The late Tortonian cheilostome Bryozoa from Niebla (Guadalquivir Basin, SW Spain): implications for Atlantic-Mediterranean environment and biogeography during the late Neogene

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Björn Berning

aus Hamburg

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und Prof. Dr. C. Betzler

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Abstract

From a late Tortonian (Late Miocene) fossil assemblage, 72 cheilostome bryozoan species are described and figured. The sampled limestone of the Formación Calcarenita de Niebla crops out in a quarry south of the town of Niebla, which is situated in the north-western Guadalquivir Basin (SW Spain). The Cuenca de Guadalquivir is the foreland basin of the Betic Cordilleras and forms an elongated triangular depression tapering towards ENE and opening towards the Atlantic. It was temporarily connected to the Mediterranean Sea via narrow straits in its south-eastern region until the early Messinian. The sampled part of the Niebla Calcarenite was deposited on a shallow shelf and comprises packstones to rudstones, dominated by encrusting red algal bioconstructions, with varying amounts of a fine grained and partly terrigenous matrix which prevented the biogenic components from excessive diagenetic alteration and cementation. The bryozoan skeletons are therefore generally well preserved.

While the number of cheilostome species present in the very facies of the Niebla Calcarenite is astonishing, bryozoans were of minor importance concerning carbonate production. Myriapora truncata, Schizotheca serratimargo and celleporinids are the only taxa contributing to the formation of the limestone in a noteworthy amount. The limited number of specimens is primarily ascribed to oligotrophic conditions prevailing in the Guadalquivir Basin during formation of this facies, which is evidenced by the faunal dominance of photoautotrophic organisms (coralline algae and large foraminifera, as well as grazing echinoids), and by a depauperate filter-feeding community. Bryozoan species richness, on the other hand, is promoted by the extensive and varied substrate provided by the 3-D coralline algal bioconstructions, which offered diverse microhabitats ranging from cryptic spaces underneath free-growing sheets to exposed sites on erect thalli. The importance of substrate is also reflected by the predominant occurrence of species (58 µ 81%) with an encrusting unilaminar mode of growth. Owing to the presence of 12 extant species in the assemblage, ecological preferences of their Recent representatives help to interpret the environment of formation of the Niebla Calcarenite. Whereas some stenobathyal species suggest a depth of production of some 30-40 m, the occurrence of a range of taxa that are known from warmtemperate to tropical environments indicate subtropical conditions during formation of the limestone.

A morphometric analysis, and subsequent intraspecific comparison of the results between taxa from the Niebla Calcarenite and nearly coeval Mediterranean fossil occurrences, revealed that zooid size is generally smaller in representatives from the Atlantic fauna. Whereas intracolonial morphometrical variability has hitherto been primarily related to an inverse correlation between temperature and zooid size, this relationship does not seem to hold up in this between-site comparison. Proliferation of coral reefs in the Late Miocene western Mediterranean Sea suggests that temperatures were slightly higher there than in the eastern Atlantic, from which reefs are absent, which would thus have resulted in the development of larger zooids in the latter region. However, a morphometrical case study on fossil and Recent specimens of the erect branching *M. truncata* indicates that nutrient availability may also be a decisive factor in controlling zooid and colony size.

According to their known biogeographic affinity, the 72 species from the Guadalquivir Basin are classified as follows: while a mere 3% were previously recorded from the Atlantic only, which may be attributed to the scarcity of taxonomic works on Late Miocene faunas from this region, 22% have been found in both the Atlantic and Mediterranean Sea before, and 38% could not be referred to any known species and thus not be biogeographically characterised. Another 38% comprise species that were formerly regarded as being endemic to the Mediterranean Sea. Their presence in the Atlantic Guadalquivir Basin suggests that there was an exchange of species between the Mediterranean Sea and the Atlantic, and that, therefore, surface water flow must have occurred in both directions. This biogeographic pattern thus corroborates previous findings concerning the Late Miocene oceanographic regime, based on the analysis of sedimentary structures in the connecting straits of southern Spain. It also shows that the eastern Atlantic region could have served as a refuge for the Mediterranean 'endemic' species to survive the drying up of the Mediterranean Sea during the Messinian salinity crisis. As a result, the number of established species present in the Guadalquivir Basin that did not survive into the Pliocene (8) is distinctly

lower than the number of species dying out by the end of the Pliocene (12), a time that was characterised by seemingly less dramatic climatic changes. Furthermore, there is only a very weak relationship between the present Spanish and Neogene Atlantic faunas further to the north (NW France, North Sea Basin), while a great number of species is shared with Middle Miocene faunas of the Paratethys, and Pliocene ones of the Mediterranean Sea. This suggests that bioprovinces were relatively stable throughout the Neogene along latitudes while species exchange between western European regions was low.

Zusammenfassung

Aus einer Fossilvergesellschaftung des späten Tortons (spätes Miozän) werden 72 Arten cheilostomer Bryozoen beschrieben und abgebildet. Die beprobten Sedimente gehören der Formación Calcarenita de Niebla an und sind in einem Steinbruch südlich der Stadt Niebla im nordwestlichen Guadalquivir Becken (Andalusien, SW Spanien) aufgeschlossen. Das Guadalquivir Becken ist ein WSW-ENE streichendes Vorlandbecken der Betischen Kordillere, welches sich zum Atlantik hin öffnet und bis in das frühe Messin im südlichen und östlichen Bereich über schmale Meeresstraßen temporär mit dem Mittelmeer verbunden war. Die untersuchten Sedimente des Niebla Kalkarenits wurden am nördlichen Rand des Beckens auf einem flachen Schelf abgelagert. Sie bestehen aus *packstones* und *rudstones*, die aus Biokonstruktionen inkrustierender Rotalgen aufgebaut sind. Der relativ hohe Anteil feinkörniger, teilweise terrigener Matrix verhinderte zudem eine starke diagenetische Umwandlung und Zementation der biogenen Komponenten; die Bryozoenskelette sind somit meist sehr gut erhalten.

Obwohl die Anzahl der Bryozoenarten in diesem einen Faziesbereich des Niebla Kalkarenits außerordentlich groß ist, trugen Bryozoen wenig zur Gesamtkarbonatproduktion bei. Myriapora truncata, Schizotheca serratimargo und celleporiforme Kolonien sind die einzigen Taxa, die in nennenswertem Volumen auftreten. Da die Fauna von photoautotrophen Organismen (Rhodophyceen und Großforaminiferen, sowie herbivore Echiniden) dominiert wird, ist die geringe Anzahl an Bryozoenkolonien, sowie anderer filtrierender Organismengruppen, im wesentlichen auf das Vorherrschen von oligotrophen Bedingungen im Guadalquivir Becken während der Produktion des biogenen Materials zurückzuführen. Der Artenreichtum bei Bryozoen wurde hingegen durch das von den Rotalgen produzierte, großflächige, dreidimensionale Hartsubstrat begünstigt, welches verschiedenartige Mikrohabitate zur Verfügung stellte, z.B. kryptisch gelegene Flächen auf der Unterseite von lagig wachsenden Algen, oder exponierte Orte an aufrecht wachsenden Thalli. Die Bedeutung des Substrats wird zudem durch die Dominanz von Bryozoenarten mit einem unilaminar inkrustierendem Wuchs (58 µ 81%) belegt. Aufgrund der Präsenz von 12 rezent lebenden Arten lassen sich, mit Hilfe eines Vergleichs der ökologischen Präferenzen ihrer heutigen Vertreter, die Paläo-Umweltbedigungen der Faunenvergesellschaftung des Niebla Kalkarenits rekonstruieren. Während einige stenobathyale Arten eine Entstehungstiefe von ca. 30-40 m anzeigen, deuten eine Reihe von Taxa, die heutzutage warm-temperierte bis tropische Gewässer bewohnen, auf subtropische Temperaturen im Guadalquivir Becken des späten Tortons hin.

Eine morphometrische Analyse der Arten des Guadalquivir Beckens, sowie ein intraspezifischer Vergleich der Ergebnisse mit fossilen Vertretern aus ungefähr zeitgleichen Mittelmeerfaunen ergab, dass die Zooide ein und derselben Art im Atlantik generell kleiner gewesen sind. Während die morphometrische Variabilität innerhalb einer Kolonie bislang hauptsächlich auf die inverse Korrelation von Temperatur und Zooidgröße zurückgeführt wurde, zeigen die Ergebnisse dieser Arbeit, dass dieses Verhältnis nicht als Ursache für die Unterschiede zwischen den Neogenen Lokationen angeführt werden kann. Das Wachstum von Riffen im Mittelmeer während des späten Torton deutet darauf hin, dass die Temperaturen dort höher gewesen sind als im östlichen Atlantik, von wo keine Riffe bekannt sind. Folglich hätten die Zooide im Guadalquivir Becken größer sein müssen als die von Vertretern derselben Art im Mittelmeer. Hingegen ergaben morphometrische Untersuchungen an fossilen und rezenten Kolonien der aufrecht und verzweigt wachsenden *M. truncata* aus unterschiedlichen Habitaten, dass, neben der Wassertemperatur, möglicherweise das Vorhandensein von Nährstoffen ein wichtiger Kontrollfaktor der Zooid- oder Koloniegröße ist.

Die 72 untersuchten Arten des Niebla Kalkarenits lassen sich aufgrund der bisherigen Kenntnisse zur paläobiogeographischen Verteilung in folgende Gruppen einteilen: lediglich 3% der Arten wurden bislang einzig in Faunenvergesellschaftungen aus dem Atlantik gefunden, was vermutlich hauptsächlich auf die spärliche Bearbeitung der ostatlantischen Faunen zurückzuführen ist. Während 22% der Arten aus dem Mittelmeer und dem Atlantik bekannt sind, konnte ein großer Anteil von 38% keiner bekannten rezenten oder fossilen Art, und somit auch nicht biogeographisch, zugeordnet werden. Das Vorkommen von weiteren 38% wurde bisher als auf das Mittelmeer beschränkt interpretiert. Die Präsenz dieser 'endemischen' Arten im Ostatlantik lässt daher den Schluss zu, dass im späten Miozän ein Austausch von Arten zwischen Atlantik und Mittelmeer stattgefunden haben muss, und dass folglich Oberflächenwasser in beide Richtungen

durch die verbindenden Meeresstraßen geflossen ist. Dieses biogeographische Muster bestätigt einerseits frühere Befunde bezüglich der ozeanographischen Bedingungen, welche auf Untersuchungen von Sedimentstrukturen innerhalb der Meeresstraßen basieren. Andererseits zeigt die Anwesenheit dieser, vornehmlich im Mittelmeer vorkommenden Arten im östlichen Atlantik, dass die Region höchstwahrscheinlich als Refugium für viele dieser Taxa während der Messinen Salinitätskrise gedient hat. Dies hatte zur Folge, dass von den etablierten Arten im Guadalquivir Becken lediglich acht nicht bis ins Pliozän überlebt haben, während deutlich mehr Arten (12) am Ende des Pliozäns ausgestorben sind, das durch einen vergleichsweise weniger dramatischen Klimawechsel gekennzeichnet ist. Des weiteren bestehen zwischen der Fauna des Guadalquivir Beckens und denen in weiter nördlich gelegenen Regionen des Atlantiks (NW Frankreich, Nordseebecken) nur sehr geringe Gemeinsamkeiten während des späten Neogens. Hingegen ist der große Anteil gemeinsamer Arten zwischen der hier behandelten Fauna und der mittelmiozänen Paratethys sowie des pliozänen Mittelmeeres ein Hinweis auf die latitudinale Stabilität von Bioprovinzen durch die Zeit, und somit auf einen geringen Austausch zwischen den Regionen des westlichen Europas.

Preface

This thesis is submitted as a semi-cumulative work. Besides a general Introduction, an overview of the Geological Setting of the sampled sites, the Material and Methods used, the Systematic Account as the main body of the thesis (Chapter 4), and the closing chapter Summarising Remarks and Conclusions, two manuscripts are presented which sort of replace the usual Discussion chapter. While the first manuscript (Chapter 5) has already been published earlier this year (Berning et al., 2005), the second one (Chapter 6) has been submitted to the journal *Lethaia* and is in the reviewing process at present (Berning, subm.). However, since the first manuscript was written before I have visited the museum collections in Vienna and London, which changed the taxonomic affiliation of some species, and additional material was measured after submission of the manuscript, species names may differ between Chapter 4 and 5, and the morphometric results originally presented in the manuscript have slightly changed. A revised table with the new morphometry data is therefore presented in the last chapter, and differences in taxonomic affiliation are given in the Material and Methods chapter.

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1. Introduction

As early as 1599, the Italian Ferrante Imperato, collector of curios and precious natural memorabilia, figured several Mediterranean bryozoan colonies in his tome *Historia Naturale*, which was later republished in 1672. And shortly after Carl Linné had published his seminal work *Systema Naturae* in 1758, the first Mediterranean species still valid today were introduced by Pallas (1766), among them *Millepora truncata* (= *Myriapora truncata*) and *Eschara ciliata* (= *Microporella ciliata*). Scientific bryozoology in the Mediterranean region thus has an outstanding record of some 350 years. Although palaeontologists started off a little later (e.g. Milne Edwards, 1836), they quickly made up for this detriment since the middle of the 19th century, when, for instance, Reuss (e.g. 1848, 1874), Manzoni (e.g. 1869a,b,c, 1870, 1875) or Seguenza (e.g. 1873) published their first voluminous compendia on Middle Miocene to Pleistocene fossil assemblages of the Mediterranean and Paratethyan basins. Besides the long standing tradition, the density of universities, and thus of scientists, around the Mediterranean Sea has led to this area being the most dealt with in the world regarding its fossil and Recent Bryozoa.

Hence, by far most of the modern and fossil bryozoan species of the Mediterranean region have already been introduced by the beginning of the 20th century. However, while more than 350 Recent species exist today, which were compiled in the works of Prenant & Bobin (1956, 1966), Gautier (1962), Zabala (1986) and, most recently, Zabala & Maluquer (1988), a systematic registration of all fossil Neogene species, that are likely to outnumber the modern ones, has not been attempted, yet. A pilot study of the Miocene to Recent evolution and diversity of Mediterranean bryozoans was presented by Taylor (2000), which was based on stratigraphic ranges of 333 species given in several more recent publications and which is thus far from being exhaustive. An obstacle in this regard is that documentation of the type-specimens of fossil species described by earlier workers using scanning electron microscopy (SEM) is still sparse (e.g. Poluzzi, 1975; Schmid, 1989; Pouyet & Moissette, 1992). Yet SEM observation techniques are essential for a precise identification of bryozoan species, and the use of SEM has led to a refined species concept and a striking increase in diversity in some genera during the last decades (e.g. Taylor & Mawatari, 2005). Thus, many of the fossil species introduced by early bryozoologists, and therefore species ranges and numbers, unfortunately remain imperfectly known to date.

Since 1973 (about the time SEM was first used to image fossil Bryozoa) the focus of many palaeontologists working in the Mediterranean region has shifted towards the evaluation and interpretation of a unique, and much debated, event: the Messinian Salinity Crisis (MSC). The discovery of evaporites with a thickness of up to some three kilometres on the floor of the main basins by the Deep Sea Drilling Project (DSDP) on Leg 13 (Hsü et al., 1973), and the idea of a completely dried up Mediterranean Sea in the latest Miocene, not only provoked conflicting points of view concerning the cause and course of the event, but also a fair bit of public sensation and publicity. However, the nature of the MSC remains controversial to date: for example, the correlation of the sedimentary records between peripheral basins (e.g. Riding et al., 1998, 1999; Fortuin et al., 2000; Steffahn & Michalzik, 2000; Aguirre & Sánchez-Almazo, 2004; Cornée et al., 2004; Matano et al., 2005); the ultimate cause for, and chronological history of, the isolation of the Mediterranean basins (e.g. Kastens, 1992; Clauzon et al., 1996; Krijgsman et al., 1999; Seidenkrantz et al., 2000; Hodell et al., 2001; Duggen et al., 2003); the question of whether the Mediterranean Sea did, in fact, dry out completely and thus the depth of origination of the evaporitic deposits in the main basins (e.g. Sonnenfeld & Finetti, 1985; Wallmann et al., 1997; Keough & Butler, 1999; Blanc, 2000; Roveri et al., 2001; Tay et al., 2002; Hardie & Lowenstein, 2004); or the effect of the crisis on the marine fauna of the Mediterranean Sea (e.g. Por & Dimentman, 1985; Dornbos & Wilson, 1999; Saint Martin et al., 2000; Néraudeau et al., 2001; Gaudant, 2002).

There are several indications that the Mediterranean Sea experienced a serious sea-level drop at least during the latest Messinian (at ca. 5.6 Myr), before hypersaline and/or brackish sediments containing a non-marine faunal assemblage, known as the 'Lago Mare' facies (e.g. Hsü et al., 1978; Rouchy & Saint Martin, 1992; Spezzaferri et al., 1998; Iaccarino & Bossio, 1999), were deposited in the main basins. These sediments could only then have formed when enough salt had been taken

out of the system and the surface of the remaining lakes had decreased to such an extent that the lighter fresh water drained by rivers could either cover the dense brines accumulating in the deep basins, or even flooding the dry main basins in case these were completely desiccated. The latter scenario is substantiated by the fact that brines trapped in deep (some 3580 m) basins in the present-day eastern Mediterranean Sea yield dissolved bischofite, which is the most soluble of all marine salts, while its bromine content suggests that it was originally precipitated in the Messinian only after the seawater had evaporated to less than 1% of the initial volume (Wallmann et al., 1997). The authors thus concluded that the eastern Mediterranean basin became evaporated to near dryness during the MSC. Meanwhile, the resulting sea-level drop of two or three kilometres left another mark in the margins of the Mediterranean basins: the incision of rivers deep into the continental crust (Barber, 1981; Stampfli & Höcker, 1989; Druckman et al., 1995; Lofi et al., 2003, 2005). The entrenchments of canyons were produced by ancient and still existing river systems such as the Rhône or Nile. The latter produced an incision with a depth in excess of three kilometres and a length of some 1200 km, cutting through resistant Mesozoic limestones and Oligocene basalts (Chumakov, 1973; Barber, 1981), while the Messinian erosional surface can be traced from today's Mediterranean margin to below the Upper Evaporites deposited in the basin centres at the toe of the River Rhône (Lofi et al., 2005).

I acknowledge that there exist different chronostratigraphic models for the MSC (compare, e.g., Clauzon et al. [1996] with Krijgsman et al. [1999]), and that the sedimentary records of some of the peripheral basins yield contrasting scenarios (see, for instance, Aguirre & Sánchez-Almazo, 2004). However, for the case I want to make here the above mentioned evidence is sufficient to show that the Mediterranean basins not in direct contact with the Atlantic temporarily experienced non-marine conditions that did not allow normal-marine, stenohaline organisms to survive.

Long before the DSDP revealed the presence of massive evaporite deposits in the main basins, the restriction of the Mediterranean Sea was known to scientists owing to the onshore occurrence of thick evaporitic successions in, for example, Italy (Ruggieri, 1967). The taxonomic difference in faunal assemblages of the last normal marine Messinian and the first marine Zanclean sediments resulted in the establishment of the Miocene/Pliocene boundary (Seguenza, 1868; for a synopsis of its history see Van Couvering et al., 2000). However, since palaeontologists have not noticed a major extinction event of Mediterranean endemics at this boundary, especially after the magnitude of the event became obvious in 1973, the scene was set for a dispute between scientists that favoured a persistence of fully marine conditions in at least some refuges in the Mediterranean region during the crisis, and those that regarded the MSC as a severe event eradicating all marine life in the Mediterranean basins (Benson, 1976a). The differential response of the various marine phyla to the MSC added to this divergence. Thus, while molluscs (Sabelli & Taviani, 1984), ostracodes (Benson, 1976b; Sissingh, 1976), larger foraminifera (Adams, 1976) as well as planktic and benthic foraminifera in general (Cita, 1976; Bizon, 1985), corals (Rosen, 1999; Dornbos & Wilson, 1999), echinoids (Néraudeau et al., 2001), odontocete cetaceans (Bianucci & Landini, 1992), and macrofaunas in general (Dermitzakis & Georgiades-Dikeoulia, 1987) show varied but marked taxonomic changes in faunal components, teleost fishes (Bianucci & Landini, 1992; Gaudant, 2002) and, at least in the Sorbas Basin, benthic foraminifera (Goubert et al., 2001) seem to have weathered the crisis without experiencing a distinct faunal turnover or larger extinction event. In Mediterranean sedimentary successions, the percentage of species becoming extinct during the Messinian range from some 5% (Goubert et al., 2001) to some 40% (Benson, 1976b). Therefore, either extra-Mediterranean refuges (Ruggieri & Sprovieri, 1976; Jones, 1984; Sabelli & Taviani, 1984; Harmelin 1992) or sanctuaries within the Mediterranean region (David & Pouvet, 1984; Saint-Martin et al., 2000; Goubert et al., 2001; Néraudeau et al., 2001) were poroposed to account for the relatively low number of extinct species in some taxa.

This discussion unveils one weak point of the current knowledge of marine fossil organisms and their biogeographic distribution: whereas Neogene Mediterranean species and assemblages are remarkably well known, very little is known from the immediate surroundings of the eastern Atlantic to compare the faunal components for their similarity. Thus, the frequently cited persistence of so-called 'endemic' taxa may be an artefact only because adjacent regions have not been studied, yet (Jones, 1984; Sabelli & Taviani, 1984). And, while endemism can never be proven but only be falsified, the few works on eastern Atlantic faunas that do exist have, in fact,

revealed a great resemblance with Mediterranean ones (Jones, 1984; Barbieri, 1998; Mayoral et al., 1998; Lauriat-Rage et al., 1999). This notion is also important concerning the question of the source area for resettlement of the Mediterranean Sea after the MSC.

The problems raised above have, to a certain extent, also been addressed using bryozoans. While Moissette & Pouyet (1987) have claimed that 17% of the 'endemic' species have survived the MSC and suggested the presence of a refuge inside the Mediterranean basins, their data also show that apparent endemics (65%) suffered a significantly greater extinction during the MSC than nonendemic species (14%) (see Taylor, 2000). Sefian et al. (1999) were the first ones to show that a great range of species formerly considered as being endemic to the Mediterranean Sea were also present in the Late Miocene eastern Atlantic off north-western Morocco. Taylor (2000) compiled data on Neogene bryozoan diversity in the Mediterranean region and found that, while diversity peaked in the Messinian, the MSC led to a drastic decrease in the number of species. He also suggested that the apparent Mediterranean endemics may have had a wider distribution outside the Mediterranean Sea. However, as with the distribution of other phyla mentioned above, knowledge of the extra-Mediterranean occurrence is poor and, as regards Bryozoa, there exists not a single study on the Miocene fauna of W and NW Europe that uses SEM for species determination and illustration. And virtually nothing is known from regions south of Morocco, with the work of Sefian et al. (1999) providing the only source of information of bryozoans from NW Morocco. It is therefore unreliable or even impossible to compare these Miocene faunas with the Mediterranean ones using literature information only. Pre-SEM works comprise studies on Late Miocene faunas from Portugal (Galopim de Carvalho, 1971) and western France (Canu & Lecointre, 1925, 1927, 1928, 1930; Buge, 1948, 1957). The Pliocene bryozoans of the NE Atlantic are somewhat better known, which is partly due to more recent publications on faunas from NW Morocco (Pouvet et al., 1999), SW Spain (Reguant, 1993), NW France (Pouyet, 1997a) and NW Europe (Bishop, 1987; Bishop & Hayward, 1989).

One aim of this project was thus to describe the bryozoan fauna of an Atlantic region that was in close proximity of the Mediterranean during the late Neogene in order to establish biogeographic patterns and pathways of distribution before onset of the MSC. The south-western Spanish Guadalquivir Basin (Fig. 2.1, 2.2) represents an ideal region for such a study due to its direct contact with the Mediterranean Sea until the early Messinian (Martín et al., 2001), and because it remained unaffected by the MSC since it was a marginal basin of the Atlantic. The results of the taxonomic account, the fundamental part of this work, will thus not only allow me to address questions concerning the impact of the MSC on the marine Mediterranean fauna and the source area for resettlement after the crisis, but also to make inferences on oceanographic characteristics of the connections between the eastern Atlantic and western Mediterranean during the late Neogene. New data from this region are furthermore crucial for our understanding of the geographical extension of fossil species, or of the exchange of species between the Mediterranean and NW European bioprovinces, and thus for the recognition of oceanic currents which may have caused these patterns.

Since Stach (1936) first noted the potential of bryozoan growth forms as (palaeo)environmental indicators, several other methods have been introduced and applied using bryozoans to obtain information on past environments. One is based on the notion that temperature is inversely related to zooid size; i.e. under increasing temperatures smaller zooids are budded in the same colony (Okamura & Bishop, 1988). The amount of zooid size change within colonies may therefore indicate the seasonal range of temperature experienced by these benthic organisms (O'Dea & Okamura, 2000). While other physical or biological parameters, such as current strength or food, may as well influence zooid or colony shape and size, special attention will be given to morphological and morphometrical features. A comparison with more or less coeval Mediterranean representatives of the same species will enable me to characterise potential differences in environmental conditions present in these different geographic regions. Additionally, information on the depth of occurrence and temperature preferences provided by the presence of Recent taxa in the Guadalquivir Basin will aid in the establishment of local conditions.

2. Geological Setting

The collision of Africa and Europe have considerably changed the Mediterranean topography during the Neogene. While the eastern connection to the Indian Ocean was sealed at the end of the Middle Miocene (e.g. Rögl, 1999), the western end of the palaeo-Mediterranean Sea was progressively closed during the Tortonian, which resulted in a restricted Mediterranean-Atlantic water exchange (Seidenkrantz et al., 2000), and ultimately lead to the complete isolation from the world's oceans, known as the Messinian salinity crisis (MSC), during the latest Miocene (e.g. Krijgsman et al., 1999). An overall compressive tectonic regime between the two continents created the Gibraltar Arc, which comprises the Betic Cordilleras in southern Spain and the Rif Mountains in northern Morocco (e.g. Sanz de Galdeano, 1990). During the Middle Miocene the foreland basins of this mountain belt formed broad and deep straits connecting the Mediterranean Sea with the Atlantic on both the Iberian and African side, the Betic and the Rifian Corridor, respectively (e.g. Benson et al., 1991; Esteban et al., 1996; Sanz de Galdeano & Rodríguez-Fernández, 1996). Large-scale but differential uplift of the region during the Late Miocene caused, on the one hand, an exposure of the eastern Gibraltar Arc and thus a shallowing and restriction of the gateways (e.g. Rodríguez-Fernández et al., 1984; Sanz de Galdeano, 1990; Gelabert et al., 2002; Duggen et al., 2003). On the other hand, especially so in southern Spain, counteracting transpressive and extensional regimes locally created smaller depressions that acted as temporal basins or channels connecting the Mediterranean Sea with the Atlantic (e.g. Esteban et al., 1996; Martín et al., 2001). While the last Spanish connection was closed by the early Messinian (Martín et al., 2001), the wider and deeper Rifian Corridor is interpreted to have made a greater contribution to the water exchange and to have stayed open until mid-Messinian times (e.g. Benson et al., 1991; Krijgsman et al., 1999; Barbieri & Ori, 2000; Münch et al., 2001; Cornée et al., 2002). Thus, whereas the deep-water circulation of the Mediterranean Sea became sluggish in the late Tortonian (Seidenkrantz et al., 2000), the MSC commenced when evaporation exceeded the ever decreasing inflow of water from the Atlantic and hypersaline conditions prevailed during the midand late Messinian (Krijgsman et al., 1999).

In concert with the Betic Cordilleras, the foreland basin of the Betics, the Guadalquivir Basin (Fig. 2.1), was differentially uplifted such as that the ENE-WSW elongated depression tapers towards the east and displays a roughly triangular shape, while Neogene sediments filling the basin crop out more than 800 m above sea-level at its far eastern end (Sanz de Galdeano, 1990; Sierro et

al., 1996; Braga et al., 2003). In contrast, the western and deepest part of the Guadalquivir Basin, opening towards the Atlantic, was less affected by the uplift. Yet, gateway configuration was now controlled by smaller-scale, temporarily existing, intramontane basins (Fig. 5.2), such as the Granada Basin (Rodríguez-Fernández et al., 1984), the Guadix Basin (Soria et al., 1999), or the Guadalhorce Corridor (Martín et al., 2001). After the successive closure of these seaways, the Guadalquivir Basin formed a mere embayment of the Atlantic Ocean from mid-Messinian to Pleistocene times (Valenzuela, 1982). A differential evolution is also observed in the sedimentological record: whereas the active and



Fig. 2.1 Overview of the structural units of Andalucía. From Sierro et al. (1996).

steep southern margin of the Guadalquivir Basin, bounded by the External Zone of the Betic Cordilleras (Fig. 2.1), is characterised by Neogene olistostrome deposits, the passive northern margin towards the Iberian Massif gradually deepens towards the basin centre and hosts a wide range of biogenic and terrigenous sediments (Valenzuela, 1982; González & Galán, 1988; Galán & González, 1993; Bustillo & López García, 1997; Riaza & Martínez del Olmo, 1996; Sierro et al.,



Fig. 2.2 Overview of all the sites sampled (solid black circles) in the Guadalquivir Basin. The asterisk marks the location of the fauna described in this work.

1996). Unconformably overlying the Paleozoic or Mesozoic basement of the northern margin are, besides a basal conglomerate, Tortonian to Messinian calcarenites, calcirudites and marls (Sierro et al., 1993).

On the quest for well-preserved bryozoan faunas I have visited several sites in different sectors of the Guadalquivir Basin (Fig. 2.2), including the Messinian/Pliocene calcirudites cropping out at Bornos and the calcarenites of Carmona (Clauss, 1991: Galán & González, 1993), Tortono-Messinian limestones of the Ronda Basin (Gläser & Betzler, 2002), as well as Messinian calcirudites at the northern exit of the Guadalhorce Corridor near Teba (Martín et al., 2001). However, while all of these sediments vielded diverse bryo-

zoan faunas, the biogenic fragments were too abraded (mainly due to reworking and a high content of siliciclastic components), extremely recrystallised, and/or too well cemented to disintegrate the rock. A precise and reliable species identification in these samples of the bryozoans in these samples was thus rendered difficult or impossible. The only suitable facies that produced bryozoans with well-preserved frontal surfaces, which were not obscured or severely altered by diagenesis, was provided by certain beds of the Calcarenita de Niebla Formation, cropping out in a quarry near the village of Niebla (Fig. 2.2, 2.3; UTM coordinates 174337 E, 4140537 N).

The Niebla Calcarenite extends along the northern margin of the Guadalquivir Basin for several kilometres and comprises a variety of facies types and sedimentary subunits, including fan-delta conglomerates, sandy beach deposits, littoral sands and silts, and marine shallow shelf grainstones to rudstones and boundstones with a varying content of siliciclastic material (Clauss Klamp & González Regalado, 1993; Civis et al., 1994; Baceta

& Pendon, 1999). According to Sierro et al. (1990b), this sedimentary sequence (Fig. 2.4) represents a part of the transgressive systems tract of the global sea level cycle 3.2 of Haq et al. (1987) and the presence of *Neogloboquadrina humerosa* (Takayanagi & Saito) in the lower part of the Niebla Calcarenite suggests a late Tortonian age (Sierro et al., 1990a). The PF-Event 1 and 2 of Sierro et al. (1993), as well as the Tortonian/ Messinian boundary, were recognised in the overlying Gibraleón Formation at a different location; at Niebla the section immediately above the Calcarenita de Niebla is condensed and the successive Gibraleón Clays show a Messinian age (Sierro et al., 1993).

The Niebla Calcarenite cropping out around the village of Niebla (Fig. 2.4) is interpreted by Baceta & Pendon (1999) to have formed on the inner part of a low gradient homoclinal ramp. Lateral and vertical facies variations are due to the local



Fig. 2.3 Location of the sampled outcrop, an active quarry south of Niebla. After Sierro et al. (1997).

presence of autochthonous coralline algal and bryozoan patches within areas of bioclastic accumulation, mostly in the form of grain- and rudstones with variable contents of finer matrix. In these grainand rudstones, larger siliciclastic components may be common to abundant, deriving from fan-delta deposits that formed at the margin of the Iberian Massif further north (Baceta & Pendon, 1999) and large bivalves (pectinids and ostreids) are commonly found. The other main carbonate producing organisms, occurring in both facies types, include coralline algae, bryozoans, echinoids (Clypeaster) and large benthic foraminifera (predominantly Heterostegina, see Tosquella et al., 2001). In general, the grain- and rudstones have a relatively open pore space and the biogenic components are thus prone to diagenetic alteration and intense cementation, and the quartzitic clasts destroy



Fig. 2.4 Sampled section in the quarry south of the village of Niebla. It is a composite section of which the lower part is cropping out at the flanks of Río Tinto just north of the quarry. Only the upper part, the asterisk marks the sampled bed, is present in the quarry, while the overlying Gibraleón Clays occur south of the quarry (see text for stratigraphic details). Modified from Baceta & Pendon (1999), incorporating own observations.

calcitic grains during compaction. In contrast, the bioconstructions of encrusting coralline algae may have acted as sediment bafflers and binders (see below). Therefore, interstices are filled by, and the presence of rather small quartzitic grains is confined to, a fine grained matrix, which reduced porosity and therefore the degree of diagenetic alteration. The coralline algal patches are interpreted to have formed local highs (Baceta & Pendon, 1999) and appear similar to the Crustose Pavement facies or the Algal Crust Packstone of Bosence & Pedley (1982) and Bosence (1983), owing to the presence of both extensive filamentous sheets, which may have been able to grow on fine-grained soft substrate (Rasser & Piller, 2004), and massive multilaminar growth with common protuberances and thick thalli forming frameworks. A diverse array of species of the genera Lithothamnion, Mesophyllum, Lithophyllum, Lithoporella and Neogoniolithon are present (Braga, 1997). The predominant occurrence of algal fragments, however, suggests that the assemblage cropping out in the Niebla quarry is allochthonous. Yet, the source of these sediments was certainly not too distant, Baceta & Pendon (1999) place it to the north of Niebla, since the bioclasts are not abraded and coralline algal fragments may reach several centimetres in size. A transport during single storm events seems to be the most plausible explanation to account for the large discrepancies in grain size and the excellent preservation of the bioclastic components.

During formation of the Niebla Calcarenite, in the early late Tortonian, the Guadalquivir Basin was connected with the Mediterranean Sea via the Guadix Basin (Sanz de Galdeano & Vera, 1992; Soría et al., 1999) and, possibly, the Granada Basin (Esteban et al., 1996). Whereas the Rifian Corridor was characterised by surface-water flowing into the Mediterranean Sea (Benson et al., 1991), sedimentary patterns suggest outflow through the Guadix Basin (Betzler et al., subm.).

3. Material and Methods

3.1 Sampling and Preparation of Material

In the Niebla quarry, bulk samples of the coralline algal dominated limestone (Fig. 2.4) were taken at several locations from the same bed. Since the quarry walls did not facilitate to recognise any bedding structures within this bed, a correlation of the samples or sample levels was not possible. However, the nature of the facies and faunal assemblages proved to be homogenous throughout the samples taken.

The bulk samples were crushed to pieces few centimetres in diameter. These were then dried in an oven and afterwards immersed in a hot, saturated solution of Glauber's salt (Na₂SO₄ x 10H₂O). After cooling down and beginning of mechanical disintegration by means of crystal growth, the process was intensified by putting the sample in a freezer overnight. The sample was then bathed in hot water to remove the ice and salt, and sieved into four size fractions (<0.5 mm; 0.5-1 mm; 1-2 mm; >2 mm), while the procedure was repeated with the remaining material not disintegrated during the first run. The disintegrated fractions of the samples were dried and placed in a 10% solution of hydrogen peroxide (H₂O₂) for several hours to remove clay and silt particles before renewed sieving, drying and, finally, picking of the bryozoan specimens. After picking and sorting, the best preserved specimens were cleaned, when necessary, by hand and by placing them (in a small flask containing a diluted liquid detergent) in an ultrasonic bath for a few seconds. If possible, several specimens of each species were mounted on a stub, sputter-coated with gold, and photographed digitally with a LEO 1455VP scanning electron microscope (SEM). Micrographs were generated at a working voltage of 15 KV, either from secondary electrons (SEI), or, when charging was a bigger problem, from a mix of back-scattered (QBSD; up to some 25%) and secondary electrons. Photos used for the morphometric analysis (see below) were taken at a 90° angle to the colony surface to enable precise measurements.

The material is, for the time being, kept in my private collection. Consecutive numbers were given to photographed specimens which are provided in the species description. Type-material of eventual future description of new species will be deposited in the bryozoan collection of the 'Bryozoenzentrum' at Senckenberg Institute (Frankfurt, Germany). Other material viewed includes specimens from the bryozoan collections of the University of Lyon (FSL), the British Natural History Museum in London (BNHM), and the Vienna Natural History Museum (VNHM). The BNHM material comprises specimens from the Department of Zoology (numbers usually starting with the year the specimen was deposited), the Department of Palaeontology (numbers starting with a capital letter, e.g. B.1684), and the photocard collection of SEM images (sometimes abbreviated PC). The collections and those taken by scientists working at the BNHM who have their own identification code followed by a consecutive number (e.g. pdt1455 stands for the photocard-series of Paul D. Taylor).

3.2 Taxonomic Account

The systematic organisation of the Cheilostomata is following the working classification of Dennis P. Gordon (pers. comm., 2003), who is currently developing the classification scheme for eventual use in the revised *Treatise of Invertebrate Paleontology*.

Synonymies provided for each species are far from complete. Reference to the original description is given together with only the most significant recent sources relating to Neogene and Recent, Mediterranean and Atlantic faunal descriptions that used SEM photography or other precise techniques (drawings, optical photography) for species illustration. Further references are given of publications of which the material was viewed. Unfortunately, in the only other relevant paper on Miocene NE Atlantic Bryozoa from Morocco, Sefian et al. (1999) did not depict many of their reported species, and those that are figured do not stand out by their state of preservation. Furthermore, species descriptions were kept at a minimum, and neither do the specimens have a

collection number nor do the authors mention at which institution the samples are kept. The material could therefore not be viewed during this study and reference to the species that were also found in NE Morocco by Sefian et al. (1999) is given, but needs to be regarded as unproven.

The ecological information on Recent species is a compilation from a range of works, which, in turn, mainly rely on the seminal studies of Gautier (1962), Prenant & Bobin (1966) and, from outside the Mediterranean Sea, Hayward & Ryland (1998, 1999). Similarly, the stratigraphic range of species was compiled from different recent works, but also includes own observations.

The number of specimens obtained of each species was counted. However, since (fragments of) colonial animals displaying different modes of growth are difficult to quantify, a semi-quantitative estimate (rare, few, common, abundant) of their contribution to the faunal assemblage is given in the Occurrence section of the species description.

Discrepancies between the taxa described in the Taxonomic Account (Chapter 4) and the species list (Table 5.1) in Chapter 5 are due to the fact that the manuscript of the latter chapter was written before I have visited the museum collections in Vienna and London, which, in concert with more experience, changed the taxonomic affiliation of some species. In addition, more material was measured after submission of the manuscript, which lead to slightly different results concerning the zooidal surface area. A revised table is therefore given in the last chapter Summarising Remarks and Conclusions (Chapter 7). The differences in taxonomic affiliation comprise the following species (in alphabetical order):

Chapter 5 (obsolete)	Chapter 4 (revised)	
Aplousina bobiesi (David & Pouyet)	?Aplousina bobiesi (David & Pouyet)	
Buffonellaria divergens (Smitt)	Buffonellaria entomostoma (Reuss)	
Buffonellodes incisa (Reuss)	Schedocleidochasma incisa (Reuss)	
Escharella grossa Moissette	Hemicyclopora sp. 2	
Escharella octodentata (Hincks)	Hemicyclopora sp. 1	
Escharella peachi (Johnston)	<i>Escharella</i> sp. 1	
Escharella reussiana (Busk)	Escharella serrulata (Reuss)	
Escharina dutertrei (Audouin)	Escharina sp.	
Herentia montenati (Pouyet)	Therenia montenati (Pouyet)	
Hippopleurifera sedgwicki (Milne Edwards)	Hippopleurifera semicristata (Reuss)	
Hippoporella pauper (Reuss)	"Hippoporella" pauper (Reuss)	
Microporella ciliata (Pallas)	<i>Microporella</i> sp.	
Onychocella angulosa (Reuss)	Onychocella cf. angulosa (Reuss)	
Prenantia cheilostoma (Manzoni)	<i>Hippoporina</i> sp.	
Schizobrachiella sanguinea (Norman)	<i>Calyptotheca</i> sp. 2	
Schizoporella longirostris (Hincks)	Schizoporella dunkeri (Reuss)	
Watersipora goniostoma (Reuss)	Watersipora sp.	

3.3 Morphometric Analysis

Zooidal measurements (Fig. 3.1) were made on digital SEM photos using the image analysis software ImageJ. Each measurement is given in the text as mean plus or minus standard deviation, observed range, and (enclosed in parantheses) number of specimens used and total number of made. The measurements are given in microns (μ m) unless otherwise stated. Measurements on the skeletons are identified by the following acronyms and abbreviations:

- aAL adventitious avicularium length
- aAW adventitious avicularium width
- AL avicularium length
- aOpL avicularian opesia length
- aOpW avicularian opesia width
- ApL aperture length

ApW aperture width

- AW avicularium width
- BD branch diameter
- DO distance between midpoints of adjacent orifices
- iAL interzooidal avicularium length
- iAW interzooidal avicularium width
- OL orifice length
- OnL onychocellarium length
- OnW onychocellarium width
- OpL opesia length
- OpW opesia width
- OvL ovicell length
- ovOL ovicellate orifice length
- ovOW ovicellate orifice width
- OvW ovicell width
- OW orifice width
- vAL vicarious avicularium length
- vAW vicarious avicularium width
- ZL zooid length as seen on colony surface
- ZW zooid width as seen on colony surface



Fig. 3.1 Main characters measured on the cheilostome bryozoan skeletons. Left: a representative of the Flustrina (*Mollia patellaria*), right: an ascophorine bryozoan (*Schedocleidochasma incisa*). See list above for abbreviations used.

3.4 Glossary of Special Terms

Adventitious avicularium: one occupying some position on the external wall of an autozooid (cf. vicarious, interzooidal).

Ancestrula: first-formed zooid of a colony, derived by metamorphosis of a free-swimming larva. **Anter:** part of the orifice distal to the condyles.

Apertural bar: fused pair of costae immediately proximal to orifice in cribriomorph Cheilostomatida.

Aperture: an opening in the frontal wall through which the tentacles are protruded, not necessarily coextensive with the (primary) orifice.

Areolar pore: marginal pore in the frontal wall of some Cheilostomatida.

Ascopore: median frontal pore which serves as an inlet of the ascus in some ascophorine bryozoans.

Ascus: sac-like hydrostatic organ in ascophorine Cheilostomatida.

Astogeny: development of a colony by budding.

Autozooid: feeding zooid.

Avicularium: specialised zooid with reduced polypide but strong muscles which operate a mandible-like operculum (see adventitious, interzooidal, vicarious).

Condyle: one of a pair of oppositely placed protuberances on which the operculum pivots.

Costa: one of the modified spines overarching the frontal membrane in cribriomorph Cheilostomatida, usually fused with the neighbouring costae to from the frontal shield.

Crossbar: a bar of calcification on which the mandible is hinged in many avicularia.

Cryptocyst: calcareous lamina on the basal side of the frontal membrane in some Neocheilostomina, developed from vertical walls of the zooid but not dividing its body cavity.

Cystid: cellular plus skeletal layers of the zooid or avicularium wall.

Distal: the direction towards the growing edge of a colony.

Ectooecium: outer, generally calcified, layer of ovicell wall.

Entooecium: inner, often membraneous, layer of ovicell wall.

Fenestrula: open space dividing the branches (cf. trabecula) in a reticulate colony (e.g. *Reteporella*).

Frontal: in the direction of the orifice-bearing surface of a zooid or colony.

- **Frontal membrane:** uncalcified part of frontal body wall in Cheilostomatida; may be exposed or covered by a frontal shield.
- **Frontal shield/wall:** calcified frontal surface of ascophorine bryozoans, coextensive with the outer body wall, formed as a partition below it, from the fusion of overarching spines or by calcification of a proximally derived fold.
- **Gymnocyst:** a calcified frontal shield formed of exterior calcification, constituting part or all of the frontal shield in cheilostomate zooids.

Intercostal pore: open space between fused costae.

- **Interzooidal avicularium:** one which extends to the basal surface of the colony, but is wedged in between zooids rather than replacing one of them in a series.
- Kenozooid: specialised zooid without polypide, and usually without either orifice or muscles.

Lacuna: median suboral perforation of costae in cribriomorph bryozoans.

- Lyrula: median tooth, often anvil-shaped, on the proximal side of the orifice in some Cheilostomatida.
- Mandible: articulated part of an avicularium, moved by muscles, and homologous with the operculum of an autozooid.

Mucro: a blunt elevation of the proximal lip of the orifice.

Mural rim: raised inner edge of the gymnocyst, often carrying marginal spines.

Onychocellarium: a special avicularium with a curved rostrum and mandible, in members of the Onychocellidae.

Ontogeny: the development of zooidal morphology from undifferentiated buds at the growing edge of the colony, through the series of zooids preceding them.

- **Operculum:** a generally uncalcified lamina, hinged or pivoting on condyles, which closes the orifice.
- **Opesia:** in zooids of Neocheilostomina, the opening below the frontal membrane which remains after development of the cryptocyst.
- **Opesiule:** groove or hole in cryptocyst in some Neocheilostomina through which muscles pass towards the frontal membrane.

Oral: in the vicinity of the orifice.

- **Orifice:** opening in the zooid wall through which the tentacles are protruded; may become surrounded by a peristome, the upper end is then known as the secondary orifice or aperture (cf. primary orifice).
- Ovicell: the globular brood chamber in some Cheilostomatida.
- Palate: part of the avicularium occupied by the mandible (syn. rostrum).
- Papilla pore: pore between bases of successive costae, bordered on one side by gymnocyst, around margin of the frontal shield in cribriomorph Bryozoa.
- Pelmatidium: small uncalcified pore in the costae of cribriomorph Bryozoa.

Peristome: a rim which may become elevated surrounding the primary orifice.

- **Polypide:** organic tissue inside autozooid consisting of tentacles, alimentary canal, musculature, and nerve ganglion.
- **Pore chamber:** small enclosed space near base of vertical walls in distal part of zooid in certain Cheilostomatida; its walls contain communication pores.

Poster: part of the orifice proximal to the condyles and leading to the ascus.

Primary orifice: the opening in the outer body wall through which the polypide is extruded, in cheilostomes coextensive with the operculum.

Proximal: in the direction of the ancestrula, the origin of colony growth.

Rostrum: distal part of avicularium occupied by mandible (syn. palate).

Scutum: a modified, usually enlarged and flattened, marginal spine which overarches the frontal membrane in members of the Scrupocellariidae.

Secondary calcification: additional deposition of skeletal material occurring as a zooid ages.

Septulum (pl. septula): perforations in the vertical walls of Cheilostomatida for the passage of communication organs.

Seta: the long bristle-like mandible of a vibraculum.

Sinus: slit at proximal edge of orifice in some ascophorine bryozoans.

Spatulate: shaped like a spoon, or a broad blunt-ended blade of an avicularian mandible/rostrum.

Spine: a tubular or flattened projection of the body wall, sometimes jointed.

Tatiform: an ancestrula with a membranous frontal wall, often surrounded by spines.

Trabecula: branch separating the fenestrulae in a reticulate colony (e.g. Reteporella).

Umbo: a blunt prominence on the frontal wall or ovicell in some cheilostomes.

Vibraculum: an avicularium with an elongate bristle-like mandible.

Vicarious avicularium: one that replaces a zooid in a series.

Zooid: single bryozoan individual; various types are distinguished by prefixes.

4. Systematic Account

4.1 Systematic List

Order Cheilostomata BUSK, 1852 Suborder Malacostegina LEVINSEN, 1902 Superfamily Membraniporoidea BUSK, 1852 Family Membraniporidae BUSK, 1852 Genus Biflustra D'ORBIGNY, 1852 Biflustra ex gr. savartii (AUDOUIN, 1826) Suborder Neocheilostomina D'HONDT, 1985 Infraorder Flustrina SMITT, 1868 Superfamily Calloporoidea NORMAN, 1903 Family Calloporidae NORMAN, 1903 Genus Amphiblestrum GRAY, 1848 *Amphiblestrum appendiculata* (REUSS, 1848) Genus Aplousina CANU & BASSLER, 1927 ?Aplousina bobiesi (DAVID & POUYET, 1974) Genus Callopora GRAY, 1848 Callopora sp. 1 ?Callopora sp. 2 Genus Copidozoum HARMER, 1926 ?Copidozoum sp. Genus Crassimarginatella CANU, 1900 ?Crassimarginatella sp. Genus Ellisina NORMAN, 1903 Ellisina gautieri FERNÁNDEZ PULPEIRO & REVERTER GIL, 1993 Family Hiantoporidae GREGORY, 1893 Genus Hiantopora MACGILLIVRAY, 1887 Hiantopora rostrata comb. nov. (MOISSETTE, 1988) **Superfamily** Flustroidea FLEMING, 1828 Family Flustridae FLEMING, 1828 Genus Hincksina NORMAN, 1903 Hincksina sp. Superfamily Buguloidea GRAY, 1848 Family Candidae D'ORBIGNY, 1851 Genus Scrupocellaria VAN BENEDEN, 1845 Scrupocellaria sp. Superfamily Microporoidea GRAY, 1848 Family Microporidae GRAY, 1848 Genus Micropora GRAY, 1848 Micropora cf. coriacea (JOHNSTON, 1847) Genus Mollia LAMOUROUX, 1816 Mollia circumcincta (HELLER, 1867) Mollia patellaria (MOLL, 1803) Family Onychocellidae JULLIEN, 1882 Genus Onychocella JULLIEN, 1882 Onychocella cf. angulosa (REUSS, 1848) Family Steginoporellidae HINCKS, 1884 Genus Steginoporella SMITT, 1873 Steginoporella cucullata (REUSS, 1848)

Superfamily Cellarioidea FLEMING, 1828 Family Cellariidae FLEMING, 1828 Genus Cellaria ELLIS & SOLANDER, 1786 Cellaria aff. melillensis EL HAJJAJI, 1987 Infraorder Ascophorina LEVINSEN, 1909 "Grade" Acanthostega LEVINSEN, 1902 Superfamily Cribrilinoidea HINCKS, 1879 Family Cribrilinidae HINCKS, 1879 Cribrilinidae gen. et sp. indet. Genus Figularia JULLIEN, 1886 *Figularia figularis* (JOHNSTON, 1847) Genus Gephyrotes NORMAN, 1903 Gephyrotes fortunensis POUYET, 2000 Genus Puellina JULLIEN, 1886 Puellina (Cribrilaria) cf. radiata (MOLL, 1803) Puellina sp. 1 Puellina sp. 2 "Grade" Hippothoomorpha GORDON, 1989 Superfamily Hippothooidea BUSK, 1859 Family Chorizoporidae VIGNEAUX, 1949 Genus Chorizopora HINCKS, 1880 Chorizopora brongniartii (AUDOUIN, 1826) Family Trypostegidae nov. Genus Trypostega LEVINSEN, 1909 Trypostega rugulosa (REUSS, 1874) "Grade" Umbonulomorpha GORDON, 1989 Superfamily Arachnopusioidea JULLIEN, 1888 Family Arachnopusiidae JULLIEN, 1888 Genus Poricella CANU, 1904 Poricella bugei (EL HAJJAJI, 1987) Superfamily Adeonoidea BUSK, 1884 Family Adeonidae BUSK, 1884 Genus Schizostomella CANU & BASSLER, 1927 ?Schizostomella cf. dubia (BUSK, 1859) Superfamily Lepralielloidea VIGNEAUX, 1949 Family Bryocryptellidae VIGNEAUX, 1949 Genus Porella GRAY, 1848 ?Porella sp. Family Romancheinidae JULLIEN, 1888 Genus Escharella GRAY, 1848 Escharella serrulata (REUSS, 1848) Escharella sp. 1 *Escharella* sp. 2 Genus Escharoides MILNE EDWARDS, 1836 Escharoides coccinea (ABILDGAARD, 1806) Escharoides megalota (REUSS, 1848) Escharoides sp. Genus Hemicyclopora NORMAN, 1894 Hemicyclopora sp. 1 Hemicyclopora sp. 2 Genus Hippopleurifera CANU & BASSLER, 1927 *Hippopleurifera semicristata* (REUSS, 1848)

"Grade" Lepraliomorpha GORDON, 1989 Superfamily Smittinoidea LEVINSEN, 1909 Family Smittinidae LEVINSEN, 1909 Genus Smittina NORMAN, 1903 Smittina messiniensis EL HAJJAJI, 1992 Genus Smittoidea OSBURN, 1952 *Smittoidea* sp. Family Bitectiporidae MACGILLIVRAY, 1895 Genus Hippoporina NEVIANI, 1895 *Hippoporina* sp. Genus Schizomavella CANU & BASSLER, 1917 ?Schizomavella sp. Family Watersiporidae VIGNEAUX, 1949 Genus Watersipora NEVIANI, 1895 *Watersipora* sp. Superfamily Schizoporelloidea JULLIEN, 1882 Family Schizoporellidae JULLIEN, 1882 Genus Schizoporella HINCKS, 1877 Schizoporella dunkeri (REUSS, 1848) Schizoporella aff. magnifica HINCKS, 1886 Schizoporella sp. Family Myriaporidae GRAY, 1841 Genus Myriapora DE BLAINVILLE, 1830 Myriapora truncata (PALLAS, 1766) Family Lanceoporidae HARMER, 1957 Genus Calyptotheca HARMER, 1957 *Calvptotheca* sp. 1 *Calvptotheca* sp. 2 Genus Emballotheca LEVINSEN, 1909 Emballotheca longidens (CIPOLLA, 1921) Family Cheiloporinidae BASSLER, 1936 Genus Cheiloporina CANU & BASSLER, 1923 *Cheiloporina campanulata* (CIPOLLA, 1921) Genus Hagiosynodos BISHOP & HAYWARD, 1989 Hagiosvnodos latus (BUSK, 1856) Family Micoporellidae HINCKS, 1879 Genus Calloporina NEVIANI, 1895 Calloporina decorata (REUSS, 1848) Genus Microporella HINCKS, 1877 *Microporella* aff. *appendiculata* (HELLER, 1867) Microporella aff. ciliata (PALLAS, 1766) Microporella aff. inamoena (REUSS, 1874) *Microporella* sp. Family Lacernidae JULLIEN, 1888 Genus Arthropoma LEVINSEN, 1909 Arthropoma ciliata CANU & LECOINTRE, 1928 **Incertae sedis** Genus Escharina MILNE EDWARDS, 1836 *Escharina* sp. Genus Therenia DAVID & POUYET, 1978 Therenia montenati comb. nov. (POUYET, 1976) Superfamily Celleporoidea JOHNSTON, 1838 Family Celleporidae JOHNSTON, 1838 Celleporidae gen. et sp. indet.

Genus Buffonellaria CANU & BASSLER, 1917 Buffonellaria entomostoma (REUSS, 1848) Genus Celleporina GRAY, 1848 Celleporina cf. canariensis ARÍSTEGUI, 1989 *Celleporina* sp. Genus Lagenipora HINCKS, 1877 *Lagenipora* sp. Genus Osthimosia JULLIEN, 1888 *?Osthimosia* sp. Genus Turbicellepora RYLAND, 1963 Turbicellepora aff. magnicostata (BARROSO, 1919) Family Phidoloporidae GABB & HORN, 1862 "Hippoporella" pauper (REUSS, 1874) Genus Reteporella BUSK, 1884 *Reteporella* sp. Genus Rhynchozoon HINCKS, 1895 Rhynchozoon monoceros comb. nov. (REUSS, 1848) Genus Schedocleidochasma SOULE, SOULE & CHANEY, 1991 Schedocleidochasma incisa comb. nov. (REUSS, 1874) Genus Schizotheca HINCKS, 1877 Schizotheca serratimargo (HINCKS, 1886) **Incertae sedis** Ascophorina indet.

4.2 Taxonomic Account

Order CHEILOSTOMATA BUSK, 1852 Suborder MALACOSTEGINA LEVINSEN, 1902 Superfamily MEMBRANIPOROIDEA BUSK, 1852 Family MEMBRANIPORIDAE BUSK, 1852 Genus BIFLUSTRA D'ORBIGNY, 1852

Biflustra ex gr. *savartii* (AUDOUIN, 1826) Plate 1, Figure 1

ex gr. 1826 Flustra savartii AUDOUIN, p. 69; Savigny, pl. 10, fig. 10.

Material:

Niebla Calcarenite: 1 specimen. examined by SEM: GNI1-019-F.

Measurements:

ZL $389 \pm 46, 302-469 (1, 9)$ ZW $267 \pm 37, 204-326 (1, 9)$ OpL $212 \pm 31, 184-286 (1, 9)$ OpW $165 \pm 25, 118-200 (1, 9)$

Description:

Colony encrusting unilaminar, multiserial. Zooids quadrangular, separated by a distinct groove; gymnocyst a thin, convex, marginal band tightly spangled with rows of small granules; cryptocyst reduced laterally to relatively well developed proximally, with less dense rows of granules than gymnocyst, forming radially arranged ridges giving the impression of a striated and toothed opesial margin, proximal and/or lateral denticles may have been present; opesia (sub)oval, large.

No spines, ovicells or avicularia.

Discussion:

Despite this species displaying so few morphological characters, the variety of morphologies described and figured in the literature are so diverse that *Biflustra savartii*, including its numerous subspecies, clearly represents a species complex. However, a great intraspecific variation, e.g. in cryptocystal development (Cook, 1968a), makes it difficult to distinguish species even in extant material, and a type-specimen has not been established, yet. Considering these obstacles, the identification of the specimen is little more than speculation, as are geographic and stratigraphic ranges given in the literature for this species. Yet, although the name *B. savartii* appears in nearly every work on Neogene Mediterranean faunas, the only presumed synonymy and morphological congruence with my material is the one depicted by Moissette (1988: p. 73, pl. 11, fig. 6, 9.), which is, however, mainly due to the lack of SEM photography in earlier studies. Sefian et al. (1999: p. 229) also note the presence of an encrusting unilaminar colony of *B. savartii* in the Messinian of NW Morocco, yet without depicting it.

Occurrence:

Species of the genus *Biflustra* (as well as morphologically related species described as *Membranipora* spp. by Cook, 1968a) are more or less confined to tropical and subtropical regions.

Only a single small specimen was found in the Niebla Calcarenite. Owing to its irregular basal wall and zooid outline it is presumed to have encrusted an ephemeral substrate.

Suborder NEOCHEILOSTOMINA D'HONDT, 1985 Infraorder FLUSTRINA SMITT, 1868 Superfamily CALLOPOROIDEA NORMAN, 1903 Family CALLOPORIDAE NORMAN, 1903 Genus AMPHIBLESTRUM GRAY, 1848

Amphiblestrum appendiculata (REUSS, 1848) Plate 1, Figure 2, 3

- v 1848 *Cellepora appendiculata* REUSS, p. 96, pl. 11, fig. 22.
- 1972 Ramphonotus appendiculata (REUSS) David et al., p. 16, pl. 7, fig. 5.
- v 1974 Ramphonotus appendiculata (REUSS) David & Pouyet, p. 108, pl. 1, fig. 2, 6.
- 1984 Ramphonotus appendiculata (REUSS) Pouyet & David, p. 93, pl. 6, fig. 5, 6.
- v 1988 Ramphonotus minax (BUSK) Moissette, p. 85, pl. 13, fig. 4, 5.
 - 1992 Ramphonotus minax (BUSK) El Hajjaji, p. 101, pl. 4, fig. 11.

1997b Ramphonotus appendiculata (REUSS) - Pouyet, p. 184.

Material:

Niebla Calcarenite: 3 colonies.

examined by SEM: GNI1-019-G; GNI1-039-D.

other: VNHM 1848.38.83 (lectotype *A. appendiculata*, Badenian, Eisenstadt; David & Pouyet, 1974, pl. 1, fig. 2, 6); 1859.50.793, 1867.40.261 (Badenian, Eisenstadt); 1878.11.102 (Badenian, Eisenstadt; Reuss, 1874, pl. 9, fig. 13-16). FSL 119068 (as *R. minax* [Busk, 1860a], Messinian, Algeria; Moissette, 1988).

Measurements:

Description:

Colony encrusting unilaminar, multiserial. Autozooids oval to rounded polygonal, separated by deep grooves; gymnocyst smooth, usually reduced laterally and well developed proximally, occasionally extending between proximal zooids; cryptocyst extensive proximally narrowing to a thin band distolaterally, with crenulate upper rim becoming smoother and depressed towards zooid centre, sometimes forming a straight edge, occupying about one-fourth to one-third of the entire frontal surface, delimiting a more or less pyriform or oval opesia. One to three (?four) spines on outer distal zooid margin.

Ovicells were not observed.

Adventitious avicularia monomorphic, single or paired, on proximal gymnocyst, usually abutting but not merging with the proximal cryptocyst, occasionally an additional avicularium on lateral gymnocyst; cystid oval (when short) to triangular; rostrum triangular to elongate triangular, pointing in various directions (usually laterally to distally, rarely proximally).

Discussion:

Although ovicells are lacking in both the type- and present material, and although specimens in the Reuss Collection are coated by a thin veneer of cement, a comparison of the autozooids with those of the lectotype and several other specimens from the type-location of *Amphiblestrum appendiculata* suggest that they may be conspecific. The shape and extension of the opesia, gymnocyst and cryptocyst, the location and shape of avicularia, and the presence of spines are the same in both samples. Although the presence of spines was not mentioned by either Reuss (1848, 1874) or David & Pouyet (1974) these can be observed in the type material and also on plate 1, fig.

2 in David & Pouyet (1974). A well preserved specimen of *A. appendiculata* is figured by Schmid et al. (2001, pl. 4, fig. 4) in which all these features can clearly be observed.

However, the absence of ovicells in both the type- and present material poses a bigger problem to an unequivocal determination of the species, and also of synonymies with other specimens and taxa in the genus *Amphiblestrum*, since these have a characteristic frontal area of uncalcified ectooecium and may or may not be associated with avicularia (see e.g. *Ramphonotus minax* [Busk, 1860a] in Moissette [1988] and El Hajjaji [1992], which may presumably be conspecific with *A. appendiculata*). In the absence of colonies with ovicellate zooids in the present samples and in the type-material the synonymies given above thus need to be taken with caution.

The consideration that *Ramphonotus minax* (Busk, 1860a) is a boreal species and absent from the Recent Mediterranean Sea (López de la Cuadra & García-Gómez, 1994) does also apply to the Neogene fossil record (see also Rosso, 2002). Most species recently described as *R. minax* are either (closely related to) *Amphiblestrum appendiculata* (e.g. Moissette, 1988; El Hajjaji, 1992) or *A. lyrulatum* (Calvet, 1907) (Pouyet & Moissette, 1992; Moissette & Spjeldnaes, 1995; Haddadi-Hamdane, 1996). Rosso (2002) synonymised the species Moissette (1988) described as *R. minax* with *A. auritum* (Hincks, 1877). I disagree with this decision and refer Moissette's species to *A. appendiculata*, since, although admittedly similar to *A. appendiculata*, *A. auritum* is characterised by zooid boundaries formed by raised margins, by the presence of only a single spine in later zooid ontogeny which is situated on the marginal cryptocyst, and by a usually proximally directed proximal avicularium (see Bishop & Hayward, 1989; Hayward & Ryland, 1998). These characters are neither present in Moissette's (1988) nor in the Niebla material and these are therefore distinct from *A. auritum*. However, this example once more shows that a revision of the Neogene occurrence of *Amphiblestrum* in the Mediterranean and Paratethyan region is essential.

Occurrence:

The colonies encrust red algae.

Distribution:

Miocene: Burdigalian (SE France), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin – Spain), Messinian (Morocco, Algeria).

Genus APLOUSINA CANU & BASSLER, 1927

Aplousina bobiesi (DAVID & POUYET, 1974) Plate 1, Figure 4-6

- v 1874 *Membranipora lacroixi* var. *diadema* REUSS, p. 181, pl. 9, fig. 9.
- 1956 Membranipora spiculata CANU & BASSLER Bobies, p. 234, pl. 5, fig. 1.
- v 1956 Membranipora tuberimargo CANU & BASSLER Bobies, p. 234, pl. 5, fig. 2.
- v 1974 Membranipora bobiesi DAVID & POUYET, p. 96, pl. 2, fig. 1.
- v 1988 Aplousina bobiesi (D. & P.) Moissette, p. 78, pl. 12, fig. 7, 11.
- 1990 Aplousina bobiesi (D. & P.) Li, p. 32, pl. 1, fig. 6-7.
- ?non 1992 Aplousina bobiesi (D. & P.) El Hajjaji, p. 93, pl. 4, fig. 4.
 - 1997b Aplousina bobiesi (D. & P.) Pouyet, p. 34, pl. 3, fig. 9-11.
 - 1999 Aplousina bobiesi (D. & P.) Sefian et al., p. 292.
- ?non 2000 Aplousina bobiesi (D. & P.) El Safori, p. 399, fig. 3: 2.

2000 Aplousina bobiesi (D. & P.) – Pouyet, p. 183.

Material:

Niebla Calcarenite: 53 colonies. examined by SEM: GNI1-006-A, B, C, D, E, F. other: VNHM 1878.11.15 (Badenian, Baden: David & Pouyet, 1974); 1867.40.270 (Badenian, Rohrbach: Reuss, 1874, pl. 9, fig. 9); 120/1955 (Badenian, Kalksburg: Bobies, 1956, pl. 5, fig. 2).

FSL 118738, 118654 (Messinian, Algeria: Moissette, 1988).

Measurements:

ZL $563 \pm 69, 461-690 (5, 20)$ ZW $421 \pm 39, 343-488 (5, 20)$ OpL $436 \pm 49, 335-519 (5, 20)$ OpW $290 \pm 25, 253-331 (5, 20)$ OvL 120-190 (1, 2)OvW 231-300 (1, 2)

Description:

Colony encrusting umilaminar, multiserial. Zooids elongated quadrangular, separated by deep grooves; gymnocyst smooth, little developed proximally and distally, almost absent laterally; cryptocyst narrow, confined to opesial margin, crenulated and granular; opesia large, oval, occupying about 80% of the frontal surface. Zooid margin with six to ten (generally eight) thin spines and a pair of prominent, distolateral, pointed tubercles separated by a raised, sometimes thickened, distal margin. Basal wall with two prominent, stalked, lateral nodules of calcification at about mid-distance.

Crescentic ovicell arching over distal part of opesia leaving a broad opening, formed by distally rising zooid margins.

No avicularia.

Discussion:

This species seems to combine characters of two different genera, namely *Aplousina* and *Crassimarginatella* Canu, 1900. Whereas the ovicell is typical for species of *Aplousina* (Pl. 1, Fig. 6), the presence of numerous spines does not match with the original genus definition of Canu & Bassler (1927). Although Cook (1968a) and Gordon (1986) recorded the occasional presence of a pair of distal spines in some species, and although Zabala & Maluquer (1988) cautiously suggested that the presence of spines in some species may need to be included in the genus definition, they certainly did not have in mind to include a species with numerous and well developed spine bases encircling the opesia in every single zooid of a colony, as is the case in *?A. bobiesi*. Furthermore, the gymnocyst and cryptocyst are usually less well developed in species of *Aplousina* (see e.g. Cook, 1968a) than in the present material. On the other hand, while the presence of numerous spines and a rather well developed gymno- and cryptocyst may suggest a placement in the genus *Crassimarginatella*, the complete absence of avicularia prohibits to classify *?A. bobiesi* with this genus. The intermediate position of this species therefore presents yet another valid argument for a revision of the family Calloporidae and its numerous genera.

Although the holotype was unfortunately not available at the Université de Lyon, comparisons with most specimens from other locations and ages, among these material from near the type-location in Austria which David & Pouyet (1974) considered conspecific, did not yield morphological differences. However, other specimens described and figured as *A. bobiesi* do show some dissimilarities: the gymnocyst is extremely reduced and the cryptocyst less well developed in the material figured in El Hajjaji (1992), while El Safori (2000) reports a narrow or absent gymnocyst and a flat cryptocyst such as that the zooid boundaries appear indistinct in this specimen. Nevertheless, both report the presence of spines and the distal part of the zooids appears to be similar to the present material. Whether this is due to a differential state of preservation or whether these are distinct species is impossible to definitely conclude for me at present.

Zooid size in the material from the Niebla Calcarenite shows to be considerably smaller than that of other records (see Chapter 5). However, a great range in zooid size within species of *Aplousina* was already noted by Cook (1968a, and references therein) and considered not to constitute a useful specific character. Of unknown function is the pair of nodular calcification on the basal wall (Pl. 1, Fig. 5), which has not been noticed before in this species.
Occurrence:

This species has been commonly reported from the Neogene of the Mediterranean and Paratethyan basins. The record from the Atlantic Morocco by Sefian et al. (1999) and SW Spain, however, was the first to show that this species does occur outside the Mediterranean as well.

Most colonies were found to encrust a stable substrate, such as red algae or other bryozoans (most commonly *S. serratimargo* Hincks, 1886), but many fragments occur unattached and show a thickened and uneven basal wall with tuberosities. This may imply either growth on soft ephemeral substrates, or growth independent of substrate in order to bridge a gap. The framework formed by the laminate red algae may have thus induced this type of growth.

Distribution:

Miocene: Burdigalian (France), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin -

Spain, Morocco), Messinian (SE Spain, Atlantic and Mediterranean Morocco, Algeria). Pliocene: SE Spain.

Genus CALLOPORA GRAY, 1848

Callopora sp. 1 Plate 1, Figure 7

Material:

Niebla Calcarenite: 1 colony. examined by SEM: GNI1-024-C.

Measurements:

ZL $392 \pm 31, 346 - 432 (1, 8)$ ZW $257 \pm 28, 234 - 324 (1, 8)$ OpL $216 \pm 27, 162 - 248 (1, 8)$ OpW $154 \pm 16, 133 - 176 (1, 8)$ OvL $163 \pm 12, 148 - 178 (1, 6)$ OvW $236 \pm 16, 211 - 258 (1, 6)$

Description:

Colony encrusting unilaminar, multiserial. Zooids oval, separated by deep grooves, zooid margin steeply inclined and proximal part strongly convex. Gymnocyst a thin band laterally but usually well developed proximally; cryptocyst reduced laterally, slightly more developed proximally, ?crenellated, steeply sloping towards zooid centre; opesia oval, usually comprising more than half of autozooid length. Eight to twelve spine bases on zooid margin.

Ovicells hemispherical, broader than long, half or more immersed in distal zooid's gymnocyst; frontal wall smooth, slightly flattened frontally with a raised, concave, proximal margin raised above distal part of opesia.

Avicularia were not observed.

Discussion:

Although the autozooids display features of *Crassimarginatella* Canu, 1900, this specimen is placed in the genus *Callopora* due to the absence of both vicarious avicularia and a crescentic frontal area in the ovicells. While most species in this genus bear adventitious avicularia, these may be absent in a few, e.g. *Callopora discreta* (Hincks, 1862).

Yet not well-preserved, the specimens described as *Electra monostachys* by Moissette (1988: p. 74, pl. 11, fig. 5, 11) may be considered conspecific with the present material. He mentions the presence of several spines and, although their frontal wall is broken off, the shape of the ovicells appears similar.

Occurrence:

The only specimen acquired encrusts a coralline alga.

Distribution:

Miocene: Tortonian (Guadalquivir Basin – Spain), ?Messinian (Algeria).

Callopora sp. 2 Plate 1, Figure 8

Material:

Niebla Calcarenite: 3 colonies. examined by SEM: GNI1-012-A, B; GNI1-016-A.

Measurements:

ZL $305 \pm 28, 269-390 (3, 18)$ ZW $234 \pm 29, 194-287 (3, 18)$ OpL $194 \pm 14, 173-218 (3, 18)$ OpW $140 \pm 16, 114-177 (3, 18)$

Description:

Colony encrusting unilaminar, multiserial. Zooids oval to rounded polygonal, usually broadest proximally, separated by distinct grooves; gymnocyst frequently well developed proximally, reduced laterally; cryptocyst narrow, restricted to opesial margin; opesia oval, large, constituting about two-thirds of total zooid length. Some ten tubercles (?spine sockets) on zooid margin, usually smaller and more distinct distally, becoming thicker and more amalgamated with gymnocyst proximally.

Ovicells and avicularia were not observed.

Discussion:

Since there are no ovicells or avicularia, a definitive generic placement is not possible. Furthermore, the marginal tubercles cannot unambiguously be identified as spines, which are rather distinct in *Callopora*; the classification with this genus thus allows for the general appearance of the zooids only. A similar species was not encountered during literature search.

Occurrence:

Only three colonies were found encrusting red algae.

Genus COPIDOZOUM HARMER, 1926

Copidozoum sp. Plate 2, Figure 1

Material:

Niebla Calcarenite: 1 colony. examined by SEM: GNI1-011-A.

Measurements:

ZL $406 \pm 18, 377-424 (1, 7)$ ZW $278 \pm 58, 234-404 (1, 7)$ OpL $353 \pm 16, 333-375 (1, 7)$ OpW $232 \pm 28, 206-290 (1, 7)$ AL $152 \pm 13, 132 - 173 (1, 6)$

AW $85 \pm 13, 66 - 103 (1, 6)$

Description:

Colony encrusting unilaminar, multiserial. Zooids oval, separated by deep grooves; some 12 basal pore chambers present; gymnocyst smooth, almost completely reduced and present only proximally; cryptocyst finely ?granular, only a very thin band proximally; opesia oval, nearly as long and wide as autozooid. No spines.

Ovicells were not observed.

Interzooidal avicularia distal to every autozooid, slightly acute to frontal plane, directed distolaterally; cystid quadrangular, rostrum elongated, tapering distally into a blunt tip, with a broad, proximal, cryptocystal shelf forming a pair of lateral condyles distally on which mandible is hinged, not joined to form a crossbar.

Discussion:

The characteristic vicarious avicularia, well enough preserved as to show the proximal cryptocystal calcification producing the condyles, as well as the reduced autozooidal gymno- and cryptocysts suggest that this specimen might belong to the genus *Copidozoum*. However, due to the absence of ovicells, a more precise specification is impossible. Moreover, although the avicularia are generally distinctly smaller in species of the genus *Ellisina*, it cannot be ruled out that the specimen could also belong to this genus.

Occurrence:

Only one specimen was found encrusting a coralline algae.

Genus CRASSIMARGINATELLA CANU, 1900

?Crassimarginatella sp. Plate 1, Figure 9, 13

cf. 1984 Copidozoum planum (HINCKS) – Pouyet & David, p. 93, pl. 7, fig. 2, 3.

Material:

Niebla Calcarenite: 35 colonies. examined by SEM: GNI1-007-A, B, C.

Measurements:

ZL	513 ± 64, 437–659 (3, 20)		
ZW	336 ± 61, 237–423 (3, 20)		
OpL	469 ± 67, 385–631 (3, 20)		
OpW	293 ± 55, 215–373 (3, 20)		
AL	732 ± 91, 635–834 (3, 4)	OpL	$490 \pm 51, 431 - 550(3, 4)$
AW	$302 \pm 32, 276 - 346(3, 4)$	OpW	$238 \pm 33, 195 - 275(3, 4)$

Description:

Colony encrusting unilaminar, multiserial. Zooids elongated hexagonal, separated by shallow indistinct grooves, vertical walls thin with some 15 septula, distolateral zooid margin slightly raised; gymnocyst absent; cryptocyst reduced to a thin band and restricted to proximolateral parts of zooid; opesia extensive, nearly as long and wide as autozooid; no spines.

Ovicell vestigial if present, possibly marked by a distinctly raised distal zooid margin.

Vicarious avicularia sporadic, large, longer than autozooid, spatulate; opesia extensive, comprising two-thirds of total length with cryptocyst covering only the tapered proximal part; distal fourth a calcified shelf at level with frontal plane covering the distalmost body cavity,

proximal edge concave, rounded distal margin slightly raised above frontal plane, recumbent on proximal part of distal zooid.

Discussion:

As ?*Aplousina bobiesi*, this species constitutes another generic borderline case. A complete absence of the gymnocyst and the extremely reduced cryptocyst are characteristic of the Membraniporoidea (unfortunately, an ancestrula was not found although the species is present with numerous colonies); however, the presence of avicularia argues against a placement in any of the genera of Membraniporoidea. On the other hand, genera of the superfamily Calloporoidea are characterised by the presence of marginal spines and usually prominent ovicells, both of which are completely absent in the present specimens. Furthermore, this very type of vicarious avicularium has, to my knowledge, not been recorded in any Recent species of the Calloporoidea.

Concerning the avicularian morphology, the vestigial ovicells, and the reduced crypto- and gymnocysts, a closer relationship may possibly exist between the present material and the Recent species Crassimarginatella tuberosa (Canu & Bassler, 1928a), as described in Cook (1968a: 151). In the latter species the ovicell is formed merely by a raised distal margin, and the gymno- and cryptocysts are greatly reduced when compared to other species of the genus, although they are still better developed than in the material from Niebla (another dissimilarity is the presence of two spines in the Recent species while these are absent in the Niebla specimens). However, the most noteworthy conformity exists in the formation of a calcified distal shelf in the similarly large vicarious avicularia of C. tuberosa, despite the development of a pair of lateral flaps that arch over part of the opesia in the central region. Another similar fossil species is Crassimarginatella *manzonii* (Cipolla, 1921), which is even more closely related to C. tuberosa in having a fairly well developed gymno- and cryptocyst as well as a similar avicularium (cf. Poluzzi, 1975: 46; El Hajjaji, 1992: 98; Pouvet & Moissette, 1992: 37). Since no other species or genus with similar features was found, the present material is warily placed in the genus Crassimarginatella. The range of disparate morphologies in this genus, e.g. compare ovicell and avicularian morphologies in C. tuberosa and C. sculpta (MacGillivray, 1895), and in the Calloporidea in general (pers. comm. D.P. Gordon, 2003), strongly suggests that these taxa need revision.

The species from the Burdigalian of SE France described as *Copidozoum planum* (Hincks, 1880) by Pouyet & David (1984) may be conspecific with the specimens from Niebla, but certainly not with the Recent species of *C. planum* as defined by Hincks (1880) (see Hayward & Ryland, 1998). Also, an assignment of the fossil species to the genus *Copidozoum* Harmer, 1926 is problematic because all of these species are characterised by prominent ovicells, whereas the genus definition of *Crassimarginatella* includes the presence of vestigial ovicells in some species (e.g. Hayward & Ryland, 1998). Whether *Callopora* sp. A and *C. planum* as described by David et al. (1970: p. 111; 1972: p. 16, respectively) are synonymic with the Recent *C. planum*, as was suggested by Pouyet & David (1984), can not be concluded here, for the authors did not figure their material. However, since David et al. (1972) mention the presence of prominent ovicells in *C. planum*, it is unlikely that their material is conspecific with the present species. *C. planum* as described by Pouyet & David (1984) differs from the Niebla specimens in that it has a better developed cryptocyst; however, this may be partly due to the fact that their material is better preserved. More SEM work is necessary before any conclusion can be drawn with respect to the introduction of a new species (and eventually genus) name.

Occurrence:

This species is common in both the red algal dominated lower part of the Niebla section, encrusting coralline algae, as well as in the upper rudstone facies, in which the interior of large oyster shells is covered by extensive colonies.

In case the Niebla specimens are conspecific with the species from the early Miocene of southeastern France, the present finding represents the youngest stratigraphic occurrence and the first appearance outside the Mediterranean basin.

Distribution:

Miocene: ?Burdigalian (SE France), Tortonian (Guadalquivir Basin - Spain).

Genus ELLISINA NORMAN, 1903

Ellisina gautieri FERNÁNDEZ PULPEIRO & REVERTER GIL, 1993 Plate 1, Figure 10-12

- 1962 Ellisina cf. levata (HINCKS) Gautier, p. 43, fig. 7.
- 1966 Ellisina cf. antarctica HASTINGS Prenant & Bobin, p. 208, fig. 64.
- 1988 Ellisina sp. Moissette, p. 79, pl. 11, fig. 4, 7.
- 1988 Ellisina cf. antarctica HAST. Zabala & Maluquer, p. 81.
- ? 1990 Ellisina cf. antarctica HAST. Li, p. 32.
 - 1993 Ellisina cf. antarctica HAST. Fernández Pulpeiro & Reverter Gil, p. 97, pl. 1, fig. 1-3.
 - 1993 Ellisina gautieri FERNÁNDEZ PULPEIRO & REVERTER GIL, p. 98. pl. 2, fig. 1, 2.
 - 1998 Ellisina gautieri FERN. P. & REV. GIL Hayward & Ryland, p. 192, fig. 56 C, D.
 - 2002 Ellisina gautieri FERN. P. & REV. GIL Hayward & McKinney, p. 18, fig. 7 E-G.

Material:

v

Niebla Calcarenite: 4 colonies. examined by SEM: GNI1-011-B; GNI1-017-A; GNI1-040-A. other: FSL 491289 (Burdigalian, Rhodanian Basin: Li, 1990).

Measurements:

ZL $281 \pm 32, 212 - 324 (3, 20)$ $212 \pm 29, 159 - 254 (3, 20)$ ZW OpL $207 \pm 18, 174 - 238(3, 20)$ OpW $151 \pm 15, 120 - 174(3, 20)$ OvL 180 OvW 147 AL $88 \pm 11,74 - 111(3,11)$ 59 ± 7, 45–68 (3, 11) AW

Description:

Colony encrusting unilaminar, multiserial. Autozooids oval, separated by distinct grooves; gymnocyst smooth and often reduced; opesia large, oval, bordered by a very narrow crenulated cryptocyst; no spines.

Ovicell slightly longer than wide, domed with an arched proximal margin and a distal avicularium similar to that of autozooids.

Avicularia interzooidal, distal to almost every autozooid; rostrum acute to frontal plane, directing distolaterally, triangular distal to and semicircular proximal to incomplete, proximomedially directed crossbar (or condyles) formed by broad cryptocystal rim.

Discussion:

This species has, for a long time, been referred to *E*. cf. *antarctica* HASTINGS, 1945 and to *E*. cf. *levata* (HINCKS, 1882) until Fernández Pulpeiro & Reverter Gil (1993) established *E. gautieri* as a new species for the Mediterranean/eastern Atlantic realm. However, why these authors continued to refer material from northern Spain to *E*. cf. *antarctica* remains curious (Hayward & Ryland, 1998).

Although morphologically indistinguishable from the Recent *E. gautieri*, the zooid length in the present material differs significantly from other Recent and fossil measurements (Table 4.1). The greatly reduced zooid length in the Guadalquivir specimen, especially when compared with Mediterranean representatives, might in part be due to it being a young colony. However, the presence of ovicells clearly shows that the colony had reached maturity, and only the largest zooids at the periphery of the colony were chosen for zooidal measurements. Furthermore, ovicell size does match with records of Recent representatives (cf. Fernández Pulpeiro & Reverter Gil, 1993).

Table	4.1	Range	e and	mean	values	of zoc	oid leng	gth (in	mm) of	E.	gautieri	give	n in s	evera	ıl publ	ication	s on
Recen	t or	fossil	mater	ial. N	ote the	large	differer	nces in	absolut	te n	ninimum	and	maxin	num	zooid	length,	and
that a	clear	cut lir	ne can	not be	e drawn	betwee	en any o	of the s	sites.								

Source	Age	Location	Range	Mean
this work	Miocene	E Atlantic	0.21-0.32	0.28
Hayward & Ryland (1998)	Recent	NE Atlantic	0.3-0.35	
Moissette (1988)	Miocene	Mediterranean	0.32-0.42	0.35
Gautier (1962)	Recent	Mediterranean	0.34-0.53	0.43
Hayward & McKinney (2002)	Recent	Mediterranean	0.47-0.6	0.52

Occurrence:

Only four specimens, encrusting red algae, have been found in samples from the Niebla Calcarenite. Other fossil records of this species are sparse and limited to the Mediterranean basin. Although similar in autozooid morphology, the viewed specimen of *E*. cf. *antarctica* of Li (1990) lacks ovicells; the Early Miocene occurrence in France is thus not proven.

In the Recent Mediterranean, *E. gautieri* may be found in caves in very shallow water. Gautier (1962) reported it on *coralligène* blocks from 40 m depth, and thus from a similar environment as suggested for the formation of the Niebla Calcarenite.

Distribution:

Miocene: ?Burdigalian (France), Tortonian (Guadalquivir Basin – Spain), Messinian (Algeria). Plio-Pleistocene: Italy.

Recent: Western Mediterranean (and Adriatic Sea), NW Spain, western English Channel.

Family HIANTOPORIDAE GREGORY, 1893 Genus HIANTOPORA MACGILLIVRAY, 1887

Hiantopora rostrata comb. nov. (MOISSETTE, 1988) Plate 2, Figure 2-4, 7

1988 Arachnopusia rostrata MOISSETTE, p. 90, pl. 15, fig. 1, 4.

Material:

Niebla Calcarenite: 11 colonies.

examined by SEM: GNI1-A, C, D, E, F.

FSL 119074 (holotype of H. rostrata, Messinian, Algeria; Moissette, 1988, pl. 15, fig. 1, 4).

other: FSL 119061 (A. rostrata, Messinian, Algeria; Moissette, 1988); 115906 (T. radicifera, Pliocene, SE Spain; Pouyet, 1976); 119480, 119535 (T. radicifera, Messinian, Algeria; Moissette, 1988).
BNHM 99.5.1.625A (lectotype of H. radicifera [Hincks, 1881], Recent, Bass Strait; chosen

by Brown, 1958).

VNHM 1848.38.57 (lectotype of *E. bipunctata* Reuss, 1848, Badenian, Eisenstadt; chosen by David & Pouyet, 1974); 1859.50.756 (*T. radicifera*, Badenian, Eisenstadt; Vávra, 1980, pl. 1, fig. 3, 5).

Measurements:

ZL $488 \pm 66, 371-636 (5, 17)$ ZW $409 \pm 62, 330-591 (5, 17)$ OpL $318 \pm 42, 276-409 (4, 14)$ OpW $245 \pm 35, 194-305 (4, 14)$

Description:

Colony encrusting unilaminar, multiserial, fixed to the substrate by five to six dorsal rhizoids per zooid. Autozooids round to oval, separated by more or less distinct grooves but usually not visible when all spines are preserved, with few, large, irregularly shaped pores at or near zooid boundaries; gymnocyst and cryptocyst smooth, reduced to a thin band, the latter steeply inclined towards zooid centre; opesia large, round or pyriform with a rather straight, narrow, distal margin. The zooid margin is raised distally and carries a pair of thick, hollow, spinous processes at the distal end, which bifurcate at least once; another larger spinous process emerges from one lateral zooid wall just proximal of the distal pair, which bifurcates some five times while branches become thinner distally, arching over the opesia leaving free the distalmost part only. On the opposite zooid wall a large complex of spines is formed by a protuberance of the lateral wall at the proximal end of an adventitious avicularium, again bifurcating some five times into successively thinner branches, covering the central and proximal part of the opesia, leaving open only oval or round spaces between branches; merging with some branch tips of the opposite spine may occur.

Ovicell partly resting on proximal wall of the distal zooid, about as long as wide, hemispherical, with parallel proximolateral walls and a straight proximal margin; ectoecium(?) forming a smooth lateral cover around a large, nodular and only slightly convex frontal area formed by the entoecium(?).

An adventitious avicularium is formed in the distal half of either one of the lateral zooid walls, pointing and incurving distally, and being slightly obliquely positioned to colony surface, thus paralleling the trend of the lateral zooid wall; cystid elongated triangular, widest at about one-third of total length where internal and external thickening marks the hinge-points for the rostrum, tapering distally; another short (bifurcating?) spine protrudes from the distolateral external cystid wall of avicularium.

Discussion:

Apart from some differences in shape of the bifurcating spinous processes, the present material is identical to the (type)specimens described by Moissette (1988). Slight variations in branching angle and branch thickness of the large protuberance, which covers most of the opesia, lead to larger and rounder 'pores' in the Algerian material. However, a certain range of flexibility in formation of this spinous process was also observed in the Niebla specimens and may reflect genetic differences between populations (although this is not much more than a guess because virtually nothing is known about intraspecific variability in Recent *Hiantopora* spp.). Nevertheless, the zooidal dimensions, the shape of the large lateral avicularium, and the morphology of ovicells are similar. Ovicells were originally not described by Moissette (1988) but were observed in the holotype during re-examination.

The species is here transferred to *Hiantopora* owing to the development of the frontal opesial cover by a spinose process. In contrast, in *Arachnopusia* Jullien, 1888 the frontal membrane is entirely covered by a porous umbonuloid shield.

Until Moissette described *H. rostrata* in 1988, only a single species of *Hiantopora*, *H. radicifera* (Hincks, 1881), was reported from the Mediterranean basin and the Paratethys (as *Tremopora radicifera*). Without viewing the type-material, David & Pouyet (1974) synonymised *Eschara bipunctata* Reuss, 1848 with the Recent *H. radicifera*, although the type-location of the latter is Bass Strait (see below). After having seen both types of *E. bipunctata* and *H. radicifera*, I suggest that Reuss' species is not conspecific with the Recent *H. radicifera* from the South Pacific and that the name *Hiantopora bipunctata* should be re-established. Furthermore, the whole genus *Hiantopora* in the Neogene Mediterranean and Atlantic region is in need of revision since, judging from the material viewed, it is very much likely that there are several species combined under the name '*Tremopora radicifera*'. Unfortunately, in much of the material the spinous processes are broken off or are incompletely preserved, which hampers a precise description and identification.

Occurrence:

Recent species of the genus *Hiantopora* are most often recorded from tropical waters (Indian Ocean, western Pacific) but some do occur in warm-temperate waters off southern Australia from where *H. radicifera* was originally described. However, since there are no records of extant Atlantic species, the Late Miocene Mediterranean and Paratethyan taxa are likely to be remnants of times when the connection to the Tethys was still in existence.

Unilaminar species usually form basal rhizoids (Pl. 2, Fig. 7) that may reach at least seven times the length of an autozooid, whereas there are up to ten rhizoids per zooid, thus forming a thick tuft of anchoring devices. These rhizoids allow the colony to encrust hard substrate as well as to attach to sandy or silty mobile sediment, as is the case in *H. radicifera* from Bass Strait. In the Niebla Calcarenite, only a few colonies of *H. rostrata* were found, encrusting red algae and other bryozoans. However, while most colonial fragments are found unattached, evidence for attachment on loose substrates, such as trapped sediment beneath the basal wall, is absent.

Unfortunately, Sefian et al. (1999) did not figure the specimens from the Late Miocene of NW Morocco they referred to *Tremopora radicifera*. Only based on their description, it is not possible to conclude whether one or two species of *Hiantopora* are present in the Late Miocene eastern Atlantic.

Distribution:

Miocene: Tortonian (Guadalquivir Basin - Spain), Messinian (Morocco).

Superfamily FLUSTROIDEA FLEMING, 1828 Family FLUSTRIDAE FLEMING, 1828 Genus HINCKSINA NORMAN, 1903

Hincksina sp.

Plate 2, Figure 5, 6

Material:

Niebla Calcarenite: 4 colonies. examined by SEM: GNI1-048-A, B.

other: VNHM 1867.40.260 (lectotype of *Callopora fenestrata* [Reuss, 1848], Badenian, Eisenstadt; chosen by David & Pouyet, 1974).

Measurements:

Description:

Colony encrusting unilaminar, multiserial. Zooids elongated oval to subrectangular, separated by deep grooves; gymnocyst smooth, well developed proximally; cryptocyst confined to a relatively broad opesial margin; opesia oval, occupying about three quarter of total zooid length. Sockets of about 12 spines badly preserved and barely visible on zooid margin.

Rudiments of immersed ovicells my be present but not well enough preserved to prove their existence.

Interzooidal avicularia in distal position to most zooids, of variable size; cystid quadrangular, smooth; rostrum oval or broadly and rounded triangular, sometimes parallel-sided, usually directing distolaterally, sometimes distally; no crossbar.

Discussion:

Due to the absence of prominent ovicells and the presence of interzooidal avicularia I choose to place this species in the genus *Hincksina*. It is different from the extant *H. flustroides* (Hincks, 1877) and its varieties occurring in the Mediterranean Sea (see Zabala & Maluquer, 1988; Hayward & Ryland, 1998), in that the gymnocyst of the latter is distinctly less developed than in the Niebla specimens. The fossil *H. loxopora* (Reuss, 1848) is, in turn, marked by larger, elongate triangular interzooidal avicularia, and its gymno- and cryptocysts are also less developed than in the present material (see David & Pouyet, 1974).

The most similar species is the one described as *Callopora fenestrata* (Reuss, 1848) by Moissette (1988) and El Hajajji (1992). Gymnocysts and cryptocysts are equally well developed and the interzooidal avicularia have an oval rostrum. Both report the presence of semicircular endozooidal ovicells with the proximal margin slightly raised above frontal plane. Since their presence in the specimens from Niebla can not be unambiguously demonstrated, more and better preserved material needs to be screened before a statement on the relationship of both species can be given. In any case, the species described as *Callopora fenestrata* by Moissette (1988: p. 79, pl. 12, fig. 8, 9) and El Hajajji (1992: p. 94, pl. 4, fig. 7) is different from the type-specimen VNHM 1867.40.260 of *C. fenestrata* chosen by David & Pouyet (1974: p. 105, pl. 1, fig. 5, 7). The latter has prominent ovicells with a strongly concave to almost triangular aperture, whilst autozooids are more elongated and narrower, and the gymnocyst of both autozooids and avicularium cystid is less developed. Moissette's (1988) and El Hajjaji's (1992) species are thus neither conspecific with *C. fenestrata* nor do they belong to the genus *Callopora* Gray, 1848 but to *Hincksina* instead, due to the presence of endozooidal ovicells and interzooidal avicularia.

Occurrence:

The colonies encrust red algae and other encrusting unilaminar bryozoans.

Superfamily BUGULOIDEA GRAY, 1848 Family CANDIDAE D'ORBIGNY, 1851 Genus SCRUPOCELLARIA VAN BENEDEN, 1845

Scrupocellaria sp. Plate 2, Figure 9-11

Material:

Niebla Calcarenite: >30 internodes. examined by SEM: GNI1-A, B, C, D, E, F, G, H, I, J, K, L.

other: VNHM 1859.50.735 (lectotype of *Bactridium granuliferum* Reuss, 1848, Badenian, Eisenstadt; chosen by David & Pouyet, 1974); 1878.11.11 (several specimens of '*S. elliptica*' Reuss, 1848, Badenian, Eisenstadt; figured by Reuss, 1974, pl. 11, fig. 2, 4, 9).

Measurements:

Description:

Colony erect flexible, biserial with alternating zooids, dichotomously branching; flat branches composed of 10 zooids. Zooids separated by thin grooves taking a zigzag course visible on both ventral and dorsal side; gymnocyst convex, smooth; opesia oval, comprising almost two-thirds of zooid length, with narrow border of cryptocystal calcification; a pair of large distolateral septula

visible in a broad, sloping, distal opesial margin. Four spines on outer opesial margin and two on inner margin plus base of scutum proximal to these.

Ovicell domed, semi-immersed in distal zooid, completely occupying proximal gymnocystal part of it, broader than long and broader near the branch axis thus forming an oblique proximal margin sloping towards the median line, distal edge rather straight and abutting the proximal part of proximal cryptocyst of distal zooid, influencing its shape; small avicularium situated on distal corner towards the median line, extending across the longitudinal branch axis and abutting neighbouring zooid, directed perpendicular to growth direction towards neighbouring zooid, rostrum plane facing distally; number of spines and position of scutum in ovicellate zooids same as in autozooids.

Each zooid with prominent distolateral avicularium projecting distinctly from branch margin at an angle of ca. 40°; rostrum distally hooked, rostrum plane facing distally. Small, frontal, adventitious avicularium frequently present on autozooids, proximal to opesia close to branch axis; short triangular rostrum perpendicular to growth direction, directing towards branch margin, rostrum plane facing more or less distally.

A small vibraculum at outer proximal corner of each zooid, setal groove long and curved; two of such on axil of dichotomy.

Discussion:

Surprisingly, only three fossil species of *Scrupocellaria*, namely *S. elliptica* (Reuss, 1848), *S. scrupea* Busk, 1851 and *S. scruposa* (Linné, 1758), are reported in recent works on late Neogene Bryozoa, whereas today at least eight species are known to occur in the Mediterranean Sea, including *S. scrupea* and *S. scruposa* (Zabala & Maluquer, 1988). This disparity is partly due to poor preservation of fossil *Scrupocellaria*, in which case, particularly in the absence of the scutum, a found classification is difficult or impossible to achieve. However, reviewing the Reuss Collection, Schmid (1989) concluded that many specimens have been wrongly assigned to *S. elliptica* as a consequence of insufficient description and illustration. This is definitely true; yet, and even more surprising, it is not clear how '*S. elliptica*' is exactly defined. There are uncertainties about the *locus typicus* of the specimen David & Pouyet (1974) chose as the type (see Schmid, 1989), and, in my opinion, too many distinct species described and figured by Reuss (1848, 1874) have been synonymised with '*S. elliptica*' by, among others, David & Pouyet (1974) and Schmid (1989).

For instance, Reuss (1848: 56) described and figured (pl. 9, fig. 7 and, with cutbacks, fig. 8) Bactridium ellipticum as having a "very large, vertical, at times long, rarely broadly elliptical" opesia and he did not mention the presence of spines. The broadly elliptical specimens may be represented in fig. 8 on pl. 9; whether or not this is a related or distinct species I can not say at this stage. In contrast, B. granuliferum is characterised by "large, semielliptical" opesia (semielliptical due to the presence of a broad, distal, suboral shelf, as shown in the figure) and the presence of four 'tubercles' or 'hunches', i.e. spine bases and scutum (p. 56, pl. 9, fig. 6). Similar morphologies are found in the specimens Schmid (1989) figured as 'S. elliptica': the specimen of fig. 1 on pl. 5 is well preserved and has elongated elliptical opesia, while spines are seemingly absent. This is also the case in the specimen of B. ellipticum Reuss (1848) figured on pl. 9 (fig. 7). In contrast, the specimen depicted in Schmid's (1989) fig. 2 (pl. 5) displays more broadly elliptical opesia and the presence of three (or four?) outer spines and one inner spine (plus scutum) on its distolateral opesial margins. It seems to me, therefore, that the species originally described by Reuss (1848) as B. ellipticum is different from most of the species ascribed to 'S. elliptica' in that it lacks spines, and may therefore be similar to, or identical with, the specimen depicted on pl. 5, fig. 1 in Schmid (1989).

Thus, judging from personal observation of some of the Reuss material, and also owing to the great discrepancies in descriptions and illustrations of species assigned to '*S. elliptica*' and the other two species mentioned, a revision of Neogene *Scrupocellaria* spp. in the Mediterranean basins and the selection of type-specimens is overdue. Since none of the figured and described specimens in the literature checked agrees in all of the characters displayed by the Niebla material, these specimens may represent a new species.

Occurrence:

Due to the taxonomic problems specified above the stratigraphic and geographic species ranges of all fossil *Scrupocellaria* spp. have to be considered as not reliable.

Scrupocellaria sp. is common in the Niebla Calcarenite, but most likely the only representative of the genus.

Superfamily MICROPOROIDEA GRAY, 1848 Family MICROPORIDAE GRAY, 1848 Genus MICROPORA GRAY, 1848

Micropora cf. *coriacea* (JOHNSTON, 1847) Plate 2, Figure 13

cf. 1847 Flustra coriacea JOHNSTON, p. 349, pl. 56, fig. 8.

cf. 1988 Micropora coriacea (JOHNST.) – Moissette, p. 93, pl. 14, fig. 9.

cf. 1988 Micropora coriacea (JOHNST.) – Zabala & Maluquer, p. 90, fig. 125.

cf. 1992 Micropora coriacea (JOHNST.) - Pouyet & Moissette, p. 40, pl. 4, fig. 9.

cf. 1998 Micropora coriacea (JOHNST.) - Hayward & Ryland, p. 288, fig. 97; fig. 99C, D.

cf. 1999 Micropora coriacea (JOHNST.) – Sefian et al., p. 230.

Material:

Niebla Calcarenite: 1 colony. examined by SEM: GNI1-075-A. other: BNHM 47.9.18.129 (lectotype, Recent, Great Britain; chosen by Brown, 1952, p. 52).

Measurements:

ZL $426 \pm 28, 380-474 (1, 8)$ ZW $319 \pm 43, 253-401 (1, 8)$ OpL $61 \pm 1, 59-62 (1, 6)$ OpW $106 \pm 8, 95-114 (1, 6)$

Description:

Colony encrusting unilaminar, multiserial. Zooids with a flat frontal surface, elliptical or polygonal in outline, separated by shallow indistinct grooves. Lateral walls thin, slightly raised, increasingly so towards the distal end of zooid, forming a rim around frontal surface. Cryptocyst finely ?granular and perforated by numerous small pores, flat and level with wall of zooid proximally, sloping and becoming slightly convex distally towards the opesiules, then rising towards the opesia where it forms its straight proximal edge. Opesiules placed in slightly different positions close to the lateral walls, either just below opesia or closer to zooid centre. Opesia slightly raised, semicircular, distinctly broader than long with a straight or slightly concave proximal margin. No spines.

Ovicells and avicularia were not observed.

Discussion:

Although otherwise indistinguishable from the autozooids of the lectotype of Recent *M. coriacea*, the Niebla specimens appear to have larger opesiules and the cryptocyst seems to lack the coarsely granular surface structure. Both differences are here interpreted to result from mechanical abrasion of the superficial layer of secondary calcification which is absent in many fossil specimens (see also *Escharoides coccinea* [Abildgaard, 1806]). However, since ovicells are unfortunately not preserved in the present material the Niebla specimens are merely conferred to *M. coriacea*.

Occurrence:

Recent *M. coriacea* occurs on shells and rocky substrates from the shallow sublittoral to deep shelf waters in all warm temperate regions of Europe. In the Mediterranean it is present from about 30 to 100 m depth. However, the record of a vast chronostratigraphic range (Eocene to Recent), geographical distribution (worldwide), and depth of occurrence (0 to 800 m), as can be found in various publications (e.g. Pouyet & Moissette, 1992), give reason to assume that several species were referred to as *M. coriacea*, which can be ascribed to the relatively simple morphology of this species. I therefore refrain from giving an overview of its chronostratigraphic and biogeographic range.

In the Niebla Calcarenite only a single specimen was found encrusting a red alga.

Genus MOLLIA LAMOUROUX, 1816

Mollia circumcincta (HELLER, 1867) Plate 2, Figure 14, 15

1867 Membranipora circumcincta HELLER, p. 96, pl. 6, fig. 5.

- v pars 1988 Mollia patellaria (MOLL) Moissette, p. 83, pl. 13, fig. 3, 6.
 - 1988 Mollia circumcincta (HELLER) Zabala & Maluquer, p. 92, fig. 130; pl. 2, fig. C, D.
 - 1992 *Mollia circumcincta* (HELLER) Alvarez, p. 285, fig. 9a.
 - 1992 *Mollia multijuncta* (WATERS) Alvarez, p. 288, fig. 9b.
 - 2002 Mollia circumcincta (HELLER) Hayward & McKinney, p. 34, fig. 13 D-H.

Material:

Niebla Calcarenite: 9 colonies. examined by SEM: GNI1-003-B, C; GNI1-050-C; GNI1-063-A. FSL 119076 (Messinian, Algeria: Moissette, 1988, pl. 13, fig. 3, 6).

Measurements:

ZL $319 \pm 26, 282-362 (3, 19)$ ZW $204 \pm 33, 151-271 (3, 19)$ OpL $74 \pm 12, 63-95 (2, 6)$ OpW $117 \pm 12, 104-139 (2, 6)$ OvL $91 \pm 5, 83-97 (1, 8)$ OvW $166 \pm 3, 161-170 (1, 8)$

Description:

Colony encrusting unilaminar, multiserial, fixed to the substrate by dorsal rhizoids. Zooecia oval, disjunct, linked to one another by 11 to 14 thick connecting tubes, frontal surface only slightly convex; granular lateral wall thin and only very little raised proximally, becoming thicker, crenulate and more elevated in the distal part around the opesia. Cryptocyst granular or nodular, imperforate, comprising about two-thirds of zooid length, slightly depressed distally towards the opesia. Opesia semielliptical, broader than long, with a concave proximal border accentuated by two opesiular indentations at each corner. Basal wall with approximately 14 small, mostly lateral pits marking the emplacement of dorsal rhizoids; just distal to the zooids' mid-distance the basal wall is divided by a concave, low but prominent ridge of calcification directing distally. No spines.

Ovicells partially immersed in distal zooid, crescent, with a slightly convex frontal surface, distolateral zooid wall discontinuous with proximal ovicell margin (a short denticle is produced by incurving lateral walls); frontal wall granular, perforated by two proximolateral pores.

Avicularia or kenozooids were not observed.

Discussion:

Zooid and ovicell morphology of the present material perfectly matches with that of the neotype of *Mollia circumcincta* depicted in Hayward & McKinney (2002). Especially the ovicell is characteristic of this species that has, especially so in the fossil record, not often been cited.

The figured specimen and most of the remaining material Moissette (1988) identified as *M. patellaria* (Moll, 1803) is, in fact, *M. circumcincta*, as is evident from the large number of connecting tubes, the shape of the opesia, and the semi-immersed crescent ovicell (*M. patellaria* has a prominent globular one). The two proximolateral pores in the ovicell (Pl. 2, Fig. 15) are also clearly visible in Moissette's (1988) and in the type-material. However, in case the zooids are closely spaced and ovicells are absent, this species may be mistaken with *Rosseliana rosselii* (Audouin, 1826), which has a similar zooid and opesia shape but broods the larvae internally, indicated by a mere shallow crescent cap at the distal end of fertile zooids.

The calcified ridge on the basal wall, here reported for the first time, is a peculiar structure of an unknown function (Pl. 2, Fig. 15). It's presence and purpose needs to be verified and examined in Recent material.

An extremely confusing case concerns the distinction between M. circumcincta, M. patellaria and *M. multijuncta* (Waters, 1879). The latter has been considered by different authors as a variety of both *M. patellaria* (e.g. Zabala & Maluquer, 1988) and *R. rosselii* (Ryland & Hayward, 1977). After Zabala & Maluquer (1988) it is characterised by a greater number of connecting tubes (8-12) than *M. patellaria* (6-8) but is reported to have similarly large round ovicells. Alvarez (1992) regarded M. multijuncta as being morphologically similar to M. circumcincta and discriminates both species by differences in the number of connecting tubes (7-11 in M. circumcincta; 12-14 in *M. multijuncta*) and zooid size (mean zooid length 466 µm in *M. circumcincta*; 396 µm in *M. multijuncta*), whereas he did not describe ovicells. The present material has an even smaller mean zooid length value (319 µm; 410 µm in material of Hayward & McKinney, 2002) than M. multijuncta of Alvarez (1992) but a similar autozooid shape and range of numbers of connecting tubes, and the ovicells are clearly those of *M. circumcincta*. I therefore assume (1) that there exists a (?sub-, ?distinct) species related to M. patellaria, as evidenced by a similar ovicell, that has a comparatively greater number of connecting tubes (the form described by Zabala & Maluquer [1988] as *M. patellaria* var. *circumcincta*), and (2) that (besides surface texture and opesia shape) zooid size and the number of connecting tubes in *M. circumcincta* is subject to great intraspecific variation and includes the form described as M. multijuncta by Alvarez (1992). However, the latter assumption is based on similarity of autozooids only whereas ovicell shape needs to be verified in his material. Also, ovicell morphology in the species from New Zealand described as M. multijuncta by Gordon (1984) clearly shows that this form is distinct from all Mediterranean/European taxa.

Furthermore, the ovicells of *M. circumcincta* as described and figured by Zabala & Maluquer (1988) are characterised by a smooth, broad, proximolateral cover that does not agree with the ovicell morphology of the neotype. However, it appears that the specimen on their pl. 2, fig. D was not bleached before the SEM photo was taken and that, possibly, adherent organic tissue may be responsible for this 'artefact'. Nevertheless, if it turns out that the conspicuous ovicell cover is calcified these specimens may represent a distinct species.

Occurrence:

M. circumcincta is reported to occur from 25 to 80 m water depth in the Mediterranean Sea where it, as *M. patellaria* by means of dorsal rhizoids, mostly encrusts red algae. The same substrate was chosen by the specimens found in the Niebla Calcarenite.

To my knowledge, neither in the fossil nor Recent has *M. circumcincta* been recorded from Atlantic waters before. Furthermore, although only a few specimens are present in the Niebla Calcarenite, this finding represents the earliest occurrence of this species, while there are no Pliocene or Pleistocene records.

Distribution:

Miocene: Tortonian (Guadalquivir Basin – Spain), Messinian (Algeria). Recent: Mediterranean.

Mollia patellaria (MOLL, 1803)

Plate 2, Figure 8, 12

- 1803 Eschara patellaria MOLL, p. 68, pl. 4, fig. 20.
- 1848 Cellepora formosa REUSS, p. 95, pl. 11, fig. 18.
- ? 1921 Floridinella formosa (REUSS) Cipolla, p. 47, pl. 2, fig. 8-10.
- v 1974 Floridinella formosa (REUSS) David & Pouyet, p. 117, pl. 1, fig. 3, 4.
- 1988 Mollia patellaria (MOLL) Zabala & Maluquer, p. 92, fig. 129.
- pars 1988 Mollia patellaria (MOLL) Moissette, p. 83, pl. 13, fig. 3, 6.
 - 1989 Mollia patellaria (MOLL) Schmid, p. 18, pl. 3, fig. 1-7.
 - 1992 Mollia patellaria (MOLL) El Hajjaji, p. 109, pl. 5, fig. 12.
 - ? 1992 Floridinella formosa (REUSS) Pouyet & Moissette, p. 41, pl. 4, fig. 12.
 1997b Mollia patellaria (MOLL) Pouyet, p. 40, pl. 3, fig. 7, 8.

Material:

v

Niebla Calcarenite: 5 colonies.

examined by SEM: GNI1-003-A; GNI1-018-A.

other: FSL 118261 (Messinian, Morocco: Moissette, 1988). BNHM 1975.7.1.32 (Recent, Chios). VNHM 1867.11.166 (lectotype of *Floridinella formosa* [Reuss, 1848], Badenian,

Eisenstadt; chosen by David & Pouyet, 1974, pl. 1, fig. 3, 4).

Measurements:

 $\begin{array}{lll} ZL & 359 \pm 19,\, 339{-}380\,(1,\,5) \\ ZW & 240 \pm 21,\, 218{-}267\,(1,\,5) \\ OpL & 113 \pm 6,\, 105{-}121\,(1,\,5) \\ OpW & 109 \pm 8,\, 101{-}121\,(1,\,5) \end{array}$

Description:

Colony encrusting unilaminar, multiserial, fixed to the substrate by dorsal rhizoids. Zooecia oval, disjunct, linked by six or seven thick, jointed connecting tubes (one per neighbouring zooid); granular lateral wall raised, becoming increasingly thicker and more elevated distally. Cryptocyst extensive, granular, slightly depressed distally. Opesia measuring about one-third of the zooid length, very pronounced, bell-shaped with a straight or slightly concave proximal margin and two stout, rounded, prominent denticles demarcating the proximal from the distal part.

Ovicells and kenozooids were not observed.

Spines and avicularia absent.

Discussion:

Due to the variation in the spacing between zooids, and its variability in zooid and opesia shape, this species may be confused with *Rosseliana rosselii* (Audouin, 1826) (see also Discussion in *Mollia circumcincta* [Heller, 1867]). Besides the presence and number of connecting tubes, other features by which *M. patellaria* can be distinguished from *R. rosseliana* and *M. circumcincta*, respectively, are the prominent denticles and thus the characteristic trifoliate shape of the opesia. However, opesia shape (as a result of varying concavity of its proximal margin and size of denticles) may vary considerably (Schmid, 1989) and a semielliptical opesia, which is characteristic of *R. rosseliana* and *M. circumcincta*, may therefore occur in some zooids and colonies of *M. patellaria*.

A detailed history and extended discussion of some fossil and Recent species that fall into synonymy with *M. patellaria* was given by Schmid (1989), including *Floridinella formosa* (Reuss, 1848). However, in the specimens described and figured as *F. formosa* by Cipolla (1921) and Pouyet & Moissette (1992) the zooids are "généralement non jointives", the zooid shape is angular and margins directly adjoined to neighbouring zooids, and opesial denticles are lacking. This species is therefore different from the lectotype in several aspects and may form an intermediate species between the genera *Mollia* and *Rosseliana* Jullien, 1888, also because Cipolla (1921)

figures a prominent ovicell (pl. 2, fig. 8). Clearly, more information about intraspecific variation in Recent *Mollia* and *Rosseliana* needs to be gathered to define species and higher taxon boundaries to interpret better the great range of morphological variation seen in the fossil record.

The specimens identified by Moissette (1988) as *M. patellaria* only partly belong to this species, owing to the presence of globular ovicells and trifoliate opesia; however, most of the material comprises specimens of *M. circumcincta* (see Discussion there).

Occurrence:

In the Mediterranean Sea *M. patellaria* occurs on pebbles, shells and coralline algae in depth of 20 to 300 m (may occur shallower in caves) with an optimum between 30-80 m. The basal rhizoids, that may reach a zooid's length (pers. observation), are presumably not only means by which this species attach to hard substrates but may also function as anchors on and in soft substrates like microbial or algal mats. In a dried Recent sample from Malta (from a cave at ca. 5 m depth, Moissette Collection) a colony was observed to bridge a gap in substrates, hanging 'freely' between settling surfaces with the rhizoids not reaching firm ground (but possibly penetrating a microbial mat not preserved in the dried sample).

In the present material, the colonies encrust coralline algaa, leaving some 40 μ m of space between the algal surface and the zooid's basal walls (Pl. 2, Fig. 8).

Since *M. patellaria* is not known as a fouling species, the almost worldwide distribution (see below) needs to be questioned. The absence of records from the Spanish and French coasts suggests instead that this species may be restricted to the Mediterranean Sea and the West African coast. Nevertheless, the (rare) presence in the Niebla Calcarenite marks the first fossil record of this species outside the Mediterranean basin.

Distribution:

Miocene: Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin and SE Spain), Messinian (Algeria, Morocco).

Pliocene: Italy.

Pleistocene: Nigeria.

Recent: Mediterranean, NE Atlantic (African coast), ?NW Atlantic (Gulf of Mexico), ?Pacific Ocean (Australia, California, Mexico).

Family ONYCHOCELLIDAE JULLIEN, 1882 Genus ONYCHOCELLA JULLIEN, 1882

Onychocella cf. *angulosa* (REUSS, 1848) Plate 3, Figure 4

- cf. 1848 Cellepora angulosa REUSS, p. 93, pl. 11, fig. 10.
- cf. 1964 Onychocella angulosa (REUSS) Cook, p. 68, fig. 11.
- cf. 1979a Onychocella angulosa (REUSS) Vávra, p. 597, pl. 2, fig. f, g.
- cf. 1988 Onychocella angulosa (REUSS) Moissette, p. 91, pl. 14, fig. 5.
- cf. 1988 Onychocella marioni (JULLIEN) Zabala & Maluquer, p. 87, fig. 108; pl. 2, fig. A.
- cf. 1989 Onychocella angulosa (REUSS) Schmid, p. 13, pl. 1, fig. 4, 5.
- cf. 1992 Onychocella angulosa (REUSS) Pouyet & Moissette, p. 40, pl. 4, fig. 8.
- cf. 1993 Onychocella angulosa (REUSS) Moissette et al., p. 93.
- cf. 1996 Onychocella angulosa (REUSS) Haddadi-Hamdane, p. 62, pl. 4, fig. 5.
- cf. 1999 Onychocella angulosa (REUSS) Sefian et al., p. 230.

Material:

Niebla Calcarenite: 27 colonies. examined by SEM: GNI1-020-A; GNI1-075-A.

Measurements:

ZL	445 ± 43, 384–521 (1, 20)
ZW	$404 \pm 39, 314 - 465 (1, 20)$
OpL	136 ± 16, 98–167 (1, 20)
OpW	$141 \pm 17, 111 - 172 (1, 20)$
OnL	449 ± 48, 395–517 (1, 6)
OnW	261 ± 61, 198–371 (1, 6)

Description:

Colony encrusting multiserial, unilaminar. Autozooids oval, polygonal or hexagonal, separated by distinct grooves. Cryptocyst well developed, finely but densely grained surface, depressed towards the zooid center; gymnocyst absent. Opesia variable in shape, usually D-shaped with either straight, slightly convex or concave proximal border, sometimes forming two short indentations in proximolateral corners; distal border occasionally with a slightly submersed, short but broad, blunt denticle.

No ovicells.

Vicarious avicularia of various size, modified as asymmetric, falciform (sickle-shaped) onychocellaria, with long, curved, pointed rostrum and elongated, oval, avicularian opesia.

Discussion:

Schmid (1989) has discussed the taxonomic problems and mophological variability of this species/species complex in greater detail. However, without further information on intraspecific variability (genetic analyses may prove to be indispensable) and revision of Recent species of *Onychocella*, little substantial knowledge can be gained from the fossil record since this species displays so few morphological characters while at the same time showing a great range of (intraspecific) variation. The present specimens differ from the material figured in Schmid (1989) in that the opesia have a rather straight proximal border with occasionally two short indentations, whereas the opesia in Schmid's specimens have a concave proximal margin and are more or less bell-shaped. Yet these differences are regarded by her as being in the range of variation in the specimens from the type-location in Austria. Furthermore, the grooves marking the zooid boundaries are somewhat deeper and more pronounced in the present material.

Occurrence:

The Recent species *Onychocella marioni* Jullien, 1882 (= *O. angulosa*?) occurs in the circalittoral or, under certain conditions (cryptic, low current energy), in the infralittoral zone in the Mediterranean Sea. It has been reported from 0 to 80 m, with an optimum between 30 and 50 m.

Due to the above mentioned uncertainties on the specific status of *O. angulosa*, an explicit account on its chronostratigraphic and geographic distribution is not given here. Its first occurrence is suggested for the Eocene and today it is reported from basically all tropical to warm-temperate seas (Cook, 1964).

Family STEGINOPORELLIDAE HINCKS, 1884 Genus STEGINPORELLA SMITT, 1873

Steginoporella cucullata (REUSS, 1848) Plate 3, Figure 1, 5

- v 1848 *Cellaria cucullata* REUSS, p. 60, pl. 7, fig. 31.
- v 1974 Steginoporella cucullata (REUSS) David & Pouyet, p. 124, pl. 10, fig. 4.
- v 1974 Steginoporella manzonii DAVID & POUYET, p. 126, pl. 4, fig. 2, 3.
- 1979 Steginoporella cucullata (REUSS) Pouyet & David, p. 774, fig. 3; pl. 3, fig. 10.
- v 1979 Steginoporella manzonii D. & P. Pouyet & David, p. 786, fig. 3; pl. 4, fig. 7.
 - 1980 Steginoporella cucullata (REUSS) Vávra, p. 53, pl. 2, fig. 1, 2.
 - 1980 Steginoporella manzonii D. & P. Vávra, p. 55, pl. 2, fig. 4.
 - 1984 Steginoporella manzonii D. & P. Vávra, p. 229, pl. 2, fig. 4, 5.
 - 1988 Steginoporella cucullata (REUSS) Moissette, p. 98, pl. 16, fig. 2, 3.
 - 1992 Steginoporella cucullata (REUSS) El Hajjaji, p. 119.
 - 1992 Steginoporella manzonii D. & P. El Hajjaji, p. 121, pl. 5, fig. 9.
 - 1997b Steginoporella manzonii D. & P. Pouyet, p. 42, pl. 3, fig. 1, 2.
 - 1999 Steginoporella cucullata (REUSS) Sefian et al., p. 231.
 - 2000 Steginoporella cucullata (REUSS) Pouyet, p. 185, fig. 2L.

Material:

Niebla Calcarenite: 11 colonies.

examined by SEM: GNI1-013-A, B, C, D, E.

other: FSL 260595 (S. manzonii, Badenian, Porzteich; David & Pouyet, 1974); 260597 (S. cucullata, Badenian, Eisenstadt; Pouyet & David, 1979, pl. 3, fig. 10). VNHM 1859.19.150 (lectotype S. manzonii, Badenian, Porzteich; David & Pouyet, 1974, pl. 4, fig. 2, 3); 1859.50.747 (lectotype S. cucullata, Badenian, Eisenstadt; chosen by David & Pouyet, 1974); 1848.38.53 (2 syntypes of S. cucullata, Badenian, Mörbisch; chosen by David & Pouyet, 1974).

Measurements:

ZL 982 ± 59, 893–1080 (4, 20)

ZW 589 ± 72, 477–740 (4, 20)

OpL 246 ± 21, 209–292 (4, 18)

OpW 306 ± 37, 243–376 (4, 18)

Description:

Colony erect rigid, branching, branches cylindrical and oval in cross section, formed by alternating zooids in up to eight longitudinal series opening towards all sides (branches broader and composed of more than eight series at bifurcations). Zooids oval, large, separated by distinct sutures. Cryptocyst extensive, the central depressed area rugose, flat and evenly perforated by relatively large pores until mid-distance of zooid, then rising towards a slightly concave distal edge; this imperforate area contains two round opesiules (diameter ~42 μ m); the broad, proximolateral, gymnocystal rim abruptly rises at level with distal rim of the central cryptocyst, forming a prominent, broad, smooth and steep-sided hood around the distolateral opesia; no spines. Opesia broader than long, D-shaped with a slightly concave proximal border, occupying about one-fourth of zooid length. Reparative growth of underlying zooids, also forming reversed polarity intramural buds, is common.

Ovicells absent.

Dimorphic zooids (B zooids = avicularia) were not observed.

Discussion:

In 1974 David & Pouyet erected a new species, *Steginoporella manzonii*, to distinguish specimens with granular and crenellate proximolateral zooid margins, and seemingly smaller

opesia, from *S. cucullata* Reuss, 1848 which was thought to be characterised by a smooth zooid border and relatively larger opesia. This distinction is here rejected for the following reasons:

(1) the crenellate zooid margins can only be seen in very well preserved fossil material, as is the case in the holotype of *S. manzonii* (VNHM 1859.19.150), which has a shiny surface and shows no signs of physical abrasion. In fact, most specimens identified as *S. cucullata* by David & Pouyet (1974) and other authors thereafter are usually badly abraded (e.g., compare the figured specimens of *S. cucullata* in David & Pouyet [1974: pl. 10, fig. 4] and Pouyet [2000: fig. 2L] with those of *S. manzonii* in David & Pouyet [1974: pl. 4, fig. 2, 3]). The present material would, due to the apparently non-crenellate margin, be classified with *S. manzonii*. However, a closer look at the lower edge of the marginal rim, where it passes into the central granular cryptocyst, shows that the smooth superficial calcification visible on the central cryptocyst has broken away from the lateral margin in the Niebla material (Plate 3, Fig. 5). Even the rudiment of a crenellation of the marginal rim can be assumed be the wavy course of the fracture zone. Loss of superficial secondary calcification is commonly observed in fossil material (e.g., see *E. coccinea* [Abildgaard, 1806]) and is obviously also the case in some specimens of *S. cucullata*, which, if incidentally present, led David & Pouyet (1974) to erect a new species.

(2) A smaller opesia size in *S. manzonii* was also put forward as an argument for the distinction of the two forms by David & Pouyet (1974). In their original species description they included morphometrical data showing that opesia length in *S. manzonii* constitutes one-eighth of autozooid length. However, the figured specimens (e.g. their pl. 4, fig. 3), and the material I have seen, clearly show that this is not correct. Instead, opesia length comprises about one fourth of zooid length, as is the case in the present material. Contributing to this error is the fact that, since the more abraded specimens were classified as *S. cucullata*, chances are greater in this material that the distalmost cryptocystal rim is not preserved (this was also frequently observed in the Niebla specimens), which may give the appearance of a larger opesia in *S. cucullata* when measurements are taken using an optical microscope. A distinction between the two forms is, therefore, not justified and *S. manzonii* is regarded here as conspecific with *S. cucullata*.

The supposed B zooid in a specimen figured by Vávra (1984) is an unusually large one only because it is the last zooid in a series before it splits up into two series (two neighbouring zooids) distally, and does not appear to be an avicularium. These are obviously truly absent in *S. cucullata*. Zooid length does not seem to vary strongly between sites, as all published data cover almost the complete range from a minimum of 0.88 mm to a maximum of 1.23 mm.

Occurrence:

Almost all of the extant species of the genus *Steginoporella* live in tropical to subtropical waters, their common occurrence my therefore be indicative of warm palaeoenvironmental conditions.

After Sefian et al. (1999) reported the presence of *S. cucullata* in Late Miocene Atlantic waters, this is the second proof that this species also occurs west of the Rifian corridors and southern Spanish gateways before onset of the Messinian salinity crisis. However, *S. cucullata* has not been found in Pliocene sediments.

Distribution:

Miocene: Burdigalian (SE France), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin and SE Spain), Messinian (Atlantic and Mediterranean Morocco, Algeria).

Superfamily CELLARIOIDEA FLEMING, 1828 Family CELLARIIDAE FLEMING, 1828 Genus CELLARIA ELLIS & SOLANDER, 1786

Cellaria aff. melillensis EL HAJJAJI, 1987 Plate 3, Figure 2, 3, 6

aff. 1987 Cellaria melillensis EL HAJJAJI, p. 127, pl. 6, fig. 2.

Material:

Niebla Calcarenite: >20 colonies. examined by SEM: GNI1-054-A, B, C, D, E, F, G.

Measurements:

Due to indistinct zooid margins, measurements of zooid and avicularia length were taken from one distal opesial margin to the proximal zooid's distal opesial margin.

ZL $369 \pm 43, 326 - 484(5, 20)$ ZW 289 ± 12, 273–313 (5, 16) OpL $75 \pm 6,65 - 87(5,20)$ $105 \pm 8,89 - 119(5,20)$ OpW OvL 42-51(2,3)OvW 80-89(2,3)AL 395-447 (3, 3) OpL 149-172(3,3)AW 284-335 (3, 3) OpW 121–163 (3, 3)

Description:

Colony erect flexible, branching, consisting of rigid cylindrical internodes made up of alternating whorls of three to five non-contiguous autozooids (seven to ten autozooidal series), zooids in direct contact in longitudinal series only; internodes at least 3.5 mm long, with a diameter between 0.33 and 0.68 mm. Zooids elongated hexagonal with finely nodular calcification and prominent, finely beaded, longitudinal, cryptocystal ridges levelling proximally and distally, separated by shallow indistinct grooves. Cryptocyst inwardly-sloping, becoming planar proximal of opesia. Opesia wider than long, about one-fifth of autozooid length; opesial margin prominent, distal rim arched and finely beaded, proximal margin convex with a blunt denticle near each proximal corner, distal margin in some zooids with a narrow immersed shelf with two small lateral denticles.

Aperture of ovicell semicircular to rounded triangular, situated immediately distal to opesia, about twice as wide as long, partially occluded by a square plate extending from proximal edge.

Vicarious avicularia slightly longer and wider than the average autozooid. Distal margin crescentic, salient, levelling to zoarial plane at mid-length of zooid. Opesia large with horseshoe-shaped distolateral rim and strongly convex proximal margin.

Circular perforations for rhizoidal kenozooids open in proximal direction, i.e. oblique to frontal plane.

Discussion:

The Guadalquivir Basin specimens are similar to *C. melillensis* El Hajjaji, 1987 mainly due to their conspicuous avicularium (Pl. 3, Fig. 2). However, the ovicell apertures of the latter are described by Moissette (1988: p. 105, pl. 3, fig. 2; pl. 17, fig. 6, 7; as *C. sinuosa*?) as being circular (although preservation of the figured material is not excellent and this feature may be an artefact), whereas in my material these are clearly semicircular. Furthermore, in *C. melillensis* the proximal opesial rim in autozooids is occasionally extremely convex (almost rounded-triangular), which has not been observed to such an extent in the present material. In addition, the longitudinal series comprising an internode are more numerous (12 on average), but this character is also subject to

some variation in the present material. For these reasons I consider the Niebla specimens as being close to *C. melillensis* (see also El Hajjaji, 1992: p. 127, pl. 6, fig. 2) but not conspecific with it.

However, as discussed at length by Schmid (1989) for *Cellaria fistulosa* and *C. salicornioides*, most characters hitherto used to discriminate Recent species in *Cellaria* are either not applicable, or at least restricted, in fossil material (growth form, length of internodes), or show such a great interand intraspecific variation (internode diameter, number of longitudinal series, zooid outline and size) that a clear discrimination of species on these grounds is impossible. In order to document intraspecific morphological variability and thus to characterise eastern Atlantic and Mediterranean species, research on Recent *Cellaria* from different environments as well as a review of the Neogene to Recent material is indispensable.

Occurrence:

Cellaria aff. *melillensis* is common in the Niebla Calcarenite, but presumably the only representative of this genus.

Infraorder ASCOPHORINA LEVINSEN, 1909 "Grade" ACANTHOSTEGA LEVINSEN, 1902 Superfamily CRIBRILINOIDEA HINCKS, 1879 Family CRIBRILINIDAE HINCKS, 1879

Cribrilinidae gen. et sp. indet. Plate 3, Figure 11, 14

Material:

Niebla Calcarenite: 4 colonies. examined by SEM: GNI1-065-D.

other: FSL 117530 (holotype of *Cribrilina messiniensis*, Messinian, SE Spain: Pouyet & Moissette, 1986); 491867 (Messinian, Morocco: El Hajjaji, 1992), 491949 (Messinian, Morocco: El Hajjaji, 1992, pl. 6, fig. 17).

Measurements:

ZL $377 \pm 28, 336-436 (1, 11)$ ZW $305 \pm 27, 272-359 (1, 11)$ OL $50 \pm 2, 48-51 (1, 6)$ OW $85 \pm 5, 79-91 (1, 6)$ OvL 198 OvW 212 AL $61 \pm 7, 52-72 (1, 12)$ AW $40 \pm 6, 29-48 (1, 12)$

Description:

Colony encrusting unilaminar, multiserial. Zooecia ovoid, separated by deep grooves; frontal wall convex. Two or three pairs of distolateral pore chambers plus a single distal one, with the uncalcified external openings approximately as wide as calcification separating them. Lateral gymnocyst very narrow, slightly more extensive proximally. Frontal shield formed of nine to eleven costae. Costae raised, distinct, each with a thickened basal portion and a slightly raised tubercle; pelmatidium not readily identifiable due to recrystallisation. Four or, more commonly, five small intercostal pores between successive costae and a slightly larger papilla pore between costal bases. Secondary orifice broader than long with a thick semicircular distal rim carrying two short stout tubercles with oval bases; concave proximal edge formed by merging of two thickened and raised costal bars.

Ovicell relatively large, globular, about as long as wide, not associated with distal zooid (Type C ovicell of Bishop & Househam, 1987); frontal surface not preserved; a pair of tubercles proximolateral to ovicell margin.

Each autozooid has a pair of small distolateral avicularia at the level of orifice, their extremely marginal position and deep placement of the cystid suggest the origin from a pore chamber; rostrum a short triangle pointing distally to laterally.

Discussion:

The present specimens resemble the species identified as *Cribrilina messiniensis* Pouyet & Moissette, 1986 by El Hajjaji (1992: p. 134, pl. 6, fig. 17), although the latter may have up to 15 costae. However, while variability in the number of costae is likely to occur in species of the related genus *Puellina* Jullien, 1886 (see below), more of El Hajjaji's material would need to be examined by SEM for an unambiguous determination, and additional colonies would have to be recovered from the Niebla Calcarenite. While both these species may be conspecific, they are clearly distinct from the type specimen of *C. messiniensis*, which has an even greater number of costae (most commonly 16; up to 18) and intercostal pores (up to eight), and the gymnocyst is nearly absent.

The generic placement of these specimens is somewhat problematic. The presence of stout oral tubercles (fused spines?), instead of (jointed) slender spines, as well as the morphology and structure of the suboral bar, do not permit a classification within the genus *Puellina*. On the other hand, while stout tubercles and a similarly structured suboral bar may occur in the genus *Cribrilina* Gray, 1848 (e.g. Bishop, 1994), the frontal shield of the Niebla specimens rather resembles that of *Puellina* spp. The present material has therefore to be left in open nomenclature until an adequate circumscription of these genera and this species exists.

Occurrence:

This species was rarely encountered in the Niebla Calcarenite, encrusting coralline algae and, on one occasion, *Therenia montenati* Pouyet, 1976.

Distribution:

Miocene: Tortonian (Guadalquivir Basin - Spain), ?Messinian (Morocco).

Genus FIGULARIA JULLIEN, 1886

Figularia figularis (JOHNSTON, 1847) Plate 3, Figure 7, 10

- 1847 Lepralia figularis JOHNSTON, p. 314, pl. 56, fig. 2.
- 1988 Figularia figularis (JOHNSTON) Moissette, p. 110, pl. 18, fig. 2, 3.
- 1988 Figularia figularis (JOHNSTON) Zabala & Maluquer, p. 110, fig. 222; pl. 7, fig. H.
- 1992 Figularia figularis (JOHNSTON) Pouyet & Moissette, p. 49, pl. 6, fig. 8.
- 1992 Figularia figularis (JOHNSTON) El Hajjaji, p. 142, pl. 7, fig. 6.
- 1993 Figularia figularis (JOHNSTON) Moissette et al., p. 100.
- 1996 Figularia figularis (JOHNSTON) Haddadi-Hamdane, p. 77, pl. 6, fig. 1.

Material:

Niebla Calcarenite: 9 colonies. examined by SEM: GNI1-009-A; GNI1-010-C, D, E. other: BNHM 47.9.16.39 (holotype, Recent, Great Britain); 1975.7.1.32 (Recent, Chios).

Measurements:

ZL $594 \pm 52, 486-685 (3, 20)$ ZW $417 \pm 67, 313-565 (3, 20)$

OL	$108 \pm 11, 92 - 127 (3, 20)$
OW	$114 \pm 12, 92 - 130(3, 20)$
OvL	$325 \pm 16, 308 - 347 (2, 4)$
OvW	382 ± 32, 347–422 (2, 4)
AL	381 ± 35, 348–427 (2, 4)
AW	$183 \pm 14, 168 - 200(2, 4)$

Description:

Colony encusting, unilaminar, multiserial. Zooids elongate, oval to rectangular, flat or slightly convex, separated by shallow grooves. Gymnocyst smooth, a broad band laterally and may be extensive proximally and/or distally, enclosing the neighbouring zooid(s). Frontal wall of 10 to 14 broad tapered costae, each having a conspicuous pseudopore on the thickened marginal end, with the distal pair being the broadest forming an apertural bar; four intercostal pores between successive costae. Orifice large with a rounded-rectangular anter that is broader than long, separated from a semielliptical poster by a pair of short blunt condyles directed proximomedially; proximal rim curved and slightly raised.

Ovicell recumbent on or incorporated into distal zooid, prominent, globular; ectoecium with a longitudinal suture, sometimes forming a central umbo, and a large, oval, curved, vertical fenestra on each side.

Vicarious avicularia infrequent, smaller than autozooids, dumbbell-shaped, with the distal rostrum being broader than the part proximal to thick crossbar.

Discussion:

The present specimens are morphologically indistinguishable from the Recent species F. *figularis*, which is widespread in the Mediterranean Sea and is often found as a fossil as well. Whether or not this species is conspecific with the morphologically closely related F. *haueri* (Reuss, 1848) and F. *peltata* (Reuss, 1874) (see also David & Pouyet, 1974) can only be addressed by investigating the latter taxa using SEM, and by studying the range of morphological variation in Recent material. Whereas F. *haueri* seems to be different only in having larger avicularia (0.5-0.6 mm) and zooids (0.56-0.72 mm, David & Pouyet, 1974) than the present specimens, zooid size in other fossil F. *figularis* is subject to great variation, given that they are all the same species (Table 4.2). Therefore, although the Niebla material has distinctly smaller zooids than Recent and fossil Mediterranean F. *figularis* and F. *haueri*, the values are overlapping and a clear line, based on morphometry alone, cannot be drawn.

Source	Age	Location	Range	Mean
this work	Miocene	E Atlantic	0.49-0.69	0.59
Moissette (1988)	Miocene	NE Atlantic	0.56-0.82	0.68
Haddadi-Hamdane (1996)	Pliocene	Mediterranean	0.61-0.69	0.62
El Hajjaji (1992)	Miocene	Mediterranean	0.64-0.96	0.73
Hayward & Ryland (1998)	Recent	NE Atlantic	0.7-1.0	
Hayward & McKinney (2002)	Recent	Mediterranean	0.71-0.91	0.82

Table 4.2 Range and mean values of zooid length (in mm) of *F. figularis* given in several publications on Recent or fossil material.

Occurrence:

F. figularis is a warm-temperate water species, and has a wide depth distribution with an optimum in the Mediterranean between 30 and 90 m. Only a few specimens were found in the Niebla Calcarenite.

Distribution:

Miocene: Langhian-Serravallian (Italy), Tortonian (Guadalquivir Basin – Spain, Crete), Messinian (Morocco, Algeria).

Pliocene: Spain, Algeria, Italy, Great Britain.

Pleistocene: Italy.

Recent: Mediterranean, northeastern Atlantic (Canary Islands to Great Britain).

Genus GEPHYROTES NORMAN, 1903

Gephyrotes fortunensis POUYET, 2000 Plate 3, Figure 8, 9

1988 Gephyrotes sp. – Moissette, p. 112, pl. 18, fig. 8, 11.

2000 Gephyrotes fortunensis POUYET, p. 186, fig. i-k.

Material:

Niebla Calcarenite: 3 colonies. examined by SEM: GNI1-011-C.

FSL117925 (holotype, Tortonian, SE Spain; Pouyet, 2000, fig. i-k).

other: FSL 119779 (Messinian, Algeria; Moissette, 1988), 119849 (Messinian, Algeria; Moissette, 1988, pl. 18, fig. 8, 11).

Measurements:

ZL $540 \pm 55, 463-649 (1, 11)$ ZW $402 \pm 88, 325-636 (1, 11)$ OL $106 \pm 14, 82-124 (1, 7)$ OW $134 \pm 13, 119-151 (1, 7)$ OvL 238-243 (1, 2)OvW 276-312 (1, 2)

Description:

Colony encrusting unilaminar, multiserial. Zooids oval to polygonal, convex, separated by deep grooves. Gymnocyst smooth, usually a narrow band but may become extensive proximally. Frontal shield formed from eight to ten broad costae (not including the ones participating in the proximal apertural lip) with two round intercostal pores between them, setiform marginal papilla pores, and pelmatidia on the slightly thickened base and on most of the central areas of costal fusion; two additional distal pairs of thick hollow costae just proximal of and distolateral to the orifice are raised and merged above the orifice to form a projecting, spout-like, proximal lip to the aperture, with two elliptical lateral and a single, large, semicircular proximal pore as well as two small, central, intercostal pores. Secondary orifice D-shaped with a slightly curved proximal edge formed by the distalmost pair of frontal wall costae, little wider than long; no spines.

Ovicell globular, wider than long, incorporated into distal zooid (Type A ovicell of Bishop & Househam, 1987), with irregularly sized and spaced, uncalcified patches on the frontal surface. In ovicellate zooids the thick, tubular, distalmost pair of costae bifurcate to form the apertural lip with the proximal branch, and abuts to the proximal part of the ovicell with the distal branch, giving the appearance of a full circle when viewed from above.

The presence of adventitious avicularia can not be proven, although these may have been situated on some of the tubular constructions abutting the ovicell, in a lateral position, pointing proximomedially (however, this may represent an artefact if the upper part of the tubes has been broken off). Avicularia are lacking in autozooids.

Discussion:

Although I believe that the synonymies given above are coherent, there are some discrepancies in morphology and (original) species descriptions between the present specimens and the other material. In both the type-specimen and those of Moissette (1988), the gymnocyst is less developed compared to the Niebla specimens; however, the extensive gymnocystal development in the present material may merely be due to the colony encrusting a rather convex substrate. Furthermore, while Moissette mentioned the presence of up to 15 costae (he did not state whether he included the distalmost pair), several zooids in those colonies have as few as ten costae and are therefore in the range of the type- and present material, and are therefore considered here as intraspecific variation. When describing *G. fortunensis*, Pouyet (2000) mentioned and figured an ovicell "avec 2 fenêtres de chaque côté d'une crête médiane saillante" being present in the type-specimen. Yet, the two fenestrae and the median carina originated by breakage of this very ovicell. Other ovicells on the same specimen do show a normal globular morphology as in the Niebla material (pers. observation).

The presence of avicularia lateral to the orifice in ovicellate zooids described by both Moissette (1988) and Pouyet (2000), the former stating that these were pointing proximally while Pouyet mentioned a distal direction, can not be proven here. Instead, these may be an artefact of mechanical abrasion of the lateral tubes of the apertural lip (see Pl. 3, Fig. 8). When the frontal part of the tubular construction is broken in an oblique way (or only the lowermost part is preserved) these may give the appearance of a hollow pointed curvature, resembling an avicularium pointing proximomedially (or distally, respectively); however, since certain Recent species do show the presence of avicularia of precisely this shape (see below), their presence is not fully rejected here either.

G. fortunensis is quite similar to the Recent *G. nitidopunctata* (Smitt, 1868), which occurs in Arctic waters. However, in the latter the peripheral papilla pores have a slit-like form elongated parallel to the costae due to the absence of an outer row of costal fusion, and prominent avicularia are present on the lateral apertural lip in autozooids (see Hayward & Ryland, 1998).

Occurrence:

Although extremely rare, only three specimens were found encrusting coralline algae, the presence of *G. fortunensis* in the Niebla Calcarenite marks the first report of this species outside the Mediterranean.

Distribution:

Miocene: Tortonian (Guadalquivir Basin and SW Spain), Messinian (Algeria).

Genus PUELLINA JULLIEN, 1886

Puellina (Cribrilaria) cf. *radiata* (MOLL, 1803) Plate 3, Figure 12, 13

- cf. 1803 Eschara radiata MOLL, p. 63, pl. 4, fig. 17.
- cf. 1848 Cellepora scripta REUSS, p. 82, pl. 9, fig. 28.
- cf. 1970 Cribrilaria radiata (MOLL) Harmelin, p. 80, fig. 1a-c, 3a; pl. 1, fig. 1-3.
- cf. 1972 *Cribrilaria radiata* (MOLL) David et al., p. 30, pl. 9, fig. 3.
- non1979b Cribrilaria radiata (MOLL) Vávra, fig. 2.
- cf. 1987 Puellina scripta (REUSS) Bishop & Househam, fig. 98.
- non1987 Cribrilaria radiata (MOLL) Ziko & Hamza, p. 305, fig. 15.
- non1988 Cribrilaria aff. radiata (MOLL) Moissette, p. 108, pl. 18, fig. 6.
- cf. 1988 *Puellina* (*C*.) *radiata* (MOLL) Zabala & Maluquer, p. 107, fig. 214; pl. 7, fig. A, B.
- non 1988 Puellina (C.) scripta (MOLL) Zabala & Maluquer, p. 108, fig. 221.
- cf. 1989 Puellina (C.) scripta (REUSS) Schmid, p. 26, pl. 6, fig. 10.

cf. 1992 Puellina (C.) scripta (REUSS) – El Hajjaji, p. 138, pl. 7, fig. 1.

cf. 1992 Puellina radiata (MOLL) – Pouyet & Moissette, p. 48, pl. 6, fig. 6.

cf. 1996 Puellina radiata (MOLL) – Reverter & Fernandez, fig. 4C.

non1997b Puellina scripta (REUSS) - Pouyet, p. 46, pl. 4, fig. 7-9.

cf. 1997 Cribrilaria innominata (COUCH) - Moissette, p. 193, pl. 2, fig 14.

Material:

Niebla Calcarenite: 14 colonies.

examined by SEM: GNI1-064-A, B; GNI1-065-C.

VNHM: 1848.38.75 (holotype *P. scripta*, Badenian, Eisenstadt; on BNHM photocards, partly figured in Bishop & Househam, 1987, fig. 98). BNHM: pdt2236 (identified as *P. radiata*; Recent, Bay of Naples).

Measurements:

ZL $467 \pm 36,400 - 534(1,20)$ ZW $344 \pm 81, 257 - 634(1, 20)$ OL $49 \pm 5, 40 - 59(1, 18)$ OW $82 \pm 5, 72 - 91(1, 18)$ OvL 164-171 (1, 2) **OvW** 175 - 177(1, 2)AL $320 \pm 102, 223 - 474(1, 5)$ AW $124 \pm 13, 102 - 137(1, 5)$

Description:

Colony encrusting unilaminar, multiserial. Zooid shape irregular ovoid, sometimes broadly bifid proximally with duplication of radiating pattern of costae on either side of proximal zooid; frontal wall convex, zooids separated by deep grooves. Each autozooid with three or four pairs of distolateral pore chambers (plus one distal pore chamber?); uncalcified external openings of pore chambers relatively large, as wide or wider than calcification separating them. Lateral gymnocyst usually absent (costae of neighbouring zooids are commonly in direct contact), if present a very thin band, occasionally little more extensive proximally, forming narrow extensions between neighbouring and proximal zooids. Frontal shield formed of 16 to 21 (most commonly 18) costae sometimes forming a narrow median ridge; up to 26 in bifid zooids (counts do not include costae associated with the formation of the suboral bar). Costae distinct, each with a thickened basal portion; pelmatidia were not observed. Five to seven small intercostal pores between successive costae and a slightly larger pore between costal bases, often hidden by closely spaced costal bases when gymnocyst absent. Orifice D-shaped, broader than long with a distinct, straight, proximal edge and five (seldom four) spines around distolateral margin in autozooids (two in ovicellate zooids). The two distalmost costae are fused to form a suboral bar fitted with indistinct umbos and a very small lacuna located just proximal to it.

Some colonies differ from the description given above in the following: zooids smaller (ZL 380 \pm 37, 291–463 [2, 20]; ZW 264 \pm 35, 195–361 [2, 20]); frontal shield of 13 to 18 costae (most commonly 15; some 21 in bifid zooids) with four to five intercostal pores.

Ovicell globular, wider than long, incorporated into distal zooid (Type A ovicell of Bishop & Househam, 1987); frontal surface imperforate, possibly with a proximal median suture and irregular short ridges or tubercles but otherwise smooth.

Interzooidal avicularia of varying size, sometimes exceeding the length of an autozooid, rostrum then recumbent on frontal wall of distal zooid, directing laterally to distally; occasionally with extensive proximal gymnocyst; uncalcified proximal area semicircular, large, delimited from palate by distinct, short, straight edges that act as pivotal bar for the mandible; palate triangular in smaller avicularia, and elongate-triangular, pointed and slightly bowed distally in large avicularia; gently inclined to substrate. Regenerative growth does occur occasionally.

Discussion:

The specimens considered here as *Puellina* cf. *radiata* display a great range of variation, which may have caused some of the confusion concerning the identification and definition of fossil and Recent *P. scripta* (Reuss, 1848) and *P. radiata* (Moll, 1803) in earlier and recent studies. Based on SEM photography, the morphological characters and occurrence of both species have, to some extent, been discussed by Bishop & Househam (1987) and Schmid (1989); however, a consensus on whether the two species are morphotypes of a single species or distinct entities could not be reached.

Recent *P. radiata* are usually characterised by having four oral spines, whereas occasionally there may be colonies where up to 60% of the zooids have five spines (Harmelin, 1970). The predominant presence of four spines is also found in Pliocene fossils from Italy (Pouyet & Moissette, 1992). In contrast, Miocene material of *P. scripta*, with a remarkably similar general appearance in zooidal morphology, are characterised by having predominantly five spines, whereas there may be zooids with only four (Bishop & Househam, 1987; Schmid, 1989), as is also the case in the present material. One may therefore argue that there was a gradual reduction in the number of oral spines in autozooids through time. Also, there may be four spines in ovicellate zooids in fossil *P. scripta* (El Hajjaji, 1992), whilst Recent *P. radiata* are characterised by having only two.

However, variability in *P. radiata/scripta* is not confined to the number of oral spines: avicularium length varies by a factor of more than two within a single colony (see Measurements), as was already noted by Schmid (1989). Although avicularia that exceed the length of an autozooid are characteristic of *P. radiata*, many avicularia in a colony may stay below this size. Furthermore, the Niebla material contains several colonies in which zooid size, as well as the number of costae and intercostal pores, is significantly reduced (Pl. 3, Fig. 13) while at the same time orifice measurements and all other characters are equal to those with greater zooid dimensions (Pl. 3, Fig. 12). Zooids with a greater length have 16 to 21 costae (most often 18) and five to seven intercostal pores, whereas the frontal wall in smaller zooids comprise 13 to 18 costae (typically 15) with four or five intercostal pores. The range of absolute length in zooids with greater dimensions is 0.4 to 0.53 mm, while it is 0.29 to 0.46 mm in colonies with generally smaller zooids. Schmid (1989) also reported the presence of 13 to 23 costae (most commonly 15 to 18) and three to five intercostal pores in zooids having a length of 0.32 to 0.52 mm. Thus, zooid dimensions as well as the number of costae and intercostal pores are overlapping in the Niebla material as well as between Niebla and Badenian specimens from Austria.

Summing up, intracolony variability in zooid size, the number of oral spines, the number of costae and intercostal pores, and avicularium length exists in Recent and fossil *P. radiata/scripta*. Without a noticeable difference in general morphology, between colony variation within a certain site and between sites are reported in several studies, yet a clear line can, due to largely overlapping numbers and measurements of characters, not be drawn. Based on these observations I am inclined to place *P. scripta* in synonymy with *P. radiata*. However, unless we know more about intraspecific variability in Recent representatives by studying colonies from different environments or using genetic analyses, or unless we find exceptionally well-preserved fossil faunas, I choose to just confer the late Tortonian specimens to this species. E.g., the present specimens cannot be distinguished from the holotype of *P. scripta* (VNHM 1848.38.75), but this is rather due to insufficient preservation of the latter and, in fact, most of the fossil material (including the specimens from Niebla) is too abraded or recrystallised to discern fine details such as intercostal pores or even the number of oral spines in autozooids or ovicellate zooids (see also Schmid, 1989).

Remarks on some other records referred to as either *P. radiata* or *scripta*: *C. radiata* in Vávra (1979b) has a better developed gmynocyst laterally and proximally, and a rather round zooid shape and is therefore reminiscent of the '*P. innominata*-type' (see Discussion in *Puellina* sp. 1) rather than *radiata* (although the suboral lacuna is not apparent in the material figured from the Badenian of Eisenstadt).

In the specimen figured by Ziko & Hamza (1987) as *P. radiata* the avicularium rests on the frontal wall of the distal zooid, a feature that has not been observed in the Recent species, but is typical for *P. hincksi* (Friedl, 1917) as figured in Zabala & Maluquer (1988; but see Hayward & McKinney, 2002).

C. aff. radiata from the Messinian of Algeria (Moissette, 1988) is, indeed, a different species since, at least in the specimen figured, the lateral gymnocyst is better developed, ovicellate zooids have four spines (but see above), and avicularia never reach the length of an autozooid although numerous avicularia were measured. Basically the same applies to specimens from the Badenian of Poland referred to as *P. scripta* by Pouyet (1997b), although no measurements are given for avicularium length.

Harmelin & Aristegui (1988) synonymised a rare and bathyal species occurring in the Strait of Gibraltar with *P. scripta* and it was as such also mentioned and figured by Zabala & Maluquer (1988). However, neither the type-location of *P. scripta* nor any other section this species was recorded from thereafter consists of bathyal sediments, but shallow to mid-shelf deposits. It is therefore highly unlikely that the species observed by Harmelin & Aristegui (1988) is conspecific with *P. scripta*. Indeed, the specimen figured as *P. scripta* in Harmelin & d'Hondt (1993) has a better developed lateral and proximal gymnocyst, a different orifice shape, a thickened suboral bar, and an even greater average number of costae (with relatively larger intercostal pores) than the large zooids in the Niebla material described above and the type-material of *P. scripta*.

All morphological characters in *C. innominata* of Moissette (1997) correspond with those of the fossil *P. radiata/scripta*. The absence of a lateral gymnocyst the greater number of costae, and the extremely large avicularium figured on his plate 2 (fig. 14) argues against it belonging to the '*P. innominata*-type'.

Occurrence:

In the absence of SEM photography, *P. radiata* has been cited from all across the world. Recent studies, however, suggest that this species is most common in the Mediterranean Sea (Harmelin, 1978; as in Bishop & Househam, 1978: 32), while Reverter & Fernández (1996) reported it from the Cape Verde Islands. In the absence of a revision of this species using SEM photography and integrating information on its morphological variability, its reported depth of occurrence (10 to 400 m) and especially its stratigraphic range back into the Oligocene and Eocene, needs to be questioned.

Distribution:

Miocene: Burdigalian (S France), Badenian (Vienna Basin), Tortonian (Guadalquivir Basin – Spain, Morocco), Messinian (Morocco, Tunisia).

Pliocene: Italy. Recent: Mediterranean, Cape Verde Islands.

Puellina **sp. 1** Plate 4, Figure 1-3

Material:

Niebla Calcarenite: 23 colonies. examined by SEM: GNI1-004-B; GNI1-017-A; GNI1-031-B; GNI1-065-B; GNI1-066-B.

Measurements:

ZL $352 \pm 32, 306-422 (4, 20)$ ZW $281 \pm 38, 232-387 (4, 20)$ OL $46 \pm 2, 42-50 (5, 20)$ OW $71 \pm 4, 63-79 (5, 20)$ AL 157-216 (1, 2)AW 79-94 (1, 2)

Description:

Colony encrusting unilaminar, multiserial. Zooid shape irregular ovoid, sometimes broadly bifid proximally with duplication of radiating pattern of costae on either side of proximal zooid; zooids

separated by deep grooves; each autozooid with three or four pairs of distolateral pore chambers plus one distal pore chamber (sometimes ?double); uncalcified external openings of pore chambers relatively large, as wide or wider than calcification separating them. Frontal wall convex; lateral gymnocyst narrow, more extensive proximally, often forming narrow extensions between neighbouring and proximal zooids. Frontal shield formed of 10 to 13 costae; up to 15 in bifid zooids (counts do not include costae associated with the formation of the suboral triangular area and mucro). Costae raised, distinct, each with thickened basal portion and a slightly raised tubercle; pelmatidia were not observed; three to five small intercostal pores between successive costae and a larger pore between costal bases. Orifice D-shaped, broader than long with straight proximal edge and five evenly spaced spines around distolateral margin in autozooids. Apertural bar forming a triangular area steeply sloping upwards to pointed suboral mucro, containing a large lacuna facing distally; suboral mucro passing into variably developed median ridge proximally.

Ovicell globular, incorporated into distal zooid (Type A ovicell of Bishop & Househam, 1987); frontal surface imperforate, with a median suture and irregular ridges or tubercles but otherwise smooth.

Interzooidal avicularia infrequent, of varying size but always considerably smaller than autozooid, rostrum positioned between zooids, directing laterally to distally, usually with well proximal gymnocyst; palate elongate-triangular, slightly inclined to substrate.

Ancestrula tatiform (ca. 130x100µm) and with about ten spines around edge of gymnocyst.

Discussion:

Owing to its suboral lacuna, these specimens resemble fossil material that has commonly been referred to as the Recent species *P. innominata* (Couch, 1844). However, in his redescription of *P. innominata*, Bishop (1986) regarded the presence of fossil representatives of this species as unproven. This statement is substantiated here since, while screening the numerous records on Neogene Mediterranean bryozoans in which *P. innominata* is mentioned, I never came across a description or illustration that showed a species having, at the same time, 10 to 13 thin and steep-sided costae, one to three intercostal pores, and a lacuna placed directly proximal to the orifice, as is the case in the neotype selected by Bishop (1986). Judging from figured material, there are several species combined under this name in the Pliocene alone: e.g., whereas the specimen figured as *P. innominata* in Marcopoulou-Diacantoni & Wuest (1999) from Crete has a large triangular area pierced by a large lacuna just proximal to the orifice, the comparatively small lacuna in a specimen from Italy lies proximal to the suboral umbo produced by the distalmost pair of costae (Pouyet & Moissette, 1992). In contrast, the suboral lacuna is placed between two suboral umbos in material from Algeria (Haddadi-Hamdane, 1996).

It is obvious that a revision of the genus *Puellina* in both Recent and especially fossil faunas is seriously needed and that, as a result, Neogene diversity within this genus will certainly drastically increase.

Occurrence:

The colonies were mostly found encrusting red algae.

Puellina sp. 2 Plate 4, Figure 5, 6

Material:

Niebla Calcarenite: 32 colonies. examined by SEM: GNI1-066-A.

Measurements:

ZL 298 ± 26, 275–353 (1, 15) ZW 234 ± 37, 185–313 (1, 15)

Description:

Colony encrusting unilaminar, multiserial. Zooid shape irregular ovoid, sometimes broadly bifid, separated by deep grooves; each autozooid with three or four pairs of distolateral pore chambers with uncalcified external openings of pore chambers relatively small. Frontal wall convex; lateral gymnocyst narrow, more extensive proximally. Frontal shield formed of eight to eleven (most often ten) costae (counts do not include costae associated with the formation of the suboral area). Costae raised, distinct, each with a thickened basal portion and a slightly raised tubercle; pelmatidia were not observed; three to four small intercostal pores between successive costae and a larger pore between costal bases. Orifice D-shaped, broader than long with straight proximal edge and five evenly spaced spines around distolateral margin in autozooids; ovicellate zooids have two closely-spaced spines on each side of the orifice. Apertural bar with a small tubercle on each side of median suture, lacuna not identifiable maybe due to recrystallisation, but must be very small if present.

Ovicell relatively large, globular, as long as wide on average but usually long and narrow or short and broad, incorporated into (sometimes large part of) distal zooid (Type A ovicell of Bishop & Househam, 1987); frontal surface non-punctate, with a (proximal) median suture and irregular short ridges or tubercles occasionally approximating to central umbo.

Avicularium interzooidal, considerably smaller than autozooid; gymnocyst well developed proximally; rostrum generally positioned between zooids but may partly rest on frontal surface of distal zooid, directing laterally to distally, palate elongate-triangular, only slightly inclined to substrate.

Discussion:

This species differs from *Puellina* sp. 1 in that the former has smaller zooidal and orificial dimensions, no lacuna (or a very small one but disguised by recrystallisation), generally fewer costae, and larger avicularian cystids. Species of similar appearance described by other authors were not encountered.

Occurrence:

This species was the most common of the genus *Puellina*, encrusting red algae and, more rarely, other bryozoans.

"Grade" HIPPOTHOOMORPHA GORDON, 1989 Superfamily HIPPOTHOOIDEA BUSK, 1859 Family CHORIZOPORIDAE VIGNEAUX, 1949 Genus CHORIZOPORA HINCKS, 1880

Chorizopora brongniartii (AUDOUIN, 1826) Plate 4, Figure 4, 7, 10

- 1826 Flustra brongniartii AUDOUIN, p. 240; Savigny, pl. 10, fig. 6.
- 1956 Trypostega circumfissa BOBIES, p. 240, pl. 7, fig. 17.
- 1974 Chorizopora brongniarti (AUD.) David & Pouyet, p. 143, pl. 6, fig. 4.
- 1976 Chorizopora brongniarti (AUD.) Pouyet, p. 62, pl. 10, fig. 3.
- 1988 Chorizopora brongniarti (AUD.) Moissette, p. 113, pl. 18, fig. 7.
- 1989 Chorizopora brongniartii (AUD.) Bishop & Hayward, p. 14, fig. 53, 54.

- 1992 Chorizopora brongniarti (AUD.) El Hajjaji, p. 157, pl. 8, fig. 5.
- 1992 Chorizopora brongniarti (AUD.) Pouyet & Moissette, p. 50, pl. 1, fig. 1.
- 1993 Chorizopora brongniarti (AUD.) Reguant, p. 132, pl. 2, fig. 6.
- 1999 Chorizopora brongniarti (AUD.) Sefian et al., p. 233.
- 2002 Chorizopora brongniartii (AUD.) Hayward & McKinney, p. 43, fig. 19 A-C.

Material:

Niebla Calcarenite: 31 colonies. examined by SEM: GNI1-004-C; GNI1-021-A, B, C; GNI1-045-B.

Measurements:

ZL $347 \pm 43, 273 - 428 (3, 20)$ $240 \pm 31, 196 - 298(3, 20)$ ZW OL $48 \pm 10, 36-69(3, 20)$ OW $59 \pm 5, 48 - 69(3, 20)$ ovOL $46 \pm 2, 44 - 50(1, 5)$ ovOW 91 ± 6, 85–100 (1, 5) $164 \pm 13, 142 - 184(2, 17)$ OvL OvW $134 \pm 9, 114 - 147 (2, 17)$ $87 \pm 9,76 - 105(2,10)$ AL $70 \pm 10, 51 - 81 (2, 10)$ AW

Description:

Colony encrusting multiserial, unilaminar. Autozooids broadly oval or fusiform (spindleshaped), disjunct, adjacent zooids linked by numerous tubular extensions of basal pore chambers. Autozooids may be closely packed, with linking tubes barely visible, or widely disjunct with intervening space filled by a mosaic of small irregular kenozooids, each of which being linked to neighbouring kenozooids or autozooids by tubular connections, and each with a small round frontal opesia. Frontal wall in autozooids slightly convex, imperforate, smooth but transversely ridged; small suboral umbo in ovicellate zooids. Orifice dimorphic, D-shaped with straight proximal border; slightly shorter than wide in autozooids; orifice in ovicellate zooids wider than those in autozooids by about one-third but with same length.

Ovicell elongate, semielliptical, imperforate, sometimes developing a stout longitudinal keel, closed by operculum; partly incorporated within cystid of avicularium.

Interzooidal avicularia distal to each autozooid, occasionally additional ones in between zooids; cystid rounded, rostrum triangular, acute to frontal plane, directed distally; crossbar complete, thin, without columella.

Discussion:

Both types of zooid shape, short and oval vs. long and slender, which are known to occur in Recent *C. brongniartii*, are also present in the Niebla material, as are colonies in which zooids are separated by several kenozooids (Pl. 4, Fig. 10) and those in which zooids are extremely closely spaced (Pl. 4, Fig. 7). However, different zooidal dimensions are produced by the variability in zooid shape which may affect zooid size measurement (for instance, mean surface area shows a deviation of some 30% between both zooid types in the present material), and therefore comparisons with other records.

Occurrence:

C. brongniartii is probably one of the few truly cosmopolitan cheilostome (morpho)species and lives in temperate and tropical zones in depths of up to 100 m. It encrusts many types of organic substrates and is, in the Niebla Calcarenite, mostly found on coralline algae, where it was frequently observed to have been overgrown by numerous other bryozoan species. The opportunistic life history of *C. brongniartii* is, besides its growth on ephemeral substrates and its low competitive abilities, also reflected by its lightly calcified frontal wall, whereas basal walls were not observed.

Distribution:

Miocene: Langhian-Serravallian (Italy), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin - Spain), Messinian (Algeria, Atlantic and Mediterranean Morocco).

Pliocene: Great Britain, Netherlands, Spain (Guadalquivir Basin, Carboneras Basin), Italy, Tunisia, Japan.

Pleistocene: Italy.

Recent: Atlantic, Mediterranean, Pacific Ocean, Indian Ocean.

Family HIPPOTHOIDAE LEVINSEN, 1909 Genus TRYPOSTEGA LEVINSEN, 1909

Trypostega rugulosa (REUSS, 1874) Plate 4, Figure 8, 9

- v 1874 Lepralia rugulosa REUSS, p. 169, pl. 3, fig. 2.
 - 1972 Hippothoa rugulosa (REUSS) David et al., p. 33, pl. 8, fig. 7.
 - 1974 Hippothoa rugulosa (REUSS) David & Pouyet, p. 142, pl. 6, fig. 6.
 - 1989 Hippothoa? rugulosa (REUSS) Schmid, p. 53, pl. 11, fig. 1.
 - 1992 Hippoporina obvia (MANZONI) Pouyet & Moissette, p. 61, pl. 9, fig. 1, 2.
 - 1992 Trypostega rugulosa (REUSS) El Hajjaji, p. 158, pl. 8, fig. 14.
 - 1996 Trypostega rugulosa (REUSS) Haddadi-Hamdane, p. 78, pl. 5, fig. 12.
 - 1997b Hippothoa rugulosa (REUSS) Pouyet, p. 48, pl. 4, fig. 3, 6.

Material:

v

Niebla Calcarenite: 21 colonies.

examined by SEM: GNI1-016-A, B; GNI1-017-B; GNI1-047-C.

other: lectotype VNHM 1878.11.65 (lectotype, Badenian, Eisenstadt; chosen by David & Pouyet, 1974, pl. 6, fig. 6).

Measurements:

ZL $384 \pm 32, 339-461 (3, 20)$ ZW $232 \pm 20, 198-268 (3, 20)$ OL $61 \pm 6, 49-69 (3, 16)$ OW $56 \pm 4, 48-66 (3, 16)$ OvL $256 \pm 24, 221-273 (3, 4)$ OvW $265 \pm 15, 246-279 (3, 4)$

Description:

Colony encrusting unilaminar, multiserial. Autozooids elongated rhomboidal or polygonal, separated by distinct grooves. Frontal wall flat to slightly convex, finely grained, regularly perforated by relatively large round pores encircled by a slightly elevated rim. Orifice cleithridiate (but not well preserved), with a round anter delimited from triangular poster by two condyles; orifice in ovicellate zooids dimorphic, shorter than in autozooids and with a broad, concave, proximal rim; no spines.

Ovicell interzooidal, globular but moderately convex, large, about as long as wide, broader than zooid; surface as frontal wall of zooids, forming a (proximo)central umbo or ridge.

Avicularia and kenozooids were not observed.

Discussion:

Since the new family Trypostegidae has not been formally established, yet (pers. comm. D.P. Gordon, 2003), *T. rugulosa* is here classified within the Hippothoidae. The present specimens are identical to the type-material, although the frontal umbo or ridge on the ovicell is more pronounced in most of the other records.

Occurrence:

This species is often recorded from Mediterranean fossil sites, but has never been found in the late Neogene eastern Atlantic area before. In most cases, coralline red algae serve as substrate for *T. rugulosa* in the Niebla Calcarenite but it is also found overgrowing other encrusting bryozoans.

Distribution:

Miocene: Burdigalian (France), Badenian (Vienna Basin, Poland), Langhian-Serravallian (France), Tortonian (Guadalquivir Basin – Spain), Messinian (Spain, Morocco, Italy). Pliocene: Spain, Algeria, Italy.

"Grade" UMBONULOMORPHA GORDON, 1989 Superfamily ARACHNOPUSIOIDEA JULLIEN, 1888 Family ARACHNOPUSIIDAE JULLIEN, 1888 Genus PORICELLA CANU, 1904

Poricella bugei (EL HAJJAJI, 1987) Plate 4, Figure 11-13

- 1987 Tremogasterina bugei EL HAJJAJI, p. 690, pl. 1, fig. 7, 8.
- 1988 Tremogasterina sp. Moissette, p. 88, pl. 15, fig. 7, 10.
- 1992 Tremogasterina bugei EL HAJJAJI El Hajjaji, p. 155, pl. 8, fig. 6.
- 2000 Tremogasterina bugei EL HAJJAJI Pouyet, p. 184.
- 2004 Poricella bugei (EL HAJJAJI) Pizzaferri, p. 74, pl. 1, fig. 1, 2.

Material:

Niebla Calcarenite: 13 colonies. examined by SEM: GNI1-044-A, B, C, D, E, F.

Measurements:

ZL $575 \pm 46, 495-667 (5, 20)$ ZW $371 \pm 40, 301-476 (5, 20)$ ApL $153 \pm 9, 129-162 (4, 11)$ ApW $130 \pm 12, 113-154 (4, 11)$ OvL $219 \pm 18, 200-253 (3, 6)$ OvW $210 \pm 18, 192-241 (3, 6)$

Description:

Colony encrusting unilaminar, multiserial. Autozooids oval, separated be deep grooves. Frontal wall convex, wrinkled (especially at transition from frontal shield to suboral mucro), imperforate except for a central area with four to seven round and/or crescent-shaped foramina, and with few, slit-like or subangular, marginal areolae; suboral mucro thick, broad and often very conspicuous and tall. Two or three large 'pore chambers' present in distolateral vertical walls. Aperture longer than wide, rounded distally and slightly concave proximally, with two short and inconspicuous proximolareral condyles delimiting a poster of equal or slightly greater length than anter; the thickened distolateral rim carries six stout spines (four in ovicellate zooids).

Ovicells globular but occasionally flattened frontally, slightly longer than wide, recumbent on frontal wall of distal zooid only with a small area; surface imperforate, smooth (in contrast to frontal wall), proximal lip convex and overarching a large part of orifice. No dimorphism in orifices of ovicellate zooids.

Avicularia were not observed.

Discussion:

Apart from the type species of *Tremogasterina* Canu, 1911, all species formerly referred to this genus were transferred to *Poricella* by Tilbrook et al. (2001). The present material is identical in morphology and morphometry to the Mediterranean species *P. bugei*, although specimens described from the Pliocene of Italy by Pizzaferri (2004) show secondary calcification of the frontal wall, resulting in the formation of a steep serrated ridge around the central pore plate. This was neither observed in the present material nor in that described by Moissette (1988) and El Hajjaji (1992). However, since aragonite is preserved in the Italian sediments of the Emilia area (pers. observation), whereas it has been dissolved in the above mentioned Miocene deposits, this species might have had a bimineralic composition producing a primary calcitic skeleton and aragonitic secondary calcification, or the latter has been lost due to mechanical abrasion. For neither interzooidal nor vicarious avicularia were observed in *P. bugei*, this species represents one of the very few *Poricella* that is lacking this feature, although Cook (1977) mentioned that these may be extremely rare in some species, and therefore seldom observed in fossil colony fragments.

P. bugei is close to the Middle Miocene *P. pouyetae* (Cook, 1977) from southern France, which, however, differs from the former in having four to six spines, a raised distal orificial margin, no suboral mucro, more numerous and conspicuous marginal areolae, and in having interzooidal avicularia, although these may be rare. The Recent *P. perplexa* (Cook, 1967) from Ghana can also be considered being related to *P. bugei*, in that the former is the only Recent species lacking avicularia. Zooid morphology is identical to *P. bugei* except that the frontal area of foramina is more extended towards the mucro in *P. perplexa*, and frontal calcification different to both the present and the Pliocene Italian material.

Occurrence:

Recent species of *Poricella* appear to occur worldwide in shallow waters between 30° latitude north and south; their presence may therefore be indicative of tropical to subtropical conditions.

P. bugei was hitherto recorded from the late Miocene and early Pliocene Mediterranean basins only. The few colonies present in the Niebla Calcarenite usually encrust red algae.

Distribution:

Miocene: Tortonian (Guadalquivir Basin and SE Spain, Morocco), Messinian (Algeria, Morocco). Pliocene: Italy.

Superfamily ADEONOIDEA BUSK, 1884 Family ADEONIDAE BUSK, 1884 Genus SCHIZOSTOMELLA CANU & BASSLER, 1927

?Schizostomella cf. dubia (BUSK, 1859) Plate 5, Figure 1

- cf. 1859 Flustra dubia BUSK, p. 132, pl. 1, fig. 3.
- cf. 1988 Schizostomella(?) dubia (BUSK) Moissette, p. 176, pl. 28, fig. 8.
- cf. 1992 Schizostomella? dubia (BUSK) El Hajjaji, p. 227, pl. 14, fig. 8.
- cf. 1999 Schizostomella? dubia (BUSK) Sefian et al., p. 239.

Material:

Niebla Calcarenite: 1 colony fragment. examined by SEM: GNI1-019-E.

Measurements:

ZL 468–568 (1, 4) ZW 182–227 (1, 4)

Description:

Colony erect bilaminar. Zooids elongated, oval or rectangular; frontal and most of lateral walls damaged and/or dissolved, basal wall rising distally, thus encroaching onto the proximal part of distal zooid; vertical walls with small oval septula, the zooid margin appears serrated since lateral walls are preferentially fractured where the septula are emplaced.

Spines, ovicells or avicularia were not observed.

Discussion:

This species presumably belongs to the superfamily Adeonoidea because these taxa may consist (partly or wholly) of aragonite (e.g. Lidgard, 1996) and usually form erect bilaminar colonies. However, since the frontal wall of ?S. cf. *dubia* is not preserved, and consequently most of the specific characters, the synonymy with the records given above are doubtful at best.

Occurrence:

For the above mentioned reasons this species is of little taxonomic and biogeographic value, besides the notion that it is one of the few taxa occurring in the Niebla Calcarenite (yet only a single specimen was found) that has a bilaminar mode of growth.

Superfamily LEPRALIELLOIDEA VIGNEAUX, 1949 Family BRYOCRYPTELLIDAE VIGNEAUX, 1949 Genus PORELLA GRAY, 1848

Porella sp. Plate 5, Figure 2-4, 8?

Material:

Niebla Calcarenite: 6 colonies. examined by SEM: GNI1-063-A, D.

Measurements:

ZL $352 \pm 12, 346-379 (2, 6)$ ZW $216 \pm 21, 187-251 (2, 6)$ ApL $89 \pm 8, 82-99 (2, 5)$ ApW $103 \pm 10, 93-118 (2, 5)$ OvL $151 \pm 6, 142-161 (2, 11)$ OvW $164 \pm 6, 158-173 (2, 11)$ AL 64-78 (1, 2)AW 61-65 (1, 2)

Description:

Colony encrusting unilaminar, multiserial. Zooids elongate ?rectangular or ?oval (vertical and basal walls are not preserved); frontal wall convex, imperforate, smooth, presumably with few, large, marginal areolae. Primary orifice wider than long; lyrula short but broad, with straight distal margin, occupying about two-thirds of total width; condyles were not observed. A conspicuous, elongated oval (in ovicellate zooids) or round (in autozooids), tubular peristome or collar structure is developed around the orifice: proximally the structure is attached to the suboral frontal wall by thin walls which extend and taper distally (proximolateral to orifice), the medioproximal rise carries an elevated suboral avicularium from which distally extending lateral walls encircle the orifice to form a peristome; the forked attachment of the (lower) proximal and (upper) lateral walls of the peristome leaves open two large lateral fenestrae proximolateral to the orifice; spines were not observed.

Ovicell globular, sometimes slightly flattened frontally, little longer than wide, recumbent on frontal wall of distal zooid and attached to peristome of mother zooid; frontal surface smooth, imperforate except for a row of some six, large, marginal pores; proximal rim slightly concave.

A small, oval, median, suboral avicularium incorporated in top of proximal peristome; rostrum pointing proximally, inclined by ca. 60° to frontal plane; crossbar thin, complete, without columella.

Discussion:

An identical structure to the 'necklace' that characterises this species could not be found in neither Recent nor fossil bryozoans. It is different from other peristomes in that, at least the proximal part incorporating the avicularium, seems to be relatively independent of both the apertural margin and frontal wall (the connection between collar and the distal, vertical, zooid walls was not observed). The most striking feature is the resulting gaps on both flanks formed between the lower attachment area on the frontal wall and the upper connection with the orifice margin.

I chose to warily place this species in *Porella* for the following reasons: (1) the frontal wall is imperforate with only marginal areolar pores; (2) the orifice is (presumably) lacking condyles while having a simple but distinct lyrula; (3) the suboral avicularium is identical in shape and position to several species of this genus, in which a peristome is also commonly present. However, one argument against this decision would be that the ovicell pores in this species are more numerous, perfectly arranged around the distolateral ovicell margin, and distinctly larger than in any of the species in *Porella*. Yet the enigmatic collar structure may, in a rudimentary state, also be present in some Recent species. Whereas several species have small pores at and around the base of the peristome, Porella minuta (Norman, 1868) and P. patula (M. Sars, 1851) even show larger pores in the lateral peristome (see Hayward & Ryland, 1999: fig. 61A, B, and fig. 61C, respectively) that may represent relicts of the larger fenestrae that characterise the Niebla material (if this is the ancestral state, that is to say). Since secondary calcification obscures many features of the primary skeleton during later ontogeny in Recent species (see Hayward & Ryland, 1999), which is obviously not preserved in my material, the resemblance with the fossil species may therefore even be greater when only the primary skeleton is taken into account. However, this needs to be proven by studying the zooid ontogeny in Recent species of Porella.

A close fossil species is *P. cheilopora* (Reuss, 1848). However, SEM figures in Schmid (1989) and El Hajjaji (1992) show that the peristome is not as well developed (especially so in autozooids), that the avicularium is not as much incorporated into the peristome and projects above it, that the peristome forms a distinct rib on the proximal ovicell margin, and that neither the marginal pores in the ovicells nor the large, lateral, peristomial fenestrae are present.

Occurrence:

Although highly reproductive, note the presence of numerous ovicells on Fig. 2 (Pl. 5), this species is rare in the Niebla Calcarenite and encrusts red algae and other bryozoans (e.g. the cyclostome *Hornera* sp.).

Family ROMANCHEINIDAE JULLIEN, 1888 Genus ESCHARELLA GRAY, 1848

Escharella serrulata (REUSS, 1848) Plate 5, Figure 5, 6, 9

V	1848	Cellepora serrulata REUSS, p. 85, pl. 10, fig. 12.
v pars?	1874	Lepralia serrulata (REUSS) – Reuss, p. 167, (non? pl. 2, fig. 2, 3).
pars?	1974	Escharella arrecta (REUSS) – David & Pouvet, p. 186 (non pl. 6, fig. 8).

- pars 1974 Escharella tenera (REUSS) David & Pouyet, p. 187 (non pl. 9, fig. 6).
 - 1992 Escharella reussiana (BUSK) El Hajjaji, p.185, pl. 13, fig. 8.
 - 1992 Escharella variolosa (JOHNSTON) Pouyet & Moissette, p. 67, pl. 10, fig. 4.

Material:

Niebla Calcarenite: 13 colonies. examined by SEM: GNI1-005-A, B, C.

other: VNHM without number (*Lepralia serrulata* [Reuss, 1848]; Badenian, Eisenstadt; figured as *E. tenera* by David & Pouyet, 1974: pl. 9, fig. 6); 1878.11.50 (lectotype of *Escharella arrecta* [Reuss, 1848], Badenian, Eisenstadt; chosen by David & Pouyet, 1974); 1878.11.57 (Badenian, Eisenstadt; identified as *L. serrulata* by Reuss, 1874: pl. 2, fig, 2; figured as *E. arrecta*, David & Pouyet, 1974, pl. 6, fig. 8).
BNHM B.1684 (holotype of *E. reussiana* [Busk, 1859], pl. 8, fig. 2; Pliocene, Coralline

BNHM B.1684 (holotype of *E. reussiana* [Busk, 1859], pl. 8, fig. 2; Pliocene, Coralline Crag); B.6786, D.55525 (*E. reussiana*, Pliocene, Coralline Crag).

Measurements:

ZL	593 ± 41, 512–666 (2, 18)		
ZW	415 ± 37, 357–488 (2, 18)		
ApL	$103 \pm 10, 89 - 126 (2, 16)$		
ApW	$160 \pm 13, 142 - 185 (2, 16)$		
OvL	260 ± 23, 218–296 (1, 7)	ApL	88–97 (1, 3)
OvW	306 ± 18, 285–342 (1, 7)	ApW	242–284 (1, 3)

Description:

Colony encrusting unilaminar, multiserial. Zooids rhomboidal to hexagonal, separated by distinct sutures; frontal wall convex, imperforate, granular, with one row of large marginal areolae (being present also at the distal zooid margin) accentuated by intervening ridges during later ontogeny. Primary orifice hemispherical; lyrula short, truncated with a straight distal edge, occupying little less than half the proximal border; condyles were not observed. Peristome well and evenly developed around orifice, tubular, protruding vertically from frontal wall, somewhat D-shaped, proximally forming a more or less pronounced lobe with a slightly raised and thickened central part; no spines.

Ovicell globular, little raised above peristome, becoming progressively immersed by secondary calcification of areolar ridges while ovicell shape becomes hemispherical to rounded triangular, not recumbent on or immersed in distal zooid, wider than long, slightly convex, surface imperforate and granular, with a distinct row of areolar pores and intervening ridges. A characteristic broad peristome develops in ovicellate zooids, shorter than in autozooids and broader by more than one-third, encroaching the ovicell forming a frontal ridge on proximal ovicell rim, peristome with two proximolateral bulges and a raised, broad, quadrate lip proximally.

No avicularia.

Discussion:

After the revision of Miocene Cheilostomata of the Vienna Basin by David & Pouvet (1974) the case of the species of Escharella Reuss (1848, 1874) described still remains an intricate one. During my short visit to the Vienna Museum, however, the many existing problems were impossible to solve. A number of uncertainties concerning the species definitions given in David & Pouyet (1974) stems from the fact that the figuration does not match the description in some cases (see also Discussion in Schedocleidochasma incisa [Reuss, 1874]). For instance, E. tenera Reuss, 1874 is described having one row (sometimes two) of areolar pores, three to five orificial spines, and globular ovicells that are immersed in the distal zooid. Yet the photo of one of the two specimens without number from Eisenstadt, referred to Lepralia serrulata by Reuss (1874, see Material), clearly shows a different species. The zooids of this specimen have a prominent peristome, no spines, always a single row of conspicuous areolar pores, and the ovicells are not immersed in the distal zooid's frontal wall but encircled, and separated from the distal zooid, by vertical walls and large areolar pores (David & Pouyet, 1974: pl. 9, fig. 6). Since this specimen resembles not only the original drawing in Reuss (1848: pl. 10, fig. 12; the figures in 1874 [pl. 2, fig. 2, 3] do not correctly represent the species and need to be revised), but also the present material, the species from Niebla is here identified as E. serrulata. However, David & Pouyet (1974) suggested to suppress the name 'serrulata' due to problems with the original material of E.
serrulata. (They mention that in one sample there are two species, *Lepralia fuchsi* Reuss, 1874 and *L. tenera*, kept under the same collection number with the name *Cellepora serrulata* on it, and that *L. tenera* was figured in the 1848 publication of Reuss. In the view of the inconsistencies in David & Pouyet's work, however, this requires re-examination.) This problem thus needs to be solved before the species can be redescribed using SEM. Nevertheless, *E. tenera* was later correctly described and figured by Pouyet (1997b), yet without her correcting the earlier mistake.

Similar problems were encountered with David & Pouyet's (1974) account on *Escharella arrecta* (Reuss, 1848). However, I refrain from going into detail and just stress that the lectotype of *E. arrecta* is characterised by a prominent ovicell which is not immersed (neither by secondary calcification nor in the distal zooid's frontal wall), by relatively small areolar pores, and by the presence of spines on the distolateral peristome. Although coated with superficial cement, the specimen identified and figured in David & Pouyet (1974: pl. 6, fig, 8; VNHM 1878.11.57) as *E. arrecta* does not show any of these features but is rather similar to *E. serrulata*, and thus the present material. For all specimens identified as *Cellepora/Lepralia serrulata* by Reuss were synonymised with either *E. arrecta* or *E. tenera* by David & Pouyet (1974), the inconsistencies specified above defy the basis for these synonymises. The species of *Escharella* described by Reuss are therefore in need of revision and a lectotype should be established for *E. serrulata*.

In the most recent publications at least two different morphospecies (compare Moissette [1988] with El Hajjaji, [1992]) have been referred to as *E. reussiana* (Busk, 1859), which was originally described from the Pliocene Coralline Crag Formation. However, neither of the two above mentioned Mediterranean species, nor any other species encountered during this work, is identical with the holotype of the British *E. reussiana*, which is characterised by a large, anvil-shaped lyrula, a single row of small and inconspicuous pores, a globular ovicell that is recumbent on the distal zooid and not encircled by areolar pores, and a rather round peristome (i.e. not as D-shaped as in the present material). Thus, on the basis of the figured specimens, the species referred to as *E. reussiana* and *E. variolosa* (see also Discussion in *Escharella* sp.) by El Hajjaji (1992) and Pouyet & Moissette (1992), respectively, are here considered conspecific with the present material. (The descriptions of both species, however, differ slightly from their figured material: El Hajjaji [1992] reports hyperstomial ovicells that are immersed in the distal zooid, which is clearly not observed on the SEM image; and Pouyet & Moissette [1992] mention the presence of two spines on the peristome, which are also not observed on the photo.)

Occurrence:

Few colonies of E. cf. serrulata were found in the Niebla Calcarenite, encrusting red algae. However, if proven to be conspecific with Reuss' species, its presence in the Guadalquivir Basin would represent the first record of this species in the Atlantic.

Distribution:

Miocene: Badenian (Vienna Basin), Tortonian (Guadalquivir Basin, Morocco), Messinian (Morocco).

Pliocene: Italy.

Escharella sp. 1

Plate 5, Figure 7, 10, 11

1976 *Escharella variolosa* (JOHNSTON) – Pouyet, p. 70, pl. 11, fig. 1.
1988 *Escharella peachi* (JOHNSTON) – Moissette, p. 155, pl. 24, fig. 5; pl. 25, fig. 7.

Material:

Niebla Calcarenite: 25 colonies. examined by SEM: GNI1-002-A, B, C, D, E, F. BNHM B1721 (SEM photocard of *L. peachii* Johnston, Pliocene, Coralline Crag). other: BNHM 47.9.16.24 (paratype of *Lepralia peachii* Johnston = *E. immersa* [Fleming, 1828]; Recent, British Isles).
FSL 115961 (as *E. variolosa*, Pliocene, SE Spain; Pouyet, 1976, pl. 11, fig. 1); 119136 (as *E. peachi*, Messinian, Algeria; Moissette, 1988, p. 155, pl. 24, fig. 5; pl. 25, fig. 7).

Measurements:

ZL 480 ± 45, 400–566 (4, 20)

ZW 361 ± 36, 296–428 (4, 20)

OL 83 ± 8, 71–95 (5, 12)

OW $120 \pm 11, 107 - 139(5, 12)$

OvL 223 ± 15, 200–248 (2, 15)

OvW 241 ± 21, 207–286 (2, 15)

Description:

Colony encrusting unilaminar to plurilaminar, multiserial. Zooids oval to rhomboidal, separated by deep furrows; frontal shield slightly convex, imperforate, finely granular, with one or two (occasionally three towards the orifice) rows of large marginal areolae with stout interareolar buttresses which, in later ontogeny, may become very accentuated forming ridges or tubes that arch over and cover the entire frontal wall. Primary orifice semicircular, a distinctly anvil-shaped lyrula with straight distal edge occupyies half to two-thirds of proximal margin; presumably without condyles. Peristome low with a stout, pointed proximal mucro; six, rarely seven, thick distolateral oral spines, the two proximal pairs only being present in ovicellate zooids.

Ovicells globular, as long as wide, finely granular, recumbent on distal zooid's frontal wall but becoming progressively immersed by a framing row of areolar tubes, proximal edge concave.

No avicularia.

Discussion:

In addition to the existing problems with some of the species Reuss (1848, 1874) introduced (see above), the Neogene Mediterranean history of *Escharella* spp. became even more complicated and confusing when bryozoologists of the 19th century started introducing names of some Recent species, originally described around the British Isles, for their fossil material. During the 20^{th} century, workers have willingly accepted these names, yet without examining the original material, without a precise species concept, and despite taxonomic changes in nomenclature. Therefore, species occurrences and stratigraphic ranges of *Escharella* spp. in the Neogene of the Mediterranean realm are not reliable and the genus is in need of a thorough revision with special reference to the Reuss Collection, as will be partly shown below.

In previous publications the present species has been referred to as *Escharella variolosa* (Johnston, 1838) and *E. peachii* (Johnston, 1847). *E. variolosa* does occur today in the Mediterranean Sea but is clearly different from the fossil material here addressed, in that the former has rectangular zooids and a single pair of spines on the distal orifice margin (in both autozooids and ovicellate zooids), in the presence of only a single row of areolar pores even in the more distal part of the zooid, and in that the lyrula is slender and not distinctly anvil-shaped (see e.g. Hayward & Ryland, 1998). Several different morphospecies have been referred to this name (compare Pouyet [1976] with El Hajjaji, [1992], Pouyet & Moissette [1992] and Haddadi-Hamdane [1996]), whereas only the specimens described as *E. variolosa* by Haddadi-Hamdane (1996) are morphologically very close to the Recent species, except that she reports a large lyrula.

Ryland (1963) has synonymised *E. peachii* with *E. immersa* (Fleming, 1828), which is a borealarctic species and, apart from its ecological preferences, differs from the material described by Moissette (1988) in that the former has a well developed peristome, a narrower lyrula with a concave edge, and only a single row of marginal areolar pores (Hayward & Ryland, 1999).

The present specimens share some similarities with *Escharella tenera* Reuss, 1874 as figured in Pouyet (1997b: pl. 7, fig. 6, 7; the figure of *E. tenera* in David & Pouyet, 1974: pl. 9, fig. 6 depicts a different species, see Discussion in *E.* cf. *serrulata* [Reuss, 1848]). However, *E. tenera* has less convex zooids, and smaller and less distinct areolar pores and buttresses. Since ovicells and the lyrula of *E. tenera* have not been documented using SEM, a precise statement on their relationship

can not be made. However, from the material viewed in Vienna and London it seems that the present material has not been described, yet, and that it is confined to the Late Miocene and Early Pliocene of the western Mediterranean/eastern Atlantic, while it is neither present in the mid-Miocene Vienna Basin nor in the Pliocene of the British Isles.

Occurrence:

Escharella sp. 1 is common in the Niebla Calcarenite, encrusting red algae.

Distribution:

Miocene: Tortonian (Guadalquivir Basin - Spain), Messinian (Algeria). Pliocene: SE Spain.

> *Escharella* sp. 2 Plate 5, Fig. 12

Material:

Niebla Calcarenite: 1 colony. examined by SEM: GNI1-024-B.

Measurements:

ZL $710 \pm 61, 639-767 (1, 5)$ ZW $538 \pm 64, 452-615 (1, 5)$ ApL 120-124 (1, 2)ApW 138-141 (1, 2)

Description:

Colony encrusting unilaminar, multiserial. Zooids hexagonal, broad, separated by distinct grooves; frontal wall imperforate, finely granular, convex proximally, passing into a steep-sided, tall, tubular peristome distally, with one to two rows of round marginal areolae. Aperture round, slightly wider than long; peristome well developed with thick rim carrying six spine bases. Primary orifice deeply immersed; lyrula low, strong, anvil-shaped with straight free margin; condyles were not observed. Basal wall only marginally calcified, or central part dissolved afterwards, if made out of aragonite.

No ovicells or avicularia present.

Discussion:

The only colony obtained of this species consists of just nine zooids which are mostly not well preserved, and a morphologically similar species could not be found in the literature. The general morphology and the well developed lyrula suggest a placement within the genus *Escharella*, although condyles are presumably absent.

As in species of the genus *Escharoides* (see below), only a broad margin of the basal wall remains firmly attached to the substrate whereas the central part was most likely never completely calcified. Weakly calcified basal walls are frequently observed in taxa growing on flexible surfaces, such as kelp fronds (McKinney & Jackson, 1989), in order to compensate flexing of the substrate. However, this colony seems to have grown *in situ* and on, albeit unknown, hard or semi-lithified substrate.

Genus ESCHAROIDES MILNE EDWARDS, 1836

Escharoides coccinea (ABILDGAARD, 1806) Plate 5, Figure 13; Plate 6, Figure 1

1806 Cellepora coccinea ABILDGAARD, p. 30, pl. 146, fig. 1, 2.

1971 Escharoides coccinea (ABILDG.) – Galopim de Carvalho, p. 115, pl. 19, fig. 1.

1984 Escharoides coccinea (ABILDG.) – Pouyet & David, p. 101, pl. 7, fig. 5, 6.

1988 Escharoides coccinea (ABILDG.) – Moissette, p. 148, pl. 24, fig. 4.

1989 Escharoides coccinea (ABILDG.) – Schmid, p. 32, pl. 8, fig. 8.

1992 Escharoides coccinea (ABILDG.) - Pouyet & Moissette, p. 63, pl. 9, fig. 6.

1993 Escharoides coccinea (ABILDG.) – Moissette et al., p. 105.

Material:

Niebla Calcarenite: 11 colonies. examined by SEM: GNI1-045-A, B, C, D, E; GNI1-067-C.

Measurements:

ZL $480 \pm 83, 369-652(3, 17)$ 425 ± 93, 298–590 (3, 17) ZW ApL $79 \pm 11,67-94(3,6)$ ApW $124 \pm 17, 109-148 (3, 6)$ OvL 231 ± 24 , 187–282 (3, 20) OvW $262 \pm 25, 210 - 310(3, 20)$ AL $165 \pm 33, 116 - 232(2, 11)$ small AW $85 \pm 11, 73 - 112(2, 11)$ small AL $329 \pm 61, 271 - 412(2, 4)$ large 144 ± 28, 111–158 (2, 4) AW large

Description:

Colony encrusting unilaminar, multiserial. Zooids broad, quadrangular to hexagonal, separated by deep grooves; frontal wall steeply convex, imperforate with large marginal areolar pores. Aperture with straight, distal, suboral shelf; a broad distolateral lip carries four to six thick spines (four in ovicellate zooids), the raised proximal lip forms two proximally directed bulges with a central notch and mucro that has a short square denticle on its inner side, which is flanked on each side by a short pointed denticle, directing medially.

Ovicell prominent, hyperstomial, round to elliptical, flattened frontally; rugose surface and with two rows of small pores around the periphery, proximal margin straight.

Adventitious avicularia usually paired, lateral to the aperture, of varying size but generally small and sometimes unequally developed; rostrum triangular to elongated-triangular, crooked distally, directing laterally to distolaterally, acute to frontal plane; crossbar complete without columella. Large avicularia common in some colonies, sometimes exceeding length of autozooid, proximolateral to orifice, pointing disto- to proximolaterally, acute to frontal plane; cystid large, swollen, with marginal pores; rostrum triangular or extremely elongated and narrow with parallel sides.

Discussion:

The nodular calcification of the frontal wall, which is used to classify Recent species of *Escharoides* (but see Zabala & Maluquer, 1988), is missing in most fossil specimens owing to mechanical abrasion. Exceptional preservation of the superficial layer in a Middle Miocene fauna from the Vienna Basin (Schmid et al., 2001), in which aragonitic fossil are not preserved, shows, on the one hand, that secondary calcification in *E. coccinea* is composed of calcite and the loss of it is due to a physical, not a chemical process. On the other hand, and more importantly, these extremely well preserved specimens show no morphological differences to Recent representatives

of the species, and therefore provide clear evidence for the existence of the morphospecies *Escharoides coccinea* for at least some 12 Ma.

The presence of giant adventitious avicularia in specimen GNI1-045-A, in addition to the common pair of smaller avicularia, provides evidence for the notion of Zabala & Maluquer (1988) that *E. coccinea* and *E. megarostris* (Canu & Bassler, 1928b) are merely ecotypes of the same species. *E. megarostris* would thus fall into synonymy with *E. coccinea*.

Occurrence:

E. coccinea is a perennial species that lives for at least two years and is characteristic for the intertidal of rocky shores, encrusting *Laminaria* holdfasts, stones and shells in warm-temperate to cool-temperate waters (Hayward & Ryland, 1999). Interestingly, in the Recent Mediterranean Sea it is abundant between 30 and 80 m and occurs down to depths of up to 100 m (Gautier, 1962).

Photographic documentations or specimens of records from the Oligocene and Eocene have not been viewed during this study. The occurrence of *E. coccinea* in the Paleogene is thus considered doubtful.

Several specimens were found in samples from Niebla, encrusting red algae and other bryozoans (e.g. *C. brongniartii*). As in *Escharoides megalota* and *Escharoides* sp., some colonies were found independent of substrate and with only the marginal basal walls calcified, which may indicate growth on an ephemeral substrate.

Distribution:

?Eocene: Germany, France, Italy, Romania.

?Oligocene: Germany, France, Italy, USA.

Miocene: Burdigalian (France), Langhian-Serravallian (France, Italy), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin - Spain), Messinian (Morocco, Algeria, Crete).

Pliocene: Portugal, Spain (Carboneras Basin), Italy, Tunisia, Algeria.

Pleistocene: Italy.

Recent: eastern Atlantic (Madeira to Shetland), Mediterranean.

Escharoides megalota (REUSS, 1848) Plate 6, Fig. 5-7

1848	Cellepora	megalota	REUSS, p.	81, pl.	10, fig. 1.
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- 1869c Lepralia fulgurans MANZONI, p. 936, pl. 1, fig. 6.
- 1972 Escharoides carboneli DAVID, MONG. & POUYET, p. 63, fig. 1, 2; pl. 4, fig. 1.
- 1974 Escharoides megalota (REUSS) David & Pouyet, p. 180, pl. 10, fig. 6.
- 1976 Escharoides fulgurans (MANZONI) Pouyet, p. 68, pl. 11, fig. 5.
- 1988 Escharoides fulgurans (MANZONI) Moissette, p. 149, pl. 24, fig. 11.
- 1989 Escharoides megalota (REUSS) Schmid, p. 33, pl. 9, fig. 1, 2, 5.
- 1992 Escharoides megalota (REUSS) El Hajjaji, p. 152, pl. 8, fig. 7.
- 1992 Escharoides fulgurans (MANZONI) Pouyet & Moissette, p. 64, pl. 9, fig. 8.
- 1997b Escharoides megalota (REUSS) Pouyet, p. 66, pl. 6, fig. 9, 10.

Material:

Niebla Calcarenite: 21 colonies. examined by SEM: GNI1-042-A, B, C, D.

Measurements:

ZL $628 \pm 44, 576-718 (4, 20)$ ZW $602 \pm 72, 480-741 (4, 20)$ ApL $166 \pm 13, 139-183 (4, 17)$ ApW $156 \pm 10, 136-170 (4, 17)$

Description:

Colony encrusting multiserial, unilaminar. Zooids broad, quadrangular to hexagonal, steeply convex, separated by deep grooves; frontal wall imperforate with one or two rows of large marginal areolae. Aperture round or elliptical, a broad distal lip carries six thick spines (four in ovicellate zooids, with the distal pair usually enlarged), proximal margin raised with a tall, thick, central mucro; above the primary orifice a short, square, median denticle and a pair of inwardly-projecting proximolateral knobs give the aperture a tridentate appearance with two drop-shaped sinuses; primary orifice with a distal, proximally sloping, straight, suboral shelf and a straight incision just above, and parallel to, the free end of the shelf.

Ovicell globular, round to elliptical, recumbent on frontal wall of distal zooid becoming slightly immersed during ontogeny, surface flattened frontally, densely punctured by small pores except for medioproximal area; proximal margin straight; ovicell may be encroached by one avicularium.

Avicularia of varying size (proximo)lateral to aperture, usually paired, one often being smaller than the other, directed distally to distomedially, acute to frontal plane; rostrum triangular to elongated-triangular, gently incurved distally, narrowing slightly distal to complete crossbar without columella.

Discussion:

E. megalota (Reuss, 1848) and *E. fulgurans* (Manzoni, 1869c) were for a long time been treated as separate species on the base of varying size of the autozooids, as well as shape and position of avicularia (e.g. Pouyet, 1976). According to Schmid (1989), who viewed many specimens of species described as either *E. megalota* or *E. fulgurans*, the variability of the number of oral spines as well as the avicularium and zooid size is great and overlapping and she therefore suggested that these two species are conspecific. This finding is supported by my data and corroborated by a comparison of these with illustrations and measurements of more recent publications (Table 4.3). In contrast, orifice and ovicell proportions do not show significant variations between these sites. However, neither for Schmid nor for me was it possible to view the type material of *E. fulgurans*. A formal revision and synonymising of these species thus remains to be accomplished.

Source	Species	Age	Location	Range	Mean
El Hajjaji (1992)	E. megalota	Miocene	Mediterranean	0.55-0.88	0.73
this work	E. megalota	Miocene	E Atlantic	0.58-0.72	0.63
Moissette (1988)	E. fulgurans	Miocene	NE Atlantic	0.64-0.84	0.74
Schmid (1989)	E. megalota	Miocene	Paratethys	0.65-0.79	
Pouyet (1976)	E. fulgurans	Pliocene	Mediterranean	0.7-0.95	

Table 4.3 Range and mean values of zooid length (in mm) of *E. megalota* given in several publications.

Occurrence:

Whereas *E. megalota* is regularly reported from Neogene Mediterranean faunas, the occurrence in the Niebla Calcarenite marks the first record of the species from the Atlantic. Most of the specimens found encrust red algae. However, several colonies occur independent of substrate and therefore indicate settlement on an ephemeral surface.

Distribution:

Miocene: Burdigalian (France, Tunisia), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin and SE Spain), Messinian (Morocco, Algeria).

Pliocene: Spain, Tunisia, Italy. Pleistocene: Italy. *Escharoides* sp. Plate 6, Figure 2-4

cf. 1930 Peristomella coccinea (ABILDGAARD) - Canu & Lecointre, p. 88, pl. 19, fig. 8-10.

Material:

Niebla Calcarenite: 14 colonies. examined by SEM: GNI1-045-F, G; GNI1-067-A.

Measurements:

ZL $541 \pm 42, 456-597 (2, 17)$ ZW $418 \pm 45, 322-493 (2, 17)$ ApL $111 \pm 20, 85-144 (3, 14)$ ApW $149 \pm 36, 118-255 (3, 14)$ OvL $224 \pm 29, 162-253 (2, 13)$ OvW $289 \pm 37, 238-359 (2, 13)$ AL $203 \pm 79, 94-307 (3, 15)$ AW $88 \pm 21, 64-145 (3, 15)$

Description:

Colony encrusting unilaminar, multiserial. Zooids broad, quadrangular to hexagonal, separated by deep grooves; frontal wall steeply convex, imperforate with large marginal areolae. Aperture with straight, distal, suboral shelf; a broad distal lip carries four thick spines (two in ovicellate zooids) whereas the steeply raised, prominent proximal lip forms a single bulge with two prominent denticles on proximolateral sides, directing distomedially, and a thin, lowered, median denticle.

Ovicell globular, round to elliptical, recumbent on and slightly immersed in frontal wall of distal zooid by costules of areolar pores; surface flattened frontally, rugose, with numerous small pores around the periphery; proximal margin straight.

Avicularia of varying size lateral to the aperture, usually paired; rostrum directing laterally to distolaterally, acute to frontal plane, triangular to elongated-triangular in shape; crossbar complete without columella.

Discussion:

Although remarkably similar to *E. coccinea* (Abildgaard, 1806), this species differs slightly in characters of the aperture: there are two proximal extending bulges separated by the notch and mucro in *E. coccinea*, whereas there is only one in this species. This is accompanied by an absence of the two lateral 'sinuses' in *Escharella* sp., and the presence of two lateral and one median denticle in the proximal aperture which are thinner than those of *E. coccinea*. Furthermore, in *Escharoides* sp. the number of oral spines is consistently four in autozooids and only two in ovicellate zooids, while in *E. coccinea* there are four to six in autozooids and four in ovicellate zooids.

The specimens from the 'faluns' in north-west France, referred to as *Peristomella coccinea* (Abildgaard, 1806) by Canu & Lecointre (1930), are likely to be conspecific with the present species. The authors mention the presence of four spines and their figures show a single median bulge in the proximal apertural rim. Therefore, since none of the known fossil or Recent species of *Escharoides* match the characters displayed by the present specimens and those from NW France, these await description as a new species.

Occurrence:

It seems that this species has not been recorded from the Mediterranean basins and is likely be restricted to the Atlantic. However, its morphological proximity to *E. coccinea* makes this species susceptible to be mistaken for the former, especially when specimens are not well preserved

In the Niebla Calcarenite *Escharoides* sp. occurs more frequently than *E. coccinea*, encrusting red algae. As in the other species of *Escharoides*, some colonies occur independent of their substrate and in these the basal zooidal walls are only marginally calcified.

Distribution:

Miocene: Tortonian (?NW France, Guadalquivir Basin - Spain).

Genus HEMICYCLOPORA NORMAN, 1894

Hemicyclopora sp. 1 Plate 6, Figure 9

Material:

Niebla Calcarenite: 1 colony. examined by SEM: GNI1-028-A.

Measurements:

ZL	633-670 (1, 3)
ZW	542-664 (1, 3)
OL	140–146 (1, 2)
OW	137–151 (1, 2)

Description:

Colony encrusting multiserial, unilaminar. Zooids hexagonal, raised towards the orifice with steep distolateral margins, separated by deep grooves; vertical walls very reduced, with numerous small pore chambers; frontal wall convex, finely granular, with two rows of marginal areolae (additional ones proximolateral to orifice). Orifice round, as wide as long, with a concave proximal margin and a pair of short thick condyles extending deeply into zooid; eight evenly spaced bases of oral spines on thick, distolateral, peristomial rim.

Ovicells or avicularia were not observed.

Discussion:

The characteristic orifice and the reduced vertical walls justify a placement in the genus *Hemicyclopora*, of which not many fossil species are described to date. To my knowledge, the species referred to as *Hemicyclopora collarina* Canu & Lecointre, 1930 by Moissette (1988) and El Hajjaji (1992) remain the only records of an already established species of this genus in the Neogene Mediterranean basins. However, in the specimens described and figured in Moissette (1988) the peristome is better developed and he mentions the presence of four spines; El Hajjaji (1992) also reports a well developed peristome and the presence of six spines, whereas another species, *Hemicyclopora* sp. 4, is lacking spines altogether. It therefore seems that the present species has not been reported before. Unfortunately, information on ovicell morphology is lacking in the present material.

Occurrence:

The only colony obtained encrusts a coralline alga.

Hemicyclopora sp. 2

Plate 6, Figure 8, 10, 11

Material:

Niebla Calcarenite: 10 colonies. examined by SEM: GNI1-039-A, B, C.

Measurements:

ZL $638 \pm 58, 545-770 (3, 20)$ ZW $526 \pm 86, 370-739 (3, 20)$ ApL $106 \pm 8, 91-121 (3, 10)$ ApW $162 \pm 26, 133-194 (3, 10)$ OvL 255-331 (1, 2)OvW 338-345 (1, 2)

Description:

Colony encrusting unilaminar, multiserial. Zooids oval to hexagonal, occasionally broadly bifid, separated by fine sutures; frontal wall convex, imperforate, granular with one or two rows of round marginal areolae, accentuated by relatively short, low, intervening costules during later ontogeny; each zooid with numerous distolateral pore chambers in slanting 'vertical' walls. Primary orifice partly hidden by peristome, with slightly concave proximal rim and a pair of short, thick and blunt condyles directing medially or proximomedially. Peristome well developed with an approximately D-shaped aperture, raised proximally, occasionally forming a variably broad, median mucro and a lobe towards the orifice; six evenly distributed distolateral spines (two pairs in ovicellate zooids).

Ovicell globular, recumbent on (and partly immersed in) distal zooid, slightly wider than long, surface imperforate and granular as frontal wall, proximal margin slightly concave. In ovicellate zooids the peristome may be distinctly broader and the lobe more pronounced than in autozooids, and extends onto the frontal surface of the ovicell forming a smooth, vertical, prominent shield on its proximal margin.

No avicularia.

Discussion:

This species poses some problems concerning its generic placement: while the presence of large and accentuated areolar pores, and pore chambers in relatively broad vertical walls may suggest that these specimens belong to *Escharella* Gray, 1848, the absence of a lyrula and presence of thick condyles argues for a placement in *Hemicyclopora*. The possibility of a loss of the lyrula due to breakage can not be excluded; however, some of the primary orifices are quite well preserved and a fractured surface on the proximal orifice margin was not observed. Since no species displaying these characters was found in the literature that could prove the presence of a lyrula, I believe that these features accord better with the genus definition of *Hemicyclopora*.

Occurrence:

The specimens were solely found on red algal substrate.

Genus HIPPOPLEURIFERA CANU & BASSLER, 1927

Hippopleurifera semicristata (REUSS, 1848) Plate 6, Figure 12-14

- v 1848 *Cellepora semicristata* REUSS, p. 82, pl. 10, fig. 3.
- v 1874 Lepralia megalota (REUSS) Reuss, p. 154, pl. 5, fig. 3.
- v 1874 Lepralia semicristata (REUSS) Reuss, p. 151, pl. 6, fig. 6.
- v 1966 *Hippopleurifera sedgwicki* (MILNE EDWARDS) Hastings, p. 75, pl. 1, fig. 4, 5.

- 1974 Hippopleurifera semicristata (REUSS) David & Pouyet, p. 153, pl. 11, fig. 7.
 - 1988 Hippopleurifera(?) sp. Moissette, p. 121, pl. 19, fig. 8.
 - 1989 Hippopleurifera semicristata (REUSS) Schmid, p. 32, pl. 8, fig. 7.
 - cf. 1992 Hippopleurifera sedgwicki (MILNE EDWARDS) El Hajjaji, p. 148, pl. 8, fig. 3.

Material:

v

Niebla Calcarenite: 18 colonies.

examined by SEM: GNI1-043-A, C, D, E.

BNHM B.0436, B.1717, D.50297-301 (*H. sedgwicki*, Pliocene, Coralline Crag; on SEM-photocards)

other: VNHM 1867.40.167 (lectotype of *H. semicristata* [Reuss, 1848], Badenian, Eisenstadt; chosen by David & Pouyet, 1974); 1859.45.655 (Badenian, Bischofswart; figured as *Lepralia megalota* [Reuss, 1848] in Reuss, 1874: pl. 5, fig. 3); 1859.50.782 (*L. semicristata*, Badenian, Eisenstadt; Reuss, 1874: pl. 6, fig. 6; David & Pouyet, 1974: pl. 11, fig. 7); without number (Badenian, Eisenstadt; figured as *H. sedgwicki* [Milne Edwards, 1836] by Hastings, 1966: pl. 1, fig. 4, 5).

Measurements:

Description:

Colony encrusting unilaminar and erect bilaminar, multiserial. Zooids broad, hexagonal to quadrangular, separated by deep grooves; frontal wall convex, imperforate with two (to proximally three) rows of large marginal areolar pores accentuated by prominent costules. Aperture large, rounded, slightly longer than wide, with a very slight demarcation of a wider anter and narrower poster, condyles extremely inconspicuous or absent; proximal aperture with a rounded median mucro, distolateral margin with six spines (four in ovicellate zooids).

Ovicell globular, slightly wider than long, partly embedded in distal zooid; surface slightly flattened frontally with ca. eight thick, prominent, radial ribs delimiting low lying areas perforated by minute pores, proximal margin relatively straight, arching over distalmost part of aperture.

Adventitious avicularium commonly single, sometimes paired or absent, of varying size, situated directly proximolateral to aperture, abutting or even merging with apertural rim; rostrum semielliptical (complete rostrum of larger avicularia not preserved), pointing in distal directions; cystid with marginal pores.

Discussion:

The present specimens occur as both encrusting and bilaminar colonies, whereas the latter growth form has not been reported before in this species. However, it is known from other species of *Hippopleurifera* (e.g. *H. biauriculata* [Reuss, 1848]) that both growth types co-occur. Besides its similarity with the type-specimens of *H. semicristata*, the present material is identical with *Hippopleurifera*(?) sp. in Moissette (1988), based on the figure and his note on the presence of the characteristic ovicells. Almost the same applies to the material described as *H. sedgwicki* (Milne Edwards, 1836) by El Hajjaji (1992), which also shows an ovicell marked by radial ribs. However, the figured specimen is not well preserved and the zooids differ slightly in that the costules separating the marginal areolar pores are more pronounced and cover a greater area of the frontal wall.

While ascertaining the type-species of the genus *Hippopleurifera*, *H. biauriculata* (Reuss, 1848), Hastings (1966) found that a second specimen, which was kept in the same sample tube

together with the type-species (VNHM 1859.50.748), belongs to a different species (and is now stored without number at the VNHM). She identified it as *H. sedgwicki*, which was described from the Pliocene Coralline Crag. However, neither does this specimen nor any other species of *Hippopleurifera* from the Mediterranean Neogene matches with the species from the NE Atlantic, as judged from SEM photos of material from the Crag at the BNHM. This conclusion was also reached by Lagaaij (1952), who mentioned that the Miocene Mediterranean records of *H. sedgwicki* should be taken with great caution. Although ovicells are not preserved in the specimen Hastings (1966: pl. 1, fig. 4, 5) figured, the zooid morphology is consistent with the type-material of *H. semicristata*.

A different problem concerning the genus definition of *Hippopleurifera* arises from the typespecies of *H. biauriculata*. In this species the ovicell has a "secondary cover with two large fossae, or with irregular smaller pits and protuberances" (Hastings, 1966: p. 74; see also *H. sedgwicki*? in Moissette, 1988: p. 118, pl. 19, fig. 10, 12), oral spines are wanting, and the frontal wall is entirely perforated. Since the only more recent genus definition of *Hippopleurifera* I could find does not mention ovicell morphologies of its species (Zabala & Maluquer, 1988: p. 112), the distinctly different ovicells of *H. semicristata* may justify its separation from *Hippopleurifera* (see also Discussion in *Hippopleurifera* sp.). However, the mere two rows of marginal areolar pores, as well as the presence of oral spines, are consistent with the genus definition. A thorough revision of the genus *Hippopleurifera*, and the late Neogene NE Atlantic and Mediterranean species complex attributed to this genus, is obviously needed.

Occurrence:

Although not very common in the Niebla Calcarenite, this is the first record of *H. semicristata* from the Atlantic.

Distribution:

Miocene: Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin - Spain), Messinian (?Morocco, Algeria).

"Grade" LEPRALIOMORPHA GORDON, 1989 Superfamily SMITTINOIDEA LEVINSEN, 1909 Family SMITTINIDAE LEVINSEN, 1909 Genus SMITTINA NORMAN, 1903

Smittina messiniensis EL HAJJAJI, 1992 Plate 7, Figure 1, 2

- 1992 Smittina messiniensis EL HAJJAJI, p. 176, pl. 10, fig. 3.
- 1999 Smittina messiniensis EL HAJJAJI Sefian et al., p. 238.

Material:

Niebla Calcarenite: 24 colonies.

examined by SEM: GNI1-004-B; GNI1-018-A, B, C, D, E.

other: FSL 491965 (holotype, Messinian, Morocco; El Hajjaji, 1992: pl. 10, fig. 3); 491966 (Messinian, Morocco); 490031 (*Smittina* sp., Messinian, Algeria; Moissette, 1988: pl. 26, fig. 9, 10).

Measurements:

- ZL $388 \pm 41, 316-451 (4, 19)$ ZW $239 \pm 39, 177-349 (4, 19)$ ApL $84 \pm 10, 65-99 (4, 16)$
- ApW 92 ± 9, 76–114 (4, 16)

OvL 186 ± 12, 165–204 (3, 12) OvW 203 ± 9, 188–217 (3, 12)

Description:

Colony encrusting unilaminar, multiserial. Zooids elongate hexagonal or polygonal, separated by deep grooves; frontal wall convex, evenly perforated by relatively large pores separated by thick nodular ridges. Primary orifice about as wide as long; proximal margin with short, quadrate or anvil-shaped lyrula, occupying about one-third to half of proximal width, and two thick pointed condyles directing (proximo)medially. Aperture slightly wider than long with a thick tubular peristome with sometimes flared thin ends developed around orifice (particularly prominent in ovicellate zooids where the lateral walls extend onto the frontal surface of ovicell), extending onto the zooids' frontal wall and forming a broad and deep fissure proximally at which end an avicularium is placed; no spines on autozooids were observed (although there are two spine bases on the distal orifice margin in some ovicellate zooids, indicating the presence of spines in early ontogeny and/or astogeny).

Ovicell globular, flattened frontally, slightly wider than long, recumbent on frontal wall of distal zooid and becoming only slightly embedded by secondary calcification; frontal surface evenly perforated by several large round pores, a thin distolateral band imperforate, proximal margin straight.

A small, single, median, suboral avicularium present on every zooid, abutting and merging with proximal walls of peristome; rostrum pointing proximally, semielliptical, slightly elevated above but normal to frontal plane.

Discussion:

Besides zooid length (the Morroccan material has longer autozooids: 0.38-0.56 mm, mean 0.45 mm), all characters are in concordance with those of the holotype of *S. messiniensis* described by El Hajjaji (1992). However, I do not agree with him synonymising the species with Moissette's (1988, p. 163, pl. 26, fig. 9, 10) material, which is not only distinctly larger (0.56-0.68 mm, mean 0.61 mm) but also, and more importantly, differ in ovicell morphology in that these have fewer but larger pores, are frontally not as flattened, and are encircled by a thick rim of calcification. Furthermore, the adventitious avicularia are more elongated than in the present or El Hajjaji's material.

Occurrence:

After the presumed presence in samples from NW Morocco (Sefian et al., 1999), this is the second record of *S. messiniensis* from the Late Miocene Atlantic, which also extends its stratigraphic range into the Tortonian. It mainly encrusts red algae and other bryozoans (e.g. *M. patellaria* Moll, 1803) in the Niebla Calcarenite.

Distribution:

Miocene: Tortonian (Guadalquivir Basin – Spain), Messinian (Atlantic and Mediterranean Morocco).

Genus SMITTOIDEA OSBURN, 1952

Smittoidea sp.

Plate 7, Figure 3, 7

Material:

Niebla Calcarenite: 6 specimens. examined by SEM: GNI1-041-C, D, E. other: BNHM 1899.5.1 (*Smittoidea reticulata* [J. Macgillivray, 1842], Recent, Cornwall), 1911.10.1.1442 (*S. reticulata*, Recent, Hardanger Fjord).

Measurements:

ZL $506 \pm 49, 449 - 582(3, 13)$ ZW $323 \pm 40, 229 - 403 (3, 13)$ ApL $158 \pm 12, 140 - 174(3, 8)$ ApW $133 \pm 9, 119 - 148(3, 8)$ OvL 248 OvW 293 AL 142 - 164(1, 3)AW 64-81(1,3)

Description:

Colony encrusting unilaminar, multiserial. Zooids elongate rectangular to hexagonal, separated by indistinct sutures on thin ridges; frontal wall convex, imperforate, nodular, with one row of large marginal areolae accentuated by intervening ridges. Primary orifice wider than long; lyrula short, narrow, occupying about one-third of total width, but (as condyles) not well preserved. Aperture longer than wide, peristome a thin wall, well developed around orifice, tubular, forming a more or less pronounced median lobe proximally; no spines.

Ovicell globular, slightly flattened frontally, wider than long, recumbent on frontal wall of distal zooid; central frontal area irregularly perforated by several pores of different size, broad distolateral walls imperforate, proximal rim straight; distal margin of peristome encroaching proximal edge of ovicell.

A single median suboral avicularium present on some zooids, abutting proximal lobe of peristome but not merging with it; rostrum pointing proximally, elongated triangular, normal to frontal plane.

Discussion:

To unravel the intricate history of species displaying a more or less similar morphology, and most often named *Smittoidea reticulata* (J. Macgillivray, 1842) in numerous publications on Neogene Mediterranean faunas, was not feasible during this project. As with several species treated of here, *S. reticulata* has served as a filing basket for several morphospecies (e.g. compare the one in David et al. [1970] with the other records mentioned below), without anyone pausing to critically compare it with Recent specimens. Today's *S. reticulata* is inferred to occur from the Barents Sea to the western Mediterranean (Hayward & Ryland, 1999), and differs from all the fossil specimens described and figured in that it has two or three spines (which may, however, be obscured by secondary calcification during later ontogeny), the peristome does not form a proximal lobe towards the avicularium, and the ovicell is, except for a narrow basal band, completely perforated by numerous pores. Neither of the described and figured material (e.g. David & Pouyet, 1974; Moissette, 1988) is characterised by these features but is rather consistent with the species description given here for *Smittoidea* sp..

The relationship between all of the above mentioned material and potential type-species, such as *Cellepora trigonostoma* Reuss, 1848, which was synonymised with *S. reticulata* by David & Pouyet (1974), needs to be elaborated using SEM, as is the status of *Schismoporella schizogaster* (Reuss, 1848), as described and figured in Moissette (1988) and El Hajjaji (1992).

Occurrence:

Owing to the above mentioned difficulties, a chronostratigraphic and biogeographic overview is not given here. Smittoidea sp. is only rarely encountered in the Niebla Calcarenite, encrusting red algae and other bryozoans.

Family BITECTIPORIDAE MACGILLIVRAY, 1895 Genus *HIPPOPORINA* NEVIANI, 1895

Hippoporina sp.

Plate 7, Figure 4-6, 8

Material:

Niebla Calcarenite: 5 colonies. examined by SEM: GNI1-029-A, B, C, D.

Measurements:

Description:

Colony encrusting unilaminar and ?plurilaminar, multiserial. Zooids rhomboidal, hexagonal or round, broad, separated by distinct sutures. Frontal wall slightly convex, evenly punctured by numerous round pores with funnel-shaped openings separated by nodular ridges, and few larger marginal pores mostly confined to zooid corners. Primary orifice orbicular with two short, thick, blunt condyles placed somewhat proximal to mid-distance of orifice and directing approximately medially, condyles are connected to each other by a slightly immersed, thin shelf along proximal orifice margin, narrowing centrally; peristome in most autozooids a smooth rim around orifice, raising and steepening distally; no spines.

Ovicell semicircular, almost completely immersed in the distal zooid; frontal surface flat and punctured by numerous pores (marginal pores being the largest), level with the peristome and sometimes with the distal zooid's frontal wall, encircled by a variably developed, smooth, vertical wall and ridge. Peristome in ovicellate zooids better developed, forming a raised, lateral rim which develops into a short, proximally extending and opening flute that rests on the frontal wall.

Avicularia were not observed.

Discussion:

I have not come across this or a related species during the literature survey. The orifice characters (prominent condyles, concave proximal margin), the absence of oral spines, and the ovicell morphology justify a placement in the genus *Hippoporina*. The difference to the Recent *H. pertusa* (Esper, 1796) lies in the better developed peristome in ovicellate zooids, in the more concave proximal margin, in a more distal location of slightly thicker condyles, and in a different ovicell shape (not as rounded as in *H. pertusa*).

Occurrence:

This species is rare in the Niebla Calcarenite, encrusting red algae and other bryozoans.

Genus SCHIZOMAVELLA CANU & BASSLER, 1917

Schizomavella sp. Plate 7, Figure 9-11

Material:

Niebla Calcarenite: 5 colonies. examined by SEM: GNI1-051-A, B; GNI1-063-B.

Measurements:

ZL $437 \pm 33, 402-492$ (3, 8) ZW $302 \pm 26, 266-343$ (3, 8) OL $84 \pm 4, 80-91$ (2, 6) OW $95 \pm 7, 87-106$ (2, 6) OvL 189-216 (2, 4) OvW 187-217 (2, 4)

Description:

Colony encrusting multilaminar, multiserial. Zooids broad but shape unknown since marginal and basal walls are not preserved. Frontal wall convex, ?smooth or ?nodular, scattered with relatively large but few round pores, suboral umbo thick, formed by avicularian cystid. Primary orifice little wider than long, anter transversely elliptical, widest at about mid-length, with a thin lining of distinct calcification broadening in proximal part of lateral orifice margins, forming the sinus, a low peristome and (presumably) the condyles; proximal margins straight, with a short Ushaped sinus occupying about one-fourth of orifice width and two broad, square, conspicuous condyles paralleling the frontal margin and slightly extending into the sinus; two distal spines.

Ovicell globular, as long as wide, recumbent on frontal wall of distal zooid; surface smooth, imperforate and flattened frontally, with a ?concave proximal margin.

Adventitious avicularia single, suboral, small, on a prominent, ?rugose and slightly swollen cystid forming a suboral umbo with two distinct distolateral pores; rostrum semielliptical, inclined by about 45-80° to frontal plane, directed proximally; crossbar thin, complete, without columella.

Discussion:

This species was exclusively encountered in a multilaminar growth form, in which zooids were chaotically budded and their basal walls are not preserved (if these were formed at all). Since zooids are apt to changes in morphology to a certain degree under this circumstance, the species description may look slightly different for unilaminar colonies.

While no similar species was encountered, also the systematic placement of this species must remain equivocal. Although identical to several species of *Schizomavella* in characters of the orifice, frontal wall, oral spines, suboral avicularium and umbo (compare with *S. sarniensis* Hayward & Thorpe, 1995, or *S. cuspidata* [Hincks, 1880], as figured in Hayward & Ryland, 1999), the present specimens have an imperforate ovicell. This is in clear conflict with the genus definition of *Schizomavella*, in which the ovicells have "conspicuous frontal perforations", while the family definition rather vaguely states that the ectooecium is "typically with pores or larger membranous fenestrae" (Hayward & Ryland, 1999). However, since there is no other genus close to *Schizomavella* that has imperforate ovicells, the present material is tentatively placed in this genus for now.

Occurrence:

Rarely encountered in the Niebla Calcarenite, the multilaminar accumulations are formed in concert with *Schizoporella dunkeri* (Reuss, 1848) (see Pl. 7, Fig. 9, 11). The relatively loose compound is remarkable in that in most or all of these zooids the basal wall is lacking and that the zooids do not seem to have settled on a firm substrate. I can merely speculate that the accumulations were formed by alternating growth of single layers of bryozoans covering thin, non-calcifying biofilms or microbial mats, and vice versa. After decay of the organic intervening laminae the zooids of the vertically not connected bryozoan layers (consisting of at least two species) became piled upon each other. Alternating proliferation between bryozoans and microbial mats do occur in several environmental settings (e.g. Scholz, 2000); however, a convincing Recent analogue of a formation of such an accumulation as found in the Niebla Calcarenite is not known to me.

Family WATERSIPORIDAE VIGNEAUX, 1949 Genus WATERSIPORA NEVIANI, 1895

Watersipora sp.

Plate 7, Figure 12, 15

1988 Dakaria aff. goniostoma (REUSS) - Moissette, p. 129, pl. 21, fig. 3, 6.

Material:

Niebla Calcarenite: 12 colonies.

examined by SEM: GNI1-049-A, B, C, D, E.

other: VNHM 1867.40.77 (lectotype of *Cellepora goniostoma* Reuss, 1848, Badenian, Steinabrunn; chosen by David & Pouyet, 1974).

Measurements:

ZL 793 \pm 77, 653–933 (4, 20) ZW 531 \pm 98, 414–815 (4, 20) OL 184 \pm 12, 165–204 (5, 13) OW 195 \pm 19, 167–228 (5, 13)

Description:

Colony encrusting unilaminar, multiserial. Autozooids rectangular or irregularly polygonal, usually with a convex distal border, separated by indistinct sutures on elevated ridges. Frontal wall slightly convex, evenly perforated by numerous round pores bounded by thickened nodular ridges, except for a small area immediately proximal to orifice; two larger pores may develop proximolateral to the orifice in the distolateral zooid corners. Primary orifice occupying the distal end of zooid, slightly wider than long, with a transversely elliptical distal part and a broadly U-shaped sinus occupying just less than half proximal width; a pair of narrow but elongated condyles along proximolateral edge; peristome a thick tubular rim; no spines.

Ovicells small, immersed, traversing the distal border of mother zooid as a narrow ribbon formed by splitting of the vertical wall, frontal surface flat, consisting of three (rarely two) distinctive fenestrae demarcated by thick ridges. Orifice in ovicellate zooids dimorphic, broader than in autozooids.

Avicularia were not observed.

Discussion:

In contrast to Recent species of the genus *Watersipora*, all or most fossil Mediterranean species have characteristic ovicells, whereas if these are absent, as in Recent species, they are difficult to distinguish. Also, the consistent presence of ovicells in fossil material makes it necessary to expand the genus definition of *Watersipora* since the lack of these is required for a species to be classified with this genus.

There are at least three Neogene Mediterranean species or species complexes that are fairly similar to each other but can be distinguished by their ovicells. The Middle Miocene *Watersipora goniostoma* (Reuss, 1848) was specified by David & Pouyet (1974) and is characterised by globular ovicells that are recumbent on, and partly embedded in, the frontal wall of the distal zooid, and are densely perforated by relatively large pores. The Late Miocene *W. crassilabia* (El Hajjaji, 1987) has ovicells that are less prominent than those of *W. goniostoma* and which are integrated in the thickened peristome, whereas the surface is described as being punctured by large pores (although fig. 7 on pl. 12 in El Hajjaji [1992] does not validate this statement). The species identified as *W.* aff. *goniostoma* by Moissette (1988) was synonymised with *W. crassilabia* by El Hajjaji (1992). This decision I reject here since the Late Miocene material from Morocco is, as my specimens, characterised by small immersed, i.e. endozooidal, ovicells which are placed between the distal end of the mother-zooid and proximal margin of the distal zooid, and are marked by three fenestrae and partitioning walls (see Moissette, 1988: pl. 21, fig. 6). Furthermore, dimorphic orifices are not as prominent in El Hajjaji's material. Although the sinus is broader in the specimen

figured by Moissette (1988), this was observed to be subject to some variation also in the present material and therefore considered as intraspecific variability.

Thus, in contrast to Recent species, a variety of ovicell morphotypes are present in fossil *Watersipora* spp. Although too few species and specimens have been dealt with here to draw any firm conclusions concerning evolutionary trends, one may argue that there was a reduction of ovicells through time, for the Middle Miocene *W. goniostoma* is characterised by the presence of non-immersed ovicells, whereas the Late Miocene *W. crassilabia* and the present material has partly immersed or endozooidal ovicells, respectively. Since autozooids in these fossil species do not show any marked differences to Recent representatives of the genus, the eventual presence of ovicells should therefore be included in the genus definition.

Remarks on other records: the specimens identified as *Dakaria goniostoma* (Reuss, 1848) by Pouyet & David (1984, p. 99, pl. 6, fig. 3, 4) and as *W*. aff. *goniostoma* by El Hajjaji (1992, p. 199, pl. 10, fig. 14) are both different from the type-material in aperture shape and frontal wall structure. *W. goniostoma* therefore seems to be restricted to the Middle Miocene. Pouyet & Moissette (1992, p. 55, pl. 7, fig. 12) do not mention or figure ovicells of their *W. goniostoma* and it is therefore impossible to come to a conclusion about its exact status.

Occurrence:

Since no other reliable record of *Watersipora* sp. exists besides that of Moissette (1988), this species appears to be restricted to the Late Miocene, and presumably represents a new species. It has also not been reported from the Atlantic region before.

The colonies encrust red algae, bryozoans and also ephemeral substrates, or may have grown independent of these, as indicated by the presence of free colony fragments having an irregular basal wall topography.

Distribution:

v

v

Miocene: Tortonian (Guadalquivir Basin - Spain), Messinian (Algeria).

Superfamily SCHIZOPORELLOIDEA JULLIEN, 1883 Family SCHIZOPORELLIDAE JULLIEN, 1883 Genus SCHIZOPORELLA HINCKS, 1877

Schizoporella dunkeri (REUSS, 1848) Plate 7, Figure 9, 11, 13, 14

- v 1848 *Cellepora dunkeri* REUSS, p. 90, pl. 10, fig. 27.
 - 1874 Lepralia ansata JOHNSTON Reuss, p. 158, pl. 6, fig. 12.
 - 1886 Schizoporella unicornis form longirostris HINCKS, p. 266, pl. 10, fig. 2.
 - 1972 Schizoporella longirostris (HINCKS) David et al., p. 43, pl. 8, fig. 3, 4.
 - 1974 Schizoporella dunkeri (REUSS) David & Pouyet, p. 159, pl. 11, fig. 6.
- non 1988 Schizoporella dunkeri (REUSS) Zabala & Maluquer, p. 133, fig. 307; pl. 18, fig. B.
 1988 Schizoporella longirostris (HINCKS) Zabala & Maluquer, p. 133, fig. 312; pl. 18, fig. C, D.
- v non 1989 Schizoporella dunkeri (REUSS) Bishop & Hayward, p. 18, fig. 67-69.
- pars 1989 ?Schizoporella longirostris (HINCKS) Schmid, p. 39, pl. 11, fig. 5-8.
 - 1992 Schizoporella longirostris (HINCKS) El Hajjaji, p. 195, pl. 12, fig. 5.
 - non1992 Schizoporella dunkeri (REUSS) Pouyet & Moissette, p. 53, pl. 7, fig. 8.
 - 1992 Schizoporella longirostris (HINCKS) Pouyet & Moissette, p. 54, pl. 7, fig. 11.
 - 1995 Schizoporella dunkeri (REUSS) Hayward & Ryland, p. 39, pl. 2, 3.
 - 1996 Schizoporella dunkeri (REUSS) Haddadi-Hamdane, p. 81, pl. 6, fig. 9.
 - 2002 Schizoporella dunkeri (REUSS) Hayward & McKinney, p. 69, fig. 31A-E.

Material:

Niebla Calcarenite: 53 colonies.

examined by SEM: GNI1-050-A, B, C; GNI1-051-A, C.

BNHM B1675 (*Lepralia unicornis* [Johnston in Wood, 1844], Pliocene, Coralline Crag; Busk, 1859: pl. 5, fig.4; on PC23243, 23244); PCpdt1455 (Recent, Adriatic Sea); PC27261-27265, PC38663-38667, PC39030-39033 (all Recent, Malta).

other: VNHM 1846.37.996 (lectotype, Badenian, Kroisbach; chosen by David & Pouyet, 1974); 1878.11.15 (Badenian, Baden; David & Pouyet, 1974: pl. 11, fig. 6); 1878.11.32 (as *Lepralia ansata* Johnston, 1847, Badenian, Baden; Reuss, 1874: pl. 6, fig. 12). BNHM 47.9.16.63 (syntype of *S. unicornis* [Johnston in Wood, 1844]; Recent, British Isles).

Measurements:

- ZL 556 ± 53, 472–644 (2, 20)
- ZW 435 ± 57, 335–576 (2, 20)
- OL $123 \pm 7, 111 134 (3, 15)$
- OW 120 ± 10, 103–136 (3, 15)
- AL 237 ± 33, 172–277 (2, 11)
- AW $123 \pm 19,97-157(2,11)$
- iAL 368–516 (2, 3)
- iAW 157–212 (2, 3)

Description:

Colony encrusting unilaminar to multilaminar, multiserial; growth pattern in unilaminar colonies regular, becoming chaotically with undetermined growth polarity in multilaminar colonies. Autozooids in unilaminar colonies usually perfectly rectangular, rarely irregular polygonal, separated by indistinct sutures on sometimes deeply immersed thin ridges. Frontal wall strongly convex (mainly due to steep lateral walls), evenly perforated by numerous small pores bounded by nodular ridges; a low, median, suboral umbo present in most zooids. Primary orifice as wide as long, may be situated in one distolateral corner of zooid with the sinus then pointing towards the opposed proximolateral corner; proximal border with a very narrow, slit-like sinus forming a drop-like proximal extremity, bounded by straight proximolateral margins; condyles broad, only slightly immersed, paralleling proximolateral orifice margin but being slightly shorter than the former. Peristome developed as a low, thickened, distolateral rim; no spines.

Ovicells were not observed.

Interzooidal avicularia relatively large, usually single, sometimes paired (the second one may then be smaller), situated proximolateral to orifice; cystid small to extremely swollen, perforated by several pores; rostrum directing distolaterally (some distally), acute to frontal plane, widest at crossbar, narrowing immediately distal to it, forming a long, slender and parallel-sided, blunt distal end, gently incurved occasionally; crossbar thick, complete, triangular, without columella, uncalcified area proximal of crossbar semicircular or triangular. Extremely large frontally budded interzooidal (here termed iAL and iAW in the Measurements section) avicularia occasionally occur on unilaminar colonial surfaces and become more numerous in multilaminar colonies; morphology same as smaller interzooidal avicularia but rostrum fused to the convex frontal wall of swollen cystid.

Discussion:

Although ovicells are not observed, the zooid, orifice, and avicularium morphology is characteristic and identical with extant representatives of *S. dunkeri*. Partly due to its variability in colony, zooid and avicularian morphology, this species has every now and then been referred to *S. longirostris* Hincks, 1886. Finally, Hayward & Ryland (1995) established the synonymy of the species Reuss (1848) described from the Vienna Basin and the Recent *S. longirostris*, the type-specimen of which is from the Adriatic Sea.

Whereas most figured specimens of the synonymy list given above are identical, or at least comparable, to the present and type-material, *S. dunkeri* of Pouyet & Moissette (1992) is clearly

not this species but related to *S. magnifica* Hincks, 1886 and allies (see Discussion there). Likewise, the species from the Dutch Pliocene described by Bishop & Hayward (1989) as *S. dunkeri* (previously identified as *S. unicornis* [Johnston in Wood, 1844] by Lagaaij, 1952; see below) is definitely not this species, either. It has a pair of avicularia (sometimes a third on lateral frontal surface) of different shape, a more pronounced suboral umbo, a broadly V-shaped orifice, and a different zooid outline. Records of fossil *S. dunkeri* outside the Mediterranean region are therefore wanting, since this was the only citation from Atlantic faunas I came across.

Schmid (1989) described two species under the name *S. longirostris*: while fig. 5 on pl. 11 shows *S. dunkeri*, fig. 6-8 are clearly a different species. The latter has fewer and larger frontal wall pores, a deep U-shaped sinus even in extremely well preserved orifices (parts of an operculum are still in place), the suboral umbo is lacking even in zooids covering a convex substrate (in present material it is best developed under this circumstance), and the avicularia do not form the long, slender, distal rostrum.

Further remarks: *S. unicornis* was described from the British Coralline Crag and was most likely rightly identified by Lagaaij (1952: p. 65, pl. 5, fig. 7), judging from observations of SEM photos of another specimen of *S. unicornis* from the Crag figured by Busk (1859: pl. 5, fig. 4). However, this species is different from the Recent specimens referred to as *S. unicornis* in the latest publications by Hayward & Ryland (1999: p. 67, fig. 30A-E) and Hayward & McKinney (2002: p. 220, fig. 90B, 91) in that the fossil species has a deeper and narrower sinus, and that the avicularian crossbar has a columella, which is absent in the Recent material. It will therefore be necessary to newly describe the Recent species previously referred to as *S. unicornis*.

Occurrence:

Although ubiquitous in Neogene faunas from the Mediterranean basins, this species is, to my knowledge, recorded here for the first time as a fossil from the Atlantic region.

In the Niebla Calcarenite *S. dunkeri* is quite common and most often found as unilaminar colonies encrusting coralline algae. However, it does also occur as frontally budded, nodular, 'multilaminar' masses, and sometimes forming these in concert with *?Schizomavella* sp. The zooids are then budded in a chaotic way and sometimes seemingly lack a basal wall, displaying a random growth polarity, and large interzooidal avicularia become common.

Distribution:

Miocene: Burdigalian (Rhodanian Basin), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin – Spain, Morocco), Messinian (Morocco, Algeria).

Pliocene: Algeria, Italy.

Recent: Isles of Scilly to Mediterranean Sea.



Fig. 4.1 Orifice shape of *Schizoporella dunkeri* (left), *S.* aff. *magnifica* (middle) and *Schizoporella* sp. (right) from the Niebla Calcarenite. Scale bar: 50 μm.

Schizoporella aff. *magnifica* HINCKS, 1886 Plate 8, Figure 1-3

aff. 1886 *Schizoporella magnifica* HINCKS, p. 268, pl. 10, fig. 1. cf. 1988 *Schizoporella lagaaiji* BUGE – Moissette, p. 125, pl. 20, fig. 8, 9.

Material:

Niebla Calcarenite: 10 colonies. examined by SEM: GNI1-053-A, B; GNI1-056-A.

Measurements:

 $418 \pm 32, 346 - 463 (3, 20)$ ZL ZW $353 \pm 59, 277 - 485 (3, 20)$ OL $94 \pm 6, 86 - 106(3, 17)$ OW $86 \pm 7,72 - 101(3,17)$ OvL $224 \pm 15, 210 - 246(1, 5)$ OvW $226 \pm 5, 221 - 232(1, 5)$ AL $115 \pm 11, 91 - 134(3, 13)$ AW $61 \pm 7, 48 - 72(3, 13)$

Description:

Colony encrusting unilaminar, multiserial; rarely multilaminar. Autozooids broad, hexagonal to irregularly polygonal, separated by distinct grooves. Frontal wall convex, densely perforated by numerous small pores bounded by thickened nodular ridges; a low median suboral umbo present in most zooids. Primary orifice longer than wide, with short and slightly upturned proximal margins, sinus comprising less than half proximal width, forming a narrow and deep U-shaped slit proximally, condyles conspicuous, short but thick, rounded and upturned; no peristome; four to two oral spines present only in earliest zooids budded from ancestrula.

Ovicells globular, as long as wide, recumbent on frontal wall of distal zooid; marginal area of frontal surface with similar morphology and perforation as frontal zooid wall, apical area imperforate and often developing a median umbo.

Adventitious avicularia paired, rarely single, situated lateral to orifice and abutting its margin, with the crossbar usually distal to the sinus; cystid slightly swollen; rostrum elongated triangular, tapering to a thin tip, acute to frontal plane, directing distally or distolaterally; crossbar complete without columella. One zooid was observed to bud an additional avicularium frontally, proximolateral of orifice, same in shape but slightly larger than the distal ones, pointing laterally.

Ancestrula oval ($320x239 \mu m$), opesia wider than long, with ?straight proximal margin, surrounded by seven thick spines (no spines proximally of proximal opesia margin).

Discussion:

This species is closely related to the Recent *S. magnifica* but differs slightly in characters of the orifice and ovicell. In the present specimens the proximal margin and condyles are slightly upturned (Fig. 4.1), the sinus is narrower, and the orifice is as long as wide, whereas the ovicells have an equal length and width, and a central mucro. In the Recent species the proximal orifice margin is not, or only minimally, upturned, while the condyles are clearly inclined towards the sinus and are also narrower (as is the sinus), while the orifice is distinctly longer than wide (Ryland, 1968: fig. 3D; Hayward & Ryland, 1999: fig. 90A; Hayward & McKinney, 2002: fig. 31F-J). Finally, the ovicells in Recent *S. magnifica* are markedly longer than wide and have a longitudinal ridge or umbo. Although identical in all other aspects (inlcuding ancestrula), and while acknowledging the presence of significant intraspecific and intracolonial variation, I consider the above mentioned disparities in character states as sufficient for treating the fossil specimens as a different species.

There also exist a close proximity to the Late Miocene *S. lagaaiji* Buge, 1966 from Morocco. However, since an SEM image of the orifice of this species does not exist to date, and the original description and photos do not precisely indicate the shape of the orifice, any conclusion on its

relationship would be insubstantial. Yet, El Hajjaji (1992: pl. 12, fig. 4) mentions the presence of a triangular sinus in the species he identified as *S. lagaiji* (while the photo is not good enough to comment on it), and Pouyet & Moissette (1992: pl. 7, fig. 8) figure such a V-shaped sinus, together with short but broad condyles. Also, their material is well enough preserved to exclude the possibility of damage of the proximal orifice rim, which may give it a different appearance. The specimen figured as *S. lagaaiji* by Moissette (1988), on the other hand, has a narrower sinus and is therefore vaguely considered here as conspecific with the present material.

Summing up, there exist at least three closely related morphotoypes in the Neogene to Recent Mediterranean basins, having in common the pair of avicularia situated distal to the sinus and abutting the orifice margin: the extant *S. magnifica*, and two fossil species of which one has a broadly triangular sinus and the other, represented by the Niebla material, a narrow one. Either of the latter species could be identical with *S. lagaaiji*, which needs to be redefined. Other records that would have to be considered during this investigation are the species identified as *S. lagaaiji* by Pouyet & David (1984) and *S. tetragona* (Reuss, 1848) by David et al. (1972).

Occurrence:

This species was rarely encountered in the Niebla Calcarenite, encrusting red algae.

Schizoporella sp.

Plate 8, Figure 4, 8, 12

Material:

Niebla Calcarenite: 65 colonies.

examined by SEM: GNI1-008-G, H; GNI1-050-D; GNI1-052-A, B, C, D.

other: VNHM 1867.40.35 (lectotype of *Schizoporella tetragona* [Reuss, 1848], Badenian, Bischofswart; chosen by David & Pouyet, 1974); 1859.45.653 (*S. tetragona*, Badenian, Bischofswart; Ryland, 1968: fig. 5).

Measurements:

Description:

Colony encrusting unilaminar to plurilaminar, multiserial, with zooids in basal layer usually regularly arranged and in succeeding layers in a rather irregular pattern. Autozooids most commonly elongate rectangular (perfectly so on planar substrates), only rarely irregular polygonal or rounded, separated by an indistinct suture on a thin ridge. Frontal wall convex, except for a small area proximal and lateral of orifice evenly perforated by numerous small pores bounded by thickened nodular ridges, and with a marginal row of larger, slit-like or round, areolar pores; a thick, conspicuous (may reach half a zooid's length or more) suboral umbo accentuated by the extension of frontal wall ridges occasionally present. Primary orifice about as wide as long, round, may be situated in one distolateral corner of zooid with the sinus then pointing towards the opposed proximolateral corner; proximal margin with a shallow and broadly U-shaped sinus, occupying more or less half proximal width of orifice, accentuated by two small rounded condyles. Peristome developed as a low thickened rim; no spines.

Ovicells were not observed.

Avicularia interzooidal, single, may be absent from a large parts of colony and abundant in others, situated lateral to sinus, abutting the peristome; size of cystid positively correlated with zooid width, perforated by several pores; rostrum directing distolaterally, usually in an angle of

>45° to frontal plane, widest at crossbar, narrowing distal to it, becoming parallel-sided and ending in a blunt tip; crossbar relatively thick, complete, without columella, uncalcified area proximal of crossbar semicircular.

Discussion:

This species has supposedly not been reported before. Due to its broad and shallow sinus, it may be referred to species with a similar orifice and which have been identified as S. tetragona (Reuss, 1848), S. errata (Waters, 1878), or S. unicornis (Johnston in Wood, 1844). Due to this similarity, all species have caused extensive confusion in the past century (see e.g. Ryland, 1968) and many problems remain to date. However, the Recent S. errata has a different orifice shape, with an even broader sinus that has angular corners, whereas the present specimens display rounded edges. S. errata is also not known for developing a very tall suboral mucro (Ryland, 1968). Whilst Recent specimens referred to S. unicornis are morphologically different from the type specimens of the Pliocene Coralline Crag (see Discussion in S. dunkeri [Reuss, 1848]), the Niebla material is clearly different from both, based on comparison of orifice shape and zooid morphology. To assess the relatedness with the Middle Miocene S. tetragona is not such a straightforward operation, basically owing to the bad state of preservation due to recrystallisation of the (type)material (see also Schmid, 1989). Although similar in outline, small-scale features of the orifice, such as the condyles, are difficult to distinguish without SEM observations, but it seems to be distinctly broader and shallower in S. tetragona, as figured by Ryland (1968). Multilaminar colonies, such as depicted by David & Pouyet (1974), were not present in the Niebla Calcarenite, and the zooids in several plurilaminar colonies do not show a such chaotic budding pattern and zooid morphology. Finally, zooid morphology and outline of some Recent specimens attributed to S. tetragona (e.g. Ryland, 1968; Hayward & McKinney, 2002) differ from the Neogene form in that the frontal wall is more convex and the zooids display a hexagonal shape. In the present specimens and in the typematerial, the zooids in encrusting unilaminar colonies are flat and have a sometimes perfectly rectangular shape, while a regular hexagonal outline was never observed in colonies of undisturbed growth.

Thus, while the original material in the Reuss Collection needs to be screened for wellpreserved specimens for SEM observations, there is no described or figured species that my specimens can unequivocally be referred to.

Occurrence:

This species is common on red algae and other bryozoans. The tallest suboral mucros are formed in zooids that are located in an exposed position on convex substrate.

Family MYRIAPORIDAE GRAY, 1841 Genus MYRIAPORA DE BLAINVILLE, 1830

Myriapora truncata (PALLAS, 1766) Plate 8, Figure 5-7

- 1766 Millepora truncata PALLAS, p. 249.
- 1848 Vaginopora polystigma REUSS, p. 73, pl. 9, fig. 2.
- 1877 Myriozoum punctatum (PHILIPPI) Manzoni, p. 70, pl. 15, fig. 52; pl. 17, fig. 55.
- 1988 Myriapora truncata (PALLAS) Moissette, p. 194, pl. 3, fig. 10, 11; pl. 31, fig. 10.
- 1988 Myriapora truncata (PALLAS) Zabala & Maluquer, p. 163, fig. 467-469.
- 1989 Myriapora truncata (PALLAS) Bishop & Hayward, p. 54, fig. 226, 227.
- 1992 Myriapora truncata (PALLAS) El Hajjaji, p. 251, pl. 15, fig. 7.
- 1999 Myriapora truncata (PALLAS) Sefian et al., p. 241.
- 2002 Myriapora truncata (PALLAS) Hayward & McKinney, p. 76, fig. 34A-D.

Material:

Niebla Calcarenite: 113 colony fragments.

examined by SEM: GNI1-068-A, B; GNI1-069-A, B; GNI1-071-A.

- own collection: ALG-082-A, B (Recent, Algeciras, SW Spain); ALV-080-A (Tortonian, Agua Amarga Basin, SE Spain), CCF-079-A, B (Pliocene, Carboneras Basin, SE Spain); CDG-084-A, B (Recent, Cabo de Gata, SE Spain); LIN-082-C, D (subrecent, Linosa, S Italy).
- other: BNHM 1951.3.16.1 (Recent, Bay of Tanger); 69.10.6.1 (Recent, Algiers); 1975.1.12.202 (Recent, Chios).

Measurements:

Description:

Colony erect rigid, robust, irregular 3-D branching, attached by an encrusting and secondarily calcified base; branches cylindrical to suboval at bifurcations. Autozooids in alternating whorls of seven to eight, individual boundaries indistinct and irregular, at the same level as frontal walls. Frontal wall finely granular, regularly perforated by small pores. Primary orifices spaced in more or less quincuncial order, slightly longer than wide, orbicular; anter semicircular, comprising two-thirds of orifice length; poster a short semi-ellipse below thick, bluntly triangular condyles. No spines or peristome.

Ovicell globose, large, length and width exceeding the distance between orifices, semiimmersed, its frontal surface scarcely projecting from colony frontal plane; frontal wall same as in autozooids; orifice of ovicellate zooids dimorphic, longer and wider than that of autozooid, with a proportionately broader poster.

No avicularia.

Discussion:

A detailed account on the morphometrical analysis of *M. truncata*, with special reference to changes in branch diameter and zooid size as well as their palaeoecological implications, is presented below in the second manuscript (Chapter 6). Despite these variations in morphology, the species has undergone no detectable change since at least the mid Miocene, whereas the diversity of species of the genus Myriapora has remained very low, being represented by only M. truncata and M. bugei (d'Hondt, 1975), in the Mediterranean region. Whereas commonly found in fossil assemblages of the Mediterranean basins, sometimes in rock-forming abundance (e.g. in the Pliocene Almería-Níjar Basin, SE Spain; pers. observation) fossil records of M. truncata from outside this region remain scarce and the species was believed to be endemic to the Mediterranean basins. Sefian et al. (1999) were the first to report it from Miocene sediments of NW Morocco. While they mention that ovicells are absent in their material, the presence of these in the eastern Atlantic Niebla specimens shows that this was not an infertile pseudopopulation. Furthermore, the finding of a single fragment with an almost bilaminar mode of growth (and reversed polarity, reparative growth at its proximal end [Lagaaij, 1952: pl. 16, fig. 7; Bishop & Hayward, 1989: fig. 226]) in the mid Pliocene of the Netherlands was substantiated by another rare occurrence in the Pliocene of NW France (Pouyet, 1997a: p. 42). On the other hand, since specimens from the German Oligocene (e.g. Dartevelle, 1952; David et al., 1968) have neither been figured nor examined by SEM, Paleogene occurrences have to be regarded with caution.

Occurrence:

Commonly known as the 'False Coral', this species is a conspicuous component of most Recent benthic communities, and widely distributed throughout, the Mediterranean Sea, from the shallow subtidal (in caves and overhangs) to at least 140 m with an optimum between 30 and 60 m (Gautier, 1962). Its deepest occurrence is bound to a narrow belt of the seasonally shifting shear zone of the MAW (eastward flowing Modified Atlantic Water) and the LIW (westward flowing Levantine Intermediate Water) where it forms 'thickets' with a patchy distribution (A. Freiwald, pers. comm. 2004). It occurs on hard substrata (rocks, crustose red algae, shells) and is, as in the fossil record, usually reported to be endemic to the Mediterranean. However, working on NW Moroccan bryozoans, Canu & Bassler (1925, p. 62) stated that *M. truncata* is "very rare in the Atlantic and in shallower water (16-24 m) than in the Mediterranean". Other affirmed records of *M. truncata* in Atlantic waters are from the southern Spanish coast (Gulf of Algeciras) described by López de la Cuadra & García-Gómez (1988, 1994) and Alvarez (1994), and from the Bay of Tanger (BNHM 1951.3.16.1).

In the Niebla Calcarenite, crustose red algae formed the substrate for *M. truncata*. In turn, basal (or dead) colony parts are often encrusted by coralline algae and other bryozoans. Besides *Schizotheca serratimargo* (Hincks, 1886), *M. truncata* is the most abundant bryozoan species, especially in regard to its contribution to the carbonate production. It occurs in numerous fragments of up to 1 cm in length.

Distribution:

?Oligocene: Germany.

Miocene: Burdigalian (France), Badenian (Vienna Basin, Romania), Middle Miocene (Italy), Tortonian (Guadalquivir Basin - Spain), Messinian (Spain, Morocco, Algeria).

Pliocene: Netherlands, NW France, Mediterranean.

Pleistocene: Mediterranean.

Recent: Mediterranean, east Atlantic (Morocco, Spain, ?Canary Islands).

Family LANCEOPORIDAE HARMER, 1957 Genus CALYPTOTHECA HARMER, 1957

Calyptotheca sp. 1

Plate 8, Figure 9-11

Material:

Niebla Calcarenite: 7 colonies. examined by SEM: GNI1-030-C, G; GNI1-031-A, B, C, D.

Measurements:

ZL $629 \pm 49, 530-708 (5, 20)$ ZW $432 \pm 71, 288-579 (5, 20)$ OL $173 \pm 16, 151-198 (6, 18)$ OV $173 \pm 16, 144-200 (2, 18)$ OvL 339-449 (3, 3)OvW 382-396 (3, 3)

Description:

Colony encrusting unilaminar, multiserial. Zooids subhexagonal, separated by salient ridges; frontal shield thick, only slightly convex, perforated by numerous relatively large pores which are separated by thick nodular ridges. Primary orifice as wide as long, encircled by a raised peristomial ridge; anter semicircular, poster semielliptical, comprising about one-fourth of orifice length with short thick condyles directing proximolaterally; no spines.

Ovicell globular, recumbent on and occupying most of the distal zooids' frontal surface but not immersed, globular, surface slightly flattened frontally and similar to zooidal frontal wall, proximal rim concave and overarching most of orifice, lateral walls extending to proximolateral corners of aperture; orifice in ovicellate zooids not dimorphic.

Adventitious avicularia common, three broken cystids were observed in a lateral or distolateral zooid corners, with marginal pores; rostrum pointing medioproximally.

Discussion:

An identical Recent or fossil species has, as far as I know, not been described. However, a morphologically related species could be *Schizobrachiella granosoporosa* (Reuss, 1874) as described by David & Pouyet (1974), but SEM work is required for a precise estimate on their relationship.

It is difficult in fossil material to find criteria for the decisive placement in either of the genera *Schizobrachiella* Canu & Bassler, 1920, *Hippoporina* Neviani, 1895, and *Calyptotheca*. I chose to assign this species to *Calyptotheca* due to its completely and evenly porous ovicell surface (which is restricted to a frontal area surrounded by a broad rim of calcification in the otherwise similar species of *Hippoporina*), and due to the presence of strong condyles and a proximal orifice margin with a well defined sinus. Although dimorphic orifices are not formed in the present species these are also not a necessary requirement for species in this genus (e.g. Gordon, 1989: p. 37).

Occurrence:

Most of the colonies encrust red algae or bryozoans, whereas some fragments are found independent of substrate. This could be indicative of growth on ephemeral substrates or, since this species is characterised by the formation of zooids by zooidal budding (see Lidgard & Jackson, 1989), that the colony margin may have been raised to tackle a competitor.

Calyptotheca sp. 2 Plate 8, Figure 14-16

Material:

Niebla Calcarenite: 14 colonies. examined by SEM: GNI1-019-A, B, C, D; GNI1-030-A, B, D, E, F. other: VNHM 1859.50.789 (partim *Lepralia tenella* Reuss, 1874; Badenian, Eisenstadt).

Measurements:

Description:

Colony encrusting unilaminar or plurilaminar, multiserial. Zooids rectangular, hexagonal, or irregularly polygonal but always with a convex distal margin, separated by distinct sutures; frontal shield thick, only slightly convex, perforated by numerous round pores separated by nodular ridges, one row of larger marginal pores; a small suboral umbo may be present. Aperture slightly longer than wide, obscuring part of the proximal primary orifice; peristomial ridge low, forming a deep U-shaped median sinus proximally; two thick, transversely positioned and slightly immersed condyles just distal to proximal rim; anter semicircular with a slightly immersed distolateral lip on which the operculum rests when closed; no spines.

Ovicell large, globular, slightly wider than long, recumbent on distal zooid; surface flattened frontally, perforated by numerous round pores, proximal edge concave and arched over orifice,

with proximolateral walls extending to proximolateral corners or aperture. Orifice in ovicellate zooids not dimorphic.

Adventitious avicularia rare, only three broken cystids were observed in distolateral or lateral zooid corners, with the rostrum pointing in a medial direction.

Discussion:

As with *Calyptotheca* sp. 1, a definite synonymy was not observed to exist with any hitherto described or figured species, and the assignment to this genus is based on the evenly perforated, non-immersed ovicells, and orifices with a distinct sinus and strong condyles. A closely related species may be part of the material Reuss (1874) referred to as *Lepralia tenella*. However, as David & Pouyet (1974) and Schmid (1989) mentioned, this sample includes specimens of a species he described earlier (namely *Schizomavella tenella* [Reuss, 1848], figured on pl. 6, fig. 4; see Schmid, 1989: p. 44, pl. 12, fig. 2-7), as well as a different set of specimens later assigned to *Schizoporella errata* (Waters, 1878) by David & Pouyet (1974: p. 155) and to *Schizoporella? tenella* by Schmid (1989: p. 42, pl. 12, fig. 1). However, since this species is distinctly different from *S. errata*, and the species name *tenella* is a primary homonym (ICZN Article 57.2; Kraus, 2000), a lectotype should be established from the samples VNHM 1878.11.46 and 1878.11.48, the specimens of which were figured by Reuss (1874: pl. 6, fig. 3 and 5, respectively; see David & Pouyet, 1974). However, the total number of samples and specimens available is quite small (Schmid, 1989) and obviously lack ovicells. It may therefore be necessary to obtain more material from the type- or other nearby regions before an unequivocal species definition can be given.

Occurrence:

Most colonies occurred in a (pluri)laminar growth mode and independent of substrate, thus possibly indicating growth on soft substrates. As *Calyptotheca* sp. 1, colony growth in this species proceeds by zooidal budding (Lidgard & Jackson, 1989).

Genus EMBALLOTHECA LEVINSEN, 1909

Emballotheca longidens (CIPOLLA, 1921) Plate 9, Figure 1-4

- 1921 Hippoporina longidens CIPOLLA, p. 96, pl. 4, fig. 17, 18.
- 1986 Emballotheca mediterranea POUYET & MOISSETTE, p. 388, pl. 1, fig. 1-4.
- 1988 Emballotheca mediterranea P. & M. Moissette, p. 130, pl. 21, fig. 9, 12.
- 1992 Emballotheca mediterranea P. & M. El Hajjaji, p. 166, pl. 9, fig. 4.
- 1992 Emballotheca longidens (CIPOLLA) Pouyet & Moissette, p. 55, pl. 8, fig. 5, 6.
- 1996 Emballotheca longidens (CIPOLLA) Haddadi-Hamdane, p. 88, pl. 7, fig. 5.
- 1997b Emballotheca longidens (CIPOLLA) Pouyet, p. 56, pl. 5, fig. 8, 9.

Material:

Niebla Calcarenite: 12 colonies. examined by SEM: GNI1-008-A, B, C, D, E, F.

Measurements:

ZL $678 \pm 71, 575 - 846 (4, 20)$ ZW $535 \pm 95, 372 - 747 (4, 20)$ OL $147 \pm 15, 120 - 173 (6, 20)$ ovOL 267 OW $159 \pm 14, 133 - 180(6, 20)$ ovOW 259 OvL 450 OvW 425 AvL 294 - 343(2, 2)AvW 163–187 (2, 2)

Description:

Colony encrusting unilaminar, multiserial. Autozooids rectangular, rhombic, or irregularly polygonal, separated by indistinct grooves on thin ridges. Frontal wall slightly convex, evenly perforated by numerous, relatively large, round pores bounded by thickened, nodular and occasionally raised ridges; areolar pores equally numerous but generally more elongated. Primary orifice rounded quadrangular, little wider than long, distal margin concave and slightly broader than proximal rim which is strongly convex; peristome a low thickened rim, no spines; a pair of long, prominent condyles emerge from the lateral walls in the proximal third or at mid distance of orifice, almost at level with rim, relatively slender when viewed from above but extending quite deep into the zooids' interior, first directing medioproximally while in the last third incurving and pointing proximally; lyrula a long denticle, slightly immersed, immediately bending downwards at almost right angle and pointing towards basal wall.

Ovicells globular, recumbent on frontal wall of distal zooid, overarching a large part of orifice; frontal wall with few large pores and thick, prominent, steeply raised, radial ribs. Orifice in ovicellate zooids dimorphic, nearly twice as long, distal and proximal rim of equal length, condyles thicker than in autozooid.

Adventitious avicularia sporadic, single, situated in one proximal corner and resting on frontal wall of zooid, directing distally or mediodistally; rostrum narrowing distal to cystid and becoming parallel-sided, ending in a rounded tip.

Discussion:

There are two morphological differences between the present material and *E. longidens* from the Mediterranean: Pouyet & Moissette (1992), who described some of the original material from Cipolla's collection, did not record the prominent ribs being present on the ovicell surface in the specimens from Niebla (Pl. 9, Fig. 4), nor did any other descriptions or illustrations thereafter. However, the ovicell surface does seem to have at least a rugose appearance in some specimens from elsewhere (see Pouyet & Moissette, 1986: pl. 1, fig. 2; El Hajjaji, 1992: pl. 9, fig. 4). Furthermore, due to downward growth, the lyrula is difficult to see in frontal view and it has not been recognised by former authors. However, since all of the remaining features of the more or less coeval Mediterranean material completely correspond with the present specimens, these are assigned to *E. longidens* and the differences in ovicell morphology may be due to abrasion or, possibly, intraspecific variability induced by secondary calcification produced during later ontogeny.

There are no significant differences in mean zooid length between Niebla specimens and those published in Pouyet & Moissette (1986: 0.69 mm), and Haddadi-Hamdane (1996), El Hajjaji (1992) and Pouyet (1997b) (all 0.7 mm). However, a greater zooid width in Niebla specimens is responsible for these being the only species having a larger frontal area compared with conspecifics from Mediterranean regions (see Chapter 5).

Occurrence:

All Recent representatives of the genus *Emballotheca* live in tropical to warm-temperate regions of the Pacific and Indian Ocean. The record of specimens from Niebla thus marks the westernmost, and the first Atlantic, occurrence of a species of this genus. *E. longidens*, although as such presumably of Mediterranean or Paratethyan origin, may therefore be a remnant of mid-Miocene times when the eastern part of the Mediterranean Sea was still connected with the Indian Ocean.

The few colony fragments found in the Niebla Calcarenite occur mostly free of their former substrate, seldom on red algae.

Distribution:

Miocene: Badenian (Poland), Tortonian (Guadalquivir Basin and SW Spain), Messinian (Spain, Morocco, Algeria).

Pliocene: Spain, Algeria, Italy.

Family CHEILOPORINIDAE BASSLER, 1936 Genus CHEILOPORINA CANU & BASSLER, 1923

Cheiloporina campanulata (CIPOLLA, 1921) Plate 8, Figure 13, 17

1921 Hippopodina campanulata CIPOLLA, p. 133, pl. 5, fig. 7-9.

1956 Hippopodina(?) campanulata CIP. – Buge, p. 71, pl. 9, fig. 5.

1975 Cheiloporina campanulata (CIP.) – Poluzzi, p. 65, pl. 20, fig. 10-12.

1976 Cheiloporina campanulata (CIP.) – Pouyet, p. 75, pl. 13, fig. 2.

1988 Cheiloporina campanulata (CIP.) – Moissette, p. 176, pl. 28, fig. 10.

1992 Cheiloporina campanulata (CIP.) – El Hajjaji, p. 171, pl. 9, fig. 6.

1992 Cheiloporina campanulata (CIP.) – Pouyet & Moissette, p. 74, pl. 11, fig. 9, 10.

1999 *Cheiloporina campanulata* (CIP.) – Sefian et al., p. 239.

Material:

Niebla Calcarenite: 2 colonies. examined by SEM: GNI1-010-A, B.

Measurements:

ZL $611 \pm 86, 493-740 (2, 20)$ ZW $339 \pm 72, 256-313 (2, 20)$ OL $179 \pm 19, 155-210 (2, 20)$ OW $163 \pm 16, 138-194 (2, 20)$ anter OW $177 \pm 26, 139-224 (2, 20)$ poster OvL $246 \pm 21, 215-277 (1, 9)$ OvW $249 \pm 20, 226-284 (1, 9)$

Description:

Colony encrusting unilaminar, multiserial. Zooids elongated subrectangular, separated by distinct grooves. Frontal wall slightly convex, regularly punctured by numerous pores separated by thick nodular ridges, a pair of relatively large and slit-like marginal pores situated proximal of aperture. Orifice in autozooids as long as wide, bell-shaped; large semicircular anter delimited from short poster with a slightly concave proximal margin by two stout condyles directing proximally; orifice in ovicellate zooids larger and bell-shape not as pronounced; no spines.

Ovicell globular, to a large part immersed in the distal zooid, slightly convex, calcification and perforation similar to frontal wall but with smaller pores and therefore denser nodular ornamentation.

Avicularia were not observed.

Discussion:

The small, single or paired avicularia that were mentioned by Cipolla (1921), Poluzzi (1975) and El Hajjaji (1992) were not observed in the present material, nor in any of the other records. Apart from this, the present specimens are identical to all of the above mentioned occurrences.

Occurrence:

After Sefian et al. (1999) recorded this species from the Atlantic side of Morocco, this is the second report of the presence of *C. campanulata* outside the Mediterranean region.

One colony encrusts a red alga, the other one occurs independent of substrate.

Distribution:

Miocene: Tortonian (Guadalquivir Basin – Spain, Morocco), Messinian (Atlantic and Mediterranean Morocco, Algeria).

Pliocene: Spain (Carboneras Basin), Tunisia, Italy.

Genus HAGIOSYNODOS BISHOP & HAYWARD, 1989

Hagiosynodos latus (BUSK, 1856) Plate 9, Figure 5, 6

- 1856 Lepralia lata BUSK, p. 309, pl. 10, fig. 1, 2.
- 1867 Lepralia kirchenpaueri HELLER, p. 105, pl. 2, fig. 11.
- 1952 Hippopodinella lata (BUSK) Lagaaij, p. 129, pl. 15, fig. 2.
- 1976 Hippopodinella lata (BUSK) Pouyet, p. 74, pl. 11, fig. 8; pl. 12, fig. 3.
- 1988 Hippopodinella lata (BUSK) Moissette, p. 178, pl. 28, fig. 1.
- 1989 *Hippopodinella lata* (BUSK) Schmid, p. 47, pl. 13, fig. 3, 5, 7.
- 1989 Hagiosynodos latus (BUSK) Bishop & Hayward, p. 46, fig. 189-191.
- 1992 Hagiosynodos latus (BUSK) El Hajjaji, p. 217, pl. 11, fig. 12.
- 1992 Hippopodinella lata (BUSK) Pouyet & Moissette, p. 75, pl. 11, fig. 11.
- 1996 Hippopodinella lata (BUSK) Haddadi-Hamdane, p. 110, pl. 10, fig. 9.
- 1997b Hagiosynodos latus (BUSK) Pouyet, p. 76, pl. 8, fig. 8.
- ? 2002 Hagiosynodos kirchenpaueri (HELLER) Hayward & McKinney, p. 76, fig. 35E-H.
- ? 2002 Hagiosynodos latus (BUSK) Hayward & McKinney, p. 79, fig. 35A-D.

Material:

v

Niebla Calcarenite: 4 colonies.

examined by SEM: GNI1-019-H, I.

own collection: CRC-078-A, CRC-081-C (Pliocene, Carboneras Basin, SE Spain). other: VNHM 1988.106.32 (Badenian, Nußdorf).

Measurements:

- ZL $386 \pm 26, 341 414(2, 9)$
- ZW $305 \pm 30, 271 370(2, 9)$
- OL $87 \pm 11, 79 107 (2, 6)$
- OW $63 \pm 11, 50-70(2, 6)$ anter
- OW $68 \pm 11, 53-82 (2, 6)$ poster
- OvL $169 \pm 11, 153 176(2, 4)$
- OvW 176 ± 3, 172–179 (2, 4)

Description:

Colony encrusting unilaminar, multiserial. Zooids rhombic, oval or irregular (polygonal) in outline, separated by shallow grooves. Frontal wall rugose or nodular, flat or only slightly convex, with evenly spaced pores. Orifice longer than wide, bell-shaped with horseshoe-shaped anter and laterally curved poster with a straight or slightly concave proximal border and distinct condyles; bell-shape in ovicellate zooids not as marked as in autozooids; no spines. Some zooids bear small paired umbones adjacent to the proximolateral corners of the orifice.

Ovicells globular but sometimes with triangular outline, to a great part immersed but independent of distal zooid, about as long as wide, frontal surface slightly convex, with large marginal pores and thick radial ribs meeting on the apex of ovicell forming a prominent central umbo.

Avicularia were not observed.

Discussion:

Ever since Heller (1867) described *Hagiosynodos kirchenpaueri* from the Recent Adriatic Sea, the distinguishing characters to delimit this species from *H. latus* were based on shaky grounds. This situation remains to date, and, unfortunately, culminated in the latest attempt to sort out the problems between the two species, when Hayward & McKinney (2002) confused figures and figure captions. On p. 79 they mention that they illustrate the lectotype of *H. kirchenpaueri* as fig. 35A (and also refer to fig. 35A-D for zooid dimensions of *H. kirchenpaueri*), while the figure caption of fig. 35A-D (p. 78) reads *Hagiosynodos latus*. Furthermore, the ovicell description of *H*.

kirchenpaueri (p. 79: "...calcification and perforation identical to frontal shield...") does not match with either of the ovicells figured.

Although Hayward & McKinney (2002), besides introducing the new species H. hadros, have given traits for discriminating H. latus (Busk, 1856) from H. kirchenpaueri (Heller, 1867), a welldefined approach to distinguish these species has, in my opinion, not satisfactorily been established. Whereas different authors have proposed a variety of characters to consider, the two taxa were principally discriminated by the generally larger zooid size of kirchenpaueri. Yet Schmid (1989) found similar ranges of zooid, orifice and ovicell dimensions when biometrically comparing Recent and fossil H. kirchenpaueri and latus from the Mediterranean and Atlantic, and consequently synonymised the species. This was rejected by Hayward & McKinney (2002), who argued that kirchenpaueri has, on average, larger zooid dimensions and a proportionally broader poster, and that *latus* has a distal lip in the primary orifice. However, one weak spot of their argumentation is that the specimens of H. latus they presented are from the British Isles and not from a nearby area in the Mediterranean Sea. Since it has been shown that zooid morphology might, to a large extent, be influenced by the environment (e.g. Harmelin, 1973, 1988; O'Dea & Okamura, 2000; see also Chapter 5, 6), the differences in zooid size and morphology may be partly related to environmental disparities between the Atlantic and Mediterranean regions. Similarly, the new species they introduced, *H. hadros*, is distinguished from the other species by its large zooid size, orifices, and spacing of pores. However, maximum zooid length and width in this species is within the range of dimensions given for *latus* and *kirchenpaueri* by Schmid (1989) and the larger orifices and spacing of pores could be a consequence of the increased zooid size.

If one considers the width of the poster as a character to distinguish *H. latus* from *kirchenpaueri*, as suggested by Hayward & McKinney (2002), most fossil material referred to *latus* would be, in fact, *kirchenpaueri*. Although the measurements given in these publications do not separately list poster and anter widths, the specimens figured clearly show a proportionally broader poster (e.g. Moissette, 1988; Bishop & Hayward, 1989; Schmid, 1989; El Hajjaji, 1992; Pouyet & Moissette, 1992; Haddadi-Hamdane, 1996). Furthermore, to update Schmid's (1989) biometric comparison, zooid length in these reports varies greatly and does not allow a line to be drawn between *H. latus, kirchenpaueri* or *hadros* (Table 4.4). Thus, poster width and zooid size do not seem to be of great value for the distinction of these species.

Table 4.4 Mean zooid length and orifice width of specimens identified as *Hagiosynodos latus*, *kirchenpaueri* or *hadros*. Most authors do not specify whether the orifice width they present is that of poster or anter; the values given below therefore refer to the greatest orifice width presented in those cases where poster and anter width are distinguished (Hayward & McKinney, 2002; Berning, unpublished; this work), which was always that of the poster. Orifice width of *H. latus* given in El Hajjaji (1992) seems to be unreasonably large and should be considered with caution.

Source	Species	Age	Location	Mean zooid length (in mm)	Mean orifice width (in mm)
this work	H. latus	Late Miocene	E Atlantic	0.39	0.07
Haddadi-Hamdane, 1996	H. latus	Early Pliocene	Mediterranean	0.4	0.1
Moissette, 1988	H. latus	Late Miocene	Mediterranean	0.41	0.1
Hayward & McKinney, 2002	H. latus	Recent	NE Atlantic	0.43	0.08
Hayward & McKinney, 2002	H. kirchenpaueri	Recent	Mediterranean	0.49	0.1
Berning, unpublished	H. latus	Early Pliocene	Mediterranean	0.53	0.08
Hayward & McKinney, 2002	H. hadros	Recent	Mediterranean	0.56	0.1
El Hajjaji, 1992	H. latus	Late Miocene	Mediterranean	0.61	0.18

As for species occurrences, it is interesting to note that both *H. latus* and *kirchenpaueri* occupy the same niche in shallow water where they preferentially encrust gastropod shells, but both were, to my knowledge, never recorded by the same author to occur together at a single site. Thus, considering these indications and the fact that there is great intra- and intercolonial variation in zooid morphology and size, it is likely that *H. kirchenpaueri* and *H. hadros* may be mere

ecophenotypes of *H. latus*. Alternatively, should a proportionally narrower poster and the distal lip in the orifice (which is also not convincingly displayed in the material figured by Hayward & McKinney [2002]) be shown to consistently occur in Atlantic and Mediterranean specimens the partition of *latus* and *kirchenpaueri* has to be held up. Until this is achieved I prefer to retain *H. kirchenpaueri* as the junior synonym of *H. latus*.

Occurrence:

Recent Mediterranean *H. latus* (as well as *H. kirchenpaueri*) is reported encrusting echinoid spines, rocks, and preferentially gastropod shells and might thus (as *H. kirchenpaueri*) be a possible facultative symbiont of hermit crabs (Taylor, 1994; Hayward & McKinney, 2002). It is common in the shallow sublittoral zone down to some 30 m and its lower limit seems to be 100 m.

H. latus is one of the few species that is present in Neogene assemblages of both the North Sea Basin, it was reported from the Pliocene of the Netherlands by Lagaaij (1952), and the Mediterranean region. In the Niebla Calcarenite *H. latus* is rare and was solely found encrusting red algae.

Distribution:

Miocene: Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin and SE Spain; Morocco), Messinian (Morocco, Algeria).

Pliocene: Netherlands, Spain, Algeria, Italy, Rhodes. Pleistocene: Italy.

Recent: Northeast Atlantic (Morocco to Great Britain), Mediterranean.

Family MICROPORELLIDAE HINCKS, 1879 Genus CALLOPORINA NEVIANI, 1895

Calloporina decorata (REUSS, 1848) Plate 9, Figure 7, 11, 14

- 1848 Cellepora decorata REUSS, p. 89, pl. 10, fig. 25.
- 1974 Calloporina decorata (REUSS) David & Pouyet, p. 184, pl. 7, fig. 2.
- 1976 Calloporina decorata (REUSS) Pouyet, p. 69, pl. 10, fig. 4.
- 1988 Calloporina decorata (REUSS) Moissette, p. 152, pl. 24, fig. 10.
- 1988 Calloporina decorata (REUSS) Zabala & Maluquer, p. 137, fig. 322.
- 1989 Calloporina decorata (REUSS) Schmid, p. 51, pl. 15, fig. 1-3.
- 1992 Calloporina decorata (REUSS) El Hajjaji, p. 221, pl. 11, fig. 6.
- 1992 Calloporina decorata (REUSS) Pouyet & Moissette, p. 66, pl. 10, fig. 3.
- 1996 Calloporina decorata (REUSS) Haddadi-Hamdane, p. 94, pl. 7, fig. 4.
- 1997b Calloporina decorata (REUSS) Pouyet, p. 68, pl. 7, fig. 10.

Material:

Niebla Calcarenite: 33 colonies.

examined by SEM: GNI1-037-A, B, C, D, E.

other: 1867.50.769 (lectotype, Badenian, Eisenstadt; chosen by David & Pouyet, 1974); 1878.11.22 (Badenian, Eisenstadt; Reuss 1874, pl. 5, fig. 2).

Measurements:

- ZL 595 ± 55, 533-713 (3, 20) ZW 478 ± 84, 388-653 (3, 20)
- OL 115 ± 8, 100–127 (5, 20)
- OW 112 ± 10, 100–131 (5, 20)
- OvL 278 ± 26, 225–316 (3, 9)
- OvW $307 \pm 10, 295 321 (3, 9)$

AL 287 ± 40, 222–358 (5, 17)

AW 93 ± 15, 73–126 (5, 17)

Description:

Colony encrusting unilaminar, multiserial. Zooids subrectangular to subhexagonal with a rounded distal margin, separated by narrow grooves, 14 to 17 septula in distolateral walls. Frontal wall slightly convex, with one to three (commonly two) rows of marginal pores, surrounded by distinct ridges tapering off towards the zooid centre; ascopore suboral, round or transversely elliptical, encircled by a thickened low rim; another less conspicuous pore is situated between the proximal orifice margin, ascopore and adventitious avicularium. Orifice semicircular with a straight proximal border surrounded by seven or (less commonly) eight oral spines, and four or six in ovicellate zooids.

Ovicell subglobular or hemispherical, partly immersed in distal zooid's frontal wall, slightly wider than long, characterised by a prominent, slightly raised, obliquely positioned, horseshoe-shaped, (perforated?) distolateral fenestra which is demarcated from the slightly convex, imperforate, proximo-frontal area by a crescent row of pores.

One (sometimes two, rarely absent) long and slender, acute, adventitious avicularium, extending from the level of ascopore to lateral margin of orifice with the mandible directing and slightly incurving distally; crossbar slightly thickened, complete, without columella.

Ancestrula tatiform (252x236 µm) with a narrow gymnocyst and about 12 spines.

Discussion:

It is noteworthy that, although zooid length is by some 10% smaller than in Mediterranean representatives (e.g. Moissette, 1988: mean zooid length 0.68 mm), the Niebla specimens have seven to eight oral spines, whereas there are usually only four to six (rarely seven) in all other described *C. decorata*. Thus, for oral spine number is obviously subject to variation, even the consistently high number in my material still seems to be in the range of intraspecific variation.

The rugose frontal calcification described by Zabala & Maluquer (1988) is lost due to mechanical abrasion, but may be present in very well preserved specimens, e.g. in the late Badenian material from St. Margarethen (Schmid et al., 2001: pl. 4, fig. 3). As a result, the costules demarcating the areolar pores are conspicuous in the present specimens. Depending on different states of preservation, the observed morphological characters are thus also subject to variation (see also David & Pouyet, 1974; Schmid, 1989). Similarly, perforation of the distolateral fenestra of the ovicell can merely be assumed in the present material.

Occurrence:

Whereas *C. decorata* is commonly found in Neogene assemblages, this species has only rarely been recorded from the Recent Mediterranean and eastern Atlantic from sites between 10 to 150m depth. Since it shared the same fossil habitats with other extant species, *C. decorata* represents one of several species for which the information gathered from the rich fossil record may be of help to infer ecological preferences for Recent representatives (Moissette, 2000).

In the Niebla Calcarenite, *C. decorata* is common and usually found to encrust coralline algae and other bryozoans (e.g. *Schizotheca serratimargo* [Hincks, 1886], *Chorizopora brongniartii* [Audouin, 1826]).

Distribution:

Miocene: Langhian (Tunisia), Langhian-Serravallian (Italy), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin and SE Spain, Italy, Romania), Messinian (Algeria, Morocco).

Pliocene: Spain, Algeria, Italy.

Pleistocene: Italy.

Recent: (western) Mediterranean, eastern Atlantic (Canary Islands, Madeira, Morocco).

Genus MICROPORELLA HINCKS, 1877

Microporella aff. *appendiculata* (HELLER, 1867) Plate 9, Figure 8

aff. 1867 *Lepralia appendiculata* HELLER, p. 31, pl. 2, fig. 8. 2000 *Microporella coronata* (AUDOUIN) – Pouyet, p. 193, fig. 2a, b.

Material:

Niebla Calcarenite: 2 colonies.

examined by SEM: GNI1-032-B.

BNHM 26.9.6.238 (*M. coronata* [Audouin, 1826], Recent, Suez Canal; on photocards pdt4465, pdt4466; figured by Hastings, 1927: fig. 83B, C, 84).

other : FSL 115941, 115944 (identified as *M. coronata* [Audouin, 1826], Pliocene, Spain; Pouyet, 1976: p. 69); 117794 (*M. inamoena* [Reuss, 1874], Badenian, Poland; figured by Pouyet, 1997b: pl. 6, fig. 1; pl. 7, fig. 8).

VNHM 1878.11.18 (*M. barrandei* [Reuss, 1848], Badenian, Eisenstadt; figured by Reuss, 1874: pl. 5, fig. 7, 8); 1878.11.21 (lectotype of *M. inamoena* [Reuss, 1874], Badenian, Baden; chosen by David & Pouyet, 1974: pl. 11, fig. 8).

Measurements:

 $499 \pm 51, 429 - 607(1, 19)$ ZL ZW $366 \pm 47, 281 - 459(1, 19)$ OL $70 \pm 3,66-76(1,7)$ OW $92 \pm 5,85 - 98(1,7)$ OvL 168 OvW 238 AL $91 \pm 9,76 - 103(1,11)$ AW $68 \pm 9, 49 - 79(1, 11)$

Description:

Colony encrusting unilaminar, multiserial. Zooids (sub)hexagonal to elongated oval, separated by distinct grooves; frontal wall convex and evenly punctured by numerous pores divided by rugose frontal calcification, and with few larger, elongated, marginal areolar pores; ascopore spaced from orifice by a distance slightly exceeding a full orifice length, surrounded by a slightly thickened rim raised proximally and levelling towards the orifice, forming a broad smooth area devoid of pores between orifice and ascopore; lumen round with denticulate border. Orifice semicircular, broader than long, slightly raised rim with a straight proximal border and five distolateral spines (one pair of slightly thickened proximal spines in ovicellate zooids).

Two elliptical adventitious avicularia, usually situated directly proximolateral to proximal orifice rim, directing distally; rostrum short, triangular, parallel to frontal plane, very slightly incurving, with a thick complete crossbar.

Ovicell partly embedded in frontal wall of distal zooid, globose, wider than long, surface imperforate and smooth, characterised by a prominent, broad, smooth, transverse rib that forms the proximal margin and passes proximolaterally into the imperforate suboral area between orifice and ascopore.

Ancestrula tatiform (278x229 µm).

Discussion:

The availability of SEM photography has revealed subtle, yet important, morphological differences between geographically distinct populations of Recent microporellids and therefore greatly increased the number of species in this genus (e.g. Soule et al., 2002; Taylor & Mawatari, 2005). Thus, although the knowledge on present-day intra- and interspecific variability as well as biogeography is far from being adequate, the strict species concept now established needs to be transferred to species of the fossil record. However, many specimens are not well enough preserved

to unveil the ascopore morphology, or species are not sufficiently described, which makes it difficult to compare closely related taxa, especially in the absence of SEM photos. As will be shown below and in the discussions of the other microporellids encountered in this study, the genus *Microporella* is in great need of a revision which will lead to a greater species diversity in the Neogene of the Mediterranean basins.

The present specimens are, owing to the transverse frontal rib on the proximal ovicell margin and the distal pair of avicularia, morphologically similar to several fossil and Recent species, including another species from Niebla, *Microporella* aff. *inamoena* (Reuss, 1874) (see also Discussion there). However, unless we know more about inter- and intraspecific variation in *Microporella* spp., bur especially without detailed SEM observation and species descriptions of most of the fossil (type)specimens, any firm conclusion on synonymy with other morphospecies must remain insubstantial.

M. barrandei (Reuss, 1848) also has a transverse frontal ovicell rib but tiny avicularia occur only sporadically, while recrystallisation and superficial cement prohibits a more precise description of the specimens (see also David & Pouyet, 1974: pl. 7, fig. 1). The ovicells of M. *inamoena* (Reuss, 1874) do not show a pronounced proximal rib and the thick proximal ridge surrounding the ascopore extends distolaterally and is connected with the proximolateral orifice margin. Both species are therefore not likely to be conspecific with the present material. Differences to M. aff. *inamoena* from Niebla will be discussed there.

While the specimen figured as *M. coronata* (Audouin, 1826) by El Hajjaji (1992: p. 220, pl. 11, fig. 11) appears to be vaguely similar to the present material, it is too badly preserved to be of any more help. The same species name was given to material from the Late Miocene and Pliocene by Poluzzi (1975: p. 58, pl. 17, fig. 7), Pouyet (1976: p. 69), and Pouyet & Moissette (1992: p. 65, pl. 9, fig. 12), which may prove to be conspecific with the Niebla specimens, judging from the SEM photos and original material. However, the distance between ascopore and orifice seems to be shorter in most of these specimens when compared with the species from Niebla. While more material would have to be examined to reach a conclusion concerning a synonymy with the above mentioned specimens, no differences were found between the present material and the Pliocene, southern Spanish specimens described as M. coronata by Pouyet (2000). In contrast, the species Moissette (1988: p. 151, pl. 24, fig. 2, 3) identified as M. coronata, although synonymised by El Hajjaji (1992) with his own specimens, is clearly a different species owing to its densely perforated frontal wall and the small prominence encircling the ascopore, while ovicells were not observed. However, none of the aforementioned species is conspecific with the Recent *M. coronata* described by Audouin (1826) from the Red Sea. SEM images of a specimen collected near the type-location that match the original description show that *M. coronata* has a crescent ascopore which is surrounded by a thin and low ridge that does not become prominent, that the frontal wall is irregularly scattered with relatively large pores, that the avicularia have a channelled and open tip, and that the ovicells have a marginal row of large pores and lack the proximal rib (BNHM 26.9.6.238). A similar fossil species was not observed in the literature during this study.

M. morrisiana (Busk, 1859) from the Pliocene Coralline Crag also agrees with the Niebla material in the proximal ovicell rib but the avicularia are illustrated as commonly pointing laterally in the original description (pl. 7, fig. 8). This was never observed in my specimens.

A very close proximity exists between the present specimens and the Recent *M. appendiculata* (Heller, 1867) from the Mediterranean and Canary Islands. Hayward & Ryland (1999) synonymised this species with *M. pseudomarsupiata* Aristegui, 1984 and some records assigned to *M. marsupiata* (Busk, 1860b) (e.g. those in Gautier, 1962; Hayward & Ryland, 1979). However, the Recent species has far fewer (but larger), and more scattered frontal wall pores. Furthermore, in the SEM photos published (Aristegui, 1984: pl. 24, fig. 6; Hayward & Ryland, 1999: fig. 134A, B), the ascopore is always round or longitudinal oval. Although Aristegui (1984: p. 325) does not mention the presence of crescentic ascopores in his species description, Hayward & Ryland (1999: p. 294) do so and their text fig. 135 depicts them. They do not, however, indicate in their species description that round or oval ascopores may exist. Thus, as stated above, we need to know more about the range of intraspecific variation in *Microporella* spp. to be able to assign (not only) fossil specimens correctly.

Occurrence:

This species is extremely rare in the Niebla Calcarenite, encrusting coralline algae.

Microporella aff. ciliata (PALLAS, 1766) Plate 9, Figure 12, 13, 15

aff. 1766 Eschara ciliata PALLAS, p. 38.

Material:

Niebla Calcarenite: 14 colonies. examined by SEM: GNI1-024-A; GNI1-033-A, C.

Measurements:

ZL $450 \pm 34, 392 - 496$ (2, 16) ZW $336 \pm 38,271 - 412(2,16)$ OL $64 \pm 6, 53 - 74(2, 13)$ OW $98 \pm 10, 86 - 118(2, 13)$ 188 ± 14, 164–218 (3, 15) OvL OvW $238 \pm 20, 207 - 277 (3, 15)$ AL $127 \pm 16,99 - 148(2,17)$ AW $84 \pm 13, 64 - 106(2, 17)$

Description:

Colony encrusting unilaminar, multiserial. Zooids (sub)hexagonal, separated by distinct grooves; frontal wall convex and evenly punctured by numerous pores divided by rugose frontal calcification; marginal areolar pores relatively large, elongated oval or slit-like, restricted to the lateral and proximal corners, plus one pair proximolateral to orifice; ascopore field situated just proximal to apertural rim without expanse of granular cryptocyst in between; lumen crescentic, presumably with a denticulate edge, raised on a more or less developed circular prominence. Orifice semicircular, length one-third less than width, with a smooth and short but distinct apertural rim, and a straight proximal border; five to six distolateral oral spines (none in ovicellate zooids).

Ovicell globose but with a relatively straight proximal margin, recumbent on only a small area of the frontal wall of distal zooid, wider than long, surface coarsely granular and with few scattered pores, especially so at distolateral margin; proximal rim in most ovicells characterised by broad, smooth, transverse lappets that extend proximolaterally towards and around the orifice (this structure may have formed a similar peristome as in the 'personate' form of *M. ciliata* of Hincks (1880) or as in the 'semipersonate' *M. agonistes* Gordon, 1984, yet it is not preserved as a whole, and there are no indications that it has encircled the ascopore).

Adventitious avicularium single, situated proximolateral of ascopore or in one centro-lateral corner, cystid oval, more or less raised above frontal wall; rostrum acute to frontal plane, directing distolaterally, broadly triangular with a distal groove ending in a blunt tip; crossbar slender, complete, no columella.

Discussion:

Many different fossil morphotypes have been assigned to the Recent *M. ciliata* (Pallas, 1766), whereas most are not very closely related to this species (see also Discussion in *Microporella* sp.). One that does get close is *M. calabra* (Seguenza, 1880) (= *M. ciliata* var. *calabra*), which was described from the Pliocene of southern Italy and is cited and figured in two other studies (Cipolla, 1921: p. 108, pl. 5, fig. 4-6; Pouyet & Moissette, 1992: p. 65, pl. 9, fig. 10). However, an adequate species definition does not exist and in what respect this species differs from the neotype of *M. ciliata* needs yet to be defined using SEM. The present material is very closely related to both of these taxa but differs in the formation of the lappets or peristome welded onto the proximal ovicell margin, as well as in overall ovicell shape, with a rather straight proximal edge that produces wider

than long ovicells. Recent *M. ciliata* (see e.g. Hayward & McKinney, 2002: p. 83, fig. 37E-J) and the fossil *M. calabra* do not show either of these characters. I interpret these differences as profound enough to regard the Niebla specimens as a distinct species.

Occurrence:

Although slightly more abundant than the other species of *Microporella*, *M*. aff. *ciliata* is also rare in the Niebla Calcarenite and was observed to encrust coralline algae, only.

Microporella aff. *inamoena* (REUSS, 1874) Plate 9, Figure 9, 10

aff. 1874 Lepralia inamoena REUSS, p. 153, pl. 5, fig. 1.

Material:

Niebla Calcarenite: 11 colonies.

examined by SEM: GNI1-032-A; GNI1-035-A, B, C, D; GNI1-036-B.

other : FSL 115941, 115944 (identified as *M. coronata* [Audouin, 1826], Pliocene, Spain; Pouyet, 1976: p. 69); 117794 (*M. inamoena* [Reuss, 1874], Badenian, Poland; figured by Pouyet, 1997b: pl. 6, fig. 1; pl. 7, fig. 8). VNHM 1878.11.18 (*M. barrandei* [Reuss, 1848], Badenian, Eisenstadt; figured by Reuss, 1874: pl. 5, fig. 7, 8); 1878.11.21 (lectotype of *M. inamoena* [Reuss, 1874], Badenian, Baden; chosen by David & Pouyet, 1974: pl. 11, fig. 8).

Measurements:

- ZL 578 ± 66, 449–677 (6, 15)
- ZW 444 ± 73, 326–602 (6, 15)
- OL $79 \pm 7, 70-92(3, 12)$
- OW 98 ± 8, 83–106 (3, 12)
- OvL 178 ± 11, 157–190 (4, 7)
- OvW $249 \pm 24, 222 285(4, 7)$
- AL $82 \pm 15, 67 105(5, 7)$
- AW 61 ± 13, 46–78 (5, 7)

Description:

Colony encrusting unilaminar, multiserial. Zooids (sub)hexagonal, separated by distinct grooves; frontal wall convex and evenly punctured by numerous small pores divided by rugose frontal calcification, and with few slightly larger, elongated, marginal areolar pores; ascopore spaced from orifice by a distance less than a full orifice length, surrounded by a thick rim steeply raised proximally and levelling towards the orifice, abutting the proximal orifice margin; lumen crescentic or transversely elliptical, with denticulate border. Orifice semicircular, broader than long, margin thickened and slightly raised, with a straight proximal border and five distolateral spines (one pair of slightly thickened proximal spines in ovicellate zooids).

Two small, elliptical, marginal, adventitious avicularia, situated proximolateral but at varying distance to proximal orifice rim, directing distally or distolaterally; rostrum short, triangular, parallel to frontal plane; crossbar complete.

Ovicell partly embedded in frontal wall of distal zooid, globose, wider than long, surface imperforate and smooth, characterised by a smooth, transverse rib that forms the proximal margin and passes proximolaterally into proximal orifice margin.

Discussion:

These specimens are very similar to *M*. aff. *appendiculata* but differ in that the frontal wall pores are slightly smaller and wider spaced, that the ascopore is located closer to the orifice and may have a different shape (but too few are well enough preserved to give a precise statement), and
that the ovicell proximal rib is not as pronounced. Furthermore, the avicularia in M. aff. *inamoena* are smaller in relation to zooid length, located further from the orifice margin, and, besides directing distally, also point in a distolateral direction. However, due to the similar appearance, synonymies with some of the species identified as M. *coronata* (Audouin, 1826) given above (see Discussion of M. aff. *appendiculata*) may also be considered to apply for M. aff. *inamoena* once more material is examined with the SEM.

Again, *M. barrandei* (Reuss, 1848) is a closely related species, but avicularia occur only sporadically and the ascopore is located too distant from the proximal orifice rim (see David & Pouyet, 1974: pl. 7, fig. 1) to be considered conspecific. However, most characters are shared with *M. inamoena* (Reuss, 1874), which was redescribed by David & Pouyet (1974: p. 183, pl. 11, fig. 8) and later also reported from the Polish Badenian by Pouyet (1997b: p. 67, pl. 6, fig. 1; pl. 7, fig. 8). Yet the ridge surrounding the ascopore extends distolaterally and is connected with the proximolateral orifice margin in ovicellate zooids, which was not observed in the present material. Furthermore, the ascopore is situated closer to the proximal orifice margin, while the lumen depicted in Pouyet's fig. 1 (pl. 6, 1997b) either consists of a pore plate, or is filled by cement or sediment, in which case nothing is known about its morphology. Since also the frontal wall pores are larger in the figured and viewed material of *M. inamoena*, the present specimens are here considered as a very close but different species.

Occurrence:

M. aff. *inamoena* is also only rarely encountered in the Niebla Calcarenite encrusting coralline algae.

Microporella sp. Plate 10, Figure 1

cf. 1988 Microporella ciliata (PALLAS) - Moissette, p. 160, pl. 24, fig. 7-9.

Material:

Niebla Calcarenite: 6 colonies. examined by SEM: GNI1-033-B, D; GNI1-034-A.

Measurements:

ZL $595 \pm 55, 465 - 661 (3, 20)$ ZW $444 \pm 73, 326-602(3, 20)$ OL $77 \pm 6, 70 - 87 (3, 12)$ OW $119 \pm 10, 101 - 131(3, 12)$ OvL 258 OvW 324 AL $171 \pm 22, 135 - 198(3, 10)$ AW $128 \pm 22, 82 - 151 (3, 10)$

Description:

Colony encrusting unilaminar, multiserial. Zooids generally hexagonal, separated by distinct grooves; frontal wall strongly convex, densely and evenly punctured by large pores with nodular ridges developing between them; one row of numerous and relatively large areolar pores; ascopore small, ?round or ?semicircular, situated directly proximal to orifice margin, with only a thin and little raised rim encircling it, occasionally becoming thicker and raised proximally. Orifice semicircular, wider than long, with a straight proximal border surrounded by five or six (rarely seven) oral spines.

Ovicell globose, wider than long, surface similar to frontal wall but with smaller pores and intervening nodular ridges (however, only one was observed in a bad state of preservation).

Adventitious avicularium single, situated just proximolateral to orifice; cystid oval, little raised above frontal wall; rostrum slightly acute to frontal plane, directing distolaterally, broadly triangular; crossbar complete, no columella.

Discussion:

These specimens are unlike any other species occurring in the Mediterranean Sea or NE Atlantic today. The dense perforation and nodular calcification of the frontal wall, the single avicularia situated proximolateral to the orifice, the perforated ovicell, and the small ascopore located directly below the proximal orifice margin characterises this species. The only presumably conspecific fossil morphospecies found was the one described by Moissette (1988) as *M. ciliata* (Pallas, 1766). However, more SEM work needs to be done until these can be synonymised and described as a new species.

Other less similar taxa were also assigned to *M. ciliata* by Poluzzi (1975: p. 57, pl. 21, fig. 12), Pouyet & Moissette (1992: p. 64, pl. 9, fig. 11), Haddadi-Hamdane (1996: p. 91, pl. 7, fig. 3), and Pouyet, (2000: p. 193, fig. 2f), yet the ascopore in these specimens is larger and distinctly separated from the proximal orifice margin and the space between both is not perforated by frontal wall pores. These species are also distinct from the Recent *M. ciliata* in that, among other characters, the avicularia are situated at level with, or distal to, the ascopore and close to the orifice. Instead, they may be assigned to *M. utriculus* (Manzoni, 1869c), as already noted by Reguant (1993).

Occurrence:

Only three colonies were found; these encrust red algae or other bryozoans.

Distribution:

Miocene: Tortonian (Guadalquivir Basin - Spain), ?Messinian (Algeria).

Family LACERNIDAE JULLIEN, 1888 Genus ARTHROPOMA LEVINSEN, 1909

Arthropoma ciliata CANU & LECOINTRE, 1928 Plate 10, Figure 2

	1928	Arthropoma ciliata CANU & LECOINTRE, p. 68, pl. 11, fig. 10, 11.
	1948	Arthropoma ciliata C. & L. – Buge, p. 75.
non	1952	Arthropoma ciliata C. & L. – Malecki, p. 199, pl. 11, fig. 8.
	1957	Arthropoma ciliata C. & L. – Buge, p. 218.

Material:

Niebla Calcarenite: 1 colony. examined by SEM: GNI1-038-A.

Measurements:

ZL	$572 \pm 55, 494 - 636(1, 6)$
ZW	549 ± 39, 508–619 (1, 6)
OL	127 ± 8, 120–140 (1, 5)
OW	$120 \pm 8, 110 - 130(1, 5)$

Description:

Colony encrusting unilaminar, multiserial. Zooids hexagonal, separated by distinct grooves; three large septula (one distal, two lateral) in vertical walls. Frontal wall slightly convex, ?smooth, regularly punctured by small round pores, and very few slit-like, marginal, areolar pores. Orifice slightly broader than long, with a D-shaped anter and a broad, straight, proximal border, indented

by a narrow, deep, U-shaped poster with straight lateral margins. Four slender spine bases widely spaced around anter.

Ovicells or avicularia were not observed.

Discussion:

This species has only rarely been encountered. It differs from the fossil and Recent *A. cecilii* (Audouin, 1826) in the presence of spines and is obviously restricted to the Atlantic. The presence in the Badenian of Poland seems somewhat spurious and the figure in Malecki (1952: pl. 11, fig. 8), although of no adequate quality to precisely determine zooid morphology, suggests that it is a different species. The frontal walls are more convex, the orifice does not show the pronounced D-shape, and Malecki mentions the presence of five thick spines in some zooids.

The latest genus definitions of *Arthropoma* (Gordon, 1984: p. 85; Hayward & Ryland, 1999: p. 224) exclude the presence of spines. Therefore, since all other features of this species are in accordance with the type species of *Arthropoma*, *A. cecilii* (Audouin, 1826), their eventual presence remains to be included in the definition.

Occurrence:

Only a single specimen was found in the Niebla Calcarenite, encrusting a coralline alga.

Distribution:

Miocene: Tortonian (NW France, Guadalquivir Basin - Spain).

Incertae sedis

Genus ESCHARINA MILNE EDWARDS, 1836

Escharina sp.

Plate 10, Figure 3, 6, 7

- 1976 Schizoporella sp. C Pouyet, p. 65, pl. 14, fig. 3.
- 1992 Escharina aff. dutertrei (AUDOUIN) El Hajjaji, p. 199, pl. 12, fig. 6.
- 1992 Escharina dutertrei (AUDOUIN) Pouyet & Moissette, p. 56, pl. 8, fig. 1.
- 1996 Escharina dutertrei (AUDOUIN) Haddadi-Hamdane, p. 82, pl. 6, fig. 7.
- ? 1997b Escharina aurita (REUSS) Pouyet, p. 57, pl. 5, fig. 3, 4.

Material:

Niebla Calcarenite: 8 colonies. examined by SEM: GNI1-047-A, B, C.

Measurements:

ZL $524 \pm 54, 428-643 (2, 20)$ ZW $435 \pm 70, 312-551 (2, 20)$ OL $65 \pm 6, 55-79 (2, 18)$ OW $79 \pm 7, 67-91 (2, 18)$ OvL $185 \pm 33, 156-229 (2, 6)$ OvW $246 \pm 4, 240-251 (2, 6)$

Description:

Colony encrusting unilaminar, multiserial. Zooids broadly hexagonal, slightly convex, separated by shallow grooves; frontal wall imperforate, finely granular with one row of numerous marginal areolar pores of varying shape. Primary orifice semicircular, broader than long; proximal border straight with a long (between half and one-third of anter length), initially slit-like sinus becoming drop-shaped proximally. Peristome only slightly raised around orifice, highest just lateral to proximal orifice margin, levelling down to frontal wall medioproximally; six spines on the distolateral rim (one pair in ovicellate zooids).

Ovicell globular, recumbent on and partly immersed in frontal wall of distal zooid, wider than long, surface imperforate and finely granular. Peristome better developed in ovicellate zooids, not levelling with frontal wall proximally and encroaching the ovicell, forming a smooth prominent ridge on its proximal edge.

Avicularia adventitious, small (ca. 70 μ m), paired, one on each distolateral side of orifice (proximal to ovicells, i.e. lateral to orifice, in ovicellate zooids); cystid oval; rostrum triangular, directing mediodistally; crossbar complete, no columella.

Discussion:

This species has often been referred to as *E. dutertrei* (Audouin, 1826), or *E.* aff. *dutertrei* in works on fossil Mediterranean assemblages. However, since there exists no type-material of this Recent species from (presumably) the Red Sea, while a neotype has not been established and thus the species not been defined yet, reference to this species is more than problematic.

The present specimens, and most of the fossil material in the literature assigned to this species, differ from the Recent Mediterranean *E*. aff. *dutertrei* (as described by Zabala & Maluquer, 1988: p. 128) in that the latter species has a proximal ovicell margin which is not encroached by the peristomial rim, has fewer marginal areolar pores, five spines only, and a broader and deeply U-shaped sinus.

On the other hand, the fossil material synonymised above agrees well with the present specimens. However, discrepancies exists between some of the species descriptions: El Hajjaji (1992) states that spines are absent in his material, yet the figured specimens show an abraded orifice margin, and under this circumstance the oral spines are impossible to observe, which is also the case in some of my material. The same applies to the material described as *E. aurita* (Reuss, 1866) by Pouyet (1997b). However, whereas El Hajjaji's (1992) figured species is without doubt conspecific with the present specimens, Reuss' species was described from the Oligocene of Germany and needs to be observed using SEM. Furthermore, Pouyet's figured specimen unfortunately has no ovicells. Finally, the material Moissette (1988: p. 131, pl. 21, fig. 5, 7) referred to *E.* aff. *dutertrei* are clearly distinct from the present material in that, among other characters, these form a prominent suboral umbo.

Occurrence:

Being most likely conspecific with several records from the Mediterranean Neogene, this species is for the first time recognised in the eastern Atlantic.

The species is rare in the Niebla Calcarenite. Most colonies were found encrusting coralline algae, while preferentially growing on the prominent algal thalli.

Distribution:

Miocene: ?Badenian (Poland), Tortonian (Guadalquivir Basin - Spain, Morocco), Messinian (Morocco).

Pliocene: Spain, Italy.

Genus THERENIA DAVID & POUYET, 1978

Therenia montenati comb. nov. (POUYET, 1976) Plate 10, Figure 4, 5

- 1976 Herentia montenati POUYET, p. 66, pl. 12, fig. 5.
- 1992 Herentia (Therenia) montenati POUYET El Hajjaji, p. 205, pl. 11, fig. 7.
- 1992 Herentia (Therenia) montenati POUYET Pouyet & Moissette, p. 57, pl. 8, fig. 7.
- 1996 Herentia (Therenia) montenati POUYET Haddadi-Hamdane, p. 84, pl. 6, fig. 3.
- 2000 Herentia (Therenia) montenati POUYET Pouyet, p. 190.

Material:

Niebla Calcarenite: 6 colonies.

examined by SEM: GNI1-038-B, C, D, E.

other: FSL 115973 (holotype, Pliocene, SE Spain; Pouyet, 1976: pl. 12, fig. 5); 115698 (Pliocene, SE Spain).

Measurements:

ZL $620 \pm 69, 523-738 (4, 20)$ ZW $504 \pm 60, 415-615 (4, 20)$ OL $111 \pm 7, 101-129 (4, 15)$ OW $123 \pm 9, 112-136 (4, 15)$ AL/W $169 \pm 16, 146-196 (2, 12)$ OvL $195 \pm 19, 177-211 (1, 4)$ OvW $313 \pm 24, 298-349 (1, 4)$

Description:

Colony encrusting unilaminar, multiserial. Zooids rhomboid or polygonal, separated by distinct grooves; frontal wall flat, closely and regularly perforated by numerous small pores, usually two or three large marginal areolar pores in proximal corners of zooid. Primary orifice slightly broader than long and widest in distal third, anter three-quarters of a transverse ellipse, proximal border straight with a short, narrow, U-shaped sinus; lining of the interior of orifice forms a low shelf along the distal margin and one paralleling the proximal orifice rim. Laterally and distally the orifice is encircled by a low, flared, smooth rim that raises and thickens distally. Spines were not observed.

Ovicell crescentic, immersed but not associated with distal zooid(s), level with frontal wall of zooid, surface imperforate, smooth or finely granular. The distal orifice rim encroaches onto the ovicell, forming a broad, smooth, prominent ridge on its proximal margin.

Avicularia interzooidal, proximolateral to orifice on either left or right side, cystid somewhat triangular, level with and not clearly demarcated from frontal shield of zooid with which it is associated, proximal part perforated like frontal wall of zooid and at least with one large areolar pore at lateral or proximal base; rostrum orbicular, pointing laterally or distolaterally; crossbar complete, without columella, not extremely thick when viewed from above but extending fairly deep into cystid, twisted along its axis, thus presumably producing a lateral component to the vertical motion of the mandible.

Discussion:

Owing to its completely porous frontal wall, this species is distinguished from the very similar taxa of the genus *Escharina* Milne Edwards, 1836, which are characterised by an imperforate shield, and placed in the genus *Therenia*. David & Pouyet (1978) originally introduced this genus as a subgenus of *Herentia* Gray, 1848, while the latter is now regarded as a junior synonym of *Escharina* (e.g. Zabala & Maluquer, 1988). However, the systematic status of both *Escharina* and *Therenia* is unclear at present, and it has been noted earlier that *Escharina sensu lato* is in need of a comprehensive systematic review (Cook, 1985; Bishop & Hayward, 1989).

The type-species of *Therenia*, the Recent *T. porosa* (Smitt, 1873) from Florida, is occasionally reported from the Mediterranean Sea (e.g. Hayward, 1974; Zabala & Maluquer, 1988) and the central East Atlantic (Cook, 1968b). This species is remarkably similar to the fossil *T. montenati*. While comparisons with figured specimens (Hayward, 1974: fig. 4A, B; Zabala & Maluquer, 1988: fig. 291, pl. 15, fig. F), do not show any major differences, more SEM work needs to be accomplished in order to accomplish a possible synonymy, and to scrutinise whether the Floridan and eastern Atlantic *T. porosa* are, in fact, conspecific.

Occurrence:

Although commonly recorded from Mediterranean fossil assemblages, this is the first report of *T. montenati* from an eastern Atlantic site. The Recent *T. porosa* occurs in the tropical and

subtropical Atlantic. In the Niebla Calcarenite, *T. montenati* encrusts red algae and is only rarely found.

Distribution:

Miocene: Tortonian (Guadalquivir Basin and SE Spain, Morocco), Messinian (Morocco). Pliocene: Spain, Algeria, Italy.

Superfamily CELLEPOROIDEA JOHNSTON, 1838 Family CELLEPORIDAE JOHNSTON, 1838

Celleporidae gen. et sp. indet.

Plate 10, Figure 8, 9

Material:

Niebla Calcarenite: 2 colonies (see Occurrence). examined by SEM: GNI1-059-D, E.

Measurements:

ZL 486 (1, 1) ZW 373 (1, 1) OL 135–145 (1, 2) OW 140–141 (1, 2) AL 513 (1, 1) AW 261 (1, 1)

Description:

Colony encrusting multilaminar, forming small (<1 cm) pisiform colonies or dome-shaped encrustations. Zooids small and short, separated by shallow grooves; frontal wall smooth with a row of large marginal pores, marginal ridges produced by calcification between pores may reach up to orifice. Shape of primary orifice was not observed. Peristome a thickened rim rising proximally to form a tall, conspicuous, suboral umbo which is slightly curved in distal direction, proximal surface of umbo marked by longitudinal grooves and ridges emerging from distal marginal pores. A small oval avicularium situated at distal end of umbo, oblique to plane of orifice, directing distally; crossbar complete.

Ovicells or vicarious avicularia were not observed.

Discussion:

A similar species was not found during the literature investigation. Furthermore, since neither the primary orifice nor ovicells were observed in any of the material from the Niebla Calcarenite, even an accurate generic determination is rendered impossible.

Occurrence:

Due to a usually bad state of preservation of the celleporiform colonies, the surfaces of most specimens are abraded and/or clogged by sediment, an exact statement on the number of colonies present per species cannot be given. The total number of celleporiform colonies obtained is 203, whereas the number given in the Material above refers to the specimens observed and identified using SEM only.

This species was encountered as small pisiform colonies or as multilayered encrustations on ephemeral substrate.

Genus BUFFONELLARIA CANU & BASSLER, 1917

Buffonellaria entomostoma (REUSS, 1848) Plate 10, Figure 10-15

- 1848 Cellepora entomostoma REUSS, p. 92, pl. 11, fig. 7.
- 1859 Lepralia biaperta? (MICHELIN) Busk, p. 47, pl. 7, fig. 5.
- 1874 Lepralia entomostoma (REUSS) Reuss, p. 157, pl. 4, fig. 11.
- 1921 Stephanosella biaperta (MICHELIN) Cipolla, p. 86, pl. 4, fig. 6.
- 1974 Stephanosella entomostoma (REUSS) David & Pouyet, p. 172, pl. 15, fig. 3.
- 1987 Buffonellaria divergens (SMITT) Bishop, p. 10, fig. 17-19.
- ? 1988 Stephanosella entomostoma (REUSS) Moissette, p. 146, pl. 24, fig. 1.
- ? 1992 Stephanosella entomostoma (REUSS) El Hajjaji, p. 214, pl. 11, fig. 13.
- ? 1992 Stephanosella entomostoma (REUSS) Pouyet & Moissette, p. 63, pl. 9, fig. 7.
- ? 1993 Stephanosella entomostoma (REUSS) Moissette et al., p. 103, fig. 6h, i.
 1997b Buffonellaria divergens (SMITT) Pouyet, p. 28, fig. 20.

Material:

Niebla Calcarenite: 11 colonies.

examined by SEM: GNI1-046-A, B, C, D, E, F.

own collection: PMP110.5-091-G (Pliocene, Italy).

BNHM B.1698 (as *Lepralia biaperta*? [Michelin, 1848], Pliocene, Coralline Crag; Busk, 1859: pl. 7, fig. 5; SEM photocard); Pk1413-1420 (as *B. biaperta*, Recent, Svalbard; Smitt, 1868: fig. 70; SEM photocards of sample number SNHM 1742 [Stockholm Natural History Museum]); 1911.10.1.1082.pt. (*B. divergens* [Smitt, 1873], Recent, Guernsey); 2000.12.5.10 (*B. divergens*, Recent, Western Channel).

other: VNHM 1878.11.31 (lectotype of *Cellepora entomostoma* Reuss, 1848, Badenian, Eisenstadt; chosen by David & Pouyet, 1974: pl. 15, fig. 3); 1860.28.12, 1867.40.222 (*B. entomostoma*, Badenian, Eisenstadt).

Measurements:

409 ± 27, 350–447 (2, 20) ZL ZW $316 \pm 43, 245 - 384(2, 20)$ OL $89 \pm 12,74 - 119(4,18)$ OW $85 \pm 7,75-98$ (4, 18) 170 ± 12, 145–186 (2, 13) OvL OvW $198 \pm 26, 169 - 262 (2, 13)$ $151 \pm 21, 111 - 179(1, 8)$ iAL iAW $69 \pm 11, 54 - 83(1, 8)$

Description:

Colony encrusting unilaminar, multiserial. Zooids hexagonal to oval, slightly convex, separated by shallow grooves; frontal wall smooth and imperforate except for very few (four to five), slitlike, marginal areolar pores, and a round distinct pore just distal to orifice, located in proximal frontal wall of distal zooid (which is presumably involved in ovicell formation). Primary orifice variable in shape and therefore in relation of length and width; anter semicircular, proximal margins straight with short distinct condyles, poster either broadly U-shaped and shallow, or deep and rounded V-shaped.

Ovicell recumbent on distal zooid's frontal wall, globular first, semicircular in later ontogeny when it becomes immersed by frontal calcification, with a smooth band of distolateral ectooecium and a less convex, hemispherical, proximofrontal area of uncovered entooecium marked with radiating ribs; often neighboured by one or two avicularia.

Small adventitious avicularia usually proximolateral or lateral to orifice, single or paired, situated on a slightly raised and swollen cystid; rostrum elliptical, directing proximally, slightly oblique to frontal plane, crossbar complete, without columella. Additional large interzooidal

avicularia present in older areas of the colony, arising anywhere on frontal zooid surface, situated on large swollen cystid with marginal pores; rostrum pointing in various directions, acute, long and slender, narrowing immediately distal to thick complete crossbar presumably lacking a columella.

The proliferation of large avicularia leads to a different appearance of these areas, in which zooidal boundaries are obscured and the orifice becomes slightly immersed. Furthermore, increasing frontal calcification in older parts of the colony results in an even more extreme zooidal and colonial morphology: the originally extensive zooidal frontal wall is reduced to a meshwork of frontal calcification punctured by areolar pores, the small adventitious avicularia, the hemispherical entooecial area, and a semicircular aperture with a straight distal margin containing the deeply immersed orifice at its bottom.

Discussion:

This species (and related taxa) stands out due to its extreme morphological variability, which is, to a great deal, produced by secondary calcification during ontogeny and affects the zooidal frontal surfaces, ovicells, and avicularia alike. Adding to the morphological plasticity, also the orifice shape is prone to variation, and may change from a broad and shallow U-shape, to deeper and rather V-shaped within a single colony. Under these premises, defining species boundaries in this genus may become a contentious issue.

Most of the (type)material of *B. entomostoma* from the Vienna Basin is quite recrystallised (see also David & Pouyet, 1974: pl. 15, fig. 3) and thus a precise definition of the species, and an unequivocal comparison with the present material, is rendered difficult. Furthermore, no SEM documentation of the types exists to date, while observation under a light microscope reveals no differences. Most of the other synonymies given above are indistinguishable from the present specimens, although some are in a bad state of preservation. The figured specimens of the synonymies indicated by a question mark, nevertheless, display some features that were not observed in the remaining material, such as a convex frontal shield, a thickened and raised orifice margin, and a frontally budded avicularium situated centrally and proximal to the orifice on a raised cystid. Since ovicell morphology is neither depicted nor specifically described in any of these works, there must remain some doubt about their affinity.

While Ryland (1969: p. 220) has clarified the taxonomic status of the Recent *B. divergens* Smitt, 1873 and the Late Miocene *Stephanosella biaperta* Michelin, 1848 from NW France. Yet a comparison with the type material of the Paratethyan *Stephanosella entomostoma*, which was regarded as very similar to (or conspecific with) the former by many palaeontologists working in the central European area, remains to be accomplished. However, there are several problems: (1) the state of preservation of the type-material of *B. entomostoma* is presumably insufficient, as mentioned above; (2) the type-material of *B. divergens* from Florida has never been studied using SEM, and, in this way, never been compared with the supposed eastern Atlantic representatives; (3) likewise, *B. divergens* or any other species of this genus from the European shores has, to my knowledge, not yet been documented using SEM, which also means that there is very little information on inter- and intraspecific variation.

As Ryland (1969) stated, there are at least two other Recent European species of *Buffonellaria* that have been assigned to *B. divergens*, one from the Arctic region (referred to as *B. biaperta* [Michelin, 1848] by e.g. Kluge, 1975) and another from Algeria. After SEM observations of specimens from the British Isles and Svalbard, the distinctness of the two species was affirmed (Berning & Kuklinski, in prep.). Furthermore, based on the fact that the East and West Atlantic share only very few species, most of which can be regarded as being introduced through fouling on ship's hulls (as, e.g., *Schizoporella errata* Waters, 1878 [Schopf & Dutton, 1976]), it is highly likely that the Floridan *B. divergens* is not conspecific with the European species. An investigation addressing this problem is currently underway (Berning & Kuklinski, in prep.).

Comparison between the present material and Recent representatives of '*B. divergens*' from the British Isles revealed that, while the latter has twice as many and more conspicuous marginal areolar pores than the fossil species, the broadly U-shaped poster is clearly dominant in extant material, whereas it is the other way round in the fossil specimens. However, as stated above, unless we know more about the range of intraspecific variation it is not of much value to decide on conspecifity between the fossil and Recent species.

Occurrence:

As with morphological variation, very little is known about the ecology of '*B. divergens*' beyond its occurrence in the southern North Atlantic and the western Mediterranean, where it is reported from depths between 20 and 200 m. *B. entomostoma/B. divergens* is fairly often been recorded in fossil assemblages from the Mediterranean basins.

In the Niebla Calcarenite it is rarely observed, encrusting coralline algae.

Distribution:

Miocene: Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin and SE Spain), Messinian (SE Spain, Algeria, Morocco, Crete).

Pliocene: Spain (Carboneras Basin), Italy, Rhodes, NW France, England, Belgium.

Genus CELLEPORINA GRAY, 1848

Celleporina cf. *canariensis* ARÍSTEGUI, 1989 Plate 11, Figure 1-4

cf. 1989 Celleporina canariensis ARÍSTEGUI, p. 147.
cf. 2002 Celleporina canariensis ARÍSTEGUI – Hayward & McKinney, p. 86, fig. 39E-G.

Material:

Niebla Calcarenite: 8 colonies. examined by SEM: GNI1-055-A, B, C, D, E; GNI1-056-C; GNI1-059-F; GNI1-060-A.

Measurements:

ZL $441 \pm 29,408 - 498(5,8)$ ZW $417 \pm 55, 364 - 508(5, 8)$ OL $135 \pm 9, 123 - 147(5, 10)$ OW $112 \pm 6, 100 - 119(5, 10)$ 155 ± 8, 142–163 (3, 6) OvL OvW $203 \pm 17, 167 - 221(3, 6)$ AL 42-50(1,3)AW 21-25(1,3)

Description:

Colony encrusting multilaminar, forming small pisiform colonies of up to ca. 3.5 mm in diameter. Zooids round to oval, swollen, separated by distinct grooves; frontal wall smooth, convex, irregularly punctured by few large pores. Primary orifice round, slightly longer than wide, with a short, rounded V-shaped sinus proximomedially. Peristome raised, tubular, thickened laterally, obscuring the proximal part of primary orifice, forming a shallowly to deeply notched proximal rim.

Ovicell wider than long, globose; planar entooecial area hemispherical with a single row of some 10 to 14 marginal pores and radiating costules; straight proximal margin and convex distal edge formed by smooth ectooecium; ovicell opening into the peristome.

A pair of small adventitious avicularia situated on lateral peristomial rim; rostrum parallel to plane of orifice, elliptical, with complete crossbar, ca. 0.5 mm long, directing distally or distolaterally Vicarious avicularia were not observed.

Discussion:

Fossil celleporinids with (remnants of) a pair of apertural avicularia were airily referred to as *Celleporina costazii* (Audouin, 1826) by numerous bryozoologists working on Neogene Mediterranean faunas. A comparison of specimens figured in some of the latest publications suggest, on the one hand, that there are several species combined under this name (e.g. Moissette,

1988, pl. 29, fig. 9, 12; El Hajjaji, 1992: pl. 15, fig. 9; Pouyet & Moissette, 1992: pl. 12, fig. 2, 3; Moissette, 1997: pl. 3, fig. 6). On the other hand, there are two problems with the assignment to this species: first, the type material of the Recent species Audouin (1826) described from an unknown locality from (presumably) the Red Sea is not available, and a neotype has not been chosen, yet. A modern species concept does therefore not exist. Secondly, fossil celleporinids are generally difficult to determine and to compare with other published records due to a commonly poor state of preservation, its few morphological characteristics, but especially owing to insufficient illustrations and descriptions, e.g. details of the primary orifice are seldom mentioned or figured. Thus, mainly due to the lack of information on other morphospecies, the present specimens can not confidently be synonymised with any other fossil species. Since the last monograph was published in 1974 by Pouyet, it is apparent that a thorough revision of Neogene Mediterranean celleporinids using modern observation techniques is overdue.

However, the species from the Niebla Calcarenite is remarkably similar to the Recent *C. canariensis* (I refer here to the Adriatic specimens described and figured in Hayward & McKinney [2002] only, since I have not seen the original publication of Arístegui [1989]). Yet, since vicarious avicularia are absent in the present material and the preservation not as good as to detect the small, medially directing processes distal to the adventitious avicularia, I prefer to merely confer my fossil specimens to *C. canariensis*.

Occurrence:

C. canariensis has not been recorded as a fossil before. However, several records of *C. costazii* may prove to be close to this species once morphological details of the orifice are identified. The Recent *C. canariensis* occurs from 5 to 40 m in the Mediterranean Sea and is common in caves along the Catalan shore.

In the Guadalquivir Basin fauna this species commonly occurs as small pisiform colonies encrusting coralline algae. (See Occurrence in Celleporidae gen et. sp. indet. for information on abundance of celleporiform colonies in the Niebla Calcarenite in general.)

Distribution:

Miocene: Tortonian (Guadalquivir Basin - Spain). Recent: ?eastern Atlantic (Canaries), Mediterranean Sea.

Celleporina sp.

Plate 11, Figure 5, 7, 8

cf. 1992 Celleporina lucida (HINCKS) – Pouyet & Moissette, p. 78, pl. 12, fig. 4, 5.

Material:

Niebla Calcarenite: 8 colonies. examined by SEM: GNI1-057-A, B, C, D; GNI1-058-A, B, C; GNI1-059-B.

Measurements:

 $305 \pm 32, 265 - 343 (2, 6)$ ZL ZW $260 \pm 14, 239 - 269(2, 6)$ 84-99 (2, 2) OL OW 78-90(2,2)108 ± 12, 93–126 (3, 11) OvL OvW $145 \pm 8, 125 - 154(3, 11)$ AL 205 ± 31 , 141–154 (3, 10) $79 \pm 10, 64 - 91 (3, 10)$ AW

Description:

Colony encrusting multilaminar, forming small (<1 cm) nodular colonies or dome-shaped encrustations. Zooids small and short, separated by distinct grooves; frontal wall convex, smooth, sloping distally towards peristome, with few marginal pores. Primary orifice longer than wide; a broad, deep, U-shaped sinus demarcated from anter by short straight proximolateral margins, occupying more than two-thirds of proximal width. Tubular peristome with an orbicular aperture formed by a thick rim, obscuring the orifice; in ovicellate zooids the proximal peristome margin is raised to form a broad suboral umbo bearing a small elliptical avicularia at its top end.

Ovicell hemispherical, frontal tabula flat, usually broad but variably developed with one row of some 14 elongated distolateral pores and radial intervening ridges, proximal margin straight; lateral walls of peristome sloping down from umbo to level with frontal surface of ovicell, encroaching proximolateral part of ovicell, producing a semicircular aperture; ectooecial rim variably developed, smooth, convex.

Adventitious avicularium single, at distal end of umbo, inclined at almost right angle to orifice plane, facing distally, directing frontally, crossbar complete. Vicarious avicularia may occur frequently, dimorphic: spatulate avicularia conspicuous, common, of varying size, with a very narrow and parallel-sided proximal part increasingly broadening towards round, spoon-shaped and slightly cupped distal end; palatal foramen short, narrow; crossbar thick, complete, without columella. Elliptical avicularia less common, elongated, parallel-sided with large palatal foramen; crossbar complete, without columella.

Discussion:

This species is very close to the one described as C. lucida (Hincks, 1880) by Pouvet & Moissette (1992). Both share the typical spatulate vicarious avicularium, a median suboral umbo associated with a distal adventitious avicularium, and the sloping lateral walls connecting umbo and ovicell. Whether the Pliocene Italian and the Miocene Guadalquivir Basin material are conspecific is not possible for me to conclude at present because the shape of the primary orifice is insufficiently described in their work. However, the species described by Pouyet & Moissette (1992) differs from the Recent Mediterranean C. lucida (as described by Zabala & Maluquer, 1988: p. 158, fig. 435, 436, pl. 26 D; I have not seen the original description or type-material) in the shape of the peristome (it is described and figured as spiralling in C. lucida) and thus the connection between umbo and ovicell. Whereas the lateral and distal peristomial rim projects above and (partly) encloses the ovicell in C. lucida, this is never the case in the fossil material, in which the lateral walls slope down towards, and level with, the proximolateral ovicell margins. Furthermore, at least in the present material, the sinus is distinctly broader than that figured for C. lucida (Zabala & Maluquer, 1988: fig. 436). Thus, the Italian and my Spanish specimens may be conspecific (which has yet to be proven) whereas both are clearly distinct from C. lucida (as defined by Zabala & Maluquer, 1988).

Occurrence:

This species is common in the Niebla Calcarenite, usually encrusting red algae. (See Occurrence in Celleporidae gen et. sp. indet. for information on abundance of celleporiform colonies in the Niebla Calcarenite in general.)

Distribution:

Miocene: Tortonian (Guadalquivir Basin - Spain). ?Pliocene: Italy.

Genus LAGENIPORA HINCKS, 1877

Lagenipora sp. Plate 11, Figure 6, 9, 10

Material:

Niebla Calcarenite: 5 colonies. examined by SEM: GNI1-059-G; GNI1-060-B.

Measurements:

ZL $455 \pm 38, 403-498 (2, 10)$ ZW $335 \pm 31, 289-388 (2, 10)$ OL 92-97 (1, 2)OW 89-97 (1, 2)ApL 141-154 (1, 3)ApW 131-143 (1, 3)OvL 104-112 (1, 2)OvW 168-173 (1, 2)

Description:

Colony encrusting unilaminar, multiserial. Zooids hexagonal but usually polygonal, separated by distinct grooves; frontal wall convex, smooth, raising distally towards peristome, with one row (proximally occasionally two) of large marginal pores accentuated by short broad ridges separating them. Primary orifice orbicular, usually disguised by the peristome. Peristome a long distinct tube with a suborbicular aperture, terminally bearing two minute lateral avicularia; no spines.

Ovicell incorporated in basal peristome, hemispherical, with a rather flat frontal surface and a large pore in each proximolateral corner accentuated by thickened and raised borders; proximal margin straight, ovicell opening into peristome.

Avicularia were not observed.

Discussion:

The autozooids of the present specimens resemble the material Pouyet & Moissette (1992: p. 76, pl. 12, fig. 11) and Haddadi-Hamdane (1996: p. 112, pl. 10, fig. 7) described as *Lagenipora lepralioides* (Norman, 1868). However, there are seemingly several differences between these fossil bryozoans. Pouyet & Moissette (1992) report a crescent area with radial ribs on the frontal ovicell surface (yet no ovicells are figured), while they do not mention the pair of lateral avicularia that exist in the present specimens, although some zooids in their fig. 11 (pl. 12) may, in fact, show remnants of these. Ovicell morphology is not described by Haddadi-Hamdane (1996), while she reports traces of spines on the peristome. However, her material is not well preserved, and the supposed spines may as well be fractures of a damaged peristome.

While more SEM work is necessary before any decision on conspecifity of these fossil specimens can be made, a comparison with the Recent *L. lepralioides* as figured in Zabala & Maluquer (1988: fig. 444) and Hayward & Ryland (1999: fig. 154, 155A, B) clearly shows that it is different from my material. *L. lepralioides* lacks avicularia as well as the proximolateral pores in the frontal surface of the ovicell.

Occurrence:

This species is rarely found in the Niebla Calcarenite, encrusting red algae.

Genus OSTHIMOSIA JULLIEN, 1888

?Osthimosia sp.

Plate 11, Figure 12, 15

Material:

Niebla Calcarenite: 2 colonies. examined by SEM: GNI1-004-A.

Measurements:

Description:

Colony encrusting unilaminar, multiserial. Individual zooid boundaries obscured by secondary calcification; frontal shield smooth, greatly reduced due to secondary thickening, punctured by large (?marginal) pores. Primary orifice immersed, orbicular, ?with a broadly U-shaped shallow sinus.

Avicularia dimorphic: small, oval, adventitious avicularia with complete crossbar incorporated in proximal or proximolateral orifice margin, oblique to frontal plane, directing proximally. Large interzooidal avicularia broadly spatulate to nearly parallel-sided, rounded distally; palate extensive, crossbar thick and complete, directing distally to distolaterally.

Ovicells were not observed.

Discussion:

Since only one specimen was found which is lacking ovicells, and in which the primary orifice is not well preserved, even the generic assignment must remain doubtful. I cautiously accomodate this species in the genus Osthimosia due to the general appearance of the autozooids only. The present specimen shares some characters with the Recent *O. virgula* Gordon, 1984 and *O. amplexa* Gordon, 1989 from New Zealand, such as that the colony surface is rather 'smooth' (single zooids or peristomes do not, or only rarely, project from the frontal surface plane, in contrast to most other celleporinids), all have a suboral avicularium directly emplaced in the proximal aperture rim, and spatulate avicularia are common between zooids. However, since all of the Recent species of *Osthimosia* occur in the Southern Hemisphere, the assignment to this genus is, as stated above, a very cautious one. No similar species has been encountered during literature survey.

Occurrence:

Only two specimens were found in the Niebla Calcarenite, encrusting coralline algal thalli.

Genus TURBICELLEPORA RYLAND, 1963

Turbicellepora aff. *magnicostata* (BARROSO, 1919) Plate 11, Figure 11, 13, 14

aff. 1919 Schismopora magnicostata BARROSO, p. 346, fig. 23-32.

Material:

Niebla Calcarenite: 3 colonies. examined by SEM: GNI1-056-B; GNI1-059-A; GNI1-060-C.

Measurements:

ZL $475 \pm 53, 404-547$ (2, 6) ZW $380 \pm 37, 319-419$ (2, 6) OL $140 \pm 6, 131-153$ (3, 10) OW $135 \pm 7, 125-145$ (3, 10) vAL 443vAW 257

Description:

Colony encrusting multilaminar, forming small (<1 cm) nodular colonies or dome-shaped encrustations. Zooids broad, separated by shallow grooves; frontal wall convex, smooth, rising distally towards peristome, with one to locally two rows of conspicuous marginal areolae which are accentuated by intervening ridges reaching up frontal wall and suboral umbo. Primary orifice longer than wide, with a broad, deep, U-shaped sinus demarcated from anter by short, inclined, proximolateral margins, occupying two-thirds proximal width. Peristome a low and slightly thickened rim with an orbicular aperture, obscuring the orifice proximally where the frontal wall raises to form a broad, conspicuous, bluntly pointed, suboral umbo directing distally.

Ovicells were not observed.

A variably developed, broadly elliptical, adventitious avicularium is situated on one distolateral face of umbo; rostrum semielliptical, inclined at almost right angle to orifice plane, directing distally, crossbar complete without columella. Vicarious avicularia rare, elongate oval and parallel-sided; rostrum deeply cupped distally, palate narrowing proximally, leaving open a large foramen; a crossbar was not observed.

Discussion:

This species resembles the Recent Mediterranean *T. magnicostata* (see Zabala & Maluquer, 1988) in the shape of the primary orifice, the conspicuous, marginal, areolar pores, and a similar shape of interzooidal avicularia. Yet the suboral umbo is distinctly larger, and the location of the associated avicularium therefore different, in the fossil specimens. Since, furthermore, ovicells were not observed, the Niebla material is here treated as closely related to *T. magnicostata*, but likely to represent a distinct species.

A closer relationship also exists between the Niebla specimens and the material described as *Turbicellepora* sp. by Moissette (1988: p. 190, pl. 30, fig. 10, 11). However, the latter differs slightly in having a more conspicuous and pointed umbo (whereas this may be induced by environmental factors), and the primary orifice is not figured; an unambiguous statement on their relatedness is therefore not feasible. No other records of morphologically similar species have been found.

Occurrence:

This species occurs frequently in the Niebla Calcarenite, forming relatively small nodular colonies. (See Occurrence in Celleporidae gen et. sp. indet. for information on abundance of celleporiform colonies in the Niebla Calcarenite in general.)

Distribution:

Miocene: Tortonian (Guadalquivir Basin - Spain), ?Messinian (Algeria).

Family PHIDOLOPORIDAE GABB & HORN, 1862

"*Hippoporella*" *pauper* (REUSS, 1874) Plate 12, Figure 1, 2, 4

V	part.	1874	Lepralia	pauper	REUSS, p.	164, p	ol. 5,	fig. 4.
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- v part. 1874 Lepralia ternata (REUSS) Reuss, p. 167, pl. 3, fig. 11; pl. 7, fig. 5.
- non 1972 Hippoporella pauper (REUSS) David et al., p. 60, pl. 9, fig. 2.
- v part. 1974 Gemelliporella ternata (REUSS) David & Pouyet, p. 178, pl. 15, non fig. 7.
- v part. 1974 Hippoporella pauper (REUSS) David & Pouyet, p. 173, pl. 7, fig. 8.
- 1988 Hippoporella pauper (REUSS) Moissette, p. 146, pl. 23, fig. 9, 12.
- v part. 1989 Hippoporella pauper (REUSS) Schmid, p. 48, pl. 14, non fig. 1-3.

Material:

Niebla Calcarenite: 78 colonies.

examined by SEM: GNI1-025-A; GNI1-026-A; GNI1-027-A, B, C; GNI1-028-B, C.

other: VNHM 1878.11.49 (partim, syntype of *Lepralia pauper* Reuss, 1874, Badenian, Garschental; partly described as *Lepralia gonversi* Reuss, 1874: pl. 5, fig. 4; chosen by David & Pouyet, 1974: pl. 7, fig. 8); 1859.50.791 (lectotype of *Cellepora ternata* Reuss, 1848, Badenian, Eisenstadt; described as *Gemelliporella ternata* by David & Pouyet, 1974: pl. 15, non fig. 7); 1878.11.59 (partim, as *Lepralia ternata*, Badenian, Eisenstadt; Reuss, 1874: pl. 3, fig. 11); 1988.106.33 (partim *H. pauper*, Badenian, Nußdorf).

Measurements:

 $377 \pm 79,278 - 506(5,20)$ ZL 291 ± 50, 218–369 (5, 20) ZW OL $128 \pm 8, 113 - 140(5, 20)$ OW $88 \pm 6,77-97(5,20)$ OvL $178 \pm 11, 164 - 192(3, 7)$ OvW $184 \pm 11, 171 - 207(3, 7)$ $90 \pm 13, 73 - 109(3, 8)$ aAL aAW $73 \pm 13, 50 - 86(3, 8)$ 315-418 (2, 4) vAL vAW 88–130 (2, 4)

Description:

Colony encrusting unilaminar to plurilaminar, multiserial. Zooids elongated oval to subhexagonal, separated by indistinct sutures; if plurilaminar, the zooids are chaotically arranged and zooid margins are not preserved (zooid length may then drastically decrease, see Measurements); frontal wall convex, raising towards the orifice, imperforate, smooth with about 14, relatively large, marginal areolar pores. Primary orifice cleithridiate, anter oval, longer than broad; round poster demarcated by thick curved condyles directing proximally, these are produced by an inner orifice rim of distinct calcification; most commonly six stout spine bases on distolateral orifice margin (less commonly five, and rarely four or seven; two to four in ovicellate zooids), whereas the most proximal pair is slightly thicker than the more distal spines.

Adventitious avicularia sporadic, small, single, emplaced in various positions on the frontal wall, usually proximolateral and less commonly lateral or proximal to orifice; cystid oval; rostrum semicircular, pointing in various directions; crossbar complete without columella. ?Interzooidal avicularia sporadic, large, single, emplaced proximolateral to orifice, may rest on a neighbouring zooid's frontal wall or ovicell; cystid elongated oval; rostrum pointing distolaterally, slightly

narrowing proximal to crossbar, becoming parallel-sided and producing a deep furrow, slightly bending downwards distally and ending in a blunt tip, uncalcified area elongate triangular; crossbar complete without columella.

Ovicell globular, as long as wide, recumbent on frontal wall of distal zooid(s), surface slightly flattened frontally, smooth and imperforate with a straight proximal edge (a proximal ovicell labellum may be formed by two lateral bars extending towards the centre, leaving a slit-like opening; however, ovicells in the present material are not well enough preserved to provide clear evidence for this).

Discussion:

Ever since its first description, and continuing during establishment of a lectotype and the generic assignment, this species has caused (and still is causing) a fair bit of confusion. I will attempt to shed some light on some of the darker parts of its history. Initially, Reuss (1874) described two species, *Lepralia pauper* (p. 164, pl. 5, fig. 4) and *L. gonversi* (p. 159, pl. 7, fig. 7) which were later synonymised by David & Pouyet (1974). (Since I have not seen the original material of *L. gonversi* I can not comment on this synonymy.) Yet, some of Reuss' samples labelled *L. pauper* (e.g. VNHM 1878.11.49) include specimens of another species, namely *Schedocleidochasma incisa* (Reuss, 1848) (see also Discussion there). Incidentally, David & Pouyet (1974: p. 173) chose this sample, consisting of two specimens, as the lectotype of *L. pauper*, which they placed in the genus *Hippoporella*. Whereas the blue-stained specimen is *S. incisa*, but remained unrecognised by them, the unstained one is *H. pauper* and was as such figured on their pl. 7, fig. 8. Both species have a similar orifice shape but *H. pauper* differs from *S. incisa* in that it has a far greater number of marginal areolar pores, and in that the spine bases are thicker and more numerous.

In the same work, David & Pouyet (1974) redescribed *Cellepora ternata* Reuss, 1848 as *Gemelliporella ternata* (p. 178), yet the species described and the lectotype figured (VNHM 1859.50.791; pl. 15, fig. 7) is that of *H. pauper* which was, in part, wrongly identified by Reuss before (as was sample VNHM 1878.11.59 with *L. ternata* on the label but several *H. pauper* in the box). The specimen has a cement coating and is not very easy to identify, e.g. the poster may be reduced to a mere slit, but the spines (the thick proximal pair may have been mistaken for avicularia) and characteristic orifice leave no doubt about it (see also Schmid [1989] for discussion on "*Gemelliporella ternata*"). (Further notes: *C. ternata* is correctly figured in Reuss [1874; pl. 3, fig. 11; as *Lepralia ternata* in the text but he gives *L. tenera* in the figure caption], and may be conspecific with *Lepralia tuba* Manzoni, 1875, which was more recently reported as *Lagenipora tuba* by, among others, Moissette [1988], El Hajjaji [1992] and Pouyet & Moissette [1992].)

Furthermore, most of the material Schmid (1989) described and figured as *H. pauper* (e.g. part of VNHM 1988.106.33) can be referred to *S. incisa* and, presumably, another distinct species (see Discussion in *S. incisa*). The specimen figured by David et al. (1972) as *H. pauper* does not belong to this species. None of the relatively well preserved orifices show the presence of a round and well defined poster and anter, and the large, triangular, interzooidal avicularia are untypical for *H. pauper*. The cases presented above are thus another prime example for the need to redefine many species by modern standards and document the type-material using SEM.

A different problem remaining to date is the generic assignment of *Hippoporella pauper*. Genera of the family Hippoporidridae Vigneaux, 1949, in which *Hippoporella* Canu, 1917 is included today (D.P. Gordon, pers. comm. 2003), are characterised by a somewhat bell-shaped orifice with a broad rounded poster, and no oral spines (Gordon, 1989: p. 65) which is inconsistent with the characters displayed by "*Hippoporella*" *pauper*. Instead, the cleithridiate orifice and the presence of spines (and, if existent, the labellum in the proximal orifice) favour a placement in the Phidoloporidae. However, none of the available genera in this family seem to combine the features of "*H*." *pauper* (numerous areolar pores, thick spines, cleithridiate orifice, interzooidal avicularia) to accommodate this species. Thus, we need to know more about ovicell morphology in this species to be able to confirm its affiliation to present genera or, perhaps more likely, to introduce a new genus.

Morphological variability in this species mainly pertains to the number of spines, which range from four to seven in the present material, whereas Mediterranean representatives are reported to have four spines only. Since the formation of spines may be induced by the presence of predators in some bryozoans (Harvell, 1984) this may thus suggest different ecological pressures between the Mediterranean sites and this eastern Atlantic environment. Furthermore, in many colonies the basal walls and basal vertical walls are missing or are damaged, respectively, which gives the zooid a different appearance and morphometry. The reason for this is unclear but it has been observed in several species occurring in the Niebla Calcarenite, especially in those with a similarly chaotic multilaminar growth (e.g. *?Schizomavella* sp., *Schizoporella dunkeri* [Reuss, 1848]).

Occurrence:

This species has not been reported from Pliocene sediments and is thus one of the few established species occurring in the Niebla Calcarenite that apparently did not survive the Messinian salinity crisis, or did not reinvade the Mediterranean Sea thereafter. Its presence in the Guadalquivir Basin marks the first find of "*H*." *pauper* beyond the Mediterranean basins.

It is one of the more abundant species in the Niebla Calcarenite and is usually found on coralline algae, while often encrusting other bryozoans as well, particularly *C. brongniartii* (Audouin, 1826).

Distribution:

Miocene: Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin & SE Spain, Morocco), Messinian (Spain, Morocco, Algeria).

Genus RETEPORELLA BUSK, 1884

Reteporella sp.

Plate 12, Figure 3, 7

Material: Niebla Calcarenite: 43 colonies. examined by SEM: GNI1-041-A, B, H, I.

Measurements:

Description:

Colony erect rigid, fenestrate; anastomosing branches form three-dimensional reticulate structures with zooids opening on one face only. Trabeculae of biserial zooids; fenestrulae elongate oval, some 0.9 to 1.1 mm long. Zooids elongate rectangular but disguised by frontal calcification, separated by indistinct sutures. Frontal wall convex, smooth, with few large pores around proximal margins; frontal shield becomes thicker and zooid boundaries less distinct during ontogeny due to secondary calcification. Primary orifice deeply immersed and concealed by a suboral avicularium and frontal calcification which forms a thick, circular, raised rim around the aperture; proximal lip with a drop-shaped notch or pore on one side of suboral avicularium; two lateral oral spines may be present proximal to mid-distance of aperture.

Ovicell semicircular, longer than wide, becoming encircled (and then being at level) with frontal calcification; proximofrontally flattened, with a narrow fissure extending for about half its length (but often obscured by secondary calcification or diagenesis) and a straight proximal edge.

Small adventitious avicularia placed in various positions: suboral, on frontal wall, on lateral walls of trabeculae, and on abfrontal surfaces; suboral avicularium round or oval, in central or more marginal position, directing proximally, with semicircular rostrum and complete crossbar; frontal avicularium placed in proximal part of zooid, oval or elongated oval with parallel sides, pointing in various directions, crossbar complete; avicularia on lateral walls oval, pointing in various directions; abfrontal avicularia oval, concentrated in regions where branches anastomose, pointing in various directions. Larger avicularia on the fenestrular axils were not observed.

Discussion:

The Neogene Mediterranean record of the genus Reteporella is a mess. Most specimens have been referred to either R. beaniana (King, 1846) or R. cellulosa (Linné, 1767), both of which are Recent species (presumably) occurring in the Atlantic only. While R. beaniana is distributed from Norway to the Bay of Biscay, where it is present below 200 m (Hayward & Ryland, 1996), the type specimens of R. cellulosa from the Atlantic have, to my knowledge, neither been documented using SEM nor redescribed and the status of this species is thus unclear. Considering this information only, it is highly unlikely that these two species were present in subtropical, relatively shallow waters of the Late Miocene Mediterranean basins. When comparing the figured material in some of the latest publications on supposed occurrences of R. beaniana (e.g. Moissette, 1988: p. 166, pl. 27, fig. 1-3; El Hajjaji, p. 234, pl. 14, fig. 14; Haddadi-Hamdane, 1996: p. 100, pl. 9, fig. 2) and R. cellulosa (e.g. Pouvet & Moissette, 1992: p. 72, pl. 11, fig. 8; Moissette et al., 1993: p. 108, fig. 6f, g; Haddadi-Hamdane, 1996: p. 101, pl. 9, fig. 3) it becomes obvious that there are several distinct species combined under the respective names, and that most specimens are not well enough preserved to enable a precise species description and specific assignment. For instance, due to the suboral avicularium the primary orifice could not be observed in the present material and will only be detected in ontogenetically younger zooids in which the avicularium is not fully developed. However, a revision of Neogene Reteporella is overdue and should, despite the generally poor state of preservation, be attempted, which will result in a drastic increase in species diversity in this genus.

None of the figured and described Recent or fossil species of the Mediterranean area seem to be conspecific with the present specimens. There may be two more species of *Reteporella* present in the Niebla Calcarenite; however, besides showing a fenestrate growth, the surface structures are completely abraded in these specimens and they are therefore not further considered here.

Occurrence:

v

Reteporiform, or fenestrate, colonies may occur in a wealth of environments, ranging from quiet cryptic habitats to areas with vigorous flow (Hass, 1948; Smith, 1995). Their colony fragments are commonly found in the Niebla Calcarenite. However, the mostly abraded surface of the specimens suggest that these were transported from their original habitat prior to deposition, which is in contrast to the excellent state of preservation encountered in most other colonies and species; the fenestrate colonies may thus be interpreted to have lived in a higher energy environment, which my also be testified by the fact that colony bases and their substrate were not found in the material.

Genus RHYNCHOZOON HINCKS, 1895

Rhynchozoon monoceros comb. nov. (REUSS, 1848) Plate 12, Figure 5, 6, 10, 11

- v 1848 *Cellepora monoceros* REUSS, p. 80, pl. 9, fig. 24.
- v 1874 Lepralia monoceros (REUSS) Reuss, p. 30, pl. 3, fig. 9.
- 1921 Umbonula? monoceros (REUSS) Cipolla, p. 128, pl. 7, fig. 8.
- 1974 Umbonula monoceros (REUSS) David & Pouyet, p. 145, pl. 12, fig. 2.
 - 1988 Umbonula monoceros (REUSS) Moissette, p. 117, pl. 19, fig. 9.
 - 1989 Umbonula monoceros (REUSS) Schmid, p. 32, pl. 8, fig. 5, 6.

- 1992 Umbonula monoceros (REUSS) Pouyet & Moissette, p. 52, pl. 7, fig. 2.
- 1992 Umbonula monoceros (REUSS) El Hajjaji, p. 146, pl. 7, fig. 11.
- 1999 Umbonula monoceros (REUSS) Sefian et al., p. 234.

Material:

Niebla Calcarenite: 121 colonies.

examined by SEM: GNI1-062-A, C, D, F, J.

own collection: CRC-083-C (Pliocene, Carboneras Basin, SE Spain).

other: VNHM 1848.38.73 (lectotype, Badenian, Eisenstadt; chosen by David & Pouyet, 1974); 1878.11.67 (Badenian, Eisenstadt; David & Pouyet, 1974: pl. 12, fig. 2).

Measurements:

389 ± 46, 329–478 (3, 20) ZL ZW $275 \pm 44, 208 - 395 (3, 20)$ OL $73 \pm 6,65 - 81(1,4)$ OW $108 \pm 9, 102 - 120(1, 4)$ OvL $165 \pm 14, 149 - 204 (2, 14)$ $163 \pm 8, 145 - 172 (2, 14)$ OvW AL $133 \pm 10, 124 - 145(1, 5)$ frontal avicularia AW $71 \pm 6,65 - 80(1,5)$ frontal avicularia

Description:

Colony encrusting multiserial, unilaminar. Zooids elongated elliptical, arranged in alternating series, separated by distinct grooves. Frontal wall strongly convex, smooth, with few, small, marginal areolar pores and a large pointed umbo on either left or right side of zooid, directed distally and covering the aperture; above the orifice an uncinate (hooked) process protrudes from the rostrum in proximal direction to form an open pseudospiramen. Primary orifice facing distally, transversely elliptical, with a concave proximal margin demarcated by two slightly immersed, short, blunt condyles; two (degenerated?) distolateral spine bases in adult zooids.

Ovicell globular, slightly longer than wide, recumbent on distal zooid's frontal wall, imperforate, flattened frontally; a proximal semicircular area of uncovered entooecium is delimited by a straight or slightly concave proximal margin.

Adventitious avicularium single, on basal side of umbo in an oblique position, acute to plane of orifice, directing distolaterally; rostrum triangular, slightly curved distally; crossbar complete without columella. Some zooids bear another monomorphic adventitious avicularium on proximal frontal wall and/or on frontal face of umbo; rostrum straight or slightly curved distally, parallel or acute to frontal plane, usually directing proximally, less commonly pointing laterally.

Ancestrula tatiform, $135x86 \ \mu m$ in size, oval opesia, with an undetermined number of spines (presumably eight), a vertically pointing umbo, and three or four spines in zooids of the first astogenetic generations.

Discussion:

Owing to the fine state of preservation, the orifice features *R. monoceros* are here described and figured for the first time. The additional, single or double, frontal avicularia that commonly occur in the present specimens have only rarely been reported or figured in Mediterranean representatives and thus marks the only morphological difference between these regions.

This species used to be included in the genus *Umbonula* Hincks, 1880 for a long time. However, besides differences in the formation of the frontal wall which can not be proven here, the orifice characteristics, general zooid morphology, and the imperforate ovicells having an uncalcified frontal area provide evidence for an assignment to *Rhynchozoon*. Although the genus *Rhynchozoon* is represented by at least six species in the Recent Mediterranean Sea (Zabala & Maluquer, 1988), surprisingly few fossil species have been reported. Thus, one possible reason may be that some were attributed to different genera, as was the case with *R. monoceros*, which may occur when specimens are poorly preserved and characteristic features are not readily observed.

Occurrence:

After Sefian et al. (1999) reported this species from the Late Miocene NW Morocco, this is the second record from an eastern Atlantic faunal assemblage. Whereas *R. monoceros* survives the Messinian salinity crisis, as evidenced by its occurrence at several post-crisis Mediterranean sites, it seems to have died out before the Pleistocene.

R. monoceros is abundant in the Niebla Calcarenite as regards number of colonies. However, since these are only lightly calcified and occur as unilaminar encrustations, their contribution to the carbonate factory are of very minor importance. The species most commonly encrusts red algae.

Distribution:

Miocene: ?Burdigalian (France), ?Langhian-Serravallian (Italy), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin – Spain; NW Morocco), Messinian (NW Morocco, SE Spain, Algeria).

Pliocene: SE Spain, Italy.

Genus SCHEDOCLEIDOCHASMA SOULE, SOULE & CHANEY, 1991

Schedocleidochasma incisa comb. nov. (REUSS, 1874) Plate 12, Figure 8, 9, 12

- v 1874 Lepralia incisa REUSS, p. 168, pl. 3, fig. 4.
- v part. 1874 Lepralia pauper REUSS, p. 164, non pl. 5, fig. 4.
 - ? 1912 Smittia incisa (REUSS) Canu, p. 215, pl. 11, fig. 8.
 - ? 1928 Buffonella incisa (REUSS) Canu & Lecointre, p. 63, pl. 12, fig. 7.
 - ? 1971 Buffonellodes incisa (REUSS) Galopim de Carvalho, p. 108, pl. 16, fig. 8.
 - 1974 Buffonellodes incisa (REUSS) David & Pouyet, p. 170, pl. 9, fig. 7.
- v part. 1974 Hippoporella pauper (REUSS) David & Pouyet, p. 173, non pl. 7, fig. 8.
 - 1976 Buffonellodes incisa (REUSS) Pouyet, p. 67, pl. 14, fig. 4.
 - 1988 Buffonellodes incisa (REUSS) Moissette, p. 143.
- v part. 1989 Hippoporella pauper (REUSS) Schmid, p. 48, pl. 14, fig. 2, ?non fig. 1, 3.
 - 1992 Buffonellodes incisa (REUSS) El Hajjaji, p. 213, pl. 11, fig. 10.
 - 1992 Buffonellodes incisa (REUSS) Pouyet & Moissette, p. 61, pl. 9, fig. 3.
 - 1997b Buffonellodes incisa (REUSS) Pouyet, p. 62, pl. 6, fig. 5.
 - 1999 Buffonellodes incisa (REUSS) Sefian et al., p. 236.

Material:

v

Niebla Calcarenite: 96 colonies.

examined by SEM: GNI1-001-A, B, C, D, E; GNI1-075-A.

other: VNHM 1878.11.61 (lectotype of *L. incisa* Reuss, 1874, Badenian, Baden; chosen by David & Pouyet, 1974: pl. 9, fig. 7); 1878.11.26 (Badenian, Baden); 1878.11.49 (partim, syntype of *Lepralia pauper* Reuss, 1874, Badenian, Garschental; chosen by David & Pouyet, 1974); 1988.106.33 (partim *H. pauper*, Badenian, Nußdorf; Schmid, 1989).

Measurements:

- ZL 347 ± 30, 281–397 (5, 20)
- ZW 294 ± 38, 206–349 (5, 20)
- OL $133 \pm 8, 123 148 (4, 13)$
- OW $100 \pm 8, 86 116(4, 13)$
- OvL 192 ± 22, 167–224 (3, 10)
- $OvW \quad 181 \pm 19,\, 159{-}214 \; (3,\, 10)$
- AL $102 \pm 9, 86 111(3, 12)$
- AW $56 \pm 6, 45 67(3, 12)$

Description:

Colony encrusting unilaminar, multiserial. Zooecia elliptical to hexagonal, separated by either distinct grooves or indistinct sutures on marked ridges; frontal wall convex, smooth, with two large elongated pores in marginal corners at mid-distance. Orifice large, comprising more than one-third of zooid length, cleithridiate, anter large, round, set off from the smaller, round or semielliptical poster by a pair of pointed condyles directing downwards and proximally; three distal oral spines (up to five in astogenetically young zooids).

Ovicell globular, recumbent on distal zooid, slightly longer than wide, surface imperforate, smooth and flattened frontally, with a pair of narrow proximolateral fissures delimiting a simple labellum with a straight or slightly concave proximal edge.

Interzooidal avicularium common, single, originating from marginal corner at mid-distance from an areolar pore, situated lateral or proximolateral to poster; cystid slightly swollen; rostrum elongated triangular, directing laterally or distolaterally; crossbar complete without columella.

Discussion:

The pair of fissures in the ovicell are, possibly due to insufficient preservation of previous material, reported here for the first time. As a result, this feature, as well as the distinct orifice and zooid morphology, makes it necessary to transfer this species from the Buffonellodidae Gordon & d'Hondt, 1997 to the Phidoloporidae. However, the generic assignment in this family is rendered a little more difficult: whereas the proximal part of the ovicell in the present specimens resembles that of Plesiocleidochasma Soule, Soule & Chaney, 1991, species of this genus form a distinctly different kind of avicularium with a double columella and a trifoliate opesia. A direct comparison between Recent and fossil specimens is further hindered by the eventual loss of secondary calcification. This can drastically influence zooid and ovicell morphology in that, for example, the ovicell is primarily recumbent on the frontal wall of the distal zooid but may later be completely covered by a thick layer of calcification and appears immersed. Furthermore, the proximal slit-like opening and lateral bars in the ovicells of these species may be a temporal phenomenon, which may coalesce and eventually close during later ontogeny. Thus, although Schedocleidochasma Soule, Soule & Chaney, 1991 has an ovicell with a transverse slit-like opening in addition to the incised proximolateral margins, Reuss' species is here tentatively assigned to this genus since zooid and avicularian morphology are very close to some species of that genus, e.g. S. immersum Soule, Soule & Chaney, 1991 (p. 482, pl. 5, fig. 1, 2). Therefore, although not even 15 years old, the genera introduced by Soule et al. (1991) already need revision concerning the usefulness of avicularian vs. ovicell morphology in genus definitions.

The present specimens are indistinguishable from the lectotype of *S. incisa* (VNHM 1878.11.61). However, the relatively close proximity to "*Hippoporella*" *pauper* (Reuss, 1874) has led to some mistakes in the identification of these species by Reuss (1848, 1874), David & Pouyet (1974), and Schmid (1989) (see also Discussion in "*H.*" *pauper*). The species Schmid (1989) figured as "*H.*" *pauper* can be referred to *S. incisa* (pl. 14, fig. 2), which shows the typical orifice and avicularia, and, presumably, to another distinct species (pl. 14, fig. 1, 3), as judged by the broader poster and the less developed frontal shield. However, although she does not mention this to be the case, if the depicted colonies are multilaminar encrustations (see e.g. fig. 1) it may be that zooid shape is greatly altered and it may then, in fact, prove to be *S. incisa*. Yet multilaminar colonies of *S. incisa* have not been recorded to date.

Occurrence:

Besides the material from the Badenian of the Vienna Basin, no other specimens have been viewed apart from optical photographs published. Therefore, any record earlier than Middle Miocene must be considered doubtful, as applies for the Tortonian specimen from NW France (Canu & Lecointre, 1928). However, since Sefian et al. (1999) report the presence of *S. incisa* in Atlantic sediments, and since it is common in the Guadalquivir Basin, the biogeographic range towards northern France is not unlikely.

S. incisa is abundant in the Niebla Calcarenite, although not important as regards cabonate production, and usually encrusts red algae.

Distribution:

 Miocene: ?Aquitanian (Portugal), ?Burdigalian (France), ?Langhian-Serravallian (France, Egypt, Italy, Portugal), Badenian (Vienna Basin, Poland), Tortonian (Guadalquivir Basin and SW Spain, ?NW France), Messinian (Algeria, NW and NE Morocco).

Pliocene: Spain, Italy.

Genus SCHIZOTHECA HINCKS, 1877

Schizotheca serratimargo (HINCKS, 1886) Plate 12, Figure 13-15

v 1886 Schizoporella serratimargo HINCKS, p. 268, pl. 10, fig. 6.

1976 Schizotheca serratimargo (HINCKS) – Pouyet, p. 73, pl. 11, fig. 3-4.

1988 Schizotheca serratimargo (HINCKS) – Moissette, p. 170, pl. 27, fig. 4, 6.

1988 Schizotheca serratimargo (HINCKS) – Zabala & Maluquer, p. 150, fig. 393, 394; pl. 22, fig. E, F.

1992 Schizotheca serratimargo (HINCKS) – El Hajjaji, p. 239, pl. 15, fig. 13.

1992 Schizotheca serratimargo (HINCKS) - Pouyet & Moissette, p. 72, pl. 11, fig. 2-4.

1993 Schizotheca serratimargo (HINCKS) – Moissette et al., p. 109, fig. 7d, e.

1996 Schizotheca serratimargo (HINCKS) – Haddadi-Hamdane, p. 104, pl. 9, fig. 4, 6.

1997 Schizotheca serratimargo (HINCKS) – Moissette, p. 196, pl. 3, fig. 2.

1999 Schizotheca serratimargo (HINCKS) – Sefian et al., p. 238, pl. 1, fig. 10.

2002 Schizotheca serratimargo (HINCKS) – Haward & McKinney, p. 98, fig. 45 A-H.

Material:

Niebla Calcarenite: 123 colony fragments.

examined by SEM: GNI1-014-A, B, C; GNI1-015-A.

own collection: CRC-077-B, C (Pliocene, Carboneras Basin, SE Spain). other: BNHM 1899.5.1.280 (co-type, Adriatic Sea, Hincks Collection).

Measurements:

ZL $463 \pm 47, 376 - 597(3, 20)$ ZW $292 \pm 36, 229 - 356(3, 20)$ $93 \pm 13,77 - 125(3,20)$ ApL ApW 89 ± 10, 77–113 (3, 20) OvL $174 \pm 12, 156 - 194(3, 13)$ OvW $186 \pm 14, 163 - 206(3, 13)$ $117 \pm 14, 102 - 138(3, 9)$ aAL aAW $88 \pm 12, 82 - 113(3, 9)$ 480 vAL vAW 400

Description:

Colony erect rigid, bilaminar; extensive and anastomosing sheets form three-dimensional structures several cm in size. Zooecia suboval to irregularly polygonal in older parts of the colony, separated by distinct grooves. Frontal wall slightly convex, nodular with six submarginal pores; frontal shield becomes thicker and zooid boundaries less distinct during ontogeny due to secondary calcification. Aperture orbicular, primary orifice round with sloping proximal margins (?condyles) and a broad, U-shaped sinus; some zooids bear a short peristome with a median sinus in proximal rim; young zooids with four, later stages with two widely spaced, distal oral spines.

Ovicell globular, resting on a very small area of the distal zooid but may become immersed during ontogeny, aperture widely open, extending distally as a rounded triangular or hemispherical fissure.

Adventitious avicularia develop on ontogenetically older zooids only, located proximolateral to orifice; rostrum elongate triangular, acute to frontal plane, pointing in different directions. Large vicarious avicularia mostly along branch or sheet margin, rarely on the colony face; cystid as long as autozooid, with marginal pores; rostrum almost as long, elongate triangular, crossbar complete, thick, without columella, concave, thus forming a crescentic foramen proximal to crossbar.

Discussion:

This species is commonly encountered in fossil and Recent faunal assemblages of the Mediterranean basins. However, whereas present-day *S. serratimargo* is reported as growing in bilaminar and anastomosing branches, the Niebla specimens consist exclusively of broad bilaminar or foliose sheets with 'triple junctions' (not site of fusion but origination of tripartite sheets) most often preserved. Furthermore, frontal budding, i.e. multilaminar growth, was commonly observed to occur in these triple junctions. In Recent representatives, multilaminar colonies were, besides adeoniform and unilaminar growth, only once observed to occur in Atlantic specimens dredged off NW Morocco by Canu & Bassler (1925). If this difference in mode of growth is triggered by environmental factors (and if yes, by which), or whether the Recent type has evolved during the Pliocene I cannot say. However, a similar pattern is observed in *Pentapora fascialis* (Pallas, 1766), which forms colonies composed of folded and anastomosed bilaminar sheets in the Atlantic, whereas Mediterranean representatives produce narrow branches (adeoniform growth).

McKinney (1989) examined the patterns of colonial water flow in *S. serratimargo* and showed that branches wider than about 4 mm usually do not exist because in branches wider than this the water outflow does not function efficiently. The present material often reaches widths in excess of 4 mm, especially when considering the bending of the continuous sheets at triple junctions, and do then sporadically form vicarious avicularia on the colony face, as observed by McKinney (1989) in one extensive sheet. Thus, one may argue that the vicarious avicularia may promote water outflow in these regions.

Another feature commonly observed in the present material was frontal budding, i.e. multilaminar growth, occurring mostly in the triple junctions (Pl. 12, Fig. 15), which has not been recorded in recent studies on *S. serratimargo* from the Mediterranean Sea (McKinney, 1989; McKinney & McKinney, 1993). Furthermore, in contrast to the Recent specimens figured in Hayward & McKinney (2002), the adventitious avicularia do not occur on the proximal frontal wall but proximolateral to the orifice. However, the location of formation of adventitious avicularia seems to be subject to variation in this species, since Zabala & Maluquer (1988) document similar suboral avicularia.

Occurrence:

S. serratimargo is considered a Mediterranean endemic; its presence in the Atlantic, where it was only once encountered off the coast of Morocco, was interpreted to be due to human introduction in Recent times (Pouyet & Moissette, 1992). In contrast, in the late Miocene this species was obviously frequently occurring on the Atlantic coasts of Spain and Morocco (Sefian et al., 1999). At the same time, the present material marks, together with a record from south-western Spain (Pouyet, 2000), the earliest occurrence of this species.

In the Mediterranean Sea, *S. serratimargo* is common on hard substrata in shallow inshore habitats as well as in biocoenoses with coralline algae and on organo-detritic sediments. It preferentially occurs in regions with low sediment accumulation and in exposed but relatively low kinetic energy conditions (McKinney & McKinney, 1993). Its known distribution ranges from 3 to 160 m depth, with an optimum between 20 and 50 m. In the Niebla Calcarenite *S. serratimargo* is, besides *Myriapora truncata*, the most frequently occurring species and most important carbonate producer among bryozoans. The prevalence of fragments of the robust triple junctions may suggest transport prior to deposition. Additionally, the fragments are often encrusted by a variety of other bryozoans, which may be another indication of an allochthonous occurrence at the site sampled.

Distribution:

Miocene: Tortonian (Guadalquivir Basin and SW Spain), Messinian (Spain, NW and NE Morocco, Algeria, Tunisia, Crete).
Pliocene: Spain, Algeria, Italy.
Pleistocene: Italy.
Recent: Mediterranean, Atlantic (?Morocco, Madeira, western English Channel).

Incertae sedis

Ascophorina indet. Plate 12, Figure 16, 17

Material:

Niebla Calcarenite: 5 colonies. examined by SEM: GNI-043-B, F.

Measurements:

ZL 905 \pm 24, 870–925 (1, 4) ZW 747 \pm 82, 664–853 (1, 4) OL 277–301 (1, 3) OW 220–232 (1, 3) AL 140–226 AW 102–126

Description:

Colony encrusting unilaminar, multiserial. Zooids large, broadly quadrangular to polygonal, separated by distinct grooves; frontal shield convex, evenly perforated by numerous round pores emphasised by funnel-shaped openings. Orifice large, oval, slightly longer than wide, widest at distal third, large anter demarcated by thin, pointed, proximomedially directing condyles from smaller poster; peristome a thick, steep-sided, smooth rim, proximal margin with large, sword-like, prominent mucro; distolateral aperture with six to eight spines.

Ovicells were not observed.

One or two adventitious avicularia of varying size lateral to orifice, sometimes absent; rostrum elongated oval with parallel sides, directing distally; cystid with marginal pores. Occasionally with an (additional) small avicularium proximally or proximolaterally to mucro; cystid may be raised.

Discussion:

Unfortunately, only three small specimens were found that lack ovicells, and therefore an important feature (i.e. if these were present at all). The general appearance of this species, with a porous frontal wall (but see below), with avicularia lateral to the orifice, and with a suboral umbo, is reminiscent of some species of the genus *Hippopleurifera* Canu, 1927, e.g. of the type-species *H. biauriculata* (Reuss, 1848). And even the third, proximal avicularium is reported in one species referred to *H. sedgwicki*? (Milne Edwards, 1836) by Moissette (1988: p. 118, pl. 19, fig. 10, 12), which has a similar ovicell as *H. biauriculata* (see also Discussion in *H. semicristata* [Reuss, 1848]). However, the presence of oral spines and distinct condyles, and the different type of frontal shield pores renders this species distinct from *Hippopleurifera*, at least from its type-species. The pores in the present specimens are not marked by prominent ridges, as is the case in *H. biauriculata*, but instead are similar to those formed in the Exechonellidae Harmer, 1957. Yet, in this family, oral spines and condyles are wanting (Gordon, 1984). Since I could not find a genus to which this species can confidently assigned to, I choose to keep it as *incertae sedis*.

Occurrence:

Only five colony fragments were found encrusting red algae, or occurring independent of their substrate.

5. Late Miocene Bryozoa from the Guadalquivir Basin (SW Spain): eastern Atlantic and western Mediterranean environment and biogeography

B. Berning¹, P. Moissette² & C. Betzler¹

¹Geologisch-Paläontologisches Institut, Universität Hamburg, Hamburg, Germany ²Université de Lyon I, UFR Sciences de la Terre/UNR 5125 CNRS PEPS, Villeurbanne Cedex, France

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5.1 Abstract

Even 30 years after the discovery of the latest Miocene desiccation of the Mediterranean Sea, the circumstances of the Messinian Salinity Crisis (MSC) are a subject of much debate. New cheilostome bryozoan data from the eastern Atlantic Guadalquivir Basin (south-western Spain), which remained unaffected by the MSC, allow us to address questions concerning the late Tortonian biogeography in concert with environmental conditions before onset of the crisis. The great similarity between this eastern Atlantic and the Mediterranean faunas suggests that, other than today, surface water exchange occurred in both directions, and that environmental conditions of the Guadalquivir Basin were sufficiently similar for Mediterranean species to survive the MSC. However, comparison of environmentally controlled autozooid morphometry of eastern Atlantic species with nearly coeval Mediterranean representatives reveals generally smaller autozooid dimensions in Atlantic specimens, thus indicating a certain dissimilarity in physical parameters between these regions.

5.2 Introduction

The isolation and desiccation of the Mediterranean Sea during the latest Miocene, an episode known as the Messinian Salinity Crisis (MSC), represents one of the most dramatic oceanographic events in the Neogene. Collision of the African and European plates induced vertical movements of the southern Spanish and northern Moroccan regions and resulted in a progressive shallowing and closure of the Mediterranean-Atlantic connections, the Betic and Rifian corridors, respectively (e.g. Esteban et al. 1996, Hodell et al. 2001, Kouwenhoven et al. 2003). Prior to and during the main phase of desiccation in the late Messinian (5.96 to 5.33 Ma) evaporites up to 3 km in thickness were deposited in the main Mediterranean basins, followed by brackish sediments of the Lago Mare facies (Hsü et al. 1973, Krijgsman et al. 1999). Re-flooding was most likely initiated by the opening of Gibraltar Strait and Mediterranean-wide normal marine conditions were re-established by the earliest Pliocene (Blanc 2000, Spezzaferri et al. 1998). The event has been thoroughly studied throughout the last three decades, yet many difficulties remain in reconstructing palaeoceanographic conditions of the connecting gateways, late Neogene biogeography of the eastern Atlantic and Mediterranean region, or the impact of the MSC on Mediterranean biota.

Owing to their great diversity and abundance in Neogene sediments, bryozoans have already played an important role in deciphering evolutionary and biogeographical consequences of the crisis to Mediterranean benthic faunas (Moissette & Pouyet 1987, Taylor 2000). Well over 400 Neogene to Recent species are described and numerous monographs have been published especially on the Western Mediterranean fossil fauna (e.g. Moissette 1988, El Hajjaji 1992, Pouyet

& Moissette 1992, Haddadi-Hamdane 1996, Pouyet 2000). However, few data exist from the immediate eastern Atlantic side of the corridors (Reguant 1993, Pouyet et al. 1999, Sefian et al. 1999) despite the fact that this region is crucial to the understanding of environmental conditions and biogeographic patterns before, during and after the MSC. In past attempts to explain the paradox of a desiccated Mediterranean Sea and relatively low late Messinian extinction rates in several benthic invertebrate groups the authors proposed either the existence of an extra-Mediterranean refuge (Ruggieri & Sprovieri 1976, Sabelli & Taviani 1984, Harmelin 1992), or the persistence of marine conditions within the Mediterranean or peripheral basins during the crisis (Moissette & Pouyet 1987, Saint-Martin et al. 2000, Goubert et al. 2001, Néraudeau et al. 2001).

In order to shed light on this issue, and to ascertain Mediterranean/Atlantic current systems and palaeoenvironmental conditions, we collected bryozoan-rich samples from the Guadalquivir Basin in Andalucía, southern Spain (Figure 5.1), which was connected to both the eastern Atlantic and the Mediterranean Sea during late Tortonian time. 51 cheilostome species from the Calcarenita de Niebla Formation were identified which, together with other pre-MSC bryozoan data available from the Moroccan Atlantic side (Sefian et al. 1999), form the basis of our investigations.



Fig. 5.1 Location of sampling site (asterisk) and simplified geology of Andalucía, southern Spain.

5.3 Geological setting

The Guadalquivir Basin in south-western Spain is the northern foreland basin of the Betic Cordilleras (Sanz de Galdeano 1990). It displays a roughly triangular shape, tapering towards the NE and opening towards the Atlantic (Figure 5.1). The late Tortonian Calcarenita de Niebla Formation (Clauss Klamp & González Regalado 1993, Civis et al. 1994, Baceta & Pendon 1999) of the north-western margin of the Guadalquivir Basin proved to comprise the best preserved and most abundant bryozoan faunas.

This formation consists of calcarenites and calcirudites with varying abundances of fine grained matrix, coralline algae, bryozoans, bivalves (large pectinids and ostreids), echinoids (*Clypeaster*) and large benthic foraminifera (*Heterostegina*). The fauna described here was extracted from

samples taken from the friable lower part of the Niebla Calcarenite which is especially abundant in coralline algae (similar to the Crustose Pavement facies [after Bosence 1983]) and has a high content of fine grained matrix, preventing excessive cementation of the biogenic grains. The limestone was deposited on the inner part of a low gradient homoclinal ramp (Baceta & Pendon 1999) and, according to Sierro et al. (1990b), represents a part of the transgressive systems tract of the global sea level cycle 3.2 of Haq et al. (1987). Lateral facies variation is due to the local presence of autochthonous coralline algal and bryozoan patches within areas of bioclastic accumulation (Baceta & Pendon 1999). Depth of deposition is estimated to have been less than 50 m and the faunal composition indicates a warm-temperate to subtropical environment. The presence of *Neogloboquadrina humerosa* (Takayanagi & Saito) in the lowermost part of the Niebla Calcarenite suggests a late Tortonian age (Sierro et al. 1990a).

The Neogene Guadalquivir Basin opened and deepened towards the eastern Atlantic and was additionally, during late Tortonian times, connected with the Mediterranean Sea via the Granada Basin (Esteban et al. 1996) in its south-central part (Figure 5.2), and via the Guadix Basin in the north-eastern region (Soría et al. 1999). The knowledge of late Neogene geography and



Fig. 5.2 Palaeogeographic reconstruction of the late Tortonian Mediterranean/Atlantic connections. Modified from Esteban et al. 1996.

morphology of the Atlantic/Mediterranean connections has greatly increased and thus inevitably changed the assumptions underlying the attempt to reconstruct the regional water exchange by Benson et al. (1991). However, no improved oceanographic model nor field data exist to test their hypothesis that during the late Tortonian influx of Atlantic surface water and outflow of deeper Mediterranean water occurred through the Rifian Straits, whereas Mediterranean surface water passed through the Spanish gateways into the Atlantic Guadalquivir Basin. Understanding the Atlantic/Mediterranean water exchange system is of particular importance when discerning the migration of species and, as a result, establishing biogeographical patterns.

5.4 Results

Although the investigation of the Niebla Calcarenite bryozoan fauna has not yet been completed, 51 cheilostome species have already been identified and their morphological characters measured. The preliminary results presented here are based upon the presence/absence of species in different regions, their variation in colonial morphology, and a morphometric analysis. A more detailed description of the sampling location, methods, bryozoan taxonomy and morphometry, and results will be published elsewhere.

5.4.1 Palaeobiogeography

Based upon known (palaeo)geographic occurrences, the identified late Tortonian bryozoan species can be grouped into cosmopolitan, eastern Atlantic/Mediterranean, and Mediterranean endemics. Additionally, the genus *Emballotheca*, represented by *E. longidens* (Cipolla, 1921) (Figure 5.3A), is the only taxon with an Indo-Pacific affinity. Cosmopolitan species [among others: *Chorizopora brongniartii* (Audouin, 1826), *Escharina dutertrei* (Audouin, 1826), *Microporella ciliata* (Pallas, 1766)], which today occur around the world but are generally absent from polar waters, make up about 16% of the total. Taxa known to occur in both the eastern Atlantic and the Mediterranean Sea predominate the fauna (45%) and comprise species like *Calloporina decorata* (Reuss, 1848), *Schizoporella longirostris* Hincks, 1886, and *Figularia figularis* (Johnston, 1847). A large part of the fauna (39%) is composed of fossil and extant species rarely or never found outside

the Mediterranean Sea and thus are considered to be endemic, such as *Steginoporella cucullata* (Reuss, 1848), *Mollia circumcincta* (Heller, 1867) and *Myriapora truncata* (Pallas, 1766).



Fig. 5.3 (A) *Emballotheca longidens* (Cipolla, 1921), late Tortonian, Guadalquivir Basin. (B) *Aplousina bobiesi* (David & Pouyet, 1974), late Tortonian, Guadalquivir Basin. (C) Variation of branch diameter in *Myriapora truncata* (Pallas, 1766), left: late Tortonian, Agua Amarga Basin, SE Spain; middle: Recent, collected onshore Cabo de Gata, SE Spain; right: late Tortonian, Guadalquivir Basin.

5.4.2 Palaeoenvironment

Most of the species identified (57%) are extant, enabling us to rank them according to their Recent distribution patterns. The Niebla fauna is, species- and specimen-wise, mainly composed of taxa that today occur in warm-temperate to subtropical environments [e.g. *Mollia patellaria* (Moll, 1803), *Schizotheca serratimargo* (Hincks, 1886)]. In addition, taxa of both tropical (*Emballotheca, Steginoporella*) and cooler water affinities [*Escharella octodentata* (Hincks, 1880), *Escharoides coccinea* (Abildgaard, 1806)] are present in the samples.

All of the Recent species of the Niebla fauna are characteristic of an inner- to mid-shelf environment, such as the stenobathic species *Hagiosynodos latus* (Busk, 1856) and *Onychocella angulosa* (Reuss, 1848), whereas species indicative of outer shelf environments are absent. Specimen-wise, the assemblage is dominated by fragments of *Schizotheca serratimargo* followed by *Rhynchozoon monoceros* (Reuss, 1848), *Myriapora truncata*, *Buffonellodes incisa* (Reuss, 1874), *Hippoporella pauper* (Reuss, 1874), as well as poorly preserved and small (usually <1 cm in diameter) celleporiform colonies represented by several species. Another indirect sign of shallow-water conditions is displayed by the faunal predominance of membraniporiform species (78%) over

all other growth forms (adeoniform 8%, celleporiform 4%, vinculariiform 4%, cellariiform 4%, reteporiform 2%).

Table 5.1 Late Tortonian Guadalquivir Basin (eastern Atlantic) mean autozooid surface area (SA, in mm²) for 33 cheilostome species in comparison with representatives from the Mediterranean late Tortonian/early Messinian Morocco (data from El Hajjaji 1992) and early Messinian Algeria (Moissette 1988). Proportional differences are given in positive (larger surface area in relation to Guadalquivir specimens) and negative values (smaller surface area in relation to Guadalquivir specimens).

	Guadalquivir Basin	Morocco		Algeria	
Species	SA	SA	Difference (%)	SA	Difference(%)
Aplousina bobiesi	0.231	0.396	+71	0.403	+74
Buffonellaria divergens	0.131	0.146	+11	0.145	+11
Buffonellodes incisa	0.096	0.136	+42	0.090	-6
Calloporina decorata	0.288	0.370	+28	0.354	+23
Cheiloporina campanulata	0.207	0.302	+46	0.297	+43
Chorizopora brongniartii	0.084	0.082	-2	0.112	+33
Ellisina gautieri	0.066	_		0.088	+33
Emballotheca longidens	0.403	0.308	-24	0.311	-23
Escharella grossa	0.333	_		0.480	+44
Escharella peachi	0.166		_	0.194	+17
Escharella reussiana	0.240	0.238	-1	0.270	+13
Escharina dutertrei	0.239	0.227	-5	0.289	+21
Escharoides coccinea	0.192	0.201	+5	0.231	+20
Escharoides megalota	0.372	0.409	+10	0.400	+8
Figularia figularis	0.242	0.402	+66	0.286	+18
Gephyrotes fortunensis	0.204		_	0.201	-1
Hagiosynodos latus	0.107	0.226	+111	0.123	+15
Herentia montenati	0.310	0.427	+38		_
Hippopleurifera sedgwicki	0.447	0.479	+7	0.558	+25
Hippoporella pauper	0.110	0.213	+94	0.170	+55
Microporella ciliata	0.241	0.192	-20	0.288	+20
Microporella coronata	0.208	0.273	+31	0.279	+34
Myriapora truncata	0.360	0.394	+9		
Onychocella angulosa	0.176	0.168	-5	0.178	+1
Poricella bugei	0.193	0.222	+15	0.207	+7
Prenantia cheilostoma	0.254	0.416	+64		
Rhynchozoon monoceros	0.107	0.124	+16	0.072	-33
Schizobrachiella sanguinea	0.348	0.413	+19	0.279	-20
Schizotheca serratimargo	0.133	0.106	-20	0.146	+10
Smittina messiniensis	0.074	0.131	+77		
Steginoporella cucullata	0.553	0.673	+22	0.747	+35
Trypostega rugulosa	0.087	0.135	+55		
Watersipora goniostoma	0.410	0.244	-40	0.416	+1

5.4.3 Variations in bryozoan zooidal and zoarial morphology

Following the approach of Jackson & Herrera Cubilla (2000), who investigated differences in zooid size from opposite sides of the Isthmus of Panama, an estimation of the surface area (length times width of the mean values) was calculated for each identified species from the Niebla Calcarenite. Only species of which the dimensions of at least ten autozooids could be measured were included in this study. We then calculated the zooid area for the same species occurring in the late Tortonian-early Messinian of the western Mediterranean using data published in Moissette (1988) and El Hajjaji (1992) and related these values to the Guadalquivir Basin specimens (Table 5.1). Given that the species are correctly identified, and despite a great inherent variability in intracolonial zooid length and width as well as significant intra-Mediterranean differences in zooid

area (e.g. *Hagiosynodos latus*, see discussion), zooidal surface area is, in most species, notably larger in the Mediterranean Sea than in the eastern Atlantic. For example, *Hagiosynodos latus* (+111%), *Hippoporella pauper* (+94%) or *Aplousina bobiesi* (+74%, see Figure 5.3B) display much larger zooid surface areas on the Mediterranean side of the connecting corridors, whereas *Watersipora goniostoma* (Reuss, 1848) (minus 40%), *Rhynchozoon monoceros* (-33%) and *Emballotheca longidens* (-24%) are some of the few species producing substantially larger surface areas on the Atlantic side (Table 5.1).

In addition, a conspicuous difference in zoarial morphology between the Niebla Calcarenite fauna and the Mediterranean Sea was detected in *Myriapora truncata*. The branch diameter of this erect robust species varies considerably not only in the two late Neogene regions we investigated, but also differs from the one measured in Recent specimens (Figure 5.3C). In the late Tortonian Niebla Calcarenite specimens the branch diameter varies between 2.0 and 3.4 mm (mean: 2.65 mm, N: 30, SD: 0.335) whereas branches of nearly coeval Mediterranean *M. truncata* vary considerably and reach diameters of 3.0 to 6.6 mm (mean: 4.75 mm, N: 25, SD: 0.974; own data, Agua Amarga Basin, SE Spain). In Recent *M. truncata* the measured values range between 2.9 and 3.9 mm (mean: 3.33 mm, N: 11, SD: 0.326; collected onshore Cabo de Gata, SE Spain). The ratio of the mean branch diameter of late Tortonian eastern Atlantic and western Mediterranean, and Recent Mediterranean *Myriapora truncata* is thus 1 : 1.8 : 1.3.

5.5 Discussion

5.5.1 Palaeobiogeography

Although environmental conditions during the main desiccation event were, due to evaporation of the deep basins and the following brackish episode, evidently unsuited for marine benthic organisms of the Mediterranean Sea to survive the MSC, many of the assumed endemic taxa are found in post-MSC deposits throughout the Mediterranean. For instance, Moissette & Pouvet (1987) estimated that 17% of the Mediterranean endemic Cheilostomata survived the crisis. These observations led some authors, working on different groups of organisms, to infer that either the main Mediterranean Basin or some peripheral basins were always in contact with the eastern Atlantic during the MSC (Moissette & Pouvet 1987, Saint-Martin et al. 2000, Goubert et al. 2001, Néraudeau et al. 2001). A great obstacle hampering the effort to obtain a consensus in this regard is caused by the scantiness of works on marine faunas from the immediate surroundings of the Mediterranean Sea before or during the MSC, i.e. from the eastern Atlantic SW Spanish or NW Moroccan coasts. Combining the available data on eastern Atlantic cheilostome bryozoans from the study of Sefian et al. (1999) and our own, 86 of the 89 species from this region are found in the Mediterranean basins, some of which have never been reported from outside the Mediterranean before. This faunal similarity to the Mediterranean, which is also evident in bivalve distribution (Lauriat-Rage et al. 1999), thus supports the suggestion that the eastern Atlantic region might have served as a refuge for marine taxa to survive the MSC (Ruggieri & Sprovieri 1976, Sabelli & Taviani 1984, Harmelin 1992).

Furthermore, the study of marine organisms from the Atlantic side of the corridors enables us to address questions concerning late Tortonian geographic dispersal of species in concert with the prevailing current system. Today, a westward migration of shallow water Mediterranean bryozoans is hindered by a constant inflow of surface water from the Atlantic through Gibraltar Strait (Harmelin & d'Hondt 1993). Outflowing intermediate water is formed in too distant regions (e.g. Gulf of Lion, Adriatic Sea) for non-planktotrophic larvae of shallow water bryozoan species to survive this lengthy transport and to reach the Atlantic. Furthermore, a physiological barrier is produced by the hydrological characteristics of the intermediate water (high oligotrophy, warm temperature) which prevents bryozoans from living in these depths (Harmelin & d'Hondt 1993). A one-way biogeographic boundary is thus created by the current regime, producing the Mediterranean province of the Atlanto-Mediterranean subregion (López de la Cuadra & García-Gómez 1994). In contrast to the modern situation, the occurrence of a great number of shallow water Mediterranean species on the eastern Atlantic side of the corridors in late Tortonian times implies the presence of a westerly surface water current flowing towards the Atlantic and thus

blurring the biogeographic boundary in this time interval. Investigating ostracodes and foraminifers of the Rifian Corridor, Benson et al. (1991) suggested that surface water influx was through the Rifian Corridor whereas the Spanish gateways were assumed to have served as outflow. Although the biogeographic reconstructions of the southern Iberian region, and thus the oceanographic mechanism producing the current pattern modelled by Benson et al. (1991), have significantly changed since then (see Esteban et al. 1996), this scenario of surface water exchange is supported by our observations. The most likely southern Spanish locations for the connecting straits are the Granada and Guadix Basins (Figure 5.2); however, a detailed reconstruction of these gateways, especially that of the northern margin of the Granada Basin, is impeded by the scarcity of outcrops due to uplift of the Betic Cordillera. The Guadix Basin was connected to the Guadalquivir Basin and displays marine sediments until the latest Tortonian when the region was uplifted (Soría et al. 1999). Evidence for current direction has not been found for either of the late Tortonian connections; yet one such gateway, the Spanish Guadalhorce Corridor, in which sedimentary structures are preserved that indicate a westerly surface water flow, has recently been established for the early Messinian by Martín et al. (2001).

5.5.2 Palaeoenvironment

The large proportion of extant species occurring in the Niebla Calcarenite provides the means to apply an actualistic approach in order to reconstruct late Tortonian environmental conditions in the north-western Guadalquivir Basin. The presence of several stenothermic taxa suggests conditions to be sufficient for a range of tropical to cool water species to thrive in the eastern Atlantic. The majority of the extant Niebla bryozoan species live in warm temperate to subtropical waters, a temperature estimate supported by the abundant occurrence of coralline red algae and the large foraminifera Heterostegina as well as the presence of Clypeaster. Whereas reefs are not reported from the eastern Atlantic southern Spanish and northern Moroccan coast, faunas of similar composition are found in distal positions of coeval Mediterranean reef complexes (Esteban et al. 1996). The absence of reefs in the Guadalquivir Basin might be explained by a high nutrient supply and cooler temperatures: although the main diatomite depositional episodes in the Guadalquivir Basin were over by the late Tortonian (Bustillo & López García 1997), the region might have been influenced by highly productive and slightly cooler water due to the mixing of Mediterranean outflow with Atlantic water, thus preventing growth of reefs and maintaining a diverse bryozoan fauna. Similarly, late Tortonian benthic and planktic foraminiferal assemblages from the NW Moroccan coast record subtropical conditions and eutrophic water masses (Barbieri 1998).

Judged by the depth distribution patterns of Recent species occurring in the Niebla Calcarenite, a distal inner- to mid-shelf depth of origination of the coralline algal-rich sections can be estimated. The high amount of fine grained matrix and an excellent state of preservation of the bryozoan specimens, owing to little transport of the grains, are further indicators of deposition below fair weather wave base. Coralline algae and bryozoans are interpreted to have formed patches of build-ups on a low gradient ramp sheltered by the presence of small islands (Baceta & Pendón 1999). An analogy to this Guadalquivir Basin fauna might be the Messinian Crustose Pavement facies from Malta (Bosence & Pedley 1982, Bosence 1983) in which coralline algae form fragile frameworks of sheets and branches providing a large surface area for bryozoans to settle upon as well as small cryptic habitats. The faunal predominance of membraniporiform species in the Niebla Calcarenite might thus not be related to a high energy subtidal environment, as is usually inferred, but might rather be a consequence of the special (and spatial) conditions offered by the coralline algal framework.

5.5.3 Variations in bryozoan zooidal and zoarial morphology

Although environmental conditions in the late Tortonian Guadalquivir Basin were sufficiently similar for Mediterranean species to thrive, the observed variation in zooidal and zoarial morphology displayed by several species indicates the presence of substantial environmental differences between these regions. Earlier morphometric studies of bryozoan zooids have shown that there is a correlation between temperature and zooid size (see references in O'Dea & Jackson 2002) and the results have been used to derive proxies for seasonality or to contrast environmental regimes (O'Dea & Okamura 2000, Jackson & Herrera Cubilla 2000, O'Dea & Jackson 2002).

However, previous studies mostly lack a comparison of intraspecific variability expressed in different natural environments.

Our results show that in most species the mean zooid area is larger in the Mediterranean Sea than in eastern Atlantic representatives (Table 5.1). If zooid size decreases with increasing temperature (Okamura & Bishop 1988) it follows that the late Tortonian eastern Atlantic Guadalquivir Basin experienced warmer temperatures than the western Mediterranean Sea. However, faunal evidence suggests that this was not the case: late Tortonian hermatypic coral reefs are absent from the eastern Atlantic shore while they flourish in western Mediterranean peripheral basins and the connecting gateways (Esteban et al. 1996); *Heterostegina* is the only large foraminifer to occur in greater abundance in the Niebla Calcarenite, a genus occurring in warm temperate (as in the easternmost Mediterranean Sea today) to tropical conditions (Betzler et al. 1997a), whereas other tropical foraminifer are absent; and the bryozoan fauna there only includes the genera *Emballotheca* and *Steginoporella* as a truly tropical component.

It is thus questionable that temperature was the only or main parameter controlling bryozoan zooid size in these contrasting environments. However, other explanations seem equally contradictory: if an increase in productivity in upwelling regions were responsible for zooid size deviation, the surface area should be larger in the Guadalquivir Basin due to the increase in nutrients and the related decrease in water temperature brought about by the upwelling of cooler water. If an increase in productivity occurred without a decrease in temperature (e.g. nutrient input from continental runoff) and turbidity would have prevented reefs from growth, the bryozoan fauna should be composed of many more tropical taxa. Salinity should not play a role either because the western Mediterranean Sea and eastern Atlantic experienced a much greater water exchange than today. Furthermore, the fact that there is a great range of zooid size at all (*Onychocella angulosa*), as well as the display of a larger surface area in Guadalquivir Basin specimens by *Emballotheca longidens*, indicates that bryozoan species do not show a uniform response to environmental change.

It must be noted, however, that our bryozoan specimens only characterise the conditions of this very facies of the Niebla Calcarenite and are, of course, not representative of the eastern Atlantic as a whole. The same holds true for western Mediterranean bryozoans used for comparison, where it is not known from which environment (e.g. reefs vs. temperate-type platform carbonates) the measured specimens were taken by Moissette (1988) and El Hajjaji (1992). The measurement of specimens from different environments might thus explain the frequent occurrence of large intraspecific differences in zooid size within the Mediterranean as, for example, in *Hagiosynodos latus* (Table 5.1), as well as some of the differences between the eastern Atlantic and Mediterranean locations. The results, interpretations and generalisations must therefore be taken with caution.

Regarding zoarial variability, Myriapora truncata shows the most obvious aberration (Figure 5.3C). Considering the minimum and maximum value measured (0.2 mm and 0.66 mm, respectively), the branch diameter is subject to more than a threefold increase in some Mediterranean locations compared to those of the Niebla Calcarenite. Due to the indistinctness of zooidal margins, resulting in a great inaccuracy when measuring zooid dimensions, the negligible difference in surface area between eastern Atlantic and Mediterranean specimens (Table 5.1) might be an artefact. Comparison of orifice surface area, with a mean value of 0.05 mm² in the Mediterranean (El Hajjaji 1992) and 0.034 mm² in the Guadalquivir Basin, suggests that variance of the branch diameter might in fact be related to zooid size. While large branch diameters are commonly observed in late Neogene *M. truncata* in the main Mediterranean basins, slender branches similar to those from the Guadalquivir Basin are also found at its northern limit of distribution, the Badenian Paratethys (N. Vávra, pers. comm.). As for zooid size differences observed between the Atlantic and Mediterranean sites discussed above, the reason for this change in branch thickness is unclear; however, it seems unlikely that it is caused by current energy. Figure 2 in Harmelin (1988) indicates that whereas branch segments between two bifurcation points become shorter with increasing current energy the branch diameter remains unaffected. The wide range of variation in branch thickness within faunas, and a notable change in diameter even within single branch fragments, suggests that these morphological variations are environmentally induced.

If, by conducting experiments with Recent colonies, the causal relationship of environment and branch diameter could be accomplished, *M. truncata* might be used as an indicator of palaeoenvironmental and seasonal change.

5.6 Conclusions

The fact that a great number of the Atlantic-influenced Guadalquivir Basin fauna are bryozoan species which were formerly thought to be endemic to the Mediterranean Sea implies that during the late Tortonian surface water transport occurred from east to west through either the Spanish gateways or the Rifian corridor. Since it has been suggested that an eastward flowing Atlantic surface water mass was present in the Rifian corridor (Benson et al. 1991), our data supports the assumption that the westward outflow of Mediterranean surface water, carrying bryozoan larvae into the Guadalquivir Basin, occurred through the Spanish corridors (Figure 5.2). Due to the exchange of species, and in contrast to the modern situation, a clear distinction between a late Tortonian eastern Atlantic and western Mediterranean shallow water bioprovince can thus not be made.

The presence of numerous Mediterranean species on the Atlantic side of the corridors furthermore shows that, prior to the beginning of the MSC, environmental conditions in this region were sufficiently similar to the Mediterranean Sea. This paper thus presents evidence for the hypothesis that many of the Mediterranean 'endemic' species were able to survive the MSC in an extra-Mediterranean refuge provided by the eastern Atlantic Guadalquivir Basin and the NW African coastal area. The presence of a large number of extant species in the Niebla Calcarenite and in NW Morocco also suggests that the eastern Atlantic accommodated the founder population for the post-MSC resettlement of the Mediterranean Sea.

However, despite the uniform faunal composition, the development of generally smaller zooid and, in *Myriapora truncata*, zoarium dimensions in Guadalquivir Basin species in contrast to Mediterranean representatives demonstrates that late Tortonian environmental conditions were notably different in these regions. The qualitative and quantitative environmental disparity between the eastern Atlantic and western Mediterranean have yet to be investigated to be fully understood.

An important conclusion which can, nevertheless, be drawn from our morphometry data is that species classifications (partly) based upon zooid or zoarial dimensions should be avoided. An over twofold increase in surface area as in *Hippoporella pauper*, or a branch diameter that varies more than threefold as in *Myriapora truncata*, strongly suggests that morphological measurements should not be taken as an argument to delimit species. Further research should concentrate on contrasting zooidal and zoarial morphology in modern environments differing in physical parameters to test for environmental variance in bryozoans.

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6. The Mediterranean bryozoan *Myriapora truncata* (Pallas, 1766): a potential indicator of (paleo)environmental conditions

B. Berning

Geologisch-Paläontologisches Institut, Universität Hamburg, Bundesstr. 55, 20146 Hamburg, Germany; [berning@geowiss.uni-hamburg.de]

submitted for publication in Lethaia.

6.1 Abstract

Fossil and Recent specimens of the Mediterranean cheilostome bryozoan Myriapora truncata show considerable intra- and intercolonial differences in branch diameter and zooid size. Statistically significant variation occurs within colonies, between colonies within sites, and between sampled sites, while the former clearly shows that branch diameter variability is largely controlled by environmental parameters. The three structural traits measured (branch diameter, zooid size and zooid depth) do not correlate, thus indicating a disconnection between the controls on zooid size and branch diameter. Possible environmental parameters that may have an influence on morphology are temperature, food supply or current energy. Whereas current energy has an effect on the colonial branching pattern, there are indications that temperature may be the main, but not the only, parameter controlling zooid size, and it is suggested that food supply largely determines the branch diameter in *M. truncata*. However, the identification of the decisive factors and quantification of the relationships between environmental and morphological change is beyond the scope of this study. The results nevertheless show that, if the control factors of morphological variability can be ascertained in Recent *M. truncata*, this species may prove to be an indicator of environmental conditions and their change at different spatial and temporal scales in Cenozoic to Recent Mediterranean habitats.

Keywords: Phenotype, variation, morphology, growth, paleoenvironment.

6.2 Introduction

In fossil and Recent non-tropical environments bryozoans are one of the dominating groups of organisms regarding both species richness and carbonate production. Owing to their formation of a variety of colonial growth forms, which are more or less restricted to certain environments by physical parameters, the relative abundance of growth forms in sediments have often been used to interpret (paleo)environments (for a review see Smith 1995). However, relatively few studies have been focused on how the environment affects intraspecific zooidal and colonial morphology, but an increasing attention is now being paid to the potential information that can be obtained from these morphological traits. In colonial animals the budding of single entities, sharing the same genetic code, provides a means to establish both microenvironmental control on and variation in zooid morphology within a colony, as well as among colony variations which are environmentally and genetically controlled (Hageman et al. 1999). Since it has been shown that at least in some Cheilostomata the fossil species concept based on morphotypes is valid (Jackson & Cheetham 1990), bryozoans prove to be exceptionally well suited for assessments of paleoenvironmental conditions and their seasonal or secular change which are reflected in the colonial and zooidal morphology of single species.

A comparison of late Tortonian (Late Miocene) bryozoan faunas from the western Mediterranean and the eastern Atlantic Guadalquivir Basin (Fig. 6.1B) revealed a general intraspecific difference in zooid morphology, mostly zooid size, between these regions (Berning et al. 2005). Being the most prominent example, fragments of the cheilostome bryozoan *Myriapora truncata* (Pallas, 1766) were observed to display a significant disparity in branch diameter. Subsequent research on other fossil specimens from different localities and on Recent material corroborated the intracolonial and site-specific variability in branching characteristics (Fig. 6.2A, B) and forms the basis of the present paper.

M. truncata has a widespread occurrence in the Recent Mediterranean Sea and a fossil record extending back to the Oligocene. Although usually reported to be endemic to the Mediterranean Sea, this species is occasionally found today on the eastern Atlantic coasts of southern Spain and northern Morocco (Canu & Bassler 1925; López de la Cuadra & García Gómez 1988, 1994; Alvarez 1994). Owing to its erect, robust, tree-like growth and large colony size, the 'false coral' is easily detected and identified both as a living organism and as a fossil. It grows on hard substrates such as rocks, crustose red algae and shells while its depth of occurrence in the Mediterranean Sea ranges from the shallow-subtidal, in sheltered sites such as caves, down to some 130 m (Gautier 1962; Hayward & McKinney 2002) where it occurs within the seasonally shifting shear zone of Mediterranean surface and intermediate water (A. Freiwald 2004: pers. comm.). Erect growth proceeds quickly after formation of an encrusting base (P. Moissette 2004: pers. comm.) from a twinned ancestrula, with radiating zooids forming in alternating whorls, producing a blunt growth tip. The space around the branch axis is, in thicker branches, filled with so called kenozooids. These are single zooids that do not possess a polypide to feed and are usually formed for constructional reasons (Fig. 6.3A). All zooidal walls are punctured by numerous pores for communication and the distribution of nutrients between zooids.



Fig. 6.1 Locations and ages of the sampled sites. A. Regional map of the western Mediterranean showing position of studied sites. B. Simplified geological map of southern Spain. Arrows indicate the studied Neogene sedimentary basins and Recent coastal sites. C. Close-up of Linosa Island.

When reviewing the potential of bryozoans as indicators of water depth, Harmelin (1988) showed that, while the branch diameter seems to be unaffected, the branching pattern of M.

truncata is largely controlled by hydrodynamics. Thus, with decreasing water currents (and possibly also with increasing sedimentation rate) the length between two bifurcations increases, i.e. bushier colonies are formed in high energy environments whereas colonies in lower energy conditions are more open spaced (Fig. 6.2B). Although site-specific differences in branch thickness were occasionally noted by early authors and are known to occur in Arctic species of the genus *Myriapora* (Kluge 1975; Schäfer 1994), variations in branch diameter in relation to environmental changes have, neither in Recent nor fossil *M. truncata*, not been registered systematically. Unfortunately, in the only study available on colony growth and integration in the genus *Myriapora*, Viskova (1986) did not include *M. truncata*. Furthermore, very little information exists about the life cycle, colony growth rate, or the diet of this species.



Fig. 6.2 Morphological and structural features of *Myriapora truncata*. A. SEM micrograph of branch section of a specimen from Algeciras showing perforated frontal wall, autozooecial orifices, and two ovicells at lower left and upper center. Note the change in branch thickness. Scale bar = 1 mm. B. Comparison of branch diameter of specimens from Agua Amarga (late Tortonian) at left, Algeciras (Recent), and Linosa (subrecent) at right. Note the intracolonial change in branch thickness and initial secondary calcification obscuring the orifices in proximal branch segment in Algeciras specimen, as well as differences in frequency of bifurcation: the short distance between branching points in Agua Amarga specimen (the right branch has become thicker perpendicular to paper plane and is about to bifurcate), an increased distance in Algeciras specimen (the distal tip is about to branch), and an extremely long branch fragment without bifurcation from Linosa. The prominent white dots in the Algeciras specimen are ovicells. Scale bar = 1 mm. D. Cross section of branch from Linosa. Scale bar = 1 mm.

The goal of this pilot study lies in revealing the great intraspecific variation in zooid and colony morphology displayed by *M. truncata* in Recent and fossil specimens, and in displaying the

potential this species has for reconstructing Cenozoic paleoenvironments in the Mediterranean realm. Morphometric analysis of several structural traits will be presented to identify (1) withincolony variability, (2) between-colony variation within a certain site, and (3) among-colony variability between temporally and spatially different sample sites. Possible environmental factors controlling morphology, such as temperature, current energy and food supply, are discussed, and the results of the present paper will hopefully stimulate, as well as serve to design, future experiments on Recent *M. truncata* in order to specifically identify the causes for morphological variability in this bryozoan.

6.3 Materials and Methods

6.3.1 Fossil localities

Fossil material was collected from both the late Tortonian (Late Miocene) eastern Atlantic Guadalquivir Basin and the peripheral Mediterranean Agua Amarga Basin, as well as from the Early Pliocene Mediterranean Carboneras Basin (Fig. 6.1B). The Niebla Calcarentie Formation crops out south-west of the town Niebla in the north-western Guadalquivir Basin. This limestone comprises coralline red algal rich packstones to rudstones and is interpreted to have formed on a shallow shelf below fair weather wave base (Civis et al. 1994; Baceta & Pendón 1999). Samples from the Agua Amarga Basin were taken from a bryozoan rich, well-bedded, coarse-grained rudstone of the Azagador Member (Betzler et al. 1997b; Brachert et al. 1998). This part of the basin hosted the carbonate factory where most of the biogenic sediment was produced by a diverse bryozoan fauna, and was situated just below fair weather wave base (Martín et al. 1996). During the Early Pliocene the Carboneras Basin formed a small and shallow embayment of the western Mediterranean Sea, partly overlapping geographically with the Agua Amarga Basin, in which a wide range of carbonate types accumulated (Braga et al. 2003; Martín et al. 2004). The samples were taken from a current-sheltered part of the sedimentary section which provided well preserved bryozoan material. The above mentioned carbonates were all formed under non-tropical conditions. A more detailed description of the sampled sites, chronostratigraphy and paleoenvironment, as well as a taxonomic account of *M. truncata* will be given elsewhere. All fossil material measured and figured in this work is stored in the author's collection.



Fig. 6.3 Morphological characters measured in *M. truncata*. A. Cross-section of branch showing the measured characters 'branch diameter' (bd) and 'zooid depth' (zd) of the radial autozooids as well as the central bundle of kenozooids (k). Note the porous zooidal walls of both autozooids and kenozooids. B. Close-up of the porous frontal surface depicting the measured 'distance between midpoints of adjacent orifices' (do). Ovicell with enlarged orifice at upper left.

6.3.2 Recent localities

Recent specimens of *M. truncata* were collected by Carlos López Fe de la Cuadra (Departamento de Fisiología y Biología Animal, Universidad de Sevilla) in the Bay of Algeciras, and by Juan Carlos Braga (Departamento de Estratigrafía y Paleontología, Universidad de Granada) off eastern Cabo de Gata (Fig. 6.1B), both by scuba-diving in about 10 m depth and from warm-temperate environments. Geographically the Bay of Algeciras belongs to the Mediterranean; however, this region is exclusively bathed by Atlantic surface water flowing into the Mediterranean Sea through the Strait of Gibraltar.

The studied material is completed by a grab-sample of iron oxide stained, relict sediment from ca. 100 m depth off Linosa Island in the Sicily Channel (Fig. 6.1C). This sample comprises numerous fragments of *M. truncata* and was taken in 1996 during RV Urania cruise 96 (sample CS96-201, 35°52,44N, 12°50,50E; samples stored at the Institut für Paläontologie, Universität Erlangen, Germany).

All measured and figured specimens of (sub)Recent locations are stored in the author's collection. Additional material of the same samples is housed in the respective institutes mentioned above.

6.3.3 Characters measured and statistical analysis

From each sampled site, 25 measurements of the branch diameter were taken with a caliper to demonstrate intercolonial variation. The fragmentary nature of most of the fossil material and the small size of fragments usually inhibited an evaluation of intracolonial variation in branch diameter. Therefore, between four and six measurements only were taken from branches of the same colony to depict intracolonial variation. Whenever possible, measurements were taken at midpoints between two bifurcations; in case of an oval cross section the smallest diameter was taken to avoid measuring the lateral increase in thickness in branching regions. Furthermore, measurements were only taken in those regions of the branches where the orifices were not obscured by secondary calcification which leads to an increase in branch diameter in older parts of the colony (Fig. 6.2B).

Zooidal measurements were determined with the analysis software ImageJ using digital SEM micrographs. Since individual zooid boundaries are indistinct on the colony surface, an approximation of the zooid size was obtained by measuring the distance between midpoints of adjacent orifices of 20 autozooids (Fig. 6.3B). Furthermore, zooid depth, the distance between the frontal surface and the termination of a zooid towards the central branch axis, was measured at a cross-section of a single branch per sample (Fig. 6.3A). These measurements represent minimum values due to cross-sectional problems of the obliquely positioned and acute termination of the zooid towards the branch center, and thus, even in the absence of central kenozooids, do not necessarily amount to half of the given branch diameter of the specific sample.

For all characters measured, the arithmetic mean, standard deviation (SD) and the coefficient of variation (CV) were calculated. One-way ANOVA and all pairs *post hoc* Tukey's tests were performed on the original measurements of intra- and intercolonial branch diameter, the distance between midpoints of orifices, and zooid depth, using a categorical *x*-axis with sample location as a category.

6.4 Results

6.4.1 Intracolonial branch diameter

Due to the fragmentary nature of the fossil material only a few within-colony measurements from four sites were obtained (Table 6.1). However, these measurements, displaying microenvironmental control on colonial morphology, yielded differences between absolute minimum and maximum branch diameter ranging from as little as 0.6 mm in subrecent specimens from Linosa (CV of 11.8) to 1.6 mm in a sample from the Pliocene Carboneras Basin (CV of 18.2), with the latter representing an increase in diameter of some 67% (min. 2.4 mm, max. 4.0 mm). Differences in intracolonial variability in branch thickness between sites proved to be significant (F= 7.59, p = <0.002) and *post hoc* Tukey's test showed that the Linosa sample is significantly

Table 6.1 Intracolonial variability in branch diameter in fossil and Recent *M. truncata*. Branch diameter values are given in mm. Abbreviations: SD: standard deviation; CV: coefficient of variation; N: number of measurements made. Branch diameter values are given in mm.

Location	Mean	SD	CV	MinMax.	Ν
Carboneras	3.3	± 0.6	18.2	2.4 - 4.9	5
Linosa	2.3	± 0.3	11.8	2.0 - 2.6	4
Algeciras	3.7	± 0.4	11.6	3.2 - 4.4	6
Cabo de Gata	3.4	± 0.4	12.6	2.8 - 4.0	6

different from all other samples. However, these results are based upon a rather small and unequally distributed number of measurements.

6.4.2 Intercolonial branch diameter

Differences in branch diameter was found to be highly significant between the studied sites (F = 58.71, p = <0.001). By far the largest mean diameter is displayed by specimens

from the Tortonian Agua Amarga Basin $(4.8 \pm 1.0 \text{ mm})$ whereas subrecent specimens from Linosa have the smallest branch diameter $(2.5 \pm 0.3 \text{ mm})$ (Table 6.2). The measured values range from an absolute minimum of 0.2 mm (in Linosa and Niebla specimens) to 6.6 mm (Agua Amarga); the branch thickness in *M. truncata* thus varies by a factor of more than three in the available material.

Having a mean branch diameter of 3.3 ± 0.4 mm (Cabo de Gata) and 3.5 ± 0.5 mm (Algeciras), the Recent shallow-water specimens are both larger than fossil representatives from Niebla and Carboneras. However, they are still considerably smaller than late Tortonian specimens from Agua Amarga. Minimum and maximum branch diameters of 2.6 to 4.0 mm (Cabo de Gata) and 2.6 to 4.4 mm (Algeciras) are in the range observed in Pliocene Carboneras specimens. *Post hoc* Tukey's test revealed that the Agua Amarga sample is significantly different from all other sites, whereas there are no significant differences between Algeciras and Cabo de Gata, nor between Linosa, Carboneras and Niebla.

Besides this between-sites variation, a striking contrast exists in within-site diameter variation: whereas minimum and maximum values range from 3.0 to 6.6 mm in Agua Amarga specimens (CV of 20.5), branches of the subrecent *M. truncata* from Linosa show the smallest absolute range of variation (2.0 to 3.1 mm, CV of 13.1).

Site	Age	Mean SD	CV	MinMax.	Ν	No. of colonial fragments measured
Agua Amarga	Tortonian	4.8 ± 1.0	20.5	3.0 - 6.6	25	17
Niebla	Tortonian	2.7 ± 0.4	13.4	2.0 - 3.4	25	22
Carboneras	Pliocene	2.9 ± 0.4	15.1	2.2 - 4.0	25	10
Linosa	subrecent	2.5 ± 0.3	13.1	2.0 - 3.1	25	11
Algeciras	Recent	3.5 ± 0.5	13.9	2.6 - 4.4	25	8
Cabo de Gata	Recent	3.3 ± 0.4	11.9	2.6 - 4.0	25	5

Table 6.2 Intercolonial variability in branch diameter in fossil and Recent *M. truncata* from the various sites studied. Abbreviations as in Table 1.

6.4.3 Zooid size

Surprisingly, the specimens with the smallest branch diameter from Linosa show by far the largest mean (672 μ m) and also the largest absolute value (817 μ m) of distance between adjacent orifices of all measured samples (Table 6.3). The control factors of zooid size are thus disconnected from those governing branch diameter. However, mean values of the remaining samples more or less correspond to branch diameter values, with specimens from Agua Amarga having large zooids (616 μ m) and Niebla specimens displaying the smallest mean (526 μ m) and absolute (409 μ m) zooid size. The great variation in absolute values in these measurements is due to structural constraints, since the distance to the distal nearest-neighbor of a given zooid may be considerably different from the distance to the distolateral nearest-neighbor. However, zooid size differences

between sampled sites are highly significant (F = 10.95, p = <0.001), whereas the sample from Niebla is significantly different from all other samples, and the sample from Linosa is indifferent only to the Agua Amarga location (*post hoc* Tukey's test).

Related to the interaction of branch thickness and zooid size, an increase in the number of zooids per whorl can be observed with increasing branch diameter. Whereas there are about six to eight zooids in every whorl in Linosa specimens, Agua Amarga branches are composed of up to 16 zooids.

Site	Age	Mean SD	CV	MinMax.	Ν	No. of colonial fragments measured
Agua Amarga	Tortonian	616 ± 49	8.0	548 - 740	20	1
Niebla	Tortonian	526 ± 63	12.0	409 - 649	20	3
Carboneras	Pliocene	585 ± 76	12.9	449 – 749	20	2
Linosa	subrecent	672 ± 75	11.1	568 - 817	20	2
Algeciras	Recent	598 ± 42	7.1	508 - 683	20	2
Cabo de Gata	Recent	601 ± 72	12.0	495 - 815	20	2

Table 6.3 Measurements (in μ m) of the distance between adjacent orifices as an approximation of zooid size (see text for explanation). Abbreviations as in Table 1.

Table 6.4 Within-colony measurements of zooid depth (in μ m) in relation to branch thickness. Branch diameter values (in mm) were taken at the position where zooid depth was measured. Abbreviations as in Table 1.

Site	Age	Mean SD	CV	MinMax.	Ν	branch diameter
Niebla	Tortonian	935 ± 42	4.5	881 - 988	9	2.3
Carboneras	Pliocene	967 ± 64	6.6	852 - 1030	9	2.2
Linosa	subrecent	962 ± 71	7.4	861 - 1108	9	2.2
Algeciras	Recent	1058 ± 69	6.6	928 - 1142	9	3.3
Cabo de Gata	Recent	971 ± 51	5.3	914 - 1065	9	3.0

6.4.4 Zooid depth

In order to be able to directly relate zooid depth to branch thickness, the cross-section of only a single branch per location was measured (Table 6.4). Although differences between sites are comparatively small, they are still highly significant (F = 5.65, p = <0.001). Post hoc Tukey's test showed that there are significant differences only between samples from Niebla and Algeciras, Cabo de Gata and Linosa, respectively, as well as between Carboneras and Algeciras. Whereas the lowest minimum values are related to the smallest branch diameter ($852 \mu m$ in the specimens from Carboneras), zooid depth does not increase arithmetically with increasing branch diameter and maximum zooid depth was never found to exceed 1.2 mm. The discrepancy between the limited zooid depth and an increasing branch diameter is balanced by the formation of central kenozooids around the central branch axis. While these are absent in the narrow branches from Linosa (Fig. 6.3D), and there are only very few in specimens from Niebla, the kenozooids become more numerous in thicker branches from Cabo de Gata and Algeciras (Fig. 6.3C).

6.5 Discussion

Fossil and Recent branches of the cheilostome bryozoan *Myriapora truncata* show significant variation in diameter between and within studied sites as well as within colonies. Overall, a more

than threefold increase in absolute branch diameter (minimum: 2.0 mm, Linosa; maximum: 6.6 mm, Agua Amarga) was observed. This discovery is in itself remarkable given the fact that in this species branch diameter variability has not been registered systematically before, although M. *truncata* is, geographically and chronostratigraphically, a well represented and often cited species in the Mediterranean region.

But what causes this variability in branch diameter? Variations between sites and between colonies excepted (but see below), major genetic control on branch thickness is precluded because of the occurrence of significant intracolonial change in diameter. Since all zooids of a colony share the same genetic code a certain branch diameter would be determined early in colony formation and would not be subject to change throughout colony growth except in regions of bifurcation or secondary calcification. The triggers thus have to be of extrinsic nature.

A variety of environmental parameters have as yet been identified that have an effect on zooid and/or colony morphology in Recent bryozoans: among others, current energy has an influence on zooid and colony shape (Harmelin 1973, 1988; Thomsen 1977; Okamura & Partridge 1999), zooid size is temperature-dependent (Okamura & Bishop 1988; Hunter & Hughes 1994; O'Dea & Okamura 1999), and food availability may affect colony growth rate and shape, or zooid size (Winston 1976; Jebram 1973; Hunter et al. 1996; O'Dea & Okamura 1999). Their possible bearing on zooid and colony morphology in *M. truncata* will be briefly discussed below.

6.5.1 Current energy

The amount of water movement has been found to be an important control factor on morphology in many sessile marine organisms from various taxonomic groups (e.g. Kaandorp 1999). However, whereas in most of these cases an increase in current energy results in the formation of thicker, more compact branches and colonies (Kaandorp 1999), branch thickness in *M. truncata* remains unaffected, as was shown by Harmelin (1988). Instead, the distance between branching points and thus the average distance between branch tips ('branch spacing'; see Kaandorp 1999) decreases with increasing water movement (and possibly also with a lowered sedimentation rate), resulting in densely spaced, bushier colonies (Harmelin 1988). Differences in branching patterns were also observed in the present study: while colony fragments from Linosa Island show extremely long (up to 4.1 cm) branch sections without bifurcation, and therefore indicate growth in a low-energy deep-water environment, colonies from shallow-water settings from the Bay of Algeciras and, in particular, Agua Amarga are formed by more frequently bifurcating branches (Fig. 6.2B). The sample from Algeciras includes both relatively bushy colonies as well as longer branch segments, thus implying changing hydrodynamic conditions during colony growth. Consequently, current energy as a control factor of primary branch diameter in *M. truncata* is, if at all, of negligible importance.

6.5.2 Temperature

Changes in temperature are interpreted to have an impact on zooid size by controlling the oxygen solubility of seawater (Okamura & Bishop 1988; Hunter & Hughes 1994; O'Dea & Okamura 1999). With rising temperature the solubility of oxygen decreases whereas the zooid's metabolic rate increases; thus, in order to increase the surface/volume ratio of the bryozoan soft parts to compensate the higher oxygen demand, smaller zooids are formed in elevated temperatures (O'Dea & Okamura 1999). This inverse temperature–size effect has been applied to both Recent (O'Dea & Okamura 2000; O'Dea & Jackson 2002) and fossil (O'Dea & Okamura 2000) bryozoan faunas to assess temperature variation, i.e. seasonality, during colony growth. However, there are two structural problems in applying the temperature–size effect to *M. truncata*: (1) lateral walls are not readily discernable on the colony surface, thus a less precise approximation of zooid dimensions (in the form of measuring the distance between adjacent orifices, see Results) must be used, and (2) unlike most other matchbox-shaped Cheilostomata, in which zooid length and width are the largest measures and the distance between the frontal and basal wall is smallest, in this species the distance between zooid surface and termination towards the branch axis, the zooid depth, accounts for the largest zooid size parameter (compare Table 6.3 and 6.4).

The morphometric results are, nevertheless, surprising: it is not the branches with the largest mean or maximum diameter from Agua Amarga that are constructed of zooids with the largest frontal surface but those with the smallest diameter from Linosa (Table 6.3). Although all other branches show a correlation, yet not a strictly linear one, of branch diameter and distance between orifices, the disparity in Linosa specimens suggest that zooid size and branch diameter are controlled by different factors. Alternatively, the increase in zooid surface area in Linosa specimens could be a consequence of its reduction in branch diameter and the associated shortening of the zooid depth, i.e. the frontal area is increased in order to volumetrically balance the loss in the zooid's third dimension. However, this scenario appears unlikely since Niebla specimens have only slightly larger branch diameters yet the shortest distance between adjacent orifices measured in all samples.

Compared to smaller zooids from Recent shallow-water sites, the formation of large zooids of subrecent Linosa specimens from an inferred deep-water and thus cooler water habitat, may reflect the inverse temperature-size effect. In turn, the presence of smaller zooids in Niebla specimens would indicate warmer temperatures in the late Tortonian eastern Atlantic compared with the larger zooids of the western Mediterranean Agua Amarga site. However, this scenario is somewhat contradictory since there are no reefs recorded from the eastern Atlantic (Esteban et al. 1996) whereas these thrive in marginal basins of the late Tortonian western Mediterranean, thus indicating lower temperatures in the eastern Atlantic. (Although the local environment of the Agua Amarga Basin could have been influenced by upwelling and thus cooler temperatures, which might also explain rather eutrophic conditions there [see below]). Temperature may therefore be not the only environmental factor controlling zooid size.

As zooid size, zooid depth comprises only a limited contribution to an increasing branch diameter due to the fact that, even in thicker branches, a zooid depth exceeding ca. 1.2 mm was not observed. Instead, circum-axial kenozooids are formed which fill the residual central space around the branch axis (Fig. 6.2C). Their presence was already noted by Donati (1750), even before M. truncata was formally described in 1766, yet the nature of these irregular, vertically elongated kenozooids that are punctured with communication pores remains unexplained. Since these kenozooids are formed coeval with the surrounding autozooids their number has to be determined during construction of each whorl. Thus, these play a vital role since the formation of an increasing number of autozooids per whorl would, due to a restricted zooid depth and without coeval construction of kenozooids, result in tubular growth of branches with a disadvantageous terminal opening. (In fact, there is an Oligocene congeneric species, Myriapora fungiformis Vávra, 1983, displaying an open chalice- or chanterelle-like growth in which there are no central kenozooids, whilst the autozooids form an inner basal wall and open out- and downwards. However, although starting from an encrusting base and a short erect trunk [Vávra 1983], as does M. truncata, no branches or bifurcations are developed.) Whether or not the kenozooids fulfil any other task, such as nutrient storage, remains as yet speculative.

6.5.3 Food supply

Compared to the factors 'temperature' and 'current energy', very little is known about the effects of quantitative changes in food supply on bryozoan zooid or colony morphology, and, even worse, the quality of food particles ingested by bryozoans is poorly understood despite the fact that it has been shown to be a factor controlling morphology (Jebram 1973; Winston 1976). Although several experimental studies showed that under optimal feeding conditions larger zooids may be formed (Jebram 1973) and the colony growth rate is increased (O'Dea & Okamura 1999) the results are inconsistent, especially regarding zooid size. For instance, in both laboratory (Hunter & Hughes 1994) and field studies (O'Dea & Okamura 1999) zooid size was controlled by temperature and genotype but was irrespective of food supply. However, since different species were studied in the above mentioned experiments the respective effects may be species-specific. Furthermore, laboratory experiments are likely not to reflect the natural environment in that, in most cases, bryozoans were fed with a monoculture of species of the flagellate algal genus *Rhodomonas*. Although representatives of this cryptophyte genus have been shown to sustain viable and reproducing bryozoan colonies during long-term studies, whereas other types of food or mixtures of various foodstuffs mostly yielded less positive results (Hunter & Hughes 1991), colony growth

under laboratory conditions proceeds nevertheless substantially slower than in natural environments (Hunter et al. 1999; Kahle et al. 2003). This is not surprising, considering that a study on British coastal waters revealed over 50 different types of potential food sources available to bryozoans (Best & Thorpe 1994); thus, natural conditions, and therefore morphological reactions to varying quantity and quality of nourishment, will be difficult to reconstruct in the laboratory.

In the Recent, Arctic, congeneric species *Myriapora coarctata* (M. Sars, 1863), Schäfer (1994) found an annual thickening of branches, in which thick growing tips were observed in summer when the samples were taken. These thick portions were mainly composed of feeding autozooids whereas non-feeding avicularia dominated the thin portions. Since temperature change is negligible at the sampled sites in these Arctic environments, Schäfer (1994) concluded that branch diameter variation may represent seasonal nutrient cycles, with phytoplankton-rich waters triggering branch thickening during summer.

A comparison of the environments of the studied sites suggest that nutrient supply may also play a role in determining branch diameter in *M. truncata*. The sampled part of the Tortonian Niebla Calcarenite is composed of photoautotroph red algal crusts and the large foraminifer *Heterostegina* as well as echinoderms, whereas filter feeding bryozoan species are diverse but volumetrically of minor importance (Baceta & Pendón 1999) and the branch diameter in *M. truncata* is small. In contrast, the Tortonian Azagador Member in the Agua Amarga Basin is dominated by filter feeding bryozoans, bivalves and barnacles, as well as smaller benthic foraminifera (Martín et al. 1996), while *M. truncata* produced thick branches in this environment. Thus, the trophic regime, with an oligotrophic environment prevailing during formation of the Niebla Calcarenite and a rather eutrophic environment prevailing during deposition of the formation of smaller or thicker branches, respectively. Similarly, the differences between thicker branches from shallow-water Recent sites and the thin branches from Linosa (Fig. 6.2B), which are interpreted to have formed in low energy and presumably deeper environments, may be due to an increased food supply in shallow waters in comparison with greater depths.

In any case, the increase in branch diameter makes possible the formation of a larger number of autozooids per whorl. This may enhance the utilization of food supply relative to colony sections with thinner branches which, in turn, may result in an increase in growth rate and, more importantly, reproductive investment. The specimen from Algeciras in Fig. 6.2B shows that ovicells abundantly, yet not exclusively, occur in thicker branch sections or in regions where the branch is beginning to thicken. It is therefore likely that the intracolonial (i.e. genetic) plasticity enables a morphological adaptation to short term (e.g. seasonal) changes in food supply in order to maximize fecundity.

6.5.4 Environmental vs. genetic control

Intracolonial change in branch diameter clearly provides evidence for fluctuating environmental conditions during growth. But can this finding be extrapolated to infer changing conditions in timeaveraged (fossil) faunas or even between (fossil) sites several hundred kilometers apart in which cases genetic divergence has to be considered? The results of several common garden experiments and field studies suggest that, in addition to environmental factors that account for a great extent of variation within colonies, genotype creates significant morphologic variation between colonies (Bayer & Todd 1996; Hageman et al. 1999; O'Dea & Okamura 1999). Therefore, to draw conclusions about the (paleo)environment from morphometric comparisons between colonies, especially in time-averaged fossil faunas, and between sites might be insubstantial. A thorough statistical analysis of variation in order to quantitatively distinguish between genetic and environmental control on branch diameter within and between colonies is, due to the fragmentary state of preservation of the available fossil material, not possible and even for Recent colonies beyond the scope of this paper. However, the present study provides some indication that in M. truncata intracolonial variation might comprise a large part of the absolute within-site variation in branch diameter (compare results in Table 6.1 and 6.2). Supposed that between-colony and -site variation were genetically controlled and that environmental conditions had a comparatively minor effect, it would be remarkable that the time-averaged late Tortonian Niebla fauna, which is composed of thin branches of homogeneous size, is so different from the more or less equally timeaveraged late Tortonian Agua Amarga fauna which consists of thick branches of inhomogeneous size. Also, in (sub)Recent faunas a vertically restricted gene flow in the water column would have to be assumed for the offset between the thin branches from Linosa, which presumably formed in a deep-water low-energy environment, and the relatively thick shallow-water specimens. In contrast, in shallow-water settings a relatively uniform branch diameter is displayed in *M. truncata* from geographically distant regions, as far apart as from Algeciras to at least the Adriatic Sea (Hayward & McKinney 2002), where the branch diameter rarely exceeds 4.0 mm. These inconsistencies and, more importantly, the occurrence of intracolonial change in diameter, therefore suggest that branch thickness between colonies and (fossil) sites is largely controlled by environmental parameters.

6.5.5 Future studies

In order to make full use of the potential *M. truncata* offers in paleoenvironmental reconstruction, the intrinsic and extrinsic factors that control branch diameter need to be assessed. Common garden experiments as well as observations in nature under monitored environmental conditions at different sites and settings need to be conducted to ascertain, among others, colony growth rate, temperature-related changes in zooidal and colonial morphology, or the effect of qualitative and quantitative changes in food supply. Furthermore, besides from the characters measured in this study (branch diameter, the distance between adjacent orifices, and zooid depth), additional information on structural composition of the branches and the interactions of single traits may be gained from measuring the orifice area, number of zooids per whorl, the diameter of the central bundle of kenozooids, and the occurrence of ovicells in relation to branch diameter. Additionally, the inverse relationship between current energy and distance between branching points needs to be quantified.

6.6 Summary

Besides the earlier notion that branching pattern is subject to alteration, substantial branch diameter and zooid size variations were detected in fossil and Recent specimens of the cheilostome bryozoan Myriapora truncata, while the specific control factors of this morphological variability remain as yet unknown. However, if the qualitative and quantitative control on branch diameter and zooid size can be ascertained, environmental information may be gained at various spatial and temporal scales for Cenozoic to Recent Mediterranean habitats. Intracolonial change clearly indicates microenvironmental short-term or seasonal changes that occur during growth and within the lifetime of a colony. In Recent faunal assemblages between-colony variation within a certain site therefore reflects the interaction of the genetic and environmental components controlling branch morphology, whereas in time-averaged fossil sites the variation between colonies (or fragments thereof) might additionally record environmental stability or variability through time. For instance, not only show late Tortonian specimens from Niebla a small mean branch diameter, but also a relatively minor disparity between minimum and maximum diameter which suggest little environmental change through time in this time-averaged faunal assemblage. Contrasting two late Tortonian sites now, the Agua Amarga Basin, in which *M. truncata* is represented by specimens with both a considerably larger mean branch diameter and CV, obviously differed in absolute microenvironmental conditions from the Niebla site as well as in the rate of environmental change through time.

Whereas there are indications that food supply and temperature may play a role in determining branch diameter and zooid size, respectively, the branching pattern of this erect robust species varies with current energy which, in case of a well preserved fossil fauna, might provide additional information for paleoenvironmental reconstruction. The frequent occurrence of *M. truncata* in Recent and fossil environments, the ease of identifying this species as well as straightforward analytical methods aid in the applicability of these procedures also for non-bryozoologists. Furthermore, the disconnection of zooid size and branch diameter, indicating differential selection pressure acting upon this species and possibly also other bryozoans during evolution, makes *M. truncata* an interesting study object beyond its potential use as an indicator of paleoenvironmental conditions.

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7. Summarising Remarks and Conclusions

7.1 Palaeoenvironment

The presence of 72 cheilostome bryozoan species in a single bed of the Niebla Calcarenite is truly remarkable. In comparison, Hayward & McKinney (2002) reported 79 species from the Recent Adriatic Sea, while their sampling stretched over about a decade, encompassed an area of several tens of square kilometres, ranged from 0 to 60 m water depth, and comprised a wealth of different substrates. However, despite the great number of species, bryozoans are far from dominating the Niebla Calcarenite fauna (most species are represented by very few specimens), and only Myriapora truncata, the celleporiform species as a whole, and Schizotheca serratimargo contribute to the carbonate production in a noteworthy amount. This pattern, great species-richness but low number of colonies, is characteristic of oligotrophic tropical environments, where Bryozoa are diverse but subordinate in respect to carbonate production (e.g. Scholz & Hillmer, 1995), in contrast to temperate, meso- or eutrophic environments in which bryozoans may occur in rockforming abundance (e.g. Nelson et al., 1982). The fauna of the sampled bed of the Niebla Calcarenite is dominated by autotrophic coralline algae, with lesser amounts of large benthic for a minifera and heterotroph echinoids, while filter-feeding organisms are of minor importance, thus indicating oligotrophic conditions. However, coral reef complexes are absent west of the straits connecting the Mediterranean Sea with the Atlantic in the Late Miocene (Esteban et al., 1996), suggesting that temperatures in the Guadalquivir Basin were below the threshold of coral growth. While most bryozoan species or genera are not strictly stenotherm, environmental conditions of the Niebla Calcarenite can be regarded as subtropical to warm temperate when the temperature preferences of recent representatives are considered (Table 7.1). This interpretation is corroborated by the presence of other subtropical organisms such as Clypeaster sp., Heterostegina sp., or planktic foraminiferal assemblages in the eastern Atlantic (Sierro et al., 1993).

Tropical to Subtropical	Biflustra spp., Emballotheca spp., Onychocella spp., Poricella spp., Steginoporella spp.
Subtropical to Warm Temperate	Calloporina decorata, Chorizopora brongniartii, Mollia circumcincta, Mollia patellaria, Myriapora truncata, Schizotheca serratimargo
Warm Temperate	Ellisina gautieri, Figularia figularis, Hagiosynodos latus, Schizoporella dunkeri
Warm Temperate to Cool Temperate	Escharoides coccinea

Table 7.1 Temperature preferences of Recent bryozoan species and genera present in the Niebla Calcarenite.

The temperature differences between the eastern Atlantic and western Mediterranean Sea, with topical conditions and reef growth in the Mediterranean realm, is, however, in conflict with the morphometric results presented in Chapter 5, when only the hitherto accepted hypothesis of an inverse relation between temperature and zooid size in Bryozoa (O'Dea & Okamura, 2000) is applied. The variable but generally smaller zooid size in species from Niebla compared to late Tortonian/Messinian representatives from the Mediterranean (Table 7.2) would suggest that temperatures were warmer in the Atlantic. Yet a continuative analysis of colonial and zooidal morphology of the erect bryozoan *Myriapora truncata* from several regions and different environments (Chapter 6) indicates that nutrients may also play a role in controlling morphology. However, this effect can not be quantified at present due to the lack of appropriate field studies and common garden experiments. Furthermore, the range of response to the environmental differences between Atlantic and Mediterranean Sea is not a uniform one, as demonstrated by several species (or even representatives of the same species) from Niebla having larger zooids than their

Table 7.2 Revised version of Table 5.1 (Chapter 5). Changes in the taxonomic affiliation of some species and measurement of additional material after publication of the manuscript lead to slightly different results concerning the zooidal surface area. The table lists the mean autozooid surface area (SA, in mm²) for 31 cheilostome species from the Niebla Calcarenite in comparison with representatives from the Mediterranean late Tortonian/early Messinian Morocco (data from El Hajjaji, 1992) and early Messinian Algeria (Moissette, 1988). Proportional differences are given in positive (larger surface area in relation to Guadalquivir specimens) and negative values (smaller surface area in relation to Guadalquivir specimens). *Myriapora truncata* is excluded from this list since a more precise analysis of its morphology is presented in Chapter 6, and zooid size not a reliable measure due to indistinct and irregular zooid margins. Note that taxonomic affiliation in this work may be different from those of El Hajjaji (1992) and Moissette (1988) for the same species; see the Taxonomic Account (Chapter 4.2) for synonymies. See Chapter 5 for detailed explanation and discussion.

	Guadalquivir Basin	Morocco		Alger	ria
Species	SA	SA	Difference (%)	SA	Difference (%)
Amphiblestrum appendiculata	0.179	0.171	-4	0.182	2 +2
?Aplousina bobiesi	0.237	0.396	+67	0.403	+70
Calloporina decorata	0.284	0.370	+30	0.354	+25
Cheiloporina campanulata	0.207	0.302	+46	0.297	43 +43
Chorizopora brongniartii	0.083	0.082	-1	0.112	+35
Ellisina gautieri	0.06	—	—	0.088	3 +47
Emballotheca longidens	0.362	0.308	-15	0.311	-14
Escharella serrulata	0.246	0.238	-3		
<i>Escharella</i> sp. 1	0.173	_		0.194	+12
Escharina sp.	0.228	0.227	± 0		
Escharoides coccinea	0.204	0.201	-1	0.231	+13
Escharoides megalota	0.378	0.409	+8	0.400) +6
Figularia figularis	0.248	0.402	+62	0.286	+15
Gephyrotes fortunensis	0.217	_	_	0.201	-7
Hagiosynodos latus	0.118	0.226	+92	0.123	+4
Hiantopora rostrata	0.2	0.187	-7		_
Hippopleurifera semicristata	0.462	_	_	0.78	+69
"Hippoporella" pauper	0.11	_	_	0.170) +55
Onychocella angulosa	0.18	0.168	-7	0.178	3 -1
Poricella bugei	0.213	0.222	+4	0.207	-3
Puellina cf. radiata	0.161	0.15	-7		
Rhynchozoon monoceros	0.107	0.124	+16	0.072	-33
Schedocleidochasma incisa	0.102	0.136	+33	0.090) -12
Schizoporella dunkeri	0.242	0.2	-17		
Schizotheca serratimargo	0.135	0.106	-21	0.146	5 +8
Smittina messiniensis	0.093	0.131	+41		
Steginoporella cucullata	0.578	0.673	+16	0.747	+29
Therenia montenati	0.312	0.427	+37		_
Trypostega rugulosa	0.089	0.135	+52		_
Watersipora sp.	0.421			0.416	- 1

Mediterranean counterparts (Table 7.2). It may therefore prove to be difficult to make predictions when zooid size is a non-linear function of temperature, food quality and quantity, and genetics (e.g. when affecting the metabolic strategy [Peck & Barnes, 2004]). However, based on the results of the study on *M. truncata*, and due to the faunal dominance of autotrophic organisms, I interpret the Niebla Calcarenite to have formed under oligotrophic conditions. Another, more general, conclusion that can be drawn from the morphometric comparison is that intraspecific zooid size may vary immensely and that, therefore, species discrimination purely based upon measurements of absolute zooidal or colonial dimensions should be avoided in bryozoans.

Coralline red algae are not only the main contributor to the carbonate factory of the sampled Niebla Calcarenite but also (and almost exclusively) provide the substrate for bryozoan settlement. The 3-D structure of algal buildups is important in promoting bryodiversity by offering a large surface with a wide range of microenvironments, from exposed sites on protuberances to cryptic habitats on the undersides of free-growing sheets. An unambiguous pattern corroborating the importance of surface area is displayed by the colony growth-form distribution present in the Niebla Calcarenite: of the 72 species, 58 (81%) are encrusting unilaminar, five (7%) encrusting multilaminar, three (4%) erect rigid bilaminar, two (3%) erect rigid robust branching and erect flexible, and one species erect rigid fenestrate (see Nelson et al. [1988] for definition of growth-forms). The clear dominance of encrusting unilaminar species is indicative of inner- to mid-shelf depths of formation of the coralline algal buildups, and the ecological preferences of Recent species present in the Niebla Calcarenite restrict the depth window to some 30 to 40 m below sea-level (Fig. 7.1).



Fig. 7.1 Bathymetric ranges of Recent species present in the Niebla Calcarenite. Thick lines indicate depth of abundant occurrence in the Recent Mediterranean Sea (data from Gautier, 1962; Hayward & Ryland, 1998, 1999; Hayward & McKinney, 2002).

Although water temperatures were presumably slightly warmer in the Mediterranean Sea, the Guadalquivir Basin fauna hosts a great number of species that were so far known from the Mediterranean basins only (see below); the environment was thus sufficiently similar to promote their growth on the other side of the connecting straits as well. However, a direct comparison of bryozoan faunas of an analogous coralline algal-dominated bioconstruction from the Mediterranean Sea is not possible since there exist no other published descriptions of species from such an environment. While numerous species survive the Messinian salinity crisis (MSC), and this most likely in the Guadalquivir Basin and NW Morocco (see below), the extinction of only four of the established Mediterranean 'endemic' species present in the Niebla Calcarenite (Fig. 7.2) may be interpreted as background extinction. (As established species of the Mediterranean Sea I refer to taxa that have often been cited from the main basins; in contrast, H. rostrata, G. fortunensis, S. messiniensis and Watersipora sp. have rarely been reported and have been found in the western part of the Mediterranean Sea only.) However, oceanographic changes during the Messinian may have also affected the eastern Atlantic faunas. Upwelling systems off NW Africa developed in the latest Miocene (e.g. Tiedemann, 1991) and changes in planktic foraminiferal assemblages in the eastern Atlantic, with northern faunal assemblages migrating southwards, suggest a cooling of that region during the Messinian (Sierro et al., 1993). The Guadalquivir Basin and southern Moroccan area was thus likely to be seized by cooler water masses coming from the north and south.

Possibly, some of the Mediterranean species adapted to warmer temperatures were affected by this cooling and did not survive into the Pliocene.

7.2 Palaeobiogeography

The history of bryozoan taxonomy and systematics can be roughly divided into two eras, separated by the introduction of SEM photography for the identification and documentation of morphological characters. Since then, the ability to observe interspecific differences at a scale of a few micrometers have not only led to a revised and substantiated (morpho)species definition and systematic order, but also to the notion that many species once interpreted to have a cosmopolitan distribution were actually confined to much smaller regions. As a result, diversity increased drastically in several genera over the last three decades (e.g. Taylor & Mawatari, 2005). Once this perception is strictly applied to fossil species or fossil representatives of Recent taxa of the Neogene Mediterranean realm, several genera considered in this work (such as, e.g., Scrupocellaria, Cellaria, Puellina, Microporella or Celleporina) will likewise turn out to contain considerably more species with rather restricted geographic ranges. A related problem encountered during this project was, besides a bad state of preservation, the insufficient definition and illustration of the type-specimens of many species described by earlier authors. A precise species identification was therefore not possible in some instances, and a revision of these earlier works (e.g. Reuss, 1848) is badly needed. To what extent biodiversity and biogeographic analyses, as well as statements on species longevity are affected by these shortcomings needs yet to be quantified.

While Neogene Mediterranean bryozoans are, despite the above mentioned problems, comparatively well-known owing to a great number of works, fossil Bryozoa from the eastern Atlantic have received less attention during the last decades. This is especially true for Miocene faunas from Portugal, northern Spain, western France and NW Europe, of which not a single recent publication exists. Therefore, without seeing the original material described in the earlier pre-SEM works, a biogeographic analysis is lacking a sound basis. Since I have visited the museum collections of the University of Lyon (hosting mostly bryozoans from the Mediterranean Neogene to Recent), and the Natural History Museums in London (Pliocene of the Coralline Crag, UK; Recent Mediterranean and Atlantic) and Vienna (Middle Miocene Bryozoa from the Paratethys region), comparisons with faunas of these ages and locations given below are more substantiated. However, analyses with a finer resolution than between bioprovinces, as given below, are not feasible or reasonable at present.

The total of the 72 species found in the Niebla Calcarenite can be roughly grouped into four clusters defined by their fossil or Recent biogeographic affinities: 2 species (3%) were hitherto recorded from the Atlantic only, 16 (22%) are known to occur in both the Atlantic and the Mediterranean Sea, 27 (38%) have never or only rarely found outside the Mediterranean region before (the so-called Mediterranean 'endemics', see Chapter 5), and another 27 species could not be referred to any known species (or figured specimen) and can therefore not be characterised biogeographically. Although the latter group may prove to comprise more species confined to the Atlantic once the fossil faunas of this region are better known, it is interesting to note that only Arthropoma ciliata and, possibly, Escharoides sp. have not been recorded from the Mediterranean Sea before. The (precautious) comparison with faunas figured and described from the Middle to Late Miocene of western France by Duvergier (1921, 1924), Canu & Lecointre (1925, 1927, 1928, 1930) and Vigneaux (1949) does therefore not suggest a substantial faunal similarity and an exchange of species to have happened between NW France and SW Spain during the Miocene, although the thermal gradient is interpreted to have been lower than today (e.g. Raffi et al. 1985). In contrast, the high number of Mediterranean species present in the Guadalquivir Basin (the modern Mediterranean Sea hosts an equal 34% of endemic species [Harmelin, 1992]) provides evidence for a strong transfer of species via the connecting straits. The region immediately west of the connecting straits thus constituted an ecotonal area characterised by the intergradation of Mediterranean and easternmost Atlantic species.

This means, however, that for the larval transport of these shallow-water bryozoans, surface water flow through the straits must have occurred in both directions. While a Late Miocene

Mediterranean surface water outflow through the Betic Strait was proposed by Benson et al. (1991), the geographic and chronological reconstruction of the evolution of the Spanish straits, on which their study was based, is now outdated (although this model is still being used in latest publications by Warny et al. [2003] or Meijer et al. [2004]). Esteban et al. (1996), Martín et al. (2001) and Betzler et al. (subm.) have shown that the broad Betic Strait has vanished by the late Tortonian and that, instead, rather short-lived and narrow gateways have connected the Mediterranean Sea with the Atlantic via the Guadalquivir Basin (Fig. 5.2). Nevertheless, in both the late Tortonian connection via the Guadix Basin (Betzler et al., subm.) and in the early Messinian Guadalhorce Corridor (Martín et al., 2001), sedimentary structures indicate surface water outflow. The observed pattern in oceanographic regime, corroborated by my biogeographic data, needs now to be re-modelled, using the recently obtained information on palaeogeography and evolution of the connecting straits, in order to understand the changing conditions in the Mediterranean Sea during the initial phase of the MSC.

Sefian et al. (1999) were the first to describe bryozoan faunas from the immediately west of the Mediterranean Sea of NW Morocco and to report the presence of 17 species (28% of their total fauna) which were considered as being endemic to the Mediterranean region before. An additional 21 of the 'endemic' species occur in the Guadalquivir Basin. Taking together the cheilostome

species described in the present study and in that of Sefian et al (1999), 33% of the total fauna (114 species) of the Late Miocene easternmost Atlantic are species that have never been reported from this region before. As mentioned above, this figure is the same for endemic species in the Recent Mediterranean Sea (Harmelin, 1992) and thus strongly favours the hypothesis of an extra-Mediterranean refuge for species to survive the MSC, and furthermore provides evidence for the eastern Atlantic having been the source are for the post-crisis resettlement of the Mediterranean Sea.

Comparison of the Guadalquivir Basin fauna with those of other regions and ages vield further important information concerning bioprovinces: while there is not a strong relationship between the SW Spanish fauna and those from western France during the Miocene, a great percentage (29%) of the total species is shared with, or at least comparable to, the Middle Miocene (Badenian) fauna of the central Paratethys (based on own observations and on publications of Reuss, 1848, 1874; David & Pouyet, 1974; Schmid, 1989; Pouyet, 1997b). A similar pattern is observed when comparing the

Stratigraphic						0	
Distribution	ene	g	e .	g	Ie	cen	
	Soc	ly	ldle	cer	cer	sto	ent
Species	Olig	Earl	Mid	Late Mic	Plio	Plei	Rec
Arthropoma ciliata				_			
Amphiblestrum appendiculata		-					
Steginoporella cucullata		-					
Hippopleurifera semicristata							
"Hippoporella" pauper							
Hiantopora rostrata							
Gephyrotes fortunensis							
Smittina messiniensis							
Watersipora sp.							
Schedocleidochasma incisa							
?Aplousina bobiesi		<u></u>			_		
Trypostega rugulosa		_					
Rhynchozoon monoceros							
Escharella serrulata							
Emballotheca longidens				-			
Buffonellaria entomostoma							
Escharina sp.							
Poricella bugei				-	_		
Escharella sp. 1							
Cheiloporina campanulata							
Therenia montenati							
Escharoides megalota		-	-		_	-	
Escharoides coccinea							
Myriapora truncata							
Puellina cf. radiata		_					_
Hagiosynodos latus		-				-	-
Schizoporella dunkeri		_					
Ellisina gautieri							
Mollia patellaria							
Figularia figularis			-			-	
Chorizopora brongniartii							
Calloporina decorata							
Schizotheca serratimargo							-
Mollia circumcincta							-

Fig. 7.2 Stratigraphic distribution of established (or of uncertain taxonomic status but previously recorded) species present in the Niebla Calcarenite. Dashed lines indicate unproven ranges.

Late Miocene Guadalquivir Basin species with those present in the Pliocene of NW Europe (7% in common, based on own observations and on publications of Busk, 1859; Lagaaij, 1952; Bishop, 1987; Bishop & Hayward, 1989; Pouyet, 1997a) and the Mediterranean Sea (42% in common). This pattern thus suggests that bioprovinces throughout the Neogene were stable through time along latitudes, while the species exchange, i.e. the number of species shared, between bioprovinces were low. Since most cheilostome bryozoan larvae are short-lived and dependent on currents as a means of transport and distribution, the low similarity between faunas of SW Spain and NW France suggests an absence of coastal parallel currents and/or differences in palaeoenvironment, and therefore the presence of a bioprovincial boundary between these regions during the Miocene. To better resolve Neogene biogeographic and oceanographic patterns, more work on especially Late Miocene faunas from Portugal, northern Spain and NW France is needed.

The stratigraphic distribution of the established (or repeatedly recorded) species present in the Niebla Calcarenite is given in Fig. 7.2. The earliest occurrence of four species was extended into the late Tortonian for Hiantopora rostrata, Mollia circumcincta, Escharella sp. 1, and Smittina messiniensis. 46% of the total number of species, thus including the species presumably encountered here for the first time, range into the Messinian, 35% range into the Pliocene, and 17% of the species are extant (the former two figures are likely to increase once the Atlantic fossil faunas are better known). Eight Mediterranean 'endemic' species (11% of the total fauna, 30% of the group with a Mediterranean affinity) became extinct during the Messinian. Based on these data, the extinction of Mediterranean species during the Messinian salinity crisis appears therefore to be distinctly less severe than the disappearance of taxa during the Plio-Pleistocene, a time characterised by the comparatively less dramatic cooling of water temperatures, as was noted before by Néraudeau et al. (2001). However, studies on species and faunas affected by the MSC were almost exclusively located in the western Mediterranean basins, while descriptions of fossil faunas of the eastern basins are scarce. Yet endemic species increase in number towards the east in the Recent Mediterranean Sea (Harmelin & d'Hondt, 1993). Since I do not see a reason why this should have been different in the Miocene, research on Aegean faunas will certainly show that the impact of the MSC was greater on faunas from the eastern basins than on those from the western ones, which obviously experienced a greater faunal exchange with the eastern Atlantic than previously acknowledged.

8. References

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PLATES

PLATE 1

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Fig. 12	<i>Microporella</i> aff. ciliata (PALLAS) Autozooids (right) and two ovicellate zooids with ovicells only partly preserved (GNI1-033-A; 200 μm).	p. 99
Fig. 13	<i>Microporella</i> aff. ciliata (PALLAS) Ovicellate zooids with secondary calcification preserved (GNI1-033-A; 200 μm).	p. 99
Fig. 14	<i>Calloporina decorata</i> (REUSS) Ovicellate zooids (GNI1-037-C; 200 μm).	p. 95
Fig. 15	<i>Microporella</i> aff. ciliata (PALLAS) Some auto- and ovicellate zooids. Secondary calcification is not preserved (GNI1-033-C; 200 μm).	p. 99



Fig. 1	<i>Microporella</i> sp Autozooids (GNI1-033-B; 200 μm).	p. 101
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Fig. 4	<i>Therenia montenati</i> (POUYET) Auto- and ovicellate zooids (centre, top right and right) (GNI1-038-B; 200 μm).	p. 104
Fig. 5	<i>Therenia montenati</i> (POUYET) Orifice and avicularia of autozooids. Note the distal shelf in the orifice (top left) and the twisted avicularian crossbar (GNI1-038-C; 100 μm).	p. 104
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Fig. 1	Celleporina cf. canariensis ARÍSTEGUI General aspect of pisiform colony (GNI1-055-B; 200 µm).	p. 109
Fig. 2	Celleporina cf. canariensis ARÍSTEGUI Autozooid and ovicellate zooid with lateral peristomial avicularia (GNI1- 056-C; 100 µm).	p. 109
Fig. 3	Celleporina cf. canariensis ARÍSTEGUI Primary autozooidal orifice (GNI1-055-B; 50 µm).	p. 109
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Fig. 15	?Osthimosia sp. Autozooids, suboral adventitious avicularia, and spatulate interzooidal avicularia (GNI1-004-A; 100 μm).	p. 113



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