

**Evolutionary systematics and reproductive biology
of two Cerithioidea snail families (Thiaridae, Planaxidae)**

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Disclaimer

This work is not issued for purposes of zoological nomenclature and is not published within the meaning of the International Code of Zoological Nomenclature (Article 8.2).

Summary

The current biodiversity crisis and associated mass extinction is undoubtedly the major challenge mankind is facing in the 21st century. To effectively take action against this threat, not only direct action but also fundamental biodiversity research must be undertaken, to assess the ‘true’ biological diversity before it is lost. Thereby, the description of new species is easily as important as the reassessment of known taxa with an ambiguous taxonomic status.

To provide a modern assessment of biodiversity in such understudied groups, an evolutionary systematics approach should be conducted, viz. studies integrating several morphological and molecular methods in a framework of evolutionary biology. The thesis at hand compiles several such studies for two families of the understudied gastropod superfamily Cerithioidea. One focus is on the tropical, freshwater Thiaridae, the other on the tropical to warm temperate, marine Planaxidae.

Here presented, is the first family-wide molecular study of representative specimens of all genera of Thiaridae. Though several morphological established lineages are not unambiguously resolved within the resulting phylogeny, the study furthers our understanding of the biogeographic history leading to the diversification of this group.

Taxonomic assessment of the thiarid *Stenomelania-Melanooides* complex have been carried out – a taxonomically highly convoluted assemblage of the genera *Stenomelania*, *Melanooides* and *Neoradina*. As major results, the *Neoradina* lineage is for the first time supported as a distinct lineage of this complex, and *Stenomelania* is outlined by its differences in developmental mode and shell shape.

With the focus on poecilogony (that is the presence of two distinctly different developmental modes within the same animal species) in the planaxid snail species *Planaxis sulcatus*, for the first time a study encompassing the entire distribution range of the species is compiled, examining its molecular genetics and developmental modes. As a result, the species was found to vary geographically in developmental mode.

With the integrative assessment of morphology and molecular biology of *Supplanaxis*, a so far unrevised planaxid snail genus has been retrieved. Twenty-two nominal species are examined, resulting in an assessment of six valid species, enabled only by the connection between different study methods.

Overall, this thesis lays the basis for further evolutionary systematic studies on a complex snail superfamily, that thus far is oftentimes overlooked due to its rough taxonomic history. Thereby this study exemplifies the need to survey all of nature’s parts to be able to assess its full picture. Only then our efforts to protect every part of it will be worthwhile.

Zusammenfassung

Die gegenwärtige Biodiversitätskrise und das damit verbundene Massenaussterben ist zweifelsfrei die größte Herausforderung der die Menschheit im 21. Jahrhundert gegenübersteht. Um ein effektives Handeln zu ermöglichen, müssen nicht nur direkte Maßnahmen ergriffen werden, sondern ebenfalls grundlegende Untersuchungen der Biodiversität vorgenommen werden, damit die ‘tatsächliche’ biologische Vielfalt ermittelt werden kann. Hierbei ist die Beschreibung bisher unbekannter Arten ebenso wichtig wie die Neubewertung bekannter Taxa, deren taxonomischer Status unklar ist.

Um zeigemäße Studien über die Vielfalt in solch wissenschaftlich vernachlässigten Gruppen durchzuführen, sollten diese im Rahmen eines evolutionssystematischen Ansatzes — also einer Integration morphologischer und molekulargenetischer Methoden vor dem Hintergrund evolutionsbiologischer Fragestellungen — durchgeführt werden. In der vorliegenden Dissertation wurden mehrere solcher Studien über zwei bisher nicht hinreichend untersuchten Schneckenfamilien innerhalb der Überfamilie Cerithioidea zusammengestellt. Hierbei stellten die in tropischen Süßgewässern lebenden Thiaridae sowie die in tropisch bis warm-temperaten Meeresküsten lebenden Planaxidae die untersuchten Fokusgruppen dar.

Zuerst wird die erste familienweite molekulargenetische Studie der Thiaridae vorgestellt, die Repräsentanten aller derzeit unterschiedenen Gattungen beinhaltet. Obschon einige morphologisch etablierte Linien in der vorliegenden Phylogenie nicht eindeutig widerspiegelt werden, erweitert die Untersuchung unser Verständnis der historischen Biogeographie, die zur Diversifikation der Gruppen innerhalb dieser Familie führte.

Innerhalb der Thiaridae wird der *Melanoides-Stenomelania* Komplex unterschieden. Dieser stellt eine taxonomisch äußerst unübersichtliche Gruppe von Arten dar, die in den Gattungen *Melanoides*, *Stenomelania* und *Neoradina* geführt werden. Im Ergebnis wird die umstrittene *Neoradina* Linie für diesen Komplex bestätigt und *Stenomelania* aufgrund ihrer Gehäuseform und ihres differenzierten entwicklungsbiologischen Mechanismus abgegrenzt.

Innerhalb der Planaxidae liegt ein Fokus auf der Untersuchung zur Poecilogonie (also dem zeitgleichen Auftreten zweier unterschiedlicher entwicklungsbiologischer Modi innerhalb derselben Art) von *Planaxis sulcatus*. Erstmals wurde hier eine Studie über den gesamten Verbreitungsraum der Art durchgeführt, bei der auf die Molekulargenetik und Entwicklungsbiologie der Populationen eingegangen wurde. In der Folge kann eine geographische Poecilogonie festgestellt werden, also eine Varianz der unterschiedlichen Entwicklungsmodi entlang des Verbreitungsgebiets.

Weiterhin wird mit einem integrativen Ansatz von morphologischen und molekularen Methoden die Planaxidengattung *Supplanaxis* revidiert. Unter den zweiundzwanzig Nominalarten dieser Gattung wurden sechs valide Arten festgestellt, die nur durch die Verbindung der angewandten Methoden erkannt werden konnten.

Die Ergebnisse aller Teilstudien dieser Dissertation bilden die Basis für eine Vielzahl weiterer evolutionssystematischer Studien an einer oftmals durch ihre unübersichtliche Taxonomie unbearbeiteten Schnecken-Überfamilie. Dabei zeigen diese Arbeiten abermals auf, dass alle noch so kleinen Teilstücke der Natur in Augenschein genommen werden müssen, um ein vollständiges Bild zu erhalten. Nur durch ein solches Vorgehen werden unsere Mühen zum Schutz all dieser Teile sich lohnen.

Chapter 1 General Introduction

Benedikt Wiggering

The taxonomic impediment and the sixth mass extinction

Although for the last quarter of the last century taxonomists have been constantly working on the naming of all extant life, a vast number of species still remain undetected (Glaubrecht, 2009, 2019; Mora et al., 2011, Costello et al., 2012; Locey & Lennon, 2016). As we enter the sixth mass extinction of so far unprecedented extent (Barnosky et al., 2011; Ceballos et al., 2017; Díaz et al., 2019, Cowie et al., 2017 for an assessment of molluscs), we need to face the plethora of threats and lessen their impact. This is the major challenge mankind and in particular nature conservation is confronted with. Simultaneously, we face the near-unsolvable problem that many species are in danger to go extinct before they are even discovered — known as one facet of the taxonomic impediment. Equally as problematic is the fact that numerous nominal species need to be reassessed, though their original habitat might no longer be existent and the species might be on the brink of extinction (Giangrande, 2003; Sluys, 2013). Numerous factors drive these threats, being especially pronounced in the tropical realms (as detail, e.g. for freshwater organisms in Dudgeon et al., 2006; Strong et al., 2008; Barlow et al., 2018).

This loss of biodiversity is mostly expressed through a focus on vertebrate species (e.g. Jenkins et al., 2013; Dirzo et al., 2014; Ceballos et al., 2017), while invertebrates are oftentimes overlooked (Cameron et al., 2018; Eisenhauer et al., 2019). Nevertheless, the latter constitute the majority of life on our planet and usually play a key role for the integrity of their respective ecosystems (Wilson, 1987). Hence, this neglect of invertebrates is rather troubling. Though more recent studies on the matter emerge (Hallmann et al., 2017; Seibold et al., 2019; Didham et al., 2020), focussing on arthropods.

Land and freshwater molluscs account for a large proportion of recorded invertebrate extinctions (Sartori et al., 2013; Régnier et al., 2009). They are some of the most threatened species in the world – especially those living in freshwater habitats (Lydeard et al., 2004; Bogan, 2006; Lysne et al., 2008; Seddon et al., 2008; Strong et al., 2008; Vaughn, 2010; Cuttelod et al., 2011; Johnson et al., 2013; Lopes-Lima et al., 2014, 2017; Neubert et al., 2019; Böhm et al., 2020). One of the reasons for this lack of attention is, that their oftentimes convoluted taxonomy hampering their accessibility. Though we certainly advanced in our knowledge on the matter (see Lydeard & Cummings, 2019 for an overview), several major groups of freshwater molluscs have been hitherto neglected by modern taxonomy. One major hurdle with the study of these molluscs is oftentimes the vast number of nominal taxa in need of reconsideration as well as a lack of easily identifiable morphological characters suited for taxonomy. Therefore, it is crucial to study these taxa using integrative approaches.

Evolutionary systematics

In contemporary taxonomy it is a common approach that several different methods are combined to constitute a reliable framework for species delimitation. However, such integrative taxonomy approaches (first conceptualized by Dayrat, 2005) oftentimes entail the danger of conducting taxonomy for taxonomy's sake, failing to consider further evolutionary concepts and histories. Therefore, the studies presented in this thesis aim to act under an evolutionary systematics framework (Glaubrecht 2007, 2010). These evolutionary systematics studies intend to access taxonomic diversity, disparity, and genetic variability and their underlying evolutionary cause of speciation, studied within the context of phylogenetic systematics. This line of thinking is crucial, when working with groups where high phenotypic plasticity, genetic entanglement and a plethora of available taxonomic names are prevalent, whilst only few lineages, deserving recognition as evolutionary entities, can be assumed. This approach has been exemplified for molluscs by Glaubrecht et al. (2009), as well as in the chapters 3, 4, 6 and 7 of this study, and for crustaceans by Schwentner et al. (2014, 2015) and Lörz et al. (2020). Furthermore, the integrative approach of these studies allows insights in the individual life histories of taxa, shrouded by more traditional lines of 'adultocentric' thinking.

'Adultocentrism'

Often in biology, the importance of the adult is emphasized by simultaneously diminishing the relevance of juvenile stages. This 'adultocentrism' subsumes the notion to perceive the juvenile as "incomplete" and the adult as the "complete" organism, rendering the latter as the final product of the former (Minelli 2003). Though this concept is deeply rooted in developmental biology (Bonner 1965, Minelli 2003, 2009, 2015), its impact is easily detectable in several fields of biology. Especially taxonomic and biogeographic studies focus on adult stages, therewith neglecting juvenile stages and their crucial importance for understanding means and modes of evolution, species distribution and dispersal. To avoid such a fallacy, lineage-specific life histories must be considered, as physiological characters, dispersal ability and habitat choice can vary throughout a species life cycle.

Contrarily, early life stages are only rarely regarded in taxonomic and biogeographic studies. In some cases this problem might be negligible, as several taxa exhibit a linear life history, taking place only in one distinct habitat. However, for taxa with a bipartite live cycle, e.g. a pelagic larval and a comparatively immobile or even sedentary adult phase, neglecting of these stages leads to the oversight of crucial information (Nathan & Nathan 2014). This is especially true within taxa where parts of the life cycle change between terrestrial, limnic and marine

habitats. Therefore, it is of utmost importance to implement evolutionary systematics studies not only on adult stages, but also factoring in early stages of life history.

Two phenomena that can easily be overlooked if only adult life stages are taken into account, are amphidromy and poecilogony — both representing key elements of the studies presented in this thesis (see Chapters 3, 4 & 6).

Poecilogony is defined as the presence of two different developmental modes with different larval types within the same species (Giard, 1891, 1892, 1905; Hoagland & Robertson, 1988; Bouchet, 1989; Chia et al., 1996; Knott & McHugh 2012). Thereby, geographic poecilogony constitutes a variant of this phenomenon, where differing developmental modes are found between populations (Giard, 1891, 1892, 1905; Chia et al., 1996; Knott & McHugh 2012), rather than within populations as suggested by more restrictive definitions (Hoagland & Robertson, 1988; Bouchet, 1989). With only thirteen thoroughly studied and supported cases of poecilogony exclusively in marine organisms (seven spionid polychaetes [Collin, 2012; Oyarzun & Brante, 2015], five sacoglossan gastropods [Vendetti et al., 2012] and one littorinimorph gastropod [McDonald et al., 2014]), this phenomenon is extremely rare. In Chapter 6 of this thesis, additionally the case of a cerithioidean snail species — *Planaxis sulcatus* (Born, 1778) — is examined and verified, as a case of geographic poecilogony.

Amphidromy constitutes a life-cycle, where adults reproduce under freshwater condition, though either an early life-stage or at least a part of the adult life is taking place within marine realms (Meyers, 1949; see McDowall, 2007 for a review of all forms of diadromy). This rare phenomenon has evolved presumably repeatedly within some families of cerithioidean gastropods.

Cerithioidea Férussac, 1819

Within the gastropods the superfamily Cerithioidea Férussac, 1819 is especially noteworthy based on its combination of both, marine and freshwater taxa, and furthermore, its partially co-dependent diversity of reproductive and developmental modes. Strong et al. (2011) consider 17 recent families and approximately 200 genera and 1100 extant species for the Cerithioidea. The vast majority of this worldwide distributed superfamily is restricted to tropical, subtropical and warm temperate realms (Houbbrick, 1988; Glaubrecht, 1996; Strong et al., 2008, 2011).

Although oftentimes constituting significant if not dominant proportions of the communities they occur in, there is still a lack of modern taxonomic studies on cerithioidean families; see e.g. Lydeard & Cummings (2019) and chapters therein for an overview of the freshwater

families, by Glaubrecht & Neiber (2019) for Thiaridae and Hourbick (1987) for marine Planaxidae Gray, 1850.

In the following chapters of this thesis a focus is laid on the freshwater Thiaridae (Chapters 2-5) and marine Planaxidae (Chapters 6 & 7).

Thiaridae Gill, 1871 (1823)

Though one of the most speciose family of freshwater Cerithioidea, the viviparous Thiaridae Gill, 1871 (1823) are taxonomically highly convoluted, as the family exhibits high rates of taxonomic redundancy, with many taxa needing revision, mainly due to their high phenotypic plasticity (for details and discussion see Glaubrecht, 1996, 2000, 2004, 2011; Glaubrecht et al., 2009; Glaubrecht & Neiber, 2019). Previously subsumed under the name Melaniidae Children, 1823, the family has long been used as a figurative “taxonomic trashcan” encompassing all freshwater lineages within the Cerithioidea. First, Thiele (1929) and then Morrison (1952, 1954) started splitting this group, though taxonomic concepts of the group have been in motion over the following decades (Starobogatov, 1970; Hourbick, 1988; Ponder & Warén, 1988; Brown, 1994). A substantiated circumscription of the “core” Thiaridae only emerged after the removal of several taxa by the description of several freshwater families (Melanopsidae Adams & Adams, 1854, Pachychilidae Fischer & Crosse, 1892, Paludomidae Stoliczka, 1868, Pleuroceridae Fischer, 1885 (1863), Semisulcospiridae Morrison, 1952), by an accumulation of molecular and/or morphological evidence (e.g., Glaubrecht, 1996, 1999, 2004, 2009, 2011; Holznagel & Lydeard, 2000; Lydeard et al., 2002; Simone, 2001; Strong & Köhler, 2009; Strong, 2011; Strong et al., 2011; Neiber & Glaubrecht, 2019; Glaubrecht et al., in prep.).

The thiarids inhabit lotic and lentic freshwater environments of South Asia and Southeast, Australia and several Pacific Islands, as well as sub-Saharan Africa. Some species are known to tolerate brackish conditions in the tailwaters of streams and rivers (Glaubrecht et al., 2009; Glaubrecht, 2011; Glaubrecht & Neiber, 2019). *Melanoides tuberculata* (Müller, 1774) and *Tarebia granifera* (Lamarck, 1822) are known to pose high invasive threats to tropical and subtropical biomes and nowadays have a global distribution (Facon et al., 2003).

Anatomically, thiarids are characterised a large textured accessory pad in the midgut, a tubular, non-glandular pallial oviduct and a spermatophore bursa (Strong, 2011). Furthermore, they possess a subhaemocoelic brood pouch in the neck region of the head-foot of the female, enabling viviparity throughout this family. Thiarids evolved two different life history strategies, based on two different modes of development. Some species are known to exhibit a developmental mode in which large amounts of free-floating planktotrophic veliger larvae are

released (“r-strategy”, ovoviviparous). Other species evolved a developmental mode where offspring is bred for a longer period of time in lower numbers, nourished directly by the parents through a “pseudoplacenta” (Glaubrecht 1996) and released after reaching the stage of a crawling juvenile (“k-strategy”, euoviviparous; see Glaubrecht 1996, 1999, 2006 for a detailed overview on these developmental modes).

Furthermore, the Thiaridae exhibit differing reproductive modes. Traditionally, all thiarids were interpreted as being parthenogenetic (Morrison, 1954). However, Jacob (1957, 1958) identified males in *Melanoides tuberculata* rendering this as a facultatively parthenogenetic species. For *Mienplotia scabra* (Müller, 1774) males have also been reported (Riech, 1937). Hence, the problem of gonochorism vs parthenogenesis in Thiaridae is not solved, pointing to at least ‘true’ and facultative parthenogenesis.

However, the results presented in this thesis point towards the existence of both sexual and asexual reproduction within Thiaridae (see the discussion of Chapter 4), albeit the frequency is not determined here either.

Shells of most thiarid species are turreted and of blackish-brown colouration. Ornamentation, colouration and shape vary heavily, from high spired needle like *Stenomelania* Fischer, 1885 to near-globose *Fijidoma* Morrison, 1952 and densely ornamented *Tarebia* Adams & Adams, 1854 to very smooth *Balanochochlis* Fischer, 1885 (see Chapter 2 Fig 1 for an overview on shells of each genus). Furthermore, intraspecific variation is very common within the Thiaridae, having led to the description of numerous nominal taxa during the 19th century, leading to high rates of taxonomic redundancy within the family and resulting in widespread confusion concerning species recognition (Glaubrecht, 1996, 1999, 2006, 2011; Kano et al., 2011; Glaubrecht & Neiber, 2019).

Potentially as a direct result of this taxonomic confusion, comprehensive molecular studies on and in this family are sparse and direly needed (Facon et al., 2003; Genner et al., 2007; Miura et al., 2008; Hidaka & Kano, 2014; Van Bocxlaer et al., 2015; Veeravechskij et al., 2018; Boonmekam et al. 2019; Wiggering et al., 2019; Lentge-Maaß et al., in press.) This thesis encompasses the first comprehensive study of representatives of all twelve currently recognised thiarid genera (see Chapter 2). A study of mitochondrial COI and 16S gene fragments as well as H3 and 28S nuclear gene fragments for a smaller subset of studied specimens has been conducted encountering rampant taxonomically incongruencies within the current morphology-based system. The study furthermore enabled a molecular dating of the split of Thiaridae and their sister family (Hemisiniidae Fischer & Crosse, 1891) at 73.5 Ma in the Late Cretaceous and the onset of diversification of the Thiaridae at 32.1 Ma in the Early Oligocene. Furthermore,

the study recovered ovoviviparity as the ancestral mode of development within the Thiaridae and the release of shelled juveniles to have evolved independently twice, with a possible reversal to releasing veligers in one lineage. Lastly (see also Chapter 2), an ancestral area estimation suggested the origin of Thiaridae in a region being composed of South Asia and Southeast Asia, Australia, and the Indo-West Pacific.

Stenomelania-Melanoides complex

Within the molecular study of all Thiaridae genera (Chapter 2), two genera have to be mentioned as excessively problematic as to their monophyly, as *Stenomelania* and *Melanoides* specimens clustered at several different independent positions within the calculated phylogenies. A third genus shell-morphologically near-indistinguishable to the two aforementioned taxa is *Neoradina* Brandt, 1974. In Chapters 3 & 4 an emphasis on this complex of genera is given, conducting evolutionary systematics studies on *Stenomelania* (Chapter 4) and *Neoradina* (Chapter 3).

Only rather recently was *Stenomelania* elevated to generic rank (Houbrick, 1987), having been initially introduced as a subspecies of the nomenclatorial available but invalid genus-name *Melania* Lamarck, 1799, and later considered as subgenus of *Melanoides* (see e.g., Pace, 1973; Rensch, 1934; Starmühlner, 1976, 1984, 1993). However, recent studies all recognise *Stenomelania* as separate (Bandel et al., 1997; Glaubrecht, 1996, 2004; Glaubrecht et al., 2009; Ginnich, 2015; Hidaka & Kano, 2014; Miura et al., 2008; Strong et al., 2011).

The type species *Melania aspirans* Hinds, 1844 has been described from Fiji, marking the easternmost border of *Stenomelania* distribution (Starmühlner, 1976). *Stenomelania* species are furthermore distributed throughout the tropical Oriental, southern Japanese, Oceanian, and Australian regions with most species exhibiting a wide ranged distribution area (Starmühlner, 1976, 1984, 1993, Chapter 3 & 4). The anatomy of several *Stenomelania* species was studied thoroughly by Starmühlner (1976, 1984, 1993) identifying it as typical for Thiaridae. All but one species currently subsumed under *Stenomelania* release a great number of offspring as small veliger larvae ('r-strategy'). This offspring is released downstream in the upper parts of lower reaches of streams and rivers. The larvae are tolerant to high salinities (Seshaiya, 1940; Okazaki & Wada 2007, Hidaka & Kano, 2014) and drift into sea currents. Juveniles re-inhabit tropical streams, rendering *Stenomelania* as a genus of amphidromous snails.

Brandt (1974) introduced *Neoradina* to encompass a then newly described species *Neoradina prasongi* Brandt, 1974 and all species previously subsumed under the subgenus *Radina* Preston, 1915. The latter was synonymized with *Stenomelania* as its type species was

found to be a junior synonym of *Stenomelania plicaria* (Born, 1778) (Schepman, 1918; Rensch, 1934).

Due to the described inconsistent taxonomic state of this complex, in Chapter 3 and Chapter 4 of this thesis evolutionary systematics approaches to *Neoradina* and *Stenomelania* were conducted, using a combination of geometric morphometrics of the shell, mitochondrial DNA based systematic approaches and an analysis of developmental mode based on examinations of brood pouch contents to study the respective genus and taxonomically revise their type species. Both studies find strong morphological support for each genus, though, in both cases genetic support is found to be low. Based on these studies the concept of *Stenomelania* is re-examined and re-defined.

In Chapter 5 the taxonomic status of *Hemicycla plicaria* (Lamarck, 1816) is conserved. If not for the assessment of this chapter, the name would have to be constituted as a junior homonym of *Stenomelania plicaria* (Born, 1778). The latter is part of the species studied in chapter 3 and 4.

Planaxidae Gray, 1850

The Planaxidae have been considered as sister taxon to the Thiaridae (Houbrick 1988, Glaubrecht 1996, Simone 2001), based on both having a subhaemocoelic brood pouch in the neck region of the female's head-foot. Contrarily, the so far most comprehensive molecular study on Cerithioidean snails (Strong et al., 2011) recovered the two families as only distantly related. Therefore, the convergent evolution of the same type of brood pouch within these families is likely, as furthermore these characters appear to have evolved several times independently within the Cerithioidea (Glaubrecht 2006). The possession of a brood pouch and the concomitant viviparity in this family sets it apart from most other marine cerithioidean families. However, besides the anatomical feature the Planaxidae share the same differentiation of developmental modes as their freshwater counterparts. Within the viviparous Planaxidae "r-strategy" brooders are common. However, with *Planaxis sulcatus* a species exists, that also includes populations with a "k-strategy" brooding mode.

Planaxids occur circumglobally in tropical, subtropical and warm-temperate marine shores. Most of its species are rock dwellers, inhabiting intertidal areas, where they are usually common (Sowerby II, 1877; Houbrick, 1987).

An exhaustive revision of the genera contained in Planaxidae has been conducted by Houbrick (1987), giving also a brief overview on the inclusion and exclusion of genera during the 19th and early 20th century. Houbrick revised each genus by examining one species per

genus anatomically. Ponder (1988) suggested to consider *Angiola* Dall, 1926 as a junior synonym of *Hinea* Gray, 1847, based on the shared ability of bioluminescence within species of these genera. Following his family-wide study, Houbrick (1990) positioned the genus *Fossarus* Philippi, 1841 within the Planaxidae. A more restricted survey on planaxids of the South Chinese Sea on the basis of morphological characters was conducted recently, revising three planaxid species occurring in that area (Chen et al., 2018). Finally, Strong & Bouchet (2020, in press) discovered two distinct lineages of *Supplanaxis* Thiele, 1929 in the Caribbean, based on the so far only molecular study of planaxid specimens. Hence, it is obvious that a comprehensive evolutionary systematics approach on the Planaxidae is missing to date.

Therefore, in Chapter 6 of this thesis the results of a comprehensive study of developmental modes of *Planaxis sulcatus* is given, encompassing for the first-time material throughout its entire distribution range. On this material basis, the species was identified to truly provide a case of geographic poecilogony. Populations in the Indo-West Pacific were found to release free-floating planktotrophic larvae from their brood pouches, whereas in the western Indian Ocean shelled and crawling juveniles are released. The molecular genetics of *P. sulcatus* did not reveal two distinct lineages correlating with these differences in life history, implying that this is truly one species with two different developmental modes. An ancestral area estimation revealed the Indo-West Pacific as the most probable area of origin for *P. sulcatus*, implying a “r-strategy” brooding as its original reproductive mode.

Finally, in Chapter 7 a first approach towards an evolutionary systematics of Planaxidae is made by thorough taxonomic evaluation of the genus *Supplanaxis*, recognising shell morphology, biometric measurement, geometric morphometrics of the shell, radula morphology and geometric morphometrics with sliding landmarks as well as molecular genetics based on sequences of the COI and 16S gene fragments, applied to a subset of overall total of six species and two subspecies.

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Chapter 2 The Indo-Australian region as key role in the evolution of diversity in an understudied group of tropical freshwater snails (Gastropoda: Cerithioidea: Thiaridae)

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Abstract

As we are faced with a biodiversity crisis, the problem is obvious that many groups in particular of invertebrates will suffer an enormous loss before we can even describe all of their taxa. Because of this situation it is even more important to investigate hitherto understudied taxa, to secure as much knowledge as possible, to allow for a conversation of as many taxa as possible. One such understudied group are the freshwater snails of the pantropically distributed Thiaridae (Gastropoda, Cerithioidea). To date, only few molecular analyses focussing on a partial set of species or genera have been carried out. We here present the results of the first family-wide phylogenetic analyses of Thiaridae including 247 specimens representative of all twelve currently accepted genera from all parts of their range based on mitochondrial and nuclear gene fragments. The analyses showed wide ranging incongruences with the current, morphology-based taxonomy of the group, suggesting non-monophyly for several well-known and speciose taxa, such as e.g. *Melanoides*, *Tarebia*, *Thiara* and *Stenomelania*, suggesting that shell characters such as the high-turreted of the latter or the stepped-shape of the former are the result of convergent evolution of conchological features rather than an expression of phylogenetic relationships. We discuss potential reasons for these incongruences, acknowledging, however, that many of the possible explanation need further testing based on genomic data sets. We use this molecular phylogeny for a biogeographical analyses and dating, which is consistent with an origin of Thiaridae in Gondwana, with an onset of diversification of extant lineages in the family starting only in the Early Oligocene and another diversification when Australia approached Asia in the Miocene. Dispersal of veliger larvae via ocean currents, anticipated as ancestral reproduction mode for Thiaridae, may have facilitated colonisation of the Indo-Australian region. The complex geological history of the region with moving terranes and emerging and subsiding islands, along with the possibly evolution of eu-viviparity in Thiaridae that limited overseas dispersal, may, have played a key role for the evolution of thiarid lineages. Although there are still many ambiguities to be resolved concerning phylogenetical relationships among thiarid genera and species, the results of the analysis presented here offer, nevertheless, considerable new insights into the evolution and biogeographic history of this group of freshwater snails, which can serve as a sound basis for further investigations.

Keywords: Asia, Australia, biogeography, Gondwana, molecular systematics, molecular dating, ancestral area estimation, evolution of reproductive modes

Introduction

The loss of biodiversity as a consequence of the proposed sixth mass extinction (e.g. Barnosky et al., 2011; Díaz et al., 2019; see also for an assessment of molluscs Cowie et al. 2017) is often exemplified by studies focussing on vertebrate species (e.g. Jenkins et al., 2013; Dirzo et al., 2014; Ceballos et al., 2017, 2020), whereas invertebrates such as arthropods or molluscs are often neglected in this regard (Cameron et al., 2018; Eisenhauer et al., 2019, but see, e.g., Hallmann et al., 2017). This is surprising considering that invertebrates represent by far the most diverse animal groups on Earth, which usually play key roles in the ecosystems they are part of (Wilson, 1987). Continental molluscs account for a large portion of recorded invertebrate extinctions (Sartori et al., 2013; Régnier et al., 2009) and they are among the most imperilled organisms on Earth, especially species living in freshwater habitats (Lydeard et al., 2004; Bogan, 2006; Lysne et al., 2008; Seddon et al., 2008; Strong et al., 2008; Vaughn, 2010; Cuttelod et al., 2011; Johnson et al., 2013; Lopes-Lima et al., 2017, 2018; Neubert et al., 2019; Böhm et al., 2020). However, several species also have high invasive potential and are considered as pests (Facon et al., 2003; Capinha et al., 2014, 2015).

Notwithstanding the fact that our knowledge on the relationships, the phylogeny and biogeography of many freshwater inhabiting gastropods has greatly increased over the past decades (see Lydeard & Kummings, 2019 and chapters therein for an overview), several groups remain problematic or have – so far – been neglected with regard to molecular genetic studies. Considering the speed with which some lineages decline or even become extinct, research efforts, therefore, ought to be focussed on these groups, especially taking into account that many freshwater taxa are thought to be particularly suitable (especially those taxa with a long evolutionary history, wide distribution and a rich fossil record) for the study of biogeographical patterns and processes and how these affect diversification dynamics (e.g. Rintelen et al., 2014; Stelbrink et al., 2020).

The Thiaridae Gill, 1871 (1823), in earlier treatments until around the mid 20th century subsumed under the name Melaniidae Children, 1823, is one such understudied group. The family has been used for a long time as a “rubbish bin” to accommodate all freshwater lineages in the Cerithioidea Fleming, 1822. By splitting the Melaniidae in the sense of Thiele (1928, 1929) into three separate clades, Morrison (1952, 1954) started a process of disassembling this large, polyphyletic assemblage of freshwater Cerithioidea. However, taxonomic concepts of the

group have largely been in flux over the following decades (Starobogatov, 1970; Houbbrick, 1988; Ponder & Warén, 1988; Brown, 1994; Glaubrecht 1996). Only during the past two decades, after the removal of Melanopsidae Adams & Adams, 1854, Pachychilidae Fischer & Crosse, 1892, Paludomidae Stoliczka, 1868, Pleuroceridae Fischer, 1885 (1863), Semisulcospiridae Morrison, 1952 and recently Zemelanopsidae Neiber & Glaubrecht, 2019 and Hemisinidae Fischer & Crosse, 1891, a better substantiated circumscription of “core” Thiaridae began to emerge on the basis of molecular and/or morphological evidence (e.g., Glaubrecht, 1993, 1996, 2011; Holznagel & Lydeard, 2000; Lydeard et al., 2002; Simone, 2001; Glaubrecht & Rintelen, 2003; Glaubrecht et al., 2009; Strong & Köhler, 2009; Strong, 2011; Strong et al., 2011; Neiber & Glaubrecht, 2019; Glaubrecht et al., in prep.). Phylogenetic analyses also suggested that Cerithioidea adapted to freshwater habitats at least twice, or possibly three times independently (Strong et al., 2011).

Thiaridae s. str. have an autochthonous distribution in Southeast and South Asia, Australia and several Pacific Islands, as well as sub-Saharan Africa, both in lotic and lentic freshwater environments, with some species also tolerating brackish conditions in the lower courses and estuaries of rivers (Glaubrecht et al., 2009; Glaubrecht, 2011; Glaubrecht & Neiber, 2019b). Some species like *Melanoides tuberculata* (Müller, 1774) or *Tarebia granifera* (Lamarck, 1822) are invasive in tropical and subtropical biomes, and today have a circum-global distribution (e.g., Brown, 1994; Glaubrecht, 1996; Glaubrecht & Neiber, 2019b).

Members of the Thiaridae play a variety of roles in aquatic ecosystems as primary herbivores, vectors of diseases and sometimes substantial contributors to biomass (Kano et al., 2011). Thiarids have often large (up to 10 cm), usually high-spired shells that can be smooth but may also bear grooves, nodules, ribs or spines (. 1). Their shells are usually dark brown or blackish because of the presence of an often relatively thick organic periostracum as the outer layer of the shell. Anatomically, Thiaridae are characterised by a tubular, non-glandular pallial oviduct, a spermatophore bursa, and a large and textured accessory pad in the midgut (Strong et al., 2011). Members of the family have realised two different life history strategies that were characterised in Glaubrecht (1996, 1999, 2006) by the duration of ontogenetic stages to remain within a subhaemocoelic brood pouch in the neck region of the cephalopodium of the female, which at the same time might also reflect a differential degree of parental investment, even including nourishment of the embryos and juveniles via nutritive tissue (Glaubrecht 1996; Glaubrecht et al., 2009; Maaß & Glaubrecht, 2012; Glaubrecht & Neiber, 2019b; Lentge-Maaß et al., in press). While in some thiarids only very early ontogenetic stages, i.e. eggs or embryos without shell, develop and are released as veligers (ovo-viviparity, here referred to as r-strategy)



Figure 1. Shells of type species of thiarid taxa. **A.** *Thiara amarula*, Indonesia, Central Sulawesi, Peleng Island, Tataban River (ZMB 107364-3). **B.** *Balanochochlis glans*, Indonesia, East Nusa Tenggara, Nangapanda, East of Ende Bay (ZMB 106468-3). **C.** *Fijidoma maculata*, Fiji, S Rokounaka, Wainimbuka R, Viti Levu (ZMB 106379-sk9). **D.** *Melanoides tuberculata*, Thailand, Khao Thong (ZMB 127444-4). **E.** *Melasma onca*, Australia, Northern Territory, Bamboo Creek, c. 3–10 m from Daly River (ZMB 106673a). **F.** *Mieniplotia scabra*, Indonesia, North Sulawesi, Minahasa, Stream between rice fields, tributary of Lake Tondano (ZMB 191037a). **G.** *Neoradina prasongi*, Thailand, Chalung City, Khlong Chalung, Muang District (ZMB 127590-2). **H.** *Plotiopsis balonnensis*, Australia, Northern Territory, Red Centre: Three Mile Point, Finke River, at crossing of Stuart Highway (ZMB 106689a-1). **J** *Ripalania queenslandica*, Australia, Queensland, North Johnston River (ZMB 106355-1); **K.** *Sermyla carbonata*; Australia, Queensland, Norman River (ZMB 106713-2). **L.** *Stenomelania aspirans*, Fiji, Sovi River, Malevu, Coral Coast (ZMB 106390-1). **M.** *Tarebia granifera*, Indonesia, Ambon, North coast, near Hitu Lama (ZMB 107442-2). **A, D, G, L.** Scale bars = 10 mm. **B, C, E, F, H, J, K, M.** Scale bars = 5 mm.

other thiarid species brood and even transform their subhaemocoelic brood pouch into a “pseudoplacenta” (Glaubrecht, 1996) that, via matrotrophy, apparently helps to nourish the developing juveniles (eu-viviparity, here referred to as k-strategy). When the eu-viviparous modus is developed, oftentimes all growth stages are present at the same time and the shell of a juvenile can comprise up to seven whorls when hatching from the brood pouch. All Thiaridae have long been assumed to reproduce by parthenogenesis (Morrison, 1954, see Glaubrecht, 1996 for a detailed discussion). However, Jacob (1957, 1958) and Ben-Ami & Heller (2005) reported sexually as well as asexually reproducing individuals for populations of *M. tuberculata* in India and Israel, thus contradicting the general assumption that indeed all thiarids reproduce asexually. Further studies point in this direction, as for e.g. *Thiara scabra* (Müller, 1774) males have also been reported (Riech, 1937) and recently, spermatophore containing sperm was described for *Thiara amarula* (Healy & Glaubrecht 2018). Colour as well as shell shape and ornamentation patterns often vary considerably within thiarid species. Like other groups of freshwater snails, this extensive intraspecific variation has produced widespread confusion concerning species recognition (Glaubrecht, 1996, 2009, 2011; Kano et al., 2011; Glaubrecht & Neiber, 2019b; Lentge-Maaß et al., in press). As a consequence, it is unknown how many species of freshwater thiarids currently really exist, and there is often little consensus in the scientific literature regarding the correct names of those that have been documented, suggesting taxonomic redundancy being as high as c. 70 percent as found for Australian thiarids (Glaubrecht et al., 2009).

Diversity on the generic level of Thiaridae is also currently rather poorly understood, especially because, for example, *Melanoides* Olivier, 1804, has been found to be polyphyletic with regard to some currently accepted species (Von Gersdorff Sørensen et al., 2005; Genner et al., 2007; Dechruksa et al., 2013; Van Bocxlaer et al., 2015), as is also the case in *Tarebia* (see Veeravechskij et al., 2018b), *Thiara* (see Boonmekam et al., 2019), *Sermyla* (see Lentge-Maaß et al., in press) and *Stenomelania* (Wiggering et al., 2019). Being both intriguing and unexpected, these findings need further investigation using a broader taxon sampling. Glaubrecht et al. (2009) surveyed the thiarid diversity of Australia, recognising about eight major groups currently subsumed under the generic names *Thiara* Röding, 1798, the type genus of the family, *Melanoides* Olivier, 1804, *Sermyla* Adams & Adams, 1854, *Melasma* Adams & Angas, 1864, *Plotiopsis* Brot, 1874, *Stenomelania* Fischer, 1885, *Ripalania* Iredale, 1943 and *Mieniplotia* Low & Tan, 2014). In addition, the following taxa belong, based on morphology, to the Thiaridae: *Tarebia* Adams & Adams, 1854, *Neoradina* Brandt, 1974, *Balanocochlis* Fischer, 1885 and *Fijidoma* Morrison, 1952.

Molecular genetic investigations of Thiaridae have been limited to specific geographic areas or included only a limited number of taxa (Facon et al., 2003; Genner et al., 2007; Miura et al., 2008; Hidaka & Kano, 2014; Van Bocxlaer et al., 2015; Veeravechsukij et al., 2018b; Boonmekam et al. 2019; Wiggering et al., 2019; Lentge-Maaß et al., in press.; Glaubrecht et al., in prep.). We here present the first family-wide analysis of Thiaridae covering the entire range of the family and including representatives of all currently recognised genera based on mitochondrial and nuclear markers. Additionally, we use ancestral area and ancestral character state estimation to infer the geographic origin of the family and to assess the evolution of reproductive modes.

Material and Methods

Sampling

The majority of sequenced specimens used in this study were collected by Matthias Glaubrecht and other members of his working group at ZMB and ZMH throughout the last two decades on numerous field expeditions. The material was inventoried under the former curatorial work of the first author in the malacozoological collection of the Museum für Naturkunde, Berlin (Germany, ZMB). Additionally, samples from the following museums were used: Australian Museum Sydney (Sydney, Australia, AMS), Florida Museum of Natural History (Gainesville, USA, FLMNH), Silpakorn University (Bangkok, Thailand, SUT) and Western Australian Museum (Perth, Australia, WAM). We included specimens belonging to the related Hemisinidae in the sense of Glaubrecht & Neiber (2019a) and Glaubrecht et al. (in prep.) (*Cubaedomus brevis* (d'Orbigny, 1842), *Hemisinus lineolatus* (Wood, 1828) and *Pachymelania fusca* (Gmelin, 1791)) as well as Paludomidae (*Paludomus siamensis* (Blanford, 1903) and *Paludomus petrosa* (Gould, 1843)) as an outgroup.

Photo imaging

Shells were placed in a standard position, in which the aperture is positioned at a 90° angle in relation to the optical axis of the camera and the columella parallel to the background. Pictures of undamaged adult specimens were taken by remote shooting with Digital Photo Professional version 3.12.51.2 (Canon Inc.) and EOS Utility version 2.12.2.1 (Canon Inc., Tokyo, Japan) using a digital camera. Photos were stacked with Helicon Focus version 5.3.14.2 (Helicon Soft, Kharkiv, Ukraine). Figures were assembled using Adobe Photoshop CS5

version 12.0.4x32 (Adobe Corporation, San José, CA, USA) and Adobe Illustrator CS5 version 15.0.0 (Adobe Corporation).

DNA extraction and amplification

We extracted DNA from foot muscle tissue samples following the CTAB protocol for molluscan tissues by Winnepenninckx et al. (1993) with slight modifications. Tissue pieces were lysed in 300 µl CTAB buffer (2% CTAB, 1.4M NaCl, 20mM EDTA, 100mM tris-HCl pH8.0), 0.6 µl b-mercaptoethanol and 10 µl serine proteinase K and incubated at 55 °C and 550 rpm in an Eppendorf R Thermomixer compact (Eppendorf AG, Hamburg, Germany) overnight. Subsequently, 300 µl chloroform: isoamyl alcohol (24:1) was added to the lysate, mixed manually for 2 min and centrifuged for 10 min at 15,000 rpm in an Eppendorf R centrifuge 5424 (Eppendorf AG). Afterwards the top layer was extracted into a new set of tubes. This washing step was repeated and the top layer of the supernatant was placed into tubes filled with 600 µl of 95% ethanol and 25 µl of 3M sodium acetate solution. The mixture was stored in a freezer at -20 °C. After three days, DNA was precipitated by centrifuging for 10 min at 15,000 rpm. The ethanol–sodium acetate solution was discarded and 1 ml 75% ethanol was added to wash the pellet. After a 5 min centrifuge step at 15,000 rpm, ethanol was removed. The DNA pellet was dried and then dissolved in 30 µl of 0.1 TE buffer for further use.

Partial sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI) and 16 S rRNA (16S) genes were amplified by the polymerase chain reaction (PCR) using the primer pairs LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3'; Folmer et al., 1994) and HCO2198var (5'-TAW ACT TCT GGG TGG CCA AAR AAA T-3'; Rintelen et al., 2004) for COI, and 16S_F_Thia2 (5'-CTT YCG CAC TGA TGA TAG CTA G-3'; Gimnich, 2015, see also Neiber & Glaubrecht, 2019) and H3059var (5'-CCG GTY TGA ACT CAG ATC ATG T-3'; Wilson et al., 2004) for 16S. Furthermore, two nuclear gene fragments, 28S and H3 were amplified using primers 28S Fmod: (5'- ACC CGC TGA ATT TAA GCA TAT -3') (modified from Van der Auwera et al., 1994) and 28S Rmod (5'- GCT ATC CTG ACG GAA ACT TC -3', Gimnich, 2015) for 28S and, H3 F (5'- ATG GCT CGT ACC AAG CAG ACV GC -3') and H3 R (5'- ATA TCC TTR GGC ATR ATR GTG AC -3') (both Colgan et al., 2000) for H3.

Amplifications were performed in 25 µl volumes containing 2.5 µl 10× amplification buffer (biolabproducts, Bebensee, Germany), 0.5 µl dNTP mix (5 mM each, biolabproducts), 0.2 µl Taq DNA polymerase (Thermo Fisher Scientific, Waltham, USA), 1 µl of each primer (Sigma-Aldrich, through Merek KGaA, Darmstadt, Germany), 18.8 µl ddH₂O and 1 µl DNA template. For the mitochondrial gene fragments amplifications were performed with an initial

denaturation at 94°C for 3 min, 35 PCR cycles (94 °C for 30 s, 50 °C (COI) or 45 °C (16S) for 1 min, 72 °C for 1 min) and final extension 72 °C for 5 min. For 28S a touchdown PCR was performed with initial denaturation at 94 °C for 3 min, 7 cycles of touchdown PCR (94 °C for 30 s, 60–53 °C annealing for 1 min and 72 °C extension for 2 min) followed by 33 cycles (94 °C for 30 s, 52 °C annealing for 1 min and 72 °C extension for 2 min) and a final extension step at 72 °C for 8 min. For H3 PCR was performed with initial denaturation at 94 °C for 3 min, 35 cycles (30 sec at 94 °C, 50 °C (16S) annealing for 1 min and 72 °C extension for 1 min) followed by a final extension step at 72 °C for 5 min. In cases where this procedure did not lead to sufficient DNA concentration, PCR was repeated under the same conditions using the QIAGENR_Multiplex PCR Kit (Qiagen, Hilden, Germany).

PCR products were purified using NucleoSpin Extract II Kits (Macherey-Nagel, Düren, Germany) or ExoSap-IT R (US Biochemicals, Salem, MA, USA) following the manufacturers protocols. Cycle sequencing reactions were carried out on an ABI 3130xl Genetic Analyser (Applied Biosystems, Waltham, MA, USA) at SMB GmbH (Berlin, Germany). See Supporting Information, Tables S1 and S2 for GenBank accession numbers and voucher information.

Phylogenetic analyses

Forward and reverse strands were assembled and edited using CodonCode Aligner 3.7.1 (CodonCode Corporation, Dedham, MA, USA). Primer sequences were removed resulting in COI sequences of ~660 bp, 16S sequences of ~990 bp, 28S sequences of ~1070 bp and H3 sequences of ~328 bp. Sequences were aligned using MUSCLE (Edgar, 2004) as implemented in GENEIOUS under default settings. Pairwise uncorrected p-distances were calculated for each gene fragment separately with MEGA 7 (Kumar et al., 2016). We analysed two datasets: 1) concatenated COI and 16S sequences (247 specimens), and 2) concatenated COI, 16S, H3 and 28S sequences (67 specimens). PARTITIONFINDER 2.1.1 (Lanfear et al., 2012) was used to select appropriate partitions and evolutionary models for both datasets. For the mitochondrial dataset four partitions were assumed initially (16S and 1st, 2nd and 3rd codon positions of COI). The results of the PARTITIONFINDER analysis using the Bayesian information criterion to select among partitions and models suggested not to partition the data and apply the GTR+G evolutionary model. We carried out the PARTITIONFINDER analysis for the concatenated COI, 16S, H3 and 28S alignment, for mitochondrial and nuclear gene respectively. Here we initially assumed eight partitions (16S and 1st, 2nd and 3rd codon positions of COI, 28S and 1st, 2nd and 3rd codon positions of H3). The results of the PARTITIONFINDER analysis suggested two partitions: 1st and 3rd codon positions of COI under the GTR+G evolutionary model and

16S, 2nd codon position of COI, 28S and 1st, 2nd and 3rd codon positions of H3 under the GTR+I+G model. The selected partitions and evolutionary models were used for the subsequent Bayesian inference (BI) and maximum likelihood (ML) analyses, respectively.

We performed a BI analysis using MRBAYES version 3.2.6 (Ronquist et al., 2012) running Metropolis-coupled Monte Carlo Markov chain (MC³) searches with four chains in two separate runs for 50,000,000 generations with trees sampled every 1,000 generations under default heating. Potential scale reduction factors close to 1 and estimated effective sample sizes above 200 from the MRBAYES output were used as diagnostics to ensure that the MC³ searches had reached stationarity and convergence. The first 5,000,000 generations of each run were discarded as burn-in.

We performed heuristic ML analyses in GARLI 2.0 (Zwickl, 2006) using the partitions and best-fit models as suggested by PARTITIONFINDER. Support values were computed by bootstrapping with 1,000 replications. Using PAUP* 4.0b10 (Swofford, 2002), we conducted heuristic maximum parsimony (MP) searches with unordered characters, 100 random sequence addition replicates, tree bisection and re-connection (TBR) branch-swapping, and gaps treated as missing data. Internal branch support was assessed in PAUP* by bootstrapping with 1,000 replications, using full heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and one tree held at each step during stepwise addition.

Posterior probabilities from the Bayesian analysis and bootstrap support values from the ML and MP analyses were mapped onto the BI 50% majority consensus tree with SUMTREES version 3.3.1 (part of the DENDROPY 3.8.0 package, Sukumaran & Holder 2010). Bootstrap support (BS) $\geq 70\%$ from the ML and MP analyses and posterior probabilities ≥ 0.95 were interpreted as positive support for a node.

Molecular dating

To infer a time frame for diversification patterns in the clade including Paludomidae, Hemisinidae and Thiaridae (only specimens for which data for all four target genes was available were included), we used the Bayesian algorithm implemented in Beast 2.1.4 (Bouckaert et al., 2014) based on mitochondrial and nuclear sequence data assuming the same partitions and nucleotide substitution models as in the ML and BI analyses. As a strict molecular clock was rejected at $\alpha = 0.05$ by the test implemented in MEGA 7 for the different partitions, a linked uncorrelated relaxed lognormal molecular clock was used for the Beast analysis and assuming the birth-death model as tree prior. The analysis was run for 50,000,000 generations with a sampling frequency set to 10,000. Tracer v1.7 (Rambaut et al., 2018) was used to assess

convergence and to check that the estimated effective population sizes (ESS) for all estimated parameters were above 200. The first 10% of generations were discarded as burn-in. A maximum clade credibility tree with median node heights was calculated from the post burn-in samples with Treeannotator 2.1.3, which is part of the Beast distribution.

The oldest fossils assigned to the Thiaridae in the sense of Strong et al. (2011), i.e. Thiaridae plus Hemisinidae, are recorded from late Albian strata of New Zealand (~100 Ma) (Beu et al., 2014) and middle to late Albian strata of New South Wales in Australia (Hamilton-Bruce et al., 2004). Although Beu et al. (2014) assign their fossil species tentatively to *Melanoides*, these authors also acknowledge a possible relationship to the South American to Mesoamerican *Hemisinus*. The age of this fossils was, therefore, used for calibrating the node uniting Paludomidae, Thiaridae and Hemisinidae assuming a lognormal-distributed prior for this calibration. Otherwise old thiarid fossils are scarce. Nuttall (1990) reported the oldest fossils assignable to the South American thiarid group from Late Oligocene deposits and Bandel & Kowalke (1999) and Kowalke (2001) report fossils similar to the West African *Pachymelania* from Eocene coastal swamp deposits in Hungary.

Ancestral area estimation

Historical distributions patterns were evaluated using ancestral range estimation. The biogeographical analyses were limited to species (or lineages in cases where species were not recovered as monophyletic groups) by pruning replicate species tips off the dated maximum clade credibility tree and removing outgroups using Phytools (Revell, 2012) in R 4.0.2 (R Core Team, 2020). For biogeographical analyses, the R package BioGeoBEARS (Matzke, 2013) was used. The following discrete areas according to the global freshwater regionalisation by Bănărescu (1992) were considered: A) Caribbean region and Middle America, B) Eastern Asia, C), South- and SouthEast Asia, D) Africa), E) Madagascar, F) South America, G) Australia and H) Indo-West Pacific. Probably human-mediated introductions of Thiaridae to Europe, as well as North and South America were not considered.

Two models were implemented in BioGeoBEARS: 1) the dispersal–extinction–cladogenesis (DEC) model (Ree et al., 2005; Ree & Smith, 2008) and 2) the DEC model allowing for founder-event speciation (+J) (Matzke, 2014). Rate multipliers for areas with direct connections were set to 1.0 and those for areas not directly adjacent to 0.01. The maximum number of areas allowed at a node was set to three corresponding to the maximum number of areas observed at a tip for a lineage. Despite alleged conceptual and statistical problems with the DEC and DEC+J models and their comparison via model selection (Ree & Sanmartín, 2018, but see the response

by D. J. Matzke at http://phylo.wikidot.com/biogeobears-validation#DEC_DECj), a likelihood ratio test (LRT) was conducted. The outcomes of the different analyses were also compared based on empirical (biological, geographic) considerations as recommended by Ree & Sanmartín (2018).

Evolution of reproductive modes

To trace the evolution of reproductive modes (oviparous, ovo-viviparous and eu-viviparous in the sense of Glaubrecht, 1996, 1999, 2006) in a maximum likelihood setting, we used R package ape (Paradis et al., 2004) assuming the one-parameter equal rates model to specify the transition probabilities between the states of the discrete character. Reproductive modes for each lineage were based on own observations and published information (Seshaiya, 1940; Abbott, 1952; Dudgeon, 1986; Haynes, 1988; Glaubrecht, 1996, 2006; Schütt & Glaubrecht, 1999; Glaubrecht et al., 2009; Gomez et al., 2011; Dechruksa et al., 2013; Veeravechskij et al., 2018b; Boonmekam et al., 2019; Wiggering et al., 2019; Lentge-Maaß et al., in press); see also Supporting Information, Table S3 for details).

Results

Sequencing

Our extractions and amplifications for both COI and 16S were successful for a total 247 specimens. However, all four targeted gene fragments were obtained only for 67 specimens. The greatest p-distance among the 247 analysed COI sequences of thiarid snails was 31 %. This value was 15% for 16S, 6% for 28S and 2% for H3.

Phylogeny based on mtDNA sequences

The analyses based on mtDNA data alone recovered the Thiaridae as delimited by Glaubrecht et al. (in prep.) as a monophyletic group, albeit only supported in the BI and MP analyses, respectively (Fig. 2, Supporting Information, Fig. S1). Only three of the twelve included thiarid genera were recovered as monophyletic groups: *Balanocochlis*, *Melasma* and *Plotiopsis*. Another three genera, all considered to be also monotypic, were represented by only one specimen each: *Ripalania*, *Fijidoma* and *Neoradina*. The remaining six genera were not recovered as monophyletic, but often represented multiple lineages (with independent occurrences in the phylogeny given): *Melanoides* (9), *Mieniplotia* (2), *Sermyla* (2), *Stenomelania* (7), *Tarebia* (3), and *Thiara* (6) (Fig. 2, Supporting Information, Fig. S1).

Moreover, a number of species that were identified based on shell morphology were not recovered as monophyletic groups: *M. tuberculata*, *Mieniplotia scabra* (Müller, 1774), *T. granifera*, *Stenomelania aspirans* (Hinds, 1844), “*Stenomelania*” *denisoniensis* (Brot, 1877) and *Thiara amarula* (Linnaeus, 1758) (Fig. 2, Supporting Information, Fig. S1).

Phylogeny based on concatenated mitochondrial and nuclear sequences

The phylogeny based on the analysis of concatenated mitochondrial (COI and 16S) and nuclear (28S and H3) sequences obtained from a total of 67 specimens, representing eleven of the studied thiarid genera (*Neoradina* could not be included because only mitochondrial data were available), was overall similar to the analysis based on mitochondrial data alone (Fig. 3). *Balanocochlis* and *Plotiopsis* were recovered as monophyla in this analysis, *Fijidoma*, *Melasma* and *Ripalania* were only represented by one specimen each. As in the previous analysis, six genera were not recovered as monophyletic groups representing often multiple lineages: *Melanoides* (6), *Mieniplotia* (2), *Sermyla* (2), *Stenomelania* (6), *Tarebia* (3), and *Thiara* (5) (Fig. 3).

Molecular dating, ancestral area estimation and evolution of reproductive modes

The results of the molecular clock analysis (assuming an age of ~100 Ma for the clade comprising Paludomidae, Hemisinidae and Thiaridae) recovered a split of Hemisinidae and Thiaridae at 73.5 Ma (95% highest posterior density interval (HPD): 48–100 Ma) in the Late Cretaceous (Fig. 4). The split of African and Neotropical representatives of Hemisinidae was dated at 38 Ma (95% HPD: 19–63 Ma) in the Late Eocene. The onset of diversification of Thiaridae was dated at 32.1 Ma (95% HPD: 18–50 Ma) in the Early Oligocene (Fig. 4).

The ancestral area estimation suggested an origin of Thiaridae in a region being composed of South Asia and Southeast Asia, Australia and the Indo-West Pacific (Fig. 5). The ancestral mode of reproduction for Thiaridae was estimated as releasing veliger larvae from the brood pouch of the female (Fig. 5). The analysis further suggests that retainment of offspring in the brood pouch and release of shelled juveniles evolved independently twice, with a possible reversal to releasing veligers in one lineage (Fig. 5).

Discussion

Previously published studies on phylogenetic relationships in the freshwater snail Thiaridae focused on only few species or a limited number of genera (Facon et al., 2003; Genner et al.,

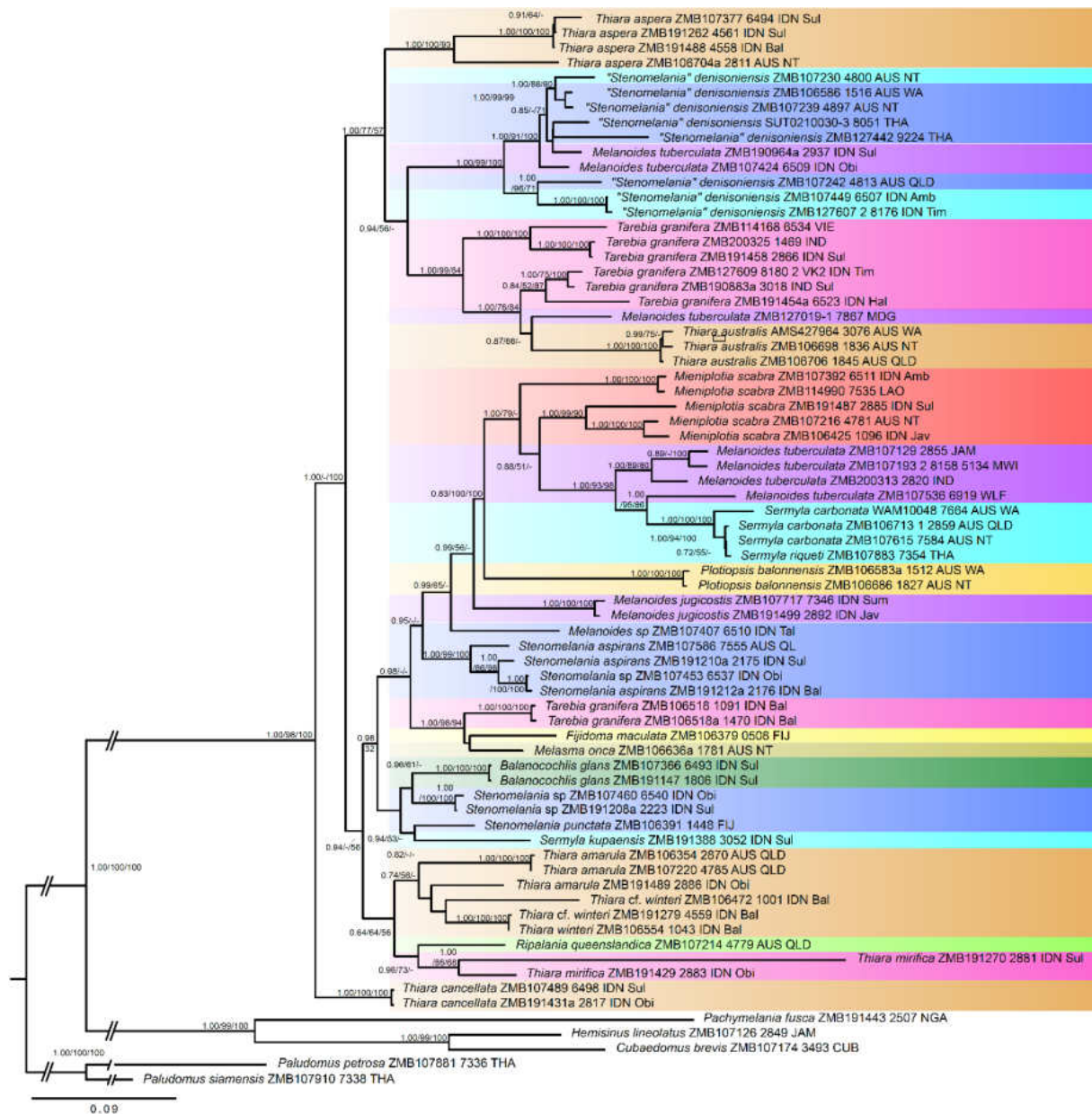


Figure 3. Bayesian 50% majority consensus tree based on concatenated COI, 16S, 28S and H3 sequences. Numbers at the nodes refer to posterior probability (PP) values (left) from the Bayesian (BI) and bootstrap support (BS) values from the maximum parsimony (MP) analysis (middle) and from the maximum likelihood (ML) analysis (right). Only nodes with PP values ≥ 0.50 and/or BS values from ML and/or MP analyses $\geq 50\%$ are annotated.

2007; Miura et al., 2008; Hidaka & Kano, 2014; Van Bocxlaer et al., 2015; Veeravechskij et al., 2018b; Boonmekam et al. 2019; Wiggering et al., 2019; Lentge-Maaß et al., in press.).

Based on wide sampling across in particular Asia and Australia we created a massive data set comprising all relevant taxa on the generic level with representative species of all thiarids, and present the first family-wide molecular phylogenetic analysis of Thiaridae utilizing a combination of mitochondrial (COI, 16S) and nuclear (H3 and 28S) molecular markers.

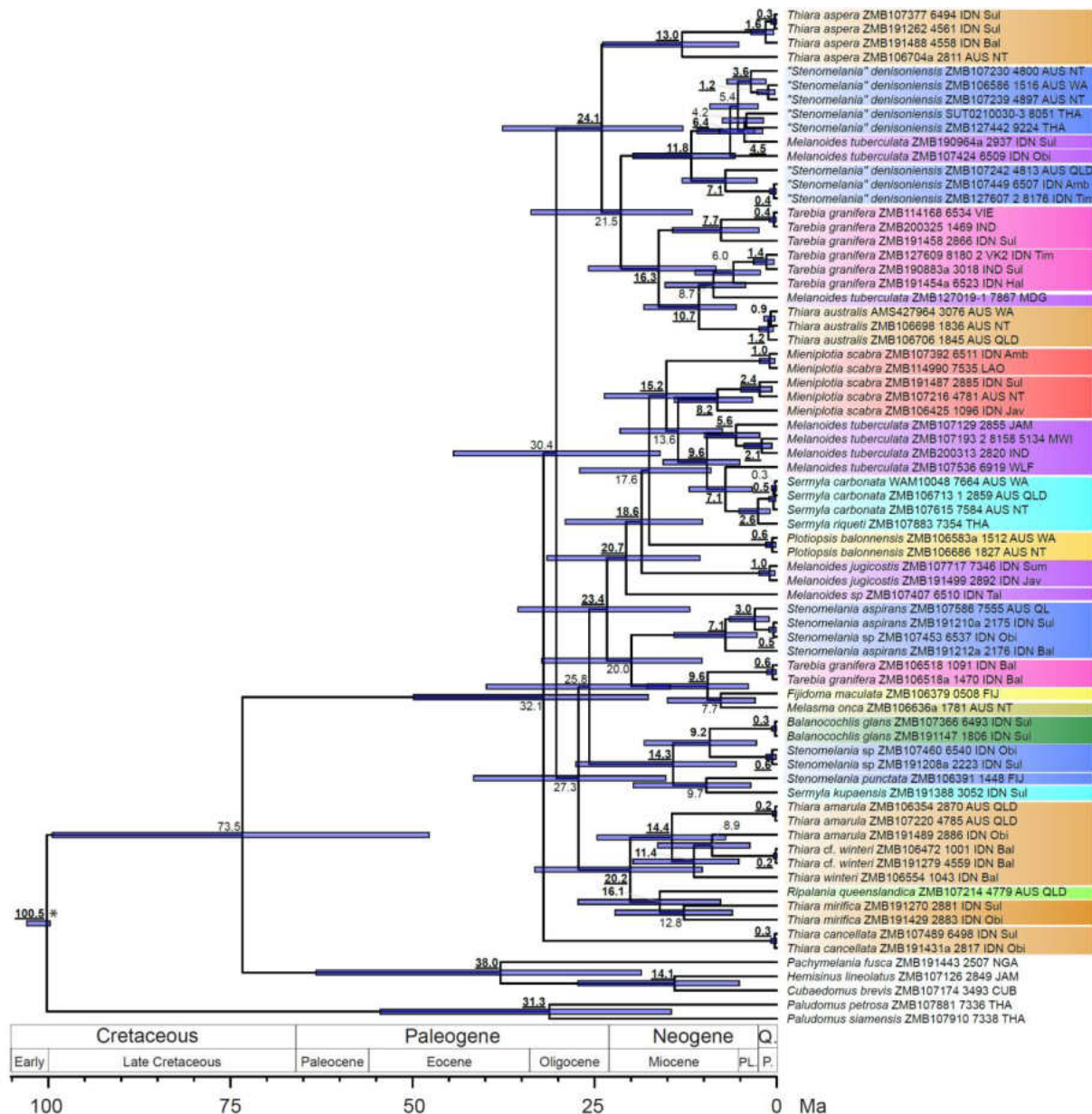


Figure 4. Time-calibrated phylogeny of Thiaridae and related families based on concatenated COI, 16S, 28S and H3 sequences. Numbers at nodes refer to the estimated ages of the nodes and the bars indicate the ranges of the 95% highest posterior density intervals. Node values in bold font indicate posterior probabilities (PP) ≥ 0.90 , underlined node values indicate PP ≥ 0.95 . *: node used for calibration, Q.: Quaternary, PL.: Pliocene, P.: Pleistocene.

The fact that estimating the phylogeny of a group based on only a few markers can be misleading is a well-known phenomenon, and the underlying mechanisms have been discussed extensively (Pamilo & Nei, 1988; Funk & Omland, 2003; Edwards, 2009; Carstens et al., 2013). The phylogenetic analyses presented here may provide another example of the potential pitfalls of inferring relationships from only a small portion of the genome, especially since many of the

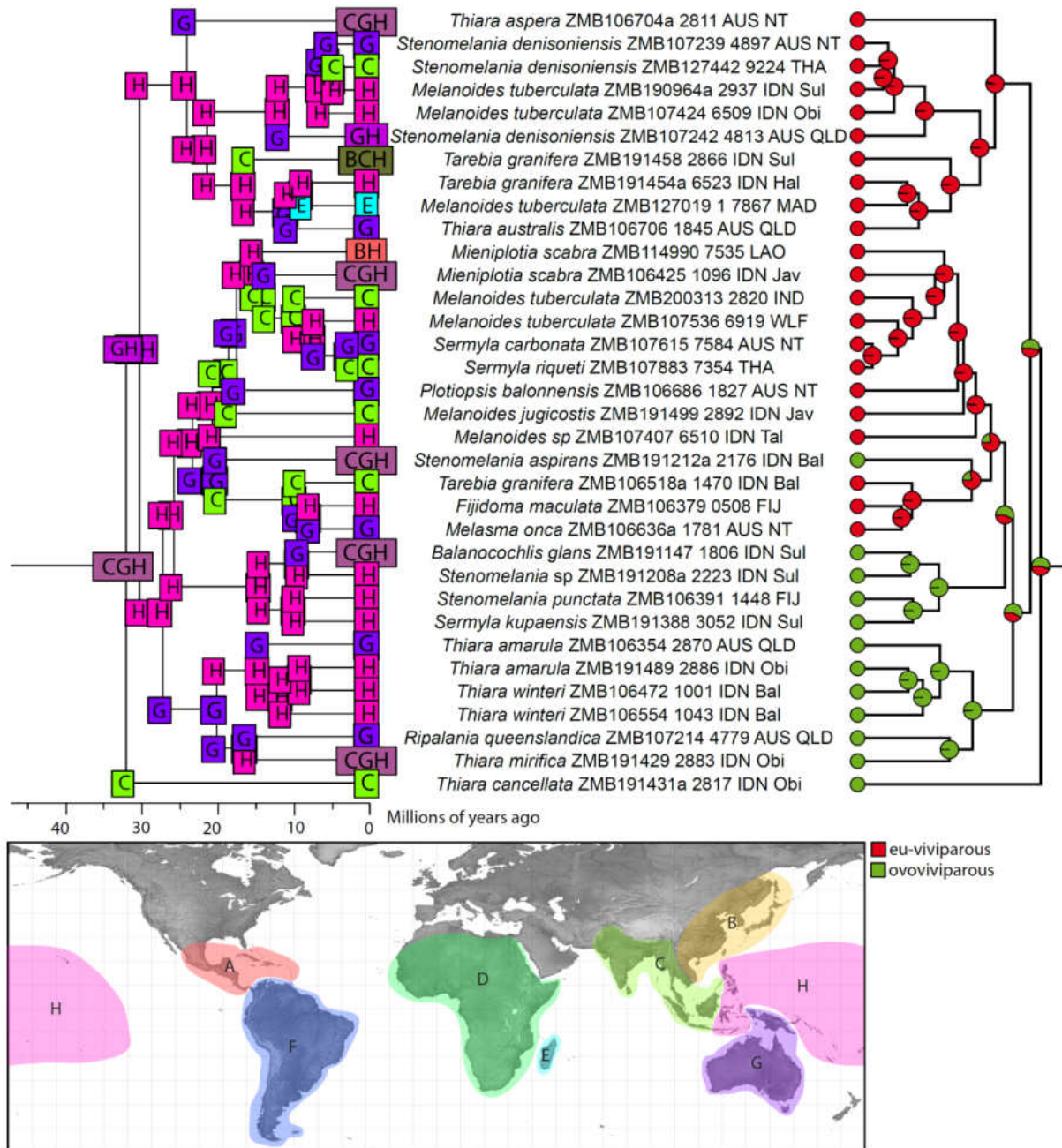


Figure 5. Time-calibrated phylogeny of Thiaridae and related families based on concatenated COI, 16S, 28S and H3 sequences. Left topology: ancestral range estimation, with letters at nodes representing the most likely area of origin, corresponding to the freshwater biogeographic regions based on Bănărescu (1992): A) Caribbean region and Middle America, B) Eastern Asia, C), South Asia and Southeast Asia, D) Africa, E) Madagascar, F) South America, G) Australia and H) Indo-West Pacific. A combination of letters represents a shared probability of ancestral range from the corresponding regions. Right topology: results of the analysis of reproductive mode evolution. Pie charts at nodes represent the probability of each reproductive mode being the ancestral state. Map made with Natural Earth. Free vector and raster map data @ naturalearthdata.com

morphologically delimited genera and species were not recovered as monophyletic groups (Figs. 2 and 3).

The incongruence of morphology-based classification with molecular phylogenies in limnic gastropods has been explained by incorrect identification, insufficient phylogenetic resolution of selected markers, taxonomic over-splitting, the presence of cryptic species or as a result of fine-scale geographical differentiation, isolation in separate drainage systems, introgression, mode of mitochondrial inheritance, presence of nuclear copies of mitochondrial genes (NUMTS), karyotypic variation, endosymbiont infection, indirect selection of the mitochondrial genome or ancestral polymorphisms (Lee et al., 2007; Köhler & Deen, 2010; Miura et al., 2013, 2018, 2020; Reid et al., 2013; Rintelen et al., 2014; Whelan & Strong, 2015; Köhler, 2016, 2017). Although limitations of our data regarding resolution power are evident (Figs. 2 and 3), this alone cannot explain all of the observed incongruences.

Many of the above-mentioned explanations for the observed incongruences can only be tested using additional, ideally multilocus molecular data, and the discussion of causes would remain purely speculative for the time being. However, our mitochondrial data are not suggesting the presence of NUMTS, as the COI sequences could be readily translated into putatively functional proteins (internal start or stop codons were not observed).

From the congruence between multilocus AFLP data and morphology in three species of *Sermyla* (Lentge-Maaß et al., in press), which are widely separate in our mitochondrial phylogeny and the phylogeny based on combined mitochondrial and nuclear data (Figs. 2 and 3), it can at least be anticipated that the phylogenetic analyses presented here do not fully reflect the actual phylogenetic structure of the family and should, therefore, be interpreted with caution. Especially, the non-monophyly of several genera and species needs further investigation, and we here refrain from proposing any changes of systematic assignment.

There has been a striking discord about the suitability of mtDNA in phylogenetics and taxonomy, not only since Hebert et al. (2003) argued that mtDNA fragments can be used as a universal barcode for all life. Although a lively debate about what it can and should be used for is continuing (e.g. Moritz & Cicero, 2004; Ebach & Holdrege, 2005; DeSalle et al., 2005; Hajibabaei et al., 2007; Waugh, 2007; Valentini et al., 2009; Casiraghi et al., 2010; Goldstein & DeSalle, 2011; Kekkonen & Hebert, 2014; Coissac et al., 2016; Deiner, 2017; Tablert, 2018; Shekhovtsov et al., 2019), DNA barcoding is a well-established molecular tool and research field currently attracting relatively large amounts of funding (Taylor & Harris, 2012; Coissac et al., 2016; Stallmann et al., 2019; Stuessy, 2020; Yang et al., 2020). Despite showing overall considerable structuring of mtDNA diversity, with often relatively little intra-lineage diversity

compared to the diversity among lineages (Fig. 2, Supporting Information, Fig. S1), the observed non-monophyly of a number of morphologically delimited thiarid species calls the practice of species identification based on mtDNA sequences alone (or few mitochondrial and nuclear markers) into question again.

A resolved phylogeny and knowledge of geographical range are prerequisites for the inference of biogeographic processes and evolutionary history in general (Hoban et al., 2019). Unfortunately, a robust molecular phylogeny of Thiaridae could not be established in the present study and many details of the historical processes and their evolutionary consequences remain to be studied in detail based on additional data in the future. Nonetheless, the timing for the onset of diversification of major lineages along with the estimation of ancestral modes of reproduction, with either veligers (ovoviviparity) or shelled juveniles (eu-viviparity) being released from the females's brood pouch, allow the discussion of scenarios that may have shaped the present-day distribution and diversity of the family.

Strong et al. (2011) and Glaubrecht et al. (in prep.) found strong support for a clade within Cerithioidea encompassing the families Paludomidae, Hemisinidae and Thiaridae, with Hemisinidae being arguably the sister group of Thiaridae as also recovered in our dated phylogeny (Fig. 4). Glaubrecht (1996) and Glaubrecht et al. (in prep.) argued in favour of a Gondwanan origin of this clade, which is consistent with the oldest fossils of the group described from Cretaceous deposits of New Zealand and Australia (Hamilton-Bruce et al., 2004; Beu et al., 2014). The dislocation of Africa and the Indian subcontinent from Antarctica during the Cretaceous (e.g. Acharyya, 2000) may have triggered the split of Paludomidae (which have an African and Oriental distribution) from Hemisinidae plus Thiaridae. The separation of Australia from Antarctica in the late Cretaceous may then account for the separation of Hemisinidae and Thiaridae, which is consistent with our molecular dating of this split (Fig. 4). Although we cannot entirely rule out an origin of Thiaridae in Africa or the Indian subcontinent where members of the family occur autochthonously today, the recovery of African and Indian lineages deeply nested within the Thiaridae (Figs 2–5, Supporting Information, Fig. S1) rather speaks against such a scenario. The relatively long branch leading to extant Thiaridae either suggests little diversification for a long period of time in Australia or the extinction of older lineages. Unfortunately, there are now fossils from Late Cretaceous to Eocene deposits from Australia to our knowledge that would lend support to either of the two views.

The onset of diversification of extant thiarid lineages was dated at c. 32 Ma into the Oligocene (with error estimates ranging from an Eocene to Miocene age, Fig. 4). This dating is

consistent with an onset of diversification when Australia approached Asia. Dispersal of veliger larvae via ocean currents, being consistent with the estimated ancestral reproduction mode for Thiaridae (Fig. 5), may have facilitated colonisation of the Indo-Australian region and the complex geological history of the region with moving terranes and emerging and subsiding islands; see Seshaiya (1940), Glaubrecht (1996) and Hidaka & Kano (2014) for an overview of knowledge on this dispersal mode in *Stenomelania*, as well as Davia & Ponder (2019) for an conceptual overview of this dispersal mode within Neritidae. Along with the possibly repeated evolution of eu-viviparity in Thiaridae limited overseas dispersal may, therefore, have played a key role for the diversification of thiarid lineages and certainly merits further investigation. Along these lines the endemic thiarid fauna of Africa assigned to *Melanooides* (see Genner et al., 2007 for the most recent molecular approach on the matter) needs also further investigation, with a colonisation pathway from South-East Asia via India, as earlier suggested in Glaubrecht (1996) being more consistent with our data, opposed to an origin of *Melanooides* in Africa as proposed by Genner et al. (2007).

Conclusion

Although there are still many ambiguities to be resolved concerning phylogenetical relationships among thiarid genera and species, the results of the analysis presented here nonetheless offer considerable new insights into the evolution and biogeographic history of this group. Australian and Southeast Asian thiarids thus represent a challenging but also extremely interesting case for studying biogeography due to their now assumed long history on the Australian continent. In the light of global warming and associated loss of biodiversity in general (Bálint et al., 2011), understanding the influence of past climate change on the biogeography, evolution and extinction of faunas is critical for the development of conservation strategies. This is also of particular importance in Australia, where intensified aridity has shaped large portions of the continent. The potential use of a phylogeographic framework to predict the possible future responses of species to climate change scenarios is noteworthy. Thiarids represent an important and realistic model system in speciation research which provides detailed insight into the dynamics of the underlying mechanisms of speciation under the influence of climate change.

It is of further concern that Thiaridae serve as first intermediate snail hosts for several trematode species, among them the human lung and intestinal fluke (Chaniotis et al., 1980; Krailas et al., 2011; Veeravechskij et al., 2018a). Regarding the known potential of some species for being invasive they might become established and spread elsewhere and of course

mollusc-transmitted diseases need recognition and emphasis due to their importance for the veterinary and public health. A focus of future work should be on the mitigation of the effect of invasive species and on preventing future invasions. The diversity of life on Earth is rapidly declining under the current biodiversity crisis (Olson et al., 2002; Ceballos et al. 2015) and invasive species are one of the most commonly cited causes of this biodiversity loss (Ricciardi, 2004; Didham et al., 2007; Hermoso et al., 2011). This situation is especially worrying in freshwater environments worldwide (Dudgeon et al., 2006; Abell et al., 2008; Stow et al., 2014). Of the global terrestrial fauna, freshwater molluscs are among the most diverse and threatened groups, so that their conservation is a matter of great concern (Lydeard et al., 2004; Lysne et al., 2008; Lopes-Lima et al., 2014).

The results of the present study offer a first basis for further, more in-depth investigations on the study of biodiversity and evolution of thiarid freshwater snails. New technological advances will facilitate the generation of large amounts of genomic sequence data which may allow for more informed decisions on phylogenetic relationships and taxonomic assignments.

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For all supplemental materials referenced in this chapter refer to Appendix II

Chapter 3 Biological diversity or nomenclatural multiplicity: the Thai freshwater snail *Neoradina prasongi* Brandt, 1974 (Gastropoda: Thiaridae).

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Research Article



Biological diversity or nomenclatural multiplicity: the Thai freshwater snail *Neoradina prasongi* Brandt, 1974 (Gastropoda: Thiaridae)

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A key aspect of evolutionary systematics research is the distinction between nomenclatural multiplicity and biological diversity. Unravelling the latter is only possible by identifying true biological entities, i.e., species and evolutionary lineages instead of an accumulation of nominal taxa. This is particularly difficult to achieve for species with high phenotypic plasticity, such as thiarid freshwater snails, a speciose family notorious for its taxonomic diversity. Exceptionally fraught with problems is a complex of nominal species in the genera *Melanooides* and *Stenomelania*. In addition to these genera, morphologically almost indistinguishable shells were the basis for the description of *Neoradina prasongi* and the establishment of *Neoradina*. To test whether these shells represent specimens from a distinct evolutionary lineage, we studied representative material of all three genera from Thailand, i.e., *Neoradina prasongi* and syntopically occurring and/or conchologically similar species, using molecular genetics, shell characters via geometric morphometrics, radula morphology, and reproductive biology. The molecular study of mitochondrial 16S rRNA and COI gene fragments unambiguously supports the distinction of the six species examined, most notably *Neoradina prasongi* as a distinct lineage. Geometric morphometrics of shell shapes allowed distinguishing species currently assigned to *Stenomelania* s. str. from the other studied species. Radula characters were uninformative. Our findings confirm the prevalence of different reproductive modes in these viviparous freshwater snails (i.e., the release of larval or juvenile stages). The combined results of our genetic analyses were ambiguous for implications on genus affiliations and did not support the classification of some species as part of *Stenomelania*, affecting the taxonomic stability of the current conception of these genera. Our results are a crucial first step towards a better understanding of the diversity found within these taxonomically problematic thiarids, emphasizing the need for evolutionary systematics approaches, in order to properly evaluate truly biological diversity in contrast to nomenclatural multiplicity.

Key words: evolutionary systematics, Indo-Australian Archipelago, *Melanooides tuberculata*, *Stenomelania aspirans*, Thailand

Introduction

One key aspect of evolutionary systematics studies, i.e., the combination of morphological, genetic, biogeographic, and/or ecological methods against the background of phylogenetic systematics to study a taxon's evolutionary history, is the evaluation of nomenclatural redundancy. The latter often hampers the identification of evolutionary lineages and true biological entities (see

Glaubrecht, 2007, 2010). Evolutionary systematics approaches are especially necessary in groups with high phenotypic plasticity and taxonomic diversity, as regularly a plethora of names have been assigned for potentially only few lineages that deserve recognition as evolutionary entities, as has been exemplified by Glaubrecht et al. (2009) for molluscs and Schwentner, Just and Richter (2015) and Schwentner, Timms and Richter (2014) for crustaceans.

As one of the most speciose families in the Cerithioidea Fleming, 1822, the viviparous freshwater

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Thiaridae Gill, 1871 (1823) represent such a taxon. Due to their high phenotypic plasticity the family exhibits high rates of taxonomic redundancy, with many taxa needing revision (for details and discussion see Glaubrecht, 1996, 2000, 2004, 2011; Glaubrecht et al., 2009; Glaubrecht & Neiber, 2019).

One especially notorious complex of morphologically similar taxa includes species currently assigned to *Stenomelania* Fischer, 1885 and *Melanoides* Olivier, 1804. In addition, the more recently described *Neoradina* Brandt, 1974 falls within this complex of morphologically nearly indistinguishable taxa, but since its brief description it has not been revised taxonomically (see Fig. 1 for an impression of shell similarities). The characters that Brandt (1974) listed for *Neoradina* can also be found in *Stenomelania* and *Melanoides*. Hence, we here study representatives of each of these three proposed lineages, in particular their respective type species based on either type and/or topotypical material. In the case of *Stenomelania* we added additional species, as previous studies (Glaubrecht et al., 2009) found higher genetic diversity within this lineage.

Stenomelania species are distributed throughout the tropical Oriental, southern Japanese, Oceanian, and Australian regions (Fig. 2), with the type species, *Melania aspirans* (Hinds, 1844), having been described from Fiji. Until its elevation to generic rank by Houbriek (1987), *Stenomelania* was generally classified as a section of *Melania* Lamarck, 1799, which today is considered invalid (see Fischer, 1885), or as a subgenus of *Melanoides* (see e.g., Pace, 1973; Rensch, 1934; Starmühlner, 1976, 1984, 1993). More recently, it has been used at generic rank (Bandel et al., 1997; Glaubrecht, 1996, 2004; Glaubrecht et al., 2009; Gimnich, 2015; Hidaka & Kano, 2014; Miura et al., 2008; Strong et al., 2011). *Stenomelania* encompasses viviparous species that release a great number of offspring as small veliger larvae ('r-strategy'). Adult *Stenomelania* snails inhabit riverine freshwater habitats, while the veligers are dispersed via marine currents (see Glaubrecht 1996, 2006; Seshaiya, 1940). The only known exception is the Australian '*Stenomelania*' *denisoniensis* (Brot, 1877 in Brot 1874–1879), which releases shelled juveniles and is genetically not closely related to other *Stenomelania* species (Glaubrecht et al., 2009). Accordingly, we here refer to *Stenomelania* with the explicit exclusion of '*Stenomelania*' *denisoniensis* as *Stenomelania* sensu stricto (s. str.).

Melanoides, with its type species *Melanoides tuberculata* (Müller, 1774) (see Glaubrecht et al., 2009), occurs in warm tropical and subtropical regions worldwide. However, the current distribution of *Melanoides tuberculata* is the result of anthropogenic influence, with the

autochthonous occurrence of this invasive species assumed to range from Africa, the Middle East, and throughout the Indo-Pacific region, with its type locality at the Coromandel Coast of India (Facon et al., 2005; Glaubrecht 1996, 2000) (Fig. 2). In contrast to *Stenomelania*, the eu-viviparous *Melanoides* releases its progeny as large, shelled juveniles with several whorls already formed ('k-strategy').

In addition to the widely distributed *Melanoides* and *Stenomelania*, a third, lesser-known genus of snails with essentially similar shells was more recently introduced as *Neoradina* by Brandt (1974). The original brief morphological description of *Neoradina* is based on material from only one site in southern Thailand (Brandt, 1974). Our study is the first since the original description to examine *Neoradina* systematically by studying not only the type material but also topotypical material of *Neoradina prasongi* Brandt, 1974, the type species of the genus, that co-occurs with species of the other two genera in southern Thailand (see Fig. 2).

The strong morphological resemblance of their constituent species makes these genera largely indistinguishable. Therefore, a systematic revision of this taxonomic complex is necessary (for discussions see Glaubrecht, 2009; Starmühlner, 1976). As a crucial first step in resolving their intricate evolutionary history, we here focus on the only weakly distinguished *Neoradina* by revisiting its type species *N. prasongi* and comparing it with confamilial and morphologically similar species. Hence, we examine six species allocated to these three morphologically very similar taxa, *Neoradina*, *Stenomelania*, and *Melanoides*, including their respective type species. In an evolutionary systematics approach, we use geometric morphometrics of the shells, radula morphology, reproductive biology, and molecular genetics to compare *N. prasongi* with species assigned to *Stenomelania* (i.e., *S. aspirans*, *S. punctata* (Lamarck, 1822), *S. torulosa* (Bruguière, 1789 in Bruguière 1789–1792), '*S. denisoniensis*') and *M. tuberculata*.

Materials and methods

Sampling

We examined *N. prasongi* and partially syntopically occurring Thai *Melanoides* and *Stenomelania* species – i.e., *M. tuberculata*, '*S. denisoniensis*', *S. torulosa*. We used topotypical material whenever possible. Hence, we included samples of *S. aspirans* from Fiji, as well as samples of *M. tuberculata* from India and samples collected during research trips in close proximity to the type locality of *N. prasongi*. To support our representation of *Stenomelania* we included additional specimens of *S. aspirans* from Australia and Indonesia, and



Fig. 1. Shells of *Neoradina*, *Stenomelania*, and *Melanooides*. **1.1.** *N. prasongi*, holotype, Thailand, stream 7 km from Krabi to Khao Thong (SMF 215933-1); **1.2.** *N. prasongi*, two of seven paratypes (SMF 215934/7-2;-7); **1.3.** *N. prasongi*, one of two specimens originally collected and identified by Brandt and used for genetic analysis, Thailand, stream 5 km from Krabi to Khao Thong (ZMH 59338-1); **1.4.** *N. prasongi*, Thailand, Mai Fad, Siako district, Pak Meng River, at Pak Meng, 30 km North of Trang (ZMB 127582-1); **1.5.** *N. prasongi*, Chalung City, Khlong Chalung, Muang district (ZMB 127590-2); **1.6.** *S. aspirans*, Fiji, Sovi River, Malevu, Coral Coast (ZMB 106390-1); **1.7.** *S. troulosa*, Thailand, Khlong Than Trip (ZMB 127458-6); **1.8.** *S. torulosa*, Thailand, Kanchanabui Province, 25.3 km Southeast Sangkhla Buri (FMNH UF 346223-2); **1.9.** *S. punctata*, Fiji, Sovi River, East of Malevu, Coral Coast (ZMB 106386-3); **1.10.** *S. punctata*, Fiji, Sovi River, Malevu, Coral Coast (ZMB 106396-2); **1.11.** '*S.*' *denisoniensis*, Thailand, Wiphiawadi waterfall, E to Khanon, below highway bridge (ZMB 127459-6); **1.12.** '*S.*' *denisoniensis*, Thailand, Ban Sa Kaewo (ZMB 127575-1); **1.13.** *M. tuberculata*, Thailand, Khao Thong (ZMB 127444-2); **1.14.** *M. tuberculata*, Thailand, 7 km north-west of Krabi (ZMB 127573-3). Scale bars = 1 cm.

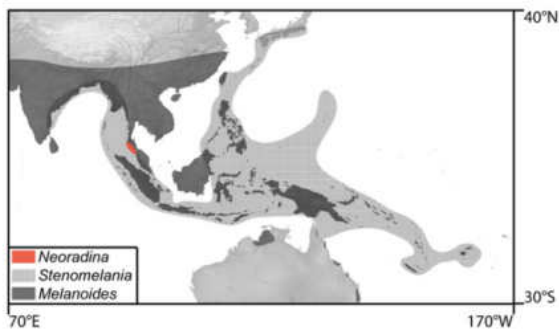


Fig. 2. Distribution map of the genera *Neoradina*, *Stenomelania*, and *Melanooides* throughout the Indo-Australian Archipelago. The Australian occurrences of *Melanooides* are the result of anthropogenic introductions of *M. tuberculata* (see Glaubrecht et al., 2009). Based on open-access map Natural Earth (Free vector and raster map data @ naturalearthdata.com).

S. punctata from Fiji. Our study is based on material collected by MG and DK in Thailand, and MG in Indonesia, Australia, and Fiji, now housed in the malacozoological collection of the Museum für Naturkunde Berlin (ZMB, Germany), and to a lesser extent on material housed in the Zoological Museum at the Center of Natural History of the Universität Hamburg (ZMH, Germany), the Senckenberg Museum Frankfurt (SMF, Germany), the Zoologische Staatssammlung München (ZSM, Germany), the Florida Museum of Natural History (FMNH, USA), the Academy of Natural Sciences, Philadelphia (ANSP, USA), the Göteborg Natural History Museum (GNM, Sweden), and Silpakorn University Thailand (SUT, Thailand). Two sequenced fragments of the mitochondrial 16S rRNA gene from specimens of *N. prasongi* (ZMH 59338) originally collected in the immediate proximity of the type locality and identified by Brandt were obtained in an ongoing study retrieving historical DNA (Gimnich, 2015) and are included here. For a detailed list of the material examined, see Appendix 1 (see online supplemental material, which is available from the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2019.1606862>).

DNA extraction and amplification

For our molecular phylogenetic study, we added two specimens of Thai *Paludomus siamensis* (Blandford, 1903) as a non-thiarid outgroup (ZMB 107721 and ZMB 107723, for sampling sites see Appendix 1 (see supplemental material online).

We performed DNA extractions of foot muscle tissue following the protocol of Sokolov (2000) with the minor modifications of Scheel and Hausdorf (2012). Partial sequences of the mitochondrial cytochrome *c* oxidase

subunit I (COI) and 16S rRNA (16S) genes were amplified by the polymerase chain reaction (PCR) using the primer pairs LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3'; Folmer et al., 1994) and HCO2198var (5'-TAW ACT TCT GGG TGK CCA AAR AAA T-3'; Rintelen et al., 2004) for COI, and 16S_F_Thia2 (5'-CTT YCG CAC TGA TGA TAG CTA G-3'; Gimnich, 2015, see also Neiber & Glaubrecht, 2018) and H3059var (5'-CCG GTY TGA ACT CAG ATC ATG T-3'; Wilson et al., 2004) for 16S. For several of the museum specimens, amplification of the complete target region was difficult or impossible. Therefore, not all ethanol-preserved (EtOH) samples were accessible for the molecular investigations, although they were included in the morphological analyses. Amplifications were performed in 20 µl volumes containing 2 µl 10× amplification buffer (biolabproducts, Bebensee, Germany), 0.4 µl dNTP mix (5 mM each, biolabproducts), 0.1 µl DreamTaq DNA polymerase (Thermo Fisher Scientific, Waltham, USA), 1 µl of each primer (Sigma-Aldrich, through Merck KGaA, Darmstadt, Germany), 13.5 µl ddH₂O and 2 µl DNA template under the following conditions: initial denaturation at 94 °C for 3 min, 35 PCR cycles (94 °C for 30 s, 50 °C for 45 s, 72 °C for 1 min), final extension 72 °C for 10 min. PCR products (10 µl) were enzymatically cleaned by adding 1 µl FastAP thermosensitive alkaline phosphatase (Thermo Fisher Scientific) and 1 µl exonuclease I (Thermo Fisher Scientific) followed by an incubation step at 37 °C for 15 min and inactivation at 85 °C for 15 min. All amplified products were sequenced at the Macrogen Europe Laboratory (Amsterdam, the Netherlands). See Table S1 (see supplemental material online) for GenBank accession numbers of sequences.

Phylogenetic analyses

Forward and reverse strands were assembled and edited using GENEIOUS R 9.1.3 (Biomatters, <http://www.geneious.com>). Primer sequences were removed resulting in COI sequences of ~660 bp and 16S sequences of ~990 bp. COI sequences were aligned using MUSCLE (Edgar, 2004) as implemented in GENEIOUS under default settings. To align the short fragments from historical, topotypic *N. prasongi* properly we partitioned the complete 16S sequences (prealigned with MUSCLE) into three parts according to presence/absence of data for the short fragments. These partitions were realigned using MAFFT (Katoh & Standley, 2013), applying the Q-INS-i iterative refinement algorithm and otherwise the default settings. Subsequently, the partitions were concatenated in the appropriate order. We used PARTITIONFINDER 2.1.1 (Lanfear et al., 2012) to

select appropriate partitions and evolutionary models. Whilst four partitions were assumed initially (16S and 1st, 2nd, and 3rd codon positions of COI), the results of the PARTITIONFINDER analysis using the Bayesian information criterion to select among partitions and models suggested two partitions with different evolutionary models: 3rd codon positions of COI (HKY + G) and 1st plus 2nd codon positions of COI plus 16S (HKY + I + G). The selected partitions and evolutionary models were used for the subsequent Bayesian inference (BI) and maximum likelihood (ML) analyses, respectively.

We performed a BI analysis using MrBAYES version 3.2.6 (Ronquist et al., 2012) running Metropolis-coupled Monte Carlo Markov chain (MC³) searches with four chains in two separate runs for 50,000,000 generations with trees sampled every 1,000 generations under default heating. Potential scale reduction factors close to 1 and estimated effective sample sizes above 200 from the MrBAYES output were used as diagnostics to ensure that the MC³ searches had reached stationarity and convergence. The first 5,000,000 generations of each run were discarded as burn-in.

We performed heuristic ML analyses in GARLI 2.0 (Zwickl, 2006) using the partitions and best-fit models as suggested by PARTITIONFINDER. Support values were computed by bootstrapping with 1,000 replications. Using PAUP* 4.0b10 (Swofford, 2002), we conducted heuristic maximum parsimony (MP) searches with unordered characters, 100 random sequence addition replicates, tree bisection and re-connection (TBR) branch-swapping, and gaps treated as missing data. Internal branch support was assessed in PAUP* by bootstrapping with 1,000 replications, using full heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and one tree held at each step during stepwise addition.

Posterior probabilities from the Bayesian analysis and bootstrap support values from the ML and MP analyses were mapped onto the BI 50% majority consensus tree with SUMTREES version 3.3.1 (part of the DENDROPY 3.8.0 package, Sukumaran & Holder 2010). Bootstrap support (BS) \geq 70% from the ML and MP analyses and posterior probabilities \geq 0.95 were interpreted as positive support for a node.

Photo imaging

Pictures of undamaged adult specimens were taken by remote shooting with EOS Utility version 2.12.2.1 for Windows (Canon Inc., Tokyo, Japan) and Digital Photo Professional version 3.12.51.2 for Windows (Canon Inc.) using a digital camera. Shells were placed in a

standard position in which the aperture is positioned at a 90° angle in relation to the optical axis of the camera and the columella is positioned parallel to the background surface. Photos were stacked with Helicon Focus version 5.3.14.2 for Windows (Helicon Soft, Kharkiv, Ukraine).

Geometric morphometrics and statistical analyses

Pictures of 139 specimens were included. We built a tps file using tpsUtil version 1.74 (Rohlf, 2017b). We then placed nine landmarks and four sliding landmarks (three with 30 points and one with 15 points, see Fig. 3 for landmark positions) in tpsDig2 version 2.30 (Rohlf, 2017a). Curves were transformed to landmarks in tpsUtil. Data were analysed in RStudio (RStudio Team, 2016), using the packages 'geomorph' (Adams & Otárola-Castillo, 2013), 'ade4' (Chessel et al., 2004), 'lawstat' (Hui et al., 2008), 'agricolae' (Mendiburu, 2010) and 'dunn.test' (Dinno, 2017). Sliding landmarks were defined followed by a Procrustes superimposition. A principal component analysis (PCA) was conducted to reduce dimensionality and to identify major axes of variation within the dataset. We included only axes with a significant proportion of variances (>0.05) for subsequent testing. All further testing was based on genetically supported species groups as predefined units. We applied the Shapiro–Wilk test for normal distribution for each of these groups on each principal component (PC) separately. If one or more groups per PC was not normally distributed, a Kruskal–Wallis-rank-sum test was used. If significant ($P < 0.05$), post-hoc testing using the Dunn test was conducted to find significant differences among groups. However, when all groups were



Fig. 3. Position of landmarks (dots) and sliding landmarks (lines). The line between landmarks 3 and 5 consists of 15 sliders, whereas the other lines are composed of 30 sliders.

normally distributed (Shapiro–Wilk test: $P > 0.05$) we conducted an analysis of variance (ANOVA). Significant ANOVA results ($P < 0.05$) were followed by a post-hoc LSD-test, testing for significant differences ($P < 0.05$) among groups.

Dissections for studying radulae and reproductive biology

EtOH preserved specimens were dissected using a stereo microscope (M125, Leica Camera AG, Wetzlar, Germany). Radulae were extracted by first removing the entire buccal apparatus. The tissue was then dissolved using proteinase K according to the protocol of Holznagel (1998). After complete digestion of the tissue, radulae were stored in 70% EtOH and cleaned using an ultrasonic bath. For imaging with a scanning electron microscope (SEM, LEO 1525 GEMINI), clean radulae were mounted on SEM object stubs (agar scientific, Stansted, Essex, UK) and coated with platinum using a sputter coater.

Across species, 106 specimens were dissected, revealing 43 gravid females. Offspring were extracted, counted, and allocated to size categories (embryos in earlier ontogenetic stages, late embryos, juveniles < 0.5 mm, juveniles 0.6–1 mm, juveniles 1.1–1.5 mm, juveniles 1.6–2 mm, juveniles 2.1–2.5 mm, juveniles 2.6–3 mm, juveniles > 3 mm).

Results

Phylogenetic analyses

The reconstructions of phylogenetic relationships of taxa assigned to *Stenomelania*, *Melanoides*, and *Neoradina*, with *P. siamensis* as outgroup, recovered the thiarids as a maximally supported group and revealed clearly distinguishable lineages within this clade. *Melanoides tuberculata* (PP: 1.00, BS (MP): 100, BS (ML): 100) and *Neoradina prasongi* (PP: 0.99, BS (MP): 92, BS (ML): 100) were well supported by the topology of the tree obtained from the analyses of combined 16S and COI sequences (see Fig. 4). The same is true for the other four species of *Stenomelania*. However, *Stenomelania* as currently understood was not recovered as a monophyletic group but divided into two lineages (Fig. 4). *Stenomelania punctata* was placed as sister group of all other in-group taxa, albeit this placement was only supported in the ML analysis but not in the BI and MP analyses (PP: 0.59, BS (MP): 32, BS (ML): 100). A second lineage with rather low support as well (PP: 0.91, BS (MP): 40, BS (ML): 99) grouped *S. torulosa* and *S. aspirans* together. Based on our topology,

this latter group was recovered as the sister group of *M. tuberculata*, albeit again without support. *Neoradina prasongi* clustered as sister to '*S.*' *denisoniensis* (PP: 0.86, BS (MP): 74, BS (ML): 31). Overall, our phylogenetic analyses showed high support values for all six species (Fig. 4), though support values for any particular phylogenetic relationship among these species was low.

Geometric morphometrics

Shell shapes show an overall high level of variance. A PCA identified the first three major axes of variance to account for a significant proportion of variance ($P > 0.05$) (PC1: 0.599; PC2: 0.158; PC3: 0.080), explaining a cumulative proportion of 0.837 of variance. The Shapiro–Wilk test was significant ($P < 0.05$) in two of the groups supported by our phylogenetic analyses (Fig. 4) on the first principal component (PC1). Subsequently, Kruskal–Wallis rank-sum testing displayed significant ($P < 0.001$) differences in PC1. The Dunn test revealed that shell shapes differed significantly between the group formed by *S. aspirans* and *S. punctata* and that formed by *M. tuberculata*, '*S.*' *denisoniensis*, and *N. prasongi* (Fig. 5). Shell shapes of *S. torulosa* did not differ significantly from any other species on PC1.

For the second principal component (PC2) the Shapiro–Wilk test was significant in one of the groups ($P < 0.05$). Hence, the Kruskal–Wallis rank-sum test was conducted and was significant ($P < 0.001$). The subsequent Dunn test showed that several significantly different ($P < 0.05$) shell shapes could be detected among supposed species clusters on PC2 (Fig. 5f): *Neoradina prasongi* was significantly different from *S. aspirans*, *S. torulosa*, *S. punctata*, and '*S.*' *denisoniensis*. In addition, *S. punctata* was significantly different from *S. aspirans*, '*S.*' *denisoniensis*, and *M. tuberculata*.

On the third principal component PC3, all groups were normally distributed (Shapiro–Wilk test: $P > 0.05$). The subsequent ANOVA was not significant ($P = 0.2063$) and no further testing along PC3 was conducted.

Radula morphology

Radula tooth formulae were variable, though only to a small extent (Table 2). All species show variable denticle configurations on all teeth, with the exception of the rachidian and marginal teeth of *S. aspirans* (Fig. 6d–f, Table 2 for tooth formulae). Though the radula morphology of *S. aspirans* turned out to be rather invariable in our study, the species cannot be distinguished from the other species by this trait as several taxa displayed the

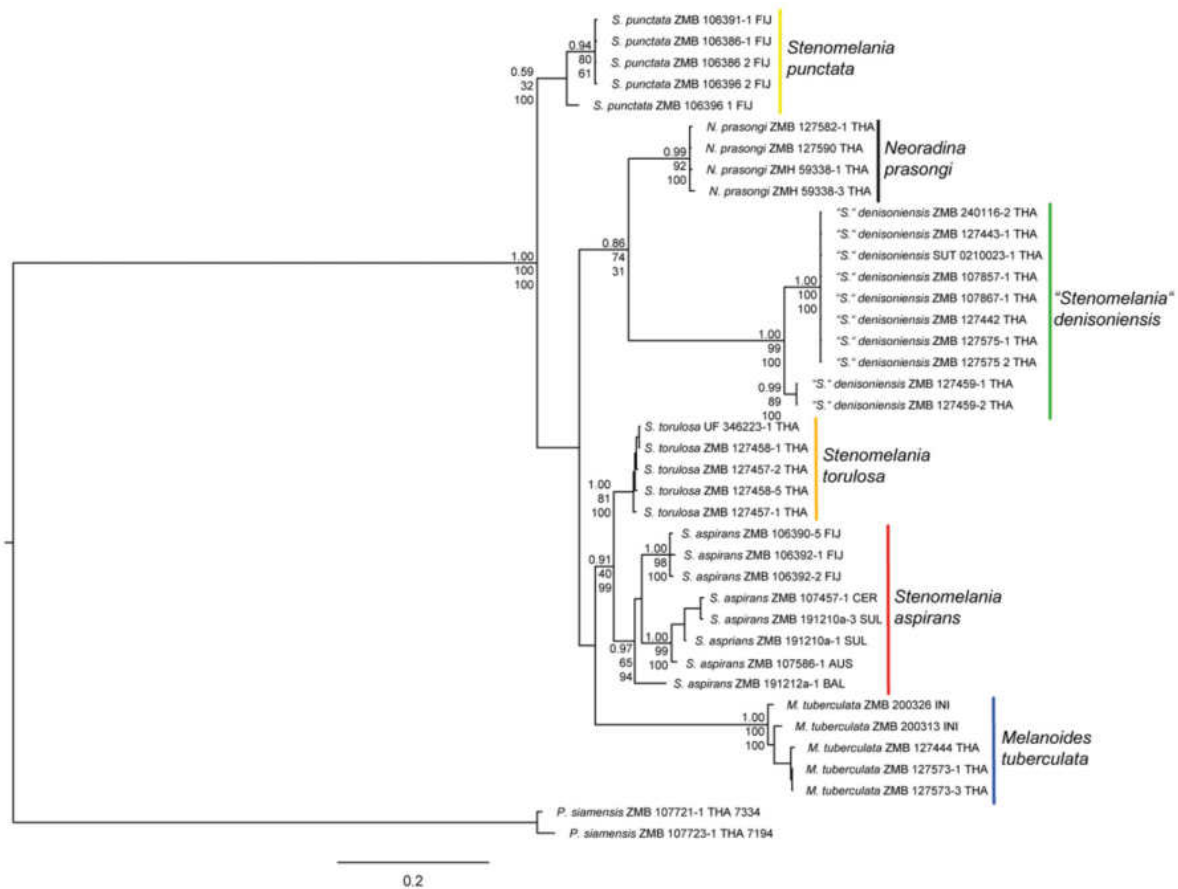


Fig. 4. Bayesian 50% majority consensus tree based on concatenated COI and 16S sequences. Numbers at the nodes refer to posterior probability (PP) values (top) from the Bayesian (BI) and bootstrap support (BS) values from the maximum parsimony (MP) analysis (middle) and from the maximum likelihood (ML) analysis (bottom). Only nodes with PP values ≥ 0.95 and/or BS values from ML and/or MP analyses $\geq 70\%$ are annotated.

same tooth formula (Table 2). Overall, radula characters were not reliable for distinguishing species, as morphologies of the different species overlapped distinctly. Tooth formulae often varied more within the radula of a single specimen than among specimens of the same species.

Reproductive biology

Approximately 40% of the 106 dissected specimens were gravid females. Brood pouches of the species of *Stenomelania* s. str. (i.e., *S. aspirans*, *S. torulosa*, and *S. punctata*, but excluding '*S. denisoniensis*') contained a large number of embryos in earlier ontogenetic stages (232–2800 per female) but in no case any larger, shelled and multi-whorled juveniles of any size class (Table 1). In contrast, specimens of *Melanoides tuberculata* and '*S. denisoniensis*' contained larger shelled offspring in all size classes but in comparatively low numbers

(1–193 individuals per female). Usually the individual females contained in their brood pouch a mixture of early life stages (Table 1) but none contained offspring of all size classes at once.

We found not a single gravid female in *Neoradina prasongi*, although we studied all available material, i.e., a total of $n = 16$ from three localities.

Systematics

Neoradina Brandt, 1974

Neoradina Brandt, 1974, pp. 169–170.

Type species: *Neoradina prasongi* Brandt, 1974 by original designation.

Taxonomic remarks: *Neoradina* was apparently introduced as a consequence of the subgenus *Radina* Preston, 1915 of *Thiara* Röding, 1798 being placed in

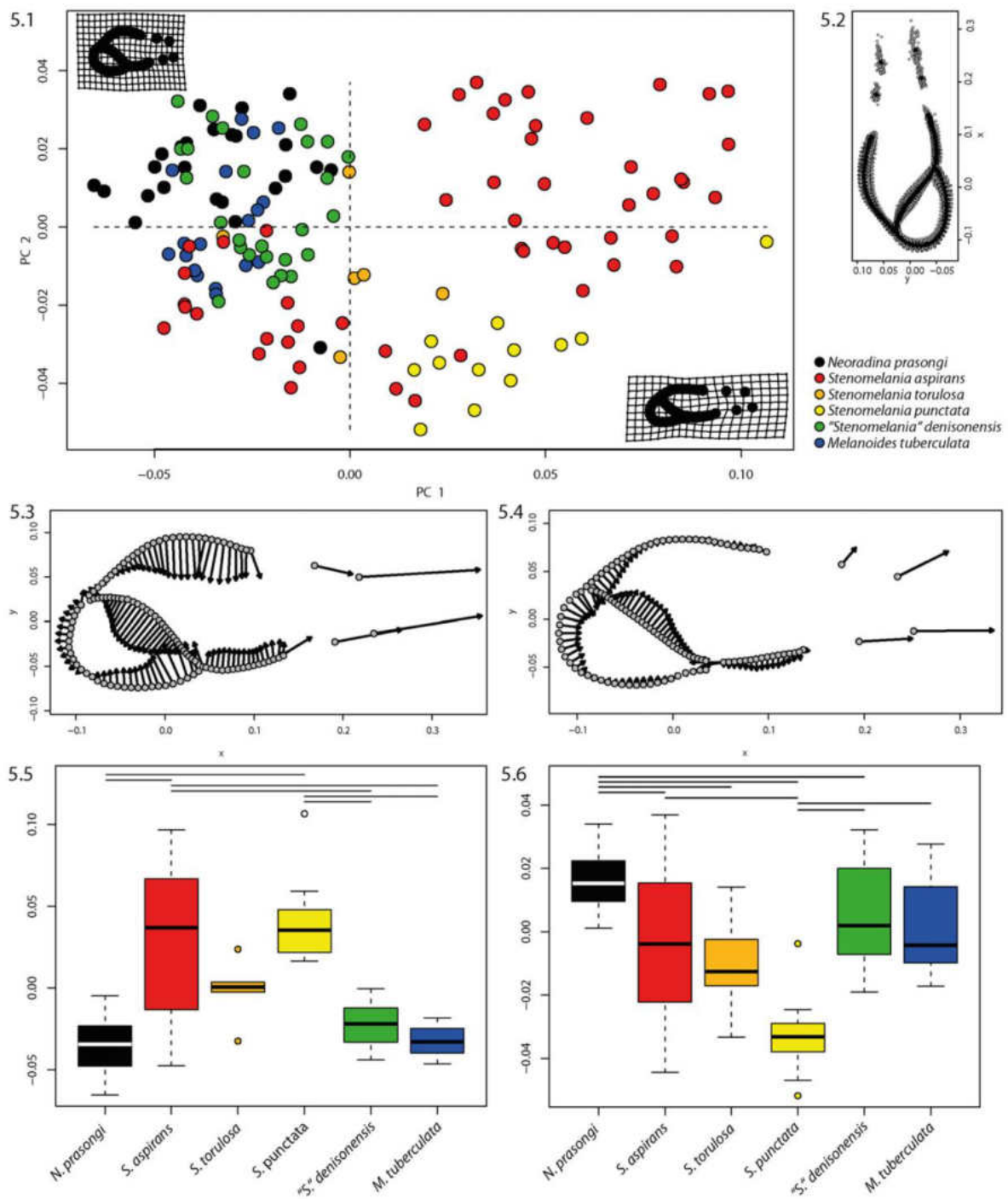


Fig. 5. Results of geometric morphometrics analysis with sliding landmarks. **5.1.** Relative variance in shell shape along PC1 and PC2. Depicted thin plate splines represent shell shapes of individuals with highest and lowest value along PC1. **5.2.** Total variance of landmark positions. Grey dots comprise all positions of landmarks. Black dots indicate the mean position of each landmark across the entire dataset. **5.3, 5.4.** Variance of shell shapes on **5.3.** PC1 and **5.4.** PC2. Arrowheads indicate the maximum value on the respective axis, grey dots indicate the minimum value. **5.5, 5.6.** Box plots for **5.5.** PC1 and **5.6.** PC2 sorted by genetic clusters. Significant differences are indicated by bars (*: $P < 0.05$).

Table 1. Results of brood pouch content analysis for the thiarid species studied. As our samples of *Neoradina prasongi* did not contain any gravid females, we cannot assess their reproductive mode. The size classes we distinguished are a, eggs/embryos in early ontogenetic stages; b, late embryos/veligers; c, juveniles < 0.5 mm; d, juveniles 0.6–1 mm; e, juveniles 1.1–1.5 mm; f, juveniles 1.6–2 mm; g, juveniles 2.1–2.5 mm; h, juveniles 2.6–3 mm; i, juveniles > 3 mm.

Species	Average amount of offspring	Lowest amount of offspring	Highest amount of offspring	Amount of different size classes	Size classes	Number of specimens examined	Number of gravid females
<i>N. prasongi</i>	n/a	n/a	n/a	n/a	n/a	15	0
<i>S. aspirans</i>	12800	12800	12800	1	a	7	1
<i>S. punctata</i>	598	598	598	1	a	10	1
<i>S. torulosa</i>	1170	232	2874	1	a	16	7
'S.' <i>denisoniensis</i>	26	1	72	9	a-i	39	21
<i>M. tuberculata</i>	74	6	193	9	a-i	19	12

Table 2. Radula formulae of all species studied. Values in brackets represent frequently observed exceptions of denticle numbers. Overall radula formulae overlap among species, in no case allowing species distinction.

Species	Rachidian tooth	Right lateral tooth	Marginal teeth
<i>N. prasongi</i>	5[4]-1-4	3[2]-1-[3]4	9–10
<i>S. aspirans</i>	3-1-3	2 -1-3[4]	9
<i>S. torulosa</i>	4[3]-1-[3]4	[3]2-1-3[4]	7–9
<i>S. punctata</i>	[4]3[2]-1-[2]3[4]	2-1-[3]4	8–9
'S.' <i>denisoniensis</i>	[4]3[2]-1-[2]3[4]	[3]2[1]-1-3[4]	8–10
<i>M. tuberculata</i>	[5]4-1-4[5]	[3]2-1-3	7–9

the synonymy of *Stenomelania* by Schepman (1918) and Rensch (1934), which at the time was considered a subgenus of *Melanoides*. The type species of *Radina*, *Melania hastula* Lea & Lea, 1851, was first synonymized with *Melania crenulata* Deshayes, 1838 by Brot (1875) in Brot (1874–1879), then placed as *Melania* (*Stenomelania*) *hastula* again by Schepman (1918) and Rensch (1934), and later synonymized with *Melanoides* (*Stenomelania*) *plicaria* by Starmühlner (1976). Brandt (1974) wanted to conserve the allocation of the remaining *Radina* species in a separate genus and therefore introduced *Neoradina* with a description of the new species *N. prasongi*, designated as the type species and transferred the 12 nominal species, varieties and subvarieties (excluding *Melania hastula*) previously included in *Thiara* (*Radina*) by Preston (1915) to *Neoradina*, elevating several of these to species rank. Without a revision of characters, Brandt (1974, p. 170) listed *N. charon* (Preston, 1908), *N. confusa* (Dohrn, 1858), *N. expatriata* (Preston, 1908), *N. fuscata* (Born, 1780), *N. multistriata* (Preston, 1908), *N. nana* (Nevill, 1884), *N. perdecollata* (Nevill, 1884), *N. pironoidea* (Nevill, 1884), *N. plana* (Brot, 1876 in Brot 1874–1879), *N. solidiuscula* (Nevill, 1884), *N. sobrius* (Lea & Lea, 1851), and *N. zelebori* (Brot, 1862) in *Neoradina*; thus, at the same time Brandt suggested that the range of the genus extends from India, the Andaman and Nicobar Islands to southern Thailand. Some of these taxa have since been placed within the synonymy of species of *Stenomelania* and *Melanoides* (see e.g.,

Starmühlner, 1984), though Brandt's (1974) allocation has never been revised since. Hence, a critical evaluation of Brandt's (1974) suggestions is necessary in future studies.

Neoradina prasongi Brandt, 1974

Neoradina prasongi Brandt, 1974, p. 170.

Type locality: 'Stream about 7 km from Grabi [sic] to Kao Tong' (Brandt, 1974, p. 170), i.e., between the town of Krabi and the village of Khao Thong, about 20 km north-west of Krabi. During collecting trips in 2012 and 2013, MG and DK collected thiarids at several places in this area, in order to search for potential topotypical material, although the type locality had been given only as a general area rather than a specific spot. However, none of the samples collected in the critical area between Krabi and Khao Thong and that we tested genetically cluster with specimens of *N. prasongi* collected originally in this area by Brandt (1974).

Type material: Holotype SMF 215933 (= SMRL 3950/A). The paratypes series specified by Brandt (1974, SMRL 3950/25) consisted of 25 specimens and has been split and sold. We located a total of 21 of these paratypes: seven paratypes SMF 215934; three paratypes ZMH 59289; two paratypes GNM Gen. kat. 1970-12684; five paratypes ZSM 19983242; four paratypes ANSP 446752. All of these specimens were collected by Brandt himself on 26 October 1969 and were all dry stored empty shells.

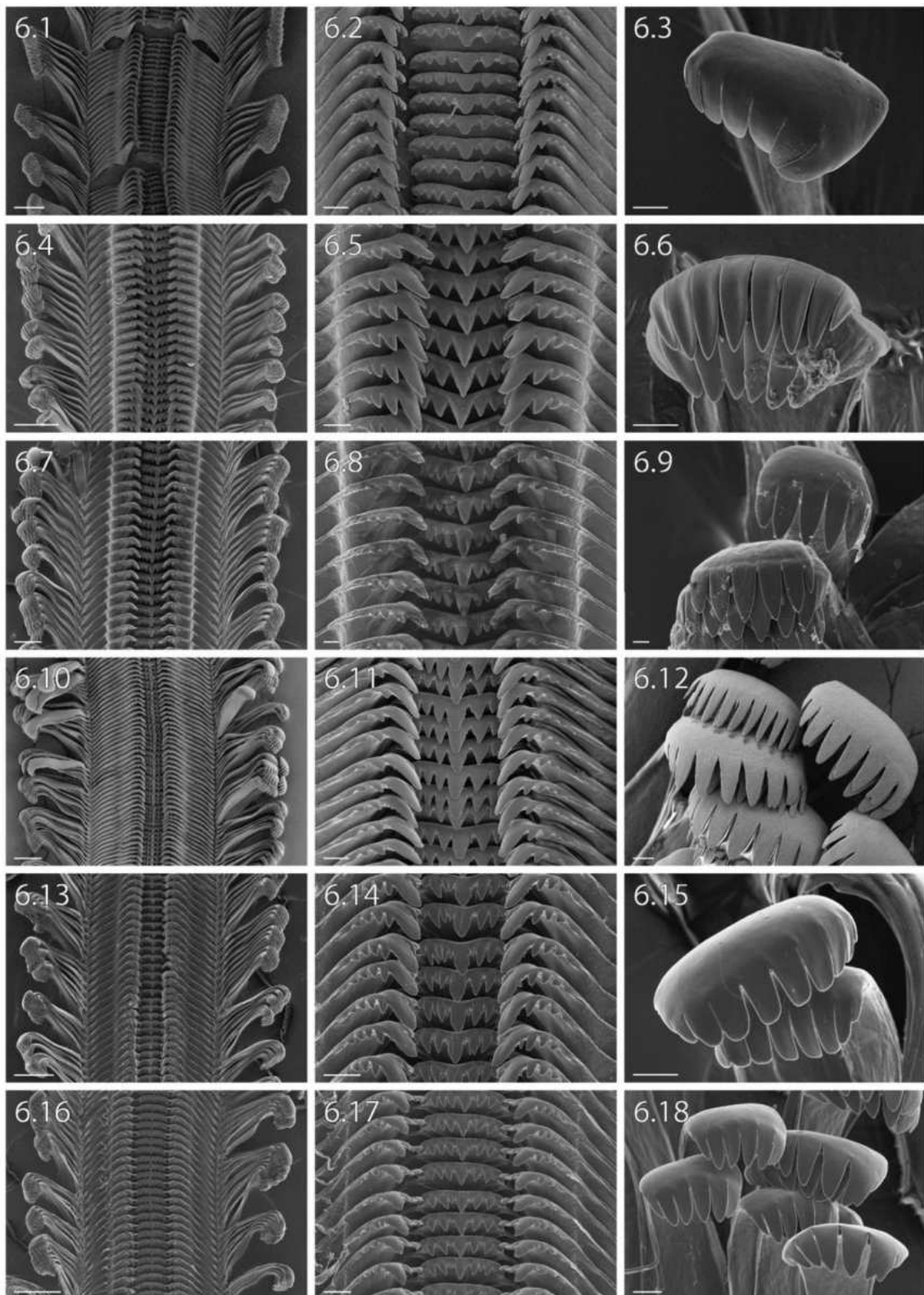


Fig. 6. Radulae of *Neoradina*, *Stenomelania*, and *Melanooides*. **6.1, 6.4, 6.7, 6.10, 6.13, 6.16.** Radula ribbon, scale bars = 100 μ m; **6.2, 6.5, 6.8, 6.11, 6.14, 6.17.** Lateral and central teeth, scale bar = 20 μ m; **6.3, 6.6, 6.9, 6.12, 6.15, 6.18.** Marginal teeth, scale bars = 10 μ m. **6.1, 6.2, 6.3.** *N. prasongi*, ZMH 3894-3; **6.4, 6.5, 6.6.** *S. aspirans*, ZMB 106392-1; **6.7, 6.8, 6.9.** *S. torulosa*, ZMB 127457-1; **6.10, 6.11, 6.12.** *S. punctata*, ZMB 106391-1; **6.13, 6.14, 6.15.** '*S.*' *denisoniensis*, ZMB 127459-1; **6.16, 6.17, 6.18.** *M. tuberculata*, ZMB 127444-2.

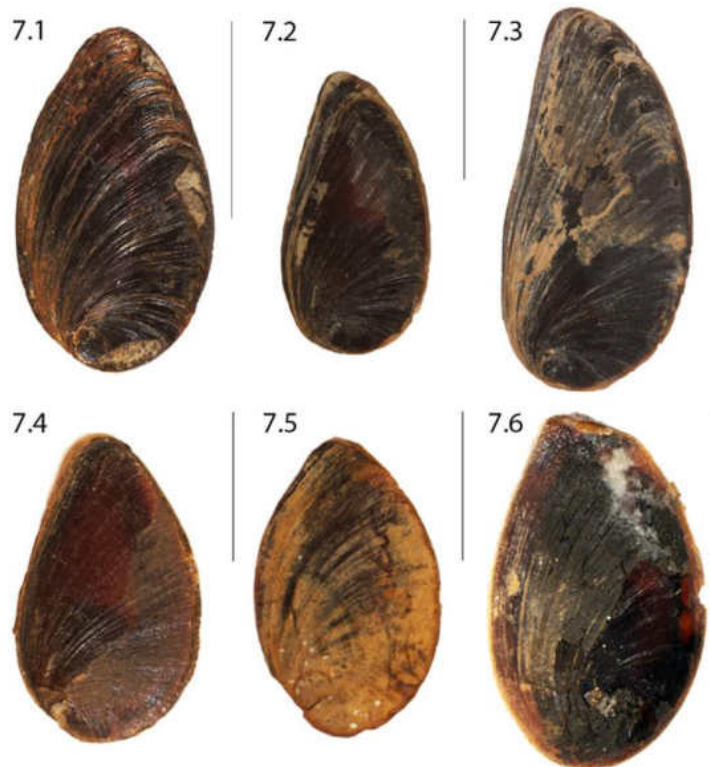


Fig. 7. Operculae of *Neoradina*, *Stenomelania*, and *Melanoides*. 7.1. *N. prasongi*, ZMB 127582-8; 7.2. *S. aspirans*, ZMB 106390-2; 7.3. *S. punctata*, ZMB 106396-1; 7.4. *S. torulosa*, ZMB 127458-6; 7.5. '*S.* *denisoniensis*', ZMB 127575-6; 7.6. *M. tuberculata*, ZMB 127573-3; 7.1–7.3. scale bars = 5 mm; 7.4–7.6. scale bars = 3 mm.

Additional material examined: Samples stored in EtOH are indicated by a '-w' following the sample ID. Thailand: 5 km from 'Grabi to Kao Tong [sic]' (ZMH 59338-w/5, coll. Brandt June 11th 1968 [*Remark:* These specimens were originally collected at the type locality and identified by Brandt, though not mentioned in his original description. Although these specimens are not paratypes, we regard them as toptotypical material of *N. prasongi*. Two of them also yielded historical mtDNA for the present study.]); Trang province, Siako district, Mai Fad, Pak Meng river, at Pak Meng, 30 km North of Trang, 7°29.681' N, 99°20.573' E (ZMB 127582-w/11, coll. Glaubrecht, Glaubrecht & Krailas February 8th 2013); Satun province, Muang district, Chalung city, Khlong Chalung, 6°43.618' N, 100°3.756' E (ZMB 127590-w/6, coll. Glaubrecht, Glaubrecht & Krailas February 9th 2013).

Description

Shell (Fig. 1.1–1.5). Elongated turreted with 10–14 whorls, 38–49 mm high and 13–16 mm wide. Dextral. Spire pointed. Darkish-brown or darkish-green to black, monochromatic. In adult specimens protoconch and early

parts of teleoconch often corroded. Sometimes last whorl with more or less pronounced keel at upper third of periphery. Whorls rounded with deep sutures. Shell shape significantly different from species of *Stenomelania*. Shell shape not significantly different from *M. tuberculata* and '*S.* *denisoniensis*' (Fig. 5.5–5.6).

Embryonic shell. Unknown. Apexes of all examined specimens corroded.

Operculum (Fig. 7). Paucispiral, nucleus basal left.

Radula (Fig. 6.1). Taenioglossate. Up to 2.2 mm long, with up to 94 rows of teeth. Rachidian pointed, with slightly elongate central denticle and four to five denticles on either side. Lateral teeth with very pronounced central denticle, two to three denticles on the rachidian side and three to five denticles on the marginal side. Marginal teeth elongated, spoon shaped with eight to 10 uniform denticles. Outer and inner marginal teeth indistinguishable.

Reproductive biology. We did not find any progeny within the subhaemocoelic brood pouches of any of the *N. prasongi* specimens available and identified by the molecular genetics as such.

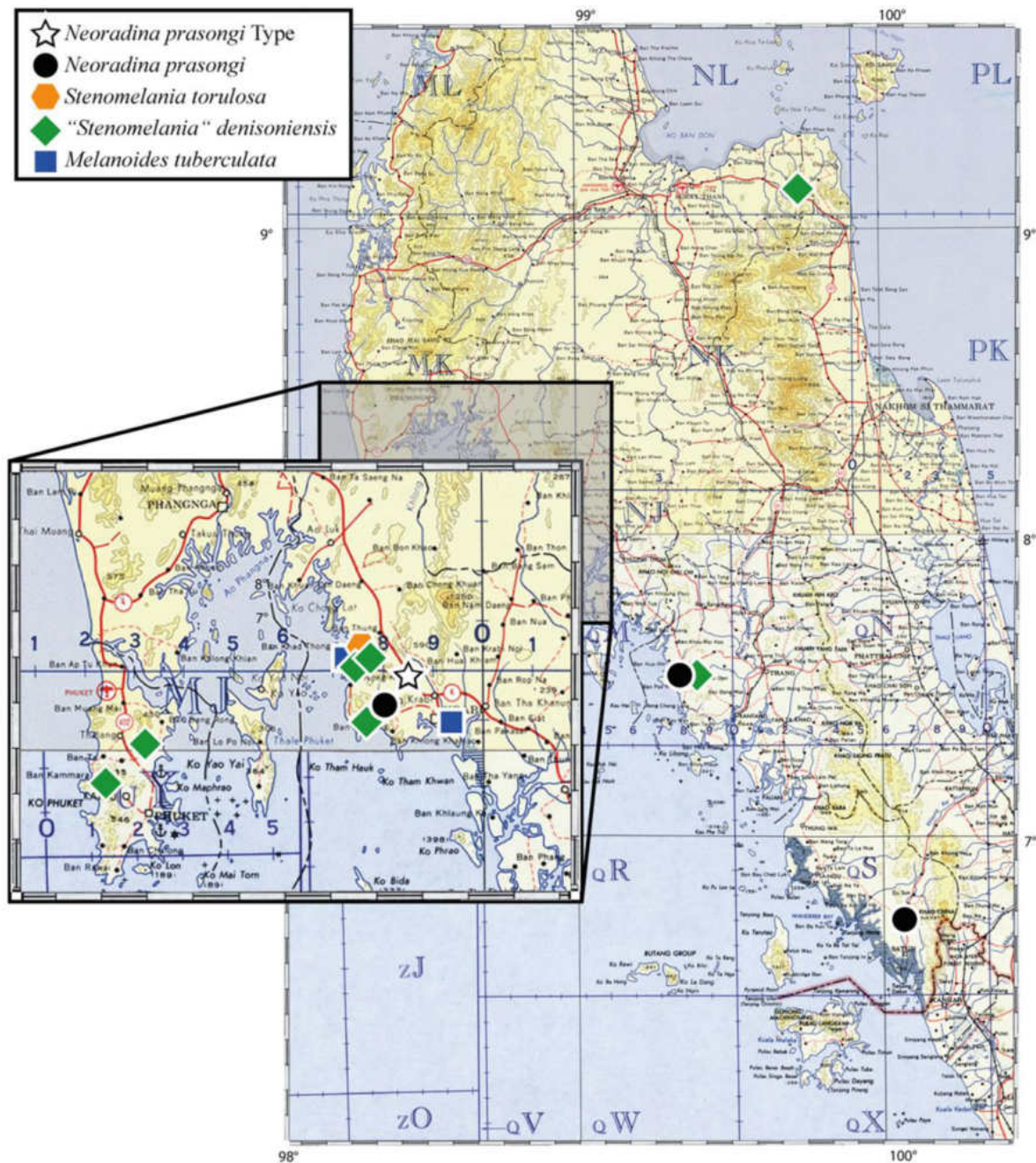


Fig. 8. Sample sites of *Neoradina*, *Stenomelania*, and *Melanoides* in southern Thailand. The open star indicates the type locality of *N. prasongi* based on Brandt (1974) and the label of the holotype. Filled symbols represent EtOH stored samples accessible for genetic studies, no other open symbols for dry material in this map. Dot shapes and colours correspond to species – see map legend. Map provided by the Perry-Castañeda Library (<http://legacy.lib.utexas.edu/maps/imw/>) in the public domain (last accessed 5 September 2018); assembled from pieces NB47 and NC47 of the 'International Map of the World'.

Ecology: Habitat preferences were not reported in the original description (Brandt, 1974). We found individuals from the two populations farther south (ZMB 127582, 127590; see additional studied specimens above), living in shallow coastal streams on muddy to sandy substrate.

Discussion

Systematics and taxonomy

The combination of different methods in our study allows new insights in this complex group of thiarids and helps to further our understanding of the lineages studied. Our molecular genetic results supported each of the six species based on reciprocal monophyly. *Stenomelania torulosa* and *S. aspirans* formed a well-supported clade. Sister to these two was *M. tuberculata*, though only weakly supported. Another weakly supported clade was formed by *N. prasongi* and '*S.*' *denisoniensis*. Finally, *S. punctata* clustered as sister to all other studied thiarid species, though only weakly supported (Fig. 3). Though no deeper phylogenetic relationships were resolved the phylogeny revealed that *Stenomelania* as currently conceived may be polyphyletic. This reflects at least two possibilities. Either our current interpretation of these genera as separate evolutionary lineages is fallacious or incomplete lineage sorting is hampering a clear interpretation of the relationship between these lineages. As our current data do not allow any unambiguous conclusion on the matter, we refrain from formalizing any possible nomenclatural changes.

In our study, the value of morphological characters to distinguish taxa within the studied thiarids has varied considerably. The radulae of the species examined were undiagnostic as they exhibited a generalized thiarid morphology (see also Bandel et al., 1997; Dechruksa et al., 2013; Glaubrecht, 1996; Glaubrecht et al., 2009). By contrast, geometric morphometrics using sliding landmarks enabled the differentiation of shell shapes of *Stenomelania* s. str. from those of *N. prasongi*, *M. tuberculata* and '*S.*' *denisoniensis*. Nonetheless, this approach did not allow the distinction of all species, as we were unable to distinguish *N. prasongi* from *M. tuberculata*, *S. torulosa* from *S. punctata*, and *S. aspirans* and '*S.*' *denisoniensis* from *M. tuberculata*.

Our study of the reproductive modes corroborates prior findings, strengthening the distinction of two reproductive strategies (Glaubrecht, 1996, 2006, 2011; Glaubrecht et al., 2009). *Stenomelania aspirans*, *S. torulosa*, and *S. punctata* are 'r-strategy' brooders, releasing marine veliger larvae (in accordance with Bandel et al.,

1997; Glaubrecht et al., 2009; Houbriek, 1987; Seshaiya, 1940; Starmühlner, 1976, 1979). On the other hand, '*S.*' *denisoniensis* and *M. tuberculata* are 'k-strategy' brooders releasing freshwater-dependent juveniles (Table 1; see also Dudgeon, 1986; Glaubrecht, 1996, 2006, 2011; Glaubrecht et al., 2009). Under the criterion of parsimony, a repeated transition between these two modes within this clade appears implausible. The evolution of such a pattern would not only involve a shift in breeding mode but also that larvae would need to have repeatedly adapted to differing salinities. Hence, although these two clades are not well supported genetically in our study and are only reliably distinguished by their reproductive mode, we see no reason at present to synonymize these genera.

In accord with Glaubrecht et al. (2009), we found that shell shape (Fig. 5), reproductive biology (Table 1), and genetics (Fig. 4) suggest excluding '*S.*' *denisoniensis* from *Stenomelania* as it is currently perceived. The genetic results also indicate a clear differentiation of '*S.*' *denisoniensis* and *M. tuberculata*, although they are indistinguishable based on their reproductive biology and shell shape. Shell shapes of freshwater snails can vary broadly and reproductive modes have evolved several times independently within the thiarids (DeWitt, 1998; Glaubrecht, 1996, 2006, 2011; Maaß & Glaubrecht, 2012; Schütt & Glaubrecht, 1999). Therefore, proposing an affiliation of the two taxa based on our data would be premature. Hence, we adopt the view of Glaubrecht et al. (2009) that '*S.*' *denisoniensis* should be separated from *Stenomelania*, especially as *Stenomelania* is not resolved as monophyletic in terms of the species currently assigned to it (see above), though we are not yet confident enough to allocate this species to any other genus.

Neoradina

The focus of our study was to assess, whether *Neoradina* (here represented by its type species *N. prasongi*) is a distinct evolutionary lineage or if *N. prasongi* is a junior synonym of syntopic *Stenomelania* species or *Melanoides tuberculata*. Brandt (1974, p. 169) introduced *Neoradina* as differing 'from *Melanoides* by lacking the axial sculpture'. We found this trait to be highly variable within *Melanoides tuberculata*, sometimes missing, and thus rendering it uninformative for distinguishing *N. prasongi* from *M. tuberculata*. Brandt (1974, p. 169) also stated that *Neoradina* 'differs from *Stenomelania* by being oviparous and having a brood-pouch'. However, *Stenomelania* is, as all thiarids are, viviparous, possessing a subhaemocoelic brood pouch (see e.g., Bandel et al., 1997; Glaubrecht, 1996; Glaubrecht et al., 2009; Seshaiya,

1936, Starmühlner, 1976). Hence, this character is unsuitable for distinguishing *Neoradina* and *Stenomelania*. As both characters that Brandt (1974) proposed for distinguishing *Stenomelania* and *Melanoides* from *Neoradina* are non-informative, no support for the taxonomic separation of *Neoradina* as a distinct evolutionary lineage can be inferred from Brandt's (1974) morphological assessment. However, *Stenomelania* and *Melanoides* are currently distinguished by their reproductive mode, i.e., either the release of veliger larvae (in the case of *Stenomelania*) or the release of large juveniles (in the case of *Melanoides*). For *Neoradina*, Brandt (1974, p. 170) claimed an oviparous reproductive mode, contradicting his own statement by mentioning that he found 'females with subhaemocoelic brood-pouch with many small embryonic shells in all stages of development'. In our study, we found no gravid females of *N. prasongi*, precluding determination of the reproductive mode in this species. However, as it would be the first and only thiarid with an oviparous reproductive mode, we anticipate *Neoradina* to be viviparous. The lack of gravid females in our *N. prasongi* samples is possibly a seasonal effect, with sampling during the non-breeding period, rather than an indication of oviparity. As our samples were collected during only two months (February and June), it is possible that these specimens were sampled outside the breeding season. We found a similar case in another thiarid species from south Thailand, i.e., *Melanoides jugicostis* (Hanley & Theobald, 1876) (see Dechruksa et al., 2013). Therefore, future sampling endeavours should factor in this possible seasonality.

The combination of all characters examined, except radula morphology and reproductive biology, enabled us to distinguish *N. prasongi* from the other five species examined. However, a close genetic relationship to any of the other species is not supported. Shell shapes of *N. prasongi* are significantly different from all *Stenomelania* s. str. species studied and '*S.* *denisoniensis*' but are indistinguishable from *M. tuberculata*. The implication of relatedness based on this morphological similarity is not supported by other evidence, such as in particular our genetic results. As freshwater snails can vary widely intraspecifically in their shell shape (see e.g., DeWitt, 1998; Glaubrecht, 1993, 1996, 2009, 2011; Glaubrecht et al. 2009), similarities between *M. tuberculata* and *N. prasongi* are likely to be convergent, rather than reflecting relatedness. Lastly, several specimens of *N. prasongi* possess a slight keel on the upper third of the periphery of the last whorl. However, this keel is of ambiguous diagnostic value as it can also be present in '*S.* *denisoniensis*' and some other *Stenomelania* s. str. species (Starmühlner, 1976).

Based on the characters mentioned in the original description (Brandt, 1974), *Neoradina* cannot be distinguished from *Stenomelania* and *Melanoides* by virtue of all supposedly distinguishing characters mentioned being present in all three or at least two groups. However, as unambiguous reproductive and genetic support for an allocation of *Neoradina prasongi* to either of the other two genera is lacking, we here refrain from any nomenclatural acts, to stand clear of adding to the taxonomic confusion in this group. Further insights on the reproductive mode of *N. prasongi* and the study of more taxa of all three lineages might help to resolve the relationships of *Stenomelania*, *Melanoides*, and *Neoradina* in future studies.

Finally, the range of *Neoradina* as provided in its original description needs to be critically examined. Brandt (1974, p. 170) gave the following range: 'India, Andamans, Nicobars, Ceylon and S Thailand: here only known from the province of Grabi'. However, he based this on his placement of all the nominal species in *Neoradina*. As several of these nominal species have subsequently been placed in the synonymy of other species referred to *Stenomelania* and *Melanoides* (Starmühlner, 1993), these nominal species should be carefully re-evaluated, potentially altering the range of *Neoradina* suggested by Brandt (1974). However, in this study we can only discuss the distribution of *N. prasongi*, which is restricted to southern Thailand. Given that Brandt (1974) did not provide exact geographic coordinates of the type locality (see above), we cannot judge whether the species is no longer present near Krabi (the type locality) or was simply not found during recent collecting attempts. We only found populations at two localities further south, in Trang and Satun provinces. This might indicate an extension of the native range in southern Thailand, but nevertheless at present *N. prasongi* must be considered a fairly restricted and narrow ranged species among South-east Asian thiarids.

Conclusion

Our study provides unambiguous support for *Neoradina prasongi* as a distinct thiarid lineage in southern Thailand. However, due to the lack of gravid females and low genetic support for the relationships of higher taxa, a clarification of the relationships of *Stenomelania*, *Melanoides*, and *Neoradina* could only be hinted at. However, the result that *N. prasongi* represents a distinct lineage is a crucial first step towards solving the intricate relationships among these thiarid genera and their respective species. With that, our study illustrates the need to further investigate this group including more taxa in an evolutionary systematics framework, to delimit true biodiversity from mere nomenclatural multiplicity.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Supplemental data

Supplemental material for this article can be accessed here: <https://doi.org/10.1080/14772000.2019.160686>.

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Erratum:

All instances of *Stenomelania punctata* (Lamarck, 1822) are misaffiliations. All instances of this species name are to be replaced with *Stenoemlania plicaria* (Born, 1778).

**Chapter 4 Towards a revision of the enigmatic *Stenomelania*
Fischer, 1885 (Gastropoda, Thiaridae), with an evaluation of its
type species**

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Abstract

We assessed the largely understudied taxon complex of highly turreted and nearly indistinguishable thiarids subsumed in various ways under either *Melanoides*, *Neoradina* and/or *Stenomelania* by conducting a combined molecular genetics and geometric morphometrics approach, including a study of brood pouch content to infer the developmental modes. For overall eight studied species, our evolutionary systematics study allowed to clearly delineate *Stenomelania* from the other two confamilial genera by its shell shape and ovoviviparous developmental mode. Adult specimens of *Stenomelania* inhabit the upper reaches of tailwaters of tropical streams and rivers where they release offspring as free-floating veliger larvae that are then dispersed downstream into ocean currents. As juveniles the offspring migrate upstream into freshwater habitats again, rendering the genus one of the few amphidromous snail taxa. By contrast, *Melanoides* is known to be eu-viviparous releasing its offspring exclusively as crawling juveniles. The reproductive biology of *Neoradina* is, however, unknown. Our molecular genetic study of these genera, based on the 16S and COI mtDNA genes, revealed a strong entanglement of representative species, lending no direct support to the genetic distinction of morphologically established genera. Therefore, our integrative approach underlines the dire need for more sophisticated genomic approaches to help further our understanding of these complex thiarid genera.

Keywords: Cerithioidea, Thiaridae, *Melanoides*, *Neoradina*, geometric morphometrics, molecular phylogeny, developmental modes, reproductive biology

Introduction

Freshwater biodiversity, as biological richness on our planet in general, faces enormous threats the current mass extinction (e.g. Ceballos et al., 2015, 2017, 2020; Cazzolla Gatti, 2016; Díaz et al., 2019; Albert et al., 2020). Here, numerous and diverse factor drive this threat hitting especially tropical realms very hard (Dudgeon et al., 2006; Strong et al., 2008; Barlow et al., 2018). To face these threads and lessen their impact is one of the major challenge nature conservation is confronted with. Especially in the tropical realm numerous threatened species are either so far undescribed or in dire need of both taxonomic revision as well as ecological assessment to enable their conservation (Giangrande, 2003; Sluys, 2013). The worst cases in

this crisis are particularly understudied groups with convoluted taxonomies and near indistinguishable morphological character traits. Understanding such difficult and understudied groups is necessary to protect as many parts of nature as possible from their impending extinction.

One such understudied group are the viviparous Thiaridae Gill, 1871 (1823). This family of tropical freshwater snails has evolved two different life history strategies based on two different modes of development, prevalent throughout this family (for an overview see e.g. Glaubrecht, 1996, 1999, 2006; Glaubrecht et al. 2009; Glaubrecht & Neiber, 2019). In one mode the offspring is released from the subhaemoeclic brood pouch of the females at the veliger stage in large numbers (ovo-viviparous, “r-strategy” brooder), whereas in the other mode offspring is contained within the brood pouch for a far longer period of time allowing for the offspring to emerge as crawling juveniles, albeit in lower numbers, from the brood pouch (eu-viviparous, “k-strategy” brooder). As the Thiaridae have been used as a kind of ‘taxonomic trashcan’ an assessment of how many species and genera truly exist within Thiaridae is so far ambiguous. However, the most recent overviews list twelve genera (Glaubrecht & Neiber, 2019) and 135 species (Strong et al., 2008), although, comprehensive taxonomic assessments using molecular or integrative approaches are still sparse. All available molecular genetic studies are either geographically scattered or taxonomically limited (Facon et al., 2003; Genner et al., 2007; Miura et al., 2008; Hidaka & Kano, 2014; Van Bocxlaer et al., 2015; Veeravechskij et al., 2018; Boonmekam et al. 2019; Wiggering et al., 2019; Lentge-Maaß et al., in press.).

Within the Thiaridae one particularly problematic group is the *Stenomelania-Melanoides* complex, composed of the three genera *Stenomelania* Fischer, 1885, *Melanoides* Olivier, 1804 and *Neoradina* Brandt, 1974 (the latter having been the spotlight of the most recent study of this group, Wiggering et al., 2019). While earlier authors have previously subsumed many species either under the invalid generic name *Melania* Lamarck, 1799 and later *Melanoides*, these three genera have only more recently been considered separately.

Stenomelania was first introduced as a sub-genus of *Melania* (see Fischer 1885) and later was used as a subgenus of *Melanoides* (see Rensch, 1934; Pace, 1973; Starmühlner, 1976, 1984, 1993). Houbriek (1987) was the first to consider *Stenomelania* at generic rank, which is the frequently used position in more recent publications (Glaubrecht, 1996, 2004; Glaubrecht et al., 2009; Bandel et al., 1997; Miura et al., 2008; Strong et al., 2011; Hidaka & Kano, 2014; Ginnich, 2015; Wiggering et al., 2019).

Species of this genus are widely distributed through the insular realm of the Indo-West Pacific, spanning throughout the tropical Oriental, southern Japanese, Oceanian, and Australian

regions, with the type species *Melania aspirans* Hinds, 1844 originating from Fiji (Hinds, 1844; Starmühlner, 1976, 1979, 1993; Hidaka & Kano, 2014; Wiggering et al., 2019). In all of these areas adults are found at the upper reaches of tailwaters of streams and rivers.

Species of *Stenomelania* s. str. are reported to encompass “r-strategy” brooders, releasing their veliger larvae in their freshwater to brackishwater habitat (Seshaiya, 1940; Starmühlner, 1976, 1979, 1993; Bandel et al., 1997). Larvae of *S. crenulata* are known to be tolerant of higher salinities and are dispersed via marine currents (Seshaiya, 1940; Okazaki & Wada, 2007; Hidaka & Kano, 2014). Hence, *Stenomelania* is known to be one of the rare examples of amphidromous snails, a life cycle, where adults live and reproduce in a freshwater-habitat, i.e. release their offspring into a marine habitat which in time remigrate into freshwater habitats to complete this cycle, as was first detailed in Glaubrecht (1996: 167-172, 304-305, 321-326).

However, the genus also encompasses “*S.*” *denisoniensis*, a species in which juveniles have been found within the brood pouches of gravid females (Glaubrecht et al., 2009). Wiggering et al. (2019) anticipated, but refrained, to transfer the species to another thiarid genus, as it is uncertain if *denisoniensis* should be considered as *Melanoides*, *Neoradina* or another lineage of its own. For the time being, we will also refer to *Stenomelania* sensu stricto (s. str.) to indicate all congeneric species other than *denisoniensis*.

Melanoides species are known to include facultative parthenogenetic species (see e.g. Livshits & Fishelson, 1983). Their offspring is released at a later developmental stage as crawling juveniles emerge (“k-strategy” brooders). The type species *Melanoides tuberculata* (Müller, 1774) is highly invasive, thus today distributed worldwide throughout tropical habitats, though its autochthonous occurrence is assumed to range from Africa, the Middle East, and throughout the Indo-Pacific region, with its type locality at the Coramandel Coast of India (Glaubrecht, 1996, 2000; Facon et al., 2005; Glaubrecht et al., 2009).

Lastly, *Neoradina* was introduced by Brandt (1974) to encompass its then newly described type species and some other loosely allocated species formerly subsumed under the subgenus *Radina* Preston, 1915. Genetic and morphological examination of the type material did verify *Neoradina prasongi* Brandt, 1974 as a distinct species within the *Stenomelania-Melanoides* complex (Wiggering et al., 2019). Unfortunately, information on the reproductive mode of this species is still missing, and hence, a potential synonymy of *Neoradina* with one of the other two genera or, alternatively, the unambiguous distinction as a different generic lineage is pending.

We here examined six representative species of *Stenomelania*, viz. *S. aspirans*, *S. crenulata*, *S. plicaria*, *S. punctata*, *S. torulosa*, as well as “*S.*” *denisoniensis* and *Neoradina prasongi*, in

comparison to *Melanoides tuberculata*. In an evolutionary systematics approach (see Glaubrecht 2010), we conducted a study of molecular genetics, geometric morphometrics of the shell and developmental modes with the aim to delineate *Stenomelania* more exactly, taking its type species *S. aspirans* as starting point. For all species type material and type material of junior synonyms was used, wherever possible. With our approach we provide a foundation for future studies on the *Stenomelania-Melanoides* complex, though our mtDNA-based approach illustrates the need to examine the complex with a more rigorous molecular method in order to solve several entanglements found throughout our study.

Materials & Methods

Sampling

For details of the 79 samples with its specimens included see Table S1, with a comprehensive list of material collected over the last three decades by the cumulative efforts of the working group of the senior author (MG), now essentially stored at the Museum für Naturkunde (ZMB, Berlin, Germany). In addition, we included 18 relevant type lots of nominal species and their junior synonyms from several malacological collections housed in the following major museums.

Museum codens:

ANSP	Academy of Natural sciences Philadelphia (USA)
GNM	Göteborg Natural History Museum (GNM, Sweden)
NHMW	Naturhistorische Museum Wien (Austria)
MHNG	Muséum d'histoire naturelle de la Ville de Genève (Geneva, Switzerland)
MNHN	Museum National d'Histoire Naturelle (Paris, France)
NHMUK	Natural History Museum Britain (London, England)
SMF	Senckenberg Naturmuseum Museum (Frankfurt, Germany)
ZMB	Museum für Naturkunde (Berlin, Germany)
ZMH	Center of Natural History (CeNak) (formerly Zoological Museum Hamburg), Universität Hamburg (Germany)
ZMUC	Natural History Museum of Denmark (Copenhagen, Denmark)

DNA extraction & amplification

DNA was extracted from foot muscle tissue based on mollusc specific protocols (see e.g. Sokolov, 2000; Scheel & Hausdorf, 2012). We performed extractions on two specimens per ethanol stored population sample (n=50). Our efforts amounted to a total of 66 successfully extracted sampled specimens, with at least one specimen per sampled population (see Table 2 for a comprehensive list of samples used for the molecular study and GenBank accession numbers). Partial sequences of the mitochondrial cytochrome c oxidase subunit I (COI) gene, with primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3' Folmer et al., 1994) and HCO2198var (5'-TAW ACT TCT GGG TGK CCA AAR AAA T-3' Rintelen et al., 2004), and 16S rRNA (16S) genes, with primers 16SF (5'-CCG CAC TAG TGA TAG CTA GTT TC-3') and H3059var (5'-CCG GTY TGA ACT CAG ATC ATG T-3', both Wilson et al., 2004) were amplified by polymerase chain reaction (PCR). Amplifications were performed in 20 µl volumes containing 2 µl 10x DreamTaq Green Buffer, 0.1 µl DreamTaq DNA polymerase (both Thermo Fisher Scientific, Waltham, MA, USA), 0.4 µl dNTP mix 10 mM each (VWR chemicals, VWR International GmbH, Darmstadt, Germany), 1 µl of each primer (Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany), 13.5 µl ddH₂O and 2 µl DNA template under the following reaction conditions: initial denaturation at 94 °C for 3 min, 35 PCR cycles (94 °C for 30 s, 50 °C for 45 s, 72 °C for 1 min), final extension at 72 °C for 10 min. PCR products (10 µl) were cleaned up enzymatically by adding 2 µl FastAP Thermosensitive Alkaline Phosphatase (1 U/µl) and 1 µl Exonuclease I (20 U/µl) (both Thermo Fisher Scientific) followed by an incubation step at 37 °C for 15 min and inactivation at 85 °C for 15 min. All amplified products were sequenced at Macrogen Europe (Amsterdam, The Netherlands). We added sequences of 25 specimens from a previous study (Wiggering et al. 2019) from overall 19 populations, and five non-thiarid cerithioidean snail species as outgroup (used in a parallel publication by Glaubrecht & Wiggering et al., in prep): *Cubaedomus brevis* (d'Orbigny, 1842), *Hemisinus lineolatus* (Wood, 1828), *Pachymelania fusca* (Gmelin, 1791), *Paludomus siamensis* (Blanford, 1903), *Paludomus petrosa* (Gould, 1843) (see Table S2 for GenBank accession numbers for all used sequences).

Phylogenetic analysis

The genetic dataset consists of 95 specimens all represented by their partial 16S and COI sequences. DNA sequences were edited and assembled using GENEIOUS R 9.1.3 (Biomatters Ltd., Auckland, New Zealand). Primer sequences were removed resulting in COI sequences of ~658 bp and 16S sequences of ~810 bp. COI sequences were aligned using MUSCLE (Edgar

2004) as implemented in GENEIOUS under default settings. For the 16S alignment MAFFT 7 (Katoh & Standley, 2013), using the Q-INS-I algorithm, the 1PAM/ $\kappa = 2$ option for the scoring matrix for nucleotide sequences and otherwise default settings, was used. We used PARTITIONFINDER 2.1.1 (Lanfear et al., 2012) to select the appropriate partitions and evolutionary models. Four partitions were assumed initially (1st, 2nd and 3rd codon positions of COI and 16S). The results of the PARTITIONFINDER analysis using the Bayesian Information Criterion suggested a single partition and the HKY+I+G evolutionary model. This model was used for the subsequent Bayesian Inference (BI) and Maximum Likelihood (ML) analyses, respectively.

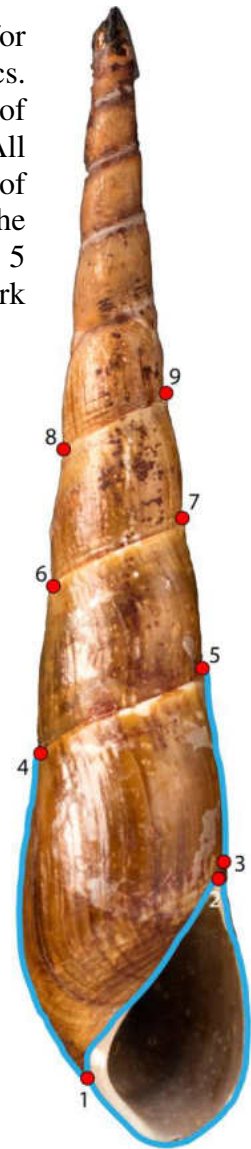
We performed BI using MRBAYES version 3.2.6 (Ronquist et al., 2012) running Metropolis-coupled Monte Carlo Markov chain (MC³) searches with four chains in two separate runs for 50,000,000 generations with trees sampled every 1,000 generations under default heating. Potential scale reduction factors close to 1 and estimated effective sample sizes above 200 from the MRBAYES output were used as diagnostics to ensure that the MC³ searches had reached stationarity and convergence. The first 5,000,000 generations of each run were discarded as burn-in. We performed heuristic ML analyses in GARLI 2.0 (Zwickl, 2006) using the best-fit model as suggested by PARTITIONFINDER. Support values were computed by bootstrapping with 1,000 replications. Using PAUP* 4.0b10 (Swofford 2002), we conducted heuristic Maximum Parsimony (MP) searches with unordered characters, 100 random sequence addition replicates, the tree bisection and re-connection (TBR) branch-swapping, and gaps treated as missing data. Internal branch support was assessed in PAUP* by bootstrapping with 1,000 replications, using full heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and one tree held at each step during stepwise addition. Posterior probabilities from the BI analysis and bootstrap support (BS) values from the ML and MP analyses were mapped onto the BI 50% majority-rule consensus tree with SUMTREES version 3.3.1 (part of the DENDROPY 3.8.0 package; Sukumaran & Holder, 2010). BS ≥ 70 % from the ML and MP analyses and posterior probabilities (PP) ≥ 0.95 were interpreted as positive support for a node.

Photo imaging

Pictures of undamaged specimens were taken by remote shooting with EOS Utility (version 2.12.2.1 for Windows) and Digital Photo Professional (version 3.12.51.2 for Windows) using a digital camera (Canon EOS 5D MKII with Canon macro photograph lens MP-E 65 mm and Canon compact macro lens EF 50 mm, Canon, Tokyo, Japan). Shells were positioned with the

aperture at a 90° angle in relation to the optical axis of the camera and the columella parallel to the background surface. Photos were stacked with Helicon Focus (version 5.3.14.2 for Windows).

Figure 1 Position of landmarks for geometric morphometrics. Landmarks (red dots) and lines of sliding landmarks (blue lines). All lines consist of 30 points of sliding landmarks, except for the line between landmark 3 and 5 consistent of 15 sliding landmark points.



Geometric morphometrics and statistical analysis

For the geometric morphometrics study we compiled a dataset of 467 suitable photographs including 44 pictures of type specimens in a .tps file using tpsUtil version 1.74 (Rohlf, 2017b). We placed 9 landmarks and 4 lines of points (three with 30 points and one with 15 points, see Fig. 1 for landmark positions) in tpsDig2 version 2.30 (Rohlf, 2017a). The latter were transformed to landmarks with tpsUtil and later defined as sliding landmarks. Data were analysed using RStudio (RStudio Team, 2016), with packages “geomorph” (Vers. 3.3.1; Adams and Otárola-Castillo, 2013), “ade4” (Chessel et al., 2004), “lawstat” (Hui et al., 2008), “agricolae” (Mendiburu, 2010) and “dunn.test” (Dinno, 2017).

We conducted a Procrustes superimposition. A principal component analysis (PCA) was conducted to reduce dimensionality and to identify major axes of variance within the dataset. Only axes with a relevant proportion of variances (> 0.05) were included for further analysing. For further analysis, we tested morphologically and genetically similar groups, based on available species descriptions and the results of our molecular phylogeny. These groups are: *S. aspirans* (201 images, including its syntypes and type specimens of its junior synonyms *Melania figurata* Hinds, 1844, *Melania picta* Hinds, 1844 and *Melania veruculum* Morelet, 1851), *S. crenulata* (4 images), *S. plicaria* (52 images, including type specimens of its junior synonyms *Melania auroriana* Hartmann, 1889 and *Melania fumosa* Hinds, 1844), *S. punctata* (40 images, including type specimens of its junior synonyms *Melania fulgurans* Hinds, 1844 and *Melania papuensis* Quoy & Gaminard, 1834), *S. torulosa* (14 images), “*S.*” *denisoniensis* (60 images, including its type specimens), “*S.*” cf. *denisoniensis* (30 images), *M. tuberculata* (38 images, including its type specimens) and *N. prasongi* (28 images, including its type specimens). Furthermore, we tested genetically diverse species clades (i.e. *S. aspirans*, *S. plicaria*, *S. punctata* and *M. tuberculata*) for

differences, in a second analysis, here, with the exclusion of all type material. Normal distribution was checked with the Shapiro-Wilk-test for each PC and predefined group, separately. If at least one group within the same PC was found to be not normally distributed ($P > 0.05$), we performed a Kruskal-Wallis-rank-sum test. If the latter showed significant results ($P < 0.05$), we executed a Bonferroni-corrected Dunn-test to identify significant differences ($P < 0.025$) between groups. If instead normal distribution was found for all groups on the same PC (Shapiro-Whilk-test $P > 0.05$) we performed an analysis of variance (ANOVA), if significant ($P < 0.05$) followed by a modified Brown-Forsythe Levene-type test. In case it scored significant ($P < 0.05$) post hoc testing with a Bonferroni-corrected LSD-test was conducted. Otherwise, a Scheffe-test was performed instead.

Brood pouch content analysis

A total of 163 EtOH preserved specimens across all species were dissected using a stereo microscope (M125, Leica Camera AG, Wetzlar, Germany). Offspring were extracted, counted, and allocated to size categories (embryos in earlier ontogenetic stages, late embryos, juveniles < 0.5 mm, juveniles 0.6–1 mm, juveniles 1.1–1.5 mm, juveniles 1.6–2 mm, juveniles 2.1–2.5 mm, juveniles 2.6–3 mm, juveniles > 3 mm). We added the already existing dataset of Wiggering et al. (2019), amounting to a final total of 263 specimens studied here.

We interpret finding only larval stages within brood pouches of a given genetic clade to represent the veliger releasing developmental mode, whereas we regard specimens of genetic clades containing any juvenile stages within brood pouches as indication for direct development. However, this interpretation is not unambiguous as the brood pouch contents only provide a snapshot of the entire ontogeny with various developmental stages, present within a population at the time of sampling. Larval stages could still develop into juveniles within the brood pouch or be released at an earlier stage. However, the more specimens studied the less likely such a misinterpretation seems.

Distribution maps and figure assembly

The species' distribution was reconstructed based on the geocoordinates of samples using QGIS version 3.16 Hannover (<https://www.qgis.org/>), with maps based on the open access Natural Earth map (free vector and raster map data @ naturalearthdata.com). Figures and maps were assembled using Adobe Photoshop CS2 version 9.0 for Windows and Adobe Illustrator CS2 version 12.0 for Windows (both Adobe Systems, San Jose, CA, USA).

Results

Phylogenetic analyses

The phylogenetic reconstruction of *Stenomelania*, *Neoradina* and *Melanoides*, with an outgroup composed of five species of Hemisinidae and Paludomidae, recovered all thiarids as a maximally supported group (see Fig. 2 for the phylogenetic tree). However, a clear distinction of the three thiarid genera discussed here is not possible based on the mtDNA only, as the basal node of the resulting phylogeny was recovered as a polytomy. Within this polytomy four lineages were found: (i) a clade consisting of three *Stenomelania* s. str. species, (ii) a combined clade of *Neoradina*, “*S.*” *denisoniensis* and another two *Stenomelania* species, and (iii) two clades of *M. tuberculata*.

(i) A well-supported clade was found composed of *Stenomelania* specimens allocable to *S. aspirans*, *S. torulosa* and *S. crenulata*. The latter two species are maximally supported (*S. crenulata* PP: 1.00, BS (MP): 100, BS (ML): 100; *S. torulosa* PP: 1.00, BS (MP): 100, BS (ML): 99). Within the *S. aspirans* further subclades are found: a basal clade encompassing specimens from West-Papua and Fiji; one encompassing only Sulawesi specimens; another consistent of one Philippine specimen, another encompassing specimens from Australia, Bali and West Papua and lastly, a large clade consistent of specimens from across Indonesia (Bali, Sulawesi, Obi, Ambon, Seram).

(ii) The second part of the basal polytomy is an only loosely supported clade of *S. plicaria* and *S. punctata*, which is sister to a clade composed of “*S.*” *denisoniensis*, *N. prasongi* and a lineage of snails from West Papua, morphologically indistinguishable from “*S.*” *denisoniensis*. Therefore, we refer to this species as “*S.*” cf. *denisoniensis* throughout this manuscript. Thereby, all latter three taxa are maximally supported (each with PP: 1.00, BS (MP): 100, BS (ML): 100). However, *S. plicaria* is relatively well-supported (PP: 0.97, BS (MP): 90, BS (ML): 48), whereas *S. punctata* is not supported (PP: 0.58, BS (MP): 32, BS (ML): 18) though this clade is composed of two well supported clades (one with PP: 1.00, BS (MP): 100, BS (ML): 87 and the other with PP: 1.00, BS (MP): 100, BS (ML): 95).

(iii) The third clade within the basal polytomy is composed of *M. tuberculata* and another *Melanoides* species. The relation of these two clades is only loosely supported (PP: 0.61, BS (MP): 42, BS (ML): 17), though both groups are maximally supported (PP: 1.00, BS (MP): 100, BS (ML): 100). A fourth branch of the basal polytomy is consistent of two specimens of *M. tuberculata* from West Papua.

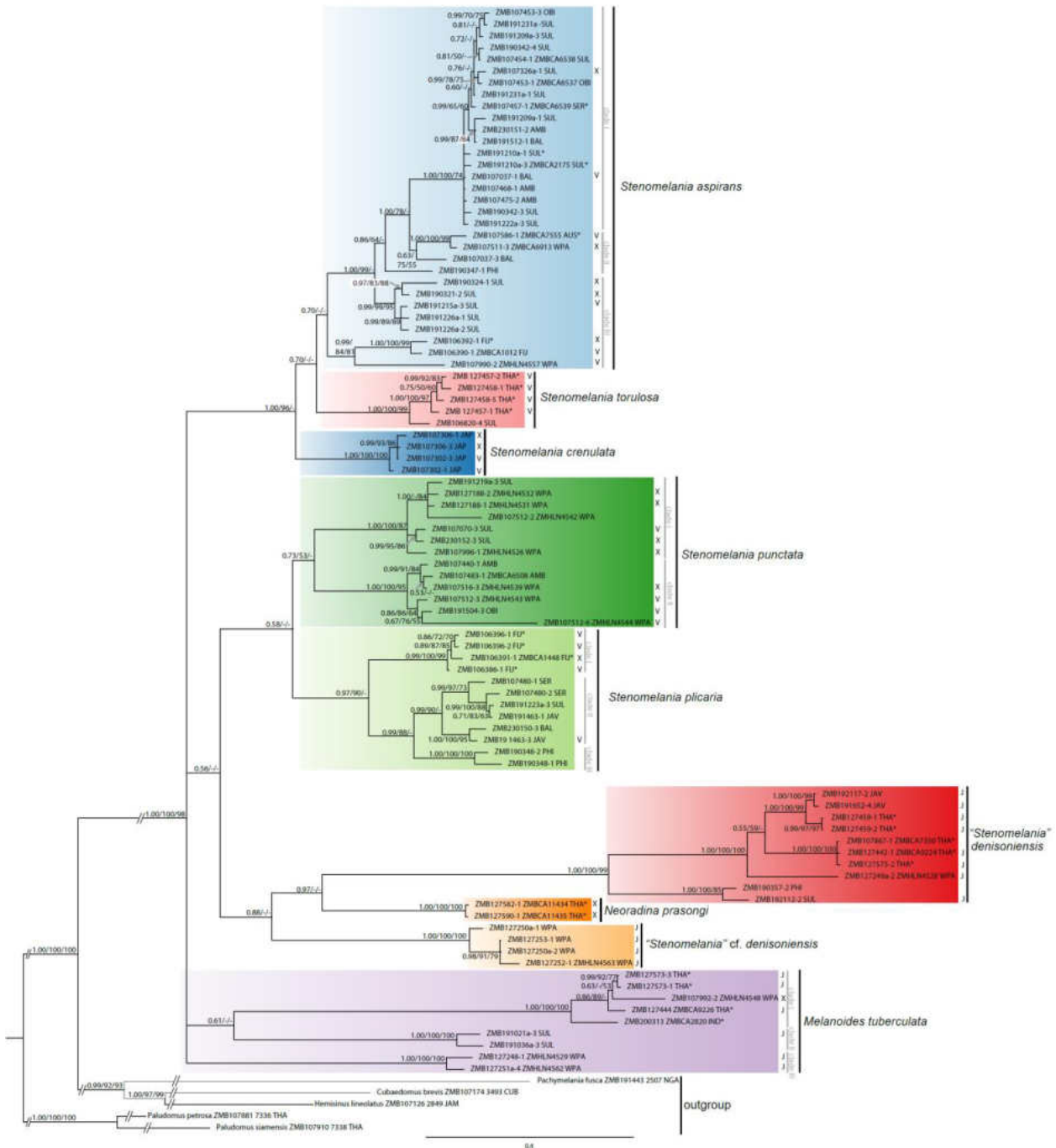


Figure 2 Bayesian 50% majority consensus tree based on concatenated COI and 16S sequences. Numbers at the nodes refer to posterior probability (PP) values (left) from the Bayesian (BI) and bootstrap support (BS) values from the maximum parsimony (MP) analysis (middle) and from the maximum likelihood (ML) analysis (right). Only nodes with PP values 0.50 and/or BS values from ML and/or MP analyses 50% are annotated. Grey clad headers indicate tested clusters for the second grouping tested in the geometrics morphometrics approach. Single letters after each sequence indicate developmental modes for each population: V = veliger stages found in brood pouches, J = juvenile stages found in brood pouches, X = no offspring found for this population. Three letter codes at the end of each sequence indicate the country or Island of origin (AMB = Ambon, Indonesia; AUS = Queensland, Australia; BAL = Bali, Indonesia; CUB = Cuba; FIJ = Fiji; IND = Indida; JAM = Jamaica; JAP = Japan; JAV = Java; NGA = Nigeria; OBI = Obi, Indonesia; PHI = Philippines; SER = Seram, Indonesia; SUL = Sulawesi, Indonesia; THA = Thailand, WPA = West Papua, Indonesia).

Geometric morphometrics

Overall, based on our the geometric morphometrics approach, we found that several of our presumed morphologically and genetically assumed species are different from each other in shell shape. There is a major difference in shell shape between all *Stenomelania* s. str. species and all other studied species. Furthermore, we found that between molecular clades of these assumed species only minor differences (that is differences on PC3) exist.

The analysis of shell shapes shows an overall high level of variance (see Figure 3A, for a scatterplot of variances on PC1 and PC2). A significant proportion of variance ($P>0.05$) was identified for the first three major axes of variance (PC = principal component axis; PC1: 0.663; PC2: 0.122; PC3: 0.056) by the PCA. These three axes explain a cumulative proportion of 0.841 of variance. We first tested for significant differences between morphologically and genetically similar groups.

On PC1 and PC2 each, the Shapiro-Wilk-test was significant ($P<0.05$) for at least one of the tested groups. The subsequent Kruskal-Wallis-rank-sum-test scored highly significant for each axis separately ($P<0.001$). Therefore, we performed a Dunn-test to identify significant differences between groups.

On PC1, shell shapes of *S. aspirans*, *S. plicaria*, *S. punctata* and *S. torulosa* were all found significantly different to those “*S.*” *denisoniensis*, “*S.*” cf. *denisoniensis*, *N. prasongi* and *M. tuberculata*. Furthermore, shells shapes of *S. aspirans* were found significantly different to those of *S. punctata* and *S. plicaria*. Shell shapes of *S. crenulata* were not significantly different to any other group (see Figure 3C).

On PC3 shell shapes of *S. aspirans*, *S. crenulata*, *S. plicaria*, *S. punctata*, *S. torulosa* and *M. tuberculata* were significantly different from those of *N. prasongi* and “*S.*” cf. *denisoniensis*. Shell shapes of *S. plicaria* and *S. punctata* were both significantly different from shell shapes of *M. tuberculata*. Additionally, *S. aspirans* shell shapes scored significantly different from those of *S. plicaria* and *S. punctata*. Further significant differences have been found between shell shapes of *S. torulosa* and *S. plicaria*. Lastly, *Stenomelania crenulata*, *S. plicaria* and *S. punctata* shell shapes were significantly different from those of “*S.*” *denisoniensis* (see Figure 3D).

For two of the nine tested group the Shapiro-Wilk-test scored significant ($P<0.05$) on PC3. The subsequent Kruskal-Wallis rank sum test was not significant ($P=0.12$). Therefore, no further testing was conducted on PC3 as no differences between shell shapes were detected.

We furthermore performed an analysis of the dataset to test for differences between genetic clusters within presumed species clades (that is the three clades of *S. aspirans*, three clades of

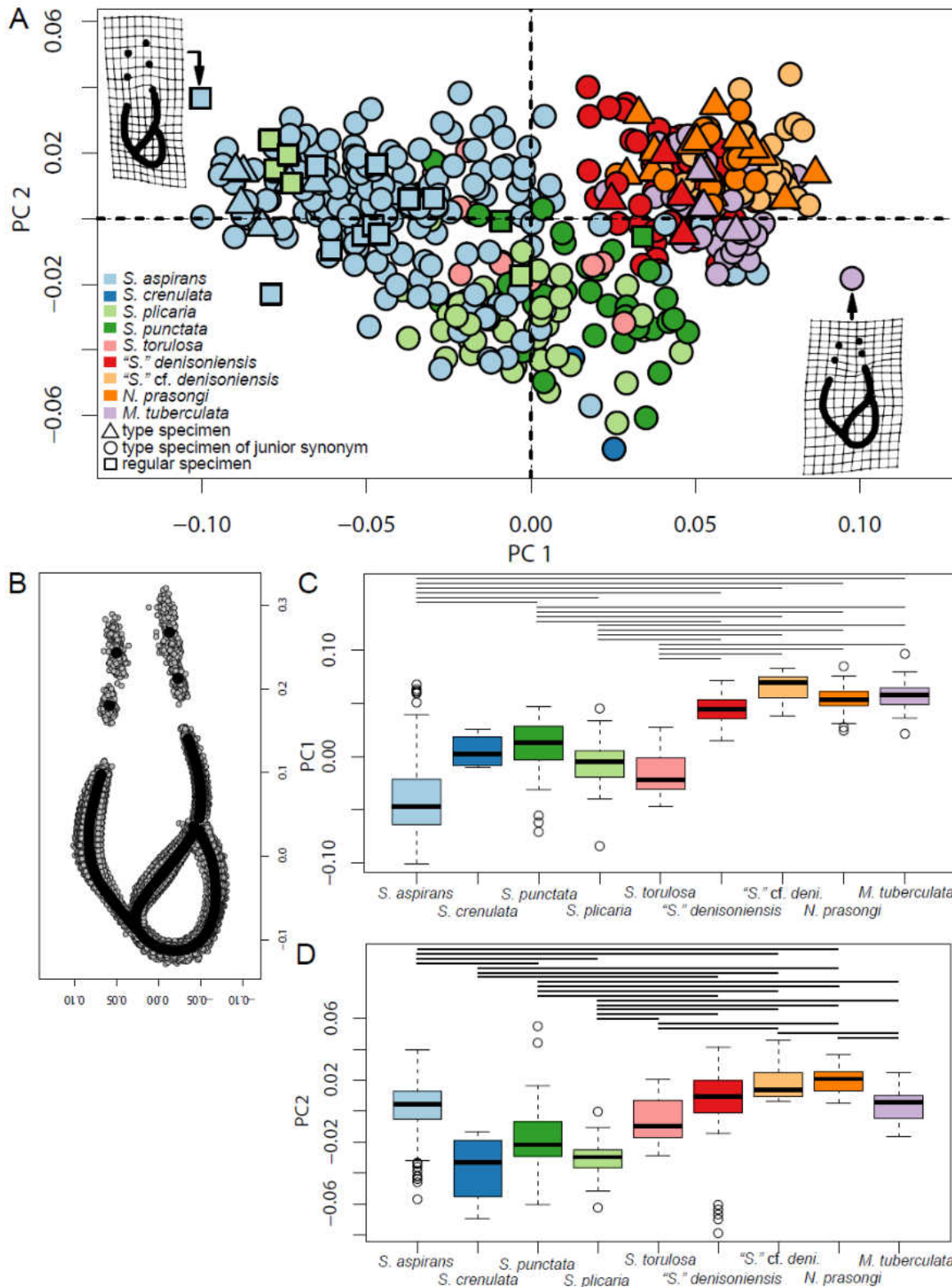


Figure 3 Results of geometric morphometrics analysis with sliding landmarks. **A** Relative variance in shell shape along PC1 and PC2. Depicted thin plate splines represent shell shapes of individuals with highest and lowest value along PC1. **B** Total variance of landmark positions. Grey dots comprise positions of all plotted landmarks. Black dots indicate the mean position of each landmark across the entire dataset. **C**, **D** Differences between shell shapes of predefined species groups on **C** PC1 and **D** PC2. Significant differences ($P < 0.05$) are indicated by bars above boxplots, with each bar beginning and end indicates significant differences between two groups.

S. plicaria, two clades of *S. punctata*, and three clades of *M. tuberculata*, see Fig. 2). On all three PC1–3 the Shapiro-Wilk-test scored significant ($P < 0.05$) for at least one studied group. Hence, for each of the three axes a Kruskal-Wallis-rank-sum-test was performed, scoring significant ($P < 0.05$) on each PC. Subsequently, Dunn-tests were performed to identify significant differences between all studied clades. On PC1 and PC2 no differences other, than those of the previous analysis were identified. Lastly, PC3 identified significant differences in shell shape between specimens belonging to clade I+III and clade II of *S. aspirans* and between specimens from clade I and clade II+III of *S. plicaria* (see Fig S1 for all details of this analysis).

Brood pouch content analysis

Our dataset contained 43.34% gravid females (114 specimens). *Stenomelania* s. str. species were all found to only contain early developmental stages in large amounts, with a range of $n = 232$ to 14423 individuals of offspring within a single brood pouch. In contrast, those species with a k-strategy, viz. "*S.*" *denisoniensis*, "*S.*" cf. *denisoniensis* and *M. tuberculata* were found with low amounts of later developmental stages only, counting $n = 1$ to 300 individuals of offspring within a single brood pouch. The highest numbers of offspring within a single brood pouch were found in *S. aspirans* ($n = 14423$) and *S. plicaria* ($n = 10200$), whereas the lowest amounts of individuals per single brood pouch were exclusively found within the three

Table 1. Results of brood pouch content analysis for the species studied. The size classes we distinguished are a, eggs/embryos/veligers in early ontogenetic stages; b, late embryos/veligers; c, juveniles < 0.5 mm; d, juveniles 0.6–1 mm; e, juveniles 1.1–1.5 mm; f, juveniles 1.6–2 mm; g, juveniles 2.1–2.5 mm; h, juveniles 2.6–3 mm; i, juveniles > 3 mm. No data is available on brood pouch contents of *Neoradina prasongi*.

Species	Average number of offspring	Lowest number of offspring	Highest number of offspring	Number of different size classes	Size classes	Number of examined specimens	Number of gravid females
<i>Stenomelania aspirans</i>	5981	940	14423	2	a, b	52	10
<i>Stenomelania crenulata</i>	656	550	830	1	b	6	3
<i>Stenomelania plicaria</i>	6746	598	10200	1	a	19	5
<i>Stenomelania punctata</i>	1009	340	2400	1	a	32	7
<i>Stenomelania torulosa</i>	1170	232	2874	2	a	16	7
" <i>Stenomelania</i> " <i>denisoniensis</i>	30	1	300	9	a-i	89	57
<i>Neoradina prasongi</i>	n/a	n/a	n/a	n/a	n/a	15	0
<i>Neoradina</i> sp.	14	14	14	5	b, d-g	2	1
<i>Melanoides tuberculata</i>	44	4	193	9	a-i	37	24

species that were found with juvenile stages (“*S.*” *denisoniensis*, “*S.*” cf. *denisoniensis* and *M. tuberculata*). Only across specimens of *M. tuberculata* and “*S.*” *denisoniensis* all size classes of offspring were found, whereas “*S.*” cf. *denisoniensis* contained five and all other species but *N. prasongi* contained either eggs or veliger stages (one to two size classes). For *Neoradina prasongi* no developmental mode is known (see Wiggering et al., 2019). For more details on brood pouch content data of each species refer to Tab. 1; for a detailed list of all brood pouch content data per individual refer to Table S3).

Lastly, the three k-strategy species among thiarids considered here had far higher frequencies of gravid females per studied samples (see Table 1). *Stenomelania* s. str. species exhibited only 19–50% gravid females across all studied specimens of each species, whereas for *M. tuberculata* 65%, and for “*S.*” *denisoniensis* 64% of gravid females across all studied specimens were found.

Systematic part

Stenomelania (Fischer, 1885)

Melania (*Stenomelania*) Fischer, 1885: 701

Melanoides (*Stenomelania*) P. Fischer, 1885 – Starmühlner, 1976: 251.

Stenomelania P. Fischer, 1885 – Houbrick, 1987: 40.

Thiara (*Radina*) Preston, 1915: 10.

Type species. *Melania aspirans* Hinds, 1844, by original designation.

Taxonomy. *Stenomelania* was first introduced by P. Fischer (1885) as a subgenus of *Melania*.

Starmühlner (1976) revised five species of this genus, placing *Stenomelania* as subgenus of *Melanoides*. Houbrick (1987) was the first to use *Stenomelania* without directly referring to *Melanoides*, though he referenced Starmühlner (1976). Glaubrecht (1996: 167-172, 304-305, 321-326) used the name at generic rank, based on the reviewed biological data in support for this distinction. This was further supported by Glaubrecht et al. (2009), repeating the assessment that *Stenomelania* constitutes an independent genus rank lineage of Thiaridae.

Preston (1915) introduced *Radina* as subgenus of *Thiara* Röding, 1798, with *Melania hastula* Lea & Lea, 1851 as its type species. However, *Melania hastula* was placed within *Stenomelania* (Schepman, 1918) and was later established as a junior synonym of *S. punctata* (Rensch, 1934). Hence, *Radina* is here considered a junior synonym of *Stenomelania*.

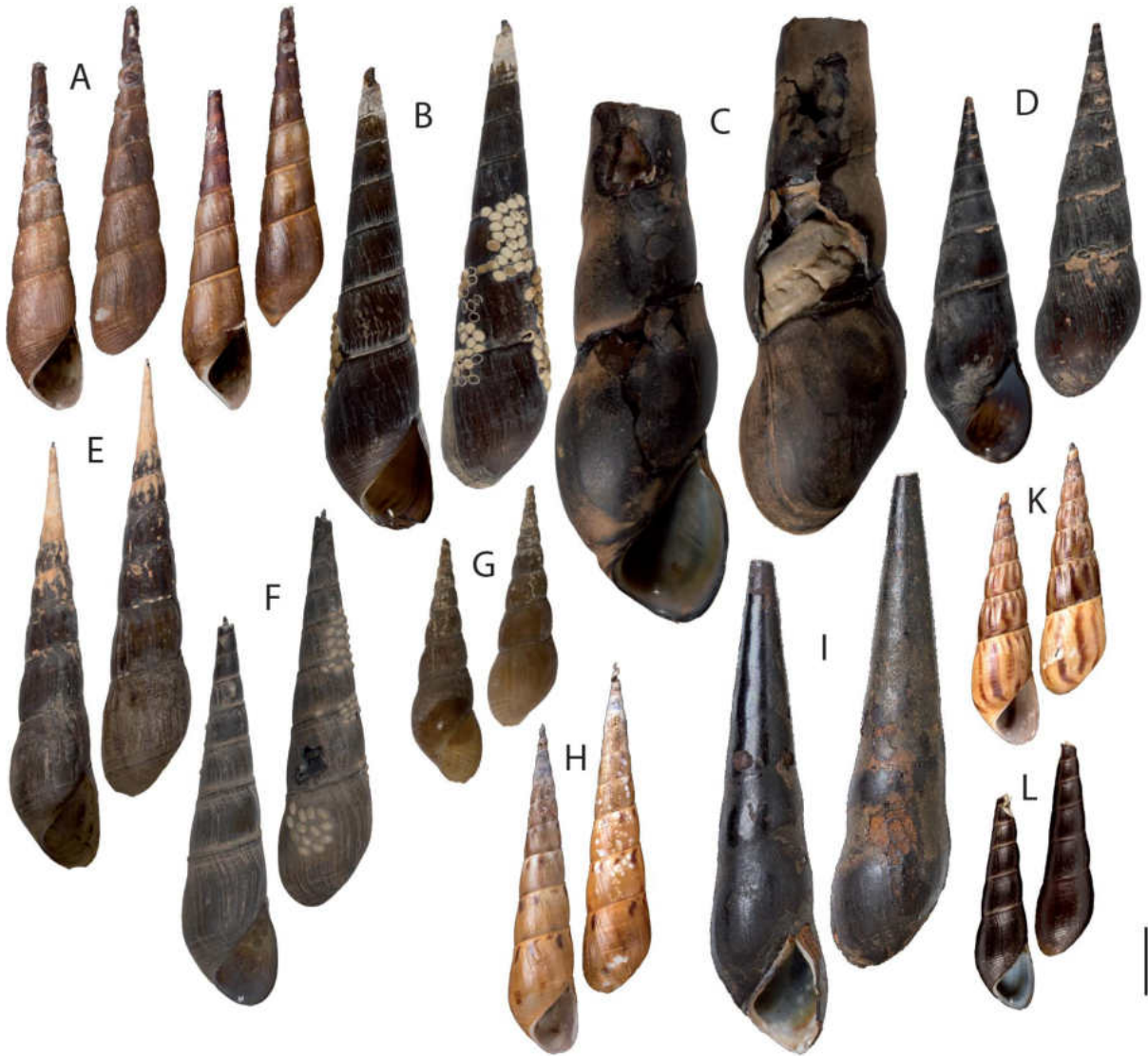


Figure 4 Shells of *Stenomelania aspirans* including types and type material of junior synonyms. **A** *Melania aspirans*, two syntypes, Fiji (NHMUK 1844.9.23.31-32); **B** Fiji, Sovi River, Malevu, Coral Coast (ZMB 106390-1); **C** Australia, Queensland, Mowbray River, near Port Douglas (ZMB 107586-2); **D** Indonesia, West Papua, South of Bird's Neck, Kaimana 35-40 km, Triton bay, River Lengguru valley upriver from Oray village (ZMB 107990-2); **E** Indonesia, Maluku, North Seram, coastal road between Piru and Latuhelu near Kawa, small stream (ZMB 107457-2); **F** Indonesia, South Sulawesi, Kupa, river, East of road between Makassar and Parepare (ZMB 191231a-2); **G** Philippines, Luzon, Barangay Masaya near Los Banos, concrete irrigation ditch (ZMB 190347-1); **H** *Melania figurata*, one of two syntypes, New Ireland (NHMUK 1844.9.23.27-28); **I** *Melania macrospira*, one of three probable syntypes, New Caledonia (NHMUK 1893.2.4.1766-1768); **K** *Melania picta*, one of two possible syntypes, New Ireland (NHMUK 20010772); **L** *Melania veruculum*, one of two syntypes, Samoa (MNHN 2000-33263). Scale bar = 10mm. **A, H, I, K**: © Images courtesy of Harry Taylor, NHMUK Photographic Unit **L**: © M. Caballer MNHN, project E-RECOLNAT: ANR-11-INBS-0004.



Diagnosis. *Stenomelania* as perceived in this study is comprised from species with rather large, high-spired, slender shells (see Figures 4-6 for shells of all studied species). Shell sculpture can vary from very smooth (as is the case for *S. aspirans*) to heavily ribbed by numerous spiral and axial ribs (as in *S. torulosa*). These shell characters can vary heavily between juvenile and adult shells, as Bandel et al. (1997) illustrated for *S. plicaria* and *S. punctata*. Furthermore, older specimens oftentimes exhibit a highly corroded shell, in extreme cases leaving the shell with only the last one or two whorls (as best illustrated by Australian specimens of *S. aspirans*, see Fig 4). *Stenomelania* species are known to inhabit the tailwaters of tropical streams and rivers, with brackish water bodies. Seshaiya (1940) observed, that specimens of *S. crenulata* produce veliger larvae, that are tolerant to moderate to high salinities. We here postulate, that this holds true in all *Stenomelania* species (see details in discussion).

← **Figure 5.** Shells of *Stenomelania* s. str. species **A** *Stenomelania crenulata*, Japan, Ryukyu Islands, Okinawa (ZMB 107306-1); **B-G** *Stenomelania plicaria*; **B** *Helix plicaria*, Holotype, (NHMW 14393); **C** Indonesia, Central Sulawesi, Pondo River, South of Uekuli, Gandalari (ZMB 191223a-1); **D** Indonesia, Maluku, Seram, West Seram, road between Masohi and Piru, South of Waisarisa, side arm of large river (ZMB 107480-1); **E** Fiji, Sovi River, Malevu, Coral Coast (ZMB 106396-2); **F** *Melania auroriana*, syntype, junior synonym, Aurora Island, New Hebrides (ANSP 60060); **G** *Melania fumosa*, syntype, junior synonym, New Ireland; in the streams about Port Carteret (NHMUK 1844.9.23.25); **H-L** *Stenomelania punctata*; **H** Indonesia, Central Sulawesi, Luwuk Peninsula, River East of Uso, North of Batui (ZMB 191219a-2); **I** Indonesia, West Papua, Pulau Batanta, Sungai Samsen, Desau Wailebet (ZMB 107516-3); **K** *Melania fulgurans*, possible syntype, junior synonym, New Ireland (NHMUK 20010766); **L** *Melania papuensis*, 1 of 3 syntypes, junior synonym, New Guinea, Harbour Dorey (MNHN-IM 2000-33241); **M-N** *Stenomelania torulosa*; **M** Thailand, Klong Than (ZMB 127458-6); **N** Indonesia, Southeast Sulawesi, Ussu River, at Ussu, Northwest of Malili (ZMB 106820-8). Scale bar = 10 mm. **B** © Anita Eschner (NHMW) **F** Images were provided by Ms. Krasimira Seizova, Department of Malacology, Academy of Natural Sciences of Philadelphia. **G, K** © Images courtesy of Harry Taylor, NHMUK Photographic Unit. **L:** © M. Caballer MNHN, project E-RECOLNAT: ANR-11-INBS-0004.



Figure 6. Shells of "*Stenomelania*" *denisoniensis*, *Melanoides tuberculata* and *Neoradina prasongi*. **A-D** "*Stenomelania*" *denisoniensis*; **A** *Melania denisoniensis*, one of five type specimens, Australia, Queensland, Port Denison (MHNG); **B** Thailand, Ban Sa Kaeow (ZMB 127575-2); **C** Philippines, Mindanao, Mountain stream near Calinan (ZMB 190357-2); **D** Indonesia, South Sulawesi, River at road between Bulukumba and Sinxi (ZMB 192112-2); **E** "*Stenomelania*" cf. *denisoniensis*, Indonesia, West Papua (ZMB 127250a-1); **F-I** *Melanoides tuberculata*; **F** one of three syntypes, India, Coramandel coast (ZMUC); **G** Thailand, 7 km Northwest of Krabi, Ban Khlong Chilat (ZMB 127573-3); **H** Indonesia, South Sulawesi, Matano catchment, Matano, stream South of village, ca. 50 m from lake (ZMB 191021a-2); **I** Indonesia, West Papua, South Bird's Neck, 35-40 km East of Kaimana, Triton bay, River Lengguru valley upriver from Oray village (ZMB 107992-1); **K & L** *Neoradina prasongi*; **K** Holotype, Thailand, Stream about 7 km from Grabi to Kao Tong (SMF 215933); **L** Thailand, Trang province, Siako district, Mai Fad, Pak Meng river, at Pak Meng, 30km North of Trang, (ZMB 127582-1). Scale bar = 10mm

***Stenomelania aspirans* (Hinds, 1844)**

Melania aspirans Hinds, 1844: 8.

Melanoides (Stenomelania) aspirans – Wenz, 1938: 714.

Melanoides (Stenomelania) aspirans (Hinds, 1847) [sic] – Starmühlner, 1976: 577.

Stenomelania cf. *aspirans* Hinds, 1844 – Glaubrecht et al., 2009: Zoosyst. Evol., 85: 247.

Melania figurata Hinds, 1844: 8. [Type material: NHMUK 20010763; 1844.9.23.27-28; see Fig 4H]

Melania picta Hinds, 1844: 8. [Type material: NHMUK 20010772; see Fig 4K]

Melania veruculum Morelet, 1851: 193 [Type material: MNHN-IM 2000-33263, see Fig. 4L]

Melania macrospira Morelet, 1857: 32. [Type material: NHMUK 1893.2.4.1766-1768; see Fig. 4I]

Type material. 2 syntypes (NHMUK 1844.9.23.31-32, see Fig 4A); eight more possible syntypes from the Hinds collection, labeled with the same locality (NHMUK 20010758, 20010759, 20010760, 20010761).

Type locality. “Feejee Islands; in rivers” (Hinds, 1844).

Taxonomy. Fischer (1885) described the new subgenus *Melania (Stenomelania)*, designating *Melania aspirans* as its original type species. Subsequently, Glaubrecht (1996) elevated *Stenomelania* to generic rank, thus implying the combination *Stenomelania aspirans*, its current taxonomic status.

We here consolidate *Melania figurata* Hinds, 1844, *Melania picta* Hinds, 1844, *Melania veruculum* Morelet, 1851, *Melania macrospira* Morelet, 1857 as junior synonyms of *S. aspirans*, based on their similarities in shell morphology, type locations and all but *M. macrospira* on their geometric shell shape. Starmühlner (1976) proposed all of these nominal species as junior synonyms, as well as *Melania scipio* Gould, 1847, *Melania ordinaria* Smith, 1884, based on shell measurements and general impression; note that we were unable to access type specimens of these nominal taxa as there were not present within all inquired collections.

Shell (Figure 4). The shell is very solid, smooth and high spired. In older specimens, oftentimes, the upper parts of the shell are corroded, in extreme cases leaving only the last few whorls of the shell intact. The apical part of the adult shell is often slightly truncated, angulated or concavely invaginated. Adults often possess only the last three to five whorls, while younger individuals show up to eleven whorls. Shells are up to 79.61 mm high. Shell coloration varies between dark brown to black whilst the inside of the aperture and corroded pieces are greyish-white or blueish-white porcelaneous. The aperture is holostome and drop-shaped. The margin protrudes to the right.

Reproductive biology. Ovo-viviparous “r-“strategy brooders. In this study, the brood pouches of *S. aspirans* specimens were found to be filled with veliger larvae. The number of veligers within a single brood pouch varied between $n = 940$ and 14423 . They were found to contain the highest amounts of offspring within the Australian populations than at all other localities.

Distribution. The species occurs through the Australasian region, spanning from Sulawesi and the Philippines, throughout the Bismarck Archipelago, West Papua, New Caledonia to Fiji. Here in addition, the range expands this vast distribution further into streams in Northeastern Queensland, Australia (Fig 7A); for details on the occurrence there see Glaubrecht et al. (2009).

Discussion

Systematics and taxonomy

Our integrative approach of combining mtDNA based molecular phylogenetics, geometric morphometrics and reproductive biology in order to study representative species of the *Melanoides-Stenomelania* complex allowed for new insights into this heavily entangled species group. Based on differences in shell shape and developmental mode, *Stenomelania* s. str. could be clearly distinguished from the other studied species. On this basis we support *Stenomelania* s. str. as a distinct lineage among thiarids. Our study of geometric morphometrics of the shell lend additional support to the distinguished species. This was also supported by our molecular genetic approach that allowed for the distinction of the five studied *Stenomelania* s. str. species, rendering each a valid species of its own.

However, the result that the basal node of this ingroup was recovered as a polytomy indicates the limitation of mtDNA based approaches within this family. In addition to the five species of *Stenomelania* s. str., *N. prasongi*, “*S.*” *denisoniensis* and “*S.*” cf. *denisoniensis* were supported as clearly distinguishable species (see Fig 2). By contrast, *Melanoides tuberculata* was not recovered as a singular lineage within our phylogeny. This is not surprising as this phenomenon was already encountered in several previous studies (Genner et al., 2007; Dechruksa et al., 2013). Furthermore, solely based on the molecular genetic approach the studied genera (*Stenomelania*, *Melanoides*, *Neoradina*) were not unambiguously supported in their morphologically established form.

By contrast, our geometric morphometrics approach was very informative in the distinction of *Stenomelania* s. str. species and all other studied species (see Fig 3C; see Figs 4–6 for an

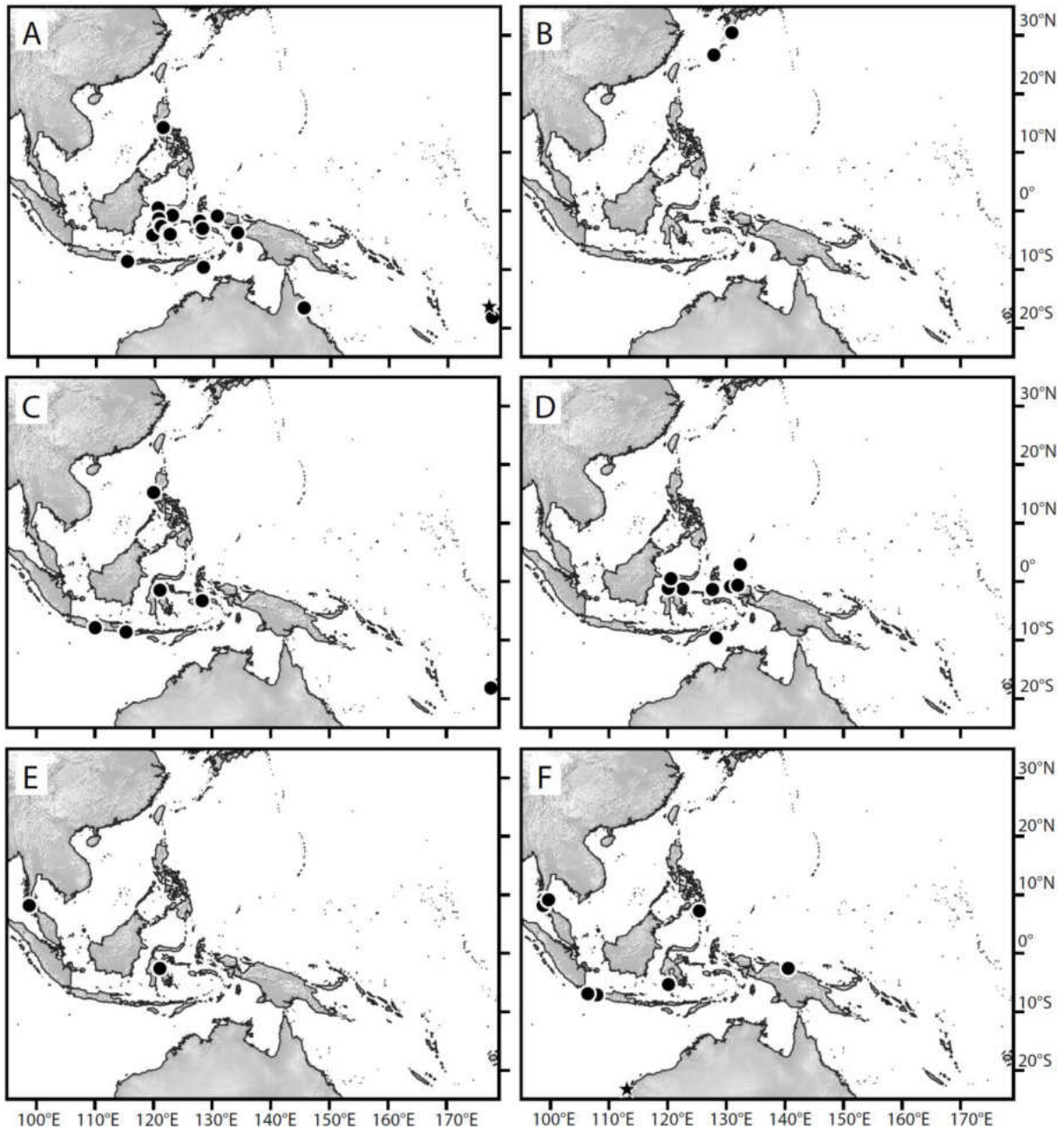


Figure 7 Distribution maps of all studied *Stenomelania* species based on all sample locations. Stars indicate type localities. **A** *S. aspirans*; **B.** *S. crenulata*; **C** *S. plicaria*; **D** *S. punctata*; **E** *S. torulosa*; **F** “*S.*” *denisoniensis*; note that this species is also widely distributed in Australia (not covered here, but see details in Glaubrecht et al., 2009).

impression of shells of all studied species). This was further supported by our examination of brood pouch contents. We found all *Stenomelania* s. str. species to be “r”-strategy brooders, these findings corroborate previous assertions about the developmental modes of these species (see for instance Seshaiya, 1940; Livshits & Fishelson, 1983; Bandel et al., 1997). “*Stenomelania*” *denisoniensis* and *M. tuberculata* were uncovered as “k”-strategy brooders. This is in accordance with prior findings and strengthens the distinction of these two

developmental modes (Glaubrecht, 1996, 2006, 2011; Glaubrecht et al., 2009). We conclude that *Stenomelania* appears to be distinguishable by shell shape and reproductive mode from the other genera in this species complex. Accordingly, we solidified this distinction within our systematic part.

Stenomelania punctata was recovered in two separate lineages that were only loosely supported in our phylogenetic tree. However, testing the shell shapes of these two clades against one another we did not find any significant differences (see Fig S1). Therefore, we do not see any reason to affiliate these clades to different species, but more so as intraspecific variation.

A similar phenomenon occurred in *S. aspirans*. Here a clade of West-Papuanese and Fijian specimens was only loosely affiliated with the other studied specimens of *S. aspirans*. The species type locality is in Fiji and *S. aspirans* is known to occur very widespread throughout the Pacific (Fig 7). It appears likely, that this problem stems from incomplete lineage sorting, as in our previous study focusing on *N. prasongi* (Wiggering et al., 2019), the same sequences were well-supported as a part of *S. aspirans*. It is therefore highly possible that with the addition of further specimens, in our analysis, differences between populations of *S. aspirans* become more apparent, leading to the structure present within our phylogeny.

Glaubrecht et al. (2009) tentatively assigned Australian specimen with a similar, yet far larger shell to *S. aspirans*. Based on reproductive mode, shell shape and the position of a representative specimen within our molecular tree, the Australian specimens used in this study can be unambiguously identified as *S. aspirans*. Hence, we confirm the finding of Glaubrecht et al. (2009) and support the wider distribution range of the species.

As our molecular phylogeny and geometric morphometrics approach do not allow for an unambiguous allocation of “*S.*” *denisoniensis* to either *Melanoides* or *Neoradina*, we here chose to leave this matter taxonomically unresolved. To indicate the disassociation of the species from *Stenomelania* we set the genus affiliation of quotation marks throughout our study.

Furthermore, a distinct genetic lineage of snails that were morphologically indistinguishable from “*S.*” *denisoniensis* was, with very low support values, recovered as sister clade to *N. prasongi* and “*S.*” *denisoniensis* within our phylogenetic reconstruction. As gravid females of this species contained juvenile stages within their brood pouches and the geometric morphometrics study did not identify any differences between this clade and “*S.*” *denisoniensis*, we here chose to tentatively call this lineage “*S.*” cf. *denisoniensis*. As *S. denisoniensis* was first described from and widely occurs in Australia (see Glaubrecht et al. 2009), the clade could very likely be just another lineage of this species. Though we expanded the material basis for “*S.*” *denisoniensis*, a clear affiliation of this species is not implied and,

thus, is a matter that should be solved in its own right, especially with an inclusion of more Australian specimens. The lack here might explain the low support values found for higher nodes related to this lineage.

Reproductive biology

Our examination of brood pouch content and subsequently assigned developmental modes suggest the distinction of *Stenomelania* s. str. from *Melanoides* and “*S.*” *denisoniensis* on the basis that the former releases large amounts of offspring at a free-floating larval stage, whereas the other two implicitly release juveniles. As our study uncovered “*S.*” *denisoniensis* as k-strategy brooder it is implied that this species should not be considered part of the genus as suggested by Glaubrecht et al. (2009) and Wiggering et al. (2019).

The evaluation of brood pouch contents might further point towards a difference not only in developmental mode but also in reproductive mode. Within *Stenomelania* s. str. species we never encountered more than 50% of studied specimens to be gravid females (*S. aspirans* 19%, *S. crenulata* 50%, *S. plicaria* 26%, *S. punctata* 22%, *S. torulosa* 44%). By contrast in the other studied species (except for *N. prasongi*), we encountered rates of gravid females above 50% (“*S.*” *denisoniensis* 64%, “*S.*” cf. *denisoniensis* 50% *M. tuberculata* 65%).

Melanoides tuberculata is known to be a facultative parthenogenetic (Jacob, 1957, 1958; Livshits & Fishelson, 1983; Ben-Ami & Hodgson, 2005; see for a comprehensive overview on the matter Ben-Ami & Heller, 2005). For all thiarids a parthenogenetic reproduction has been suggested, discussed and in the past widely accepted (Morrison, 1954; see Glaubrecht, 1996 for a detailed discussion). However, in truly parthenogenetic species, it is normal to encounter skewed gender proportions, that would manifest in a higher gravidity rate in studied specimens (as we encountered here for *M. tuberculata* and “*S.*” *denisoniensis*). Hence, we propose that *Stenomelania* s. str. is not reproducing parthenogenetically and the hypothesis that all thiarids are parthenogenetic should be rejected and replaced by more thorough research on the reproductive biology of this family. However, it should be noted that for both, “*S.*” cf. *denisoniensis* and *S. torulosa* less than ten specimens could be studied, rendering their implications less reliable than those of the other species (Table 1).

Biogeography

The distribution areas of most *Stenomelania* species are large (see Fig 7) and spanning through remote areas of the Indo-West Pacific. The distribution area of *S. aspirans* as presented in this study, is spanning far across the Indo-Pacific and Australian regions (Sulawesi and the

Philippines, the Bismarck Archipelago, West Papua, New Caledonia, Fiji and Australia). As adults of these species are relatively large and, thus, cannot be easily dispersed as ‘hitchhikers’ on birds and are not tolerant to higher, i.e. marine, salinity, the question arises how these animals can be dispersed so far. As larval stages of *S. crenulata* were found to be tolerant of high salinities (Seshaiya 1940), *Stenomelania* s. str. species might disperse via marine currents, potentially allowing for long-distance dispersal, which we propose here. We see this assumption justified, as in all *Stenomelania* s. str. species only early developmental stages were present. Additionally, all *Stenomelania* s. str. species regularly have a very wide area of distribution, which is unexplainable based on other modes of dispersal.

The proposed dispersal ability of *Stenomelania* s. str. is enabled by the multitude of wide-ranging sea currents within the Australasian region. A system of ocean currents, viz. the Indonesian Throughflow and the North Equatorial Current (NEC), carry water westwards from the Pacific to the Indian Ocean, taking routes where the winds are light or variable, i.e. such as through deep passages of the Indonesian Archipelago (NCMI Information and Data Centre, CSIRO). The NEC turns southwards as the East Australian Current (EAC) and flows back from the west by Tasmania to the east as the South Pacific Current (SPC). At the northern Australian coasts of Queensland, the EAC intertwines with several Coral Sea Currents. Consequently, larval stages of *S. aspirans* could be dispersed throughout the Australasian region by prevailing ocean currents. Similar phenomena have been described for amphidromous Neritidae snails (Crandall, et al 2010; Davis & Ponder, 2019) and giant clams (Keyse et al., 2018), as well as for the recent (Castelin et al., 2013; Iacchei, 2016) and historical (Page, 2005) dispersal of Crustaceans.

Studies of ocean currents and presumable barriers to larval dispersal in respect to giant clams of the genus *Tridacna* occurring in this region have revealed that there might be a putative barrier to dispersal such as the Pleistocene land barrier of Torres Strait (Keyse et al., 2018) which could also constitute a barrier for other larvae, such as those of *Stenomelania*.

This could potentially explain the restriction of *S. aspirans* to northern Queensland within Australia, which holds also true for other amphidromous Neritidae species (Davis & Ponder, 2019). Additionally, it can be assumed that the larval dispersion is limited to the tropical Australasian region as veliger stages might only tolerate certain salinities and temperatures, that might be lethally different in other areas (see discussion in Glaubrecht et al. 2009). This might best be exemplified by the distribution ranges of *Stenomelania* species, as they regularly lie in the Australasian region with a concentration on the Indo-Polynesian province. A similarly distribution is found in the “r-strategy” brooder *Thiara amarula* (Linné, 1758). Schütt &

Glaubrecht (1999) show, that the species has a disjunct distribution, being present within Australasia and the southern Western Indian Ocean, but lacking from India and the Arabian sea, where very different salinities prevail. However, at this point more detailed studies on the larval development and dispersal ability of *Stenomelania* species are needed in order to then access and model the dispersion passageways and evolutionary history of *Stenomelania*.

Conclusion

The combination of methods (i.e. molecular phylogenetics, geometric morphometrics and the analysis of brood pouch content) provided in this study allowed us to reconstitute *Stenomelania* s. str. and confirm this lineage as a distinct genus of Thiaridae different from *Melanoides* and *Neoradina* in shell shape and developmental mode. Furthermore, all studied species were supported by our geometric morphometrics approach, as well as our genetic approach based exclusively on partial mtDNA sequences.

However, our limited genetic approach based exclusively on partial mtDNA sequences illustrated that within the Thiaridae a more sophisticated genomic approach might be needed to truly resolve the systematic issues within this gastropod family. Future studies will need broader sampling both in number of examined nominal species as well as specimens to resolve the entanglement of the enigmatic *Stenomelania-Melanoides* complex, hopefully disentangling its evolutionary systematics.

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For all supplemental materials refenced in this chapter refer to Appendix III

Chapter 5 Case 3838 – *Helix plicaria* Lamarck, 1816 (currently *Hemicycla plicaria*; Gastropoda, Eupulmonata, Stylommatophora, HELICIDAE): proposed conservation of the specific name

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Abstract

The purpose of this application, under Article 23.9.5 of the Code, is to conserve the specific name *Helix plicaria* Lamarck, 1816, a junior primary homonym of *Helix plicaria* Born, 1778. These names are currently in use for two different groups of land and freshwater snails, respectively, and have not been treated as congeneric since 1828. *Helix plicaria* Born, 1778 was first transferred to the genus *Bulimus* Scopoli, 1777 and subsequently to the genera *Thiara* Röding, 1798, *Melania* Lamarck, 1799, *Melanoides* Olivier, 1804 and *Stenomelania* Fischer, 1885. *Helix plicaria* Lamarck, 1816 has either been treated as belonging to *Helix* Linnaeus, 1758, *Cochlea* Da Costa, 1778 or has been included in *Hemicycla* Swainson, 1840. It is proposed that *Helix plicaria* Lamarck, 1816 be conserved by ruling it is not invalid by reason of being a junior homonym of *Helix plicaria* Born, 1778.

Keywords Nomenclature; taxonomy; Gastropoda; Heterobranchia; Caenogastropoda; HELICIDAE; THIARIDAE; *Bulimus*; *Helix*; *Cochlea*; *Hemicycla*; *Melania*; *Melanoides*; *Stenomelania*; *Thiara*; *plicaria* Lamarck, 1816; *plicaria* Born, 1778; Canary Islands; Indo-Pacific region

Case 3838

1. The name *Helix plicaria* Born, 1778 was introduced by Born (1778) on p. 403 as *Helix plicata* (and corrected on p. 2 of the corrigendum to *Helix plicaria*) for a freshwater gastropod, which is, according to the current delimitation of the taxon, thought to be widespread in the Indo-Pacific region (Starmühlner, 1976, 1982). On p. 376, Born (1778) had already introduced the name *Helix plicata* for another species (with a depressed conical shell and an aperture with plicae inside), and Born (1780) on p. 368 used the name again for the same species. Although not explicitly stated, Born (1778) probably recognised that he had used the name for two different species and corrected the name for the species introduced on p. 403. With the correction to *Helix plicaria* in the corrigendum, *Helix plicata* as introduced on p. 403 became therefore an incorrect original spelling. Coan & Petit (2011) erroneously considered the usage of the name *plicaria* by Born (1780) to be unavailable as these authors considered it a subsequent misspelling of the name *plicata*, overlooking Born's corrigendum. The name *plicaria* Born, 1778 was thus correctly used in the combination *Helix plicaria* by Born (1780)

on p. 389 and a specimen was figured on pl. 16, fig. 14 of that work. A single specimen of *Helix plicaria* Born, 1778 corresponding well to the specimen figured by Born (1780) (Fig. 1A) is present in the collection of the Naturhistorisches Museum Wien (NHMW 14393, Fig. 1D, see also Brauer, 1878: 184). The specimens figured by Gualtieri (1742: pl. 6 fig. H) (Fig. 1B) and the specimen figured by Martini (1767: pl. 10 fig. 51) (Fig. 1C), which were cited by Born (1778: 403), are also part of the type series (Article 72.4.1). The specimen figured by Gualtieri (1742) is not present in the N. Gualtieri collection housed at the Museo di Storia Naturale dell'Università di Pisa, and since the whereabouts of the collection of F. H. W. Martini is unknown (Cernohorsky, 1974), the specimen figured by Martini (1767) is probably lost, too. Furthermore, at least the specimen figured by Martini (1767) is probably not conspecific with the specimen in the collection of the NHMW. In order to stabilise the usage of the name, we here select the specimen NHMW 14393 (Fig. 1D) as the lectotype of the nominal species *Helix plicaria* Born, 1778.

2. Relatively few authors used the name *plicaria* Born, 1778 in the combination *Helix plicaria* at the end of the 18th and during the first decades of the 19th century (six usages, see Supplementary Material). Already Bruguière (1792: 328–329) transferred the taxon to the genus *Bulimus* Scopoli, 1777, and the name was also used in the combination *Bulimus plicarius* in the three editions of the ‘Histoire naturelle des coquilles’ by L. A. G. Bosc (see Supplementary Material). Subsequent authors used the name (see Supplementary Material), although sometimes with the year given as 1780, in the binomial combination *Melania plicaria* (eight usages), *Melanoides plicarius* (three usages), *Melanoides plicaria* (44 usages), *Thiara plicaria* (five usages) or *Stenomelania plicaria* (18 usages). Additional sources using the name in combination with the genus-group names *Thiara* Röding, 1798, *Melania* Lamarck, 1799, *Melanoides* Olivier, 1804 or *Stenomelania* Fischer, 1885 could probably be found, but although there is some dissent among researchers as to the generic placement of *plicaria* Born, 1778, its placement in THIARIDAE Gill, 1871 (1823) (= MELANIIDAE Children, 1823) is widely accepted.

3. The specific name *Helix plicaria* was introduced by Lamarck (1816: 13, pl. 462 fig. 3a, b) and is a junior primary homonym of *Helix plicaria* Born, 1778. There are two specimens in the Lamarck collection housed at the Muséum d’Histoire naturelle Genève (MHNG 1091/87; see Mermod, 1951, fig. 54 and Ibáñez et al. 1987: pl 1 fig. 2), which were collected by René Maugé on Tenerife according to Lamarck (1822: 88, referred to as *Helix plicatula* Lamarck, 1822, with *Helix plicaria* mentioned in the synonymy). René Maugé visited Tenerife between November 1796 and March 1797 during an expedition onboard the fluyt ‘*La Belle Angelique*’ led by Nicolas-Thomas Baudin from Le Havre to the Antilles (Ledru, 1810) and the type

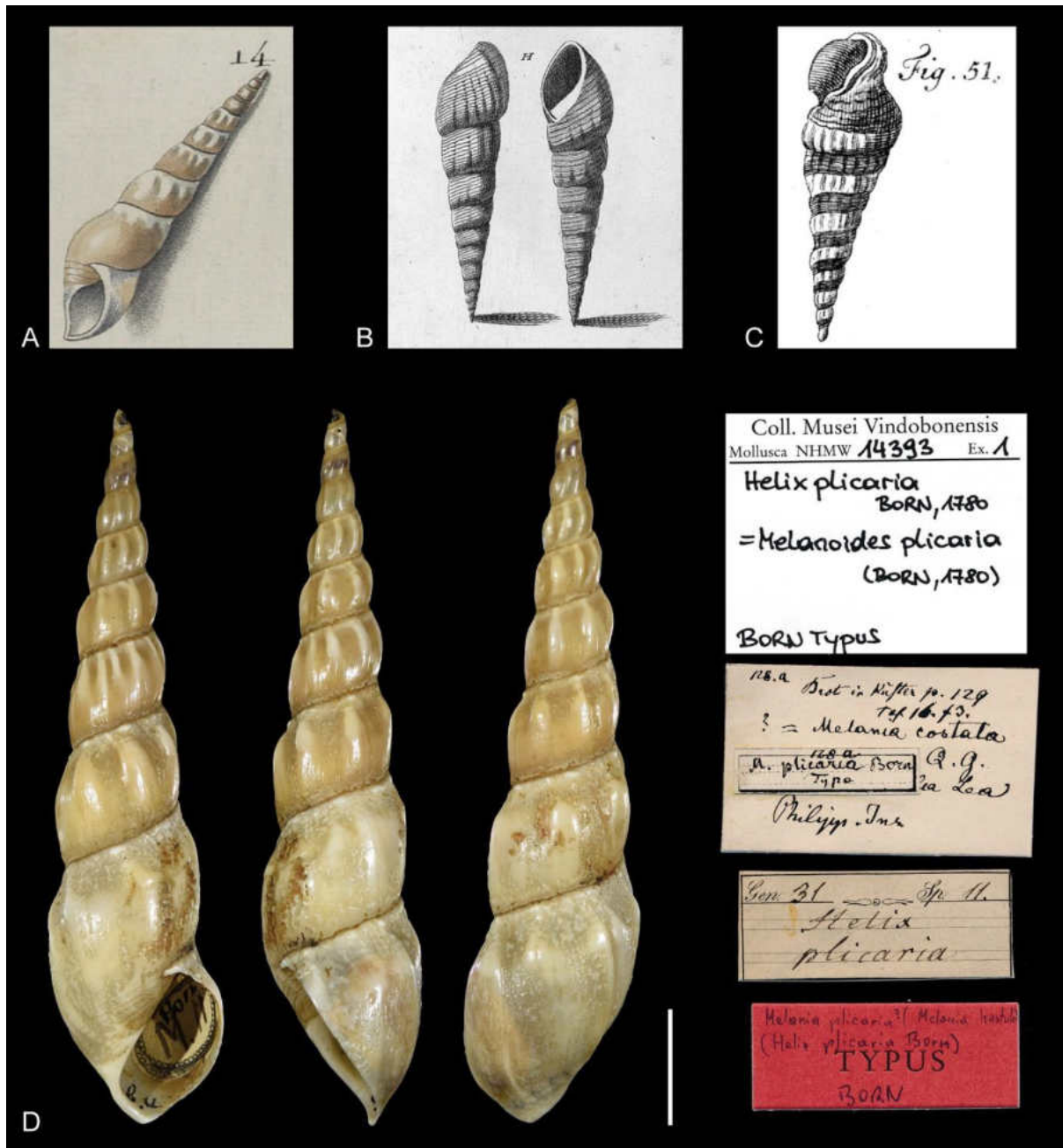


Figure 1. Specimens included in the type series of *Helix plicaria* Born, 1778 **A.** Figure from Born, 1780. **B.** Figure from Gualtieri, 1742. **C.** Figure from Martini, 1767. **D.** Lectotype of *Helix plicaria* Born, 1778 with its accompanying labels (NHMW 14393). Scale bar: 1 cm. **A–C.** Digitised through the Göttinger Digitalisierungszentrum (GDZ), Niedersächsische Staats- und Universitätsbibliothek Göttingen (SUB).

material was certainly collected during this visit. Ibáñez et al. (1987: 80, pl. 1 fig. 2) selected the specimen with the more expanded apertural margin as the lectotype, with the other specimens becoming a paralectotype (figured by Mermod, 1951: fig 54.1). The taxon is known only from a small area near Candelaria in the lower part of the Güimar Valley on Tenerife (Ibáñez et al. 1987), which was also reportedly visited by the members of the ‘La Belle Angélique’ expedition (Ledru, 1810).

4. Although there has been confusion as to the identity of *Helix plicaria* Lamarck, 1816 (Ibáñez et al., 1987, 1988; Ibáñez & Alonso, 2007), the name has been widely used (see Supplementary Material), either in the combination with the genus-group name *Helix* Linnaeus, 1758 (45 usages), *Cochlea* Da Costa, 1778 (one usage) or *Hemicycla* Swainson, 1840 (54 usages).

5. The next available names for the species from Tenerife are *Helix plicatula* Lamarck, 1822 (apparently a new name for *Helix plicaria* Lamarck, 1816, but not expressly stated as such; an objective junior synonym of *Helix plicaria* Lamarck, 1816 because Ibáñez et al., 1987 selected the same specimen as lectotype) and *Helix chersa* Mabilie, 1882 (two syntypes in the collection of the Muséum national d'Histoire naturelle, Paris, see Ibáñez et al., 1987). Both names have only been rarely used by subsequent authors: *plicatula* Lamarck, 1822 (Blainville, 1825; Deshayes, 1832; Beck, 1837; Deshayes & Milne Edwards, 1838; Catlow & Reeve, 1845; Graells, 1846; Gray, 1847; Chenu, 1852; Gray, 1859; Mermod, 1951) and *chersa* Mabilie, 1882 (Mabilie, 1884, 1885; Gude, 1896; Odhner, 1931; Hesse, 1931; Oromí Masoliver et al., 1985, 1987). The name *Helix orbiculata* Wood, 1828a for this species is preoccupied by *Helix orbiculata* Férussac, 1822 and has to our knowledge only been used as the valid name of a taxon by Hanley (1856) in the fourth edition of Wood's 'Index testaceologicus'.

6. *Helix plicaria* Lamarck, 1816 is the type species (by monotypy) of *Hemicycla* Swainson, 1840 and the taxonomic confusion relating to the name *plicaria* Lamarck, 1816 has been resolved in the revision of Ibáñez et al. (1987). The species is currently considered as critically endangered and has been consistently included in conservation literature, faunal listings, distribution atlases and national and international Red Lists as well as in molecular genetic studies in the combination *Hemicycla plicaria* (Lamarck, 1816) since 1987 (Alonso et al., 1990, 1991; Thornback et al., 1990; Groombridge, 1993; Baillie & Groombridge, 1996; Koomen & van Helsdingen, 1996; Gómez Moliner et al., 2000; Ibáñez & Alonso, 2001, 2005, 2006, 2009; Ibáñez et al., 2001; Bank et al., 2002; Groh & García, 2004; Martínez-Ortí, 2005; Arechavaleta Hernández, 2006; Arechavaleta & Martín, 2008; Verdú & Galante, 2009; Cuttelod et al., 2011; Neiber et al., 2011; Hernández-Manrique et al., 2012; Groh & Alonso, 2013; Neiber & Hausdorf, 2015, 2016; Neubert et al., 2019). Replacing the currently used species name would therefore have the potential not only to cause confusion in the nomenclature of the species again, but also has the potential to cause confusion with regard to conservation issues.

7. Both, the names *plicaria* Born, 1778 and *plicaria* Lamarck, 1816 have frequently been used in the past (see Supplementary Material), but Wood (1828b) was the last – to our knowledge – who used the name *plicaria* Born, 1778 in the combination *Helix plicaria*. Both

taxa have, therefore, not been considered congeneric for 192 years and belong to very distantly related gastropod lineages, with *Helix plicaria* Born, 1778 currently classified in the family THIARIDAE Gill, 1871 (1823) (Caenogastropoda) and *Helix plicaria* Lamarck, 1816 in the family HELICIDAE Rafinesque, 1815 (Heterobranchia). Their shells look very different and it is very unlikely that the two taxa could be confounded in museum collections (see Fig. 1D and pl. 1 fig 2 in Ibáñez et al., 1987, respectively).

8. Using the name *plicatula* Lamarck, 1822 for the species from Tenerife would be possible, we think however that nomenclatural stability in this case would be best achieved by disregarding the primary homonymy because the name *plicatula* Lamarck, 1822 has only been used infrequently in the 19th century (see above) and only once after 1859 by Mermod 1951 (who recommended, however, that the name *plicaria* Lamarck, 1816 ought to be adopted).

9. The International Commission on Zoological Nomenclature is accordingly asked:

- (1) to use its plenary power to rule that the specific name *plicaria* Lamarck, 1816 as published in the binomen *Helix plicaria*, is not invalid by reason of being a junior primary homonym of *plicaria* Born, 1778; and
- (2) to place on the Official List of Specific Names in Zoology the name *plicaria* Lamarck, 1816 as published in the binomen *Helix plicaria*, with the endorsement that it is not invalid by reason of being a junior primary homonym of *plicaria* Born, 1778, as published in the binomen *Helix plicaria*, as ruled in (1) above.

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For all supplemental materials referenced in this chapter refer to Appendix IV

Chapter 6 One species, two developmental modes: a case of geographic poecilogony in marine gastropods.

Benedikt Wiggering, Marco T. Neiber, Katharina Gebauer & Matthias Glaubrecht

RESEARCH ARTICLE

Open Access

One species, two developmental modes: a case of geographic poecilogony in marine gastropods



Benedikt Wiggering^{*} , Marco T. Neiber[†] , Katharina Gebauer and Matthias Glaubrecht

Abstract

Background: Poecilogony, the presence of two developmental modes in the same animal species, is a rare phenomenon. Few cases of poecilogony have been suggested for marine invertebrates including molluscs and even less so extensive testing, mostly revealing a species pair with differing developmental modes. We studied a textbook example of poecilogony in the viviparous snail *Planaxis sulcatus* (Gastropoda: Planaxidae), for the first time throughout its entire distribution range.

Results: In the Western Indian Ocean and Red Sea this intertidal species is observed to have large, shelled juveniles, whereas in the Indo-West Pacific planktotrophic veliger larvae are released from a subhaemocoelic brood pouch. We uncovered a shift in developmental modes across its range: from west to east successively earlier developmental stages are released. Furthermore, genetic data based on mitochondrial DNA suggests to recognize *P. sulcatus* as a single species rather than a group of cryptic species. A reconstruction of the ancestral area of *P. sulcatus* based on molecular data outlines the Western Indian Ocean and the Indo-West Pacific as area of origin.

Conclusion: The findings supporting *Planaxis sulcatus* as a single widespread species and the geographical shift from one reproductive mode to another suggest for this species to truly represent a case of geographic poecilogony, i.e. differing developmental modes between populations of the same species. Furthermore, the results of our ancestral range estimation imply the release of planktotrophic larvae as the ancestral developmental mode.

Keywords: Reproductive biology, Poecilogony, Cryptic species, Larval development, Viviparity, Planaxidae, Gastropoda

Background

Developmental biology and diversity on a geographic scale are major fields of evolutionary biology studies as they oftentimes influence the interpretation and recognition of groups of individuals as species [1]. Thereby, cases where a polymorphic development is present, are of great interest as they influence our view on species recognition and interpretation of biological phenomena. Poecilogony, the presence of two different developmental modes with

alternative larval types [2–8], is one of these phenomena. Such differing larval types are e.g. planktotrophic larvae (free floating larvae that feed on plankton) or lecithotrophic larvae (larvae that are nursed exclusively by the yolk originally contained within the egg). Some interpretations of the definition of poecilogony require phenotypic differences between larval types and the possibility to encounter singular female specimens producing both types of larvae in the same brood [5, 6]. Others (including the very first), differentiate geographic poecilogony including cases with phenotypically indifferent larvae but differing developmental modes while such differences are found among rather than within populations [2–4, 7, 8].

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Only thirteen cases of poecilogony in marine organisms have been thoroughly studied and supported (seven spionid polychaetes [9, 10], five sacoglossan gastropods [11] and one littorinimorph gastropod [12]). For molluscs, a total of 42 cases have been suggested [5, 6], though only six cases are supported [11, 12]. The remaining cases of proposed poecilogony are either rejected or in need of detailed investigation.

The marine snail *Planaxis sulcatus* (Born, 1780) is a textbook example for poecilogony [13]. This viviparous intertidal species is widespread throughout the tropical Indo-West Pacific Region (IWP, geographic delimitations following [14]), with populations known from the Red Sea (RS), Western Indian Ocean (WIO) and Indo-Polynesian (IP) provinces. In this species, fertilized eggs are kept in a subhaemocoelic brood pouch (i.e. located in the neck region of the headfoot) until larvae or juveniles are released. Based on records from the Iranian Gulf and Pakistan populations, it has been suggested that *P. sulcatus* releasing juveniles are adelphophagic (offspring grow large by consuming other earlier developmental stages or other juveniles within the mother's brood pouch), supplying nutrition eggs for juveniles within the brood pouch [15–17]. Concordantly, in these populations it was found that broods do not represent single cohorts, but rather that eggs can be added sequentially [17]. As in these populations later developmental stages (viz. juveniles) are far larger than earlier stages (viz. larvae), an adelphophagic nourishment is highly probable. However, no differences in larval morphology between veliger and juvenile releasing specimens has been recorded [15–20].

Six reports on the reproductive biology of this species have been published — all from singular, geographically scattered populations. In the Persian Gulf [15] and in Pakistan [16, 17] populations with long breeding periods releasing comparably large, shelled juveniles were found, whereas in Japan, Thailand [18], New Caledonia [19] and Northeast Australia [20] only planktotrophic veliger larvae were reported. These different developmental modes were either considered as an indication for poecilogony [13, 15, 21], or as revealing the presence of cryptic species [6]. In all populations studied, reproductive modes were the same within populations, differing only among populations. However, a thorough investigation of the reproductive modes throughout this species' whole range is currently lacking, as is a molecular genetic study on potentially present cryptic species.

In this study we aim at evaluating the developmental modes in *P. sulcatus*, for the first time encompassing specimens from 71 populations across its entire range, in context with analysing molecular genetic data to clarify the potential existence of cryptic species. To investigate the geographic origin of this species and its plesiomorphic

developmental mode, we conducted an ancestral range estimation based on the molecular data.

Results

Reproductive biology

Developmental modes of *P. sulcatus* differ distinctly between geographic regions (Fig. 1). Brood pouches of IP populations contained large amounts of larvae (offspring only exhibiting a protoconch). By contrast, in RS and WIO populations, both larval stages and large juveniles (shelled offspring with a teleoconch) were present. Of the overall 364 dissected specimens 64 (17.6%) were gravid females (for a detailed list of each studied specimen and their exact brood pouch content refer to Table S3).

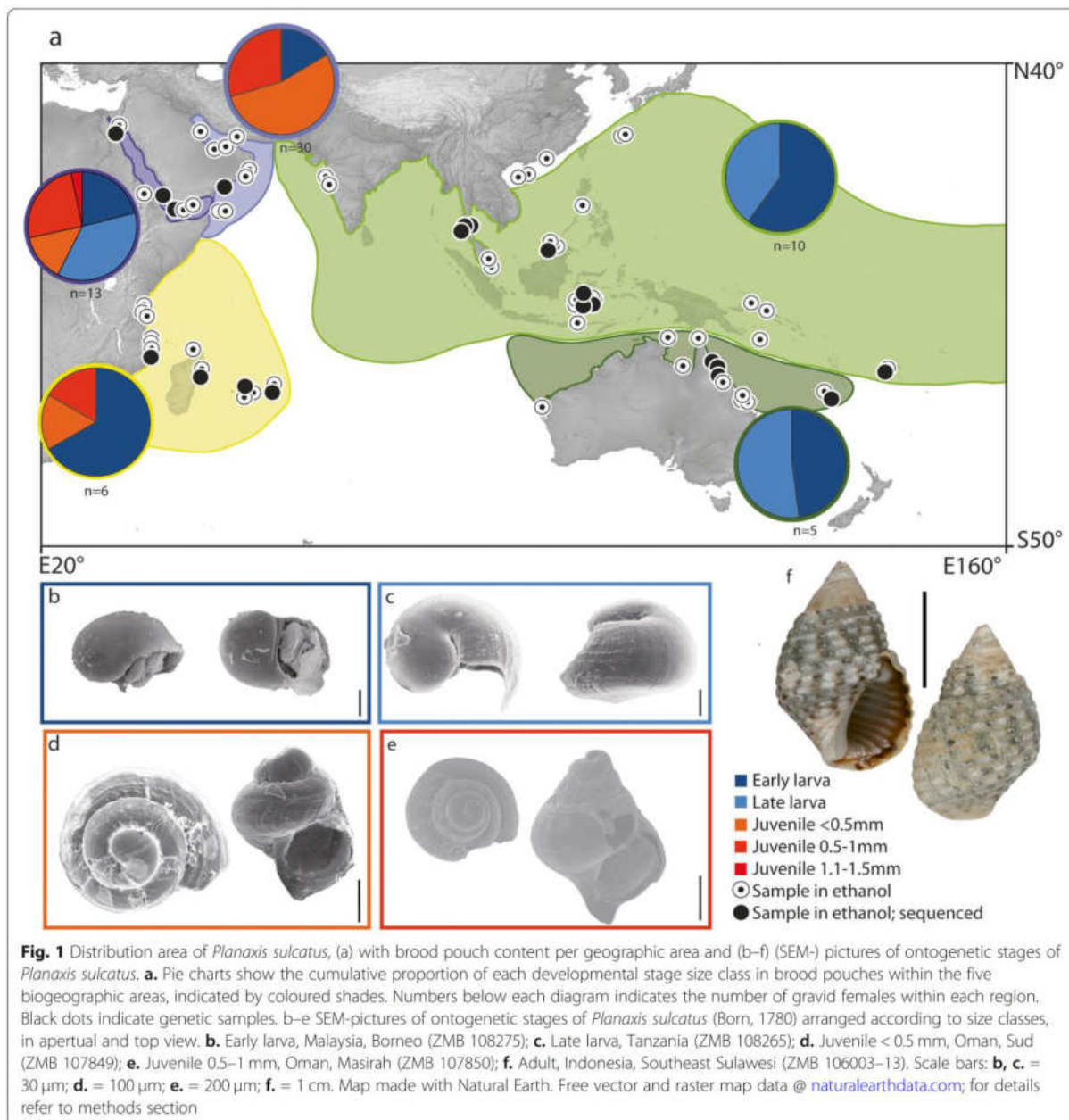
The number of offspring found in each brood pouch varied broadly, ranging from as few as 28 up to 10,500 individuals. Irrespective of the geographic origin, larval stages were always found in large amounts, whereas fewer individuals were present in each brood pouch when juveniles in an advanced state of development were present. In general, we found that the further developed the ontogenetic stages within a brood pouch, the fewer the amount of offspring therein.

The largest size class (juveniles 1–1.5 mm) was exclusively found within the RS populations. Regularly, all offspring within each individual brood pouch were of the same developmental stage and size class. Only 12.6% of all gravid females harboured more than one size class of offspring. In these cases, a mixture of successive size classes (for instance an admixture of 0.6–1 mm juveniles and 1.1–1.5 mm juveniles) was found.

Only within one Yemenite and one Eritrean population (both RS) one gravid female each was present containing a mixture of larval and juvenile stages within their brood pouches. The Yemenite specimen (CWR 129/84–4) contained a mixture of late larvae ($n = 15$) and small juveniles (< 0.5 mm, $n = 80$) within its brood pouch. By contrast, the Eritrean specimen (SMF 346144–4) contained a mixture of few late larvae ($n = 35$) and a relatively many large juveniles (0.6–1.5 mm, $n = 80$) within its brood pouch. Other than these two specimens, we never encountered females from any populations containing both larvae and juveniles within the same brood pouch. Furthermore, we did not find any phenotypic differences between larvae from WIO and IP populations with different reproductive modes.

Molecular genetics

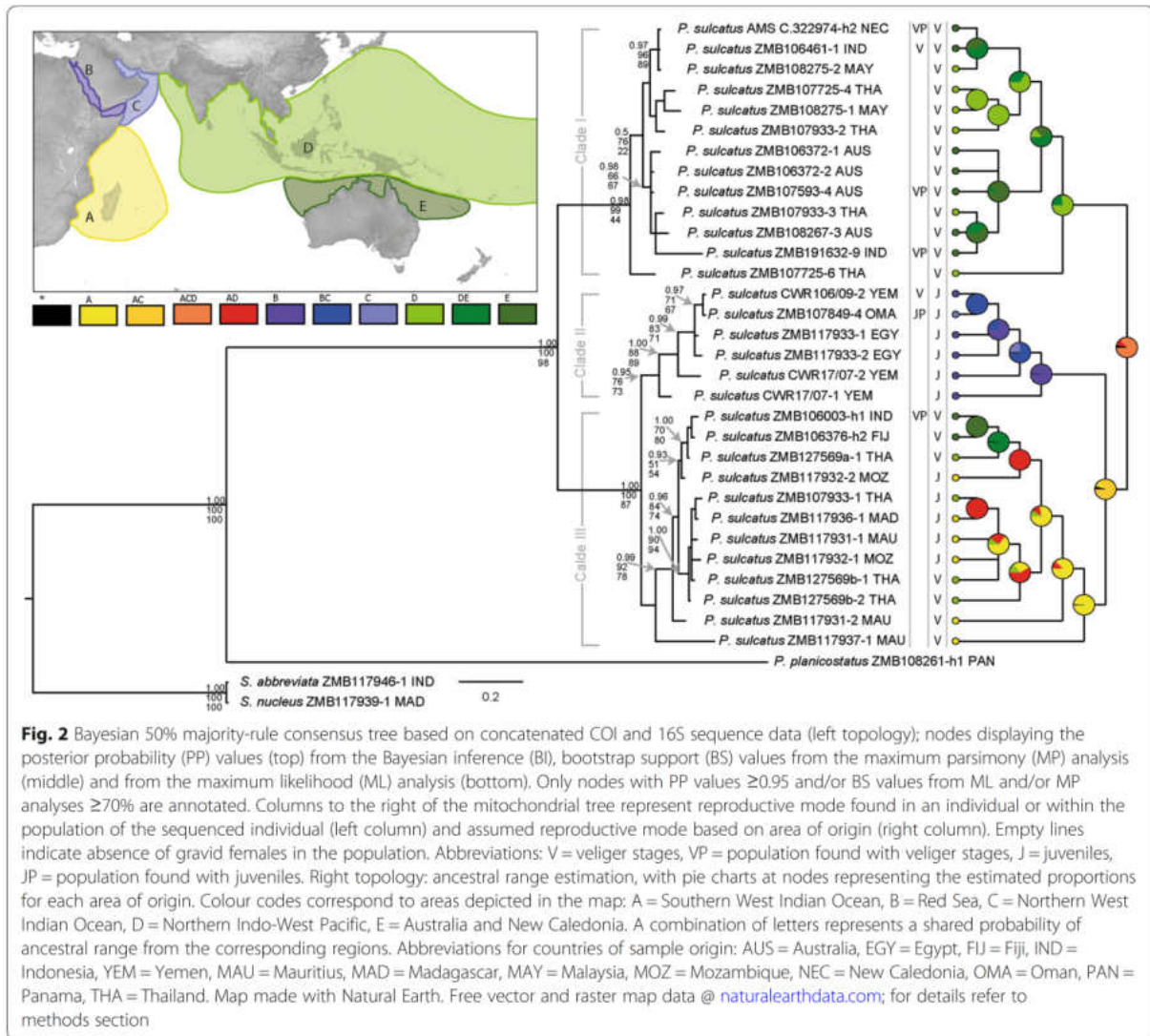
Our genetic study yielded 28 16S and 16 COI sequences from a total of 32 *P. sulcatus* specimens (see Table S2 for a list of these specimens and GenBank accession numbers of individual sequences). Therefore, 19.6% of the 163 genetically sampled specimens yielded genetic data. The 32 specimens that were successfully amplified



and sequenced originated from 20 populations, with eleven populations represented by one, seven populations represented by two and two populations represented by three specimens. The molecular phylogeny based on all available sequences of *P. sulcatus* revealed three distinct clades within this taxon (Fig. 2): one consisting of IP specimens (clade I), being sister to the other two, a second clade including specimens from the RS and northern WIO (clade II) and its sister clade consisting of specimens from southern WIO and IP (clade III).

The ABGD approach revealed that up to three groups can be distinguished within our COI dataset. At a K2P-value of 0.1% three groups were distinguished, aligning with clades I-III, at 1.3% two groups were found, one representing clade I and another representing clades II and III. At 3.08% all partitions collapsed (see Table S4 for more details).

The bGMYC approach based on the COI dataset suggested the same groupings as the ABGD approach (see Fig. S1 for a probability matrix based on the BEAST COI tree).



The ancestral range estimation suggests a highly probable combined IP and WIO origin (RASP Value (SV) = 86.68%) of *P. sulcatus* (Fig. 2). The different genetic clades, however, show different probabilities of origin: clade I is of mainly IP (SV = 77.35%) origin, whereas clade II is proposed to be of mainly Northern WIO origin (SV = 99.58%). Lastly, although consisting of samples from Southern IP and Southern WIO specimens, clade II is highly probable to be of combined Southern WIO and RS (SV = 86.23%) origin.

Discussion

This study corroborates the presence of two developmental modes within *P. sulcatus*: one with large amounts of planktotrophic veliger larvae being released, and a second one with small amounts of shelled juveniles hatching from

the female's brood pouch. Contrasting prior studies that provided snapshots of distant populations [15–20], our more comprehensive study uncovered a gradually changing pattern of variation within developmental modes across the entire distribution range (Fig. 1). Generally, the further to the east and south the smaller were the juvenile shells within brood pouches with only larval stages being present in populations east of Pakistan (i.e. IP populations). Within the RS only juvenile stages were present. However, in the WIO both, juveniles and larvae, were found.

A co-occurrence of larval and juvenile stages within the same brood pouch was only observed at one Yemenite and one Eritrean locality. The Yemenite population contained one gravid female with late larvae and small juveniles (CWR 129/84–4). In this case we assume that

all larvae of this specimen would have developed into juveniles, rather than being released as a mixture of veligers and juveniles as the encountered offspring was from consecutive developmental stages and class sizes. In other populations in this region, much larger juveniles were present, lending support for our assumption. The Eritrean specimen (SMF 346144–4) is an outstanding exception, as the presence of early larvae and large juveniles (0.6–1.5 mm) could potentially be interpreted as two reproductive modes being present. As specimens from both this Yemenite and the Eritrean population did not yield any molecular data, we cannot provide further insights into these critical populations. Neither our nor any other study on *P. sulcatus* indicated in any other case the presence of both reproductive modes within the same population [15–20].

Interpreting larval stages within brood pouches of conserved specimens as direct implications for present reproductive mode could, however, be ambiguous. As each specimen is sampled at a fixed point in time, there is no saying if larvae would have been released as veliger or developed further into juveniles within the brood pouch. However, the alternative – determining reproductive mode by observing the hatching/release of offspring from brood pouches directly – is logistically very challenging, due to the geographic scope of the present study. As our samples have been collected between 1921 and 2013, and throughout different seasons of these years, we regard the potential hypotheses that brood pouch content patterns are just coincidental as unlikely and, accordingly, assume the approach to infer reproductive mode by this trait as valid.

The findings of the Eritrean specimen (SMF 346144–4) containing both early larvae and large juveniles could alternatively be a hint at adelphophagy in *P. sulcatus*, as it has been suggested that larger offspring feed on developing eggs (so called nurse eggs) [15–17]. This is further hinted at by the observation that the further developed the ontogenetic stages within a brood pouch are the fewer the amount of offspring present therein. This correlation might be an indication to not only nurse eggs being consumed by developing offspring but rather all kinds of siblings might be the nourishment of the offspring. In contrast to other studies [15–17], we did not find any distinct nurse eggs. Therefore, to unambiguously solve the question of offspring nourishment in *P. sulcatus* further studies, expanding the limits of our dataset, are needed.

The genetic study reveals three clades of *P. sulcatus* (Fig. 2). The ABGD approach showed that the maximum K2P-distance within the COI gene of all specimens is 3.08%. Other marine caenogastropods show an intraspecific variance between 0.31 and 4.11%. For instance, the intraspecific variance of two similarly distributed littorinid

species is 1.36 and 3.48% [22]. The bGMYC approach suggested similar groupings as the ABGD approach (Fig. S1). It must be noted that molecular species delimitation models work best for groups with a low intraspecific and high interspecific variation. In other cases, these methods usually show a tendency to oversplitting [23]. The potential intraspecific variance of 3.08% that we found for *P. sulcatus* might suggest that population structure is detected in this case rather than distinct species. Except for developmental modes, no morphological differentiation within *P. sulcatus* can be observed [see also 15, 17, 18, 20] and a geographic restriction without partial overlap is not present within the molecular clades. Furthermore, developmental modes do not entirely correlate with genetic clades. Hence, we see the genetic differences found in our study to represent intraspecific variation and reject the hypothesis [6] that *P. sulcatus* should be considered as a complex of cryptic species.

However, only 36% of the individuals, from which DNA was extracted proved to be suitable for PCR amplification. Besides the protocol listed in the material and method section [24, 25] we tried other protocols that, however, all failed to extract any additional specimens. As our study was based on museum material sampled between 1921 and 2013, with most samples collected during the 1980s and 1990s, a major hurdle of this study was finding primers and extraction protocols that actually yield DNA given this rather “old” – i.e. degraded – museum material. Consequently, an exact genetic coverage of each gravid specimen could not be realized. Hence, we interpret genetic and brood pouch content information as proxies for their respective geographic areas, rather than as direct information obtained from specific individuals in all cases.

Alternatively, the two or three genetic lineages in *P. sulcatus* could be interpreted as representing distinct species. However, this still would include at least one lineage in which the two differing developmental modes are present (see clade III in Fig. 2). Following the notion of not unnecessarily multiplying additional arguments (and taxa), we here refrain from expanding our discussion beyond the scope covered by our data, which hint at the existence of only one poecilogonous species. *Planaxis sulcatus* therefore exhibits a developmental mode, in which planktotrophic veliger larvae are released (predominant in IP populations) and another where larvae are retained for a longer period only to be released as juveniles (predominant in WIO and RS populations).

We did not find any obvious morphological differences between larval stages, excluding poecilogony in *P. sulcatus* according to the strict definition suggested by Hoagland & Robertson [5]. However, following the original definition of poecilogony [3] and more recent discussions [8], we adhere to a broader definition of the term where no morphological

difference but only a polymorphism of developmental modes is the necessary criterion. Consequently, we see *P. sulcatus* to represent a case of geographic poecilogony.

Finally, the results of the ancestral range estimations imply a shared geographic origin of *Planaxis sulcatus* from IP and WIO (Fig. 2). As most other Planaxidae release veliger larvae from their brood pouches, it was assumed that this is the plesiomorphic mode of reproduction in this family [20]. Therefore, it appears likely that the spawning of pelagic veliger larvae is the ancestral developmental mode in *P. sulcatus* as well, as this is the main developmental mode of *P. sulcatus* in the ancestral regions.

Thus, we infer a scenario where from the centre of the IP adjacent areas have been colonised by ancestral lineages of this species. These consecutively evolved the developmental mode we now see within WIO and RS populations. Brooding larger juveniles may have ensured a higher rate of survival by sheltering the progeny from environmental conditions being different in the WIO and RS.

Prior studies suggested higher sea surface salinity [6] and intertidal zoning [17] as factors influencing the emergence of different reproductive modes. Especially changing salinities might be important as it has often been proposed that the evolution of viviparity in freshwater snails is correlated with adaptation to lower salinities [21]. However, in *P. sulcatus* it would be an increase in salinity triggering the same response. Although these factors are plausible, sea current activity might play an important role as well, as veligers are more prone to sea current drift. In a non-poeciologous species it has been shown that depending on substrate (as an indicator for sea current activity), different life history stages hatch from laid eggs [26]. A similar factor might be at hand here, where sea currents are unfavourable for dispersal of WIO and RS populations and, hence, the longer breeding in this area evolved. In other species, poecilogony was proposed as a bet-hedging strategy, to evade unstable conditions in mudflat estuaries [27]. As *P. sulcatus* inhabits intertidal rocky shores, a similar effect might be possible.

However, to further identify the ecological drivers behind geographic poecilogony in *P. sulcatus*, controlled aquaria experiments should be conducted. Life samples from WIO, RS and IP populations could each be held under the same salinity and temperature conditions, examining at which stage each population releases its offspring, potentially revealing one of the factors as a trigger for one of the developmental modes. Unfortunately, our current dataset is not suitable to address this question. However, we anticipate that poecilogony in *P. sulcatus* is a direct result of an ecological component leading to and maintaining these differential modes of development.

Conclusion

Our study implies the presence of poecilogony in the widespread *Planaxis sulcatus*, with a pattern of geographic variation from one developmental mode to another across its distribution range, varying in the developmental stage at which offspring are released. The ancestral range estimation shows that *P. sulcatus* originated in the WIO or IP, thereby suggesting the release of larval stages to be the initial reproductive mode. Hence, instead of assuming cryptic species our study corroborates *P. sulcatus* to truly represent a textbook example of poecilogony.

Methods

Material

We studied museum specimens of *P. sulcatus*, originating from a total of 71 populations from throughout the IWP, accumulated from several independent collecting trips of MG during the 1990th to early 2000 years, now stored in the Museum für Naturkunde, Berlin (ZMB, Germany), supplemented by material from several other museum collections, including ZMB, Universität Rostock (CWR, Germany), Senckenberg Naturmuseum, Frankfurt (SMF, Germany), Australian Museum, Sydney (AMS) and the Natural History Museum, London (NHMUK, United Kingdom). These samples were collected between 1921 and 2013, though most samples (42) were collected before the year 2000 (see Table S1 for a detailed list of all used samples and sample locations).

(a) Analysis of brood pouch content for developmental mode evaluation

We studied brood pouch contents of gravid females, to identify reproductive modes within *P. sulcatus* populations. As all previous studies on the matter [15–20] never identified a co-occurrence of reproductive modes within the same population, we interpret finding only larval stages within brood pouches of a given population to represent the veliger releasing mode, whereas we regard populations containing any juvenile stages within brood pouches as indication of direct development. However, this interpretation is not unambiguous as the brood pouch contents only provide a snapshot of the developmental stages present within a population at the time of sampling. Larval stages could still develop into juveniles within the brood pouch or be released at an earlier stage. To account for this ambiguity we combined results from singular populations with other populations from the same area, to infer the reproductive biology in a given region. As our samples were collected between 1921 and 2013 it is highly unlikely that for any given region all samples were collected during the same season, reducing the possibility of a seasonal sampling bias.

In total, 365 adult specimens were dissected using a Leica M125 stereo microscope (Leica Microsystems GmbH, Wetzlar, Germany). If present, ontogenetic stages were extracted and counted according to predefined size classes: early larva, late larva, juveniles < 0.5 mm, juveniles 0.5–1 mm, juveniles 1–1.5 mm; see Fig. 2 b–e. We here define larvae as individuals with only a protoconch and juveniles as individuals with a teleoconch. This transition is easily spotted in *P. sulcatus* as the transition from teleoconch to protoconch is marked by a deep sinusigeral notch [20]. Following Nation [28], larval and juvenile stages were dried for subsequent imaging with a LEO 1525 GEMINI scanning electron microscope (SEM, LEO Electron Microscopy Inc., Thornwood, NY, USA). Dried larval and juvenile stages were mounted on SEM object stubs (Agar Scientific Ltd., Stansted, UK) and coated with platinum using a Polaron SC7640 sputter coater (Quorum Technologies Ltd., Ashford, UK).

DNA extraction & amplification

DNA was extracted from foot muscle tissue using mollusc specific protocols [24, 25]. Wherever possible specimens with offspring of known developmental mode in their brood pouches were preferentially used. We performed extractions on 2–3 specimens per studied population, amounting to a total 163 genetically sampled specimens. We added sequences of a confamilial species to our dataset as outgroup: *Supplanaxis abbreviata* (Pease, 1865) (see Table S1 for a comprehensive list of used samples). Partial sequences of the mitochondrial cytochrome c oxidase subunit I (COI) gene, with primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3' [29]) and HCO2198var (5'-TAW ACT TCT GGG TGG CCA AAR AAA T-3' [30]), and 16S rRNA (16S) gene, with primers 16SF (5'-CCG CAC TAG TGA TAG CTA GTT TC-3' [31]) and H3059var (5'-CCG GTY TGA ACT CAG ATC ATG T-3' [31]) were amplified by polymerase chain reaction (PCR). Amplifications were performed in 20 µl volumes containing 2 µl 10x DreamTaq Green Buffer, 0.1 µl DreamTaq DNA polymerase (both Thermo Fisher Scientific, Waltham, MA, USA), 0.4 µl dNTP mix 10 mM each (VWR chemicals, VWR International GmbH, Darmstadt, Germany), 1 µl of each primer (Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany), 13.5 µl ddH₂O and 2 µl DNA template under the following reaction conditions: initial denaturation at 94 °C for 3 min, 35 PCR cycles (94 °C for 30 s, 50 °C for 45 s, 72 °C for 1 min), final extension at 72 °C for 10 min. PCR products (10 µl) were cleaned enzymatically by adding 2 µl FastAP Thermosensitive Alkaline Phosphatase (1 U/µl) and 1 µl Exonuclease I (20 U/µl) (both Thermo Fisher Scientific) followed by an incubation step at 37 °C for 15 min and inactivation at 85 °C

for 15 min. All amplified products were sequenced at MacroGen Europe (Amsterdam, The Netherlands). See Table S2 for GenBank accession numbers for all obtained sequences.

Phylogenetic analysis

DNA sequences were edited and assembled using GENEIOUS R 9.1.3 (Biomatters Ltd., Auckland, New Zealand). Primer sequences were removed resulting in COI sequences of ~ 658 bp and 16S sequences of ~ 810 bp. COI sequences were aligned using MUSCLE [32] as implemented in GENEIOUS under default settings. For the 16S alignment MAFFT 7 [33], using the Q-INS-I algorithm, the 1PAM/κ=2 option for the scoring matrix for nucleotide sequences and otherwise default settings, was used. We used PartitionFinder 2.1.1 [34] to select the appropriate partitions and evolutionary models. Four partitions were assumed initially (1st, 2nd and 3rd codon positions of COI and 16S). The results of the PartitionFinder analysis using the Bayesian information criterion suggested a single partition and the HKY + G model, which was used for the subsequent Bayesian inference (BI) and maximum likelihood (ML).

We performed a BI using MrBayes version 3.2.6 [35] running Metropolis-coupled Monte Carlo Markov chain (MC³) searches with four chains in two separate runs for 50,000,000 generations with trees sampled every 1000 generations under default heating. Potential scale reduction factors close to 1 and estimated effective sample sizes above 200 from the MrBayes output were used as diagnostics to ensure that the MC³ searches had reached stationarity and convergence. The first 5,000,000 generations of each run were discarded as burn-in. We performed heuristic ML analyses in GARLI 2.0 [36] using the best-fit model as suggested by PartitionFinder. Support values were computed by bootstrapping with 1000 replications. Using PAUP* 4.0b10 [37], we conducted heuristic maximum parsimony (MP) searches with unordered characters, 100 random sequence addition replicates, the tree bisection and re-connection (TBR) branch-swapping, and gaps treated as missing data. Internal branch support was assessed in PAUP* by bootstrapping with 1000 replications, using full heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and one tree held at each step during stepwise addition. Posterior probabilities from the BI analysis and bootstrap support (BS) values from the ML and MP analyses were mapped onto the BI 50% majority-rule consensus tree with SumTrees version 3.3.1 (part of the DendroPy 3.8.0 package [38]). BS ≥ 70% from the ML and MP analyses and posterior probabilities (PP) ≥ 0.95 were interpreted as positive support for a node.

Molecular species delimitation models

To test for the presence of potential cryptic lineages we used the Automated Barcode Gap Discovery (ABGD method) [39], via its online application (<http://www.abgd.jussieu.fr/public/abgd/abgdweb.html>). For the COI gene we used the Kimura (K80) TS/TV 2.0 distance (K2P). We entered previously established [22] minimum ($P_{min} = 0.0031$) and maximum ($P_{max} = 0.0411$) COI K2P values for marine caenogastropod snails (Littoriniidae) and otherwise default settings.

We also used the general mixed Yule-coalescent (GMYC) approach in its Bayesian implementation (bGMYC) [40] for DNA sequence-based species delimitation. We constructed ultrametric trees based on COI data with BEAST 2.4.1 [41]. The chain was run for 11,000,000 generations, with a sample frequency of 1000. The first 1,000,000 of the generations were discarded as burn-in. The GTR + I + G model was applied; otherwise default settings were used. Tracer 1.7.1 [42] was used to check that all effective sample sizes were above 200. GMYC and bGMYC analyses were conducted with the Split [43] and bGMYC R packages [44], respectively. The single-threshold as well as the multiple-threshold analyses were both conducted using the maximum clade credibility tree from the BEAST analysis constructed with TreeAnnotator 2.1.2 (part of the BEAST software suite) setting the posterior probability limit to 0. The bGMYC analysis was based on 100 trees drawn equidistantly from the post burn-in generations obtained from the BEAST analysis. For each of the 100 trees, the Markov-chain Monte Carlo sampler was run for 100,000 generations, discarding the first 90,000 generations as burn-in and sampling every 100 generations.

Ancestral range estimation

An ancestral range estimation was conducted based on 1000 randomly selected post-burn-in trees from the BI analysis of the dataset accounting for statistical uncertainty and the 50% majority-rule consensus tree from the BI analysis using the statistical dispersal-vicariance analysis (S-Diva) method [45] implemented in RASP 4.0 beta [46]. We constructed a matrix in which each individual was assigned to one of five geographic regions (roughly following [14]): A) Southwest Africa, Madagascar and Mauritius; B) the Red Sea; C) the Arabian Sea (including the Gulf of Yemen); D) the Indo-West Pacific (including Indonesia, Malaysia and Thailand) and; E) Australia and New Caledonia. For our analysis, we allowed transitions from B only to A and C, as well as from E only to D. All other areas were assumed as directly connected. The analysis was run allowing a maximum of three areas at each node and otherwise default settings.

Distribution maps and figure assembly

The species' distribution was reconstructed on a dot by dot basis based on ethanol stored specimens from the aforementioned collections, with maps based on the open access Natural Earth map (free vector and raster map data @ naturalearthdata.com). Figures and maps were assembled using Adobe Photoshop CS2 version 9.0 for Windows and Adobe Illustrator CS2 version 12.0 for Windows (both Adobe Systems, San Jose, CA, USA).

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s12862-020-01644-1>.

Additional file 1 Table S1 Material examined. **Table S2** Specimens examined for the molecular genetic analysis of this study with GenBank accession and inventory numbers. **Table S3** Results of brood pouch content analysis of *Planaxis sulcatus*. If present, content was counted according to five predefined size classes. **Table S4** Results of ABGD analysis for the COI mt rRNA dataset using the K2P model to calculate pairwise distances. P is the prior maximum intraspecific divergence. **Fig. S1** Probability matrix of the bGMYC analysis based on the COI mt rRNA dataset. Colours correspond to p-values depicted at the right side. Clades are entered corresponding to those shown in Fig. 2.

Abbreviations

16S: 16S rRNA gene; ABGD: Automated Barcode Gap Discovery; AMS: Australian Museum, Sydney; AUS: Australia; bGMYC: Bayesian general mixed Yule-coalescent approach; BI: Bayesian inference; BS: Bootstrap support; COI: Mitochondrial cytochrome c oxidase subunit I gene; CWR: Universität Rostock (Germany); DNA: Deoxyribonucleic acid; EGY: Egypt; FIJ: Fiji; GMYC: General mixed Yule-coalescent approach; IND: Indonesia; IP: Indo-Polynesian Province; J: Juveniles; JP: Population found with juveniles; K2P: Kimura (K80) TS/TV 2.0 distance; MAU: Mauritius; MAD: Madagascar; MAY: Malaysia; MC³: Metropolis-coupled Monte Carlo Markov chain; ML: Maximum likelihood; MOZ: Mozambique; MP: Maximum parsimony; NEC: New Caledonia; NHMUK: Natural History Museum, London (United Kingdom); OMA: Oman; PAN: Panama; PCR: Polymerase chain reaction; rRNA: Ribosomal ribonucleic acid; RS: Red Sea Province; S-Diva: Statistical dispersal-vicariance analysis; SEM: Scanning electron microscope; SMF: Senckenberg Naturmuseum, Frankfurt (Germany); SV: RASP Value; TBR: Tree bisection and re-connection branch-swapping; THA: Thailand; V: Veliger stages; VP: Population found with veliger stages; WIO: Western Indian Ocean Province; YEM: Yemen; ZMB: Museum für Naturkunde, Berlin (Germany)

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Authors' contributions

MG designed the study, organized funding, collected ZMB material and co-authored paper drafts. BW carried out morphological studies and wrote the manuscript. KG carried out the molecular lab work. MN and BW analysed the data. BW, MG, MN and KG proof read manuscript drafts and final versions. All authors have read and approved the manuscript for submission and publication.

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Availability of data and materials

The morphological datasets supporting the conclusions of this article are included within the article and its additional files. The genetic dataset supporting the conclusions of this article is available in the GenBank repository, see Table S2 of the supporting files for accession numbers.

Ethics approval and consent to participate

Our study is based exclusively on museum material collected in and mainly before the year 2013. We have a permission to collect the samples from the museum (listed in the methods section) and adhered to the specified terms of use of the respective collections.

Consent for publication

Not applicable.

Competing interests

We declare to have no competing interests.

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Chapter 7 Reducing taxonomic redundancy: geometric morphometrics delineates species in *Supplanaxis* Thiele, 1929 (Gastropoda: Planaxidae).

Benedikt Wiggering, & Matthias Glaubrecht

Abstract

In light of the impending global biodiversity loss, a main challenge of modern taxonomy and evolutionary systematics - besides the description of new species - is the reassessment of previously described nominal taxa to ensure recognition of true biological entities rather than nomenclatural multiplicity. As accurate taxonomic knowledge is urgently needed, we examine 22 nominal species group taxa of the viviparous, marine snail genus *Supplanaxis* (Cerithioidea, Planaxidae) and expand the concept of the genus. We studied these nominal taxa by morphological comparison of shell features, using shell biometry and a geometric morphometrics approach with sliding landmarks of more than 400 shells, radula morphology of representative specimens and a molecular genetic study of a subset of suitable material based on mitochondrial 16S rRNA and COI gene fragments. Our combined approach revealed six species and two subspecies that are significantly different in shell shape and measurements from one another. Radula features proved unsuited for species delimitation; however, they confirmed the positioning of *S. planicostatus* within *Supplanaxis*, rather than *Planaxis*. This positioning is corroborated by our molecular genetic data.

Keywords: Cerithioidea, Pacific Ocean, marine, evolutionary systematics, shell morphology

Introduction

Although taxonomists have been working on describing and naming species for over 250 years, a large amount of biodiversity remains undiscovered (Glaubrecht, 2009, 2019; Mora *et al.*, 2011, Costello *et al.*, 2012; Locey & Lennon, 2016). This is problematic as we face another mass extinction of so far unprecedented extent (Ceballos *et al.*, 2017). To conserve our global biodiversity, it is crucial to conduct modern taxonomic studies (Thomson *et al.*, 2018). Besides discovering new taxa it remains one of the core objectives of biodiversity research to revisit nominal taxa using modern methods to uncover true biological diversity, otherwise taxonomic redundancy prevails (see for instance Glaubrecht, 2009; Vaidya *et al.*, 2018). However, a major hurdle in reassessing previously described species is the delimitation and differentiation of nominal taxa that can be overcome by methodologically integrative approaches. Such evolutionary systematics approaches (Glaubrecht, 2010) are especially needed in groups where a plethora nominal taxa have been introduced for potentially far fewer lineages that deserve

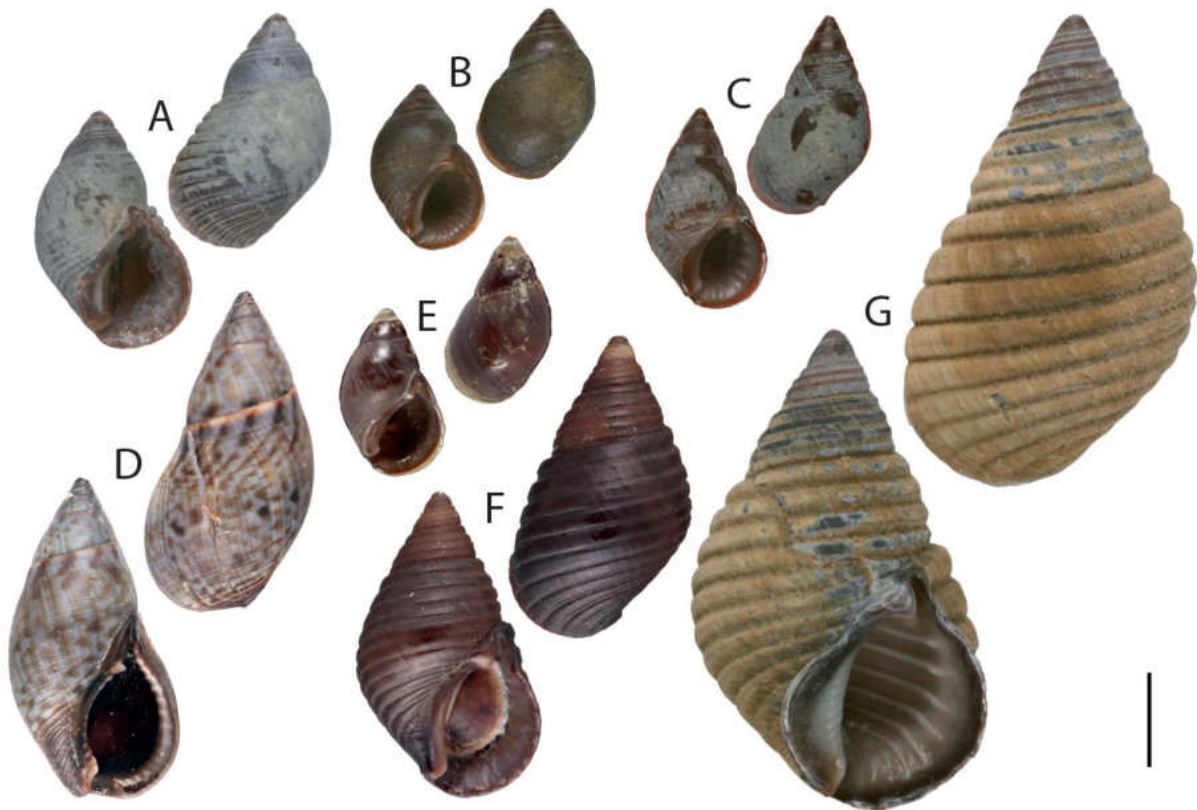


Figure 1. Shells of *Supplanaxis* species; **A** *Supplanaxis nucleus*, topotypic material, Barbados (AMS C. 323610-8). **B** *Supplanaxis abbreviata abbreviata*, Samoa (ZMB 18294-2). **C** *Supplanaxis abbreviata ogasawarana*, Seychelles, Mahé Island, Northolme (ZMB 108269-6). **D** *Supplanaxis leyteensis*, paratype, Leyte, Caminagan (FW 8566); **E**. *Supplanaxis niger*; syntype, New Ireland, Lamassa Bay (MNHN-IM-2000-27769-3). **F** *Supplanaxis obsoletus*, Mexico, Jalisco, Bahia de Cuastecomates (GP 1014114). **G** *Supplanaxis planicostatus*; Panama, Paitilla (ZMB 108261-9). Scale bar = 5 mm. **E** © M. Caballer MNHN, project **E-RECOLNAT**: ANR-11-INBS-0004.

recognition as evolutionary entities (see for instance Glaubrecht *et al.*, 2009; Schwentner *et al.*, 2014, 2015; Wiggering *et al.*, 2019).

We used an evolutionary systematics approach to assess the species of a genus of planaxid snails. The Planaxidae Gray, 1850, is a rather small, intertidal cerithioidean gastropod family, inhabiting rocky shores of tropical and subtropical regions throughout the world. In contrast to most other marine Cerithioidea families, all known taxa in this clade are viviparous with a subhaemocoelic brood pouch, in which eggs are laid, and later released either as planktonic, free-floating larvae or as well-developed, shelled juveniles (Houbrick, 1987). Even though the planaxids are widely distributed, the last taxonomic evaluation of the group was conducted on only a few species, seen as representatives of their respective genera (Houbrick, 1987). Detailed taxonomic assessments of most nominal species are missing.

We studied one widely distributed genus within this family, viz *Supplanaxis* Thiele, 1929, with a range spanning throughout the tropical Pacific, the Caribbean, and along the West coast

of Africa. Two brief accounts on the reproductive biology of *Supplanaxis nucleus* (Bruguière, 1789) have been published (Thorson, 1940; Bandel, 1976) identifying it to release veliger larvae from its brood pouch. Subsequently, a more detailed account on the subhaemocoelic brood pouch anatomy and breeding in *S. nucleus* was provided by Houbriek (1987), confirming viviparity within this species. In the same publication (Houbriek, 1987), the genus was elevated from sub-generic rank based on features of the radula. Only two species, *Supplanaxis nucleus* and *Supplanaxis niger* (Quoy & Gaimard, 1833), have been revised on a very small geographic scale (Houbriek, 1987; Chen *et al.*, 2018). The entire genus, however, has never been subjected to a monographic treatment by considering all nominal species, described in or in close affiliation to it.

We compiled samples from 117 *Supplanaxis* populations (including type specimens of nominal species wherever possible), to provide a thorough taxonomic revision of the nominal species affiliated with *Supplanaxis*. We studied shell morphology, by standardised biometric measurements and using geometric morphometrics with sliding landmarks, as well as radula morphology. Furthermore, a suitable subset of specimens was used in a molecular genetic study, based on sequences of the COI and 16S gene fragments. This combination of methods led us to acknowledge six species and two subspecies of *Supplanaxis*: *Supplanaxis nucleus*, *Supplanaxis abbreviata abbreviata* (Pease, 1865), *Supplanaxis abbreviata ogasawarana* (Pilsbry, 1905), *Supplanaxis leyteensis* Poppe, Tagaro and Stahlschmidt, 2015, *Supplanaxis niger*, *Supplanaxis obsoletus* (Menke, 1851) and *Supplanaxis planicostatus* (Sowerby I, 1825) (see Fig. 1 for shells of all species).

Materials & Methods

Sampling

Our study is based on 117 samples (each including of several specimens) of the malacological collections of several major museums; we used type material or topotypical material wherever possible.

Museum codens:

ANSP	Academy of Natural sciences Philadelphia (USA)
AMS	Australian Museum Sydney (Australia)
CWR	Private Collection of Wolfgang Wranik (Universität Rostock, Germany)
FMNH	Field Museum of Natural History (Chicago, USA)
FW	Private Collection of Frank Walther (Essen, Germany)
GP	Guido Poppe, Conchology Inc. (Cebu, Philippines)

MNHN	Museum National d'Histoire Naturelle (Paris, France).
NHMUK	Natural History Museum Britain (London, England),
NHMW	Naturhistorische Museum Wien (Austria)
SMF	Senckenberg Naturmuseum Museum (Frankfurt, Germany)
USNM	National Museum of Natural History, Smithsonian Institution (Washington, D. C., USA)
ZMB	Museum für Naturkunde (Berlin, Germany)
ZMH	Center of Natural History (CeNak) (formerly Zoological Museum Hamburg), Universität Hamburg (Germany)

Distribution maps were prepared in Adobe Illustrator CS5 (version 15.0.0 for Windows) on a dot-by-dot basis, using Natural Earth (@natureearthdata.com, last access 18 December 2019) as base map. Delineation and definition of biogeographic regions and provinces used in this study are based on Briggs & Bowen (2012).

Photo imaging

Pictures of undamaged adult specimens (in *Supplanaxis* juvenile specimens are easily identified by the lack of the columellar tooth and a sharp lipped aperture) were taken by remote shooting with EOS Utility (version 2.12.2.1 for Windows) and Digital Photo Professional (version 3.12.51.2 for Windows) using a digital camera (Canon EOS 5D MKII with Canon macro photograph lens MP-E 65 mm and Canon compact macro lens EF 50 mm, Canon, Tokyo, Japan). Shells were positioned with the aperture at a 90° angle in relation to the optical axis of the camera and the columella parallel to the background surface. Photos were stacked with Helicon Focus (version 5.3.14.2 for Windows). Pictures for illustrations were assembled using Adobe Photoshop CS5 (version 12.0.4 for Windows) and Adobe Illustrator CS5 (version 15.0.0 for Windows).

Geometric morphometrics and statistical analysis

For our geometric morphometrics study we also included specimens of *Planaxis sulcatus* to function as outgroup, as *Planaxis* is considered the most closely related genus to *Supplanaxis* (Houbrick, 1987). As *P. sulcatus* is the type species of *Planaxis* we included this species and its type specimen (see Table 1 for a detailed list of *P. sulcatus* samples used in this study). In addition to our own compilation of material (245 adult specimens) we added pictures of 147

Table 1. Samples of *Planaxis sulcatus* used in this study for comparison. Note that material examined from *Supplanaxis* species is listed for each species separately in the systematic part.

Museum ID	Country	Location	Coordinates	Comment
NHMW 14249				Syntype
SMF 256114	India	Bombay		
SMF 346144	Eritrea	Massawa		
SMF 346145	Saudi Arabia	Jubali, Ras-al-Bukhara		
SMF 346146	Saudi Arabia	Ras-al-Zour		
SMF 346148	Yemen	Sokotra, northeast coast , near Saqarah	12°36.109'N 54°20.931'E	
SMF 346149	China	Hainan, Tien ya hai jiao		
AMS C.322974	New Caledonia	Ilot Maitre, in channel near Noumea	22°20 S 166°24 E	
ZMB 106003	Indonesia	Southeast Sulawesi, Muna Island, Raha	04°54.19 S 122°45.43 E	
ZMB 106372	Australia	Archer Point		
ZMB 106376	Fiji	Musket Cove, Malololailai Island	17°46.26 S 177°11.83 E	
ZMB 107850	Oman	Masirah, Sea Plane Jetty		
ZMB 108271	Australia	Queensland, Cape York, GBR		
CWR 106/09	Yemen	al-Hudeida		
CWR 14/90	Yemen	Aden MSRC		
CWR 129/84	Yemen	Little Aden		
CWR 17/07	Yemen	Little Aden		
CWR 25/85	Yemen	Little Aden		
CWR 47/84	Yemen	Little Aden		
CWR 4/83	Yemen	Ras al Ara		

adult specimens, oriented in the exact same way as ours, kindly provided by Philippe Poppe (Conchology Inc.) and pictures of several type specimens from the above mentioned collection (34 adult specimens). Overall, pictures of 426 specimens (including type specimens) were used to build a .tps file in tpsUtil version 1.74 (Rohlf, 2017b). We placed 9 landmarks and 8 lines of points (three with 30 points, three with 15 points and two with 10 points, see Fig. 2A for landmark positions) in tpsDig2 version 2.30 (Rohlf, 2017a). The latter were

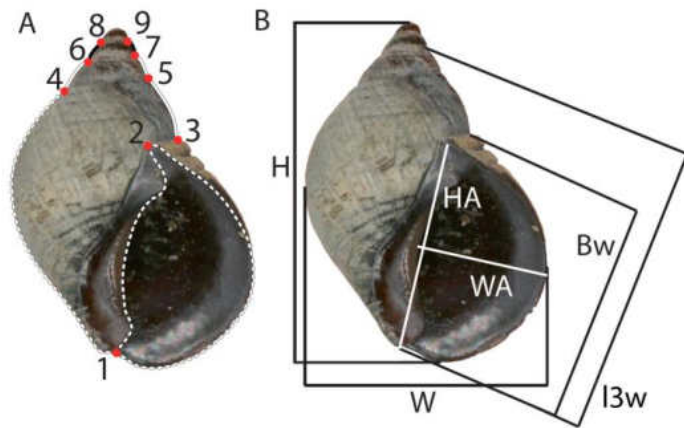


Figure 2. Position of landmarks for geometric morphometrics and shell measurements. **A** Position of landmarks (red dots) and lines of sliding landmarks. Dotted lines represent 30, white lines 15 and black lines 10 sliding landmarks. **B** Shell parameters measured on adult shells. H – shell height; W – shell width; Bw – Last whorl height; l3w – last three whorls height; HA – aperture height; WA – aperture width.

transformed to landmarks with tpsUtil and later defined as sliding landmarks. Data were analysed using RStudio (RStudio Team, 2016), with packages “geomorph” (Adams and Otárola-Castillo, 2013), “ade4” (Chessel *et al.*, 2004), “lawstat” (Hui *et al.*, 2008), “agricolae” (Mendiburu, 2010) “dunn.test” (Dinno, 2017) and “cluster” (Maechler *et al.*, 2019). We conducted a Procrustes superimposition. Based on the resulting centroid sizes we conducted an Agglomerative Nesting (AGNES) cluster analysis, including all specimens to test for an emergent clustering pattern. For further analysis, the material was sorted into morphologically similar groups, based on available species descriptions. For further testing all type specimens of nominal taxa represented by less than 10 specimens were removed, as these would not be valid for further statistical tests. Hence, the type specimens of *Planaxis albersii* Dunker, 1853, *P. circinatus* Lesson, 1842, *P. castaneus* Smith, 1872, *P. hanleyi* Smith, 1872, *P. (Supplanaxis) nancyae* Petuch, 2013, *P. nicobaricus* Zelebor, 1866, *P. nigrifella* Forbes, 1850, *P. obscurus* A. Adams, 1853 [“1851”] and *P. similis* Smith, 1872 were excluded from our analysis. This reduced the dataset to 412 specimens. A principal component analysis (PCA) was conducted to reduce dimensionality and to identify major axes of variance within the dataset. Only axes with a relevant proportion of variances (> 0.05) were included for further analysing. We tested for significant difference between potential species clusters: *Supplanaxis nucleus* (128 images), *S. abb. abbreviata* (19 images), *S. abb. ogasawarana* (39 images), *S. leyteensis* (20 images), *S. niger* (86 images), *S. obsoletus* (35 images),

S. planicostatus (30 images) and *P. sulcatus* (55 images). Normal distribution was checked with the Shapiro-Wilk test for each PC and predefined group, separately. If at least one group within the same PC was found to be not normally distributed ($P > 0.05$), we performed a Kruskal-Wallis-rank-sum test. If the latter showed significant results ($P < 0.05$), we executed a Bonferroni-corrected Dunn-test to identify significant differences ($P < 0.025$) between groups. If instead normal distribution was found for all groups on the same PC (Shapiro-Whilk-test $P > 0.05$) we performed an analysis of variance (ANOVA), if significant ($P < 0.05$) followed by a modified Brown-Forsythe Levene-type test. In case it scored significant ($P < 0.05$) post hoc testing with a Bonferroni-corrected LSD-test was conducted. Otherwise, a Scheffe-test was performed instead.

Shell biometry and characters

For our biometric study of *Supplanaxis* shell characters, we measured 412 adult specimens (including type specimens, if more than 10 specimens of a nominal taxon were available). Our standardised measurements were shell height and width, aperture height and width, height of the last whorl, height of the last three whorls (see Fig. 2B for position of measurement axes). Measurements were all performed on images of the specimens using ImageJ version 1.51 (Schneider *et al.*, 2012), including those provided by Philippe Poppe. For these measurement axes statistic testing was conducted using RStudio with packages listed above. We deployed the same testing cascade as we used for our geometric morphometrics approach, without the Procrustes super imposition and PCA. Furthermore, we counted the total number of whorls, number of spiral grooves on the last whorl, number of spiral grooves on the penultimate whorl, number of columellar teeth and number of palatal grooves (all examined in apertural view). Palatal and spiral grooves were also examined based on markedness and position. As these latter characters are non-metric, we did not perform any statistical test based on this data.

Radula morphology

EtOH preserved specimens were dissected using a stereo microscope (Leica M125). For each species with EtOH preserved specimens radulae of 35 representative specimens were examined (*S. nucleus* $n = 10$, *S. abbreviata ogasawarana* $n = 10$, *S. niger* $n = 10$ and *S. planicostatus* $n = 5$). Radulae were extracted by removing the entire buccal apparatus. The tissue was then dissolved using proteinase K according to the protocol of Holznagel (1998). After complete digestion of the tissue, radulae were stored in 70% EtOH and cleaned using an ultrasonic bath (Sonorex Super 10T, Bandelin, Berlin, Germany). For imaging with a scanning electron

microscope (SEM, LEO 1525 GEMINI, LEO Electron Microscopy Inc., One Zeiss Drive, Thornwood, NY, USA), clean radulae were mounted on SEM object stubs (Agar Scientific, Stansted, Essex, UK) and coated with platinum using a sputter coater (Polaron SC7640 Sputter Coater, Quorum Technologies Ltd, Ashford, UK).

DNA extraction & amplification

DNA was extracted from foot muscle tissue based on mollusc specific protocols (Sokolov, 2000; Scheel & Hausdorf, 2012). We performed extractions on two specimens per ethanol stored population sample (n=30), amounting to a total of 60 genetically sampled specimens. We added sequences of *S. abbreviata ogasawarana*, four specimens of *Planaxis sulcatus* and of three species of pachychilid snails to our dataset as outgroups, all of which have been used in our previous studies and are available via GenBank: *Brotia costula* (Rafinesque, 1833), *Faunus ater* (Linnaeus, 1758) and *Pachychilus nigratus* (Poey, 1858) (see Table 2 for a comprehensive list of samples used for the molecular study and GenBank accession numbers). Partial sequences of the mitochondrial cytochrome c oxidase subunit I (COI) gene, with primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3' Folmer *et al.*, 1994) and HCO2198var (5'-TAW ACT TCT GGG TGG CCA AAR AAA T-3' Rintelen *et al.* 2004), and 16S rRNA (16S) genes, with primers 16SF (5'-CCG CAC TAG TGA TAG CTA GTT TC-3') and H3059var (5'-CCG GTY TGA ACT CAG ATC ATG T-3', both Wilson *et al.*, 2004) were amplified by polymerase chain reaction (PCR). Amplifications were performed in 20 µl volumes containing 2 µl 10x DreamTaq Green Buffer, 0.1 µl DreamTaq DNA polymerase (both Thermo Fisher Scientific, Waltham, MA, USA), 0.4 µl dNTP mix 10 mM each (VWR chemicals, VWR International GmbH, Darmstadt, Germany), 1 µl of each primer (Sigma-Aldrich Chemie GmbH, Taufkirchen, Germany), 13.5 µl ddH₂O and 2 µl DNA template under the following reaction conditions: initial denaturation at 94 °C for 3 min, 35 PCR cycles (94 °C for 30 s, 50 °C for 45 s, 72 °C for 1 min), final extension at 72 °C for 10 min. PCR products (10 µl) were cleaned up enzymatically by adding 2 µl FastAP Thermosensitive Alkaline Phosphatase (1 U/µl) and 1 µl Exonuclease I (20 U/µl) (both Thermo Fisher Scientific) followed by an incubation step at 37 °C for 15 min and inactivation at 85 °C for 15 min. All amplified products were sequenced at Macrogen Europe (Amsterdam, The Netherlands). See Table 2 for GenBank accession numbers for all obtained sequences.

Table 2. Specimens successfully sequenced for the molecular genetic analysis of this study, with GenBank accession and inventory numbers.

Species	Inventory number	Country of origin	16S	COI	Reference
<i>Supplanaxis nucleus</i>	ZMH 140713-1	Curacao	MT593017	MT587875	
<i>Supplanaxis nucleus</i>	ZMH 140713-11	Curacao	MT593016	MT587874	
<i>Supplanaxis nucleus</i>	ZMB 117940-1	Dominica	MT593019	MT587877	
<i>Supplanaxis nucleus</i>	ZMB 117940-2	Dominica	MT593018	MT587876	
<i>Supplanaxis planicostatus</i>	ZMB 117941-1	Costa Rica	MT593015	MT587873	
<i>Supplanaxis planicostatus</i>	ZMB 117941-2	Costa Rica	MT593014	MT587872	
<i>Supplanaxis abbreviata ogasawarana</i>	ZMB 117939-1	Madagascar	MT593021	MT587879	Wiggering <i>et al.</i> (2020)
<i>Supplanaxis abbreviata ogasawarana</i>	ZMB 117938-1	Oman	MT593022	MT587880	
<i>Supplanaxis abbreviata ogasawarana</i>	ZMB 108274-4	Malaysia	MT593024	MT587882	
<i>Supplanaxis abbreviata ogasawarana</i>	ZMB 108274-5	Malaysia	MT593023	MT587881	
<i>Supplanaxis abbreviata ogasawarana</i>	ZMB 117946-1	Indonesia	MT593020	MT587878	Wiggering <i>et al.</i> (2020)
<i>Planaxis sulcatus</i>	ZMB 117933-1	Egypt	MT593025	MT587883	Wiggering <i>et al.</i> (2020)
<i>Planaxis sulcatus</i>	ZMB 117931-2	Mauritius	MT593026	MT587884	Wiggering <i>et al.</i> (2020)
<i>Planaxis sulcatus</i>	ZMB 107725-6	Thailand	MT593027	MT587885	Wiggering <i>et al.</i> (2020)
<i>Planaxis sulcatus</i>	ZMB 106461-1	Indonesia	MT593028	MT587886	Wiggering <i>et al.</i> (2020)
<i>Brotia costula</i>	ZMB 112660	Nepal	DQ284985	DQ284986	Köhler & Glaubrecht (2007)
<i>Faunus ater</i>	ZMB 106456	Indonesia	GU079666	MT590757	16S: Köhler & Glaubrecht (2010)
<i>Pachychilus nigratus</i>	ZMB 200290	Cuba	AY311947	AY312053	Rintelen <i>et al.</i> (2004)

Phylogenetic analysis

DNA sequences were edited and assembled using GENEIOUS R 9.1.3 (Biomatters Ltd., Auckland, New Zealand). Primer sequences were removed resulting in COI sequences of ~658 bp and 16S sequences of ~810 bp. COI sequences were aligned using MUSCLE (Edgar, 2004) as implemented in GENEIOUS under default settings. For the 16S alignment MAFFT 7 (Kato & Standley, 2013), using the Q-INS-I algorithm, the 1PAM/ $\kappa = 2$ option for the scoring matrix for nucleotide sequences and otherwise default settings, was used. We used PARTITIONFINDER 2.1.1 (Lanfear *et al.*, 2012) to select the appropriate partitions and evolutionary models. Four partitions were assumed initially (1st, 2nd and 3rd codon positions of COI and 16S). The results of the PARTITIONFINDER analysis using the Bayesian Information Criterion suggested three partitions and evolutionary models: 16S (HKY+I+G), 1st and 2nd codon position of COI (GTR+I+G) and 3rd codon position of COI (GTR+I+G). All partitions and models were used for the subsequent Bayesian Inference (BI) and Maximum Likelihood (ML) analyses, respectively.

We performed BI using MRBAYES version 3.2.6 (Ronquist *et al.*, 2012) running Metropolis-coupled Monte Carlo Markov chain (MC³) searches with four chains in two separate runs for 50,000,000 generations with trees sampled every 1,000 generations under default heating. Potential scale reduction factors close to 1 and estimated effective sample sizes above 200 from the MRBAYES output were used as diagnostics to ensure that the MC³ searches had reached stationarity and convergence. The first 5,000,000 generations of each run were discarded as burn-in. We performed heuristic ML analyses in GARLI 2.0 (Zwickl, 2006) using the best-fit model as suggested by PARTITIONFINDER. Support values were computed by bootstrapping with 1,000 replications. Using PAUP* 4.0b10 (Swofford, 2002), we conducted heuristic Maximum Parsimony (MP) searches with unordered characters, 100 random sequence addition replicates, the tree bisection and re-connection (TBR) branch-swapping, and gaps treated as missing data. Internal branch support was assessed in PAUP* by bootstrapping with 1,000 replications, using full heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and one tree held at each step during stepwise addition. Posterior probabilities from the BI analysis and bootstrap support (BS) values from the ML and MP analyses were mapped onto the BI 50% majority-rule consensus tree with SUMTREES version 3.3.1 (part of the DENDROPY 3.8.0 package; Sukumaran & Holder, 2010). BS $\geq 70\%$ from the ML and MP analyses and posterior probabilities (PP) ≥ 0.95 were interpreted as positive support for a node.

Results

Geometric morphometrics

We found the shapes of the studied specimens to show an overall high amount of variance (Fig. 3). After the Procrustes superimposition, a diagram of the total variance within the axes of variance within the dataset. The first four axes account for a relevant proportion of variance ($P > 0.05$; PC1: 0.53; PC2: 0.15; PC3: 0.08; PC4: 0.06), explaining a cumulative proportion of 0.82 of variance.

dataset was produced (see Fig. 3B). A principal component analysis (PCA) identified major

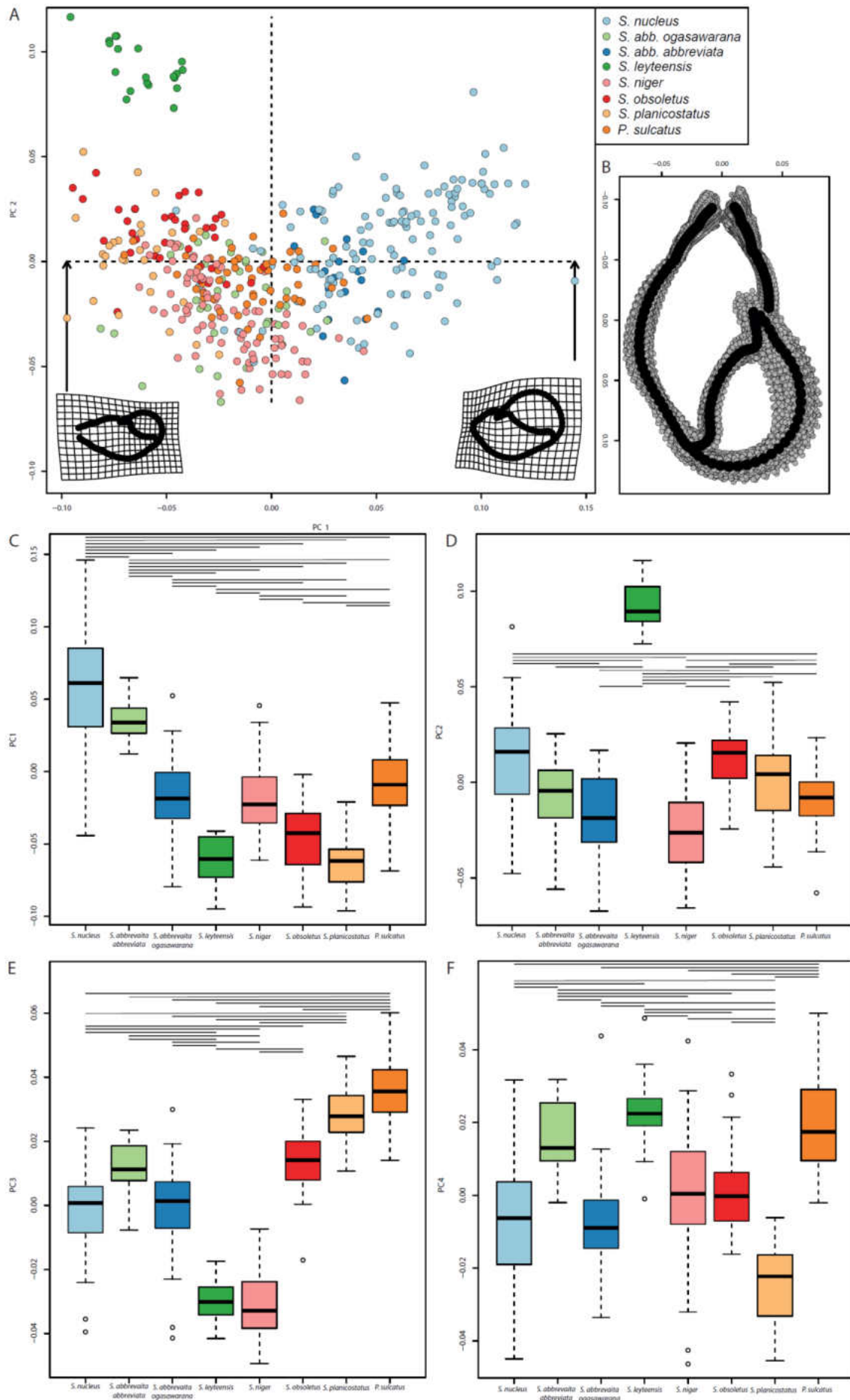
The testing of potential species groups uncovered significant differences between the assumed groups on all four studied Principle component axes. For all but the first Principle component (PC1) at least one group was not normally distributed (Shapiro-Wilk test $P < 0.05$). Accordingly, PC1 was tested with an ANOVA whereas all other axes (PC2–4) were each independently tested with the Kruskal-wallis-rank-sum-test, all scoring significant ($P < 0.05$), followed by a Dunn test to uncover significant differences between groups.

For PC1 the modified robust Brown-Fortsythe Levene-type test was highly significant ($P < 0.001$). The subsequent LSD-Test identified four significantly different groups: 1) *S. nucleus*, 2) *S. abb. abbreviata* 3) *S. abb. ogasawarana*, *S. niger* and *P. sulcatus*, and 4) *S. leyteensis*, *S. obsoletus* and *S. planicostatus* (see Fig. 3C).

On the second principle component (PC2) highly significant differences ($P < 0.001$) between *S. leyteensis* and all the taxa were uncovered. *S. abb. abbreviata* was indistinguishable from any other group. *S. nucleus* and *S. obsoletus* were found significantly different from *S. abb. ogasawarana*, *S. niger* and *P. sulcatus*. Lastly, *S. niger* is additionally significantly different from *P. sulcatus* and *P. planicostatus* (Fig. 3D).

The third Principle component (PC 3) contained significant differences ($P < 0.001$) between several potential species groups (Fig. 3E): *S. planicostatus* and *P. sulcatus* were significantly different from all other groups. Also, *S. leyteensis* and *S. niger* were found significantly different from all other groups. Both subspecies of *S. abbreviata* were significantly different

> **Figure 3.** Results of geometric morphometrics analysis with sliding landmarks. **A** Relative variance in shell shape along PC1 and PC2. Depicted thin plate splines represent shell shapes of individuals with highest and lowest value along PC1. **B** Total variance of landmark positions. Grey dots comprise all positions of 793 landmarks. Black dots indicate the mean position of each landmark across the entire dataset. **C–F** Differences between shell shapes of predefined species groups on **C** PC1, **D** PC2, **E** PC3, **F** PC4. Significant differences ($P < 0.001$) are indicated by bars above or below boxplots, with each bar beginning and end indicates significant differences between two groups.



from all species but *S. nucleus* and *S. obsoletus*. In addition, *S. obsoletus* was significantly different from *S. nucleus*.

On the fourth principle component (PC4) highly significant differences ($P < 0.001$) between three groups were found (Fig. 3F): *S. planicostatus* was found significantly different from all other potential species groups. *S. abb. abbreviata*, *S. leyteensis* and *P. sulcatus* formed a second significantly different group. Lastly, *S. nucleus*, *S. abb. ogasawarana*, *S. niger* and *S. obsoletus* were significantly different from all other species groups.

The cluster analysis based on centroid sizes did not produce groups that can be interpreted as biological species. Several of the type series do not group with one another or their respective species group. Even taxa as different as *P. sulcatus* and *S. leyteensis* were grouped together, indicating that unreliable result are to be expected in terms of taxonomy when based solely on the similarity of centroid sizes (see Supplemental Fig. S1).

Shell biometry and morphology

For all measured traits, at least one group was not normally distributed (Shapiro-Whilk test $P > 0.05$). The subsequent Kruskal-Wallis-rank-sum-tests scored highly significant ($P < 0.0001$), for each trait. Hence Dunn-tests were performed to identify significant differences between potential species groups. For shell height three significantly different ($P < 0.05$) groups were found (Fig. 4A): One formed by *P. sulcatus*, *S. planicostatus* and *S. leyteensis*, another formed by *S. nucleus* and *S. obsoletus* and lastly one consistent of the two subspecies of *S. abbreviata* and *S. niger*. Based on shell width (see Fig. 4B), four significantly different groups were uncovered, however, one groups overlaps with two other: *P. sulcatus* and *S. planicostatus* formed one group, *S. planicostatus* and *S. leyteensis* formed another, *S. nucleus*, *S. leyteensis* and *S. obsoletus* formed a third and lastly the two subspecies of *S. abbreviata* and *S. niger* formed another group. The height/width-index uncovered several significant differences (Fig. 4C). *Supplanaxis nucleus* was significantly different from all other species but *P. sulcatus*. The latter was significantly different from all species other than *S. nucleus* and *S. abb. abbreviata*. Furthermore, *S. leyteensis* was significantly different from all species but *S. planicostatus*. However, the latter formed a significantly different group with *S. abb. ogasawarana*, *S. niger* and *S. obsoletus*. *Supplanaxis abbreviata abbreviata* was found to group with *S. abb. ogasawarana*, *S. niger* and *S. obsoletus*. A similar pattern was found for the index of aperture height to aperture width (Fig. 4D). Here, *Supplanaxis nucleus* was significantly different from all other species but *P. sulcatus*. The latter was found significantly

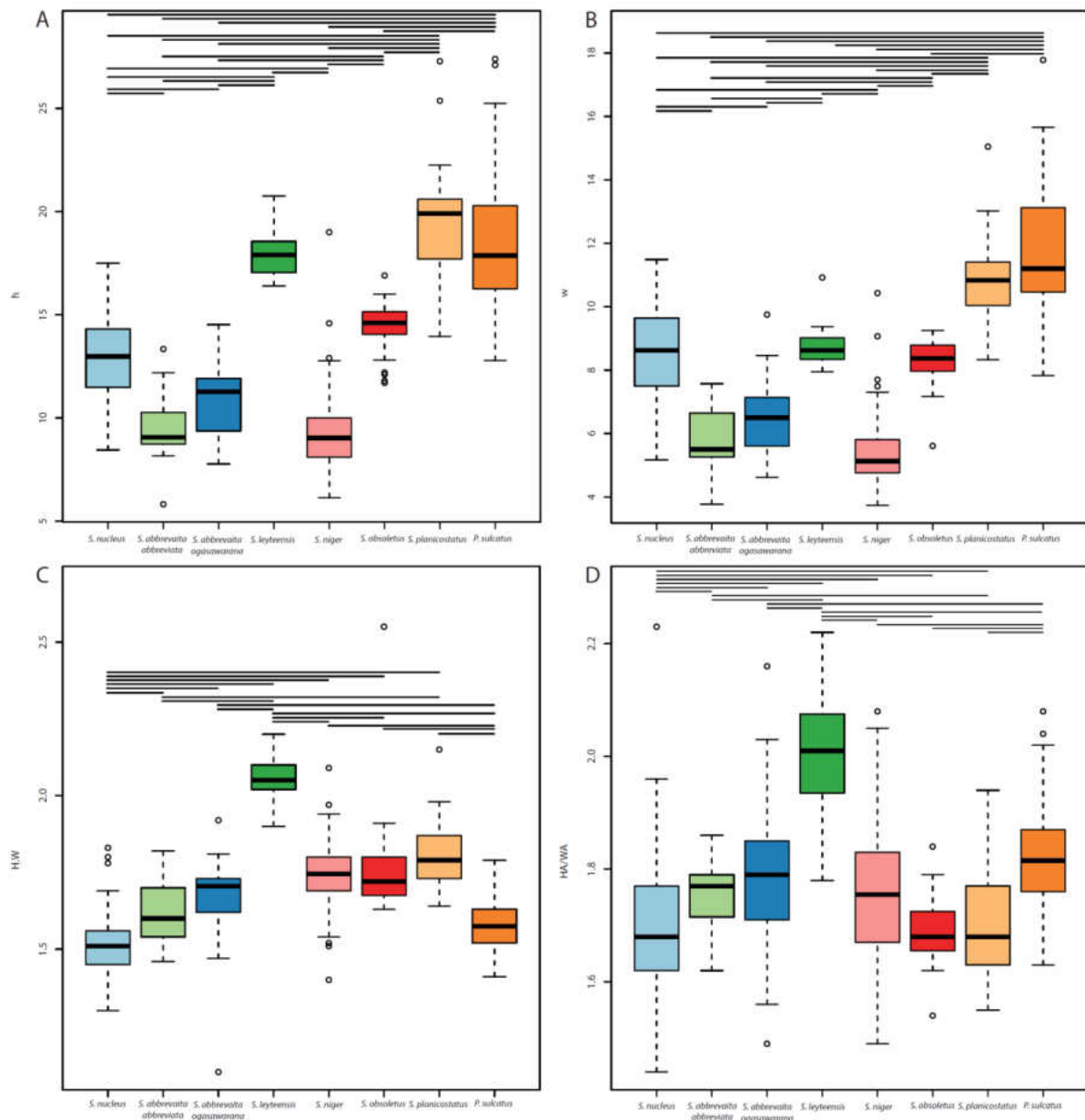


Figure 4. Results of shell parameter measurements per species. Boxplots of **A** shell height, **B** shell width, **C** index of shell height/width and **D** index of aperture height/width. Significant differences ($P < 0.001$) are indicated by bars above or below boxplots, with each bar beginning and end indicates significant differences between two groups.

different from all species but *S. nucleus* and *S. abb. abbreviata*. *Supplanaxis leyteensis* was significantly different from all groups but *S. planicostatus*. The latter additionally was significantly different from all groups but *S. abb. ogasawarana*, *S. planicostatus* and *S. niger*.

All examined adult specimens varied between 4–7 whorls, with only *S. niger*, *S. planicostatus* and *P. sulcatus* encompassing specimens with more than six whorls as a rare exception. In *S. nucleus*, *S. abbreviata* and *S. niger* we found specimens with both none or fewer than three and more than eighteen palatal and spiral grooves as (Table 3). By contrast the number of palatal grooves in *S. leyteensis* with only 0–2 palatal grooves, *S. obsoletus* with 6–

Table 3. Average (AVG), median (MED), minimum (MIN) and maximum (MAX) values of measured specimens per species. Note that of *S. leyteensis* only two specimens were available, hence we only show average/median values of this species. For non-metric characters MED is displayed, whereas metric characters are displayed with their AVG. Abbreviations for metric characters: h = shell height, w = shell width, ha = height of aperture, wa = width of aperture, bw = height of last whorl, l3w = height of last three whorls, h/w = index of h divided by w, ha/wa = index of ha divided by wa. Non-metric data were: wh = number of whorls (counted in half digit steps), sg = number of spiral grooves, pw = number of grooves at penultimate whorl, ct = number of collumellar teeth, and pg = palatal grooves.

Species		h	w	ha	wa	bw	l3w	h/w	ha/wa	wh	sg	pw	ct	pg
<i>S. nucleus</i>	AVG/MED	12.88	8.56	8.02	4.75	10.80	12.55	1.51	1.69	4.5	9	2	1	12
	MIN	8.45	5.17	5.08	2.75	6.87	7.90	1.30	1.44	4.0	0	0	1	0
	MAX	17.50	11.49	10.78	6.53	14.30	16.73	1.83	2.23	6.5	23	8	1	19
<i>S. abbreviata abbreviata</i>	AVG/MED	9.52	5.86	5.68	3.25	7.77	9.25	1.63	1.75	4.5	7	1	1	10
	MIN	5.82	3.77	3.60	1.99	4.86	5.68	1.46	1.62	4.0	2	0	1	0
	MAX	13.34	7.57	7.29	4.20	10.30	12.92	1.82	1.86	5.5	19	5	1	20
<i>S. abbreviata ogasawarana</i>	AVG/MED	10.89	6.55	6.20	3.51	8.57	10.55	1.67	1.78	5.0	13	5	1	10
	MIN	7.77	4.62	4.81	2.49	6.53	7.85	1.10	1.49	4.0	4	0	1	0
	MAX	14.52	9.75	9.26	4.89	12.01	14.12	1.92	2.16	6.0	22	9	1	20
<i>S. leyteensis</i>	AVG/MED	17.96	8.73	9.74	4.87	14.19	17.01	2.06	2.00	6.0	15	1	1	16
	MIN	16.40	7.95	8.19	4.32	12.68	15.07	1.90	1.78	5.5	13	0	1	14
	MAX	20.75	10.92	11.69	6.10	15.90	19.91	2.20	2.22	6.5	18	2	10	17
<i>S. niger</i>	AVG/MED	9.34	5.37	5.27	3.01	7.39	8.99	1.74	1.76	5.0	5	1	1	4
	MIN	6.13	3.74	3.45	2.00	4.96	6.07	1.40	1.49	4.0	0	0	1	0
	MAX	19.00	10.43	10.72	5.87	14.49	17.89	2.09	2.08	7.0	17	7	10	18
<i>S. obsoletus</i>	AVG/MED	14.44	8.25	7.35	4.36	10.94	13.51	1.76	1.69	5.5	13	4	1	10
	MIN	11.70	5.61	5.19	2.93	7.75	9.37	1.63	1.54	4.5	8	2	1	6
	MAX	16.90	9.25	8.25	4.95	12.55	16.04	2.55	1.84	6.5	17	5	1	12
<i>S. planicostatus</i>	AVG/MED	19.44	10.78	9.08	5.35	13.99	17.80	1.80	1.70	6.0	11	4	1	8
	MIN	13.95	8.33	7.19	3.95	10.65	13.34	1.64	1.55	4.5	10	3	1	7
	MAX	27.28	15.05	12.80	7.64	18.78	24.70	2.15	1.94	7.0	12	5	1	10

12 palatal grooves and *S. planicostatus* with 7–10 palatal grooves rather constant amounts were present. Spiral grooves varied heavily in all species; however, variation was lower in *S. abb. ogasawarana*, *S. obsoletus* and *S. planicostatus*. *Supplanaxis abbreviata*, *S. leyteensis*, *S. obsoletus* and *S. planicostatus* contained only specimens with at least some but never no spiral grooves, whereas in both *S. nucleus* and *S. niger* individuals without spiral grooves were identified. All species but *S. planicostatus* and *S. obsoletus* contained specimens with and without grooves on the penultimate whorl, though *S. abbreviata* displayed this character more frequently with overall more grooves. *Supplanaxis niger* had far fewer specimens with high amounts of palatal grooves. Consistently spiral grooves and palatal grooves of *S. niger* were far weaker than those of other species. In *S. nucleus* all states of spiral and palatal grooves were found, with varying degree of intensity. *Supplanaxis leyteensis* displayed high amounts of spiral and palatal grooves and was the only species with more than one (16) columellar teeth. Other than *S. leyteensis* all adult specimens displayed a single columellar tooth, no matter the species.

Radula morphology

The examined specimens showed rather variable tooth formulae (Table 4). All species show variable denticle configurations on all teeth. As radula morphologies of all species overlap and are indistinguishable between species. However, the square shape of the rachidian tooth and allows to distinguish *Supplanaxis* from other planaxid genera. Furthermore, we found the teeth of *S. planicostatus* specimens to distinctly resemble this the rachidian formula of *Supplanaxis* rather than that of *Planaxis*.

Table 4. Overview on the radula teeth formulae of *Supplanaxis* species. Numbers in squared brackets show variations found within examined specimens. As *S. abb. abbreviata*, *S. leyteensis* and *S. obsoletus* were only studied from dry material no radula formulae of these species can be provided.

Species	Rachidian	Lateral	Inner/outer marginal (number of denticles)
<i>S. nucleus</i>	$\frac{[4-]2-1-2[-4]}{1-1}$	[4-]3-1-3[-2]	8-10/ 20-26
<i>S. abb. ogasawarana</i>	$\frac{[5-]2-1-2[-5]}{1-1}$	[4-]3-1-3[-4]	8-14/ 18-24
<i>S. niger</i>	$\frac{[5-]2-1-2[-5]}{1-1}$	[4-]2-1-2[-4]	8-12/ 20-24
<i>S. planicostatus</i>	$\frac{[5-]2-1-2[-5]}{1-1}$	[3-]2-1-2[-3]	6-8/10-14

Phylogenetic analyses

Our genetic study yielded sequences of nine *Supplanaxis* specimens, each with both 16S and COI sequences, from seven independent populations, representing three of the six studied species. We recovered four sequences of *S. nucleus*, five of *S. abb. ogasawarana*, and two of *S. planicostatus*. The phylogenetic reconstruction of *Supplanaxis* and *Planaxis sulcatus* with three pachychilid species recovered the planaxids as a maximally supported group (Fig. 5). In accordance with our findings on radula morphology we found *Planaxis* (represented by its type species) as sister group of *Supplanaxis* representing distinguishable lineages, with *S. planicostatus* nested within *Supplanaxis* rather than as sister taxon of *P. sulcatus* (as previously assumed, see Houbriek, 1987). The *Supplanaxis* lineage is composed of two distinct geographic lineages: One consistent of Caribbean and Panamanian specimens, viz. *S. nucleus* and *S. planicostatus* (the latter being from the pacific side of the Panama) and one composed of Western Indian Ocean and Indo-Polynesian specimens, viz. *S. abb. ogasawarana*. However, the

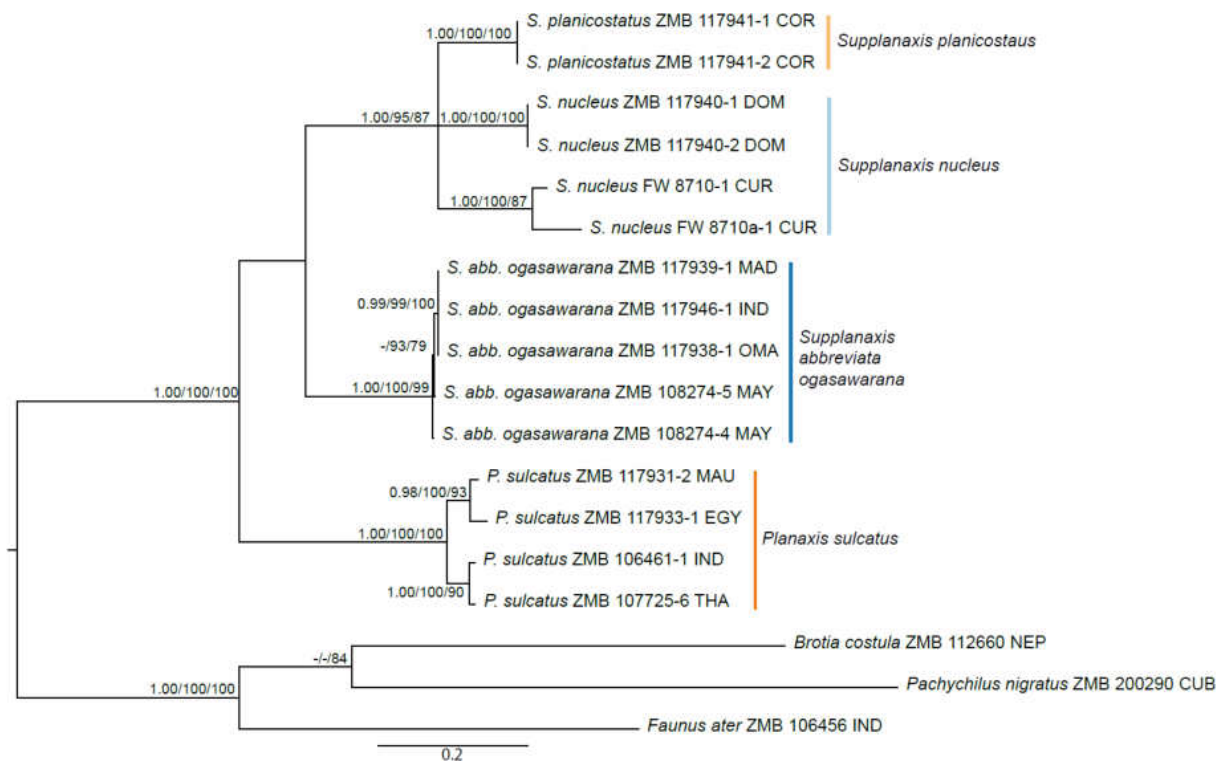


Figure 5. Bayesian 50% majority consensus tree based on concatenated COI and 16S sequences; Numbers at the nodes refer to posterior probability (PP) values (left) from the Bayesian (BI) and bootstrap support (BS) values from the maximum parsimony (MP) analysis (middle) and from the maximum likelihood (ML) analysis (right). Only nodes with PP values 0.95 and/or BS values from ML and/or MP analyses 70% are annotated. Three letter codes at the end of each sequence label indicate the country of origin (CUB = Cuba, COR = Costa Rica, CUR= Curacao, DOM = Dominica, EGY = Egypt, IND = Indonesia, MAD = Madagascar, MAU = Mauritius, MAY = Malaysia, NEP = Nepal, OMA = Oman, THA = Thailand).

Caribbean/Panamanian cluster was unfortunately unresolved, posing *S. planicostatus* and *S. nucleus* as polytomous. However, *S. abb. ogasawarana* is well supported as a distinct lineage of *Supplanaxis*.

Identification key to the *Supplanaxis* species

1. Specimen from the Caribbean.....:*Supplanaxis nucleus* (Fig. 1A)
- 1.* Pacific specimen.....:2
- 2 Shell with very deep spiral grooves on all whorls.....3
- 2.* Shell with rather shallow spiral grooves, on no more than the last 3 whorls.....4
3. Shell height >18 mm.....*Supplanaxis planicostatus* (Fig. 1G)
- 3.* Shell height <18 mm.....*Supplanaxis obsoletus* (Fig. 1F)
4. Shell higher than 15 mm, aperture pointed-oval, spire high and slender, Philippine specimen*Supplanaxis leyteensis* (Fig. 1D)
- 4.* Shell height below 15 mm, aperture roundish-oval.....5
5. Aperture without or only with weak palatal grooves, Spiral grooves weak and few if any, regularly only on the last whorl.....*Supplanaxis niger* (Fig. 1E)
- 5.* Aperture with very pronounced 12–20 palatal grooves, regularly with >12 spiral grooves, at least on the last whorl.....*Supplanaxis abbreviata*.....6
6. Spire flat-conical, shell rather obtuse, specimen from Eastern Pacific:*S. abb. abbreviata* (Fig. 1B)
- 6.* Spire high-conical, shell comparably slender, specimen from Western Pacific:*S. abb. ogasawarana* (Fig. 1C)

Systematic part

Supplanaxis Thiele, 1929

Planaxis (*Supplanaxis*) Thiele, 1929: 204.

Planaxis (*Proplanaxis*) Thiele, 1929: 203.

Supplanaxis Thiele, 1929 – Houbrick, 1987: 25.

Type species. *Buccinum nucleus* Bruguière, 1789, by monotypy.

Taxonomy. First described by Thiele (1929) as subgenus of *Planaxis*, *Supplanaxis* was elevated to generic rank by Houbrick (1987) based on several features of shell, radula, anatomy of the soft body and embryonic development. His main differentiation, though, was based on *Supplanaxis* having a radula with rachidial lateral denticles, whereas *Planaxis* has an undenticulated rachidial tooth. We identified 22 nominal species matching the characters of this genus, based exclusively on shell features. However, based on our results we here recognise six species as valid: *Supplanaxis nucleus*, *S. abbreviata*, *S. leyteensis*, *S. niger*, *S. obsoletus* and *S. planicostatus*. The latter species is also the type species of the subgenus *Planaxis* (*Proplanaxis*) Thiele, 1929. *Planaxis* (*Proplanaxis*) and *Planaxis* (*Supplanaxis*) have been described simultaneously. As we transfer *Planaxis planicostatus* to *Supplanaxis* we give precedence to *Supplanaxis* over *Proplanaxis*.

Shell. Shape variable pointed- to flat-conical, rarely globose (see Fig. 1 for an overview of shells from all *Supplanaxis* species). Shells rather small (5.8–27.3 mm high; 3.7–15 mm wide; 4–7 whorls), 0–23 spiral grooves. If present, spiral grooves can be present across the entire shell, the last up to three whorls or only at the lower and/or higher part of the columella of last whorl. Dark brown to black, rarely spotted. Aperture shape can vary heavily, as discussed below for each species separately. Aperture of adults with one columellar tooth (only *S. leyteensis* differs in this trait with 10 minute columellar teeth; columellar tooth missing in juveniles of all species) and 0 – 20 more or less pronounced palatal grooves. The outer margin of the aperture (lip) of adults is slightly widened and rounded, as opposed to the sharp aperture margin in juveniles.

Radula. Taenioglossate, each row of teeth consisting of 5 teeth. Rachidians with one sharp to ovate central denticle, with two to five denticles on both sides. Basal rachidial processes sturdy, slightly angular. Lateral teeth are shaped typically for planaxids (see Houbrick 1987) with a slight tilt towards the rachidian and deviating numbers of side denticles (occasionally two or up to five on each side, varying independently). Marginal teeth vary heavily in

denticle numbers; with the inner teeth usually having 8–14 denticles, whereas the outer teeth are waved with 18–26 denticles (Figs 7, 10, 15, and 20).

Reproductive biology: Houbrick (1987) gave a detailed account on the reproductive biology of *S. nucleus*, identifying it as typical for the planaxids: offspring are bred in a subhaemocoelic brood pouch (positioned in the neck region of the head-foot) until shelled veliger larvae hatch and become planktonic; i.e. the species is viviparous (see Glaubrecht, 2006, 2009 for detailed discussion on reproductive strategies in Cerithioidea).

Ecology. Most species live in intertidal, rocky shores, where they can be found in large numbers scattered on rocks or in puddles. Few accounts exist, reporting specimens of the nominal species *P. nancyae* (= *S. nucleus*) from subtidal habitats of 2–5 m depth, also stating a comparably low frequency of specimens occurring in these depths (Petuch 2013).

***Supplanaxis nucleus* (Bruguière, 1789)**

Lister, 1770: Pl. 976, fig. 32. [Figure and description of the species from Barbados without a Linnean name]

Martini and Chemnitz, 1780: 46f, Pl. 125 fig. 1183. [Figured specimen from Barbados without a description or name]

Buccinum nucleus Bruguière, 1789: 254f.

Purpura nucleus Brug. – Lamarck, 1822: 249f.

Planaxis nucleus (Bruguière) – Deshayes, 1828: 13.

Planaxis (Supplanaxis) nucleus (Lamarck) – Thiele, 1929: 204. [mis-affiliation of original author]

Supplanaxis nucleus (Bruguière, 1789) – Houbrick, 1987: 445: 25ff.

Buccinum strigosum Gmelin, 1791: 3488. [not *Buccinum strigosum* Gmelin, 1791 (p. 3476) or *Buccinum strigosum* Gmelin, 1791 (p. 3494)]

Planaxis semisulcatus Sowerby I, 1823: 74; Pl 70 fig. 3 [no type locality indicated]

Planaxis (Supplanaxis) nancyae Petuch, 2013: 193, fig. 6.13 [Holotype FMNH IZ 328402; Fig. 6I; type locality Southern Gonave Island, Haiti]

Type material. Whereabouts of original type series unknown (see *Taxonomy*).

Type locality. “Barbadense” as given in his description by Bruguière (1789), in addition to “Madagascar” and “New Zealand”; here restricted to Barbados.

Taxonomy. In his original description Bruguière (1789) focused on three ‘morphs’, two from his own collection found in Madagascar and one he apparently saw stitched onto clothing in the possession of “Mr. Broussonet”, which he allocated to New Zealand. In addition, he lists shells from Barbados depicted by Lister (1770) and further shells figured by Martini and Chemnitz (1780) without a sample location. Although the latter authors gave no Linnean name or species description of the material, these should be accounted for as part of Bruguière’s understanding of the species. Throughout all inquired collections (see section

‘museum codens’) where searched, neither Bruguiere’s nor Lister’s (1770) or Martini and Chemnitz’s (1780) material could be located.

We found two accounts using the name for Pacific specimens after Bruguière’s (1789) original account, viz. Bosc (1802) and Dillwyn (1817), both reproducing his work, albeit without an indication of material examined but exclusively giving New Zealand and Madagascar as geographical origin. However, in subsequent publications this species name is exclusively allocated to specimens from the Caribbean (e.g. Sowerby II, 1877; Thiele 1929; Wenz 1940; Abbott 1955, 1974; Sterrer 1986; Houbriek 1987; Hewitt 2013; Petuch 2013). Hence, we here determine *S. nucleus* to be an exclusively Caribbean species and suggest Barbados as its proper type locality in accordance with Lister’s proposition.

We place three nominal taxa into the synonymy of *S. nucleus*. *Buccinum strigosum* Gmelin, 1791 (p. 3488, not *Buccinum strigosum* Gmelin, 1791, p. 3476, or *Buccinum strigosum* Gmelin, 1791 (p. 3494), was described with reference to Martini & Chemnitz (1780), specifying the illustration that Bruguière (1789) is referencing in his original description of *S. nucleus*. Hence, *B. strigosum* constitutes a junior synonym of *S. nucleus*. *Planaxis semisulcatus* Sowerby I, 1823, described without specifying a type locality, is nearly identical to the typical morph of *S. nucleus* found throughout the Caribbean.

Furthermore, *Planaxis (Supplanaxis) nancyae*, as described by its author differs from *S. nucleus* “in being a smaller, more slender and less inflated shell; in in having a proportionally higher and narrower spire; in being highly polished and shiny; in lacking the strong spiral cords and deeply incised spiral grooves around the shoulder, subsutural area, and anterior end [...]; in having weaker and less developed teeth on the inner edge of the lip; and in having a reddish-brown shell color instead of black or dark brown-black” (Petuch, 2013: 193). However, we found spiral grooves of *S. nucleus* to vary in these traits and to also encompassing specimens with very low amounts and even lacking spiral grooves, as well as palatal grooves. This variation is also true for the shell color, which also varied between the picture provided by the FMNH collection (Fig. 6I) and the one provided in Petuch (2013), with the latter being far more reddish than other pictures of the same specimen. Petuch (2013) suggests a difference in habitat but also states that, while *P. nancyae* is found in deeper waters, it is also less frequent there. Furthermore, based on an underdeveloped columellar tooth and a rather sharp aperture margin, the holotype seems to be a subadult specimen, potentially a juvenile of *S. nucleus*. The reported decrease in abundance (Petuch, 2013) alone does not conflict with the suggested synonymy of these nominal taxa, as fewer snails may be expected at lower depth if this habitat is sub-optimal.

Based on these morphological and ecological traits we here consider *P. nancyae* (with its type locality Southern Gonave Island, Haiti) a junior synonym of *S. nucleus*.

In contrast, Strong & Bouchet (2020) found in their study two distinct genetic clades of Caribbean *Supplanaxis* specimens, occurring syntopically in three Caribbean populations. Based on their implications we evaluated exclusively our Caribbean specimens, grouping together those with a more ovoid aperture shape and overall smaller shell height. However, we found no clear distinction of these entities based on this criterion alone and, thus, we were unable to identify any significant differences between Caribbean *Supplanaxis* specimens based on our data. Nevertheless, in case this suggested distinction holds true in future studies we agree to use *P. nancyae* as the name for a second clade of *Supplanaxis* in the Caribbean.

Shell. (Fig. 6). Shell shape very variable with flat- and pointed-conical forms. Regularly, the last whorl is heavily inflated, leading to a very broad to globose impression of shell shape. 8.5–17.5 mm high, 5.2–11.5 mm wide. The 4–6.5 whorls can be very short to rather slender, varying heavily within and between populations. Dark brown to black, sometimes with a greyish coating. The last whorl can have 0–23 spiral grooves, though averaging at 9 grooves

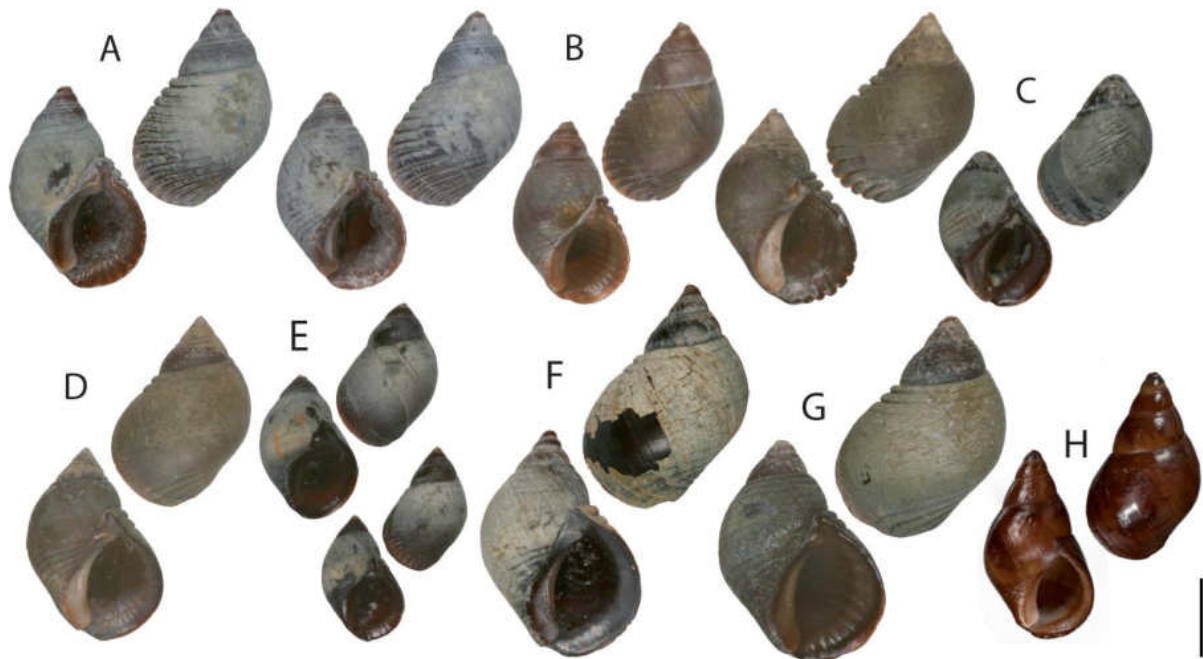


Figure 6. Shells of *Supplanaxis nucleus* and type specimens of junior synonyms. **A** Topotypical specimens, Barbados (AMS C. 323610-8, -6). **B** Cuba (ZMB 121059-1; -3). **C** Virgin Islands, St. Thomas (ZMB 193436-3). **D** Virgin Islands, St. Thomas (ZMB 121060-4). **E** Dominica, Thibaud (NHMUK 2014.0847-2;-6). **F** Venezuela, Margarita Island (ZMB 108278-6). **G** Trinidad, Maracas Bay (AMS C.323604-6). **H** *Planaxis nancyae*, holotype (FMNH IZ 328402). Scale bar = 5 mm. **H** © Images were provided by Jochen Gerber, Field Museum of Natural History (FMNH).

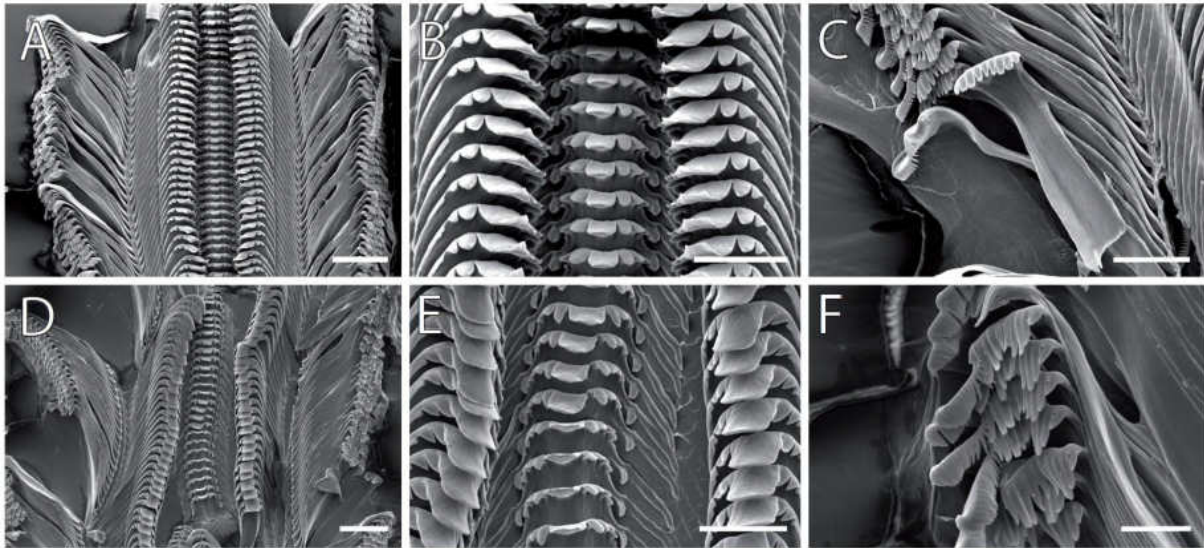


Figure 7. Radulae of *Supplanaxis nucleus*. **A–C** Barbados, St. Lucy, Archer Bay (AMS C.323610-6). **D–F** Venezuela, Margarita Island (ZMB 108278-6). **A, D** Radula ribbon. Scale bar = 100µm. **B, E** Lateral and central teeth. Scale bar = 50µm. **C** Marginal teeth. Scale bar = 50µm. **F** Marginal teeth. Scale bar = 5µm.

in our material, regularly positioned at the upper and lower part of the whorl. The rather ovate aperture (5–10.7 mm high; 2.7–6.5 mm wide) has one columellar tooth and 0–19 palatal grooves. Lip only slightly widened.

Radula. Radulae of this species (Fig. 7) were found to be of typical *Supplanaxis* shape, differing in the following characters: radulae are at least 340 rows long. Rachidian teeth exhibit usually only two denticles on each side of the central denticle, rarely rachidians with three or four denticles on each side of the central denticle can be found. Marginals were found with 20–26 denticles (see also Table 4).

Distribution. This species can be found throughout the Caribbean province, ranging from Florida in the north, along the West Indian islands to Barbados in the east and the Caribbean main land to the south, with the southernmost occurrence known from Trinidad (see Fig. 8).

Material examined

USA: Florida, Key Largo (GP 639708, 639709).

Cuba: (ZMB 121059).

Jamaica: (ZMB 28724).

Haiti: (ZMB 28725, 110432, 121066) (SMF 218276); St. Mare (ZMB 110557) (SMF 218275).

Dominican Republic: Barahona, 5km of Barahona, Playazul beach, 18°9'19.8"N 71°2'17.16"W (FW 12373-w); Samaná, small beach west of Las Galeras, 19°17'32.28"N; 69°12'42.12"W (FW 12372-w).

Puerto Rico: (ZMB 121065).

West Indies: (ZMB 121054; 121055) (SMF 304766).

Virgin Islands: St. Thomas (ZMB 2874, 28723, 121060, 121061, 121062, 121083, 193436-w) (SMF 304765).

Antigua and Barbudas: Redonda (USNM 714035).

Dominica: Thibaut (ZMB 117940-w) (NHMUK 2014.0847-w).

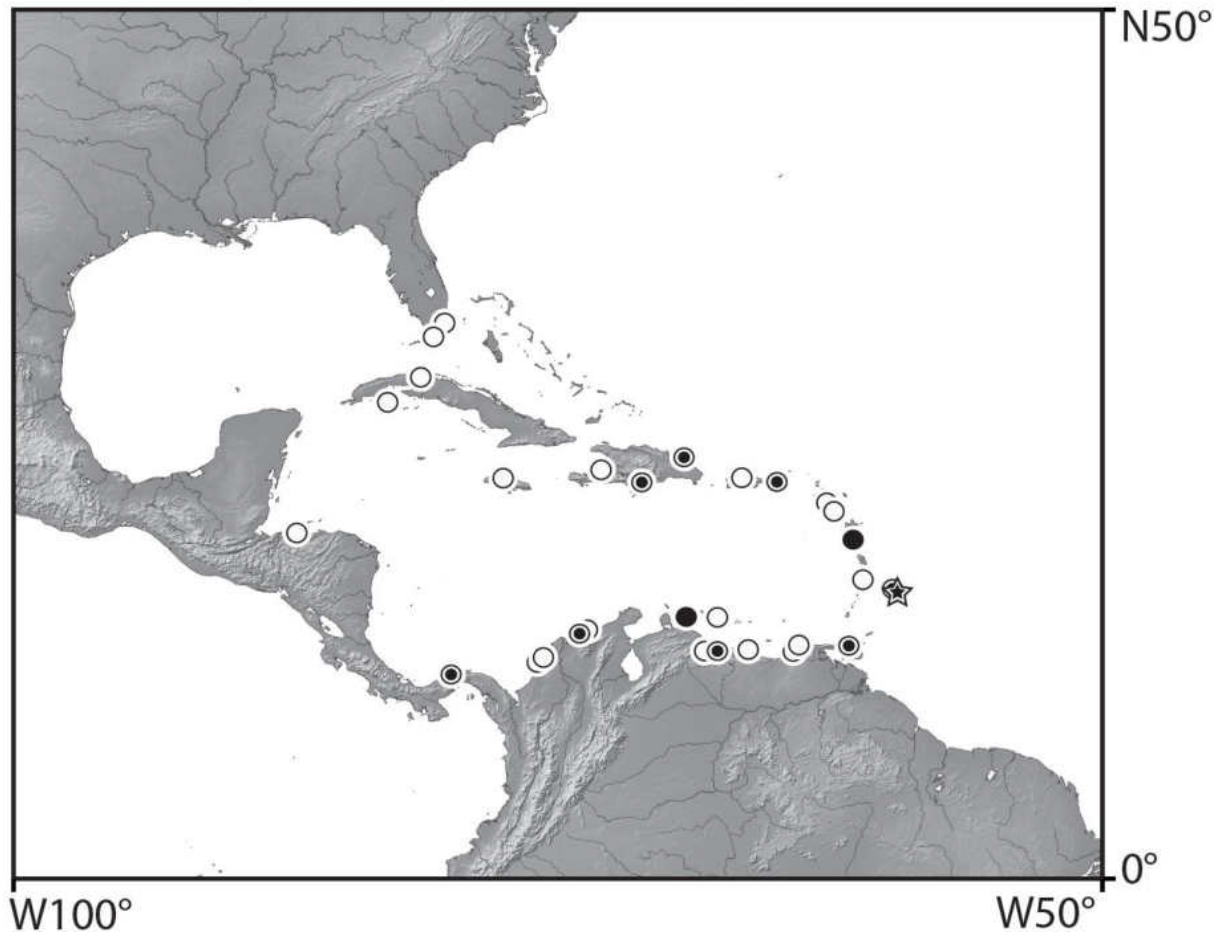


Figure 8. Occurrences of *Supplanaxis nucleus* throughout the Caribbean. Open circles represent dry stored shells, whereas concentric circles represent ethanol stored specimens, entirely filled symbols represent ethanol stored specimens that yielded genetic sequences, the star indicates the type locality.

Barbados: St Lucy, Archer Bay (13°20'N; 59°37'W) (AMS C.323610-w).

Trinidad: Maracas Bay, N of Port of Spain, on rocks on beach (10°45'N; 61°34'W) (AMS C.323604-w).

Curacao: Soto, Playa Mansalina, 12°14'49.2"E; 69°6'24.84"W (FW7810-w, ZMH 140713), Curacao, West point, Playa Kalki, 12°22'32.88"N; 69°9'29.16"W (FW 8721-w); Boka Grandi, 12°21'30.96"N; 69°5'48.84"W (FW 8722-w).

Colombia: Bahía de Nenguange near Sta. Marta (SMF 257244).

ABC Islands: Bonaire, Shoreline rocks (GP 958027).

Venezuela: (ZMB 32401); Puerto Cabello (ZMB 121056, 121057); Caracas (ZMB 225-w); Margarita Island, near Porlamar, water depth 3m (GP 114269-114278, 236134, 268488-268493, 675595-675597, 675599-675605, 727170-727173, 771817, 771818, 771831, 771832, 921466, 921467); Margarita Island (ZMB 108278-w); Margarita Island, Playa Valdez (GP 977447-977449, 1061535-1061537, 1061539, 1061540, 1061542).

***Supplanaxis abbreviata* (Pease, 1865) (new combination)**

Planaxis abbreviata Pease, 1865: 515.

Planaxis abbreviata ogasawarana Pilsbry, 1905: 105.

Planaxis similis Smith, 1872: 41 [one syntype NHMUK 1907.12.30.165; Fig. 9J, type locality Hawaii]

Type material. Pease (1865) did not specify any type material. Johnson (1994) designated ANSP 18261 (Fig. 9A) as lectotype and thus ANSP 394492 and MCZ 187833, 187834 are paralectotypes. He states that no specimens were located a NHMUK (see also Kay, 1965). However, we found one specimen in this collection labelled as “holotype” (NHMUK 1964.320) with a reference to the original description (Pease, 1865), a figure of the shell in Reeve (1878) and a note stating that the holotype was designated by “Kay 1964”, that apparently was never published, as Kay (1965) in her later work states to have not found any types of the species in London. As Pease (1865) did not specify any type material, ANSP 18261 remains the lectotype.

For the subspecies *Supplanaxis abbreviata ogasawarana* ANSP 87769 (see Fig. 9E) has been listed by the describing author (Pilsbry, 1905), comprising four syntypes.

Type locality. Pease (1865) did not specify a type locality in his original description. The lectotype (ANSP 18261) originates from Tahiti Island (Johnson, 1994). The types of *Supplanaxis abbreviata ogasawarana* (ANSP 87769) are from Hahajima, Ogasawara in Japan (see Fig. 9E).

Taxonomy. Chen *et al.* (2018) listed *S. abbreviata* as a junior synonym of *S. niger*. As we here found strong support in shell shape and characters to distinguish *S. abbreviata* and *S. niger*, we reject their hypothesis, considering the former also as a proper species. Therefore, we here place *P. abbreviata* in *Supplanaxis*, as a new combination.

Furthermore, Pilsbry (1905) described *Planaxis abbreviata ogasawarana* for a distinct morph from Hahajima, Ogasawara, Japan (four syntypes ANSP 87769; Fig. 9E). We found specimens from the Western Indian Ocean and Eastern Indo-Pacific to be morphologically similar to this subspecies, whereas western Indo-Polynesian specimens are morphologically similar to *S. abb. abbreviata*. Morphologically these subspecies are different in spire height and amount of spiral grooves on the penultimate whorl. However, as the high morphological variance of *S. nucleus* implies that a high morphological variance might also be present for other congeneric species, we do not separate these two variants into different species, although future genetic studies might reveal species differences.

We found *Planaxis similis* Smith, 1872 described from Hawaii to represent a junior synonym of *Supplanaxis abb. abbreviata* based on its high morphological similarity, as the position and number of spiral grooves, as well as shell shape are typical of *S. abbreviata*.

Shell. (Fig. 9). Pointed- to flat-conical. 5.82–14.5 mm high, 3.7–9.7 mm in wide. 4–6 whorls. Shells dark to reddish brown. Aperture 3.6–9.2 mm high, 2–4.9 mm wide, white, porcelaneous coloured, with 8–20 deep palatal grooves and one columellar tooth. Lip slightly widened.

Supplanaxis abbreviata abbreviata (Fig. 9A–D) spire flat-conical, shell shape obtuse, shells slightly smaller, with 4–15 spiral grooves only on last whorl.

Supplanaxis abbreviata ogasawarana (Fig. 9 E–I) spire pointed-conical, shell shape slender, larger than *S. abb. abbreviata*. 10–22 spiral grooves on last whorl, regularly 2–9 spiral grooves on penultimate whorl.

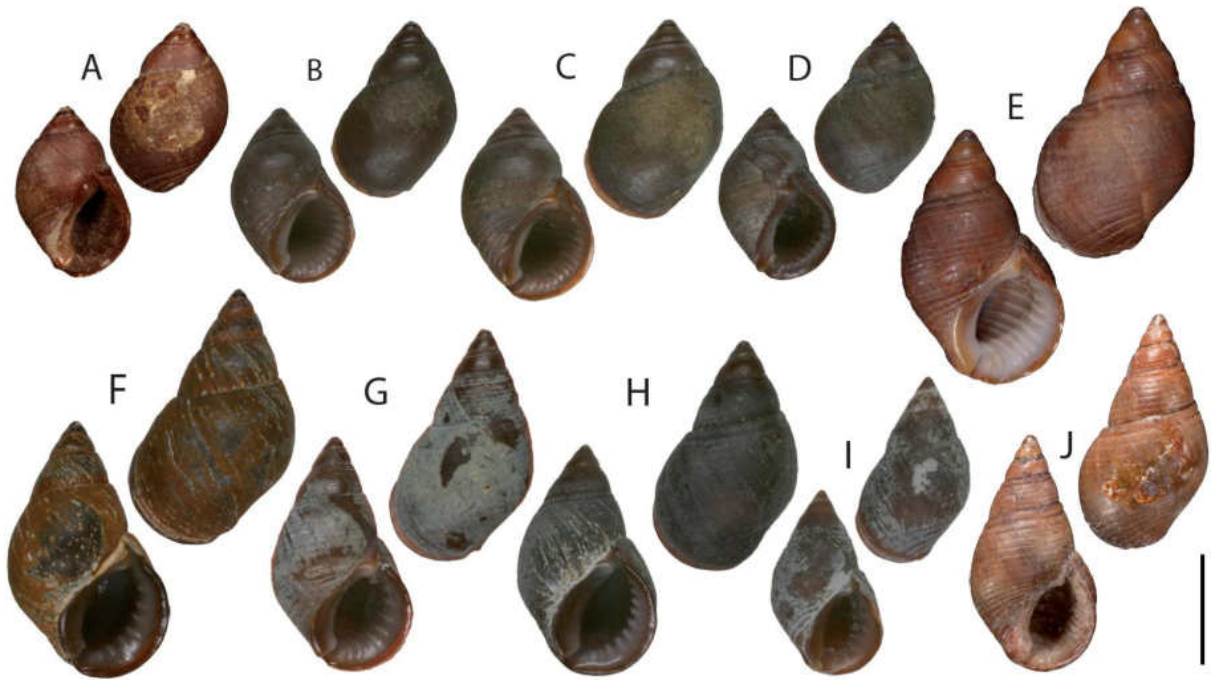


Figure 9. Shell morphology of *Supplanaxis abbreviata* and type specimens of junior synonyms. **A–D** *S. abbreviata abbreviata*. **E–I** *S. abbreviata ogasawara*. **A** Lectotype, French Polynesia, Tahiti (ANSP 18261). **B** Papua New Guinea, Milne Bay (ZMB 121084-2). **C** Samoa (ZMB 18294-2). **D** French Polynesia, “Otaheite”, Tahiti (ZMB 121078). **E** One of four syntypes; Japan; Hahajima, Ogasawara (ANSP 87769). **F** Oman, Mirbat, Dofar (NHMUK 2014.0856-2). **G** Seychelles, Mahé Island, Northolme (ZMB 108269). **H** Indonesia, Sumatra, Aceh, Ule-le (NHMUK 2014.0863-2). **I** Malaysia, Borneo, Tanjung Aru (ZMB 108274). **J** *Planaxis similis*, Syntype, Sandwich Island (Hawaii, NHMUK 1907.12.30.165). Scale bar = 5 mm. **A, E** © Images were provided by Ms. Krasimira Seizova, Department of Malacology, Academy of Natural Sciences of Philadelphia. **J.** © Images courtesy of Harry Taylor, NHMUK Photographic Unit.

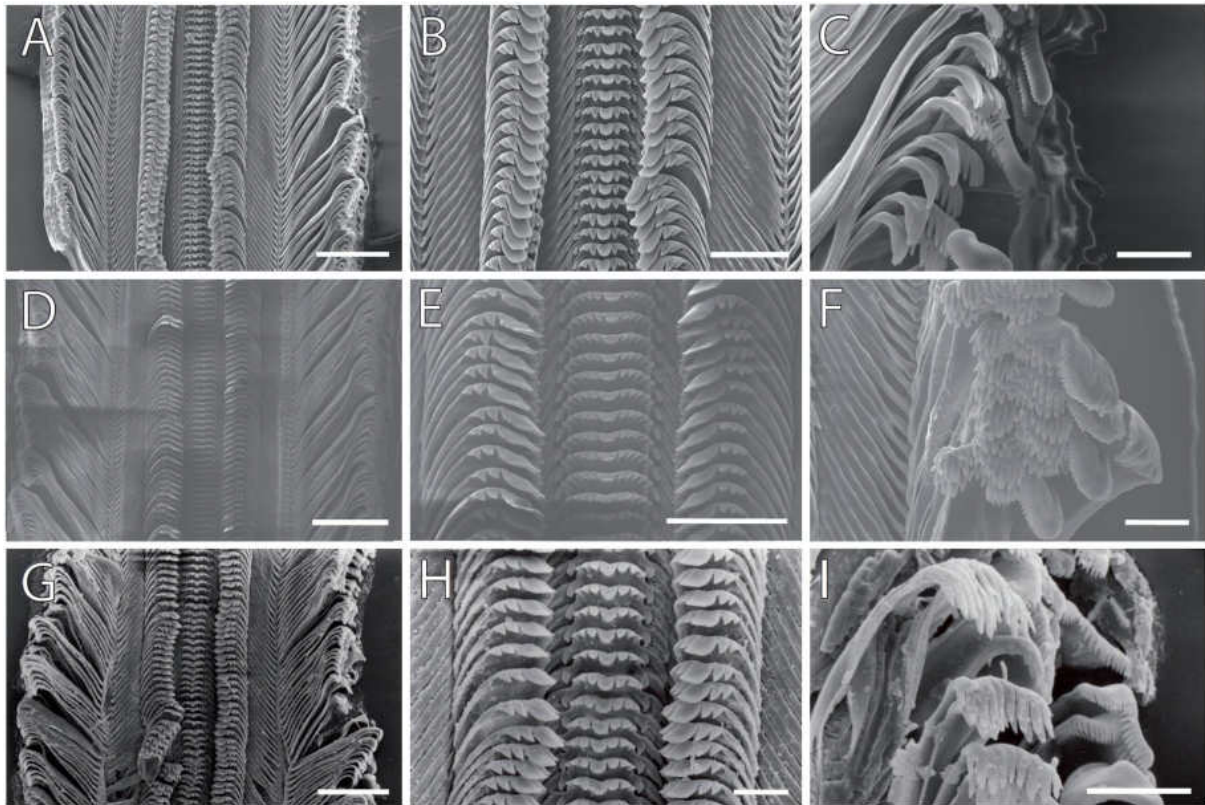


Figure 10. Radula of *Supplanaxis abbreviata ogasawarana*. **A–C.** Seychelles, Mahé Island, Northolme (ZMB 108269). **D–F** Yemen, Sokotra, west of Hadiboh (SMF 346151). **G–I.** Malaysia, Borneo, Tanjung Aru (ZMB 108274). **A, D, G** Radula ribbon. Scale bar = 100µm. **B, E, H** Lateral and central teeth. **B, E** Scale bar = 50 µm. **H** Scale bar = 25 µm. **C, F, I** Marginal teeth. **C** Scale bar = 10 µm. **F, I** Scale bar = 25 µm.

Radula. As only dry stored shells of *S. abb. abbreviata* were available, we studied only the radula of *S. abb. ogasawarana* (Fig. 10). Radula typical of *Supplanaxis*. Rachidians regularly with two denticles beside the central denticle, though specimens with up to 5 side denticles were identified. Lateral teeth with three side denticles on each side, rarely with four. Outer marginals with 18–24 denticles, inner marginal with 8–14 denticles (see Table 4).

Distribution. (Fig. 11). *Supplanaxis abbreviata* can be found from Madagascar across the western Indian Ocean and throughout the Indo-Polynesian province and south Japan, as well as in Hawaii. *Supplanaxis abb. abbreviata* occurs from east Papua New Guinea to Tahiti. *S. abb. ogasawarana* is found throughout the Western Indian Ocean province, South Japan and the Eastern Indo-Polynesian province.

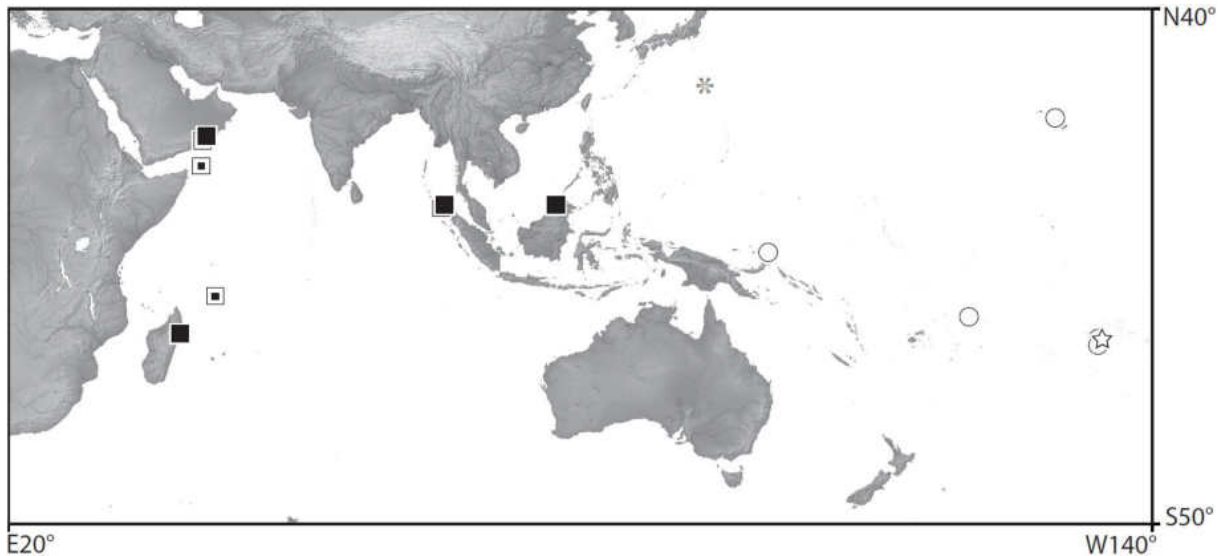


Figure 11. Occurrences of *Supplanaxis abbreviata* throughout the Western Indian and Indo-Pacific regions. Circles and the star indicate sample sites of *S. abb. abbreviata*, whereas squares and the asterisk indicate sites of *S. abb. ogasawarana*. The star and asterisk indicate the respective type localities. Open circles represent dry stored shells, whereas concentric symbols represent ethanol stored specimens, filled symbols represent ethanol stored specimens that yielded genetic sequences.

Material examined

Supplanaxis abbreviata abbreviata

“Pacific”: (ZMB 121085).

Papua New Guinea: Milne Bay (ZMB 121084).

Samoa: (ZMB 18294).

French Polynesia: “Otaheite”, Tahiti (ZMB 20097, 121078).

Hawaii: (NHMUK 1907.12.30.165) [Syntype of *Planaxis similis*, here considered a junior synonym].

Supplanaxis abbreviata ogasawarana

Indonesia: Sumatra, Aceh, Ule-le (ZMB 117946-w) (NHMUK 2014.0863-w).

Malaysia: Borneo, Sabah, Kota Kinabalu, Tanjung Aru, Pulau (ZMB 108274-w); Borneo (ZMB 121079).

Yemen: Sokotra, north coast, West of Hadiboh, between Qadub and Hadiboh (SMF 346151-w).

Oman: Mirbat, Dofar (ZMB 117938-w) (NHMUK 2014.0856-w).

Seychelles: Mahé Island, Northolme (ZMB 108269-w).

Madagascar: (ZMH 41636); Southeast Island St. Marie (ZMB 117939-w) (NHMUK 2014.0850-w).

Supplanaxis leyteensis Poppe, Tagaro and Stahlschmidt, 2015

Supplanaxis leyteensis Poppe, Tagaro and Stahlschmidt, 2015: 22f.

Type material. Holotype MNHN 2000-30332

(Fig. 12A). Additionally, the original authors list 23 paratypes in the collection of Guido T. Poppe (GP 643587, 646299, 646302, 646303, 646305-646316, 646318-646321, FW 8566 = GP 646317). These paratypes stand for sale in the original author's venture (Conchology Inc). Hence, the type series is already and will further be split in the future.

Type locality. Philippines, Leyte, Caminagan.

Shell. (Fig. 12) High-conical, spire more slender than in all other *Supplanaxis* species, providing the impression of an elongated shell by contrast to the other species. 16.4–20.8 mm high, 7.9–10.9 mm wide, 5.5–6.5 whorls. 15–18 very weak spiral grooves, densely and very shallow covering the last whorl. Black to greyish-green coloured with several radial spotted lines. Aperture oval, slightly elongated. 8.2–11.69 mm high, 4.3–6.1 mm wide. 16–18 rather deep palatal and 8–10 columellar grooves, one pronounced columellar tooth, contrasting all congeneric species it is minute and pointed, with the tip facing horizontally in standardised position.

Radula. As only the dry shell material of the type

specimens was available to us, the radular of this species has so far not been studied.

Distribution. So far, this species is only known from Leyte (its type locality in the Philippines) and one other location in Mindanao, (Philippines, Fig. 13).

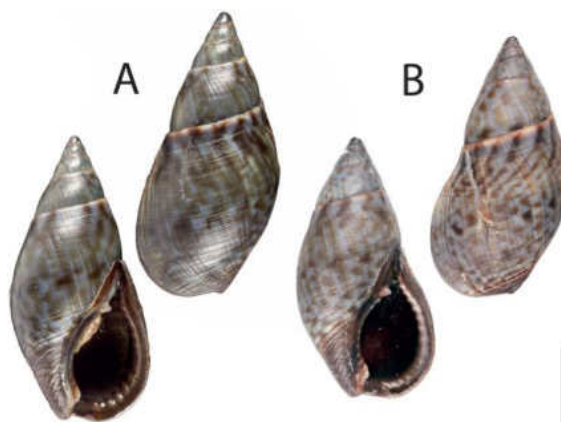


Figure 12. Shells of *Supplanaxis leyteensis* from Leyte. **A** Holotype (MNHN 2000-30332). **B** Paratype (FW 8566). Scale bar = 5 mm. **A** © M. Caballer MNHN, project E-RECOLNAT: ANR-11-INBS-0004.

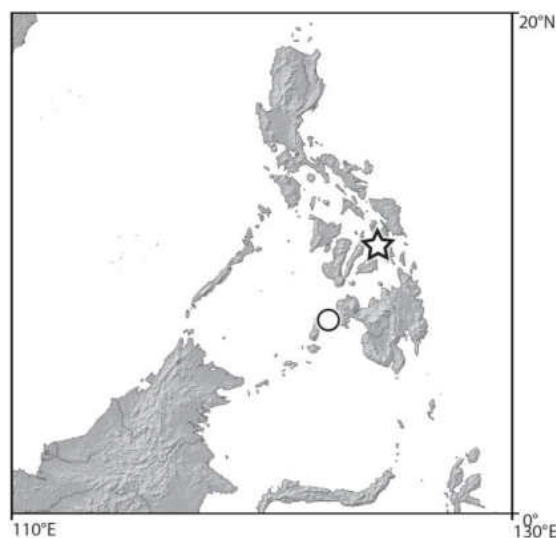


Figure 13. Map of the type locations of *Supplanaxis leyteensis* within the Philippines. Open symbols represent dry stored specimens, the star indicates the type location.

Ecology. Lives between 50–100 cm water depths between and under round big rocks and on sand (Poppe *et al.*, 2015).

Material examined

Philippines: Mindanao, Surigao, Barangay Ipil, Baliti, water depth 1–2 m (GP 777185).

***Supplanaxis niger* (Quoy & Gaimard, 1833)**

Planaxis nigra Quoy & Gaimard, 1833: 491f.

Planaxis niger Quoy & Gaimard – Smith 1872: 44.

Supplanaxis niger Quoy & Gaimard, 1833 – Cernohorsky 1972: 52.

Planaxis acuta Krauss, 1848: 103. [not *Planaxis acutus* Menke 1851 [type locality: “In littore nataelensis”; that is the South-East African Natal region]

Planaxis nicobaricus Zelebor, 1866 in Dunker and Zelebor 1866: 910 [two syntypes ZMB 12329; Fig. 14G type locality: Nicobar Islands].

Planaxis nicobaricus Frauenfeld, 1867 [sic] – Chen *et al.* 2018: 552. [mis-affiliation of the describing authors]

Planaxis castaneus Smith, 1872: 40 [three syntypes NHMUK 2014.0091; Fig. 14E; type locality unknown].

Planaxis hanleyi Smith, 1872: 41 [two syntypes NHMUK 1907.10.25.93; Fig. 14F; type locality: “Sandwich islands”, i.e. Hawaii].

Type material. 22 syntypes MNHN-IM-2000-27769.

Type locality. “...at the harbour of Carteret New Ireland” (Quoy & Gaimard, 1833), i.e. Carteret’s Harbour (named after Philipp Carteret, 1733-1796), also known as Lamassa Bay, at the southern tip of the island of New Ireland.

Taxonomy. First described by Quoy & Gaimard (1833) as *Planaxis nigra*. Smith (1872) changed the species epithet to *niger* to match the grammatical gender of the generic name. The species was later placed in *Supplanaxis* by Cernohorsky (1972). We identified four junior synonyms. *Planaxis acuta* Krauss, 1848, described from the South-East African Natal region, and *Planaxis nicobaricus* Zelebor, 1866 (two syntypes ZMB 12329; Fig. 14G), described from the Nicobar Islands, based on their respective original descriptions which closely mirror the description and overall appearance of *S. niger*. Chen *et al.* (2018) referenced *Planaxis nicobaricus* to “Frauenfeld, 1867”. In Frauenfeld, 1867, the author allocates the name *P. nicobaricus* to Zelebor but only in the German introduction, which might have been overlooked by non-German speaking authors. Therefore, the applicable combination is *Planaxis nicobaricus* Zelebor, 1866, a junior synonym of *S. niger*. The type specimens of both *P. castaneus* Smith, 1872 (NHMUK 2014.009) and *P. hanleyi* Smith,

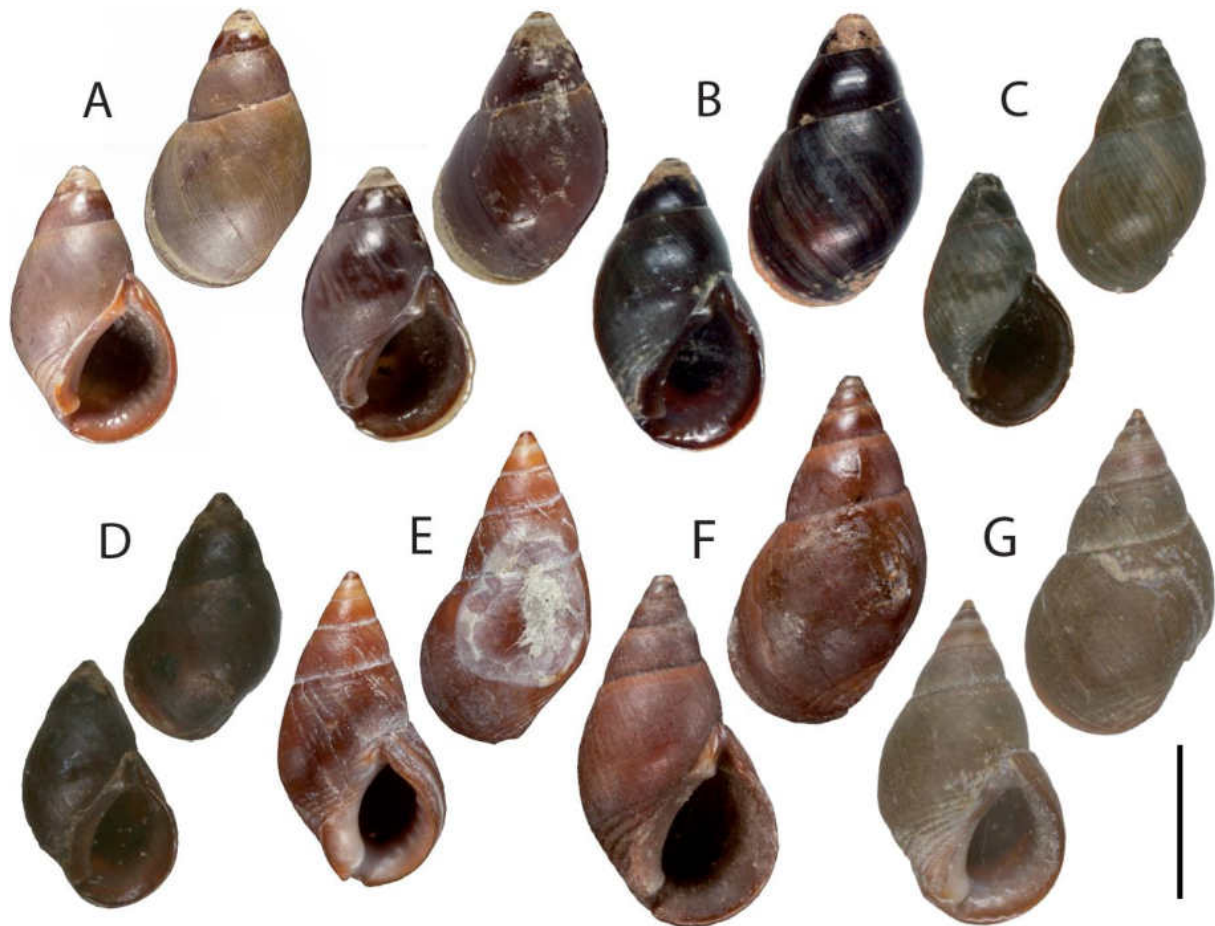


Figure 14. Shells of *Supplanaxis niger* and type specimens of junior synonyms. **A** Two of twenty-two syntypes, New Ireland, Lamassa Bay (MNHN-IM-2000-27769). **B** Indonesia, West Irian, Manokwari (AMS C.323602-9). **C** Papua New Guinea, E side of Beliau Island, Madang Harbour, in coral (5°12 S 145°50 E) (AMS C. 322982-9). **D** Fiji, Viti (ZMB 121077-5). **E** *Planaxis castaneus*, one of three syntypes (NHMUK 2014.0091). **F** *Planaxis hanleyi*, one of two syntypes (NHMUK 1907.10.28). **G** *Planaxis nicobaricus*, one of two syntypes (ZMB12329-2). Scale bar = 5 mm. **A** © M. Caballer MNHN, project E-RECOLNAT: ANR-11-INBS-0004. **E, F** © Images courtesy of Harry Taylor, NHMUK Photographic Unit.

1872 (NHMUK 1907.10.28, from Hawaii) are slightly larger than the average *S. niger*. However, the smooth aperture and mostly smooth shell account for a close affiliation to *S. niger*. Chen *et al.* (2018) position *Planaxis atra* Pease, 1869 (lectotypes ANSP 18282, paralectotypes ANSP 391038) as a junior synonym of *S. niger*. However, *Planaxis atra* is by its size, spiral bands and missing aperture grooves clearly to be allocated to *Angiola*. Hence, we do not consider this nominal species as a junior synonym of *S. niger*.

Shell. (Fig. 14) Rather flat-conical. 6.13–19 mm high, 3.7–10.4 mm wide, 4–7 whorls. 0–17 spiral grooves, on upper and lower third of the last whorl, most specimens with less than 5. Regularly, no spiral grooves on the penultimate whorl, rarely up to 5. Light to dark brown, sometimes with reddish aperture margin. Aperture 3.5–10.7 mm high, 8.3–5.6 mm wide, 0–

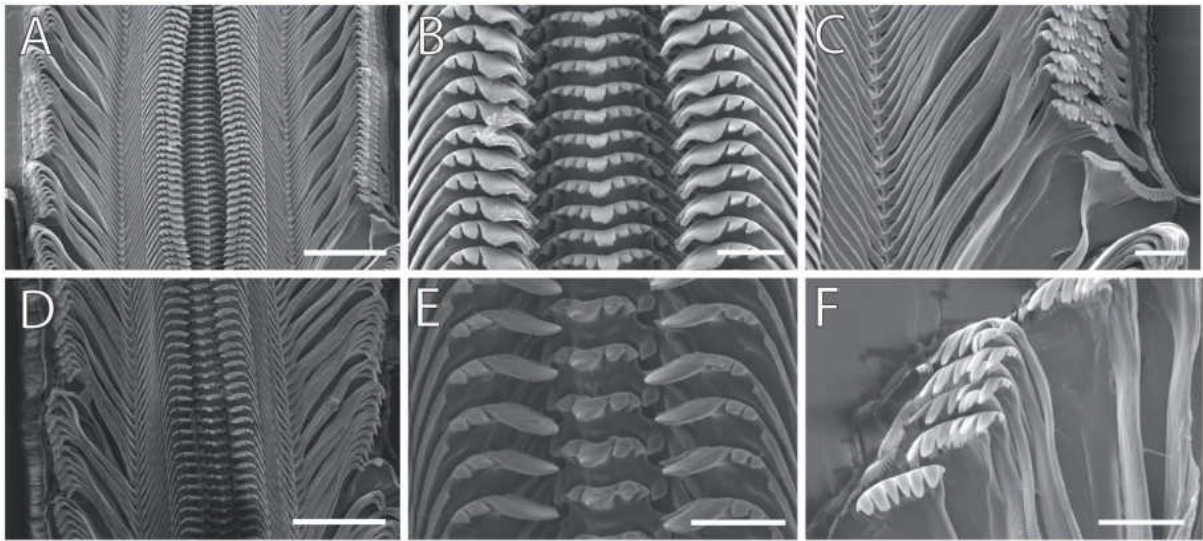


Figure 15. Radula of *Supplanaxis niger*. **A–C** Madagascar, Southeast Island, St. Marie (NHMUK 2014.0850). **D–F** Papua New Guinea, Madang Harbour (AMS C.322982). **Q–S** French Polynesia, Ua Huka Island (NHMUK 2014.0862). **A, D** Radula ribbon. Scale bar = 100 μm . **B, E** Lateral and central teeth. Scale bar = 25 μm . **C, F** Marginal teeth. Scale bar = 25 μm .

18 palatal grooves, 4 on average. Adults with on columellar tooth, lip only slightly widened, rarely light brown, whitish.

Radula. (Fig. 15) Radulae of this species are at least 650 rows long. Rachidian teeth had two to five denticles on each side of the central denticle. Other radula features of this species did not vary in any way from the general description of *Supplanaxis* radulae.

Distribution. *Supplanaxis niger* is found to range from the Western Indian Ocean to Indo-Polynesian Province (Fig. 16). It ranges from Madagascar along Yemen, Saudi-Arabia, into the Indo-Polynesian Province, where it is widespread. Several samples from the Philippines and New Guinea, as well as New Caledonia, even ranging to Samoa as its easternmost sample location, have been found, while to the south the distribution does not reach Australia.

Material examined

Yemen: Little Aden (CWR 51/07-w); Sokotra (CWR 65/96-w); Hawlaf (CWR 32/97-w).

Philippines: Bohol, Maribojoc, Abatan River, in mangroves (GP 515577, 515579); Camotes Islands, Pilar, water depth 1m (GP 160676-160683, 161460, 307118, 307121-307123, 307125-307127, 515580, 727553, 727554, 950668); Coron, Palawan (GP 114309, 114312, 114316, 114317, 306949-306958, 986681-986683); Mactan Island, Punta Engano, intertidal (GP 723081, 723082); Mactan Island, Punta Engano, Coral Point, intertidal (GP 685458, 685459, 773692-773698, 773700); Palawan, Bubusawin, Apurawan (GP 874300-874302).

Indonesia, West Irian: Manokwari (0°52'S; 134°5'E) (AMS C.323602-w).

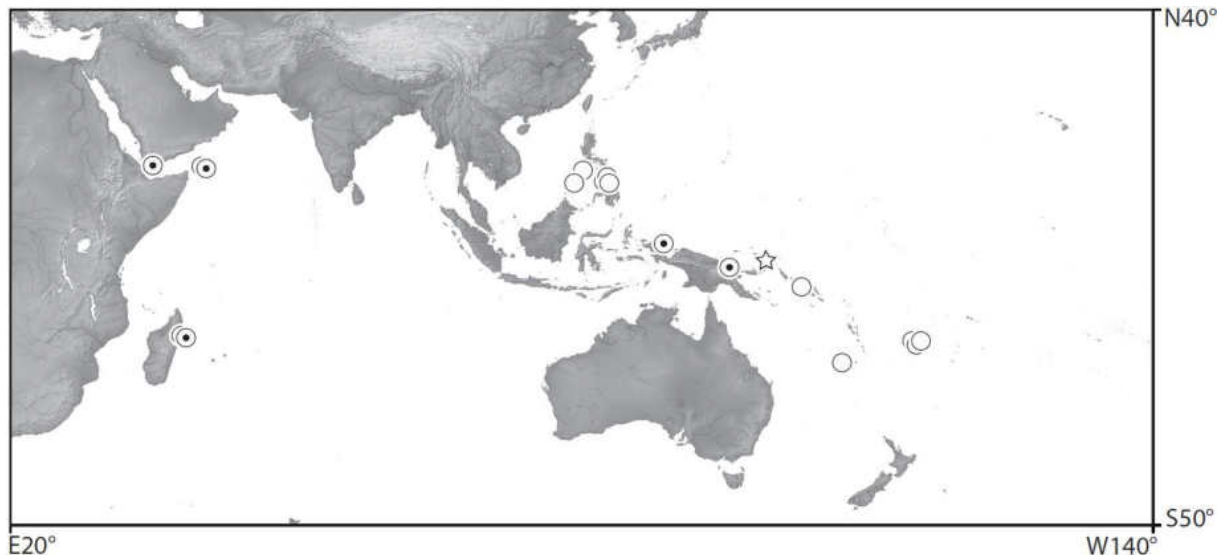


Figure 16. Occurrences of *Supplanaxis niger* throughout the Western Indian and Indo-Polynesian regions. The star indicates the type locality. Open circles represent dry stored shells, whereas filled symbols represent ethanol stored specimens.

Papua New Guinea: East side of Beliau Island, Madang Harbour, in coral (5°12'S; 145°50'E) (AMS C.322982-w);

Solomon Islands: (GP 1040781, 1061756-1061766)

New Caledonia: (ZMB 121075).

Fiji: (ZMB 4494); Viti (ZMB 121076, 121077).

***Supplanaxis obsoletus* (Menke, 1851) (new combination)**

Planaxis obsoletus Menke, 1851: 170.

Planaxis (Supplanaxis) obsoletus Menke, 1851 – Abbott 1974: 102.

Planaxis acutus Menke, 1851: 169f. [also a junior homonym of *Planaxis acuta* Krauss, 1848; type locality “Mazatlan region”]

Planaxis obscura A. Adams, 1853 [“1851”]: 271. [NHMUK 2014.0096; Fig. 17C; type locality unknown]

Planaxis obscurus A. Adams, 1851 (sic.) – Sowerby II 1878: Pl. I, spec. 5.

Type material. Whereabouts unknown.

Type locality. Mazatlán region, Mexico (Mencke, 1851).

Taxonomy. First described by Menke (1851) as *Planaxis obsoletus*. We here allocate this species to *Supplanaxis*, based on similarities in shell size, form and groove patterns, following the subgeneric position established by Abbott (1974).

The shell description of *Planaxis acutus* Menke, 1851, described from the “Mazatlan region”, clearly represent specimens of *S. obsoletus*, based on morphological similarity and geographic overlap. Of the two names (*P. acutus* and *P. obsoletus*) that Mencke (1851) described, *P. acutus* is the one occurring earlier in his text. However, *Planaxis acutus*

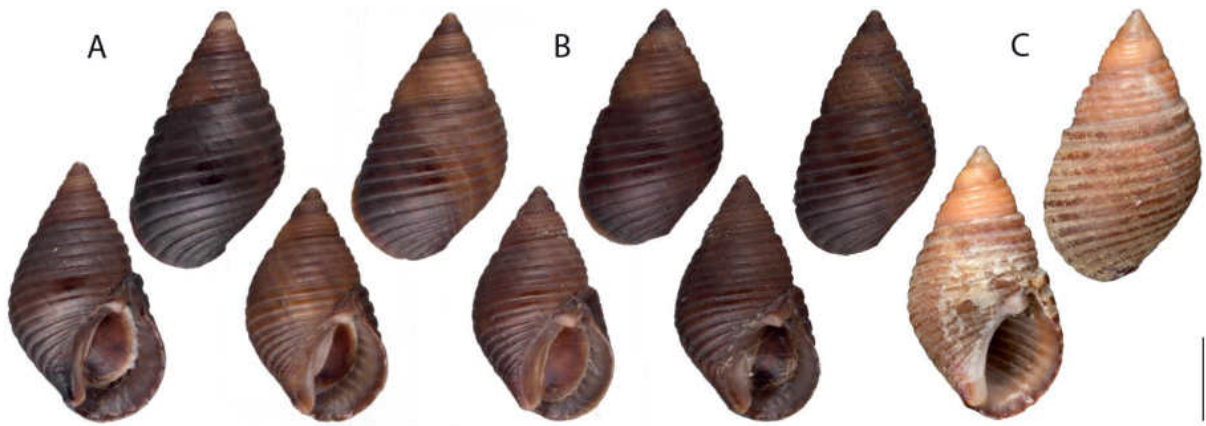


Figure 17. Shells of *Supplanaxis obsoletus* and type specimens of junior synonyms. **A** Mexico, Jalisco, Bahia de Cuastecomates (GP 1014114; 1014115). **B** Mexico, Jalisco, Melaque (GP 924660, 928879). **C** *Planaxis obscurus*, one of four syntypes (NHMUK 2014.0096). Scale bar = 5 mm. C © Image courtesy of Harry Taylor, NHMUK Photographic Unit.

Menke, 1851 represents a junior homonym of *Planaxis acuta* Krauss, 1848 and has therefore to be considered invalid, suggesting *P. obsoletus* as the proper taxon name.

Furthermore, we place *Planaxis obscura* A. Adams, 1853 [“1851”] (see Fig. 17D) as a junior synonym of *S. obsoletus*, as all shell features and dimensions are identical. The account of *Planaxis obscurus* given in Sowerby II (1878) appears to be erroneous: Even though the reference to “Adams, 1851” (Adams 1853) is correct, the species descriptions and depiction vary heavily, rather describing a specimen of *Planaxis sulcatus* (Born, 1780) than any *Supplanaxis* species. Hence, Sowerby II (1878) provided a miss-affiliation of this name.

Shell. (Fig. 17) Conical, 11.7–16.9 mm high, 5.6–9.3 mm wide, with 4.5–6.5 whorls. Entire shell covered by 8–17 deep spiral grooves. Mid to dark brown. Aperture 5.2–8.2 mm high and 2.9–4.9 mm wide, with 6–12 palatal grooves and one columellar tooth. The lip is slightly widened.

Radula. As all specimens examined of this species are dry stored shells no examination of the radula was possible.

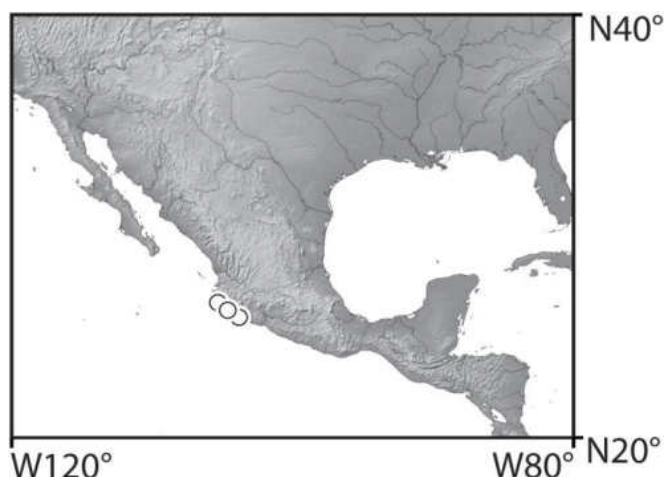


Figure 18. Occurrences of *Supplanaxis obsoletus* at the west coast of Mexico. Open circles represent dry stored shells.

Distribution. Based on available material it appears to be restricted to locations along the Pacific coast in Mexico (Fig. 18).

Material examined

Mexico: Jalisco, Bahía el Dorado, amongst small stones, near high tide line (GP 284359-284406, 283488, 283489, 283492, 283495, 283496, 283528-283531, 28349115); Jalisco, Bahía de Cuastecomates, found between and under rocks at low tide (GP 1014114-1014119); Jalisco, Melaque, low tide on and under rocks (GP 924654-924661, 928872, 928873, 928875-928883, 928885).

Supplanaxis planicostatus Sowerby I, 1825

Planaxis planicostatus Sowerby I, 1825: xiii.

Supplanaxis planicostatus (Sowerby) – Laidre & Vermej 2012: 177

Planaxis canaliculata Duval, 1840 in Porro 1840: 107 [type locality: “Iles Gallapagos”].

Planaxis circinatus Lesson, 1842: Rev. Zool.: 187 [two syntypes (MNHN-IM-2000-33882); type locality: Acapulco].

Type material. 9 syntypes (NHMUK 1966.623, coll. Cuming) (Fig. 19A).

Type locality. “Gallapagos Islands” (Sowerby I, 1825); a misspelling of the Galapagos Islands.

Taxonomy. This species was described by Sowerby I (1825). Sowerby II (1878) places *P. canaliculata* Duval, 1840, described from the Galapagos Islands and *P. circinatus* Lesson, 1842, two syntypes (MNHN-IM-2000-33882) described from Acapulco as junior synonyms, which is followed here, based on shell descriptions and distribution ranges of these species. Houbriek (1987) elevated *Supplanaxis* to generic rank and differentiated it from *Planaxis* having a radula with rachidial side denticles, whereas all known species of *Planaxis* exhibit an un-denticulated rachidial tooth. *Supplanaxis planicostatus* has also been briefly examined by Houbriek (1987) including the radula of Panamanian specimens, though without depicting it, and found no difference to *Planaxis sulcatus*. By contrast, we found all examined *S. planicostatus* specimens to possess rachidian teeth with two side denticles on each side (including specimens from Panama). Furthermore, in our molecular genetic study, two specimens from the same Panamanian population grouped next to Caribbean *S. nucleus* specimens, rather than with *P. sulcatus* (the type species of *Planaxis*; Fig 5). Laidre & Vermej (2012) already suggested the combination *Supplanaxis nucleus*, albeit without providing any details for this transfer, which we here support based on our findings. *Supplanaxis planicostatus* is differentiated from *S. obsoletus* by its larger size and wider distribution area. As juveniles of *Supplanaxis* species exhibit no columellar tooth and a sharp apertural lip, it can be ruled out that the *S. obsoletus* specimens in our study represent juveniles of *S. planicostatus*.

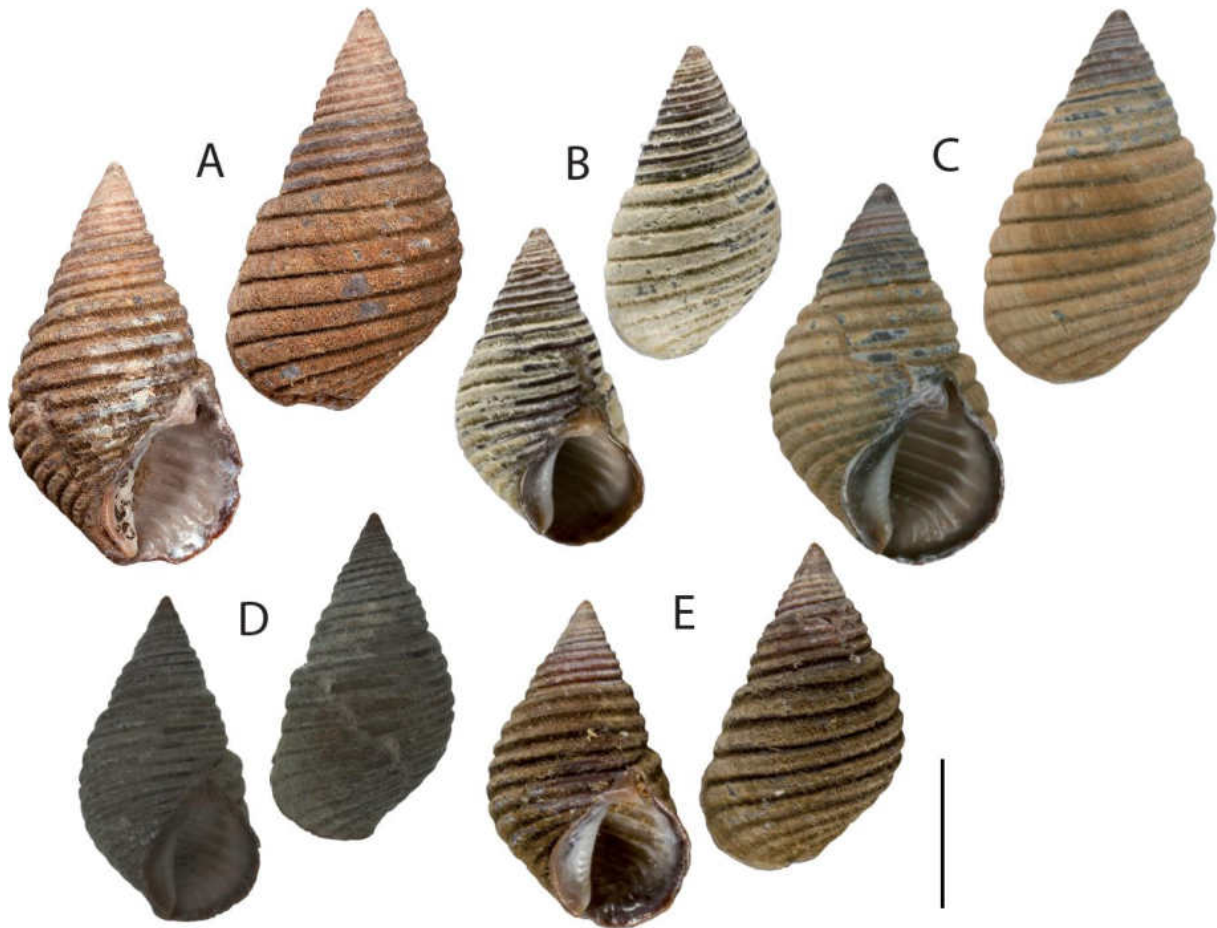


Figure 19. Shells of *Supplanaxis planicostatus* and type specimens of junior synonyms. **A** Syntype, Galapagos Islands (BNHM 1966623). **B** Costa Rica, Playa de Coco (AMS C.323001). **C** Panama, Paitilla (ZMB 108261). **D** Australia, Port Philipps [location doubtful, see text for more] (ZMH 41607). **E** *Planaxis circinatus*, Mexico, Acapulco, one of two syntypes (MNHN-IM-2000-33882). Scale bar = 10 mm. **A** © Image courtesy of Harry Taylor, NHMUK Photographic Unit. **E** © M. Caballer MNHN, project E-RECOLNAT: ANR-11-INBS-0004.

Shell. (Fig. 19) Pointed-conical. 14–27.3 mm high, 8.3–15 mm wide, largest *Supplanaxis* species, with unusually high spire. 4.5–7 whorls. 10–12 spiral grooves across all whorls. Yellowish-brown to dark-brown in colour. Aperture 7.2–12.8 mm high, 4–7.6 mm wide, with 7–10 palatal well pronounced grooves. Adults with one columellar tooth. Lip substantially widened, often porcelaneous greyish-white.

Radula. The radula (Fig. 20) length spans at least 380 rows. The rachidian of *S. planicostatus* has five (rarely six) denticles. The middle denticle is significantly larger than the other denticles, denticle tips are rounded. The processes at the rachidian base are long, slender and arced without being angulate. Inner lateral teeth have six to eight denticles, whereas outer lateral teeth show 22 to 26 denticles. The comb-like outer lateral tooth tips are undulated.

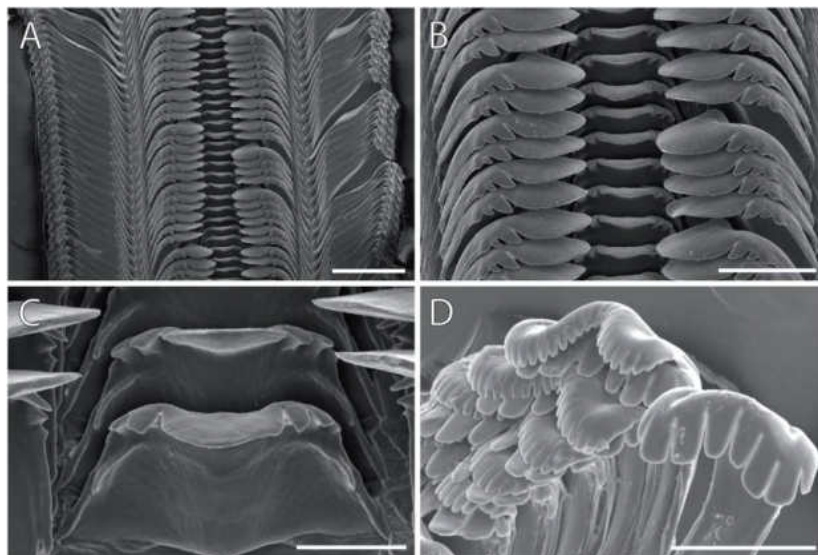


Figure 20. Radula of *Supplanaxis planicostatus*, Costa Rica, Playa de Coco (AMS C.323001). **A** Radula ribbon. Scale bar = 200 µm. **B** Lateral and central teeth. Scale bar = 100 µm. **C** Rachidian Scale bar = 50 µm. **D** Marginal teeth. Scale bar = 50 µm.

Distribution. While the examined material mainly originates from the Eastern Pacific Region (Galapagos, Cortez and Panamanian Province) (Fig. 21), we found one sample exceeding this range: In the collection of the Zoological Museum Hamburg one sample of *P. planicostatus* (ZMH 41607) is labelled to come from Port Philipps in Australia. Unfortunately, the lack of sampling date and collector does hamper any investigation of this

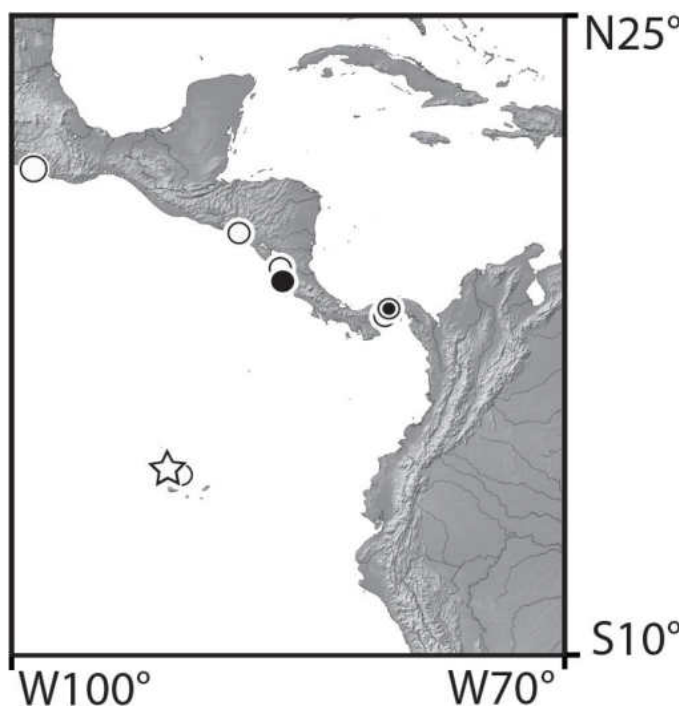


Figure 21. Occurrences of *Supplanaxis planicostatus* throughout the Eastern Pacific Region. Note that open dots represent dry shell samples whereas concentric dots represent samples stored in ethanol, filled dots represent ethanol stored specimens that yielded genetic sequences. The star marks the type locality.

unlikely location. As we doubt this species to occur this far in the south, for its main distribution is well within tropical areas, we therefore propose the location data to be erroneous.

Material examined.

Costa Rica: Playa de Coco, west of Liberia (10°39'N; 85°35'W) (AMS C.323001-w); Guanacaste (ZMB 117941-w) (NHMUK 2014.0860-w); Jesusita Island (GP 637497).

Panama: Paitilla, Bay of Panama, Pacific (ZMB 108261-w); Paitilla and Naos, Bay of Panama (ZMB 108282); Naos Island (USNM 742818); Taboga Island, on rocks at low tide, in exposed waters (GP 114260-114268, 183253, 183254, 194342, 261235, 268185-268189, 589162-589168, 674215-674225, 674450, 685455, 685456, 771803-771811, 771829, 771830).

Galapagos: (SMF 304767).

Incertae sedis

Planaxis albersii Dunker, 1853

Planaxis albersii Dunker, 1853: 16,
Tab. II fig. 35–37

Comment. In the collection of the Natural History Museum in Berlin we found three syntypes of this nominal species (ZMB 108675, Fig. 22A), described by Dunker (1853) from Luanda, Angola. However, we only know of three other specimens in the private collection of Guido Poppe from South Africa: Nataö

South Coast, found on rocks at low tide (GP 346676), and Natal, Park Rynie, on rocks (GP 136204, 136207). Based on these few specimens, we were unable to encompass this species in our analysis. Hence, this species stands for further examination in later studies.

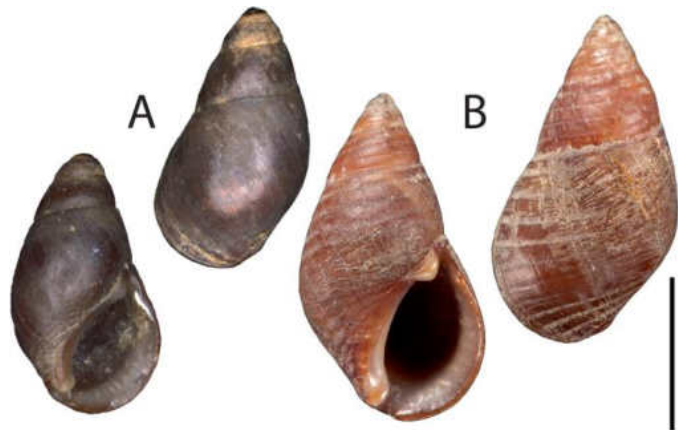


Figure 22. Incertae sedis taxa. **A** *Planaxis albersii*, one of three syntypes (ZMB 108675-2). **B** *Planaxis nigritella*, holotype (NHMUK 1855.4.5.20/1). Scale = 5 mm. **A** © provided by Christine Zorn, Malacological Collection, ZMB. **B** © Image courtesy of Harry Taylor, NHMUK Photographic Unit.

Planaxis nigritella Forbes, 1850

Planaxis nigritella Forbes, 1850:273, Pl. 11 fig. 6.

Comment. We found the Holotype (NHMUK 1855.4.5.20/1; see Fig. 22B) and 7 syntypes (NHMUK 1855.4.5.20/2-4;1851.2.19.20-23) of this species. Forbes (1850) lists “Straits of Juan del Fuaco”- certainly strait of Juan de Fuca in British Columbia - as type locality. *Planaxis nigritella* has been suggested as synonym of *Planaxis obsoletus* (Keen, 1971; Abbott 1974), though we find the morphology of the two to differ too significantly from each other. However, no other species of similar morphology are known from the West coast of America. The specimens were part of the material collected during the voyages of HMS Pandora and HMS Herald. The latter circumnavigated the globe during 1845 and 1851, also visiting the Caribbean (Seemann 1853). Forbes (1850: 270f) states that “unfortunately, the precise locality of many of the individual specimen had not been noted at the time”. However, he ensures the reader that “the new species are all from the American shores”. This does not specifically state whether these were all from the Pacific or Atlantic side. Hence, there is a slight chance that these specimens are originally collected in the Caribbean

and therefore would be potentially be samples of *S. nucleus*. The location originally provided, however, is so precise that without an investigation at the presumable type locality, we cannot clearly decide in this case.

The shell height of the holotype and the adult paratypes ranges between 9.4 and 11.6 mm, the shell width between 6.1 and 6.4 mm. Each shell exhibits about 13 spiral grooves. Therefore, the morphology of the holotype of *P. nigritella* lies in the spectrum known from *S. nucleus*. Hence, there is no clear morphological distinction between these two species.

Nomina dubia

***Planaxis incisus* Philippi, 1951**

Planaxis incisus Philippi, 1951: 92.

Comment: Type material missing. Philippi (1951) does not provide any description that is unambiguous, as both *S. nucelus* and *S. niger* (as understood in this study) fit his description. As Philippi (1951) does not provide a type locality and no type material could be identified, *P. incisus* must be seen as an invalid nomen dubium.

Discussion

Species differentiation

Based on our geometric morphometrics and shell biometry approach, we were able to recognize overall six *Supplanaxis* species, and two subspecies of one of these. Thereby, the geometric morphometrics analysis uncovered an overall high amount of shell shape variations within *Supplanaxis*. Four species were uncovered as significantly different from all other groups on at least one PC axis: *S. nucleus* (PC1), *S. abb. abbreviata* (PC1), *S. leyteensis* (PC2) and *S. planicostatus* (PC4). For these the strongest support based on shell shape was found. The other species are supported as well, as no species clustered with the exact same species on each of the four studied PCs. For instance *Supplanaxis niger* on PC1 formed a group with *S. abb. ogasawarana* and *P. sulcatus*, on PC2 with the two subspecies of *S. abbreviata*, on PC3 with *S. leyteensis* and on PC4 with *S. nucleus*, *S. abb. ogasawarana* and *S. obsoletus*. We have to assume an overall similarity in shell shape between *S. niger* and *S. abb. ogasawarana* (as they form a group on PC 1, 2, 4), though a significant difference on PC3 underlines further

differences. However, other characters of shell biometry, viz. number of spiral grooves and palatal grooves, clearly differentiate the two species. As in case of *S. niger*, we can find such a differentiation for each of the seven taxa recognized in this study.

In the resulting molecular phylogeny, two populations of *S. nucleus* and one of *S. planicostatus* were unresolved as a polytomous group. However, this molecular similarity is not suitable to imply that these specimens are from the same species, as all morphological characters, such as shell size, spiral groove patterns and palatal grooves distinctly differ between the two species. However, it might be possible that this result points in the same direction as suggested in a study by Strong & Bouchet (2020), though our limited dataset is not exhaustive enough to account for this topic. A common ancestry of Caribbean *Supplanaxis* and *S. planicostatus* is likely, due to their close geographic distribution and relatedness in the phylogeny.

In addition to shell shape, spiral grooves, palatal grooves, and shell biometry gravely informed our taxonomic decisions, allowing for a clear distinction of morphotypes resembling the six distinguished species. Especially spiral and palatal groove patterns allowed for the distinction of Pacific *Supplanaxis* species. Radula morphologies studied for four of the six *Supplanaxis* species, were non-informative for species differentiation in this genus, as tooth formulae heavily overlapped and general shape and size appeared to be indifferent (see Tab. 4).

The relationship of Planaxis and Supplanaxis

Contrasting Houbriek's (1987) statement that the rachidian teeth of *P. sulcatus* and *S. planicostatus* are both undenticulated, we found the radula of *S. planicostatus* to feature the characters proposed for the distinction of *Supplanaxis* from *Planaxis*. All examined specimens of *S. planicostatus* had a distinctly denticulated rachidial tooth which, according to Houbriek (1987), *Planaxis* species should not possess. Even specimens collected in the same area as those on which Houbriek's (1987) study was based on showed this denticulation. Furthermore, our molecular genetic study of three *Supplanaxis* species and *P. sulcatus* grouped *S. planicostatus* into a polytomy with *S. nucleus* and this clade as sister to *S. abb. ogasawarana* (Fig. 5). Hence, besides the morphological support for the positioning of *S. planicostatus* in *Supplanaxis* there are genetic implications strengthening the argument.

This positioning questions the distinction of *Planaxis* and *Supplanaxis* as separate genera, as the generic border drawn by Houbriek (1987) might be more fluid than previously assumed. For a brief insight into this matter we included *P. sulcatus*, the type species of *Planaxis*, in the geometric morphometrics study, which indicates similarities in shell shape between this species

and most *Supplanaxis* species. The previously proposed close relatedness of *Supplanaxis* and *Planaxis* (Houbrick, 1987) is here confirmed: Based on PC1 and PC2 the shell shape of *P. sulcatus* is very similar to that of several other *Supplanaxis* species (see Fig. 4A). This close relationship is inherently suggested, as upon its original description *Supplanaxis* has been a subgenus of *Planaxis* (Thiele, 1929). However, the elevation of *Supplanaxis* to generic rank was based on features of the rachidial tooth, and thus a resemblance of shell characters and shape was to be expected for this genus pair.

To clearly resolve this matter a more comprehensive molecular genetic study of all planaxid genera and all *Planaxis* and *Supplanaxis* species should be conducted as soon as more suitable material becomes available. For the time being the differentiation based on radular characters is the most reliable method, as has been shown in this study. However, even then a differentiation of two genera is, as always, arbitrary rather than dictated based on genetic clustering, revealing them as being closely related within the Planaxidae.

Molecular phylogeny

For our study we, first, had only a limited amount of ethanol stored specimens from which, second, DNA could be extracted successfully only from very few specimens. As we based our study almost entirely on museum material, several of the studied specimens were found unsuited for genetic studies, as the material was either too old or was stored unsuitable for such an approach. Thus, in total we retrieved sequences of eleven specimens (out of a total of 60 specimens used for the genetic study), limited to only three *Supplanaxis* species which further diminished the explanatory value of this approach. However, we were able to clearly allocate *S. planicostatus* to *Supplanaxis* and support *S. abb. ogasawarana* based on this approach (Fig. 5).

To fully understand the diversity in this taxon, a more comprehensive molecular genetic study should be conducted as soon as fresh material of all relevant nominal species becomes available. This particularly would help resolving our critical evaluation of *Planaxis nancyae*, the question if *S. abb. abbreviata* and *S. abb. ogasawarana* represent species or subspecies (the latter was here proposed for lack of unambiguous support of the alternative hypothesis) and the relation of *Supplanaxis abbreviata* and *Supplanaxis niger*, as prior studies suggested the synonymy of the latter species pair (Chen *et al.*, 2018). Furthermore, a future study should give special emphasis on the African nominal species *P. albersii* and the identity of *P. nigrifella*, which both were unresolved in the study at hand due to a lack of unavailable material.

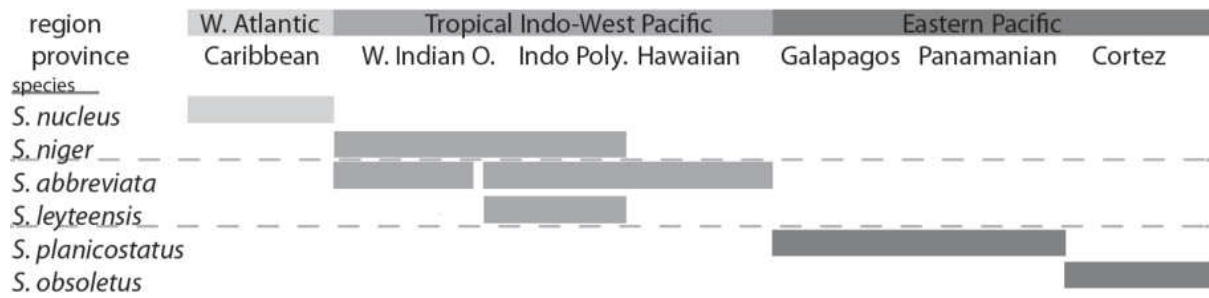


Figure 23. Summary of the geographic ranges of *Supplanaxis* species. Biogeographic regionalisation following Briggs & Bowen (2012). The bars indicate the occurrence of each species within a marine province. Grey shades imply occurrences in marine regions. Note the two separate bars for *S. abbreviata*, with the left one representing *S. abb. ogasawarana* and the right one *S. abb. abbreviata*.

Biogeographic patterns and implications

The *Supplanaxis* species under study here exhibit a clear biogeographical pattern. Excluding only the two unresolved nominal species (see under Incertae sedis) all congeneric species occur within three marine biogeographic regions (for comparison of marine region and provinces see Briggs & Bowen, 2012): West Atlantic (one species), Tropical Indo-West Pacific (three species) and Eastern Pacific region (two species), which are distributed throughout seven marine provinces (Fig. 23). More speciose are the western Indian Ocean (two species) and the Indo-Polynesian province (three species), while in all other provinces only a single species is present.

This biogeographic pattern is very conspicuous, as it is in accordance with general patterns of biodiversity spanning across multiple taxa (Tittensor *et al.*, 2010). These patterns have been found to be different for gastropod assemblages in rocky shores in general, to which the *Supplanaxis* species belong as well (Miloslavich *et al.*, 2013): here the Mediterranean and the Gulf of Alaska were identified as the most speciose areas. However, the study by Miloslavich *et al.* (2013) did not encompass any tropical Pacific sites. Another study of latitudinal species richness gradients for rocky shore gastropods underlines the canonical pattern of species richness being highest within the tropics (Rivadeneira *et al.*, 2015). A worldwide study of species of the marine gastropod *Echinolittorina* Habe, 1956 clearly uncovered the Indo-Polynesian province as unambiguous center of species richness (Williams & Reid, 2004), hence, the pattern we found in *Supplanaxis* falls perfectly in line with other studies of marine biodiversity patterns.

Taxonomic redundancy

In this study we examined overall 22 nominal taxa allocable to *Supplanaxis*. Of these our revision supported six species with two subspecies. Furthermore, we identified two nominal species (*P. albersii* and *P. nigritella*) where available material was too sparse to give a proper diagnosis. With these results we find a taxonomic redundancy of 65% or synonymy ratio of 1:3 within this genus, meaning that only every third nominal taxon can be considered to represent a valid species. A similar higher rate in the order of two third redundant names was found for several freshwater gastropods, as discussed in Glaubrecht (2009; see also Glaubrecht *et al.* 2009). Accordingly, these rates in limnic and marine Cerithioidea are apparently far higher compared to the generally proposed rate of 38% of names being redundant for molluscs (see Glaubrecht, 2009). Bouchet (1997) suggested an overall synonymy ratio of 1:6 within molluscs in general, based on a subsample of his comprehensive data, which by comparison is also twice as high as that found here for *Supplanaxis*, rendering our findings to lie well within the recently proposed ratio of taxonomic redundancy in molluscs.

With that our findings on *Supplanaxis* underline the need of modern evolutionary systematics studies as necessities to identify true biodiversity rather than merely projecting taxonomic redundancy.

Conclusions

We evaluated 22 nominal taxa recognisable as *Supplanaxis* species. Of these our evolutionary systematics approach combining geometric morphometrics, biometry and characters of the shell as well as radular morphology with an (albeit limited) molecular genetics approach identified six species containing two subspecies. Hence, we uncovered a synonymy ratio of 1:3 for this genus. Furthermore, it allowed for the transfer of one species to this genus. The distribution of these species underlines general patterns of global species diversity, with the Indo-West Pacific as centre of species richness.

However, due to a lack of available material we were unable to assess the status of one African nominal taxon, as well as covering only three species with our molecular approach. Lastly our results imply a close relationship between *Supplanaxis* and *Planaxis* that needs to be studied further in context of a revision of additional planaxid species and genera.

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For all supplemental materials referenced in this chapter refer to Appendix V

Chapter 8 General Discussion

Benedikt Wiggering

Evolutionary systematics of Thiaridae and Planaxidae

Overall, the studies included within the chapters of this thesis heavily emphasize the need of an evolutionary systematics approach; see e.g. Glaubrecht (2007, 2010) for progressive studies on biodiversity and its evolution. Chapters 3, 4, and 7 exemplify how the integration of different methods enable a more nuanced systematic view. In these chapters, different genera and species of the Cerithioidea Fleming, 1822 snail families Thiaridae Gill, 1871 (1823) and Planaxidae Gray, 1850 have been examined by combining morphological and molecular genetic studies to gain more advanced insights on their systematics and the evolution of these lineages. In all cases, a clear distinction was only enabled by the combination of these different methods. However, Chapters 3, 4 and 6 furthermore include specific topics — viz. diversity of reproductive modes, life-stage dependent dispersal and poecilogony — that are solved or at least further clarified. In Chapter 6 the question if *Planaxis sulcatus* (Born, 1778) represents a case of poecilogony, was the driving force to study the intraspecific variance of the species (Chapter 6), and also triggering the study of its sister clade *Supplanaxis* Thiele, 1929 (Chapter 7). Chapters 2, 3 and 4 include a molecular genetic approach towards the systematics of the Thiaridae and the first family-wide molecular genetic study including specimens representing all genera of this family. However, only through the examination of brood pouch content and biogeographic assessment (in Chapters 3 and 4) more precise delimitation of taxa is enabled. By contrast, Chapter 2 illustrates the potential fallacies provided if only a singular methodological approach is conducted, through even by this single method approach the understanding of the numerous factors driving diversification in this group is furthered, mainly through an ancestral area estimation, providing biogeographic context for the family's origin. On a side note, in Chapter 5 a junior homonym of a thiarid species is stabilized.

Family-wide systematics of Thiaridae

All currently available studies on the phylogenetic relationships within the freshwater Thiaridae concentrate on very few species and genera (Facon et al., 2003; Genner et al., 2007; Miura et al., 2008; Hidaka & Kano, 2014; Van Bocxlaer et al., 2015; Veeravechskij et al., 2018b; Boonmekam et al. 2019; Wiggering et al., 2019 (Chapter 3); Lentge-Maaß et al., in press.). In Chapter 2 the first molecular genetic analysis encompassing a family-wide sampling of representative specimens of all twelve currently recognised (see Glaubrecht & Neiber, 2019) genera was conducted. The study is based on the mitochondrial cytochrome c oxidase subunit I (COI) and 16 S rRNA (16S) gene fragments (see Figure 1 for a reproduction of this phylogeny) and for a smaller subset the nuclear gene fragments 28S and H3. In both phylogenies, several

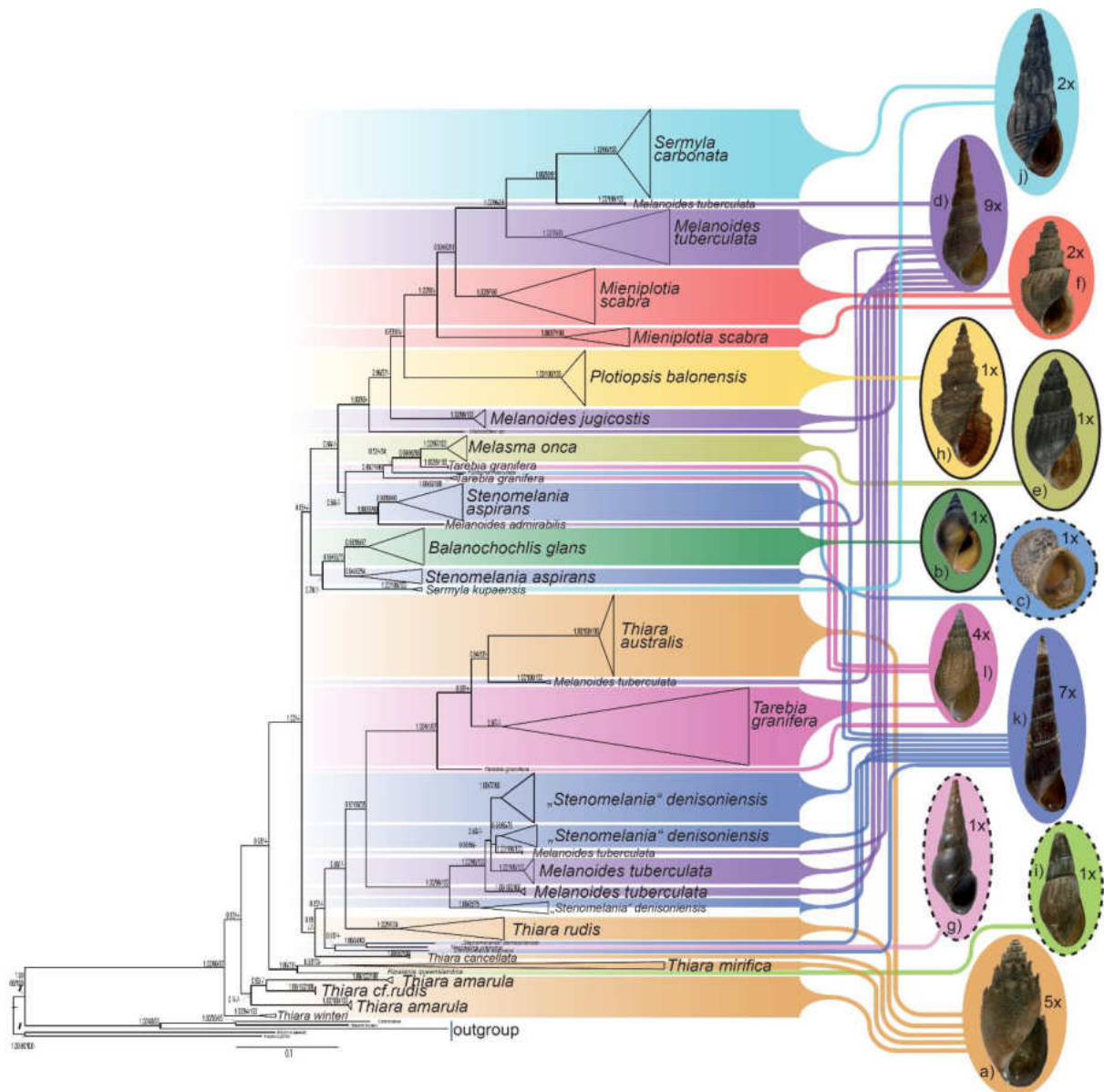


Figure 2. Bayesian 50% majority consensus tree based on concatenated COI and 16S sequences. Numbers at the nodes refer to posterior probability (PP) values (left) from the Bayesian (BI) and bootstrap support (BS) values from the maximum parsimony (MP) analysis (middle) and from the maximum likelihood (ML) analysis (right). Only nodes with PP values ≥ 0.50 and/or BS values from ML and/or MP analyses $\geq 50\%$ are annotated. Line Leading to shells imply genus affiliation. Shells are specimens representative for the type species of each genus. The number in each circle corresponds to the number of independent occurrences of specimens from the genus within the phylogeny. **a)** *Thiara amarula*, (ZMB 107364-3); **b)** *Balanochochlis glans* (ZMB 106468-3); **c)** *Fijidoma maculata*, (ZMB 106379-sk9); **d)** *Melanoides tuberculata* (ZMB 127444-4); **e)** *Melasma onca* (ZMB 106673a); **f)** *Mieniplotia scabra* (ZMB 191037a); **g)** *Neoradina prasongi* (ZMB 127590-2); **h)** *Plotiopsis balonnensis* (ZMB 106689a-1); **i)** *Ripalania queenslandica* (ZMB 106355-1); **j)** *Sermyla carbonata* (ZMB 106713-2); **k)** *Stenomelania aspirans* (ZMB 106390-1); **l)** *Tarebia granifera* (ZMB 107442-2). For further details see Chapter 2 Figures 1 & 2.

morphologically distinguished lineages have been recovered multiple times independently. For overall six genera this problem has been encountered, in both the phylogeny based only on COI

and 16S as well as the concatenated nuclear and mt-DNA based phylogeny. A similar problem occurred within the molecular phylogenies presented in Chapters 3 and 4, where in both studies, based on COI and 16S sequences, the basal node of the ingroup has been only resolved as a polytomy.

The phylogenies in Chapter 2 (though this effect may also be present in those of Chapters 3 and 4) may represent an example of the potential “stumbling rocks” of inferring higher taxonomic relationships from only a small portion of the genome. It is well-known that an estimation of a group phylogeny based on few genetic markers may be misleading and has been discussed rigorously, including the potential mechanisms underlying this phenomenon (Pamilo & Nei, 1988; Funk & Omland, 2003; Edwards, 2009; Carstens et al., 2013).

For freshwater gastropods, the incongruence of morphology-based taxonomy with molecular genetic phylogenies is an established problem with numerous factors driving this phenomenon, having been discussed including insufficient phylogenetic resolution of selected markers, introgression, mode of mitochondrial inheritance, indirect selection of the mitochondrial genome, ancestral polymorphisms, karyotypic variation, incorrect identification, taxonomic over-splitting, the presence of cryptic species, isolation in separate drainage systems and lastly potential endosymbiont infection (see e.g. Lee et al., 2007; Köhler & Deen, 2010; Miura et al., 2013, 2018, 2020; Reid et al., 2013; von Rintelen et al., 2014; Whelan & Strong, 2015; Köhler, 2016, 2017). It is very likely, that within the exhaustive dataset presented in Chapter 2, multiple of these factors might drive the rampant taxonomic incongruencies observed. However, the abovementioned factors can only be studied further by including multi-locus molecular genetic approaches or additional methodological approaches. Pointing at any of these factors would be highly speculative and is consequently refrained from within this study. Therefore, to provide a better understanding of the molecular systematics of Thiaridae, a more comprehensive genetic approach including genomic methods such as AFLP (Vos et al., 1995; as exemplified for Thiaridae by Lentge-Maaß et al., in press) or ddRADSeq (Peterson et al., 2012) should be conducted.

Biogeographic origin of Thiaridae

Even though the results of intrafamilial relationships of the Thiaridae provided in Chapter 2 must be considered with caution, the ancestral range estimation of thiarids provided in this study enable new insights on their biogeographic origin. Strong et al. (2011) and Glaubrecht et al. (in prep) found strong support for a cerithioidean clade composed of Paludomidae, Hemisinidae and Thiaridae. Here, Hemisinidae were positioned as sister of the Thiaridae, a notion also

recovered in the phylogenies provided in Chapter 2. The oldest fossils of this three-family clade date back to Cretaceous fossils from New Zealand and Australian deposits (Hamilton-Bruce et al., 2004; Beu et al., 2014). This strengthens a Gondwana origin of this clade, as Glaubrecht (1996) and Glaubrecht et al. (in prep.) also discuss. The split of Paludomidae from Hemisinidae and Thiaridae might have been triggered during the Cretaceous by the dislocation of the Indian and African subcontinent (Acharya, 2000). During the late Cretaceous Australia was separated from Antarctica, possibly initiating the split of Thiaridae and Hemisinidae (at 73.5 Ma according to the analysis in Chapter 2). As the reconstruction within Chapter 2 did recover specimens from Africa and the Indian subcontinent deeply nested within the phylogeny, this theory is further strengthened, though the alternative — the origin of the Thiaridae being Africa or the Indian subcontinent — cannot be ruled out entirely.

The onset of diversification of Thiaridae dated with c. 32 Ma within the Oligocene, coinciding with the approach of Australia to Asia. As discussed below, the dispersal of veliger larvae through ocean currents is assumed as the ancestral mode of reproduction within the Thiaridae (Seshaiya, 1940; Glaubrecht, 1996; Hidaka & Kano, 2014; as well as Chapter 4 and below). This unique dispersal method, together with the complex geological history of this region with its moving terranes and emerging and subsiding islands may have enabled the thiarid colonialization of the Indo-Australian region. Combined with possibly repeated evolutions of developmental modes in Thiaridae, a diverse interplay of plate tectonics and dispersal of individual taxa is certainly a manifold subject worthwhile for further research. However, the results presented in Chapter 2 clearly illustrate the key role the Indo-Australian region played for the diversification within the Thiaridae, though the taxonomic entanglement of many of its species complexes were not resolved in this study.

Insights in the Stenomelania-Melanoides complex

Within the family-wide thiarid phylogeny presented in Chapter 2 *Stenomelania* Fischer, 1885 and *Melanoides* Olivier, 1804 were represented each by several independent lineages. As mentioned above the reasons for these findings may be manifold. However, to assess the biodiversity found within the *Stenomelania-Melanoides* complex, two additional studies, one on *Neoradina* Brandt, 1974 (Chapter 3) and another on *Stenomelania* (Chapter 4), have been conducted.

Neoradina was introduced by Brandt (1974) as a new genus to encompass all species but the type species previously subsumed in *Radina* Preston, 1915. Brandt saw this as necessary consequence of as the type species *Melania hastula* Lea & Lea, 1851, was synonymised with

Stenomelania plicaria (Born, 1778), synonymising *Radina* with *Stenomelania* (see Schepman, 1918; Rensch, 1934). As type species of *Neoradina*, a new species — *Neoradina prasongi* Brandt, 1974 — from Thailand was described. As based on simple impression of the shell morphology, this species appears near indistinguishable from other *Melanoides* and *Stenomelania* species, the introduction of this lineage was far from unambiguous.

In Chapter 3, a study of molecular genetics based on the COI and 16S gene fragments, geometric morphometrics of the shell, radula morphology and brood pouch content has been conducted on *N. prasongi* from Thailand and syntopically occurring *Stenomelania* and *Melanoides* species. The molecular genetics approach also includes a fragment of the 16S gene extracted from material originally collected by the original author (Brandt, 1974), strengthening the molecular approach of the study. Both geometric morphometrics and molecular genetics uncovered *N. prasongi* as separate lineage, distinct from all other examined species within the *Stenomelania-Melanoides* complex.

In his account on the developmental modes of *Neoradina*, Brandt (1974) only provides an ambiguous description of the brood pouch content, stating on the one hand that *Neoradina* “differs from *Stenomelania* by being oviparous and having a brood pouch” (p. 169) and on the other hand, that *N. prasongi* has “females with subhaemocoelic brood-pouch with many small embryonic shells in all stages of development” (p. 170). *Stenomelania* females, however, are known to possess a subhaemocoelic brood pouch and all *Stenomelania* species studied so far reproduce viviparously (see Chapters 3 and 4). Hence, Brandt’s (1974) account must be considered doubtful towards the developmental mode displayed in *Neoradina*. As *N. prasongi* specimens in both studies (that is Chapters 3 and 4) clustered with “*Stenomelania*” *denisoniensis*, “k-strategy” brooding in *N. prasongi* seems likely. However, as support values for higher nodes were expectedly low, it cannot be clearly resolved, if *Neoradina* constitutes a synonym of *Melanoides*. Given that the recently collected samples and the few available specimens originally sampled by Brandt and stored in Ethanol did not contain any gravid females, it is likely that breeding in this species is seasonal. With that it would be distinctly different to *Melanoides*, from which at least its type species *Melanoides tuberculata* (Müller, 1774) is reported to breed throughout the year (Dudgeon, 1986). Lastly, the study of radula morphology within the *Melanoides-Stenomelania* complex revealed, that no diagnostic characters could be found separating species or genera. This reflects the canon on the matter, as previous studies revealed that within the Thiaridae only very small differences exist between genera as well as species radula morphology (see also Bandel et al., 1997; Dechruksa et al.,

2013; Glaubrecht, 1996; Glaubrecht et al., 2009). Hence, in the second study (Chapter 4) the study of radula morphology was omitted.

By contrast to *Neoradina*, *Stenomelania* had been established as a subgenus of *Melania* Lamarck, 1799 (see Fischer, 1885). Later it was positioned as subgenus of *Melanoides* (see eg. Pace, 1973; Rensch, 1934; Starmühlner, 1976, 1984, 1993). It has first been used a genus level by Houbrick (1987), albeit without a detailed taxonomic assessment. Though the subsequent studies of Glaubrecht (1996), Bandel et al. (1997) and Glaubrecht et al. (2009) place *Stenomelania* at generic rank, in each publication, the need of a taxonomic assessment of the genus is emphasised.

In Chapter 4 such a systematic study, including overall six species currently subsumed under *Stenomelania* as well as *M. tuberculata* and *N. prasongi*, has been conducted. Through the study of molecular genetics based on 16S and COI sequences combined with a geometric morphometrics approach examining shell morphologies, and a study about developmental mode via brood pouch content examination, *Stenomelania* and its type species *S. aspirans* have been taxonomically revised, including a formal characterisation of the genus. As in the two afore mentioned studies (Chapters 2 and 3), support for the basal nodes within the molecular phylogeny provided in chapter 4 was low. Hence, the molecular genetics approach was not able to unambiguously support any predetermined genus. However, the study of shell shapes via geometric morphometrics and developmental mode clearly separated *M. tuberculata*, *N. prasongi* and "*S.*" *denisoniensis* from all other studied *Stenomelania* species. Therefore, *Stenomelania* was formally revised to be a genus of high spired, relatively large freshwater thiarid genus, with an "r-strategy" brooding mode. Based on the studies of Seshaiya (1940), Okazaki & Wada (2007) and Hidaka & Kano (2014) it has been established, that *Stenomelania* species are amphidromous. Therefore, adult *Stenomelania* species populate upper reaches of tailwaters of Indo-West Pacific streams and rivers, releasing their larvae downstream into ocean currents. After a planktonic phase in the marine realm, the juveniles return into freshwater habitats, where this cycle is started anew. This mode of dispersal is explanatory for the wide distribution ranges of all *Stenomelania* species presented in chapter 4. Davis and Ponder (2019) sketched out the details of this amphidromous life cycle for Neritidae gastropods, providing important implications already established by (Glaubrecht 1996) and Glaubrecht et al. (2009). The latter authors preliminarily assigned a very large, high spired thiarid snail group, found in North-Eastern Queensland, Australia, to *Stenomelania* cf. *aspirans*. Within the phylogenetic reconstruction of *Stenomelania* species (Chapter 4) this taxon clustered deeply nested within

S. aspirans. Hence, the assumption of Glaubrecht et al (2009), that *S. aspirans* is reaching into Australia can be supported.

Glaubrecht et al. (2009) already noted, that Australian “*S.*” *denisoniensis* constitutes a “k-strategy” brooder and suggested a new generic affiliation. The results presented in Chapter 3 and 4 both underline this finding. However, as a clear affiliation with *Melanoides* was not supported, the species cannot be transferred to this genus. In both phylogenies, “*S.*” *denisoniensis* specimens form a clade with *N. prasongi* specimens. Due to the missing information of developmental mode of *Neoradina*, however, it would be premature to position “*S.*” *denisoniensis* as part of *Neoradina*. Due to these ambiguities, a formal revision of “*S.*” *denisoniensis* was not conducted, though in both chapters (3 and 4), the species is excluded from *Stenomelania* sensu stricto (s. str.).

The two studies (Chapters 3 and 4) on the *Stenomelania-Melanoides* complex provided in this thesis can only be seen as a first detailed foray into the intricate evolutionary model this taxonomic complex represents. Especially the clade of African *Melanoides* species, so far seen as another polytomous lineage (see Genner et al. 2007), calls for an in-depth evaluation, as does the plethora of available nominal taxa recognisable as potential *Stenomelania* species. As most of these names are a consequence of 19th century over-splitting, most of these nominal taxa certainly constitute junior synonyms of other species. However, as they mostly are accompanied by valid taxonomic descriptions, these potential species may not be neglected in future studies.

Gonochory vs parthenogenesis in Thiaridae and Planaxidae

Morrison (1954) proclaimed that the Thiaridae are obligatory parthenogenetic. By contrast a plethora of studies on the reproductive biology of *Melanoides tuberculata* is available, most outlining the species as facultatively parthenogenetic (Jacob, 1957, 1958; Livshits & Fishelson, 1983; Livshits et al., 1984; Heller & Farstay, 1989; Hodgeson & Heller, 1990; Ben-Ami & Heller, 2005; Genner et al 2007; Dagan et al., 2017). Furthermore, other Thiaridae species have been reported to contain males. In *Tarebia granifera* (Lamarck, 1816) Jacob (1959), Brandt (1974) and Chanotis et al. (1980) reported sterile males. Riech (1937), Pace (1973) and Muley (1977) reported males in *Mienplotia scabra* (Müller, 1774), Starmühlner (1976) and Healy & Glaubrecht (2018) in *Thiara amarula* (Linné, 1758) and Jacob (1959) and Seshaiya (1936) for *Stenomelania crenulata* (Deshayes, 1838).

In Chapter 3 and 4 studies on brood pouch content of five *Stenomelania* species as well as *Melanoides* have been conducted. The frequency of gravid females in all *Stenomelania* s. str. stayed always at or below 50% (see Table 1), whereas the frequency of gravid females in

“*S.*” *denisoniensis* and *M. tuberculata* were 64% and 65% respectively. These frequencies across populations need to be estimated very modestly, as effects of seasonality and sampling bias might skew the given perspective. However, combining these findings with the report of males in *S. crenulata* (Seshayia, 1936; Jacobs, 1959), implies a gonochoristic or at least facultative parthenogenetic mode of reproduction. As only few accounts studying the reproductive modes of Thiaridae species directly exist, it is obvious that further studies on the matter are needed.

Besides these more restricted approaches of studying the reproductive modes of singular Thiaridae species, only few comprehensive accounts on the reproductive biology of Thiaridae exist (Glaubrecht 1996, Glaubrecht 2006, Glaubrecht et al., 2009). In Chapter 2, an ancestral state reconstruction, based on literature records of reproductive modes within thiarid genera and the provided molecular phylogeny of all Thiarid genera, has been conducted. Based on its results, the study showed, that “r-strategy” brooding represents the ancestral mode of reproduction within Thiaridae. The same has been found for *P. sulcatus* within Chapter 6. As oviparity is the presumed ancestral mode of reproduction in Certithioidea (Glaubrecht, 1996, Strong et al., 2011), a stepwise evolution from one mode to the others, seems to be the most parsimonious assumption. The reconstruction of reproductive modes in Chapter 2 furthermore implies that “k-Strategy brooding might have evolved twice within the Thiaridae,

Table 1 Results of brood pouch content analysis assembled from the data provided in Chapters 3, 4 and 6. The size classes distinguished are a, eggs/embryos/veligers in early ontogenetic stages; b, late embryos/veligers; c, juveniles < 0.5 mm; d, juveniles 0.6–1 mm; e, juveniles 1.1–1.5 mm; f, juveniles 1.6–2 mm; g, juveniles 2.1–2.5 mm; h, juveniles 2.6–3 mm; i, juveniles > 3 mm. No data is available on brood pouch contents of *Neoradina prasongi*. Results on *Planaxis sulcatus* were differentiated according to biogeographic region (IP = Indo-Polynesian, RS = Red Sea, WIO = Western Indian Ocean; see Bowen et al 2016).

Species	Average number of offspring	Lowest number of offspring	Highest number of offspring	Size classes	Number of examined specimens	Number of gravid females	Percentage of gravid females
<i>Planaxis sulcatus</i> IP	1958	30	4900	a, b	217	15	7%
<i>Planaxis sulcatus</i> WIO	620	26	6980	a, b, c, d	88	36	41%
<i>Planaxis sulcatus</i> RS	764	1	5160	a, b, c, d, e	59	13	22%
<i>Stenomelania aspirans</i>	5981	940	14423	a, b	52	10	19%
<i>Stenomelania crenulata</i>	656	550	830	b	6	3	50%
<i>Stenomelania plicaria</i>	6746	598	10200	a	19	5	26%
<i>Stenomelania punctata</i>	1009	340	2400	a	32	7	22%
<i>Stenomelania torulosa</i>	1170	232	2874	a	16	7	44%
" <i>Stenomelania</i> " <i>denisoniensis</i>	30	1	300	a-i	89	57	64%
<i>Neoradina prasongi</i>	n/a	n/a	n/a	n/a	15	0	
<i>Melanoides tuberculata</i>	44	4	193	a-i	37	24	65%

though it is likely that this is a consequence of the poor support for the *Stenomelania* lineage. However, it is very remarkable, that in the phylogeny presented in Chapter 2 the reproductive modes clustered overall rather unambiguously.

For the Planaxidae Morrison (1954) stated the same as for the Thiaridae – a family-wide obligatory parthenogenesis. Based on the observation, that Iranian specimens of *P. sulcatus* showed a very high frequency of gravid females, Thorson (1940) assumed the specimens from the region to have evolved a parthenogenetic reproduction, arguing also, that otherwise a fertilisation of eggs within is uterus would be hard to explain as cerithioidean snails do not possess a penis (see discussion in Glaubrecht, 1996). Gonochoristic species within this taxon use spermatophores for fertilisation. Albeit, Thorson (1940) argues that the frequency of gravid females as well as the lack of a penis and spermatophores imply parthenogenesis in western Indian populations of *P. sulcatus*. However, Houbrick (1987) conducted a detailed survey of specimens from all Planaxidae genera reporting males in New Caledonian populations. Furthermore, Zehra & Perveen, (1988) and Ahmed & Siddiqui (1997) reported only males for a year-long survey within a Pakistan population.

The brood pouch data content reported upon in Chapter 6 is not and cannot be entirely conclusive on the matter, as it is only an implication of the reproduction. Albeit, across all studied populations the frequency of gravid females never surpassed 41% in *P. sulcatus* (see Table 1). It must be noted, though, that within the Western Indian Ocean two Saudi-Arabian and two Yemenite populations showed heightened frequencies of gravid females. In all four populations 5-6 specimens were studied and between 80-100% of these were gravid female. In species with obligatory parthenogenesis no males should occur and in those with facultative parthenogenesis usually a lowered frequency of males is observed (Philipps, 1903; Suomalainen, 1950; Mittwoch, 1987). Hence, the data within this study point towards traditional gonochoristic reproduction within *P. sulcatus* though a shift towards parthenogenesis might be implied in western populations. For the time being, the question of the reproductive mode of *P. sulcatus* is not entirely solvable, however, a correlation of developmental and reproductive mode might be very possible within this species. Further studies on the matter (as here presented in Chapter 6, see also subsequent discussion) might allow for insights on the modes sexual evolution in cerithioidean snails.

Poecilogony in Planaxis sulcatus

Planaxis sulcatus is remarkable among all cerithioidean snails, as it exhibits an outstanding deviation in developmental modes, differing between populations of this species. Risbec (1936) identified a New-Caledonian population as “r-strategy” brooders, releasing its offspring as veliger larvae. The same finding was later reported from Northeast Australia (Houbrick, 1987), Thailand, and Japan (Ohgaki, 1997). Contrarily, Thorson (1940) identified the species as “k-strategy” brooders, releasing their offspring in low numbers as shelled juveniles, based on a population from the Persian Gulf. His findings were later supported by studies on populations from Pakistan (Barkati & Ahmed, 1982; Ahmed & Siddiqui, 1997). Thorson (1940) already noted the differences apparent through his and Risbec’s (1936) work, assuming, that the different environmental conditions of the Indo-West pacific and the Western Indian Ocean triggered this shift accompanied by a change towards a parthenogenetic reproduction. Tardent (1979) used *P. sulcatus* as textbook example for poecilogony. In contrast, Bouchet (1989) advertised the idea that the populations of *P. sulcatus* have to be seen as two cryptic species that have so far only been recognised by their differing reproductive mode. However, due to lack of a study examining reproductive modes throughout the whole distribution area of the species, and the lack of a molecular genetic study, the subject was not resolved any further.

In Chapter 6 the results of the first study of molecular genetics and developmental modes across the species entire distribution range are presented. Three distinct genetic clades of *P. sulcatus* have been found, based on COI and 16S sequences. Two of the three clades showed only one of the two developmental modes and were geographically restricted. However, the third clade consisted of an admixture of Western Indian Ocean and Indo-West Pacific specimens and both kinds of development. If the three clades would be interpreted as three different species, still one lineage containing populations with both developmental modes would have to be delineated. Hence, the most parsimonious solution is proposed in that the studied populations only represent on widely distributed species with two differing developmental modes. Therefore, the assumption of Bouchet (1989) needs to be rejected. Due to the spatial correlation of reproductive modes, that is that in the Western Indian Ocean, “k-strategy” breeding is the predominant form, whereas in the Indo-West Pacific “r-strategy” brooding is dominant, *P. sculatus* is a clear case of geographic poecilogony (Chia et al., 1996; Knott & McHugh, 2012), constituting the overall 14th supported case of poecilogony across all animal species. More importantly it is only the second case supported in shelled gastropods and the only known species with this form of development within the Cerithioidea.

Escaping from Adultocentrism – the impact of studying snail broods

Adultocentrism in biology is defined as the restricted focus on the adult by simultaneously neglecting of the juvenile, perceiving the former as ‘complete’ and the latter as ‘incomplete’ (Minelli, 2003). In systematics and biogeography, this hampers perception most impactful when different developmental stages a) develop different ecological niches, or b) exhibit differing dispersal abilities.

Within the Chapters of this study two major examples for the impact of differences between different developmental stages are given. Chapters 2, 3 and 4 illustrate how the differences in developmental modes gravely informed taxonomic decisions, as developmental mode directly informed a taxonomic signal differentiating *Stenomelania* and *Melanoides*, where molecular genetics failed to grasp these differences. Furthermore, the difference in dispersal intrinsic dispersal ability influence the distribution ranges of *Stenomelania* s. str. species, though due to its wide distribution as invasive species *M. tuberculata* shrouds the lucidity of these differences. The topic of differing dispersal abilities through larval stages need to be incorporated even more for considerations on the historic biogeography of the Thiaridae, as pointed out above. Lastly, the study of poecilogony in *P. sulcatus* easily elucidates how the consideration of developmental modes as taxonomic character can be misleading, though it is obvious, that without considering the developmental modes of this species, a most fascinating evolutionary phenomenon would have been overlooked.

Taxonomic redundancy

Though these studies on the *Stenomelania-Melanoides* complex allow for new systematic insights on the species group, a study clarifying the taxonomy of this complex is still direly needed. However, besides the account on thiarid systematics, this study also encompasses a taxonomic study of *Supplanaxis*, the presumed sister clade to *Planaxis*, reducing the existent taxonomic redundancy found within this genus.

A problem inherent to taxonomy has always been the delineation of a species and how to distinguish it from other such entities. The means to differentiate species and the plethora of literature on this topic is so vast, that it exceeds the boundaries of reasonability of this thesis (for an overview of this topic, however, see e.g. the discussions in Glaubrecht, 2009 and Hausdorf, 2011; as well as Zachos, 2016 for an exhaustive review on the matter). However, as an result of these disputes and the description of species being always a ‘child of its time’ (meaning that with advancement of study techniques, the possibilities of character distinction also changed) the description of nominal taxa that either constitute junior synonyms of other taxa as well as homonyms of others is unavoidable. Hence a major challenge besides the

description of biodiversity before it is lost, is the reassessment of already described biodiversity to allow for a ‘true’ portrayal of extant biodiversity (see eg. Giangrande, 2003; Glaubrecht, 2009; Sluys, 2013; Vaidya et al., 2018). Thereby taxonomic redundancy describes the rate of junior synonyms and homonyms in correlation to true biological entities found (Glaubrecht, 2009).

In Chapter 7, last but not least, an evolutionary systematics study on *Supplanaxis* was conducted. Twenty-two nominal species were examined based on Geometric morphometrics of the shell, shell characters and shell biometry, as well as radular morphology and molecular genetics, wherever applicable. Based on the combination of methods, overall six species and two subspecies were recovered as valid species. Consequentially, a taxonomic redundancy of 65% or synonymy ratio of 1:3 was recovered for the genus. These rates translate to the fact that roughly a third of available names can be considered valid. Glaubrecht (2009) and Glaubrecht et al. (2009) reported similarly high rates for freshwater gastropods, including Australian thiarids. These rates are excessively higher than the proposed 38% of redundant names proposed for mollusks in general (Glaubrecht, 2009), though Bouchet (1997) proposes a far higher rate of 1:6. The rates found for Freshwater Thiaridae by Glaubrecht et al. (2009) and Planaxidae in this study suggest that in Cerithioidean snail a lot of taxonomic ‘busywork’ still needs to be conducted, as several families within this superfamily have not been accessed by modern evolutionary systematic studies.

However, not all taxonomic acts conducted and implied in the thesis at hand lead to synonymisation. In Chapter 5 lies in the periphery of the *Stenomelania-Melanoides* complex, as the main focus of this taxonomic assessment is not a species within this complex but rather on a junior homonym of one of its species. The name *Helix plicaria* has been introduced for two very different snail species. *Helix plicaria* Born, 1778 was introduced for a high spired, tropical freshwater snail now assigned to the genus *Stenomelania* (though it was actually introduced as *Helix plicata* Born, 1778 and corrected in an erratum to *Helix plicaria*, for details refer to Chapter 5). However, *Helix plicaria* Lamarck, 1816 was introduced for a flat-conical land-snail species now assigned to the genus *Hemicycla* Swainson, 1840. As both names have been used separately since 1792 (with the transfer of *H. plicaria* Born, 1778 to *Bulimus* Scopoli, 1777 by Bruguière (1792)), and both are used in current literature on the taxa, a conservation of the name *Helix plicaria* Lamarck, 1816 was requested from the International Commission of Zoological Nomenclature.

Conclusion and Outlook

The combination of evolutionary systematics studies compiled in this thesis, illustrates advancements on our knowledge towards cerithioidean freshwater snail of the family Thiaridae as well as the related, marine Planaxidae.

Therewith, the first family wide molecular phylogeny of thiarids, encompassing all of its currently accepted genera, has been conducted. Based solely on a molecular genetics approach with only a few genes, the study produced very ambiguous results. Hence, it can only be an intermediate step, inevitably calling for a family-wide study, based on genomic approaches. Notwithstanding, the study emphasizes the importance of the Indo-Australian region as key factor in the family's evolution and, furthermore, a clear distinction of developmental mode evolution.

Moreover, the current understanding of the genera constituting the *Stenomelania-Melanoides* complex, is furthered by revising *Neoradina* and *Stenomelania* and their respective type species, based on a combination of different molecular and morphological methods. The combined results of these studies allow a better conceptualisation of the genera and provide a foundation for future studies, using more exhaustive material and species samplings. In addition, a junior homonym of a *Stenomelania* species has been conserved, reducing the taxonomic convolutedness of both lineages.

As an assessment towards the flexibility of developmental modes in cerithioidean snails, the poecilogony in *Planaxis sulcatus* has been studied. Traditionally, the species was held as a textbook example for poecilogony. Subsequently its status, standing for this form of development, was doubted. However, the study at hand lends support to this unique phenomenon being present within the species, expanding the possibilities feasible for Cerithioidean snails.

As an inevitable step, the planaxid genus *Supplanaxis* has been accessed in an evolutionary systematics approach. Overall, six species and two subspecies were supported by means of shell and radula morphology as well as molecular genetics. The study allowed for a considerable reduction of taxonomic redundancy in this clade, furthering the understanding of this group and thus easing future studies on this family.

The collective knowledge gained from this thesis constitutes a direly needed foundation for future studies on the taxonomically convoluted Thiaridae, which now should be accessed with more sophisticated genetic and morphological approaches. Furthermore, the study illustrates how it is of utmost importance to consider all developmental stages of the studied model

organisms, to avoid the oversight of key features necessary to access the evolutionary history of any group.

Land and freshwater molluscs account for a large proportion of recorded invertebrate extinctions and are some of the most threatened species in the world. As consequence of their oftentimes convoluted taxonomy, however, the accessibility of these species is regularly hampered. Due to this lack of knowledge on the matter, some major groups of freshwater molluscs have been hitherto neglected by modern taxonomy, since, usually a vast number of nominal taxa is in need of reconsideration and the fact in many groups only few taxonomically sound morphological characters are accessible.

Simultaneously, mankind faces the largest biodiversity crises to date, threatening an immeasurable amount of species, potentially including ourselves. Though countless small acts of economic adaptation as well as nature conservation will be needed if we are to prevent the worst from happening. However, to monitor and access the threat as well as our success in preventing it, studies on biodiversity and taxonomy are crucial. It is one of biology's universal truths that nature can only be protected by studying its parts – and I wholeheartedly hope that this study plays its part in it, by providing some pieces of the puzzle that has to put together.

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Appendix I List of publications

Published

- Wiggering B, Neiber M T, Krailas D, Glaubrecht M. 2019. **Biological diversity or nomenclatural multiplicity: the Thai freshwater snail *Neoradina prasongi* Brandt, 1974 (Gastropoda: Thiaridae).** Systematics and Biodiversity 17(3): 260-276. <https://doi.org/10.1080/14772000.2019.1606862>
- Wiggering, B., Neiber, M., Gebauer, K., & Glaubrecht, M. **One species, two developmental modes: Validating a case of geographic poecilogony in marine gastropods.** – BMC Evolutionary Biology 20: Article Number 76. <https://doi.org/10.1186/s12862-020-01644-1>

Submitted & under review

- Wiggering B, Glaubrecht M. Neiber M T, **Case 3838 – *Helix plicaria* Lamarck, 1816 (currently *Hemicycla plicaria*; Gastropoda, Eupulmonata, Stylommatophora, HELICIDAE): proposed conservation of the specific name.**

To be submitted soon

- Glaubrecht M*, Wiggering B*, Gimmich F, Rintelen T v, Neiber M T **The Indo-Australian region as key role in the evolution of diversity in an understudied group of tropical freshwater snails (Gastropoda: Cerithioidea: Thiaridae).**
- Wiggering B, Krivohlavek L, Glaubrecht M **Towards a revision of the enigmatic *Stenomelania* Fischer, 1885 (Gastropoda, Thiaridae), with an evaluation of its type species.**
- Wiggering B, Glaubrecht M **Reducing taxonomic redundancy: geometric morphometrics delineates species in *Supplanaxis* Thiele, 1929 (Gastropoda: Planaxidae).**

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Appendix II Supplemental material for Chapter 2

Figure S1. Bayesian 50% majority consensus tree based on concatenated COI and 16S sequences. Numbers at the nodes refer to posterior probability (PP) values (left) from the Bayesian (BI) and bootstrap support (BS) values from the maximum parsimony (MP) analysis (middle) and from the maximum likelihood (ML) analysis (right). Only nodes with PP values ≥ 0.50 and/or BS values from ML and/or MP analyses $\geq 50\%$ are annotated. Labels at nodes refer to museum voucher numbers and geographic origin, see also Supporting Information.

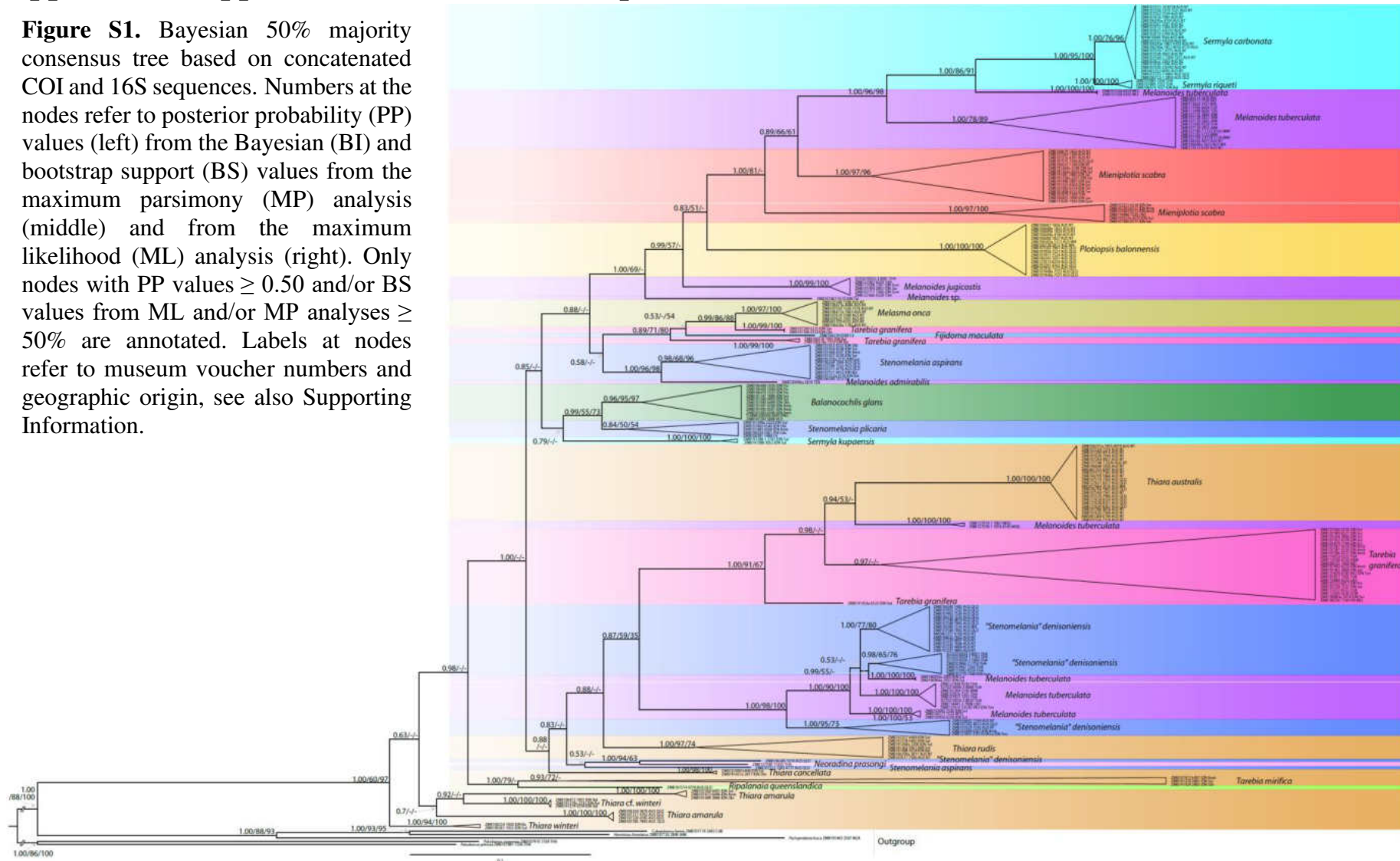


Table S1. List of examined material, including information on vouchers, sampling sites, collector and date of collection.

Species	Collection ID	Location	Collector	Sampling date
<i>Balanocochlis glans</i> (P. Fischer, 1885)	FLMNH308204	Melanesia: Papua New Guinea: Milne Bay Province: Rabaraba, Kigara River nr Rabaraba Airfield, swift rocky river; S 9° 58.594' E 149° 49.716'	Slapcinsky	12.02.2003
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB106468	Asia: Indonesia: East Nusa Tenggara: Nangapanda, E of Ende Bay; S 8° 47.703' E 121° 28.273'	Glaubrecht, Brinkmann	03.10.2003
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB106469	Asia: Indonesia: East Nusa Tenggara: Wailengga River, W of Aimere; S 8° 49.434' E 120° 49.086'	Glaubrecht, Brinkmann	04.10.2003
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB106470	Asia: Indonesia: East Nusa Tenggara: River at Mborong, 1-1,5 km upstream; S 8° 48.851' E 120° 37.028'	Glaubrecht, Brinkmann	04.10.2003
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB107292	Melanesia: Vanuatu: Santo: Cumberland Cape, Pwamel Village, rapids nr mouth of river; S 14° 43.29' E 166° 39.673'	Bouchet, Fontaine, Gargominy	29.11.2007
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB107366	Indonesia: Central Sulawesi: Luwuk Peninsula: River Biak, at Biak; S 0° 55.395' E 122° 52.962'	Stelbrink	07.11.2008
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB107490	Indonesia: North Maluku: Obi: Nika River; S 1° 41.347' E 127° 44.118'	von Rintelen	26.10.2008
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB107491	Indonesia: North Maluku: Ambon: Western part of Leihitu, road Lima - Lahe, E of Asilulu, small stream; S 3° 39.586' E 127° 57.404'	Glaubrecht	24.10.2008
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB107492	Indonesia: North Maluku: Ambon: North coast, near Hitu Lama; S 3° 35.293' E 128° 9.903'	Glaubrecht	21.10.2008
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB107493	Indonesia: North Maluku: Ambon: East coast of Leihitu, road Waai to Liang, few km N of bay, c. 500m from sea; S 3° 33.534' E 128° 19.221'	Glaubrecht	26.10.2008
<i>Balanocochlis glans</i> (P. Fischer, 1885)	ZMB191147	Asia: Indonesia: Central Sulawesi: Pondo River, S of Uekuli, Gandalari; S 1° 27.585' E 121° 6.406'	Glaubrecht, von Rintelen, Zitzler	28.05.2005
<i>Fijidoma maculata</i> (Mousson, 1865)	ZMB106379	Melanesia: Fiji: Viti Levu: at Wainimbuka River, S of Rokovuaka; S 17° 39.19' E 178° 15.63'	Glaubrecht	11.06.2002
<i>Melanoides admirabilis</i> (E.A. Smith, 1880)	ZMB220096a	Africa: Tanzania: Malagarasi (-1m); S 5° 13' E 29° 50'	Wilson	12.12.2000
<i>Melanoides jugicostis</i> (Hanley & Theobald, 1876)	ZMB107717	Asia: Indonesia: Riau: Kampar River, 60m, Sumatra Riau, SUM020; S 0° 17.512' E 100° 53.457'	Balke	
<i>Melanoides jugicostis</i> (Hanley & Theobald, 1876)	ZMB113598	Asia: Indonesia: Sumatra Barat: Pangkalan, 140m, Sumatra Barat, SUM019; S 0° 5.991' E 100° 44.213'	Balke	
<i>Melanoides jugicostis</i> (Hanley & Theobald, 1876)	SUT0210025 ZMB113746	Asia: Thailand: Ra Mon Waterfall, Phangnga;	Silpa Korn University	
<i>Melanoides jugicostis</i> (Hanley & Theobald, 1876)	ZMB127446	Asia: Thailand: Erawan waterfall, tributary to main Kwai River; N 14° 22.503' E 99° 8.665'	Glaubrecht, Krailas, Boonmekam	03.03.2012
<i>Melanoides jugicostis</i> (Hanley & Theobald, 1876)	ZMB127447	Asia: Thailand: Klong Palian River, at Yan Ta Khao; N 7° 22.308' E 99° 40.719'	Glaubrecht, Krailas, Boonmekam	08.03.2012
<i>Melanoides jugicostis</i> (Hanley & Theobald, 1876)	ZMB127448	Asia: Thailand: Klong Palian River, at Yan Ta Khao; N 7° 22.308' E 99° 40.719'	Glaubrecht, Krailas, Boonmekam	08.03.2012

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<i>Melanoides jugicostis</i> (Hanley & Theobald, 1876)	ZMB191499	Asia: Indonesia: West Java: River in Sukawayana, N of road Pelabuhan Ratu - Cisolok; S 6° 57.439' E 106° 30.238'	von Rintelen	27.10.2005
<i>Melanoides nodicincta</i> (Dohrn, 1865)	ZMB107180	Africa: Malawi: Lake Malawi: Lake Malawi, Chilumba, shore 300m E of Karonga Preventing Station (KPS); S 10° 25.535' E 34° 15.007'	Schultheiß, Geertz	16.08.2006
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB104177	Central America and the Antilles: Martinique: Martinique; N 14° 37' W 61° '	Pointier	
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB106592	Australia: Northern Territory: Darwin: George Brown Botanic Garden, pool; S 12° 26.739' E 130° 50.179'	Glaubrecht, Brinkmann, von Rintelen	25.06.2004
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB106690a	Australia: West Australia: Kimberley Region: Lilly Lagoon, nr. Lake Kununurra, above Diversion Dam; S 15° 46.825' E 128° 44.477'	Glaubrecht, Brinkmann	27.09.2005
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107125	Jamaica: Cornwall: Trelawny: Quashies River sink, nr Albert Town; N 18° 18.03' W 77° 33.95'	Schubart	20.03.2003
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107128	Central America and the Antilles: Jamaica: Rio Negro; N 18° 24.864' W 77° 12.648'	Schubart, Reuschel, Santl	21.10.2005
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107129	Jamaica: Cornwall: Westmorland: Rio Magno;	Schubart, Reuschel, Santl	19.10.2005
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107130	Jamaica: Cornwall: Westmorland: Green Island River; N 18° 21.958' W 78° 13.851'	Schubart, Reuschel, Santl	15.10.2005
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107183	Africa: Malawi: Lake Malawi: Ngora Resort (Ngora Town), beach between restaurant & hot springs; S 10° 12.608' E 34° 5.673'	Schultheiß, Geertz	17.08.2006
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107193	Africa: Malawi: Lake Malawi: Chilumba, rocky shore next to DEMAG harbour; S 10° 25.946' E 34° 15.366'	Schultheiß, Geertz	16.08.2006
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107204	Africa: Malawi: Lake Malawi: Lake Malawi, N of Chipoka, offshore: between Namkoma Island and lake shore; S 13° 55.708' E 34° 34.151'	Schultheiß, Geertz	12.08.2006
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107424	Indonesia: North Maluku: Obi: Lake Sagu, W shore, small bay just S of peninsula; S 1° 29.84' E 127° 26.862'	von Rintelen	24.10.2008
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107536	Europe: France: Hoorn Islands (COM): Wallis Island (Uvea), Lac Kikila, NW-shore, Lake and shore line with shrub vegetation alt. 30m; S 13° 17.707' W 176° 11.388'	Richling	13.11.2007
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107538	Europe: France: Hoorn Islands (COM): Futuna Island: Tarodièrè Nuku;	Richling	17.11.2008
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107876	Asia: Thailand: S of Chumphon, creek NW of Lang Suan, on road to Phato, turn right, after 5km from NW junction; N 9° 59.189' E 99° 0.786'	Glaubrecht, Brinkmann, Krailas	26.07.2010
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB107921	Asia: Thailand: Mae Sa Waterfall, N Chiang Mai, W Mae Rin; N 18° 54.334' E 98° 54.055'	Glaubrecht, Brinkmann, Krailas	03.08.2010
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB112662	Nepal: Koshi: Sunsari: Hariपुर, tributary of Sapta Koshi River near Indian border; N 26° 33.28' E 86° 59.6'	Bößneck	23.04.2003
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	SUT0210006 ZMB113749	Asia: Thailand: 42 Km, Wang Thong , Pitsanulok;		
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	SUT0210024 ZMB113763	Asia: Thailand: Ton Sai Waterfall, Phuket;	Silpa Korn University	

Benedikt Wiggering

<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB114441	Asia: Laos: Vientiane: Chin River in Phônông, highway 13; N 18° 31.657' E 102° 23.54'	Köhler	07.10.2006
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB117496	Asia: Turkey: Provinz Hatay/TR, Vilayet Reyhanlı, am südlichen Ufer des Yenişehir Gölü, südlich der Stadt Reyhanlı; am Fuße eines künstlichen Wasserfalles, unmittelbar am südlichen Rand der Ringstraße, ~187m NN; N 36° 14.164' E 36° 34.109'	Hartz	27.09.2010
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB117498	Asia: Turkey: Provinz Hatay/TR, Vilayet Kırıkhan, östliches Ufer des Gölbaşı Gölü am südlichen Ortsrand des Dorfes Adalar, ~83m NN; N 36° 30.189' E 36° 29.873'	Hartz	27.09.2010
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB127019	Africa: Madagascar: Ihosy (Stream), River Basin : Mangoky upper part, First bridge RN7 to the south after Ihosy, 773m, (Sample 23A); S 22° 23.32' E 46° 6.58'	Ferreux	28.12.2009
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB127078	Africa: Madagascar: Befandriana, Mangoky (Stream), River Basin : Mangoky, Left bank close to Ambiky village, 61m, (Sample 65A); S 21° 52.813' E 43° 53.783'	Ferreux	16.02.2010
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB127444	Asia: Thailand: Khao Thong; N 8° 10.405' E 98° 44.939'	Glaubrecht, Krailas, Boonmekam	08.03.2012
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB127610	Asia: Indonesia: Timor: Lutu-Ira, Ira-Ara village, Lautern District, Large spring pool, Quite strongly running outflow stream in the village, limestone; S 8° 20.535' E 127° 1.132'	Kessner	23.05.2011
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB127613	Australia: Northern Territory: Top End: Bitter Springs, at Mataranka; S 14° 54.642' E 133° 5.362'	Glaubrecht, Gimnich 2, Maaß	16.09.2011
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB190830a	Asia: Indonesia: Central Sulawesi: Lake Poso, N shore, Leboni; S 1° 47.153' E 120° 33.143'	Glaubrecht, von Rintelen	28.03.2004
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB190964a	Asia: Indonesia: Central Sulawesi: Lake Poso, S shore, Pendolo, beach at Hotel Mulia; S 2° 3.876' E 120° 41.587'	Glaubrecht, von Rintelen	27.03.2004
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB193926	Asia: Indonesia: South Sulawesi: Pucue River, Datae, road Parepare - Sidenreng; S 3° 54.893' E 119° 42.571'	Schubart	12.11.2008
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB193945	Indonesia: South Sulawesi: Palopo plain: Makawa River, tributary, road Palopo - Sabbang; S 2° 45.763' E 120° 8.503'	Schubart, Kolbinger, Wirdmann	12.11.2008
<i>Melanoides tuberculata</i> (O.F. Müller, 1774)	ZMB200313	Asia: India: Tamil Nadu: Moyar River in Theppakadu, Bandipur N.P.;	Köhler, Schütt	
<i>Melanoides</i> sp.	ZMB107407	Asia: Indonesia: North Maluku: Taliabu: limestone outcrop, uphill E of Bobong; S 1° 57.001' E 124° 23.506'	Slapcinsky	02.10.2008
<i>Melasma onca</i> (A. Adams & Angas, 1864)	AMS461370	Australia: Northern Territory: Arnhem Land: eastern Goyder River crossing, Central Arnhem Road; S 13° 1.619' E 134° 58.62'	Ponder, Kessner	02.07.2007
<i>Melasma onca</i> (A. Adams & Angas, 1864)	ZMB106617a	Australia: Northern Territory: Top End: Katherine River, at Katherine, Low Level crossing, downstream from bridge; S 14° 29.441' E 132° 14.991'	Glaubrecht, Brinkmann, von Rintelen	30.06.2004
<i>Melasma onca</i> (A. Adams & Angas, 1864)	ZMB106636a	Australia: Northern Territory: Top End: Roper River, at Roper Bar; S 14° 42.802' E 134° 30.474'	Glaubrecht, Brinkmann, von Rintelen	02.07.2004
<i>Melasma onca</i> (A. Adams & Angas, 1864)	ZMB106673a	Australia: Northern Territory: Top End: Bamboo Creek, c. 3-10m from Daly River; S 13° 40.118' E 130° 39.501'	Glaubrecht, Brinkmann	14.09.2005
<i>Melasma onca</i> (A. Adams & Angas, 1864)	ZMB107549	Australia: Northern Territory: Top End: Ooloo Crossing, Daly River; S 14° 4.24' E 131° 15.056'	Glaubrecht, Brinkmann	24.10.2007

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<i>Melasma onca</i> (A. Adams & Angas, 1864)	ZMB107550	Australia: Australia: Northern Territory: Bamboo Creek at Daly River; S 13° 40.083' E 130° 39.542'	Glaubrecht, Brinkmann	30.09.2009
<i>Melasma onca</i> (A. Adams & Angas, 1864)	ZMB107619	Australia: Australia: Northern Territory: Wabalarr, Roper River, E of 4 Mile Point on way to Jalmurark; S 14° 56.028' E 133° 10.44'	Glaubrecht, Brinkmann	22.10.2009
<i>Melasma onca</i> (A. Adams & Angas, 1864)	ZMB107625	Australia: Australia: Northern Territory: Mulurark, Roper River, 2km W of Jalmurark, 6km E of Wabalarr; S 14° 56.789' E 133° 12.626'	Glaubrecht, Brinkmann	22.10.2009
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB191487	Asia: Indonesia: Central Sulawesi: Peleng Island, W shore, stream; S 1° 23.999' E 122° 47.615'	von Rintelen, Zitzler	27.09.2005
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB191258a	Indonesia: Central Sulawesi: Luwuk Peninsula: Freshwater spring in Malotong, W of Ampana, brackish water pool; S 0° 53.125' E 121° 31.371'	Glaubrecht, von Rintelen, Zitzler	27.05.2005
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB106425	Asia: Indonesia: West Java: River at road Cipatujah - Tasikmalaya; S 7° 41.12' E 108° 2.52'	von Rintelen	03.05.2002
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107216	Australia: Northern Territory: Top End: Ooloo Crossing, Daly River; S 14° 4.24' E 131° 15.056'	Glaubrecht, Brinkmann	24.10.2007
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107392	Indonesia: North Maluku: Ambon: Leitimur, south coast, Kalo Kilang at Kilang; S 3° 44.276' E 128° 13.8'	Glaubrecht	26.10.2008
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB114990	Asia: Laos: Champasak Prov.: river Xe Set above Tat Lo waterfall (mud and rocks); N 15° 30.66' E 106° 16.66'	Köhler, Püschel	11.11.2007
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB106552	Asia: Indonesia: East Nusa Tenggara: Wailangga River, W of Aimere; S 8° 49.434' E 120° 49.086'	Glaubrecht, Brinkmann	04.10.2003
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB106679	Australia: Northern Territory: Top End: Little Roper River, South bank at old crossing; S 14° 55.589' E 133° 7.137'	Glaubrecht, Brinkmann	16.09.2005
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107371	Indonesia: Maluku: Seram: West Seram, road Masohi - Piru, S of Piru, small stream; S 3° 8.924' E 128° 14.59'	Glaubrecht	23.10.2008
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107382	Indonesia: North Maluku: Ternate: West coast, ring road S of Togafo, small stream nr Afetaduma; N 0° 48.55' E 127° 17.666'	Glaubrecht	29.10.2008
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107386	Indonesia: Maluku: Seram: North Seram, coastal road Piru - Latuhelu, nr. Kawa, small stream; S 3° 0.321' E 128° 7.416'	Glaubrecht	23.10.2008
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107408	Indonesia: North Maluku: Ternate: Lake Tolire Besar; N 0° 50.283' E 127° 18.279'	Glaubrecht	29.10.2008
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107443	Indonesia: North Maluku: Ambon: North coast, near Hitu Lama; S 3° 35.293' E 128° 9.903'	Glaubrecht	21.10.2008
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107564	Australia: Australia: Northern Territory: Little Roper River at crossing; S 14° 55.63' E 133° 7.105'	Glaubrecht, Brinkmann	02.10.2009
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107575	Australia: Australia: Queensland: Gregory River at Riversleigh; S 19° 1.101' E 138° 43.5'	Glaubrecht, Brinkmann	05.10.2009
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB107879	Asia: Thailand: Klong Tha Sae, N of Chumphon; N 10° 44.648' E 99° 12.747'	Glaubrecht, Brinkmann, Krailas	26.07.2010
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB113595	Asia: Indonesia: Sumatra Barat: Talawi, Ombilin River, 210m, Sumatra Barat, SUM005; S 0° 35.379' E 100° 43.684'	Balke	
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB191037a	Indonesia: North Sulawesi: Minahasa: Stream between rice fields, tributary of Lake Tondano, c. 500m from lake; N 1° 11.228' E 124° 52.192'	von Rintelen, Zitzler	13.08.2004

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<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB191253	Indonesia: Central Sulawesi: Luwuk Peninsula: Stream in mountains nr Sape, SW of Balantak, E coast of Balantak Peninsula; S 0° 56.682' E 123° 21.38'	Glaubrecht, von Rintelen, Zitzler	25.05.2005
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB191264a	Asia: Indonesia: Southeast Sulawesi: Adayu River, W of Alenggae; S 4° 16.879' E 122° 9.07'	Glaubrecht, von Rintelen, Zitzler	31.05.2005
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB191265a	Asia: Indonesia: Southeast Sulawesi: River along road Kolono - Lapuko, N of Lamotua; S 4° 16.726' E 122° 42.592'	Glaubrecht, von Rintelen, Zitzler	31.05.2005
<i>Mieniplotia scabra</i> (O. F. Müller, 1774)	ZMB191498	Asia: Indonesia: Central Sulawesi: Peleng Island, W peninsula, SW of Alani, small lake, close to river outlet; S 1° 29.26' E 122° 51.487'	von Rintelen, Zitzler	27.09.2005
<i>Neoradina prasongi</i> (Brandt, 1974)	ZMB127590	Asia: Thailand: Chalung city, Klong Chalung, Muang district; N 6° 43.618' E 100° 3.756'	Glaubrecht, Glaubrecht Krailas	09.02.2013
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB106345	Australia: Australia: Queensland: nr. Gregory Falls; S 17° 35.57' E 145° 52.29'	Glaubrecht, von Rintelen, Brinkmann	15.05.2002
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB106583a	Australia: Australia: West Australia: Murchinson River, Kalbarri N.P., at Ross Graham Lookout; S 27° 48.77' E 114° 28.54'	Glaubrecht, Brinkmann	22.07.2004
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB106686	Australia: Northern Territory: Red Centre: Ormiston Gorge, outlet, waterhole with vegetation; S 23° 37.704' E 132° 43.375'	Glaubrecht, Brinkmann	19.09.2005
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB106687	Australia: Northern Territory: Red Centre: Finke River, at Glen Helen Gorge nr. resort; S 23° 41.322' E 132° 40.606'	Glaubrecht, Brinkmann	23.09.2005
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB106688a	Australia: Northern Territory: Red Centre: Boggy Hole, Campground, Finke River; S 24° 8.174' E 132° 51.768'	Glaubrecht, Brinkmann	21.09.2005
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB106689a	Australia: Northern Territory: Red Centre: Three Mile Point, Finke River at crossing of Stuart HWY; S 24° 33.182' E 133° 14.355'	Glaubrecht, Brinkmann	25.09.2005
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB106728	Australia: Australia: West Australia: Pilbara Region, Hamersley Range (Karijini) National Park, Dales Gorge riverside, loose gravel, 0-0,2 m; S 22° 28.521' E 118° 33.08'	Albrecht	25.07.2004
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB107583	Australia: Australia: Queensland: Mareeba, upper Barron River; S 16° 59.134' E 145° 25.158'	Glaubrecht, Brinkmann	10.10.2009
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB107946a	Australia: Australia: Queensland: Upper Brisbane River, at Fernvale, W Brisbane, at old bridge crossing; S 27° 26.226' E 152° 38.056'	Glaubrecht, Brinkmann	25.09.2010
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB107948a	Australia: Australia: Queensland: South Maroochy River at Yandina, Coleman's Road crossing; S 26° 33.626' E 152° 56.629'	Glaubrecht, Brinkmann	26.09.2010
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB107950	Australia: Australia: Queensland: Litte Widgee Creek, trib. to Mary River, W Gympie; S 26° 12.31' E 152° 27.193'	Glaubrecht, Brinkmann	27.09.2010
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB107951	Australia: Australia: Queensland: Euri Creek, at Bowen to Collinsville road; S 20° 12.294' E 147° 57.613'	Glaubrecht, Brinkmann	29.09.2010
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB107956	Australia: Australia: Queensland: Broken River, trib. to Bowen River, at Eungella; S 21° 10.13' E 148° 30.129'	Glaubrecht, Brinkmann	01.10.2010
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB127615	Australia: Australia: Queensland: Porcupine Creek at Porcupine Gorge; S 20° 21.197' E 144° 28.01'	Glaubrecht, Gimnich, Maaß	30.09.2011
<i>Plotiopsis balonnensis</i> (Conrad, 1850)	ZMB192391	Australia: Australia: Queensland: Dawson River, Theodore; S 24° 57.417' E 150° 4.443'	Page, Cook	18.08.2007

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<i>Ripalania queenslandica</i> (Smith, 1882)	ZMB107214	Australia: Australia: Queensland: North Johnston River; S 17° 30.34' E 145° 59.55'	Glaubrecht, Brinkmann	19.10.2007
<i>Sermyla carbonata</i> (Reeve, 1859)	AMS461353	Australia: Northern Territory: Arnhem Land: Numbulwar - Roper River road, Mumpumumpu Outstation, Phelp River drainage, Mumpumampu Waterhole; S 14° 22.979' E 135° 19.559'	Ponder, Kessner	10.07.2007
<i>Sermyla carbonata</i> (Reeve, 1859)	WAM10048	Australia: Australia: West Australia: Bundera Sinkhole (Cenote), C-28; S 22° 25' E 113° 46'	Humphreys	07.06.2005
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB106700a	Australia: Northern Territory: Top End: Howard Springs; S 12° 27.345' E 131° 3.146'	Glaubrecht, Brinkmann	01.10.2005
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB106593a	Australia: Northern Territory: Top End: Howard Springs; S 12° 27.345' E 131° 3.146'	Glaubrecht, Brinkmann, von Rintelen	27.06.2004
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB106595a	Australia: Northern Territory: Top End: Howard Springs Creek, N of Howard Springs; S 12° 27.268' E 131° 3.108'	Glaubrecht, Brinkmann, von Rintelen	27.06.2004
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB106713	Australia: Australia: Queensland: Norman River, 4 km East of Normanton; S 17° 39.332' E 141° 6.048'	Kessner	03.09.2005
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107210	Australia: Northern Territory: Top End: Berry Springs, S of Darwin; S 12° 42.111' E 130° 59.854'	Glaubrecht, Brinkmann	24.10.2007
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107228	Australia: Northern Territory: Top End: Howard Springs Creek, N of Howard Springs; S 12° 27.268' E 131° 3.108'	Glaubrecht, Brinkmann	02.10.2007
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107231	Australia: Northern Territory: Top End: Elsey Creek on Roper Highway (Roper River Catchment); S 15° 0.627' E 133° 15.096'	Glaubrecht, Brinkmann	04.10.2007
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107235	Australia: Australia: Queensland: Norman River, Billabong 1 km N of Normanton; S 17° 39.712' E 141° 6.154'	Glaubrecht, Brinkmann	11.10.2007
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107544	Australia: Australia: Northern Territory: Berry Springs on Stuart Highway; S 12° 42.309' E 131° 0.401'	Glaubrecht, Brinkmann	29.09.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107545	Australia: Australia: Northern Territory: Berry Springs on Stuart Highway; S 12° 42.309' E 131° 0.401'	Glaubrecht, Brinkmann	29.09.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107557	Australia: Australia: Northern Territory: Roper River at Jalmurark camp; S 14° 57.1' E 133° 13.42'	Glaubrecht, Brinkmann	02.10.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107558	Australia: Australia: Northern Territory: Roper River at Jalmurark camp; S 14° 57.1' E 133° 13.42'	Glaubrecht, Brinkmann	02.10.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107561	Australia: Australia: Northern Territory: Little Roper River at crossing; S 14° 55.63' E 133° 7.105'	Glaubrecht, Brinkmann	02.10.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107562	Australia: Australia: Northern Territory: Little Roper River at crossing; S 14° 55.63' E 133° 7.105'	Glaubrecht, Brinkmann	02.10.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107615	Australia: Australia: Northern Territory: Wabalarr, Roper River, E of 4 Mile Point on way to Jalmurark; S 14° 56.028' E 133° 10.44'	Glaubrecht, Brinkmann	22.10.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107616	Australia: Australia: Northern Territory: Wabalarr, Roper River, E of 4 Mile Point on way to Jalmurark; S 14° 56.028' E 133° 10.44'	Glaubrecht, Brinkmann	22.10.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107621	Australia: Australia: Northern Territory: Mulurark, Roper River, 2km W of Jalmurark, 6km E of Wabalarr; S 14° 56.789' E 133° 12.626'	Glaubrecht, Brinkmann	22.10.2009

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<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107627	Australia: Australia: Northern Territory: Howard Springs Creek; S 12° 27.268' E 131° 3.108'	Glaubrecht, Brinkmann	24.10.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB107630	Australia: Australia: Northern Territory: Howard Springs Creek; S 12° 27.268' E 131° 3.108'	Glaubrecht, Brinkmann	24.10.2009
<i>Sermyla carbonata</i> (Reeve, 1859)	ZMB192019	Australia: Australia: Northern Territory: Warloch Ponds on Elsey Creek, near old Stuart Hwy, Elsey Station, Mataranka area; S 16° 5.042' E 133° 7.258'	Kessner	13.07.2006
<i>Sermyla kupaensis</i>	ZMB191388	Asia: Indonesia: South Sulawesi: Kupa, river, E of road Makassar - Parepare; S 4° 7.567' E 119° 37.426'	Glaubrecht, von Rintelen, Zitzler	02.06.2005
<i>Sermyla riqueti</i> (Grateloup, 1840)	ZMB106474	Indonesia: Bali: South Bali: Gumbrih River, 500m from sea at river bank; S 8° 26.542' E 114° 52.598'	Glaubrecht, Brinkmann	10.10.2003
<i>Sermyla riqueti</i> (Grateloup, 1840)	ZMB107883	Asia: Thailand: Puek Tian Beach, N of Hua Hin, S of Phetchaburi; N 12° 57.495' E 100° 1.91'	Glaubrecht, Brinkmann, Krailas	27.07.2010
<i>Sermyla riqueti</i> (Grateloup, 1840)	ZMB107886	Asia: Thailand: Puek Tian Beach, N of Hua Hin, S of Phetchaburi; N 12° 57.495' E 100° 1.91'	Glaubrecht, Brinkmann, Krailas	27.07.2010
<i>Stenomelania aspirans</i> (Hinds, 1844)	ZMB106390	Fiji: Viti Levu: Coral Coast: Sovi River, Malevu; S 18° 10.49' E 177° 34.36'	Glaubrecht	15.06.2002
<i>Stenomelania aspirans</i> (Hinds, 1844)	ZMB107211	Australia: Australia: Queensland: Granite Creek, W of Bloomsfield; S 15° 55.99' E 145° 19.54'	Glaubrecht, Brinkmann	14.10.2007
<i>Stenomelania aspirans</i> (Hinds, 1844)	ZMB107212	Australia: Australia: Queensland: Mowbray River; S 16° 33.87' E 145° 27.83'	Glaubrecht, Brinkmann	16.10.2007
<i>Stenomelania aspirans</i> (Hinds, 1844)	ZMB107586	Australia: Australia: Queensland: Mowbray River, near Port Douglas; S 16° 33.812' E 145° 27.877'	Glaubrecht, Brinkmann	11.10.2009
<i>Stenomelania aspirans</i> (Hinds, 1844)	ZMB191210a	Asia: Indonesia: Southeast Sulawesi: Small river at Sukamaju, road Kendari - Lapuko; S 3° 59.28' E 122° 34.96'	von Rintelen, Zitzler	01.06.2005
<i>Stenomelania aspirans</i> (Hinds, 1844)	ZMB191212a	Asia: Indonesia: Bali: South Bali: Stream at Kangkang, NW of Denpasar; S 8° 37.945' E 115° 8.143'	Glaubrecht, von Rintelen, Zitzler	04.06.2005
<i>Stenomelania plicaria</i> (Born, 1778)	ZMB106391	Melanesia: Fiji: Viti Levu: Creek at Lawai, tributary of Singatoka River; S 18° 7.05' E 177° 31.42'	Glaubrecht	16.06.2002
<i>Stenomelania punctata</i> (Lamarck, 1822)	ZMB107483	Indonesia: North Maluku: Ambon: Eastern part of Leihitu, at Watatiri, road Passo - Natsepa; S 9° 37.052' E 128° 16.262'	Glaubrecht	21.10.2008
<i>Stenomelania</i> sp.	ZMB106344	Australia: Australia: Queensland: Mowbray River; S 16° 33.87' E 145° 27.83'	Glaubrecht, Brinkmann	31.05.2002
<i>Stenomelania</i> sp.	ZMB107453	Indonesia: North Maluku: Obi: S coast, Wayaloar, mouth of river c. 20-50m from sea, c. 300m W of 37-08; S 1° 43.122' E 127° 36.855'	von Rintelen	27.10.2008
<i>Stenomelania</i> sp.	ZMB107454	Asia: Indonesia: Central Sulawesi: Peleng Island, W peninsula, Tataban River; S 1° 32.294' E 122° 51.465'	Glaubrecht, Schultz	05.11.2008
<i>Stenomelania</i> sp.	ZMB107457	Indonesia: Maluku: Seram: North Seram, coastal road Piru - Latuhelu, nr. Kawa, small stream; S 3° 0.321' E 128° 7.416'	Glaubrecht	23.10.2008
<i>Stenomelania</i> sp.	ZMB107460	Indonesia: North Maluku: Obi: Nika River; S 1° 41.347' E 127° 44.118'	von Rintelen	26.10.2008
<i>Stenomelania</i> sp.	ZMB107468	Indonesia: North Maluku: Ambon: Western part of Leihitu, river NE of Liliboi at road Passo - Liliboi; S 3° 44.747' E 128° 1.558'	Glaubrecht	22.10.2008

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<i>Stenomelania</i> sp.	ZMB107511	Indonesia: West Papua: Batanta: Sungai Samsen, Desau Wailebet;	EWIN II Expedition	02.05.2008
<i>Stenomelania</i> sp.	ZMB190354	Asia: Philippines: Cebu: Small river at Kawasan waterfalls, Matutinao, limestone; N 9° 48.49' E 123° 22.1'	Köhler, Schütt	19.04.2000
<i>Stenomelania</i> sp.	ZMB191208a	Indonesia: Central Sulawesi: Luwuk Peninsula: Small tributary of large river W of Sukamaju at Tumpujaya; S 1° 19.956' E 122° 24.063'	Glaubrecht, von Rintelen, Zitzler	23.05.2005
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	AMS461371	Australia: Northern Territory: Arnhem Land: Numbulwar - Roper River road, Mumpumumpu Outstation, Phelp River drainage, Mumpumampu Waterhole; S 14° 22.979' E 135° 19.559'	Ponder, Kessner	10.07.2007
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	SUT0210034	Thailand		
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB106339	Australia: Australia: Queensland: Laura River; S 15° 34.68' E 144° 27.41'	Glaubrecht, von Rintelen, Brinkmann	26.05.2002
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB106340	Australia: Australia: Queensland: South Mission Beach; S 17° 56.84' E 146° 3.29'	Glaubrecht, von Rintelen, Brinkmann	15.05.2002
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB106586	Australia: Australia: West Australia: SE of Geraldton, Ellendale Pool at Greenough River; S 28° 51.63' E 114° 58.43'	Glaubrecht, Brinkmann	19.07.2004
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB106632	Australia: Northern Territory: Top End: Salt Creek nr Elsey Creek, at crossing of Roper Highway; S 15° 0.703' E 133° 14.417'	Glaubrecht, Brinkmann, von Rintelen	02.07.2004
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB106682	Australia: Northern Territory: Top End: Stevie's Hole at Waterhouse River, Elsey N.P.; S 14° 55.782' E 133° 8.732'	Glaubrecht, Brinkmann	16.09.2005
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107230	Australia: Northern Territory: Top End: Salt Creek nr Elsey Creek, at crossing of Roper Highway; S 15° 0.703' E 133° 14.417'	Glaubrecht, Brinkmann	04.10.2007
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107233	Australia: Australia: Northern Territory: Kangaroo Creek; S 16° 47.553' E 137° 6.107'	Glaubrecht, Brinkmann	06.10.2007
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107237	Australia: Northern Territory: Top End: Little Roper River, at crossing; S 14° 55.581' E 133° 7.176'	Glaubrecht, Brinkmann	23.10.2007
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107239	Australia: Northern Territory: Top End: Towns River, at crossing; S 15° 2.57' E 135° 12.718'	Glaubrecht, Brinkmann	05.10.2007
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107242	Australia: Australia: Queensland: Normanton River, Glenmore, SE of Normanton River; S 15° 51.199' E 141° 8.048'	Glaubrecht, Brinkmann	11.10.2007
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107248	Australia: Australia: Queensland: Meelele River; S 15° 58.25' E 145° 23.85'	Glaubrecht, Brinkmann	14.10.2007
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107449	Indonesia: North Maluku: Ambon: Stream at road Hunut - Hitu Lama; S 3° 37.817' E 128° 12.286'	Glaubrecht	21.10.2008
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107584	Australia: Australia: Queensland: Mareeba, upper Barron River; S 16° 59.134' E 145° 25.158'	Glaubrecht, Brinkmann	10.10.2009
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107588	Australia: Australia: Queensland: Mowbraw River, near Port Douglas; S 16° 33.812' E 145° 27.877'	Glaubrecht, Brinkmann	11.10.2009
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107629	Australia: Australia: Northern Territory: Howard Springs Creek; S 12° 27.268' E 131° 3.108'	Glaubrecht, Brinkmann	24.10.2009

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<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107719	Asia: Indonesia: Riau: Kampar River, 60m, Sumatra Riau, SUM020; S 0° 17.512' E 100° 53.457'	Amran & Balke	02.10.2009
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107866	Asia: Thailand: Khao Tong, Klong Sai, highway to Krabi; N 8° 10.482' E 98° 47.433'	Glaubrecht, Brinkmann, Krailas	24.07.2010
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107867	Asia: Thailand: W of Ko Nang to Kao Tong, W of Krabi; N 8° 5.772' E 98° 48.535'	Glaubrecht, Brinkmann, Krailas	25.07.2010
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107955	Australia: Australia: Queensland: Euri Creek, at Bowen to Collinsville road; S 20° 12.294' E 147° 57.613'	Glaubrecht, Brinkmann	29.09.2010
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB107963	Australia: Australia: Queensland: Botanic Garden, Mackay, on Bruce Hwy; S 21° 9.485' E 149° 9.582'	Glaubrecht, Brinkmann	30.09.2010
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	SUT0210026 ZMB113764	Asia: Thailand: Klong Sai, Krabi;	Silpa Korn University	
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	SUT0210030-3 ZMB113778	Asia: Thailand: Sai Ku Waterfall, Prachuabkirikhan;	Silpa Korn University	
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB127442	Asia: Thailand: Khao Thong; N 8° 10.405' E 98° 44.939'	Glaubrecht, Krailas, Boonmekam	08.03.2012
<i>"Stenomelania" denisoniensis</i> (Brot, 1877)	ZMB127607	Asia: Indonesia: Timor: Lutu-Ira, Ira-Ara village, Lautern District, Large spring pool, Quite stronly running outflow stream in the village, limestone; S 8° 20.535' E 127° 1.132'	Kessner	23.05.2011
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB106518	Indonesia: Bali: South Bali: Yehembang, E of Mendaya; S 8° 23.641' E 114° 45.064'	Glaubrecht, Brinkmann	25.09.2003
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB106518a	Indonesia: Bali: South Bali: Yehembang, E of Mendaya; S 8° 23.641' E 114° 45.064'	Glaubrecht, Brinkmann	25.09.2003
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107360	Indonesia: Maluku: Seram: West Seram, road Kairatu - Rumahkai, N of Rumahkai, stream c. 50m from sea; S 3° 27.276' E 128° 31.556'	Glaubrecht	25.10.2008
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107367	Indonesia: North Maluku: Ambon: Western part of Leihitu, road Lima - Said, river at Nahai nr Lima, W of Fort Rotterdam, c. 600m from sea; S 3° 37.363' E 127° 59.912'	Glaubrecht	24.10.2008
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107381	Indonesia: North Maluku: Ambon: Central part of Leihitu, road Hila - Hitu Lama, E of Hila, small stream; S 3° 35.664' E 128° 2.704'	Glaubrecht	24.10.2008
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107384	Indonesia: North Maluku: Obi: S coast, Wayaloar, mouth of river c. 20m from sea; S 1° 43.122' E 127° 36.855'	von Rintelen	27.10.2008
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107396	Indonesia: North Maluku: Ambon: Eastern part of Leihitu, at Watatiri, road Passo - Natsepa; S 9° 37.052' E 128° 16.262'	Glaubrecht	21.10.2008
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107400	Asia: Indonesia: Central Sulawesi: Peleng Island, central peninsula, Telen River; S 1° 27.554' E 123° 13.063'	Glaubrecht, von Rintelen	03.11.2008
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107409	Asia: Indonesia: Central Sulawesi: Peleng Island, NE peninsula, road Luksagu - Sambiu; S 1° 19.011' E 123° 27.035'	Glaubrecht, von Rintelen	04.11.2008
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107422	Asia: Indonesia: South Sulawesi: Malino, Takapala waterfall; S 5° 16.494' E 119° 51.5'	Stelbrink, Glaubrecht, von Rintelen	30.10.2008
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107442	Indonesia: North Maluku: Ambon: North coast, near Hitu Lama; S 3° 35.293' E 128° 9.903'	Glaubrecht	21.10.2008

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<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107533	Asia: Indonesia: Flores, below Ruteng;	Amran & Balke	
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB107877	Asia: Thailand: Klong Tha Sae, N of Chumphon; N 10° 44.648' E 99° 12.747'	Glaubrecht, Brinkmann, Krailas	26.07.2010
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB113272	Central America and the Antilles: Cuba: Pinar del Rio: Rio Santiago; N 22° 51.59' W 83° 2.81'	Schneider	13.12.2007
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB113295	Central America and the Antilles: Guatemala: Izabal: Rio Sauce, E El Estor (Izabal); N 15° 33.03' W 89° 16.97'	Schneider	23.03.2007
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB114033	Asia: Thailand: Phitsanulok Prov.: Kaek River, K5, Poi waterfall, 60 km E of Phitsanulok; N 16° 50.75' E 100° 45.06'	Köhler	20.02.2006
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB114168	Asia: Vietnam: Lao Cai: river 10km W of Lao Cai (town); N 22° 25.408' E 104° 1.579'	Köhler	17.03.2006
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB114980	Asia: Laos: Savannakhet Prov.: clear creak Houay Ki in Ban Phon Xay 12 km SW Sepone (on rocks); N 16° 40.7' E 106° 7.77'	Köhler, Püschel	11.11.2007
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB127609	Asia: Indonesia: Timor: Lutu-Ira, Ira-Ara village, Lautern District, Large spring pool, Quite stronly running outflow stream in the village, limestone; S 8° 20.535' E 127° 1.132'	Kessner	23.05.2011
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB190256	Asia: Philippines: Mindanao: Mountain stream nr Calinan; N 7° 14.77' E 125° 23.92'	Köhler, Schütt	06.04.2000
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB190883a	Asia: Indonesia: Central Sulawesi: Lake Poso, W shore, bay of Bancea; S 1° 59.489' E 120° 35.223'	Glaubrecht, von Rintelen	29.03.2004
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB191454a	Indonesia: North Maluku: Halmahera: River, road Sidangoli - Tobelo; N 0° 55.176' E 127° 37.711'		19.09.2005
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB191458	Asia: Indonesia: Central Sulawesi: Peleng Island, W peninsula, E of Alani, river with lake-like extension; S 1° 28.315' E 122° 52.473'	von Rintelen, Zitzler	27.09.2005
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB191465	Asia: Indonesia: Central Java: Karanganyat, river, Tributary of Ci Tanduy River, at road Ciamis - Yogyakarta; S 7° 19.863' E 108° 38.519'	Zitzler, Lamers	14.09.2005
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB191879	Asia: Indonesia: South Sulawesi: Lake Mahalona, E shore; S 2° 35.56' E 121° 30.77'	von Rintelen	16.11.2002
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB192758	Asia: Indonesia: East Java: Malang: Batu: Ngantang; S 7° 51' E 122° 22'	Heryanto, Isnaningsih, Afi	04.07.2006
<i>Tarebia granifera</i> (Lamarck, 1822)	ZMB200325	India: Karnataka: Western Ghats: Mountain river c. 40km W of Madikeri, Road 88 Mangalore – Mysore;	Köhler, Schütt	
<i>Thiara amarula</i> (Linnaeus, 1758)	ZMB106354	Australia: Australia: Queensland: North Johnston River; S 17° 30.34' E 145° 59.55'	Glaubrecht, von Rintelen, Brinkmann	15.05.2002
<i>Thiara amarula</i> (Linnaeus, 1758)	ZMB107217	Australia: Australia: Queensland: Granite Creek, W of Bloomsfield; S 15° 55.99' E 145° 19.54'	Glaubrecht, Brinkmann	14.10.2007
<i>Thiara amarula</i> (Linnaeus, 1758)	ZMB107220	Australia: Australia: Queensland: Barron River, below 150 m Lake Placid; S 16° 52.17' E 145° 40.405'	Glaubrecht, Brinkmann	17.10.2007
<i>Thiara amarula</i> (Linnaeus, 1758)	ZMB107364	Asia: Indonesia: Central Sulawesi: Peleng Island, W peninsula, Tataban River; S 1° 32.294' E 122° 51.465'	Glaubrecht, Schultz	05.11.2008

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<i>Thiara amarula</i> (Linnaeus, 1758)	ZMB107472	Indonesia: North Maluku: Ambon: Central part of Leihitu, between Wakal and Hitu Lama, small stream; S 3° 35.46' E 128° 8.697'	Glaubrecht	24.10.2008
<i>Thiara amarula</i> (Linnaeus, 1758)	ZMB107585	Australia: Queensland: Mowbraw River, near Port Douglas; S 16° 33.812' E 145° 27.877'	Glaubrecht, Brinkmann	11.10.2009
<i>Thiara amarula</i> (Linnaeus, 1758)	ZMB191489	Indonesia: North Maluku: Obi: River, close to sea, c. 20km SW of Laiwui; S 1° 26.71' E 127° 29.01'	von Rintelen	24.09.2005
<i>Thiara australis</i> (Lea & Lea, 1851)	AMS427964	Australia: West Australia: Ord River, 150m below Kununurra Diversion Dam, on W side of River; S 15° 47.48' E 128° 41.58'	Ponder, Walker, Puslednik	13.06.2003
<i>Thiara australis</i> (Lea & Lea, 1851)	AMS461355	Australia: Northern Territory: Arnhem Land: Numbulwar - Roper River road, Mumpumumpu Outstation, Phelp River drainage, Mumpumumpu Waterhole; S 14° 22.979' E 135° 19.559'	Ponder, Kessner	10.07.2007
<i>Thiara australis</i> (Lea & Lea, 1851)	AMS461368	Australia: Northern Territory: Arnhem Land: eastern Goyder River crossing, Central Arnhem Road; S 13° 1.619' E 134° 58.62'	Ponder, Kessner	02.07.2007
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB106698	Australia: Northern Territory: Top End: Katherine River, 500 m downstream from Lower Land Bridge at Springvale Homestead detour; S 14° 29.49' E 132° 14.73'	Glaubrecht	29.09.2005
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB106701a	Australia: Northern Territory: Top End: Howard River, crossing; S 12° 27.752' E 131° 5.008'	Glaubrecht, Brinkmann	01.10.2005
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB106706	Australia: Queensland: Gregory River at Riversleigh (Gregory River Catchment); S 19° 1.116' E 138° 43.529'	Page	
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB106709	Australia: Northern Territory: Top End: Blueys Creek on The Savannah Way (Clavert River Catchment); S 16° 56.066' E 137° 21.578'	Page	
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107264	Australia: Northern Territory: Top End: Daly River Crossing; S 13° 46.026' E 130° 42.688'	Glaubrecht, Brinkmann	02.10.2007
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107286	Australia: Northern Territory: Top End: Little Roper River, at crossing; S 14° 55.581' E 133° 7.176'	Glaubrecht, Brinkmann	23.10.2007
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107290	Australia: Northern Territory: Top End: Berry Springs, S of Darwin; S 12° 42.111' E 130° 59.854'	Glaubrecht, Brinkmann	24.10.2007
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107554	Australia: Northern Territory: Adelaide River; S 13° 10.353' E 131° 11.501'	Glaubrecht, Brinkmann	01.10.2009
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107556	Australia: Northern Territory: Elsey Falls at junction of Salt Creek, 50 m above confluence with Roper River, below Mataranka Falls; S 14° 57.412' E 133° 15.103'	Glaubrecht, Brinkmann	02.10.2009
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107569	Australia: Northern Territory: MacArthur River, Borroloola; S 16° 4.889' E 136° 19.148'	Glaubrecht, Brinkmann	04.10.2009
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107573	Australia: Northern Territory: Robinson River, West of border to Queensland; S 16° 28.27' E 137° 2.995'	Glaubrecht, Brinkmann	04.10.2009
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107574	Australia: Queensland: O'Shanassy River, nr Riversleigh; S 19° 1.322' E 138° 45.697'	Glaubrecht, Brinkmann	05.10.2009
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107579	Australia: Queensland: Bynoe River, west of Normanton; S 17° 51.685' E 140° 48.231'	Glaubrecht, Brinkmann	06.10.2009
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107620	Australia: Northern Territory: Wabalarr, Roper River, E of 4 Mile Point on way to Jalmurark; S 14° 56.028' E 133° 10.44'	Glaubrecht, Brinkmann	22.10.2009
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB107628	Australia: Northern Territory: Howard Springs Creek; S 12° 27.268' E 131° 3.108'	Glaubrecht, Brinkmann	24.10.2009

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<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB127628	Australia: Australia: Queensland: Gregory River, at crossing, Gregory Downs; S 18° 38.829' E 139° 14.912'	Glaubrecht, Gimmich, Maaß	26.09.2011
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB127630	Australia: Australia: Queensland: Bynoe River, at crossing; S 17° 51.719' E 140° 48.067'	Glaubrecht, Gimmich, Maaß	27.09.2011
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB127631	Australia: Australia: Queensland: Norman River, at Glenmore, crossing at old bridge; S 17° 51.228' E 141° 8.047'	Glaubrecht, Gimmich, Maaß	28.09.2011
<i>Thiara australis</i> (Lea & Lea, 1851)	ZMB127748	Australia: Northern Territory: Top End: Daly River, at Ooloo crossing; S 14° 4.24' E 131° 15.084'	Glaubrecht, Gimmich, Maaß	03.10.2011
<i>Thiara cancellata</i> Röding, 1798	ZMB107489	Asia: Indonesia: Central Sulawesi: Peleng Island, W peninsula, Tataban River; S 1° 32.294' E 122° 51.465'	Glaubrecht, Schultz	05.11.2008
<i>Thiara cancellata</i> Röding, 1799	ZMB191431a	Indonesia: North Maluku: Obi: Small river, W of Laiwui; S 1° 21.613' E 127° 36.421'	von Rintelen	23.09.2005
<i>Thiara mirifica</i> (A. Adams, 1853)	ZMB107473	Indonesia: North Maluku: Ambon: Central part of Leihitu, between Wakal and Hitu Lama, small stream; S 3° 35.46' E 128° 8.697'	Glaubrecht	24.10.2008
<i>Thiara mirifica</i> (A. Adams, 1853)	ZMB191270	Asia: Indonesia: Southeast Sulawesi: Small river at Sukamaju, road Kendari - Lapuko; S 3° 59.28' E 122° 34.96'	von Rintelen, Zitzler	01.06.2005
<i>Thiara mirifica</i> (A. Adams, 1853)	ZMB191429	Indonesia: North Maluku: Obi: River, close to sea, c. 20km SW of Laiwui; S 1° 26.71' E 127° 29.01'	von Rintelen	24.09.2005
<i>Thiara winteri</i> (von dem Busch, 1842)	ZMB106554	Indonesia: Bali: South Bali: Yehembang, E of Mendaya; S 8° 23.641' E 114° 45.064'	Glaubrecht, Brinkmann	25.09.2003
<i>Thiara winteri</i> (von dem Busch, 1842)	ZMB190261	Indonesia: South Sulawesi: Kalaena catchment: Kalaena River; S 2° 35.57' E 120° 54.17'	Glaubrecht, von Rintelen, Schütt	27.08.1999
<i>Thiara cf. winteri</i> (von dem Busch, 1842)	ZMB106472	Indonesia: Bali: South Bali: Yehembang, E of Mendaya; S 8° 23.641' E 114° 45.064'	Glaubrecht, Brinkmann	25.09.2003
<i>Thiara cf. winteri</i> (von dem Busch, 1842)	ZMB191279	Asia: Indonesia: Bali: South Bali: Yehembang River, at Yehembang; S 8° 23.602' E 114° 45.067'	Glaubrecht, von Rintelen, Zitzler	04.06.2005
<i>Thiara cf. winteri</i> (von dem Busch, 1842)	ZMB191279a	Asia: Indonesia: Bali: South Bali: Yehembang River, at Yehembang; S 8° 23.602' E 114° 45.067'	Glaubrecht, von Rintelen, Zitzler	04.06.2005
" <i>Thiara</i> " <i>aspera</i> (Lesson, 1831)	ZMB106704a	Australia: Northern Territory: Top End: Berry Springs; S 12° 42.153' E 130° 59.875'	Glaubrecht, Brinkmann	01.10.2005
" <i>Thiara</i> " <i>aspera</i> (Lesson, 1831)	ZMB107377	Asia: Indonesia: Central Sulawesi: Peleng Island, W peninsula, Tataban River; S 1° 32.294' E 122° 51.465'	Glaubrecht, Schultz	05.11.2008
" <i>Thiara</i> " <i>aspera</i> (Lesson, 1831)	ZMB107378	Asia: Indonesia: Central Sulawesi: Peleng Island, W peninsula, Tataban River; S 1° 32.294' E 122° 51.465'	Glaubrecht, Schultz	05.11.2008
" <i>Thiara</i> " <i>aspera</i> (Lesson, 1831)	ZMB107617	Australia: Australia: Northern Territory: Wabalarr, Roper River, E of 4 Mile Point on way to Jalmurark; S 14° 56.028' E 133° 10.44'	Glaubrecht, Brinkmann	22.10.2009
" <i>Thiara</i> " <i>aspera</i> (Lesson, 1831)	ZMB191262	Asia: Indonesia: Southeast Sulawesi: Simbune River, c. 1km NE of Raterate, road Kendari - Kolaka; S 4° 2.326' E 121° 54.204'	Glaubrecht, von Rintelen, Zitzler	30.05.2005
" <i>Thiara</i> " <i>aspera</i> (Lesson, 1831)	ZMB191268a	Asia: Indonesia: Southeast Sulawesi: River at Tinobu, road Andowia - Kendari; S 3° 39.461' E 122° 13.861'	Glaubrecht	01.06.2005
" <i>Thiara</i> " <i>aspera</i> (Lesson, 1831)	ZMB191488	Asia: Indonesia: Bali: South Bali: Stream SW of Gumicik; S 8° 38.648' E 115° 16.626'	Glaubrecht	27.10.2005

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<i>Cubaedomus brevis</i> (Orbigny, 1832)	ZMB107174	Central America and the Antilles: Cuba: Pinar del Rio: El Punto;	Gutiérrez	18.10.2006
<i>Hemisinus lineolatus</i> (W. Wood, 1828)	ZMB107126	Jamaica: Middlesex: Manchester: Black River, N of Oxford, 212m and upstream; N 18° 12.341' W 77° 37.67'	Schubart, Reuschel, Santl	10.10.2005
<i>Pachymelania fusca</i> (Gmelin, 1791)	ZMB191443	Africa: Nigeria		
<i>Paludomus petrosa</i> (Gould, 1844)	ZMB107881	Asia: Thailand Pranburi river at Palak Waterfall, SW of Phetchaburi; N 12° 32.24' E 99°28.092`	Glaubrecht, Brinkmann, Krailas	27.07.2010
<i>Paludomus siamensis</i> W.T. Blanford, 1903	ZMB107910	Asia: Thailand: Lampang Ban Mae Tha, SE of Lampang, from NE to Mae Nam Wang River drainage; N 18°7.117'E 99°37.414`	Glaubrecht, Brinkmann, Krailas;	31.07.2010

Table S2. GenBank accession and voucher numbers for specimens used in this study. For locality data, see Supporting Information, Table S1. Sequences marked with na are not yet submitted to GenBank

Taxon	Museum ID	Extract. No.	COI	16S	28S	H3
<i>Balanocochlis glans</i>	ZMB191147	1806	na	na	na	na
<i>Balanocochlis glans</i>	ZMB107366	6493	na	na	na	na
<i>Balanocochlis glans</i>	ZMB107493	6506	na	na		
<i>Balanocochlis glans</i>	ZMB107492	6501	na	na		
<i>Balanocochlis glans</i>	ZMB107491	6500	na	na		
<i>Balanocochlis glans</i>	ZMB107490	6499	na	na		
<i>Balanocochlis glans</i>	ZMB106470	1025	na	na		
<i>Balanocochlis glans</i>	ZMB106469	1044	na	na		
<i>Balanocochlis glans</i>	ZMB106468	1026	na	na		
<i>Balanocochlis glans</i>	ZMB107292	5806	na	na		
<i>Balanocochlis glans</i>	FLMNH308204	6683	na	na		
<i>Fijidoma maculata</i>	ZMB106379	0508	na	na	na	na
<i>Melanoides admirabilis</i>	ZMB220096a	2819	na	na		
<i>Melanoides jugicostis</i>	ZMB191499	2892	na	na	na	na
<i>Melanoides jugicostis</i>	ZMB107717	7346	na	na	na	na
<i>Melanoides jugicostis</i>	ZMB113598	7347	na	na	na	na
<i>Melanoides jugicostis</i>	ZMB127446	9228	na	na		
<i>Melanoides jugicostis</i>	SUT0210025	8081	na	na		
<i>Melanoides jugicostis</i>	ZMB127447	9229	na	na		
<i>Melanoides jugicostis</i>	ZMB127448	9230	na	na		
<i>Melanoides nodicincta</i>	ZMB107180	5122 8165	na	na		
<i>Melanoides tuberculata</i>	ZMB107129	2855	na	na	na	na
<i>Melanoides tuberculata</i>	ZMB107193	8158 5134	na	na	na	na
<i>Melanoides tuberculata</i>	ZMB200313	2820	MK879274 ^a	MK879411 ^a	na	na
<i>Melanoides tuberculata</i>	ZMB200313	7530	na	na		
<i>Melanoides tuberculata</i>	ZMB107128	2857	na	na	na	na
<i>Melanoides tuberculata</i>	ZMB107125	2860	na	na	na	na
<i>Melanoides tuberculata</i>	ZMB107130	2865	na	na		
<i>Melanoides tuberculata</i>	ZMB127613	8187	na	na		
<i>Melanoides tuberculata</i>	ZMB106690a	1823	na	na		
<i>Melanoides tuberculata</i>	ZMB106592	4077	na	na		
<i>Melanoides tuberculata</i>	ZMB107183	5125	na	na		
<i>Melanoides tuberculata</i>	ZMB112662	7531	na	na		
<i>Melanoides tuberculata</i>	ZMB117498	8606	na	na		
<i>Melanoides tuberculata</i>	ZMB117496	8604	na	na		
<i>Melanoides tuberculata</i>	ZMB127444	9226	na	na		
<i>Melanoides tuberculata</i>	ZMB107536	6919	na	na	na	na
<i>Melanoides tuberculata</i>	ZMB107538	6920	na	na		
<i>Melanoides tuberculata</i>	ZMB127019	7867	na	na	na	na
<i>Melanoides tuberculata</i>	ZMB127078	7876 8145	na	na		
<i>Melanoides tuberculata</i>	ZMB193945	7540	na	na		
<i>Melanoides tuberculata</i>	ZMB104177	7533	na	na		
<i>Melanoides tuberculata</i>	ZMB193926	6330	na	na		
<i>Melanoides tuberculata</i>	ZMB190964a	2937	na	na	na	na
<i>Melanoides tuberculata</i>	ZMB190830a	3000	na	na		
<i>Melanoides tuberculata</i>	ZMB107424	6509	na	na	na	na
<i>Melanoides tuberculata</i>	ZMB127610	8182	na	na		
<i>Melanoides tuberculata</i>	SUT0210024	8050	na	na		
<i>Melanoides tuberculata</i>	ZMB114441	7908	na	na		
<i>Melanoides tuberculata</i>	ZMB107921	7353	na	na		
<i>Melanoides tuberculata</i>	SUT0210006	8088	na	na		
<i>Melanoides tuberculata</i>	ZMB107876	7351	na	na		
<i>Melanoides tuberculata</i>	ZMB107204	5145	na	na		
<i>Melanoides</i> sp.	ZMB107407	6510	na	na	na	na

<i>Melasma onca</i>	ZMB106636a	1781	na	na	na	na
<i>Melasma onca</i>	ZMB107549	7598	na	na		
<i>Melasma onca</i>	ZMB106673a	4086	na	na		
<i>Melasma onca</i>	ZMB107625	7591	na	na		
<i>Melasma onca</i>	ZMB107619	7588	na	na		
<i>Melasma onca</i>	ZMB106617a	1863	na	na		
<i>Melasma onca</i>	ZMB107550	7326 7314	na	na		
<i>Melasma onca</i>	AMS461370	6105	na	na		
<i>Mieniplotia scabra</i>	ZMB191487	2885	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB191258a	2227	na	na		
<i>Mieniplotia scabra</i>	ZMB107564	7340	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB107216	4781	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB191264a	2199	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB191498	2891	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB106552	1140	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB191265a	4563	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB106679	1832	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB191253	4564	na	na		
<i>Mieniplotia scabra</i>	ZMB107408	6515	na	na		
<i>Mieniplotia scabra</i>	ZMB107382	6514	MK879279 ^a	MK879416 ^a		
<i>Mieniplotia scabra</i>	ZMB107879	7349	na	na		
<i>Mieniplotia scabra</i>	ZMB107575	7344	na	na		
<i>Mieniplotia scabra</i>	ZMB106425	1096	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB113595	7345	na	na		
<i>Mieniplotia scabra</i>	ZMB107392	6511	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB114990	7535	na	na	na	na
<i>Mieniplotia scabra</i>	ZMB191037a	4570	na	na		
<i>Mieniplotia scabra</i>	ZMB107443	6512	na	na		
<i>Mieniplotia scabra</i>	ZMB107386	6517	na	na		
<i>Mieniplotia scabra</i>	ZMB107371	6516	na	na		
<i>Neoradina prasongi</i>	ZMB127590	11435	na	na		
<i>Plotiopsis balonnensis</i>	ZMB106583a	1512	na	na	na	na
<i>Plotiopsis balonnensis</i>	ZMB106686	1827	na	na	na	na
<i>Plotiopsis balonnensis</i>	ZMB106728	2815	na	na	na	na
<i>Plotiopsis balonnensis</i>	ZMB106345	1031	na	na		
<i>Plotiopsis balonnensis</i>	ZMB107946a	7521	na	na		
<i>Plotiopsis balonnensis</i>	ZMB107951	7524	na	na		
<i>Plotiopsis balonnensis</i>	ZMB107956	7527	na	na		
<i>Plotiopsis balonnensis</i>	ZMB107950	7523	na	na		
<i>Plotiopsis balonnensis</i>	ZMB107948a	7522	na	na		
<i>Plotiopsis balonnensis</i>	ZMB192391	4165	na	na		
<i>Plotiopsis balonnensis</i>	ZMB106689a	4100	na	na		
<i>Plotiopsis balonnensis</i>	ZMB106689a	1824	na	na		
<i>Plotiopsis balonnensis</i>	ZMB106688a	1825	na	na		
<i>Plotiopsis balonnensis</i>	ZMB106687	1826	na	na		
<i>Plotiopsis balonnensis</i>	ZMB107583	7991	na	na		
<i>Plotiopsis balonnensis</i>	ZMB127615	8224	na	na		
<i>Ripalania queenslandica</i>	ZMB107214	4779	na	na	na	na
<i>Sermyla carbonata</i>	ZMB107615	7584	na	na	na	na
<i>Sermyla carbonata</i>	WAM10048	7664	na	na	na	na
<i>Sermyla carbonata</i>	ZMB106713	2859	na	na	na	na
<i>Sermyla carbonata</i>	ZMB192019	3799	na	na	na	na
<i>Sermyla carbonata</i>	ZMB106595a	4104	na	na		
<i>Sermyla carbonata</i>	ZMB107627	7593	na	na		
<i>Sermyla carbonata</i>	ZMB107545	8742	na	na		
<i>Sermyla carbonata</i>	ZMB107228	7605	na	na		
<i>Sermyla carbonata</i>	ZMB107210	4775	na	na		
<i>Sermyla carbonata</i>	ZMB107630	7596	na	na		
<i>Sermyla carbonata</i>	ZMB106700a	1857 4016 4110	na	na		

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<i>Sermyla carbonata</i>	ZMB106593a	1867 4103	na	na		
<i>Sermyla carbonata</i>	ZMB107544	7309 7321	na	na		
<i>Sermyla carbonata</i>	ZMB107231	8728	na	na		
<i>Sermyla carbonata</i>	ZMB107558	7319 7331	na	na		
<i>Sermyla carbonata</i>	ZMB107616	7585	na	na		
<i>Sermyla carbonata</i>	ZMB107621	8733	na	na		
<i>Sermyla carbonata</i>	ZMB107562	7529	na	na		
<i>Sermyla carbonata</i>	ZMB107561	7597	na	na		
<i>Sermyla carbonata</i>	ZMB107557	8729	na	na		
<i>Sermyla carbonata</i>	ZMB107235	4805	na	na		
<i>Sermyla carbonata</i>	AMS461353	6095	na	na		
<i>Sermyla kupaensis</i>	ZMB191388	3052	na	na	na	na
<i>Sermyla kupaensis</i>	ZMB191388	2181	na	na		
<i>Sermyla riqueti</i>	ZMB107883	7354	na	na	na	na
<i>Sermyla riqueti</i>	ZMB106474	1027	na	na		
<i>Sermyla riqueti</i>	ZMB107886	7355	na	na		
<i>Stenomelania aspirans</i>	ZMB107586	7555	na	na	na	na
<i>Stenomelania aspirans</i>	ZMB107211	4776	na	na		
<i>Stenomelania aspirans</i>	ZMB107511	6913	na	na		
<i>Stenomelania aspirans</i>	ZMB191212a	2176	na	na	na	na
<i>Stenomelania aspirans</i>	ZMB191210a	2175	na	na	na	na
<i>Stenomelania aspirans</i>	ZMB106390	1012	na	na		
<i>Stenomelania aspirans</i>	ZMB107212	7582 4777	na	na		
<i>Stenomelania plicaria</i>	ZMB106391	1448	na	na	na	na
<i>Stenomelania punctata</i>	ZMB107483	6508	na	na	na	na
<i>Stenomelania</i> sp.	ZMB106344	1064	na	na		
<i>Stenomelania</i> sp.	ZMB107453	6537	na	na	na	na
<i>Stenomelania</i> sp.	ZMB107457	6539	na	na	na	na
<i>Stenomelania</i> sp.	ZMB107454	6538	na	na		
<i>Stenomelania</i> sp.	ZMB107468	6541	na	na		
<i>Stenomelania</i> sp.	ZMB107460	6540	na	na	na	na
<i>Stenomelania</i> sp.	ZMB191208a	2223	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107449	6507	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB127607	8176	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107242	4813	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB106682	7599	MK879288 ^a	MK879425 ^a		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107629	7595	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107239	4897	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107233	7606	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB106632	7602	MK879287 ^a	MK879424 ^a		
" <i>Stenomelania</i> " <i>denisoniensis</i>	AMS461371	6106	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB106586	1516	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107248	4819	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107584	7992	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107588	7995	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB106339	1035	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107963	7526	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107955	7525	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB106340	1485	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB106340	1018	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB127442	9224	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	SUT0210030	8051	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	SUT0210034	7763	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107719	7348	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	SUT0210026	7860	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107866	7754	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107867	7350	na	na		
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107230	4800	na	na	na	na
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107237	4895	na	na		
<i>Stenomelania</i> sp.	ZMB190354	1061	na	na		

<i>Tarebia granifera</i>	ZMB107396	6521	na	na		
<i>Tarebia granifera</i>	ZMB106518	1091	na	na	na	na
<i>Tarebia granifera</i>	ZMB106518a	1470	na	na	na	na
<i>Tarebia granifera</i>	ZMB107384	6524	na	na		
<i>Tarebia granifera</i>	ZMB107360	6525	na	na		
<i>Tarebia granifera</i>	ZMB200325	1469	na	na	na	na
<i>Tarebia granifera</i>	ZMB114168	6534	na	na	na	na
<i>Tarebia granifera</i>	ZMB191458	2866	na	na	na	na
<i>Tarebia granifera</i>	ZMB114033	6533	na	na		
<i>Tarebia granifera</i>	ZMB191879	1144	na	na		
<i>Tarebia granifera</i>	ZMB107409	6527	na	na		
<i>Tarebia granifera</i>	ZMB107400	6526	na	na		
<i>Tarebia granifera</i>	ZMB107381	6520	na	na		
<i>Tarebia granifera</i>	ZMB107367	6518	na	na		
<i>Tarebia granifera</i>	ZMB107442	6522	na	na		
<i>Tarebia granifera</i>	ZMB107422	6528	na	na		
<i>Tarebia granifera</i>	ZMB190883a	3018	na	na	na	na
<i>Tarebia granifera</i>	ZMB191454a	6523	na	na	na	na
<i>Tarebia granifera</i>	ZMB127609	8180	na	na	na	na
<i>Tarebia granifera</i>	ZMB191465	2869	na	na	na	na
<i>Tarebia granifera</i>	ZMB107533	6917	na	na	na	na
<i>Tarebia granifera</i>	ZMB192758	7537	na	na		
<i>Tarebia granifera</i>	ZMB190256	1104	na	na		
<i>Tarebia granifera</i>	ZMB113295	6530	na	na		
<i>Tarebia granifera</i>	ZMB113272	6531	na	na		
<i>Tarebia granifera</i>	ZMB114980	6532	na	na		
<i>Tarebia granifera</i>	ZMB107877	7356	na	na		
<i>Thiara amarula</i>	ZMB106354	2870	na	na	na	na
<i>Thiara amarula</i>	ZMB107220	4785	na	na	na	na
<i>Thiara amarula</i>	ZMB107217	4782	na	na		
<i>Thiara amarula</i>	ZMB107585	7993	na	na		
<i>Thiara amarula</i>	ZMB191489	2886	MK879289 ^b	MK879426 ^b	na	na
<i>Thiara amarula</i>	ZMB107364	6491	na	na		
<i>Thiara amarula</i>	ZMB107472	6496	MK094074 ^a	MK098355 ^a		
<i>Thiara australis</i>	ZMB106698	1836	na	na	na	na
<i>Thiara australis</i>	AMS427964	3076	na	na	na	na
<i>Thiara australis</i>	ZMB106706	1845	na	na	na	na
<i>Thiara australis</i>	ZMB106709	1866	na	na	na	na
<i>Thiara australis</i>	ZMB107264	4837	na	na	na	na
<i>Thiara australis</i>	ZMB107290	4916	na	na	na	na
<i>Thiara australis</i>	ZMB107579	7990	na	na	na	na
<i>Thiara australis</i>	ZMB107286	4878	na	na		
<i>Thiara australis</i>	ZMB107569	7341	na	na		
<i>Thiara australis</i>	ZMB107620	7589	na	na		
<i>Thiara australis</i>	ZMB107573	7342	na	na		
<i>Thiara australis</i>	AMS461368	6104	na	na		
<i>Thiara australis</i>	ZMB106701a	1855 4019	na	na		
<i>Thiara australis</i>	ZMB107554	7316	na	na		
<i>Thiara australis</i>	ZMB107556	7318	na	na		
<i>Thiara australis</i>	ZMB127630	8367	na	na		
<i>Thiara australis</i>	ZMB127631	8377	na	na		
<i>Thiara australis</i>	ZMB127748	9320	na	na		
<i>Thiara australis</i>	ZMB107628	7594	na	na		
<i>Thiara australis</i>	ZMB127628	8320	na	na		
<i>Thiara australis</i>	ZMB127628	8321	na	na		
<i>Thiara australis</i>	ZMB107574	7343	na	na		
<i>Thiara australis</i>	AMS461355	6097	na	na		
<i>Thiara cancellata</i>	ZMB107489	6498	na	na	na	na
<i>Thiara cancellata</i>	ZMB191431a	2817	na	na	na	na
<i>Thiara mirifica</i>	ZMB191429	2883	na	na	na	na

<i>Thiara mirifica</i>	ZMB191270	2881	na	na	na	na
<i>Thiara mirifica</i>	ZMB107473	6497	na	na		
<i>Thiara winteri</i>	ZMB106554	1043	MK879301 ^a	MK879439 ^a	na	na
<i>Thiara winteri</i>	ZMB190261	1055	MK879302 ^a	MK879440 ^a		
<i>Thiara cf. winteri</i>	ZMB191279	4559	MK879300 ^a	MK879438 ^a	na	na
<i>Thiara cf. winteri</i>	ZMB191279a	2232	MK879299 ^a	MK879437 ^a		
<i>Thiara cf. winteri</i>	ZMB106472	1001	MK879298 ^a	MK879436 ^a	na	na
" <i>Thiara</i> " <i>aspera</i>	ZMB107377	6494	MK879293 ^a	MK879429 ^a	na	na
" <i>Thiara</i> " <i>aspera</i>	ZMB191262	4561	na	na	na	na
" <i>Thiara</i> " <i>aspera</i>	ZMB191488	4558	MK879297 ^a	MK879435 ^a	na	na
" <i>Thiara</i> " <i>aspera</i>	ZMB107378	6495	MK879294 ^a	MK879430 ^a	na	na
" <i>Thiara</i> " <i>aspera</i>	ZMB191268a	2200	MK879296 ^a	MK879434 ^a		
" <i>Thiara</i> " <i>aspera</i>	ZMB106704a	2811	na	na	na	na
" <i>Thiara</i> " <i>aspera</i>	ZMB107617	7586	MK879295 ^a	MK879295 ^a		
<i>Cubaedomus brevis</i>	ZMB107174	3493	na	na	na	na
<i>Hemisinus lineolatus</i>	ZMB107126	2849	na	na	na	na
<i>Pachymelania fusca</i>	ZMB191443	2507	na	na	na	na
<i>Paludomus petrosa</i>	ZMB107881	7336	na	na	na	na
<i>Paludomus siamensis</i>	ZMB107910	7338	na	na	na	na

^aBoonmekam, D., Krailas, D., Gimnich, F., Neiber, M. T., & Glaubrecht, M. (2019). A glimpse in the dark? A first phylogenetic approach in a widespread freshwater snail from tropical Asia and northern Australia (Cerithioidea, Thiariidae). *Zoosystematics and Evolution*, 95(2), 373–390.

^bNeiber, M. T., & Glaubrecht, M. (2019). Unparalleled disjunction or unexpected relationships? Molecular phylogeny and biogeography of Melanopsidae (Caenogastropoda: Cerithioidea), with the description of a new family and a new genus from the ancient continent Zealandia. *Cladistics*, 35(4), 401–425.

Table S3. Clades observed in the phylogeny based on mitochondrial and nuclear sequences and their reproductive mode. K = eu-viviparous, R = ovo-viviparous, O = oviparous.

Clade (represented by one specimen each)	Reproductive mode	Reference for reproductive mode
<i>Thiara aspera</i> _ZMB106704a_2811	K	Boonmekam (2019)
<i>Stenomelania denisoniensis</i> _ZMB107239_4897	K	Glaubrecht et al. (2009)
<i>Stenomelania denisoniensis</i> _ZMB127442_9224	K	Wiggering et al. (2019)
<i>Melanoides tuberculata</i> _ZMB190964a_2937	K	Dudgeon (1986)
<i>Melanoides tuberculata</i> _ZMB107424_6509	K	Dudgeon (1986)
<i>Stenomelania denisoniensis</i> _ZMB107242_4813	K	Glaubrecht et al. (2009)
<i>Tarebia granifera</i> _ZMB191458_2866	K	Abbott (1952), Veeravechsukij et al. (2018)
<i>Tarebia granifera</i> _ZMB191454a_6523	K	Abbott (1952), Veeravechsukij et al. (2018)
<i>Melanoides tuberculata</i> _ZMB127019_1_7867	K	Dudgeon (1986)
<i>Thiara australis</i> _ZMB106706_1845	K	Glaubrecht et al. (2009)
<i>Mieniplotia scabra</i> _ZMB114990_7535	K	Glaubrecht et al. (2009)
<i>Mieniplotia scabra</i> _ZMB106425_1096	K	Glaubrecht et al. (2009)
<i>Melanoides tuberculata</i> _ZMB200313_2820	K	Dudgeon (1986)
<i>Melanoides tuberculata</i> _ZMB107536_6919	K	Dudgeon (1986)
<i>Sermyla carbonata</i> _ZMB107615_7584	K	Lentge-Maaß et al. (in press)
<i>Plotiopsis balonensis</i> _ZMB106686_1827	K	Glaubrecht et al. (2009)
<i>Melanoides jugicostis</i> _ZMB191499_2892	K	Dechruska et al. (2013)
<i>Melanoides sp.</i> _ZMB107407_6510	K	Dudgeon (1986)
<i>Stenomelania aspirans</i> _ZMB191212a_2176	R	Seshaiya (1940), Glaubrecht (1996, 2006), Wiggering et al. (2019)
<i>Tarebia granifera</i> _ZMB106518a_1470	K	Abbott (1952), Veeravechsukij et al. (2018)
<i>Fijidoma maculata</i> _ZMB106379_0508	K	Haynes (1988)
<i>Melasma onca</i> _ZMB106636a_1781	K	Glaubrecht et al. (2009)
<i>Balanocochlis glans</i> _ZMB191147_1806	R	Glaubrecht (2006)
<i>Stenomelania sp.</i> _ZMB191208a_2223	R	Seshaiya (1940), Glaubrecht (1996, 2006), Wiggering et al. (2019)
<i>Stenomelania punctata</i> _ZMB106391_1448	R	Seshaiya (1940), Glaubrecht (1996, 2006), Wiggering et al. (2019)
<i>Sermyla kupaensis</i> _ZMB191388_3052	R	Lentge-Maaß et al. (in press)
<i>Thiara amarula</i> _ZMB106354_2870	R	Schütt & Glaubrecht (1999)
<i>Ripalania queenslandica</i> _ZMB107214_4779	R	Glaubrecht et al. (2009)
<i>Thiara mirifica</i> _ZMB191429_2883	R	Glaubrecht (2006)
<i>Thiara cancellata</i> _ZMB191431a_2817	R	Glaubrecht (2006)
<i>Cubaensis brevis</i> _ZMB107174_3493	K	Glaubrecht (1996)
<i>Hemisinus lineolatus</i> _ZMB107126_2849	K	Gomez (2011)
<i>Pachymelania fuscus</i> _ZMB191443_2507	O	Glaubrecht (1996)
<i>Paludomus siamensis</i> _ZMB107910_7338	O	Abbott (1952)

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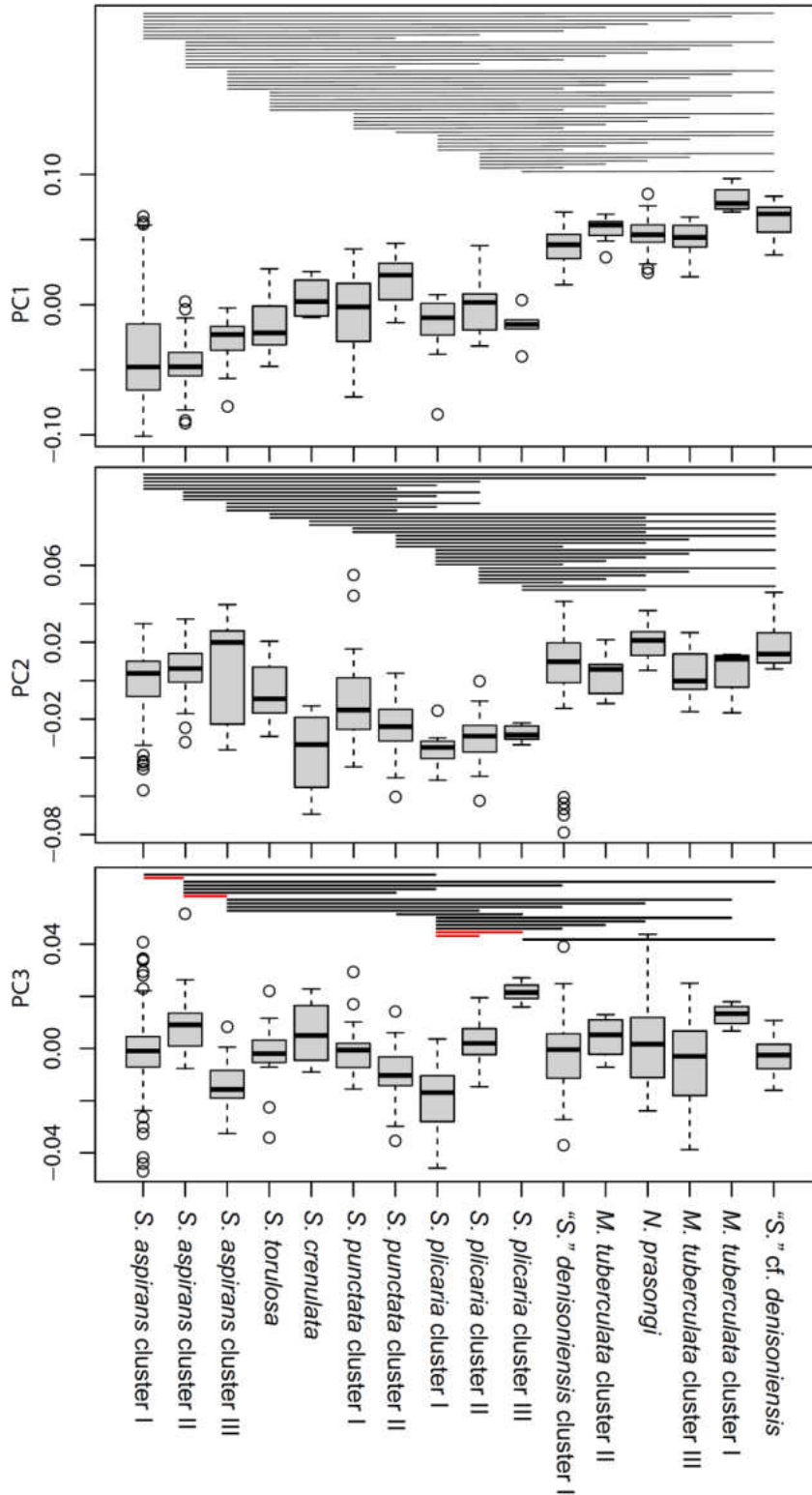


Figure S1 Results of geometric morphometrics analysis with sliding landmarks. Differences between shell shapes of genetic clusters on PC1 PC2 and PC3. Significant differences ($P < 0.05$) are indicated by bars above boxplots, with each bar beginning and end indicates significant differences between two groups. Bars coloured red indicate significant differences within a species.

Table S1 Material examined with all collectors and sample dates, as well as sample localities.

Species	Museum ID	Type status	Location	Collector	Date collected	Coordinates	Remarks
<i>Melania aspirans</i>	NHMUK 1844.9.23.3 1-32	Syntype s	Fiji				
<i>Melania aspirans</i>	NHMUK 20010760	Possible Syntype s	Fiji				
<i>Melania aspirans</i>	NHMUK 20010761	Possible Syntype s	Fiji				
<i>Stenomelania aspirans</i>	ZMB107586		Australia Queensland Mowbray River, near Port Douglas	Glaubrecht, Brinkmann	11-Okt-09	S16°33.812' E145°27.877'	
<i>Stenomelania aspirans</i>	ZMB106392		Fiji, Sovi River, Malevu, Coral Coast	Glaubrecht	16-Jun-02	S18°10,49' E177°34,36'	
<i>Stenomelania aspirans</i>	ZMB106390		Fiji Viti Levu Coral Coast Sovi River, Malevu	Glaubrecht	15-Jun-02	S18°10,49' E177°34,36'	
<i>Stenomelania aspirans</i>	ZMB107454		Indonesia Central Sulawesi Peleng Island, W peninsula, Tataban River;	Glaubrecht, Schultz	05-Nov-08	S1°32,294' E122°51,465'	
<i>Stenomelania aspirans</i>	ZMB191222		Indonesia, Central Sulawesi, Luwuk Peninsula, Freshwater spring in Malotong, West of Ampana, brackish water pool	Glaubrecht, von Rintelen, Zitzler	27-Mai-05	S0°53,125' E121°31,371'	
<i>Stenomelania aspirans</i>	ZMB191222 a		Indonesia, Central Sulawesi, Luwuk Peninsula, Freshwater spring in Malotong, West of Ampana, brackish water pool	Glaubrecht, von Rintelen, Zitzler	27-Mai-05	S0°53,125' E121°31,371'	
<i>Stenomelania aspirans</i>	ZMB191215		Indonesia, Central Sulawesi, Luwuk Peninsula, River in Samaku, North coast of Balantak Peninsula	Glaubrecht, von Rintelen, Zitzler	24-Mai-05	S0°37.804' E122°54.844'	
<i>Stenomelania aspirans</i>	ZMB191215 a		Indonesia, Central Sulawesi, Luwuk Peninsula, River in Samaku, North coast of Balantak Peninsula	Glaubrecht, von Rintelen, Zitzler	24-Mai-05	S0°37.804' E122°54.844'	
<i>Stenomelania aspirans</i>	ZMB191209		Indonesia, Central Sulawesi, Luwuk Peninsula, Stream into Bolo Bay	Glaubrecht, von Rintelen, Zitzler	24-Mai-05	S0°45.131' E122°58.478'	
<i>Stenomelania aspirans</i>	ZMB191209 a		Indonesia, Central Sulawesi, Luwuk Peninsula, Stream into Bolo Bay	Glaubrecht, von Rintelen, Zitzler	24-Mai-05	S0°45.131' E122°58.478'	
<i>Stenomelania aspirans</i>	ZMB107326		Indonesia, Central Sulawesi, River at road between Tinombo and Moutong	Glaubrecht, von Rintelen	23-Mai-07	N0°30.756' E120°32.765'	
<i>Stenomelania aspirans</i>	ZMB107326 a		Indonesia, Central Sulawesi, River at road between Tinombo and Moutong	Glaubrecht, von Rintelen	23-Mai-07	N0°30.756' E120°32.765'	

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<i>Stenomelania aspirans</i>	ZMB190342		Indonesia, Central Sulawesi, Stream at road between Poso and Palu	von Rintelen, Brinkmann	24-Mär-00	S1°19.06' E120°38.34'	
<i>Stenomelania aspirans</i>	ZMB107475		Indonesia, Maluku Utara, Ambon, Central part of Leihitu, between Wakal and Hitu Lama, small stream	Glaubrecht	24-Okt-08	S3°35.46' E128°8.697'	
<i>Stenomelania aspirans</i>	ZMB107468		Indonesia North Maluku Ambon Western part of Leihitu, river NE of Liliboi at road Passo - Liliboi	Glaubrecht	22-Okt-08	S3°44.747' E128°1.558'	
<i>Stenomelania aspirans</i>	ZMB107453		Indonesia North Maluku Obi S coast, Wayaloar, mouth of river c. 20-50m from sea	von Rintelen	27-Okt-08	S1°43.122' E127°36.855'	
<i>Stenomelania aspirans</i>	ZMB107457		Indonesia Maluku Seram North Seram, coastal road Piru - Latuhelu, nr. Kawa, small stream;	Glaubrecht	23-Okt-08	S3°0.321' E128°7.461'	
<i>Stenomelania aspirans</i>	ZMB107037		Indonesia, South Bali, Gumbrih River, 500m from sea at river bank	Glaubrecht, Brinkmann	10-Okt-03	S8°26.542' E114°52.598'	
<i>Stenomelania aspirans</i>	ZMB191512		Indonesia, South Bali, Petanu River, between road crossing Sothwest of Saba and estuary	Glaubrecht	27-Okt-05	S8°36.569' E115°18.789'	
<i>Stenomelania aspirans</i>	ZMB190324		Indonesia, South Sulawesi, Kalaena catchment, Kalaena River	Glaubrecht, von Rintelen, Schütt	27-Aug-99	S2°35.57' E120°54.17'	
<i>Stenomelania aspirans</i>	ZMB191231		Indonesia, South Sulawesi, Kupa, river, East of road between Makassar and Parepare	Glaubrecht, von Rintelen, Zitzler	02-Jun-05	S4°7.567' E119°37.426'	
<i>Stenomelania aspirans</i>	ZMB191231 a		Indonesia, South Sulawesi, Kupa, river, East of road between Makassar and Parepare	Glaubrecht, von Rintelen, Zitzler	02-Jun-05	S4°7.567' E119°37.426'	
<i>Stenomelania aspirans</i>	ZMB190321		Indonesia, South Sulawesi, Malili catchment, Malili River estuary	Glaubrecht, von Rintelen, Schütt	27-Aug-99	S2°38.48' E121°5.11'	
<i>Stenomelania aspirans</i>	ZMB191226		Indonesia, Sulawesi, Southeast Sulawesi, River at Tinobu, road between Andowia and Kendari	Glaubrecht	01-Jun-05	S3°39.461' E122°13.861'	
<i>Stenomelania aspirans</i>	ZMB191226 a		Indonesia, Sulawesi, Southeast Sulawesi, River at Tinobu, road between Andowia and Kendari	Glaubrecht	01-Jun-05	S3°39.461' E122°13.861'	
<i>Stenomelania aspirans</i>	ZMB191210		Indonesia Southeast Sulawesi Small river at Sukamaju, road Kendari - Lapuko;	von Rintelen, Zitzler	01-Jun-05	S3°59.28' E122°34.96'	
<i>Stenomelania aspirans</i>	ZMB191210 a		Indonesia Southeast Sulawesi Small river at Sukamaju, road Kendari - Lapuko	von Rintelen, Zitzler	01-Jun-05	S3°59.28' E122°34.96'	
<i>Stenomelania aspirans</i>	ZMB107511		Indonesia West Papua Batanta Sungai Samsen, Desau Wailebet;	EWIN II Expedition	02-Mai-08	S0°52.136' E130°38.368'	

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<i>Stenomelania aspirans</i>	ZMB107990		Indonesia, West Papua, South of Bird's Neck, Kaimana 35-40 km, Triton bay, River Lengguru valley upriver from Oray village	Greke	13-Sep-10	S3°43.433' E134°6.1'	
<i>Stenomelania aspirans</i>	ZMB190347		Philippines, Luzon, Barangay Masaya near Los Banos, concrete irrigation ditch	Köhler, Schütt	28-Mär-00	N14°15.31' E121°24.4'	
<i>Stenomelania aspirans</i>	ZMB230151		Indonesia, Maluku Utara, Ambon, Eastern part of Leihitu, at Watatiri, road between Passo and Natsepa	Glaubrecht	21-Okt-08	S9°37,052' E128°16,262'	
<i>Melania figurata</i>	NHMUK 1844.9.23.2 7-28	Syntype s	New Ireland				junior synonym of <i>S. aspirans</i>
<i>Melania figurata</i>	NHMUK 20010763	Possible Syntype s	New Ireland				junior synonym of <i>S. aspirans</i>
<i>Melania macrospira</i>	NHMUK	Possible Syntype s	New Caledonia				junior synonym of <i>S. aspirans</i>
<i>Melania picta</i>	NHMUK 20010772	Possible Syntype	New Ireland				junior synonym of <i>S. aspirans</i>
<i>Melania veruculum</i>	MNHN-IM- 2000-33263	Syntype s	Samoa				junior synonym of <i>S. aspirans</i>
<i>Stenomelania crenulata</i>	ZMB107306		Japan, Ryukyu Islands, Okinawa		03.08.2008	N26°39' E127°53'	
<i>Stenomelania crenulata</i>	ZMB107302		Japan, Ryukyu Islands, Tanegashima		03.07.2008	N30°27' E130°57'	
<i>Helix plicaria</i>	NHMW 14393	Holotyp e					
<i>Stenomelania plicaria</i>	ZMB230150		Indonesia, South Bali, Petanu River, between road crossing South of Saba and estuary	Glaubrecht	27-Okt-05	S8°36.569' E115°18.789'	
<i>Stenomelania plicaria</i>	ZMB106391		Melanesia Fiji Viti Levu Creek at Lawai, tributary of Singatoka River	Glaubrecht	16-Jun-02	S18°7,05' E177°31,42'	
<i>Stenomelania plicaria</i>	ZMB106396		Fiji, Sovi River, Malevu, Coral Coast	Glaubrecht	15-Jun-02	S18°10,49' E177°34,36'	
<i>Stenomelania plicaria</i>	ZMB106386		Fiji, Sovi River, Malevu, Coral Coast	Glaubrecht	15-Jun-02	S18°10,49' E177°34,36'	
<i>Stenomelania plicaria</i>	ZMB191223		Indonesia, Central Sulawesi, Pondo River, South of Uekuli, Gandalari	Glaubrecht, von Rintelen, Zitzler	28-Mai-05	S1°27.585' E121°6.406'	

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<i>Stenomelania plicaria</i>	ZMB191223a		Indonesia, Central Sulawesi, Pondo River, South of Uekuli, Gandalari	Glaubrecht, von Rintelen, Zitzler	28-Mai-05	S1°27.585' E121°6.406'	
<i>Stenomelania plicaria</i>	ZMB191463		Indonesia, Java, Central Java, River South of Bagelen, tributary of Bogowonio River, at road between Purworejo and Yogyakarta	Zitzler, Lamers	14-Sep-05	S7°52.001' E110°2.539'	
<i>Stenomelania plicaria</i>	ZMB107480		Indonesia, Maluku, Seram, West Seram, road between Masohi and Piru, South of Waisarisa, side arm of large river	Glaubrecht	23-Okt-08	S3°15.681' E128°18.354'	
<i>Stenomelania plicaria</i>	ZMB190348		Philippines, Luzon, Stream near coast at Botolan	Köhler, Schütt	30-Mär-00	N15°14' E120°1'	
<i>Melania auroriana</i>	ANSP 60060	Type	Aurora Island, New Hebrides				junior synonym of <i>S. plicaria</i>
<i>Melania fumosa</i>	NHMUK 20010767	Possible Syntype	New Ireland; in the streams about Port Carteret				junior synonym of <i>S. plicaria</i>
<i>Melania fumosa</i>	NHMUK 1844.9.23.25	Syntypes	New Ireland; in the streams about Port Carteret				junior synonym of <i>S. plicaria</i>
<i>Stenomelania punctata</i>	ZMB191219a		Indonesia, Central Sulawesi, Luwuk Peninsula, River East of Uso, North of Batui	Glaubrecht, von Rintelen, Zitzler	26-Mai-05	S1°15.42' E122°34.651'	
<i>Stenomelania punctata</i>	ZMB107440		Indonesia, Maluku Utara, Ambon, Eastern part of Leihitu, at Watatiri, road between Passo and Natsepa	Glaubrecht	21-Okt-08	S9°37.052' E128°16.262'	
<i>Stenomelania punctata</i>	ZMB107483		Indonesia North Maluku Ambon Eastern part of Leihitu, at Watatiri, road Passo - Natsepa	Glaubrecht	21-Okt-08	S9°37.052' E128°16.262'	
<i>Stenomelania punctata</i>	ZMB191504		Indonesia, Maluku Utara, Obi, Laiwui River, at Laiwui	von Rintelen, Zitzler, Lamers	21-Sep-05	S1°20.367' E127°38.763'	
<i>Stenomelania punctata</i>	ZMB107070		Indonesia, Sulawesi, North East Sulawesi, Minahasa, near Batuputih, small river	Kotrba	01.08.2004	S1°8.04' E120°4.53'	
<i>Stenomelania punctata</i>	ZMB107512		Indonesia, West Papua, Pulau Batanta, Sungai Pangkarin, Desau Wailebet	EWIN II Expedition	03-Mai-08	- 0.852022081239 8939,130.48441 89583405	
<i>Stenomelania punctata</i>	ZMB107516		Indonesia, West Papua, Pulau Batanta, Sungai Samsen, Desau Wailebet	EWIN II Expedition	03-Mai-08	- 0.834124689223 0909,130.73876 265410306	
<i>Stenomelania punctata</i>	ZMB127188		Indonesia, West Papua, Warboy River, close to Kampung Mega	Franz	06-Sep-10	S0°36.457' E131°57.42'	
<i>Stenomelania punctata</i>	ZMB107996		Indonesia, West Papua, Fak-Fak peninsula, 10km East of Fak-Fak	Greke	26-Sep-10	N2°56.533' E132°23.016'	

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<i>Stenomelania punctata</i>	ZMB230152		Indonesia, Central Sulawesi, River at road between Tinombo and Moutong	Glaubrecht, von Rintelen	23-Mai-07	N0°30.756' E120°32.765'	
<i>Melania fulgurans</i>	NHMUK 20010766	Possible Syntype	New Ireland				junior synonym of <i>S. punctata</i>
<i>Melania papuensis</i>	MNHN-IM 2000-33241	Type	New Guinea, Harbour Dorey				junior synonym of <i>S. punctata</i>
<i>Stenomelania torulosa</i>	ZMB106820		Indonesia, Southeast Sulawesi, Ussu River, at Ussu, Northwest of Malili	Glaubrecht	09-Sep-03	- 2.594127776347 762,121.088174 3408659	
<i>Stenomelania torulosa</i>	ZMB127457		Thailand, Klong Than Trip	Glaubrecht, Krailas, Boonmekam	09-Mär-12	N8°9.939' E98°47.661'	
<i>Stenomelania torulosa</i>	ZMB127458		Thailand, Klong Than Trip	Glaubrecht, Krailas, Boonmekam	09-Mär-12	N8°9.939' E98°47.661'	
<i>Melania denisoniensis</i>	MHNG (Syntype series)	Syntype s	Australia, Queensland, Port Denison				
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB191652		Indonesia, Java, West Java, Lake Cangkuang, East of Leles on road to Cibatu	Glaubrecht, von Rintelen	23-Mär-06	S7°6.012' E107°55.036'	
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB192117		Indonesia, Java, West Java, Rice paddy and canal at road between Cisolok and Bayah	von Rintelen	05-Mai-07	S6°54.626' E106°21.845'	
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB192112		Indonesia, South Sulawesi, River at road between Bulukumba and Sinxi	Glaubrecht, von Rintelen	27-Mai-07	S5°19.659' E120°7.97'	
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB192112 a		Indonesia, South Sulawesi, River at road between Bulukumba and Sinxi	Glaubrecht, von Rintelen	27-Mai-07	S5°19.659' E120°7.97'	
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB127249		Indonesia, West Papua, Sentani			- 2.569872701953 0954,140.56115 184840914	
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB127249 a		Indonesia, West Papua, Sentani			- 2.569872701953 0954,140.56115 184840914	
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB190357		Philippines, Mindanao, Mountain stream near Calinan	Köhler, Schütt	06-Apr-00	N7°14.77' E125°23.92'	
" <i>Stenomelania</i> " <i>denisoniensis</i>	ZMB107867		Thailand W of Ko Nang to Kao Tong, W of Krabi	Glaubrecht, Brinkmann, Krailas	25-Jul-10	N8°5.772' E98°48.535'	

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<i>"Stenomelania" denisoniensis</i>	ZMB127575		Thailand, Ban Sa Kaeow	Glaubrecht, Glaubrecht 2, Krailas	08-Feb-13	N9°10,112' E98°48,457	
<i>"Stenomelania" denisoniensis</i>	ZMB127442		Thailand Khao Thong	Glaubrecht, Krailas, Boonmekam	08-Mär-12	N8°10,405' E98°44,939'	
<i>"Stenomelania" denisoniensis</i>	ZMB127459		Thailand, Wiphiawadi waterfall, East to Khanon, below highway bridge	Glaubrecht, Krailas, Boonmekam	10-Mär-12	N9°8.266' E99°40.309'	
<i>"Stenomelania" cf. denisoniensis</i>	ZMB127253		Indonesia, Westpapua	von Rintelen	10.10.2015		
<i>"Stenomelania" cf. denisoniensis</i>	ZMB127250		Indonesia, Westpapua	von Rintelen	06.10.2015		
<i>"Stenomelania" cf. denisoniensis</i>	ZMB127250 a		Indonesia, Westpapua	von Rintelen	06.10.2015		
<i>"Stenomelania" cf. denisoniensis</i>	ZMB127252		Indonesia, Westpapua	von Rintelen			
<i>Neritida tuberculata</i>	ZMUC	Syntype s	India Coramandel coast				
<i>Melanoides tuberculata</i>	ZMB200313		India Tamil Nadu Moyar River in Theppakadu, Bandipur N.P.;	Köhler, Schütt			
<i>Melanoides tuberculata</i>	ZMB191036 a		Indonesia, North Sulawesi, Minahasa, stream between rice fields, tributary of Lake Tondano, ca. 500 m from lake	von Rintelen, Zitzler	13-Aug-04	S1°11,228' E124°52,192'	
<i>Melanoides tuberculata</i>	ZMB191021		Indonesia, South Sulawesi, Matano catchment, Matano, stream South of village, ca. 50 m from lake	von Rintelen, Zitzler	23-Jul-04		
<i>Melanoides tuberculata</i>	ZMB191021 a		Indonesia, South Sulawesi, Matano catchment, Matano, stream South of village, ca. 50 m from lake	von Rintelen, Zitzler	23-Jul-04		
<i>Melanoides tuberculata</i>	ZMB127248		Indonesia, West Papua, outlet Sentani				
<i>Melanoides tuberculata</i>	ZMB127251 a		Indonesia, West Papua, Sentani	von Rintelen			
<i>Melanoides tuberculata</i>	ZMB107992		Indonesia, West Papua, South Bird's Neck, 35-40 km East of Kaimana, Triton bay, River Lengguru valley upriver from Oray village	Greke	13-Sep-10	S3°43.433' E134°6.1'	
<i>Melanoides tuberculata</i>	ZMB127573		Thailand, 7 km Northwest of Krabi, Ban Khlong Chilat	Glaubrecht, Glaubrecht 2, Krailas	08-Feb-13	8°5.185'N98°52. 613' E	

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<i>Melanoides tuberculata</i>	ZMB127444		Thailand Khao Thong	Glaubrecht, Krailas, Boonmekam	08-Mär-12	8°10.405'N98°4 4.939' E	
<i>Neoradina prasongi</i>	SMF 215933	Holotyp e	Thailand, Stream about 7 km from Grabi to Kao Tong				
<i>Neoradina prasongi</i>	GMN 3950	Paratype s	Thailand, Stream about 7 km from Grabi to Kao Tong				
<i>Neoradina prasongi</i>	ZMH 59289	Paratype s	Thailand, Stream about 7 km from Grabi to Kao Tong				
<i>Neoradina prasongi</i>	SMF 215934	Paratype s	Thailand, Stream about 7 km from Grabi to Kao Tong				
<i>Neoradina prasongi</i>	ZMB127590		Thailand Chalung city, Klong Chalung, Muang distict	Glaubrecht, Glaubrecht 2, Krailas	09-Feb-13	N6°43.618' E100°3.756'	
<i>Neoradina prasongi</i>	ZMB127582		Thailand, Trang province, Siako district, Mai Fad, Pak Meng river, at Pak Meng, 30km North of Trang,	Glaubrecht, Glaubrecht 2, Krailas	08-Feb-13	N7°29.681' E99°20.573'	
<i>Cubaensis brevis</i>	ZMB107174		Central America and the Antilles Cuba Pinar del Rio El Punto;	Gutiérrez	18-Okt-06		
<i>Hemisinus lineolatus</i>	ZMB107126		Jamaica Middlesex Manchester Black River, N of Oxford, 212m and upstream;	Schubart, Reuschel, Santl	10-Okt-05	N18°12.341' W77°37.67'	
<i>Pachymelania fuscus</i>	ZMB191443		Africa, Nigeria				
<i>Paludomus petrosa</i>	ZMB107881		Asia: Thailand Pranburi river at Palak Waterfall, SW of Phetchaburi	Glaubrecht, Brinkmann, Krailas	27.07.2010	32.24` E99°28.092`	
<i>Paludomus siamensis</i>	ZMB107910		Asia: Thailand: Lampang Ban Mae Tha, SE of Lampang, from NE to Mae Nam Wang River drainage;	Glaubrecht, Brinkmann, Krailas	31.07 2010	N18°7.117` E99°37.414`;	

Table S2 GenBank accession numbers for each genetic sequence provided by this study, as well as other sequences and their respective source. Sequences marked with na are not yet submitted to GenBank

	ID	Lab no	16S	COI	Source
<i>Stenomelania aspirans</i>	ZMB107037-1		na	na	
<i>Stenomelania aspirans</i>	ZMB107037-3		na	na	
<i>Stenomelania aspirans</i>	ZMB191512-1		na	na	
<i>Stenomelania aspirans</i>	ZMB190347-1		na	na	
<i>Stenomelania aspirans</i>	ZMB107326a-1		na	na	
<i>Stenomelania aspirans</i>	ZMB191215a-3		na	na	
<i>Stenomelania aspirans</i>	ZMB191209a-1		na	na	
<i>Stenomelania aspirans</i>	ZMB191209a-3		na	na	
<i>Stenomelania aspirans</i>	ZMB191222a-3		na	na	
<i>Stenomelania aspirans</i>	ZMB190342-3		na	na	
<i>Stenomelania aspirans</i>	ZMB190342-4		na	na	
<i>Stenomelania aspirans</i>	ZMB107454-1	ZMBCA6538	na	na	
<i>Stenomelania aspirans</i>	ZMB191226a-1		na	na	
<i>Stenomelania aspirans</i>	ZMB191226a-2		na	na	
<i>Stenomelania aspirans</i>	ZMB191210a-1	ZMBCA2175	MK719184	MK697736	Wiggering et al 2018
<i>Stenomelania aspirans</i>	ZMB191210a-3		MK719185	MK697737	Wiggering et al 2018
<i>Stenomelania aspirans</i>	ZMB190324-1	ZMBCA1528	na	na	
<i>Stenomelania aspirans</i>	ZMB190321-2		na	na	
<i>Stenomelania aspirans</i>	ZMB191231a-1		na	na	
<i>Stenomelania aspirans</i>	ZMB191231a-2		na	na	
<i>Stenomelania aspirans</i>	ZMB107453-1	ZMBCA6537	na	na	
<i>Stenomelania aspirans</i>	ZMB107453-3		na	na	
<i>Stenomelania aspirans</i>	ZMB107457-1	ZMBCA6539	MK719182	MK697723	Wiggering et al 2018
<i>Stenomelania aspirans</i>	ZMB107475-2		na	na	
<i>Stenomelania aspirans</i>	ZMB107468-1		na	na	
<i>Stenomelania aspirans</i>	ZMB107511		na	na	
<i>Stenomelania aspirans</i>	ZMB107990-2	ZMHLN4557	na	na	
<i>Stenomelania aspirans</i>	ZMB106392-1		MK719177	MK697718	Wiggering et al 2018
<i>Stenomelania aspirans</i>	ZMB106390-1	ZMBCA1012	MK719175	MK697716	Wiggering et al 2018
<i>Stenomelania aspirans</i>	ZMB107586-1	ZMBCA7555	MK719183	MK697724	Wiggering et al 2018
<i>Stenomelania aspirans</i>	ZMB230151-2		na	na	
<i>Stenomelania crenulata</i>	ZMB107306-1		na	na	
<i>Stenomelania crenulata</i>	ZMB107306-3		na	na	
<i>Stenomelania denisoniensis</i>	ZMB127575-2		MK719198	MK697734	Wiggering et al 2018
<i>Stenomelania denisoniensis</i>	ZMB127442-1	ZMBCA9224	MK719190	MK697727	Wiggering et al 2018
<i>Stenomelania denisoniensis</i>	ZMB127459-1		MK719195	MK697732	Wiggering et al 2018
<i>Stenomelania denisoniensis</i>	ZMB127459-2		MK719196	MK697733	Wiggering et al 2018
<i>Stenomelania denisoniensis</i>	ZMB192117-2		na	na	
<i>Stenomelania denisoniensis</i>	ZMB191652-4	ZMBCA3754	na	na	
<i>Stenomelania denisoniensis</i>	ZMB190357-2		na	na	
<i>Stenomelania denisoniensis</i>	ZMB192112-2		na	na	

<i>Stenomelania denisoniensis</i>	ZMB127249a-2	ZMHLN4528	na	na	
<i>Stenomelania denisoniensis</i>	ZMB127250a-1		na	na	
<i>Stenomelania denisoniensis</i>	ZMB127250a-2		na	na	
<i>Stenomelania denisoniensis</i>	ZMB127252-1	ZMHLN4563	na	na	
<i>Stenomelania denisoniensis</i>	ZMB127253-1		na	na	
<i>Stenomelania denisoniensis</i>	ZMB107867-1	ZMBCA7350	MK719189	MK697726	Wiggering et al 2018
<i>Stenomelania plicaria</i>	ZMB191463-1		na	na	
<i>Stenomelania plicaria</i>	ZMB191463-3		na	na	
<i>Stenomelania plicaria</i>	ZMB190348-1		na	na	
<i>Stenomelania plicaria</i>	ZMB190348-2		na	na	
<i>Stenomelania plicaria</i>	ZMB191223a-3		na	na	
<i>Stenomelania plicaria</i>	ZMB107480-1		na	na	
<i>Stenomelania plicaria</i>	ZMB107480-2		na	na	
<i>Stenomelania plicaria</i>	ZMB106391-1	ZMBCA1448	MK719176	MK697717	Wiggering et al 2018
<i>Stenomelania plicaria</i>	ZMB106396-1		MK719180	MK697721	Wiggering et al 2018
<i>Stenomelania plicaria</i>	ZMB106396-2		MK719181	MK697722	Wiggering et al 2018
<i>Stenomelania plicaria</i>	ZMB106386-1		MK719179	MK697719	Wiggering et al 2018
<i>Stenomelania plicaria</i>	ZMB230150-3		na	na	
<i>Stenomelania punctata</i>	ZMB191504-3		na	na	
<i>Stenomelania punctata</i>	ZMB107070-3		na	na	
<i>Stenomelania punctata</i>	ZMB191219a-3		na	na	
<i>Stenomelania punctata</i>	ZMB107440-1		na	na	
<i>Stenomelania punctata</i>	ZMB107483-1	ZMBCA6508	na	na	
<i>Stenomelania punctata</i>	ZMB107996-1	ZMHLN4526	na	na	
<i>Stenomelania punctata</i>	ZMB127188-1	ZMHLN4531	na	na	
<i>Stenomelania punctata</i>	ZMB127188-2	ZMHLN4532	na	na	
<i>Stenomelania punctata</i>	ZMB107516-3	ZMHLN4539	na	na	
<i>Stenomelania punctata</i>	ZMB107512-2	ZMHLN4542	na	na	
<i>Stenomelania punctata</i>	ZMB107512-3	ZMHLN4543	na	na	
<i>Stenomelania punctata</i>	ZMB107512-6	ZMHLN4544	na	na	
<i>Stenomelania punctata</i>	ZMB230152-3		na	na	
<i>Stenomelania crenulata</i>	ZMB107302-1		na	na	
<i>Stenomelania crenulata</i>	ZMB107302-3		na	na	
<i>Stenomelania torulosa</i>	ZMB127457-1		MK719191	MK697728	Wiggering et al 2018
<i>Stenomelania torulosa</i>	ZMB127457-2		MK719192	MK697729	Wiggering et al 2018
<i>Stenomelania torulosa</i>	ZMB127458-1		MK719193	MK697730	Wiggering et al 2018
<i>Stenomelania torulosa</i>	ZMB127458-5		MK719194	MK697731	Wiggering et al 2018
<i>Stenomelania torulosa</i>	ZMB106820-4		na	na	
<i>Melanoides tuberculata</i>	ZMB191036a-3		na	na	
<i>Melanoides tuberculata</i>	ZMB191021a-3		na	na	
<i>Melanoides tuberculata</i>	ZMB127248-1	ZMHLN4529	na	na	
<i>Melanoides tuberculata</i>	ZMB107992-2	ZMHLN4548	na	na	
<i>Melanoides tuberculata</i>	ZMB127251a-4	ZMHLN4562	na	na	
<i>Melanoides tuberculata</i>	ZMB127444-1	ZMBCA9226	MK719160	MK697710	Wiggering et al 2018
<i>Melanoides tuberculata</i>	ZMB127573-1	ZMBCA11432	MK719161	MK697711	Wiggering et al 2018

<i>Melanoides tuberculata</i>	ZMB127573-3		MK719162	MK697712	Wiggering et al 2018
<i>Melanoides tuberculata</i>	ZMB200313-1	ZMBCA2820	MK719163	MK697735	Wiggering et al 2018
<i>Neoradina prasongi</i>	ZMB127582-1	ZMBCA11434	MK719166	MK697713	Wiggering et al 2018
<i>Neoradina prasongi</i>	ZMB127590-1	ZMBCA11435	MK719165	MK697738	Wiggering et al 2018
<i>Cubaedomus brevis</i>	ZMB107174	ZMBCA3493	na	na	Glaubrecht & Wiggering et al
<i>Hemisinus lineolatus</i>	ZMB107126	ZMBCA2849	na	na	Glaubrecht & Wiggering et al
<i>Pachymelania fusca</i>	ZMB191443	ZMBCA2507	na	na	Glaubrecht & Wiggering et al
<i>Paludomus petrosa</i>	ZMB107881	ZMBCA7336	na	na	Glaubrecht & Wiggering et al
<i>Paludomus siamensis</i>	ZMB107910	ZMBCA7338	na	na	Glaubrecht & Wiggering et al

Table S3 Brood pouch content data. * in the sources collum refers to Wiggering et al. (2019).

Species	Museum ID	Amount of offspring	eggs	embryos	to 0.5 mm	0.6 to 1.0 mm	1.1 to 1.5 mm	1.6 to 2.0 mm	2.1 to 2.5 mm	2.6 to 3.0 mm	over 3.0 mm	source
<i>Stenomelania aspirans</i>	ZMB 106390-1	12800	12800	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 106390-2	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 106390-3	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 106390-4	9470	9470	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 106390-5	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 106390-6	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 106390-7	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 106392-10	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-11	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-12	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-3	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-4	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-5	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-6	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-7	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-8	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 106392-9	0	0	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 107037-1	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107037-2	3200	3200	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107037-3	2800	2800	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107037-4	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107037-5	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107511-4	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107511-5	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107511-6	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107511-7	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107511-8	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107511-9	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107586-1	14423	14423	0	0	0	0	0	0	0	0	*
<i>Stenomelania aspirans</i>	ZMB 107990-1	8074	8074	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107990-2	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 191215-1	3500	0	3500	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 191215-2	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 191215a-1	940	940	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 191215a-2	1410	1410	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 191215a-3	3200	3200	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107326-1	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107326-2	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107326-3	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107326a-1	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 107326a-2	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB190321-1	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB190321-2	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB190321-3	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 190324-1	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 190324-2	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 190324-3	0	0	0	0	0	0	0	0	0	0	
<i>Stenomelania aspirans</i>	ZMB 190324-4	0	0	0	0	0	0	0	0	0	0	

Stenomelania aspirans	ZMB 190324-5	0	0	0	0	0	0	0	0	0	0	
Stenomelania aspirans	ZMB 190324-6	0	0	0	0	0	0	0	0	0	0	
Stenomelania aspirans	ZMB 190324-7	0	0	0	0	0	0	0	0	0	0	
Stenomelania crenulata	ZMB 107306-1	0	0	0	0	0	0	0	0	0	0	
Stenomelania crenulata	ZMB 107306-2	0	0	0	0	0	0	0	0	0	0	
Stenomelania crenulata	ZMB 107306-3	0	0	0	0	0	0	0	0	0	0	
Stenomelania crenulata	ZMB 107302-1	590	0	590	0	0	0	0	0	0	0	
Stenomelania crenulata	ZMB 107302-2	550	0	550	0	0	0	0	0	0	0	
Stenomelania crenulata	ZMB 107302-3	830	0	830	0	0	0	0	0	0	0	
Stenomelania plicaria	ZMB 106386-1	5232	5232	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106386-2	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106386-3	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106391-1	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-1	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-10	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-2	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-3	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-4	598	598	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-5	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-6	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-7	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-8	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 106396-9	0	0	0	0	0	0	0	0	0	0	*
Stenomelania plicaria	ZMB 191463-1	9700	9700	0	0	0	0	0	0	0	0	
Stenomelania plicaria	ZMB 191463-2	10200	10200	0	0	0	0	0	0	0	0	
Stenomelania plicaria	ZMB 191463-4	8000	8000	0	0	0	0	0	0	0	0	
Stenomelania plicaria	ZMB 191463-5	0	0	0	0	0	0	0	0	0	0	
Stenomelania plicaria	ZMB 191463-6	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-1	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-10	1556	1556	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-2	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-3	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-4	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-5	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-6	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-7	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-8	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107512-9	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107516-1	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107516-2	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107516-3	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107516-4	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107996-1	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 127188-1	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 127188-2	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 127188-3	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 127188-4	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 127188-5	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 127188-6	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107070-1	350	350	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107070-2	460	460	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107070-3	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107070-4	340	340	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 107070-5	420	420	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 191504-1	1540	1540	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 191504-2	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 191504-3	2400	2400	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 191504-4	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 191504-5	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 191504-6	0	0	0	0	0	0	0	0	0	0	
Stenomelania punctata	ZMB 230152-3	0	0	0	0	0	0	0	0	0	0	
Stenomelania torulosa	ZMB 127457-1	2874	2874	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127457-2	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127457-3	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127457-4	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127457-5	1976	1976	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127457-6	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127457-7	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127458-1	537	537	0	0	0	0	0	0	0	0	*

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Stenomelania torulosa	ZMB 127458-2	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127458-3	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127458-4	232	232	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127458-5	973	973	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127458-6	1242	1242	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127458-7	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127458-8	0	0	0	0	0	0	0	0	0	0	*
Stenomelania torulosa	ZMB 127458-9	355	355	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127249-1	5	0	0	0	0	2	1	1	1	0	
"Stenomelania" denisoniensis	ZMB 127249-10	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127249-2	8	0	0	0	0	6	1	0	0	1	
"Stenomelania" denisoniensis	ZMB 127249-3	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127249-4	1	0	0	0	1		0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127249-5	8	0	0	5	1	0	0	1	0	1	
"Stenomelania" denisoniensis	ZMB 127249-6	4	0	0	0	2	0	1	0	1	0	
"Stenomelania" denisoniensis	ZMB 127249-7	6	0	0	1	2	1	1	1	0	0	
"Stenomelania" denisoniensis	ZMB 127249-8	4	0	0	0	2	1		0	1	0	
"Stenomelania" denisoniensis	ZMB 127249-9	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127249a-1	5	0	0	0	0	2	0	2	0	1	
"Stenomelania" denisoniensis	ZMB 127249a-2	5	0	0	0	1	2	0	0	1	1	
"Stenomelania" denisoniensis	ZMB 127249a-3	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127250a-1	17	0	3	3	5	3	3	0	0	0	
"Stenomelania" denisoniensis	ZMB 127250a-2	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127250a-3	7	0	2	0	0	0	2	3	0	0	
"Stenomelania" denisoniensis	ZMB 127250a-4	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127250a-5	8	5	0	0	3	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127250a-6	10	2	2	0	6	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 127442-1	21	0	0	8	0	0	11	2	0	0	*
"Stenomelania" denisoniensis	ZMB 127442-10	32	0	2	7	6	9	7	1	0	0	*
"Stenomelania" denisoniensis	ZMB 127442-2	24	0	10	4	0	2	3	2	0	3	*
"Stenomelania" denisoniensis	ZMB 127442-3	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127442-4	24	0	4	10	3	6	1	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127442-5	17	0	0	11	3	2	1	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127442-6	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127442-7	13	0	0	0	2	0	2	6	2	1	*
"Stenomelania" denisoniensis	ZMB 127442-8	12	0	0	3	1	3	0	2	0	3	*
"Stenomelania" denisoniensis	ZMB 127442-9	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-1	30	0	12	0	17	1	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-10	29	0	0	12	7	6	4	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-2	44	19	10	3	6	5	1	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-3	20	0	0	6	12	0	2	0	0	0	*

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"Stenomelania" denisoniensis	ZMB 127459-4	44	0	12	10	19	3	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-5	47	0	19	16	8	4	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-6	33	0	0	3	6	8	16	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-7	72	26	20	8	3	6	9	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-8	14	0	0	5	4	2	3	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127459-9	26	0	10	3	5	8	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-1	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-10	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-2	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-3	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-4	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-5	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-6	1	0	0	0	0	1	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-7	14	0	0	14	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-8	0	0	0	0	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 127575-9	7	2	1	4	0	0	0	0	0	0	*
"Stenomelania" denisoniensis	ZMB 191652-1	31	0	0	3	7	10	5	3	3	0	
"Stenomelania" denisoniensis	ZMB 191652-2	15	0	0	0	4	3	1	2	3	2	
"Stenomelania" denisoniensis	ZMB 191652-3	300	300	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-1	50	50	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-10	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-2	79	35	13	30	1	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-3	31	0	0	12	8	3	4	2	0	2	
"Stenomelania" denisoniensis	ZMB 192117-4	55	0	0	8	21	17	9	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-5	3	0	0	0	1	2	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-6	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-7	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-8	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192117-9	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192112-1	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192112-2	9	0	0	5	2	1	1	0	0	0	
"Stenomelania" denisoniensis	ZMB 192112-3	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192112-4	0	0	0	0	0	0	0	0	0	0	
"Stenomelania" denisoniensis	ZMB 192112-5	3	0	0	0	0	1	2	0	0	0	
"S." cf denisoniensis	ZMB 127253-1	27	0	0	0	6	6	5	8	2	0	
"S." cf denisoniensis	ZMB 127253-10	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127253-11	48	0	7	2	8	18	12	1	0	0	
"S." cf denisoniensis	ZMB 127253-12	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127253-2	18	0	1	0	8	6	2	1	0	0	
"S." cf denisoniensis	ZMB 127253-3	61	0	0	3	13	20	18	7	0	0	

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"S." cf denisoniensis	ZMB 127253-4	50	0	4	1	19	10	14	2	0	0	
"S." cf denisoniensis	ZMB 127253-5	44	0	0	0	16	5	20	3	0	0	
"S." cf denisoniensis	ZMB 127253-6	58	0	2	2	18	13	21	2	0	0	
"S." cf denisoniensis	ZMB 127253-7	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127253-8	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127253-9	60	0	3	3	31	11	11	1	0	0	
"S." cf denisoniensis	ZMB 127250-10	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127250-8	14	0	1	0	7	1	3	2	0	0	
"S." cf denisoniensis	ZMB 127252-1	40	16	24	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127252-10	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127252-2	19	11	7	0	0	1	0	0	0	0	
"S." cf denisoniensis	ZMB 127252-3	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127252-4	28	0	0	0	8	2	7	11	0	0	
"S." cf denisoniensis	ZMB 127252-5	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127252-6	39	5	16	0	5	5	6	2	0	0	
"S." cf denisoniensis	ZMB 127252-7	0	0	0	0	0	0	0	0	0	0	
"S." cf denisoniensis	ZMB 127252-8	32	0	4	0	10	14	4	0	0	0	
"S." cf denisoniensis	ZMB 127252-9	23	2	4	0	5	2	8	2	0	0	
Melanoides tuberculata	ZMB 107992-1	0	0	0	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 127248-1	0	0	0	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 127248-2	14	0	2	1	7	1	3	0	0	0	
Melanoides tuberculata	ZMB 127251a-1	12	3	1	6	2	0	0	0	0	0	
Melanoides tuberculata	ZMB 127251a-2	25	15	6	0	1	2	1	0	0	0	
Melanoides tuberculata	ZMB 127251a-3	8	7	0	0	0	0	1	0	0	0	
Melanoides tuberculata	ZMB 127251a-4	16	4	12	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 127251a-5	4	0	0	0	0	0	3	1	0	0	
Melanoides tuberculata	ZMB 127251a-6	7	0	6	0	0	0	1	0	0	0	
Melanoides tuberculata	ZMB 127251a-7	0	0	0	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 127444-1	46	0	0	25	15	6	0	0	0	0	*
Melanoides tuberculata	ZMB 127444-10	0	0	0	0	0	0	0	0	0	0	*
Melanoides tuberculata	ZMB 127444-2	193	80	45	32	12	5	9	2	7	1	*
Melanoides tuberculata	ZMB 127444-3	86	17	35	15	5	4	3	6	1	0	*
Melanoides tuberculata	ZMB 127444-4	0	0	0	0	0	0	0	0	0	0	*
Melanoides tuberculata	ZMB 127444-5	57	0	5	20	4	14	7	5	1	1	*
Melanoides tuberculata	ZMB 127444-6	72	0	0	36	7	10	14	2	3	0	*
Melanoides tuberculata	ZMB 127444-7	29	0	0	0	5	12	8	3	1	0	*
Melanoides tuberculata	ZMB 127444-8	28	0	0	16	7	0	2	0	2	1	*
Melanoides tuberculata	ZMB 127444-9	0	0	0	0	0	0	0	0	0	0	*
Melanoides tuberculata	ZMB 127573-1	22	0	0	3	0	2	17	0	0	0	*
Melanoides tuberculata	ZMB 127573-10	6	0	0	0	1	3	0	1	0	1	*
Melanoides tuberculata	ZMB 127573-2	0	0	0	0	0	0	0	0	0	0	*
Melanoides tuberculata	ZMB 127573-4	0	0	0	0	0	0	0	0	0	0	*
Melanoides tuberculata	ZMB 127573-5	0	0	0	0	0	0	0	0	0	0	*
Melanoides tuberculata	ZMB 127573-6	189	0	115	37	16	12	9	0	0	0	*
Melanoides tuberculata	ZMB 127573-7	48	0	24	11	6	3	2	1	0	1	*
Melanoides tuberculata	ZMB 127573-8	0	0	0	0	0	0	0	0	0	0	*
Melanoides tuberculata	ZMB 127573-9	117	0	63	10	32	7	5	0	0	0	*
Melanoides tuberculata	ZMB 191021-1	0	0	0	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 191021-2	4	0	0	4	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 191021-3	10	3	4	1	0	1	0	1	0	0	
Melanoides tuberculata	ZMB 191021-4	0	0	0	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 191021-5	5	5	0	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 191021a-1	0	0	0	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 191021a-2	0	0	0	0	0	0	0	0	0	0	
Melanoides tuberculata	ZMB 191021a-3	15	0	0	8	3	4	0	0	0	0	
Neoradina prasongi	ZMB 127582a-1	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127582a-10	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127582a-11	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127582a-12	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127582a-8	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127590-1	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127590-2	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127590-3	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127590-4	0	0	0	0	0	0	0	0	0	0	*
Neoradina prasongi	ZMB 127590-5	0	0	0	0	0	0	0	0	0	0	*

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Usages of the names *plicaria* Born, 1778 and *plicaria* Lamarck, 1816

Usages of the name *plicaria* Born, 1778 in combination with *Helix* Linnaeus, 1758 as the valid name of a taxon
Schröter (1784), Gmelin (1791), Dillwyn (1817), Wood (1818, 1825, 1828b).

Usages of the name *plicaria* Born, 1778 in combination with *Bulimus* Scopoli, 1777 as the valid name of a taxon
Bruguère (1792); Bosc (1802, 1824, 1830).

Usages of the name *plicaria* Born, 1778 in combination with *Thiara* Röding, 1798 as the valid name of a taxon
Van Benthem Jutting (1941), Habe (1974), Subba Rao (1989), Kress (2000), Ho et al. (2010).

Usages of the name *plicaria* Born, 1778 in combination with *Melania* Lamarck, 1799 as the valid name of a taxon
Hanley (1856), Chenu (1859), Martens (1897), Leschke (1912, 1914), Degner (1928), van Benthem Jutting (1929),
Rensch (1934).

Usages of the name *plicaria* Born, 1778 in combination with *Melanoides* Olivier, 1804 as the valid name of a
taxon (as *Melanoides plicaria*)

Van Benthem Jutting (1956), Knipper (1958), Pace (1973), Starmühlner (1976, 1982, 1984, 1992, 1993), Holthuis
(1978), Bright (1979); Haynes (1983, 1984, 1985, 1987, 1988, 1990, 1993, 2000), Brown & Gallagher (1985),
Hartoto & Marwoto (1986), Smith (1989, 1991), McLaughlin & Murray (1990), Monk et al. (1997), Cowie (1998,
2000, 2001), Neubert (1998), Feulner & Green (1999), Kartamihardja et al. (1999), Bragado et al. (2000), Joordens
et al. (2009), Purnama et al. (2011), Sulawesty et al. (2013), Beu et al. (2014), Kariono et al. (2014), Morales &
Llorente-Rodríguez (2016), Rizka et al. (2016), Sidik et al. (2016), Assuyuti et al. (2017), Dewiyanti et al. (2017),
Rijaluddin et al. (2017), Purnama et al. (2019), Wiggering et al. (2019).

Usages of the name *plicaria* Born, 1778 in combination with *Melanoides* Olivier, 1804 as the valid name of a
taxon (as *Melanoides plicarius*)

Van Benthem Jutting (1963), Gerber & Schechter (2011), Golitko et al. (2016).

Usages of the name *plicaria* Born, 1778 in combination with *Stenomelania* Fischer, 1885 as the valid name of a
taxon

Glaubrecht (1996), Bandel et al. (1997), Bandel & Riedel (1998), Sasaki (2002), Smith (2003), Benbow et al.
(2004), Strong & Glaubrecht (2007) Ramakrishna & Dey (2007), Ito et al. (2008), Glaubrecht & Podlacha (2010),
Kano et al. (2011), Strong et al. (2011), Kerr (2013), Ayu et al. (2015), Tripathy & Mukhopadhyay (2015), Ng et
al. (2016), Mukhopadhyay et al. (2017), Tsai (2019).

Usages of the name *plicaria* Lamarck, 1816 in combination with *Helix* Linnaeus, 1758 as the valid name of a taxon

Férussac (1821a, b, 1822), Martens (1832), Webb & Berthelot (1833), d'Orbigny (1839), Villa & Villa (1841),
Pfeiffer (1846, 1847, 1850, 1851, 1874), Swainson (1840), Albers (1850) Deshayes (1850), Chenu (1852),
Herrmannsen (1852), Mörch (1852), Reeve (1852), Gray (1854), Albers & Martens (1860), Hidalgo (1869), Paetel
(1869, 1873, 1883, 1889), Mousson (1872), Nevill (1878), Wollaston (1878) Kobelt (1879), Mabilie (1885),

Theobald (1889), Krause (1895), Pilsbry (1895), Dautzenberg (1900), Trechmann (1943), Mermod (1951), Chevallier (1965), Backhuys (1975), Shuttleworth (1975), Vega-Luz & Vega-Luz (2008), Yanes et al. (2009a), Castro et al. (2012), Matsukuma (2012a, b).

Usages of the name *plicaria* Lamarck, 1816 in combination with *Cochlea* Da Costa, 1778 as the valid name of a taxon

Dautzenberg (1891).

Usages of the name *plicaria* Lamarck, 1816 in combination with *Hemicycla* Swainson, 1840 as the valid name of a taxon

Gude (1896), Boettger (1908), Haas (1911), Hesse (1912, 1931), Leschke (1913), Boettger & Wenz (1921), Wenz (1923), Fischer-Piette (1942, 1946), Wenz & Zilch (1960), Martín et al. (1985, 2005), Groh (1985), Ibáñez et al. (1987, 1988, 2001), Kempermann & Gittenberger (1988), Abbott (1989), Alonso et al. (1990, 1991, 2001), Thornback et al. (1990), Groombridge (1993), Baillie & Groombridge (1996), Koomen & van Helsdingen (1996), Gómez Moliner et al. (2000), Siepel et al. (2000), Ibáñez & Alonso (2001, 2005, 2006, 2007, 2009), Bank et al. (2002), Groh & García (2004), Martínez-Ortí (2005), Arechavaleta Hernández (2006), Schileyko (2006), Lizana & Viejo (2007), Alonso & Ibáñez (2007), Arechavaleta & Martín (2008), Verdú & Galante (2009), Cuttelod et al. (2011), Contreras González (2009), Yanes et al. (2009b), Moro et al. (2011), Neiber et al. (2011), Pannell et al. (2011), Hernández-Manrique et al. (2012), Groh & Alonso (2013), Neiber & Hausdorf (2015, 2016), Felix et al. (2019), Neubert et al. (2019).

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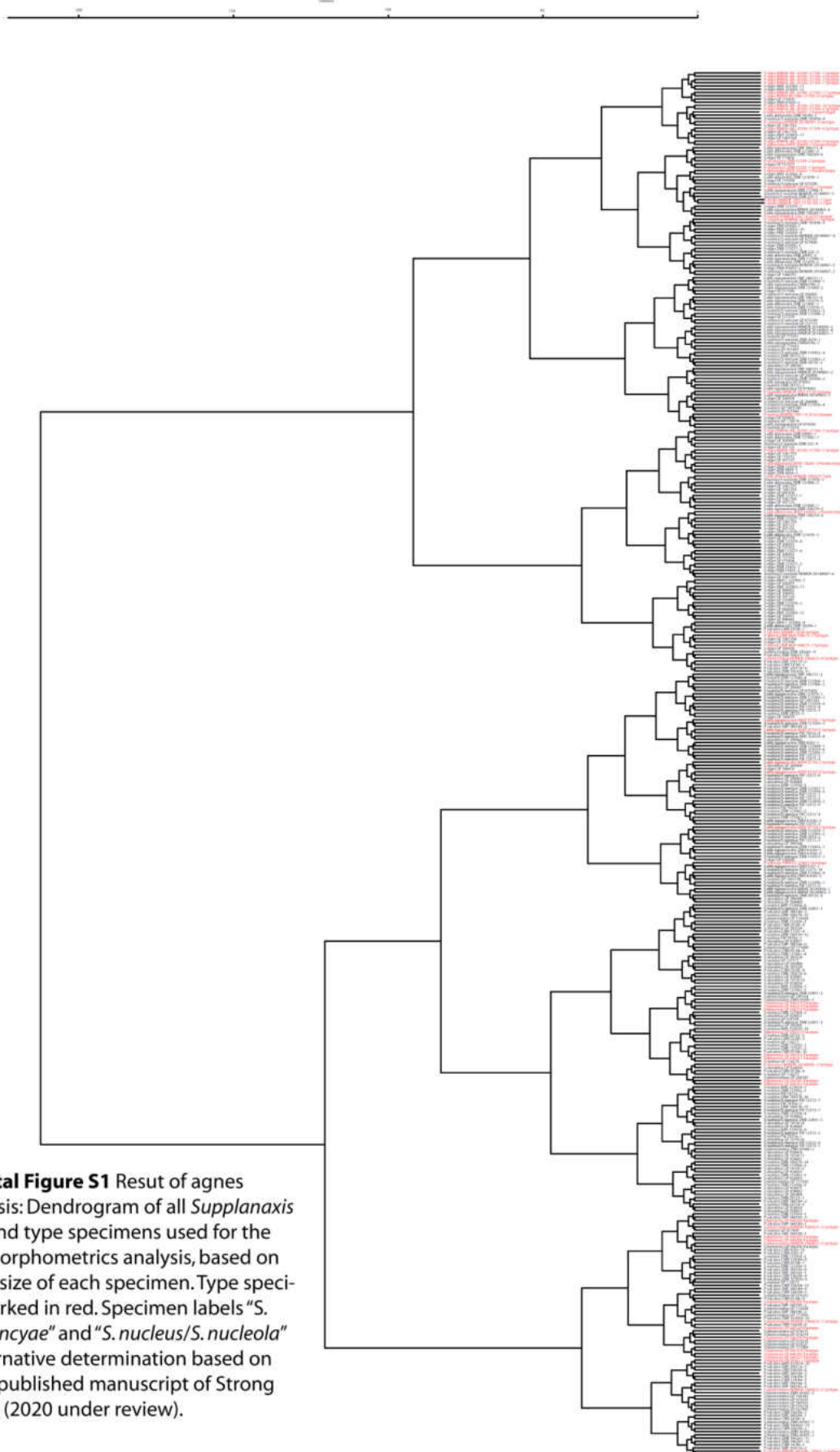
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Appendix V Supplemental material for Chapter 7



Supplemental Figure S1 Result of agnes cluster analysis: Dendrogram of all *Supplanaxis* specimens and type specimens used for the geometric morphometrics analysis, based on the centroid size of each specimen. Type specimens are marked in red. Specimen labels "*S. nucleus/S. nancyae*" and "*S. nucleus/S. nucleola*" indicate alternative determination based on the so far unpublished manuscript of Strong and Bouchet (2020 under review).

Table S1 Shell measurements of *Supplanaxis* and *Planaxis sulcatus* specimens. h – shell height; w – shell width; ha – aperture height; wa – aperture width; bw – last whorl height; l3w – last three whorls height; H/W – index of shell height to width

<i>Species</i>	ID	h	w	ha	wa	bw	l3w	H/W	HA/WA	whorls	Spiral grooves	strength of grooves	grooves at	grooves at next to last whorl	Collumelar teeth	palatal grooves	Strength of palatal grooves
<i>S. nucleus</i>	AMS 323604-6	14.59	10.43	9.45	5.87	12.36	14.30	1.40	1.61	4.5	17	2	4	5	1	12	1
<i>S. nucleus</i>	AMS 323604-7	15.85	10.56	9.95	5.94	13.03	15.31	1.50	1.68	5.0	14	2	4	4	1	13	1
<i>S. nucleus</i>	AMS 323610-10	15.71	10.88	10.01	5.98	13.27	15.51	1.44	1.67		17	2	4	5	1	15	2
<i>S. nucleus</i>	AMS 323610-6	13.07	8.62	8.31	4.93	10.57	12.86	1.52	1.69		8	1	2	4	1	15	1
<i>S. nucleus</i>	AMS 323610-7	13.71	8.43	8.40	5.13	11.30	13.33	1.63	1.64		6	1	2	3	1	14	2
<i>S. nucleus</i>	AMS 323610-8	12.84	7.93	7.46	4.65	10.56	12.44	1.62	1.60	4.0	12	2	2	5	1	16	1
<i>S. nucleus</i>	AMS 323610-9	13.76	8.88	8.58	4.86	11.61	13.61	1.55	1.77	4.0	15	3	4	5	1	15	2
<i>S. nucleus</i>	ZMB 108278-12	14.95	10.02	9.50	5.28	12.26	14.59	1.49	1.80		9	3	2	2	1	13	2
<i>S. nucleus</i>	ZMB 108278-13	15.17	9.98	9.45	5.84	12.65	14.84	1.52	1.62		18	2	4		1	14	2
<i>S. nucleus</i>	ZMB 108278-14	13.91	9.82	9.25	5.26	12.02	13.62	1.42	1.76		3	1	1	3	1	17	1
<i>S. nucleus</i>	ZMB 108278-15	13.30	8.83	8.46	5.18	11.27	13.18	1.51	1.63		7	1	1	1	1	4	1
<i>S. nucleus</i>	ZMB 108278-16	13.79	8.70	8.38	4.45	11.19	13.22	1.59	1.88		19	2	4	5	1	5	1
<i>S. nucleus</i>	ZMB 110432-2	12.01	7.92	7.78	4.07	9.96	11.71	1.52	1.91		23	1	4	4	1	13	2
<i>S. nucleus</i>	ZMB 110557-2	11.23	7.88	7.68	4.11	9.64	11.08	1.43	1.87		20	1	4	0	1	4	1
<i>S. nucleus</i>	ZMB 121054-1	16.45	11.18	10.71	5.85	14.04	16.17	1.47	1.83		11	1	2	5	1	12	1
<i>S. nucleus</i>	ZMB 121054-2	16.67	11.46	10.11	5.93	13.53	16.13	1.45	1.70	5.5	16	1	4	5	1	15	2
<i>S. nucleus</i>	ZMB 121054-3	17.11	11.49	10.21	6.29	13.58	16.25	1.49	1.62	5.5	16	1	4	5	1	15	2
<i>S. nucleus</i>	ZMB 121054-4	13.65	9.01	8.47	4.87	11.09	13.22	1.51	1.74	5.0	7	1	2	1	1	13	1
<i>S. nucleus</i>	ZMB 121054-5	13.50	8.60	7.82	4.96	10.69	13.01	1.57	1.58	5.0	16	1	4	7	1	13	2
<i>S. nucleus</i>	ZMB 121055-1	16.53	10.71	10.28	5.73	13.54	15.96	1.54	1.79		17	2	4	4	1	16	2
<i>S. nucleus</i>	ZMB 121056-1	15.79	10.37	9.50	5.47	12.39	14.98	1.52	1.74	5.0	10	1	2	2	1	13	1
<i>S. nucleus</i>	ZMB 121056-2	14.77	10.28	9.24	5.66	12.13	14.33	1.44	1.63		12	1	2	5	1	13	2
<i>S. nucleus</i>	ZMB 121056-3	14.78	10.55	9.52	5.71	12.15	14.43	1.40	1.67		19	1	4	3	1	14	2
<i>S. nucleus</i>	ZMB 121057-1	12.81	7.98	8.01	4.66	10.60	12.69	1.61	1.72	4.0	10	1	2	3	1	10	1
<i>S. nucleus</i>	ZMB 121059-2	13.45	8.63	7.86	4.69	10.93	13.09	1.56	1.68		15	1	4	5	1	15	1
<i>S. nucleus</i>	ZMB 121059-3	12.48	8.68	8.13	4.85	10.48	12.19	1.44	1.68		7	1	2	1	1	15	1
<i>S. nucleus</i>	ZMB 121059-5	12.86	8.03	7.50	4.33	10.45	12.65	1.60	1.73		10	1	2		1	14	2
<i>S. nucleus</i>	ZMB 121060-1	10.62	7.81	7.50	4.14	9.57	10.57	1.36	1.81		5	1	1		1	19	2

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<i>S. nucleus</i>	ZMB 121060-2	12.07	8.20	7.77	4.51	10.12	11.70	1.47	1.72		7	1	2		1	0	0
<i>S. nucleus</i>	ZMB 121060-4	12.49	8.61	8.35	4.85	10.66	12.17	1.45	1.72	4.0	7	1	2	1	1	8	2
<i>S. nucleus</i>	ZMB 121061-2	13.06	9.11	8.33	5.06	11.11	12.94	1.43	1.65		6	1	2	1	1	14	2
<i>S. nucleus</i>	ZMB 121061-3	14.36	9.26	9.30	4.75	11.71	13.90	1.55	1.96	5.0	12	2	4	2	1	15	1
<i>S. nucleus</i>	ZMB 121061-4	15.08	9.62	9.22	5.40	12.46	14.35	1.57	1.71		7	2	2	0	1	16	1
<i>S. nucleus</i>	ZMB 121061-5	13.70	9.79	8.98	5.61	12.10	13.43	1.40	1.60		8	1	2		1	14	2
<i>S. nucleus</i>	ZMB 121062-1	13.12	9.10	8.29	4.75	10.99	12.75	1.44	1.75	4.0	16	3	4	5	1	15	1
<i>S. nucleus</i>	ZMB 121062-2	9.12	5.89	6.12	2.75	7.64	8.72	1.55	2.23	5.0	21	2	4	5	1	12	2
<i>S. nucleus</i>	ZMB 121064-1	13.09	7.77	7.18	4.44	10.19	12.68	1.68	1.62		8	1	2	4	1	12	1
<i>S. nucleus</i>	ZMB 121064-2	14.79	10.22	9.53	5.84	12.94	14.70	1.45	1.63	4.5	7	1	1	0	1	13	2
<i>S. nucleus</i>	ZMB 121064-3	13.78	9.45	8.87	5.30	11.92	13.69	1.46	1.67	4.0	8	1	2	0	1	15	2
<i>S. nucleus</i>	ZMB 121065-1	12.75	8.19	7.33	4.68	10.55	12.55	1.56	1.57		7	2	2	1	1	13	2
<i>S. nucleus</i>	ZMB 121065-2	12.58	7.05	7.00	4.01	9.80	11.77	1.78	1.75	5.0	7	1	2	2	1	15	1
<i>S. nucleus</i>	ZMB 225-2	8.88	6.17	6.07	3.61	8.26	8.82	1.44	1.68	4.0	0	0	0	0	1	0	0
<i>S. nucleus</i>	ZMB 225-5	9.06	5.77	5.08	3.40	7.53	8.97	1.57	1.49	4.0	0	0	0	0	1	15	1
<i>S. nucleus</i>	ZMB 28723-1	14.60	9.64	9.20	5.42	11.96	13.97	1.51	1.70	5.0	10	1	4	1	1	12	1
<i>S. nucleus</i>	ZMB 28723-2	15.80	11.45	10.78	6.44	13.80	15.69	1.38	1.67	4.5	5	1	1	0	1	11	3
<i>S. nucleus</i>	ZMB 28724-1	14.79	9.78	9.48	4.96	12.24	14.50	1.51	1.91	4.5	13	1	4	1	1	13	3
<i>S. nucleus</i>	ZMB 28724-2	15.51	10.24	10.28	5.70	13.76	15.37	1.51	1.80	4.5	5	1	2	1	1	15	4
<i>S. nucleus</i>	ZMB 28724-3	15.58	9.39	9.42	5.69	13.17	15.21	1.66	1.66		3	1	2	1	1	16	4
<i>S. nucleus</i>	ZMB 28725-1	11.62	7.89	7.89	4.55	10.10	11.53	1.47	1.73		9	2	2	0	1	5	3
<i>S. nucleus</i>	ZMB 28725-2	11.37	7.73	7.58	4.28	9.86	11.05	1.47	1.77		6	1	1	0	1	9	2
<i>S. nucleus</i>	ZMB 28725-3	10.56	7.04	7.33	3.86	9.47	10.46	1.50	1.90		5	1	1	0	1	5	1
<i>S. nucleus</i>	ZMB 28725-4	11.86	7.58	7.61	4.18	10.00	11.64	1.56	1.82	5.0	7	1	1	0	1	15	2
<i>S. nucleus</i>	ZMB 28725-5	12.44	7.85	8.25	4.53	10.37	11.97	1.58	1.82		6	1	0	0	1	0	0
<i>S. nucleus</i>	ZMB 32401-1	14.26	10.95	10.57	6.53	13.25	14.12	1.30	1.62	4.0	5	1	1	0	1	15	1
<i>S. nucleus</i>	ZMB 32401-2	15.38	10.91	10.50	6.50	13.53	15.18	1.41	1.62		0	0	0	0	1	15	1
<i>S. nucleus</i>	ZMB 32401-3	14.75	11.08	10.58	6.23	13.17	14.75	1.33	1.70		0	0	0	0	1	16	1
<i>S. nucleus</i>	ZMB 32401-4	13.57	9.62	8.98	5.05	11.67	13.39	1.41	1.78		0	0	0	0	1	10	1
<i>S. nucleus</i>	ZMB 32401-5	13.26	9.41	8.58	5.18	11.47	13.18	1.41	1.66	4.0	0	0	0	0	1	13	1
<i>S. nucleus</i>	ZMB 108278-11	14.52	9.75	9.26	4.89	12.01	14.12	1.49	1.89	4.0	5	1	2	1	1	10	1
<i>S. nucleus</i>	ZMB 108278-6	14.97	10.53	9.30	5.69	12.42	14.40	1.42	1.63	4.0	9	1	2	2	1	13	1
<i>S. nucleus</i>	FW 12372- 1	13.01	9.08	8.60	5.02	11.24	12.83	1.43	1.71	5.0	7	1	2	1	1	15	2
<i>S. nucleus</i>	FW 12372- 10	13.24	8.76	8.63	4.55	11.06	12.62	1.51	1.90		15	2	4	2	1	16	1
<i>S. nucleus</i>	FW 12372- 2	14.36	9.11	8.55	5.08	11.62	13.55	1.58	1.68	5.0	18	2	4	6	1	14	2
<i>S. nucleus</i>	FW 12372- 3	12.98	9.07	8.53	4.92	11.25	12.66	1.43	1.73		15	2	4	3	1	14	2
<i>S. nucleus</i>	FW 12372- 4	13.15	9.30	8.55	5.03	11.00	12.81	1.41	1.70		7	2	2	3	1	16	2

<i>S. nucleus</i>	FW 12372-5	12.78	8.97	8.24	5.16	10.82	12.39	1.42	1.60		16	1	4		1	12	1
<i>S. nucleus</i>	FW 12372-6	13.49	9.59	8.35	5.06	11.14	13.22	1.41	1.65	4.0	14	1	4	3	1	15	3
<i>S. nucleus</i>	FW 12372-7	13.69	8.62	8.55	5.05	11.13	13.15	1.59	1.69	5.0	17	3	4	4	1	18	2
<i>S. nucleus</i>	FW 12372-8	12.33	8.68	7.98	4.50	10.27	11.82	1.42	1.77	5.0	9	2	2	2	1	13	2
<i>S. nucleus</i>	FW 12372-9	12.89	9.62	8.73	5.26	10.96	12.58	1.34	1.66		21	3	4	4	1	13	2
<i>S. nucleus</i>	FW 12373-2	13.10	8.95	8.30	4.95	11.03	12.86	1.46	1.68		7	2	2		1	14	2
<i>S. nucleus</i>	FW 12373-6	12.96	8.55	8.25	4.57	10.87	12.67	1.52	1.81		13	2	4	2	1	11	2
<i>S. nucleus</i>	FW 12373-8	13.00	8.86	8.09	4.87	10.92	12.64	1.47	1.66		11	1	4	2	1	12	2
<i>S. nucleus</i>	FW 12373-9	11.67	7.84	7.46	4.41	9.95	11.48	1.49	1.69		13	2	2	3	1	15	1
<i>S. nucleus</i>	ZMH 140713-1	14.48	10.10	9.69	5.70	12.69	14.34	1.43	1.70	4.0	9	1	2		1	15	2
<i>S. nucleus</i>	ZMH 140713-3	12.98	9.64	9.17	5.28	11.70	12.84	1.35	1.74	4.0	15	2	4	2	1	15	2
<i>S. nucleus</i>	FW 7821a-1	13.94	9.82	9.53	5.08	11.95	13.52	1.42	1.88	6.0	17	1	4	0	1	3	1
<i>S. nucleus</i>	FW 7821a-2	13.07	9.33	9.11	5.07	11.60	12.85	1.40	1.80	4.0	6	1	1	0	1	5	1
<i>S. nucleus</i>	FW 7821a-3	13.22	8.67	8.23	4.81	11.11	12.84	1.52	1.71	5.0	7	1	2	1	1	11	2
<i>S. nucleus</i>	FW 7821a-5	13.42	9.22	8.79	5.11	11.23	12.97	1.46	1.72	5.0	7	1	2	0	1	9	1
<i>S. nucleus</i>	BMNH 20140847-2	9.59	6.35	6.49	3.51	8.31	9.44	1.51	1.85	4.5	0	0	0	0	1	3	1
<i>S. nucleus</i>	BMNH 20140847-3	9.84	6.43	6.37	3.60	8.26	9.59	1.53	1.77	4.0	2	1	1	0	1	16	1
<i>S. nucleus</i>	BMNH 20140847-4	9.59	5.95	6.29	3.63	8.40	9.49	1.61	1.73		0	0	0	0	1	18	1
<i>S. nucleus</i>	BMNH 20140847-6	8.45	5.31	5.16	2.9	6.87	7.9	1.59	1.78	4	1	1	1	0	1	10	1
<i>S. nucleus</i>	ZMB 110432-3	13.06	8.99	8.73	5.10	11.68	13.00	1.45	1.71	4.0	0	0	0	0	1	0	0
<i>S. nucleus</i>	ZMB 110432-4	11.18	7.53	7.39	4.23	9.96	10.97	1.48	1.75	4.5	0	0	0	0	1	11	1
<i>S. nucleus</i>	ZMB 110557-1	12.07	7.59	6.99	4.33	9.93	11.94	1.59	1.61		8	1	2	1	1	16	1
<i>S. nucleus</i>	ZMB 121056-4	10.76	6.71	7.03	3.58	9.01	10.56	1.60	1.96		0	0	0	0	1	0	0
<i>S. nucleus</i>	ZMB 121056-5	8.70	5.17	5.23	2.89	6.90	8.43	1.68	1.81		5	1	1	0	1	0	0
<i>S. nucleus</i>	ZMB 121059-4	11.79	7.72	7.60	4.55	10.25	11.64	1.53	1.67		2	1	1	0	1	7	1
<i>S. nucleus</i>	ZMB 121062-4	11.60	7.53	7.32	4.25	9.92	11.43	1.54	1.72		5	2	1	1	1	13	2
<i>S. nucleus</i>	ZMB 121063-1	13.42	9.16	8.28	5.09	11.11	13.04	1.47	1.63		3	1	1	1	1	9	1
<i>S. nucleus</i>	ZMB 121066-1	12.25	7.25	6.32	3.94	9.56	11.94	1.69	1.60		6	1	2	1	1	0	0
<i>S. nucleus</i>	ZMB 121086-1	12.05	7.45	6.71	4.03	8.85	11.44	1.62	1.67	5.5	7	2	2	1	1	8	1
<i>S. nucleus</i>	ZMB 121086-2	12.04	6.70	6.65	3.71	8.90	11.38	1.80	1.79	5.0	6	1	2	1	1	12	1
<i>S. nucleus</i>	ZMB 193436-2	9.80	6.52	6.67	3.50	8.65	9.67	1.50	1.91	4.0	3	1	1	0	1	6	1
<i>S. nucleus</i>	ZMB 193436-5	9.35	5.68	6.11	3.57	8.24	9.24	1.65	1.71	4.0	0	0	0	0	1	13	1
<i>S. nucleus</i>	ZMB 2874-1	11.20	7.97	7.73	4.28	10.04	11.15	1.41	1.81		3	1	1	0	1	15	1
<i>S. nucleus</i>	ZMB 2874-2	11.8	7.82	7.10	3.86	10.00	11.76	1.50	1.84		4	2	1	1	1	12	1
<i>S. nucleus</i>	GP 1061536	11.8	8.06	6.48	4.46	9.7	11.6	1.46	1.45	5.5	14	1	4	5	1	15	1
<i>S. nucleus</i>	GP 1061540	10.7	6.64	5.76	3.77	8.77	10.5	1.61	1.53	4.5	16	1	4	4	1	14	1
<i>S. nucleus</i>	GP 1061542	12.3	7.62	6.61	4.48	10.4	11.9	1.61	1.48	4.5	8	1	3	0	1	12	1

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<i>S. nucleus</i>	GP 114273	17	10.6	10.1	6.08	13.8	16.3	1.61	1.65	5.5	9	1	3	2	1	12	1
<i>S. nucleus</i>	GP 114274	10.6	7.23	6.33	4.06	9.03	10.3	1.47	1.56	4.5	8	1	3	2	1	13	1
<i>S. nucleus</i>	GP 114275	16	10.7	9.81	5.93	13.3	15.4	1.49	1.65	4.5	17	2	4	3	1	11	2
<i>S. nucleus</i>	GP 114277	16.2	10.7	9.91	5.98	13.4	15.7	1.51	1.66	5.5	16	1	4	5	1	12	2
<i>S. nucleus</i>	GP 114278	16.8	11.3	10.1	6.31	13.8	16.1	1.49	1.60	6.5	7	1	3	4	1	11	1
<i>S. nucleus</i>	GP 268488	10.7	6.91	5.6	3.76	8.84	10.5	1.55	1.49	5.5	3	1	1	2	1	15	1
<i>S. nucleus</i>	GP 268490	11.1	7.3	6.36	4.14	9.55	10.8	1.52	1.54	4.5	5	1	1	1	1	16	1
<i>S. nucleus</i>	GP 268491	11.3	7.11	6.7	4.1	9.31	11	1.59	1.63	4.5	6	1	3	1	1	15	2
<i>S. nucleus</i>	GP 639708	15	10.2	8.9	5.81	12.4	14.6	1.46	1.53	4.5	6	1	3	1	1	14	1
<i>S. nucleus</i>	GP 675596	10	6.44	5.42	3.62	8.25	9.6	1.55	1.50	5.5	6	1	3	4	1	13	1
<i>S. nucleus</i>	GP 675597	10	6.46	5.31	3.67	8.3	9.79	1.55	1.45	4.5	5	1	3		1	16	1
<i>S. nucleus</i>	GP 675599	11	7.02	6.38	3.96	9.34	10.9	1.57	1.61	4.5	5	1	3	1	1	17	1
<i>S. nucleus</i>	GP 675600	10	6.5	5.6	3.7	8.37	9.81	1.54	1.51	5.5	6	1	3	1	1	13	1
<i>S. nucleus</i>	GP 675602	12.5	8.21	7.15	4.58	10.7	12.4	1.52	1.56	4.5	4	1	3	1	1	17	1
<i>S. nucleus</i>	GP 727172	14.9	9.64	8.68	5.67	12.2	14.3	1.55	1.53	4.5	5	1	3	1	1	13	1
<i>S. nucleus</i>	GP 727173	11	7.14	6.36	4.07	9.39	10.9	1.54	1.56	4.5	6	1	3	1	1	15	1
<i>S. nucleus</i>	GP 771818	10.7	7.07	6.11	3.86	9.01	10.3	1.51	1.58	4.5	8	1	3	1	1	14	1
<i>S. nucleus</i>	GP 771831	11.2	7.6	6.28	4.22	9.43	10.3	1.47	1.49	4.5	5	1	3	1	1	17	1
<i>S. nucleus</i>	GP 771832	11.6	7.47	6.33	4.39	9.74	11.2	1.55	1.44	4.5	3	1	3	1	1	17	1
<i>S. nucleus</i>	GP 921466	10.7	6.94	5.8	3.74	8.95	10.4	1.54	1.55	4.5	15	1	4	5	1	15	1
<i>S. nucleus</i>	GP 921467	11.6	7.53	6.37	4.21	9.74	11.4	1.54	1.51	4.5	7	1	3	2	1	15	1
<i>S. nucleus</i>	GP 977449	17.5	11.4	10.2	6.21	14.3	16.7	1.54	1.64	5.5	15	2	4	5	1	14	2
<i>S. abb. abbreviata</i>	ANSP 18260	9.73	6.39	5.52	3.28	7.90	9.32	1.52	1.68	5.5	15	2	4	5	1	16	
<i>S. abb. abbreviata</i>	ANSP 18260	8.99	5.63	5.22	3.12	7.43	8.89	1.60	1.67	4.5	6	2	2	1	1	13	4
<i>S. abb. abbreviata</i>	ANSP 18260	8.49	5.33	4.89	3.16	7.13	8.38	1.59	1.55	4.5	4	2	2	0	1	13	4
<i>S. abb. abbreviata</i>	ANSP 18261	6.27	4.06	3.79	2.09	5.31	6.15	1.54	1.81		15	1	4	1	1	16	4
<i>S. abb. abbreviata</i>	ANSP 394492	8.86	5.67	5.25	3.18	7.43	8.60	1.56	1.65	4.5	7	1	2	1	1	18	3
<i>S. abb. abbreviata</i>	ANSP 394492	8.03	5.16	4.58	2.91	6.88	7.93	1.56	1.57	4.5	6	1	2	1	1	13	3
<i>S. abb. abbreviata</i>	NHMUK 1964320.tif	8.21	5.60	4.81	2.75	6.84	8.02	1.47	1.75	5.5	5	2	1	0	1	13	3
<i>S. abb. abbreviata</i>	ZMB 121078-1	9.75	6.25	6.23	3.49	8.22	9.52	1.56	1.79	5.0	5	1	2	1	1	17	3
<i>S. abb. abbreviata</i>	ZMB 121078-2	9.01	5.96	5.48	3.14	7.71	8.91	1.51	1.75	4.5	9	1	2	1	1	15	3
<i>S. abb. abbreviata</i>	ZMB 121078-3	8.16	5.21	4.86	2.76	6.84	7.94	1.57	1.76	5.5	16	1	4	4	1	13	3
<i>S. abb. abbreviata</i>	ZMB 121084-1	8.37	5.23	4.87	2.87	7.13	8.23	1.60	1.70	4.0	5	2	2	1	1	20	3
<i>S. abb. abbreviata</i>	ZMB 121084-2	8.22	5.61	4.97	2.93	7.03	7.99	1.47	1.70	4.0	19	2	4	1	1	16	3
<i>S. abb. abbreviata</i>	ZMB 20097-1	8.59	5.50	5.26	2.95	7.31	8.41	1.56	1.78	4.0	4	1	1	1	1	14	3
<i>S. abb. abbreviata</i>	ZMB 20097-2	8.87	6.08	5.59	3.31	7.87	8.74	1.46	1.69	4.5	7	2	2	1	1	13	2
<i>S. abb. ogasawarana</i>	SMF 346151-1	11.67	6.69	6.60	4.41	9.17	11.20	1.74	1.50	5.0	6	2	2	1	1	11	
<i>S. abb. ogasawarana</i>	SMF 346151-2	12.77	7.30	7.41	3.95	9.83	12.24	1.75	1.88	5.0	4	2	2	1	1	11	
<i>S. abb. ogasawarana</i>	SMF 346151-3	11.15	5.83	5.96	3.46	8.62	10.68	1.91	1.72	5.0	12	1	4	5	1	13	
<i>S. abb. ogasawarana</i>	SMF 346151-4	10.86	5.61	5.87	3.01	8.17	10.07	1.94	1.95	5.5	5	2	2	7	1	3	
<i>S. abb. ogasawarana</i>	SMF 346151-5	11.14	6.52	6.36	3.56	8.64	10.80	1.71	1.79	4.5	6	2	2	1	1	11	

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<i>S. abb. ogasawarana</i>	SMF 346151-6	11.30	6.65	6.53	3.65	8.59	10.74	1.70	1.79	5.5	7	1	2	6	1	12	
<i>S. abb. ogasawarana</i>	ANSP 87769	12.12	7.26	6.53	3.93	9.23	11.55	1.67	1.66	5.5	16	2	4	8	1	11	4
<i>S. abb. ogasawarana</i>	ANSP 87769	13.49	8.42	7.67	4.51	10.41	13.16	1.60	1.70	5.5	12	1	2	9	1	13	3
<i>S. abb. ogasawarana</i>	ANSP 87769	12.59	8.46	7.43	4.35	10.00	12.42	1.49	1.71	4.5	14	2	2	8	1	13	3
<i>S. abb. ogasawarana</i>	ANSP 87769	12.83	7.51	7.03	4.17	9.86	12.25	1.71	1.69	5.5	16	2	4	8	1	14	3
<i>S. abb. ogasawarana</i>	BMNH 20140856-1	11.75	7.57	6.84	3.79	9.21	11.48	1.55	1.80	5.0	12	1	2	5	1	8	2
<i>S. abb. ogasawarana</i>	BMNH 20140856-2	12.09	7.57	6.58	3.89	9.02	11.52	1.60	1.69		5	1	4	0	1	8	2
<i>S. abb. ogasawarana</i>	BMNH 20140863-1	11.99	6.54	6.35	3.84	9.01	11.38	1.83	1.65	5.0	8	1	1	1	1	12	2
<i>S. abb. ogasawarana</i>	BMNH 20140863-2	11.08	6.72	6.27	3.51	8.62	10.66	1.65	1.79	5.5	18	1	4	8	1	11	3
<i>S. abb. ogasawarana</i>	BMNH 20140863-3	11.73	6.88	6.72	3.90	9.29	11.24	1.70	1.72	6.0	22	1	4	9	1	13	3
<i>S. abb. ogasawarana</i>	BMNH 20140863-4	10.94	6.41	6.54	3.52	8.72	10.66	1.71	1.86	5.0	19	1	4	6	1	11	3
<i>S. abb. ogasawarana</i>	BMNH 20140863-5	11.38	6.34	6.09	3.50	8.78	10.87	1.79	1.74	5.0	19	2	4	9	1	8	3
<i>S. abb. ogasawarana</i>	BMNH 20140863-6	10.22	6.06	5.75	3.19	7.84	9.73	1.69	1.80	5.0	20	2	4	7	1	10	3
<i>S. abb. ogasawarana</i>	ZMB 108269-6	10.70	6.38	5.79	3.38	7.97	10.08	1.68	1.71	5.0	21	2	4	9	1	11	2
<i>S. abb. ogasawarana</i>	ZMB 108269-9	10.79	6.63	6.18	3.30	7.88	10.04	1.63	1.87	5.5	18	1	4	5	1	10	2
<i>S. abb. ogasawarana</i>	ZMB 108274-4	8.62	5.19	4.88	2.64	6.62	8.13	1.66	1.85	5.0	15	1	4	7	1	8	2
<i>S. abb. ogasawarana</i>	ZMB 108274-5	8.93	4.96	4.87	2.68	6.74	8.35	1.80	1.82	6.0	16	1	2	4	1	9	1
<i>S. abb. ogasawarana</i>	ZMB 117946-1	10.28	5.93	5.43	3.11	7.71	9.78	1.73	1.75	5.0	15	2	4	8	1	10	3
<i>S. abb. ogasawarana</i>	ZMB 117946-2	9.63	5.61	5.09	2.95	7.32	9.30	1.72	1.73	5.5	18	2	4	9	1	9	3
<i>S. abb. ogasawarana</i>	ZMH 41636-1	7.77	7.08	7.12	4.35	9.95	11.89	1.10	1.64	5.0	14	2	4	6	1	12	2
<i>S. abb. ogasawarana</i>	ZMH 41636-3	11.85	7.07	6.95	3.87	9.53	11.65	1.68	1.80		14	2	4	1	1	11	1
<i>S. abb. ogasawarana</i>	ZMH 41636-4	11.99	7.74	7.18	4.14	9.66	11.62	1.55	1.73		20	2	4	5	1	12	1
<i>S. abb. ogasawarana</i>	ZMH 41636-5	13.52	8.43	7.89	4.60	10.98	12.90	1.60	1.72	5.0	17	2	4	4	1	18	2
<i>S. abb. ogasawarana</i>	CWR51/07-1	12.30	7.20	6.70	3.44	8.84	11.48	1.71	1.95	5.0	14	2	4	6	1	10	1
<i>S. abb. ogasawarana</i>	GP 346676	13.9	8.23	6.95	4.46	10.5	12.9	1.69	1.56	5.5	15	1	4	7	1	12	2
<i>S. abb. ogasawarana</i>	GP 874300	11.4	6.63	5.9	3.6	8.48	10.7	1.72	1.64	5.5	17	1	4	5	1	13	1
<i>S. abb. ogasawarana</i>	GP 874301	11.7	6.57	5.56	3.74	8.67	11	1.78	1.49	5.5	18	1	4	5	1	16	1
<i>S. abb. ogasawarana</i>	GP 874302	12	6.25	5.78	3.59	8.77	11.1	1.92	1.61	5.5	16	1	4	6	1	14	1
<i>S. leyteensis</i>	FW 8566-1	20.75	10.92	11.69	6.10	15.90	19.91	1.90	1.92	6.0	18	1	2	2	10	17	2
<i>S. leyteensis</i>	MNHN 2000-30332	19.00	9.07	10.72	5.15	14.49	17.89	2.09	2.08	6.0	15	1	2	1	10	16	1
<i>S. leyteensis</i>	GP 643587	17	8.29	9.28	4.88	13.2	16.2	2.05	1.90	6.5	15	1	3	1	1	17	0
<i>S. leyteensis</i>	GP 646299	20	9.35	10.4	5.13	15.6	18.9	2.14	2.02	6.5	15	1	3	1	1	14	1
<i>S. leyteensis</i>	GP 646302	18.7	9.37	10.3	5.17	15.3	18.1	2.00	1.99	5.5	15	1	3	2	1	17	1
<i>S. leyteensis</i>	GP 646303	17.9	8.66	9.61	4.56	14.1	16.6	2.07	2.11	6.5	15	1	3	1	1	16	1
<i>S. leyteensis</i>	GP 646305	18.4	9.26	10.4	5.34	14.9	17.5	1.99	1.95	5.5	15	1	3	0	1		1
<i>S. leyteensis</i>	GP 646306	18.1	8.45	9.76	4.84	14.2	17.2	2.14	2.02	5.5	17	1	3	1	1	16	1
<i>S. leyteensis</i>	GP 646307	18.2	8.87	9.35	4.92	14.2	17.1	2.05	1.90	6.5	16	1	3	1	1		0
<i>S. leyteensis</i>	GP 646308	17.8	8.59	10.1	4.83	14.3	17.1	2.07	2.09	5.5	13	1	3	0	1		1
<i>S. leyteensis</i>	GP 646310	16.5	8.03	8.19	4.61	12.7	15.1	2.05	1.78	5.5	15	1	3	0	1	16	1

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<i>S. leyteensis</i>	GP 646311	17.4	8.64	9.62	4.74	13.7	16.5	2.01	2.03	6.5	16	1	3	0	1	15	1
<i>S. leyteensis</i>	GP 646312	17.3	8.12	9.22	4.47	13.7	16.2	2.13	2.06	6.5	13	1	3	1	1	15	1
<i>S. leyteensis</i>	GP 646314	16.6	8.01	9.45	4.43	13.2	15.6	2.07	2.13	6.5	14	1	3	1	1	16	1
<i>S. leyteensis</i>	GP 646315	17.1	8.39	9.36	4.74	13.7	16.1	2.04	1.97	5.5	15	1	3	1	1	16	1
<i>S. leyteensis</i>	GP 646316	16.9	8.62	9.28	4.97	13.8	16.1	1.96	1.87	5.5	16	1	3	1	1	17	1
<i>S. leyteensis</i>	GP 646318	19.1	8.69	10.3	4.88	15.1	18.4	2.20	2.11	5.5	17	1	3	1	1	16	1
<i>S. leyteensis</i>	GP 646319	16.4	7.95	8.49	4.32	12.7	15.3	2.06	1.97	5.5	15	1	3	1	1	16	1
<i>S. leyteensis</i>	GP 646320	18.5	8.46	10	4.5	14.5	17.5	2.19	2.22	5.5	13	1	3	1	1	14	1
<i>S. leyteensis</i>	GP 646321	18.6	9.17	10.4	5.18	14.9	17.8	2.03	2.01	5.5	15	1	3	1	1		0
<i>S. niger</i>	AMS C.322982-8	6.13	3.78	3.65	2.00	4.96	6.07	1.62	1.83	4.0	3	1	1	0	1	0	
<i>S. niger</i>	MNHN- IM-20100- 27769-1	9.25	5.10	5.46	3.09	7.28	8.99	1.81	1.77		5	1	1	0	1	16	2
<i>S. niger</i>	MNHN- IM-20100- 27769-11	9.01	5.36	5.12	2.90	7.13	8.90	1.68	1.77		3	1	1	0	1	0	0
<i>S. niger</i>	MNHN- IM-20100- 27769-2	9.06	5.04	5.20	2.93	6.97	8.77	1.80	1.77		4	1	1	0	1	13	2
<i>S. niger</i>	MNHN- IM-20100- 27769-3	9.08	5.50	5.72	3.22	7.44	8.89	1.65	1.78		4	1	1	0	1	0	0
<i>S. niger</i>	MNHN- IM-20100- 27769-4	9.06	5.31	5.36	2.97	7.08	8.78	1.71	1.80		6	1	2	0	1	4	2
<i>S. niger</i>	MNHN- IM-20100- 27769-5	9.08	5.38	5.39	3.11	7.08	8.74	1.69	1.73		6	1	1	0	1	0	0
<i>S. niger</i>	MNHN- IM-20100- 27769-6	9.07	5.39	5.42	2.99	7.41	8.88	1.68	1.81	4.5	4	1	1	0	1	0	0
<i>S. niger</i>	MNHN- IM-20100- 27769-7	9.11	5.28	5.37	2.91	7.27	8.95	1.73	1.85		4	1	1	0	1	10	2
<i>S. niger</i>	MNHN- IM-20100- 27769-8	9.11	5.31	5.43	2.93	7.32	8.91	1.72	1.85		4	1	0	0	1	3	2
<i>S. niger</i>	MNHN- IM-20100- 27769-9	8.98	5.02	5.39	2.97	7.27	8.84	1.79	1.81		6	1	1	0	1	9	2
<i>S. niger</i>	ZMB 000-1	11.33	6.56	6.20	3.35	8.73	10.59	1.73	1.85	5.5	17	2	4	4	1	15	2
<i>S. niger</i>	ZMB 000-2	10.44	5.89	5.93	3.36	8.36	10.08	1.77	1.76	5.5	12	1	4	3	1	0	0
<i>S. niger</i>	ZMB 121076-1	9.13	5.21	5.37	2.81	7.13	8.86	1.75	1.91	5.0	7	1	2	0	1	0	0
<i>S. niger</i>	ZMB 121076-2	7.90	4.80	4.80	2.65	6.44	7.68	1.65	1.81	4.5	4	1	1	1	1	0	0
<i>S. niger</i>	ZMB 121076-4	8.36	4.73	5.10	2.66	6.72	8.16	1.77	1.92	4.5	6	1	1	0	1	0	0
<i>S. niger</i>	ZMB 121077-1	8.69	5.09	5.05	2.65	7.09	8.42	1.71	1.91	4.5	5	1	1	0	1	0	0
<i>S. niger</i>	ZMB 121077-2	9.24	5.67	5.85	3.13	7.59	9.09	1.63	1.87	4.5	2	1	1	0	1	2	1
<i>S. niger</i>	ZMB 121077-3	8.35	4.86	5.21	2.74	6.85	8.12	1.72	1.90	4.5	4	1	1	0	1	0	0
<i>S. niger</i>	ZMB 121077-4	8.03	4.66	5.01	2.65	6.54	7.98	1.72	1.89	4.5	2	1	1	0	1	0	0
<i>S. niger</i>	ZMB 121077-5	8.25	4.93	5.09	2.80	6.80	8.04	1.67	1.82	4.5	3	1	1	0	1	0	0
<i>S. niger</i>	ZMB 121079-1	12.19	7.33	6.82	4.20	9.50	11.76	1.66	1.62		14	1	4	5	1	6	2
<i>S. niger</i>	ZMB 121079-2	11.10	7.22	7.07	3.81	9.46	10.97	1.54	1.86	5.0	7	3	2	1	1	15	1
<i>S. niger</i>	ZMB 121079-3	11.22	6.98	6.76	3.75	9.19	10.87	1.61	1.80	4.5	10	2	2	5	1	16	2
<i>S. niger</i>	ZMB 121080-1	10.00	5.80	5.74	3.04	7.90	9.57	1.72	1.89	4.5	12	1	2	4	1	5	1

<i>S. niger</i>	ZMB 121080-2	11.66	6.44	6.39	3.52	9.01	11.15	1.81	1.82	5.0	14	1	4	4	1	12	2
<i>S. niger</i>	ZMB 121085-1	10.69	6.78	6.59	4.07	9.32	10.49	1.58	1.62	4.5	3	2	1	0	1	20	3
<i>S. niger</i>	ZMB 121085-2	9.84	6.52	6.25	3.62	8.75	9.78	1.51	1.73	4.0	3	2	1	0	1	20	2
<i>S. niger</i>	ZMB 18294-1	5.82	3.77	3.60	1.99	4.86	5.68	1.54	1.81	4.0	3	1	1	0	1	14	2
<i>S. niger</i>	ZMB 18294-2	8.92	5.80	5.68	3.24	7.65	8.40	1.54	1.75	5.0	15	2	4	1	1	15	3
<i>S. niger</i>	ZMB 21803-2	8.46	4.92	5.05	2.72	6.66	8.11	1.72	1.86	5.5	2	2	1	0	1	0	0
<i>S. niger</i>	ZMB 4303- 1	13.34	7.32	7.29	3.95	10.30	12.92	1.82	1.85		8	2	2	3	1	5	1
<i>S. niger</i>	ZMB 4494- 1	9.05	5.43	5.50	3.12	7.25	8.83	1.67	1.76		4	1	1	0	1	0	0
<i>S. niger</i>	ZMB 4494- 3	9.18	5.32	5.27	3.03	7.33	8.82	1.73	1.74	4.5	3	1	1	0	1	0	0
<i>S. niger</i>	AMS 322982-10	8.00	4.62	5.05	2.49	6.53	7.85	1.73	2.03		4	1	1	0	1	0	0
<i>S. niger</i>	AMS 322982-11	9.45	5.26	5.41	3.07	7.46	9.32	1.80	1.76		2	1	1	0	1	0	0
<i>S. niger</i>	AMS 322982-12	7.79	4.40	4.83	2.36	6.32	7.68	1.77	2.05		3	1	1	0	1	0	0
<i>S. niger</i>	AMS 322982-13	7.49	4.38	4.69	2.51	6.15	7.33	1.71	1.87	4.5	3	1	1	0	1	0	0
<i>S. niger</i>	AMS 322982-14	7.86	4.56	4.63	2.35	6.37	7.68	1.72	1.97	4.0	3	1	1	0	1	0	0
<i>S. niger</i>	AMS 323602-10	10.08	5.98	6.13	3.40	8.04	9.87	1.69	1.80	4.5	7	1	2	1	1	15	2
<i>S. niger</i>	AMS 323602-11	9.48	5.30	5.45	2.90	7.21	9.20	1.79	1.88		6	1	1	1	1	0	0
<i>S. niger</i>	AMS 323602-12	9.28	5.37	5.28	3.26	7.43	9.04	1.73	1.62		3	1	1	0	1	5	1
<i>S. niger</i>	AMS 323602-8	10.00	5.97	6.00	3.38	7.97	9.70	1.68	1.78	6.0	6	1	1	0	1	15	2
<i>S. niger</i>	AMS 323602-9	9.82	5.55	5.94	3.17	8.00	9.67	1.77	1.87	4.5	6	1	1	0	1	9	1
<i>S. niger</i>	CWR65/96- 1	11.73	6.98	6.50	3.64	8.82	11.23	1.68	1.79	5.0	7	2	1	1	1	11	2
<i>S. niger</i>	CWR65/96- 2	11.43	6.61	6.37	3.56	8.77	11.15	1.73	1.79	4.0	6	1	1	1	1	14	2
<i>S. niger</i>	ZMB 108269-13	9.85	5.60	5.82	2.70	7.52	9.18	1.76	2.16	6.0	9	1	2	4	1	0	0
<i>S. niger</i>	GP 1040781	9.9	5.81	5.25	3.22	8.04	9.33	1.70	1.63	4.5	3	1	1	0	1	0	
<i>S. niger</i>	GP 1061756	8.7	4.87	4.88	2.72	6.66	8.29	1.79	1.79	4.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 1061757	8.9	4.95	5	2.86	6.58	8.52	1.80	1.75	5.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 1061758	9.8	4.98	5.24	2.8	7.48	9.29	1.97	1.87	5.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 1061759	9.5	5.1	5.04	2.86	7.21	8.92	1.86	1.76	5.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 1061760	9	5.03	5.07	3.03	7.2	8.56	1.79	1.67	5	4	1	1	0	1	0	
<i>S. niger</i>	GP 1061761	8.4	4.89	4.84	2.78	6.57	8.05	1.72	1.74	4.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 1061762	9.7	5.37	5.44	2.84	7.35	9.28	1.81	1.92	4.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 1061763	9	4.88	5.27	2.74	6.91	8.44	1.84	1.92	5.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 1061764	10	5.35	5.38	2.98	7.41	9.1	1.87	1.81	7	6	1	1	0	1	0	
<i>S. niger</i>	GP 1061766	6.9	4.44	4.31	2.66	5.87	6.79	1.55	1.62	4.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 114309	10.5	5.93	5.59	3.2	8.03	10.1	1.77	1.75	4.5	0			0	1	12	0
<i>S. niger</i>	GP 114312	9.3	4.97	5.12	2.73	7.2	8.93	1.87	1.88	4.5	4	1	1	0	1	0	0
<i>S. niger</i>	GP 160679	12.7	7.49	6.87	3.91	9.72	11.8	1.70	1.76	5.5	13	1	4	6	1	9	0
<i>S. niger</i>	GP 160680	12.9	7.7	6.5	3.86	9.87	12	1.68	1.68	5.5	16	1	4	5	1	11	1
<i>S. niger</i>	GP 306949	9	4.94	4.79	2.81	7.09	8.66	1.82	1.70	5.5	5	1	1	0	1	0	

Appendix V Supplemental material for Chapter 7

<i>S. niger</i>	GP 306951	8	4.58	4.26	2.64	6.27	7.6	1.75	1.61	4.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 306952	8.1	4.67	4.49	2.43	6.33	7.92	1.73	1.85	4.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 306953	8.5	4.92	4.33	2.71	6.43	8.05	1.73	1.60	4.5	6	1	1	0	1	0	
<i>S. niger</i>	GP 306954	10.9	6.16	6.12	3.45	8.5	10.4	1.77	1.77	5.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 306955	7.5	4.25	4.28	2.36	5.99	7.28	1.76	1.81	4.5	2	1	1	0	1	0	
<i>S. niger</i>	GP 306956	6.5	3.74	3.45	2.02	5.02	6.17	1.74	1.71	5.5	6	1	1	0	1	0	
<i>S. niger</i>	GP 306957	7.4	4.15	4.31	2.27	5.77	7.08	1.78	1.90	4.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 307118	8.6	4.82	4.83	2.74	6.77	8.33	1.78	1.76	5.5	6	1	1	0	1	0	
<i>S. niger</i>	GP 307121	8.7	4.79	4.71	2.58	6.75	8.47	1.82	1.83	4.5	6	1	1	0	1	0	
<i>S. niger</i>	GP 307122	9.1	5.1	5.21	2.98	7.2	8.85	1.78	1.75	4.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 307123	8.8	5.03	5.04	2.87	7.17	8.69	1.75	1.76	4.5	3	1	1	0	1	0	
<i>S. niger</i>	GP 307125	9.1	4.63	4.66	2.69	6.81	8.44	1.97	1.73	6.5	3	1	1	0	1	0	
<i>S. niger</i>	GP 307126	7.6	4.18	3.98	2.35	5.88	7.17	1.82	1.69	5.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 307127	9.4	5.22	4.95	2.93	7.22	8.91	1.80	1.69	5.5	6	1	1	0	1	0	
<i>S. niger</i>	GP 515580	12.4	6.56	6.41	3.69	9.12	11.4	1.89	1.74	6.5	8	1	3	0	1	16	0
<i>S. niger</i>	GP 685458	8.8	5.01	4.75	2.82	6.87	8.5	1.76	1.68	4.5	5	1	1	0	1		
<i>S. niger</i>	GP 723081	8	4.31	4.13	2.27	5.71	7.3	1.86	1.82	6.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 727553	8.3	4.8	4.71	2.69	6.8	8.23	1.73	1.75	4.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 727554	8.1	4.76	4.75	2.89	6.44	7.84	1.70	1.64	4.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 773692	11.1	6.07	5.69	3.46	8.5	10.6	1.83	1.64	5.5	4	1	1	0	1	12	0
<i>S. niger</i>	GP 773693	9.2	5.25	4.86	3.01	7.33	9.09	1.75	1.61	4.5	3	1	1	0	1	13	0
<i>S. niger</i>	GP 773694	8.2	4.69	4.36	2.66	6.37	7.9	1.75	1.64	4.5	6	1	1	0	1	15	0
<i>S. niger</i>	GP 773695	8.1	4.27	4.08	2.45	6.37	7.8	1.90	1.67	6	6	1	1	0	1	12	0
<i>S. niger</i>	GP 773700	6.8	4.1	3.79	2.36	5.56	6.63	1.66	1.61	4.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 950668	11	6.49	5.74	3.67	8.74	10.8	1.69	1.56	4.5	6	1	1	0	1	12	0
<i>S. niger</i>	GP 986681	7.7	4.37	4.19	2.44	6.21	7.44	1.76	1.72	4.5	5	1	1	0	1	13	0
<i>S. niger</i>	GP 986682	7.8	4.63	4.09	2.75	6.24	7.56	1.68	1.49	4.5	4	1	1	0	1	0	
<i>S. niger</i>	GP 986683	8.1	4.81	4.33	2.84	6.68	7.81	1.68	1.52	5.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 515577	11	6.44	6.15	3.4	8.9	10.6	1.71	1.81	5.5	5	1	1	0	1	0	
<i>S. niger</i>	GP 515579	11.7	6.63	6.3	3.82	9.29	11.3	1.76	1.65	5.5	4	1	1	0	1	0	
<i>S. niger</i>	ZMH 41603-1	9.13	5.46	5.32	3.16	7.57	8.81	1.67	1.68	4.5	4	1	1	0	1	0	
<i>S. niger</i>	ZMH 41603-2	9.66	5.55	5.22	3.1	7.83	9.27	1.74	1.68	4.5	4	1	1	0	1	0	
<i>S. niger</i>	ZMH 41604-1	10.3	5.53	5.23	3.07	8.01	9.78	1.85	1.70	5.5	4	1	1	0	1	0	
<i>S. niger</i>	ZMH 41604-3	10.5	5.69	5.69	3.06	8.28	9.99	1.84	1.86	5.5	4	1	1	0	1	0	
<i>S. obsoletus</i>	GP 1014114	15.4	9.07	8.05	4.95	12.1	14.7	1.70	1.63	5.5	13	3	4	4	1	9	1
<i>S. obsoletus</i>	GP 1014115	14.6	8.44	7.78	4.53	11.6	13.8	1.73	1.72	5.5	15	3	4	5	1	9	1
<i>S. obsoletus</i>	GP 1014116	14.4	8.54	7.63	4.54	11.4	13.8	1.69	1.68	5.5	15	3	4	4	1	10	1
<i>S. obsoletus</i>	GP 1014117	14.3	5.61	5.19	2.93	7.75	9.37	2.55	1.77	5	12	3	4	4	1	9	2
<i>S. obsoletus</i>	GP 1014118	14.4	8.34	7.71	4.41	11.1	13.6	1.73	1.75	5.5	14	3	4	5	1	8	2
<i>S. obsoletus</i>	GP 284397	11.7	7.17	6.63	4.04	9.44	11.3	1.63	1.64	5	9	1	3	3	1	10	1
<i>S. obsoletus</i>	GP 284398	12.2	7.46	6.69	3.93	9.76	11.6	1.64	1.70	5.5	11	1	3	3	1	12	1
<i>S. obsoletus</i>	GP 284399	12.1	7.19	6.41	4.17	9.33	11.6	1.68	1.54	4.5	9	1	3	4	1	9	1
<i>S. obsoletus</i>	GP 284400	11.8	7.22	6.53	3.88	9.6	11.6	1.63	1.68	4.5	8	1	3	5	1	11	1

<i>S. obsoletus</i>	GP 284401	12.8	7.36	6.64	3.98	10.2	12.3	1.74	1.67	4.5	9	1	3	3	1	12	1
<i>S. obsoletus</i>	GP 284402	13	7.61	7.03	4.1	10.4	12.5	1.71	1.71	4.5	10	1	3	4	1	12	1
<i>S. obsoletus</i>	GP 284403	13.4	7.93	7.3	4.45	10.6	12.8	1.69	1.64	5.5	9	1	3	4	1	12	1
<i>S. obsoletus</i>	GP 284406	13.4	8.12	7.32	4.48	10.8	12.9	1.65	1.63	6	9	1	3	2	1	11	1
<i>S. obsoletus</i>	GP 924654	15.5	8.67	7.72	4.47	11.7	14.6	1.79	1.73	5.5	11	3	4	4	1	6	1
<i>S. obsoletus</i>	GP 924655	15.1	8.03	7.26	4.11	11.2	14.1	1.88	1.77	6	14	3	4	5	1	8	2
<i>S. obsoletus</i>	GP 924657	16	9.11	8.14	4.55	11.8	15	1.76	1.79	6	14	3	4	4	1	10	1
<i>S. obsoletus</i>	GP 924658	16.9	8.85	8.25	4.48	12.6	16	1.91	1.84	5.5	11	3	4	5	1	8	1
<i>S. obsoletus</i>	GP 924659	14.7	8.83	7.89	4.79	11.2	13.9	1.66	1.65	5	16	3	4	5	1	11	2
<i>S. obsoletus</i>	GP 924660	14.1	8.45	7.38	4.43	10.7	12.9	1.67	1.67	5.5	17	3	4	5	1	10	1
<i>S. obsoletus</i>	GP 924661	14.3	8.55	7.84	4.54	11.1	13.6	1.67	1.73	6	16	3	4	5	1	9	1
<i>S. obsoletus</i>	GP 928873	15	8.37	7.3	4.36	11.3	14.1	1.79	1.67	5.5	15	3	4	5	1	10	1
<i>S. obsoletus</i>	GP 928875	15.2	8.27	7.28	4.37	11.2	14.3	1.84	1.67	6	13	3	4	4	1	11	2
<i>S. obsoletus</i>	GP 928877	15.7	8.65	7.63	4.4	11.9	14.9	1.82	1.73	5.5	16	3	4	5	1	10	2
<i>S. obsoletus</i>	GP 928878	14.4	8	7.11	4.27	10.5	13.5	1.80	1.67	5.5	15	3	4	4	1	9	1
<i>S. obsoletus</i>	GP 928879	14.6	8.09	7.51	4.48	11	13.9	1.80	1.68	5.5	13	3	4	5	1	9	1
<i>S. obsoletus</i>	GP 928880	14	7.79	6.61	3.85	10.1	12.9	1.80	1.72	6.5	15	3	4	4	1	9	1
<i>S. obsoletus</i>	GP 928881	15.7	8.55	7.46	4.42	11.3	14.7	1.84	1.69	6.5	16	3	4	5	1	10	2
<i>S. obsoletus</i>	GP 928882	14.2	8.26	7.09	4.35	10.5	13.3	1.72	1.63	5.5	16	3	4	4	1	9	1
<i>S. obsoletus</i>	GP 928883	15	8.24	7.24	4.33	11.4	14.2	1.82	1.67	5.5	15	3	4	4	1	9	2
<i>S. obsoletus</i>	GP 283488	15	8.97	7.91	4.56	11.5	14.2	1.67	1.73	6.5	15	3	4	5	1	9	1
<i>S. obsoletus</i>	GP 283489	14.9	8.81	7.52	4.43	11.5	14	1.69	1.70	5.5	15	3	4	4	1	8	1
<i>S. obsoletus</i>	GP 283492	16	9	8.14	4.87	12	14.6	1.78	1.67	6	16	3	4	4	1	10	1
<i>S. obsoletus</i>	GP 283528	15	9.01	7.85	4.86	11.5	14.2	1.66	1.62	5.5	16	3	4	5	1	9	1
<i>S. obsoletus</i>	GP 283529	15	8.77	7.45	4.49	11.2	14.2	1.71	1.66	5.5	16	3	4	4	1	8	2
<i>S. obsoletus</i>	GP 283530	15.5	9.25	7.69	4.69	11.6	14.2	1.68	1.64	5.5	13	3	4	4	1	9	1
<i>S. planicostaus</i>	ZMH 41607-1	22.3	11.3	9.97	5.79	15.8	20.3	1.98	1.72	6.5	11	4	4	4	1	8	2
<i>S. planicostaus</i>	ZMH 41607-2	22	13	10.3	6.07	16.3	20.5	1.69	1.70	5.5	10	4	4	4	1	7	2
<i>S. planicostaus</i>	ZMB 108261-9	25.4	15.1	12.8	7.64	18.6	23.4	1.69	1.68	6.5	10	4	4	4	1	8	3
<i>S. planicostaus</i>	ZMH 41606-2	14	8.33	7.19	4	10.7	13.3	1.67	1.80	4.5	11	4	4	4	1	7	2
<i>S. planicostaus</i>	ZMH 41606-3	16.9	9.32	8.62	4.72	12.3	15.6	1.81	1.83	5.5	12	4	4	4	1		
<i>S. planicostaus</i>	GP 114264	16.3	8.92	7.79	4.25	11.9	15.1	1.83	1.83	6	11	4	4	4	1	8	2
<i>S. planicostaus</i>	GP 114268	19.2	10	8.05	5.04	13.5	17.4	1.91	1.60	5.5	10	4	4	4	1	8	1
<i>S. planicostaus</i>	GP 194342	20.8	11.9	9.47	5.8	14.8	18.7	1.75	1.63	7	11	4	4	4	1	7	2
<i>S. planicostaus</i>	GP 268185	17.4	9.21	8.3	4.68	12.4	15.9	1.89	1.77	6.5	12	4	4	4	1	7	1
<i>S. planicostaus</i>	GP 589163	20.6	11	9.09	5.5	14.3	18.4	1.87	1.65	6.5	10	4	4	4	1		
<i>S. planicostaus</i>	GP 589164	16.9	9.83	7.99	5.16	12.3	15.8	1.72	1.55	6.5	10	4	4	4	1		
<i>S. planicostaus</i>	GP 637497	20.2	11.6	9.48	5.93	14.8	18.8	1.75	1.60	5.5	10	4	4	4	1	7	2
<i>S. planicostaus</i>	GP 674215	20.1	10.7	8.75	5.32	14.2	17.9	1.87	1.64	6.5	11	4	4	4	1	9	2
<i>S. planicostaus</i>	GP 674216	20.8	11.4	8.91	5.71	14.5	18.6	1.82	1.56	7	10	4	4	4	1	9	2
<i>S. planicostaus</i>	GP 674218	20	10.6	8.64	5.33	14.1	17.7	1.89	1.62	6.5	11	4	4	5	1	8	2
<i>S. planicostaus</i>	GP 674219	19.9	11.5	9.68	5.45	14.3	18.1	1.73	1.78	7	10	4	4	4	1	9	2
<i>S. planicostaus</i>	GP 674221	19.9	10.9	8.64	5.25	14.1	18	1.82	1.65	7	11	4	4	4	1	8	2
<i>S. planicostaus</i>	GP 674222	19.1	11	8.64	5.39	13.4	17.4	1.74	1.60	7	11	4	4	4	1	8	2

Appendix V Supplemental material for Chapter 7

<i>S. planicostaus</i>	GP 674225	20.1	11.2	8.81	5.52	13.7	18	1.79	1.60	6.5	10	4	4	4	1	7	2
<i>S. planicostaus</i>	GP 771803	18.7	10.7	8.57	5.05	13.4	17.2	1.75	1.70	6.5	11	4	4	4	1	9	1
<i>S. planicostaus</i>	GP 771806	20.2	10.5	8.63	5.06	13.8	18.1	1.92	1.71	6.5	10	4	4	4	1	9	1
<i>S. planicostaus</i>	GP 771809	16.2	8.55	7.38	4.28	11.4	14.9	1.89	1.72	6.5	11	4	4	4	1	8	2
<i>S. planicostaus</i>	GP 771829	15	8.42	7.54	3.95	11	13.9	1.78	1.91	6.5	11	4	4	4	1	7	2
<i>S. planicostaus</i>	NHMUK 1966623-1	18.6	10.7	8.79	5.4	13.3	17	1.74	1.63	5.5	10	4	4	4	1	7	2
<i>S. planicostaus</i>	NHMUK 1966623-2	17.7	10.4	9.06	5.38	13.2	16.7	1.70	1.68	5.5	11	4	4	4	1		
<i>S. planicostaus</i>	NHMUK 1966623-3	17.9	10.5	9.1	5.49	13.5	16.7	1.71	1.66	5.5	12	4	4	4	1	9	2
<i>S. planicostaus</i>	NHMUK 1966623-5	20.1	11.2	9.93	5.79	14.4	18.3	1.79	1.72	5.5	11	4	4	4	1	8	1
<i>S. planicostaus</i>	NHMUK 1966623-8	27.3	12.7	12.8	6.88	18.8	24.7	2.15	1.86	6.5	12	4	4	4	1	7	1
<i>S. planicostaus</i>	ZMH 41605-1	21.3	11.7	10.2	5.29	16.3	20	1.81	1.94	5.5	11	3	4	3	1	10	2
<i>S. planicostaus</i>	ZMH 41605-2	18.4	11.2	9.3	5.52	14.9	17.9	1.64	1.68	4.5	11	3	4	3	1	9	2
<i>P. sulcatus</i>	SMF 346144-1	19.6	13.3	11.5	6.62	16.1	18.9	1.47	1.74	4.5	14	2	4		1	11	2
<i>P. sulcatus</i>	SMF 346144-3	18.2	12.9	10.2	6.16	14.6	17.1	1.41	1.65	5.5	12	2	4		1	11	1
<i>P. sulcatus</i>	SMF 346144-4	17.8	11.8	10.3	5.99	14.1	16.3	1.52	1.72	4.5	11	1	4		1	9	1
<i>P. sulcatus</i>	SMF 346144-5	18.8	12	10.9	6.1	14.8	17.4	1.56	1.78	4.5	18	1	4		1	9	1
<i>P. sulcatus</i>	AMS C.322974- 10	21.2	12.9	12	6.07	16.3	19.6	1.64	1.97	6.5	12	3	4	5	1	12	2
<i>P. sulcatus</i>	SMF 256114-2	20.6	13.6	11.3	6.56	17.1	19.7	1.51	1.73	4.5			4		1	11	
<i>P. sulcatus</i>	SMF 256114-3	23.1	14	11.7	7.15	18.1	21.5	1.65	1.63	5.5	14	2	4		1	10	1
<i>P. sulcatus</i>	SMF 256114-4	23.4	14.3	12.4	6.8	18	21.7	1.63	1.82	5.5	13	2	4		1	11	2
<i>P. sulcatus</i>	SMF 256114-5	18.5	12.2	10.3	5.85	15.2	17.7	1.52	1.77	4.5						10	2
<i>P. sulcatus</i>	SMF 346145-1	17.1	10.5	9.36	5.27	12.9	15.6	1.64	1.78	4.5	12	2	4	5	1	9	1
<i>P. sulcatus</i>	SMF 346145-2	18.4	11.2	9.37	5.26	13.7	16.6	1.65	1.78	7.5	12	1	4	4	1	9	2
<i>P. sulcatus</i>	SMF 346145-3	16.9	11.1	9.26	5.36	12.8	15.8	1.52	1.73	5.5	12	1	4	3	1	9	1
<i>P. sulcatus</i>	SMF 346145-4	19.3	12.2	9.96	5.87	15.1	18.2	1.58	1.70	5.5	13	1	4	4	1	8	1
<i>P. sulcatus</i>	SMF 346145-6	15.9	9.4	8.24	4.78	11.9	14.8	1.69	1.72	6.5	12	2	4	4	1	8	2
<i>P. sulcatus</i>	SMF 346146-2	18.3	11.1	10.2	5.49	13.7	16.8	1.65	1.85	6.5	12	2	4	4	1	7	1
<i>P. sulcatus</i>	SMF 346146-6	15.9	9.48	8.35	4.91	11.9	15	1.68	1.70	5.5	11	1	4	4	1	10	1
<i>P. sulcatus</i>	SMF 346148-1	16.4	10.4	9.79	5.24	13.8	16.2	1.58	1.87		15	1	4		1	7	1
<i>P. sulcatus</i>	SMF 346148-2	14.6	8.76	7.67	4.29	11.2	14	1.66	1.79	5.5	15	2	4	4	1	8	1
<i>P. sulcatus</i>	SMF 346149-1	17.1	10.6	8.81	5.09	13.5	16.8	1.62	1.73		12	2	4		1	10	2
<i>P. sulcatus</i>	SMF 346149-3	15.6	9.68	8.53	4.22	12.1	14.8	1.61	2.02	5.5	14	2	4	4	1	10	2
<i>P. sulcatus</i>	SMF 346149-4	12.8	7.83	6.91	3.74	10.1	12.2	1.63	1.85	4.5	12	2	4	4	1	10	2
<i>P. sulcatus</i>	ZMB 106003-12	27.4	17.8	14.7	7.88	21.6	26.5	1.54	1.87	4.5	13	2	4	4	1	9	1
<i>P. sulcatus</i>	ZMB 106003-13	20.5	13.2	11.9	5.83	16.7	19.8	1.56	2.04	4.5	16	2	4	4	1	10	2
<i>P. sulcatus</i>	ZMB 106307-11	21.8	14	12.5	6.75	17	20.6	1.56	1.86	5.5	13	2	4	5	1	10	2
<i>P. sulcatus</i>	ZMB 106307-12	21.6	13.1	12.5	6.42	17.2	20.6	1.65	1.95	4.5	15	2	4	5	1	11	2

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<i>P. sulcatus</i>	ZMB 106376-11	22.5	15.1	12.8	6.71	18.2	21.6	1.49	1.90	4.5	15	2	4		1	9	2
<i>P. sulcatus</i>	ZMB 107850-10	16.9	11.1	9.46	5.29	14.2	16.4	1.52	1.79	4.5					1	8	1
<i>P. sulcatus</i>	ZMB 107850-9	15.9	11.1	10.1	5.16	13.3	15.9	1.44	1.95	4.5	14	1	4		1	9	1
<i>P. sulcatus</i>	ZMB 108271-10	23.9	15	13.4	6.98	19.1	23.1	1.59	1.92	4.5	13	2	4	4	1	8	2
<i>P. sulcatus</i>	MNHN- IM-2000- 27771	17	10.6	8.53	5.12	12.8	15.7	1.61	1.67	5.5	16	2	4	3	1	10	2
<i>P. sulcatus</i>	CWR 106_09-10	16.1	11.1	9.52	5.55	13.5	15.8	1.45	1.72	4.5	14	2	4		1	10	1
<i>P. sulcatus</i>	CWR 106_09-2	20	13.1	11.6	6.62	16.3	19.6	1.53	1.75	4.5	16	2	4	4	1	10	2
<i>P. sulcatus</i>	CWR 106_09-3	17.4	11.4	10.5	5.82	14.7	17.2	1.53	1.80	4.5	15	2	4	4	1	11	2
<i>P. sulcatus</i>	CWR 106_09-5	18	12.4	10.6	5.97	15.6	17.9	1.44	1.77		14	2	4		1	10	1
<i>P. sulcatus</i>	CWR 106_09-6	18.6	11.9	11.1	6.12	15.9	18.6	1.56	1.81	4.5	15	2	4		1	11	2
<i>P. sulcatus</i>	CWR 106_09-8	17.6	11.2	9.79	5.65	14	16.9	1.57	1.73	5.5	14	2	4	5	1	10	2
<i>P. sulcatus</i>	CWR 106_09-9	16.5	11.2	9.9	5.58	13.7	16.2	1.48	1.77	4.5	14	2	4		1	9	2
<i>P. sulcatus</i>	CWR 106_092-7	19.3	12.3	11.3	6.08	15.8	18.7	1.57	1.86	4.5	15	2	4	4	1	10	1
<i>P. sulcatus</i>	CWR 129_84-5	18.9	11.8	10.4	5.76	15.2	18.4	1.60	1.81	4.5	14	2	4	4	1	10	1
<i>P. sulcatus</i>	CWR 129_84-9	16.1	10.8	9.03	4.84	13.2	15.9	1.49	1.87		15	2	4		1	10	1
<i>P. sulcatus</i>	CWR 14_90-1	25.2	15.7	13.5	7.57	21.2	25	1.61	1.78	4.5					1	12	1
<i>P. sulcatus</i>	CWR 14_90-2	22.8	15.6	13.5	7.02	19.6	22.6	1.47	1.92		12	2	4		1	10	1
<i>P. sulcatus</i>	CWR 14_90-5	20.6	14.6	11.9	6.08	17.4	20.6	1.41	1.95		14	2	4		1	10	1
<i>P. sulcatus</i>	CWR 14_90-6	19.2	13.2	11.1	6.26	16.3	19.2	1.45	1.78	4.5	13	2	4		1	12	1
<i>P. sulcatus</i>	CWR 17_07-8	14.2	9.48	8.59	4.62	12.2	14	1.49	1.86	4.5	14	2	4		1	10	1
<i>P. sulcatus</i>	CWR 25_85-3	16	9.98	9.06	4.95	12.9	15.8	1.60	1.83	4.5	16	2	4		1	10	1
<i>P. sulcatus</i>	CWR 25_85-8	14.2	9.25	7.72	4.16	11.7	13.8	1.53	1.86	5	14	2	4		1	11	2
<i>P. sulcatus</i>	CWR 25_85-9	15	9.29	8.39	4.62	11.9	14.7	1.61	1.82	4.5	15	2	4		1	10	1
<i>P. sulcatus</i>	CWR 47_84-10	16.6	10.5	9.4	5.08	13.2	15.7	1.58	1.85	5.5	15	2	4	5	1	10	1
<i>P. sulcatus</i>	CWR 47_84-4	17.9	10.8	10.2	5.46	14.4	17.2	1.66	1.87	4.5	16	1	4	4	1	11	2
<i>P. sulcatus</i>	CWR 47_84-7	17.2	10.3	9.62	5.21	13.5	16.5	1.67	1.85	5.5	15	2	4	5	1	10	1
<i>P. sulcatus</i>	CWR 47_84-8	15.6	10.1	9.42	4.78	12.7	14.9	1.55	1.97	5.5	14	2	4	4	1	10	2
<i>P. sulcatus</i>	CWR 47_84-9	15.4	9.38	8.99	4.72	12.2	14.6	1.64	1.90	5.5	14	2	4	5	1	9	2
<i>P. sulcatus</i>	CWR 4_83- 10	17.1	10.5	9.2	5.1	13.4	16.5	1.63	1.80	4.5	14	2	4		1		
<i>P. sulcatus</i>	CWR 4_83- 9	17	10.5	9.75	5.08	13.9	16.4	1.61	1.92	4.5	12	2	4		1		
<i>P. sulcatus</i>	NHMW 14249	27.1	15.1	13.8	6.63	20.3	24.9	1.79	2.08	5.5	13	3	4	5	1	11	1

Table S2 List of images used for the Geometric morphometrics approach.

Species	Included Image and Museum ID
<i>S. nucleus</i>	AMS 323604-6 sh1.JPG'
<i>S. nucleus</i>	AMS 323604-7 sh1.JPG'
<i>S. nucleus</i>	AMS 323610-10 sh1.JPG'
<i>S. nucleus</i>	AMS 323610-6 sh1.JPG'
<i>S. nucleus</i>	AMS 323610-7 sh1.JPG'
<i>S. nucleus</i>	AMS 323610-8 sh1.JPG'
<i>S. nucleus</i>	AMS 323610-9 sh1.JPG'
<i>S. nucleus</i>	BMNH 20140847-2 sh1.JPG'
<i>S. nucleus</i>	BMNH 20140847-3 sh1.JPG'
<i>S. nucleus</i>	BMNH 20140847-4 sh1.JPG'
<i>S. nucleus</i>	BMNH 20140847-5 sh1.JPG'
<i>S. nucleus</i>	BMNH 20140847-6 sh1.JPG'
<i>S. nucleus</i>	ZMB 108278-12 sh1.JPG'
<i>S. nucleus</i>	ZMB 108278-13 sh1.JPG'
<i>S. nucleus</i>	ZMB 108278-14 sh1.JPG'
<i>S. nucleus</i>	ZMB 108278-15 sh1.JPG'
<i>S. nucleus</i>	ZMB 108278-16 sh1.JPG'
<i>S. nucleus</i>	ZMB 110432-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 110432-3 sh1.JPG'
<i>S. nucleus</i>	ZMB 110432-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 110557-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121054-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121054-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121054-3 sh1.JPG'
<i>S. nucleus</i>	ZMB 121054-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 121054-5 sh1.JPG'
<i>S. nucleus</i>	ZMB 121055-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121055-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121056-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121056-3 sh1.JPG'
<i>S. nucleus</i>	ZMB 121056-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 121056-5 sh1.JPG'
<i>S. nucleus</i>	ZMB 121057-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121059-1sh1.JPG'
<i>S. nucleus</i>	ZMB 121059-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121059-3 sh1.JPG'
<i>S. nucleus</i>	ZMB 121059-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 121059-5 sh1.JPG'
<i>S. nucleus</i>	ZMB 121060-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121060-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121060-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 121061-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121061-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121061-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 121061-5 sh1.JPG'
<i>S. nucleus</i>	ZMB 121062-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121062-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 121063-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121064-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121064-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121064-3 sh1.JPG'
<i>S. nucleus</i>	ZMB 121065-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121065-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121066-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121066-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121083-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 121086-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 121086-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 193436-3 sh1.JPG'
<i>S. nucleus</i>	ZMB 193436-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 193436-5 sh1.JPG'
<i>S. nucleus</i>	ZMB 225-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 225-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 225-5 sh1.JPG'
<i>S. nucleus</i>	ZMB 28723-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 28723-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 28724-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 28725-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 28725-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 28725-3 sh1.JPG'
<i>S. nucleus</i>	ZMB 28725-4 sh1.JPG'
<i>S. nucleus</i>	ZMB 28725-5 sh1.JPG'
<i>S. nucleus</i>	ZMB 2874-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 2874-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 32401-1 sh1.JPG'
<i>S. nucleus</i>	ZMB 32401-2 sh1.JPG'
<i>S. nucleus</i>	ZMB 32401-3 sh1.JPG'
<i>S. nucleus</i>	ZMB 32401-5 sh1.JPG'
<i>S. nucleus</i>	ZMB 108278-6 sh1.JPG'
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<i>S. nucleus</i>	FW 12372-2 sh1.tif'
<i>S. nucleus</i>	FW 12372-3 sh1.tif'
<i>S. nucleus</i>	FW 12372-4 sh1.tif'
<i>S. nucleus</i>	FW 12372-5 sh1.tif'
<i>S. nucleus</i>	FW 12372-6 sh1.tif'
<i>S. nucleus</i>	FW 12372-7 sh1.tif'
<i>S. nucleus</i>	FW 12372-8 sh1.tif'
<i>S. nucleus</i>	FW 12372-9 sh1.tif'
<i>S. nucleus</i>	FW 12373-1 sh1.tif'
<i>S. nucleus</i>	FW 12373-10 sh1.tif'
<i>S. nucleus</i>	FW 12373-2 sh1.tif'
<i>S. nucleus</i>	FW 12373-3 sh1.tif'
<i>S. nucleus</i>	FW 12373-4 sh1.tif'
<i>S. nucleus</i>	FW 12373-5 sh1.tif'
<i>S. nucleus</i>	FW 12373-7 sh1.tif'
<i>S. nucleus</i>	FW 12373-8 sh1.tif'
<i>S. nucleus</i>	FW 12373-9 sh1.tif'
<i>S. nucleus</i>	ZMH 140713-1 sh1.tif'
<i>S. nucleus</i>	ZMH 140713-3 sh1.tif'
<i>S. nucleus</i>	FW 7821a-1 sh1.tif'
<i>S. nucleus</i>	FW 7821a-2 sh1.tif'
<i>S. nucleus</i>	FW 7821a-4 sh1.tif'
<i>S. nucleus</i>	FW 7821a-5 sh1.tif'
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<i>S. nucleus</i>	GP 1061540 10_7mm.jpg'
<i>S. nucleus</i>	GP 1061542 12_3mm.jpg'
<i>S. nucleus</i>	GP 114273 17mm.jpg'
<i>S. nucleus</i>	GP 114274 10_6mm.jpg'
<i>S. nucleus</i>	GP 114275 16mm.jpg'
<i>S. nucleus</i>	GP 114277 16_2mm.jpg'
<i>S. nucleus</i>	GP 114278 16_8mm.jpg'
<i>S. nucleus</i>	GP 268488 10_7mm.jpg'
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<i>S. nucleus</i>	GP 268491 11_3mm.jpg'
<i>S. nucleus</i>	GP 639708 15mm.jpg'
<i>S. nucleus</i>	GP 675596 10mm.jpg'
<i>S. nucleus</i>	GP 675597 10mm.jpg'
<i>S. nucleus</i>	GP 675599 11mm.jpg'
<i>S. nucleus</i>	GP 675600 10mm.jpg'
<i>S. nucleus</i>	GP 675602 12_5mm.jpg'
<i>S. nucleus</i>	GP 727172 14_9mm.jpg'
<i>S. nucleus</i>	GP 727173 11mm.jpg'
<i>S. nucleus</i>	GP 771818 10_7mm.jpg'
<i>S. nucleus</i>	GP 771831 11_2mm.jpg'

<i>S. nucleus</i>	GP 771832 11_6mm.jpg'	<i>S. leyteensis</i>	GP 646299 1 20mm.jpg'
<i>S. nucleus</i>	GP 921466 10_7mm.jpg'	<i>S. leyteensis</i>	GP 646302 4 18_7mm.jpg'
<i>S. nucleus</i>	GP 921467 11_6mm.jpg'	<i>S. leyteensis</i>	GP 646303 5 17_9mm.jpg'
<i>S. nucleus</i>	GP 977449 17_5mm.jpg'	<i>S. leyteensis</i>	GP 646305 7 18_4mm.jpg'
<i>S. abb. abbreviata</i>	ANSP 18260 shell1 apt Paralectotype.jpg'	<i>S. leyteensis</i>	GP 646306 8 18_1mm.jpg'
<i>S. abb. abbreviata</i>	ANSP 18260 shell2 apt Paralectotype.jpg'	<i>S. leyteensis</i>	GP 646307 9 18_2mm.jpg'
<i>S. abb. abbreviata</i>	ANSP 18260 shell3 apt Paralectotype.jpg'	<i>S. leyteensis</i>	GP 646308 10 17_8mm.jpg'
<i>S. abb. abbreviata</i>	ANSP 18261 apt Lectotype.tif'	<i>S. leyteensis</i>	GP 646310 12 16_5mm.jpg'
<i>S. abb. abbreviata</i>	ANSP 394492 shell1 apt Paralectotype.jpg'	<i>S. leyteensis</i>	GP 646311 13 17_4mm.jpg'
<i>S. abb. abbreviata</i>	ANSP 394492 shell2 apt Paralectotype.jpg'	<i>S. leyteensis</i>	GP 646312 14 17_3mm.jpg'
<i>S. abb. abbreviata</i>	NHMUK 1964320.tif'	<i>S. leyteensis</i>	GP 646314 16 16_6mm.jpg'
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<i>S. abb. abbreviata</i>	ZMB 121078-2 sh1.JPG'	<i>S. leyteensis</i>	GP 646316 18 16_9mm.jpg'
<i>S. abb. abbreviata</i>	ZMB 121078-3 sh1.JPG'	<i>S. leyteensis</i>	GP 646317 19 17_3mm FW 8566.jpg'
<i>S. abb. abbreviata</i>	ZMB 121082-1 sh1.JPG'	<i>S. leyteensis</i>	GP 646318 20 19_1mm.jpg'
<i>S. abb. abbreviata</i>	ZMB 121084-1 sh1.JPG'	<i>S. leyteensis</i>	GP 646319 21 16_4mm.jpg'
<i>S. abb. abbreviata</i>	ZMB 121084-2 sh1.JPG'	<i>S. leyteensis</i>	GP 646320 22 18_5mm.jpg'
<i>S. abb. abbreviata</i>	ZMB 121085-1 sh1.JPG'	<i>S. leyteensis</i>	GP 646321 23 18_6mm.jpg'
<i>S. abb. abbreviata</i>	ZMB 121085-2 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-1.jpg'
<i>S. abb. abbreviata</i>	ZMB 18294-1 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-10.jpg'
<i>S. abb. abbreviata</i>	ZMB 18294-2 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-11.jpg'
<i>S. abb. abbreviata</i>	ZMB 20097-1 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-2.jpg'
<i>S. abb. abbreviata</i>	ZMB 20097-2 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-3.jpg'
<i>S. abb. ogaswarana</i>	SMF 346151-1 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-4.jpg'
<i>S. abb. ogaswarana</i>	SMF 346151-2 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-5.jpg'
<i>S. abb. ogaswarana</i>	SMF 346151-4 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-6.jpg'
<i>S. abb. ogaswarana</i>	SMF 346151-5 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-7.jpg'
<i>S. abb. ogaswarana</i>	SMF 346151-6 sh1.JPG'	<i>S. niger</i>	MNHN-IM-20100-27769-8.jpg'
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<i>S. abb. ogaswarana</i>	ANSP 87769 shell1 apt Syntype.jpg'	<i>S. niger</i>	AMS C. 322982-7 sh1.JPG'
<i>S. abb. ogaswarana</i>	ANSP 87769 shell2 apt Syntype.jpg'	<i>S. niger</i>	AMS C. 322982-8 sh1.JPG'
<i>S. abb. ogaswarana</i>	ANSP 87769 shell3 apt Syntype.jpg'	<i>S. niger</i>	ZMB 121075-1 sh1.JPG'
<i>S. abb. ogaswarana</i>	ANSP 87769 shell4 apt Syntype.jpg'	<i>S. niger</i>	ZMB 121076-1 sh1.JPG'
<i>S. abb. ogaswarana</i>	BMNH 20140856-1 sh1.JPG'	<i>S. niger</i>	ZMB 121076-2 sh1.JPG'
<i>S. abb. ogaswarana</i>	BMNH 20140856-2 sh1.JPG'	<i>S. niger</i>	ZMB 121076-3 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 121079-1 sh1.JPG'	<i>S. niger</i>	ZMB 121076-4 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 121079-2 sh1.JPG'	<i>S. niger</i>	ZMB 121077-1 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 121079-3 sh1.JPG'	<i>S. niger</i>	ZMB 121077-2 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 121080-2 sh1.JPG'	<i>S. niger</i>	ZMB 121077-3 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 4303-1 sh1.JPG'	<i>S. niger</i>	ZMB 121077-4 sh1.JPG'
<i>S. abb. ogaswarana</i>	BMNH 20140863-1 sh1.JPG'	<i>S. niger</i>	ZMB 121077-5 sh1.JPG'
<i>S. abb. ogaswarana</i>	BMNH 20140863-2 sh1.JPG'	<i>S. niger</i>	ZMB 21803-1 sh1.JPG'
<i>S. abb. ogaswarana</i>	BMNH 20140863-3 sh1.JPG'	<i>S. niger</i>	ZMB 21803-2 sh1.JPG'
<i>S. abb. ogaswarana</i>	BMNH 20140863-4 sh1.JPG'	<i>S. niger</i>	ZMB 4494-1 sh1.JPG'
<i>S. abb. ogaswarana</i>	BMNH 20140863-5 sh1.JPG'	<i>S. niger</i>	ZMB 4494-3 sh1.JPG'
<i>S. abb. ogaswarana</i>	BMNH 20140863-6 sh1.JPG'	<i>S. niger</i>	AMS 322982-11 sh1.JPG'
<i>S. abb. ogaswarana</i>	CWUR10-1 sh1.tif'	<i>S. niger</i>	AMS 322982-12 sh1.JPG'
<i>S. abb. ogaswarana</i>	CWUR10-2 sh1.tif'	<i>S. niger</i>	AMS 322982-13 sh1.JPG'
<i>S. abb. ogaswarana</i>	CWUR11-1 sh1.tif'	<i>S. niger</i>	AMS 323602-10 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 108269-6 sh1.JPG'	<i>S. niger</i>	AMS 323602-11 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 108269-9 sh1.JPG'	<i>S. niger</i>	AMS 323602-12 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 108274-4 sh1.JPG'	<i>S. niger</i>	AMS 323602-8 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 108274-5 sh1.JPG'	<i>S. niger</i>	AMS 323602-9 sh1.JPG'
<i>S. abb. ogaswarana</i>	ZMB 117946-1 sh1.JPG'	<i>S. niger</i>	Type MNHN IM 2000-27769.jpg'
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<i>S. abb. ogaswarana</i>	ZMH 41636-1 sh1.jpg'	<i>S. niger</i>	GP 1061756 8_7mm.jpg'
<i>S. abb. ogaswarana</i>	ZMH 41636-3 sh1.jpg'	<i>S. niger</i>	GP 1061757 8_9mm.jpg'
<i>S. abb. ogaswarana</i>	ZMH 41636-4 sh1.jpg'	<i>S. niger</i>	GP 1061758 9_8mm.jpg'
<i>S. abb. ogaswarana</i>	ZMH 41636-5 sh1.jpg'	<i>S. niger</i>	GP 1061759 9_5mm.jpg'
<i>S. abb. ogaswarana</i>	GP 874300 11_4mm.jpg'	<i>S. niger</i>	GP 1061760 9mm.jpg'
<i>S. abb. ogaswarana</i>	GP 874301 11_7mm.jpg'	<i>S. niger</i>	GP 1061761 8_4mm.jpg'
<i>S. abb. ogaswarana</i>	GP 874302 12mm.jpg'	<i>S. niger</i>	GP 1061762 9_7mm.jpg'
<i>S. leyteensis</i>	FW 8566-1 Paratype.tif'	<i>S. niger</i>	GP 1061763 9mm.jpg'
<i>S. leyteensis</i>	GP 643587 17mm.jpg'	<i>S. niger</i>	GP 1061764 10mm.jpg'

Appendix V Supplemental material for Chapter 7

<i>S. niger</i>	GP 1061766 6_9mm.jpg'	<i>S. obsoletus</i>	GP 928879 14_6mm.jpg'
<i>S. niger</i>	GP 114309 10_5mm.jpg'	<i>S. obsoletus</i>	GP 928880 14mm.jpg'
<i>S. niger</i>	GP 114312 9_3mm.jpg'	<i>S. obsoletus</i>	GP 928881 15_7mm.jpg'
<i>S. niger</i>	GP 160679 12_7mm.jpg'	<i>S. obsoletus</i>	GP 928882 14_2mm.jpg'
<i>S. niger</i>	GP 160680 12_9mm.jpg'	<i>S. obsoletus</i>	GP 928883 15mm.jpg'
<i>S. niger</i>	GP 306949 9mm.jpg'	<i>S. obsoletus</i>	GP 283488 15mm.jpg'
<i>S. niger</i>	GP 306951 8mm.jpg'	<i>S. obsoletus</i>	GP 283489 14_9mm.jpg'
<i>S. niger</i>	GP 306952 8_1mm.jpg'	<i>S. obsoletus</i>	GP 283492 16mm.jpg'
<i>S. niger</i>	GP 306953 8_5mm.jpg'	<i>S. obsoletus</i>	GP 283528 15mm.jpg'
<i>S. niger</i>	GP 306954 10_9mm.jpg'	<i>S. obsoletus</i>	GP 283529 15mm.jpg'
<i>S. niger</i>	GP 306955 7_5mm.jpg'	<i>S. obsoletus</i>	GP 283530 15_5mm.jpg'
<i>S. niger</i>	GP 306956 6_5mm.jpg'	<i>S. planicostatus</i>	ZMH 41607-1 sh1.jpg'
<i>S. niger</i>	GP 306957 7_4mm.jpg'	<i>S. planicostatus</i>	ZMH 41607-2 sh1.jpg'
<i>S. niger</i>	GP 307118 8_6mm.jpg'	<i>S. planicostatus</i>	ZMB 108261-9 sh1.JPG'
<i>S. niger</i>	GP 307121 8_7mm.jpg'	<i>S. planicostatus</i>	ZMH 41606-2 sh1.jpg'
<i>S. niger</i>	GP 307122 9_1mm.jpg'	<i>S. planicostatus</i>	ZMH 41606-3 sh1.jpg'
<i>S. niger</i>	GP 307123 8_8mm.jpg'	<i>S. planicostatus</i>	GP 114264 16_3mm.jpg'
<i>S. niger</i>	GP 307125 9_1mm.jpg'	<i>S. planicostatus</i>	GP 114268 19_2mm.jpg'
<i>S. niger</i>	GP 307126 7_6mm.jpg'	<i>S. planicostatus</i>	GP 194342 20_8mm.jpg'
<i>S. niger</i>	GP 307127 9_4mm.jpg'	<i>S. planicostatus</i>	GP 268185 17_4mm.jpg'
<i>S. niger</i>	GP 515580 12_4mm.jpg'	<i>S. planicostatus</i>	GP 589163 20_6mm.jpg'
<i>S. niger</i>	GP 685458 8_8mm.jpg'	<i>S. planicostatus</i>	GP 589164 16_9mm.jpg'
<i>S. niger</i>	GP 723081 8mm.jpg'	<i>S. planicostatus</i>	GP 637497 20_2mm.jpg'
<i>S. niger</i>	GP 727553 8_3mm.jpg'	<i>S. planicostatus</i>	GP 674215 20_1mm.jpg'
<i>S. niger</i>	GP 727554 8_1mm.jpg'	<i>S. planicostatus</i>	GP 674216 20_8mm.jpg'
<i>S. niger</i>	GP 773692 11_1mm.jpg'	<i>S. planicostatus</i>	GP 674218 20mm.jpg'
<i>S. niger</i>	GP 773693 9_2mm.jpg'	<i>S. planicostatus</i>	GP 674219 19_9mm.jpg'
<i>S. niger</i>	GP 773694 8_2mm.jpg'	<i>S. planicostatus</i>	GP 674221 19_9mm.jpg'
<i>S. niger</i>	GP 773695 8_1mm.jpg'	<i>S. planicostatus</i>	GP 674222 19_1mm.jpg'
<i>S. niger</i>	GP 773700 6_8mm.jpg'	<i>S. planicostatus</i>	GP 674225 20_1mm.jpg'
<i>S. niger</i>	GP 950668 11mm.jpg'	<i>S. planicostatus</i>	GP 771803 18_7mm.jpg'
<i>S. niger</i>	GP 986681 7_7mm.jpg'	<i>S. planicostatus</i>	GP 771806 20_2mm.jpg'
<i>S. niger</i>	GP 986682 7_8mm.jpg'	<i>S. planicostatus</i>	GP 771809 16_2mm.jpg'
<i>S. niger</i>	GP 986683 8_1mm.jpg'	<i>S. planicostatus</i>	GP 771829 15mm.jpg'
<i>S. niger</i>	GP 515577 11mm.jpg'	<i>S. planicostatus</i>	NHMUK 1966623-1 Syntype.tif'
<i>S. niger</i>	GP 515579 11_7mm.jpg'	<i>S. planicostatus</i>	NHMUK 1966623-2 Syntype.tif'
<i>S. niger</i>	ZMH 41603-1 sh1.tif'	<i>S. planicostatus</i>	NHMUK 1966623-3 Syntype.tif'
<i>S. niger</i>	ZMH 41603-2 sh1.tif'	<i>S. planicostatus</i>	NHMUK 1966623-5 Syntype.tif'
<i>S. niger</i>	ZMH 41604-1 sh1.tif'	<i>S. planicostatus</i>	NHMUK 1966623-8 Syntype.tif'
<i>S. niger</i>	ZMH 41604-3 sh1.tif'	<i>S. planicostatus</i>	ZMH 41605-1 sh1.tif'
<i>S. obsoletus</i>	GP 1014114 15_4mm.jpg'	<i>S. planicostatus</i>	ZMH 41605-2 sh1.tif'
<i>S. obsoletus</i>	GP 1014115 14_6mm.jpg'	<i>P. sulcatus</i>	SMF 346144-1 sh1.JPG'
<i>S. obsoletus</i>	GP 1014116 14_4mm.jpg'	<i>P. sulcatus</i>	SMF 346144-3 sh1.JPG'
<i>S. obsoletus</i>	GP 1014117 14_3mm.jpg'	<i>P. sulcatus</i>	SMF 346144-4 sh1.JPG'
<i>S. obsoletus</i>	GP 1014118 14_4mm.jpg'	<i>P. sulcatus</i>	SMF 346144-5 sh1.JPG'
<i>S. obsoletus</i>	GP 284397 11_7mm.jpg'	<i>P. sulcatus</i>	AMS C.322974-10 sh1.JPG'
<i>S. obsoletus</i>	GP 284398 12_2mm.jpg'	<i>P. sulcatus</i>	SMF 256114-2 sh1.JPG'
<i>S. obsoletus</i>	GP 284399 12_1mm.jpg'	<i>P. sulcatus</i>	SMF 256114-3 sh1.JPG'
<i>S. obsoletus</i>	GP 284400 11_8mm.jpg'	<i>P. sulcatus</i>	SMF 256114-4 sh1.JPG'
<i>S. obsoletus</i>	GP 284401 12_8mm.jpg'	<i>P. sulcatus</i>	SMF 256114-5 sh1.JPG'
<i>S. obsoletus</i>	GP 284402 13mm.jpg'	<i>P. sulcatus</i>	SMF 346145-1 sh1.JPG'
<i>S. obsoletus</i>	GP 284403 13_4mm.jpg'	<i>P. sulcatus</i>	SMF 346145-2 sh1.JPG'
<i>S. obsoletus</i>	GP 284406 13_4mm.jpg'	<i>P. sulcatus</i>	SMF 346145-3 sh1.JPG'
<i>S. obsoletus</i>	GP 924654 15_5mm.jpg'	<i>P. sulcatus</i>	SMF 346145-4 sh1.JPG'
<i>S. obsoletus</i>	GP 924655 15_1mm.jpg'	<i>P. sulcatus</i>	SMF 346145-6 sh1.JPG'
<i>S. obsoletus</i>	GP 924657 16mm.jpg'	<i>P. sulcatus</i>	SMF 346146-2 sh1.JPG'
<i>S. obsoletus</i>	GP 924658 16_9mm.jpg'	<i>P. sulcatus</i>	SMF 346146-6 sh1.JPG'
<i>S. obsoletus</i>	GP 924659 14_7mm.jpg'	<i>P. sulcatus</i>	SMF 346148-1 sh1.JPG'
<i>S. obsoletus</i>	GP 924660 14_1mm.jpg'	<i>P. sulcatus</i>	SMF 346148-2 sh1.JPG'
<i>S. obsoletus</i>	GP 924661 14_3mm.jpg'	<i>P. sulcatus</i>	SMF 346149-1 sh1.JPG'
<i>S. obsoletus</i>	GP 928873 15mm.jpg'	<i>P. sulcatus</i>	SMF 346149-3 sh1.JPG'
<i>S. obsoletus</i>	GP 928875 15_2mm.jpg'	<i>P. sulcatus</i>	SMF 346149-4 sh1.JPG'
<i>S. obsoletus</i>	GP 928877 15_7mm.jpg'	<i>P. sulcatus</i>	ZMB 106003-12 sh1.JPG'
<i>S. obsoletus</i>	GP 928878 14_4mm.jpg'	<i>P. sulcatus</i>	ZMB 106003-13 sh1.JPG'

<i>P. sulcatus</i>	ZMB 106307-11 sh1.JPG'
<i>P. sulcatus</i>	ZMB 106307-12 sh1.JPG'
<i>P. sulcatus</i>	ZMB 106376-11 sh1.jpg'
<i>P. sulcatus</i>	ZMB 107850-10 sh1.JPG'
<i>P. sulcatus</i>	ZMB 107850-9 sh1.JPG'
<i>P. sulcatus</i>	ZMB 108271-10 sh1.JPG'
<i>P. sulcatus</i>	CWR 106_09-10 sh1.jpg'
<i>P. sulcatus</i>	CWR 106_09-2 sh1.jpg'
<i>P. sulcatus</i>	CWR 106_09-3 sh1.jpg'
<i>P. sulcatus</i>	CWR 106_09-5 sh1.jpg'
<i>P. sulcatus</i>	CWR 106_09-6 sh1.jpg'
<i>P. sulcatus</i>	CWR 106_09-8 sh1.jpg'
<i>P. sulcatus</i>	CWR 106_09-9 sh1.jpg'
<i>P. sulcatus</i>	CWR 106_092-7 sh1.jpg'
<i>P. sulcatus</i>	CWR 129_84-5 sh1.jpg'
<i>P. sulcatus</i>	CWR 129_84-9 sh1.jpg'
<i>P. sulcatus</i>	CWR 14_90-1 sh1.JPG'
<i>P. sulcatus</i>	CWR 14_90-2 sh1.JPG'
<i>P. sulcatus</i>	CWR 14_90-5 sh1.JPG'
<i>P. sulcatus</i>	CWR 14_90-6 sh1.JPG'
<i>P. sulcatus</i>	CWR 17_07-8 sh1.jpg'
<i>P. sulcatus</i>	CWR 25_85-3 sh1.JPG'
<i>P. sulcatus</i>	CWR 25_85-8 sh1.JPG'
<i>P. sulcatus</i>	CWR 25_85-9 sh1.JPG'
<i>P. sulcatus</i>	CWR 47_84-10 sh1.jpg'
<i>P. sulcatus</i>	CWR 47_84-4 sh1.jpg'
<i>P. sulcatus</i>	CWR 47_84-7 sh1.jpg'
<i>P. sulcatus</i>	CWR 47_84-8 sh1.jpg'
<i>P. sulcatus</i>	CWR 47_84-9 sh1.jpg'
<i>P. sulcatus</i>	CWR 4_83-10 sh1.JPG'
<i>P. sulcatus</i>	CWR 4_83-9 sh1.JPG'
<i>P. sulcatus</i>	NHMW 14249 type.tif

Contributions

Contributions of the author (Benedikt Wiggering) to already published or to be published chapters of the dissertation entitled “Evolutionary systematics and Reproductive Biology of two Cerithioidea snail families (Thiaridae, Planaxidae)”.

Chapter 2

Glaubrecht M, Wiggering B, Gimnich F, Rintelen T v, Neiber M T **The Indo-Australian region as key role in the evolution of diversity in an understudied group of tropical freshwater snails (Gastropoda: Cerithioidea: Thiaridae).**

Matthias Glaubrecht and Marco T. Neiber designed the study. Matthias Glaubrecht, Thomas von Rintelen and France Gimnich collected material. Thomas von Rintelen and France Gimnich carried out the molecular lab work. France Gimnich conducted pre-analyses of the sequence data. Marco T. Neiber and Benedikt Wiggering analysed the data. Benedikt Wiggering handled the data and provided all figure drafts. The first manuscript draft of the Material and Methods section and Results section were written by Benedikt Wiggering; first drafts of Introduction and Discussion were written by Marco T. Neiber and France Gimnich, with contributions then to the final version by BW and MG. Matthias Glaubrecht acquired funding. All authors proofread final manuscript versions and approved the manuscript for submission and publication.

Chapter 3

Wiggering B, Neiber M T, Krailas D, Glaubrecht M. 2019. **Biological diversity or nomenclatural multiplicity: the Thai freshwater snail *Neoradina prasongi* Brandt, 1974 (Gastropoda: Thiaridae).** Systematics and Biodiversity 17(3): 260-276. <https://doi.org/10.1080/14772000.2019.1606862>

Matthias Glaubrecht designed the study, organized funding, collected ZMB material and co-authored paper drafts. Benedikt Wiggering carried out morphological and molecular lab work and wrote the manuscript, including the first draft. Marco T. Neiber and Benedikt Wiggering analysed the data. Duangduen Krailas collected SUT material. All authors proofread manuscript drafts and final versions. All authors have read and approved the manuscript for submission and publication.

Chapter 4

Wiggering B, Krivohlavek L, Glaubrecht M **Towards a revision of the enigmatic *Stenomelania* Fischer, 1885 (Gastropoda, Thiaridae), with an evaluation of its type species.**

Matthias Glaubrecht and Benedikt Wiggering designed the study. Benedikt Wiggering corresponded with other collections, carried out morphological and molecular studies, analysed data and wrote the manuscript, including the first draft, with contributions by MG. Laura Krivohlavek conducted parts of the morphological study. Matthias Glaubrecht organized funding, collected ZMB material and co-authored paper drafts. All three authors have proof-read and approved the manuscript for submission and publication.

Chapter 5

Wiggering B, Glaubrecht M, Neiber M T, **Case 3838 – *Helix plicaria* Lamarck, 1816 (currently *Hemicycla plicaria*; Gastropoda, Eupulmonata, Stylommatophora, HELICIDAE): proposed conservation of the specific name.**

Marco T. Neiber designed the study and wrote the first manuscript draft. Benedikt Wiggering corresponded with other collections, assembled the figure and co-authored all manuscript drafts. Matthias Glaubrecht acquired funding and proof-read the final manuscript version. All three authors have read the manuscript and the manuscript for submission and publication.

Chapter 6

Wiggering, B., Neiber, M., Gebauer, K., & Glaubrecht, M. **One species, two developmental modes: Validating a case of geographic poecilogony in marine gastropods.** – BMC Evolutionary Biology 20: Article Number 76. <https://doi.org/10.1186/s12862-020-01644-1>

Matthias Glaubrecht designed the study, organized funding, collected ZMB material and co-authored paper drafts. Benedikt Wiggering carried out morphological studies and wrote the manuscript, including the first draft. Katharina Gebauer carried out the molecular lab work. Marco T. Neiber and Benedikt Wiggering analysed the data. All authors proofread manuscript drafts and final versions and approved the manuscript for submission and publication.

Chapter 7

Wiggering B, Glaubrecht M **Reducing taxonomic redundancy: geometric morphometrics delineates species in *Supplanaxis* Thiele, 1929 (Gastropoda: Planaxidae).**

Benedikt Wiggering designed the study, corresponded with other collections, carried out morphological and molecular studies, analysed data and wrote the manuscript, including the first draft. Matthias Glaubrecht co-designed the study, organized funding, collected ZMB material and co-authored paper drafts. Both authors have read and approved the manuscript for submission and publication.

Eidesstattliche Versicherung/Declaration on oath

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation by my own and have not used any other than the acknowledged resources and aids.

Kiel, 19.11.2020 _____


Benedikt Wiggering

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