Life and death of the Mesozoic grasshoppers (Insecta: Orthoptera) – their diversity, phylogeny and fate during mass extinctions.

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Hiermit erkläre ich, dass die vorliegende Arbeit vollständig ohne den Einsatz künstlicher Intelligenz verfasst wurde. Einzige Ausnahme bildet die KI-Übersicht der Google-Suche, welche standardmäßig bei Google-Suchanfragen antwortet.

I hereby declare that the presented work was completely written without the use of artificial intelligence. The only exception is the AI-overview of the Google search engine, which answers Google searches by default.

Zusammenfassung der Forschungsergebnisse:

Die nachfolgende Arbeit beschreibt 20 neue Arten von mesozoischen Heuschrecken, darunter vier der Familie Ripipterygidae („Schlammgrillen“), zwei Tridactylidae („Zwerg-Maulwurfsgrillen“), fünf Elcanidae („Lagunengrillen“), acht Locustopsidae (ohne deutschen Namen) und eine Eumastacoidea („Affen-Grashüpfer“). Viele bereits beschriebene Arten dieser Gruppen werden hinsichtlich ihrer taxonomischen Position neu beurteilt. Der Fokus der meisten Kapitel liegt auf den Faunen der brasilianischen Crato Formation (ca. 122-113 Millionen Jahre) und des Burmesischen Bernsteins (ca. 110-99 Millionen Jahre), die beide in die Frühe bis Mittlere Kreidezeit datieren. Ein Kapitel behandelt außerdem die Revision jurassischer Elcaniden Zentraleuropas. In drei weiteren Kapiteln wird mit Hilfe des neu erworbenen Wissens eine taxonomische Neubeurteilung der Tridactyliden, Locustopsiden und Elcaniden vorgenommen. Während zu den Locustopsiden noch zu wenige Daten vorliegen, um begründete Schlüsse zu ziehen, scheint es wahrscheinlich, dass die Elcaniden und insbesondere die Tridactyliden in der Kreidezeit (ca. 143-66 Millionen Jahre) deutlich formenreicher waren als bisher angenommen. Neben dem taxonomischen Teil wird die Phylogenie der gesamten Ordnung Orthoptera anhand von morphologischen Merkmalen und mit Fokus auf die beiden fossilen Gruppen Elcanidea und Locustopsoidea erforscht. Dabei werden die Elcaniden als basale Gruppe der Ensifera („Langfühlerheuschrecken“) vorgeschlagen, während die Locustopsiden die basale Gruppe der Caelifera („Kurzfühlerheuschrecken“) bilden. Ein abschließendes Kapitel untersucht schließlich die Diversitätsentwicklung der großen Heuschreckengruppen seit Beginn deren Entwicklung vor ca. 300 Millionen Jahren bis in die Gegenwart. Anhand des Artenreichtums im Fossilbericht lassen sich die Heuschrecken in drei distinkte Faunengemeinschaften ordnen: Eine paläozoische, die die Linie der Heuschrecken im Karbon begründete und bis zum Ende des Perms erfolgreich blieb; eine mesozoische, deren Linien die dominanten Heuschrecken während der Herrschaft der Dinosaurier waren; und eine Känozoische, die vermutlich bereits ab der mittleren Kreidezeit begann die mesozoische Fauna abzulösen und schließlich die Arten hervorgehen ließ, die heute unsere Ökosysteme bevölkern. Insgesamt leistet diese Arbeit damit einen wichtigen Beitrag zum Verständnis des Artenreichtums und der Evolution der Heuschrecken, sowohl im Hinblick auf deren Vergangenheit als auch der Herkunft der modernen Formen.

Summary of research results:

The following dissertation describes 20 new species of Mesozoic grasshoppers, among them four of the family Ripipterygidae (mud crickets), two Tridactylidae (pygmy mole crickets), five Elcanidae (lagoon crickets), eight Locustopsidae (without common name) and one Eumastacoidea (monkey grasshoppers). Several previously described species from these groups are revised in regards to their taxonomic position. The focus of most chapters is on the faunas of the Brazilian Crato Formation (ca. 122-133 million years ago) and Burmese amber (ca. 110-99 million years ago), both of which date to the Early to mid-Cretaceous. Another chapter also deals with the revision of the Jurassic elcanids from Central Europe. Using the newly obtained knowledge, three more chapters cover a taxonomic review of the tridactylids, locustopsids and elcanids. While there is no sufficient data to draw conclusions for Locustopsidae, it seems likely that Elcanidae and especially Tridactyloidea were much more diverse during the Cretaceous (ca. 143-66 million years ago) than previously assumed. In addition to the taxonomic contents, the phylogeny of the entire order Orthoptera is analyzed based on morphological characters. The focus of the phylogeny was to determine the position of Elcanidea and Locustopsoidea within Orthoptera. Results suggest that Elcanidea were probably a basal lineage of the Ensifera ("long horned grasshoppers"), whereas Locustopsoidea were a basal lineage of the Caelifera ("short horned grasshoppers"). A final chapter is on the topic of diversity evolution of the major lineages of Orthoptera from the beginning of their kin ca. 300 million years ago all the way to present day. According to their species richness in the fossil record, Orthoptera can be grouped into three distinct faunal communities: a Paleozoic fauna, which started the lineage of Orthoptera in the Carboniferous and remained successful until the end of the Permian; a Mesozoic fauna which included the dominant lineages during the reign of the dinosaurs; and a Cenozoic fauna, that probably began to take over from their Mesozoic predecessors by the mid-Cretaceous and eventually brought forward the species which populate our ecosystems today. Overall, this dissertation is an important milestone towards understanding the diversity and evolution of grasshoppers; not just in regards to their past, but also to the origin of the present forms.

Liste der (Vor-) Veröffentlichungen/*List of (pre-) publications*

1. Schall, O. K. O., Cao, C. Q., Husemann, M. (2025). New genera and species of Ripipterygidae (Orthoptera, Tridactyloidea) from mid-Cretaceous Kachin amber.

Contributions to Entomology 75(2): 253-262. https://doi.org/10.3897/contrib.entomol.75.e154529
Eigener Beitrag: Beschreibung der neuen Taxa, Analyse der Beinlänge.
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Beitrag Koautoren: Rezension des Manuskripts.

2. Schall, O. K. O., Heads, S. W. & Husemann, M. (in press). New species of Tridactyloidea (Orthoptera: Caelifera) from mid-Cretaceous Kachin amber show intermediate evolutionary state between extant lineages. *Evolutionary systematics*.
Eigener Beitrag: Beschreibung der neuen Taxa, Bestimmungsschlüssel.
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3. Schall, O. K. O., Gu, J.-J. & Husemann, M. (in press). Two new members of Tridactylidae (Orthoptera: Caelifera) from mid-Cretaceous Kachin amber. *Zootaxa*.
Eigener Beitrag: Beschreibung der neuen Taxa.
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4. Schall, O. K. O., Lima, D., Heads, S. W., Pinheiro, A. P., Kotthoff, U. & Husemann, M. (submitted). New species of Cretaceous Locustopsidae (Orthoptera: Caelifera) from the Crato Formation of Brazil and a taxonomic revision of the family. *Zootaxa*.
Eigener Beitrag: Beschreibung der neuen Taxa, Taxonomische Revision.
Ausarbeitung und Konzeption: 95%. Sammlungsarbeit (Fotos & Abbildungen): 80%.
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5. Schall, O. K. O., Lima, D., Kotthoff, U., Pinheiro, A. P., Heads, S. W. & Husemann, M. (in prep./chapter 5). New species of Locustopsidae (Orthoptera: Caelifera) from the Crato Formation including a new subfamily Pseudoacridinae subfam. nov.

Eigener Beitrag: Beschreibung der neuen Taxa, Diversitätsvergleich.
Ausarbeitung und Konzeption: 100%. Sammlungsarbeit (Fotos & Abbildungen): 90%. Anteil am Manuskript: 90%.
Beitrag Koautoren: Rezension des Manuskripts; DL Sammlungsarbeit, Mitarbeit am Text.

6. Schall, O. K. O., Lima, D., Heads, S. W., Pinheiro, A. P. & Husemann, M. (in prep./chapter 6). First Eumastacoidea and new Locustopsidae (Orthoptera: Caelifera) from the Crato Formation of Brazil.
   Eigener Beitrag: Beschreibung der neuen Taxa.
   Ausarbeitung und Konzeption: 100%. Sammlungsarbeit (Fotos & Abbildungen): 95%. Anteil am Manuskript: 95%.
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7. Schall, O. K. O., Kotthoff, U. & Husemann, M. (in press). The first species of *Parelcana* and the second species of *Longioculus* (Orthoptera: Elcanidae) from mid-Cretaceous Kachin amber. *Journal of Orthoptera Research*.
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8. Schall, O. K. O., Heads, S. W., Lima, D., Pinheiro, A. P., Kotthoff, U. & Husemann, M. (submitted). Revision of the lagoon crickets Elcanidae (Insecta: Orthoptera) of the Lower Cretaceous Crato Formation of Brazil with the description of new taxa. *Cretaceous Research*.
   Eigener Beitrag: Beschreibung der neuen Taxa, Analyse der innerartlichen Variabilität.
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9. Schall, O. K. O., Husemann, M. (in prep./chapter 9). A new hypothesis for the phylogenetic placement for fossil grasshopper (Insecta: Orthoptera) lineages.
   Eigener Beitrag: Phylogenetische Analysen
   Ausarbeitung und Konzeption: 100%. Sammlungsarbeit (Fotos & Abbildungen): 100%. Analysen: 100%. Anteil am Manuskript: 95%.
   Beitrag Koautoren: Rezension des Manuskripts.

10. Schall, O. K. O., Husemann, M. (in prep./chapter 10). Towards a revision of the Elcanidae genus *Panorpidium* (Insecta: Orthoptera) – a review of many misplaced taxa.
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Anmerkung/*Comment*

Kapitel 11-14 sind aus den erweiterten Schlussfolgerungen entstanden und in ihrer in dieser Arbeit enthaltenen Fassung ausschließlich vom Doktoranden (Ole-Kristian Odin Schall) selbst verfasst. Bis auf Kapitel 12 sind auch diese zur späteren Publikation in einer wissenschaftlichen Zeitschrift vorgesehen./*Chapters 11-14 were created from the expanded conclusions and the versions included in this dissertation were exclusively written by the doctoral candidate (Ole-Kristian Odin Schall). Except for chapter 12 these are supposed to be published in a scientific journal at a later time, too.*

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Welcome to a tropical forest, 100 million years ago…

Waves broke on the shoreline at the feet of the araucarian trees[1]. Out on the horizon, the Cretaceous sun was rising as an orange fiery sphere to ring in a new dawn. On the sandy beach the carcass of a dead shark washed on during last night's storm had attracted one of the island's large theropod dinosaurs. Enjoying its free meal, the dinosaur ripped apart the flesh of the fish, shaking out parts of a parasitic tapeworm that had resided in the shark's intestines[2]. Thrown beneath the roots of the nearby forest, a small enantiornithine bird[3] fluttered out from behind the spiny leaves where it had hidden during the night and inspected the invertebrate's leftovers. Curiously, the bird picked at the tentacle of the worm with its long third claw. Then, he took it in its beak serrated with small needle-sharp teeth and flew back within the concealed safety of the forest.

Under the cover of the trees, the world was darker and more shaded. A network of gurgling rivers and still swamps sourced by freshwater and periodic influx from the nearby sea ran through the woods like a set of arteries, giving life to the thriving community of creatures around. The small bird targeted a branch heavily masked by a flowering shrub. Several wasps that were feeding on the pollen provided by the flowers[4] buzzed in annoyance as the bird interrupted their business and set on the branch to more closely inspect its marine catch. Pinning the worm down with its foot, the bird began piercing the invertebrate with its teeth when a rustle in the leaves behind him caught its attention. Fearsome, the bird looked up and with a shriek dropped its meal down to the forest floor when a large agamid lizard[5] reached its scaly head out of the branches, investigating what was going on. While the bird flew away, broadcasting its frustration over the lost meal into the forest, down in the leaf litter by the riverside a great rushing and hushing was caused by the dropping from above. Just at the top layer of the humid forest floor, the earth was bustling alive with all kinds of invertebrates. On the banks of the running stream a colony of vividly colored tiny pygmy mole crickets was digging burrows into the ground[6]. Not few jumped by surprise when the enantiornithines' price had hit the earth and hurriedly retreated in the safety of their tunnels[7].

Meanwhile, above the heads of the smaller distant relatives, very different crickets were flying. These were larger than a lot of the leaf litter fauna, although still nowhere near big enough as to not fall victim to one of the toothed birds or lizards that were scurrying about. They belong to a family of Orthoptera that would, 100 million years later, become known as Elcanidae. One of the elcanids, a female with its many eggs about to be laid landed on a flowering shrub on the river's edge that had many blossoms with long filamentous leaves and lower branches still

charred from the last forest fire that had ravaged the forest a couple of weeks ago[8]. After checking its surroundings for potential danger, the female then proceeded to the ground right by the shoreline of the river and using the long ovipositor on her abdomen began depositing her precious eggs in the moist soil[9]. Suddenly, the surface of the river exploded as a frog burst out from beneath the water[10]. The female elcanid spread her forewings wide apart, flashing the two large spots on each of them, trying to scare the amphibian off[11]. But the predator was not fooled by the insect's attempt. Just when the tongue of the frog shot out at the female, she made a desperate leap, landing directly on the surface of the streaming river. Then she expanded her hindlegs and used the large spurs on the tibiae to create more surface of which to push off from. A second later, intensely flapping her two wing pairs, she escaped onto a large conifer on the other side of the river, while the surprised predator blankly gazed after her[12]. Having barely escaped certain death, the female came to rest on the rough bark of the tree, her long antennae quivering above her head. She did not react at first, when some sticky resin excreted from the conifer flowed around her tarsi. When she tried to move, it was already too late. The resin flowed all over her body, entrapping her in the orange blood of the tree and soon enough the female suffocated in the transparent prison that would become her tomb for eternity. Our elcanid had met an unfortunate end, but unbeknownst to it, one hundred million years later the amber piece containing her perfectly preserved body would be unearthed in a part of the world that nowadays belongs to northern Myanmar. It, alongside all the other extraordinary creatures it had shared an ecosystem with, would gather great attention from the scientific community and provide fascinating insights into the life that had once roamed in a tropical forest, 100 million years ago.

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Research goals

This doctoral thesis explores the diversity, evolutionary relationships and responses to (mass) extinctions of the insect order Orthoptera, which includes grasshoppers, katydids, crickets and their allies. More specifically, the following goals shall be achieved: **1)** Determining the diversity of Tridactyloidea (families Tridactylidae, pygmy mole crickets and Ripipterygidae, mud crickets) from mid-Cretaceous Burmese amber. This group is one of the most abundant orthopteran taxa in the amber. The aim is to describe additional taxa and use the new, plus already available taxonomic data, to develop a first understanding of the true diversity of

Tridactyloidea. **2)** Determining the diversity of Elcanidae from Burmese amber and the Early Cretaceous Crato Formation of Brasil. Elcanidae is another abundant family of orthopterans in Burmese amber and several new species have been described in the past few years. Here, a couple more specimens will be described. However, the focus is going to be on the elcanids of the Brazilian Crato Formation. This fauna offers a rare glimpse into the orthopteran community in a Gondwanan locality, but it has been largely ignored for more than thirty years. In addition, several taxa of Elcanidae described more than a hundred years ago will be reviewed in regards to their taxonomic position. Based on the newly obtained data, the taxonomic relationships inside Elcanidae will be explored. **3)** Determining the diversity of Locustopsidae from the Crato Formation. While Elcanidae were diverse in Burmese amber, in the Crato Formation another family of Orthoptera, the Locustopsidae, seem to have been far more speciose. Because they likely were the very first members of the Caelifera suborder of Orthoptera, Locustopsidae are probably crucial towards understanding the evolutionary history of these insects. Nonetheless, they are severely understudied, something that will change in this dissertation. **4)** With the new knowledge about Elcanidae, Locustopsidae, Tridactylidae and Ripipterygidae, a phylogenetic analysis based on morphology will be performed. It aims towards understanding the phylogenetic position of the major fossil and extant lineages of Orthoptera on the infraorder/superfamily level. This will be the first time that a phylogenetic analysis of the entire order Orthoptera with representatives from most major fossil and extant lines is performed. **5)** Using my findings from the diversity and phylogeny studies, I will analyze diversity patterns of the major lineages over deep time. Here, the goal is to identify patterns in large scale Orthoptera evolution (i.e. on a higher taxonomic level) and estimate the susceptibility of Orthoptera to major extinction events that occurred in the fossil record.

Note by the author: the following introduction to this dissertation is written in a 'popular science' style of writing. I hope this makes the reading experience more enjoyable, while offering a comprehensive overview of the topics that come up during the later chapters.

Introduction

The Orthoptera: a history, part 1 – From their early beginnings to the greatest mass extinction of all times

The first to hop – Orthoptera of the Carboniferous

100 million years ago, during the Cretaceous period, when the most iconic species of dinosaurs evolved, Elcanidae Handlirsch, 1906 and pygmy mole crickets (or Tridactyloidea Brullé, 1835, to call them by their scientific name) likewise had reached potentially some of their highest levels of diversity (Clapham et al., 2016). However, the order of animals they belong to – the Orthoptera Olivier, 1789 or grasshoppers, crickets and katydids – are much older than the Cretaceous. If we want to meet the earliest orthopterans in evolution, we must travel far back in time, several millions of years before the first dinosaurs stepped on stage, and to a period known today as the Carboniferous, ca. 359-299 Mya (million years ago). During this era, the land was covered by the first large forests to develop, vertebrate life had taken the evolutionary step from a water-bound life to fully terrestrial small reptiles and early griffenflies (stem-group relatives of modern dragonflies), Palaeodictyoptera Goldenberg, 1877 and millipedes of enormous sizes roamed the coal forests (Kukalova, 1969; Lhéritier et al., 2024; Marchetti et al., 2021). Although phylogenomics-based estimates suggest the earliest insects perhaps appeared as early as the Ordovician (ca. 479 Mya) and the first flying insects during the Devonian (ca. 406 Mya) (Misof et al., 2014), first fossil evidence of major extant insect lineages is found in deposits dating to the Carboniferous (Wang et al., 2022) and the Orthoptera were among them. We have found fossil remains of two groups of grasshoppers from this period in France and Portugal (Brongniart, 1885; Correia and Nel, 2023; Meunier, 1911; Schubnel et al., 2021). *Theiatitan azari* Schubnel, Roques & Nel, 2021 belongs to the Titanoptera Sharov, 1968. The relationship of this group with the rest of Orthoptera is a matter of debate (e.g. Huang et al., 2020). Currently they are regarded as an extinct suborder, next to the two other suborders Ensifera Chopard, 1921 (crickets and katydids) and Caelifera Ander, 1936 (grasshoppers, locusts and pygmy mole crickets) which both have a plethora of living representatives today (Cigliano et al., 2025). Titanoptera brought foreward some giant-sized species of up to 400 mm wingspan (Park et al., 2022) when they diversified during the later Permian and Triassic period,

but *Theiatitan azari* was no "giant", with a wingspan that would not have exceeded 40 mm (Schubnel et al., 2021). Based on findings from later Titanoptera, these insects were voracious predators as indicated by their raptorial forelegs with stout spines and the forewings of both sexes showed specialized areas that were probably used in some kind of acoustic or visual communication (Park et al., 2022; Schubnel et al., 2021).

The other group of Orthoptera occurring in Carboniferous-age rocks is regarded as the most basal family of the two extant lineages (Caelifera and Ensifera) that evolved before they separated sometime in the Permian (Song et al., 2015): the Oedischiidae Handlirsch, 1906. This family is attributed to the Ensifera (Gorochov, 1995; 2021) and known from two species that were found in the Commentry Shales of France, namely *Oedischia williamsoni* Brongniart, 1885 and *Anhomalophlebia couloni* (Meunier, 1911) as well as *Lusitadischia sai* Correia and Nel, 2023 from Portugal. Unfortunately, most Oedischiidae are known only from isolated forewings and most aspects of their paleobiology, therefore, remain a mystery. Rare parts of hind- and forelegs suggest they were saltatorial and predatorial, as well as active flyers (Sharov, 1968), in contrast to the Titanoptera which likely were not good flyers (Schubnel et al., 2021).

Although some early extinct relative orders of Orthoptera (Caloneurodea Zeuner, 1939, Cnemidolestodea Handlirsch, 1937) as well as other taxa of uncertain taxonomic status were relatively diverse during the Carboniferous (Correia and Nel, 2023), Orthoptera itself appears to begin diversifying only in the following Permian.

Diverse in dry lands – Orthoptera of the Permian

The Permian saw the rise of tetrapods as rulers of the land. Famous animals like the sphenacodontid *Dimetrodon* Cope, 1878 were the first large-bodied apex predators among terrestrial amniotes. Later, the sphenacodontids would give rise to the therapsids, the earliest ancestors of mammals (Brink and Reisz, 2014; Matamales-Andreu et al., 2024). The climate became much dryer during the Permian than it had been in the Carboniferous and large parts of the supercontinent Pangea were characterized by arid environments subjected to distinct seasonal changes in precipitation and/or moisture availability (Tabor and Poulsen, 2008). The extensive coastal swamps and wetland vegetation of seed ferns, clubmosses and calamite trees had been forced to retreat to shrinking "wet spots" during the Early Permian and by the Middle Permian the land was dominated by plants adapted to seasonal drought and a deep water table (DiMichele et al., 2006). For the Orthoptera, the Permian was the age of the Oedischioidea Handlirsch, 1906. Currently, 45 species of the superfamily are described from this time, almost all of them belonging either to the family Oedischiidae or Pruvostitidae Zalessky, 1929. Fossil

remains of Permian oedischiids were found throughout the continents of Laurasia (North America, Europe and Asia), but are missing from Gondwana (South America, Africa, Australia and Antarctica). But while the Permian orthopteran fauna contained many species of Oedischiidae, other groups were present too. The Titanoptera had diversified as well and since their small beginnings during the Carboniferous had produced species justifying the name of the order, such as *Tcholmanvissiella gigantea* Gorochov, 1987 with a forewing wingspan of ca. 200 mm (Béthoux and Nel, 2002). Among the dominating oedischiids and titanopterans a completely new group had evolved during the Permian, a group that would become very successful in the upcoming Mesozoic era: the Elcanidea Gorochov, 1995. These earlier members of the infraorder did not yet have the large spurs on the tibiae of their hind legs that would be characteristic for their Jurassic and Cretaceous descendants (see for example *Permoraphidia magnifica* in Béthoux and Nel, 2002a). Permian elcanids are found in the same formations as titanopterans and oedischiids (Iva-Gora and Koshelevka Formation of Russia, Wellington Formation of Kansas among the most important ones), and one exceptionally well-preserved specimen was found in an unknown location of Madagascar (the aforementioned *P. magnifica*) (https://paleobiodb.org/#/, 2025 [= PBDB in the following]). With the Laurasian parts of Pangea inhabited by Oedischioidea, Titanoptera and Elcanidea, other taxa evolved in Gondwanaland. The Xenopteroidea Riek, 1955, relatives of the Laurasian oedischiids, would become somewhat diverse during the Triassic. Their earliest member was relatively recently described from South Africa (van Dijk and Gorochov, 2011). All the taxa we met so far during the Carboniferous and Permian (except for the Titanoptera, which are their own separate suborder) belong to the suborder Ensifera. Modern ensiferans are characterized by antennae that are longer than their bodies and the females having striking ovipositors, that look like the blades of long or curved swords and are used to deposit their eggs into soil, plants or other organic matter (the name Ensifera means “sword bearing” in reference to this structure). However, among the many early ensiferans, Gondwana during the Permian had given rise to the first ancestors of the second suborder Caelifera, the group that would eventually evolve species such as the famous and notorious migratory locusts (e.g. *Locusta migratoria* (Linnaeus, 1758)). These early caeliferans belong to a superfamily called Locustopsoidea Handlirsch, 1906 and the first members were found in Middle Permian deposits of South Africa (Geertsema and van Dijk, 1999; the authors placed *Afroedischia oosthuizeni* in the Oedischiidae, but the forewing characters suggest a placement in Locustopsoidea). More specimens were unearthed from the Late Permian of South Africa as well as Russia (Riek, 1976; Sharov, 1968); hence, they had reached Laurasia early.

The Permian period had seen the diversification of the earliest orthopterans (Titanoptera and Oedischiidea Handlirsch, 1906) as well as the evolution of Elcanidea and the first Caelifera (i.e. Locustopsoidea), which would become characteristic lineages among the Mesozoic orthopterans. However, at the end of the Permian, ca. 252 Mya, life on earth was tested to its core.

Death from below – the Permian-Triassic mass extinction

On the boundary of the Paleozoic to the Mesozoic era something devastating happened on planet earth, something that caused 81-94% of marine species and 70% of vertebrate families to go extinct (Dal Corso et al., 2022). The ultimate cause of this Permian-Triassic mass extinction is a matter of ongoing debate, but recent findings point towards massive eruptions of the giant Siberian Traps flood basalt province as the likely culprit (Wignall and Bond, 2024). Over the cause of ca. 55.000 years a cascade of environmental changes including global warming, oceanic anoxia and acidification, (potentially) ozone reduction, acid rain and metal poisoning (Dal Corso et al., 2022; Wignall and Bond, 2024) led to the demise of many lifeforms that had developed up to this point, but also left behind many ecological niches ready to be taken over again.

Insects suffered major losses during the latest Permian mass extinction, too. Jouault et al. (2022) found an extinction of 82.6% of insect genera ca. 252 Mya. Moreover, two additional extinction events in the vicinity of the mass extinction (ca. 266.9 Mya and ca. 237 Mya) caused further loss of 64.5% and 74.8% of insect genera, respectively. However, Jouault and colleagues did not find evidence for the three extinction events at the family level across all insects.

In the case of Orthoptera, two Permian and one Triassic formation stand out in the fossil record for having revealed a large portion of species from these periods. For the Permian, these are the Koshelevka Formation (upper Early Permian, ca. 279-272 Mya) and the Iva-Gora Beds Formation (lower Middle Permian, ca. 272-269 Mya) from Russia (PBDB). The Triassic Orthoptera fauna is represented by the Madygen Formation of Kyrgyzstan (upper Middle Triassic, ca. 242-237 Mya) (PBDB). Although the deposits in these formations date to roughly 20 My prior and 10 My post the Permian mass extinction, comparing the faunas from both places still indicates a clear picture. None of the genera that had occurred in the Permian Formations can be found in the Madygen Formation (or any other Triassic formation) (Cigliano et al., 2025; PBDB), meaning there was a 100% extinction rate on the generic level. Now, clearly, some genera we are not aware of must have survived, because, although certain less-speciose superfamilies (for example Permorhaphidioidea Tillyard, 1932 and Tettoedischioidea

Gorochov, 1987) are not found in deposits postdating the Permian extinction, most superfamilies such as Tcholmanvissioidea Zalessky, 1934 and Oedischioidea still occur in Triassic formations, despite their diversity having declined after the extinction events. Jouault et al., (2022) noticed a 3.5x increased genera origination rate (as compared to normal rates at times longer before or after the extinction event) just before the Permian mass extinction and a 3.8x increase during the Middle Triassic. These findings suggest that Orthoptera had quickly recovered from the "Great Dying", as the Permian-Triassic mass extinction is often colloquially referred to, a phenomenon known as flash recovery (Jouault et al., 2022).

From Paleozoic to Mesozoic – Orthoptera of the Triassic

But by the time things had returned to normal during the Middle Triassic, the orthopteran fauna was a very different one. Schachat and Labandeira (2021) remarked that the Permian mass extinction was "more of a faunal turnover than a mass extinction for insects". Indeed, when the Orthoptera of Koshelevka, Iva-Gora Beds and Madygen are compared on a higher taxonomic level such as the superfamily, we can see that the previously dominant Oedischioidea had lost much of their Permian diversity and made room for a new group of ensiferans: the Hagloidea Handlirsch, 1906, the very first members of the infraorder Tettigoniidea Kevan, 1982 which include all the many species of extant katydids (Fig. 1.1). The Triassic fauna was more diverse too, with ten superfamilies that were found in the Madygen Formation as opposed to six from the Russian formations.

On the boundary to the Jurassic, ca. 201 Mya, magmatic activities in the Central Atlantic magmatic province (Whiteside et al., 2010) caused temperature increases of 2.5-5°C (Steinthorsdottir et al., 2011) and ocean acidification (Greene et al., 2012) that led to two pulses of extinctions especially in the marine realm (Hallam, 1981; Wignall and Atkinson, 2020). Terrestrial vertebrates were also affected (Allen et al., 2019), although the exact course of their demise throughout the Late Triassic is a matter of debate (Lucas and Tanner, 2018). The impact of the end-Triassic mass extinction on insects is little studied, but findings from Schachat and Labandeira (2021) suggest they were relatively unaffected. However, the authors mention that this impression may be obscured by the dearth of Triassic lagerstätten. This is most certainly also true for Orthoptera, for which the majority of Triassic findings comes from the Madygen Formation of Kyrgyzstan (see S*tudying fossil Orthoptera, part 1: the fossil record and its limitations*, p. 50). Nonetheless, the abundant Oedischiidea and charismatic Titanoptera of the Carboniferous and Permian disappear from the fossil record after the Triassic, indicating orthopterans were not unaffected by the end-Triassic extinction. In the ensuing Jurassic, the

Hagloidea, Elcanidea and Locustopsoidea further diversified and a new group of orthopterans that would become very successful, the Gryllidea Vickery, 1977, appeared. They were the characteristic grasshoppers of the Mesozoic, the contemporaries of the dinosaurs.

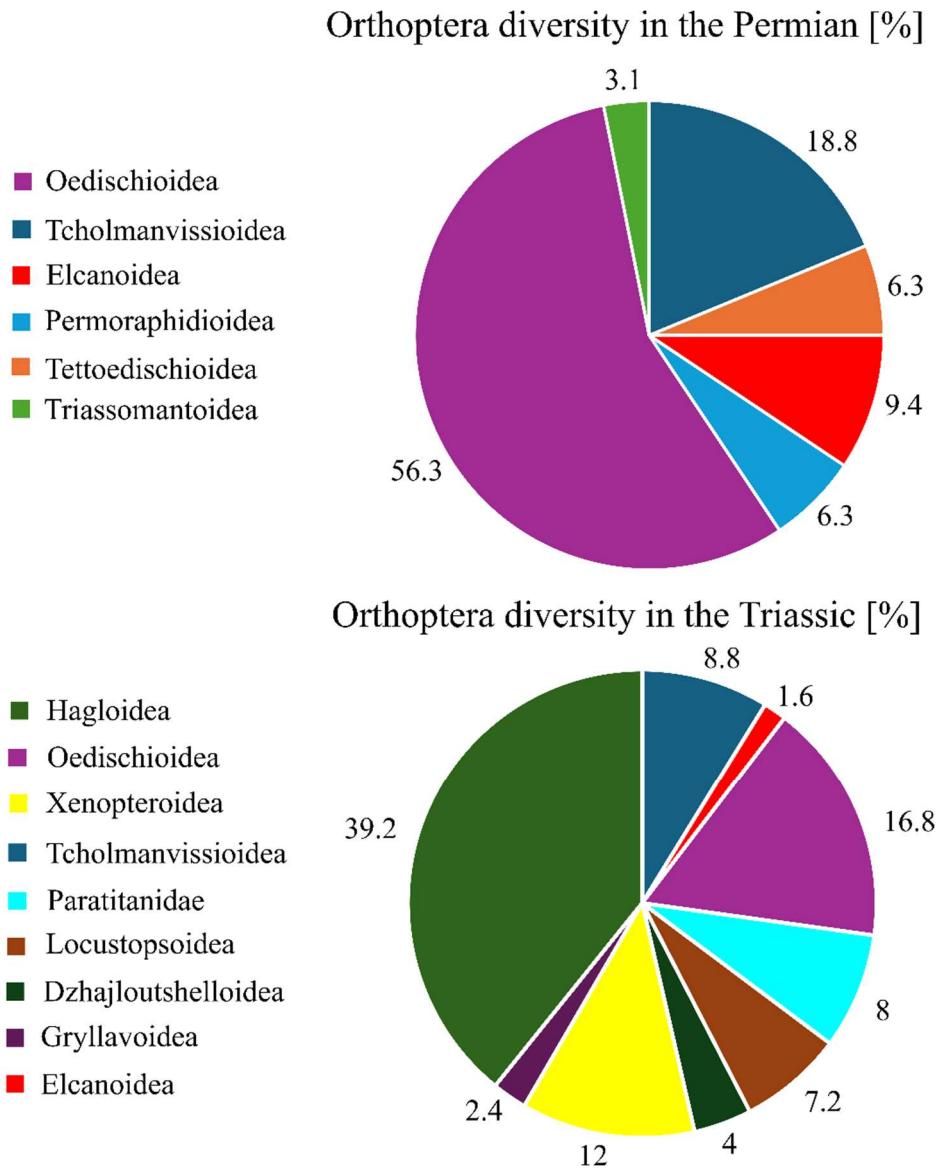

Fig. 1.1 Comparison of superfamily (sf) diversity of Orthoptera Olivier, 1789 in the Permian and Triassic. Values for each sf indicate the number of species [%] of the total species discovered. The Permian is represented by the Iva-Gora-Beds and Koshelevka Formation of Russia (species of both formations were combined). The Triassic is represented by the Madygen Formation of Kyrgyzstan. Note especially the turnover from Oedischioidea as the most speciose sf during the Permian to the Hagloidea during the Triassic, as well as the three sf that went extinct after the Permian and six sf that occurred in the Triassic for the first time.

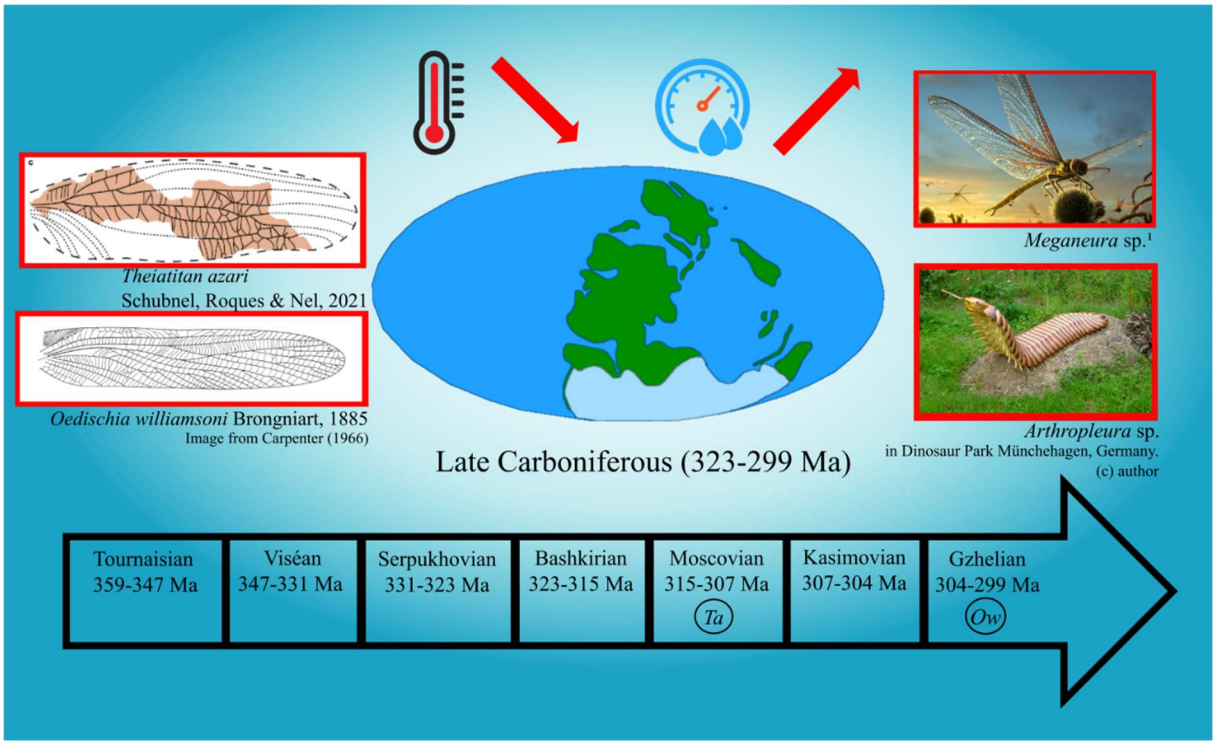

Fig. 1.2: Constellation of the continents, geological stages, climate indicators, and faunal examples of the Late Carboniferous, the period from which the oldest fossil Orthoptera are known. Pictogram of thermometer indicates general temperature trend (cooler/warmer climate), where cooler is similar to modern day temperatures and warmer is closer to the warmest climates probably ever experienced on the planet for a longer interval (e.g. Late Permian, Late Triassic, mid-Cretaceous. Pictogram of hygrometer indicates general climate conditions trend (more humid or more arid). Colors used in the world map indicate sea (deep blue), continents (green) and ice (light blue). Circles in the timeline indicate occurrence of example orthopterans on the left. [1]Image of *Meganeura* sp. uploaded to Fandom.com by Sunsandstars344, CC 3.0 (https://creativecommons.org/licenses/by-sa/3.0/deed.de).

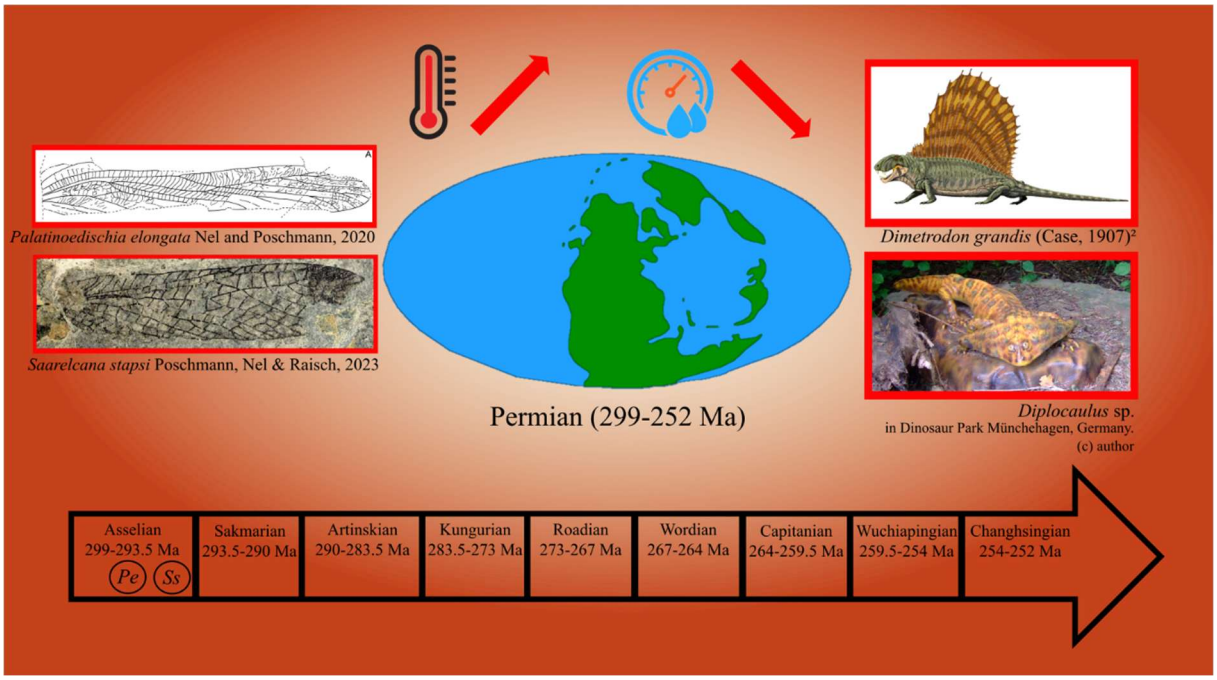

Fig. 1.3: Constellation of the continents, geological stages, climate indicators, and faunal examples of the Permian during which Titanoptera Sharov, 1968 and especially Oedischiidea Handlirsch, 1906 greatly diversified. Pictogram of thermometer indicates general temperature trend (cooler/warmer climate). Pictogram of hygrometer indicates general climate conditions trend (more humid or more arid). Colors used in the world map indicate sea (deep blue) and continents (green). Circles in the timeline indicate occurrence of example orthopterans on the left. [2]Image of *Dimetrodon grandis* uploaded to Wikimedia commons, created by DiBgd; CC 3.0 (https://creativecommons.org/licenses/by-sa/3.0/deed.de).

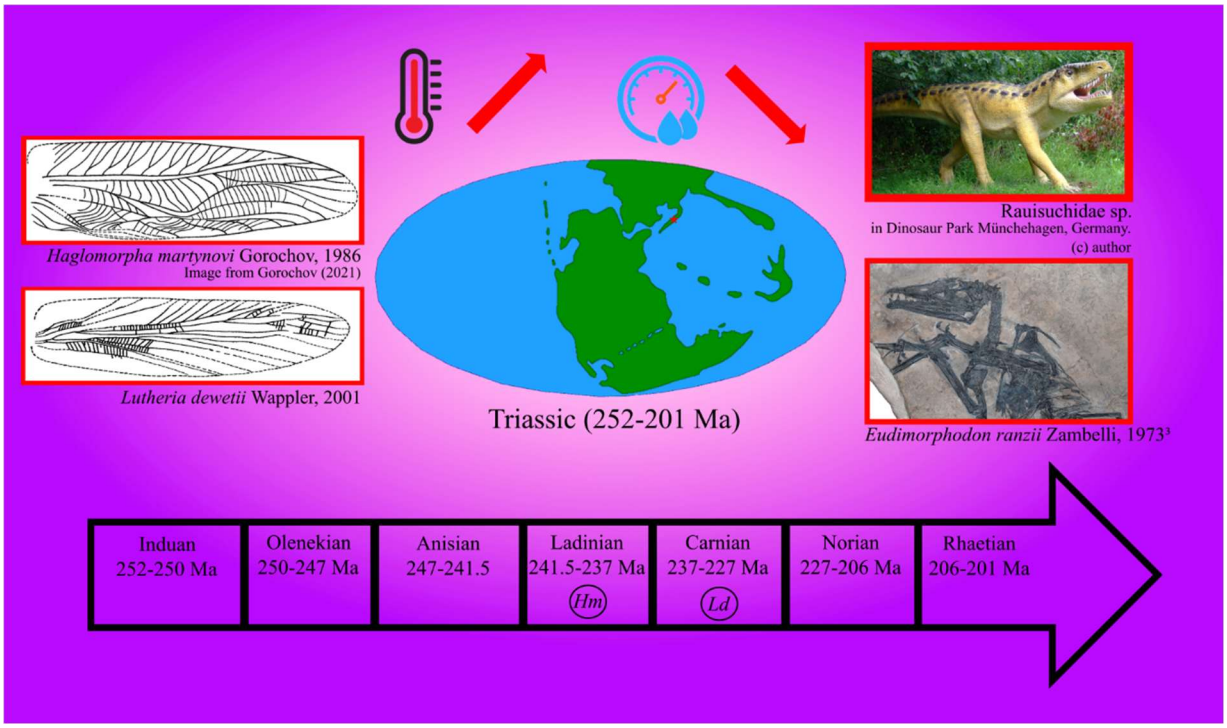

Fig. 1.4: Constellation of the continents, geological stages, climate indicators, and faunal examples of the Triassic during which Hagloidea Handlirsch, 1906 rose to become the dominant group of orthopterans. Pictogram of thermometer indicates general temperature trend (cooler/warmer climate). Pictogram of hygrometer indicates general climate conditions trend (more humid or more arid). Colors used in the world map indicate sea (deep blue) and continents (green). Red star marks the approximate position of the Madygen Formation in Kyrgyzstan, the most important discovery site for Triassic Orthoptera. Circles in the timeline indicate occurrence of example orthopterans on the left. [3]Image of *Eudimorphodon ranzii* uploaded to Wikimedia commons, created by 'Tommy from Arad' (with small modifications); CC 2.0 (https://creativecommons.org/licenses/by/2.0/).

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The Orthoptera: a history, part 2 - Strange families that lived alongside the dinosaurs

The rule of Hagloidea – Orthoptera of the Jurassic

In the Jurassic period (145-201 Mya), the dinosaurs became the undisputed rulers of the terrestrial ecosystems. Pterosaurs soared through the skies; along coastlines and the shallows and deep oceans, large marine reptiles such as ichthyosaurs and plesiosaurs roamed. Among the Orthoptera the dominating group still was the superfamily Hagloidea (see Fig. 1.5). Nearly 50% of described orthopterans from the Jurassic are assigned to this subfamily with most species from the families Haglidae Handlirsch, 1906 and Prophalangopsidae Kirby, 1906. Significantly less diverse but still increasing in species-count from their beginnings in the Permian and Triassic, were the Jurassic Elcanidea and Locustopsoidea, both present now in their type families Elcanidae Handlirsch, 1906 and Locustopsidae Handlirsch, 1906. Many of the Jurassic elcanids and locustopsids were found in deposits from Germany (Solnhofen and Dobbertin), indicating that they lived side by side in the archipelago at the margin of the Jurassic Neotethys Sea (Meyer and Schmidt-Kaler, 1989; Zessin, 1987).

Also, for the first time occurring in the fossil record of the Jurassic, were the Grylloidea Laicharting, 1781, despite molecular studies suggesting they had already evolved during the Triassic, ca. 234 Mya (Song et al., 2015). These early crickets do not yet belong to any extant modern family, but to the completely extinct Protogryllidae Zeuner, 1937 (which are only found in Jurassic deposits) and Baissogryllidae Gorochov, 1985 (Jurassic-Cretaceous) (Cigliano et al., 2025).

Hagloidea, Locustopsidae, Elcanidae and Grylloidea were the iconic taxa among the Jurassic Orthoptera. However, two other rather enigmatic groups are known from this period, before being lost again in the fossil record of the Cretaceous. The Phasmomimidae Sharov, 1968, a family of the Ensifera, were named after the Phasmida Leach, 1815, commonly known as stick insects. Phasmida is a relative order of Orthoptera and the first specimens of Phasmomimidae described by Sharov (1968) had a forewing venation resembling that of fossil stick insects

(Gorochov, 2000). Originally, there were 25 species included in this family (Cigliano et al., 2025), but most of them are now considered to belong to the real Phasmida instead (Gorochov, 2000). According to Gorochov (2000) only two species of Phasmomimidae should be regarded as valid, both were found in the Jurassic deposits of the Karabastau Formation of Kazakhstan (PBDB). The Ensifera were clearly thriving in the Mesozoic, whereas the Caelifera were only represented by the Locustopsoidea up until the Triassic. However, in the Triassic Madygen Formation of Kyrgyzstan a separate group of caeliferans had evolved. Perhaps in a somewhat convergent evolution with the ensiferan crickets (as superficially they are morphologically similar) the Tridactylidea Brullé, 1835 first appeared as the family Dzhajloutshellidae Gorochov, 1994. For the Jurassic, the Regiatidae were recorded from the UK and Germany (Handlirsch, 1939; Whalley, 1985). Both these early tridactyloids are enigmatic due to the few specimens known. Gorochov (2001) suggested a connection to early Locustopsoidea as well as Xenopteroidea, whereby the latter are usually considered ensiferans and relatives of the Oedischioidea.

The unsatisfying truth is that the evolutionary origins of modern Tridactyloidea are not very well understood. Body fossils of this group from the Triassic and Jurassic are entirely absent and the assignment of Dzhajlousthellidae and Regiatidae relies on similarities in forewing venation. Additionally, the third family of extant Tridactyloidea, the subterranean Cylindrachetidae Giglio-Tos, 1914, are suggested to have evolved as the first lineage of modern tridactylids by molecular findings (Song et al., 2015), but not a single specimen of fossil sand gropers (how they are colloquially referred to) is known so far. This absence of information on Tridactyloidea changes drastically in the Cretaceous period. A combination of complex and interrelated factors from the Barremium to Campanium (ca. 54 My from the Lower to Upper Cretaceous) caused an increase in the development of amber yielding macroscopic bioinclusions (Delclòs et al., 2023). Thanks to this so-called Cretaceous Resinous Interval (CREI), a plethora of small organisms was preserved in astonishing detail, providing us with an unparalleled look into the Late Mesozoic fauna, not last the diversity of Cretaceous Orthoptera.

Diversity peak – Orthoptera of the Cretaceous

From the Late Jurassic to mid-Cretaceous (ca. 150-100 Mya) flowering plants (angiosperms) began to diversify (Dimitrov et al., 2023). This is thought to have caused the Cretaceous or Angiosperm Terrestrial Revolution (Lloyd et al., 2008; Benton et al., 2022), a term used to refer to a time interval of ca. 50 My from the Cretaceous to Early Paleogene (100-50 Mya) where

several groups of organisms from pollinating insects to mammals experienced an apparent burst of diversification (Weaver et al., 2024). How did orthopterans respond during this time? From the Jurassic period 212 species are described, from the Cretaceous 256. This would suggest that the abundance of Orthoptera as an order in faunal communities did not significantly increase from one era to the other. However, on the superfamily level things look different (Fig. 1.5). After their diversity peak during the Jurassic, the Hagloidea have become much less speciose during the Cretaceous. Species were mostly found in the Yixian Formation of China (ca. 126-124 Mya (Zhong et al., 2021)) and Zaza Formation of Russia (ca. 125-113 Mya (PBDB)). In China, they shared their habitat with the Elcanidae. Elcanidae were not remarkably diverse in most faunas, but they were widespread in the Cretaceous and found in South America as well as several places across Europe and Asia. One fossil resource in particular, the amber found in modern-day Myanmar, has revealed an unusually high taxonomic diversity of elcanids (21 species). The amber, often referred to as Burmese or Kachin amber (after the Kachin State in Myanmar, where several amber mines are located), is dated to be around 110-99 My old, depending on the exact location where the resin was excavated (Shi et al., 2012; Xing and Qiu, 2020). At this time, during the middle Cretaceous, the Burma Terrane (a tectonic microplate mainly lying within the borders of Myanmar today, also called the West Burma Block) where the amber formed was located on an isolated island-arc off the coast of Southeast Asia (Westerweel et al., 2025). The amber has revealed many important findings, from a feathered dinosaur tail (Xing et al., 2016) to enantiornithine birds (Xing et al., 2019), lizards (Wagner et al., 2021) and countless arthropods (Ross, 2024). Several species of Orthoptera were described too, namely members of the families Trigonidiidae, Oecanthidae, Mogoplistidae and Gryllidae (Ensifera: Grylloidea), Tridactylidae Brullé, 1835 and Ripipterygidae Ander, 1939 (Caelifera: Tridactyloidea), a nymph of the (as fossils) rare Eumastacoidea Burr, 1899 (Husemann et al., 2025), the enigmatic Burmecaelidae Uchida, Husemann & Kotthoff, 2024 and Elcanidae. Perhaps the elcanids were able to diversify so much because of the absence of Hagloidea or Locustopsidae competitors, compared to other Cretaceous deposits where these three taxa shared the same environment, such as in the aforementioned Yixian Formation, the Crato Formation of Brasil (ca. 122-113 Mya (Bezerra and Mendes, 2024)) ore the Weald Clay, Durlston and Lulworth Formations of the UK (Berriasian-lower Aptian (Gorochov and Coram, 2022)), where Elcanidae are far less speciose.

As indicated, Grylloidea diversified extensively during the Cretaceous with several extant lineages being recorded as fossils for the first time, after the Jurassic had only seen the primitive and extinct Baissogryllidae and Protogryllidae. Indeed, most fossils of Cretaceous Orthoptera

belong to Grylloidea. The Cretaceous also saw the diversification of the Caelifera, which almost doubled in species recorded from 40 Jurassic to 75 Cretaceous species, although they were still severely outmatched by the Ensifera of which 200 species are recorded from the last era of the Mesozoic. Nonetheless, the first of the two main clades of Caelifera, the Tridactylidea showed a remarkable diversity, especially, once again, in Burmese amber. Almost 30 species attributed to Tridactylidae and Ripipterygidae are described from the Myanmar resin, with species reports increasing every year. The second major group of the Caelifera, the Acrididea Targioni-Tozzetti, 1882, was mainly represented by the Locustopsidae during the Mesozoic (although the Eumastacoidea (Husemann et al., 2025; chapter 6) and Proscopioidea Serville, 1838 (Heads, 2008; Mendes et al., 2019) were present, they appear very rarely in the fossil record of this time). Locustopsidae were very diverse in the Crato Formation of Brasil, where their species number even surpassed that of Burmese amber Elcanidae. Although they occurred through large parts of Europe and Asia as well during the Jurassic and Cretaceous, this suggests Acrididea may have had a diversity stronghold in Gondwana and more precisely the Crato Formation.

The Cretaceous period had been a time when the Orthoptera, along with many other animals, had thrived and evolved many new forms. But while life on earth was prospering, out of space impending doom was nearing at cosmic speed.

Death from above - the Cretaceous-Paleogene mass extinction

66 million years ago a gigantic asteroid struck earth, leaving behind a 200-kilometers wide impact crater in Yucatán, Mexico. Material both from Earth and the asteroid were ejected into the atmosphere and formed a cloud of dust, soot, and sulfate aerosols among others, shrouding the planet in darkness. The resulting winter, following the impact, would have lasted for decades or even millennia (Morgan et al., 2022). At around the same time, the deccan traps, a large volcanic province in India erupted over the cause of several 100ky and many large-volume magmatic pulses, further straining environmental conditions (Keller et al., 2020; Schoene et al., 2019). When life recovered in the Early Paleocene, 76% of species had been wiped out by the end-Cretaceous mass extinction (Jablonski, 1995), including all non-avian dinosaurs, the iconic marine reptiles and pterosaurs of the Mesozoic, ammonites and rudists. Several other lineages did not completely die out, but suffered major losses, such were the land plants, planktic foraminifera and calcareous nannofossils (Schulte et al., 2010).

Unfortunately, the fossil record of insects around the Cretaceous-Paleogene Extinction (KPg) is patchy. The last lagerstätten to predate the extinction, Canadian amber deposits from the provinces Alberta and Manitoba, formed ca. ten million years before the KPg. The first

lagerstätte for insects after the extinction is the Menat Formation in France, with deposits more than five million years younger than the impact date of the asteroid (Schachat and Labandeira, 2021). Wilf et al. (2023) and Schachat and Labandeira (2021) argue, based on broad range analyses of the fossil record of insects by Labandeira and Sepkoski (1993) as well as trace fossils on plants by Labandeira et al. (2002), that insects experienced a drop in diversity of specialized herbivorous species during the KPg, but no global extinctions at the family level occurred.

The order Orthoptera, however, seems to have faced a different situation. Of the "big five" Mesozoic superfamilies (Grylloidea, Elcanoidea, Hagloidea, Locustopsoidea and Tridactyloidea) only the Grylloidea and Tridactyloidea survived the Cretaceous to witness the Cenozoic sunrise. Although an isolated wing from the Menat Formation was attributed to Elcanidae (Schubnel et al., 2020) and another wing from the Paleogene-Early Eocene Niubao Formation of China was first described as a Hagloidea (Lin and Huang, 2006), both these records should probably be treated with caution. In fact, Wang et al. (2019) suggested that the Chinese specimen should be transferred to Palaeorehniidae Zeuner, 1937 (= Zeuneropterinae Kevan and Wighton, 1983). There is also a Miocene species *Macrelcana ungeri* (Heer, 1849) from Croatia attributed to Elcanidae (Heer, 1849), but the forewing venation features of the specimen may suggest that this placement was incorrect. Grylloidea did not seem to be affected by the extinction and diversified plentiful, reaching almost 6000 extant species described (Cigliano et al., 2025), making them the third-biggest superfamily alive today, surpassed only by Acridoidea MacLeay, 1821 and Tettigonioidea Krauss, 1902. Tridacytloidea did survive the extinction, however, they apparently suffered heavy losses. The family Tridactylidae remains widespread today, but the second family Ripipterygidae is only found in South and Central America in modern times. This means the entire population of ripipterygids once present in the Burmese amber fauna (see chapters 1 and 2) must have died out at some point in history.

Although the end-Cretaceous mass extinction was doubtless catastrophic to Earth's ecosystems, a much less well-known crisis apparently affected insects during the mid-Cretaceous (Labandeira, 2005). This time marked a transitionary period where the older Mesozoic lineages started to decline because they were less adapted to thrive in the changing ecosystems of the Angiosperm Terrestrial Revolution (see above) (Labandeira, 2005). Because of the virtually non-existent fossil record of orthopterans during the latter half of the Cretaceous, it is currently impossible to say for certain if the demise of elcanids, locustopsids, haglids and tridactyloids was caused by the end-Cretaceous mass extinction or had already set in by the mid-Cretaceous (the topic of Orthoptera and mass extinctions is discussed in depth in chapter 14).

After the great Permian-Triassic mass extinction Orthoptera had experienced a faunal turnover, where the Oedischioidea of the Permian were largely replaced by the Hagloidea of the Mesozoic. Tracing the fossil record over the Cretaceous-Cenozoic transition, something similar can be seen. Following the devastating fate that had overtaken the two large lineages of Ensifera - Hagloidea and Elcanoidea -, the modern Tettigonioidea or katydids diversified. Additionally, Caelifera evolution finally stepped into proper action during the Cenozoic. Gaining advantage of the demise of the other suborder, the large gap in species count between them and Ensifera that had been present for the entire past of their evolutionary history started to close.

In the upcoming chapters of this dissertation, we will take closer looks into the diversity of the Mesozoic Orthoptera, namely the Tridactyloidea (chapters 1-3, 11), Locustopsoidea (chapters 4-6, 12) and Elcanoidea (chapters 7-10, 13). But before we dive deep into the tropical forests of Cretaceous Myanmar and seasonal wetlands of the Crato Formation, it is time to follow the Orthoptera on their final 66 million years of evolution and meet the direct ancestors of the many species alive today.

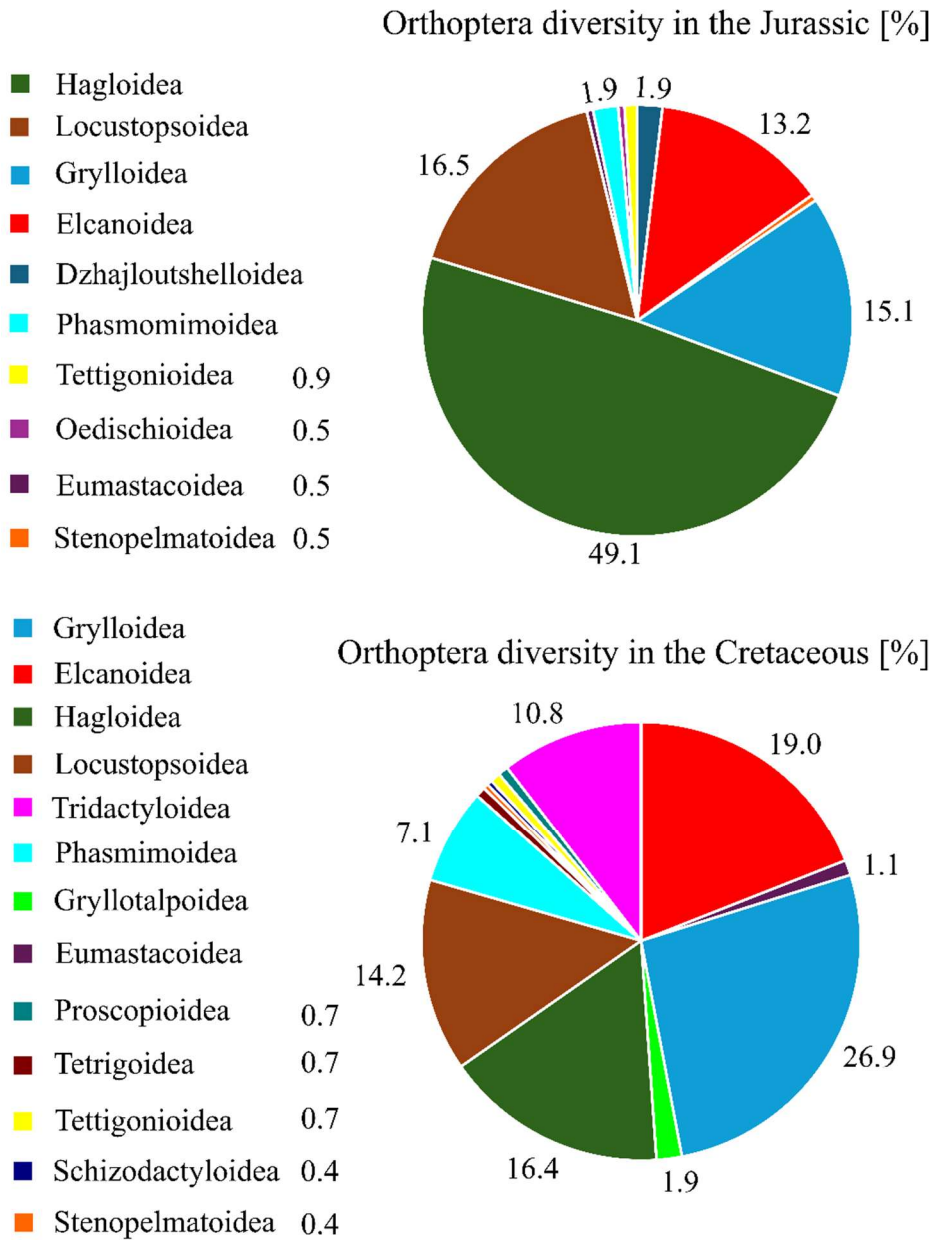

Fig. 1.5 Comparison of superfamily (sf) diversity of Orthoptera Olivier, 1789 in the Jurassic and Cretaceous. Values for each sf indicate the number of species [%] of the total species discovered. The Jurassic orthopteran fauna is represented by several sites across Europe and Asia with most notable ones from Germany, Kyrgyzstan, Kazakhstan and China. Important lagerstätten of Cretaceous age include the Crato Formation of Brazil, Burmese amber from Myanmar, the Russian Zaza Formation, the Durlston and Weald Clay Formation in the UK and the Yixian Formation of China. Several of the modern superfamilies begin to occur in the fossil record of the Jurassic (Grylloidea Laicharting, 1781, Tettigonioidea Krauss, 1902, Stenopelmatoidea Burmeister, 1838, Eumastacoidea Burr, 1899), but of these only the Grylloidea seem to have radiated early on in their evolution. The large majority of Jurassic Orthoptera consisted of the Mesozoic taxa Hagloidea Handlirsch, 1906, Locustopsoidea

Handlirsch, 1906 and Elcanoidea Handlirsch, 1906. In the Cretaceous, Orthoptera became more diverse than ever before, and still more modern subfamilies occur among the fossils of this time. The overall fauna, however, continued to be dominated by Grylloidea and the large Mesozoic taxa mentioned before. As a novelty – and due to their abundance in Burmese amber – Tridactyloidea accompany these groups as the last of the "big five" in terms of diversity of Cretaceous Orthoptera groups.

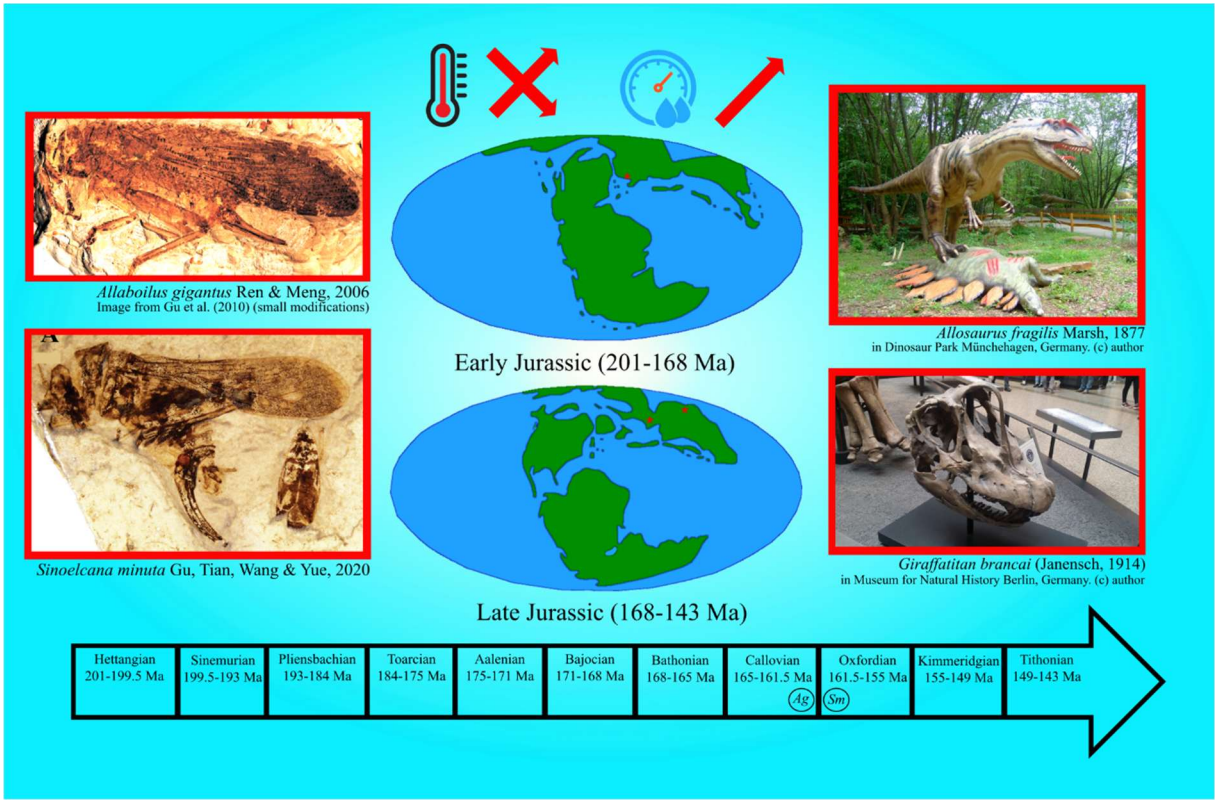

Fig. 1.6: Constellation of the continents, geological stages, climate indicators and faunal examples of the Jurassic during which Hagloidea Handlirsch, 1906 were still the dominant grasshoppers and Gryllidea Vickery, 1977 showed up in the fossil record. Pictogram of thermometer indicates general temperature trend (cooler/warmer climate). Pictogram of hygrometer indicates general climate conditions trend (more humid or more arid). Colors used in the world maps indicate sea (deep blue) and continents (green). Red stars mark the approximate position of Dobbertin in Germany (Early Jurassic) and Karabastau Formation in Kazakhstan (left) as well as Daohugou Formation in China (right) (Late Jurassic), the most important discovery sites for Jurassic Orthoptera. Circles in the timeline indicate occurrence of example orthopterans on the left.

Fig. 1.7: Constellation of the continents, geological stages, climate indicators and faunal examples of the Cretaceous during which Orthoptera and insects may have reached their highest levels of diversity ever (Clapham et al., 2016). Pictogram of thermometer indicates general temperature trend (cooler/warmer climate). Pictogram of hygrometer indicates general climate conditions trend (more humid or more arid). Colors used in the world maps indicate sea (deep blue) and continents (green). Red stars mark the approximate position of the Weald Clay Formation in the UK, Zaza Formation in Russia, Burmese amber from Myanmar and Crato Formation of Brasil (clockwise from top left), the most important discovery sites for Cretaceous Orthoptera. Circles in the timeline indicate occurrence of example orthopterans on the left.

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The Orthoptera: a history, part 3 - Orthoptera of the Cenozoic: familiar faces develop

Aftermath and a new beginning – Orthoptera of the Cenozoic

As the dust of the Cretaceous asteroid impact settled, the Cenozoic unfolded. This last of the three eras of the Phanerozoic (the eon in which complex life diversified on the planet) started after the KPg extinction and continues to the modern day. It began with the Paleocene (66-56 Mya) and Eocene (56-33.9 Mya). Global temperature increases eventually culminated to a Paleocene-Eocene Thermal Maximum ca. 55 Mya that had major negative effects on the benthic marine biota and dinoflagellate assemblages, however, led to thriving terrestrial plant ecosystems (Smith et al., 2020). Since the start of the Cenozoic, placental mammals experienced major diversification (Goswami et al., 2022), giant flightless birds roamed the forests (Mayr et al., 2024) and early whales were in the process of their transition from land to water (Gingerich et al., 2001), to fill in the niche left behind by the Cretaceous mosasaurs.

The warm temperatures caused global biomes to change and the extension of temperate climates to high latitudes (Korasidis et al., 2022). This would likely have influenced diversity patterns of insects, allowing them to disperse and colonize new habitats, while perishing from others (Jouault et al., 2023). But the timing of insect diversification is debated (Benton et al., 2022); fossil-calibrated molecular phylogenetic analyses estimate that 80% of modern insect species

are in families that first appeared in the Cretaceous (Benton et al., 2022). Findings by Clapham et al (2016) and Schachat et al. (2019) noticed a peak in diversity in the Early Cretaceous Aptian 125 Mya that is not connected to a biased fossil record (see *studying fossil Orthoptera, part 1: the fossil record and its limitations*, p. 50), but instead possibly due to the rise of many parasitic lineages (especially Hymenoptera). Clapham et al. (2016) argue that the negligible net richness change after the Cretaceous peak implies that major radiations within extant groups were offset by reduced diversity in declining relic groups or such that went fully extinct.

These findings correspond well to what we have seen in the Orthoptera. Unfortunately, the fossil record of this group after the Mesozoic becomes incredibly patchy and it is difficult to follow the diversification of the extant superfamilies Tettigonioidea and Acridoidea. Instead of 659 species described from Mesozoic deposits, only 171 are known from the Cenozoic. The most important fossil sites of this era are the Florissant and Green River Formations from the Eocene of Colorado, USA, Eocene Baltic amber from Russia (and other countries on the coast of the Baltic Sea), Miocene amber from the Dominican Republic and the old sulfur mine of Radoboj, Croatia that has revealed flora and fauna from the middle Miocene (Mileusnić et al., 2021). In these lagerstätten the superfamilies found most commonly are the Grylloidea, Acridoidea and Tettigonioidea, but also other taxa present in the extant fauna such as Stenopelmatoidea Burmeister, 1838, Rhaphidophoroidea Walker, 1869, Tetrigoidea Rambur, 1838 and Eumastacoidea.

After the Mesozoic had been a time of more ancient, stem-group Ensifera and Caelifera, during the Cenozoic Orthoptera communities developed to resemble the faunal assemblages found today (Fig. 1.8). Even in the small sample size of Eocene vs. Miocene Orthoptera, an increase in Acridoidea species can be seen from 7 to 14, closely matching the Tettigonioidea with 11 species from the Miocene. This fits well with the ca. 8400 species found in both superfamilies today (Cigliano et al., 2025). Although the Cenozoic fossil record of Orthoptera is as scarce as it is, present findings indicate that the familiar faces of the group we know today only diversified after the end-Cretaceous mass extinction. Once the Elcanoidea and Hagloidea of the Ensifera that had been very successful during the Mesozoic had disappeared, Caelifera quickly became more speciose. Nowadays, Ensifera consists of the two major clades Tettigoniidea (Tettigonioidea, Stenopelmatoidea etc.) and Gryllidea Vickery, 1977, Caelifera of the three major clades Acridomorpha MacLeay, 1821 (Acridoidea, Eumastacoidea etc.), Tetrigoidea and Tridactylidea. Some of these lineages, namely Gryllidea, Tridactylidea and some Acridomorpha (Eumastacoidea, Proscopioidea) are present today with families that can trace their ancestors all the way back to the Cretaceous diversity peak, more than 100 Mya, where

they were numerous already. Others, like the Tettigoniidea, Acridoidea and Tetrigoidea only appeared in their modern forms later or were severely underrepresented in the Mesozoic. Because the age of the dinosaurs was not just witness to the greatest reptiles of all time, but also to some remarkable Orthoptera that would meet their demise along with the big lizards, capturing the imagination of paleoentomologists for many years to come.

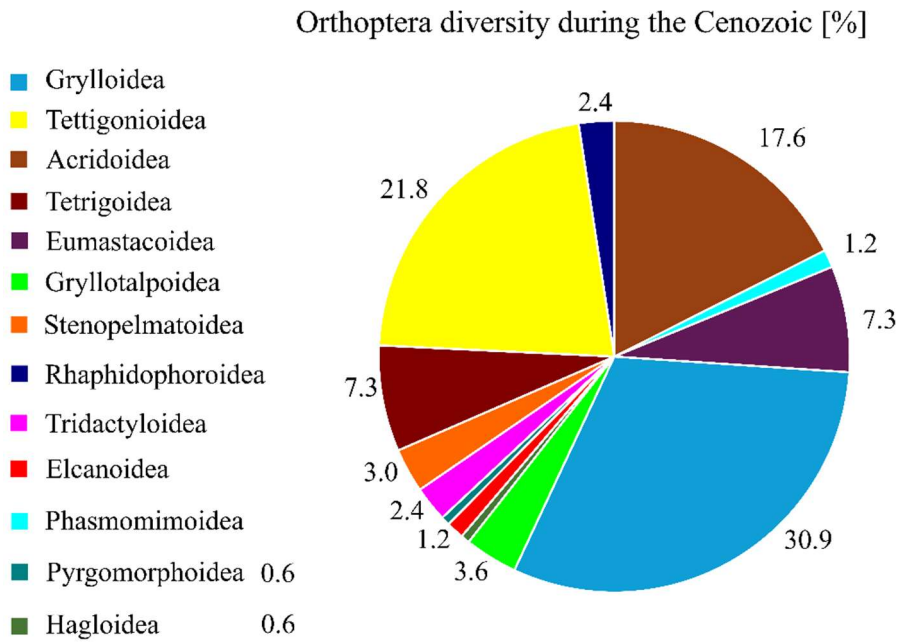

Fig. 1.8 Comparison of superfamily (sf) diversity of Orthoptera Olivier, 1789 in the Cenozoic (combined occurrences during the Paleocene, Eocene, Oligocene, Miocene, Pliocene and Quaternary; fossils only). Values for each sf indicate the number of species [%] of the total species discovered. Important Cenozoic fossil sites for Orthoptera include Dominican amber (Miocene), the Florissant Formation in the US (Eocene), Baltic amber from Russia and Poland (Eocene), Green River Formation in the US (Eocene), Radoboj in Croatia (Miocene), the Menat Formation of France (Paleocene) and the Bouldnor Formation in the UK (Eocene). The list of deposits illustrates a limitation of the post-Cretaceous fossil record, i.e. it is highly biased towards the Eocene and Miocene. Nonetheless, the discoveries made so far generally reflect on the faunal composition of Orthoptera found today. The biggest superfamilies are by far the Grylloidea Laicharting, 1781, Tettigonioidea Krauss, 1902 and Acridoidea MacLeay, 1821. The presence of two alleged Elcanidae species (*Cenoelcanus menatensis* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020 and *Macrelcana ungeri* (Heer, 1849) should be treated with caution.

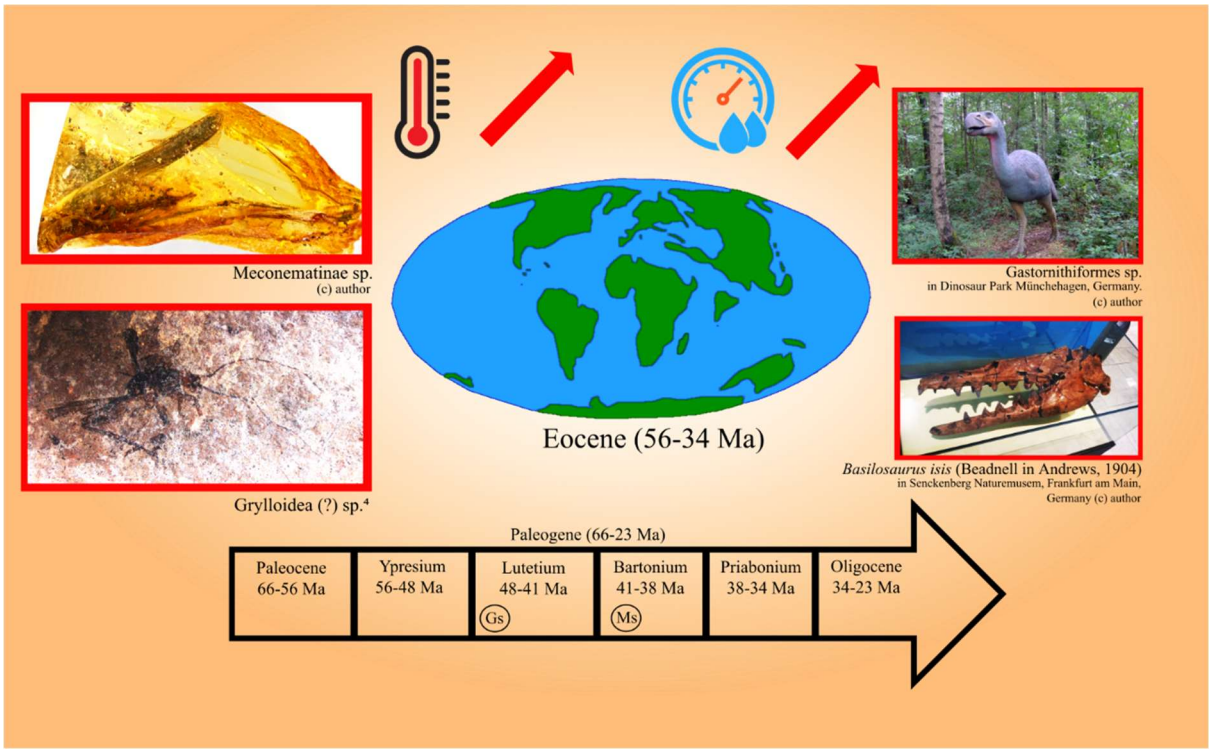

Fig. 1.9: Constellation of the continents, geological stages, climate indicators and faunal examples of the Eocene, during which the modern orthopteran infraorders became diverse. Pictogram of thermometer indicates general temperature trend (cooler/warmer climate). Pictogram of hygrometer indicates general climate conditions trend (more humid or more arid). Colors used in the world maps indicate sea (deep blue) and continents (green). Circles in the timeline indicate occurrence of example orthopterans on the left.

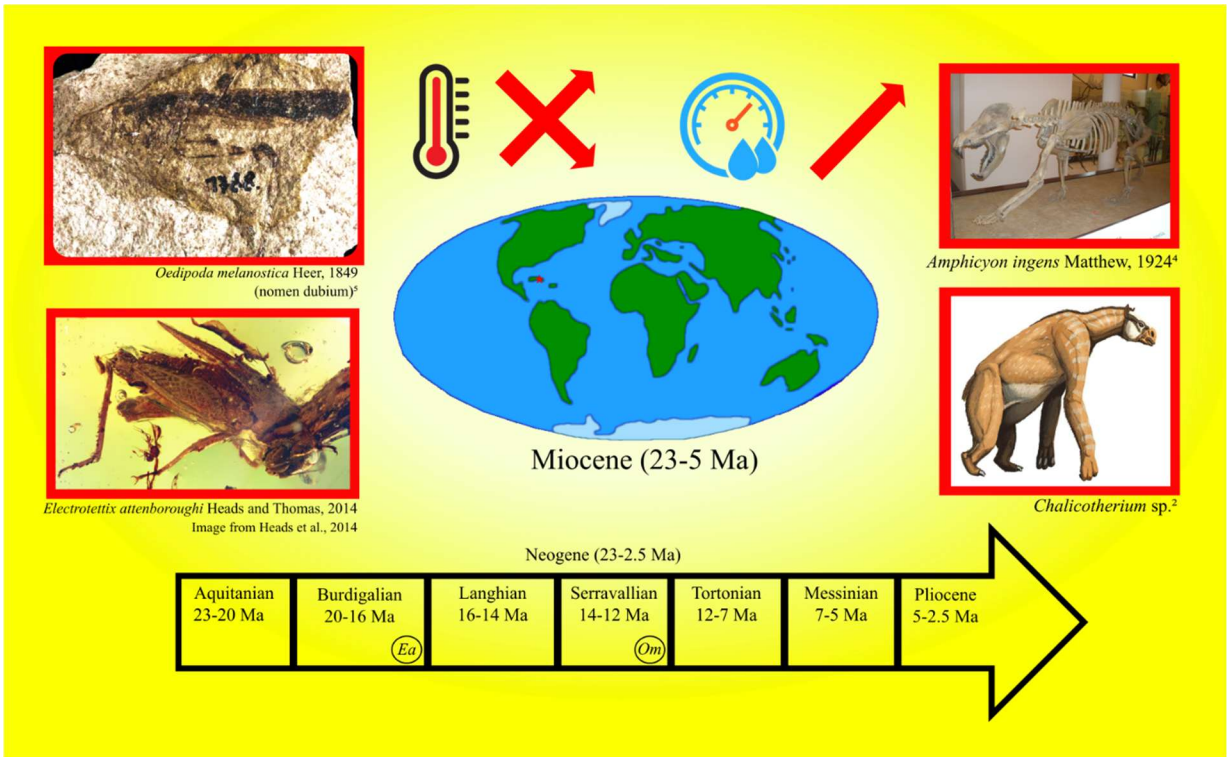

Fig. 1.10: Constellation of the continents, geological stages, climate indicators and faunal examples of the Miocene. Pictogram of thermometer indicates general temperature trend (cooler/warmer climate). Pictogram of hygrometer indicates general climate conditions trend (more humid or more arid). Colors used in the world maps indicate sea (deep blue), continents (green) and ice (light blue). Red star marks the location of Miocene amber from the Dominican Republic, the most important discovery site of Miocene orthopterans. Circles in the timeline indicate occurrence of example orthopterans on the left. [2]Image of *Chalicotherium* uploaded to Wikimedia commons, created by DiBgd; CC 3.0. [4]Image of *Amphicyon ingens* uploaded to Wikipedia.org by Ghedoghedo; no copyrights withheld. [5]Specimen of *Oedipoda melanostica* in the collection of Croatian Natural History Museum, image by Martin Husemann.

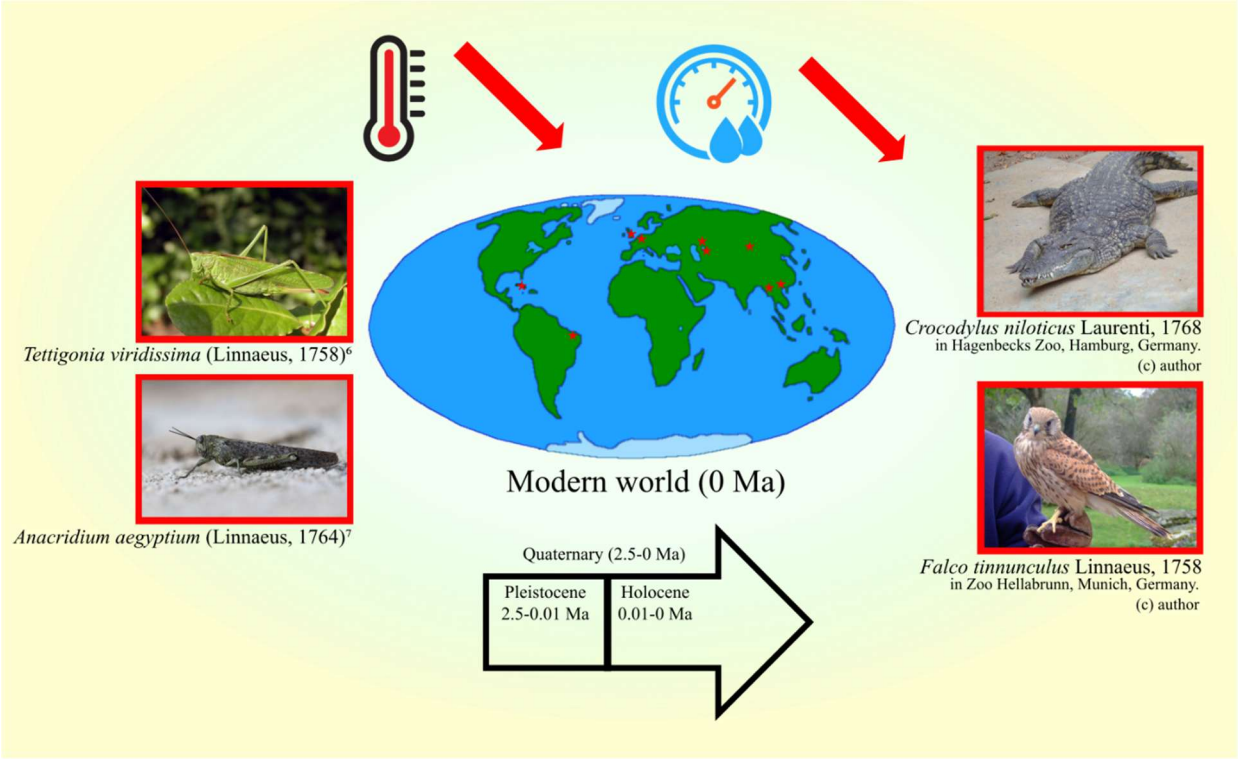

Fig. 1.11: Constellation of the continents, geological stages, climate indicators and faunal examples of the modern world. Pictogram of thermometer indicates general temperature trend (cooler/warmer climate). Pictogram of hygrometer indicates general climate conditions trend (more humid or more arid). Colors used in the world maps indicate sea (deep blue), continents (green) and ice (light blue). Red stars mark the location of all discovery sites featured in the previous era posters. They are (from left to right): Miocene amber from the Dominican Republic; Crato Formation of Brasil (Cretaceous); Weald Clay Formation of UK (Cretaceous); Dobbertin in Germany (Jurassic); Karabastau Formation of Kazakhstan (Jurassic); Madygen Formation of Kyrgyzstan (Triassic); Zaza Formation of Russia (Cretaceous); Burmese amber of Myanamar (Cretaceous); Daohugou Formation of China (Jurassic). Formations

corresponding to Fig. 1.12 (the richest fossillagerstätten for Orthoptera in the world). [6]Image of *Tettigonia viridissima* uploaded to Wikipedia.org by Fritz Geller-Grimm; CC 2.5 (https://creativecommons.org/licenses/by-sa/2.5/). [7]Image of *Anacridium aegyptium* uploaded to the Orthoptera species file by Karmela Adžic (https://orthoptera.speciesfile.org/otus/819169/overview).

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Studying fossil Orthoptera, part 1: the fossil record and its limitations

The things we know about the Orthoptera of the past, their diversity, phylogenetic relationships and biology, are inferred from the fossil record. Unfortunately, the fossil record has many limitations (both in general as well as for insects specifically) which are important to keep in mind when interpreting results such as the diversity of lineages across deep time and space. Schachat and Labandeira (2021) point out several key factors biasing the fossil record of insects:

1. The comparatively frail exoskeleton of insects has a lower chance of being preserved than, for example, vertebrate teeth or shells.
2. The fossil record of insects is especially fragmentary across space and time. A large portion of the known taxonomic diversity of Orthoptera (almost 50%) comes from only nine lagerstätten (so-called konzentrat lagerstätten, due to the high concentration of fossils) (Fig. 1.12). Here, I considered every deposit that has yielded more than 20 species of Orthoptera a konzentrat lagerstätte. They are (in order of geological age):
    a. The Madygen Formation of Kyrgyzstan – Middle Triassic (ca. 242-237 Mya), 125 species
    b. Dobbertin in Germany – Lower Jurassic (ca. 184-183 Mya (PBDB)), 28 species
    c. Daohugou Formation of China – Middle to Upper Jurassic (ca. 166-152 Mya (PBDB)), 30 species
    d. Karbastau Formation of Kazakhstan - Upper Jurassic (ca. 164-157 Mya (PBDB)), 25 species
    e. Weald Clay Formation of the United Kingdom – Lower Cretaceous (ca. 133-125 Mya (PBDB)), 21 species
    f. Zaza Formation of Russia – Lower Cretaceous (ca. 125-113 Mya), 26 species
    g. Crato Formation of Brasil – Lower Cretaceous (ca. 122-113 Mya), 81 species
    h. Burmese amber of Myanmar – Lower Cretaceous (ca. 110-100 Mya), 64 species
    i. Dominican amber from the Dominican Republic - Early Miocene (ca. 20-14 Mya (PBDB)), 22 species

    This selection clearly indicates a strong bias towards specific temporal ranges with ca. 20 to 50 My gaps between deposits of the Mesozoic and an even larger gap of ca. 80 My between the last largerstätte of the Cretaceous (Myanmar) and Dominican amber, which is the only deposit of its taxonomic magnitude for Orthoptera throughout the Cenozoic. The spatial bias becomes evident as well; for example, the Triassic Madygen

Formation, while having revealed an abundance of fossils, exerts a strong bias on our understanding of Triassic Orthoptera communities as more than three quarters of Triassic species are described from this location. This is problematic, as Flannery-Sutherland et al. (2022) showed that global diversity dynamics are regionally heterogenous. So, if 39% of Orthoptera species in the Madygen Formation belonged to the Hagloidea, does this also apply to regions elsewhere? Or is it merely a matter of the Madygen Formation having had an exceptionally rich diversity of Hagloidea, similar to the many species of Elcanidae in the Burmese amber biota, but not in other contemporary Early Cretaceous deposits?

3. Lagerstätten usually develop in certain types of habitats (for example in an ancient lake or around trees that produce large amounts of resins). This way, insects that live in or near these habitats have higher chances of being preserved than others. Much of what is known about Cretaceous amber Orthoptera is based on faunal communities from tropical rainforests, while the species that lived in more temperate environments are less well known (Martínez-Delclòs et al., 2004). On a similar note, environmental conditions of the habitat (such as temperature and moisture) can influence resin production (Langenheim, 1995), causing shifts in quantity between seasons (Martínez-Delclòs et al., 2004).
4. Some body parts of insects are more easily preserved than others. For example, in Orthoptera often isolated fore- or hindwings are found. These structures fossilize easier than the multi-segmented thorax, abdomen or legs which can become readily disarticulated on their way to a depositional setting (Smith, 2000). Also, predators that may feed on an entrapped insect before burial sometimes regurgitate wings (Martínez-Delclòs et al., 2004).
5. Smaller insects are more likely to be preserved than larger ones, because they are buried quicker in a body of water and have a much higher risk of becoming entrapped in amber (Labandeira, 2014a). According to Poinar (1992), insects of less than 5 mm body length are most common in Cretaceous ambers. However, it should be noted that Elcanidae (which are larger than 5 mm in most cases and sometimes exceed 15 mm forewing length [e.g. *Letoelcana artemisapollonque* Schall, Kotthoff & Husemann, 2024]), are relatively common in Cretaceous amber from Myanmar.
6. Of the smaller insects, the larger specimens are recognized more often by researchers and are easier to study, favoring intermediate-sized insects overall.

7. Some findings, such as first and last occurrences of a given taxa gain more attention and are therefore more likely to be published (Schachat et al., 2019).
8. Personal taxonomic preferences of researchers can additionally influence the intensity at which taxa are studied.

In addition to these, further biases are reported by Martínez-Delclòs et al. (2004):

9. Insects with a behavior that has them closely associated with plants that exude resin are more likely to become trapped in amber (Poinar and Poinar, 1999, Solórzano Kraemer et al., 2018). Willmott et al. (2025) reported on three different types of ovipositors found in Elcanidae, which indicate great diversity regarding the egg-laying sites of this family. Perhaps, some members may have deposited their eggs directly under the bark of resin producing trees.
10. Resin may attract some insects (floral resins attract pollinators [Armbruster, 1984]), while deterring others as well as protecting against fungi and bacterial infection. In the case of Orthoptera, Rácz et al. (2023) summarize several instances of extant pollinivorous orthopterans and Labandeira et al. (2007) mention the presence of fresh pollen in the gut of some Prophalangopsidae Kirby, 1906 (superfamily Hagloidea Handlirsch, 1906).

While the limitations affecting the fossil record should not be ignored when conducting studies of larger scope (for example analyses of faunal communities across deep time intervals), it remains a powerful and indispensable mean if we want to understand life on Earth today and in the future. Whether this is for calibrating molecular clocks for estimating divergence times of major clades in phylogenetic analyses (e. g. Song et al., 2015), trying to predict the impact of anthropogenic disturbances on the extinction rates of insects (Schachat and Labandeira, 2021) or determining the ecological role of higher-level taxa in their ecosystem (for example by comparing the faunal assemblages and paleoenvironment of the four Lower Cretaceous lagerstätten mentioned before). The fossil record of insects is continuously growing, revealing new insights into their evolution the more specimens are discovered (Nicholson et al., 2015).

This is why taxonomy is the steppingstone to all other research in paleobiology – it is the groundwork that provides the data of which everything else is conducted (Singh, 2025). The fossil record truly is an ever-expanding treasure trove of knowledge. Growing richer publication by publication. Species by species.

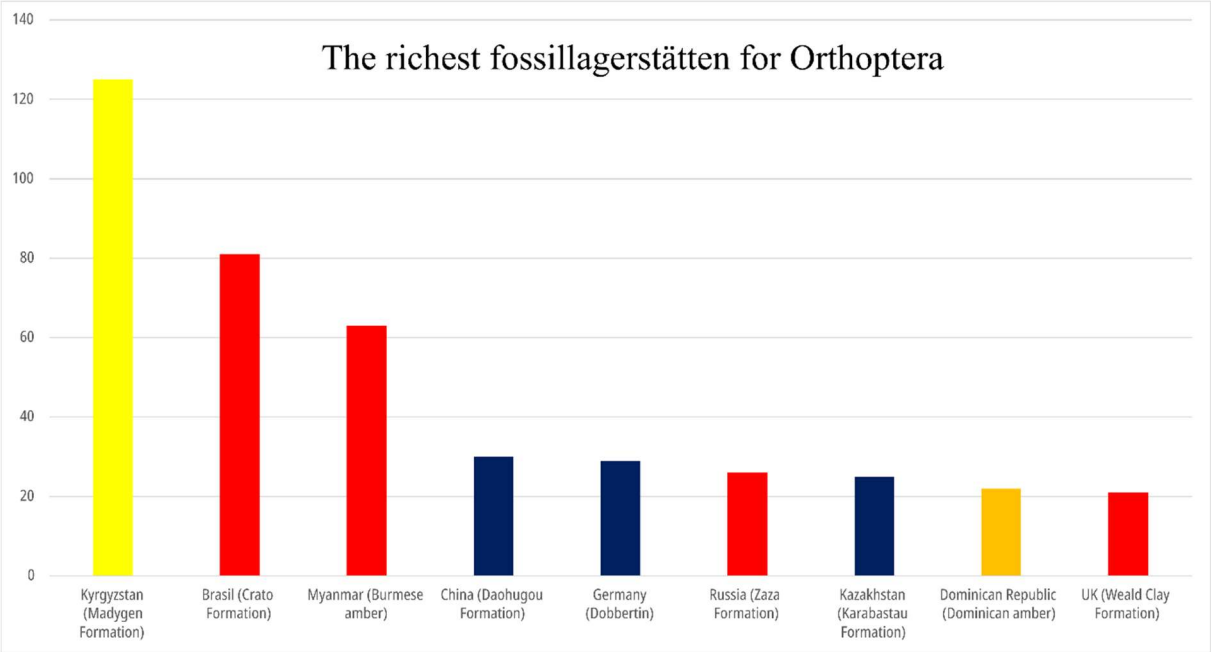

Fig. 1.12 The richest fossillagerstätten in the world for Orthoptera. Yellow = Triassic; Blue = Jurassic; Red = Cretaceous; Orange = Cenozoic (Miocene). The Triassic and Cenozoic especially are affected by strong temporal and geographic biases of the lagerstätten. The situation is better for the Jurassic, but still most findings are from Europe and Asia. The Cretaceous is the period best represented by the fossil record, with rich lagerstätten from parts of Laurasia (Russia, UK) and Gondwana (Brazil, Myanmar). Unfortunately, we are missing a high-yielding deposit of the Late Cretaceous.

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Studying fossil Orthoptera, part 2: morphology (body & wing venation)

The following chapters of this dissertation will cover four different families of Orthoptera Olivier, 1789: Tridactylidae Brullé, 1835, Ripipterygidae Ander, 1939, Locustopsidae Handlirsch, 1906 and Elcanidae Handlirsch, 1906. Although the texts and figures provided in each chapter make it possible to understand the morphological terms featured in the description of specimens, here I present a general overview for each family. Besides the morphology of aspects of the head, thorax (this includes the legs) and abdomen, for families with an elaborate

wing venation (such as Locustopsidae and Elcanidae) this is of high taxonomic value as well. Therefore, venation terminology of these two families will be illustrated based on typical fore- and hindwings.

Ripipterygidae

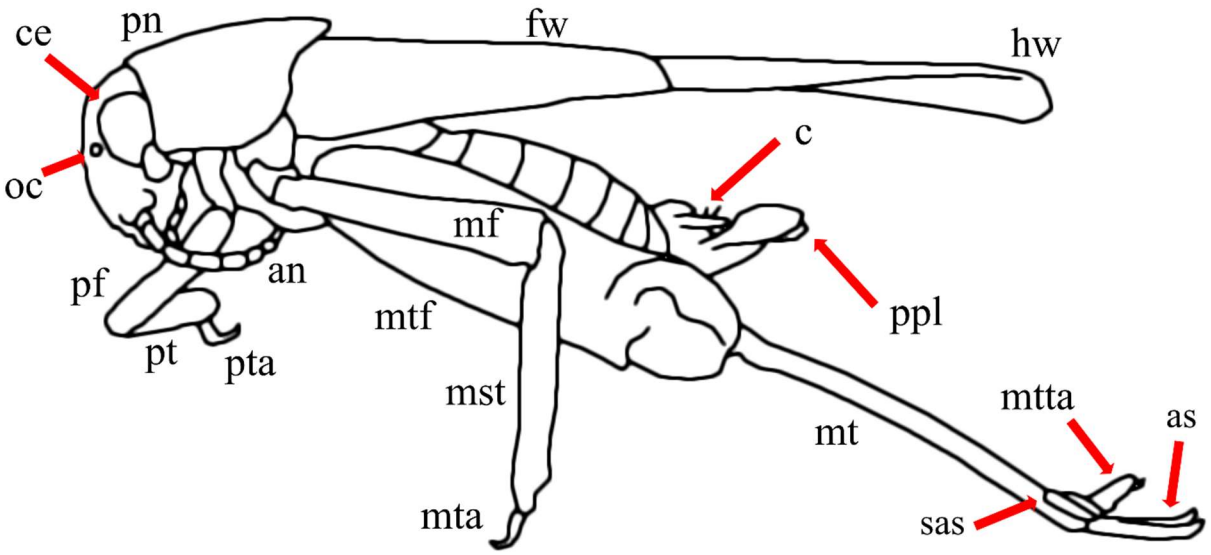

Fig. 1.13 Morphology of Ripipterygidae Ander, 1939 after *Ripipteryx notata* (Burmeister, 1838) (drawing based on CollectionObject 1537546 in the Orthoptera species file: https://orthoptera.speciesfile.org/otus/806060/overview). Abbreviations: ce = compound eye; oc = ocellus; pn = pronotum; fw = forewing; hw = hindwing; pf = profemur; pt = protibia; pta = protarsus; an = antenna; mf = mesofemur; mst = mesotibia; mta = mesotarsus; mtf = metafemur; mt = metatibia; mtta = metatarsus; sas = subapical spur; as = apical spur; c = cercus; ppl = paraproctal lobe.

Tridactylidae

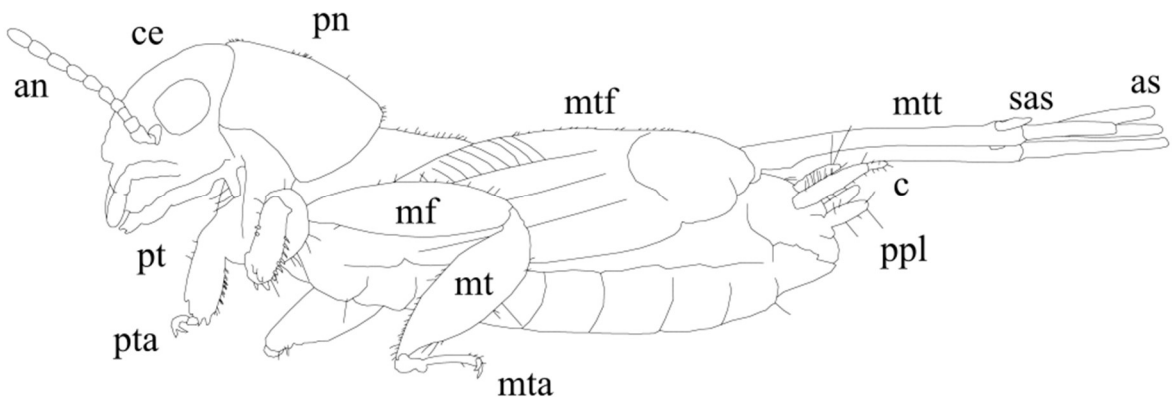

Fig. 1.14 Morphology of Tridactylidae Brullé, 1835 after *Ellipes deyrupi* Woo, 2021 (drawing based on Figure 3B in Woo, 2021). Abbreviations: an = antenna; ce = compound eye; pn =

pronotum; pt = protibia; pta = protarsus; mf = mesofemur; mt = mesotibia; mta = mesotarsus; mtf = metafemur; mtt = metatibia; c = cercus; ppl = paraproctal lobe; sas = subapical spur; as = apical spur.

Ripipterygidae and Tridactylidae share many common features (see Heads, 2009), since they do belong to the same superfamily Tridactyloidea Brullé, 1835 and are close relatives of each other. Main differences between the two families include 1) the inflated mesotibiae of Tridactylidae, which is at least as wide as the mesofemur or wider (less wide than mesofemur in Ripipterygidae); 2) the two-segmented cerci of Tridactylidae; 3) Valvulae of ovipositor just visible in females of Ripipterygidae (not visible in Tridactylidae). Additionally, some extant species of Tridactylidae have very reduced metatarsi, that are barely visible with the naked eye and appear absent without closer look (see Fig. 1.14). Members of several genera (*Xya* Latreille, 1809, *Bruntridactylus* Günther, 1979, *Afrotridactylus* Günther, 1994 and *Neotridactylus* Günther, 1972, as well as the fossil *Guntheridactylus* Azar and Nel, 2008) feature characteristic swimming lamellae on the tibiae of their hind legs. These adaptations that help to move on the surface of water (Kim et al., 2021), are not known from any Cretaceous tridactyloids, however.

Elcanidae

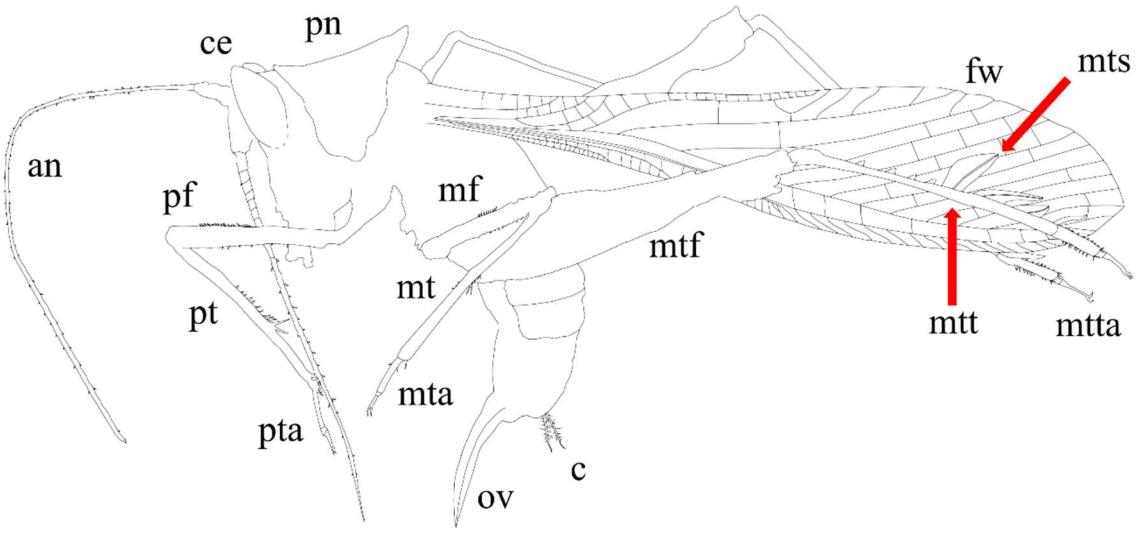

Fig. 1.15 Morphology of Elcanidae Handlirsch, 1906 after *Longioculus poinari* (see chapter 7). Drawing with some aspects reconstructed to depict complete specimen. May deviate from real *L. poinari*. Abbreviations: an = antenna; ce = compound eye; pn = pronotum; pf = profemur; pt = protibia; pta = protarsus; mf = mesofemur; mt = mesotibia; mta = mesotarsus; mtf = metafemur; mtt = metatibia; mts = metatibial spur; mtta = metatarsus; fw = forewing c = cercus; ov = ovipositor.

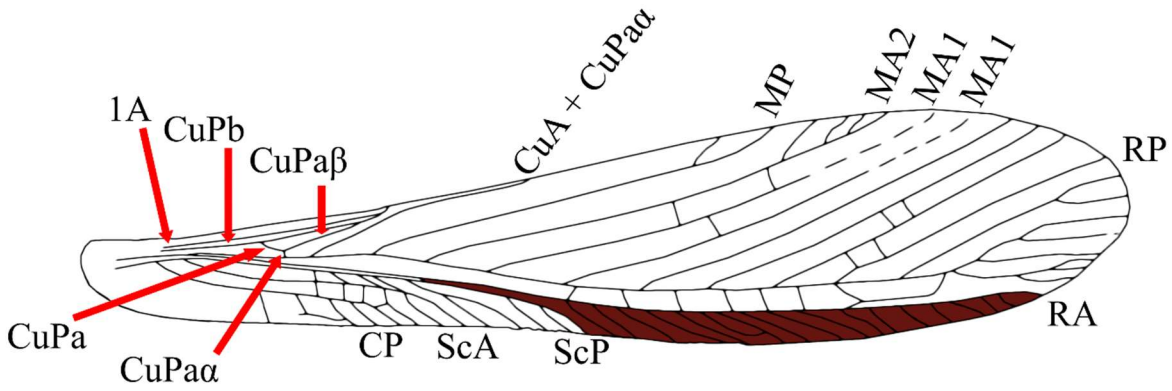

Fig. 1.16 Morphology of a typical elcanid forewing, after *Pseudopanorpidium inversa* Schall, Kotthoff & Husemann, 2025. Length of CuA + CuPaα reconstructed and posterior wing base reconstructed. Abbreviations: 1A = anterior anal vein. CuPb = second posterior cubitus; CuA = anterior cubitus; CuPa = first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPaα = anterior branch of first posterior cubitus; MA, MP = anterior/posterior media; R = radius; RA, RP = anterior/posterior radius; ScA, ScP = anterior/posterior subcosta; CP = posterior costa.

Notice the terminal fusion of the veins 1A, CuPb and CuPaβ in the forewing of *Pseudopanorpidium inversa* vs. the unfused state of *Longioculus poinari* (Fig. 1.17). This difference separates the two subfamilies of Elcanidae, the Elcaninae Handlirsch, 1906 (veins are fused) and the Archelcaninae Gorochov et al., 2006 (veins are not fused).

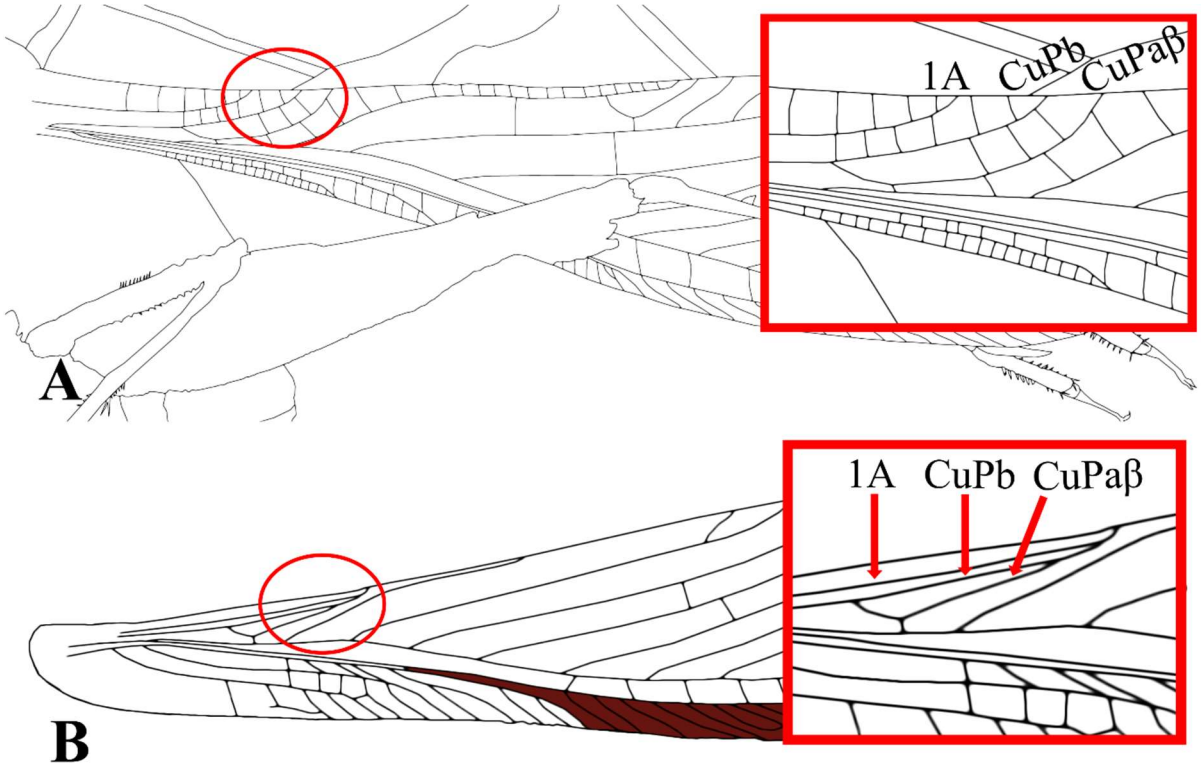

Fig. 1.17: Comparison of unfused ('free') state of veins 1A, CuPb and CuPaβ in the forewing of *Longioculus poinari* sp. nov. (chapter 7) from the subfamily Archelcaninae Gorochov, Jarzembowski & Coram, 2006 (**A**) to the fused state in *Pseudopanorpidium inversa* Schall, Kotthoff & Husemann, 2025 from the subfamily Elcaninae Handlirsch, 1906 (**B**).

Locustopsidae

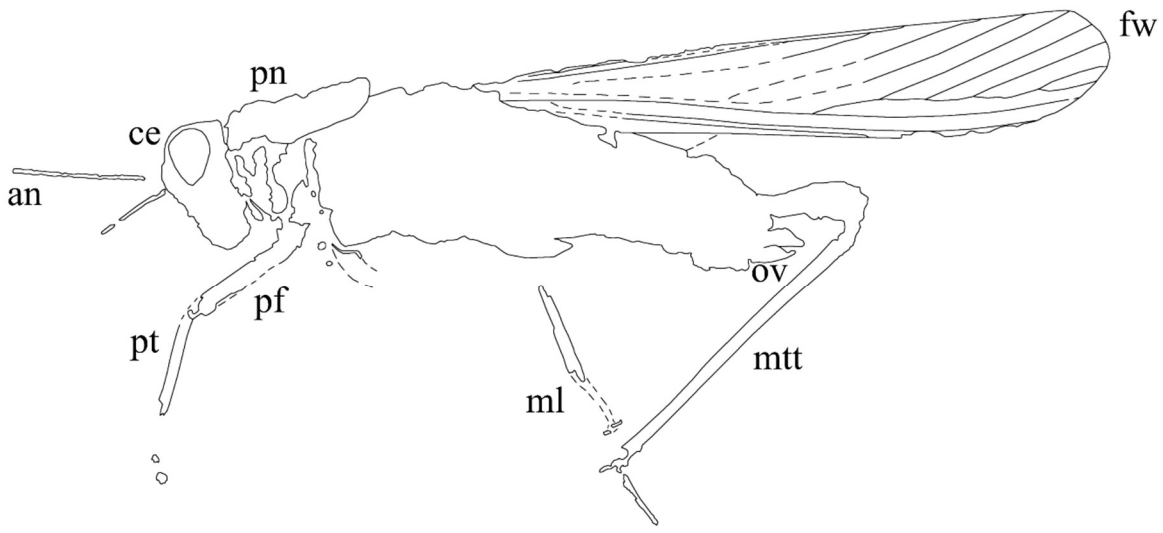

Fig. 1.18 Morphology of Locustopsidae Handlirsch, 1906 after an undescribed specimen from the University of Illinois Collection (INHSP_1123a). Because the morphology of Locustopsidae is less well understood than for Elcanidae (due to the absence of amber specimens), reconstructions were not applied. Dotted lines represent features of uncertain morphology. Abbreviations: an = antenna; ce = compound eye; pn = pronotum; pf = profemur; pt = protibia; ml = mesothoracic leg; mtt = metatibia; fw = forewing; ov = ovipositor.

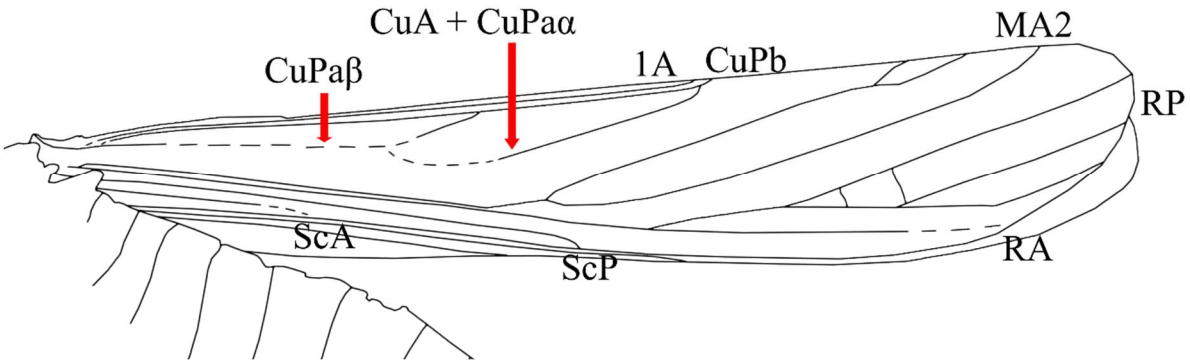

Fig. 1.19 Morphology of a typical locustopsid forewing, after specimen MH0066 (*Locustrix gallegoi* Martins-Neto, 2003; see chapter 6) from the private collection of Martin Husemann (State Museum of Natural History, Karlsruhe, Germany). Dotted lines represent veins with uncertain morphology. Abbreviations: 1A = anterior anal vein. CuPb = second posterior cubitus; CuA = anterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPaα = anterior branch of first posterior cubitus; MA, MP = anterior/posterior media; R = radius; RA, RP = anterior/posterior radius; ScA, ScP = anterior/posterior subcosta.

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Part I: Tridactyloidea – little gems of the riverside

Fig. 2.1 An undescribed specimen (MH_0012) of Tridactyloidea (family Tridactylidae, cf. *Burmadactylus tenuicerci* Fan, Gu & Cao, 2023) from Burmese amber of Myanmar. Notice the distinct three-fingered look of the apical spines and metatarsus of the hind leg, namesake of the superfamily.

Preface

Orthoptera Olivier, 1789 are split into two suborders, the Ensifera Chopard, 1921 and the Caelifera Ander, 1936. While the extant diversity of Ensifera is relatively equally distributed among its two infraorders Tettigoniidea Kevan, 1982 and Gryllidea Vickery, 1977, the majority of extant Caelifera species is found in the Acrididea Targioni-Tozzetti, 1882. Today, ca. 98% of Caelifera belong to this infraorder (Cigliano et al., 2025). But that was not always the case. In the Cretaceous (ca. 143-66 Mya), the sister group of Acrididea contributed almost 40% to the overall diversity of the suborder: this was the Tridactylidea Brullé, 1835. Not only was Tridactylidea proportionally much more diverse in ancient times, but they are also significantly older than the rest of the Caelifera alive today. The first members of this taxon, a group called Dzhajloutshelloidea Gorochov, 1994 appear in the fossil record as early as the Triassic of Madygen. It took ca. 80 My longer for the very first Acrididea to show up in the Jurassic of the Karabastau Formation in Kazakhstan (PBDB) (this refers to *Archaeomastax jurassicus* Sharov, 1968, an alleged Eumastacoidea Burr, 1899).

The modern infraorder Tridactylidea is organized in three families: Tridactylidae Brullé, 1835, the type family has a cosmopolitan distribution and includes 165 species, 20 of them fossil (Cigliano et al., 2025; chapter 3). They are commonly referred to as pygmy mole crickets due to the superficial resemblance of the true mole crickets of the superfamily Gryllotalpoidea Leach, 1815 within the Gryllidea. The sister group of Tridactylidae is the family Ripipterygidae Ander, 1939 (Song et al., 2015). In modern times, this family is exclusively found in South and Middle America, however, findings from Burmese amber show it was more widely spread during the Cretaceous period (Zhao et al., 2024). Ripipterygidae includes 83 species, 11 of them fossils (Cigliano et al., 2025; chapters 1-2). They are sometimes referred to as mud crickets but often called pygmy mole crickets as well. The third family of Tridactyloidea and sister group to Tridactylidae + Ripipterygidae is the Cylindrachetidae Giglio-Tos, 1914 (Song et al., 2015; Yahyaoğlu et al., 2023). These enigmatic animals exhibit great adaptations to a subterranean lifestyle, such as the reduced antennae, compound eyes, cerci and mid- and hind legs as well as the cylindrical, almost worm-like body shape (Houston, 2007). They are found in Australia, New Guinea and South America and include 16 species. Despite divergence time estimates by Song et al., (2015) suggesting that they evolved from the common ancestor of Tridactyloidea as early as ca. 200 Mya, no fossils of this group have been found so far.

Tridactyloidea are characterized by 1) the pronotum and prosternum being connected via a precoxal bridge; 2) a protarsus with two tarsomeres, inserted on the inner surface of the protibia

(in most other orthopterans, the protarsus has three tarsomeres); 3) mesotarsus with two tarsomeres (three in most other orthopterans); 4) metatarsus always reduced to only one tarsomere; 5) arolia entirely absent; 6) abdomen with nine fully sclerotized sterna in both sexes, the ninth forming a simple subgenital plate lacking styli; 7) abdominal repugnatorial glands; 8) male paraproct with distinctive sclerotized hooks (list of apomorphies after Heads, 2009).

In fossil specimens, several of the characters mentioned can be difficult to assess based on the quality and visibility of the fossil. Extinct members of Tridactyloidea are therefore best recognized by their 1) heavily inflated metafemurs. 2) Short antennae. 3) The characteristic shape of the metatibia with the subapical and apical spines and reduced metatarsus displaying a "three-finger look" from which the name Tridacytloidea is derived. 4) Morphology of the abdomen with distinct paraproctal lobes, visible ovipositor valvulae in Ripipterygidae and two-segmented cerci in Tridactylidae.

The biology of Tridactylidae and Ripipterygidae is little studied, especially of the latter family. Members of the taxa are usually found within reach of water bodies, where they live in colonies and dig burrows into the sand or soil (Burrows and Picker, 2010; Woo, 2021). They feed mainly on organic detritus (Kuřavová and Kočárek, 2016) and algae (Woo, 2021). Some species of Ripipterygidae, like *Ripipteryx insignis* Chopard, 1937*, Ripipteryx biolleyi* Saussure, 1896 and *Ripipteryx saopauliensis* Günther, 1969 exhibit striking coloration of orange, yellow and black patterns. When populating the banks of a nearby forest stream, they truly represent little living gems with their elusiveness completing this image.

The next three chapters will showcase the diversity of Tridactyloidea from mid-Cretaceous Burmese amber of Northern Myanmar. The amber has revealed numerous species of this group in most recent times (e.g. Fan et al., 2023; Gu et al., 2022; Zhao et al., 2024). Here, we will meet three new species of Ripipterygidae plus a most unusual, putative member of this family (chapters 1 and 2) and two new species of Tridactylidae (chapter 3).

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Chapter 1

New genera and species of Ripipterygidae (Orthoptera: Tridactyloidea) from mid-Cretaceous Kachin amber†

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AUTHOR'S COMMENT

This article was previously published as **Schall, O. K. O., Cao, C. Q. & Husemann, M. (2025). New genera and species of Ripipterygidae (Orthoptera, Tridactyloidea) from mid-Cretaceous Kachin amber. *Contributions to Entomology*, *75*(2), 253-262** in a slightly different version (all author names behind the first mention of a taxon name are included in the dissertation version of the article).

Abstract

Two new genera and species of Ripipterygidae Ander, 1939 are described from mid-Cretaceous Kachin amber of Northern Myanmar. *Ozymandipteryx campana* gen. et sp. nov. is remarkable for its absent or very reduced metatarsus. In modern species of Tridactyloidea, a reduced metatarsus can only be found in the Tridactylidae Brullé, 1835 genera *Ellipes* Scudder, 1902 and *Xya* Latreille, 1809, but not in Ripipterygidae. *Magnidactylus robustus* Xu, Fang & Jarzembowski, 2020, type species of the genus, is found to share the character of a fully reduced metatarsus (apical spurs were previously misinterpreted as metatarsus), but *M. robustus* differs from *O. campana* in several important characters and hence remains a separate genus. However, a new genus *Yakkhapipteryx* is erected to include the other two former *Magnidactylus* species *M. mirus* Gu, Zheng, Cao & Yue, 2022 (*Yakkhapipteryx mirus* comb. nov.) and *M. gracilis* Gu, Zheng, Cao & Yue, 2022 (*Yakkhapipteryx gracilis* comb. nov.), which both have a metatarsus in normal condition. Another newly described taxon is *Ciconipteryx bidactylus* gen. et sp. nov. This species is the first fossil Ripipterygidae with only two dactyls on its protibia, a feature it shares with the modern species *Mirhipipteryx pulicaria* (Saussure, 1896). *Ciconipteryx bidactylus* stands out due to its long mid- and hindlegs in relation to body size. This character may have enabled it to perform very efficient jumps. The new species add to the diversity of Ripipterygidae from Kachin amber, expanding our knowledge of this little studied family and raising new possibilities for interpreting their evolutionary history.

Keywords: Caelifera, fossil, jumping behavior, mud crickets, pygmy mole crickets, taxonomy

Introduction

Alongside the more diverse and well-known Acrididea Targioni-Tozzetti, 1882, Tridactylidea Brullé, 1835 is one of the two infraorders of the Caelifera Ander, 1936, the short-horned grasshoppers, which include more than 40% of modern-day orthopteran diversity (Cigliano et al., 2025). However, next to their grasshopper relatives, which are larger, more conspicuous, and generally gain far more attention both from science and laypersons alike, the Tridactylidea are a group with many aspects of their behaviour and ecology still poorly understood (Ugolini, 2021).

Systematically, Tridactylidea consist of two superfamilies, the Dzhajloutshelloidea Gorochov, 1994 (entirely fossil, 9 species) and the Tridactyloidea Brullé, 1835 (257 species, both extant and fossil). A third taxon, the enigmatic Burmecaelidae Uchida et al., 2024, is currently considered Tridactylidea *incerta sedis* (Schall et al., 2025). Within Tridactyloidea are three families. The Cylindrachetidae Giglio-Tos, 1914 are exclusively found in Argentina, Australia and Papua New Guinea, and are heavily adapted to an underground lifestyle. Their habitus has become almost worm-like with completely reduced or absent wings and ovipositor and very shortened legs. There is no fossil record of this family as of yet. The other two families are the Tridactylidae Brullé, 1835 and the Ripipterygidae Ander, 1939. In modern representatives, Ripipterygidae can be differentiated from Tridactylidae by 1) their cerci being one-segmented (two-segmented in Tridactylidae), 2) their mesotibiae being of roughly the same width as their mesofemora (in Tridactylidae the mesotibiae are distinctly inflated and wider than the mesofemora), 3) visible valves of the ovipositor (the ovipositor is reduced to the point where it is invisible in Tridactylidae), and 4) paraproctal lobes apically with a distinct array of setae (distinct apical setae not present in Tridactylidae) (Gorochov, 2010; Heads, 2010; Gu et al., 2022). Tridactylidae have a cosmopolitan distribution (except for Antarctica), whereas Ripipterygidae are only known from South and Central America (Cigliano et al., 2025).

The fossil record of Tridactylidae and Ripipterygidae is not very extensive, but several findings have been made during recent years in Kachin amber from the mid-Cretaceous of Myanmar which has revealed a stunning diversity of these groups in that ecosystem (Zhao et al., 2024). Other localities with reported occurrences of fossil Tridactylidae and Ripipterygidae are the Crato-Formation of Brazil (Lower Cretaceous) (Martins-Neto, 1990), amber from the Dominican Republic (Miocene) (Heads, 2010; Poinar, 2018), France (Eocene) (Azar and Nel, 2008), Great Britain (Lower Cretaceous) (Gorochov et al., 2006), Russia (Lower Cretaceous) (Gorochov in Kopylov et al., 2020; Sharov, 1968) and Mongolia (Lower Cretaceous)

(Gorochov, 1992) (for a comprehensive table of the known fossil record of Tridactyloidea see Zhao et al., 2024). The Tridactyloidea found in amber from Myanmar are especially important for understanding the evolution of the superfamily, because they are very diverse (ca. 50% of fossil Tridactyloidea have been found in Kachin amber) and are often preserved with almost life-like detail.

In this study, we describe three new genera and two new species of Ripipterygidae from mid-Cretaceous Kachin amber. Both exhibit an intriguing combination of characters which provide important insights into the evolutionary history that led to the distinct modern clades Ripipterygidae and Tridactylidae.

Materials and methods

The amber pieces presented in this study are housed in the collection of the Leibniz Institute for the Analysis of Biodiversity Change (Hamburg) (collection numbers GPIH07209 and GPIH07210). They originate from Myanmar and were discovered at a mining site either near Tanai village or Hkamti village. The age of the two amber sites differs by ca. 10 my.; amber from Tanai is estimated to be 98.79 ± 0.62 My old (Shi et al. 2012), whereas amber from Hkamti is ca. 110 My old (Xing and Qiu, 2020). Tragically, political instability and enforcement of human rights continue to be problematic in Myanmar. Unfortunately, we do not know the year the amber pieces in this study were originally obtained, i. e. pre- or post-2017. However, after considering the local situation in Myanmar as described in Peretti (2020) and Peretti (2021), we think that stopping scientific amber research (as demanded by Engel (2020)) is unjustified.

Imaging of the specimens was conducted using a DUN. Inc. stacking system with a Canon EOS 5Dsr Camera. We used a 65 mm lens and a magnification of 2.5x. Individual pictures were taken with VD Passport and Capture One program (Capture One A/S, Denmark) and stacked with Zerene Stacker (Zerene Systems LLC, Washington, USA). They were edited with Photoshop CS6 Extended application by Adobe Inc. (USA; https://www.adobe.com). Further modifications (e. g. scale-bars) and creation of image collections was done in Inkscape (v. 1.3.2) (the INKSCAPE Team, 2025). Drawings were created in GIMP (v. 2.10.30) (the GIMP Team, 2025).

The jitter plot featured in the comparison of leg lengths of Tridactyloidea Brullé, 1835 species in the discussion was created with PAST5 (Hammer et al., 2001) and Inkscape.

The taxonomy in this study follows the Orthoptera Species File (OSF) (https://orthoptera.speciesfile.org/, Cigliano et al., 2025).

Systematic paleontology

Order: Orthoptera Olivier, 1789
Suborder: Caelifera Ander, 1936
Infraorder: Tridactylidea Brullé, 1835
Superfamily: Tridactyloidea Brullé, 1835
Family: Ripipterygidae Ander, 1939

Genus ***Ozymandipteryx*** gen. nov.

Type species: *Ozymandipteryx campana* sp. nov.

Zoobank-ID: urn:lsid:zoobank.org:act:A66BF25D-834A-4457-97B9-6419485A66E8

Etymology: Named after Ozymandias, a poem by Percy Bysshe Shelley (1818) about the loss of greatness and forgetting of glory by the passing of time. It refers to the state of absent/very reduced metatarsi in the genus, which can be found in the modern-day Tridactylidae genera *Ellipes* Scudder, 1902 and *Xya* Latreille, 1809, but is not present in any extant Ripipterygidae.

Diagnosis: Absence or almost complete reduction of the metatarsus. Protibiae without dactyls. Mesotibiae not inflated. Cerci one-segmented, cylindrical, with long hairs. Forewing and hindwing present. Metafemur with two small apical protrusions. Dorsal metatibial ridge distally with slight serration. Apical spurs of metatibia much longer (4x) than subapical spurs.

Ozymandipteryx campana sp. nov.

Figs 1-2

Zoobank-ID: urn:lsid:zoobank.org:act:49DE4348-1B1C-4B44-B2FC-9087CACB8272

Etymology: The species' name is Latin for "bell". It is meant to refer to the "Great Bell of Dhammazedi", a treasure lost in time.

Locality and horizon: The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My and the amber from Tanai ca. 99 My old.

Holotype: Sex unknown. Specimen part of the LIB-Hamburg collection; collection number GPIH07209 (ex collection Martin Husemann MH0082).

Diagnosis of species: As for genus (monotypic).

Description: Preservation of complete specimen, unfortunately with some parts obscured by structural damage inside the amber.

Measurements: Some measurements could not be precisely made, because the corresponding feature was somewhat obscured. Such measurements are indicated with a "ca.". Body length ca. 1.72 – 1.76 mm (head to abdominal apex). Forewing length ca. 0.72 mm. Hindwing length ca. 1.26 mm. Head height ca. 0.5 mm. Mesofemur length 0.89 mm. Mesotibia length 0.72 mm. Mesofemur width/mesotibia width 1.18 (both at max. width). Pronotum length (dorsal) 0.42 mm. Metafemur length 1.18 mm, width 0.54 mm. Metatibia length 1.17 mm, width 0.09 mm. Length of subapical spurs 0.08 mm and of apical spurs 0.32 mm. Cercus length ca. 0.24 mm.

Head: Antennae 10-segmented (including scape and pedicel). 10^{th} antennomere larger than previous seven and bean shaped. Compound eyes protruding from head. Ocelli not visible.

Thorax: Pronotum not prolonged over abdomen, with elevation from thorax. Both forewings and hindwings present. Hindwings not prolonged over abdomen.

Legs:

Prothoracic leg: Tibia inflated. Dorsal margin with four evenly spaced hairs. No dactyls present. Tarsus very slender, with two claws.

Mesothoracic leg: Femur without hair or appendages. Tibia not inflated, with hairs on ventral margin along the entire length and also on dorsal margin towards apex. Tarsus two-segmented, bearing two claws.

Metathoracic leg: Femur greatly inflated along its entire length. Two small protrusions apically. Dorsal tibial ridge distally with slight serration proximal to subapical spurs. Two subapical and two apical spurs present. Apical spurs much longer than subapical spurs. Metatarsus not visible, either absent or too vestigial to be seen.

Abdomen: Only one cercus visible, one-segmented and cylindrical in shape. Setulose with long hair.

Remarks: The new species can be assigned to the Ripipterygidae based on the following characters: 1) Cercus one-segmented and 2) mesotibiae not inflated. In this family, it differs from the other members found in Kachin amber by an absent or very vestigial metatarsus, a protibia without dactyls and two small protrusions on the apex of its metafemur. The protibia without dactyls is a character the new species shares with some members of fossil Tridactylidae: *Burmadactylus grimaldii* Heads, 2009, *Paraxya hui* Cao, Chen & Yin, 2019 and *Ellipes dominicana* Poinar, 2020. Likewise, a vestigial metatarsus is also present in some extant Tridactylidae, namely the genera *Ellipes* Scudder, 1902 and *Xya* Latreille, 1809 (Günther, 1977; Heads, 2010).

Based on our current understanding of Tridactyloidea morphology, the presence of characters only known from Tridactylidae among the extant fauna in a fossil specimen that should be placed in Ripipterygidae, suggests four possible conclusions: 1) Our understanding of Tridactyloidea morphology is not complete. 2) A fully reduced metatarsus and protibial without dactyls were present for some time in the ancestors of modern Ripipterygidae, but this lineage was subsequently lost. 3) *Ozymandipteryx* does not actually belong to the Ripipterygidae but is instead a member of a stem-group Tridactyloidea occurring prior to the split of Tridactylidae and Ripipterygidae. 4) *Ozymandipteryx* is part of a separate lineage of Tridactyloidea not yet described. If one of the last two hypotheses is true, attribution of fossil Tridactyloidea from the Cretaceous may have to be reconsidered; however, this can only be validated by future findings.

Interestingly, *O. campana* is not the first fossil species with a fully reduced metatarsus. In the description of *Magnidactylus robustus* Xu, Fang & Jarzembowski, 2020, the apical spurs of the specimen were interpreted as the metatarsus. But in fact, the metatarsus appears to be absent in *M. robustus* just like in *O. campana*. This finding may suggest a closer phylogenetic relationship between the two species. However, *M. robustus* differs from *O. campana* by the presence of four dactyls on its protibia, no hairs on the cerci and no apical protrusions on the metafemur. Further, *M. robustus* is more than three times the size of *O. campana* (Xu et al., 2020). With this re-interpretation of the morphology of *M. robustus*, the species does not belong in the same genus as *Magnidactylus mirus* Gu, Zheng, Cao & Yue, 2022 and *M. gracilis* Gu, Zheng, Cao & Yue, 2022, which both posess a normal (for Tridactyloidea) metatarsus. We propose *Yakkhapipteryx* gen nov. as a new genus to house *M. mirus* and *M. gracilis*.

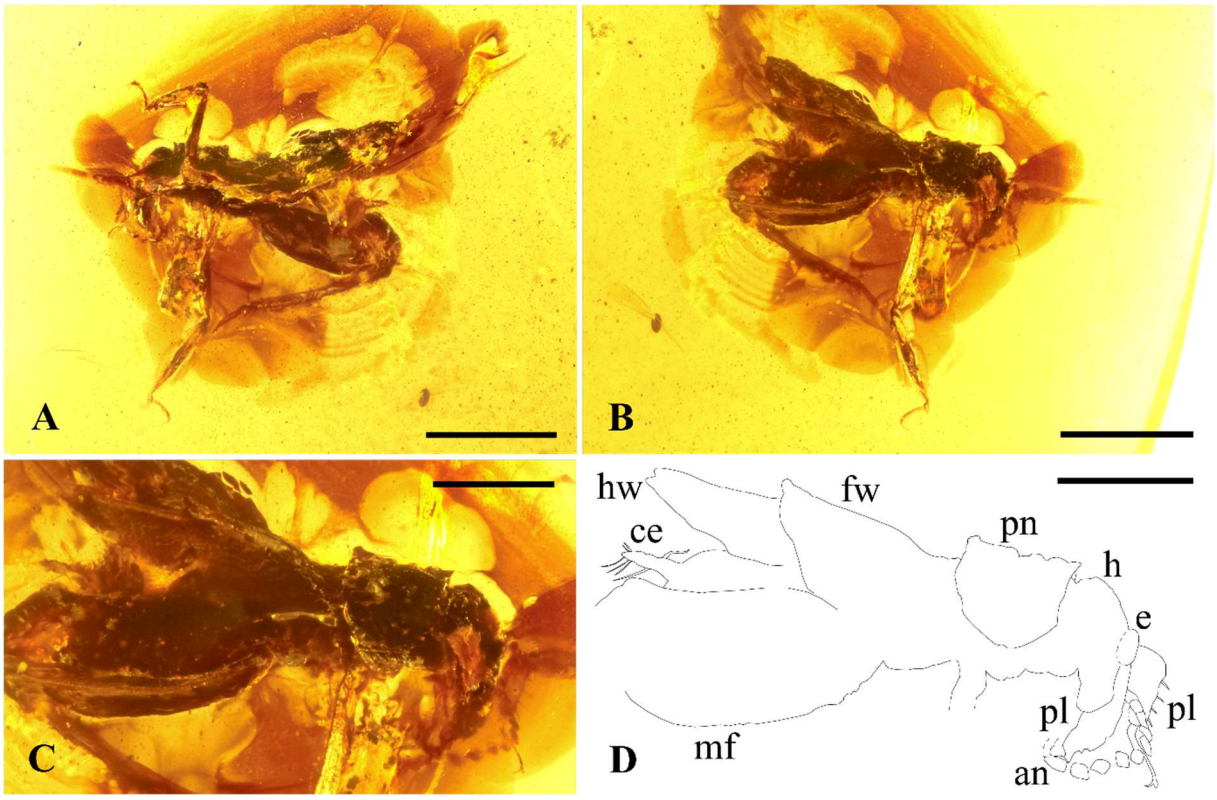

Fig. 1: *Ozymandipteryx campana* gen. et sp. nov. holotype (sex unknown), collection number GPIH07209. **A.** Specimen, left. **B.** Specimen, right. **C.** and **D.** Detail of body excluding legs as image and schematic drawing. **Abbreviations:** hw = hindwing; ce = cercus; fw = forewing; pn = pronotum; h = head; e = compound eye; pl = prothoracic leg; an = antenna; mf = metafemur. **Scale bars** = 1 mm (**A**, **B**); 0.5 mm (**C**, **D**).

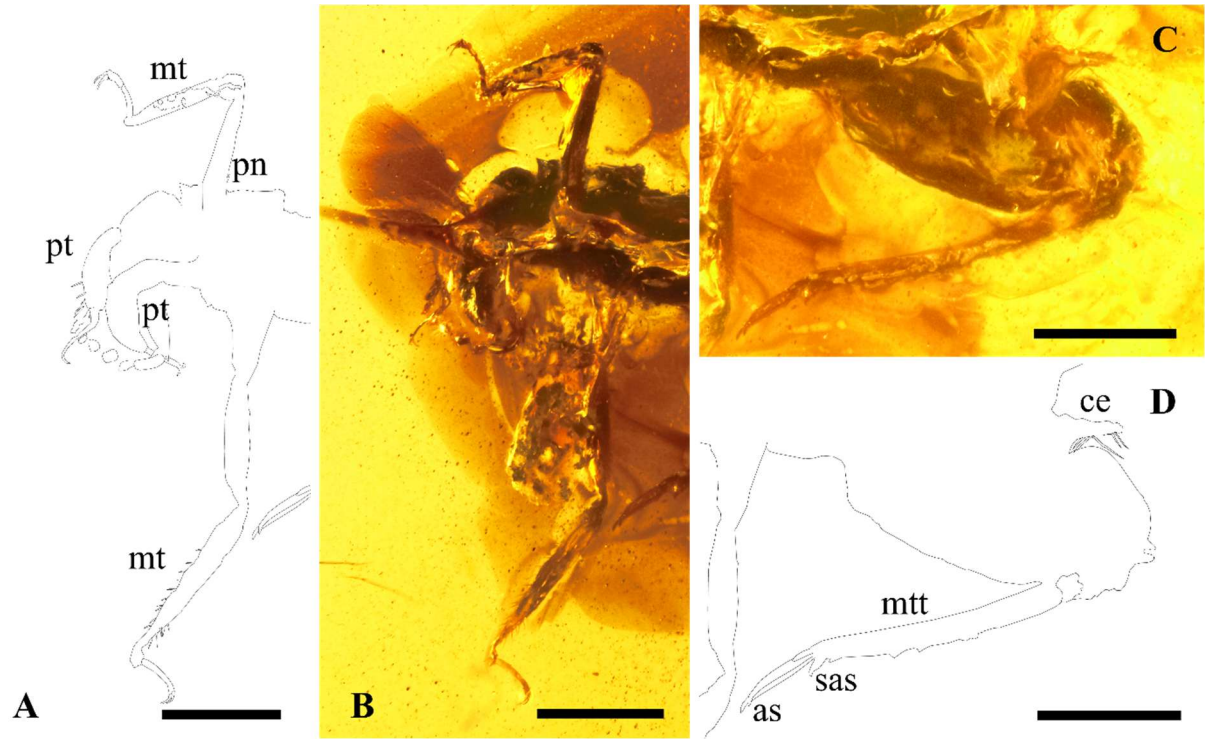

Fig. 2: *Ozymandipteryx campana* gen. et sp. nov. holotype (sex unknown), collection number GPIH07209. **A.** and **B.** Detail of head, prothoracic- and mesothoracic legs as image and schematic drawing. **Abbreviations:** pt = protibia; mt = mesotibia; pn = pronotum. **C.** and **D.** Detail of metathoracic leg and cercus as image and schematic drawing. **Abbreviations:** as = apical spurs; sas = subapical spurs; mtt = metatibia; ce = cercus. **Scale bars** = 0.5 mm.

Genus ***Yakkhapipteryx*** gen. nov.

Type species: *Yakkhapipteryx mirus* comb. nov. (Gu, Zheng, Cao & Yue, 2022)

Included species: *Yakkhapipteryx mirus* comb. nov., *Y. gracilis* comb. nov. (Gu, Zheng, Cao & Yue, 2022)

Zoobank-ID: urn:lsid:zoobank.org:act:CB55611A-D029-4FB1-A374-7154C54C006B

Etymology: Named after the Yakkha (Sanskrit: Yaksha), guardians of buried treasures (in reference to amber) from Burmese mythology.

Diagnosis: As provided by Gu et al. (2022) for *Magnidactylus*, which the authors based on the specimens now assigned to *Yakkhapipteryx*.

Genus ***Ciconipteryx*** gen. nov.

Type species: *Ciconipteryx bidactylus* sp. nov.

Zoobank-ID: urn:lsid:zoobank.org:act:984DDC59-027C-466D-8AF0-7C2A8758B3C4

Etymology: The new genus is named after its long legs. Ciconi- is derived from the bird family Ciconiidae, the storks.

Diagnosis: Very small body. Interocular distance larger than width of compound eye. Protibia with two dactyls. Mesothoracic leg longer than body (head to abdominal apex) and very slender along entire length (femur and tibia not much wider than tarsus). Metafemur as long as body. Forewings present, four to five veins visible. Cercus somewhat longer than paraproctal lobes. Both structures setulose; setae more prominent on paraproctal lobes. Valves of ovipositor visible, much shorter than paraproctal lobes.

Ciconipteryx bidactylus sp. nov.

Figs 3-6

Zoobank-ID: urn:lsid:zoobank.org:act:209312AD-9098-4290-A0F6-ED5A0D9D2814

Etymology: The species' name refers to the protibia with (only) two dactyls.

Locality and horizon: The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My and the amber from Tanai ca. 99 My old.

Holotype: Female. Specimen part of the LIB-Hamburg collection, collection number GPIH07210 (ex collection Martin Husemann MH0093).

Diagnosis of species: As for genus (monotypic).

Description: The specimen is relatively well preserved, but unfortunately the apical region of the metatibia and the metatarsus are missing.

Measurements: Body length (head to abdominal apex) 1.4 mm. Head height 0.6 mm. Eye height 0.21 mm, width 0.11 mm. Interocular distance (mid-eye level) ca. 0.2 mm. Protibia 0.24 mm long. Longest dactyl 0.05 mm long. Mesofemur 0.67 mm long. Mesotibia 0.59 mm long. Mesotarsus 0.27 mm long. Metafemur 1.4 mm. Cercus 0.12 mm long. Paraproctal lobes 0.1 mm long.

Head: Antennae not preserved. Interocular distance wider than compound eye width. Eyes somewhat tear shaped, laterally protruding from head. Ocelli not visible.

Thorax: Pronotum with posterior margin straight (not rounded or pointed), covering base of forewings. Pronotum without elevation. Forewings present with four or five simple veins visible. Hindwings present, shorter than abdomen.

Legs:
Prothoracic leg: Femur and tibia setulose with long hairs. Tibia only slightly inflated with two relatively long dactyls. Tarsus with two claws.
Mesothoracic leg: Very long and slender along entire length. Femur inconspicuous. Tibia not inflated. With 8-11 fine spines on the ventral margin of the distal half and five hairs subapically on the dorsal side. Tarsus two-segmented with first segment much shorter than second. Bulbous apical lobe on first tarsal segment. Second tarsal segment with two claws.
Metathoracic leg: Femur long and inflated along its entire length. Only ca. proximal third of metatibia preserved.

Abdomen: Cercus one-segmented, cylindrical in shape with some hairs. Paraproctal lobes one-segmented, thin clavate and slightly shorter than cercus; setulose with long hair, especially apically. From a dorsal view apices of ovipositor valves just visible between paraproctal lobes.

Remarks: Ciconipteryx bidactylus gen. et sp. nov. is assigned to Ripipterygidae based on the following characters: 1) Cercus one-segmented. 2) Mesotibiae not inflated. 3) Ovipositor visible. 4) Paraproctal lobes with distinct array of setae. It differs from previously described genera of Kachin amber Ripipterygidae by its two dactyls on the protibia (in other species from this locality and horizon there are either four dactyls or 0, as in *Ozymandipteryx campana* gen. et sp. nov.) and the markedly longer mesothoracic leg and metafemur which are longer or just as long as the body, respectively. The two dactyls on the protibia represent a character shared between *Ciconipteryx* and some species of the fossil as well as extant genus *Mirhipipteryx* Günther, 1969. While certain species of this genus, such as *M. antillarum* Heads, 2010, are reported to have three protibial dactyls (Heads, 2010), some modern species such as *M. pulicaria* (Saussure, 1896) are said to have only two (Baena-Bejarano et al., 2018), as in *C. bidactylus*. However, *Ciconipteryx* can be differentiated from *Mirhipipteryx* by its proportionally longer legs (in *M. pulicaria* the mesothoracic leg length is only ca. 60% of the total body length) and its interocular distance between the compound eyes, which is wider than the compound eye width in *Ciconipteryx*, but significantly shorter in *Mirhipipteryx* (Heads,

2010; Baena-Bejarano, 2018). Species of the other extant Ripipterygidae genus, *Ripipteryx* Newman, 1834, are much larger than *Ciconipteryx* and *Mirhipipteryx* (Heads, 2010).

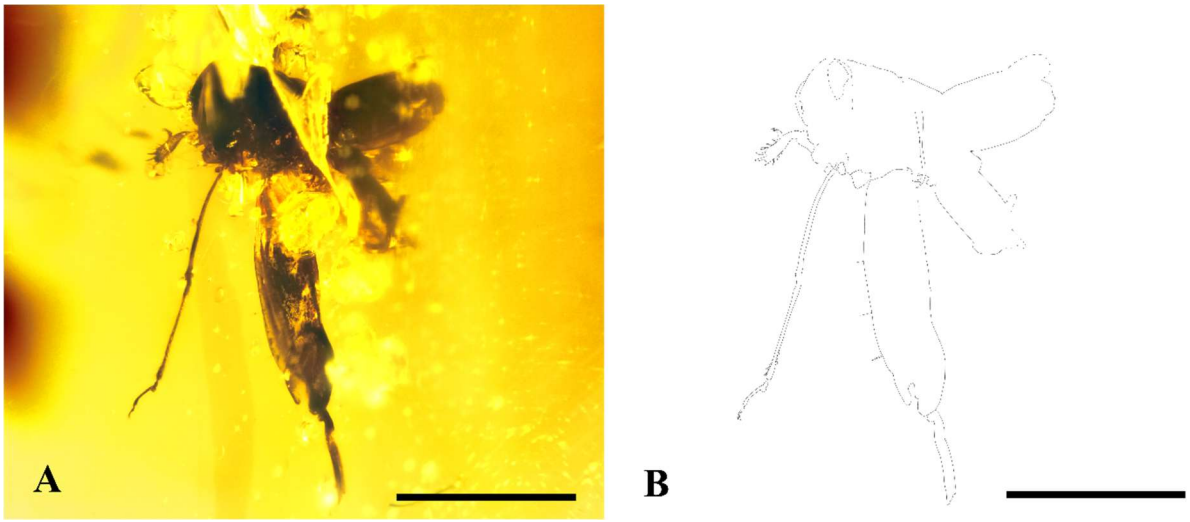

Fig. 3: *Ciconipteryx bidactylus* gen. et sp. nov. holotype female, collection number GPIH07210. **A.** and **B.** Specimen in frontal view. **Scale bars** = 1 mm.

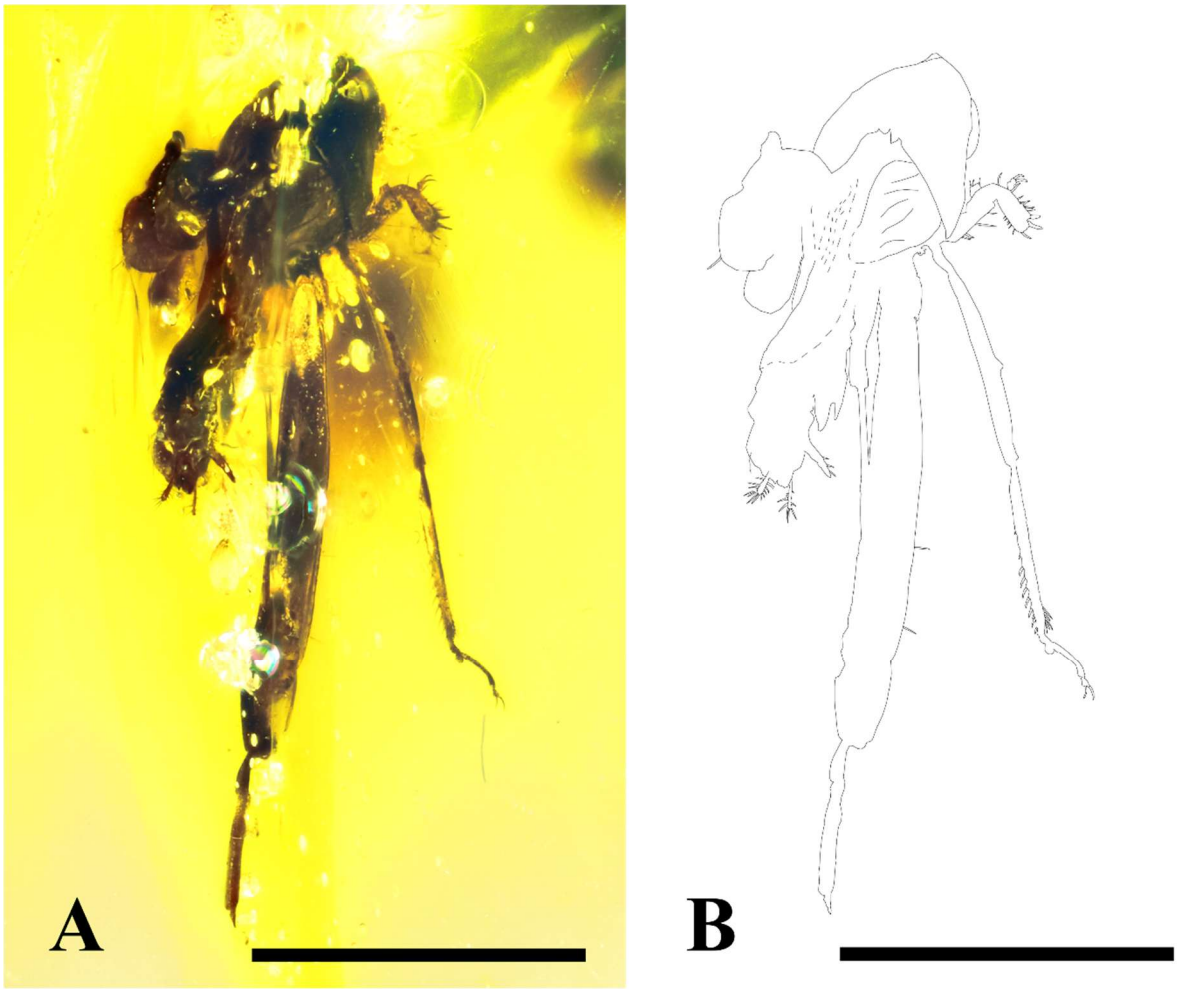

Fig. 4: *Ciconipteryx bidactylus* gen. et sp. nov. holotype female, collection number GPIH07210. **A.** and **B.** Specimen in dorsal view. **Scale bars** = 1 mm.

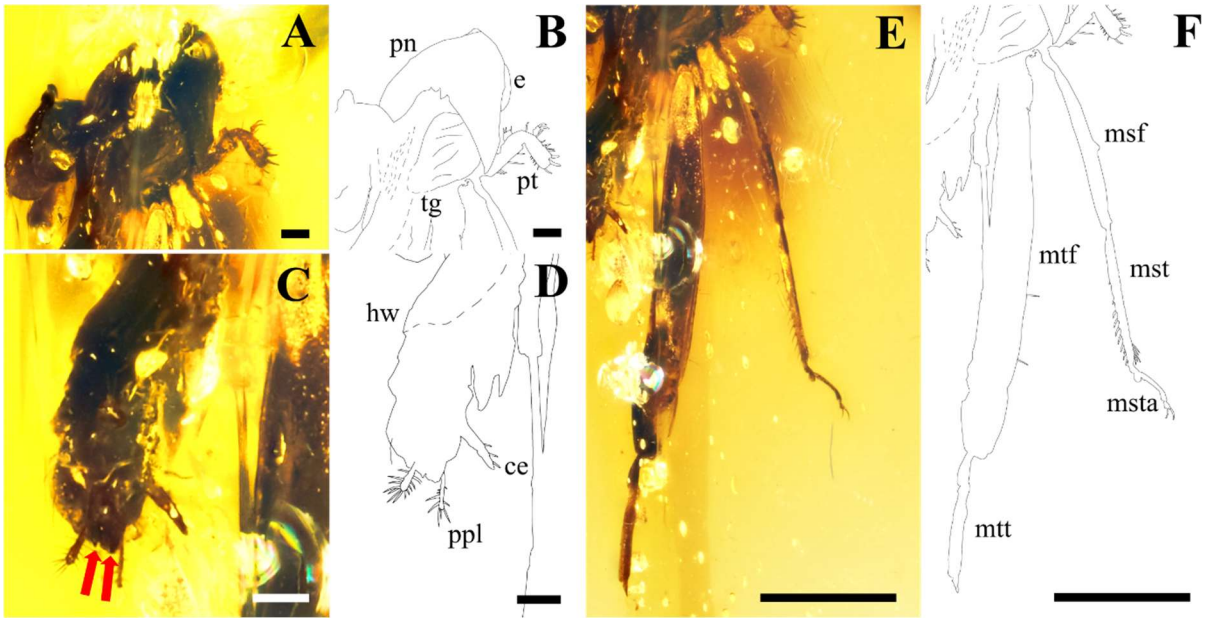

Fig. 5: *Ciconipteryx bidactylus* gen. et sp. nov. holotype female, collection number GPIH07210. **A.** and **B.** Detail of head region in dorsal view as image and schematic drawing. **Abbreviations:** pn = pronotum; tg = tegmen; e = eye; pt = prothoracic leg. **C.** and **D.** Detail of abdominal region in dorsal view as image and schematic drawing. Red arrows in C mark valves of ovipositor just visible between paraproctal lobes. **Abbreviations:** hw = hindwing; ppl = paraproctal lobe; ce = cercus. **E.** and **F.** Detail of meso- and metathoracic leg in dorsal view as image and schematic drawing. **Abbreviations:** mtt = metatibia; mtf = metafemur; msf = mesofemur; mst = mesotibia; msta = mesotarsus. **Scale bars** = 0.1 mm (**A-D**); 0.5 mm (**E**, **F**).

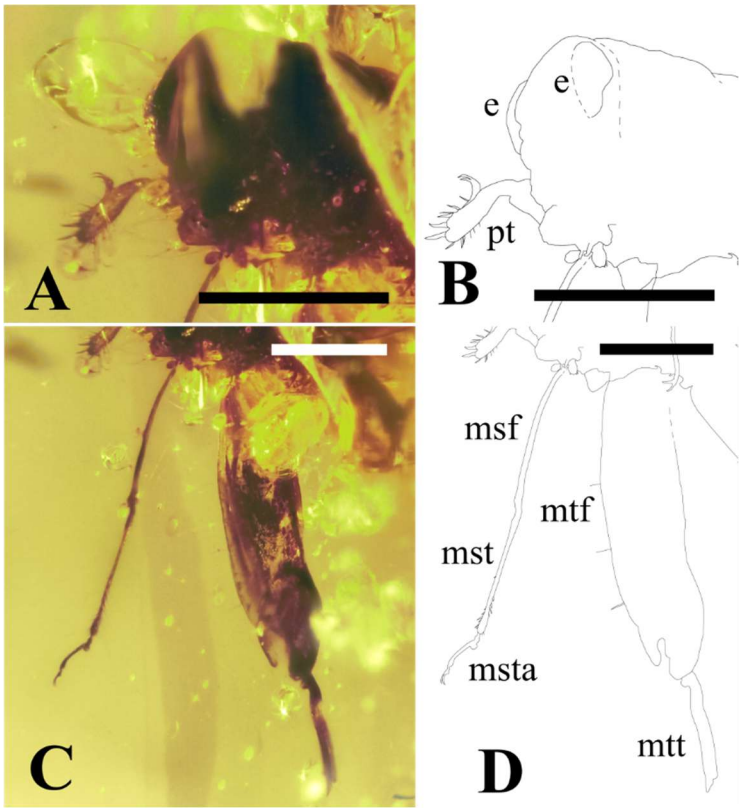

Fig. 6: *Ciconipteryx bidactylus* gen. et sp. nov. holotype female, collection number GPIH07210. **A.** and **B.** Detail of head and prothoracic leg in frontal view as image and schematic drawing. **Abbreviations:** e = compound eye; pt = prothoracic leg. **C.** and **D.** Detail of meso- and metathoracic leg in frontal view as image and schematic drawing. **Abbreviations:** msf = mesofemur; mst = mesotibia; msta = mesotarsus; mtf = metafemur; mtt = metatibia. **Scale bars** = 0.5 mm.

Discussion

Fig 7

In this study, we described two new members or Ripipterygidae Ander, 1939 from mid-Cretaceous Kachin amber from Myanmar, *Ozymandipteryx campana* gen. et sp. nov. and *Ciconipteryx bidactylus* gen. et sp. nov. Both taxa stand out from previously described fossil ripipterygids as well as extant representatives due to their unique combination of morphological characters. These findings have intriguing implications for the diversity and evolution of Ripipterygidae and also Tridactyloidea Brullé, 1835. Numerous findings during recent years (Xu et al., 2020; Xu et al., 2020; Gu et al., 2022; Zhu et al., 2023; Zhao et al., 2023, 2024) strongly suggest that diversity of ripipterygids was high in the Myanmar amber forest. Not only were numerous species present, these taxa also show a surprising variation of characters, many

of which cannot be found in modern members of the family, but are present in members of the sister family Tridactylidae Brullé, 1835. These include the presence of a vestigial metatarsus (fossil: *O. campana*, *Magnidactylus robustus* Xu, Fang & Jarzembowski, 2020 – Ripipterygidae; extant: *Xya* Latreille, 1809, *Ellipes* Scudder, 1902 – Tridactylidae), the inflation of the mesotibia (fossil *Kallosripipteryx zhangi* Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024 – Ripipterygidae; extant: Tridactylidae (an inflated mesotibia is diagnostic of all modern tridactylids) and the presence of a subapical denticular process of the metatarsus, which can be found in fossil members of Ripipterygidae (e. g. Gu et al., 2022; Zhao et al., 2023) and Tridactylidae (Heads, 2009; Fan et al., 2023), but is exclusively present in the latter family in the extant fauna.

The presence of several characters in fossil Ripipterygidae that were previously considered to be diagnostic of certain groups within Tridactylidae (or in the case of an inflated mesotibia for Tridactylidae as a whole) presents both a problem and an opportunity for resolving phylogenetic relationships within both families. Ideally, attempts towards this endeavor should either be based on molecular data (which cannot be fooled by the conflicting presence/absence of certain morphological characters in fossil vs. extant forms) or, better still, should incorporate as much of the fossil diversity of pygmy mole crickets and mud crickets as possible.

An aspect of morphology that is not known from any extant or fossil form and, therefore, currently completely unique, is the disproportionate relationship of mid- and hindleg length compared to body length of *Ciconipteryx bidactylus* gen. et sp. nov. Noticeably, it is not the legs itself that are unusually long in the new species, but rather the body seems to be strangely short in relation to them (Tabel 1, Fig. 7). The extant species *Ripipteryx guacharoensis* Baena-Bejarano and Heads, 2015 shares the character of extensively long mesothoracic legs in relation to body length, but the species has normal-sized metafemora in comparison to the over proportionate metafemora of *C. bidactylus*. Tridactyloidea are generally thought to exhibit a four-legged walking behaviour, whereby they use only their fore- and mid-legs and the hind legs are kept completely off the ground (Zhang et al., 2022). To compensate for the posteriorly shifted center of gravity due to their heavy hindlegs, tridactylids use the abdomen as a fifth fulcrum for support during walking (Zhang et al., 2022). Perhaps the proportionally long mid-legs and shorter abdomen allowed *C. bidactylus* to walk without dragging the abdomen, as the center of gravity was shifted anteriorly. This may have led to an increase in mobility.

The hindlegs and strong femora of tridactylids enable them to be among the most efficient jumpers within Orthoptera and the insect world (Burrows and Picker, 2010). Because they serve no function in walking, it is likely that they evolved to be specialized for jumping (Zhang et al.,

2022). As the metafemora of *C. bidactylus* are the largest currently known for any tridactyloid, it is possible that this species may have been the best jumper of the taxon.

Table 1: Some length ratios of Tridactyloidea Brullé, 1835. For the mesothoracic leg only the length of the mesofemur and mesotibia was combined for each species, as other parts were sometimes difficult to observe.

Family	**Species**	**Mesothoracic leg/metafemur length**	**Mesothoracic leg/body length**	**Metafemur/body length**	**Reference**
Ripipterygidae Ander, 1939	*Kallosripipteryx zhangi* Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024	0.96	0.67	0.7	Zhao et al., 2024
	Ripipteryx gorgonaensis Baena-Bejarano and Heads, 2015	1.11	0.7	0.62	Baena-Bejarano and Heads, 2015
	Ripipteryx guacharoensis Baena-Bejarano and Heads, 2015	1.44	0.99	0.69	Baena-Bejarano and Heads, 2015
	Mirhipipteryx pulicaria (Saussure, 1896)	0.92	0.53	0.58	Baena-Bejarano et al., 2018
	Ciconipteryx bidactylus gen. et sp. nov.	0.9	0.9	1	herein
Tridactylidae Brullé, 1835	*Xya sichuanensis* Cao, Shi & Yin, 2018	0.84	0.61	0.57	Zhang et al., 2022
	Burmadactylus tenuicerci Fan, Gu & Cao, 2023	1	0.67	0.67	Fan et al., 2023

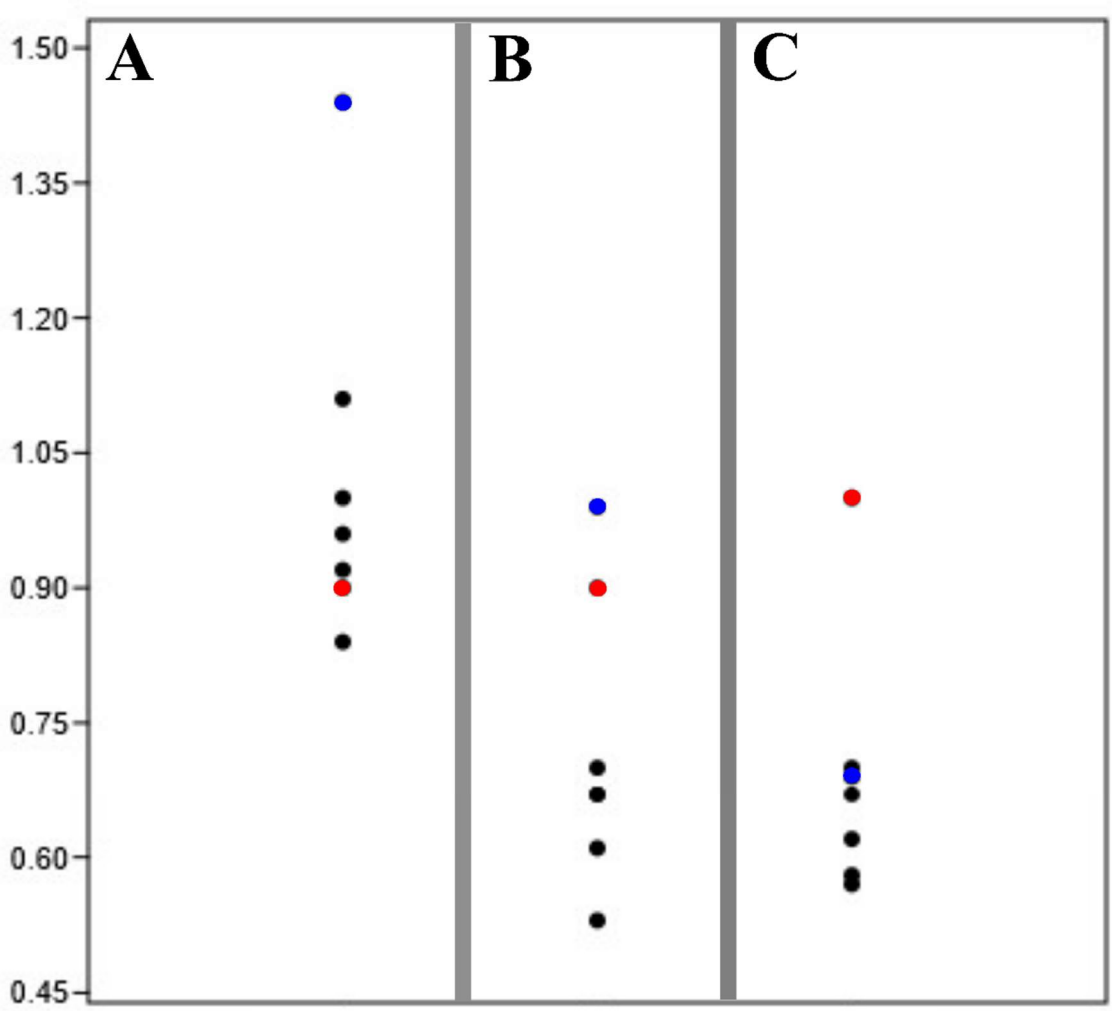

Fig. 7 Data from Table 1 as jitter plot. **A**: mesothoracic leg/metafemur length; **B**: mesothoracic leg/body length; **C**: metafemur/body length. *Ciconipteryx bidactylus* gen. et sp. nov. marked by red dots. *Ripipteryx guacharoensis* Baena-Bejarano and Heads, 2015 marked by blue dots.

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Chapter 2

New species of Tridactyloidea (Orthoptera: Caelifera) from mid-Cretaceous Kachin amber show intermediate evolutionary state between extant lineages[†]

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AUTHOR'S COMMENT

This article was submitted to *Evolutionary Systematics* and has finished its review process. Currently awaiting publication in the journal.

Abstract

Two new genera and species of Tridactyloidea Brullé, 1835 from mid-Cretaceous Kachin amber are described. *Abaddonella nwarrngaal* gen. et sp. nov. is based on a well-preserved male specimen. It is assigned to Ripipterygidae Ander, 1939 due to its cercus being one-segmented and mesotibia not being significantly wider than mesofemur. The new genus is similar to *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023 in regard to its abdominal and external genitalia morphology, but it differs from the latter genus (as well as other Ripipterygidae) by two small bumps on the vertex in front of the eyes. The second new taxon described is named *Naginipteryx pinna* gen. et sp. nov. Despite exhibiting a distinct ripipterygid-like morphology of the external genitalia, it shows a very inflated mesotibia with a marked triangular shape. This feature is usually considered to be diagnostic of Tridactylidae Brullé, 1835. The taxonomic position of *N. pinna* therefore, is difficult. For now, the species is placed outside both families (Ripipterygidae and Tridactylidae) and is suggested to be an ancestor to both lineages, prior to the evolutionary separation of them being completed. An identification key to the genera of Ripipterygidae from Kachin amber is provided.

Keywords: Burmese, fossil, identification key, mud crickets, pygmy mole crickets, taxonomy

Introduction

Tridactyloidea Brullé, 1835 is a superfamily inside the Caelifera Ander, 1936 suborder of the Orthoptera Olivier, 1789. It includes three families which are the Cylindrachetidae Giglio-Tos, 1914, Ripipterygidae Ander, 1939 and Tridactylidae Brullé, 1835. Cylindrachetidae are heavily adapted to a fossorial lifestyle with an almost worm-like habitus and can be found in 16 species throughout Australia and New Guinea as well as parts of South America (Heads, 2009). For now, they are not known from the fossil record. Ripipterygidae and Tridactylidae are similar in appearance however, they can be told apart by several morphological characters: 1) The cercus of Ripipterygidae is one segmented, in Tridactylidae two-segmented. 2) The mesotibia of Ripipterygidae is roughly of the same width as the mesofemur, in Tridactylidae the mesotibia is distinctly inflated and of greater width than the mesofemur. 3) The ovipositor is still visible in female Ripipterygidae, whereas in Tridactylidae it is too reduced to be seen. 4) Paraproctal lobes of Ripipterygidae apically with distinct array of setae, which is not present in Tridactylidae (characters after Gorochov 2010; Heads, 2010; Gu et al., 2022). Some authors also mention 5) modified paraproctal lobes in Ripipterygidae of a more elaborate shape while the paraproctal lobes of Tridactylidae look like a second pair of cerci (Gu et al., 2022).

The fossil record of Tridactylidae and Ripipterygidae is not rich, but especially during the last 15 years, many remarkable findings have been made in Kachin amber from the mid-Cretaceous of what is now Myanmar (Zhao et al., 2024). In fact, both families appear to have been incredibly diverse in the Kachin amber fauna with seven genera of Tridactylidae (compared to ten extant genera) and also seven (!) genera of Ripipterygidae (compared to only two extant genera) having been reported from this origin (Cigliano et al., 2025; Zhao et al., 2024).

In this study we report two new genera and species of Tridactyloidea from Kachin amber. One of them is assigned to Ripipterygidae based on the diagnostic characters mentioned above. The second new addition could possibly hold a taxonomic position closer to the base of Tridactyloidea, as an ancestor to both lineages Ripipterygidae and Tridactylidae.

Materials and methods

Amber pieces in this study are in the collection of the Leibniz Institute for the Analysis of Biodiversity Change (Hamburg) (collection numbers GPIH07231 and GPIH07232). They were excavated in Myanmar in a mining site either near Tanai village or Hkamti village. The age of

the two amber sites differs by ca. 10 My. Amber from Tanai is estimated to be 98.79 ± 0.62 My old (Shi et al. 2012), amber from Hkamti is ca. 110 My old (Xing and Qiu, 2020). We think it important not to let the severe humanitarian situation currently in place in Myanmar go unmentioned. Regarding the use of amber specimens from Kachin state for scientific purpose we take the position of Haug et al. (2020). We wish to recognize the fossils' origin described herein by giving them names to connect them with their home country.

Imaging of the specimens was conducted using a DUN. Inc. stacking system with a Canon EOS 5Dsr Camera having a 65mm lens and a magnification of 2.5x. Individual pictures were taken with VD PASSPORT and CAPTURE ONE program (CAPTURE ONE A/S, Denmark) and stacked with ZERENE STACKER (Zerene Systems LLC, Washington, USA). They were edited with the PHOTOSHOP CS6 Extended application by Adobe Inc. (USA; https://www.adobe.com). Further modifications (e. g. scale-bars) and creation of image collections was done in INKSCAPE (v. 1.4.2) (Inkscape-Team, 2025). Drawings were created in GIMP (v. 3.0.2-1) (GIMP Team, 2025) by direct layer copying.

Taxonomy in this study follows the Orthoptera Species File (OSF) (https://orthoptera.speciesfile.org/, Cigliano et al., 2025).

Systematic paleontology

Order: Orthoptera Olivier, 1789
Suborder: Caelifera Ander, 1936
Infraorder: Tridactylidea Brullé, 1835
Superfamily: Tridactyloidea Brullé, 1835
Family: Ripipterygidae Ander, 1939

Genus ***Abaddonella*** gen. nov.

Type species: *Abaddonella nwarrngaal* sp. nov.

Zoobank-ID: urn:lsid:zoobank.org:act:2961DF57-95B1-41A1-9CF0-803E1B9808F2

Etymology: Named after Abaddon, angel of the abyss from the Book of Revelation in connection with -ella meant as a suffix functioning as diminutive. A translation would be "little abaddon" or "little demon", referring to the small bumps on the type species' vertex which remind a little of demon horns.

Diagnosis: Antenna ten-segmented. Compound eyes laterally placed on head. Two small bumps on vertex in front of the compound eyes. Pronotum more or less quadrangular in shape. Forewings and hindwings present. Hindwings slightly longer than abdomen. Protibia with hairs on entire surface. Apically with three strong dactyls. Mesotibia not distinctly wider than mesofemur. Metafemur inflated along entire length. Metatibial fin with distinct serration. Subapical and apical spurs approximately of equal length, much shorter than metatarsus. Metatarsus with rather long fine hairs on ventral margin. Abdomen with cercus one-segmented and heavily setulose. Paraproctal lobes much shorter than cercus, inconspicuous and not setulose. Subgenital plate elongated, much longer than paraproctal lobes and with long hairs. Coloration on head with distinct light/dark contrast over the eye. Pronotum with light coloration and several dark colored spots.

Abaddonella nwarrngaal sp. nov.

Figs 1-2

Zoobank-ID: urn:lsid:zoobank.org:act:BA107602-EA55-4D8D-A787-C1BEE259D095

Etymology: Nwarr ngaal is Burmese and means “little cow”. It refers to the conspicuous color markings on the species’ head and pronotum.

Locality and horizon: The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My and the amber from Tanai ca. 99 My old.

Holotype: Male. Specimen part of the LIB-Hamburg collection; collection number GPIH07231 (ex coll. Martin Husemann, coll. no. MH0086).

Diagnosis of species: as for genus (monotypic).

Description: A fully preserved specimen, except for left metathoracic leg.

Measurements: Values given with a “ca.” indicate measurements based partly on estimation. Body-length ca. 1.83 mm. Head height 0.68 mm. Compound eye height 0.31 mm, width 0,21 mm. Antenna length 0.85 mm. Pronotum length 0.54 mm, height 0.4 mm. Forewing length 0.55 mm, hindwing length 1.64 mm. Prothoracic leg: femur 0.38 mm long. Tibia 0.36 mm long. Mesothoracic leg: tibia 0.5 mm long. Femur/Tibia width = 1.07 (at mid of both). Metathoracic leg: femur ca. 0.86 mm long, 0.51 mm wide. Tibia ca. 0.79 mm long, ca. 0.09 mm wide (around mid-length). Tarsus > 0.31 mm long. Cercus 0.15 mm long. Paraproctal lobe ca. 0.05 mm long. Subgenital plate 0.18 mm long.

Head: Antennae 10-segmented, moniliform. Pedicel and scape wider than antennomeres. Head with two small bumps on the vertex in front of the compound eyes. Compound eyes placed laterally on the head. Head with distinct coloration; a lighter area crosses the eye dividing it into two equal parts and continuing on the dorso-lateral portion of the head. Ocelli not seen.

Thorax: Pronotum with similar light/dark contrasting colors as head, but here the base color is light and several dark spots are scattered across the surface. Pronotum without elevation. Both fore- and hindwings present. Forewings with same color pattern as pronotum, hindwings uniformly dark. Hindwing slightly longer than abdomen.

Legs:

Prothoracic leg: femur bearing some long hairs. Tibia slightly inflated, completely covered with shorter to longer hairs. Apically with three dactyls, the longest of which is 0.05 mm long. Tarsus slender, only distal segment can be seen, bearing two curved claws.

Mesothoracic leg: femur with some short hairs on both margins. Femur rather slender towards coxa, becoming wider towards tibia. Tibia slightly inflated but not as wide as distal part of femur. Tibia apically with dense long hair. Tarsus slender with two claws.
Metathoracic leg: femur inflated along its entire length. Tiger stripe coloration which can be seen on the metafemur of the specimen is probably due to fissures in the amber and not actual coloration. Connection to tibia damaged. Tibia with lateral carina that runs until apex. Fin with distinct serration. Subapical and apical spurs present, approximately the same length. Tarsus proportionally long and rather thin. Ventrally with eight to nine hairs. Apex of tarsus hidden behind mesotibia.

Abdomen: Epiproct short, not covering cercus. Cercus one-segmented, cylindrical in shape and with many long hairs. Paraproct distinct with paraproctal lobe in ventral position. Paraproctal lobe significantly smaller than cercus (both length and width), cylindrical without hairs. Subgenital plate elongated, approximately the length of the cercus and with long hairs; one especially long hair on the apex. Subgenital plate mostly dark in coloration becoming slightly lighter towards apex. Cercus completely of lighter color.

Remarks: The new genus is assigned to Ripipterygidae based on the following characters: 1) cercus one-segmented. 2) Mesotibia not inflated. It is most similar to *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023 but differs from the latter by the two bumps on its forehead and the coloration pattern of the head, pronotum as well as external genitalia (*B. oblongus* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023, only species of the genus, has cerci with the basal half light in color and the distal half dark, while the subgenital plate is completely light. Head and pronotum show no noteworthy color pattern). These characters also differentiate *Abaddonella* from any other ripipterygid-genus. The underdeveloped paraproctal lobes of this genus and also *Burmaripipteryx* (much smaller than cerci, of no distinct shape and without apical setae) are rather unusual for Ripipterygidae. According to Song et al. (2015) the estimated split between the lineages of Ripipterygidae and Tridactylidae occurred 153.45 Mya, ca. 50 My prior to the formation of the Kachin amber from Tanai. Maybe, at this point in time the separation of the two families had not yet been fully completed and a third lineage, ancestral to both, still existed. This is a question that will be answered with more findings of Tridactyloidea from Kachin amber in the future. For now, we follow Zhao et al. (2023) and place *Abaddonella* in Ripipterygidae.

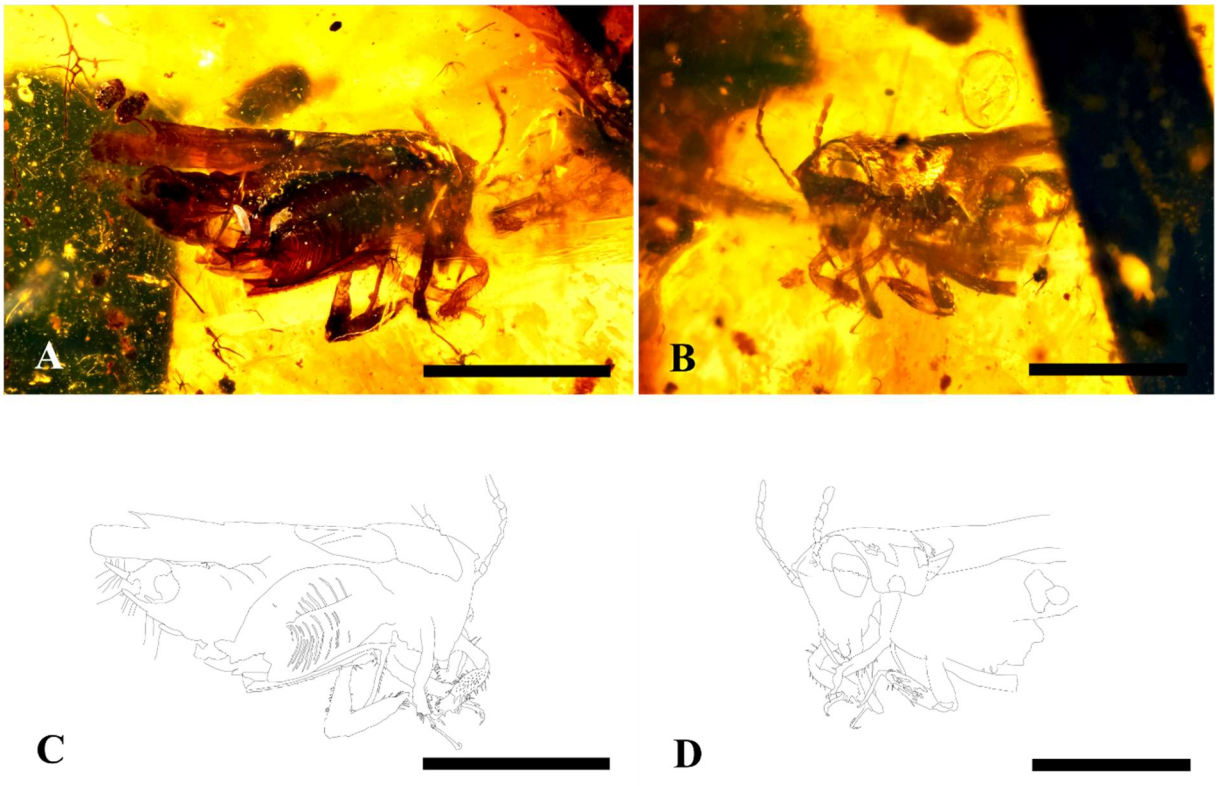

Figure 1 *Abaddonella nwarrngaal* gen. et sp. nov. holotype male GPIH07231 (ex collection Martin Husemann MH0086). **A** and **C** Specimen in postero-lateral view. **B** and **D** Specimen in antero-lateral view. **Scale bars** = 1 mm.

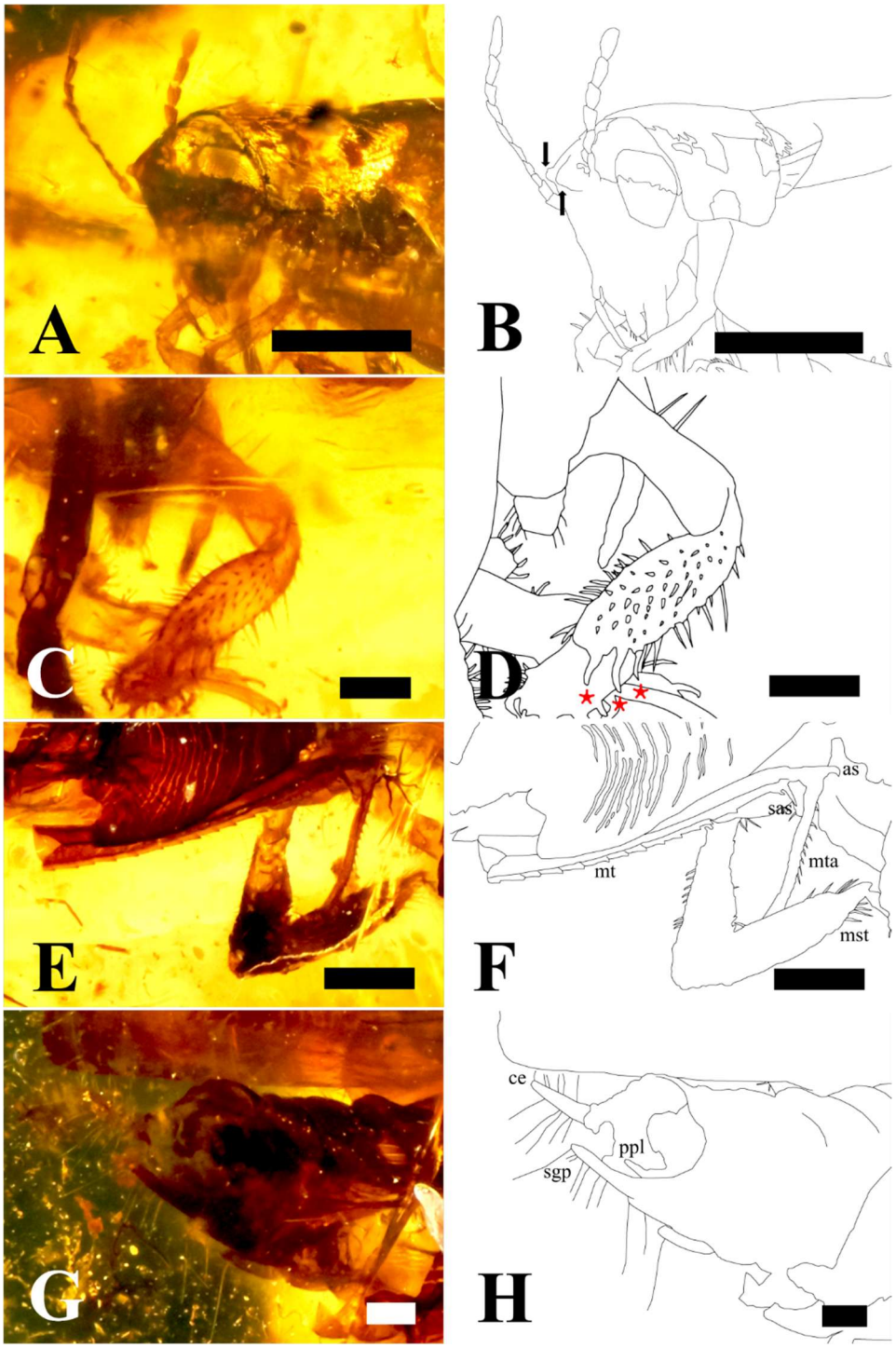

Figure 2 *Abaddonella nwarrngaal* gen. et sp. nov. holotype male GPIH07231.

A and **B** Detail of head and pronotum. Black arrows mark little bumps on the vertex. **Scale bars** = 0.5 mm. **C** and **D** Detail of prothoracic leg. Red stars mark dactyls. **Scale bars** = 0.1 mm. **E** and **F** Detail of metatibia and mesothoracic leg. **Abbreviations:** as = apical spur; mst = mesotibia; mt = metatibia; mta = metatarsus; sas = subapical spur **Scale bars** = 0.2 mm. **G** and **H** Detail of abdominal apex. **Abbreviations:** ce = cercus; ppl = paraproctal lobe; sgp = subgenital plate. **Scale bars** = 0.1 mm.

Superfamily: Tridactyloidea Brullé, 1835

Genus ***Naginipteryx*** gen. nov.

Type species: *Naginipteryx pinna* sp. nov.

Zoobank-ID: urn:lsid:zoobank.org:act:91DB496C-97FC-4723-8872-9D67C3217368

Etymology: Named after the naga (female nagini), a mythological creature from Asian religions such as Hinduism and Buddhism. It is also found in the mythology of Myanmar. Nagas is usually portrayed as half-human, half serpent beings, but can also be found as dragons. This is why the name has been chosen, for the triangularly shaped mesotibia of the genus, reminding of a classical dragons' tail.

Diagnosis: Protibia with four dactyls. Fore- and hindwings present, hindwings just as long as abdomen. Apical metatibial spurs slightly longer than subapical. Ventral margin of apical spurs with four distinct long hairs. External genitalia very similar to *Yakkhapipteryx* Schall, Cao & Husemann, 2025 more specifically *Y. gracilis* (Gu, Zheng, Cao & Yue, 2022) (this includes morphology of the cerci, paraproctal lobes and ovipositor valves): cercus one-segmented, cylindrical and setulose with long hairs. Paraproctal lobes two-segmented and longer than cerci, apically swollen and clavate with distinct long hair. Ovipositor visible, approximately as long as cerci, valve rather thick (more similar to *Y. gracilis* than *Y. mira* (Gu, Zheng, Cao & Yue, 2022)). Differs from *Yakkhapipteryx* by 1) the mesotibia being distinctly inflated and triangular in shape. 2) Ventral appendages with an inserted hair on the abdomen. 3) A blunt (rather than pointed) metatarsus with one row of serration and one row with hairs (rather than no row).

Naginipteryx pinna sp. nov.

Figs 3-5

Zoobank-ID: urn:lsid:zoobank.org:act:9A6AD0E2-F314-40D2-BC0A-858307362D97

Etymology: Named after the latin word "pinna" (fin) because of the ventral appendages on the abdomen, reminding of the dorsal fin of some fish, for example male sea goldies or the threadfin butterflyfish.

Locality and horizon: The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My and the amber from Tanai ca. 99 My old.

Holotype: Female. Specimen part of the LIB-Hamburg collection; collection number GPIH07232 (ex coll. Martin Husemann, coll. no. MH0011).

Diagnosis of species: as for genus (monotypic).

Description: The specimen is well preserved, but most of the head and thorax are somewhat contorted due to internal damage of the amber structure.

Measurements: Body-length 2.52 mm (head to abdominal apex). Pronotum length 0.62 mm, height 0.38 mm. Prothoracic leg: femur ca. 0.35 mm long. Tibia ca. 0.27 mm long. Tarsus ca. 0.25 mm long (including claws). Forewing ca. 0.79 mm long. Hindwing ca. 1.53 mm long. Mesothoracic leg: tibia 0.39 mm long, 0.25 mm wide (max width). Tarsus 0.35 mm long. Metathoracic leg: femur 1.36 mm long. Tibia 1.41 mm long, 0.09 mm wide. Tarsus 0.32 mm long. Subapical spurs ca. 0.05 mm long. Apical spurs 0.08 mm long. Cercus 0.19 mm long. Paraproctal lobes 0.3 mm long (not including hairs). Ovipositor (longest valve) 0.17 mm long.

Head: Morphology uncertain due to internal damage in the amber.

Thorax: Pronotum without elevation. Very deep laterally, covering the entire height of the thorax. Fore- and hindwings present. Venation undiscernible (lines seen on the wings are fissures in the amber, not actual veins). Hindwings just as long as abdomen.

Legs:

Prothoracic leg: Coxa big, about 2.5x the width of femur with sparse hair. Trochanter halfway in width between coxa and femur. Femur with numerous hairs. Tibia with numerous hairs, too. Apically with four dactyls, the longest of which is 0.05 mm long. Tarsus damaged. Slender without hair and ending in two claws.

Mesothoracic leg: only tibia and tarsus can be seen. Tibia with very distinct shape, looking like it is made up of two triangles, where the distal half is inserted into the bigger (both wider and thicker) proximal half. Greatly inflated. Apically with some hairs. Tarsus two-segmented, slender, no hair and with two claws.

Metathoracic leg: femur apically with sparse hair. Tapering toward apex, only somewhat inflated. Tibial fin with serration. A pair of subapical and apical spurs. Apical spurs with four conspicuous hairs on ventral margin. Tarsus blunt with two rows ventrally, one metatibial fin serrated, the other with hair.

Abdomen: Proximal to abdominal apex are three fin-like appendages of which the anterior two have singe hair inserted. Posterior fin probably lost the hair during preservation. More fins may be present but are covered by the metafemur. Cercus one-segmented, cylindrical in shape and setulose. Paraproctal lobes two-segmented, longer than cercus. Distal segment swollen, clavate in shape with distinct long hairs, especially on the apex of distal segment. Ovipositor visible, with narrower pointed end.

Remarks: Based on the structure of the external genitalia (cercus one-segmented; paraproctal lobes longer than cercus, modified in shape and with distinct apical hair; ovipositor visible), the new species should be assigned to Ripipterygidae. However, this family is usually recognized by an uninflated mesotibia, too (Heads, 2010). Some species of Kachin amber that were previously assigned to Ripipterygidae were noted to have an untypical mesotibia, for example Zhao, Xu, Cao, Jarzembowski, Fang & Xiao (2024) remarked in their description of *Kallosripipteryx zhangi* "mesotibia slightly fusiform, not slender as typical of ripipterygids". In *Naginipteryx pinna*, this character is extremely pronounced, with an inflation of the mesotibia surpassing what is common for Tridactylidae (who are characterized by an inflation of the mesotibia) (compare for example *Latedactylus longapedi* Zheng, Cao & Gu, 2023 or *Burmadactylus tenuicerci* Fan, Gu & Cao, 2023). As suggested for *Abaddonella nwarrngaal* gen. et sp. nov. (see above), this strange combination of characters may indicate the presence of an ancestral lineage (or perhaps several ancestral lineages?) of Tridactyloidea in the Kachin amber forest that had not yet completed the evolutionary separation between Tridactylidae and Ripipterygidae.

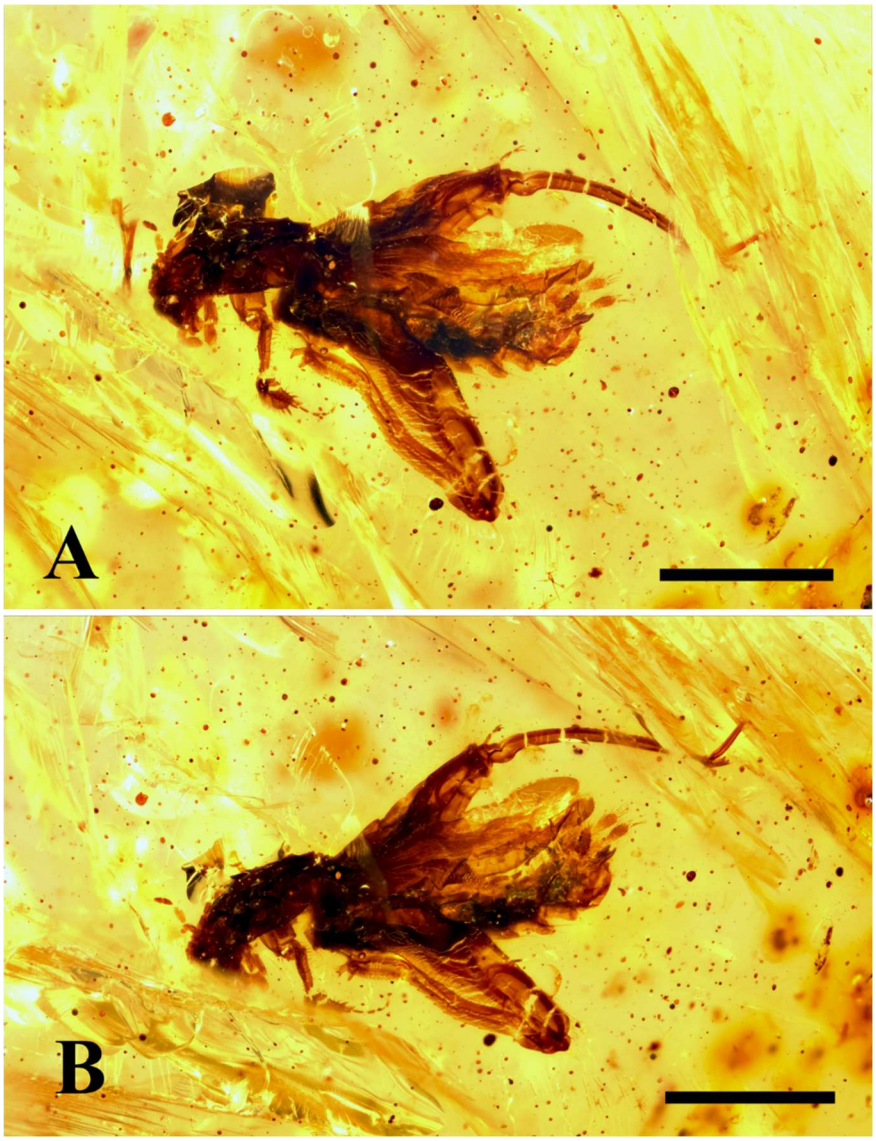

Figure 3 *Naginipteryx pinna* gen. et sp. nov. holotype female GPIH07232 (ex collection Martin Husemann MH0011). **A** and **B** Specimen, left side. B is taken from a slightly different angle. **Scale bars** = 1 mm.

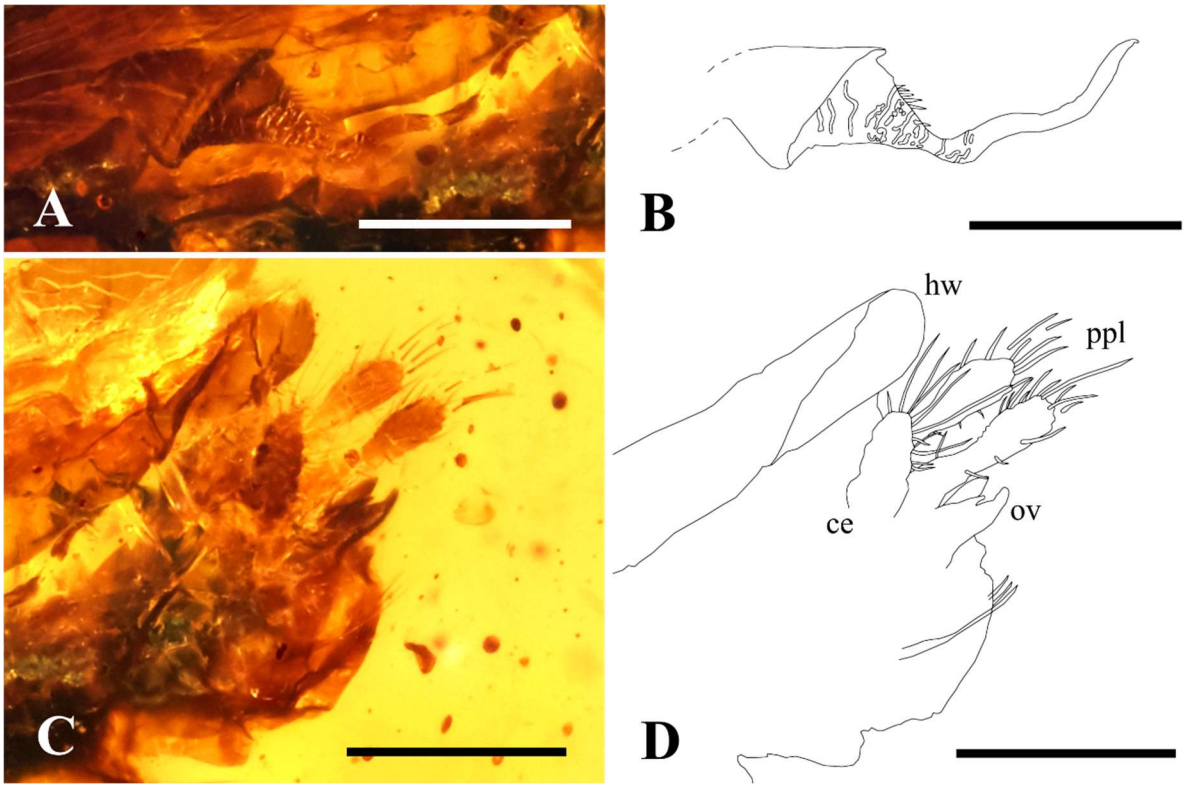

Figure 4 *Naginipteryx pinna* gen. et sp. nov. holotype female GPIH07232.

A and **B** Detail of mesothoracic leg with triangularly shaped tibia. **Scale bars** = 0.1 mm. **C** and **D** Detail of abdominal apex (including tip of hindwing). **Abbreviations:** ce = cercus; hw = hindwing; ov = ovipositor; ppl = paraproctal lobe. **Scale bars** = 0.1 mm.

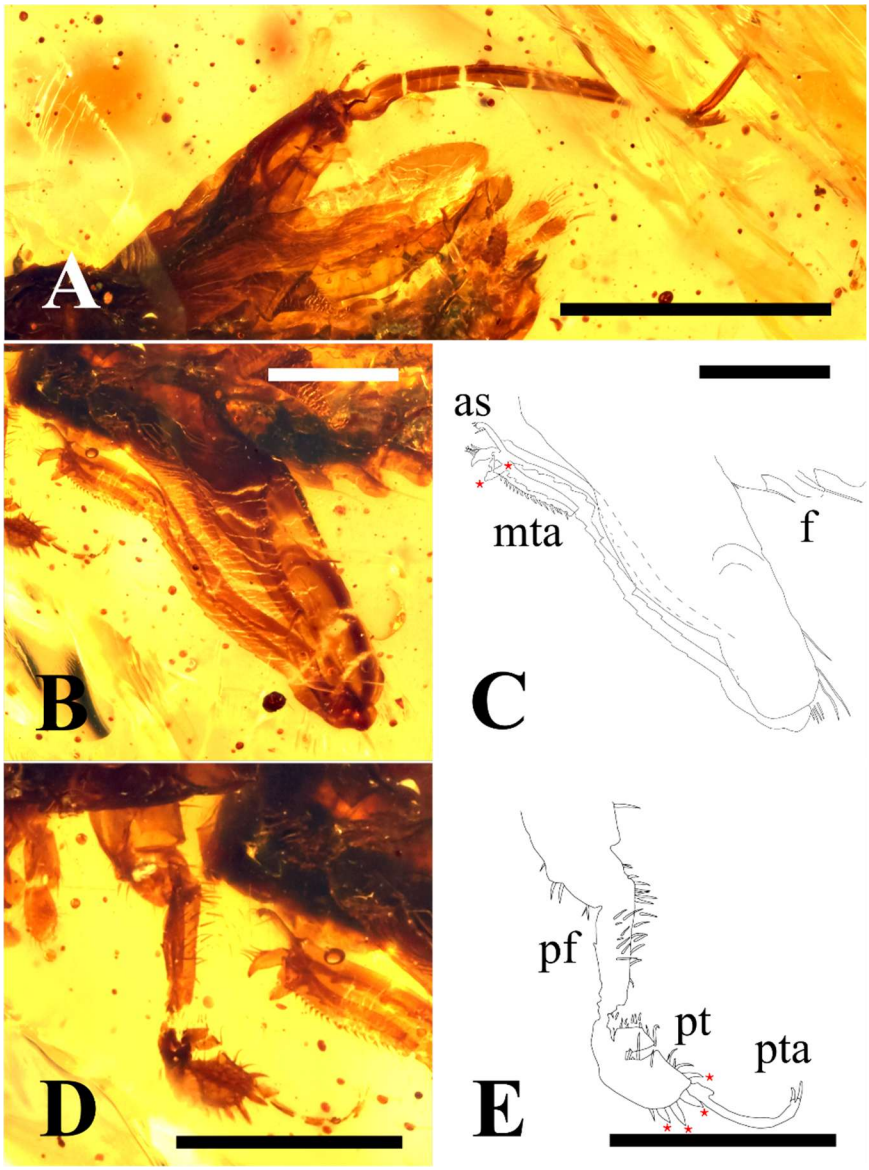

Figure 5 *Naginipteryx pinna* gen. et sp. nov. holotype female GPIH07232.
A Detail of right metathoracic leg. **Scale bar** = 1 mm. **B** and **C** Detail of left metathoracic leg (including abdominal fins). Red stars mark subapical spurs. **Abbreviations:** as = apical spurs; f = fins; mta = metatarsus. **Scale bars** = 0.5 mm. **D** and **E** Detail of prothoracic leg. Red stars mark dactyls. **Abbreviations:** pf = profemur; pt = protibia; pta = protarsus. **Scale bars** = 0.5 mm.

Key to the genera of Ripipterygidae found in Kachin amber

The increasing number of Ripipterygidae genera described from Kachin amber makes it appropriate to provide an up-to-date identification key to the diversity of the family known from this locality. As most of the genera are currently monotypic, this key is restricted to the genus-level.

Included genera (n species): *Abaddonella* gen. nov., herein (1); *Archaicaripipteryx* Xu, Zhang, Jarzembowski & Fang, 2020 (2); *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023 (1); *Ciconipteryx* Schall, Cao & Husemann, 2025 (1); *Kallosripipteryx* Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024 (1); *Magnidactylus* Xu, Fang & Jarzembowski, 2020 (1); *Naginipteryx* gen. nov., herein (1); *Ozymandipterx* Schall, Cao & Husemann, 2025 (1); *Yakkhapipteryx* Schall, Cao & Husemann, 2025 (2).

1. Metatarsus absent/fully reduced (not visible in the fossil) – 2
   Metatarsus visible – 3
2. Body-length ca. 6 mm; protibia with dactyls – *Magnidactylus*
   Body-length < 2 mm; protibia without dactyls – *Ozymandipteryx*
3. Cercus longer than paraproctal lobe – 4
   Cercus shorter than paraproctal lobe or equally long - 5
4. Two small bumps on the vertex in front of the compound eyes; distinct light and dark coloration on head and pronotum – *Abaddonella*
   No such bumps; coloration different – *Burmaripipteryx*
5. Mesotibia very inflated and with distinct triangular shape; abdomen with fin-like appendages – *Naginipteryx*
   Mesotibia without triangular shape; abdomen without fin-like appendages – 6
6. Mesothoracic leg longer than body; metafemur as long as body – *Ciconipteryx*
   Mesothoracic leg and metafemur both shorter than body - 6
7. Cercus as long as paraproctal lobe – *Archaicaripipteryx*
   Cercus shorter than paraproctal lobe - 7
8. Presence of one prosternal process – *Kallosripipteryx*
   Presence of no such prosternal process – *Yakkhapipteryx*

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We wish to thank Eileen Nguyen from the LIB Hamburg for her help with imaging the specimens.

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Chapter 3

Two new members of Tridactylidae (Orthoptera: Caelifera) from mid-Cretaceous Kachin amber†

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AUTHOR'S COMMENT

This article was submitted to *Zootaxa* and has finished its review process. Currently awaiting publication in the journal.

Abstract

Two new members of Tridactylidae Brullé, 1835 are described based on specimens found in mid-Cretaceous Kachin amber from Northern Myanmar. *Duappendactylus melanocephalus* gen. et sp. nov. is assigned to the family based on its two-segmented cerci and inflated mesotibia. It is similar to *Birmitoxya* Gorochov, 2010 by its lack of (visible) paraproctal processes and the presence of an elongated, upward-facing subgenital plate, but differs from that genus in several other aspects of its morphology. Additionally, we describe *Hiemalidactylus eileenae* gen. et sp. nov. based on a well preserved, presumably nymphal specimen. It is assigned to Tridactylidae based on the two-segmented cerci and the inflated mesotibia. Like the two aforementioned genera, *Hiemalidactylus* does not have cerciform paraproctal processes. However, this genus differes from *Birmitoxya* and *Duappendactylus* by not having an elongated subgenital plate. Instead, the paraproct is elongated and reaches almost the length of the basal segment of the cercus. These new species of Tridactylidae raise the diversity of this family known from Kachin amber to nine genera and eleven species.

Keywords: Burmese, fossil, nymph, pygmy mole crickets, taxonomy, Tridactyloidea

1.Introduction

Tridactylidae Brullé, 1835 is a family within the superfamily Tridactyloidea Brullé, 1835 (infraorder Tridactylidea Brullé, 1835), which is one of the two main groupings of the Caelifera Ander, 1936 (the other is the more diverse and commonly known Arcididea Targioni-Tozzetti, 1882). Tridactyloidea consists of three families: Tridactylidae, Ripipterygidae Ander, 1939 and Cylindrachetidae Giglio-Tos, 1914 (Cigliano et al., 2025). Their monophyly is well supported by several morphological characters as stated by Heads (2010): 1) the prosternum directly connected to the pronotum via a precoxal bridge. 2) Pro- and mesotarsus with only two tarsomeres. 3) Metatarsus reduced to a single tarsomere. 4) Absence of arolia. 5) Abdomen with nine fully sclerotized sterna in both sexes, the ninth forming a simple subgenital plate lacking styli. 6) Presence of abdominal repugnatorial glands. 7) Paraproct bearing distinctive cerciform processes (secondarily lost in Cylindrachetidae). This grouping is further supported by recent molecular phylogenetic data (Song et al., 2015).

Cylindrachetidae are known from Australia and New Guinea as well as parts of South America and are heavily adapted to a subterranean lifestyle (Houston, 2007). This is reflected in their anatomy with forelegs highly modified for digging, reduced mid- and hindlegs, simple eyes instead of compound eyes, reduced antennae and cerci, and entirely absent wings (Houston, 2007). For now, there are no representatives of this family known from fossils. Tridactylidae and Ripipterygidae are superficially similar. Both taxa are present in the fossil record with a few species, 8 for Ripipterygidae and 21 for Tridactylidae (Cigliano et al., 2025). Most of these findings were made in amber from the mid-Cretaceous found in Kachin state of northern Myanmar (Zhao et al., 2024). Other findings have been made in Cretaceous deposits of Russia, Mongolia and the UK (Tridactylidae: Mongoloxyinae Gorochov, 1992) (Gorochov, 1992; Gorochov et al., 2006; Sharov, 1968) as well as in the Crato Formation of Brazil (Tridacytlidae: Tridactylinae Brullé, 1835) (Martins-Neto, 1990). No tridactyloid has been discovered from older than the Cretaceous, however, the Triassic to Jurassic superfamily Dzhajloutshelloidea Gorochov, 1994 is believed to be a close relative of Tridactyloidea (Gorochov, 2005). Dated molecular phylogenies suggest the origin of Tridactyloidea in the Late Triassic, ca. 203 Mya (Song et al., 2015).

Tridactylidae differ from Ripipterygidae as follows: 1) two-segmented cerci (Ripipterygidae one-segmented). 2) Inflated mesotibiae (the mesotibia is wider than or at least of equal width as the mesofemur) (in Ripipterygidae the mesotibia is narrower than the mesofemur). 3) The ovipositor not being visible in female Tridactylidae (in Ripipterygidae, the ovipositor is visible).

4) The paraproctal lobes do not feature a distinct array of long setae, which is present in Ripipterygidae. 5) The paraproctal processes look like a second pair of cerci, but in Ripipterygidae they can have more modified shapes (Gorochov, 2010; Gu et al., 2022; Heads, 2010).

In this study we describe two new genera and species of Tridactylidae from mid-Cretaceous Kachin amber. The new taxa add to the diversity of fossil species known from the family and are important for a better understanding of their evolutionary history.

Materials and methods

Amber pieces used in this study are deposited in the collection of the Leibniz Institute for the Analysis of Biodiversity Change (Hamburg) (collection numbers GPIH07246 and GPIH07247). They were excavated in Myanmar in a mining site either near Tanai village or Hkamti village. The age of the two amber sites differs by ca. 10 My. Amber from Tanai is estimated to be 98.79 ± 0.62 My old (Shi et al. 2012), amber from Hkamti is ca. 110 My old (Xing & Qiu, 2020). Studies on amber from Myanmar, especially if it was obtained post 2017, are connected to a controversial ethical debate. However, reports such as Peretti (2021) illustrate the possible problems for the indigenous people of Myanmar that a generalized ban on Myanmar amber studies as requested by the Society of Vertebrate Paleontology (Engel, 2020) may hold. With the situation being as described by Peretti (2021), we agree with Haug et al. (2020) that scientific studies on amber from Myanmar should continue, as they open the door to an invaluable treasure of knowledge, especially in the case of Cretaceous invertebrate evolution and diversity.

The specimens presented in this study were imaged using a DUN. Inc. stacking system with a Canon EOS 5Dsr Camera (65mm lens, magnification 2.5x). Individual pictures were taken with VD Passport and Capture One Pro (v. 9.3.0.85) (Capture One A/S, Denmark) and stacked with Zerene Stacker (v. 1.04) (Zerene Systems LLC, Washington, USA). They were edited with the Photoshop CS6 extended application by Adobe Inc. (version Adobe Photoshop 2024) (USA; https://www.adobe.com). Further modifications were applied in Inkscape (v. 1.3.2) (the Inkscape Team, 2025). Drawings were created in GIMP (v. 3.0.2-1) (the GIMP Team, 2025).

Taxonomy in this study follows the Orthoptera Species File (OSF) (https://orthoptera.speciesfile.org/, Cigliano et al., 2025).

Systematic paleontology

Order: Orthoptera Olivier, 1789
Suborder: Caelifera Ander, 1936
Infraorder: Tridactylidea Brullé, 1835
Superfamily: Tridactyloidea Brullé, 1835
Family: Tridactylidae Brullé, 1835

Genus ***Duappendactylus*** gen. nov.

Type species: *Duappendactylus melanocephalus* sp. nov.

Zoobank-ID: urn:lsid:zoobank.org:act:6C168A1C-3C14-44BA-86CE-F2AA01693B34

Etymology: The genus name is a combination of the Latin words “duo” (two) and “appendix” (appendage) as well as the ending -dactylus which is commonly used in Tridactylidae. It refers to the absence of the paraproctal processes of the genus, meaning there are only two and not four (as usually in Tridactylidae) abdominal appendages.

Diagnosis: Very small body size, 1.41 mm (head to abdominal apex; not including subgenital plate). Antennae ten-segmented. Only forewings present, with very reduced venation. Protibia with three dactyls. Mesotibia distinctly inflated. Metafemur heavily inflated along entire length, dorsally with rather distinct setae. Metatibia shorter than metafemur and without swimming plates. Apical metatibial spurs slightly longer than subapical tibial spurs. Metatarsus one-segmented, present (i.e. not very reduced as in *Ellipes* Scudder, 1902 or *Xya* Latreille, 1809). Cerci two-segmented, basal segment much wider and longer than distal segment; both segments with setae. Paraproct very prominent, broadly triangular, but without paraproctal processes. Subgenital plate elongated, reaching to ca. half the length of basal cercus segment; directed upwards and with long distinct apical setae.

Duappendactylus melanocephalus sp. nov.

Figs. 1-2

Zoobank-ID: urn:lsid:zoobank.org:act:B8C217F9-6655-4F0D-97FA-6BC398BE05B0

Etymology: The species is named after its dark-colored head (ancient Greek “mélas” = black and “kefáli” = head).

Locality and horizon: The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My and the amber from Tanai ca. 99 My old.

Holotype: sex unknown. Specimen part of the LIB-Hamburg collection; collection number GPIH07246 (ex collection Martin Husemann MH0108).

Diagnosis of species: As for genus (monotypic).

Description: Preservation of an entire specimen with parts of the head and thorax somewhat obscured by additional matter in the amber.

Measurements (mm): Values given with a “ca.” are partly based on estimation as structures are not clearly or fully visible. Body length 1.41 (head to abdominal apex; not including subgenital plate). Head-height 0.54. Antenna length 0.55. Forewing length 0.47. Mesotibia length 0.45. Metafemur length 0.96. Metafemur width 0.38 mm. Metatibia length ca. 0.89. Paraproct 0.34 mm. Subgenital plate extending beyond paraproct by 0.16 mm. Basal cercus segment length 0.21. Basal cercus segment width 0.06. Distal cercus segment length 0.09. Distal cercus segment width 0.01 mm. Apical setae of subgenital plate up to ca. 0.15 mm long.

Head: Antennae ten-segmented (including pedicel and scape), moniliform and with antennomeres relatively thick. Coloration of both head and antennae dark, close to black.

Thorax: Pronotum smooth, without elevation; of dark color. Forewings present, with reduced venation. Hindwings absent.

Legs:
Prothoracic leg: Femur and tibia with setae which are more numerous on the tibia. Tibia apically with three dactyls, the longest of which is 0.04 mm long. Tarsus slender, with two claws.
Mesothoracic leg: Middle of tibia distinctly inflated.
Metathoracic leg: Femur greatly inflated along the entire length. Distal half of dorsal margin with evenly spaced setae of varying length. Tibia with a pair of subapical and apical spurs. Tarsus morphology uncertain due to poor visibility in the amber (Fig. 2B shows best interpretation of what is visible).

Abdomen: Cerci two-segmented with basal segment longer and wider than distal segment. Distal segment very slender. Both segments with setae. Paraproct prominent, broad-triangularly shaped. Paraproctal processes absent. Subgenital plate prominent, orientated upwards and elongated far beyond paraproct, reaching up to half of the basal cercus segment; apically with long setae.

Remarks: The new specimen can be assigned to Tridactylidae based on the two-segmented cerci and the distinctly inflated mesotibia. Triddactylidae consists of three subfamilies: the Cretaceous to recent Tridactylinae Brullé, 1835 and Dentridactylinae Günther, 1979 and the Cretaceous Mongoloxyinae Gorochov, 1992. The first two are separated by a subapical denticular process which is present in Dentridactylinae, but not in Tridactylinae (Heads, 2009). Because the morphology of the metatarsus is obscured, the presence or absence of a subapical denticular process cannot be confirmed. Mongoloxyinae is characterized by a more elaborate forewing venation than in the other subfamilies (Gorochov et al., 2006). The forewing venation of *Duappendactylus melanocephalus* gen. et sp. nov. seems to be reduced (as in Tridactylinae and Dentridactylinae), but this aspect of morphology is somewhat difficult to see in the fossil. Gorochov (2010) attributed the Burmese amber species *Birmitoxya intermedia* Gorochov, 2010 to Mongoloxyinae, but this act was solely based on the species not matching known characters of the other two subfamilies and the body morphology of Mongoloxyinae is rather unknown (Gorochov, 2010). Recently, Schall et al. (2025) have speculated that the Burmecaelidae Uchida et al., 2024 may be allied to Mongoloxyinae as they share similar venation characters. Because of the above, the subfamily position of *Duappendactylus melanocephalus* cannot be determined for now.

Within Tridactylidae, *D. melanocephalus* differs from all other members of the family except *Birmitoxya intermedia* by the absence of paraproctal processes. From *Birmitoxya*, the new taxon is separated by 1) a proportionally shorter metatibia. 2) Two-segmented cerci. In *Birmitoxya* the cerci were one-segmented. It is unlikely that the reason for this is found in the nymphal status of the specimen described by Gorochov (2010) as modern nymphs of the species *Ellipes deyrupi* Woo, 2021 and *Ellipes eisneri* Deyrup, 2005 already have two-segmented cerci like the adults (Woo, 2021). 3) Three strong dactyli on the protibia. Gorochov (2010) mentions “small fossorial denticles” in his description of *B. intermedia*, but they are not shown in Figure 6A of the species. 4) Smaller body size. In total, the scale of these differences appears to justify generic separation from *Birmitoxya* despite the shared absence of paraproctal processes.

The absence of paraproctal processes is unusual for Tridactylidae and also the closely related Ripipterygidae Ander, 1939. However, it is an apomorphy of Cylindrachetidae Giglio-Tos,

1914, but this family differs from the rest of Tridactyloidea in several other important characters (see introduction). Cylindrachetidae were estimated to have evolved 202.67 Mya, ca. 50 My prior to the other two families of Tridactyloidea (Song et al., 2015). This would make a relationship between Cylindrachetidae and the Kachin amber Tridactyloidea without paraproctal processes seem unlikely. For now, it seems more conclusive to suggest this character state was once present in Tridactylidae and subsequently lost in their evolutionary history.

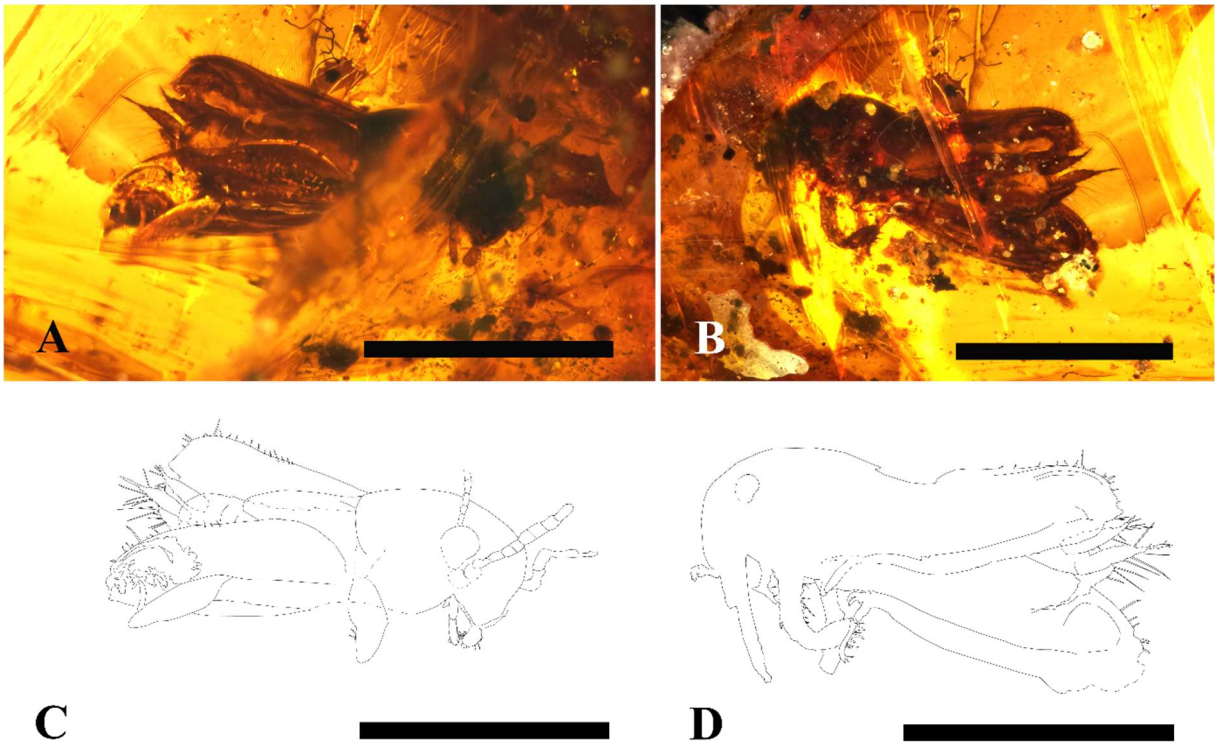

Fig. 1: *Duappendactylus melanocephalus* gen. et sp. nov. holotype (sex unknown) GPIH07246. **A.** and **C.** Specimen, right lateral view. **B.** and **D.** Specimen, left lateral view. **Scale bars** = 1 mm.

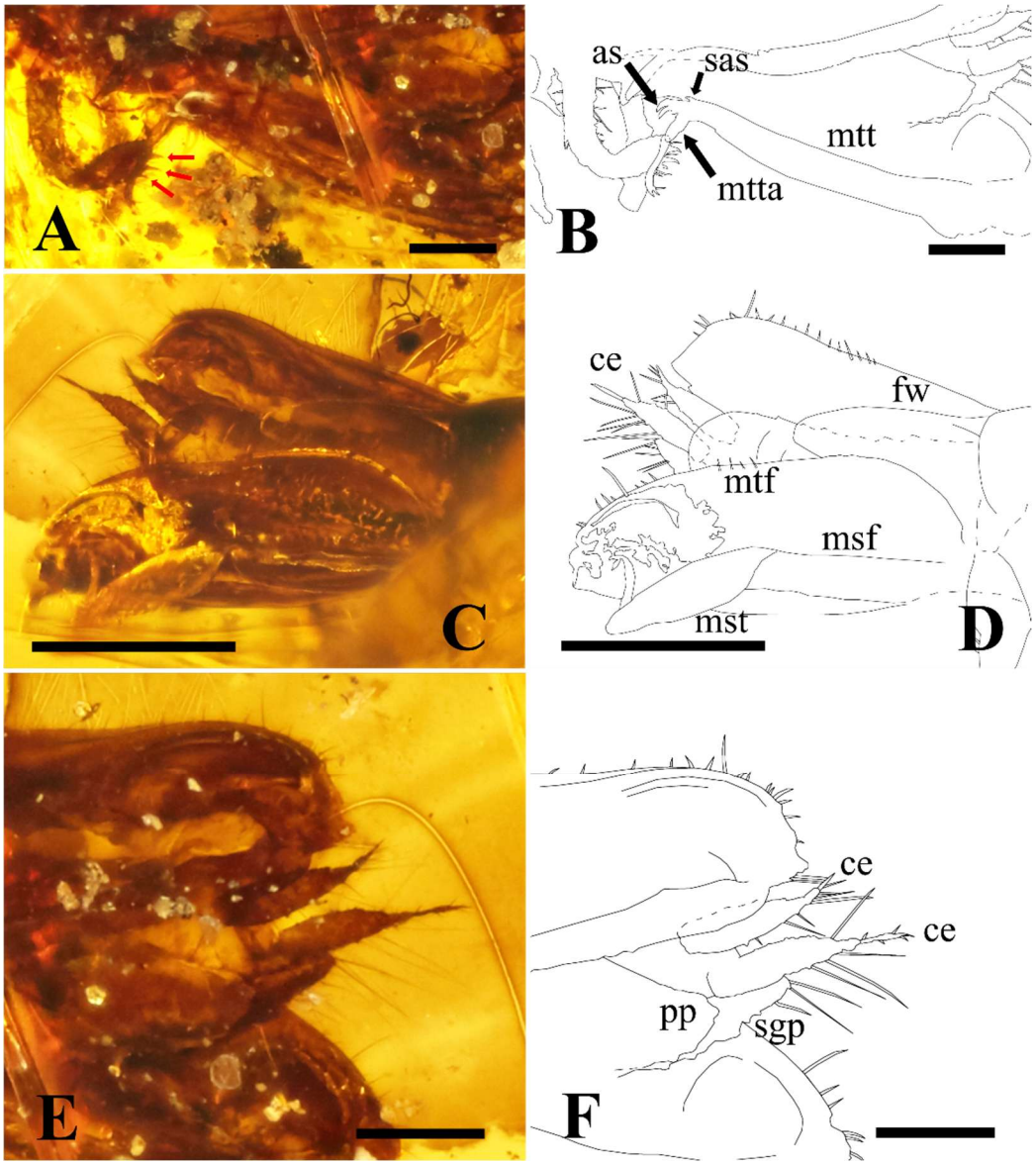

Fig. 2: *Duappendactylus melanocephalus* gen. et sp. nov. holotype (sex unknown) GPIH07246. **A.** and **B.** Detail of prothoracic leg and metathoracic tibia. Red arrows in A mark dactyli on protibia. **Abbreviations:** as = apical spurs; sas = subapical spurs; mtta = metatarsus; mtt = metatibia. **Scale bars** = 0.2 mm. **C.** and **D.** Detail of forewing, mesothoracic leg and metafemur. **Abbreviations:** ce = cerci; fw = forewing; mtf = metafemur; msf = mesofemur; mst = mesotibia. **Scale bars** = 0.5 mm. **E.** and **F.** Detail of abdomen. **Abbreviations:** pp = paraproct; sgp = subgenital plate; ce = cerci. **Scale bars** = 0.2 mm.

Subfamily Tridactylinae Brullé, 1835

Genus ***Hiemalidactylus*** gen. nov.

Type species: *Hiemalidactylus eileenae* sp. nov.

Zoobank-ID: urn:lsid:zoobank.org:act:CA6C708A-EC4E-492F-8ECC-DDF91638C3E6

Etymology: The genus is named after the coloration of its face; a contrasting dark and light pattern, looking like the specimen just came in from a wintery, snowy walk (from Latin "hiemalis" meaning "wintery").

Diagnosis: Distinct facial coloration consisting of highly contrasting darker and lighter areas, including the compound eye. Protibia with three long dactyls. Metafemur inflated along entire length, but comparably slender for a Tridactylidae (length/width ratio 3.4). Metatibia with few small denticles. Subapical and apical spurs approximately of equal length. Metatarsus pointed apically, without denticular process, hairs, or spines. Cerci two-segmented, basal segment longer than distal segment and tapering consistently with no clear constriction between segments. Both segments with sparse long setae. Paraproct elongated and prominent, narrow triangular and reaching almost length of basal cercus segment. Paraproct without paraproctal processes. Subgenital plate not elongated (not visible).

Hiemalidactylus eileenae sp. nov.

Figs. 3-4

Zoobank-ID: urn:lsid:zoobank.org:act:DDCE5FA5-DACC-4A60-BD71-7D65BC0559CB

Etymology: The species is named for Eileen Nguyen from the LIB Hamburg in thanks of her continued help concerning imaging and collection access during the first authors' doctoral studies.

Locality and horizon: The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 My and the amber from Tanai ca. 99 My old.

Holotype: sex unknown. Specimen part of the LIB-Hamburg collection; collection number GPIH07247 (ex collection Martin Husemann MH0110).

Diagnosis of species: As for genus (monotypic).

Description: Well-preserved, probably late instar nymph. Only missing distal parts of the left metathoracic leg (right side fully intact).

Measurements (mm): Body length 1.12 (head to abdominal apex; not including cerci or paraproct). Head height 0.4. Compound eye width 0.14. Compound eye height 0.16. Pronotum length 0.32. Pronotum height ca. 0.24. Forewing bud 0.09. Prothoracic leg: tibia 0.34, tarsus 0.12. Mesothoracic leg: tibia length 0.42, tibia width 0.15, tarsus 0.17. Metathoracic leg: Femur length 0.85, femur width 0.25, tibia length 0.81, tibia width 0.05. Tarsus 0.2. Subapical spurs 0.06, apical spurs 0.05. Paraproct ca. 0.2. Basal cercus segment length 0.17. Basal cercus segment width 0.04. Distal cercus segment length 0.05-0.08. Distal cercus segment width 0.01.

Head: With conspicuous coloration of contrasting light and dark areas, including compound eye. Compound eye not protruding, lateral position on head. Antennomeres with short setae.

Thorax: Pronotum without elevation, bearing sparse setae, especially on posterior margin. Forewings present as underdeveloped buds. Hindwings absent.

Legs:

Prothoracic leg: Femur rather short. Tibia with setae and three long apical dactyli, the longest of which is 0.04 mm long. Tarsus two-segmented; basal segment shorter than distal segment; distal segment bearing two claws.

Mesothoracic leg: Femur inconspicuous. Tibia distinctly inflated with triangularly shaped extension at widest point on one side. Distal part with setae. Tarsus two-segmented; basal segment shorter than distal segment; distal segment bearing two claws.

Metathoracic leg: Femur apically with few dorsal setae. Inflated along entire length, but still rather slender. Tibia with small denticles placed at a distance along the entire length. Subapical and apical spurs present (only one subapical spur can be seen, apical spurs as pair); approximately of same length. Tarsus much longer than spurs, pointed apically and without hair, spines, or denticular process.

Abdomen: Cerci two-segmented, basal segment longer than distal segment. Tapering consistently without distinct reduction in width from basal to distal segment. Both segments with very few setae. Paraproct prominent, narrow triangular, extending far beyond the abdominal apex to almost the length of the basal cercus segment; not setulose. Paraproctal processes absent. Subgenital plate not elongated and not visible.

Remarks: The new species is placed in Tridactylidae based on the distinct inflation of the mesotibia as well as the two-segmented cerci. It is suggested to be part of the subfamily

Tridactylinae due to the absence of a subapical denticular process on the metatarsus. *Hiemalidactylus* can be differentiated from all previously described genera of the family except for *Birmitoxya* Gorochov, 2010 and *Duappendactylus* described herein, by the absence of paraproctal processes. From these two genera it can be readily separated by the absence of an elongated subgenital plate. Due to the underdeveloped forewings as well as the very small body size of *Hiemalidactylus eileenae*, the specimen is probably a nymph. The classification of nymphs of Tridactylidae is problematic, because very little is known about morphological differences between adult and nymphs of the family (Baena-Bejarano et al., 2018). However, Gorochov (2010) described *Birmitoxya intermedia* based on a nymphal specimen and in this species the subgenital plate was clearly visible, suggesting that the absence/presence of an elongated subgenital plate can be used as a diagnostic character even in nymphs of Tridactylidae. Likewise, the presence/absence of paraproctal processes can be used to diagnose nymphal specimens too, as paraproctal processes - if present in the adults - are usually found in the nymphs as well (see *Ellipes deyrupi* Woo, 2021 and *Ellipes eisneri* Deyrup, 2005 in Woo (2021)). In terms of species identification, Baena-Bejarano et al. (2018) considered the coloration pattern a reliable character for associating nymphs with the correct species in *Mirhipipteryx pulicaria* (Saussure, 1896). The likeness of coloration between nymphs and adults of *Ellipes deyrupi* and *Ellipes eisneri* is apparent too (see Fig. 2 and 7 in Woo (2021)), although coloration is lighter in the nymphs. *Hiemalidactylus eileenae* has distinct head coloration which should facilitate species identification once adult specimens are found. The description of this well-preserved individual improves understanding nymph morphology in Tridactylidae.

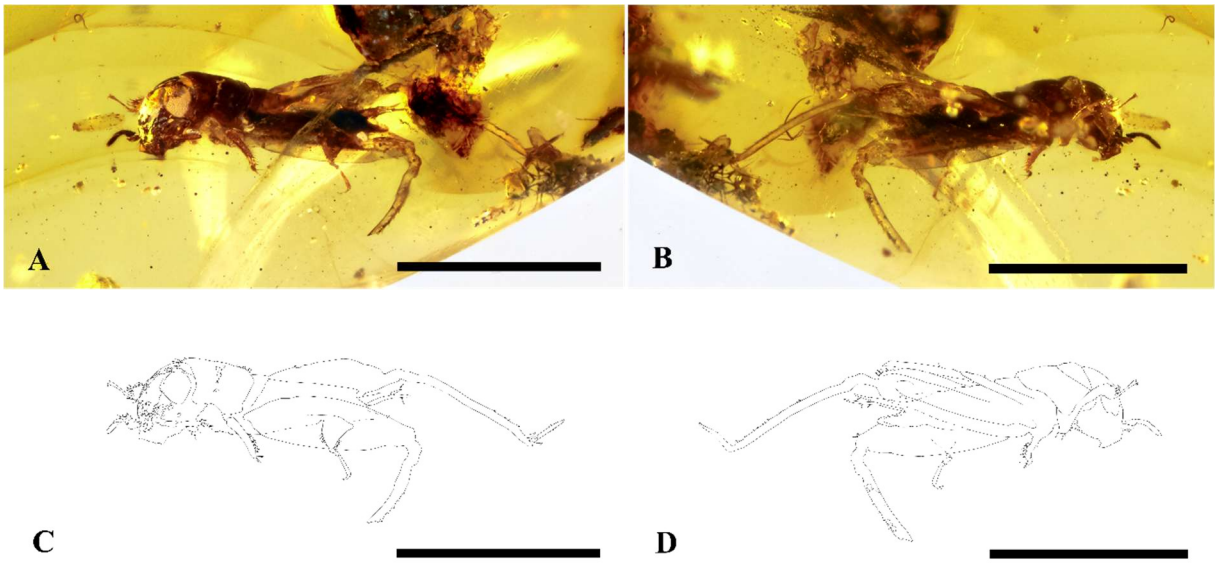

Fig. 3: *Hiemalidactylus eileenae* gen. et sp. nov. holotype (sex unknown; nymph) GPIH07247. **A.** and **C.** Specimen, left lateral view. **B.** and **D.** Specimen, right lateral view. **Scale bars** = 1 mm.

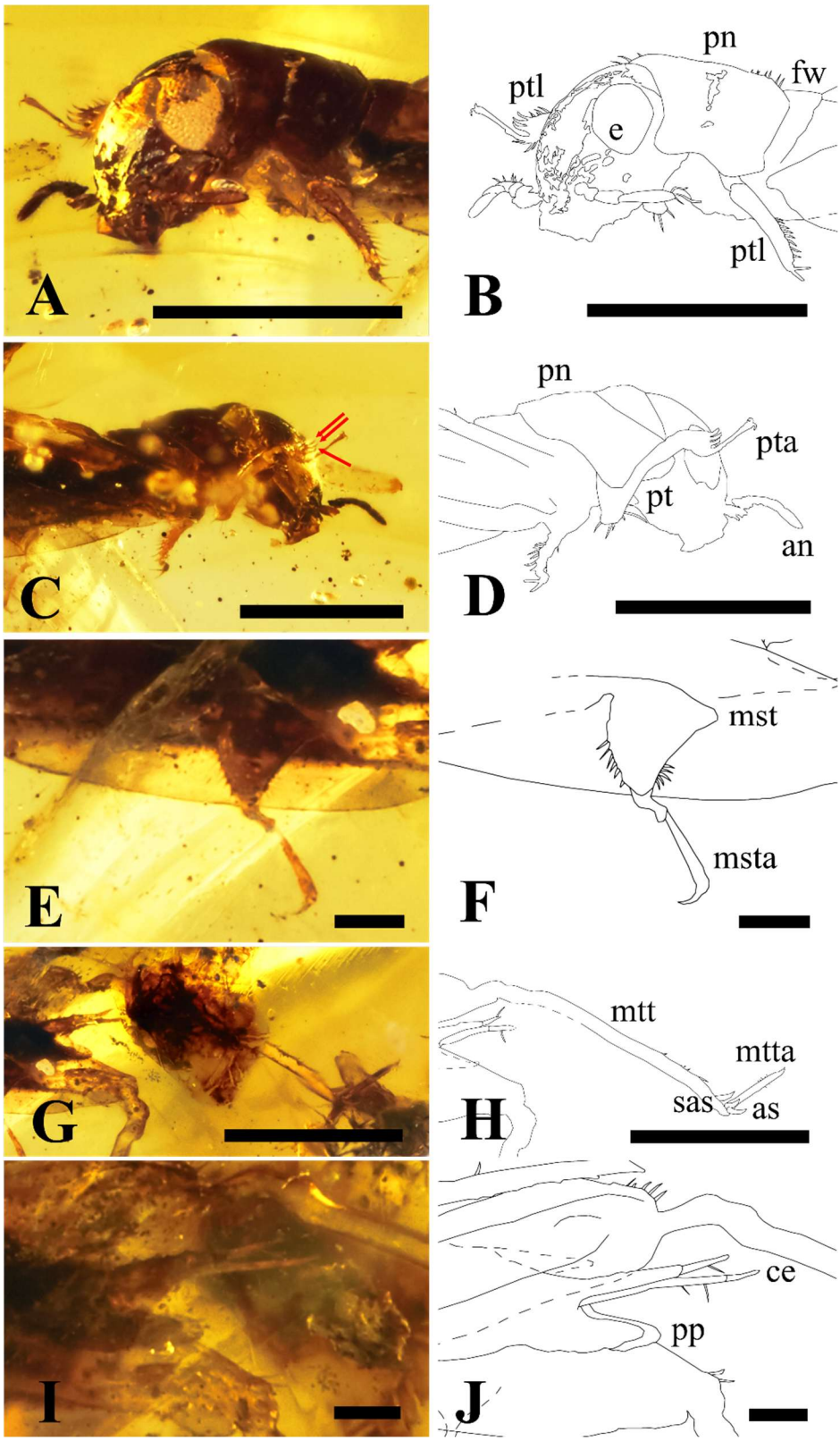

Fig. 4: *Hiemalidactylus eileenae* gen. et sp. nov. holotype (sex unknown; nymph) GPIH07247. **A.** and **B.** Detail of head, thorax and prothoracic leg. **Abbreviations:** ptl = prothoracic leg; e = eye; pn = pronotum; fw = forewing. **Scale bars** = 0.5 mm. **C.** and **D.** Detail of pronotum and prothoracic leg. Red arrows mark dactyli of protibia. **Abbreviations:** an = antenna; pn = pronotum; pt = protibia; pta = protarsus. **Scale bars** = 0.5 mm. **E.** and **F.** Detail of mesothoracic leg. **Abbreviations:** mst = mesotibia; msta = mesotarsus. **Scale bars** = 0.1 mm. **G.** and **H.** Detail of metathoracic leg. **Abbreviations:** mtt = metatibia; sas = subapical spur; as = apical spurs; mtta = metatarsus. **Scale bars** = 0.5 mm. **I.** and **J.** Detail of abdomen. **Abbreviations:** pp = paraproct; ce = cerci. **Scale bars** = 0.1 mm.

Discussion

This study describes two new genera and species of Tridactylidae Brullé, 1835 from mid-Cretaceous amber of Myanmar. Previously, nine species of this family had been known from the Burmese amber forest, whereby two – *Latedactylus longapedi* Zheng et al., 2023 and *Phyllotridactylus wangi* Xu et al., 2022 – were assigned to the subfamily Tridactylinae Brullé, 1835, four – *Burmadactylus grimaldii* Heads, 2009, *B. tenuicerci* Fan et al., 2023, *Cascogryllus lobiferus* Poinar, 2020 and *C. setosus* Du et al., 2021 – were assigned to Dentridactylinae Günther, 1979, one was preliminarily placed into Mongoloxyinae Gorochov, 1992 (*Birmitoxya intermedia* Gorochov, 2010), and two were not assigned to a subfamily (*Amberotridactylus cheni* Du et al., 2021 and *Paraxya hui* Cao et al., 2019) (for references see the publications of the original description). In the case of *Cascogryllus*, the metatarsal structure (i.e. presence of a subapical denticular process) is unknown for *C. setosus*, because the distal portion of the metatibia and -tarsus were not preserved in the holotype specimen (Du et al., 2021). The characters listed by Poinar (2020) to justify placement of *C. lobiferus* in Dentridactylinae (absence of leaf-like tibial spurs [sometimes referred to as swimming lamellae], antennae nine-segmented, hind tibiae with denticles on dorsal surface, extended metatarsus longer than metatibial spurs, two-segmented cerci and well-developed paraproctal lobes) are not unique to members of this subfamily, but can also be found in species of Tridactylinae. Instead, the author has considered the absence of a subapical denticular process in *C. lobiferus* as a unique character of this genus in Dentridactylinae (Poinar, 2020). However, the presence of a subapical denticular process on the metatarsus is what unites the subfamily Dentridactylinae (Heads, 2009). Thus, its absence in *C. lobiferus* suggests that the genus should be placed in the other subfamily Tridactylinae. The new species from this study were placed in Tridactylinae

(*Hiemalidactylus eileenae* gen. et sp. nov.) and Tridactylidae *incertae sedis* (*Duappendactylus melanocephalus* gen. et sp. nov.).

Both new species feature an unusual morphology of their abdominal structure, i.e. the absence of paraproctal processes in both taxa and absence of subgenital plate in *H. eileenae*. The absence of paraproctal processes is shared with *Birmitoxya intermedia*. However, this species was described as having a metatarsus somewhat bifurcated apically (Gorochov, 2010), which may indicate a placement within Dentridactylinae; anyhow, it certainly seems to contradict a position within Tridactylinae, thus the taxon is separated from *Hiemalidactylus*. The shared morphology of absent paraproctal lobes seems to be a rather distinct feature, however. Perhaps it is possible that these three genera constituted a separate subfamily within Tridactylidae. If so, the presence/absence of a subapical denticular process might be a plesiomorphic character in Tridactylidae. Hopefully, future findings can enlighten our understanding of these enigmatic little orthopterans and help to resolve the internal systematics of Tridactylidae.

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Part II: Locustopsidae and other early Acridomorpha – the rise of grasshoppers

Fig. 3.1 Holotype (CNBS_00419) of *Araripelocusta imperatrix* sp. nov. from the Crato Formation of Brazil (chapter 4).

Preface

In 1906, Austrian entomologist and paleontologist Anton Handlirsch described a new family of fossil Orthoptera Olivier, 1789: the Locustopsidae. According to his studies, this group is characterized by a long subcosta (contrary to the Elcanidae where the subcosta encompasses ca. half the length of the posterior tegminal margin), a well-developed free medial vein (MP, MA) with two branches (contrary to the Elcanidaa, where the median vein and the posterior radius (RP) are fused) and a free cubitus (he likely refers to CuA + CuPaα) with one to two branches (Handlirsch, 1906). Interestingly, Handlirsch (1906) also noted long antennae for Locustopsidae; it is unclear on what evidence this is based on. To my knowledge, no locustopsid with antennae so long that they would match those of, for example, Elcanidae has been discovered so far. As to the other apomorphies suggested by Handlirsch (1906), they are not sufficient to support monophyly of the taxon, because they can be found in various modern species of Acrididea Targioni-Tozetti, 1882 as well, for example the Pamphagidae Burmeister, 1840 species *Lobosceliana femoralis* (Walker, 1870). In fact, this species bears such a high similarity to Locustopsidae, that a morphology-based phylogeny of Orthoptera (chapter 10) consistently placed them in the same clade as a basal sister group to the remaining Caelifera Ander, 1936.

Gorochov (1995b) suggested these characters to support Locustopsidae: forewing with a three-branched medial vein; CuA + CuPaα with two branches and the medial vein of the hindwing with two branches. Although this is true for the genus *Locustopsis* Handlirsch, 1906, we now know various taxa of Locustopsidae (e. g. Araripelocustinae Martins-Neto, 1995 or Pseudoacridinae, chapter 6) to which these characters do not apply. Zessin (1983) proposed features similar to Gorochov (1995b), although a bit more elaborate, stating: forewings slender; medial vein splitting into three long parallel branches near the base of RP; CuA + CuPaα branching off anteriorly in an arc-shaped way; CuA + CuPaα with two to four branches; base of RP in proximal half of wing, with several branches (information from Gorochov, 1995b and Zessin, 1983 after Nel and Jouault, 2022). However, these characters too, do not apply to every taxon of Locustopsidae known today and are thus not adequate to diagnose the family.

The unpleasant truth is that it is difficult to propose apomorphies for the family Locustopsidae or the superfamily Locustopsoidea Handlirsch, 1906 (which, besides Locustopsidae itself, includes three more families of which only the Locustavidae Sharov, 1968 are well supported) based on wing venation alone. In fact, the similarity of Locustopsoidea to other Acridomorpha MacLeay, 1821 is so strong, that they are currently included within the nanorder (Cigliano et

al., 2025). However, a phylogenetic analysis based on morphology of extant and fossil Orthoptera (chapter 10) recovered Locustopsoidea as a basal sister clade to the rest of Caelifera (i. e. Tridactylidea Brullé, 1835 + Acrididea). According to the character matrix used they were separated from almost all modern Caelifera by a greater ratio of forewing length to body length, which exceeded 1.25 in Locustopsidae, but was less in the rest of Caelifera sampled. Still, the earlier mentioned Pamphagidae *Lobosceliana femoralis* also had a forewing length/body length ratio of 1.27, thus making it unable to characterize monophyly of Locustopsoidea based on this character alone.

It is likely that in order to fully understand the taxonomic relationships of Locustopsoidea, more characters other than from wing venation will have to be considered. Unfortunately, most specimens of this superfamily are known from isolated forewings. Here, I present 13 new specimens of Locustopsidae from the Cretaceous Crato Formation of Brazil (chapters 4-6). They provide some new details of body morphology of this family, however, most of them are still incompletely preserved. Hopefully, the near future will reveal additional findings of well-preserved Locustopsidae that help to resolve the relationships within the family. This group possibly represents the first Caelifera in evolution. Thus, understanding their diversity is essential for tracking the relationship between the two suborders of Orthoptera through time.

Despite Locustopsoidae likely having been the first caeliferans to walk the Earth, and certainly the most diverse taxon of this suborder until the Cretaceous-Paleogene mass extinction event (perhaps rivalled only by the Tridactylidea Brullé, 1835, see before), there were others to follow in their path and survive until today. Although they are exceedingly rare, Eumastacoidea Burr, 1899 are found in the fossil record from the Jurassic onwards (Sharov, 1968). Husemann et al. (2025) described a stunning nymph specimen from Cretaceous Burmese amber. Here, I describe an adult eumastacoid from the Crato Formation of Brazil (chapter 6), indicating that these acridomorphs lived in the same area as their more abundant relatives from the Locustopsidae. Other superfamilies of Caelifera found in the fossil record of the Mesozoic include the Proscopioidea Serville, 1838 (Heads, 2008; Mendes et al., 2019), Tetrigoidea (Sharov, 1968) and the enigmatic Burmecaelidae Uchida, Husemann & Kotthoff, 2024 (which, despite sharing some similarities with select superfamilies of Acridomorpha, likely belongs to Tridactylidea (Schall et al., 2025)).

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Chapter 4

New species of Cretaceous Locustopsidae (Orthoptera: Caelifera) from the Crato Formation of Brazil and a taxonomic revision of the family

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AUTHOR'S COMMENT

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Abstract

A new genus and four new species of Locustopsidae Handlirsch, 1906 are described from the Crato Formation of northeastern Brazil. *Aestuacrida stereofemoris* gen. et sp. nov. differs from previous genera of the family by having four branches of CuA + CuPaα. A new species of *Araripelocusta* Martins-Neto, 1995, *Araripelocusta imperatrix* sp. nov., is much larger than previous congeners with a wingspan of ca. 39 mm and features two little leaf-like appendages on the dorsal front part of the head. *Parapleurites brasiliensis* sp. nov. is the first Cretaceous member of this genus following two Jurassic predecessors. *Parapleurites morrisonensis* Smith, Gorman, Pardo and Small, 2011 has a wing venation that more closely resembles *Mesolocustopsis* Hong and Wang, 1990 and is moved to this genus as *M. morrisonensis* comb. nov. *Cratolocustopsis aquila* sp. nov. joins *C. cretacea* (Martins-Neto, 1990) and *C. contumax* Martins-Neto, 2003 as the third member of this genus, helping to solidify its separate position from other genera of Locustopsidae. A comprehensive taxonomic revision of all known species of Locustopsidae is given to improve our understanding of the diversity of these short-horned Mesozoic grasshoppers. The genus *Cratozeunerella* Martins-Neto, 1998 is considered a junior synonym of *Zeunerella* Sharov, 1968. *Cratozeunerella godoii* Martins-Neto, 2003, *C. nervosa* Martins-Neto, 2003, *C. soaresi* Martins-Neto, 2003 and *C. titanella* Martins-Neto, 2003 are suggested to be included in *Locustopsis* Handlirsch, 1906. *Plesioschwinzia* Zessin, 1988 is considered a junior synonym of *Locustopsis*. Further changes on the species level concern former *Zeunerella reticulata* (Handlirsch, 1939) which is moved to *Cratolocustopsis* Martins-Neto, 2003. *Mesolocustopsis petruleviciusi* (Martins-Neto, 2003) is considered a junior synonym of *M. caririensis* (Martins-Neto, 1990). In *Locustopsis* two synonyms are proposed: *Locustopsis elongata* Handlirsch, 1906 syn. nov. of *L. elegans* Handlirsch, 1906, and *Locustopsis lacera* (Zessin, 1983) (former *Plesioschwinzia lacera*) syn. nov. of *L. gyra* Zessin, 1983. Additionally, *Locustopsis anatolica* Sharov, 1968 is moved to *Schwinzia* Zessin, 1983. The recently described species of the Chinese *Sinolocustopsis* Huang and Nel, 2024 are removed to *Locustopsis elongatus* comb. nov. (Huang and Nel, 2024) and *Mesolocustopsis brevis* comb. nov. (Huang and Nel, 2024). *Liadolocusta auscultans* Handlirsch, 1906 is considered a *nomen nudum*. *Locustopsites gigantea* Théobald, 1937 is probably a member of Tettigoniidae Krauss, 1902 and should be excluded from Locustopsidae.

Keywords: Araripe Basin, Lower Cretaceous, fossil grasshoppers, Konservat-Lagerstätte

1. Introduction

Locustopsidae Handlirsch, 1906 represents an extinct clade of Caelifera Ander, 1936, nested within Acridomorpha Macleay, 1821. Despite its longstanding recognition, the monophyly of Locustopsidae remains questionable due to the absence of unambiguous apomorphies defining the group (Nel and Jouault, 2022). Nonetheless, the family is traditionally distinguished from other fossil Orthoptera Olivier, 1789 by a combination of wing venation features: the CuA + CuPaα, M, and RP remain distinct, unconnected by pseudo cross veins–contrasting with the (presumably) closely related Locustavidae Sharov, 1968, in which these veins are proximally fused by such pseudo cross veins. Also, Locustopsidae have a single main branch of RA and an elongated ScP reaching near the wing apex (with exception of *Locustrix* Martins-Neto, 2003, which exhibits a reduced ScP).

The family currently comprises two subfamilies–Araripelocustinae Martins-Neto, 1995 and Locustopsinae Handlirsch, 1906–as well as a set of genera of uncertain subfamilial affinity (Cigliano et al., 2025). Araripelocustinae, characterized by a single M branch in the tegmina, includes *Araripelocusta* Martins-Neto, 1995 from the Crato Formation (Brazil) and *Britannacrida* Gorochov, Jarzembowski & Coram, 2006 from the Lower Cretaceous beds of Dorset (UK) (Gorochov et al., 2006). In contrast, Locustopsinae are characterized by featuring multiple branches of M (two or three), including *Orichalcum* Whalley, 1985–taxonomically ambiguous due to its fused M and RP veins resembling the ensiferan Elcanidae Handlirsch, 1906–and *Conocephalella* Strand, 1926, which remains poorly known since its original description (Deichmüller, 1886).

The remaining genera of Locustopsinae are broadly distributed across Jurassic and Cretaceous localities in Europe (UK, Germany), Asia (China), Africa (Egypt), and the Americas (Brazil, USA), as documented in formations such as Jiulongshan, Morrison, and Crato (Tab. 1) (Ansorge, 1991; Gorochov & Coram, 2023; Gu et al., 2016; Martins-Neto, 2003; Smith et al., 2011; Zessin, 1983). Their taxonomy relies primarily on the number and arrangement of M and CuA + CuPaα branches, especially the relative positions of MA1, MA2, and MP (Tab. 2) (Gorochov et al., 2006). The genus *Plesioschwinzia* Zessin, 1988 is very similar to *Locustopsis*. In fact, the genera are separated only by the number of branches of ScP (1–4 in *Plesioschwinzia*, 6–8 in *Locustopsis*) (Gorochov & Coram, 2023).

Some genera remain unplaced within either subfamily due to incomplete or atypical material. *Liadolocusta* Handlirsch, 1906 is known solely from a foreleg, while *Locustopsites* Théobald,

1937 was described on a possibly overlapping pair of forewings with tettigoniid-like venation (pers. comm. O. Béthoux). *Locustrix* resembles *Cratolocustopsis* Martins-Neto, 2003 in M and CuA + CuPaα branching (i.e., two), but differs in its shorter ScP, which extends only halfway along the wing (Martins-Neto, 2003). *Pseudoacrida* Lin, 1982 is distinguished by a tegminal CuA + CuPaα that extends beyond its connection with CuPaβ as a separate branch of CuA. More recently, *Sinolocustopsis* Nel and Huang, 2024, described from the Middle Jurassic of China, displays forewing venation similar to *Locustopsis*, with three M, MA2 in direct contact to MA1, and two CuA + CuPaα branches.

The Crato Formation, a Lower Cretaceous Koservat-Lagerstätte in northeastern Brazil, is a major source of well-preserved fossil orthopterans. As of July 2024, the Locustopsidae are represented by 19 valid species across seven genera in this unit, making them the second most diverse orthopteran group in the formation after Baissogryllidae Gorochov, 1985 (20 spp. (Cigliano et al., 2025) (Tab. 1). Other orthopteran families from Crato include Gryllidae Laicharting, 1781 (13 spp.), and several with much lower diversity (compared to Baissogryllidae and Locustopsidae) such as Tridactylidae Brullé, 1835, Proscopiidae Serville, 1838, Prophalangopsidae Kirby, 1906, Gryllotalpidae Leach, 1815, Elcanidae Handlirsch, 1906, and Bouretidae Martins-Neto, 2001, each with one to three known species (Cigliano et al., 2025; Mendes et al., 2019; de Moura-Júnior et al., 2018; Nel & Jouault, 2022).

In this study, we describe a new genus and four new species of Locustopsidae from the Lower Cretaceous deposits of the Crato Formation, Brazil. These taxa contribute to our understanding of the morphological diversity and taxonomic boundaries of the family. A critical reassessment of the diagnostic criteria and subfamily placements within Locustopsidae is also provided, aiming to refine the taxonomy of this lineage of extinct Orthoptera.

Tab. 1: Species of Locustopsidae Handlirsch, 1906, their geographical origin, and associated era. Due to their uncertain/misidentified taxonomic status *Liadolocusta auscultans* Handlirsch, 1906, *Conocephalella capito* (Deichmüller, 1886) and *Locustopsites gigantea* Théobald, 1937 are excluded. Locality information from Cigliano et al., 2025 and Paleobiology Database (https://paleobiodb.org/#/, 25.10.2024).

Species	**Publication**	**Locality**	**Era**
Parapleurites morrisonensis	Smith, Gorman, Pardo & Small, 2011	USA/Morrison Formation	Upper Jurassic
Araripelocusta brevis	Martins-Neto, 1995	Brazil/Crato Formation	Lower Cretaceous

Araripelocusta longinota	Martins-Neto, 1995	Brazil/Crato Formation	Lower Cretaceous
Cratolocustopsis contumax	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Cratolocustopsis cretacea	(Martins-Neto, 1990)	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella amedegnatoi	Martins-Neto, 1998	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella godoii	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella neotropica	Martins-Neto, 1998	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella nervosa	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella soaresi	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Cratozeunerella titanella	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Mesolocustopsis araripensis	(Martins-Neto, 1990)	Brazil/Crato Formation	Lower Cretaceous
Mesolocustopsis caririensis	(Martins-Neto, 1990)	Brazil/Crato Formation	Lower Cretaceous
Mesolocustopsis petruleviciusi	(Martins-Neto, 2003)	Brazil/Crato Formation	Lower Cretaceous
Mesolocustopsis vikingi	(Martins-Neto, 2003)	Brazil/Crato Formation	Lower Cretaceous
Zessinia pulcherrima	Martins-Neto, 1990	Brazil/Crato Formation	Lower Cretaceous
Zessinia reticulata	Martins-Neto, 1990	Brazil/Crato Formation	Lower Cretaceous
Locustrix audax	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Locustrix gallegoi	Martins-Neto, 2003	Brazil/Crato Formation	Lower Cretaceous
Pseudoacrida sennlaubi	Nel & Jouault, 2022	Brazil/Crato Formation	Lower Cretaceous
Britannacrida distincta	Gorochov, Jarzembowski & Coram, 2006	UK/Lulworth Formation	Lower Cretaceous

Locustopsis posterior	Gorochov, Jarzembowski & Coram, 2006	UK/Lower Purbeck	Lower Cretaceous
Mesolocustopsis anglica	Gorochov, Jarzembowski & Coram, 2006	UK/Durlston Formation	Lower Cretaceous
Mesolocustopsis angusta	Gorochov, Jarzembowski & Coram, 2006	UK/Weald Clay Formation	Lower Cretaceous
Mesolocustopsis problematica	Gorochov, Jarzembowski & Coram, 2006	UK/Weald Clay Formation	Lower Cretaceous
Zessinia borealis	Gorochov, Jarzembowski & Coram, 2006	UK/Lulworth Formation	Lower Cretaceous
Zeunerella prior	Gorochov, Jarzembowski & Coram, 2006	UK/Weald Clay Formation	Lower Cretaceous
Locustopsis bucklandi	(Brodie, 1845)	UK/Grafton	Lower Jurassic
Locustopsis cockerelli	Handlirsch, 1939	UK/Binton	Lower Jurassic
Orichalcum ornatum	Whalley, 1985	UK/Shales with Beef Formation	Lower Jurassic
Plesioschwinzia lacoei	(Cockerell, 1916)	UK/Binton	Lower Jurassic
Plesioschwinzia uvarovi	(Zeuner, 1942)	UK/unknown	Lower Jurassic
Locustopsis constricta	Zeuner, 1942	UK/Lilstock Formation	Upper Triassic
Locustopsis cubitalis	Zeuner, 1942	UK/Lilstock Formation	Upper Triassic
Locustopsis spectabilis	Zeuner, 1942	UK/Lilstock Formation	Upper Triassic
Plesioschwinzia gracilis	(Zeuner, 1942)	UK/Lilstock Formation	Upper Triassic
Plesioschwinzia sharovi	Gorochov & Coram, 2023	UK/Lilstock Formation	Upper Triassic
Locustopsis dubia	Handlirsch, 1939	Germany/Dobbertin	Lower Jurassic
Locustopsis elegans	Handlirsch, 1906	Germany/Dobbertin	Lower Jurassic
Locustopsis elongata	Handlirsch, 1906	Germany/Dobbertin	Lower Jurassic
Locustopsis gyra	Zessin, 1983	Germany/Dobbertin	Lower Jurassic
Locustopsis maculosa	Bode, 1953	Germany/Posidonia Shale Formation	Lower Jurassic
Locustopsis nana	Handlirsch, 1939	Germany/Dobbertin	Lower Jurassic
Locustopsis pulchella	Zessin, 1983	Germany/Dobbertin	Lower Jurassic
Locustopsis reducta	Handlirsch, 1939	Germany/Dobbertin	Lower Jurassic
Locustopsis sippeli	Zessin, 1983	Germany/Lehmhagen	Lower Jurassic
Plesioschwinzia bernstorffi	(Geinitz, 1880)	Germany/Dobbertin	Lower Jurassic

Plesioschwinzia kruegeri	(Zessin, 1983)	Germany/Schandelah	Lower Jurassic
Plesioschwinzia lacera	(Zessin, 1983)	Germany/Dobbertin	Lower Jurassic
Plesioschwinzia procera	(Zessin, 1983)	Germany/Dobbertin	Lower Jurassic
Plesioschwinzia thalassophila	Zessin, 1988	Germany/Dobbertin	Lower Jurassic
Schwinzia sola	Zessin, 1983	Germany/Dobbertin	Lower Jurassic
Zeunerella mecklenburgica	(Zessin, 1983)	Germany/Dobbertin	Lower Jurassic
Zeunerella reticulata	(Handlirsch, 1939)	Germany/Dobbertin	Lower Jurassic
Locustopsis germari	(Münster, 1842)	Germany/Solnhofen Formation	Upper Jurassic
Locustopsis africanus	Ansorge, 1991	Egypt/Tonsteinserie Formation	Lower Cretaceous
Locustopsis anatolica	Sharov, 1968	Kyrgyzstan/Dzhil Formation	Lower Jurassic
Locustopsis karatavica	Sharov, 1968	Kazakhstan/Karabastau Formation	Upper Jurassic
Zeunerella arborea	Sharov, 1968	Kazakhstan/Kzyl-Zhar	Upper Cretaceous
Locustopsis apicalis	Zherikhin, 1985	Siberia/Itat Formation	Lower Jurassic
Locustopsis picta	Zherikhin, 1985	Siberia/Itat Formation	Lower Jurassic
Locustopsis ferghanensis	Martynov, 1937	Kyrgyzstan/Sulyukta Formation	Lower Jurassic
Locustopsis shurabica	Sharov, 1968	Kyrgyzstan/Sagul Formation	Lower Jurassic
Parapleurites gracilis	Brauer, Redtenbacher & Ganglbauer, 1889	Siberia/Cheremkhovskaya Formation	Lower Jurassic
Parapleurites sibiricus	Sharov, 1968	Siberia/Cheremkhovskaya Formation	Middle Jurassic
Mesolocustopsis sinica	Hong & Wang, 1990	China/Laiyang Formation	Lower Cretaceous
Pseudoacrida costata	Lin, 1982	China/Liupanshan Basin	Lower Cretaceous
Locustopsis rhytofemoralis	Gu, Yue, Shi, Tan & Ren, 2016	China/Jiulongshan Formation	Middle Jurassic
Sinolocustopsis elongatus	Nel and Huang, 2024	China/Yan'an Formation	Middle Jurassic
Sinolocustopsis brevis	Nel and Huang, 2024	China/Yan'an Formation	Middle Jurassic

Tab. 2: Generic separation of Locustopsidae Handlirsch, 1906 on the basis of wing venation. Missing are *Liadolocusta* Handlirsch, 1906 and *Conocephalella* Strand, 1926 because they are

insufficiently known to be included in a comparison and *Locustopsites* Théobald, 1937 because it probably does not belong in Locustopsidae.

Genus	**Branches of CuA + CuPaα**	**Branches of M**	**Contact of MA2**	**Separating character from similar genus**
Araripelocusta Martins-Neto, 1995	1	1	-	-
Britannacrida Gorochov et al., 2006	2	1	-	-
Cratolocustopsis Martins-Neto, 2003	2	2	-	-
Locustrix Martins-Neto, 2003	2	2	-	ScP markedly shorter, ca. 50% of total wing length
Cratozeunerella Martins-Neto, 1998	2	3	MP	ScP with many cross veins
Zeunerella Sharov, 1968	2	3	MP	ScP without cross veins
Locustopsis Handlirsch, 1906	2	3	MA1	ScP with 6–8 branches
Sinolocustopsis Nel and Huang, 2024	1-2	3	MA1	ScP with 2–3 branches
Plesioschwinzia Zessin, 1988	2	3	MA1	ScP with 1–4 branches
Orichalcum Whalley, 1985	2	3	MA1	M and RP fused to one branch
Mesolocustopsis Hong & Wang, 1990	1	3	MA1	CuA + CuPaα does not continue past fusion to CuPaβ
Pseudoacrida Lin, 1982	1	3	MA1	CuA + CuPaα continues past fusion to CuPaβ as separate CuA
Zessinia Martins-Neto, 1990	1	3	MP	-
Parapleurites Brauer et al., 1889	3	2	-	-
Schwinzia Zessin, 1983	3	3	MA1	-

2. Geological Setting

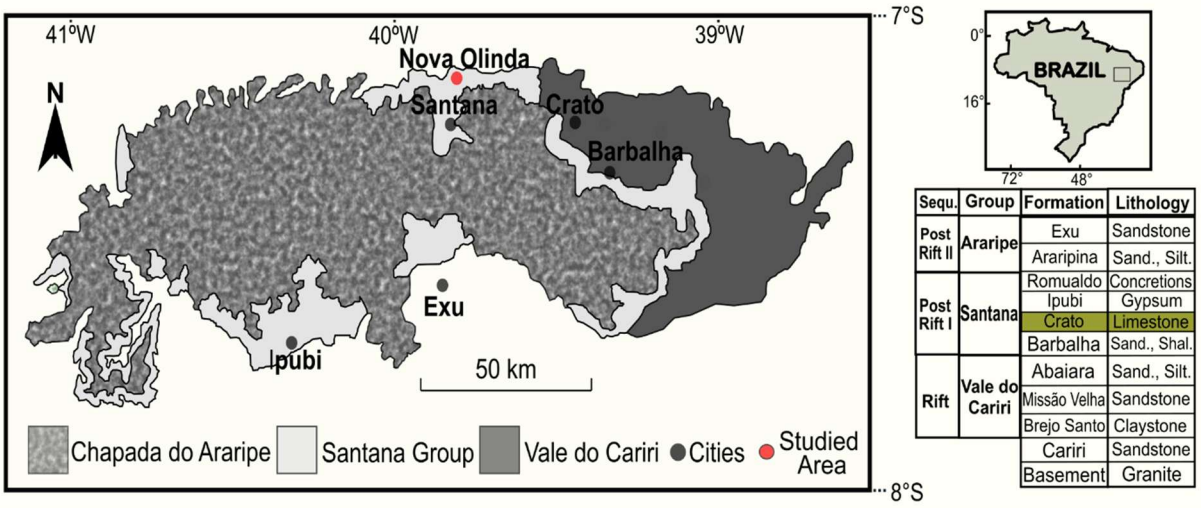
Fig. 1

The break-up of Africa and South America led to the formation of several hinterland basins in Brazil during the Jurassic–Cretaceous interval. The Araripe Basin is the largest and most complete basin in the interior of northeastern Brazil, being one of the most prominent examples of this phase (Assine, 2007). The sedimentary history of this basin is linked to rifting processes and can be divided into pre-rift, rift, and post-rift tectonic sequences (Ponte and Ponte Filho, 1996). The post-rift tectonic sequence is divided into two events: the post-rift I and post-rift II (Assine et al., 2014). The post-rift I is represented from base to top by the Barbalha, Crato, Ipubi, and Romualdo Formations, stacked within the Santana Group (Assine et al., 2014).

The Crato Formation is characterized by lacustrine carbonates, which are interlayered, at least at its top, by green shales and fine-to-coarse sandstones (Santos et al., 2017). The carbonates of the Crato Formation can be distinguished into six informal layers (C1–C6), of which C6 at the top of the formation is exposed in quarries near Nova Olinda and Santana do Cariri, Ceará State (Neumann et al., 2003) (Fig. 1). Crato limestones are famous for their abundance of high-quality fossils. The excellent preservation of Crato fossils have made it known worldwide as a Fossil Konservat-Lagerstätte. This Lagerstätte is a para-autochthonous to allochthonous assemblage with diverse invertebrates, vertebrates, fungi, and plants (Mendes et al., 2020). The Crato biota are almost exclusively conserved in the C6 limestone layer (Corecco et al., 2022). Crato fossils commonly appear as an orange to brown friable material or as a seemingly amorphous dark matter (Bezerra et al., 2020; Dias & Carvalho, 2022). The orange to brown specimens are preserved by oxy-hydroxide after pyrite, while the coalified fossils occur as carbonaceous compressions (Bezerra et al., 2021). The strata of the Crato Formation are of uncertain age as estimates vary depending on the method applied (e.g., isotope-analysis, ostracod and palynomorph assemblages, microfossil data) (Arai, 2014; Arai & Assine, 2020; Coimbra et al., 2002; Coimbra & Freire, 2021; Heimhofer & Hochuli, 2010; Lúcio et al., 2020; Melo et al., 2020). However, all methods agreed on an age constraint between the Late Barremian and Early Albian or ca. 122–113 mya (Bezerra & Mendes, 2024).

The Crato fossils have primarily been interpreted as having lived in a lacustrine environment because of the absence of typically marine specimens (Heimhofer et al., 2010; Catto et al., 2016). The presence of halite pseudomorphs in different carbonate levels of the Crato Formation suggests deposition under fluctuating salinity conditions (Martill et al., 2007). Several authors have suggested that these carbonates were deposited in a hypersaline lagoon

system with restricted connection to an epeiric sea (Assine et al., 2016). Whether the Crato limestones were deposited in a freshwater lake, or temporarily in a brackish lagoon is still a matter of debate.



Sequ.	Group	Formation	Lithology
Post Rift II	Araripe	Exu	Sandstone
		Araripina	Sand., Silt.
Post Rift I	Santana	Romualdo	Concretions
		Ipubi	Gypsum
		Crato	Limestone
		Barbalha	Sand., Shal.
Rift	Vale do Cariri	Abaiara	Sand., Silt.
		Missão Velha	Sandstone
		Brejo Santo	Claystone
		Cariri	Sandstone
		Basement	Granite

Fig. 1: Simplified geological map of the Araripe Basin. The stratigraphic column is summarized at the right (modified from Assine, 2007).

3. Materials and methods

The specimens presented in this study were part of two German collections (the Husemann Research Collection (HRC) managed by author MH and the collection of the Museum der Natur – Paläontologie/Geologie, Hamburg, Germany, managed by author UK). As part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future" they were donated to the Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil. Specimens MPSC 9841 (ex coll. no. CNBS00410), MPSC 9842 (ex coll. no. CNBS00419), and MPSC 9840 (ex coll. no. CNBS00421) were donated from the latter institution. MPSC 9839 (ex coll. no. HC0008) and MPSC 9838 (ex coll. no. HC0011) were donated from the HRC. The non type specimen CNBS00417 is housed in the Museum der Natur – Paläontologie/Geologie collection.

Imaging of the specimens was done using a Keyence VHX-6000 digital microscope (KEYENCE Corporation, 2024, Osaka, Japan; https://www.keyence.com/). All images are composite images assembled via the stitching method. Drawings of the specimens were created in GIMP (v. 3.0.2-1) (the GIMP Team, 2025; https://www.gimp.org/). Figures were assembled

and modified (scale bars and labelling) in Inkscape (v. 1.4.2) (the Inkscape Team, 2025; https://inkscape.org/).

The taxonomy in this study follows the Orthoptera species file (Cigliano et al., 2025; https://orthoptera.speciesfile.org/). Wing venation nomenclature follows Béthoux & Nel (2002) with abbreviations: CP posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

4. Systematic paleontology

Order Orthoptera Latreille, 1810

Suborder Caelifera Ander, 1936

Family Locustopsidae Handlirsch, 1906

Genus ***Aestuacrida*** new genus

Type species: *Aestuacrida stereofemoris* sp. nov. by monotypy and present designation. Gender feminine.

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The genus name is a combination of the Latin *aestuarium* (lagoon) and the suffix -*acrida*. It refers to the hypothesized habitat of the Crato Formation in which the genus is thought to have lived.

Diagnosis: The new genus is characterized by having two branches of M as well as four branches of CuA + CuPaα in the forewing.

Remarks: The new genus can be attributed to Locustopsidae by its separated RP, M, and CuA + CuPaα, as well as a long ScP and singular RA. Its main diagnostic character–the presence of four branches of CuA + CuPaα–highlights the great diversity of this family in the Crato Formation, as the trait is unique to this genus and locality.

Aestuacrida stereofemoris new species

Fig. 2

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The species name refers to the heavily built metafemora. It is derived from the Ancient Greek *stereós* (solidly built) and Latin *femur*.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype male in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9838.

Diagnosis: Overall stocky body and very sturdy hind femurs (length/width-ratio ca. 3.0). Origin of tegminal RP distinctly posterior to forking of M. RP with five or six branches. Cross vein pattern relatively simple.

Description: The specimen has body, wings, left hindleg and part of the right hindleg preserved.

Measurements: Body length 12.9 mm, height (measure taken at thorax) 4.7 mm. Head height 3.3 mm. Forewing length 16 mm, height 2.8 mm. Metafemur 8.3 mm long, ca. 2.8 mm wide. Metatibia 7.1 mm long. Metatarsus 2.2 mm long.

Body: Body rather stocky (length/height-ratio 2.74). Head rather short, much shorter than thorax.

Legs: Metathoracic femur very sturdy, length/height-ratio 3.0. Oblique lateral carinae present. Metatibia narrow with no apparent spination other than 2 (?) apical spurs. Metatarsus with no spines or lobes.

Forewing: Length/height-ratio 5.7. ScP long and narrow, at least 81.5% of total wing length (twl) (venation not preserved in most distal part of wing; ScP would have been longer). Space between ScP and RA 9.4% of total wing height (twh). Origin of RP at 54.5% of twl, distinctly posterior to fork of M. Space between RA and RP 11.3% of wing height. RP with 5 or 6

branches (attribution of RP3 to forewing or hindwing unsure due to strong wing overlap; we suggest RP of forewing with 5 branches). M with two branches; fork of M at 44.5% of twl. CuA + CuPaα with four branches; anterior branch reaching anal margin of forewing at ca. 69.8% of twl. Second branch probably reaching anal wing margin too. Third and fourth branch do not reach anal wing margin but make contact with CuPaβ. CuPaβ reaching anal wing margin at ca. 62.6% of twl. Cross vein pattern rather simple; consisting mainly of simple orthogonal cross veins set at rather wider distance.

Remarks: The single species of this genus is characterized by relatively thick hindfemora. Whether this trait is a common feature of *Aestuacrida* remains unanswered until additional species are described. Unfortunately, most locustopsids do not have their hindlegs well-preserved, hence providing little applicability to the character of femur width regarding taxonomy of the family.

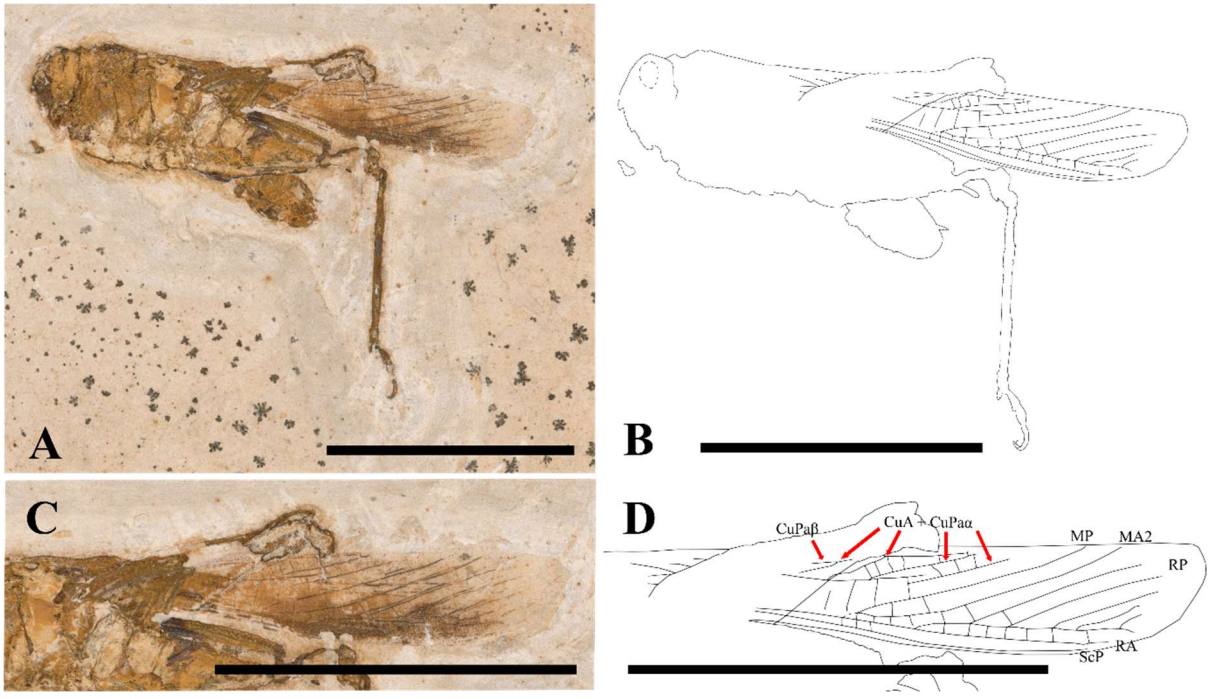


Fig. 2: *Aestuacrida stereofemoris* gen. et sp. nov. holotype male, MPSC 9838. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

Genus ***Parapleurites*** Brauer, Redtenbacher & Ganglbauer, 1889

Included species: *Parapleurites gracilis* Brauer, Redtenbacher & Ganglbauer, 1889 (type species); *P. sibiricus* Sharov, 1968; *P. brasiliensis* sp. nov.

Parapleurites brasiliensis new species

Fig. 3

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The species is named after its home country Brazil.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype male, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9839.

Diagnosis: Characterized by having three branches of CuA + CuPaα and two branches of M–a combination that places it within the genus *Parapleurites*. Third and second branches of CuA + CuPaα strongly concave, first branch convex. RP with four branches. Fork of M above between second and third branches of CuA + CuPaα, slightly inclined toward third branch. Origin of RP distinctly posterior to fork of M. Pronotum possibly rather shallow with elongated hind lobe (pronotal shape not clearly discernible).

Description: Specimen with impression of body, forewing, metafemurs and proximal part of the right metatibia preserved.

Measurements: Body length 18 mm. Metafemur ca. 11.2 mm long, 2.4 mm wide. Forewing length 21.6 mm, height 4.05 mm. Pronotum 7.9 mm long (?), 2.1 mm high (pronotum outline unclear).

Body: Body cylindrical, little alteration in height, “sausage-like” shape. Pronotum outline unclear; possibly very elongate and shallow. Abdominal height dominated by tergites (ca. 79%). Ventral side with conspicuous structure of uncertain identity; possibly associated with fossilized plant material present in matrix).

Legs: Only metafemur and proximal portion of metatibia preserved. Metafemur length/height ratio 4.7; oblique lateral carinae present; genicular joint not significantly wider than metatibia. Three small spines discernible on posterior half of metatibia.

Forewing: Length/height ratio 5.3. ScP long, narrow, extending beyond 89.2% of twl. RA distinctly curved upward near distal margin. Distance between ScP and RA 10.9% of twh. RP originates at 53.9% of twl, posterior to fork of M. Distance between RA and RP broad (15.2% of wing height). RP with four branches. M with two branches; fork of M at 46.3% of twl. CuA + CuPaα with three branches, all reaching anal margin at 76.3%, 68.5%, and 60.2% of twl, respectively. Anterior branch convex; second and third strongly concave. CuPaβ reaches anal margin at 51.2% of twl. CuPaβ, CuPb, and 1A narrow and parallel.

Remarks: The new species can be assigned to *Parapleurites* based on the presence of two branches of M and three branches of CuA + CuPaα. It differs from the type species, *P. gracilis*, in several characters: it is significantly larger (forewing length 14 mm in *P. gracilis*) and exhibits a longer ScP (72.7% of total wing length in *P. gracilis*). Additionally, the second branch of CuA + CuPaα is strongly concave in *P. brasiliensis* sp. nov., whereas both the first and second branches are strongly convex in *P. gracilis* (third branch in *P. gracilis* is likely concave). Another distinguishing feature is the position of the RP origin, which is anterior to the fork of M in *P. gracilis*, but posterior in *P. brasiliensis*. The stratigraphic and geographic provenance further differentiates the species: *P. gracilis* originates from the Lower Jurassic of Siberia, while *P. brasiliensis* is from the Lower Cretaceous of Brazil. From *P. sibiricus*, the new species differs by having one fewer branch of RP as well as the position of RP origin, which is proximal to the fork of M in *P. brasiliensis*. *Parapleurites sibiricus* is known from the Middle Jurassic of Siberia. *Parapleurites morrisonensis* Smith, Gorman, Pardo & Small, 2011 from the Upper Jurassic Morrison Formation of North America, does not have three branches of CuA + CuPaα and should not be retained in *Parapleurites*. Its venation features–three branches of M and single branch of CuA + CuPaα, with MP and CuA + CuPaα fused in the holotype–suggests a more appropriate placement in *Mesolocustopsis*.

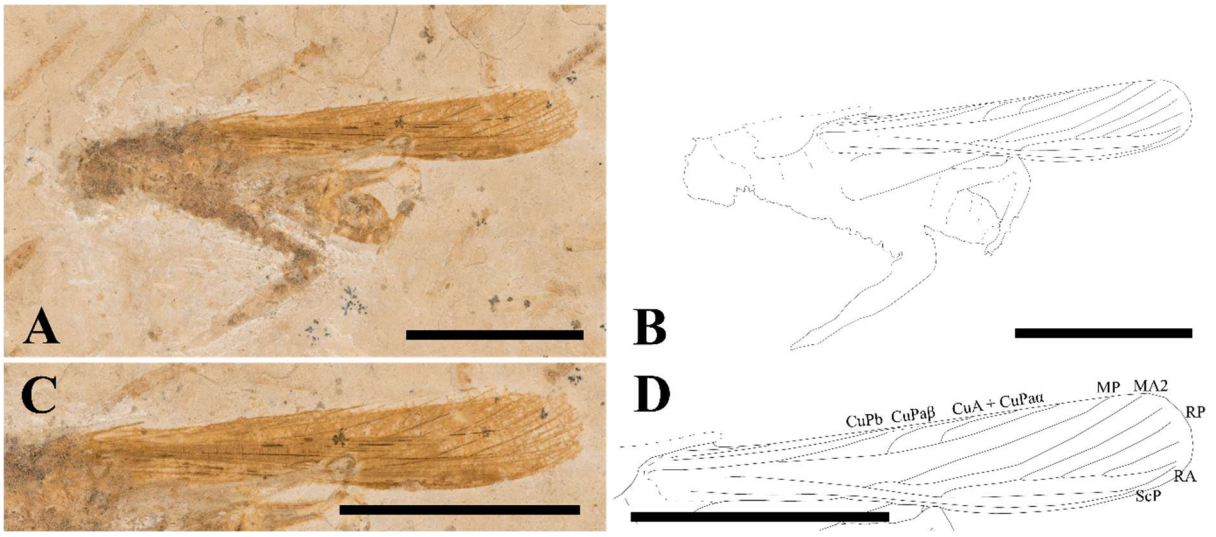


Fig. 3: *Parapleurites brasiliensis* sp. nov. holotype male, MPSC 9839. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

Genus *Cratolocustopsis* Martins-Neto, 2003

Included species: *Cratolocustopsis cretacea* (Martins-Neto, 1990) (type species); *C. contumax* Martins-Neto, 2003; *C. aquila* sp. nov.

Remarks: *Cratolocustopsis* was originally described by Martins-Neto (2003) as having forewing with two branches of CuA + CuPaα (referred to as MP + CuA in the original text) and a relatively short and robust hindfemur, with a width/length ratio ranging from 0.2 to 0.35. Unfortunately, the drawings given in the same publication for species assigned to *Cratolocustopsis* did not match this description, leading to taxonomic uncertainty regarding the validity of the genus (e.g., Gorochov et al., 2006). In addition to the new species of *Cratolocustopsis* described herein, we report a new specimen that, based on its morphology and original description of *Cratolocustopsis cretacea* (Martins-Neto, 1990), can be confidently assigned to that species. This new specimen reveals the presence of two branches of CuA + CuPaα–features that were not depicted in the original figure provided by Martins-Neto–thus reaffirming the diagnostic traits of the genus.

Cratolocustopsis aquila sp. nov.

Fig. 4

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The species name derives from the Latin *aquila*, meaning “eagle”. It refers to the head shape of the specimen, which resembles the beak of a bird of prey. This appearance is the result of damage to the fossil and does represent the actual morphology of the species.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype, sex unknown, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9840.

Diagnosis: Species recognized by MP strongly concave in distal fourth, almost parallel to anal wing margin. RP originates posterior to fork of M. RP bifurcates shortly after origin. Note: latter character may represent an individual aberration.

Description: Body, forewing and left metafemur as well as most of metatibia preserved.

Measurements: Body length 20.4 mm; abdomen ca. 10.3 mm. Head height 4.3 mm. Metafemur 12.1 mm long, 2.6 mm wide. Preserved part of metatibia 8.8 mm long. Forewing length 24.6 mm, 4.1 mm high.

Legs: Length/height-ratio of metafemur 4.65. Oblique lateral carinae present. Metatibia with 7 small dorsal spines on preserved part (probably ca. 80% of metatibia length preserved).

Forewing: Length/height-ratio 6. ScP length at least 85.9% of twl. Space between ScP and RA 11.4% of total wing height. Origin of RP at 50.5% of twl, posterior to M bifurcation. Space between RA and RP rather wide, 15% of wing height. RP with four branches. Shortly after its origin, RP is bifurcated; the upper branch is the “normal” RP, considered as RP1. Lower branch is fused to RA slightly anterior to branching of RP4. M with two branches. Fork of M at 45.9% of twl. Anterior and posterior branch of M parallel along most of their length, however MP describing a strong concave curve distally, almost making contact with MA2 as the latter touches wing margin. CuA + CuPaα with two branches. Anterior branch relatively parallel to MA2, reaching wing margin at 72.7% of twl. Posterior branch strongly concave similar to distal part of MP. Base of CuA + CuPaα (connection to CuPaβ) at 30% of twl. CuPaβ reaching anal

wing margin at ca. 42.5% of twl (anal wing margin slightly damaged in the fossil, last millimeters of branch are lost). Cross vein pattern rather simple, consisting mainly of straight cross veins.

Remarks: Cratolocustopsis aquila sp. nov. is assigned to *Cratolocustopsis* based on the presence of two branches of CuA+ CuPaα and two branches of M. It differs from *C. cretacea* by its MP being strongly concave distally (MP is parallel to MA2 along its entire length in *C. cretacea* (Fig. 6A in Martins-Neto (2003) and Fig. 5 from this study). *Cratolocustopsis aquila* further differs from the type species by the distal extent of the CuA + CuPaα branches: in the new species, both branches reach the wing margin, whereas in *C. cretacea*, only the anterior branch does so, with the posterior branch terminating in contact with CuPaβ. The new species also differs from *C. contumax* by being significantly larger; the forewing of *C. contumax* measures 18 mm in length, whereas that of *C. aquila* is 24.6 mm long.

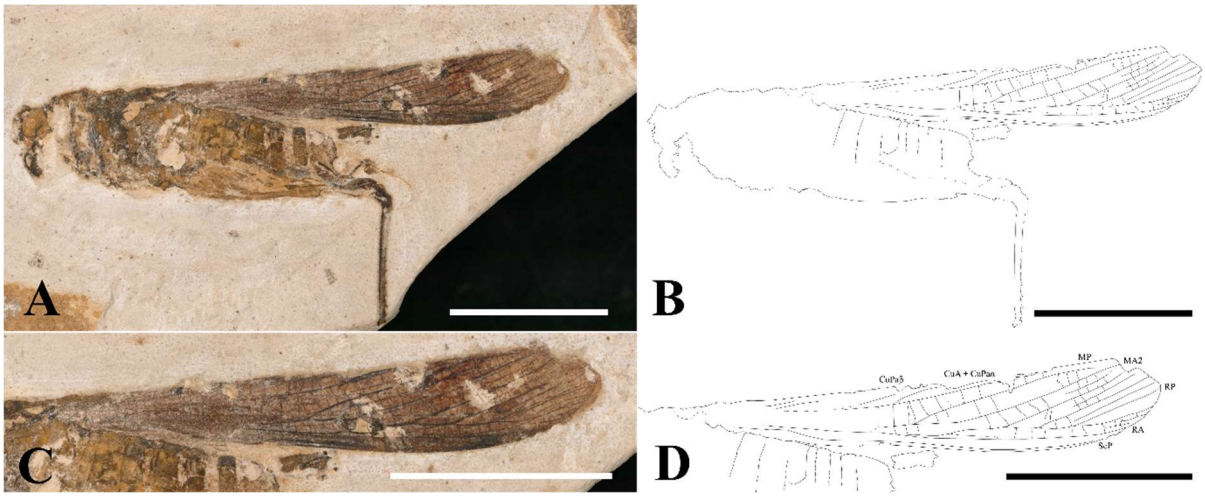


Fig. 4: *Cratolocustopsis aquila* sp. nov. holotype, sex unknown, MPSC 9840. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

Cratolocustopsis cretacea (Martins-Neto, 1990)

Figs. 5, 6

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype male (coll. no. GP/1T-1671) and paratype male (coll. no. GP/1T-1618a), both specimens are in the collection of Instituto de Geociências da Universidade de São Paulo (IGc/USP) (Fig. 6).

Additional material examined in this study: A relatively well-preserved specimen of uncertain sex in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9841. Donation from Museum der Natur – Paläontologie/Geologie (Museum of Nature – Palaeontology/Geology), Hamburg, Germany (Collection number CNBS_00410), as part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future".

Description of new material: Large parts of the body and wings preserved. Missing are most details of the prothoracic leg, the mesothoracic leg as well as the tarsus of the metathoracic leg. Structures of the abdominal apex obscured by metathoracic legs.

Measurements: Body length (head to abdominal apex) 17.9 mm. Head height 3.6 mm. Pronotum length 8.65 mm. Metafemur ca. 11.4 mm long. Metatibia (as preserved) 9.9 mm long. Forewing 20.6 mm long, 3.4 mm high.

Body: Head relatively small. Pronotum rather large and posteriorly elongated. Lateral margin with very prominent concave curve.

Legs: Prothoracic leg inconspicuous. Femur slightly wider than tibia. Metathoracic leg: femur relatively slender. Distal half of tibia dorsally with some small spines of which four are preserved.

Forewing: Length/height-ratio 6.1. ScP length at least 89% of twl. Termination of ScP (costal wing margin or fused to RA) not preserved. Space between ScP and RA 13.6% of total wing height (measured between RP4 and RP5). Origin of RP at 48.1% of twl, posterior to M bifurcation. Space between RA and RP 14% of wing height. RP with five branches. M with two branches. Fork of M at 43% of twl. Branches of M and RP more or less parallel. CuA + CuPaα with two branches. Anterior branch relatively parallel to M and RP, reaching wing margin at 61.3% of twl. Posterior branch strongly concave and fused to CuPaβ. Base of CuA + CuPaα (connection to CuPaβ) at 31.5% of twl. CuPaβ not reaching anal wing margin but fused to CuPb at 43.3% of twl. CuPb long and narrow, reaching anal wing margin after 54.8% of twl. 1A

narrow, reaching anal wing margin after 27% of twl. Cross vein pattern unsure due to overlapping of fore- and hindwings.

Remarks: The specimen MPSC 9841 originates from the same stratigraphic unit (Crato Formation) and general geographic region as the holotype of *Cratolocustopsis cretacea*. It preserves diagnostic features consistent with the original description and emended diagnosis of *C. cretacea*, including a forewing with two branches of CuA + CuPaα and two branches of M. The description of the additional specimen will hopefully provide reference for future comparative and systematic studies.

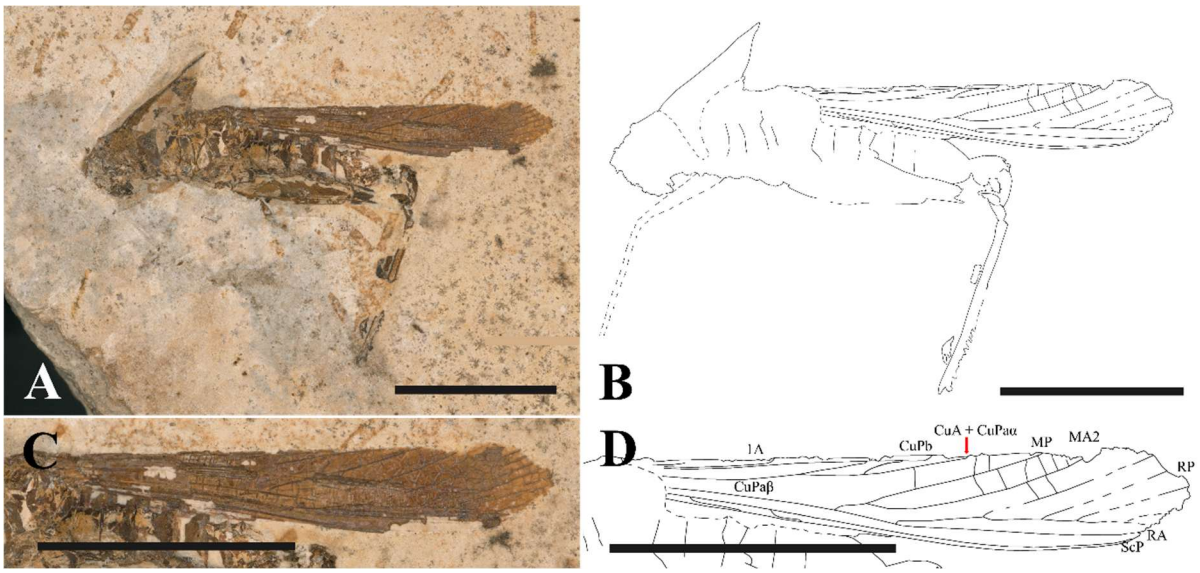


Fig. 5: *Cratolocustopsis cretacea* (Martins-Neto, 1990), specimen MPSC 9841 (not a type). **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

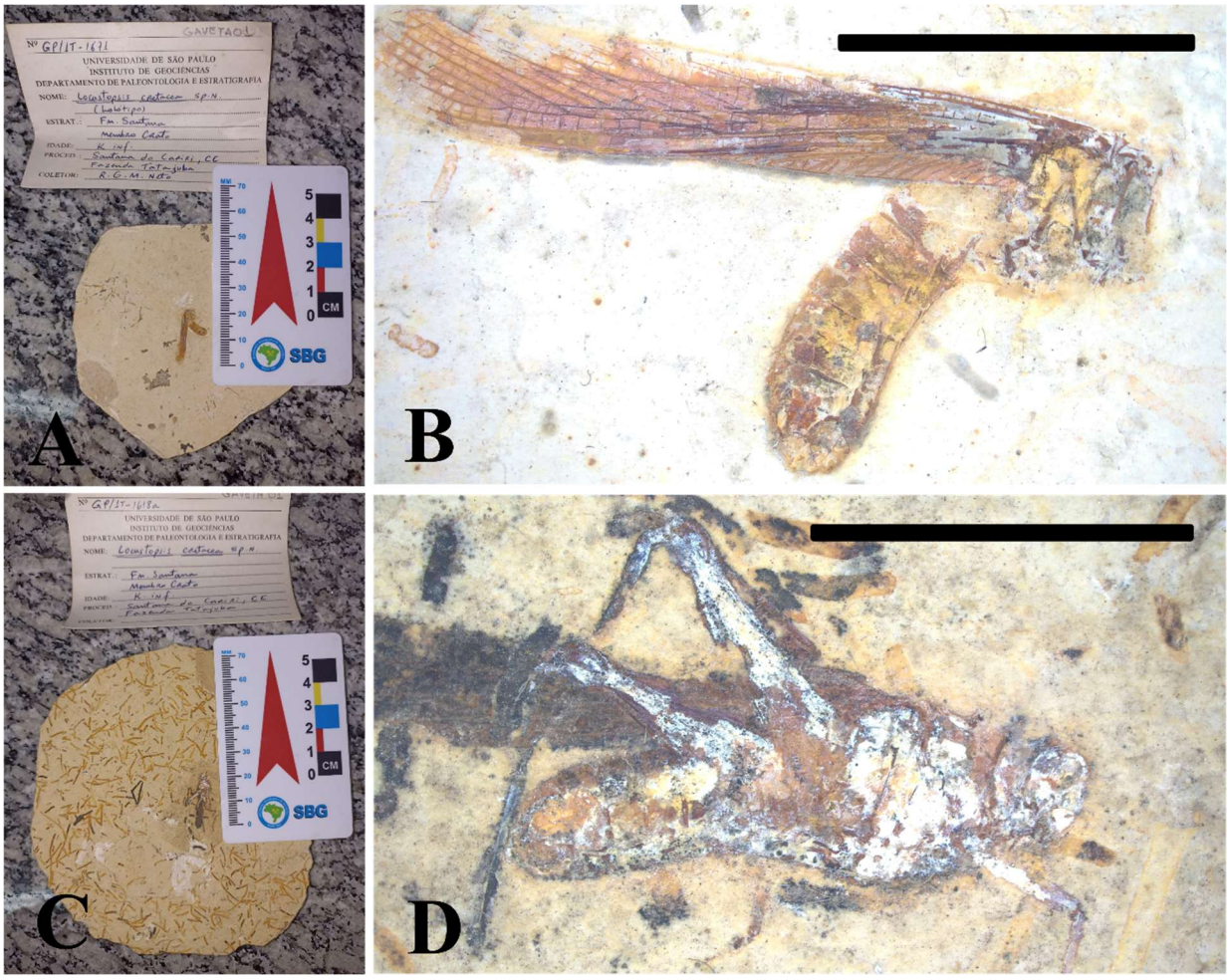


Fig. 6: Holotype (GP/1T-1671) and paratype (GP/1T-1618a) in the collection of Instituto de Geociências da Universidade de São Paulo (IGc/USP) of *Cratolocustopsis cretacea* (Martins-Neto, 1990). **A.** and **B.** Holotype. **A.** shows a museum label proving the identity of the holotype. **C.** and **D.** Paratype. **C.** shows a museum label proving the identity of the paratype. Image credits to Marcela F. Colombo.

Subfamily Araripelocustinae Martins-Neto, 1995

Genus *Araripelocusta* Martins-Neto, 1995

Included species: *Araripelocusta longinota* Martins-Neto, 1995 (type species); *A. brevis* Martins-Neto, 1995; *A. imperatrix* sp. nov.

Araripelocusta imperatrix new species

Figs. 7–9

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The species name is derived from the Latin word *imperatrix*, meaning “female sovereign”. It refers to the rather large size of the specimen, which makes it the largest known species of its genus. The name also alludes to the leaf-like appendages on the head, which resembles a crown or antlers.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type *material:* Holotype female, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, MPSC 9842. Paratype female, in the collection of Museum der Natur – Paläontologie/Geologie, Hamburg Germany, coll. no. CNBS00417.

Diagnosis of species: Large species; forewing length 37.8–39.1 mm. Hindwing with conspicuous dark band near distal margin and irregular dark blotches across wing surface. Wings very elongate with length/width-ratio of forewing 7.4. RP with five branches. Apex of head bearing two leaf-like appendages with fine lateral spines/hairs (Fig. 9). Ovipositor straight, 5.5 mm long.

Description of holotype: Head, body, wings and fragmented metathoracic leg.

Measurements: Body length 30.1 mm. Head height 6.2 mm. Appendages of head 0.85 mm. Ovipositor 2.1 mm (fragmented). Forewing length 37 mm, 5 mm high.

Body: Head conically pointed with front convexly curved. On the top of the head above the eyes is a pair of leaf-shaped appendages somewhat like little antlers. Anterolateral margin of appendages distally with fine spines or hairs. Pronotum saddle-shaped, exact outline unsure. Valvulae of ovipositor broad.

Legs: Attribution of fragmentary metathoracic leg parts unsure; either rather broad metafemur or metatibial folded in front of metafemur. Apparently with oblique lateral carinae on metafemur.

Forewing: Length/height-ratio 7.4. ScA narrow with multiple branches, reaching anterior wing margin at 41% of twl. ScP length 97.8% of wing length, slightly turned upwards distally. Space between RA and ScP 13.3% of total wing height. Origin of RP at 41.5% of twl, relatively close to M veering off RA. Space between RA and RP 10.7% of total wing height. RA distinctly turned upwards distally. RP with five branches; RP1 distinctly turned upwards parallel to RA. M with one branch, parallel to RP branches. CuA + CuPaα with one branch, reaching anal wing margin at ca. 67.6% of twl (contact point not discernible). CuPaβ parallel to CuA + CuPaα. Base of CuA + CuPaα at 25.8% of twl. Cross vein pattern rather simple over majority of wing surface but getting very complicated and net-like towards distal area between M and RP as well as branches of RP.

Description of paratype: Body outline with fragmented pro- and mesothoracic leg as well as ovipositor preserved. Wing apparatus fully intact.

Measurements: Body length 31.6 mm. Head height 5.9 mm. Eye height 2.0 mm. Ovipositor 5.5 mm. Forewing length 39.1 mm, 5.3 mm high.

Body: Head conically pointed. Valvulae of ovipositor rather prominent (for Caelifera), possibly serrated distally (impression of serration could be due to state of preservation).

Legs: Pro- and mesothoracic extremities slim, almost looking fragile compared to the animal's larger size.

Forewing: Length/height-ratio 7.4. ScA narrow with multiple branches (18+), reaching anterior wing margin at 52% of twl. ScP length at least 72.5% of twl, but likely significantly longer (the branch is lost in the dark coloration present towards the anterior wing margin). Origin of RP at 49.6% of twl, relatively close to M veering of RA. Space between RA and RP 10.5% of total wing height. RP with five branches. M with one branch, parallel to RP branches. CuA + CuPaα with one branch, reaching anal wing margin at 73.1% of twl. CuPaβ parallel to CuA + CuPaα; not reaching wing margin but in contact with CuPb at 60.7% of twl. CuPb very long and narrow, reaching wing margin very shortly anterior of CuA + CuPaα reaching wing margin. Cross vein pattern rather simple over majority of wing surface but getting very complicated and net-like towards distal area between M and RP as well as branches of RP.

Remarks: The new species is assigned to Araripelocustinae based on the presence of a single branch of M, and to *Araripelocusta* due to the presence of a single branch of CuA + CuPaα.

Araripelocusta imperatrix sp. nov. is clearly distinct from the other two species of the genus known from the Crato Formation by being significantly larger, exceeding 37 mm (*A. longinota* and *A. brevis* have forewings about 22.5 mm long (Martins-Neto & Gallego, 2006)). It further differs from its congeners as well as all known species of Locustopsidae so far by having a pair of small, leaf-like appendages located dorsally above the eyes, reminiscent of antlers. The precise identity of this structure remains uncertain; however, the presence of similar shape in the same position in the paratype specimen (Fig. 8), albeit less clearly preserved, supports the interpretation that this appendage is part of its morphology rather than an extrinsic element of the matrix.

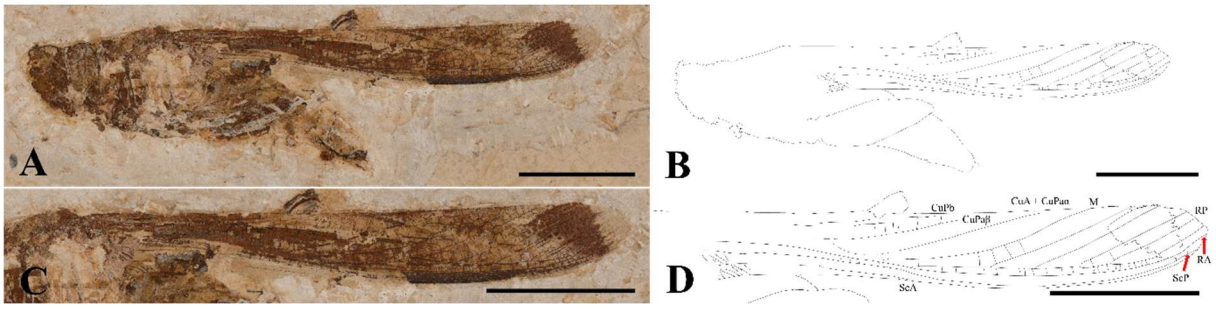


Fig. 7: *Araripelocusta imperatrix* sp. nov. holotype female, MPSC 9842. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

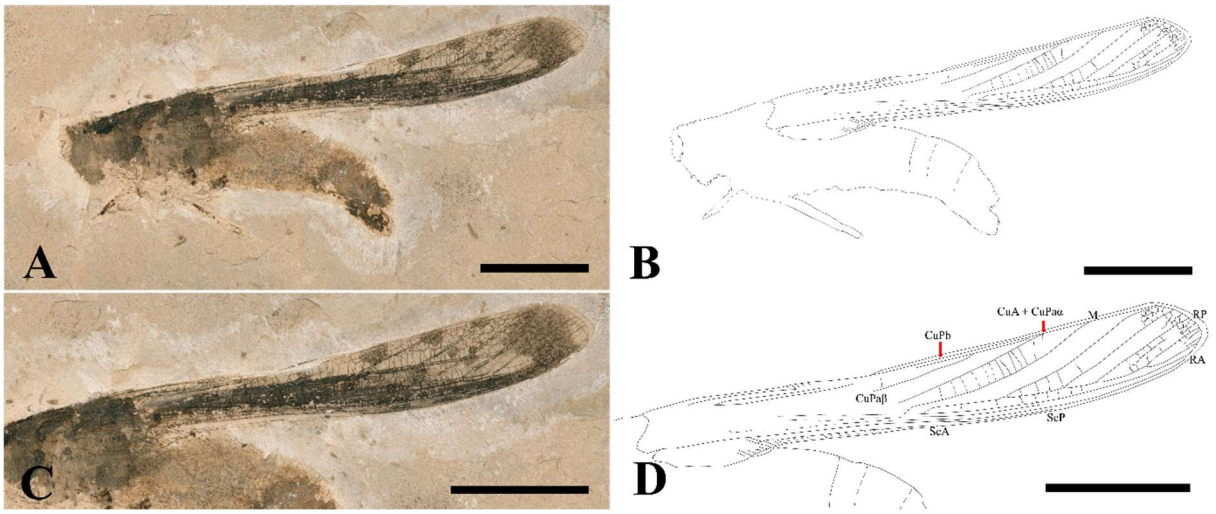


Fig. 8: *Araripelocusta imperatrix* sp. nov. paratype CNBS_00417. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of the forewing. **Scale bars** = 10 mm.

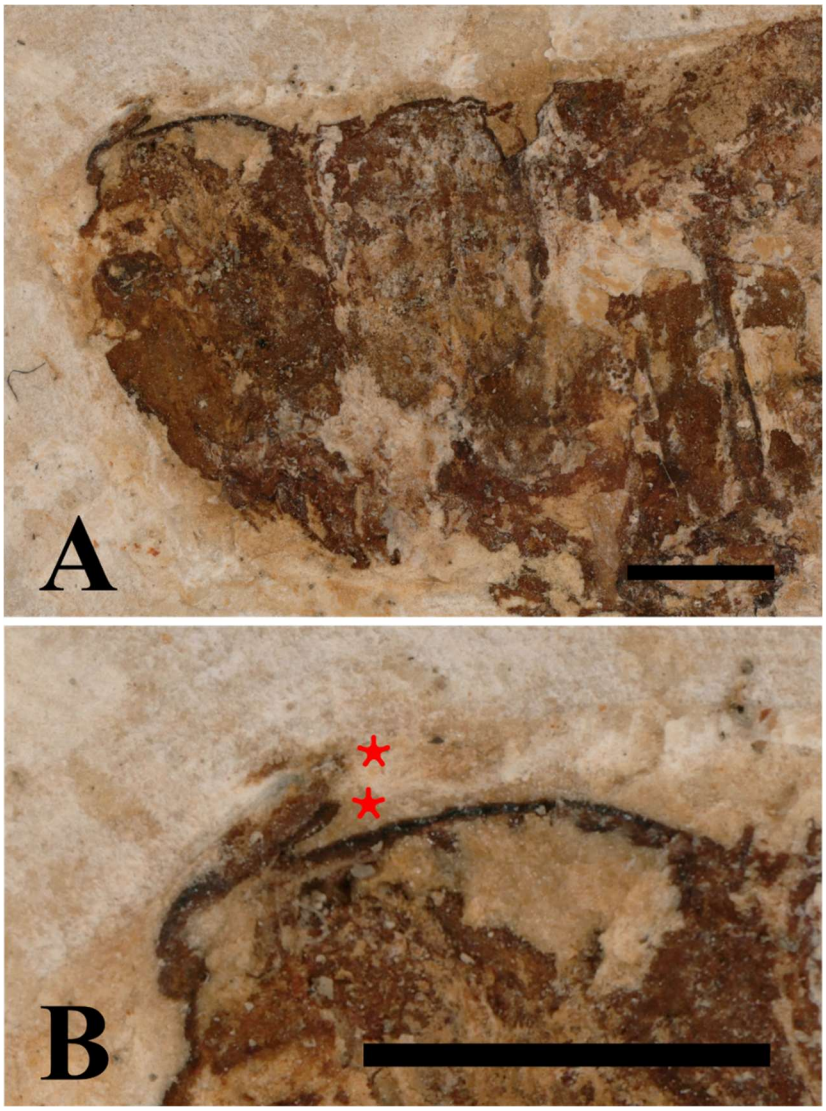


Fig. 9: *Araripelocusta imperatrix* sp. nov. holotype female, coll. no. MPSC 9842. **A.** Detail of head with appendages. **B.** Close-up of antler-like appendages (red stars). **Scale bars** = 2 mm.

5. Taxonomic revision of Locustopsidae

The taxonomy of Locustopsidae is predominantly based on forewing venation, particularly the number of branches of CuA + CuPaα and M, and the relative position of MA2 in relation to either MP or MA1 when three M branches are present (Tab. 2) (Gorochov et al., 2006). Previous revisions of Gorochov et al. (2006) and Gorochov & Coram (2023) proposed several significant changes to the internal classification of the family. These include the tentative synonymy of *Cratozeunerella* Martins-Neto, 1998 with *Zeunerella* Sharov, 1968, and *Cratolocustopsis* Martins-Neto, 2003 with *Mesolocustopsis* Hong & Wang, 1990 (Gorochov & Coram, 2023). The inclusion of *Locustopsis anatolica* Sharov, 1968 in *Schwinzia* Zessin, 1983 was also

suggested (Gorochov & Coram, 2023). Furthermore, *Zessinia caririensis* Martins-Neto, 1990, *Z. petruleviciusi* Martins-Neto, 2003, and *Z. vikingi* Martins-Neto, 2003 were proposed to be transferred to *Mesolocustopsis* (Gorochov et al., 2006). Gorochov & Coram (2023) also pointed out the marginal difference between *Locustopsis* Handlirsch, 1906 and *Plesioschwinzia* Zessin, 1988 (number of branches of ScP) and questioned whether it would suffice to generic separation.

Building upon these prior assessments and incorporating newly examined specimens, we propose the following taxonomic revisions to Locustopsidae:

1. Synonymy of *Cratozeunerella* with *Zeunerella*

The characters originally used (Martins-Neto, 2003) to distinguish *Cratozeunerella*–presence of cross veins in subcostal area, one to two additional RP branches in fore- and hindwings–are insufficient for generic separation and better reflect species-level differences. We agree with Gorochov & Coram (2023) that *Cratozeunerella* should be synonyized with *Zeunerella*. However, four species formerly attributed to *Cratozeunerella–C. godoii* Martins-Neto, 2003, *C. nervosa* Martins-Neto, 2003, *C. soaresi* Martins-Neto, 2003, and *C. titanella* Martins-Neto, 2003–exhibit MA2 in contact with MA1 (rather than MP), a venational pattern diagnostic of *Locustopsis*, and are thus should be transferred to that genus. *Cratozeunerella amedegnatoi* Martins-Neto, 1998 and *C. neotropica* Martins-Neto, 1998 are proposed to be moved to *Zeunerella*.

2. Transfer of *Locustopsis anatolica* to *Schwinzia*

Locustopsis anatolica displays three branches of both CuA + CuPaα and M, a combination considered apomorphic for *Schwinzia* (Zessin, 1983). We therefore support the transfer of this species to *Schwinzia anatolica* (Sharov, 1968) comb. nov., as proposed by Gorochov & Coram (2023).

3. Transfer and synonymy within *Mesolocustopsis*

Mesolocustopsis is characterized by a single branch of CuA + CuPaα and three branches of M, with MA2 in direct contact to MA1. The species *Zessinia caririensis*, *Z. petruleviciusi*, and *Z. vikingi* match this venation pattern (see Martins-Neto, 2003; figs. 3A & 5A, 5D & 5F, 4A & 4C), and are thus retained within *Mesolocustopsis*. We further propose M. *petruleviciusi* as a

junior synonym of *M. carirensis*, as the only difference between them–the origin of RP slightly anterior vs. posterior to the fork–is likely due to intraspecific variation.

4. Synonymy of *Plesioschwinzia* with *Locustopsis*

We agree with Gorochov & Coram (2023) that the variation in the number of ScP branches (1–4 in *Plesioschwinzia*; 6–8 in *Locustopsis*) does not warrant generic distinction. This variation is likely due to intraspecific or interspecific differences rather than deeper phylogenetic divergence. We therefore propose *Plesioschwinzia* as a junior synonym of *Locustopsis*.

5. *Cratolocustopsis* and *Mesolocustopsis* are not synonyms

While *Mesolocustopsis* is defined by one branch of CuA + CuPaα and three branches of M (with MA2 contacting MA1), *Cratolocustopsis* possesses two branches of both CuA + CuPaα and M. These character combinations justify their distinction as separate genera. Unfortunately, earlier figures of *C. cretacea* and *C. contumax* (Martins-Neto, 2003) did not clearly depict these venation patterns. However, review of the holotype as well as new material of *C. cretacea* confirms the diagnostic features of *Cratolocustopsis* and supports its validity.

6. Synonymy of German *Locustopsis* species

A detailed re-evaluation of *Locustopsis* species from the Lower Jurassic of Germany (Handlirsch, 1906, 1939; Zessin, 1983) revels substantial morphological overlap:

- *Locustopsis elongata* Handlirsch, 1906 is morphologically indistinguishable from *L. elegans* Handlirsch, 1906 and is herein considered a junior synonym of the latter.

- *Locustopsis lacera* (originally *Plesioschwinzia lacera* Zessin, 1983) is highly similar to *L. gyra* Zessin, 1983 from the same region and era (Lower Jurassic of Germany) and is proposed as junior synonym of *L. gyra*.

7. Transfer of *Zeunerella reticulata* to *Cratolocustopsis*

Zeunerella reticulata (Handlirsch, 1939) has two branches of both CuA + CuPaα and M (Zessin, 1983, Fig. 21), consistent with the diagnosis of *Cratolocustopsis*. Although a distal bifurcation of MP may indicate a relic third M branch, the overall venation pattern supports the transfer of this species to *Cratolocustopsis reticulata* (Handlirsch, 1939) comb. nov.

8. Taxonomic status of *Sinolocustopsis* Nel and Huang, 2024

Sinolocustopsis elongatus was recently described from the Middle Jurassic of Yan'an Formation, China based on a well-preserved forewing by Nel and Huang (2024). Its venation–particularly the three M branches and two CuA + CuPaα branches–closely matches *Locustopsis*, and we propose its transfer to *Locustopsis* as *L. elongatus* (Nel and Huang, 2024) comb. nov. (not to be confused with *L. elongata* (Handlirsch, 1906), considered a junior synonym of *L. elegans* Handlirsch, 1906; see above).

The second species, *Sinolocustopsis brevis* Nel and Huang, 2024, is based on an almost complete forewing with only the basal part missing and two partly preserved paratypes. The holotype shows M as in *Locustopsis* but has only a single branch of CuA + CuPaα. Therefore, it should probably be included in *Mesolocustopsis* as *M. brevis* comb. nov. (Nel and Huang, 2024). The two paratypes of *S. brevis* are insufficiently preserved for precise placement. The paratype NIGP206135 (Fig. 2B in Nel and Huang, 2024) may belong to *M. brevis* or *Pseudoacrida* Lin, 1982, depending on the trajectory of CuA + CuPaα. The second paratype NIGP206073 (Fig. 2C in Nel and Huang, 2024), with only probably two M branches and uncertain CuA + CuPaα branches, may represent *Cratolocustopsis* or a new genus, though this cannot be confirmed due to the poor preservation.

9. Additional notes on genera of uncertain status

In addition to the taxonomic changes proposed above, two genera currently assigned to Locustopsidae are problematic and require re-evaluation. *Liadolocusta* Handlirsch, 1906 (single species *L. auscultans* Handlirsch, 1906) from the Lower Jurassic of England and *Locustopsites* Théobald, 1937 (single species *L. gigantea* Théobald, 1937) from the Oligocene of France. *Liadolocusta* was described by Handlirsch (1906) based on a single foreleg with a well preserved tympanal opening. This material lacks sufficient diagnostic material and should be considered a *nomen nudum*.

Locustopsites gigantea is based on an almost completely preserved forewing. The figure given in Théobald (1937) does not match Locustopsidae and more closely resembles Tettigoniidae Krauss, 1902 (as suggested by Gorochov, 1995) and confirmed via pers. comm. from Dr. Olivier Béthoux (MNHN). We therefore propose *Locustopsites* be removed from Locustopsidae and transferred to Tettigoniidae.

Below is a full list of the genera and species of Locustopsidae with the changes to taxonomy proposed above applied:

Tab. 3: Genera and species of Locustopsidae with taxonomic changes from this study. Species and genera affected by any change to taxonomy are marked by an *. *Locustopsites gigantea* Théobald, 1937 is likely a Tettigoniidae and not featured in this list.

Genus (Author)	**Species (Author)**
Araripelocusta Martins-Neto, 1995	
	longinota Martins-Neto, 1995
	brevis Martins-Neto, 1995
	*imperatrix** sp. nov.
Britannacrida Gorochov et al., 2006	
	distincta Gorochov et al., 2006
Liadolocusta Handlirsch, 1906	
	auscultans Handlirsch, 1906
Conocephalella Strand, 1926	
	capito (Deichmüller, 1886)
Cratolocustopsis Martins-Neto, 2003	
	*aquila** sp. nov.
	contumax Martins-Neto, 2003
	cretacea (Martins-Neto, 1990)
	*reticulata** comb. nov. (Handlirsch, 1939)
Locustopsis (= *Plesioschwinzia** syn. nov.) Handlirsch, 1906	
	africanus Ansorge, 1991
	apicalis Zherikhin, 1985
	*bernstorffi** comb. nov. (Geinitz, 1880)
	bucklandi (Brodie, 1845)
	cockerelli (Handlirsch, 1939)
	constricta Zeuner, 1942
	cubitalis Zeuner, 1942
	dubia Handlirsch, 1939
	elegans (= *elongata** syn. nov.) Handlirsch, 1906
	*elongatus** comb. nov. (Nel and Huang, 2024)
	ferghanensis Martynov, 1937
	germari (Münster, 1842)
	*godoii** comb. nov. (Martins-Neto, 2003)
	*gracilis** comb. nov. Zeuner, 1942
	gyra (= *lacera** syn. nov.) Zessin, 1983
	karatavica Sharov, 1968
	*kruegeri** comb. nov. Zessin, 1983

	*lacoei** comb. nov. Cockerell, 1916
	maculosa Bode, 1953
	nana Handlirsch, 1939
	*nervosa** comb. nov. (Martins-Neto, 2003)
	picta Zherikhin, 1985
	posterior Gorochov et al., 2006
	*procera** comb. nov. Zessin, 1983
	pulchella Zessin, 1983
	reducta Handlirsch, 1939
	rhytofemoralis Gu et al., 2016
	*sharovi** comb. nov. (Gorochov & Coram, 2023)
	shurabica Sharov, 1968
	sippeli Zessin, 1983
	*soaresi** comb. nov. (Martins-Neto, 2003)
	spectabilis Zeuner, 1942
	*thalassophila** comb. nov. (Zessin, 1988)
	*titanella** comb. nov. (Martins-Neto, 2003)
	*uvarovi** comb. nov. Zeuner, 1942
Mesolocustopsis Hong & Wang, 1990	
	anglica Gorochov et al., 2006
	angusta Gorochov et al., 2006
	araripensis (Martins-Neto, 1990)
	*brevis** comb. nov. (Nel and Huang, 2024)
	carirensis (= *petruleviciusi** syn. nov.) (Martins-Neto, 1990)
	morrisonensis comb. nov. (Smith et al., 2011)
	problematica Gorochov et al., 2006
	sinica Hong & Wang, 1990
	vikingi (Martins-Neto, 2003)
*Aestuacrida** gen. nov.	
	*stereofemoris** sp. nov.
Orichalcum Whalley, 1985	
	ornatum Whalley, 1985
Parapleurites Brauer et al., 1889	
	gracilis Brauer et al., 1889
	sibiricus Sharov, 1968
	*brasiliensis** sp. nov.
Schwinzia Zessin, 1983	
	*anatolica** comb. nov. (Sharov, 1968)
	sola Zessin, 1983
Zessinia Martins-Neto, 1990	

	borealis Gorochov et al., 2006
	pulcherrima Martins-Neto, 1990
	reticulata Martins-Neto, 1990
Zeunerella Sharov, 1968	
	*amedegnatoi** comb. nov. (Martins-Neto, 1998)
	arborea Sharov, 1968
	mecklenburgica (Zessin, 1983)
	*neotropica** comb. nov. (Martins-Neto, 1998)
	prior Gorochov et al., 2006
Locustrix Martins-Neto, 2003	
	audax Martins-Neto, 2003
	gallegoi Martins-Neto, 2003
Pseudoacrida Lin, 1982	
	costata Lin, 1982
	sennlaubi Nel & Jouault, 2022

6. Conclusions

This study significantly expands the known diversity of Locustopsidae from the Early Cretaceous Crato Formation, Brazil, through the description of one new genus and four new species. These taxa contribute to a better understanding of the morphological variability and evolutionary differentiation within the family, particularly in terms of forewing venation patterns—currently the primary diagnostic basis for genus-level taxonomy in Locustopsidae.

In addition to the new taxa, we provide a taxonomic revision of several genera previously assigned to Locustopsidae. This includes the synonymizing of *Cratozeunerella* with *Zeunerella*, and *Plesioschwinzia* with *Locustopsis*, as well as the reallocation of multiple species to more appropriate genera such as *Mesolocustopsis*, *Schwinzia*, *Cratolocustopsis*, and *Locustopsis*. Furthermore, we clarify the status of problematic taxa such as *Sinolocustopsis* and recommend the exclusion of *Liadolocusta* and *Locustopsites* from Locustopsidae based on insufficient or contradictory morphological evidence.

Taken together, our findings reinforce the Crato Formation as a hotspot for caeliferan diversity during the Early Cretaceous and demonstrate the importance of rigorous morphological re-evaluation in fossil Orthoptera. The taxonomic refinements proposed herein lay the groundwork for future phylogenetic analyses of Locustopsidae and underscore the need for continued investigation of underexplored fossil insect assemblages in South America.

Acknowledgements

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Further thanks to Dr. Robert A. Coram (University of Bristol) for sending a copy of his work on *Plesioschwinzia sharovi*, the reading of which greatly helped in writing the present study.

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Chapter 5

New species of Locustopsidae (Orthoptera: Caelifera) from the Crato Formation including a new subfamily Pseudoacridinae subfam. nov.

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Abstract

Three new species, a new genus, and a new subfamily of Locustopsidae Handlirsch, 1906 are described from the Early Cretaceous Crato Formation of Brazil. *Pseudoacrida eumastacoimima* sp. nov. represents the third global record of the genus and the second species named from the Crato Formation, following *P. sennlaubi* Nel & Jouault, 2022. The head morphology of *P. eumastacoimima* sp. nov. resembles that of members of Eumastacoidea. A newly discovered specimen of *P. sennlaubi* is also presented herein, providing additional morphological data beyond the two previously known forewings, including preserved body structures that enhance our understanding of the species. A new genus, *Auroralocusta* gen. nov., is described from the formation. *Auroralocusta restituta* gen et sp. nov. shares with *Pseudoacrida* the diagnostic feature of CuA + CuPaα branch that continues beyond its fusion with CuPaβ. However, it differs by possessing only two branches of M, whereas *Pseudoacrida* has three. Based on these differences and shared features, a new subfamily, Pseudoacridinae subfam. nov., is proposed to house *Pseudoacrida* and *Auroralocusta* gen. nov. Lastly, a new species of *Mesolocustopsis* Hong & Wang, 1990 is described as *Mesolocustopsis levis* sp. nov., further expanding the locustopsid diversity of the Crato Formation. With the inclusion of these new taxa, the known diversity of Locustopsidae from the formation now comprises 26 species distributed across eleven genera. A comparative analysis of Locustopsidae diversity from the Crato Formation, the Lower Jurassic of Germany, and the Lower Cretaceous of UK suggests that the Crato Formation represents a major hotspot of locustopsid evolution, with a greater number of taxa recorded than from any other locality worldwide.

Keywords: *Pseudoacrida*, *Auroralocusta*, *Mesolocustopsis*, Crato Formation, diversity

1. Introduction

Locustopsidae Handlirsch, 1906 is an extinct family of short-horned grasshoppers (Caelifera) known from the Triassic of England, the Jurassic of Laurasia, and the Cretaceous of Laurasia, South America, and Africa (Ansorge, 1991; Gorochov et al., 2006; Gorochov & Coram, 2023; Martins-Neto, 2003; Smith et al., 2011; Zessin, 1983). The apomorphies originally proposed by Handlirsch (1906)–such as M with two branches, CuA + CuPaα with one or two branches and a long ScP–are no longer applicable to the entire diversity of taxa currently assigned to the family. For instance, the number of M branches varies from one in *Araripelocusta* Martins-Neto, 1995, to two in *Cratolocustopsis* Martins-Neto, 2003, and up to three in *Locustopsis* Handlirsch, 1906. Similarly, CuA + CuPaα may present from one to four branches (Schall et al., 2025a). Despite these inconsistencies regarding family-level synapomorphies, the apomorphies of most genera within Locustopsidae are relatively well understood and provide a robust basis for taxonomic assignment at the generic level.

Locustopsidae currently comprises two subfamilies (Cigliano et al., 2025). Locustopsinae Handlirsch, 1906 includes the majority of genera within the family, notably *Locustopsis*, which alone accounts for nearly half of the described species (35 out of 73; Schall et al., 2025a). Genera assigned to Locustopsinae typically exhibit two or three branches of M and two or three branches of CuA + CuPaα. In contrast, Araripelocustinae Martins-Neto, 1995 includes only two genera, which are characterized by a reduced venation pattern: a single branch of M and one or two branches of CuA + CuPaα.

Five genera within Locustopsidae remain unassigned to a subfamily. *Liadolocusta* Handlirsch, 1906 is based solely on a single foreleg and may warrant consideration as a *nomen nudum*. *Locustopsites* Théobald, 1937 has been suggested to belong to Tettigoniidae rather than Locustopsidae (Schall et al., 2025a). *Locustrix* Martins-Neto, 2003 is characterized by two branches of M and a single branch of CuA + CuPaα (Martins-Neto, 2003). *Pseudoacrida* Lin, 1982 is currently known by two species: *Pseudoacrida costata* Lin, 1982 from the Early Cretaceous of China, and *P. sennlaubi* Nel & Jouault, 2022 from the Early Cretaceous Crato Formation of Brazil. Although *Pseudoacrida* shares some venational features with *Mesolocustopsis* Hong & Wang, 1990 (Locustopsinae)–notably three branches of M and one of CuA + CuPaα– it can be distinguished from all other Locustopsidae by the unique extension of its CuA + CuPaα beyond its fusion with CuPaβ, towards the wing base (Nel & Jouault, 2022).

Aestuacrida Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025 has two branches of M and four of CuA + CuPaα. However, the basal origin of CuA + CuPaα remains unknown in the type species, preventing formal assignment of the genus to any existing subfamily.

In this study, we described three new species of Locustopsidae from the Crato Formation, including one new genus and a newly established subfamily. The fossil record Locustopsidae in the Crato deposits are remarkedly diverse, representing one of the richest assemblages of the family globally. This diversity surpasses or rivals that observed in other well-sampled localities, such as the Lower Jurassic of Germany and the Lower Cretaceous of the UK (Cigliano et al., 2025; Gorochov et al., 2006; Gorochov & Coram, 2023; Mendes et al., 2019; de Moura-Júnior et al., 2018; Nel & Jouault, 2022; Zessin, 1983). A comparative analysis of Locustopsidae diversity across these regions will be presented and discussed in detail.

2. Geological Setting

Fig. 1

The Araripe Basin is located at the confluence of the states of Ceará, Pernambuco, Piauí and Paraíba in Northeastern Brazil, with an area of about 12000 km^2 (Carvalho et al., 2012). This basin lies over Precambrian terrains of the Transversal Fold Zone of Borborema Province, northwards of Pernambuco lineament and southwards of Patos lineament (Assine, 1992). These lineaments would have controlled the installation of the basin, which began to form during the opening of the Brazilian Atlantic margin (Fambrini et al., 2019; Ponte & Ponte Filho, 1996).

Structurally, the Araripe Basin is organized into megasequences classified as Pre-Rift, Syn-Rift, and Post-Rift (Assine et al., 2014). The Pre-Rift consists of continental siliciclastic units deposited during the Jurassic, while the Syn-Rift phase is characterized by lacustrine and alluvial settings (Berriasian–Early Aptian). The Post-Rift megasequence is divided into two tectonic events: (1) Post-Rift I (Aptian–Early Albian) and (2) Post-Rift II (Albian–Cenomanian), with fluvial deposits (Assine et al., 2014).

The Crato Formation is part of the Santana Group. This group comprehends the Post-Rift I megasequence, which records a mixed siliciclastic-carbonate-evaporite succession (Santos et

al., 2017; Nascimento Jr et al., 2016). The Santana Group is represented from base to top by the Barbalha, Crato, Ipubi, and Romualdo formations, which correspond to the apex of the thermal subsidence of the Araripe Basin during the Cretaceous (Assine et al., 2014). This depositional sequence is formed at base by fluvial and lacustrine deposits of the Barbalha Formation followed by the highstand Crato Formation and culminates in the evaporites of the Ipubi Formation (Assine et al., 2014).

The Crato Formation represents a 60-m-thick succession and is composed of metric-scale laminated carbonate units interfingered with siliciclastic sediments (Santos et al., 2017). This unit contains six informal limestone layers (C1–C6) (Neumann, 1999; Neumann et al., 2003). Much of the C6 layer, at the top of the formation, is exposed in quarries near Nova Olinda and Santana do Cariri, Ceará (Nascimento Jr et al., 2023). The quarry fronts exhibit a tabular unit of micritic limestones, approximately 10 m thick, which are commercially excavated as "Pedra Cariri" for use as a building material in civil construction (Fig. 1). The finely laminated rhythmic carbonates of the Crato Formation were originally interpreted as having been deposited in a non-marine setting, probably in a saline lacustrine environment close to marine environments (Heimhofer et al., 2010; Catto et al., 2016). The age of the Crato Formation has been estimated from different methods (e. g. isotope-analysis, ostracod and palynomorph assemblages, microfossil data) (Arai, 2014; Arai & Assine, 2020; Coimbra et al., 2002; Coimbra & Freire, 2021; Heimhofer & Hochuli, 2010; Lúcio et al., 2020; Melo et al., 2020). Although it is not possible to constrain the exact age, the Crato strata encompassing the Late Barremian and Early Albian or ca. 122–113 mya (Bezerra & Mendes, 2024).

The Crato Formation yields an important Gondwanan Konservat-Lagerstätte, due to its well-preserved fossil content (Nascimento Jr et al., 2023). This fossil assemblage includes arthropods (i.e., insects, ostracods, crustaceans, and arachnids), fishes, chelonids, pterosaurs, crocodilians, fungi, gymnosperms, and angiosperms (Mendes et al., 2020). The Crato biota is almost exclusively recorded in layer C6. However, the exact level within layer C6 is rarely known because fossil specimens are collected by quarry workers, who do not report the position of the individuals. As a rare attempt to understand the stratigraphic position of fossils within the Crato Lagerstätte, Corecco et al. (2022) identified that most insects are recovered from the uppermost portion of the C6 layer in Nova Olinda. The insect fossils in this interval are mostly preserved as pyrite (iron sulfide) replacements that were later weathered to more stable oxides/hydroxides (goethite and hematite) (Alberto et al., 2023; Bezerra et al., 2023).

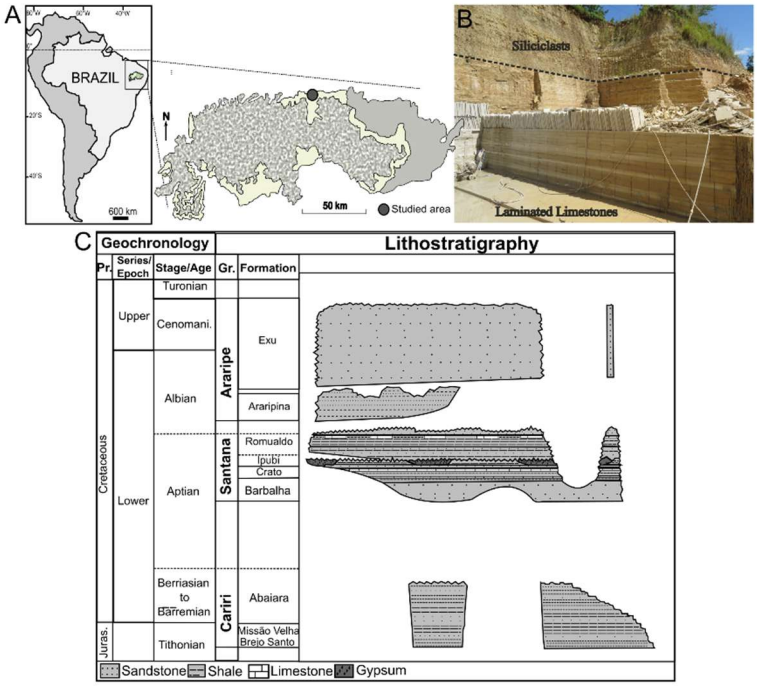

Fig. 1: Location of the studied area. **A.** Simplified map of the Araripe Basin with the position of the basin in Northeastern Brazil. **B.** Geological section exposed in a quarry near Nova Olinda, Ceará state. **C.** Chronostratigraphic chart of the Araripe Basin (adapted from Assine, 2007).

3. Materials and methods

Specimens presented in this study are housed in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil [collection numbers MPSC 9835 (ex Husemann Research Collection, Staatliches Museum für Natrukunde Karlsruhe, Germany, coll. no. HC0045); MPSC 9836 (ex-collection Museum der Natur – Paläontologie/Geologie, Hamburg, Germany, coll. no. CNBS00420); MPSC 9837 (ex Husemann Research Collection, Staatliches Museum für Natrukunde Karlsruhe, Germany, coll. no. HC0046)]. They were donated to their Brazilian home as part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future". A fourth non-type specimen featured in this study is housed in the collection of Museum der Natur – Paläontologie/Geologie, Hamburg, Germany, coll. no. CNBS_00416.

Imaging of the specimens was done using a Keyence VHX-6000 digital microscope (KEYENCE Corporation, 2025, Osaka, Japan; https://www.keyence.com/). All images are composite images assembled via the stitching method. Drawings of the specimens were created in GIMP (v. 3.0.2-1) (the GIMP Team, 2025; https://www.gimp.org/). Figures were assembled and modified (scale bars and labelling) in Inkscape (v. 1.4.2) (Moini et al., 2025;

https://inkscape.org/). The diagram in Fig. 6 was created in Microsoft Excel (Microsoft, 2025; https://www.microsoft.com).

The taxonomy in this study follows the Orthoptera species file (Cigliano et al., 2025; https://orthoptera.speciesfile.org/). Wing venation nomenclature follows Béthoux & Nel (2002) with abbreviations: CP = posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

4. Systematic palaeontology

Order Orthoptera Latreille, 1810

Suborder Caelifera Ander, 1936

Family Locustopsidae Handlirsch, 1906

Subfamily **Pseudoacridinae** subfam. nov.

Type genus: *Pseudoacrida* Lin, 1982.

Included genera: *Auroralocusta* gen. nov.; *Pseudoacrida* Lin, 1982.

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: After the type genus *Pseudoacrida* Lin, 1982.

Diagnosis of subfamily: General forewing morphology as in Locustopsinae Handlirsch, 1906 or Araripelocustinae Martins-Neto, 1995, but with main branch of CuA + CuPaα continuing beyond the fusion to CuPaβ and terminating much closer to wing base than in any other Locustopsidae.

Remarks: Pseudoacridinae differs from Locustopsinae and Araripelocustinae in its CuA + CuPaα continuing beyond the fusion to CuPaβ and terminating much further towards the wing base than in the latter two subfamilies. In Locustopsinae and Araripelocustinae CuA + CuPaα

ends in the fusion to CuPaβ. The currently described genera of Pseudoacridinae have three (*Pseudoacrida*) or two (*Auroralocusta* gen. nov.) branches of M and one branch of CuA + CuPaα. Yet, knowing the many combinations of M and CuA + CuPaα branches present especially in Locustopsinae it is possible that branch numbers also varied substantially in Pseudoacridinae. Thus, for now the only apomorphy is the continuation of CuA + CuPaα.

Genus ***Auroralocusta*** new genus

Type species: *Auroralocusta restituta* sp. nov. by monotypy and present designation. Gender feminine.

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The genus' name comes from the Latin word "aurora" for dawn.

Diagnosis: As for the type species by monotypy.

Remarks: Auroralocusta differs from all other genera of Locustopsidae except *Pseudoacrida* by its CuA + CuPaα continuing beyond the fusion with CuPaβ until proximal to wing base. It differs from *Pseudoacrida* by having just two branches of M whereas the latter genus has three M-branches.

Auroralocusta restituta sp. nov.

Fig. 2

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The specific epithet *restituta* is derived from the Latin verb *restituere*, meaning "to restore, to give back, to reinstate." The feminine singular participle *restituta* translates as "restored" or "returned." The name refers to the repatriation of the type specimen, which had been removed from Brazil and later returned through a scientific cooperation agreement between Brazil and Germany. Thus, the epithet honors the act of restitution and the restoration of the fossil to its homeland.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype female in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9835.

Diagnosis: Forewing length 25.1 mm, 4.4 mm wide. Body length 19.7 mm. M of the forewing with two branches. CuA + CuPaα with one branch that continues beyond its fusion with CuPaβ and is fused to M/RA close to wing base. ScA prominent with 12+ branches. ScP fused to RA at 89.4% of total forewing length. RP with four branches. Ovipositor of the female with broad valvulae that show serration.

Description: Entire body except legs and antennae as well as wings preserved. Parts of mesothoracic (?) leg somewhat visible.

Measurements: Eye height 1.2 mm, interocular distance 0.85 mm. Body length 19.7 mm. Ovipositor 3.4 mm. Forewing length 25.1 mm, 4.4 mm wide.

Body: Body features mostly described under measurements. Abdomen with tergites covering 80% of abdomen hight. Ovipositor 3.4 mm long with two valvulae visible, the outer of which is serrated. Ovipositor with some resemblance to other Caelifera, e.g., *Anacridium aegyptium* (Linnaeus, 1764).

Forewing: Length/width-ratio 5.7. ScA reaching anterior margin at 43.8% of total wing length; fairly broad and with 12+ branches. ScP much narrower and without cross veins, not connected to wing margin but fused to RA at 89.4% of wing length. Space between ScP and RA 9.1% of total wing height. Space between RA and RP 9.1% of wing height (measured below RP4). RP with four branches. RP1 distinctly curved upwards, path parallel to other RP-branches. Origin of RP at 45.6% of wing length, slightly anterior of M-fork. M with two branches, both very much parallel to RP branches. CuA + CuPaα one-branched, slightly concave, but mostly parallel to M and RP, too. Base of CuA + CuPaα fused to M close to wing base. CuPaβ and CuPb both long and narrow, exact path distally unsure. Cross vein pattern of the forewing consisting mainly of straight veins with a more complex pattern of net cells and intermediary branches between M and especially RP.

Remarks: This species' ovipositor may allow for hypotheses regarding the habitat used for egg laying. However, the knowledge of Caelifera ovipositor morphology in connection to egg laying substrate is limited (opposed to the Ensifera, where it is better studied (Barbosa and Fianco, 2024)) and no conclusions can be derived at this point.

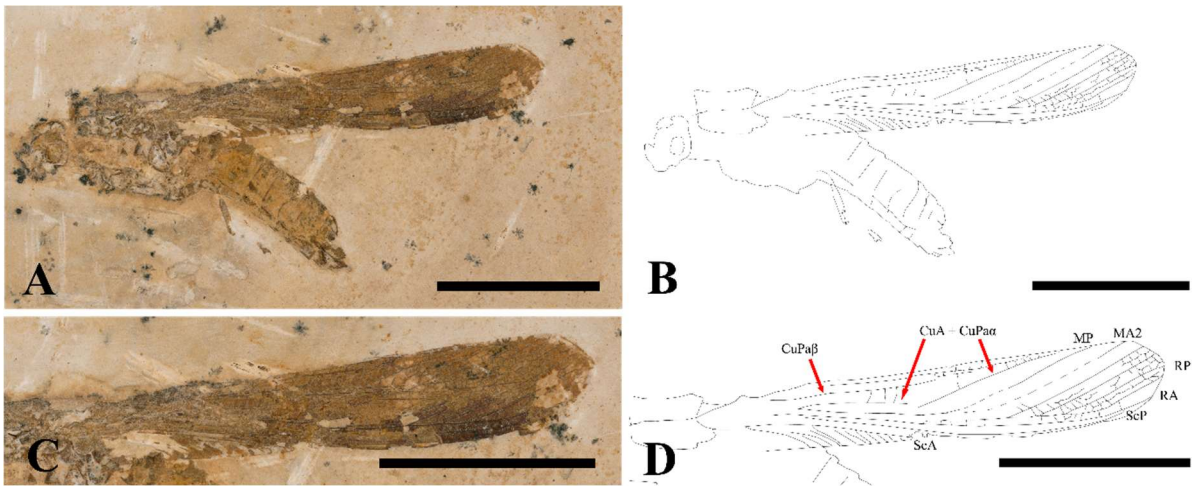

Fig. 2: *Auroralocusta restituta* gen. et sp. nov. holotype female, coll. no. MPSC 9835. **A.** and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of wings. **Scale bars** = 10 mm.

Genus *Pseudoacrida* Lin, 1982

Included species: *P. costata* Lin, 1982 (type species); *P. sennlaubi* Nel & Jouault, 2022; *P. eumastacoimima* sp. nov.

Pseudoacrida eumastacoimima new species

Fig. 3

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The species' name derives from its characteristic head shape with an oblique face and eye. It reminds of some extant members of Pyrgomorphidae Brunner von Wattenwyl, 1874, such as the Malagasy *Ambositracris ornata* Dirsh, 1963 and Eumastacoidea Burr, 1899, for example the Middle American *Episactus brunneri* Burr, 1899.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype male in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9836.

Diagnosis: Head elongated, eye ellipsoid in shape, reminding of Eumastacoidea. Forewing 22.3 mm long (in *P. sennlaubi* the forewing is 36-37 mm long), 3.9 mm wide (length/width-ratio 5.7). Branches of RP parallel to MA1 and MA2. MP slightly concave, rather parallel to CuA + CuPaα. CuA + CuPaα does not reach wing margin but stops at CuPaβ.

Description: Body and wings well preserved. Antennae and legs missing, except for fragmental metathoracic (?) tarsus.

Measurements: Forewing 22.3 mm long, 3.9 mm wide. Body length 19.5 mm. Head height 5.2 mm. Eye height 1.9 mm, width 1.0 mm.

Body: Head very oblique, conical in shape. Compound eye oblique too, ellipsoid in shape. Metabasitarsus (?) with lobulate spurs.

Forewing: Length/width-ratio 5.7. ScP very narrow, length at least 87.4% of total wing length. Space between ScP and RA 11.8% of total wing height. Space between RA and RP rather narrow, 7.9% of wing height. Origin of RP at 43.7% of wing length, proximal to furcation of MP and anterior to bifurcation of MA-branches. RP with 4 branches. M with three branches. Branches of RP parallel to MA1 and MA2. MP slightly concave. CuA + CuPaα with one branch, slightly concave and rather parallel to MP. CuA + CuPaα does not reach anal wing margin but stops at reaching CuPaβ. Base of CuA + CuPaα at 31.8% of wing length. CuPaα oblique. CuA + CuPaα continuing beyond fusion with CuPaβ as CuA and reaching M or RA proximal of wing base. CuPaβ, CuPb and 1A all long and narrow, especially former two with CuPaβ stretching until at least 73.3% of wing length. Cross vein pattern rather complex (as typical for this genus) with straight cross venation found only in proximal half of forewing. Cross vein pattern in distal half consisting of complex net-pattern and intermediary branches.

Remarks: Pseudoacrida eumastacoimima sp. nov. differs from *P. sennlaubi*, the only other species of the genus known from the Crato Formation, by its significantly smaller size (forewing length: 22 mm vs. 36–37 mm in *P. sennlaubi*). In addition, the characteristic eumastacoid-like head shape morphology observed in the new species is of uncertain presence in *P. sennlaubi*. A newly identified specimen (CNBS00416, Fig. 4), here assigned to *P. sennlaubi* based on forewing venation patterns congruent with the holotype, provides partial insight into head morphology of the species. Although the head is incompletely preserved, its general outline appears to resemble that of modern Acrididae MacLeay, 1821 more than that of Eumastacoidea or Pyrgomophidae, suggesting that the eumastocoid-like condition may be absent in *P. sennlaubi*. It is important to note that CNBS00416 is not part of the type series of *P. sennlaubi*, but is presented herein to augment the morphological understanding of the species, whose holotype is based solely on isolated wings (Nel & Jouault, 2022). *Pseudoacrida eumastacoimima* sp. nov. also differs from its Early Cretaceous Chinese congener, *P. costata* Lin, 1982, by the proportionally broader area between CuA + CuPaα and CuPaβ. This condition is shared with *P. sennlaubi*, in which the same respective area is similarly expanded (Nel & Jouault, 2022), potentially representing a synapomorphy uniting the Crato species.

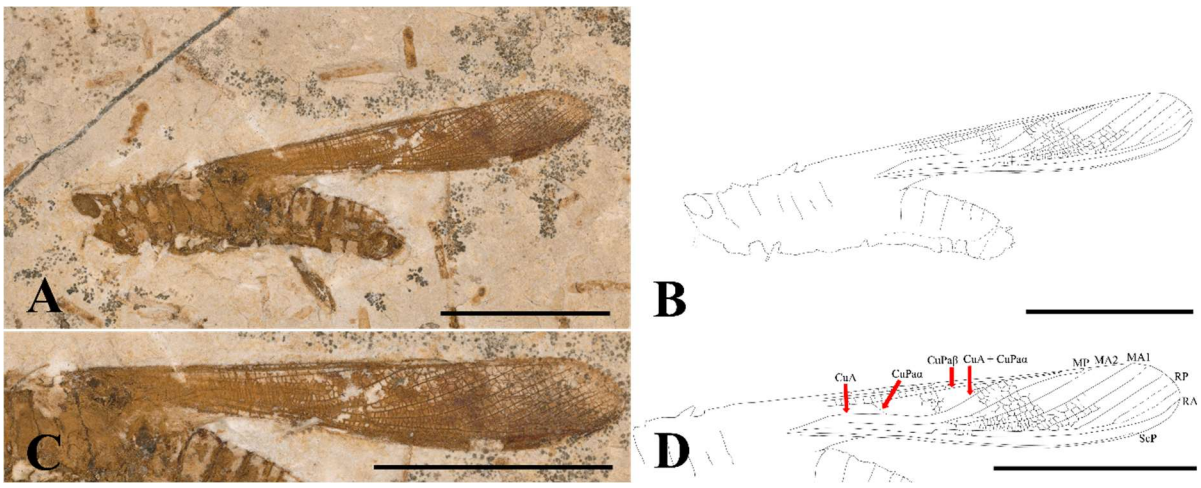

Fig. 3: *Pseudoacrida eumastacoimima* sp. nov. holotype male, coll. no. MPSC 9836. **A**. and **B.** Image and drawing of complete specimen. **C.** and **D.** Image and drawing of wings. **Scale bars** = 10 mm.

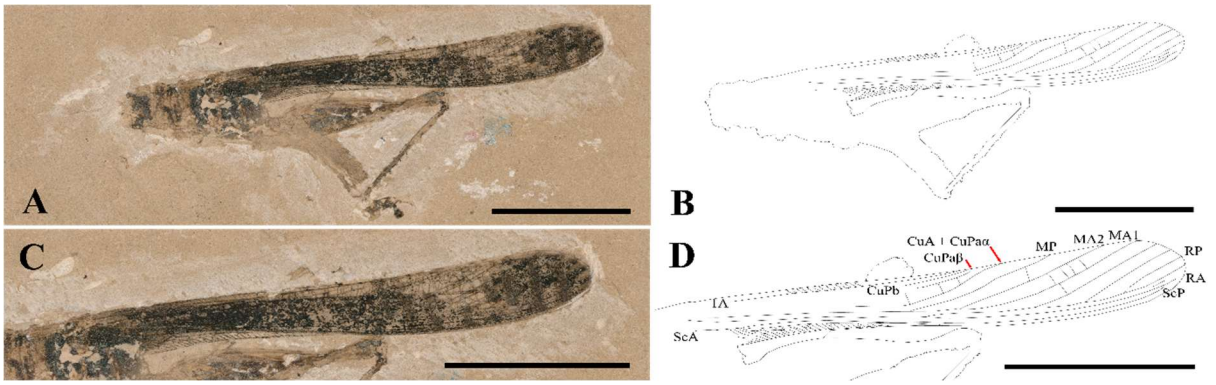

Fig. 4: *Pseudoacrida sennlaubi* Nel & Jouault, 2022, not type specimen CNBS_00416. **A.** and **B.** Image and drawing of complete specimen. **C**. and **D.** Image and drawing of wings. **Scale bars** = 10 mm.

Subfamily Locustopsinae Handlirsch, 1906

Genus *Mesolocustopsis* Hong & Wang, 1990

Included species: *M. sinica* Hong & Wang, 1990 (type species); *M. anglica* Gorochov et al., 2006; *M. angusta* Gorochov et al., 2006; *M. araripensis* (Martins-Neto, 1990); *M. caririensis* Martins-Neto, 1990; *M. morrisonensis* (Smith et al., 2011); *M. problematica* Gorochov et al., 2006; *M. vikingi* (Martins-Neto, 2003); *M. levis* sp. nov.

Mesolocustopsis levis new species

Fig. 5

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The specific name is derived from the Latin word “levis” meaning “smooth” or “polished”. It refers to the unserrated ovipositor of this species, that is longer, narrower, and smooth compared to the broader, shorter, and serrated ovipositor of other Crato locustopsids like *Auroralocusta restituta* (see above).

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Type material: Holotype female in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9837.

Diagnosis: Head rather high, 7.3 mm. Forewing length 30.5 mm, 4.9 mm high. Tegminal RP with two branches. Ovipositor with valvulae rather narrow and elongated, non-serrated.

Description: Wings and full body preserved, except antennae and legs.

Measurements: Head height 7.3 mm. Body length 24.6 mm (without ovipositor). Ovipositor length 4.8mm. Forewing length 30.5 mm, 4.9 mm high.

Body: Head conical. Abdomen with seven to eight tergites/sternites. Cercus one-segmented, 1.8 mm long, non-setulose. Ovipositor rather narrow and elongated, somewhat reminiscent of a knives' blade.

Forewing: Length/width-ratio 6.2. ScP long and narrow, fused to RA after 88.6% of total wing length. Width between ScP and RA 11.8% of total wing height (measured below RP origin). Width between RA and RP narrow, 5.4% of wing height (measured below RP2). RA and RP1 curved upwards. Origin of RP at 70.2% of wing length, posterior to furcation of MP and MA2, shortly anterior to MA1. RP with two branches. M with three branches, parallel to RP. MA2 in direct contact to MA1. M closing in on RA at 47.8% of wing length. CuA + CuPaα with one branch, parallel to M and RP. Base of CuA + CuPaα at 42.4% of wing length. CuA + CuPaα reaching posterior wing margin at 77.6% of wing length. CuPaβ reaching posterior margin at 69.8%. CuPaβ almost parallel to CuA + CuPaα (and M and RP) with subtle concave turning distally. CuPb apparently reaching wing margin at 51% of wing length. 1A not discernible. Cross vein pattern mostly simple, with straight evenly spaced cross veins; becoming more complex into net-pattern with intermediary branches between MA2, MA1 and branches of RP.

Remarks: Mesolocustopsis levis sp. nov. can be differentiated from all known congeners by the combination of a relatively large forewing (30.5 mm length) and a reduced branching pattern of RP, which exhibits only two branches. This character state contrasts with other species of the genus possessing forewings of comparable or greater length, e.g., *M. vikingi* (Martins-Neto, 2003) and *M. caririensis* (Martins-Neto, 1990), both of which exhibit five RP branches. The

reduced number of RP branches in *M. levis* sp. nov. may therefore represent a derived condition within the genus, independent of overall wing size.

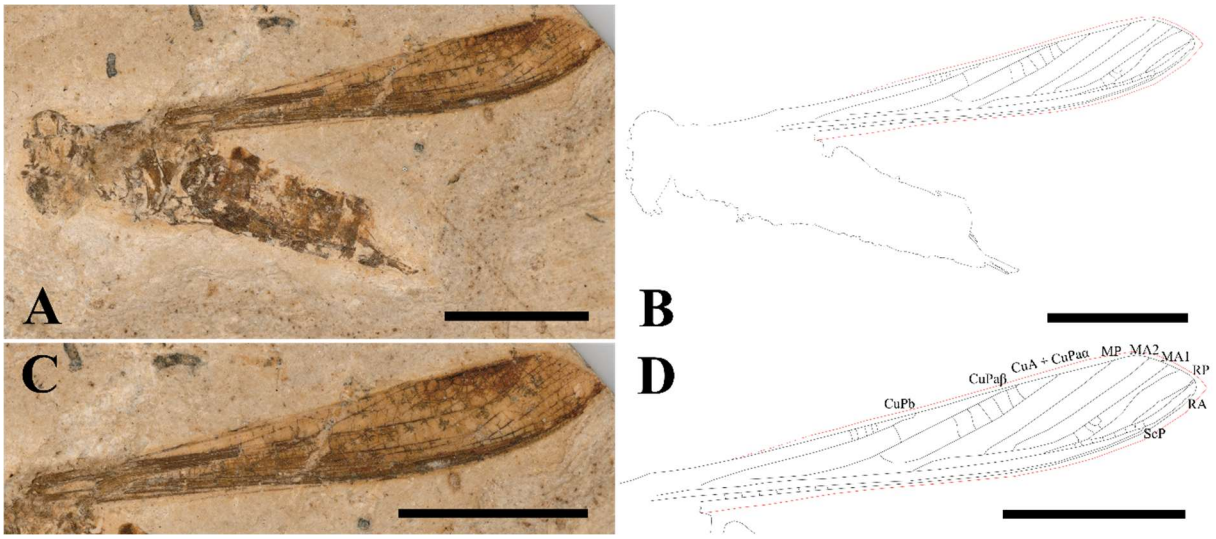

Fig. 5: *Mesolocustopsis levis* sp. nov. holotype female, coll. no. MPSC 9837. **A**. and **B.** Image and drawing of complete specimen. **C**. and **D.** Image and drawing of wings. Red lines represent hind wing. **Scale bars** = 10 mm.

5. Discussion

In this study, we described three new species of Locustopsidae Handlirsch, 1906 from the Early Cretaceous Crato Formation of northeastern Brazil. Among them, *Auroralocusta restituta* gen. et sp. nov., is assigned to a new genus within the newly proposed subfamily Pseudoacridinae subfam. nov., which is diagnosed by the extension of CuA + CuPaα beyond its fusion with CuPaβ, terminating much closer to the wing base than in any other known genus of Locustopsidae. The other two species, *Mesolocustopsis levis* sp. nov. and *Pseudoacrida eumastacoimima* sp. nov., further expand the known morphological and taxonomic diversity of Locustopsidae in the Crato Formation.

Diversity of Locustopsidae in the Crato Formation

Fig. 6

In a recent overview of Locustopsidae (Schall et al., 2025a), we compiled a comprehensive table summarizing all formally known species of the family, along with and their respective

geographic and stratigraphic distributions. Three fossil sites stand out for their substantial contributions to locustopsid diversity: the Lower Cretaceous of England (Gorochov et al., 2006), the Lower Jurassic of Germany (Handlirsch, 1906; Zessin, 1983), and the Aptian-aged Crato Formation of Brazil (Martins-Neto, 2003).

With the addition of the two new genera and seven new species described across our current and previous studies (Schall et al., 2025a), and in light of recent taxonomic revisions, the Crato Formation now harbors the highest known diversity of Locustopsidae worldwide (Fig. 6). A total, of 26 species assigned to 11 genera are currently known from this unit. Notably, the Crato Formation is the only locality where representatives of all three subfamilies–Araripelocustinae Martins-Neto, 1995, Locustopsinae Handlirsch, 1906, and the newly proposed Pseudoacridinae–co-occur.

In contrast, the Lower Jurassic of Germany yield 16 species but only three genera: *Locustopsis* Handlirsch, 1906, *Schwinzia* Zessin, 1983, and *Cratolocustopsis* Martins-Neto, 2003) (Schall et al., 2025a; Zessin, 1983). The Lower Cretaceous of England, while more diverse at the generic level (five genera), contains comparatively fewer species, with only seven formally described to date (Gorochov et al., 2006).

The remarkable diversity and morphological disparity of Locustopsidae in the Crato Formation underscore its paleontological significance as a key locality for understanding evolutionary dynamics of early Acrididea. The co-occurrence of multiple lineages, including highly derived and morphologically divergent forms, suggests that this paleoenvironment may have represented a center of diversification for the group during the Early Cretaceous.

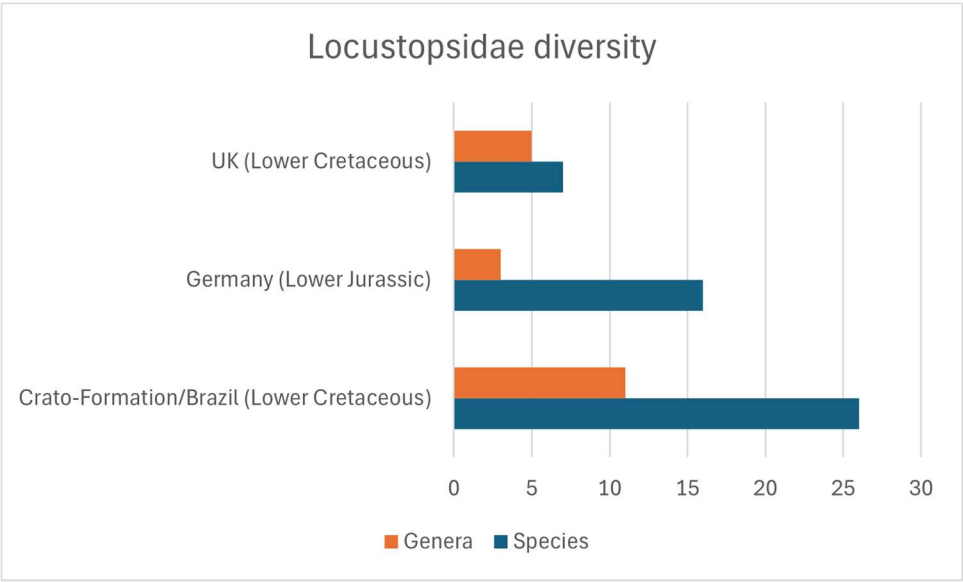

Fig. 6: Locustopsidae Handlirsch, 1906 diversity in different fossil sites. The highest number of genera and species were found in the Early Cretaceous Crato Formation of Brazil (11 genera

and 26 species), followed by the Lower Cretaceous of England in case of genera (5) and the Lower Jurassic of Germany in case of species (16).

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Chapter 6

First Eumastacoidea and new Locustopsidae (Orthoptera: Caelifera) from the Crato Formation of Brazil

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Abstract

The first genus and species of Eumastacoidea Burr, 1899 is described from the Early Cretaceous Crato Formation of northeastern Brazil. *Cratomastax mariellaae* gen. et sp. nov. is reported from a relatively well-preserved specimen with wing, head, and metathoracic leg aspects in good condition. It is assigned to the Eumastacoidea based on its forewing venation feature of M and CuA + CuPaα being fused. Due to its two branches of M + CuA it could be assigned to Chorotypidae Stål, 1873, but the forewing venation of other families of Eumastacoidea is not sufficiently known to confidently exclude it from these taxa. *Cratomastax mariellaae* gen. et sp. nov. is evidence that Eumastacoidea were present in the fauna of the Crato Formation. Additionally, a second species of *Aestuacrida* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, *submitted* (chapter 4) is described from the Crato Formation. *Aestuacrida mikronaulion* sp. nov. is significantly bigger than *A. stereofemoris* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, *submitted* (chapter 4) and its wing venation is more fully preserved. The new species suggests *Aestuacrida* belongs to the subfamily Pseudoacridinae Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, chapter 5 increasing the diversity of this recently established taxon. Lastly, we report a new specimen of *Locustrix gallegoi* Martins-Neto, 2003. Individuals of this genus seem to be rather rare and the apomorphies of *Locustrix* Martins-Neto, 2003 were not well understood. The new specimen helps to resolve this issue. *Locustrix* can now be assigned to the *Locustopsinae* Handlirsch, 1906. It is characterized by having two branches of M and CuA + CuPaα and a short ScP of only about 50% of total forewing length.

Keywords: Caelifera, Crato Formation, *Cratomastax, Locustrix, Aestuacrida, Pseudoacridinae*

1. Introduction

With over 29,000 extant species, Orthoptera Olivier, 1789 are the most diverse order of Polyneoptera insects (Cigliano et al., 2025). The order is traditionally divided into two major suborders: Ensifera Chopard, 1921– encompassing katydids, bush-crickets, and true crickets– and Caelifera Ander, 1936, which includes short-horned grasshoppers and locusts. Both lineages have a deep evolutionary history, with definite fossil representatives of each suborder having been reported from the Late Permian (255.7 Ma) (Riek, 1976; Béthoux et al., 2002).

During the Mesozoic (251.9–66 Ma), one of the most distinctive caeliferan families was Locustopsidae Handlirsch, 1906. These orthopterans resemble several morphological traits reminiscent of the extant Acridoidea Macleay, 1821, particularly in wing venation and general body shape and proportions. Locustopsidae are known from multiple fossiliferous formations worldwide, with notable occurrences in Lower Jurassic and Lower Cretaceous deposits of Europe–particularly the UK (Brodie, 1845; Cockerell, 1916; Gorochov et al., 2006; Handlirsch, 1939; Whalley, 1985; Zeuner, 1942) and Germany (Bode, 1953; Geinitz, 1880; Handlirsch, 1906; 1939; Zessin, 1983)

Among these, the Lower Cretaceous Crato Formation of northeastern Brazil stands out for its exceptional preservation and taxonomic richness. Recent studies have revealed a remarkable diversity of Locustopsidae in this Konservat-Lagerstatte, with more than twice the number of genera described from this single locality compared to any other known site worldwide (Martins-Neto, 1995; 1998; 2003; Nel and Jouault, 2022; Schall et al., chapter 5). Remarkably, representatives of all three subfamilies currently recognized within the family occur exclusively in the Crato assemblage (Schall et al., chapter 5).

Locustopsidae are mainly characterized by their forewing venation, i.e., the number of branches of CuA + CuPaα and M. Genera within Araripelocustinae Martins-Neto, 1995 are distinguished by a simplified venation pattern, displaying a single branch of M and one to two branches of CuA + CuPaα (Gorochov et al., 2006). In contrast, Locustopsinae Handlirsch, 1906–the most speciose subfamily–typically exhibit two to three branches of M and one to three branches of CuA + CuPaα. The most recently established subfamily, Pseudoacridinae Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, chapter 5 is characterized by a CuA + CuPaα that extends significantly beyond its point of fusion with CuPaβ and terminates markedly closer to the wing base than in any other locustopsid.

Among extant Caelifera, the second most diverse superfamily after Acridoidea is Eumastacoidea Burr, 1899 (Cigliano et al., 2025). The fossil record of this group is dominated by isolated wing imprints, which can often be recognized by the characteristic fusion of M and CuA veins (Schubnel et al., 2020; Zessin, 2017). Nonetheless, a limited number of eumastocoid species with preserved body morphology have also been documented, primarily from amber. These specimens are generally wingless or brachypterous and may represent nymphal stages (Husemann et al., 2025; Perez-Gelabert, 1997).

The classification of fossil Eumastacoidea remains problematic duo to the reliance on detailed analysis of external and internal genitalia for extant taxa (Descamps, 1979; Rowell and Perez-Gelabert, 2006). As a result, most fossil identifications are tentative and based solely on wing venation. To date, fossil eumastacoids have been assigned to Episactidae Burr 1899 (Perez-Gelabert et al., 1997), Eumastacidae Burr 1899 (e.g. Zessin, 2017), and Chorotypidae Stål, 1873 (Schubnel et al., 2020). However, the venation of extant representatives remains poorly characterized, and many extant species are brachy- or apterous, further complicating comparison with fossil material.

Until now, no formal description of a eumastacoid from the Crato Formation had been published, although the possible existence of the group was previously hypothesized by Martins-Neto (1991). More recently, Husemann et al. (2025) speculated on the presence of Eumastacoidea in South American Gondwana, based on a brachypterous specimen recovered from Burmese amber–an ecosystem with proposed Gondwanan biogeographic affinities.

In this study, we formally describe the first confirmed Eumastacoidea from the Crato Formation. Additionally, we present a new species of Locustopsidae from this unit and report a new specimen of *Locustrix gallegoi* Martins-Neto, 2003, which contributes valuable morphological data toward refining the taxonomy of the genus.

2. Geological Setting

Fig. 1

The Mesozoic sedimentary succession of the Araripe Basin developed within the Borborema Province, interior of northeastern Brazil, by the reactivation of Neoproterozoic faults in response to the opening of the South Atlantic (Matos, 1992; Fig. 1). The Early Cretaceous transitional phase of this basin is represented by the Barbalha, Crato, Ipubi, and Romualdo formations that constitute the Santana Group (Assine et al., 2014). These units encompass a

mixed carbonate-evaporite-siliciclastic depositional system tract (Arai, 2014; Assine et al., 2016; Varejão et al., 2016).

The Crato-Formation is a 90-m-thick succession of interbedded limestone, shale, mudstone and sandstone, is one of the most-studied units of the Araripe Basin due to its fossil content (Santos et al., 2017; Nascimento Jr. et al., 2023). Crato strata are interpreted as a lacustrine system due to the presence of continental fauna, flora, and particular carbon and oxygen isotopic values (Heimhofer et al., 2010; Varejão et al., 2021). The Crato Formation contains abundant and exceptionally preserved fossils, making it one of the most important Cretaceous *Konservat-Lagerstätten* worldwide (Mendes et al., 2020). Fish, arthropods, turtles, pterosaurs, fungi, gymnosperms, and early flowering plants are found in the Crato biota (Mendes et al., 2020). Among these, insects are recognized as the best-preserved fossils and thrived in the margins of a lake (or several lakes) under frequent hypersaline and alkaline conditions (Bezerra and Mendes, 2024). Currently, there are two models of insect preservation in the Crato Formation: kerogenization and pyritization (Osés et al., 2016; Bezerra et al., 2018). Kerogenized insects consist of amorphous carbon while pyritized insects are preserved as oxyhydroxides after pyrite (Barling et al., 2020; Bezerra et al., 2021).

Paleontological works often solely referencing "limestones" of the Crato Formation without specifying the carbonate unit where the fossils are found. To address this, Corecco et al. (2022) adopted an informal nomenclature to specify the stratigraphic position of the fossils. In particular, the insects of the Crato Formation are collected in the uppermost portion of the laminated limestones, informally named "veio do besouro" (beetle vein). The absence of diagnostic microfossils or volcanic ash challenges the robust establishment of the age of this unit. Lúcio et al. (2020) proposed a late Barremian age for this interval based on isotopic analysis. However, a series of studies based on micropaleontological data converge in placing the Crato strata in the late Aptian-early Albian interval (Coimbra et al., 2002; Heimhofer and Hochuli, 2010; Arai, 2014; Coimbra and Freire, 2021). Arai and Assine (2020) and Melo et al. (2020), based on microfossil assemblages, consider placing the Crato Formation in the Late Aptian.

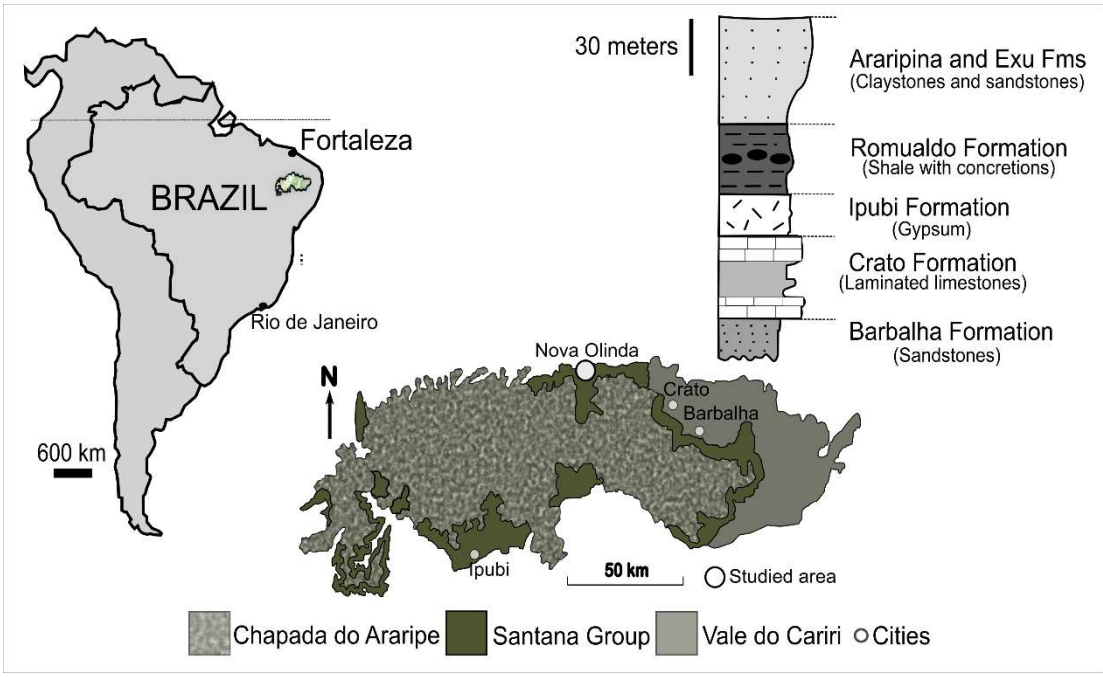

Fig. 1: Geologic map and location of the Araripe Basin in North-Eastern Brazil.

3. Materials and methods

Type specimens are deposited in the Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, collection numbers MPSC 9664 and MPSC 9665. A non-type specimen is part of the Husemann Research Collection, collection number MH_Fossil_0066.

Imaging of the specimens was done using a Keyence VHX-6000 digital microscope (MPSC 9664) and a Keyence VHX-7000 digital microscope (MPSC 9665; MH_Fossil_0066) (KEYENCE Corporation, 2024, Osaka, Japan; https://www.keyence.com/). All images are composite images assembled via the stitching method. Drawings of the specimens were created in GIMP (v. 3.0.2-1) (the GIMP Team, 2025; https://www.gimp.org/) by direct layer copying. Figures were assembled and modified (scale bars and labelling) in Inkscape (v. 1.4.2) (Moini et al., 2025; https://inkscape.org/).

The taxonomy in this study follows the Orthoptera species file (Cigliano et al., 2025; https://orthoptera.speciesfile.org/). Wing venation nomenclature follows Béthoux & Nel (2002) with abbreviations: CP posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

4. Systematic paleontology

Order Orthoptera Olivier, 1789

Suborder Caelifera Ander, 1936

Superfamily Eumastacoidea Burr, 1899

Genus ***Cratomastax*** new genus

Type species: *Cratomastax mariellaae* sp. nov. by monotypy and present designation. Gender feminine.

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The genus name is derived from the Crato Formation, type locality of the fossil, combined with “eumastax”, refering to its systematic position within Eumastacoidea.

Diagnosis: As for the type species by monotypy.

Remarks: Cratomastax gen. nov. is attributed to Eumastacoidea based on the fusion of M and CuA of the tegmina. Despite morphological similarities to *Paleochina duvergeri* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020 and *P. minuta* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020 from the Paleocene of France (compare species remarks), we refrain from assigning *Cratomastax* gen. nov. to Chorotypidae Stål, 1873 (the family of *Paleochina* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020) or to any other family within Eumastacoidea. The classification of fossil eumastacoids remains problematic due to limited availability of morphologic characters that define modern taxa. Extant Eumastacoidea are either organized based on molecular data (Matt et al., 2008) or detailed examination of the external and especially internal genitalia (Rowell and Perez-Gelabert, 2006)–features that rarely preserve in fossils. While external genitalia are occasionally visible (e.g., Husemann et al., 2025), this is not the case in *C. mariellaae* gen. et sp. nov. Although some modern Chorotypidae (e.g., *Erucius dimidiatipes* Bolívar, 1898) share a similar wing venation to *Paleochina* or *Cratomastax* gen. nov., the lack of information regarding the wing venation of the ancestors of many extant apterous or brachypterous genera across Eumastacoidea offers few chances for comparison to base phylogenetic relationships on. Because the wing venation of modern Eumastacoidea is almost unstudied, it cannot be considered a reliable character for family placement in the absence of further corroborating morphological data. From the other fossil genera of Eumastacoidea *Taphacris* Scudder, 1890 (Eocene of Colorado, USA and Cretaceous–Eocene of China) and *Eoerianthus* Gorochov, 2012

(Eocene of Colorado, USA), *Cratomastax* gen. nov. can be differentiated by the much narrower space between CuPaβ and CuPb. It further differs from *Eozaenhuepfer* Zessin, 2017 (Eocene of Denmark), which has a similarly narrow CuPaβ and CuPb space, by having one fewer branch of M (two in *E. erteboellei* Zessin, 2017) and one additional branch of RP (four in *E. erteboellei*). *Cratomastax* gen. nov. also differs from *Archaeomastax* Sharov, 1968 (Jurassic of Kazakhstan) in having a longer ScP and ScP fused to RA (instead reaching costal margin in *Archaeomastax*). This feature also distinguishes it from *Promastax* Handlirsch, 1910 (Eocene of British Columbia) and the problematic *Promastacoides* Kevan and Wighton, 1981 (Eocene of Alberta). From the two Eumastacoidea preserved in amber–*Paleomastacris* Perez-Gelabert, Hierro, Dominici & Otte, 1997 (Dominican amber, Miocene) and *Burmeumastax* Husemann, Schall, Uchida & Kotthoff, 2025 (Kachin amber, mid-Cretaecous)–*C. mariellae* gen. et sp. nov. differs by its much larger and fully developed wings (the single type species of *Paleomastacris* is apterous; the single type species of *Burmeumastax* is brachypterous (Perez-Gelabert et al., 1997; Husemann et al., 2025)).

Cratomastax mariellaae new species

Fig. 2

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The species is named in honor of Prof. Dr. Mariella Herberstein, currently Head of the Center for Taxonomy and Morphology at the Leibniz Institute for the Analysis of Biodiversity Change (LIB), Hamburg, Germany, in recognition of her kind support of the first author's dissertation work.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Holotype: Unsexed specimen in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9664. Donation from the Husemann Research Collection of Dr. Martin Husemann at the Public Museum of Natural History Karlsruhe, Karlsruhe, Germany (collection number HC_0042) as part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future".

Diagnosis of species: Forewing length 30.2 mm. Forewing length/height 7. M and CuA fused to one branch. CuA + CuPaα and M one branched. RP with 5 branches. ScP long, reaching origin of RP2, fused terminally with RA. ScA reaching up to 37.2% of total wing length. 1A very long, reaching anal margin almost as far distally as CuA + CuPaα. CuPb and CuPaβ parallel to 1A but each slightly shorter. Space between 1A, CuPb and CuPaβ narrow. Head height 6.67 mm. Eye height ca. 2.09 mm, oval shaped and not protruding above head. Metafemur ca. 19.8 mm long, ca. 3.54 mm high. Metatibia at least 19 mm long, with distinct armature consisting of 16 + spines up to 0.83 mm long (spine length measured along dorsal line of longest spine).

Description: Wings, head, and metathoracic leg preserved up to distal metatibia. Pro-, mesothoracic leg and body fragmentary.

Forewing: Length/height-ratio 7. ScP long and narrow, 93.1% of total wing length (twl). ScA reaching costal wing margin after 37.2% of twl. ScP distally with slight upwards path, fused to RA. Space between ScP and RA 7.4% of total wing height (measured at meeting point of CuA + CuPaα reaching anal margin). Origin of RP at 52.2% of twl, slightly posterior to bifurcation of M + CuA. Space between RA and RP 12% of wing height (measured at same point as before). RP with 5 branches. M and CuA + CuPaα simple; bifurcation of M + CuA at 48.2% of twl. M reaching anal wing margin at 88.5% of twl. CuA + CuPaα reaching anal wing margin at 80.2% of twl. CuPaβ simple, fused to CuPb at 61.7% of twl. CuPb fused to 1A at 65.4% of twl. 1A reaching anal wing margin after 78.3% of twl. Space between 1A and CuPb and CuPaβ and CuPb narrow. All three veins run parallel. Cross vein pattern simple, except for between RP branches, especially distally where it becomes a more complex net pattern.

Head: 6.67 mm high and 3.96 mm wide at widest point (at mid eye level). Without any appendages or anything to "break the shape". Fastigium not prolongated. Antennae not preserved. Eye height ca. 2.09 mm, oval shape, not protruding above head height.

Metathoracic leg: 19.8 mm long, 3.54 mm wide (widest point). Metatibia at least 19 mm long (broken off distally), 0.81 mm wide (widest point). A single row of spines is visible on the dorsal margin of the metatibia, consisting of 16 preserved spines. Spines vary in (preserved) length between 0.18 (first preserved spine) and 0.83 mm (spine at middle). Tarsus not preserved, except for possible fragment at distal end of preserved tibia.

Remarks: Among known fossil species of Eumastacoidea*, Cratomastax mariellaae* sp. nov. most closely resembles *Paleochina duvergeri* and *P. minuta* from the Early Cenozoic of France,

although it is closer in size to *P. duvergeri*. *Cratomastax mariellaae* differs from *P. duvergeri* by its larger forewing length (30.2 mm vs 23.3 mm in *P. duvergeri*), a different forewing length-to-height ratio (7.0 to 8.6), and a narrower spacing between CuPaβ and CuPb. The presence of a eumastacoid in the Crato Formation is not unexpected, although this is the first species formally described. Martins-Neto (1991) had already suggested the presence of such forms based on preliminary observations of undetermined specimens. Today, several subfamilies of Eumastacidae Burr, 1899 are represented in the modern faunas of Brazil and surrounding countries. In contrast, Chorotypidae are absent from the extant South American fauna and are currently restrict to Africa and Southeast Asia (Cigliano et al., 2024).

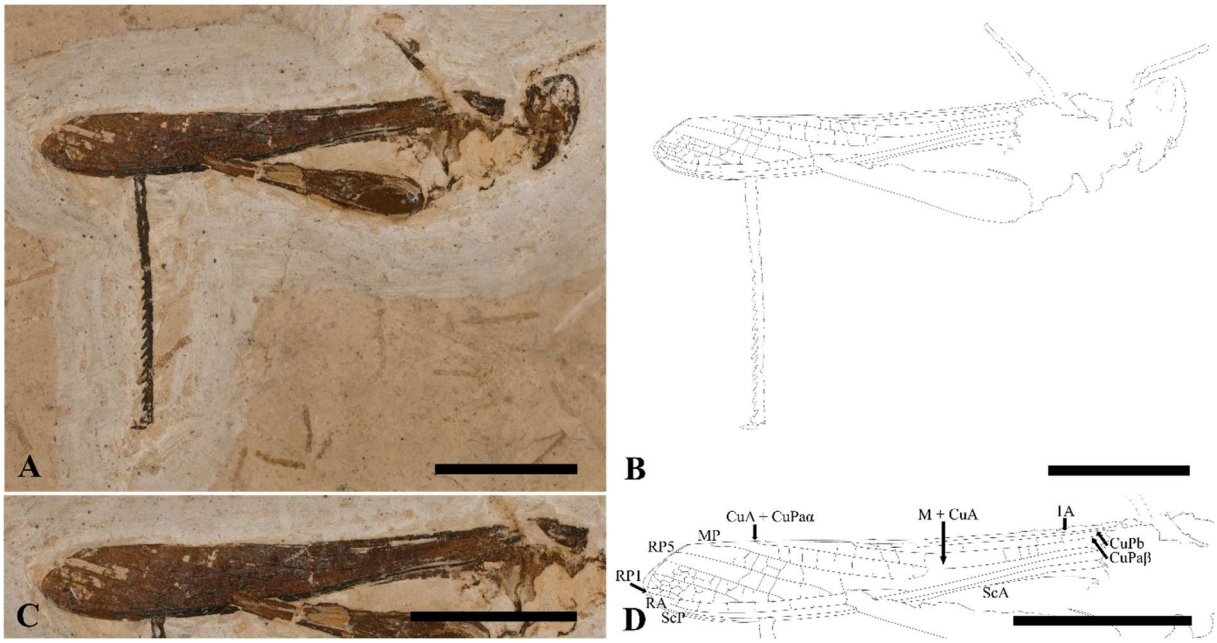

Fig. 2: *Cratomastax mariellaae* gen. et sp. nov. holotype (sex unknown), coll. no. MPSC 9664. **A.** and **B.** Image and schematic drawing of holotype, respectively. **C.** and **D.** Detail and schematic drawing of wings. **Scale bars** = 10 mm.

Superfamily Locustopsoidea Handlirsch, 1906

Family Locustopsidae Handlirsch, 1906

Subfamily Pseudoacridinae Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, (chapter 5)

Genus *Aestuacrida* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, *submitted* (chapter 4)

Type species: *Aestuacrida stereofemoris* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, *submitted* (chapter 4)

Emended diagnosis: 2 branches of M and four branches of CuA + CuPaα (*after Schall et al. *submitted* (chapter 4)). CuA + CuPaα do not terminate at fusion to CuPaβ (which, if present, looks like a cross vein), but near wing base.

Aestuacrida mikronaulion new species

Fig. 3

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: The species name is a combination of the Ancient Greek *mikron* (small) and *aulion* (farm), in reference to Dr. Ulrich Kotthoff (Leibniz-Institute for the Analysis of Biodiversity Change, Hamburg) who has co-authored several studies on fossil Orthoptera with the first author.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Holotype: Male specimen in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9665. Donation from the Private Collection of Dr. Martin Husemann at the Public Museum of Natural History Karlsruhe, Karlsruhe, Germany (collection number MH_Fossil_0075) as part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future".

Diagnosis: Generic characters (see above). Forewing: RP with five branches. Anterior two branches of CuA + CuPaα reaching anal wing margin, posterior two fused to CuPaβ. ScP long and fused to RA. Forewing length 27.9 mm, maximum height 4.8 mm. Body length 19.1 mm, height (measured at wing base) 6.28 mm. Head height 4.8 mm.

Description: Preservation of wings and body without legs (or the legs are pressed to the body and hardly visible). Measurements of the body and head are given under diagnosis of species.

Forewing: Length/height-ratio 5.8. ScP long and narrow, 92.15% of total wing length (twl). ScP distally with slight upwards path, fused to RA. Space between ScP and RA 7.9% of total

wing height (measured at origin of RP3). Origin of RP at 53.9% of twl, posterior to bifurcation of M. Space between RA and RP 7.9% of wing height (measured at same point as before). RP with 5 branches. M with two branches; bifurcation of M at 49.1% of twl. MA2 reaching anal wing margin at 91.5% of twl. Anterior most branch of CuA + CuPaα reaching anal wing margin at 82.9% of twl. MP reaching anal wing margin in the middle of MA2 and anterior branch of CuA + CuPaα (precise reaching point damaged). Branches of RP up to first two anterior branches of CuA + CuPaα more or less parallel. Posterior two branches of CuA + CuPaα fused to CuPaβ at 55.3% and 49.8% of twl, respectively. CuPaβ and CuPb long, parallel and with narrow space in between. 1A relatively short, reaching anal wing margin after 35.8% of twl. Cross vein pattern simple between cubital branches and more complex net pattern between branches of M and RP.

Remarks: Aestuacrida mikronaulion sp. nov. differs from its congeneric species *A. stereofemoris* mainly by being significantly larger (forewing length 27.9 mm vs. 16 mm; body length 19.1 mm vs. 12.9 mm). This size difference is unlikely to result from sexual dimorphism, as both known specimens of *Aestuacrida* are probably males. In the new species, the pathing of CuA + CuPaα can be seen, which was obscured in the holotype of *A. stereofemoris*. The absence of fusion between CuA + CuPaα and CuPaβ, and the continuation of CuA + CuPaα toward the wing base, supports the placement of *Aestuacrida* within Pseudoacridinae. However, the genus differs from *Pseudoacrida* Lin, 1982 in having one fewer branch of M and three additional branches of CuA + CuPaα. It can also be distinguished from *Auroralocusta* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, *submitted* by having three more branches of CuA + CuPaα. The addition of *Aestuacrida* in Pseudoacridinae reinforces the exceptional taxonomic diversity of Locustopsidae in the Crato Formation. Notably, two of the three currently recognized genera within the subfamily– *Aestuacrida* and *Auroralocusta*–are endemic to this deposit.

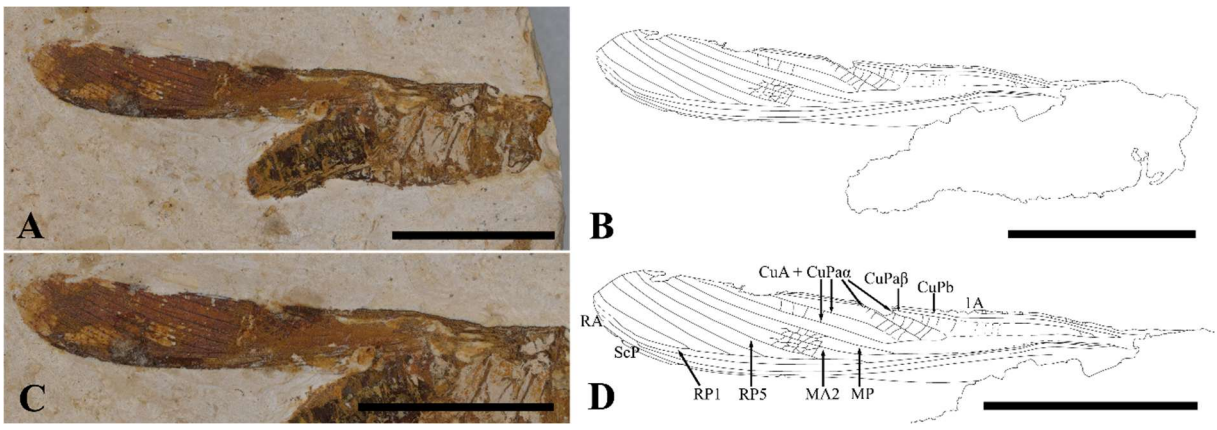

Fig. 3: *Aestuacrida mikronaulion* sp. nov. holotype male, coll. no. MPSC 9665. **A.** and **B.** Image and schematic drawing of holotype, respectively. **C.** and **D.** Detail and schematic drawing of wings. **Scale bars** = 10 mm.

Subfamily Locustopsinae Handlirsch, 1906

Genus *Locustrix* Martins-Neto, 2003

Species included: *Locustrix audax* Martins-Neto, 2003; *Locustrix gallegoi* Martins-Neto, 2003 (type species).

Diagnosis: After Martins-Neto (2003) the genus is diagnosed by a short ScP, MA (= M, consisting of MP and MA) two-branched, MP + CuA (= CuA + CuPaα) two-branched and fore- and hindwing with RP three-branched. This diagnosis is herein confirmed. It is possible, that the new specimen of *Locustrix gallegoi* described below has RP of the forewing with four branches instead of three, but preservation of venation features in the most distal part of the specimen's wings is not ideal.

Remarks: The new specimen is attributed to *Locustrix* based on the short ScP as well as the presence of two branches in both M and CuA + CuPaα, all observed in the forewing. Although Martins-Neto (2003) illustrated the CuA + CuPaα vein in both original *Locustrix* specimens as a single-branched, the generic diagnosis explicitly states the presence of two branches. *Locustrix* can be separated from *Cratolocustopsis* Martins-Neto, 2003–another genus exhibiting two branches of M and CuA + CuPaα–by the markedly shorter ScP in the forewing. In *Cratolocustopsis*, the ScP is of typical locustopsid length, reaching close to the wing apex. *Locustrix* can be assigned to the subfamily Locustopsinae based on forewing venation features–namely, the presence of more than one branch of M and CuA + CuPaα that does not extend beyond its connection with CuPaβ. Gorochov et al. (2006) tentatively suggested that *Locustrix* may belong to an as-yet undescribed subfamily of Locustopsidae, characterized by a shortened ScP. However, based on currently available evidence, we consider the abbreviated ScP better interpreted as a genus-level diagnostic feature. Given the limited number of specimens (n= 3), no additional characters currently support the recognition of *Locustrix* as representing a distinct subfamily. This interpretation may be revised should further material become available in the future.

Locustrix gallegoi Martins-Neto, 2003

Fig. 4

Material examined: Male specimen (not of the type series) currently in the private collection of Dr. Martin Husemann (Staatliches Museum für Naturkunde Karlsruhe). Collection number MH_Fossil_0066.

Remarks: Locustrix was established by Martins-Neto (2003) based on two specimens, with description of two species: *L. gallegoi* (the type species) and *L. audax*. *Locustrix audax* differs from *L. gallegoi* by having a longer ScP reaching the costal margin posterior to the origin of RP (anterior in *L. gallegoi*), and by the bifurcation point of M posterior to the RP origin (anterior in *L. gallegoi*). At the species level, the new specimen can be assigned to *L. gallegoi* based on the shared position of the ScP termination and the anterior location of the M bifurcation point relative to RP.

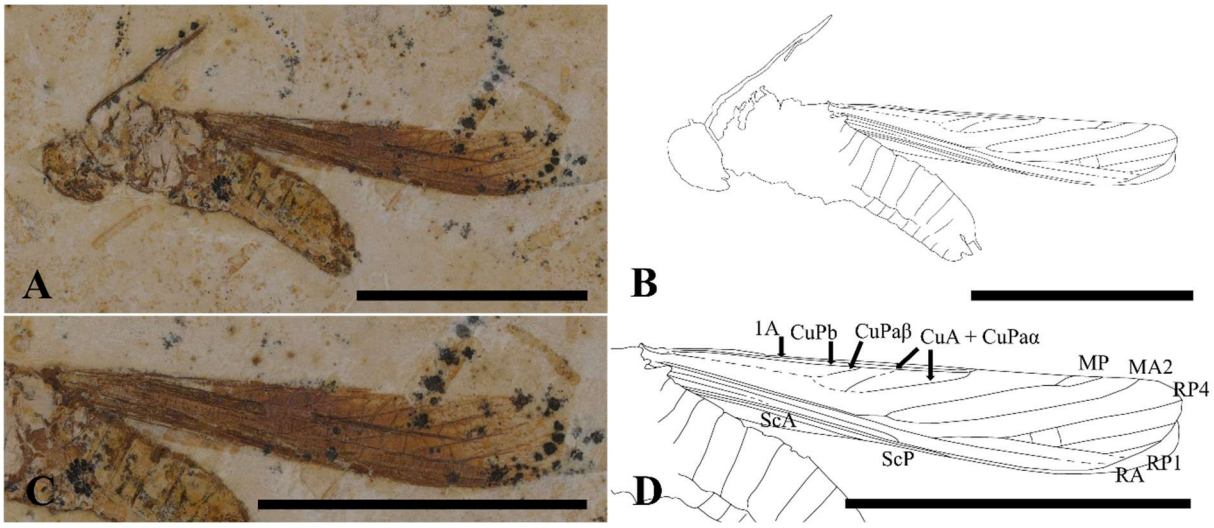

Fig. 4: *Locustrix gallegoi* Martins-Neto, 2003. Male specimen, coll. no. MH_Fossil_0066, not a type. **A.** and **B.** Image and schematic drawing of specimen, respectively. **C.** and **D.** Detail and schematic drawing of wings. **Scale bars** = 10 mm.

Discussion

The new species of Eumastacoidea, Locustopsidae described in this study further highlight the diversity of the Caelifera suborder present in the Early Cretaceous of Brazil. *Cratomastax mariellaae* gen. et sp. nov. proves for the first time that early eumastacoids were present in this time and area among the much more speciose locustopsids (26 species of Locustopsidae have been described from the Crato Formation, including the new species *Aestuacrida mikronaulion*

from this study). Unfortunately, the taxonomy of Locustopsidae and Eumastacoidea is insufficiently understood. A lack of defined apomorphies based on morphological aspects observable in fossils for the families of Eumastacoidea means that all classifications to the family of fossil eumastacoids should be considered with caution (Husemann et al., 2025). Likewise, no clear apomorphies have been defined for Locustopsidae yet (Nel and Jouault, 2022). This is bothersome, because this group likely holds a key role in the evolution of Caelifera, possibly as an ancient sister lineage or "ancestors" of the extant Acridomorpha (Gorochov, 1995b). If early acridomorphs, like the Cretaceous Eumastacoidea, share a common ancestor with Locustopsidae, then the definition of clear apomorphies to separate both groups and date the origin of Eumastacoidea (and extant Acridomorpha) is essential. Hopefully, in the future more well-preserved specimens of both taxa will help shed more light on this issue and allow for a more comprehensive understanding of Caelifera evolution, one of the most charismatic suborders in hemimetabolous insect evolution.

Acknowledgements

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Part III: Elcanidae – mysterious crickets of the ancient swamps and lagoons

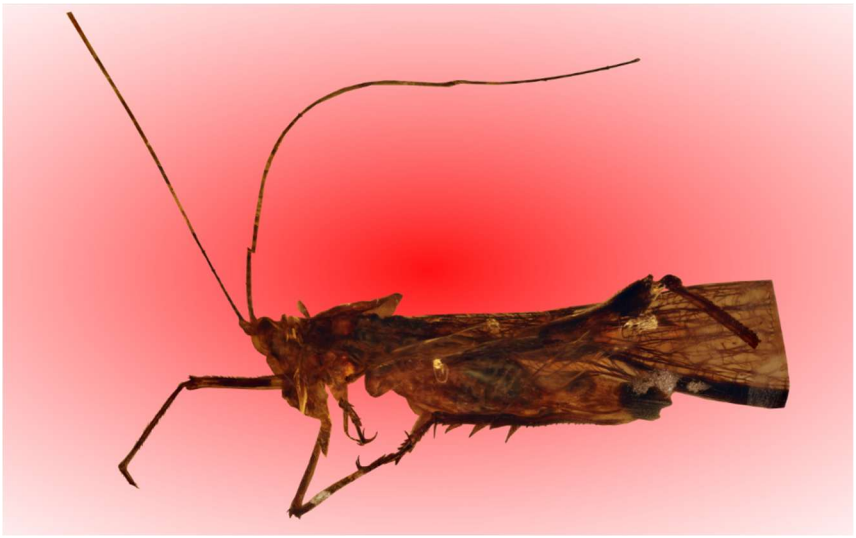

Fig. 4.1 An undescribed specimen (MH_0043) of Elcanidae Handlirsch, 1906 (cf. *Elcanodentes alatus* Willmott, Schall, Kotthoff & Husemann, 2025) from Cretaceous Burmese amber.

Preface

The Elcanidae Handlirsch, 1906, like the Locustopsidae Handlirsch, 1906, were first described as a family more than 100 years ago by Austrian entomologist and paleontologist Anton Handlirsch. Back then, they were known from “a large number of forms in the Jurassic deposits” of Germany and the United Kingdom (after Handlirsch, 1906). Today, although new Jurassic and some rare Triassic findings of this family were made (Fang et al., 2018; Heads et al., 2022), most of their diversity is of Cretaceous age. This is largely, albeit not singularly, due to the rise of mid-Cretaceous Burmese amber of northern Myanmar in the paleontologic literature (Ross, 2024). In Kachin amber 21 species of elcanids were discovered so far, making the tropical coastal forest, the trees of which produced the resin about 100 Mya, the place with the highest species-diversity of the family (Cigliano et al., 2025; chapter 7).

Other than is the case with the Locustopsidae, where our best sources for understanding body morphology is from better-preserved compression fossils, the abundancy of Elcanidae in Burmese amber has provided much knowledge about the diversity of characters that were previously unknown.

Handlirsch (1906) had already noticed the long antennae and ovipositors of the family which strongly suggest a position in the suborder Ensifera (Gorochov and Coram, 2022; Ragge, 1955; Sharov, 1968; Zessin, 1987). Contrary, Handlirsch (1906) further commented on the wing venation of elcanids being more similar to “acridoids” (= Caelifera) than extant “locustoids” (= Ensifera). This circumstance was corroborated by the only phylogenetic analysis including Elcanidae until now, performed by Béthoux and Nel (2002), who proposed that the family should be included in the Caelifera based on their forewing venation. Because of this juxtaposition of characters, the phylogenetic position of Elcanidae continued to be a matter of debate.

Among the many insights into prehistoric life that Burmese amber has enabled us to glimpse at, is the possibility to speculate on the biology of the organisms preserved (e. g. Arce et al., 2024; Grimaldi et al., 2019; Haug et al., 2024). In the case of Elcanidae, three characters of their body plan stand out and have been the focus of previous studies. Fang et al. (2018), Kočárek (2020) and Schall et al. (2024) commented on a peculiar area in the forewing of elcanids visible as a distinctly darkened field towards the posterior wing margin. This area was interpreted as a pterostigma, a structure that is common in Hymenoptera and Odonata (although it is much smaller in these groups) and thought to play some role in the enhancement of flight abilities (Kočárek, 2020; Norberg, 1972). According to Kočárek (2020) and Schall et al. (2024)

there are two types of pterostigmata present in elcanids: one that does feature cross veins and is more commonly found and one without cross veins that has only been reported for some Burmese amber elcanids.

The apomorphy of Elcanidae are three pairs of large moveable spurs on the dorsal side of their metatibiae. Before the discovery of the family in Burmese amber, these spurs appeared to always bear a leaf-like morphology. The Myanmar elcanids, however, have shown that this character is of much higher diversity than had previously been assumed. *Ellca nevelka* Kočárek, 2020 has long, straight spine-like spurs that feature numerous small setae. Many species, such as *Elcanonympha diana* Heads and Thomas, 2018, *Trigonelca jennywinterae* Schall, Kotthoff & Husemann, 2024 or *Pseudopanorpidium inversa* Schall, Kotthoff & Husemann, *in press* have a type of spur referred to as ensiform. Willmott, Schall, Kotthoff & Husemann (2025) have described three species in the genus *Elcanodentes*, which have rows of small teeth along the lateral margins of their spurs. Also, nymphs found in Spanish amber possess paddle-like spurs (Peñalver and Grimaldi, 2010) and these were present in one species from the Cretaceous Yixian Formation of China, too (Fang et al., 2015).

The functional role of the spurs of Elcanidae is not certain. Kočárek (2020) speculated on a use for stabilizing or influencing the direction of flight, similar to a rudder. Since the spurs bear a high likeness to the ones found in many modern Tridactylidae Brullé, 1835, another possibility supported by Tian et al. (2019) and Kim et al. (2021), is that they were used to maneuver in the water (swimming) or jumping over the water's surface. This theory gains support by the fact that Elcanidae are often found in deposits representing ancient lakes or lagoons (chapter 8).

The third distinct morphological feature of elcanids is their ovipositor. Many specimens discovered are female. Willmott et al. (2025) demonstrated that there are three types of ovipositors found in Elcanidae: a long, broad and rather straight type is called "sword". This seems to have been the most common type (Willmott et al., 2025). Next, there is a shorter, broad and more or less strongly recurved one that is referred to as "scythe". It is present in some Burmese amber forms as well as *Sinoelcana minuta* Gu, Tian, Wang & Yue, 2020 from the Jurassic of China (Willmott et al., 2025). Lastly, the third type is short, thin and somewhat s-shaped. This one is called "saber" and it was thought to be the rarest type by Willmott et al. (2025), occurring only in two Burmese amber species. But a saber ovipositor was fairly common in Elcanidae of the Brazilian Crato Formation, although it had been overlooked for more than 30 years (chapter 8).

Elcanidae were divided into two subfamilies by Gorochov et al. (2006) based on a character of forewing venation, namely whether the veins 1A, CuPb and CuPaβ are terminally fused or not (see Introduction, "studying fossil Orthoptera, part 2"). If the veins are not fused this means the taxon is placed in the subfamily Archelcaninae Gorochov, Jarzembowski & Coram, 2006. If they are, the taxon belongs to the subfamily Elcaninae Handlirsch, 1906. Most of the conventions regarding the taxonomy of Elcanidae are based on forewing venation. This is because most specimens, especially before the Burmese amber species, consisted of isolated forewings, thus no other characters were available for comparison. The discovery of the Cretaceous elcanids of Myanmar and the Crato Formation tremendously increases our understanding of their morphology and allows for more inclusive evidence to determine evolutionary relationships within the family and to other fossil as well as extant Orthoptera (chapter 10 and 13).

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Chapter 7

The first species of *Parelcana* and the second species of *Longioculus* (Orthoptera: Elcanidae) from mid-Cretaceous Kachin amber[†]

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AUTHOR'S COMMENT

This article is currently awaiting publication in the *Journal of Orthoptera Research*.

Abstract

A new species of *Parelcana* Handlirsch, 1906, *Parelcana xena* sp. nov., is described from mid-Cretaceous Kachin amber. The specimen consists of a well-preserved wing apparatus as well as parts of the thorax including pro- and mesothoracic legs. It stands out by its unusual morphology of tegminal CuA + CuPaα fused to MP, which is suggested to be caused by individual variation. Additionally, the second species of the genus *Longioculus* Poinar, Gorochov and Buckley, 2007 is reported. *Longioculus burmensis* Poinar, Gorochov and Buckley, 2007 was the first Elcanidae Handlirsch, 1906 to be described from Kachin amber and pioneer of the many that were to follow. The new species *Longioculus poinari* sp. nov. is a female specimen in very good condition. It is assigned to the subfamily Archelcaninae Gorochov, Jarzembowski and Coram, 2006 based on its free 1A, CuPb and CuPaβ, along with the genus *Longioculus*. The metatibial spurs of this species, not preserved in the holotype of *L. burmensis*, are leaf-like. *Longioculus poinari* differs from *L. burmensis* by some aspects of metatibial armature. The new species increase the diversity of Burmese amber Elcanidae, raising their total species to 23.

Keywords: Archelcaninae, Burmese, fossil, individual variation, taxonomy

Introduction

Elcanidae Handlirsch, 1906 is an extinct family of Orthoptera Olivier, 1789 that appears in the fossil record throughout the Mesozoic and of all continents, except for Africa and Antarctica (e. g. Fang et al., 2018; Gu et al., 2020; Martins-Neto, 1991; Tillyard, 1918; Zessin, 1987). They are characterized by a large dark area near the anterior margin of the forewing (pterostigma) and an overall appearance similar to many extant Ensifera Chopard, 1921 (i.e. antennae longer than body and ovipositor very prominent, often shaped like the blade of a scythe or sword.) Apomorphy of the family are three pairs of large moveable spurs on the dorsal side of the metatibiae which vary in shape and are either leaf-like, ensiform, spine-like or paddle-shaped (e.g. Heads and Thomas, 2018; Hu and He, 2023; Kočárek, 2020; Peñalver and Grimaldi, 2010).

A plethora of Elcanidae species have been found since 2007 in Kachin amber from Northern Myanmar (Poinar et al., 2007). The amber dates back to the mid-Cretaceous (ca. 110–100 Ma) (Shi et al., 2012; Xing and Qui, 2020) and is remarkable for its high abundance of arthropod inclusions, among them many families of Orthoptera (Ross, 2024).

Elcanidae were organised into two subfamilies by Gorochov et al. (2006). The Elcaninae Handlirsch, 1906 and the Archelcaninae Gorochov, Jarzembowski and Coram, 2006. The main point of differentiation between the two is the state of the forewing veins 1A, CuPb and CuPaβ, which are fused in Elcaninae, but not in Archelcaninae (Gorochov et al., 2006). In the case of Elcanidae from Kachin amber (and for the entire family), the Elcaninae are more diverse than their sister taxon (Cigliano et al., 2025). So far, only four species of Archelcaninae are known from the amber, but fourteen species of Elcaninae (Cigliano et al., 2025; Schall et al., 2025).

In this study, we describe two new species of Archelcaninae from Kachin amber.

Materials and methods

Taxonomy in this study follows the Orthoptera Species File (OSF) (Cigliano et al., 2025). Wing venation nomenclature follows Béthoux and Nel (2002). Abbreviations: CP = posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch

of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

Specimens presented in this study are housed in the collection of the Leibniz Institute for the Analysis of Biodiversity Change (Hamburg) (GPIH07233 and GPIH07234). They were discovered at a mining site in Myanmar, either near Tanai village or Hkamti village. The age of the two amber sites differs by ca. 10 Ma. Amber from Tanai is estimated to be 98.79 ± 0.62 Ma old (Shi et al., 2012), amber from Hkamti is ca. 110 Ma old (Xing and Qiu, 2020). Tragically, political stability and enforcement of human rights continue to be problematic in Myanmar. For a detailed discussion of the situation of conflict and ethical problems surrounding amber fossils of Burmese origin see Haug et al. (2020). Unfortunately, we do not know the year the amber pieces in this study were originally obtained (pre- or post-2017), but we argue that material already present in collections should not be ignored for scientific examination.

For imaging of the specimens, we used a DUN. Inc. stacking system with a Canon EOS 5Dsr Camera with a 65 mm lens and a magnification of 1x for GPIH07233 and 2x for GPIH07234, respectively. Individual pictures were taken with VD Passport and Capture One program (Capture One A/S, Denmark) and stacked with Zerene Stacker (Zerene Systems LLC, Washington, USA). They were edited with the Photoshop CS6 Extended application by Adobe Inc. (USA; https://www.adobe.com). Further modifications (e. g. scale bars) and creation of image collections was done in Inkscape (v. 1.3.2) (the Inkscape Team, 2024). Drawings were created in GIMP (v. 2.10.38) (the GIMP Team, 2025).

Systematic palaeontology

Order: Orthoptera Olivier, 1789

Superfamily: Elcanoidea Handlirsch, 1906

Family: Elcanidae Handlirsch, 1906

Subfamily: Archelcaninae Gorochov, Jarzembowski and Coram, 2006

Genus: *Parelcana* Handlirsch, 1906

Type species: *Parelcana tenuis* Handlirsch, 1906

Parelcana xena sp. nov.

Figures 1–2

Zoobank ID: urn:lsid:zoobank.org:act:96AA6449-DF4B-4A15-92D5-A38E5E410234

Etymology: Xena derives from the ancient Greek word “ξένος” for “strange”. It alludes to the unusual morphology of the type specimen’s CuA + CuPaα, probably an individual aberration.

Locality and horizon: The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 Ma and the amber from Tanai ca. 99 Ma old.

Holotype: Sex unknown. Specimen part of the LIB-Hamburg collection; collection number GPIH07233 (ex coll. Martin Husemann MH0051) (Fig. 1). The amber piece containing the specimen has some syninclusions, including tiny beetles and fragments of larger unspecified invertebrates. It is relatively transparent. Measurements are 31.4 mm x 24 mm, weight is 1.59 g. The amber is in good condition.

Diagnosis of species: Tegminal M with four branches. Stem of RP just posterior of second MA1 branch. RP with six to seven branches. RA with numerous comb–like cross veins. ScP with four secondary branches and ScA with two secondary branches. Two wing spots present, the anterior of which is distinctly larger than the posterior (Fig 2A, B).

Description: Preserved are the wings, the pro- and the mesothoracic leg. The rest of the body appears to have dissolved.

Prothoracic leg: Femur 2.5 mm long, same as tibia. First tarsal segment 0.85 mm, second 0.07 mm, third 0.4 mm (not including claws). Femur dorsally with evenly spaced short hairs, ventrally and on the surface with finer and far more abundant hairs. Subapically with a cuspidal lobe. Tibia thinner than femur, with similar "hair pattern" as on femur, but dorsal hairs slightly more frequent and prominent, here interspersed with finer hairs. Apically with two large spines. First tarsal segment dorsally with short hairs. Third tarsal segment with two long claws (0.27 mm long); arolium absent.

Mesothoracic leg: Tibia 2.6 mm. Femur approximately same length, but exact scale obscured by object in the amber. First tarsal segment 0.87 mm, second 0.17 mm, third (as preserved, with distal part/claws missing) 0.67 mm. Hair pattern of femur and tibia inversed to prothoracic leg (evenly spaced short hairs on ventral side of femur etc.). Femur without subapical cuspidal lobe. Tibia without long apical spines. First tarsal segment dorsally with short hairs. Apically with three claw-like spines. Second tarsal segment with cuspidal lobe bearing short hairs. Third tarsal segment with short hairs, more evenly spaced than on first tarsal segment and cuspidal lobe of second tarsal segment (Fig 2C).

Wings: The wings of the species show two dark wing spots, the anterior one being noticeably larger than the posterior one. Anterior wing spot 1.4 mm in diameter. Posterior wing spot 0.84 mm in diameter. The spots appear to be located on the hindwing. However, this cannot be said for certain due to the strong wing overlap (Fig 2A).

Forewing: ca. 12.6 mm long (with most distal part reconstructed). CuPb and CuPaβ free. CuPaα fused with free CuA. M with four branches, all of them anterior to stem of RP. RP with six to seven branches. Pterostigma present, area with numerous cross veins (> 14). ScP with 5 branches. ScA and CP each with three branches (Fig 2B).

Hindwing: Slightly shorter and of slightly less hight than forewing. Venation pattern unsure, because mainly overlapped by the forewing.

Remarks: The new specimen is attributed to the subfamily Archelcaninae based on the tegminal veins 1A, CuPb and CuPaβ reaching the anterior wing margin independently. It is assigned to *Parelcana* because of its morphology of CuPaα fused with free CuA (Gu et al., 2020) and the very short, nearly vertical CuA (Tian et al., 2019). The four branches of M anterior of the RP stem clearly separate it from *Cascadelcana* Fang, Muscente, Heads, Wang and Xiao, 2018. In

Parelcana, there are usually three branches of M anterior of the RP stem, however, we think that the four branches in *P. xena* are probably due to intraspecific variation, especially because the RP stem is very close to the posterior MA1. The position of the RP stem in relation to the branches of M was proposed an important diagnostic character by Gorochov et al. (2006). However, in rare instances where intraspecific variability in Elcanidae was possible to be analyzed (Tian et al., 2019; Zessin, 1987), it was indicated that the RP stem may be somewhat variable in its position. For example, the RP stem was located posterior of the anterior MA1 in three specimens of *Parelcana pulchmacula*, but right below the anterior MA1 in a fourth specimen (CNU-ORT-NN2016042). Zessin (1987), who studied dozens of specimens of Jurassic Elcanidae from Germany, noted that "the proximal beginning of RP in relation to its position to MA1 [= MA2] is subject of considerable variation within the same species (*E. minima*) [now *Panorpidium minimum* (Handlirsch, 1906)] already" (translated from German). Indeed, this variation is clearly visible in several of the specimens depicted in Zessin (1987), for example in Figures 23 and 25.

The specimen is characterized by CuA + CuPaα of the forewing very short and fused to MP, which is most unusual and not known from any described Elcanidae. It is likely, that this morphology can be interpreted as individual aberration again. In *Jeholecana yanensis* Fang, Heads, Wang, Zhang and Wang, 2018 from the Lower Cretaceous Yixian Formation of China CuPaβ is fused to CuA + CuPaα in a similarly unique way. Fang et al. (2018) considered this as sufficient for generic separation, but Gu et al. (2020) stated that they found the same state in one of six specimens of *Calliptamus abbreviatus* Ikonnikov, 1913, strongly indicating individual variation.

Among its congeners, *Parelcana xena* shares similarities to the type species *P. tenuis*. Both species have six branches of RP, nearly the same number of ScP branches (four in *P. tenuis* and five in *P. xena*) and they are of similar size, too (holotype (forewing) of *P. tenuis* ca. 14 mm long (Zessin, 1987); holotype (forewing) of *P. xena* ca. 12.6 mm long). Aside from the great temporal (ca. 80 Ma) and spatial (Germany vs Myanmar) distance, *P. tenuis* differs from *P. xena* in the morphology of the anal veins, which are more numerous in *P. tenuis* (three longitudinal veins below 1A vs. none in *P. xena*). The new species differs from *P. pulchmacula* Tian, Gu, Yin and Ren, 2019 from the middle Jurassic of China by being smaller (holotype (forewing) of *P. pulchmacula* 18.4 mm long (Tian et al., 2019)) and having no color pattern of the wing besides the two spots. Although the wing spots of *P. xena* may be located on the hindwings (which are not known for *P. pulchmacula*), the forewing of the Chinese species shows clear sings of the abstract color pattern present in many Jurassic elcanids such as

Archelcana numbergerae Heads, Thuy and Tamarri, 2022. This abstract color pattern is not present in *P. xena*. Taxonomy of *P. dubia* Handlirsch, 1939 and *P. anglicana* Handlirsch, 1939 is problematic. In *P. dubia* important diagnostic characters for subfamily and generic diagnosis are missing. *Parelcana anglicana* may be closer to *Archelcana* Sharov, 1968 based on its CuPaα fused with CuA + CuPaα (Handlirsch, 1939).

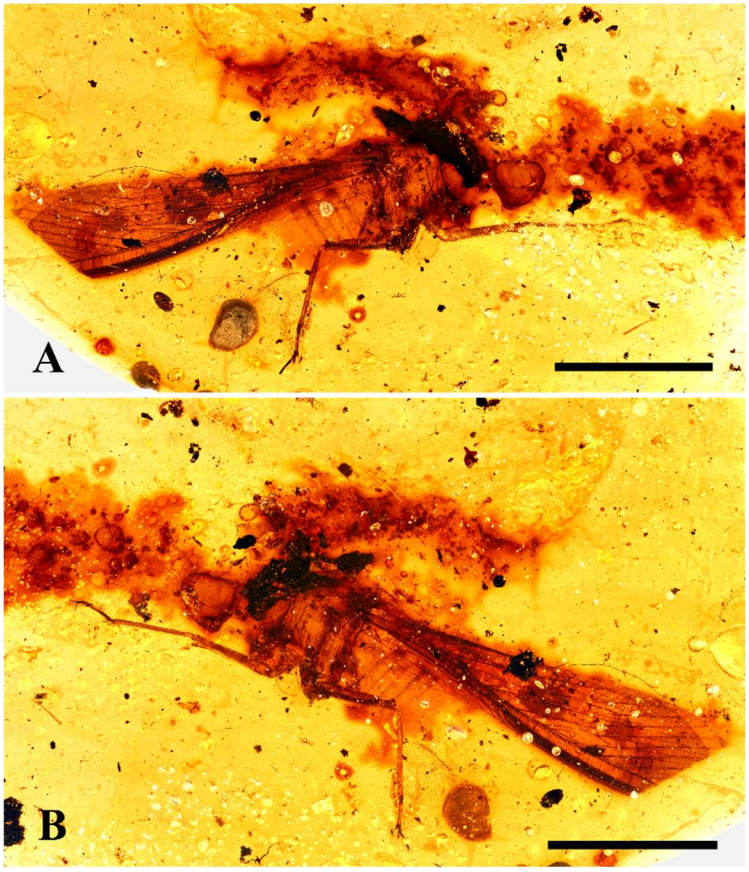

Figure 1 *Parelcana xena* sp. nov. holotype (sex unknown) GPIH07233. **A** Specimen (right side). **B** Specimen (left side). **Scale bars** = 5 mm.

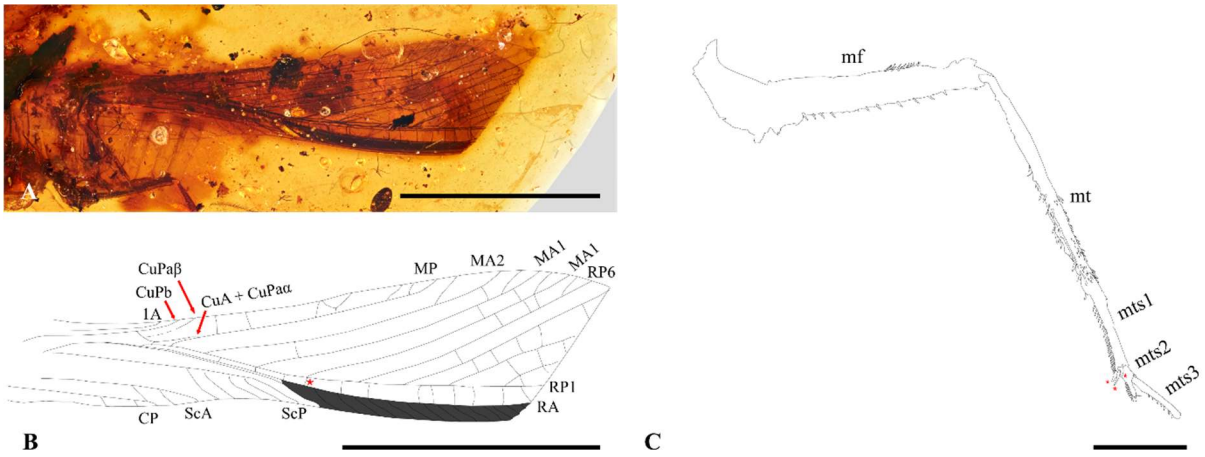

Figure 2 *Parelcana xena* sp. nov. holotype (sex unknown) GPIH07233. **A** Detail of wings (forewing overlapping the hindwing). **B** Schematic drawing of the forewing. **C** Line drawing of the mesothoracic leg. **Abbreviations:** mf = metafemur; mt = metatibia; mts1-3 = metatarsal segment 1-3. **Scale bars** for **A** and **B** = 5 mm; for **C** = 1 mm.

Genus *Longioculus* Poinar, Gorochov and Buckley, 2007

Type species: *Longioculus burmensis* Poinar, Gorochov and Buckley, 2007

Longioculus poinari sp. nov.

Figures 3–4

Zoobank ID: urn:lsid:zoobank.org:act:C8472E79-33F8-4DDC-8384-E382E1E098D7

Etymology: The species is named after George O. Poinar, who has described the genus and first species of *Longioculus* alongside many more contributions about prehistoric insects found in amber.

Locality and horizon: The specimen was included in amber found in Hkamti, Sagaing Division, Myanmar or Tanai, Kachin State Burma, Myanmar, two nearby amber mining locations. The amber from Hkamti is ca. 110 Ma and the amber from Tanai ca. 99 Ma old.

Holotype: Female. Specimen part of the LIB-Hamburg collection; collection number GPIH07234 (ex. coll. Martin Husemann MH0065) (Fig 3). Syninclusions include several insect fragments and insects covered by other objects. Among these are two dipterans, one of which belongs to Nematocera Latreille, 1825 and a well-preserved mite. Some trichoms are included as well. The amber piece appears rather dark due to many particles clouding the interior. Its measurements are 13.7 mm x 10 mm, and it weighs 1.15 g. The piece is in overall good condition, but has some fragments broken off on the opposite margin of the specimen and should be handled with care.

Diagnosis: Forewing characters: 1A, CuPb and CuPaβ free. CuPaα fused with CuA + CuPaα. M with three branches. RP with nine branches. RA with 16 or more cross veins. Body characters: Proximal part of metatibia dorsally with denticles the same height as metatibia. Metatibial spurs leaf-like. Apically with four spine-like spurs, one small, two medium, one

large. Metabasitarsus dorsally with smaller, ventrally with longer spines; dorsally less numerous than or equally as much as ventrally. Ovipositor sword shaped (Fig 4).

Description: Completely preserved specimen with only parts of the antennae and ovipositor missing. Body length ca. 5.2-5.5 mm.

Wings: Forewing 6.9 mm long. 1A, CuPb and CuPaβ free. CuPaα fused with CuA + CuPaα. MP with regularly spaced cross veins, one of them Y-shaped. M with three branches. RP with nine branches, no terminal bifurcation of any RP branch. Pterostigma present. Pterostigma area with cross veins (> 16). Subcostal venation not visible. Hindwing 6.64 mm long (Fig 4A).

Head: Antennal scapes large, same width as antennal cavities. Antennomeres with small spines, irregularly placed. Eyes strongly protruding, oval shaped and much higher than wide. Eyes 0.94 mm high (ca. half of head height) (Fig 4C).

Thorax: Pronotum 1.4 mm long (dorsally), elevated from thorax (Fig 4C).

Legs:

Prothoracic leg: Femur 1.6 mm long. Dense short hairs dorsally, few fine denticles/short hairs ventrally. Tibia ca. 1.4 mm long. Ventral spination starting at ca. half the length and increasing in size towards apex. Two apical large spines at a V-angle. Tarsus three-segmented. First tarsus looking like continuation of tibia, but without spines, except one or two large apical spines (perhaps again at V-angle). Second tarsal segment much shorter than first, bearing a lobe. Third tarsal segment ca. 70% of first tarsal segment in length, slender. Claws missing (Fig 4C).

Mesothoracic leg: With some damage. Small spines present on femur and tibia. At least one large spine apically on tibia. Tarsus with hairs and two claws (Fig 4C).

Metathoracic leg: Femur 3.56 mm long, 0.76 mm high. Tibia 3.51 mm long, much thinner than femur. Proximally with small denticles. Metatibial spurs leaf-like. Apical spurs spine–like, two small, two medium and one large one. Only basitarsus preserved (cut off at amber). Dorsally with smaller, ventrally with longer spines (Fig 4A, B–D).

Abdomen: One cercus preserved, straight, 0.78 mm long. A single hair near the cercus tip might be a detached appendage of the tip, however, in the holotype no appendage was present.

Ovipositor broken off shortly after base, but apparently sword-shaped (general direction does not indicate a scythe-like curve) (Fig 4C).

Remarks: The new species is placed in the subfamily Archelcaninae based on its free 1A, CuPb and CuPaβ. It is attributed to the genus *Longioculus* based on the large protruding eyes, which are much higher than wide, RA with visible cross veins, the absence of wing spots, postero–lateral margin of pronotum without concave curve, metatarsus with denticles and cerci not setulose. A detailed comparison of the known species of Archelcaninae from Kachin amber is provided in Table 1. The state of 1A, CuPb and CuPaβ is unknown in *L. burmensis*, but now, the genus can be assigned to the Archelcaninae based on the free state of these veins in the new species.

Poinar et al. (2007) described the forewing of *L. burmensis* with a stem of RP (orig. "base of RS") between the third and fourth branch of RP ("RA") (RP branches counted in the direction towards wing apex). In *L. poinari*, the position of the stem of RP is unsure, however, it would not be further posterior than behind the ninth branch of RP as the area of the wing from there can be well seen. We estimate that the stem of RP in *L. poinari* would either be between MA1 and RP9 or RP9 and RP8. This position is much more in line with where the stem of RP can usually be found in the forewings of Elcanidae. It would be helpful, if the type specimen of *L. burmensis* could be reviewed to confirm the position of the RP-stem in this species. Unfortunately, its whereabouts in the collection of R. Buckley are currently unknown.

Longioculus poinari differs from *L. burmensis* by not having seven circular light blotches on the dorsal surface of the pronotum and by the denticles on the proximal half of the metatibia being broader and more prominent.

Table 1 Comparison of *Longioculus poinari* sp. nov. with other members of the Archelcaninae Gorochov, Jarzembowski and Coram, 2006 from Kachin amber.

Species	**Compound eyes strongly protruding above head**	**RA with visible cross veins**	**Presence of wing spots**	**Postero–lateral margin of pronotum with concave curve**	**Metatarsus with denticles**	**Branches of RP**	**Branches of M anterior of RP stem**	**Cercus setulose**	**CuPaα fused with…**
Longioculus poinari sp. nov.	Yes	Yes	No	No	Yes	Nine	Three	No	CuA + CuPaα
Longioculus burmensis Poinar,	Yes	Yes	No	No	Yes	NN	NN	No	NN

Gorochov and Buckley, 2007									
Caelielca spinocrus Uchida, 2022	No	Yes	No	Yes	Yes	Eight	NN	Yes	CuA + CuPaα
Hukawnelca gracile Uchida, 2022	No	Yes	Yes	Yes	Yes	Six	NN	Yes	CuA + CuPaα
Specimen GPIH07022 Archelcaninae gen. et sp. nov. Schall, Kotthoff and Husemann (accepted for publication)	NN	No	Yes	Yes	NN	Ten	Three	No	CuA + CuPaα
Parelcana xena sp. nov., described herein	NN	Yes	Yes	NN	NN	Six	Four	No	Free CuA

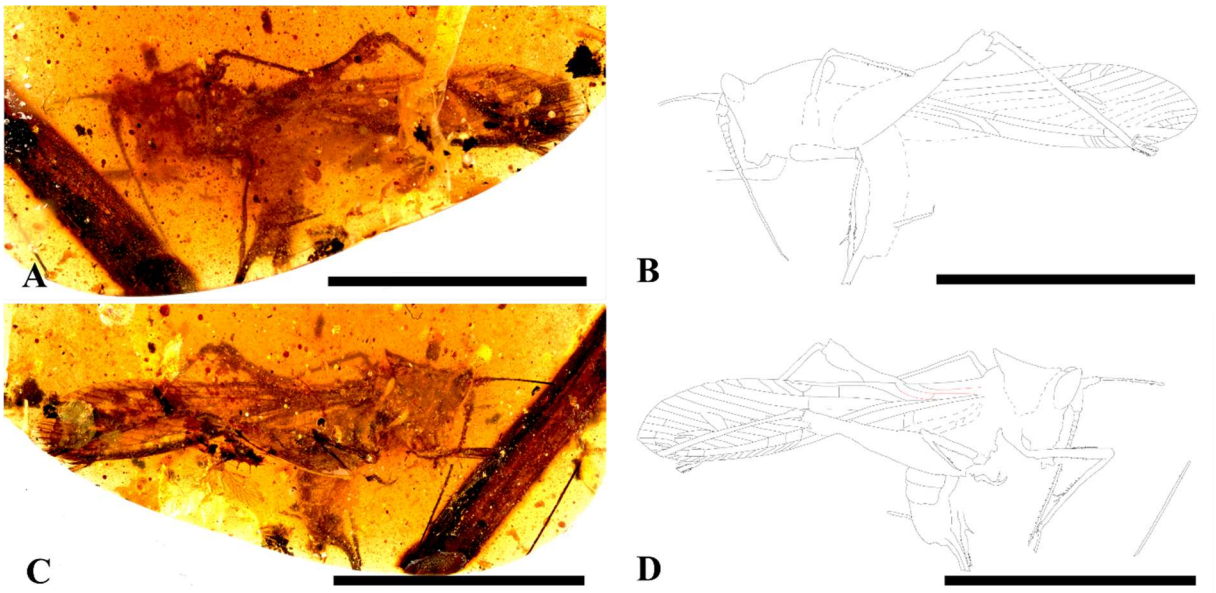

Figure 3 *Longioculus poinari* sp. nov. holotype female GPIH07234. **A** and **B** Specimen (left side). **C** and **D** Specimen (right side). **Scale bars** = 5 mm.

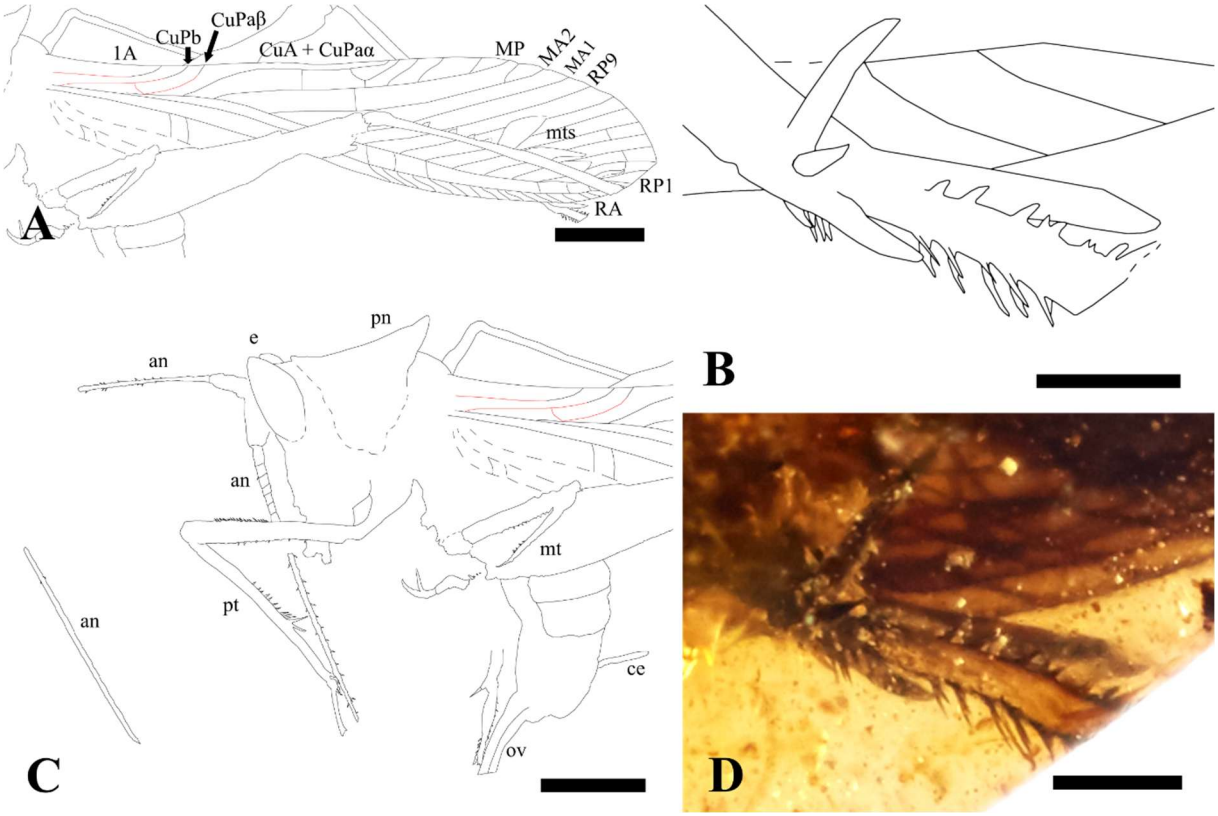

Figure 4 *Longioculus poinari* sp. nov. holotype female GPIH07234. **A** Schematic drawing of the forewing. **B** Schematic drawing of the apical spines on the metatibia and metabasitarsus. **C** Schematic drawing of the body aspects. **Abbreviations:** an = antenna; pt = prothoracic leg; e = eye; pn = pronotum; ov = ovipositor; mt = mesothoracic leg; ce = cercus. **D** Apical spines on the metatibia and metabasitarsus. **Scale bars** for **A** and **C** = 1 mm; for **B** and **D** = 0.2 mm.

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Chapter 8

Revision of the lagoon crickets Elcanidae (Insecta: Orthoptera) of the Lower Cretaceous Crato Formation of Brazil with the description of new taxa

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AUTHOR'S COMMENT

This article was submitted to *Cretaceous Research*.

Abstract

Elcanidae is a Mesozoic family of grasshoppers with many species known from Laurasia, but only very few from Gondwana. Here, a total of 88 specimens of Elcanidae from the Lower Cretaceous Crato Formation of Brazil were examined. Three new genera and species are described: *Argentoelcana intermedia* gen. et sp. nov.; *Ensiferelcana brachyptera* gen. et sp. nov.; *Gondwanaelcana brasiliensis* gen. et sp. nov. In addition, the new genus *Mesembrelcana* gen. nov. is described to accommodate *Cratoelcana rasnitsini* Nel and Jouault, 2022, resulting in the new combination *Mesembrelcana rasnitsini* (Nel and Jouault, 2022) comb. nov. Finally, *Cratoelcana damianii* Martins-Neto, 1991 is transferred to *Panorpidium* Westwood, 1854, resulting in the new combination *Panorpidium damianii* (Martins-Neto, 1991) comb. nov., thus rendering *Cratoelcana* Martins-Neto, 1991 monotypic, containing only the type species *Cratoelcana zessini* Martins-Neto, 1991. Trait variability across the species based on the 88 specimens is presented and possible conclusions for the taxonomy of the family are discussed. Reasons explaining the high abundance of females among the specimens (69.3%) may include 1) a female-biased population of Elcanidae with the possible presence of parthenogenesis. 2) A stronger association of females with an aquatic habitat, for example for egg-laying use (thus leading to females being more likely to be preserved). The common name lagoon crickets is proposed for the family Elcanidae due to their apparent connection to bodies of water. The present work is the most comprehensive study about the Elcanidae of the Crato Formation since the contributions of Martins-Neto over 30 years ago.

Keywords: Ceará, Chapada do Araripe, Ensifera, fossil, Nova Olinda Member, taxonomy

1. Introduction

Elcanidae Handlirsch, 1906 is an unusual and enigmatic family of Orthoptera Olivier, 1789. While its general morphology superficially resembles members of Ensifera Chopard, 1921, its position inside this suborder remains unresolved. Elcanids are usually found in Mesozoic deposits, with an almost worldwide distribution during that era–although no representatives have been recorded from Africa and Antarctica (Zhou et al., 2024).

Recently, elcanids found in Kachin amber from northern Myanmar have gained significant attention due to their exquisite preservation, which has revealed previously unknown morphologic details (e.g., Kočárek, 2020; Willmott et al., 2025). The amber deposits are thought to represent an island ecosystem with a Gondwanan origin and possible later faunal input from Laurasia (Jouault, 2021; Westerweel et al., 2019). Owing of this peculiar biogeographic history, the taxonomic relationships of Burmese elcanids to their relatives remain uncertain.

Whereas the Elcanidae from Laurasian mainland deposits (i.e., North America, Europe, and Asia) have been relatively well studied (see Fang et al., 2018; Heads et al., 2022; Tian et al., 2022), those from former Gondwana regions (South America, Africa, and Australia) remain poorly understood. No species have yet been reported from Africa, and only a single fragmentary wing tentatively attributed to the family has been recovered from the Triassic Hawkesbury Sandstone in Sydney, Australia (Jell, 2004; Tillyard, 1918).

In contrast, the fossil record of Elcanidae in South America is more informative. The Crato Formation of northeastern Brazil, a Lower Cretaceous *Koservat*- and *Konzentratlagerstätte* (ca. 122–113 mya), has yielded a remarkably diverse insect fauna, including several families of Orthoptera and Elcanidae in particular (Bezerra and Mendes, 2024; Mendes et al., 2019; Nel and Jouault, 2022). Despite this diversity, only two taxonomic studies have been published on Crato-Elcanidae: Martins-Neto (1991) and Nel and Jouault (2022). The first examined 99 specimens and described two species within a new genus, *Cratoelcana*: *Cratoelcana zessini* Martins-Neto, 1991 and *C. damianii* Martins-Neto, 1991. According to Martins-Neto, the two species can be readily differentiated by their forewing size and the number of branches of the posterior radius (RP). *Cratoelcana zessini* exhibits forewings ranging from 22–26 mm in length and has more than nine RP branches, whereas *C. damianii* has shorter forewings (9–14 mm) and only 5–7 RP branches (Martins-Neto, 1991).

More than 30 years later, Nel and Jouault (2022) described a third species, *Cratoelcana rasnitsyni*, which falls within the size range of *C. zessini* but differs from it by having a distinct tegminal color pattern, notably consisting of two round wing spots absent in the latter species (Nel and Jouault, 2022).

In this study we revisit the taxonomy of Elcanidae from the Crato Formation based on 88 new, previously unpublished specimens. Our aim is to provide a comprehensive assessment of their morphological features and re-evaluate their taxonomy and systematics in light of recent advances in Elcanidae research.

Geological and Paleontological Context of the Crato Formation

The Crato Formation, located in the Araripe Basin of northeastern Brazil, constitutes one of the most significant *Konservatlagerstätte* of the Lower Cretaceous and is globally renowned for the exceptional preservation of its fossil biota. Chronostratigraphically assigned to the Aptian (ca. 113–125 Ma), the Crato Formation is the basal unit of the post-rift sequence of the Santana Group and comprises finely laminated limestones interbedded with greenish shales and fine-grained sandstones (Assine, 2007). These sedimentary successions were deposited in a shallow, intermittently hypersaline lacustrine system under predominantly anoxic or dysoxic bottom conditions that favored the preservation of both hard and soft tissues (Martill et al., 2007; Heimhofer et al., 2010).

A notable and recently emphasized component of the Crato paleoenvironment is the widespread occurrence of stromatolitic microbialites within the lower laminated limestones of the formation. These structures—ranging from domes to pseudo-columns—are composed of finely laminated carbonate boundstones and are interpreted as the result of biologically induced mineralization by benthic microbial mats (Warren et al., 2017). Stromatolite levels occur at several stratigraphic intervals in both the Nova Olinda and Santana quarries, with evidence of preserved extracellular polymeric substances (EPS), calcified coccoid and filamentous microbial cells, and organominerals. These microbialites likely developed in shallow photic zones under high-stress conditions (e.g., elevated salinity, low oxygen availability), providing substrates for microbial colonization and sediment trapping (Catto et al., 2016; Warren et al., 2017). Their presence strengthens the hypothesis that microbial activity played a central role in the carbonate precipitation and taphonomic conditions that characterize this Lagerstätte.

The fossil assemblage of the Crato Formation is extraordinarily diverse and includes an extensive representation of both aquatic and terrestrial organisms. The flora comprises water plants, conifers, gnetales, ferns, and early angiosperms, many preserved with fine anatomical detail (Kunzmann et al., 2021). The fauna includes an abundance of arthropods (notably insects, but also crustaceans, arachnids, and myriapods), fishes, amphibians, reptiles, avian and non-avian dinosaurs, and pterosaurs (Martins-Neto et al., 2005; Martill et al., 2007; Carvalho et al., 2015; Martill & Smith, 2025). Insects, in particular, are among the most taxonomically diverse and abundant groups in the formation, contributing to its paleobiological significance as one of the richest Cretaceous insect localities worldwide (Menon, 2008; Macário et al., 2025 *in press*).

Collectively, sedimentological, micropaleontological, and geochemical data suggest that the Crato Formation was deposited in a saline to hypersaline lacustrine setting, episodically influenced by freshwater influxes and subject to water-level fluctuations (Heimhofer et al., 2010; Warren et al., 2017). The presence of halite hoppers, gypsum layers, and microbialites points to a dynamic chemical environment, where carbonate precipitation was modulated by microbial processes and limited benthic activity. These factors contributed directly and indirectly to the exceptional preservation of fossils, allowing insights into trophic structure, evolutionary processes, and paleoecological dynamics of Lower Cretaceous continental ecosystems.

2. Materials and methods

Eighty-eight specimens of Elcanidae from the Crato Formation were considered for this study. These specimens are currently housed in the following collections:

1. AMNH: American Museum of Natural History, New York, USA;
2. INHS-P: Illinois Center for Paleontology, University of Illinois, USA;
3. LIB: Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany;
4. MHRC: Husemann Research Collection, Staatliches Museum für Naturkunde, Karlsruhe, Germany;
5. MPSC: Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Brazil;
6. SMNK: Staatliches Museum für Naturkunde, Karlsruhe, Germany.

Images of the specimens from (3) and (4) were taken using a Keyence VHX-6000 digital microscope (KEYENCE Corporation, 2024, Osaka, Japan; https://www.keyence.com/). Specimens from (6), were taken with a Keyence VHX-7000 digital microscope. Images of the MPSC collection were taken using a Canon EOS 6D camera equipped with a 100 mm macro lens. All images are composite photographs generated via the stitching method. Specimens from (1) were kindly made available by Agnieszka Pierwola and Prof. Dr. David Grimaldi from AMNH. Along with specimens from (2), these were photographed by Dr. Sam W. Heads and Michael Jared Thomas from the University of Illinois. Line drawings of the specimens were created using GIMP (v. 3.0.2-1) (the GIMP Team, 2025; https://www.gimp.org/). Final figures plates were assembled and edited (scale bars and labelling) using Inkscape (v. 1.4.2) (Moini et al., 2025; https://inkscape.org/). Taxonomic nomenclature in this study follows the Orthoptera Species File (Cigliano et al., 2025; https://orthoptera.speciesfile.org/). Wing venation terminology follows Béthoux & Nel (2002), with the following abbreviations: CP posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein. Ovipositor morphology in Elcanidae follows Willmott et al. (2025).

3. Results

3.1 Systematic paleontology

Order Orthoptera Olivier, 1789

Infraorder Elcanidea Gorochov, 1995

Superfamily Elcanoidea Handlirsch, 1906

Family Elcanidae Handlirsch, 1906

**Common name:*

As no common name has been proposed to date, we propose the colloquial name “lagoon crickets” for the family Elcanidae, reflecting the frequent association of its species with aquatic or semi-aquatic environments.

Subfamily Elcaninae Handlirsch, 1906

Genus ***Argentoelcana*** new genus

Type species: *Argentoelcana intermedia* sp. nov. by monotypy and present designation. Gender feminine.

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: Named after the Latin "argentum" (silver) and "elcana" after the family Elcanidae. Translates as "the silver lagoon cricket" and refers to its middle position (size wise) between the smaller *Panorpidium damianii* and *Gondwanaelcana brasiliensis* and the larger *Cratoelcana zessini* and *Mesembrelcana rasnitsyni*; in an analogy to competitions awarding gold, silver and bronze to the first, second and third placed athlete, respectively.

Diagnosis: As for the type species by monotypy.

Remarks: The genus is assigned to the Elcanidae based on the large spurs on the metatibia and the forewing venation characters of a fused M and RP, stem of RP as cross vein between RA and RP and CuA + CuPaα single. Its suggested affiliation with the subfamily Elcaninae is preliminary; the holotype specimen appears to show a fusion of tegminal 1A + CuPb + CuPaβ, but the preservation in this area is not clear and interpretation might be erroneous. *Argentoelcana* gen. nov. differs from all other Elcanidae genera described so far except for *Cratoelcana* and *Mesembrelcana* gen. nov. (see below) by the stem of RP being located posterior of the last RP branch. It differs from *Cratoelcana* and *Mesembrelcana* gen. nov. by being smaller (forewing length ca. 16 mm vs. more than 22 mm; body length ca. 10 mm vs. 10.8-16.7 mm (12.8 mm in *Ensiferelcana brachyptera* gen. et sp. nov., see below); see also Figs. 30 and 33). The genus *Longioculus* Poinar, Gorochov & Buckley, 2007 which might have the RP stem in a similar position (Schall & Husemann, in press) is much smaller than *Argentoelcana* gen. nov. (forewing size ca. 7 mm).

Argentoelcana intermedia new species

Fig. 1

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: After the intermediate state between the aforementioned taxa.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Lower Cretaceous, Aptian.

Holotype: Female, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Brazil, coll. no. MPSC 9832 (ex-collection Illinois Center for Paleontology, University of Illinois, USA, coll. no. INHS-P1872).

Diagnosis: Forewing length 16.1 mm. Tegminal M with three branches. Distance between CuA + CuPaα and MP rather narrow. Tegminal RP with 10 branches. Stem of RP located posterior of last RP. Ovipositor morphology similar to *Cratoelcana*, estimated ovipositor length/forewing length 0.54. Body length 9.9 mm. Head height/forewing length 0.3.

Description:

Measurements: Forewing length 16.1 mm. Forewing height 4.2 mm. Forewing length/height 3.8. Body length 9.9 mm. Ovipositor length 8.7 mm. Metafemur 8.7 mm long. Metatibia 8 mm long. Metatarsus (including claws) 4.1 mm long.

Body: Metatibia with three large spurs. Ovipositor long and slender with a slow upwards curve.

Wings: Forewing with the distance between CuA + CuPaα and MP rather narrow, 16.2% of total wing length. M with three branches. RP with ten branches. Fusions occurring in the wing apex in the area of RP1 and RP2. Stem of RP posterior of last RP. ScP with at least seven branches.

Remarks: While it is possible that *A. intermedia* sp. nov. is just a smaller variation of *Cratoelcana zessini* (since they share a similar ovipositor length/forewing length ratio), the decreased number of RP branches (10 vs. 11–13) indicates a more pronounced distinction from the latter, rather than just an undergrown individual. These middle-sized elcanids are rare in the fossil record (only three specimens among 88), suggesting that they were also less common in the Crato-orthopteran fauna. A male specimen INHS–P1937 may belong to this species or the following one.

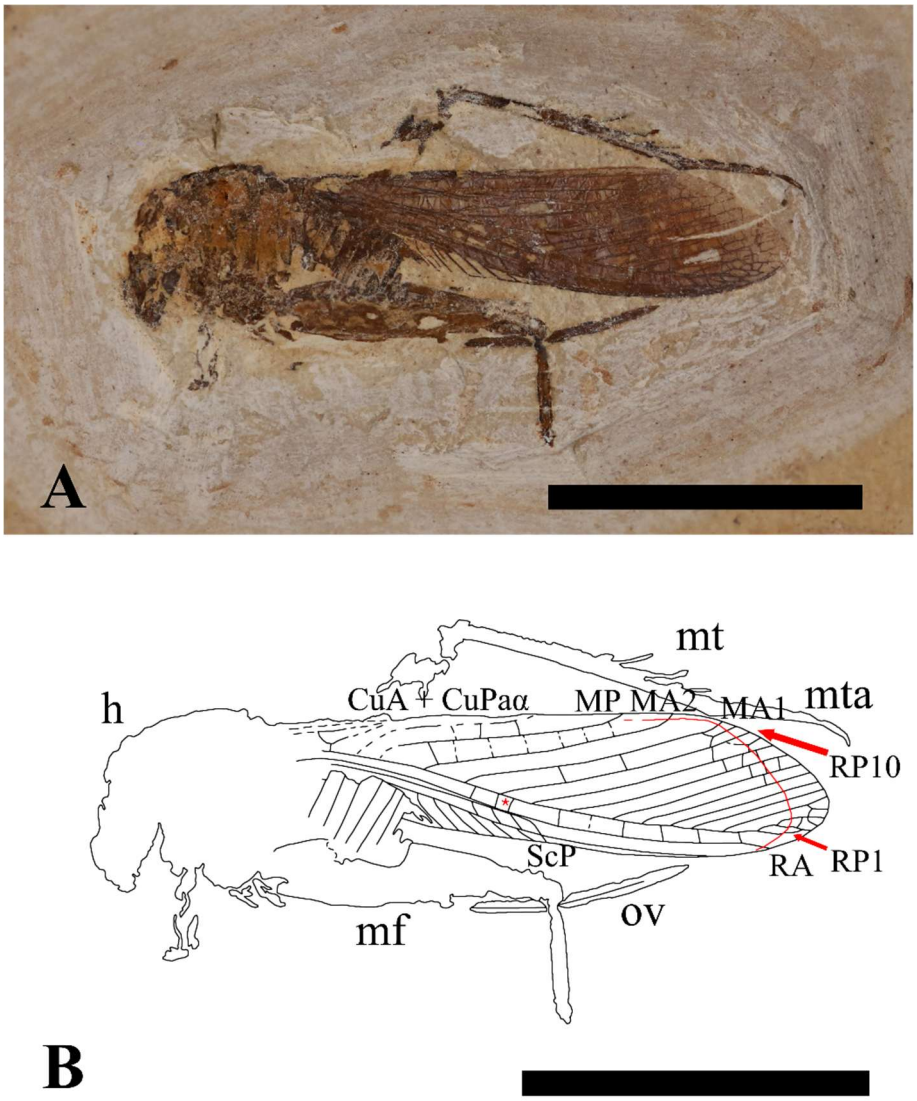

Fig. 1: *Argentoelcana intermedia* gen. et sp. nov. holotype MPSC 9832, female. **A.** and **B.** Specimen. **Abbreviations:** h = head; mf = metafemur; mt = metatibia; mta = metatarsus; ov = ovipositor. **Scale bars** = 10 mm.

Subfamily Elcaninae Handlirsch, 1906

Genus *Cratoelcana* Martins-Neto, 1991

Type species: *Cratoelcana zessini* Martins-Neto, 1991

Emended diagnosis: As for the type species by monotypy.

Cratoelcana zessini Martins-Neto, 1991

Figs. 2–12

Holotype: Female, in the collection of Instituto de Geociências da Universidade de São Paulo, coll. no. GP/1T-1619 [(not RGMN-1619 as provided in Martins-Neto (1991)] (Fig. 2). Type locality: between Santana do Cariri and Nova Olinda, Crato Formation Ceará, Brazil. Collected by R.G. Martins-Neto.

Further specimens from this study: HC0001; HC0026; HC0040; HC0041; MH1111; SMNK_PAL_47253; AMNH_SA_45367; INHS-P1131; INHS-P1626; INHS-P1619; INHS-P1879; INHS-P1824 (all ♀). Three more specimens were discovered in the collection of MPSC at a later point during the writing of this article. They are included as figures (Figs. 10–12) but were not considered for the rest of the study (such as the analysis of characters variation): MPSC 5729; MPSC 5770; MPSC 5811 (part and counterpart) (all ♀).

Emended diagnosis: Forewing 22.7–27.4 mm long (*22–26 mm according to the diagnosis of Martins-Neto (1991)). 1A + CuPb + CuPaα fused. Wing margin length between CuA + CuPaα and MP short. Tegminal RP with 11–13 branches (*more than nine branches after Martins-Neto (1991). Comment: Martins-Neto only counted the secondary branches of RP, i.e. not the RP1 as counted in this study; hence, he gave "more than eight branches" as the original number). Tegminal M with four branches. Location of stem of RP from below second MA1 to after second last RP. Body length 10.8–16.7 mm. Ovipositor long and thin, needle shaped; ovipositor length/forewing length 0.51–0.64.

Description of specimen INHS-P1131:

Specimen INHS-P1131 (Fig. 3) is a very well-preserved female specimen and offers valuable morphological data to refine the diagnosis of *Cratoelcana zessini*.

Measurements: Forewing length 26 mm, height 5.4 mm. Forewing length/height 4.8. Body length 10.8 mm. Head height/forewing length 0.19. Ovipositor length/forewing length 0.55. Ovipositor length 14.4 mm. First metatibial spur length 1.7 mm (along midline). Metatibia 11 mm long. Metatarsus (including claws) 4.8 mm long. Antennae (longest preservation) ca. 50 mm long.

Body: Antennae thin, much longer than body. Front of head in profile with convex curve. Pronotum with posterolateral concave curve. Metatibia with small proximal spur, little less than half the size of first main spur. Three main spurs preserved, possibly ensiform in shape. No apical spurs preserved. Metatarsus without preserved armature. Ovipositor long and thin, needle-shaped; almost straight.

Wings: Forewing M with four branches and RP with 13 branches. RP2 probably consists of fused former RP1–3 (former RP1 and 2 can be seen as horizontal cross veins). Stem of RP between RP12 and RP11 (= after second last RP). Pterostigma area of RA with 23 cross veins. ScP with 15 branches, rather wide along costal wing margin. Forewing coloration possibly with colored broad apical margin and one round spot close to margin (see remarks of *Mesembrelcana rasnitsyni* below on the reliability of tegminal coloration in Crato-Elcanidae). Forewing tapering almost symmetrically with apical tip roughly at mid-wing level. Hindwing 2.9 mm shorter than forewing, tapering asymmetrically with apical tip in bottom third of wing height.

Remarks: Cratoelcana was established by Martins-Neto (1991). Originally, it included three species: *C. zessini* Martins-Neto, 1991 (the type species), *C. damianii* Martins-Neto, 1991, and *C. rasnitsyni* Nel and Jouault, 2022. The taxonomic status of the latter two species is discussed below. *Cratoelcana zessini* can be attributed to the Elcanidae based on a suite of diagnostic characters, including the presence of large metatibial spurs, antennae longer than body, a long prominent ovipositor, and distinctive forewing venation patterns–particularly the fusion of M and RP and the presence of the RP stem as a pseudo-cross vein. Within Elcanidae, *C. zessini* is further assigned to the subfamily Elcaninae Handlirsch, 1906, based on the fusion of tegminal veins 1A + CuPb + CuPaβ, a feature clearly visible in specimens AMNH_SA_45367 and SMNK_PAL_47253. *Cratoelcana* can be differentiated from other elcanid genera by the more posteriorly located RP stem. In the newly examined specimen INHS-P1131, described above, the RP stem emerges posterior to the second last RP branch. The position of the RP stem appears to be variable, however (see discussion), as in other specimens the RP stem may originate posterior to the first or second branch of MA1. Such variation could suggest potential affinity with *Panorpidium* Westwood, 1854, but in that genus the RP stem is consistently located after the first MA1branch and never more posteriorly. *Cratoelcana zessini* also exhibits a remarkably high number of RP branches (11–13), a condition otherwise known only in certain Kachin amber taxa, such as *Kolymbelcana phantasma* Schall, Kotthoff & Husemann, 2025 (11 RP branches) and *Letoelcana artemisapollonque* Schall, Kotthoff & Husemann, 2023 (14 RP branches). While *K. phantasma* is markedly smaller (forewing length 9.5 mm), *L. artemisapollonque* bears a strong resemblance to *Cratoelcana*, differing mainly in the absence of crossveins within RA (pterostigma area). Given the morphological affinities, it is plausible that *L. artemisapollonque* may represent a descendant lineage of *C. zessini*.

Cratoelcana zessini specimens examined in this study:

Fig. 2: *Cratoelcana zessini* Martins-Neto, 1991 holotype female in the collection of Instituto de Geociências da Universidade de São Paulo, coll. no. GP/1T-1619. **A.** Overview of the specimen with museum note proving its holotype status. **B.** Metathoracic leg (left) and forewing. Note the presence of a proximal metatibial spur on the holotype specimen. **C.** Detail of the body. **D.** Detail of other metathoracic leg and ovipositor. For a drawing of the venation features of this specimen see Fig. 28. **Scale bars** = 10 mm (**B**), 5 mm (**C**, **D**). Image credits: Marcela F. Colombo.

The following figures 3–12 depict specimens of *Cratoelcana zessini* examined in this study and never featured in the literature before. None of the specimens is of type status. Three more specimens (Figs. 10–12) that were not included in the analysis of character variation or considered during the review of *Cratoelcana zessini* presented above were discovered in the collection of Museu de Paleontologia Plácido Cidade Nuvens during a later stage of this manuscript's production. They are figured here to provide a broader range of individuals of this species.

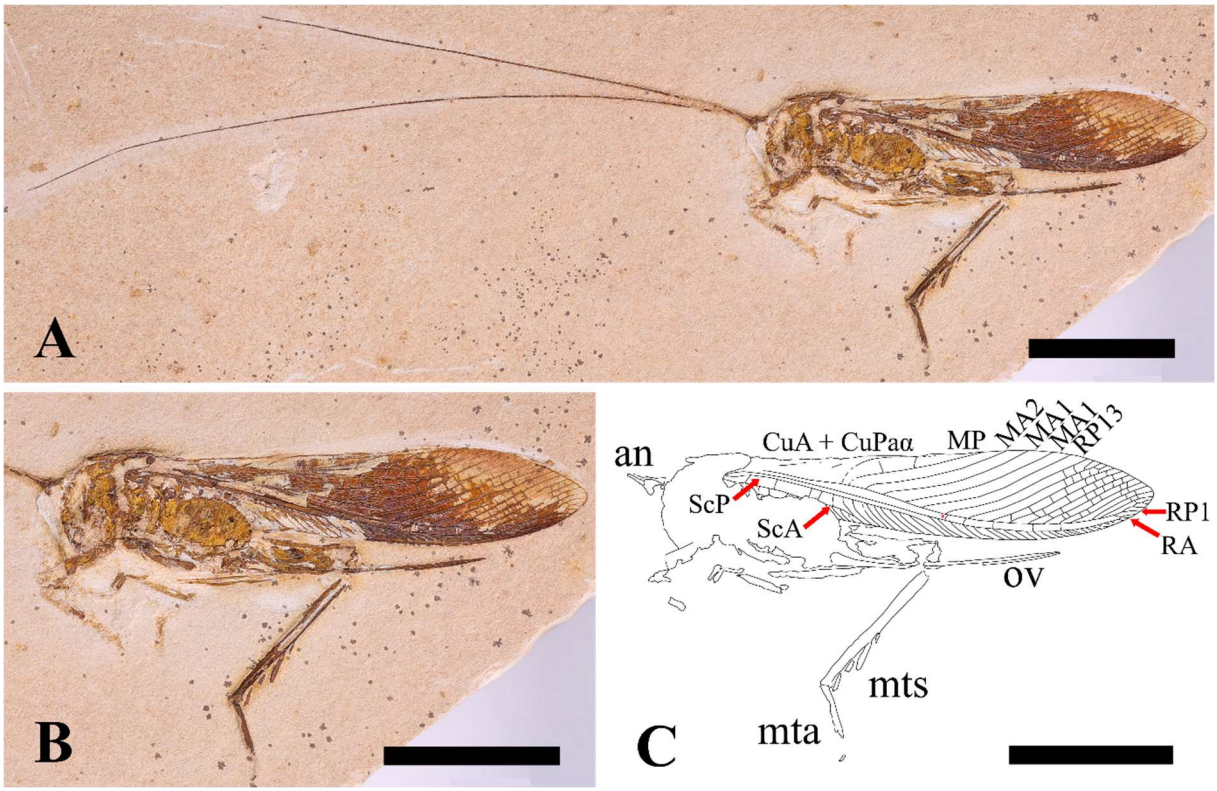

Fig. 3: *Cratoelcana zessini* Martins-Neto, 1991. Specimen INHS-P1131, female. **A.** View of complete specimen. **B.** A, but without the antennae. **C.** Drawing of B. Red asterisk marking stem of RP. **Abbreviations:** an = antennae; mts = metatibial spurs; mta = metatarsus; ov = ovipositor. **Scale bars** = 10 mm.

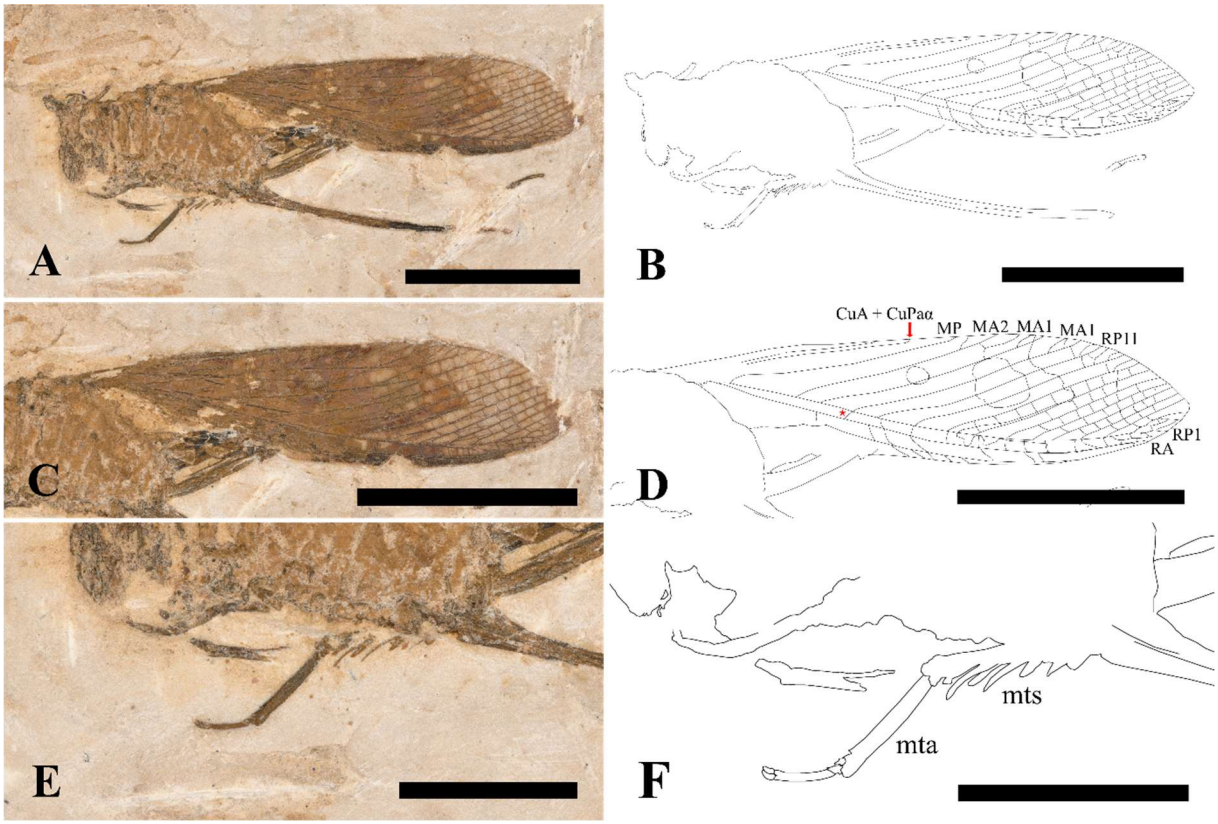

Fig. 4: *Cratoelcana zessini* Martins-Neto, 1991. Specimen HC0040, female. **A.** and **B.** Complete specimen. **C.** and **D.** Detail of wings. Note the partly preserved wing spots of this specimen. Red asterisk marking the stem of RP. **E.** and **F.** Detail of metathoracic tibia and tarsus. **Abbreviations:** mts = metatibial spurs; mta = metatarsus. **Scale bars** = 10 mm (A–D); 5 mm (E, F).

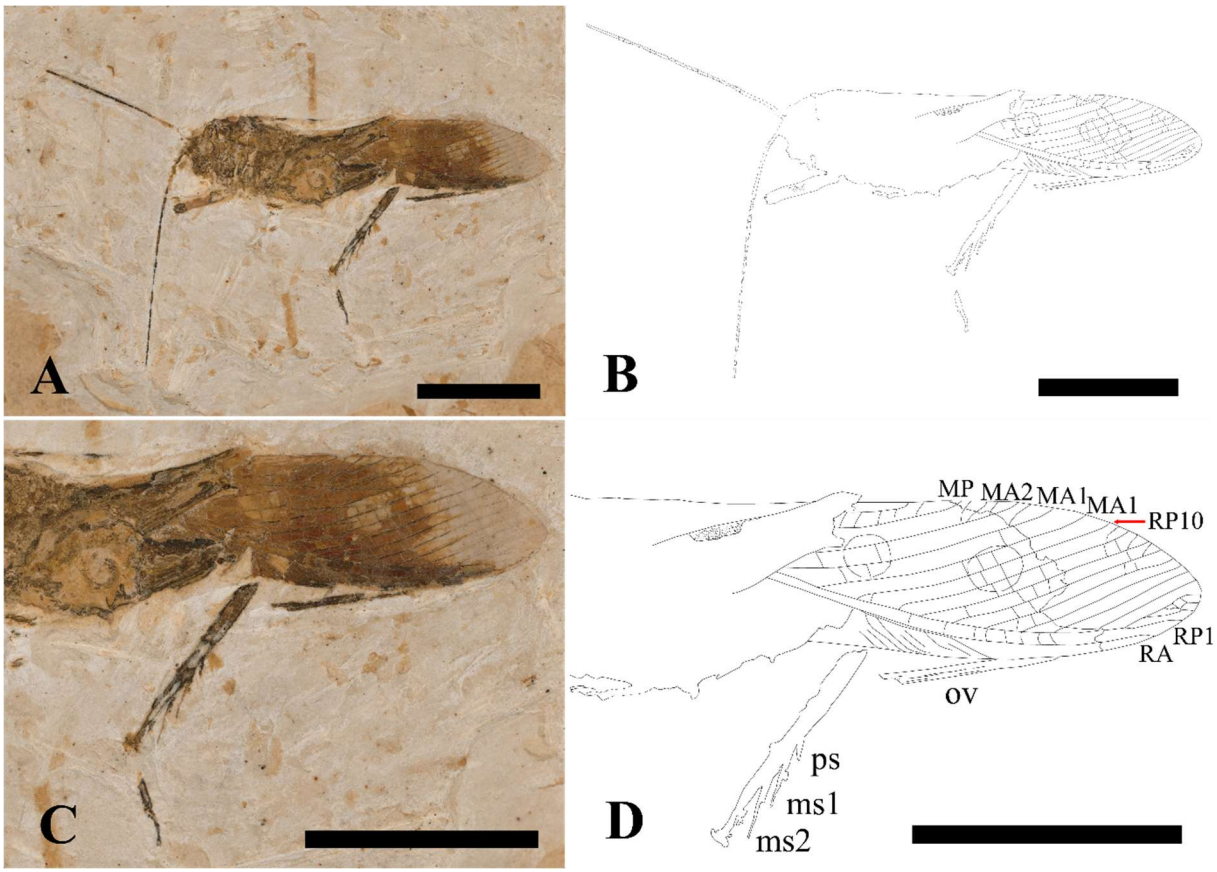

Fig. 5: *Cratoelcana zessini* Martins-Neto, 1991. Specimen HC0041, female. **A.** and **B.** Complete view of the specimen. **C.** and **D.** Detail of wings, ovipositor and metathoracic leg. Note the clear wing spots on this specimen. **Abbreviations:** ov = ovipositor; ps = proximal spur; ms1 = first metatibial spur; ms2 = second metatibial spur. **Scale bars** = 10 mm.

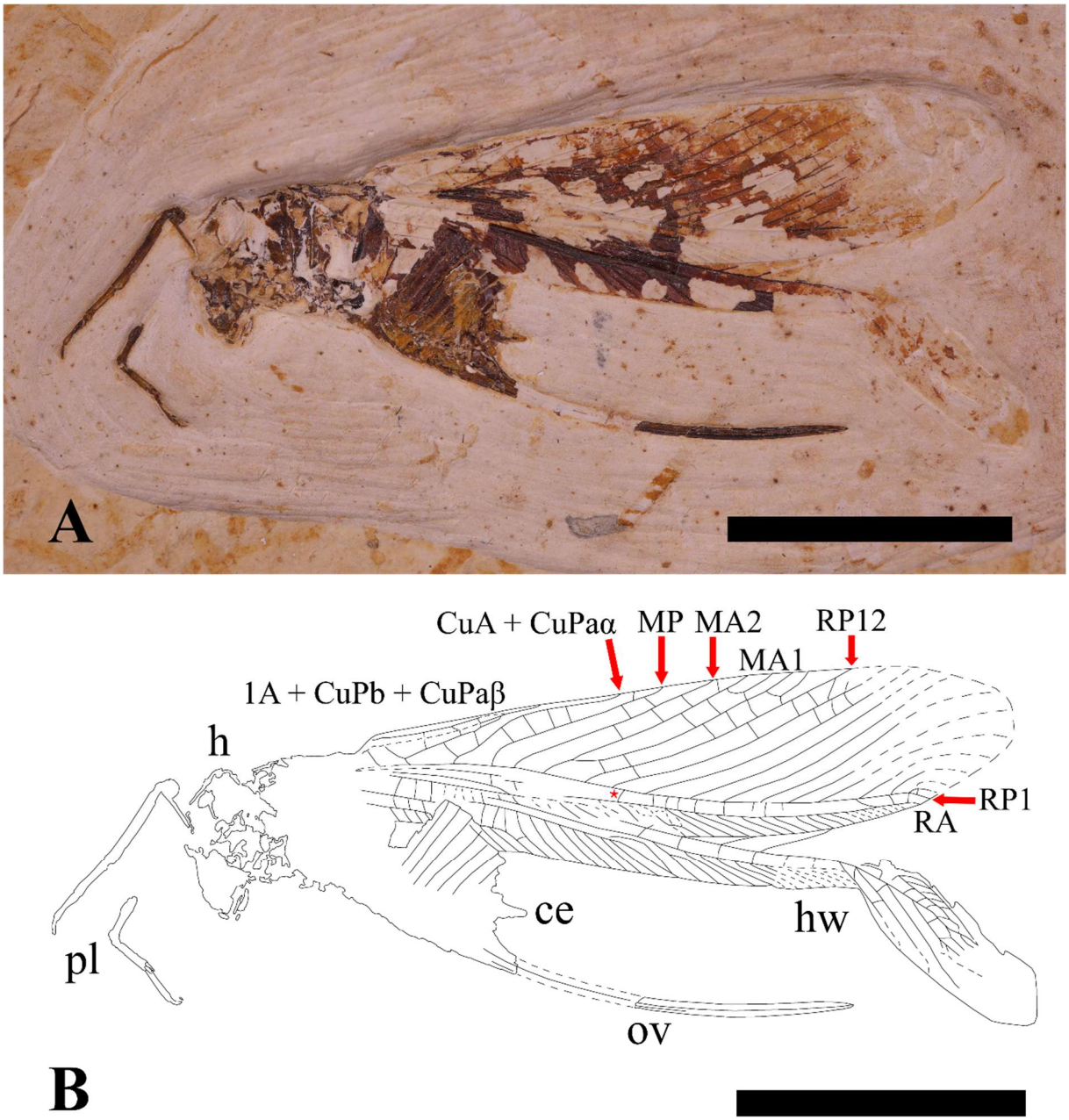

Fig. 6: *Cratoelcana zessini* Martins-Neto, 1991. Specimen AMNH_SA_45367, female. **A.** and **B.** Complete specimen. Red asterisk marking stem of RP. Note the fusion of the branches of MA1. **Abbreviations:** pl = prothoracic legs; h = head; ce = cercus; ov = ovipositor; hw = hindwing. **Scale bars** = 10 mm.

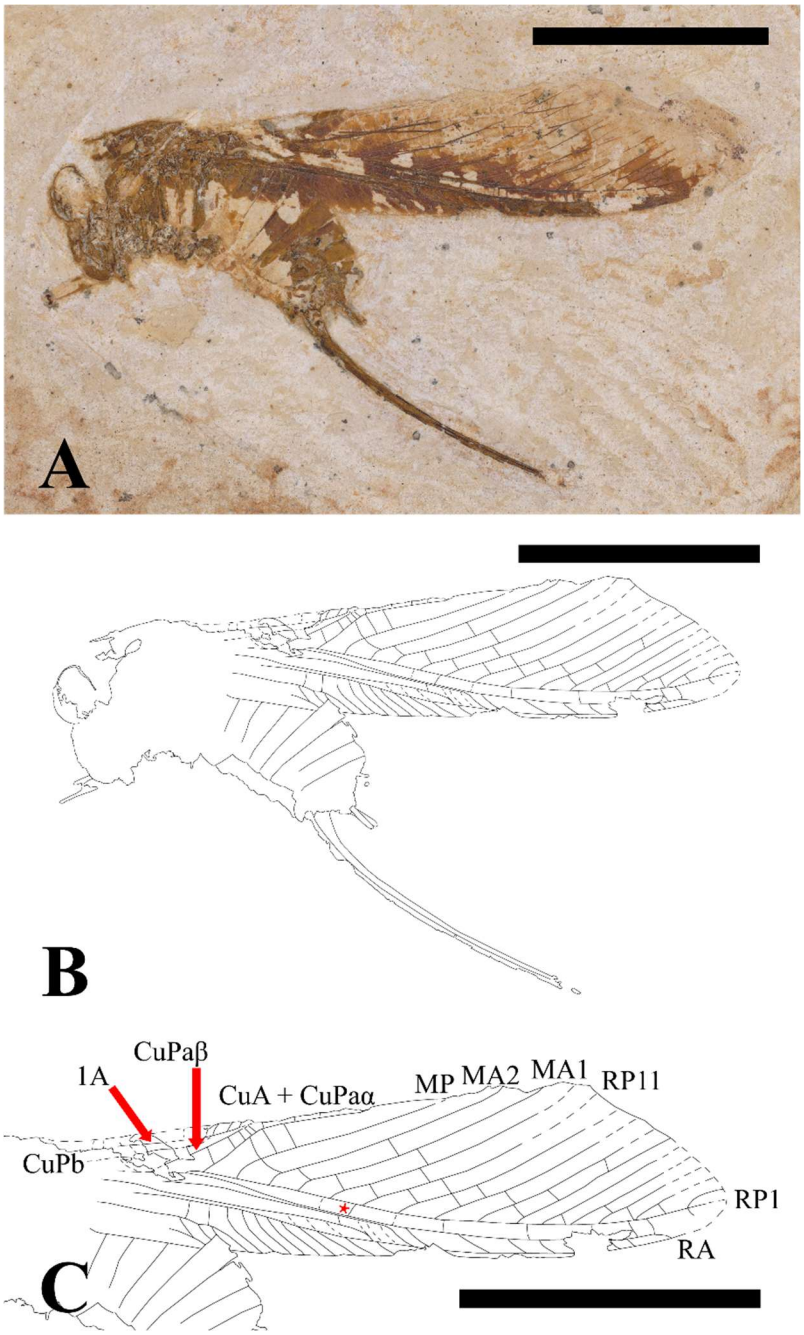

Fig. 7: *Cratoelcana zessini* Martins-Neto, 1991. Specimen SMNK_PAL_47253, female. **A.** and **B.** Complete specimen. **C.** Detail of the forewing with red asterisk marking the stem of RP. **Scale bars** = 10 mm.

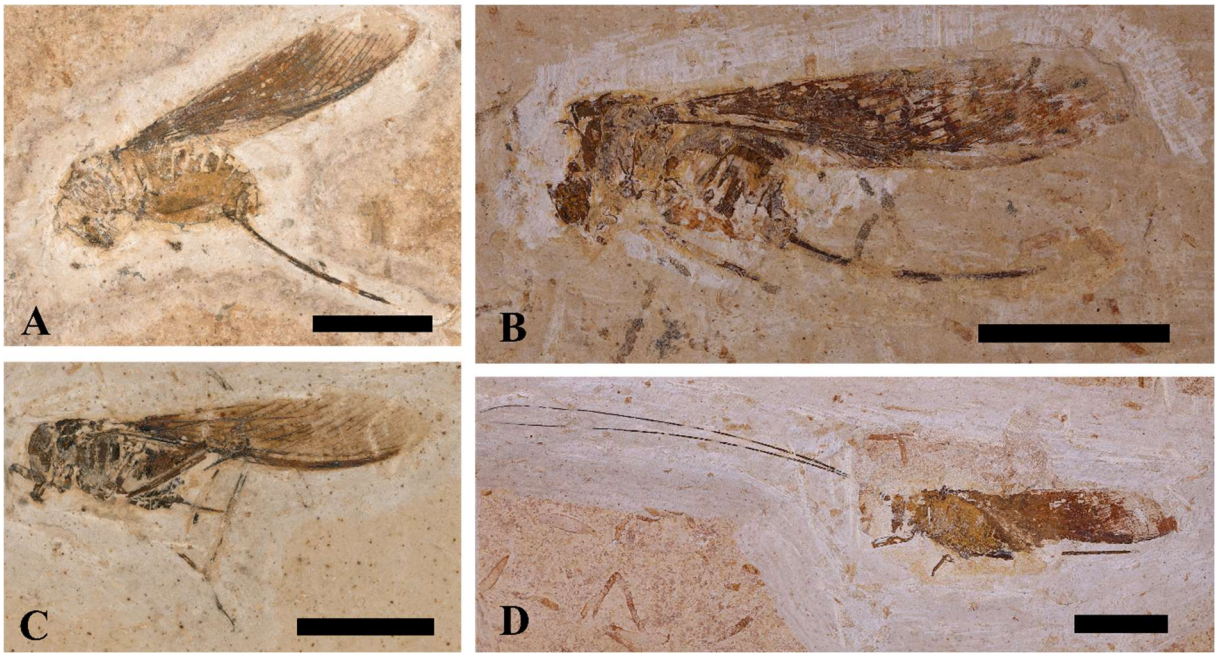

Fig. 8: *Cratoelcana zessini* Martins-Neto, 1991. Further specimens. **A.** HC0001, female. **B.** INHSP_1619, female. **C.** HC0026, female. **D.** INHSP_1626, female. **Scale bars** = 10 mm.

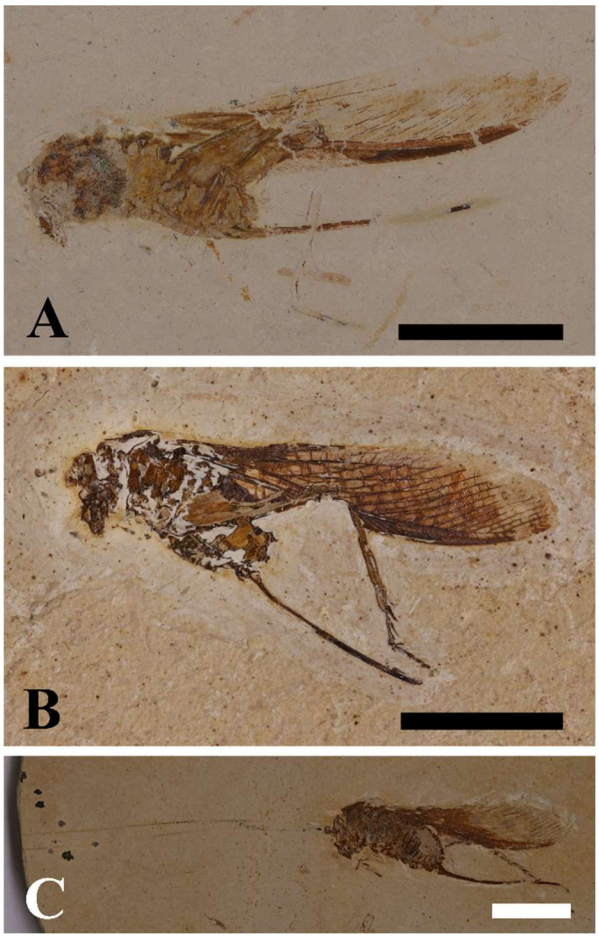

Fig. 9: *Cratoelcana zessini* Martins-Neto, 1991. Further specimens. **A.** MH1111, female. **B.** INHSP_1879, female. **C.** INHSP_1824, female. **Scale bars** = 10 mm.

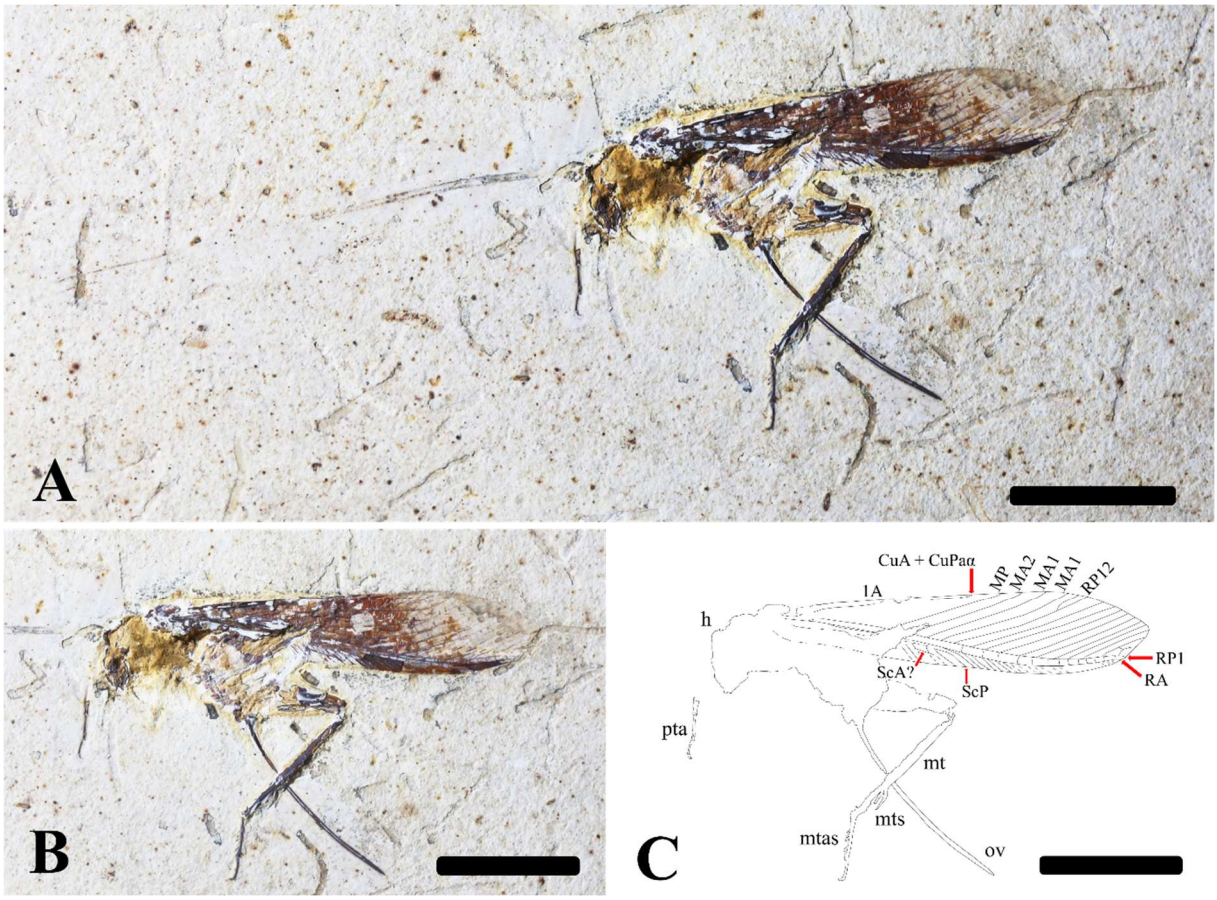

Fig. 10: *Cratoelcana zessini* Martins-Neto, 1991. Specimen MPSC 5570, female **A.** Overview of complete specimen. **B.** and **C.** Image and drawing of specimen without the antennae. The cubital area of the forewing (except for CuA + CuPaα) could not be distinguished. **Abbreviations:** h = head; mt = metatibia; mts = metatibial spur; mtas = metatarsus spurs/denticles; ov = ovipositor; pta = protarsus. **Scale bars** = 10 mm.

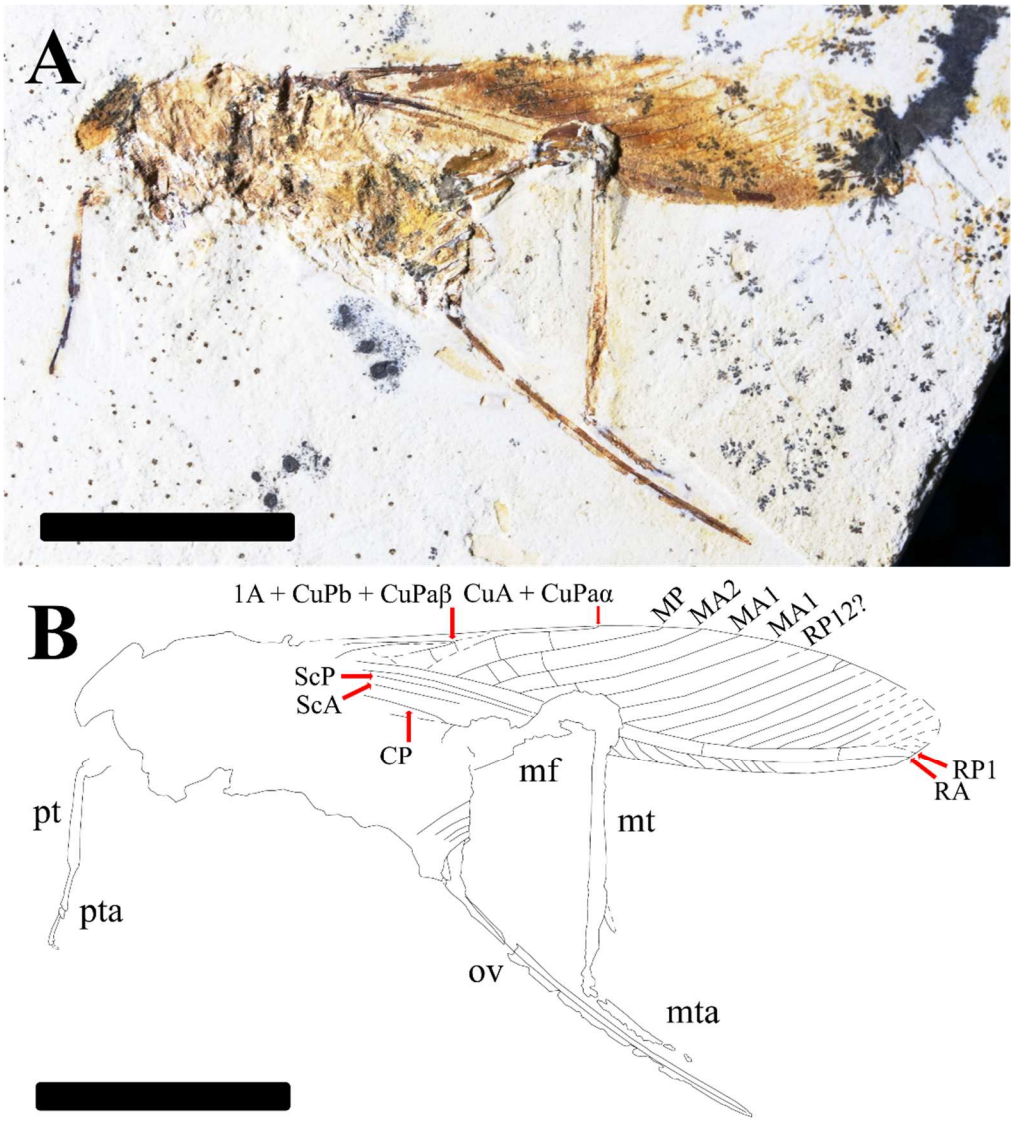

Fig. 11: *Cratoelcana zessini* Martins-Neto, 1991. Specimen MPSC 5729, female. **A.** and **B.** Overview (image and drawing) of complete specimen. **Abbreviations:** mf = metafemur; mt = metatibia; mta = metatarsus; ov = ovipositor; pt = protibia; pta = protarsus. **Scale bars** = 10 mm.

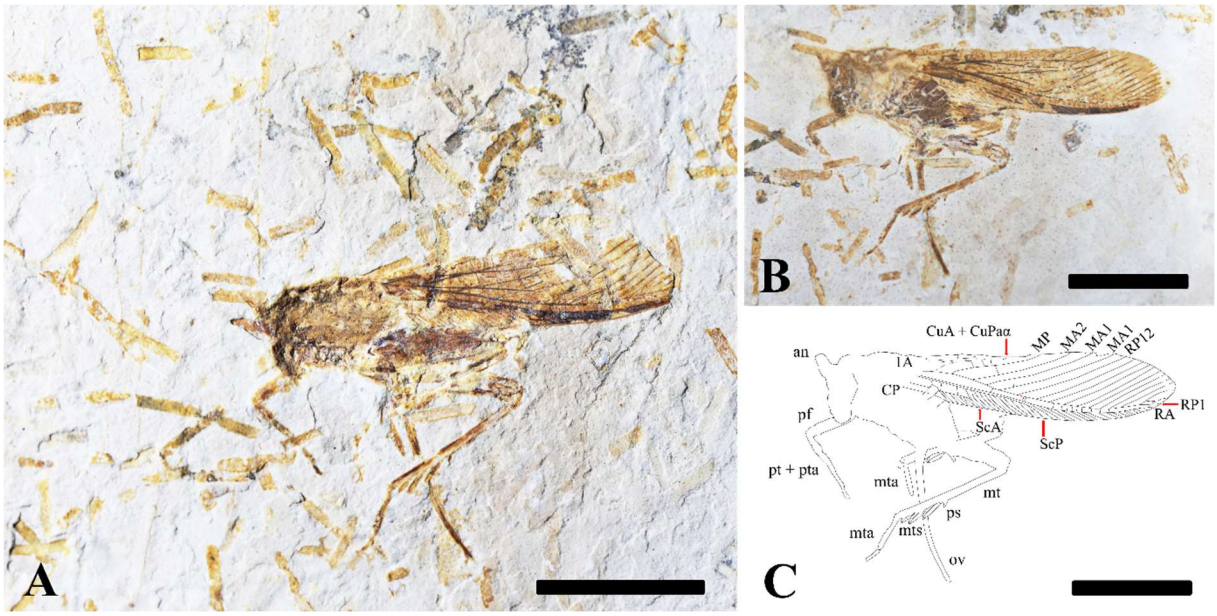

Fig. 12: *Cratoelcana zessini* Martins-Neto, 1991. Specimen MPSC 5811, female, part and counterpart. **A.** Overview of complete specimen (counterpart). **B.** and **C.** Image and drawing of specimen (part). Orientation of specimen was mirrored to allow for optimal comparison. Red star in C marks position of the RP stem (posterior of RP12). **Abbreviations:** an = antenna; mt = metatibia; ps = proximal metatibial spur; mts = metatibial spurs; mta = metatarsus; ov = ovipositor; pf = profemur; pt + pta = protibia and -tarsus. **Scale bars** = 10 mm.

Subfamily *Incertae sedis*

Genus ***Ensiferelcana*** new genus

Type species: *Ensiferelcana brachyptera* sp. nov. by monotypy and present designation. Gender feminine.

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: After the Latin “ensifer” (sword bearing) and “elcana” after the family Elcanidae. Translates as “sword bearing lagoon cricket” and refers to the proportionally long ovipositor of the type species.

Diagnosis: As for the type species by monotypy.

Remarks: The new genus is attributed to the Elcanidae based on the fusion of tegminal M and RP, single CuA + CuPaα, antennae longer than body and the prominent ovipositor.

Unfortunately, the metatibial spurs of this specimen are not preserved. The basal area of the tegmen cannot be distinguished, making assignment to a subfamily problematic. *Ensiferelcana* gen. nov. can be differentiated from all other genera of Elcanidae known so far by its proportionally very long ovipositor, surpassing the tip of the forewing by a distinct amount. Interestingly, this is not due to the ovipositor itself being long, but rather the forewings being comparably short. Because of its smaller number of RP branches (10 vs. 11–13) compared to *Cratoelcana zessini*, one less branch of tegminal M (3 vs. 4) and a different orientation of the ovipositor (straight and pointed upwards vs. slightly curved and pointing downwards in most specimens of *C. zessini*), it seems unlikely for now that specimen MPSC 9831 (the holotype of *E. brachyptera* sp. nov.) is a short-wing morph of *C. zessini*. It is possible that future findings might point towards this direction, as short-wing morphs are known from many modern-day orthopterans (e.g., *Decticus verrucivorus verrucivorus* (Linnaeus, 1758) or *Eobiana engelhardti subtropica* (Bey-Bienko, 1949). No apparent short-wing morph has been described for Elcanidae, however.

Ensiferelcana brachyptera new species

Fig. 13

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: After the ancient Greek “brachys” (short) and “pteryx” (wing). Translates to “short winged” and refers to the wings of the type species being surpassed by the ovipositor.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Lower Cretaceous, Aptian.

Holotype: Female, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Brazil, coll. no. MPSC 9831 (ex-collection Illinois Center for Paleontology, University of Illinois, USA, coll. no. INHS-P1866).

Diagnosis: Forewing length 16.6 mm. Distance between CuA + CuPaα and MP rather narrow. Tegminal M with three branches. Tegminal RP with 10 branches. Ovipositor length/forewing

length ratio very high, at least 0.86. Ovipositor completely straight. Body length 12.8 mm. Head height/forewing length 0.35. Antennae longer than body.

Description: Measurements: Forewing length 16.6 mm. Forewing height 3.5 mm. Forewing length/height 4.7. Body length 12.8 mm. Ovipositor length 14.2 mm or longer (tip possibly missing). Antennae length preserved (possibly full) 30.3 mm. Profemur 5.1 mm long. Cercus 2.6 mm long.

Body: Cercus one-segmented, relatively long. Ovipositor very long, distinctly surpassing forewing; angled upwards and completely straight.

Forewing: Distance between CuA + CuPaα and MP rather narrow, ca. 14.9% of total wing length. M with three branches. RP with ten branches.

Remarks: The female specimen of *Cratoelcana zessini* INHS-P1131 (see above) exhibits an ovipositor length of 14.4 mm and a body length of 10.8 mm, dimensions that are comparable to those of *E. brachyptera* sp. nov., which possesses an ovipositor of 14.2 mm length and 12.8 mm body length. However, the forewing length of *C. zessini* exceeds that of *E. brachyptera* by ca. 10 mm–a key distinction that underlines the specific epithet "*brachyptera*", denoting the relatively short wings of the latter taxon, meaning "short-winged". Similar to *Argentoelcana* gen. nov., *Ensiferelcana* appears to have been rare among the Elcanidae assemblage of the Crato-Formation, with only one out of 88 examined specimens attributed to this genus. The male specimen (INHS-P1937), mentioned above, may tentatively be considered as conspecific with *E. brachyptera*. However, its notably shorter cerci length (1.5 mm) argues against this assignment. Given that male orthopterans typically exhibit cerci that are longer than those of females, the morphology of INHS-P1937 aligns more closely with *Argentoelcana*.

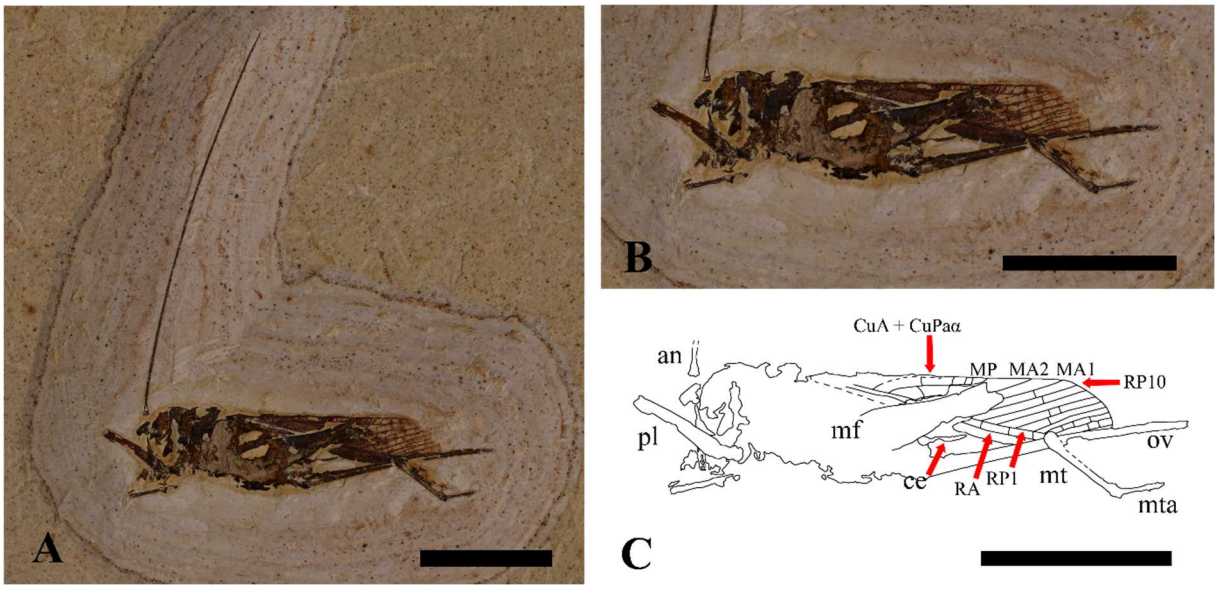

Fig. 13: *Ensiferelcana brachyptera* gen. et sp. nov. holotype MPSC 9831, female. **A.** Complete specimen. **B.** and **C.** Specimen with only part of antenna. **Abbreviations:** an = antennae; pl = prothoracic leg; mf = metafemur; mt = metatibia; mta = metatarsus; ce = cercus; ov = ovipositor. **Scale bars** = 10 mm.

Subfamily Elcaninae Handlirsch, 1906

Genus ***Gondwanaelcana*** new genus

Type species: *Gondwanaelcana brasiliensis* sp. nov. by monotypy and present designation. Gender feminine.

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: After the southern supercontinent Gondwana and "elcana" after the family Elcanidae. Translates as "lagoon cricket from Gondwana".

Diagnosis: As for the type species by monotypy.

Gondwanaelcana brasiliensis new species

Figs. 14–19

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: After the country Brazil where the Crato Formation is located. Translates as “from Brazil”.

Locality and horizon: Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Lower Cretaceous, Aptian.

Holotype: Female, in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Brazil, coll. no. MPSC 9830. Donation from the Husemann Research Collection of Dr. Martin Husemann at the Public Museum of Natural History Karlsruhe, Karlsruhe, Germany (collection number HC0037) as part of the guidelines discussed at the “Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future” (Fig. 14).

Paratype specimens: CNBS00422; HC0002; HC0025; HC0038; SMNK_PAL_45251; AMNH_SA_45082; AMNH_SA_45092; INHSP_1125; INHS-P1168 (all ♀)

Diagnosis: Forewing length 9.8–12.2 mm. Tegminal RP with 6–8 branches. Tegminal M with three branches. Stem of RP located after MA1. Body length 5.7–6.7 mm. Ovipositor short, saber type of Willmott et al., 2025; ovipositor length/forewing length <0.1.

Description of holotype:
Measurements: Forewing length 12.2 mm. Forewing length/height 3.9. Body length 6.4 mm. Ovipositor length/forewing length 0.05. Ovipositor length 1.1 mm. Metatibia 5.2 mm long.

Body: Metatibia with three partly preserved large spurs. No proximal or apical spur preserved. Metabasitarsus with some prominent denticles preserved. Ovipositor short and thin, slightly s-curved; of the saber-type.

Wings: Distance between CuA + CuPaα and MP rather short, ca. 14.8% of total wing length. M with three branches, RP with eight branches. RP2 with fusion of former RP2 and RP3.

Additional characters shown only by the paratypes:
Antennae significantly longer than body, ca. 20.3 mm (SMNK_PAL_45251). Compound eye very large, almost as wide as head and 1.16 mm high (HC0002). Cerci heavily setulose across

the entire surface (HC0038) and with a hair-like tip (INHS-P1168). A smaller proximal spur (CNBS0422) and a large apical spur (SMNK_PAL_45251) is preserved on the metatibiae of some specimens (AMNH_SA_45092 with proximal and apical spur).

Remarks: Gondwanaelcana brasiliensis sp. nov. and *Panorpidium damianii* comb. nov. are the pair of small-sized elcanids of the Crato Formation, while *Mesembrelcana rasnitsyni* comb. nov. and *Cratoelcana zessini* are the large-sized pair. The first species of each pair is best differentiated from the second by the much shorter ovipositor of the saber type instead of the sword type. The saber ovipositor separates *Gondwanaelcana* gen. nov. from *Panorpidium*. It can be differentiated from the other taxa of Elcanidae bearing this type of ovipositor (*Elcanodentes alatus* Willmott, Schall, Kotthoff and Husemann, 2025 and *Pseudoprobaisselcana oculata* (Hu and He, 2023)) by a shorter distance between tegminal CuA + CuPaα and MP (14.8% of total wing length in *G. brasiliensis* sp. nov., 21% in *P. oculata*, 32.8% in *E. alatus*). The subfamily assignment to Elcaninae is preliminary for now, as the state of tegminal 1A + CuPb + CuPaβ cannot be stated without possible error due to less-than-ideal preservation of this area in all specimens of this species. It is based on the previous three genera clearly showing the fusion of these veins. In two specimens of *G. brasiliensis* sp. nov. (MPSC 9830 and HC0025, holotype and paratype, respectively) the area below RA, interpreted as a pterostigma in Elcanidae by various authors such as Kočárek (2020) or Fang et al. (2018), shows signs of being absent of cross veins. A pterostigma without cross veins is known from several taxa of Kachin amber Elcanidae and has been used as a character of taxonomic value for example by Schall et al., (2025). However, it is possible that the veins in these two specimens just are not preserved, as this appears to be a problem with other characters in Crato-Elcanidae too (see the discussion about tegminal coloration in the remarks on *Mesembrelcana rasnitsyni* comb. nov. below). Another structure possibly affected by this issue are proximal and apical metatibial spurs which are clearly present in some specimens of *G. brasiliensis* sp. nov. but missing in others. Unfortunately, it is difficult to determine whether missing features like this are due to true absence (i.e., they were not present in the live animal) or false absence (i.e. they were present in the live animal but are not preserved in the fossil). In this study, we decided to rely on characters with a high chance of preservation (forewing length, RP branches, position of RP stem, ovipositor morphology), because they are less prone to overestimating species richness among Crato-Elcanidae. Nonetheless, it is (quite) possible that more species hide among the six taxa presented here.

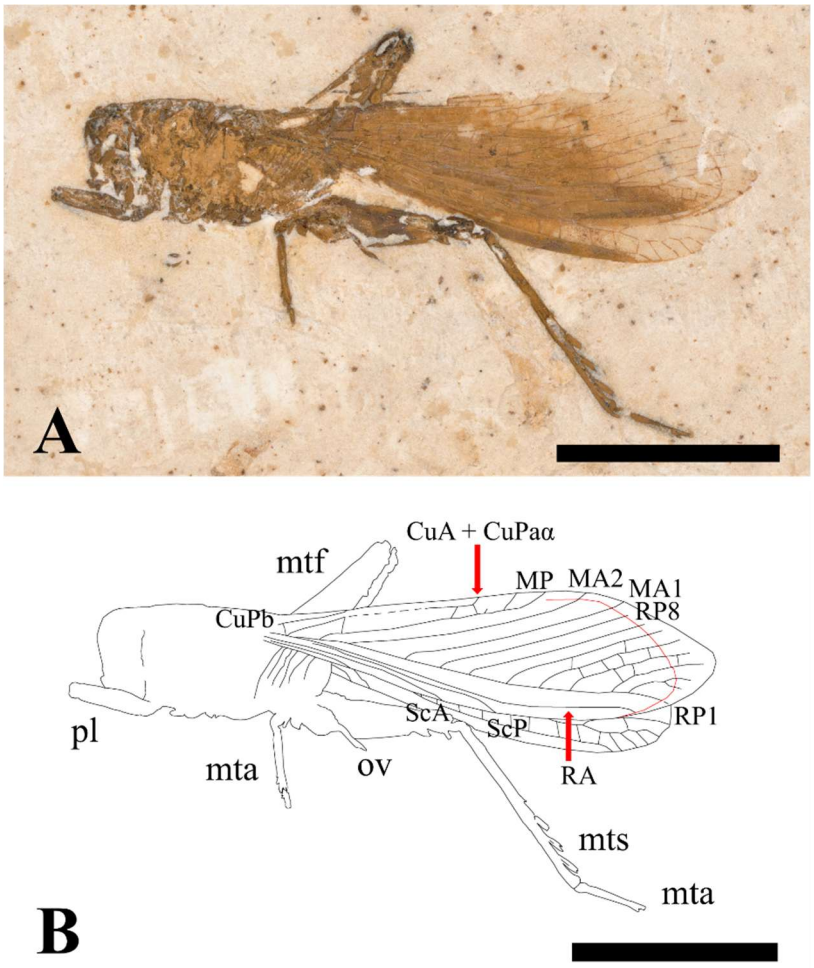

Fig. 14: *Gondwanaelcana brasiliensis* gen. et sp. nov. holotype MPSC 9830, female. **A.** and **B.** Complete specimen. **Abbreviations:** pl = prothoracic leg; mtf = metafemur; mts = metatibial spurs; mta = metatarsus; ov = ovipositor. **Scale bars** = 5 mm.

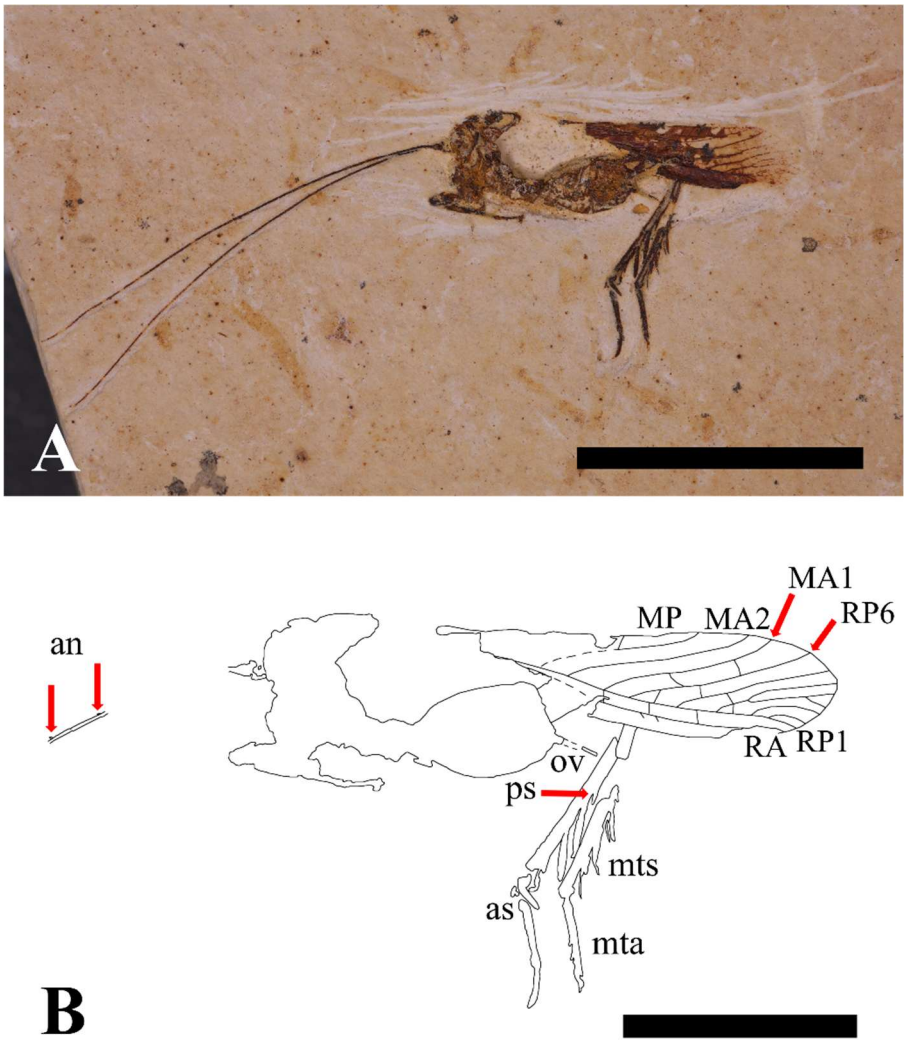

Fig. 15: *Gondwanaelcana brasiliensis* gen. et sp. nov. paratype AMNH_SA_45092, female. **A.** and **B.** Complete specimen (B with antennae partly drawn). Red arrows on piece of antenna mark two small spines on the antennomeres. Note the apparent difference in metatibial spination from right to left leg of this specimen (presence/absence of large apical spine; metatibial main spur size). It suggests that metatibial spur morphology may not be a reliant character for determining taxonomy of Crato Formation Elcanidae. **Abbreviations:** an = antenna; ov = ovipositor; ps = proximal spur; mts = metatibial spurs; as = apical spur; mta = metatarsus. **Scale bars** = 5 mm.

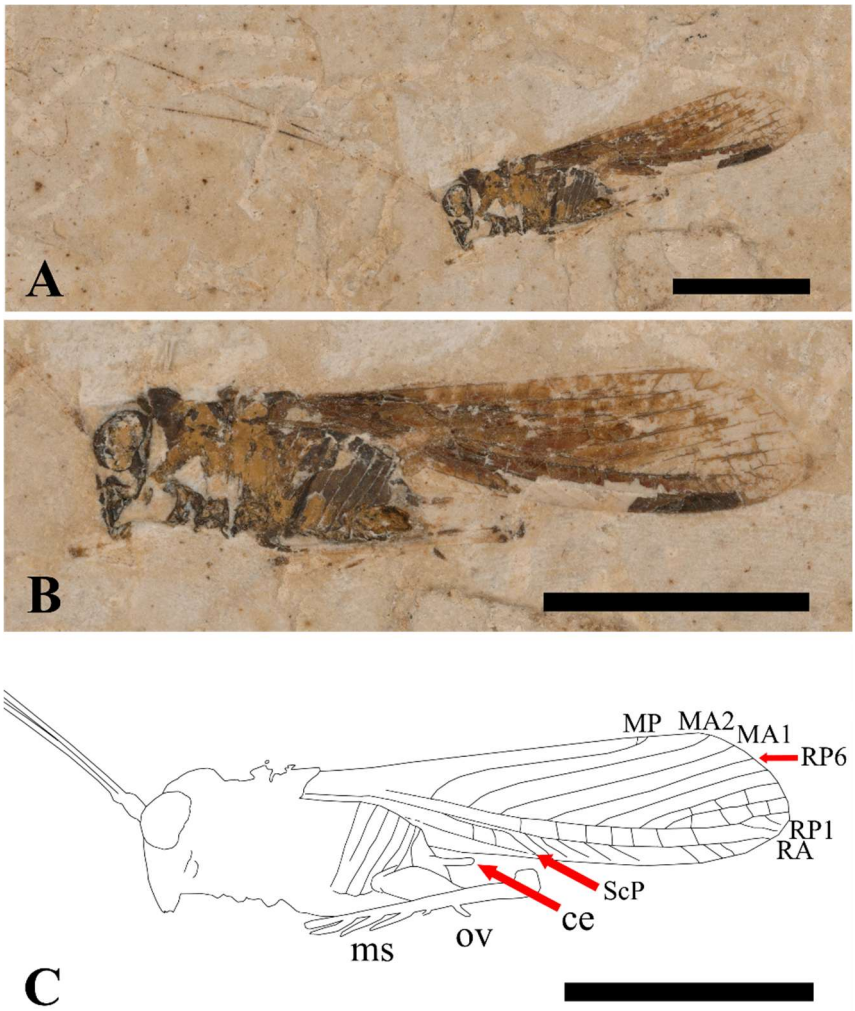

Fig. 16: *Gondwanaelcana brasiliensis* gen. et sp. nov. paratype HC0002, female. **A.** Complete specimen. **B.** and **C.** Specimen with only part of antennae. Note the large compound eyes visible on this specimen. **Abbreviations:** ms = metatibial spurs; ov = ovipositor; ce = cercus. **Scale bars** = 5 mm.

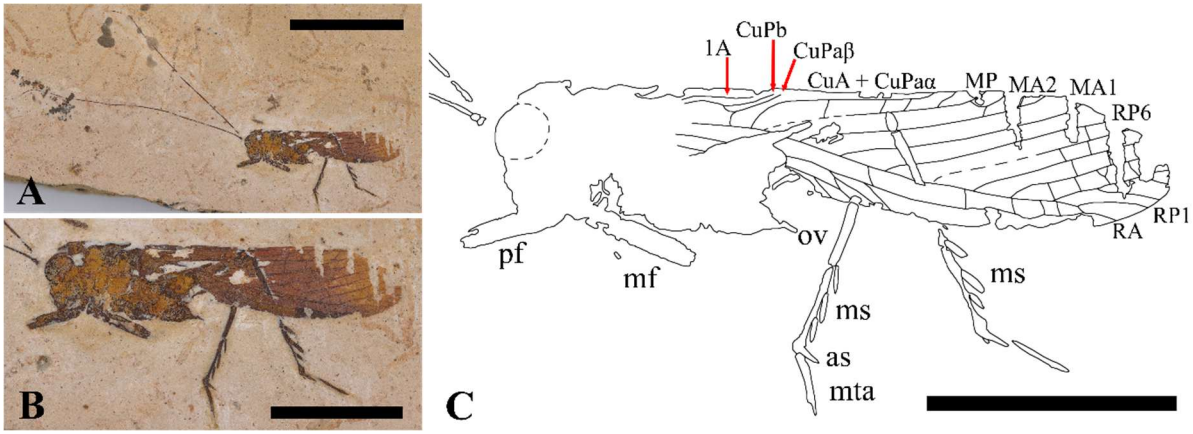

Fig. 17: *Gondwanaelcana brasiliensis* gen. et sp. nov. paratype SMNK_PAL_45251, female. **A.** Complete specimen. **B.** and **C.** Specimen with only part of antennae. Unfortunately, the endings of tegminal 1A, CuPb and CuPaβ are not distinguishable. **Abbreviations:** pf =

profemur; mf = mesofemur; ov = ovipositor; ms = metatibial spurs; as = apical spur; mta = metatarsus. **Scale bars** = 5 mm.

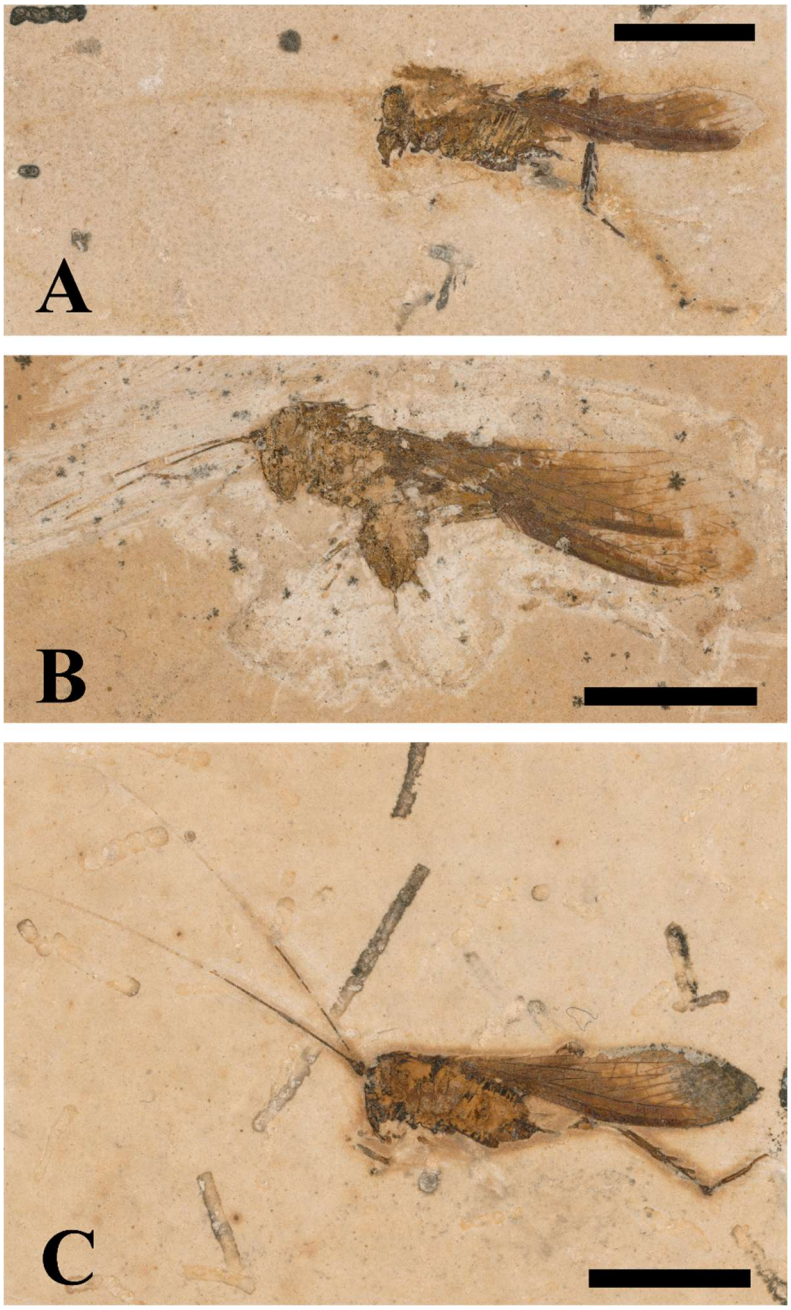

Fig. 18: *Gondwanaelcana brasiliensis* gen. et sp. nov. paratype specimens. **A.** HC0038, female. **B.** HC0025, female. **C.** CNBS00422, female. **Scale bars** = 5 mm.

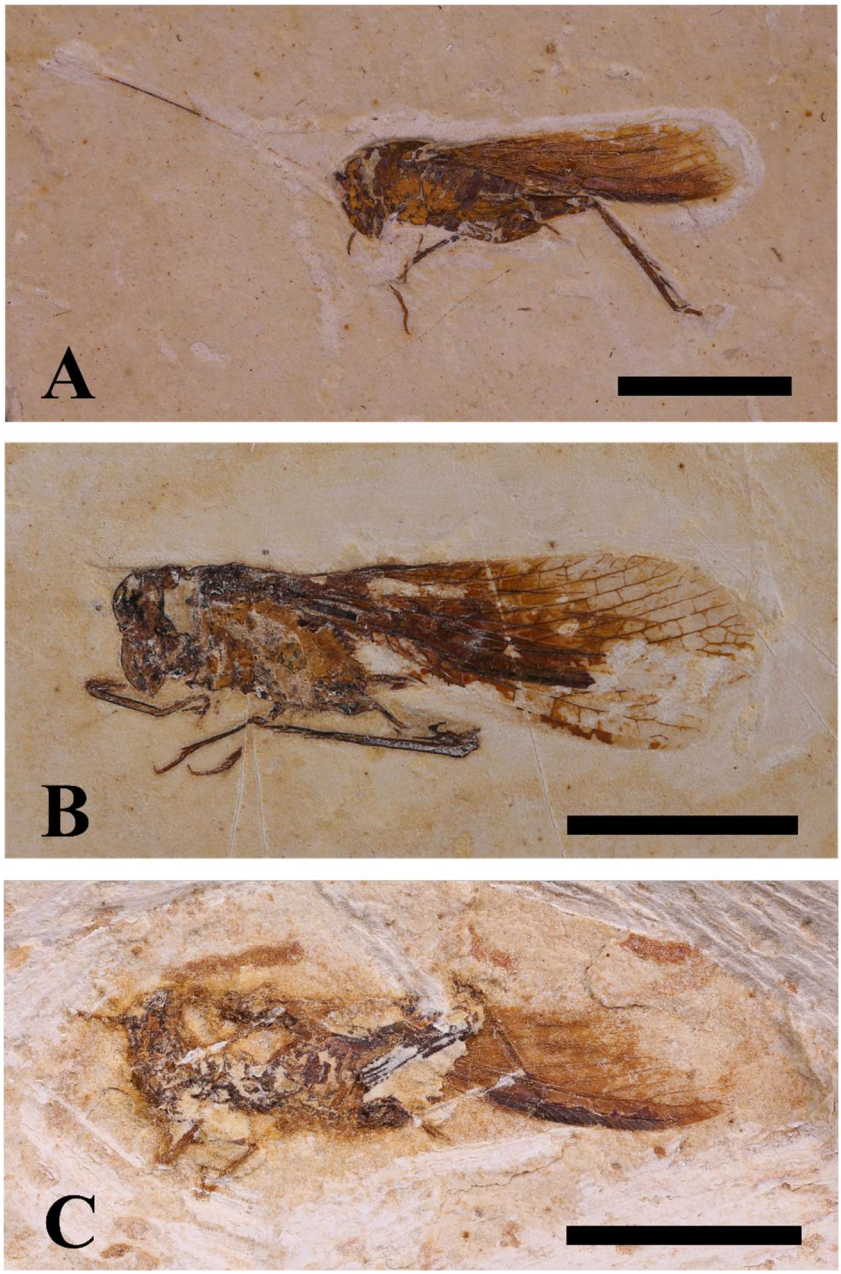

Fig. 19: *Gondwanaelcana brasiliensis* gen. et sp. nov. paratype specimens. **A.** AMNH_SA_45082, female. **B.** INHS-P1168, female. **C.** INHSP_1125, female. **Scale bars** = 5 mm.

Genus ***Mesembrelcana*** new genus

Type species: *Cratoelcana rasnitsyni* Nel and Jouault, 2022.

Zoobank-ID: Will be added in the article version of this chapter.

Etymology: After ancient Greek “mesembria” (south) and “elcana” for the family Elcanidae. The name translates as “Elcanidae from the south” or “lagoon cricket from the south”.

Diagnosis: As for the type species by monotypy.

Remarks: *Mesembrelcana* gen. nov. is conspicuously similar to *Cratoelcana* Martins-Neto, 1991 and the same character for generic separation from other elcanids applies (i.e. the stem of RP is more posteriorly located, varying from below last RP to posterior of second last RP). Females of *Mesembrelcana* and *Cratoelcana* can easily be differentiated by the different type of ovipositor, which is the sword-type in *Cratoelcana* and the saber-type in *Mesembrelcana*. Males of the two taxa cannot be differentiated at the current state of knowledge.

Mesembrelcana rasnitsyni (Nel and Jouault, 2022) comb. nov.
Figs. 20–26

Holotype: The holotype specimen is currently in the private collection of Markus Seenlaub (identifier number 13,068) and is supposed to be deposited in a Brazilian museum (Nel and Jouault, 2022).

Examined specimens (not of type status): HC0024; HC0028; HC0044; INHS-P1179; INHS-P1874; INHS-P1878; INHS-P1887; INHS-P1935 (all ♀). Two more specimens were discovered in the collection of MPSC at a later point during the writing of this article. They are included as figures (Figs. 25, 26) but were not considered for the rest of the study (such as the analysis of characters variation): MPSC 5771; MPSC 5792 (all ♀).

Emended diagnosis: Forewing length 23.8–26.4 mm (*tegmen large after Nel and Jouault (2022)). 1A + CuPb + CuPaβ fused. Tegminal RP with 10–14 branches (*11-12 after Nel and Jouault (2022)). Tegminal M with four branches. Stem of RP located below last RP to posterior of second last RP. Body length 12.1–15 mm. Tegminal surface with color pattern consisting of two round wing spots of equal size and a broad colored apical margin (* tegmen with a small dark apical zone, a hyaline transverse band and dark basal part of tegmen with two rounded hyaline spots in the middle after Nel and Jouault (2022)). Ovipositor short, saber type; ovipositor length/forewing length <0.1.

Remarks: The taxon currently referred to as *Mesembrelcana rasnitsyni* comb. nov. was originally described as the third species of *Cratoelcana* by Nel and Jouault (2022). In their

diagnosis, the authors primarily relied on forewing coloration patterns to distinguish the holotype of *M. rasnitsyni* comb. nov. from *C. zessini*, noting the presence of distinct wing spots in the former and their supposed in the latter. While such pigmentation differences may appear taxonomically significant, the reliability of wing coloration as a diagnostic feature in Elcanidae from the Crato Formation is questionable due to the variable preservation of pigments. For example, specimen HC0024 (Fig. 23A) apparently shows a colored apical wing margin and just anterior of it what could be interpreted as the remains of a partially preserved wing spot. In HC0028 (Fig. 23B), two wing spots can arguably be interpreted, though with considerably less clarity than in the holotype of *M. rasnitsyni* comb. nov. Specimen INHS-P1179 (Fig. 21) preserves wing spots with relative clarity, but the presence of damage on both markings underscores the influence of taphonomic alteration on their visibility. Moreover, specimens attributed herein to *Cratoelcana zessini*, such as HC0041 (Fig. 5) and INHS-P1626 (Fig. 8D), also exhibit traces of partially preserved wing spots. These observations collectively suggest that wing coloration patterns are not consistently preserved and should therefore be regarded with caution in taxonomic assessments of Crato Formation Elcanidae. In contrast, ovipositor morphology of the *M. rasnitsyni* comb. nov. holotype–as figured by Nel and Jouault (2022)–differs markedly from the elongate, needle-like ovipositor of *C. zessini*. Instead, it resembles a robust, saber-shaped structure, comparable to the ovipositors described by Willmott et al. (2025) for the Kachin amber species *Elcanodentes alatus* and *Pseudoprobaisselcana oculata*. This structure, overlooked in the original description of *M. rasnitsyni* comb. nov., represents the most consistent character for distinguishing *Mesembrelcana* gen. nov. from *Cratoelcana*, which are otherwise morphologically similar. *Mesembrelcana* gen. nov. can further be differentiated from *E. alatus* and *P. oculata* by its substantially larger size and the more posterior origin of the RP stem.

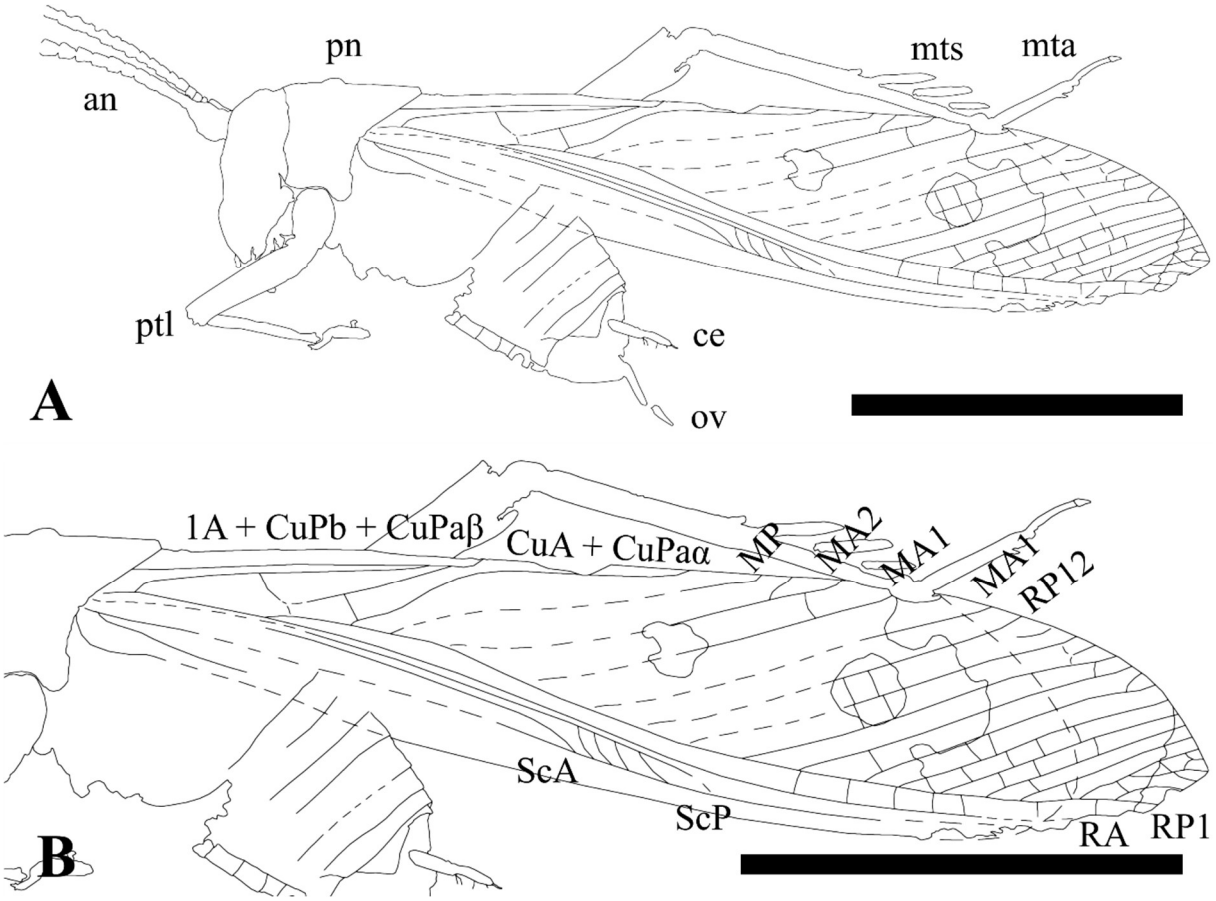

Fig. 20: *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) comb. nov. holotype 13,068 from Markus Seenlaub private collection, female. Drawing after the specimen depicted in Nel and Jouault (2022). Fig. 1. Due to copyright issues with the publisher of the original material, we are not able to reproduce photographs of the holotype. **A.** Specimen overview. **Abbreviations:** an = antenna; pn = pronotum; ptl = prothoracic leg; mts = metatibial spurs; mta = metatarsus; ce = cercus; ov = ovipositor. **B.** Detail of forewing with apical margin of hindwing indicated by dotted line. Note the two wing spots clearly visible on this specimen of *M. rasnitsyni*. **Scale bars** = 10 mm.

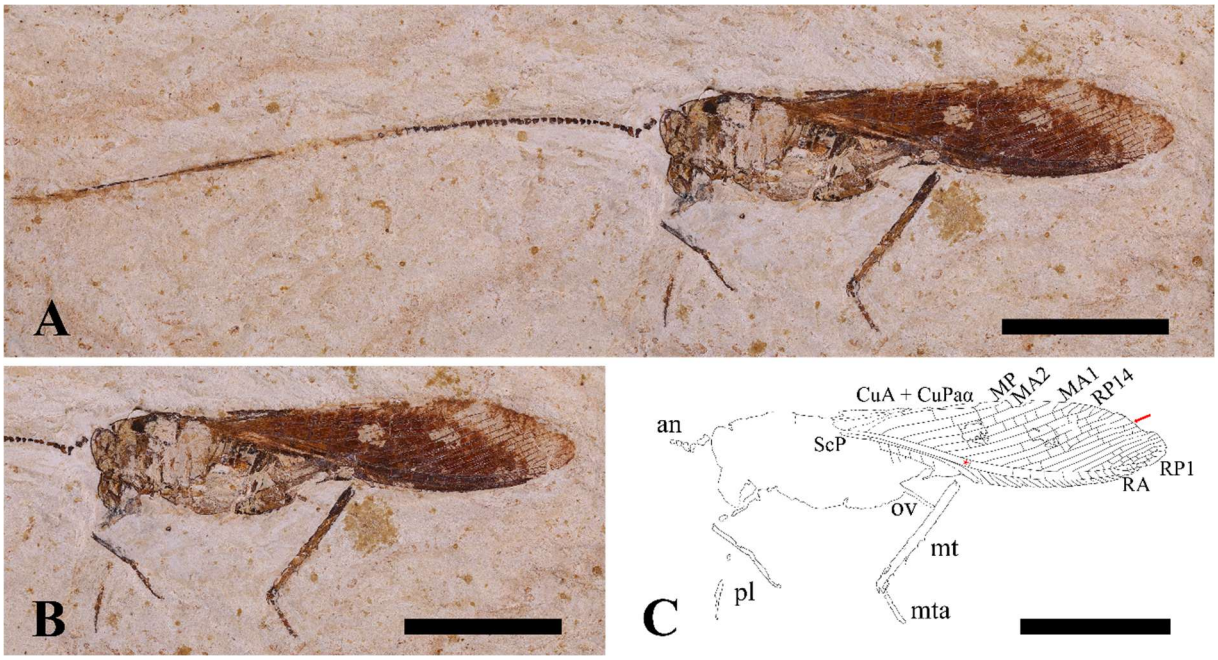

Fig. 21: *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) comb. nov. specimen INHS-P1179 (not of type status), female. **A.** Complete specimen. **B.** and **C.** Specimen without antennae. Red asterisk marking the stem of RP. Note the fusion happening at RP10 (red arrow). **Abbreviations:** an = antennae; pl = prothoracic legs; mt = metatibia; mta = metatarsus; ov = ovipositor. **Scale bars** = 10 mm.

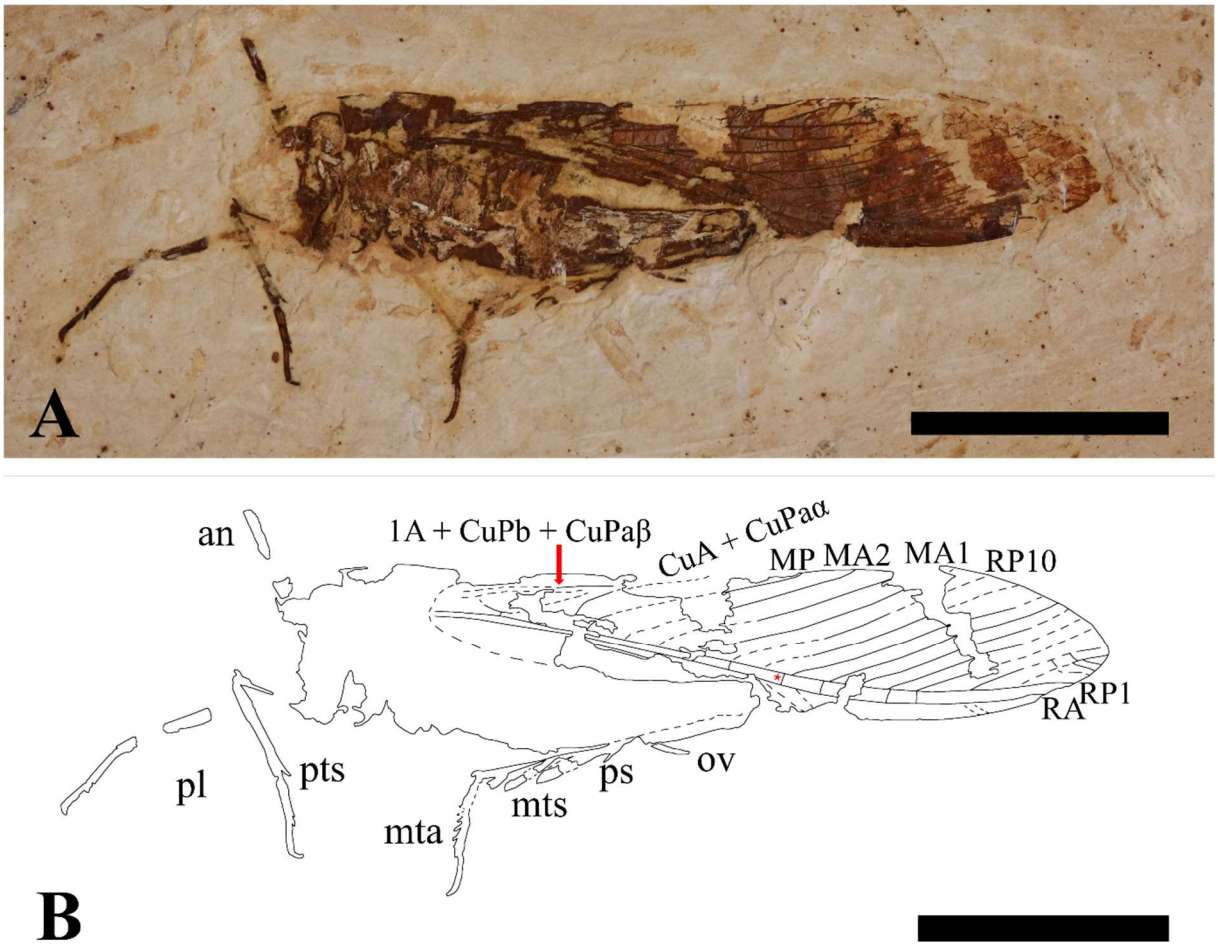

Fig. 22: *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) comb. nov. specimen INHS-P1887 (not of type status), female. **A.** and **B.** Complete specimen. Red asterisk marking the stem of RP. **Abbreviations:** an = antenna; pl = prothoracic legs; pts = protibial spine; ps = proximal spur; mts = metatibial spurs; mta = metatarsus; ov = ovipositor. **Scale bars** = 10 mm.

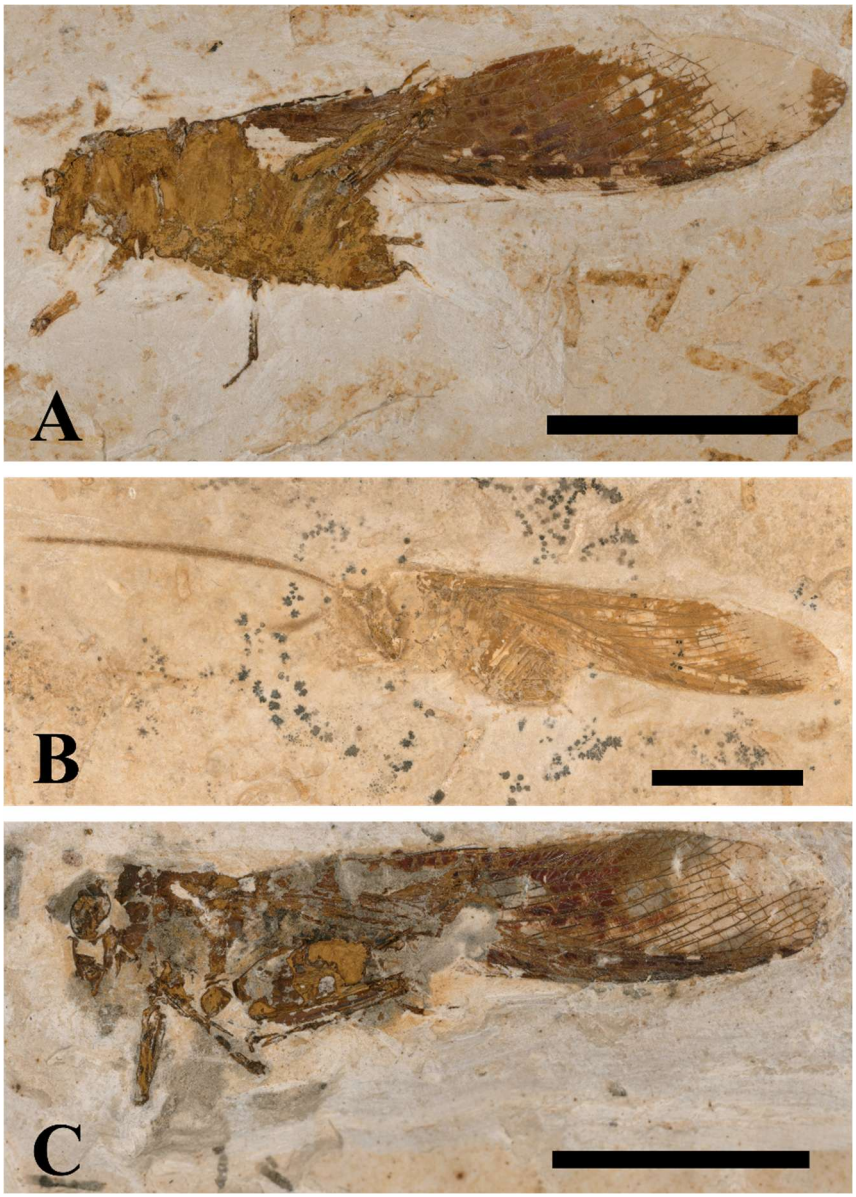

Fig. 23: *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) comb. nov. non-type specimens. **A.** HC0024, female. **B.** HC0028, female. **C.** HC0044, female. Note the differences in wing color pattern preservation between these three specimens (wing spots). **Scale bars** = 10 mm.

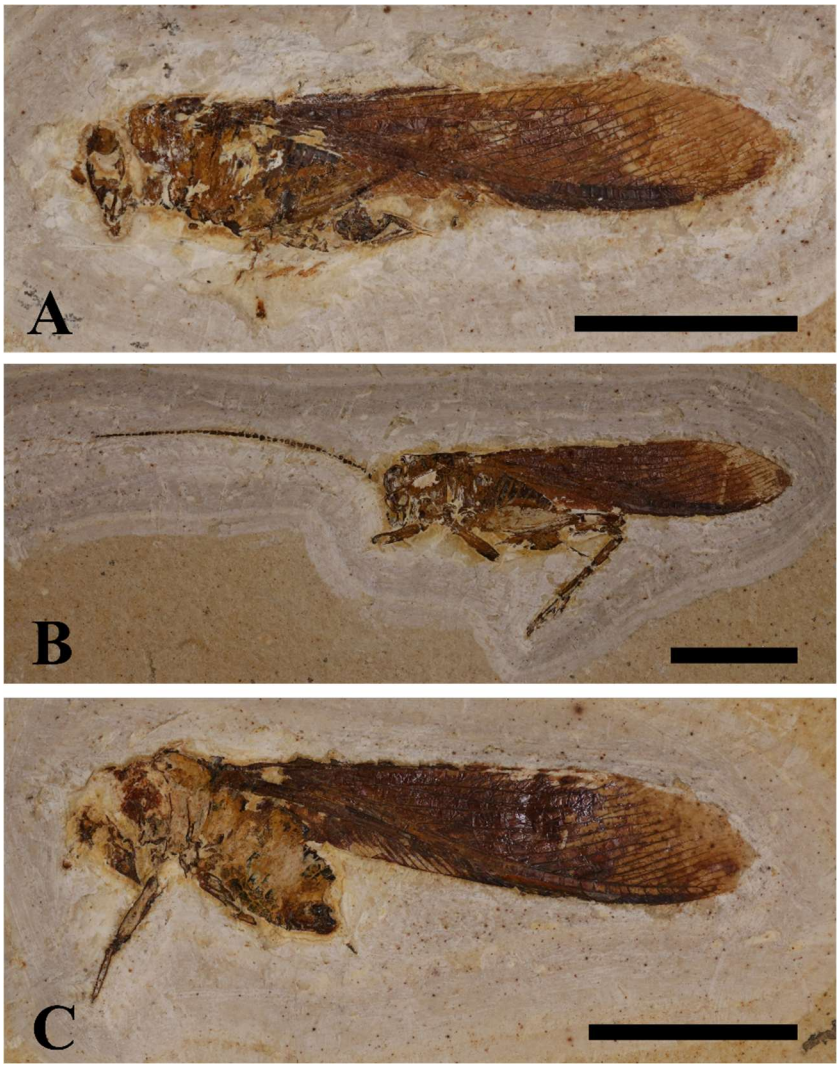

Fig. 24: *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) comb. nov. non-type specimens. **A.** INHS-P1874, female. **B.** INHS-P1878, female. **C.** INHS-P1935, female. **Scale bars** = 10 mm.

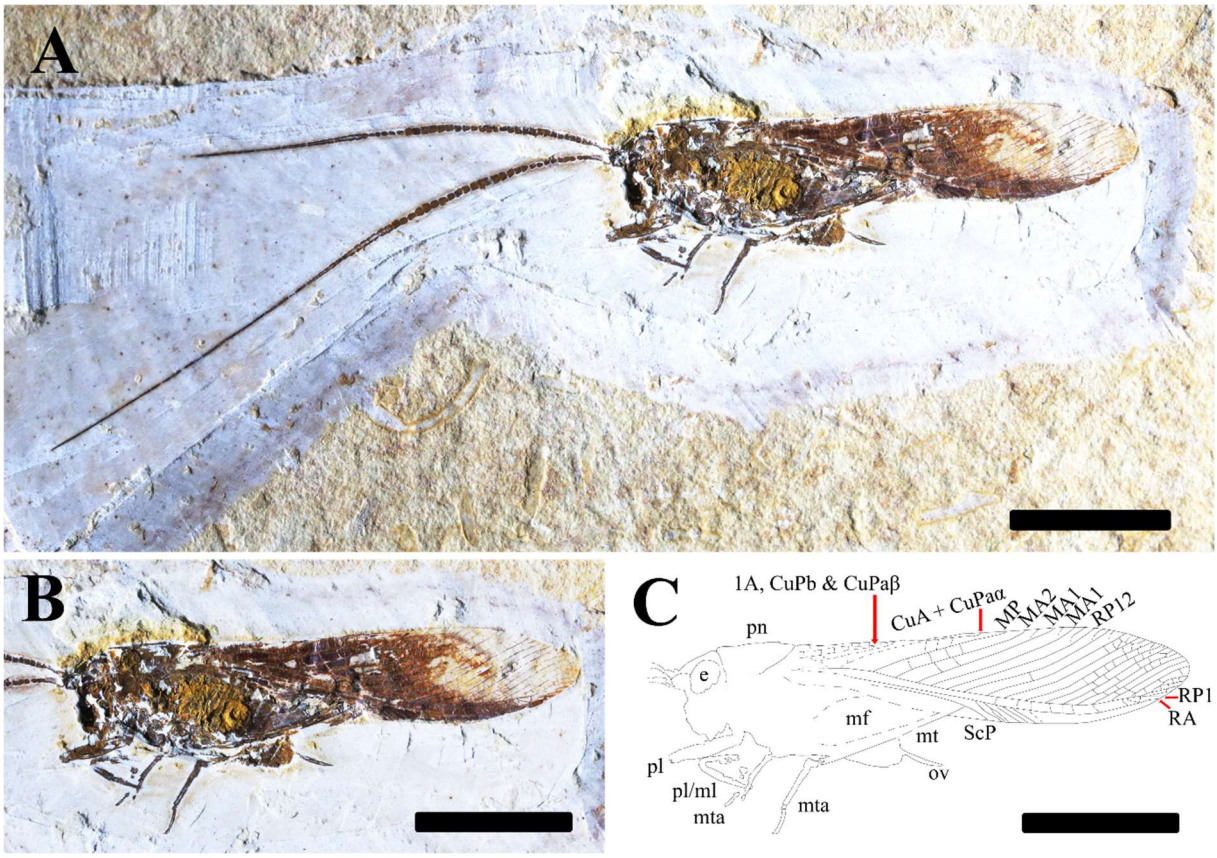

Fig. 25: *Mesembrelcana rasnitsyni* comb. nov. (Nel and Jouault, 2022). Non-type female specimen MPSC 5771. **A.** Overview of complete specimen. **B.** and **C.** Image and drawing of specimen without the antennae. **Abbreviations:** e = compound eye; mf = metafemur; mt = metatibia; mta = metatarsus; ov = ovipositor; pl = prothoracic leg; pl/ml = pro- or mesothoracic leg (identity unclear); pn = pronotum. **Scale bars** = 10 mm.

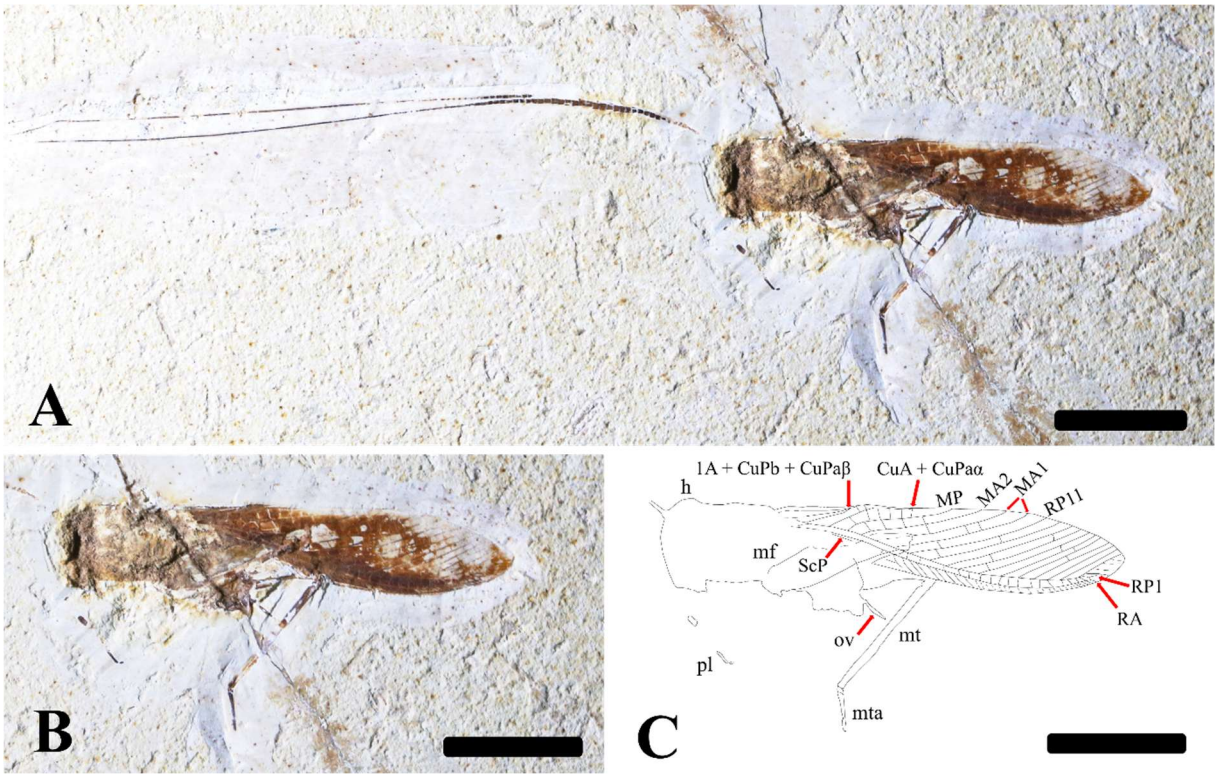

Fig. 26: *Mesembrelcana rasnitsyni* comb. nov. (Nel and Jouault, 2022). Non-type female specimen MPSC 5792. **A.** Overview of complete specimen. **B.** and **C.** Image and drawing of specimen without the antennae. **Abbreviations:** h = head; mt = metatibia; mta = metatarsus; ov = ovipositor; pl = prothoracic leg. **Scale bars** = 10 mm.

Subfamily Elcaninae Handlirsch, 1906

Genus *Panorpidium* Westwood, 1854

Type species: *Panorpidium tessellatum* Westwood, 1854.

Panorpidium damianii (Martins-Neto, 1991) comb. nov.

Figs. 27–37

Examined specimens: HC0005; HC0006; HC0007; HC0009; HC0013; HC0030; HC0031; HC0032; HC0033; MH1112; MH1119; SMNK_PAL_45252; AMNH_SA_44506; AMNH_SA_44508; INHS-P1173; INHS-P1756 (all ♀)

Type material: Holotype male in the collection of Instituto de Geociências da Universidade de São Paulo, coll. no. GP/1T-1620 [(not RGMN-1620 as provided in Martins-Neto (1991)] (Fig.

27). Type locality: Type locality: between Santana do Cariri and Nova Olinda, Crato Formation Ceará, Brazil. Collected by R.G. Martins-Neto.

Emended diagnosis: Forewing 9.7-13.7 mm long (*9-14 mm after Martins-Neto (1991)). 1A + CuPb + CuPaα fused. Wing margin length between CuA + CuPaα and MP rather short. Tegminal RP with 6-9 branches (*5-7 after Martins-Neto (1991)). Tegminal M with three branches. Location of stem of RP after MA1. Body length 5.6–8.2 mm. Ovipositor rather long and broad, sword-shaped; ovipositor length/forewing length ca. 0.3–0.4.

Description of HC0006:
HC0006 is a specimen examined in this study with well-preserved forewing characters (Fig. 29). It is described here to elucidate the similarities of this species to other members of *Panorpidium*.

Measurements: Forewing length 13.7 mm. Forewing length/height 3.9. Body length 6.4 mm. Ovipositor length/forewing length 0.32. Ovipositor length 4.4 mm.

Body: Body features not well preserved. Antennae longer than body with many thin segments. Antennal scape, pedicel and first segment enlarged. Metatibia with large spurs, however their morphology cannot be described in detail due to their state of preservation. Ovipositor shorter than in *Cratoelcana zessini* but relatively broader; almost straight.

Wings: Forewing with 1A + CuPb + CuPaβ fused. 1A with cross veins. CuPaα present as vertical cross vein on top of CuPaβ. Distance between CuA + CuPaα and MP 17.9% of total wing length. M with three branches. RP with eight branches. RP2 probably consists of fusion of former RP2 and RP3. Stem of RP located posterior of MA1. Pterostigma area of RA with 15 cross veins. ScP with at least nine branches, rather wide. ScA narrow with at least three branches. No apparent coloration patterns visible.

Remarks: Panorpidium damianii comb. nov. (Martins-Neto, 1991) was originally described as *Cratoelcana damianii* and for over decades considered the second valid species within the genus, alongside *C. zessini*.

Because the holotype specimen of *P. damianii* is a male, its identity as either this species or *Gondwanaelcana brasiliensis* gen. et sp. nov. is problematic. Martins-Neto (1991) described a long, sword-shaped ovipositor for *Cratoelcana damianii* (Martins-Neto, 1991, Fig. 2–31 J–L). Because of this, we assign the specimens with this type of ovipositor to *Panorpidium damianii* comb. nov. whereas the forewing venation-wise very similar specimens with a short saber-type ovipositor–which was not recognized as such by Martins-Neto (1991)–are attributed to the new taxon *G. brasiliensis*.

At the time of its description, Martins-Neto was unable to reconstruct the complete forewing venation of *P. damianii*, particularly the basal region, which limited a more precise taxonomic placement. Additionally, the diagnostic relevance of the RP stem position in elcanid taxonomy was only emphasized later, following Gorochov et al. (2006). With advances in our understanding of Elcanidae morphology, particularly in regard to tegminal vein fusion and RP stem placement, we propose the transfer of *C. damianii* to *Panorpidium*. This reassignment is justified by the presence of the diagnostic fusion of veins 1A + CuPb + CuPaβ and by the position of the RP stem arising posterior to MA1–both consistent with *Panorpidium*. No characters observed in the available specimens support generic separation from *Panorpidium*, a genus with broad paleogeographical distribution, including numerous species from Europe and Asia (e.g., Gorochov et al., 2006; Kim et al., 2021). *Panorpidium damianii* comb. nov. differs from most of its congeners by its relatively small forewing length, which does not exceed 13.7 mm. This feature excludes comparison with larger representatives of *Panorpidium.* However, *P. damianii* is cryptically similar to *P. parvum* Gorochov, Jarzembowski and Coram, 2006 from the Lower Cretaceous of Britain, which is known only from a forewing. Due to this limited material, differentiation between the two species is challenging. Nonetheless, we suggest retaining *P. damianii* as a distinct species based on biogeographic considerations, as the significant geographic and temporal separation between the Crato Formation and the Weald Clay Formation of southern England likely precluded any gene flow between the two populations.

Specimens of Panorpidium damianii comb. nov. examined in this study:

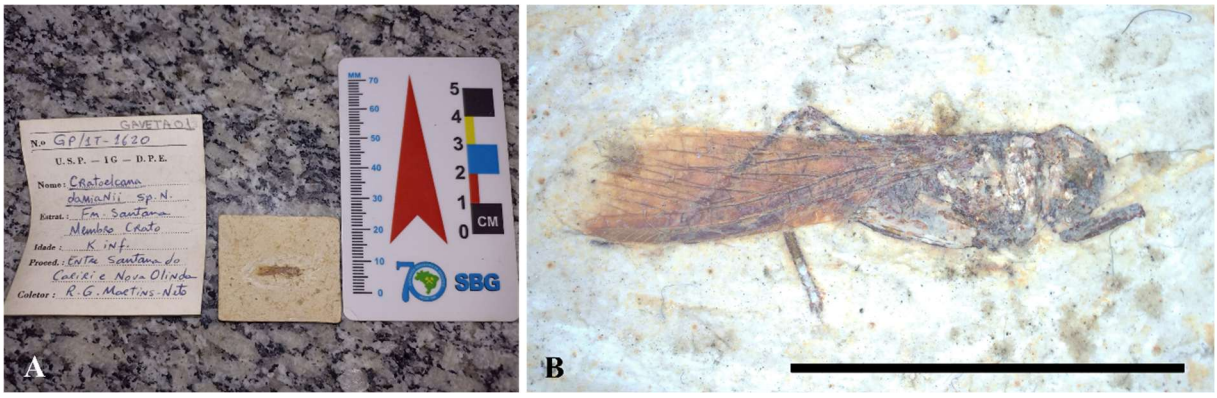

Fig. 27: *Panorpidium damianii* comb. nov. (Martins-Neto, 1991) holotype male in the collection of Instituto de Geociências da Universidade de São Paulo, coll. no. GP/1T-1620. **A.** Overview of the specimen with museum note proving its holotype status. **B.** Overview of the specimen in detail.

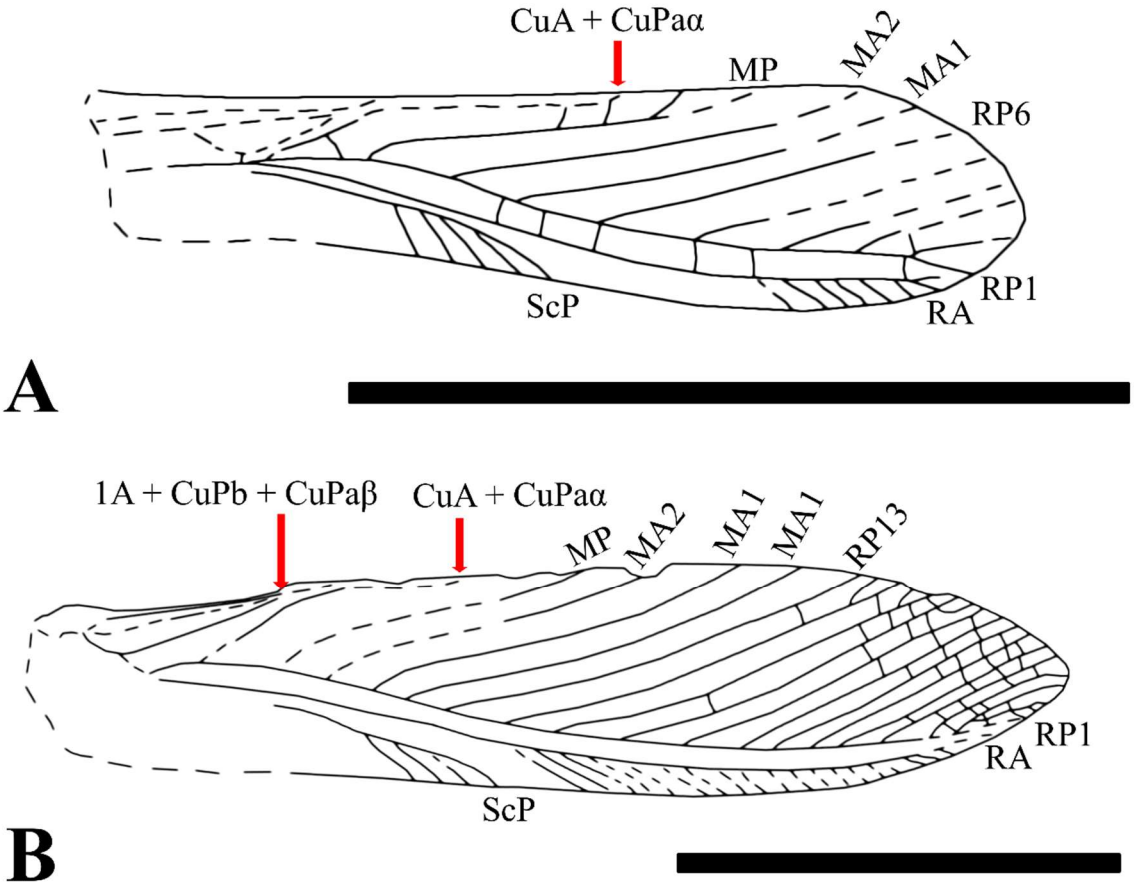

Fig. 28: Comparison of the forewing venation of **A.** *Panorpidium damianii* comb. nov. (Martins-Neto, 1991) and **B.** *Cratoelcana zessini* Martins-Neto, 1991.

The following figures 29–37 depict specimens of *Panorpidium damianii* comb. nov. examined in this study and never featured in the literature before. None of the specimens are of type status.

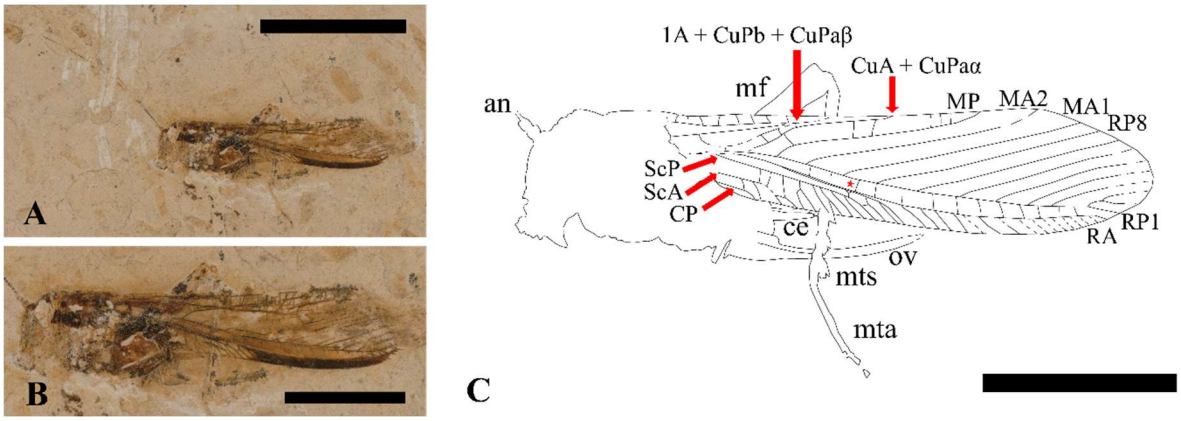

Fig. 29: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Specimen HC0006, female. **A.** View of complete specimen. **B.** and **C.** Specimen without antennae. Red asterisk marking position of the stem of RP. **Abbreviations:** an = antennae; mf = metafemur; mts = metatibial spur; mta = metatarsus; ce = cerci; ov = ovipositor. **Scale bars** = 10 mm (A); 5 mm (B-C).

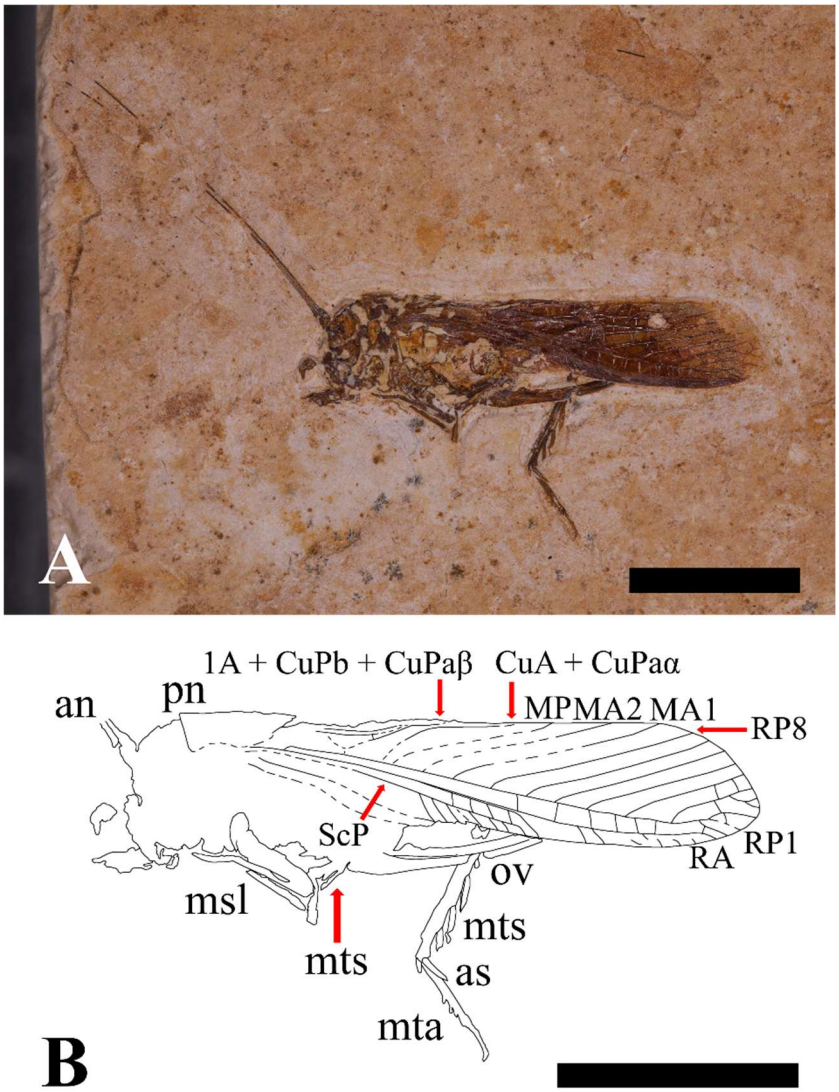

Fig. 30: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Specimen AMNH_SA_44506, female. **A.** and **B.** Specimen (B drawn without antennae). **Abbreviations:** an = antennae; pn = pronotum; msl = mesothoracic leg; mts = metatibial spur; as = apical spur; mta = metatarsus; ov = ovipositor. **Scale bars** = 5 mm.

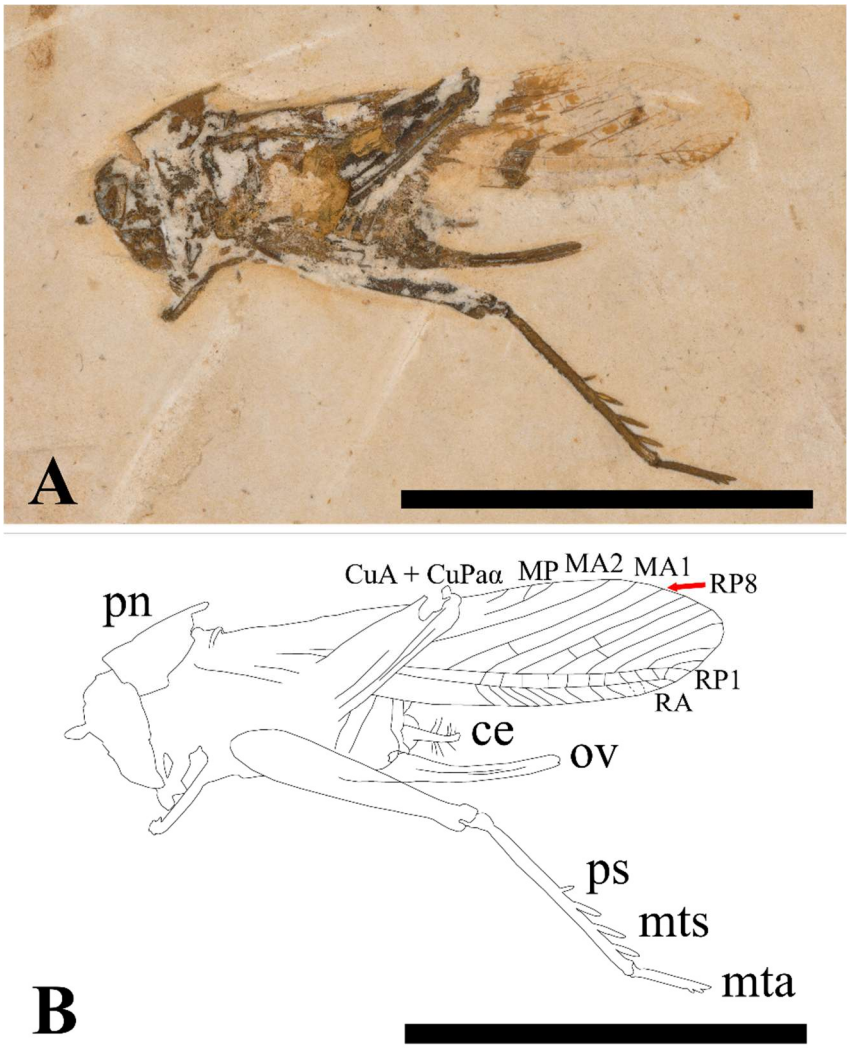

Fig. 31: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Specimen HC0030, female. **A.** and **B.** Complete specimen. **Abbreviations:** pn = pronotum; ce = cercus; ov = ovipositor; ps = proximal spur; mts = metatibial spurs; mta = metatarsus. **Scale bars** = 10 mm.

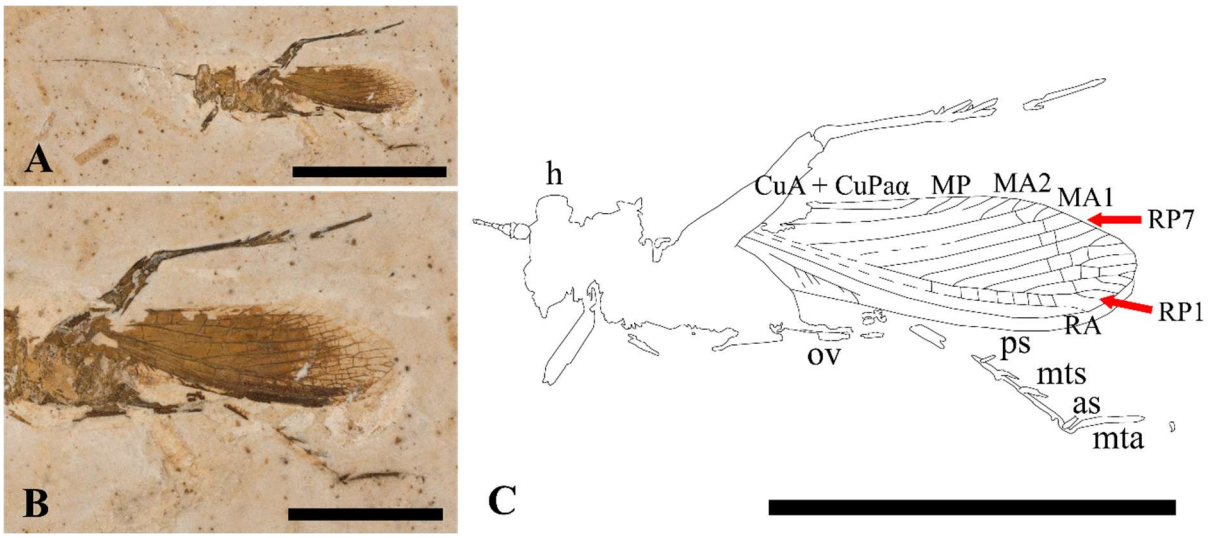

Fig. 32: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Specimen HC0032, female. **A.** Complete specimen. **B.** Detail of wings and metathoracic legs. **C.** Drawing of specimen (without antennae). **Abbreviations:** h = head; ov = ovipositor; ps = proximal spur; mts = metatibial spurs; as = apical spur; mta = metatarsus. **Scale bars** = 10 mm (A, C); 5 mm (B).

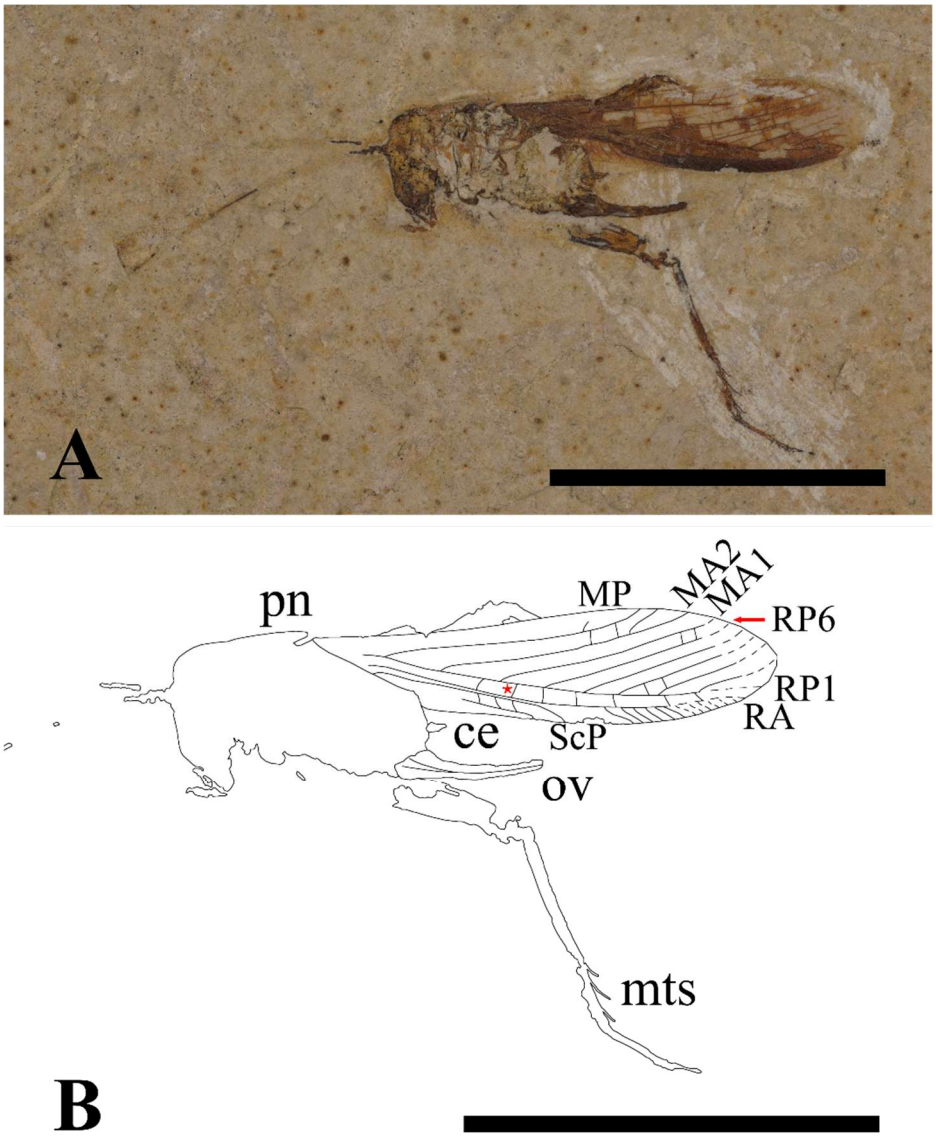

Fig. 33: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Specimen MH1119, female. **A.** and **B.** Specimen (B with antennae only partly drawn). Red asterisk marking the stem of RP. **Abbreviations:** pn = pronotum; ce = cercus; ov = ovipositor; mts = metatibial spurs. **Scale bars** = 10 mm.

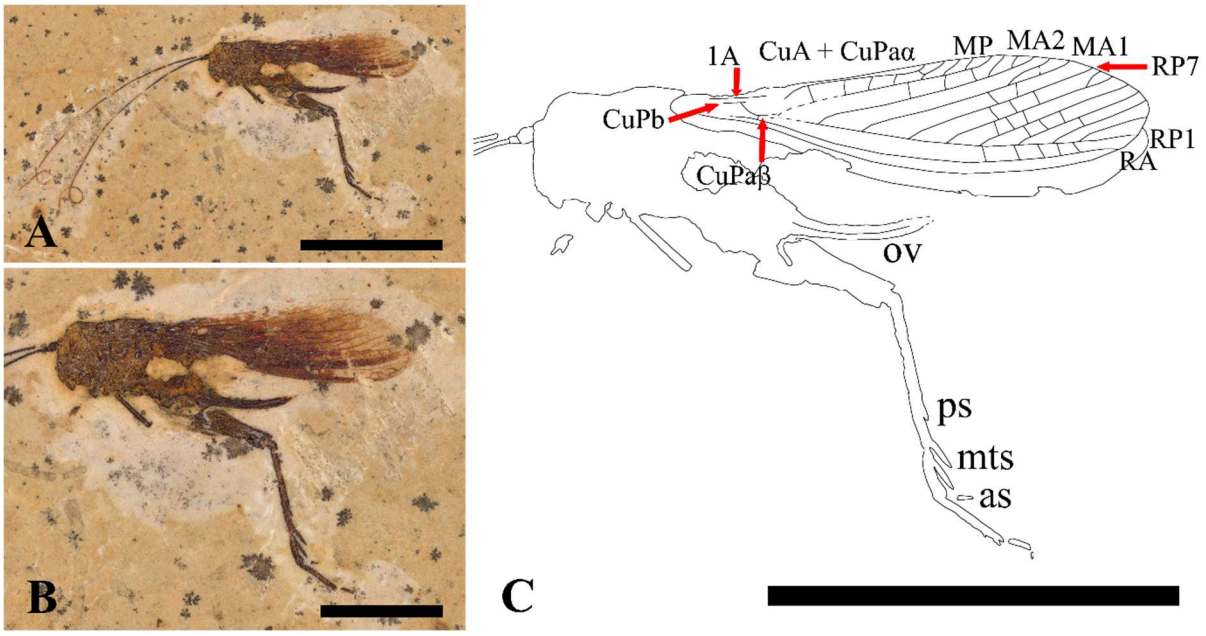

Fig. 34: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Specimen SMNK_PAL_45252, female. **A.** Complete specimen. **B.** and **C.** Specimen without antennae. Note the peculiar appearance of CuPaβ in this specimen. It looks similar to the Kachin amber species *Parelcana xena* Schall and Husemann, in press, but in this case, it is probably rather due to incomplete preservation or wing overlapping. **Abbreviations:** ov = ovipositor; ps = proximal spur; mts = metatibial spurs; as = apical spur. **Scale bars** = 10 mm (A, C); 5 mm (B).

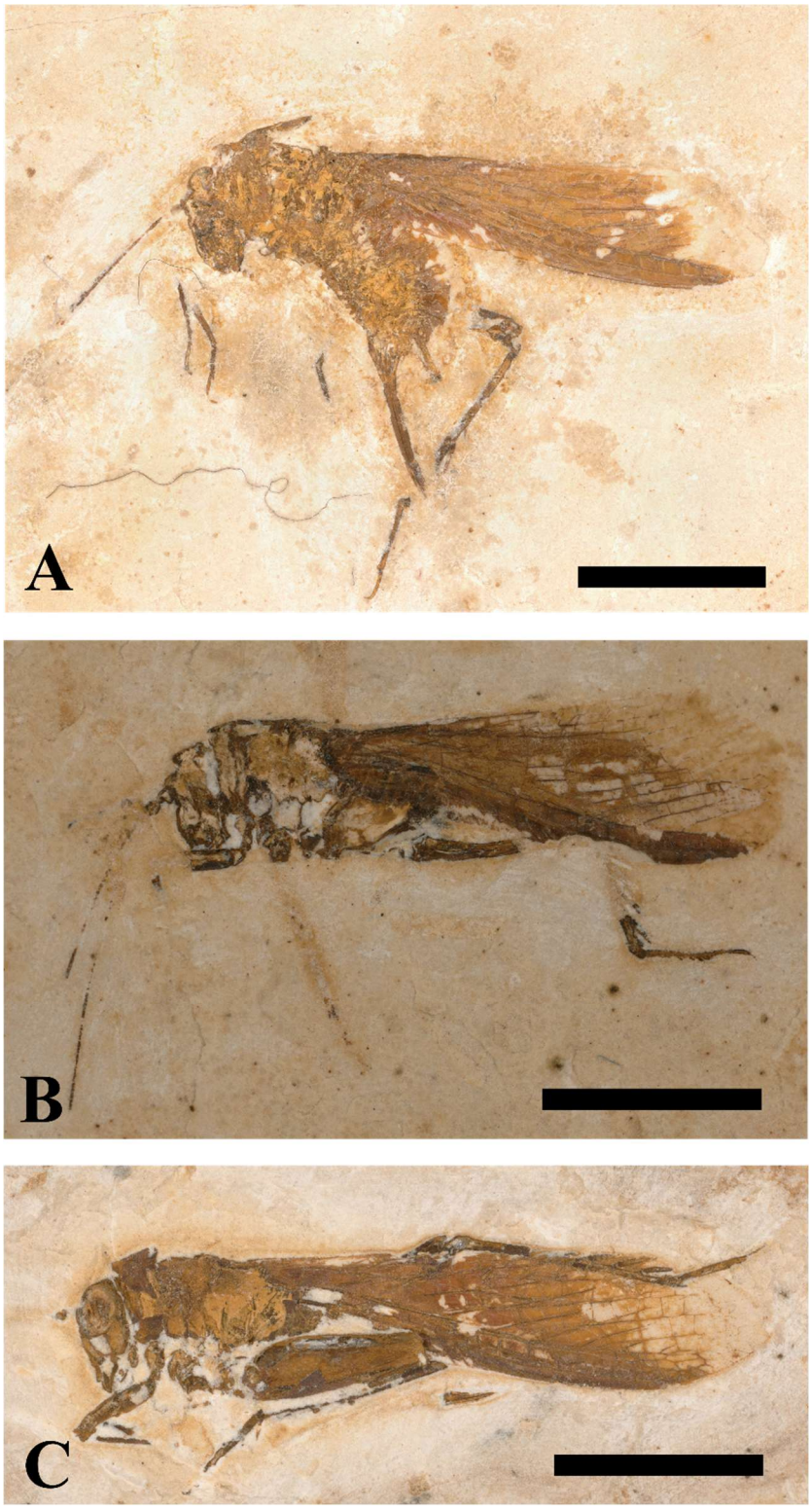

Fig. 35: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Further specimens. **A.** HC0009, female. **B.** HC0007, female. **C.** HC0033, female. In this specimen only a fragment of the ovipositor is preserved, but it still suggests HC0033 belongs to *P. damianii* rather than *G. brasiliensis*. **Scale bars** = 5 mm.

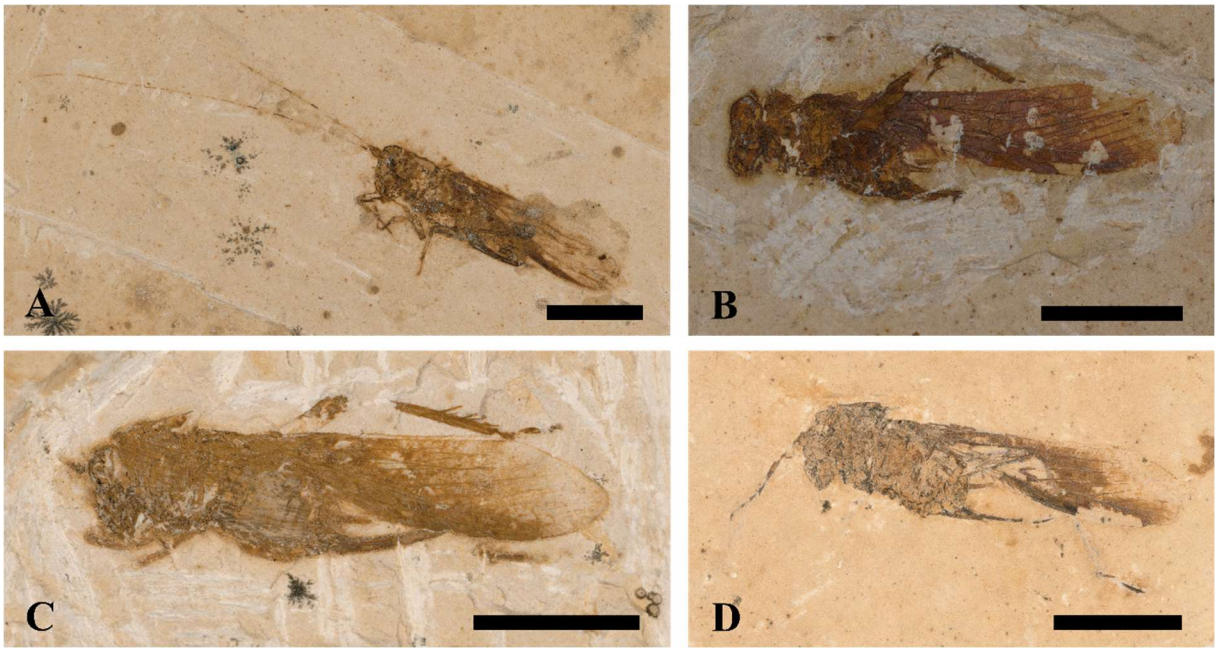

Fig. 36: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Further specimens. **A.** HC0031, female. **B.** MH1112, female. **C.** HC0005, female. **D.** HC0013, female. **Scale bars** = 5 mm.

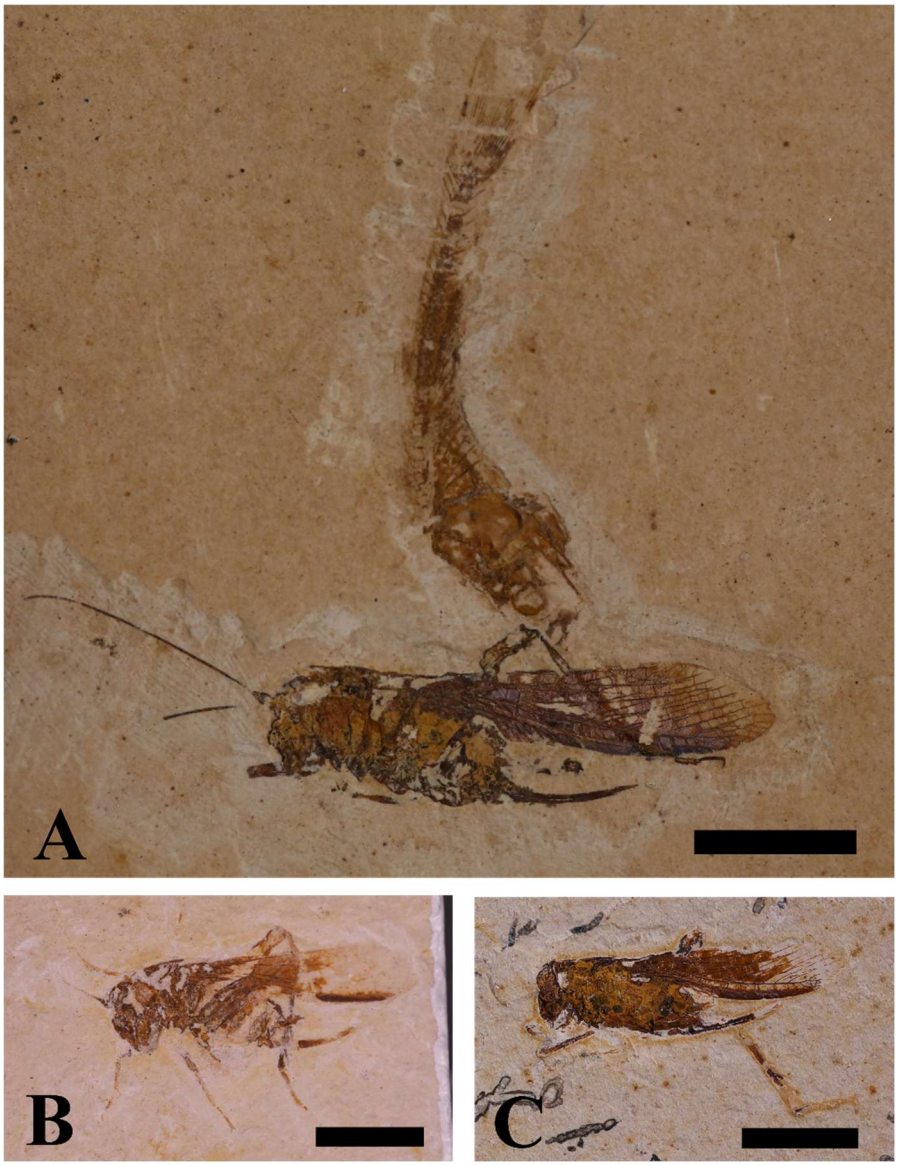

Fig. 37: *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. Further specimens. **A.** INHS-P1756, female. The fish preserved with this fossil likely belongs to the species *Dastilbe crandalli* Jordan, 1910. Judging by its small size, it would be a juvenile. **B.** AMNH_SA_44508, female. **C.** INHSP_1173, female. **Scale bars** = 5 mm.

3.2 Character variation of Crato Formation Elcanidae

In order to determine the taxonomy of the Elcanidae from the Crato Formation as presented above, selected morphological features of the 88 specimens were considered. The resulting data for each specimen (both assigned and unassigned to one of the species) is presented in the supplementary Table 1. Characters include: forewing length; forewing length/width; branches of RP; (position of the) stem of RP; body length (head to abdominal apex); head height/forewing length; ovipositor length/forewing length. Below the characters of all specimens assigned to one of six species of Crato Elcanidae are statistically analyzed in detail.

Forewing length:

Forewing length of all specimens that were able to be assigned to one of the six described species was measured from base to apex. The results (mean, max., min. and standard deviation) are given in Table 1 and illustrated in Fig. 38, statistical results of Mann-Whitney pairwise test can be seen in Table 2.

Table 1: Variation of forewing length in Crato Elcanidae. SD = standard deviation. All values in centimeters (cm).

Value	*Cratoelcana zessini* Martins-Neto, 1991 N = 12	*Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) N = 9	*Panorpidium damianii* (Martins-Neto, 1991) N = 15	*Gondwanaelcana brasiliensis* gen. et sp. nov. N = 10	*Argentoelcana intermedia* gen. et sp. nov. N = 1	*Ensiferelcana brachyptera* gen. et sp. nov. N = 1
Mean	24.7	25.5	12	10.5	16.1	16.6
Max	27.4	26.4	13.7	12.2	-	-
Min	22.7	23.8	9.7	9.1	-	-
SD	1.5	0.8	1	0.8	-	-

Table 2: Mann-Whitney pairwise test of variation in forewing length of *Cratoelcana zessini*, *Mesembrelcana rasnitsyni*, *Panorpidium damianii* and *Gondwanaelcana brasiliensis*. Significant p-values are marked.

	C. zessini	*M. rasnitsyni*	*P. damianii*	*G. brasiliensis*
C. zessini		0.145	0.00001259	0.00008654
M. rasnitsyni	0.145		0.00006443	0.0002746
P. damianii	0.00001259	0.00006443		0.003247
G. brasiliensis	0.00008654	0.0002746	0.003247	

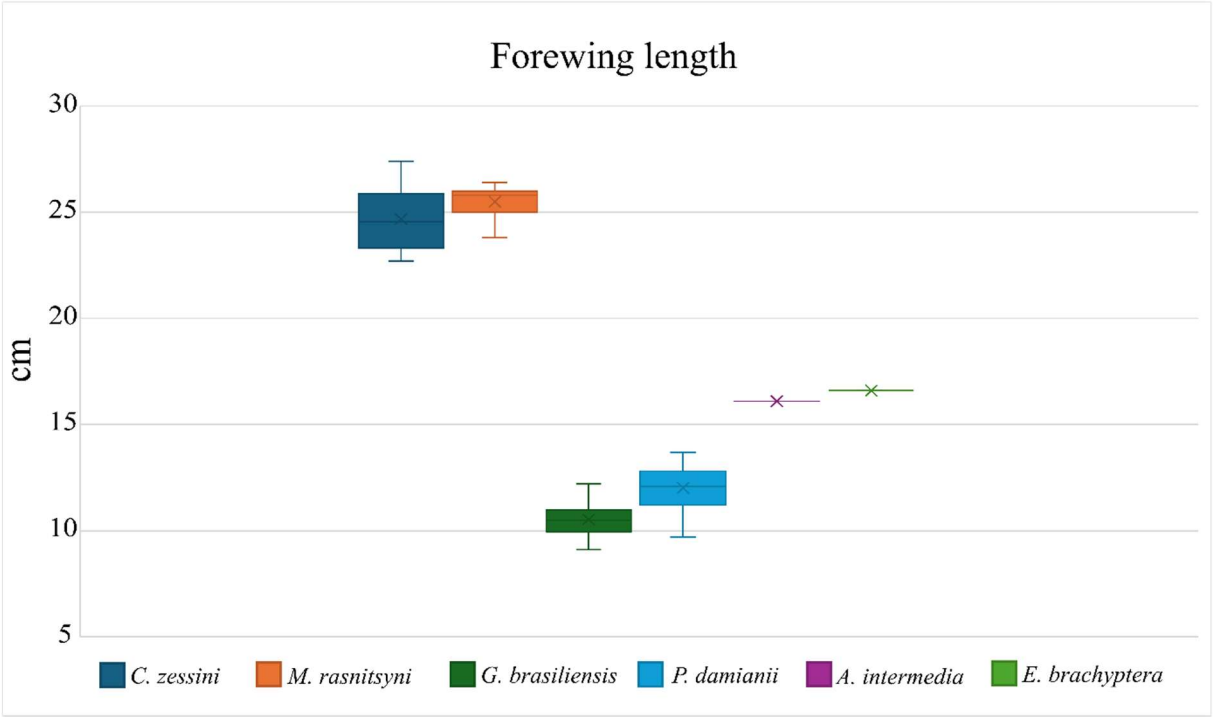

Fig. 38: Boxplots of the variation in forewing length of Crato Formation Elcanidae. The distinction between the large, intermediate and small species is clear. Boxes represent first and third quartile. X is the mean; solid horizontal line is the median. Solid vertical line is minimum and maximum value.

Forewing length/width:

The ratio of forewing length/width of all specimens that were able to be assigned to one of the six species described was calculated. For this, the forewing length measured from base to apex was divided by the maximum width of the forewing. The results (mean, max., min. and standard deviation) are given in Table 3 and illustrated in Fig. 39, statistical results of Mann-Whitney pairwise test can be seen in Table 4.

Table 3: Variation of forewing length/width in Crato Elcanidae. SD = standard deviation. The slightly different number of n specimens for *Gondwanaelcana brasiliensis* gen. et sp. nov. is caused by two specimens with the forewing in a condition where maximum width could not be measured confidently.

Value	*Cratoelcana zessini* Martins-Neto, 1991 N = 12	*Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) N = 9	*Panorpidium damianii* (Martins-Neto, 1991) N = 15	*Gondwanaelcana brasiliensis* gen. et sp. nov. N = 8	*Argentoelcana intermedia* gen. et sp. nov. N = 1	*Ensiferelcana brachyptera* gen. et sp. nov. N = 1
Mean	4.3	4.3	4.1	4	3.8	4.7

Max	4.8	4.5	4.3	4.3	-	-
Min	4	4.1	3.7	3.8	-	-
SD	0.26	0.14	0.14	0.15	-	-

Table 4: Mann-Whitney pairwise test of variation in forewing length/width ratio of *Cratoelcana zessini*, *Mesembrelcana rasnitsyni*, *Panorpidium damianii* and *Gondwanaelcana brasiliensis*. Significant p-values are marked.

	C. zessini	*M. rasnitsyni*	*P. damianii*	*G. brasiliensis*
C. zessini		1	0.02808	0.00889
M. rasnitsyni	1		0.00407	0.005492
P. damianii	0.02808	0.00407		0.2318
G. brasiliensis	0.00889	0.005492	0.2318	

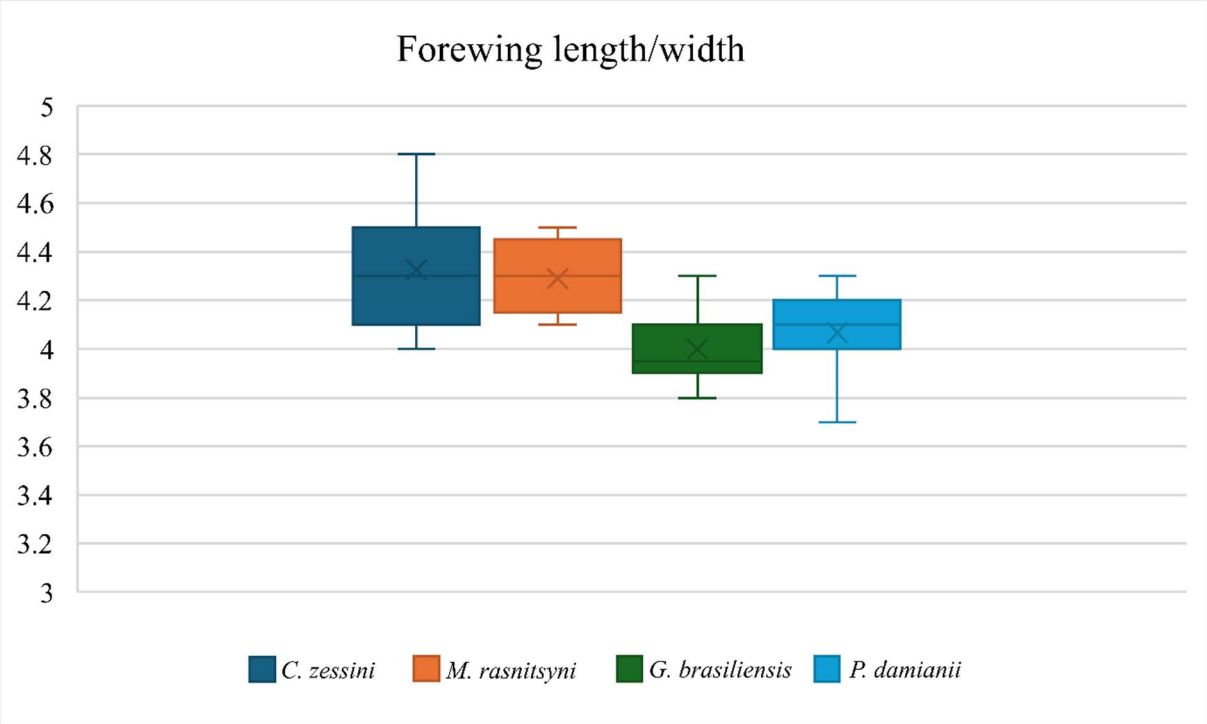

Fig. 39: Boxplots of the variation in forewing length/width of Crato Formation Elcanidae. The distinction between species is rather small, however the Mann-Whitney pairwise still found a significant difference between the larger species (*C. zessini* + *M. rasnitsyni*) and the smaller (Table 4). Boxes represent first and third quartile. X is the mean; solid horizontal line is the median. Solid vertical line is minimum and maximum value.

Branches of RP:

The number of RP branches was counted for all specimens that were able to be assigned to a species. The results can be seen in Table 5 and are illustrated in Fig. 40, statistical results of Mann-Whitney pairwise test can be seen in Table 6.

Table 5: Number of RP branches in Crato Elcanidae. In *Panorpidium damianii* (Martins-Neto, 1991) 7 and 8 branches of RP were present in an equal number of specimens (5).

Value	*Cratoelcana zessini* Martins-Neto, 1991 N = 12	*Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) N = 9	*Panorpidium damianii* (Martins-Neto, 1991) N = 12	*Gondwanaelcana brasiliensis* gen. et sp. nov. N = 8	*Argentoelcana intermedia* gen. et sp. nov. N = 1	*Ensiferelcana brachyptera* gen. et sp. nov. N = 1
Max	13	14	9	8	10	10
Min	11	10	6	6	10	10
Most common	11	12	7-8	6	10	10

Table 6: Mann-Whitney pairwise test of variation of the number of RP branches of *Cratoelcana zessini*, *Mesembrelcana rasnitsyni*, *Panorpidium damianii* and *Gondwanaelcana brasiliensis*. Significant p-values are marked.

	C. zessini	*M. rasnitsyni*	*P. damianii*	*G. brasiliensis*
C. zessini		0.4616	0.00002715	0.0001895
M. rasnitsyni	0.4616		0.0001086	0.0005087
P. damianii	0.00002715	0.0001086		0.03073
G. brasiliensis	0.0001895	0.0005087	0.03073	

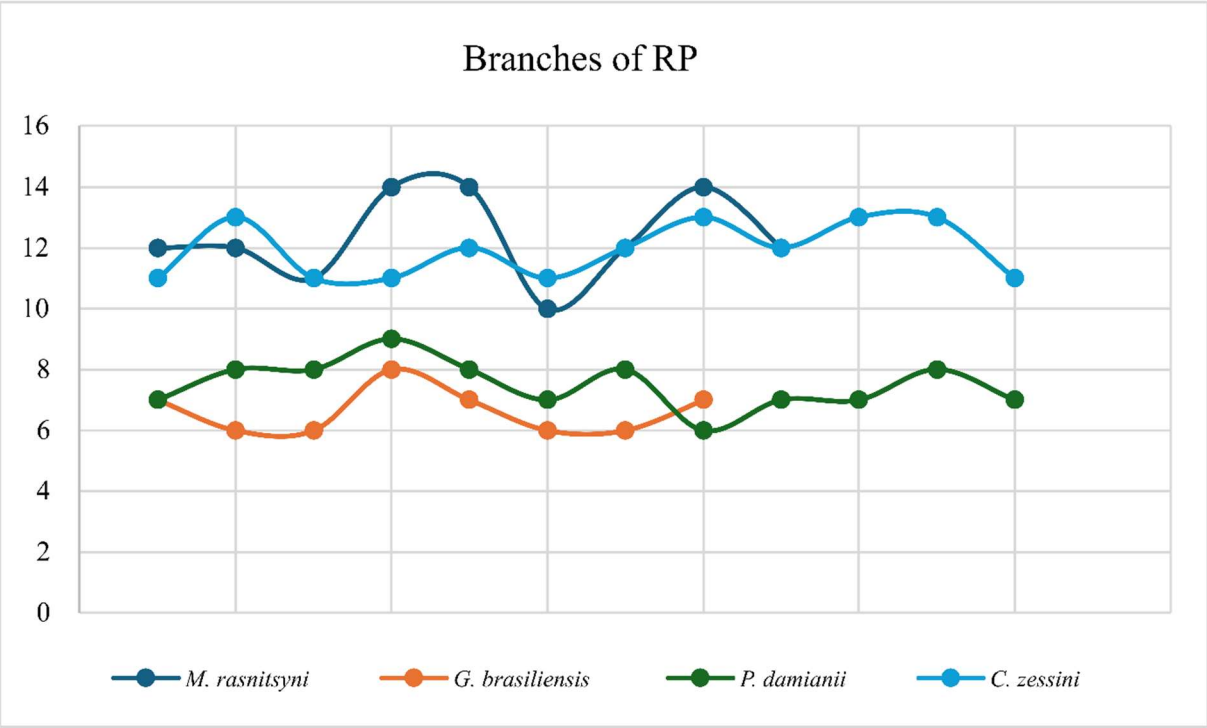

Fig. 40: Scatter plot of the variation in forewing length/width of Crato Formation Elcanidae where each dot represents a specimen, and the number of RP branches is given on the Y-axis. Distinction between the larger species with more RP branches and the smaller species with less RP branches is clear. Mann-Whitney pairwise scored small significance ($p = 0.03$) between the small species *P. damianii* and *G. brasiliensis* as well (Table 6). Dots are connected to improve visualization (the variables "RP branches" and "specimen" are of course not continuous).

Position of the stem of RP:

The position of the stem of RP is considered to be of high taxonomic importance for generic separation in Elcanidae, for example to distinguish *Probaisselcana* Gorochov, 1989 from *Panorpidium* Westwood, 1854. In *Cratoelcana zessini* Martins-Neto, 1991 the stem of RP varies in position from right below the posterior branch of MA1 (Fig. 4) to posterior of the second last branch of RP (e.g. Fig. 6). In *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) the RP stem varied in position from right below the last branch of RP (Fig. 24C) to posterior of second last RP (Fig. 21). In the smaller species *Panorpidium damianii* (Martins-Neto, 1991) and *Gondwanaelcana brasiliensis* gen. et sp. nov. the position of the RP stem was always posterior of MA1. However, for *P. damianii* this character could only be determined for four specimens and for *G. brasiliensis* only for three specimens. In *Argentoelcana intermedia* gen. et sp. nov. the RP stem was located posterior of the last branch of RP. In *Ensiferelcana brachyptera* gen. et sp. nov. the RP stem could not be determined.

Body length (head to abdominal apex):

The body length of all specimens that were able to be assigned to one of the six described species was calculated. The results (mean, max., min. and standard deviation) are given in Table 7 and illustrated in Fig. 41, statistical results of Mann-Whitney pairwise test can be seen in Table 8.

Table 7: Variation of body length in Crato Elcanidae. SD = standard deviation. All values in centimeters (cm).

Value	*Cratoelcana zessini* Martins-Neto, 1991 N = 12	*Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) N = 9	*Panorpidium damianii* (Martins-Neto, 1991) N = 15	*Gondwanaelcana brasiliensis* gen. et sp. nov. N = 10	*Argentoelcana intermedia* gen. et sp. nov. N = 1	*Ensiferelcana brachyptera* gen. et sp. nov. N = 1
Mean	13	14	6.9	6.2	9.2	12.8
Max	16.7	15	8.2	6.7	-	-
Min	10.8	12.1	5.6	5.7	-	-
SD	1.5	0.8	0.8	0.3	-	-

Table 8: Mann-Whitney pairwise test of variation in body length of *Cratoelcana zessini*, *Mesembrelcana rasnitsyni*, *Panorpidium damianii* and *Gondwanaelcana brasiliensis*. Significant p-values are marked.

	C. zessini	*M. rasnitsyni*	*P. damianii*	*G. brasiliensis*
C. zessini		0.05422	0.00001232	0.00008574
M. rasnitsyni	0.05422		0.00006256	0.0000695
P. damianii	0.00001232	0.00006256		0.00828
G. brasiliensis	0.00008574	0.0002695	0.00828	

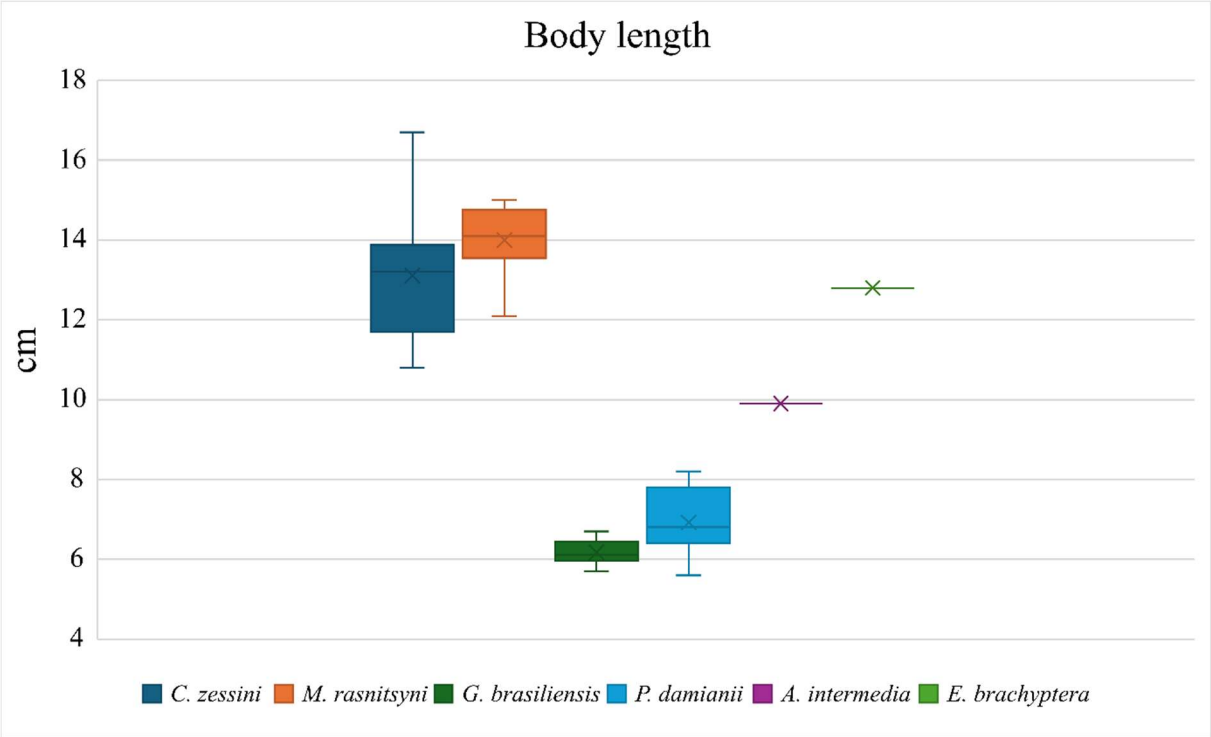

Fig. 41: Boxplots of the variation in body length of Crato Formation Elcanidae. Similar to the forewing length (Fig. 38), distinction between the large, intermediate and small species is clear, except for *E. brachyptera* gen. et sp. nov. of which the body length matches that of the large species. Mann-Whitney pairwise test also scored a significant difference between *P. damianii* and *G. brasiliensis* ($p = 0.008$). Boxes represent first and third quartile. X is the mean; solid horizontal line is the median. Solid vertical line is minimum and maximum value.

Head height/forewing length:

The ratio of forewing length/width of all specimens that were able to be assigned to one of the six species described was calculated. For this, the forewing length measured from base to apex was divided by the maximum width of the forewing. The results (mean, max., min. and standard deviation) are given in Table 9 and illustrated in Fig. 42, statistical results of Mann-Whitney pairwise test can be seen in Table 10. In general, the large species *Cratoelcana zessini* Martins-Neto, 1991 and *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) had heads slightly larger in comparison to their forewing length than the smaller and intermediate species.

Table 9: Variation of head height/forewing length in Crato Elcanidae. SD = standard deviation. Different number of specimens from previous results caused by poor preservation of the head in some specimens.

Value	*Cratoelcana zessini* Martins-Neto, 1991 N = 11	*Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) N = 9	*Panorpidium damianii* (Martins-Neto, 1991) N = 12	*Gondwanaelcana brasiliensis* gen. et sp. nov. N = 10	*Argentoelcana intermedia* gen. et sp. nov. N = 1	*Ensiferelcana brachyptera* gen. et sp. nov. N = 1
Mean	0.22	0.21	0.26	0.27	0.3	0.35
Max	0.27	0.24	0.3	0.35	-	-
Min	0.17	0.18	0.22	0.19	-	-
SD	0.03	0.02	0.02	0.04	-	-

Table 10: Mann-Whitney pairwise test of variation in head height/forewing length ratio of *Cratoelcana zessini*, *Mesembrelcana rasnitsyni*, *Panorpidium damianii* and *Gondwanaelcana brasiliensis*. Significant p-values are marked.

	C. zessini	*M. rasnitsyni*	*P. damianii*	*G. brasiliensis*
C. zessini		0.263	0.01327	0.02537
M. rasnitsyni	0.263		0.000373	0.003074
P. damianii	0.01327	0.000373		0.5256
G. brasiliensis	0.02537	0.003074	0.526	

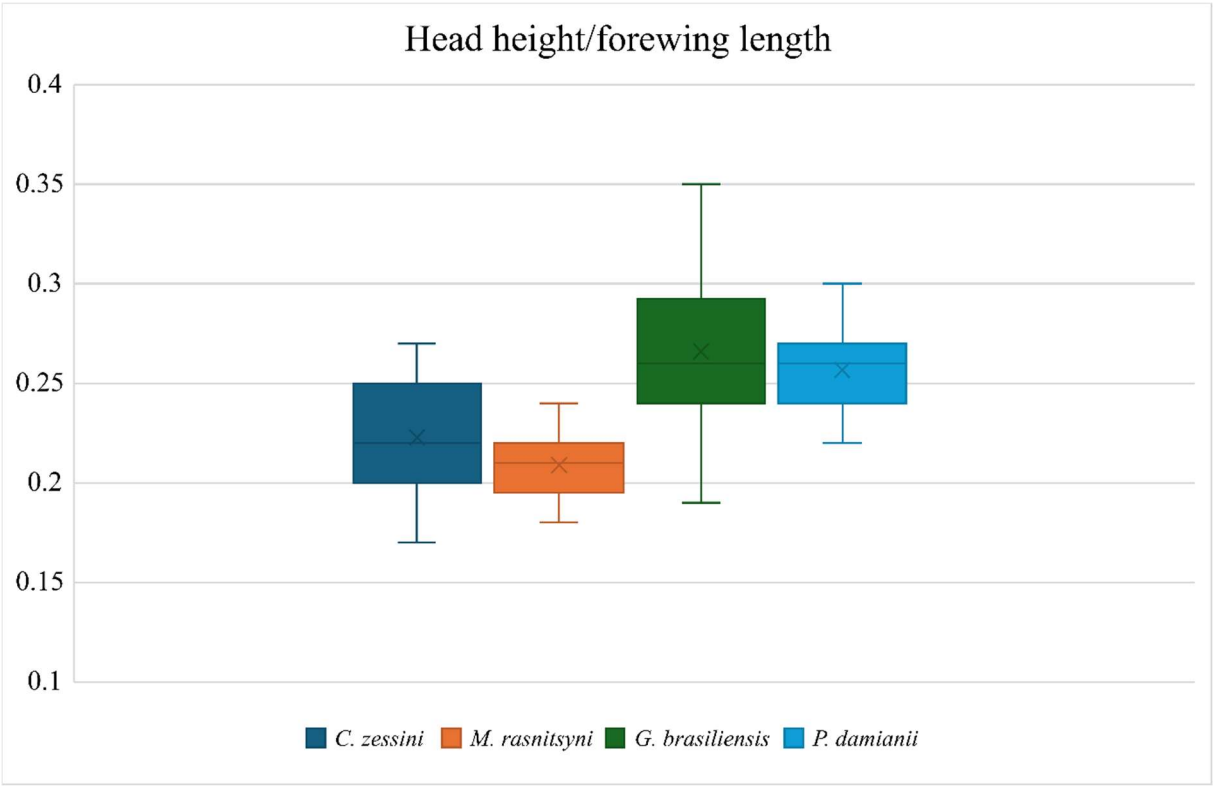

Fig. 42: Boxplots of the variation in head height/forewing length of Crato Formation Elcanidae. Similar to the forewing length/width, the variation of this character is rather small between

species. However, the smaller species had heads proportionally somewhat larger in relation to forewing size than the larger species. Boxes represent first and third quartile. X is the mean; solid horizontal line is the median. Solid vertical line is minimum and maximum value.

Ovipositor length/forewing length:

The ratio of ovipositor length/forewing length of all specimens that were able to be assigned to one of the six described species was calculated. For this, the forewing and ovipositor were measured from base to apex and the values were divided. The results (mean, max., min. and standard deviation) are given in Table 11 and illustrated in Fig. 43, statistical results of Mann-Whitney pairwise test can be seen in Table 12.

Table 11: Variation of ovipositor length/forewing length in Crato Elcanidae. SD = standard deviation. Different number of specimens from previous results caused by poor preservation of the ovipositor in some specimens.

Value	*Cratoelcana zessini* Martins-Neto, 1991 N = 11	*Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) N = 9	*Panorpidium damianii* (Martins-Neto, 1991) N = 14	*Gondwanaelcana brasiliensis* gen. et sp. nov. N = 10	*Argentoelcana intermedia* gen. et sp. nov. N = 0	*Ensiferelcana brachyptera* gen. et sp. nov. N = 1
Mean	0.57	0.06	0.32	0.07	-	0.86
Max	0.64	0.09	0.4	0.11	-	-
Min	0.51	0.03	0.21	0.05	-	-
SD	0.03	0.02	0.05	0.02	-	-

Table 12: Mann-Whitney pairwise test of variation in ovipositor length/forewing length ratio of *Cratoelcana zessini*, *Mesembrelcana rasnitsyni*, *Panorpidium damianii* and *Gondwanaelcana brasiliensis*. Significant p-values are marked.

	C. zessini	*M. rasnitsyni*	*P. damianii*	*G. brasiliensis*
C. zessini		0.0001822	0.00002639	0.0001091
M. rasnitsyni	0.0001822		0.00007917	0.2788
P. damianii	0.00002639	0.00007917		0.00004347
G. brasiliensis	0.0001091	0.2788	0.00004347	

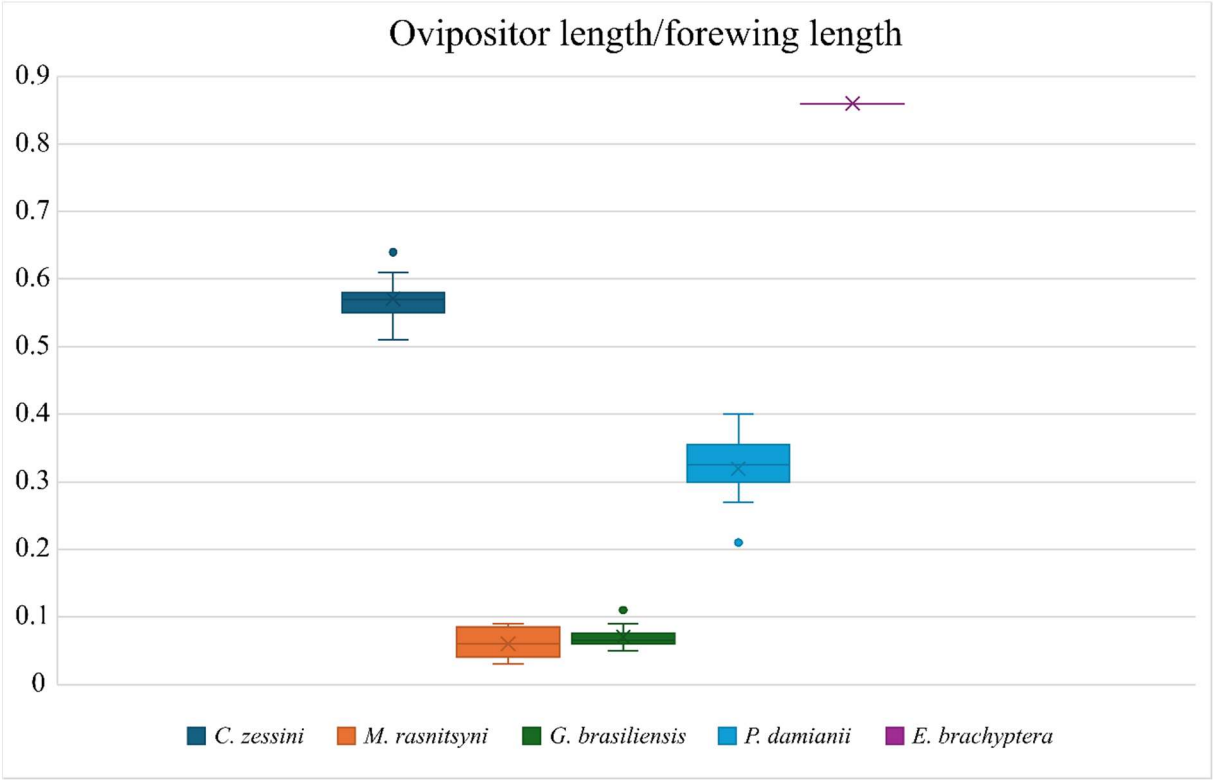

Fig. 43: Boxplots of the variation in ovipositor length/forewing length of Crato Formation Elcanidae. The stark difference between the saber-type bearing species (*M. rasnitsyni* (Nel and Jouault, 2022) and *G. brasiliensis* gen. et sp. nov.) to the other species is very apparent. The ovipositor morphology of *C. zessini* Martins-Neto, 1991 and *P. damianii* (Martins-Neto, 1991) is also different ($p = 0.00003$). The ovipositor of the first may be considered a "long sword" whereas that of the latter is rather a "short sword". The extreme relation of ovipositor length/forewing length of *E. brachyptera* gen. et sp. nov. can be seen well, too. Boxes represent first and third quartile. X is the mean; solid horizontal line is the median. Solid vertical line is minimum and maximum value. Singular dots show outliers.

4. Discussion

This study examined 88 specimens of Elcanidae from the Crato Formation of northeastern Brazil based on morphological features. We organized the specimens in six distinct genera, mostly due to their forewing size and ovipositor length/forewing length ratio. The rare opportunity of being able to study a greater number of specimens of Elcanidae allowed us to analyze character variability in this group. In the following section, implications for the taxonomy of elcanids derived from our findings are discussed. Additionally, we noticed a skewed sex ratio of Crato Elcanidae towards a female biased fossil record. Of the 88 specimens, 61 were female (69.3%), 22 were male (25%), and in 5 specimens (5.7%) the abdominal apex

was obscured or not preserved. An 89th specimen – the holotype of *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) comb. nov. was found to also be female. Possible implications of this high number of females for the biology of Elcanidae are discussed.

Character variation in Elcanidae from the Crato Formation

Forewing length

Differences in forewing length was one of the main characters used to differentiate between the taxa of Crato Elcanidae described herein. In the only other study where fossil material was abundant enough to analyze character variability in Elcanidae, Zessin (1987) used this character as well to separate the four Jurassic species of Elcanidae from Dobbertin (Germany). Both these findings suggest that variation in forewing length is probably a reliable character for estimating taxonomic diversity in Elcanidae.

Forewing length/width

Although the statistical test did find $p < 0.05$ for the smaller species compared to the larger species in regard to this character, we do not suggest it to be a reliable trait for taxonomic separation. Overlap of the range of larger and smaller species was present in our data (the maximum value recorded in both small species was a ratio of 4.3, which is higher than the minimum value recorded for each larger species, see Table 3).

Branches of RP

Next to the forewing length, the number of RP branches was the second character used by Martins-Neto (1991) to differentiate between the larger and smaller specimens he examined. Indeed, our statistical analysis found significant difference in the number of RP branches between the larger and smaller species and between the two smaller species as well ($p = 0.03$). Generally, the longer the forewing the more branches has RP (although exceptions occur, such as the Burmese amber species *Kolymbelcana phantasma* Schall, Kotthoff & Husemann, 2025, which has eleven branches of RP while the forewing is only 9.5 mm long). Our findings demonstrate that the number of RP branches is fairly consistent within species of Elcanidae and a variation of three branches or more in smaller and four branches or more in larger species should probably justify the separation of species.

Position of the stem of RP

The variation of the stem of RP is of highest interest to the study of Elcanidae, because it is the main reason for the generic separation of species-rich genera *Panorpidium* Westwood, 1854 and *Probaisselcana* Gorochov, 1989. The location of the RP stem is stable in the species with small forewings *G. brasiliensis* and *P. damianii*, always being located posterior of MA1 (although N specimens only three and four, respectively). However, in the species with large forewings *C. zessini* and *M. rasnitsyni,* it varies significantly between posterior of the first (out of two) MA1 to posterior of the second last RP and below the last RP to posterior of second last RP, respectively. Zessin (1987) noted variation of the RP stem in the Jurassic elcanids of Dobbertin as well, stating that "the beginning of proximal RP is subject of considerable variation in its position to MA2 (*sic* MA1) already within the same species" (translated from Zessin, 1987). Zhou et al. (2024) found fore- and hindwing variation even in the same specimen of *Probaisselcana kachinensis* Zhou, Xu & Xiao, 2024 (although this did not affect the stem of RP), which they suggested may have been caused by stressful environmental conditions. The findings mentioned make the generic separation of Elcanidae taxa such as *Panorpidium* and *Probaisselcana* problematic. Their status may have to be re-evaluated in the future.

Body length

The body length is usually correlated to the forewing length (i. e. species with a larger forewing have longer bodies too.). As many species of Elcanidae are known from isolated forewings, that character is better suited for comparison within the family, however body length is likely a reliable trait for taxonomic separation as well. It should be noted that exceptions can occur, though, as was seen with *Ensiferelcana brachyptera* gen. et sp. nov. which has a body of similar length to *Cratoelcana zessini* and *Mesembrelcana rasnitsyni*, despite featuring forewings significantly shorter.

Head height/forewing length

Although overlap did occur between them, generally the smaller species had heads somewhat higher in proportion to the forewing length than the larger species. Despite this difference being statistically significant (see Table 10), we would suggest being cautious with this character, especially when dealing with compression fossils as the perceived head height can easily be influenced by the state of preservation. However, for amber specimens where the head morphology is less error-prone, this character may be quite useful. A difference of 0.05 for the ratio head height/forewing length could probably suffice to separate species.

Ovipositor length/forewing length

Beside the forewing length and RP branches, the ovipositor length/forewing length ratio was another key factor for the taxonomic results applied inhere to the species of Crato Elcanidae. Willmott et al. (2025) recognized the saber-type ovipositor only recently in the genus *Elcanodentes* Willmott et al., 2025 from Burmese amber. This type of ovipositor is very short in comparison to the other types found in Elcanidae (sword and scythe) and can be missed quite easily or interpreted as, for example, a cercus. The deposition site associated with the saber ovipositor is unknown, but so far it was only recorded from Burmese amber and the Crato Formation. The different forms of ovipositor present (saber, "long sword" in *Cratoelcana zessini*, "short sword" in *Panorpidium damianii* and the variation of "long sword" seen in *Ensiferelcana brachyptera*) suggest high rates of adaptation in this family to different kind of habitats.

Sex ratio of Elcanidae in the Crato Formation

The sex ratio of Elcanidae from the Crato Formation shows a strong bias towards females: considering all 88 specimens analyzed for this study as well as the type specimen of *M. rasnitsyni*, 69.7% of published specimens are female (excluding the specimens from Martins-Neto (1991)). This is supported by the sex ratio of specimens found in Kachin amber, where 61.9% were females, only 19% were males and 19% were of unknown sex (Table 2). One interpretation is that this sex ratio reflects on actual population composition. Biased sex ratios have been reported from extant species of Orthoptera, such as in the ground weta *Anderus maculifrons* (Walker, 1869) (male-biased) (Chappell et al., 2014) or the conehead *Ruspolia differens* (Serville, 1838) (female- or male-biased depending on seasonality) (Matojo and Yarro, 2010). There are also rare examples of almost exclusively female populations in parthenogenetic species like the tettigoniid *Saga pedo* (Pallas, 1771) or the ant-loving cricket *Myrmecophilus acervorum* (Panzer, 1799) which has been shown to reproduce both sexually and via parthenogenesis (Iorgu et al., 2023). Another possible explanation for the female-biased fossil record of Elcanidae could be the common character of deposit they are found in: they are often associated with bodies of water (the Crato Formation was probably deposited in a prehistoric lake or lagoon (Bezerra and Mendes, 2024); Kachin amber has been shown to include marine organisms and the trees that produced the resin may have stood near shore (Yu et al., 2019)). Possibly, females of Elcanidae had a stronger association with the aquatic habitat than males, using it for example for egg laying purposes. The oviposition site in orthopterans is chosen based on the availability of suitable substrates and microclimatic conditions such as

temperature and moisture (Wünsch et al., 2012). The morphologic diversity of ovipositors found in Elcanidae from the Crato Formation and elsewhere suggests that they were adapted to several kinds of substrates (Zhou et al., 2024; Willmott et al., 2025). The eggs of most Orthoptera need water for development, those of ensiferans more than those of caeliferans (Ingrisch and Köhler, 1998). Perhaps the eggs of elcanids found best conditions for development near shores of lakes or swamps. They may have even been deposited into aquatic plants as is known from some extant Acrididae MacLeay, 1821 (Song, 2019). Nymphs of this family already possessed the long metatibial spurs characteristic of Elcanidae (Peñalver and Grimaldi, 2010; Heads et al., 2018), hypothesized to be used for moving over the water's surface or swimming (Tian et al., 2019; Kim et al., 2021). Therefore, the ancient Mesozoic shorelines may have been a nursery ground for Elcanidae.

Table 2: Sex ratio of Elcanidae from Kachin/Burmese amber. Females 13, males four. Specimens of unknown sex (four) are not listed.

Species	**Sex**	**Publication**
Longioculus burmensis	male	Poinar et al., 2007
Ellca nevelka	female	Kočárek, 2020
Paraxelcana zhengi (holotype)	female	(Gu et al., 2022)
Hukawnelca gracile	male	Uchida, 2022
Caelielca spinocrus	male	Uchida, 2022
Pseudoprobaisselcana oculata	female	(Hu and He, 2023)
Paraxelcana zhengi (additional specimen, no type)	female	Schall et al., 2024
Letoelcana artemisapollonque	female	Schall et al., 2024
Trigonelca jennywinterae	female	Schall et al., 2024
Probaisselcana kachinensis	female	Zhou et al., 2024
Elcanodentes alatus	female	Willmott et al., 2025
Elcanodentes cretaceus holotype	male	Willmott et al., 2025
Elcanodentes cretaceus paratype	female	Willmott et al., 2025
Elcanodentes thanatos	female	Schall et al., 2025 in Willmott et al., 2025

Paraxelcana simplicissima	female	(Schall et al., 2025)
Kolymbelcana phantasma	female	Schall et al., 2025
Thagyaminana atawedeia	female	Schall et al., in press

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Supplementary material

Table 1 – Character variation of Crato Formation Elcanidae

Sheat 1: All 88 specimens + *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022) comb. nov. holotype (formerly *Cratoelcana rasnitsyni*).

Sheat 2: The “large group” specimens (forewing size >20 mm).

Sheat 3: The “small group” specimens (forewing size <14 mm).

Sheat 4: The “medium group” specimens (forewing size ca. 16-18 mm).

Character	Forewing length	Forewing length/width	Branches of RP	Stem of RP	body length (head to abdon	head height/forewing length	ovipositor length/forewing length	
Specimen								
CNBS00422 ♀	9,8	3,8	7	after MA1	5,7	0,28		0,06
CNBS00411 ♂	22,4	4,5	15	after second last RP	11,2	0,21	nn	
CNBS00423 ♂	25,3	4,4 nn		below 2 MA1	13,3	0,23	nn	
HC0001 ♀	27,2	4,5	11	nn	16,7	0,21		0,55
HC0002 ♀	ca. 10,8	3,9	6	after MA1	6,3	ca. 0,3	ca. 0,05	
HC0003 ♂	11,8	4,4	7	after MA1	6,3	>0,21	nn	
HC0004 ♂	nn	nn	nn	nn	5,7	nn	nn	
HC0005 ♀	12,7	4,1	7	nn	7,9	nn	>0,27	
HC0006 ♀	13,7	3,9	8	after MA1	6,4	nn		0,32
HC0007 ♀	nn	nn	nn	nn	5,6	nn	nn	
HC0009 ♀	12,1	ca. 4	nn	nn	ca. 7,8	nn		0,32
HC0012 ♂	11,4	3,9	7	after MA1	>6,3	0,24	nn	
HC0013 ♀	12,5	4,2	8	nn	6,8	0,26		0,33
HC0023 ♂	12,1	3,7	9	after last RP	7,8	0,26	nn	
HC0024 ♀	24,7	4,1	12	nn	14,6	>0,2	>0,04	
HC0025 ♀	11,5	nn	6	nn	6,1	0,24		0,06
HC0026 ♀	24,2	4,5	13	nn	11,4	0,21	>0,28	
HC0027 ♂	26,1	4,5 nn		nn	>11,7	>0,19	nn	
HC0028 ♀	25,8	4,3	12	below second last RP	14,1	0,24		0,05
HC0030 ♀	13,1	4,1	9	nn	8,2	0,24	>0,33	
HC0031 ♀	ca. 11,4	4,1 nn		nn	6,9	0,26		0,35
HC0032 ♀	11,9	3,9	8	nn	6,8	0,26	>0,21	
HC0033 ♀	12,8	3,7	7	after MA1	nn	0,22	nn	
HC0034 ♂	12,8	4,2 nn		right below MA1	6,4	0,18	nn	
HC0035 ♂	13,1	nn	nn	nn	7	ca. 0,25	nn	
HC0036 ♀	12,5	3,8	8	after 2 (!) MA1	9,2	0,21	nn	
HC0037 ♀	12,2	3,9	8	nn	6,4	>0,19		0,07
HC0038 ♂	10,4	nn	nn	nn	6,1	0,29		0,07
HC0040 ♀	25,1	4,1	11	below 2 MA1	12,7	0,22		0,64
HC0041 ♀	22,7	4	11	nn	12,6	nn	ca. 0,57	
HC0044 ♀	23,8	4,2	11	below second last RP	12,1	>0,19	>0,04	
MH1112 ♀	13,4	4,1	8	after MA1	6,8	0,24	>0,21	
MH1113 ♂	10	4,3	7	nn	5,7	0,25	nn	
MH1114 ♀	12,5	4,1 nn		nn	8,3	nn	nn	
MH1115 ♀	nn	nn	8	nn	nn	nn	nn	
MH1117 ♂	nn	nn	nn	nn	nn	nn	nn	
MH1118 ?	10	3,8 nn		nn	5,9	0,24	nn	
MH1119 ♀	11,1	4,2	6	after MA1	6,2	0,28	>0,32	
MH1111 ♀	27,4	4,7	12	nn	13,9	0,25	>0,58	
SMNK2672 ?	9,4	4	7	after MA1	5,7	0,24	nn	
SMNK45251 ♀	10,6	4	7	after MA1	5,8	0,25		0,06
SMNK45252 ♀	11,5	4	7	nn	6,7	0,24		0,31
SMNK47253 ♀	23,4	4	11	after 2 MA1	13,8	0,25		0,57
AMNH_SA_45123 ?	nn	nn	7	nn	nn	nn	nn	
AMNH_SA_45166 ♀	11,9	ca. 4,4	8	nn	7	0,3	>0,39	
AMNH_SA_45175 ♀	12,2	4,1	8	nn	6,6	>0,2	>0,31	
AMNH_SA_45181 ♀	nn	nn	9	nn	ca. 5,7	nn	nn	
AMNH_SA_45192 ♀	13,6	4	7	nn	6,8	0,28		0,4
AMNH_SA_45367 ♀	25,5	4,5	12	after second last RP	11,4	0,23		0,61
AMNH_SA_44504 ?	11	4,1	8	nn	5,9	0,22	nn	
AMNH_SA_44506 ♀	11,2	4,3	7	nn	5,8	0,27	>0,35	
AMNH_SA_44508 ♀	10,8	4,1 nn		nn	7,9	0,3		0,37
AMNH_SA_45082 ♀	10	4,3 nn		nn	6	0,27		0,06
AMNH_SA_45092 ♀	>9,1	>4,1	6	nn	6,6	<0,35	<0,11	
AMNH_SA_43881 ♀ (?)	24,1	4,4	12	after last RP	12	0,23	nn	
AMNH_SA_43893 ♂	9,6	4,1	7	nn	5,7	0,3	nn	
INHSP_1638 ♂	11	3,8 nn		nn	7	0,26	nn	
INHSP_1633 ♀	nn	nn	nn	nn	7,6	nn	nn	
INHSP_1631 ♂	11,4	4 nn		nn	5,5	0,24	nn	
INHSP_1626 ♀	23,5	4,1	13	nn	13,3	0,17		0,57
INHSP_1619 ♀	23,3	4,2	12	nn	13,3	0,27		0,57
INHSP_1614 ♀	11,4	4,3	8	nn	6,7	>0,2	nn	
INHSP_1179 ♀	25,6	4,1	14	below second last RP	13,3	0,23	>0,03	
INHSP_1131 ♀	26	4,8	13	after second last RP	10,8	0,19		0,55
INHSP_1168 ♀	10,8	3,9	6	nn	6	0,25		0,07
INHSP_1173 ♀	9,7	4,1	8	nn	6,6	0,27		0,4
INHSP_1166 ♀	23,3	4,2 nn		nn	13,3	0,23	>0,34	
INHSP_1169 ♀	nn	nn	nn	nn	5,8	nn	nn (saber)	
INHSP_1151 ?	26,1	4,1	12	below last RP	<16,5	0,2	nn	
INHSP_1145 ♂	11,2	4 nn		nn	5,8	0,21	nn	
INHSP_1125 ♀	10	4,1	7	nn	6,7	0,24		0,09
INHSP_1944 ♂	28,2	5,2 10 to 12		after third last RP	14,6	nn	nn	
INHSP_1937 ♂	18,7	4,3	10	after last RP	9,2	0,27	nn	
INHSP_1935 ♀	26,1	4,2	14	below last RP	13,8	>0,18		0,06
INHSP_1933 ♂	23,6	4,1	12	nn	12,9	0,21	nn	
INHSP_1918 ♂	24,5	4,2 nn		nn	12	0,22	nn	
INHSP_1887 ♀	26,4	4,5	10	after second last RP	14,1	>0,21		0,06
INHSP_1879 ♀	24,9	4,4	13	nn	13,1	0,2		0,56
INHSP_1878 ♀	25,9	4,4	12	nn	15	0,21		0,09
INHSP_1872 ♀	16,1	3,8	10	after last RP	9,9	0,3	>0,45	
INHSP_1874 ♀	25,3	4,3	14	nn	14,1	0,21		0,09
INHSP_1867 ♂	23,3	4,4 nn		nn	12	0,22	nn	
INHSP_1866 ♀	16,6	4,7	10	nn	12,8	0,35		0,86
INHSP_1851 ♂	27,7	4,6	12	nn	13,1	0,19	nn	
INHSP_1824 ♀	23	4,1 10 to 11		after last RP	14,3	0,25		0,51
INHSP_1817 ♀	25,2	4,2	14	nn	14,1	0,21	>0,41	
INHSP_1820 ♀	23,5	4,4	11	nn	12,4	>0,21	>0,39	
INHSP_1756 ♀	12,3	4,2	7	nn	7,4	0,24		0,38
C. rasnitsyni type specimen ♀	25,9	4,5	12	below last RP	14,9	0,21		0,08

Character	Forewing length	Forewing length/width	Branches of RP	Stem of RP	body length (head to abdom	head height/forewing length	ovipositor length/forewing length
Specimen							
CNBS00411 ♂	22,4	4,5	15	after second last RP		11,2	0,21 nn
CNBS00423 ♂	25,3	4,4 nn		below 2 MA1		13,3	0,23 nn
HC0001 ♀	27,2	4,5	11	nn		16,7	0,21 0,55
HC0024 ♀	24,7	4,1	12	nn		14,6 >0,2	>0,04
HC0026 ♀	24,2	4,5	13	nn		11,4	0,21 >0,28
HC0027 ♂	26,1	4,5 nn		nn	>11,7	>0,19	nn
HC0028 ♀	25,8	4,3	12	below second last RP		14,1	0,24 0,05
HC0040 ♀	25,1	4,1	11	below 2 MA1		12,7	0,22 0,64
HC0041 ♀	22,7	4	11	nn		12,6 nn	ca. 0,57
HC0044 ♀	23,8	4,2	11	below second last RP		12,1 >0,19	>0,04
MH1111 ♀	27,4	4,7	12	nn		13,9	0,25 >0,58
SMNK47253 ♀	23,4	4	11	after 2 MA1		13,8	0,25 0,57
AMNH_SA_45367 ♀	25,5	4,5	12	after second last RP		11,4	0,23 0,61
AMNH_SA_43881 ♀ (?)	24,1	4,4	12	after last RP		12	0,23 nn
INHSP_1626 ♀	23,5	4,1	13	nn		13,3	0,17 0,57
INHSP_1619 ♀	23,3	4,2	12	nn		13,3	0,27 0,57
INHSP_1179 ♀	25,6	4,1	14	below second last RP		13,3	0,23 >0,03
INHSP_1131 ♀	26	4,8	13	after second last RP		10,8	0,19 0,55
INHSP_1166 ♀	23,3	4,2 nn		nn		13,3	0,23 >0,34
INHSP_1151 ?	26,1	4,1	12	below last RP	<16,5		0,2 nn
INHSP_1944 ♂	28,2	5,2 10 to 12		after third last RP		14,6 nn	nn
INHSP_1935 ♀	26,1	4,2	14	below last RP		13,8 >0,18	0,06
INHSP_1933 ♂	23,6	4,1	12	nn		12,9	0,21 nn
INHSP_1918 ♂	24,5	4,2 nn		nn		12	0,22 nn
INHSP_1887 ♀	26,4	4,5	10	after second last RP		14,1 >0,21	0,06
INHSP_1879 ♀	24,9	4,4	13	nn		13,1	0,2 0,56
INHSP_1878 ♀	25,9	4,4	12	nn		15	0,21 0,09
INHSP_1874 ♀	25,3	4,3	14	nn		14,1	0,21 0,09
INHSP_1867 ♂	23,3	4,4 nn		nn		12	0,22 nn
INHSP_1851 ♂	27,7	4,6	12	nn		13,1	0,19 nn
INHSP_1824 ♀	23	4,1	11	after last RP		14,3	0,25 0,51
INHSP_1817 ♀	25,2	4,2	14	nn		14,1	0,21 >0,41
INHSP_1820 ♀	23,5	4,4	11	nn		12,4 >0,21	>0,39
C. rasnitsyni type specimen ♀	25,9	4,5	12	below last RP		14,9	0,21 0,08

Cratoelcana zessini
Mesembrelcana rasnitsyni

Character	Forewing length	Forewing length/width	Branches of RP	Stem of RP	body length (head to abdo	head height/forewing length	ovipositor length/forewing length
Specimen							
CNBS00422 ♀	9,8		3,8	7 after MA1	5,7	0,28	0,06
HC0002 ♀	ca. 10,8		3,9	6 after MA1	6,3	ca. 0,3	ca. 0,05
HC0003 ♂	11,8		4,4	7 after MA1	6,3	>0,21	nn
HC0005 ♀	12,7		4,1	7 nn	7,9	nn	>0,27
HC0006 ♀	13,7		3,9	8 after MA1	6,4	nn	0,32
HC0007 ♀	nn	nn	nn	nn	5,6	nn	nn
HC0009 ♀	12,1	ca. 4	nn	nn	ca. 7,8	nn	0,32
HC0012 ♂	11,4		3,9	7 after MA1	>6,3	0,24	nn
HC0013 ♀	12,5		4,2	8 nn	6,8	0,26	0,33
HC0023 ♂	12,1		3,7	9 after last RP	7,8	0,26	nn
HC0025 ♀	11,5	nn		6 nn	6,1	0,24	0,06
HC0030 ♀	13,1		4,1	9 nn	8,2	0,24	>0,33
HC0031 ♀	ca. 11,4		4,1	nn nn	6,9	0,26	0,35
HC0032 ♀	11,9		3,9	8 nn	6,8	0,26	>0,21
HC0033 ♀	12,8		3,7	7 after MA1	nn	0,22	nn
HC0034 ♂	12,8		4,2	nn right below MA1	6,4	0,18	nn
HC0035 ♂	13,1	nn	nn	nn	7	ca. 0,25	nn
HC0036 ♀	12,5		3,8	8 after 2 (!) MA1	9,2	0,21	nn
HC0037 ♀	12,2		3,9	8 nn	6,4	>0,19	0,07
HC0038 ♂	10,4	nn	nn	nn	6,1	0,29	0,07
MH1112 ♀	13,4		4,1	8 after MA1	6,8	0,24	>0,21
MH1113 ♂	10		4,3	7 nn	5,7	0,25	nn
MH1114 ♀	12,5		4,1	nn nn	8,3	nn	nn
MH1118 ?	10		3,8	nn nn	5,9	0,24	nn
MH1119 ♀	11,1		4,2	6 after MA1	6,2	0,28	>0,32
SMNK2672 ?	9,4		4	7 after MA1	5,7	0,24	nn
SMNK45251 ♀	10,6		4	7 after MA1	5,8	0,25	0,06
SMNK45252 ♀	11,5		4	7 nn	6,7	0,24	0,31
AMNH_SA_45166 ♀	11,9	ca. 4,4		8 nn	7	0,3	>0,39
AMNH_SA_45175 ♀	12,2		4,1	8 nn	6,6	>0,2	>0,31
AMNH_SA_45192 ♀	13,6		4	7 nn	6,8	0,28	0,4
AMNH_SA_44504 ?	11		4,1	8 nn	5,9	0,22	nn
AMNH_SA_44506 ♀	11,2		4,3	7 nn	5,8	0,27	>0,35
AMNH_SA_44508 ♀	10,8		4,1	nn nn	7,9	0,3	0,37
AMNH_SA_45082 ♀	10		4,3	nn nn	6	0,27	0,06
AMNH_SA_45092 ♀	>9,1	>4,1		6 nn	6,6	<0,35	<0,11
AMNH_SA_43893 ♂	9,6		4,1	7 nn	5,7	0,3	nn
INHSP_1638 ♂	11		3,8	nn nn	7	0,26	nn
INHSP_1631 ♂	11,4		4	nn nn	5,5	0,24	nn
INHSP_1614 ♀	11,4		4,3	8 nn	6,7	>0,2	nn
INHSP_1168 ♀	10,8		3,9	6 nn	6	0,25	0,07
INHSP_1173 ♀	9,7		4,1	8 nn	6,6	0,27	0,4
INHSP_1145 ♂	11,2		4	nn nn	5,8	0,21	nn
INHSP_1125 ♀	10		4,1	7 nn	6,7	0,24	0,09
INHSP_1756 ♀	12,3		4,2	7 nn	7,4	0,24	0,38

Gondwanaelcana brasiliensis
Panorpidium damianii

Character	Forewing length	Forewing length/width	Branches of RP	Stem of RP	body length (head to abdominal apex)	head height/forewing length	ovipositor length/forewing length
Specimen							
INHSP_1937 ♂	18,7	4,3	10	after last RP	9,2	0,27	nn
INHSP_1872 ♀	16,1	3,8	10	after last RP	9,9	0,3	>0,45
INHSP_1866 ♀	16,6	4,7	10	nn	12,8	0,35	0,86

Argentelcana intermedia
Ensiferelcana brachyptera

Supplementary Figures – 1-6

Figs. 1-4: undetermined specimens of the “small group” featured in Table 1.

Fig. 5: undetermined specimens of the “large group” featured in Table 1.

Fig. 6: undetermined male specimen of the “medium group” featured in Table 1.

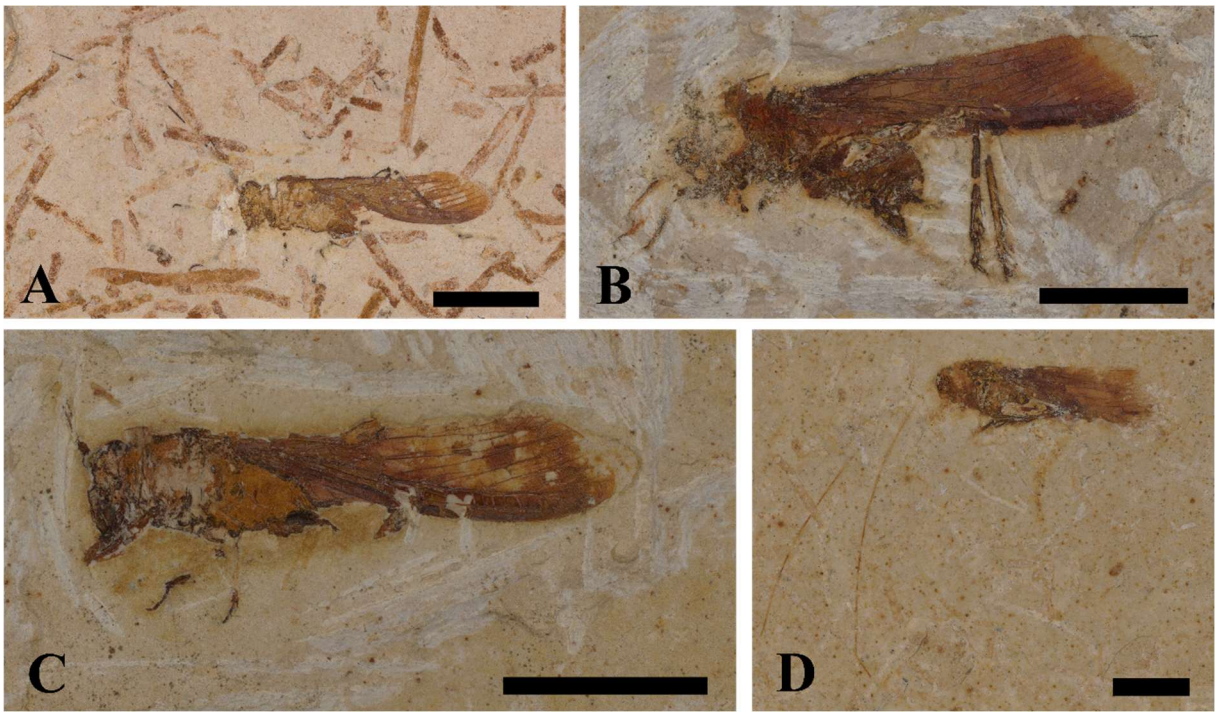

Fig. 1: Undetermined specimens of Crato Formation Elcanidae (“small group”): **A.** SMNK_PAL_2672, male. **B.** MH1114, female. This specimen shows the very base of an ovipositor that appears to have been rather broad. It probably belongs to *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. **C.** MH1118. In this specimen the abdomen was damaged; the gender is unknown. **D.** MH1117, probably a male. Note the metatibial spurs of this specimen which show distinct leaf-like morphology. **Scale bars** = 5 mm.

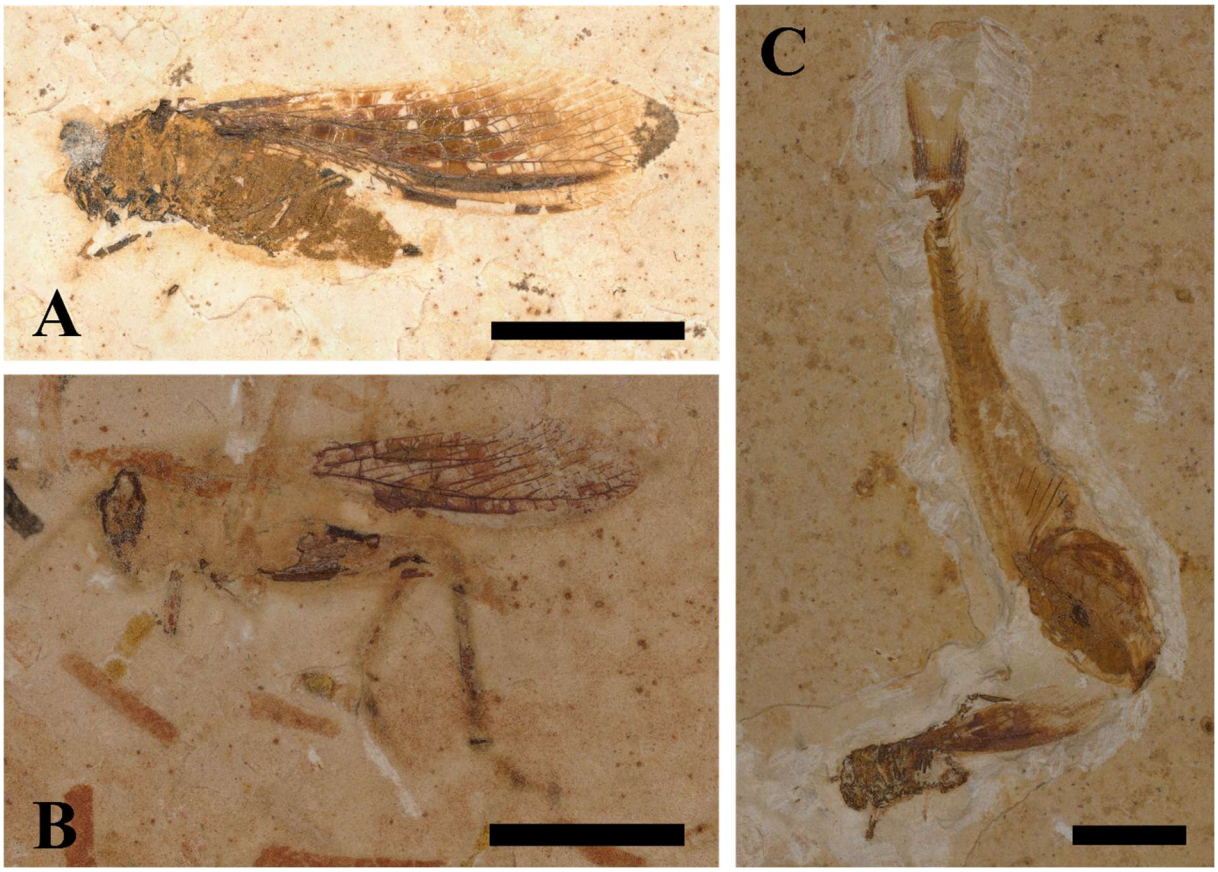

Fig. 2: Undetermined specimens of Crato Formation Elcanidae ("small group"): **A.** HC0036, probably female. Similar to MH1114 (previous figure, B), at the abdomen of this specimen something can be seen that likely belongs to a rather broad ovipositor; this suggests this specimen may belong to *Panorpidium damianii* (Martins-Neto, 1991) comb. nov. **B.** MH1115, maybe female. There is a small fragment in the knee region of the metathoracic leg that may belong to an ovipositor (it would once again indicate *P. damianii*). However, attribution of this fragment is doubtful. **C.** MH1113, male. Like in Fig. 16A from the main study, this specimen was preserved together with a fish probably of the taxon *Dastilbe crandalli* Jordan, 1910. In this case, the fish is slightly larger than the one from 16A. Maybe, at this size the juvenile *D. crandalli*s were predating on the elcanids if they got close to the water. **Scale bars** = 5 mm.

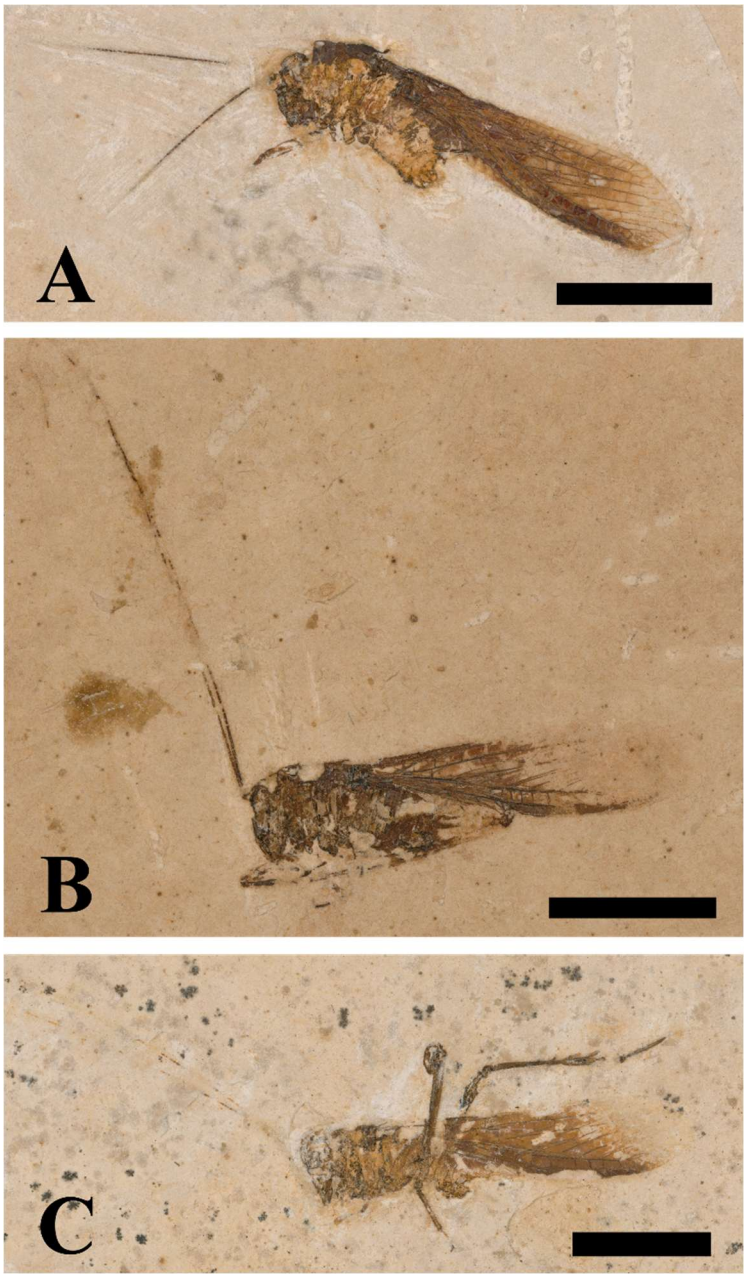

Fig. 3: Undetermined specimens of Crato Formation Elcanidae ("small group"): **A.** HC0003, male. **B.** HC0004, probably male. **C.** HC0012, abdominal apex damaged, gender unknown. **Scale bars** = 5 mm.

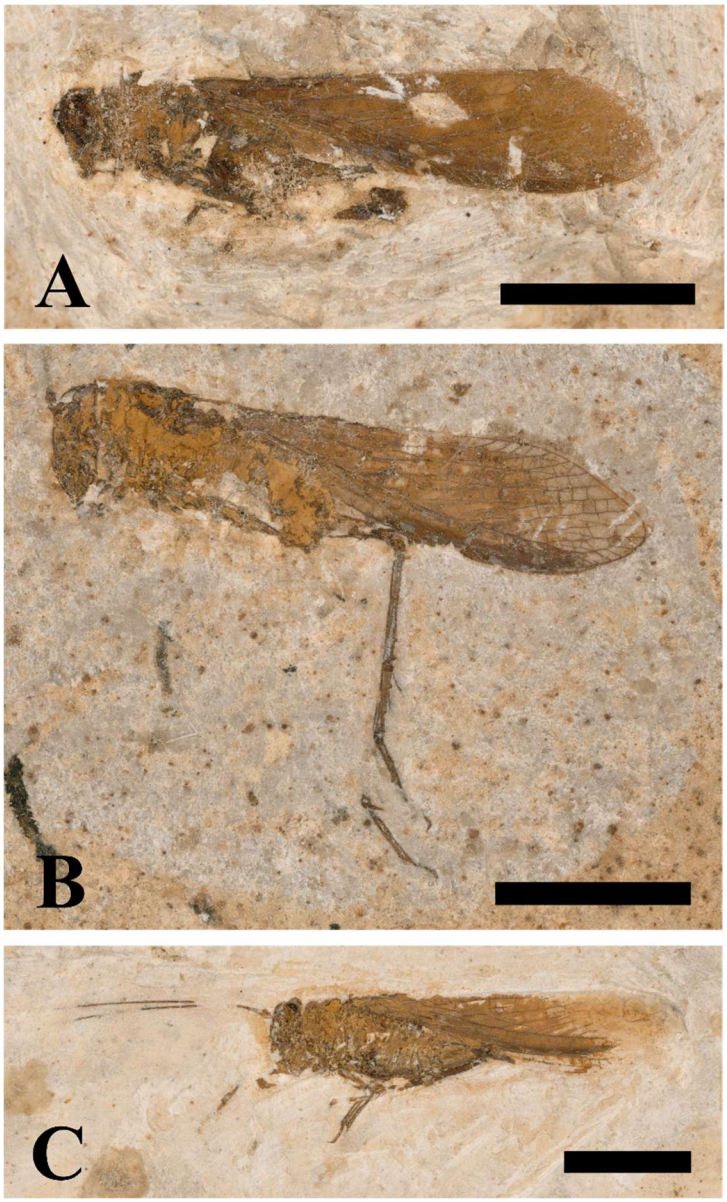

Fig. 4: Undetermined specimens of Crato Formation Elcanidae ("small group"): **A.** HC0034, abdomen obscured/damaged, gender unknown. **B.** HC0023, male. **C.** HC0035, male. **Scale bars** = 5 mm.

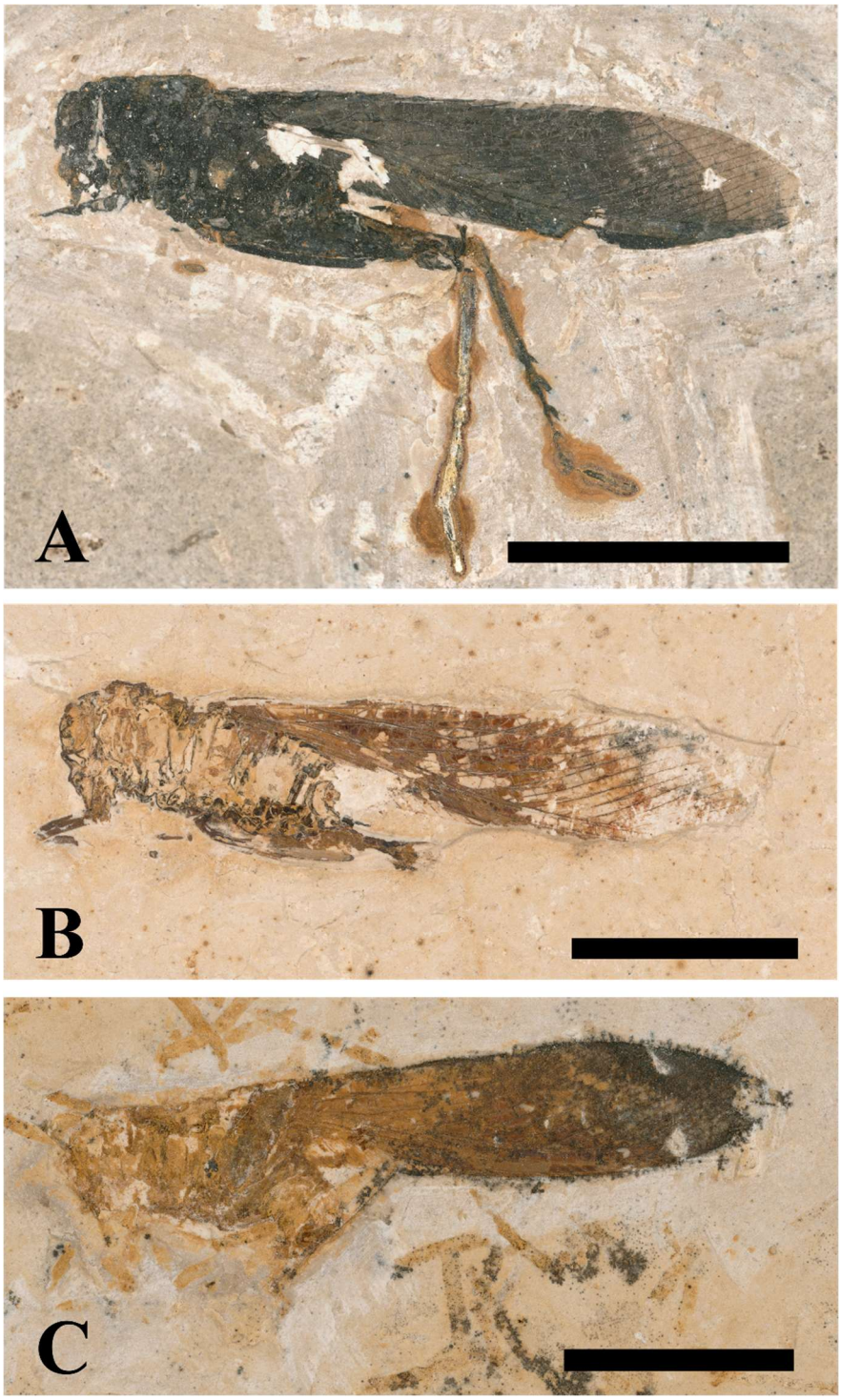

Fig. 5: Undetermined specimens of Crato Formation Elcanidae ("large group"): **A.** CNBS00411, male. **B.** CNBS00423, probably male. **C.** HC0027, abdominal apex obscured/damaged, gender unknown. **Scale bars** = 10 mm.

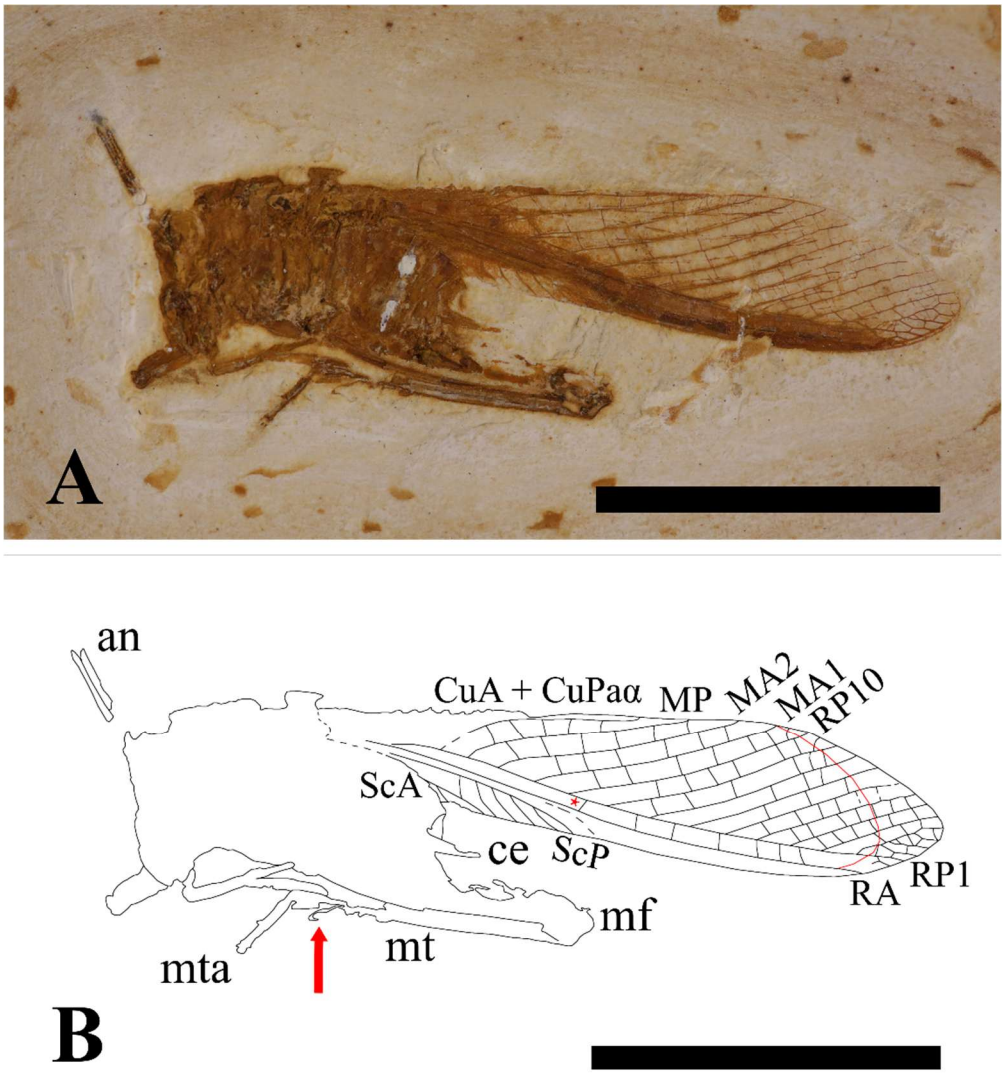

Fig. 6: Undetermined specimen of Crato Formation Elcanidae ("medium group"), INHSP_1937, male: **A.** and **B.** Complete specimen. Red asterisk marking the position of the stem of RP, red arrow marking metatibial spur, red line marking apical margin of hindwing. Based on the shorter cerci (1.5 mm) of this specimen it may belong to *Argentelcana* rather than *Ensiferelcana*, but it could also be a separate taxon. **Scale bars** = 10 mm.

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Chapter 9

A new hypothesis for the phylogenetic placement of fossil grasshopper (Insecta: Orthoptera) lineages

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Abstract

The Elcanidea Gorochov, 1995 is an extinct infraorder of the Orthoptera Olivier, 1789. Due to their morphological traits, which on the one hand largely resemble Ensifera Chopard, 1921, but also share characters with Caelifera Ander, 1936, their systematic position has long been debated. We here try to tackle this issue by performing a morphology-based phylogenetic analysis of Orthoptera using a Maximum Likelihood approach. By combining our findings with earlier hypotheses based on molecular and morphological evidence as well as analysis of the fossil record of Orthoptera, we propose new phylogenetic relationships for major higher-level taxa of the order, including Oedischiidea Handlirsch, 1906, Elcanidea Gorochov, 1995, Hagloidea Handlirsch, 1906, Tettigoniidea Kevan, 1982, Gryllidea Vickery, 1977, Locustopsoidea Handlirsch, 1906, Tridactylidea Brullé, 1835, Tetrigoidea Rambur, 1838 and Acridomorpha MacLeay, 1821. Oedischiidea are suggested to be the ancestors of Ensifera and Caelifera (Oedischiidea should be excluded from Ensifera, if monophyly of Caelifera is to be maintained). Elcanidea are suggested as basal Ensifera and sister taxon of Hagloidea and Gryllidea + Tettigoniidea, a position that matches some previous hypotheses, but rejects others which have suggested placement inside Caelifera. Locustopsoidea are basal Caelifera and sister taxon to Tridactylidea and Acridomorpha + Tetrigoidea (= Acrididea). This finding refutes the current placement of the group as a member of Acridomorpha and sister group to Acridoidea. Our findings highlight the importance to include fossil species in phylogenetic studies of Orthoptera if the goal is to resolve higher-level taxa relationships.

Keywords: Ensifera; Caelifera; Hagloidea; Locustopsoidea; fossil record; Maximum Likelihood

1. Introduction

Resolving the phylogenetic position of an extinct group of organisms is challenging. The fossil record is inherently incomplete, and few specimens are perfectly preserved, often resulting in plenty of missing data (Swalla and Smith, 2008). Additionally, aspects of morphology can be subject to ambiguous interpretation, causing errors in data composition not present in molecular phylogenies (Swalla and Smith, 2008). On the other hand, fossils provide invaluable insights into the evolutionary history of a lineage by exhibiting ancestral character states not found in present forms, which are key to understanding their complete relationships (Ware and Barden, 2016). Accordingly, Beutel et al. (2011) remark that the neglect of fossils can lead to serious misinterpretation of phylogenetic relationships.

The Elcanidea Gorochov, 1995 are a Permian-Cretaceous infraorder of Orthoptera Olivier, 1789 with a global distribution (except Africa and Antarctica). Currently (as of July 2025), 107 species are known (Cigliano et al., 2025; Schall et al., in press a; Schall et al., in press b; Schall et al., submitted), making them one of the better known exclusively fossil groups of Orthoptera, alongside the Hagloidea Handlirsch, 1906 (222 species) and Locustopsoidea Handlirsch, 1906 (93 species) (Cigliano et al., 2025; Schall et al., chapters 4-6). However, whereas Locustopsoidea and Hagloidea are confidently attributed to the suborders Caelifera Ander, 1936 and Ensifera Chopard, 1921, respectively, the phylogenetic position of Elcanidea has remained a matter of debate. Despite most studies having suggested a placement within Ensifera (Gorochov and Coram, 2022; Handlirsch, 1906; Ragge, 1955; Sharov, 1968; Zessin, 1987), some authors have articulated an opposing opinion, placing them in the Caelifera instead (Béthoux and Nel, 2002; Zeuner, 1942c). Today, especially the phylogenetic analysis based on parsimony conducted by Béthoux and Nel (2002) is commonly cited in reference to the phylogeny of Elcanidea, as this also represents the only cladistic analysis of the matter so far. Based on 74 morphological characters of forewing venation they recovered a position of Elcanidea within Caelifera. In the past 23 years, many new species of Elcanidae Handlirsch, 1906 (Elcanidea: Elcanoidea) were discovered, among them several (nearly) complete specimens found in Cretaceous amber of Northern Myanmar (Kachin amber) (e.g. Kočárek, 2020; Willmott et al. 2025). These new findings have greatly improved our understanding of Elcanidae anatomy, providing additional morphological data for a phylogenetic analysis including characters of forewing venation and other body features. Based on this data, we performed a Maximum Likelihood phylogenetic analyses to determine the position of the infraorder Elcanidea Gorochov, 1995 in relation to other major infraorders and superfamilies

(Gryllidea Vickery, 1977; Tettigoniidea Kevan, 1982; Acrididea Targioni-Tozzetti, 1882 (without Locustopsoidea Handlirsch, 1906); Locustopsoidea; Tetrigoidea Rambur, 1838; Tridactylidea Brullé, 1835) within Orthoptera.

2. Materials and methods

The taxonomy in this study follows the Orthoptera Species File (Cigliano et al., 2025 https://orthoptera.speciesfile.org/).

2.1 Data collection

We constructed a multistep character matrix based on morphological data of the forewing and body with the aim to resolve the phylogenetic position of main infraorders and superfamilies of Orthoptera (= main matrix, suppl. mat. 1). This taxonomic level was selected to allow for a more complete dataset (i.e. reduce missing data), as below the superfamily level, some fossil taxa are represented only by isolated wings. In total, 133 species of Orthoptera from 47 families (both extinct and extant) and one outgroup (*Fragosublatta pectinata* Chen et al., 2021, an extinct species of cockroach) were included and analysed by comparing 50 characters. Character selection was based on apomorphies of different taxa of Orthoptera (e. g. "presence of metatibial spurs" for Elcanidae Handlirsch, 1906; "mesotibia inflated" for Tridactylidae Brullé, 1835), conspicuous morphological traits (e. g. "well-developed spines on fore- and middle tibiae" for Gryllacrididae Blanchard, 1845; "habitus stick-like" for Proscopioidea Serville, 1838) and general aspects of morphology (e.g. "branches of M" [medial vein of the forewing]; metafemur/body length). All characters were newly selected for this analysis and were weighted equally. The full character list used in our analysis is provided in Supplementary Material 2. Our analysis included less characters than some previous ones that focused on fossil lineages (for example Béthoux and Nel (2002) analyzed 74 characters of the forewing morphology). The overall goal of our analysis was to keep the ratio of missing data as low as possible to avoid incorrect reconstruction of relationships influenced by a shared number of N (= missing data). Including more detailed characters (such as information of genital structure) obtainable from extant forms, would have made the fossil forms artificially more similar to each other, because they would have all shared the "N" character state in that position.

The number of taxa per family was decided based on the species richness of each family. Families with a species number between 1 and 29 were included with one representative (since our goal was to resolve the phylogeny of Orthoptera on the infraorder/superfamily-level, testing monophyly of each family did not meet the scope of this study); 30-99 species - two representatives; 100-199 species – three representatives. 200-999 species – four representatives; more than 1000 species – five representatives. The only exceptions are the Elcanidae Handlirsch, 1906 and Permelcanidae Sharov, 1962, which have four and two representatives, respectively. This was done to more fully cover morphologic variation for the taxon of main interest. We included fossil species of each family if available and well-preserved. Morphological data of the species was collected using the Orthoptera Species File, as well as published studies. Additionally, some species were included based on collection material of the Leibniz Institute for the Analysis of Biodiversity Change (LIB), Hamburg (see supplementary material 3 for all species used and supplementary figures 1-9 for images of the LIB Hamburg specimens).

2.2 Phylogenetic analyses

Firstly, we performed a Neighbor Joining (NJ) analysis using PAUP (v. 4.0) (Swofford, 2025; https://paup.phylosolutions.com/) with default settings. Secondly, a phylogenetic analysis based on Maximum Parsimony (MP) was performed in PAUP. Input data was a standard nexus file (supplementary material 4), which was manually constructed. We conducted a heuristic search with all settings as default and increased the number of retained trees to 1000. A consensus tree of all 1000 trees was computed. Finally, we performed a phylogenetic analysis using Maximum Likelihood (ML) via the online-tool IQ-TREE (Nguyen et al., 2015 http://www.iqtree.org/, December 2024). IQ-TREE analyses are based on a ML algorithm. Source data was again the manually constructed nexus file. The data type was set to morphology. All other options were left as default (substitution model "Auto"; bootstrap analysis "Ultrafast" with 1000 replicates; Hoang et al., 2017). We used the integrated substitution model finder by IQ-TREE, "ModelFinder" (Kalyaanamoorthy et al., 2017) and performed three runs with the same data ngMK+FQ+ASC+G4 as the best fitting model for our analysis in all runs. A 50% majority rule consensus tree was constructed with IQ-TREE.

Consensus trees from the MP and ML approach and the NJ tree were visualized in the online webtool ITOL (Interactive Tree Of Life) (Letunic and Bork, 2024, https://itol.embl.de/) and

further graphically improved with Inkscape v.1.4.2 (Moini et al., 2025, https://inkscape.org/, 28.07.2025). Shapes of Orthoptera taxa were created in GIMP v. 3.0.2-1 (the GIMP Team, 2025; https://www.gimp.org/). Sources for the shapes were: Gryllidea = *Miogryllus patagonicus* Cadena-Castañeda et al., 2024 after an image in Castelli et al. (2024); Elcanidea = *Panorpidium damianii* (Martins-Neto, 1991), specimen HC0030. Tettigoniidea = *Tettigonia viridissima* (Linnaeus, 1758), specimen ZMH71558 from the LIB Hamburg collection (Suppl. Fig. 1); Locustopsoidea = *Locustopsis rhytofemoralis* Gu et al., 2016; Tetrigoidea = *Phelene turgida* (Bolívar, 1887), specimen depicted in Kasalo et al. (2024); Acrididea = *Dericorys millierei* Bonnet and Finot, 1884, specimen ZMH862113 from the LIB Hamburg collection (Suppl. Fig. 3); Tridactylidea after *Ellipes deyrupi* Woo, 2021 (Fig. 4B in Woo (2021)); Hagloidea (Tettigoniidea) after *Allaboilus gigantus* Ren and Meng, 2006 (Fig. 5,5 in Gu et al. (2010)); Eumastacoidea after *Afromastax zebra zebra* (Gerstaecker, 1889), specimen ZMH862120 from the LIB Hamburg collection (Suppl. Fig. 7); Proscopioidea after *Proscopia gigantea* Klug, 1820 (collection object 1500894, otus 827235 on Cigliano et al. (2025); image by Sigfrid Ingrisch, DORSA).

2.3 Reconstructing missing data

We reconstructed missing characters in the matrix with a composite morphology approach for each species. For example, if the character is "amorph metatibial spurs present: yes/no" and this character is unknown in the species *Meselcana madygenica* Sharov, 1968, but known in another species of Elcanoidea Handlirsch, 1906 the same character state from this other species is assumed for *M. madygenica*. This method of composite character reconstruction reduced the ratio of unknown character states in our phylogenetic matrix by 80.7%. To test if this approach was superior to an unreconstructed matrix and to find the best parameters for reconstruction, we performed a test phylogenetic analysis using only extant species of Orthoptera of which the phylogenetic relationships are rather well-known thanks to comprehensive studies based on molecular evidence such as Song et al. (2015, 2020). The test analysis was conducted similarly as stated in 2.1 and 2.2. The fossil species of extant families were replaced by extant species. Exclusively fossil families were removed. To reconstruct the missing data, we followed these steps:

a. Setting the same N-rate

In our phylogenetic analysis, to determine the position of Elcanidae within Orthoptera, we had an N-rate (missing data = an unknown character state) of 29.3%. In our test matrix the N rate was only 24.1%. Hence, as a first step we randomly changed characters in our test matrix to N until the same N-ratio as of the main matrix was achieved. In total, 313 known character states were randomly set to N.

b. Applying threshold values

For every lower-level taxon (= species), missing character states were reconstructed based on the higher-level taxon (which was either infraorder or superfamily). To do this, different threshold requirements were set for how often a character had to obtain the same state to serve as a model for related taxa with that character unknown (an example: an infraorder (higher-level taxon) includes 15 species. In five of them the character X is unknown. In the remaining ten species, three have X as "present", seven have it as "absent". If we apply a 60% threshold, this means of the species with character X known (ten), six or more need to have the same character for that character state to also be applied to the five species in which X is unknown. In our example, seven species have the character state "absent", so the five species with X unknown would get the character state reconstructed as "absent", too). Four different thresholds were tested: 60%, 40%, 20% and 0%. Reliability of each threshold was ranked by determining how many species clustered in the correct infraorder. The results can be seen in Table 1. With a decrease in threshold, the number of N replaced increased. The reliability (species clustering in correct infraorder) increased up to the 20% threshold, but did not improve by lowering further to 0%. To determine if 0% or 20% was the better value for a threshold, we counted the species clustering in the correct superfamily for these two thresholds. The result of both thresholds were very similar, with 86 species clustering in the correct superfamily using the 20% threshold and 85 species using 0%. Further, we tested whether this result could be improved by applying the 20% threshold not on the infraorder as the higher-level taxon, but on the superfamily. However, in this case only 103 species clustered in the correct infraorder, whereas previously (20% applied on infraorder) 120 species clustered in the correct infraorder (100% of species used in the test analysis).

c. The hybrid approach

Finally, we tested whether the results could be improved by applying the 20% threshold first at the superfamily level and, in a second step, at the infraorder level. In this analyses, all 120 species clustered in the correct infraorder. Using this hybrid approach, 111 species also clustered in the correct superfamily (in other approaches only 86). Thus, the hybrid approach was chosen as the most reliable method of trait reconstruction for our phylogenetic analysis and was applied to the main matrix. Curiously, all test matrices, no matter the method of reconstruction, found Ensifera nested within Caelifera. This was changed once the fossil taxa were included.

Table 1: Results of the character reconstruction testing. The hybrid approach was the most reliable method to determine the placement of superfamilies within Orthoptera with all species of the test matrix clustering in the correct infraorder and almost all of them (111/120) clustering in the correct superfamily. *A rate of 100% for N replaced was not reached even if no threshold was applied (0%-threshold), because we applied the general rule that if two characters (that were not N) were present at equal number for one given character, N was not replaced for that character.

Threshold for reconstruction	**Number of species clustering in correct infraorder**	**Number of species clustering in correct superfamily**	**N replaced**
Raw (without reconstruction of missing data)	80 (66.67%)	Not tested	0 (0%)
60% (on infraorder)	85 (70.8%)	Not tested	309 (17.4%)
40% (on infraorder)	93 (77.5%)	Not tested	385 (21.7%)
20% (on infraorder)	120 (100%)	86 (71.67%)	1298 (73.2%)
0% (= no threshold) (on infraorder)	120 (100%)	85 (70.8%)	1503 (84.8%*)
20% (on superfamily)	103 (85.8%)	Not tested	989 (55.8%)
20% (hybrid = superfamily first, then infraorder)	120 (100%)	111 (92.5%)	1430 (80.7%)

3 Results

Figs. 1-4

Neighbour Joining

In the NJ tree (Fig. 1), Elcanidea is the most-basal taxon of Orthoptera. The two extant infraorders of Ensifera, Gryllidea and Tettigoniidea, are monophyletic, but Tridactylidea (Caelifera) shares a common ancestor with Tettigoniidea, thus is nested within the ensiferan taxa. The remaining Caelifera (extant Acridomorpha, Locustopsoidea and Tetrigoidea) are monophyletic, and more closely related to Tettigoniidea than the rest of Ensifera or Tridactylidea. Locustopsoidea forms a clade at the base of Caelifera that includes *Lobosceliana femoralis* (Walker, 1870), a pamphagid (Acridoidea). The NJ as well as the MP analysis below were performed without the implementation of a branch support test. Bootstrap analysis was attempted in an earlier run of both approaches (using PAUP), but resulted in trees affected by major polytomies.

Maximum Parsimony

The heuristic search option with MP as the optimality criterion finds similar relationships as in the NJ tree in terms of Ensifera relationships (Fig. 2). Two noteworthy differences are that Tridactylidea is now included in Caelifera, as were members of the superfamily Tettigonioidea Krauss, 1902. Within Acridomorpha, a major polytomy is present among the deeper nodes. Locustopsoidea is not placed at the base of Caelifera anymore. Tetrigoidea is not monophyletic, because two species (*Tripetalocera ferruginea* Westwood, 1834 and *Discotettix belzebuth* Serville, 1838) cluster in a different position from the other three tetrigids in the analysis as a sister group to some Acridoidea.

Maximum Likelihood

Three runs with the same data (i. e. Nexus file) were conducted using ML as the algorithm. They resulted in two different tree topologies with similar bootstrap support values (Fig. 3 = run 1 and 4 = run 2 & 3). The first topology (Fig. 3) finds Gryllidea at the base of Ensifera (and Orthoptera as a whole) instead of Elcanidea, which is more closely related to Tettigoniidea. The node marking the last common ancestor (LCA) of Gryllidea and Elcanidea has a bootstrap support of ca. 70%. The node marking the LCA of Elcanidea and Tettigoniidea has a bootstrap support of ca. 92%. All ensiferan clades are monophyletic. Tettigoniidea shares a common ancestor with Caelifera. The node marking the LCA of Tettigoniidea and Caelifera has a bootstrap support of ca. 72% and the LCA of Caelifera of ca. 90% (= split between Locustopsoidea and the rest of Caelifera). Among Caelifera, Locustopsoidea is once more the

most basal taxon (similar to NJ) and again includes *Lobosceliana femoralis*. Tetrigoidea and Tridactylidea are monophyletic taxa within Acridomorpha (bootstrap ca. 100%).

The second topology (Fig. 4) is mostly similar to the first, however, with the noteworthy difference that Caelifera forms a monophyletic sister clade to a clade consisting of (Gryllidea + Elcanidea) Tettigonioidea. The split between these clades has a bootstrap support of ca. 80%. The remaining Tettigoniidea are the common ancestor of the other groups. The bootstrap support for the LCA between the remaining Tettigoniidea and the two sister clades is ca. 80%. LCA of Elcanidea and Gryllidea has ca. 90% bootstrap support, as does the LCA of Locustopsoidea and the rest of Caelifera. Monophyly of Tetrigoidea and Tridactylidea (both nestes within Acridomorpha) is supported by bootstrap values of ca. 100%. In this version of the ML analysis, Tetrigoidea and Tridactylidea cluster as sister clades in an almost monophyletic clade (bootstrap ca. 80%), yet including two (out of four) species of Euschmidtiidae Rehn, 1948 and the single species of Tristiridae Rehn, 1906.

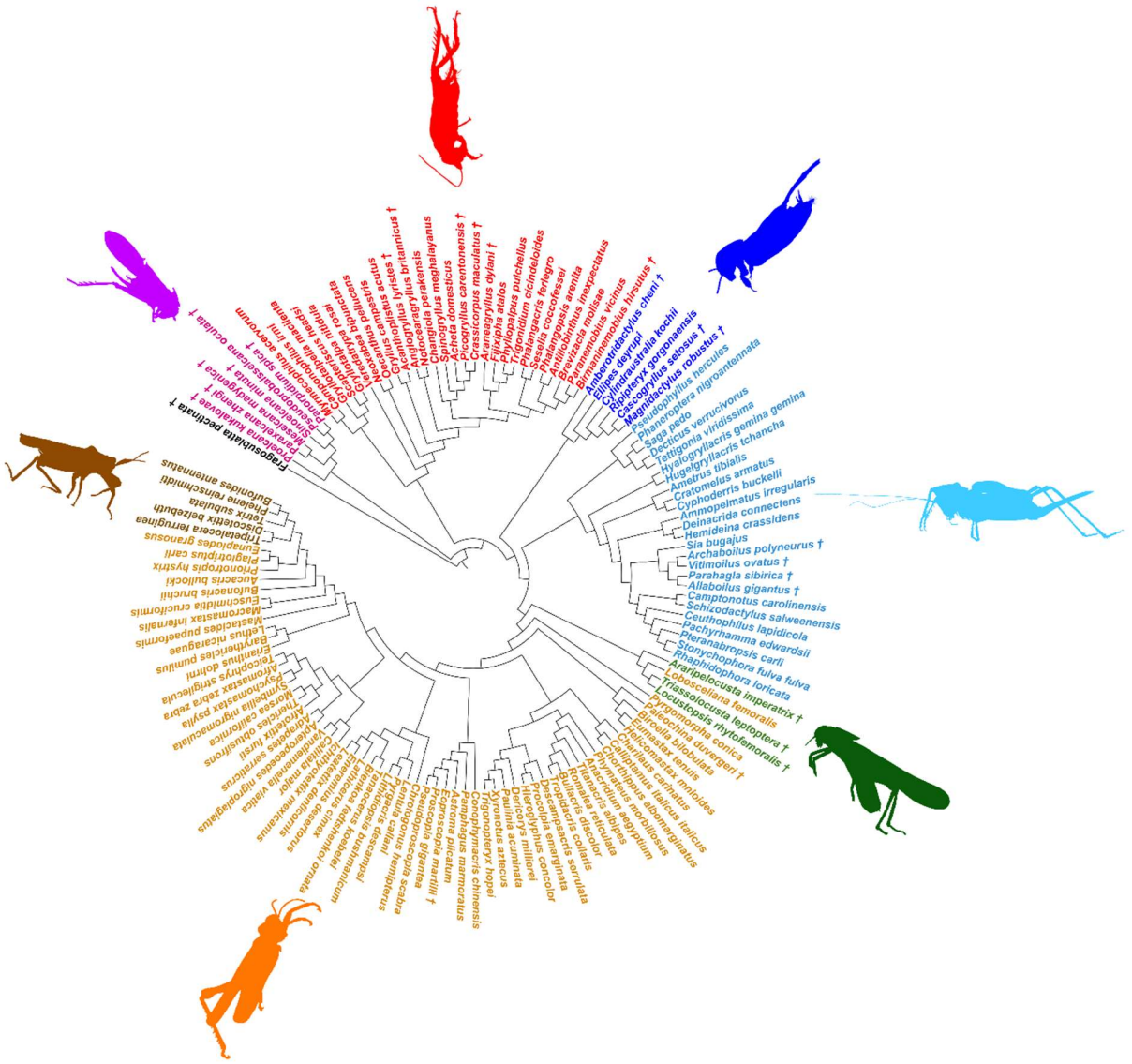
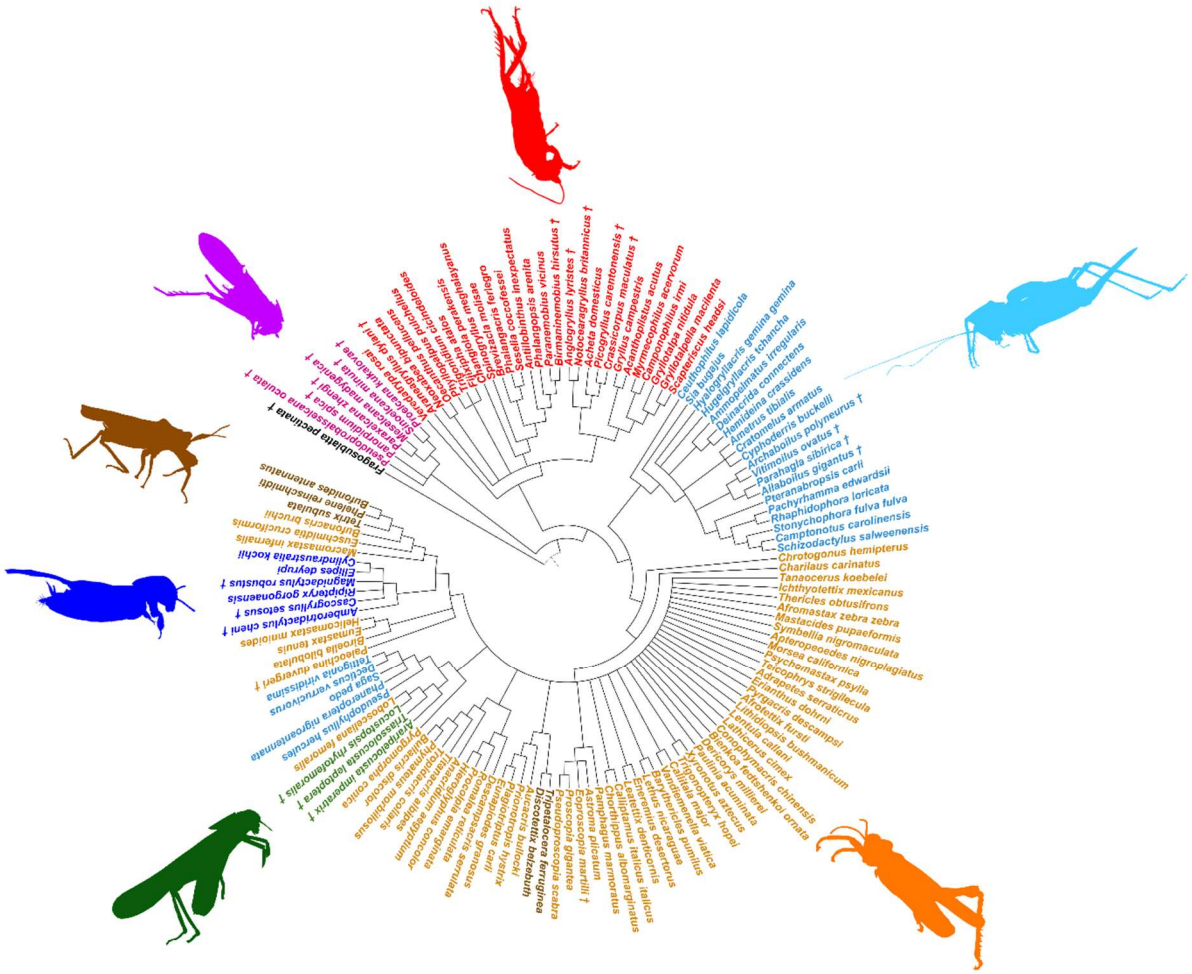


Fig. 1 Morphology-based phylogeny of Orthoptera Olivier, 1789 using neighbor joining and focusing on the major clades Gryllidea Vickery, 1977 (red), Elcanidea Gorochov, 1995 (pink), Tettigoniidea Kevan, 1982 (light blue), Locustopsoidea Handlirsch, 1906 (green), Tetrigoidea Rambur, 1838 (brown), Acrididea Targioni-Tozzetti, 1882 (orange) and Tridactylidea Brullé, 1835 (dark blue). Extinct taxa are marked with †. The tree was computed in PAUP (Swofford, 2025). *Fragosublatta pectinata* Chen et al., 2021 (an extinct species of Blattodea Latreille, 1810) was picked as outgroup.


Fragosublatta pectinata †
Archaboilus musicus †
Archaeogryllus lyristes †
Angiogryllus britannicus †
Birmaninemobius hirsutus †
Paranemobius vicinus
Anaxipha longipennis
Sclerogryllus inexpectatus
Sclerogryllus sp.
Gryllus campestris
Acheta domesticus
Picogryllus sp.
Grassicorpa maculatus †
Acanthogryllus acutus
Myrmecophilus acervorum
Myrmecophilus imni
Gryllotalpa macilenta
Gryllotalpa fossilis
Scapteriscus tetradactylus
Ceuthophilus gracilipes
Hugogryllacris gemina gemina
Hugogryllacris schancha
Hugogryllacris irregularis
Hemideina crassidens
Hemideina thoracica
Deinacrida connectens
Anabropsis dilatata
Amusurgus armatus
Cyphoderris buckelli
Cyphoderris polyneurus †
Archaboilus sibirica †
Vitimollus ovatus †
Allabropsis gigantus †
Allabropsis carli
Pteranabropsis edwardsii
Pachyrhamma loricata
Rhaphidophora fulva fulva
Stonychophora sp.
Camptonotus carolinensis
Schizodactylus salweenensis
Chrotogonus hemipterus
Charilaus carinatus
Tanaocerus koebelei
Ichthyotettix mexicanus
Thericles obtusifrons
Afromastax zebra zebra
Mastacides pupaeformis
Symbellia nigromaculata
Apteropeodes nigroplagiatus
Morsea californica
Teichonastax psylla
Eremochrys strigilecula
Eidrapates serraticrus
Eidrapates dohrni
Xyronotus hirsti
Xyronotus descimpsi
Lentidictix hirsti
Lentidictix bushmanicum
Lentidictix cilian
Lentidictix climex
Lentidictix chinensis
Bonnetophrys femoralis
Bonnetophrys antennalis
Bonnetophrys acuminata
Bonnetophrys sp.
Bonnetophrys ? hopei
Trigonopteryx sp.
Trigonopteryx vatica
Chilalia major
Chilalia sp.
Eremopolemicus punctatus
Eremopolemicus deserticus
Eremopolemicus peregrinus
Eremopolemicus sp.
Eremopolemicus ? sp.
Eremopolemicus ? sp.
Eremopolemicus ?

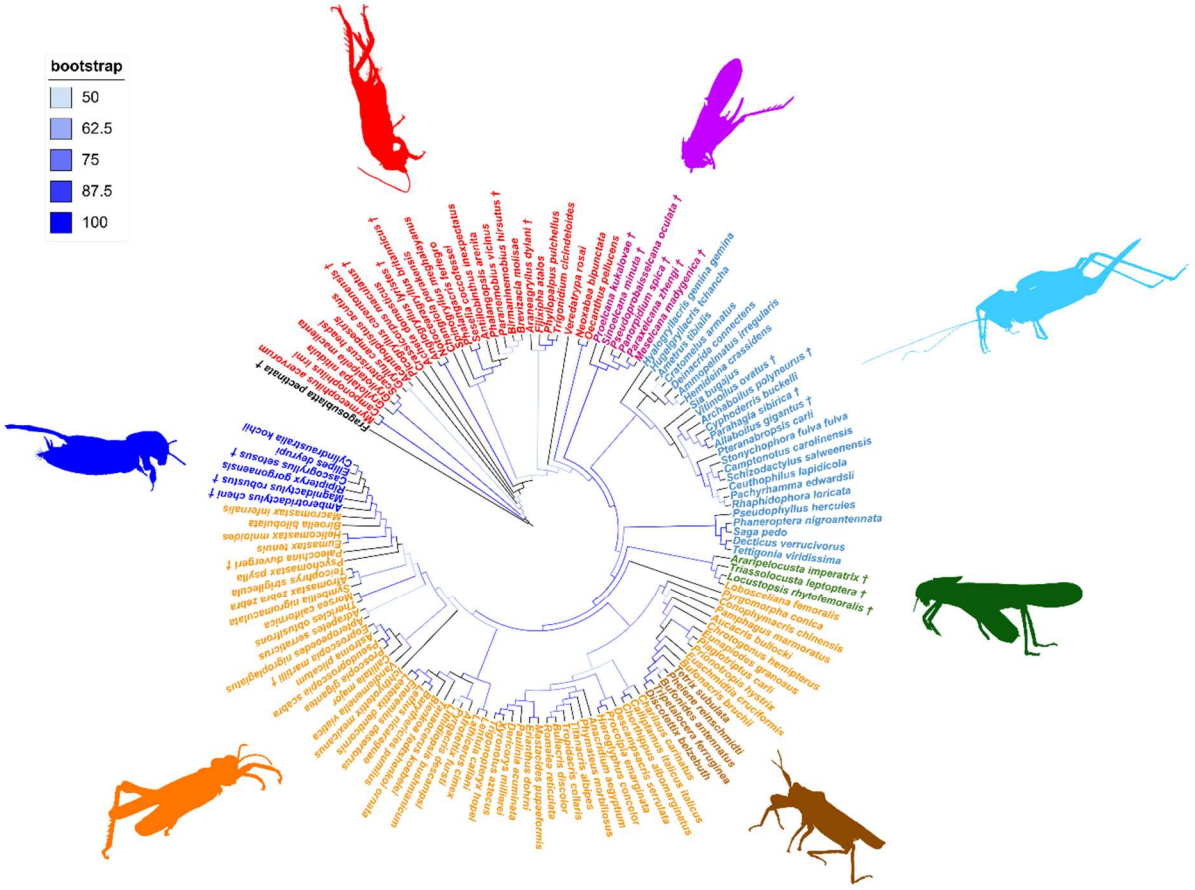


Fig. 3 First of two topologies based on the analyses of morphological data of Orthoptera Olivier, 1789 using Maximum Likelihood and focusing on the major clades Gryllidea Vickery, 1977 (red), Elcanidea Gorochov, 1995 (pink), Tettigoniidea Kevan, 1982 (light blue), Locustopsoidea Handlirsch, 1906 (green), Tetrigoidea Rambur, 1838 (brown), Acridiidea Targioni-Tozzetti, 1882 (orange) and Tridactylidea Brullé, 1835 (dark blue). Extinct taxa are marked with †. The tree was computed in IQ-TREE (Nguyen et al., 2015) and is the consensus tree based on 1000 bootstrap replicates. Bootstrap values (from 50-100) are indicated by different shades of blue. Black branches indicate bootstrap values < 50. *Fragosublatta pectinata* Chen et al., 2021 (an extinct species of Blattodea Latreille, 1810) was picked as outgroup. The log-likelihood of the consensus tree is -3900.547311

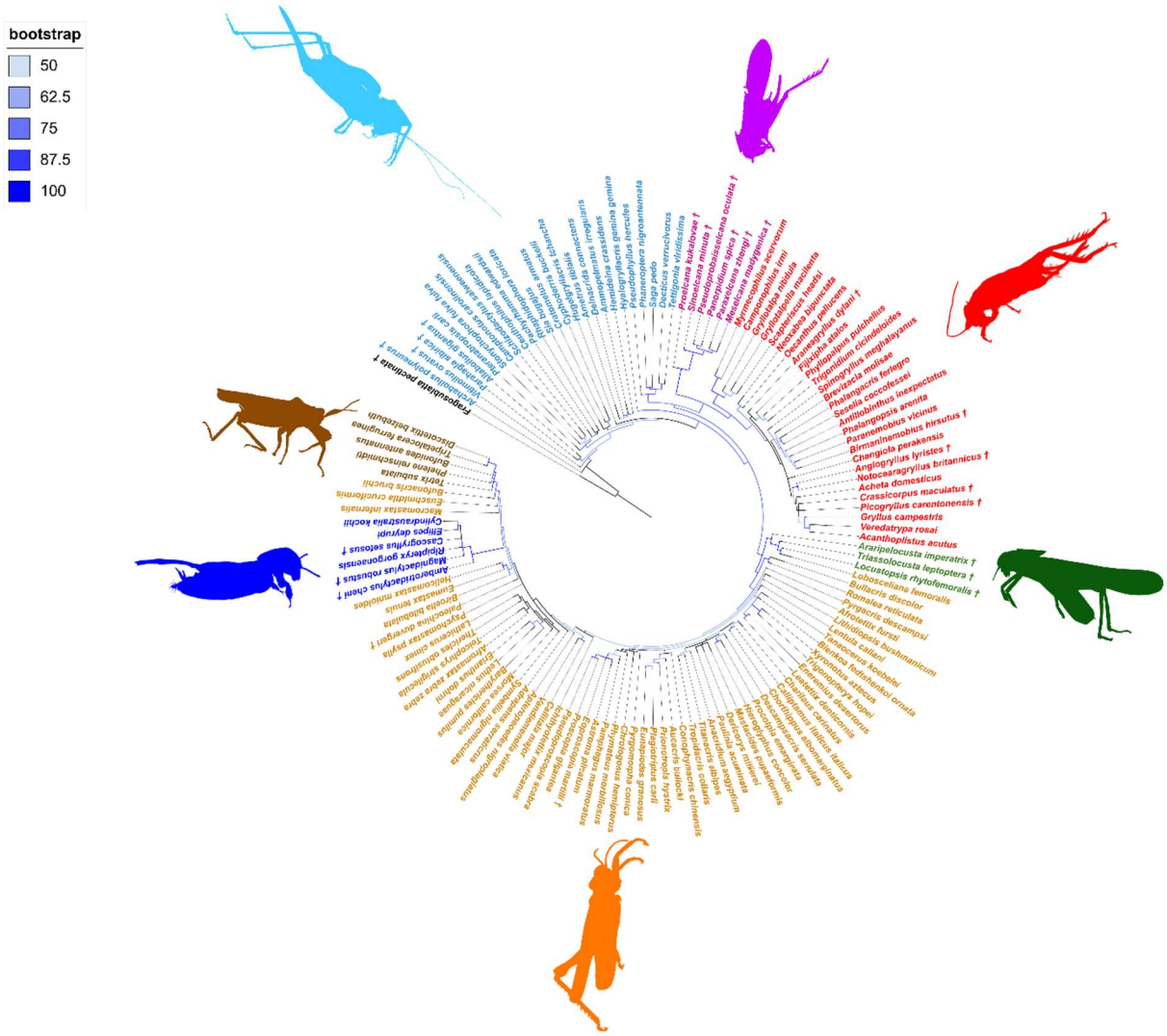


Fig. 4 Second of two topologies based on the analyses of morphological data of Orthoptera Olivier, 1789 using Maximum Likelihood and focusing on the major clades Gryllidea Vickery, 1977 (red), Elcanidea Gorochov, 1995 (pink), Tettigoniidea Kevan, 1982 (light blue), Locustopsoidea Handlirsch, 1906 (green), Tetrigoidea Rambur, 1838 (brown), Acrididea Targioni-Tozzetti, 1882 (orange) and Tridactylidea Brullé, 1835 (dark blue). Extinct taxa are marked with †. The tree was computed in IQ-TREE (Nguyen et al., 2015) and is the consensus tree based on 1000 bootstrap replicates. Bootstrap values (from 50-100) are indicated by different shades of blue. Black branches indicate bootstrap values < 50. *Fragosublatta pectinata* Chen et al., 2021 (an extinct species of Blattodea Latreille, 1810) was picked as outgroup. The log-likelihood of the consensus tree is -3916.7033.

4. Discussion

In this study, we present a morphology-based phylogenetic analysis of the Orthoptera Olivier, 1789 with the goal of determining relationships of seven major clades: Gryllidea Vickery, 1977; Elcanidea Gorochov, 1995; Tettigoniidea Kevan, 1982; Locustopsoidea Handlirsch, 1906; Acrididea Targioni-Tozzetti, 1882; Tetrigoidea Rambur, 1838 and Tridactylidea Brullé, 1835. Here, we discuss the hypotheses found in our analyses and compare them with previous morphological and molecular findings as well as conclusions derived from the fossil record.

The phylogenetic position of Elcanidea within Orthoptera

Comparison with previous molecular and morphological findings

The phylogeny of Orthoptera has been worked on by many researchers over the years, in pre-cladistic times and by means of morphological as well as molecular analyses (Flook et al., 1999; Gorochov, 1995; Jost and Shaw, 2006; Song et al., 2015; Song et al., 2020; Zeuner, 1942; Zhang et al., 2013). Molecular studies generally tend to find the following results (Song et al., 2015; Song et al., 2020; Zhang et al., 2013):

1. Ensifera Chopard, 1921 and Caelifera Ander, 1936 are monophyletic.
2. Ensifera consists of two monophyletic sister groups, Tettigoniidea and Gryllidea.
3. Caelifera consists of two monophyletic sister groups, Acrididea and Tridactylidea.
4. Acrididea itself consists of two monophyletic sister groups, Tetrigoidea and Acridomorpha MacLeay, 1821.

There are, however, differences in results when it comes to the choice of molecular markers as well as the tree reconstruction method applied. Zhang et al. (2013) found the above-mentioned relationships when using mitochondrial DNA from concatenated cytochrome oxidase subunits (COX) and COX + cytochrome b and using Bayesian Inference and Maximum Likelihood (Fig. 5a). Additionally, the same results were obtained by analysing mitochondrial NADH data with Bayesian Inference, but using ML on the dataset yielded conflicting relationships (Tridactylidea and Tettigoniidea included in Gryllidea) (Fig. 5d). Likewise, rRNA seemed less suitable for determining the phylogeny of Orthoptera (Tetrigoidea sister clade to Acridomorpha + Gryllidea (including Tridactylidea and Tettigoniidea; Tettigoniidea included in Gryllidea) (Fig. 5b, c).

Morphology based analyses of the entire order Orthoptera are rare. One that stands out and has gotten a lot of attention for the placement of Elcanidae was performed by Béthoux and Nel

(2002). The authors are experts on wing venation in the Orthoptera and used their extensive knowledge of the fossil record of this group to conduct parsimony based analysis of fossil forms. They mainly included members of Oedischiidea Handlirsch, 1906 and Hagloidea Handlirsch, 1906 (which belong to the Tettigoniidea) with some representatives of Gryllidea, Elcanidea and Locustopsoidea. They recovered two main clades, one consisting of Hagloidea (Gryllidea), the other of Oedischiidea + Elcanidea/Locustopsoidea (Fig. 5g). The clustering of Elcanidae with Locustopsoidea led Béthoux and Nel (2002) to propose Elcanidae as members of the Caelifera. However, their taxon sampling of Caelifera was limited, with only three species of Locustopsoidea, which may have influenced tree topology.

Including fossils in phylogenetic analyses is difficult, because of a plethora of missing information. Béthoux and Nel (2002) circumvented this issue by relying solely on forewing venation, as isolated forewings make up a large majority of the fossil record of Orthoptera. On the downside, this means other evidence is neglected, for example the long antennae and ovipositors of elcanids, which clearly represent Ensifera. These traits may even be of higher weight in reconstructions, as they are easier homologized and secondary evolution of similar traits seems less likely. However, it may be argued, that wing venation is a well-suited trait for phylogenetic reconstruction as it may evolve more neutrally than traits under strong selection as egg laying and sensory structures. Further, another important trait of many extant Ensifera, the stridulation apparatus and the tympanum, located at the tibia of the fore legs is missing in Elcanidae, which may suggest either a very basal position in the phylogeny or secondary loss.

Another problem concerning a morphology-based approach to the phylogeny of Orthoptera is a lack of knowledge regarding apomorphies of Caelifera: Acrididea. The relationships between extant taxa of this infraorder often rely on molecular studies. Morphological characters that have been used to suggest hypotheses of Acrididea evolution include the structure of the external and especially internal genitalia as well as different mechanisms of stridulation (Flook et al., 2000; Matt et al., 2008). Genitalia morphology is rarely preserved in fossil Orthoptera, and no findings of stridulatory organs have been reported from Locustopsoidea so far; whether due to absence in the group or lack of preservation remains unanswered. The knowledge gap in Acrididea morphology applicable to fossil forms may explain why the infraorder is poorly resolved in the phylogenetic approaches used in this study. They may further be the reason why the pamphagid *Lobosceliana femoralis* (Walker, 1870) clustered within Locustopsoidea in all four phylogenies presented in the results (Figs. 1-4). This combination is probably due the similar ratio of forewing length to body length of Locustopsoidea and *L. femoralis*. All other

Caelifera in the analyses have shorter forewings in relation to their body length (see values for character 'forewing length/body length' in the main matrix, supplementary material 4). However, the other three Pamphagidae Burmeister, 1840 do not cluster with Locustopsoidea, because they are brachypterous. The unusual occurrence of *L. femoralis* within Locustopsoidea is probably an artefact of the limitations in knowledge regarding morphology of Acrididea. Because of this, it is not considered for the hypotheses of Orthoptera evolution presented below.

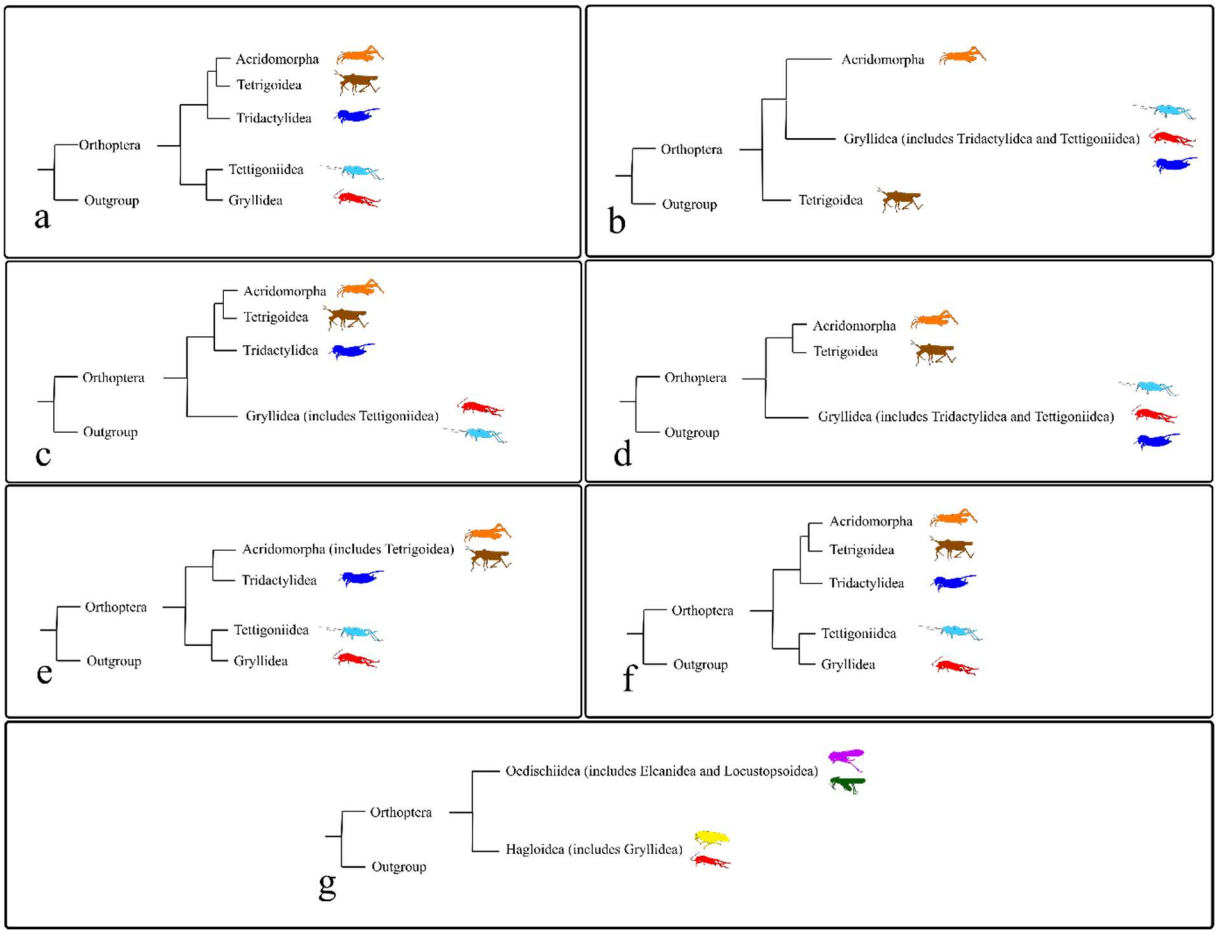


Fig. 5 a-d: Hypotheses of Orthoptera phylogeny after Zhang et al. (2013) based on extant taxa. **a** Method: Bayesian Inference (BI). Data: NADH dehydrogenase (mtDNA). And: Method: BI/Maximum Likelihood (ML). Data: Cytochrome oxidase + cytochrome b (mtDNA). And: Method: BI/ML. Data: Cytochrome oxidase (mtDNA). **b** Method: BI/ML. Data: concatenated variable domain of rRNA. In the BI dendrogram, one of the outgroup taxa clustered with Tetrigoidea. **c** Method: BI/ML. Data: concatenated conserved domain of rRNA. One eumastacoid clustered with Tetrigoidea (not shown). **d** Method: ML. Data: NADH dehydrogenase (mtDNA). **e-f:** Hypotheses after Song et al. (2015) and (2020). The authors used fossils as calibration points and to perform divergence time estimates, but morphological data was not included. **e** Method: Maximum Parsimony. Data: complete mitogenome.

Schizodactyloidea Blanchard, 1845 included in Gryllidea Vickery, 1977 (from Song et al. (2015)). **f** Method: ML. Data: complete mitogenome. Schizodactyloidea included in Gryllidea (from Song et al. (2015)). And: Method: ML. Data: total evidence (complete mitogenome + nuclear RNA + 15 protein coding genes). Schizodactyloidea in Tettigoniidea Kevan, 1982 (from Song et al. (2015)). And: Method: Divergence time estimate analysis. Data: complete transcriptome (from Song et al. (2020)). And: Method: ML. Data: complete transcriptome + complete mitogenome (from Song et al. (2020)). **g:** Hypothesis after Béthoux and Nel (2002), exclusively based on fossils. Method: Maximum Parsimony. Data: Morphology of forewing venation. Diagrams were created manually. Branch lengths not to scale.

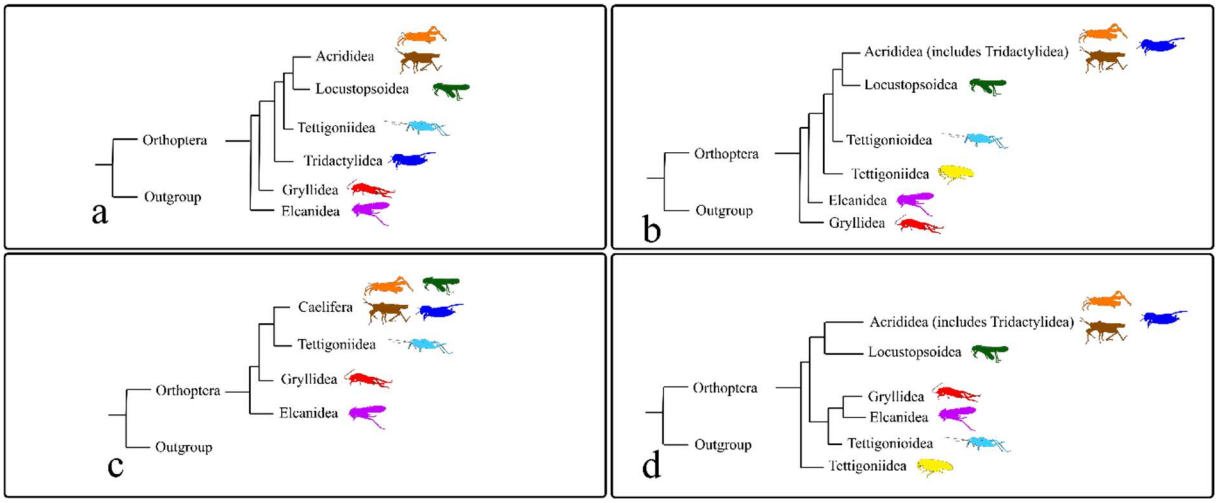


Fig. 6 Hypothesis of Orthoptera phylogeny according to this study, based on fossil and extant taxa. **a** Method: Neighbor Joining. Data: Morphology. **b** Method: ML. Data: Morphology. **c** Method: Maximum Parsimony. Data: Morphology. **d** Method: ML. Data: Morphology. All hypotheses are based on the exact same data set. **b** and **c** represent two alternative hypotheses derived from the same method and data. Diagrams were created manually. Branch lengths not to scale.

Implications for Orthoptera evolution from the fossil record

More than 900 species of fossil Orthoptera are described to date (Cigliano et al., 2025). The fossil record is unlikely to be complete, but we can attempt to derive inferences of orthopteran evolution based on current knowledge (Table 2; Fig. 7). The first orthopteroid lineages to appear in the fossil record are the Oedischiidea Handlirsch, 1906 and Titanoptera Sharov, 1968, the latter represented by one species, *Theiatitan azari* Schubnel et al., 2021. Currently, the Titanoptera are considered a suborder of Orthoptera, next to Caelifera and Ensifera (Cigliano

et al., 2025). However, Park et al. (2021) remarked that their relationships are a matter of debate and positions outside Orthoptera, as a separate order, have been suggested. These early Oedischiidea and Titanoptera are from the Late Carboniferous of France (ca. 304-299 Mya) and Portugal (ca. 301-300 Mya) (the Paleobiology Database; https://paleobiodb.org (PBDB)). (*Prototettix lithanthraca* (Goldenberg, 1854) from the Carboniferous of Germany was assigned to Tettigoniidae. This is very likely incorrect, and the species needs revision. Based on the figures in Goldenberg (1854) it could possibly belong to the Legendreiidae Huang et al., 2020). Hence, in the following, we will consider Oedischiidea as the first definite lineage of Orthoptera.

In the following Permian period (ca. 299-252 Mya), Elcanidea and Locustopsoidea make their first appearances. The Triassic (ca. 252-201 Mya) saw the first occurrences of Tridactylidea and Tettigoniidea, which were very diverse with the superfamily Hagloidea in the Madygen Formation of Kyrgyzstan (PBDB). The first fossils of Gryllidea are of Jurassic age (ca. 201-143 Mya). Also from the Jurassic is the first record of the Acridomorpha superfamily Eumastacoidea with *Archaeomastax jurassicus* Sharov, 1968. In Cretaceous deposits (143-66 Mya), the oldest known remains of Tetrigoidea, and the extant superfamilies of Tettigoniidea (Tettigonioidea, Schizodactyloidea and possibly Stenopelmatoidea (see Martins-Neto, 2007)), and Proscopioidea (Acrididea: Acridomorpha) were discovered. It is curious, that the current picture of the fossil record would make the Eumastacoidea older than the Tetrigoidea, suggesting Tetrigoidea might have evolved from Eumastacoidea. Zhang et al. (2013) found a species of Eumastacoidea to cluster basally of Tetrigoidea in an analysis of the concatenated conserved domain of rRNA. Still, most molecular studies suggest a position for Tetrigoidea as the sister group to Acridomorpha (including Eumastacoidea) (Lin et al., 2017; Song et al., 2015; Song et al., 2020) and morphological similarities would suggest them to be closer to Tridactylidea (Heads et al., 2014). Other extant superfamilies of Acridomorpha, like the Acridoidea MacLeay, 1821 themselves, only appear in the fossil record after the Cretaceous-Paleogene mass extinction 66 Mya.

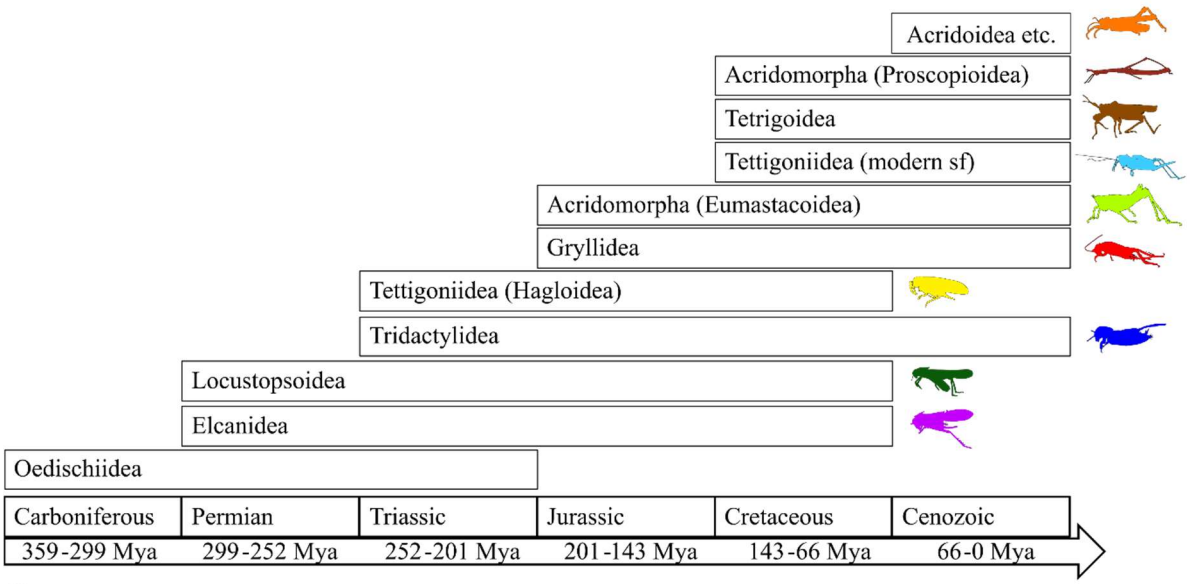
Given the assumption that the fossil record at the infraorder/superfamily level is largely complete (or at least not missing any earlier occurrences), we can infer the phylogeny of Orthoptera (Fig. 7): Oedischiidea were probably the earliest lineage of Orthoptera. Consequently, all following lineages would have derived from oedischiid ancestors. In the Permian, Elcanidea and Locustopsoidea evolved from Oedischiidea, maybe within a short time

frame. Based on the phylogenetic analyses presented above, Elcanidea could be an early diverging lineage of Ensifera (the earliest if Oedischiidea is excluded from Ensifera). Locustopsoidea on the other hand may be the earliest diverging lineage of the Caelifera. Among the Ensifera, Hagloidea evolved next, probably at some time in the Late Permian/Early Triassic (Gorochov, 2021). Within Caelifera, Tridactylidea is the next major lineage that probably evolved sometime in the Triassic. Finally in the evolution of Ensifera, Gryllidea evolved during the Jurassic and the first modern superfamilies of Tettigoniidea during the Cretaceous. It is possible, that Hagloidea may be a common ancestor of both. Last among the Caelifera were early superfamilies of Acridomorpha (like the Eumastacoidea (Husemann et al., 2025; Sharov, 1968)) and Tetrigoidea (Sharov, 1968) which appeared during the Jurassic and Cretaceous. The main diversification of Acridomorpha probably only set in after the end-Cretaceous mass extinction.

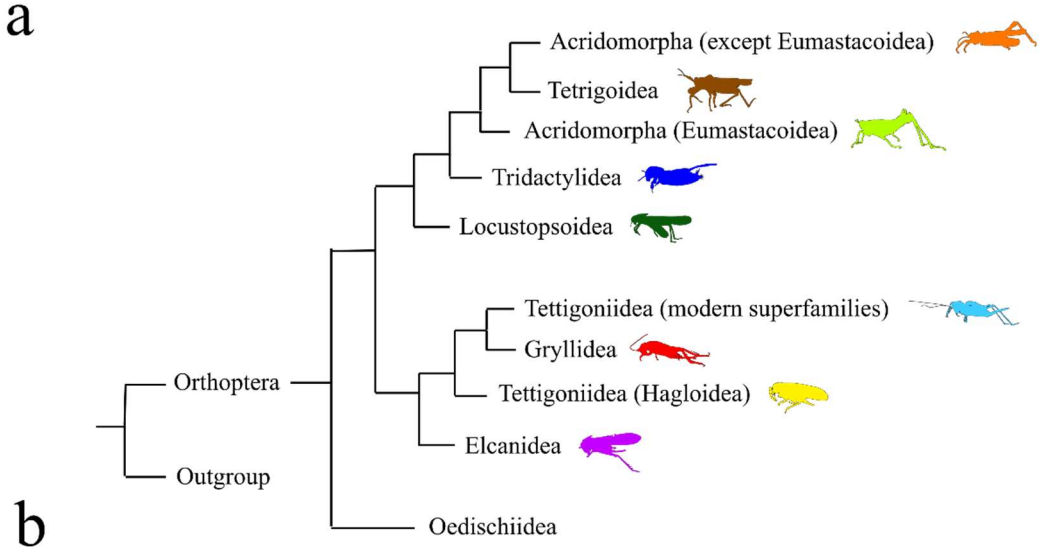
Table 2 The earliest and last occurrences of higher-level taxa of Orthoptera Olivier, 1789. Taxonomic data from Cigliano et al., 2025. Occurrence data (including age constraints) from Paleobiology Database (https://paleobiodb.org/). [1]There are four fossil species attributed to Tettigoniidae Krauss, 1902 and Gryllacrididae Blanchard, 1845 from the Jurassic and Triassic. *Pseudogryllacris propinqua* (Deichmüller, 1886) does not belong to Gryllacrididae, but possibly to Hagloidea Handlirsch, 1906 (*Pycnophlebia* Deichmüller, 1886) according to Handlirsch (1906). *Xenogryllacris reductus* Riek, 1955 (Gryllacrididae) may belong to Oedischiidea Handlirsch, 1906. The identity of the two tettigoniids from the Jurassic of Germany is also dubious. Here, we consider the Haglotettigoniidae Gorochov, 1988 (Tettigonioidea Krauss, 1902) and *Brauckmannia groeningae* Martins-Neto, 2007 (Schizodactyloidea Blanchard, 1845) from the Cretaceous as the first records of modern superfamilies (sf) of Tettigoniidea Kevan, 1982. [2]Sharov (1968) described *Archaeomastax jurassicus* from the Jurassic of Kazakhstan. [3]Proscopioidea Serville, 1838 occurs in the fossil record of the Cretaceous. Acridoidea MacLeay, 1821 occurs only after the Cretaceous-Paleogene mass extinction. A species of Pyrgomorphoidea Brunner von Wattenwyl, 1874 is known from the Miocene of Germany (Kevan and Akbar, 1964). Alleged recordings of Acridoidea: Pamphagidae Burmeister, 1840 from the Triassic of UK (Giebel, 1856) were likely incorrectly assigned.

Taxon	**Earliest occurrence**	**Last occurrence**
Oedischiidea	Carboniferous (ca. 315-310 Ma)	Triassic (ca. 227-206 Ma)

Tettigoniidea (Hagloidea)	Triassic (ca. 252-251 Ma)	Cretaceous (ca. 113-106 Ma)
Tettigoniidea (modern sf[1])	Cretaceous (ca. 121-113 Ma)	Extant
Elcanidea	Permian (ca. 299-295 Ma)	Cretaceous (ca. 110-99 Ma)
Gryllidea	Jurassic (ca. 201-193 Ma)	Extant
Locustopsoidea	Permian (ca. 264-260 Ma)	Cretaceous (ca. 121-133 Ma)
Tridactylidea	Triassic (ca. 242-237 Ma)	Extant
Tetrigoidea	Cretaceous (ca. 121-113 Ma)	Extant
Acridomorpha (Eumastacoidea[2])	Jurassic (ca. 162-155 Ma)	Extant
Acridomorpha (Proscopioidea + rest[3])	Cretaceous (ca. 126-113 Ma)	Extant



a



b

Fig. 7 Earliest and last occurrences of high-level taxa of Orthoptera in the fossil record (**a**) and possible inferences for their phylogeny (**b**). Diagram in **b** was created manually. Branch lengths not to scale.

Combining all the evidence

Comparing the findings of molecular studies with the fossil record, both suggest similar relationships among extant lineages of Orthoptera. That means, Ensifera consists of Tettigoniidea + Gryllidea and Caelifera consists of Tridactylidea + Acrididea = Acridomorpha + Tetrigoidea. They differ mainly in one argument. Caelifera and Ensifera are monophyletic according to molecular studies, whereas the fossil record suggests that both suborders derived from Oedischiidea. Since Oedischiidea are thought to belong to Ensifera (Cigliano et al., 2025), this would imply that Ensifera are paraphyletic with respect to a derived and monophyletic Caelifera. Morphological findings support this hypothesis (Béthoux and Nel, 2002; this study). But, as pointed out by Béthoux and Nel (2002), the divergence point of the two suborders is very ancient and strictly molecular analyses may not be able to detect this because they cannot include fossil taxa. Our morphological analyses suggest that Elcanidea belongs to Ensifera and Locustopsoidea belongs to Caelifera. Their early appearance in the fossil record suggests that both are basal representatives of their respective suborders. This is further implied by the findings of Béthoux and Nel (2002), who recovered Elcanidea and Locustopsoidea within Oedischiidea, suggesting that the evolutionary distance between the three taxa is not large. Lastly, according to the fossil record, the Hagloidea appeared long before the other members of Tettigoniidea. Béthoux and Nel (2002) noted that extant taxa considered as ‘Hagloidea’ by Flook et al. (1999) and Gwynne (1995) are Prophalangopsidae and no longer ‘Hagloidea’.

Combining all the evidence from molecular and morphological findings as well as from the fossil record, we suggest the following relationships of Orthoptera (Fig. 8):

1. Oedischiidea are the earliest Orthoptera and ancestors of Ensifera + Caelifera.
2. Elcanidea are basal Ensifera and sister taxon to the remaining Ensifera.
3. Locustopsoidea are basal Caelifera and sister taxon to the rest of Caelifera.
4. Hagloidea are the sister taxon to the extant Tettigoniidea + Gryllidea.
5. Tridactylidea are the sister taxon to Acrididea which consists of Tetrigoidea + Acridomorpha.

Our findings suggest that molecular analyses are very powerful and potentially more informative than morphology-based studies to determine lower-level (superfamily and below) phylogenetic relationships of extant taxa. However, to understand the evolutionary history of the entire order Orthoptera and of its infraorders, morphological findings from fossil species need to be included.

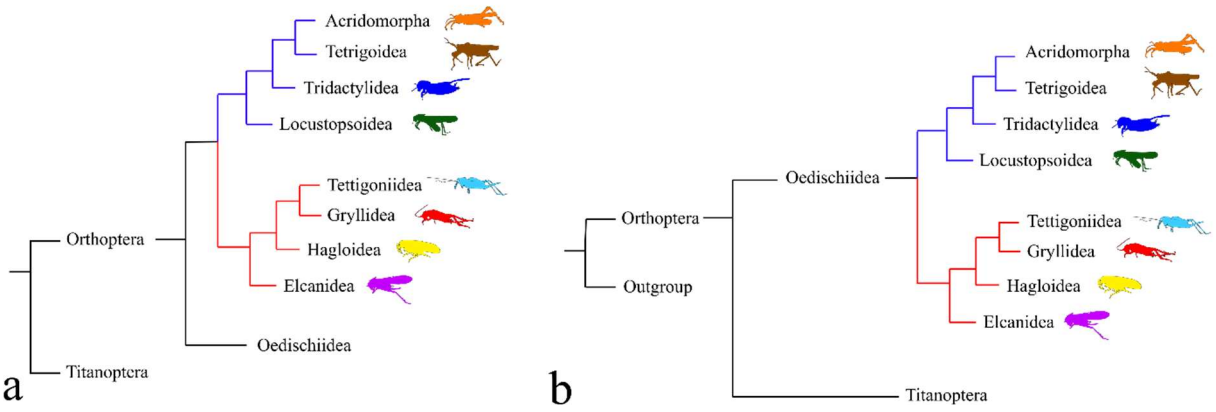


Fig. 8 Hypotheses of the phylogeny of Orthoptera based on molecular, morphological and fossil record evidence. Monophyletic Caelifera Ander, 1936 in blue, monophyletic Ensifera Chopard, 1921 in red. Oedischiidea Handlirsch, 1906 are considered to be Ensifera, thus, according to these hypotheses, Caelifera is a taxonomic subunit within Ensifera. The taxonomic position of Titanoptera Sharov, 1968 is uncertain. **a** Phylogeny with Titanoptera not included in Orthoptera (as supported for example by Schubnel et al. (2021). **b** With Titanoptera as a suborder of Orthoptera (as it is currently listed in Cigliano et al. (2025)).

Acknowledgements

We wish to thank several Orthoptera experts who sent copies of their works on respective taxa which greatly helped determining characters for our analysis. Namely, we thank Dr. S. Bruce Archibald (Beaty Biodiversity Museum, Canada), Prof. Dr. Carolin Haug (LMU Munich), Oscar Javier Cadena-Castañeda (Universidad Distrital Francisco José de Caldas), Assoc. Prof. Jun-Jie Gu (Sichuan Agricultural University), Dr. Olivier Béthoux (Muséum National d'Histoire Naturelle), Prof. Dr. André Nel (Muséum National d'Histoire Naturelle) and Thomas Schubnel (Muséum National d'Histoire Naturelle).

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Supplementary materials

Matrix:

Supplementary material 1: excel file including character states, character matrix and hybrid-reconstructed character matrix table sheets. Red numbers in the hybrid table mark reconstructed characters.

| Character states | | |

Character states	Character	Cryptostaurum	Stalked vs invisible	Antennal length (% of body length without cornicles or ovipositor)	Ovipositor morphology (% of body length)	Fe and RP scone branch	Fe wedge with three broadened areas for sensory pegs	Branches of CuA + CuPaa (main branches)	HA1 connected via stem of RP1+2 (stalk with HA)	Position of stem of RP	Pterostigma	CuA + CuPaa and RP-S cut and length metatibia (can't connect if in spiral) (different from normal emarsion)	Vein can in circulation in naturalis/advisory apparatus of forewing	Orientation of nerve cross vein	Fe wedge present	Metatarsus spurs	Prominent cicatrices on vertex and front	Body covered in dense long yellow hairs	Protrochlear groove defective/digging	RA distal to r-rs/SP and anal vein (margin of wing)	HA1 sclerotized stripes on fe+ti and hind tibiae (vein/CV/Ax-like)	Compound eye height/head height	Metatarsus inflated during preimaginal	Prosternum cone fully with elevated sternopleurite	Mesosternum inflated	Hind tibia stick-like	Fe wing length/body length	Head/thorax width	Metatibia inflated	Cerci segments	Fe wing pos- ventral m	Length of SpS (%)	Length of CuPaa1 (%)	Length of CuA+CuPaa (%)	Branches of HA (main branches)	Branches of RP (main branches)	Fe wing length/body length	Prosternum length/body length	Prosternum length/height	Head height/body length	Metatarsus/body length	Metatarsus/forewing length	Metatarsus metatibia length	Metatarsus metatibia width	Largest gap of metathoracic sternopleurite width (not including apical spurs)	Largest apical spur/metatibia width	Metatarsus (including claw)/metatibia length	Cerci size length/forewing length	Cerci size length/body length	Antenna segments (all of them)
Suborder	**Family**	**Species**																																												
Caelifera	Morabidae	*Biroella bilobulata*	yes	yes	14,8	15,6	nn	no	nn	nn	nn	nn	nn	nn	nn	yes	no	no	no	no	no	no	0,44	no	no	no	>1	no	no	1	no	nn	nn	0,38	0,16	1,05	0,27	0,81	1,7	1,15	6	3,5	2,5	0,39	0,09 (female)	0,03 (female)	nn	
Caelifera	Thericleidae	*Afromastax zebra zebra*	yes	yes	13,7	12,2	nn	nn	nn	nn	nn	nn	nn	nn	nn	no	no	no	no	no	no	no	0,4	no	no	no	nn	no	no	nn	nn	nn	nn	nn	nn	nn	0,2	0,77	0,38	0,77	nn								0,39	nn	ca. 0,08 (male) (OSF)	9 (OSF)
Caelifera	Thericleidae	*Thericles obtusifrons*	yes	yes	6,6	11,3	nn	nn	nn	nn	nn	nn	nn	nn	nn	no	no	no	no	no	nn	no	0,47	no	no (?)	no	no	nn	no	no	1 (?)	nn	nn	nn	nn	nn	nn	nn	0,16	0,62	0,26	0,54	nn								1,05	6,75	0,25	2	0,44	nn	0,04 (male)	10
Caelifera	Thericleidae	*Flagiotriptus carli*	yes	yes	9,1	15,9	nn	no	nn	nn	nn	nn	no	no	no (?)	nn	nn	yes	no	no	no	nn	0,24	no (?)	yes	no	no	ca. 1	no	no	1	no	nn	nn	nn	nn	nn	nn	0,26	0,66	1,37	ca. 0,3	0,52	1,6							1,03	6,8	0,8	2,2	0,54	0,16 (male)	0,09 (male)	ca. 10
Caelifera	Thericleidae	*Baerythericles pumilus*	yes	yes	6,4 (possibly broken off)	8,2	nn	nn	nn	nn	nn	nn	nn	nn	nn	no	yes (?)	no	no	no	nn	no	0,33	no	no	no	no	nn	no	no	1 (?)	nn	nn	nn	nn	nn	nn	nn	0,17	0,87	0,31	0,62	nn								1,01	5,4	0,5	3,75	0,39	nn	0,02 (female)	nn
Caelifera	Locustopsidae	*Locustopsis rhytidomorpha*	yes	yes	nn	nn	no	no		2	no	branchine of RA near base	no	no	no	no	yes	yes	no	no	no	no	0,34	no	no	no	no	nn	no	no		1	no	82,4	49,1	67,8	3	4	1,26	0,27	1,38	0,23	0,55	0,43							1,23	4	0,3	1,1	0,47	0,05	0,07	nn	
Caelifera	Locustopsidae	*Ananjelocusta imperatrix*	yes	yes	nn	ca. 20,8	no	no		1	no	branchine of RA near middle	yes (?)	no	nn	no	yes	nn	no	no	no	nn	ca. 0,34	no	no	no	no	1,03	no	nn	nn	no	97,9	56,9	71,8	no	1	6	1,29	0,3 (?)	1,64 (?)	0,21	nn	nn	nn		nn	nn	nn	nn	nn															
Caelifera	Locustopsidae	*Traxoplocuca lostcatlora*	nn	nn	nn	nn	no	no		2	yes (?)	branching of RA near base (almost middle)	no	no	nn	no	no	yes	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	64,1	57,4	71,8	3	6 or 7	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn	nn
Caelifera	Pneumoridae	*Bullacris discolor*	yes	yes	ca. 22,1	13,4	nn	no		2	no	branchine of RA near middle	no	no	no	no	yes	no	no	no	no	no	0,25	no	yes	yes	no	1,05	no	no	1	no	37,9	63,7	80,9	1	4	1,09	ca. 0,52	ca. 0,58	0,22	0,41	ca. 0,36	1,07	2,75	0,2 (OSF)	1,2 (OSF)	ca. 0,35	nn	nn	24 (OSF, female)	
Caelifera	Proscopiidae	*Eoproscopia martilli*	no (based on Heads, 2008)	yes	25,9	ca. 4,1	nn	no	nn		nn	nn	no	no	no	no	nn	yes	nn	no	no	no	0,33	no	no	no	yes	nn	no	no	nn	no	nn	nn	nn	nn	ca. 0,65	0,12 +	5,1 +	0,08	ca. 0,53	0,85	1,27	1,75	0	0	nn	nn	nn		
Caelifera	Proscopiidae	*Pseudoproscopia scabra*	yes	yes	3,2	5	nn	nn	nn		nn	nn	no	no	no	no	no	no (?)	no	no	no	no	0,16	no	no	no	yes	nn	no	no	1	nn	nn	nn	nn	nn	nn	0,26	10,1	0,18	0,31	nn								0,92	2,25	0,6	0,9	0,14	nn	ca. 0,02 (female)	nn
Caelifera	Proscopiidae	*Proscopia gigantea*	yes	yes	3,8	5	nn	nn	nn		nn	nn	no	no	no	no	nn	no	no	no	no	no	0,12	no	no	no	yes	nn	no	no	nn	nn	nn	nn	nn	nn	nn	0,24	6,3	0,16	0,34	nn								0,95	2,3	0,33	nn	0,12	nn	<0,02 (female)	nn
Caelifera	Proscopiidae	*Astroma plicatum*	yes	yes	4,4	5,8	nn	nn	nn		nn	nn	no	no	no	no	nn	yes (?)	no	no	no	no	0,11	no	no	no	yes	>1	no	no	nn	no	nn	nn	nn	nn	0,03	0,36	4	0,24	0,42	11,75	1,07	2,6	0,29	nn	0,16	nn	nn	6
Caelifera	Pyrgomorphidae	*Chrotogonus hemipterus*	yes	yes	32,3	nn	no	no		1	no	stantine off at wind base (?)	no	no	no	no	nn	yes (radicoid)	no	no	no	no	0,32	no	no	no	no	1,84	no	no	1 (?)	no	55,7 (?)	72,1	94,1	2	3 (?)	0,54	0,18	1	0,32	0,56	0,87	1,44	5,7	0,8	2,6	0,43	0,1 (female) (OSF)	0,02 (female) (OSF)	15-17	
Caelifera	Pyrgomorphidae	*Phymateus morbillosus*	yes	yes	37,4	8,5	no	no		1	no	branchine of RA near middle	no	no	no	no	nn	yes	no	no	no	no	0,28	no	no	no	no	1,83	no	no	1 (?)	no	89,7	72,4	72,4	2	4	1,07	0,25	1,2	0,21	0,54	0,51	1,06	2,6	1	ca. 2	ca. 0,36	0,02	0,03 (?) (female)	20-21	
Caelifera	Pyrgomorphidae	*Pyrgomorpha conica*	yes	yes	18,9	10,7	no	no		1	no	branchine of RA near middle	no	no	no	no	nn	yes	no	no	no	no	0,25	no	no	no	no	1,83	no	no	1 (?)	no	86,4	77,7	91,6	1	2	0,87	0,2	1,4	0,28	0,51	0,56	1,13	5,8	1	2,1	0,27	<0,04 (female)	0,02 (female)	14	
Caelifera	Pyrgomorphidae	*Ichthyotettix mexicanus*	yes	yes	23,4	12,1	nn	nn	nn		nn	nn	no	no	no	no	nn	no	no	no	no	no	0,24	no	no	no	no (?)	nn	no	no	1	nn	nn	nn	nn	nn	nn	0,18	1,06	0,29	0,48	nn								1,14	4,1	0,7	1	0,35	nn	0,02 (female)	14
Caelifera	Tanaocercidae	*Tanaocerus koebelei*	yes	yes	227,6	ca. 12,6		nn	nn	nn	nn	nn	nn	nn	no	no	no	no	no	no	no	no	0,36	no	no	no	no	nn	no	no	1	nn	nn	nn	nn	nn	nn	nn	0,28	0,62	0,46	1,07	nn								0,88	6,3	0,8	1,2	0,35	nn	0,1 (male)	27
Caelifera	Trigonopterygidae	*Trigonopteryx huxei*	yes	yes	46,4	ca. 10,9		no	no		5	no	branchine of RA near apex	no	no	no	no	nn	yes	no (?)	no	no	no	0,25	no	no	no	no	1,13	no	no	1 (?)	no	80,7	42,9	78,2	3 (?)	3	1,05	0,25	1,2	0,34	0,68	0,55	1,13 (OSF male)	4,83	1	1,2	0,32 (OSF male)	0,02 (female)	0,02 (female)	17-18	
Caelifera	Xyronotidae	*Xyronotus aztecus*	yes	yes	44,8	11,6	nn	nn	nn		nn	nn	nn	nn	nn	no	no	no	no	no	nn	no	0,2	no	yes (?)	no	no	nn	no	no	1	nn	nn	nn	nn	nn	nn	nn	0,24	0,97	0,35	0,64	nn								1,17	6,3	1,3	0,8	0,29	nn	0,05 (female)	21
Caelifera	Cylindrachetidae	*Cylindraustralia sochi*	yes	no	nn	nn		nn	nn	nn		nn	nn	nn	no	no	no	no	yes	nn	no	ca. 0,67	yes (?)	no	no	no	nn	yes	yes	nn	nn	nn	nn	nn	nn	nn	nn	0,15	1,3	ca. 0,11	0,09	nn								1,21	1,4	0	0	nn	nn	nn	4 to 6
Caelifera	Ripipterygidae	*Magnistictylus robustus*	yes	yes	20,4	nn	no	no	nn		nn	nn	no	no	no	no	nn	yes	no (?)	no	no	yes	0,52	yes	no	no	no	ca. 0,51	no	yes		2	no	nn	nn	nn	1 (?)	nn	ca. 0,49	0,25	1	0,25	0,67	1,36	1,03	nn	0	nn	0,23	nn	nn	9
Caelifera	Ripipterygidae	*Ripipteryx gorgonaensis*	yes	yes	21,7	nn	nn	nn	nn		nn	nn	no	no	no	no	nn	yes	no	no	yes	nn	0,49	yes	no	no	no	0,61	no	no	nn	no	nn	nn	nn	nn	nn	0,62	0,3	1,35	0,35	0,7	1,13	1,06	4,4	0	4,2	ca. 0,25	nn	nn	10
Caelifera	Tridactylidae	*Ambeinhidactylus cheni*	yes	yes	nn	nn	no	no	nn		no	no stem of RP	no	no	no	nn	nn	yes	no	no	no	yes	no	no	no	no	0,67	no	yes	2	no	nn	nn	nn	nn	1	nn	ca. 1,65	1,09	6,3	0,1	3,4	0,24	nn	nn	9	
Caelifera	Tridactylidae	*Clipex depugi*	yes	yes	23,9	< 25%	nn	nn	nn		nn	nn	no	no	no	no	nn	yes	no	no	yes	nn	0,29	yes	no	no	no	>1 (hindwing absent)	no	yes	2	no	nn	nn	nn	nn	nn	0,22	0,2	1,03	0,29	0,52	2,24	1,27	5,5	0	10	< 0,05		0,48	0,09	10
Caelifera	Tridactylidae	*Cancagrillus setosus*	yes	yes	35	nn	nn	nn	nn		nn	nn	nn	nn	no (?)	no	nn	yes	nn	no	yes	nn	0,41	yes	no	no	no	ca. 0,47	no	yes	2	no	96,9	nn	nn	nn	nn	0,48	0,26	1,3	0,28	0,74	1,5	nn	3,4	nn	nn	nn		0,29	0,14	10
Blattodea	Corydiidae	*Fragosublatta pectinata*	no	no	84,1	nn		nn	no	8 +	no (?)	nn	no	no	no	no	yes	yes	nn	no	no	yes	nn	yes	no	no	no	0,95 (?)	no	no	9	no	33,9	24,6 (?)	nn	2 (?)	nn	0,95	nn	nn	nn	0,27	0,28	0,67	3	ca. 1,9	ca. 1,9	0,76	0,18	0,19	40+	

Character matrix

Suborder	Family	Species	Cryptopleuron	Saltatorial hindlegs	Antennae length [% of body length without cercus or ovipositor]	Ovipositor morphology [% of body length]	M and RP are one branch	Forewing with three broadened areas for communication	Branches of CuA + CuPac (main branches)	MA1 connected via stem of RP in Z-shape with RA	Position of stem of RP	Pterostigma	CuA + CuPac1 and MP S-curved	Amorph metatibial spurs present (no apical) (different from normal armation)	Mirror (as in crickets) in male stridulatory apparatus of forewing	Orientation of mirror cross veins	Forewings present	Metatarsus spurs	Prominent bristles on vertex and frons	Body covered densely with long setae	Prothoracic legs modified for digging	Width b/w ScP and anal wing margin higher than usual	Well-developed spines on fore- and middle tibiae (as in Gryllacrididae)	Compound eye height/head height	Metafemur inflated along entire length	Pronotum dorsally with elevated sharpened keel	Abdomen inflated	Habitus stick-like	Forewing/hindwing length	Habitus worm-like	Mesotibia inflated	Cercus segments	Forewing apex rolled in	Length of ScP [%]	Length of CuPaβ [%]	Length of CuA + CuPac [%]	Branches of M (main branches)	Branches of RP (main branches)	Forewing length/body length	Pronotum length/body length	Pronotum length/height	Head height/body length	Metafemur/body length	Metafemur/forewing length	Metafemur/metatibia length	Metafemur/metatibia width	Largest spine of metathoracic leg/metatibia width (not including apical spurs!)	Largest apical spur/metatibia width	Metatarsus (including claws)/metatibia length	Cercus length/forewing length	Cercus length/body length	Antennal segments (all of them)
Ensifera	Permelcanidae	*Proelcana kukalovae*	1	1	1	N	1	0	1	0	0	1	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	N	0	0	N	0	0	1	4	0	0	1	2	0	1	1	N	1	0	N	N	N
Ensifera	Permelcanidae	*Meselcana madygenica*	N	N	N	N	1	0	2	0	0	N	1	N	0	N	1	N	N	N	0	N	N	N	N	N	N	N	0	1	0	0	2	0	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Ensifera	Elcanidae	*Panorpidium spica*	1	1	N	1	1	0	0	0	0	1	0	1	0	N	1	1	0	0	0	0	0	N	0	0	0	0	0	0	0	0	2	3	4	1	3	N	1	0	1	1	2	2	1	0	1	N
Ensifera	Elcanidae	*Sinoelcana minuta*	1	1	N	1	1	0	0	0	0	1	0	1	0	N	1	N	0	0	0	0	0	1	0	0	0	0	N	0	0	0	0	0	0	2	1	3	0	0	2	1	0	1	1	2	0	N	1	1	N
Ensifera	Elcanidae	*Pseudoprobaisselcana oculata*	1	1	N	1	1	0	0	0	0	1	0	1	0	N	1	1	0	0	0	0	0	N	0	0	0	0	0	0	0	0	2	3	4	0	2	N	2	0	1	1	2	2	1	N	N	N
Ensifera	Elcanidae	*Paraxelcana coronakanthodis*	1	1	1	N	1	0	0	0	0	1	0	1	0	N	1	1	0	0	0	0	0	N	0	0	0	1	0	1	0	0	2	2	4	1	2	N	1	0	1	1	2	0	N	1	1	4
Ensifera	Baissogryllidae	*Notocearagryllus britannicus*	N	N	N	N	0	0	6	0	N	0	0	N	1	2	1	N	N	N	N	1	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Ensifera	Baissogryllidae	*Anglogryllus lyristes*	N	N	N	N	0	0	6	0	N	0	0	N	1	2	1	N	N	N	N	1	N	N	N	N	N	N	N	N	0	1	1	1	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Ensifera	Gryllidae	*Antillobinthus inexpectatus*	1	1	1	1	N	0	N	0	N	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	N	N	N	N	N	1	0	2	1	1	1	1	1	2	2	1	3	2	5
Ensifera	Gryllidae	*Acheta domesticus*	1	1	1	1	1	0	N	0	N	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	N	N	0	0	2	0	0	1	0	0	1	0	1	2	2	2	2	5
Ensifera	Gryllidae	*Spinogryllus meghalayanus*	1	1	1	N	1	0	N	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	N	N	N	N	2	0	1	2	2	1	1	2	2	1	2	2	5
Ensifera	Gryllidae	*Acanthoplistus acutus*	1	1	2	0	1	0	N	0	N	0	0	0	N	N	1	1	0	0	0	N	0	1	0	0	0	0	0	0	0	N	N	N	N	2	0	3	2	0	0	1	1	1	1	2	1	3
Ensifera	Gryllidae	*Gryllus campestris*	1	1	2	1	1	N	N	0	N	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	N	N	N	N	2	0	2	2	0	0	1	1	0	3	1	2	1	5
Ensifera	Oecanthidae	*Crassicorpus maculatus*	1	1	1	N	N	0	1	0	N	0	0	0	1	0	1	1	0	1	0	0	0	2	0	0	0	0	0	0	0	0	1	N	N	N	N	2	0	N	1	0	0	1	1	1	3	1	2	2	5
Ensifera	Oecanthidae	*Picogryllus carentonensis*	1	1	0	N	1	0	5	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	N	1	0	0	2	0	2	1	0	0	1	1	1	3	1	2	2	N
Ensifera	Oecanthidae	*Oecanthus pellucens*	1	1	1	1	1	0	N	0	N	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	N	N	N	N	2	0	4	1	0	0	0	1	1	2	0	2	1	5
Ensifera	Oecanthidae	*Neoxabea bipunctata*	1	1	1	1	1	N	N	N	0	N	0	0	1	N	1	0	0	0	0	0	0	1	0	0	0	0	0	N	0	N	N	N	N	2	0	N	0	0	0	0	0	0	1	1	5
Ensifera	Oecanthidae	*Veredatrypa rosai*	1	1	1	0	1	0	0	0	N	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	N	N	1	2	2	0	3	0	0	0	1	1	1	2	0	1	1	5
Ensifera	Phalangopsidae	*Brevizacla molisae*	1	1	1	1	N	0	N	N	N	N	N	N	0	N	N	1	1	1	1	0	N	0	N	0	0	0	0	0	0	N	N	N	N	0	0	N	N	2	2	1	1	1	2	1	3	3	5
Ensifera	Phalangopsidae	*Seselia coccofessei*	1	1	1	1	N	0	N	0	N	0	0	0	0	0	N	1	1	0	0	0	0	0	1	0	0	0	0	2	0	0	0	N	N	0	0	1	0	2	1	2	1	1	1	1	2	1	3	3	N
Ensifera	Phalangopsidae	*Phalangacris ferlegro*	1	1	1	1	1	0	0	0	N	0	0	0	0	0	N	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	N	N	0	0	1	0	2	2	2	1	0	1	N	N	1	3	3	5
Ensifera	Phalangopsidae	*Araneagryllus dylani*	1	1	1	1	N	N	N	N	N	N	N	N	0	N	N	0	1	0	0	0	N	0	2	0	0	0	0	0	N	N	N	N	N	N	N	0	N	1	2	N	1	1	2	0	N	1	N
Ensifera	Phalangopsidae	*Phalangopsis arenita*	1	1	1	1	N	N	N	N	N	N	N	N	0	N	N	1	1	0	0	0	N	0	1	0	0	0	0	0	0	N	N	N	N	N	1	0	2	1	2	1	0	1	2	3	0	3	2	5
Ensifera	Pteroplistidae	*Changiola perakensis*	1	1	1	1	1	0	N	0	N	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	N	N	N	N	N	2	0	4	1	1	0	1	1	0	1	1	3	2	5
Ensifera	Trigonidiidae	*Birmaninembius hirsutus*	1	1	1	N	N	0	N	0	N	0	0	0	1	1	1	1	1	1	0	0	0	0	N	0	0	0	0	0	0	N	N	N	N	N	1	0	N	N	1	1	0	1	1	2	3	1	3	2	5
Ensifera	Trigonidiidae	*Fijixipha atalos*	1	1	N	1	N	0	N	0	N	0	0	0	1	1	1	1	1	0	0	0	N	0	2	0	0	0	0	0	0	0	N	N	N	N	N	2	0	2	N	1	0	1	1	2	2	1	1	1	N
Ensifera	Trigonidiidae	*Trigonidium cicindeloides*	1	1	1	1	N	0	N	N	N	0	0	0	0	N	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	N	N	N	N	N	2	0	0	1	1	1	0	1	2	2	1	1	1	5
Ensifera	Trigonidiidae	*Paranemobius vicinus*	1	1	N	1	N	0	N	0	N	0	0	0	1	0	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	N	N	0	0	1	0	2	2	2	1	1	1	2	3	1	3	3	N
Ensifera	Trigonidiidae	*Phyllopalpus pulchellus*	1	1	1	1	N	0	N	N	N	0	0	0	0	N	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	N	N	N	0	N	2	0	1	0	1	0	0	1	2	N	1	1	1	5
Ensifera	Gryllotalpidae	*Gryllotalpa nitidula*	1	1	0	N	1	0	1	0	N	0	0	0	0	N	1	1	0	0	0	1	1	0	1	0	0	0	0	N	0	0	0	0	1	1	1	3	0	0	0	0	1	0	0	0	1	3	1	4
Ensifera	Gryllotalpidae	*Scapteriscus headsi*	1	1	N	0	N	0	N	0	N	0	0	0	0	N	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	N	N	N	N	2	1	4	1	0	0	1	0	0	0	1	1	N
Ensifera	Gryllotalpidae	*Gryllotalpella macilenta*	1	1	1	0	N	0	N	0	N	0	0	0	0	N	1	1	0	0	0	1	N	0	N	0	0	0	0	0	0	0	0	0	0	1	0	N	N	0	0	1	0	0	0	N	N	3	2	1	5
Ensifera	Myrmecophilidae	*Camponophilus irmi*	1	1	2	1	N	N	N	N	N	N	N	N	0	N	N	0	1	0	0	0	N	0	0	1	0	0	0	N	0	0	N	N	N	N	N	N	N	N	1	2	1	1	N	1	1	1	1	1	4
Ensifera	Myrmecophilidae	*Myrmecophilus acervorum*	1	1	2	1	N	N	N	N	N	N	N	N	0	N	N	0	1	0	0	0	N	0	0	1	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	1	0	2	1	N	1	0	2	1	1	0	1	2	N	2	4
Ensifera	Prophalangopsidae	*Allaboilus gigantus*	1	1	N	1	0	0	4	0	1	0	0	0	0	N	1	N	0	0	0	0	0	1	N	0	0	0	N	0	1	N	0	1	1	1	1	3	4	0	3	1	0	0	1	0	0	0	0	N	N	N
Ensifera	Prophalangopsidae	*Cyphoderris buckelli*	1	1	1	N	N	0	N	0	N	0	0	0	0	N	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	N	N	N	N	1	1	4	2	0	1	0	0	0	0	0	1	1	1	4
Ensifera	Prophalangopsidae	*Parahagla sibirica*	1	N	N	1	0	0	2	0	1	0	0	0	0	N	1	N	0	0	0	N	0	N	N	N	0	0	0	0	0	N	N	0	1	1	0	2	3	4	0	N	N	N	N	N	N	N	0	1	N	N	N	N
Ensifera	Haglidae	*Vitimoilus ovatus*	N	N	N	N	0	0	3	0	2	0	0	N	0	N	1	N	N	N	N	0	N	N	N	N	N	N	N	N	N	0	1	1	1	2	1	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Ensifera	Haglidae	*Archaboilus polyneurus*	N	N	N	N	0	0	3	0	2	0	0	N	0	N	1	N	N	N	N	0	N	N	N	N	N	N	N	N	N	0	1	0	1	1	0	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Ensifera	Rhaphidophoridae	*Rhaphidophora loricata*	1	1	1	1	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	1	1	0	0	0	0	N	N	N	N	N	N	N	N	1	2	2	2	N	1	1	0	3	0	N	1	5
Ensifera	Rhaphidophoridae	*Stonychophora fulva fulva*	1	1	N	1	N	N	N	N	N	N	N	0	N	N	0	1	0	0	0	N	1	1	0	0	0	0	N	N	N	N	N	N	1	3	2	2	N	1	1	0	2	2	1	N	2	N	5
Ensifera	Rhaphidophoridae	*Ceuthophilus lapidicola*	1	1	1	1	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	1	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	0	2	1	1	N	1	1	1	2	1	N	1	5
Ensifera	Rhaphidophoridae	*Pachyrhamma edwardsii*	1	1	1	1	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	0	3	1	2	N	0	1	0	3	1	N	1	5
Ensifera	Schizodactylidae	*Schizodactylus salweenensis*	1	1	1	0	N	0	N	0	0	0	0	0	0	N	1	1	0	0	1	0	1	1	0	0	0	0	1	0	1	N	N	N	N	N	0	3	2	1	N	1	1	0	2	1	N	1	5
Ensifera	Anostostomatidae	*Pteranabropsis carli*	1	1	1	1	0	0	1	0	2	0	0	0	0	N	1	0	0	0	0	0	1	1	0	0	0	0	N	0	0	0	0	1	1	1	1	1	4	0	3	2	2	0	0	1	0	2	0	1	1	5
Ensifera	Anostostomatidae	*Hemideina crassidens*	1	1	1	1	N	N	N	N	N	N	N	0	0	N	0	0	0	0	0	N	1	1	0	0	0	0	N	N	N	N	N	N	N	N	0	4	2	0	N	0	0	0	1	N	0	N	0	5
Ensifera	Anostostomatidae	*Deinacrida connectens*	1	1	1	1	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	1	1	0	0	0	0	N	N	N	N	N	N	N	N	0	4	1	0	N	0	0	0	0	1	1	N	0	5
Ensifera	Anostostomatidae	*Cratomelus armatus*	1	1	1	1	N	N	N	0	N	0	0	0	0	N	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	N	N	N	N	1	1	4	2	1	1	1	1	0	1	1	2	1	5
Ensifera	Gryllacrididae	*Hugelgryllacris tchancha*	1	1	1	1	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	N	0	4	2	0	N	1	1	N	N	N	1	N	N	5
Ensifera	Gryllacrididae	*Hyalogryllacris gemina gemina*	1	1	1	1	0	0	2	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	1	4	0	3	1	0	0	1	1	0	N	1	0	0	5
Ensifera	Gryllacrididae	*Ametrus tibialis*	1	1	1	N	N	N	N	N	N	N	N	0	N	N	1	0	0	0	0	N	1	1	0	0	0	0	N	0	0	0	0	N	N	N	N	N	1	0	2	2	1	1	0	0	0	0	0	2	0	N	5
Ensifera	Gryllacrididae	*Camptonotus carolinensis*	1	1	1	2	N	N	N	N	N	N	N	0	0	N	0	1	0	0	0	0	N	1	1	0	0	0	0	N	N	N	N	N	N	N	N	0	3	2	1	N	1	1	1	0	0	1	N	0	5
Ensifera	Stenopelmatidae	*Sia bugajus*	1	1	1	N	0	0	2	0	1	0	0	0	0	N	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	2	0	2	1	0	0	1	1	0	1	1	1	5
Ensifera	Stenopelmatidae	*Ammopelmatus irregularis*	1	1	2	0	N	N	N	N	N	N	N	0	0	N	0	0	0	0	1	N	1	1	0	0	0	0	0	N	N	N	N	N	N	N	0	4	2	0	N	0	0	0	0	1	2	N	1	4
Ensifera	Tettigoniidae	*Tettigonia viridissima*	1	1	1	2	0	0	2	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	3	0	3	2	2	0	1	1	0	0	0	0	5	5
Ensifera	Tettigoniidae	*Decticus verrucivorus*	1	1	2	2	0	0	0	0	1	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	3	0	2	2	2	0	1	1	0	2	0	0	0	5

Character matrix

Suborder	Family	Species	Character	Cryptopleuron	Saltatorial hindlegs	Antennae length [% of body length without cercus or ovipositor]	Ovipositor morphology [% of body length]	M and RP are one branch	Forewing with three broadened areas for communication	Branches of CuA + CuPac (main branches)	MA1 connected via stem of RP in Z-shape with RA	Position of stem of RP	Pterostigma	CuA + CuPac1 and MP S-curved	Amorph metatibial spurs present (no apical) (different from normal armation)	Mirror (as in crickets) in male stridulatory apparatus of forewing	Orientation of mirror cross veins	Forewings present	Metatarsus spurs	Prominent bristles on vertex and frons	Body covered densely with long setae	Prothoracic legs modified for digging	Width b/w ScP and anal wing margin higher than usual	Well-developed spines on fore- and middle tibiae (as in Gryllacrididae)	Compound eye height/head height	Metafemur inflated along entire length	Pronotum dorsally with elevated sharpened keel	Abdomen inflated	Habitus stick-like	Forewing/hindwing length	Habitus worm-like	Mesotibia inflated	Cercus segments	Forewing apex rolled in	Length of ScP [%]	Length of CuPaβ [%]	Length of CuA + CuPac [%]	Branches of M (main branches)	Branches of RP (main branches)	Forewing length/body length	Pronotum length/body length	Pronotum length/height	Head height/body length	Metafemur/body length	Metafemur/forewing length	Metafemur/metatibia length	Metafemur/metatibia width	Largest spine of metathoracic leg/metatibia width (not including apical spurs!)	Largest apical spur/metatibia width	Metatarsus (including claws)/metatibia length	Cercus length/forewing length	Cercus length/body length	Antennal segments (all of them)
Ensifera	Tettigoniidae	*Saga pedo*	1	1	2	2	N	N	N	N	N	N	N	0	N	N	1	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	0	N	N	N	N	N	1	0	4	1	1	0	0	0	0	0	N	0	4
Ensifera	Tettigoniidae	*Phaneroptera nigroantennata*	1	1	1	2	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	N	N	0	0	4	0	2	1	2	0	0	1	0	0	0	0	5
Ensifera	Tettigoniidae	*Pseudophyllus hercules*	1	1	1	2	0	0	0	0	1	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	4	0	2	1	1	0	1	0	0	0	0	0	5
Caelifera	Acrididae	*Chorthippus albomarginatus*	1	1	0	0	0	N	0	0	4	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	N	0	1	1	0	1	0	2	0	2	1	1	0	1	1	0	1	0	0	2
Caelifera	Acrididae	*Calliptamus italicus italicus*	1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	N	0	1	1	0	1	0	2	0	2	1	1	0	1	1	0	1	0	0	2
Caelifera	Acrididae	*Anacridium aegyptium*	1	1	0	0	0	0	1	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	2	3	0	2	1	0	0	1	1	1	1	0	2
Caelifera	Acrididae	*Hieroglyphus concolor*	1	1	0	0	0	0	1	0	3	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	3	1	0	0	1	1	1	1	0	N
Caelifera	Acrididae	*Paulinia acuminata*	1	1	0	0	0	0	0	0	4	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	N	1	1	0	0	3	0	2	1	1	0	1	N	N	N	0	0	2
Caelifera	Dericorythidae	*Dericorys millierei*	1	1	0	N	0	0	1	0	2	0	0	0	0	N	1	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	1	1	2	0	2	0	2	1	1	0	1	1	1	1	0	2
Caelifera	Dericorythidae	*Bienkoa fedtshenkoi ornata*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	1	N	N	N	N	N	N	N	0	0	2	1	N	1	1	1	N	0	2
Caelifera	Dericorythidae	*Conophymacris chinensis*	1	1	0	0	N	N	N	N	N	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	N	0	1	1	0	N	N	N	1	0	2	1	0	1	1	1	0	N	0	2
Caelifera	Lathiceridae	*Lathicerus cimex*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	2	0	N	1	1	1	2	0	N	0	0
Caelifera	Lentulidae	*Lentula callani*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	1	0	N	1	1	1	2	0	N	0	2
Caelifera	Lentulidae	*Lithidiopsis bushmanicum*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	1	0	N	1	1	1	1	1	N	0	2
Caelifera	Lentulidae	*Afrotettix fursti*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	2	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	1	0	N	0	1	1	0	1	N	0	1
Caelifera	Lentulidae	*Leatettix denticornis*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	2	1	N	1	1	1	1	0	N	0	1
Caelifera	Lithidiidae	*Eneremius desertorus*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	2	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	2	1	N	1	1	1	1	1	N	0	1
Caelifera	Ommexechidae	*Descampsacris serrulata*	1	1	0	N	0	0	0	0	3	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	N	0	1	1	1	3	1	2	0	2	1	0	0	1	1	1	1	N	N	0	1
Caelifera	Ommexechidae	*Aucacris bullocki*	1	1	0	0	N	0	N	N	N	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	N	N	N	N	1	0	3	1	0	1	1	1	1	1	1	1	0	2
Caelifera	Pamphagidae	*Pamphagus marmoratus*	1	1	0	N	N	0	N	N	N	N	N	0	0	N	1	0	0	0	0	N	0	1	0	1	0	0	N	0	0	N	0	N	N	N	N	1	0	0	0	0	1	1	0	0	0	0	0	2
Caelifera	Pamphagidae	*Lobosceliana femoralis*	1	1	0	0	0	0	1	0	1	0	0	0	0	N	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	4	1	2	1	0	0	1	1	0	0	0	N	N	1
Caelifera	Pamphagidae	*Prionotropis hystrix*	1	1	0	0	0	0	0	0	4	0	0	0	0	N	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	3	1	0	1	1	1	0	1	1	0	1
Caelifera	Pamphagidae	*Eunapiodes granosus*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	1	0	0	0	0	N	0	1	0	1	0	0	0	0	N	0	N	N	N	N	N	1	1	2	2	0	1	1	1	0	N	1	N	0	2
Caelifera	Pamphagodidae	*Charilaus carinatus*	1	1	0	0	1	0	0	0	N	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	2	1	0	0	1	1	1	1	2	0	0	2
Caelifera	Pyrgacrididae	*Pyrgacris descampsi*	1	1	0	N	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	1	N	0	0	0	N	N	N	N	N	0	3	1	0	N	1	1	1	1	N	0	2
Caelifera	Romaleidae	*Procolpia emarginata*	1	1	0	0	0	0	1	0	3	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	2	0	3	0	0	0	1	1	1	2	0	0	2
Caelifera	Romaleidae	*Tropidacris collaris*	1	1	0	0	0	0	2	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	1	2	3	0	3	1	0	0	1	0	1	1	0	2
Caelifera	Romaleidae	*Romalea reticulata*	1	1	0	0	0	0	0	0	4	0	0	0	0	N	1	0	0	0	0	0	0	1	0	1	0	0	0	0	N	0	1	N	1	0	1	2	1	3	1	0	0	1	1	1	1	0	0	2
Caelifera	Romaleidae	*Titanacris albipes*	1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	3	0	2	0	0	0	1	1	1	1	0	0	2
Caelifera	Tristiridae	*Bufonacris bruchii*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	2	2	0	N	1	1	1	1	1	N	0	1
Caelifera	Tetrigidae	*Tetrix subulata*	1	1	0	0	N	0	N	N	N	0	N	0	0	N	1	0	0	0	0	N	0	1	0	0	0	0	1	0	0	0	N	N	N	N	N	1	2	4	2	1	1	1	1	0	1	0	1	0	1
Caelifera	Tetrigidae	*Discotettix belzebuth*	1	1	0	N	N	N	N	N	N	N	N	0	N	N	1	0	0	0	0	N	0	1	0	0	0	0	0	0	N	0	N	N	N	N	N	1	2	4	1	0	1	1	1	0	0	1	N	N	0
Caelifera	Tetrigidae	*Tripetalocera ferruginea*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	1	1	0	0	0	N	0	1	0	0	0	0	1	0	0	1	0	N	N	N	N	N	1	2	4	1	0	1	1	1	0	0	1	1	0	0
Caelifera	Tetrigidae	*Bufonides antennatus*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	N	0	0	0	0	N	0	1	0	0	0	0	N	0	0	N	N	N	N	N	N	2	4	2	1	N	1	1	1	0	0	0	N	N	1
Caelifera	Tetrigidae	*Phelene reinschmidti*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	1	0	0	0	0	N	0	1	0	1	0	0	1	0	0	0	N	N	N	N	N	1	2	4	2	1	1	1	1	0	0	1	0	0	1
Caelifera	Chorotypidae	*Paleochina duvergeri*	N	1	N	N	0	0	N	0	2	1	0	N	0	N	1	N	N	N	N	0	N	N	N	N	N	N	0	N	N	N	N	1	1	N	1	1	N	N	N	N	N	0	1	1	N	N	N	N	N	N
Caelifera	Chorotypidae	*Erianthus dohrni*	1	1	0	0	0	0	N	0	2	0	0	0	0	N	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	N	1	0	3	0	2	2	1	0	1	1	0	0	N	N	1
Caelifera	Chorotypidae	*Adrapetes serraticrus*	1	1	N	0	0	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	0	0	N	N	N	N	N	N	N	0	2	1	1	N	0	0	1	2	0	N	0	N
Caelifera	Episactidae	*Lethus nicaraguae*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	1	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	1	2	2	N	1	1	1	0	0	N	0	0
Caelifera	Episactidae	*Teicophrys strigilecula*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	1	0	0	0	N	0	2	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	2	1	1	N	0	1	1	0	0	N	0	2
Caelifera	Eumastacidae	*Helicomastax mnioides*	1	1	0	0	0	0	0	0	3	0	0	0	0	N	1	1	0	0	0	0	0	2	0	0	0	0	0	0	N	1	1	0	0	2	0	2	1	2	1	0	1	2	2	0	0	0	1
Caelifera	Eumastacidae	*Psychomastax psylla*	1	1	0	N	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	2	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	2	1	1	N	1	1	1	0	2	0	N	N	1
Caelifera	Eumastacidae	*Morsea californica*	1	1	0	N	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	2	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	3	2	2	N	1	1	1	0	2	1	N	N	1
Caelifera	Eumastacidae	*Eumastax tenuis*	1	1	0	0	0	0	N	0	N	0	0	0	0	N	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	N	1	N	0	0	2	0	2	1	2	1	1	1	0	2	2	0	0	1
Caelifera	Euschmidtiidae	*Euschmidtia cruciformis*	1	1	0	0	N	N	N	N	N	N	N	0	0	N	1	0	0	0	0	N	0	2	0	0	0	0	N	0	0	0	0	N	N	N	N	N	1	0	0	2	1	1	1	1	0	1	1	1	0	1
Caelifera	Euschmidtiidae	*Apteropeoedes nigroplagiatus*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	0	N	N	N	N	N	N	0	2	1	1	0	1	1	1	2	1	N	0	1
Caelifera	Euschmidtiidae	*Macromastax infernalis*	1	1	N	0	N	0	N	N	N	0	0	0	0	N	1	0	0	0	0	0	0	2	0	0	0	0	0	0	N	0	N	N	N	N	N	1	0	2	1	1	1	0	1	2	1	0	1	0	N
Caelifera	Euschmidtiidae	*Symbellia nigromaculata*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	2	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	3	1	1	N	1	1	1	0	N	0	N	0	N
Caelifera	Mastacideidae	*Mastacides pupaeformis*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	1	0	0	0	0	N	0	1	0	0	0	0	0	0	N	0	N	N	N	N	N	0	0	2	1	1	2	1	1	1	1	0	3	1	1
Caelifera	Morabidae	*Vandiemenella viatica*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	1	N	0	0	0	N	N	N	N	N	N	N	N	0	3	2	0	N	1	1	1	0	1	0	N	0	1
Caelifera	Morabidae	*Callitala major*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	1	N	0	0	0	N	N	N	N	N	N	N	N	0	4	1	0	N	1	1	1	1	N	0	N	0	1
Caelifera	Morabidae	*Biroella bilobulata*	1	1	0	0	N	0	N	N	N	N	0	0	0	N	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	N	N	N	N	N	1	0	2	1	2	1	1	1	2	2	0	0	0	N
Caelifera	Thericleidae	*Afromastax zebra zebra*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	2	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	2	1	N	0	1	1	0	1	0	N	0	0
Caelifera	Thericleidae	*Thericles obtusifrons*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	2	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	1	0	N	1	1	1	0	2	1	N	0	0
Caelifera	Thericleidae	*Plagiotriptus carli*	1	1	0	0	N	0	N	N	N	0	0	0	0	N	1	0	0	0	0	N	0	1	0	1	0	0	0	0	0	0	N	N	N	N	N	1	1	2	2	0	1	1	1	0	2	1	1	0	0
Caelifera	Thericleidae	*Barythericles pumilus*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	1	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	N	0	0	2	1	N	1	1	1	0	2	0	N	0	N

Character matrix

Suborder	Family	Species	Cryptopleuron	Saltatorial hindlegs	Antennae length [% of body length without cercus or ovipositor]	Ovipositor morphology [% of body length]	M and RP are one branch	Forewing with three broadened areas for communication	Branches of CuA + CuPac (main branches)	MA1 connected via stem of RP in Z-shape with RA	Position of stem of RP	Pterostigma	CuA + CuPac1 and MP S-curved	Amorph metatibial spurs present (no apical) (different from normal armation)	Mirror (as in crickets) in male stridulatory apparatus of forewing	Orientation of mirror cross veins	Forewings present	Metatarsus spurs	Prominent bristles on vertex and frons	Body covered densely with long setae	Prothoracic legs modified for digging	Width b/w ScP and anal wing margin higher than usual	Well-developed spines on fore- and middle tibiae (as in Gryllacrididae)	Compound eye height/head height	Metafemur inflated along entire length	Pronotum dorsally with elevated sharpened keel	Abdomen inflated	Habitus stick-like	Forewing/hindwing length	Habitus worm-like	Mesotibia inflated	Cercus segments	Forewing apex rolled in	Length of ScP [%]	Length of CuPaβ [%]	Length of CuA + CuPac [%]	Branches of M (main branches)	Branches of RP (main branches)	Forewing length/body length	Pronotum length/body length	Pronotum length/height	Head height/body length	Metafemur/body length	Metafemur/forewing length	Metafemur/metatibia length	Metafemur/metatibia width	Largest spine of metathoracic leg/metatibia width (not including apical spurs!)	Largest apical spur/metatibia width	Metatarsus (including claws)/metatibia length	Cercus length/forewing length	Cercus length/body length	Antennal segments (all of them)
Caelifera	Locustopsidae	*Locustopsis rhytofemoralis*	1	1	N	N	0	0	1	0	1	0	0	0	0	N	1	1	0	0	0	0	0	1	0	0	0	0	N	0	0	0	0	1	0	0	2	1	4	0	2	1	0	0	1	1	0	1	1	0	0	N
Caelifera	Locustopsidae	*Araripelocusta imperatrix*	1	1	N	0	0	0	0	0	2	1	0	N	0	N	1	N	0	0	N	0	N	1	0	0	0	0	0	N	N	0	1	1	1	0	2	4	0	3	1	N	N	N	N	N	N	N	N	N	N	N
Caelifera	Locustavidae	*Triassolocusta leptoptera*	N	N	N	N	2	0	1	1	1	0	0	N	0	N	1	N	N	N	N	0	N	N	N	N	N	N	N	0	1	1	1	2	2	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Caelifera	Pneumoridae	*Bullacris discolor*	1	1	0	0	N	0	1	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	1	3	1	0	1	0	0	1	0	0	1	0	N	N	2
Caelifera	Proscopiidae	*Eoproscopia martilli*	0	1	0	0	N	0	N	N	N	0	0	0	0	N	1	N	0	0	0	0	0	1	0	0	0	1	N	0	0	N	N	N	N	N	2	0	4	0	0	0	1	0	0	0	N	N	N
Caelifera	Proscopiidae	*Pseudoproscopia scabra*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	1	N	0	0	0	N	N	N	N	N	N	0	4	0	0	N	0	0	0	0	N	0	N
Caelifera	Proscopiidae	*Proscopia gigantea*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	1	N	0	0	N	N	N	N	N	N	N	N	0	4	0	0	N	0	0	0	N	0	N
Caelifera	Proscopiidae	*Astroma plicatum*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	1	0	0	0	0	N	0	1	0	0	0	1	0	0	0	N	0	N	N	N	N	N	0	1	4	1	0	2	1	0	0	N	N	0
Caelifera	Pyrgomorphidae	*Chrotogonus hemipterus*	1	1	0	N	0	0	0	0	4	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	1	1	1	1	0	2	0	1	2	0	0	1	1	0	2	1	1	0	2
Caelifera	Pyrgomorphidae	*Phymateus morbillosus*	1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	3	0	2	1	0	0	1	0	0	2	0	0	0	2
Caelifera	Pyrgomorphidae	*Pyrgomorpha conica*	1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	3	1	0	0	1	1	0	2	0	0	0	1
Caelifera	Pyrgomorphidae	*Ichthyotettix mexicanus*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	0	2	1	0	N	1	1	0	1	0	N	0	1
Caelifera	Tanaoceridae	*Tanaocerus koebelei*	1	1	1	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	0	0	0	N	0	0	0	N	N	N	N	N	N	N	0	0	2	2	N	0	1	0	1	0	N	1	2
Caelifera	Trigonpterygidae	*Trigonopteryx hopei*	1	1	0	0	0	0	4	0	3	0	0	0	0	N	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	2	0	3	0	2	2	1	0	1	1	0	1	0	0	0	2
Caelifera	Xyronotidae	*Xyronotus aztecus*	1	1	0	0	N	N	N	N	N	N	N	0	N	N	0	0	0	0	0	N	0	1	0	1	0	0	0	N	N	N	N	N	N	N	N	N	0	0	2	1	N	1	1	1	1	1	0	N	0	2
Caelifera	Cylindrachetidae	*Cylindraustralia kochii*	1	0	N	N	N	N	N	N	N	N	N	0	N	N	0	0	0	0	1	N	0	0	1	0	0	0	N	1	1	N	N	N	N	N	N	N	N	0	2	0	0	N	N	N	0	0	0	N	N	0
Caelifera	Ripipterygidae	*Magnidactylus robustus*	1	1	0	N	0	N	N	N	N	N	0	0	0	N	1	0	0	0	1	0	0	2	1	0	0	0	0	0	1	1	0	N	N	N	0	N	1	0	1	1	1	1	1	N	0	N	N	N	0
Caelifera	Ripipterygidae	*Ripipteryx gorgonaensis*	1	1	0	N	N	N	N	N	N	0	0	0	0	N	1	0	0	0	1	0	N	0	2	1	0	0	0	0	0	0	N	0	N	N	N	N	N	2	0	2	2	1	1	1	1	0	3	0	N	N	0
Caelifera	Tridactylidae	*Amberotridactylus cheni*	1	1	N	N	0	0	N	0	5	0	0	0	0	N	1	0	0	0	1	0	0	N	1	0	0	0	0	0	1	1	0	N	N	N	N	N	N	N	N	N	1	1	1	1	0	2	0	N	N	0
Caelifera	Tridactylidae	*Ellipes deyrupi*	1	1	0	0	N	N	N	N	N	0	0	0	0	N	1	0	0	0	1	N	0	1	1	0	0	0	0	1	1	0	N	N	N	N	N	1	0	2	1	0	1	1	1	0	3	0	1	0	0
Caelifera	Tridactylidae	*Cascogryllus setosus*	1	1	0	N	N	N	N	N	N	N	N	0	0	N	1	N	0	0	1	N	0	2	1	0	0	0	0	0	1	1	0	1	N	N	N	N	1	0	2	1	1	1	N	1	N	N	N	1	1	0
Blattodea	Corydiidae	*Fragosublatta pectinata*	0	0	2	N	N	0	6	0	N	0	0	0	0	N	1	1	N	0	0	0	1	N	1	N	0	0	0	0	0	3	0	0	0	N	1	N	2	N	N	N	0	0	0	0	1	1	1	1	1	3

Character matrix (hybrid reconstructed)

Suborder	Infraorder	Superfamily	Family	Species	Character	Cryptopleuron	Sattorial hindlegs	Antennae length [% of body length without cercus or ovipositor]	Ovipositor morphology [% of body length]	M and RP are one branch	Forewing with three broadened areas for communication	Branches of CuA + CuPaa (main branches)	MA1 connected via stem of RP in Z-shape with RA	Position of stem of RP	Pterostigma	CuA + CuPaa and MP S-curved	Amorph metatibial spurs present (no apical) (different from normal armation)	Mirror (as in crickets) in male stridulatory apparatus of forewing	Orientation of mirror cross veins	Forewings present	Metatarsus spurs	Prominent bristles on vertex and frons	Body covered densely with long setae	Prothoracic legs modified for digging	Width b/w ScP and anal vein/ margin higher than usual	Well-developed spines on fore- and middle tibiae (as in Gryllacrididae)	Compound eye height/head height	Metafemur inflated along entire length	Pronotum dorsally with elevated sharpened keel	Abdomen inflated	Habitus stick-like	Forewing/hindwing length	Habitus worm-like	Mesotibia inflated	Cercus segments	Forewing apex rolled in	Length of ScP [%]	Length of CuPa@ [%]	Length of CuA + CuPaa [%]	Branches of M (main branches)	Branches of RP (main branches)	Forewing length/body length	Pronotum length/body length	Pronotum length/height	Head height/body length	Metafemur/body length	Metafemur/forewing length	Metafemur/metatibia length	Metafemur/metatibia width	Largest spine of metathoracic leg/metatibia width (not including apical spurs!)	Largest apical spur/metatibia width	Metatarsus (including claws)/metatibia length	Cercus length/forewing length	Cercus length/body length	Antennal segments (all of them)
Ensifera	Elcanidea	Elcanoidea †	Permelcanidae †	*Proelcana kukalovae*	1	1	1	1	1	0	1	0	0	1	0	0	N	1	0	0	0	0	0	0	0	0	0	N	0	0	0	0	1	0	0	1	4	0	0	1	2	0	1	1	2	1	0	1	1	N
Ensifera	Elcanidea	Elcanoidea †	Permelcanidae †	*Meselcana madygenica*	1	1	1	1	1	0	2	0	0	1	1	1	0	N	1	1	0	0	0	0	0	0	1	0	0	0	0	N	0	0	0	0	1	0	0	2	0	4	0	N	N	1	0	1	1	2	N	1	1	1	N
Ensifera	Elcanidea	Elcanoidea †	Elcanidae †	*Panorpidium spica*	1	1	1	1	1	0	0	0	0	1	0	1	0	N	1	1	0	0	0	0	0	0	1	0	0	0	0	N	0	0	0	0	0	0	0	2	3	4	1	3	N	1	0	1	1	2	2	1	0	1	N
Ensifera	Elcanidea	Elcanoidea †	Elcanidae †	*Sinoelcana minuta*	1	1	1	1	1	0	0	0	0	1	0	1	0	N	1	1	0	0	0	0	0	0	1	0	0	0	0	N	0	0	0	0	0	0	0	2	1	3	0	0	2	1	0	1	1	2	0	1	1	1	N
Ensifera	Elcanidea	Elcanoidea †	Elcanidae †	*Pseudoprobaisselcana oculata*	1	1	1	1	1	0	0	0	0	1	0	1	0	N	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	3	4	0	2	N	2	0	1	1	2	2	1	1	1	N
Ensifera	Elcanidea	Elcanoidea †	Elcanidae †	*Paraxelcana zhengi*	1	1	1	1	1	0	0	0	0	1	0	1	0	N	1	1	0	0	0	0	0	0	1	0	0	0	0	N	0	0	1	0	1	0	0	2	2	4	1	2	N	1	0	1	1	2	0	1	1	1	4
Ensifera	Gryllidea	Grylloidea	Baissogryllidae †	*Notocearagryllus britannicus*	1	1	1	1	0	0	6	0	N	0	0	0	1	2	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	1	0	0	1	1	1	2	1	3	2	5
Ensifera	Gryllidea	Grylloidea	Baissogryllidae †	*Anglogryllus lyristes*	1	1	1	1	0	0	6	0	N	0	0	0	1	2	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	1	0	0	1	1	1	2	1	3	2	5
Ensifera	Gryllidea	Grylloidea	Grylidae	*Antillobinthus inexpectatus*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	1	1	1	1	1	2	2	1	3	2	5
Ensifera	Gryllidea	Grylloidea	Grylidae	*Acheta domesticus*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	0	1	0	1	1	2	2	2	2	5
Ensifera	Gryllidea	Grylloidea	Grylidae	*Spinogryllus meghalayanus*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	1	2	2	1	1	1	2	1	2	2	5
Ensifera	Gryllidea	Grylloidea	Grylidae	*Acanthoplistus acutus*	1	1	2	0	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	3	2	0	0	1	1	1	2	1	3
Ensifera	Gryllidea	Grylloidea	Grylidae	*Gryllus campestris*	1	1	2	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	2	0	0	1	1	1	0	3	1	2	1	5
Ensifera	Gryllidea	Grylloidea	Oecanthidae	*Crassicorpus maculatus*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	1	0	0	1	1	1	3	1	2	2	5
Ensifera	Gryllidea	Grylloidea	Oecanthidae	*Picogryllus carentonensis*	1	1	0	1	1	0	5	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	1	0	0	1	1	1	3	1	2	2	5
Ensifera	Gryllidea	Grylloidea	Oecanthidae	*Oecanthus pellucens*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	4	1	0	0	0	1	1	2	0	2	1	5
Ensifera	Gryllidea	Grylloidea	Oecanthidae	*Neoxabea bipunctata*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	0	0	0	0	0	0	0	0	1	1	5
Ensifera	Gryllidea	Grylloidea	Oecanthidae	*Veredatrypa rosai*	1	1	1	0	1	0	0	0	N	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	0	3	0	0	0	1	1	1	2	0	1	1	5
Ensifera	Gryllidea	Grylloidea	Phalangopsidae	*Brevizacla molisae*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2	1	2	2	1	1	1	2	1	3	3	5
Ensifera	Gryllidea	Grylloidea	Phalangopsidae	*Seselia coccofessei*	1	1	1	1	1	0	1	0	N	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	1	1	1	0	0	1	0	2	1	2	1	1	1	1	2	1	3	3	5
Ensifera	Gryllidea	Grylloidea	Phalangopsidae	*Phalangacris ferlegro*	1	1	1	1	1	0	0	0	N	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	2	2	1	0	1	1	2	1	3	3	5
Ensifera	Gryllidea	Grylloidea	Phalangopsidae	*Araneagryllus dylani*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	1	1	1	0	0	2	0	2	1	2	0	1	1	1	2	0	3	1	5
Ensifera	Gryllidea	Grylloidea	Phalangopsidae	*Phalangopsis arenita*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	1	2	1	0	1	1	2	3	0	3	2	5
Ensifera	Gryllidea	Grylloidea	Pteroplistidae	*Changiola perakensis*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	2	0	4	1	1	0	1	1	0	1	1	3	2	5
Ensifera	Gryllidea	Grylloidea	Trigonidiidae	*Birmaninemobius hirsutus*	1	1	1	1	1	0	1	0	N	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	1	1	1	1	1	1	2	3	1	3	2	5
Ensifera	Gryllidea	Grylloidea	Trigonidiidae	*Fijixipha atalos*	1	1	1	1	1	0	1	0	N	0	0	0	1	1	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	1	1	0	1	1	1	2	2	1	1	1	5
Ensifera	Gryllidea	Grylloidea	Trigonidiidae	*Trigonidium cicindeloides*	1	1	1	1	1	0	1	0	N	0	0	0	0	0	1	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	0	1	1	1	0	1	2	2	1	1	1	5
Ensifera	Gryllidea	Grylloidea	Trigonidiidae	*Paranemobius vicinus*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	2	2	1	1	1	1	2	3	1	3	3	5
Ensifera	Gryllidea	Grylloidea	Trigonidiidae	*Phyllopalpus pulchellus*	1	1	1	1	1	0	1	0	N	0	0	0	1	0	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	1	0	1	0	0	1	1	2	2	1	1	1	5
Ensifera	Gryllidea	Gryllotalpoidea	Gryllotalpidae	*Gryllotalpa nitidula*	1	1	0	1	1	0	1	0	N	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	3	0	0	0	1	0	0	1	1	3	1	4
Ensifera	Gryllidea	Gryllotalpoidea	Gryllotalpidae	*Scapteriscus headsi*	1	1	2	0	1	0	1	0	N	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	1	4	1	0	0	1	0	0	0	0	1	1	4
Ensifera	Gryllidea	Gryllotalpoidea	Gryllotalpidae	*Gryllotalpella macilenta*	1	1	1	0	1	0	1	0	N	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	1	0	0	1	0	1	1	1	3	2	5
Ensifera	Gryllidea	Gryllotalpoidea	Myrmecophilidae	*Camponophilus irmi*	1	1	2	1	1	0	1	0	N	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	2	1	1	0	1	1	1	1	1	2	3	1	4
Ensifera	Gryllidea	Gryllotalpoidea	Myrmecophilidae	*Myrmecophilus acervorum*	1	1	2	1	1	0	1	0	N	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	2	1	0	1	1	0	1	1	2	3	2	4
Ensifera	Tettigoniidea	Hagloidea	Prophalangopsidae	*Allaboilus gigantus*	1	1	1	1	0	0	4	0	1	0	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1	3	4	0	3	1	0	0	1	1	0	0	0	1	1	4
Ensifera	Tettigoniidea	Hagloidea	Prophalangopsidae	*Cyphoderris buckelli*	1	1	1	1	0	0	3	0	2	0	0	0	0	0	N	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	3	1	1	4	2	0	1	0	0	0	0	0	1	1	4
Ensifera	Tettigoniidea	Hagloidea	Prophalangopsidae	*Parahagla sibirica*	1	1	1	1	0	0	2	0	1	0	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	2	3	4	0	3	2	0	0	1	1	0	0	1	1	4
Ensifera	Tettigoniidea	Hagloidea	Haglidae †	*Vitimoilus ovatus*	1	1	1	1	0	0	3	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	2	1	4	0	3	2	0	0	1	1	0	0	1	1	4
Ensifera	Tettigoniidea	Hagloidea	Haglidae †	*Archaboilus polyneurus*	1	1	1	1	0	0	3	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	4	0	3	2	0	0	1	1	0	0	1	1	4
Ensifera	Tettigoniidea	Rhaphidophoroidea	Rhaphidophoridae	*Rhaphidophora loricata*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	1	2	2	2	0	1	1	0	3	0	1	1	5
Ensifera	Tettigoniidea	Rhaphidophoroidea	Rhaphidophoridae	*Stonychophora fulva fulva*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	1	3	2	2	0	1	1	0	2	1	1	2	5
Ensifera	Tettigoniidea	Rhaphidophoroidea	Rhaphidophoridae	*Ceuthophilus lapidicola*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	2	1	1	0	1	1	0	1	2	1	1	5
Ensifera	Tettigoniidea	Rhaphidophoroidea	Rhaphidophoridae	*Pachyrhamma edwardsii*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	3	1	2	0	0	1	1	0	3	1	1	5
Ensifera	Tettigoniidea	Schizodactyloidea	Schizodactylidae	*Schizodactylus salweenensis*	1	1	1	0	0	0	2	0	0	0	0	0	0	N	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	4	0	3	2	1	0	1	1	0	2	1	1	1	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Anostostomatidae	*Pteranabropsis carli*	1	1	1	1	0	0	1	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	3	2	2	0	0	1	1	0	2	0	1	1	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Anostostomatidae	*Hemideina crassidens*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	4	2	0	0	0	1	1	0	1	0	1	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Anostostomatidae	*Deinacrida connectens*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	4	1	0	0	0	0	1	1	0	1	0	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Anostostomatidae	*Cratomelus armatus*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	4	2	1	1	1	0	0	0	1	1	0	1	2	1	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Gryllacrididae	*Hugelgryllacris tchancha* (+ Eremini)	1	1	1	1	0	0	0	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	4	0	4	2	0	0	1	1	0	1	0	5	1	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Gryllacrididae	*Hyalogryllacris gemina gemina*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	1	4	0	3	1	0	0	1	1	0	1	0	0	0	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Gryllacrididae	*Ametrus tibialis*	1	1	1	1	0	0	2	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	2	2	1	1	0	0	0	0	0	2	0	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Gryllacrididae	*Camptonotus carolinensis*	1	1	1	2	0	0	2	0	2	0	0	0	0	0	N	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	3	2	1	0	1	1	0	0	0	1	1	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Stenopelmatidae	*Sia bugajus*	1	1	1	1	0	0	2	0	1	0	0	0	0	0	N	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	2	0	2	1	0	0	1	1	1	0	1	1	1	1	5
Ensifera	Tettigoniidea	Stenopelmatoidea	Stenopelmatidae	*Ammopelmatus irregularis*	1	1	2	0	0	0	2	0	2	0	0	0	0	0	N	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	4	0	4	2	0	0	0	0	0	1	2	1	1	4
Ensifera	Tettigoniidea	Tettigonioidea	Tettigoniidae	*Tettigonia viridissima*	1	1	1	2	0	0	2	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	3	0	3	2	2	0	1	1	0	0	0	0	0	5
Ensifera	Tettigoniidea	Tettigonioidea	Tettigoniidae	*Decticus verrucivorus*	1	1	2	2	0	0	0	0	1	0	0	0	0	0	N	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	2	2	2	0	1	1	0	0	2	0	0	5
Ensifera	Tettigoniidea	Tettigonioidea	Tettigoniidae	*Saga pedo*	1	1	2	2	0	0	0	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	4	1	1	0	0	0	0	0	0	0	0	4
Ensifera	Tettigoniidea	Tettigonioidea	Tettigoniidae	*Phaneroptera nigroantennata*	1	1	1	2	0	0	0	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	4	0	2	1	2	0	0	1	0	0	0	0	0	5
Ensifera	Tettigoniidea	Tettigonioidea	Tettigoniidae	*Pseudophyllus hercules*	1	1	1	2	0	0	0	0	1	0	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	4	0	2	1	1	0	1	1	0	0	0	0	0	5
Caelifera	Acrididea	Acridoidea	Acrididae	*Chorthippus albomarginatus*	1	1	0	0	0	0	0	0	4	0	0	0	0	0	N	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	2	0	2	1	1	0	1	1	0	1	0	0	2
Caelifera	Acrididea	Acridoidea	Acrididae	*Calliptamus italicus italicus*	1	1	0	0	0	0	0	0	2	0	0	0	0	0	N	1	0	0	0	0	0	0	0	1	0	0

Character matrix (hybrid reconstructed)

Suborder	Infraorder	Superfamily	Family	Species	Character	Cryptopleuron	Sattorial hindlegs	Antennae length [% of body length without cercus or ovipositor]	Ovipositor morphology [% of body length]	M and RP are one branch	Forewing with three broadened areas for communication	Branches of CuA + CuPaa (main branches)	MA1 connected via stem of RP in Z-shape with RA	Position of stem of RP	Pterostigma	CuA + CuPaa and MP S-curved	Amorph metatibial spurs present (no apical) (different from normal armation)	Mirror (as in crickets) in male stridulatory apparatus of forewing	Orientation of mirror cross veins	Forewings present	Metatarsus spurs	Prominent bristles on vertex and frons	Body covered densely with long setae	Prothoracic legs modified for digging	Width b/w ScP and anal vein/ margin higher than usual	Well-developed spines on fore- and middle tibiae (as in Gryllacrididae)	Compound eye height/head height	Metafemur inflated along entire length	Pronotum dorsally with elevated sharpened keel	Abdomen inflated	Habitus stick-like	Forewing/hindwing length	Habitus worm-like	Mesotibia inflated	Cercus segments	Forewing apex rotied in	Length of ScP [%]	Length of CuPa@ [%]	Length of CuA + CuPaa [%]	Branches of M (main branches)	Branches of RP (main branches)	Forewing length/body length	Pronotum length/body length	Pronotum length/height	Head height/body length	Metafemur/body length	Metafemur/forewing length	Metafemur/metatibia length	Metafemur/metatibia width	Largest spine of metathoracic leg/metatibia width (not including apical spurs!)	Largest apical spur/metatibia width	Metatarsus (including claws)/metatibia length	Cercus length/forewing length	Cercus length/body length	Antennal segments (all of them)
Caelifera	Acrididea	Acridoidea	Ommexechidae	*Aucacris bullocki*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	0	2
Caelifera	Acrididea	Acridoidea	Pamphagidae	*Pamphagus marmoratus*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	2
Caelifera	Acrididea	Acridoidea	Pamphagidae	*Lobosceliana femoralis*		1	1	0	0	0	0	1	0	1	0	0	0	0	N	1	0	0	0	0	0	0	0	1	0	1	1	1	1	4	1	2	1	0	0	1	1	0	0	0	0	0	0	1
Caelifera	Acrididea	Acridoidea	Pamphagidae	*Prionotropis hystrix*		1	1	0	0	0	0	0	0	4	0	0	0	0	N	1	0	0	0	0	0	0	0	1	1	1	1	0	1	1	3	1	0	1	1	1	0	1	1	1	0	1	1	0	1
Caelifera	Acrididea	Acridoidea	Pamphagidae	*Eunapiodes granosus*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	1	1	1	1	0	1	1	2	2	0	1	1	1	0	1	1	1	0	1	1	0	2
Caelifera	Acrididea	Acridoidea	Pamphagodidae	*Charilaus carinatus*		1	1	0	0	1	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	2	1	0	0	1	1	0	2	0	0	0	0	2
Caelifera	Acrididea	Acridoidea	Pyrgacrididae	*Pyrgacris descampsi*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	3	1	0	0	1	1	0	1	1	0	1	1	0	2
Caelifera	Acrididea	Acridoidea	Romaleidae	*Procolpia emarginata*		1	1	0	0	0	0	1	0	3	0	0	0	0	N	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
Caelifera	Acrididea	Acridoidea	Romaleidae	*Tropidacris collaris*		1	1	0	0	0	0	2	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	3	0	3	1	0	0	1	0	2
Caelifera	Acrididea	Acridoidea	Romaleidae	*Romalea reticulata*		1	1	0	0	0	0	0	0	4	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	2	1	3	1	0	0	1	1	0	2
Caelifera	Acrididea	Acridoidea	Romaleidae	*Titanacris albipes*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	3	0	2	0	0	0	1	1	1	1	0	2
Caelifera	Acrididea	Acridoidea	Tristiridae	*Bufonacris bruchii*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	2	2	0	1	1	1	1	0	1
Caelifera	Acrididea	Tetrigoidea	Tetrigidae	*Tetrix subulata*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	1	0	1	0	1	0	1
Caelifera	Acrididea	Tetrigoidea	Tetrigidae	*Discotettix belzebuth*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	0	0	0	1	1	0	0	1	1	0	0
Caelifera	Acrididea	Tetrigoidea	Tetrigidae	*Tripetalocera ferruginea*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	1	1	1	0	1	0	1	2	4	1	0	1	1	1	0	0	1	1	0	0
Caelifera	Acrididea	Tetrigoidea	Tetrigidae	*Bufonides antennatus*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	2	4	2	1	1	1	1	0	0	0	1	0	1
Caelifera	Acrididea	Tetrigoidea	Tetrigidae	*Phelene reinschmidti*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	1	1	1	0	1	0	1	2	4	2	1	1	1	1	0	0	0	1	0	1
Caelifera	Acrididea	Eumastacoidea	Chorotypidae	*Paleochina duvergeri*		1	1	0	0	0	0	0	0	2	1	0	0	0	N	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	1	2	0	2	1	1	0	1	1	0	2	0	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Chorotypidae	*Erianthus dohrni*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	3	0	2	2	1	0	1	1	1	0	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Chorotypidae	*Adrapetes serraticrus*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	2	0	2	1	1	1	0	1	1	2	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Episactidae	*Lethus nicaraguae*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	2	0	1	2	2	1	1	1	1	0	0	0	0	0	0
Caelifera	Acrididea	Eumastacoidea	Episactidae	*Teicophrys strigilecula*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	1	1	0	1	0	2	0	2	1	1	1	1	0	1	1	0	0	0	2
Caelifera	Acrididea	Eumastacoidea	Eumastacidae	*Helicomastax mnioides*		1	1	0	0	0	0	0	0	3	0	0	0	0	N	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	1	2	1	0	1	1	2	2	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Eumastacidae	*Psychomastax psylla*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	2	0	2	1	1	1	1	1	0	2	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Eumastacidae	*Morsea californica*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	2	1	2	1	1	1	1	1	0	2	1	0	0	1
Caelifera	Acrididea	Eumastacoidea	Eumastacidae	*Eumastax tenuis*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	0	0	2	0	2	1	2	1	1	1	2	2	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Euschmidtiidae	*Euschmidtia cruciformis*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	2	1	1	1	1	1	1	0	1	1	1	0	1
Caelifera	Acrididea	Eumastacoidea	Euschmidtiidae	*Apteropeoedes nigroplagiatus*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	2	1	0	1	1	0	1	1	2	1	0	0	1
Caelifera	Acrididea	Eumastacoidea	Euschmidtiidae	*Macromastax infernalis*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	2	1	1	1	1	0	1	1	2	1	0	1	1
Caelifera	Acrididea	Eumastacoidea	Euschmidtiidae	*Symbellia nigromaculata*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	2	0	3	1	1	1	1	1	0	1	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Mastacideidae	*Mastacides pupaeformis*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	2	1	1	2	1	1	1	1	1	0	3	1	1
Caelifera	Acrididea	Eumastacoidea	Morabidae	*Vandiemenella viatica*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	2	0	3	2	0	1	1	1	0	1	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Morabidae	*Callitala major*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	4	1	0	1	1	1	1	1	0	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Morabidae	*Biroella bilobulata*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	2	1	2	1	1	1	2	2	0	0	0	1
Caelifera	Acrididea	Eumastacoidea	Thericleidae	*Afromastax zebra zebra*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	0	2	2	1	1	0	1	1	0	0	0	0	0
Caelifera	Acrididea	Eumastacoidea	Thericleidae	*Thericles obtusifrons*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	0	1	0	2	1	1	1	0	0	2	1	0	0	0
Caelifera	Acrididea	Eumastacoidea	Thericleidae	*Ptagiotriptus carli*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	2	2	0	1	1	1	1	0	2	1	1	0	0
Caelifera	Acrididea	Eumastacoidea	Thericleidae	*Barythericles pumilus*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	0	2	1	1	1	1	1	0	2	0	0	0	1
Caelifera	Acrididea	Locustopsoidea †	Locustopsidae †	*Locustopsis rhytofemoralis*		1	1	0	0	0	0	1	0	1	0	0	0	0	N	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	4	0	2	1	0	0	1	1	0	0	1
Caelifera	Acrididea	Locustopsoidea †	Locustopsidae †	*Araripelocusta imperatrix*		1	1	0	0	0	0	0	0	2	1	0	0	0	N	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	2	4	0	3	1	0	0	1	1	0	0	1
Caelifera	Acrididea	Locustopsoidea †	Locustavidae †	*Triassolocusta leptoptera*		1	1	0	0	2	0	1	1	1	0	0	0	0	N	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	4	0	2	1	0	0	1	1	0	0	1	1	0	0	1
Caelifera	Acrididea	Pneumoroidea	Pneumoridae	*Bullacris discolor*		1	1	0	0	0	0	1	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	0	1	3	1	0	1	0	0	1	1	0	0	0	0	2
Caelifera	Acrididea	Procopioidea	Proscopiidae	*Eoproscopia martilli*		0	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	2	0	4	0	0	0	1	0	0	0	0	0	0	0
Caelifera	Acrididea	Procopioidea	Proscopiidae	*Pseudoproscopia scabra*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	2	0	4	0	0	0	0	0	0	0	0	0	0	0
Caelifera	Acrididea	Procopioidea	Proscopiidae	*Proscopia gigantea*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	2	0	4	0	0	0	0	0	0	0	0	0	0	0
Caelifera	Acrididea	Procopioidea	Proscopiidae	*Astroma plicatum*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	2	1	0	1	4	1	0	2	1	0	0	0	0	0
Caelifera	Acrididea	Pyrgomorphoidea	Pyrgomorphidae	*Chrotogonus hemipterus*		1	1	0	0	0	0	0	0	4	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	1	1	1	1	0	2	0	1	2	0	0	1	1	0	2	1	1	0	2
Caelifera	Acrididea	Pyrgomorphoidea	Pyrgomorphidae	*Phymateus morbillosus*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	3	0	2	1	0	0	1	1	0	2	0	0	0	2
Caelifera	Acrididea	Pyrgomorphoidea	Pyrgomorphidae	*Pyrgomorpha conica*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	3	1	0	0	1	1	0	2	0	0	0	1
Caelifera	Acrididea	Pyrgomorphoidea	Pyrgomorphidae	*Ichthyotettix mexicanus*		1	1	0	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	2	1	0	0	1	1	0	0	0	0	0	1
Caelifera	Acrididea	Tanaoceroidea	Tanaoceridae	*Tanaocerus koebelei*		1	1	1	0	0	0	0	0	2	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	0	0	2	2	0	0	1	0	1	2	0	1	1
Caelifera	Acrididea	Trigonopterygoidea	Trigonpterygidae	*Trigonopteryx hopei*		1	1	0	0	0	0	4	0	3	0	0	0	0	N	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	2	0	3	0	2	2	1	0	1	1	0	0	0	0	0	2
Caelifera	Acrididea	Trigonopterygoidea	Xyronotidae	*Xyronotus aztecus*		1	1	0	0	0	0	4	0	3	0	0	0	0	N	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	2	0	3	0	0	2	1	0	1	1	0	0	0	2
Caelifera	Tridactylidea	Tridactyloidea	Cylindrachetidae	*Cylindraustralia kochii*		1	0	0	N	0	N	N	N	0	0	0	0	0	N	1	0	0	0	0	0	0	0	0	0	1	1	1	0	N	N	N	0	N	1	0	2	0	0	1	1	N	N	0	0	0	0	1	1	N	0
Caelifera	Tridactylidea	Tridactyloidea	Ripipterygidae	*Magnidactylus robustus*		1	1	0	N	0	N	N	N	N	0	0	0	0	N	1	0	0	0	1	0	0	0	0	2	1	0	0	0	0	0	1	1	0	N	N	N	0	N	1	0	1	1	1	1	1	1	0	3	0	1	N	0
Caelifera	Tridactylidea	Tridactyloidea	Ripipterygidae	*Ripipteryx gorgonaensis*		1	1	0	N	0	N	N	N	N	0	0	0	0	N	1	0	0	0	1	0	0	0	0	2	1	0	0	0	0	0	1	0	N	N	N	0	N	2	0	2	2	1	1	1	1	0	3	0	1	N	0
Caelifera	Tridactylidea	Tridactyloidea	Tridactylidae	*Amberotridactylus cheni*		1	1	0	N	0	0	N	0	5	0	0	0	0	N	1	0	0	0	1	0	0	0	0	2	1	0	0	0	0	0	1	1	0	N	N	N	0	N	1	0	2	1	1	1	1	1	0	2	0	1	N	0
Caelifera	Tridactylidea	Tridactyloidea	Tridactylidae	*Ellipes deyrupi*		1	1	0	0	0	N	N	N	N	0	0	0	0	N	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	N	N	N	0	N	1	0	2	1	0	1	1	1	0	3	0	1	0	0
Caelifera	Tridactylidea	Tridactyloidea	Tridactylidae	*Cascogryllus setosus*		1	1	0	N	0	N	N	N	N	0	0	0	0	N	1	0	0	0	1	0	0	0	0	2	1	0	0	0	0	0	1	1	0	N	N	N	0	N	1	0	2	1	1	1	1	1	0	3	0	1	1	0
Blattodea		Corydioidea	Corydiidae	*Fragosublatta pectinata*		0	0	2	N	N	0	6	0	N	0	0	0	0	N	1	1	N	0	0	0	0	0	1	N	1	N	0	0	0	0	0	3	0	0	0	N	1	N	2	N	N	N	0	0	0	0	1	1	1	1	1	3

Supplementary material 2: annotated character list.

Annotated character list (used for test and main matrix)

1. Presence of a cryptopleuron/large saddle-shaped pronotum

0 = no; 1 = yes

2. Saltatorial hindlegs

0 = no; 1 = yes

3. Antennae length

0 = less than 51%; 1 = 90% or more; 2 = 51-89%

4. Ovipositor morphology

0 = less than 25%; 1 = 25% or more

5. M and RP are one branch

0 = no; 1 = yes; 2 = no (fused to RP via cross vein)

6. Forewing with three broadened areas hypothesized to be associated with communication (as in Titanoptera)

0 = no; 1 = yes

7. Branches of CuA + CuPaα (main branches)

0 = 1; 1 = 2; 2 = 3; 3 = 4; 4 = 5; 5 = 6-7; 6 = 8-9; 7 = more than 9

8. MA1 connected via stem of RP in Z-shape with RA (as in Oedischia williamsoni*)*

0 = no; 1 = yes

9. Position of stem of RP

0 = as cross vein between RA and M + RP; 1 = branching of RA near base; 2 = branching of RA near middle; 3 = branching of RA near apex; 4 = starting off at wing base; 5 = no stem of RP

10. Presence of pterostigma

0 = no; 1 = yes

11. CuA + CuPaα and MP S-curved (as in Meselcana*)*

0 = no; 1 = yes

12. Presence of enlarged metatibial spurs (as in Elcanidae)

0 = no; 1 = yes

13. Mirror (as in crickets) in male stridulatory apparatus of forewing

0 = no; 1 = yes

14. Orientation of mirror cross veins

0 = vertical; 1 = horizontal; 2 = oblique (right to left)

15. Forewings present

0 = no; 1 = yes

16. Metatarsus spurs

0 = no; 1 = yes

17. Prominent bristles on vertex and frons

0 = no; 1 = yes

18. Body covered densely with long setae

0 = no; 1 = yes

19. Prothoracic legs modified for digging

0 = no; 1 = yes

20. *Width b/w ScP and anal wing margin higher than usual (more than 30% of total wing height)*

0 = no; 1 = yes

21. Well-developed spines on fore- and middle tibiae

0 = no; 1 = yes

22. Compound eye height/head-height

0 = less than 0.1; 1 = 0.1-0.39; 2 = 0.4 or more

23. Metafemur inflated along entire length

0 = no; 1 = yes

24. Pronotum dorsally with sharpened keel

0 = no; 1 = yes

25. Abdomen inflated (as in Pneumoridae)

0 = no; 1 = yes

26. Habitus stick-like

0 = no; 1 = yes

27. Forewing/hindwing length

0 = 0.3-1.5; 1 = less than 0.3; 2 = more than 1.5

28. Habitus worm-like (as in Cylindrachetidae)

0 = no; 1 = yes

29. Mesotibia inflated (as in Tridactylidae)

0 = no; 1 = yes

30. Cercus segments

0 = 1; 1 = 2; 2 = 3 or more

31. Apex of forewing rolled in (as in Schizodactylidae)

0 = no; 1 = yes

32. Length of ScP [% of total wing length]

0 = up to 50%; 1 = more than 50%

33. Length of CuPaβ [%]

0 = up to 50%; 1 = more than 50%

34. Length of CuA + CuPaα [%]

0 = less than 70%; 1 = more than 70%

35. Branches of M (main branches)

0 = 1; 1 = 2; 2 = 3; 3 = 4

36. Branches of RP (main branches)

0 = 1-3; 1 = 4-5; 2 = 6-7; 3 = 8-10; 4 = RP absent

37. Forwing length/body length

0 = less than 0.1; 1 = 0.1-0.5; 2 = 0.5-0.99; 3 = 1.0-1.2; 4 = more than 1.2

38. Pronotum length/body length

0 = up to 0.3; 1 = 0.3-1.0; 2 = more than 1.0

39. Pronotum length/height

0 = less than 1; 1 = 1; 2 = 1.01-1.39; 3 = 1.4-1.8; 4 = more than 1.8

40. Head height/body length

0 = less than 0.2; 1 = 0.2-0.29; 2 = 0.3 +

41. Metafemur/body length

0 = less than 0.6; 1 = 0.6-0.79; 2 = 0.8 +

42. Metafemur/forewing length

0 = less than 1.0; 1 = 1.0-7.0; 2 = more than 7.0

43. Metafemur/metatibia length

0 = less than 1.0; 1 = 1.0 or more

44. Metafemur/metatibia width

0 = up to 3.0; 1 = more than 3.0

45. Largest spine of metathoracic leg/metatibia width

0 = up to 1.0 (including no spines); 1 = 1.01-2.0; 2 = more than 2.0

46. Largest apical spur/metatibia width

0 = less than 1; 1 = 1-1.9; 2 = 2-4; 3 = more than 4

47. Metatarsus (including claws)/metatibia length

0 = up to 0.4; 1 = 0.41-0.8; 2 = 0.81-0.99; 3 = 1.0 or more

48. Cercus length/forewing length

0 = less than 0.1; 1 = 0.1-0.49; 2 = 0.5-0.99; 3 = 1.0 or more

49. Cercus length/body length

0 = less than 0.1; 1 = 0.1-0.49; 2 = 0.5-0.89; 3 = 0.9 or more

50. Antennal segments (all of them)

0 = up to 10; 1 = 11-15; 2 = 16-30; 3 = 31-49; 4 = 50-100; 5 = 100 or more

Supplementary material 3: reference list for all species featured in the phylogenetic analyses.

Infraorder	**Superfamily**	**Family**	**Species**	**Reference**
Ensifera Chopard, 1921	Elcanoidea Handlirsch, 1906	Permelcanidae Sharov, 1962	*Proelcana kukalovae* (Sharov, 1968)	Zessin, W. (1987). Variabilität, Merkmalswandel und Phylogenie der Elcanidae im Jungpaläozoikum und Mesozoikum und die Phylogenie der Ensifera (Orthopteroida, Ensifera). *Deutsche Entomologische Zeitschrift*, *34*(1-3), 1-76. https://doi.org/10.1002/mmnd.19870340102

Ensifera	Elcanoidea	Permelcanidae	*Meselcana madygenica* Sharov, 1968	Zessin, W. (1987). Variabilität, Merkmalswandel und Phylogenie der Elcanidae im Jungpaläozoikum und Mesozoikum und die Phylogenie der Ensifera (Orthopteroida, Ensifera). *Deutsche Entomologische Zeitschrift*, *34*(1-3), 1-76. https://doi.org/10.1002/mmnd.19870340102
Ensifera	Elcanoidea	Elcanidae Handlirsch, 1906	*Panorpidium spica* Kim, Lee, Nam & Park, 2021	Kim, D. Y., Lee, M., Nam, G. S., & Park, T. Y. S. (2021). The first orthopteran fossils from the Lower Cretaceous (Albian) Jinju Formation of Korea: Ethological implications for elcanids. *Cretaceous Research*, *125*, 104843. https://doi.org/10.1016/j.cretres.2021.104843
Ensifera	Elcanoidea	Elcanidae	*Sinoelcana minuta* Gu, Tian, Wang & Yue, 2020	Gu, J. J., Tian, H., Wang, J., Zhang, W., Ren, D., & Yue, Y. (2020). A world key to the genera of Elcanidae (Insecta, Orthoptera), with a Jurassic new genus and species of Archelcaninae from China. *ZooKeys*, *954*, 65. doi: 10.3897/zookeys.954.52088
Ensifera	Elcanoidea	Elcanidae	*Pseudoprobaisselcana oculata* (Hu and He, 2023)	Hu, T. H., & He, Z. Q. (2023). A new species of genus *Probaisselcana* (Orthoptera: Elcanidae)

				from mid-Cretaceous Burmese amber. *Cretaceous Research*, *151*, 105671. https://doi.org/10.1016/j.cretres.2023.105671
Ensifera	Elcanoidea	Elcanidae	*Paraxelcana zhengi* (Gu, Tian & Ren, 2022)	Specimen GPIH05133; Schall, O. K. O., Kotthoff, U. & Husemann, M., in review. A review of the Elcanidae (Insecta: Orthoptera) species *Paraxelcana coronakanthodis*, *Letoelcana artemisapollonque* and *Trigonelca jennywinterae* Schall et al., 2023. *PalZ.*
Ensifera	Grylloidea Laicharting, 1781	Baissogryllidae Gorochov, 1985	*Notocearagryllus britannicus* Gorochov, Jarzembowski & Coram, 2006	Gorochov, A. V., Jarzembowski, E. A., & Coram, R. A. (2006). Grasshoppers and crickets (Insecta: Orthoptera) from the Lower Cretaceous of southern England. *Cretaceous Research*, *27*(5), 641-662. https://doi.org/10.1016/j.cretres.2006.03.007
Ensifera	Grylloidea	Baissogryllidae	*Anglogryllus lyristes* Gorochov, Jarzembowski & Coram, 2006	Gorochov, A. V., Jarzembowski, E. A., & Coram, R. A. (2006). Grasshoppers and crickets (Insecta: Orthoptera) from the Lower Cretaceous of southern England. *Cretaceous Research*, *27*(5), 641-662. https://doi.org/10.1016/j.cretres.2006.03.007
Ensifera	Grylloidea	Gryllidae Laicharting, 1781	*Anthillobintus inexpectatus* Yong and Desutter-Grandcolas, 2020	Yong, S., Desutter-Grandcolas, L., Teruel, R., & Leguin, E. A. (2020). A new genus and species of cricket from eastern Cuba: the first Antillean true Eneopterinae (Orthoptera: Gryllidae: Eneopterinae). *Zootaxa*, *4858*(2), 261-273.

Ensifera	Grylloidea	Gryllidae	*Acheta domesticus* (Linnaeus, 1758)	https://www.orthoptera.ch/wiki/arten/ensifera/gryllinae/item/acheta-domesticus
Ensifera	Grylloidea	Gryllidae	*Spinogryllus meghalayanus* Vasanth, 1993	https://orthoptera.speciesfile.org/otus/829166/overview
Ensifera	Grylloidea	Gryllidae	*Acanthoplistus acutus* Saussure, 1877	https://orthoptera.speciesfile.org/otus/829718/overview
Ensifera	Grylloidea	Gryllidae	*Gryllus campestris* Linnaeus, 1758	https://orthoptera.speciesfile.org/otus/829396/overview
Ensifera	Grylloidea	Oecanthidae Blanchard, 1845	*Crassicorpus maculatus* Zheng, Yuan & Gu, 2023	Zheng, C., Yuan, W., Chen, H., & Gu, J. J. (2023, November). Two new genera and species of Oecanthidae (Orthoptera: Grylloidea) from Mid-Cretaceous of Myanmar. In *Annales de la Société entomologique de France (NS)* (Vol. 59, No. 6, pp. 417-427). Taylor & Francis. https://doi.org/10.1080/00379271.2023.2284172
Ensifera	Grylloidea	Oecanthidae	*Picogryllus carentonensis* Josse and Desutter-Grandcolas, 2023	Desutter-Grandcolas, L., Josse, H., Laurent, M., De Campos, L. D., Hugel, S., Soriano, C., ... & Perrichot, V. (2023). New Cretaceous crickets of the subfamilies Nemobiinae and Podoscirtinae (Orthoptera, Grylloidea: Trigonidiidae, Oecanthidae) attest the antiquity of these clades. *Geological Magazine*, *160*(5), 927-940. https://doi.org/10.1017/S0016756823000055
Ensifera	Grylloidea	Oecanthidae	*Oecanthus pellucens* (Scopoli, 1763)	https://orthoptera.speciesfile.org/otus/836475/overview
Ensifera	Grylloidea	Oecanthidae	*Neoxabea bipunctata* (De Geer, 1773)	https://orthoptera.speciesfile.org/otus/836564/overview
Ensifera	Grylloidea	Oecanthidae	*Veredatrypa rosai* de Campos, Souza-	de Campos, L. D., Souza-Dias, P. G., & Nihei, S. S. (2020). New Brazilian Tafaliscina increase the

			Dias & Nihei, 2020	diversity of this Neotropical cricket clade (Orthoptera: Grylloidea: Gryllidae: Oecanthinae: Paroecanthini). *Zoosystema*, *42*(19), 331-353. https://doi.org/10.5252/zoosystema2020v42a19
Ensifera	Grylloidea	Oecanthidae	*Euscyrtus bivittatus bivittatus* Guérin-Méneville, 1844	https://orthoptera.speciesfile.org/otus/834916/overview
Ensifera	Grylloidea	Oecanthidae	*Calyptotrypus helvolus* (Serville, 1838)	https://orthoptera.speciesfile.org/otus/834986/overview
Ensifera	Grylloidea	Phalangopsidae Blanchard, 1845	*Brevizacla molisae* Desutter-Grandcolas, 2012	Desutter-Grandcolas, L. (2012). Phalangopsidae crickets from Espiritu Santo Island, Vanuatu (Insecta, Orthoptera, Grylloidea). *Zoosystema*, *34*(2), 287-304. https://doi.org/10.5252/z2012n2a7
Ensifera	Grylloidea	Phalangopsidae	*Seselia coccofessei* Hugel and Desutter-Grandcolas, 2021	Hugel, S., Warren, B. H., & Desutter-Grandcolas, L. (2021). The Phalangopsidae crickets (Orthoptera, Grylloidea) of the Seychelles Archipelago: Taxonomy of an ecological radiation. *Zootaxa*, *5047*(3), 201-246. 10.11646/zootaxa.5047.3.1
Ensifera	Grylloidea	Phalangopsidae	*Phalangacris ferlegro* Hugel and Desutter-Grandcolas, 2021	Hugel, S., Warren, B. H., & Desutter-Grandcolas, L. (2021). The Phalangopsidae crickets (Orthoptera, Grylloidea) of the Seychelles Archipelago: Taxonomy of an ecological radiation. *Zootaxa*, *5047*(3), 201-246. 10.11646/zootaxa.5047.3.1

Ensifera	Grylloidea	Phalangopsidae	*Araneagryllus dylani* Heads, 2010	Heads, S. W. (2010). The first fossil spider cricket (Orthoptera: Gryllidae: Phalangopsinae): 20 million years of troglobiomorphosis or exaptation in the dark?. *Zoological Journal of the Linnean Society*, *158*(1), 56-65. https://doi.org/10.1111/j.1096-3642.2009.00587.x
Ensifera	Grylloidea	Phalangopsidae	*Phalangopsis arenita* Mews and Sperber, 2008	https://orthoptera.speciesfile.org/otus/832860/overview
Ensifera	Grylloidea	Phalangopsidae	*Vescelia variegata* (Chopard, 1937)	https://orthoptera.speciesfile.org/otus/831879/overview
Ensifera	Grylloidea	Pteroplistidae Chopard, 1936	*Changiola perakens*is (Chopard, 1969)	Tan, M. K., Muhammad, A. A., & Robillard, T. (2021). A review of the genus Changiola (Orthoptera: Grylloidea: Pteroplistinae) and description of the first species from Borneo. *Zootaxa*, *4941*(1), 101-114. 10.11646/zootaxa.4941.1.6
Ensifera	Grylloidea	Trigonidiidae Saussure, 1874	*Birmaninemobius hirsutus* Xu, Zhang, Jarzembowski & Fang, 2020	Xu, C., Zhang, H., Jarzembowski, E. A., & Fang, Y. (2020). The first ground cricket (Orthoptera: Trigonidiidae: Nemobiinae) from mid-Cretaceous Burmese amber. *Cretaceous Research*, *115*, 104481. https://doi.org/10.1016/j.cretres.2020.104481
Ensifera	Grylloidea	Trigonidiidae	*Fijixipha atalos* Otte and Cowper, 2007	Otte, D., & Cowper, G. (2007). New cricket species from the Fiji Islands (Orthoptera: Grylloidea). *Proceedings of the Academy of Natural Sciences of Philadelphia*, *156*(1), 217-303. https://doi.org/10.1635/0097-

				3157(2007)156[217:NCSFTF]2.0.CO;2
Ensifera	Grylloidea	Trigonidiidae	*Trigonidium cicindeloides* Rambur, 1838	https://orthoptera.speciesfile.org/otus/834467/overview
Ensifera	Grylloidea	Trigonidiidae	*Paranemobius vicinus* Chopard, 1928	https://orthoptera.speciesfile.org/otus/833897/overview
Ensifera	Grylloidea	Trigonidiidae	*Phyllopalpus pulchellus* Uhler, 1864	https://orthoptera.speciesfile.org/otus/834062/overview
Ensifera	Grylloidea	Trigonidiidae	*Pepoyara jagoi* de Mello and Capellari, 2012	Bolfarini, M. P., Capellari, R. S., & De Mello, F. D. A. (2012). Two new genera of Pteronemobiini crickets from the Brazilian Atlantic forest (Orthoptera, Grylloidea, Trigonidiidae, Nemobiinae). *Zootaxa*, *3478*(1), 19-31.
Ensifera	Gryllotalpoidea Leach, 1815	Gryllotalpidae Leach, 1815	*Gryllotalpa nitidula* Serville, 1838	Tindale, N. B. (1928). Australasian mole-crickets of the family Gryllotalpidae (Orthoptera). South Australian Museum.
Ensifera	Gryllotalpoidea	Gryllotalpidae	*Scapteriscus headsi* Cadena-Castañeda, 2011	Cadena-Castaneda, O. J. (2011). Two new species of mole crickets (Orthoptera: Gryllotalpidae: Scapteriscinae) from the Colombian Amazon and Orinoquia rainforests. *Zootaxa*, *3126*(1), 62-68.
Ensifera	Gryllotalpoidea	Gryllotalpidae	*Gryllotalpella macilenta* (Saussure, 1874)	https://orthoptera.speciesfile.org/otus/837573/overview
Ensifera	Gryllotalpoidea	Myrmecophilidae Saussure, 1874	*Camponophilus irmi* Ingrisch, 1995	Ingrisch, S. (1995). Eine neue Ameisengrille aus Borneo (Ensifera: Grylloidea). *Entomologische Zeitschrift*, *105*(21), 421-427.
Ensifera	Gryllotalpoidea	Myrmecophilidae	*Myrmecophilus acervorum* (Panzer, 1799)	https://orthoptera.speciesfile.org/otus/837642/overview

Ensifera	Hagloidea Handlirsch, 1906	Prophalangopsidae Kirby, 1906	*Allaboilus gigantus* Ren and Meng, 2006	Gu, J. J., Qiao, G. X., & Ren, D. (2010). Revision and new taxa of fossil Prophalangopsidae (Orthoptera: Ensifera). *Journal of Orthoptera Research*, 41-56. https://www.jstor.org/stable/20789566
Ensifera	Hagloidea	Prophalangopsidae	*Cyphoderris buckelli* Hebard, 1934	Vickery, V.R. & Kevan, D.K.M.E. (1986) The grasshoppers, crickets, and related insects of Canada and adjacent regions. Ulonata: Dermaptera, Cheleutoptera, Notoptera, Dictuoptera, Grylloptera, and Orthoptera. *The Insects and Arachnids of Canada*, 14, 1–918.
Ensifera	Hagloidea	Prophalangopsidae	*Parahagla sibirica* Sharov, 1968	Gu, J. J., Qiao, G. X., & Ren, D. (2010). Revision and new taxa of fossil Prophalangopsidae (Orthoptera: Ensifera). *Journal of Orthoptera Research*, 41-56. https://www.jstor.org/stable/20789566
Ensifera	Hagloidea	Prophalangopsidae	*Prophalangopsis obscura* (Walker, 1869)	https://orthoptera.speciesfile.org/otus/837767/overview
Ensifera	Hagloidea	Prophalangopsidae	*Paracyphoderris erebeus* Storozhenko, 1980	Storozhenko, S. Y., Molodtsov, V. V., & Sergeev, M. G. (2023). The mysterious Amurian grig Paracyphoderris erebeus Storozhenko, 1980 (Orthoptera: Prophalangopsidae): New data on its distribution, ecology and biology. *Insects*, *14*(10), 789. https://doi.org/10.3390/insects14100789
Ensifera	Hagloidea	Haglidae Handlirsch, 1906	*Vitimoilus ovatus* Gu, Tian, Yin, Shi & Ren, 2017	Gu, J. J., Tian, H., Yin, X., Shi, F., & Ren, D. (2017). A new species of Cyrtophyllitinae (Insecta: Ensifera) from the Cretaceous China. *Cretaceous Research*, *74*, 151-154.

				https://doi.org/10.1016/j.cretres.2016.12.023
Ensifera	Hagloidea	Haglidae	*Archaboilus polyneurus* Gu, Yue & Ren, 2021	Gu, J. J., Yang, X., Huang, R., Yang, G., Yue, Y., & Ren, D. (2021). New species and material of Hagloidea (Insecta, Ensifera) from the Yanliao biota of China. *ZooKeys*, *1033*, 183. 10.3897/zookeys.1033.63571
Ensifera	Rhaphidophoroidea Walker, 1869	Rhaphidophoridae Walker, 1869	*Rhaphidophora loricata* (Burmeister, 1838)	https://orthoptera.speciesfile.org/otus/838742/overview
Ensifera	Rhaphidophoroidea	Rhaphidophoridae	*Stonychophora fulva fulva* (Brunner von Wattenwyl, 1888)	https://orthoptera.speciesfile.org/otus/838853/overview
Ensifera	Rhaphidophoroidea	Rhaphidophoridae	*Ceutophilus lapidicola* (Burmeister, 1838)	https://orthoptera.speciesfile.org/otus/839047/overview
Ensifera	Rhaphidophoroidea	Rhaphidophoridae	*Pachyrhamma edwardsii* (Scudder, 1869)	https://orthoptera.speciesfile.org/otus/839299/overview
Ensifera	Schizodactyloidea Blanchard, 1845	Schizodactylidae Blanchard, 1845	*Schizodactylus salweenensis* Dawwrueng, Panitvong, Mooltham, Meebenjamart & Jaitrong, 2018	Dawwrueng, P., Panitvong, N., Mooltham, K., Meebenjamart, P., & Jaitrong, W. (2018). First record of the family Schizodactylidae (Orthoptera: Ensifera) from Thailand, with the description of a new species. *Zootaxa*, *4472*(1), 60-70.
Ensifera	Stenopelmatoidea Burmeister, 1838	Anostostomatidae Saussure, 1859	*Pteranabropsis carli* (Griffini, 1911)	Crickets, K. (2001). The Biology of Wetas, King Crickets, and Their Allies.
Ensifera	Stenopelmatoidea	Anostostomatidae	*Hemideina crassidens* (Blanchard, 1851)	https://orthoptera.speciesfile.org/otus/841350/overview
Ensifera	Stenopelmatoidea	Anostostomatidae	*Deinacrida connectens* (Ander, 1939)	https://orthoptera.speciesfile.org/otus/841335/overview
Ensifera	Stenopelmatoidea	Anostostomatidae	*Cratomelus armatus* Blanchard, 1851	https://orthoptera.speciesfile.org/otus/840994/overview

Ensifera	Stenopelmatoidea	Gryllacrididae Blanchard, 1845	*Hugelgryllacris tchancha* (Hugel, 2009)	Cadena-Castañeda, O. J. (2019). A proposal towards classification of the Raspy Crickets (Orthoptera: Stenopelmatoidea: Gryllacrididae) with zoogeographical comments: An initial contribution to the higher classification of the Gryllacridines. *Zootaxa*, *4605*(1), 1-100. 10.11646/zootaxa.4605.1.1
Ensifera	Stenopelmatoidea	Gryllacrididae	*Hyalogryllacris gemina gemina* (Brunner von Wattenwyl, 1888)	https://orthoptera.speciesfile.org/otus/840487/overview
Ensifera	Stenopelmatoidea	Gryllacrididae	*Ametrus tibialis* Brunner von Wattenwyl, 1888	https://orthoptera.speciesfile.org/otus/839614/overview
Ensifera	Stenopelmatoidea	Gryllacrididae	*Camptonotus carolinensis* (Gerstaecker, 1860)	https://orthoptera.speciesfile.org/otus/839905/overview
Ensifera	Stenopelmatoidea	Stenopelmatidae Burmeister, 1838	*Sia bugajus* Gorochov, 2020	Gorochov, A. V. (2020). The families Stenopelmatidae and Anostostomatidae (Orthoptera). 1. Higher classification, new and little known taxa. *Entomological Review*, *100*, 1106-1151. https://doi.org/10.1134/S0013873820080084
Ensifera	Stenopelmatoidea	Stenopelmatidae	*Ammopelmatus irregularis* (Brunner von Wattenwyl, 1888)	https://orthoptera.speciesfile.org/otus/841453/overview
Ensifera	Tettigonioidea Krauss, 1902	Tettigoniidae Krauss, 1902	*Tettigonia viridissima* (Linnaeus, 1758)	LIB specimen ZMH71558 (Supplementary figure 4); https://orthoptera.speciesfile.org/otus/805907/overview
Ensifera	Tettigonioidea	Tettigoniidae	*Decticus verrucivorus* (Linnaeus, 1758)	https://orthoptera.speciesfile.org/otus/849730/overview

Ensifera	Tettigonioidea	Tettigoniidae	*Saga pedo* (Pallas, 1771)	https://orthoptera.speciesfile.org/otus/804627/overview
Ensifera	Tettigonioidea	Tettigoniidae	*Phaneroptera nigroantennata* Brunner von Wattenwyl, 1878	https://orthoptera.speciesfile.org/otus/848741/overview
Ensifera	Tettigonioidea	Tettigoniidae	*Pseudophyllus hercules* (Karny, 1923)	https://orthoptera.speciesfile.org/otus/803307/overview
Caelifera Ander, 1936	Acridoidea MacLeay, 1821	Acrididae MacLeay, 1821	*Chorthippus albomarginatus* (De Geer, 1773)	LIB specimen ZMH826245 (supplementary figure 5); https://orthoptera.speciesfile.org/otus/812450/overview
Caelifera	Acridoidea	Acrididae	*Calliptamus italicus italicus* (Linnaeus, 1758)	https://orthoptera.speciesfile.org/otus/819657/overview
Caelifera	Acridoidea	Acrididae	*Anacridium aegyptium* (Linnaeus, 1764)	https://orthoptera.speciesfile.org/otus/819169/overview
Caelifera	Acridoidea	Acrididae	*Hieroglyphus concolor* (Walker, 1870)	https://orthoptera.speciesfile.org/otus/819729/overview
Caelifera	Acridoidea	Acrididae	*Paulinia acuminata* (De Geer, 1773)	https://orthoptera.speciesfile.org/otus/814186/overview
Caelifera	Acridoidea	Dericorythidae Jacobson and Bianchi, 1905	*Dericorys millierei* Bonnet and Finot, 1884	LIB specimen ZMH862113 (supplementary figure 6); https://orthoptera.speciesfile.org/otus/825041/overview
Caelifera	Acridoidea	Dericorythidae	*Bienkoa fedtshenkoi ornata* (Ramme, 1931)	https://orthoptera.speciesfile.org/otus/825281/overview
Caelifera	Acridoidea	Dericorythidae	*Conophymacris chinensis* Willemse, 1933	https://orthoptera.speciesfile.org/otus/825091/overview
Caelifera	Acridoidea	Lathiceridae Dirsh, 1954	*Lathicerus cimex* Saussure, 1888	https://orthoptera.speciesfile.org/otus/824907/overview
Caelifera	Acridoidea	Lentulidae Dirsh, 1956	*Lentula callani* Dirsh, 1956	https://orthoptera.speciesfile.org/otus/822803/overview
Caelifera	Acridoidea	Lentulidae	*Lithidiopsis bushmanicum* (Dirsh, 1956)	https://orthoptera.speciesfile.org/otus/825010/overview
Caelifera	Acridoidea	Lentulidae	*Afrotettix fursti* Brown, 1970	https://orthoptera.speciesfile.org/otus/822864/overview

Caelifera	Acridoidea	Lentulidae	*Leatettix denticornis* (Brown, 1970)	https://orthoptera.speciesfile.org/otus/822888/overview
Caelifera	Acridoidea	Lithidiidae Dirsh, 1961	*Eneremius desertorus* (Brown, 1962)	https://orthoptera.speciesfile.org/otus/824992/overview
Caelifera	Acridoidea	Ommexechidae Bolívar, 1884	*Descampsacris serrulata* (Thunberg, 1824)	LIB specimen ZMH862112 (supplementary figure 6); https://orthoptera.speciesfile.org/otus/822617/overview
Caelifera	Acridoidea	Ommexechidae	*Aucacris bullocki* Rehn, 1943	https://orthoptera.speciesfile.org/otus/822590/overview
Caelifera	Acridoidea	Pamphagidae Burmeister, 1840	*Pamphagus marmoratus* Burmeister, 1838	LIB specimen ZMH862110 (supplementary figure 7); https://orthoptera.speciesfile.org/otus/824074/overview
Caelifera	Acridoidea	Pamphagidae	*Lobosceliana femoralis* (Walker, 1870)	https://orthoptera.speciesfile.org/otus/824494/overview
Caelifera	Acridoidea	Pamphagidae	*Prionotropis hystrix* (Germar, 1817)	https://orthoptera.speciesfile.org/otus/824844/overview
Caelifera	Acridoidea	Pamphagidae	*Eunapiodes granosus* (Stål, 1876)	https://orthoptera.speciesfile.org/otus/823969/overview
Caelifera	Acridoidea	Pamphagodidae Bolívar, 1884	*Charilaus carinatus* Stål, 1875	https://orthoptera.speciesfile.org/otus/825304/overview
Caelifera	Acridoidea	Pyrgacrididae Kevan, 1974	*Pyrgacris descampsi* Kevan, 1976	https://orthoptera.speciesfile.org/otus/822584/overview
Caelifera	Acridoidea	Romaleidae Pictet and Saussure, 1887	*Procolpia emarginata* (Serville, 1831)	LIB specimen ZMH862115 (supplementary figure 8)
Caelifera	Acridoidea	Romaleidae	*Tropidacris collaris* (Stoll, 1813)	https://orthoptera.speciesfile.org/otus/823474/overview
Caelifera	Acridoidea	Romaleidae	*Romalea reticulata* (Fabricius, 1781)	https://orthoptera.speciesfile.org/otus/823229/overview; https://www.inaturalist.org/taxa/1501182-Romalea-reticulata
Caelifera	Acridoidea	Romaleidae	*Titanacris albipes* (De Geer, 1773)	https://orthoptera.speciesfile.org/otus/823459/overview

Caelifera	Acridoidea	Tristiridae Rehn, 1906	*Bufonacris bruchii* Brancsik, 1901	https://orthoptera.speciesfile.org/otus/824933/overview
Caelifera	Tetrigoidea Rambur, 1838	Tetrigidae Rambur, 1838	*Tetrix subulata* (Linnaeus, 1758)	LIB specimens ZMH862117 and ZMH862118 (supplementary figure 9); https://orthoptera.speciesfile.org/otus/809090/overview
Caelifera	Tetrigoidea	Tetrigidae	*Discotettix belzebuth* (Serville, 1838)	https://orthoptera.speciesfile.org/otus/808158/overview
Caelifera	Tetrigoidea	Tetrigidae	*Tripetalocera ferruginea* Westwood, 1834	https://orthoptera.speciesfile.org/otus/809541/overview
Caelifera	Tetrigoidea	Tetrigidae	*Bufonides antennatus* Bolívar, 1898	https://orthoptera.speciesfile.org/otus/806600/overview
Caelifera	Tetrigoidea	Tetrigidae	*Phelene reinschmidti* Kasalo et al., 2024	Kasalo, N., Husemann, M., van de Kamp, T., & Skejo, J. (2024). Description of *Phelene reinschmidti* from Ecuador with notes on the subfamily Lophotettiginae (Orthoptera, Tetrigidae). *Evolutionary Systematics*, *8*, 119-125.
Caelifera	Eumastacoidea Burr, 1899	Chorotypidae Stål, 1873	*Paleochina duvergeri* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020	Schubnel, T., Desutter-Grandcolas, L., Garrouste, R., Hervet, S., & Nel, A. (2020). Paleocene of Menat Formation, France, reveals an extraordinary diversity of orthopterans and the last known survivor of a Mesozoic Elcanidae. *Acta Palaeontologica Polonica*, *65*(2). doi.org/10.4202/app.00676.2019
Caelifera	Eumastacoidea	Chorotypidae	*Erianthus dohrni* Bolívar, 1914	https://orthoptera.speciesfile.org/otus/825453/overview
Caelifera	Eumastacoidea	Chorotypidae	*Adrapetes serraticrus* Karsch, 1889	https://orthoptera.speciesfile.org/otus/825535/overview
Caelifera	Eumastacoidea	Chorotypidae	*Chorotypus fenestratus* Serville, 1838	https://orthoptera.speciesfile.org/otus/825350/overview

Caelifera	Eumastacoidea	Episactidae Burr, 1899	*Lethus nicaraguae* Descamps, 1974	Rowell, C. H. F., & Perez-Gelabert, D. E. (2006). The status of the Espagnolinae (Rehn 1948) and other subfamilies of the Episactidae (Descamps 1973)(Eumastacoidea, Caelifera, Orthoptera), with description of two new genera, *Paralethus* and *Neibamastax*. *Journal of Orthoptera Research*, *15*(2), 191-240. https://doi.org/10.1665/1082-6467(2006)15[191:TSOTER]2.0.CO;2
Caelifera	Eumastacoidea	Episactidae	*Teicophrys strigilecula* Rehn and Rehn, 1939	https://orthoptera.speciesfile.org/otus/825707/overview
Caelifera	Eumastacoidea	Eumastacidae Burr, 1899	*Helicomastax mnioides* Rowell and Bentos-Pereira, 2001	Rowell, C. H. F., & Bentos-Pereira, A. (2001). *Helicomastax*, a new genus of Central American eumastacid grasshoppers. *Journal of Orthoptera Research*, *10*(2), 255-262. https://doi.org/10.1665/1082-6467(2001)010[0255:HANGOC]2.0.CO;2
Caelifera	Eumastacoidea	Eumastacidae	*Psychomastax psylla* Rehn and Hebard, 1918	https://orthoptera.speciesfile.org/otus/826787/overview
Caelifera	Eumastacoidea	Eumastacidae	*Morsea californica* Scudder, 1898	https://orthoptera.speciesfile.org/otus/826771/overview
Caelifera	Eumastacoidea	Eumastacidae	*Eumastax tenuis* (Perty, 1832)	https://orthoptera.speciesfile.org/otus/826649/overview
Caelifera	Eumastacoidea	Euschmidtiidae Rehn, 1948	*Euschmidtia cruciformis* (Bolívar, 1895)	https://orthoptera.speciesfile.org/otus/825755/overview
Caelifera	Eumastacoidea	Euschmidtiidae	*Apteropeoedes nigroplagiatus* Bolívar, 1903	https://orthoptera.speciesfile.org/otus/825857/overview
Caelifera	Eumastacoidea	Euschmidtiidae	*Macromastax infernalis* Karsch, 1889	https://orthoptera.speciesfile.org/otus/825833/overview
Caelifera	Eumastacoidea	Euschmidtiidae	*Symbellia nigromaculata* Bruner, 1910	https://orthoptera.speciesfile.org/otus/826017/overview

Caelifera	Eumastacoidea	Mastacideidae Rehn, 1948	*Mastacides pupaeformis* Bolívar, 1899	https://orthoptera.speciesfile.org/otus/825334/overview
Caelifera	Eumastacoidea	Morabidae Rehn, 1948	*Vandiemenella viatica* (Erichson, 1842)	LIB specimen ZMH862119 (supplementary figure 7); https://orthoptera.speciesfile.org/otus/826502/overview
Caelifera	Eumastacoidea	Morabidae	*Callitala major* Sjöstedt, 1921	https://orthoptera.speciesfile.org/otus/826432/overview
Caelifera	Eumastacoidea	Morabidae	*Biroella bilobulata* Bolívar, 1925	https://orthoptera.speciesfile.org/otus/826576/overview
Caelifera	Eumastacoidea	Thericleidae Burr, 1899	*Afromastax zebra zebra* (Gerstaecker, 1889)	LIB specimen ZMH862120 (supplementary figure 10); https://orthoptera.speciesfile.org/otus/826161/overview
Caelifera	Eumastacoidea	Thericleidae	*Thericles obtusifrons* Stål, 1875	https://orthoptera.speciesfile.org/otus/826258/overview
Caelifera	Eumastacoidea	Thericleidae	*Plagiotriptus carli* (Bolívar, 1914)	https://orthoptera.speciesfile.org/otus/826104/overview
Caelifera	Eumastacoidea	Thericleidae	*Barythericles pumilus* (Karny, 1910)	https://orthoptera.speciesfile.org/otus/826237/overview
Caelifera	Locustopsoidea Handlirsch, 1906	Locustopsidae Handlirsch, 1906	*Locustopsis rhytofemoralis* Gu, Yue, Shi, Tian & Ren, 2016	Gu, J. J., Yue, Y., Shi, F., Tian, H., & Ren, D. (2016). First Jurassic grasshopper (Insecta, Caelifera) from China. *Zootaxa*, *4169*(2), 377-380. https://doi.org/10.11646/zootaxa.4169.2.9
Caelifera	Locustopsoidea	Locustopsidae	*Araipelocusta imperatrix* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025	Schall, O. K. O., Lima, D., Heads, S. W., Pinheiro, A. P., Kotthoff, U. & Husemann, M. (submitted). New species of Cretaceous Locustopsidae (Orthoptera: Caelifera) from the Crato Formation of Brail and a taxonomic revision of the family. *Zootaxa*. Chapter 4, this dissertation.

Caelifera	Locustopsoidea	Locustopsidae	*Triassolocusta leptoptera* Tillyard, 1922	Tillyard, R.J. (1922) Mesozoic Insects of Queensland. No. 9. Orthoptera and additions to the Protorthoptera, Odonata, Hemiptera and Planipennia. *Proceedings of the Linnean Society of New South Wales*, 47, 447–470.
Caelifera	Pneumoroidea Thunberg, 1810	Pneumoridae Thunberg, 1810	*Bullacris discolor* (Thunberg, 1810)	LIB specimen ZMH862108 (supplementary figure 11); https://orthoptera.speciesfile.org/otus/828683/overview
Caelifera	Proscopioidea Serville, 1838	Proscopiidae Serville, 1838	*Eoproscopia martilli* Heads, 2008	Heads, S. W. (2008). The first fossil Proscopiidae (Insecta, Orthoptera, Eumastacoidea) with comments on the historical biogeography and evolution of the family. *Palaeontology*, *51*(2), 499-507. https://doi.org/10.1111/j.1475-4983.2008.00756.x
Caelifera	Proscopioidea	Proscopiidae	*Pseudoproscopia scabra* (Klug, 1820)	https://orthoptera.speciesfile.org/otus/827265/overview
Caelifera	Proscopioidea	Proscopiidae	*Proscopia gigantea* Klug, 1820	https://orthoptera.speciesfile.org/otus/827235/overview
Caelifera	Proscopioidea	Proscopiidae	*Astroma plicatum* Liana, 1980	https://orthoptera.speciesfile.org/otus/827299/overview
Caelifera	Proscopioidea	Proscopiidae	*Bolidorhynchus insignis* (Hebard, 1931)	https://orthoptera.speciesfile.org/otus/827315/overview
Caelifera	Pyrgomorphoidea Brunner von Wattenwyl, 1874	Pyrgomorphidae Brunner von Wattenwyl, 1874	*Chrotogonus hemipterus* Schaum, 1853	LIB specimen ZMH862111 (supplementary figure 12); https://orthoptera.speciesfile.org/otus/827839/overview
Caelifera	Pyrgomorphoidea	Pyrgomorphidae	*Phymateus morbillosus* (Linnaeus, 1758)	https://orthoptera.speciesfile.org/otus/828190/overview
Caelifera	Pyrgomorphoidea	Pyrgomorphidae	*Pyrgomorpha conica* (Olivier, 1791)	https://orthoptera.speciesfile.org/otus/828398/overview

Caelifera	Pyrgomorphoidea	Pyrgomorphidae	*Ichthyotettix mexicanus* (Saussure, 1859)	https://orthoptera.speciesfile.org/otus/827686/overview
Caelifera	Tanaoceroidea Rehn, 1948	Tanaoceridae Rehn, 1948	*Tanaocerus koebelei* Bruner, 1906	https://orthoptera.speciesfile.org/otus/828674/overview
Caelifera	Trigonopterygoidea Walker, 1870	Trigonopterygidae Walker, 1870	*Trigonopteryx hopei* (Westwood, 1841)	LIB specimen ZMH862109 (supplementary figure 9); https://orthoptera.speciesfile.org/otus/827379/overview
Caelifera	Trigonopterygoidea	Trigonopterygidae	*Xyronotus aztecus* Saussure, 1884	https://orthoptera.speciesfile.org/otus/827347/overview
Caelifera	Tridactyloidea Brullé, 1835	Cylindrachetidae Giglio-Tos, 1914	*Cylindraustralia kochii* (Saussure, 1877)	LIB-specimen ZMH862116 (supplementary figure 12)
Caelifera	Tridactyloidea	Ripipterygidae Ander, 1939	*Magnidactylus robustus* Xu, Fang & Jarzembowski, 2020	Xu, C., Fang, Y., & Jarzembowski, E. A. (2020). A new pygmy mole cricket (Orthoptera: Tridactyloidea: Tridactylidae) from mid-Cretaceous Burmese amber. *Cretaceous Research*, *111*, 104371. https://doi.org/10.1016/j.cretres.2020.104371
Caelifera	Tridactyloidea	Ripipterygidae	*Ripipteryx gorgonaensis* Baena-Bejarano and Heads, 2015	Baena-Bejarano, N., & Heads, S. W. (2015). Three new species of the genus *Ripipteryx* from Colombia (Orthoptera, Ripipterygidae). *ZooKeys*, (502), 129. 10.3897/zookeys.502.8871
Caelifera	Tridactyloidea	Ripipterygidae	*Mirhipipteryx pulicaria* (Saussure, 1896)	Baena-Bejarano, N., Heads, S. W., & Taylor, S. J. (2018). Comments on the neglected nymphs of mud crickets in the genus Mirhipipteryx (Caelifera: Tridactyloidea: Ripipterygidae). *Zootaxa*, *4486*(2), 180-188. https://doi.org/10.11646/zootaxa.4486.2.7
Caelifera	Tridactyloidea	Tridactylidae	*Amberotridactylus cheni* Du, Xu & Zhang, 2022	Du, X., Xu, C., & Zhang, L. (2022). Two new pygmy mole crickets from mid-Cretaceous Kachin amber of northern

				Myanmar (Orthoptera: Tridactyloidea: Tridactylidae). *Cretaceous Research*, *129*, 105002. https://doi.org/10.1016/j.cretres.2021.105002
Caelifera	Tridactyloidea	Tridactylidae	*Ellipes deyrupi* Woo, 2021	Woo, B. (2021). A new species of pygmy mole cricket (Orthoptera: Tridactylidae) from the Lake Wales ridge of Florida and new records of *Ellipes eisneri* from the northern Brooksville ridge. *Journal of Orthoptera Research*, *30*(2), 131-143. https://doi.org/10.3897/jor.30.65603
Caelifera	Tridactyloidea	Tridactylidae	*Cascogryllus setosus* Du, Xu & Zhang, 2022	Du, X., Xu, C., & Zhang, L. (2022). Two new pygmy mole crickets from mid-Cretaceous Kachin amber of northern Myanmar (Orthoptera: Tridactyloidea: Tridactylidae). *Cretaceous Research*, *129*, 105002. https://doi.org/10.1016/j.cretres.2021.105002
Caelifera	Tridactyloidea	Tridactylidae	*Dentridactylus quadratus* Baena-Bejarano and Heads, 2018	Baena-Bejarano, N., & Heads, S. W. (2018). First records of Dentridactylinae (Orthoptera: Tridactylidae) from Colombia, with description of two new species of *Dentridactylus* Günther. *Zootaxa*, *4402*(3), 575-584.
Caelifera	Tridactyloidea	Tridactylidae	*Xya sichuanensis* Cao, Shi & Yin, 2018	Cao, C. Q., Shi, J. P., & Yin, Z. (2018). A new species of the genus Xya Latreille, 1809 from China (Orthoptra, Tridctyloidea, Tridactylidae). *Zootaxa*, *4413*(2), 397-400. https://doi.org/10.11646/zootaxa.4413.2.13

Blattodea Brunner von Wattenwyl, 1882 (order)	Corydioidea Saussure, 1864	Corydiidae Saussure and Zehntner, 1893	*Fragosublatta pectinata* Chen, Xiao, Liang, Shih & Ren, 2021	Chen, G., Xiao, L., Liang, J., Shih, C., & Ren, D. (2021). A new cockroach (Blattodea, Corydiidae) with pectinate antennae from mid-Cretaceous Burmese amber. *ZooKeys*, *1060*, 155. 10.3897/zookeys.1060.67216
Phasmatodea Jacobson and Bianchi, 1902 (order)	Pseudophasmatoidea Rehn, 1904	Agathemeridae Engel and Bradler, 2024	*Agathemera crassa* (Blanchard, 1851)	https://phasmida.speciesfile.org/otus/852053/overview

Supplementary material 4: Nexus file of hybrid-reconstructed matrix (used in the phylogenetic analyses corresponding to Figs. 1-4) (compare supplementary material 2 for translation of the code).

Nexus file of the hybrid-reconstructed matrix (phylogenetic tree in Fig. 3 and 4).

#NEXUS

BEGIN DATA;

DIMENSIONS NTAX=134 NCHAR=50;

FORMAT SYMBOLS= " 0 1 2 3 4 5 6 7 N "

;

MATRIX

Fragosublatta_pectinata 0 0 2 N N 0 6 0 N 0
0 0 0 N 1 1 N 0 0 0 1 N
1 N 0 0 0 0 0 3 0 0 0 N
1 N 2 N N N 0 0 0 0 1 1
1 1 1 3

Proelcana_kukalovae 1 1 1 1 1 0 1 0 0 1 0
0 0 N 1 0 0 0 0 0 0 1 0
0 0 0 N 0 0 0 0 0 1 0 0
1 4 0 0 1 2 0 1 1 2 1 0
1 1 N

Meselcana_madygenica 1 1 1 1 1 0 2 0 0 1
1 1 0 N 1 1 0 0 0 0 0 1
0 0 0 0 N 0 0 0 0 1 0 0
2 0 4 0 N N 1 0 1 1 2 N
1 1 1 N

Panorpidium_spica 1 1 1 1 1 0 0 0 0 1 0
1 0 N 1 1 0 0 0 0 0 1 0
0 0 0 N 0 0 0 0 0 0 0 2
3 4 1 3 N 1 0 1 1 2 2 1
0 1 N

Sinoelcana_minuta 1 1 1 1 1 0 0 0 0 1 0
1 0 N 1 1 0 0 0 0 0 1 0
0 0 0 N 0 0 0 0 0 0 0 2
1 3 0 0 2 1 0 1 1 2 0 1
1 1 N

Pseudoprobaisselcana_oculata 1 1 1 1 1 0 0 0 0 1
0 1 0 N 1 1 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 0 0 0

2	3	4	0	2	N	2	0	1	1	2	2
1	1	1	N								
Paraxelcana_zhengi	1	1	1	1	1	0	0	0	0	1	0
1	0	N	1	1	0	0	0	0	0	1	0
0	0	0	N	0	0	1	0	1	0	0	2
2	4	1	2	N	1	0	1	1	2	0	1
1	1	4									
Notocearagryllus_britannicus	1	1	1	1	0	0	6	0	N	0	
0	0	1	2	1	1	0	0	0	1	0	1
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	2	1	0	0	1	1	1	2
1	3	2	5								
Anglogryllus_lyristes	1	1	1	1	0	0	6	0	N	0	0
0	1	2	1	1	0	0	0	1	0	1	0
0	0	0	0	0	0	0	0	1	1	1	0
0	2	0	2	1	0	0	1	1	1	2	1
3	2	5									
Antillobinthus_inexpectatus	1	1	1	1	1	0	1	0	N	0	
0	0	1	0	1	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
0	0	1	0	2	1	1	1	1	1	2	2
1	3	2	5								
Acheta_domesticus	1	1	1	1	1	0	1	0	N	0	0
0	1	0	1	1	0	0	0	1	0	1	0
0	0	0	0	0	0	0	0	1	1	1	0
0	2	0	0	1	0	0	1	0	1	2	2
2	2	5									
Spinogryllus_meghalayanus	1	1	1	1	1	0	1	0	N	0	
0	0	1	0	1	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	1	2	2	1	1	1	1	2
1	2	2	5								
Acanthoplistus_acutus	1	1	2	0	1	0	1	0	N	0	
0	0	1	0	1	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	3	2	0	0	1	1	1	1
1	2	1	3								
Gryllus_campestris	1	1	2	1	1	0	1	0	N	0	0
0	1	0	1	1	0	0	0	1	0	1	0
0	0	0	0	0	0	0	0	1	1	1	0
0	2	0	2	2	0	0	1	1	0	3	1
2	1	5									
Crassicorpus_maculatus	1	1	1	1	1	0	1	0	N	0	
0	0	1	0	1	1	0	1	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	2	1	0	0	1	1	1	3
1	2	2	5								
Picogryllus_carentonensis	1	1	0	1	1	0	5	0	0	0	
0	0	1	0	1	1	0	0	0	1	0	1
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	2	1	0	0	1	1	1	3
1	2	2	5								
Oecanthus_pellucens	1	1	1	1	1	0	1	0	N	0	0
0	1	0	1	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	1	1	1	0
0	2	0	4	1	0	0	0	1	1	2	0
2	1	5									
Neoxabea_bipunctata	1	1	1	1	1	0	1	0	N	0	0
0	1	0	1	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	1	1	1	0
0	2	0	2	0	0	0	0	0	0	0	0
1	1	5									
Veredatrypa_rosai	1	1	1	0	1	0	0	0	N	0	0
0	1	0	1	1	0	0	0	1	0	1	0
0	0	0	0	0	0	0	0	1	1	1	1

2	2	0	3	0	0	0	1	1	1	2	0
1	1	5									
Brevizacla_molisae	1	1	1	1	1	0	1	0	N	0	0
0	1	0	1	1	1	1	0	0	0	1	0
0	0	0	0	0	0	0	0	1	1	1	0
0	0	0	2	1	2	2	1	1	1	2	1
3	3	5									
Seselia_coccofessei	1	1	1	1	1	0	1	0	N	0	0
0	0	0	1	1	0	0	0	0	0	1	0
0	0	0	2	0	0	0	0	1	1	1	0
0	1	0	2	1	2	1	1	1	1	2	1
3	3	5									
Phalangacris_ferlegro		1	1	1	1	1	0	0	0	N	0
0	0	0	0	1	1	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
0	0	1	0	2	2	2	1	0	1	1	2
1	3	3	5								
Araneagryllus_dylani	1	1	1	1	1	0	1	0	N	0	0
0	1	0	0	1	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	1	1	1	0
0	2	0	2	1	2	0	1	1	1	2	0
3	1	5									
Phalangopsis_arenita	1	1	1	1	1	0	1	0	N	0	0
0	1	0	1	1	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	1	1	1	0
0	1	0	2	1	2	1	0	1	2	3	0
3	2	5									
Changiola_perakensis		1	1	1	1	1	0	1	0	N	0
0	0	1	0	1	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	4	1	1	0	1	1	0	1
1	3	2	5								
Birmaninemobius_hirsutus		1	1	1	1	1	0	1	0	N	0
0	0	1	1	1	1	1	1	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
0	0	1	0	2	1	1	1	1	1	2	3
1	3	2	5								
Fijixipha_atalos	1	1	1	1	1	0	1	0	N	0	0
0	1	1	1	1	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	1	1	1	0
0	2	0	2	1	1	0	1	1	2	2	1
1	1	5									
Trigonidium_cicindeloides		1	1	1	1	1	0	1	0	N	0
0	0	0	0	1	1	1	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	0	1	1	1	0	1	2	2
1	1	1	5								
Paranemobius_vicinus		1	1	1	1	1	0	1	0	N	0
0	0	1	0	1	1	1	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
0	0	1	0	2	2	2	1	1	1	2	3
1	3	3	5								
Phyllopalpus_pulchellus		1	1	1	1	1	0	1	0	N	0
0	0	1	0	1	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	1	0	1	0	0	1	2	2
1	1	1	5								
Gryllotalpa_nitidula	1	1	0	1	1	0	1	0	N	0	0
0	0	1	1	0	0	0	1	1	0	1	0
0	0	0	0	0	0	0	0	1	1	1	0
0	1	1	3	0	0	0	1	0	0	1	1
3	1	4									
Scapteriscus_headsi	1	1	2	0	1	0	1	0	N	0	0
0	0	1	1	0	0	0	1	1	0	1	0
0	0	0	0	0	1	0	0	1	1	1	0

0	2	1	4	1	0	0	1	0	0	0	1
1	1	4									
Gryllotalpella_macilenta		1	1	1	0	1	0	1	0	N	0
0	0	0	1	1	0	0	0	1	1	0	1
0	0	0	0	0	0	1	0	0	1	1	1
0	0	1	0	2	1	0	0	1	0	1	1
3	2	1	5								
Camponophilus_irmi	1	1	2	1	1	0	1	0	N	0	0
0	0	1	0	1	0	0	0	1	0	0	1
0	0	0	0	0	0	0	0	1	1	1	0
0	1	1	2	1	1	0	1	1	1	1	2
3	1	4									
Myrmecophilus_acervorum		1	1	2	1	1	0	1	0	N	0
0	0	0	1	0	1	0	0	0	1	0	0
1	0	0	0	0	0	0	0	0	1	1	1
0	0	1	1	0	2	1	0	1	0	1	1
2	3	2	4								
Allaboilus_gigantus	1	1	1	1	0	0	4	0	1	0	0
0	0	N	1	0	0	0	0	0	1	1	0
0	0	0	0	0	1	0	0	1	1	1	1
3	4	0	3	1	0	0	1	0	0	0	1
1	1	4									
Cyphoderris_buckelli	1	1	1	1	0	0	3	0	2	0	0
0	0	N	1	0	0	0	0	1	0	1	0
0	0	0	0	0	0	0	0	1	1	1	1
3	1	1	4	2	0	1	0	0	0	0	1
1	1	4									
Parahagla_sibirica	1	1	1	1	0	0	2	0	1	0	0
0	0	N	1	0	0	0	0	0	1	1	0
0	0	0	0	0	0	0	0	1	1	0	2
3	4	0	3	2	0	0	1	0	0	1	1
1	1	4									
Vitimoilus_ovatus	1	1	1	1	0	0	3	0	2	0	0
0	0	N	1	0	0	0	0	0	1	1	0
0	0	0	0	0	0	0	0	1	1	1	2
1	4	0	3	2	0	0	1	0	0	0	1
1	1	4									
Archaboilus_polyneurus		1	1	1	1	0	0	3	0	2	0
0	0	0	N	1	0	0	0	0	0	1	1
0	0	0	0	0	0	0	0	0	1	0	1
1	0	4	0	3	2	0	0	1	0	0	0
1	1	1	4								
Rhaphidophora_loricata		1	1	1	1	0	0	2	0	2	0
0	0	0	N	0	0	0	0	0	0	1	1
0	0	0	0	0	0	0	0	0	1	1	1
1	1	4	1	2	2	2	0	1	1	0	3
0	1	1	5								
Stonychophora_fulva_fulva		1	1	1	1	0	0	2	0	2	0
0	0	0	N	0	1	0	0	0	0	1	1
0	0	0	0	0	0	0	0	0	1	1	1
1	1	4	1	3	2	2	0	1	1	0	2
1	1	2	5								
Ceuthophilus_lapidicola		1	1	1	1	0	0	2	0	2	0
0	0	0	N	0	0	0	0	0	0	1	1
0	0	0	0	0	0	0	0	0	1	1	1
1	1	4	0	2	1	1	0	1	1	1	2
1	1	1	5								
Pachyrhamma_edwardsii		1	1	1	1	0	0	2	0	2	0
0	0	0	N	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
1	1	4	0	3	1	2	0	0	1	0	3
1	1	1	5								
Schizodactylus_salweenensis		1	1	1	0	0	0	2	0	0	0
0	0	0	N	1	1	0	0	1	0	1	1
0	0	0	0	0	0	1	0	1	1	1	1

1 1 4 0 3 2 1 0 1 1 0 2
1 1 1 5

Pteranabropsis_carli 1 1 1 1 0 0 1 0 2 0 0
0 0 N 1 0 0 0 0 0 1 1 0
0 0 0 0 0 0 0 0 1 1 1 1
1 4 0 3 2 2 0 0 1 0 2 0
1 1 5

Hemideina_crassidens 1 1 1 1 0 0 2 0 2 0
0 0 0 N 0 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 1 1 1
1 1 4 0 4 2 0 0 0 0 1 1
0 1 0 5

Deinacrida_connectens 1 1 1 1 0 0 2 0 2 0
0 0 0 N 0 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 1 1 1
1 1 4 0 4 1 0 0 0 0 0 1
1 1 0 5

Cratomelus_armatus 1 1 1 1 0 0 2 0 2 0 0
0 0 N 1 0 0 0 0 1 1 1 0
0 0 0 0 0 0 0 0 1 1 1 1
1 1 1 4 2 1 1 1 1 0 1 1
2 1 5

Hugelgryllacris_tchancha 1 1 1 1 0 0 0 0 2 0
0 0 0 N 1 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 1 1 1
1 0 4 0 4 2 0 0 1 1 0 1
1 1 0 5

Hyalogryllacris_gemina_gemina 1 1 1 1 0 0 2 0 2 0
0 0 0 N 1 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 1 1 1
0 1 4 0 3 1 0 0 1 1 0 1
1 0 0 5

Ametrus_tibialis 1 1 1 1 0 0 2 0 2 0 0
0 0 N 1 0 0 0 0 0 1 1 0
0 0 0 0 0 0 0 0 1 1 1 1
1 1 0 2 2 1 1 0 0 0 0 0
2 0 5

Camptonotus_carolinensis 1 1 1 2 0 0 2 0 2 0
0 0 0 N 0 1 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 1 1 1
1 1 4 0 3 2 1 0 1 1 0 0
1 1 0 5

Sia_bugajus 1 1 1 1 0 0 2 0 1 0 0
0 0 N 1 0 0 0 1 1 1 1 0
0 0 0 0 0 0 0 0 1 1 1 1
1 2 0 2 1 0 0 1 1 0 1 1
1 1 5

Ammopelmatus_irregularis 1 1 2 0 0 0 2 0 2 0
0 0 0 N 0 0 0 0 1 0 1 1
0 0 0 0 0 0 0 0 0 1 1 1
1 1 4 0 4 2 0 0 0 0 0 1
2 1 1 4

Tettigonia_viridissima 1 1 1 2 0 0 2 0 2 0
0 0 0 N 1 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 1 0 0
0 1 3 0 3 2 2 0 1 1 0 0
0 0 0 5

Decticus_verrucivorus 1 1 2 2 0 0 0 0 0 1 0
0 0 0 N 1 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 1 0 0
0 0 3 0 2 2 2 0 1 1 0 2
0 0 0 5

Saga_pedo 1 1 2 2 0 0 0 0 2 0 0
0 0 N 1 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 0 0 0

0 1 0 4 1 1 0 0 0 0 0 0
0 0 4

Phaneroptera_nigroantennata 1 1 1 2 0 0 0 0 2 0
0 0 0 N 1 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 0 0
0 0 4 0 2 1 2 0 0 1 0 0
0 0 0 5

Pseudophyllus_hercules 1 1 1 2 0 0 0 0 1 0
0 0 0 N 1 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 1
0 0 4 0 2 1 1 0 1 0 0 0
0 0 0 5

Chorthippus_albomarginatus 1 1 0 0 0 0 0 0 4 0
0 0 0 N 1 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 0
1 0 2 0 2 1 1 0 1 1 0 1
0 0 0 2

Calliptamus_italicus_italicus 1 1 0 0 0 0 0 0 2 0
0 0 0 N 1 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 0
1 0 2 0 2 1 1 0 1 1 0 1
0 0 0 2

Anacridium_aegyptium 1 1 0 0 0 0 0 1 0 2 0
0 0 0 N 1 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 1
1 2 3 0 2 1 0 0 1 1 1 1
0 0 0 2

Hieroglyphus_concolor 1 1 0 0 0 0 0 1 0 3 0
0 0 0 N 1 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 1
1 0 2 0 3 1 0 0 1 1 1 1
0 0 0 2

Paulinia_acuminata 1 1 0 0 0 0 0 0 4 0 0
0 0 N 1 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 1 1 0
0 3 0 2 1 1 0 1 1 1 1 0
0 0 2

Dericorys_millierei 1 1 0 0 0 0 1 0 2 0 0
0 0 N 1 0 0 0 0 0 0 2 0
1 0 0 0 0 0 0 0 1 1 1 2
0 2 0 2 1 1 0 1 1 1 1 0
0 0 2

Bienkoa_fedtshenkoi_ornata 1 1 0 0 0 0 0 0 0 2 0
0 0 0 N 0 0 0 0 0 0 0 1
0 0 0 0 0 0 0 1 0 1 1 1
1 0 2 0 0 2 1 0 1 1 0 1
1 0 0 2

Conophymacris_chinensis 1 1 0 0 0 0 0 0 0 2 0
0 0 0 N 1 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 1
1 0 1 0 2 1 0 1 1 1 0 1
0 0 0 2

Lathicerus_cimex 1 1 0 0 0 0 0 0 0 2 0 0
0 0 N 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 1 1 1
0 2 0 0 2 0 0 1 1 1 2 0
0 0 0

Lentula_callani 1 1 0 0 0 0 0 0 0 2 0 0
0 0 N 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 1 1 1
0 2 0 0 1 0 0 1 1 0 2 0
0 0 2

Lithidiopsis_bushmanicum 1 1 0 0 0 0 0 0 0 2 0
0 0 0 N 0 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 1

1	0	2	0	0	1	0	0	1	1	1	1
1	0	0	2								
Afrotettix_fursti	1	1	0	0	0	0	0	0	2	0	0
0	0	N	0	0	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	1	1	1	1
0	2	0	0	1	0	0	0	1	0	1	1
0	0	1									
Leatettix_denticornis	1	1	0	0	0	0	0	0	2	0	0
0	0	N	0	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	1	1	1	1
0	2	0	0	2	1	0	1	1	1	1	0
0	0	1									
Eneremius_desertorus	1	1	0	0	0	0	0	0	2	0	
0	0	0	N	0	0	0	0	0	0	2	
0	0	0	0	0	0	0	0	0	1	1	1
1	0	2	0	0	2	1	0	1	1	1	1
0	0	0	1								
Descampsacris_serrulata	1	1	0	0	0	0	0	0	3	0	
0	0	0	N	1	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
3	1	2	0	2	1	0	0	1	1	1	1
0	0	0	1								
Aucacris_bullocki	1	1	0	0	0	0	0	0	2	0	0
0	0	N	1	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	1	1	1	1
0	1	0	3	1	0	1	1	1	1	1	1
1	0	2									
Pamphagus_marmoratus	1	1	0	0	0	0	0	0	2	0	
0	0	0	N	1	0	0	0	0	0	0	1
0	1	0	0	0	0	0	0	0	1	1	1
1	0	1	0	0	0	0	1	1	0	0	0
0	0	0	2								
Lobosceliana_femoralis	1	1	0	0	0	0	1	0	1	0	
0	0	0	N	1	0	0	0	0	0	0	1
0	1	0	0	0	0	0	0	0	1	0	1
1	1	4	1	2	1	0	0	1	1	0	0
0	0	0	1								
Prionotropis_hystrix	1	1	0	0	0	0	0	0	4	0	0
0	0	N	1	0	0	0	0	0	0	1	0
1	0	0	0	0	0	0	0	1	1	1	1
0	1	1	3	1	0	1	1	1	0	1	1
1	0	1									
Eunapiodes_granosus	1	1	0	0	0	0	0	0	2	0	
0	0	0	N	1	0	0	0	0	0	0	1
0	1	0	0	0	0	0	0	0	1	1	1
1	0	1	1	2	2	0	1	1	1	0	1
1	0	0	2								
Charilaus_carinatus	1	1	0	0	1	0	0	0	2	0	0
0	0	N	1	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	1	0	0	1
0	2	0	2	1	0	0	1	1	1	2	0
0	0	2									
Pyrgacris_descampsi	1	1	0	0	0	0	0	0	2	0	0
0	0	N	0	0	0	0	0	0	0	1	0
0	0	1	0	0	0	0	0	1	1	1	1
0	2	0	3	1	0	0	1	1	0	1	1
0	0	2									
Procolpia_emarginata	1	1	0	0	0	0	0	1	0	3	0
0	0	0	N	1	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
1	1	2	0	3	0	0	0	1	1	2	0
0	0	0	2								
Tropidacris_collaris	1	1	0	0	0	0	2	0	2	0	0
0	0	N	1	0	0	0	0	0	0	1	0
1	0	0	0	0	0	0	0	1	1	1	1

2 3 0 3 1 0 0 1 0 1 1 0
0 0 2

Romalea_reticulata 1 1 0 0 0 0 0 0 4 0 0
0 0 N 1 0 0 0 0 0 0 1 0
1 0 0 0 0 0 0 0 1 1 1 0
1 2 1 3 1 0 0 1 1 1 1 1
0 0 2

Titanacris_albipes 1 1 0 0 0 0 0 0 2 0 0
0 0 N 1 0 0 0 0 0 0 1 0
1 0 0 0 0 0 0 0 1 1 1 1
1 3 0 2 0 0 0 1 1 1 1 0
0 0 2

Bufonacris_bruchii 1 1 0 0 0 0 0 0 2 0 0
0 0 N 0 0 0 0 0 0 0 1 0
0 0 0 1 0 0 0 0 1 1 1 1
0 1 0 2 2 0 1 1 1 1 1 0
1 0 1

Tetrix_subulata 1 1 0 0 0 0 0 0 2 0 0
0 0 N 1 0 0 0 0 0 0 1 0
0 0 0 1 0 0 0 0 1 1 1 1
0 1 2 4 2 1 1 1 1 0 1 0
1 0 1

Discotettix_belzebuth 1 1 0 0 0 0 0 0 2 0 0
0 0 N 1 0 0 0 0 0 0 1 0
0 0 0 1 0 0 0 0 1 1 1 1
0 1 2 4 1 0 1 1 1 0 0 1
1 0 0

Tripetalocera_ferruginea 1 1 0 0 0 0 0 0 2 0
0 0 0 N 1 1 0 0 0 0 0 1
0 0 0 0 1 0 0 1 0 1 1 1
1 0 1 2 4 1 0 1 1 1 0 0
1 1 0 0

Bufonides_antennatus 1 1 0 0 0 0 0 0 2 0
0 0 0 N 1 0 0 0 0 0 0 1
0 0 0 0 1 0 0 0 0 1 1 1
1 0 1 2 4 2 1 1 1 1 0 0
0 1 0 1

Phelene_reinschmidti 1 1 0 0 0 0 0 0 2 0 0
0 0 N 1 0 0 0 0 0 0 1 0
1 0 0 1 0 0 0 0 1 1 1 1
0 1 2 4 2 1 1 1 1 0 0 0
1 0 1

Paleochina_duvergeri 1 1 0 0 0 0 0 0 2 1
0 0 0 N 1 0 0 0 0 0 0 2
0 0 0 0 0 0 0 0 0 1 1 1
1 1 2 0 2 1 1 0 1 1 0 2
0 0 0 1

Erianthus_dohrni 1 1 0 0 0 0 0 0 2 0 0
0 0 N 1 1 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 1 1 1
0 3 0 2 2 1 0 1 1 1 0 0
0 0 1

Adrapetes_serraticrus 1 1 0 0 0 0 0 0 2 0
0 0 0 N 0 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 1
1 0 2 0 2 1 1 1 0 1 1 2
0 0 0 1

Lethus_nicaraguae 1 1 0 0 0 0 0 0 2 0 0
0 0 N 0 1 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 1 1 1
0 2 0 1 2 2 1 1 1 1 0 0
0 0 0

Teicophrys_strigilecula 1 1 0 0 0 0 0 0 2 0
0 0 0 N 0 1 0 0 0 0 0 2
0 0 0 0 0 0 0 0 0 1 1 1

1	0	2	0	2	1	1	1	0	1	0	1
0	0	0	2								
Helicomastax_mnioides		1	1	0	0	0	0	0	0	3	0
0	0	0	N	1	1	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
0	0	2	0	2	1	2	1	0	1	2	2
0	0	0	1								
Psychomastax_psylla	1	1	0	0	0	0	0	0	2	0	0
0	0	N	0	0	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	1	1	1	1
0	2	0	2	1	1	1	1	1	0	2	0
0	0	1									
Morsea_californica	1	1	0	0	0	0	0	0	2	0	0
0	0	N	0	0	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	1	1	1	1
0	2	0	3	2	2	1	1	1	0	2	1
0	0	1									
Eumastax_tenuis	1	1	0	0	0	0	0	0	2	0	0
0	0	N	1	0	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	1	1	1	0
0	2	0	2	1	2	1	1	1	2	2	0
0	0	1									
Euschmidtia_cruciformis		1	1	0	0	0	0	0	0	2	0
0	0	0	N	1	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
1	0	1	0	0	2	1	1	1	1	0	1
1	1	0	1								
Apteropeoedes_nigroplagiatus		1	1	0	0	0	0	0	0	2	0
0	0	0	N	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
1	0	2	0	2	1	0	1	1	1	1	2
1	0	0	1								
Macromastax_infernalis		1	1	0	0	0	0	0	0	2	0
0	0	0	N	1	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
1	0	1	0	2	1	1	1	0	1	2	1
0	1	0	1								
Symbellia_nigromaculata		1	1	0	0	0	0	0	0	2	0
0	0	0	N	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1
1	0	2	0	3	1	1	1	1	1	0	1
0	0	0	1								
Mastacides_pupaeformis		1	1	0	0	0	0	0	0	2	0
0	0	0	N	1	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
1	0	0	0	2	1	1	2	1	1	1	1
0	3	1	1								
Vandiemenella_viatica		1	1	0	0	0	0	0	0	2	0
0	0	0	N	0	0	0	0	0	0	0	1
0	0	0	1	0	0	0	0	0	1	1	1
1	0	2	0	3	2	0	1	1	1	0	1
0	0	0	1								
Callitala_major	1	1	0	0	0	0	0	0	2	0	0
0	0	N	0	0	0	0	0	0	0	1	0
0	0	1	0	0	0	0	0	1	1	1	1
0	2	0	4	1	0	1	1	1	1	1	0
0	0	1									
Biroella_bilobulata	1	1	0	0	0	0	0	0	2	0	0
0	0	N	1	0	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	1	1	1	1
0	1	0	2	1	2	1	1	1	2	2	0
0	0	1									
Afromastax_zebra_zebra		1	1	0	0	0	0	0	0	2	0
0	0	0	N	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	1	1	1

1	0	2	0	0	2	1	1	0	1	0	1
0	0	0	0								
Thericles_obtusifrons	1	1	0	0	0	0	0	0	2	0	0
0	0	N	0	0	0	0	0	0	0	2	0
0	0	0	0	0	0	0	0	1	1	1	1
0	2	0	0	1	0	1	1	1	0	2	1
0	0	0									
Plagiotriptus_carli	1	1	0	0	0	0	0	0	2	0	0
0	0	N	1	0	0	0	0	0	0	1	0
1	0	0	0	0	0	0	0	1	1	1	1
0	1	1	2	2	0	1	1	1	0	2	1
1	0	0									
Barythericles_pumilus		1	1	0	0	0	0	0	0	2	0
0	0	0	N	0	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
1	0	2	0	0	2	1	1	1	1	0	2
0	0	0	1								
Locustopsis_rhytofemoralis		1	1	0	0	0	0	1	0	1	0
0	0	0	N	1	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	0	0
2	1	4	0	2	1	0	0	1	1	0	1
1	0	0	1								
Araripelocusta_imperatrix		1	1	0	0	0	0	0	0	2	1
0	0	0	N	1	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
0	2	4	0	3	1	0	0	1	1	0	1
1	0	0	1								
Triassolocusta_leptoptera		1	1	0	0	2	0	1	1	1	0
0	0	0	N	1	1	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1
2	2	4	0	2	1	0	0	1	1	0	1
1	0	0	1								
Bullacris_discolor	1	1	0	0	0	0	1	0	2	0	0
0	0	N	1	0	0	0	0	0	0	1	0
1	1	0	0	0	0	0	0	0	1	1	0
1	3	1	0	1	0	0	1	0	0	1	0
0	0	2									
Eoproscopia_martilli	0	1	0	0	0	0	0	0	2	0	0
0	0	N	1	0	0	0	0	0	0	1	0
0	0	1	0	0	0	0	0	1	1	1	1
0	2	0	4	0	0	0	1	0	0	0	0
0	0	0									
Pseudoproscopia_scabra		1	1	0	0	0	0	0	0	2	0
0	0	0	N	0	0	0	0	0	0	0	1
0	0	0	1	0	0	0	0	0	1	1	1
1	0	2	0	4	0	0	0	0	0	0	0
0	0	0	0								
Proscopia_gigantea	1	1	0	0	0	0	0	0	2	0	0
0	0	N	0	0	0	0	0	0	0	1	0
0	0	1	0	0	0	0	0	1	1	1	1
0	2	0	4	0	0	0	0	0	0	0	0
0	0	0									
Astroma_plicatum	1	1	0	0	0	0	0	0	2	0	0
0	0	N	1	0	0	0	0	0	0	1	0
0	0	1	0	0	0	0	0	1	1	1	1
0	0	1	4	1	0	2	1	0	0	0	0
0	0	0									
Chrotogonus_hemipterus		1	1	0	0	0	0	0	0	4	0
0	0	0	N	1	0	0	0	0	0	0	1
0	0	0	0	2	0	0	0	0	1	1	1
1	0	2	0	1	2	0	0	1	1	0	2
1	1	0	2								
Phymateus_morbillosus		1	1	0	0	0	0	0	0	2	0
0	0	0	N	1	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	1	1	1

1 1 3 0 2 1 0 0 1 0 0 2
0 0 0 2

Pyrgomorpha_conica 1 1 0 0 0 0 0 0 2 0 0
0 0 N 1 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 1 1 0
0 2 0 3 1 0 0 1 1 0 2 0
0 0 1

Ichthyotettix_mexicanus 1 1 0 0 0 0 0 0 2 0
0 0 0 N 0 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 1 1 1
1 0 2 0 2 1 0 0 1 1 0 1
0 0 0 1

Tanaocerus_koebelei 1 1 1 0 0 0 0 0 2 0 0
0 0 N 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 1 1 1
0 2 0 0 2 2 0 0 1 0 1 0
0 1 2

Trigonopteryx_hopei 1 1 0 0 0 0 4 0 3 0 0
0 0 N 1 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 0 1 2
0 3 0 2 2 1 0 1 1 0 1 0
0 0 2

Xyronotus_aztecus 1 1 0 0 0 0 4 0 3 0 0
0 0 N 0 0 0 0 0 0 0 1 0
1 0 0 0 0 0 0 0 1 0 1 2
0 3 0 0 2 1 0 1 1 1 0 0
0 0 2

Cylindraustralia_kochii 1 0 0 N 0 N N N N 0
0 0 0 N 0 0 0 0 1 0 0 0
1 0 0 0 0 1 1 1 0 N N N
0 N 1 0 2 0 0 1 1 0 0 0
0 1 N 0

Magnidactylus_robustus 1 1 0 N 0 N N N N 0
0 0 0 N 1 0 0 0 1 0 0 2
1 0 0 0 0 0 1 1 0 N N N
0 N 1 0 1 1 1 1 1 1 0 3
0 1 N 0

Ripipteryx_gorgonaensis 1 1 0 N 0 N N N N 0
0 0 0 N 1 0 0 0 1 0 0 2
1 0 0 0 0 0 0 1 0 N N N
0 N 2 0 2 2 1 1 1 1 0 3
0 1 N 0

Amberotridactylus_cheni 1 1 0 N 0 0 N 0 5 0
0 0 0 N 1 0 0 0 1 0 0 2
1 0 0 0 0 0 1 1 0 N N N
0 N 1 0 2 1 1 1 1 1 0 2
0 1 N 0

Ellipes_deyrupi 1 1 0 0 0 N N N N 0 0
0 0 N 1 0 0 0 1 0 0 1 1
0 0 0 0 0 1 1 0 N N N 0
N 1 0 2 1 0 1 1 1 0 3 0
1 0 0

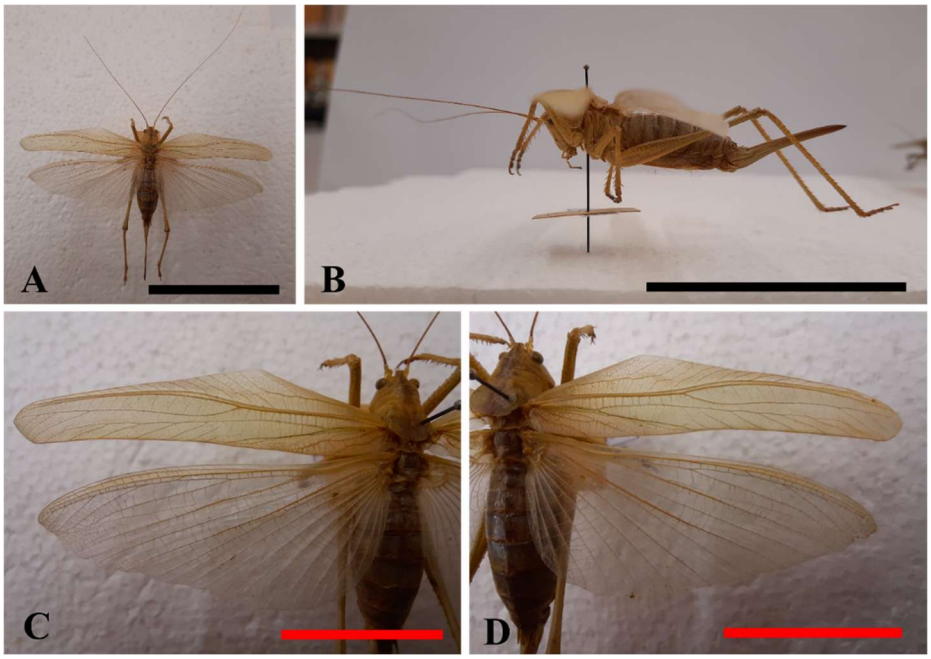
Cascogryllus_setosus 1 1 0 N 0 N N N N 0 0
0 0 N 1 0 0 0 1 0 0 2 1
0 0 0 0 0 1 1 0 1 N N 0
N 1 0 2 1 1 1 1 1 0 3 0
1 1 0

;

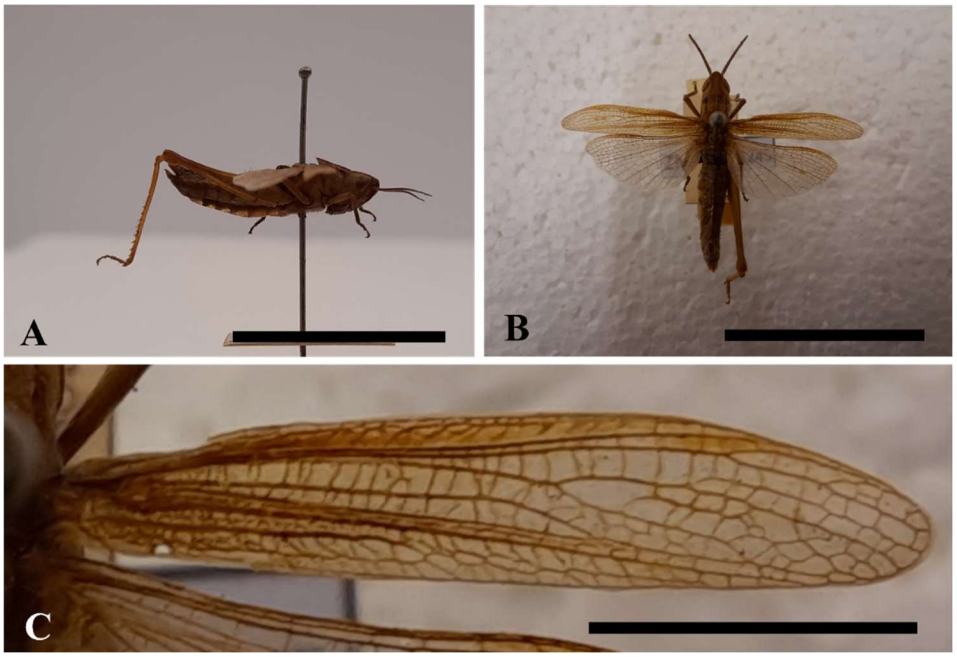
END;

Supplementary figures:

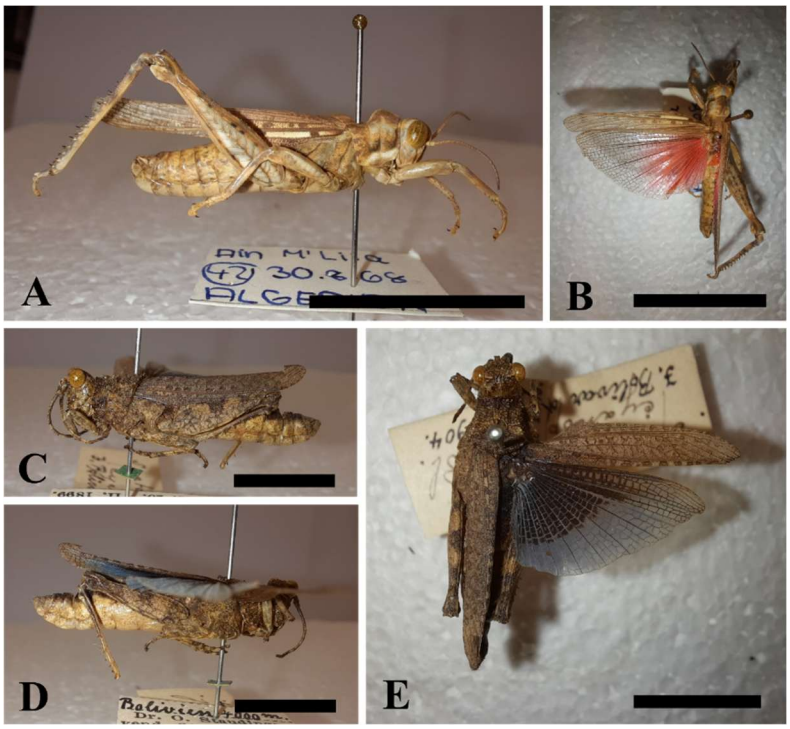
Supplementary figures 1-9: Orthoptera specimens from the LIB Hamburg used for reference in the phylogenetic analysis.



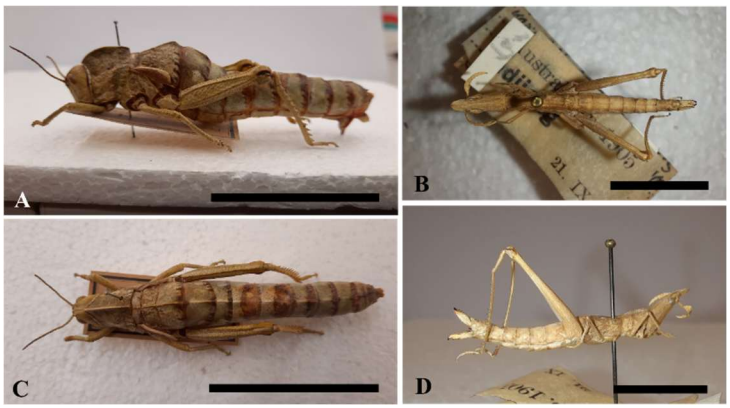
Supplementary figure 1: *Tettigonia viridissima* (Linnaeus, 1758), female specimen ZMH71558 from the LIB Hamburg collection (not of type status). **A.** Dorsal view. **B.** Left lateral view. **C.** Detail of left wing pair. **D.** Detail of right wing pair. **Scale bars** = 5 cm (A, B); = 2 cm (C, D).



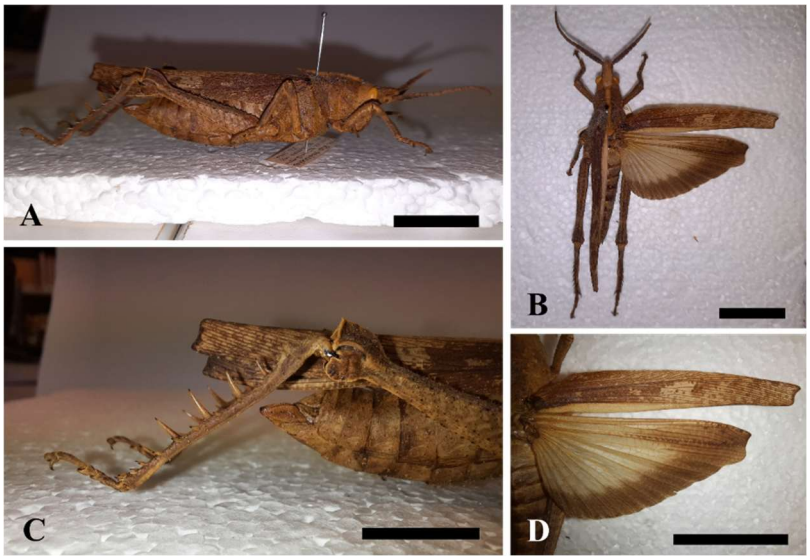
Supplementary figure 2: *Chorthippus albomarginatus* (De Geer, 1773), female specimen ZMH826245 from the LIB Hamburg collection (not of type status). **A.** Right lateral view. **B.** Dorsal view. **C.** Detail of right forewing. **Scale bars** = 2 cm (A, B); = 0.5 cm (C).



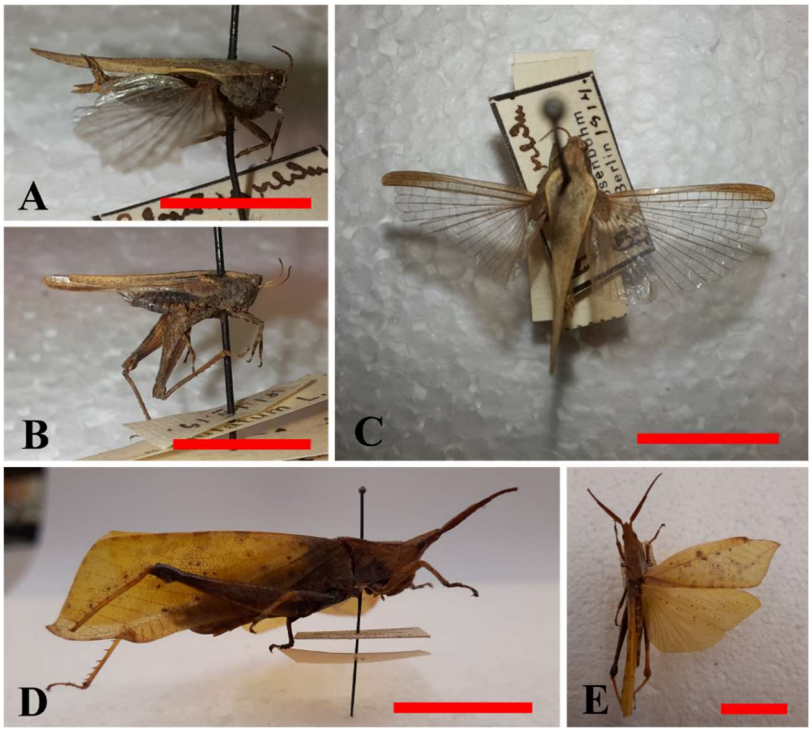
Supplementary figure 3: *Dericorys millierei* Bonnet and Finot, 1884, male specimen ZMH862113 from the LIB Hamburg collection (not of type status). **A.** Right lateral view. **B.** Dorsal view. **Scale bars** = 2 cm. *Descampsacris serrulata* (Thunberg, 1824), male specimen ZMH862112 from the LIB Hamburg collection (not of type status). **C.** Left lateral view. **D.** Right lateral view. **E.** Dorsal view. **Scale bars** = 1 cm.



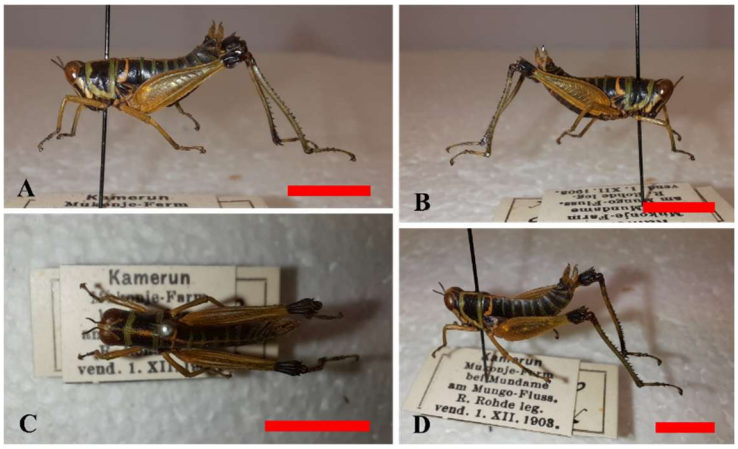
Supplementary figure 4: *Pamphagus marmoratus* Burmeister, 1838, female specimen ZMH862110 from the LIB Hamburg collection (not of type status). **A.** Left lateral view. **C.** Dosal view. **Scale bars** = 5 cm. *Vandiemenella viatica* (Erichson, 1842), female specimen ZMH862119 from the LIB Hamburg collection (not of type status). **B.** Dorsal view. **D.** Right lateral view. **Scale bars** = 1 cm.



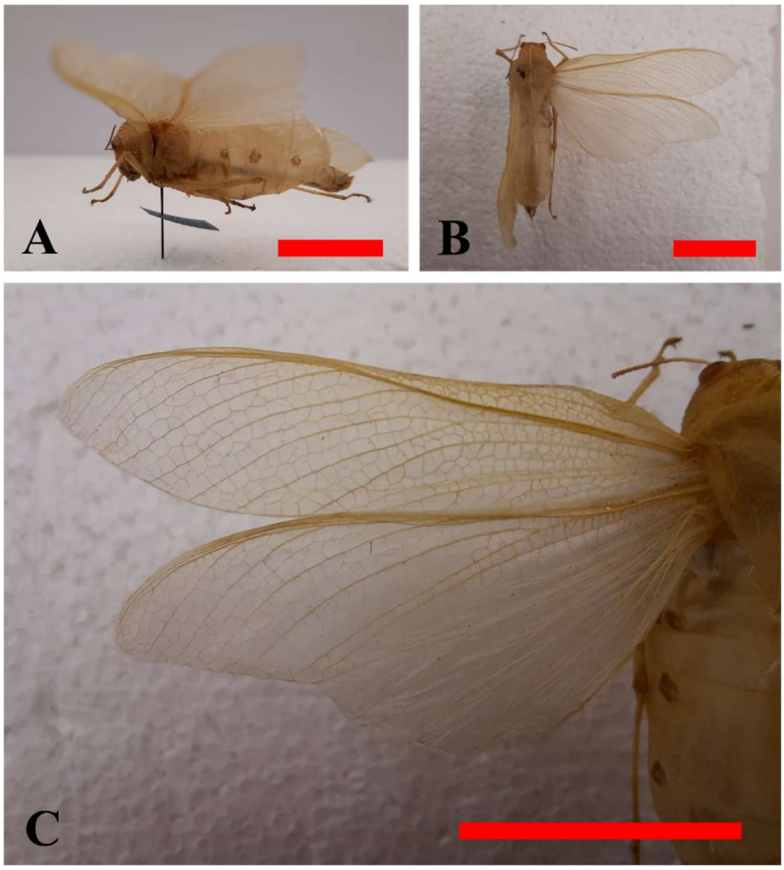
Supplementary figure 5: *Procolpia emarginata* (Serville, 1831), male specimen ZMH862115 from the LIB Hamburg collection (not of type status). **A.** Right lateral view. **B.** Dorsal view (mirrored). **C.** Detail of metathoracic leg and abdomen. **D.** Detail of left wing pair (mirrored). **Scale bars** = 2 cm (A, B, D); = 1 cm (C).



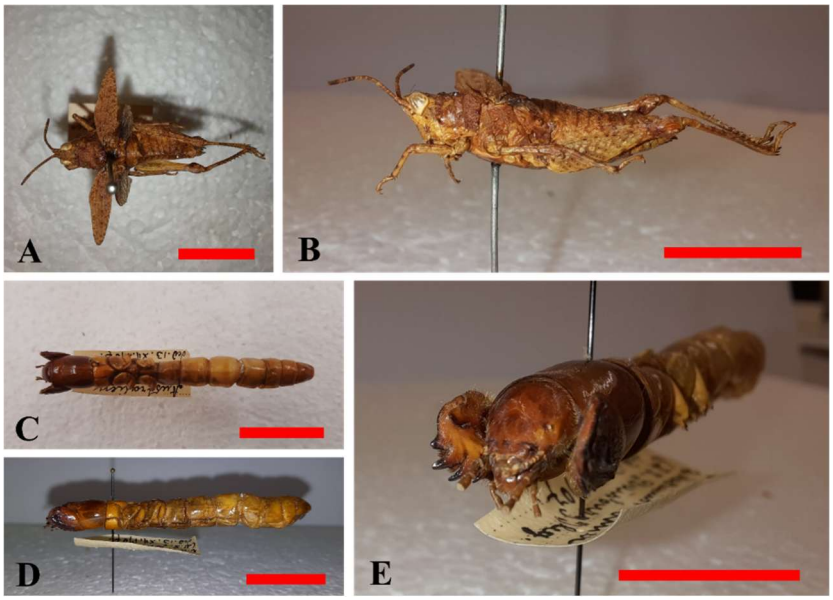
Supplementary figure 6: *Tetrix subulata* (Linnaeus, 1758), female specimens ZMH862117 (A, C) and ZMH862118 (B) from the LIB Hamburg collection (not of type status). **A.** Right lateral view. **B.** Right lateral view. **C.** Dorsal view. **Scale bars** = 1 cm. *Trigonopteryx hopei* (Westwood, 1841), female specimen ZMH862109 (not of type status). **D.** Left lateral view. **E.** Dorsal view (mirrored). **Scale bars** = 2 cm.



Supplementary material 7: *Afromastax zebra zebra* (Gerstaecker, 1889), female specimen ZMH862120 from the LIB Hamburg collection (not of type status). **A.** Left lateral view. **B.** Right lateral view. **C.** Dorsal view. **D.** Left dorso-lateral view. **Scale bars** = 1 cm.



Supplementary figure 8: *Bullacris discolor*, male specimen (Thunberg, 1810) ZMH862108 from the LIB Hamburg collection (not of type status). **A.** Left lateral view. **B.** Dorsal view (mirrored). **C.** Detail of left wing pair. **Scale bars** = 2 cm.



Supplementary figure 9: *Chrotogonus hemipterus* Schaum, 1853, female specimen ZMH862111 from the LIB Hamburg collection (not of type status). **A.** Dorsal view. **B.** Left lateral view. **Scale bars** = 1 cm. *Cylindraustralia kochii* (Saussure, 1877), specimen ZMH862116 from the LIB Hamburg collection (not of type status). **C.** Dorsal view. **D.** Left lateral view. **E.** Detail of head and prothoracic legs. **Scale bars** = 2 cm (C, D); = 1 cm (E).

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Chapter 10

Towards a revision of the Elcanidae genus *Panorpidium* (Insecta: Orthoptera) – a review of many misplaced taxa

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Abstract

The taxonomic position of eleven species formerly assigned to the genus *Panorpidium* Westwood, 1854 within the extinct Orthopteran family Elcanidae Handlirsch, 1906 is reviewed. Five of the eleven species are moved to the genus *Archelcana* Sharov, 1968: *Archelcana geinitzi* (Heer, 1880) comb. nov.; *Archelcana minima* (Handlirsch, 1906) comb. nov.; *Archelcana media* (Handlirsch, 1906) comb. nov.; *Archelcana magna* (Handlirsch, 1906) comb. nov. and *Archelcana phyllophora* (Handlirsch, 1906) comb. nov. For a single species, *Panorpidium liasinum* (Giebel, 1856), a position in *Archelcana* is suggested, but no formal nomenclatural act is performed, because the holotype of this species had not been available for review. Two of the eleven species are proposed as synonyms of *Archelcana media*, namely *Panorpidium mesostenum* (Handlirsch, 1939) syn. nov. and *Panorpidium reticulatum* (Handlirsch, 1920) syn. nov. *Panorpidium deichmuelleri* (Handlirsch, 1906) is moved to *Jeholelcana* Fang, Heads, Wang, Zhang & Wang, 2018 (*Jeholelcana deichmuelleri* comb. nov). *Panorpidium plagiatus* (Hagen, 1858) is moved to *Probaisselcana* (*Probaisselcana plagiata* comb. nov). Lastly, *Panorpidium oppenheimi* (Handlirsch, 1906) is the only species in this review for which a position in *Panorpidium* is confirmed. With these taxonomic acts, this study represents an important step towards understanding the evolutionary transition of the Elcanidae from the Jurassic to Cretaceous. Our findings indicate that *Panorpidium* was probably absent during the Early Jurassic of Central Europe, when Archelcaninae were the dominant elcanids, but the genus had evolved by the Late Jurassic. Eight more species currently assigned to *Panorpidium* are still in need of review.

Keywords: Dobbertin, fossil, grasshopper, insects, Solnhofen

1. Introduction

Elcanidae Handlirsch, 1906 is a family of extinct Orthoptera Olivier, 1789 with a wide distribution during the Mesozoic. Taxonomically, they are divided into two subfamilies: the Elcaninae Handlirsch, 1906 and the Archelcaninae Gorochov et al., 2006. The main difference between the subfamilies is the fusion of the tegminal veins 1A, CuPb and CuPaβ, which is present only in the Elcaninae (in the Archelcaninae, the three veins reach the anterior wing margin independently) (Gorochov et al., 2006). The Elcanidae were first described as a family 100 years before the recognition of the subfamilies. Back then, Handlirsch (1906) had placed most species of Elcanidae in the genus *Elcana* Giebel, 1856. Later, Gorochov (1995) suggested *Elcana* to be a synonym of the Elcaninae genus *Panorpidium* Westwood, 1854. Consequently, most species formerly in *Elcana* were moved to *Panorpidium*, which became the most speciose genus of Elcanidae. However, several authors such as Heads et al. (2022) and Gorochov and Coram (2022) pointed out that many species included in *Panorpidium* share strong resemblance to genera from the Archelcaninae and especially the type genus *Archelcana* and should probably be removed from *Panorpidium*.

In this study, we review the taxonomy of ten species of *Panorpidium* originally described as *Elcana*. In this context, images of the holotypes of four species are published for the first time alongside a novel interpretation of their tegminal venation.

2. Materials and methods

Holotype specimens of *Panorpidium* species in need of revision (see Table 1, green + red species) were located from literature review and information available in the Paleobiology Database (https://paleobiodb.org/#/). Unfortunately, not all species could be acquired and reviewed in this study, but the assembly presented here includes more than half of the species requiring revision. The remaining taxa, if located, will be considered in a future study.

We follow the taxonomy used in the Orthoptera Species File (Cigliano et al., 2025). Wing venation nomenclature follows Béthoux and Nel (2002). Abbreviation of the veins are: CP = posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα =

anterior branch of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

Drawings of specimens were created in GIMP v. 3.0.2-1 (the GIMP Team, 2025; https://www.gimp.org/). Figures were composed in Inkscape (v. 1.4) (the Inkscape Team, 2025; https://inkscape.org/).

3. Systematic palaeontology

Eight species of the genus *Panorpidium* Westwood, 1854 are reviewed based on new images and drawings of the holotype. Of a single species, previously unpublished images of non-type material are presented and the possible status of the species is discussed. Two species are declared synonyms based on comparison of available figures with the new images presented in this study. An updated status of all species of *Panorpidium* is given at the end of this section in Table 1.

Order: Orthoptera Olivier, 1789

Infraorder: Elcanidea Gorochov, 1995

Superfamily: Elcanoidea Handlirsch, 1906

Family: Elcanidae Handlirsch, 1906

Subfamily: Archelcaninae Gorochov et al., 2006

Genus: *Archelcana* Sharov, 1968

Included species: *A. britannica* (Handlirsch, 1906); *A. durnovaria* Whalley, 1985; *A. numbergerae* Heads et al., 2022; *A. ornata* Zherikhin, 1985; *A. shurabica* Sharov, 1968; *A. tina* Heads et al., 2022

Species ***Archelcana geinitzi*** (Heer, 1880) comb. nov.

Nomenclatural history: *Clathrotermes geinitzi* Heer, 1880; *Elcana geinitzi* (Heer, 1880) in Geinitz, 1880; *Panorpidium geinitzi* (Heer, 1880) by Cigliano et al. (2025)

Fig. 1

Remarks on nomenclature: Heer (1865) originally described a species he called *Clathrotermes signatus* from Switzerland (Schambelen), which he believed to be a termite. A second specimen from Dobbertin (Germany) was later described as *Clathrotermes geinitzi* by Heer, 1880 who identified the specimen upon request of Geinitz. Heer had described the specimen, but its

description was featured in a publication by Geinitz. Thus, the full taxon combination would be *Elcana geinitzi* Heer, 1880 in Geinitz (1880). However, usually, only Heer, 1880 gets mentioned as author of the species. When Geinitz (1880) published the Dobbertin specimen he had recognized the similarity to the genus *Elcana*, which had been established by Giebel (1856) based on material published in Westwood (1854). The two latter authors believed *Elcana* to be members of the scorpionflies (Panorpidae Latreille, 1802). Thus, *Clathrotermes geinitzi* became *Elcana geinitzi* upon publication due to the priority of the earlier genus name over *Clathrotermes*. Handlirsch (1906) was the first to include *Elcana geinitzi* as a species of Orthoptera in his newly erected family Elcanidae.

When Zessin (1987) revised the Elcanidae known at the time, he synonymized several of the species described by Handlirsch (1906). Among them were the six species of 'termites' described by Heer (1865) from Switzerland in the genera *Clathrotermes* and *Calotermes*. One of the synonyms recognized for *Elcana geinitzi* by Zessin was *Clathrotermes signatus*. Technically, recognition of *Clathrotermes* as a synonym of *Elcana* would had to have resulted in the combination *Elcana signata* (Heer, 1865) in Geinitz (1880) comb. nov., but this name was never explicitly implemented until Handlirsch (1906). Because *Elcana signata* (Heer, 1865) was named prior to *Elcana geinitzi* (Heer, 1880), the latter should have become a synonym of the former rather than vice versa. According to Cigliano et al. (2025) *Clathrotermes signatus* is to be treated as a *nomen oblitum* of *Elcana geinitzi*. On that note, the same should be true for the combination *Elcana signata*.

Elcana geinitzi was pro forma moved to *Panorpidium* Westwood, 1854 when *Elcana* became a synonym of *Panorpidium* in Jarzembowski (1996) as *Panorpidium geinitzi*. (Heer, 1880) comb. nov.

Holotype: The holotype of this species is a forewing in the collection of the Museum für Naturkunde (Museum for Natural History) in Berlin, Germany (collection number MB.I.15.1, part and counterpart).

Locality and horizon: Late Triassic to Early Jurassic of Switzerland (Schambelen), Germany (Dobbertin, Grimmen, Braunschweig) and UK.

Diagnosis: This species (as well as *Archelcana magna* (Handlirsch, 1906) comb. nov., *A. media* (Handlirsch, 1906) comb. nov. and *A. minima* (Handlirsch, 1906) comb. nov., see below) has been thoroughly covered by Zessin (1987), who also analysed its intraspecific variation. Here

only the holotype specimen shall be redescribed based on the understanding and terminology of Elcanidae morphology in 2025.

Description of holotype specimen MB.I.15.1: Forewing length 13.2 mm (base to apex), maximum width 3.5 mm. Anal vein with two branches, A1 and A2 plus a third anal vein terminating very close to wing base. Anal vein cross vein pattern hardly visible, but apparently regular (compare to 'complex' cross vein pattern of *Archelcana magna* comb. nov., below). 1A, CuPb and CuPaβ reach the posterior wing margin independently (= free 1A, CuPb and CuPaβ). CuA + CuPaα long. M with three branches, proximal two anterior of RP stem. RP with eight branches. RA with numerous (ca. 15+) cross veins. ScP with seven branches. ScA narrow, with two branches. Coloration of wing poorly preserved.

Remarks: Based on the free state of 1A, CuPb and CuPaβ this species belongs to the subfamily Archelcaninae Gorochov et al., 2006. Thus, its current position in *Panorpidium*, a genus in the subfamily Elcaninae Handlirsch, 1906, is incorrect. Within the Archelcaninae, MB.I.15.1 can be attributed to one of the genera *Archelcana* Sharov, 1968, *Sinoelcana* Gu, Tian, Wang & Yue, 2020, *Synelcana* Zessin, 1988, *Sibelcana* Gorochov, 1990 and possibly *Caelielca* Uchida, 2022 based on the two branches of M anterior of the RP stem. Among these genera, the taxonomic position is somewhat difficult to assess. The status of *Sinoelcana* in regards to *Archelcana* is problematic. Gu et al. (2020) state that the latter differs from the former by having only one longitudinal vein (i.e. MP) between CuA + CuPaα and the stem of RP. Although this appears to be true for some specimens of *Archelcana*, for example the holotype specimen of *A. minima* comb. nov. (Handlirsch, 1906) (see below), most specimens currently assigned to *Archelcana* have two longitudinal veins (i.e. MP and MA2) between CuA + CuPaα and the stem of RP. Either *Archelcana* consists of two genera, characterized by either two or just one branch of M between CuA + CuPaα and RP, or a variation of one or two longitudinal branches falls under intraspecific variation (this was the view of Zessin (1987)). Considering the plethora of figures in Zessin (1987), the RP stem appears to be somewhat variable indeed, being located clearly between MP and MA2, just or almost just below MA2 and clearly posterior of MA2. This continuous (rather than distinct) variation is more suggestive of intraspecific variation. Furthermore, recent findings from Elcanidae of the Brazilian Crato Formation support this theory too (Schall et al., submitted). Therefore, we follow Zessin (1987) and suggest that *Archelcana* probably has a variable RP stem position, varying between posterior of MP to posterior of MA2. Gu et al. (2020) further propose that *Archelcana* differs from *Sinoelcana, Sibelcana* and *Synelcana* by only having two branches of M instead of three. This is confusing,

because the morphology of RP and M is very similar in all four genera, giving no reason to assume absence of MA1 in *Archelcana* in our opinion. Additionally, both Heads et al. (2022), as well as Gorochov and Coram (2022) acknowledge the presence of three M branches in *Archelcana*. It is doubtful whether the small differences suggested by Gu et al. (2020) and Gorochov and Coram (2022) (minor morphologic differences of cubital branches and number of anal branches) are sufficient for generic separation.

Differences between *Sibelcana* and *Archelcana* are obscure, as the diagnostic characters of *Sibelcana* as stated by Gorochov and Coram (2022) (i.e. ScP reaching or extending beyond the position of the RP stem and proximal part of CuPaα in contact with base of CuA + CuPaα) is also found in most specimens of *Archelcana* (also *A. geinitzi*, see Fig. 1).

Synelcana differs from *Archelcana* by the morphology of the anal veins, which are more numerous and less horizontal in the former vs the latter. Regarding this character, *Synelcana* resembles *Parelcana* Handlirsch, 1906, indicating that *Synelcana* may represent an intermediate state between *Parelcana* and *Archelcana*.

The monotypic *Caelielca* Uchida, 2022 from mid-Cretaceous Burmese amber can probably be separated from *Archelcana* and *Sinoelcana* by the absence of secondary branches of ScP. Its forewing is also smaller than that of *A. geinitzi* (8.41 mm vs. 13.2 mm) (Uchida, 2022).

Based on the differences of the genera discussed, MB.I.15.1 could belong to *Archelcana*, *Sinoelcana* or *Sibelcana*. Because differentiation of these taxa based on forewing venation alone is problematic, we assign the specimen (and the species *Panorpidium geinitzi*) to *Archelcana* as this seems to be the most conservative decision until the taxonomy of the Archelcaninae is better resolved.

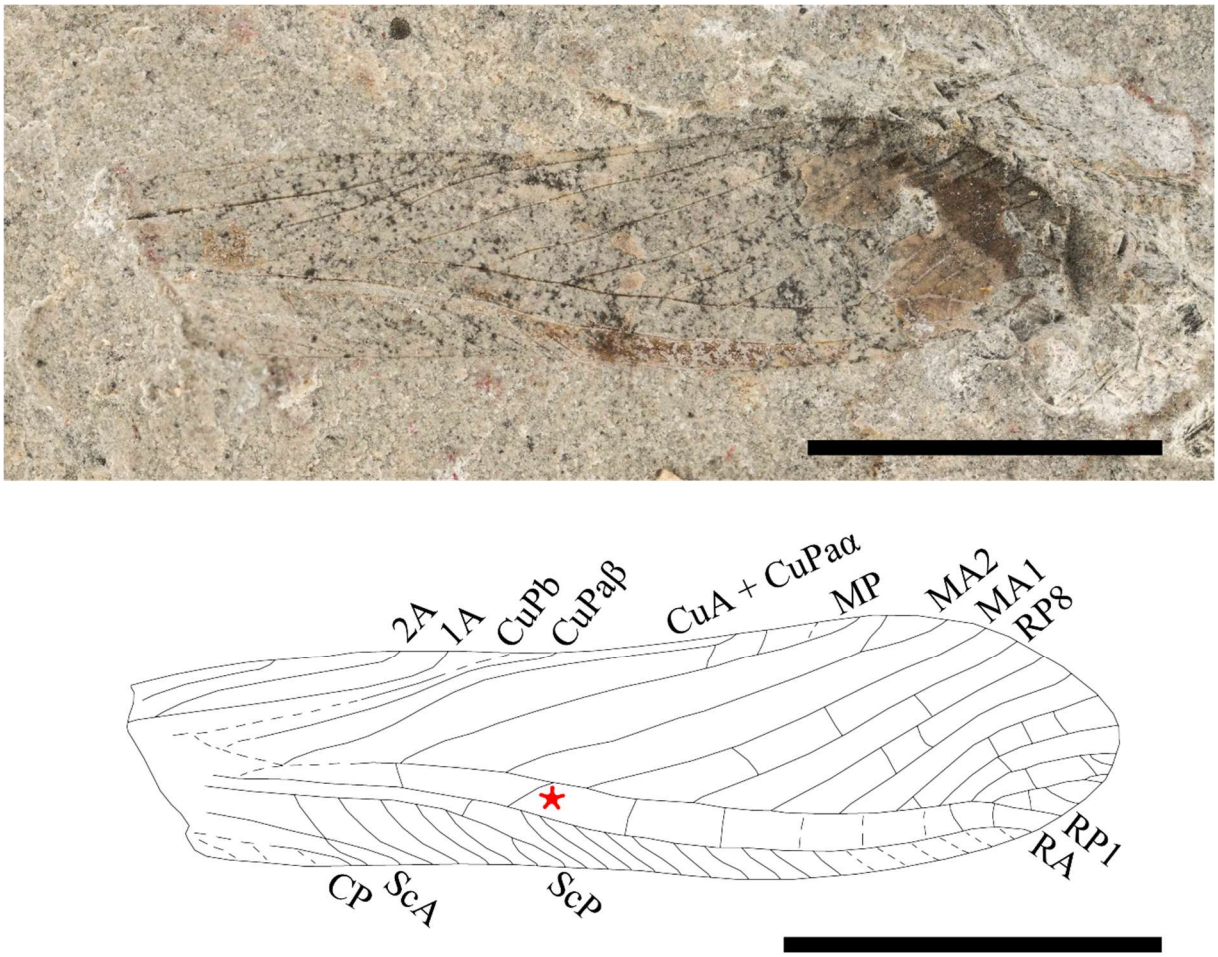


Fig. 1: *Archelcana geinitzi* (Heer, 1880) comb. nov. holotype MB.I.15.1. Image and drawing. Red star marks position of the RP stem. **Scale bars** = 5 mm. © Eran Wolff, MfN Berlin.

Species: **cf. *Archelcana liasina*** (Giebel, 1856)

Nomenclatural history: *Rapha liasina* Giebel, 1856; *Elcana liasina* (Giebel, 1856) in Handlirsch, 1906; *Archelcana liasina* (Giebel, 1856) in Gorochov, 1995; *Panorpidium liasinum* (Giebel, 1856) in Cigliano et al. (2025)

Fig. 2-3

Remarks on nomenclature: Originally believed to be a mayfly (Ephemeroptera Hyatt and Arms, 1890), the species was described as *Rapha liasina* Giebel, 1856 from the Late Triassic (Rhaetian) Lilstock Formation of the UK. Handlirsch (1906) included it in its new family Elcanidae as *Elcana liasina*. It had kept this name until its pro forma inclusion in *Panorpidium* after *Elcana* had become a synonym of *Panorpidium* post the revision by Jarzembowski (1996). Interestingly, Gorochov (1995) already mentioned the combination *Archelcana liasina*, but apparently, that name was subsequently ignored.

Holotype: NHMUK I.11676 in the collection of the Natural History Museum in London, UK.

Additional material: Unfortunately, the holotype of this species was not available to us at the time of writing this study. However, a total of five specimens attributed to cf. *Archelcana liasina* by Cockerell (1916) are housed in the collection of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (coll. no. USNM PAL 61389 [3490, 3491, 3493, 3494, 3495]). The best-preserved specimen USNM PAL 61389, 3490 is redescribed here. All specimens are shown in Fig. 2. Images can be obtained at GUID http://n2t.net/ark:/65665/30c17a132-68bc-4e72-b497-3746a2c3d632.

Locality and horizon: Late Triassic (Rhaetian) to possibly Early Jurassic (Toarcian) of the United Kingdom. Jurassic occurrence based on *Elcana brodiei* Handlirsch, 1906 (Cockerell, 1916).

Description of USNM PAL 61389, 3490: Forewing 11.0 mm long (base to apex), 2.8 mm wide (maximum width). Anal vein with two branches, A1 and A2 plus a third anal vein terminating close to wing base. Regular cross vein pattern in anal vein region. 1A, CuPb and CuPaβ reach the posterior wing margin independently (= free 1A, CuPb and CuPaβ). CuA + CuPaα shorter (than for example in *A. geinitzi*). M with three branches, proximal two anterior of RP stem. RP with five branches. RA with numerous (at least twelve) cross veins. ScP with three to five branches (presence of proximal two uncertain due to preservation). ScA narrow, with two branches preserved. Wing color consists of the abstract color pattern typical for Jurassic and Early Cretaceous European elcanids.

Remarks: Based on the material reviewed, the same considerations discussed above for *Archelcana geinitzi* also apply to this species. Hence, we suggest a position in *Archelcana* as *Archelcana liasina*. However, because we were unable to review the holotype specimen of this species, we refrain from officially moving it to *Archelcana* until this step has been performed. It is suggested as a likely member of this genus as cf. *Archelcana liasina* (Giebel, 1856) for now.

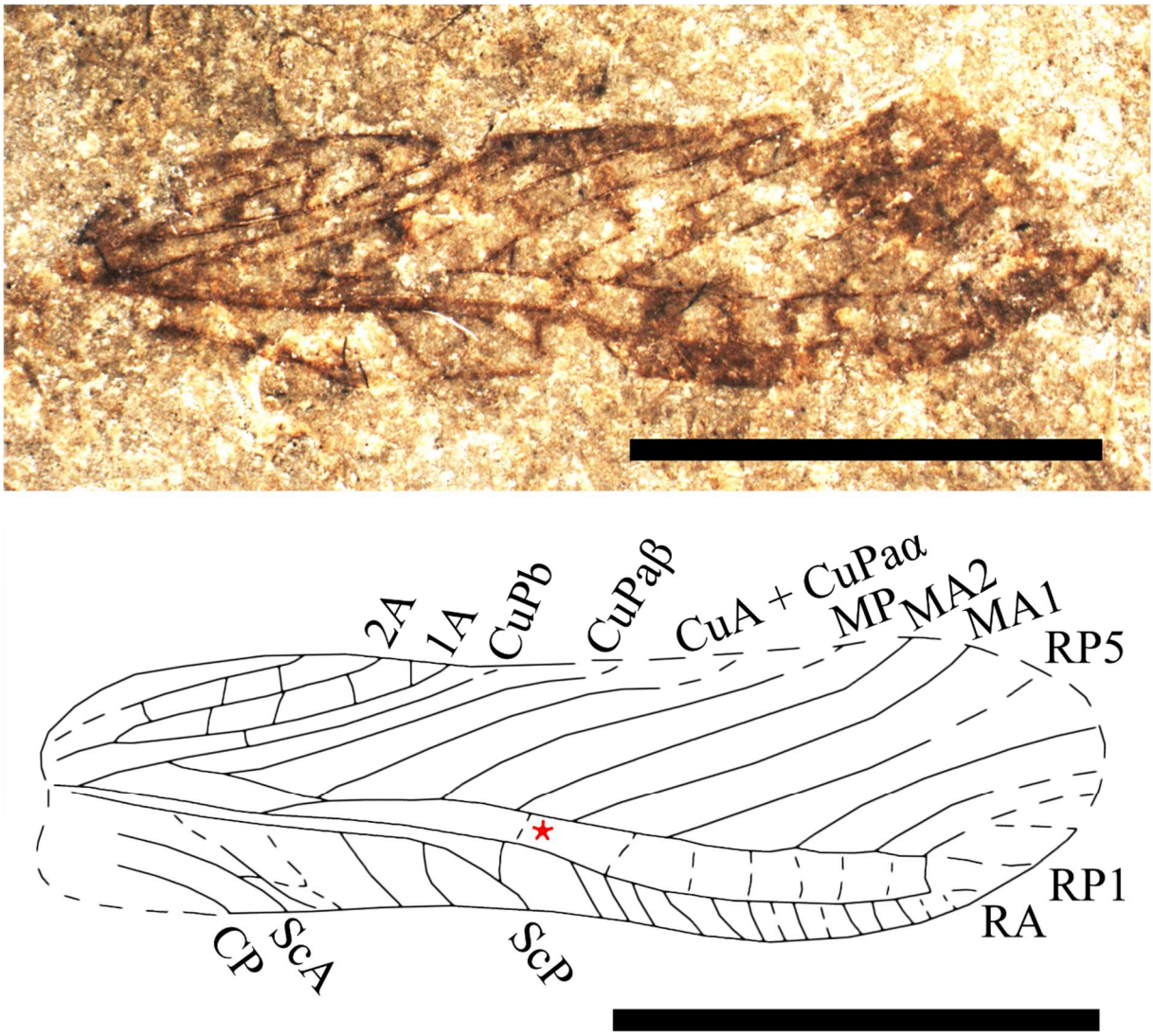


Fig. 2: cf. *Archelcana liasina* (Giebel, 1856) specimen USNM PAL 61389, 3490 (not of type status). Image and drawing. Red star marks likely position of RP stem (preservation not ideal). **Scale bars** = 5 mm. Image courtesy of the Smithsonian Institution.

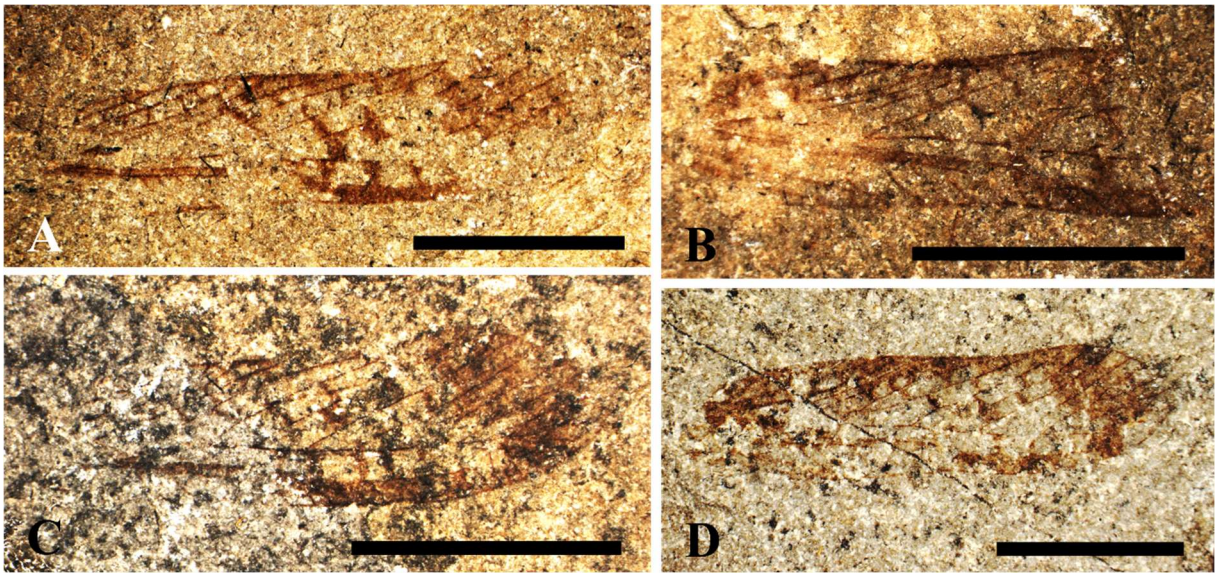


Fig. 3: cf. *Archelcana liasina* (Giebel, 1856) USNM PAL 61389 (not of type status). **A.** 3494. **B.** 3491. **C.** 3493. **D.** 3495. **Scale bars** = 5 mm. Images courtesy of the Smithsonian Institution.

Species: ***Archelcana magna*** (Handlirsch, 1906) comb. nov.

Nomenclatural history: *Elcana magna* Handlirsch, 1906; *Panorpidium magnum* (Handlirsch, 1906) in Cigliano et al. (2025)

Fig. 4

Remarks on nomenclature: This species has experienced a similar nomenclatural history as *Archelcana geinitzi* described above. Among the many species of Elcanidae described by Handlirsch (1906) were *Elcana magna* Handlirsch, 1906 and *Elcana obtecta* (Heer, 1865), whereby the latter was a new combination of *Calotermes obtectus* Heer, 1865, another alleged Swiss termite species. Upon revision of the Elcanidae by Zessin (1987), the author recognized *Elcana obtecta* as a synonym of *Elcana magna* rather than the other way around, which would have been more appropriate given the priority of the earlier name over the more recent *Elcana magna*. According to Cigliano et al. (2025) *Calotermes obtectus* (and hence *Elcana obtecta*) should be treated a *nomen oblitum* of *Elcana magna*.

Holotype: MB.I.06.1 (part and counterpart), a forewing in the collection of the Museum für Naturkunde (Museum for Natural History), Berlin, Germany.

Locality and horizon: Early Jurassic of Germany and Switzerland.

Description of holotype specimen MB.I.06.1: Forewing 20.6 mm long (base to apex), 5.0 mm wide (maximum width). Anal vein likely with two branches, but termination of posterior branch

(2A) obscured by complex cross vein pattern below the anal veins. 1A, CuPb and CuPaβ reach the posterior wing margin independently (= free 1A, CuPb and CuPaβ). CuA + CuPaα long. M with three branches, proximal two anterior of RP stem. RP with seven branches. RA with numerous (20+) cross veins. ScP with eight to nine branches. ScA with five branches. Wing color consists of the abstract color pattern typical for Jurassic and Early Cretaceous European elcanids.

Remarks: In terms of generic assignment, the same considerations as discussed for *Archelcana geinitzi* above apply to *Archelcana magna*. Besides the difference in size, *A. magna* differs from *A. geinitzi* by the complex cross vein pattern in the region of the anal veins and more branches of ScA. However, both characters vary between specimens of either species (compare Zessin (1987)) and probably do not imply taxonomic information. It is perhaps noteworthy that despite the size difference, *A. magna* does not have more branches of RP than *A. geinitzi*. Contrary, in the Crato Formation Elcanidae, *Cratoelcana zessini* Martins-Neto, 1991 has more branches of RP than the smaller *Panorpidium damianii* (Martins-Neto, 1991) (ca. 11 vs. ca. 7-8) (Schall et al., submitted (chapter 8, this dissertation)). However, smaller species with many RP branches are also known, like the Burmese amber *Kolymbelcana phantasma* Schall et al., 2025 (forewing length 9.5 mm, 11 RP branches).

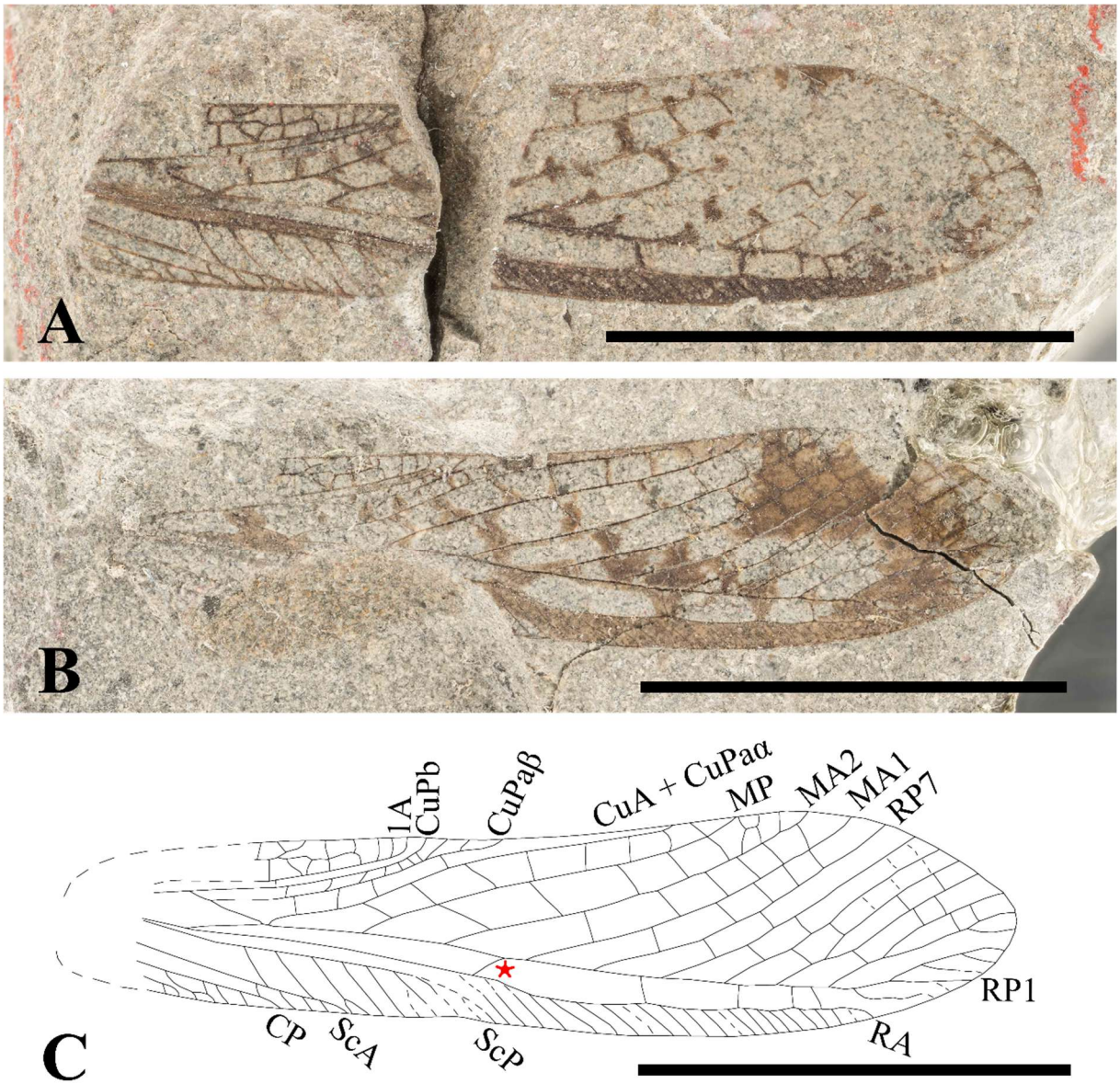


Fig. 4: *Archelcana magna* (Handlirsch, 1906) comb. nov., holotype MB.I.06.1. **A.** Part. **B.** Counterpart. **C.** Drawing (combining details from part and counterpart). Red star marks position of the RP stem. **Scale bars** = 10 mm. © Eran Wolff, MfN Berlin.

Species: ***Archelcana media*** (Handlirsch, 1906) comb. nov.

= *Panorpidium mesostenum* (Handlirsch, 1939) syn. nov.; = *Panorpidium reticulatum* (Handlirsch, 1920) syn. nov.

Nomenclatural history: *Elcana media* Handlirsch, 1906; *Panorpidium medium* (Handlirsch, 1906) in Cigliano et al. (2025)

Fig. 5

Remarks on nomenclature: Although Bode (1905) featured a specimen likely attributable to *A. media*, he regarded this specimen as a larger variation of *A. geinitzi*. The specimen mentioned is a wing of good preservation discovered at Schandelah (near Braunschweig, Germany) which is 17.7 mm long and 3.8 mm wide (Bode, 1905). Handlirsch (1906) described *Elcana media* based on a 16 mm long forewing from Dobbertin (Germany), although Handlirsch (1939) apparently had changed his mind, as he listed *Elcana media* as a synonym of *Elcana geinitzi* again. Nonetheless, Zessin (1987) recognized both species. *Elcana media* was moved pro forma to *Panorpidium* in Cigliano et al. (2025) after *Elcana* had become a synonym of *Panorpidium* post revision by Jarzembowski (1996).

Holotype: The holotype is a forewing in the Museum für Naturkunde collection (Museum for Natural History), Berlin, Germany. Its collection number is MB.I.09.1 and it consists of a part and a counterpart.

Locality and horizon: Early Jurassic of Germany.

Description of holotype specimen MB.I.09.1: Forewing 16.8 mm long (base to apex), 4.0 mm wide (maximum width). Anal vein with two branches with regular cross vein pattern. 1A, CuPb and CuPaβ reach the posterior wing margin independently (= free 1A, CuPb and CuPaβ). CuA + CuPaα relatively long. M with three branches, proximal two anterior of RP stem. RP with six branches. RA with ca. sixteen cross veins. Subcostal branches not preserved. Wing color pattern unclear (the entire wing is of uniform black coloration which is unlikely to have represented color in the live animal).

Remarks: Generic assignment follows the same reasoning as for the above-mentioned species. Zessin (1987) separated *A. media* and *A. geinitzi* based on the difference in forewing size (17.3 mm vs. 14.3 mm mean), as well as a more elaborate cross vein pattern in the hindwing of *A. media*. The last point appears to be misleading, as one of the specimens of *A. geinitzi* figured by Zessin (1987) (LDA422/1/2, Fig. 71) also shows an elaborate cross vein pattern, in no way less developed than in *A. media*. The size difference between *A. media* and *A. geinitzi* is minimal. Schall et al. (submitted) noticed a size range of 0.9 to 2.7 mm in elcanids from the Crato Formation. This means the size difference between the two Jurassic species may just be enough to justify specific separation, but it may also represent intraspecific variation slightly greater than in Crato elcanids. A final word in this decision is difficult based on just characters of the forewing. The Brazilian elcanids could be differentiated by their ovipositor type; perhaps aspects of the body morphology revealed by future findings will help understand true taxonomic

diversity of Elcanidae in the Jurassic formations of Central Europe and elucidate on the species problem *A. geinitzi* / *A. magna*.

The holotype specimens of *Panorpidium (Elcana) mesostenum* (Handlirsch, 1939) and *Panorpidium (Elcana) reticulatum* (Handlirsch, 1920) figured in both respective works show clear resemblance to *Archelcana media*. They only differ by having two more branches of RP than the holotype, but a variation of two RP branches falls into the range that can be expected for intraspecific variation in elcanids (Schall et al., submitted; Zessin, 1987). Therefore, *Panorpidium mesostenum* and *Panorpidium reticulatum* are proposed as synonyms of *Archelcana media*.

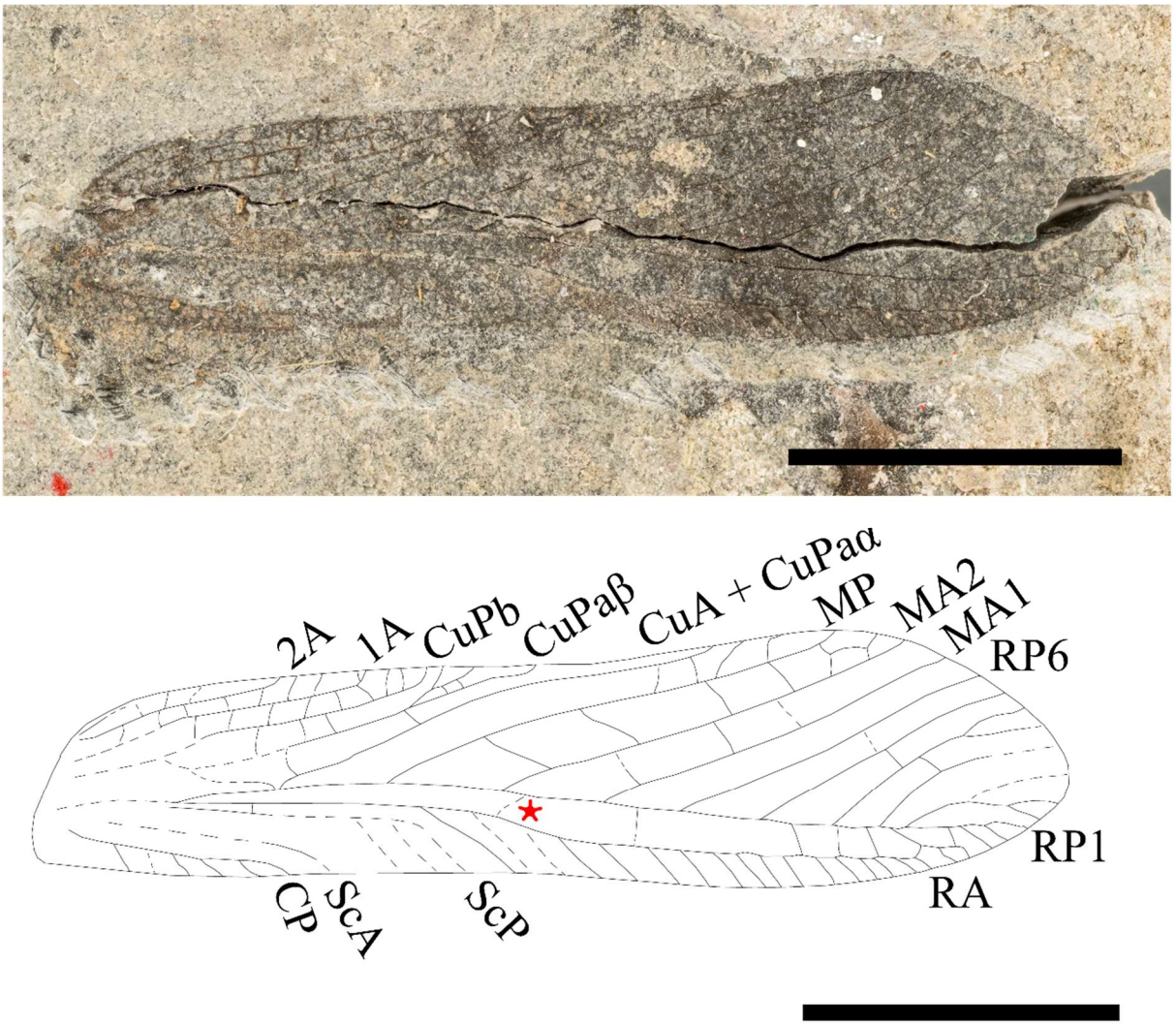


Fig. 5: *Archelcana media* (Handlirsch, 1906) comb. nov., holotype MB.I.09.1. Red star in the drawing marks the position of the RP stem. **Scale bars** = 5 mm. © Eran Wolff, MfN Berlin.

Species: ***Archelcana minima*** (Handlirsch, 1906) comb. nov.

Nomenclatural history: *Termes troglodytes* Hagen, 1858; *Calotermes troglodytes* (Hagen, 1858) in Heer, 1865; *Elcana minima* Handlirsch, 1906; *Panorpidium minimum* (Handlirsch, 1906) in Cigliano et al., 2025

Fig. 6

Remarks on nomenclature: This species is another one that was originally perceived to be a termite, first by Hagen (1858), who named it *Termes troglodytes* and then by Heer (1865), who placed it in the genus *Calotermes*. Similar to *A. geinitzi* and *A. magna*, Handlirsch (1906) described *Elcana minima* as one species, while moving *Calotermes troglodytes* to *Elcana* as *Elcana troglodytes* (Hagen, 1858). When Zessin (1987) revised the Elcanidae, he recognized *Elcana troglodytes* as a synonym of *Elcana minima* rather than giving priority to the older name. *Termes troglodytes* (and *Elcana troglodytes*) should be treated as a *nomen oblitum* of *Archelcana minima* (Handlirsch, 1906) comb. nov.

Holotype: A forewing in the collection of Museum für Naturkunde (Museum for Natural History), Berlin Germany (coll. no. MB.I.25.1, part and counterpart).

Locality and horizon: Early Jurassic of Germany and Switzerland.

Description of holotype specimen MB.I.25.1: Forewing ca. 8.9 mm long (base to apex), 2.2 mm wide (maximum width). Anal vein region not well-preserved. 1A (presumably), CuPb and CuPaβ reach the posterior wing margin independently (= free 1A, CuPb and CuPaβ). CuA + CuPaα long. M with three branches, only MP anterior of RP stem. RP with four branches. RA with eight to nine cross veins. ScP with five branches. ScA and CP without branches. Wing color pattern apparently representing the abstract color pattern typical of Jurassic elcanids.

Remarks: Generic assignment follows the same considerations as for the species discussed above. The most distinguishing aspect of forewing morphology of this species is the position of the RP stem, i.e. it is posterior only of MP (and not MP and MA2). However, this character is only known from some specimens, including the holotype (!), but not others (mostly non-type specimens assigned to *A. geinitzi* by Zessin (1987)) where it is in its 'normal' position posterior of MA2. The specimens of *A. minima* currently attributed to this taxon exhibit continuous variation of the RP stem position, i.e. it shifts between from posterior of MP to right at the level of MA2 to posterior of MA2 (Zessin, 1987). This pattern would support the view of Zessin (1987), that the variation of the RP stem in *A. minima* is due to intraspecific variation. A hypothesis that is corroborated by the findings from Schall et al. (submitted), who noticed similar variation in the forewing of specimens attributed to *Cratoelcana zessini* Martins-Neto,

1991 and *Mesembrelcana rasnitsyni* (Nel and Jouault, 2022). On the other hand, it would contradict the opinion of Gorochov et al. (2006), who proposed a variation of the RP stem posterior of MA2 and MA1 respectively, as diagnostic for the genera *Panorpidium* and *Probaisselcana*. Furthermore, variation of the RP stem position seems to only occur in certain species (*Archelcana minima*, *Cratoelcana zessini*, *Mesembrelcana rasnitsyni*), but not others (*Archelcana geinitzi*, *Archelcana magna*, *Panorpidium damianii*, *Gondwanaelcana brasiliensis* Schall et al., submitted), suggesting that it is in fact not usual for elcanids, hence, pointing towards separate taxa. Hopefully, future findings of Elcanidae from Crato, Dobbertin or other places will shed light on this issue.

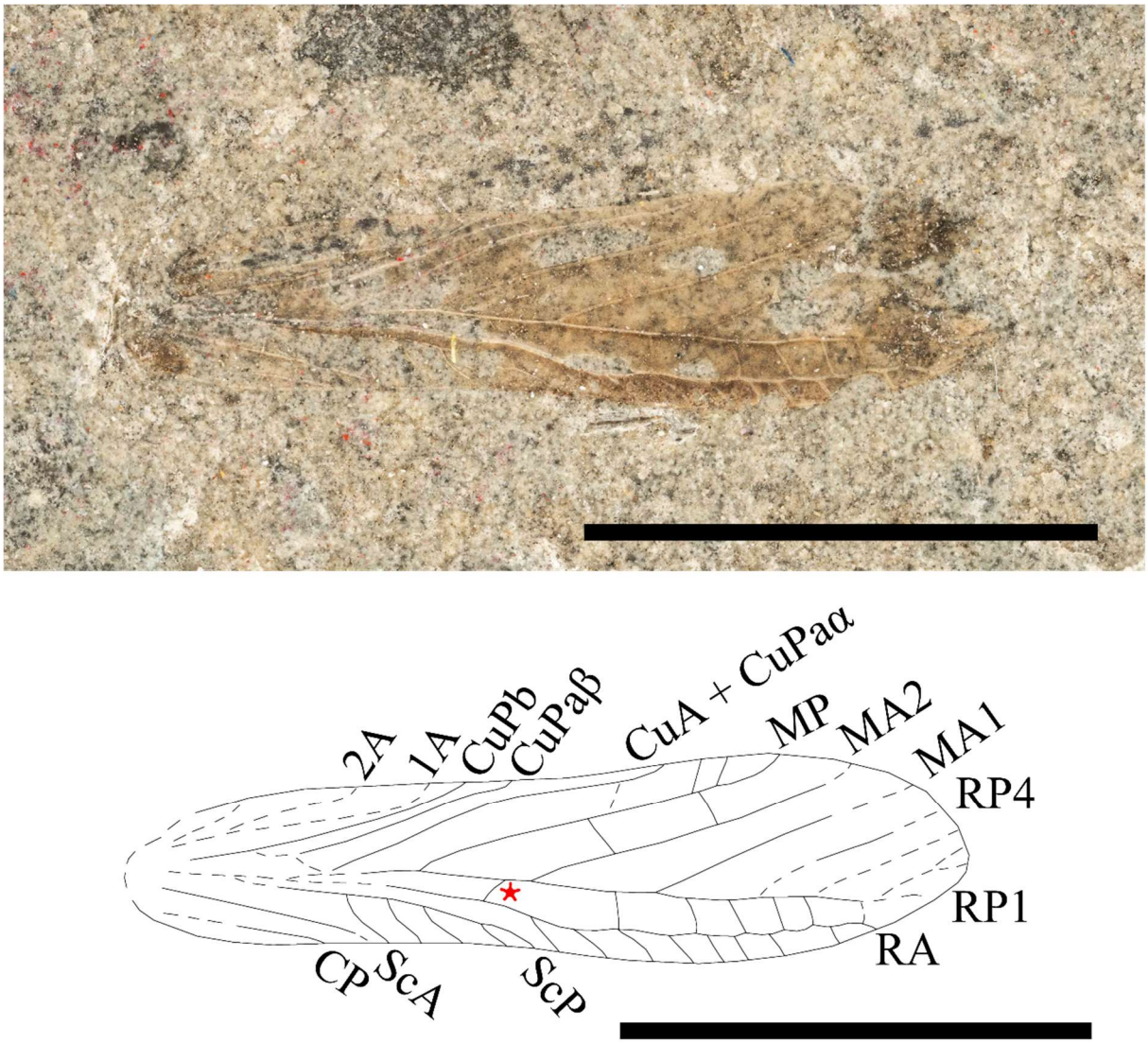


Fig. 6: *Archelcana minima* (Handlirsch, 1906) comb. nov., holotype MB.I.25.1. Red star marks the position of the RP stem. **Scale bars** = 5 mm. © Eran Wolff, MfN Berlin.

Species: ***Archelcana phyllophora*** (Handlirsch, 1906) comb. nov.

= *Elcana bavarica* Handlirsch, 1906

Nomenclatural history: *Elcana phyllophora* Handlirsch, 1906

Fig. 7

Remarks on nomenclature: This species was described by Handlirsch (1906) as *Elcana phyllophora* and pro forma moved to *Panorpidium* in Cigliano et al. (2025), following the revision of *Elcana* by Jarzembowski (1996).

Holotype: The holotype specimen is in the collection of the Naturhistorisches Museum Wien, collection number 2007z0142/0006. At the time of writing, it is registered under the old name *Elcana pyhllophora*. It had previously been depicted in Handlirsch (1906, Plate 44, Figure 1).

Locality and horizon: Eichstätt, a German town in the country of Bavaria. The limestone of this region dates back to the early Tithonian, ca. 152.1-145 Mya (Röper and Reich, 2023).

Emended diagnosis: Forewing as preserved 20.6 mm long (almost full length). M with four branches. RP with 10-12 branches. RA with numerous (16+) comb-like branches. Metatibial spurs leaf-like.

Emended description: The holotype specimen consists of a reasonably well-preserved forewing as well as some aspects of the body including parts of the metathoracic leg. Metatibial spurs leaf-like. Forewing: 1A not seen. CuPb and CuPaβ independently reaching anterior wing margin. Morphology of CuA and CuPaα not certain, but interpreted as seen in Fig. 2B (CuPaα fused with CuA + CuPaα). M with four branches. RP with ten to twelve branches. Stem of RP posterior of MA2. RA with numerous comb-like branches, 16 of which are preserved. ScP with five branches preserved.

Remarks: The holotype of *Archelcana phyllophora* comb. nov. in the collection of the Natural History Museum Vienna shows CuPb and CuPaβ of the forewing reaching the anterior wing margin independently and not fused as is the case in *Panorpidium*. The free state of these veins and two branches of M anterior of the RP stem suggest a position in one of the genera of Archelcaninae already discussed (*Archelcana*, *Caelielca*, *Sibelcana*, *Sinoelcana* and *Synelcana*). Because the situation is like with the previous species, *Panorpidium phyllophorum* is placed in *Archelcana* for now, as *Archelcana phyllophora* comb. nov. Due to its larger size, it is most similar to *Archelcana magna*. The two species differ in the more elaborate medial

(M) and posterior radial (RP) vein of *A. phyllophora*, which has one and three to five branches more than in *A. magna*, respectively.

In addition to the holotype of *Archelcana phyllophora,* we also examined the holotype of *Elcana bavarica* Handlirsch, 1906, which has been considered a synonym of *A. phyllophora* by Zessin (1987). After reviewing the specimen (Fig. 2C-D), we agree with this interpretation. The holotype of *E. bavarica* is in a similar state of preservation as that of *A. phyllophora*, but with the venation features towards the base more obscured. However, aside from being slightly larger (forewing length 25.8 mm), the specimen of *E. bavarica* exhibits no features on the basis of which it could be differentiated from *A. phyllophora*.

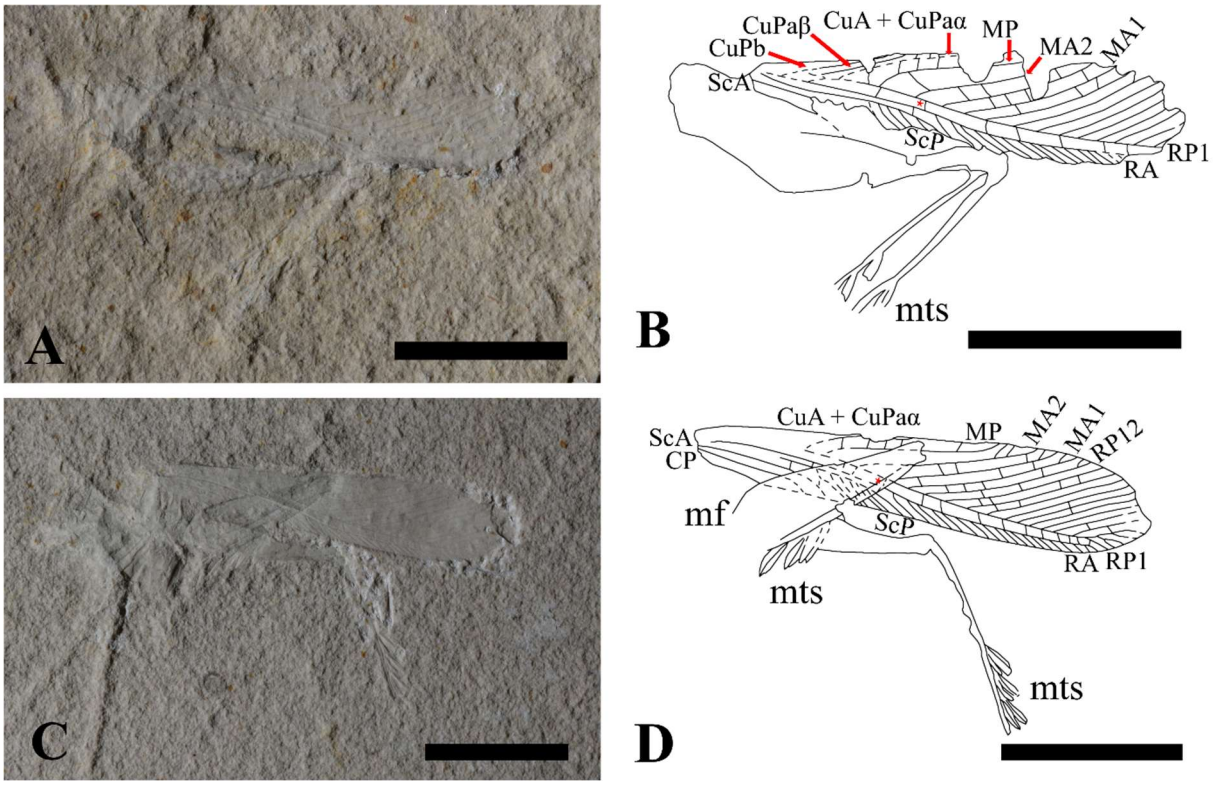


Fig. 7: A-B. *Archelcana phyllophora* (Handlirsch, 1906) comb. nov. holotype in the collection of Naturhistorisches Museum Wien (NMW), coll. no. 2007z0142/0006. **A.** Image of the specimen. Image kindly provided by Prof. Mathias Harzhauser from NMW. **B.** Drawing of the specimen. **C-D.** *Archelcana phyllophora*, holotype specimen of *Elcana bavarica* Handlirsch, 1906, a synonym of *A. phyllophora* as recognized by Zessin (1987). Specimen in the collection of NMW, coll. no. 2007z0140/0003. **D.** Drawing of the specimen. **Abbreviations:** mf = metafemur; mts = metatibial spur(s). **Scale bars** = 10 mm.

Genus: *Jeholelcana* Fang, Heads, Wang, Zhang & Wang, 2018

Type species: *Jeholelcana yanensis* Fang, Heads, Wang, Zhang & Wang, 2018

Species: ***Jeholelcana deichmuelleri*** (Handlirsch, 1906) comb. nov.

Nomenclatural history: *Locusta amanda* Hagen, 1862; *Elcana amanda* (Hagen, 1862) in Deichmüller (1886); *Elcana deichmuelleri* Handlirsch, 1906; *Panorpidium deichmuelleri* (Handlirsch, 1906) in Cigliano et al. (2025)

Fig. 8

Remarks on nomenclature: Hagen (1862) described a specimen of Elcanidae as *Locusta amanda* (known today as *Panorpidium lithophilum* (Germar, 1842)). This species was transferred to *Elcana* by Deichmüller (1886) as *Elcana amanda* (Hagen, 1862), but based on a different specimen in the collection of the Senckenberg Naturhistorische Sammlungen Dresden that was much larger than the holotype of *Locusta amanda*. This view (i.e. both specimens belonging to the same species) was supported by Oppenheimer (1888), who studied four specimens from the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. Handlirsch (1906) resolved this likely error by establishing two species, *Elcana deichmuelleri* Handlirsch, 1906 (after the Dresden specimen described by Deichmüller (1886) as *Elcana amanda*) and *Elcana amanda* (Hagen, 1862) after the original specimen (location currently unknown) regarded by Deichmüller (1886) as *Elcana amanda* (Hagen, 1862). Handlirsch also established a third species *Elcana lithophila* (Germar, 1842) after *Assilicus lithophilus* Germar, 1842. However, he had already speculated that *E. lithophila* might be identical with *E. amanda* (Hagen, 1862).

In his revision of Elcanidae, Zessin (1987) agreed with this opinion by Handlirsch. He moved *Assilicus lithophilus* Germar, 1842 to *Elcana* as *Elcana lithophila* (Germar, 1842), meanwhile recognizing *Locusta/Elcana amanda* Hagen, 1862 as a synonym of *Elcana lithophila*, since the original combination was published twenty years earlier. Zessin (1987) also supported *Elcana deichmuelleri* Handlirsch, 1906 as a distinct species. Confusingly, Zessin (1987) regarded the Munich specimens studied by Oppenheimer (1888) as belonging to *Elcana phyllophora* Handlirsch, 1906. This species was reviewed above; the Munich specimens are reviewed below. They do not belong to the same species or the same genus.

Elcana lithophila and *Elcana deichmuelleri* were pro forma moved to *Panorpidium* in Cigliano et al. (2025) following the revision of *Elcana* by Jarzembowski (1996). In this review the

holotype of the species *Elcana deichmuelleri* is redescribed. The holotype of *Elcana lithophila* will hopefully be covered in a future review that will cover the remaining species of *Panorpidium*.

Holotype: The holotype of *Panorpidium (Elcana) deichmuelleri* is a female in the collection of the Senckenberg Naturhistorische Sammlungen Dresden, collection number BaJ1485.

Locality and horizon: The type specimen was found in Eichstätt, a German town in the country of Bavaria. The limestone of this region is early Tithonian in age, ca. 152.1-145 Mya (Röper and Reich, 2023).

Emended diagnosis: Large species with a forewing length of 27.7 mm in the holotype. Metatibial spurs leaf-like. Ovipositor sword shaped. Forewing with CuPaβ free. CuPaα fused with CuA + CuPaα. M with four branches. RP with nine branches. RA with numerous comb-like branches.

Emended description:

Measurements: Forewing length (max.) 27.7 mm, height (max.) 6.1 mm. Body length (head to abdominal apex) ca. 20 mm. Metafemur ca. 12.7 mm long. Ovipositor (preserved length) 12.9 mm long.

Characters: Head almost completely destroyed. Thoracic region only discernible by the outline. Metathoracic leg preserved up to metatibial spur region. No appendages/spination visible proximal of metatibial spurs. Anterior metatibial spur fully, second partly preserved, large and leaf-like. Abdomen with ovipositor straight and sword shaped; likely not preserved with full length. Forewing with 1A and CuPb hardly visible due to damage at the wing base' anal region. CuPaβ free. CuA + CuPaα relatively long. M with four branches, presumably proximal three anterior of RP stem. RP with nine branches. RA with numerous (16+) comb-like branches, preservation fading distally. ScP with five branches. ScA and CP without branches. Color pattern not preserved.

Remarks: The free CuPaβ and likely free CuPb as well as 1A of this species suggest a placement in the subfamily Archelcaninae rather than in *Panorpidium* in the subfamily Elcaninae. In the Archelcaninae, BaJ1485 is assigned to *Jeholelcana,* because it has three branches of MA. Additionally, comparison with other elcanids allows to estimate the position of the RP stem not anterior of between the two branches of MA1, because the RP stem is always located towards where ScP fuses to the posterior wing margin. In most Archelcaninae the stem of RP is located posterior of MA2. In *Jeholelcana yanensis*, the single and type species of the genus, the RP

stem is located between the two branches of MA1. *Jeholelcana yanensis* also still retains the cryptic color pattern of the Jurassic elcanids, despite being from the Lower Cretaceous of China. *Jeholelcana* differs from *Parelcana* Handlirsch, 1906, which shares the three branches of M between CuA + CuPaα and the stem of RP, by having CuPaα fused with CuA + CuPaα instead of with the free CuA (as is the case in *Parelcana* (Gu et al., 2020)). It differs from *Thagyaminana* Schall et al., 2025 by being much larger (forewing size of *Thagyaminana atawedeia* Schall et al., 2025, the single species of the genus, is 13.5 mm) and by the presence of cross veins of RA. *Thagyaminana atawedeia* also has two dark wing spots which is common in Cretaceous elcanids, but not known in most Jurassic forms.

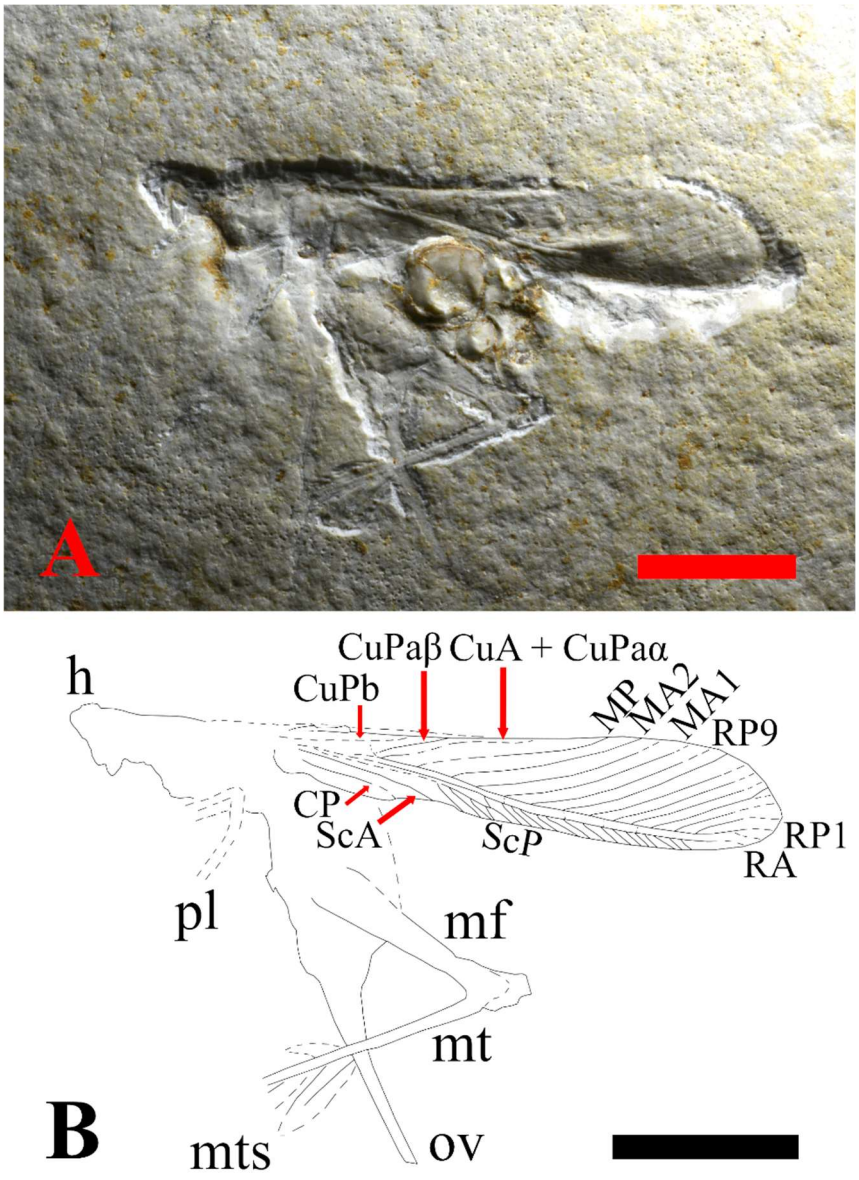


Fig. 8: *Jeholelcana deichmuelleri* (Handlirsch, 1906) comb. nov. holotype female in the collection of Senckenberg Naturhistorische Sammlungen Dresden (SNSD), coll. no. BaJ1485. **A.** Image of the specimen. Photographed and kindly provided by Ronald Winkler from SNSD. **B.** Drawing of the specimen. **Abbreviations:** h = head; pl = prothoracic leg; mf = metafemur; mt = metatibia; mts = metatibial spur(s); ov = ovipositor. **Scale bars** = 10 mm.

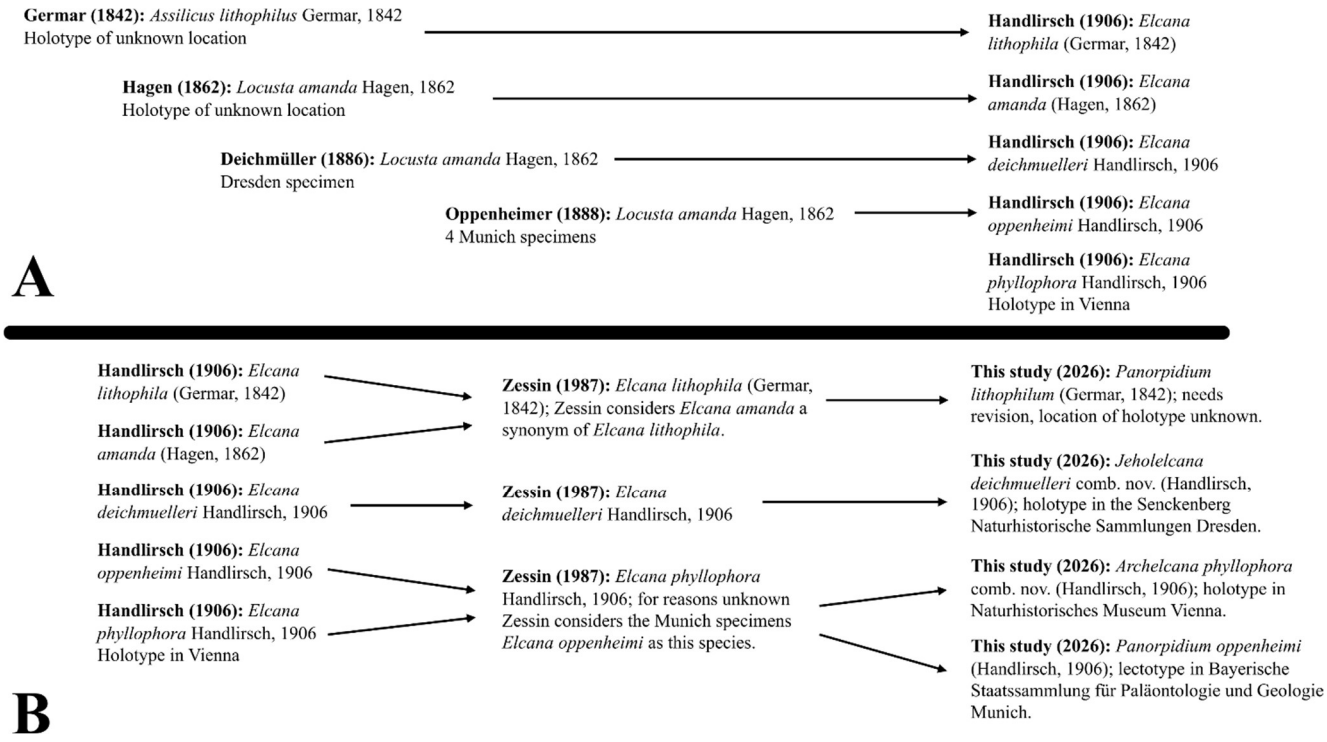


Fig. 9: Taxonomic history of the "*Locusta amanda*-complex". **A.** Development from Germar (1842) and Hagen (1862) to Handlirsch (1906). **B.** Development from Handlirsch (1906) to this study (2026).

Subfamily: Elcaninae Handlirsch, 1906

Genus: *Panorpidium* Westwood, 1854

Type species: *Panorpidium tessellatum* Westwood, 1854

Species: ***Panorpidium oppenheimi*** (Handlirsch, 1906)

Nomenclatural history: *Elcana oppenheimi* Handlirsch, 1906; *Panorpidium oppenheimi* (Handlirsch, 1906) in Cigliano et al. (2025)

Fig. 10-11

Remarks on nomenclature: Oppenheimer (1888) said there were four specimens of *Elcana amanda* (Hagen, 1862) in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie (Bavarian state collection for paleontology and geology), Munich, Germany. Based on two of these specimens (AS VII 799 and AS VII 799 [ex 1891 VI 5]), Handlirsch (1906) established a new species *Elcana oppenheimi*. Following the revision of *Elcana* by Jarzembowski (1996), *E. oppenheimi* was moved to *Panorpidium* in Cigliano et al. (2025).

Holotype: Handlirsch (1906) did not specify which of the two specimens was the designated holotype of its new species (Martin Nose, pers. comm.). He only mentioned that the specimen was presumable a male and had a forewing length of 24 mm. These specifications apply to both specimens (Fig. 11-12). According to Bechly (2015), the holotype of *P. oppenheimi* is supposed to be in the collection of Senckenberg Naturhistorische Sammlungen Dresden, Germany. However, the labels of the Munich specimens clearly state that they are the original and voucher specimens to Handlirsch (1906-1908) (Fig. 12). We asked in Dresden about the holotype of *P. oppenheimi*, but this collection has no records of the specimen (Markus Wilmsen, pers. comm.). Because one of the Munich specimens presented in this study clearly must be the holotype of *P. oppenheimi*, but identification due to lack of information in Handlirsch (1906) is dubious, we here designate the specimen_AS VII 799 [ex 1891 VI 5] (Fig. 11) as the lectotype of *Panorpidium oppenheimi* (Handlirsch, 1906), because the wing venation is slightly better preserved than in the other specimen (AS VII 799) (Fig. 12).

Locality and horizon: Late Jurassic (Tithonian) of Germany (Solnhofen).

Emended diagnosis: Large species with a forewing length of 21.4–25.6 mm and forewing width of 4.5–5.8 mm (values for AS VII 799–AS VII 799 [ex 1891 VI 5]). CuA + CuPaα long. MP short. RP with 11–10 branches. RA with numerous cross veins (ca. 20). ScP with nine to ten branches. ScA with three branches. CP with numerous cross veins (ca. 11) (last three characters based on AS VII 799 [ex 1891 VI 5]).

Emended description: Aspects of the body are almost entirely lost due to preservation. Both specimens have antennae longer than the body (nearly three times longer in AS VII 799 [ex 1891 VI 5]). Pronotum of AS VII 799 shaped like an inverted triangle, with postero-lateral margin without concave curve. Metafemur of AS VII 799 ca. 9 mm long. Metatibia with large spurs, presumably leaf-shaped; smaller spur proximal to leaf-like spurs apparently absent.

Forewing of AS VII 799 [ex 1891 VI 5]: the forewing of this specimen is slightly better preserved than that of AS VII 799. 1A, CuPb and CuPaβ probably fused (however, somewhat

unclear due to preservation). M with four branches, proximal three anterior of RP stem. Coloration pattern not preserved. Other characters are stated in the emended diagnosis. The forewing of the second specimen does not provide any other information.

Remarks: Based on the (assumed) fusion of the anal and cubital veins 1A, CuPb and CuPaβ this species belongs to the subfamily Elcaninae. The three branches of M anterior of the RP stem indeed suggest placement in *Panorpidium*, meaning that this species is the first (and only) in this review that was already placed in the correct genus. This makes *Panorpidium oppenheimi* an important finding, because it is the oldest record of the genus currently recognized (aside from the remaining species in need of revision). As such, its presence in the limestone formation of Late Jurassic Bavaria indicates that the transition from an Archelcaninae dominated Elcanidae fauna in the Early Jurassic to an Elcaninae dominated one had already started by this time.

Panorpidium oppenheimi differs from its congeners most notably in the following aspects (species in need of review not considered; species in need of review are highlighted in Table 1 at the end of the systematic paleontology section): from *P. bimaculatum* Gorochov, Jarzembowski & Coram, 2006), *P. damianii* (Martins-Neto, 1991), *P. parvum* Gorochov, Jarzembowski & Coram, 2006 and *P. spica* Kim, Lee, Nam & Park, 2021 it differs by being larger to much larger. From the Chinese *P. acusicaudum* Tian, Ren & Gu, 2022, *P. validum* Tian, Ren & Gu, 2022 and *P. yixianensis* Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015 it differs by having significantly more branches of RP (seven branches in the Chinese species vs. ten to eleven in *P. oppenheimi*). It differs from *P. proximum* Gorochov et al., 2006 by having more branches of ScP distal of the termination of ScA (five to six vs. three). Lastly, differences from *P. sibiricum* (Sharov, 1968) and *P. tessellatum* Westwood, 1854 are unclear, but probably include less numerous and elaborate branches of ScA as well as cross veins of 1A. However, this impression may be due to a low degree of preservation in these areas in both specimens of *P. oppenheimi*.

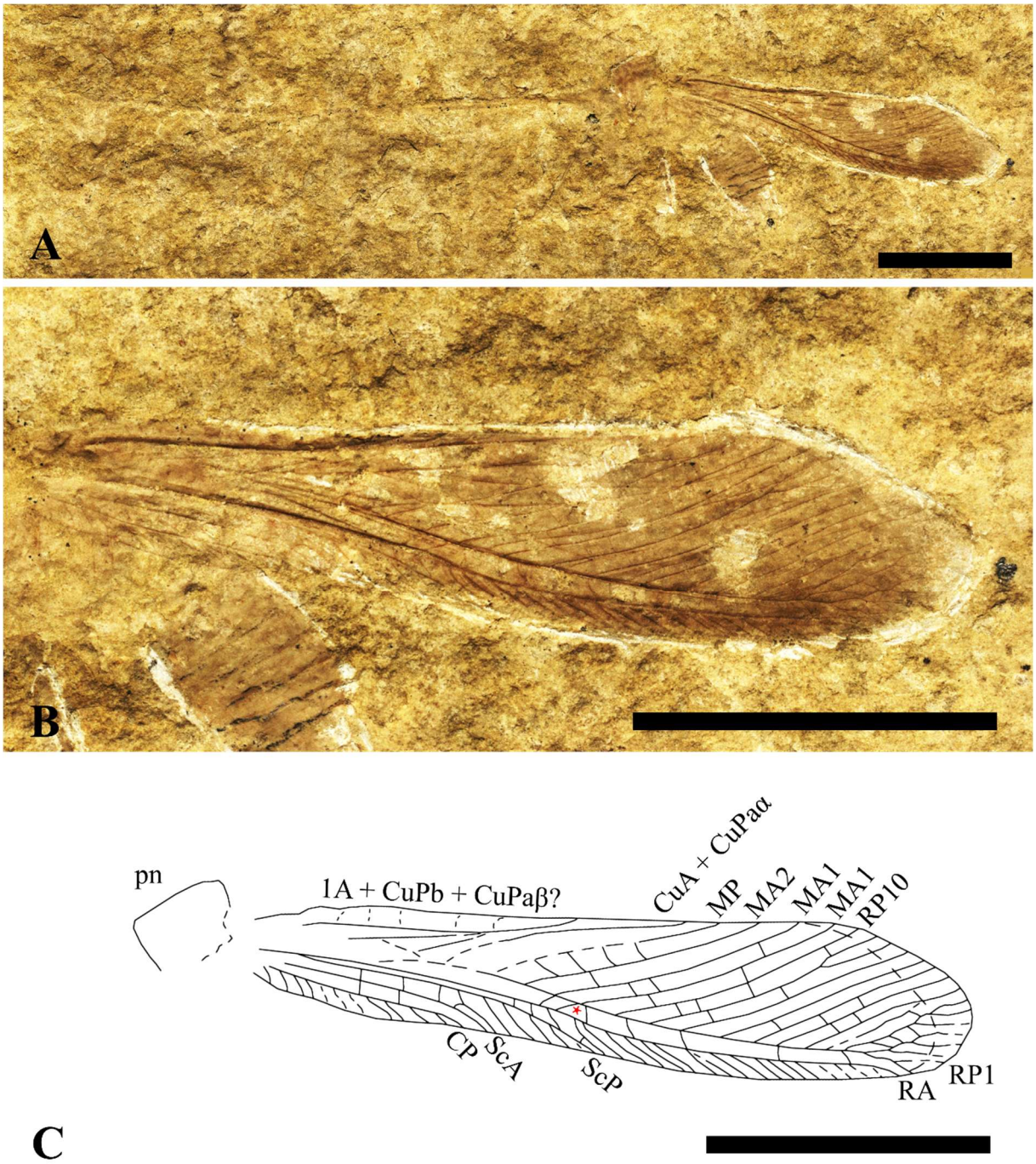


Fig. 10: *Panorpidium oppenheimi* (Handlirsch, 1906) lectotype AS VII 799 [ex 1891 VI 5]. **A.** Overview of complete specimen. **B.** and **C.** Detail and drawing of the forewing. Red star marks the position of the RP stem. **Scale bars** = 10 mm. © SNSB-BSPG/Imelda Hausmann.

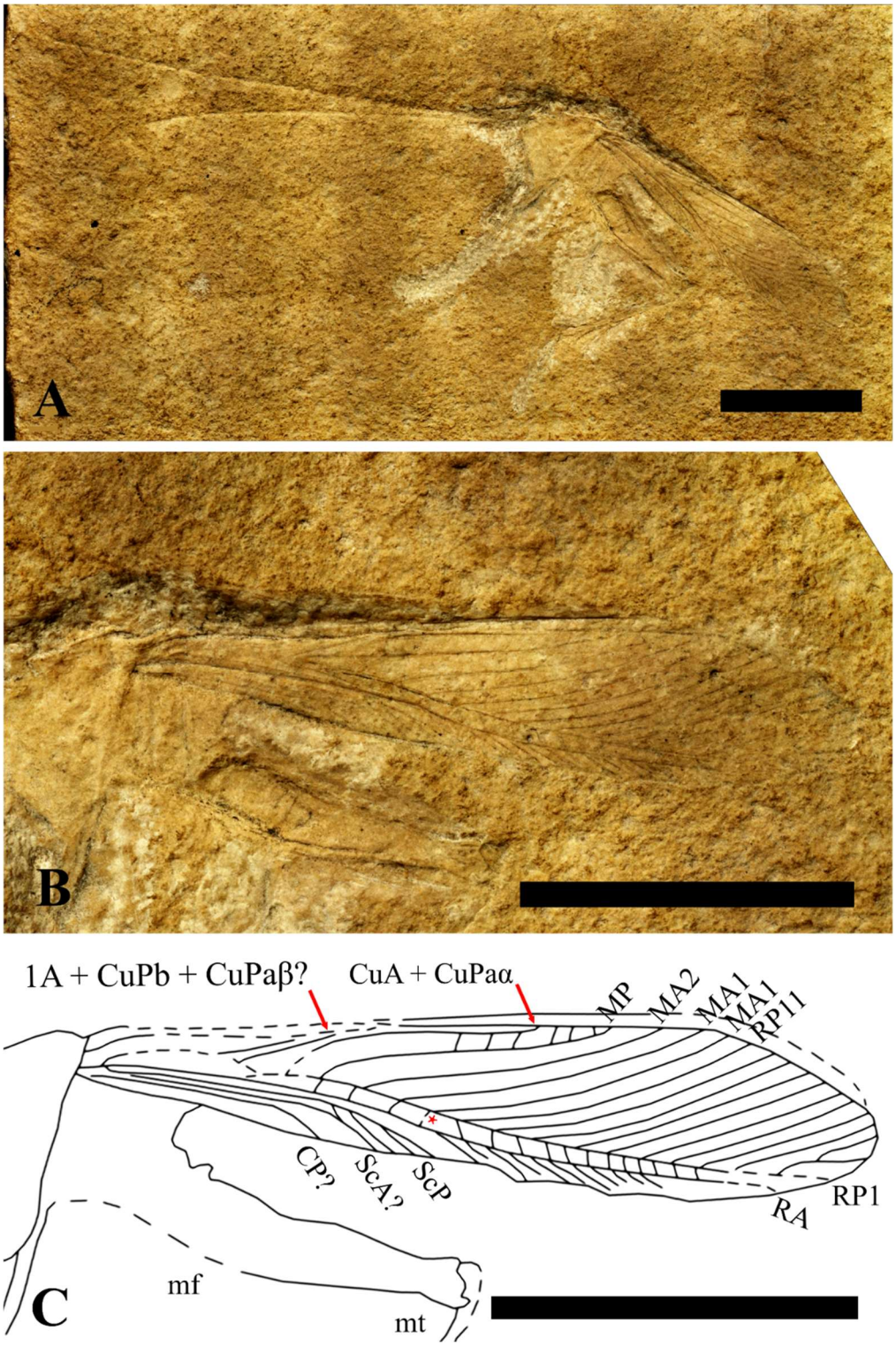


Fig. 11: *Panorpidium oppenheimi* (Handlirsch, 1906) specimen AS VII 799. **A.** Overview of complete specimen. **B.** and **C.** Detail and drawing of the forewing. Red star marks the position of the RP stem. **Scale bars** = 10 mm. © SNSB-BSPG/Imelda Hausmann.

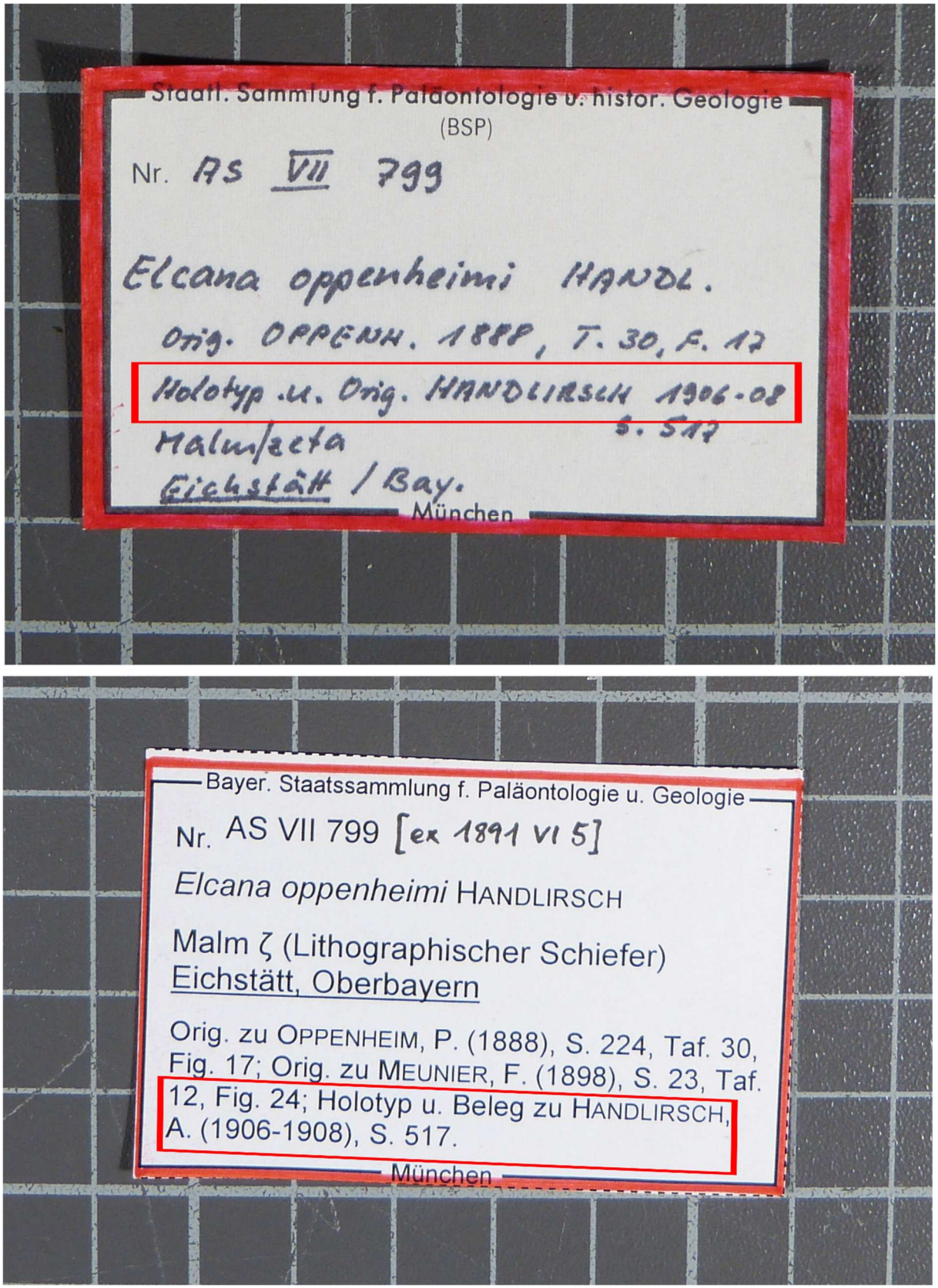


Fig. 12: Label of both specimens of *Panorpidium oppenheimi* (Handlirsch, 1906) in the Bayerische Staatssammlung für Paläontologie und Geologie. Red box marks the part where it indicates both specimens as possible holotypes and originals to Handlirsch (1906-1908). © SNSB-BSPG/Imelda Hausmann.

Genus: ?*Probaisselcana* Gorochov, 1989

Type species: *P. karatavica* (Sharov, 1968)

Species: ***?Probaisselcana plagiata*** (Hagen, 1858) comb. nov.

Nomenclatural history: *Termes plagiatus* Hagen, 1858; *Calotermes plagiatus* (Hagen, 1858) in Heer, 1865; *Elcana plagiata* Handlirsch, 1906; *Panorpidium plagiatus* (Hagen, 1858) in Cigliano et al. (2025)

Fig. 13

Remarks on nomenclature: Another one of Hagen's (1858) alleged termites, this species was included as *Calotermes plagiatus* in Heer (1865). Handlirsch (1906) included it in *Elcana*. After this, the specimen was ignored for over 100 years and pro forma moved to *Panorpidium* in Cigliano et al. (2025) following the revision of *Elcana* by Jarzembowski (1996).

Holotype: A hindwing in the collection of the ETH Zürich, collection number 18070.2. It is currently registered under the old name *Termes plagiatus* as used in the original description by Hagen (1858).

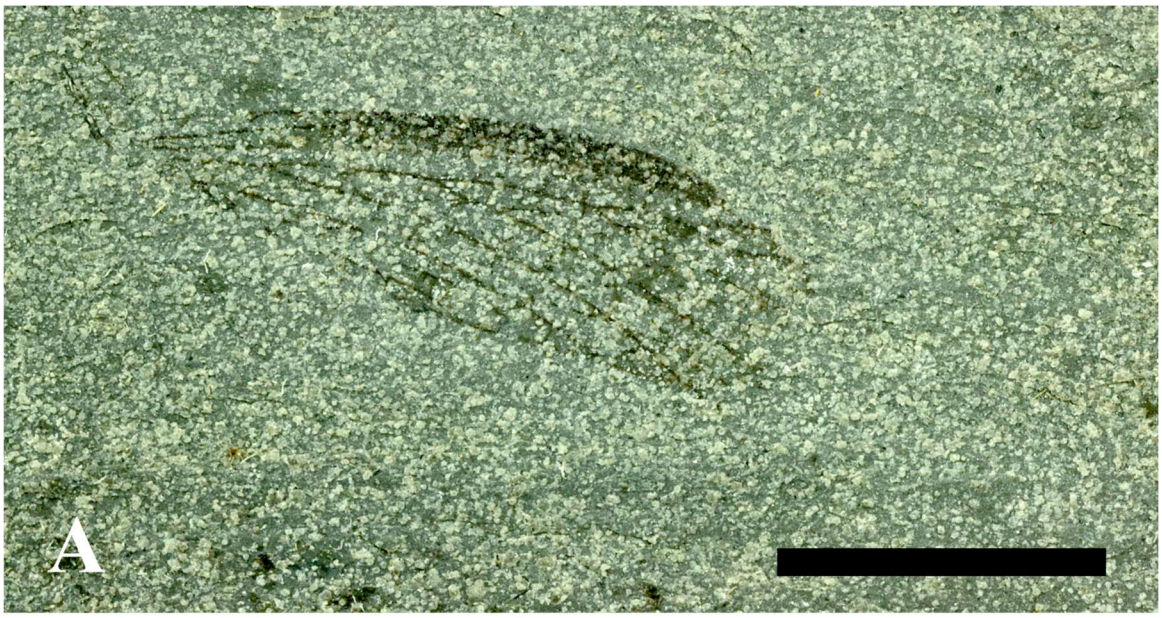
Locality and horizon: Switzerland, Schambelen-Member of the Staffelegg Formation (Insektenmergel), Lower Jurassic (Etter and Felber, 2018)

Emended diagnosis: Hindwing as preserved 10.3 mm long. ScP reaching posterior margin halfway between MP and MA2. RP with three branches.

Emended description: The hindwing is not well preserved. Coloration (if present) is lost, except for in the pterostigma area which is darkened. Cross veins are mostly lost. Otherwise, same as emended diagnosis.

Remarks: The identity of this specimen is dubious. Based on the fusion of M and RP and the short ScP it probably does belong to Elcanidae, but the generic position is difficult to determine due to lack of diagnostic characters in the holotype. The hindwings are known for several species of Elcanidae, among them *Panorpidium acusicaudum* Tian et al., 2022, *Probaisselcana kachinensis* Zhou et al., 2024, *Thagyaminana atawedeia* Schall et al., 2025 and *Archelcana geinitzi* (Heer, 1880) comb. nov. In *P. kachinensis*, *T. atawedeia* and *A. geinitzi,* the stem of RP is located posterior of MP, whereas it is located posterior of MA2 in *P. acusicaudum*.

Unfortunately, the stem of RP is not preserved in *P. plagiatus*. *Thagyaminana atawedeia* and *A. geinitzi* have six and five to six (intraspecific variation in *A. geinitzi*) branches of RP, respectively (Schall et al., 2025; Zessin, 1987). *Panorpidium acusicaudum* has four branches of RP in the left and six branches of RP in the right hindwing (Tian et al., 2022). *Probaisselcana kachinensis* has three branches of RP in both hindwings. However, the species *Probaisselcana euryptera* Tian et al., 2019 has six branches of RP again. In conclusion, the Swiss hindwing could have belonged to *Probaisselcana* as this is the only Elcanidae genus we have definite evidence of having three branches of RP in the hindwing. However, if other Elcanidae species from different genera should be discovered that also feature just three RP branches, *Probaisselcana plagiata* may have to be considered a nomen dubium, because the combination of characters in the hindwing of this species does not allow for an unambiguous diagnosis.



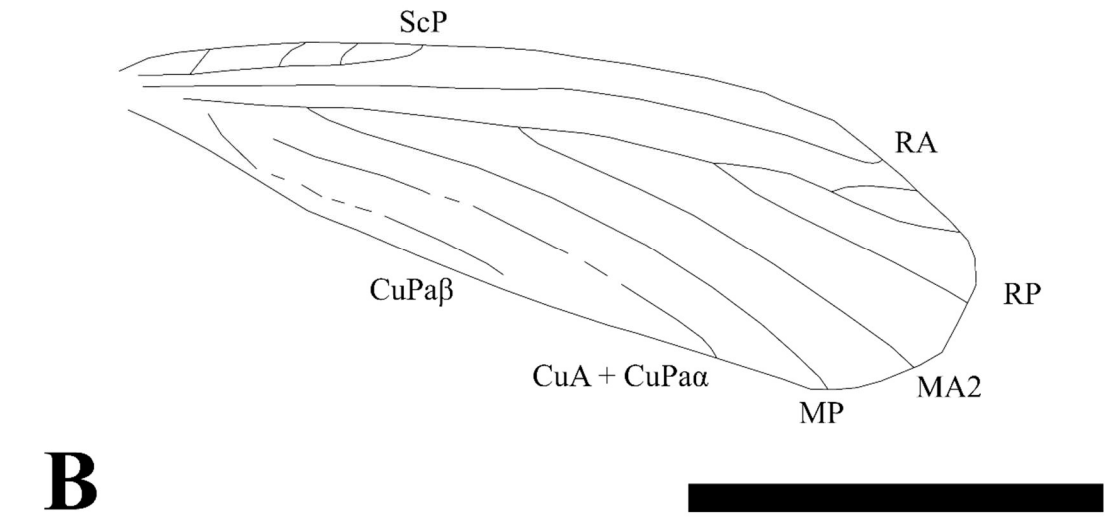


Fig. 13: ?*Probaisselcana plagiata* (Hagen, 1858) comb. nov. holotype in the collection of ETH Zürich, coll. no. 18070.2. **A.** Image of the specimen. **B.** Drawing of the specimen. **Scale bars** = 5 mm.

Table 1: Updated status of the species of *Panorpidium* Westwood, 1854. Green species were reviewed in this study; red species are still in need of revision.

Species prior revision	**Original author**	**Holotype**	**Locality and horizon**	**Suggested new genus post revision**
Panorpidium acusicaudum	Tian, Ren & Gu, 2022	CNU-ORT-LB2011041P/C; Key Lab of Insect Evolution & Environmental Changes, Capital Normal University (CNU), Beijing, China.	China, Yixian; Lower Cretaceous.	Unchanged.
P. angustior	(Handlirsch, 1939)	Forewing; the only record is a figure in Handlirsch, 1939; suspected location of the holotype in the collection of Natural History Museum London (BMNH) (unconfirmed).	UK, Gloucester; Lower Jurassic.	Not considered.
P. beyrichi	(Giebel, 1856)	Fragmentary forewing (missing the base) according to Handlirsch, 1906; location of the holotype in the collection of Natural History Museum London (BMNH) according to Paleobiology Database (unconfirmed).	UK, Purbeck Group; Lower Cretaceous.	Not considered.
P. bimaculatum	Gorochov, Jarzembowski & Coram, 2006	BMB 016391/-2 (part and counterpart); Booth Museum of Natural History, Brighton, UK.	UK, Upper Weald Clay; Lower Cretaceous.	Unchanged.

P. damianii	(Martins-Neto, 1991)	RGMN-1620; image in chapter 8 of this dissertation (p. 287).	Brazil, Crato; Lower Cretaceous.	Unchanged; prior to revision in chapter 8 was *Cratoelcana damianii* Martins-Neto, 1991
P. deichmuelleri	(Handlirsch, 1906)	BaJ1485; Senckenberg Naturhsitorische Sammlungen Dresden, Germany; Fig. 8.	Germany, Eichstätt; Upper Jurassic.	**Jeholelcana deichmuelleri* comb. nov.
P. geinitzi	(Heer, 1880)	MB.I.15.1 (part and counterpart); Museum für Naturkunde (MfN), Berlin, Germany; Fig. 1.	Germany, Dobbertin; Lower Jurassic.	**Archelcana geinitzi* comb. nov.
P. lata	(Sharov, 1968)	PIN 2066/808; Paleontological Museum Juri Orlow, Moscow, Russia.	Kazakhstan, Karatau; Upper Jurassic.	Not considered.
P. liasinum	(Giebel, 1856)	NHMUK I.11676; Natural History Museum, London, UK. Additional specimens (not of type status) with collection number USNM PAL 61389 (3490, 3491, 3493, 3494, 3495), National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.	UK, Strensham and Gloucester; Upper Triassic to Lower Jurassic.	Holotype unavailable for review. USNM PAL 61389 (USA specimens) shown Figs. 2-3.
P. lithophilum	(Germar, 1842)	Location of the holotype unknown (it is not in Munich, Vienna, Dresden or Münster).	Solnhofen, Germany; Upper Jurassic.	Not considered.
P. longicorne	(Handlirsch, 1906)	Location of the holotype unknown (it is not in Munich, Vienna, Dresden or Münster).	Solnhofen, Germany; Upper Jurassic.	Not considered.
P. magnum	(Handlirsch, 1906)	MB.I.06.1 (part and counterpart); Museum für Naturkunde (MfN), Berlin, Germany; Fig. 4.	Germany, Dobbertin; Lower Jurassic.	**Archelcana magna* comb. nov.

P. medium	(Handlirsch, 1906)	MB.I.09.1 (part and counterpart); Museum für Naturkunde (MfN), Berlin, Germany; Fig. 5.	Germany, Dobbertin; Lower Jurassic.	**Archelcana media* comb. nov.
P. mesostenum	(Handlirsch, 1939)	MB.I.0031.1 (part and counterpart); Museum für Naturkunde (MfN), Berlin, Germany.	Germany, Dobbertin; Lower Jurassic.	**Archelcana media* syn. nov.
P. minimum	(Handlirsch, 1906)	MB.I.25.1 (part and counterpart); Museum für Naturkunde (MfN), Berlin, Germany; Fig. 6	Germany, Dobbertin; Lower Jurassic.	**Archelcana minima* comb. nov.
P. minutum	(Sharov, 1968)	PIN 2066/814; Paleontological Museum Juri Orlow, Moscow, Russia.	Kazakhstan, Karatau; Upper Jurassic.	Not considered.
P. oppenheimi	(Handlirsch, 1906)	Lectotype (designated herein) AS VII 799 [ex 1891 VI 5]; Bayerische Staatssammlung für Paläontologie und Geologie, Munich Germany. Fig. 11	Solnhofen, Germany; Upper Jurassic.	Unchanged (but see review of the species above).
P. parvum	Gorochov, Jarzembowski & Coram, 2006	MNEMG 2003.39 [Co34] part and counterpart; Maidstone Museum and Bentlif Art Gallery, Kent, UK.	UK, Lower Weald Clay; Lower Cretaceous.	Unchanged.
P. phyllophorum	(Handlirsch, 1906)	2007z0142/0006; Naturhistorisches Museum Wien, Vienna, Austria; Fig. 7.	Germany, Eichstätt; Upper Jurassic.	**Archelcana phyllophora* comb. nov.
P. plagiatus	(Hagen, 1858)	18070.2; Eidgenössische Technische Hochschule (ETH) Zürich, Zurich, Switzerland; Fig. 13.	Switzerland, Schambelen; Lower Jurassic.	*?*Probaisselcana plagiata* comb. nov.
P. proximum	Gorochov, Jarzembowski & Coram, 2006	MNEMG 2003.33 [DB175/ORTH 1], part and counterpart; Maidstone Museum and Bentlif Art Gallery, Kent, UK.	UK, Durlston Formation; Lower Cretaceous.	Unchanged.

P. reticulatum	(Handlirsch, 1920)	MB.I.0032.1 (part and counterpart); Museum für Naturkunde (MfN), Berlin, Germany.	Germany, Dobbertin; Lower Jurassic.	**Archelcana media* syn. nov.
P. sibiricum	(Sharov, 1968)	PIN 1668/1651; Paleontological Museum Juri Orlow, Moscow, Russia.	Russia, Transbaikalika; Lower Cretaceous.	Unchanged.
P. spica	Kim, Lee, Nam & Park, 2021	GNUE212001; Gongju National University of Education; Republic of Korea.	Korea; Jinju Formation; Lower Cretaceous.	Unchanged.
P. tessellatum	Westwood, 1854	NHM I. 3982 and NHM I. 12262 (part and counterpart); Natural History Museum, London, UK.	UK, Middle Purbeck; Lower Cretaceous.	Unchanged.
P. validum	Tian, Ren & Gu, 2022	CNU-ORT-LB2016067; Key Lab of Insect Evolution & Environmental Changes, Capital Normal University (CNU), Beijing, China.	China, Yixian; Lower Cretaceous	Unchanged.
P. westwoodi UK	(Handlirsch, 1906)	According to PBDB, the holotype is in the collection of the Natural History Museum, London, UK (BMNH) (coll. no. unknown).	UK, Lower Purbeck; Lower Cretaceous.	Not considered.
P. yixianensis	Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015	NIGP159068; Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), China.	China, Yixian; Lower Cretaceous.	Unchanged.

4. Discussion

The results presented in this study show that many species that had previously been assigned to *Panorpidium* Westwood, 1854 were incorrectly placed in the genus. Of the ten species considered in our review, we moved five to *Archelcana* Sharov, 1968, two became synonyms

of *Archelcana media* (Handlirsch, 1906) and one each was assigned to *Jeholecana* Fang et al., 2018 and *Probaisselcana* Gorochov, 1989, respectively. Only a single species, *Panorpidium oppenheimi* (Handlirsch, 1906), could be confirmed as correctly placed in the genus. *Panorpidium*, which included 29 species prior to this revision, now only includes 19 species. Of these, one will probably be moved to *Archelcana* or a closely associated genus of Archelcaninae once the holotype has been reviewed (cf. *Archelcana liasina* (Giebel, 1856)). A further seven still require revision. On the other hand, *Archelcana* now includes eleven species instead of the former six. The present review has been an important step towards understanding the Elcanidae diversity in the Jurassic of Central Europe, after this community was largely ignored during the last decade due to the increased interest in discoveries from Asia (especially China and Burmese amber). Hopefully, the remaining eight species of *Panorpidium* can be reviewed soon too, to finally conclude the taxonomic issue surrounding this genus.

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Part IV: Orthoptera among dinosaurs – their rise to and fall from diversity

Fig. 5.1 *The Tyrant and the Cricket.* After the Cretaceous had ended ca. 66 Mya, non-avian dinosaurs and several major lineages of Mesozoic orthopterans disappeared from the fossil record. But others, like the crickets (Gryllidea Vickery, 1977) and pygmy mole crickets (Tridactylidea Brullé, 1835) survived to the present day.

Skull model from REBOR, depicting *Yutyrannus huali* Xu, Wang, Zhang, Ma, Xing, Sullivan, Hu, Cheng & Wang, 2012 (Scale ca. 1:7.5 based on *Y. huali* specimen ZCDM V5000). The cricket is a female of *Gryllus assimilis assimilis* (Fabricius, 1775) (Jamaican field cricket). Credits: Author.

Preface

The previous three parts of this dissertation have presented investigations of three of the major five lineages of Orthoptera Olivier, 1789 found in the Mesozoic fossil record (Tridactylidea Brullé, 1835 [chapters 1-3], Locustopsoidea Handlirsch, 1906 [chapters 4-6] and Elcanidea Gorochov, 1995 [chapters 7-8, 10]). In chapter 9 I have proposed new phylogenetic relationships of these and the other big fossil lineages, namely Oedischiidea Handlirsch, 1906, Titanoptera Sharov, 1968, Hagloidea Handlirsch, 1906, Gryllidea Vickery, 1977, Tettigoniidea Kevan, 1982 and Acrididea Targioni-Tozzetti, 1882.

The unusual combination of morphological characters revealed by *Ozymandipteryx campana* Schall, Cao & Husemann, 2025 (chapter 1) as well as *Naginipteryx pinna* Schall, Heads & Husemann, in press (chapter 2) has hinted towards the presence of extinct lineages yet unknown. In the first chapter of this fourth part (chapter 11), new taxonomic relationships of Ripipterygidae Ander, 1936 and Tridactylidae Brullé, 1835 are suggested based on findings from the last five years of research on these groups.

Next (chapter 12) we will revisit the Locustopsidae Handlirsch, 1906 and look at aspects of their morphology which have been little known so far but may provide important clues towards deciphering their taxonomy in the future.

In chapter 13 the taxonomic relationships of Elcanidae Handlirsch, 1906 will be analyzed. The new specimens from Burmese amber in this study and previous research have revealed a stunning degree of diversity and new distinct aspects of morphology about this family that suggest the possible existence of previously unrecognized lineages.

The evolution of diversity patterns of Orthoptera over deep time, from their earliest steps in the lush forests of the Carboniferous 300 million years ago to the extant communities that sing in our meadows, fields and forests today, will be the topic of the final chapter of this work (chapter 14). We will witness how the predecessors of Ensifera Chopard, 1921 and Caelifera Ander, 1936 conquered the Paleozoic landscape, how the Big Five Mesozoic lineages diversified and brought Orthoptera to their peak diversity in the Early to mid-Cretaceous, and how the modern fauna rose in the final stages of the Cretaceous to displace elcanids and locustopsids in the changing ecosystems.

This concludes the history of Orthoptera as we know it so far.

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Chapter 11

The lost fossil lineages of Tridactyloidea (Orthoptera: Caelifera)

Abstract

The taxonomy of Tridactyloidea Brullé, 1835 for the families Tridactylidae Brullé, 1835 (pygmy mole crickets) and Ripipterygidae Ander, 1936 (mud crickets) is reviewed, including several fossil discoveries made in the last five years in mid-Cretaceous Burmese amber. Based on a UPGMA cluster analysis of six characters recognized as important for tridactyloid taxonomy, several new lineages are proposed. Ripipterygidae consists of two subfamilies, Ripipteryginae Ander, 1939 and Yakkhapipteryginae subfam. nov., whereby all extant species are found in Ripipteryginae. Yakkhapipteryginae consists of two tribes, Yakkhapipterygini trib. nov. and Naginipterygini trib. nov. Ripipteryginae also consists of two tribes, Ripipterygini trib. nov. and Ozymandipterygini trib. nov. Tridactylidae consists of at least two subfamilies, Xyaninae subfam. nov. and Burmadactylinae subfam. nov. Burmadactylinae consists of two tribes, Burmadactylini trib. nov. and Latedactylini trib. nov. Apomorphies of the new taxa are described. The new study highlights the remarkable diversity of Tridactyloidea in the past, which was likely much greater than in the present day. Thus, tridactyloids should likely be viewed as relics of the Mesozoic fauna that have survived until today.

Keywords: Dentridactylinae, fossil, insect, swimming lamellae, Tridactylinae

1. Introduction

Tridactyloidea Brullé, 1835 or pygmy mole crickets are a little-studied superfamily within the Caelifera Ander, 1936 suborder of the Orthoptera Olivier, 1789. 233 extant species in three families (Tridactylidae Brullé, 1835, Ripipterygidae, Ander, 1939 and Cylindrachetidae Giglio-Tos, 1914) are found on every continent except for Antarctica (Cigliano et al., 2025). No fossils are known of Cylindrachetidae, but Tridactylidae and Ripipterygidae were discovered in various Cretaceous deposits (e.g. Gorochov et al., 2006; Martins-Neto, 1990; Zhao et al., 2024) and in Eocene (Azar and Nel, 2008) and Miocene amber (Heads, 2010; Poinar, 2020).

Recently, three new species of Ripipterygidae (chapters 1-2), one putative new ripipterygid (*Naginipteryx pinna* Schall, Heads & Husemann, in press (chapter 2)) and two new species of Tridactylidae Brullé, 1835 (chapter 3) from mid-Cretaceous amber of Northern Myanmar were reported. With these additions, a total of 22 fossil species of Tridactyloidea Brullé, 1835 are now described from this lagerstätte. This is a remarkable degree of diversity, considering the taxon's low diversity today. In combination with the remaining ten fossil species from other localities, this means fossil Tridactyloidea constitute about 12% of overall diversity of the taxon – significantly more than in any other higher-level taxon of Orthoptera present in modern times (except Hagloidea Handlirsch, 1906, but see chapter 9 for Prophalangopsidae Kirby, 1906 – the suspected relic family of Hagloidea – not actually belonging to this taxon).

The small diversity of extant Tridactyloidea, paling in comparison with their better known cousins from the Acrididea Targioni-Tozzetti, 1882, is perhaps the reason why they are severely underrepresented in the literature. Except for one study by Baena-Bejarano et al. (2015), who attempted to solve the phylogeny of modern Ripipterygidae based on morphology, no phylogenetic analysis on Tridactyloidea has been conducted so far.

After the enigmatic Cylindrachetidae Giglio-Tos, 1914 (which are absent from the fossil record and not a subject of this study), the Ripipterygidae or mud crickets are the smaller of the families within Tridactyloidea. They include 82 species (83 if one counts the earlier mentioned *N. pinna*). The fossil forms - 11 (12) species – are known exclusively from Cretaceous amber of Myanmar, whereas extant diversity is restricted to the northern half of South America as well as Central America (Cigliano et al., 2025). Ripipterygidae include one subfamily, the Ripipteryginae Ander, 1939 which houses the two extant genera *Mirhipipteryx* Günther, 1969 and *Ripipteryx* Newman, 1834. The fossil forms are not assigned to a subfamily as of yet. *Ripipteryx* differs from *Mirhipipteryx* by 1) a larger body size (> 5 mm), 2) greater interocular distance between compound eyes (at least half the width of compound eyes), 3) metatarsus approximately equal in length to apical metatibial spurs (smaller than apical spurs in *Mirhipipteryx*) and 4) the distinctly sclerotized lateral valvulae of the phallus (Baena-Bejarano and Heads, 2015).

The genus *Ripipteryx* is organized in five superspecies groups (Günther, 1969; Heads, 2010), which are diagnosed mainly based on morphological differences of the male terminalia and phallic complex (Baena-Bejarano and Heads, 2015). However, Heads (2010) questioned the monophyly of some of these groups, and this was apparently supported by a preliminary phylogenetic analysis based on morphology by Baena-Bejarano that was never published.

The type family of Tridactyloidea are the Tridactylidae. With a total of 146 extant species and a distribution on every continent except for Antarctica, they are the most diverse taxon of the superfamily. Tridactylidae includes three superfamilies. The fossil Mongoloxyinae Gorochov, 1992 are known from the Early Cretaceous and are characterized by a forewing venation consisting of more well-developed veins in comparison with the reduced venation of extant Tridactylidae (Gorochov et al., 2006). A nymph specimen *Birmitoxya intermedia* Gorochov, 2010 from mid-Cretaceous Burmese amber was attributed to this subfamily, because the unusual combination of characters did not allow placement in any other taxon of Tridactyloidea. Yet, the forewing of this species is unknown, thus placement in Mongoloxyinae is not unambiguous. Recently, Schall et al. (2025) found the forewing venation of *Burmecaelinus yungyenwangae* Schall, Cumming, Lian & Husemann, 2025, a member of the enigmatic Burmese amber family Burmecaelidae Uchida, Husemann & Kotthoff, 2024 conspicuously similar to Mongoloxyinae. However, as no body fossils of unambiguous members of the subfamily are known, the relationship between Mongoloxyinae and Burmecaelidae remains unanswered for now.

The two largely extant subfamilies of Tridactylidae are the Tridactylinae Brullé, 1835 and Dentridactylinae Günther, 1979. They differ by the presence of a subapical denticular process which is present in Dentridactylinae but absent in Tridactylinae (Baena-Bejarano and Heads, 2018). Systematics of Tridactylidea are little explored. A mitogenome-based phylogenetic analysis supported the relationships of the extant families as Cylindrachetidae + (Tridactylidae + Ripipterygidae) (Yahyaoğlu et al., 2023). The analysis suggested the Tridactylidae genus *Ellipes* Scudder, 1902 as a sister group to a crown clade consisting of *Xya* Latreille, 1809 and *Tridactylus* Olivier, 1789. However, the authors used a small taxon sampling, comprising only of one member of Cylindrachetidae and Ripipterygidae each, as well as five members of Tridactylidae, whereby all five specimens were from the subfamily Tridactylinae (Yahyaoğlu et al., 2023).

Standing taxonomic relationships within Ripipterygidae + Tridactylidae are based on morphological aspects of extant forms. However, numerous discoveries of the last five years (e.g. Zhao et al., 2024; chapters 1-3) suggest that the diversity of these groups in the ancient past may have been higher than today. Therefore, when delimiting lineages of Tridactyloidea, fossil forms should be considered more directly. Here, I present a new hypothesis for the taxonomy and systematics of pygmy mole crickets (Tridactylidae and Ripipterygidae) based on a cluster analysis of morphological characters. Taking both the most recent fossil findings as well as extant taxa into account, relationships within both families reveal several possible

lineages exclusive to the fossil record, suggesting that modern Tridactyloidea, and especially Ripipterygidae, are merely a relic taxon compared to their once thriving Mesozoic diversity.

2. Materials and methods

2.1 Taxon sampling

In total, 32 species of Tridactyloidea (12 Ripipterygidae [3 extant + 9 fossil] and 20 Tridactylidae [11 extant + 9 fossil] were compared based on six morphological characters: 1) cercus segmentation, 2) inflation of mesotibia, 3) presence of swimming lamellae, 4) ratio metatarsus/apical metatibial spur length, 5) presence of metatarsal denticular process, 6) presence of hindwings (Table 1). Characters 1 and 2 are used to differentiate between Tridactylidae and Ripipterygidae (chapter 2). Swimming lamellae are a conspicuous character found in many extant Tridactylidae genera and the fossil *Guntheridactylus grimaulti* Azar and Nel, 2008 from Eocene French amber. Character 4 is used to differentiate between *Mirhipipteryx* and *Ripipteryx* (see introduction) and varies significantly between fossil and extant taxa. Character 5 separates the extant subfamilies of Tridactylidae (see introduction), but some fossil species attributed to Ripipterygidae feature a denticular process on their metatarsus, too (see Gu et al., 2022). The presence of hindwings (character 6) was included, because many of the fossil tridactylids lack hindwings (e.g. Fan et al., 2023; Zheng et al., 2023; chapter 3), whereas they are usually present in fossil ripipterygids (e.g. Xu et al., 2020; Zhao et al., 2023; chapters 1-2).

Table 1 Taxon and character sampling of Tridactyloidea Brullé, 1835 for a cluster analysis based on morphological data. [1]https://www.gbif.org/occurrence/4160966651. [2]Available at: https://www.ideals.illinois.edu/items/113054. [3]https://inaturalist.ca/taxa/755769-Bruntridactylus-tartarus. "Ref." (= Reference) in column "Data obtained from" means data in columns 3-8 is based on the publication stated after the taxon name in column two (i.e. the original description of the species) and provided in the reference list. "Ch." (= Chapter) refers to a chapter of this dissertation where the respective species is described. The question mark (?) for *Naginipteryx pinna* in column 7 is because presence of denticular process is suggested for this species but cannot be confirmed based on the only known specimen.

Family	Species	Cercus two-segmented	Mesotibia distinctly inflated	Swimming lamellae present	Metatarsus/apical metatibial spur length	Presence of metatarsal denticular process	Hindwings present	Data obtained from
Ripipterygidae Ander, 1939	*Archaicaripipteryx rotunda* † Xu, Zhang, Jarzembowski & Fang, 2020	no	no	no	2.2	yes	yes	Ref.
	Burmaripipteryx oblongus † Zhao, Xu, Jarzembowski, Fang & Xiao, 2023	no	yes	no	3.4	yes	yes	Ref.
	Yakkhapipteryx gracilis †	no	no	no	3.6	yes	yes	Ref.

	(Gu, Zheng, Cao & Yue, 2022)							
	Yakkhapipteryx mirus † (Gu, Zheng, Cao & Yue, 2022)	no	no	no	2.2	yes	yes	Ref.
	Magnidactylus robustus † (Xu, Fang & Jarzembowski, 2020)	no	yes	no	0.02	no (tarsus vestigial)	yes	Ref.
	Kallosripipteryx zhangi † (Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024)	no	yes	no	2.5	yes	yes	Ref.
	Ozymandipteryx campana † Schall, Cao & Husemann, 2025	no	no	no	0.03	no (tarsus vestigial)	yes	Ch. 1
	Naginipteryx pinna † Schall, Heads & Husemann, in press (chapter 2)	no	yes	no	2.5	yes (?)	yes	Ch. 2

	Mirhipipteryx antillarum † Heads, 2010	no	no	no	0.68	no	yes	Ref.
	Ripipteryx diegoi Baena-Bejarano and Heads, 2015	no	no	no	1.1	no	yes	Ref.
	Ripipteryx guacharoensis Baena-Bejarano and Heads, 2015	no	no	no	0.74	no	yes	Ref.
	Ripipteryx gorgonaensis Baena-Bejarano and Heads, 2015	no	no	no	0.85	no	yes	Ref.
Tridactylidae Brullé, 1835	*Burmadactylus tenuicerci* † Fan, Gu & Cao, 2023	yes	yes	no	3.5	yes	no	Ref.
	Burmadactylus grimaldii † Heads, 2009	yes	yes	no	2.7	yes	no	Ref.
	Cascogryllus lobiferus † Poinar, 2020	yes	yes	no	2.1	no	no	Ref.

	Guntheridactylus grimaulti † Azar and Nel, 2008	yes	yes	yes	1.4	yes	no	Ref.
	Archaeoellipes engeli † Heads, 2010	yes	yes	no	0.69	no	yes	Ref.
	Latedactylus longapedi † Zheng, Cao & Gu, 2023	yes	yes	no	3.3	no	no	Ref.
	Phyllotridactylus wangi † Xu, Wang, Fan, Jarzembowski, Fang, Wang, Li, Zhuo, Ding & Engel, 2022	yes	yes	no	2.9	no	no	Ref.
	Ellipes dominicana † Poinar, 2020	yes	yes	no	0.95	no	no	Ref.
	Hiemalidactylus eileenae † in press (chapter 3)	yes	yes	no	3.2	no	no	Ch. 3
	Ellipes deyrupi Woo, 2021	yes	yes	no	0.02	no	no	Ref.

	Ellipes eisneri Deyrup, 2005	yes	yes	no	0.03	no	no	Woo et al. (2021)
	Ellipes monticolus Günther, 1977	yes	yes	no	0.03	no	no	Woo et al. (2020)
	Xya sichuanensis Cao, Shi & Yin, 2018	yes	yes	yes	0.03	no	yes	Zhang et al. (2022)
	Xya yunnaensis Cao, Rong & Naveed, 2020	yes	yes	yes	< 0.05	no	yes	Ref.
	Xya xishangbanna Cao, Rong & Naveed, 2020	yes	yes	yes	< 0.05	no	yes	Ref.
	Neotridactylus apicialis (Say, 1825)	yes	yes	yes	1.1	no	yes	GBIF[1]
	Dentridactylus quadratus Baena-Bejarano and Heads, 2018	yes	yes	no	2.7	yes	no	Ref.
	Dentridactylus truncatus	yes	yes	no	2.2	yes	no	Ref.

	Baena-Bejarano and Heads, 2018							
	Afrotridactylus spiralatus Günther, 1994	yes	yes	yes	0.23	no	yes	Dissertation of Baena-Bejarano (2019)[2]
	Bruntridactylus tartarus (Saussure, 1874)	yes	yes	yes	1.3	yes	yes	iNaturalist Canada[3]

2.2 Cluster analysis

The data from Table 1 was translated into a multistep matrix. Columns 3, 4, 5, 7, 8 were coded as no = 0; yes = 1. Column 6 was coded as < 0.5 = 0; 0.5-1.5 = 1; > 1.5 = 2.

The matrix was manually translated into a Nexus file (appendix 1). A UPGMA (unweighted pair-group method with arithmetic mean) analysis was performed in PAUP v. 4.0a169 (Swofford, 2003) with all settings kept at default. The resulting dendrogram was saved and uploaded to iTOL (Letunic and Bork, 2024). UPGMA is a clustering method based on the average differences of (in this case) morphological data from different taxa (Gronau and Moran, 2007). However, it is not a sufficient method for providing robust hypotheses of evolution (phylogenies) (Farris, 1971). Here, I use UPGMA as a means of illustrating groups of taxa that are clustering together based on the presence/absence of certain characters. In that sense, the interpretations derived from the analysis are of taxonomic nature (i.e. depict distinct taxonomic units based on proposed apomorphies), but do not necessarily depict phylogenetic relationships.

Further modifications to the dendrogram were made in Inkscape v. 1.4 (the Inkscape Team, 2025). Images of apomorphies adjacent to the results shown in Fig. 1 were created in GIMP v. 3.0.2-1 (the GIMP Team, 2025).

3. Results

UPGMA recovered the two families Ripipterygidae Ander, 1939 and Tridactylidae Brullé, 1835 as monophyletic. Ripipterygidae consists of two clades. One of them includes most fossil taxa, the other the extant representatives of *Ripipteryx* Newman, 1834 and the Miocene amber species *Mirhipipteryx antillarum* Heads, 2010 next to the Cretaceous Burmese amber species *Magnidactylus robustus* Xu, Fang & Jarzembowski, 2020 and *Ozymandipteryx campana* Schall, Cao & Husemann, 2025 (chapter 1). The clade exclusively comprised of fossil taxa had two subclades. The first includes *Yakkhapipteryx* Schall, Cao & Husemann, 2025 (chapter 1) and *Archaicaripipteryx* Xu, Zhang, Jarzembowski & Fang, 2020. The second subclade includes *Naginipteryx* Schall, Heads & Husemann, in press (chapter 2), *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023, and *Kallosripipteryx* Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024.

Tridactylidae consist of two clades. The first includes all the genera with swimming lamellae on their metatibia, namely *Xya* Latreille, 1809, *Afrotridactylus* Günther, 1994, *Neotridactylus* Günther, 1972, *Bruntridactylus* Günther, 1979 and the Eocene *Guntheridactylus grimaulti* Azar

and Nel, 2008. The second clade includes *Ellipes* Scudder, 1902 and *Archaeoellipes* Heads, 2010, the Burmese amber genera *Hiemalidactylus* Schall, Gu & Husemann, in press (chapter 3), *Phyllotridactylus* Xu, Wang, Fan, Jarzembowski, Fang, Wang, Li, Zhuo, Ding & Engel, 2022, *Latedactylus* Zheng, Cao & Gu, 2023, *Cascogryllus* Poinar, 2020 and *Burmadactylus* Heads, 2009 as well as *Dentridactylus* Günther, 1974. Among the Burmese amber taxa and *Dentridactylus*, two clades can be recognized. One includes *Dentridactylus* and *Burmadactylus*, the other *Hiemalidactylus*, *Phyllotridactylus*, *Latedactylus* and *Cascogryllus*.

Based on the findings presented, I propose several new taxa on the subfamily and tribe level within Tridactylidae and Ripipterygidae which are formally described below.

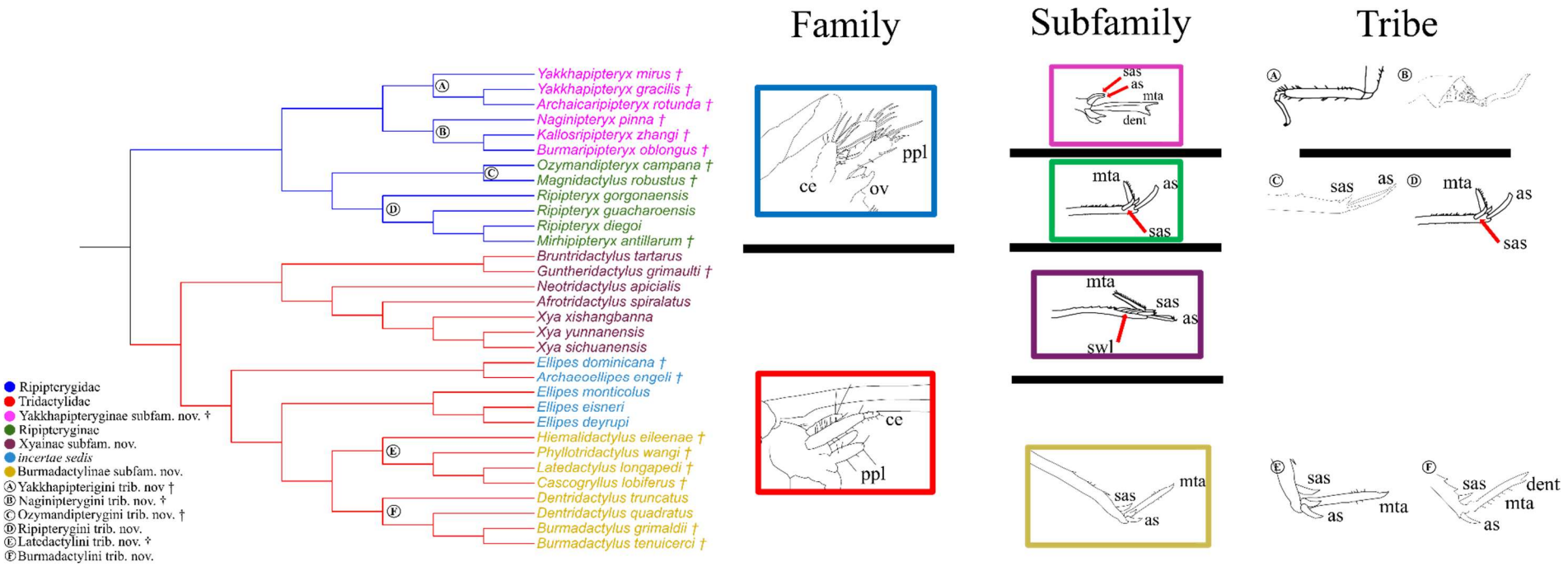
Family
Subfamily
Tribe
Yakkhapipteryx mirus †
Yakkhapipteryx gracilis †
Archaicaripipteryx rotunda †
Naginipteryx pinna †
Kallosripipteryx zhangi †
Burmaripipteryx oblongus †
Ozymandipteryx campana †
Magnidactylus robustus †
Ripipteryx gorgonaensis
Ripipteryx guacharoensis
Ripipteryx diegoi
Mirhipipteryx antillarum †
Bruntridactylus tartarus
Guntheridactylus grimaulti †
Neotridactylus apicialis
Afrotridactylus spiralatus
Xya xishangbanna
Xya yunnanensis
Xya sichuanensis
Ellipes dominicana †
Archaeoellipes engeli †
Ellipes monticolus
Ellipes eisneri
Ellipes deyrupi
Hiemalidactylus eileenae †
Phyllotridactylus wangi †
Latedactylus longapedi †
Cascogryllus lobiferus †
Dentridactylus truncatus
Dentridactylus quadratus
Burmadactylus grimaldii †
Burmadactylus tenuicerci †
Ⓐ
Ⓑ
Ⓒ
Ⓓ
Ⓔ
Ⓕ
Ripipterygidae
Tridactylidae
Yakkhapipteryginae subfam. nov. †
Ripipteryginae
Xyainae subfam. nov.
incertae sedis
Burmadactylinae subfam. nov.
Ⓐ Yakkhapipterigini trib. nov †
Ⓑ Naginipterygini trib. nov. †
Ⓒ Ozymandipterygini trib. nov. †
Ⓓ Ripipterygini trib. nov.
Ⓔ Latedactylini trib. nov. †
Ⓕ Burmadactylini trib. nov.
ppl
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Fig. 1 Morphology-based UPGMA of 32 species of Tridactyloidea Brullé, 1835 and six characters. Blue branches mark Ripipterygidae Ander, 1939, red branches mark Tridactylidae Brullé, 1835. Colorations of taxa names correspond to different (newly proposed) subfamilies. Letters in circles indicate newly proposed tribes. On the right, apomorphies of families, subfamilies and tribes are shown. **Family (blue):** abdominal morphology of *Naginipteryx pinna* Schall, Heads & Husemann, in press (chapter 2), specimen GPIH07232 (holotype), female. **Family (red):** the same of *Ellipes deyrupi* Woo, 2021 (after Woo (2021), Fig. 3B). **Subfamily (pink):** apical metatibia and metatarsus of *Yakkhapipteryx gracilis* (Gu, Zheng, Cao & Yue, 2022), specimen SICAU-A-085 (holotype), female. **Subfamily (green):** the same of *Ripipteryx gorgonaensis* Baena-Bejarano and Heads, 2015, specimen IvaH-E 113896 (holotype), male (after Baena-Bejarano and Heads (2015), Fig. 4). **Subfamily (violet):** the same of *Guntheridactylus grimaulti* Azar and Nel, 2008 (after Azar and Nel (2008) Fig. 3D), specimen PA 15270 1/7 (holotype), male. **Subfamily (gold):** the same of *Hiemalidactylus eileenae* Schall, Gu & Husemann, in press (chapter 3), specimen GPIH07247 (holotype), sex unknown. **Tribe A:** Mesotibia and tarsus of *Yakkhapipteryx gracilis*. **Tribe B:** the same of *Naginipteryx pinna*. **Tribe C:** apical metatibia and tarsus (not seen) of *Ozymandipteryx campana* Schall, Cao & Husemann, 2025 (chapter 1), specimen GPIH07209 (holotype), sex unknown. **Tribe D:** apical metatibia and tarsus of *Ripipteryx gorgonaensis*. **Tribe E:** apical metatibia and tarsus of *Hiemalidactylus eileenae*. **Tribe F:** the same of *Burmadactylus tenuicerci* Fan, Gu & Cao, 2023 (after Fan et al. (2023), Fig. 1F), specimen LNU-22 (holotype), sex unknown. **Abbreviations:** as = apical spur; ce = cercus; dent = denticular process; mta = metatarsus; ov = ovipositor; ppl = paraproctal lobe; sas = subapical spur; swl = swimming lamellae.

4. Systematic paleontology

Order Orthoptera Olivier, 1789

Suborder Caelifera Ander, 1936

Infraorder Tridactylidea Brullé, 1835

Superfamily Tridactyloidea Brullé, 1835

Family Ripipterygidae Ander, 1939

Subfamily Ripipteryginae Ander, 1939

Included tribes: Ozymandipterygini trib. nov.; Ripipterygini trib. nov.

Included genera: *Magnidactylus* Xu et al., 2020; *Mirhipipteryx* Günther, 1969; *Ozymandipteryx* Schall, Cao & Husemann, 2025 (chapter 1); *Ripipteryx* Newman, 1834

Horizon: Cretaceous amber of Myanmar (Ozymandipterygini) and Miocene-today of South and Central America (Ripipterygini).

Emended diagnosis: Within the Ripipterygidae, members of this subfamily are characterized by the absence of a subapical denticular process of the metatarsus. If the metatarsus is too vestigial to be seen (*Ozymandipteryx* and *Magnidactylus*), the absence of a denticular process is assumed. This is based on *Xya* and *Ellipes* from the Tridactylidae, which do not feature a denticular process either, while having metatarsi of very similar morphology.

Remarks: This subfamily, originally a formal taxon to house all extant diversity of Ripipterygidae, is now expanded to include the fossil Cretaceous forms without a subapical denticular process. Interestingly, in these fossil forms, the metatarsus cannot be seen. It is assumed that this is because it is vestigial, similar to the Tridactylidae genera *Ellipes* and *Xya*. The Ripipteryginae include two tribes, Ripipterygini trib. nov. (Miocene-today) and the Ozymandipterygini (Cretaceous).

Tribe **Ripipterygini** trib. nov.

Included genera: *Mirhipipteryx* Günther, 1969; *Ripipteryx* Newman, 1834

Etymology: After the type genus *Ripipteryx*, assigned herein.

Horizon: Miocene of Central America-today in South and Central America.

Diagnosis: Differs from Ozymandipterygini by a ratio of the metatarsus/apical metatibial spur length of 0.68-1.1 (vs. smaller than 0.5 in Ozymandipterygini).

Remarks: This tribe is formally equal to Ripipteryginae prior to the recognition of Ozymandipterygini. It houses the extant diversity of Ripipteryginae as well as their direct ancestors from Miocene amber of the Dominican Republic. This is the only one of four tribes of Ripipterygidae currently recognized that has survived the end-Cretaceous mass extinction.

Tribe **Ozymandipterygini** trib. nov.

Included genera: *Magnidactylus* Xu, Fang & Jarzembowski, 2020; *Ozymandipteryx* Schall, Cao & Husemann, 2025 (chapter 1)

Etymology: After the type genus *Ozymandipteryx*, assigned herein.

Horizon: Cretaceous amber of Myanmar.

Diagnosis: Differs from Ripipterygini by a ratio of the metatarsus/apical metatibial spur length less than 0.5. More specifically, in the two genera assigned to this tribe, the metatarsus is too small to be seen in the fossil specimens. It is likely vestigial, similar to the tridactylids *Ellipes* and *Xya*.

Remarks: This tribe is only known from the Cretaceous amber of Myanmar. Whether or not it truly forms a sister clade to the Ripipterygini or should rather be interpreted as a separate subfamily is unclear. More findings of this apparently rare lineage (only two specimens are known) will help answer this question in the future.

Subfamily **Yakkhapipteryginae** subfam. nov.

Included tribes: Naginipterygini trib. nov.; Yakkhapipterygini trib. nov.

Included genera: *Abaddonella* Schall, Heads & Husemann, in press (chapter 2); *Archaicaripipteryx* Xu, Zhang, Jarzembowski & Fang, 2020; *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023; *Kallosripipteryx* Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024; *Naginipteryx* Schall, Heads & Husemann, in press (chapter 2); *Yakkhapipteryx* Schall, Cao & Husemann, 2025 (chapter 1)

Etymology: After the type genus *Yakkhapipteryx*, assigned herein.

Horizon: Cretaceous amber of Myanmar.

Diagnosis: This subfamily differs from the Ripipteryginae by the presence of a subapical denticular process on the metatarsus. This process can be very conspicuous (see for example *Yakkhapipteryx gracilis* (Fig. 1)) or much less pronounced (compare *Kallosripipteryx*).

Remarks: This subfamily is only known from the Cretaceous amber of Myanmar. The presence of a subapical denticular process in Ripipterygidae is interesting, as this character is only associated with Tridactylidae: Dentridactylinae in modern Tridactyloidea. Therefore, it is perhaps more likely that the denticular process was present in the common ancestor of Tridactylidae + Ripipterygidae and secondarily lost in the groups where it is not featured.

Tribe **Naginipterygini** trib. nov.

Included genera: *Abaddonella* Schall, Heads & Husemann, in press (chapter 2); *Burmaripipteryx* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023; *Kallosripipteryx* Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024; *Naginipteryx* Schall, Heads & Husemann, in press (chapter 2)

Etymology: After the type genus *Naginipteryx*, assigned herein.

Horizon: Cretaceous amber of Myanmar.

Diagnosis: Differs from Yakkhapipterygini by an inflated mesotibia. As with the denticular process in the entire subfamily described before, this character can be very conspicuous (*Naginipteryx pinna* Schall, Heads & Husemann, in press (chapter 2)) or rather subtly developed (*Burmaripipteryx oblongus* Zhao, Xu, Jarzembowski, Fang & Xiao, 2023). In some cases, namely *Burmaripipteryx* and *Abaddonella*, this makes attribution to this subfamily not unambiguous. Further diagnostic characters that may become apparent with future findings will help to resolve this issue.

Tribe **Yakkhapipterygini** trib. nov.

Included genera: *Archaicaripipteryx* Xu, Zhang, Jarzembowski & Fang, 2020; *Yakkhapipteryx* Schall, Cao & Husemann, 2025, chapter 1

Etymology: After the type genus *Yakkhapipteryx*, assigned herein.

Horizon: Cretaceous amber of Myanmar.

Diagnosis: Differs from Naginipterygini by an uninflated mesotibia.

Remarks: The third tribe of Ripipterygidae that is only known from Cretaceous Myanmar amber. Diversity of this family in the amber is remarkable. It shows that they once where far more diverse than today and also more broadly distributed, as Ripipterygini are only found in South and Central America.

Genera *incertae sedis*: *Ciconipteryx* Schall, Cao & Husemann, 2025 (chapter 1).

Possible placements: Because the metatarsus of this genus is unknown, subfamily assignment is not possible. The uninflated mesotibia exclude it from Naginipterygini, but all other three tribes are potential affiliations.

Family Tridactylidae Brullé, 1835

Subfamily **Xyainae** subfam. nov.

> Included genera: *Afrotridactylus* Günther, 1994; *Bruntridactylus* Günther, 1979; *Guntheridactylus* Azar and Nel, 2008; *Neotridactylus* Günther, 1972; *Tibetxya* Cao, Yang, Shen & Yin, 2021; *Tridactylus* Olivier, 1789; *Xya* Latreille, 1809

Etymology: After the type genus *Xya*, assigned herein.

Horizon: Eocene of France until today with global distribution (except for Antarctica).

Diagnosis: Characterized by the presence of swimming lamellae on the dorsal side of the metatibiae (secondarily absent in *Tibetxya*). The metatarsus is reduced in members of *Afrotridactylus* and very reduced in *Xya* and *Tibetxya*.

Remarks: Xyainae is a successful surviving lineage of Tridactyloidea. Genera of this subfamily are globally distributed (except for Antarctica) and include the modern diversity of Tridactylidae (Cigliano et al., 2025). *Guntheridactylus grimaulti* Azar and Nel, 2008 from Eocene French amber is the oldest known member of Xyainae. Until now, no tridactyloid with swimming lamellae was discovered from the Cretaceous, suggesting that this subfamily evolved relatively recently, supposedly after the end-Cretaceous mass extinction. The genus *Tridactylus* was not included in the cluster analysis presented above. However, it can be attributed to this subfamily, because it is very similar to *Neotridactylus* (in fact, they would have the exact same combination of characters in the multistep matrix resulting from Table 5.1, see above). The genus *Ellipes* Scudder, 1902 and the associated *Archaeoellipes* Heads, 2010 from Miocene amber may belong to this subfamily (see below).

Subfamily **Burmadactylinae** subfam. nov.

> Included genera: *Burmadactylus* Heads, 2009; *Cascogryllus* Poinar, 2020; *Dentridactylus* Günther, 1974; *Hiemalidactylus* Schall, Gu & Husemann, in press

(chapter 3); *Latedactylus* Zheng, Cao & Gu, 2023; *Phyllotridactylus* Xu, Wang, Fan, Jarzembowski, Fang, Wang, Li, Zhuo, Ding & Engel, 2022

Etymology: After the type genus *Burmadactylus*, assigned herein.

Horizon: Cretaceous amber of Myanmar-today in South America, Africa and Australia.

Diagnosis: Characterized by a metatarsus/apical spur length ratio > 2. Swimming lamellae always absent.

Remarks: Contrary to the Ripipterygidae, where the Burmese amber fauna was distributed among several taxa, all members of Tridactylidae from the amber belong to this subfamily. While they were diverse during the Cretaceous, only one lineage has persisted into present times, the genus *Dentridactylus*.

Tribe **Latedactylini** trib. nov.

Included genera: *Cascogryllus* Poinar, 2020; *Hiemalidactylus* Schall, Gu & Husemann, in press (chapter 3); *Latedactylus* Zheng, Cao & Gu, 2023; *Phyllotridactylus* Xu, Wang, Fan, Jarzembowski, Fang, Wang, Li, Zhuo, Ding & Engel, 2022

Etymology: After the type genus *Latedactylus*, assigned herein.

Horizon: Cretaceous amber of Myanmar.

Diagnosis: Differs from the other tribe in the subfamily Burmadactylinae by the absence of a subapical denticular process of the metatarsus.

Remarks: Known only from the Cretaceous amber of Myanmar, this tribe was relatively diverse, including four genera and possibly *Duappendactylus* Schall, Gu & Husemann, in press (chapter 3) as well. Based on the absence of the paraproctal lobes, *Duappendactylus* and *Hiemalidactylus* may constitute a third distinct tribe of Burmadactylinae. This character was not compared in the cluster analysis performed here, because it is exclusively known from these two genera. Additional specimens sharing the trait (i.e. paraproctal lobes absent) may give support to this hypothesized third tribe.

Tribe **Burmadactylini** trib. nov.

Included genera: *Burmadacytlus* Heads, 2009; *Dentridactylus* Günther, 1974

Etymology: After the type genus *Burmadactylus*, assigned herein.

Horizon: Cretaceous amber of Myanmar-today in South America, Africa and Australia.

Diagnosis: Differing from Latedactylini trib. nov. (see above) by the presence of a subapical denticular process on the metatarsus.

Remarks: This tribe is remarkable, because it is the only one to have existed all the way from the Cretaceous (genus *Burmadactylus*) to today (genus *Dentridactylus*). Because *Burmadactylus* is only known from the type locality (Burmese amber), but *Dentridactylus* occurs in relic areas of South America, Africa and Australia (Cigliano et al., 2025), it is likely, that this tribe had extinct unknown members from other parts of the world. Perhaps, the genus *Cratodactylus* Martins-Neto, 1990 belongs to this genus, yet this is very difficult to prove given the delicate detail of the denticular process, which could only be traced in the best-preserved compression fossils.

Genera *incertae sedis*: *Amberotridactylus* Du, Xu & Zhang, 2021; *Archaeoellipes* Heads, 2010; *Asiotridactylus* Günther, 1995; *Cratodactylus* Martins-Neto, 1990; *Duappendactylus* Schall, Gu & Husemann, in press (chapter 3); *Ellipes* Scudder, 1902; *Paratridactylus* Ebner, 1943; *Paraxya* Cao, Chen & Yin, 2019

Possible placements for Archaeoellipes and Ellipes: The genus *Ellipes* consists of 28 species distributed across the new world (Cigliano et al., 2025). A fossil species (*E. dominicana* Poinar, 2020) was described from Dominican amber that is dated to the Middle Miocene (20-15 Mya) (Iturralde-Vinent and MacPhee, 2019). Additionally, another Dominican amber specimen (*Archaeoellipes engeli* Heads, 2010) is considered to be closely associated with *Ellipes*. In the case of *E. dominicana*, the metatarsus was mistaken for a fifth apical spur and thus interpreted as underdeveloped (as typical for *Ellipes*). Because of this, it seems more likely to move *E. dominicana* to *Archaeoellipes*, which also has a normally developed metatarsus (Heads, 2010). The genera *Ellipes* and *Archaeoellipes* are considered *incertae sedis* for now. The taxon sampling in my UPGMA only included species that do not feature swimming lamellae. Although this character state is accurate for most members of *Ellipes* (and *Archaeoellipes*) (Günther, 1977; Heads, 2010), some species of *Ellipes* were reported to feature swimming lamellae by Günther (1977) (e.g. *E. wagneri wagneri* (Chopard, 1920) and *E. minuta minuta* (Scudder, 1862)). Taking this into account, the character combination of an *Ellipes* species with swimming lamellae would be identical to *Xya* once transcribed into the binary character matrix used to perform the UPGMA above. Also, the monotypic *Tibetxya* from China does not have

swimming lamellae and has a vestigial metatarsus (Cao et al., 2021), just like most species of *Ellipes*. Therefore, it is likely that *Ellipes* and *Archaeoellipes* can be attributed to Xyainae. However, they are regarded here as taxa *incertae sedis* within Tridactylidae, because their combination of characters does not suggest clear apomorphies. In the future, a phylogenetic analysis based on morphological and molecular data should help to resolve this issue.

Possible placements for Amberotridactylus: The single species *A. cheni* Du, Xu & Zhang, 2021 from Cretaceous Burmese amber is missing the abdominal terminalia. The authors assigned it to Tridactylidae based on the inflated mesotibia (Du et al., 2021), but this character is present in Naginipterygini trib. nov. too (see above). However, *Amberotridactylus* differs from Naginipterygini by the absence of a denticular process on the metatarsus and a smaller metatarsus/apical spur-length ratio (ca. 1.4). Assuming the species does belong to Tridactylidae, it is most similar to *Archaeoellipes engeli* Heads, 2010. This would be remarkable, as it would extend the earliest record of Ellipesinae subfam. nov. back by ca. 80 My. For confident placement of *Amberotridactylus* in the new taxonomic framework of Tridactyloidea proposed here, it is necessary to wait for future findings of the genus with preserved abdominal structures.

Possible placements for Asiotridactylus: This extant genus is known from two species found in Africa and parts of Asia. Unfortunately, I was not able to review any material of this little-known group.

Possible placements for Cratodactylus: Currently known from two species found in the Cretaceous Crato Formation of Brazil, this genus is very difficult to assign to one of the newly described taxa. Although Crato insects are often well preserved compared to other compression fossils, they can not match the detail observable in amber. The holotypes of *C. ferreirai* Martins-Neto, 1990 and *C. kellneri* Martins-Neto, 1990 do not have preserved cerci (or paraproctal lobes), thus they cannot even be assigned to the family level with confidence.

Possible placements for Duappendactylus: In the single type species of this new genus described herein (chapter 3), the metatarsus is not quite visible. Because of this, a position in either Ellipesinae subfam. nov. of Burmadactylinae subfam. nov. is possible, as the absence of swimming lamellae exclude it from Xyainae subfam. nov. Based on the shared absence of paraproctal lobes of this genus and *Hiemalidactylus*, it is possible that they are more closely related. This would suggest that *Duappendactylus* should be placed in Burmadactylinae, which is corroborated by the matching horizon of this subfamily. It is further conceivable, that *Duappendactylus* and *Hiemalidactylus* form yet another distinct clade within Tridactylidae, one

that is diagnosed by the absence of parapoctal lobes. However, as this character is otherwise completely unknown in Tridactyloidea, more findings are needed to confirm this hypothesis.

Possible placements for Paratridactylus: This genus is based on a single species from the island of Bioko in the Gulf of Guinea. I was not able to review any material on it, but it seems likely that this genus would have evolved as an island-endemic from one of the tridactylid-genera present in Africa. Based on its assignment to Dentridactylinae Günther, 1979 (Cigliano et al., 2025) - a subfamily concept diagnosed by the presence of a denticular process on the metatarsus (but probably not monophyletic, as a denticular process is a common feature among fossil Tridactyloidea) – the genus likely has a denticular process as well. Two genera of Tridactylidae with a denticular process are known from Africa: *Dentridactylus* Günther, 1974 and *Bruntridactylus* Günther, 1979 (Cigliano et al., 2025). Because the former occurs only in a relic area near the city of Durban, South Africa (Cigliano et al., 2025), *Bruntridactylus* may be the likely ancestor of an island-endemic *Paratridactylus*. Thus, the genus may belong to Xyainae subfam. nov.

Possible placements for Paraxya: This genus is known from the single species *P. hui* Cao, Chen & Yin, 2019 discovered in Cretaceous Burmese amber. It is not visible, whether the cercus of this species is one- or two-segmented and it was not specified in the description of the species (Cao et al., 2019). If the cercus was two-segmented (indicative of Tridactylidae), the genus would be most closely associated with Burmdactylini trib. nov., however, with the presence of hindwings, which are absent in the currently known members of this tribe. In fact, *Paraxya hui* is very similar to *Burmaripipteryx* and *Kallosripipteryx* (although hindwings of the latter species are less prominent than in *P. hui*). Therefore, I wonder whether the genus may in fact belong to Ripipterygidae (and there in the tribe Naginipterygini trib. nov.) rather than Tridactylidae.

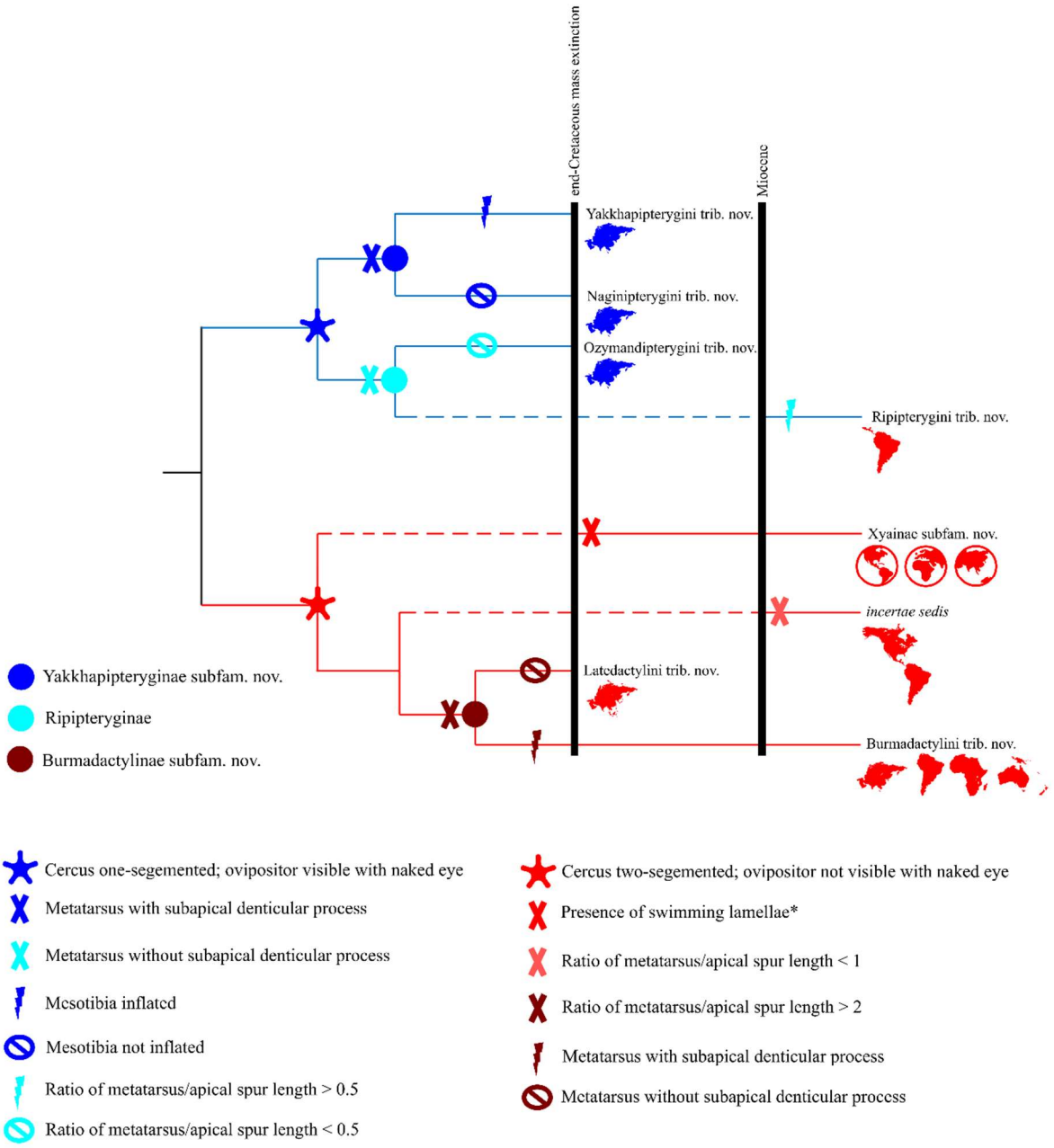

Fig. 2 Suggested taxonomic framework of Tridactyloidea Brullé, 1835 after dendrogram in Fig. 1 with tips collapsed to represent subfamilies or tribes. Blue = Ripipterygidae Ander, 1939. Red = Tridactylidae Brullé, 1835. Abstract symbols state autapomorphies of each taxon. Continental shapes indicate distribution of each taxon throughout time, whereby Asia is equivalent to Cretaceous Burmese amber. Two vertical black bars mark the end-Cretaceous mass extinction and the horizon of Miocene amber (ca. 20-15 My old). *Swimming lamellae of Xyainae subfam. nov. are secondarily absent in the Tibetian *Tibetxya motuoensis* Cao, Yang, Shen & Yin, 2021.

5. Discussion

Above, I have reviewed the taxonomic relationships of the families Ripipterygidae Ander, 1939 and Tridactylidae Brullé, 1835 (Caelifera: Tridactyloidea). My findings suggest that both families once were more diverse than today with several extinct lineages on the subfamily and tribe level found in Cretaceous amber of Myanmar (ca. 110-99 My old (Shi et al., 2012; Xing and Qiu, 2020)). In total, one new subfamily and three new tribes for Ripipterygidae as well as three new subfamilies and two new tribes of Tridactylidae are recognized.

Glory Days: Past diversity of Tridactyloidea

The extinct diversity of Tridactyloidea Brullé, 1835 discovered in Burmese amber is remarkable, as the group makes up only 2% of the extant diversity of Caelifera Ander, 1936 (Cigliano et al., 2025). It is, therefore, not surprising that deciphering taxonomic relationships of Tridactyloidea has proven quite a challenge prior to the description of the Cretaceous species – taxonomists were dealing with a puzzle that included only a handful of pieces necessary to complete the full picture.

Although unexpected, the increased diversity of ancient Tridactyloidea compared to the modern members is not surprising. Schachat et al. (2019) found evidence for a diversity peak of insect families during the Early Cretaceous. Uchida, Husemann & Kotthoff (2024) recently described the Burmecalidae, an enigmatic new Caelifera family, attributed to Tridactylidea Brullé, 1835 by Schall et al. (2025). What is astonishing, however, are the implications for the evolution of Tridactyloidea. Beside the Gryllidea Vickery, 1977, they are the only Orthoptera with high levels of diversity in the past that have persisted into the present. In some cases, as with the genus *Dentridactylus* Günther, 1974 apparently with little changes to morphology, meaning they can be considered “living fossils”.

Reliability of the UPGMA

The fossil forms have shed light on some characters previously assumed staples of certain taxa. For example, the subapical denticular process of the metatarsus had been considered an autapomorphy of the subfamily Dentridactylinae Günther, 1979. But this character is present in several species of Burmese amber Ripipterygidae as well (subfamily Yakkhapipteryginae subfam. nov.) and may have been present in the common ancestor of Ripipterygidae and Tridactylidae. It was then secondarily lost in the Ripipteryginae Ander, 1939, Latedactylini trib. nov., and Xyainae subfam. nov. Therefore, instead of by the presence/absence of a subapical denticular process, the UPGMA cluster analysis separated Tridactylidae by the

presence/absence of swimming lamellae. Additionally, an inflated mesotibia, formerly an exclusive attribute of Tridactylidae was present in at least one lineage of Ripipterygidae as well (Naginipterygini subfam. nov.).

Although the estimate of phylogenetic relationships of Tridactyloidea suggested by the UPGMA may better reflect on the true diversity levels of the taxon than the classification currently employed (with only a single subfamily in Ripipterygidae) (Cigliano et al., 2025), but accuracy of UPGMA is probably low (Rohlf et al., 1990). Despite model studies finding UPGMA to be comparable with Bayesian analyses, this was true when the number of characters sampled was much higher than the number of taxa, as is generally the case when using molecular data (Khan et al., 2008). However, when using morphological data, it is expected that the accuracy of UPGMA decreases the more taxa per character are being sampled (Rohlf et al., 1990). In the analysis used in this study only a few characters were selected, because they were regarded as possible apomorphies of the lineages described. In this context, the UPGMA was meant to test if and how the Tridactyloidea described up until now were able to be grouped based on these presumed apomorphies (i.e. which presumed apomophy may be more suitable than others to diagnose lineages of Tridactyloidea). However, the UPGMA used in this study cannot serve to accurately give a reliable reconstruction of phylogenetic relationships. Therefore, it is to be taken as a preliminary new hypothesis of Tridactyloidea systematics until a more comprehensive total evidence phylogeny can be performed.

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Appendix

Appendix 1: Nexus file of the cluster analysis of Tridactyloidea (Tridactylidae + Ripipterygidae).

#NEXUS

BEGIN DATA;

DIMENSIONS NTAX=32 NCHAR=6;

FORMAT SYMBOLS= " 0 1 2 "

;

MATRIX

Archaicaripipteryx_rotunda	0	0	0	2	1	1
Burmaripipteryx_oblongus	0	1	0	2	1	1
Yakkhapipteryx_gracilis	0	0	0	2	1	1
Yakkhapipteryx_mirus	0	0	0	2	1	1
Magnidactylus_robustus	0	1	0	0	0	1
Kallosripipteryx_zhangi	0	1	0	2	1	1
Ozymandipteryx_campana	0	0	0	0	0	1
Naginipteryx_pinna	0	1	0	2	1	1
Mirhipipteryx_antillarum	0	0	0	1	0	1
Ripipteryx_diegoi	0	0	0	1	0	1
Ripipteryx_guacharoensis	0	0	0	1	0	1
Ripipteryx_gorgonaensis	0	0	0	1	0	1
Burmadactylus_tenuicerci	1	1	0	2	1	0

Burmadactylus_grimaldii 1 1 0 2 1 0

Cascogryllus_lobiferus 1 1 0 2 0 0

Guntheridactylus_grimaulti 1 1 1 1 1 0

Archaeoellipes_engeli 1 1 0 1 0 1

Latedactylus_longapedi 1 1 0 2 0 0

Phyllotridactylus_wangi 1 1 0 2 0 0

Ellipes_dominicana 1 1 0 1 0 0

Hiemalidactylus_eileenae 1 1 0 2 0 0

Ellipes_deyrupi 1 1 0 0 0 0

Ellipes_eisneri 1 1 0 0 0 0

Ellipes_monticola 1 1 0 0 1 0

Xya_sichuanensis 1 1 1 0 0 1

Xya_yunnanensis 1 1 1 0 0 1

Xya_xishangbanna 1 1 1 0 0 1

Neotridactylus_apicialis 1 1 1 1 0 1

Dentridactylus_quadratus 1 1 0 2 1 0

Dentridactylus_truncatus 1 1 0 2 1 0

Afrotridactylus_spiralatus 1 1 1 0 0 1

Bruntridactylus_tartarus 1 1 1 1 1 1

;

END;

Chapter 12

Beyond the wings – using aspects of body morphology to better understand taxonomy of Locustopsidae (Orthoptera: Caelifera)

Abstract

Important characteristics of body morphology of the family Locustopsidae Handlirsch, 1906 are compared in well-preserved specimens. Specifically, the ovipositor morphology of *Araripelocusta imperatrix* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025 (chapter 4), *Auroralocusta restituta* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, 2025 (chapter 5) and *Mesolocustopsis levis* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, 2025 (chapter 5) as well as the pronotum morphology of *A. imperatrix*, *Locustrix gallegoi* Martins-Neto, 2003, *Locustopsis rhytofemoralis* Gu, Yue, Shi, Tian & Ren, 2016 and *Cratolocustopsis cretacea* (Martins-Neto, 1990). Possible implications derived from these characters for the taxonomy of Locustopsidae are discussed. However, it will take additional well-preserved specimens to improve knowledge of body morphology in locustopsids before taxonomic changes can be applied.

Keywords: Crato Formation, fossil, grasshopper

1. Introduction

Locustopsidae Handlirsch, 1906 is a family of early Caelifera Ander, 1936 that first appears in the fossil record of the Triassic (Zeuner, 1942) and disappears after the Cretaceous. A total of 76 species make this group one of the most abundant Mesozoic grasshoppers with findings reported from every continent except for Antarctica and Australia (Cigliano et al., 2025, chapters 4-6).

The species are distributed among three subfamilies: the Locustopsinae Handlirsch, 1906 house the majority with 65 species. They are known from across the entire geographic and temporal range of the family. Araripelocustinae Martins-Neto, 1995 with four species were found in deposits from the Early Cretaceous of Brazil and the UK and six species of Pseudoacridinae

subfam. nov., herein (chapter 5) were discovered in the Early Cretaceous of Brazil and China. One species, *Liadolocusta auscultans* Handlirsch, 1906, was considered a *nomen dubium* (chapter 4).

For all their history, taxonomy in Locustopsidae relied on characters of the forewing venation (see chapter 4 for a comparison of venation characters between genera of Locustopsidae). This was born virtually out of necessity, as the majority of specimens from the family are known based on isolated (fore-) wings. However, limiting systematics of a group to only one character set (i.e. characters of forewing venation) can be problematic: up to this day autapomorphies of Locustopsidae are unclear. According to the character matrix used to perform the phylogenetic analysis presented in chapter 9, Locustopsidae can be separated from most extant Acridomorpha MacLeay, 1821 by a proportionally longer forewing (forewing length/body length > 1.25). Yet, this makes them indistinguishable from some modern species such as *Lobosceliana femoralis* (Walker, 1870), which consistently placed in the same clade as Locustopsidae in the chapter 9 phylogeny.

Further, I have demonstrated the intraspecific variation in the forewing characters of some species of Elcanidae from the Crato Formation (chapter 8). The above-mentioned phylogeny suggests that Locustopsidae and Elcanidae evolved early on in Orthoptera evolution from a common (presumably oedischiid) ancestor sometime during the Permian. If the wing venation of elcanids is somewhat variable already within the same species, a similar variation must be assumed for Locustopsidae, especially when comparing genera. Consequently, this casts doubt on the validity of for example *Parapleurites* Brauer, Redtenbacher & Ganglbauer, 1889 which is separated from *Cratolocustopsis* Martins-Neto, 2003 only by the presence of one additional branch of CuA + CuPaα. Moreover, species separation in locustopsids is often based on relatively minor differences in wing characters, such as the origin point or trajectory of certain veins and width or area between them (e.g. Gorochov et al., 2006).

In order to develop a better understanding of Locustopsidae diversity, it will be necessary to take more aspects of their morphology into account other than just the forewings. Here, I comprise information about pronotum and ovipositor forms available from the current fossil record of locustopsids and discuss possible implications for their taxonomy.

2. Materials and methods

Thirty-one out of 76 or 41% of Locustopsidae species are known from more than isolated wings (Table 1). Of these, only 6 species show aspects of their body morphology (pronotum and ovipositor) in good detail: *Araripelocusta imperatrix* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025 (chapter 4), *Auroralocusta restituta* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, 2025 (chapter 5), *Cratolocustopsis cretacea* (Martins-Neto, 1990), *Locustopsis rhytofemoralis* Gu, Yue, Shi, Tian & Ren, 2016, *Locustrix gallegoi* Martins-Neto, 2003 and *Mesolocustopsis levis* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, 2025 (chapter 5). The pronotum and/or ovipositor morphology of these species is described based on the newly presented specimens from chapters 4-6 of this dissertation as well as the material described in Gu et al. (2016).

Table 1: Species of Locustopsidae (post taxonomic revision as presented in chapter 4) and whether body parts apart from isolated wings are known or not. Thirty-one out of 76 species are known from more than just wings. Species marked in green show aspects of body morphology (pronotum and ovipositor) in good detail and are considered in the results. The two species described by Zherikhin (1985) and *Mesolocustopsis sinica* Hong and Wang, 1990 are insufficiently featured in the literature available online and need revision. *Liadolocusta auscultans* Handlirsch, 1906 is a *nomen dubium* and not included in this list. *A new specimen of *Pseudoacrida sennlaubi* Nel and Jouault, 2022 with aspects of the body preserved was described in chapter 5 of this dissertation. References in the 'Quality of preservation' column refer to publications that feature an image or figure of the species or at least give a text-based description and were considered in this study.

Species	**(Parts of) body known**	**Quality of preservation**
Araripelocusta brevis Martins-Neto, 1995	Yes	Full body fossil (according to Martins-Neto and Gallego, 2006). Publication record poor.
Araripelocusta imperatrix Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, submitted (chapter 4)	Yes	Full body fossils missing the legs and antennae (chapter 4).
Araripelocusta longinota Martins-Neto, 1995	Yes	Full body fossil (according to Martins-Neto and Gallego, 2006). Publication record poor.
Britannacrida distincta Gorochov, Jarzembowski & Coram, 2006	No	An isolated forewing (Gorochov et al., 2006).

Conocephalella capito (Deichmüller, 1886)	Yes	Complete specimen (Zessin, 1983). Images and detailed drawings are missing.
Cratolocustopsis aquila Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, submitted (chapter 4)	Yes	Full body fossil with some appendages missing.
Cratolocustopsis contumax Martins-Neto, 2003	Yes	Full body fossil (Martins-Neto, 2003).
Cratolocustopsis cretacea (Martins-Neto, 1990)	Yes	Full body fossils known. The holotype is missing legs and head (chapter 4).
Cratolocustopsis reticulata (Handlirsch, 1939)	No	An isolated forewing with about the apical half preserved (Zessin, 1983).
Locustopsis africanus Ansorge, 1991	No	Isolated hindwing (Ansorge, 1991).
Locustopsis apicalis Zherikhin, 1985	No (?)	No online records available. Needs revision.
Locustopsis bernstorffi (Geinitz, 1880)	No	Isolated forewing. Holotype lost (Zessin, 1983).
Locustopsis bucklandi (Brodie, 1845)	Yes	Full body fossil. Wing venation missing (Zessin, 1983).
Locustopsis cockerelli Handlirsch, 1939	No	Isolated forewing? The holotype with the coll. no. USNM3461, Lacoe coll. (US National Museum of Natural History) (Zessin, 1983) was never figured and needs revision.
Locustopsis constricta Zeuner, 1942	No	Isolated forewing (Zessin, 1983).
Locustopsis cubitalis Zeuner, 1942	No	Isolated forewing (Zessin, 1983).
Locustopsis elegans Handlirsch, 1906	No	Isolated forewing (Zessin, 1983).
Locustopsis elongata Handlirsch, 1906	No	Isolated forewing (Zessin, 1983).

Locustopsis ferghanensis Martynov, 1937	No	Isolated fragmentary forewing. No figure/image available in the online literature (Zessin, 1983).
Locustopsis germari (Münster, 1842)	Yes	Full body fossil with poorly preserved venation features; this complicates identification of the species which has been disputed by Zeuner (1942) (Zessin, 1983).
Locustopsis godoii (Martins-Neto, 2003)	Yes	Full body fossils (Martins-Neto, 2003).
Locustopsis gracilis Zeuner, 1942	No	Isolated forewing (Zessin, 1983).
Locustopsis gyra Zessin, 1983	No	Isolated forewing (Zessin, 1983).
Locustopsis karatavica Sharov, 1968	Yes	Well-preserved fore- and hindwing (Zessin, 1983).
Locustopsis kruegeri Zessin, 1983b	No	Probably an isolated forewing. No online figure/image available.
Locustopsis lacoei Cockerell, 1916	No	Isolated forewing (Zessin, 1983).
Locustopsis maculosa Bode, 1953	No	Isolated forewing (Zessin, 1983).
Locustopsis nana Handlirsch, 1939	No	Apical part of a forewing (Handlirsch, 1939). Nomen dubium according to Cigliano et al. (2025).
Locustopsis nervosa (Martins-Neto, 2003)	Yes	Mostly a forewing (Martins-Neto, 2003).
Locustopsis picta Zherikhin, 1985	No (?)	No online records available. Needs revision.
Locustopsis posterior Gorochov, Jarzembowski & Coram, 2006	No	Isolated forewing (Gorochov et al., 2006).
Locustopsis procera Zessin, 1983	No	Isolated forewing (Zessin, 1983).
Locustopsis pulchella Zessin, 1983	No	Isolated forewing (Zessin, 1983).

Locustopsis reducta Handlirsch, 1939	No	Isolated forewing (Zessin, 1983).
Locustopsis rhytofemoralis Gu, Yue, Shi, Tian & Ren, 2016	Yes	Full and well-preserved body fossil (Gu et al., 2016).
Locustopsis sharovi (Gorochov and Coram, 2023)	No	Isolated forewing (Gorochov and Coram, 2023).
Locustopsis shurabica Sharov, 1968	No	Isolated forewing with parts of the posterior base and apex missing (Zessin, 1983).
Locustopsis sippeli Zessin, 1983	No	Isolated forewing (Zessin, 1983).
Locustopsis soaresi (Martins-Neto, 2003)	Yes	Full body fossils (Martins-Neto, 2003).
Locustopsis spectabilis Zeuner, 1942	No	Isolated forewing (Zessin, 1983).
Locustopsis thalassophila Zessin, 1988	No	Isolated forewing (Gorochov and Coram, 2023).
Locustopsis titanella (Martins-Neto, 2003)	Yes	Full body fossils (Martins-Neto, 2003).
Locustopsis uvarovi Zeuner, 1942	No	Isolated forewing (Zessin, 1983).
Mesolocustopsis anglica Gorochov, Jarzembowski & Coram, 2006	No	Isolated forewing (Gorochov et al., 2006).
Mesolocustopsis angusta Gorochov, Jarzembowski & Coram, 2006	No	Isolated forewing (Gorochov et al., 2006).
Mesolocustopsis araripensis (Martins-Neto, 1990)	Yes	Full body fossil (Martins-Neto, 2003).
Mesolocustopsis levis Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, in prep. (chapter 5)	Yes	Full body fossil (chapter 5).
Mesolocustopsis brevis (Huang and Nel, 2024)	No	Three isolated forewings of different preservation; basal part missing in all of them (Huang and Nel, 2024).
Mesolocustopsis caririensis (Martins-Neto, 1990)	Yes	Full body fossils (Martins-Neto, 2003).

Mesolocustopsis morrisonensis (Smith, Gorman, Pardo & Small, 2011)	No	Isolated forewing (Smith et al., 2011).
Mesolocustopsis problematica Gorochov, Jarzembowski & Coram, 2006	No	Isolated forewing (Gorochov et al., 2006).
Mesolocustopsis sinica Hong and Wang, 1990	No	No online records available. Needs revision.
Mesolocustopsis vikingi (Martins-Neto, 2003)	Yes	Full body fossils (Martins-Neto, 2003).
Orichalcum ornatum Whalley, 1985	No	Isolated forewing (Whalley, 1985).
Parapleurites brasiliensis Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, submitted (chapter 4)	Yes	Full body fossil missing legs and antennae (chapter 4).
Parapleurites gracilis Brauer, Redtenbacher & Ganglbauer, 1889	No	Isolated forewing (Zessin, 1983).
Parapleurites sibiricus Sharov, 1968	No	Isolated forewing (Zessin, 1983).
Schwinzia anatolica Sharov, 1968	No	Fore- and hindwing (Zessin, 1983).
Schwinzia sola Zessin, 1983	No	Isolated forewing (Zessin, 1983).
Zessinia borealis Gorochov, Jarzembowski & Coram, 2006	No	Isolated forewing (Gorochov et al., 2006).
Zessinia pulcherrima Martins-Neto, 1990	Yes	Forewing figured in Martins-Neto (2003), but probably a full body fossil. Needs revision.
Zessinia reticulata Martins-Neto, 1990	Yes	Forewing figured in Martins-Neto (2003), but probably a full body fossil. Needs revision.
Zeunerella amedegnatoi (Martins-Neto, 1998)	Yes	No online figure/image available. Needs revision.
Zeunerella arborea Sharov, 1968	No	Fore- and hindwings (Zessin, 1983).
Zeunerella mecklenburgica (Zessin, 1983)	No	Isolated forewing (Zessin, 1983).
Zeunerella neotropica (Martins-Neto, 1998)	Yes	Fore- and hindwings and probably full body fossils (Martins-Neto, 2003).

Zeunerella prior Gorochov, Jarzembowski & Coram, 2006	No	Isolated forewing (Gorochov et al., 2006).
Locustrix audax Martins-Neto, 2003	Yes	Full body fossil (Martins-Neto, 2003).
Locustrix gallegoi Martins-Neto, 2003	Yes	Full body fossil (Martins-Neto, 2003 and chapter 6).
Aestuacrida mikronaulion Schall, Lima, Heads, Pinheiro & Husemann, in prep. (chapter 6)	Yes	Full body fossil missing legs and antennae (chapter 6).
Aestuacrida stereofemoris Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, submitted (chapter 4)	Yes	Full body fossil missing most appendages except for metathoracic legs (chapter 4).
Auroralocusta restituta Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, in prep. (chapter 5)	Yes	Full body fossil missing most appendages except for one mesothoracic leg (chapter 5).
Pseudoacrida costata Lin, 1982	No	Isolated forewing (probably), but figure/image not available online.
Peudoacrida eumastacoimima Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, in prep. (chapter 5)	Yes	Full body fossil missing legs and antennae (chapter 5).
Pseudoacrida sennlaubi Nel and Jouault, 2022	Yes*	Isolated forewing (holotype in Nel and Jouault, 2022) and full body fossil (chapter 5).

3. Results

Araripelocusta imperatrix Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, submitted (chapter 4)

The paratype (CNBS00417) of this new species shows both the pronotum as well as the ovipositor and relatively good detail. The pronotum of this species is characterized by not being elongated posteriorly as well as a postero-lateral margin without concave curve. Instead, the

postero-lateral margin declines without curve (Fig. 1A, B). The ovipositor can be seen with two lower valvulae. Each valve is broad and features apical serration (Fig. 2A, B).

Locustrix gallegoi Martins-Neto, 2003

The description of the pronotum of this species is based on the specimen MH_Fossil_0066, described in chapter 6 of this dissertation. The pronotum is posteriorly distinctly elongated (described as "seliform" by Martins-Neto (2003)). Postero-lateral margin unknown (Fig. 1C, D).

Locustopsis rhytofemoralis Gu, Yue, Shi, Tian & Ren, 2016

The shape of the pronotum of this species can be described based on the material published by Gu et al. (2016) of specimen CNU-ORT-NN2011010PC (holotype). The pronotum is posteriorly not elongated (similar to *Araripelocusta imperatrix*). However, it differs from *A. imperatrix* by the concave curve of the postero-lateral margin (Fig. 1E, F).

Cratolocustopsis cretacea (Martins-Neto, 1990)

The pronotum of *C. cretacea* is described based on the neotype specimen CNBS_00410 (chapter 4). It is posteriorly elongated, slightly less than in *Locustrix gallegoi*. Postero-lateral margin with concave curve (Fig. 1G, H).

Mesolocustopsis levis Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, in prep. (chapter 5)

Based on the holotype specimen MPSC 9837, the ovipositor of this species has two or three lower valvulae. They are thin and blade-like, without serration (Fig. 2E, F).

Auroralocusta restituta Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, in prep. (chapter 5)

The ovipositor of this species is described based on the holotype specimen MPSC 9835. It has two lower valvulae. They are broad, one of them with apical serration, the other tapering to a single pointed apex (Fig. 2C, D). The ovipositor morphology of *A. restituta* is very similar to *Araripelocusta imperatrix*. Differences might be due to preservation issues.

4. Discussion

Pronotum

Currently, the pronotum morphology of four species of Locustopsidae is known. One of them (*Araripelocusta imperatrix*) belongs to the subfamily Araripelocustinae. The other three (*Locustrix gallegoi*, *Locustopsis rhytofemoralis* and *Cratolocustopsis cretacea*) belong to the Locustopsinae. The pronotum morphology of *L. rhytofemoralis* is more similar to *A. imperatrix* than to the other two members of Locustopsinae, in that they are not posteriorly elongated. Likewise, a closer phylogenetic relationship between *L. gallegoi* and *C. cretacea* is possible based on the posterior elongation of the pronotum that they share.

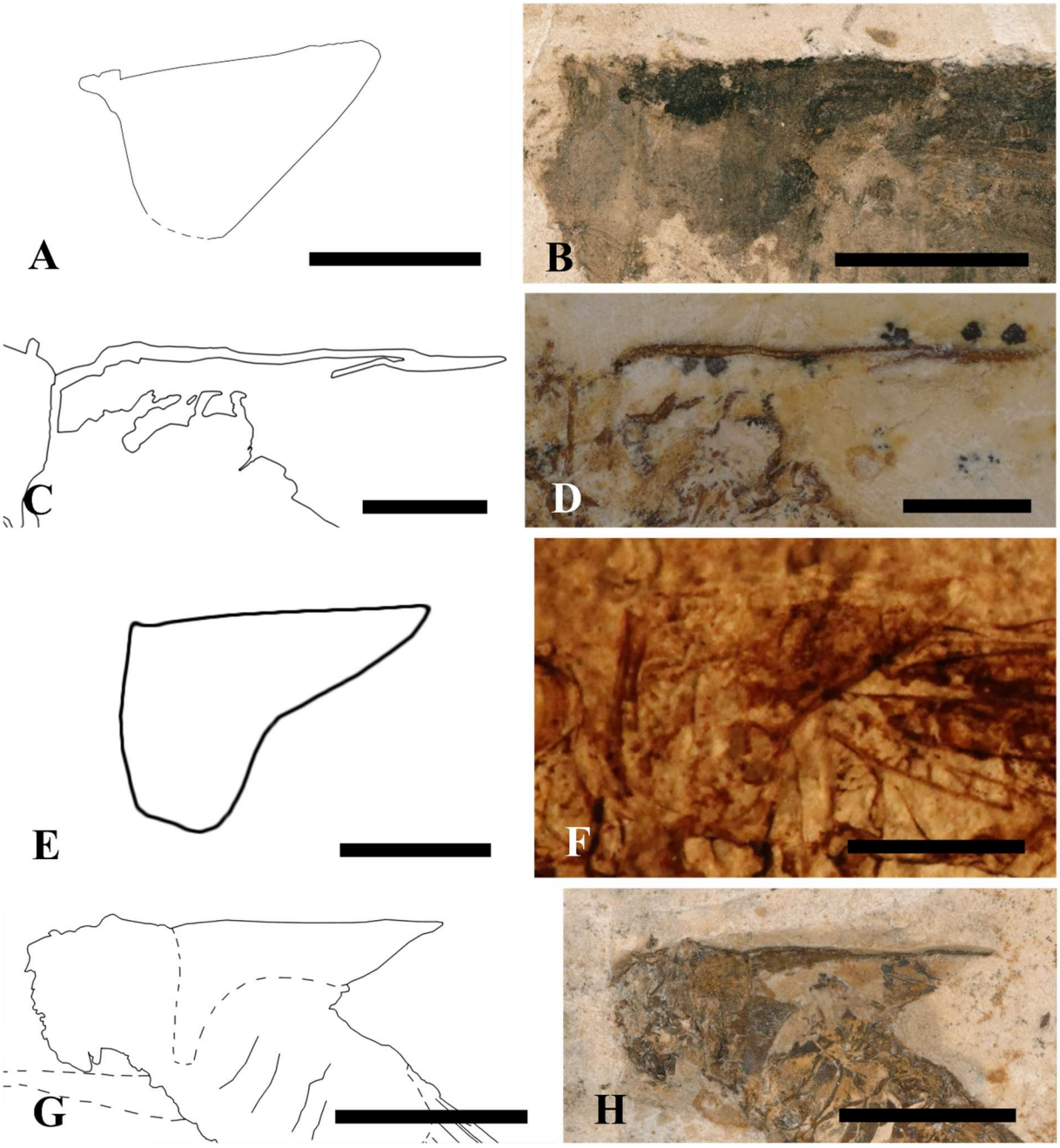

Fig. 1: Comparison of pronotal morphology in Locustopsidae. **A** and **B** *Araripelocusta imperatrix* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, submitted (chapter 4).

CNBS00417 (paratype), female. **C.** and **D** *Locustrix gallegoi* Martins-Neto, 2003. MH_Fossil_0066, male. **E** and **F** *Locustopsis rhytofemoralis* Gu, Yue, Shi, Tian & Ren, 2016. CNU-ORT-NN2011010PC (holotype), male. **G** and **H** *Cratolocustopsis cretacea* (Martins-Neto, 1990). CNBS_00410 (neotype) (chapter 4). **Scale bars** = 5 mm for A, B, G, H; 2 mm for C-F.

Ovipositor

Regarding ovipositor morphology, the structure of valvulae of three species is known, namely *Araripelocusta imperatrix* from the subfamily Araripelocustinae, *Auroralocusta restituta* from the subfamily Pseudoacridinae and *Mesolocustopsis levis* from the subfamily Locustopsinae. The ovipositor of *A. imperatrix* is very different from the one of *M. levis*, but similar to what can be seen in *A. restituta*. This could indicate an earlier lineage divergence of Araripelocustinae and *Mesolocustopsis*, however, the pronotum morphology described above suggests closer association of Araripelocustinae with *Locustopsis* – and both genera are from the same subfamily Locustopsinae. It is possible, therefore, that *Mesolocustopsis* and *Locustopsis* need to be assigned to different subfamilies. Likewise, *Locustrix* and *Cratolocustopsis* may have to be placed in a different subfamily from *Locustopsis* due to the differences in pronotal shape.

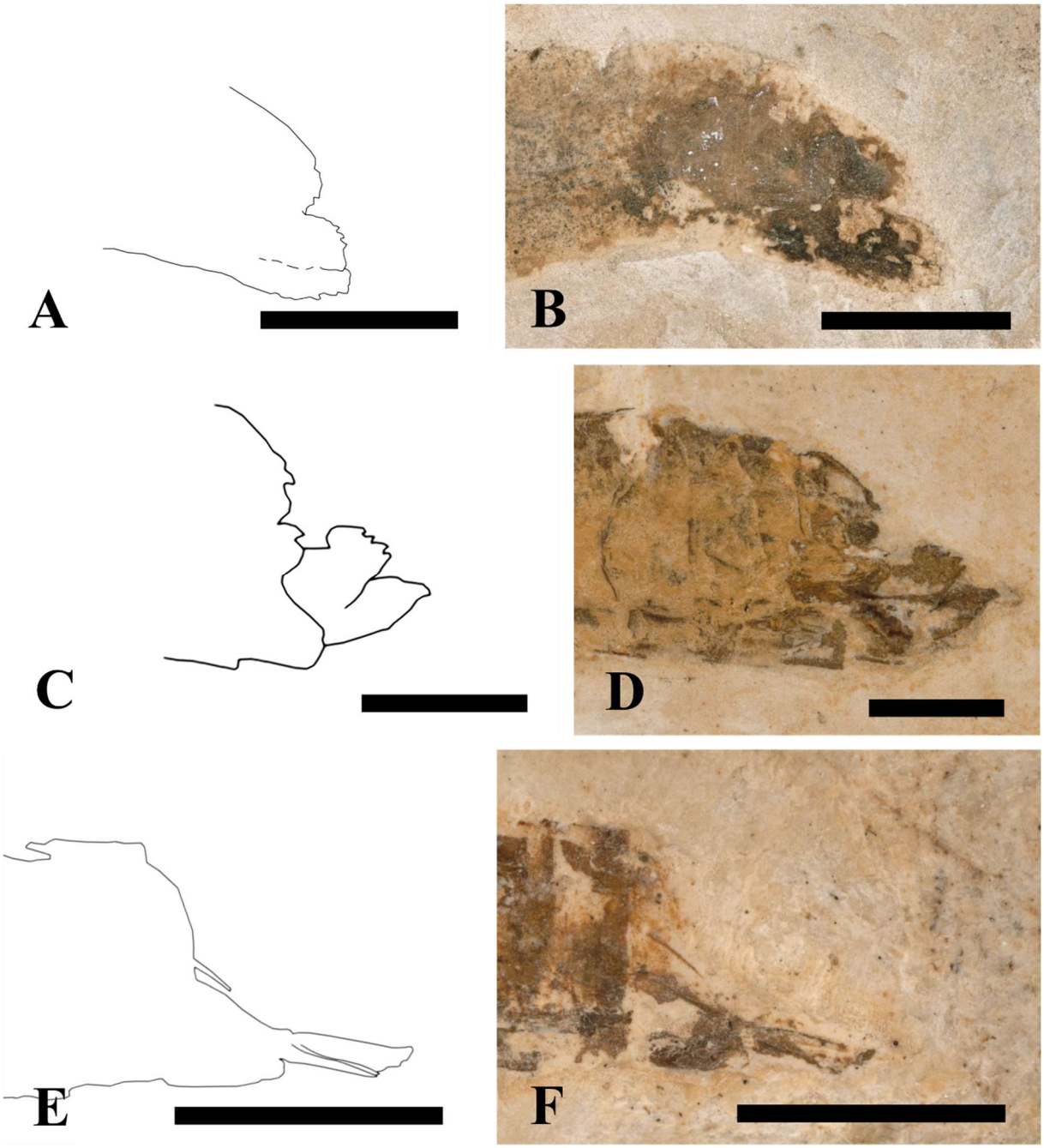

Fig. 2 Comparison of ovipositor morphology in Locustopsidae. **A** and **B** *Araripelocusta imperatrix* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025 (chapter 4). CNBS00417 (paratype), female. **C** and **D** *Auroralocusta restituta* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, in prep. (chapter 5). MPSC 9835 (holotype). **E** and **F** *Mesolocustopsis levis* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, in prep. (chapter 5). MPSC 9837 (holotype). **Scale bars** = 5 mm for A, B, E, F; 2 mm for C, D.

5. Conclusions

Despite the suggestions derived from the morphology of the characters presented above, it is too early to propose changes to locustopsid taxonomy. Still, far too little is known about their diversity, especially with respect to aspects of body morphology. The conflicting information derived from the characters presented here demonstrated that our current understanding of relationships within the group is insufficient to reliably estimate true diversity levels of Locustopsidae. However, this knowledge is essential in order to comprehend the evolution of these pioneering Caelifera, especially their rates of speciation in comparison to the rest of Orthoptera – both to the rare members of modern Acridomorpha found in the pre-Cenozoic fossil record (e.g. Eumastacoidea, see chapter 6), but also to the Ensifera.

Hopefully, the future will provide many more findings of well-preserved body fossils of Locustopsidae. They will enlighten our understanding of the family's taxonomy and finally resolve the mystery that surrounds it since what has already been more than a century.

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Chapter 13

A review of the taxonomy of Elcanidae (Orthoptera: Ensifera) reveals several new lineages

Abstract

Based on recent findings of lagoon crickets (family Elcanidae Handlirsch, 1906) in Cretaceous amber from Myanmar, a revised taxonomy of the family is proposed. Next to the fusion of basal tegminal veins 1A, CuPb and CuPaβ (as recognized by Gorochov et al., 2006), patterns of wing color are suggested as apomorphies of the new clades. Specifically, Elcanidae are organized as Archelcaninae Gorochov et al., 2006 + Elcaninae Handlirsch, 1906 (Panorpidini trib. nov. + Stellacanini trib. nov. + Paraxelcanini trib. nov.). Additionally, some taxonomic revisions on the genus and species level are performed to adjust for monophyly of the new taxa. Namely, five species of *Panorpidium* Westwood, 1854 are moved to *Stellacana* gen. nov., including *S. spica* comb. nov. (Kim, Lee, Nam & Park, 2021), *S. acusicauda* comb. nov. (Tian, Ren & Gu, 2022), *S. bimaculata* comb. nov. (Gorochov, Jarzembowski & Coram, 2006), *S. sibirica* comb. nov. (Sharov, 1968) and *S. yixianensis* comb. nov. (Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015); two species of *Parelcana* Handlirsch, 1906 are moved to *Atopoelcana* gen. nov., including *A. pulchmacula* comb. nov. (Tian, Gu, Yin & Ren, 2019) and *A. xena* comb. nov. Schall and Husemann, in press (chapter 7); *Panorpidium damianii* (Martins-Neto, 1991) is moved to *Cratopidium* gen. nov. as *C. damianii* comb. nov. (Martins-Neto, 1991); *Probaisselcana kachinensis* Zhou, Xu & Xiao, 2024 is moved to *Pseudoprobaisselcana* Schall, Willmott, Kotthoff & Husemann, 2025 as *Pseudoprobaisselcana kachinensis* comb. nov. The new taxonomy proposed for Elcanidae highlights the diversity of the family, especially during the Early- and mid-Cretaceous when insect diversity in general was probably at its peak.

Keywords: Burmese amber, cluster analysis, Crato Formation, fossil, UPGMA

1. Introduction

The Elcanidae or lagoon crickets is a family of Mesozoic orthopterans occupying a phylogenetic position towards the base of Ensifera Chopard, 1921 evolution (chapter 9). When the group was first described by Handlirsch (1906), it was almost exclusively based on the various Jurassic forms found in Germany and the United Kingdom. These species do not exhibit great variation in their morphology and many specimens are based on isolated forewings (Handlirsch, 1906; 1939; Zessin, 1987). Because of this, it does not surprise that they were originally considered to belong mostly to the same genus *Elcana* Giebel, 1856.

It took 90 years since their first description, when more Cretaceous specimens from the Early Cretaceous fossil beds of the UK were discovered, that Gorochov (1995) and Jarzembowski (1996) noticed the similarities of *Elcana* with an earlier described specimen by the name of *Panorpidium tessellatum* Westwood, 1854 and declared *Elcana* a synonym of *Panorpidium*. It was here that *Panorpidium* became by far the most speciose genus of Elcanidae until its revision performed in chapter 9 of this dissertation.

An important step towards understanding the taxonomic relationships within Elcanidae was made by Gorochov et al. (2006), who noticed a crucial difference in forewing venation of some specimens compared to others. In the majority of Jurassic elanids, the three basal veins 1A, CuPb and CuPaβ of the forewing reached the wing margin independently (they are "free"). On the other hand, in most of the Cretaceous specimens, these veins were fused together and reached the wing margin as a single, combined vein (see for example Fig. 4). Based on this difference, Gorochov et al. (2006) proposed two subfamilies for the Elcanidae. They named the group with the free veins Archelcaninae Gorochov, Jarzembowski & Coram, 2006 and the one with the fused veins Elcaninae Handlirsch, 1906.

The description of Elcaninae and Archelcaninae preceded the discovery of the first elcanid from Cretaceous Burmese amber by only a single year (Poinar et al., 2007). Over the course of the next two decades and especially during the 2020s, this resource proved an invaluable treasure for the study of Elcanidae, with numerous findings having been reported on a regular basis (e.g. Hu and He, 2023; Schall et al., 2024; Uchida, 2022; Willmott et al., 2025). Other than before, where many elcanids were mainly diagnosed based on their (often isolated) forewings, the new amber species allowed for a more complete assessment of Elcanidae morphology (for example Willmott et al., 2025).

The newly known characters made for some problematic cases regarding the separation into Archelcaninae and Elcaninae. Species such as *Hukawnelca gracile* Uchida, 2022 were placed into Archelcaninae by Willmott et al. (2025) based on the three free forewing veins, despite the general morphology of *H. gracile* being similar to other Burmese amber elcanids placed in Elcaninae. Furthermore, the presence of two conspicuous wing spots on the forewing (and sometimes possibly the hindwing, see chapter 7) of several Burmese Elcanidae (e.g. *Hukawnelca gracile* Uchida, 2022; *Letoelcana artemisapollonque* Schall, Kotthoff & Husemann, 2024; *Pseudopanorpidium maculosum* (Zhou, Xu, Jarzembowski & Xiao, 2022); *Pseudoprobaisselcana oculata* (Hu and He, 2023)) is curious, as it apparently occurred in both subfamilies (*H. gracile* from the Archelcaninae, the other species from Elcaninae). It is possible that Archelcaninae and Elcaninae evolved in common ways, with either subfamily independently acquiring similar morphological traits (i. e. pattern of wing color). But the close resemblance of Elcanidae species from Burmese amber attributed to Archelcaninae (*Caelielca spinocrus* Uchida, 2022; *Hukawnelca gracile* Uchida, 2022; *Longioculus poinari* Schall and Husemann, in press (chapter 7); *Parelcana xena* Schall and Husemann, in press (chapter 7)) compared with their Elcaninae relatives, seriously questions whether the current hypothesis of Elcanidae taxonomy continues to hold up.

To test this, I performed a cluster analysis based on morphology including the “old” elcanids, formerly members of *Elcana*, and “new” ones from Cretaceous Burmese amber.

2. Materials and methods

In this study I followed the taxonomic framework of Cigliano et al. (2025). Wing venation nomenclature follows Béthoux and Nel (2002), with the following abbreviation for veins: CP = posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch of first posterior cubitus; CuPaβ = posterior branch of first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

2.1 Taxon sampling

A total of 44 specimens of Elcanidae attributed to 42 species were compared by four morphological characters (Table 1). Characters included 1) presence of abstract wing color (i.e. the pattern of most Jurassic elcanids considered to be Archelcaninae, for example *Archelcana geinitzi* comb. nov. (Heer, 1880 in Geinitz, 1880). 2) Presence of large prominent wing spots.

3) Wings without color (i.e. absence of characters 1 and 2). 4) 1A, CuPb and CuPaβ fused. Several test runs were also performed including more characters, namely 5) ovipositor type and 6) metatibial spur type as well as reducing the number of characters corresponding to wing color (1-3). However, these alternative runs led to less convincing results than relying on just characters 1-4. An example is given in Fig. 2, where character 5 (ovipositor type) was added to the analysis (ovipositor types after Willmott et al. (2025)).

The species of Elcanidae used in the analysis represent members from the Archelcaninae and Elcaninae as well as multiple different localities and horizons. Species selection was based on how well a specimen is preserved and represented in the literature. The Crato Formation Elcanidae discussed in chapter 8 of this dissertation were not considered, because different states of preservation between specimens allow for varying interpretations regarding their wing color patterns.

Table 1: Taxon sampling of Elcanidae Handlirsch, 1906 for morphology-based UPGMA. "N" indicates missing information on the character state. MH_0041 and MH_0043 are figured below (Fig. 4 and 5). "Ref." (= Reference) in column "Data obtained from" means data in columns 3-6 is based on the publication stated after the taxon name in column two and provided in the reference list. "Ch." (= Chapter) refers to a chapter of this dissertation where the respective species is described.

Subfamily	Species	Presence of abstract wing color	Presence of large prominent wing spots	Wings without color (absence of char. 1 and 2)	1A, CuPb and CuPaβ fused	Data obtained from
Archelcaninae Gorochov, Jarzembowski & Coram, 2006	*Archelcana durnovaria* Whalley, 1985	yes	no	no	no	Ref.
	Archelcana geinitzi comb. nov., herein (Heer, 1880 in Geinitz, 1880)	yes	no	no	no	Ch. 9
	Archelcana magna comb. nov., herein (Handlirsch, 1906)	yes	no	no	no	Ch. 9
	Archelcana media comb. nov., herein (Handlirsch, 1906)	yes	no	no	no	Ch. 9
	Archelcana minima comb. nov., herein (Handlirsch, 1906)	yes	no	no	no	Ch. 9

	Archelcana numbergerae Heads, Thuy & Tamarri, 2022	yes	no	no	no	Ref.
	Archelcana tina Heads, Thuy & Tamarri, 2022	yes	no	no	no	Ref.
	Caelielca spinocrus Uchida, 2022	yes	no	no	no	Ref.
	Cascadelcana virginiana Fang, Muscente, Heads, Wang & Xiao, 2018	yes	no	no	no	Ref.
	Hukawnelca gracile Uchida, 2022	no	yes	no	no	Ref.
	Jeholelcana yanensis Fang, Heads, Wang, Zhang & Wang, 2018	yes	no	no	no	Ref.
	Longioculus poinari Schall and Husemann, in press (chapter 7)	no	no	yes	no	Ch. 7
	Parelcana pulchmacula Tian, Gu, Yin & Ren, 2019	no	yes	no	no	Ref.
	Parelcana xena Schall and Husemann, in press (chapter 7)	no	yes	no	no	Ch. 7

	Sinoelcana minuta Gu, Tian, Wang & Yue, 2020	yes	no	no	no	Ref.
	Thagyaminana atawedeia Schall, Kotthoff & Husemann, in press	no	yes	no	no	Ref.
Elcaninae Handlirsch, 1906	*Elcanodentes alatus* Willmott, Schall, Kotthoff & Husemann, 2025	no	no	yes	N	Ref.
	MH_0041 (*Elcanodentes alatus*), Fig. 5.10	no	no	yes	yes	Fig. 5.10 (this dissertation)
	MH_0043 (*Elcanodentes alatus*), Fig. 5.11	no	no	yes	yes	Fig. 5.11 (this dissertation)
	Elcanodentes cretaceus Willmott, Schall, Kotthoff & Husemann, 2025	no	no	yes	yes	Ref.
	Elcanodentes thanatos Schall, Willmott, Kotthoff & Husemann, 2025 in Willmott et al., 2025	no	no	yes	yes	Ref.

	Ellca nevelka Kočárek, 2020	no	no	yes	yes	Ref.
	Kolymbelcana phantasma Schall, Kotthoff & Husemann, 2025	no	yes	no	yes	Ref.
	Minelcana membranacea Gorochov, Jarzembowski & Coram, 2006	yes	no	no	yes	Ref.
	Panorpidium acusicaudum Tian, Ren & Gu, 2022	no	yes	no	yes	Ref.
	Panorpidium bimaculatum Gorochov, Jarzembowski & Coram, 2006	no	yes	no	yes	Ref.
	Panorpidium parvum Gorochov, Jarzembowski & Coram, 2006	yes	no	no	yes	Ref.
	Panorpidium proximum Gorochov,	yes	no	no	yes	Ref.

	Jarzembowski & Coram, 2006					
	Panorpidium sibiricum (Sharov, 1968)	no	yes	no	yes	Zessin, 1987
	Panorpidium spica Kim, Lee, Nam & Park, 2021	no	yes	no	yes	Ref.
	Panorpidium tessellatum Westwood, 1854	yes	no	no	yes	Gorochov et al., 2006
	Panorpidium validum Tian, Ren & Gu, 2022	yes	no	no	yes	Ref.
	Panorpidium yixianensis Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015	no	yes	no	yes	Ref.
	Paraxelcana simplicissima (Schall, Kotthoff & Husemann, 2025)	no	no	yes	yes	Ref.
	Paraxelcana zhengi (Gu, Tian & Ren, 2022)	no	no	yes	yes	Schall, Kotthoff & Husemann (submitted)
	Probaisselcana cretacea Gorochov,	yes	no	no	yes	Ref.

	Jarzembowski & Coram, 2006					
	Probaisselcana euryptera Tian, Gu & Ren, 2019	yes	no	no	yes	Ref.
	Probaisselcana kachinensis Zhou, Xu & Xiao, 2024	no	yes	no	yes	Ref.
	Pseudopanorpidium maculosum (Zhou, Xu, Jarzembowski & Xiao, 2022)	no	yes	no	yes	Ref.
	Pseudopanorpidium inversa Schall, Kotthoff & Husemann, 2025	no	yes	no	yes	Ref.
	Pseudoprobaisselcana oculata (Hu and He, 2023)	no	yes	no	yes	Ref.
Incertae sedis	*Letoelcana artemisapollonque* Schall, Kotthoff & Husemann, 2024	no	yes	no	N	Ref.
	Trigonelca jennywinterae Schall,	no	no	yes	N	Ref.

	Kotthoff & Husemann, 2024					

2.2 Cluster analysis

The data from Table 1 was translated into a binary matrix. All characters were coded no = 0; yes = 1. The matrix was written to a Nexus file (appendix 1). A UPGMA was performed in PAUP v. 4.0a169 (Swofford, 2003) with all settings kept as default. The resulting dendrogram was saved and uploaded to iTOL (Letunic and Bork, 2024). The taxon *Cascadelcana virginiana* Fang, Muscente, Heads, Wang & Xiao, 2018 was selected as root for the tree, because it is the earliest known species of Elcanidae. Including a different outgroup (attempted with *Pseudoacrida sennlaubi* Nel and Jouault, 2022 from the Locustopsidae Handlirsch, 1906 family) did not result in any changes to tree topology due to the limited character sampling (*P. acrida* had the same combination of 0 and 1 as the Archelcaninae in the character matrix, see appendix 1). Limitations of the UPGMA (i.e. unsuitable for depicting phylogenetic relationships) apply as stated above for Tridactyloidea Brullé, 1835. In this study I used the UPGMA to organize species of Elcanidae in distinct clusters that represent operational taxonomic units and are based on morphological differences. Further modifications (font style of labels) to the dendrogram were made in Inkscape v. 1.4 (the Inkscape Team, 2025). Images of apomorphies adjacent to the results in Fig. 1were created in GIMP v. 3.0.2-1 (the GIMP Team, 2025).

3. Results

The UPGMA recovered one paraphyletic and three monophyletic clades (Fig. 1). The paraphyletic clade formed the ancestors to the monophyletic clades and included the Jurassic Elcanidae of the genus *Archelcana* Sharov, 1968 (including those revised in chapter 9), *Jeholelcana yanensis* Fang, Heads, Wang, Zhang & Wang, 2018, *Sinoelcana minuta* Gu, Tian, Wang & Yue, 2020 and *Caelielca spinocrus* Uchida, 2022 from Cretaceous Burmese amber. This clade was united by the presence of abstract wing color and free 1A, CuPb and CuPaβ.

The first monophyletic clade included *Minelcana membranacea* Gorochov, Jarzembowski & Coram, 2006 (UK, Lower Cretaceous), *Probaisselcana cretacea* Gorochov, Jarzembowski & Coram, 2006 (UK, Lower Cretaceous), *Probaisselcana euryptera* Tian, Gu & Ren, 2019 (China, Lower Cretaceous), *Panorpidium parvum* Gorochov, Jarzembowski & Coram, 2006 (UK, Lower Cretaceous), *Panorpidium proximum* Gorochov, Jarzembowski & Coram, 2006 (UK, Lower Cretaceous), *Panorpidium tessellatum* Westwood, 1854 (UK, Lower Cretaceous) and *Panorpidium validum* Tian, Ren & Gu, 2022 (China, Lower Cretaceous). Like the taxa

mentioned before, this clade was characterized by an abstract wing color pattern, but these species had 1A, CuPb and CuPaβ fused.

The second and third monophyletic clades were part of a larger clade that was the sister group to the previous clade. This clade was characterized by elcanids without an abstract wing color pattern. One of these groups included the species without any wing pattern (although some species, for example *Elcanodentes alatus* Willmott, Schall, Kotthoff & Husemann, 2025 may exhibit some color on the apical wing margin; the "pterostigma" area on the anterior margin of the forewing is always colored in elcanids). It featured the genera *Longioculus* Poinar, Gorochov & Buckley, 2007, *Trigonelca* Schall, Kotthoff & Husemann, 2024, *Ellca* Kočárek, 2020, *Elcanodentes* Willmott, Schall, Kotthoff & Husemann, 2025 and *Paraxelcana* Schall , Kotthoff & Husemann, 2024. As *Longioculus poinari* Schall and Husemann, in press (chapter 7) has 1A, CuPb and CuPaβ free (but all other taxa listed have these veins fused [unknown for *Trigonelca*]), monophyly of this clade was not characterized by absence/presence of fusion of these veins. All taxa included in this group were discovered in Cretaceous amber from Myanmar.

The other group consisted of species which forewings (or possibly hindwings) show two (or sometimes just one) conspicuous round wing spots. The presence of wing spots is often, but not necessarily, accompanied by a colored apical wing margin. Included in this group were the genera *Letoelcana* Schall, Kotthoff & Husemann, 2024, *Thagyaminana* Schall, Kotthoff & Husemann, in press, *Hukawnelca* Uchida, 2022, *Pseudoprobaisselcana* Schall, Willmott, Kotthoff & Husemann, 2025, *Pseudopanorpidium* Schall, Willmott, Kotthoff & Husemann, 2025 and *Kolymbelcana* Schall, Kotthoff & Husemann, 2025. Additionally, the species *Parelcana pulchmacula* Tian, Gu, Yin & Ren, 2019, *Parelcana xena* Schall and Husemann, in press (chapter 7), *Probaisselcana kachinensis* Zhao, Xu & Xiao, 2024, *Panorpidium yixianensis* Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015, *Panorpidium spica* Kim, Lee, Nam & Park, 2021, *Panorpidium sibiricum* (Sharov, 1968), *Panorpidium acusicaudum* Tian, Ren & Gu, 2022 and *Panorpidium bimaculatum* Gorochov, Jarzembowski & Coram, 2006. Like in the previous clade, species with 1A, CuPb and CuPaβ free as well as fused were present in this group. All species were discovered in Cretaceous amber from Myanmar, except for: *Parelcana pulchmacula* (China, Jurassic), *Panorpidium acusicaudum* (China, Lower Cretaceous), *Panorpidium bimaculatum* (UK, Lower Cretaceous), *Panorpidium sibiricum* (Russia, Lower Cretaceous), *Panorpidium spica* (Korea, Lower Cretaceous) and *Panorpidium yixianensis* (China, Lower Cretaceous).

Below, I describe the three monophyletic clades as new tribes of Elcanidae. The subfamily concept of Elcaninae Handlirsch, 1906 and Archelcaninae Gorochov, Jarzembowski & Coram, 2006 *sensu* Gorochov et al. (2006) is re-considered. The final results of the taxonomic revision are summarized in Table 2.

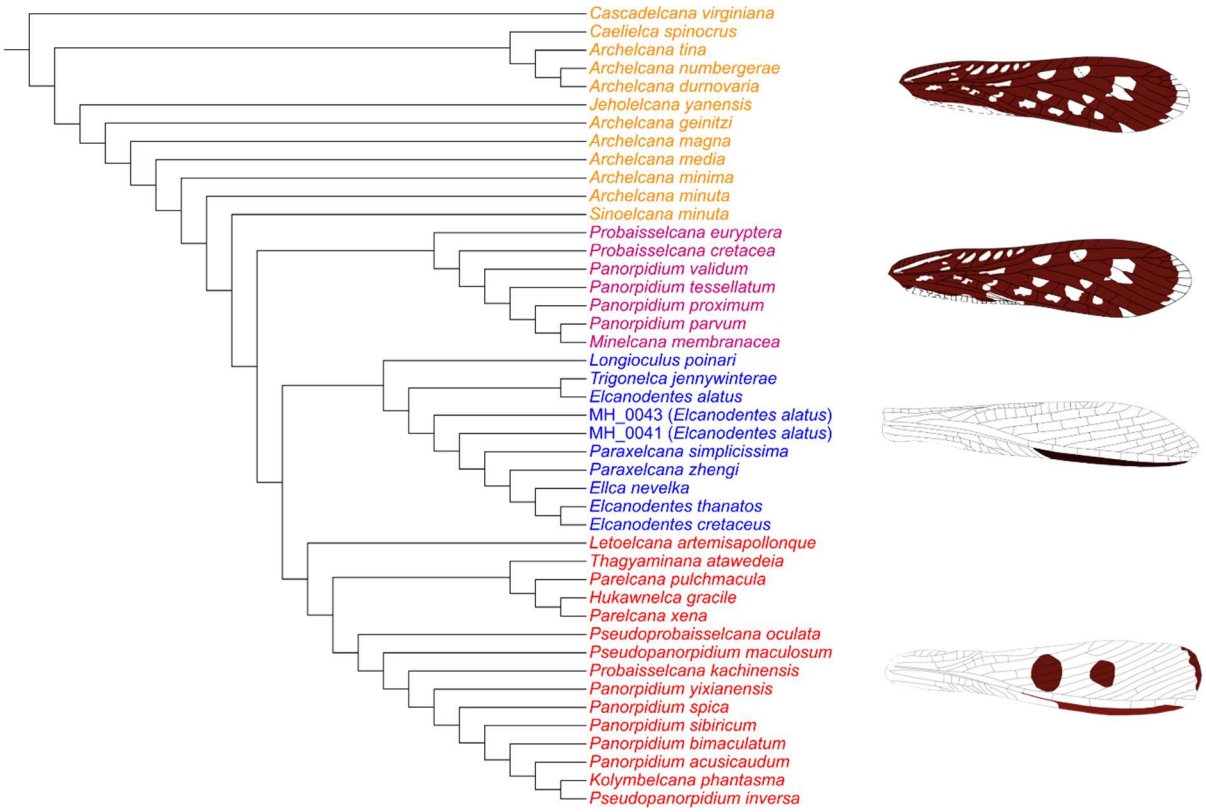

Fig. 1 UPGMA of Elcanidae Handlirsch, 1906 taxonomy based on morphological characters of wing pattern and fusion of forewing veins 1A, CuPb and CuPaβ. To the right wing pattern of clades are shown (clades are color-coded).

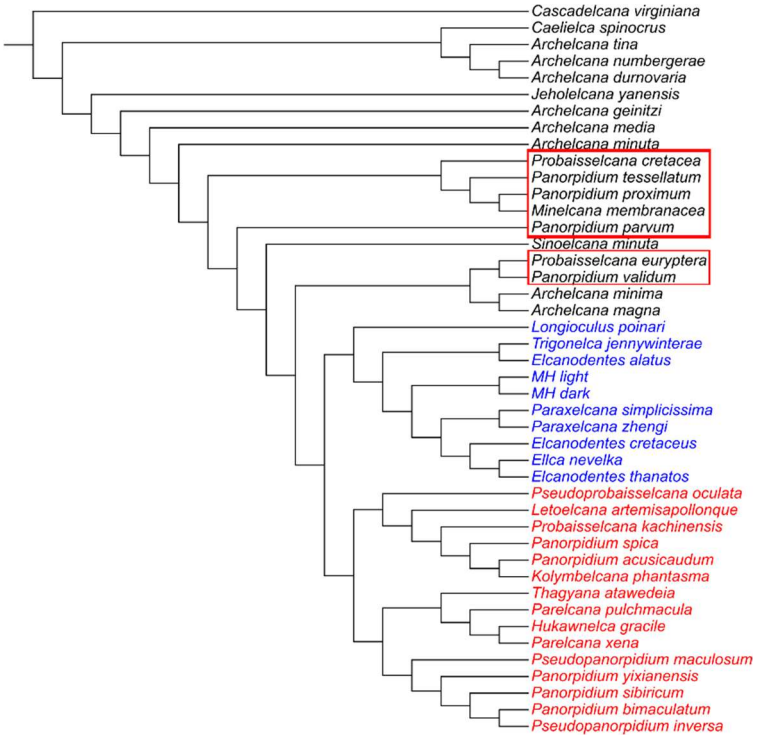

Fig. 2 same as Fig. 1, but with "ovipositor type" (after Willmott et al., 2025) added as a character. Although the "blue clade" and "red clade" are resolved in this version too, some species colored in orange and violet in Fig. 1 cluster strangely. The bottom red square shows two species of *Panorpidium* Westwood, 1854/*Probaisselcana* Gorochov, 1989 that cluster together with the species in the top red square in Fig. 1 (i.e. the expected outcome), but are instead more closely associated with two species of *Archelcana* Sharov, 1968 here. Because of this, the ovipositor type was excluded from the cluster analysis. However, note the improved resolution of the red and blue clade. Once more data is available, including additional characters in the UPGMA may improve its quality down to the genus level.

4. Systematic paleontology

Order Orthoptera Olivier, 1789

Suborder Ensifera Chopard, 1921

Infraorder Elcanidea Gorochov, 1995

Superfamily Elcanoidea Handlirsch, 1906

Family Elcanidae Handlirsch, 1906

Subfamily Archelcaninae Gorochov, Jarzembowski & Coram, 2006

Included genera: *Archelcana* Sharov, 1968; *Caelielca* Uchida, 2022; *Cascadelcana* Fang, Muscente, Heads, Wang & Xiao, 2018; *Jeholelcana* Fang, Heads, Wang, Zhang

& Wang, 2018; *Parelcana* Handlirsch, 1906; *Sibelcana* Gorochov, 1990; *Sinoelcana* Gu, Tian, Wang & Yue, 2020; *Synelcana* Zessin, 1988

Emended diagnosis: This – possibly paraphyletic – subfamily is characterized by an abstract wing color pattern, whereby the area of wing that is colored can vary somewhat drastically; further characterized by the free state of tegminal veins 1A, CuPb and CuPaβ.

Remarks: This taxon was recovered as paraphyletic in the UPGMA presented in the previous section. However, a cluster analysis based on four morphological character sets is unlikely to fully resolve taxonomic relationships within any group. Consequently, the subfamily Archelcaninae is preliminarily kept as a valid taxon until a proper phylogenetic analysis of Elcanidae is conducted (I attempted this, but taxon and/or character sampling is still too small in Elcanidae to resolve relationships). Archelcaninae had their highest levels of diversity during the Jurassic, where they are known from localities in Europe and China. *Caelielca spinocrus* Uchida, 2022 from mid-Cretaceous Burmese amber is an anomaly in that its presence post-dates the existence of the next youngest member (*Sibelcana websteri* Gorochov and Coram, 2022) by ca. 40 My. Furthermore, no other elcanid with an abstract color pattern has been discovered from Burmese amber so far.

Subfamily Elcaninae Handlirsch, 1906

Included genera: *Argentoelcana* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, 2025 (chapter 8); *Atopoelcana* gen. nov., herein (see below); *Cratoelcana* Martins-Neto, 1991; *Elcanodentes* Willmott, Schall, Kotthoff & Husemann, 2025; *Ellca* Kočárek, 2020; *Ensiferelcana* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, 2025 (chapter 8); *Gondwanaelcana* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, 2025 (chapter 8); *Hukawnelca* Uchida, 2022; *Kolymbelcana* Schall, Kotthoff & Husemann, 2025; *Letoelcana* Schall, Kotthoff & Husemann, 2024; *Longioculus* Poinar, Gorochov & Buckley, 2007; *Mesembrelcana* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, 2025 (chapter 8); *Minelcana* Gorochov, Jarzembowski & Coram, 2006; *Paraxelcana* Schall, Kotthoff & Husemann, 2024; *Panorpidium* Westwood, 1854; *Probaisselcana* Gorochov, 1989; *Pseudopanorpidium* Schall, Willmott, Kotthoff & Husemann, 2025; *Pseudoprobaisselcana* Schall, Willmott, Kotthoff & Husemann, 2025; *Stellacana* gen. nov., herein (see below); *Thagyaminana* Schall, Kotthoff & Husemann, in press; *Trigonelca* Schall, Kotthoff & Husemann, 2024

Emended diagnosis: Characterized by either an abstract wing color pattern, but with tegminal veins 1A, CuPb and CuPaβ fused; or by the wing color pattern different, i.e. presence of conspicuous wing spots (1-2) or wing without coloration (except "pterostigma area" and sometimes apical wing margin).

Remarks: The Elcaninae *sensu novum* are mostly known from the Early-middle Cretaceous from Europe, Asia (including Burmese amber) and South America (Crato Formation). One curious exception is *Atopoelcana pulchmacula* comb. nov. (Tian, Gu, Yin & Ren, 2019) from the middle Jurassic of China. In this species, which is known from four specimens (all are isolated forewings), two wing spots are fully developed. Yet, remnants of what looks like the abstract color pattern of the Jurassic Archelcaninae is present alongside those (Tian et al., 2019). As this is the first record of an Elcaninae *sensu novum* and it seems to represent an intermediary state, it is possible that this subfamily originated during the Jurassic in Asia.

Elcaninae consists of two tribes, the Panorpidini trib. nov. and the Stellacanini trib. nov.

Tribe **Panorpidini** trib. nov.

> Included genera: *Minelcana* Gorochov, Jarzembowski & Coram, 2006; *Panorpidium* Westwood, 1854; *Probaisselcana* Gorochov, 1989

Etymology: After the type genus *Panorpidium*, assigned herein.

Locality and horizon: Early Cretaceous of the UK and China.

Diagnosis: Wing color pattern abstract, with pigmention developed to varying degrees (covering more or less area of the wing). Tegminal 1A, CuPb and CuPaβ fused.

Remarks: Panorpidini includes the species of Elcaninae that have retained the abstract wing color pattern of their ancestors in the Archelcaninae. It consists of three genera from the Early Cretaceous of the UK and China. Most species formerly assigned to *Panorpidium* (and some species of *Probaisselcana*) are removed from these genera, because they show different wing color patterns. Their new taxonomic status is discussed below.

Tribe **Paraxelcanini** trib. nov.

> Included genera: *Argentoelcana* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8); *Cratopidium* gen. nov., herein (see below); *Elcanodentes*

Willmott, Schall, Kotthoff & Husemann, 2025; *Ellca* Kočárek, 2020; *Ensiferelcana* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8); *Gondwanaelcana* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8); *Longioculus* Poinar, Gorochov & Buckley, 2007; *Paraxelcana* Schall, Kotthoff & Husemann, 2024; *Trigonelca* Schall, Kotthoff & Husemann, 2024

Etymology: After the type genus *Paraxelcana*, assigned herein.

Locality and horizon: Confirmed members of this tribe are exclusively known from mid-Cretaceous amber of Myanmar. Some taxa of Crato-Formation Elcanidae may also belong to Paraxelcanini, namely *Argentoelcana* (chapter 8), *Ensiferelcana* (chapter 8), *Gondwanaelcana* (chapter 8) and *Cratopidium* gen. nov., herein (see below), which is erected to accommodate former *Panorpidium damianii* (Martins-Neto, 1991).

Diagnosis: Paraxelcanini is characterized by the absence of wing color except for in the "pterostigma" area. Some specimens of the genus *Elcanodentes* show coloration on the apical margin of the forewing (see Fig. 3).

Remarks: This tribe is well-represented from several specimens discovered in amber from Myanmar (Kočárek, 2020; Poinar et al., 2007; Schall et al., 2024; Willmott et al., 2025). The holotypes of the Crato Formation *Argentoelcana intermedia* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8), *Ensiferelcana brachyptera* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8), *Gondwanaelcana brasiliensis* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8) and *Cratopidium damianii* comb. nov. (Martins-Neto, 1991) may also belong to this group, because their wings seemingly do not to show wing spots or an abstract color pattern. However, varying degrees of preservation accuracy as was observed with *Cratoelcana* and *Mesembrelcana* (see below) might have influenced reliability of what can be seen in the fossils. Their taxonomic position may, therefore, change with future findings. The genus *Longioculus* may be the most basal taxon within this subtribe, as the species still exhibit the non-fused state of tegminal 1A, CuPb and CuPaβ.

Subtribe **Stellacanini** trib. nov.

Included genera: *Atopoelcana* gen. nov., herein (see below); *Cratoelcana* Martins-Neto, 1991; *Hukawnelca* Uchida, 2022; *Kolymbelcana* Schall, Kotthoff & Husemann, 2025; *Letoelcana* Schall, Kotthoff & Husemann, 2024; *Mesembrelcana* Schall, Heads, Lima,

Pinheiro, Kotthoff & Husemann, submitted (chapter 8); *Pseudopanorpidium* Schall, Willmott, Kotthoff & Husemann, 2025; *Pseudoprobaisselcana* Schall, Willmott, Kotthoff & Husemann, 2025; *Stellacana* gen. nov., herein (see below); *Thagyaminana* Schall, Kotthoff & Husemann, in press

Etymology: After the type genus *Stellacana* gen. nov., herein (below), assigned herein.

Locality and horizon: Middle Jurassic of China (*Atopoelcana pulchmacula* comb. nov. (Tian, Gu, Yin & Ren, 2019)); Early Cretaceous of Brazil; mid-Cretaceous of Myanmar (Burmese amber).

Diagnosis: Members of this tribe are easily recognized by the presence of either a single or two large round wing spots, prominently located on the forewing (or sometimes hindwing).

Remarks: This tribe may have evolved during the Lower or middle Jurassic in China and was widespread with many species in the Lower and middle Cretaceous. Many previous members of *Panorpidium* are removed to the type genus *Stellacana* gen. nov. to account for monophyly of *Panorpidium sensu novum* in the Panorpidini tribe. Some specimens assigned to *Cratoelcana* and *Mesembrelcana* (chapter 8) clearly show two wing spots (including the holotype of *Mesembrelcana rasnitsyni* comb. nov. (Nel and Jouault, 2022). This proves that Stellacanini were present in the Crato Formation of Brazil, too. Differences regarding presence/absence of wing spots in some specimens versus others are probably caused by varying degrees of preservation accuracy.

Genus ***Atopoelcana*** gen. nov.

Included species: *Atopoelcana pulchmacula* comb. nov. (Tian, Gu, Yin & Ren, 2019); *A. xena* comb. nov. (of *Parelcana xena* Schall and Husemann, in press (chapter 7))

Etymology: From the ancient Greece “atopos” (strange, incorrect) and -elcana. The name refers to the rare and unusual wing venation found in this genus and *Parelcana*, which may have been its ancestor.

Type species: Atopoelcana pulchmacula comb. nov. (Tian, Gu, Yin & Ren, 2019)

Locality and horizon: Known only from the middle Jurassic of China and middle Cretaceous of Myanmar.

Diagnosis: Forewing with three branches of M between CuA + CuPaα and the stem of RP. CuPaα fused with free CuA. Forewing or hindwing with two prominent wing spots.

Remarks: Both *Parelcana* and *Atopoelcana* are strange taxa. The different morphology of anal veins below 1A in *Parelcana* (i.e. 2A is not fused to 1A as is usually the case in Elcanidae) may suggest that the genus rather belongs to Permelcanidae Sharov, 1962. In *Atopoelcana* the state of 2A in respect to 1A is typical for Elcanidae (i.e. 2A is fused to 1A). Still, the unusual morphology of the cubital veins is puzzling, more so because of its rarity. Anomalies regarding wing venation are known to occur in Elcanidae (fusion of CuPaβ into CuA + CuPaα in *Jeholelcana yanensis*; fusion of CuA + CuPaα into MP in *Atopoelcana xena* (compare chapter 7, Fig. 2); fusion of CuPaβ and CuA + CuPaα in only one hindwing of *Pseudoprobaisselcana kachinensis* comb. nov. (see below) (Zhou, Xu & Xiao, 2024)). It should probably be considered whether the character "CuPaα in contact with MP" is merely an unusual variation within *Pseudopanorpidium* (for *A. xena*) and *Stellacana* (for *A. pulchmacula*), rather than a diagnostic character of a separate genus. On the other hand, *A. pulchmacula* is known from four specimens and it is unlikely that the "unusual variation" would have been present in all of them.

Differences between *A. pulchmacula* and *A. xena* (namely the elongated tegminal margin of MP, the absence of the remnants of abstract color still visible in *A. pulchmacula* and possibly the position of the wing spots on the hindwing rather than forewing) suggest these species belong to different genera. As this work is already rather extensive regarding its changes to taxonomy, I refrain here from proposing a new genus for *A. xena*, as it would not serve to advance the main findings of this section of the study (which is the revision of higher-level Elcanidae taxonomy).

Genus ***Cratopidium*** gen. nov.

Included species: *Cratopidium damianii* comb. nov. (Martins-Neto, 1991)

Etymology: The name is a combination of "Crato" (after the type locality of the genus), and "Panorpidium" due to the likeness it shares with that taxon.

Type species: Cratopidium damianii.

Locality and horizon: Early Cretaceous (Late Barremian-Early Albian) Crato Formation of Brazil.

Diagnosis: Similar to *Panorpidium* in having tegminal 1A, CuPb and CuPaβ fused and three branches of M between CuA+ CuPaα and the stem of RP. However, wings without color pattern (vs. abstract color pattern in *Panorpidium*). Differences from the other members of Paraxelcanini trib. nov. were already discussed in chapter 8 of this dissertation.

Remarks: This taxon was already discussed in chapter 8 of this dissertation.

Genus ***Stellacana*** gen. nov.

> Included species: *Stellacana acusicauda* comb. nov. (Tian, Ren & Gu, 2022); *S. bimaculata* comb. nov. (Gorochov, Jarzembowski & Coram, 2006); *S. sibirica* comb. nov. (Sharov, 1968); *S. spica* comb. nov. (Kim, Lee, Nam & Park, 2021); *S. yixianensis* comb. nov. (Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015)

Etymology: After the Latin "stella", meaning "star" and -cana from "elcana", the original name of the type genus of Elcanidae. Refers to the characteristic wing spots of this group, reminiscent of "stars" on a night sky.

Type species: Stellacana spica, assigned herein.

Locality and horizon: Early Cretaceous of UK and Asia (Siberia, China, Korea).

Diagnosis: Similar to *Panorpidium* in terms of venation morphology (i.e. 1A, CuPb and CuPaβ fused; 3 branches of M between CuA + CuPaα and the stem of RP; CuPaα short, fused in vertical orientation with CuA + CuPaα), but differs from *Panorpidium* by the replacement of the abstract wing color pattern (see above) with one or two conspicuous wing spots.

Remarks: This genus comprises species formerly attributed to *Panorpidium*. After the taxonomic revision of Elcanidae, *Panorpidium* is definded by the presence of abstract wing color and absence of wing spots. Thus, a new genus is proposed for the species listed above.

Species *Pseudoprobaisselcana kachinensis* comb. nov. (Zhou, Xu & Xiao, 2024)

Remarks: This species was recently described from Burmese amber as *Probaisselcana kachinensis*. The holotype feature a distinct wing spot on the forewing, which is otherwise bare of color. The presence of a wing spot excludes this species from *Probaisselcana sensu novum*. The genus *Pseudoprobaisselcana* Schall, Willmott, Kotthoff & Husemann, 2025 (in Willmott et al., 2025) until now included only *P. oculata* (Hu and He, 2023). That species shares important characteristics with *P. kachinensis*, including the absence of abstract wing color, but

the presence of wing spots (there are two wing spots in *P. oculata*). Another diagnostic feature of *Pseudoprobaisselcana* is an elongated tegminal margin of MP (21% of total wing length (twl) in *P. oculata* vs. a mean of 11% of twl in *Probaisselcana*) (Willmott et al., 2025). The tegminal margin of *P. kachinensis* is 14% of twl on the left forewing and ca. 20.7% of twl on the right forewing. This is a noteworthy degree of variation, as the prior value is closer to *Probaisselcana*, while the second is closer to *Pseudoprobaisselcana*. But, based on the wing color pattern of *P. kachinensis* it seems conclusive to place it into the latter genus. As the tegminal margin of MP of at least the right forewing matches that of *P. oculata*, no new genus needs to be erected.

Genera *incertae sedis*: *Burmelcana* Peñalver and Grimaldi, 2010; *Cenoelcanus* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020; *Elcanonympha* Heads and Thomas, 2018; *Elcanopsis* Tillyard, 1918; *Eubaisselcana* Gorochov, 1986; *Hispanelcana* Peñalver and Grimaldi, 2010; *Liaonemobius* Ren, 1998; *Macrelcana* Karny, 1932; *Monitelcana* Xu, Luo, Jarzembowski, Fang & Wang, 2022

Possible placements of Burmelcana: This genus is based on the single nymph *B. longirostris* Peñalver and Grimaldi, 2010 from Cretaceous Burmese amber. *Burmelcana* was proposed as a synonym of *Panorpidium* by Zhou et al. (2022) on the basis of shared morphology of metatibial and -tarsal spines. *Panorpidium maculosum*, the species described in Zhou et al. (2022) has been transferred to *Pseudopanorpidium* by Willmott er al. (2025). It has leaf-like metatibial spurs, whereas *B. longirostris* has spine-like spurs. Given the hypothesized importance of wing patterns for the taxonomic placement of elcanids, assignment of any nymphal specimen is problematic. Considering current evidence, *Burmelcana* should probably be re-instated as its own genus and considered Elcanidae *incertae sedis*, until more knowledge regarding nymph morphology in this family is available.

Possible placements of Cenoelcanus: The genus includes a single species *C. menatensis* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020, described from an isolated wing found in the Paleocene deposits of the French Menat Formation. If the specimen truly belongs to Elcanidae, it would be a remarkable finding as it would prove survival of the group post the end-Cretaceous mass extinction. However, the affinity of *C. menatensis* with Elcanidae is dubious. The anal and cubital veins (except for CuA + CuPaα) have a very different morphology compared to the Mesozoic elcanids. ScP of *C. menatensis* almost reaches the wing apex, whereas it only extends to about the middle of the wing in other Elcanidae. Lastly, *C.*

menatensis only has two branches of M and three branches of RP, which is an unusually small number. Nonetheless, the apparent fusion of M and RP, as suggested by Schubnel et al. (2020), does support placement of *C. menatensis* in Elcanidae.

The identity of *C. menatensis* remains dubious and intriguing at the same time. Hopefully, future findings from the Menat Formation (or other places of Paleocene origin) can confirm the presence of post-Cretaceous Elcanidae or, alternatively, help assign *Cenoelcanus* to the correct family.

Possible placements of Elcanonympha: Like *Burmelcana*, this genus is based on a single species known from a Burmese amber nymph (Heads et al., 2018). As mentioned previously, assigning elcanid nymphs to taxonomic ranks is difficult due to the absence of wings. Analyzing nymph morphology of the group may be a worthwhile subject for a future study. For now, like *Burmelcana*, *Elcanonympha* is considered Elcanidae *incertae sedis*.

Possible placements of Elcanopsis: Based on the single species *E. sydneiensis* Tillyard, 1918, the holotype is an isolated wing fragment consisting of ca. the distal two thirds. Originally, *E. sydneiensis* was thought to be of Permian age, which would have made it the only pre-Mesozoic record of the family. Later age estimates for the type locality of the species (Hawkesbury Sandstone Formation, Balmain, Sydney Harbor, Australia) suggest a Triassic age instead (Jell, 2004; Mc Loughlin et al., 2021). Therefore, *E. sydneiensis* would only be slightly older than *Cascadelcana virginiana* Fang, Muscente, Heads, Wang & Xiao, 2018 from the Upper Triassic of North America. Tillyard (1918) states that the specimen of *E. sydneiensis* is "not spotted, but marked with brown pigment along the costal space" (which refers to the "pterostigma" area of Elcanidae). If *Elcanopsis* belongs to the Archelcaninae (like *C. virginiana*), it would be expected that the wing showed traces of the abstract color pattern diagnostic of the group. Perhaps the pigmentation was lost. Tillyard (1918) remarks that the specimen is "so faint in outline" that it is hard to even locate. On the other hand, pigmentation in the pterostigma area was preserved. Another possibility is that *E. sydneiensis* represents a separate lineage, perhaps at the subfamily level, of early Gondwanan Elcanidae. Because nothing is known of Elcanidae from the southern hemisphere between *Elcanopsis* and the Crato Fauna ca. 120 My later, this hypothesis can neither be confirmed nor rejected with the current knowledge. It seems rather unlikely that *Elcanopsis* should represent a basal member of Paraxelcanini trib. nov. due to the 120 My that separate them.

Possible placements of Eubaisselcana: This genus includes two species from the Aptian (Early Cretaceous) of Mongolia (the Paleobiology Database,

https://paleobiodb.org/classic/basicTaxonInfo?taxon_no=250571, accessed 11.08.2025). They are diagnosed based on the fusion of anal veins 1A and CuPb, but free CuPaβ. The wing color pattern is indicated by Gorochov (1986): *Eubaisselcana sharovi* Gorochov, 1986 seems to show an abstract wing color pattern. *Eubaisselcana mongolica* Gorochov, 1986 has faint traces of an abstract wing color pattern, but also something that could be seen as partly preserved wing spots. It would be helpful if images of the holotypes of both species could be published. Unfortunately, access to specimens located in Russian collections is difficult at the moment.

Possible placements of Hispanelcana: This genus is known from three nymphs discovered in Early Albian Spanish amber (Peñalver and Grimaldi, 2010). As previously stated, placement of nymphs of Elcanidae is difficult with our current understanding of the family's taxonomy. It would be most interesting to find adult specimens of Spanish amber Elcanidae, as they could reveal novel aspects of morphology.

Possible placements of Liaonemobius: Another nymph, this time from the Early Cretaceous Yixian Formation of China. Other elcanids from the Yixian-Formation include *Probaisselcana minuta* Gu, Tian & Ren, 2022 and *P. euryptera* Tian, Gu & Ren, 2019, *Panorpidium validum* Tian, Ren & Gu, 2022, *Stellacana acusicaudum* comb. nov. (Tian, Ren & Gu, 2022), *S. yixianensis* comb. nov. (Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015) and *Jeholelcana yanensis* Fang, Heads, Wang, Zhang & Wang, 2018. Because of the relatively high diversity of elcanids found in the Formation, assignment of *Liaonemobius* to one of the taxa inside Elcanidae is difficult. The genus remains *incertae sedis*.

Possible placements of Macrelcana: An almost complete specimen from the Miocene of Radoboj, constituting the single species of this genus *M. ungeri* (Heer, 1849). Over the course of the roughly 150 years since its discovery, the species has been regarded either as a member of Elcanidae (Karny, 1932) or of Gryllacrididae Blanchard, 1845 (Poncrácz, 1928; Sharov, 1968). Karny (1932), main advocate of the Elcanidae hypothesis, argues that the oblique vein orientation of the forewing (especially of the anal veins) is reminiscent of Elcanidae much more than of the straight path found in Gryllacrididae. Prompted by this assumption, Karny made a closer inspection of the hindtibiae of *M. ungeri* and states: "I […] noticed four slightly concave bulges and then believe that I have also perceived that each of these bulges is covered by a flat, oval scale-like leaf" (translated from German). A little bit further down the text he continues: "distally, the hindtibia shows the flat, half-oval bulges mentioned previously and you get the impression – as far as this can still be observed, given the less-than-ideal state of preservation of the fossil – that each of these bulges is covered by a flat, oval scale, very similar to the

Mesozoic elcanids, but less acutely angled, more closely adjacent to the tibia than there" (Karny, 1932, pp. 66-67). Both claims sound rather vague.

The forewing morphology of *M. ungeri* differs from Elcanidae in several ways: the area below RA (the "pterostigma" area) which is usually colored in elcanids is inconspicuous in *M. ungeri*. M and RP are distinctly separate branches (vs they are fused to one branch in elcanids). The morphology of CuA + CuPaα is completely different from elcanids and much more closely resembles Gryllacrididae. ScP of *M. ungeri* covers almost the entire length of the forewing whereas it reaches only to about 50% of it in Elcanidae.

Overall, the forewing morphology of *M. ungeri* strongly suggests the species as part of Gryllacrididae instead of Elcanidae. As to the possible tibial spurs stated by Karny (1932), it would be helpful if the holotype of *M. ungeri* could be reviewed with some high-resolution images to resolve the question of this – admittedly intriguing – alleged character.

Possible placements of Monitelcana: The genus is based on a single species known from a Burmese amber nymph that faces the same taxonomic difficulties as *Burmelcana, Elcanonympha, Liaonemobius* and *Hispanelcana*. It is considered Elcanidae *incertae sedis*.

Table 2: Taxonomy of Elcanidae Handlirsch, 1906 with revisions and changes proposed in this study. The table includes all species currently described.

Subtaxon	**Species new**	**Species old**	**Comment**
Archelcaninae Gorochov, Jarzembowski & Coram, 2006	***Archelcana*** *anglicana* (Handlirsch, 1939)	Unchanged	From *Parelcana anglicana* (see chapter 7).
	Archelcana britannica (Handlirsch, 1906)		
	Archelcana durnovaria Whalley, 1985		
	Archelcana geinitzi (Heer, 1880)		
	Archelcana magna (Handlirsch, 1906)		
	Archelcana media (Handlirsch, 1906)		
	Archelcana minima (Handlirsch, 1906)		

	Archelcana minuta (Sharov, 1968)		
	Archelcana numbergerae Heads et al., 2022		
	Archelcana ornata Zherikhin, 1985		
	Archelcana phyllophora (Handlirsch, 1906)		
	Archelcana shurabica (Sharov, 1968)		
	Archelcana tina Heads, Thuy & Tamarri, 2022		
	Caelielca *spinocrus* Uchida, 2022		
	Cascadelcana *virginiana* Fang, Muscente, Heads, Wang & Xiao, 2018		
	Jeholelcana *deichmuelleri* (Handlirsch, 1906)		
	Jeholelcana yanensis Fang, Heads, Wang, Zhang & Wang, 2018		
	Parelcana *tenuis* Handlirsch, 1906		
	Parelcana dubia Handlirsch, 1939		Nomen dubium (chapter 7)
	Sibelcana *rossica* Gorochov, 1990		
	Sibelcana transbaicalica Gorochov, 1990		
	Sibelcana websteri		
	Sinoelcana *minuta* Gu, Tian, Wang & Yue, 2020		
	Synelcana *muelleri* Zessin, 1988		
Elcaninae Handlirsch, 1906: Panorpidini trib. nov.	***Minelcana*** *dubia* (Giebel, 1856)	Unchanged	
	Minelcana membranacea Gorochov, Jarzembowski & Coram, 2006		

	Panorpidium *angustior* (Handlirsch, 1939)		Needs revision.
	Panorpidium beyrichi (Giebel, 1856)		Needs revision.
	Panorpidium lata (Sharov, 1968)		Needs revision.
	Panorpidium liasinum (Giebel, 1856)		Needs revision.
	Panorpidium lithophilum (Germar, 1842)		Needs revision.
	Panorpidium longicorne (Handlirsch, 1906)		Needs revision.
	Panorpidium oppenheimi (Handlirsch, 1906)		
	Panorpidium parvum Gorochov, Jarzembowski & Coram, 2006		
	Panorpidium proximum Gorochov, Jarzembowski & Coram, 2006		
	Panorpidium tessellatum Westwood, 1854		
	Panorpidium validum Tian, Ren & Gu, 2022		
	Panorpidium westwoodi (Handlirsch, 1906)		Needs revision.
	Probaisselcana *cretacea* Gorochov, Jarzembowski & Coram, 2006		
	Probaisselcana euryptera Tian, Gu & Ren, 2019		
	Probaisselcana karatavica (Sharov, 1968)		
	Probaisselcana minuta Gu, Tian & Ren, 2022		
Elcaninae: Paraxelcanini trib. nov.	***Argentoelcana*** *intermedia* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8)	U	

	Cratopidium *damianii* (Martins-Neto, 1991) (chapter 8)	*Panorpidium damianii*	
	Elcanodentes *alatus* Willmott, Schall, Kotthoff & Husemann, 2025	U	
	Elcanodentes cretaceus Willmott, Schall, Kotthoff & Husemann, 2025		
	Elcanodentes thanatos Schall, Willmott, Kotthoff & Husemann, 2025		
	Ellca *nevelka* Kočárek, 2020		
	Ensiferelcana *brachyptera* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8)		
	Gondwanaelcana *brasiliensis* Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, submitted (chapter 8)		
	Longioculus *burmensis* Poinar, Gorochov & Buckley, 2007		
	Longioculus poinari Schall and Husemann, in press (chapter 7)		
	Paraxelcana simplicissima (Schall, Kotthoff & Husemann, 2025)		
	Paraxelcana zhengi (Gu, Tian & Ren, 2022)		
	Trigonelca *jennywinterae* Schall, Kotthoff & Husemann, 2024		
Elcaninae: Stellacanini trib. nov.	***Atopoelcana*** *pulchmacula* (Tian, Gu, Yin & Ren, 2019)	*Parelcana pulchmacula*	

	Atopoelcana xena Schall and Husemann, in press (chapter 7)	*Parelcana xena*	*A. pulchmacula* and *A. xena* are probably different genera.
	Cratoelcana *zessini* Martins-Neto, 1991	U	
	Hukawnelca *gracilis* Uchida, 2022		
	Kolymbelcana *phantasma* Schall, Kotthoff & Husemann, 2025		
	Letoelcana *artemisapollonque* Schall, Kotthof & Husemann, 2024		
	Mesembrelcana *rasnitsyni* (Nel and Jouault, 2022)		
	Pseudopanorpidium *maculosum* (Zhou, Xu, Jarzembowski & Xiao, 2022)		
	Pseudopanorpidium inversa Schall, Kotthoff & Husemann, 2025		
	Pseudoprobaisselcana *oculata* (Hu and He, 2023)		
	Pseudoprobaisselcana kachinensis comb. nov. (Zhou, Xu & Xiao, 2024)	*Probaisselcana kachinensis*	
	Stellacana *spica* comb. nov. (Kim, Lee, Nam & Park, 2021)	*Panorpidium spica*	
	Stellacana acusicauda comb. nov. (Tian, Ren & Gu, 2022)	*Panorpidium acusicaudum*	
	Stellacana bimaculata comb. nov. (Gorochov, Jarzembowski & Coram, 006)	*Panorpidium bimaculatum*	
	Stellacana sibirica comb. nov. (Sharov, 1968)	*Panorpidium sibiricum*	

	Stellacana yixianensis comb. nov. (Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015)	*Panorpidium yixianensis*	
	Thagyaminana *atawedeia* Schall, Kotthoff & Husemann, in press	U	
Incertae sedis	***Burmelcana*** *longirostris* Peñalver and Grimaldi, 2010	*Panorpidium longirostris*	A nymph; *Panorpidium* according to Zhou et al. (2022) but evidence is not clear.
	Cenoelcanus *menatensis* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020	U	A specimen of uncertain identity.
	Elcanonympha *diana* Heads and Thomas, 2018		A nymph that is difficult to assign.
	Elcanopsis *sydneiensis* Tillyard, 1918		A mysterious Triassic specimen of uncertain position within Elcanoidea.
	Eubaisselcana *mongolica* Gorochov, 1986		Position within Elcanidae uncertain; photographs are needed.
	Eubaisselcana sharovi Gorochov, 1986		Position within Elcanidae uncertain; photographs are needed.
	Hispanelcana *arilloi* Peñalver and Grimaldi, 2010		A nymph of uncertain position within Elcanidae.
	Hispanelcana alavensis Peñalver and Grimaldi, 2010		A nymph of uncertain position within Elcanidae.
	Hispanelcana lopezvallei Peñalver and Grimaldi, 2010		A nymph of uncertain position within Elcanidae.
	Liaonemobius tanae Ren, 1998		A nymph of uncertain position within Elcanidae.
	Macrelcana *ungeri* (Heer, 1849)		A Miocene specimen of uncertain position within

			Ensifera; probably from the Gryllacrididae Blanchard, 1845
	Monitelcana *penalveri* Xu, Luo, Jarzembowski, Fang & Wang, 2022		A nymph of uncertain position within Elcanidae.

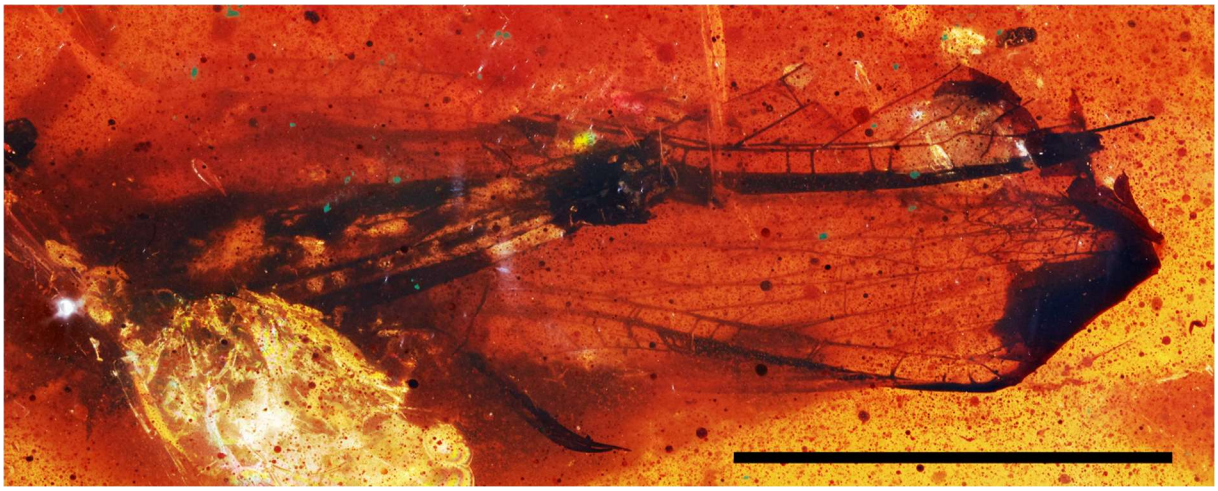

Fig. 3 Forewing of the holotype of *Elcanodentes alatus* Willmott, Schall, Kotthoff & Husemann, 2025 from the subfamily Elcaninae Handlirsch, 1906, tribe Paraxelcanini trib. nov. Members of this tribe usually have forewings without any coloration, but in some specimens of *Elcanodentus* Willmott, Schall, Kotthoff & Husemann, 2025 the apical margin shows the semicircular pattern that can be seen in the holotype of *E. alatus* as well. **Scale bar** = 5 mm.

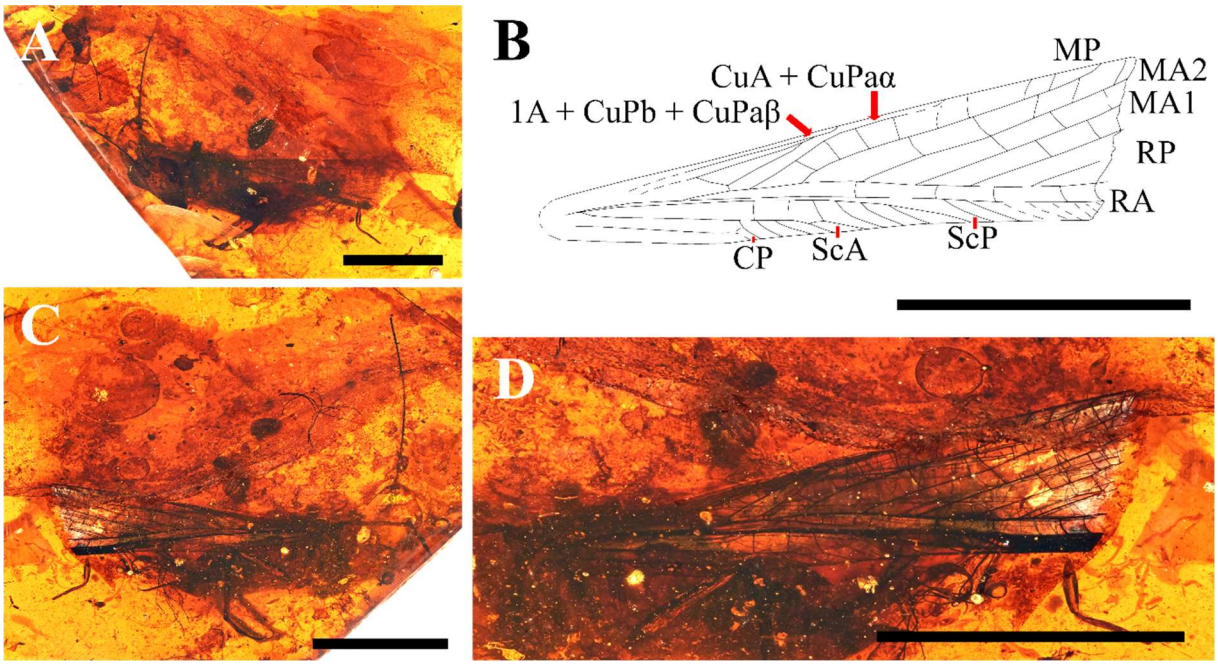

Fig. 4 Specimen MH_0041 (featured in the UPGMA presented above), determined as *Elcanodentus alatus* Willmott, Schall, Kotthoff & Husemann, 2025, female. **A.** Specimen, left side (head twisted towards front). **B.** Drawing of the forewing. **C.** Specimen, right side. **D.** Detail of the forewing. **Scale bars** = 5 mm.

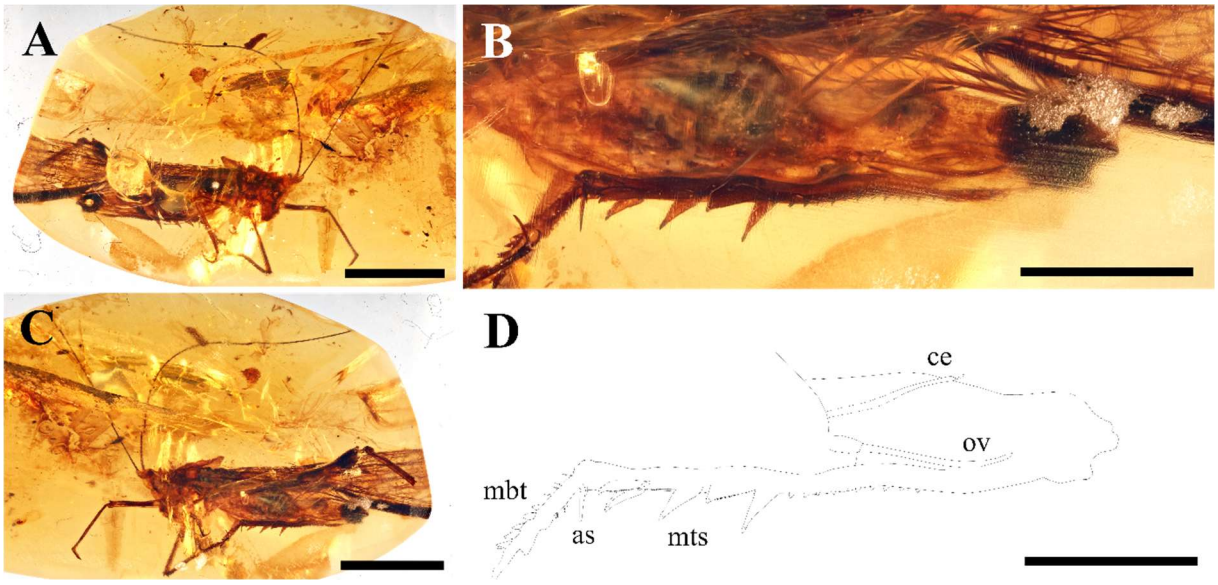

Fig. 5 Specimen MH_0043 (featured in the UPGMA presented above), determined as *Elcanodentus alatus* Willmott, Schall, Kotthoff & Husemann, 2025, female. **A.** Specimen, right side. **B.** Detail of cercus, ovipositor and metathoracic leg. **C.** Specimen, left side. **D.** Drawing of B. **Abbreviations:** as = apical spur; ce = cercus; mbt = metabasitarsus; mts = metatibial spurs; ov = ovipositor. **Scale bars** = 5 mm (A, B); 2 mm (C, D).

5. Discussion

When the previous taxonomic system for Elcanidae Handlirsch, 1906 was proposed by Gorochov et al. (2006), none of the Burmese amber species was known. Because of this, besides a few rare examples (such as *Stellacana bimaculata* comb. nov. (Gorochov, Jarzembowski & Coram, 2006)), all specimens of Elcanidae featured the abstract color pattern seen in Archelcaninae Gorochov, Jarzembowski & Coram, 2006 and Panorpidini trib. nov. The diverse Burmese amber species greatly expanded our knowledge of wing coloration in the family and the new system of Elcanidae taxonomy accounts for that. While in the old system the presence of wing spots and the absence of wing color would have had to evolve twice independently in Archelcaninae and Elcaninae (and following that in several genera, too), the new system allows for the evolution of wing spots in the common ancestor of Stellacanini trib. nov. and absence of wing color in the common ancestor of Paraxelcanini trib. nov.

Moreover, the new system displays the increase in higher-rank taxonomic diversity that should be expected based on the steep increase in family diversity of insects in general during the Aptian (Early Cretaceous) (Schachat et al., 2019). A similar trend has been demonstrated for Tridactyloidea Brullé, 1835 from Burmese amber (see chapter 11, this dissertation). Additionally, the issue of some problematic species formerly assigned to Archelcaninae, including *Hukawnelca gracile* Uchida et al., 2022, *Thagyaminana atawedeia* Schall, Kotthoff & Husemann, in press, *Longioculus poinari* Schall & Husemann, in press (chapter 7) and *Atopoelcana xena* comb. nov. (formally *Parelcana xena* Schall & Husemann, in press (chapter 7)), is resolved. These species do not differ from their relatives in Burmese amber that were assigned to Elcaninae in any more way than among each other, but their free state of tegminal veins 1A, CuPb and CuPaβ meant they had to be assigned to Archelcaninae according to the previous taxonomic framework.

However, the newly proposed taxonomy of Elcanidae has problematic cases too. First and foremost, *Caelielca spinocrus* Uchida, 2022 from Burmese amber is an unusual species, because it clearly features an abstract wing color pattern and free 1A, CuPb and CuPaβ, suggesting a position in Archelcaninae. While it is possible that Archelcaninae were present among the abundant Stellacanini trib. nov., their presumed occurrence in the Cretaceous Burmese amber fauna nonetheless stands out among the otherwise mostly Jurassic members of the subfamily. Another curious case is *Atopoelcana pulchmacula* comb. nov. (Tian, Gu, Yin & Ren, 2019) from the middle Jurassic of China. This species is the earliest known member of Stellacanini, predating the next occurrence (*S. bimaculata*) by over 30 My. *Atopoelcana pulchmacula* clearly retains some traces of an abstract color pattern and has 1A, CuPb and CuPaβ free. This combination of characters, presumably an intermediate state between Archelcaninae and Stellacanini, may indicate that this tribe did not evolve from Panorpidini, but instead both tribes evolved from an Archelcaninae ancestor.

The taxonomic framework for Elcanidae presented above is meant to 1) propose a logic position of the Archelcaninae species that have been discovered in Burmese amber. 2) More accurately represent Cretaceous levels of diversity of the family. 3) Take into account the different wing color patterns revealed by the Myanmar amber fauna that could not have been considered by the previous system (Gorochov et al., 2006) because it pre-dated the first report of a Burmese amber elcanid (Poinar et al., 2007). Although the study of Elcanidae has greatly advanced since 2007, knowledge of essential aspects of their morphology (ovipositor, metatibial spurs) is still limited. Data available right now was not sufficient to include these traits in the cluster analysis, let alone a full phylogenetic analysis. In this context, the present study should be taken as a

preliminary hypothesis of Elcanidae systematics, until enough knowledge has been gained to perform a more comprehensive phylogeny. UPGMA using only very little characters in comparison to the number of taxa sampled is likely to be inaccurate (Rohlf et al., 1990). However, the increase in estimated diversity proposed in this study and use of additional apomorphies (i.e. wing color patterns) complementing the previously established state of tegminal veins 1A, CuPb and CuPaβ is probably a step in the right direction towards understanding true richness of Elcanidae. Nonetheless, the goal for accurately reconstructing phylogenetic relationships in the lagoon crickets should be a phylogenetic analysis, which will hopefully be performed in the next years.

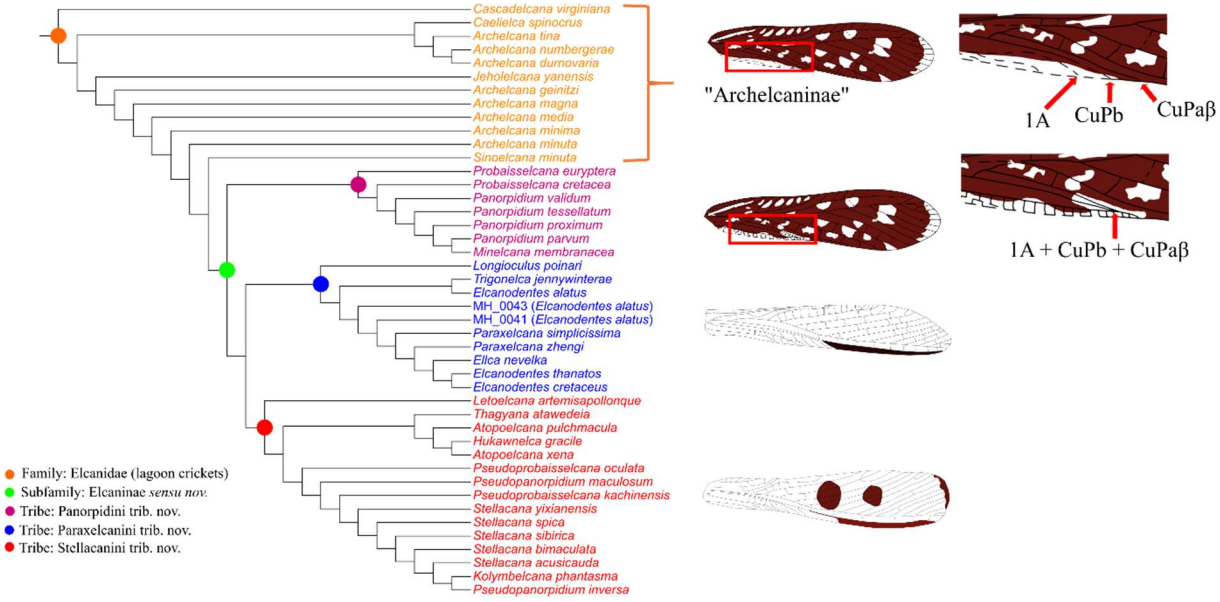

Fig. 6 Fig. 1, but with updated taxon names. UPGMA of Elcanidae Handlirsch, 1906 taxonomy based on morphological characters of wing coloration and fusion of forewing veins 1A, CuPb and CuPaβ. To the right, wing color of clades (= apomorphies) are shown. Because the taxa attributed to the Archelcaninae Gorochov, Jarzembowski & Coram, 2006 are not monophyletic (they are paraphyletic with respect to Elcaninae *sensu nov.*) according to this cluster analysis, the name "Archelcaninae" is indicated in quotation marks. The taxon is kept for now, but its validity requires further study.

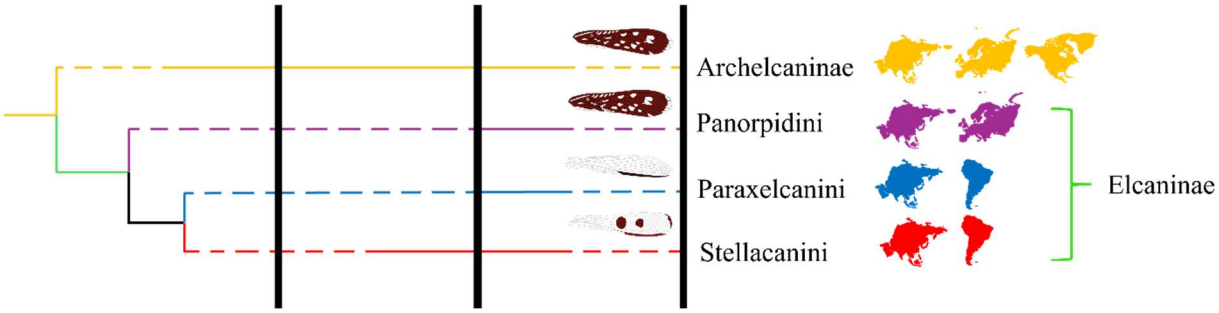

Fig. 7 Tree from previous figure, but with species names collapsed to make the subfamily/tribe the terminal taxon. Pictograms of continents indicate distribution, drawing of forewing color pattern of terminal taxon. Dashed lines indicate absence of terminal taxon from the fossil record with each black line marking the end of the Triassic, Jurassic and Cretaceous period, respectively. Note the interval during the Early Cretaceous, the only time when all terminal taxa are found in the fossil record.

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Appendix

Appendix 1: Nexus file of the cluster analysis of Elcanidae.

BEGIN DATA;

DIMENSIONS NTAX=44 NCHAR=4;

FORMAT SYMBOLS= " 0 1 2 N "

;

MATRIX

Archelcana_durnovaria 1 0 0 0

Archelcana_numbergerae 1 0 0 0

Archelcana_tina 1 0 0 0

Pseudopanorpidium_inversa 0 1 0 1

Caelielca_spinocrus 1 0 0 0

Cascadelcana_virginiana 1 0 0 0

Elcanodentes_alatus 0 0 1 N

Elcanodentes_cretaceus 0 0 1 1

Elcanodentes_thanatos 0 0 1 1

Ellca_nevelka 0 0 1 1

Parelcana_xena 0 1 0 0

Hukawnelca_gracile 0 1 0 0

Jeholelcana_yanensis 1 0 0 0

Kolymbelcana_phantasma 0 1 0 1

Letoelcana_artemisapollonque 0 1 0 N

Longioculus_poinari	0	0	1	0
Minelcana_membranacea	1	0	0	1
Panorpidium_acusicaudum	0	1	0	1
Panorpidium_bimaculatum	0	1	0	1
Panorpidium_geinitzi	1	0	0	0
Panorpidium_magnum	1	0	0	0
Panorpidium_medium	1	0	0	0
Panorpidium_minimum	1	0	0	0
Panorpidium_minutum	1	0	0	0
Panorpidium_parvum	1	0	0	1
Panorpidium_proximum	1	0	0	1
Panorpidium_sibiricum	0	1	0	1
Panorpidium_spica	0	1	0	1
Panorpidium_tessellatum	1	0	0	1
Panorpidium_validum	1	0	0	1
Panorpidium_yixianensis	0	1	0	1
Paraxelcana_zhengi	0	0	1	1
Paraxelcana_simplicissima	0	0	1	1
Parelcana_pulchmacula	0	1	0	0
Probaisselcana_cretacea	1	0	0	1
Probaisselcana_euryptera	1	0	0	1
Probaisselcana_kachinensis	0	1	0	1
Pseudopanorpidium_maculosum	0	1	0	1
Pseudoprobaisselcana_oculata	0	1	0	1
Sinoelcana_minuta	1	0	0	0

Thagyana_atawedeia 0 1 0 0

Trigonelca_jennywinterae 0 0 1 N

MH_0041 0 0 1 1

MH_0043 0 0 1 1

;

END;

Chapter 14

Diversity patterns of Orthoptera (Insecta: Polyneoptera) over deep time: three phases of dominance and impact off mass extinctions

Abstract

The complete fossil record of Orthoptera Olivier, 1789 (as of 06/2025) is analyzed with respect to the diversity patterns of higher-level taxa Oedischiidea Handlirsch, 1906, Titanoptera Sharov, 1968, Elcanidea Gorochov, 1995, Locustopsoidea Handlirsch, 1906, Hagloidea Handlirsch, 1906, Gryllidea Vickery, 1977, Tridactylidea Brullè, 1835, Tettigoniidea Kevan, 1982 and Acrididea Targioni-Tozzetti, 1882. Diversity curves show three distinct faunal compositions: a Paleozoic phase with dominant taxa Oedischiidea and Titanoptera, a Mesozoic phase with dominant taxa Elcanidea, Locustopsoidea, Hagloidea, Tridactylidea and Gryllidea, and a Cenozoic pahse with dominant taxa Tettigoniidea, Acrididea and Gryllidea (Gryllidea can be attributed to the Mesozoic or Cenozoic fauna). The transitions between orthopteran faunal phases align with mass extinction events recognized for insects in general and are characterized by representing intervals of faunal turnover. The timing of turnover intervals supports both the Triassic Revolution as well as the Angiosperm Terrestrial Revolution.

Keywords: end-Triassic extinction, extinction risk, insect extinction, Late Jurassic extinction, Permian-Triassic mass extinction

1. Introduction

The insect order Orthoptera Olivier, 1789, which includes grasshoppers, crickets, katydids and their allies, includes more than 29.000 living species (Cigliano et al., 2025). Looking at the fossil record, over 900 fossil Orthopterans have been described (Cigliano et al., 2025) and many more are being added every year. The majority of fossil Orthoptera can be assigned to one of nine higher level taxa (Fig. 1).

1) Oedischiidea Handlirsch, 1906

Fig. 2

Along with the Titanoptera Sharov, 1968 (see below) the Oedischiidea are the earliest Orthopterans to appear in the fossil record. Three species are known from the Late Pennsylvanian (Gzhelian, ca. 304-299 Mya) of France and Portugal (Brongniart, 1885; Correia and Nel, 2022; Meunier, 1911). In the Permian (ca. 299-252 Mya) they diversified and were the dominant group among Orthoptera. Although their species count in the fossil record from the Triassic (ca. 252-201 Mya) is almost the same as the Permian (48 Permian vs. 46 Triassic species (Paleobiology Database)), they were no longer the dominant group and eventually disappeared from the fossil record in the Jurassic (ca. 201-143 Mya) (according to the taxonomy used by Cigliano et al. (2025), the last occurrence of Oedischiidea is *Bintoniella brodiei* Handlirsch, 1939 from the Jurassic of the UK. However, the family Bintoniellidae Handlirsch, 1939 was not included in Oedischiidea in Béthoux and Grauvogel-Stamm (2022) who did not classify its position within Orthoptera. Oedischiidea are ranked in Ensifera Chopard, 1921 by Cigliano et al. (2025), but the most recent findings suggest they may be ancestral to Ensifera and Caelifera Ander, 1936 (chapter 9, this dissertation).

2) Titanoptera

Fig. 3

Along with the Oedischiidea, these were the first orthopteroid insects to appear in the fossil record (PBDB), with the oldest record being *Theiatitan azari* Schubnel, Roques & Nel, 2021 from the Moscovian (ca. 315-307 Mya) of France (Schubnel et al., 2021). They are considered to have been carnivorous with raptorial forelegs and could reach large sizes with a wingspan of ca. 400 mm reported for *Gigatitan vulgaris* Sharov, 1968 (Sharov, 1968; Park et al., 2022). Like Oedischiidea, the Titanoptera diversified during the Permian and were most speciose in the Triassic, especially in the Madygen Formation of Kyrgyzstan (PBDB). After the Triassic, they disappeared from the fossil record. The taxonomic position of Titanoptera (i.e. whether it is a suborder of Orthoptera or a close relative order) is a matter of ongoing debate (Béthoux, 2007; Huang et al., 2020; Schubnel et al., 2021).

3) Elcanidea Gorochov, 1995

Fig. 4

The oldest Elcanidea are found in the fossil record of the Permian and belong to the superfamily Permoraphidioidea Tillyard, 1932 and family Permelcanidae Sharov, 1962 (Cigliano et al., 2025; PBDB). The Permelcanidae probably is the closest relative to the Elcanidae Handlirsch, 1906 (lagoon crickets), which appear in the fossil record of the Triassic (Fang et al., 2018) and

greatly diversified during the Jurassic and Cretaceous (ca. 143-66 Mya). In more recent years, the family has become more prominent due to the numerous occurrences in Cretaceous amber from Myanmar (e.g. Kočárek, 2020; Hu and He, 2023). Elcanidea disappear from the fossil record after the Cretaceous (although two putative records exist from the Paleocene (ca. 66-56 Mya) of France (Schubnel et al., 2020) and the Miocene (ca. 23-5 Mya) of Croatia (Karny, 1932), but these findings are under scrutiny (see chapter 13, this dissertation)). A recent phylogenetic analysis (chapter 9, this dissertation) suggests they are a basal member of the Ensifera, a view supported by many (though not all (see Béthoux and Nel, 2002) researchers (Gorochov, 1995; Handlirsch, 1906; Zessin, 1987).

4) Locustopsoidea Handlirsch, 1906

Fig. 5

While most orthopterans discovered in the fossil record of pre-Cenozoic times probably belong to the Ensifera, the Locustopsoidea show clear morphological characters of the second suborder Caelifera Ander, 1936 (see chapters 4-6, this dissertation). Although their overall resemblance of modern day Acridoidea is high and the taxon is currently placed within Acridomorpha MacLeay, 1821 (Cigliano et al., 2025), most recent phylogenetic findings (chapter 9, this dissertation) suggest a placement at the base of Caelifera, similar to how the Elcanidea are at the base of Ensifera. Like the elcanids, the Locustopsoidea appear in the fossil record of the Permian as the basal families Locustavidae Sharov, 1968 and Eolocustopsidae Riek, 1976 (PBDB). They diversified throughout the Mesozoic, probably reached peak diversity during the Cretaceous (the Crato Formation of Brazil has revealed a very high number of locustopsid species, see chapters 4-6, this dissertation) and disappeared after the Cretaceous.

5) Hagloidea Handlirsch, 1906

Fig. 6

The most species rich group of fossil orthopterans are the Hagloidea or grigs (Cigliano et al., 2025). The superfamily belongs to the infraorder Tettigoniidea Kevan, 1982 and is a truly Mesozoic taxon (after a review by Wang et al. (2019) determined the only non-Mesozoic occurrence – *Hylophalangopsis chinensis* Lin and Huang, 2006 – a member of Palaeorehniidae Zeuner, 1937 which do not belong to Hagloidea). Hagloidea were extremely abundant during the Triassic and especially Jurassic periods, where they constituted the majority of Orthoptera found in the fossil record (almost 50% in the Jurassic) (PBDB). By the Cretaceous, their numbers had decreased to a still respectable 16% of overall Orthoptera species, as the faunal

composition of the order became more diverse and two other groups (Gryllidea Vickery, 1977 and Tridactylidea Brullè, 1835) rose to significant levels of diversity (see below). Some researchers (Flook et al., 1999; Gwynne, 1995) consider the extant species of Prophalangopsidae Kirby, 1906 to be members of Hagloidea, however, this view has been challenged by others (Béthoux and Nel, 2002; chapter 9, this dissertation).

6) Gryllidea

Fig. 7

The crickets (Grylloidea Laicharting, 1781) and mole crickets (Gryllotalpoidea Leach, 1815) comprise the Gryllidea, one of the two extant infraorders of the Ensifera, next to the Tettigoniidea (Cigliano et al., 2025). Gryllidea are successful today with over 6200 described species (Cigliano et al., 2025). In the fossil record they are abundant as well. They first appeared during the Jurassic with the more basal families Baissogryllidae Gorochov, 1985 and Protogryllidae Zeuner, 1937, but by the Cretaceous most modern families were present as well (PBDB). The Cenozoic fossil record of crickets is also quite extensive. Numerous findings were made from the Eocene (e.g. Gorochov, 2012; Gorochov, 2019) and Miocene (e.g. Gorochov, 2010; Vickery and Poinar, 1994), but occasional discoveries have also been reported from the Paleocene (Cockerell, 1925; Schubnel et al., 2020), Oligocene (ca. 34-23 Mya) (Handschin, 1944, a gryllotalpoid) and Holocene (ca. 0.01 Mya-present) (Chopard, 1936; Gorochov, 2010; in Tanzanian copal).

7) Tridactylidea

Fig. 8

Tridactylidea and Acrididea Targioni-Tozzetti, 1882 are the two extant infraorders of the Caelifera. Nowadays, Tridactylidea is a relatively small group with only 233 extant species in three families (Cigliano et al., 2025). However, numerous findings of Cretaceous tridactyloids from Myanmar amber suggest that this taxon was once far more diverse than today with multiple lineages that went extinct during the Cretaceous period (chapter 11, this dissertation). Tridactylidea are rarely found in the fossil record of the Triassic and Jurassic, however, their diversity levels were high in the Cretaceous, an impression that may be majorly influenced by their abundance in Myanmar amber (Zhao et al., 2024). Four species of Tridactylidea were discovered in Cenozoic amber, from the Eocene (ca. 56-34 Mya) of France (Azar and Nel, 2008) and the Miocene of the Dominican Republic (Heads, 2010; Poinar, 2020).

8) Tettigoniidea (without Hagloidea)

Fig. 9

The sister taxon to the Gryllidea within Ensifera is Tettigoniidea (Cigliano et al., 2025). With over 10.700 extant species this is the most successful group of extant Orthoptera, second only to Acrididea (see below) (Cigliano et al., 2025). The occurrence of a gryllacridid species in the Triassic of Australia (Riek, 1955) is dubious, as this specimen may rather belong to Oedischiidea (chapter 9, this dissertation). Other early findings of Tettigoniidea include the enigmatic Phasmomimoidea (Sharov, 1968) – the taxonomic position of which (i.e. if they are Orthoptera or Phasmida Leach, 1815) is uncertain (Gorochov, 2000; Wang et al., 2014) – from the Jurassic and Cretaceous (PBDB). The first unequivocal findings of fossil Tettigoniidea are two species of the family Haglotettigoniidae Gorochov, 1988 from the Cretaceous of Russia and in Lebanon amber (Gorochov, 1988; Gorochov, 2010), as well as a schizodactyloid (Martins-Neto, 2007; reviewed by Heads and Leuzinger, 2011) and an anostostomatid (Martins-Neto, 2007), from the Brazilian Crato Formation. Forty-seven species of Tettigoniidea are known from the Cenozoic (two species of Phasmomimoidea, four species of Rhaphidophoroidea Walker, 1869, five species of Stenopelamtoidea Burmeister, 1838 and thirty-six species of Tettigoniidae Krauss, 1902 (Tettigonioidea Krauss, 1902), representing numerous subfamilies.

9) Acrididea (without Locustopsoidea)

Fig. 10

The most successful group in terms of species number of Orthoptera alive today are the Acrididea (Cigliano et al., 2025). More than 12.000 extant species are distributed across eight superfamilies of which the majority (over 8.000 species) are housed within Acridoidea MacLeay, 1821. The fossil record of Acrididea starts in the Jurassic with *Archaeomastax jurassicus* Sharov, 1968 (superfamily Eumastacoidea Burr, 1899), as alleged findings from the Triassic (Giebel, 1856) were likely incorrectly assigned (chapter 9, this dissertation). Members of the superfamilies Eumastacoidea (e.g. Husemann et al., 2025), Proscopioidea Serville, 1838 (e.g. Heads, 2008) and Tetrigoidea Rambur, 1838 (Sharov, 1968) were found in Cretaceous deposits of Russia, Brazil, Myanmar and China, but they were far less abundant than the dominant caeliferans of that age, the Locustopsoidea (see above). During the Cenozoic, Acrididea diversified into its many modern taxa and the group has been reported from about 50 findings throughout the northern hemisphere (PBDB).

The fossil record of insects separates them into two distinct faunae that are separated by the Permian-Triassic mass extinction (ca. 252 Mya) (Jarzembowski and Ross, 1996; Zherikhin, 2002), the greatest mass extinction of all time (Bambach, 2006; Marshall, 2023). The older Paleozoic fauna up to the Late Permian consists of basal clades of apterygotes, paleopterans, orthopteroids and hemipteroids. After the Permian-Triassic extinction, the modern lineages become abundant, comprising derived clades of odonates, orthopteroids and hemipteroids as well as the diverse holometabolous insects (Labandeira, 2005). Bambach (2006) recognized 18 peaks of elevated extinction rates throughout the course of the Phanerozoic. Three (the Permian-Triassic or end-Permian event, end-Triassic event (ca. 201 Mya) and Cretaceous-Paleogene or end-Cretaceous event (ca. 66 Mya)) had extinction rates severe enough to be classified as mass extinctions (Foote, 2003; Lu et al., 2006; Raup and Sepkoski, 1982) and occurred late enough in earths' history to have affected insects (the Late Devonian Kellwasser event, ca. 372 Mya affected only marine organisms (Bambach et al., 2004)). While the Permian-Triassic mass extinction is considered to have had a major impact on insect diversity, the end-Triassic and end-Cretaceous event were likely less severe (Schachat and Labandeira, 2021). However, three other intervals of elevated extinction rates that specifically impacted insects occurred in the Late Pennsylvanian, Late Jurassic (ca. 150 Mya) and late Early Cretaceous (ca. 110 Mya), of which the latter one rivalled extinction rates observed from the end-Permian event (Labandeira, 2005).

The intervals of mass extinction in the insect fossil record should be interpreted as faunal turnovers (Schachat and Labandeira, 2021). This means that while extinction rates were elevated due to the demise of some lineages, origination rates were also increased, with new taxa quickly replacing the lost ones (Schachat and Labandeira, 2021).

In this study the fossil record of the insect order Orthoptera is analyzed. Specifically, three questions are in focus: 1) Can Orthoptera be split into two distinct faunae like other insects, i.e. a basal pre-Permian-Triassic mass extinction fauna and a more derived, 'modern' fauna post end-Permian extinction? 2) Does the rise/fall of major Orthoptera lineages (1-9 from above) correspond to the intervals of elevated extinction rates identified by Labandeira (2005)? 3) Did Orthoptera experience faunal turnover during extinctions?

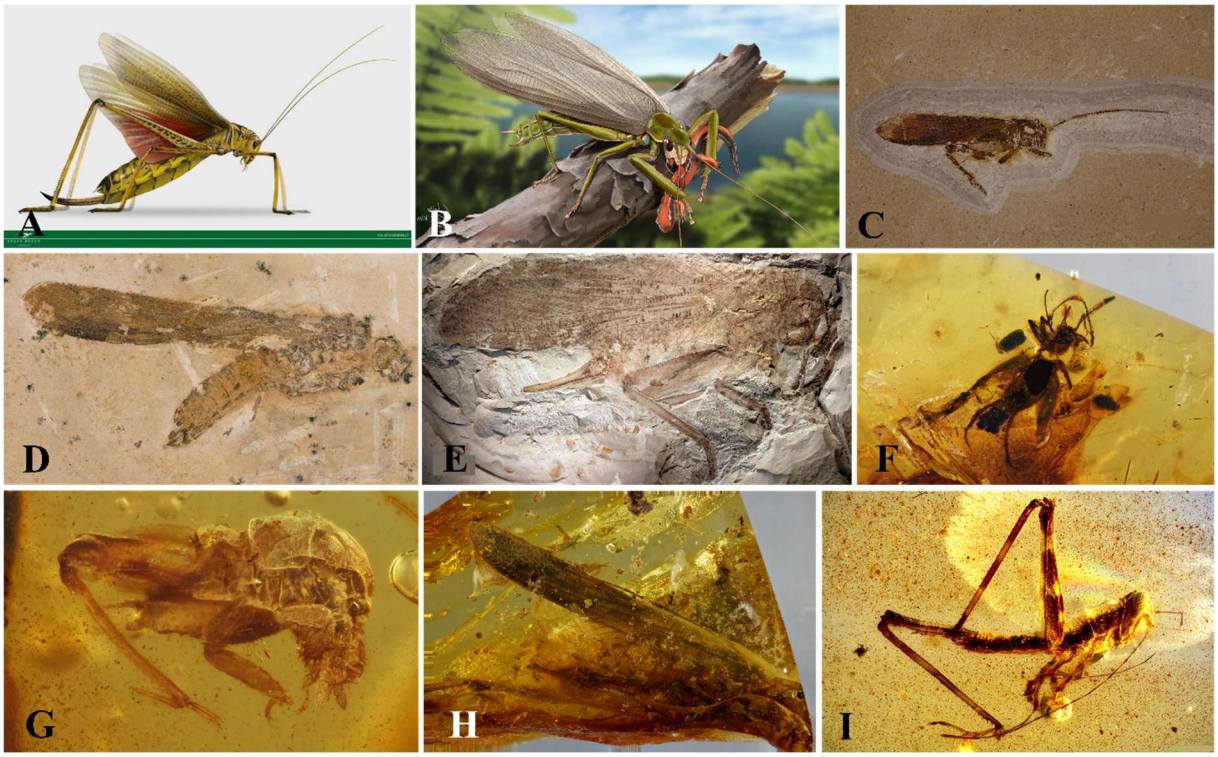

Fig. 1: Major lineages of fossil Orthoptera Olivier, 1789. **A.** Oedischiidea Handlirsch, 1906 (*Lusitadischia sai* Correia and Nel, 2022); artwork by Vito Silva – Paleoartista. **B.** Titanoptera Sharov, 1968 (*Magnatitan jongheoni* Park, Kim, Nam & Lee, 2022); illustration © Doyoon Kim, reproduced from Park et al. (2022), Journal of Paleontology, with permission (mirrored). **C.** Elcanidea Gorochov, 1995 (*Mesembrelcana rasnitsyni* (Nel and Jouault, 2022); specimen INHS-P1878, photographed by Michael J. Thomas (University of Illinois, USA). **D.** Locustopsoidea Handlirsch, 1906 (*Auroralocusta restituta* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, chapter 5); holotype MPSC 9835. **E.** Hagloidea Handlirsch, 1906 (*Allaboilus gigantus* Ren and Meng, 2006); specimen CNU-ORT-NN2006081 after an image in Cigliano et al. (2025), probably by Jun-Jie Gu (Sichuan Agricultural University, China). **F.** Gryllidea Vickery, 1977 (MH0112, an undescribed specimen from Burmese amber). **G.** Tridactylidea Brullé, 1835 (MH0094, an undescribed specimen from Burmese amber). **H.** Tettigoniidea Kevan, 1982 (SMNK-PAL 76082; this specimen was assigned to Tettigoniidae Krauss, 1902: Meconematinae Burmeister, 1838: Phlugidini Eichler, 1938 and described as a new genus and species from Eocene Baltic amber in an unpublished work by Schall and Husemann. Unfortunately, the specimen got lost in post transfer from the first to second author). **I.** Acrididea Targioni-Tozzetti, 1882 (BPM1121, holotype of *Monolophomastax disantoi* Schall, Bonino & Husemann (submitted) (mirrored).

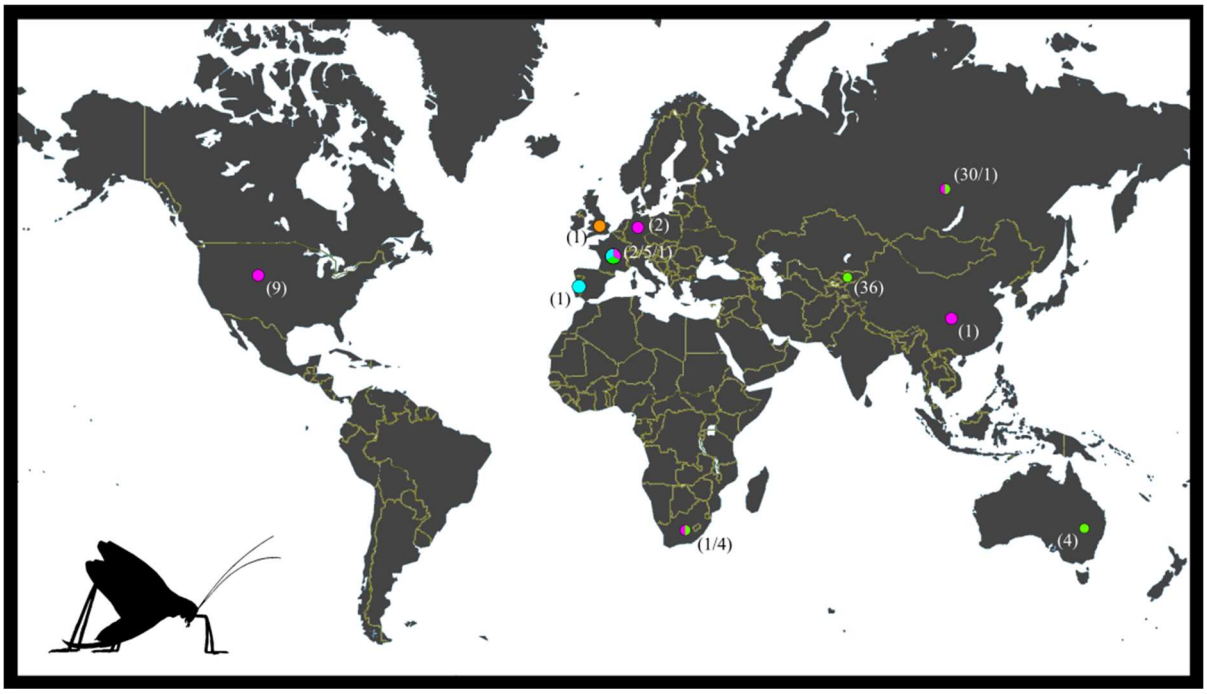

Fig. 2: Distribution map of fossil Oedischiidea Handlirsch, 1906. Light blue = Carboniferous; pink = Permian; light green = Triassic; orange = Jurassic. Numbers in brackets indicate fossil species per era. For example, in Russia 30 species of Permian and 1 species of Triassic Oedischiidea were found.

Fig. 3: Distribution map of fossil Titanoptera Sharov, 1968. Light blue = Carboniferous; pink = Permian; light green = Triassic. Numbers in brackets indicate fossil species per era. For example, in Russia 11 species of Permian Titanoptera were found. [1]The fossil *Steinhardtia*

maryae Jell and Lambkin, 1993 from Australia may be part of a plant leaf (Schubnel et al., 2021).

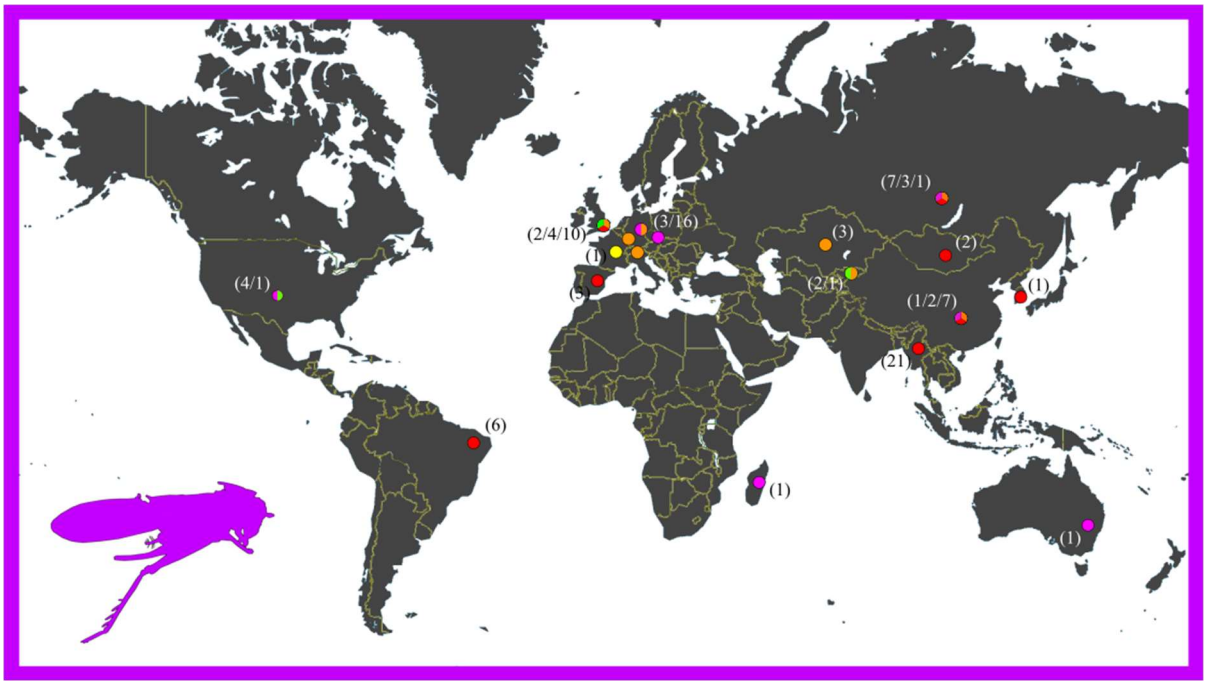

Fig. 4: Distribution map of fossil Elcanidea Gorochov, 1995. Pink = Permian; light green = Triassic; orange = Jurassic; red = Cretaceous; yellow = Cenozoic. Numbers in brackets indicate fossil species per era. For example, in Russia 7 species of Permian, 3 species of Jurassic and 1 species of Cretaceous Elcanidea were found. Occurrences from Germany, Switzerland, Luxembourg and the Czech Republic are collected in (3/16).

Fig. 5: Distribution map of fossil Locustopsoidea Handlirsch, 1906. Pink = Permian; light green = Triassic; orange = Jurassic; red = Cretaceous. Numbers in brackets indicate fossil species per era. For example, in Russia 2 species of Permian and 4 species of Jurassic Locustopsoidea were found.

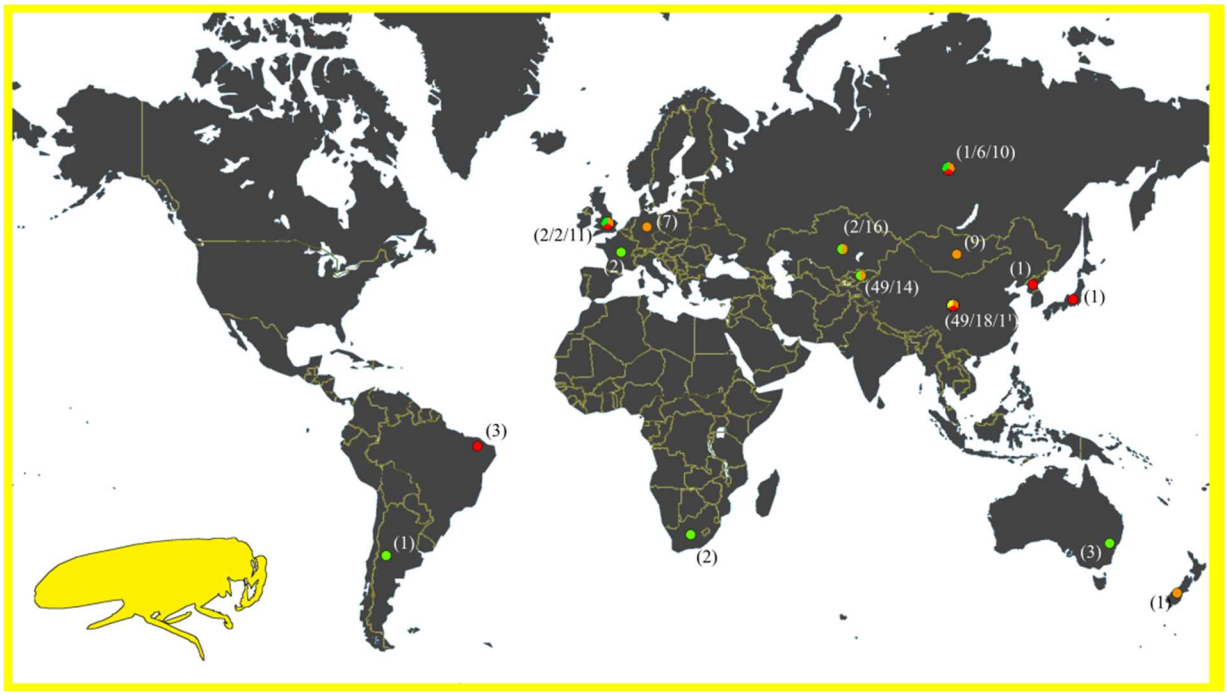

Fig. 6: Distribution map of fossil Hagloidea Handlirsch, 1906. Light green = Triassic; orange = Jurassic; red = Cretaceous; yellow = Cenozoic. Numbers in brackets indicate fossil species per era. For example, in Russia 1 species of Triassic, 6 species of Jurassic and 10 species of Cretaceous Hagloidea were found. [1]The occurrence of a Hagloidea from the Paleocene of China (*Hylophalangopsis chinensis* Lin and Huang, 2006) may belong to Palaeorehniidae Zeuner, 1937, which is not included in Hagloidea (Wang et al., 2019).

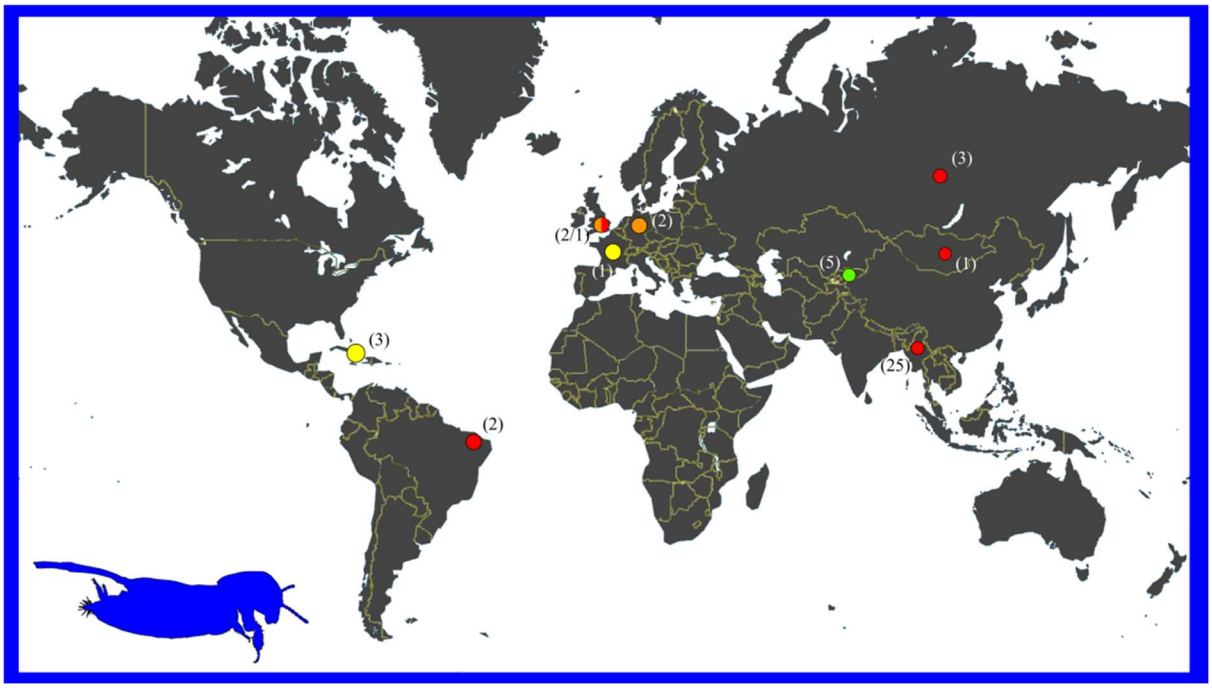

Fig. 7: Distribution map of fossil Tridactylidea Brullé, 1835. Light green = Triassic; orange = Jurassic; red = Cretaceous; yellow = Cenozoic. Numbers in brackets indicate fossil species per era. For example, in the UK 2 species of Jurassic and 1 species of Cretaceous Tridactylidea were found.

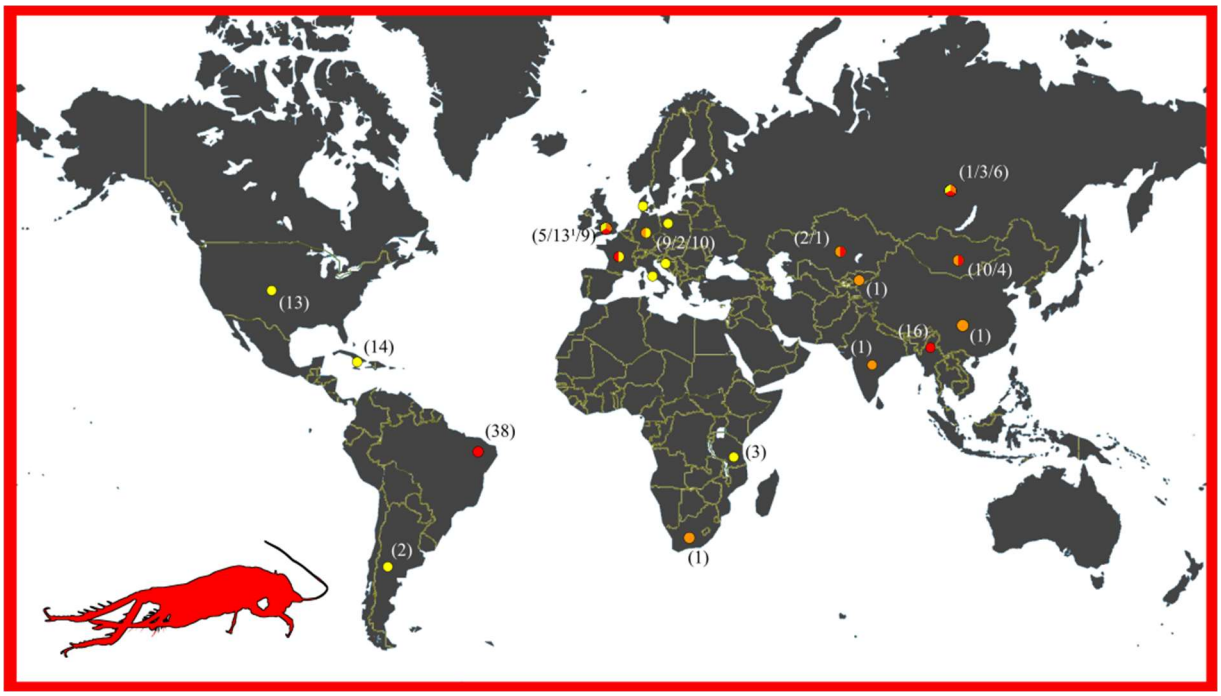

Fig. 8: Distribution map of fossil Gryllidea Vickery, 1977. Orange = Jurassic; red = Cretaceous; yellow = Cenozoic. Numbers in brackets indicate fossil species per era. For example, in Russia

1 species of Jurassic, 3 species of Cretaceous and 6 species of Cenozoic Gryllidea were found. Findings from Central Europe (except for UK) are collected in (9/2/10). [1]A Cretaceous finding from the UK (*Gryllidium oweni* Westwood, 1854) may belong to Phasmida Leach, 1815 (Coram and Jepson, 2012).

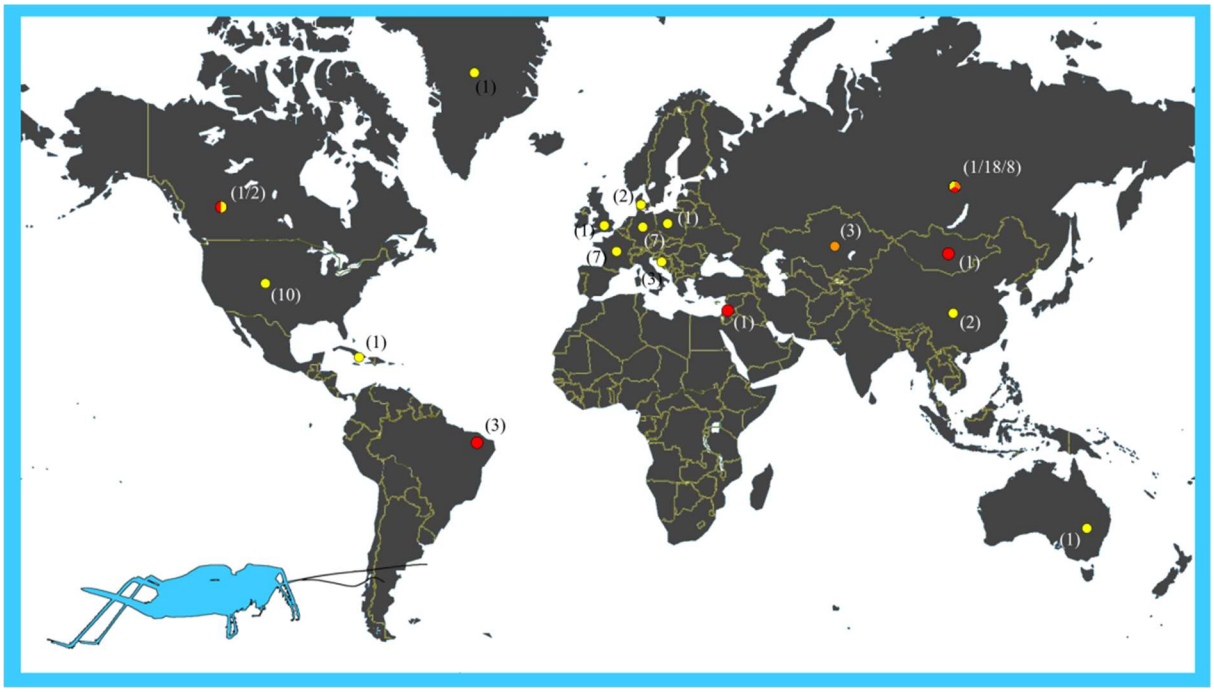

Fig. 9: Distribution map of fossil Tettigoniidea Kevan, 1982 (without Hagloidea). Orange = Jurassic; red = Cretaceous; yellow = Cenozoic. Numbers in brackets indicate fossil species per era. For example, in Russia 1 species of Jurassic, 18 species of Cretaceous and 8 species of Cenozoic Tettigoniidea were found.

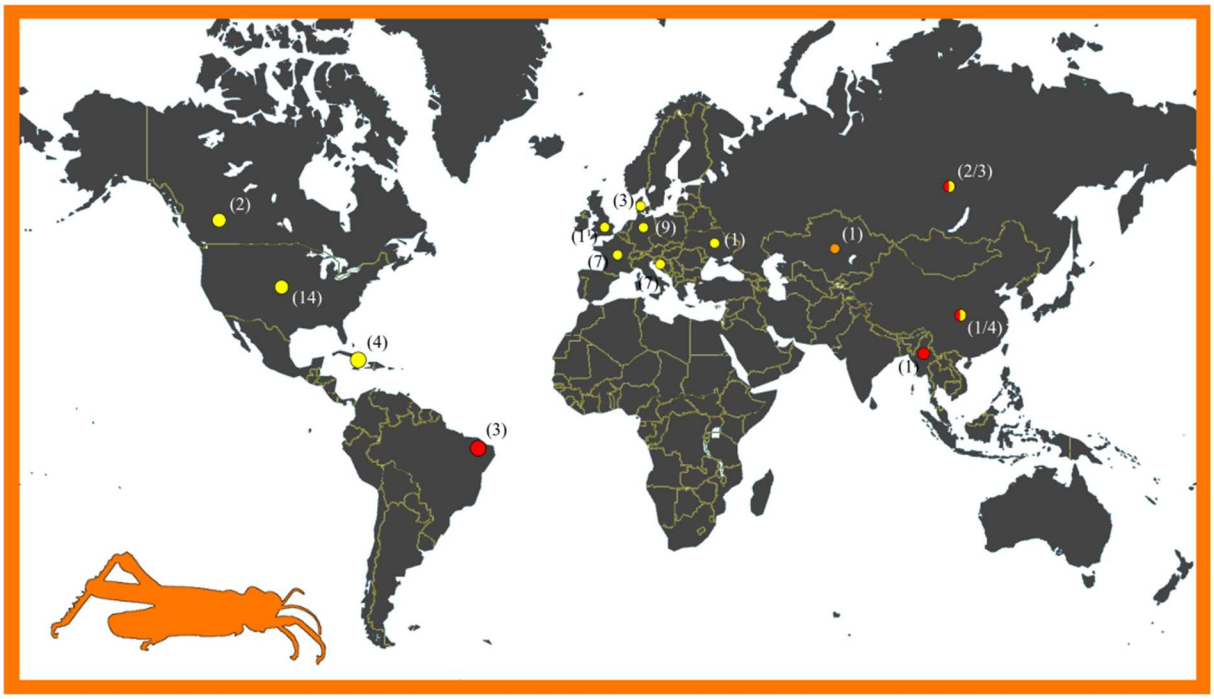

Fig. 10: Distribution map of fossil Acrididea Targioni-Tozzetti, 1882 (without Locustopsoidea). Orange = Jurassic; red = Cretaceous; yellow = Cenozoic. Numbers in brackets indicate fossil species per era. For example, in Russia 2 species of Cretaceous and 3 species of Cenozoic Acrididea were found. [1]Two Triassic findings from the UK (*Akicera frauenfeldi* Giebel, 1856 and *A. heeri* Giebel, 1856) are not considered on this map due to doubtful identity of the species.

2. Materials and methods

To perform the analyses required for this study, an Excel-File (Microsoft Corporation, USA) was created including every species of fossil Orthoptera with information on their taxonomy, type locality and horizon. The Excel file is included as a pdf-version at the end of this chapter (supplemental material 1). Data in the Excel file is based on the taxonomy of Cigliano et al. (2025), occurrence data of species (age constraint and type locality) were collected from the Paleobiology Database (https://paleobiodb.org/classic/basicTaxonInfo). For analysis 1, all fossil species of Orthoptera were sorted by taxon (see Introduction 1-9) and era (Carboniferous, Permian, Triassic, Jurassic, Cretaceous, Cenozoic) and the relative diversity per taxon per era was determined (i.e. how many % species belong to a taxon per era). Additionally, the number of extant Orthoptera species per taxon was calculated by subtracting the number of fossil species listed in the Excel file from the total species number stated in Cigliano et al. (2025). I

chose a rough temporal resolution over dividing eras into stages (e.g. Berriasian-Maastrichtian for the Cretaceous) to avoid bias of overrepresentation of some taxa in certain fossillagerstätten. For example, based on the current record, Locustopsidae seem to have been more diverse in the Brazilian Crato Formation from the Aptian (ca. 121-113 Mya) than anywhere else. Therefore, higher temporal resolution in the analysis would have causes a sudden spike in locustopsid diversity only in the Aptian, which is unlikely to reflect true diversity patterns of the family.

For analysis 2 for every taxon 1-9 the sum of relative diversity per eon (Paleozoic, Mesozoic and Cenozoic) was taken. Depending on which eon showed the highest diversity, the taxon was assigned to one of three categories. In each category, diversity values per era (values from analysis 1) were added for every included taxon.

Both analyses include fossil Orthoptera that cannot be assigned to one of the taxa 1-9 in the overall diversity of the order or, in other words, 100% of Orthoptera diversity per era includes unassigned forms. Findings *incertae sedis* within Orthoptera as of now are: *Legendreia magnifica* Huang, Schubnel & Nel, 2020, *Tillyardiella distincta* Martynov, 1930 and *Thnetus stuckenbergi* Handlirsch, 1904 from the Permian, *Liassogrylloides basifastigatus* Bode, 1953 and *Yuxiania jurassica* Hong, 1997 from the Jurassic, *Falsirameus ravus* Zhang, 1985 and *Gryllobencain patrickmuelleri* Haug, Hörnig, Kiesmüller, Pazinato, Baranov & Haug, 2022 as well as four species of Gryllavoidea Gorochov, 1986 from the Triassic, 3 species of Vitimiidae Sharov, 1968 from the Cretaceous and five species of Paleorehniidae Zeuner, 1937 from the Paleocene and Eocene.

Resulting diagrams illustrating diversity patterns were created in Microsoft Excel and modified in Inkscape v. 1.4 (the Inkscape-Team, 2025). Additional graphical elements were created in GIMP v. 3.0.2-1 (the GIMP-Team, 2025). Silhouette images of Orthoptera used in this study are: for Oedischiidea after *Lusitadischia sai* Correia and Nel, 2022 from paleoart created by Vito Silva – Paleoartista. For Titanoptera after *Magnatitan jongheoni* Park, Kim, Nam & Lee, 2022 from the beautiful artwork by Dr. Do-Yoon Kim in Park et al. (2022). For Elcanidea after *Cratopidium damianii* (Martins-Neto, 1991) (specimen HC0030) from chapter 8 of this dissertation; Locustopsoidea after *Locustopsis rhytofemoralis* Gu, Yue, Shi, Tian & Ren, 2016 from that publication; Hagloidea after *Allaboilus gigantus* Ren and Meng, 2006 from Gu et al., 2010; Gryllidea after *Miogryllus patagonicus* Cadena-Castañeda, Castelli & Cheli, 2024 in Castelli et al. (2024); Tridactylidea after *Ellipes deyrupi* Woo, 2021 from that publication; Tettigoniidea after *Tettigonia viridissima* Linnaeus, 1758 picturing specimen ZMH71558 from

the LIB Hamburg collection. Acrididea after *Dericorys millierei* Bonnet and Finot, 1884 picturing specimen ZMH862113 from the LIB Hamburg collection.

3. Results

Analysis 1 – Diversity patterns of taxa 1-9 through deep time

1. Oedischiidea

Fig. 11

Oedischiidea were the dominant component in terms of species number in the Permian, comprising over 50% of the total orthopteran community during this era. By the Triassic, their part in the overall faunal assemblage of Orthoptera had decreased considerably, to just under 30%. However, it should be noted that total species number of Oedischiidea has stayed almost the same compared to the Permian (Triassic: 48 species, Permian: 46 species). Thus, although maintaining their numbers, Oedischiidea had lost the spot of most speciose orthopterans to the Hagloidea in the Triassic (compare Fig. 12). Only one species of Oedischiidea (*Bintoniella brodiei*) is known from the Jurassic of the UK. Other than that, the taxon had disappeared from the orthopteran fauna.

2. Titanoptera

Fig. 11

Although less speciose overall, the diversity history of Titanoptera shows similarity to the Oedischiidea. Their greatest relative diversity was during the Permian, when they comprised almost 20% of the orthopteran fauna. During the Triassic, despite their absolute diversity increasing (Triassic: 27 species, Permian: 16 species), their part in the overall fauna of Orthoptera slightly decreased (but much less than Oedischiidea). After the Triassic, Titanoptera seem to have met the same fate as Oedischiidea, because so far, no fossil of this group has been discovered from the Jurassic.

3. Elcanidea

Fig. 12

Elcanidea or lagoon crickets first appear in the fossil record of the Permian, where they are represented by the Permelcanidae and the Permoraphidioidea. In the Triassic their diversity apparently experienced a drop (but see discussion), before rising again during the Jurassic and

Cretaceous, where they made up about 15-20% of the orthopteran fauna. Although this may not seem as much compared to the dominance of Oedischiidea during the Permian or Hagloidea during the Triassic and Jurassic (see below), many taxa of Orthoptera were already present by the Cretaceous and contributed to the fauna. In fact, the only group of orthopterans more diverse during the Cretaceous than the lagoon crickets were the true crickets and mole crickets from the Gryllidea (see below). After the Cretaceous, Elcanidea disappeared from the fossil record with only two alleged findings from the Cenozoic.

4. Locustopsoidea

Fig. 12

Locustopsoidea show a similar deep-time diversity pattern to the elcanids and their relative part of the orthopteran community in the different areas is roughly alike, too. Unlike the elcanids, Locustopsoidea was not as diverse during the Permian, but experienced an increase in relative (and absolute) diversity during the Triassic. They reached their highest diversity during the Jurassic and declined slightly in the Cretaceous. After the Cretaceous, Locustopsoidea disappeared from the fossil record.

5. Hagloidea

Fig. 12

No species of Hagloidea is recorded from the pre-Mesozoic fossil record, but when the superfamily first appeared during the Triassic, their numbers immediately rose, making up almost 40% of the orthopteran fauna during this time. Diversity of Hagloidea further increased in the Jurassic, where they comprised nearly 50% of the Orthoptera community. However, during the Cretaceous, they decreased in diversity, now only constituting 16% of the overall fauna, with absolute species numbers reflecting this trend (Jurassic: 105 species, Cretaceous: 44 species). No fossil Hagloidea species is known from the Cenozoic (but see introduction).

6. Gryllidea

Fig. 12

No gryllid species is known from the Permian or Triassic period. However, from their first appearance in the fossil record during the Jurassic they became a major component of the Orthoptera community. In the Cretaceous, Gryllidea constituted the most species of any grasshopper group. Contrary to other large Mesozoic taxa, like the Elcanidea, Locustopsoidea and Hagloidea, the crickets did not disappear after the Cretaceous but continued to be very

diverse also in the Cenozoic. Among the extant fauna, Gryllidea is one of the three large infraorders within Orthoptera, totaling more than 6200 species.

7. Tridactylidea

Fig. 12

Tridactylidea occurs in the fossil record of the Triassic (family Dzhajloutshellidae Gorochov, 1994) and Jurassic (family Regiatidae Gorochov, 1995). Both families are known from just a handful of species (D = 5, R = 4). In the Cretaceous, diversity significantly increased to an all-time high of 11%, whereby the many species discovered in Kachin amber of Myanmar constitute a large part to this number. Like the Gryllidea, Tridactylidea survived the Cretaceous period and is present in the Cenozoic and today, however, their relative diversity has never come close to Cretaceous times again. Among the extant fauna, Tridactylidea contributes just 0.8% to overall Orthoptera diversity.

8. Tettigoniidea (without Hagloidea)

Fig. 13

First findings of members attributed to Tettigoniidea are from the Jurassic (but the identity of each species or their affiliation with Tettigoniidea is under scrutiny). The earliest unequivocal members of this taxon are from the Cretaceous and belong to the families Anostostomatidae Saussure, 1859 and Haglotettigoniidae Gorochov, 1988. In the Cenozoic Tettigoniidea increased a lot in diversity, constituting almost 30% of overall orthopteran diversity, close to the Gryllidea. In the extant fauna, Tettigoniidea has surpassed their cricket relatives with a total of more than 10700 species, making them the second most diverse taxon alive today.

9. Acrididea (without Locustopsoidea)

Fig. 13

The Acrididea show a similar diversity pattern as the Tettigoniidea. The first members of this group belong to the superfamilies Eumastacoidea Burr, 1899 (monkey grasshoppers), Proscopioidea Serville, 1838 (stick grasshoppers) and Tetrigoidea Rambur, 1838 (pygmy grasshoppers) which appeared in the Jurassic–Cretaceous. After the Cretaceous, Acrididea experienced rapid increase of diversity, rising from 2.5% in the Cretaceous to 31.8% in the Cenozoic. Today, Acrididea is the most successful infraorder of Orthoptera, with over 12000 species.

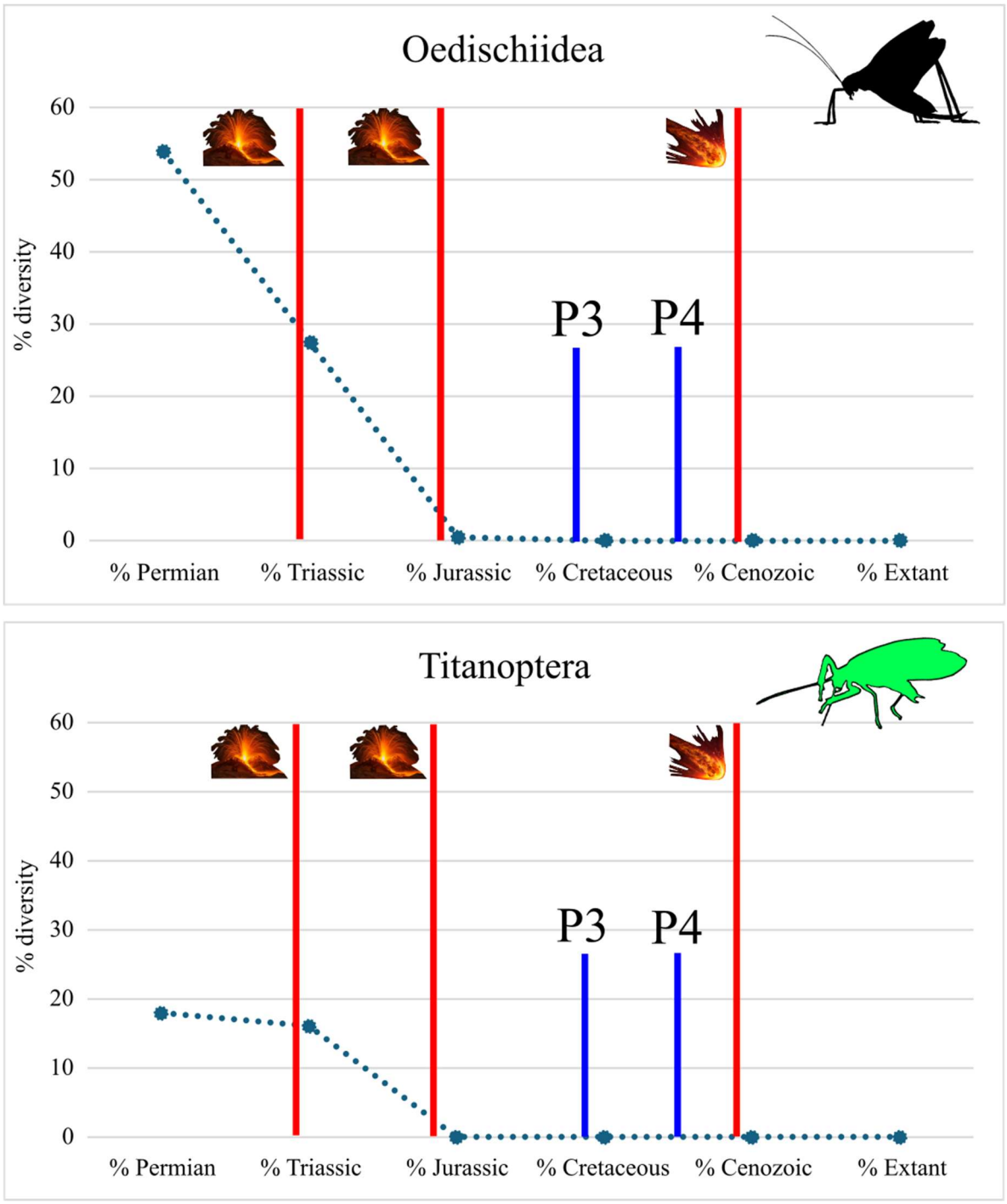

Fig. 11 Diversity pattern of Oedischiidea Handlirsch, 1906 and Titanoptera Sharov, 1968 over deep time. Y-axis represents relative diversity (relative number of species known from the given taxon of the total number of fossil Orthoptera species per era, values are %). Red bars indicate Permian-Triassic mass extinction (ca. 252 Mya), end-Triassic mass extinction (ca. 201 Mya) and Cretaceous-Paleogene mass extinction (ca. 66 Mya). Blue bars indicate additional mass extinctions affecting insects as determined by Labandeira (2005). P3 = peak 3 from Labandeira (2005) during the Late Jurassic (Kimmeridgian); P4 = peak 4 from Labandeira (2005) during

the mid-Cretaceous (Aptian-Albian). Volcano image from DPA/Salvatore Allegra (cutout). Asteroid image from IMAGO/Panthermedia (cutout).

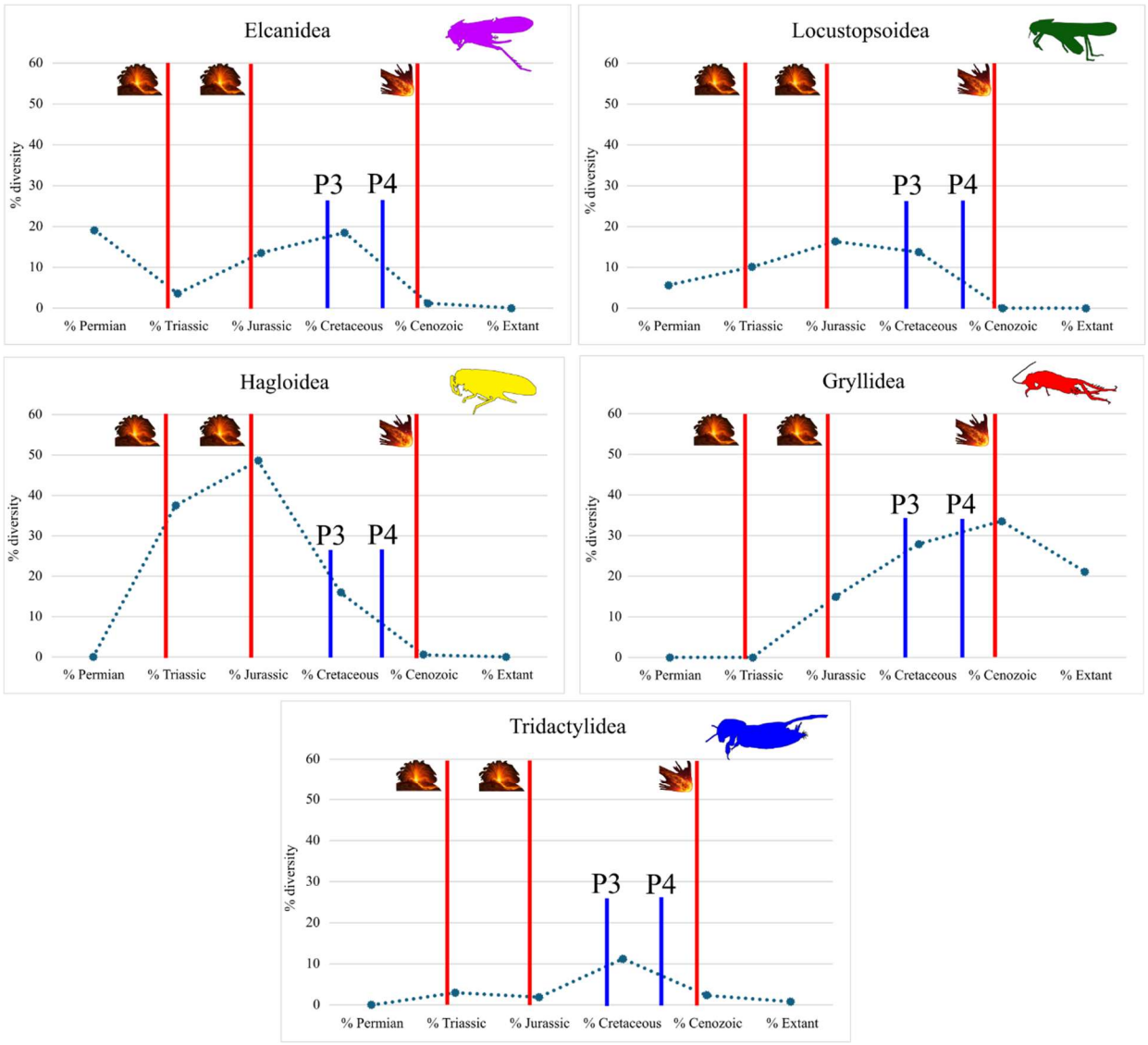

Fig. 12 Diversity pattern of Elcanidea Gorochov, 1995, Locustopsoidea Handlirsch, 1906, Hagloidea Handlirsch, 1906, Gryllidea Vickery, 1977 and Tridactylidea Brullé, 1835 over deep time. Y-axis represents relative diversity (relative number of species known from the given taxon of the total number of fossil Orthoptera species per era, values are %). Red bars indicate Permian-Triassic mass extinction (ca. 252 Mya), end-Triassic mass extinction (ca. 201 Mya) and Cretaceous-Paleogene mass extinction (ca. 66 Mya). Blue bars indicate additional mass extinctions affecting insects as determined by Labandeira (2005). P3 = peak 3 from Labandeira (2005) during the Late Jurassic (Kimmeridgian); P4 = peak 4 from Labandeira (2005) during the mid-Cretaceous (Aptian-Albian). Volcano image from DPA/Salvatore Allegra (cutout). Asteroid image from IMAGO/Panthermedia (cutout).

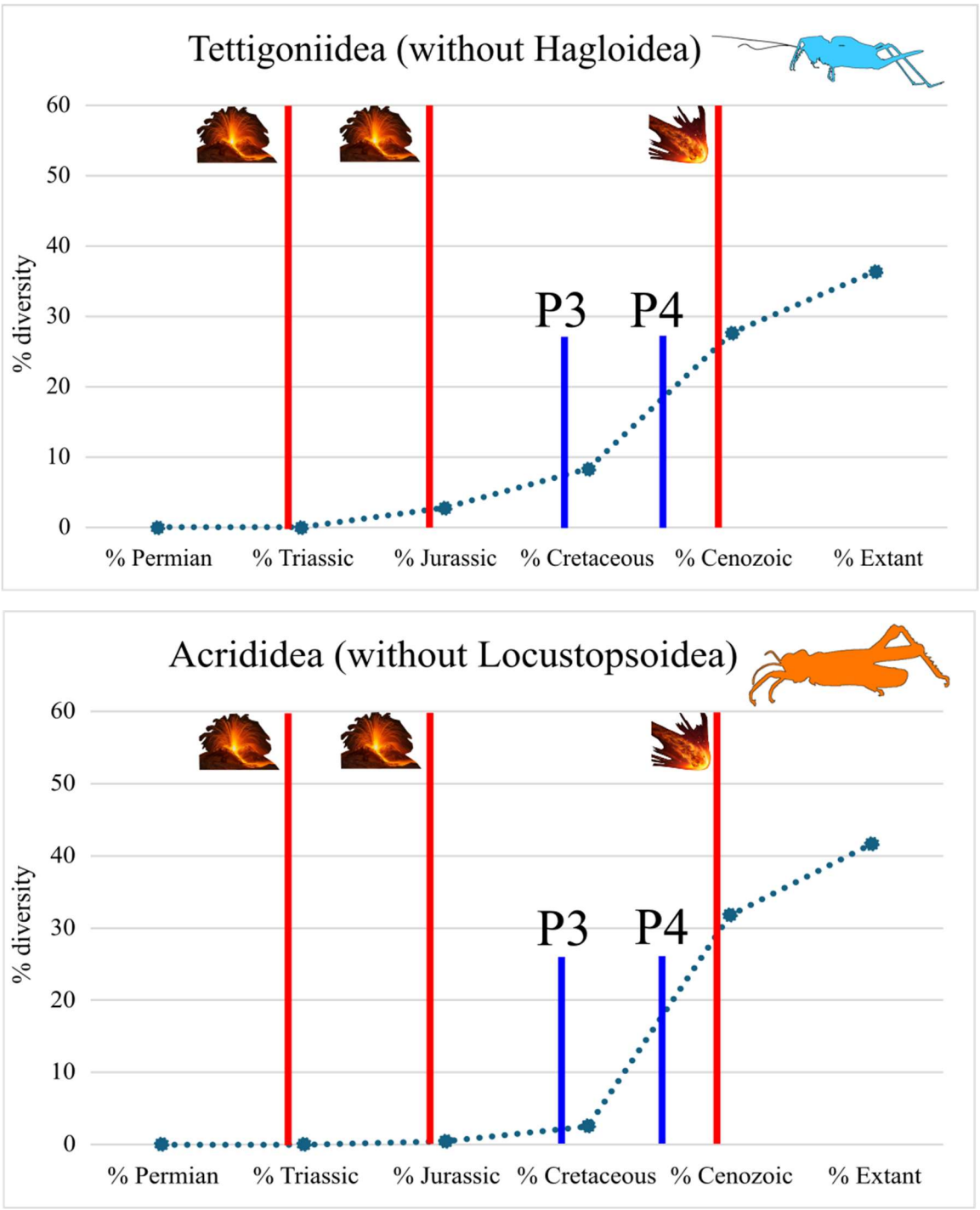

Fig. 13 Diversity pattern of Tettigoniidea Kevan, 1982 (without Hagloidea) and Acrididea Targioni-Tozzetti, 1882 (without Locustopsoidea) over deep time. Y-axis represents relative diversity (relative number of species known from the given taxon of the total number of fossil Orthoptera species per era, values are %). Red bars indicate Permian-Triassic mass extinction (ca. 252 Mya), end-Triassic mass extinction (ca. 201 Mya) and Cretaceous-Paleogene mass extinction (ca. 66 Mya). Blue bars indicate additional mass extinctions affecting insects as determined by Labandeira (2005). P3 = peak 3 from Labandeira (2005) during the Late Jurassic (Kimmeridgian); P4 = peak 4 from Labandeira (2005) during the mid-Cretaceous (Aptian-

Albian). Volcano image from DPA/Salvatore Allegra (cutout). Asteroid image from IMAGO/Panthermedia (cutout).

Analysis 2 – eon of highest diversity

The results from analysis 1 (i.e. % diversity per era) were summed up per eon (Paleozoic (Carboniferous + Permian), Mesozoic and Cenozoic (extant + fossil taxa) for taxa 1-9 (Table 1) to determine the eon of highest diversity per taxon. Oedischiidea (128.9%; values above 100% are due to the combination of Carboniferous and Permian values that were added together) and Titanoptera (43%) had highest values during the Paleozoic. Values for the Carboniferous were not included in analysis 1, because only 4 species of Orthoptera (3 Oedischiidea and 1 Titanoptera) are known from that period. Thus, Oedischiidea had a 75% part in the overall diversity of Orthoptera during the Carboniferous, while Titanoptera had 25% part. Elcanidea (35.7%), Locustopsoidea (40.3%), Hagloidea (102%) and Tridactylidea (16.1%) were most diverse during the combined Mesozoic. Gryllidea (54.6%), Tettigoniidea (without Hagloidea) (64%) and Acrididea (without Locustopsoidea) (73.4%) were most diverse during the Cenozoic. However, it should be noted that the value for Gryllidea for combined Mesozoic was almost as high (42.9%) as for Cenozoic.

Table 1: % diversity of taxa 1-9 per eon. [1]Cenozoic findings of Elcanidea based on *Cenoelcanus menatensis* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020 and *Macrelcana ungeri* (Heer, 1849). Both findings are under scrutiny (chapter 13, this dissertation). [2]Cenozoic finding of Hagloidea based on *Hylophalangopsis chinensis* Lin and Huang, 2006. This finding is under scrutiny (Wang et al., 2019). [3]All findings attributed to Tettigoniidea in Cigliano et al. (2025) from the Triassic and Jurassic that do not belong to Phasmomimoidea Sharov, 1968 are under scrutiny (*Xenogryllacris reductus* Riek, 1955, an alleged gryllacridid from the Triassic of Australia was considered a protoblattodean by Cadena-Castañeda (2019)). *Pseudogryllacris propinqua* (Deichmüller, 1886), another alleged gryllacridid from the Jurassic of Germany may belong to *Pycnophlebia* Deichmüller, 1886, a genus of Hagloidea according to Handlirsch (1906). *Locustophanes rhipidophorus* Handlirsch, 1939, an alleged tettigoniid from the Jurassic of Germany is based on a partially preserved fore- and hindwing (only apical portion) and should probably be considered a *nomen dubium*. Its attribution to Tettigoniidae Krauss, 1902 is doubtful. *Locustites priscus* (Germar, 1839) also from the Jurassic of Germany is not figured in any literature that was available to me; the species needs revision. The position of Phasmomimoidea is debated over (see introduction). Tettigoniidea is unequivocally reported only from the Cretaceous onwards (Gorochov, 1988,

2010, Heads and Leuzinger, 2011, Martins-Neto, 2007). [4]Two alleged species of Pamphagidae Burmeister, 1840 (*Akicera frauenfeldi* Giebel, 1856 and *A. heeri* Giebel, 1856) from the Triassic of UK can not be validated due to missing documentation of the specimens (need revision). However, the presence of Pamphagidae in the Triassic is very unlikely, given the overall fossil record of Acrididea.

Taxon	**Sum of % of overall Orthoptera fauna/eon (Paleozoic/Mesozoic/Cenozoic)**
Oedischiidea Handlirsch, 1906	128.9/27.9/0
Titanoptera Sharov, 1968	43.0/16.1/0
Elcanidea Gorochov, 1995	19.1/35.7/1.2[1]
Locustopsoidea Handlirsch, 1906	5.6/40.3/0
Hagloidea Handlirsch, 1906	0/102/0.6[2]
Gryllidea Vickery, 1977	0/42.9/54.6
Tridactylidea Brullé, 1835	0/16.1/3.2
Tettigoniidea Kevan, 1982 (without Hagloidea)	0/11.1[3]/64
Acrididea Targioni-Tozzetti, 1882 (without Locustopsoidea)	0/3[4]/73.4

Based on these results, every taxon was assigned to a category reflecting during which eon it had the highest levels of relative diversity. Oedischiidea and Titanoptera had their highest value during the Paleozoic and were grouped together in the 'Paleozoic' category. Elcanidea, Locustopsoidea, Hagloidea and Tridactylidea had their highest value in the Mesozoic and were grouped together in the 'Mesozoic' category. Acrididea and Tettigoniidea had their highest value in the Cenozoic and were grouped together in the 'Cenozoic' category. Gryllidea also had their highest value in the Cenozoic. However, because their diversity level during the Mesozoic was already high and comparable to the Mesozoic group taxa, it was included in both categories, one each in two different versions (Fig. 14). Results show three distinct phases of Orthoptera evolution. The Paleozoic phase/fauna (Oedischiidea + Titanoptera) was most diverse during the Carboniferous and Permian. Although they remained relatively diverse during the Triassic, in this period the Mesozoic fauna was already more diverse. This trend continued in the Jurassic and Cretaceous, when the Mesozoic fauna comprised nearly 100% of Orthoptera diversity in the model including the Gryllidea in the Mesozoic category, and about 80% (60%) in the Jurassic (Cretaceous) in the model where Gryllidea was put in the Cenozoic category, respectively. In the Cenozoic the Cenozoic group was most diverse, comprising 80% of relative diversity in the model with Gryllidea in the Mesozoic group and 100% in the model with

Gryllidea in the Cenozoic group. Both hypotheses of faunal community evolution of Orthoptera yield similar results. The main difference is that, if Gryllidea is included in the Cenozoic fauna, the Cenozoic group has almost reached diversity levels of the Mesozoic fauna by the Cretaceous, whereas they do not get close to them until the Cenozoic in the variation that puts Gryllidea as a Cenozoic group taxon.

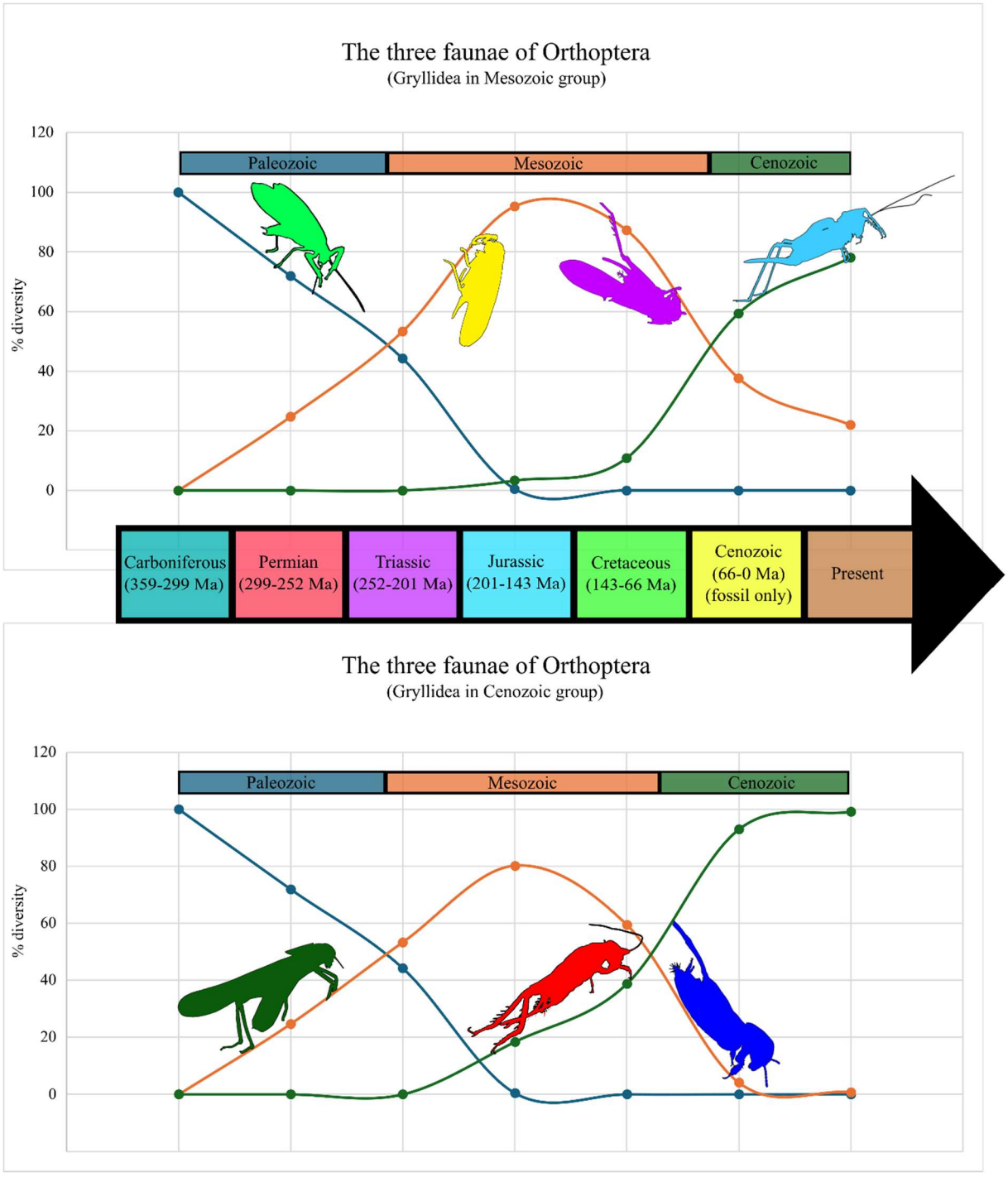

Fig. 14 Three faunae of Orthoptera. Paleozoic fauna with typical components consisting of Oedischiidea Handlirsch, 1906 and Titanoptera Sharov, 1968. Mesozoic fauna with typical

components being Hagloidea Handlirsch, 1906, Elcanidea Gorochov, 1995, Locustopsoidea Handlirsch, 1906, Tridactylidea Brullé, 1835 and Gryllidea Vickery, 1977 (Gryllidea only in top hypothesis). Cenozoic fauna with typical components being Tettigoniidea Kevan, 1982, Acrididea Targioni-Tozzetti, 1882 and Gryllidea (only in bottom hypothesis). The relative abundance in the overall Orthopteran community (measured in species number) of each component is shown on the Y-axis (%). Species number of taxa for each 'fauna' were added together.

4. Discussion

Based on the results of Orthoptera diversity over deep time presented above, evolutionary patterns of faunal community assemblages of the order can be determined. Specifically, hypotheses to answer the questions raised in the introduction are proposed.

1) Can Orthoptera be split into two distinct faunae like other insects, i.e. a basal pre-Permian-Triassic mass extinction fauna and a more derived, 'modern' fauna post end-Permian extinction?

Faunal communities of insects, and terrestrial and marine ecosystems in general, can be recognized as two different assemblages, a Paleozoic and a post-Paleozoic or 'modern' one. They are set apart by the Permian-Triassic mass extinction 252 Mya (Benton and Wu, 2022; Jarzembowski and Ross, 1996; Labandeira, 2005). This theory is sometimes referred to as the Triassic Revolution (Benton and Wu, 2022), Mesozoic Marine Revolution (due to the abundant marine fossils often used in analyses of faunal community evolution through deep time) (Sepkoski, 1984; Vermeij, 1977) or Mesozoic Lacustrine Revolution (based on fossil communities from lacustrine deposits) (Buatois et al., 2016; Zheng et al., 2018). The Triassic Revolution hypothesis postulates that faunal communities on a higher taxonomic level (usually order-level) (Gui et al., 2024; Zheng et al., 2018) and physiologic innovations (Benton and Wu, 2022) resembled modern ecosystems by the early stages of the Mesozoic with enhanced rates of diversification during the Carnian Pluvial Episode (233-232 Mya) (Benton and Wu, 2022).

In the case of Orthoptera, faunal community evolution can be separated into three phases instead of two (Fig. 14). After the Paleozoic fauna, which dominated the ecosystems prior to the end-Permian extinction, follows a Mesozoic fauna that was dominant through the Triassic, Jurassic and Cretaceous period. This Mesozoic fauna, although overlapping in some taxa like the Gryllidea and Tridactylidea, is still distinct from the following Cenozoic fauna, which

became dominant either after the Cretaceous-Paleogene mass extinction or perhaps somewhat earlier during the early Late Cretaceous (the timing of this faunal turnover is discussed below). The Mesozoic was characterized by the ensiferan groups Elcanidea and Hagloidea and the Locustopsoidea from the Caelifera, whereas the Cenozoic saw the radiation of the extant Acrididea and Tettigoniidea.

This three-stage faunal development is perhaps more in line with the Angiosperm Terrestrial Revolution - another, seemingly contrasting hypothesis to the Triassic Revolution. This theory suggests that, in a time-interval from about 100-50 Mya, angiosperm evolution drove the diversification of life on land, especially of pollinating and herbivorous insect lineages (Benton et al., 2022). Insect diversity reached its peak in the late Early Cretaceous ca. 125 Mya. From that point on, no increase in net diversity can be recorded, suggesting that the origination of new taxa was balanced by the extinction of previous ones (Clapham et al., 2016; Schachat et al., 2019). This finding aligns well with the apparent demise of the Mesozoic orthopteran fauna and simultaneous rise of the Cenozoic fauna (Fig. 14). Indeed, research from dragonflies (Nel et al., 2015) and plant-herbivore interactions (Labandeira, 2006) support that around the mid-Cretaceous (115-100 Mya) several first and last occurrences of multiple lineages overlapped, resulting in many extinction and origination events at the same time and creating the observed diversity peak. A few million years later, the diversification of angiosperms during the Angiosperm Terrestrial Revolution seems to have had a buffering effect for many of the new modern lineages, i.e. keeping extinction rates low and further benefitting their rise by providing new ecological niches and additional resources (Jouault et al., 2024; Peris and Condamine, 2024).

Although the Triassic Revolution and Cretaceous Angiosperm Terrestrial Revolution are sometimes understood as contradicting theories (Gui et al., 2024), the evolution of Orthoptera faunal communities indicates that they are rather complementary, once applied on the appropriate taxonomic scale. Titanoptera is mostly regarded as a separate and sister order to Orthoptera (Gorochov, 2007; Huang et al., 2020; Schubnel et al., 2021), but other researchers place it within Orthoptera (Bethoux, 2007) and it is currently listed as a suborder of Orthoptera by Cigliano et al. (2025). Oedischiidea, on the other hand, are listed within the Ensifera Chopard, 1921 suborder of Orthoptera in Cigliano et al. (2025), however, a recent hypothesis (chapter 9, this dissertation) suggests they may be stem-Orthoptera that preceded the split of Ensifera and Caelifera Ander, 1936 and thus, should be excluded from Ensifera. In accordance with the Triassic Revolution hypothesis at the suborder/order taxonomic level Orthoptera (and Titanoptera) can be divided into a Paleozoic and a ‘modern’ fauna. That being said, on the

infraorder level (Locustopsoidea and the Mesozoic Hagloidea should probably be treated as infraorders) Orthoptera can be divided into three distinct faunae. In accordance with the Angiosperm Terrestrial Revolution hypothesis, the 'modern' fauna can be further divided into a Mesozoic and a Cenozoic fauna, whereby the transition from one to the other may have occurred around the mid-Cretaceous, contemporary to other major insect lineages (Schachat et al., 2019). However, due to the paucity of orthopteran fossils in the interval from 99 Mya (post-Burmese amber) to ca. 60 Mya (Menat Formation), there is little evidence to document the decline of the Mesozoic fauna during its final stages. If it in fact was about to meet its demise in the following Million years, the Orthoptera from Burmese amber may be the last representatives of a still – but not for much longer – flourishing Mesozoic fauna.

2) Does the rise/fall of major Orthoptera lineages correspond to the intervals of elevated extinction rates identified by Labandeira (2005)?

Labandeira (2005) identified four occasions in the history of insect evolution with rates of extinction so high they could be classified as mass extinctions. These are a Late Carboniferous event (Late Pennsylvanian), the end-Permian mass extinction, a Late Jurassic event (Kimmeridgian stage) and a mid-Cretaceous event (Albian/Aptian stages). Two other extinction events that may have affected insects, but generally are thought to have been less impactful for their evolution (Schachat and Labandeira, 2021), are the end-Triassic event (ca. 201 Mya) and the end-Cretaceous mass extinction. How did orthopterans respond during these times?

<u>The Late Carboniferous event</u>

This earliest mass extinction event to fall into the time of Orthoptera evolution was caused by the climatic and environmental change from the Late Pennsylvanian to Permian (Labandeira, 2005). The fossil record of Orthoptera from the Carboniferous is scarce, and no impact of this extinction can be traced in the group so far. Based on the limited data available, it seems as if Orthoptera were not affected by the Late Carboniferous extinction. They had only risen to existence relatively recently and continued to diversify in the Permian.

<u>The end-Permian mass extinction</u>

The end-Permian mass extinction (first red bar in Figs. 11-13) left some traces in the fossil record of Orthoptera, however, perhaps not as significant as would be expected from one of the greatest mass extinctions to have affected life on earth (Sepkoski, 1982). Although it caused the disappearance of major insect taxa like the order Meganisoptera Martynov, 1932 (which housed the famous giant Paleozoic dragonflies) and superorder Paleodictyopterida Bechly,

1996 (including four extinct orders), the orthopterans almost seemed non-affected by the event. Recorded species of Oedischiidea dropped from 48 to 46 from the Permian to Triassic and the Titanoptera even increased from 16 Permian species to 27 in the Triassic. However, in the Elcanidea the superfamily Permoraphidioidea Tillyard, 1932 completely died out and the family Permelcanidae Sharov, 1962 was almost fully gone, leaving just two members discovered in the Madygen Formation of Kyrgyzstan (ca. 237 Mya). The transition of the Permian-Triassic for Orthoptera is most notable as a time of transition between the Paleozoic fauna dominated by Oedischiidea and Titanoptera to a more diverse fauna of the Triassic, dominated by Hagloidea, with several other groups like the Locustopsoidea and early Tridactylidea appearing for the first time. Since the Paleozoic taxa did not decrease in number, it would be more appropriate to view the Permian-Triassic transition as a period of origination for Orthoptera rather than extinction. This suggestion, quite contradictory to the general impact of the end-Permian extinction on life on earth, may change with future findings. The Triassic fossil record of Orthoptera is extremely limited. 125 of 162 findings of described species were discovered in the Madygen Formation of the Middle Triassic, by which insects may have already rebounded from the effects of the extinction (Labandeira, 2005). New Triassic discoveries from an interval closer to the end-Permian extinction may reveal evidence for a depauperate early Mesozoic orthopteran community right after the devastation.

The end-Triassic mass extinction

Unlike the end-Permian event, the end-Triassic mass extinction (second red bar in Figs. 11-13) is thought to generally not having had a major impact on insect diversity (Schachat and Labandeira, 2021). However, again, Orthoptera seem to be somewhat different. Oedischiidea and Titanoptera went extinct in the Triassic (except for one species of Oedischiidea from the early Jurassic in the UK). Thus, this period – and potentially the end-Triassic extinction – marked the true end of the Paleozoic orthopteran fauna and ushered in the unrivaled dominance of the Mesozoic grasshoppers.

The Late Jurassic mass extinction

The Late Jurassic mass extinction (P3 in Figs. 11-13) did not seem to affect most Orthoptera, but it did have great impact on the Hagloidea. They had contributed almost 50% to overall orthopteran diversity in the Jurassic; a value that dropped below 20% in the Cretaceous. In other numbers, more than 100 species of Hagloidea are recorded from the Jurassic, but only 44 from the Cretaceous.

The mid-Cretaceous and end-Cretaceous mass extinction

Because of the lack of orthopteran fossils in the interval from ca. 100-60 Mya, it is difficult to say with certainty whether the patterns observable in the faunal community evolution of Orthoptera from the Cretaceous to the Cenozoic were caused by the mid-Cretaceous (P4 in Figs. 11-13), end-Cretaceous (third red bar in Figs. 11-13), or both mass extinctions. However, what can be said is that a significant change happened, with the dominance shifting from the Mesozoic to the Cenozoic fauna. The Mesozoic groups Elcanidea, Locustopsoidea and Hagloidea completely disappeared (see earlier comments on putative records of Cenozoic elcanids and hagloids). The Mesozoic Tridactylidea suffered major losses and were reduced from a once important faunal element (11% relative diversity in the Cretaceous) to a relic taxon in the extant faunal assemblage. The only Mesozoic taxon apparently unaffected by any ongoing extinctions were the Gryllidea. The crickets and mole crickets, after already having been diverse in the Cretaceous, even showed a small increase in the Cenozoic, with relative diversity increasing by 5.6%.

Although it is uncertain whether these changes are associated with the mid-Cretaceous or end-Cretaceous mass extinction (or if it was a simultaneous effect from both), conclusions made previously may point towards one direction. The pattern of faunal development of Orthoptera aligns well with the observations made for other insect lineages prior and during the Angiosperm Terrestrial Revolution (i.e. overlapping of first and last occurrences of many lineages). This may suggest that the changes also to Orthopteran communities were indeed caused by the mid-Cretaceous extinction. It should be noted, however, that these changes appear to have set in slowly. In the Crato Formation of Brazil (ca. 122-113 Mya) 27 species of Caelifera discovered so far belong to the Mesozoic faunal element Locustopsoidea while only three belong to the Cenozoic Proscopioidea Serville, 1838 and Eumastacoidea Burr, 1899 (infraorder Acrididea). A similar picture can be seen in the slightly younger Burmese amber (ca. 110-99 Mya), where almost all findings of Orthoptera can be attributed to the Mesozoic Elcanidea, Tridactylidea and Gryllidea (could be interpreted as Cenozoic, see above). Thus, if the Angiosperm Terrestrial Revolution can be traced in the evolution of faunal communities of orthopterans, it started of slowly. In the beginning, ecosystems were still dominated by the Mesozoic taxa for a considerable amount of time, before tipping over to the Cenozoic assemblages we see today.

3) Did Orthoptera experience faunal turnover during extinctions?

The evolution of insect diversity during mass extinctions is considered to represent faunal turnover rather than 'true' extinction (Schachat and Labandeira, 2021). Whereas during an extinction many taxa disappear without origination rates increasing above background levels, during episodes of faunal turnover both extinction and origination rates increase simultaneously, hence net diversity remains largely unchanged.

The principle of faunal turnover is apparently also observable in the Orthoptera. Generally, two intervals can be recognized that correspond to the shift from the Paleozoic fauna to the Mesozoic fauna and from the Mesozoic fauna to the Cenozoic fauna (Fig. 13). The first faunal turnover (Paleozoic fauna-Mesozoic fauna), perhaps initiated in the Permian, may have been facilitated by the end-Permian extinction. It continued throughout the Triassic and culminated in the end-Triassic extinction with the disappearance of Oedischiidea and Titanoptera, the typical elements of the Paleozoic orthopteran community.

The second faunal turnover (Mesozoic-Cenozoic fauna) may have started in the Late Jurassic, facilitated by the Late Jurassic extinction, when Hagloidea started to significantly decrease in diversity. However, evidence for an impact of the Late Jurassic extinction on Orthoptera is limited. Based on the trajectory in other insect lineages (Nel et al., 2015; Schachat et al., 2019) it seems likely that the main transition between the two faunae was initiated in the mid-Cretaceous and in association with the Angiosperm Terrestrial Revolution and the shift from phase 3 to 4 of the plant-herbivore associations recognized by Labandeira (2006).

It is noteworthy that both faunal turnovers apparently did not happen over the course of a short time interval that could be directly assigned to a single mass extinction event. Instead, they took a long time (> 50 My), at least from the end-Permian to end-Triassic and Late Jurassic to probably Late Cretaceous/Early Cenozoic, respectively. Understanding of the timing of turnover progress may change with future discoveries, as knowledge of the Orthoptera fauna of the Triassic is heavily biased towards findings from the Madygen Formation of Kyrgyzstan (ca. 75% of Triassic Orthoptera species). The paucity of Orthoptera fossils from the second half of the Cretaceous has already been mentioned above.

The faunal turnover affected almost all higher-level taxa of Orthoptera addressed in this study with the apparent exception of Gryllidea. This group seems to have experienced a constant increase in diversity since its appearance in the Jurassic. In fact, the diversity pattern of Gryllidea is so unusual that the infraorder cannot be assigned with certainty to either the Mesozoic or the Cenozoic orthopteran fauna. Why were the crickets unaffected by the events during the Cretaceous, which had great impact on their grasshopper and katydid relatives as

well as other insects? Perhaps Gryllidea was more resistant than other groups to the changing environment, i.e. the shifting in vegetation from lycophytes and crown spermatophytes (gymnosperms) to angiosperm dominated ecosystems (Labandeira, 2006) and Late Cretaceous climate cooling (Linnert et al., 2014). Or perhaps the new vegetation buffered crickets against extinction similar to ants (Jouault, 2024), whereas the other Mesozoic orthopterans were negatively affected.

Diversity patterns of insects over deep time can have important implications for the current diversity crisis. If we understand the factors that drove insect extinction/origination rates in the past (e.g. climate change, vegetation change) it may allow to pre-determine the future of faunal communities in modern ecosystems. However, reasons that may have increased the extinction risk of the ancient orthopteran lineages (i.e. Hagloidea, Elcanidea and Locustopsoidea) are not well understood. Superficially, Hagloidea and Elcanidea bear reasonable likeness to modern Tettigoniidea, and Locustopsoidea are virtually indistinguishable from modern Acrididea (so much so, that no apomorphies to define Locustopsoidea have been postulated so far). Understanding differences in ecology and lifestyle of these groups will be essential to understand the drivers of faunal turnover during the most recent shift in community assemblage of the Orthoptera.

5. Conclusions

Based on their fossil record, the order Orthoptera can be split into three distinct faunae with certain typical taxonomic units: a Paleozoic fauna characterized by the dominance of Oedischiidea and Titanoptera; a Mesozoic fauna characterized by the dominance of Elcanidea, Locustopsoidea, Hagloidea, Tridactylidea and Gryllidea; and a Cenozoic fauna characterized by the dominance of Gryllidea, Tettigoniidea and Acrididea. The transition from one fauna to the other was characterized by a long interval (>50 My) of faunal turnover and can be associated with major extinction events (i.e. the end-Permian and end-Triassic mass extinction for the faunal turnover from Paleozoic to Mesozoic fauna and the Late Jurassic to mid-Cretaceous/end-Cretaceous mass extinction for the faunal turnover from Mesozoic to Cenozoic fauna). The second transition during the Cretaceous was likely facilitated by the changes in vegetation (Angiosperm Terrestrial Revolution) affecting insect communities in general. Interestingly, the infraorder Gryllidea seems to have been the only taxon in the history of insects not affected by a faunal turnover so far. Understanding drivers of extinction and origination in Orthoptera may

hold important implications for conservation issues, but ecological factors affection extinction risk in the Mesozoic orthopteran lineages are not explored.

Supplemental material

Supplemental material 1: Excel file (pdf version) including every species of fossil Orthoptera described so far. Data based on Cigliano et al. (2025) and the Paleobiology Database (2025).

Suborder	Infraorder	Nanorder	Superfamily	Family	Subfamily	Species	Era	Location	Original Author(s)	Year of publication
Titanoptera			Tcholmanvissioidea	Mesotitanidae	Jubilaeinae	*Jubilaeus beybienkoi*	Permian	Russia (Koshelevka Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae	Mesotitaninae	*Clatrotitan andersoni*	Triassic	Australia (Hawkesbury Sandstone Formation)	McKeown, 1937	1937
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Clatrotitan scullyi*	Triassic	Australia (Hawkesbury Sandstone Formation)	(Tillyard, 1925)	1925
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Clatrotitan tillyardi*	Triassic	Australia (Hawkesbury Sandstone Formation)	(McKeown, 1937)	1937
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Gigatitan ovatus*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Gigatitan similis*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Gigatitan vulgaris*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Mesotitan giganteus*	Triassic	Australia (Ashfield Shale Formation)	Tillyard, 1925	1925
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Nanotitan extentus*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Nanotitan magnificus*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Ootitan curtis*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Tcholmanvissiella gigantea*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Mesotitanodes similis*	Triassic	Kyrgyzstan (Madygen Formation)	(Sharov, 1968)	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Mesotitanodes tillyardi*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Ultratitan superior*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae	Prototitaninae	*Prototitan primitivus*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			Tcholmanvissioidea	Mesotitanidae		*Prototitan sharovi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2003	2003
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae	Tcholmanvissiinae	*Pinegia craticius*	Permian	?	(Martynov, 1928)	1928
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Pinegia distincta*	Permian	?	(Martynov, 1930)	1930
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Pinegia martynovi*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Pinegia meidigouensis*	Permian	China (Xiashihezi Formation)	Hong, 1985	1985
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Pinegia mirabilis*	Permian	?	(Zalessky, 1929)	1929
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Pinegia oknowae*	Permian	Russia (Iva-Gora Beds Formation)	Martynov, 1928	1928
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Pinegia zalesskyi*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Tcholmanvissia longipes*	Permian	Russia (Koshelevka Formation)	(Martynov, 1940)	1940
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Tcholmanvissia noinskii*	Permian	Russia (Baitugan Formation)	Zalessky, 1929	1929

Suborder	Infraorder	Nanorder	Superfamily	Family	Subfamily	Species	Era	Location	Original Author(s)	Year of publication
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Tcholmannvissia uralica*	Permian	?	Zalessky, 1929	1929
Titanoptera			Tcholmanvissioidea	Tcholmanvissiidae		*Yinpingia caesia*	Permian	China (Yinping Formation)	Lin, 1982	1982
Titanoptera			Tettoedischioidea	Tettoedischiidae	Tettoedischiinae	*Macroedischia elongata*	Permian	Russia (Koshelevka Formation)	Sharov, 1968	1968
Titanoptera			Tettoedischioidea	Tettoedischiidae		*Tettoedischia minuta*	Permian	Russia (Koshelevka Formation)	Sharov, 1968	1968
Titanoptera			-	Deinotitanidae		*Deinotitan orenburgensis*	Permian	Russia	Gorochov, 2007	2007
Titanoptera			-	Deinotitanidae		*Monstrotitan monstrosus*	Permian	Russia (Poldarsa Formation)	Gorochov, 2013	2013
Titanoptera			-	Paratitanidae		*Magnatitan jongheoni*	Triassic	South Korea (Amisan Formation)	Park, Kim, Nam & Lee, 2022	2022
Titanoptera			-	Paratitanidae		*Minititan zherichini*	Triassic	Kyrgyzstan (Madygen Formation)	(Gorochov, 2003)	2003
Titanoptera			-	Paratitanidae		*Paratitan bispeculum*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2003	2003
Titanoptera			-	Paratitanidae		*Paratitan intermedius*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2003	2003
Titanoptera			-	Paratitanidae		*Paratitan latispeculum*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2003	2003
Titanoptera			-	Paratitanidae		*Paratitan libelluloides*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			-	Paratitanidae		*Paratitan longispeculum*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2003	2003
Titanoptera			-	Paratitanidae		*Paratitan modestus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2003	2003
Titanoptera			-	Paratitanidae		*Paratitan ovalis*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Titanoptera			-	Paratitanidae		*Paratitan reductus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2003	2003
Titanoptera			-	Paratitanidae		*Paratitan venosus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2003	2003
Titanoptera			-	Theiatitanidae		*Theiatitan azari*	Carboniferous	France	Schubnel, Roques & Nel, 2021	2021
Titanoptera			-	-		*Steinhardtia maryae*	Triassic	Australia (Esk Formation)	Jell & Lambkin, 1993	1993
-	-	-	-	Legendreiidae		*Legendreia magnifica*	Permian	China (Yinping Formation)	Huang, Schubnel & Nel, 2020	2020
-	-	-	-	-	-	*Tillyardiella distincta*	Permian	Russia (Baitugan Formation)	Martynov, 1930	1930
Caelifera	Tridactylidea		-	Burmecaelidae		*Burmecaelinus armis*	Cretaceous	Myanmar (Burmese amber)	Uchida, Husemann & Kotthoff, 2023	2023
Caelifera	Tridactylidea		-	Burmecaelidae		*Burmecaelinus yungyenwangae*	Cretaceous	Myanmar (Burmese amber)	Schall, Cumming, Lian & Husemann, 2025	2025
Caelifera	Tridactylidea		-	Burmecaelidae		*Moban zhengzhemini*	Cretaceous	Myanmar (Burmese amber)	Hu & He, 2024	2024
Caelifera	Acrididea	Acridomorpha	Acridoidea	Acrididae	Calliptaminae	*Calliptamus strausi*	Pliocene (?)	Germany (Willershausen)	Harz, 1973	1973
Caelifera	Acrididea		Acridoidea	Acrididae	Cyrtacanthacridinae	*Orthacanthacris incertus*	Paleocene	France (Menat Formation)	Piton, 1940	1940
Caelifera	Acrididea		Acridoidea	Acrididae		*Orthacanthacris lineata*	?	France	Théobald, 1937	1937
Caelifera	Acrididea		Acridoidea	Acrididae		*Orthacanthacris rhenana*	Oligocene	Germany (Salt Formation)	Théobald, 1937	1937
Caelifera	Acrididea		Acridoidea	Acrididae		*Proschistocerca oligocaenica*	Eocene	UK (Bouldnor Formation)	Zeuner, 1937	1937
Caelifera	Acrididea		Acridoidea	Acrididae	Gomphocerinae	*Gomphocerus abstrusus*	Eocene	USA (Florissant Formation)	Scudder, 1890	1890

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Caelifera	Acrididea		Acridoidea	Acrididae		*Gomphocerus femoralis*	Miocene	Germany (Oeningen)	Heer, 1849	1849
Caelifera	Acrididea		Acridoidea	Acrididae		*Ochrilidia lineata*	Paleocene	France (Menat Formation)	Piton, 1940	1940
Caelifera	Acrididea		Acridoidea	Acrididae		*Stenobothrus posthumoides*	Quaternary	Ukraine	Zeuner, 1934	1934
Caelifera	Acrididea		Acridoidea	Acrididae	Melanoplinae	*Melanoplus spretus*	Quaternary	USA	(Walsh, 1866)	1866
Caelifera	Acrididea		Acridoidea	Acrididae	Oedipodinae	*Bryodema croatica*	Miocene	Croatia (Radoboj)	Poncrácz, 1928	1928
Caelifera	Acrididea		Acridoidea	Acrididae		*Pardalophora hungarica*	Miocene	Croatia (Radoboj)	Poncrácz, 1928	1928
Caelifera	Acrididea		Acridoidea	Acrididae		*Oedipoda germari*	Miocene	Germany (Oeningen)	Heer, 1865	1965
Caelifera	Acrididea		Acridoidea	Acrididae		*Oedipoda haidingeri*	Miocene	Croatia (Radoboj)	Heer, 1865	1865
Caelifera	Acrididea		Acridoidea	Acrididae		*Oedipoda longipennis*	Miocene	Croatia (Radoboj)	Poncrácz, 1928	1928
Caelifera	Acrididea		Acridoidea	Acrididae		*Oedipoda nigrofasciolata*	Miocene	Croatia (Radoboj)	Heer, 1849	1849
Caelifera	Acrididea		Acridoidea	Acrididae		*Oedipoda praefocata*	Eocene	USA (Florissant Formation)	Scudder, 1890	1890
Caelifera	Acrididea		Acridoidea	Acrididae		*Oedipoda pulchra*	Miocene	Croatia (Radoboj)	Poncrácz, 1928	1928
Caelifera	Acrididea		Acridoidea	Acrididae		*Aestilocusta graminea*	Miocene	China (Shanwang Formation)	Zhang, 1989	1989
Caelifera	Acrididea		Acridoidea	Acrididae		*Mioedipoda reisereri*	Miocene	USA (Buffalo Canyon Formation)	Stidham & Stidham, 2000	2000
Caelifera	Acrididea		Acridoidea	Acrididae		*Nymphacrida discrita*	Miocene	China (Shanwang Formation)	Zhang, Sun & Zhang, 1994	1994
Caelifera	Acrididea		Acridoidea	Acrididae		*Oedemastopoda grammaca*	Miocene	China (Shanwang Formation)	Zhang, Sun & Zhang, 1994	1994
Caelifera	Acrididea		Acridoidea	Acrididae		*Acridium atrum*	?	?	Eichwald, 1830	1830
Caelifera	Acrididea		Acridoidea	Acrididae		*Oedipoda melanosticta*	Miocene	Croatia (Radoboj)	Heer, 1849	1849
Caelifera	Acrididea		Acridoidea	Acrididae	-	*Heeracris oeningense*	Miocene	Germany (Oeningen)	(Scudder, 1895)	1895
Caelifera	Acrididea		Acridoidea	Acrididae		*Menatacridium eocenicum*	Paleocene	France (Menat Formation)	Piton, 1936	1936
Caelifera	Acrididea		Acridoidea	Acrididae		*Nanthacia torpida*	Eocene	USA (Florissant Formation)	Scudder, 1890	1890
Caelifera	Acrididea		Acridoidea	Acrididae		*Taeniopodites pardalis*	Eocene	USA (Florissant Formation)	Cockerell, 1909	1909
Caelifera	Acrididea		Acridoidea	Acrididae		*Tyrbula russelli*	Eocene	USA (Florissant Formation)	Scudder, 1885	1885
Caelifera	Acrididea		Acridoidea	Acrididae		*Tyrbula scudderi*	Eocene ?	USA (Florissant Formation) ?	Cockerell, 1914	1914
Caelifera	Acrididea		Acridoidea	Acrididae		*Acridium barthelemyi*	Oligocene	France	(Hope, 1847)	1847
Caelifera	Acrididea		Acridoidea	Pamphagidae	Akicerinae	*Akicera frauenfeldi*	Triassic	UK (Wainlode Cliff)	Giebel, 1856	1856
Caelifera	Acrididea		Acridoidea	Pamphagidae		*Akicera heeri*	Triassic	UK (Wainlode Cliff)	Giebel, 1856	1856
Caelifera	Acrididea		Eumastacoidea	Chorotypidae	Eruciinae	*Erucius lewisi*	Oligocene	Montana (Renova Formation)	Kevan and Wighton, 1981	1981
Caelifera	Acrididea		Eumastacoidea	Chorotypidae		*Paleochina duvergeri*	Paleocene	France (Menat Formation)	Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020	2020
Caelifera	Acrididea		Eumastacoidea	Chorotypidae		*Paleochina minuta*	Paleocene	France (Menat Formation)	Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020	2020
Caelifera	Acrididea		Eumastacoidea	Episactidae	Espagnolinae	*Paleomastacris ambarinus*	Miocene	Dominican Republic (Dominican amber)	Perez-Gelabert, Hierro, Dominici & Otte, 1997	1997
Caelifera	Acrididea		Eumastacoidea	Eumastacidae	-	*Archaeomastax jurassicus*	Jurassic	Kazakhstan (Karabastau Formation)	Sharov, 1968	1968
Caelifera	Acrididea		Eumastacoidea	Eumastacidae		*Eoerianthus eocaenicus*	Eocene	USA (Green River Formation)	Gorochov, 2012	2012
Caelifera	Acrididea		Eumastacoidea	Eumastacidae		*Eoerianthus multispinosus*	Eocene	USA (Florissant Formation)	(Scudder, 1890)	1890
Caelifera	Acrididea		Eumastacoidea	Eumastacidae		*Eozaenhuepfer erteboellei*	Eocene	Denmark	Zessin, 2017	2017
Caelifera	Acrididea		Eumastacoidea	Eumastacidae		*Taphacris bittaciformis*	Eocene	USA (Florissant Formation)	Cockerell, 1926	1926
Caelifera	Acrididea		Eumastacoidea	Eumastacidae		*Taphacris reliquata*	Eocene	USA (Florissant Formation)	Scudder, 1890	1890

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Caelifera	Acrididea		Eumastacoidea	Eumastacidae		*Taphacris stenosis*	Paleocene	China	Lin, 1977	1977
Caelifera	Acrididea		Eumastacoidea	Eumastacidae		*Taphacris tillyardi*	Eocene	USA (Florissant Formation)	Cockerell, 1926	1926
Caelifera	Acrididea		Eumastacoidea	Eumastacidae		*Taphacris turgis*	Cretaceous	China (Hengshan Formation)	Lin, 1980	1980
Caelifera	Acrididea		Eumastacoidea	Promastacidae		*Promastacoides albertae*	Paleocene	Canada (Paskapoo Formation)	Kevan and Wighton, 1981	1981
Caelifera	Acrididea		Eumastacoidea	Promastacidae		*Promastax archaicus*	Eocene	Canada	Handlirsch, 1910	1910
Caelifera	Acrididea		Eumastacoidea	-	-	*Burmeumastax lexiae*	Cretaceous	Myanmar (Burmese amber)	Husemann, Schall, Uchida & Kotthoff, 2025	2025
Caelifera	Acrididea		Eumastacoidea	-	-	*Cratomastax mariellaae*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Heads, Pinheiro & Husemann, 2025	2025
Caelifera	Acrididea		Locustopsoidea	Bouretidae		*Bouretia elegans*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2001	2001
Caelifera	Acrididea		Locustopsoidea	Eolocustopsidae		*Eolocustopsis primitiva*	Permian	South Africa	Riek, 1976	1976
Caelifera	Acrididea		Locustopsoidea	Eolocustopsidae		*Protettavus exilis*	Permian	South Africa	Riek, 1976	1976
Caelifera	Acrididea		Locustopsoidea	Locustavidae	Locustavinae	*Alekhosara reticulata*	Permian	Russia	Aristov, 2008	2008
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Brevilocustavus distinctus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Brevilocustavus microscopicus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Locustavus deformatus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Locustavus intermedius*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Locustavus lanceolatus*	Triassic	Kyrgyzstan (Madygen Formation)	(Sharov, 1968)	1968
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Locustavus madygensis*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Locustavus minutus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Locustavus problematicus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Mesacridites elongata*	Triassic	Australia (Hawkesbury Sandstone Formation)	Riek, 1954	1954
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Miolocustavus reductus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Acrididea		Locustopsoidea	Locustavidae	Praelocustopsinae	*Praelocustopsis mirabilis*	Permian	Russia (Bugarikta Formation)	Sharov, 1968	1968
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Triassolocusta leptoptera*	Triassic	Australia (Blackstone Formation)	Tillyard, 1922	1922
Caelifera	Acrididea		Locustopsoidea	Locustavidae	-	*Afroedischia oosthuizeni*	Permian	South Africa (Laingsburg Formation)	Geertsema & van Dijk, 1999	1999
Caelifera	Acrididea		Locustopsoidea	Locustavidae		*Hejiafanga tongchuanensis*	Triassic	China (Yanchang Formation)	Xu, Fang, Heads, Zhang, Jarzembowski & Wang, 2020	2020
Caelifera	Acrididea		Locustopsoidea	Locustopsidae	Araripelocustinae	*Araripelocusta brevis*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1995	1995
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Araripelocusta imperatrix*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025	2025

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Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Araripelocusta longinota*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1995	1995
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Britannacrida distincta*	Cretaceous	UK (Lulworth Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Caelifera	Acrididea		Locustopsoidea	Locustopsidae	Locustopsinae	*Conocephalella capito*	Jurassic	Germany (Solnhofen)	(Deichmüller, 1886)	1886
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Cratolocustopsis aquila*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025	2025
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Cratolocustopsis contumax*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2003	2003
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Cratolocustopsis cretacea*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1990)	1990
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Cratolocustopsis reticulata*	Jurassic	Germany (Dobbertin)	(Handlirsch, 1939)	1939
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis africanus*	Cretaceous	Egypt (Tonsteinserie Formation)	Ansorge, 1991	1991
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis apicalis*	Jurassic	Russia (Itat Formation)	Zherikhin, 1985	1985
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis bernstorffi*	Jurassic	Germany (Dobbertin)	(Geinitz, 1880)	1880
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis bucklandi*	Jurassic	UK	(Brodie, 1845)	1845
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis cockerelli*	Jurassic	UK	(Handlirsch, 1939)	1939
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis constricta*	Triassic	UK (Lilstock Formation)	Zeuner, 1942	1942
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis cubitalis*	Triassic	UK (Lilstock Formation)	Zeuner, 1942	1942
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis elegans*	Jurassic	Germany (Dobbertin)	Handlirsch, 1906	1906
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis elongatus*	Jurassic	China (Yan'an Formation)	(Nel & Huang, 2024)	2024
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis ferghanensis*	Jurassic	Kyrgyzstan (Sulyukta Formation)	Martynov, 1937	1937
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis germari*	Jurassic	Germany (Solnhofen)	(Münster, 1842)	1842
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis godoii*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 2003)	2003
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis gracilis*	Triassic	UK (Lilstock Formation)	Zeuner, 1942	1942
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis gyra*	Jurassic	Germany (Dobbertin)	Zessin, 1983	1983
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis karatavica*	Jurassic	Kazakhstan (Karabastau Formation)	Sharov, 1968	1968
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis kruegeri*	Jurassic	Germany (Posidonia Shale Formation)	Zessin, 1983	1983
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis lacoei*	Jurassic	UK	Cockerell, 1916	1916
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis maculosa*	Jurassic	Germany (Posidonia Shale Formation)	Bode, 1953	1953
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis nana*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis nervosa*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 2003)	2003
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis picta*	Jurassic	Russia (Itat Formation)	Zherikhin, 1985	1985
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis posterior*	Cretaceous	UK	Gorochov, Jarzembowski & Coram, 2006	2006
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis procera*	Jurassic	Germany (Dobbertin)	Zessin, 1983	1983
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis pulchella*	Jurassic	Germany (Dobbertin)	Zessin, 1983	1983
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis reducta*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis rhytofemoralis*	Jurassic	China (Jiulongshan Formation)	Gu, Yue, Shi, Tian & Ren, 2016	2016
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis sharovi*	Triassic	UK (Lilstock Formation)	(Gorochov & Coram, 2023)	2023
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis shurabica*	Jurassic	Kyrgyzstan (Sagul Formation)	Sharov, 1968	1968

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Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis sippeli*	Jurassic	Germany	Zessin, 1983	1983
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis soaresi*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 2003)	2003
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis spectabilis*	Triassic	UK (Lilstock Formation)	Zeuner, 1942	1942
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis thalassophila*	Jurassic	Germany (Dobbertin)	(Zessin, 1988)	1988
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis titanella*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 2003)	2003
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsis uvarovi*	Jurassic ?	UK	Zeuner, 1942	1942
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis anglica*	Cretaceous	UK (Durlston Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis angusta*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis araripensis*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1990)	1990
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis levis*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, 2025	2025
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis brevis*	Jurassic	China (Yan'an Formation)	(Nel & Huang, 2024)	2024
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis caririensis*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1990)	1990
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis morrisonensis*	Jurassic	USA (Morrison Formation)	Smith, Gorman, Pardo & Small, 2011	2011
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis problematica*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis sinica*	Cretaceous	China (Laiyang Formation)	Hong & Wang, 1990	1990
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Mesolocustopsis vikingi*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 2003)	2003
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Orichalcum ornatum*	Jurassic	UK (Shales with Beef Formation)	Whalley, 1985	1985
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Parapleurites brasiliensis*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025	2025
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Parapleurites gracilis*	Jurassic	Russia (Cheremkhovskaya Formation)	Brauer, Redtenbacher & Ganglbauer, 1889	1889
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Parapleurites sibiricus*	Jurassic	Russia (Cheremkhovskaya Formation)	Sharov, 1968	1968
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Schwinizia anatolica*	Jurassic	Kyrgyzstan (Dzhil Formation)	(Sharov, 1968)	1968
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Schwinzia sola*	Jurassic	Germany (Dobbertin)	Zessin, 1983	1983
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Zessinia borealis*	Cretaceous	UK (Lulworth Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Zessinia pulcherrima*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1990	1990
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Zessinia reticulata*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1990	1990
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Zeunerella amedegnatoi*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1998)	1998
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Zeunerella arborea*	Cretaceous	Kazakhstan	Sharov, 1968	1968
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Zeunerella mecklenburgica*	Jurassic	Germany (Dobbertin)	(Zessin, 1983)	1983
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Zeunerelle neotropica*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1998)	1998
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Zeunerella prior*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006

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Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustrix audax*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2003	2003
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustrix gallegoi*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2003	2003
Caelifera	Acrididea		Locustopsoidea	Locustopsidae	Pseudoacridinae	*Aestuacrida mikronaulion*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Heads, Pinheiro & Husemann, 2025	2025
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Aestuacrida stereofemoris*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025	2025
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Auroralocusta restituta*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, 2025	2025
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Pseudoacrida costata*	Cretaceous	China (Liupanshan Basin)	Lin, 1982	1982
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Pseudoacrida eumastacoimima*	Cretaceous	Brasil (Crato Formation)	Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, 2025	2025
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Pseudoacrida sennlaubi*	Cretaceous	Brasil (Crato Formation)	Nel & Jouault, 2022	2022
Caelifera	Acrididea		Locustopsoidea	Locustopsidae	-	*Liadolocusta auscultans*	Jurassic	UK	Handlirsch, 1906	1906
Caelifera	Acrididea		Locustopsoidea	Locustopsidae	-	*Liadolocusta ornata*	Jurassic	Germany	Bode, 1953	1953
Caelifera	Acrididea		Locustopsoidea	Locustopsidae		*Locustopsites gigantea*	?	?	Théobald, 1937	1937
Caelifera	Acrididea		Proscopioidea	Proscopiidae		*Eoproscopia martilli*	Cretaceous	Brasil (Crato Formation)	Heads, 2008	2008
Caelifera	Acrididea		Proscopioidea	Proscopiidae		*Eoproscopia reliquum*	Cretaceous	Brasil (Crato Formation)	Mendes, Lopes de Vasconcelos & Bezerra de Oliveira, 2019	2019
Caelifera	Acrididea		Pyrgomorphoidea	Pyrgomorphidae	Pyrgomorphinae	*Miopyrgomorpha fischeri*	Miocene	Germany (Oeningen)	(Heer, 1865)	1865
Caelifera	Acrididea	-	Tetrigoidea	Tetrigidae	Batrachideinae	*Archaeoarmatus messelensis*	Eocene	Germany (Messel Formation)	Kasalo, Skejo, Tumbrinck, Wedmann & Husemann, 2024	2024
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Eotetrix unicornis*	Eocene	USA (Green River Formation)	Gorochov, 2012	2012
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Tettigidea gracilis*	Miocene	Germany (Oeningen)	(Heer, 1865)	1865
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Danatettix hoffeinsorum*	Eocene	Russia (Baltic amber)	Thomas, Skejo and Heads, 2019	2019
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Messeltettix cryptoantennatus*	Eocene	Germany (Messel Formation)	Kasalo, Skejo, Tumbrinck, Wedmann & Husemann, 2024	2024
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Rusmithia gorochovi*	Eocene	Russia (Baltic amber)	Skejo, Kasalo, Thomas & Heads, 2023	2023
Caelifera	Acrididea		Tetrigoidea	Tetrigidae	Metrodorinae	*Antillotettix electrum*	Miocene	Dominican Republic (Dominican amber)	Heads, 2009	2009
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Baeotettix lottiae*	Miocene	Dominican Republic (Dominican amber)	Heads, 2009	2009
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Electrotettix attenboroughi*	Miocene	Dominican Republic (Dominican amber)	Heads & Thomas, 2014	2014
Caelifera	Acrididea		Tetrigoidea	Tetrigidae	Tetriginae	*Succinotettix bachofeni*	?	?	(Zeuner, 1937)	1937
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Succinotettix chopardi*	Eocene	Russia (Baltic amber)	Piton, 1938	1938
Caelifera	Acrididea		Tetrigoidea	Tetrigidae	-	*Archaeotetrix locustopseiformis*	Cretaceous	Russia (Zaza Formation)	Sharov, 1968	1968
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Eozaentetrix furi*	Eocene	Denmark (Moler Formation)	Zessin, 2017	2017
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Eozaentetrix wittecki*	Eocene	Denmark (Moler Formation)	Zessin, 2017	2017
Caelifera	Acrididea		Tetrigoidea	Tetrigidae		*Prototetrix reductus*	Cretaceous	Russia (Zaza Formation)	Sharov, 1968	1968

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Caelifera	Tridactylidea		Dzhajloutshelloidea	Dzhajloutshellidae		*Adzhajloutshella plana*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Tridactylidea		Dzhajloutshelloidea	Dzhajloutshellidae		*Adzhajloutshella talis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1994	1994
Caelifera	Tridactylidea		Dzhajloutshelloidea	Dzhajloutshellidae		*Dzhajloutshella arcanum*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1994	1994
Caelifera	Tridactylidea		Dzhajloutshelloidea	Dzhajloutshellidae		*Dzhajloutshella flexuosa*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Tridactylidea		Dzhajloutshelloidea	Dzhajloutshellidae		*Triassoxya novozhilovi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Caelifera	Tridactylidea		Dzhajloutshelloidea	Regiatidae		*Micromacula gracilis*	Jurassic	UK (Shales with Beef Formation)	Whalley, 1985	1985
Caelifera	Tridactylidea		Dzhajloutshelloidea	Regiatidae		*Protochaeta lanceolata*	Jurassic	Germany (Dobbertin)	(Handlirsch, 1939)	1939
Caelifera	Tridactylidea		Dzhajloutshelloidea	Regiatidae		*Protochaeta masculina*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Caelifera	Tridactylidea		Dzhajloutshelloidea	Regiatidae		*Regiata scutra*	Jurassic	UK (Charmouth Mudstone Formation)	Whalley, 1985	1985
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Abaddonella nwarrngaal*	Cretaceous	Myanmar (Burmese amber)	Schall, Heads & Husemann, 2025	2025
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Ciconipteryx bidactylus*	Cretaceous	Myanmar (Burmese amber)	Schall, Cao & Husemann, 2025	2025
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Mirhipipteryx antillarum*	Miocene	Dominican Republic (Dominican amber)	Heads, 2010	2010
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Ozymandipteryx campana*	Cretaceous	Myanmar (Burmese amber)	Schall, Cao & Husemann, 2025	2025
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Yakkhapipteryx gracilis*	Cretaceous	Myanmar (Burmese amber)	Gu, Zheng, Cao & Yue, 2022	2022
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Yakkhapipteryx mirus*	Cretaceous	Myanmar (Burmese amber)	Gu, Zheng, Cao & Yue, 2022	2022
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Archaicaripipteryx burmensis*	Cretaceous	Myanmar (Burmese amber)	Zhu, Li, Xu, Jarzembowski, Fang & Zhang, 2023	2023
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Archaicaripipteryx rotunda*	Cretaceous	Myanmar (Burmese amber)	Xu, Zhang, Jarzembowski & Fang, 2020	2020
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Burmaripipteryx oblongus*	Cretaceous	Myanmar (Burmese amber)	Zhao, Xu, Jarzembowski, Fang & Xiao, 2023	2023
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Kallosripipteryx zhangi*	Cretaceous	Myanmar (Burmese amber)	Zhao, Xu, Cao, Jarzembowski, Fang & Xiao, 2024	2024
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Magnidactylus robustus*	Cretaceous	Myanmar (Burmese amber)	Xu, Fang & Jarzembowski, 2020	2020
Caelifera	Tridactylidea		Tridactyloidea	Ripipterygidae		*Naginipteryx pinna*	Cretaceous	Myanmar (Burmese amber)	Schall, Heads & Husemann, 2025	2025
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Archaeoellipes engeli*	Miocene	Dominican Republic (Dominican amber)	Heads, 2010	2010
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Cascogryllus lobiferus*	Cretaceous	Myanmar (Burmese amber)	Poinar, 2020	2020
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Cascogryllus setosus*	Cretaceous	Myanmar (Burmese amber)	Du, Xu & Zhang, 2021	2021
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Cratodactylus ferreirai*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1990	1990

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Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Cratodactylus kellneri*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1990	1990
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Hiemalidactylus eileenae*	Cretaceous	Myanmar (Burmese amber)	Schall, Gu & Husemann, 2025	2025
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Ellipes dominicana*	Miocene	Dominican Republic (Dominican amber)	Poinar, 2020	2020
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Latedactylus longapedi*	Cretaceous	Myanmar (Burmese amber)	Zheng, Cao & Gu, 2023	2023
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Tridactylinae	*Phyllotridactylus wangi*	Cretaceous	Myanmar (Burmese amber)	Xu, Wang, Fan, Jarzembowski, Fang, Wang, Li, Zhuo, Ding & Engel, 2021	2021
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Dentridactylinae	*Burmadactylus grimaldii*	Cretaceous	Myanmar (Burmese amber)	Heads, 2009	2009
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Dentridactylinae	*Burmadactylus tenuicerci*	Cretaceous	Myanmar (Burmese amber)	Fan, Gu & Cao, 2023	2023
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Dentridactylinae	*Guntheridactylus grimaulti*	Eocene	France (Argiles d'lignite du Soissonnais Formation)	Azar & Nel, 2008	2008
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Mongoloxyinae	*Baisoxya dolichopterus*	Cretaceous	Russia (Zaza Formation)	(Sharov, 1968)	1968
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Mongoloxyinae	*Birmitoxya intermedia*	Cretaceous	Myanmar (Burmese amber)	Gorochov, 2010	2010
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Mongoloxyinae	*Cretoxya rasnitsyni*	Cretaceous	UK (Lulworth Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Mongoloxyinae	*Mongoloxya fossor*	Cretaceous	Russia (Khasurty)	Gorochov, 2021	2021
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Mongoloxyinae	*Mongoloxya ponomarenkoi*	Cretaceous	Mongolia (Dzun Bain Formation)	Gorochov, 1992	1992
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	Mongoloxyinae	*Monodactyloides curtipennis*	Cretaceous	Russia (Zaza Formation)	Sharov, 1968	1968
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	-	*Amberotridactylus cheni*	Cretaceous	Myanmar (Burmese amber)	Du, Xu & Zhang, 2021	2021
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	-	*Duappendactylus melanocephalus*	Cretaceous	Myanmar (Burmese amber)	Schall, Gu & Husemann, 2025	2025
Caelifera	Tridactylidea		Tridactyloidea	Tridactylidae	-	*Paraxya hui*	Cretaceous	Myanmar (Burmese amber)	Cao, Chen & Yin, 2019	2019
Ensifera	Elcanidea		Elcanoidea	Elcanidae	Elcaninae	*Argentoelcana intermedia*	Cretaceous	Brasil (Crato Formation)	Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Cratoelcana zessini*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Elcanodentes alatus*	Cretaceous	Myanmar (Burmese amber)	Willmott, Schall, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Elcanodentes cretaceus*	Cretaceous	Myanmar (Burmese amber)	Willmott, Schall, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Elcanodentes thanatos*	Cretaceous	Myanmar (Burmese amber)	Schall, Willmott, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Ellca nevelka*	Cretaceous	Myanmar (Burmese amber)	Kočárek, 2020	2020
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Ensiferelcana brachyptera*	Cretaceous	Brasil (Crato Formation)	Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Eubaisselcana mongolica*	Cretaceous	Mongolia (Gurvan Eren Formation)	Gorochov, 1986	1986
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Eubaisselcana sharovi*	Cretaceous	Mongolia (Gurvan Eren Formation)	Gorochov, 1986	1986

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Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Gondwanaelcana brasiliensis*	Cretaceous	Brasil (Crato Formation)	Schall, Heads, Lima, Pinheiro, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Kolymbelcana phantasma*	Cretaceous	Myanmar (Burmese amber)	Schall, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Mesembrelcana rasnitsyni*	Cretaceous	Brasil (Crato Formation)	(Nel & Jouault, 2022)	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Minelcana dubia*	Cretaceous	UK (Lulworth Formation)	(Giebel, 1856)	1856
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Minelcana membranacea*	Cretaceous	UK (Durlston Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium acusicaudum*	Cretaceous	China (Yixian Formation)	Tian, Ren & Gu, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium angustior*	Triassic (?)	UK	(Handlirsch, 1939)	1939
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium beyrichi*	Cretaceous	UK	(Giebel, 1856)	1856
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium bimaculatum*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium damianii*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1991)	1991
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium lata*	Jurassic	Kazakhstan (Karabastau Formation)	(Sharov, 1968)	1968
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium liasinum*	Triassic (?)	UK (Lilstock Formation)	(Giebel, 1856)	1856
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium lithophilum*	Jurassic	Germany (Solnhofen)	(Germar, 1842)	1842
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium longicorne*	Jurassic	Germany (Solnhofen)	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium minutum*	Jurassic	Kazakhstan (Karabastau Formation)	(Sharov, 1968)	1968
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium oppenheimi*	Jurassic	Germany (Solnhofen)	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium parvum*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium proximum*	Cretaceous	UK (Durlston Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium sibiricum*	Cretaceous	Russia (Zaza Formation)	(Sharov, 1968)	1968
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium spica*	Cretaceous	South Korea (Jinju Formation)	Kim, Lee, Nam & Park, 2021	2021
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium tesselatum*	Cretaceous	UK (Durlston Formation)	Westwood, 1854	1854
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium validum*	Cretaceous	China (Yixian Formation)	Tian, Ren & Gu, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium westwoodi*	Cretaceous	UK (Lulworth Formation)	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Panorpidium yixianensis*	Cretaceous	China (Yixian Formation)	Fang, Wang, Zhang, Wang, Jarzembowski, Zheng, Zhang, Lia & Liu, 2015	2015
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Paraxelcana simplicissima*	Cretaceous	Myanmar (Burmese amber)	(Schall, Kotthoff & Husemann, 2025)	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Paraxelcana zhengi*	Cretaceous	Myanmar (Burmese amber)	(Gu, Tian & Ren, 2022)	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Probaisselcana cretacea*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Probaisselcana euryptera*	Cretaceous	China (Yixian Formation)	Tian, Gu & Ren, 2019	2019
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Probiasselcana kachinensis*	Cretaceous	Myanmar (Burmese amber)	Zhou, Xu & Xiao, 2024	2024

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Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Probaisselcana karatavica*	Jurassic	Kazakhstan (Karabastau Formation)	(Sharov, 1968)	1968
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Probaisselcana minuta*	Cretaceous	China (Yixian Formation)	Gu, Tian & Ren, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Probaisselcana plagiata*	Jurassic	Switzerland (Insektenmergel Formation)	(Hagen, 1858)	1858
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Pseudopanorpidium maculosum*	Cretaceous	Myanmar (Burmese amber)	Zhou, Xu, Jarzembowski & Xiao, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Pseudopanorpidium inversa*	Cretaceous	Myanmar (Burmese amber)	Schall, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Pseudoprobaisselcana oculata*	Cretaceous	Myanmar (Burmese amber)	(Hu & He, 2023)	2023
Ensifera	Elcanidea		Elcanoidea	Elcanidae	Archelcaninae	*Archelcana britannica*	Jurassic	UK	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana durnovaria*	Jurassic	UK (Charmouth Mudstone Formation)	Whalley, 1985	1985
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana geinitzi*	Jurassic	Germany (Dobbertin)	(Heer, 1880)	1880
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana magna*	Jurassic	Germany (Dobbertin)	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana media*	Jurassic	Germany (Dobbertin)	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana minima*	Jurassic	Germany (Dobbertin)	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana numbergerae*	Jurassic	Luxembourg	Heads, Thuy & Tamarri, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana ornata*	Jurassic	Russia (Cheremkhovskaya Formation)	Zherikhin, 1985	1985
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana phyllophora*	Jurassic	Germany (Solnhofen)	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana shurabica*	Jurassic	Kyrgyzstan (Sagul Formation)	Sharov, 1968	1968
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Archelcana tina*	Jurassic	Luxembourg	Heads, Thuy & Tamarri, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Caelielca spinocrus*	Cretaceous	Myanmar (Burmese amber)	Uchida, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Cascadelcana virginiana*	Triassic	USA (Cow Branch Formation)	Fang, Muscente, Heads, Wang & Xiao, 2018	2018
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Hispanelcana alavensis*	Cretaceous	Spain (Escucha Formation)	Peñalver & Grimaldi, 2010	2010
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Hispanelcana arilloi*	Cretaceous	Spain (Escucha Formation)	Peñalver & Grimaldi, 2010	2010
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Hispanelcana lopezvallei*	Cretaceous	Spain (Escucha Formation)	Peñalver & Grimaldi, 2010	2010
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Hukawnelca gracilis*	Cretaceous	Myanmar (Burmese amber)	Uchida, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Jeholelcana deichmuelleri*	Jurassic	Germany (Solnhofen)	(Handlirsch, 1906)	1906
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Jeholelcana yanensis*	Cretaceous	China (Yixian Formation)	Fang, Heads, Wang, Zhang & Wang, 2018	2018
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Longioculus burmensis*	Cretaceous	Myanmar (Burmese amber)	Poinar, Gorochov & Buckley, 2007	2007
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Longioculus poinari*	Cretaceous	Myanmar (Burmese amber)	Schall & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Parelcana anglicana*	Jurassic	UK	Handlirsch, 1939	1939
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Parelcana dubia*	Triassic/Jurassic	UK	Handlirsch, 1939	1939
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Parelcana pulchmacula*	Jurassic	China (Daohugou Formation)	Tian, Gu, Yin & Ren, 2019	2019
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Parelcana tenuis*	Jurassic	Germany (Dobbertin)	Handlirsch, 1906	1906

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Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Parelcana xena*	Cretaceous	Myanmar (Burmese amber)	Schall & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Sibelcana rossica*	Jurassic	Russia (Glushkovo Formation)	Gorochov, 1990	1990
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Sibelcana transbaicalica*	Jurassic	Russia (Ukurei Formation)	Gorochov, 1990	1990
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Sibelcana websteri*	Cretaceous	UK (Durlston Formation)	Gorochov & Coram, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Sinoelcana minuta*	Jurassic	China (Daohugou Formation)	Gu, Tian, Wang & Yue, 2020	2020
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Synelcana muelleri*	Jurassic	Germany (Dobbertin)	Zessin, 1988	1988
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Thagyaminana atawedeia*	Cretaceous	Myanmar (Burmese amber)	Schall, Kotthoff & Husemann, 2025	2025
Ensifera	Elcanidea		Elcanoidea	Elcanidae	-	*Cenoelcanus menatensis*	Paleocene	France (Menat Formation)	Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020	2020
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Elcanonympha diana*	Cretaceous	Myanmar (Burmese amber)	Heads & Thomas, 2018	2018
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Elcanopsis sydneiensis*	Permian (?)	Australia	Tillyard, 1918	1918
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Letoelcana artemisapollonque*	Cretaceous	Myanmar (Burmese amber)	Schall, Kotthoff & Husemann, 2023	2023
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Liaonemobius tanae*	Cretaceous	China (Yixian Formation)	Ren, 1998	1998
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Macrelcana ungeri*	Miocene	Croatia (Radoboj)	(Heer, 1849)	1849
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Monitelcana penalveri*	Cretaceous	Myanmar (Burmese amber)	Xu, Luo, Jarzembowski, Fang & Wang, 2022	2022
Ensifera	Elcanidea		Elcanoidea	Elcanidae		*Trigonelca jennywinterae*	Cretaceous	Myanmar (Burmese amber)	Schall, Kotthoff & Husemann, 2023	2023
Ensifera	Elcanidea		Elcanoidea	Permelcanidae	Meselcaninae	*Meselcana madygenica*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Elcanidea		Elcanoidea	Permelcanidae		*Meselcana permelcanoides*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Elcanidea		Elcanoidea	Permelcanidae		*Meselcana udmurtica*	Permian	Russia	Gorochov, 2013	2013
Ensifera	Elcanidea		Elcanoidea	Permelcanidae		*Meselcana vologodica*	Permian	Russia (Poldarsa Formation)	Gorochov, 2013	2013
Ensifera	Elcanidea		Elcanoidea	Permelcanidae	Permelcaninae	*Permelcana sojanense*	Permian	Russia (Iva-Gora Beds Formation)	Sharov, 1962	1962
Ensifera	Elcanidea		Elcanoidea	Permelcanidae		*Proelcana kukalovae*	Permian	Russia (Koshelevka Formation)	(Sharov, 1968)	1968
Ensifera	Elcanidea		Elcanoidea	Permelcanidae		*Proelcana uralica*	Permian	Russia (Koshelevka Formation)	Sharov, 1962	1962
Ensifera	Elcanidea		Elcanoidea	Permelcanidae		*Promartynovia venicosta*	Permian	Kansas (Wellington Formation)	Tillyard, 1937	1937
Ensifera	Elcanidea		Elcanoidea	Permelcanidae	-	*Saarelcana stapsi*	Permian	Germany (Meisenheim Formation)	Poschmann, Nel & Raisch, 2023	2023
Ensifera	Elcanidea		Elcanoidea	Permelcanidae		*Sinelcana azari*	Permian	China (Yinping Formation)	Gu, Tian, Wang & Yue, 2020	2020
Ensifera	Elcanidea		Elcanoidea	-		*Acridiites liasinus*	Jurassic	Switzerland (Insektenmergel Formation)	Heer, 1865	1865
Ensifera	Elcanidea		Elcanoidea	-		*Acridomima deperdita*	Jurassic	Switzerland (Insektenmergel Formation)	(Heer, 1865)	1865
Ensifera	Elcanidea		Permoraphidioidea	Permoraphidiidae		*Permoraphidia americana*	Permian	Kansas (Wellington Formation)	Tillyard, 1932	1932

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Ensifera	Elcanidea		Permoraphidioidea	Permoraphidiidae		*Permoraphidia grandis*	Permian	Kansas (Wellington Formation)	Carpenter, 1943	1943
Ensifera	Elcanidea		Permoraphidioidea	Permoraphidiidae		*Permoraphidia magnifica*	Permian	Madagascar	Béthoux & Nel, 2002	2002
Ensifera	Elcanidea		Permoraphidioidea	Pseudelcanidae		*Pseudelcana permiana*	Permian	Russia (Koshelevka Formation)	Gorochov, 1987	1987
Ensifera	Elcanidea		Permoraphidioidea	Pseudelcanidae		*Pseudelcana uralensis*	Permian	Russia (Koshelevka Formation)	Gorochov, 1987	1987
Ensifera	Elcanidea		Permoraphidioidea	Thueringoedischiidae		*Hymenelcana initialis*	Permian	New Mexico (Bursum Formation)	Gorochov, 2004	2004
Ensifera	Elcanidea		Permoraphidioidea	Thueringoedischiidae		*Permoedischia moravica*	Permian	Czech Republic (Padochov Formation)	Kukalová-Peck, 1955	1955
Ensifera	Elcanidea		Permoraphidioidea	Thueringoedischiidae		*Thueringoedischia trostheidei*	Permian	Germany (Goldlauter Formation)	Zessin, 1997	1997
Ensifera	Oedischiidea		Oedischioidea	Anelcanidae		*Anelcana dilatata*	Permian	Kansas (Wellington Formation)	(Carpenter, 1966)	1966
Ensifera	Oedischiidea		Oedischioidea	Anelcanidae		*Petrelcana elongata*	Permian	Kansas (Wellington Formation)	Carpenter, 1966	1966
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae	Bintoniellinae	*Bintoniella brodiei*	Jurassic	UK	Handlirsch, 1939	1939
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae		*Eubintoniella ferganica*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae	Oshiellinae	*Paroshiella alia*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae		*Probintoniella crassa*	Triassic	Kyrgyzstan (Madygen Formation)	(Gorochov, 1987)	1987
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae		*Probintoniella oblonga*	Triassic	Kyrgyzstan (Madygen Formation)	(Gorochov, 1987)	1987
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae		*Probintoniella triassica*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae		*Stenoshiella angusta*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae	Proshiellinae	*Proshiella ramivenosa*	Triassic	Kyrgyzstan (Madygen Formation)	(Sharov, 1968)	1968
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae		*Provitimia pectinata*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Bintoniellidae	-	*Parabintoniella papierae*	Triassic	France (Grès à Voltzia Formation)	Béthoux & Grauvogel-Stamm, 2022	2022
Ensifera	Oedischiidea		Oedischioidea	Mesoedischiidae		*Mesoedischia kirgizica*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Mesoedischiidae		*Mesoedischia madygenica*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Mesoedischiidae		*Mesoedischia obliqua*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Mesoedischiidae		*Sonoedischia shmakovi*	Triassic	Russia (Maltsevo Formation)	Gorochov, 2005	2005
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae	Elcanoedischiinae	*Elcanoedischia major*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Elcanoedischia minor*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987

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Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Kansasoedischia maculata*	Permian	Kansas (Wellington Formation)	(Carpenter, 1966)	1966
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Metoedischia kamensis*	Permian	Russia (Baitugan Formation)	Martynov, 1928	1928
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Metoedischia magnifica*	Permian	Russia (Iva-Gora Beds Formation)	Martynov, 1928	1928
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae	Mezenoedischiinae	*Mezenoedischia maculosa*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Mezenoedischia martynovi*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Pseudoiasvia sinuosa*	Permian	Oklahoma (Wellington Formation)	Béthoux & Beckemeyer, 2007	2007
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Uraloedischia permiensis*	Permian	Russia (Koshelevka Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae	Oedischiinae	*Anhomalophlebia couloni*	Carboniferous	France (Commentry Shale Formation)	(Meunier, 1911)	1911
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Lusitadischia sai*	Carboniferous	Portugal (Douro Carboniferous Basin)	Correia & Nel, 2022	2022
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Oedischia williamsoni*	Carboniferous	France (Commentry Shale Formation)	Brongniart, 1885	1885
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Palatinoedischia elongata*	Permian	Germany (Meisenheim Formation)	Nel & Poschmann, 2020	2020
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Iasvia reticulata*	Permian	Russia (Solikamsk Formation)	Zalessky, 1934	1934
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Iasvia secunda*	Permian	France (Salagou Formation)	Béthoux, Nel, Gand, Lapeyrie & Galtier, 2002	2002
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Nobloedischia rasnitsyni*	Permian	Oklahoma (Wellington Formation)	Beckemeyer, 2011	2011
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Plesioidischia baentschi*	Permian	Germany (Lebacher Schichten Formation)	Schlechtendal, 1906	1906
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Rimnosentomon grande*	Permian	Russia (Koshelevka Formation)	Zalessky, 1955	1955
Ensifera	Oedischiidea		Oedischioidea	Oedischiidae		*Sinoedischia carbonica*	Permian	China (Shanxi Formation)	Hong, 1985	1985
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae	Ademirsoyinae	*Ademirsoyus reductus*	Triassic	Kyrgyzstan (Madygen Formation)	(Sharov, 1968)	1968
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Archifergania isadyensis*	Permian	Russia (Poldarsa Formation)	Gorochov, 2013	2013
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Parafergania sharovi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae	Madygeniinae	*Madygenia extremalis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Madygenia longissima*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Madygenia orientalis*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Madygenia ovalis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Platymadygenia grandis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987

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Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae	Oedischimiminae	*Oedischimima deficientis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae	Proparagryllacridinae	*Dordrechtia aasvoelbergensis*	Triassic	South Africa (Molteno Formation)	Wappler, 2001	2001
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Dordrechtia robusta*	Triassic	South Africa (Molteno Formation)	Riek, 1976	1976
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Gryllacrimima abscisa*	Triassic	Kyrgyzstan (Madygen Formation)	(Gorochov, 1987)	1987
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Gryllacrimima johnski*	Triassic	South Africa (Molteno Formation)	Wappler, 2001	2001
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Gryllacrimima perfecta*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Mesogryllacris giganteus*	Triassic	Australia	Riek, 1955	1955
Ensifera	Oedischiidea		Oedischioidea	Proparagryllacrididae		*Proparagryllacris crassifemur*	Triassic	Australia (Blackstone Formation)	Riek, 1956	1956
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae	Kamiinae	*Adumbratus curtus*	Permian	Russia (Mitina Formation)	Sharov, 1961	1961
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Adumbratus extentus*	Permian	Russia (Mitina Formation)	Sharov, 1961	1961
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Kamia angustovenosa*	Permian	Russia (Baitugan Formation)	Martynov, 1928	1928
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Raphogla rubra*	Permian	France (Salagou Formation)	Béthoux, Nel, Lapeyrie, Gand & Galtier, 2002	2002
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae	Kargalariinae	*Eukargalaria parallela*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Kargalaria maculata*	Permian	Russia (Amanak Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae	Maculoedischiinae	*Maculoedischia abnormis*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Maculoedischia sojanensis*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Vologdoptera maculata*	Permian	Russia (Poldarsa Formation)	Aristov, 2009	2009
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae	Pruvostitinae	*Kitjakoedischia pruvostitoides*	Permian	Russia (Belebeevo Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Paroedischia recta*	Permian	Kansas (Wellington Formation)	Carpenter, 1966	1966
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Pruvostites takhtachurensis*	Permian	Russia (Kazan Formation)	Zalessky, 1928	1928
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Sharovoedischia aberrans*	Permian	Russia (Koshelevka Formation)	(Sharov, 1968)	1968
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Sojanoedischia sharovi*	Permian	Russia (Iva-Gora Beds Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Suchonoedischia incompleta*	Permian	Russia (Poldarsa Formation)	Gorochov, 2013	2013
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Suksonoedischia breviuscula*	Permian	Russia (Koshelevka Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Tshekardoedischia ancestralis*	Permian	Russia (Koshelevka Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae	Sylvoedischiinae	*Stenoedischia sylvensis*	Permian	Russia (Koshelevka Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Sylvoedischia circummaculosa*	Permian	Russia (Lek-Vortuka Formation)	(Aristov, 2005)	2005

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Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Sylvoedischia crassa*	Permian	Russia (Koshelevka Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Sylvoedischia curvovenosa*	Permian	Russia (Iva-Gora Beds Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Sylvoedischia uralica*	Permian	Russia (Koshelevka Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae	Tettavinae	*Tettavus fenestrata*	Permian	Russia (Baitugan Formation)	(Martynov, 1930)	1930
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Crinoedischia buttsi*	Permian	Kansas (Wellington Formation)	Béthoux & Beckemeyer, 2007	2007
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Crinoedischia lapeyriei*	Permian	France (Salagou Formation)	Rodrigues Fernandes, Prokop &Nel, 2014	2014
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Crinoedischia noblensis*	Permian	Oklahoma (Wellington Formation)	Béthoux & Beckemeyer, 2007	2007
Ensifera	Oedischiidea		Oedischioidea	Pruvostitidae		*Loxoedischia drewi*	Permian	Oklahoma (Wellington Formation)	Beckemeyer, 2011	2011
Ensifera	Oedischiidea		Triassomantoidea	Adumbratomorphidae		*Adumbratomorpha tettigonioides*	Permian	Russia (Koshelevka Formation)	Gorochov, 1987	1987
Ensifera	Oedischiidea		Triassomantoidea	Triassomantidae		*Triassomantis pygmaeus*	Triassic	Australia (Blackstone Formation)	Tillyard, 1922	1922
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae	Axenopterinae	*Axenopterum venosum*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Triassomanteodes madygenicus*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Xenoferganella pini*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae	Ferganopterinae	*Ferganopterodes reductus*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Ferganopterus clarus*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Ferganopterus longus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Ferganotriassia lata*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Permoxenopterum laticostum*	Permian	South Africa (Estcourt Formation)	van Dijk & Gorochov, 2011	2011
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Pseudoferganopsis zini*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Pteroferganella crassa*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Pteroferganella minuta*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Pteroferganella sharovi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Pteroferganodes decipiens*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Pteroferganodes rieki*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989

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Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae	Xenopterinae	*Lutheria dewetii*	Triassic	South Africa (Molteno Formation)	Wappler, 2001	2001
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Proxenopterum primitivum*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Triassoferganella angusta*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1989	1989
Ensifera	Oedischiidea		Xenopteroidea	Xenopteridae		*Xenopterum crosbyi*	Triassic	Australia	Riek, 1955	1955
Ensifera	Oedischiidea		-	Permotettigoniidae		*Permotettigonia gallica*	Permian	France (Cians Formation)	Nel & Garrouste, 2016	2016
Ensifera	Oedischiidea			-		*Permophyllum rotundatum*	Permian	France (Salagou Formation)	Prokop, Szwedo, Lapeyrie, Garrouste & Nel, 2015	2015
Ensifera	-		Gryllavoidea	Gryllavidae	Gryllavinae	*Galliagryllavus vogesiacus*	Triassic	France (Grès à Voltzia Formation)	Marchal-Papier, Nel & Grauvogel-Stamm, 2000	2000
Ensifera			Gryllavoidea	Gryllavidae		*Gryllavus madygenicus*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera			Gryllavoidea	Gryllavidae		*Paragryllavus curvatus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera			Gryllavoidea	Gryllavidae		*Zagryllavus elongatus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera			-	Palaeorehniidae		*Albertoilus cervirufi*	Paleocene	Canada (Paskapoo Formation)	Kevan & Wighton, 1981	1981
Ensifera			-	Palaeorehniidae		*Palaeorehnia maculata*	Eocene	Colorado (Florissant Formation)	(Scudder, 1890)	1890
Ensifera			-	Palaeorehniidae		*Republicopteron douseae*	Eocene	Washington (Klondike Mountain Formation)	Archibald, Gu & Mathewes, 2022	2022
Ensifera			-	Palaeorehniidae		*Ypopteron nicola*	Eocene	Canada (Tranquille Formation)	Archibald, Gu & Mathewes, 2022	2022
Ensifera			-	Palaeorehniidae		*Zeuneroptera scotica*	Paleocene	UK (interbasaltic plant-beds Formation)	(Zeuner, 1939)	1939
Ensifera			-	Vitimiidae		*Deinovitimia insolita*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1989	1989
Ensifera			-	Vitimiidae		*Deinovitimia occidentalis*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera			-	Vitimiidae		*Vitimia evoluta*	Cretaceous	Russia (Zaza Formation)	Sharov, 1968	1968
Ensifera			-	-		*Falsirameus ravus*	Cretaceous	China (Laiyang Formation)	Zhang, 1985	1985
Ensifera			-	-		*Gryllobencain patrickmuelleri*	Cretaceous	Myanmar (Burmese amber)	Haug, Hörnig, Kiesmüller, Pazinato, Baranov & Haug, 2022	2022
Ensifera			-	-		*Liassogrylloides basifastigatus*	Jurassic	Germany (Posidonia Shale Formation)	Bode, 1953	1953
Ensifera			-	-		*Thnetus stuckenbergi*	Permian	Russia	Handlirsch, 1904	1904
Ensifera			-	-		*Yuxiania jurassica*	Jurassic	China (Houcheng Formation)	Hong, 1997	1997
Ensifera	Gryllidea		Grylloidea	Baissogryllidae	Baissogryllinae	*Baissogryllus sharovi*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1985	1985
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Baissogryllus sibiricus*	Cretaceous	Russia (Zaza Formation)	Sharov, 1968	1968
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Eubaissogryllus vitimicus*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1985	1985
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Ponomarenkoana probontzagania*	Jurassic	Mongolia (Sharteg Formation)	Gorochov, 1992	1992

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Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Sinagryllus xinjiangensis*	Jurassic	China (Sangonghe Formation)	Wang, Fang, Fang & Jarzembowski, 2019	2019
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Speculogryllus acutispeculum*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Storozhenkoana parvispeculum*	Jurassic	Mongolia (Sharteg Formation)	Gorochov, 1992	1992
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Transigryllus edmundi*	Cretaceous	UK (Weald Clay Formation)	Gorochov & Coram, 2022	2022
Ensifera	Gryllidea		Grylloidea	Baissogryllidae	Bontzaganiinae	*Anglogryllus lyristes*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Anglogryllus rotundispeculum*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Bontzagania perfecta*	Cretaceous	Mongolia (Dzun Bain Formation)	Gorochov, 1985	1985
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Castillogryllus complicatus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1995	1995
Ensifera	Gryllidea		Grylloidea	Baissogryllidae	Cearagryllinae	*Allocearagryllus leipnitzi*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 2002)	2002
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Cearagrylloides microcephalus*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1991)	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Cearagrylloides perforatorius*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1991)	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Cearagrylloides previstus*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1999)	1999
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Cearagryllus gorochovi*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Cearagryllus monstruosus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Cearagryllus robustus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Cryptocearagryllus revelatus*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1999)	1999
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Notocearagryllus arturandradai*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2009	2009
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Notocearagryllus britannicus*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Notocearagryllus cordispeculum*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Notocearagryllus dutrae*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1999	1999
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Notocearagryllus grandispeculum*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Paracearagryllus poliacanthus*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1991)	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Santanagryllus hesselae*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae	Olindagryllinae	*Olindagryllus obliteratus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1999	1999
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Olindagryllus rotundus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1999	1999
Ensifera	Gryllidea		Grylloidea	Baissogryllidae	Sharategiinae	*Caririgryllus arthaudi*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Caririgryllus brachypterus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2002	2002
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Caririgryllus elongatus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Caririgryllus mesai*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Caririgryllus pilosus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Mongologryllus martynovi*	Cretaceous	Mongolia (Dzun Bain Formation)	Gorochov, 1985	1985
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Neosharategia paradoxa*	Jurassic	Mongolia (Sharteg Formation)	Gorochov, 1992	1992

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Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Sharategia baldocki*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Sharategia batchelorae*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Sharategia davisi*	Cretaceous	UK (Durlston Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Gryllidea		Grylloidea	Baissogryllidae		*Sharategia rasnitsyni*	Jurassic	Mongolia (Sharteg Formation)	Gorochov, 1992	1992
Ensifera	Gryllidea		Grylloidea	Gryllidae	Gryllinae	*Gryllus fuchsi*	Miocene	Croatia (Radoboj)	Handlirsch, 1907	1907
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Gryllus vociferans*	Paleocene	Argentina (Margas Verdes Formation)	Cockerell, 1925	1925
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Eogryllus elongatus*	Eocene	Colorado (Green River Formation)	Gorochov, 2012	2012
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Eogryllus unicolor*	Eocene	Colorado (Green River Formation)	Gorochov, 2012	2012
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Pronemobius induratus*	Eocene	Wyoming (Green River Formation)	Scudder, 1890	1890
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Pronemobius ornatipes*	Eocene	Colorado (Green River Formation)	Cockerell, 1921	1921
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Pronemobius tertiarius*	Eocene	Wyoming (Green River Formation)	(Scudder, 1878)	1878
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Burmagryllotalpa longa*	Cretaceous	Myanmar (Burmese amber)	Wang, Lei, Zhang, Xu, Fang & Zhang, 2019	2019
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Chunxiania fania*	Cretaceous	Myanmar (Burmese amber)	Xu, Wang & Fang, 2022	2022
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Pherodactylus micromorphus*	Cretaceous	Myanmar (Burmese amber)	Poinar, Su & Brown, 2020	2020
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Pherodactylus rectanguli*	Cretaceous	Myanmar (Burmese amber)	(Xu, Fang & Wang, 2020)	2020
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Ontogryllus oligocenus*	Eocene	UK (Bouldnor Formation)	(Cockerell, 1921)	1921
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Ontogryllus rossi*	Eocene	UK (Bouldnor Formation)	Gorochov, 2019	2019
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Ontogryllus vetus*	Eocene	UK (Bouldnor Formation)	(Cockerell, 1921)	1921
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Araripegryllus camposae*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1987	1987
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Araripegryllus femininus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Araripegryllus marianoi*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Araripegryllus megacephalus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Araripegryllus nanus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Araripegryllus romualdoi*	Cretaceous	Brasil (Romualdo Formation)	Freitas, de Moura & Saraiva, 2016	2016
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Araripegryllus serrilhatus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Araripegryllus spinosus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Gryllospeculum mongolicum*	Cretaceous	Mongolia (Dzun Bain Formation)	Gorochov, 1985	1985
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Mongolospeculum minutum*	Cretaceous	Mongolia (Dzun Bain Formation)	Gorochov, 1985	1985
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Proararipegryllus andrewi*	Cretaceous	UK (Weald Clay Formation)	Gorochov & Coram, 2022	2022

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Ensifera	Gryllidea		Grylloidea	Gryllidae		*Proararipegryllus orientalis*	Cretaceous	UK (Weald Clay Formation)	(Gorochov, Jarzembowski & Coram, 2006)	2006
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Cratogryllus cigueli*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Cratogryllus guimaraesae*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Cratogryllus pentagonalis*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Sharovella caucasica*	?	Russia	(Sharov, 1968)	1968
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Trichogryllus macrocercus*	Eocene	Poland (Baltic amber)	(Germar & Berendt, 1856)	1856
Ensifera	Gryllidea		Grylloidea	Gryllidae	Eneopterinae	*Brontogryllus excelsus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Proecanthus anatolicus*	Cretaceous	Kazakhstan	Sharov, 1968	1968
Ensifera	Gryllidea		Grylloidea	Gryllidae	Pentacentrinae	*Apentacentrus copalicus*	Holocene	Tanzania (amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Eopentacentrus borealis*	Eocene	Russia (Baltic amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Grossoxipha feminea*	Miocene	Dominican Republic (Dominican amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Grossoxipha yaque*	Miocene	Dominican Republic (Dominican amber)	Vickery & Poinar, 1994	1994
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Proanaxipha bicolorata*	Miocene	Dominican Republic (Dominican amber)	Vickery & Poinar, 1994	1994
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Proanaxipha latoca*	Miocene	Dominican Republic (La Toca Formation; Dominican amber)	Vickery & Poinar, 1994	1994
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Proanaxipha madgesuttonae*	Miocene	Dominican Republic (Dominican amber)	Heads & Penney, 2012	2012
Ensifera	Gryllidea		Grylloidea	Gryllidae	-	*Achetomorpha irregularis*	Eocene	UK (Bouldnor Formation)	Gorochov, 2019	2019
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Achetomorpha schindewolfi*	Eocene	UK (Bouldnor Formation)	(Zeuner, 1937)	1937
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Eneopterotrypus chopardi*	Eocene	UK (Bouldnor Formation)	Zeuner, 1937	1937
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Fanzus grandis*	Eocene	Germany (Fur Formation)	Zessin, 2019	2019
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Gryllidium oweni*	Cretaceous	UK	Westwood, 1854	1854
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Lithogryllites lutzii*	Eocene	Colorado (Florissant Formation)	Cockerell, 1908	1908
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Menatgryllus longixiphus*	Paleocene	France (Menat Formation)	Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020	2020
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Nanaripegryllus pygmaeus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2002	2002
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Proeneopterotrypus danicus*	Eocene	Denmark (Ølst Formation)	(Rust, 1999)	1999
Ensifera	Gryllidea		Grylloidea	Gryllidae		*Gryllus troglodytes*	Miocene	Germany (Oeningen)	(Heer, 1865)	1865
Ensifera	Gryllidea		Grylloidea	Mogoplistidae	Mogoplistinae	*Ornebius ambericus*	Miocene	Dominican Republic (Dominican amber)	Vickery & Poinar, 1994	1994
Ensifera	Gryllidea		Grylloidea	Mogoplistidae		*Archornebius balticus*	Eocene	Russia (Baltic amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Mogoplistidae		*Pseudarachnocephalus dominicanus*	Miocene	Dominican Republic (Dominican amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Mogoplistidae		*Pseudarachnocephalus latiusuculus*	Miocene	Dominican Republic (Dominican amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Mogoplistidae		*Eomogoplistes longipennis*	Eocene	Colorado (Green River Formation)	Gorochov, 2012	2012
Ensifera	Gryllidea		Grylloidea	Mogoplistidae		*Pteromogoplistes grandis*	Eocene	Colorado (Green River Formation)	Gorochov, 2012	2012

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Ensifera	Gryllidea		Grylloidea	Mogoplistidae		*Pteromogoplistes smithii*	Eocene	Colorado (Green River Formation)	(Scudder, 1890)	1890
Ensifera	Gryllidea		Grylloidea	Mogoplistidae	Protomogoplistinae	*Protomogoplistes asquamosus*	Cretaceous	Myanmar (Burmese amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Oecanthidae	Oecanthinae	*Apiculatus cretaceus*	Cretaceous	Myanmar (Burmese amber)	Yuan, Ma & Gu, 2022	2022
Ensifera	Gryllidea		Grylloidea	Oecanthidae		*Birmanioecanthus haplostichus*	Cretaceous	Myanmar (Burmese amber)	Yuan, Ma & Gu, 2022	2022
Ensifera	Gryllidea		Grylloidea	Oecanthidae		*Crassicorpus maculatus*	Cretaceous	Myanmar (Burmese amber)	Zheng, Yuan & Gu, 2023	2023
Ensifera	Gryllidea		Grylloidea	Oecanthidae	Podoscirtinae	*Madasumma europensis*	Eocene	Russia (Baltic amber)	Chopard, 1936	1936
Ensifera	Gryllidea		Grylloidea	Oecanthidae		*Allopterites multilineatus*	Eocene	UK (Poole Formation)	Cockerell, 1920	1920
Ensifera	Gryllidea		Grylloidea	Oecanthidae		*Stenogryllodes brevipalpis*	Eocene	Russia (Baltic amber)	Chopard, 1936	1936
Ensifera	Gryllidea		Grylloidea	Oecanthidae		*Ordicalcaratus inconditus*	Cretaceous	Myanmar (Burmese amber)	Zheng, Yuan & Gu, 2023	2023
Ensifera	Gryllidea		Grylloidea	Oecanthidae		*Picogryllus carentonensis*	Cretaceous	Myanmar (Burmese amber)	Josse & Desutter-Grandcolas, 2023	2023
Ensifera	Gryllidea		Grylloidea	Phalangopsidae	Phalangopsinae	*Araneagryllus dylani*	Miocene	Dominican Republic (Dominican amber)	Heads, 2010	2010
Ensifera	Gryllidea		Grylloidea	Phalangopsidae		*Eotrella mira*	Eocene	Colorado (Green River Formation)	Gorochov, 2012	2012
Ensifera	Gryllidea		Grylloidea	Phalangopsidae		*Eozacla arachnomorpha*	Eocene	Colorado (Green River Formation)	Gorochov, 2012	2012
Ensifera	Gryllidea		Grylloidea	Phalangopsidae		*Eozacla problematica*	Eocene	Colorado (Green River Formation)	Gorochov, 2012	2012
Ensifera	Gryllidea		Grylloidea	Phalangopsidae	Phaloriinae	*Electrogryllus septentrionalis*	Eocene	Russia (Baltic amber)	(Chopard, 1936)	1936
Ensifera	Gryllidea		Grylloidea	Protogryllidae	Falsispeculinae	*Angarogryllus angaricus*	Jurassic	Russia (Cheremkhovskaya Formation)	(Sharov, 1968)	1968
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Asiogryllus asiaticus*	Jurassic	Kyrgyzstan (Dzhil Formation)	(Sharov, 1968)	1968
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Falsispeculum bacharicum*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1984	1984
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Falsispeculum karatavicum*	Jurassic	Kazakhstan (Karabastau Formation)	(Sharov, 1968)	1968
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Parangarogryllus brevis*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1984	1984
Ensifera	Gryllidea		Grylloidea	Protogryllidae	Karataogryllinae	*Karataogryllus gryllotalpiformis*	Jurassic	Kazakhstan (Karabastau Formation)	Sharov, 1968	1968
Ensifera	Gryllidea		Grylloidea	Protogryllidae	Protogryllinae	*Archaegryllodes magnus*	Jurassic	UK	(Zeuner, 1937)	1937
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Archaegryllodes stormbergensis*	Jurassic	South Africa (Clarens Formation)	(Haughton, 1924)	1924
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Bacharogryllus mongolicus*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1984	1984
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Bacharogryllus ponomarenkoi*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1984	1984
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Daniilacheta aristovi*	Jurassic	UK (Charmouth Mudstone Formation)	Gorochov & Coram, 2023	2023
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus acutipennis*	Jurassic (?)	?	Handlirsch, 1920	1920
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus dobbertinensis*	Jurassic	Germany (Dobbertin)	(Geinitz, 1880)	1880
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus femina*	Jurassic	Germany (Dobbertin)	Handlirsch, 1906	1906
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus fissus*	Jurassic	Germany	Bode, 1953	1953
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus fossilis*	Jurassic	Germany	(Karny, 1928)	1928
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus germanicus*	Jurassic (?)	Germany	Handlirsch, 1920	1920
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus grandis*	Jurassic (?)	UK	Zeuner, 1937	1937

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Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus irregularis*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus lakshmi*	Jurassic	India (Kota Formation)	Pérez-de la Fuente, Heads, Hinojosa-Díaz & Engel, 2012	2012
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus liadis*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus major*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus parallelus*	Jurassic (?)	UK	Zeuner, 1937	1937
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus sedgwicki*	Jurassic (?)	UK	(Brodie, 1845)	1845
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus stenobasis*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Protogryllus vicinus*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Ensifera	Gryllidea		Grylloidea	Protogryllidae	-	*Aenigmagryllus indistinctus*	Jurassic	Mongolia (Sharteg Formation)	Gorochov, 1992	1992
Ensifera	Gryllidea		Grylloidea	Protogryllidae		*Aenigmagryllus obscurus*	Jurassic	Mongolia (Sharteg Formation)	Gorochov, 1992	1992
Ensifera	Gryllidea		Grylloidea	Trigonidiidae	Nemobiinae	*Pteronemobius anglicus*	Eocene	UK (Bouldnor Formation)	Zeuner, 1937	1937
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Baltonemobius fossilis*	Eocene	Russia (Baltic amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Palaeonemobius occidentalis*	Cretaceous	France (La Buzinie amber)	Laurent & Desutter-Grandcolas, 2023	2023
Ensifera	Gryllidea		Grylloidea	Trigonidiidae	Trigonidiinae	*Abanaxipha incongrua*	Miocene	Dominican Republic (Dominican amber)	Vickery & Poinar, 1994	1994
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Abanaxipha longispina*	Miocene	Dominican Republic (Dominican amber)	Vickery & Poinar, 1994	1994
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Amusurgus africanus*	Holocene	Tanzania (amber)	Chopard, 1936	1936
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Anaxipha dominica*	Miocene	Dominican Republic (La Toca Formation; Dominican amber)	Vickery & Poinar, 1994	1994
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Cyrtoxipha electrina*	Miocene	Dominican Republic (Dominican amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Cyrtoxipha illegibilis*	Miocene	Dominican Republic (Dominican amber)	Gorochov, 2010	2010
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Rhicnogryllus zeuneri*	Holocene	Tanzania (amber)	Chopard, 1936	1936
Ensifera	Gryllidea		Grylloidea	Trigonidiidae	-	*Birmaninemobius hirsutus*	Cretaceous	Myanmar (Burmese amber)	Xu, Zhang, Jarzembowski & Fang, 2020	2020
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Curvospurus huzhengkun*	Cretaceous	Myanmar (Burmese amber)	He, 2022	2022
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Palaeotrigonidium concavoculus*	Cretaceous	Myanmar (Burmese amber)	Gu, Zhou & Yuan, 2024	2024
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Palaeotrigonidium defectivum*	Cretaceous	Myanmar (Burmese amber)	Gu, Zhou & Yuan, 2024	2024
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Qiongqi crinalis*	Cretaceous	Myanmar (Burmese amber)	Yuan, Ma & Gu, 2023	2023
Ensifera	Gryllidea		Grylloidea	Trigonidiidae		*Tricalcaratus longilineus*	Cretaceous	Myanmar (Burmese amber)	Gu, Zhou & Yuan, 2024	2024
Ensifera	Gryllidea		Grylloidea	-		*Bellosichnus tripartitus*	Eocene	Argentina (Sarmiento Formation)	Genise & Sánchez, 2017	2017
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae	Gryllotalpinae	*Gryllotalpa aveyronensis*	Oligocene	France	Handschin, 1944	1944
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Gryllotalpa miocaenica*	Miocene	Germany (Thermalsinterkalk Formation)	Zeuner, 1931	1931
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Gryllotalpa stricta*	?	?	Heer, 1865	1865
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Neocurtilla schmidtgeni*	Miocene	Germany (Hydrobienkalk Formation)	Zeuner, 1937	1937

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Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Pterotriamescaptor americanus*	Eocene	Colorado (Green River Formation)	Gorochov, 2012	2012
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Pterotriamescaptor primus*	Eocene	UK (Bouldnor Formation)	(Cockerell, 1921)	1921
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Pterotriamescaptor tridactylinus*	Eocene	Italy	(Secretan, 1975)	1975
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae	Marchandiinae	*Archaeogryllotalpoides ornatus*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Cratotetraspinus fossorius*	Cretaceous	Brasil (Crato Formation)	(Martins-Neto, 1995)	1995
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Marchandia magnifica*	Cretaceous	France (Charentese amber)	Perrichot, Neraudeau, Azar, Menier & Nel, 2002	2002
Ensifera	Gryllidea		Gryllotalpoidea	Gryllotalpidae		*Palaeoscapteriscops cretacea*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Gryllidea		Gryllotalpoidea	Myrmecophilidae	Myrmecophilinae	*Araripemyrmecophilops gracilis*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Tettigoniidea		Hagloidea	Eospilopteronidae		*Eospilopteron ornatum*	Triassic/Jurassic	UK	Cockerell, 1916	1916
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Angarohaglinae	*Angarohagla variegata*	Jurassic	Russia (Cheremkhovskaya Formation)	Zherikhin, 1985	1985
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Microvoliopus bacharicus*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1990	1990
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Archaboilinae	*Archaboilus kisylkiensis*	Jurassic	Kyrgyzstan	Martynov, 1937	1937
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Archaboilus martynovi*	Jurassic	Kyrgyzstan (Dzhil Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Archaboilus musicus*	Jurassic	China (Daohugou Formation)	Gu, Engel & Ren, 2012	2012
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Archaboilus ornatus*	Jurassic	China (Jiulongshan Formation)	Gu, Ren & Chen, 2024	2024
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Archaboilus polyneurus*	Jurassic	China (Daohugou Formation)	Gu, Yue & Ren, 2021	2021
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Archaboilus shurabicus*	Jurassic	Kyrgyzstan (Sulyukta Formation)	Martynov, 1937	1937
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Archaboilus similis*	Jurassic	Russia (Cheremkhovskaya Formation)	Zherikhin, 1985	1985
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Pararchaboilus cretaceus*	Cretaceous	UK (Lulworth Formation)	(Gorochov, Jarzembowski & Coram, 2006)	2006
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Tasgorosailus orlovskajae*	Jurassic/Cretaceous	Kazakhstan	Gorochov, 1990	1990
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Vitimoilus captiosus*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Vitimoilus gigantus*	Cretaceous	China (Yixian Formation)	Gu, Ren & Chen, 2024	2024
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Vitimoilus ovatus*	Cretaceous	China (Dabeigou Formation)	Gu, Tian, Yin, Shi & Ren, 2017	2017
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Bachariinae	*Bacharia zherichini*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Paratshorkuphlebia multivenosa*	Jurassic	Kyrgyzstan (Dzhil Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Pseudotshorkuplebia pritykinae*	Jurassic	Kyrgyzstan (Sagul Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Pseudotshorkuplebia sharovi*	Jurassic	Kyrgyzstan (Sagul Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Sharovophlebia angusta*	Jurassic	Kyrgyzstan (Sagul Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Sogutophlebia issykkulensis*	Jurassic	Kyrgyzstan (Dzhil Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Cyrtophyllitinae	*Cyrtophyllites rogeri*	Jurassic	Germany (Solnhofen)	Oppenheim, 1888	1888

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Ensifera	Tettigoniidea		Hagloidea	Haglidae	Haglinae	*Archihagla tenuis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Archihagla zeuneri*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Cantohagla gracilis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Dinohagla corrugata*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Dolichohagla longa*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Dulcihagla beybienkoi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Dulcihagla mistshenkoi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Euhagla saurensis*	Triassic	Kazakhstan (Tologoi Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Euspilopteron ornatum*	?	UK (?)	Cockerell, 1916	1916
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Hagla gracilis*	Triassic	UK (Lilstock Formation)	Giebel, 1856	1856
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Haglomorpha martynovi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Lyrohagla decipiens*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Lyrohagla pravdini*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Lyrohagla uvarovi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Microhagla minuta*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Modihagla ovalis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Neohagla sinuata*	Triassic	Australia	Riek, 1955	1955
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Prohagla imperfecta*	Triassic	Australia	Riek, 1955	1955
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Prohagla superba*	Triassic	Australia (Hawkesbury Sandstone Formation)	Riek, 1954	1954
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Protohagla langi*	?	UK	Zeuner, 1962	1962
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Protshorkuphlebia kirgizica*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Protshorkuphlebia similis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Protshorkuphlebia triassica*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Pseudohumbertiella grandis*	Jurassic	Russia (Cheremkhovskaya Formation)	(Brauer, Redtenbacher & Ganglbauer, 1889)	1889
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Sharovohagla plana*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Sonohagla chopardi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Sonohagla curta*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986

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Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Sonohagla saussurei*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Tinnihagla handlirschi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Tinnihagla zeuneri*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Vocohagla clara*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Vocohagla tarbinskyi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Yenshania hebeiensis*	Cretaceous	China (Yixian Formation)	Hong, 1982	1982
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Haglopterinae	*Hagloptera intermedia*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Isfaropterinae	*Isfaroptera grylliformis*	Jurassic	Kyrgyzstan (Sulyukta Formation)	Martynov, 1937	1937
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Isfaroptera yujiagouensis*	Jurassic	China (Haifanggou Formation)	Hong, 1983	1983
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Triassaginae	*Eumaraga madygenica*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Maragella reducta*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Paramaraga fusca*	Triassic	Kazakhstan (Koldzat Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Triassaga angusta*	Triassic	Kyrgyzstan (Madygen Formation)	(Gorochov, 1986)	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Triassaga tshorkuphlebioides*	Triassic	Kyrgyzstan (Madygen Formation)	(Gorochov, 1986)	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Zamaraga reticulata*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Tshorkuphlebiinae	*Tshorkuphlebia compressa*	Jurassic	Kyrgyzstan (Sulyukta Formation)	Martynov, 1937	1937
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Tshorkuphlebia shurabica*	Jurassic	Kyrgyzstan (Sagul Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Haglidae	Voliopinae	*Asiovoliopus kirgizicus*	Jurassic	Kyrgyzstan (Dzhil Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Bacharovoliopus pulcherrimus*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Bajanchongoria modesta*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Euvoliopus giganteus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Jurovoliopus sinuatus*	Jurassic	Kyrgyzstan (Sulyukta Formation)	(Martynov, 1937)	1937
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Macrovoliopus declivus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Melovoliopus fasciatus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Mongolovoliopus sonorus*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1988	1988

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Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Paravoliopus dorsalis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Phonovoliopus musicus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Phyllovoliopus isufficiens*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Platyvoliopus maximus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Stenovoliopus elongatus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Voliopellus latus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Voliopus ancestralis*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Voliopus margueritae*	Triassic	South Africa (Molteno Formation)	Wappler, 2001	2001
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Zavoliopus densus*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Zeunerophlebia gigas*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Haglidae	-	*Afrohagla contorta*	Triassic	South Africa (Molteno Formation)	(Riek, 1974)	1974
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Ahagla mira*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 2005	2005
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Archaeohagla sinensis*	Jurassic	China	Lin, 1965	1965
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Gurenia caii*	Jurassic	China (Jiulongshan Formation)	(Gu & Ren, 2012)	2012
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Haglopsis parallela*	Triassic	UK (Lilstock Formation)	(Giebel, 1856)	1856
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Huabeius suni*	Cretaceous	China (Yixian Formation)	Hong, 1982	1982
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Laiyangohagla beipoziensis*	Cretaceous	China (Laiyang Formation)	Wang & Liu, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Mesohagla xinjiangensis*	Jurassic	China (Badaowan Formation)	Zhang, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Mongolohagla unicolor*	Jurassic	Mongolia (Zhargalant Formation)	Zherikhin, 1985	1985
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Notopamphagopsis bolivari*	Triassic	Argentina (Potrerillos Formation)	Cabrera, 1928	1928
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Permohagla tomica*	Triassic	Russia (Maltsevo Formation)	Gorochov, 2021	2021
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Proisfaroptera martynovi*	Triassic	Kyrgyzstan (Madygen Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Shanxius meileyingziensis*	Cretaceous	China (Shahai Formation)	Hong, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Shanxius reticulatus*	Jurassic	China	Hong, 1984	1984
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Sinohagla anthoides*	Jurassic	China	Lin, 1965	1965
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Sinohagla pleioneura*	Cretaceous	China (Yixian Formation)	Ren, 1995	1995
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Turkestania deviata*	Cretaceous	China (Yixian Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Haglidae		*Zhemengia sinica*	Jurassic	China	Hong, 1982	1982
Ensifera	Tettigoniidea		Hagloidea	Hagloedischiidae		*Hagloedischia primitiva*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986

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Ensifera	Tettigoniidea		Hagloidea	Hagloedischiidae		*Voltziahagla pseudoveinosa*	Triassic	France (Grès à Voltzia Formation)	Marchal-Papier, Nel & Grauvogel-Stamm, 2000	2000
Ensifera	Tettigoniidea		Hagloidea	Prezottophlebiidae		*Prezotophlebia helbae*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae	Aboilinae	*Aboilus abbreviatus*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus amplus*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus aulietus*	Jurassic	Kazakhstan (Karabastau Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus bresobasovae*	Jurassic	Kazakhstan (Karabastau Formation)	Cockerell, 1928	1928
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus chinensis*	Jurassic	China (Daohugou Formation)	Fang, Zhang & Wang, 2009	2009
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus columnatus*	Jurassic (?)	Kazakhstan (Karabastau Formation) (?)	Martynov, 1934	1934
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus cornutus*	Jurassic	China (Daohugou Formation)	Li, Ren & Wang, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus dilutus*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus faciatus*	Cretaceous	China (Yixian Formation)	(Hong, 1982)	1982
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus fasciatus*	Jurassic	Kazakhstan (Karabastau Formation)	Martynov, 1925	1925
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus femineus*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus huanghuachunensis*	Cretaceous	China (Shahai Formation)	(Hong, 1982)	1982
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus jiyuanensis*	Jurassic	China (Ma'ao Formation)	Lin & Huang, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus khasurty*	Cretaceous	Russia	Gorochov, 2021	2021
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus krassilovi*	Jurassic	Russia (Talynzhan Formation)	Zherikhin, 1985	1985
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus lamina*	Jurassic	China	(Lin, 1982)	1982
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus longitudinalis*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus perbellus*	Jurassic	China (Daohugou Formation)	Wang, Li, Zhang, Fang, Wang & Zhang, 2015	2015
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus pullus*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus stratosus*	Jurassic	China (Daohugou Formation)	Li, Ren & Wang, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus tigris*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus transversalis*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus tuzigouensis*	Jurassic	China (Badaowan Formation)	Lin & Huang, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Aboilus zebra*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Allaboilus dicrus*	Jurassic	China (Daohugou Formation)	Ren & Meng, 2006	2006

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Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Allaboilus gigantus*	Jurassic	China (Daohugou Formation)	Ren & Meng, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Allaboilus hani*	Cretaceous	China (Yixian Formation)	Gu, Qiao & Ren, 2010	2010
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Allaboilus robustus*	Jurassic	China (Daohugou Formation)	Gu, Qiao & Ren, 2010	2010
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Angustaboilus fangianus*	Jurassic	China (Daohugou Formation)	Li, Ren & Meng, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Apsataboilus sibiricus*	Cretaceous	Russia (Apsat Formation)	Gorochov, 1990	1990
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Ashangopsis daohugouensis*	Jurassic	China (Daohugou Formation)	Lin, Huang & Nel, 2008	2008
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Bacharaboilus curvus*	Jurassic	China (Jiulongshan Formation)	Gu, Xu & Ren, 2021	2021
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Bacharaboilus jurassicus*	Jurassic	China (Daohugou Formation)	Li, Ren & Wang, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Bacharaboilus lii*	Jurassic	China (Daohugou Formation)	Gu, Qiao & Ren, 2011	2011
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Bacharaboilus mongolicus*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Baissaboilus paradoxus*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Brunneus haifanggouensis*	Jurassic	China (Haifanggou Formation)	Hong, 1983	1983
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Circulaboilus aureus*	Jurassic	China (Daohugou Formation)	Li, Ren & Wang, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Circulaboilus priscus*	Jurassic	China (Daohugou Formation)	Gu, Qiao & Ren, 2010	2010
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Karatailus micropterus*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Nipponohagla kaga*	Cretaceous	Japan (Kuwajima Formation)	Fujiyama, 1978	1978
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Notohagla mauii*	Jurassic	New Zealand (Puti Siltstone Formation)	Johns, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Novaboilus multifurcatus*	Jurassic	China (Daohugou Formation)	Li, Ren & Meng, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Novaboilus ovatus*	Jurassic	China (Daohugou Formation)	Gu, Xu & Ren, 2021	2021
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pamphagopsis maculata*	Jurassic	Kazakhstan (Karabastau Formation)	Martynov, 1925	1925
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pamphagopsis modesta*	Jurassic	Kazakhstan (Karabastau Formation)	Martynov, 1925	1925
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Procyrtophyllites britannicus*	Cretaceous	UK (Durlston Formation)	Zeuner, 1935	1935
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Prophalangopseides vitimicus*	Cretaceous	Russia (Zaza Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pseudohagla pospelovi*	Jurassic	Russia (Osinovo Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pseudohagla shihi*	Jurassic	China (Daohugou Formation)	Li, Ren & Wang, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pycnophlebia deichmulleri*	Jurassic	Germany (Solnhofen)	Zeuner, 1939	1939
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pycnophlebia minor*	Jurassic	Germany (Solnhofen)	Handlirsch, 1906	1906
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pycnophlebia obesa*	Jurassic	China (Haifanggou Formation)	Wang, 1987	1987
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pycnophlebia robusta*	Jurassic	Germany (Solnhofen)	Zeuner, 1939	1939

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Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pycnophlebia speciosa*	Jurassic	Germany (Solnhofen)	(Germar, 1839)	1839
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Scalpellaboilus angustus*	Jurassic	China (Daohugou Formation)	Gu, Qiao & Ren, 2010	2010
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sigmaboilus calophlebius*	Jurassic	China (Daohugou Formation)	Wang, Fang & Zhang, 2018	2018
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sigmaboilus fuscus*	Jurassic	China (Daohugou Formation)	Gu, Zhao & Ren, 2009	2009
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sigmaboilus gorochovi*	Jurassic	China (Daohugou Formation)	Fang, Zhang, Wang & Zhang, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sigmaboilus longus*	Jurassic	China (Daohugou Formation)	Fang, Zhang, Wang & Zhang, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sigmaboilus peregrinus*	Jurassic	China (Daohugou Formation)	Gu, Zhao & Ren, 2009	2009
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sigmaboilus sinensis*	Jurassic	China (Daohugou Formation)	Fang, Zhang, Wang & Zhang, 2007	2007
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sinoprophalangopsis reticulata*	Jurassic	China (Jiulongshan Formation)	Hong, 1983	1983
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sunoprophalangopsis clathrata*	Jurassic	China (Jiulongshan Formation)	Hong, 1982	1982
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sunoprophalangopsis elegantis*	Jurassic	China (Jiulongshan Formation)	Hong, 1982	1982
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sunoprophalangopsis scupta*	Jurassic	China (Jiulongshan Formation)	Hong, 1982	1982
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sunoprophalangopsis sparsula*	Jurassic	China (Jiulongshan Formation)	Ren, 1995	1995
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sunoprophalangopsis superba*	Jurassic	China (Haifanggou Formation)	Ren, 1995	1995
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Tettaboilus distinctus*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Tettaboilus pulcher*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Utanaboilus bellus*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Utanaboilus pulchellus*	Cretaceous	Russia (Utan Formation)	Gorochov, 1990	1990
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae	Chifengiinae	*Aenigmoilus minutus*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Ashanga borealis*	Cretaceous	China (Yixian Formation)	Fang, Zhang, Wang & Zheng, 2013	2013
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Ashanga clara*	Jurassic	Russia (Uda Formation)	Zherikhin, 1985	1985
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Ashanga hongi*	Cretaceous	China (Yixian Formation)	(Meng & Ren, 2006)	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Ashanga jiuquanensis*	Cretaceous	China (Zhonggou Formation)	Wang, Zheng, Lei, Zhang, Ren, Wang, Fang, Jarzembowski & Zhang, 2017	2017
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Chifengia batuyingziensis*	Jurassic	China (Haifanggou Formation)	Wang, 1987	1987
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Chifengia mosaica*	Cretaceous	China (Yixian Formation)	Hong, 1982	1982
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Parahagla cheni*	Jurassic	China (Badaowan Formation)	Xu, Fang, Fang, Wang, Zhou, Jiang & Zhang, 2024	2024

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Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Parahagla sibirica*	Cretaceous	Russia (Zaza Formation - Holotype)/China (Yixian Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae	Prophalangopsinae	*Jurassobatea gryllacroides*	Jurassic	Germany (Solnhofen)	Zeuner, 1937	1937
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Mesoprophalangopsis liaoxiensis*	Jurassic	China (Haifanggou Formation)	Hong, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Zalmonites geinitzi*	Jurassic	Germany (Dobbertin)	Handlirsch, 1906	1906
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae	Protaboilinae	*Protaboilus amblus*	Jurassic	China (Daohugou Formation)	Ren & Meng, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Protaboilus lini*	Jurassic	China (Daohugou Formation)	Ren & Meng, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Protaboilus praedictus*	Jurassic	Kyrgyzstan	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Protaboilus rudis*	Jurassic	China (Daohugou Formation)	Ren & Meng, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae	Termitidiinae	*Agrionidium aetna*	Cretaceous	UK (Lulworth Formation)	Westwood, 1854	1854
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Agrionidium obscurum*	Cretaceous	UK (Durlston Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Mesogryllus achelous*	Cretaceous	UK (Lulworth Formation)	(Westwood, 1854)	1854
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pseudaboilus ningchengensis*	Cretaceous	China (Yixian Formation)	Wang, Fang, Wang & Zhang, 2018	2018
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pseudaboilus purbeckensis*	Cretaceous	UK (Durlston Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Pseudaboilus wealdensis*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Termitidium ignotum*	Cretaceous	UK (Durlston Formation)	Westwood, 1854	1854
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Tettigoilus sonorus*	Cretaceous	UK (Weald Clay Formation)	Gorochov, Jarzembowski & Coram, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Zalmona brodiei*	Cretaceous	UK (Lulworth Formation)	Giebel, 1856	1856
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae	Tettohaglinae	*Tettohagla problematica*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1996	1996
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae	-	*Cratohaglopsis santanaensis*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Hylophalangopsis chinensis*	Paleocene	China (Niubao Formation)	Lin & Huang, 2006	2006
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Kevania araripensis*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Parahaglopsis posteria*	Cretaceous	China (Yingcheng Formation)	Hong, 1992	1992
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Shangxiania fengjiashanensis*	Cretaceous	China (Fengjiashan Formation)	Zhang, 1993	1993
Ensifera	Tettigoniidea		Hagloidea	Prophalangopsidae		*Sinuijus baektoensis*	Cretaceous	North Korea (Sinuiju Formation)	Fang & So, 2020	2020
Ensifera	Tettigoniidea		Hagloidea	Tuphellidae	Paracyrtophyllitinae	*Paracyrtophyllites popovi*	Jurassic	Mongolia (Sharteg Formation)	Gorochov, 1985	1985
Ensifera	Tettigoniidea		Hagloidea	Tuphellidae		*Paracyrtophyllites undulatus*	Jurassic	Kazakhstan (Karabastau Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Hagloidea	Tuphellidae		*Triassoparacyrtophyllites bifurcatus*	Triassic	France (Grès à Voltzia Formation)	Marchal-Papier, Nel & Grauvogel-Stamm, 2000	2000

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Ensifera	Tettigoniidea		Hagloidea	Tuphellidae	Tuphellinae	*Neotuphella minor*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Tuphellidae		*Tuphella rasnitzyni*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Tuphellidae		*Tuphella rohdendorfi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Tuphellidae		*Tuphella sharovi*	Triassic	Kyrgyzstan (Madygen Formation)	Gorochov, 1986	1986
Ensifera	Tettigoniidea		Hagloidea	Tuphellidae	-	*Liassophyllum abbreviatum*	Jurassic	UK	Zeuner, 1935	1935
Ensifera	Tettigoniidea		Hagloidea	Tuphellidae		*Liassophyllum patriciae*	Jurassic	UK	Gorochov, Coram, Jarzembowski & Webster, 2024	2024
Ensifera	Tettigoniidea		Hagloidea	-		*Tzetzenulia dilutemaculata*	Jurassic	Mongolia (Bakhar Formation)	Gorochov, 1990	1990
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae	Kolymopterinae	*Kolymoptera magadanica*	Cretaceous	Russia (Arkagalinskaya Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Palaeopteron complexus*	Cretaceous	Canada (Redmond Formation)	Rice, 1969	1969
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Paraphasmomimella chetanica*	Cretaceous	Russia (Amka Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Paraphasmomimella longa*	Cretaceous	Russia (Zaza Formation)	Kuzmina, 1985	1985
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Phasmomimella antiqua*	Cretaceous	Russia (Zaza Formation)	Kuzmina, 1985	1985
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Phasmomimella araripensis*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 1991	1991
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Phasmomimella paskapoensis*	Paleocene	Canada (Paskapoo Formation)	Kevan & Wighton, 1981	1981
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae	Phasmomiminae	*Jurophasmomima punctata*	Jurassic	Kazakhstan (Karabastau Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Paraphasmomima sharovi*	Jurassic	Russia (Cheremkhovskaya Formation)	Zherikhin, 1985	1985
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Phasmomima maculomarginata*	Jurassic	Kazakhstan (Karabastau Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Phasmomimula enigma*	Paleocene	Canada (Paskapoo Formation)	Kevan & Wighton, 1981	1981
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae	Phasmomimoidinae	*Phasmomimoides baissiense*	Cretaceous	Russia (Zaza Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Phasmomimoides lineatus*	Jurassic	Kazakhstan (Karabastau Formation)	Sharov, 1968	1968
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae	Susumaniinae	*Cretophasmomima arkagalica*	Cretaceous	Russia (Arkagalinskaya Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Cretophasmomima burjatica*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Cretophasmomima clara*	Cretaceous	Russia (Ola Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Cretophasmomima vitimica*	Cretaceous	Russia (Zaza Formation)	Kuzmina, 1985	1985
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Cretophasmomimoides reductus*	Cretaceous	Mongolia (Anda-Khuduk Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Eosusumania fusca*	Cretaceous	Russia (Amka Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Eosusumania lata*	Cretaceous	Russia (Zaza Formation)	(Kuzmina, 1985)	1985
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Eosusumania maculata*	Cretaceous	Transbaikalia	(Kuzmina, 1985)	1985
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Eosusumania ornata*	Cretaceous	Russia (Zaza Formation)	(Kuzmina, 1985)	1985
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Eosusumania reticulata*	Cretaceous	Transbaikalia	(Kuzmina, 1985)	1985
Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Prosusumania semenica*	Cretaceous	Russia (Argun Formation)	Gorochov, 1988	1988

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Ensifera	Tettigoniidea		Phasmomimoidea	Phasmomimidae		*Susumania flexuosa*	Cretaceous	Russia (Arkagalinskaya Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Rhaphidophoroidea	Rhaphidophoridae	Protroglophilinae	*Prorhaphidophora antiqua*	Eocene	Russia (Baltic amber)	Chopard, 1936	1936
Ensifera	Tettigoniidea		Rhaphidophoroidea	Rhaphidophoridae		*Protroglophilus sukatshevae*	Eocene	Russia (Baltic amber)	Gorochov, 1989	1989
Ensifera	Tettigoniidea		Rhaphidophoroidea	Rhaphidophoridae		*Protroglophilus tachycinoides*	Eocene	Poland (Baltic amber)	(Chopard, 1936)	1936
Ensifera	Tettigoniidea		Rhaphidophoroidea	Rhaphidophoridae		*Protroglophilus zeuneri*	Eocene	Russia (Baltic amber)	(Chopard, 1936)	1936
Ensifera	Tettigoniidea		Schizodactyloidea	Schizodactylidae	Schizodactylinae	*Brauckmannia groeningae*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2007	2007
Ensifera	Tettigoniidea		Stenopelmatoidea	Anostostomatidae	Euclydesinae	*Euclydes ramosfernandesi*	Cretaceous	Brasil (Crato Formation)	Martins-Neto, 2007	2007
Ensifera	Tettigoniidea		Stenopelmatoidea	Gryllacrididae	Gryllacridinae	*Gryllacris bodei*	?	somewhere in Asia	Karny, 1928	1928
Ensifera	Tettigoniidea		Stenopelmatoidea	Gryllacrididae		*Gryllacris cineris*	Eocene	Colorado (Florissant Formation)	Scudder, 1890	1890
Ensifera	Tettigoniidea		Stenopelmatoidea	Gryllacrididae		*Gryllacris kittli*	Miocene	Croatia (Radoboj?)	Handlirsch, 1907	1907
Ensifera	Tettigoniidea		Stenopelmatoidea	Gryllacrididae		*Gryllacris mutilata*	Eocene	Colorado (Florissant Formation)	Cockerell, 1909	1909
Ensifera	Tettigoniidea		Stenopelmatoidea	Gryllacrididae		*Plesiolarnaca prior*	Eocene	Russia (Baltic amber)	Gorochov, 2010	2010
Ensifera	Tettigoniidea		Stenopelmatoidea	Gryllacrididae	-	*Pseudogryllacris propinqua*	Jurassic	Germany (Solnhofen)	(Deichmüller, 1886)	1886
Ensifera	Tettigoniidea		Stenopelmatoidea	Gryllacrididae		*Xenogryllacris reductus*	Triassic	Australia	Riek, 1955	1955
Ensifera	Tettigoniidea		Stenopelmatoidea	Stenopelmatidae	Stenopelmatinae	*Electrosia baltica*	Eocene	Russia (Baltic amber)	Gorochov, 2010	2010
Ensifera	Tettigoniidea		Tettigonioidea	Haglotettigoniidae		*Haglotettigonia aenigmatosa*	Cretaceous	Lebanon (Lebanese amber)	Gorochov, 2010	2010
Ensifera	Tettigoniidea		Tettigonioidea	Haglotettigoniidae		*Haglotettigonia egregia*	Cretaceous	Russia (Zaza Formation)	Gorochov, 1988	1988
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Phaneropterinae	*Amblycorypha perdita*	Miocene	Colorado (Florissant, Wilson Ranch)	Cockerell, 1915	1915
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Arethaea solterae*	Eocene	Colorado (Green River Formation)	Heads, Thomas & Hedlund, 2023	2023
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Nephoptera harzensis*	Pliocene	Germany (Willershausen)	Harz, 1967	1967
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Phaneroptera vetusta*	Miocene	Germany (Oeningen)	Heer, 1849	1849
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Pseudophyllinae	*Archepseudophylla fossilis*	Oligocene	France	Nel, Prokop & Ross, 2008	2008
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Archepseudophylla melanospila*	Eocene	UK (Bouldnor Formation)	(Cockerell, 1921)	1921
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Archepseudophylla nanzhaoica*	Oligocene	China (Xiaolongtan Formation)	Nel, Wang, Engel, Huang, Jia, Su & Wappler, 2020	2020
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Archepseudophylla wenshanensis*	Oligocene	China (Xiaolongtan Formation)	Nel, Wang, Engel, Huang, Jia, Su & Wappler, 2020	2020
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Conocephalinae	*Senexifigia reticulata*	Oligocene	France	(Piton & Théobald, 1939)	1939
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Conocephalus martyi*	Paleocene	France (Menat Formation)	Piton, 1940	1940
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Orchelimum placidum*	Eocene	Colorado (Florissant Formation)	Scudder, 1890	1890
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Lipotactinae	*Eomortoniellus bispinatus*	Eocene	? (Baltic amber?)	(Weidner, 1956)	1956
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Eomortoniellus handlirschi*	Eocene	Russia (Baltic amber)	Zeuner, 1936	1936
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Eomortoniellus martynovi*	Eocene	? (Baltic amber?)	(Zeuner, 1936)	1936
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Meconematinae	*Archixizicus occidentalis*	Eocene	Russia (Baltic amber)	Gorochov, 2010	2010
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Eogrigoriora gracilis*	Eocene	Russia (Baltic amber)	Gorochov, 2010	2010
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Miophlugis rostratus*	Miocene	Dominican Republic (Dominican amber)	Gorochov, 2010	2010
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Pseudotettigoniinae	*Arctolocusta groenlandica*	Paleocene	Greenland (Atanikerluk Formation)	(Heer, 1883)	1883

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Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Lithymnetes guttatus*	Eocene	Colorado (Florissant Formation)	Scudder, 1878	1878
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Lithymnetoides laurenti*	Eocene	France	(Théobald, 1937)	1937
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Nymphomorpha medialis*	Eocene	Denmark (Fur Formation)	Henriksen, 1922	1922
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Pseudotettigonia amoena*	Eocene	Denmark (Moler Formation)	(Henriksen, 1929)	1929
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Pseudotettigonia leona*	Eocene	Montana (Kishenehn Formation)	Greenwalt & Rust, 2014	2014
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Rammeinae	*Rammea laticeps*	Miocene	Germany (Thermalsinterkalk Formation)	Zeuner, 1931	1931
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Tettigoidinae	*Tettigoides pectinata*	Eocene	Australia (Redbank Plains Formation)	Riek, 1952	1952
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	Tettigoniinae	*Decticus umbraceus*	Miocene (?)	Germany (Freudenhain Braunkohle)	Frič, 1869	1869
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Platycleis pongraczi*	Miocene	Croatia (Radoboj)	Zeuner, 1929	1929
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Platycleis speciosa*	Miocene	Germany (Oeningen)	(Heer, 1865)	1865
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Anabrus caudelli*	Eocene	Colorado (Florissant Formation)	Cockerell, 1908	1908
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Tettigonia bricei*	Miocene	France	Greenwalt & Rust, 2014	2014
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Eodecticus maculatus*	Miocene	Croatia (Radoboj)	Poncrácz, 1928	1928
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae	-	*Locustites exstinctus*	Miocene	Germany	Giebel, 1852	1852
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Locustites maculatus*	Miocene	Germany	Heer, 1849	1849
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Locustites prisca*	Jurassic	Germany (Solnhofen)	(Germar, 1839)	1839
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Locustophanes rhipidophorus*	Jurassic	Germany (Dobbertin)	Handlirsch, 1939	1939
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Prophasgonura lineatocollis*	Paleocene	France (Menat Formation)	Piton, 1940	1940
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Protempusa incerta*	Paleocene	France (Menat Formation)	Piton, 1940	1940
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Prototettix lithanthraca*	Carboniferous	Germany (Lower Saarbrucker layer Formation)	(Goldenberg, 1854)	1854
Ensifera	Tettigoniidea		Tettigonioidea	Tettigoniidae		*Locusta silens*	Eocene	Colorado (Florissant Formation)	Scudder, 1890	1890
Ensifera	Tettigoniidea		-	-		*Tettoraptor maculatus*	Eocene	Wyoming (Green River Formation)	Gorochov, 2012	2012

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Conclusions

Note by the author: the following part adopts a somewhat 'popular science' style of writing. I hope this provides a more fun-to-read experience.

Although they are not as species rich as the great holometabolous orders of the insect world (like beetles, hymenopterans or flies), the Orthoptera Olivier, 1789 are certainly among the most charismatic insects in modern ecosystems. New evidence in this dissertation suggests that this would not have been different in the prehistoric world. From the tiny hopping Tridactyloidea Brullé, 1835 on the ancient river banks, to the enigmatic Locustopsidae Handlirsch, 1906 with their head-crest bearing species, and the mesmerizing Elcanidae Handlirsch, 1906 from the tropical amber forest of Myanmar, the Mesozoic grasshoppers are no less captivating than the giant vertebrates they shared their habitat with – at least once you begin to properly dive into their world.

Throughout the chapters of this dissertation, I have described six new species of Tridactyloidea, eight new species of Locustopsidae, one new species of Eumastacoidea, and five new species of Elcanidae. The taxonomic positions of many species were reviewed and, if necessary, changed, based on the newest scientific discoveries. The increase in knowledge provided by the continuous efforts of paleontologists over the past eighteen years since the discovery of the first elcanid from Burmese amber (Poinar et al., 2007) have set the basis for a new understanding of Orthoptera evolution. In this dissertation I have expanded upon these findings by combining all the information together, to provide a new taxonomic framework for Tridactyloidea and Elcanidae and explore the phylogenetic relationships of Orthoptera, both of the extant as well as the extinct forms.

We have learned that Oedischiidea Handlirsch, 1906 were likely the first Orthoptera to evolve in the Late Carboniferous (ca. 300 Mya) and that they are considered the ancestors of the suborders Ensifera Chopard, 1921 and Caelifera Ander, 1936. They were accompanied by the mysterious Titanoptera Sharov, 1968, those ferocious giant predators of the Paleozoic insect world, the phylogenetic position of which continues to be enigmatic. Do they belong inside Orthoptera as a sister group to Oedischiidea and the clades that evolved from them? Or are they a separate order and sister to the whole of Orthoptera? It remains to be seen with future discoveries.

Elcanidea and Locustopsoidea probably evolved at a similar stage during the Permian, the former being the earliest infraorder of the Ensifera, the latter the same of Caelifera. The Permian

mass extinction event (ca. 252 Mya) apparently did not have the major impact on Orthoptera that would have been expected based on the severe consequences it had on other organisms (Chen and Benton, 2012). However, it marked the transition from the Paleozoic faunal community of Orthoptera (Oedischiidea + Titanoptera) to the faunal community of the Mesozoic that begun with the appearance of Hagloidea Handlirsch, 1906 in the Triassic. This group, which quickly rose to become the most speciose taxon of Orthoptera in the Triassic and following Jurassic period (that means for roughly 100 million years!) may have been the common ancestor of the modern lineages of Ensifera, Tettigoniidea Kevan, 1982 and Gryllidea Vickery, 1977.

Although the end-Triassic mass extinction caused the demise of the Paleozoic orthopterans Oedischiidea and Titanoptera, it could not stop the further triumph of Hagloidea in the Jurassic. Also, the Gryllidea (crickets) appeared in the Jurassic for the first time with their diversification rates quickly picking up pace. Meanwhile, the other taxon of the Ensifera, the Elcanidea also became more diverse in the Jurassic, as did the Locustopsoidea for the Caelifera. The mass extinction event towards the dawn of the Jurassic perhaps caused the end to the Hagloidea-dominated orthopteran landscape, anyway, their numbers had dwindled considerably in the Cretaceous. Right before their possible breakdown due to the mid-Cretaceous insect crisis (or, less likely, end-Cretaceous mass extinction), the orthopteran fauna had reached what was possibly their most diverse community assemblage ever. All Mesozoic lineages were present and abundant and among them had evolved the lineages of the Cenozoic fauna, which are the grasshoppers that are still around today.

After the Cretaceous had ended the great lineages of the Mesozoic, the Hagloidea, Elcanidea and Locustopsoidea had disappeared. Tridactyloidea were still around, but their diversity levels had taken a major beating, and they never recovered back to what they likely once were during the Cretaceous period. The crickets from the Gryllidea infraorder alone persisted through every crisis apparently unfaced and they continued to be abundant in the Cenozoic and are also commonly encountered in modern times. Meanwhile, Tettigoniidea (katydids) had replaced the Hagloidea and Elcanidea while Acrididea Targioni-Tozzetti, 1882 took over from Locustopsoidea.

What allowed Gryllidea to persist while the other Mesozoic taxa were eradicated? Why were the Hagloidea, Elcanidea, Locustopsoidea and even, in parts, Tridactylidea nearing their end while Tettigoniidea and Acrididea became more and more diverse? It seems obvious to look

for explanations in the changing ecosystems over the Cretaceous-Cenozoic transition, but to the precise reasons we will have to await the findings of future researchers.

I hope my work has outlined the fascinating world of Mesozoic Orthoptera and incentivizes many more studies on this exciting, swiftly developing subject. Every stone, every amber piece and every specimen enlarges our knowledge of the life in the past. And, who knows – maybe the next groundbreaking discovery is just one drawer away. Over there, in that creaky museum cabinet, waiting to be inspected closely by an aspiring paleontologist and reveal its secrets, intriguingly preserved for one hundred million years…

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