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Seagrass Mollusks as a Model Group for Paleoecological and Paleodiversity Studies

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Seagrass Mollusks as a Model Group for Paleoecological and Paleodiversity Studies

Weekdieren van het Zeegras als Modelgroep voor Paleomilieu en Biodiversiteit Studies

(met een samenvatting in het Nederlands)

Seegrass Mollusken als Modelgruppe für Studien der Paläoökologie und Paläodiversität

(mit einer Zusammenfassung in deutscher Sprache)

PROEFSCHRIFT

ter verkrijging van de graad van doctor aan de Universiteit Utrecht op gezag van de rector magnificus, prof.dr. G.J. van der Zwaan, ingevolge het besluit van het college voor promoties in het openbaar te verdedigen op

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Today's global marine diversity hotspot, or center of maximum biodiversity, is located in the Indo-West Pacific (IWP), namely in the Indo-Malayan region, including Malaysia, the Philippines, Indonesia, and Papua New Guinea (Hoeksma, 2007; Renema et al., 2010). Numerous groups of marine organisms, for instance foraminifera, mollusks, and corals contribute to the high taxonomic richness (e.g., Bellwood et al., 2005; Hoeksema, 2007; Kohn, 1990; Wilson and Rosen, 1998). The exceptional biodiversity in the region is thought to have originated in the Early Neogene with the diversification of scleractinian coral reefs and associated organisms (e.g., Wilson and Rosen, 1998; Chapter 6). Because the available fossil data to document patterns of diversification of marine organisms in the Cenozoic of SE-Asia are comparatively sparse, the collection of new data is needed in order to document the timing and context of diversification. To perform this task, the Marie-Curie Initial Training Network (ITN) Throughflow was formed in 2010, focusing on Miocene fossils and their paleohabitats of East Kalimantan, Indonesia. This thesis represents one of eleven projects of the Throughflow program.

The initial aim of the research presented in this thesis was the reconstruction of marine mollusk biodiversity in the Miocene of Indonesia. To make useful comparisons of species diversity over time it is necessary to compare faunas from the same paleohabitat, because species richness varies considerably among different environments (Chapter 3). For the following reasons seagrass meadows and associated mollusk assemblages were selected as a model habitat and model group for this research:

1. *Significance*. Seagrass meadows are ecologically important marine habitats with a worldwide distribution and are of high scientific interest (Chapter 1). They are highly productive and play an important role in the ocean's carbon cycle. Seagrass roots stabilize sediments and therefore help prevent coastal erosion. Seagrass meadows can reduce eutrophication and bind organic pollutants. Furthermore, their three-dimensional structuring provides a habitat for numerous associated organisms, including economically important species. For instance, seagrass meadows act as a nursery habitat for fish. Like other shallow marine environments seagrass meadows are threatened by human impact, therefore studies on the response of this ecosystem (e.g., indicated by the diversity of associated organisms) to small and large scale

environmental changes in the past are of critical importance.

2. *Abundance and species richness*. Mollusca represent a large animal phylum that includes amongst others snails, mussels and clams, and squids. They are an important seagrass-associated higher taxon, because they contribute significantly to the species richness in the habitat and are usually very abundant or even numerically dominant in seagrass-associated invertebrate communities. Yet, compared to other marine environments (e.g., coral reefs), mollusk diversity is not exceedingly high, providing a good opportunity to study this group within a restricted time frame without being overwhelmed by species numbers (Chapters 2, 3, 6).

3. *Biodiversity.* Seagrasses and associated organisms follow global diversity patterns. Seagrasses, like numerous other shallow marine organisms, have their highest species diversity in the Indo-Malayan region, as do a number of highly speciose mollusk families that occur commonly in modern seagrass meadows (Chapter 6).

4. *Preservation*. Seagrass meadows are mainly located in areas where the plants are protected from strong currents and wave action; the plant cover itself additionally reduces water flow velocities. Seagrasses trap and stabilize sediments, therefore sediments within meadows are often finer-grained than in adjacent unvegetated areas (Chapter 1). These parameters increase the preservation potential of associated organisms and decrease the chance of transport of material out of the habitat. Additionally, increased pH-values in seagrass environments may enhance calcification rates of associated organisms and might therefore be another control for reduced taphonomic shell loss in seagrass habitats. Seagrass-associated mollusk faunas are among the best preserved in marine Miocene deposits in the study area, whereas the record of reef-associated mollusks is highly biased against by diagenetic loss of shell carbonate (Chapters 2, 3, 5, 6).

5. *Availability.* The presence of seagrasses in the Miocene of Indonesia in combination with the increased fossilization potential of mollusks in seagrass meadows led to the availability of several fossil seagrass-associated mollusk faunas in the study area that represent different stratigraphic intervals (Chapters 2, 5, 6).

However, the focus on a specific paleohabitat also comes with challenges; in particular the addressed paleohabitat has to be reliably identified in the geological record.

Seagrasses as well as their pollen easily disintegrate. Therefore, seagrasses have a poor fossil record and their former presence has to be inferred using other approaches (Chapter 1). This is why the focus of this research shifted towards investigating possibilities of the successful identification of paleo-seagrass meadows from other data as a base for future biodiversity studies. This includes the characterization of mollusk assemblages from seagrass meadows and other marine environments in the study area (Chapters 2 and 3) as well as studies on the potential of mollusk assemblages as paleoenvironmental indicators (Chapter 4 and 5). Subsequently this has led to a first attempt of reconstructing Miocene biodiversity of seagrass-associated mollusk assemblages in today's biodiversity hotspot (Chapter 6). The latter chapter also addresses challenges that come with such studies, such as analysis of material obtained from differing collection methods and post-collection treatment of samples.

Although taxonomy is fundamental to studies on ecology and biodiversity, detailed taxonomic revisions and the description of new species were not the principal goals in this research. However, four new seagrass-associated gastropod species are described from the early Burdigalian (early Miocene) of Banyunganti, Java, Indonesia (Chapter 2). It is assumed that a high percentage of the taxa presented here (Chapters 2, 3, and 6) is still undescribed. The use of open nomenclature in this research provided a pragmatic approach to conducting studies on highly diverse and largely unknown faunas whilst preventing unreasonable expenditure of time.

As seagrasses rarely fossilize, their former presence in earth history has been commonly inferred by the occurrence of indirect indicators, represented by fossil organisms, and sedimentological, taphonomical or geochemical signatures. The successful identification of seagrass environments in the fossil record was a major challenge in this research. Not only mollusks, but also other organisms groups and proxies were explored for their potential as indirect seagrass indicators (IPSIs). A comprehensive review of formerly applied IPSIs that provides a catalogue for the identification of seagrass environments in the fossil record for future researchers has been made (**Chapter 1 - Introduction**). This chapter also introduces habitat characteristics of seagrass meadows and stresses their ecological importance.

The topic of the first section of this thesis (Chapters 2 and 3) is mollusk faunas from the Miocene of Indonesia. In this section two fossil mollusk assemblages from two different paleohabitats are presented to provide an insight in the exceptional preservation and high species richness of mollusks, especially gastropods. Furthermore, these chapters address the following questions: How are mollusk faunas characterized and assigned to certain paleohabitats? How do they differ ecologically and may this allow the possibility of differentiating habitats?

Chapter 2 presents a fossil mollusk assemblage from the early Miocene of Banyunganti, Java, Indonesia, that has been identified as seagrass-associated based on its taxonomic and ecological composition, the presence of the seagrass indicator taxon *Smaragdia*, and the composition of the accompanying foraminifera fauna. The mollusk assemblage has been extensively studied, providing an overview over all present taxa, including rare species and shell fragments. The sampled fauna contains 184 mollusk taxa of which 159 are gastropods. Most presented taxa are considered to be undescribed. Four common gastropod taxa are introduced as new species and all taxa are figured. The Banyunganti assemblage is characterized by high species richness, a high abundance of small grazing gastropods, and exceptional preservation of shell ornamentation.

Chapter 3 presents a well-preserved mollusk assemblage from the Tortonian (late Miocene) of Bontang, East Kalimantan, Indonesia. The fauna is associated with abundant ramose corals, the paleohabitat is therefore interpreted as a coral carpet environment. The fauna is characterized in terms of species abundances, species richness, and feeding ecology. In comparison with the seagrass-associated mollusk assemblage from Java (Chapter 2) it differs in feeding guild composition: predatory gastropods are more abundant in the coral carpet assemblage. Therefore, the present assessment of a mollusk assemblage from a coral carpet environment supports the assumption that feeding ecology might provide a tool for distinguishing seagrass meadows from other shallow marine habitats in the fossil record.

The second section of this thesis (Chapters 4 and 5) deals with two approaches to the use of mollusk assemblages as IPSIs (see also Chapter 1). The studies presented here do not focus on specific taxa but try to identify proxies based on the species composition of whole assemblages (Chapter 4) and on the geochemical signature of shells (Chapter 5).

Chapter 4 addresses the question whether the species composition of mollusk assemblages from seagrass meadows differs from assemblages sampled at adjacent environments (in this case unvegetated sandflats). In this study gastropod death assemblages from modern day ecosystems at San Salvador, Bahamas were used. This, other than studies carried out on fossil material, provides control over the sampled habitat. The results of the study show a highly significant difference between the species composition of gastropod death assemblages sampled from seagrass-vegetated sandflats and those sampled from unvegetated sandflats. Furthermore, the species composition of assemblages sampled within seagrass meadows differs from that of samples from the unvegetated zone adjacent to seagrass meadows. Furthermore, the taphonomic signature of shelly assemblages shows obvious differences between vegetated and unvegetated areas with poorly preserved shells being more abundant at unvegetated sites.

Chapter 5 provides a study of the stable isotopic signals of more than 150 shells from different marine paleohabitats in the Miocene of Java and East Kalimantan. The studied material includes seagrass-associated shells from Banyunganti (Chapter 2) and from three other localities with inferred seagrass vegetation in the Tortonian of East Kalimantan. Furthermore, material from a coral carpet environment (Chapter 3), from a mixed seagrass-coral habitat and from an estuarine, brackish water, locality are included. The results of $\delta^{18}O$ and $\delta^{13}C$ analyses herein show consistently higher $\delta^{13}C$ ratios in shells from seagrass habitats, leading to the conclusion that carbon isotopes yield an additional tool to confirm assemblage-based paleoenvironmental interpretations within regions and limited stratigraphic time intervals. It is furthermore investigated which processes in seagrass meadows may influence the isotopic composition of associated shells.

The synthesis of this thesis is a comparison of three seagrass-associated mollusk assemblages from the Miocene of Indonesia, which are characterized in terms of feeding ecology, species abundance and diversity (**Chapter 6**). Each fauna occurs within a different stratigraphic interval extending from the early Burdigalian (early Miocene; Banyunganti fauna, Chapter 2), the middle Miocene and the Tortonian (late Miocene, Chapter 5). For comparison also an early Tortonian (late Miocene) coral carpet fauna (Chapter 3) is included in the study. The study provides a first attempt of reconstructing the historical development of biodiversity of seagrass-associated mollusks during the Miocene within today's hotspot of marine biodiversity. Late Miocene samples were somewhat more diverse then early Miocene samples, and both were considerable more diverse then a paratropical seagrass-associated mollusk assemblage from the middle Miocene of the Paratethys (Chapter 6).

In summary, a suite of indirect paleo-seagrass indicators has been established in order to differentiate paleo-seagrass meadows from other shallow marine habitats in the geological record (Chapter 1). Especially, assessments of feeding ecology, $\delta^{13}C$ signals of shells and the presence of the obligate seagrass feeder *Smaragdia* enable the identifications of paleo-seagrass habitats (Chapters 1 to 5). Using these indicators paleo-seagrass meadows can be discriminated and the study of timing and context of diversification of associated mollusk assemblages becomes possible. High species richness and high numbers of undescribed taxa make such studies challenging. In order to investigate the timing and context of diversification standardized analyses are required, and material from existing museum collections appears to be of limited use as unknown collecting biases may apply (Chapters 3 and 6).

Much additional sampling, especially from middle Miocene, Pliocene and Quaternary settings, will be required to extend this research and rigorously establish patterns through space and deep time. In addition, future research will require the assessment of the role of environmental parameters (for example, depth) in controlling diversity variation among seagrass habitats (Chapter 6).

Introduction

Chapter 1 – Introduction

Indirect Paleo-Seagrass Indicators (IPSIs): A Review

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and Willem Renema

Earth Science Reviews

(manuscript in review)

Keywords: seagrass, seagrass meadow, seagrass fauna, fossil record, proxy, (paleo)-ecology

Abstract

Seagrass meadows are marine habitats with high ecological importance. Their detection in the fossil record will contribute to our understanding of the development of patterns of marine biodiversity through time and the response of coastal marine habitats to environmental change. Due to the low probability of fossilization of seagrass macrofossils, the reliable identification of seagrass meadows in the fossil record is often challenging. A wide range of indirect indicators has been applied to infer paleo-seagrass habitats in late Cretaceous and Cenozoic deposits. The usefulness of those indicators is determined by various factors, such as their stratigraphic range, fossilization potential, and habitat restriction. Although they have sometimes been briefly summarized in the literature, a comprehensive review of indirect paleo-seagrass indicators, including an assessment of their value for recognition of this habitat, is not yet available. We summarize them here and explore their usefulness. We aim to assist future workers to identify facies and fossil assemblages associated with seagrass beds. In conclusion, apart from a few truly diagnostic proxies, combinations of several indicators turn out to be most reliable when aiming to identify the presence of paleo-seagrass habitats.

1. Introduction

The deeper understanding of paleo-habitats and their successful recognition in the geological past help us to investigate their ecological responses to small- and large-scale environmental change, such as climate change and sea-level fluctuations. In order to evaluate the development of coastal biodiversity through time it is necessary to reliably discriminate different marine habitats, because species numbers and assemblage compositions may vary considerably between environments (Chapter 3; Gray, 2001). Therefore, the successful recognition of different paleohabitats is an indispensable basis for studies on biodiversity, climate and sea level history.

Here the terms ‘seagrass habitat’, ‘seagrass meadow’, etc. refer to environments with an area-wide vegetation cover (10s to 100s of m^2) dominated by marine angiosperms. Patchy seagrass occurrences in other, for instance coral-dominated, environments are not further considered, because the recognition of dispersed seagrass vegetation appears to be limited, although not impossible (Chapter 3).

Seagrass meadows are distributed worldwide from Australia and New Zealand to Iceland, Norway and Greenland, spanning the coasts of Africa, India, The Middle East, North and South America and Europe with the exception of Antarctica (Fig. 1). The habitat is characterized by a three-dimensional structuring of marine angiosperms and associated macroalgae.

Seagrasses are a polyphyletic functional group comprising approximately 60 species in 13 genera, assigned to five different plant families (Les et al., 1997). They are the only angiosperms that live permanently in fully marine environments, involving several physiological adaptations (Touchette and Burkholder, 2000). The highest diversity of seagrass species is found in the tropical Indo-West Pacific around the Philippines, New Guinea, and Indonesia (Green and Short, 2003; Mukai, 1993). Marine angiosperms predominantly occur in the tidal and subtidal zone, but have also been reported from depths down to 90 m, depending on light attenuation (Duarte, 1991). In the tropics seagrasses often grow on reef flats and form compound associations with corals in the transition zone between intertidal meadows and subtidal reefs (Hoeksema, 2007; Nienhuis et al., 1989). In the Caribbean the presence of fringing reefs, which have been

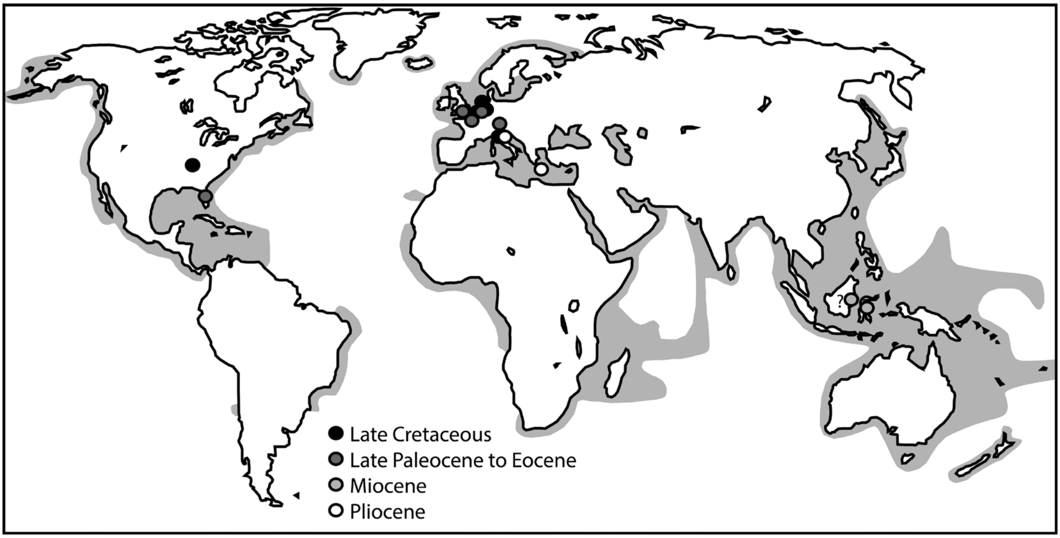

Figure 1: Worldwide occurrences of fossil seagrasses, see legend for stratigraphic assignments. The shaded areas represent the range of modern seagrass distribution (after Green and Short, 2000).

the dominant reef type in that region since the Plio/Pleistocene, is critical for sheltering and facilitating the accumulation of back-reef seagrass meadows and landward fringes of mangroves (Budd et al. 1999; Johnson et al., 2007; Spalding et al., 2001). Where the three components are present, seagrasses, coral reefs, and mangroves are intimately linked both in terms of the genesis of the wider reef system and its sedimentation patterns, and chemically through nutrient transfer (McCoy and Heck, 1976; Ogden, 1997).

Seagrass meadows provide a number of functions that make them an ecologically highly valuable habitat. Constanza et al. (1997) estimated the commercial value of ecosystems based on the ecological functions they provide, and rated seagrass meadows as one of the most valuable biotopes in the world. They contribute significantly to the oceanic primary production on a global scale and play an important role in the oceanic carbon cycle, especially in carbon storage (Duarte and Chiscano, 1999; Hemminga and Duarte, 2000). Due to their ability of rapid nutrient uptake in combination with slow decomposition rates, they can reduce eutrophication, bind organic pollutants and therefore play an important role in nutrient cycling (Spalding et al., 2003). Because seagrasses, in contrast to other marine macrophytes, have true roots, they trap and stabilize sediments and therefore prevent coastal erosion even under extreme conditions such as hurricanes (Ball et al., 1967; Scoffin, 1970). Seagrass meadows support local biodiversity by providing food, stable sediment conditions, and a three-dimensional structuring, offering attachment surfaces and shelter against predation, for numerous associated organisms (e.g., Boström and Bonsdorff, 1997). Seagrasses form complex ecosystems that consist of several microhabitats for different groups of organisms, i.e., the infauna in the sediment, the benthic community on the sediment surface, the epiphytic community, and planktonic as well as nektonic organisms in the water column (Den Hartog, 1979). Meadows are also an important nursery habitat for fish, crustaceans, mollusks and echinoderms, including reef-associated and economically important species (Hemminga and Duarte, 2000). Therefore, species richness and abundance is often higher in seagrass meadows than in adjacent unvegetated areas that lack a three-dimensional structuring (Barnes and Barnes, 2012; Brasier, 1975; Hemminga and Duarte, 2000; Mikkelsen et al., 1995). However, diversity often does not exceed that of other shallow marine phytal habitats, such as mangrove forests or algal mats, or that of nearby coral reefs (Hemminga and Duarte, 2000, and references therein; Sheridan, 1997). Like other coastal marine ecosystems, seagrass meadows are severely threatened by climate change, eutrophication, over-exploitation, and mechanical disturbance (Hughes et al., 2009; Jackson, 2001; Orth et al., 2006; Short and Neckles, 1999; Waycott, 2009).

Fundamental to studies of seagrass habitats in deeper time is the assumption that seagrass meadows in the geological past since the late Cretaceous provided habitat functions comparable to modern seagrass meadows and were inhabited by a comparable community of associated organisms. Despite their ecological importance, our knowledge of the biodiversity of modern seagrass habitats remains surprisingly limited, with faunal inventories often being restricted to specific groups, such as fish or arthropods (e.g., Heck, 1995). Other studies focus on the macrobenthic invertebrate community, often combined with an assessment of the infauna (e.g., Barnes and Barnes, 2012; Boström and Bonsdorff, 1997), or that of epiphytes (e.g., Marsh, 1973). Studies of the composition and diversity of the entire macrofauna present in Recent seagrass meadows are comparatively scarce (Brouns and Heijs, 1985). Likewise, detailed studies of distribution patterns of seagrass meadows and their response to environmental change during the Cenozoic are very few in number (Brasier, 1975; Domning, 2001; Eva, 1980; Vélez-Juarbe, 2013). There are no studies examining patterns of biodiversity change of seagrasses and associated organisms over global or regional scales. One likely explanation is the challenge of reliable identification of seagrass meadows in the fossil record. Seagrasses easily disintegrate, therefore marine angiosperm macrofossils are rare (Brasier, 1975). In contrast to most land plants, the pollen of seagrasses is prone to decay, because it lacks the resistant pollen wall used by land plants for protection against dehydration (Hesse et al., 1999). Therefore, a widely used approach has been to infer the former presence of paleo-seagrass vegetation through lithological, sedimentological and taphonomical indicators, and the presence of fossil organisms that are interpreted as typical for seagrass associations (Brasier, 1975; Domning, 1981; Eva, 1980; James and Bone, 2007; Reuter et al., 2010). All these indicators can only provide indirect evidence of seagrass meadows and are therefore here referred to as IPSIs (Indirect Paleo-Seagrass Indicators). IPSIs have often been of limited use because of their low fossilization potential, limited geographical distribution, or occurrences in habitats others than seagrass meadows. To date no comprehensive summary of indirect paleo-seagrass indicators is available, neither is an assessment of the value of those indicators.

In this study we review previous studies of seagrass meadows in the late Cretaceous and Cenozoic, focusing on the methods used to identify this habitat. Our aim is to provide an overview of previously used IPSIs, to assess their usefulness, and to identify which indicators or combinations of them are most reliable to infer paleo-seagrass vegetation in the geological record.

2. Material and Methods

This study is largely based on a review of the available literature on modern seagrass meadows, previously identified paleo-seagrass meadows, and IPSIs of various kinds. Observations made on our own (in part unpublished) material and results are included. Specimens deposited in the Naturalis Biodiversity Center, Leiden, the Netherlands are indicated by RGM numbers.

We provide a classification for each reviewed IPSI, referring to its appearance in modern seagrass meadows, the way it has been used as an indicator, and possible limitations of itsusefulness (2.1.1-2.1.4).

2.1 Definition and Quality of IPSIs

The term IPSI is used for every proxy that has been previously applied to infer seagrass-dominated environments in the fossil record. This includes the presence and/or abundance of various organisms, the species and ecological composition of fossil assemblages, sediment characteristics, taphonomic features, and geochemical approaches (4.-5.). The most commonly used IPSIs are organisms that are characteristic of paleo-seagrass vegetation.

The ideal IPSI would occur abundantly in all seagrass meadows worldwide but in no other habitat, and would have a high potential for fossilization. Such an ideal IPSI does not exist. The quality of an IPSI, that is its ability to reliably identify paleo-seagrass meadows, depends on several factors. For instance, one IPSI can be strictly confined to seagrass meadows, but is limited by a low preservation potential. Another IPSI can occur frequently in fossil assemblages, but its occurrence is not restricted to seagrass environments. To assess the usefulness of IPSIs each indicator is reviewed for its compliance with four criteria (see below). In conclusion, the indicators are ranked as strong IPSIs (including conclusive and highly suggestive indicators), suggestive IPSIs, and weak IPSIs. The latter are only applicable to strengthen the argument when other IPSIs are present.

A common concern with paleoenvironmental indicators, including IPSIs, is the possibility of transport out of the original habitat and mixing of indicators from different environments. Therefore, an otherwise strong IPSI might not be able to indicate the exact locality of a seagrass meadow but only its proximity. When using assemblage compositions as IPSIs, use of autochthonous assemblages is essential. Assemblages that contain taxa characteristic for a number of different habitats or that are significantly variable in the taphonomic condition among shells should be excluded from such analyses (e.g., Davies et al., 1989). However, out-of-habitat transport is generally rare for fossil organisms, especially in flat-bottomed settings, and it is likely that fossil assemblages represent the original ecological signal (Kidwell and Bosence, 1991; Kidwell and Flessa, 1996). Where transport is occurring, it usually takes place over short distances of less than 50 m (Miller and Cummins, 1990).

2.1.1 Stratigraphic and Geographic Range

Seagrasses are distributed worldwide with the exception of Antarctica (Fig. 1), and known since the late Cretaceous (3.1). An ideal IPSI would have a geographic distribution and stratigraphic range congruent with that of seagrasses, and would therefore be able to indicate seagrass vegetation across all time intervals and regions. However, many IPSIs have a narrower geographic range and their use is therefore limited to their region of occurrence. Furthermore, any feature or organism that is highly characteristic for modern seagrass meadows is still not useful as an IPSI when it is unknown in the fossil record.

2.1.2 Fossilization Potential

To be useful as an indicator for seagrasses in the fossil record, an IPSI should have a high potential for preservation. Here we categorize the fossilization potential of IPSIs as 'high', 'moderately high', and 'low'. IPSIs with a high potential for preservation include organisms with solid, carbonate shells such as mollusks. IPSIs with a moderately high potential for preservation include organisms that tend to disarticulate and are usually represented by parts of their skeleton (e.g., echinoid spines). IPSIs with a low potential for preservation include fragile encrusters and non-skeletal organisms, although they may be abundant at certain sites (e.g., 4.4).

2.1.3 Frequency of Occurrence

The frequency of occurrence specifies how likely it is that the addressed IPSI occurs in a randomly chosen seagrass meadow. 'Frequent' means that the addressed IPSI is almost exclusively confined to seagrass meadows. Other IPSIs are ranked as 'moderately frequent' or 'rare'. For this classification it is necessary to define a frame of reference. For instance, an IPSI can occur frequently in modern seagrass meadows, but is very rare in the fossil record (according to its fossilization potential). Another IPSI may occur very frequently, but only within its limited geographic range. We here define the frame of reference for the frequency of every IPSI individually.

2.1.4 Habitat Restriction

Whether the indicator is strictly confined to seagrass meadows, or if it occurs outside this habitat, is of critical importance. Some IPSIs characterize marine macrophyte vegetation, including seagrasses but also macroalgae. Other IPSIs occur in a wide range of marine habitats.

3. Seagrass Associations in the Fossil Record

Seagrass associations in the fossil record can be divided into two categories: 1) associations with seagrass preservation (3.1), and 2) associations identified based on IPSIs. In addition, the presence of IPSIs can strengthen the interpretation of a sedimentary deposit containing only rare remains of seagrasses or of ‘seagrass-like’ plants that cannot be reliably identified (Collinson, 1996). Studies on fossil associations including preserved seagrass remains reveal similarities to modern seagrass habitats, indicating that observations on today’s seagrass systems are applicable to the past and vice versa. For instance, the use of seagrass leaves as an attachment surface is attested by encrusting organisms preserved on seagrass leaves from the Eocene of Florida and France and the Pliocene of Greece (Ivany et al., 1990; Moisette et al., 2007; Taylor and Todd, 2001). Another example is the high abundance of juvenile echinoderms, also observed in the Eocene of Florida, which may indicate the function of seagrass meadows as nursery habitats in the geological past (Ivany et al., 1990).

3.1. Plant Macrofossils

Considering the worldwide distribution of seagrasses and their origination in the late Cretaceous, records of fossilized seagrass remains are very sparse (Fig. 1). The oldest known seagrass fossil comprises a stem of *Thalassocharis muelleri* from the early Campanian of the Netherlands (Debey, 1848, 1851; Pomel, 1849). Late Campanian seagrass stems, occasionally with attached leaves, have been described from Westphalia, Germany (Hosius and von der Marck, 1880). Two early Maastrichtian seagrass leaves are known from Tennessee, USA (Dilcher, in press). Anatomically preserved seagrass stems and roots are described from the late Maastrichtian of the Netherlands (Voigt, 1981; Voigt and Domke, 1955). Those seagrass fossils are associated with various bryozoan species and also include examples of bioimmuration (Voigt, 1981; 3.2). Van der Ham et al. (2007) described silicified fragments and chert imprints of seagrass leaves from the late Maastrichtian and earliest Danian of Belgium and the Netherlands. A late Paleocene seagrass record is known from Belgium (De Saporta and Marion, 1878). Chandler (1961) and Collinson (1996) have recorded remains of seagrass-like leaves, axes and rhizomes (some possibly representing *Posidonia*-like seagrass), associated with diverse foraminifera, bryozoans, and a highly diverse mollusk fauna, from a thin bed within the middle Eocene Selsey Formation (formerly Upper Bracklesham Beds) of southern England. Both Curry (1965) and Tracey et al. (1996) have briefly discussed the fauna and have interpreted it as indicating a seagrass or mixed seagrass/macroalgal habitat, which contrasts strongly with the assemblages and inferred habitats present throughout much of this formation. Plant remains similar to those from Selsey are known from the London Clay Formation (early Eocene) of Herne Bay, UK (Chandler, 1961; Collinson, 1983) and from the Brussels Sand Formation (middle Eocene), Belgium (Stockmans, 1936). A well-preserved seagrass bed with a rich associated fauna is known from the middle Eocene Avon Park Formation, Florida (Benzecry and Brack-Hanes, 2008; Ivany et al., 1990; Lumbert et al., 1984). Associated organisms include various epiphytes and juvenile echinoids, but also sirenian bones and remains of a sea turtle (Ivany et al., 1990). Further Eocene records of seagrasses are from the Paris Basin, France (Phillips and Meñez, 1988), southern Germany (Gregor, 2003), and northern Italy (Gregor, 1991). Laurent and Laurent (1926) reported fossil seagrass from the Miocene of Sulawesi.

Furthermore, recently we have found a locality with preserved probable seagrass leaves of early Tortonian (late Miocene) age in East Kalimantan, Indonesia, but the plant identifications have yet to be verified. Fossilized *Posidonia* leaves as well as in-situ rhizomes are known from the late Pliocene Kritika Section, Rhodes Formation of Rhodes, Greece (Moisette et al., 2007). A diverse assemblage of organisms, such as coralline algae, foraminifera, serpulids, mollusks, bryozoans, and ostracods, was collected from this section, including 121 species associated with the leaves and 57 species associated with the rhizomes. Another Pliocene record of seagrass leaves is from northern Italy (Gregor, 1991).

Two records are not further considered here: a fossil from the late Cretaceous Izumi sandstone in Japan (Koriba and Miki, 1960) that was later doubted to represent a marine angiosperm (Brasier, 1975; Kuo et al., 1989), and an Oligocene record of *Cymodocea* seagrass mentioned by Brasier (1975) that actually refers to the freshwater plant *Cymodoceites* (Chesters et al., 1967).

3.2 Bioimmured Seagrass

Bioimmuration is both the process and the result of the organic overgrowth of an organism by the skeleton of another. This process provides a route by which unmineralized or weakly mineralized taxa may enter the fossil record, in some cases the only means (Todd and Taylor, 1992). In the fossil record, just as today, seagrass provides a substratum for relatively large skeletonized epiphytic organisms, such as encrusting bivalves (e.g., true oysters: Ostreidae). These encrusters, in turn, preserve an external mould of the seagrass, in this example the leaf, on their basal attachment surface. Typically this becomes visible after the seagrass tissue itself disintegrates. This manner of preservation of body fossils has been termed substratum bioimmuration (Taylor, 1990). Because encrusters secrete their skeletons in different ways, the degree of fidelity of the resulting external mould differs between organisms. The most accurate moulders are cementing bivalves, such as oysters, and serpulid worms. Both of these taxa may reproduce a negative with sub-micrometer scale fidelity of the surface they attach to (Todd, 1994). External moulds of seagrass leaves and stems (the latter referred to *Thalassocharis*) bioimmured by the base of encrusting bryozoans (especially cyclostomes) have been described and illustrated from the Maastrichtian (late Cretaceous) of Limburg, the Netherlands (Voigt, 1956, 1981). This assemblage comprised 50 species of bryozoans on stems, roots and leaves preserved by bioimmuration. The growth direction of most colonies was parallel to the axes of the roots and stems, although some were transversely oriented and enveloped the substrate (Voigt, 1981). Other examples of basal surfaces of encrusting bryozoans that bioimmure seagrasses are known from Burdigalian celleporiform bryozoans from India (Reuter et al., 2010) and from attachment surfaces of arborescent colonies belonging to the genera; *Metrarhabdotos, Adeonellopsis, Cigclisula* and *Gemelliporella* from the Mio-Pliocene of the Cibao Valley, Dominican Republic (Cheetham and Jackson, 1996; see 4.6 for more information on bryozoans in seagrass meadows). These external molds may be surprisingly common; Cheetham and Jackson (1996) report their presence on 75% of the basal surfaces of 125 colonies of *Metrarhabdotos* examined. These bryozoans comprised seven species and occurred over 5 million years of deposition.

At best such fossils preserve details of the leaf epidermis and therefore allow confident taxonomic attribution. A good example is the bioimmured epidermal patterns recorded by Cheetham and Jackson (1996: fig. 8.10) that strongly resemble the epidermis of the Recent seagrass *Halodule*. Importantly, when taken together with *Metrarhabdotos*' preferred paleo-bathymetries at the present day, this suggested taxonomic affinity allows one to infer the presence of relatively deep-water seagrass assemblages. However, frequently the encruster's attachment surface is worn or, in the case of cementing bivalves, has been subject to diagenesis so that the thin aragonitic cement layer (so-called Harper Layer) has been lost. In this case a lower resolution mould ('undermould') may be preserved in the underlying outer shell layer of the encruster (Todd, 1993). In these cases unambiguous interpretation of the taxonomic identity of flat 'vegetal' substrates as being of macroalgal or seagrass origin may be difficult (see illustrations in Voigt 1956, 1979). The same accounts for the bioimmuration of seagrass rhizomes by oysters as reported from upper Oligocene deposits of NW Germany (Diedrich, 2008). Such imprints can be conclusive indications of seagrass vegetation, but only if the external mould preserved on a shell can be confidently identified.

4. IPSIs - Taxonomic Groups

4.1 Benthic Foraminiferal Assemblages

The assemblage composition of foraminifera and the occurrence of individual species associated with seagrasses have received considerable attention (e.g., Langer, 1993; Semeniuk, 2001). Worldwide, numerous species (>100) are reported in association with seagrasses. Species numbers per seagrass leaf can be up to 24 (Richardson, 2004), and typical densities range from 14-80 specimens/cm^2 (Richardson, 2000, 2004; Wilson, 1998; W. Renema, unpublished data on various seagrass meadows in Indonesia). Foraminifera inhabit both leaves and exposed rhizomes of seagrasses, which can bear distinctly different communities (Langer, 1993; Ribes et al., 2000). Langer (1993) distinguished between four functional groups of foraminifera in phytal habitats. Those are defined by distinct morphotypes and different life modes, i.e., permanently attached (4.1.1), motile with attachment surface, permanently motile suspension feeders, and permanently motile grazers. All functional groups were found on most types of seagrass and macroalgae (Langer, 1993). For tropical environments, a fifth group is here proposed: motile photosymbiotic foraminifera (4.1.2-3). Interpretations especially of symbiont-bearing, benthic foraminifera assemblages as seagrass-associated are frequently justified by citing only one of a limited number of publications (e.g., Cushman, 1922; Eva, 1980; Langer, 1993, Steinker and Clem, 1984), which is not sufficient for such a general statement. Murray (1970) and Steinker and Steinker (1976) argue that seagrass-associated assemblages are more diverse than assemblages from adjacent non-vegetated habitats. However, as far as we can tell, there are no quantitative analyses that would support this statement. Available comparisons, at most, are restricted to vegetated versus directly adjacent unvegetated environments, and are limited concerning the identified taxonomic levels (Murray, 1970; Scoffin, 1970). Higher species diversity was not confirmed for seagrass-associated foraminifera occurring on reef flats in the Spermonde Archipelago, Indonesia (W. Renema, unpublished data). Furthermore, Ribes et al (2000) found that assemblages on natural and artificial seagrass leaves did not differ significantly, suggesting that foraminifera are mainly attracted to long-lived flat surfaces and do not necessarily depend on seagrasses.

4.1.1 Abundance of Permanently Attached Foraminifera

In modern seagrass meadows: Sessile epiphytic foraminifera are characterized by a comparatively large size, a complex internal structure, and a discoidal shape (e.g., Eva, 1980). Groups that are commonly reported as associated with seagrasses include soritids (*Marginopora*, *Amphisorus*, and *Sorites*), planorbulids (*Planorbulina*), cymbaloporids (*Cymbaloporetta*), nubeculariids (*Nubecularia*), and the acervulinid genus *Gypsina*. Primary sources that report these taxa as more abundant on seagrass leaves compared to other phytal substrates, or even as restricted to seagrasses, are rare. Wilson (1998) found that *Gypsina squamiformis* was the most abundant species living attached to seagrass leaves of *Thalassia* and *Syringodium*. Wilson (2008) found that planorbulinids dominate the biocoenosis on seagrass leaves in Nevis (West Indies), but that they also occur in the thanatocoenosis in sediments outside the studied seagrass meadows. Furthermore, densities of *Sorites* sp. were reported as much higher on seagrass leaves compared to most other substrates (Kloos, 1984; Fujita and Hallock, 1999; Richardson, 2000; W. Renema, pers. obs. on diverse reefs in Indonesia).

Use as IPSI: The above-listed taxa were reported from fossil assemblages interpreted as seagrass- associated (Renema; 2008a; Reuter et al., 2010; O'Connell et al., 2012). Moisette et al. (2007) is the only of these studies in which encrusting foraminifera were actually found still attached to seagrass moulds. Occurrences of *Marginopora vertebralis* in the fossil record have frequently been associated with seagrass environments (e.g., Brasier, 1975; Cann and Clarke, 1993; James and Bone, 2007; O'Connell et al., 2012). However, many of these occurrences include misidentifications due to frequent confusion within the genera *Amphisorus* and *Marginopora*. The genus *Nubecularia* was also reported as IPSI (e.g., Cann et al. 2006; O'Connell et al. 2012).

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: Moderately high. Attached foraminifers have a limited potential for preservation in seagrass-surrounding sediments compared to free-living forms due to their thinner tests (Buchan and Lewis, 2008; Martin, 1986; Martin and Wright, 1988).

Frequency of occurrence: Frequently occurring in modern seagrass environments, moderately frequent in the fossil record.

Habitat restriction: Most permanently attached foraminifera that are common on seagrasses also encrust macroalgae, such as *Halimeda* and *Sargassum*, and occur furthermore on coral rubble covered by coralline algae (Hohenegger, 1994; Renema, 2006; Renema and Troelstra, 2001). Modern *Marginopora vertebralis* has been found on seagrasses, but is more abundant on other shallow marine, exposed substrates (e.g., Lobegeier, 2002; Maxwell, 1968; Ross, 1972), whereas other taxa occur on sand and rubble substrates, sometimes overgrown by macroalgae (Reymond et al., 2011; Great Barrier Reef, Vanuatu: W. Renema, pers. obs.). In addition, Debenay and Payri (2010) found that *M. vertebralis* changed their position from being attached to seagrasses in the warm season, to being mainly attached to macroalgae in the cold season.

Most occurrences of the genus *Amphisorus* are in reefal habitats (Hohenegger, 1994; Renema and Troelstra, 2001; Renema, 2006). However, the occurrence of large ?*Amphisorus* sp. along the West Australian coast is highly localized and associated with seagrass beds. *Sorites orbiculus*, although occurring more frequently on seagrass leaves than on any algae species, is not exclusive to seagrasses (Kloos, 1984; Fujita and Hallock, 1999; Renema 2006; W. Renema, pers. obs.). In a comparison between assemblages of attached foraminifera from *Caulerpa* versus seagrass, Mateu-Vicens et al. (2010) found that the taxonomic composition was similar, but seagrass was inhabited by longer-lived species, such as *Planorbulina mediterranense*. In the same study, *Nubecularia* was more abundant in the *Caulerpa* thanatocoenosis (Mateu-Vicens et al., 2010).

Conclusions: Suggestive IPSI. It is likely that the abundant occurrence of epiphytic encrusters, such as *Planorbulina*, discorbids, and others in fossil assemblages is associated with seagrass vegetation. A high abundance of *Sorites* in a fossil assemblage, although the genus also occurs on macroalgae, is more likely to be associated with seagrass meadows, because seagrasses occur in stands of meters to hundreds of meters, and macroalgae mostly as individual plants. The genera *Marginopora* and *Amphisorus* are weak IPSIs (taxonomic issues: e.g., Gudmundson, 1994; Lee et al., 2004; lacking habitat restriction).

4.1.2 Abundance of Motile Porcelaneous Photosymbiotic Foraminifera

In modern seagrass meadows: The group includes motile forms, such as *Austrotrillina*, peneroplids (e.g., *Peneroplis*), and archaiasinids (e.g., *Archaias*). The latter group is most frequently associated with seagrasses, but modern representatives are also found living on algae or sediment (Fujita and Hallock, 1999). Modern *Peneroplis* was observed attached to seagrass rhizomes (Renema, 2006), but can also be abundant on sandy or algal substrates (Hohenegger, 1994; Renema, 2006).

Use as IPSI: Various papers report porcelaneous photosymbiotic foraminifera as frequently associated with seagrasses (e.g., Brachert et al., 1998; Brandano et al., 2009; Cann et al., 2006; O'Connell et al., 2012; Reuter et al., 2010). For instance, the high abundance of the extinct archaiasanid genus *Pseudotaberina* in Indonesia and India was used to indicate the presence of seagrass vegetation (Renema, 2008b; Reuter et al., 2010). Most of these taxa likely had chlorophytes as photosymbiotic algae and are therefore indicative of shallow, well-illuminated environments (which are also preferred by seagrasses), but may not depend on seagrasses.

Stratigraphic and geographic range: Archaiasinids: Eocene-Recent, circumtropical, most abundant in the fossil record in the Paleogene of the Middle East and the Pliocene of the Caribbean. *Austrotrillina*: early Oligocene-early Miocene, Eurasia (Adams, 1968; Renema 2008b). Peneroplids are scarcely mentioned in literature on fossil larger benthic foraminifera.

Fossilization potential: High.

Frequency of occurrence: Frequently occurring in modern seagrass meadows and in the fossil record.

Habitat restriction: None of the modern taxa included in this group is confined to seagrasses (Fujita and Hallock, 1999; Hallock and Peebles, 1993; Hohenegger, 1994; Renema, 2006). Most taxa (e.g., *Borelis* and *Peneroplis*) have been observed in other environments as or even more frequently than in seagrass meadows (Hallock and Peebles, 1993; Hohenegger, 1994; Renema and Troelstra, 2001; Renema, 2006). Out of three extant taxa of archaiasinids, the optimal habitat of only one, *Archais angulatus*, was found to be in seagrass meadows (Hallock and Peebles, 1993). Furthermore, *A. angulatus* was abundant on seven out of ten epiphytic substrates including five species of macroalgae (Fujita and Hallock, 1999). *Pseudotaberina* is likely to be associated with seagrasses, but the genus is extinct, therefore it is not possible to observe its habitat relation in modern environments.

Conclusions: *Pseudotaberina* is probably the best suggestive IPSI in this group, but only within its very restricted stratigraphic and geographic range. Possibly *Archaias* can be used as a suggestive IPSI when occurring in high abundance.

4.1.3 Abundance of Motile Hyaline Photosymbiotic Foraminifera

In modern seagrass meadows: The group includes for instance calcarinids (*Calcarina*), amphisteginids (e.g., *Amphistegina*), and elphidiids (*Elphidium*), which can be very abundant in seagrass meadows. The spines of calcarinids are adaptations to living attached to phytal substrates by pseudoplasm plugs (Hohenegger, 1994; Renema, 2010).

Use as IPSI: Some species of *Elphidium* (e.g., *E. crispum*) have been found in high abundance on seagrasses, and were therefore used as IPSIs (Betzler et al., 2000; Puga-Bernabéu et al., 2007). Riordan et al. (2012) used the occurrence of *Amphistegina* as an IPSI. We are not aware of any studies that have used calcarinids as seagrass indicators.

Stratigraphic and geographic range: Most of the Cenozoic, circumtropical, apart from calcarininids which are late Miocene-Recent, Indo-West Pacific (Renema, 2010).

Fossilization potential: High.

Frequency of occurrence: Frequently occurring in modern environments and fossil associations. Listed taxa, apart from calcarinids, are among the most abundant fossils in shallow marine environments. Calcarinids are frequent only in the Pleistocene of the West Pacific.

Habitat restriction: In turbid-water reefs near Java some species of *Calcarina* appear to prefer macroalgal stands, and others seagrasses, but this difference is most likely not related to sea grass specific substrate characters (Renema, 2008a). In more oceanic reefs, the same species that are found in seagrass meadows and macroalgal stands have their highest densities on turf algae in high-energy settings (Hohenegger, 1996; Renema, 2006). In addition, the taxonomy of calcarinids is not well understood (e.g., Renema and Hohenegger, 2005; Renema, 2008a). Elphidiids are also hard to identify; *Elphidium* itself is one of the most eurytopic genera and its use as IPSI is restricted to cases where it can be reliably identified to species level. However, even if species-level identifications are possible, the problem remains that at least *E. crispum* occurs abundantly in habitats other than seagrass meadows.

Conclusions: Weak IPSI (taxonomic uncertainty and lacking habitat restriction).

4.2 Specific Growth Forms of Crustose Coralline Red Algae

In modern seagrass meadows: The epiphytic algal community in seagrass meadows is often dominated by red algae in terms of species numbers and biomass (Borowitzka et al., 2006). Red algae encrusting seagrass leaves or stems may preserve a distinct morphology (see below).

Use as IPSI: Crustose coralline red algae were suggested as IPSIs, because the morphology of their attachment surface is influenced by the encrusted substrate, e.g. seagrass leaves (Pusey, 1975). Beavington-Penney et al. (2004) proposed coralline red algae with a flat attachment surface and a ‘hooked’ shape as IPSI. The ‘hooked’ forms were observed in a modern seagrass habitat; they originate when coralline algae grow over the leaf margin. Similar forms have been found in the Eocene of Oman (Beavington-Penney et al., 2004) and the late Miocene of Spain (Sola et al., 2013). In the Mediterranean coralline algae, mainly belonging to the genus *Mesophyllum*, grow attached to *Posidonia* seagrass. They develop relatively large structures, several tens of cm wide, that form a variably complex framework of foliose, contorted ‘branches’. This kind of growth form is likewise found in the Miocene of Spain (Sola et al., 2013). Furthermore, crustose coralline algae can form tubes around stems and leaf axes of seagrasses (Davies, 1970; Sola et al., 2013).

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: Low. Red algae crusts are usually thin and fragile, only the thickest forms have a chance of preservation (Beavington-Penney et al., 2004).

Frequency of occurrence: Frequently occurring in modern seagrass meadows, rare in the fossil record. 'Hooked' and 'tubular' coralline algae crusts occur less frequently than crusts with simple, flat attachment surfaces.

Habitat restriction: Flattened expanses, which are regarded as typical for seagrass-attached algae, also develop through encrustation of other substrates (Woelkerling et al., 1993). 'Hooked' and 'tubular' coralline red algae are more characteristic of seagrasses, but may also occur on other marine macrophytes (Beavington-Penney et al., 2004).

Conclusions: (Highly) suggestive IPSI. 'Hooked' and 'tubular' crustose coralline red algae are good indicators for marine macrophyte vegetation. Their high abundance is likely to be associated with seagrass meadows.

4.3 Abundance of Articulated Coralline Red Algae

In modern seagrass meadows: The abundance of fragments of articulated coralline red algae is often higher in seagrass-associated sediments than in adjacent unvegetated areas (Davies, 1970).

Use as IPSI: A high abundance of articulated coralline red algae was observed in Oligocene-middle Miocene and in late Pliocene-early Pleistocene seagrass facies in Australia (James and Bone, 2007; Lukasik et al., 2000).

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: Low, but higher than for crustose coralline red algae. Articulated coralline algae easily disarticulate, hindering taxonomic identifications (Aguirre et al., 2000). However, the abundance of articulated red algae in general is here considered as IPSI, therefore identifications to lower taxonomic levels are not needed.

Frequency of occurrence: Frequently occurring in modern seagrass meadows, moderately frequent to rare in the fossil record.

Habitat restriction: Not restricted to seagrass meadows. Articulated coralline red algae occur abundantly in a wide range of marine environments including rocky shores and coral reefs (e.g., Benedetti-Cecchi, 2001, Shears et al., 2002).

Conclusions: Weak IPSI. Useful additional facies-character when other indicators are present.

4.4 Occurrence of the Hydroid *Dynamena*

In modern seagrass meadows: The extant hydroid genus *Dynamena* is found as an epiphyte on seagrasses (e.g., Ben Brahim et al., 2010).

Use as IPSI: A single site in the 'Sables Moyens' (middle Eocene, Paris Basin, France) preserves numerous examples of a species of a thecate hydroid, belonging to the genus *Dynamena*, preserved as epibiont bioimmurations (*sensu* Taylor, 1990) in the attachment area of the small ostreid oyster *Cubitostrea cubitus*. This oyster is frequently, but not obligately, cemented via a large amount of its attached valve to flat, strap-like vegetal substrates. A few specimens preserve fine details of venation in the Harper Layer cement, indicating in these cases that the substratum was seagrass rather than macroalgae. As an oyster grew over the substratum its shell and cement engulfed and bioimmured any epiphytes present. The hydroid *Dynamena* is common and occurs on > 25% of substratum bioimmurations (J.A. Todd, pers. obs.), and both its basal stolonal system and its erect branches are preserved, the latter pushed over by the oyster in its direction of growth (Fig. 2; Taylor and Todd, 2001).

Stratigraphic and geographic range: Known from a few horizons from a single site in the middle Eocene (Lutetian). We are not aware of other fossil occurrences of the genus. Currently distributed worldwide.

Fossilization potential: In general low for soft-bodied organisms. Common, at a single site, in part due to the abundance of well-preserved encrusters with large attachment areas.

Frequency of occurrence: Moderately frequent in modern seagrass meadows, rare in the fossil record.

Habitat restriction: Not restricted to seagrass meadows. The genus is abundantly recorded from macroalgae (e.g., Rossi et al., 2000).

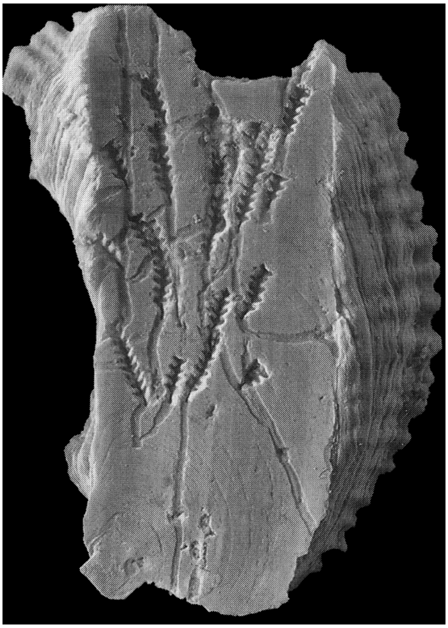

Figure 2: Bioimmuration of *Dynamena* hydroids attached to a seagrass leaf, preserved by the oyster *Cubitostrea*, middle Eocene, Paris Basin (from Taylor and Todd, 2001).

Conclusion: The majority of the substratum bioimmurations at this site (including that in Fig. 2) lack fine surface detail, and despite their suggestive form this obviates their conclusive identification as seagrass. The shared presence of common *Dynamena* and other typical seagrass epiphytes on confirmed seagrass, as well as the less well preserved substrates, suggests that all of the strap-like substrates at this site represent seagrass. This occurrence of bioimmured seagrass epiphytes is currently unique. Pending further discoveries in the fossil record, where the bioimmured epiphyte helps identification of the substratum, such records cannot be regarded as generally useful IPSIs.

4.5 Abundance of Specific Coral Taxa

In modern seagrass meadows: Shallow-water seagrass beds in the Caribbean have a characteristic associated coral community including the free-living *Manicina areolata* and *Siderastrea radians* (Johnson, 1992; Lewis, 1989) as well as attached forms (*Cladocora arbuscula*, *Porites divaricata*). Free-living *Meandrina braziliensis* are found in seagrass meadows off Brazil (Laborel, 1967). In contrast, modern free-living corals in the Indo-West Pacific are commonly found on flat, undisturbed sand flats, often in reef-base or inter-reef environments, and only occasionally associated with rather sparse seagrass vegetation (Fisk, 1983; Hoeksema and Best, 1991; B.W. Hoeksema, pers. comm., 2013).

Use as IPSI: Abundant free-living meandroid corals (*Teleiophyllia*, *Thyasanus*, *Trachyphyllia*, *Placocyathus*) were associated with seagrass vegetation in the Miocene and Pliocene in the Dominican Republic (Budd et al., 1996; Costa et al., 2001). This is supported by the presence of seagrass bioimmured by the basal attachment surface of *Metrarhabdotos* bryozoans (Cheetham and Jackson, 1996; 3.2.) and by occurrences of the snail *Smaragdia viridis* (Costa et al., 2001; 4.7.4).

Stratigraphic and geographic range: Modern *Manicina-Siderastrea-Porites* assemblage*:* middle/late Holocene to Recent, with the exception of *Cladocara arbuscula*: late Pleistocene to Recent, Caribbean. *Meandrina braziliensis*: late Pleistocene to Recent; Brazil (occurred in the Caribbean until ~ 2000 years BP). Fossil *Teleiophyllia-Thyasanus*-*Trachyphyllia*-*Placocyathus* assemblage: Miocene to Plio-Pleistocene, Caribbean. The group largely became extinct during the Plio-Pleistocene turnover of Caribbean reef corals (Johnson et al., 1995, 2008).

Fossilization potential: High.

Frequency of occurrence: Frequent occurrence in modern environments and in the fossil record but only within their limited stratigraphic and geographic ranges.

Habitat restriction: None of the above-listed modern species is restricted to seagrass vegetation (Goreau, 1959). It remains unclear whether or not the Caribbean Mio/Pliocene free-living coral association was confined to seagrass vegetation.

Conclusions: Suggestive IPSI within their limited stratigraphic and geographic ranges, if a reef framework has been inferred to be absent.

4.6 Morphology and Species Composition of Bryozoans

In modern seagrass meadows: Bryozoans colonize leaves and stems as well as exposed rhizomes of seagrasses (see review of seagrass-associated modern and fossil bryozoans: Di Martino and Taylor, 2014). An estimated total of at least 154 bryozoan species has been reported from *Posidonia oceanica* meadows from different parts of the Mediterranean Sea (e.g., Geraci, 1974; Harmelin, 1976; Hayward, 1974). Epiphytic bryozoans on seagrass leaves are photophilous and adapted to the relatively ephemeral nature and flexibility of the substrate with unilaminar encrusting forms predominant (Balata et al., 2007). Encrusting bryozoans often develop small colonies orientated parallel to growth direction of the leaf, whereas bryozoans growing on exposed rhizomes are shade-loving and long-lived (Zabala, 1986). However, the assemblage composition of rhizomes and leaves may change according to depth: rhizomes from shallow sites are often colonized by species otherwise considered characteristic of leaves, whereas shade-loving species characteristic of rhizomes may colonize the leaves in deeper sites (e.g., Geraci and Cattaneo, 1980; Nesti et al., 2009). Over 60 bryozoan species have been reported from seagrass meadows of geographical areas other than the Mediterranean, such as tropical America, Japan and Australia. Many of those develop cylindrical colonies that wrap around seagrass stems (Bone and James, 1993; Davies, 1970).

Use as IPSI: Encrusting bryozoans that preserve external moulds of seagrass leaves on their underside and therefore provide direct evidence of seagrasses are discussed in section 3.2. In addition, bryozoans may perform as IPSIs based on holdfasts (Lukasik et al., 2000). Holdfast morphologies are difficult to identify as seagrass-related and are therefore here considered as indirect indicators. Bryozoans in association with seagrasses are already known from the Maastrichtian (late Cretaceous) of the Netherlands (Voigt, 1981; 3.2). Voigt (1981) described a few distinctive and unusual morphological characters observed mainly on species encrusting seagrass or algae, and not found in species encrusting hard substrates. Seagrasses as bryozoan substrates become more common in the fossil record since the Miocene (Taylor and James, 2013). Vávra (1984) reported a dominance of the cheilostome *Schizoporella geminipora* in a middle Miocene bryozoan association from Poland. The presence of holes on the undersides of the zooids was tentatively interpreted as an adaptation for attaching the colony to seagrass leaves. This species, although extinct, has been used as IPSI (Vávra, 1979). Moissette (2012) listed 58 species of seagrass-associated bryozoans from the late Pliocene of Greece, most of which are extant and occur in present-day *Posidonia oceanica* meadows. Additionally, celleporiform colonies offer evidence for seagrass environments in the tube-like form of the colony, indicating encrustation of an organic stem (Reuter et al., 2010). For instance, *Celleporaria cristata* at the present day grows only on the stems of *Amphibolis*, and its presence in late Pliocene-early Pleistocene carbonates in Western Australia strongly suggests that seagrass was one of the major components of this paleoenvironment (James and Bone, 2007).

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: Low for thin encrusters of leaves, moderate for more robust forms.

Frequency of occurrence: Frequently occurring in modern seagrass meadows, moderately frequent to rare in the fossil record.

Habitat restriction: Voigt (1981) interpreted the cheilostomes *Kunradina bicincta* and *Onychocella spinifera* from the Maastrichtian of the Netherlands as restricted to seagrass habitats. However, Recent encrusting bryozoans show almost no restriction habits. Unilaminar encrusting forms, often found as epiphytes, may also dominate bryozoan associations on hard substrates (e.g., shells, corals and rocks). Likewise, bryozoans growing on exposed rhizomes are similar to the community on hard rocky substrates (Zabala, 1986). Exceptions include: the Mediterranean *Electra posidoniae*, which may be considered as an obligate epiphyte of *P. oceanica* leaves (Gautier, 1952); *Microporella trigonellata*, which has been found exclusively on seagrass leaves in Japan (Kouchi et al., 2006); and the above-mentioned *C. cristata*. *Hagiosynodos tregouboffi* encrusts small gastropods living in *Posidonia* meadows (Gautier, 1952). None of the seagrass-associated bryozoans listed by Moissette (2012) is confined to seagrasses.

Conclusions: The species composition of bryozoans is a weak IPSI, because only a few modern species from different regions are confined to seagrasses (Gautier, 1952; Kouchi et al., 2006). Abundant tube-like bryozoan colonies and holdfast structures perform as highly suggestive IPSIs.

4.7 Mollusks

4.7.1 Species Composition of Bivalves

In modern seagrass meadows: Bivalves occurring in seagrass meadows include taxa with various life modes, such as epifaunal, semi-infaunal and infaunal forms. Infaunal bivalves in seagrass meadows include common and widespread families of suspension and deposit feeders, such as Nuculidae, Carditidae, Cardiidae, Veneridae, and Tellinidae (Brasier, 1975; Davies, 1970; Deehr et al., 2001; Jackson, 1972, Mikkelsen et al,. 1995). Furthermore, chemosymbiotic bivalves, such as Lucinidae and Solemyidae, are often common in seagrass beds (4.7.2). Commonly-occurring epifaunal species include members of the families Arcidae, Mytilidae, Pteriidae, Pectinidae, and Ostreidae. Pinnidae may be present among semi-infaunal bivalves. A comparative study of bivalve death assemblages from modern seagrass meadows versus unvegetated sand flats from San Salvador, Bahamas, suggests a significant difference in species composition between the two neighboring environments (Careres and Reich, in prep.).

Use as IPSI: We are not aware of the previous use of the species composition of bivalve assemblages in itself as IPSI, but bivalves are included when entire mollusk faunas have been used to indicate paleo-seagrass meadows (James and Bone, 2007; Chapter 2). A higher abundance of deposit feeders such as tellinids and nuculids might be expected in seagrass beds compared to neighboring areas. Bivalve assemblages with abundant deposit-feeders are present in the Caribbean since the Pliocene when the food webs in seagrass meadows became commonly detritus-based (Domning, 2001; Leonard-Pingel et al., 2012). In addition, the occurrence of Pinnidae in life-position has been used as IPSI in the early Miocene of the Styrian Basin, Austria (Reuter and Piller, 2011; Reuter et al., 2012). Other more specific cases are discussed below, i.e. the abundance of lucinids (4.7.2), and the bivalve/gastropod ratio (4.7.6).

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: High.

Frequency of occurrence: Highly variable: ranging from frequent to absent in modern seagrass meadows, and therefore in fossil assemblages (4.7.6).

Habitat restriction: An inventory of Recent mollusks living in the Indian River Lagoon, Florida (Mikkelsen et al., 1995) illustrates that seagrass-dwelling bivalves are generally not restricted to this habitat. Of 61 infaunal species recorded in seagrass vegetation only 11 species were found exclusively in seagrass. Each of those was recorded only once or twice. Of 14 epifaunal taxa five species, including all four present species of Pectinidae, were only found associated with seagrass vegetation, suggesting that the additional attachment surface provided by marine angiosperms supports higher species-richness of epifaunal bivalves. Fossil Pinnidae in life position (used as an IPSI by Reuter and Piller, 2011; Reuter et al., 2012), although present in seagrass meadows, also occur in other habitats, such as unvegetated sand and mud bottoms, for instance in the London Clay Formation (early Eocene) of England, and are widespread in Jurassic deposits when no seagrasses existed (Davis and Elliot, 1957; Fürsich, 1980).

Conclusions: The abundance and species composition of seagrass-associated bivalve communities are highly variable, therefore it is difficult to characterize a single association typical for seagrass meadows. However, abundant deposit-feeders and additionally the high abundance of small, potentially epiphytic, epifaunal bivalves may strengthen the argument when other indicators are present. Pinnidae are a weak IPSI (lack of habitat restriction).

4.7.2 Occurrence of Lucinids (and other Chemosymbiotic Bivalves)

In modern seagrass meadows: Lucinidae (e.g., *Anodontia*, *Codakia*, *Lucina* among the larger genera) can be abundant or may even numerically dominate the deeper infauna in seagrass meadows (Barnes and Hickman, 1999; Greenway, 1995; Jackson, 1972; Johnson et al., 2002; Meyer et al., 2008; Mikkelsen et al., 1995; Nakaoka, 2002). Members of the family live in symbiosis with sulfide-oxidizing bacteria and therefore require habitats with high input of organic matter and sufficient oxygen levels (e.g., Glover and Taylor, 2007; Taylor et al., 2011), which also characterizes seagrass meadows on muddy substrates. A mutualistic relationship among seagrasses, lucinids, and their chemosymbionts has been hypothesized: lucinids and their associated bacteria reduce sulfide levels in seagrass beds that otherwise would reach toxic levels, and lucinids profit from the oxygen release of seagrass roots in a sulfide-rich depositional environment (Fisher and Hand, 1984; Van der Heide et al., 2012). Lucinidae were present in 97 % of tropical and 90 % of subtropical seagrass beds investigated by Van der Heide et al. (2012). Other chemosymbiont-bearing bivalves, for instance Ungulinidae (e.g., *Diplodonta*) and *Solemya,* are frequently reported from Recent seagrass meadows as well (Greenway, 1995; Mikkelsen et al., 1995).

Use as IPSI: Lucinids are common in fossil faunas associated with seagrasses (Chapter 2; James and Bone, 2007; Moisette et al., 2007; Reuter et al., 2010). Bretsky (1978) used the presence of lucinid bivalves to support Petta and Gerhard's (1977) interpretation of the Cretaceous Pierre Shale, Colorado, USA, as representing a seagrass habitat. Nowadays it is know that the locality represents a deep-sea methane seep deposit (Kauffman et al, 1996). In a seagrass horizon of the middle Eocene Selsey Formation, southern England, a more diverse lucinid fauna is present than in neighboring horizons, and a species of *Solemya* is fairly frequent, though absent elsewhere in the British Paleogene stratigraphic succession (J.A. Todd, pers. obs.).

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: High.

Frequency of occurrence: Frequent in modern seagrass meadows, especially in the tropics and subtropics, and in the fossil record.

Habitat restriction: Not restricted to seagrass meadows. Lucinids (like other chemosymbionts) occur in a wide range of habitats and can be very abundant in non-seagrass environments, for instance coral reefs or mangrove swamps (Beesley et al., 1998; Glover and Taylor, 2007, and references therein).

Conclusions: Lucinids cannot indicate seagrasses by their mere presence, because they lack habitat restriction. However, if chemosymbiotic bivalves are absent in a well-preserved mollusk assemblage it might rather exclude the assemblage from being a seagrass association.

4.7.3 Species Composition of Gastropods

In modern seagrass meadows: Gastropods are a common and diverse component of the benthic macrofaunal assemblage in seagrass beds, and are often more abundant wwand species-rich in meadows than in other adjacent habitats (e.g., Barnes and Barnes, 2012; Mikkelsen et al., 1995; Sheridan, 1997). The benthic gastropod assemblage commonly includes cerithioideans; for example, several species of cerithiids are reported to be associated with seagrasses (Davies, 1970; Houbrick, 1992; Taylor and Lewis, 1970; Table 1). The only extant diastomatid species, *Diastoma melanoides,* is restricted to seagrass and algal beds in south to west Australia (Houbrick, 1981, 1984; Table 1). Gastropods are also common, or even dominant, as epiphytes in seagrass meadows (Boström and Bonsdorff, 1997; Jackson, 1972; Marsh, 1973). Common epiphytic gastropods include small cerithiodeans in the subfamily Bittiinae that graze on microalgae occurring on seagrasses (Houbrick, 1993; Table 1). *Bittium* and related genera are often reported as significantly abundant or even numerically dominant in seagrass habitats worldwide (Albano and Sabelli, 2011; Greenway, 1995; Marsh, 1976; Mikkelsen et al., 1995; Morgan and Kitting, 1984; Rueda et al., 2009a). The shallow-water species of shallow infaunal gastropods of the families Ringiculidae and Cylichnidae occur predominantly close to seagrass beds (Beesley et al, 1998). Chapter 4 shows that significant differences exist between the compositions of gastropod death assemblages from seagrass-vegetated and unvegetated sand flats at San Salvador, Bahamas, and identified several statistically significant indicator species.

Use as IPSI: The composition of gastropod assemblages as well as the presence and abundance of certain taxa have been commonly used to infer the presence of seagrass meadows (Chapter 2; James and Bone, 2007; Mandic et al., 2012; Reuter et al., 2010). Paleo-environmental interpretations of different seagrass localities in the late Miocene of East Kalimantan are likewise largely based on common gastropod taxa (Chapter 5; Fig. 3).

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: High.

Frequency of occurrence: Frequently occurring in modern seagrass habitats worldwide. Moderately frequent in the fossil record considering that autochthonous assemblages are needed.

Table 1: Gastropod taxa commonly reported from modern seagrass meadows.

Reported life mode	**Taxon**	**References**
Benthic	Trochidae: Cantharidinae, e.g. *Jujubinus*	Barnes and Barnes, 2012; Beesley et al., 1998; Davies, 1970; Rueda et al., 2009a
	Calliostomatidae: *Calliostoma*	Davies, 1970; Rueda, et al. 2009a
	Phasianellidae: *Eulithidium*, *Tricolia*	Barnes and Barnes, 2012; Beesley et al., 1998; Davies, 1970; Reich, submitted
	Cerithiidae spp.	Davies, 1970; Houbrick, 1992; Taylor and Lewis, 1970
	Diastomidae: *Diastoma melanoides*	Houbrick, 1981, 1984
	Strombidae: *Strombus*	Greenway, 1995; Stoner and Waite, 1991; Taylor and Lewis, 1970
	Rissoidae	Barnes and Barnes, 2012
	Columbellidae: e.g. *Mitrella*	Arroyo et al., 2006; Davies, 1970; Greenway, 1995; Rueda et al., 2009a
	Conidae spp.	Taylor, 1971
Infaunal	Ringiculidae: *Ringicula*	Beesley et al., 1998
	Cylichnidae: e.g., *Cylichna*	Beesley et al., 1998
Epiphytic	Trochidae spp.	Nakaoka et al., 2001
	Colloniidae: *Bothropoma*	Zuschin and Hohenegger, 1998; Zuschin et al., 2009
	Neritiidae: *Smaragdia*	see 4.7.4
	Cerithiidae: Bittiinae	Albano and Sabelli, 2011; Greenway, 1995; Houbrick, 1993; Marsh, 1976; Mikkelsen et al., 1995; Morgan and Kitting, 1984; Rueda et al., 2009a
	Cerithiidae: *Cerithium*	Houbrick, 1992; Jackson, 1972; Taylor and Lewis, 1970
	Dialidae: *Diala*	Jernakoff and Nielsen, 1998; Ponder and De Keyzer, 1992; Zuschin and Hohenegger, 1998
	Modulidae: *Modulus modulus*	Houbrick, 1980
	Hydrobiidae: *Hydrobia*	Boström and Bonsdorff, 1997
	Rissoidae: *Rissoina*, *Zebina*	Greenway, 1995

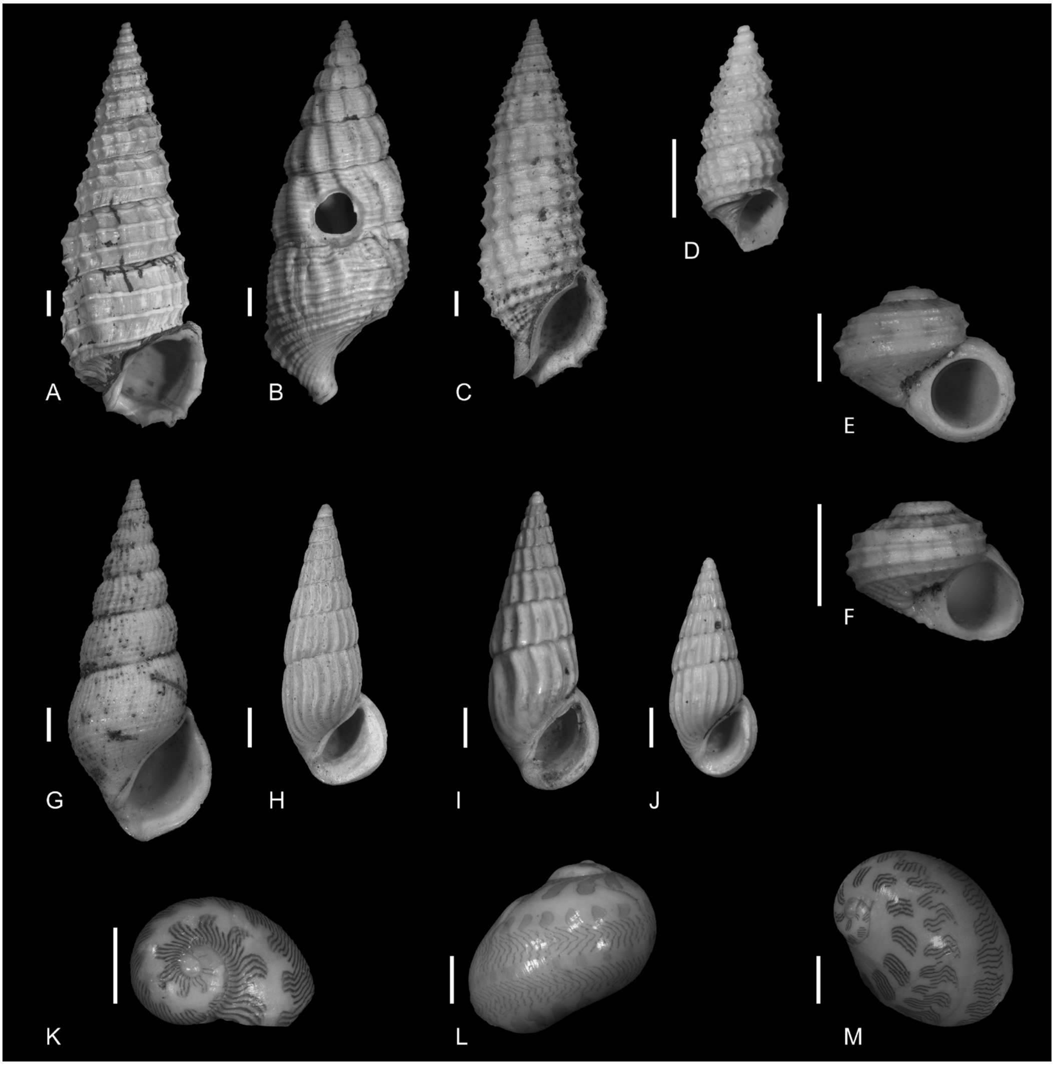

Figure 3: Common seagrass-associated gastropods in the Miocene of Indonesia. A-D) Cerithiidae. A) *Cerithium* sp. 4 (RGM.794.000), locality TF 508, East Kalimantan, Tortonian. B) *Cerithium* sp. 5 (RGM.794.011), locality TF 517, East Kalimantan, Tortonian. C) *Rhinoclavis* sp. 2 (RGM.793.996), locality TF 110, East Kalimantan, Tortonian. D) *Cerithidium* cf. *perparvulum* (RGM.784.758), Java, early Burdigalian. E-F) Collonidae. E) *Bothropoma mediocarinata* (RGM.784.746), Java, early Burdigalian. F) *Bothropoma* sp. 2 (RGM.794.013), locality TF 517, East Kalimantan, Tortonian. G-J) Rissoidae. G) *Rissoina* (*Phosinella*) sp. 1 (RGM.793.997), locality TF 110, East Kalimantan, Tortonian. H) *Rissoina* (*Rissoina*) sp. 2 (RGM.794.008), locality TF 508, East Kalimantan, Tortonian. I) *Rissoina* (*Rissoina*) sp. 5 (RGM.794.012), locality TF 517, East Kalimantan, Tortonian. J) *Rissoina* (*Rissoina*) *banyungantiensis* (RGM.784.843), Java, early Burdigalian. K-M) Neritidae – Smaragdininae. K) *Smaragdia jogjacartensis* (RGM.784.754), Java, early Burdigalian. L) *Smaragdia gelingsehensis* (RGM.793.999), locality TF 110, East Kalimantan, Tortonian. M) *Smaragdia semari* (RGM.794.002), locality TF 508, East Kalimantan, Tortonian.

Habitat restriction: None of the here-listed gastropod taxa (Table 1) is restricted to seagrass meadows. *Bittium*, for instance, also occurs abundantly on macroalgae (Chemello and Millazo, 2002; Leite et al., 2009). The lack of habitat restriction of most gastropods is shown using Mikkelsen et al.'s (1995) inventory of mollusks in the Indian River Lagoon, Florida: of 103 gastropod species (including Sacoglossa and Nudibranchia) that have been recorded in seagrasses, 86 species occurred in at least one additional habitat. The 17 remaining species, including the only obligate seagrass feeder, *Smaragdia viridis* (4.7.4), occurred at low frequencies. Likewise, all indicator species identified in Chapter 2, apart from *S. viridis*, were also reported from non-seagrass habitats.

Conclusions: Suggestive IPSI (lack of habitat restriction). Future studies might reveal that the taxonomic compositions of gastropod faunas yield a characteristic seagrass signal; the ecological composition should be taken into consideration as well (4.7.5).

4.7.4 Occurrence of *Smaragdia*

In modern seagrass meadows: The neritid snail *Smaragdia* is closely associated with seagrass vegetation worldwide (Higo et al., 1999; Kay, 1979; Rueda et al., 2009a; Taylor and Lewis, 1970; Zuschin et al., 2009). Two species, *S. viridis* and the Hawaiian endemic *S. bryanae*, have been demonstrated to be selective feeders on seagrass tissue (Rueda and Salas, 2007; Unabia, 2011). The radular characteristics of the genus, which are different from other neritids, suggest that all other species are obligate seagrass feeders too (Rueda et al., 2009b). In addition, the validity of *Smaragdia* as an indicator taxon for seagrass vegetation is confirmed in Chapter 4 using modern-day associations.

Use as IPSI: As an obligate associate, the genus is a useful IPSI (Unabia, 1980). Its occurrence was applied as an indicator in the Miocene to Pliocene of the Dominican Republic (Costa et al., 2001) and the early Miocene of India and Indonesia (Chapter 2; Reuter et al., 2010; Fig. 3K). The genus also occurs at various localities in the late Miocene of Indonesia (Chapter 5; Fig. 3L-M). *Stratigraphic and geographic range*: Early Miocene-Recent; Indo-West Pacific, Red Sea, West Atlantic (Florida to Brazil, including the Caribbean), East Atlantic (Straits of Gibraltar to Senegal), Mediterranean Sea (based on the geographic distribution of *S. viridis* and *S. rangiana*, the most widespread Recent species; Costa et al., 2001; Dekker, 2000).

Fossilization potential: High.

Frequency of occurrence: Moderately frequent in modern seagrass meadows and in the fossil record.

Habitat restriction: Restricted to seagrass vegetation.

Conclusions: Highly suggestive, especially when occurring in high abundance. In addition, low specimen numbers of *Smaragdia* may indicate the presence of dispersed seagrasses in other shallow marine environments, such as coral carpets (Chapter 3).

4.7.5 Trophic Composition of Gastropod Assemblages

In modern seagrass meadows: Small gastropods grazing on microalgae (e.g., Rissoidae, Cerithiidae, Trochidae, Phasianellidae) have often been reported as most abundant in modern seagrass-associated mollusk communities (e.g., Arroyo et al., 2006; Nakaoka et al. 2001). Taylor (1978) showed that species numbers of predatory gastropods in different habitats at Addu Atoll, Maldives, were higher in seagrass beds compared to adjacent algal-dominated habitats, but lower than in reefal environments. The comparatively high diversity of seagrass-associated organisms (see 1.), including the common occurrence of sessile, filter-feeding organisms, such as sponges, sea anemones and others (Ogden, 1980), may lead to a comparatively high diversity of gastropod feeding ecologies present in seagrass habitats, including parasites and other highly specialized carnivores.

Use as IPSI: The high abundance of small grazers has been often considered as IPSI (Chapter 2; Brasier, 1975; Davies, 1970; Ivany et al., 1990; James and Bone, 2007; Moisette et al., 2007; Moulinier and Picard, 1952; Reuter et al., 2010). Furthermore, the feeding guild composition of whole mollusk assemblages, including herbivorous as well as carnivorous taxa, may be a useful indicator. In view of the high variability in the abundance of infaunal bivalves in seagrass habitats (4.7.6) we suggest that only gastropods should be considered when comparing feeding guild compositions. A comparison of patterns in feeding ecology of fossil mollusk assemblages from different shallow marine habitats has been made in Chapter 3, showing a clear difference between the feeding guild composition of an early Miocene seagrass-associated mollusk fauna (Banyunganti, Java, Indonesia) and a late Miocene fauna from a coral carpet environment (Bontang, East Kalimantan, Indonesia). The seagrass fauna showed a significant difference between the feeding guild compositions based on species richness and based on abundance, whereas no such difference was observed

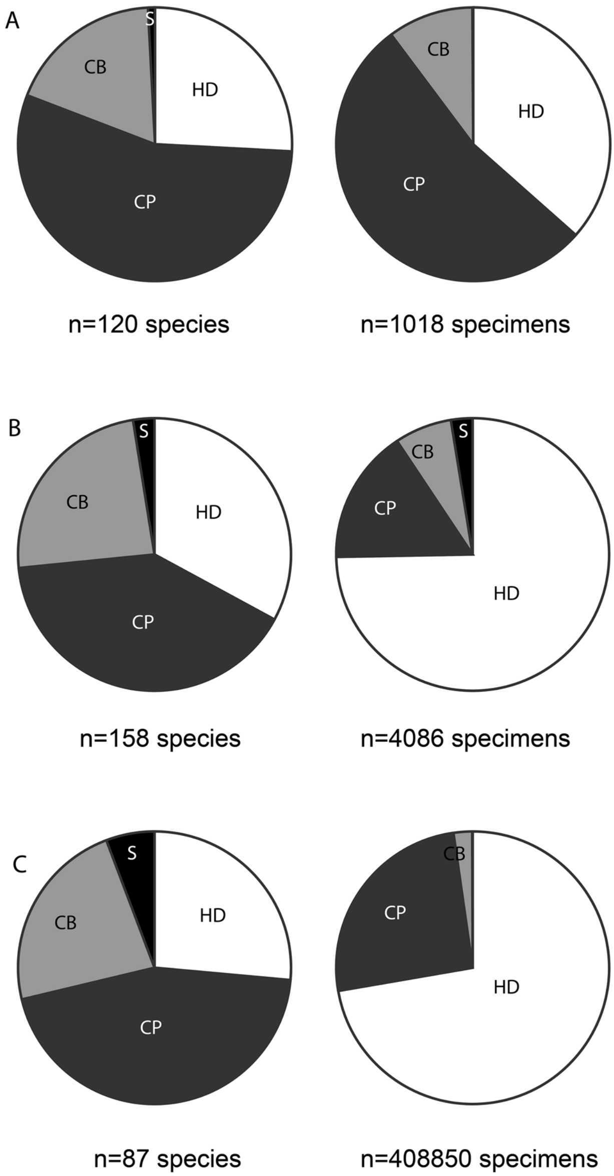

Figure 4: Feeding guild composition of gastropod faunas based on numbers of species (right column) and numbers of specimens (left column). A) Fossil assemblage from a coral-carpet habitat. Late Miocene, TF 102, East-Kalimantan, Indonesia. B) Fossil assemblage from a seagrass meadow. Early Miocene, Banyunganti, Java, Indonesia. C) Modern assemblage from a seagrass meadow. Alboran Sea, Spain (Data from Rueda et al., 2009; nudibranchs removed).

in the coral-associated fauna (Fig. 4A-B). This might be a characteristic feature of seagrass-associated mollusk communities. Gastropods from the Miocene of Java, Indonesia (Chapter 2) and a modern assemblage from Spain (Rueda et al., 2009a) show almost the same feeding guild composition, in terms of both species richness and abundance (Fig. 4B-C), suggesting that a consistent ecological signature of seagrass-inhabiting mollusks may exist both across regions and over larger time-scales. A comparative study of Panamanian Caribbean Holocene and modern mollusk death assemblages showed no significant difference in the trophic ecological composition of seagrass-associated faunas (Fredston-Hermann et al., 2013), likewise indicating that feeding ecology of seagrass-associated mollusks remained constant. Macroalgae-associated mollusk assemblages that are also dominated by herbivores appear to be less diverse in carnivorous gastropods than seagrass-associated assemblages (Leite et al., 2009). Modern gastropod death assemblages from seagrass-vegetated versus unvegetated sandflats at San Salvador, Bahamas (Chapter 4) showed a significant difference in feeding guild composition between assemblages only when measured using species richness, but not using abundance. In this case, this might be due to mixing of shells from different habitats (including seagrass meadows) at unvegetated sandflats, stressing that autochthonous assemblages should be used for this type of study.

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: High.

Frequency of occurrence: Data are not sufficient to make a statement about the frequency of occurrence of a specific feeding guild pattern in seagrass-associated gastropod assemblages. Autochthonous assemblages are needed.

Habitat restriction: A high abundance of herbivorous gastropods is also found in other habitats, for instance in estuarine faunas (Lozouet and Plaziat, 2008), in death assemblages from unvegetated sandflats (Chapter 4), and especially in macroalgae assemblages (Chemello and Milazzo, 2002; Leite et al., 1995). However, studies based on species richness and abundance of all feeding guilds suggest that the ecological composition of gastropod faunas may be characteristic for seagrass environments (Chapter 3; S. Reich, pers. obs.).

Conclusions: Suggestive IPSI. Additional research is needed to confirm the generality of this pattern over space and time.

4.7.6 High Gastropod/Bivalve Ratio

In modern seagrass meadows: Cummins et al. (1995) found that gastropod/bivalve ratios (epifaunal/infaunal ratios) of whole shells from death assemblages sampled at seagrass sites and unvegetated sites in Pigeon Creek, San Salvador Bahamas, were considerably higher in seagrass meadows. This might be due to a reduced food supply for infaunal filter-feeders at densely vegetated sites, because dense vegetation results in reduced near-bottom water flow (Hemminga and Duarte, 2000). Furthermore, dense seagrass vegetation also results in a dense rhizome mat that can inhibit the establishment of an infauna (Davies, 1970; James and Bone, 2007).

Use as IPSI: We are not aware of comparative studies of gastropod-bivalve ratios from different marine paleohabitats.

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: High.

Frequency of occurrence: Moderately frequent. The abundance of infaunal bivalves, and therefore the gastropod/bivalve ratio, varies remarkably between seagrass meadows. Although infaunal bivalves can be entirely absent in some seagrass environments (Davies, 1970), they can be the most abundant mollusk group in others (Taylor and Lewis, 1970), which would result in a low gastropod/bivalve ratio.

Habitat restriction: A study by Jarochowska (2012) at the same locality investigated by Cummins et al. (1995) showed high gastropod/bivalve ratios in various environments, with the highest ratio recorded in mangroves.

Conclusions: Weak IPSI. Probably high gastropod/bivalve ratios at sites that can be identified as seagrass meadows based on other IPSIs can be applied to infer high vegetation densitiy, but additional research is needed to confirm such a relation.

4.8 Species Composition of Ostracod Assemblages

In modern seagrass meadows: Some ostracod species preferentially live on marine macrophytes (Benson, 1961, Frenzel et al., 2005, and references therein; Kamiya, 1988). Kamiya (1988) compared ostracod assemblages associated with different microhabitats in a *Zostera* bed in central Japan, namely the epiphytic assemblage and the assemblage associated with the sandy sediment surface. The studied assemblages contained congeneric taxa, but differed in species composition and in carapace morphology (4.9).

Use as IPSI: The species compositions of ostracod assemblages might offer a good tool for the discrimination of marine vegetated and unvegetated areas (Cronin et al., 2001; Frenzel et al. 2005). A high abundance of epiphytic ostracod genera (e.g., *Aurila*, *Loxoconcha*, *Xestoleberis*, *Hemicytherura*, *Cythere* and *Paradoxostoma*) suggests the presence of nearby seagrass vegetation (M. Yasuhara, pers. comm., 2013). However, most (if not all) of these genera include benthic species living in or on soft sediment as well ass epiphytic species. Epiphytic species can be recognized by carapace morphology (4.9) or known habitat information of each species if available.

Stratigraphic and geographic ranges: *Loxoconcha* and *Xestoleberis*: Cretaceous-Recent; *Paradoxostoma*: ?Cretaceous/Eocene-Recent; *Cythere*: Eocene-Recent; *Aurila* and *Hemicytherura*: Pliocene-Recent (Moore, 1961; Yamaguchi and Goedert, 2010). Each of these genera have a worldwide distribution.

Fossilization potential: High, but lower than for foraminifera and mollusks.

Frequency of occurrence: Frequently occurring in modern seagrass meadows; moderately frequent in the fossil record.

Habitat restriction: In Kamiya's (1988) comparative study, only the dominant *Zostera*-associated species *Loxoconcha japonica* was restricted to seagrass leaves; all other taxa in the epiphytic assemblage occurred on macroalgae as well. Benthic taxa are not confined to any vegetated habitat (Kamiya, 1988).

Conclusions: Suggestive IPSI. Ostracod assemblages largely composed of epiphytic taxa most likely represent phytal environments, although not necessarily seagrass meadows. Due to the occurrence of epiphytic and benthic species within the same genus, it could be difficult to discriminate vegetated from other habitats if identifications at species level are not possible, but carapace morphology can additionally be applied to identify epiphytic taxa (4.9).

4.9 Carapace Morphology of Ostracods

In modern seagrass meadows: In a comparative study of ostracod assemblages from a seagrass meadow in Japan, Kamiya (1988) found that seagrass leaf-associated ostracods differ from substrate-associated congeneric species in carapace morphology. The latter have elongated carapaces with a flat ventral area, whereas epiphytic species have round carapaces with a convex ventral area. The differing morphologies reflect adaptations of copulation behavior of epiphytic species to the unstable nature of the substrate (Kamiya, 1988).

Use as IPSI: Carapace morphology has so far not been applied as an IPSI. Only Yamaguchi and Goedert (2010) suggested that *Loxocorniculum* sp. from the Eocene McIntosh Formation, Washington State, USA, was a dweller in marine macrophytes based on its round ventral margin in lateral view.

Stratigraphic and geographic range: So far only observed in a Recent seagrass meadow in Japan (Kamiya, 1988).

Fossilization potential: High, but lower than for foraminifera or mollusks.

Frequency of occurrence: Frequently occurring in modern seagrass meadows; moderately frequent in the fossil record.

Habitat restriction: Further studies on modern and fossil faunas from different habitats are needed to confirm the general possibility of distinguishing between environments using carapace morphology. It still remains difficult to discriminate epiphytic assemblages from seagrass meadows from those occurring in macroalgae habitats (Frenzel et al., 2005; Rosenfeld, 1979).

Conclusions: Has potential to be a useful suggestive IPSI, at least for marine macrophyte vegetation. An advantage may be that non-specialists on ostracod taxonomy perhaps will be able to identify epiphytic assemblages in the fossil record based on carapace morphology.

4.10 Abundance and Occurrence of Specific Taxa of Echinoderms

In modern seagrass meadows: Common echinoderms in seagrass meadows include the regular echinoid genera *Diadema*, *Tripneustes*, *Lytechinus*, *Toxopneustes*, the irregular *Clypeaster*, and deposit-feeding holothurians (Brasier, 1975). Some echinoids (e.g., *Lytechinus variegatus*) graze extensively on seagrass material, occasionally resulting in defoliation and loss of entire seagrass patches (Larkum and West, 1990; Valentine and Heck, 1991).

Use as IPSI: Bałuk and Radwański (1977) mentioned, among other indicators, the abundance of echinoid and holothurian remains in general, as well as the echinoid genus *Echinocyamus* and free-living comatulid crinoids of the *Antedon* type in particular, as characteristic for seagrass vegetation in the Miocene of Poland. Ivany et al. (1990) reported the high abundance of juvenile echinoderms (ophiuroids, oreasterid asteroids, and regular echinoids) in a seagrass bed in the Eocene of Florida.

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: Moderately high. Often only fragments, spines and disarticulated plates are found (Greenstein, 1991; Kier, 1977).

Frequency of occurrence: Moderately frequent in modern seagrass meadows and in the fossil record.

Habitat restriction: The echinoid *Lytechinus variegatus*, although abundant in modern seagrass meadows, also occurs on rocks and open sandflats (Greenway, 1995; Moore et al., 1963). Studies on modern *Echinocyamus* species show a preference for coarse-grained sediments in high-energy settings (Telford et al., 1983). *Echinocyamus crispus* is reported as rare in seagrass beds, but abundant in other habitats (Nebelsick and

Kowalewski, 1999). Studies on modern *Antedon* species show affinities to types of environments other than seagrass meadows, such as soft-corals on rocky walls (Fishelson, 1974).

Conclusions: Weak IPSI (lack of habitat restriction; even taxa characteristic of modern seagrass meadows are not restricted to the environment).

4.11 Otoliths (of Juvenile Sciaenids)

In modern seagrass meadows: Fish are abundant and species-rich in seagrass meadows. The habitat also serves as an important nursery habitat for juvenile fish (Hemminga and Duarte, 2000, and references therein).

Use as IPSI: Green (2002) used the presence of sciaenid otoliths of primarily 2-4 mm size as an additional character for the interpretation of the Eocene Moody's Branch Formation, Louisiana and Mississippi, USA, as a seagrass habitat. For sciaenids the predominant otolith size in the studied assemblage is small and indicates the presence of juveniles (Waessle at al., 2003).

Stratigraphic and geographic range: Eocene-Recent; worldwide.

Fossilization potential: Generally high for otoliths.

Frequency of occurrence in the fossil record: Moderately frequent to rare.

Habitat restriction: Although often most abundant in seagrass meadows, juvenile sciaenids in the Gulf of Mexico were also observed in unvegetated areas and, sometimes abundantly, along the edge of marshes (Neahr et al., 2010). Little habitat selection was observed for adult specimens.

Conclusions: Weak IPSI. May offer additional indication in combination with stronger IPSIs.

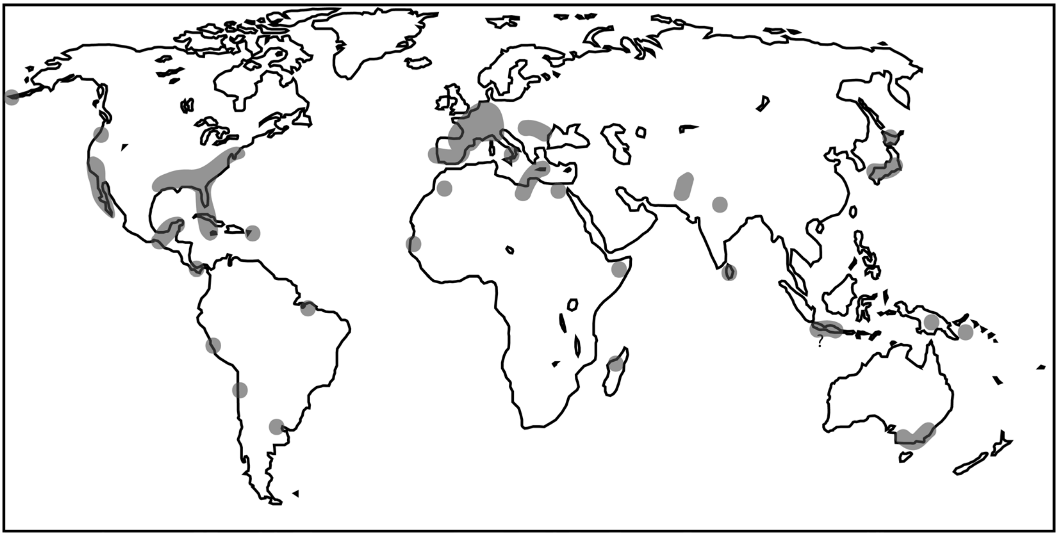

Figure 5: Worldwide distribution of fossil prorastomid, protosirenid and dugongid findings (after Domning, 1996).

4.12 Occurrence of Prorastomid, Protosirenid and Dugongid Remains

In modern seagrass meadows: Sirenians (dugongs and manatees) are the only extant herbivorous marine mammals (Domning, 2001). Dugongs predominantly feed on marine angiosperms, although algae may be used to supplement limited seagrass supply (MacFadden et al, 2004). Manatees feed on a variety of plants, including freshwater plants and true grasses, and occur in a wider range of habitats than dugongs (Ames et al., 1996; Domning, 1982). Sirenians have been extensively studied and much more data on their ecology and evolution is available (e.g., Domning, 1981, 2001; Marsh et al., 2011).

Use as IPSI: Because of the high dependence of modern dugongs on seagrasses as a food source, their fossil remains are considered as IPSIs (Domning, 1981, 2001; Ivany et al., 1990; Veléz-Juarbe, 2013; Vélez-Juarbe et al., 2012). Sirenian remains in association with fossilized seagrasses are known from the Eocene of Florida (Domning et al., 1982; Ivany et al., 1990). Seagrass herbivory of extinct dugongids and protosirenids from the middle Eocene onwards has been inferred from dental and rostral features, particularly a high angle of rostral deflection (Domning, 1977). Furthermore, the large tusks of some species are regarded as an adaptation for harvesting seagrass rhizomes (Domning and Beatty, 2007). Seagrass herbivory is also supported by isotopic evidence on teeth of prorastomids, protosirenids and dugongids, including records from the middle to late Eocene of Egypt and France (Clementz et al., 2006), the middle Eocene to Pliocene of the Tethys-Mediterranean (Clementz et al., 2009), and the middle Eocene to Pliocene of Florida (MacFadden et al, 2004).

Stratigraphic and geographic range: Middle Eocene-Recent. The distribution of prorastomid, protosirenid and dugongid fossils is shown in Figure 5. It should be noted that their fossil occurrences are concentrated in the Caribbean and Europe and are comparatively scarce around the Indo-Pacific. That might reflect a pattern of search effort. Today dugongs live only in coastal areas of the (sub)-tropical Indo-Pacific, whereas manatees inhabit the (sub)tropical Atlantic and Caribbean.

Fossilization potential: High compared to other mammals because of dense bone structure (Vélez-Juarbe, 2013).

Frequency of occurrence in the fossil record: Moderately frequent to rare, depending on region (Fig. 5).

Habitat restriction: Although dugongids largely rely on seagrasses as their primary food source, they are active swimmers and therefore not strictly confined to seagrass meadows. Because of their wider habitat and food range, the interpretation of manatees as seagrass-associated should be regarded with caution.

Conclusions: Not strictly associated with seagrass facies, but strongly suggestive for the presence of paleo-seagrass beds within a region. Particularly useful in time intervals and regions where records of seagrass remains and/or other IPSIs are lacking (Vélez-Juarbe, 2013).

5. IPSIs – Sedimentology, Taphonomy, and Geochemistry

5.1 Occurrence of Unsorted Fine Sediments

In modern seagrass meadows: Sedimentological features of seagrass meadows are linked to the ability of seagrasses to baffle currents and trap and stabilize sediments. Reduced re-suspension promotes the accumulation of fine-grained sediments, partly sourced from the in-habitat production of skeletal carbonate (Scoffin, 1970; Nelsen and Ginsburg, 1986; Fornos and Ahr, 1997). As observed in seagrass meadows in the Mediterranean, seagrass-associated sediments are usually poorly sorted, with abundant silt, carbonate mud and coarse skeletal components, typically of carbonate-producing invertebrates and foraminifera (Fornos and Ahr, 1997). In contrast, sediments that surround the seagrass meadow are sorted and display sedimentary structures (Fornos and Ahr, 1997). In addition, the selective concentration of sediment can result in the formation of low mounds that are elevated compared to the unvegetated seafloor (Pérès and Picard, 1964). However, there are other examples of seagrass beds in sub-tropical and temperate seas, where a dense vegetation cover does not promote the deposition of muddy sediment. This occurs where carbonate mud production is low and does not balance sediment re-suspension (Perry and Beavington-Penney, 2005).

Use as IPSI: The presence of unsorted fine grained sediments with surrounding higher-energy deposits may indicate the former presence of a seagrass meadow (Davies, 1970; Scoffin, 1970). Such sedimentological features were interpreted as seagrass facies in late Miocene inner carbonate ramp deposits in the Balearic Islands, Spain (Pomar, 2001). Poorly-defined, undulated bedding in bryozoan-bivalve floatstone to rudstone in the late Miocene of southern Spain was likewise interpreted as a result of a mounded seafloor due to seagrass vegetation (Betzler et al., 2000).

Habitat restriction: Sedimentary features such as grain size and sorting depend on various parameters (depth, energy, etc.) and cannot be regarded as restricted to any habitat.

Conclusions: Weak IPSI, but a useful additional facies-character when other indicators are present.

5.2 Fining-Upward Sequences

In modern seagrass meadows: Wanless (1981) described fining-upward sedimentary sequences in a modern, very shallow (1-2 m depth) seagrass setting off Florida. Those are generated by the seaward migration of blowout structures; crescent-shaped, grass-free depressions within seagrass meadows that formed under increased wave-action (*sensu* Patriquin, 1975).

Use as IPSI: Wanless (1981) suggested the application of characteristic fining-upward sedimentary sequences as IPSI. However, we are not aware that they actually have been used to identify paleo-seagrass meadows.

Frequency of occurrence: Moderately frequent in modern seagrass meadows: The formation of fining-upward sequences is restricted to predominately clastic settings, and mainly occurs in shallow environments that are exposed to wave and current action (Wanless, 1981). Fining-upward sedimentary sequences are frequent in the fossil record, but no information is available on the occurrence of strictly seagrass-associated fining-upward sequences.

Habitat restriction: Not restricted to seagrass meadows. Fining-upward sedimentary sequences are generated by changes in depth, energy, or distribution of depositional systems.

Conclusions: Weak IPSI. Fining-upward sequences are common in many sedimentary contexts. Additional facies-character for seagrass environments when other indicators are present.

5.3 Abundance of ‘Constructive’ Micrite Envelopes

In modern seagrass meadows: Reduced energy conditions and the high supply of organic material in seagrass environments create favorable conditions for the formation of so-called ‘constructive’ micrite envelopes that occur on carbonate grains and are associated with biofilms comprising mucilage, cyanobacteria, bacteria, and diatoms (Perry, 1999).

Use as IPSI: The high abundance of carbonate grains with distinctive ‘constructive’ micrite envelopes is considered to be a useful IPSI (Perry, 1999). Such envelopes have also been identified in a seagrass facies in the Eocene of Oman (Beavington-Penney et al., 2004).

Fossilization potential: High.

Frequency of occurrence: Moderately frequent to rare. Besides their being restricted to carbonate environments, high levels of water energy may prevent the development of micrite envelopes in seagrass environments with otherwise favorable conditions (Jarochowska, 2012).

Habitat restriction: 'Constructive' micrite envelopes do occur in other low-energy environments as well, but they are less abundant and thinner than in seagrass beds (Perry, 1999).

Conclusions: Highly suggestive IPSI when very abundant.

5.4 Taphonomic Signature of Skeletal Remains

In modern seagrass meadows: The taphonomic signature of skeletal remains includes all alterations a shell or test has undergone after death, for instance fragmentation, abrasion, and bioerosion. Leonard-Pingel (2005) studied the taphonomic signatures of mollusk shells from seagrass versus beach environments in different modern situations at the Bahamas, Florida and Mexico. She found that the best taphonomic characters to discriminate between the two environments were a combination of edge-rounding, abrasion, dissolution and fragmentation. Seagrass-associated shells were typically characterized by comparatively low rates of edge-rounding and abrasion, and comparatively high rates of bioerosion. Buchan and Lewis (2008) performed a study on benthic foraminifer tests from modern sites with different seagrass density. They found that dense vegetation protects the tests, resulting in higher densities, lower numbers of broken tests, and higher rates of grain cementation at densely vegetated sites. In Chapter 4 it was likewise concluded that mollusk shells sampled from seagrass meadows are less affected by taphonomic alteration than shells from unvegetated sandflats due to the protective nature of seagrasses, especially at densely vegetated sites.

Use as IPSI: Leonard-Pingel (2005) included fossil, presumably seagrass-associated mollusk assemblages from Louisiana, USA (late Eocene) and Panama (Pleistocene) in the above-described study. Based on an evaluation of taphonomic signatures, both assemblages were assigned to seagrass environments, but high error rates preclude those results from being truly significant (Leonard-Pingel, 2005). Miocene seagrass-associated shell assemblages from siliciclastic environments in Indonesia are characterized by high rates of fragmentation, but very low rates of edge rounding and abrasion, with exceptionally well-preserved details of the ornament (Fig. 3; Chapter 2).

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: High.

Frequency of occurrence: Frequent (applicable for all environments with preserved mollusk assemblages).

Habitat restriction: Not restricted to seagrass meadows (Leonard-Pingel, 2005).

Conclusions: Weak IPSI; a seagrass-specific taphonomic signature does not exist. Useful for additional support, if other IPSIs are present.

5. 5 Root Etchings on Shells

In modern seagrass meadows: Unlike macroalgae, seagrasses have real roots and rhizomes. When in contact with shells, marginal dissolution may occur due to locally corrosive pore waters caused by the plant’s metabolism (Parsons and Brett, 1991). Root etchings are distinctive features that consist of fine, chalky, sometimes branched lines, and can be distinguished from carbonate crusts that originated from algae-induced precipitation (Cutler, 1995).

Use as IPSI: The oldest published record of shell etchings we are aware of is from the middle Miocene of Poland (Bałuk and Radwański, 1977). However, root etchings have also been observed on bivalve shells from the Miocene Choptank and Calvert Formations, Maryland, USA and from the Lutetian (early Eocene) Calcaire Grossiere of the Paris Basin, France, housed in the collections at University of Rochester, USA (J. Cottrell, pers. comm., 2014).

Stratigraphic and geographic range: The oldest record is possibly from the early Eocene (see above), but root etchings might potentially be present since the late Cretaceous, worldwide.

Fossilization potential: High.

Frequency of occurrence: Rare compared to other taphonomic signatures.

Habitat restriction: Restricted to seagrass meadows.

Conclusions: Conclusive IPSI, if reliably identifiable.

5.6 Presence of Root Casts

In modern seagrass meadows: Root casts are calcified structures that originate due to the transport of nutrients towards roots during transpiration. By this means Ca-cations may accumulate in and around the roots, leading to the formation of $CaCO_3$ and the preservation of the root shape (Cramer and Hawkins, 2009).

Use as IPSI: Froede (2012) used seagrass root casts, preserved in the late Holocene of Florida, as an indicator for sea-level highstand.

Stratigraphic and geographic range: Only published from the Holocene of Florida, but potentially present since the late Cretaceous, worldwide.

Fossilization potential: Low.

Frequency of occurrence: Rare in the fossil record.

Habitat restriction: Restricted to seagrass meadows.

Conclusions: Conclusive IPSI if provided that the preserved structures can be distinguished from other roots, e.g. from mangroves or marsh plants (Froede, 2012).

5.7 Carbon Isotope Signals of Mollusk Shells

In modern seagrass meadows: Seagrasses are characterized by comparatively enriched δ^{13}C values of typically -10 to -11‰ (Hemminga and Mateo, 1996; Smith and Epstein, 1971), especially in the tropics. Seagrass meadows are highly productive ecosystems and store a considerable amount of their net primary production within the habitat (Duarte and Cebrián, 1996; Duarte and Chiscano, 1999), resulting in enriched δ^{13}C values of sedimentary organic carbon in modern seagrass beds (-9.8 to – 14‰, in contrast to -20‰ in other marine sediments; Fry et al., 1977, and references therein).

Use as IPSI: A study of the potential value of stable carbon and oxygen isotope ratios of fossil mollusk shells as indicators for paleo-seagrass habitats has been recently made (Chapter 5). Carbon isotopic signals were able to discriminate paleo-seagrass environments from coral-dominated environments within the same region and time frame. Shells from seagrass environments had enriched carbon isotopic values of 2‰ on average; shells from other habitats had values < 1‰.

Stratigraphic and geographic range: Applicable for all time intervals and regions.

Fossilization potential: Moderately high. Chemically unaltered shells are needed for this type of study.

Frequency of occurrence: Data are not sufficient to investigate how frequently enriched carbon values occur in modern and fossil seagrass habitats. However, this signature is not conclusive, because seagrass-associated shells may be comparatively depleted in ^{13}C due to freshwater or light organic carbon input (Lin et al., 1991; Simenstad and Wissmar, 1985).

Habitat restriction: Data are not sufficient to support the existence of a seagrass-specific carbon isotope signature of mollusk shells. Although shells from modern marine settings lacking seagrass vegetation commonly display depleted δ^{13}C values >

1‰, exceptions with values > 2‰ can be found in shallow marine settings (Keith et al., 1964).

Conclusions: Weak IPSI, but can offer additional support of environmental interpretations, if material from different environments of the same region and time interval is available for comparison.

5.8 Molecular Fossils of Seagrass Biomolecules

In modern seagrass meadows: Biological molecules of different organisms differ chemically, for instance concerning the structure of the carbon skeleton (e.g., the lengths of carbon chains). This is also the case for seagrass leaves, for which it was demonstrated that their outer membrane differs chemically from that found in terrestrial higher plants (Eglington and Hamilton, 1963; Frewin, 1993 in De Leeuw et al., 1995). Because seagrass meadows may cover large areas of 100s of m^2 and store a high amount of organic carbon within the habitat, their specific organic compounds may contribute considerably to the sediments accumulated in a meadow (Duarte and Cebrián, 1996; De Leeuw et al., 1995).

Use as IPSI: A small percentage of biologically derived organic matter (0.1 to 1%) gets selectively preserved in the sedimentary record, and therefore differs from the composition of organic compounds in living organisms (De Leeuw et al., 1995). Those preserved organic compounds can be used as so-called molecular biomarkers to indicate paleoenvironmental conditions using methods outlined in De Leeuw et al. (1995). Molecular fossils of seagrass-specific biomolecules are higher-plant long-chain α,ω-dicarboxylic acids (C_{26}-C_{28}), and in the case of *Zostera marina* from temperate regions a specific series of α,β-diOH-fatty acids (Frewin, 1993; De Leeuw et al., 1995; Nichols and Johns, 1985; Nichols et al., 1982). Frewin (1993 in De Leeuw et al., 1995) detected the presence of seagrasses in the lower section of a Holocene core from Florida Bay, USA, based on the presence of long-chain carbon molecules, whereas the upper part of the core was characterized by shorter carbon chains attributed to mangrove vegetation. Sonshine (2012) reconstructed the eelgrass-derived organic carbon input in sediments of Maquoit Bay and Casco Bay, Maine, USA, over the past

50 years. Furthermore, the relative abundance of *n*-alkane lipid biomarkers was confirmed as an indicator for seagrass-derived organic matter in modern settings (e.g., Hernandez et al., 2001; Kennedy et al., 2010).

Stratigraphic and geographic range: We are not aware of studies of seagrass-derived biomolecules in sediments older than Holocene. Occurring worldwide.

Fossilization potential: Higher-plant long-chain acids found in leaf waxes appear to remain constant over time (Huang et al., 1996; Logan et al., 1995; Pancost and Pagani, 2006). However, their preservation in sediments, disconnected from preserved plant remains, depends on factors such as sedimentation rate and nature of different lipids and different plant species as studied for Miocene lacustine sediments (Huang et al., 1996; Logan et al., 1995). Plant fossils were still present in the sediments investigated in the latter studies.

Frequency of occurrence: Occurring in all seagrass meadows.

Habitat restriction: Although lipid biomarkers from seagrass leaves can be distinguished from lipids derived from a number of other organism groups, such as terrestrial higher plants (e.g., Eglington and Hamilton, 1963), they are not strictly confined to seagrasses (J.W. De Leeuw and R.D. Pancost, pers. comm., 2014). Studies in modern settings use two- or three-endmember mixing models to infer the percentage of seagrass organic carbon, and exclude (for instance) the contribution of marsh plants (e.g., Kennedy et al., 2010; Sonshine, 2012).

Conclusions: A set of methods to identify seagrass-derived biomolecules in the geological record has not yet been established (Sonshine, 2012). Further research in this field is required before a generally useful IPSI can be characterized. However, biomarkers cannot be applied as an indicator independent of other IPSIs (J.W. De Leeuw and R.D. Pancost, pers. comm., 2014).

6. Discussion and Conclusions

The strength of an IPSI is context-dependent. We have yet to find an IPSI that can provide straightforward identification of paleo-seagrass habitats on a global scale throughout the stratigraphic range of seagrasses and that is common in the fossil record. However, tropical paleo-seagrass meadows are likely to be easier to identify than those occurring in temperate regions, because some IPSIs (e.g., photosymbiotic foraminifers, corals, and 'constructive' micrite envelopes) are restricted to the tropics.

The frequency of occurrence of an IPSI in the fossil record is related to its fossilization potential. In theory, when characterizing an ideal IPSI, preservation potential and frequency of occurrence play important roles. However, in practice, a researcher aiming to characterize a paleohabitat will work with the available material regardless of its state of preservation or its general frequency of occurrence. The better the preservation, the more likely is a reliable interpretation, because poor preservation may preclude the identification of fossils to the required taxonomic level.

A common problem is that many IPSIs are not restricted in their occurrence to seagrass meadows. Taxa that commonly occur in modern-day seagrass habitats have often been used to infer paleo-seagrass meadows without taking into consideration that they may be equally abundant in other habitats. This concerns, for instance, the presence of various foraminifera (e.g., *Elphidium*), mollusks and echinoids. Similarities occur particularly between seagrass associations and macroalgal associations. Relatively poorly-preserved substrate bioimmurations may not contain enough information to conclusively identify the systematic affinities of the vegetal substrate (J.A.Todd, pers. obs.). Therefore, caution must be observed in inferring that strap-shaped 'vegetal' substrates are indeed seagrass leaves. A high abundance of certain IPSIs, such as specific foraminifera or 'hooked' red algae, is more likely to indicate seagrass meadows, because seagrasses occur in dense stands of meters to hundreds of meters in diameter, but macroalgae mostly occur as individual plants, with a few exceptions such as kelp forests. In conclusion, all IPSIs should be thoroughly checked for their habitat restriction when aiming to identify seagrass vegetation in the fossil record. A high abundance in modern seagrass habitats is not sufficient to qualify them as strong IPSIs.

Table 2 provides the here proposed classification of IPSIs, divided into strong (conclusive or highly suggestive), suggestive, and weak indicators. This classification is only intended to be a practical guide reflecting our current understanding.

Conclusive IPSIs are those that document the presence of seagrasses by preserving imprints, etchings, or casts of roots, rhizomes, stems, or leaves. These IPSIs have in common that they are rare in the fossil record and represent structures that can be difficult to distinguish from structures related to other plants. Suggestive IPSIs are most reliable for identifying seagrass meadows in the fossil record when a combination of at least two indicators can be applied. They also strengthen the interpretation in combination with highly suggestive IPSIs. Weak IPSIs may always be used to additionally support a seagrass interpretation when other indicators are present, but are not independent indicators for paleo-seagrass. Furthermore, they can be useful for an additional characterization of paleo-seagrass meadows. For instance, a high gastropod/bivalve ratio and a low abrasion rate of shells suggest a dense vegetation cover; abundant lucinid bivalves and comparatively high carbon isotope ratios point to a high organic content; and abundant juvenile organisms confirm the use of seagrass meadows as nursery habitats in the past.

In conclusion, the more numerous the IPSIs present are, the stronger is the argument for the presence of a paleo-seagrass meadow. In previous works a combination of IPSIs was often applied to infer seagrasses. For instance, a paleo-seagrass bed in the early Miocene of India was identified based on foraminifera, lucinids, gastropods, tube-like bioimmurations of bryozoans, and sedimentological features (Reuter et al., 2010). An early Miocene seagrass locality in Java, Indonesia could be identified according to foraminifera and mollusks (including feeding guild composition); the paleoenvironment was later confirmed using the carbon isotope signal of mollusk shells (Chapter 2 and 5). Seagrass facies in the Plio/Pleistocene of Australia were identified based on foraminifera, coralline algae, bryozoans, mollusks (including lucinids), and sedimentological features (James and Bone, 2007). In conclusion, an integrative approach of sedimentology, paleontology, paleoecology, taphonomy, and (if possible) geochemistry is preferable when characterizing potential seagrass facies and fossil associations.

Mollusks represent the organism group providing the most various IPSIs, including indicator species, taxonomic and ecological composition of assemblages, bioimmuration, and carbon isotopic signals of shells (Table 2). All together, one conclusive, one strongly indicative, two suggestive, and seven weak IPSIs are provided by mollusks. They have a high preservation potential, are abundant in seagrass environments, and are common in the fossil record. Therefore, mollusks are a useful group to identify seagrass vegetation in the geological record. Likewise, foraminifera are abundant and commonly preserved organisms in seagrass meadows. A combination of fossil mollusk and foraminiferal faunas that can be interpreted as seagrass-characteristic provides a good suggestive IPSI. Both organism groups are often common and comparatively diverse in fossil assemblages and therefore offer an excellent first approach for paleohabitat interpretations.

Table 2: Classification of IPSIs.

Direct seagrass indicators	
Plant fossils	
High-resolution bioimmurations of seagrasses	
Strong IPSIs	
Conclusive IPSIs	Highly suggestive IPSIs
Rhizome imprints preserved by oysters Root casts	Abundance of tube-like encrustaions of coralline algae and bryozoans
Root etchings on shells	Abundance of ‘hooked’ crustose coralline red algae
Seagrass specific biomolecules	Occurrence of *Smaragdia*
	Occurrence of prorastomid/protosirenid/dugongid remains
	Abundance of constructive micrite envelopes
Suggestive IPSIs	
Low-resolution bioimmurations (undermoulds) of leaf like structures	
Abundance of permanently attached foraminifera (*Planorbulina*, *Sorites*)	
Abundance of motile porcelaneous photosymbiotic foraminifera (*Pseudoteberina*, *Archais*)	
other specific growth forms of crustose coralline red algae	
Species composition of coral associations	
Species composion of gastropod assemblages	
Feeding guild composition of gastropod assemblages	
Species composition of ostracod assemblages	
Carapace morphology of ostracods	

Table 2 (continued): Classification of IPSIs.

Weak IPSIs (Additional characters)
Abundance of permanently attached foraminifera (*Marginopora*, *Amphisorus*)
Abundance of specific hyaline foraminifera
Abundance of articulated coralline red algae
Occurrence of ‘*Dynamena*’
Species composition of bryozoans
General species composition of bivalves (abundant deposit-feeders)
Pinnidae in life position
Occurrence of lucinids (and other chemosymbiotic bivalves)
High gastropod/bivalve ratio
Abundance of small epifaunal bivalves
Species composition and occurrence of specific echinoderm taxa
Otoliths (of juvenile sciaenids)
Occurrence of unsorted fine sediments
Fining-upward sequences
Taphonomic signature of shells
Carbon isotope signals of mollusk shells
Molecular fossils of seagrass biomolecules

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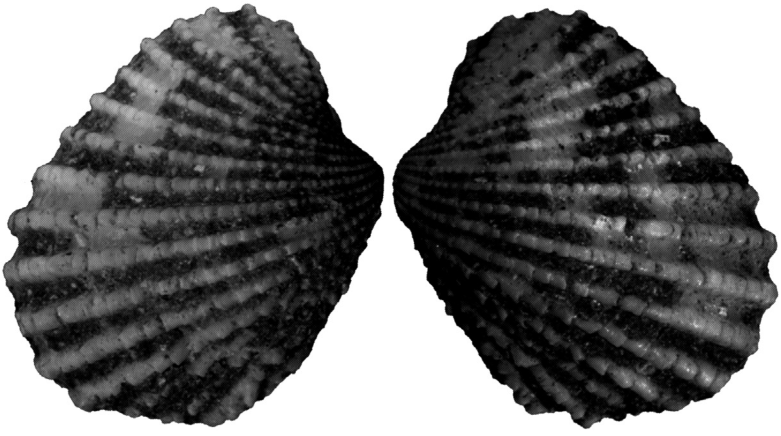
Section 1

Mollusk Assemblages from the Miocene of Indonesia



Chapter 2

A Highly Diverse Molluscan Seagrass Fauna from the Early Burdigalian (Early Miocene) of Banyunganti (South-Central Java, Indonesia)

with 20 plates

Sonja Reich, Frank P. Wesselingh and Willem Renema

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Keywords: biodiversity, faunal composition, Gastropoda, Bivalvia, new species, Indo-Pacific, Miocene

Abstract

The faunal composition of an early Miocene shallow marine mollusk fauna from South-central Java (Indonesia) is investigated. Age determination is based on the accompanying assemblage of large benthic foraminifera. The mollusk fauna includes 184 species represented by 4,424 individuals of which 159 species (4,081 individuals) are gastropods. In species numbers the fauna is dominated by carnivorous gastropods, but herbivorous gastropods, including grazers and detritivores, dominate in terms of abundance. The ecological composition as well as the presence and abundance of certain gastropod taxa (*Smaragdia*, *Bothropoma*, Bittiinae) points to seagrass environments. The excellent preservation of the material hints to relatively low energetic depositional conditions. The mollusk taxa are briefly characterized and/or discussed. Four gastropod species, *Bothropoma mediocarinata*, *Plesiotrochus hasibuani*, *Rissoina* (*Rissoina*) *banyungantiensis*, and *Rissolina reticuspiralis*, are described as new.

1. Introduction

The Progo Mountains west of Yogyakarta (Java, Indonesia) contain fossil-rich Paleogene and Neogene deposits that have been subject of various classical paleontological studies (e.g., Martin, 1916, 1917). The mountains form the western flank of the deep Yogyakarta Basin. During a fieldwork in 2006 performed by F.P. Wesselingh and W. Renema a rich and well-preserved Miocene mollusk fauna was encountered in one of the outcrops located near the village of Banyunganti. The fauna, attributed to the early Miocene, contained a shallow marine assemblage and sheds light on the mollusk diversity during those times. Currently, Java is located in the modern center of maximum marine biodiversity. The new fauna might contribute to the understanding of the development of this diversity hotspot.

The scope of this study is the characterization of the Miocene mollusk fauna sampled in Banyunganti, Java in terms of abundances, diversity and ecology. A complete overview of the fauna including rare and poorly preserved specimens is given. The aim is to make the material accessible and reproducible for future taxonomists working on specific Indo-Pacific molluskan groups. Although, many taxa are described in open nomenclature it is highly likely that the vast majority represents undescribed species. A full taxonomic review of the fauna is beyond scope of this work.

2. Study Area

The studied sample was collected from marine Miocene deposits of the Jonggrangan Formation (Kadar, 1986) that are exposed on the eastern flank of the Menoreh Mountains west of Yogyakarta (Java, Indonesia, Fig. 1). Samples were collected near the village of Banyunganti in the western side of the road from Jongranggan to Niten (-7.760731 S, 110.128372 E), close to Goa Kiskendo.

The lower part of the Jonggrangang Formation comprises a thick succession of Oligocene–lowermost Miocene andesitic volcaniclastics, overlying the middle–upper

Eocene marls of the Nanggulan Formation (Kadar, 1986). The fauna was collected from a 1.5 m thick interval of not consolidated to slightly consolidated carbonate rich fine-middle sand grainstone with very common shells, coral fragments and larger benthic foraminifera. This interval is located about 20 m above the volcaniclastic interval in a transitional zone that contains volcaniclastics with calcareous sand and lignite intervals. The calcareous sands increase in thickness up section, until the first massive carbonate bank, directly above the sampled layer. Above this carbonate no lignites and only very fine clastic sediments were observed.

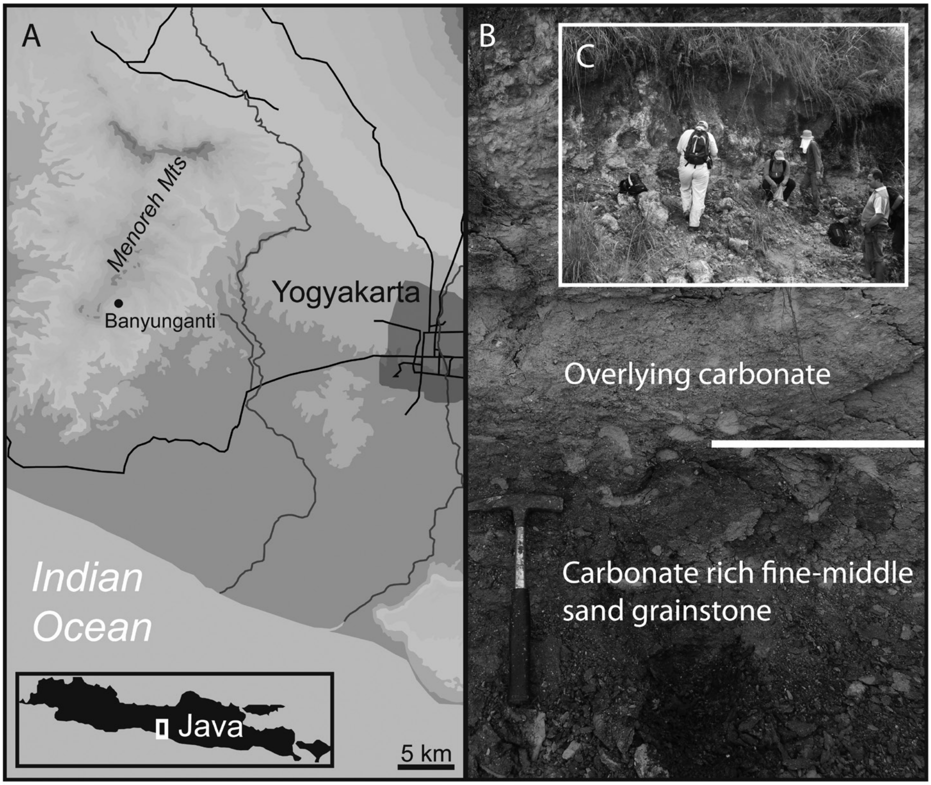

Figure 1: A) Locality map with overview map of Java included below. B) Close-up of the sampled interval and the overlying carbonate (2006). C) Overview of the sampled outcrop (2006).

Accompanying larger benthic foraminifera (LBF) are among others *Miogypsina kotoi* Hanzawa, 1935, *Austrotrillina howchini* (Schlumberger, 1893), *Flosculinella globulosa* Rutten, 1917, and *Planogypsina* sp. In the overlying carbonates also *Cycloclypeus eidae* Tan, 1930 is present, accompanied by *Nephrolepidina* spp., but *Eulepidina* and

Spiroclypeus species are lacking. This association is a typical LBF zone Tf1 fauna, approximately equivalent to early Burdigalian (Lunt and Allen, 2004; Renema 2007, 2008a). Strontium isotope stratigraphy analysis on two well-preserved isolated mollusks from the same sample as investigated both resulted in an age of ~18.9 Ma.

Active volcanism in the area has been dated at ~25-29 Mya (Smyth et al., 2005). This indicates that the Jonggrangan Formation forms a transgressive sequence over extinct volcanic cores. During the oldest phase of the transgression, where the Banyunganti fauna was sampled, a coastal environment with local patch reefs and branching coral gardens, and a considerable terrestrial influence existed. The younger part of the section represents a more open marine succession.

3. Material and Methods

The original sample size was 5.9 kg. The fraction > 1 mm was sorted following procedures outlined by other authors (Janssen et al., 2011; Rueda et al., 2009a; Zuschin et al., 2009). The sampled fauna is dominated by gastropods followed by bivalves, whereas just two scaphopod and one polyplacophoran species were found. Other faunal components are benthic foraminifers, corals, articulated bryozoans, echinoderms, crustaceans (ostracods, decapods), and fish remains (otoliths, one tooth). The mollusk specimens were counted and identified to at least superfamily level. Whenever possible, incomplete or poorly preserved material was included.

Each gastropod columella (including incomplete specimens and fragments) was counted for one individual. Each articulated bivalve was counted for one individual. Disarticulated valves were sorted into right and left valves and counted if the hinge and/or the umbo were preserved in the material. Each valve was counted for a half individual. For each species the higher number of valves (right or left) represents the minimum number of present individuals within the abundance data set. Each fully circular fragment of a scaphopod was counted for one individual. All material for which an attribution to at least superfamily level was possible and which was clearly distinguishable from other species present in the fauna was included in the investigation. Only 20 of 4448 sampled specimens remain unidentified and are excluded from this work which therefore should represent a complete characterization of the mollusk fauna > 1 mm sampled at Banyunganti.

The material was compared to the original type material of mollusk species from Java described by Martin (1879, 1884, 1899, 1905, 1906, 1916, 1917, 1921) and species from East Kalimantan identified or described by Beets (1941, 1986). All type material referred to in the systematic part is housed at Naturalis Biodiversity Center, Leiden, The Netherlands (formerly Rijksmuseum van Geologie en Mineralogie). For more information on the type material by Martin and localities see Leloux and Wesselingh (2009). Material referred to in the systematic part that is identified or described by Beets is mainly from the middle Miocene Menkrawit Beds, northern Mangkalihat Peninsula, East Kalimantan (Beets, 1941: L 114; age according to Shuto, 1975) or from the late Miocene lower Gelingseh Beds, Sangkulirang area, East Kalimantan (Beets 1986: L B; age according to Leupold and van der Vlerk, 1931).

Identifications in open nomenclature are based on the general literature on modern mollusks from the Philippines (Poppe, 2008a, b, 2010a, b), Thailand (Robba et al., 2003), Japan (Okutani, 2000), and Australia (Beesley et al., 1998), and on reviews of certain groups (e.g., Houbrick, 1992; Laseron, 1957; Ponder, 1984; Ponder and de Keyzer, 1992).

In total 182 mollusk species where attributed to at least superfamily level. Many of those taxa are described in open nomenclature because of their incomplete preservation, an insufficient number of individuals, or the general lack of knowledge of several mollusk groups in the Cenozoic of the Indo-Pacific, precluding a meaningful taxonomic revision at the moment. For material that could be only attributed to family or superfamily level it remains unresolved if undescribed taxa are present. The same accounts for material with questionable generic assignments and for material only containing incomplete, poorly preserved and/or juvenile individuals, although it could be attributed to genus level. For the majority of other taxa described in open nomenclature it is likely that they represent undescribed species, but confirmation would require more material and/or careful taxonomic revisions of several mollusk groups which was beyond scope of this work. With this documentation we intend to enable specialists on different mollusk groups to include the Banyunganti material in their works.

The mollusk fauna has been assigned to five different feeding guilds (5.2). The assignments are based on the Neogene Marine Biota of Tropical America molluskan life habits database (Todd, 2001) and the comprehensive ecological information provided in Beesley et al. (1998, and references therein). Assignments based on Todd (2001) concern mollusk families with a worldwide distribution that are represented by a single feeding guild and genera that occur in tropical America as well as in the Indo-Pacific.

The material is housed at Naturalis Biodiversity Center, Leiden, the Netherlands (indicated by RGM-numbers). Paratypes of the new taxa are housed at Pusat Survei Geologi (Center for Geological Survey), Bandung, Java, Indonesia (indicated by PSG-numbers).

Illustrations of all taxa are provided and remarks are given for all species if their level of identification is superfamily or lower. Remarks often include brief morphological characterizations of the species.

3.1 Abbrevations

Institutions: RGM = Naturalis Biodiversity Center (formerly Rijksmuseum van Geologie en Mineralogie), department fossil Molluska, Leiden, The Netherlands; PSG = Pusat Survei Geologi (Center for Geological Survey), Bandung, Java, Indonesia.

Localities: L 114 = Locality 114, Menkrawit Beds, northern Mangkalihat Peninsula, East Kalimantan (Beets, 1941); L B = Locality B, Gelingseh Beds, Sangkulirang area, East Kalimantan (Beets, 1986).

Material: h = height, w = width, frag./frags = fragment/s, p-t boundary = protoconch-teleoconch boundary, rv = right valve(s), lv = left valves(s), TN = temporary number.

4. Systematic Paleontology

For gastropod families we follow the taxonomic order proposed by Bouchet and Rocroi (2005) with a few exceptions: Colloniidae and Phasianellidae are ranked as families in the superfamily Phasianelloidea (Williams et al., 2008). For the taxonomy of Conoidea we follow Bouchet et al. (2011). The ranking of Pyramidelloidea follows Robba (2013). For the taxonomic order of bivalve families we follow Bieler et al. (2010).

Class Gastropoda Cuvier, 1795

Clade Vetigastropoda Salvini-Plawen, 1980

Superfamily Fissurelloidea Fleming, 1822

Family Fissurellidae Fleming, 1822

Remarks: All specimens in the family Fissurellidae investigated in this study are incomplete and appear in low abundances, therefore it remains unsolved if undescribed taxa are present in the material.

Genus *Scutus* Montfort, 1810

Scutus sp.

(Pl. 1, Fig. 1)

Material: RGM.783.219 (1)

Remarks: Approximately half a shell of this ovate, solid species is present. It is partly abraded. The original ornament consists of irregular, narrow spiral ribs with a wavy character.

Subfamily Emarginulinae Children, 1834

Genus *Emarginula* Lamarck, 1801

Emarginula sp.

(Pl. 1 , Fig. 2)

Material: RGM.784.739 (1); RGM.784.740 (1)

Remarks: Two damaged apical fragments are present in the material. The specimens have a very regular reticulate ornamentation of approximately 15 robust primary and finer secondary ribs. Equally thin concentric ribs bound square depressions.

Subfamily Fissurellinae Fleming, 1822

Genus *Puncturella* Lowe, 1827

Puncturella sp.

(Pl. 1 , Fig. 3)

Material: RGM.784.741 (1); RGM.784.742 (2)

Remarks: The available specimens are incomplete. The shells are low and ovate with a more or less centered apex and a large elliptical foramen. The ornamentation consists of approximately 30 low radial ribs; fine concentric ribs are drapped over the primaries and have a wavy appearance.

Superfamily Trochoidea Rafinesque, 1815

Family Trochidae Rafinesque, 1815

Subfamily Cantharidinae Gray, 1857

Genus *Jujubinus* Monterosato, 1884

Jujubinus cf. *polychromus* (A. Adams, 1853a)

(Pl. 1, Fig. 4)

cf. 1853a *Ziziphinus polychromus* A. Adams: 168

For a synonymy of the junior synonym *Trochus gilberti* Montrouzier in Fischer, 1878 see Herbert (1996: 421).

Material: RGM.784.743 (1); RGM.784.744 (9)

Remarks: The shell is conical with slightly rounded early and straight-sided late teleoconch whorls. It is ornamented with up to 22 regularly spaced, shallow spiral grooves. A slight suprasutural ridge appears on later teleoconch whorls. The partly preserved color pattern consists of axially orientated brown and narrower white blotches which form a flaming pattern. The aperture is subquadrate, the apertural base slightly contracted. A shallow umbilicus is present. The material resembles the modern Indo-Pacific species *Jujubinus gilberti* (Montrouzier in Fischer, 1878) in shell shape and color pattern (see e.g., Poppe, 2008a: pl. 44, fig. 7). The Recent specimens illustrated by Poppe and Poppe (1996a) show a high intraspecific variation regarding the strength of the suprasutural ridge. It is often distinctively stronger than in our material. According to Herbert (1996) *Jujubinus gilberti* (described from the Philippines) is a junior synonym of *Ziziphinus polychromus* A. Adams, 1853a. Herbert (1996) states that the generic affinity of the species is uncertain but assigns it to the *Cantharidus*-*Jujubinus*-*Thalotia*-*Komaitrochus* complex. We place the species in the genus *Jujubinus* because of the high conical spire and the slight constriction of the body whorl; the latter well visible in the specimens illustrated by Herbert (1996: figs 26-27, 65-66).

Family Calliostomatidae Thiele, 1924

Subfamily Calliostomatinae Thiele, 1924

Genus *Calliostoma* Swainson, 1840

Calliostoma sp.

(Pl. 1, Fig. 5)

Material: RGM.784.745 (1)

Remarks: The specimen is incomplete, the body whorl not preserved. It slightly resembles *Calliostoma butacianum* (Martin, 1905). The latter shows a more strongly imbricated shell and is ornamented with only five spiral cords containing regularly spaced knobs. The studied specimen has seven spirals on the latest preserved whorl. The protoconch of *Calliostoma* sp. is poorly preserved and therefore lacks the reticulate ornament typical for all calliostomids (Hickman and McLean, 1990). Considering the relatively poor preservation of the single specimen it is unclear if it concerns an undescribed species.

Trochoidea indet. sp.

(Pl. 1, Fig. 6)

Material: RGM.784.753 (1)

Remarks: The incomplete character and poor preservation of the single specimen only allows an assignment to the superfamily. It concerns a low dome-shaped shell with relatively round whorls and a reticulate ornament dominated by the spiral ribs.

Superfamily Phasianelloidea Swainson, 1840

Family Colloniidae Cossmann, 1917

Subfamily Colloniinae Cossmann, 1917

Genus *Bothropoma* Thiele, 1924

Bothropoma mediocarinata Reich and Wesselingh, 2014

(Pl. 2, Figs 1-7)

Holoype: Rijksmuseum van Geologie en Mineralogie (Naturalis Biodiversity Center) 784.746 (h: 2.3 mm, w: 2.7 mm);

Paratypes: RGM.784.747 (h: 2.5 mm, w: 3.0 mm); RGM.784.748 (h: 2.5 mm, w: 2.8 mm); RGM.784.749 (h: 2.2 mm, w: 2.5 mm); PSG TN1 (h: 2.2 mm, w: 2.6 mm); RGM.784.750 (h: 2.0 mm, w: 2.3 mm).

Additional material: RGM.608.185 (1); RGM.608.186 (1); RGM.608.187 (1); RGM.784.751 (1 operculum); RGM.784.752 (355 + 2 opercula).

Derivatio nominis: referring to the distinct median spiral ridge characterizing the species.

Locus typicus: western side of road at the village Banyunganti, province Yogyacarta, South-central Java, Indonesia.

Stratum typicum: unnamed fossiliferous bed of medium coarse sand, below Jongranan Formation, early Burdigalian (early Miocene).

Diagnosis: Small, turbiniform shell; rounded whorl profile with up to three more or less pronounced keels and additional ornamentation of secondary and tertiary spiral threads; median primary ridge forms a strong keel; moderately strong basal cord entrenching a deep umbilicus; large circular aperture with complete peristome.

Description: The species is typically about 2-2.5 mm high and 2.3-3 mm wide. The protoconch is composed of 0.6 whorls. It is shallow and smooth. The p-t boundary is formed by a prosocline riblet, not visible in all specimens. The teleoconch is composed of 2.2-2.4 rounded whorls rapidly increasing in size. The suture is deeply impressed. The shell is ornamented with distinct spiral cords and threads of different order. The ornamentation initiates at approximately 0.3 teleoconch whorls after the p-t-boundary. It consists of three primary spiral cords that soon form pronounced ridges. The upper ridge forms a shoulder at about one third of the whorl. The middle ridge develops into a distinct keel at the body whorl. The lower ridge is situated in the middle between the median ridge and the lower suture. A straight to slightly convex or slightly concave subsutural ramp is present. Between the three ridges the whorl profile is about straight. Three to four secondary spiral threads are present on the subsutural ramp, increasing to six on the body whorl. The upper thread is wider than the lower ones. One secondary spiral cord develops between the upper and the middle primary ridge. Usually it becomes nearly as prominent as the upper primary spiral ridge, but in some specimens it remains weak. Tertiary spiral threads might develop on the body whorl between primary and secondary spiral ribs. Two to three spiral cords develop between the median keel and the lower primary spiral ridge. Usually they are of same strenght, but in some specimens the median is strongest. The base of the body whorl is ornamented with six to nine secondary and tertiary spiral threads and a moderately strong basal ridge. Axial ornamentation is weak and only developed on the upper half of the subsutural ramp and on the base of the body whorl. The subsutural ramp is ornamented with low prosocline axial ribs that form low, roundish tubercles with the upper and sometimes with the middle primary spiral rib. Thin, prosocline axial ribs are present on the base of the body whorl. They are most pronounced when overrunning the basal ridge where distinct roundish tubercles are formed. The growth lines are prosocline and best visible at the interspaces of the spiral ornamentation. In some specimens the color pattern is preserved. It consists of about ten to twelve regularly spaced, somewhat rectangular light brown blotches on the subsutural ramp. Smaller light brown blotches are present along the median keel. The base of the body whorl seems to bear brown markings as well, but those are poorly preserved in the material. The body whorl is almost twice as high as the aperture. The base of the body whorl is straight to slightly convex. The aperture is large, circular, and with a complete thickened peristome. The outer lip coincides with a prosocyrt, smooth varix which is slightly bend outwards. The inner lip is thickened. It forms a rounded, somewhat elongate basal swelling. The umbilicus is open and deep. It is entrenched by the basal ridge. The operculum is circular with a diameter of about 1 mm. The outer surface is rugose with a pit in the middle. The inner surface is flat with a multispiral pattern.

Discussion: *Bothropoma mediocarinata* resembles *Bothropoma* cf. *munda* (H. Adams, 1873) from the Red Sea (Zuschin et al., 2009: pl. 14, figs. 3-5). The latter has approximately a half teleoconch whorl more and a higher spire. Sometimes the shoulder of *B*. cf. *munda* appears smooth (Zuschin et al., 2009), but the spiral ornamentation is visible all over the shell of *B*. *mediocarinata*. *Bothropoma* cf. *munda* from Eastern Arabia (Bosch et al., 1995: p. 40, fig. 87) shows an evenly rounded whorl profile without a median keel. *Bothropoma* sp. from the early Miocene of south-west India has a higher spire, the shoulder of the body whorl is sloping, more numerous spiral cords are present, and the median keel is less pronounced (Reuter et al., 2010; M. Harzhauser pers. comm.). *Bothropoma pilula* (Dunker, 1860) sensu Beets, 1941 (published as *Leptothyra pilula* Dunker, 1860 from L 114) can be easily distinguished from our species by its beaded spiral ornamentation and the less pronounced median primary spiral cord.

Occurrence: *Bothropoma mediocarinata* is only known from the type locality.

Clade Neritimorpha

Superfamily Neritoidea Rafinesque, 1815

Family Neritidae Rafinesque, 1815

Subfamily Neritininae Poey, 1852

Smaragdia Issel, 1869

Smaragdia jogjacartensis Martin, 1916

(Pl. 2, Fig. 8)

1916 *Neritina jogjacartensis* Martin: 259, pl. 3, figs 82-83

1966 *Smaragdia* (*Smaragdia*) *jogjacartensis* (Martin) – Ladd: 58, pl. 10, figs 28-31, pl. 11, figs 1-2

2009 *Neritina jogjacartensis* Martin, 1916– Leloux and Wesselingh 2009: 146 (cum. syn.).

Material: RGM.784.754 (1); RGM.784.755 (28)

Remarks: The species has a thin, convex shell that is strongly flattened at the apertural side. The button-shaped protoconch consists of less than one whorl. The inner lip callus is thickened and restricted to the parietal margin. The inner lip is weakly crenulated. The color pattern consists of three spiral bands on the body whorl, composed of prosocline, tightly packed, brown axial lines. The new material from Banyunganti shows more variation in coloration than the type series. Especially the juvenile specimens (included in RGM.784.755) show a more simple pattern of more or less curved axial lines that appear at the upper suture.

Genus *Smaragdia* sp.

(Pl. 2, Fig. 9)

Material: RGM.784.756 (1); RGM.784.757 9 (3)

Remarks: *Smaragdia* sp. has a very similar color pattern as *S. jogjacartensis* Martin, 1916 but has an oblique egg-shape and seems to have a more prominent crenulation of the inner lip. However, the inner lip is worn or lacking in the available specimens for which reason this attribute can not be used to distinguish the material. *Smaragdia* sp. resembles *Smaragdia semari* Beets, 1941 (L 114) in shell shape but can be distinguished by its color pattern. *Smaragdia semari* has a pattern of two spiral bands composed of brown axial lines arranged in blotches. Two more bands appear on the body whorl. Axial lines always develop with some distance below the suture while they appear with contact to the suture in *Smaragdia* sp. (and *S. jogjacartensis*). Neritids often show a high intraspecific variation in color pattern and shell shape (e.g., Tan and Clements, 2008). For that reason the distinction between *Smaragdia* sp. and *S. jogcarcartensis* remains somewhat questionable. *Smaragdia* sp. probably represents an undescribed species.

Superorder Caenogastropoda Cox, 1960

Superfamily Cerithioidea Fleming, 1822

Family Cerithiidae Fleming, 1822

Remarks: The material investigated in this study that is assigned to Cerithiidae but not identified beyond generic level likely includes undescribed species. Confirmation will require a thorough revision of the Indo-Pacific cerithiids which is beyond scope of this work.

Subfamily Bittiinae Cossmann, 1906

Genus *Bittium* Gray, 1847

Bittium sp.

(Pl. 3, Fig. 1)

Material: RGM.784.761 (1); RGM.784.762 9 (1)

Remarks: *Bittium* sp. is represented by relatively thin-shelled specimens with an elongate-conical shell, rounded whorls and a very regular cancellate ornamentation. The ornament consists of numerous axial ribs, four spiral cords on early teleoconch whorls, and five spiral cords on later teleoconch whorls.

Genus *Cerithidium* Monterosato, 1884

Cerithidium cf. *perparvulum* (Watson, 1886)

(Pl. 3, Figs 2-3)

cf. 1886 *Bittium perpavulum* Watson: 555, pl. 38, fig. 4.

2006 Cerithidium perpavulum (Watson, 1886) – van Aartsen: 35 (cum. syn.).

Material: RGM.784.758 (1); RGM.784.890 (1); RGM.784.759 (534)

Remarks: The shell is small, elongate-conical to slender with an ornamentation of thin, slightly prosocline axial ribs and spiral cords, two on early, four on later whorls. Axial and spiral ribs form a cancellate pattern with beads at the intersections. Varices might be present on later teleoconch whorls. The species shows a variation in shell shape from elongate-conical to slender. The width of the whorls was measured in 15 specimens including conical, slender, and intermediate shells to exclude the possibility that more than a single species is present. The variation in whorl-width initiates after the second teleoconch whorl. This observation leads to the assumption that only one species with some intraspecific variation in shell shape is present. Our material resembles the Indo-Pacific species *Cerithidium perparvulum* (Watson, 1886) (van Aartsen, 2006: figs 4-5, 10, 13) and *Clathrofenalla cerithina* (Philippi, 1849) from the Red Sea and the Gulf of Aden (Janssen et al., 2011: pl. 7, figs 3-7). According to Bosch et al. (1995) *C. perparvulum* is a synonym of *C. cerithina*. Janssen et al. (2011) note a high variability in the ornamentation of their material ranging from two to four spiral elements. They conclude that their material should be attributed to a single, highly variable species with *C. cerithina* being the oldest available name. Because our material does not show a high variability in ornamentation, but four spiral cords on later whorls of all 536 specimens, we follow van Aartsen (2006) and use *C.* cf. *perparvulum*.

Cerithidium sp.

(Pl. 3, Fig. 4)

Material: RGM.784.760 (1)

Remarks: *Cerithidium* sp. resembles *C.* cf. *perparvulum* (Watson, 1886), but it lacks the upper middle spiral cord on the penultimate whorl and only shows weakly developed beads at the intersections of axial and spiral ribs. The whorls are less rounded and tend to have a steep subsutural ramp.

Subfamily Cerithiinae Fleming, 1822

Genus *Cerithium* Bruguière, 1789

Cerithium aff. *balteatum* Philippi, 1848

(Pl. 3, Fig. 5)

aff. 1848 *Cerithium balteatum* Philippi: 22-23.

2003 *Cerithium balteatum* Philippi, 1848 – Robba et al., 2003: 26 (cum. syn.).

Material: RGM.784.763 (1); RGM.784.764 (1); RGM.784.765 (1)

Remarks: The material includes subadult shells only. Robba et al. (2003) illustrated a juvenile shell of *C. balteatum* (pl. 2, fig. 8). The identification of the former authors is based on a juvenile individual illustrated by Houbrick (1992: fig. 18 D). The material from Banyunganti agrees quite well with both illustrated specimens. However, the present shells are lacking varices and seem to have more slender and regularly spaced axial ribs than *C. balteatum*. The species ranges from Australia to the Tonga Islands in the east and the Ryukyu Islands in the north. It is known from the Miocene of Saipan (Northern Mariana Islands), the Quaternary of Indonesia, and the Holocene of Thailand (Robba et al., 2003).

Cerithium deningeri (Martin, 1916) comb. nov.

(Pl. 3, Fig. 6)

1916 *Potamides* (*Terebralia*) *deningeri* Martin: 249, pl. 2, figs 56-58

2009 *Clypeomorus deningeri* (Martin, 1916)– Leloux and Wesselingh: 132 (cum. syn.).

Material: RGM.784.766 (1), RGM.784.767 (5)

Remarks: The shell is characteristically cerithiiform: slender-conoidal and clearly tapering towards the apex. Early teleoconch whorls are ornamented with regularly spaced low axial ribs that become wider spaced and rounded on later teleoconch whorls. Low spiral ribs develop over the wide spaced axial ribs on later whorls. The species was assigned to *Clypeomorus* Jousseaume, 1888, by Shuto (1978) based on its conoidal shape and moderately high spire. The assignment is doubtful, because typical characteristics for the genus such as a spire/aperture ratio of 2:1, a large aperture, a prominent spiral ornamentation, and beads formed at the intersections of axial and spiral elements (after Houbrick, 1985) are lacking. Assignment to *Cerithium* is favoured, because the species shows resemblance with modern representatives of the genus (see Houbrick, 1992 for comparison).

Cerithium dolfusi (Martin, 1916)

(Pl. 3, Fig. 7)

1916 *Potamides* (*Terebralia*) *dolfusi* Martin: 250, pl. 3, fig. 61

2009 *Cerithium dolfusi* (Martin, 1916) – Leloux and Wesselingh: 130 (cum. syn.).

Material: RGM.784.768 (1)

Remarks: The shell is slender-conoidal with a weakly rounded whorl profile. The ornamentation of realatively low axial and spiral ribs is poorly preserved, but roundish knobs at the intersections of axial and spiral ribs are seen on late teleoconch whorls. The body whorl of the Banyunganti specimen is damaged.

?*Cerithium* “*ickei*” (Martin, 1916) comb. nov.

(Pl. 3, Fig. 8)

1916 *Potamides* (*Terebralia*) *ickei* Martin: 252, pl. 3, fig. 6

2009 *Potamides (Terebralia) ickei* Martin, 1916 – Leloux and Wesselingh: 130 (cum. syn.).

Material: RGM.784.778 (1)

Remarks: The studied specimen has a strongly convex whorl profile and is ornamented with wide, rounded axial ribs and numerous spiral cords. The material is tentatively assigned to *Cerithium*, but it is not sufficiently preserved for a doubtless generic assignment. The strongly convex whorl profile is unusual for the genus. Houbrick (1978) suggested an assigment of *Clava ickei* (Schepman, 1906) to the genus *Cerithium* which would make *C. ickei* (Schepman, 1906) the oldest valid name. However, Houbrick (1985) later stated that the available material is insufficient to make a generic assignment of the species. In addition, the name *C. ickei* has also been used for *C.* (*Ptychocerithium*) *ickei* Martin, 1914 (accepted as *Cerithium coralium* Kiener, 1841, see Houbrick, 1992: 61-68). In case of an attribution to the genus *Cerithium* a new name has to be attributed to the specimen from Banyunganti.

*Cerithium progoens*e (Martin, 1916)

(Pl. 3, Fig. 9)

1916 *Potamides* (*Cerithidea*) *progoënsis* Martin: 253, pl. 3, figs 67-68

1941 *Cerithium* (*Ptycocerithium*) *progoënse* – Beets: 52, pl. 2, figs 95-98

2009 *Cerithium progoens*e – Leloux and Wesselingh: 131 (cum. syn.).

Material: RGM.784.769 (1); RGM.784.771 (2); RGM.784.770 (22)

Remarks: The species is a relatively wide *Cerithium* with subrounded whorls and an ornament of regularly spaced, slightly wavy, opisthocline axial ribs and some varices.

Most specimens from Banyunganti are represented by small apical fragments (RGM.784.770) but two relatively large specimens with a maximum height of 43 mm are present in the material (RGM.784.771).

Cerithium teschi (Martin, 1916)

(Pl. 4, Fig. 1)

1916 *Potamides* (*Terebralia*) *teschi* Martin: 252, pl. 3, fig. 65

2009 *Cerithium* (*Cerithium*) *teschi* (Martin, 1916) – Leloux and Wesselingh: 130 (cum. syn.).

Material: RGM.784.772 (1); RGM.784.773 (1)

Remarks: This comparatively large species is represented by two incomplete specimens with a maximum height of 34 mm. The whorls are prominently shouldered. The teleoconch ornamentation consists of widely spaced axial ribs overrun by narrow, sharp spiral cords. Along the shoulder distinct upward pointing spines are formed at the intersections of the axial ribs and the upper primary spiral cord. Given the identical shape and ornamentation the Banyunganti material is assigned to *C. teschi*, although spines are not present in the type material. The possession or lack of spines lies within the intraspecific variation of cerithiid species and might be linked to their occurrence in different habitats [see *Cerithium zonatum* (Wood, 1828) in Houbrick, 1992].

Cerithium s.s. sp. 1

(Pl. 4, Fig. 2)

Material: RGM.784.774 (1); RGM.784.775 (141)

Remarks: The specimens are medium-sized cerithiids with a subrounded whorl profile and a slightly impressed suture. The ornament is rather low and consists of regularly spaced, orthocline to slightly opisthocline, slightly sigmoidal axial ribs and three to ten spiral ribs. Varices are present and most prominent on the body whorl which is damaged in all specimens.

Cerithium s.s. sp. 2

(Pl. 4, Fig. 3)

Material: RGM.784.776 (1); RGM.784.777 (7)

Remarks: All present specimens are damaged. They are characterized by relatively flat whorls and an ornamentation of rounded axial ribs and regularly spaced spiral cords. The body whorl is slightly constricted below the penultimate whorl with an almost straight outline. The axial ribs become more slender and irregular on the body whorl.

Cerithium s.l. sp. 1

(Pl. 4, Fig. 4)

Material: RGM.784.779 (1)

Remarks: The single individual is incomplete and relatively poorly preserved but can be easily distinguished from the other Banyunganti cerithiids by its high, slender spire and an ornament of few orthocline axial ribs.

Cerithium s.l. sp. 2

(Pl. 4, Fig. 5)

Material: RGM.784.780 (1)

Remarks: The single shell is too incomplete for an accurate classification. Its ornamentation consists of relatively wide spaced, narrow, roundish axial ribs crossed by two spiral cords on early teleoconch whorls and up to five spiral cords and additional spiral threads on later whorls. The specimen shows slight resemblance with *Cerithium* aff. *balteatum* Philippi, 1848 from Banyunganti (see above) but has wider and more rounded axial ribs.

Genus *Clypeomorus* Jousseaume, 1888

Clypeomorus sp. 1

(Pl. 4, Fig. 6)

Material: RGM.784.781 (1); RGM.784.782 (5)

Remarks: The shell is conical with straight-sided early and slightly rounded later teleoconch whorls. The ornament consists of low, prosocline axial ribs and three distinct primary spiral ribs which form tubercles at the intersections with the axial ornament. Varices are present. The material has been assigned to *Clypeomorus* rather than to *Cerithium* according to a spire/aperture ratio of 2:1, a large aperture, and the presence of three prominent primary spiral cords, although the beaded ornamentation characteristical for the genus is not developed (see Houbrick, 1985 for comparison).

?*Clypeomorus* sp. 2

(Pl. 4, Fig. 7)

Material: RGM.784.783 (1); RGM.784.784 (2)

Remarks: ?*Clypeomorus* sp. 2 is a relatively wide, straight-sided cerithiid with a narrow subsutural ridge and relatively evenly and widely spaced orthocline axial ribs. The material resembles *Clypeomorus* sp. 1. The two species share features like a spire/aperture ratio of 2:1 and a large aperture (which is larger in *Clypeomorus* sp. 1). However, a prominent spiral ornament and hence a beaded ornamenation are lacking in ?*Clypeomorus* sp. 2 for which reason an assignment to the genus remains open for future scrutiny.

Family Dialidae Kay, 1979

Genus *Diala* Adams, 1861

Diala semistriata s.l. (Philippi, 1849)

(Pl. 4, Figs 8-9)

1849 *Rissoa semistriata* Philippi: 34-35

2011 *Diala semistriata* (Philippi, 1849) – Janssen et al., 2011: 395 (cum. syn.).

Material: RGM.784.785 (1); RGM.784.786 (1); RGM.784.787 (107)

Remarks: The material falls within the morphological variation as illustrated and described by Ponder and de Keyzer for this highly variable species (1992: 1022, figs 1A-E, 2B, C, E, G, H, 3I-P, 4, 5D-I, 6A-F, 7, 8C, D, 9A, B). For instance, six to 11 spiral lirae separated by grooves are present on the base of the body whorl which range from being “about equal in width to lirae to linear” (Ponder and de Keyzer, 1992). Due to the high variation within this genus with few shell characteristics it remains unclear if *D. semistriata* does not include more than a single species. The species is widely distributed in the tropical Indo-West Pacific (Ponder and de Keyzer, 1992). *Diala semistriata* is known since the early Miocene from Bikini and Eniwetok Atolls (Ladd, 1972).

Diala sp.

(Pl. 4, Fig. 10)

Material: RGM.784.788 (1); RGM.784.789 (6)

Remarks: *Diala* sp. is easily distinguished from *D. semistriata* s.l. (Philippi, 1849) by its subrounded whorl profile and the entirely smooth shell. Potentially, the specimens represent an undescribed species.

Family Modulidae Fischer, 1884

Genus *Modulus* Gray, 1840

Modulus sp. 1

(Pl. 4, Fig. 11a-b)

Material: RGM.784.794 (1); RGM.784.795 (12)

Remarks: The available specimens have trochiform shells with a straight whorl profile. Early teleoconch whorls become slightly convex on later whorls. The shell is ornamented with regularly spaced, narrow spiral ribs and fine spiral threads, and regularly spaced, wide, pronounced axial ribs initiating on later teleoconch whorls. The spiral ornamentation forms a cancellate pattern with the growthlines at the base of the body whorl. The aperture is large and semi-circular. The umbilicus is shallow and slitlike. Up to 16 well-developed ridges are present in the interior of the outer lip. The material neither resembles any of the modern Indo-Pacific species nor *Modulus preangerensis* Martin, 1905 from the Miocene of Java and might belong to an undescribed species.

Additional remark: The species has been revised and is described as a new species by Landau et al. (submitted).

Modulus sp. 2

(Pl. 4, Fig. 12)

Material: RGM.784.796 (1)

Remarks: A single incomplete specimen with a relatively high spire is present. The specimen has more strongly inflated whorls and lower, more closely spaced axial ribs than *Modulus* sp. 1, resulting in an undulating appearance of the spiral ornamentation. It resembles *Modulus praeangerensis* Martin, 1916, but the latter species has a lower spire with clearly shouldered whorls. Additional material is needed to verify whether it concerns an undescribed species.

Family Planaxidae Gray, 1850

Subfamily Planaxinae Gray, 1850

Genus *Planaxis* Lamarck, 1822

Planaxis s.l. sp.

(Pl. 5, Fig. 1)

Material: RGM.784.797 (1)

Remarks: The material contains a single incomplete spire with a wide apical angle and an ornamentation of regularly spaced spiral grooves. The assignment to Planaxidae is based on the resemblance of our material with *Fissilabia decollata* (Quoy and Gaimard, 1833) (Poppe, 2008a: pl. 94, fig. 10). Additional material is needed to verify whether it concerns an undescribed species.

Family Potamididae Adams and Adams, 1854

Genus *Cerithideopsilla* Thiele, 1929

?*Cerithideopsilla* sp.

(Pl. 5, Figs 2-3)

Material: RGM.784.798 (1); RGM.784.799 (1); RGM.784.800 (1); RGM.784.801 (1)

Remarks: The shells have an almost straight outline, an overall beaded ornamentation with three primary spiral cords of which the median one is weaker on early teleoconch whorls, and a strong columellar fold. The material is fragmented and insufficient for an accurate classification, but it resembles modern *Cerithideopsilla* species illustrated in Poppe (2008a: pl. 87, figs 5, 9; pl. 88, figs 1-3).

Family Scaliolidae Jousseaume, 1912

Genus *Finella* A. Adams, 1860

Finella cf. *pupoides* A. Adams, 1860

(Pl. 5, Figs 4-5)

cf. 1860 *Finella pupoides* A. Adams: 336

2011 *Finella pupoides* A. Adams, 1860 – Janssen et al., 2011: 399 (cum. syn.).

Material: RGM.784.802 (1); RGM.784.803 (1); RGM.784.804 (1)

Remarks: The studied material contains thin-walled, elongate-ovate shells with a subrounded whorl profile and a low reticulate ornament of spiral cords and rather prominent growth marks. The species shows variation in shell shape from being more ovate to more elongate. The most characteristic feature of the species is the constriction of the last one to two teleoconch whorls. One specimen from Banyunganti

(RGM.784.803) resembles well a specimen of *F. pupoides* illustrated by Janssen et al. (2011) from the Red Sea (pl. 7, fig. 10a). The other two specimens in the material are more ovate.

Finella sp. 1

(Pl. 5, Fig. 6)

Material: RGM.784.805 (1); RGM.784.805 (1)

Remarks: The shells are elongate and slender. Although they show some resemblance with *F.* cf. *pupoides* from Banyunganti and a specimen of *F. pupoides* from the Red Sea (Janssen et al., 2011: pl. 7, fig. 9), the material was separated due to its profile of early teleoconch whorls which differs from the above mentioned species. Furthermore, a constriction of the last whorls was not observed in the Banyunganti material. Additional material is needed to verify whether it concerns an undescribed species.

Finella sp. 2

(Pl. 5, Fig. 7)

Material: RGM.784.807 (1)

Remarks: The body whorl of the available specimen is damaged and the protoconch and earliest whorls are lacking. The specimen shows resemblance with the modern South African species *Finella natalensis* Smith, 1899 (Poppe and Poppe, 1996b) in shell shape and whorl profile, but differs from that species by having an ornamentation of more numerous axial ribs and weaker spiral cords. *Finella* sp. 2 can be distinguished from the other *Finella* material from Banyunganti by having an ornamentation of relatively pronounced axial ribs. The matarial is insufficient to confirm an undescribed species.

Family Turritellidae Lovén, 1847

Subfamily Turritellinae Lovén, 1847

Genus *Archimediella* Sacco, 1895

Archimediella spolongensis (Martin, 1916)

(Pl. 5, Fig. 8)

1916 *Turritella spolongensis* Martin: 256, pl. 3, fig. 73

2009 *Archimediella spolongensis* (Martin, 1916) – Leloux and Wesselingh: 127 (cum. syn.).

Material: RGM.784.808 (1); RGM.784.809 (1); RGM.784.810 (24)

Remarks: All present specimens are incomplete. The species is characterized by a strong median spiral ridge which forms a pronounced keel on early teleoconch whorls and weakens gradually on later whorls. A weaker but still distinct suprasutural spiral ridge is present. A subsutural spiral ridge might be pronounced as well. Secondary regularly spaced spirals are present and grow in number on later teleoconch whorls.

Genus *Haustator* Montfort, 1810

Haustator sp.

(Pl. 5, Fig. 9)

Material: RGM.784.811 (1); RGM.784.812 (74)

Remarks: The apex and the body whorl are damaged or lacking in the material. The teleoconch is preserved with at most nine whorls. The specimens have a strong spiral ridge creating a slightly sub-median angulated whorl profile. The spiral ornamentation consists of very subtle sub- and suprasutural ridges and a median spiral ridge which is located at approxiamtely 45% of the height of the whorl. The latter is often the strongest on late teleoconch whorls. Additional weaker spiral threads and strongly curved growthlines are present all over the whorls, but the spiral threads are worn on most specimens. The material is easily distinguished from *Archimediella spolongensis* (Martin, 1916) by its sub-median angulated whorl profile. Possibly it concerns an undescribed species, but a thorough revision of Indo-Pacific turritellids would be required for confirmation.

Cerithioidea indet. sp. 1

(Pl. 5, Fig. 10)

Material: RGM.784.813 (1); RGM.784.814 (2)

Remarks: The specimens are conical-ovate with a slightly convex whorl profile. The ornament is dominated by slender, well defined axial ribs and two spiral cords on early teleoconch whorls. A single suprasutural spiral cord is present on later whorls. A siphonal notch is developed. The classification remains open. The material is for now placed in the superfamily Cerithioidea because of the presence of two distinct spiral cords on early whorls.

Cerithioidea indet. sp. 2

(Pl. 5, Fig. 11)

Material: RGM.784.815 (1)

Remarks: The single specimen is too incomplete for an accurate classification. It has an evenly convex whorl profile. The low ornamentation consists of thin axial ribs and four to five primary spiral cords and secondary threads. The axial ribs are about the same strenght as the primary spiral cords, both form a slightly irregular cancellate pattern. Low varices are present. The base of the last preserved whorl appears flat and smooth.

Cerithioidea indet. sp. 3

(Pl. 5, Fig. 12)

Material: RGM.784.816 (1)

Remarks: The single specimen is too incomplete for an accurate classification. The species is characterized by evenly convex whorls separated by a deep suture, and a weak ornamentation of prosocline, thin, low axial ribs and spiral cords and threads of different order forming an irregular cancellate pattern. The two spiral cords on the lower half of the whorl are most prominent. Varices are absent. The material shows some resemblance with Cerithioidea indet. sp. 2 regarding the whorl profile and the overall appearance of the ornament.

?Cerithioidea sp. 4

(Pl. 6, Fig. 1)

Material: RGM.784.790 (1); RGM.784.791 (1)

Remarks: Only the spire is present in the material. It is conical with an almost straight whorl profile. The ornament consists of two dominant spiral cords on early whorls. On later whorls regular, prosocline axial ribs and weaker spiral cords form a cancellate pattern. Low varices are present. The classification remains open.

?Cerithioidea sp. 5

(Pl. 6, Fig. 2)

Material: RGM.784.792 (1); RGM.784.793 (2)

Remarks: Only the spire is preserved. The material can be distinguished from ?Cerithioidea sp. 4 by slightly more rounded whorls, a shallow suture, and more numerous, less regularly spaced axial ribs. The classification remains open, but it is assumed that ?Cerithioidea sp. 4 and ?Cerithioidea sp. 5 belong to the same genus.

Superfamily Campaniloidea Douvillé, 1904

Family Ampullinidae Cossman, 1918

Genus *Ampullina* Bowdich, 1822

Ampullina s.l. sp.

(Pl. 6, Fig. 3)

Material: RGM.784.817 (1); RGM.784.818 (2)

Remarks: The material contains apical fragments too incomplete for a further identification. The generic assignment is based on the thin shell, the rounded whorls and the deeply impressed suture. These characters distinguish ampullinids from otherwise similar naticids. The specimens can be easily distinguished from other ampullid material from Banyunganti (?*Cernina* sp., see below) by their lower spire, a lower number of whorls, and a larger protoconch. Today the family is represented by a single living Philippine species, *Cernina fluctuata* (Sowerby I, 1825) (e.g., Kase and

Ishikawa, 2003).

Genus *Cernina* Gray, 1840

?*Cernina* sp.

(Pl. 6, Fig. 4)

Material: RGM.784.819 (1)

Remarks: Eight fragments of a single individual are present. The material is insufficient for a complete reconstruction. The thin shell is approximately 3 cm high. It is globular with a relatively low spire, although the spire is more elevated than in *Ampullina* s.l. sp. The whorls are well rounded with a deeply impressed suture. The number of whorls is significantly higher and the protoconch is smaller in ?*Cernia* sp. than in *Ampullina* s.l. sp.

Family Plesiotrochidae Houbrick, 1990

Genus *Plesiotrochus* Fischer, 1878

Remarks: Three *Plesiotrochus* species from Banyunganti are described in open nomenclature due to insufficient specimen numbers and poor preservation. The material yields potentially undescribed species.

Plesiotrochus hasibuani Reich and Wesselingh, 2014

(Pl. 6, Figs 5-10)

Holotype: Rijksmuseum van Geologie en Mineralogie (Naturalis Biodiversity Center) 784.820 (h: 6.7 mm, w: 3.5 mm);

Paratypes: RGM.784.821 (h: 7.4 mm, w: 3.6 mm); RGM.784.822 (h: 6.7 mm, w: 3.4 mm); RGM.784.823 (h: 5.9 mm, w: 3.0 mm); RGM.784.824 (h: 6.2 mm, w: 3.3 mm); PSG TN2 (h: 5.7 mm, w: 3.2 mm).

Additional material: RGM.608.188 (1); RGM.608.189 (1); RGM.608.190 (1); RGM.784.825 (150).

Derivatio nominis: in honour of Prof. Fauzie Hasibuan, geologist at the Pusat Survei Geologi (Center for Geological Survey), Bandung, Java.

Locus typicus: western side of road at the village Banyunganti, province Yogyacarta, South-central Java, Indonesia.

Stratum typicum: unnamed fossiliferous bed of medium coarse sand, below Jongranan Formation, early Burdigalian (early Miocene).

Diagnosis: Small, elongate-conical *Plesiotrochus* species; whorl-profile angular on early teleoconch whorls and evenly rounded on later whorls; ornamentation of regularly spaced, rounded axial ribs, increasingly pronounced and more widely spaced on later whorls; spiral ornamentation of regularly spaced cords; pronounced basal spiral cord.

Description: The elongate-conical shell is typically 6-7 mm high and 3-3.5 mm wide, but all shells are damaged in the present material and may have been higher. The protoconch is composed of about one smooth whorl. The p-t boundary is poorly delimited. The teleoconch is composed of about six convex whorls separated by a well-defined suture. The initial teleoconch whorls show a clear angulation at about one third to one fourth of the whorl height and a straight subsutural ramp. The angulation weakens gradually; later teleoconch whorls are evenly rounded. The shell is ornamented with up to 15 axial ribs on early and eight to ten axial ribs on later whorls. Early axial ribs are narrow, low, prosocline, and relatively regularly spaced with their interspaces about as wide as the ribs. Later ribs become more pronounced, more rounded, and slightly more irregular in shape. The width of their interspaces becomes more variable: from approximately the width of the rib to twice that wide. On average, later ribs are wider spaced than early ribs. Spiral ornamentation consists of numerous, thin, regularly spaced, low cords. It is uniform on early whorls, but some spiral elements become more distinct on the penultimate whorl. Up to five pronounced spiral cords are present on the body whorl. One additional spiral cord is situated at the body whorl's periphery, and another distinct roundish cord runs along the base. Growthlines are prosocline and best visible on the body whorl where they form an irregular rectangular pattern with the spiral ornament. The subovate aperture occupies two fifth of the shell height. The outer lip is damaged in the material. The siphonal canal is short and oblique.

Discussion: The studied material is easily distinguishable from modern *Plesiotrochus* species known from the Philippines and Japan by its well rounded profile of later teleoconch whorls (see Poppe, 2008a: pl. 97; Okutani, 2000: pl. 67). The shell shape of *Plesiotrochus tomlini* Beets, 1941 (L 114) shows some resemblance to *P. hasibuani*. However, the former has clearly weaker axial ribs and varices are present (not seen in *P. hasibuani*).

Occurrence: *Plesiotrochus hasibuani* is only known from the type locality.

Plesiotrochus sp. 1

(Pl. 6, Fig. 11)

Material: RGM.784.826 (1); RGM.784.827 (6)

Remarks: The available specimens are easily distinguished from the other *Plesiotrochus* material from Banyunganti by the presence of a distinct suprasutural keel and numerous, narrow, relatively weak axial ribs. Furthermore, *Plesiotrochus* sp. 1 is the only *Plesiotrochus* from Banyunganti having varices. The material shows some resemblance with the modern *Plesiotrochus unicinctus* (A. Adams, 1853a) concerning shell shape and ornament, although the latter lacks varices (Poppe, 2008a: pl. 97, figs 1-2).

Plesiotrochus sp. 2

(Pl. 6, Fig. 12)

Material: RGM.784.828 (1)

Remarks: The single specimen is poorly preserved but can be distinguished from the other *Plesiotrochus* material from Banyunganti by the presence of widely spaced, low, roundish axial ribs. Those are thickened at about one third above the suture caused by an indistinct overrunnig spiral cord. The whorls are less convex than in *P. hasibuani* Reich and Wesselingh, 2014.

?*Plesiotrochus* sp. 3

(Pl. 6, Fig. 13)

Material: RGM.784.829 (1)

Remarks: The present specimen differs from the other *Plesiotrochus* forms from Banyunganti by having flat whorls with a distinct suprasutural carina and an ornament of dominant thin, narrow spaced spiral threads and weak axial elements. We are not entirely sure about the assignment to the genus *Plesiotrochus*. There are some similarities with the planaxid genus *Fissilabia* as well.

Clade Hypsogastropoda Ponder and Lindberg, 1997

Clade Littorinimorpha Golikov and Starobogatov, 1975

Superfamily Capuloidea Fleming, 1822

Family Capulidae Fleming, 1822

Genus *Capulus* Montfort, 1810

Capulus sp.

(Pl. 7, Fig. 1)

Material: RGM.784.830 (1)

Remarks: A juvenile shell is present that can not be further identified. It can be distinguished from the javanese *C. junghuhni* Martin, 1905 by the following characters: *Capulus junghuhni* has a rather round than ovate aperture like in our specimen. The protoconch of *C. junghuhni* is small, narrowly coiled, and consists of more than one whorl, whereas the protoconch in the present specimen is bulbiform and consists of 0.7 whorls. Furthermore, *Capulus* sp. changes the direction of the coiling axis after the p-t boundary, a feature lacking in *C. junghuhni*.

Superfamily Cingulopsoidea Fretter and Patil, 1958

Family Eatoniellidae Ponder, 1965

Remarks: Eatoniellids are present in low numbers in our material. This and the few shell characters of the family impede an accurate taxonomic revison of the shells from Bayunganti.

Genus *Eatoniella* Dall, 1876

Eatoniella s.l. sp. 1

(Pl. 7, Fig. 2)

Material: RGM.784.831 (1); RGM.784.832 (2)

Remarks: The shell is ovate-conical with a subrounded whorl profile. It is smooth apart from fine, slightly sigmoid growthlines. The protoconch is poorly delimited. The aperture is ovate and occupies about two fifth of the shell height. A rimate umbilicus is present. The few characters of the shell make an attribution to a genus or even a family somewhat difficult. Several families and some genera of for example Rissoidae have very similar appearances. However, the smooth nature of the protoconch and the lack of a clear p-t boundary are typical of *Eatoniella* and some related genera (Beesley et al., 1998).

Eatoniella s.l. sp. 2

(Pl. 7, Fig. 3)

Material: RGM.784.833 (1); RGM.784.834 (3)

Remarks: The material is distinguished from *Eatoniella* s.l. sp. 1 by its elongate-conical shell, a slightly rounded whorl profile, and a spire/aperture ratio of 2:1. The illustrated specimen RGM.784.833 contains numerous predation scars possibly caused by decapod crustaceans.

Superfamily Cypraeoidea Rafinesque, 1815

Family Cypraeidae Rafinesque, 1815

Cypraeidae indet. sp.

(Pl. 7, Figs 4-5)

Material: RGM.784.835 (1 frag.); RGM.784.836 (1 frag.); RGM.784.837 (9 frags)

Remarks: The material contains several fragments and is too incomplete for identification.

Superfamily Naticoidea Guilding, 1834

Family Naticidae Guilding, 1834

Remarks: Little naticid material is known from Banyunganti. All taxa are documented in open nomenclature. A revision of Indo-Pacific Naticidae might reveal that undescribed species are present.

Genus *Natica* Scopoli, 1777

Natica s.l. sp. 1

(Pl. 7, Fig. 6)

Material: RGM.784.839 (1)

Remarks: The single specimen contains a weakly shouldered body whorl and has a well visible ornamentation of fine growthlines which form weak grooves on the upper part of the body whorl.

Natica s.l. sp. 2

(Pl. 7, Fig. 7)

Material: RGM.784.840 (1); RGM.784.841 (1)

Remarks: The specimens are distinguished from *Natica* s.l. sp. 1 by their larger size, an evenly rounded body whorl lacking a shoulder, and most characteristicly by their smooth shells.

Genus *Naticarius* Duméril, 1805

Naticarius sp.

(Pl. 7, Fig. 8)

Material: RGM.784.838 (1)

Remarks: The present specimen resembles *Naticarius marochiensis* (Gmelin, 1791) sensu Beets, 1986 (L B). That species is also known as *Natica* (*Natica*) *marochiensis* (Gmelin, 1971) sensu Beets, 1941 (L 114). The most characteristic feature of the Banyunganti specimen and *N. marochiensis* are the well-defined, regularly spaced grooves radiating from the suture. The Banyunganti material is distinguished from *N. marochiensis* by its more rounded shell, a slightly lower spire, and a less open, crescent shaped umbilical chink.

Naticidae indet.

(Pl. 7, Fig. 9)

Material: RGM.784.842 (1 operculum)

Remarks: One generically unassigned naticid operculum is found in the Banyunganti material. It is larger than the naticid shells present in the fauna and might belong to a different species.

Superfamily Rissooidea Gray, 1874

Family Rissoidae Gray, 1874

Remarks: Rissoids from Banyunganti that are described in open nomenclature contain single, damaged specimens that are regarded as insufficient for a further taxonomic assignment.

Subfamily Rissoininae Stimpson, 1865

Genus *Rissoina* d'Orbigny, 1840

Subgenus *Rissoina* d'Orbigny, 1840

Rissoina (*Rissoina*) *banyungantiensis* Reich and Wesselingh, 2014

(Pl. 7, Fig. 10, Pl. 8, Figs 1-4)

Holotype: Rijksmuseum van Geologie en Mineralogie (Naturalis Biodiversity Center) 784.843 (h: 5.5 mm, w: 2.2 mm);

Paratypes: RGM.784.844 (h: 6.2 mm, w: 2.8 mm); RGM.784.845 (h: 5.7 mm, w: 2.3 mm); RGM.784.846 (h: 5.6 mm, w: 2.3 mm); RGM.784.847 (h: 5.7 mm, w: 2.6 mm); PSG TN3 (h: 5.7 mm, w: 2.4 mm).

Additional material: RGM.608.191 (1); RGM.608.192 (1); RGM608.193 (1); RGM.784.848 (1414).

Derivatio nominis: referring to the type locality.

Locus typicus: western side of road at the village Banyunganti, province Yogyacarta, South-central Java, Indonesia.

Stratum typicum: unnamed fossiliferous bed of medium coarse sand, below Jongranan Formation, early Burdigalian (early Miocene).

Diagnosis: Small, elongate-conical, high-spired *Rissoina* species; whorl profile almost straight; shell with slender but robust, slightly opisthocline axial ribs and very weak spiral threads; strong varix just behind the outer lip; wide and shallow spiral depression just above base of the body whorl.

Description: The elongate-conical, high-spired shell is on average 5.7 mm high and typically 2.2-2.8 mm wide. The smooth, dome-shaped protoconch is composed of 1.3-1.5 whorls. The p-t boundary is defined by an indistinct opisthocline line. The teleoconch consists of 6.5-7 whorls. The whorl profile is straight to convex. The suture is moderately deep impressed and undulating. The shell is ornamented with regularly spaced, slender axial ribs; interspaces are as wide as the ribs. About 15 axial ribs are present on early teleoconch whorls, increasing to 20-25 on the body whorl. The ribs are slightly opisthocline and continue on the base of the body whorl. The spiral ornamentation is very weakly developed. Numerous regular, fine spiral threads are present between the interspaces of the axial ribs, best visible on the slightly rounded body whorl. A wide spiral depression is developed at the base of the body whorl. The fusiform to subovate aperture occupies about one third of the height of the shell. The outer lip is rounded. A very heavy opisthocline varix is present just behind the apertural margin, covered by up to six additional axial ribs which are less prominent and narrower spaced than the regular axial ribs. The former are often worn in the material. The inner lip is narrow, moderately thickened and slightly curved. The base of the inner lip is located to the left of the shell's axis. A moderately deep, wide basal apertural notch is present. It is entrenched by a slight swelling at the lower part of the inner lip. A shallow posterior canal is well-defined.

Discussion: *Rissoina* (*R.*) *banyungantiensis* resembles *Rissoina indrai* Beets, 1941 (various Miocene localities, East Kalimantan). The latter species is clearly larger being around 10 mm high. The holotype of *R. indrai* (RGM.312.250) is ornamented with widely spaced axial ribs on early whorls. The ribs become progressively more close-set. The body whorl bears more than 30 axial ribs that become weaker on the base of the body whorl. The spiral ornamentation becomes clearly evident on the base of the body whorl where it forms a reticulate pattern with the weak axials, a feature lacking in *R.* (*R.*) *banyungantiensis*. The modern Japanese species *Rissoina* (*Rissoina*) *rosea* (Deshayes, 1862) (Okutani, 2000: pl. 75, fig. 19) resembles *R.* (*R.*) *banyungantiensis* superficially but has a lower number of axial ribs and a more convex whorl profile.

Rissoina (*Rissoina*) sp.

(Pl. 8, Fig. 5)

Material: RGM.784.856 (1)

Remarks: The shell is fusiform with a relatively rounded whorl profile and an ornamentation of distinct axial ribs and weak spiral threads. The convex whorls and the strong axial ornament clearly distinguish the specimen from *Rissoina* (*R.*) *banyungantiensis* Reich and Wesselingh, 2014.

?*Rissoina* s.l. sp.

(Pl. 8, Fig. 6)

Material: RGM.784.855 (1)

Remarks: The shell is fusiform with a subrounded whorl profile and strong axial ribs and weaker spiral threads. The specimen resembles *Rissoina* (*Rissoina*) sp. but can be distinguihed by a lower number of stronger spiral threads and weaker axial ribs. Due to the incomplete preservation of the body whorl a distinction on genus level based on the presence or absence of a basal spiral ridge is not possible.

Genus *Rissolina* Gould, 1861

Rissolina reticuspiralis Reich and Wesselingh, 2014

(Pl. 8, Figs 7-11)

Holotype: Rijksmuseum van Geologie en Mineralogie (Naturalis Biodiversity Center) 784.849 (h: 3.5 mm, w: 1.4 mm);

Paratypes: RGM.784.850 (h: 3.9 mm, w: 1.6 mm); RGM.784.851 (h: 3.2 mm, w: 1.4 mm); RGM.784.852 (h: 3.6 mm, w: 1.5 mm); RGM.784.853 (h: 3.2 mm, w: 1.3 mm); PSG TN4 (h: 3.5 mm, w: 1.5 mm).

Additional material: RGM.608.194 (1); RGM.608.195 (1); RGM.608.196 (1); RGM.784.854 (72).

Derivatio nominis: referring to the presence of well-developed spiral cords that form a reticulate pattern with the axial ribs.

Locus typicus: western side of road at the village Banyunganti, province Yogyacarta, South-central Java, Indonesia.

Stratum typicum: unnamed fossiliferous bed of medium coarse sand, below Jongranan Formation, early Burdigalian (early Miocene).

Diagnosis: *Rissolina* species with small, elongate-conical high-spired shell; whorl profile convex; with sharp, slightly opisthocline axial ribs, thinner but sharply delimited spiral cords, and microscopic, very densely spaced spiral striae; outer lip coinciding with strong varix, ornamented with well defined low knobs; strong, beaded spiral ridge at base of body whorl.

Description: The elongate-conical, high-spired shell is typically about 3-4 mm high and on average 1.5 mm wide. The dome-shaped protoconch is smooth apart from thin irregular axial folds which are often worn in the material. The p-t boundary at about 1.2-1.5 whorls is indistinct and appears to coincide with the onset of the teleoconch ornamentation. The teleoconch consists of 5.5 to 6 convex whorls. A subtle subsutural angulation is present. The suture is moderately deep impressed. The shell is ornamented with regularly spaced, very slender and sharp axial ribs. The concave interspaces are about four times as wide. About 13 axial ribs are present on early teleoconch whorls, increasing to about 18 on the body whorl. The ribs are slightly opisthocline and extend on the base of the body whorl. The thin and sharp, regularly spaced spiral cords are visible in the axial interspaces and overrun the axials on the terminal part of the body whorl. They are well visible on the outer lip as small pointed knobs. The shell is covered by a dense micro-ornamentation of numerous thin spiral threads with their interspaces equating their width (see Pl. 8, Fig. 11c). The fusiform to subovate aperture is about one quarter the height of the shell. The outer lip is rounded. It coincides with an opisthocline varix containing the ultimate two to four (usually three) narrow spaced axial ribs. The spiral ornamentation is well developed on the entire terminal varix. The inner lip is slightly curved. A shallow, wide basal apertural notch is present. A shallow posterior canal is moderately well defined. The base of the body whorl contains a very robust spiral ridge. The ornamentation on the ridge is well developed. Where axial and spiral ribs meet narrow, low beads are formed.

Discussion: The attribution to *Rissolina* is based on the presence of a well-developed ridge on the lower half of the body whorl (Ponder, 1984). The sharply delimited spiral cords are exceptional for the subgenus. The species resembles *Rissolina ramai* (Beets, 1941) (various Miocene localities, East Kalimantan). The latter species is slightly larger and has a rounded whorl profile. The axial ribs of *R. ramai* are more numerous and clearly opisthocline, whereas the axial ribs of *R. reticuspiralis* are almost straight. Spiral ribs are usually weaker and more variable in *R. ramai*. That species also has a more clearly defined siphonal notch. The modern Philippine species *Rissoina laevicostulata* Pilsbry, 1904 (Poppe, 2010b: pl. 1306, fig. 8) resembles *R. reticuspiralis* in shape, but it lacks the beaded ornamentation of the varix and the basal ridge. Furthermore, the axial ribs of *R. laevicostulata* seem to be slightly wider, but narrower spaced than in *R. reticuspiralis*. *Rissoina* s.l sp. from Banyunganti resembles *R. reticuspiralis* in ornamentation, but it can be distinguished by its fusiform shape, the stronger rounded whorls, and the slightly stronger axial ribs.

Genus *Stosicia* Brusina, 1870

Subgenus *Isseliella* Weinkauff, 1881

Stosicia (*Isseliella*) sp.

(Pl. 8, Fig. 12)

Material: RGM.784.857 (1)

Remarks: A fragment of a rissoid body whorl is present in the material. It is attributed to the genus *Stosicia* based on the knob in the upper part of the columellar lip. The reticulate ornament typifies subgenus *Isseliella* (Ponder, 1984).

Superfamily Stromboidea Rafinesque, 1815

Family Strombidae Rafinesque, 1815

Genus *Strombus* Linnaeus, 1758

Strombus s.l. sp.

(Pl. 9, Fig. 1)

Material: RGM.784.858 (1 frag.)

Remarks: One fragment of the outer lip of a comparetively large specimen is present. The character of the fragment allows an assignment to Strombidae but is not sufficient for a further classification.

Genus *Varicospira* Eames, 1952

Varicospira sokkohensis (Martin, 1916)

(Pl. 9, Fig. 2)

1916 *Rimella sokkohensis* Martin: 247–248, pl. 2, fig. 50

1931 *Rimella sokkohensis* – van der Vlerk: 245

1994 *Rimella sokkohensis* – Skwarko and Sufiati: g10.

Material: RGM.784.859 (1); RGM.784.860 (48)

Remarks: We follow the assignment to *Varicospira* made by Harzhauser (2007) for *Rimella mordax* Martin, 1916. *Varicospira sokkohensis* was regarded as a synonym of *V. mordax* by van den Hoek Ostende et al. (2002) (see also Leloux and Wesselingh, 2009: *Rimella mordax*; Harzhauser, 2007). In this study we follow the original distinction of the two species made by Martin (1916). *Varicospira mordax* has a somewhat squat shell, whereas the shell of *V. sokkohensis* is higher, slender and acuminated. The long posterior canal is almost straight to the shell axis in *V. mordax*, but it is clearly inclined towards the axis in *V. sokkohensis*. The material from Banyunganti agrees with the type material of *V. sokkohensis*.

Family Seraphsidae Gray, 1853

Genus *Terebellum* Röding, 1798

Terebellum sp. 1

(Pl. 9, Fig. 3)

Material: RGM.784.861 (1)

Remarks: A relatively large fragment of the spire is present. The distinguishing feature of the material is a low suprasutural ridge clearly demarcated from the upper part of the whorl by a furrow.

Terebellum sp. 2

(Pl. 9, Fig. 4)

Material: RGM.784.862 (1)

Remarks: A fragment of the uppermost part of the spire is present. The specimen can be distinguished from *Terebellum* sp. 1 by the absence of a suprasutural ridge.

Superfamily Tonnoidea Suter, 1913 (1825)

Family Ranellidae Gray, 1854

Subfamily Cymatiinae Iredale, 1913

Genus *Sassia* Bellardi, 1873

Sassia (*Cymatiella*) *fennemai* (Martin, 1899)

(Pl. 9, Figs 5-6)

1899 *Triton* (*Colubraria*) *fennemai* Martin: 141, pl. 22, fig. 322

2009 *Sassia* (*Cymatiella*) *fennemai* (Martin, 1899) – Leloux and Wesselingh: 107 (cum. syn.).

Material: RGM.784.863 (2); RGM.784.864 (23)

Remarks: The present shells are conical with straight to slightly convex tangents. The multispiral protoconch appears smooth and is clearly delimited from the teleoconch. The teleoconch is ornamented with regularly spaced axial and spiral ribs of equal strenght that form a reticulate pattern. Additional spiral threads and varices are present. The Banyunganti material represents the first record of *S*. (*C*.) *fennemai* from the early Miocene. Previously the species was only known from the middle and late Miocene of Java (Beu, 2005) and East Kalimantan (Beets, 1986).

?Ranellidae indet. sp.

(Pl. 9, Fig. 7)

Material: RGM.784.865 (1); RGM.784.866 (1)

Remarks: Two apical fragments that do not allow a further identification are present in the material. The large, smooth paucispiral protoconch in combination with the dense teleoconch ornamentation of axial and spiral elements and the presence of varices suggest a placement in Ranellidae.

Superfamily Vermetoidea Rafinnesque, 1815

Family Vermetidae Rafinesque, 1815

Genus *Vermetus* Daudin, 1800

Vermetus s.l. sp.

(Pl. 9, Fig. 8)

Material: RGM.784.867 (1 frag.)

Remarks: The material contains a single fragment with a slightly ovate cross section and an ornamentation of irregular axial ridges that does not allow a further classification.

Informal group Ptenoglossa Gray, 1853

Superfamily Epitonioidea Berry, 1910

Family Epitoniidae Berry, 1910

Genus *Amaea* Adams and Adams, 1853

Amaea sp.

(Pl. 9, Fig. 9)

Material: RGM.784.868 (1); RGM.784.869 (11)

Remarks: The available specimens have an elongate-conical shell with convex whorls regularly increasing in size and an ornamentation of weak, slender axial ribs and narrowly spaced, fine spiral threads forming a cancellate pattern. On later whorls weak tubercles develop on the intersections of axial and spiral ornamentation. The body whorl is lacking in all specimens. The material represents a potentially undescribed species.

Genus *Epitonium* Röding, 1798

Epitonium sp.

(Pl. 9, Fig. 10)

Material: RGM.784.870 (1)

Remarks: A single strongly convex teleoconch whorl is present. The material is insufficient for a species assignment. The convex whorl profile and the ornamentation of straight axial ribs, that are widely spaced, slender and distinctively elevated, are characteristic for the genus.

Superfamily Eulimoidea Philippi, 1853

Family Eulimidae Philippi, 1853

Genus *Melanella* Bowdich, 1822

Melanella sp.

(Pl. 9, Fig. 11)

Material: RGM.784.871 (1); RGM.784.872 (1)

Remarks: The specimens show typical features of the genus, such as an elongate-conical to lanceolate, glossy shell with a straight whorl profile, an indistinct suture, and a spindle-shaped aperture. The protoconch forms a small tip on top of the shell which resembles the modern Indo-Pacific *Melanella teinostoma* (Adams, 1853b) (Poppe, 2008a: pl. 302, figs 5-6), but that species has a more cylindrical shape. A careful revision of Indo-Pacific Eulimidae would be required for a further taxonomic assignment of the species.

Eulimidae indet. sp.

(Pl. 9, Fig. 12)

Material: RGM.784.873 (1); RGM.784.874 (2)

Remarks: The small shells are elongate-ovate and have a subrounded whorl profile that shows the highest convexity on the lower part of the whorl. The protoconch is incomplete in the material. Together with the first teleoconch whorl it forms a tip that is disctinctively smaller than the following teleoconch whorls. The shell is smooth apart from strongly sinuous growthlines. The aperture is ovate to widely spindle-shaped and anteriorly extended. The columella is twisted. The body whorl is slightly turreted. The material shows resemblance with several genera within the family but could not be assigned to a genus beyond doubt.

Superfamily Triphoroidea Gray, 1847

Remarks: Triphoroidea from Banyunganti are present in low numbers. Specimens are ofen incomplete and lack important diagnostic characters, such as the protoconch. Therefore the material is described in open nomenclature, although undescribed species might be present.

Family Triphoridae Gray, 1847

Subfamily Metaxiinae Marshall, 1977

Genus *Metaxia* Monterosato, 1884

Metaxia sp. 1

(Pl. 9, Fig. 13)

Material: RGM.784.875 (1); RGM.784.876 (1)

Remarks: Up to the last 2-2.5 dextrally coiled teleoconch whorls are preserved in the material. The specimens are characterized by their ornamentation of numerous slender, slightly opisthocline axial ribs and three spiral cords forming a slightly irregular cancellate pattern with tubercles at the intersections of axial and spiral ribs.

Metaxia sp. 2

(Pl. 9, Fig. 14)

Material: RGM.784.877 (1)

Remarks: The single specimen is preserved with 4.7 dextrally coiled teleoconch whorls. The material resembles *Metaxia* sp. 1 but can be distinguished by its more strongly rounded whorl profile and the lower number of axial ribs.

Subfamily Triphorinae Gray, 1847

Genus *Triphora* De Blainville, 1828

Triphora s.l. sp. 1

(Pl. 10, Fig. 1)

Material: RGM.784.878 (1); RGM.784.879 (32)

Remarks: The specimens have a subrounded whorl profile. The protoconch is preserved: Protoconch I is smooth and consists of about a half whorl. Protoconch II consists of 1.5 whorls and is ornamented with two spiral ridges and slender sigmoidal axial ribs. The teleoconch is ornamented with regularly spaced, slender, prosocline axial ribs and two widely spaced primary spiral cords. Distinct roundish tubercles form at the intersections of axial and spiral ribs. A single secondary spiral cord developes between the two primary spiral ribs on later teleoconch whorls and becomes progressively more prominent. A short, wide siphonal canal is pointing left-backwards. *Triphora* s.l. sp. 1 resembles *T.* (*Inella*) *javana* (Martin, 1899) in external ornamentation. However, the latter is larger and has a straight overall appearance, whereas *Triphora* s.l. sp. 1 has a somewhat spindle shape.

Triphora s.l. sp. 2

(Pl. 10, Fig. 2)

Material: RGM.784.880 (1); RGM.784.881 (4)

Remarks: The protoconch is lacking in the material. *Triphora* s.l. sp. 2 contains two spiral ribs, whereas *Triphora* s.l. sp. 1 contains three. Furthermore, *Triphora* s.l. sp. 2 has a deeper impressed suture.

Family Cerithiopsidae Adams and Adams, 1853
Genus *Cerithiopsis* Forbes and Hanley, 1851

Cerithiopsis s.l. sp. 1

(Pl. 10, Fig. 3)

Material: RGM.784.882 (1); RGM.784.883 (3)

Remarks: The material contains high, slender shells with an almost straight whorl profile and an ornamentation of numerous slender, slightly opisthocline axial ribs and three spiral cords that form a regular quadrate pattern with tubercles at the intersections of axial and spiral ribs. The protoconch is lacking.

Cerithiopsis s.l. sp. 2

(Pl. 10, Fig. 4)

Material: RGM.784.884 (1)

Remarks: The specimen can be easily distinguished from *Cerithiopsis* s.l. sp. 1 by the more straight-sided whorls and the slightly prosocline position of the axial ribs.

Infraorder Neogastropoda Thiele, 1929

Superfamily Buccinoidea Rafinesque, 1815

Family Columbellidae Swainson, 1840

Genus *Mitrella* Risso, 1826

Mitrella s.l. cf. *njalindungensis* (Martin, 1921)

(Pl. 10, Fig. 5)

cf. 1921 *Columbella* (*Atilia*) *njalindungensis* Martin: 464, pl. 59, figs 47–48

2009 *Atilia njalindungensis* (Martin, 1921) – Leloux and Wesselingh: 48 (cum. syn.).

Material: RGM.784.885 (1); RGM.784.886 (1); RGM.784.887 (23)

Remarks: The shell is conical with a weakly rounded whorl profile. It is widest right above the base of the body whorl. Ornamentation is restricted to the base of the body whorl. Here regularly spaced spiral grooves are present. The aperture is spindle-shaped. Denticulation is present on the inner side of outer and inner lip. It remains unclear if the syntypes designed by Martin (1921) belong to a single species. The specimens from Banyunganti agree especially well with syntype RGM.9615b but remain smaller.

Columbellidae indet. sp.

(Pl. 10, Fig. 6)

Material: RGM.784.888 (1); RGM.784.889 (1)

Remarks: The material differs from *Atilia* cf. *njalindungensis* (Martin, 1921) from Banyunganti by its larger size, the more constricted body whorl resulting in a slightly concave outer lip, the higher number of grooves on the base of the body whorl, and the longer and narrower aperture. The shell of Columbellidae indet. sp. is widest just below the spire, whereas the shell of *A*. cf. *njalindungensis* is widest right above the base of the body whorl.

Family Fasciolariidae Gray, 1853

Subfamily Fusininae Wrigley, 1927

Genus *Fusinus* Rafinesque, 1815

Fusinus sp.

(Pl. 10, Fig. 7)

Material: RGM.784.891 (1)

Remarks: The single spire present in the material precludes a further identification.

Genus *Fasciolaria* Lamarck, 1799

Fasciolaria s.l. sp.

(Pl. 10, Fig. 8)

Material: RGM.784.892 (1); RGM.784.893 (2)

Remarks: Incomplete, subadult specimens are present. The material could not be identified on species level nor equivocally attributed to a genus of fasciolariids. The paucispiral protoconch suggests a close relationship with *Fusinus* (G. Vermeij, pers. comm., 2010).

Superfamily Muricoidea Rafinesque, 1815

Family Muricidae Rafinesque, 1815

Subfamily Coralliophilinae Chenu, 1858

Genus *Coralliophilia* Adams and Adams, 1853

Coralliophila sp.

(Pl. 10, Fig. 9)

Material: RGM.784.895 (1)

Remarks: The genus assignment of the present material is based on the dense ornamentation of closely positioned spiral cords with a characteristic scaled appearance. The specimen resembles modern representatives of the genus as illustrated in Poppe, 2008b (e.g., *Coralliophila infantula* Kosuge, 1985: pl. 416, figs 1-2) but does not fully confirm any of the illustrated species in that work. It might represent an undescribed species.

Subfamily Muricinae Rafinesque, 1815

Genus *Calotrophon* Hertlein and Strong, 1951

Subgenus *Panamurex* Woodring, 1959

Calotrophon (*Panamurex*) sp.

(Pl. 10, Fig. 10)

Material: RGM.784.894 (1)

Remarks: The available specimen resembles well modern representatives of *Calotrophon* (*Panamurex*) [e.g., *Calotrophon* (*Panamurex*) *lychnia* (Gardner, 1947) in Merle et al., 2011: pl. 147, fig. 4]. Fossil representatives of the subgenus are known from the western Atlantic, Europe, and the eastern Pacific; the oldest record is from the early Oligocene. Modern species are known from the western Atlantic and Somalia (Merle et al., 2011). The present specimen is the first fossil record of the subgenus in the Indo-Pacific and may represent an undescribed species.

Subfamily Typhinae Cossman, 1903

Genus *Typhina* Jousseaume, 1880

Typhina cf. *macropterus* (Martin, 1884)

(Pl. 10, Fig. 11)

cf. 1884 *Typhis macropterus* Martin: 98, pl. 6, fig. 100

2009 *Talityphis macropterus* (Martin, 1884) – Leloux and Wesselingh: 94 (cum. syn.).

Material: RGM.784.896 (1)

Remarks: Only one apical fragment is present. The material is insufficient for an accurate species identification. Nevertheless, the spire fragment resembles the type material quite well.

Typhinae indet. sp.

(Pl. 10, Fig. 12)

Material: RGM.784.897 (1 frag.)

Remarks: One fragment of a distinct wing-shaped outer lip is present. The shape is characteristic for species within the subfamily Typhinae.

Muricidae indet. sp.

(Pl. 10, Fig. 13)

Material: RGM.784.898 (1)

Remarks: The present poorly preserved apical fragment is not sufficient for a further classification.

Family Costellariidae MacDonald, 1860

Genus *Vexillum* Röding, 1798

Remarks: The costellariids from Banyunganti are assigned to eight different species and for the moment attributed to *Vexillum*. The material almost certainly includes undescribed species, but confirmation would require an extensive revision of Indo-Pacific Costellariidae which is beyond scope of this study.

Vexillum sp. 1

(Pl. 11, Fig. 1)

Material: RGM.784.899 (1); RGM.784.900 (20)

Remarks: The small shells have a smooth, bulbous protoconch of about 1.4 whorls. The teleonconch whorls are slightly convex to almost straight and ornamented with up to 11 strong, regularly spaced, gently curved axial ribs, resulting in a wavy appearance of the suture and a slightly stepped periphery. Four oblique columellar folds are present; the uppermost is strongest and the lowest is very weak. A moderately strong denticulation is present in the interior of the outer lip.

Vexillum sp. 2

(Pl. 11, Fig. 2)

Material: RGM.784.901 (1); RGM.784.902 (5)

Remarks: The material closely resembles *Vexillum* sp. 1 in size and shell shape but has a teleoconch ornamentation of more numerous axial ribs (approximately 17 on the body whorl). The ribs are furthermore slightly more slender, and less elevated than in *Vexillum* sp. 1.

Vexillum sp. 3

(Pl. 11, Fig. 3)

Material: RGM.784.903 (1)

Remarks: The small individual is more slender than *Vexillum* sp. 1 and *Vexillum* sp. 2. The ornamentation of the shell resembles *Vexillum* sp. 1, but the material can be distinguished by the protoconch. The protoconch of *Vexillum* sp. 3 is higher, narrower, and comprises about 0.25 whorls more than the protoconch of *Vexillum* sp. 1.

Vexillum sp. 4

(Pl. 11, Fig. 4)

Material: RGM.784.904 (1); RGM.784.905 (8)

Remarks: *Vexillum* sp. 4 can be distinguished from the previous *Vexillum* forms by its larger size. The shell is elongate-ovate with evenly convex whorls and a slightly stepped whorl profile. It is ornamented with up to 18 distinct, straight to slightly opisthocline, regularly spaced axial ribs. Four columellar folds are present; the upper one is strongest and less oblique than the lower three. The siphonal canal is short and straight. Numerous narrow ridges are seen in the interior of the inner lip.

Vexillum sp. 5

(Pl. 11, Fig. 5)

Material: RGM.784.906 (1); RGM.784.907 (7)

The material resembles *Vexillum* sp. 4 but can be distinguished by its wider shell shape, the more strongly inflated later teleoconch whorls, and the wider and less numerous axial ribs (approximately 15 on the body whorl).

Vexillum sp. 6

(Pl. 11, Fig. 6)

Material: RGM.784.908 (1)

Remarks: The apical fragment belongs to a relatively wide shell with a clearly stepped whorl profile. It most closely resembles *Vexillum* sp. 5 but can be distinguished by the lower number of axial ribs on early whorls (approximately nine, wheras *Vexillum* sp. 5 has 13). The ribs are furthermore wider and slightly lower than in *Vexillum* sp. 5.

Vexillum sp. 7

(Pl. 11, Fig. 7)

Material: RGM.784.909 (1)

Remarks: The single incomplete specimen is small with a wide, squat shell and up to eleven wide, roundish axial ribs. It can be easily distinguished from the other present *Vexillum* forms by the combination of small size and squat shape.

Vexillum sp. 8

(Pl. 11, Fig. 8)

Material: RGM.784.910 (1); RGM.784.911 (1)

Remarks: Although only one spire (RGM.784.910) and one subadult specimen (RGM.784.911) are present, the material can be easily distinguished from the other *Vexillum* forms present in the fauna by its conical shape, the straight whorl profile, and the character of the axial ribs that are opisthocline and thickened on the lower half of the whorl and have a slightly prosocyrt profile on the upper half.

Family Cystiscidae Stimpson, 1865

Remarks: Cystiscidae from Banyunganti are described in open nomenclature but presumably include undescribed species. Confirmation would require a thorough revision of the family in the Indo-Pacific.

Subfamily Cystiscinae Stimpson, 1865

Genus *Cystiscus* Stimpson, 1865

Cystiscus sp.

(Pl. 11, Fig. 9)

Material: RGM.784.912 (1); RGM.784.913 (5)

Remarks: The material is characterized by its widely ovate shape, being widest at the shoulder of the aperture, and a depressed spire. Three oblique columellar folds occupy less than half of the inner lip with the uppermost fold being the weakest. A distinctively thickened outer lip with a smooth interior is present. The anterior end of the shell is rounded. The placement in genus *Cystiscus* is based on the genus classification for *Euliginella* Laseron, 1957 which is a synonym of *Cystiscus* (Coovert and Coovert, 1995). The material resembles the modern species *Cystiscus triangularis* Cossignani, 2008 (Poppe, 2008b: pl. 510, figs 5a,b), but the latter lacks a thickened outer lip.

Subfamily Persiculinae Coovert and Coovert, 1995

Genus *Gibberula* Swainson, 1840

Gibberula sp. 1

(Pl. 11, Fig. 10)

Material: RGM.784.914 (1); RGM.784.915 (5)

Remarks: The specimens are ovate and have slightly elevated, rounded spires. Three oblique columellar folds occupy about the lower third of the inner lip with the uppermost fold being the weakest. A moderately strong denticulation is seen on the inner side of the outer lip. A shallow anterior sinus is present.

Gibberula sp. 2

(Pl. 11, Fig. 11)

Material: RGM.784.916 (1); RGM.784.917 (25)

Remarks: The material contains ovate shells with moderately elevated spires. Four oblique columellar folds occupy the lower half of the inner lip with the uppermost fold being the weakest. A moderately strong denticulation is seen on the inner side of the outer lip. A deep anterior sinus is present. *Gibberula* sp. 2 resembles the modern Indo-West-Pacific *Gibberula poppei* Cossignani, 2001 (Poppe, 2008b: pl. 510, figs 10a-b), but *Gibberula* sp. 2 has a stronger developed anterior sinus and a more strongly rounded shell outline.

Family Marginellidae Fleming, 1828

Remarks: All marginellids from Banyunganti that are described in open nomenclature represent potentially undescribed species. Confirmation requires an extensive revision of the family in the Indo-Pacific.

Subfamily Marginellinae Fleming, 1828

Genus *Dentimargo* Cossmann, 1899

Dentimargo sp. 1

(Pl. 12, Fig. 1)

Material: RGM.784.918 (1); RGM.784.919 (41)

Remarks: The available specimens have biconical shells with an elevated, long, conical spire that occupies more than one third of the shell height. The whorl profile is weakly convex. Four distinct columellar folds occupy more than the lower half of the inner lip. The upper pair is perpendicular to the shell's vertical axis and the lower pair is oblique. A distinctively thickened outer lip forms a rounded external varix, clearly demarcated by a groove. Roundish plications are present at the interior of the outer lip, the upper two to three are clearly the strongest. An anterior sinus is lacking.

Dentimargo sp. 2

(Pl. 12, Fig. 2)

Material: RGM.784.920 (1); RGM.784.921 (18)

Remarks: The material is distinguished from *Dentimargo* sp. 1 by its biconical-ovate shape, the elevated, rounded spire that occupies about one third of the shell height, and a smooth interior of the outer lip. The body whorl is almost straight-sided to slightly concave.

Genus *Mesoginella* Laseron, 1957

Mesoginella nanggulanensis (martin, 1916) comb. nov.

(Pl. 12, Fig. 3)

1916 *Marginella* (*Cryptospira*) *nanggulanensis* Martin: 232, pl. 1, fig. 18

2009 *Cryptospira nanggulanensis* (Martin, 1916) – Leloux and Wesselingh: 96 (cum syn.).

Material: RGM.784.922 (1); RGM.784.923 (4 + 2 frags)

Remarks: The material resembles the type material well, although the columella is not preserved or very incomplete in the Banyunganti specimens. The species is placed in the genus *Cryptospira* Hinds, 1844 by Leloux and Wesselingh (2009), but the type material does not have the columellar folds occupying the lower half or more of the inner lip like it is characteristic for the genus (Wakefield, 2010). Therefore, the species is transferred to the genus *Mesoginella* Laseron, 1957, because of the shell shape; the discrete, somewhat rounded whorls; the terminal varix; and the distinct columellar folds occupying less than the lower half of the inner lip (Marshall, 2004).

Genus *Volvarina* Hinds 1844

Volvarina sp. 1

(Pl. 12, Fig. 4)

Material: RGM.784.924 (1), RGM.784.925 (3)

Remarks: The shells are elongate cylindrical with a moderately elevated conical spire. Four oblique columellar folds occupy the lower half of the inner lip, the upper fold is weakest. Narrow ridges are present in the interior of the outer lip. An anterior sinus is lacking. *Volvarina* sp. 1 resembles the modern Indo-West-Pacific *Volvarina hirasei*

Bavay, 1917 in shell shape but has more distinct columellar folds (Poppe, 2008b: pl. 512, figs 6a-b). Furthermore, *V. hirasei* has a sloping shoulder and seems to lack denticles at the interior of the outer lip.

Volvarina sp. 2

(Pl. 12, Fig. 5)

Material: RGM.784.926 (1); RGM.784.927 (9)

Remarks: *Volvarina* sp. 2 and *Volvarina* sp. 1 share features like four oblique columellar folds occupying the lower half of the inner lip with the upper one being weakest, a denticulation of the interior of the outer lip, and a lacking anterior sinus. However, they can be easily distinguished by shell shape. *Volvarina* sp. 2 is elongate-ovate and has a short rounded spire, whereas *Volvarina* sp. 1 is elongate cylindrical with a conical spire.

Family Mitridae Swainson, 1829

Subfamily Mitrinae Swainson, 1829

Genus *Mitra* Lamarck, 1798

Mitra cf. *sokkohensis* Martin, 1916

(Pl. 12, Fig. 6)

cf. 1916 *Mitra* (*Cancilla*) *sokkohensis* Martin: 237, Pl. 1, Figs 29-30

2009 *Vexillum sokkohensis* Martin, 1916 – Leloux and Wesselingh: 96 (cum. syn.).

Material: RGM.784.928 (1)

Remarks: The species is represented by a spire only. It resembles *M. sokkohensis* Martin, 1916, but it differs slightly from the type material in ornamentation. *Mitra sokkohensis* has narrower spaced growth lines that give the interspaces of the spiral cords a slightly more punctuated appearance rather than forming a quadrate pattern like in the studied specimen. The species has been assigned to *Vexillum* by Leloux and Wesselingh (2009), but the original genus assignment is favoured, because the species is lacking distinct axial ribs.

Superfamily Olivoidea Latreille, 1825

Family Olividae Latreille, 1825

Subfamily Ancillariinae Swainson, 1840

Genus *Ancilla* Lamarck, 1799

Ancilla cf. *cinnamomea* sensu Beets, 1941 non Lamarck, 1801

(Pl. 12, Fig. 7)

cf. 1941 *Ancilla cinnamomea* Lamarck, 1801 – Beets: 105–106.

Material: RGM.784.929 (1)

Remarks: Beets (1941) identified four ancillarid specimens from L 114 as *A. cinnamomoea* Lamarck, 1801. His classification is not correct, because *A. cinnamomoea* has seven to eleven lirae on the columellar pillar (Kilburn, 1981), whereas the material from L 114 contains only five lirae. The columella of the Banyunganti specimen is incomplete and poorly preserved but a low number of lirae appears to be present. Three of the specimens documented by Beets (1941) can be distinguished from the present material by their higher, narrower, and more acuminate spire, whereas the fourth specimen resembles the material quite well. However, important diagnostic characters like the columellar pillar and the labral denticle are incomplete or missing in the Banyunganti specimens as well as in the single specimen that resembles our material. It is possible that *A. cinnamomea* from L 114 actually comprises two species one of which resembles the species from Banyunganti.

Ancilla sp.

(Pl. 12, Fig. 8)

Material: RGM.784.930 (1)

Remarks: The material is not sufficiently preserved for a further classification. It is distinguished from *A.* cf. *cinnamomea* Beets, 1941 non Lamarck, 1801 from Banyunganti by its much wider apical angle.

Genus *Oliva* Bruguière, 1789

Oliva s.l. sp.

(Pl. 12, Fig. 9)

Material: RGM.784.931 (1)

Remarks: The material contains one juvenile specimen that could not be identified beyond genus level. It has convex whorls well separated by a deeply channeled suture.

Family Olivellidae Troschel, 1869

Genus *Olivella* Swainson, 1831

Olivella sp.

(Pl. 12, Fig. 10)

Material: RGM.784.932 (1); RGM.784.933 (68)

Remarks: Diagnostic characters of the available specimens are their elongate-ovate shape, a deeply channeled suture, four oblique columellar folds, the ribbed interior of the outer lip, and the lack of an anterior sinus. It is quite possible that it concerns an undescribed species.

Superfamily Conoidea Fleming, 1822

Remarks: The large superfamily Conoidea includes several families currently under revision that yield multiple unresolved issues regarding their taxonomy (e.g., Bouchet et al., 2011). Conoidea present in the Banyunganti material are often represented by fragments or single juveniles precluding an accurate classification. The material is therefore largely described in open nomenclature.

Family Conidae Flemming, 1822

Genus *Fusiconus* Da Motta, 1991

?*Fusiconus arntzenii* (Martin, 1916)

(Pl. 13, Fig. 2)

1916 *Conus arntzenii* Martin: 228, pl. 1, figs 9-10

2009 *Lautoconus*? *arntzenii* (Martin, 1916) – Leloux and Wesselingh: 71 (cum. syn.).

Material: RGM.784.937 (1); RGM.784.938 (50)

Remarks: The species is placed in genus *Fusiconus* by Tucker and Tenorio (2009). The shell contains a single spiral groove dissecting the whorls before the body whorl. That is characteristic for the genus (Tucker and Tenorio, 2009). However, *F. arntzenii* lacks a distinct scalariform outline of the spire which also appears characetristic for the genus. We are uncertain about the base for the assignment by Tucker and Tenorio (2009) as another conid species described by Martin does confirm the generic characteristics of *Fusiconus* (Tucker and Tenorio, 2009: 85–86). We can not rule out that the authors mixed up the two species.

Fusiconus spolongensis (Martin, 1916) comb. nov.

(Pl. 13, Fig. 1)

1916 *Conus* (*Leptoconus*) *spolongensis* Martin: 228, pl. 1, fig. 8

2009 *Leptoconus spolongensis* (Martin, 1816) – Leloux and Wesselingh: 71 (cum. syn.).

Material: RGM.784.939 (1); RGM.784.940 (5)

Remarks: The most characteristic feature of the species is the highly elevated spire with a distinct scalariform outline. The species is placed in genus *Austroconus* by Tucker and Tenorio (2009) while ?*F. arntzenii* is placed in genus *Fusiconus*, although it lacks the scalariform outline typifying the genus (see also remarks under ?*F. arntzenii* above). We suspect that the two species might have been accidentally mixed up by Tucker and Tenorio (2009). Because of the distinct scalariform spire of *F. spolongensis* an assignment to the genus *Fusiconus* is here favoured.

Genus *Phasmoconus* Mörch, 1852

Phasmoconus aff. *hulshofi* (Martin, 1906)

(Pl. 13, Fig. 3)

1906 *Conus hulshofi* Martin: 290, pl. 42, figs 695-697

2009 *Conus hulshofi* Martin, 1906 – Leloux and Wesselingh: 68 (cum. syn).

Material: RGM.784.941 (1)

Remarks: The species is represented by a spire that resembles the type material very well. However, *P. hulshofi* (Martin, 1906) shows only three spiral grooves on the upper part of the base of the body whorl, but a spiral ornamentation of at least ten grooves continues on the Banyunganti specimen. The genus assignment follows Tucker and Tenorio (2009).

Conidae indet. sp. 1

(Pl. 13, Fig. 4)

Material: RGM.784.934 (1); RGM.784.935 (9)

Remarks: The material only contains juvenile and subadult specimens mainly represented by apical fragments. The main diagnostic characteristics are a low spire and a lack of ornamentation apart from well visible, crescent shaped growthlines.

Conidae indet. sp. 2

(Pl. 13, Fig. 5)

Material: RGM.784.936 (1)

Remarks: A single juvenile specimen is present that is not sufficient for a further identification. It resembles Conidae indet. sp. 1 in shape but is distinguished by a suprasutural bulge and spiral grooves on the upper half of the whorls.

Family Clathurellidae Adams and Adams, 1858

Genus *Lienardia* Jousseaume, 1884

Lienardia sp.

(Pl. 13, Fig. 6)

Material: RGM.784.942 (1); RGM.784.943 (4)

Remarks: The specimens show all characteristics for the genus after Powell (1966): a small, solid shell with a strong ornamentation of rounded axial ribs and sharp spirals; a smooth paucispiral protoconch; a narrow aperture; a short deeply notched siphonal canal; a terminal varix; a very deep u-shaped subsutural sinus; and denticles on the inside of outer and inner lip. In the present material the uppermost denticle on the inner side of the outer lip is clearly the strongest.

Family Mangeliidae Fischer, 1883

Genus *Eucithara* Fischer, 1883

Eucithara sp. 1

(Pl. 13, Fig. 7)

Material: RGM.784.944 (1); RGM.784.945 (6)

Remarks: The present material shows resemblance to *Eucithara sawitrae* (Beets, 1941) (L 114) *Eucithara* sp. 1 can be distinguished from that species by its smaller size and the lower number of axial ribs on later whorls. Furthermore, *Eucithara* sp. 1 is more slender than the holotype of *E. sawitrae* (RGM.312.527).

Eucithara sp. 2

(Pl. 13, Fig. 8)

Material: RGM.784.946 (1); RGM.784.947 (11)

Remarks: *Eucithara* sp. 2 clearly differs from *Eucithara* sp. 1 by a larger, spindle-shaped shell and by ornamentation. It has a conical spire and an almost straight whorl profile.The axial ribs of *Eucithara* sp. 2 are wider and prosocline, but they are very narrow and opisthocline in *Eucithara* sp. 1.

Eucithara sp. 3

(Pl. 13, Fig. 9)

Material: RGM.784.948 (1)

Remarks: The specimen is lacking the body whorl. It shows more resemblance to *Eucithara* sp. 2 than to *Eucithara* sp. 1 concerning the shape of the spire, but it can be easily distinguished from the former by its more convex whorls and the opisthocline axial ribs. The specimen contains clearly wider, less sharp, and narrower spaced spiral ribs than *Eucithara* sp. 1 and *Eucithara* sp. 2.

Eucithara sp. 4

(Pl. 13, Fig. 10)

Material: RGM.784.949 (1)

Remarks: One incomplete spire is present in the material. It has been assigned to the genus based on the resemblance with *Eucithara* sp. 1. The two species share a convex whorl profile; narrow, widely spaced opisthocline axial ribs; and a fine spiral ornament. However, *Eucithara* sp. 4 is larger and the axial ribs remain strongly opisthocline to prosocyrt in, wheras they become straighter on later whorls in *Eucithara* sp. 1.

Family Raphitomidae Bellardi, 1875

Genus *Pseudodaphnella* Boettger, 1895

Pseudodaphnella sp. 1

(Pl. 14, Fig. 1)

Material: RGM.784.950 (1); RGM.784.951 (3)

Remarks: The shells have subrounded whorls with a subsutural angulation. The material most closely resembles species of the genus *Pseudodaphnella* regarding the teleoconch ornament of sharp, slender axial ribs crossed by sharp spiral cords, resulting in a distinct reticulate pattern with acuminate beads at the intersections of axial and spiral ribs. The protoconch ornamentation of fine spirals and thin axial riblets that form a lattice ornament is consistent with Powell's (1966) definition of the genus. The only disagreement between the Banyunganti specimens and the genus definition by Powell (1966) concerns the number of protoconch whorls of two to three in Powell's description and less than two in our specimens.

Pseudodaphnella sp. 2

(Pl. 14, Fig. 2)

Material: RGM.784.952 (1)

Remarks: The genus assignment is based on the protoconch and teleoconch ornamentation as described by Powell (1966). The specimen is distinguished from

Pseudodaphnella sp. 1 by evenly convex whorls lacking an angulation and by a lower number of axial ribs. The ribs are furthermore clearly opisthocline in *Pseudodaphnella* sp. 2 but slightly prosocline in *Pseudodaphnella* sp. 1.

Pseudodaphnella sp. 3

(Pl. 13, Fig. 3)

Material: RGM.784.953 (1); RGM.784.954 (2)

Remarks: The material resembles *Pseudodaphnella* sp. 2 in teleoconch as well as in protoconch ornamentation. It can be distinguished by a shouldered whorl profile and a subsutural ramp that lacks spiral ornamentation.

Raphitomidae indet. sp. 1

(Pl. 14, Fig. 4)

Material: RGM.784.955 (1)

Remarks: The material contains an incomplete spire that is insufficient for a genus assignment. Characteristics of the teleoconch are convex, slightly angulated whorls and a strong reticulate ornamentation of evenly spaced, narrow, rounded axial ribs and elevated, narrow, sharp spiral lirae. The ultimate protoconch whorl is preserved. It has a diagonally cancellate ornament.

Raphitomidae indet. sp. 2

(Pl. 14, Fig. 5)

Material: RGM.784.956 (1)

Remarks: An incomplete spire including the last protoconch whorl is present. The material is insufficient for a further classification. The specimen resembles Raphitomidae indet. 1 in protoconch as well as in teleoconch ornamentation, but it has a clearly defined shoulder, a concave subsutural ramp, wider spaced axial ribs, and stronger tubercles at the intersections of axial and spiral ribs. Raphitomidae indet. sp. 1 and Raphitomidae indet. sp. 2 likely belong to the same genus.

Family Drilliidae Olsson, 1964

Genus *Splendrillia* Hedley, 1922

?*Splendrillia* sp.

(Pl. 14, Fig. 6)

Material: RGM.784.957 (1)

Remarks: Only a spire lacking the protoconch is present in the material, making a genus assignment difficult. The specimen is tentatively placed in *Splendrillia* because of the shell's glossy appearance and the presence of a distinct subsutural bulge followed by a deep shoulder sulcus and prominent axial ribs. A fine spiral liration like in our material might be present in the genus (Powell, 1966).

Genus *Tylotiella* Habe, 1958

Tylotiella sp.

(Pl. 14, Fig. 7)

Material: RGM.784.958 (1); RGM.784.959 (1)

Remarks: The two specimens, although relatively poorly preserved, are consistent with Powell's (1966) definition of the genus. Characters for the genus are moderate size; solid, claviform shell with a tall spire and a truncated body whorl; smooth, paucispiral protoconch; teleoconch ornamentation of "fold-like, slightly oblique axials, extending from suture to suture and partly over the base, weaker over the shoulder sulcus, and nowhere developed into peripheral nodes or tubercles" (Powell, 1966).

?Drilliidae indet.

(Pl. 14, Fig. 8)

Material: RGM.784.960 (1)

Remarks: A single incomplete body whorl that does not match any of the other specimens from Banyunganti is present. The material is considered to be insufficient for a further classification. The species is for now placed in Drillidae because of the dominant axial ribs and the weak, very low spiral ornamentation (Bouchet et al., 2011).

Family Pseudomelatomidae Morrison, 1965

Genus *Crassispira* Swainson, 1840

Crassispira molengraafi (Martin, 1916)

(Pl. 14, Fig. 9)

1916 *Drillia* (s. str.) *molengraaffi* Martin: 230, Pl. 1, Fig. 14

2009 *Crassispira molengraafi* (Martin, 1916) – Leloux and Wesselingh: 64 (cum. syn.).

Material: RGM.784.961 (1); RGM.784.962 (17)

Remarks: The shell is slender with a conical spire and an ornamentation of rounded axial ribs and spiral cords and threads. A distinct subsutural bulge divided by a spiral groove is present. The shoulder sulcus is deep and ornamented with only spiral threads. The deep u-shaped anal sinus is located at the shoulder sulcus.

Genus *Inquisitor* Hedley, 1918

Inquisitor sp. 1

(Pl. 14, Figs 10-11)

Material: RGM.784.963 (1); RGM.784.964 (1); RGM.784.965 (3)

Remarks: Powell (1966: p. 79) noted a “strong subsutural fold composed of two linear spaced cords, followed by a rather deep and narrow spirally lirate shoulder sulcus” as typical for the genus. The Banyunganti material agrees with these characters. The material is also in agreement with the genus definition in shell shape and teleoconch ornamentation. The only disagreement between the present specimens and the genus definition by Powell (1966) concerns the small size of the specimens from Banyunganti and the number of protoconch whorls. That is 2.5 whorls for smooth, rounded protoconchs in the genus definition and less than 2 whorls in the present material.

?*Inquisitor* sp. 2

(Pl. 14, Figs 12-13)

Material: RGM.784.966 (1); RGM.784.967 (1); RGM.784.968 (2)

Remarks: The genus assignment of the material is problematic, because only early teleoconch whorls are known. The specimens have a very characteristic conical protoconch of about four whorls that are smooth apart from a fine supersutural ridge. The protoconch is delimited from the teleoconch by a strongly developed, highly elevated axial riblet. The teleoconch ornamentation of axial ribs and spiral cords suggests a placement in the Pseudomelatomidae. According to the multispiral, conical protoconch the species likely belongs to *Inquisitor*.

Pseudomelatomidae indet. 1

(Pl. 15, Fig. 1)

Material: RGM.784.969 (1)

Remarks: A single body whorl is present. The material is considered to be insufficient for a further classification. The Banyunganti specimen resembles the genus *Austrotoma* Finlay, 1924 as illustrated in Powell (1966: text figure A3, 18) in shape and position of the sinus.

Pseudomelatomidae indet. 2

(Pl. 15, Fig. 2)

Material: RGM.784.970 (1)

Remarks: A single body whorl is present, considered as insufficient for a further classification.

?Pseudomelatomidae indet. 3

(Pl. 15, Fig. 3)

Material: RGM.784.971 (1)

Remarks: The material contains an incomplete spire lacking the protoconch and is therefore insufficient for a further classification. The ornament of the fragment resembles the ornament of *Crassispira molengraafi* (Martin, 1916). The fragment can be distinguished from that species by its steeper and wider shoulder sulcus and the presence of only two distinct primary spiral cords. The species is assigned to Pseudomelatomidae because of the presence of well developed spiral elements overrunning the axial ribs.

Family Clavatulidae Gray, 1853

Genus *Clavatula* Lamarck, 1801

Clavatula s.l. sp.

(Pl. 15, Fig. 4)

Material: RGM.784.974 (1); RGM.784.975 (4)

Remarks: The shell has an almost biconical shape. The protoconch is paucispiral and smooth. The teleoconch shows a reticulate ornamentation with slightly more dominant axial ribs. A distinct, somewhat angulated subsutural bulge is present. Below it a shoulder sulcus and a clearly angulated shoulder are developed. The siphonal canal is relatively short and straight. Ridges are seen on the inner side of the outer lip. Because the anal sinus is not located at the whorl periphery, an assignment to Clavatulidae rather than Turridae is favoured (E. Robba, pers. comm., 2012).

Genus *Turricula* Schuhmacher, 1817

?*Turricula kelirensis* (Martin, 1916)

(Pl. 15, Fig. 5)

1916 *Surcula kelirensis* Martin: 228, pl. 1, figs 11-12

2009 *Turricula kelirensis* (Martin, 1916) – Leloux and Wesselingh: 80 (cum. syn.).

Material: RGM.784.972 (1); RGM.784.973 (19)

Remarks: The turreted shell is ornamented with very regular, thin but distinct axial ribs and three primary spiral cords on the lower half of the whorl. Axial and spiral ribs form a reticulate pattern. A distinct shoulder at the middle of the whorl and a deep shoulder sulcus with well visible concave growthlines develop on later teleoconch whorls. Thin spiral ridges are present on the inner side of the outer lip. It is questionable if the assignment to *Turricula* (Leloux and Wesselingh, 2009; Skwarko and Sufiati, 1994; van den Hoek Ostende et al., 2002) is correct, because the distinct reticulate ornament is untypical for the genus.

Family Strictispiridae McLean, 1971

Genus *Strictispira* McLean, 1971

Strictispira sp.

(Pl. 15, Fig. 6)

Material: RGM.784.976 (1); RGM.784.977 (3)

Remarks: The specimens are assigned to genus *Strictispira* according to their resemblance with modern *Strictispira* species such as *Strictispira solida* (C.B. Adams, 1850) (Bouchet et al., 2011: fig. 11 E). However, *S. solida* shows a clearly higher number of axial ribs. If confirmed, our material would represent the first Indo-Pacific record of a likely undescribed *Strictispira* species. The genus is so far known from the tropical Atlantic only.

Family Terebridae Mörch, 1852

Subfamily Terebrinae Mörch, 1852

Genus *Terebra* Bruguière, 1789

Terebra s.l. sp.

(Pl. 15, Fig. 7)

Material: RGM.784.978 (1); RGM.784.978 (1)

Remarks: The material is incomplete and poorly preserved and therefore remains unclassified.

Superfamily Cancellarioidea Forbes and Hanley, 1851

Family Cancellariidae Forbes and Hanley, 1851

Cancellariidae indet. sp.

(Pl. 15, Fig. 8)

Material: RGM.784.980 (1)

Remarks: A large multispiral protoconch of 3.1 whorls rapidly increasing in size is present. It is ornamented with two thin but distinct spiral ridges on the upper half of the whorl which is characteristic for cancellariids.

Clade Heterobranchia Gray, 1840

Informal group "Lower Heterobranchia"(= Allogastropoda)

Superfamily Acteonoidea d'Orbigny, 1843

Family Acteonoidae d'Orbigny, 1843

Genus *Acteon* Montfort, 1810

Acteon s.l. sp.

(Pl. 15, Fig. 9)

Material: RGM.785.008 (1); RGM.785.009 (1 + 1 frag.)

Remarks: The material contains subadult specimens with an ornamentation of low, narrowly spaced spiral cords. Growthlines are well visible in the interspaces of the spiral ribs, resulting in a pattern of punctuated grooves that is characteristic for the genus. It remains unclear if one additional fragment of a body whorl of a larger individual (RGM.785.009) belongs to same species.

?Acteonidae indet. sp.

(Pl. 15, Fig. 10)

Material: RGM.785.010 (1)

Remarks: A fragment of a lower columella is present in the material. It is characterized by the presence of deep spiral grooves that become shallower and more widely spaced towards the abapical end of the shell. The material does not allow a further classification.

Superfamily Architectonicoidea Gray, 1850

Family Architectonicidae Gray, 1850

Remarks: Bieler (1993) used an eloborate system to name the various spiral ribs of architectonicids that we follow here.

Genus *Adelphotectonica* Bieler, 1987

Adelphotectonica sp.

(Pl. 16, Fig. 1)

Material: RGM.784.981 (1); RGM.784.982 (10)

Remarks: The shell of this potentially undescribed species is widely conical with an almost straight whorl-profile. The upper point of whorl attachment is located at the peripheral keel. The teleoconch ornamentation shows a low subsutural and upper peripheral rib, whereas the middle part of the teleoconch whorls lacks spiral ribs or grooves. Strong growth marks are present. The wide, low, strongly ribbed proxumbilical cord is unusual for the genus (Bieler, 1993).

Genus *Discotectonica* Marwick, 1931

?*Discotectonica* sp.

(Pl. 16, Fig. 2)

Material: RGM.784.983 (1); RGM.784.984 (5)

Remarks: Only the first one to two teleoconch whorls are present in the Banyunganti material, precluding a further taxonomic assignment. The specimens have depressed shells with bulging whorls and a very prominent peripheral keel. A nodulose subsutural rib and two nodulose midribs of equal strength are present. A narrow upper peripheral rib consists of narrower spaced nodules than those on the subsutural and the median ribs. The area between the peripheral keel and the upper peripheral rib is sligthly concave and lacks spiral ornamentation. A narrow, distinct, infraperipheral rib and a weak spiral ridge at the concave area between the peripheral keel and the infraperipheral rib are developed. The umbilical cord is low and strongly ribbed. Four nodulose proxumbilical cords that increase in width towards the umbilicus are present. The material could not be equivocally assigned to a genus. It most closely agrees with the description of *Discotectonica* Marwick, 1931 (Bieler, 1993), although the number of spiral cords on the apical as well as on the adapical side is lower in our material than it is described for the genus.

Genus *Heliacus* d'Orbigny in Sagra, 1842

Subgenus *Heliacus* (*Torinista*) Iredale, 1936

Heliacus (*Torinista*) *implexus* (Mighels, 1845)

(Pl. 16, Fig. 3)

1845 *Solarium implexum* Mighels: 22

1993 *Heliacus* (*Torinista*) *implexus* (Mighels, 1845) – Bieler: 205-207 (cun. syn.).

Material: RGM.784.985 (1)

Remarks: The available specimen has a depressed cone-shaped shell and two prominent peripheral keels, the upper one being stronger. The apical side of the shell is ornamented with four nodolar spiral ribs. A strong umbilical cord and five nodular spiral ribs, that regularly decrease in width with distance from the umbilicus, are present on the base of the shell. The Banyunganti material agrees with Bieler's (1993) description of the species. The species has a continous range in the Indo-Pacific (Bieler, 1993). The present material represents the first fossil record of *H*. (*T*.) *implexus*.

Genus *Psilaxis* Woodring, 1928

Psilaxis cf. *radiatus* (Röding, 1798)

(Pl. 16, Fig. 4)

cf. 1798 *Architectonica radiata* Röding: 79

1993 *Psilaxis radiatus* (Röding, 1798) – Bieler: 117-120 (cun. syn.).

Material: RGM.784.986 (1)

Remarks: The present specimen shows moderately inflated whorls that appear smooth and glossy. A prominent peripheral keel is present. It is accompanied by two weaker but distinct spiral ribs of which one is located above and one below the median keel. *Psilaxis radiatus* (Röding, 1798) can be distinguished from the very similar *Psilaxis oxytropis* (A. Adams, 1855) by its smaller protoconch. Nevertheless, the protoconch diameter of our specimen is slightly smaller than the smallest recorded protoconch of 105 specimens of *P. radiatus* (Bieler, 1993). At the same time the anal keel is distinctively longer. Our specimen has a 0.47 mm long anal keel, but the mean length for the species is 0.27 mm for 217 measured specimens (Bieler, 1993). For that reasons the species assignment remains somewhat uncertain.

Superfamily Pyramidelloidea Gray, 1840

Remarks: Paleogene to Quarternary Pyramidelloidea from Indonesia were recently revised by Robba (2013). None of the taxa from Banyunganti fully confirms the species recognized in that work. Therefore, it is likely that the majority of the Banyunganti material, here described in open nomenclature, could be attributed to new species. However, the low abundance and often incomplete preservation of the available specimens precludes a full taxonomic revision at the moment.

Family Odostomiidae Pelseneer, 1928

Subfamily Odostomiinae Pelseneer, 1928

Genus *Odostomia* Fleming, 1813

Odostomia sp.

(Pl. 16, Fig. 5)

Material: RGM.784.994 (1)

Remarks: The available specimen lacks the protoconch. It has a narrowly conical shell, a moderately convex whorl profile with a subtle suprasutural angulation, a well impressed suture, a smooth shell apart from growthlines, a single very distinct columellar ridge, and a smooth interior of the outer lip. The fossil Indonesian *Odostomia* species illustrated in Robba (2013: pl. 3, figs 3-5) can be distinguished from the studied material by an evenly convex whorl profile lacking an angulation.

Genus *Parodostomia* Laseron, 1959

Parodostomia sp.

(Pl. 16, Fig. 6)

Material: RGM.784.995 (1); RGM.784.996 (35)

Remarks: The present specimens resemble *Odostomia* sp. in shape, but have a slightly convex to almost straight whorl profile, a narrow umbilicus and distinct, elevated ridges at the interior of the outer lip. The genus assignment is based on the latter character and on the intorted protoconch. According to Robba (2013) both are diagnostic characters for the genus in the Paleogene to Quarternary of Indonesia. A grooved suture is considered an additional character for the genus (Robba, 2013), but is lacking in the present material by which it can be distinguished from the fossil Indonesian species illustrated in Robba (2013: pl. 4, figs 1-5, pl. 5, fig. 1).

Subfamily Chrysallidinae Saurin, 1958

Genus *Babella* Dall and Bartsch, 1906

Babella sp.

(Pl. 16, Fig. 7)

Material: RGM.784.987 (1)

Remarks: The specimen is characterized by a stout shell with a conical spire and a straight whorl profile. The teleoconch ornamentation consists of regular, prosocline, slender axial ribs. The body whorl is angular, one distinct spiral cord is present at the base. A single moderately strong columellar fold is developed.

Genus *Pyrgulina* Adams, 1863

Pyrgulina sp. 1

(Pl. 16, Fig. 8)

Material: RGM.784.988 (1); RGM.784.989 (6)

Remarks: Characteristic features of the specimens are an elongate-conical shape, an intorted protoconch, a weak columellar ridge, an ornamentation of strong, prosocline axial ribs that extend on the base, and regular spiral threads best visible in the interspaces of the axial elements. The species most closely resembles *Pirgulina* *wesselinghi* Robba (2013: pl. 11, figs 6-7), but it can be distinguished from that species by its elongate-conical shape, whereas *P. wesselinghi* is more cylindrical.

Pyrgulina sp. 2

(Pl. 16, Fig. 9)

Material: RGM.784.990 (1); RGM.784.991 (1)

Remarks: The available material can be distinguished from *Pyrgulina* sp. 1 by the more slender shape and the straight axial ribs that are prosocline in *Pyrgulina* sp. 1. The columellar fold is strong for the genus.

Family Pyramidellidae Gray, 1840

Subfamily Pyramidellinae Gray, 1840

Genus *Longchaeus* Mörch, 1875

Longchaeus sp.

(Pl. 16, Fig. 10)

Material: RGM.784.997 (1); RGM.784.998 (1)

Remarks: The available specimens have a partially immersed but not fully intorted protoconch, a conical spire with a straight outline, a grooved suture resulting in a peripheral furrow, a smooth shell, three distinct columellar ridges of which the uppermost one is strongest and least oblique, and teeth of different strength in the interior of the outer lip. The characters agree with Robba's (2013) description of the genus. The five fossil Indonesian species illustrated in Robba (2013: pl. 13, figs 3-5, 7-12, pl. 14, figs 1-4) differ from our material in shell shape, convexity of the whorls and/or in the presence of a slight crenulation just below the suture.

Genus *Pyramidella* Lamarck, 1799

Pyramidella sp.

(Pl. 17, Fig. 1)

Material: RGM.784.999 (1)

Remarks: The protoconch is lacking in the studied specimen. It resembles *Longchaeus* sp. in shell shape, in being smooth, and in the characters of the interior of the outer lip and the columellar folds. It can be distinguished by the lack of a grooved suture and the associated peripheral furrow, regarded as the distinctive character between the genera *Pyramidella* and *Longchaeus* according to Robba (2013).

Family Turbonillidae Bronn, 1849

Subfamily Turbonillinae Bronn, 1849

Genus *Asmunda* Dall and Bartsch, 1904

Asmunda sp.

(Pl. 17, Fig. 2)

Material: RGM.785.000 (1); RGM.785.001 (1)

Remarks: The genus assignment is based on the following characters (after Robba 2013): the protoconch is situated perpendicular to the first teleoconch whorl, being slightly immersed in it; a peripheral spiral cord at which the axial ribs end abruptly is present. The material can be easily distinguished from *Asmunda rebjongensis* Robba, 2013 (pl. 17, fig. 7) by its cylindro-conical shape with an almost straight whorl profile.

Asmunda rebjongensis is elongate-conical with more convex whorls. The Banyunganti specimens have a single spiral cord located right above the suture on early whorls, and moving upwards on later whorls.

Genus *Pyrgiscus* Philippi, 1841

?*Pyrgiscus* sp.

(Pl. 17, Fig. 3)

Material: RGM.785.002 (1); RGM.785.003 (5)

Remarks: The specimens have slender elongate-conical shells. The protoconch is helicoid and does not protrude over the first teleoconch whorl. The teleoconch is ornamented with straight to slightly prosocline axial ribs that continue on the base of the body whorl, and numerous spiral threads that are visible at the interspaces of the axial ribs. The columella is slightly twisted. A single prominent spiral cord is present at the upper part of the base of the body whorl.

Genus *Turbolidium* Robba, 2013

Turbolidium sp. 1

(Pl. 17, Fig. 4)

Material: RGM.785.004 (1); 785.005 (4)

Remarks: The genus assignment is based on the following characters (after Robba, 2013): The helicoid protoconch is almost at a right angle to the shell axis with the apex lying at the suture of the first teleoconch whorl. The aperture is ovate-quadrangular. The columella is very gently twisted. The axial ribs fade out over the upper part of the otherwise smooth base of the body whorl. Our material can be distinguished from the type species *Turbolidium schroederi* (Wissema, 1947) (Robba, 2013: pl. 22, fig. 6) by its more slender shell and its whorl profile that is slightly intended at the upper half of the whorl, whereas the whorls of *T. schroederi* are evenly convex. Spiral ornamentation is lacking in our material.

?*Turbolidium* sp. 2

(Pl. 17, Fig. 5)

Material: RGM.785.006 (1)

Remarks: The studied specimen is incomplete. The shell is cylindrical. The columella is slightly twisted but lacks a ridge. Classification of the species is somewhat problematic, because the protoconch is lacking in the material. However, a lack of spiral ornamentation in combination with axial ribs that fade out over the upper part of the otherwise smooth base suggest a placement in genus *Turbolidium* (Robba, 2013). The specimen is distinguished from other Turbonillinae from Banyunganti by a high number of slender, slightly sigmoidal axial ribs. The whorls are more convex than in *Turbolidium* sp. 1.

Genus *Turbonilla* Risso, 1826

Turbonilla sp.

(Pl. 17, Fig. 6)

Material: RGM.785.007 (1)

Remarks: The specimen has an elongate-conical shell with a moderately convex whorl profile, a protoconch with a short spire not projecting over the first teleoconch whorl, a teleoconch ornamentation of axial ribs stopping at the periphery of the last whorl without a peripheral spiral cord being present. Spiral ornamentation is lacking.

Subfamily Eulimellinae Saurin, 1958

Genus *Eulimella* Forbes and MacAndrew, 1846

Eulimella sp.

(Pl. 17, Fig. 7)

Material: RGM.784.992 (1); RGM.784.993 (1)

Remarks: The specimens have high, elongate-conical spires with a slightly convex to almost straight whorl profile, smooth, shiny shells, and a twisted columella bearing a single moderately strong fold. The protoconch is damaged or lacking in the material. The specimens are assigned to the genus *Eulimella* according to shape, the presence of a smooth shell and the absence of a distinct collumellar ridge. *Eulimella* sp. does not resemble any of the fossil Indonesian *Eulimella* species illustrated by Robba (2013: pl. 23, fig. 7; pl. 24, figs 1-6; pl. 25, figs 1, 2).

Superfamily Ringiculoidea Philippi, 1853

Family Ringiculidae Philippi, 1853

Remarks: The following taxa from Bayunganti assigned to genus *Ringicula* are potentially undescribed species. A revision of fossil and modern Indo-Pacific ringiculids is required for confirmation.

Genus *Ringicula* Deshayes, 1838

Ringicula sp. 1

(Pl. 17, Fig. 8)

Material: RGM.785.011 (1); RGM.785.012 (122)

Remarks: The available specimens have small, narrowly ovate shells with a rounded whorl profile and a slight shoulder angulation. The height of the spire equals that of the body whorl. The teleoconch is ornamented with up to approximately 16 regular, closely spaced spiral cords. The aperture is ovate and strongly modified by two very pronounced columellar folds, the upper of which is oblique, and a parietal tooth. The thickened outer lip forms a low, wide, well pronounced bulge with an elongated internal swelling at the middle part of the outer lip. Inner and outer lip are clearly differentiated from the body whorl and surround the aperture completely. The ornamentation of elevated spiral cords instead of grooves seems unusual for the family (e.g., Poppe, 2010a: pl. 741). In addition, none of the *Ringicula* species described by Martin (1879, 1884) is ornamented with spiral cords.

Ringicula sp. 2

(Pl. 17, Fig. 9)

Material: RGM.785.013 (1); RGM.785.014 (91)

Remarks: The material resembles *Ringicula* sp. 1 in shell shape but is provided with spiral grooves with interspaces varying in width instead of elevated cords. In most specimens the interspace between the second and the third or between the third and the fourth spiral groove below the suture on the body whorl are widest. Among the ringiculid species described by Martin (1879, 1884) *Ringicula pygmaea* Martin, 1884 resembles the Banyunganti material most closely but has a narrower spire and lacks the slight shoulder angulation. The first subsutural groove on the body whorl appears to be strongest in *R. pygmaea*, a feature lacking in *Ringicula* sp. 2. The other ringiculids described by Martin (1879, 1884) can easily be distinguished from the Banyunganti material by their larger size and wider, more convex whorls.

Ringicula sp. 3

(Pl. 17, Fig. 10)

Material: RGM.785.015 (1); RGM.785.016 (1)

Remarks: The specimens are distinguished from the other ringiculids from Banyunganti by being more widely ovate and having a spiral ornamentation of approximately up to 20 narrowly spaced spiral grooves. The interspaces between the grooves do not show a variation in width like in *Ringicula* sp. 2. Although the specimens are more ovate than *Ringicula* sp. 2, they remain smaller and less inflated than the *Ringicula* species described by Martin (1879, 1884).

Order Opisthobranchia Milne-Edwards, 1848

Suborder Cephalaspidea Fischer, 1883

Superfamily Philinoidea Gray, 1850 (1815)

Family Cylichnidae adams and adams, 1854

Genus *Cylichna* Lovén, 1846

Cylichna triplicata (Martin, 1916)

(Pl. 17, Fig. 11)

1916 *Bullinella triplicata* Martin: 224, pl. 1, fig. 3

1941 *Cylichna triplicata* – Beets: 144-145, pl. 7, fig. 294

2009 *Cylichna triplicata* – Leloux and Wesselingh: 40 (cum. syn.).

Material: RGM.785.017 (1); RGM.785.018 (49)

Remarks: This *Cylichna* species is characterized by the presence of three columellar folds. Furthermore, spiral grooves are present at the abapical and adapical side of the body whorl but are lacking on the middle segment.

Cylichnidae indet. sp. 1

(Pl. 17, Fig. 12)

Material: RGM.785.019 (1); RGM.785.020 (2)

Remarks: The only more or less complete specimen (RGM.785.019) is slightly compressed and abraded precluding a further taxonomic assignment. The shell is elongate-cylindrical and contains regularly spaced spiral grooves all over the shell's surface.

Cylichnidae indet. sp. 2

(Pl. 17, Fig. 13)

Material: RGM.785.021 (1); RGM.785.022 (2)

Remarks: The studied material contains fragments that preclude a further classification. The shells are solid and show a distinct ornamentation of low, imbricated spiral ridges separated by narrow grooves.

Class Bivalvia Linnaeus, 1758

Subclass Autobranchia Grobben, 1894

Superorder Pteriomorphia Beurlen, 1944

Order Arcida Gray, 1854

Superfamily Arcoidea Lamarck, 1809

Family Glycymerididae Dall, 1908 (1847)

Subfamily Glycimeridinae Dall, 1908 (1847)

Genus *Tucetona* Iredale, 1931

?*Tucetona* sp.

(Pl. 18, Fig.1)

Material: RGM.785.031 (1/2); RGM.785.032 (2 frags)

Remarks: The fragments present in the studied material are ornamented with radial ribs bearing irregularly shaped roundish tubercles varying in size. The material is tentatively assigned to the genus *Tucetona* based on the presence of axial ribs (Nicol, 1956).

Order Pectinida Gray, 1854

Superfamily Pectinoidea Rafinesque, 1815

Family Pectinidae Rafinesque, 1815

Subfamily Chlamydinae Teppner, 1922

Tribe Mimachlamydini Waller, 1993

Genus *Mimachlamys* Iredale, 1929

Mimachlamys sp.

(Pl. 18, Fig. 2)

Material: RGM.785.033 (1 frag.); RGM.785.034 (5 frags)

Remarks: The fragments present in the studied material have evenly spaced, low radial ribs that bear regularly spaced tubercles and are flanked with secondary costallae. The ornament is characteristic for the genus (Dijkstra, 2013).

Family Spondylidae Gray, 1826

Genus *Spondylus* Linnaeus, 1758

Spondylus sp.

(Pl. 18, Fig. 3)

Material: RGM.785.035 (1/2); RGM.785.036 (1 frag.)

Diagnosis: The available material is insufficient for a taxonomic classification. The genus assignment is based on the spinose radial ribs and a partly preserved hinge (RGM.785.035) with very weak primary teeth and well developed secondary teeth and sockets.

Clade Heterodonta Neumayr, 1884

Order Lucinida Gray, 1854

Superfamily Lucinoidea Fleming, 1828

Family Lucinidae Fleming, 1828

Subfamily Lucininae Fleming, 1828

Genus *Cardiolucina* Sacco, 1901

Cardiolucina civica (Yokoyama, 1927)

(Pl. 18, Figs 4-6)

1927 *Cardium civica* Yokoyama, 1927: 179, pl. 48, figs 3-4

1997 *Cardiolucina civica* (Yokoyama, 1927) – Taylor and Glover: 99–102, figs 7–8 (cum. syn.).

Material: RGM.785.041 (1); RGM.785.040 (1 rv); RGM.785.039 (1 lv); RGM.785.042 (3 + 60 rv, 44 lv)

Remarks: The present material agrees with the description and the illustrated material of the modern Indo-Pacific *Cardiolucina civica* (Yokoyama, 1927) provided by Taylor and Glover (1997: 99-102, figs 7-8). This is the first fossil record of the species. The material also shows resemblance with *Cardiolucina antjamensis* (Beets, 1986) from L B [published as *Linga* (*Bellucina*) *antjamensis* Beets, 1986]. Although paratype RGM.312.173 of the latter species contains more strongly elevated and more numerous commarginal ridges than our material, *C. antjamensis* (Beets, 1986) might be a synonym of *C. civica*.

Cardiolucina sp.

(Pl. 18, Figs 7-9)

Material: RGM.785.044 (1); RGM.785.043 (1 rv); RGM.785.045 (1 lv); RGM.785.046 (9 rv, 9 lv)

Remarks: *Cardiolucina* sp. resembles *Cardiolucina civica* (Yokoyama, 1927) in almost all shell characters. However, a clear difference is the lack of strong commarginal ridges. Regarding the latter character *Cardiolucina* sp. might represent an undescribed species.

Order Carditida Dall, 1889

Superfamily Carditoidea Férussac, 1822

Family Carditidae Férussac, 1822

Subfamily Carditinae Férussac, 1822

Genus *Cardita* Bruguière, 1792

Cardita s.l. sp.

(Pl. 18, Fig. 10)

Material: RGM.785.037 (1); RGM.785.038 (3 + 107 rv, 100 lv)

Remarks: The present specimens have subquadrate shells with largest height near the posterior margin. The radial ornamentation consists of 18 well defined ribs. The commarginal ornament forms roundish nodules when crossing the anterior ribs, deloping into scales on the posterior side. The hinge teeth show the fine transversal striation characteristic for carditids. The material appears to include only juvenile and subadult specimens, therefore an accurate identification is difficult.

Order Venerida Gray, 1854

Superfamily Cardioidea Lamarck, 1809

Family Cardiidae Lamarck, 1809

Remarks: Cardiidae from Banyunganti are only represented by damaged valves and fragments in low numbers, therefore they are presented in open nomenclature.

Subfamily Fraginae Stewart, 1930

Genus *Fragum* Röding, 1798

Fragum sp.

(Pl. 18, Fig. 11)

Material: RGM.785.048 (1 lv); RGM.785.049 (4 rv, 3 lv)

Remarks: The shells are strongly inequivalve. The anterior ventral shell margin is short and rounded. The anterior margin is narrow and gently curved ventrally to almost straight dorsally. The posterior part of the shell is extended showing a distinct wing like shape with a long, straight ventral margin, a slightly wavy dorsal margin, and a sharp almost 90° angulation between the two. The shell is ornamented with low radial ribs and a commarginal striation. The most prominent rib runs in a gentle curve from the umbo to the dorsal point where the narrow anterior margin meets with the wing-like posterior margin.

Subfamily Laevicardiinae Keen, 1951

Genus *Nemocardium* Meek, 1876

Nemocardium sp.

(Pl. 19, Fig. 1)

Material: RGM.785.050 (1 rv); RGM.785.051 (1 rv); RGM.785.052 (1 rv)

Remarks: The material is damaged. The ornamentation consists of numerous, regularly spaced, low radial ribs. At some distance from the umbo the narrow interspaces of the ribs bear commarginal riblets. The anterior shell area is almost smooth apart from widely spaced commarginal threads. Those are only present close to the umbo and do not continue over the radial ribs. The genus assignment is based on this latter character.

Subfamily Trachycardiinae Stewart, 1930

Genus *Acrosterigma* Dall, 1900

?*Acrosterigma* sp.

(Pl. 19, Fig. 2)

Material: RGM.785.053 (1 frag.)

Remarks: A single fragment is present in the material. It has a strongly dentate shell margin, a radial ornamentation of wide, low ribs that coincide with the interspaces of the marginal denticles, and strongly sinuouse growthlines. The distinct denticles at the shell margin show some resemblance with modern *Acrosterigma* species, but the material is insufficient for a certain assignment, because other cardiids show similar characters .

Cardiidae indet. sp. 1

(Pl. 19, Fig. 3)

Material: RGM.785.054 (1 rv)

Remarks: An incomplete right valve is available. It has a radial ornamentation of regularly spaced, wide, low ribs that bear distinct roundisch knobs. A narrow keel bearing very small, spiny tubercles is running from the umbo ventro-posteriorly.

Cardiidae indet. sp. 2

(Pl. 19, Fig. 4)

Material: RGM.785.055 (1 lv); RGM.785.056 (1 lv)

Remarks: Two incomplete left valves with a radial ornamentation of regularly spaced, low, slender ribs are available from Banyunganti. A slightly more prominent keel is running from the umbo to the ventro-posterior margin. The material is distinguished from Cardiidae indet. sp. 1 by the lack of spines along the keel.

Cardiidae indet. sp. 3

(Pl. 19, Fig. 5)

Material: RGM.785.057 (1 frag.)

Remarks: A fragment with a clearly dentate shell margin is distinguished from ?*Acrosterigma* sp. by its more elevated radial ribs, and its blunter, more angular marginal denticles. Furthermore, the denticles coincide with the radial ribs in Cardiidae indet. sp. 3, whereas they coincide with the interspaces of the ribs in ?*Acrosterigma* sp.

Superfamily Glossoidea Gray, 1847 (1840)

Family Kelliellidae Fischer, 1887

Genus *Kelliella* Sars, 1870

Kelliella sp.

(Pl. 19, Fig. 6)

Material: RGM.785.058 (1 rv)

Remarks: One right valve is present in the Banyunganti material. It resembles *Kelliella japonica* Hayami and Kase, 1993 (Okutani, 2000: pl. 495, fig. 2), but an attribution to that species needs further confirmation. Today the genus is almost entirely restricted to abyssal depths, but shallow-water records are known from late Eocene to Miocene deposits (Studencka, 1987).

Superfamily Tellinoidea Blainville, 1814

Family Tellinidae Blainville, 1814

Remarks: Only low numbers of damaged valves and fragments of tellinids are present in the Banyunganti material. This and the general difficulties occuring with identifications of tellinids preclude a further identification.

Genus *Arcopagia* Leach, 1927

?*Arcopagia* sp.

(Pl. 19, Fig. 7)

Material: RGM.785.059 (1 lv)

Remarks: The incomplete left valve is relatively thick and moderately inflated. The shell surface is worn, but an ornament of fine widely spaced commarginal striae is still visible. The small, pointed umbo in combination with the appearance of the hinge, although incomplete, supports an assignment to the Tellinidae. According to the relatively thick shell and the semicircular outline the species might belong in the genus *Arcopagia*.

Genus *Tellina* Linnaeus, 1758

Tellina s.l. sp. 1

(Pl. 19, Fig. 8)

Material: RGM.785.060 (1 lv); RGM.785.061 (1 lv); RGM.785.062 (1 lv); RGM.785.063 (2 lv)

Remarks: The material consists of very incomplete left valves only. The thin shells are flat with a small, pointed umbo and a long, straight hinge line. The shell surface is smooth apart from a fine commarginal striation. The hinge consists of two cardinal teeth. The anterior tooth is clearly bifurcate.

Tellina s.l. sp. 2

(Pl. 19, Fig. 9)

Material: RGM.785.064 (1 lv)

Remarks: The incomplete valve is characterized by a well developed ornamentation of narrow but prominent commarginal ridges that dominate a very fine cancellate pattern of numerous, narrowly spaced radial and commarginal striae. The distinct ornamentation is unusual for tellinids, but a typical tellinid hinge is present.

Superfamily Veneroidea Rafinesque, 1815

Remarks: The Banyunganti material in the family Veneroidea that is described in open nomenclature contains only damaged or juvenile specimens, mainly in low numbers, precluding more accurate classifications.

Family Veneridae Rafinesque, 1815

Subfamily Gouldinae Stewart, 1930

Genus *Circe* Schumacher, 1817

Circe junghuhni Martin, 1917

(Pl. 20, Fig. 1)

1917 *Circe* (s. str.) *junghuhni* Martin: 271, pl. 5, figs 128–129

2009 *Circe* (*Circe*) *junghuhni* Martin, 1917 – Leloux and Wesselingh 2009: 14 (cum. syn.).

Material: RGM.785.065 (1 rv); RGM.785.064 (2 + 94 rv, 82 lv + frags)

Remarks: The valves from Banyunganti are all incomplete apart from one small left valve (RGM.785.064). The shells are ovate with a small pointed umbo and an ornament of distinct, regularly spaced commarginal ridges. At the posterior side of the ventral shell margin the ridges end in characteristic thickened nodules.

Circe sp.

(Pl. 20, Fig. 2)

Material: RGM.785.067 (1 rv); RGM.785.068 (1 rv)

Remarks: The two available juvenile valves are subcircular and moderately inflated. The anterior shell margin is slightly bulging. Ornamentation consists of numerous, narrowly spaced commarginal striae. The umbo is small and pointed. Traces of the original color pattern are preserved. The material resembles the modern species *Circe scripta* (Linnaeus, 1758) (Poppe, 2010 b: Pl. 1129, Figs 1-5) in shell shape and ornamentation.

Veneridae indet. sp. 1

(Pl. 20, Figs 3-4)

Material: RGM.785.070 (1 rv); RGM.785.069 (1 lv); RGM.785.071 (12 rv, 13 lv)

Remarks: The material is incomplete. The valves are ornamented with equally spaced, thin and low, well defined commarginal ridges. A strongly prosogyrate umbo and a well-defined large lunula demarcated by a furrow are present.

Veneridae indet. sp. 2

(Pl. 20, Figs 5-6)

Material: RGM.785.072 (1 lv); RGM.785.073 (1 lv); RGM.785.074 (2 lv)

Remarks: Only incomplete left valves are available. The main characteristic feature of the shells is a dense ornamentation of thin, equally spaced commarginal striae instead of slightly elevated ridges like in Veneridae indet. sp. 1.

Veneroidea indet. sp. 1

(Pl. 20, Fig. 7)

Material: RGM.785.075 (1 rv)

Remarks: An incomplete right valve is present in the material. It is solid, inflated and has a circular outline. The umbo is strongly prosogyrate. The hinge is incomplete. One large cardinal tooth parallel to the margin and a deep socket situated above the cardinal are preserved in the specimen. The shell surface appears to be partly covered with sandgrains. It remains unclear if this is a preservational or biological effect.

?Veneroidea indet. sp. 2

(Pl. 20, Fig. 8)

Material: RGM.785.076 (1)

Remarks: The available specimen was originally paired but the valves got separated during investigation, damaging the hinge. The shell is small, subtriangular, and ornamented with fine commarginal striae.

Class Scaphopoda Bronn, 1862

Order Dentaliida Starobogatov, 1974

Family Dentaliidae Children, 1834

Genus *Dentalium* Linnaeus, 1758

Dentalium sp. 1

(Pl. 20, Fig. 9)

Material: RGM.783.220 (1); RGM.783.221 (4)

Remarks: The specimens are relatively robust and thick-shelled. Primary and secondary ribs are irregularly spaced, the finer secondary ribs dissapear during growth.

Dentalium sp. 2

(Pl. 20, Fig. 10)

Material: RGM.783.222 (1); RGM.783.223 (4)

Remarks: The specimens are smaller and thinner-shelled than those of *Dentalium* sp.

1. Ten well defined, regularly spaced primary ribs are present.

Class Polyplacophora Blainville, 1816

Subclass Neoloricata Bergenhayn, 1955

Order Chitonida Thiele, 1909

Suborder Chitonina Thiele, 1909

Superfamily Schizochitonoidea Dall, 1889

Family Schizochitonidae Dall, 1889

Genus *Schizochiton* Gray, 1847

Schizochiton incisus (Sowerby II, 1841)

(Pl. 20, Fig. 11)

Material: RGM.783.224 (1)

Remarks: A single damaged intermediate valve with closely-spaced well-defined longitudinal riblets is present in the material.

5. Results

5.1 Composition of the Fauna

Gastropods (n = 4,086; 92%) are dominant over bivalves (n = 333). The most abundant families are Rissoidae (n = 1,507) and Cerithiidae (n = 747) followed by Ringiculidae (n = 221) and Veneridae (n = 120).

The three most abundant species in the Banyunganti fauna are *Rissoina banyungantiensis* (n = 1,423; 32%), *Cerithidium* cf. *perparvulum* (n = 543; 12%) and *Bothropoma mediocarinata* (n = 365; 8%). Other common species are *Plesiotrochus hasibuani* (4%), *Diala semistriata* s.l., *Cerithium* s.s. sp. 1 and *Ringicula* sp. 1 (3% each). The remaining 35% of the fauna comprise 177 species.

In terms of species numbers gastropods are the most diverse mollusk group in the Banyunganti fauna with 158 species. Bivalves are represented by 22 species, scaphopods by two species, and polyplacophorans by one species.

The most species-rich families are Cerithiidae (15 species), Costellariidae (8 species) and Pseudomelatomidae, Torbonillidae, and Cardiidae (6 species each). Almost 50% of the molluskan families are represented by one or two species only.

5.2 Feeding Ecology

The Banyunganti mollusk fauna has been assigned to five feeding guilds: herbivores and detritivores (HD), predatory carnivores (CP), browsing carnivores (CB), suspension feeders (S), and chemosymbiotic deposit feeders (CD) (Todd, 2001).

Herbivores (e.g., grazers on microalgae) and non-selective detritivores were merged to one feeding guild, because an assignment to one of these groups might vary by genus or even species level (e.g., in Cerithiidae, Rissoidae; Beesley et al., 1998).

Gastropods assigned to the CP-group prey on vagile and whole sedentary organisms. Scavengers were included in the group, because most of them also prey on living organisms and shift facultative to carrion (Britton and Morton, 1994). Assignment to a guild is problematic for the Columbellidae, because the family combines several feeding modes. The food of the majority of columbellids includes some sort of animal material, thus they are here considered as predatory carnivores. Feeders on foraminifera, such as cylichnids and scaphopods, are included in the CP-guild as well.

The guild CB includes highly specialized feeders on predominantly sedentary animals and ectoparasites on a variety of organisms (see "browsing carnivores" in Bouchet et al., 2002; Johnson et al., 2007; Todd, 2001). The assignment of the Marginellidae and Cystiscidae to the group was somewhat problematic, because the feeding habits of both families are not well known. Marginellidae feed on a wide range of animal material, are often highly specialized (e.g., Fretter, 1976), and parasitism is known within the family, hence it is assigned to the CB-group. Cystiscidae were included in the Marginellidae until the division of the two families by Coovert and Coovert (1995). No information on the feeding ecology of cystiscid species has been found in the literature. The family is therefore assigned to the same feeding guild as the Marginellidae.

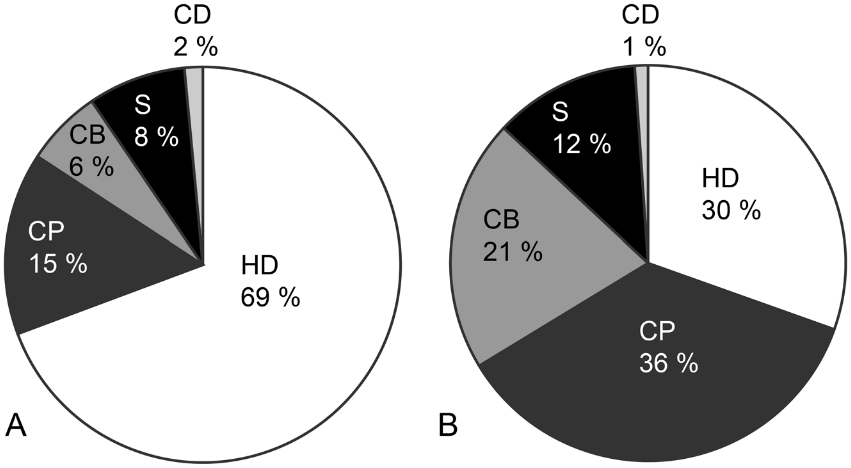

Figure 2: Feeding guild composition of the Banyunganti fauna. A) Abundances of feeding guilds with nspecimens = 4.428. B) Species numbers of feeding guilds with nspecies = 182.

Suspension feeders include most of the bivalves and the Turritellidae, Capulidae, and Vermetidae.

The chemosymbiont guild contains two lucinid species (Williams et al., 2004).

In terms of numbers of specimens the fauna is clearly dominated by herbivores and detritivores (Fig. 2A). In terms of species numbers the fauna is dominated by carnivorous species (Fig. 2B).

5.3 Preservation

For much of the material fine surface ornamentation details and sometimes color patterns are retained. Wear is very rare. Although fragmentation is high, the non-abraded edges of fragments and the predominantly excellent preservation of the ornament of shells suggest shell breakage due to biogenic interactions rather than due to postmortal transportation (e.g., Stanton, 1980). Shell breakage due to sediment compaction, collecting and post-collecting effects likely plays a role as well. Preservation of color patterns occurs in the neritids, *Bothropoma mediocarinata*, *Diala semistriata* s.l., *Cerithium deningeri,* and *Circe* sp. Two specimens of *B. mediocarinata* were found with their opercula still in place. Bivalves are predominantly disarticulated, but left and right valves of common species (> 50 specimens) occur in similar numbers indicating little post-mortem transport (e.g., Lever, 1958).

6. Discussion - Paleoenvironment

The overall excellent preservation of shells including color pattern preservation and in-situ opercula suggests deposition in a low energetic environment and very little to no post-mortem transport of the material. The lack of very fine-grained sediments suggests that the preservation cannot be attributed to rapid “sealing” by mud.

The mollusk fauna is considered to represent a seagrass-associated assemblage.

This assumption is based on a number of arguments. Herbivores and detritivores, particularly small grazers on microalgae, are the most abundant feeding guild in the Banyunganti fauna (Fig. 2A). The numerous occurrence of small herbivores has been used before to infer seagrass vegetation (Brasier, 1975; Davies, 1970; Ivany et al., 1990; Moulinier and Picard, 1952). Within the small herbivores the Bittiinae are very abundant (*Cerithidium* cf. *perparvulum*, n = 543). All living, observed members of *Bittium* graze on epiphytic microalgae that commonly occur on seagrasses (Houbrick, 1993). Another indicator might be *Bothropoma mediocarinata* (n = 365). *Bothropoma* is predominantly associated with seagrasses in the northern Red Sea, although it occurs less abundantly in other habitats as well (Zuschin and Hohenegger, 1998; Zuschin et al., 2009). Reuter et al. (2010) used the numerous occurrence of *Bothropoma* sp. among others as an indicator for an ancient seagrass habitat in the Miocene of India.

The high abundance of small herbivorous species might also be relatively higher as a result of the different life spans of herbivorous and carnivorous gastropod species. Shorter life spans of herbivores compared to carnivores might result in the accumulation of herbivore's shells in a fossil fauna (Albano and Sabelli, 2011; Cadée, 1968).

In general, the ecological composition of the Banyunganti mollusk fauna in terms of feeding guilds appears typical for seagrass-associated mollusk communities (see e.g., Rueda et al., 2009a for comparison), but further research is needed to confirm this assumption. Characteristical elements of the ecological composition of the Banyunganti fauna and likely of other seagrass-associated mollusk faunas are, besides the high abundance of herbivores and detritivores, the high diversity in the CP and CB-guilds and the presence of lucinids (Van der Heide et al., 2012; J.L. Rueda, pers. comm., 2009).

Modern representatives of *Smaragdia*, present in the Banyunganti fauna as well, are closely associated with seagrasses as observed for several species in different parts of the world (Higo et al., 1999; Kay, 1979; Rueda et al., 2009a; Taylor and Lewis, 1970; Zuschin et al., 2009). The modern species *Smaragdia viridis* and *Smaragdia bryanae* feed selectively on seagrass tissue (Rueda and Salas, 2007; Rueda et al., 2009a, b; Unabia, 2011). The radula of the genus differs from those of other neritids and might have evolved for breaking the cell walls of seagrasses. This would indicate a general relation of the genus to marine angiosperms (Rueda and Salas, 2007; Unabia, 2011). The occurrence of *Smaragdia* within a fossil fauna has therefore been used as an indicator for seagrass vegetation before (e.g., Reuter et al., 2010) and is generally regarded as the best available indicator for seagrass vegetation within a fossil mollusk fauna.

The assemblage of associated benthic foraminifera hints to seagrass vegetation as well. Members of the permanently attached morpho-group (*sensu* Langer, 1993), such as *Sorites* sp., *Planogypsina* sp. and *Planorbulina* sp,. occur in the fauna. Especially higher concentrations of *Sorites* species are associated with seagrass environments (Chapter 1; Hohenegger et al., 1999; Renema, 2006, 2008a). Also *Pseudotaberina* sp. and *Flosculinella* sp., both present in Banyunganti, have been associated with seagrass vegetation (Chapter 1; Renema, 2008b, Reuter et al., 2010). *Pseudotaberina vandervlerki* (de Neve, 1947) is the most common foraminifera species in the fauna.

An assessment of the paleo-water depth for the Banyunganti fauna remains somewhat speculative. Considering the terrestrial influence in the environment the associated foraminifera and the scleractinian coral assemblage point to a shallow depositional depth in the upper photic zone in not more than 20 m waterdepth (Tomascik et al., 2007). Modern Indonesian seagrasses occur in waterdepths of down to at least 20 m in clear waters, but are most abundant in the intertidal zone often growing on reef flats (Hoeksema, 2007; Nienhuis et al., 1989; D. Kneer, pers. comm., 2012). The excellent preservation of the Banyunganti material suggests a deposition in a slightly deeper environment than the latter, because modern seagrass associated shells from intertidal reef flats show much higher rates of wear (own observation). Therefore a paleodepth of ~5-20 m is assumed.

Acknowledgements

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Plates

All scale bars equal 1 mm unless indicated otherwise

Plate 1

Scutus sp.

Fig. 1 dorsal view RGM.783.219

Emarginula sp.

Fig. 2a dorsal view RGM.784.739

Fig. 2b lateral view

Puncturella sp.

Fig. 3a dorsal view RGM.784.741

Fig. 3b lateral view

Jujubinus cf. *polychromus* (A. Adams, 1853a)

Fig. 4a rear view RGM.784.743

Fig. 4b frontal view

Calliostoma sp.

Fig. 5a rear view RGM.784.745

Fig. 5b frontal view

Trochoidea indet. sp.

Fig. 6a rear view RGM.784.753

Fig. 6b dorsal view

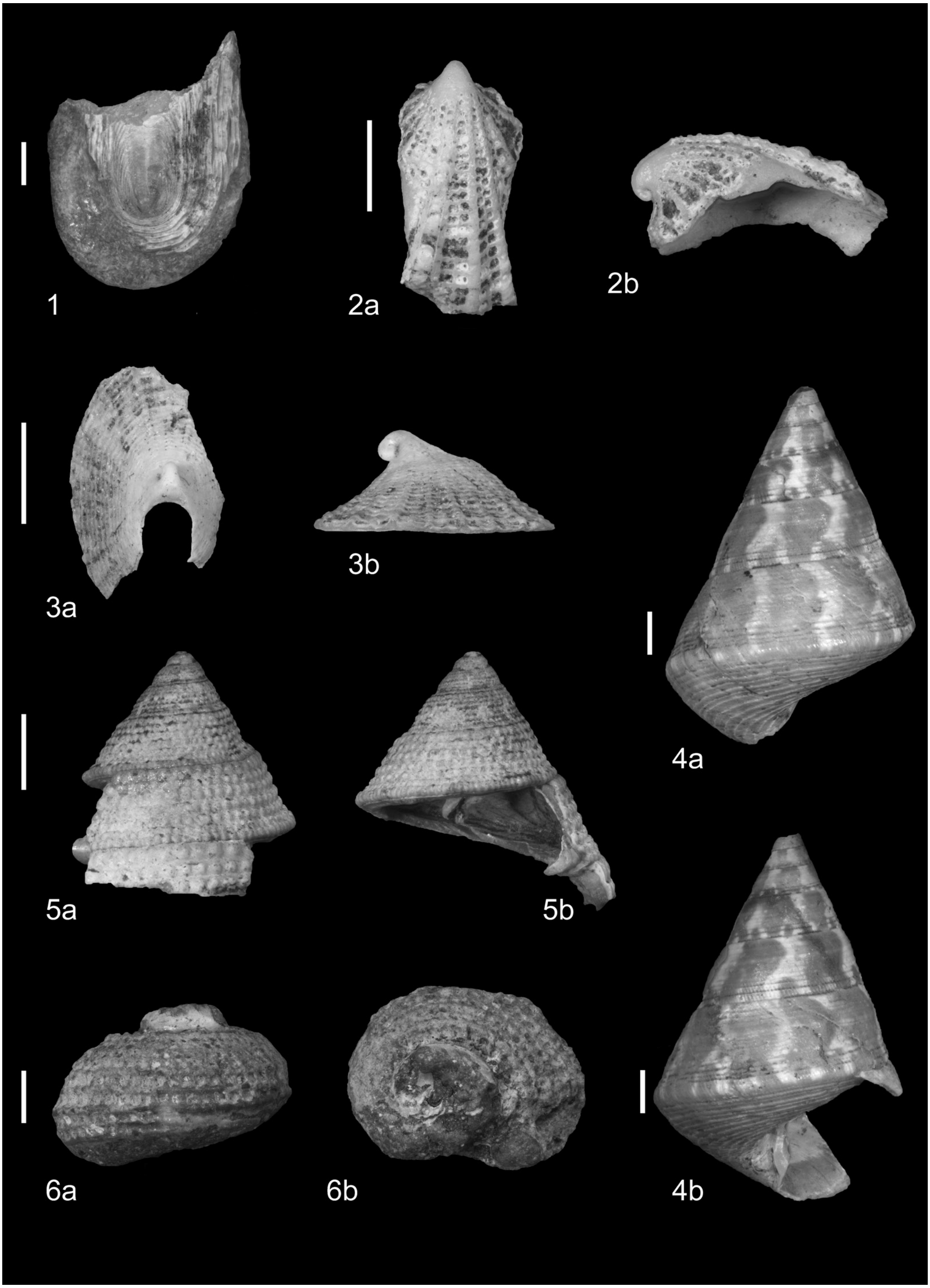
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Plate 2

Bothropoma mediocarinata Reich and Wesselingh, 2014

Fig. 1a rear view holotype RGM.784.746

Fig. 1b lateral view

Fig. 1c frontal view

Fig. 1d dorsal view

Fig. 1e ventral view

Fig. 2 frontal view paratype 1 RGM.784.747

Fig. 3 frontal view paratype 2 RGM.784.748

Fig. 4 frontal view paratype 3 RGM.784.749

Fig. 5 frontal view paratype 5 RGM.784.750

Fig. 6a rear view operculum RGM.784.751

Fig. 6b frontal view

Fig. 7 SEM dorsal view, enlargement protoconch RGM.608.186

Smaragdia jogjacartensis (Martin, 1916)

Fig. 8a rear view RGM.784.754

Fig. 8b frontal view

Fig. 8c dorsal view

Smaragdia sp.

Fig. 9a rear view RGM.784.756

Fig. 9b frontal view

Fig. 9c dorsal view

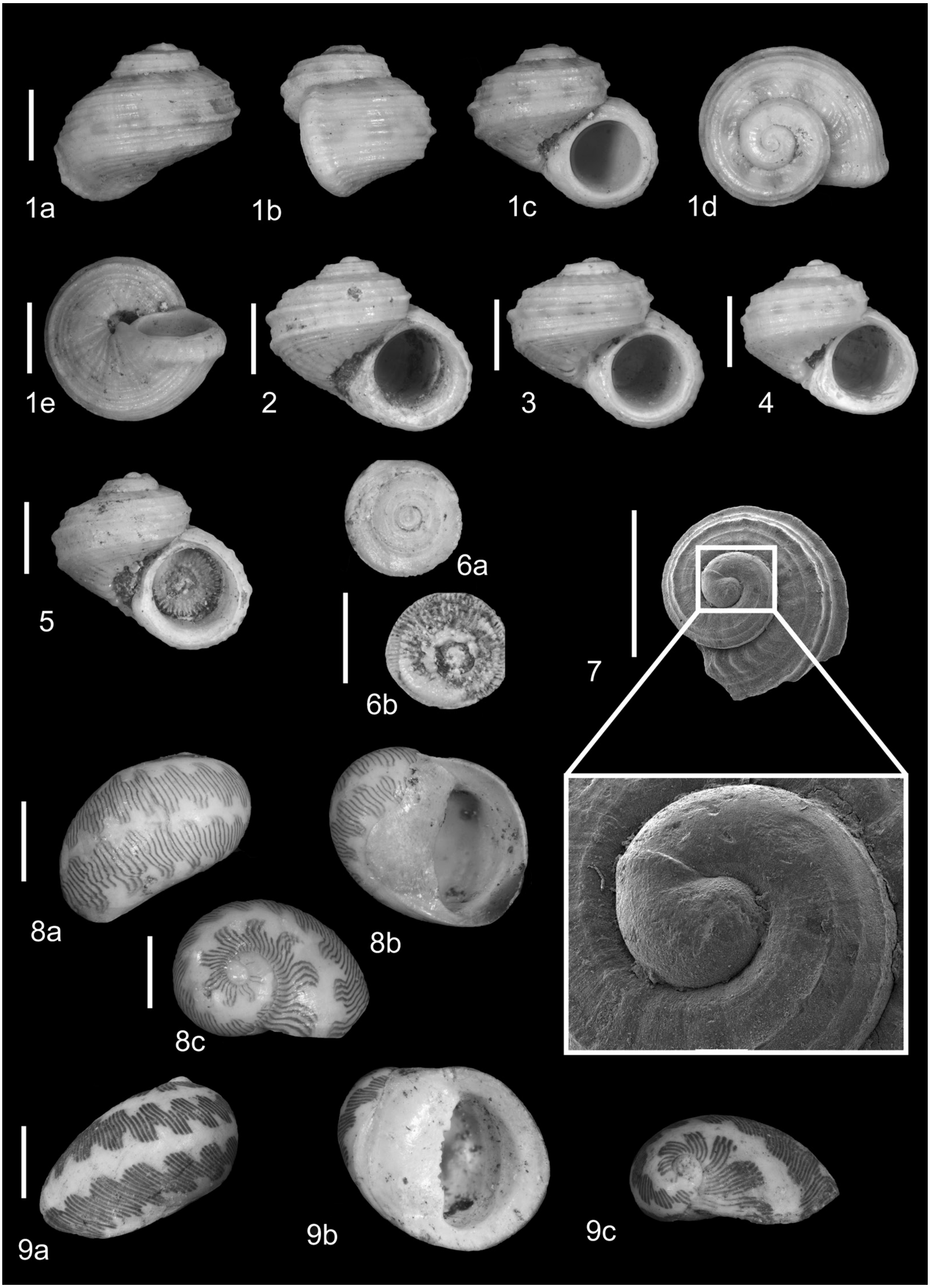
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Plate 3

Bittium sp.

Fig. 1a rear view RGM.784.761

Fig. 1b frontal view

Cerithidium cf. *perparvulum* (Watson, 1886)

Fig. 2a rear view RGM.784.758

Fig. 2b frontal view

Fig. 3a rear view RGM.784.890

Fig. 3b frontal view

Cerithidium sp.

Fig. 4 spire RGM.784.760

Cerithium aff. *balteatum* Philippi, 1848

Fig. 5 spire RGM.784.764

Cerithium deningeri (Martin, 1916)

Fig. 6a rear view RGM.784.766

Fig. 6b frontal view

Cerithium dolfusi (Martin, 1916)

Fig. 7a lateral view RGM.784.768

Fig. 7b frontal view

?*Cerithium* “*ickei*” (Martin, 1916)

Fig. 8a rear view RGM.784.778

Fig. 8b frontal view

Cerithium progoense (Martin, 1916)

Fig. 9a rear view RGM.784.769

Fig. 9b lateral view

Fig. 9c frontal view

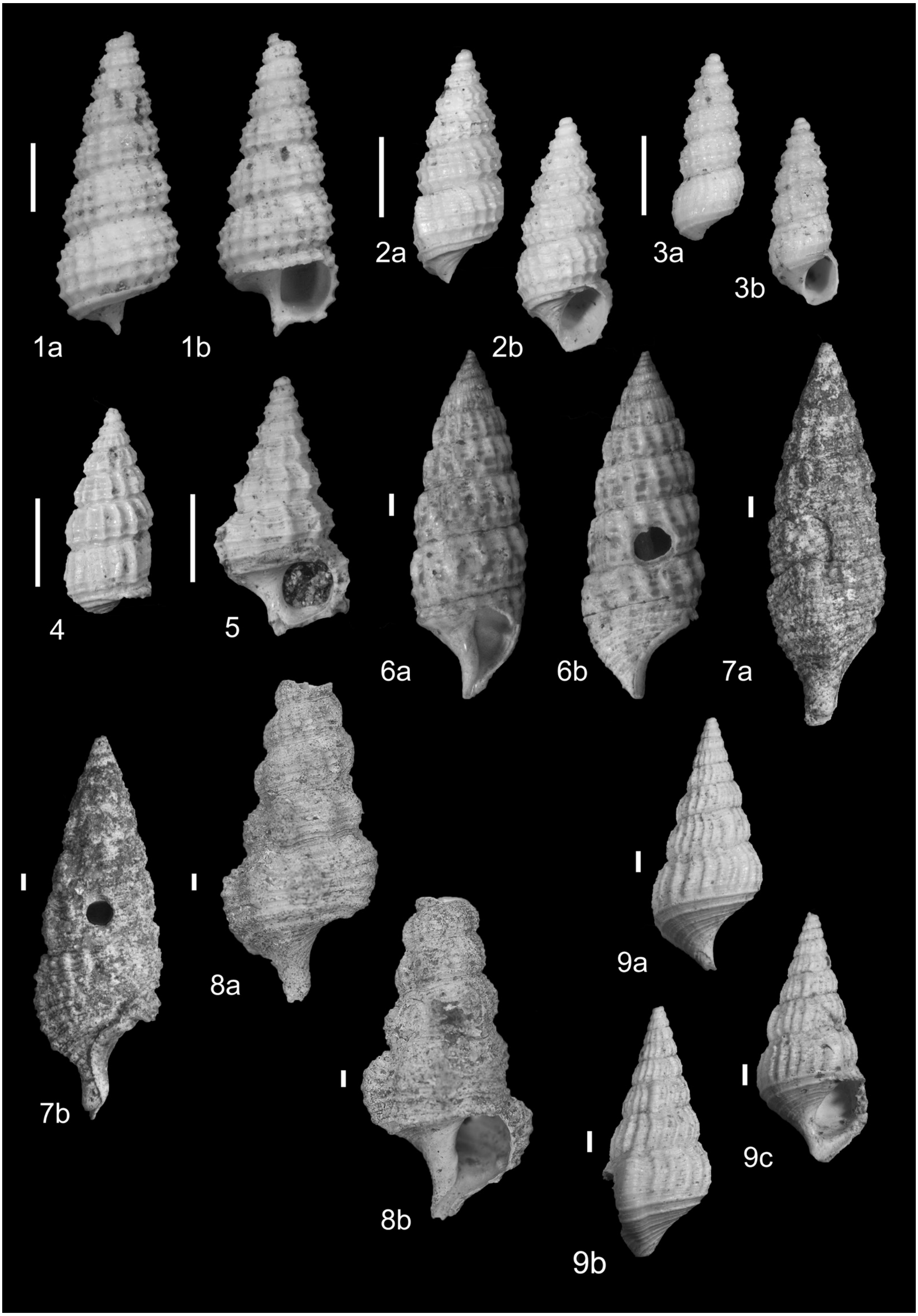
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Plate 4

Cerithium teschi (Martin, 1916)
Fig. 1 spire RGM.784.772

Cerithium s.s. sp. 1
Fig. 2a rear view RGM.784.774
Fig. 2b frontal view

Cerithium s.s. sp. 2
Fig. 3a rear view RGM.784.776
Fig. 3b frontal view

Cerithium s.l. sp. 1
Fig. 4a rear view RGM.784.779
Fig. 4b frontal view

Cerithium s.l. sp. 2
Fig. 5 rear view RGM.784.780

Clypeomorus sp. 1
Fig. 6a rear view RGM.784.781
Fig. 6b frontal view

?*Clypeomorus* sp. 2
Fig. 7a rear view RGM.784.783
Fig. 7b frontal view

Diala semistriata s.l. (Philippi, 1849)
Fig. 8a rear view RGM.784.785
Fig. 8b frontal view
Fig. 9a rear view RGM.784.786
Fig. 9b frontal view

Diala sp.
Fig. 10a rear view RGM.784.788
Fig. 10b frontal view

Modulus sp. 1
Fig. 11a rear view RGM.784.794
Fig. 11b frontal view

Modulus sp. 2
Fig. 12 spire RGM.784.796

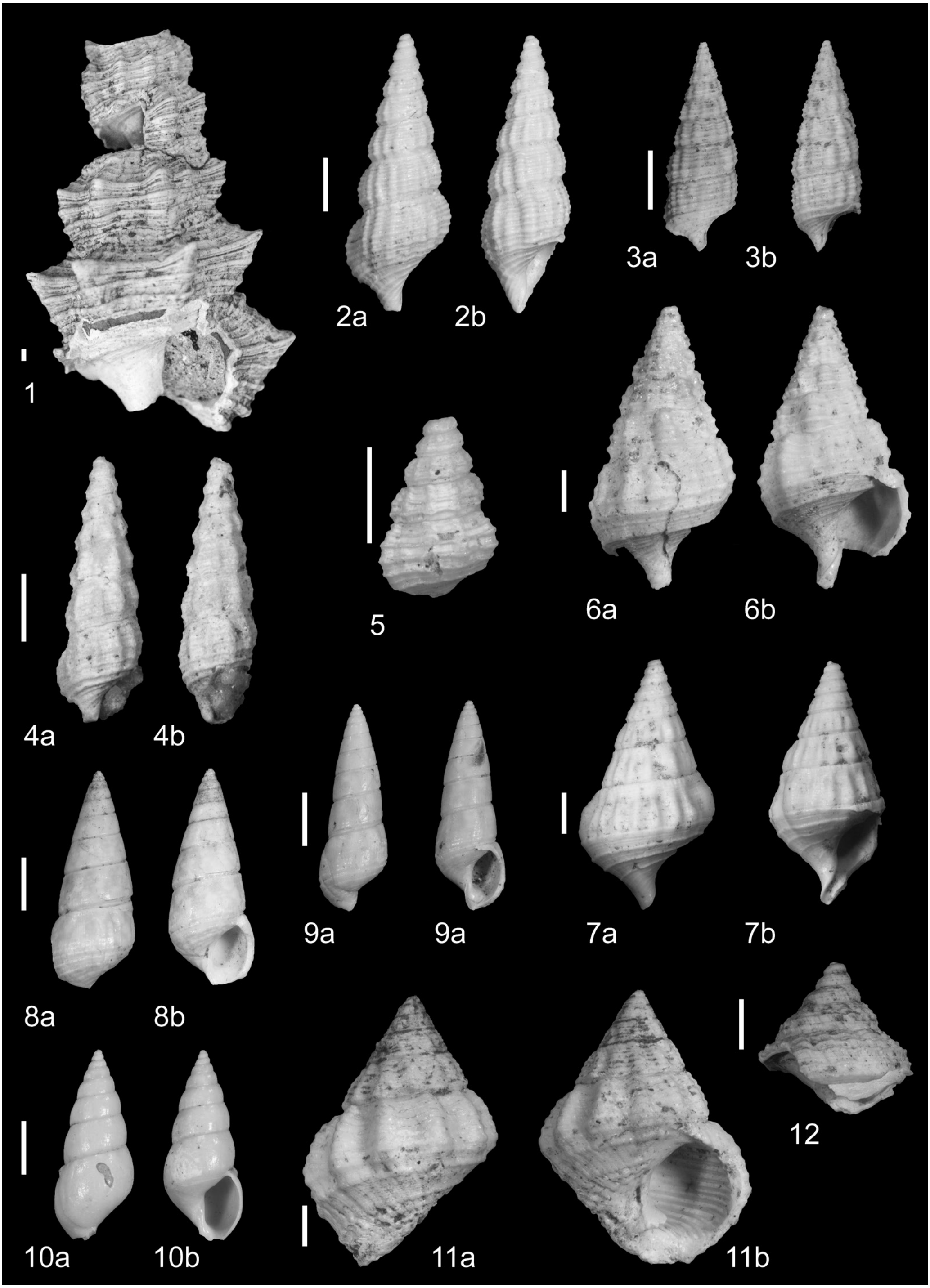
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Plate 5

Planaxis s.l. sp.

Fig. 1 spire RGM.784.797

?*Cerithideopsilla* sp.

Fig. 2 incomplete teleoconch RGM.784.798

Fig. 3 incomplete teleoconch RGM.784.800

Finella cf. *pupoides* A. Adams, 1860

Fig. 4a rear view RGM.784.802

Fig. 4b frontal view

Fig. 5a rear view RGM.784.803

Fig. 5b frontal view

Finella sp. 1

Fig. 6a rear view RGM.784.805

Fig. 6b frontal view

Finella sp. 2

Fig. 7a rear view RGM.784.807

Fig. 7b frontal view

Archimediella spolongensis (Martin, 1916)

Fig. 8 spire RGM.784.808

Haustator sp.

Fig. 9 spire RGM.784.811

Cerithioidea indet. 1

Fig. 10a rear view RGM.784.813

Fig. 10b frontal view

Cerithioidea indet. sp. 2

Fig. 11 spire RGM.784.815

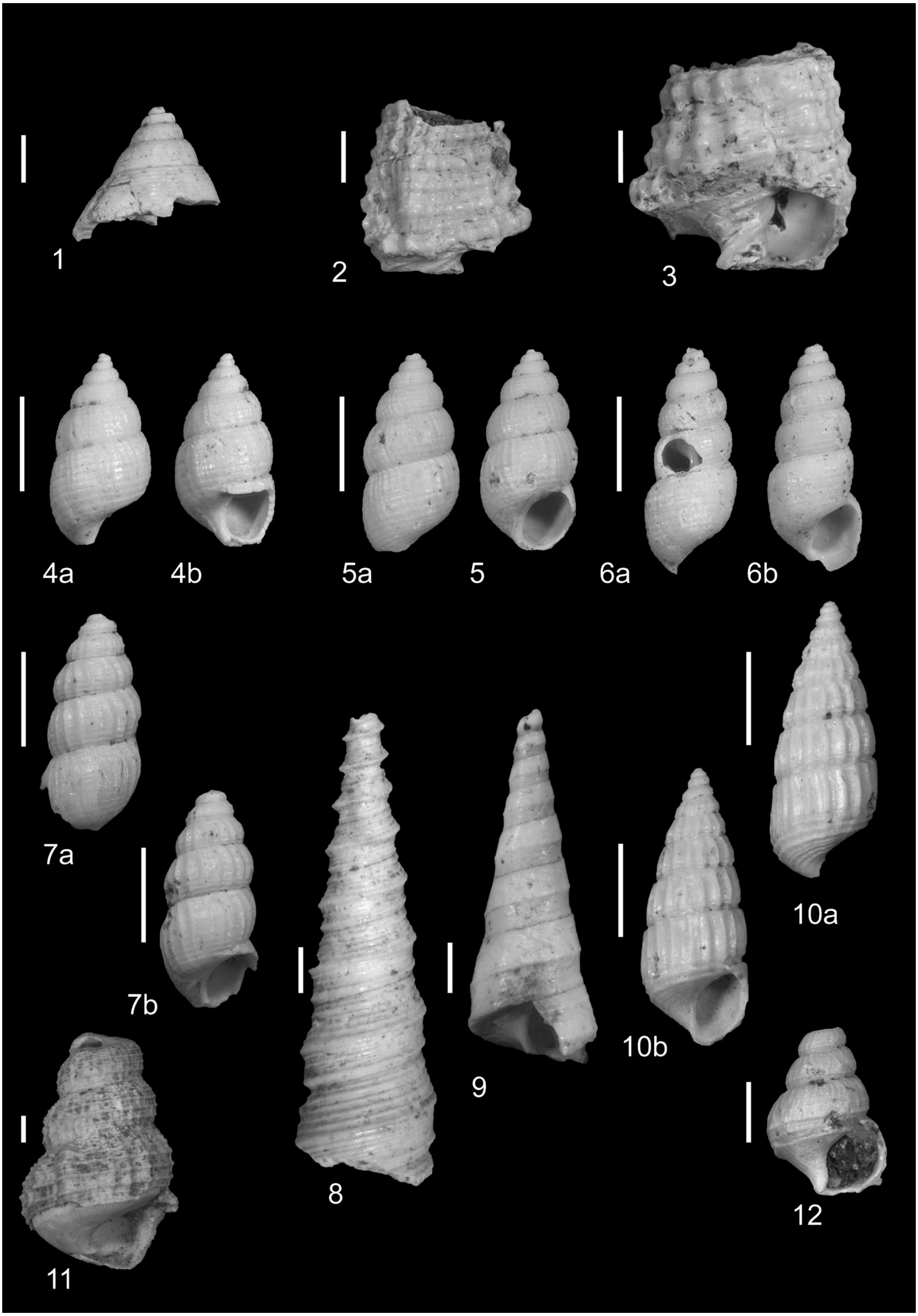
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Plate 6

?Cerithioidea indet. sp. 4
Fig. 1 spire 784.790

?Cerithioidea indet. sp. 5
Fig. 2 spire 784.792

Ampullina s.l. sp.
Fig. 3a lateral view RGM 784.817
Fig. 3b dorsal view

?*Cernina* sp.
Fig. 4a lateral view RGM 784.819
Fig. 4b dorsal view

Plesiotrochus hasibuani Reich and Wesselingh, 2014
Fig. 5 rear view holotype RGM 784.820
Fig. 5b lateral view
Fig. 5c frontal view
Fig. 6 frontal view paratype 1 RGM 784.821
Fig. 7 frontal view paratype 2 RGM 784.822
Fig. 8 frontal view paratype 3 RGM 784.823
Fig. 9 frontal view paratype 4 RGM 784.824
Fig. 10a SEM spire RGM 608.189
Fig. 10b SEM protoconch

Plesiotrochus sp. 1
Fig. 11 spire RGM 784.826

Plesiotrochus sp. 2
Fig. 12a rear view RGM 784.828
Fig. 12b frontal view

?*Plesiotrochus* sp. 3
Fig. 13 frontal view RGM 784.829

Cerithioidea indet. sp. 3
Fig. 12 spire RGM.784.816

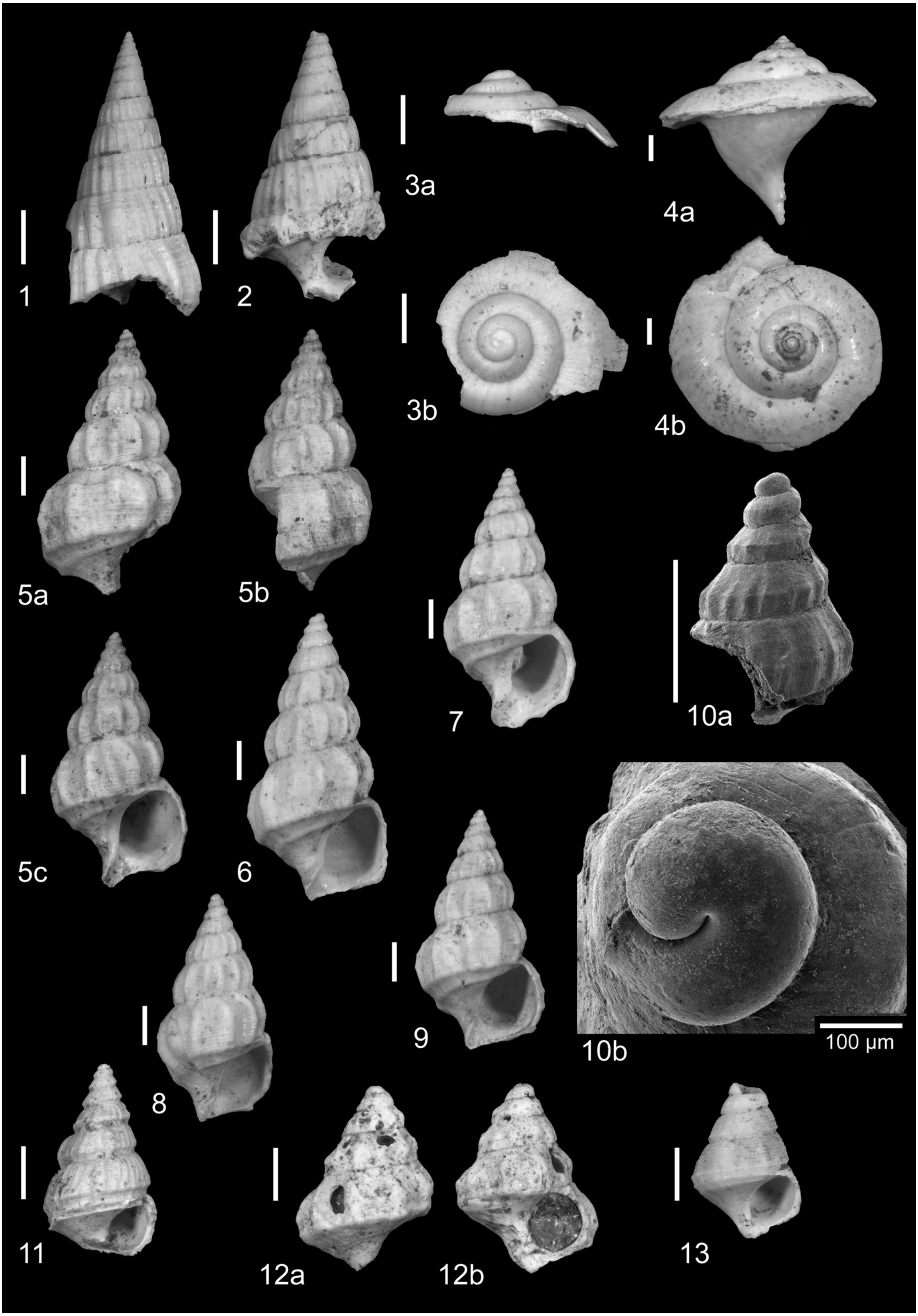
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Plate 7

Capulus sp.
Fig. 1a dorsal view RGM 784.830
Fig. 1b lateral view

Eatoniella s.l. sp. 1
Fig. 2a rear view RGM 784.831
Fig. 2b frontal view

Eatoniella s.l. sp. 2
Fig. 3a rear view RGM 784.833
Fig. 3b frontal view

Cypraeidae indet. sp.
Fig. 4 dorsal view RGM 784.835
Fig. 5 ventral view RGM 784.836

Natica s.l. sp. 1
Fig. 6a frontal view RGM 784.839
Fig. 6b dorsal view

Natica s.l. sp. 2
Fig. 7a frontal view RGM 784.840
Fig. 7b dorsal view

Naticarius sp.
Fig. 8a frontal view RGM 784.838
Fig. 8b dorsal view

Naticidae indet.
Fig. 9a frontal view RGM 784.842
Fig. 9b rear view

Rissoina (*Rissoina*) *banyungantiensis*
Reich and Wesselingh, 2014
Fig. 10a rear view holotype
RGM 784.843
Fig. 10b lateral view
Fig. 10c frontal view

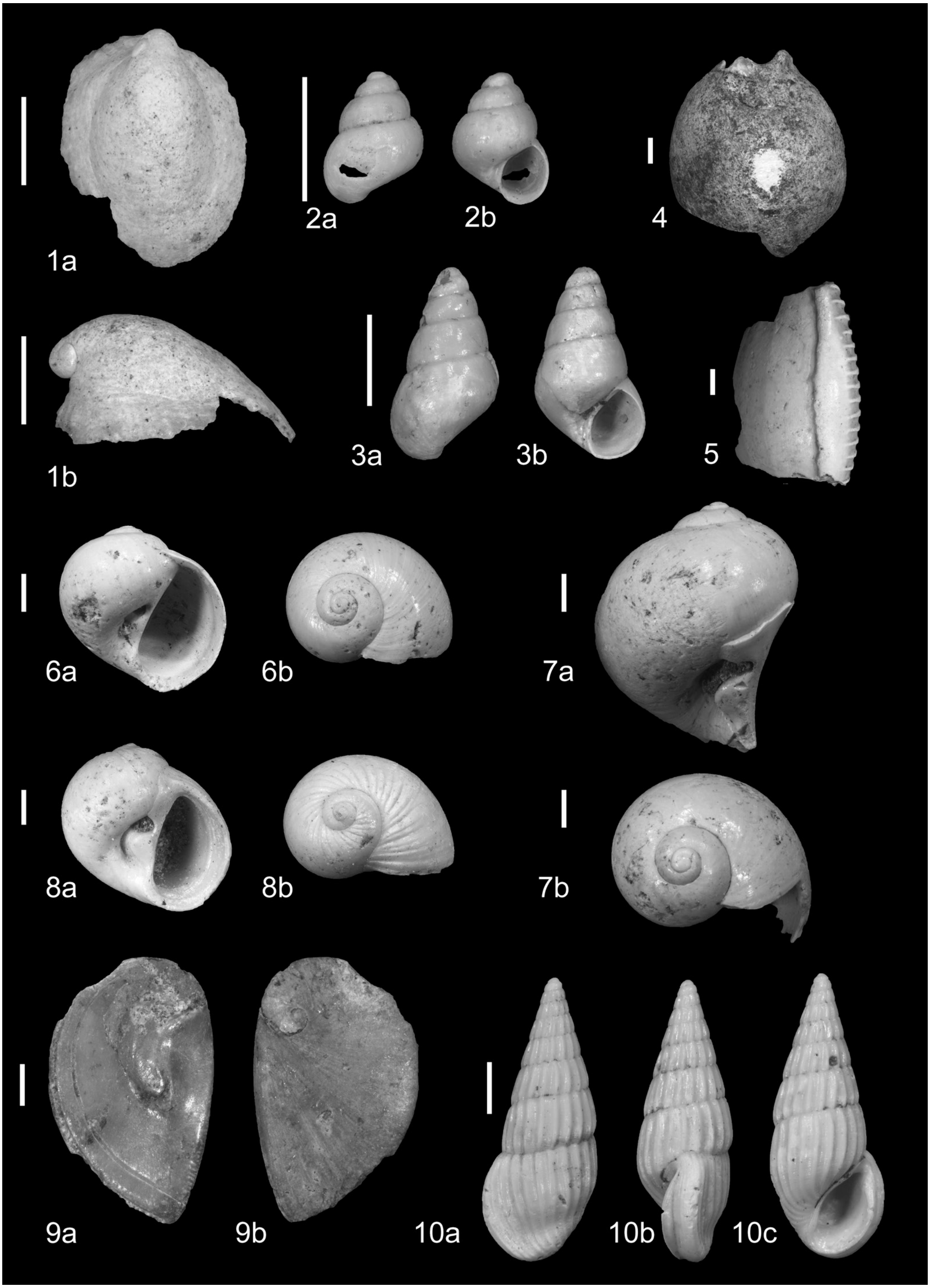
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Plate 8

Rissoina (*Rissoina*) *banyungantiensis*

Reich and Wesselingh, 2014

Fig. 1 frontal view paratype 1

RGM 784.844

Fig. 2 frontal view paratype 2

RGM 784.845

Fig. 3 frontal view paratype 3

RGM 784.846

Fig. 4a SEM protoconch RGM 608.193

Fig. 4b SEM spire

Rissoina (*Rissoina*) sp.

Fig. 5a rear view RGM 784.856

Fig. 5b frontal view

?*Rissoina* s.l. sp.

Fig. 6a rear view RGM 784.855

Fig. 6b frontal view

Rissolina reticuspiralis Reich and

Wesselingh, 2014

Fig. 7a rear view holotype RGM 784.849

Fig. 7b lateral view

Fig. 7c frontal view

Fig. 8 frontal view paratype 1

RGM 784.850

Fig. 9 frontal view paratype 2

RGM 784.851

Fig. 10 frontal view paratype 3

RGM 784.852

Fig. 11a SEM spire RGM 608.196

Fig. 11b SEM protoconch

Fig. 11c SEM detail teleoconch microstriation

Stosicia (*Iseliella*) sp.

Fig. 12 frontal view RGM 784.857

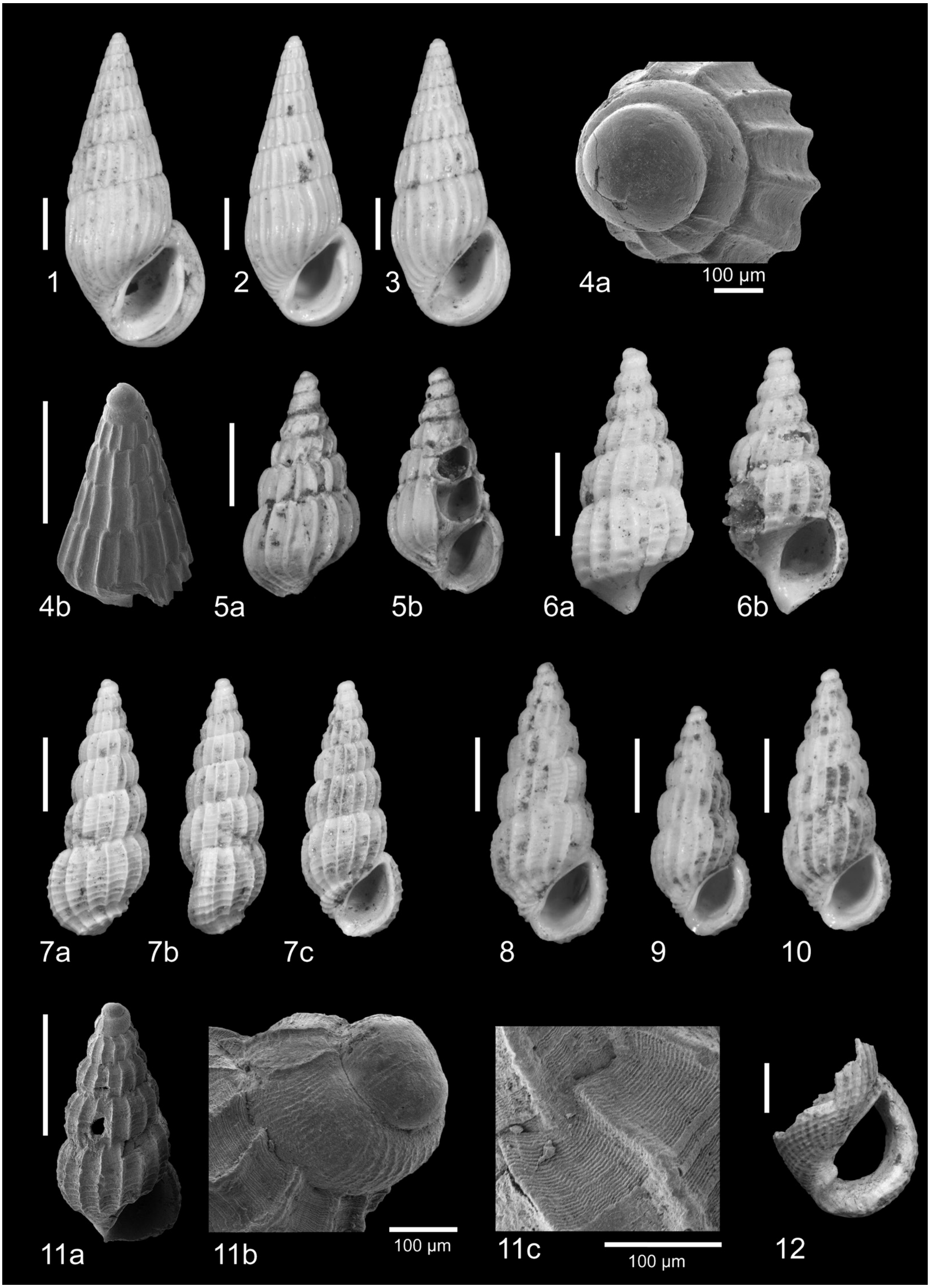
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Plate 9

Strombus s.l. sp.

Fig. 1a rear view fragment RGM 784.858

Fig. 1b lateral view

Varicospira sokkohensis (Martin, 1916)

Fig. 2a rear view RGM 784.859

Fig. 2b lateral view

Fig. 2c frontal view

Terebellum sp. 1

Fig. 3 spire RGM 784.861

Terebellum sp. 2

Fig. 4 spire RGM 784.862

Sassia (*Cymatiella*) *fennemai* (Martin, 1899)

Fig. 5a rear view RGM 784.863

Fig. 5b lateral view

Fig. 5c frontal view

Fig. 6a rear view juvenile RGM 784.863

Fig. 6b frontal view

Ranellidae indet. sp.

Fig. 7a spire RGM 784.865

Fig. 7b inclined dorsal

Vermetus s.l. sp.

Fig. 8 fragment RGM 784.867

Amaea sp.

Fig. 9 spire RGM 784.868

Epitonium sp.

Fig. 10 teleoconch whorl RGM 784.870

Melanella sp.

Fig. 11 frontal view RGM 784.871

Eulimidae indet. sp.

Fig. 12a rear view RGM 784.873

Fig. 12b frontal view

Metaxia sp. 1

Fig. 13 incomplete teleoconch RGM 784.875

Metaxia sp. 2

Fig. 14 incomplete teleoconch RGM 784.877

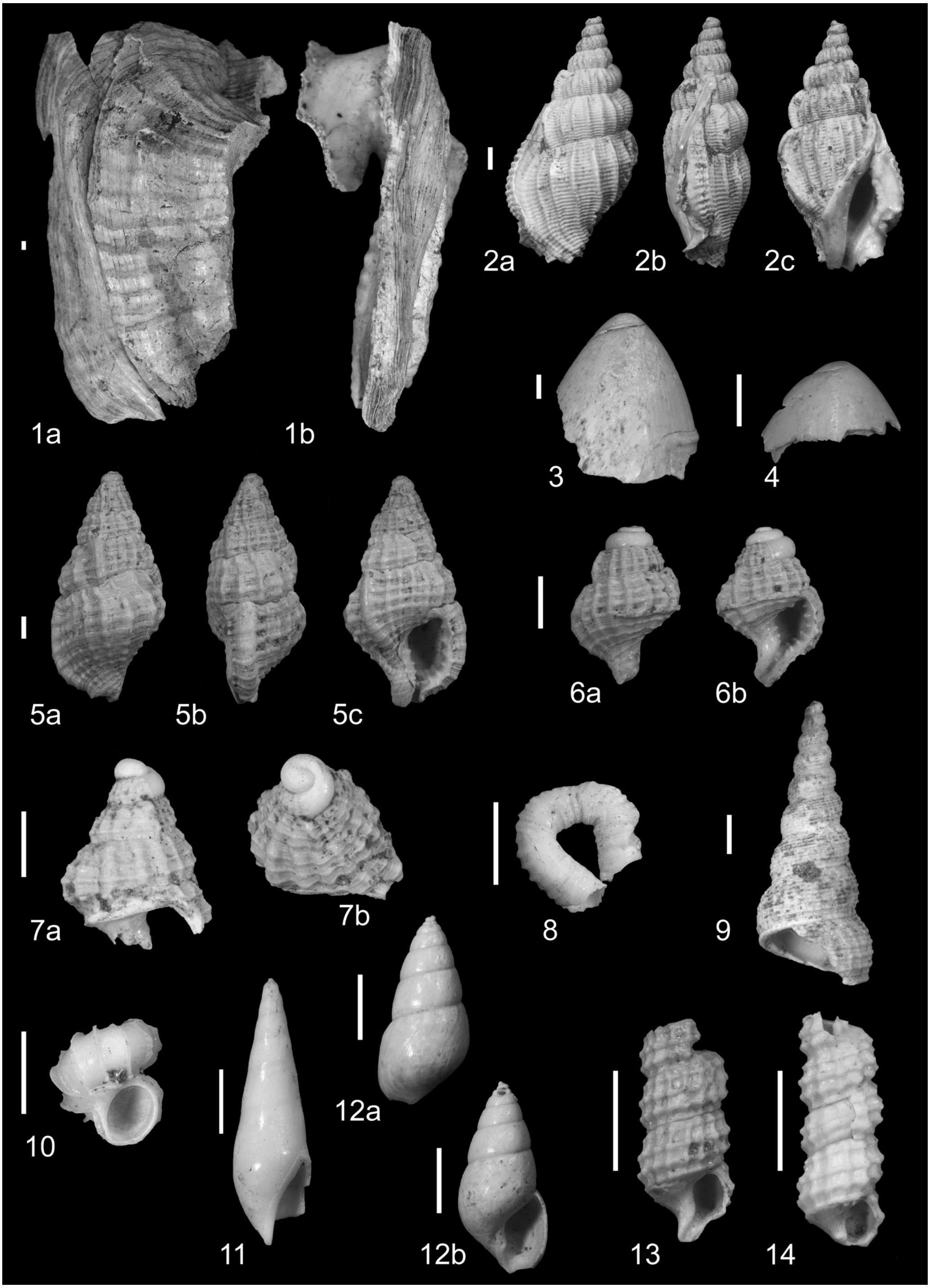
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Plate 10

Triphora s.l. sp. 1

Fig. 1a frontal view RGM 784.878

Fig. 1b lateral view

Fig. 1c rear view

Triphora s.l. sp. 2

Fig 2a frontal view RGM 784.880

Fig 2b rear view

Cerithiopsis s.l. sp. 1

Fig. 3 frontal view RGM 784.882

Cerithiopsis s.l. sp. 2

Fig. 4 frontal view RGM 784.884

Mitrella s.l. cf. *njalindungensis* Martin, 1921

Fig. 5a rear view RGM 784.885

Fig. 5b lateral view

Fig 5c frontal view

Columbellidae indet. sp.

Fig. 6a rear view RGM 784.888

Fig. 6b lateral view

Fig. 6c frontal view

Fusinus sp.

Fig. 7 spire RGM 784.891

Fasciolaria s.l. sp.

Fig. 8a rear view RGM 784.892

Fig 8b frontal view

Coralliophila sp.

Fig. 9a side view RGM 784.895

Fig. 9b frontal view

Calotrophon (*Panamurex*) sp.

Fig. 10a rear view RGM 784.894

Fig. 10b frontal view

Typhina cf. *macropterus* (Martin, 1884)

Fig. 11 spire RGM 784.896

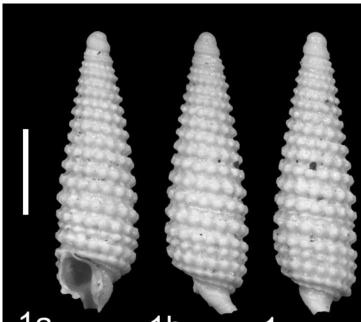
Typhinae indet. sp.

Fig. 12a frontal view fragment RGM 784.897

Fig. 12b rear view fragment

Muricidae indet. sp.

Fig. 13 spire RGM 784.898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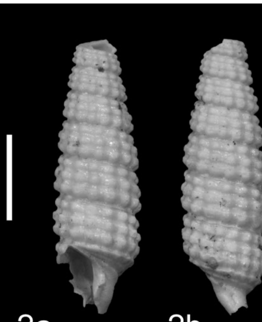
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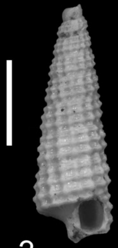
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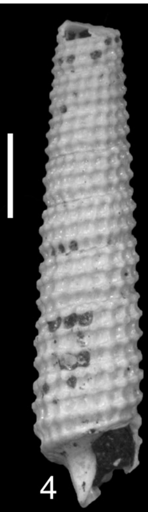
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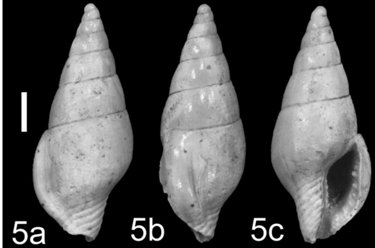
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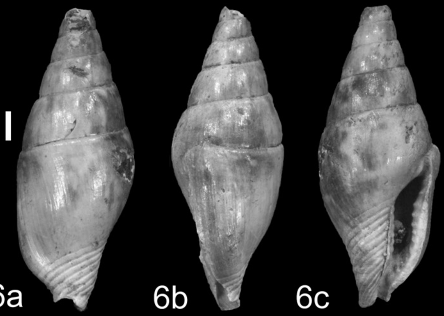
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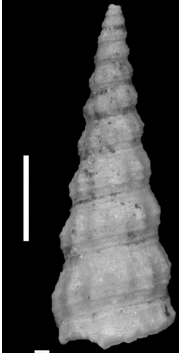
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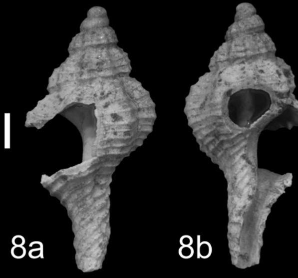
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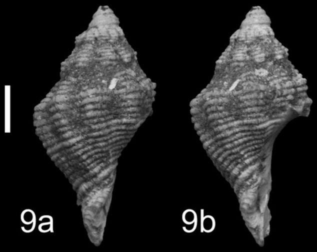
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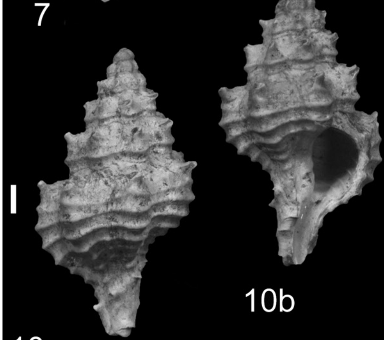
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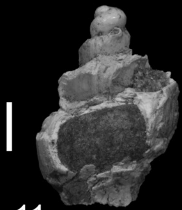
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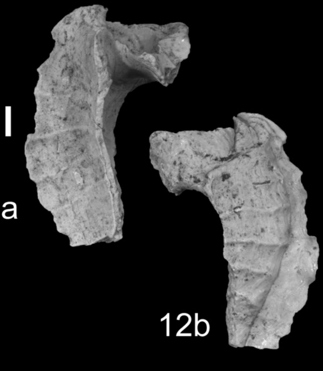
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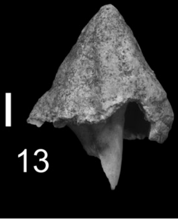
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Plate 11

Vexillum sp. 1

Fig. 1a rear view RGM.784.899

Fig. 1b frontal view

Vexillum sp. 2

Fig. 2a rear view RGM.784.901

Fig. 2b frontal view

Vexillum sp. 3

Fig. 3a rear view RGM.784.903

Fig. 3b frontal view

Vexillum sp. 4

Fig. 4a rear view RGM.784.904

Fig. 4b frontal view

Vexillum sp. 5

Fig. 5a rear view RGM.784.906

Fig. 5b frontal view

Vexillum sp. 6

Fig. 6 spire RGM.784.908

Vexillum sp. 7

Fig. 7a rear view RGM.784.909

Fig. 7b frontal view

Vexillum sp. 8

Fig. 8 spire RGM.784.910

Cystiscus sp.

Fig. 9a rear view RGM.784.91

Fig. 9b lateral view

Fig. 9c frontal view

Gibberula sp. 1

Fig. 10a rear view RGM.784.914

Fig. 10b lateral view

Fig. 10c frontal view

Gibberula sp. 2

Fig. 11a rear view RGM.784.916

Fig. 11b lateral view

Fig. 11c frontal view

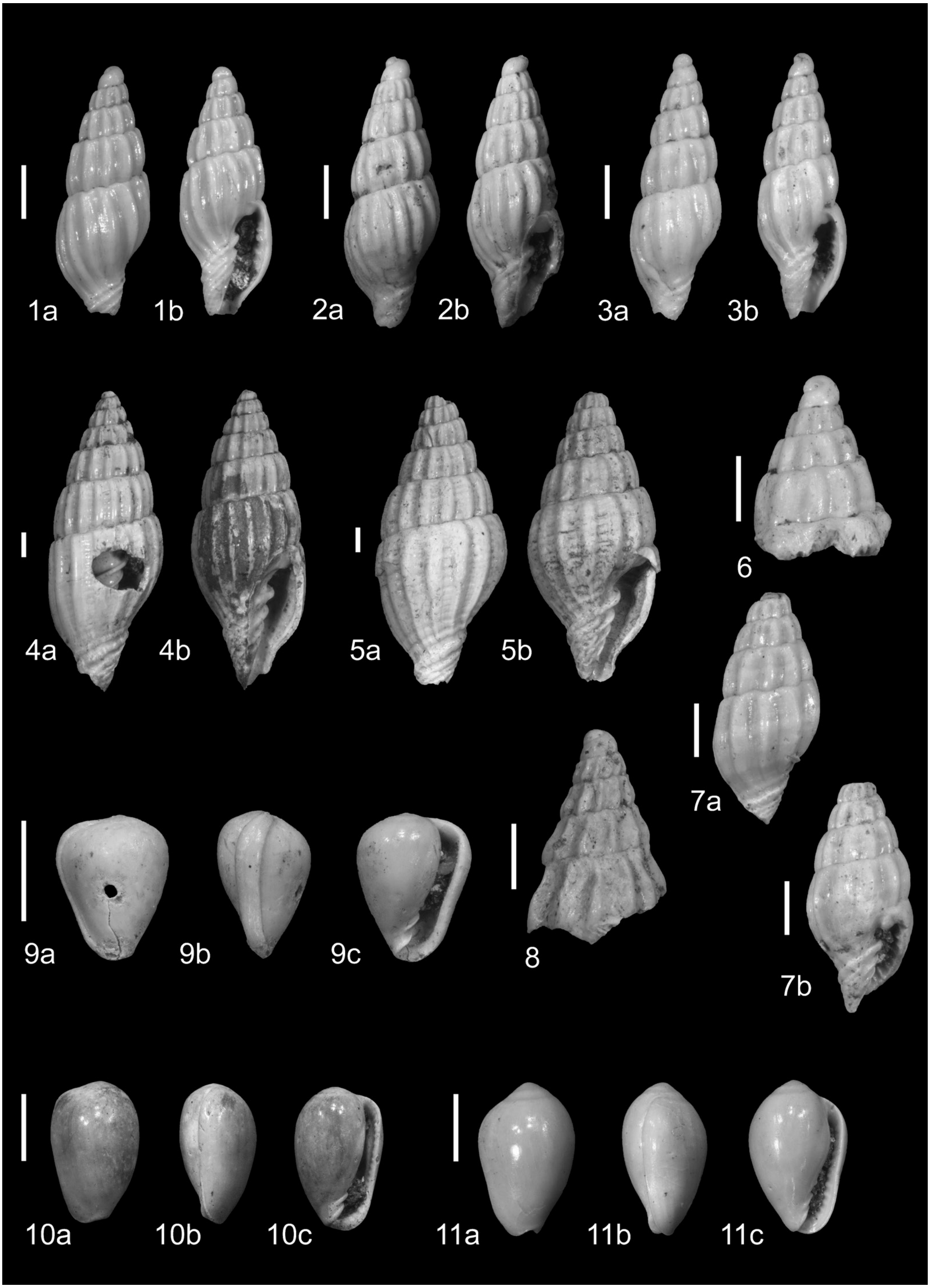
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Plate 12

Dentimargo sp. 1
Fig. 1a rear view RGM.784.918
Fig. 1b lateral view
Fig. 1c frontal view

Dentimargo sp. 2
Fig. 2a rear view RGM.784.920
Fig. 2b frontal view

Mesoginella nanggulanensis (Martin, 1916)
Fig. 3a rear view RGM.784.922
Fig. 3b lateral view
Fig. 3c frontal view

Volvarina sp. 1
Fig. 4a rear view RGM.784.924
Fig. 4b frontal view

Volvarina sp. 2
Fig. 5a rear view RGM.784.926
Fig. 5b frontal view

Mitra cf. *sokkohensis* Martin, 1916
Fig. 6a rear view spire RGM.784.928
Fig. 6b frontal view spire

Ancilla cf. *cinnamomea* sensu Beets, 1941 non Lamarck, 1801
Fig. 7a rear view RGM.784.929
Fig. 7b frontal view

Ancilla sp.
Fig. 8a rear view RGM.784.930
Fig. 8b frontal view

Oliva s.l. sp.
Fig. 9a rear view RGM.784.931
Fig. 9b frontal view

Olivella sp.
Fig. 10a rear view RGM.784.932
Fig. 10b frontal view

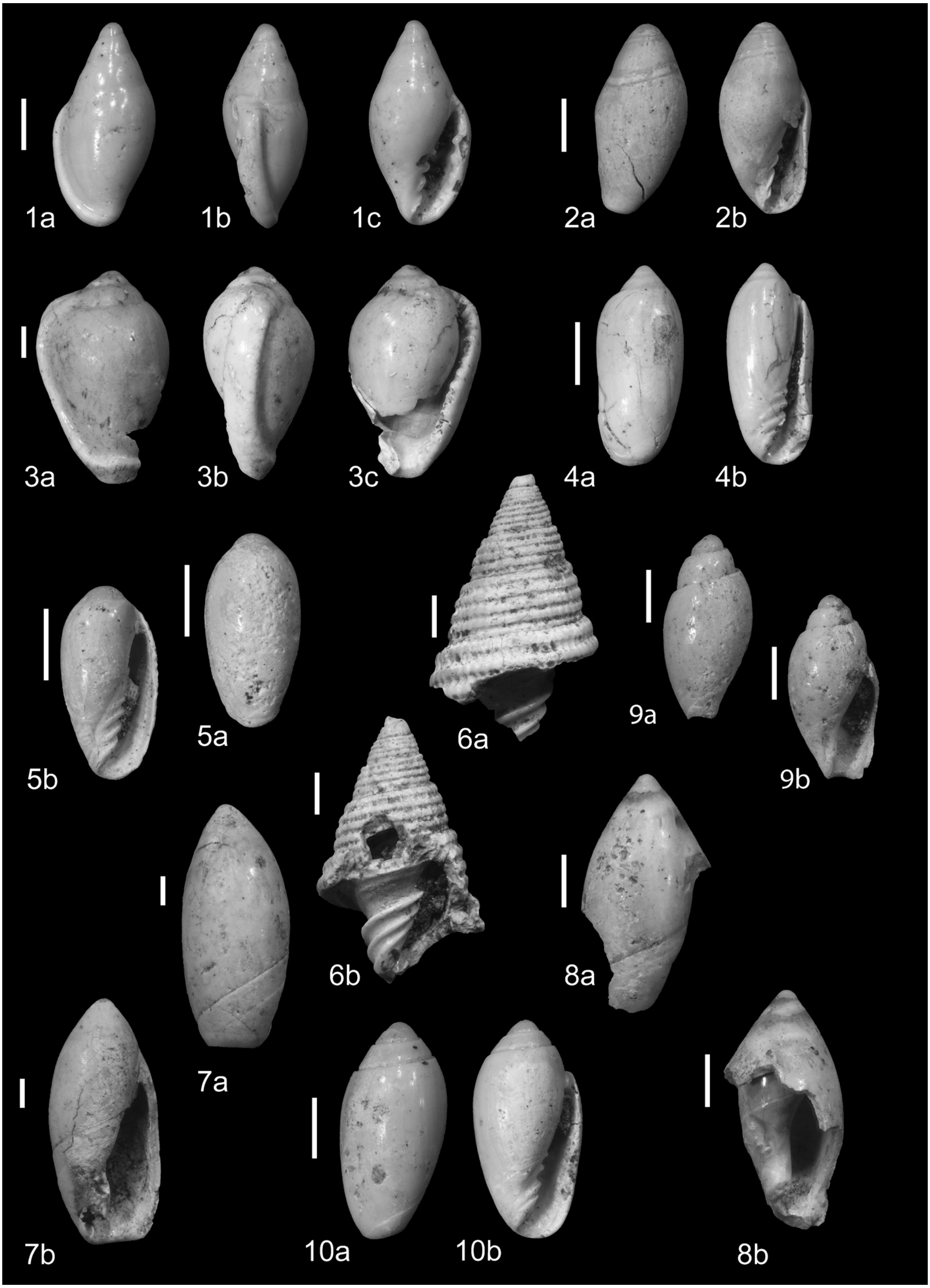
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Plate 13

Fusiconus spolongensis Martin, 1916
Fig. 1a rear view RGM.784.939
Fig. 1b frontal view

?*Fusiconus arntzenii* (Martin, 1916)
Fig. 2a rear view RGM.784.937
Fig. 2b frontal view

Phasmoconus aff. *hulshofi* (Martin, 1906)
Fig. 3 spire RGM.784.941

Conidae indet. sp. 1
Fig. 4a rear view RGM.784.934
Fig. 4b frontal view

Conidae indet. sp. 2
Fig. 5a rear view RGM.784.936
Fig. 5b frontal view

Lienardia sp.
Fig. 6a rear view RGM.784.942
Fig. 6b lateral view
Fig. 6c frontal view

Eucithara sp. 1
Fig. 7a rear view RGM.784.944
Fig. 7b lateral view
Fig. 7c frontal view

Eucithara sp. 2
Fig. 8a rear view RGM.784.946
Fig. 8b lateral view
Fig. 8c frontal view

Eucithara sp. 3
Fig. 9 spire RGM.784.948

Eucithara sp. 4
Fig. 10 spire RGM.784.949

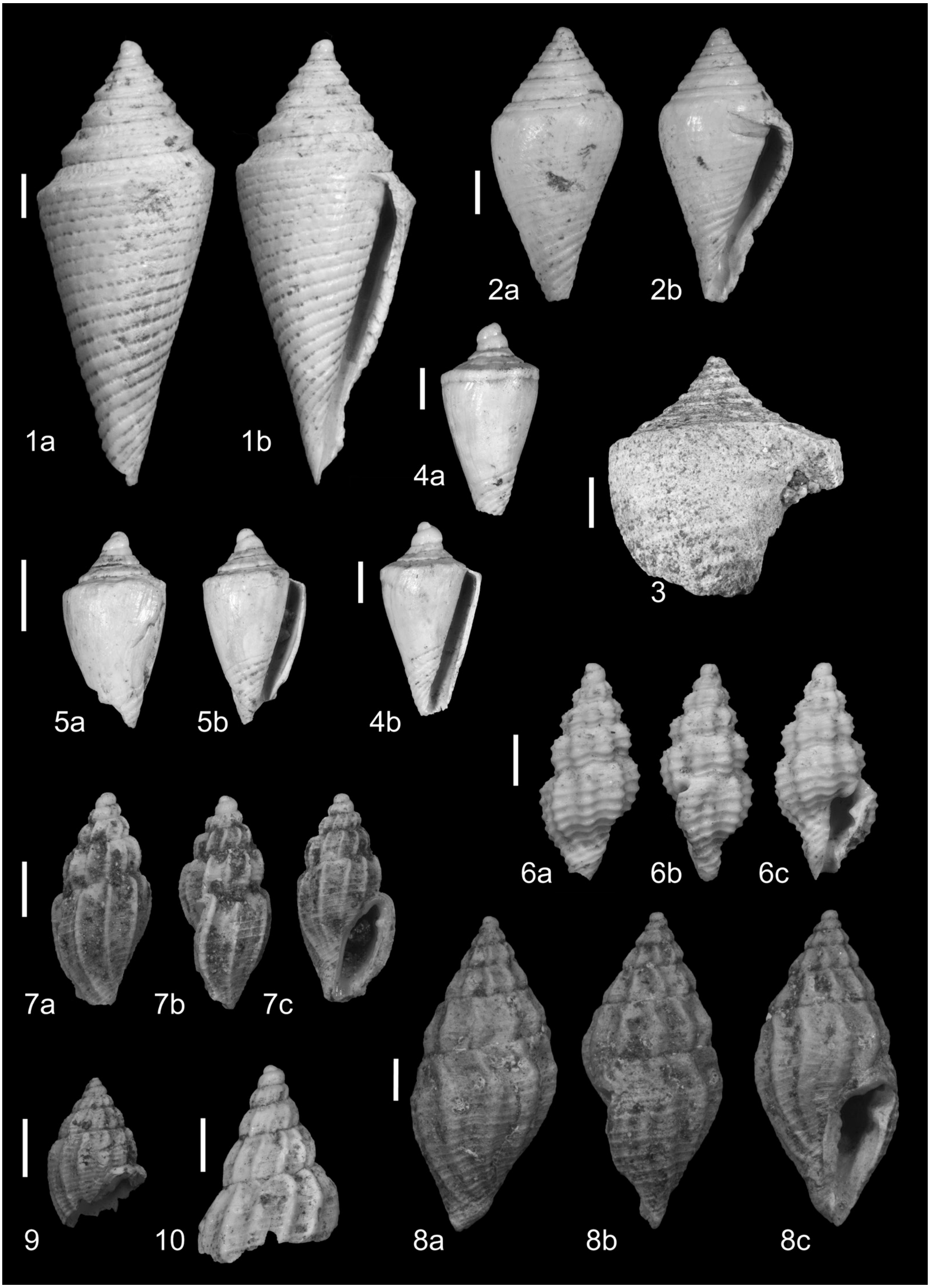
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Plate 14

Pseudodaphnella sp. 1

Fig. 1a rear view RGM.784.950

Fig. 1b frontal view

Pseudodaphnella sp. 2

Fig. 2 spire RGM.784.952

Pseudodaphnella sp. 3

Fig. 3 spire RGM.784.953

Raphitomidae indet. sp. 1

Fig. 4 spire RGM.784.955

Raphitomidae indet. sp. 2

Fig. 5 spire RGM.784.956

?*Splendrillia* sp.

Fig. 6 spire RGM.784.957

Tylotiella sp.

Fig. 7a rear view RGM.784.958

Fig. 7b frontal view

?Drilliidae indet.

Fig. 8 frontal view body whorl RGM.784.960

Crassispira molengraafi (Martin, 1916)

Fig. 9a rear view RGM.784.961

Fig. 9b lateral view

Fig. 9c frontal view

Inquisitor sp. 1

Fig. 10a rear view RGM.784.963

Fig. 10b frontal view

Fig. 11 rear view juvenile RGM.784.964

?*Inquisitor* sp. 2

Fig. 12a rear view RGM.784.966

Fig. 12b frontal view

Fig. 13 rear view juvenile RGM.784.967

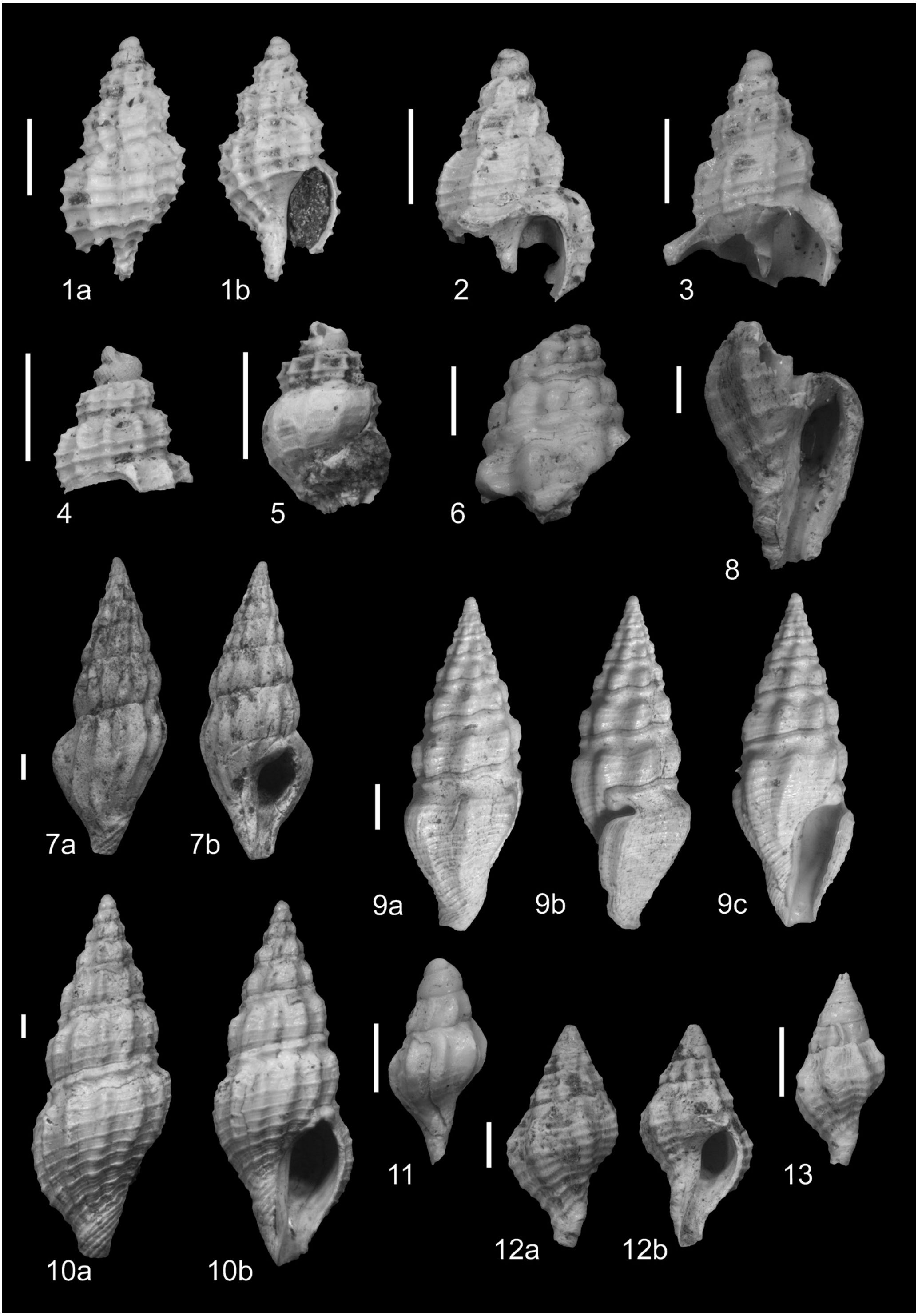
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Plate 15

Pseudomelatomidae indet. 1
Fig. 1a rear view body whorl
RGM.784.969
Fig. 1b lateral view
Fig. 1c frontal view

Pseudomelatomidae indet. 2
Fig. 2a rear view body whorl
RGM.784.970
Fig. 2b frontal view

Pseudomelatomidae indet. 3
Fig. 3 spire RGM.784.971

Clavatula s.l. sp.
Fig. 4a rear view RGM.784.974
Fig. 4b frontal view

?*Turricula kelirensis* (Martin, 1916)
Fig. 5a rear view RGM.784.972
Fig. 5b frontal view

Strictispira sp.
Fig. 6a rear view RGM.784.976
Fig. 6b lateral view
Fig. 6c frontal view

Terebra sp.
Fig. 7a rear view RGM.784.978
Fig. 7b frontal view

Cancellariidae indet. sp.
Fig. 8a lateral view protoconch
RGM.784.980
Fig. 8b dorsal view

Acteon sp.
Fig. 9a rear view RGM.785.008
Fig. 9b frontal view

?Acteonidae indet. sp.
Fig. 10 frontal view fragment
RGM.785.010

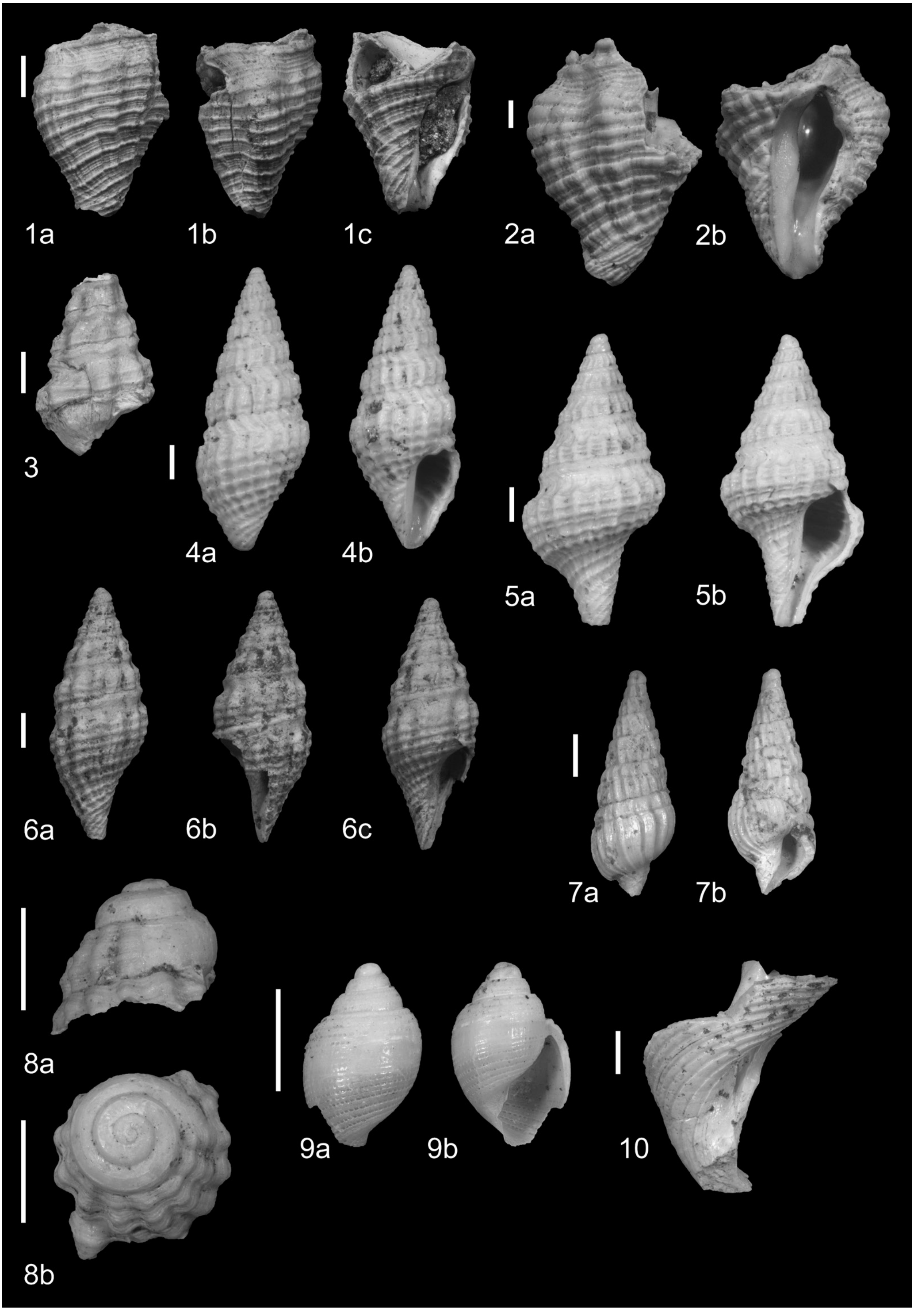
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Plate 16

Adelphotectonica sp.
Fig. 1a dorsal view RGM.784.981
Fig. 1b ventral view
Fig. 1c lateral view

?*Discotectonica* sp.
Fig. 2a lateral view RGM.784.983
Fig. 2b dorsal view
Fig. 2c ventral view

Heliacus (*Torinista*) *implexus* (Mighels, 1845)
Fig. 3a dorsal view RGM.784.985
Fig. 3b ventral view
Fig. 3c lateral view

Psilaxis radiatus (Röding, 1798)
Fig. 4a dorsal view RGM.784.986
Fig. 4b ventral view
Fig. 4c lateral view

Odostomia sp.
Fig. 5a rear view
Fig. 5b frontal view

Parodostomia sp.
Fig. 6a rear view
Fig. 6b frontal view

Babella sp.
Fig. 7a rear view RGM.784.987
Fig. 7b frontal view

Pyrgulina sp. 1
Fig. 8a rear view RGM.784.988
Fig. 8b frontal view

Pyrgulina sp. 2
Fig. 9a rear view RGM.784.990
Fig. 9b frontal view

Longchaeus sp.
Fig. 10a rear view RGM.784.997
Fig. 10b frontal view

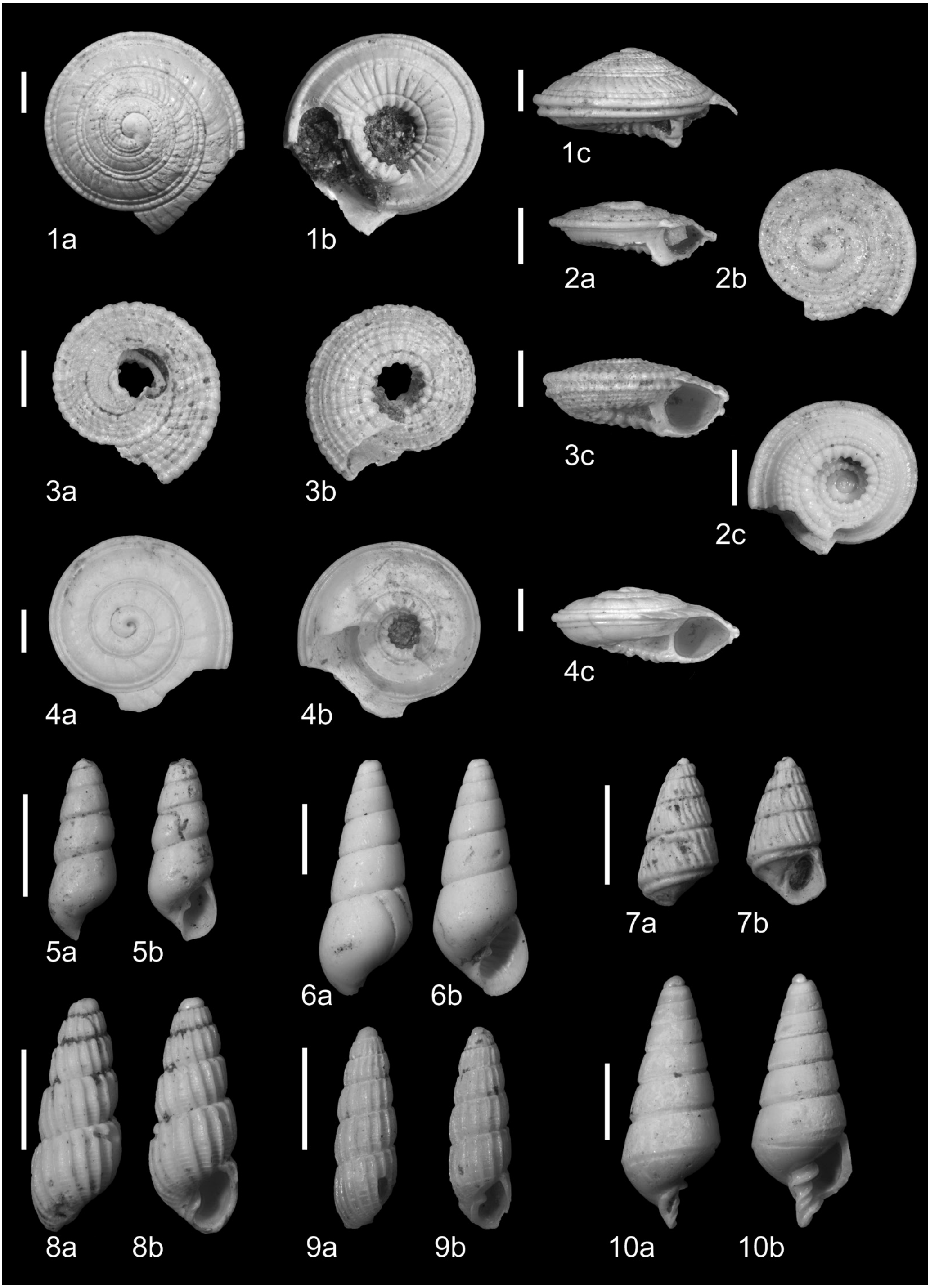
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Plate 17

Pyramidella sp.
Fig. 1a rear view RGM.784.999
Fig. 1b frontal view

Asmunda sp.
Fig. 2a rear view RGM.785.000
Fig. 2b frontal view

?*Pyrgiscus* sp.
Fig. 3a rear view RGM.785.002
Fig. 3b frontal view

Turbolidium sp. 1
Fig. 4a rear view RGM.785.004
Fig. 4b frontal view

?*Turbolidium* sp. 2
Fig. 5a rear view RGM.785.004
Fig. 5b frontal view

Turbonilla sp.
Fig. 6a rear view RGM.785.007
Fig. 6b frontal view

Eulimella sp.
Fig. 7a rear view RGM.784.992
Fig. 7b frontal view

Ringicula sp. 1
Fig. 8a rear view RGM.785.011
Fig. 8b lateral view
Fig. 8c frontal view

Ringicula sp. 2
Fig. 9a rear view RGM.785.013

Fig. 9b lateral view
Fig. 9c frontal view

Ringicula sp. 3
Fig. 10a rear view RGM.785.015
Fig. 10b lateral view
Fig. 10c frontal view

Cylichna triplicata (Martin, 1916)
Fig. 11a rear view RGM.785.017
Fig. 11b frontal view

Cylichnidae indet. sp. 1
Fig. 12a rear view RGM.785.019
Fig. 12b frontal view

Cylichnidae indet. sp. 2
Fig. 13 dorsal view fragment
RGM.785.021

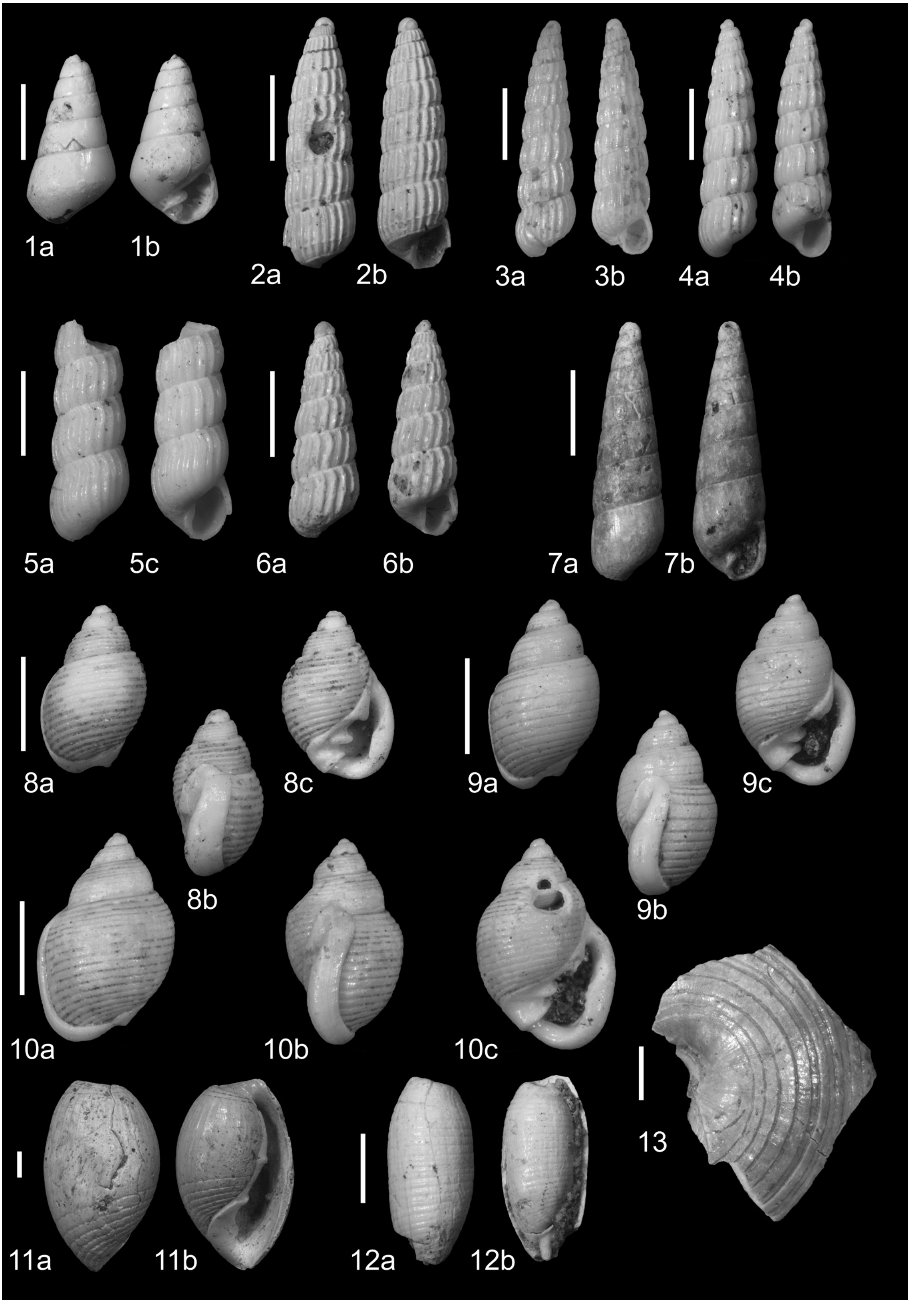
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Plate 18

?*Tucetona* sp.

Fig. 1a external view RGM.785.031

Fig. 1a internal view

Mimachlamys sp.

Fig. 2 external view fragment

RGM.785.033

Spondylus sp.

Fig. 3 external view RGM.785.035

Cardiolucina civica (Yokoyama, 1927)

Fig. 4a external view left valve

RGM.785.039

Fig. 4b internal view

Fig. 5a internal view right valve

RGM.785.040

Fig. 5b external view

Fig. 6 dorsal view RGM.785.041

Cardiolucina sp.

Fig. 7 external view right valve

RGM.785.043

Fig. 8 internal view left valve

RGM.785.045

Fig. 9 dorsal view RGM.785.044

Cardita s.l. sp.

Fig. 10a internal view left valve

RGM.785.037

Fig. 10b external view

Fig. 10c external view right valve

Fig. 10d internal view

Fragum sp.

Fig. 11 external view RGM.785.048

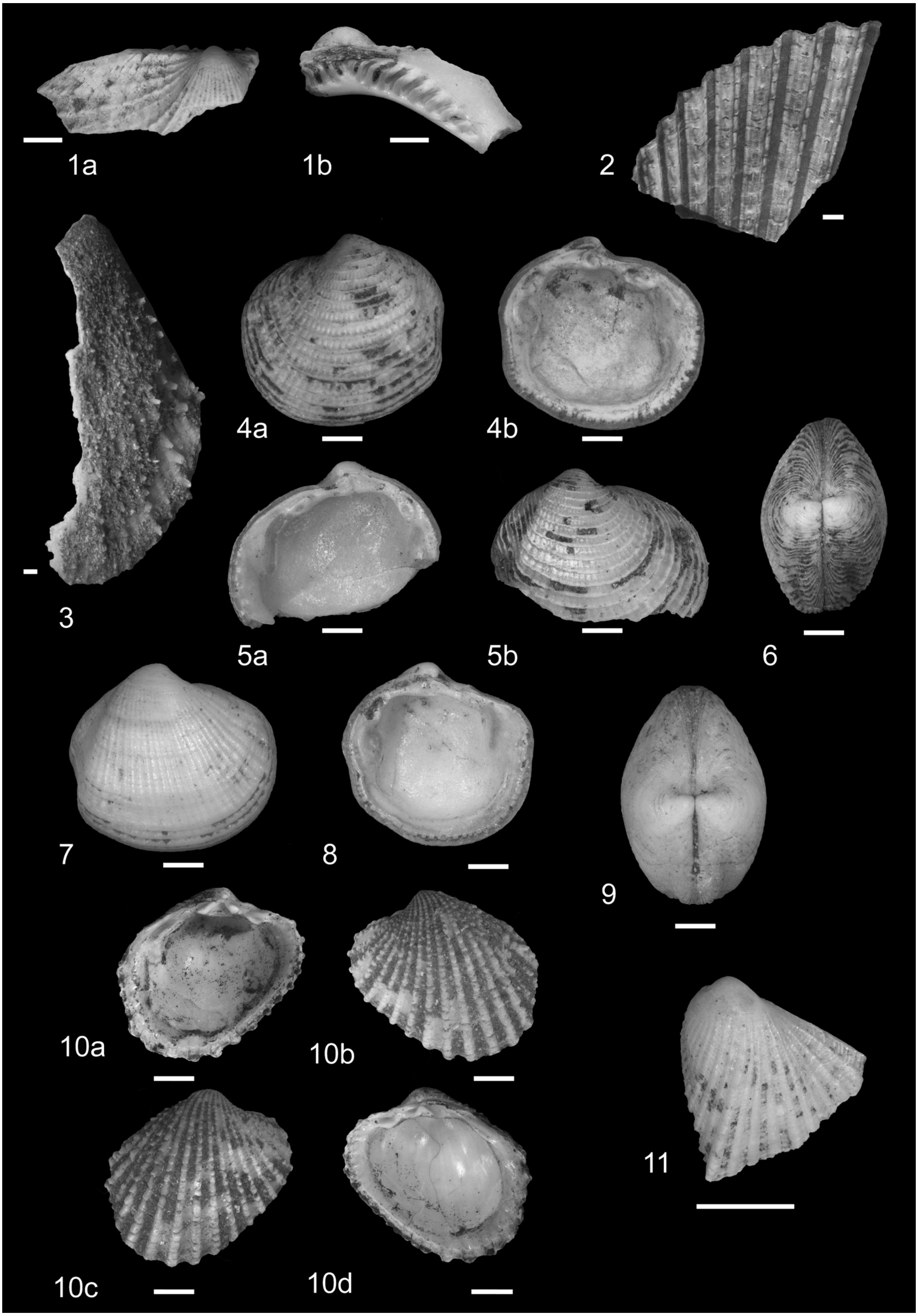
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Plate 19

Nemocardium sp.

Fig. 1 external view RGM.785.050

?*Acrosterigma* sp.

Fig. 2 external view fragment RGM.785.053

Cardiidae indet. sp. 1

Fig. 3 external view RGM.785.054

Cardiidae indet. sp. 2

Fig. 4 internal view RGM.785.055

Fig. 4b external view

Cardiidae indet. sp. 3

Fig 5a external view fragment RGM.785.057

Kelliella sp.

Fig. 6a external view RGM.785.058

Fig. 6b internal view

?*Arcopagia* sp.

Fig 7a internal view RGM.785.059

Fig. 7b external view

Tellina s.l. sp. 1

Fig. 8a external view RGM.785.060

Fig. 8b hinge

Tellina s.l. sp. 2

Fig. 9a external view

Fig. 9b hinge

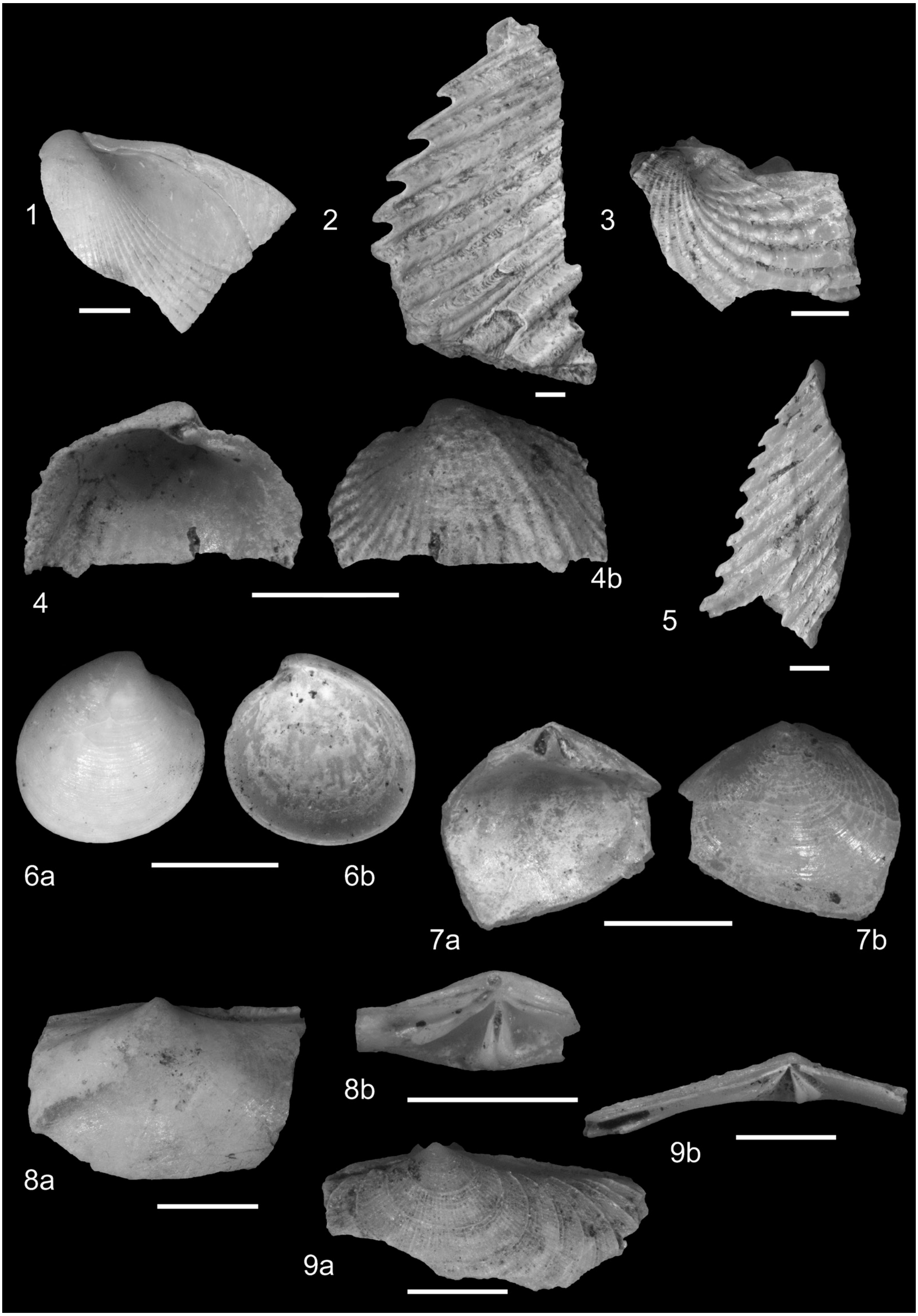
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Plate 20

Circe junghuhni Martin, 1917

Fig. 1 external view RGM.785.065

Circe sp.

Fig. 2a external view RGM.785.067

Fig. 2b internal view

Veneridae indet. sp. 1

Fig. 3 external view right valve RGM.785.070

Fig. 4a internal view left valve RGM.785.069

Fig. 4b external view

Veneridae indet. sp. 2

Fig. 5a internal view subadult RGM.785.072

Fig. 5b external view

Fig 6 external view RGM.785.073

Veneroidea indet. sp. 1

Fig. 7a external view Material: RGM.785.075

Fig. 7b hinge

?Veneroidea indet. sp. 2

Fig. 8a internal view left valve RGM.785.076

Fig. 8b external view

Fig. 8c external view right valve

Fig. 8d internal view

Dentalium sp. 1

Fig. 9a lateral view RGM.783.220

Fig. 9b cross section

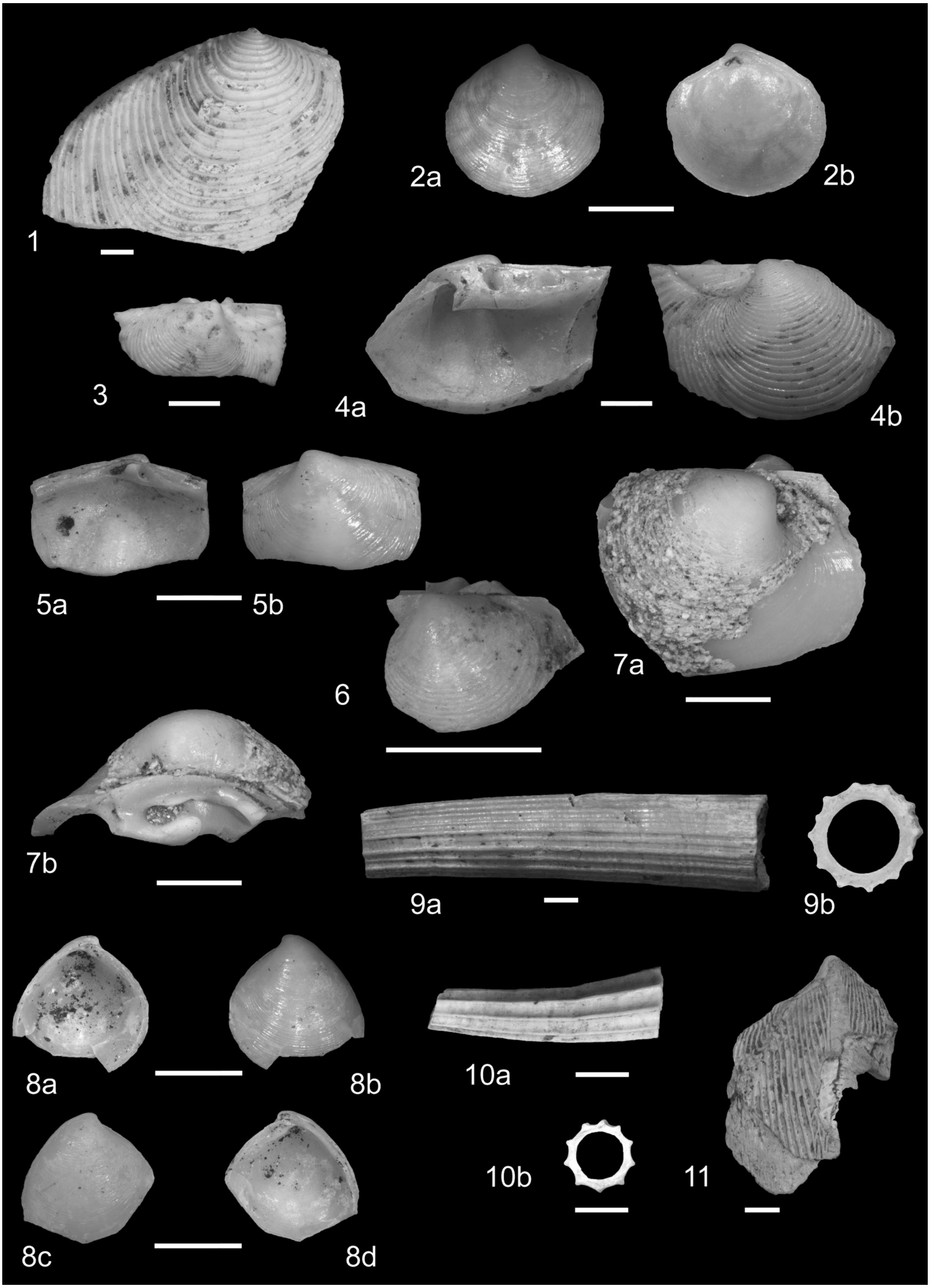
Dentalium sp. 2

Fig. 10a lateral view RGM.783.222

Fig. 10b cross section

Schizochiton incisus (Sowerby, 1841)

Fig. 11 dorsal view RGM.783.224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Chapter 3

Diversity and Paleoecology of Miocene Coral-Associated Mollusks from East Kalimantan, Indonesia

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Kenneth Johnson, Jon A. Todd, and Willem Renema

Adapted from *Palaios*

(submitted manuscript)

Keywords: Mollusca, Tortonian, feeding ecology, biodiversity, coral carpet

Abstract

This study represents a preliminary assessment of a diverse Tortonian (late Miocene) mollusk assemblage from a coral carpet environment preserved at Bontang (East Kalimantan, Indonesia). Although coral-associated aragonitic faunas rarely preserve well, the sampled assemblage is well-preserved that allows us to study its taxonomic and ecological composition. The mollusk assemblage is dominated by predatory snails and includes typical modern coral-associated taxa, such as the gastropod *Coralliophila* and the bivalve *Tridacna*. Our sampling of the species-rich assemblage implies that adequate documentation of Cenozoic mollusk diversity in the Indo-Pacific will be even more challenging than previously expected. Further assessments of fossil faunas from coral-dominated habitats will be required to provide insight to development of diversity in the Indo-Pacific biodiversity hotspot through time.

1. Introduction

The Indo-West Pacific (IWP), extending from the Red Sea and East Africa to the Central Pacific, is the largest of four major oceanic biogeographic regions, and the one holding the highest taxon diversity (Briggs, 1974; Ekman, 1934; Paulay, 1997). Within the IWP, the centre of maximum marine biodiversity (species richness) is located in the Indo-Malayan region where local species richness peaks in and around coral habitats (Hoeksma, 2007; Renema et al., 2008). A large variety of organisms, including corals, fish, mollusks, crustaceans, and echinoderms contribute to the high diversity in the region (Bellwood et al., 2005; Bouchet et al., 2002; Hoeksema, 2007; Renema et al., 2008). Documentation of the fossil record is required in order to understand the ecological and environmental context of the origin of the biodiversity hotspot, as well as its development through time (Renema et al., 2008). Although the sampling of ancient coral reef-associated habitats is necessary to document levels of biodiversity this is frequently difficult, because coral facies often suffer strong diagenesis, compromising the preservation of associated organisms, especially those with aragonitic hard-parts, such as mollusks (Wright et al., 2003). This results in highly biased mollusk assemblages from reefal environments that largely comprise taxa with more diagenetically resistant and largely calcitic shells, such as oysters and pectinids (Santodomingo et al., submitted; Wright et al., 2003, and references therein).

In this study an unusually well-preserved association of ramose corals and mollusks from late Miocene deposits in Bontang (East Kalimantan, Indonesia) is presented. The material provides the opportunity to investigate a rare diagenetically largely unfiltered Neogene coral-associated mollusk assemblage from the marine biodiversity hotspot. The aim of this study is to reconstruct the paleoenvironment and to characterize the mollusk assemblage in terms of diversity and ecology. The assemblage is furthermore compared to the early Miocene seagrass-associated Banyunganti assemblage (Chapter 2) in terms of feeding guild composition. This enables us to gain insight in the variation of the assemblage compositions of fossil faunas from similar regions and time frames, but from different paleohabitats.

2. Study Area

The Miocene outcrops of Bontang are located on the eastern side of the Kutai Basin, the southeastern-most extension of the Sunda platform on the east coast of Kalimantan, Indonesia (Fig. 1A-B). The Kutai Basin is confined by the Sangkulirang fault zone in the north, the Adang fault zone in the south, the Kalimantan High in the west, and the Makassar Strait in the east. The formation of the Kutai Basin initiated during the Eocene (Moss and Chambers, 1999). Subsequently the basin developed in various phases during the Cenozoic, including major changes of the basin architecture and depositional systems. During the Late Neogene and Quaternary the basin development was regressive, a result of sediment fill, inversion and uplift (Allen and Chambers, 1998). In Miocene times the study area was located in a coastal zone that received considerable input of terrigenous clastic sediments (Cibaj, 2009; Marshall et al., accepted). In spite of relatively turbid water conditions, rich coral communities could develop in the region (Novak and Renema, submitted; Santodomingo et al., submitted; Wilson, 2005).

The sampling locality TF 102 (0.16821° N, 117.44350° E) is an abandoned quarry on the north side of the northern entrance road of Bontang (Fig. 1B). The locality represents the upper part of a marine interval of about 150 cm

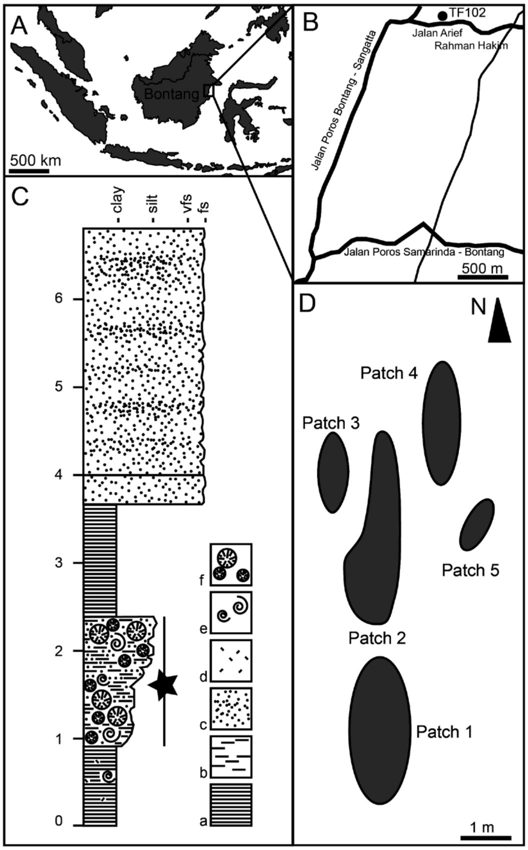

Figure 1 (left): Overview over locality TF 102, Bontang, East-Kalimantan. A) Location of the Bontang area. B) Location of TF 102. (C) Lithological column of the TF102 quarry section with a) clay, b) silt, c) sand, d) organic matter, e) shells, f) corals. The asterisk denotes the sampled interval. D) Situation sketch of coral patches on the quarry floor.

of fossiliferous, coarsening-upward, silty clay to fine sandy silt (Fig. 1C). Below this interval gray blue clay with dispersed fossiliferous lenses occurs. Above the marine interval lies a non-fossiliferous undulating clay bed of approximately 160 cm thickness followed by approximately three meters of barren fine sandstones. Those sediments represent the basal part of an overlying fluvial unit.

Based on benthic foraminifera the TF 102 locality, as well as other fossiliferous localities nearby, was assigned an early Tortonian age. This was confirmed by strontium isotope stratigraphy (Chapter 5; Renema et al., submitted).

3. Material and Methods

Fossil assemblages were collected from discrete patches of fragmented ramose corals, weathering out on the approximately horizontal surface of a bedding plane of marine silts and clays (Fig. 1D, 2). Although these patches had been rain-washed, leading to some concentration of the fauna, specimens showed no signs lateral transport. In addition, many of the thinner-shelled mollusks were whole suggesting patches had been exposed on the quarry floor for only a short period of time. This is confirmed by the lack of any surficial features on larger mollusks that might indicate partial dissolution of aragonite. Therefore we could largely discount compositional distortion through atmospheric weathering of the recovered assemblage. Size and shape of each coral patch was measured in the field along a line transect of 10 m length. A total of five coral patches, each with an area of about 1-3 m2, were studied (Fig. 1D).

The first set of samples was obtained by hand-picking every mollusk seen at the surface of each coral patch. One additional handpicked surface collection includes larger, well-preserved coral colonies, selected to complement the taxonomic inventory. Subsequently, two bulk sediment samples were collected from each patch, resulting in a total of 10 bulk samples with weights ranging from 3 to 6 kg. One of each two samples (numbered for each site: SR50 to SR54) was used to study the taxonomic and ecological composition of the mollusk assemblage. The second sample of each pair (numbered for each site: NS50 to NS54) was used to study the composition of the coral assemblage.

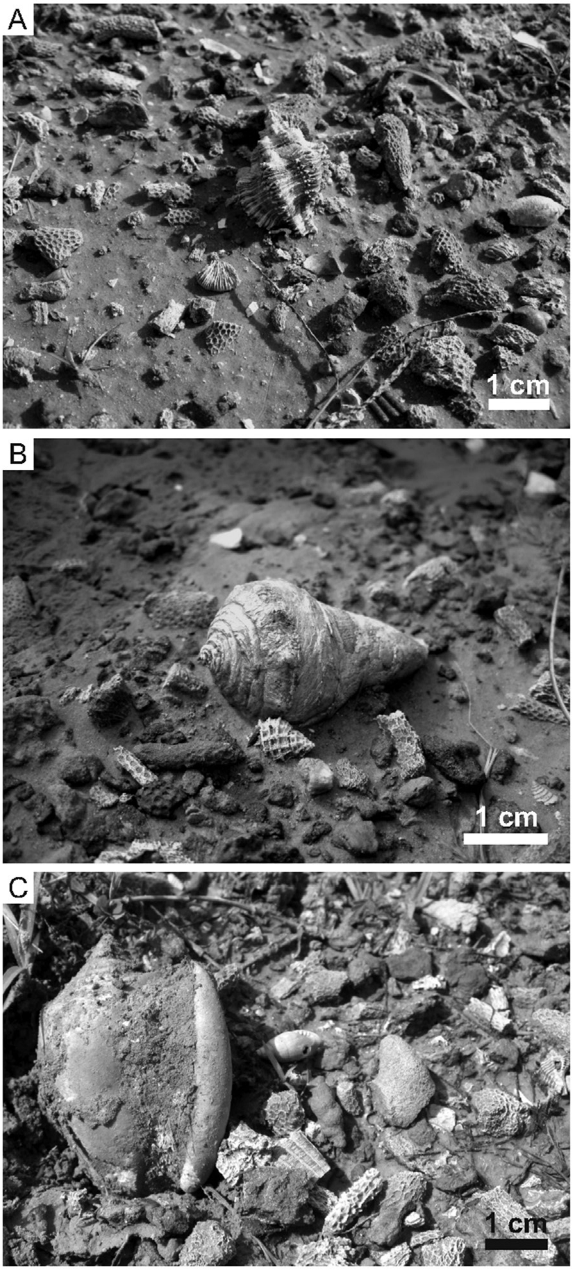

Figure 2: Snapshots of coral-mollusk patches on the floor of the TF 102 quarry. A) Coral fragments and mollusks; a larger muricid gastropod is visible in the center. B) Melongena in the center; the smaller gastropod shell in front is a Coralliophila. C) A comparatively large strombid shell on the left.

Bulk samples used for the study of mollusks were treated following the procedures outlined in Chapter 2 (3. Material and Methods), assessing all mollusk remains retained on a sieve with a mesh of 1 mm. Counting of specimens was likewise done as described in Chapter 2 (3. Material and Methods). Taxonomic identifications follow publications on fossil faunas of Indonesia (Beets, 1941, 1986; Leloux and Wesselingh, 2009) as well as descriptions of modern Indo-Pacific faunas (e.g., Okutani, 2000; Poppe, 2008a, 2008b, 2010a, 2010b). Specimens that could not be identified due to their poor preservation are labeled as Gastropoda indet. spp. and treated as a single taxon in the statistical analyses. The mollusk material is housed in the collection of Naturalis Biodiversity Center, Leiden, the Netherlands (indicated by RGM-numbers).

Bulk samples used for the study of corals were soaked in water, washed and sieved. The size fraction retained on a sieve mesh of 3.5 mm was studied. Identifications of corals are based on macro- and micromorphological features of colonies and corallites, following taxonomic accounts of Indonesian fossil faunas (Gerth, 1921, 1923; Umbgrove, 1929; mostly illustrated by Leloux and Renema, 2007). Taxon names were assigned according to the recent revision on Indo-Pacific fossil corals by Johnson et al. (submitted). Specimens identified as Acropora were classified into morphological species groups sensu Wallace (1999). The coral material is deposited in the collections of the Natural History Museum, London, UK (indicated by NHMU numbers).

According to the state of preservation and the available taxonomic frameworks both mollusks and corals were identified to the lowest possible rank (species). Otherwise, taxa were left in open nomenclature indicating their genus or family. Because part of the assemblages could not be identified below family level, the term taxon is used in this study, rather than species. In addition to the taxonomic classification, feeding guilds of mollusk taxa were defined as outlined in Chapter 2 (see 5.2). Coral abundances were estimated based on number of colony fragments as well as on weight of material (dry weight in grams) of each taxon per coral patch.

The adequacy of samples was explored using sample rarefaction, also providing an estimate of mollusk diversity. Analysis was performed using PAST (Paleontological Statistics; Hammer et al., 2001). Raup-Crick dissimilarities were calculated to assess how taxonomic composition varied among the assemblages, using the vegan package provided in the R statistical programming environment (Oksanen et al., 2013; R Core Team, 2013). The method is specifically designed for cases where sampling is incomplete and uneven among sites, because Raup-Crick dissimilarities are based on the probability that the compared sampling units have non-identical compositions (Raup and Crick, 1979). Two versions of Raup-Crick dissimilarities were applied. The first is based on analytic results of a hypergeometric distribution to find probabilities with the underlying assumption that all species occurrences are equally probable. The second is based on permutation results that allow sampling probabilities to be proportional to species frequencies. Raup-Crick dissimilarity for almost identical assemblages is close to zero. Raup-Crick dissimilarity for two assemblages with only a few shared species is close to 1.

4. Results

4.1 Taxonomic Composition of the Mollusk Assemblage

A total number of 178 identified mollusk taxa were obtained from the samples (Appendix 1). The five surface collections contained on average 31 taxa (ranging from 17 to 54). The five bulk sediment samples contained on average 70 taxa (ranging from 45 to 96). The overall most abundant taxa are illustrated in Figure 3. Twenty-four species were present only in surface- collected samples, whereas 102 species only occurred in bulk samples. Gastropods represent the most abundant and most species-rich mollusk group in all samples. They make up more than 70% in terms of specimens and species numbers in bulk samples. Bivalves make up around a quarter of the assemblage. A single polyplacophoran plate was found. The most abundant mollusk taxon in bulk samples is a medium-sized (~10 mm) cerithiid (Fig. 3G). The second most abundant taxon is a comparatively large (~25 mm) turrid (‘*Lophiotoma*’ sp. 1, Fig. 3R) that also represents the most abundant taxon in surface samples. The next most abundant taxa in bulk samples are represented by the genera *Dendostrea*, *Zafra*, *Nassarius*, *Plesiotrochus*, *Arcopsis*, *Anadara*, and *Iredalea* (Fig. 3).

4.2 Sample Size and Dissimilarity

The species accumulation curves show undersaturation for all samples, particularly for the assemblages recovered from hand-picked surface collections (Fig. 4). Because rarefaction curves unambiguously showed that the surface-picked collections were too small to provide enough data to accurately characterize assemblage composition (Fig. 4), we excluded them from further analyses.

Raup-Crick sample dissimilarity of all five bulk samples using equal probability ranges from 0 to 0.18 (mean = 0.02, Table 1A). Using abundance-based dissimilarities sample SR50 differs from almost all other samples apart from sample SR52 (Table 1B). Raup-

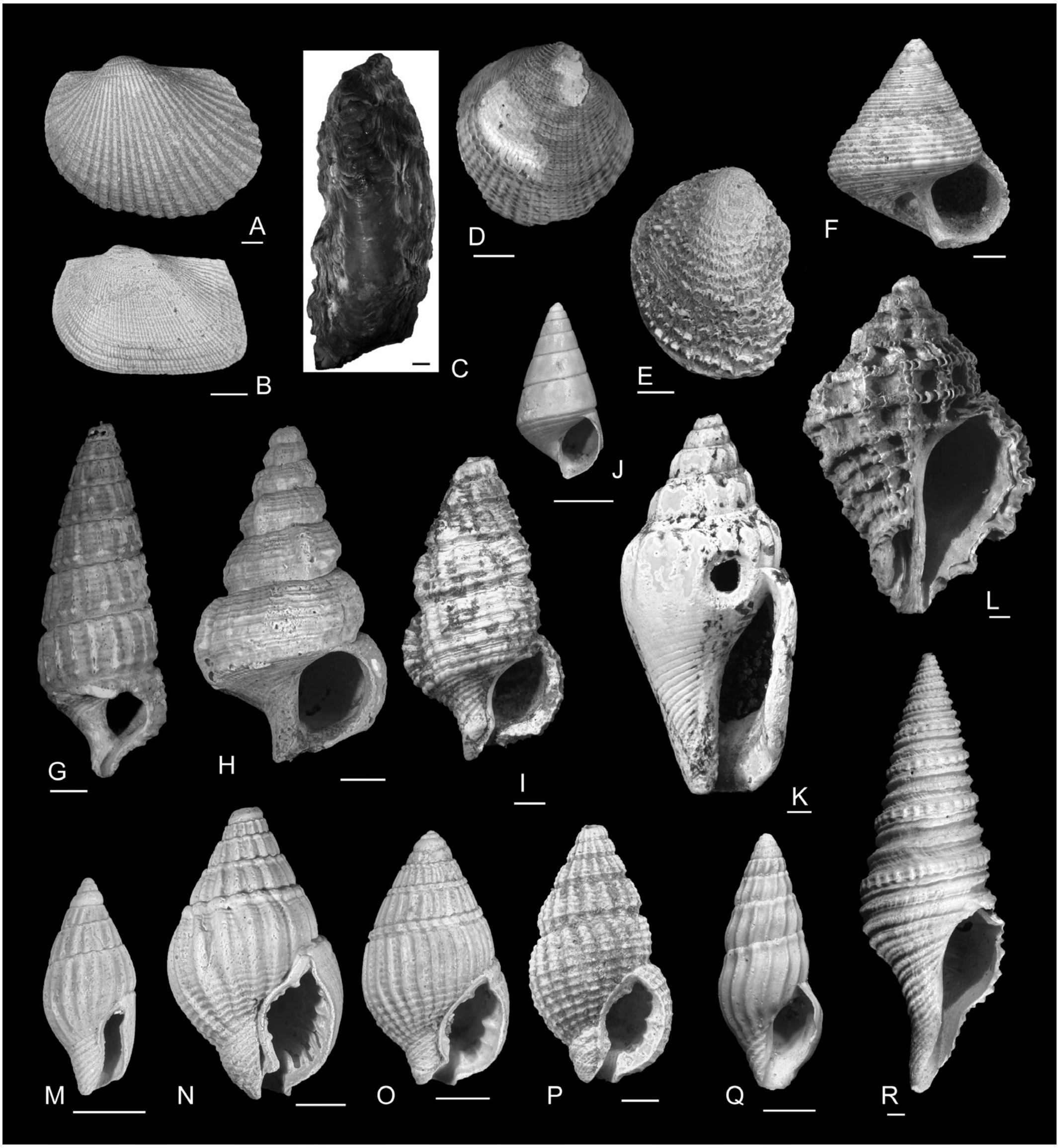

Figure 3: Abundant mollusk taxa in the TF 102 assemblage and some characteristic ecological indicator species. A) *Anadara* sp. 3, RGM.793.987, L 9.9 mm. B) *Arcopsis sculptilis* sensu Beets, 1941, RGM.793.986, L 5.0 mm. C) *Dendostrea* sp. 1, RGM.793.965, L 18 mm. D) *Cardiolucina* sp. 2, RGM.793.967, L 4.4 mm. E) *Chama* sp. 3, RGM.793.992, L 5.5 mm. F) *Gibbula leopoldi*, RGM.793.994, L 6.6 mm. G) *Cerithium* sp. 7, RGM.793.966, L 9.5 mm. H) *Plesiotrochus* sp. 6, RGM.793.985, L 7.6 mm. I) *Cerithium* sp. 3, RGM.793.993, L 9.6 mm. J) *Diala semistriata* s.l., RGM.793.995, L 2.9 mm. K) *Canarium unifasciatum* s.l., RGM.793.990, L 15.5 mm. L) *Coralliophila* aff. *clathrata*, RGM.793.969, L 16.2 mm. M) *Zafra* sp. 1, RGM.793.983, L 2.9 mm. N) *Nassarius* sp. 2, RGM.793.984, L 5.7 mm. O) *Nassarius* sp. 5, RGM.793.988, L 4.7 mm. P) *Nassarius* sp. 3, RGM.793.991, L 7.1 mm. Q) *Iredalea* sp. 1, RGM.793.989, L 4.7 mm. R) ‘*Lophiotoma*’ sp. 1, RGM.793.968, L 25 mm.

Crick dissimilarity between SR50 and SR54 is highest. A moderate dissimilarity is seen between SR50 and samples SR51 and 53. The only other samples that display a moderate dissimilarity are samples SR51 and 54.

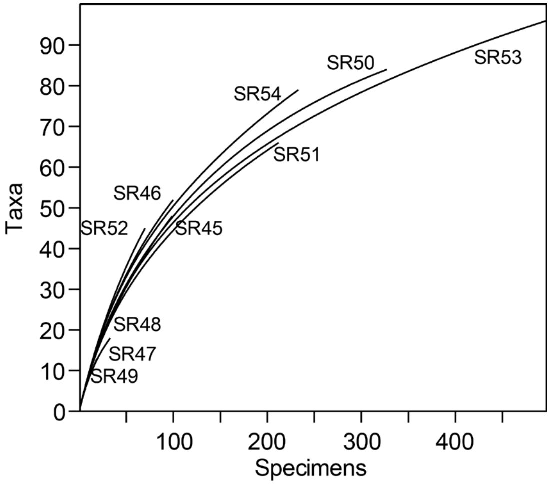

Figure 4 (left): Rarefaction curves of all mollusk samples from TF102.

Table 1: Raup-Crick sample dissimilarity. (A) Based on equal probability. (B) Based on proportional species abundance with highlighted values indicating dissimilarity.

A	SR50	SR51	SR52	SR53	B	SR50	SR51	SR52	SR53
SR51	0.010				SR51	**0.497**			
SR52	0.000	0.000			SR52	0.049	0.001		
SR53	0.011	0.000	0.000		SR53	**0.545**	0.121	0.008	
SR54	0.181	0.039	0.000	0.000	SR54	**0.936**	**0.704**	0.013	0.136

4.3 Ecological Composition of the Mollusk Assemblage

Feeding ecology was reconstructed for the assemblage obtained from adding all bulk-samples patches together (Appendix 1; Fig. 5). The assemblage is dominated by predatory and scavenging carnivorous gastropods, both in terms of species numbers (55%) and in abundance (48%). The most numerous carnivore, '*Lophiotoma*' sp. 1

(Fig. 3G) belongs to the superfamily Conoidea, which is represented by a total of 25 taxa (193 specimens) in the sampled assemblage as a whole. The likewise abundant *Iredalea* (Fig. 3G) is a conoidean as well. Both genera were formerly lumped together in the Turridae, the members of which commonly prey on polychaetes (Beesley et al., 1998; Bouchet et al., 2011). Nassariidae are also common, represented by four species (123 specimens; Fig. 3N-P), two of which are among the ten most abundant taxa. Members of the family largely feed on carrion, although they may shift facultatively to plant matter (Brown, 1969). Suspension feeders and herbivores (including detritivores) typically make up about a quarter of the assemblage. The latter group is slightly more prominent (28%) in the abundance data set. Suspension feeders are represented by bivalves, apart from a single capulid gastropod. Within the suspension feeding bivalves, shallow infaunal as well as epifaunal taxa are present. Whereas infaunal and epifaunal bivalves are represented by the same number of taxa, epifaunal bivalves are much more abundant and make up almost 80% of the bivalve assemblage in terms of specimens. This is due to the presence of a few very abundant taxa, such as *Dendostrea* and *Arcopsis* (Fig. 3B-C). The most abundant herbivorous/detritivorous gastropods are *Cerithium*, *Plesiotrochus*, and *Canarium unifasciatum* (Fig. 3G-I, K).

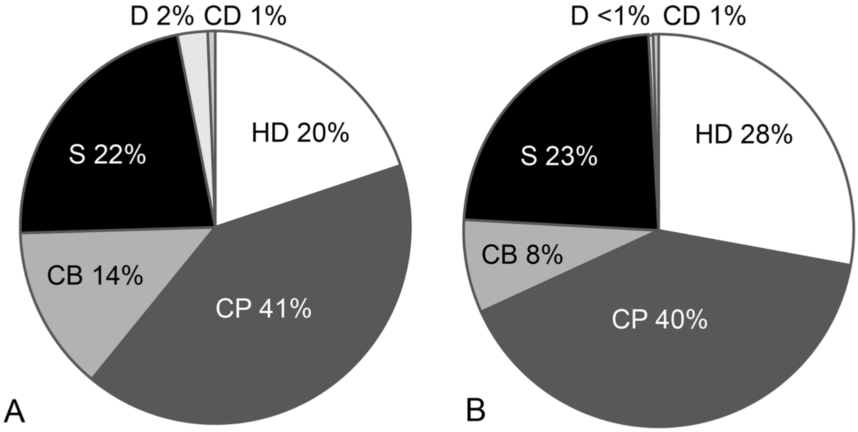

Figure 5: Feeding guild composition of the TF 102 assemblage. HD = herbivores and detritivores, CP = predatory carnivores, CB = browsing carnivores, S = suspension feeders, D = deposit-feeding bivalves, CD = chemosymbiotic deposit-feeders. A) Species numbers of feeding guilds with n = 163. B) Abundances of feeding guilds with n = 1452.

The obligate seagrass-feeding gastropod *Smaragdia* (Chapter 1; Rueda et al., 2009b; Unabia, 2011) is present in low numbers. Browsing carnivores are the least abundant gastropod feeding guild present. The guild is more prominent in species richness than in abundance. The most common included taxon is the marginellid *Dentimargo*, followed by the coral-feeder *Coralliophila* (Fig. 3L), and *Triphora*, an ectoparasite on sponges. The most species-rich, though not very abundant group included in the latter guild are the ectoparasitic pyramidelloids. Infaunal, deposit-feeding bivalves include tellinids and chemosymbiotic deposit-feeders, the latter represented by a species of *Cardiolucina* (Fig. 3D). Both families contribute little to the abundance and species richness of mollusks from the sampled units (< 1% to 2%).

4.4 Taxonomic Composition of the Coral Assemblage

Nineteen coral taxa were identified from the bulk sediment samples. Material from handpicked surface collections was better preserved and included larger colonies, but did not yield any additional taxa (Table 2). Taxon abundances measured as weight of colonies indicate that corals are mainly represented by ramose forms (67.5%) with subordinate columnar forms (21.5%). The most abundant ramose corals are taxa in the genus *Dictyaraea* (50.2%; Fig. 6A-C). Of these, three taxa could be identified as *Dictyaraea* sp. 1 (29.6%), *Dictyaraea* sp. 2 (19.2%) and *Dictyaraea micrantha* var. *spinosa* (1.4%). Other abundant ramose corals are *Alveopora* sp. (13.2%), *Seriatopora irregularis* (2.6%) and *Acropora* sp. aspera group (1.5%). Columnar forms include *Platygyra* sp. (9.6%) and *Goniopora* sp. (5.9%). Other coral forms make up less than 10% of the total assemblage. They include amongst others a free-living mushroom coral (*Fungia* sp.), fragments of small massive *Oulophyllia* sp., and the flabello-meandroid *Trachyphyllia* sp. No significant difference was seen when abundances were estimated as number of colony fragments.

Table 2 (right): Coral taxa abundances and growth forms. Data is presented as the dry weight of each taxon in grams and the number of fragments per sample. Ra=Ramose, Col=Columnar, Ma= small massive, Pl=Platy, Fm=Flabello meandroid, Fr=Free-living.

Taxon	**Form**	**Weight/g**							
		NS50	**NS51**	**NS52**	**NS53**	**NS54**	**Hand picked**	**Total**	**%**
Dictyaraea sp.1	Ra	95.50	39.50	47.50	139.00	73.00	14.50	409.00	29.60
Dictyaraea sp.2	Ra	121.0	53.5	19.5	23.5	10.0	37.5	265.0	19.2
Dictyaraea micrantha	Ra	2.5	5.0	0.5	6.0	0.0	5.0	19.0	1.4
Porites sp.	Ra	0.5	0.5	0.5	3.5	0.0	0.0	5.0	0.4
Goniopora sp.	Ra/Co	5.0	2.5	5.0	13.5	0.5	54.5	81.0	5.9
Seriatopora irregularis	Ra	25.0	0.5	7.0	3.0	0.5	0.5	36.5	2.6
Seriatopora hystrix	Ra	0.5	0.5	0.5	0.0	0.0	0.0	1.5	0.1
Stylophora sp.	Ra	0.5	0.5	0.5	0.0	0.0	0.0	1.5	0.1
Acropora sp. *aspera* group	Ra	0.0	21.0	0.0	0.0	0.0	0.0	21.0	1.5
Alveopora sp.	Ra/Co	55.0	26.5	11.5	28.0	14.0	47.0	182.0	13.2
Montipora sp.	Ra	0.5	12.5	3.0	2.0	0.0	6.0	18.0	1.3
Fungiidae sp.	Fr	0.5	2.0	2.5	0.5	0.5	74.0	80.0	5.8
Leptastrea -like	Co	0.0	13.0	0.0	2.0	0.0	5.5	20.5	1.5
Oulophyllia sp.	Ma	0.0	0.0	0.5	0.0	0.0	27.0	27.5	2.0
Platygyra sp.	Co	0.0	0.0	3.5	47.0	9.5	72.0	132.0	9.6
Pectinia sp.	Co	0.0	0.5	0.0	0.0	0.0	3.5	4.0	0.3
Trachyphyllia sp.	Fm	0.5	3.0	0.5	0.0	0.5	70.0	74.5	5.4
Pavona sp.	Pl	0.0	0.0	0.5	1.0	0.0	0.0	1.5	0.1
Millepora sp.	Ra	0.0	0.5	0.0	0.5	0.0	0.0	1.0	0.1
Total		307.0	181.5	103.0	269.5	108.5	417.0	1380.5	100.1

Taxon	**Form**	**Count of fragments**							
		NS50	**NS51**	**NS52**	**NS53**	**NS54**	**Hand picked**	**Total**	**%**
Dictyaraea sp.1	Ra	309	189	108	317	136	11	1070	51.0
Dictyaraea sp.2	Ra	134	123	16	25	8	17	323	15.4
Dictyaraea micrantha	Ra	7	14	4	16	0	3	44	2.1
Porites sp.	Ra	6	45	1	24	0	0	76	3.6
Goniopora sp.	Ra/Co	9	13	3	1	2	11	39	1.9
Seriatopora irregularis	Ra	108	10	11	12	4	4	149	7.1
Seriatopora hystrix	Ra	4	10	2	0	0	0	16	0.8
Stylophora sp.	Ra	1	5	1	0	0	0	7	0.3
Acropora sp. *aspera* group	Ra	0	52	0	0	0	0	52	2.5
Alveopora sp.	Ra/Co	55	20	21	31	13	9	149	7.1
Montipora sp.	Ra	6	38	7	5	0	2	56	2.7
Fungiidae sp.	Fr	2	13	6	3	1	2	27	1.3

Table 2 (continued): Coral taxa abundances and growth forms. Data is presented as the dry weight of each taxon in grams and the number of fragments per sample. Ra=Ramose, Col=Columnar, Ma= small massive, Pl=Platy, Fm=Flabello meandroid, Fr=Free-living.

Leptastrea -like	Co	0	2	0	4	0	2	8	0.4
Oulophyllia sp.	Ma	0	0	1	0	0	2	3	0.1
Platygyra sp.	Co	0	0	1	21	6	11	39	1.9
Pectinia sp.	Co	0	4	0	0	0	2	6	0.3
Trachyphyllia sp.	Fm	5	15	1	0	2	6	29	1.4
Pavona sp.	Pl	0	0	1	1	0	0	2	0.1
Millepora sp.	Ra	0	1	0	1	0	0	2	0.1
Total		646	554	184	461	172	82	2097	100.1

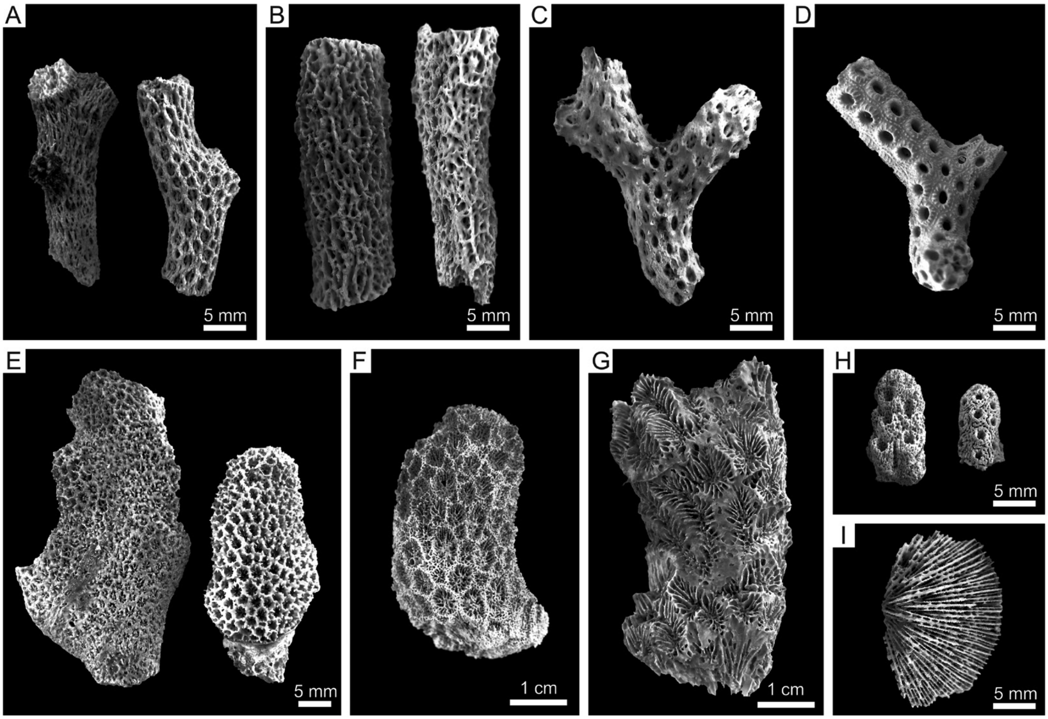

Figure 6: Abundant coral taxa in the TF 102 assemblage. A) *Dictyaraea* sp. 1, BMNH AZ6065. B) *Dictyaraea* sp. 2, BMNH AZ6035. C) *Dictyaraea micrantha* var. *spinosa*, BMNH AZ8797. D) *Seriatopora irregularis*, BMNH AZ8796. E) *Alveopora polyacantha*, BMNH AZ8788. F) *Goniopora* sp., BMNH AZ8790. G) *Platygyra* sp. AZ8786. H) *Acropora* sp. *aspera* group, BMNH AZ6006. I) *Fungia* sp., BMNH AZ8793.

5. Discussion

5.1 Paleoenvironment

Corals are abundant at the sampling locality, but they form small clumps evidently following the sea-floor morphology instead of build-up structures. We therefore refer to the paleoenvironment as a coral carpet sensu Riegl and Piller (1999, 2000).

The dominance of ramose forms in the coral assemblage is interpreted as a response to high sedimentation rates and high turbidity in the water column, because ramose colonies are more likely to overcome potential burial and suffocation caused by constant or episodic sediment discharge (Reuter et al., 2012; Sanders and Baron-Szabo, 2005). Among the ramose corals present, *Dictyaraea* species are the most abundant in our samples. *Dictyaraea* is an extinct genus of the family Poritidae, with the oldest fossil occurrence in the Oligocene of France (Chevalier, 1956). The genus is commonly reported from Miocene fossil coral faunas of Indonesia (Gerth, 1923; Umbgrove, 1929) and became extinct in the Pleistocene (Johnson et al., submitted). Modern representatives of the family Poritidae in reefal habitats include the genera *Porites* and *Goniopora*. Both genera include species that are common in relatively calm waters and that are tolerate comparatively high input of sediments into their habitat (Stafford-Smith and Ormond, 1992). Assuming *Dictyaraea* shares similar ecologies with its modern counterparts, it is proposed that these sediment-tolerant coral assemblages occupied the niche developed in calm, shallow waters influenced by high siliclastic input in the Miocene of East Kalimantan.

Fossil mollusks were predominantly observed within the coral patches and not in the sediments in between. This suggests that the occurrence of mollusks is associated with the presence of corals in the studied environment. Therefore, we assume that *Dictyaraea* corals offered a microhabitat that supported the rich mollusk community presented in this study. The assumed high rates of clay-grade sedimentation probably provided a preservation window for the aragonitic mollusks.

Close association of components of the mollusk assemblage to the once-living coral assemblage is also indicated by the presence of the obligate coral grazer *Coralliophila* (Beesley et al., 1998). Furthermore, fragments of the reef-associated bivalve *Tridacna* were recovered from the quarry floor and in some of the samples. The high abundance of the small epifaunal ostreid genus *Dendostrea* may indicate the presence of gorgonians (sea whips, sea fans) in the environment, the preferred substrate of modern *Dendostrea frons* in tropical America (Forbes, 1971). Although the assemblage is assumed to be largely diagenetically unfiltered, we cannot exclude the possibility that the numerical dominance of that taxon in the bivalve assemblage is due to its higher preservation potential because of its calcitic shell. Possibly thinner-shelled bivalve taxa got more affected by weathering and fragmented and were therefore not counted.

In addition, some shells of the obligate seagrass-feeding gastropod *Smaragdia* (Chapter 1) were found. Specimen numbers are very low, but considering that mollusk shells are rarely transported out of their original environment, we can assume they reflect the original life assemblage on a spatial scale (e.g., Kidwell, 2008; Kidwell and Bosence, 1991; Kidwell and Flessa, 1996). This leads to the assumption that interspersed seagrasses or seagrass patches were also present in this habitat.

5.2 Variation among Samples

The very low Raup-Crick dissimilarities based on equal probability among samples indicate little variation in their taxonomic composition. Therefore, the samples from different coral patches represent a single coral-associated mollusk assemblage, albeit sampled over a small horizontal distance. This justifies the combined analysis of all five merged bulk samples as a single assemblage.

The high abundance-based dissimilarity between sample SR54 and samples SR50 and 51 is probably due to comparatively low abundances of overall very common species, such as *Cerithium* sp. 7 and ‘*Lophiotoma*’ sp. 1 in sample SR54 (e.g., 59 specimens of *Ceritium* sp. 7 in SR51 vs. 13 specimens in SR54).

5.3 Ecological Variation between Environments

The TF 102 mollusk assemblage is dominated both in species richness and in abundance by predatory gastropods. A similar pattern may be present in modern tropical coral-associated mollusk assemblages based on the limited numerical data available. Taylor (1977, 1978) observed that the richness of predatory gastropods is highest in modern reef-associated gastropod assemblages compared to those from other shallow tropical marine environments in his study area at the Maldives.

Because of the similarity of the applied sample processing and counting methods the feeding-guild composition of the TF 102 assemblage can be directly compared to the composition of the seagrass-associated Banyunganti assemblage (Fig. 7; Chapter 2).

The Banyunganti assemblage and the assemblage from TF 102 have a similar composition of feeding guilds when species data is used. However, the abundance data discriminate clearly between both

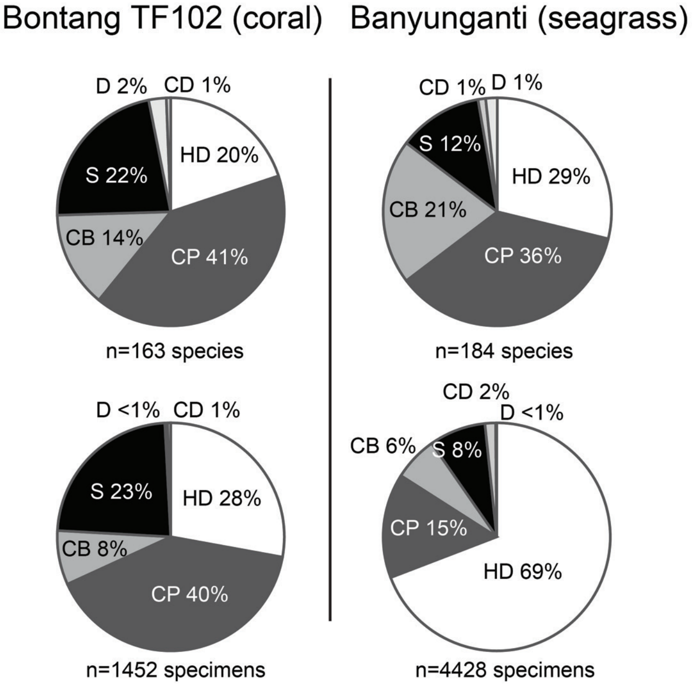

Figure 7: Comparison of mollusk feeding ecology using species richness (upper diagrams) and abundance data (lower diagrams) of the late Miocene coral carpet assemblage from TF102 (Bontang) and an early Miocene seagrass assemblage from Bayunganti (Java; Chapter 2). HD = herbivores and detritivores, CP = predatory carnivores, CB = browsing carnivores, S = suspension feeders, D = deposit-feeding bivalves, CD = chemosymbiotic deposit-feeders.

environments, with the seagrass assemblage being dominated by herbivores and the coral carpet assemblage by predators. Suspension feeders are less species-rich and abundant in the seagrass environment. A dominance of herbivorous and detritivorous gastropods is expected for seagrass-associated mollusk communities and has been used previously to identify seagrass meadows in the fossil record (Chapters 1 and 2; Brasier, 1975; Davies, 1970; Ivany et al., 1990; Moulinier and Picard, 1952). The comparatively low abundance and species richness of bivalves in the Banyunganti assemblage might be attributed to the presence of a dense rhizome mat that largely inhibited the establishment of an infauna (Chapter 1; Davies, 1970; James and Bone, 2007). However, the majority of filter-feeding bivalves in the TF 102 assemblage is represented by epifaunal taxa, and it remains unknown why those taxa are largely lacking in the Banyunganti assemblage, although they are often common in modern seagrass associations (Chapters 1 and 6; Mikkelsen et al., 1995). The here presented data may be applied for further studies on differences in feeding ecologies of mollusk assemblages from different habitats as a possible indicator for different paleohabitats (Chapter 1).

5.4 Biodiversity and Future Research

The rarefaction curve shows that the overall species richness of the seagrass assemblage is lower than that of the coral carpet assemblage (Fig. 8). However, it remains unresolved if the observed difference is based on environmental parameters or is due to the time difference between early Miocene (Banyunganti) and late Miocene (TF 102) assemblages. This stresses the necessity for comparisons of assemblages from the same habitat when reconstructing biodiversity over time.

To our knowledge, the TF 102 mollusk assemblage is at present the only detailed numerical analysis of a Neogene coral-associated mollusk assemblage from the region, so no comparisons with diversity from other coral-associated assemblages can be made. Quantitative shell data from comparable modern settings (e.g., Zuschin et al., 2001) were not available for comparison.

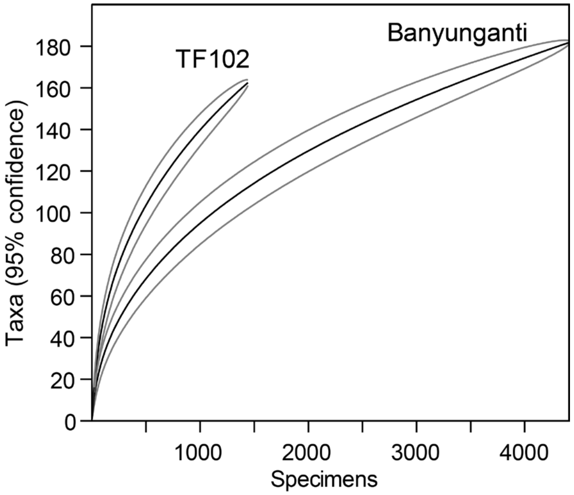

Fig.ure 8 (left): Rarefaction curves of the mollusk assemblages from TF102 (5 combined bulk samples; late Miocene) and Banyunganti (early Miocene).

Our results indicate that it is essential to make abundance counts based on bulk sediment samples in order to be able to make standardized diversity estimates and ecological characterizations (e.g., Jackson et al., 1999). Furthermore, with over a thousand specimens counted the rarefaction curve is not saturated, implying the need of larger sample-sizes in order to estimate species richness. When considered in isolation, the hand-picked samples yield far too low specimen numbers to be useful in analyses. Another obstacle is that the taxonomic impediment is huge. In the current assemblage we were able to identify only slightly more than 12% of the present taxa to species level, and several of these identifications remain uncertain.

6. Conclusions

1. The paleoenvironment of the late Miocene TF 102 site from Bontang (East Kalimantan, Indonesia) can be interpreted as a coral carpet that developed in calm, shallow waters influenced by high inputs of fine-grained sediments. Ramose corals of the extinct genus Dictyaraea were dominant in these settings and provided a suitable microhabitat for a diverse mollusk community.

2. The mollusk assemblage associated with the TF 102 coral carpet is dominated in species richness and abundance by various types of predatory gastropods. Modern

tropical coral-dominated environments may show a similar composition of molluscan feeding guilds.

3. The proportion of taxon-based and abundance-based feeding guilds in the studied coral carpet assemblage is very similar. A Miocene seagrass assemblage from the same region is typified by an increase in the proportion of the herbivore/detritivore guild in the abundance data when compared to the taxon data. Therefore, feeding guild composition of shallow marine tropical mollusk assemblages might yield a tool for the discrimination of paleo-habitats in addition to sedimentological or other information, but a lot more data and further studies are required to determine the generality of the pattern (Chapter 1).

4. We can infer species richness of the coral carpet mollusk assemblage to be very high and made up mostly of rare species. With over 1000 specimens counted the rarefaction curves show no sign of saturation, indicating that our level of sampling is too incomplete to adequately estimate total species richness in this and comparable environments.

5. The coral-associated mollusk assemblage is more diverse than a Miocene seagrass-associated assemblage from Indonesia, however it is unknown if this is based on diversity variations over time or between different environments. This indicates the importance of carefully distinguishing paleohabitats in order to make meaningful comparisons of habitat biodiversity.

6. Our results indicate that standardized bulk sampling is the preferred method over surface collecting when characterizing fossil assemblages, because only bulk sampling facilitates the collection of large numbers of shells required to adequately describe the taxonomic composition and abundance structure of diverse assemblages such as tropical shallow marine mollusks.

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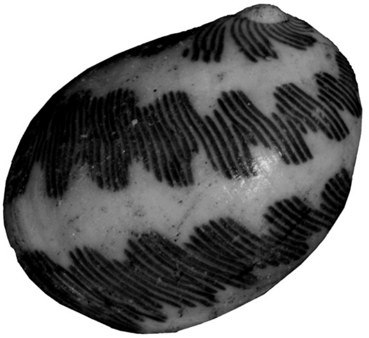
Section 2

Shelly IPSIs



Chapter 4

Gastropod Associations as a Proxy for Seagrass Vegetation in a Tropical, Carbonate Setting (San Salvador, Bahamas)

Sonja Reich

Palaios

(accepted manuscript)

Keywords: Marine angiosperms, snails, species composition, feeding ecology, Holocene

Abstract

Seagrass meadows are productive marine ecosystems that stabilize sediments and provide food and shelter for a diverse associated community. The recognition of these important habitats in the geological record is problematic, because marine angiosperms rarely fossilize. Thus, the presence of paleo-seagrass vegetation often has to be inferred from the occurrence of associated organisms with a higher potential for fossilization, such as mollusks. Because most mollusk taxa are not restricted to seagrass meadows, the species composition and feeding ecology of fossil mollusk faunas need to be considered when distinguishing paleo-seagrass meadows from other marine habitats. In this study the utility of faunal composition and feeding ecology of gastropods as an indicator of seagrass vegetation was tested using present-day ecosystems. Bulk sediment samples containing gastropod death assemblages from shallow water seagrass meadows and unvegetated sandflats from San Salvador Island, Bahamas were collected in July 2012. Vegetation varied across localities in terms of density and number of seagrass species. Twenty-four standardized (n=200) samples of gastropods were compared in terms of species composition and relative abundance of feeding guilds. Multivariate analyses indicate that species composition is an effective tool for distinguishing between gastropod assemblages from vegetated versus unvegetated areas. To a lesser extent, species composition differs among vegetation zones on sandflats with seagrass cover. Feeding guild composition based on species richness also differs on seagrass-vegetated and unvegetated sandflats. The results suggest that gastropod assemblages are a useful proxy for seagrass meadows in the fossil record.

1. Introduction

The importance of seagrass meadows has been highlighted by numerous authors. Seagrass beds are relevant primary producers and sediment stabilizers, they can be a source of biogenic carbonates, provide food and refuge for numerous associated organisms, and they play a considerable role in coastal nutrient cycling (Scoffin, 1970; Brasier, 1975; Constanza et al., 1997; Duarte and Chiscano, 1999; Hemminga and Duarte, 2000; De Falco et al., 2003; Green and Short, 2003; and others). The earliest fossil seagrasses occur in the Late Cretaceous and they apparently diversified during the Miocene, however, marine angiosperms have a low preservation potential, and as a result possess a relatively poor and incomplete fossil record (e.g., Brasier, 1975). Therefore, the former presence of seagrasses often has to be inferred from indirect fossil, sedimentological, and taphonomic evidence (Brasier, 1975; Eva, 1980; Domning, 2001; Beavington-Penney et al., 2004; Leonard-Pingel, 2005; Reuter et al., 2010). This study investigates if gastropods are a useful model group for the characterization of seagrass associated communities. They are suitable for this kind of analysis, because they are common or even dominant in the benthic and epiphytic community in modern seagrass meadows (Jackson, 1972; Marsh, 1973; Greenway, 1995; Barnes and Barnes, 2012), and they have a high potential for preservation (e.g., Moisette et al., 2007). Nevertheless, the majority of common seagrass-inhabiting gastropods occur in shallow marine habitats that are not characterized by seagrass (Mikkelsen et al., 1995; Zuschin and Hohenegger, 1998; this study). Because useful indicator taxa are rare, the species composition and feeding ecology of whole gastropod assemblages can be used to indicate unpreserved paleo-seagrass vegetation (Davies, 1970; James and Bone, 2007; Reuter et al., 2010; Reich et al., 2014). In particular, the high abundance of small herbivores is considered characteristic for seagrass associated mollusk communities (Moulinier and Picard, 1952; Davies, 1970).

In this study, I evaluate if gastropod death assemblages (*sensu* Kidwell and Bosence, 1991) from modern shallow-water seagrass vegetated habitats are different from assemblages in unvegetated sandflats. I test whether the observed differences in species composition and feeding ecology can be used to infer the presence of seagrass in fossil deposits. I will also explore differences in the grade of taphonomic alteration of shells to test if seagrass vegetation protects shells from taphonomic processes that may lead to the loss of identifiable specimens.

I gathered samples from seagrass vegetated sandflats within the meadow, as well as from the landward margin of the vegetated zone and from the unvegetated zone close to the shore. Subsequently, I evaluate if differences in seagrass vegetation (density, species composition) induce variation in the taxonomic and ecological composition of gastropod death assemblages.

2. Methods

2.1 Study Area and Sampling

San Salvador is a subtropical island (24° 06´ N) that is part of an isolated carbonate platform on the eastern edge of the Grand Bahama Bank (Fig. 1A). A wide range of depositional environments occur along the margins of the island, including numerous shallow water lagoons that host a patchy mosaic of seagrass communities with varying densities, as well as unvegetated sandflats. Samples were taken from three vegetated and two unvegetated sandflats around San Salvador (Table 1). Sampling at all five localities was carried out within a 0.25 m^2 large

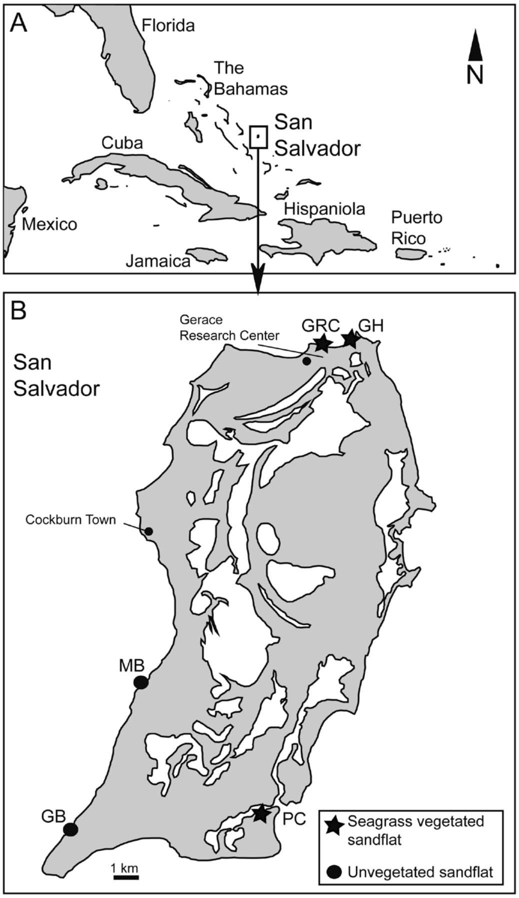


Figure 1 (left): Study area. A) Geographical setting of San Salvador. B) Locality map including sampling sites. GRC: Gerace Research Center. GH: Graham's Harbor. PC: Pigeon Creek. MB: Monument Beach. GB: Grotto Beach.

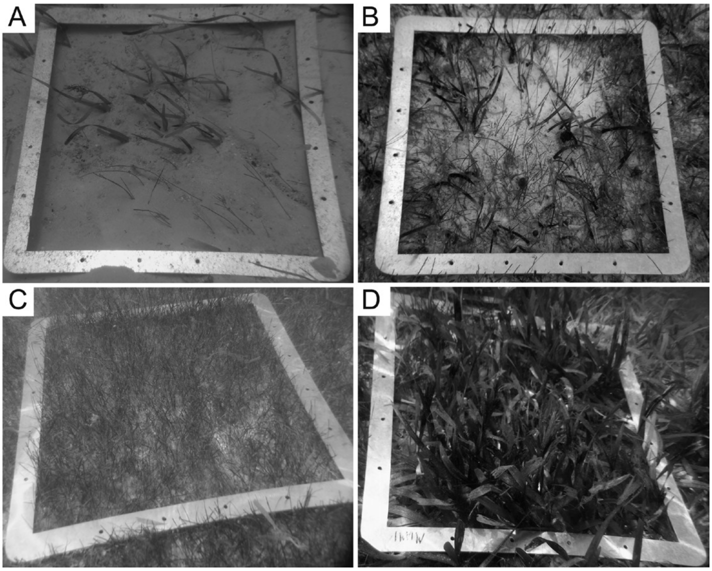


Figure 2 (right): Examples of sample sites at seagrass-vegetated sandflats displaying differences in vegetation density and species composition. A) Site PC2_B: Scarce vegetation of *T. testudinum* and *S. filiforme*. B) Site GRC1_C: Moderately dense vegetation of *T. testudinum* and *S. filiforme* intergrowing with *Penicillus capitatus*. C) Site PC1_B: Dense monospecific vegetation of *S. filiforme*. D) Site PC1_C: Dense vegetation of *T. testudinum* and *S. filiforme*.

frame using the same sieve (mesh width: 1 mm, d: 30 cm). Prior to sampling the quadrates were photographed to document vegetation density (Fig. 2). Vegetation cover was estimated using a comparison chart for visual estimation of percentage cover for each quadrate (Terry and Chilingar, 1955). A percentage cover of 1-10% was classified as ‘sparsely vegetated’, a percentage cover of 11-50% was classified as ‘moderately-well vegetated’, and a vegetation cover of >50% was classified as ‘densely vegetated’. At each sampling site the sieve was filled with surficial sediment, achieving approximately 500 g of material for each sample.

Two of the three vegetated localities are situated at Graham’s Harbor, a lagoon between Singer Bar and North Point at the north coast of San Salvador (Fig. 1B). Graham’s Harbor is located windward and is here classified as a moderate energy setting (Colby and Boardman, 1989). The first sample locality (GRC) is located opposite the entrance of the Gerace Research Center. The second locality (GH) is located further east on the right side of the old dock close to North Point. Both localities represent scarcely to moderately well vegetated seagrass dominated sandflats (Fig. 2B), with both *Thalassia testudinum* and *Syringodium filiforme*. Plant communities in these settings also include green algae commonly associated with tropical and subtropical seagrass meadows, such as *Halimeda* and *Penicillus* (Den Hartog, 1979).

Table 1: Sampling site attributes: water energy; coordinates; water depth; sample (including indication of represented vegetation zone: A = unvegetated, B = landward margin of seagrass meadow, C = seagrass meadow); seagrass density (estimated using the comparison chart for visual estimation of percentage cover after Terry and Chilingar, 1955: 0 = unvegetated, 1 = 1-10%, sparsely vegetated, 2 = 11-50%, moderately-well vegetated, 3 = >50%, densely vegetated); seagrass species (0 = unvegetated, 1 = *S. filiforme*, 2 = *T. testudinum* and *S. filiforme*).

Locality	Water energy	Coordinates	Sample site	Water depth/ cm	Seagrass density	Seagrass species
Gerace Research Center	Moderate	24.12002° N, 74.46397° W	GRC1_A	90	0	0
			GRC1_B	120	1	1
			GRC1_C	190	2	2
			GRC2_A	70	0	0
			GRC2_B	90	2	2
			GRC2_C	140	2	2
Graham's Harbor	Moderate	24.12071° N, 74.46070° W	GH1_A	80	0	0
			GH1_B	100	1	2
			GH1_C	120	2	2
			GH2_A	80	0	0
			GH2_B	100	1	2
			GH2_C	120	2	2
Pigeon Creek	High	23.95898° N, 74.48965° W	PC1_A	40	0	0
			PC1_B	70	3	1
			PC1_C	130	3	2
			PC2_A	60	0	0
			PC2_B	110	1	2
			PC2_C	120	3	2
Monument Beach	Low	24.00260° N, 74.51840° W	MB_A.1	80	0	0
			MB_A.2	110	0	0
			MB_A.3	130	0	0
Grotto Beach	Low	23.95429° N, 74.55412° W	GB_A.1	80	0	0
			GB_A.2	165	0	0
			GB_A.3	200	0	0

The third vegetated sample locality is situated at Pigeon Creek (PC), a tidal inlet at the southeastern end of the island (Fig. 1B). Pigeon Creek experiences strong current velocities of up to 25m/min near the inlet channel, and about 11m/min at the sampling locality (Mitchell, 1986), and is therefore classified as a high energy setting. Salinity at the sampling locality is at or slightly above offshore salinity (Curran and Martin, 2003; Mitchell, 1986). The subtidal area is characterized by a vegetation of *T. testudinum* and *S. filiforme*, which is considerably denser than at Graham's Harbor (Fig. 2C–D).

Two additional sampling localities represent unvegetated sandflats in front of small patch reefs and are located at Monument Beach (MB) and Grotto Beach (GB). Both localities are situated on the leeward west coast of San Salvador (Fig. 1B), are therefore protected from storms, and classified as low energy settings.

Six samples were taken at each of the three vegetated localities. Two samples (A) were derived from the unvegetated zone at the landward side of the meadow in a water depth ranging from 40-90 cm. Two samples (B) were taken from the landward margin of the vegetated zone in a water depth ranging from 70-112 cm. The final two samples (C) were taken within the vegetated zone in a water depth ranging from 110-190 cm. Sample sites representing the same zone were approximately 10 m apart. Mixed *Thalassia*-*Syringodium* vegetation occurs at all vegetated sampling sites apart from GRC1_B and PC1_B (Fig. 2C). The latter sites are located within an approximately 70 cm wide transition zone that is vegetated with *Syringodium* only. At each of the two unvegetated localities, three samples were taken in different water depths ranging from 80-200 cm.

2.2. Sample Processing

Samples were washed over a 1 mm sieve, dried, and sorted for shells. A total of 200 gastropods were randomly picked from each sample including incomplete specimens and fragments if a part of the columella was preserved. Fragments representing <50% of the original shell were included in the analysis and counted for one individual. Only two living gastropods were found among 4690 picked shells, and they were excluded from the analysis. The volume of sediment residue that was sorted to yield 200 specimens was weighed, and the number of specimens was divided by the weight of sorted material, and used as an estimate of shell abundance (number of gastropods/ 1 g sediment residue). Only one sample (GB_A.2) did not include the required number of gastropods, as only 90 specimens were found in this sample. The number of specimens for each species was counted based on Redfern (2001). Due to the applied counting method, it cannot be ruled out that two fragments representing the same individual were counted as two individuals, therefore the assembled data is not suitable for a comparison of relative abundance with a living assemblage. Identified species were assigned to four feeding guilds based on Todd (2001). A list of all taxa, their proportional abundance and assignments to feeding guilds is provided in the Supplementary Data. No direct data on the age of the collected shells, the time represented, or the significance of time-averaging (*sensu* Kowalewski, 1996) is available for the assemblages treated in this study.

2.3 Evaluation of Taphonomy

The number of specimens that could not be identified due to alteration (often a rather thick coating of carbonate) was used as a proxy for the general taphonomic state of samples. Spearman's correlation was used to test for a relation between the abundance of shells and the number of unidentifiable gastropods. A quantification of different types of alteration was beyond scope of this work.

2.4 Ecological Indices

Ecological indices, used for comparisons between samples and sample groups in this study, are species richness and dominance/evenness (Etter, 1999; Hammer et al., 2011). Species richness is expressed as the number of identified species occurring per sample. Dominance D (= 1-Simpson index) ranges from 0 to 1, indicating if the tested death assemblage is dominated by one species (D = 1) or if species are evenly distributed (D = 0). Conversely, the Simpson index (1-D) measures the evenness of the assemblage ranging from 0 to 1, with 1 indicating an even distribution of the present species. Similarity between species richness and dominance/evenness of samples from seagrass vegetated versus unvegetated sandflats was tested with one-way Analysis of Similarity (ANOSIM) using Bray Curtis similarity.

2.3 Analyses of Species Composition

Rare species were not excluded from the analyses following Etter (1999). Species abundance data are expressed as proportions to control for the effect of differing total abundances (Clifford and Stephenson, 1975). For example, without standardization sample GB_A2 would appear as an outlier, because it contained few specimens. Initial analyses of species composition and feeding ecology were carried out based on identified gastropods. In a later analysis, the proportional abundance of indeterminate gastropods was included by treating indeterminate specimens as unique category. Samples were initially grouped according to ‘seagrass vegetated sandflat’ and ‘unvegetated sandflat’. Analyses of samples from vegetated sandflats only are based on different grouping variables all referring to seagrass vegetation (vegetation zone, seagrass density, seagrass species; see Table 1). Similarity of species composition between sample groups was tested by one-way ANOSIM based on Bray-Curtis distance. Similarity is expressed by R and p-values ranging from 0 to 1, with high R and low p-values indicating dissimilarity between sample groups (Clarke, 1993). The data was log(x+1)-transformed for this analysis to reduce the effect of very abundant taxa (Krebs, 1989). Significant dissimilarities between sample groups, identified by ANOSIM, are visualized by non-metric multidimensional scaling (NMDS). The analysis is an indirect ordination method that reduces the data to fewer dimensions and shows overall relationships between samples (Hammer and Harper, 2006; Clapham, 2011). By using the same distance measure, the NMDS provides a visualization of the same patterns tested by ANOSIM. Alternative data-transformations [e.g., log(x+1), square-root] yielded similar results, but led to increased stress values of sample ordination. Therefore, the NMDS results presented here are based on untransformed data. Similarity percentage analysis (SIMPER) was applied to reveal which taxa are responsible for dissimilarities between sample groups (Clarke, 1993). Indicator species analysis was used to reveal the presence of taxa potentially indicative for seagrass vegetation. Indicator values are given as percentage of perfect indication, based on a combination of the relative abundance and the relative frequency of species. Species with a difference >60% between indicator value for seagrass vegetation and indicator value for unvegetated sandflat are here considered as potential indicator species for seagrass vegetation. The significance of indicator values was tested by Monte Carlo test of significance (expressed in p-values). Indicator species analysis was carried out using PC-ORD 6 (Peck, 2010). All other analyses were performed using PAST 2.16 (Hammer et al., 2001)

2.4 Analyses of Feeding Ecology

All identified gastropods were assigned to one of four feeding guilds, (1) herbivores (including detritivores, grazers, and feeders on seagrass tissue), (2) predatory carnivores (including scavengers and feeders on foraminifers; after Todd, 2001), (3) browsing carnivores (including parasites; after Todd, 2001), and (4) suspension feeders. Feeding guild abundance data is based on specimen numbers and species richness, expressed as proportions. The results presented in this study are based on untransformed data. Data analyses (NMDS, ANOSIM and SIMPER) are equivalent to analyses performed on species composition data.

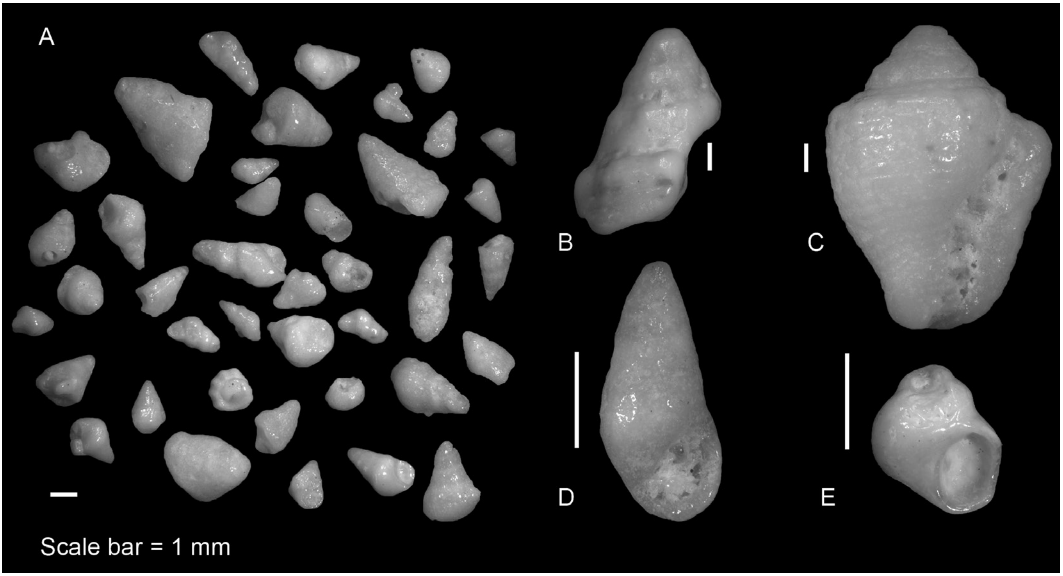


Figure 3: Examples of alteration of shells from unvegetated sandflats; showing fragmentation, abrasion and carbonate coating (sample sites and registration numbers are given). A) Gastropoda indet. spp., GB_A.1, RGM.794.355. B) Fragment of *Cerithium litteratum*, GB_A.3, RGM.794.356. C) *Columbella mercatoria*, GB_A.1, RGM.794.359. D) *Zebina browniana*, GB_A.2, RGM.794.358. E) *Eulithidium thalassicolum*, GB_A.2, RGM.794.357.

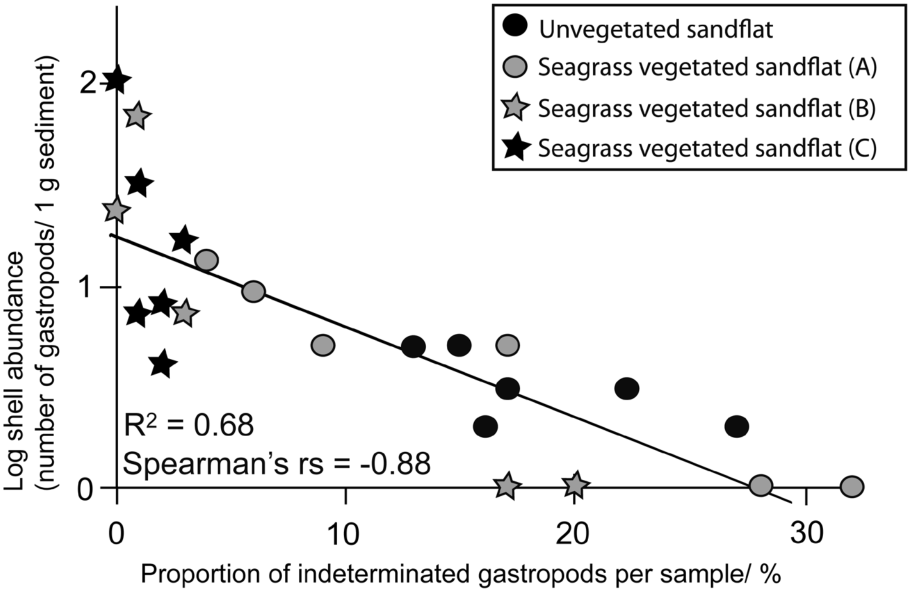


Figure 4: Scatterplot and line of best fit of log shell abundance and proportional abundance of indeterminate gastropods for 24 gastropod death assemblages from vegetated and unvegetated sandflats.

Table 2: Taphonomical and ecological indices of 24 gastropod death assemblages. $N_{specimens}$ = 200, except sample GB_A.2* with $N_{specimens}$ = 90.

Sampling site	Shell abundance (individuals/1 g sediment residue)	Unidentifiable shells/%	Species richness	Dominance D (1-Simpson index)	Eveness (Simpson index 1-D)
GRC1_A	1	27.5	31	0.13	0.87
GRC1_B	1	20.0	34	0.11	0.89
GRC1_C	4	2.0	37	0.16	0.84
GRC2_A	1	32.0	22	0.22	0.78
GRC2_B	1	17.0	30	0.10	0.90
GRC2_C	7	1.0	24	0.15	0.85
GH1_A	5	8.5	39	0.10	0.90
GH1_B	7	3.0	33	0.12	0.88
GH1_C	16	2.5	25	0.12	0.88
GH2_A	13	4.0	29	0.16	0.84
GH2_B	7	2.5	28	0.14	0.86
GH2_C	8	1.5	22	0.15	0.85
PC1_A	5	16.5	28	0.15	0.88
PC1_B	66	0.5	22	0.37	0.63
PC1_C	103	0.0	16	0.41	0.59
PC2_A	9	5.5	36	0.11	0.88
PC2_B	23	0.0	29	0.15	0.85
PC2_C	32	1.0	30	0.09	0.90
MB_A.1	3	16.5	29	0.15	0.85
MB_A.2	5	15.0	34	0.16	0.84
MB_A.3	5	12.5	32	0.19	0.81
GB_A.1	2	27.0	33	0.14	0.86
GB_A.2*	1	22.2	32	0.10	0.90
GB_A.3	2	16.0	31	0.16	0.84

3. Results

3.1 Shell Abundance and Taphonomic Alteration

The abundance of gastropod shells varies among samples from 1 to 103 specimens/g residue. Observed taphonomic features of the present shells are fragmentation, edge rounding, abrasion and carbonate-coating (Fig. 3). The number of indeterminate gastropods as an indication for taphonomic alteration ranges from 0 to 64 (Table 2).

The two variables 'shell abundance' and 'number of unidentifiable specimens' show a strongly negative correlation (Fig. 4). Total abundance and number of indeterminate specimens are inversely correlated such that samples with many indeterminate gastropods included relatively fewer shells overall than samples with few indeterminate gastropods. Furthermore, samples from unvegetated sandflats generally have low shell densities and high numbers of indeterminate gastropods while samples from seagrass meadows have high shell densities and low numbers of indeterminate gastropods. Samples from unvegetated areas close to seagrass meadows show the highest variation of shell abundance per sample.

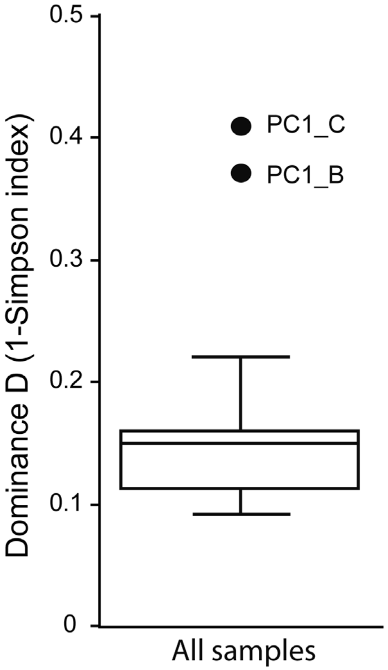


Figure 5: Boxplot of dominance D (1-Simpson index) of 24 gastropod death assemblages.

3.2 Species Richness and Dominance/Evenness

A total number of 114 species was found in 24 samples ($n_{specimens}$ = 4690). The number of identified species per sample ranges from 16 to 39 with a mean value of 29 (Table 2). On average, samples from unvegetated sandflats seem to have the highest species richness (n = 32), followed by samples from the unvegetated zone of seagrass vegetated sandflats (n = 31), and samples from the landward margin of seagrass meadows (n = 29). Samples collected inside seagrass meadows display the lowest mean species richness (n = 26) but also the widest range (min = 16, max = 37). ANOSIM reveals a significant dissimilarity of species richness between samples from unvegetated sandflats and samples collected inside seagrass meadows (R = 0.34, p = 0.014).

Dominance is low in most samples, ranging from 0.10 to 0.22 (mean = 0.14, STD = 0.03), with two exceptions: samples PC1_B and PC1_C appear as outliers with higher values of 0.37 (PC1_B) and 0.41(PC1_C) (Table 2; Fig. 5). No significant dissimilarity is seen between dominance/evenness of samples from seagrass vegetated versus unvegetated sandflats (R = -0.10, p = 0.75).

3.3 Abundance and Distribution

The ten most common species are listed in Table 3, and the most common species from seagrass vegetated localities are figured (Fig. 6). Among a total of 114 species, only four are present in all samples (*Eulithidium thalassicolum*, *Cerithium litteratum*, *Cerithium eburneum*, *Zebina browniana*). Fifty-four species are present in only one sample. Forty-five species (18 singletons) are only present in samples from seagrass vegetated localities. Eighteen species are only present in samples from unvegetated areas including 11 species that are represented by a single specimen.

Table 3 (left): The ten most common gastropod species from all localities, from seagrass-vegetated sandflats, and from unvegetated sandflats ranked for proportional abundance.

Species	Number of specimens	Proportional abundance/ %
All samples		
Eulithidium thalassicolum	740	17.59
Zebina browniana	687	16.33
Cerithium eburneum	517	12.29
Cerithium litteratum	382	9.08
Acteocina spp.	360	8.56
Finella adamsi	255	6.06
Cerithium lutosum	222	5.28
Tegula fasciata	56	1.33
Patelloidea pustulata	48	1.14
Atys sharpi/*Atys*. sp. 1	45	1.07
Samples from seagrass vegetated sandflats		
Eulithidium thalassicolum	679	20.51
Zebina browniana	663	20.03
Cerithium eburneum	397	11.99
Acteocina spp.	338	10.21
Cerithium lutosum	215	6.5
Finella adamsi	121	3.66
Cerithium litteratum	105	3.17
Patelloidea pustulata	48	1.45
Atys sharpi/*Atys*. sp. 1	45	1.36
Tegula fasciata/ *Smaragdia viridis*	41	1.24
Samples from unvegated sandflats		
Cerithium litteratum	277	30.92
Finella adamsi	134	14.95
Cerithium eburneum	120	13.39
Eulithidium thalassicolum	61	6.81
Zebina browniana	24	2.68
Acteocina spp.	22	2.46
Columbella mercatoria	19	2.12
Tegula fasciata/ *Dentimargo reductus*	15	1.67
?*Arene* sp. 1/ *Granoturris* sp. 1/ *Bulla occidentalis*	11	1.23
Rissoina sp. B	9	1.12

Figure 6: The ten most common gastropod species from seagrass-vegetated sandflats (sample sites and registration numbers are given). A) *Patelloidea pustulata*, GRC1_C, RGM.783.151. B) *Tegula fasciata*, GRC1_C, RGM.783.152. C) *Eulithidium thalassicolum*, GRC1_C, RGM.783.153. D) *Smaragdia viridis*, PC1_C, RGM.783.154. E) *Cerithium eburneum*, PC1_C, RGM.783.155. F) *Cerithium litteratum*, GRC1_C, RGM.783.156. G) *Cerithium lutosum*, PC2_C, RGM.783.157. H) *Finella adamsi*, PC2_C, RGM.783.158. I) *Zebina browniana*, PC1_C, RGM.783.159. J) *Acteocina* sp., PC2_C, RGM.783.160. K) *Atys sharpi*, GRC1_C, RGM.783.161. L) *Atys* sp. 1, GRC1_C, RGM.783.162.

Table 4 (right): ANOSIM results for comparisons of species composition and feeding guild composition between different sample groups, based on different grouping variables (vegetation zone: A = unvegetated, B = landward margin of seagrass meadow, C = seagrass meadow; vegetation density: 0 = unvegetated, 1 = 1-10%, sparsely vegetated, 2 = 11-50%, moderately-well vegetated, 3 = >50%, densely vegetated; occurrence of seagrass species 0 = unvegetated, 1 = *S. filiforme*, 2 = *T. testudinum* and *S. filiforme*). Significant results are highlighted.

<table>
<tr><th colspan="5">Species composition - All samples</th></tr>
<tr><th>Grouping variable</th><th>Dataset</th><th>Comparison between groups</th><th></th><th>p-value</th></tr>
<tr><td>Presence of vegetation</td><td>Identified gastropods</td><td>seagrass vs. unvegetated</td><td>0.894</td><td>0.000</td></tr>
<tr><td></td><td>Identified gastropods (outliers removed)</td><td>seagrass vs. unvegetated (outliers removed)</td><td>0.985</td><td>< 0.0001</td></tr>
<tr><th colspan="5">Species composition - Samples from seagrass vegetated sandflats</th></tr>
<tr><td>Vegetation zone</td><td>Identified gastropods</td><td>A vs. B</td><td>-0.135</td><td>0.938</td></tr>
<tr><td></td><td></td><td>A vs. C</td><td>0.230</td><td>0.010</td></tr>
<tr><td></td><td></td><td>B vs. C</td><td>0.056</td><td>0.230</td></tr>
<tr><td></td><td>Identified gastropods</td><td>A vs. B</td><td>-0.184</td><td>0.933</td></tr>
<tr><td></td><td>(outliers removed)</td><td>A vs. C</td><td>0.371</td><td>0.015</td></tr>
<tr><td></td><td></td><td>B vs. C</td><td>0.312</td><td>0.041</td></tr>
<tr><td></td><td>Gastropoda spp. included</td><td>A vs. B</td><td>-0.061</td><td>0.706</td></tr>
<tr><td></td><td></td><td>A vs. C</td><td>0.430</td><td>0.002</td></tr>
<tr><td></td><td></td><td>B vs. C</td><td>0.063</td><td>0.284</td></tr>
<tr><td></td><td>Gastropoda spp. included</td><td>A vs. B</td><td>-0.069</td><td>0.666</td></tr>
<tr><td></td><td>(outliers removed)</td><td>A vs. C</td><td>0.579</td><td>0.003</td></tr>
<tr><td></td><td></td><td>B vs. C</td><td>0.340</td><td>0.039</td></tr>
<tr><td>Vegetation density</td><td>Gastropoda spp. included</td><td>0 vs. 1</td><td>-0.119</td><td>0.761</td></tr>
<tr><td></td><td></td><td>0 vs. 2</td><td>0.525</td><td>0.006</td></tr>
<tr><td></td><td></td><td>0 vs. 3</td><td>0.778</td><td>0.012</td></tr>
<tr><td></td><td></td><td>1 vs. 2</td><td>0.306</td><td>0.072</td></tr>
<tr><td></td><td></td><td>1 vs. 3</td><td>0.593</td><td>0.027</td></tr>
<tr><td></td><td></td><td>2 vs. 3</td><td>0.713</td><td>0.017</td></tr>
<tr><td></td><td>Gastropoda spp. included</td><td>0 vs. 1</td><td>-0.119</td><td>0.756</td></tr>
<tr><td></td><td>(outliers removed)</td><td>0 vs. 2</td><td>0.525</td><td>0.006</td></tr>
<tr><td></td><td></td><td>0 vs. 3</td><td>0.422</td><td>0.142</td></tr>
<tr><td></td><td></td><td>1 vs. 2</td><td>0.306</td><td>0.071</td></tr>
<tr><td></td><td></td><td>1 vs. 3</td><td>-0.250</td><td>1.000</td></tr>
<tr><td></td><td></td><td>2 vs. 3</td><td>0.520</td><td>0.339</td></tr>
<tr><td>Seagrass species</td><td>Gastropoda spp. included</td><td>0 vs. 1</td><td>0.375</td><td>0.177</td></tr>
<tr><td></td><td></td><td>0 vs. 2</td><td>0.052</td><td>0.302</td></tr>
</table>

Table 4 (continued): ANOSIM results for comparisons of species composition and feeding guild composition between different sample groups, based on different grouping variables (vegetation zone: A = unvegetated, B = landward margin of seagrass meadow, C = seagrass meadow; vegetation density: 0 = unvegetated, 1 = 1-10%, sparsely vegetated, 2 = 11-50%, moderately-well vegetated, 3 = >50%, densely vegetated; occurrence of seagrass species 0 = unvegetated, 1 = *S. filiforme*, 2 = *T. testudinum* and *S. filiforme*). Significant results are highlighted.

		1 vs. 2	0.009	0.480
		0 vs. 1	-0.200	0.714
		0 vs. 2	0.122	0.138
		1 vs. 2	-0.222	0.799
Feeding guild composition - All samples				
Presence of vegetation	Specimen numbers	seagrass vs. unvegetated	0.021	0.398
	Species richness	seagrass vs. unvegetated	**0.476**	**< 0.001**
Feeding guild composition - Samples from seagrass vegetated sandflats				
Vegetation zone	Species richness	A vs. B	-0.014	0.479
		A vs. C	0.023	0.298
		B vs. C	-0.026	0.515
	Species richness	0 vs. 1	-0.052	0.573
		0 vs. 2	0.000	0.365
		1 vs. 2	**0.549**	**0.033**
		0 vs. 1	-0.025	0.507
		0 vs. 2	0.222	0.145
		1 vs. 2	0.272	0.109

3.4 Species Composition

NMDS analyses of species composition data in a two-dimensional ordination space result in stress values greater than 1.15, indicating that no close agreement exists between the ordination and the original data (Hammer and Harper, 2006). Therefore, all NMDS analyses of patterns of species composition are performed in a three-dimensional space. ANOSIM was performed on proportional species abundances

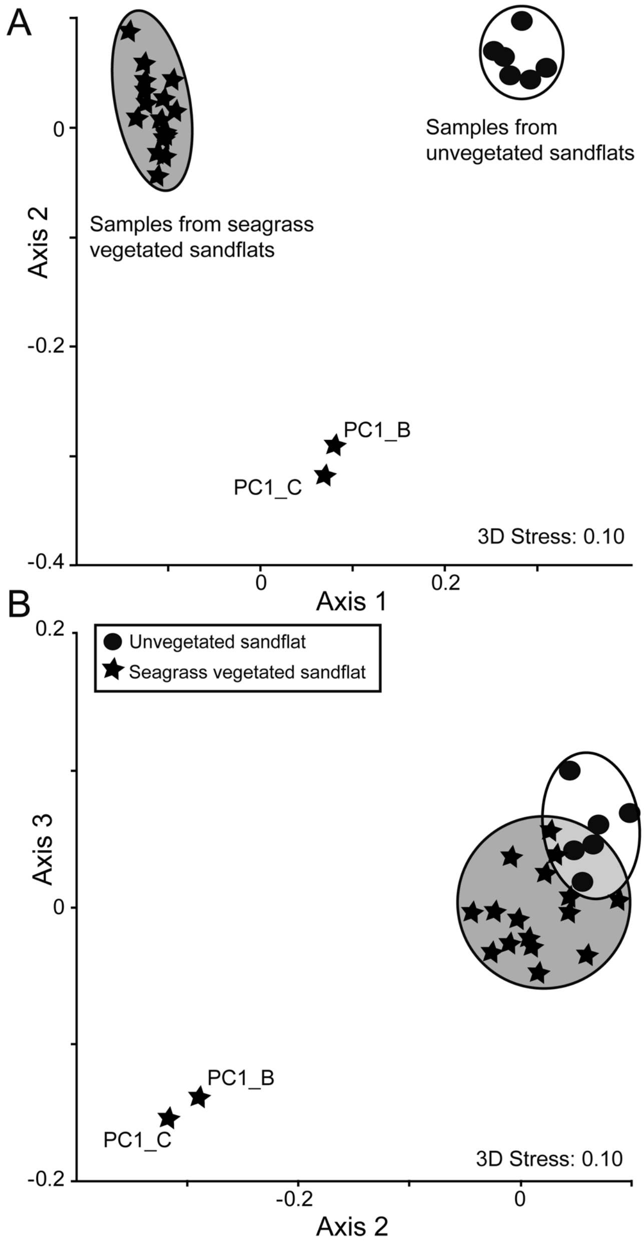


Figure 7: Three-dimensional NMDS ordination of 24 gastropod death assemblages based on proportional abundance of identified species, grouped by locality, using Bray Curtis distance. A) Axis 1 and 2. B) Axis 2 and 3.

of identified species from all samples grouped for seagrass vegetated versus unvegetated sandflats. Results reveal a highly significant dissimilarity between the two sample groups (R = 0.894, p = 0.0001; Table 4). NMDS analysis confirms a clear separation with no overlap of samples from seagrass vegetated sandflats and samples from unvegetated sandflats along axis 1(Fig. 7A). Two samples from a densely vegetated locality in Pigeon Creek are very different from all other samples along axis 2 (PC1_B, PC1_C; Fig. 7). Samples from unvegetated sandflats group together along axis 3 as do samples from seagrass vegetated sandflats, but the groups are overlapping (Fig. 7B). According to SIMPER results (Table 5), the most important contributor to the dissimilarity is *Cerithium litteratum*, followed by *Zebina browniana* and *Eulithidium thalassicolum*.

Dataset	Grouping	Average dissimilarity	Species
All samples	Seagrass vegetated sandflats vs. unvegetated sandflats	66.33	*Cerithium litteratum* *Zebina browniana* *Eulithidium thalassicolum* *Finella adamsi* *Acteocina* spp.
All samples, except outliers	Seagrass vegetated sandflats vs. unvegetated sandflats	64.89	*Cerithium litteratum* *Eulithidium thalassicolum* *Zebina browniana* *Finella adamsi* *Acteocina* spp.
Samples from seagrass vegetated sandflats, except outliers	vegetation zone A vs. C	37.20	*Zebina browniana* *Acteocina* spp. *Eulithidium thalassicolum* *Cerithium lutosum* *Cerithium eburneum*
Samples from seagrass vegetated sandflats, except outliers	vegetation zone B vs. C	35.12	*Zebina browniana* *Cerithium lutosum* *Eulithidium thalassicolum* *Cerithium eburneum* *Acteocina* spp.
Samples from seagrass vegetated sandflats, except outliers, Gastropoda indet. included	vegetation zone A vs. C	39.61	Gastropoda indet. spp. *Zebina browniana* *Eulithidium thalassicolum* *Cerithium eburneum* *Cerithium lutosum*
Samples from seagrass vegetated sandflats, except outliers, Gastropoda indet. included	vegetation zone B vs. C	36.93	*Zebina browniana* *Eulithidium thalassicolum* Gastropoda indet. spp. *Cerithium lutosum* *Cerithium eburneum*

Contribution to dissimilarity	Cummulative %
13.50	20.35
8.35	32.94
7.34	44.00
5.63	52.49
4.38	59.10
13.62	20.99
8.13	33.53
5.74	42.37
5.50	50.83
4.79	58.21
5.09	13.68
4.26	25.12
3.90	35.62
3.09	43.92
2.93	51.80
4.65	13.24
3.83	24.14
3.66	34.57
2.13	40.64
1.70	45.49
6.06	15.31
4.65	27.05
3.95	37.02
2.99	44.57
2.93	51.96
4.01	10.87
3.97	21.63
3.76	31.82
3.73	41.91
1.94	47.16

Table 5 (left): SIMPER results: Five most important species contributing to the dissimilarity between sample groups using different groupings (A = unvegetated, B = landward margin of seagrass meadow, C = seagrass meadow; 0 = unvegetated, 1 = 1-10%, sparsely vegetated, 2 = 11-50%, moderately-well vegetated, 3 = >50%, densely vegetated).

To exclude the possibility that the dissimilarity between sample groups is induced by the two outlying samples, PC1_B and PC1_C were removed, and the ANOSIM analysis was repeated, leading to an increase of significance ($R = 0.985$, $p < 0.0001$, Table 4). After removal of the outliers, *Z. browniana* contributes less to the dissimilarity between sample groups.

To examine differences between samples from different zones of seagrass vegetated sandflats, analysis on identified gastropods was carried out excluding samples from unvegetated sandflats, with the remaining samples grouped into three vegetation zones (unvegetated zone, margin of seagrass meadow, and seagrass meadow; Table 1).

Excluding the outlying samples PC1_B and PC1_C leads to an increased significance of dissimilarity between samples from seagrass meadows (C) and samples from unvegetated zones (A), as well as between samples from seagrass meadows (C) and samples from the margin of meadows (B) (Table 4). Only samples from unvegetated zones (A) and samples from the margin of meadows (B) do

All samples from seagrass vegetated sandflats, Gastropoda indet. included	vegetation density 0 vs. 3	59.47	*Zebina browniana* Gastropoda indet. spp. *Acteocina* spp. *Eulithidium thalassicolum* *Cerithium eburneum*
All samples from seagrass vegetated sandflats, Gastropoda indet. included	vegetation density 1 vs. 3	56.92	*Zebina browniana* *Eulithidium thalassicolum* *Cerithium eburneum* *Acteocina* spp. *Cerithium lutosum*
All samples from seagrass vegetated sandflats, Gastropoda indet. included	vegetation density 2 vs. 3	52.03	*Zebina browniana* *Eulithidium thalassicolum* *Cerithium eburneum* *Acteocina* spp. *Cerithium lutosum*
All samples from seagrass vegetated sandflats, Gastropoda indet. included	vegetation density 0 vs. 2	40.87	Gastropoda indet. spp. *Zebina browniana* *Eulithidium thalassicolum* *Cerithium eburneum* *Cerithium lutosum*

not differ significantly. To illustrate the pattern, NMDS was performed on the reduced proportional abundance data set, grouped for vegetation zone. The results show that the sample groups strongly overlap when plotted against axis 1 and 2 (Fig. 8A), but samples from seagrass meadows separate from other samples along axis 3 (Fig. 8B). The species mainly contributing to the dissimilarity of samples from seagrass meadows to other sample groups is *Z. browniana*, but other species (e.g., *Acteocina* spp., *C. litteratum*, and *E. thalassicolum*) are almost as important (Table 5).

The proportional abundance of indeterminate gastropods was included in the analysis. ANOSIM results display significant dissimilarities between sample groups A and C, and C and B, as revealed by the analysis carried out on identified species only. However, the addition of the proportional abundance of indeterminate gastropods leads to increased R-values and decreased p-values, indicating that dissimilarities between

18.24	30.66
7.58	43.41
5.21	52.17
4.57	59.86
3.18	65.20
17.63	30.97
5.77	41.11
4.40	48.83
3.48	54.94
3.46	61.02
15.67	30.11
6.32	42.25
3.62	49.20
3.30	55.54
2.88	61.08
6.55	16.03
5.31	29.02
3.81	38.34
3.26	46.31
2.82	53.20

Table 5 (continued): SIMPER results: Five most important species contributing to the dissimilarity between sample groups using different groupings (A = unvegetated, B = landward margin of seagrass meadow, C = seagrass meadow; 0 = unvegetated, 1 = 1-10%, sparsely vegetated, 2 = 11-50%, moderately-well vegetated, 3 = >50%, densely vegetated).

sample groups were enhanced (Table 4). NMDS results show a separation with some overlap between samples from seagrass meadows and other sample groups along axis 1 (Fig. 8C); only two samples from seagrass meadows separate from other samples along axis 2 (Fig. 8D). SIMPER analysis confirms that the proportional abundance of indeterminate specimens significantly contributes to the dissimilarity between samples groups, especially between samples from unvegetated zones and samples from seagrass meadows (Table 5).

Figure 8 (next page): Three-dimensional NMDS ordination of 16 gastropod death assemblages from seagrass-vegetated sandflats, grouped by vegetation zone, using Bray Curtis distance. A) Proportional abundance of identified species; axis 1 and 2. B) Proportional abundance of identified species; axis 2 and 3. C) Proportional species abundances including Gastropoda indet.; axis 1 and 2. D) Proportional species abundances including Gastropoda indet.; axis 2 and 3.

Figure 9 (next page): Three-dimensional NMDS ordination of 16 gastropod death assemblages from seagrass-vegetated sandflats (including Gastropoda indet.), grouped by vegetation density, using Bray Curtis distance. A) Axis 1 and 2. B) Axis 2 and 3.

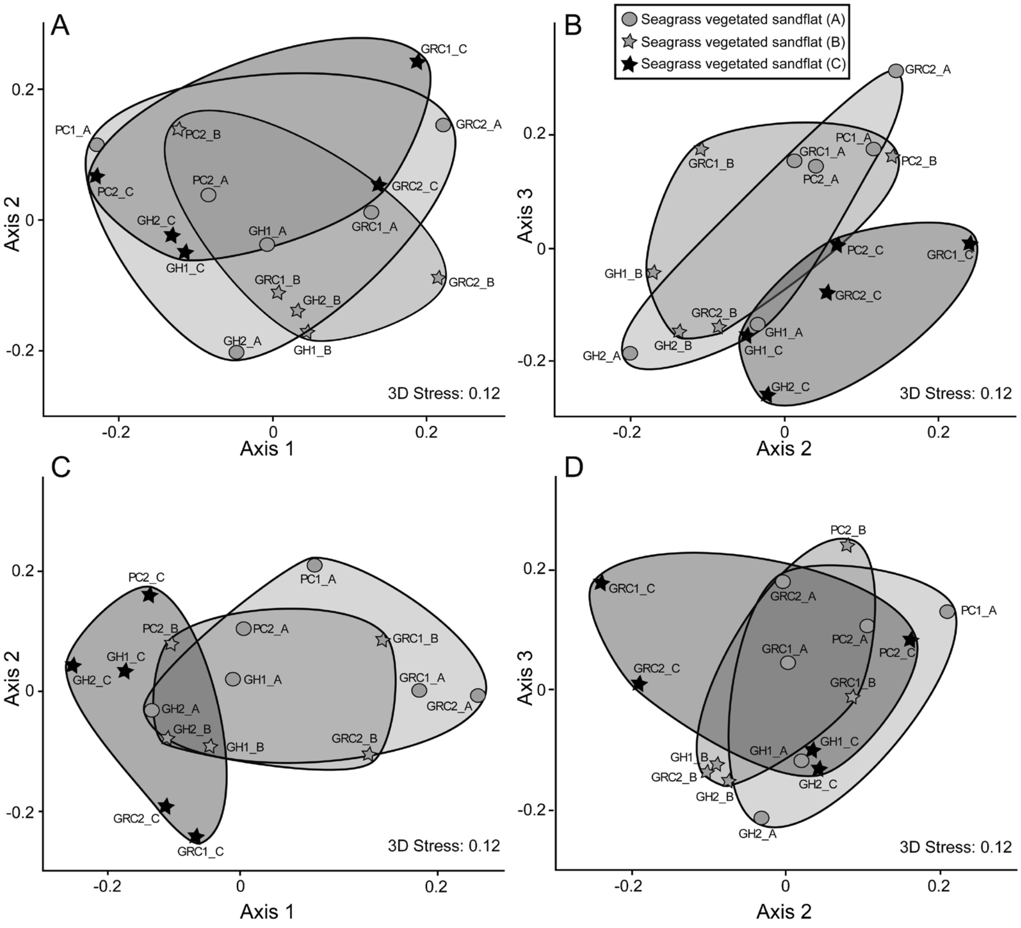
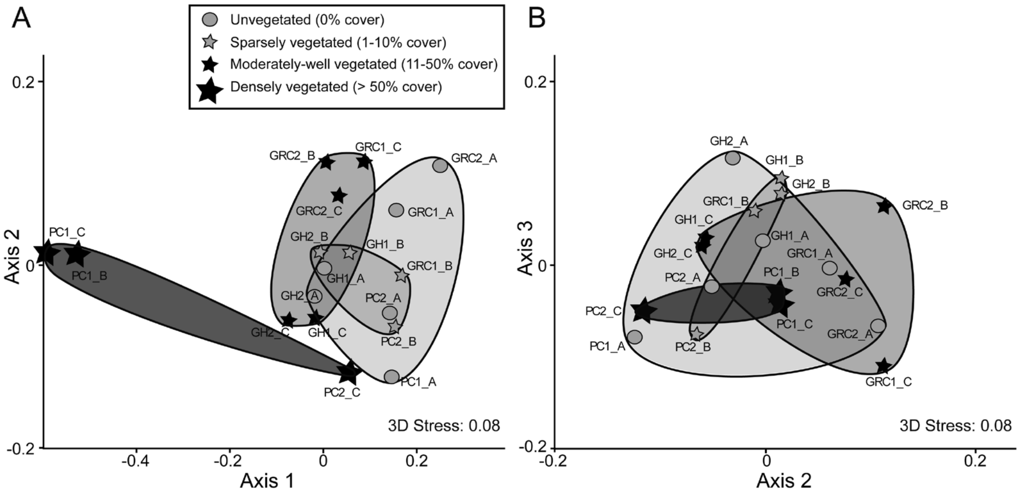


Figure 8 (above) and Figure 9 (below)



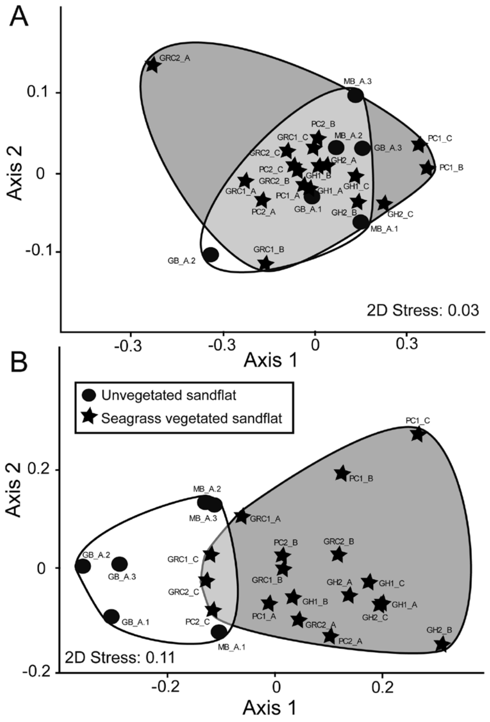


Figure 10: Two-dimensional NMDS ordination of 24 gastropod death assemblages based on proportional abundance of feeding guilds, grouped by locality, using Bray Curtis distance. A) Feeding guild composition based on specimen numbers. B) Feeding guild composition based on species richness.

Similarity was also quantified between samples grouped according to seagrass species composition using three variables (0-2 seagrass species present; Table 1), and according to vegetation density using four variables (unvegetated to densely vegetated; Table 1). The outliers PC1_B and PC1_C were included in these analyses, because they contribute considerably to the groups 'one seagrass species' and 'densely vegetated'. When excluding the outliers, R-values are relatively small, negative values (Table 4), indicating that differences within samples are greater than differences among samples (Chapman and Underwood, 1999). The proportional abundance of indeterminate gastropods was included in both analyses. There were no significant differences among samples grouped by seagrass species composition, but samples from sites with different seagrass density do show significant differences in mollusk species composition (Table 4). Although, dissimilarity between samples from densely vegetated sites and other sample groups is likely caused by the inclusion of the outlying samples PC1_B and PC1_C. In addition, samples from the unvegetated zone differ significantly from samples from moderately dense vegetated sites (R = 0.525, p = 0.006). NMDS is used to visualize the pattern tested by ANOSIM for samples grouped according to seagrass density (Fig. 9). The included outliers strongly separate from other samples along axis 1; as do samples from moderately-well and unvegetated sites, although the groups are overlapping (Fig. 9A). All sample groups strongly overlap when plotted against axis 2 and 3 (Fig. 9B). SIMPER results reveal that *Z. browniana* is the main contributor to dissimilarities between samples from densely vegetated and samples from other sites; Gastropoda indet. contributes slightly more than *Z. browniana* to the dissimilarity between samples from unvegetated and moderately dense vegetated sites (Table 5).

3.5 Feeding Guild Composition

Herbivores are by far the most abundant and species-rich group in all samples, making up 60% on average in terms of species richness (STD = 8%, min = 45%, max = 75%) and up to 94% in terms of specimen numbers (mean = 80%, STD = 8%, min = 60%). Predatory carnivores are the next most abundant and species-rich feeding guild in all samples and display the highest variation in terms of species richness (max = 41%, min = 7%). Browsing carnivores make up 15% on average in terms of species richness (STD = 5%, min = 0%, max = 22%) and 5% in terms of specimen numbers (STD = 2%, min = 0%, max = 10%). Suspension feeders are only present in very low numbers ($\text{max}_{\text{species richness}}$ = 7%, $\text{max}_{\text{specimen numbers}}$ = 3%). The group is absent in 15 of 24 samples.

There are significant differences in feeding guild composition between assemblages from vegetated and unvegetated sandflats based on species richness, but not for specimen abundance (Table 4; Fig 10A, B). NMDS results for species richness confirm a separation of the two sample groups with a slight overlap along axis 1 (Fig. 10B). According to SIMPER, predatory carnivores and herbivores are both important contributors to the dissimilarity between sample groups (average dissimilarity = 16. 9, contribution of predatory carnivores = 6.4, contribution of herbivores = 6.1). There are more predatory carnivore species on unvegetated sandflats (mean proportional abundance of predatory species = 33.61%) than on seagrass vegetated sandflats (mean proportional abundance of predatory species = 20.28 %). The proportional abundance of herbivorous species is higher at seagrass vegetated sandflats (mean = 63.00%; mean proportional abundance of herbivorous species at unvegetated sandflats = 51.03%). There is significant variation in guild composition among sites with different vegetation density, with samples from unvegetated sandflats distinct from samples from densely vegetated sandflats, but this pattern is likely to be a result of including the outlying sites. No differences occur among sites with differing vegetation zone (Table 4).

3.6 Indicator Species Analysis

Eight out of 114 gastropod species have a difference greater than 60% between indicator value for seagrass vegetation and indicator value for unvegetated sandflats, and are therefore considered as potential indicator species for seagrass vegetation (Table 6). However, the indicator value for one of those species, *Gibberula* sp. 1 is not significant, so this species is not valuable as a proxy for seagrass cover. Two out of the remaining seven species have high indicator values for seagrass vegetation but also occur less frequently at unvegetated sandflats (*Z. browniana* and *Cerithium lutosum*). *Atys sharpi* has the highest indicator value for seagrass vegetation (94%).

Table 6: Species with indicator values >60% for seagrass vegetation.

Species	IV1 (Indicator value for seagrass vegetation)/ %	IV2 (Indicator value for unvegetated sandflat)/ %	IV1-IV2/ %	p
Atys sharpi	94	0	94	0.000
Atys sp. 1	83	0	83	0.001
Gibberula sp. 1	78	0	78	0.267
Zebina browniana	88	12	76	0.001
Smaragdia viridis	72	0	72	0.013
Suturoglypta albella	72	0	72	0.012
Cerithium lutosum	79	8	71	0.008
Patelloidea pustulata	67	0	67	0.018

4. Discussion

4.1 Time, Taphonomy, and Transport

The time span that is represented by a death assemblage is determined by time-averaging

(*sensu* Kowalewski, 1996). Mollusk death assemblages may contain shells of various ages that derived from different sources, but age determination is cost as well as resource intensive (Kosnik et al., 2009). It is not known how much time is represented by the death assemblages used in this study, but assemblages collected in comparable settings yielded radiocarbon ages between 0 and 4805 years and represented time spans between 175 years in the Bahamas and 3085 years in Baja California (Taft and Harbaugh, 1964). Strasser and Samankassou (2003) dated Holocene shell material in lagoonal and intertidal settings in Florida Bay and Bermuda at about 1000 to 5600 years and calculated sediment accumulation rates ranging from 0.5 to 1.1 mm/a. However, their samples derived from deeper sediments (65 to 130 cm) than the material used in this study that was collected from the seafloor. The upper 20 cm of reef sediments at the Great Barrier Reef, Australia contained an essentially modern mollusk assemblage, but some shells were up to 2000 years old (Kosnik et al., 2009). Mollusk death assemblages from San Salvador are also thought to reflect up to hundreds of years (Colby and Boardman, 1989), and differ from living assemblages in species composition and abundance (Deehr et al., 2001), indicating that time-averaging plays an important role in shaping these communities. In addition, the high density of *Callianassid* shrimp burrows at sampling sites GRC and GH potentially led to an increased availability of recycled older shell material from deeper sediments (e.g., Meldahl, 1987).

Shells from unvegetated areas (unvegetated sandflats and unvegetated areas proximal to seagrass meadows) are more often taphonomically altered than shells from vegetated localities, and are therefore more difficult to identify or even unidentifiable. Therefore, shell abundance is highest in samples from densely vegetated localities at Pigeon Creek, and the number of unidentifiable gastropods is very low or even zero at those localities. Jarochowska (2012) observed low rates of abrasion in carbonate sediments from vegetated localities in Pigeon Creek. The strongly negative correlation between proportional abundance of indeterminate gastropods and shell abundance suggests that a low abundance of shells results from taphonomic alteration rather than from low abundance of living gastropods. Results of SIMPER analysis confirm that the dissimilarity between sample groups from vegetated and unvegetated sandflats is highly sensitive to the proportional abundance of indeterminate shells. Lower level of taphonomic shell loss in vegetated areas might be due to the protective nature of seagrass vegetation (Beavington-Penney et al., 2006). Additionally, pH-values in seagrass environments are often increased due to the photosynthetic activity of marine angiosperms and macroalgae, enhancing calcification rates of associated organisms (Semesi et al., 2009). High pH-values might therefore be another control for reduced taphonomic shell loss in seagrass habitats. However, pH-values of pore-water in seagrass meadows decrease with sediment depth leading to an increase of shell dissolution at about 4 cm sediment depth on the Bahamas Bank (Burdige et al., 2010).

High shell abundance and low levels of taphonomic alteration were likewise observed at some sampling sites at unvegetated areas close to seagrass meadows (e.g., GH2_A). A possible explanation is that those unvegetated areas might have been vegetated just a few years ago. Seagrass meadows are dynamic ecosystems and their boundaries may change on short time-scales of years or even months (e.g., Patriquin, 1975).

The occurrence of more altered shells in the unvegetated parts of sandflats dominated by seagrass cover is thought to result from a lack of protective vegetation, and possibly also from transport of shell material out of seagrass meadows. Generally, little transport is likely to occur between vegetated and adjacent unvegetated areas because of the trapping effect of the plants (Scoffin, 1970; Miller, 1988; Albano and Sabelli, 2011), but this study shows that gastropod death assemblages from the unvegetated zone of seagrass meadows differ from those collected at entirely unvegetated sandflats, while they do not significantly differ from assemblages collected on the margin of the vegetated zone. This may indicate that transported shells from within seagrass meadows are influencing death assemblages from the adjacent unvegetated zone. In a high-energy setting such as Pigeon Creek, material is transported out of the meadow and re-deposited at unvegetated sites (Leonard-Pingel, 2005). Graham’s Harbor is exposed to winds and vegetation at sampling sites is scarce to moderately dense, so that transport of material out of seagrass meadows is likely to be common.

It remains questionable if the altered death assemblages from low-energy, unvegetated sandflats, where material is not trapped by plants, are more affected by transport than shells from seagrass meadows. Lower dominance/higher evenness indices at unvegetated sites compared to seagrass beds would suggest higher levels of transport of shells at unvegetated sandflats (Tomašových and Kidwell, 2009), but dominance/evenness shows no significant variation between vegetated and unvegetated localities. However, gastropod death assemblages from unvegetated sandflats are significantly richer than assemblages sampled within seagrass meadows. It seems unlikely that this reflects species richness in the living population, because comparative studies of living assemblages from seagrass meadows and adjacent unvegetated areas usually reveal a higher abundance and species richness in seagrass meadows (Brasier, 1975, and references therein; Mikkelsen et al., 1995; Hemminga and Duarte, 2000, and references therein; Barnes and Barnes, 2012). Possibly higher species richness at unvegetated localities is a result of the addition of transported shells from adjacent habitats (Kidwell and Bosence, 1991), but this interpretation remains to be supported with additional data.

In contrast to other studies that show how seagrass vegetation supports the development of constructive micrite envelopes (Perry, 1999), in this case shells from unvegetated sampling sites are more frequently coated with carbonate than shells from seagrass meadows. This might relate to the present energy conditions with lowest water energy at unvegetated sandflats and moderately-high to high-energy conditions at vegetated sites. High water energies might prevent the establishment of micrite envelopes on grains deposited in seagrass beds (Jarochowska, 2012).

4.2 Species Composition

When comparing assemblages from seagrass covered versus unvegetated sandflats, samples from the seagrass localities at Graham's Harbor and most sites in Pigeon Creek (apart from PC1_B and PC1_C) are similar to one another, but assemblages from unvegetated sandflats differ significantly. Axis 1 of the NMDS ordination (Fig. 7) follows the occurrence of marine macro-vegetation at the sampling sites. This strongly suggests that gastropod death assemblages from seagrass-vegetated localities preserve a typical species composition that can be distinguished from death assemblages collected from unvegetated areas, although species composition in the death assemblages might differ from that of living assemblages. Two samples from Pigeon Creek are very different from all other samples derived from seagrass vegetated sandflats as well as from samples taken at unvegetated sandflats. The samples represent a densely vegetated mixed meadow (PC1_C, Fig. 2D) and the very proximal monospecific *Syringodium* zone at the landward margin of the same meadow (PC1_B, Fig. 2C). The samples differ from all other samples by the high dominance of *Z. browniana* (65% proportional abundance in PC1_C, 59% proportional abundance in PC1_B). The proportional abundance of the species does not exceed 27% at any other sampling site including close-by sites at Pigeon Creek. At the latter, the proportional abundance of *Z. browniana* is actually relatively low (e.g., 13% in PC2_C). Death assemblages are frequently dominated by individuals that died recently (Tomašových and Kidwell, 2011), leading to the assumption that a localized reproduction event followed by the death of multiple individuals was sampled at PC1_B and PC1_C. Axis 2 in the NMDS-ordination is thought to reflect the abundance of *Z. browniana*.

Analyses of samples from different vegetation zones of seagrass-vegetated sandflats reveal differences between samples collected in seagrass meadows and other sample groups (margin of meadow, unvegetated zone), reflected by axis 2 and 3 of the NMDS ordination. When including indeterminate gastropods, samples from seagrass meadows are distinct from other samples along axis 1 that likely corresponds to vegetation cover. A similar pattern is observed when samples are grouped according to seagrass density, suggesting that the two variables ‘vegetation zone’ and ‘vegetation density’ are closely connected and the main control for differences in species composition of gastropod assemblages, whereas the species composition of seagrasses does not induce any dissimilarity between samples. On one hand, the dissimilarity between gastropod death assemblages from seagrass meadows and adjacent zones shows that the species composition is sensitive to small-scale spatial changes, supporting the suitability of the species composition of gastropod death assemblages as an indicator for seagrass vegetation in the fossil record.

4.3 Feeding Ecology

A high abundance of herbivores is regarded as characteristic for seagrass habitats in comparison to other shallow marine environments (Moulinier and Picard, 1952; Davies, 1970; Reich et al., 2014), but I found no difference in feeding guild composition between death assemblages from seagrass vegetated versus unvegetated sandflats based on specimen numbers. Potential explanations for the similarity of herbivore abundance between seagrass associated assemblages and those from unvegetated sandflats include:

1. The abundance of herbivores at unvegetated sandflats is not different from seagrass vegetated sites. The high abundance of herbivorous gastropods can therefore not be considered as an exclusive proxy for seagrass vegetation in the fossil record.

2. The assemblages from unvegetated sandflats are influenced by mixing of shells from different habitats including seagrass meadows, stressing that comparative studies of feeding ecology of fossil gastropod assemblages should be carried out with assemblages that show minimal evidence for between-facies transport.

However, there are distinct differences in species richness of feeding guilds from vegetated and unvegetated sandflats, mainly due to the dissimilarity between the proportional abundance of herbivore and predatory carnivore species. Future research on shallow marine gastropod death assemblages should include feeding guild analysis to reveal, if the observed patterns are characteristical for seagrass associated assemblages, and how they compare to the ecological composition of assemblages from other tropical shallow marine environments such as mangroves and coral reefs.

4.4 Seagrass Indicator Species

Seven gastropod species have been identified as potential indicator species for seagrass vegetation. *Zebina browniana* and *Cerithium lutosum* also occur less frequently at unvegetated localities, and are therefore considered as useful indicators only when found in high abundances. According to their indicator values, *Atys sharpi* and *Atys* sp. 1 are the most useful indicator species for seagrass vegetation in the studied assemblages at San Salvador. However, the general use of those species as seagrass indicators appears to be limited. *Atys sharpi* is recorded up to a depth of 52 m from various substrates including sponges and submerged logs, and only occasionally from seagrass beds at Abaco, Bahamas (Redfern, 2001). Likewise, none of the other *Atys* species reported by Redfern (2001) shows an affinity to seagrass vegetation. Possibly the restriction of those species to seagrass vegetated localities at San Salvador is a preservational effect, because relatively small, thin-shelled individuals have a higher chance for preservation when protected by marine vegetation. *Patelloidea pustulata* has the lowest indicator value of the remaining potential indicator species. The species was observed living on *Thalassia* blades at Pigeon Creek (PG1_C), but Redfern (2001) commonly found larger specimens under rocks and recorded empty shells from beach drift at Abaco, Bahamas. Nevertheless, the occurrence of small well-preserved shells of this species might indicate seagrass vegetation. The remaining two potential seagrass indicators are *Smaragdia viridis* and *Suturoglypta albella*. Both have an indicator value of 72%, and both are associated to seagrass vegetation at Abaco (Redfern, 2001). The general use of *S. albella* as a seagrass indicator remains questionable, because records are scarce. The species was recorded from the Caribbean coast of Panama, but further information on its habitat is lacking (Olsson and McGinty, 1958). *Smaragdia viridis*, however, is generally closely associated with seagrasses (Mikkelsen et al., 1995; Redfern, 2001; Rueda et al., 2009 a; this study). The species has been identified as a selective feeder on seagrass tissue (Rueda and Salas, 2007; Rueda et al., 2009 a, 2009 b; Holzer et al., 2011). Shells might be present in samples from unvegetated sand close to the vegetated zone (Redfern, 2001; this study), but they were not observed at any sandflat lacking seagrass vegetation or in beach drift at unvegetated localities (personal observations, 2012). *Smaragdia* species other than *S. viridis* are closely associated with seagrasses as well (Taylor and Lewis, 1970; Kay, 1979; Higo et al., 1999; Zuschin et al., 2009; Unabia, 2011). The radula of the genus differs from that of other gastropods in the family Neritidae by having strong cusps and few denticulate cutting edges, possibly an adaption of all included taxa on the direct consumption of seagrass tissue (Rueda and Salas, 2007; Unabia 2011). Therefore, the genus *Smaragdia* appears to be in general the best available indicator taxa for seagrass vegetation. It has previously been used to infer marine angiosperms in the early Miocene (Reuter et al., 2010; Reich et al., 2014).

4.5 Faunal Composition as a Seagrass Indicator in the Fossil Record

This study is a first step towards the possible establishment of gastropod death assemblages as seagrass indicators in the fossil record. Results indicate that the faunal composition of Holocene gastropod death assemblages is significantly different from the composition of assemblages found at unvegetated sandflats at San Salvador. Paleogene and Neogene assemblages likely differ in species composition from those of the Holocene, but the generic and/or ecological composition may still be a useful tool to identify seagrass associated faunas. For a general use of shell assemblages as seagrass indicators in different geographical areas and in deeper time, further research on the characterization of seagrass associated gastropod faunas is necessary.

5. Conclusions

1. The species composition of gastropod death assemblages clearly distinguishes vegetated and unvegetated sandflats at San Salvador, Bahamas. Therefore, the faunal composition of gastropod death assemblages may serve as an useful proxy for seagrass vegetation in the fossil record.

2. Variation in assemblages sampled from different vegetation zones on seagrass vegetated sandflats (unvegetated, margin of meadow, meadow) are less obvious, probably due to transport of shell material out of seagrass meadows and because of shifting boundaries of seagrass meadows on relatively short timescales. Nevertheless, assemblages from seagrass meadows might be distinguishable from assemblages derived from the proximal unvegetated area and the margin of the meadow, indicating that gastropod death assemblages are sensitive to small-scale spatial variation.

3. Variation in assemblages sampled at different vegetation zones on seagrass vegetated sandflats likely relates to seagrass density, whereas seagrass species composition does not induce differences between sample groups.

4. The taphonomic signature of shells, indicated by the number of unidentifiable gastropods, should be considered as a supporting feature when distinguishing assemblages from vegetated versus unvegetated shallow water habitats, because the proportional abundance of indeterminate gastropods contributes significantly to the differences between samples from seagrass vegetated and unvegetated sampling sites, likely reflecting the protective nature of the seagrass canopy.

5. The high abundance of herbivores as a proxy for seagrass vegetation in the fossil record should be regarded with caution, as gastropod death assemblages from unvegetated sandflats may display equally high abundances of herbivores as those from seagrass meadows.

6. Gastropod death assemblages from seagrass vegetated areas at San Salvador are characterized by a higher species richness of herbivores and a lower species richness of predatory carnivores compared to assemblages from unvegetated sandflats.

7. *Atys* species and *Sutoroglypta albella* are useful seagrass indicators in death assemblages at San Salvador, Bahamas. The high abundance of *Zebina browniana* and *Cerithium lutosum*, and the occurrence of small, well-preserved specimens of *Patelloidea pustulata* likewise indicate seagrass vegetation in the study area. The neritid genus *Smaragdia* is confirmed to be generally useful as an indicator taxa for seagrass vegetation in the fossil record.

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Chapter 5

Paleoecological Significance of Stable Isotope Ratios in Miocene Tropical Shallow Marine Habitats (Indonesia)

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Palaios

(manuscript in review)

Keywords: Stable isotopes, mollusks, paleoecology, Cenozoic, Indo-Pacific

Abstract

For numerous reasons seagrass meadows are important shallow water habitats, but their detection in the fossil record is problematic. Indirect indicators are often needed to discriminate seagrass beds from other shallow marine paleohabitats. Here, the stable isotope signatures of mollusk shells are tested to determine if they might provide such an indicator in addition to the faunal composition of mollusk assemblages. Aragonitic shells of 167 gastropods and bivalves from Burdigalian and Tortonian deposits in Java and East Kalimantan (Indonesia) were analyzed for their $\delta^{18}O$ and $\delta^{13}C$ ratios. The faunas represent fully marine to brackish water environments and include seagrass meadows (with dispersed corals), mixed seagrass-coral, and coral dominated habitats (with dispersed seagrass). We assess processes and settings that shape inorganic isotope signals in the Miocene ambient waters and fractionation processes occurring at the time of shell deposition. Depleted $\delta^{18}O$ and $\delta^{13}C$ ratios are shown in brackish water samples. Furthermore, chemosymbiotic species show depleted $\delta^{13}C$ ratios. A significant difference is found between the carbon isotopic signatures of coral and seagrass dominated environments within a stratigraphic interval. Seagrass communities consistently yield comparatively enriched $\delta^{13}C$ ratios. Hence, stable isotope ratios do provide additional evidence for distinguishing paleoenvironments and are helpful in identifying ecological processes and settings within these environments.

1. Introduction

The successful recognition of different habitats in the geological past is an indispensable base for studies on climate history, sea-level changes, and biodiversity. In order to evaluate marine biodiversity through time it is necessary to reliably discriminate habitats, because species numbers may vary considerably among environments (Gray, 2001). A good example is the challenge of recognizing seagrass vegetation in the fossil record. Seagrass meadows are highly productive ecosystems that play an important role in coastal nutrient cycling and yield a diverse community of associated organisms (Chapter 1; Duarte and Chiscano, 1999; Hemminga and Duarte, 2000), but marine angiosperms rarely fossilize. Therefore, independent indicators such as associations of benthic foraminifera and mollusks are often used to infer their presence in the geological past (Chapter 1; e.g., Brasier, 1975; James and Bone, 2007). In most cases these indicators are indirect and not exclusive. For mollusks, the high abundance of small herbivorous gastropods and the occurrence of the neritid gastropod genus *Smaragdia* may be useful indicators (Chapters 1 and 2). Furthermore, seagrass meadows and coral environments are difficult to distinguish if not indistinguishable, because marine angiosperms and scleractinian corals often occur in the same habitat. Patches of corals are common in tropical seagrass beds and compound seagrass-coral associations occur in the transition zone between coral reefs and seagrass meadows (Brasier, 1975; Nienhuis et al., 1989). Patches of seagrass might also be present in coral carpet environments (sensu Riegl and Piller, 1999, 2000).

In this study we aim to test whether stable carbon and oxygen isotope signatures of mollusk shells provide an additional tool for the discrimination of paleohabitats ranging from seagrass meadows to coral carpets. Habitat assignments are based on the abundance of coral remains and on the species and ecological composition of mollusk assemblages, and in one case on the fossilized remains of probable seagrass. We do not expect to find an isotope signature exclusively indicative for seagrass meadows, but a probable trend that reflects the preliminary habitat assignments. The method is thought to be restricted to material derived from the same geographical region and time frame. In addition, we aim to investigate which processes in seagrass meadows influence the isotopic composition of associated shells including the influence of different ecologies of mollusks on the carbon isotope signals of their shells.

Stable isotope signatures of mollusk shells are widely used to reconstruct paleoenvironmental conditions (e.g., Latal et al., 2006 a,b; McConnaughey and Gillikin, 2008). They precipitate near ^{18}O equilibrium with ambient seawater, therefore kinetic isotopic effects are likely to be small (Epstein, 1953; McConnaughey, 1989; McConnaughey et al., 1997). However, carbon signals of marine mollusk shells are difficult to interpret. They largely reflect ambient DIC (dissolved inorganic carbon), but can be influenced by other factors as well. This includes for instance salinity or physiologic processes (McConnaughey and Gillikin, 2008). The animal’s former diet has relatively little influence on $\delta^{13}C$ in marine shells compared to those of landsnails (McConnaughey and Gillikin, 2008, and references therein; McConnaughey et al., 1997). Furthermore, $\delta^{13}C$ provides a record of seasonality during bivalve growth and commonly becomes depleted with age of the shell (e.g., Kennedy et al., 2001; McConnaughey and Gillikin, 2008, and references therein).

2. Localities and Paleoenvironments

An overview of sampling localities, their age and paleoenvironmental interpretation is provided in Table 1.

Table 1: Sampling localities, estimated ages, sample set indications, and preliminary paleoenvironmental interpretations based on associated fossil assemblages. Banyunganti is located on Java, all other localities are located on East Kalimantan.

Locality	Age	Sample set	Paleoenvironment
Banyunganti	early Burdigalian	BA 18	seagrass meadow
Bontang	early Tortonian	TF 102	coral carpet
Bontang	early Tortonian	TF 110	seagrass meadow
Bontang	early Tortonian	TF 508_FW1	sandflat, sparse seagrass vegetation
Bontang	early Tortonian	TF 508_FW6	estuarine, brackish
Bontang	early Tortonian	TF 508_FW7	mixed seagrass-coral
Sangatta	early Tortonian	TF 517	seagrass meadow

2.1 Banyunganti, Java, Indonesia (Sample BA 18) – Early Burdigalian (Early Miocene)

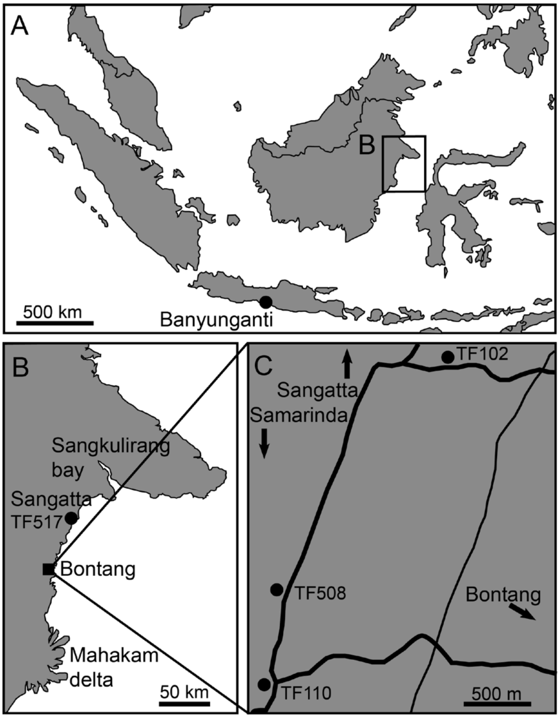

Figure 1: Locality map. A) Overview map of Indonesia including the locality of Banyunganti. B) Overview map of the coast of central East Kalimantan including the localities Sangatta (TF 517) and Bontang. C) Map of the Bontang area showing the TF-localities 102, 110 and 508.

The sample locality (-7.760731 S, 110.128372 E) is situated near the village of Banyunganti (province Yogyacarta, Java, Indonesia: Fig 1A). The shells used in this study derive from a bulk sample collected from marine, early Burdigalian deposits of the Jonggrangan Formation west of the city of Yogyakarta. The locality is described in detail in Chapter 2.

The excellently preserved mollusk fauna was interpreted as a seagrass-associated assemblage based on the high dominance of small grazing gastropods (69 % abundance; e.g., *Rissoina*, *Cerithidium*, *Bothropoma*, Figs 2A-C) and the occurrence of the indicator genus *Smaragdia* (Fig. 2D). The associated assemblage of benthic foraminifera, including the large benthic genus *Pseudotaberina*, hints at seagrass vegetation as well (Chapters 1 and 2; Renema, 2008b; Reuter et al., 2010). The associated branching coral fragments are dominated by *Seriatopora* sp. (N. Santodomingo, pers. comm., 2012). The paleoenvironment is considered to be a seagrass meadow with dispersed intergrowing corals (Chapter 2).

2.2 Bontang, East Kalimantan, Indonesia (Localities TF 102, TF 110, TF 508) – Early Tortonian (Late Miocene)

The city of Bontang is located at the coast of central East Kalimantan (Fig. 1B), within the Kutai Basin, the largest Cenozoic sedimentary basin of Kalimantan (Moss and Chambers, 1999). The Bontang area has recently witnessed a surge in construction work leading to the temporary availability of outcrops at building sites, most of which are located along roads. The outcropping sediments are predominantly marine clay-, silt-, and fine sandstones occasionally interbedded with carbonates and lignites. Fluvial deposits occur to the east, stratigraphically above the marine successions. The Bontang marine interval is underlain by older (early-middle Miocene) fluviatile, swamp and shallow marine sediments outcropping to the west in the area of the Indominco coal mine. Samples used in this study were collected at three localities within the Bontang area (Fig. 1C): TF 102 (0.16821° N, 117.44350° E; visited in 2010), TF 110 (0.14048° N, 117.42692° E; visited in 2010) and TF 508 (0.14870° N, 117.42908° E, visited in 2011). Based on benthic foraminifera the age has been estimated as Tortonian (late Miocene) for all localities in the Bontang area referred to in this study. Strontium isotope stratigraphy analysis on mollusks and corals from Bontang (including TF 102, TF 110 and other localities) results in an age of 9.8 (± 0.2) Ma, and thus confirms an early Tortonian age for the stratigraphy of the Bontang area (Renema et al., submitted).

TF 102. The locality represents the upper part of a marine interval of fossiliferous coarsening upward silty clay to fine sandy silt with abundant mollusks and corals. Those sediments are covered by non-fossiliferous clay and fine sandstones likely representing the lowest deposits of a fluvial series. The locality is described in detail in Chapter 3. The shells used in this study were collected from patches of branching coral remains found on a bedding plane of marine silty clay (hand-collected sample SR45) and a bulk sample taken from the same bed (sample SR50). Shells from both samples were combined and hereafter referred to as TF 102. The fossil assemblage is dominated by corals of the genus *Dictyaracea*. The associated mollusk fauna is dominated by carnivorous gastropod species including abundant '*Lophiotoma*' sp. (Fig. 2E) and the coral-feeder *Coralliophila* (Fig. 2F). In total, carnivores make up 48% of the fauna based on specimen numbers. Herbivores make up only 28% of the

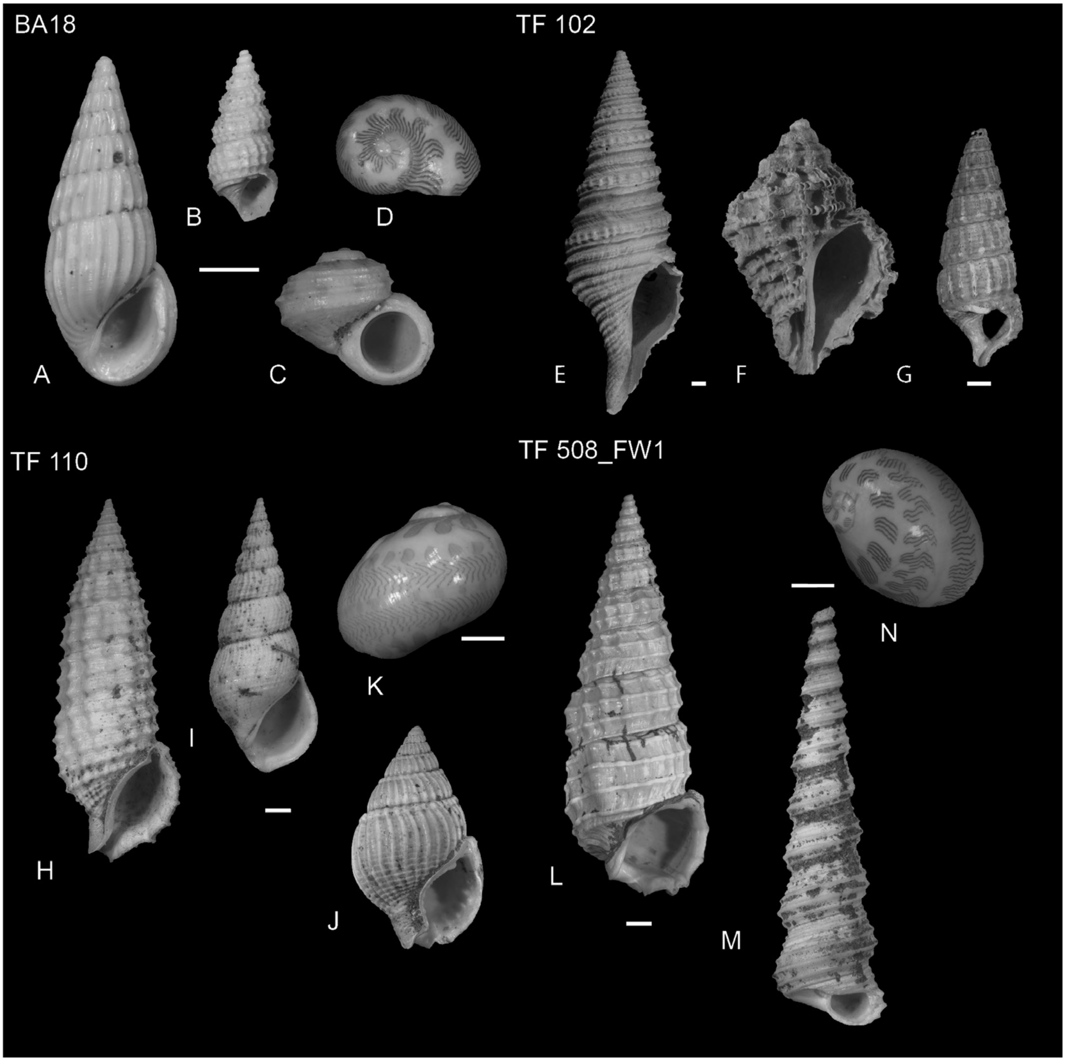

Figure 2: Some common and/or indicative gastropods from samples BA 18, TF 102, TF 110, and TF 508_1. Scale bars equal 1 mm. A) *Rissoina* (*Rissoina*) *banyungantiensis* (RGM.784.843). B) *Cerithidium* cf. *perparvulum* (RGM.784.758). C) *Bothropoma mediocarinata* (RGM.784.746). D) *Smaragdia jogjacartensis* (RGM.784.754) E) '*Lophiotoma*' sp. (RGM.793.968). F) *Coralliophila* aff. *clathrata* (RGM.793.969) G) *Cerithium* sp. 7 (RGM.793.966). H) *Rhinoclavis* sp. 2 (RGM.793.996). I) *Rissoina* (*Phosinella*) sp. 1 (RGM.793.997). J) *Nassarius* sp. 1 (RGM.793.998). K) *Smaragdia gelingsehensis* (RGM.793.999). L) *Cerithium* sp. 4. (RGM.794.000). M) '*Turritella*' sp. (RGM.794.001). N) *Smaragdia semari* (RGM.794.002).

fauna in terms of abundance. They are mainly represented by medium-sized species (e.g., *Cerithium*, Fig. 2G). However, six specimens of *Smaragdia semari* were found in sample SR50. Their number is very low, but considering that mollusk shells are rarely transported out of their original environment, we can assume they reflect the original life assemblage on a spatial scale (e.g., Kidwell, 2008; Kidwell and Bosence, 1991; Kidwell and Flessa, 1996). This leads to the assumption that seagrasses might have been present as well. Therefore, the paleoenvironment is considered to be a coral carpet environment with dispersed seagrasses (Chapter 3).

TF 110. Bulk sample TF 110_SR38 (hereafter referred to as TF 110) was collected from fossiliferous dark gray silty clays. The sampled mollusk fauna is diverse and excellently preserved. Herbivorous gastropods are species-rich and numerous, including species of *Rhinoclavis*, *Rissoina* (Figs 2H-I) and *Cerithium*. Carnivorous gastropods are abundant as well. *Nassarius* sp. (Fig. 2J) is the most common species in the assemblage; Costellariidae and omnivorous Columbellidae are likewise very abundant. Two species of the seagrass-indicator *Smaragdia* are present in high numbers (*S. gelingsehensis*, 114 specimens, Fig. 2K; *S. semari*, 96 specimens). Coral-remains are present in the sample. The locality is inferred to represent a paleo-seagrass meadow with dispersed intergrowing corals.

TF 508. The locality provides a 25 m long stratigraphic succession of clastic marine and brackish sediments with variable content of mollusks and branching coral fragments. Three samples from different intervals representing different habitats were selected for this study.

Bulk sample TF 508_FW1 was collected at ~8 m from the base of the succession from a bed of clayey siltstone. The sample contains a well preserved mollusk assemblage characterized by the gastropods *Cerithium* (Fig. 2L) and '*Turritella*' (Fig. 2M) and the bivalve *Placuna*. *Smaragdia semari* (Fig. 2N) is present and indicates seagrass vegetation. Fragments of branching corals are rare, but the free-living coral genus *Heterocyathus* is common. The genus indicates a flat undisturbed sandflat probably in a reef-base or inter-reef environment. Its occurrence points to sparse to moderate seagrass vegetation rather than to the presence of a dense meadow (Fisk, 1983; Hoeksema and Best, 1991; B.W. Hoeksema, pers. comm., 2013). The paleohabitat is therefore interpreted as a sandflat with seagrass vegetation in low density.

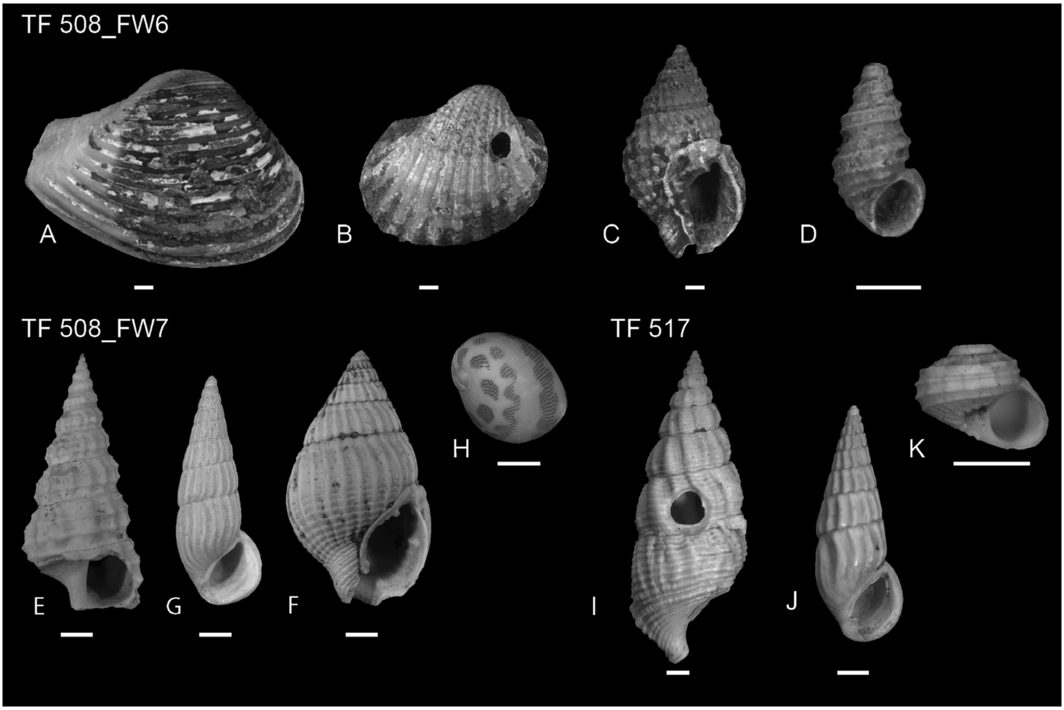

Figure 3: Some common and/or indicative gastropods and bivalves from samples TF 508-6, TF 508_7 and TF 517. Scale bars equal 1 mm. A) *Corbula* sp. 2 (RGM.794. 003). B) *Anadara granosa* (RGM.794.004). C) *Nassarius* sp. 6 (RGM.794.005). D) *Iravadia* sp. 1 (RGM.794.006). E) *Cerithium* sp. 4 (RGM.794.007). F) *Rissoina* (*Rissoina*) sp. 2 (RGM.794.008). G) *Nassarius* sp. 1 (RGM.794.009). H) *Smaragdia semari* (RGM.794.010). I) *Cerithium* sp. 5 (RGM.794.011). J) *Rissoina* (*Rissoina*) sp. 5 (RGM.794.012). *Bothropoma* sp. 2 (RGM.794.013).

Bulk sample TF 508_FW6 was collected ~ 20 m from the base of the succession from the upper level of a calcareous siltstone bed. The fossil material is rust-colored and the sample contains gypsum crystals. The latter is likely a post-depositional product of partial carbonate dissolution. The associated mollusk fauna is less diverse, with more evenly distributed species abundances than the other faunas used in this study. Bivalves are dominated by *Corbula* sp. and *Anadara granosa* (Figs 3A-B), both are often preserved articulated. Common gastropod genera are *Nassarius* (Fig. 3C) and medium-sized *Cerithium*. Furthermore, iravadiids are present (Fig. 3D). This faunal composition is comparable to that of estuarine faunas reported from the Philippines (Lozouet and Plaziat, 2008). Therefore, the sample likely represents a brackish environment.

Bulk sample TF 508_FW7 was collected ~ 21.5 m from the base of the succession from organic rich marls. It is dominated by fragments of branching corals and contains well-preserved mollusk shells. Abundant genera are the gastropods *Cerithium*, *Rissoina* and *Nassarius* (Figs 3E-G) and the bivalves *Nucula* and *Dendostrea*. The mollusk fauna shares common species with the material from TF 110. Sample TF 508_FW7 contains abundant corals but at the same time four *Smaragdia* species (including e.g., *S. semari*, Fig. 3H) indicating a mixed coral-seagrass habitat.

2.3 Sangatta, East Kalimantan, Indonesia (Locality TF 517, Sample TF 517 _FW3) – Early Tortonian (Late Miocene)

Locality TF 517 (00.56780N, 117.63420 E; Fig. 1B) is an artisanal limestone quarry located about 16 km east of the Sangatta coal mine and about 1.3 km north-west of the Tanjung Bara airport. The succession is poorly exposed due to the nature of the excavation process. The base of the succession consists of one meter of lignite with abundant gypsum crystals. A sharp contact exists with the overlying dark-gray clayey silt that contains abundant mollusks and coral fragments. Bulk sample TF 517_FW3 (hereafter referred to as TF 517) was collected from a clay block dug by an excavator, the exact position within the clay layer is therefore unknown. Strontium isotope stratigraphy analysis on corals and mollusk shells from TF 517 resulted in an early Tortonian age of 9.2 (± 0.2) Ma, therefore the locality is younger than localities in the Bontang area (Renema et al., submitted).

The sample contains a diverse and excellently preserved mollusk assemblage interpreted as a seagrass-associated fauna. This is based on the high abundance of small herbivorous gastropods (e.g., *Cerithium*, *Rissoina*, *Bothropoma*; Figs 2I-K). Furthermore, plant remains found at the locality show resemblance with marine angiosperms and might therefore be direct evidence for seagrass vegetation, although confirmation is needed. The paleoenvironment is interpreted as a seagrass meadow with dispersed intergrowing corals.

3. Material and Methods

3.1 Samples

Gastropod and bivalve shells representing 43 species in 31 genera and eight different feeding guilds were chosen from the seven fossil samples. In total 167 shells were analyzed. All selected individuals represent species that are common in the original bulk samples. Attention was also paid to choosing taxa that occur in several samples, such as the gastropod species *Diala semistriata* s.l. and the bivalve '*Arcopsis sculptilis*' or the gastropod genera *Rissoina*, *Cerithium* and *Cylichna*. Shells and shell fragments were first cleaned in the ultrasonic bath and thereafter manually ground resulting in a visually homogenous fine powder. Weights of prepared samples ranged between 540 and 20 µg with an average weight of about 300 µg. Remaining sample material is stored at Naturalis Biodiversity Center, Leiden, The Netherlands (indicated by RGM numbers). A list of samples, including identifications and feeding guild assignments, and results for oxygen and carbon stable isotope analyses is provided in Appendix 1.

3.2 Species Identification and Feeding Guild Assignment

The mollusk fauna from Banyunganti, Java (BA 18) is described in Chapter 2. Species identifications of mollusks from other localities are based on the works of Beets (1941, 1986), on reviews (Houbrick, 1990, 1992; Laseron, 1957; Ponder, 1984; Ponder and De Keyzer, 1992), and on the works of Poppe (2008a, b; 2010a, b).

The selected mollusk shells represent eight different feeding guilds which are herbivores (including grazers as well as detritivorous gastropods, e.g. *Cerithium* and *Rissoina*), seagrass feeders (*Smaragdia*; Rueda and Salas, 2007; Rueda et al., 2009; Unabia, 2011), predators on invertebrates (e.g., *Naticarius*), predators on foraminifera (*Cylichna*), browsing carnivores (*Dentimargo*), suspension feeders (e.g., *Circe*), deposit-feeding bivalves (Tellinidae), and chemosymbiotic deposit feeders (Lucinidae;

Williams et al., 2004). Assignments to feeding guilds are based on the Neogene Marine Biota of Tropical America molluscan life habits database (Todd, 2001) and the comprehensive ecological information provided by Beesley et al. (1998). Assignments based on Todd (2001) concern mollusk families with a worldwide distribution that are represented by a single feeding guild and genera that occur in tropical America as well as in the Indo-Pacific.

3.3 Preservation State

Shell mineralogy was analyzed by Raman spectroscopy using a Thermo DXR Raman microscope with 532 nm laser excitation at Naturalis. Raman spectra were collected at room temperature in the confocal mode which is necessary for analysis of individual layers of a sample on a micron scale (1-2 µm). A grating of 1800 grooves/mm and a pinhole size of 25 µm was used which, combined with the optical path length, yields a spectral resolution of 1.0 cm^{-1}. Spectra were collected in the range of 100-1800 cm^{-1}. In this range, the vibrations of the carbonate anion $(CO_3)^{2-}$ can be detected. The most intense signals of symmetric stretching and in-plane bending of this anion can be used to distinguish aragonite and calcite (e.g., Wehrmeister et al., 2010). Measurements were performed on the outside as well as on the inside of shells. The analysis is nondestructive, therefore the same specimens could be used for Raman-testing and stable isotope analysis.

3.4 Stable Isotope Analyses

Analyses were performed on entire shells of very small specimens and shell fragments of small to medium-sized individuals. Samples (70 - 400 µg) from Banyunganti, TF 110, TF 517, TF 508_7 and TF 102 were analyzed using a Micromass Multiflow head space system connected to a GV Instruments Isoprime IRMS at Royal Holloway University of London, United Kingdom. Samples were digested in 103% orthophosphoric acid at 90°C. After a minimum of four hours reaction time, the evolved CO^2 was expanded into the sample loop, and then delivered to the Isoprime mass spectrometer within continuous He-carrier gas flow. Duplicate analyses were performed for each sample and standard, and averaged. Averaged precision (1SD) of duplicates was 0.03‰ for $\delta^{13}C$ and 0.06‰ for $\delta^{18}O$. Isotopic ratios are calibrated against the Vienna Peedee belemnite (VPDB) through NBS-19 and LSVEC international standards and an in-house standard (RHBNC calcite).

Samples TF 508_FW1 and TF 508_FW6 and two additional specimens of *Smaragdia* from TF 110 (all > 350 µg) were analyzed at Faculty of Earth Sciences at Utrecht University, The Netherlands using an ISOCARB common bath system which is directly coupled to a VG SIRA 24 mass spectrometer. Prior to the analysis, each sample was roasted for 30 minutes at 380°C under vacuum to remove any organic remains. To exclude the possibility that roasting affected the isotopic signals, we re-analyzed the same material without roasting it. The isotopic values of roasted versus unroasted samples display no significant differences and correlate with linear R = 0.996 (Appendix 2). During one run 40 samples were measured including one international (IAEA-CO-1) and nine in-house (NAXOS) standards. The samples reacted with 103% phosphoric acid for 7.5 minutes at 90°C. After (linear) correction of the samples using the NAXOS standard as reference, the analytical precision and accuracy were determined by the comparison with international (IAEA-CO-1 and NBS-19) standards. The relative standard deviations, analytical precision and accuracy were better than 0.05 and 0.1‰ for $\delta^{13}C$ and $\delta^{18}O$ respectively. Three samples (each from TF 110, TF 508, and TF 517) yielded an amount of < 70 µg, therefore they were too small for the requirements of the above described machines. Those samples were analyzed using a Finnigan MAT Kiel III individual acid bath carbonate system coupled to a Finnigan MAT 253 mass spectrometer. Each sample reacted with 103% phosphoric acid (H_3PO_4) for 7 minutes at 70°C. Calibration using the international standard NBS-19 and the in-house standard Naxos revealed an analytical precision better than 0.03‰ and 0.09‰ for $\delta^{13}C$ and $\delta^{18}O$ respectively. The same method was applied for an additional analysis of 9 shell samples from a modern seagrass habitat from Sulawesi, Indonesia.

All isotopic ratios are expressed in conventional delta notation per mil values.

3.5 Statistical Analyses

Statistical analyses were performed using PAST 2.16 (Hammer et al., 2001). One-way ANOVA analyses were used to test whether isotope ratios from different localities or attributed to different feeding guilds display significant differences. Afterwards ratios from localities and guilds were compared pairwise using Tukey's HSD (Honestly Significant Difference). Significant differences between localities or feeding guilds are expressed by q-values > 4 and p-values < 0.05.

4. **Results**

4.1 Preservation

Only specimens of *Smaragdia* display a mixed aragonite-calcite signal on the outer shell surface. This represents their original shell mineralogy (Bandel, 2008) and is therefore almost certainly not a sign of diagenesis. All other shells are entirely aragonitic. Additional specimens from the same localities were investigated by Scanning Electron Microscopy and showed the original shell structure.

4.2 ANOVA Analyses

Significant differences were found for oxygen isotope ratios grouped by localities (F = 34.82, p = 1.002E-26), carbon isotope ratios grouped by feeding guilds (F = 22.58, p = 3.289E-20), carbon isotope ratios grouped by localities (F = 31.89, p = 4.738E-25), and are enhanced when using a reduced dataset for $\delta^{13}C$ ratios grouped by localities (chemosymbiotic deposit feeders removed; F = 82.85; p = 6.626E-44). Tuckey's HSD furthermore reveals pairwise differences between localities or feeding guilds (see below).

Table 2: Summary of δ^{13}C and δ^{18}O ratios of mollusks according to sampling locality; * outlier *Strombus* additionally removed.

Paleo-environment	**Seagrass**				**Coral carpet**	**Mixed coral-seagrass**	**Brackish**
Sample set	BA 18	TF 110	TF 517	TF 508_FW1	TF 102	TF 508_FW7	TF 508_FW6
n	37	37	30	9	9	25	20
δ^{18}O mean	-3.02	-2.66	-2.86	-2.79	-2.61	-2.82	-3.97
std	0.29	0.34	0.36	0.2	0.28	0.47	0.4
δ^{18}O min	-3.72	-3.41	-3.64	-2.97	-3.09	-3.60	-4.66
δ^{18}O max	-2.48	-1.88	-2.22	-2.38	-2.27	-1.95	-3.09
δ^{13}C mean	1.46	2.03	1.63	1.03	-0.33	0.16	-1.19
std	1.0	0.55	1.19	1.10	0.95	1.30	0.89
δ^{13}C min	-1.32	0.65	-1.93	-0.75	-1.86	-3.35	-2.42
δ^{13}C max	3.65	3.66	2.94	2.38	0.91	1.33	0.43
δ^{13}C mean, lucinids removed	1.82	2.08	2.04	1.47	0.10*	0.62	-
std	0.61	0.52	0.57	0.76	0.52	0.36	-

4.3 Oxygen and Carbon Values Grouped by Localities

Stable isotope ratios of samples from seven investigated localities are shown in Table 2, Figure 4 and are provided in Appendix 1. Samples (apart from TF 508_FW6) yield similar δ^{18}O ratios ranging from-1.88 to-3.72. Shells from TF 508_FW6 have depleted oxygen isotope ratios which significantly differ from all other localities (Tukey's HSD: $q > 11$, $p = 2.569E-5$). Also samples from BA 18 are slightly depleted in oxygen; significant differences are seen between BA 18 and TF 102 (Tukey's HSD: $q = 4.88$; $p = 0.01$) and BA 18 and TF 110 (Tukey's HSD: $q = 4.27$, $p = 0.04$).

Delta ^{13}C ratios are scattered over a wider range than δ^{18}O ratios (-3.35 to 3.66). Some samples show depleted δ^{13}C ratios compared to the bulk, mostly concerning lucinid

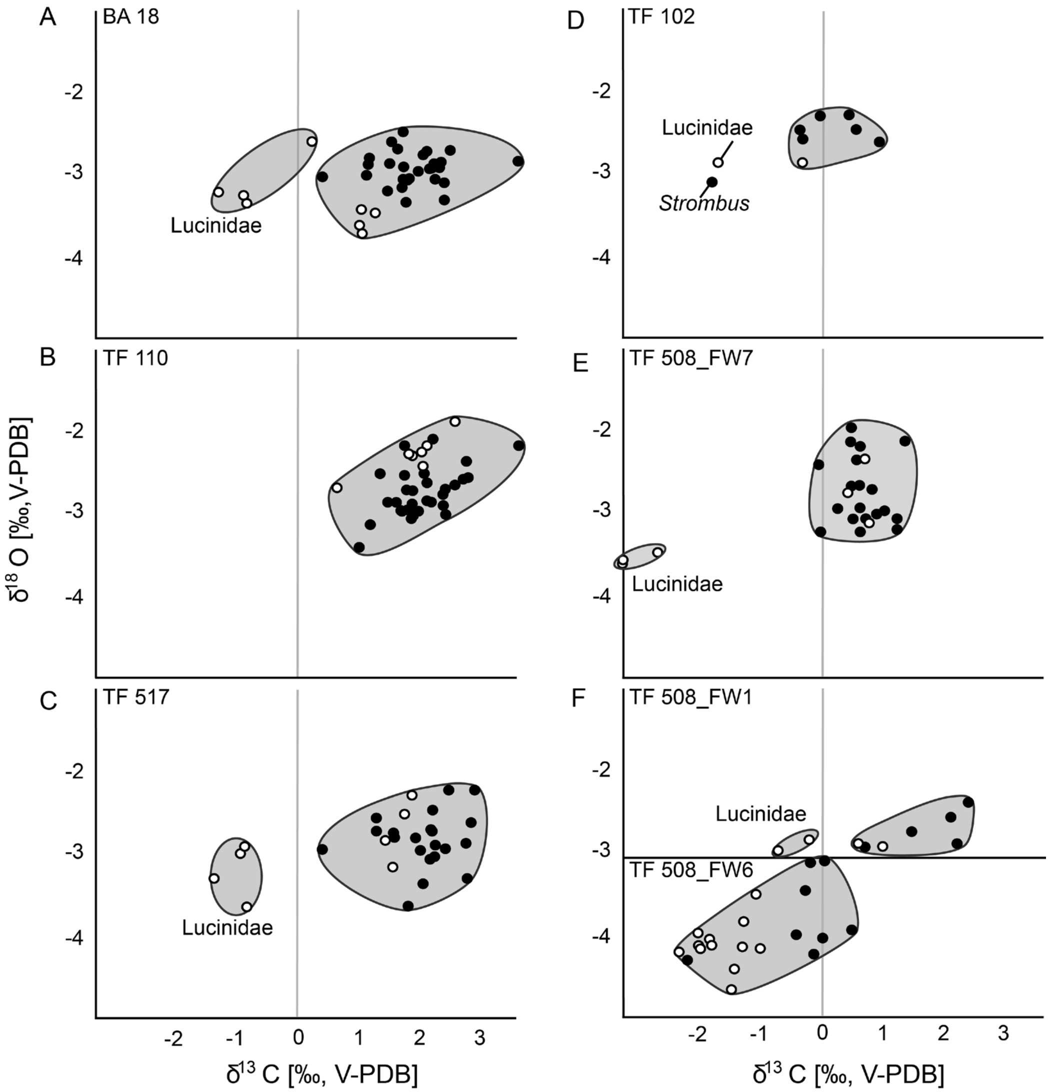

Figure 4: δ^{13}C and δ^{18}O ratios of gastropods (indicated by black dots) and bivalves (indicated by open circles) arranged according to sampling locality. A) BA 18. B) TF 110. C) TF 517. D) TF 102. E) TF 508_7. F) TF 508_1 and TF 508_6.

bivalves (Fig. 4A, C-F). The depleted carbon isotopic ratios from TF 508_FW6 differ significantly from all other localities (Tukey's HSD: $q > 5$; $p < 0.001$), apart from TF 102. No significant differences of $\delta^{13}C$ ratios occur between samples interpreted as seagrass-associated (BA 18, TF 110, TF 508_FW1, and TF 517; Tukey's HSD: $q < 2$; $p > 0.7$). Furthermore, the $\delta^{13}C$ signals of samples TF 102, TF 508_FW1, and TF 508_FW7 display no significant variation (Tukey's HSD: $q < 4$; $p > 0.1$)

4.4 Carbon and Oxygen Values Grouped by Feeding Guilds

Stable isotope ratios grouped by feeding guilds are shown in Table 3 and Figure 5. Feeding guild assignments for each taxon are provided in Appendix 1.

Herbivores and predators on invertebrates yield a wide range of isotope signatures (typically -2.0 to -4.0 $\delta^{18}O$ and -0.5 to +3.0 $\delta^{13}C$). The depleted carbon isotope ratio of -1.86 in a single herbivorous *Strombus* is considered an outlier.

Predators on foraminifera (Cylichnidae), browsing carnivores (*Dentimargo*, Marginellidae) and suspension feeders have very similar ratios typically ranging between -2.0 to -3.5 $\delta^{18}O$ and 0 to +3.0 $\delta^{13}C$. These ranges are therefore less wide than those of herbivores or predators on invertebrates.

Carbon ratios of seagrass feeders (*Smaragdia*) differ significantly from those of predators on foraminifera (Tukey's HSD: $q = 4.46$, $p = 0.034$) and suspension feeders (TF 508_FW 6 excluded; Tukey's HSD: $q = 6.04$, $p = 0.00053$) by being comparatively enriched.

Chemosymbiotic deposit feeders (Lucinidae) from all localities, apart from TF 508_FW6 where the family is not present, show a wide range of relatively depleted $\delta^{18}O$ and $\delta^{13}C$ signals. Their carbon isotope ratios differ significantly from those attributed to other feeding guilds (Tukey's HSD: $q > 9$; $p = 3.222E-5$). Only three of four specimens from TF 110 show enriched $\delta^{13}C$ and $\delta^{18}O$ values compared to other lucinids, and plot together with the deposit feeding tellinids from the same locality (Fig. 5F).

Specimens from sample TF 508_FW6 have depleted isotope ratios regardless of their

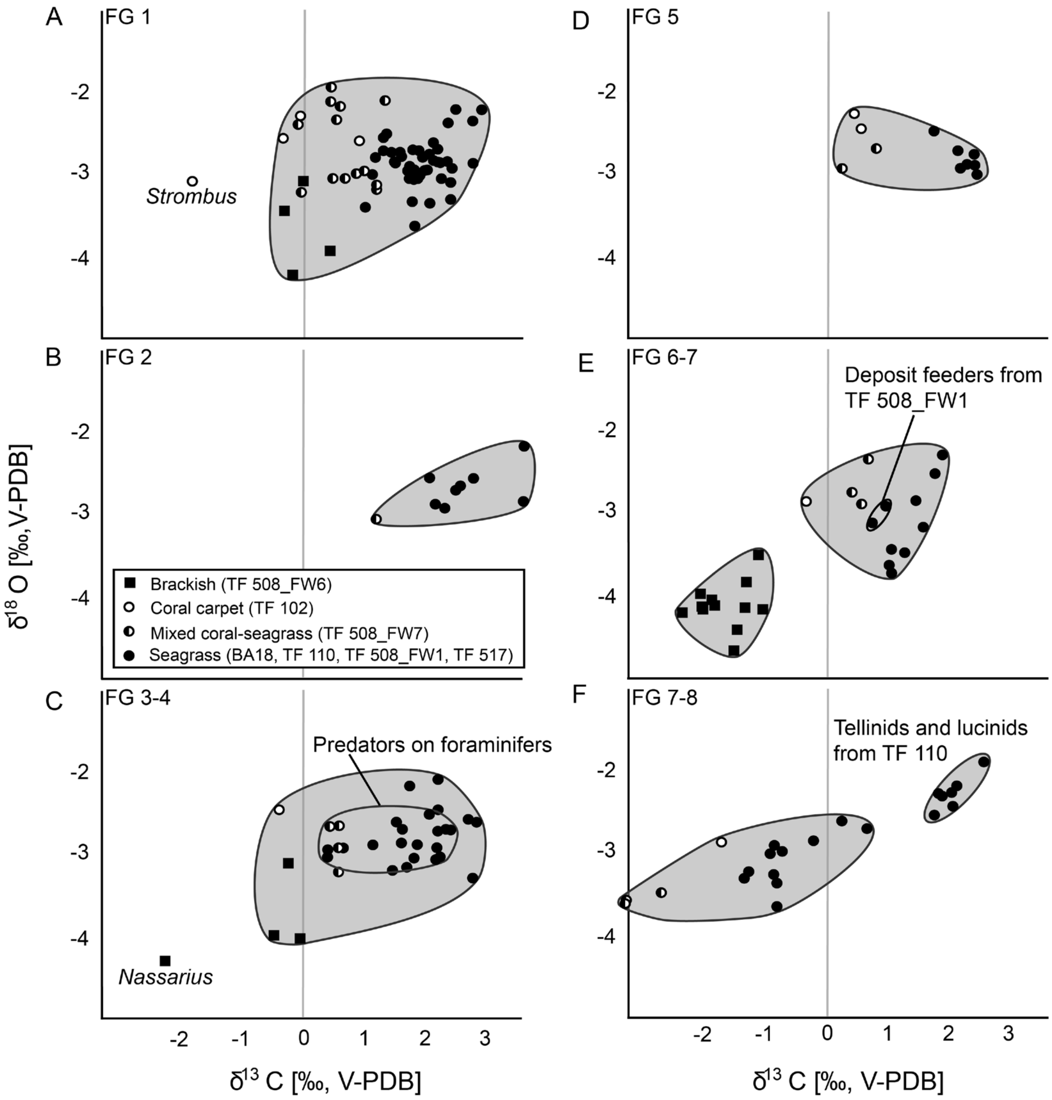

Figure 5: $\delta^{13}C$ and $\delta^{18}O$ ratios of mollusks arranged according to feeding guilds (FG 1-8) and paleoenvironmental interpretation (see legend). A) FG 1 (herbivores). B) FG 2 (seagrass feeders). C) FG 3-4 (predators on invertebrates and feeders on foraminifera). D) FG 5 (browsing carnivores). E) FG 6-7 (suspension feeders and part of deposit-feeders. F) FG 7-8 (part of deposit feeders and chemosymbiotic deposit feeders).

Table 3: Summary of $\delta^{13}C$ and $\delta^{18}O$ ratios of mollusks according to feeding guild (FG): 1 = herbivore, 2 = seagrass feeder, 3 = predator on invertebrates, 4 = predator on foraminifera, 5 = browsing carnivore, 6 = infaunal suspension feeder, 7 = infaunal deposit feeder, 8 = chemosymbiotic deposit feeder. * one outlier removed, ** three outliers removed.

FG	**FG 1 (all data*)**	**FG 2 (all data)**	**FG 3 (all data*)**	**FG 4 (all data)**	**FG 5 (all data)**	**FG 6 (TF 508_ FW6)**	**FG 6 (all data excl. TF 508_FW6)**	**FG 7 (all data)**	**FG 8 (all data **)**
n	65	9	17	15	11	12	12	6	15
$\delta^{18}O$ mean	-2.86	-2.71	-2.94	-2.81	-2.73	-4.11	-3.00	-2.44	-3.15
std	0.41	0.26	0.54	0.17	0.24	0.28	0.49	0.40	0.34
$\delta^{18}O$ min	-4.23	-3.06	-4.03	-3.06	-3.01	-4.66	-3.72	-2.91	-3.64
$\delta^{18}O$ max	-1.95	-2.17	-2.09	-2.51	-2.27	-3.50	-2.28	-1.88	-2.60
$\delta^{13}C$ mean	1.48	2.56	1.42	1.44	1.59	-1.71	1.05	1.65	-1.23
std	0.84	0.26	1.17	0.78	0.90	0.43	0.63	0.76	1.17
$\delta^{13}C$ min	-0.35	1.20	-0.49	0.40	0.22	-2.42	-0.36	0.56	-3.35
$\delta^{13}C$ max	2.94	3.66	2.88	2.44	2.45	-1.08	1.90	2.60	0.65

feeding ecology (Fig. 5A,C, E). However, the most striking difference appears between the isotope ratios of infaunal suspension feeders from TF 508_FW6 compared to those from other localities (Fig. 5E)

4.5 Stable Isotope Ratios and Inferred Paleoenvironments

The stable isotope ratios of mollusks from different paleoenvironments are shown in Figure 6. In order to compare between inferred paleoenvironments we exclude chemosymbiotic lucinids, as their stable isotope signature differs significantly from that of all other feeding guilds.

The brackish water sample TF 508_FW6 has depleted oxygen and carbon isotope ratios compared to other samples (see also discussion below). After removal of isotope ratios from lucinid bivalves the sample also differs from TF 102 (Tukey's HSD: q = 6.49; p = 0.0001), whereas no difference between the two localities was seen before.

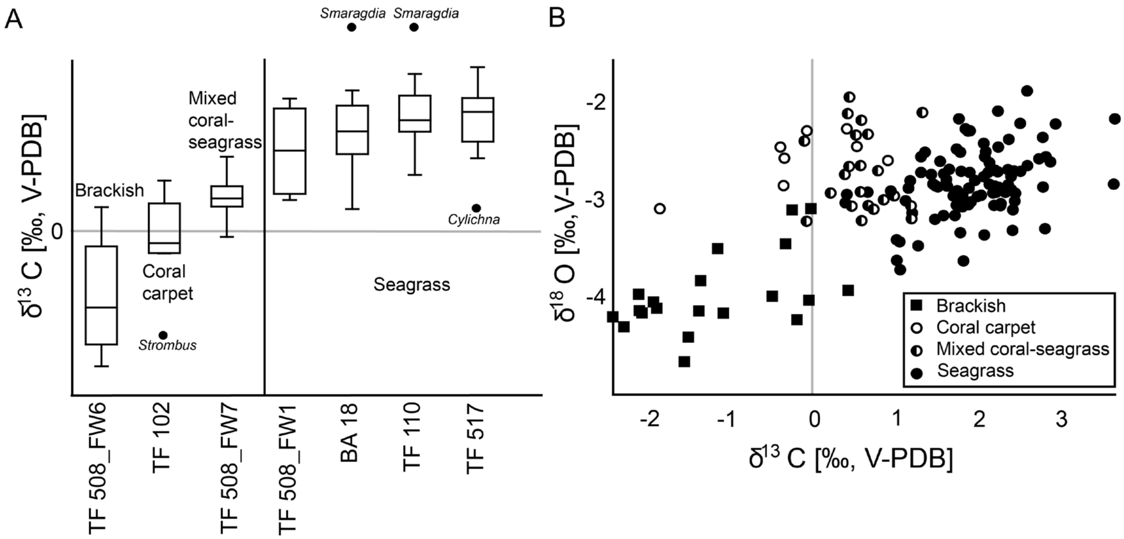

Figure 6: Comparison of all isotopic ratios. A) Interpolated box plots of δ13C values of all localities, outliers indicated by black dots. B) δ^{13}C and δ^{18}O ratios of all samples (including outliers); see legend for paleoenvironmental assignment.

The carbon isotope ratios of the six marine localities distinguish between coral carpet (depleted $\delta^{13}C$), mixed coral seagrass (intermediate $\delta^{13}C$ in TF 508_FW7) and seagrass (enriched $\delta^{13}C$ ratios). The seagrass localities BA 18, TF 110, TF 517, and TF 508_FW1 show significantly different carbon isotopic ratios than samples from the mixed coral-seagrass habitat TF 508_FW7 (Tukey's HSD: $q > 4$, $p < 0.01$) and the coral carpet environment TF 102 (Tukey's HSD: $q > 4$, $p < 0.01$).

When including carbon isotope ratios of lucinids, TF 508_FW1 (with presumably sparse seagrass vegetation) differs slightly from TF 110 (Tukey's HSD: $q = 4.18$, $p = 0.049$), whereas no difference is seen compared to TF 508_FW7 (Tukey's HSD: $q = 3.64$, $p = 0.13$).

5. **Discussion**

In order to understand processes and factors involved in the isotope signature of the shells we distinguish between processes affecting the composition of the ambient waters and fractionation processes that may occur between the water and the deposition of the shell. We assess factors in order to identify paleoecological processes and settings.

5.1 Factors Controlling the Isotopic Composition of Miocene Seawater

Global Ice-Volume. The increase of global ice-volume during the middle Miocene generally results in enriched oxygen isotope ratios of early Miocene carbonates compared to late Miocene carbonates (Lear et al., 2000; Prentice and Matthews, 1988;). In this study, the Kalimantan samples are of a Tortonian (late Miocene) age while the material from Banyunganti, Java has a Burdigalian (early Miocene) age. The latter has the most depleted $\delta^{18}O$ signals of samples assigned to fully marine environments. This likely reflects a different seawater composition at the time of shell formation due to a lower global ice-volume in the early Miocene.

Temperature and Salinity. Temperature and salinity are major factors controlling stable isotope composition of ambient waters; temperature is also known to affect kinetic processes (e.g., Dettman et al. 1999; McConnaughey and Gillikin, 2008). The narrow range of $\delta^{18}O$ ratios implies very similar temperature/salinity settings for the six marine samples of this study. Shells from sample TF 508_FW6 are on average 1‰ more depleted in $\delta^{18}O$ (and $\delta^{13}C$: Tab. 2), in this case indicating reduced salinities in a brackish environment (e.g., Eisma et al., 1976). The assemblage composition confirms the paleoenvironmental interpretation. We assume that the samples represent an environment with relatively low residence times (estuarine, see Eisma et al., 1976) and we assume an averaged salinity of 35‰ for marine waters. In comparison to isotope ratios of *Tridacna* shells from the Miocene of Indonesia (-2.3 to -2.2 $\delta^{18}O$ and 1.4 to 2.4 $\delta^{13}C$; Batenburg et al., 2011; Warter et al., this issue) and freshwater ratios of -4.6 $\delta^{18}O$ and -10.5 $\delta^{13}C$ in the Mahakam river south of the sample sites (S. Troelstra, pers. comm., 2011), we extrapolate that TF 508_FW6 (-3.97 $\delta^{18}O$ and -1.19 $\delta^{13}C$) was deposited in water with mesohaline conditions (9‰ based on $\delta^{18}O$ and 17-20‰ based on $\delta^{13}C$, conservative mixing assumed).

Air-Sea Exchange. Air-sea exchange is a controlling factor for oceanic $\delta^{13}C$, because atmospheric and oceanic carbon reservoirs tend towards isotopic equilibrium. Today's equatorial regions have a net transfer of isotopic light CO^2 from the ocean to the atmosphere resulting in ^{13}C enriched surface waters (Lynch-Stieglitz et al., 1995). All samples used in this study, apart from BA 18, derive from the same region and time frame, therefore air-sea exchange is not considered to be a contributing factor to isotope differences among those localities. Samples from BA 18 seem slightly depleted in ^{13}C compared to other seagrass-associated samples, but no significant difference between carbon ratios of seagrass localities is revealed by Tukey's HSD. The slight depletion in ^{13}C in samples from BA 18 cannot be attributed to a process without doubt, and might also be just a chance occurrence regarding the statistical insignificance. Other possible explanations are differences of the isotopic composition of atmospheric CO^2 and/or the mode of air-sea exchange in early Miocene compared to late Miocene times, or environmental differences between localities, such as the influence of ^{13}C depleted organic matter from other sources (see 5.2 '*Productivity and Organic Matter*' below).

5.2 Factors and Fractionation Processes Controlling the Isotope Signatures in Shell Formation

Mineralogy. Members of the seagrass feeding genus *Smaragdia* have slightly enriched $\delta^{13}C$ ratios compared to other mollusks from the same localities. Most likely this is a result of their calcitic outer shell layer (confirmed by Raman testing), because $\delta^{13}C$ of calcite is generally enriched compared to co-precipitated aragonite (Krantz et al., 1987).

Feeding Ecology. Numerous previous studies have attempted to identify food sources and reconstruct food webs in seagrass meadows using carbon isotopes, based on the assumption that a close similarity exists between the carbon signal of organisms and their diet (e.g., DeNiro and Epstein, 1978; Fry et al., 1982; Thayer et al., 1978). However, marine mollusks use largely ambient DIC to build their shells rather than respired CO_2 derived from dietary organic carbon (McConnaughey and Gillikin, 2008, and references therein). Several studies estimated parts of respired carbon in aquatic (marine and freshwater) mollusk shells at around 10% or less (Gillikin et al., 2006; Lorrain et al., 2004; McConnaughy et al., 1997).

In this study, isotope ratios grouped by feeding guilds overlap considerably and largely group according to localities (Fig. 5). Therefore, different feeding habits seem to have very little influence on the isotope composition of the shells, with a single exception. Lucinid bivalves differ in their isotopic composition from other mollusks in almost all samples (apart from TF 110) by their comparatively depleted $\delta^{13}C$ ratios. This is thought to be a result of bacteria induced carbon fractionation during carbon fixation, and therefore reflects their chemosymbiotic mode of life (CoBabe, 1991). Depleted $\delta^{13}C$ ratios of oxygen depleted sediments might also result in ^{13}C-depletion of infaunal lucinids (Latal et al. 2006a). In this study non-lucinid infaunal bivalves from the marine sites BA 18, TF 102, TF 508_1, TF 508_FW7 and TF 517 display an enriched $\delta^{13}C$ signal compared to lucinids from the same localities, indicating that the physiology of lucinids is the very likely cause of the depleted $\delta^{13}C$ ratios in their shells. The relatively enriched ^{13}C ratios of three lucinid specimens from TF 110, and possibly also of the fourth specimen and in one *Cardiolucina* from BA 18, may reflect deposit-feeding. In case of limited supply with reduced sulfur, lucinids can compensate the nutritional limitations by feeding on particles, or additional deposit-feeding might provide an advantage in highly productive depositional environments (Duplessis et al., 2004).

Infaunal versus Epifaunal Habitat. Previous studies found that infaunal bivalves are depleted in ^{13}C compared to epifaunal bivalves from the same locality (Krantz et al., 1987; Stevens and Vella, 1981), whereas in other studies no differences were seen (Tanaka et al., 1986). Comparatively depleted $\delta^{13}C$ values of infaunal bivalves are attributed to ^{13}C depleted pore water due to the decomposition of ^{13}C depleted organic matter in the sediment (Krantz et al., 1987, and references therein). Likewise, depleted $\delta^{18}O$ values may result from the degradation of organic matter by sulfate ions in oxygen depleted pore waters (Sass et al., 1991). However, none of the above mentioned studies included material from seagrass meadows.

Seagrass beds store a high amount of organic carbon and generally have high rates of sulfate reduction (Duarte and Cebrián, 1996; Holmer et al. 2003, 2009), therefore depleted isotopic values in infaunal bivalves could be expected. However, $\delta^{13}C$ values of sedimentary organic carbon from modern seagrass beds are often comparatively enriched (-9.8 to – 14, rather than -20 in other marine sediments; Fry et al., 1977, and references therein). This reflects the comparatively enriched $\delta^{13}C$ values of marine angiosperms especially in the tropics (typically -10 to -11; Hemminga and Mateo, 1996; Smith and Epstein, 1971).

In our study, four specimens of the infaunal venerid *Circe junghuhni* from BA 18 show comparatively depleted $\delta^{18}O$ values (Fig. 4A), whereas infaunal bivalves (excluding lucinids) from other localities (seagrass localities and TF 508_FW7) do not show such a depletion in oxygen compared to epifaunal species. A depletion of oxygen of infaunal bivalves might be prohibited in some seagrass environments due to the release of oxygen through seagrass roots and rhizomes (Fisher and Hand, 1984; Pedersen et al., 1998).

The infaunal bivalves from TF 508_FW6, where indications for seagrass vegetation are lacking, show a depletion of ^{13}C compared to epifaunal gastropods. This likely reflects the decomposition of ^{13}C depleted organic matter in the sediment. Infaunal bivalves (excluding lucinids) from coral carpet and the sparsely vegetated sandflat habitat of TF 508_FW1 also display rather depleted isotopic values, but data points are too few to make a clear statement.

However, $\delta^{13}C$ values of infaunal mollusks from seagrass habitats are mostly equally enriched as $\delta^{13}C$ values of epifaunal taxa, indicating that sedimentary organic matter in seagrass meadows displays enriched carbon isotope ratios compared to other marine environments as outlined above. Only two specimens of the shallow infaunal *Cylichna* from BA 18 and TF 517 are depleted in ^{13}C compared to other seagrass-associated cylichnids (Fig. 5C). This probably reflects depleted pore water on a very small spatial or temporal scale.

Furthermore, infaunal deposit-feeders from site TF 110 (including Lucinidae) and Veneridae from BA 18 have very small variation in their isotope ratios possibly reflecting very similar environmental conditions in the sediment. At other localities (TF 517, TF 508_7) the isotopic ratios of infaunal bivalves are found scattered between those of epifaunal gastropods, probably reflecting more variable parameters in the sediment, or a negligible variability between the conditions above and below the sediment-water interface. In addition, we cannot rule out that the variation of isotope values in the bivalve material results from the use of shell fragments in our analyses. Because carbon isotope values often become more depleted with growth of the bivalve shell (e.g., McConnaughey and Gillikin, 2008, and references therein), the use of fragments may result in an isotope record biased towards a fraction of some years.

Productivity and Organic Matter. Photosynthetic organisms, such as seagrasses, preferably incorporate the lighter ^{12}C leading to ^{13}C enriched ambient seawater when productivity is high (e.g., Lynch-Stieglitz et al., 1995). Epifaunal mollusk shells with comparatively enriched $\delta^{13}C$ values from seagrass localities (BA 18, TF 110, TF 508_FW1, TF 517) therefore may indicate a high primary production as known for modern seagrass environments (Duarte and Chiscano, 1999). As outlined in '*Epifaunal versus Infaunal Habitat*' the organic matter stored in seagrass meadows is relatively enriched in ^{13}C resulting in enriched $\delta^{13}C$ values of infaunal mollusks. However, $\delta^{13}C$ measured in modern habitats varies between different seagrass environments. For example, shells from mangrove adjacent seagrass beds show depleted $\delta^{13}C$ ratios due to the input of ^{13}C depleted mangrove carbon (Hemminga et al., 1994; Lin et al., 1991; McMillan et al., 1980). Samples from mangrove areas had carbon isotope values ranging from -0.8 to -3.7, whereas shells from seagrass meadows where mangroves where lacking display enriched values of +0.0 to +1.0 (Lin et al., 1991). Estuarine seagrasses display a more depleted $\delta^{13}C$ signal than those lacking riverine influence (Simenstad and Wissmar, 1985), likely resulting in comparatively depleted shells.

5.3 Stable Isotope Signatures as Paleoenvironmental Indicators

The similar $\delta^{18}O$ ratios occurring in our samples, suggest that $\delta^{13}C$ ratios are more likely to discriminate between different habitats. However, $\delta^{18}O$ records are useful to exclude the possibility that variations in $\delta^{13}C$ are based on temperature or salinity differences. In coastal settings the influence of freshwater and/or depleted organic carbon, for instance from mangroves, often leads to depleted carbon isotope values of mollusk shells (Lin et al., 1991; Simenstad and Wissmar, 1985; this study: sample TF 508_FW6). Depleted $\delta^{18}O$ values can indicate such depressed salinities.

It is presumed that mollusks in Recent open marine conditions precipitate their shells close to seawater-atmosphere equilibrium, therefore the $\delta^{13}C$ values of their shells should be around 0 (Hoefs, 1987). However, in our study, the mollusk shells from seagrass settings are significantly enriched compared to the expected $\delta^{13}C$ value for marine conditions and compared to contemporary samples from coral-dominated environments. This suggests that it is possible to distinguish seagrass from non-seagrass marine environments by the carbon isotope signal of mollusk shells at least within the same region and time frame. Therefore carbon isotope signals may serve as a control over paleohabitat assignments made based on the composition of fossil assemblages. Carbon isotope ratios of mollusk shells show a positive correlation with carbon values of seagrass tissue (Lin et al., 1991), therefore this method might be restricted to (sub)-tropical environments because of the relative depletion of $\delta^{13}C$ of seagrasses in temperate areas (Hemminga and Mateo, 1996). When only considering tropical, fully marine settings it is also unlikely that a specific carbon signature for seagrass meadows exists. Keith et al. (1964) presented stable isotope signatures of Recent mollusk shells derived from various marine and freshwater environments. Carbon isotope values of marine mollusks ranged from -1.7 to +4.2. Highest values were found in shells from shallow waters at the Pacific coast of Mexico, including three samples with a value > +2. Although no environmental indications are given in that work, all three samples derived from localities where seagrass meadows were most likely absent (Green and Short, 2003). Further studies on the isotope signals of mollusk shells from different modern shallow marine habitats, including seagrass meadows, are necessary to confirm a general trend of enrichment of shell carbon in seagrass habitats. Unfortunately many studies on isotope ratios displayed by organisms in modern seagrass habitats are performed on organic material/tissue and not on shells (e.g., Fry et al., 1982). However, Recent epifaunal gastropod shells collected from a seagrass-vegetated reef flat (depth = ~1m) off the island of Lankadea (Spermonde, Sulawesi, Indonesia) have enriched carbon isotope values ranging from +1.45 to +2.68 (mean = +2.14) comparable to those from the here investigated fossil seagrass assemblages (own data: Tab. 4). The wide range of oxygen isotope ratios in those samples (-1.37 to -3.13, Tab. 4) may suggest that the stable isotope composition of the investigated shells was additionally influenced by varying salinities, possibly indicating that they were partly transported from different environments. At least for *Smaragdia rangiana* (δ^{13}C = +2.26) an in-habitat deposition can be assumed. More studies are needed for comparison.

Table 4: Stable isotope values of Recent mollusk shells from a seagrass-vegetated reef-flat (Lankadea, Spermonde, Indonesia).

Sample	Species	13C V-PDB	18O V-PDB
UPG16_1	*Bothropoma* sp.	1.94	-1.99
UPG16_1.2	*Bothropoma* sp.	2.52	-2.16
UPG16_2	*Smaragdia rangiana* Récluz, 1841	2.26	-1.69
UPG16_4	Conidae indet.	1.98	-3.13
UPG16_4.2	Conidae indet.	1.45	-2.98
UPG16_5.2	*Diala semistriata* (Philippi, 1849)	1.61	-2.49
UPG16_7.2	*Euplica* sp.	2.68	-1.55
UPG16_8.2	*Euplica* sp.	2.58	-1.65
UPG16_9.2	*Ervilia bisculpata*	2.39	-1.37
Mean		**2.14**	**-2.12**
Min		1.45	-3.13
Max		2.68	-1.37

6. Conclusions

The shell isotope composition in the studied samples reflects a number of paleoecological conditions and processes. The following conclusions can be made based on our results.

1. Feeding ecology, in most cases, has very little to no influence on the isotopic values of mollusk shells in this study, with the exception of chemosymbiotic taxa. The life mode of most lucinids analyzed seems to be well preserved in a distinctively depleted $\delta^{13}C$ signature. Such taxa should be removed from data sets when aiming for a paleoenvironmental comparison among samples.

2. An ability to switch to deposit-feeding by chemosymbiotic lucinids is possibly documented in the stable isotope record of samples from TF 110.

3. Infaunal taxa in seagrass meadows are more likely to have shells enriched in ^{13}C compared to shells from other habitats due to the enriched $\delta^{13}C$ values of sedimentary organic seagrass carbon.

4. High rates of productivity in seagrass meadows likely cause the enriched $\delta^{13}C$ values of epifaunal mollusk shells from seagrass habitats.

5. Shells from paleo-seagrass meadows do not display a unique isotope signal that can serve as an independent indicator for the biotope, but in comparison with contemporary samples from non-seagrass environments they have enriched $\delta^{13}C$ ratios. Therefore, the carbon isotopic ratios of shells can be used to confirm habitat assignments based on the taxonomy and ecology of fossil mollusks within regions and limited stratigraphic time intervals. A control over the context is indispensable.

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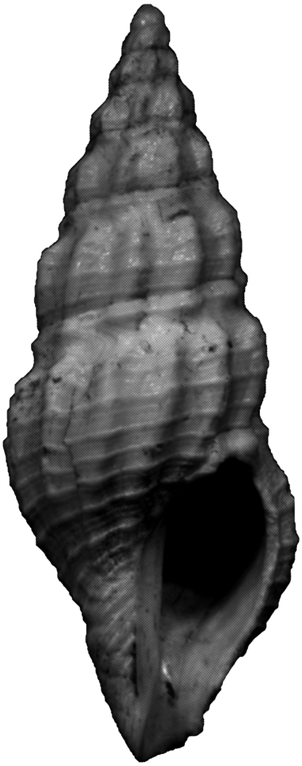
Synthesis



Chapter 6 - Synthesis

Composition, Ecology and Diversity of Seagrass-Associated Mollusk Faunas in the Miocene of the Marine Biodiversity Hotspot, Indonesia

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Manuscript in preparation

Keywords: seagrass meadow, mollusks, species composition, biodiversity, feeding guild ecology, Indonesia, Miocene

Abstract

Today's marine global biodiversity hotspot, located in in the South-West Pacific, yields the highest species richness of numerous organisms including mollusks. For this study seagrass-associated mollusk assemblages were chosen as a model group to document variation in taxonomic and ecological composition over time and gain insight on diversity change during the Miocene of Indonesia. Three seagrass-associated assemblages, including one historical museum collection, were available for comparison. They belong to the early, the middle, and the late Miocene. In addition, a late Miocene coral carpet assemblage is used for comparison to gain insight on variation between assemblages from distinct seagrass-bearing paleohabitats. All investigated assemblages are large in terms of mollusk abundance (1486-8212 specimens per sample) and species richness (161-271 species per sample) and contain a high number of undescribed species. Analyses of species composition reveal high dissimilarity among all assemblages with the lowest dissimilarity found between two contemporaneous assemblages from different paleohabitats (seagrass meadow and coral carpet, late Miocene). Biodiversity of the assemblages is generally high, but data are not sufficient for a diversity reconstruction over time, stressing the huge effort that is required for data acquisition when aiming for such assessments. Furthermore, a comparison of feeding ecology reveals that seagrass-characteristic feeding ecological patterns show more variation than previously assumed, and potential environmental differences among seagrass meadows are addressed.

1. Introduction

Today's center of maximum marine biodiversity is located in the Indo-Malayan region, including Malaysia, the Philippines, Indonesia, and Papua New Guinea. The area is often referred to as today's global marine biodiversity hotspot or the coral triangle (Hoeksma, 2007; Renema et al., 2008). The latter refers to the worldwide highest diversity of about 500-600 species of corals in the region (Hoeksema, 2007). The high coral diversity apparently originated in the Early Neogene, although this might be a result of a lack of sampling of Paleogene deposits (McMonagle et al., 2011). The Early Neogene is marked by a change from larger benthic foraminifera to coral dominated carbonates in the sedimentological record, and by an increase of the distribution and extent of carbonate sediments (Wilson and Rosen, 1998). The increase and diversification of scleractinian coral reefs also contributed to the radiation of reef-associated biota (Kohn, 1990; Wilson and Rosen, 1998). The Neogene rise of reefs and associated assemblages probably led to an increase of steepness of latitudinal mollusk diversity gradients (Rex et al., 2005). Several extant molluscan clades have their peak species diversity in the Indo-Malayan region, including the class Bivalvia (Crame, 2000) and several speciose gastropod families such as Conidae (Kohn, 1967, 1985, 1997; Vallejo, 2005), Strombidae (Roy et al., 2001), and Cerithiidae (Houbrick, 1985, 1992). Likewise, shallow marine ecosystem engineers (*sensu* Jones et al., 1996) other than corals, such as mangroves and seagrasses, also have their diversity peaks in the Indo-Malayan region (Spalding et al., 2001). Where the three components are present in the same environment; seagrasses, coral reefs, and mangroves are closely connected (McCoy and Heck, 1976; Ogden, 1997; Spalding et al., 2003). Examples are for instance, the protective function of reefs for seagrasses and mangroves against wave action, or the function of seagrass meadows as nursery habitats for reef-associated fish (Hemminga and Duarte, 2000; Spalding et al., 2003).

Seagrass meadows themselves are complex ecosystems that consist of several microhabitats and play an important ecological role as; providers of food and refuge for numerous associated organisms, primary producers, a source of biogenic carbonate, sediment stabilizers, and in nutrient cycling (Chapter 1).

As part of the ITN Throughflow program (www. ipaeg.org/throughflow) we aim to document Neogene organismal diversification in shallow marine habitats based on museum collections as well as on newly collected fossil material. This study focusses on mollusk diversity. Because taxonomic diversity does not only vary through time, but also among different habitats (e.g. Gray, 2001), seagrass-associated mollusk assemblages were chosen as a model group. Mollusks are common and diverse in seagrass environments, have a high preservation potential, and are furthermore useful paleohabitat indicators (Chapter 1).

The four faunas investigated in this study are all dominated by mollusks, and by gastropods in particular. Three of the four faunas were identified as seagrass-associated based on mollusk assemblages and other indicators (Chapters 1, 2, 5). The assemblages represent different Miocene time intervals (early Burdigalian, early Miocene; middle Miocene; and early Tortonian, late Miocene). The fourth assemblage was derived from a coral carpet environment (Chapter 3: TF 102, early Tortonian, late Miocene). In this study we aim to reconstruct and compare seagrass faunal composition, ecology and diversity in the different Miocene time intervals.

In Chapter 4 it was shown that the species composition of seagrass associated gastropod assemblages differs significantly from that of assemblages derived from adjacent unvegetated sandflats in modern environments at San Salvador, Bahamas. Here we test whether taxonomic composition of assemblages from different regions and/or time intervals can also delimit paleoenvironments. Furthermore, we investigate if feeding guild composition has a characteristic pattern in seagrass assemblages as is suggested in Chapters 1 and 3.

2. Sampling Localities

2.1 Banyunganti, Java

The sampling locality is situated near the village of Banyunganti in the province of Yogyacarta, Java, Indonesia (Fig. 1A; see Chapter 2 for detail map). The studied bulk sample (BA 18) derived from a 1.5 m thick interval of fine to medium-grained sand in marine Miocene deposits of the Jonggrangan Formation (Chapter 2; Kadar, 1986). The studied assemblage is early Burdigalian (early Miocene) in age. Geological context, sedimentology, and stratigraphy of the sampling locality are described in detail in Chapter 2.

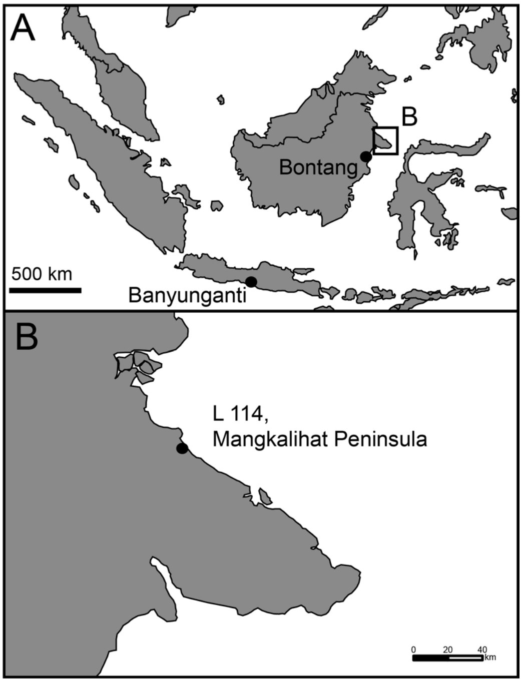

Figure 1: Locality map. A) Overview map of Indonesia including the localities Banyunganti and Bontang. B) Overview map of Mangkalihat Peninsula indicating the assumed position of historical sampling locality L 114 (map by V. Novak).

2.2 L 114, Mangkalihat Peninsula, East Kalimantan

The historical sample locality L 114 (after Leopold, 1921-1927) is situated on the Menkrawit River in the northern Mangkalihat Peninsula (East Kalimantan, Indonesia), but the exact locality is unknown (Fig. 1B). In the 1920s Leopold measured a coastal section from Gunung (hill) Taballar to Tandjung (cape) Domaring, along the northern shore of the Mangkalihat Peninsula. His research was part of a survey for the Dienst van het Mijnwezen in Nederlands Oost-Indie. The area was revisited in 2010, but the exact locality could not be retraced.

During most of the Cenozoic the Mangalihat Peninsula formed a topographic high that separated the Kutai Basin in the south and the Tarakan Basin in the north. The deposition of shallow marine carbonates on top of the high began in the late middle Eocene (Wilson et al., 1999). Leupold's study section comprised two massive limestone packages, separated by an interval of alternating marls, clay-rich sandstones and thin limestone beds, known as the Menkrawit Beds. The outcrop is situated on the coast in proximity of a low cliff (1-2 m high) and some rivers (Leopold, unpublished report, collection archive NCB Naturalis). Sample L 114 was collected near the mouth of the Menkrawit River. From Leupold's descriptions it appears that a trench had been dug in the river, upstream from the cliff. Sediments at the sampled locality were described as slightly sandy, gray clays containing abundant mollusks and corals (Beets, 1941).

Samples were sent by Leuopold to van der Vlerk, and formed the basis of the letter classification of larger benthic foraminifera (LBF) subsequently used for shallow marine biostratigraphy in Indonesia (van der Vlerk and Umbgrove, 1927). Benthic foraminifera in sample L 114 unambiguously indicate a (late) Tf2 or middle Miocene age (Lunt and Allen, 2004; Renema, 2007; van der Vlerk and Umbgrove, 1927). Other samples taken in the same stretch of marls contained the planktonic foraminifer *G. menardii*, consistent with the age range indicated by LBF (Wade et al., 2011).

2.3 Bontang, East Kalimantan

The city of Bontang is located on the coast of central East Kalimantan south of the Mangkalihat Peninsula (Fig. 1A). The Bontang area has recently witnessed a surge in construction works leading to the temporary availability of several outcrops at building sites. The outcropping sediments are predominantly marine clay-, silt-, and fine sandstones of early Tortonian (late Miocene) age. Geological context and stratigraphy of the study area are discussed in more detail in Chapter 5 (see also Renema et al., submitted). Bulk samples from two sample localities in the Bontang area are investigated in this study: sample TF110_SR38 from locality TF 110 and samples TF102_SR 50 to SR 54 from locality TF 102 (see Chapter 5 for detail map). For convenience samples will be further referred to by locality name only. Sample TF 110 was collected from a bed of highly fossiliferous dark-gray silty clays within an interval of shallow marine clastic sediments (Chapter 5). Five bulk samples from TF 102, derived from five closely associated coral patches on a bedding plane of marine silty clay, were combined into one data set (Chapter 3). Further information on the locality and the sampling method used is provided in Chapter 3.

3. Material and Methods

3.1 Sample Treatment and Species Identification

The material investigated in this study is housed at Naturalis Biodiversity Center (Leiden, the Netherlands), indicated by RGM numbers. The samples we collected from Banyunganti and Bontang were washed over a 1 mm sieve and sorted for biogenic components.

Mollusk shells were counted as outlined in Chapter 2 to create a comparable dataset. There is no general agreement on which of the several existing counting methods is most suitable. Our counting method is quick and easily reproducible, because all gastropod shells of at least one whorl were counted when a part of the columella was present. In contrast, a counting method using a certain percentage of the available shell as representative of one individual will be biased by the perception and judgment of different workers. However, we are aware that the method used raises other issues, especially concerning the original number of specimens present, because an increased degree of fragmentation (e.g., due to sample treatment) will increase the apparent number of specimens. This issue will be discussed later (see 5.4).

Both the collecting (sampling) method used at the historical sampling locality L 114 (Mangkalihat) and sample treatment after collection are unknown. From its appearance it is likely that the collection contains specimens sorted out from a bulk sample as well as larger specimens collected from float. Indications for this include the numerical dominance of one strombid species that is represented only by comparatively large specimens and the general scarcity of small individuals. Furthermore, it appears that fragmented specimens were largely excluded from the collection, and therefore could not be counted. This raises issues concerning the numerical comparability of the material with the other studied assemblages that will be discussed later (5.3-5.5).

Species identification of mollusks from samples was undertaken as outlined in Chapters 2 and 3, resulting in material that is largely presented in open nomenclature. It is highly likely that the majority of those faunas is undescribed, but a full taxonomic revision was beyond scope of this study. However, we would like to raise awareness of the availability and accessibility of this excellently preserved material among molluscan taxonomic specialists (see also Chapters 2 and 3). Some incomplete specimens could not unequivocally be assigned to a taxon and are therefore grouped together as Gastropoda indet. spp. Other specimens could only be assigned to a family, but could not been placed in one of the identified species (e.g., Columbellidae indet. spp.).

The mollusk fauna from L 114 was described by Beets (1941), but the material is in need of taxonomic revision. Later Beets and other workers changed species and generic names within the collection, but those changes are so far unpublished. We briefly revised the fauna to make identifications consistent among our samples and to limit the inaccuracies that would result from clear misidentifications. For instance, most species identified by Beets as species described by Martin from Cenozoic deposits of Java we consider to be misidentifications based on our direct comparisons with the type material housed in the Naturalis collection (Leloux and Wesselingh, 2009). For species identifications of living species, it is doubtful that these are correct, but no comparisons with the type material were made. Therefore those species are referred to as ‘species *sensu* Beets, 1941’. Generic assignments of Conidae follow Tucker and Tenorio (2009). A full taxonomic review of the fauna is pending and was beyond scope of this study. For now we use the revised, largely unpublished taxonomic assignments made by us and other workers, because they are probably more accurate and are certainly more consistent across our data set than the original names. The original published names are given in Appendix 1.

3.2 Paleoenvironmental Interpretations

The paleohabitats of the studied assemblages, apart from TF 102, have been interpreted as seagrass meadows based on the composition of the mollusk faunas, including the occurrence of the seagrass-feeding gastropod *Smaragdia*, and accompanying foraminifera (Chapters 1, 2 and 5). TF 102 was interpreted as a coral carpet environment, presumably with dispersed seagrass vegetation (Chapter 3).

The paleohabitat assignments were supported by carbon isotope signals displayed by mollusk shells (Chapter 5). For the fauna from L 114 no habitat assignment was yet available. The mollusk assemblage is here tentatively interpreted as a seagrass-associated assemblage based on its taxonomic and ecological composition and the presence of *Smaragdia* (Chapter 1).

3.3 Associated Faunas

The fauna from Banyunganti is dominated by excellently preserved mollusks, both in terms of abundance and species richness, followed by benthic foraminifera (in terms of species richness) and scleractinian corals (in terms of abundance). Other biogenic components are much rarer in abundance and richness and include bryozoans, echinoderm fragments, ostracods, fragments of crab claws, and fish remains. The mollusk fauna was described in Chapter 2. It includes 184 species of which 159 species are gastropods. Four gastropod species were described as new (Chapter 2).

The fauna from L 114 includes 161 mollusk species of which 69 species were described as new (Beets, 1941). Other biogenic components are benthic foraminifera, scleractinian corals, a single ostracod, and otoliths (Umbgrove, 1929; Posthumus, 1929; Doeglas, 1931, Leopold and van der Vlerk, 1931).

The fauna from TF 102 is dominated by scleractinian corals in terms of abundance, and mollusks in terms of species richness. The composition of both mollusks and corals is discussed in Chapter 2. Other fossils are scarce and include foraminifera, fragments of crustacean claws, and rare fish remains (1 otolith, 3 teeth).

Apart from the use of some of the material from TF 110 in a comparative study of stable isotope signals from shells from different paleohabitats (Chapter 5) the fauna is largely unpublished. Besides a species-rich mollusk assemblage (271 species), the sample contained benthic foraminifera, scleractinian corals, calcified worm tubes, bryozoans (Di Martino and Taylor, in press), ostracods, fragments of crustacean claws, abundant echinoderm remains, and fish remains (otoliths, teeth, bone fragments).

3.4 Analyses of Taxonomic Composition

Analyses of taxonomic composition were performed using PAST 2.16 (Hammer et al., 2001). Analyses of abundance were carried out on the same data set at three taxonomic levels; species, genus, and family. For the analyses the complete datasets including rare species were used (Etter, 1999). Groups of gastropods that could not be identified beyond family level, such as Columbellidae indet. spp., and likewise Gastropoda indet. spp., were included and treated as unique units. To compare samples with very different total abundances, species abundance data are expressed as proportions (Clifford and Stephenson, 1975). Similarity of species composition among samples was tested by Bray-Curtis distance measure with a value of 1 indicating a complete match of the assemblage composition, whereas a value of 0 indicates complete dissimilarity (Bray and Curtis, 1957). The overall relationship among samples is visualized by non-metric multidimensional scaling (NMDS) likewise using Bray-Curtis distance measure. The method is an indirect ordination that reduces the data to fewer dimensions (Hammer and Harper, 2006; Clapham, 2011). In this analysis the composition of the five sub-samples from TF 102 (SR50-ST54) is presented together with the composition of the combined sample.

3.5 Analysis of Feeding Guild Composition

Each taxon present in the assemblages was assigned to one of seven feeding guilds (herbivores/detritivores, predatory carnivores, browsing carnivores, suspension feeders, deposit feeders, chemosymbiotic deposit feeders, and borers) as outlined in detail in Chapter 2. Unidentified gastropods (Gastropoda indet. spp.) were not included in this analysis. Feeding guild composition is shown based on abundance data (number of specimens) as well as based on species richness, and is reconstructed for the entire mollusk assemblage as well as for gastropods only.

3.6 Analyses of Biodiversity

Analyses of biodiversity were performed using PAST 2.16 (Hammer et al., 2001), including the calculation of the following biodiversity indices: species richness (number of species), dominance (D), Simpson index (1-D), and Shannon index (H) as well as rarefaction analysis. The later additionally provides an estimate of sampling adequacy.

The only available data set directly comparable to our is a middle Miocene, presumably seagrass-associated, assemblage from Karaman, Turkey that has been sorted and counted applying the same methods used in this study (Landau et al., 2013; Wesselingh, unpublished data).

4. **Results**

4.1 Taxonomic Composition

The complete abundance data for species all samples are given in Appendix 2. Abundance data for genera and families can be downloaded (https://www.dropbox.com/s/uo2mtoufbm591wy/Chapter_6_Supplementary_Data.xls). Bray-Curtis distance values show high dissimilarity between the species composition of all assemblages (Tab. 1). The highest value, indicating a comparatively higher similarity, is found between the contemporaneous assemblages TF 102 and TF 110. Values for all other samples are <0.05 indicating almost complete dissimilarity among species composition. As expected, Bray-Curtis distance values increase as the precision of identification is decreased (or the taxonomic hierarchy is ascended) from species to genus to family-levels. Interestingly, the general relationship of values among samples remains the same, with the highest similarity found between samples TF 102 and TF 110 and the lowest similarity found between samples BA 18 and L 114 (Tab. 1).

Table 1: Bray-Curtis distance measures for all assemblages based on proportional abundance of species, genera and families.

Species composition				
	BA 18	L 114	TF 110	TF 102
BA 18	1	0.016	0.044	0.033
L 114	0.016	1	0.036	0.043
TF 110	0.044	0.036	1	0.189
TF 102	0.033	0.043	0.189	1
Generic composition				
	BA 18	L 114	TF 110	TF 102
BA 18	1	0.14	0.23	0.22
L 114	0.14	1	0.17	0.19
TF 110	0.23	0.17	1	0.44
TF 102	0.22	0.19	0.44	1
Family composition				
	BA 18	L 114	TF 110	TF 102
BA 18	1	0.20	0.39	0.33
L 114	0.20	1	0.22	0.31
TF 110	0.39	0.22	1	0.52
TF 102	0.33	0.31	0.52	1

Of a total of 705 identified species only two occur in all four samples (Appendix 3). However, both represent a species complex (indicated by the suffix s.l.), and therefore might represent different species that could not be separated due to a lack of distinguishing characters. Thirteen species were found in three of the samples. Of those only one occurs at Banyunganti, L 114 and TF 110; but this also represents a species complex. The remaining 12 species were found in all samples apart from Banyunganti. Fifty-seven species are represented by two samples. The majority of these, 40 species, were found in the contemporaneous samples TF 110 and TF 102. Nine species occur in both samples L 114 and TF 110. Three species occur each at Banyunganti and L 114 and at L 114 and TF 102, and two species have shared occurrences at Banyunganti and TF 110. This makes a total of 603 species that only occur at one of the four sampling sites. It also should be noted that abundances of co-occurring species often differ distinctively among samples (Appendix 3).

All NMDS results of abundance data based on species, genera and family level identifications confirm that most sub-samples from TF 102 have a similar species composition and can therefore be combined into one data set as already concluded in Chapter 3 (Fig. 2). The only exception is sample SR52 that most likely differs from the other samples due to its low overall abundance of mollusks of only 78 specimens. The difference was not detected by Raup-Crick sample dissimilarity as applied in Chapter 3, because that method is specifically designed for use in cases where sampling is uneven among sites.

All NMDS results illustrate the difference in the taxonomic composition of the four investigated assemblages (Fig. 3). NMDS based on species abundances reflects a trend of diversity as revealed by rarefaction (see 4.3) with TF 102 and TF 110 being similar in composition along axis 1, whereas axis 2 reflects richness of species-level taxa (Gastropoda indet. spp. included) from TF 110 with 272 taxa over BA 18 and L 114, each with about 180 taxa, and TF 102 with the lowest richness of 162 (Fig. 3A, Tab. 2).

Axis 2 of NMDS based on generic abundances reflects a trend of diversity similar to that seen in the NMDS based on species abundances, but here TF 102 and TF 110 are more separated (Fig. 3A-B). To some extent, axis 2 might reflect dominance of the assemblages from higher to lower, (Fig. 3B, Tab. 2). NMDS results based on family

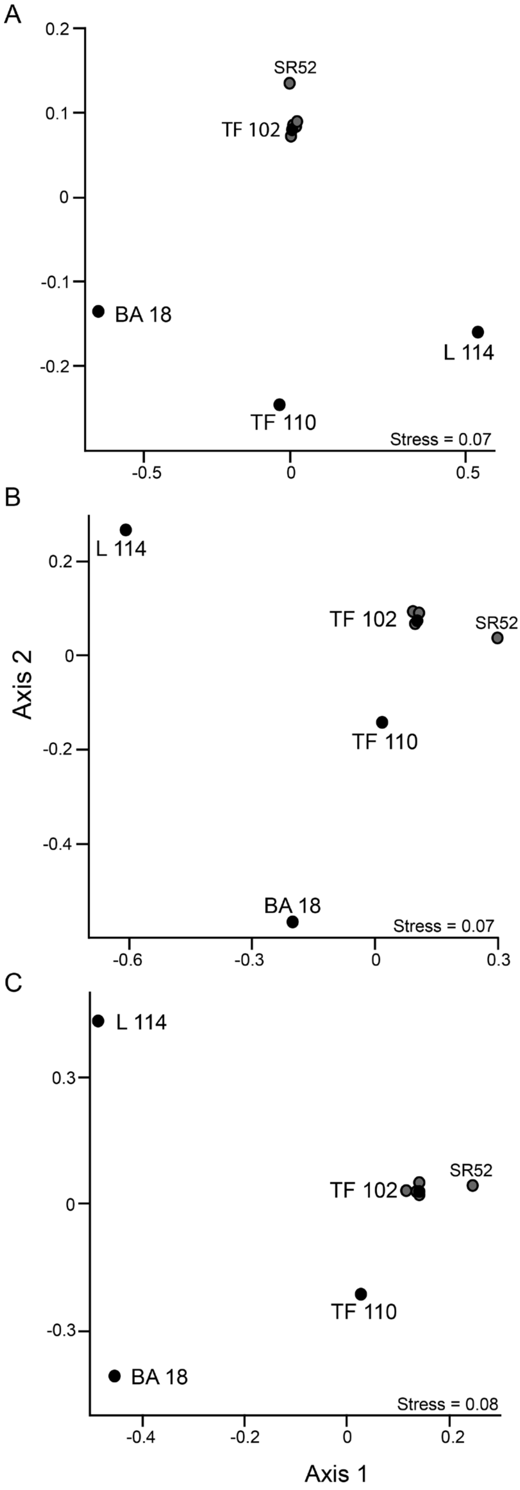

Figure 2 (left): Two-dimensional NMDS ordination of 4 Miocene mollusk assemblages (black dots) and five sub-samples (gray dots) of TF 102, using Bray Curtis distance. A) Based on proportional abundance of species. B) Based on proportional abundance of genera. C) Based on proportional abundance of families.

abundances are very similar to those of generic abundance based analysis (Fig. 3B-C). The most obvious difference is the very small distance between L 114 and BA 18 along axis 1.

Apart from a closer relation between the contemporaneous samples TF 102 and TF 110 along axis 1 of the NMDS based on species composition (Fig. 3A) than for the other samples, the assemblages do not group by age or by paleoenvironment. However, the few data points available prevent a generalized statement.

4.2 Feeding Guild Composition

When using gastropod assemblages, herbivory/detritivory is the most abundant feeding guild in the seagrass-associated assemblages (BA 18, L 114, and TF 110) with at least 70% abundance in BA 18 and L 114 (Fig. 3A). In the assemblage from TF 110 predatory gastropods make up 41% and are therefore almost as abundant as herbivores and detritivores (45%). In the coral carpet assemblage from TF 102 predatory gastropods are most abundant (54%), followed by herbivores/detritivores (36%). When using species richness, the feeding guild composition of all four assemblages is similar with 40-45% predatory gastropod species and 26-36% herbivorous/detritivorous species (Fig. 3B). Predatory gastropod species are most abundant at TF 102 and least abundant at Banyunganti, whereas herbivorous/detritivorous species are most abundant at L 114 and least abundant at TF 102.

When including all mollusks (gastropods, bivalves and a few scaphopod and chiton specimens), the feeding guild composition of seagrass-associated assemblages remains overall similar to that based on gastropods only (Fig. 3A, C). The abundance of suspension feeders increases due to the addition of bivalve specimens involving a slight decrease of the abundance of feeding guilds primarily made up of gastropods. The overall pattern of feeding guild composition based on species richness remains similar to that using gastropods only (Fig. 3B, D). Seagrass faunas are dominated by herbivores/detritivores in terms of abundance, but predatory carnivores are dominant in terms of species richness, whereas the coral carpet assemblage is dominated by predatory gastropods both in terms of abundance and species richness.

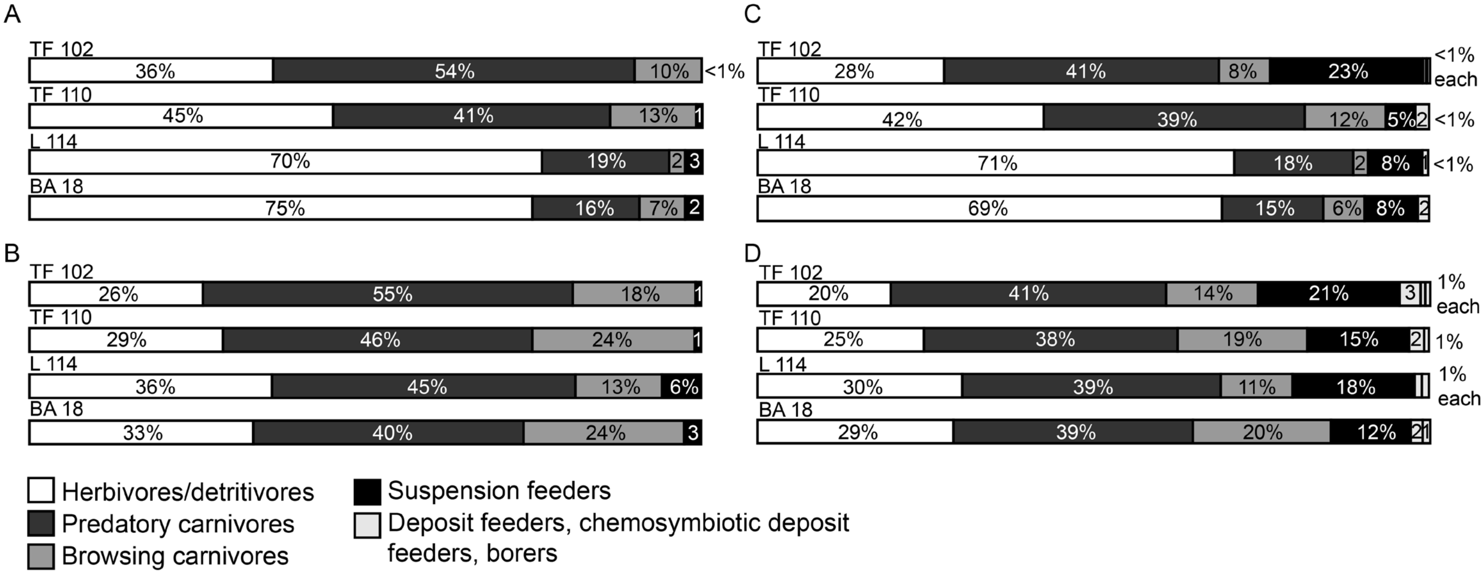

Figure 3: Comparison of feeding guild composition of three seagrass-associated mollusk assemblages (samples BA 18, L 114, and TF 110) and one coral carpet assemblage (TF 102). A) Based on numbers of gastropod specimens with NTF 102 = 1033, NTF 110 = 7645, NL 114 = 1316, and NBA 18 = 4087. B) Based on numbers of gastropod species with NTF 102 = 120, NTF 110 = 215, NL 114 = 156, and NBA 18 = 159. C) Based on numbers of all mollusk specimens with NTF 102 = 1354, NTF 110 = 8139, NL 114 = 1410, and NBA 18 = 4417. D) Based on numbers of all mollusk species with NTF 102 = 161, NTF 110 = 271, NL 114 = 187, and NBA 18 = 182.

4.3 Biodiversity

All four assemblages have low dominance D and accordingly high evenness expressed by Simpson index 1-D (Tab. 2). However, the stratigraphic older assemblages BA 18 and L 114 have higher dominance than the late Miocene assemblages collected at Bontang (TF 102 and TF 110). According to Shannon index H, species diversity of the assemblages increases with time from the early Miocene (early Burdigalian, BA 18) to the late Miocene (early Tortonian, TF 102 and TF 110). When using generic richness the overall picture remains the same, but variation among assemblages increases. Other than for species and genera, BA 18 has a slightly higher family richness than L 114, but the general pattern of diversity increase over time remains the same. The coral carpet assemblage TF 102 has the highest diversity indices when using generic or family richness.

According to the diversity estimates based on rarefaction curves using species-data, L 114 is the most diverse assemblage, followed by TF 102 and 110, and Banyunganti has the lowest diversity (Fig. 4). The assemblage from the coral carpet environment TF 102 is slightly more diverse than the contemporaneous seagrass-associated assemblage TF 110.

The seagrass-associated assemblage from the middle Miocene of Karaman, Turkey is included to provide a preliminary comparison of biodiversity between the Miocene Indo-Pacific and the Miocene of the Paratethys. The Karaman sample has a lower diversity than the Indonesian assemblages according to diversity indices as well as according to rarefaction curves (Tab. 2, Fig. 4A).

The rarefaction curves for species level taxa clearly show undersampling for all assemblages (Fig 4A). When using generic and family-taxa the curve for the largest sample (TF 110) seems to approach an asymptote in each case at around 8000 specimens. In addition, the curve for sample TF 102 using family-level taxa appears to level off at <2000 specimens (Fig. 4B-C).

Table 2: Mollusk abundance and diversity indices of all samples, including indication of age and paleoenvironment.

Sample	**Age**	**Paleoenvironment**
BA 18	early Miocene (early Burdigalian)	seagrass meadow
L 114	middle Miocene	seagrass meadow
TF 110	late Miocene (early Tortonian)	seagrass meadow
TF 102	late Miocene (early Tortonian)	coral carpet
Karaman	middle Miocene	seagrass meadow

Sample	**Number of specimens**	**Species richness**	**Dominance D**	**Simpson 1-D**	**Shannon index H**
BA 18	4444	185	0.13	0.87	3.06
L 114	1410	188	0.14	0.86	3.41
TF 110	8212	272	0.03	0.97	4.07
TF 102	1468	162	0.03	0.97	4.10
Karaman	1744	96	0.28	0.72	2.21
		Generic richness	**Dominance D**	**Simpson 1-D**	**Shannon index H**
BA 18		123	0.13	0.87	2.89
L 114		132	0.14	0.86	3.22
TF 110		154	0.05	0.95	3.56
TF 102		108	0.04	0.96	3.74
		Family richness	**Dominance D**	**Simpson 1-D**	**Shannon index H**
BA 18		70	0.16	0.84	2.60
L 114		65	0.15	0.85	2.85
TF 110		86	0.09	0.91	3.08
TF 102		73	0.05	0.95	3.45

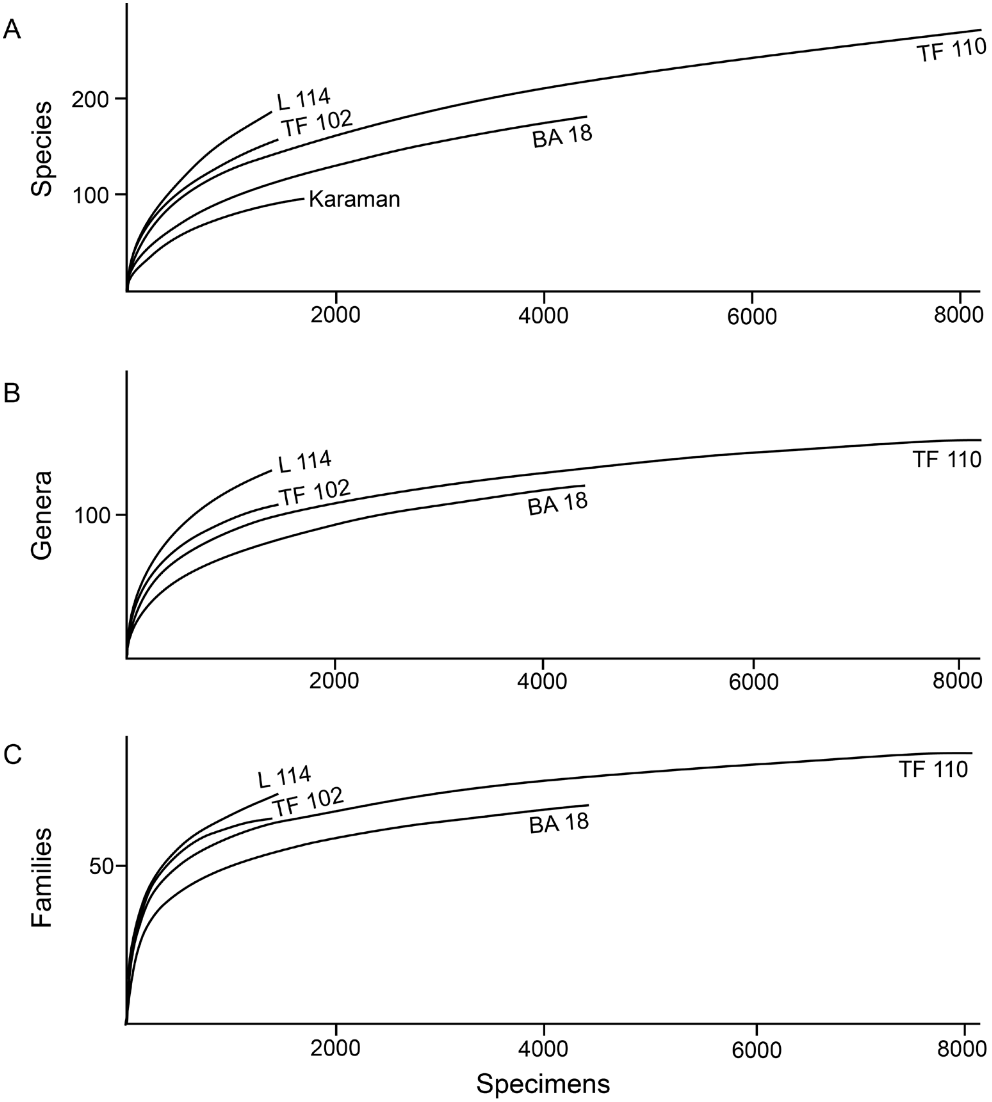

Figure 4: Rarefaction curves of three Miocene seagrass-associated mollusk assemblages (BA 18, early Miocene; L 114, middle Miocene; and TF 110, late Miocene) and one coral carpet assemblage (TF 102, late Miocene). A) Based on species abundance; a middle Miocene parathetyan assemblage is additionally included. B) Based on generic abundance. C) Based on family abundance.

5. **Discussion**

5.1 Size of Assemblages and Level of Taxonomic Identifications

The size of the studied assemblages appears large in terms of both specimen numbers per sample (> 1400 per sample) and in terms of taxonomic richness (for instance compared to the assemblage from Karaman, see 4.3), but the sampled horizons are still severely undersampled as indicated by rarefaction curves. Furthermore, the assemblages include high numbers of previously unknown taxa. The sorting, counting and the taxonomic identification of such assemblages, especially, are very time consuming (see also Chapter 3). Due to the major effort required to assemble the data, the number of samples suitable for the present study is limited to four, including one pre-sorted and pre-identified museum collection. However, the effort might be reduced in some ways depending on the aim of the individual study performed. The use of open nomenclature is recommended, because full taxonomic revisions of assemblages like the ones presented here would require at least several years of work and very detailed knowledge of the taxonomy of numerous mollusk groups. Although we hope the material will be at least partly revised and described in the future, for studies on paleoecology and biodiversity of assemblages in space and time the effort of full revisions is not advisable given the huge richness of the assemblages.

We compared the results based on species, genus and family data. Analysis at a range of taxonomic hierarchical levels did not lead to changes in the overall pattern of sample dissimilarity displayed by Bray-Curtis distance measure and NMDS, but trends displayed along axes of NMDS plots do differ according to the taxonomic level of identification (Fig. 3). Biodiversity indices and rarefaction curves remained similar when using different levels of taxonomic identifications; only subtle differences occur. Family level identifications appear adequate when dealing with general questions about the composition of highly diverse assemblages, but one should be aware of the possibility that the use of species data may lead to different results, such as the greater difference in diversity expressed by indices between the assemblages TF 102 and TF 110 when using generic or family data, whereas an opposite effect is seen in rarefaction curves. Furthermore, the relatively closer distance between the contemporaneous samples TF 102 and TF 110 along axis 1 of the NMDS based on species composition was not displayed by NMDS results based on generic or family composition, but is evident from all Bray-Curtis distance measures (Tab. 1).

5.2 Variation in Species Composition

Species composition among samples varies remarkably, even in the contemporaneous assemblages TF 110 and TF 102 that derive from geographically proximate localities, but that represent slightly different paleoenvironments. In addition, several species that were found in two or more samples represent species complexes that likely comprise more than one species, but shell characters were too few for a reliable separation of species. This large variation implies that species turnover in many higher mollusk taxa may have occurred on short time-scales in the Miocene of the South-West Pacific, in contrast to the long species durations inferred for the gastropod family Tonnoidae in that region (Beu, 2005)

It can be concluded that the taxonomic composition of mollusk assemblages from seagrass meadows derived from different time intervals does not yield a characteristic seagrass signal unlike that in modern assemblages from San Salvador, Bahamas (Chapters 1 and 4; see also 5.4, this Chapter). In addition, it cannot be excluded that the dissimilarity between sample L 114 and the other samples is partly due to differences in the applied collecting method and/or post-collection treatment, because the former sample is an historical museum collection and applied sampling methods are unknown (see also 5.3).

5.3 Collection and Post-Collection Treatment and Impact on Measures of Biodiversity

From the rarefaction curves it appears that the historical collection from L 114 (Mangaklihat, middle Miocene) is most diverse. However, this is not supported by diversity indices. On one hand we may expect differences in the results of biodiversity analyses when applying different methods, because of the differing assumptions they make (e.g., Nagendra, 2002; Purvis and Hector, 2000). On the other hand, this contradiction may be a result of different sample collection and post-collection treatment of L 114 compared to that of the other samples. We doubt that for this historical collection standardized sampling as for our own collections was applied. Possibly comparatively large and therefore distinct specimens of the most common species (*Strombus preoccupatus* sensu Beets, 1941) were collected from float and added to the collection. Furthermore, fragmented material, especially of medium-sized and small mollusks, was possibly removed and could therefore not be counted. This could result in lower specimen numbers per taxon and therefore in a steeper rarefaction curve. Because the analyses of all other assemblages do not show differing results when applying different diversity measures, the latter case seems more likely. Such a bias might occur commonly in historical collections.

5.4 Biodiversity and Paleoecolgy

Considering the unknown sampling method applied for collection at L 114 and the resulting potential biases (5.2-5.3), the assemblage cannot be used for a reliable reconstruction of biodiversity over time. This is also shown by the different levels of diversity displayed for this assemblage by biodiversity indices versus rarefaction curves. When removing the assemblage from the data set only two time intervals, the early Burdigalian (early Miocene) and the early Tortonian (late Miocene) are represented. A literal comparison may suggest an increase in seagrass-associated molluscan diversity from the early to the late Miocene, however the number of data points is clearly insufficient for further speculation.

In Chapter 3 the early Miocene seagrass assemblage from Banyunganti was compared to the late Miocene coral carpet assemblage from TF 102, leading to the question to what extent the observed difference in diversity results from a variation in time or paleohabitat. Here a seagrass-associated assemblage contemporaneous with TF 102 was included. The two assemblages TF 102 and TF 110 are both more diverse than

Banyunganti and very similar to each other with the coral carpet assemblage being slightly more diverse than the seagrass-associated assemblage. To minimize the effect of differing biodiversity in contemporaneous assemblages from different habitats it was advised to compare assemblages from the same paleohabitat when aiming for biodiversity reconstructions over time (Chapter 3). Although regional diversity and macroecological patterns in deep time could emerge even from analyses without detailed identification of facies, the amount of data needed for this analysis is not given for the present study (Jackson et al., 1999; Johnson et al., 2007; Todd et al., 2002). In addition, also for the seagrass-associated assemblages from different time intervals it is still not possible to rule out differences in species composition and diversity based on environmental factors (Vermeij and Leighton, 2003). Seagrass meadows are influenced by many factors, such as depth, substrate, seagrass species composition, and seagrass density (e.g., Hemminga and Duarte, 2000). Such factors are difficult or even impossible to reliably reconstruct for past environments. The very few samples available also ruled out a comparison of within-habitat variation. Some speculations on the different environmental factors affecting the seagrass habitats of Banyunganti and TF 110 can be made based on the sedimentology, accompanying foraminifera, and the presence or absence of specific mollusk groups in the assemblages.

Depth and sediment. Depth and lithology of sediments are two primary controlling factors that affect the composition of benthic mollusk assemblages in tropical level-bottom settings (Bergen et al., 2001; Jayaraj et al., 2008, and references therein). The depositional depth of sample BA 18 was inferred to range somewhere between 5 and 20 m (Chapter 2), whereas foraminifera present at TF 110 point to a possibly shallower paleoenvironment of 2 to 10 m (W. Renema, unpublished data). The sediments present at the sampling localities, fine to medium-grained sand at Banyunganti versus silty clay at TF 110, indicate a higher input of fine grained terrestrial material into the latter system, or a denser vegetation cover that decreased the chance of re-suspension of fine-grained material at TF 110. Sediments at the nearby coral carpet locality TF 102 are fine-grained as well. High amount of terrigenous input was assumed for this environment, also based on its coral assemblage (Chapter 3). Therefore, it is likely that the amount of fine-grained material deposited in the habitat was indeed higher in the late Miocene of Bontang than in the early Miocene of Banyunganti. The sediments at L 114 were described as slightly sandy clay, the depositional depth has not been estimated.

Table 3: Abundance and species richness of two functional bivalve groups and gastropods of all assemblages, * Gastropoda indet. spp. excluded.

Sample	Epifaunal bivalves			Infaunal bivalves			Gastropods		
	Number of epifaunal bivalves	%	Species richness	Number of infaunal bivales	%	Species richness	Number of gastropods	%	Species richness *
Banyunganti	3	<1	3	329	7	19	4101	93	159
L 114	60	4	16	31	2	13	1316	94	156
TF 110	179	2	19	295	4	29	7703	94	215
TF 102	243	17	17	78	5	23	1146	78	120

Deposit-feeding. Studies on paleo-seagrass meadows in the Caribbean indicate a shift from deeper seagrass habitats towards shallower environments with an increase of the abundance of deposit-feeders such as tellinid bivalves in the Plio/Pleistocene (Domning, 2001; Leonard-Pingel, 2012). Tellinids are represented by more than 100 specimens at TF 110 (22% of the bivalve fauna), whereas they occur only with 3-7 individuals (2-3% of the bivalve fauna) at other localities. Likewise deposit-feeding Nuculidae are very abundant at TF 110 (67 specimens, 14%), but they are comparatively rare at L 114 (7 specimens, 8%) and absent at Banyunganti. Nuculidae occur rarely in a seagrass-associated bivalve assemblage from the Burdigalian (early Miocene) of Kerala, India (Reuter et al., 2010), whereas Tellinidae are absent in that assemblage, however quantitative data was not available (O. Mandic, pers. comm., 2014). From this very limited data, it remains unclear if this represents a shift of environmental characteristics of seagrass habitats from the early to the late Miocene in the Indo-Pacific, comparable to that observed later in the southwest Caribbean, or if it is just a chance occurrence due to the sampling of differing environments that were all present throughout the Miocene. In the latter case, grain-size may have been a controlling factor, because deposit-feeders such as Nuculidae often occur preferably in settings with fine-grained sediments (Beesley et al., 1998) which is the case for locality TF 110. It also has to be noted that chemosymbiotic deposit-feeders (lucinid bivalves) are more abundant at Banyunganti (76 specimens, 23%) than at TF 110 (3 specimens, < 1%) or L 114 (2 specimens, 2%). Probably conditions for chemosymbiont-bearing taxa were not ideal in the latter two environments. This could be due to a limited supply of reduced sulfur in the sediment. The comparatively enriched carbon isotope ratios detected in lucinid shells from TF 110 indicate that they may have switched to deposit-feeding, supporting the assumption of limited availability of reduced sulfur in the environment (Chapter 5).

Infaunal bivalves and vegetation cover. The abundance of infaunal bivalves compared to epifaunal taxa, including gastropods, may provide an indication of seagrass density. High gastropod/bivalve rations were assumed to be characteristic of seagrass meadows, because a dense rhizome mat may inhibit the establishment of infauna (Cummins et al., 1995, Davies, 1970; James and Bone, 2007). Although it was concluded that high gastropod/bivalve ratios are not conclusive for identifying or characterizing seagrass meadows, they may still provide a useful tool to indicate the density of the vegetation cover (Chapter 1). The counting method for gastropods applied in this study for the assemblages from Banyunganti and TF 110 will skew the data towards gastropods, because fragmented individuals were possibly counted more than once, whereas the number of bivalves is more likely to reflect the true number of specimens present in the assemblage. Due to the likely removal of fragmented material from the museum collection L 114 this issue is solved for that assemblage, but here the inclusion of float-collected material may have altered the original assemblage composition. For those reasons a numerical comparison of gastropod/bivalve abundances would not lead to reliable results. However, in all samples, abundance as well as species richness is much lower for infaunal bivalves than for gastropods. In addition, the coral-carpet environment has the lowest gastropod abundance (78%), whereas all seagrass associated faunas have a gastropod abundance of at least 93% (Tab. 3).

*Epifaunal bivalve*s. Epifaunal bivalves, that commonly occur in modern seagrass meadows (Chapter 1; Mikkelsen et al., 1995), are very rare at Banyunganti (Tab. 3). Only three epifaunal singletons were found in the assemblage. In contrast, 35% of the bivalve fauna from TF 110 is represented by epifaunal taxa, mainly by the most abundant ostreid bivalve *Dendostrea* (125 specimens, 26% of the bivalve fauna). That taxon likely indicates the presence of gorgonians (sea whips, sea fans) in the environment, and is also the most abundant bivalve in the coral carpet habitat TF 102 (Chapter 3; Forbes, 1971). Oysters are entirely absent at Banyunganti. Another group of epifaunal bivalves that is common in modern seagrass meadows is the family

Arcidae (Chapter 1; Mikkelsen et al., 1995). This is also the most abundant and species-rich bivalve family at L 114 (43% abundance; 12 species), and is likewise present at TF 110 (3% abundance, 6 species), but is entirely absent at Banyunganti. It remains unresolved why epifaunal bivalves are so rare at this early Miocene locality, and if this reflects habitat specific conditions (e.g., limited supply of suspended particles in the water column) or a trend over time. Epifaunal taxa seem to occur more abundantly in a seagrass-associated bivalve assemblage from the early Burdigalian of Kerala, India (Reuter et al., 2010) than at Banyunganti, but are much less abundant than infaunal bivalves in that assemblage, however no quantitative data is available (O. Mandic, pers. comm., 2014).

5.5 Feeding Ecology as Paleoenvironmental Indicator

The feeding guild composition of mollusk assemblages based on both abundance data and species richness is considered to be a suggestive indicator of paleo-seagrass meadows (IPSI: Chapter 1) based on data from Banyunganti, TF 102, and a modern assemblage from Spain (Chapters 1 and 3). In particular, seagrass-associated assemblages are typified by a high abundance of herbivorous/detrivorous gastropods and a high species richness of predatory gastropods, a pattern that leads to a distinct increase of the proportion of the herbivore/detritivore guild based on abundances when compared to the feeding guild composition based on species richness. In contrast, the coral carpet assemblage from TF 102 displays a similar feeding guild composition when comparing abundance to species richness data, with predatory gastropods being the most species-rich but also the most abundant feeding guild (Chapters 1 and 3).

Additionally, it was suggested that feeding guild composition should be based only on the abundance and species richness of gastropods, because the composition of bivalve assemblages may vary considerably among different seagrass environments (Chapter 1).

Overall feeding guild composition is most similar between assemblages from Banyunganti and L 114. The latter also agrees well with the feeding guild composition of a modern seagrass-associated assemblage from Spain (Rueda et al., 2009a), displaying the pattern suggested to be typical for seagrass associations (Chapter 1). However, as for species composition, the data set of L 114 is not reliable (see 5.2), although the high abundance of one herbivorous gastropod (*Strombus preoccupatus* sensu Beets, 1941), presumably due to the addition of float-collected specimens, might have reduced the effect of the overall comparatively low abundance of small herbivores, presumably due to small bulk sample size and/or removal of fragmented material.

The composition of the assemblage from TF 110 is intermediate between the composition of assemblages from Banyunganti (seagrass) and TF 102 (coral carpet) with predatory gastropods being almost as abundant as herbivores/detritivores (Fig. 4A). The carbon isotope composition of mollusk shells supported the identification of the assemblage from TF 110 as a seagrass-associated assemblage, because it displayed a similar isotopic signature as shells from other seagrass localities such as Banyunganti, whereas the carbon isotopic signature of a mixed seagrass-coral habitat was significantly lower (Chapter 5). Probably corals were more common in the environment of TF 110 than at Banyunganti. This assumption can be supported by the observed, although not numerically determined, higher abundance of coral remains at TF 110. The high abundance of the seagrass-feeding gastropod *Smaragdia* at TF 110 (210 specimens, 2.6%) still indicates a significant seagrass component, because the genus is a highly suggestive IPSI (Chapter 1).

The use of a distinct feeding-guild composition as an indicator for paleo-seagrass environments seems to be less generally applicable than previously assumed, because it shows more variation among seagrass associated assemblages, even within the same region. However, it is still possible that a ‘typical’ feeding guild composition, as previously recognized, provides evidence of seagrass meadows when present, although it may not typify all seagrass environments.

5.6 Time-averaging, Transport and Taphonomy

As for modern death assemblages sampled at San Salvador, Bahamas (Chapter 4), we do not have direct data on the time span represented by each investigated sample or on the influence of time-averaging (*sensu* Kowalewski, 1996). Comparisons of life and death assemblages from seagrass environments reflect differences in species composition and abundance (Albano and Sabelli, 2011; Deehr et al., 2001), indicating that time-averaging plays an important role in shaping these assemblages. Species composition of seagrass-associated assemblages varies on annual cycles, for instance reflecting reproductive cycles of organisms (e.g., Baron et al., 1993; Rueda et al., 2008), and it is unknown how many such cycles are captured by our fossil samples. Furthermore, the abundance of small herbivorous species might be relatively higher in fossil assemblages than in the original living assemblage as a result of differing life spans of herbivorous versus carnivorous gastropod taxa. Shorter life spans of small-sized herbivores, at least, compared to carnivores might result in the accumulation of herbivore's shells in fossil assemblages (Chapter 2; Albano and Sabelli, 2011; Cadée, 1968).

It is likely that our samples represent largely autochthonous assemblages. In general, out-of habitat transport is rare for mollusk shells, especially in flat-bottomed settings, and it is therefore likely that our assemblages reflect the original ecological signal (Chapters 1, 3 and 5; Kidwell and Bosence, 1991; Kidwell and Flessa, 1996). When transport occurs, it usually takes place over short distances of less than 50 m (Miller and Cummins, 1990). Other studies concluded that little transport is likely to occur between seagrass meadows and adjacent unvegetated areas because of the trapping effect of seagrasses (Albano and Sabelli, 2011; Miller, 1988; Scoffin, 1970). No to little transport of shells was previously concluded for the mollusk assemblage from Banyunganti (Chapter 2).

Taphonomic signature may serve as additional character allowing identification of seagrass-associated shells (weak IPSI: Chapter 1; Chapter 4; Leonard-Pingel, 2005). A quantitative assessment of taphonomic signatures of shells was beyond the scope of this study, but a few qualitative observations indicate an increased potential for preservation of seagrass-associated assemblages in the Miocene of Indonesia. This includes the excellent preservation of shell ornamentation, the preservation of shell colour patterns, and the presence of two in-situ opercula (Chapter 2). However, fragmentation rates are comparatively high in our samples. That is likely a result of in-habitat biotic interactions, sediment compaction, and/or collecting and post-collecting effects, because shell edges are not abraded (Chapter 2; Stanton, 1980). The number of gastropods that could not be identified due to poor preservation was applied as an indicator for taphonomic alteration for seagrass-associated assemblages and assemblages from unvegetated sandflats at San Salvador, Bahamas, showing that seagrass-associated shells were generally better preserved (Chapter 4; Buchan and Lewis, 2008). Likewise in this study unidentified gastropods are most abundant at the coral carpet locality TF 102 where they make up about 8% of the proportional abundance of all mollusks, whereas they represent less than 1% of proportional mollusk abundance at seagrass sites.

6. Conclusions and Suggestions for Future Research

1. The effort of sampling and taxonomic identification of highly diverse shallow marine mollusk assemblages is huge. It might be reducible to some extent by using higher levels of taxonomic identifications such as generic or family level instead of species level. This study shows that results of analysis of taxonomic composition as well as biodiversity estimates did generally not differ among analyses using different taxonomic levels. Therefore, further studies on this topic are highly recommended and may enable us to more rapid estimates of (paleo)-biodiversity by working at higher taxonomic levels.

2. Quantitative analysis of historical museum collections has to be regarded with caution, when parameters such as sampling method (e.g., bulk sampling and collection from float) and sorting method (e.g., removal of fragmented material or small individuals) are unknown.

3. Shallow marine mollusk assemblages from the Miocene of Indonesia are characterized by high species richness and evenness, and a numerical dominance of gastropods, especially in seagrass-associated assemblages.

4. Diversity of Miocene seagrass-associated assemblages is higher than that of a comparable assemblage from the middle Miocene of the Paratethys.

5. Species composition differs significantly among seagrass-associated assemblages from different time intervals and a coral carpet assemblage, contemporaneous with one of the seagrass-associated assemblages, and is therefore neither indicative for a time interval nor for a paleohabitat.

6. Variation of the feeding guild composition of gastropod and whole mollusk assemblages from seagrass meadows is higher than expected based on our previous works (Chapters 1 and 3). However, the general signal of highest abundance of herbivores/detritivores compared to highest species richness of carnivores remains the same. Our results did not vary considerably between comparisons based on mollusk assemblages and comparisons based on gastropods only. More comparative studies are needed.

7. Environmental factors that may additionally control for differences among seagrass habitats are often impossible to reliably reconstruct, but can influence numerical assessments such as biodiversity calculations. Only further studies including present-day assemblages can potentially assess the influence of environmental variability among seagrass meadows on the composition of associated assemblages.

8. Possibly the composition of seagrass-associated bivalve assemblages changed over time during the Miocene of the Indo-Pacific, resulting in an increase of the abundance of deposit-feeders (e.g., Tellinidae, Nuculidae) and the abundance of epifaunal taxa (e.g., Pectinidae, Ostreidae). This needs to be further investigated in future studies and tested with considerably more data.

9. The present study supports an assumption that seagrass-associated shells have an increased preservation potential compared to those from other neighboring shallow water tropical environments. However, a quantitative assessment of taphonomic characteristics is still pending.

10. It is highly recommended to continue the present research with the inclusion of more samples from other Miocene and also younger time intervals, such as Pliocene, Pleistocene and modern assemblages. It is expected that this will produce; more robust patterns of biodiversity change in space and time, including within the IWP biodiversity hotspot, the usefulness of feeding ecology as a paleoenvironmental indicator, estimated rates of taxonomic and ecological turn-over, and the effect

of differing environmental conditions in seagrass meadows on the taxonomic composition and biodiversity of associated assemblages.

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Supplementary

Material

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Chapter 3

Appendix 3.1: List of all taxa from surface collected and bulk samples with feeding guild assignments (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Chapter 4

Appendix 4.1: List of all taxa from unvegetated sandflats with assignment to feeding guild (FG) and proportional abundance per sample. $N_{specimens}$ = 200 except sample GB_A.2 with $N_{specimens}$ = 90. Feeding guilds: 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder.

Appendix 4.2: List of all taxa from seagrass-vegetated sandflats with proportional abundance per sample. $N_{specimens}$ = 200. See Appendix 4.1 for assignments to feeding guilds.

Chapter 5

Appendix 5.1: List of all samples, assigned to taxon and feeding guild (FG), and ^{13}C V-PDB and ^{18}O V-PDB values, including the lab where the sample was analyzed (RH = Royal Hollow University, London; UU = Utrecht University). Feeding guilds: 1 = herbivore, 2 = seagrass feeder, 3 = predator on invertebrates, 4 = predator on foraminifera, 5 = browsing carnivore, 6 = infaunal suspension feeder, 7 = infaunal deposit feeder, 8 = chemosymbiotic deposit feeder.

Appendix 5.2: δ^{13}C and δ^{18}O ratios of roasted versus unroasted samples, including figure: linear correlation of roasted versus unroasted samples.

Chapter 6

Appendix 6.1: List of species that deviate from originally published name.

Appendix 6.2: List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Appendix 6.3: Shared species of all assemblages.

Appendix 3.1: List of all taxa from surface collected and bulk samples with feeding guild assignments (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Taxon	**FG**	**SR45**	**SR46**	**SR47**
Diodora sp. 1	1	0	0	0
Gibbula leupoldi Beets, 1941	1	1	0	0
?*Gibbula* sp. 1	1	0	0	0
Stomatolina sp. 2	1	0	0	0
Trochidae indet. sp. 1	1	0	0	0
Turbo s.l. operculum	1	0	1	0
Angaria aff. *spaerula* (Kiener, 1873) sensu Beets, 1941	1	0	0	0
Bothropoma sp. 1	1	0	0	0
Smaragdia semari Beets, 1941	1	0	0	0
Cerithium nodulosum Bruguière, 1792 sensu Beets, 1984	1	0	0	1
Cerithium sp. 3	1	1	1	0
Cerithium sp. 7	1	2	0	0
Cerithium sp. 8	1	2	0	0
Colina sp. 1	1	2	2	0
Rhinoclavis sp. 1 s.l.	1	1	3	0
Diala semistriata s.l. (Philippi, 1849)	1	0	0	0
Modulus praeangerensis Martin, 1905	1	1	0	0
?Potamididae indet. sp. 1	1	0	0	0
Finella sp. 3	1	0	0	0
Ampullina s.l. sp. 2	1	0	0	0
Ampullospira sp. 1	1	0	0	0
Ampullospira sp. 2	1	1	0	0
Ampullospira sp. 4	1	0	0	0
Plesiotrochus sp. 6	1	1	2	0
?*Capulus* sp. 2	4	0	0	0
Eatoniella s.l. sp. 3	1	0	0	0
Cypraeidae indet. sp. 3	1	0	0	0
Natica spadicea (Gmelin, 1791) sensu Beets, 1941	2	7	6	2
Rissoina (*Rissoina*) sp. 3	1	0	1	0
Rissoina (*Phosinella*) sp. 2	1	0	0	0
Rissoina indet.	1	0	0	0
Rissolina sp. 2	1	0	0	0
Cyclostremiscus novemcarinatus (Melvill, 1906) sensu Beets, 1986	1	0	0	0

SR48	SR49	SR50	SR51	SR52	SR53	SR54	Total bulk samples	Total all samples
0	0	2	2	1	2	2	9	9
0	0	5	2	2	11	4	24	25
0	0	0	1	0	2	0	3	3
0	0	0	0	0	1	0	1	1
0	0	0	1	0	0	0	1	1
0	0	0	0	0	0	0	0	1
0	0	0	0	1	0	0	1	1
0	0	1	0	0	0	0	1	1
0	0	6	1	2	5	1	15	15
0	0	0	0	0	0	0	0	1
1	0	3	2	0	13	7	25	28
0	0	24	21	4	48	10	107	109
0	0	0	0	0	0	0	0	2
1	0	7	5	2	0	0	14	19
0	0	0	0	0	0	1	1	5
0	0	2	4	1	10	9	26	26
0	0	0	0	0	4	1	5	6
0	0	0	2	0	0	0	2	2
0	0	1	0	0	0	0	1	1
0	0	1	0	0	0	0	1	1
0	0	2	2	0	1	0	5	5
0	1	3	0	0	2	1	6	8
0	1	0	0	0	0	0	0	1
3	0	14	13	1	18	8	54	60
0	0	0	0	0	0	1	1	1
0	0	1	0	0	0	0	1	1
1	0	0	0	0	0	0	0	1
0	1	2	4	0	4	8	18	34
0	0	0	0	0	0	0	0	1
0	0	5	2	0	8	2	17	17
0	0	0	0	0	0	1	1	1
0	0	3	1	1	4	0	9	9
0	0	0	0	0	0	1	1	1

Appendix 3.1 (continued): List of all taxa from surface collected and bulk samples with feeding guild assignments (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Taxon	**FG**	**SR45**	**SR46**	**SR47**
Varicospira sp. 1	1	0	2	0
Canarium unifasciatum s.l. (Martin, 1884)	1	1	4	1
Strombus s.l. sp. 2	1	5	1	0
Strombus s.l. sp. 3	1	0	1	2
Strombus s.l. sp. 4	1	0	1	1
Terebellum sp.	1	0	0	0
Cymatium (*Turritriton*) cf. *tenuiliratum* (Lischke, 1873)	2	0	0	0
Cymatium (*Reticutriton*) sp. 1	2	0	0	0
Gyrineum lacunatum (Mighels, 1845)	2	1	1	0
Ranellidae indet. sp. 2	2	0	0	0
Eratoena sp. 1	3	1	0	0
Epitonium sp. 3	3	0	0	0
Triphora s.l. sp. 3/*Triphora* indet. [Beets]	3	0	0	0
Seila sp. 1	3	0	0	0
?Buccinidae indet. sp. 1	2	1	0	0
Euplica sp. 1	2	5	4	0
Mitrella s.l. cf. *gembacana* (Martin, 1921)	2	1	1	0
Mitrella s.l. aff. *njalindungensis* sensu (Beets, 1941) non (Martin, 1921)	2	0	0	0
Zafra sp. 1	2	0	0	0
Mitrella s.l. sp. 1	2	0	0	0
Mitrella s.l. sp. 2	2	0	0	0
Mitrella s.l. sp. 3	2	0	0	0
?*Mitrella* s.l. sp. 4	2	0	0	0
?*Pyreneola* sp. 1	2	0	0	0
Fasciolaria sp. 1	2	1	0	0
Peristernia beberiana sensu Beets, 1941 non Martin, 1921	2	3	1	0
Nassarius sp. 2	2	1	3	0
Nassarius sp. 3	2	4	1	0
Nassarius sp. 4	2	0	2	0
Nassarius sp. 5	2	0	0	0
Melongena sp. 1	2	0	1	0
Melongena sp. 2	2	1	2	0
Chicoreus sp. 1	2	2	2	0

SR48	SR49	SR50	SR51	SR52	SR53	SR54	Total bulk samples	Total all samples
0	0	0	0	0	1	0	1	3
0	0	14	3	1	7	8	33	39
0	0	0	0	0	1	2	3	9
2	0	0	0	0	0	1	1	6
2	0	2	0	0	0	0	2	6
0	0	1	1	0	0	1	3	3
0	0	0	1	0	0	0	1	1
0	0	0	0	1	0	0	1	1
0	0	0	0	0	0	0	0	2
0	0	1	0	0	0	0	1	1
0	0	0	0	0	0	1	1	2
0	0	0	0	0	0	1	1	1
0	0	3	2	2	5	3	15	15
0	0	1	0	0	1	0	2	2
0	0	1	1	0	1	0	3	4
0	0	1	0	0	4	0	5	14
2	0	4	1	1	5	6	17	21
0	0	2	1	1	4	2	10	10
0	0	14	10	2	23	10	59	59
0	0	2	0	0	2	0	4	4
0	0	0	0	0	1	0	1	1
0	0	0	0	0	0	1	1	1
0	0	0	0	0	0	1	1	1
0	0	1	0	0	0	0	1	1
0	0	0	0	0	0	0	0	1
1	1	2	0	1	7	1	11	17
2	0	19	9	7	13	7	55	61
0	0	7	5	2	16	1	31	36
0	1	0	0	0	2	0	2	5
0	0	7	4	1	19	4	35	35
1	1	0	0	1	0	0	1	4
0	0	0	0	0	0	0	0	3
0	0	0	2	0	4	0	6	10

Appendix 3.1 (continued): List of all taxa from surface collected and bulk samples with feeding guild assignments (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Taxon	**FG**	**SR45**	**SR46**	**SR47**
Chicoreus sp. 2	2	0	0	0
Coralliophila aff. *clathrata* (A. Adams, 1854)	3	15	6	1
Coralliophila sp. 2	3	1	1	0
Coralliophila sp. 3	3	1	3	1
?Muricidae indet. sp. 1	2	2	0	0
Vexillum sp. 9	2	2	3	0
Vexillum sp. 10	2	1	0	0
Vexillum sp. 11	2	1	0	0
Vexillum sp. 12	2	0	1	0
Vexillum sp. 13	2	0	0	0
Vexillum sp. 14	2	0	0	0
Vexillum sp. 15	2	0	0	0
Vexillum sp. 16	2	0	0	0
Vexillum sp. 17	2	0	0	0
Costellariidae indet. spp.	2	0	0	0
Cysticsus sp. 3	3	0	0	0
Granulina menkrawitensis (Beets, 1986)	3	0	0	0
Granulina sp. 2	3	0	0	0
Cryptospira sp. 1	3	4	5	0
Cryptospira sp. 2	3	1	0	0
Dentimargo sp. 1 sl.	3	0	0	0
Volvarina sp. 3	3	0	1	0
Marginellidae indet.	3	0	0	0
Mitra bayeri Beets, 1941	2	0	0	0
Mitra sp. 1	2	1	1	0
Mitra sp. 2	2	0	1	0
Mitra sp. 3	2	0	1	0
Mitra sp. 4	2	0	0	0
Mitra sp. 5	2	0	0	0
Oliva sp. 2	2	0	2	0
Olividae indet.	2	1	0	0
Oliviella sp. 2	2	0	0	0
Dendroconus odengensis s.l. (Martin, 1895)	2	4	0	0

SR48	SR49	SR50	SR51	SR52	SR53	SR54	Total bulk samples	Total all samples
0	0	1	0	0	0	0	1	1
0	0	3	3	2	7	1	16	38
0	0	2	0	0	0	0	2	4
0	0	5	1	0	1	3	10	15
0	0	0	0	0	2	0	2	4
2	0	4	1	1	8	2	16	23
0	0	0	0	0	0	0	0	1
0	0	5	6	1	5	4	21	22
1	0	4	5	0	0	0	9	11
3	0	0	0	0	0	0	0	3
0	0	4	0	1	5	1	11	11
0	0	1	0	0	0	0	1	1
0	0	0	1	0	0	0	1	1
0	0	0	0	0	1	0	1	1
0	0	0	0	0	11	0	11	11
0	0	2	0	0	9	0	11	11
0	0	0	0	0	0	1	1	1
0	0	0	0	0	1	0	1	1
0	3	3	0	0	2	0	5	17
0	0	1	0	0	0	0	1	2
0	0	4	6	1	7	5	23	23
0	0	0	0	0	0	0	0	1
0	0	0	2	1	0	0	3	3
1	0	0	0	0	0	0	0	1
0	0	0	0	0	1	1	2	4
0	0	2	0	0	0	0	2	3
0	0	0	0	0	0	0	0	1
0	0	0	1	0	0	0	1	1
0	0	0	0	0	1	0	1	1
0	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	1
0	0	3	0	0	3	2	8	8
1	0	0	1	0	1	0	2	7

Appendix 3.1 (continued): List of all taxa from surface collected and bulk samples with feeding guild assignments (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Taxon	**FG**	**SR45**	**SR46**	**SR47**
Rolaniconus tjilonganensis (Martin, 1906)	2	0	0	0
Conidae indet. sp. 3	2	2	2	0
Conidae indet. sp. 4	2	1	2	0
Conidae indet. sp. 5	2	0	3	0
Conidae indet. sp. 6	2	0	0	0
Conidae indet.	2	0	0	2
Tomopleura sp. 1	2	0	0	0
Lienardia sp. 2	2	0	0	0
Clathurellidae indet. sp. 1	2	0	0	0
Clathurellidae indet. sp. 2	2	0	0	0
Eucithara sp. 5	2	0	0	0
Eucithara sp. 6	2	0	0	0
Eucithara sp. 7	2	0	0	0
Raphitomidae indet. sp. 3	2	0	0	0
Raphitomidae indet. sp. 4	2	0	0	0
Raphitomidae indet. sp. 5	2	0	0	0
Iredalea sp. 1	2	0	0	0
?*Iredalea* sp. 2	2	0	0	0
Tylotiella sp. 2	2	0	1	0
Drilliidae indet. sp. 2	2	0	0	0
Crassispira sp. 2	2	1	0	0
Pseudomelatomidae indet. sp. 4	2	0	0	0
Pseudomelatomidae indet. sp. 5	2	0	0	0
Pseudomelatomidae indet. sp. 6	2	0	0	0
Strictispira sp. 2	2	3	3	0
Strictispira sp. 3	2	1	0	0
'Lophiotoma' sp. 1	2	5	8	0
'Lophiotoma' sp. 2	2	1	0	0
Terebra s.l. sp. 2	2	1	0	0
Terebra s.l. sp. 3	2	1	0	0
Pupa sp. 1	2	0	0	0
Pupa sp. 2	2	0	0	0
Adelphotectonica karikalensis (Cossmann, 1910) sensu (Beets, 1941)	3	0	0	0

SR48	SR49	SR50	SR51	SR52	SR53	SR54	Total bulk samples	Total all samples
1	1	0	0	0	0	0	0	2
0	0	2	1	0	2	0	5	9
0	0	1	0	0	3	0	4	7
0	0	3	0	0	0	0	3	6
0	0	1	0	0	0	0	1	1
0	0	0	0	0	0	0	0	2
0	0	1	0	0	0	0	1	1
0	0	1	0	0	0	3	4	4
0	0	1	1	0	2	0	4	4
0	0	1	0	0	1	1	3	3
0	0	2	1	1	5	3	12	12
0	0	4	1	2	4	2	13	13
0	0	0	0	0	1	0	1	1
0	0	1	0	0	1	0	2	2
0	0	0	2	0	0	0	2	2
0	0	0	0	1	0	1	2	2
0	0	2	8	5	12	11	38	38
0	0	1	0	0	0	0	1	1
1	0	0	0	0	3	1	4	6
0	0	0	0	0	0	2	2	2
0	0	0	0	0	0	0	0	1
0	0	0	1	0	0	0	1	1
0	0	0	0	0	0	1	1	1
0	0	0	0	0	0	1	1	1
0	1	2	0	2	2	2	8	15
0	0	0	0	0	1	0	1	1
7	3	23	15	1	30	9	78	101
0	0	0	0	0	0	0	0	1
0	0	0	1	0	0	0	1	2
0	1	0	0	0	0	0	0	2
1	0	0	0	0	0	0	0	1
0	0	0	1	0	0	0	1	1
0	0	0	1	0	0	1	2	2

Appendix 3.1 (continued): List of all taxa from surface collected and bulk samples with feeding guild assignments (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Taxon	**FG**	**SR45**	**SR46**	**SR47**
Heliacus sp. 1	3	0	0	0
Odostomiinae indet. sp. 1	3	0	0	0
Linopyrga sp. 1	3	0	0	0
Pyramidella sp. 2	3	0	0	0
?*Tibersyrnola* sp. 1	3	0	0	0
Pyramidellidea indet. sp. 1	3	0	0	0
Pyramidellidea indet. sp. 2	3	0	0	0
Pyramidellidea indet. sp. 3	3	0	0	0
Talahabia cf. *dentifera* Martin, 1921	2	0	0	0
Cylichnidae indet. sp. 3	2	0	1	0
Cylichnidae indet. sp. 4	2	0	0	0
Gastropoda indet. spp.		1	1	0
Nucula sp. 1	4	0	0	0
Brachidontes sp. 1	4	0	0	0
Modiolus sp. 1	4	0	0	0
Acar sp. 1	4	0	2	1
Anadara sp. 3	4	0	2	1
?*Barbatia* sp. 1	4	0	0	0
Arcopsis sculptilis sensu Beets, 1941	4	2	1	1
Pteria s.l. sp. 1	4	0	0	0
Malleidae indet. sp.	4	0	0	0
Dendostrea folia (Linnaeus, 1758) *sensu* Beets, 1941	4	0	0	1
Lopha sp. 1	4	0	0	0
Ostreidae indet.	4	2	1	3
Mimachlamys aff. *menkrawitensis* (Beets, 1941)	4	1	1	1
Gloripallium sp. 1	4	0	0	1
Spondylus sp. 2	4	0	0	0
Plicatula sp. 1	4	0	1	0
Cardiolucina sp. 2	5	0	0	0
Cardita s.l. sp. 3	4	0	0	0
Trachycardium denticostulatum (Beets, 1941)	4	0	1	0
Vasticardium sp. 1	4	0	1	0
Cardiidae indet. sp. 4	4	0	1	0

SR48	SR49	SR50	SR51	SR52	SR53	SR54	Total bulk samples	Total all samples
0	1	0	0	0	0	0	0	1
0	0	0	0	0	1	0	1	1
0	0	0	1	0	1	0	2	2
0	0	0	0	0	0	1	1	1
0	0	0	1	0	1	0	2	2
0	0	1	0	0	0	0	1	1
0	0	0	0	0	1	0	1	1
0	0	0	0	0	1	0	1	1
0	0	1	1	0	0	2	4	4
0	0	0	0	0	0	2	2	3
0	0	1	0	0	0	0	1	1
0	0	17	20	4	59	13	113	115
0	0	0	0	0	0	1	1	1
0	0	0	0	0	1	1	2	2
0	0	0	0	0	1	0	1	1
0	0	2	0	0	1	2	5	8
0	1	13	6	1	13	8	41	45
0	0	0	0	0	1	1	2	2
0	0	18	7	2	19	7	53	57
0	0	1	0	0	2	1	4	4
0	0	0	1	0	1	0	2	2
0	0	11	14	4	26	11	66	67
0	0	0	0	0	0	2	2	2
0	3	1	3	1	5	5	15	24
0	0	3	2	1	6	1	13	16
0	0	0	1	1	2	1	5	6
0	0	0	0	0	0	1	1	1
0	0	0	0	1	0	0	1	2
0	0	2	1	0	1	2	6	6
0	0	2	1	0	2	1	6	6
0	0	0	1	0	1	0	2	3
0	0	0	0	0	1	0	1	2
0	0	0	0	0	0	0	0	1

Appendix 3.1 (continued): List of all taxa from surface collected and bulk samples with feeding guild assignments (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Taxon	**FG**	**SR45**	**SR46**	**SR47**
Cardiidae indet. sp. 5	4	0	0	1
Cardiidae indet. sp. 6	4	0	0	0
Cardiidae indet. sp. 7	4	0	0	0
Tridacna (*Camatrachea*) *mbalavuana* Ladd, 1934	4	1	1	0
Chama sp. 3	4	1	0	0
Tellina s.l. sp. 3	6	0	0	0
Tellina s.l. sp. 4	6	0	0	0
Tellina s.l. sp. 5	6	0	0	0
Tellina s.l. sp. 6	6	0	0	0
Circe ickeae sensu (Beets, 1941) non Martin, 1922	4	0	0	0
Dosinia sp. 1	4	0	0	0
Gafrarium sp. 1	4	0	1	1
?*Timoclea* sp. 1	4	0	0	0
?*Timoclea* sp. 2	4	0	0	0
Veneridae indet. sp. 3	4	0	1	0
Veneridae indet. sp. 4	4	0	0	0
Veneridae indet. sp. 5	4	0	0	0
Corbula solidula Hinds, 1843 sensu Beets 1941	4	0	0	0
Corbula sp. 1	4	0	0	0
Corbula sp. 2	4	0	0	0
Pholadidae indet. sp. 1	7	0	0	0
Chitonoidea indet. sp. 4	1	0	0	0
Total specimens		**104**	**103**	**22**
Total species		**49**	**52**	**17**

SR48	SR49	SR50	SR51	SR52	SR53	SR54	Total bulk samples	Total all samples
0	0	0	0	0	0	0	0	1
0	0	0	0	1	1	0	2	2
0	0	2	0	3	4	2	11	11
0	0	1	0	0	0	0	1	3
0	0	3	3	2	15	7	30	31
0	0	0	0	1	0	0	1	1
0	0	0	0	0	0	1	1	1
0	0	0	0	0	1	1	2	2
0	0	0	0	0	1	0	1	1
0	0	2	2	0	4	4	12	12
0	0	0	0	0	2	0	2	2
0	0	3	1	1	3	0	8	10
0	0	0	1	0	1	0	2	2
0	0	0	0	0	1	0	1	1
0	0	1	0	0	0	0	1	2
0	0	0	0	0	2	0	2	2
0	0	0	0	0	1	0	1	1
0	0	4	2	1	4	0	11	11
0	0	1	0	0	0	0	1	1
0	0	0	0	0	0	1	1	1
0	0	0	0	0	0	1	1	1
0	0	0	0	0	0	1	1	1
34	**20**	**344**	**232**	**78**	**568**	**246**	**1468**	**1739**
19	**14**	**84**	**66**	**45**	**97**	**79**	**161**	**185**

Appendix 4.1: List of all taxa from unvegetated sandflats with assignment to feeding guild (FG) and proportional abundance per sample. $N_{specimens}$ = 200 except sample GB_A.2 with $N_{specimens}$ = 90. Feeding guilds: 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder.

Species	**FG**	**Unvegetated sandflat**					
		MB_A.1	**MB_A.2**	**MB_A.3**	**GB_A.1**	**GB_A.2**	**GB_A.3**
Eulithidium thalassicolum	1	9.50	6.00	5.00	3.50	2.22	5.50
Zebina browniana	1	3.50	1.50	1.00	3.00	1.11	2.50
Cerithium eburneum	1	7.50	13.50	17.00	8.00	7.78	10.50
Cerithium litteratum	1	23.00	28.50	33.00	18.00	20.00	27.00
Acteocina spp.	2	3.00	1.50	2.00	1.50	2.22	2.00
Finella adamsi	1	17.00	8.50	6.50	17.50	7.78	14.00
Cerithium lutosum	1	2.00	0.50	0.00	0.50	1.11	0.00
Tegula fasciata	1	2.00	2.00	2.00	0.50	1.11	0.50
Patelloidea pustulata	1	0.00	0.00	0.00	0.00	0.00	0.00
Atys sharpi	1	0.00	0.00	0.00	0.00	0.00	0.00
Atys sp. 1	1	0.00	0.00	0.00	0.00	0.00	0.00
“Nassarius ambiguus”	2	0.50	0.50	0.50	0.50	1.11	0.00
Smaragdia viridis	1	0.00	0.00	0.00	0.00	0.00	0.00
Sayella laevigata	3	0.50	0.00	0.00	0.50	2.22	1.00
Eulithidium bellum	1	0.50	1.00	1.00	0.00	1.11	0.50
Granulina sp.	3	0.00	0.00	0.00	0.00	0.00	0.00
Suturoglypta albella	2	0.00	0.00	0.00	0.00	0.00	0.00
Gibberula sp.	3	0.50	0.50	0.00	1.50	0.00	0.00
Columbella mercatoria	2	0.50	3.00	3.50	0.50	1.11	1.50
Dentimargo reductus	3	3.00	2.00	0.00	1.00	2.22	0.50
Granoturris sp.	2	0.50	1.00	1.00	0.50	3.33	1.00
Turbo castanea	1	0.00	0.00	0.00	0.00	0.00	0.00
Cerithidea costata	1	0.00	0.00	0.00	0.00	0.00	0.00
Eulithidium affine	1	0.00	0.50	0.00	0.00	0.00	0.00
Rissoina dyscrita	1	0.50	1.50	0.00	0.00	0.00	3.00
Rissoina elegantissima	1	0.50	0.50	0.50	0.00	0.00	1.50
“Bittium” turriculum	1	0.00	0.50	1.00	1.00	0.00	1.00
Bulla occidentalis	1	0.00	1.50	0.50	1.00	1.11	2.00
Modulus modulus	1	1.00	0.00	1.00	1.00	0.00	1.00
?*Naticarius* sp.	2	0.00	0.50	0.00	0.00	1.11	1.00
Rissoina sp. B	1	1.50	1.00	0.00	1.50	1.11	0.00

Appendix 4.1 (continued)

Litiopa melanostoma	1	0.00	0.00	0.00	0.00	0.00	0.00
Hinea lineata	1	0.00	0.00	0.50	0.00	0.00	0.00
Schwartziella sp.	1	0.00	0.00	0.50	0.50	1.11	1.50
?*Arene* sp.	1	1.00	1.00	1.50	1.00	0.00	1.00
Triphora s.l. sp. 1	3	0.50	1.00	0.50	0.50	0.00	0.00
Conus cf. *mindanus*	2	0.00	0.00	0.00	0.00	1.11	0.50
Brachycythara biconica	2	1.00	2.00	0.00	0.00	1.11	0.50
Cerithium sp.	1	0.00	0.00	0.00	0.00	0.00	0.00
Vermetidae indet. spp.	4	0.50	0.50	2.00	0.00	0.00	0.00
Atys sp. 2	1	0.00	0.00	0.00	0.00	0.00	0.00
Atys sp. 3	1	0.00	0.00	0.00	0.00	0.00	0.00
Teinostoma clavium	1	0.00	0.00	0.00	0.00	0.00	0.00
Cerithiopsis s.l. sp. 2	3	0.00	0.00	0.00	0.00	1.11	0.50
Conidae indet. spp.	2	0.00	0.50	0.00	0.00	1.11	0.00
Fissurella barbadensis	1	0.00	0.50	0.50	0.00	0.00	0.00
Olivella nivea	2	0.00	0.50	1.00	0.00	0.00	0.00
Triphora s.l. sp. 2	3	0.00	0.00	0.00	0.50	2.22	0.00
Columbella s.l. sp. 1	2	0.50	0.00	0.50	1.00	1.11	0.00
Melanella sp.	3	0.00	0.00	0.00	0.00	0.00	0.00
Haminoea elegans	1	0.00	0.00	0.00	0.00	0.00	0.00
Vexillum cf. chickcharneorum	2	0.00	0.50	0.00	0.00	1.11	0.50
Parviturbo weberi	1	0.00	0.00	0.00	0.00	0.00	0.00
Nodilittorina dilatata	1	0.00	0.50	0.00	0.00	0.00	0.00
Natica sp.	2	0.00	0.00	0.00	1.00	0.00	0.50
Columbella s.l. sp. 3	2	0.00	0.00	0.00	2.50	0.00	0.00
Olivella sp. 2	2	0.00	0.00	0.00	0.00	0.00	0.00
Alaba incerta	1	0.00	0.00	0.00	0.00	2.22	0.00
Astralium phoebium	1	0.00	0.00	0.00	0.00	1.11	0.00
Lottia sp.	1	0.50	0.00	0.50	0.50	0.00	0.50
Schwartziella cf. *bryerea*	1	0.00	0.00	1.00	0.00	0.00	0.00
Hipponix sp.	4	0.50	0.50	0.50	0.00	0.00	0.00

Appendix 4.1: List of all taxa from unvegetated sandflats with assignment to feeding guild (FG) and proportional abundance per sample. $N_{specimens}$ = 200 except sample GB_A.2 with $N_{specimens}$ = 90. Feeding guilds: 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder.

Species	FG	Unvegetated sandflat					
		MB_A.1	**MB_A.2**	**MB_A.3**	**GB_A.1**	**GB_A.2**	**GB_A.3**
Engina turbinella	2	0.00	0.00	0.50	1.00	0.00	0.50
Brachycythara sp.	2	0.00	0.00	0.00	0.00	0.00	0.00
Rictaxis punctostriatus	2	0.00	0.00	0.00	0.00	0.00	0.00
Turbonilla kumpermani	3	0.00	0.00	0.00	0.00	0.00	0.00
Bittiolum varium	1	0.00	0.00	0.00	0.00	1.11	0.00
Rissoina sp.	1	0.00	0.00	0.00	0.50	1.11	0.00
Truncatella caribaeensis	1	0.00	0.00	0.00	0.00	0.00	0.00
Truncatella clathrus	1	0.00	0.00	0.00	0.00	0.00	0.00
Cerithiopsis cf. iontha	3	0.00	0.00	0.00	0.50	0.00	0.00
?*Seila* sp.	3	0.00	0.00	0.00	0.00	0.00	0.50
Aesopus stearnsii	2	0.00	0.00	0.50	0.50	0.00	0.00
Vexillum epiphaneum	2	0.00	0.00	0.00	0.00	0.00	0.00
Terebra alba	2	1.00	0.50	0.00	0.00	0.00	0.00
Arene cruenatata	1	0.00	0.00	0.00	0.00	1.11	0.00
Natica s.l. sp. 2	2	0.00	0.00	0.00	0.00	1.11	0.00
Conus sp.	2	0.00	0.00	0.00	0.00	1.11	0.00
Ithycythara sp.	2	0.00	0.00	0.00	0.00	1.11	0.00
Diodora dysoni	1	0.50	0.50	0.00	0.00	0.00	0.00
Turritella sp.	4	0.00	0.00	0.00	0.00	0.00	0.00
Cenchritis muricatus	1	0.00	0.00	0.00	0.00	0.00	0.00
Caecum sp.	1	0.00	0.00	0.00	0.00	0.00	0.00
Cochliolepsis parasitica	1	0.00	0.00	0.50	0.00	0.00	0.00
Olivellidae indet. spp.	2	0.00	0.00	0.00	0.50	0.00	0.00
Turbonilla cf. riisei	3	0.00	0.00	0.00	0.00	0.00	0.00
Hemitoma cf. octoradiata	1	0.00	0.50	0.00	0.00	0.00	0.00
Diodora sp.	1	0.00	0.00	0.50	0.00	0.00	0.00
Nerita versicolor	1	0.00	0.00	0.00	0.00	0.00	0.00
?*Nodilittorina* sp.	1	0.00	0.00	0.00	0.00	0.00	0.00
Natica s.l. sp. 1	2	0.00	0.00	0.00	0.00	0.00	0.00
Caecum cf. regulare	1	0.00	0.00	0.00	0.00	0.00	0.00
Cymatium sp. 1	2	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 4.1 (continued)

Cymatium sp. 2	2	0.00	0.00	0.50	0.00	0.00	0.00
Ranellidae indet. sp. 1	2	0.00	0.00	0.00	0.50	0.00	0.00
Ranellidae indet. sp. 2	2	0.00	0.00	0.00	0.00	0.00	0.50
Hipponix cf. subrufus	4	0.00	0.00	0.00	0.00	0.00	0.00
Epitonium sp.	3	0.00	0.00	0.00	0.00	0.00	0.00
Cerithiopsis s.l. sp. 1	3	0.00	0.00	0.00	0.00	0.00	0.00
Zafrona sp.	2	0.00	0.00	0.00	0.00	0.00	0.00
Columbella s.l. sp. 2	2	0.00	0.00	0.00	0.50	0.00	0.00
Columbella s.l. sp. 4	2	0.00	0.00	0.00	0.00	0.00	0.50
Granulina ovuliformis	3	0.00	0.00	0.00	0.00	0.00	0.00
Volvarina sp.	3	0.00	0.00	0.50	0.00	0.00	0.00
Olivella sp. 1	2	0.00	0.00	0.00	0.00	0.00	0.00
Crassispira sp.	2	0.00	0.00	0.00	0.00	0.00	0.00
Hastula hastata	2	0.00	0.00	0.00	0.00	0.00	0.50
Heliacus cf. *cylindricus*	3	0.50	0.00	0.00	0.00	0.00	0.00
Turbonilla cf. ornata	3	0.00	0.00	0.00	0.00	0.00	0.00
Turbonilla sp. 1	3	0.00	0.00	0.00	0.00	0.00	0.00
Turbonilla sp. 2	3	0.00	0.00	0.00	0.00	0.00	0.00
Haminoea succinea	1	0.00	0.00	0.00	0.00	0.00	0.00
Melampus monile	1	0.00	0.00	0.00	0.00	0.00	0.00
Pedipes ovalis	1	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda indet. spp.		16.50	15.00	12.50	27.00	22.22	16.00

Appendix 4.2: List of all taxa from seagrass-vegetated sandflats with proportional abundance per sample. $N_{specimens}$ = 200. See Appendix 4.1 for assignments to feeding guilds.

Species	Seagrass vegetated sandflat						
	GRC1_A	**GRC1_B**	**GRC1_C**	**GRC2_A**	**GRC2_B**	**GRC2_C**	**GH1_A**
Eulithidium thalassicolum	20.00	20.00	35.00	22.00	13.50	28.00	14.50
Zebina browniana	6.00	2.00	6.00	1.50	14.50	20.00	16.50
Cerithium eburneum	7.00	13.00	10.50	4.50	9.00	8.50	14.00
Cerithium litteratum	3.00	3.50	1.50	2.00	6.50	2.50	2.00
Acteocina spp.	12.00	8.00	9.00	22.00	10.50	13.00	11.50
Finella adamsi	0.50	3.00	3.50	4.00	1.50	2.00	4.00
Cerithium lutosum	4.50	6.00	0.50	2.00	0.00	0.00	4.50
Tegula fasciata	0.00	1.00	1.50	1.00	1.50	1.00	0.50
Patelloidea pustulata	0.00	0.50	3.50	0.00	0.50	3.50	2.50
Atys sharpi	0.50	2.50	2.00	0.50	2.00	1.00	0.50
Atys sp. 1	1.50	0.00	2.00	1.00	2.00	3.50	2.50
"*Nassarius ambiguus*"	1.00	2.50	1.00	0.50	1.00	2.00	0.50
Smaragdia viridis	0.50	1.50	3.00	0.00	0.00	1.00	0.50
Sayella laevigata	0.00	0.50	0.00	0.50	0.00	1.00	0.50
Eulithidium bellum	1.00	0.50	0.50	0.00	2.50	0.50	1.00
Granulina sp.	1.00	2.00	1.50	1.50	1.00	2.00	1.00
Suturoglypta albella	0.50	0.50	1.50	0.50	0.50	1.00	0.00
Gibberula sp.	2.00	2.00	0.50	1.00	2.00	0.00	0.50
Columbella mercatoria	0.00	1.00	0.00	0.00	1.00	0.50	0.00
Dentimargo reductus	1.00	2.00	0.50	0.00	0.50	0.50	0.50
Granoturris sp.	0.50	0.00	0.50	0.00	0.00	1.00	0.00
Turbo castanea	0.00	0.00	2.50	0.00	3.50	4.00	0.50
Cerithidea costata	0.00	0.50	0.00	0.00	0.00	0.00	0.50
Eulithidium affine	0.50	0.50	1.00	0.50	1.50	0.00	0.00
Rissoina dyscrita	0.50	0.50	0.00	0.50	0.00	0.00	1.00
Rissoina elegantissima	1.00	0.00	0.00	0.00	2.00	0.00	1.00
"*Bittium*" *turriculum*	0.00	0.50	0.00	0.00	0.00	0.00	0.50
Bulla occidentalis	0.00	0.00	1.00	0.00	0.50	0.00	0.00
Modulus modulus	0.00	0.00	1.00	0.00	0.00	0.00	0.50
?*Naticarius* sp.	0.50	0.00	0.00	0.00	0.00	0.00	0.50
Rissoina sp. B	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Litiopa melanostoma	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Hinea lineata	1.00	0.00	0.00	0.00	1.00	0.00	0.00

Seagrass vegetated sandflat										
GH1_B	**GH1_C**	**GH2_A**	**GH2_B**	**GH2_C**	**PC1_A**	**PC1_B**	**PC1_C**	**PC2_A**	**PC2_B**	**PC2_C**
21.00	15.50	18.50	21.00	15.50	17.50	6.50	6.00	21.00	25.50	18.50
17.50	21.50	22.00	22.00	27.00	5.00	59.00	63.00	8.50	6.50	13.00
15.00	16.50	23.50	17.00	18.00	6.50	3.00	4.00	8.00	11.50	9.00
2.50	3.00	2.00	4.50	0.50	2.50	7.50	3.00	2.50	1.50	2.00
10.50	6.50	7.50	8.50	5.00	10.00	0.50	0.00	15.50	11.50	7.50
1.50	3.00	1.00	1.00	4.00	11.00	2.50	0.00	5.00	4.50	8.50
2.50	9.00	2.00	2.00	10.50	13.50	4.00	2.00	10.50	21.50	12.50
0.00	0.00	0.50	1.00	1.50	0.50	2.00	5.00	0.00	0.50	3.00
0.00	3.50	0.00	2.00	3.00	0.00	1.50	2.50	0.50	0.00	0.50
1.00	2.00	1.00	0.50	1.00	2.00	0.50	0.00	1.50	1.50	2.50
0.50	3.00	0.50	1.50	2.00	0.50	0.50	0.00	0.50	1.00	0.00
0.50	1.00	2.00	0.50	1.00	0.50	0.00	1.00	1.00	0.50	2.00
1.50	1.50	0.00	0.00	1.00	0.50	2.50	4.00	1.00	0.00	2.00
0.00	2.50	1.50	1.50	0.50	2.00	1.00	0.00	1.50	1.00	2.00
2.50	0.00	1.50	2.00	0.00	0.50	0.50	0.00	1.00	0.00	1.50
0.50	0.50	1.50	1.00	3.00	0.00	0.00	0.00	1.50	0.00	0.50
0.50	1.50	0.00	0.00	0.00	0.00	2.50	5.00	0.50	0.50	3.00
1.00	1.00	0.50	1.00	0.50	1.00	0.00	0.00	0.50	0.50	0.50
0.50	0.00	2.50	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
1.50	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.00	0.00	0.50	0.00	0.00	1.00	0.50	0.00	0.00	0.50	1.50
0.00	0.00	0.00	0.00	0.00	0.00	2.00	1.00	0.00	0.00	0.50
0.00	1.00	0.00	1.00	0.00	2.50	0.00	0.00	4.00	2.00	1.50
4.00	0.00	0.00	1.50	0.00	0.00	0.00	0.50	0.00	0.00	0.50
1.00	0.00	0.50	0.50	0.00	0.00	0.00	0.00	0.50	1.00	0.00
0.50	0.00	0.00	0.50	0.00	1.00	1.00	0.00	0.50	0.00	0.00
1.00	0.50	0.50	2.50	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.50	0.00	0.00	0.00	1.00	0.00	0.00	0.50	0.50	0.00
0.50	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.50	1.00	1.50
0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
3.00	0.50	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.50	0.00
0.00	0.00	1.00	0.50	0.00	0.50	0.50	1.50	0.00	0.00	0.00

Appendix 4.2 (continued): List of all taxa from seagrass-vegetated sandflats with proportional abundance per sample. $N_{specimens}$ = 200. See Appendix 4.1 for assignments to feeding guilds.

Species	**Seagrass vegetated sandflat**						
	GRC1_A	**GRC1_B**	**GRC1_C**	**GRC2_A**	**GRC2_B**	**GRC2_C**	**GH1_A**
Schwartziella sp.	0.50	0.50	0.00	0.00	0.00	0.00	0.00
?*Arene* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triphora s.l. sp. 1	0.00	0.50	0.00	0.00	0.00	0.00	1.00
Conus cf. *mindanus*	0.50	1.00	0.50	0.00	0.00	0.50	0.00
Brachycythara biconica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerithium sp.	0.00	0.50	0.00	0.00	0.00	0.00	1.50
Vermetidae indet. spp.	0.00	0.50	0.00	0.50	0.00	0.00	0.50
Atys sp. 2	0.00	0.00	2.00	0.00	0.00	1.00	0.00
Atys sp. 3	1.50	0.00	0.50	0.00	1.00	0.00	0.50
Teinostoma clavium	1.00	0.00	0.00	0.00	0.50	0.00	0.50
Cerithiopsis s.l. sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Conidae indet. spp.	0.50	0.50	0.00	0.00	0.00	0.00	0.00
Fissurella barbadensis	1.00	0.50	0.00	0.50	0.50	0.00	0.00
Olivella nivea	0.50	0.50	0.00	0.00	0.50	0.00	0.50
Triphora s.l. sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Columbella s.l. sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Melanella sp.	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Haminoea elegans	0.00	0.00	0.50	0.00	0.00	0.00	1.00
Vexillum cf. chickcharneorum	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Parviturbo weberi	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Nodilittorina dilatata	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Natica sp.	0.00	0.00	0.50	0.00	0.00	0.00	0.50
Columbella s.l. sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Olivella sp. 2	0.50	0.00	0.50	0.00	0.00	0.00	0.00
Alaba incerta	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Astralium phoebium	0.00	0.00	0.50	0.00	0.00	0.00	0.50
Lottia sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Schwartziella cf. *bryerea*	0.00	0.00	0.00	0.00	0.50	0.00	0.00
Hipponix sp.	0.00	0.50	0.00	0.00	0.00	0.00	0.00
Engina turbinella	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brachycythara sp.	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Rictaxis punctostriatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turbonilla kumpermani	0.00	0.00	0.50	0.00	0.50	0.00	0.50

Seagrass vegetated sandflat										
GH1_B	**GH1_C**	**GH2_A**	**GH2_B**	**GH2_C**	**PC1_A**	**PC1_B**	**PC1_C**	**PC2_A**	**PC2_B**	**PC2_C**
0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	1.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.50	0.00	0.50
0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	1.00	0.50	0.00	0.00	0.50	0.00	0.00	0.00	0.50	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.50	0.00
0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	1.00	0.50	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	1.00	0.50
0.00	0.00	0.50	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.50	0.00	0.00	1.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.50	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.50	1.00
0.50	0.50	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.50
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00	0.00	1.00
0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 4.2 (continued): List of all taxa from seagrass-vegetated sandflats with proportional abundance per sample. $N_{specimens}$ = 200. See Appendix 4.1 for assignments to feeding guilds.

Species	Seagrass vegetated sandflat						
	GRC1_A	GRC1_B	GRC1_C	GRC2_A	GRC2_B	GRC2_C	GH1_A
Bittiolum varium	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rissoina sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Truncatella caribaeensis	0.50	0.00	0.00	0.00	0.00	0.00	0.00
Truncatella clathrus	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerithiopsis cf. iontha	0.00	0.00	0.00	0.00	0.00	0.00	0.00
?*Seila* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aesopus stearnsii	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vexillum epiphaneum	0.00	0.00	0.50	0.50	0.00	0.50	0.00
Terebra alba	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arene cruenatata	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Natica s.l. sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Conus sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ithycythara sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diodora dysoni	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turritella sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cenchritis muricatus	0.00	0.50	0.00	0.00	0.00	0.00	0.00
Caecum sp.	0.00	0.00	0.00	0.50	0.00	0.00	0.00
Cochliolepsis parasitica	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Olivellidae indet. spp.	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Turbonilla cf. riisei	0.00	0.00	0.00	0.50	0.00	0.00	0.00
Hemitoma cf. octoradiata	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diodora sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nerita versicolor	0.00	0.50	0.00	0.00	0.00	0.00	0.00
?*Nodilittorina* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Natica s.l. sp. 1	0.00	0.00	0.00	0.00	0.50	0.00	0.00
Caecum cf. regulare	0.00	0.00	0.00	0.00	0.50	0.00	0.00
Cymatium sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cymatium sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ranellidae indet. sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ranellidae indet. sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hipponix cf. subrufus	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epitonium sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerithiopsis s.l. sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Seagrass vegetated sandflat										
GH1_B	**GH1_C**	**GH2_A**	**GH2_B**	**GH2_C**	**PC1_A**	**PC1_B**	**PC1_C**	**PC2_A**	**PC2_B**	**PC2_C**
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00
0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 4.2 (continued): List of all taxa from seagrass-vegetated sandflats with proportional abundance per sample. $N_{specimens} = 200$. See Appendix 4.1 for assignments to feeding guilds.

Species	**Seagrass vegetated sandflat**						
	GRC1_A	**GRC1_B**	**GRC1_C**	**GRC2_A**	**GRC2_B**	**GRC2_C**	**GH1_A**
Zafrona sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Columbella s.l. sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Columbella s.l. sp. 4	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Granulina ovuliformis	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Volvarina sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Olivella sp. 1	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Crassispira sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hastula hastata	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Heliacus cf. *cylindricus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turbonilla cf. ornata	0.00	0.00	0.00	0.00	0.00	0.50	0.00
Turbonilla sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Turbonilla sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Haminoea succinea	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Melampus monile	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pedipes ovalis	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda indet. spp.	27.50	20.00	2.00	32.00	17.00	1.00	8.50

Seagrass vegetated sandflat										
GH1_B	**GH1_C**	**GH2_A**	**GH2_B**	**GH2_C**	**PC1_A**	**PC1_B**	**PC1_C**	**PC2_A**	**PC2_B**	**PC2_C**
0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
3.00	2.50	4.00	2.50	1.50	16.50	0.50	0.00	5.50	0.00	1.00

Appendix 5.1: List of all samples, assigned to taxon and feeding guild (FG), and ^{13}C V-PDB and ^{18}O V-PDB values, including the lab where the sample was analyzed (RH = Royal Hollow University, London; UU = Utrecht University). Feeding guilds: 1 = herbivore, 2 = seagrass feeder, 3 = predator on invertebrates, 4 = predator on foraminifera, 5 = browsing carnivore, 6 = infaunal suspension feeder, 7 = infaunal deposit feeder, 8 = chemosymbiotic deposit feeder.

Sample Set	**Sample**	**Taxon**	**FG**	**^{13}C V-PDB**	**^{18}O V-PDB**	**Lab**
BA 18	BA18_01a	*Rissoina* (*Rissoina) banjunantensis*	1	2.27	-3.06	RH
	BA18_01b	*Rissoina* (*Rissoina) banjunantensis*	1	1.99	-2.96	RH
	BA18_01c	*Rissoina* (*Rissoina) banjunantensis*	1	2.25	-2.87	RH
	BA18_01d	*Rissoina* (*Rissoina) banjunantensis*	1	1.75	-2.91	RH
	BA18_02b	*Cerithidium* cf. *perparvulum*	1	1.74	-3.06	RH
	BA18_02c	*Cerithidium* cf. *perparvulum*	1	2.42	-3.10	RH
	BA18_02d	*Cerithidium* cf. *perparvulum*	1	1.51	-2.87	RH
	BA18_03a	*Diala semistriata* s.l.	1	2.07	-2.76	RH
	BA18_03b	*Diala semistriata* s.l.	1	1.81	-3.07	RH
	BA18_03c	*Diala semistriata* s.l.	1	2.42	-3.31	RH
	BA18_03d	*Diala semistriata* s.l.	1	2.37	-2.85	RH
	BA18_04b	*Bothropoma mediocarinata*	1	1.79	-3.34	RH
	BA18_04c	*Bothropoma mediocarinata*	1	1.13	-3.01	RH
	BA18_04d	*Bothropoma mediocarinata*	1	1.18	-2.80	RH
	BA18_05b	*Smaragdia jogjacartensis*	2	3.65	-2.84	RH
	BA18_05c	*Smaragdia jogjacartensis*	2	2.34	-2.92	RH
	BA18_05d	*Smaragdia jogjacartensis*	2	2.52	-2.71	RH
	BA18_06a	*Cylichna triplicata*	4	0.40	-3.03	RH
	BA18_06b	*Cylichna triplicata*	4	1.55	-2.60	RH
	BA18_06c	*Cylichna triplicata*	4	1.65	-2.69	RH
	BA18_06d	*Cylichna triplicata*	4	1.16	-2.88	RH
	BA18_07a	*Dentimargo* sp.	5	2.18	-2.93	RH
	BA18_07b	*Dentimargo* sp.	5	2.13	-2.72	RH
	BA18_07c	*Dentimargo* sp.	5	1.74	-2.48	RH
	BA18_07d	*Dentimargo* sp.	5	2.25	-2.87	RH
	BA18_08a	?*Fusiconus arntzenii*	3	2.22	-2.92	RH
	BA18_08b	?*Fusiconus arntzenii*	3	1.72	-3.16	RH
	BA18_08c	?*Fusiconus arntzenii*	3	1.84	-3.05	RH

Appendix 5.1 (continued)

BA 18	BA18_08d	?*Fusiconus arntzenii*	3	1.48	-3.20	RH
	BA18_09a	*Circe junghuhni*	6	1.05	-3.43	RH
	BA18_09b	*Circe junghuhni*	6	1.28	-3.47	RH
	BA18_09c	*Circe junghuhni*	6	1.02	-3.62	RH
	BA18_09d	*Circe junghuhni*	6	1.06	-3.72	RH
	BA18_10a	*Cardiolucina civica*	8	-0.90	-3.25	RH
	BA18_10b	*Cardiolucina civica*	8	-1.32	-3.22	RH
	BA18_10c	*Cardiolucina civica*	8	-0.85	-3.36	RH
	BA18_10d	*Cardiolucina civica*	8	0.23	-2.60	RH
TF 102	TF102_01	*Strombus* s.l. sp. 2	1	-1.86	-3.09	RH
	TF102_02	*Cerithium* sp. 7	1	0.91	-2.60	RH
	TF102_03	*Colina* sp.	1	-0.07	-2.29	RH
	TF102_04	*Gibbula leopoldi*	1	-0.35	-2.57	RH
	TF102_06	*Coralliophila* aff. *clathrata*	4	0.53	-2.45	RH
	TF102_07	*Dentimargo* sp.	5	0.41	-2.27	RH
	TF102_08	*Natica helvacea* sensu Beets, 1941	3	-0.40	-2.46	RH
	TF102_09	*Arcopsis sculptilis*sensu Beets, 1941	6	-0.36	-2.85	RH
	TF102_10	*Cardiolucina* sp. 2	8	-1.76	-2.86	RH
TF 110	TF110_01a	*Rissoina* (*Phosinella*) sp. 1	1	2.14	-2.84	RH
	TF110_01b	*Rissoina* (*Phosinella*) sp. 1	1	2.79	-2.36	RH
	TF110_01c	*Rissoina* (*Phosinella*) sp. 1	1	2.14	-2.62	RH
	TF110_01d	*Rissoina* (*Phosinella*) sp. 1	1	2.21	-2.86	RH
	TF110_02a	*Cerithium* sp. 3	1	1.81	-2.95	RH
	TF110_02b	*Cerithium* sp. 3	1	1.20	-3.13	RH
	TF110_02c	*Cerithium* sp. 3	1	1.49	-2.86	RH
	TF110_02d	*Cerithium* sp. 3	1	1.01	-3.41	RH
	TF110_03a	*Diala semistriata* s.l.	1	1.36	-2.51	RH
	TF110_03b	*Diala semistriata* s.l.	1	1.80	-2.71	RH

Appendix 5.1 (continued): List of all samples, assigned to taxon and feeding guild (FG), and ^{13}C V-PDB and ^{18}O V-PDB values, including the lab where the sample was analyzed (RH = Royal Hollow University, London; UU = Utrecht University). Feeding guilds: 1 = herbivore, 2 = seagrass feeder, 3 = predator on invertebrates, 4 = predator on foraminifera, 5 = browsing carnivore, 6 = infaunal suspension feeder, 7 = infaunal deposit feeder, 8 = chemosymbiotic deposit feeder.

Sample Set	Sample	Taxon	FG	^{13}C V-PDB	^{18}O V-PDB	Lab
TF 110	TF110_03c	*Diala semistriata* s.l.	1	1.90	-2.72	RH
	TF110_03d	*Diala semistriata* s.l.	1	1.91	-3.02	RH
	TF110_04a	*Rhinoclavis* sp. 2	1	1.88	-3.06	RH
	TF110_04b	*Rhinoclavis* sp. 2	1	1.99	-2.96	RH
	TF110_04c	*Rhinoclavis* sp. 2	1	1.71	-2.96	RH
	TF110_04d	*Rhinoclavis* sp. 2	1	1.72	-2.97	RH
	TF110_05b	*Smaragdia gelingsehensis*	2	3.66	-2.17	RH
	TF110_05e	*Smaragdia gelingsehensis*	2	2.82	-2.56	UU
	TF110_05f	*Smaragdia gelingsehensis*	2	2.60	-2.65	UU
	TF110_06a	*Cylichna triplicata*	4	2.09	-2.51	RH
	TF110_06b	*Cylichna triplicata*	4	2.44	-2.70	RH
	TF110_06c	*Cylichna triplicata*	4	1.63	-2.86	RH
	TF110_06d	*Cylichna triplicata*	4	1.89	-2.88	RH
	TF110_07a	*Dentimargo* sp.	5	2.45	-3.01	RH
	TF110_07c	*Dentimargo* sp.	5	2.41	-2.90	RH
	TF110_07d	*Dentimargo* sp.	5	2.40	-2.76	RH
	TF110_08a	*Naticarius marochiensis*sensu Beets, 1941	3	1.77	-2.17	RH
	TF110_08b	*Naticarius marochiensis*sensu Beets, 1941	3	2.24	-2.09	RH
	TF110_08c	*Naticarius marochiensis*sensu Beets, 1941	3	2.74	-2.58	RH
	TF110_09a	"*Tellina*" sp. 3	7	1.89	-2.29	RH
	TF110_09b	"*Tellina*" sp. 3	7	2.07	-2.42	RH
	TF110_09c	"*Tellina*" sp. 3	7	1.85	-2.27	RH
	TF110_09d	"*Tellina*" sp. 3	7	2.60	-1.88	RH
	TF110_10a	"*Lucina*" sp. 1	8	0.65	-2.68	UU
	TF110_10b	"*Lucina*" sp. 1	8	1.77	-2.53	RH
	TF110_10c	"*Lucina*" sp.1	8	2.05	-2.25	RH
	TF110_10d	"*Lucina*" sp. 1	8	2.14	-2.17	RH
TF 508_FW1	TF508_1_01a	*Cerithium* sp. 4	1	2.38	-2.38	UU

Appendix 5.1 (continued)

	TF508_1_01b	*Cerithium* sp. 4	1	1.44	-2.74	UU
	TF508_1_02a	*Smaragdia semari*	2	2.20	-2.88	UU
	TF508_1_02b	*Smaragdia semari*	2	2.09	-2.56	UU
	TF508_1_03a	*Turris* s.l. sp. 1	3	0.67	-2.92	UU
	TF508_1_04a	*Nuculana* cf. *ventricosa* sensu Beets, 1986	6	0.56	-2.88	UU
	TF508_1_04b	*Nuculana* cf. *ventricosa* sensu Beets, 1986	6	0.95	-2.91	UU
	TF508_1_05a	*Cardiolucina* sp. 2	8	-0.24	-2.85	UU
	TF508_1_05b	*Cardiolucina* sp. 2	8	-0.75	-2.97	UU
TF 508_FW6	TF508_6_01a	*Cerithium* sp. 4	1	-0.33	-3.45	UU
	TF508_6_01b	*Cerithium* sp. 4	1	0.43	-3.93	UU
	TF508_6_02a	*Cerithium* sp. 5	1	-0.02	-3.09	UU
	TF508_6_02b	*Cerithium* sp. 5	1	-0.19	-4.23	UU
	TF508_6_03a	*Nassarius* sp. 6	3	-0.25	-3.11	UU
	TF508_6_03b	*Nassarius* sp. 6	3	-0.49	-3.99	UU
	TF508_6_03c	*Nassarius* sp. 6	3	-2.29	-4.30	UU
	TF508_6_03d	*Nassarius* sp. 6	3	-0.05	-4.03	UU
	TF508_6_04a	*Anadara granosa*	6	-2.09	-4.13	UU
	TF508_6_04b	*Anadara granosa*	6	-2.42	-4.20	UU
	TF508_6_04c	*Anadara granosa*	6	-1.89	-4.11	UU
	TF508_6_04d	*Anadara granosa*	6	-2.11	-3.97	UU
	TF508_6_05a	Arcidae indet.	6	-1.93	-4.05	UU
	TF508_6_05b	Arcidae indet.	6	-1.56	-4.66	UU
	TF508_6_05c	Arcidae indet.	6	-1.36	-3.83	UU
	TF508_6_05d	Arcidae indet.	6	-2.07	-4.16	UU
	TF508_6_06a	*Corbula* sp. 2	6	-1.38	-4.14	UU
	TF508_6_06b	*Corbula* sp. 2	6	-1.51	-4.41	UU
	TF508_6_06c	*Corbula* sp. 2	6	-1.08	-4.16	UU
	TF508_6_06d	*Corbula* sp. 2	6	-1.15	-3.50	UU

Appendix 5.1 (continued): List of all samples, assigned to taxon and feeding guild (FG), and ^{13}C V-PDB and ^{18}O V-PDB values, including the lab where the sample was analyzed (RH = Royal Hollow University, London; UU = Utrecht University). Feeding guilds: 1 = herbivore, 2 = seagrass feeder, 3 = predator on invertebrates, 4 = predator on foraminifera, 5 = browsing carnivore, 6 = infaunal suspension feeder, 7 = infaunal deposit feeder, 8 = chemosymbiotic deposit feeder.

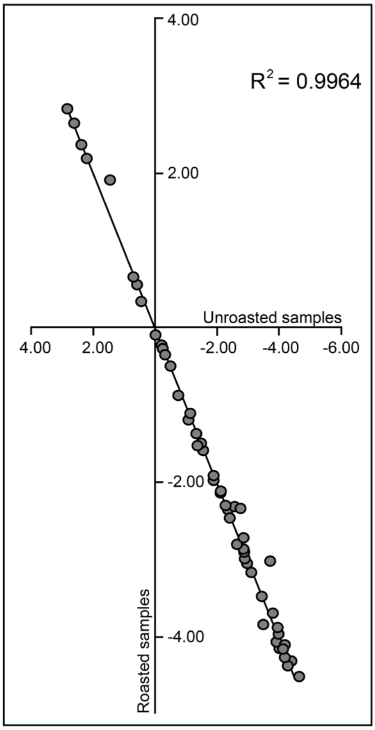
Sample Set	Sample	Taxon	FG	^{13}C V-PDB	^{18}O V-PDB	Lab
TF 508_FW7	TF508_01a	*Rissoina* (*Phosinella*) sp. 1	1	0.44	-1.95	RH
	TF508_01b	*Rissoina* (*Phosinella*) sp. 1	1	0.59	-2.18	RH
	TF508_01c	*Rissoina* (*Phosinella*) sp. 1	1	0.43	-2.12	RH
	TF508_02a	*Cerithium* sp. 4	1	1.33	-2.11	RH
	TF508_02b	*Cerithium* sp. 4	1	-0.07	-3.22	RH
	TF508_02c	*Cerithium* sp. 4	1	0.68	-3.06	RH
	TF508_03a	*Cerithium* sp. 6	1	0.99	-2.96	RH
	TF508_03b	*Cerithium* sp. 6	1	1.20	-3.19	RH
	TF508_03c	*Cerithium* sp. 6	1	0.86	-3.00	RH
	TF508_04a	*Gibbula leupoldi*	1	0.53	-2.34	RH
	TF508_04b	*Gibbula leupoldi*	1	-0.10	-2.40	RH
	TF508_04c	*Gibbula leupoldi*	1	0.47	-3.06	RH
	TF508_05a	*Smaragdia semari*	2	1.20	-3.06	RH
	TF508_06a	*Talahabia* cf. *dentifera*	4	0.58	-2.65	RH
	TF508_06b	*Talahabia* cf. *dentifera*	4	0.58	-2.92	RH
	TF508_06c	*Talahabia* cf. *dentifera*	4	0.44	-2.66	RH
	TF508_07a	*Dentimargo* sp.	5	0.79	-2.70	RH
	TF508_07c	*Dentimargo* sp.	5	0.22	-2.93	RH
	TF508_08c	*Naticarius marochiensis* sensu Beets, 1941	3	0.59	-3.22	RH
	TF508_09a	*Arcopsis sculptilis* sensu Beets, 1941	6	0.39	-2.74	RH
	TF508_09b	*Arcopsis sculptilis* sensu Beets, 1941	6	0.67	-2.33	RH
	TF508_09c	*Arcopsis sculptilis* sensu Beets, 1941	6	0.74	-3.10	RH
	TF508_10a	*Lamellolucina* sp. 1	8	-3.35	-3.60	RH
	TF508_10b	*Lamellolucina* sp. 1	8	-2.77	-3.47	RH
	TF508_10c	*Lamellolucina* sp. 1	8	-3.33	-3.56	RH
TF 517	TF517_01a	*Rissoina* (*Rissoina*) sp. 5	1	1.59	-2.74	RH
	TF517_01b	*Rissoina* (*Rissoina*) sp. 5	1	1.31	-2.72	RH
	TF517_01c	*Rissoina* (*Rissoina*) sp. 5	1	1.96	-2.80	RH

Appendix 5.1 (continued)

TF 517	TF517_01d	*Rissoina* (*Rissoina*) sp. 5	1	2.21	-2.70	RH
	TF517_02a	*Cerithium* sp. 5	1	2.28	-2.89	RH
	TF517_02b	*Cerithium* sp. 5	1	2.45	-2.93	RH
	TF517_02c	*Cerithium* sp. 5	1	2.94	-2.22	RH
	TF517_02d	*Cerithium* sp. 5	1	2.51	-2.22	RH
	TF517_03c	*Diala semistriata* s.l.	1	2.79	-2.87	RH
	TF517_04a	*Bothropoma* sp. 2	1	2.08	-3.36	RH
	TF517_04b	*Bothropoma* sp. 2	1	1.83	-3.63	RH
	TF517_04d	*Bothropoma* sp. 2	1	1.61	-2.79	RH
	TF517_05b	*Plesiotrochus* sp. 5	1	2.04	-2.95	RH
	TF517_05c	*Plesiotrochus* sp. 5	1	1.31	-2.56	RH
	TF517_06a	*Cylichna* indet.	4	2.27	-3.03	RH
	TF517_06b	*Cylichna* indet.	4	2.20	-3.06	UU
	TF517_06c	*Cylichna* indet.	4	0.41	-2.94	RH
	TF517_06d	*Cylichna* indet.	4	2.36	-2.69	RH
	TF517_08a	*Conus* s.l. *arntzenii* sensu Beets, 1941	3	2.24	-2.46	RH
	TF517_08b	*Conus* s.l. *arntzenii* sensu Beets, 1941	3	2.23	-2.72	RH
	TF517_08c	*Conus* s.l. *arntzenii* sensu Beets, 1941	3	2.88	-2.61	RH
	TF517_08d	*Conus* s.l. *arntzenii* sensu Beets, 1941	3	2.81	-3.29	RH
	TF517_09a	*Arcopsis sculptilis* sensu Beets, 1941	6	1.90	-2.28	RH
	TF517_09b	*Arcopsis sculptilis* sensu Beets, 1941	6	1.46	-2.84	RH
	TF517_09c	*Arcopsis sculptilis* sensu Beets, 1941	6	1.78	-2.51	RH
	TF517_09d	*Arcopsis sculptilis* sensu Beets, 1941	6	1.58	-3.16	RH
	TF517_10a	*Cardiolucina* sp. 3	8	-0.89	-2.90	RH
	TF517_10b	*Cardiolucina* sp. 3	8	-0.85	-3.64	RH
	TF517_10c	*Cardiolucina* sp. 3	8	-1.39	-3.30	RH
	TF517_10d	*Cardiolucina* sp. 3	8	-0.96	-3.00	RH

Appendix 5.2: δ^{13}C and δ^{18}O ratios of roasted versus unroasted samples, including figure: linear correlation of roasted versus unroasted samples.

Sample	Roasted		Unroasted	
	^{13}C V-PDB	^{18}O V-PDB	^{13}C V-PDB	^{18}O V-PDB
508_1_1a	2.37	-2.34	2.38	-2.38
508_1_1b	1.92	-2.33	1.44	-2.74
508_1_2a	2.20	-2.86	2.20	-2.88
508_1_3a	0.66	-2.99	0.67	-2.92
508_1_3b	0.79	-3.13	-	-
508_1_4a	0.57	-2.90	0.56	-2.88
508_1_5a	-0.26	-2.71	-0.24	-2.85
508_1_5b	-0.87	-3.03	-0.75	-2.97
mean	**0.92**	**-2.79**	**0.89**	**-2.80**
508_6_1a	-0.34	-3.48	-0.33	-3.45
508_6_1B	0.34	-4.05	0.43	-3.93
508_6_2a	-0.08	-3.15	-0.02	-3.09
508_6_2b	-0.21	-4.25	-0.19	-4.23
508_6_3a	-0.23	-3.15	-0.25	-3.11
508_6_3b	-0.49	-3.95	-0.49	-3.99
508_6_3c	-2.29	-4.36	-2.29	-4.30
508_6_3d	-0.08	-4.13	-0.05	-4.03
508_6_4a	-2.13	-4.14	-2.09	-4.13
508_6_4b	-2.45	-4.10	-2.42	-4.20
508_6_4c	-1.92	-4.11	-1.89	-4.11
508_6_4d	-2.11	-3.87	-2.11	-3.97
508_6_5a	-1.96	-3.95	-1.93	-4.05
508_6_5b	-1.57	-4.51	-1.56	-4.66
508_6_5c	-1.36	-3.69	-1.36	-3.83
508_6_5d	-2.11	-4.14	-2.07	-4.16
508_6_6a	-1.52	-4.11	-1.38	-4.14
508_6_6b	-1.51	-4.31	-1.51	-4.41
508_6_6c	-1.18	-4.11	-1.08	-4.16
508_6_6d	-1.10	-3.84	-1.15	-3.50
mean	**-1.22**	**-3.97**	**-1.19**	**-3.97**
110_5e	2.829	-2.309	2.82	-2.56
110_5f	2.652	-2.798	2.60	-2.65



Appendix 6.1: List of species that deviate from originally published name.

Species with new, unpublished taxonomic assignments	**Published name**
Macrochisma sp. 1	*Macrochisma* spec. indet. [Beet, 1941]
Hemitoma sp.	*Hemitoma tricarinata* (Born, 1778) [Beets, 1981]
Thalotia erinacea (Beets, 1941)	*Cantharidus erinaceaus* Beets, 1941
Ethalia minolina grooti spec. nov. Beets	*Ethalia guamensis* (Quoy & Gaimard, 1834)
Bothropoma pilula (Dunker, 1860) *sensu* Beets, 1941	*Leptothyra pilula* Dunker, 1860 [Beets, 1841]
Phasianella variegata Lamarck, 1822 *sensu* Beets, 1941	*Phasianella aethiopica* Philippi, 1853 [Beets, 1941]
Colina menkrawitense (Beets, 1941)	*Cerithium menkrawitense* (Beets, 1941)
Pseudovertagus aluco (Linnaeus, 1758) *sensu* (Beets, 1941)	*Cerithium aluco* Linnaeus, 1758 [Beets, 1941]
Rhinoclavis leupoldi (Beets, 1941)	*Cerithium leupoldi* Beets, 1941
Rhinoclavis sawitrae (Beets, 1941)	*Cerithium sawitrae* Beets, 1941
Diala semistriata s.l. (Philippi, 1849)	*Melanella* spec. indet. [Beets, 1941]
Conomodulus praeangerensis (Martin, 1905)	*Modulus* spec. nov. [Beets, 1941]
Conomodulus pseudotectum spec. nov. Landau et al., 2014	*Modulus tectum* (Gmelin, 1791) [Beets, 1941]
Conomodulus renemai spec. nov. Landau et al., 2014	*Modulus* sp.1 [Reich et al., 2014]
Indomodulus miocenicus spec. nov. Landau et al., 2014	*Modulus tectum* (Gmelin, 1791) [Beets, 1941]
Modulidae indet. sp.	*Modulus* sp. 2 [Reich et al., 2014]
Turritella s.l. *damarwulani* Beets, 1941	*Turritella damarwulani* Beets, 1941
Turritella s.l. *talarensis* Eames, 1950	*Turritella subulata* Martin, 1884 [Beets, 1941]
Turritellidae indet. sp.	*Turritella* spec. indet. [Beets, 1941]
Ampullina berauensis (Beets, 1941)	*Globularia berauensis* Beets, 1941
Cernina fluctuata (Sowerby I, 1824)	*Globularia fluctuata* (Sowerby I, 1824) [Beets, 1941]
Plesiotrochus inopinatum (Cossmann, 1910) *sensu* Beets, 1941	*Cerithium inopinatum* (Cossmann, 1910) [Beets, 1941]

Appendix 6.1 (continued)

Plesiotrochus semari (Beets, 1941)	*Cerithium semari* Beets, 1941
Capulus sp. 2	*Capulus* spec. 1 [Beets, 1941]
Capulus sp. 3	*Capulus* spec. 2 [Beets, 1941]
Capulus sp. 4	*Capulus* spec. 3 [Beets, 1941]
Barycypraea spec. nov.	*Zoila murisimilis* (Martin, 1879) [Beets, 1941]
Cleotrivia berauensis Schilder	*Trivia smithi* (Martin, 1884)/*Trivia scabriusscula* Gray, 1828 [Beets, 1941]
Cypraea vandervlerki Schilder	*Cypraea vitellus* Linnaeus, 1758 [Beets, 1941]
Erronea berauensis Schilder	*Erronea kamai* Beets, 1941
Pustularia fisiformis Schilder, 1932	*Erronea kamai* Beets, 1941
Natica spadicea (Gmelin, 1791) *sensu* Beets, 1941	*Natica helvacea* Lamarck, 1822 [Beets, 1941], unaccepted name
Tanea undulata (Röding, 1798) *sensu* Beets, 1941	*Natica zebra* Lamarck, 1822 [Beets, 1941], unaccepted name
Naticarius marochiensis (Gmelin, 1791) *sensu* Beets, 1941	*Natica marochiensis* (Gmelin, 1791) [Beets, 1941]
Rissolina ramai Beets, 1941	*Rissoina*? *ramai* Beets, 1941
Cyclostremiscus novemcarinatus (Melvill, 1906) *sensu* Beets, 1987	*Vitrinella novemcarinata* (Melville, 1906) [Beets, 1941]
Canarium unifasciatum s.l. Martin, 1984	*Strombus unifasciatus* Martin, 1984 [Beets, 1941]
Cymatium cf. *vespaceum* (Lamarck, 1822) [det. Beu]	*Cymatium pileare* (Linnaeus, 1758) [Beets, 1941]
Sassia (*Cymatiella*) *fennemai* (Martin, 1899)	*Charonia fennemai* (Martin, 1899) [Beets, 1941]
Sassia menkrawitensis (Beets, 1941)	*Charonia menkrawitensis* Beets, 1941
Gyrineum bituberculare (Lamarck, 1816) *sensu* Beets	*Argobuccinum bituberculare* (Lamarck, 1816) [Beets, 1941]
Hipponix conicus (Schuhmacher, 1917) *sensu* Beets, 1941	*Amalthea conica* Schuhmacher, 1817 [Beets, 1941]
Vermetus (?*Spiroglyphus*) sp.	*Vermetus* (*Spiroglyphus*?) spec. indet. [Beets, 1941]
Vermetus (?*Serpulorbis*) sp.	*Vermetus* (*Serpulorbis*?) spec. indet. [Beets, 1941]
Vermetidae indet. sp. 1	*Vermetus* s.l. sp. [Reich et al., 2014]
Triphora s.l. *maharatai* Beets, 1941	*Triphora maharatai* Beets, 1941

Appendix 6.1: List of species that deviate from originally published name.

Triphora s.l. *indrai* Beets, 1941	*Triphora indrai* Beets, 1941
Triphora javana berauensis Beets, 1981	*Triphora javana* (Martin, 1899) [Beets, 1941]
Triphora s.l. sp. 3/ *Triphora* spec. indet. [det. Beet]	*Triphora javana* (Martin, 1899) [Beets, 1941]
Phos dijki Martin, 1884 *sensu* Beets, 1941	*Phos teschi* Koperberg, 1931 [Beets, 1941]
Engina sp.	*Engina* spec. nov. [Beets, 1941]
Mitrella s.l. *njalindungensis* sensu (Beets, 1941) non (Martin, 1921)	*Pyrene njalindungensis* (Martin, 1921) [Beets, 1941]
Mitrella s.l. cf. *njalindungensis* s.l. Martin, 1921	*Atilia* cf. *njalindungensis* Martin, 1921 [Reich et al., 2014]
Mitrella s.l. *gembacana* (Martin, 1884)	*Pyrene gembacanus* (Martin, 1884) [Beets, 1941]
Chicoreus juttingae (Beets, 1941)	*Murex juttingae* Beets, 1941
Chicoreus microphyllus (Lamarck, 1816)	*Murex microphyllus* Lamarck, 1816 [Beets, 1941]
Haustellum haustellum (Linnaeus, 1758) *sensu* Beets, 1941	*Murex haustellum* Linnaeus, 1758 [Beets, 1941]
Hexaplex ardjunoi (Beets, 1941)	*Murex ardjunoi* Beets, 1941
Vitularia cf. *miliaris* (Gmelin, 1791)	*Tritonalia* cf. *miliaris* (Gmelin, 1791) [Beets, 1941]
Vexillum ardjunoi (Beets, 1941)	*Pusia ardjunoi* Beets, 1941
Vexillum cf. *ardjunoi* (Beets, 1941)	*Pusia* cf. *ardjunoi* Beets, 1941
Vexillum escheri Beets, 1941	*Pusia escheri* Beets, 1941
Vexillum menkrawitensis Beets, 1941	*Pusia menkrawitensis* Beets, 1941
Vexillum kopenbergae	*Pusia kopenbergae* Beets, unpublished
*Morum*spec. nov. [Beets, 1941]	*Lambidium* spec. nov. [Beets, 1941]
Granulina maduparensis Beets unpublished	*Persicula* spec. 1 [Beets, 1941]
Canalispira indrai (Beets, 1941)	*Marginella indrai* Beets, 1941
Dentimargo ringicula (Sowerby III, 1901) *sensu* Beets, 1941	*Marginella ringicula* Sowerby III, 1901 [Beets, 1941]
Volvarina berauensis (Beets, 1941)	*Marginella berauensis* Beets, 1941
Mitra cf. *lipaiana* (?) (det. Beets)	*Mitra sokkohensis* Martin, 1916 [Beets, 1941]

Appendix 6.1 (continued)

Phasmoconus menkrawitensis Beets, 1941	*Conus menkrawitensis* Beets, 1941
Pionoconus achatinus Gmelin, 1791 *sensu* Beets, 1941	*Conus achatinus* Gmelin, 1791 [Beets, 1941]
Pionoconus magus Linnaeus, 1758 *sensu* Beets, 1941	*Conus magus* Linnaeus, 1758 [Beets, 1941]
Asprella sulcata Hwass *in* Bruguière, 1792 *sensu* Beets, 1941	*Conus sulcatus* Hwass in Bruguière, 1792
Dendroconus odengensis s.l. (Martin, 1895)	*Conus odengensis* Martin, 1895 [Beets, 1941]
Dendroconus pamotanensis Martin, 1906 *sensu* Beets, 1941	*Conus pamotanensis* Martin, 1906 [Beets, 1941]
Rolaniconus tjilonganensis Martin, 1906	*Conus tjilonganensis* Martin, 1906 [Beets, 1941]
Turriconus acutangulus Lamarck, 1810 *sensu* Beets, 1941	*Conus acutangulus* Lamarck, 1810 [Beets, 1941]
?*Fusiconus arntzenii* sensu (Beets, 1941) non (Martin, 1916)	*Conus arntzenii* Martin, 1916 [Beets, 1941]
Conus s.l. cf. *mutabilis* Reeve, 1844	*Conus* cf. *mutabilis* Reeve, 1844 [Beets, 1941]
Benthomangelia vandervlerki (Beets, 1941)	*Turris vandervlerki* Beets, 1941
Eucithara sawitrae (Beets 1941)	*Cythara sawitrae* Beets, 1941
Inquisitor durgae (Beets, 1941)	*Drillia durgae* Beets, 1941
Clavatula s.l. *berauensis* (Beets, 1941)	*Clavatula berauensis* (Beets, 1941)
Gemmula imitatrix (Martin, 1916) *sensu* Beets, 1941	*Turris imitatrix* (Martin, 1916) [Beets, 1941]
Strioterebrum ardjunoi (Beets, 1941)	*Terebra ardjunoi* Beets, 1941
Strioterebrum indrai (Beets, 1941)	*Terebra indrai* Beets, 1941
Strioterebrum mangkalihatensis (Beets, 1941)	*Terebra mangkalihatensis* Beets, 1941
Adelphotectonica karikalensis (Cossmann, 1903) *sensu* (Beets, 1941)	*Phillipia karikalensis* Cossman, 1910 [Beets, 1941]
Heliacus sokkohensis (Martin, 1916) *sensu* (Beets, 1941)	*Solarium sokkohense* (Martin, 1916) [Beets, 1941]
Acteocina sumatrana (Thiele, 1925) *sensu* Beets	*Acteocina* spec. 1 [Beets, 1941]
Cylichnidae indet. sp. 2	Retusidae indet. sp. [Reich et al., 2014]
Nucula njalindungensis s.l. Martin, 1919	*Nucula njalindungensis* Martin, 1919 [Beets, 1941]

Appendix 6.1: List of species that deviate from originally published name.

Anadara antiquata (Linneaus, 1758) *sensu* Beets, 1941	*Arca antiquata* Linnaeus, 1758 [Beets, 1941]
Anadara mangkalihatensis (Beets, 1941)	*Arca mangkalihatensis* Beets, 1941
Anadara nodosa (Martin, 1879) *sensu* Beets, 1941	*Arca nodosa* Martin, 1879 [Beets, 1941]
Barbatia leupoldi spec. nov. [Beets, 1941]	*Arca fusca* Bruguière, 1789
Barbatia wendti (Lamy, 1950) *sensu* Beets, 1941	*Arca oosthingii* Beets, 1941
Scapharca multiformis (Martin, 1879) *sensu* Beets, 1941	*Arca multiformis* Martin, 1879 [Beets, 1941]
Trisidios semitorta (Lamarck, 1819) *sensu* Beets, 1941	*Arca semitorta* Lamarck, 1819 [Beets, 1941]
Arcopsis sculptilis (Reeve, 1844) sensu *Beets*	*Arca menkrawitensis* Beets, 1941
Pteria s.l. spec indet. Beets, 1941	*Pteria* spec. indet. [Beets, 1941]
Dendostrea folia (Linnaeus, 1758) *sensu* Beets, 1941	*Ostrea* (*Lopha*) spec. [Beets, 1941]
Ostreidae indet. spp.	*Ostrea* (*Ostrea*) spec. indet. [Beets, 1941]
Mimachlamys menkrawitensis (Beets, 1941)	*Pecten menkrawitensis* Beets, 1941
Gloripallium cf. *pallium* (Linnaeus, 1758) *sensu* Beets, 1941	*Pecten* cf. *pallium* Linnaeus, 1758 [Beets, 1941]
Linga indrai Beets, 1941	*Phacoides indrai* Beets, 1941
Freneixicardia bomasense (Martin, 1916) *sensu* Beets, 1941	*Cardium bomasense* Martin, 1916 [Beets, 1941]
Fragum menkrawitense spec. nov. [Beets, 1941]	*Corculum* spec. [Beets, 1941]
Laevicardium njalindungense (Martin, 1922) *sensu* Beets, 1941	*Cardium njalindungense* Martin, 1922 [Beets, 1941]
Trachycardium denticostulatum (Beets, 1941)	*Cardium denticostulatum* Beets, 1941
Chama asperella Lamarck, 1819 *sensu* Beets, 1941	*Chama fibula* Reeve, 1846 [Beets, 1941]
Atopodonta sawitrae (Beets, 1941)	*Cypremeria sawitrae* Beets, 1941
Circe ickeae sensu (Beets, 1941) non Martin, 1922	*Gafrarium ickeae* (Martin, 1922) [Beets, 1941]
Timoclea imbricata (Sowerby II, 1853) *sensu* Beets, 1941	*Venus imbricata* Sowerby II, 1853 [Beets, 1941]

Family	**Taxon**	**FG**
Fissurellidae	*Diodora* sp.	3
	Emarginula sp.	3
	Puncturella sp.	2
	Scutus sp. 1	1
	Scutus sp. 2	1
	Macrochisma sp. 1	1
	Macrochisma sp. 2	1
	Hemitoma sp.	1
Calliostomatidae	*Calliostoma* sp.	3
Skeneidae	*Leucorhynchia* sp.	1
Trochidae	*Cantharidus berauensis* Beets, 1941	1
	Gibbula leupoldi Beets, 1941	1
	?*Gibbula* sp.	1
	Jujubinus cf. *polychromus* (A. Adams, 1853)	1
	Thalotia erinacea (Beets, 1941)	1
	Stomatia rubra Lamarck, 1816 *sensu* Beets, 1941	1
	Stomatolina sp.	1
	Trochus maculatus Linneaus, 1758 *sensu* Beets, 1941	1
	Ethalia minolina grooti spec. nov. Beets	1
	Trochidae indet. sp.	1
Turbinidae	*Astralium* sp.	1
	Turbo petholatus Linnaeus, 1758 *sensu* Beets, 1941	1
	Turbo sp.	1
	Trochoidea indet. sp.	1
Angariidae	*Angaria delphinus* Linneaus, 1758 *sensu* Beets, 1941	1
	Angaria spaerula (Kiener, 1873) *sensu* Beets, 1941	1
	Angaria aff. *spaerula* (Kiener, 1873) *sensu* Beets, 1942	1
Chilodontidae	*Euchelus atratus* (Gmelin, 1971) *sensu* Beets 1941	1
	Euchelus cf. *atratus* (Gmelin, 1971) *sensu* Beets, 1941	1
	Turcica suryai (Beets, 1941)	1
Colloniidae	*Bothropoma mediocarinata* Reich & Wesselingh, 2014	1
	Bothropoma pilula (Dunker, 1860) *sensu* Beets, 1941	1
	Bothropoma sp.	1
Phasianellidae	*Phasianella variegata* Lamarck, 1822 *sensu* Beets, 1941	1

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	0	5	9	2	2	1	2	2
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	1	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	4	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	3	89	24	5	2	2	11	4
0	0	0	3	0	1	0	2	0
10	0	13	0	0	0	0	0	0
0	25	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
0	0	1	1	0	0	0	1	0
0	1	0	0	0	0	0	0	0
0	5	0	0	0	0	0	0	0
0	0	0	1	0	1	0	0	0
0	0	1	0	0	0	0	0	0
0	5	0	0	0	0	0	0	0
0	0	4	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	7	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	2	1	0	0	1	0	0
0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
365	0	0	0	0	0	0	0	0
0	11	0	0	0	0	0	0	0
0	0	25	1	1	0	0	0	0
0	164	0	0	0	0	0	0	0

Appendix 6.2 (left): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Family	**Taxon**	**FG**
	Tricolia sp. 1	1
	Tricolia sp. 2	1
Neritidae	*Smaragdia gelingsehensis* Beets, 1986	1
	Smaragdia jogjacartensis (Martin, 1916)	1
	Smaragdia rangiana sensu Beets, 1941 non (Recluz, 1841)	1
	Smaragdia semari Beets, 1941	1
	Smaragdia sp.	1
Cerithiidae	*Cerithidium* cf. *pervarvulum* (Watson, 1886)	1
	Cerithidium sp. 1	1
	Cerithidium sp. 2	1
	Bittium sp. 1	1
	?*Bittium* sp. 2	1
	Cerithium bayeri Beets, 1941	1
	Cerithium deningeri (Martin, 1916)	1
	Cerithium dolfusi (Martin, 1916)	1
	Cerithium mangkalihatense Beets, 1941	1
	Cerithium noetlingi Martin, 1899	1
	Cerithium progoense (Martin, 1916)	1
	Cerithium teschi (Martin, 1916)	1
	Cerithium aff. *balteatum* Philippi, 1848	1
	Cerithium (*Vulgocerithium*) spec. nov. (Beets, 1941)	1
	Cerithium sp. 1	1
	Cerithium sp. 2	1
	Cerithium sp. 3 (morphotype A)	1
	Cerithium sp. 4	1
	Cerithium sp. 5 (*Cerithium* sp. 3 morphotype B)	1
	Cerithium sp. 6	1
	Cerithium sp. 7	1
	Cerithium s.l. sp. 1	1
	Cerithium s.l. sp. 2	1
	non *Cerithium ickei* Shepman, 1906	1
	Colina menkrawitense (Beets, 1941)	1
	Colina sp. 1	1
	Colina sp. 2	1

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	0	2	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	114	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	13	96	15	6	1	2	5	1
4	0	0	0	0	0	0	0	0
543	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	4	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	17	0	0	0	0	0	0	0
25	32	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
144	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0
0	0	346	25	3	2	0	13	7
0	0	165	0	0	0	0	0	0
0	0	149	0	0	0	0	0	0
0	0	315	0	0	0	0	0	0
0	0	138	107	24	21	4	48	10
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	5	0	0	0	0	0	0	0
0	0	4	14	7	5	2	0	0
0	0	13	0	0	0	0	0	0

Family	Taxon	FG
	Clypeomorus sp. 1	1
	?*Clypeomorus* sp. 2	1
	Clypeomorus sp. 3	1
	Pseudovertagus aluco (Linnaeus, 1758) *sensu* (Beets, 1941)	1
	Rhinoclavis leupoldi (Beets, 1941)	1
	Rhinoclavis sawitrae (Beets, 1941)	1
	Rhinoclavis sp. 1 s.l.	1
	Rhinoclavis sp. 2	1
Dialidae	*Diala semistriata* s.l. (Philippi, 1849)	1
	Diala sp.	1
	Gibborissoia sp.	1
Modulidae	*Conomodulus praeangerensis* (Martin, 1905)	1
	Conomodulus pseudotectum spec. nov. Landau et al., submitted	1
	Conomodulus renemai spec. nov. Landau et al., submitted	1
	Indomodulus miocenicus spec. nov. Landau et al., submitted	1
	Modulidae indet. sp.	1
Planaxiidae	*Planaxis* s.l. sp. 1	1
Potamididae	*Cerithidea hochstetteri* Martin, 1879	1
	Menkrawia callosalabiata Beets, 1941	1
	Potamides menkrawitensis Beets, 1941	1
	Telescopium titan Martin, 1889 *sensu* Beets, 1941	1
	Terebralia kelirensis (Martin, 1916) *sensu* Beets, 1941	1
	Terebralia s.l. sp.	1
	Vicarya callosa Jenkins, 1863 *sensu* Beets, 1941	1
	?Potamididae indet. sp. 1	1
	Potamididae indet. sp. 2	1
Scaliolidae	*Finella* cf. *pupoides* A. Adams, 1860	1
	Finella sp. 1	1
	Finella sp. 2	1
	Finella sp. 3	1
	Finella sp. 4	1
Thiaridae	"*Paludomus*" *conicus* Gray, 1834 *sensu* Beets, 1941	1
	"*Terebripirena*" *javana* (Martin, 1879) *sensu* Beets, 1941	1
Turritellidae	*Archimediella spolongensis* (Martin, 1916)	4

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
6	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	126	1	0	0	0	0	1
0	0	597	0	0	0	0	0	0
114	4	372	26	2	4	1	10	9
7	0	0	0	0	0	0	0	0
0	0	55	0	0	0	0	0	0
0	1	15	5	0	0	0	4	1
0	1	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0
0	4	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	10	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	8	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
0	12	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	0	0	2	0	2	0	0	0
0	0	2	0	0	0	0	0	0
3	0	322	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0
0	0	2	0	0	0	0	0	0
0	4	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Family	Taxon	FG
	Haustator sp.	4
	Turritella s.l. *damarwulani* Beets, 1941	4
	Turritella s.l. *talarensis* Eames, 1950	4
	Turritellidae indet. sp.	4
	Cerithiodea indet. 1	1
	Cerithiodea indet. 2	1
	Cerithiodea indet. 3	1
	?Cerithoidea indet. sp. 1	1
	?Cerithoidea indet. sp. 2	1
Campanilidae	*Campanile acutispinosum* Beets, 1941	1
	Campanile gigas (Martin, 1881) *sensu* Beets, 1941	1
Ampullinidae	*Ampullina berauensis* (Beets, 1941)	1
	Ampullina s.l. sp. 1	1
	Ampullina s.l. sp. 2	1
	Ampullospira martini Beets, 1941	1
	Ampullospira sp. 1	1
	Ampullospira sp. 2	1
	Ampullospira sp. 3	1
	?*Cernina* sp.	1
	Cernina fluctuata (Sowerby I, 1824)	1
Plesiotrochidae	*Plesiotrochus inopinatum* (Cossmann, 1910) *sensu* Beets, 1941	1
	Plesiotrochus aff. *inopinatum* (Cossmann, 1910) *sensu* Beets, 1942	1
	Plesiotrochus semari (Beets, 1941)	1
	Plesiotrochus tomlini Beets, 1941	1
	Plesiotrochus hasibuani Reich & Wesselingh, 2014	1
	Plesiotrochus sp. 1	1
	Plesiotrochus sp. 2	1
	?*Plesiotrochus* sp. 3	1
	Plesiotrochus sp. 4	1
	Plesiotrochus sp. 5	1
	Plesiotrochus sp. 6	1
Capulidae	*Capulus* sp. 1	4
	?*Capulus* sp. 2	4
	Capulus sp. 2	4

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
75	0	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	14	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
0	14	0	0	0	0	0	0	0
0	23	0	0	0	0	0	0	0
0	6	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0
0	13	0	0	0	0	0	0	0
0	0	36	5	2	2	0	1	0
0	0	8	6	3	0	0	2	1
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	7	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	15	0	0	0	0	0	0
0	27	0	0	0	0	0	0	0
0	4	0	0	0	0	0	0	0
159	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	16	0	0	0	0	0	0
0	0	11	0	0	0	0	0	0
0	0	0	54	14	13	1	18	8
1	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1
0	2	0	0	0	0	0	0	0

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Family	Taxon	FG
	Capulus sp. 3	4
	Capulus sp. 4	4
Eatoniellidae	*Eatoniella* s.l. sp. 1	1
	Eatoniella s.l. sp. 2	1
	Eatoniella s.l. sp. 3	1
Cypraeidae	*Barycypraea* spec. nov.	1
	Cleotrivia berauensis Schilder	1
	Cypraea vandervlerki Schilder	1
	Cypraea s.l. sp.	1
	Cypraeopsis vandervlerki Schilder, 1936	1
	Erronea berauensis Schilder	1
	Erronea aff. *berauensis* Schilder	1
	Pustularia fisiformis Schilder, 1932	1
Naticidae	*Natica spadicea* (Gmelin, 1791) *sensu* Beets, 1941	2
	Tanea undulata (Röding, 1798) *sensu* Beets, 1941	2
	Naticarius marochiensis (Gmelin, 1791) *sensu* Beets, 1941	2
	Naticarius sp.	2
	Natica s.l. sp. 1	2
	Natica s.l. sp. 2	2
	Polinices callosior (Martin, 1879) *sensu* Beets, 1941	2
	Polinices candidissima (Récluz, 1850) *sensu* Beets, 1941	2
	Polinices mammilia (Linnaeus, 1758) *sensu* Beets, 1941	2
	Sinum sp.	2
Rissoidae	*Microstelma* sp.	1
	Rissoina indrai Beets, 1941	1
	Rissoina fragileplicata (Beets, 1941)	1
	Rissoina semari Beets, 1941	1
	Rissoina (*Rissoina*) *banyungantiensis* Reich & Wesselingh, 2014	1
	Rissoina (*Rissoina*) sp. 1	1
	Rissoina (*Rissoina*) sp. 2	1
	Rissoina (*Phosinella*) sp. 1	1
	Rissoina (*Phosinella*) sp. 2	1
	?*Rissoina* s.l. sp.	1
	Rissoina indet.	1

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0
0	1	1	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	1	0	0	0	0	0	0
0	15	0	0	0	0	0	0	0
0	8	0	18	2	4	0	4	8
0	4	0	0	0	0	0	0	0
0	2	165	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
0	5	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	8	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1423	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	52	0	0	0	0	0	0
0	0	103	0	0	0	0	0	0
0	0	0	17	5	2	0	8	2
1	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1

Family	**Taxon**	**FG**
	Rissolina ramai Beets, 1941	1
	?*Rissolina* aff. *ramai* Beets, 1942	1
	Rissolina reticuspiralis Reich & Wesselingh, 2014	1
	Rissolina sp. 1	1
	Rissolina sp. 2	1
	Stosicia (*Stosicia*) sp.	1
	Stosicia (*Iseliella*) sp.	1
Iravadiidae	*Iravadia* (*Pseudonoba*) sp. 1	1
	Iravadia (*Pseudonoba*) sp. 2	1
Tornidae	*Cyclostremiscus novemcarinatus* (Melvill, 1906) *sensu* Beets, 1987	1
	Cyclostremiscus sp.	1
	Vitrinella sp.	1
Rostellariidae	*Rimella javana* (Martin, 1897)	1
	Varicospira sokkohensis (Martin, 1916)	1
	Varicospira sp.	1
Strombidae	*Canarium unifasciatum* s.l. Martin, 1984	1
	Strombus preoccupatus Finlay, 1927 *sensu* Beets, 1941	1
	Strombus s.l. sp. 1	1
	Strombus s.l. sp. 2	1
	Strombus s.l. sp. 3	1
	Strombus s.l. sp. 4	1
Seraphsidae	*Terebellum* spec. indet. [Beets, 1941]	1
	Terebellum sp. 1	1
	Terebellum sp. 2	1
	Terebellum spp.	1
Cassidae	?*Cassis martini* Beets, 1941	2
	Phalium menkrawitense Beets, 1941	2
Ranellidae	*Cymatium pileare* (Linnaeus, 1758)	2
	Cymatium cf. *vespaceum* (Lamarck, 1822) [det. Beu]	2
	Cymatium (*Turritriton*) cf. *tenuiliratum* (Lischke, 1873)	2
	Cymatium (*Reticutriton*) sp. 1	2
	Cymatium (*Reticutriton*) sp. 2	2
	Cymatium s.l. sp.	2
	Sassia (*Cymatiella*) *fennemai* (Martin, 1899)	2

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	1	0	0	0	0	0	0	0
0	0	8	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0
0	0	31	0	0	0	0	0	0
0	0	0	9	3	1	1	4	0
0	0	9	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	1	33	1	0	0	0	0	1
0	0	1	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	1	0
0	5	7	33	14	3	1	7	8
0	493	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	3	0	0	0	1	2
0	0	0	1	0	0	0	0	1
0	0	0	2	2	0	0	0	0
0	1	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	72	3	1	1	0	0	1
0	3	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
0	0	0	1	0	1	0	0	0
0	0	0	1	0	0	1	0	0
0	0	2	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
25	1	0	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Sassia menkrawitensis (Beets, 1941)	2
	Gyrineum bituberculare (Lamarck, 1816) *sensu* Beets	2
	Gyrineum lacunatum (Mighels, 1845)	2
	Ranellidae indet. sp. 1	2
	Ranellidae indet. sp. 2	2
Hipponicidae	*Hipponix conicus* (Schuhmacher, 1917) *sensu* Beets, 1941	4
Triviidae	*Eratoena* sp.	3
Vermetidae	*Vermetus* (?*Spiroglyphus*) sp.	4
	Vermetus (?*Serpulorbis*) sp.	4
	Vermetus javanus Martin, 1879 *sensu* Beets, 1941	4
	Vermetidae indet. sp. 1	4
	Vermetidae indet. sp. 2 s.l.	4
	Vermetidae indet. sp. 3 s.l.	4
Epitoniidae	*Amaea* sp. 1	3
	Amaea sp. 2	3
	Epitonium sp. 1	3
	Epitonium sp. 2	3
	Epitonium sp. 3	3
Eulimidae	*Melanella* sp. 1	3
	Melanella sp. 2	3
	Melanella sp. 3	3
	Melanella sp. 4	3
	Eulimidae indet. sp. 1	3
Triphoridae	*Metaxia* sp. 1	3
	Metaxia sp. 2	3
	Triphora s.l. *maharatai* Beets, 1941	3
	Triphora s.l. *indrai* Beets, 1941	3
	Triphora javana berauensis Beets, 1981	3
	Triphora s.l. sp. 1	3
	Triphora s.l. sp. 2	3
	Triphora s.l. sp. 3/ *Triphora* spec. indet. [det. Beet]	3
	Triphora s.l. sp. 4	3
	Triphora s.l. sp. 5	3
Cerithiopsidae	*Cerithiopsis* s.l. sp. 1	3

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	1	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	0	7	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0
0	21	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1
0	3	0	0	0	0	0	0	0
0	5	0	0	0	0	0	0	0
0	4	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	52	0	0	0	0	0	0
0	0	18	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0
0	0	6	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1
2	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	3	3	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
0	1	214	15	3	2	2	5	3
0	0	8	0	0	0	0	0	0
0	0	35	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Cerithiopsis s.l. sp. 2	3
	Cerithiopsis s.l. sp. 3	3
	Seila sp.	3
Buccinidae	*Phos dijki* Martin, 1884 *sensu* Beets, 1941	2
	Engina sp.	2
	?*Metula* sp.	2
	?Buccinidae indet. sp. 1	2
Columbellidae	*Euplica* sp. 1	2
	Euplica sp. 2	2
	Metanachis sp.	2
	Mitrella s.l. *njalindungensis* sensu (Beets, 1941) non (Martin, 1921)	2
	Mitrella s.l. cf. *njalindungensis* s.l. Martin, 1921	2
	Mitrella s.l. aff. *njalindungensis* sensu (Beets, 1941) non (Martin, 1921)	2
	Mitrella s.l. *gembacana* (Martin, 1884)	2
	Mitrella s.l. cf. *gembacana* (Martin, 1921)	2
	Mitrella s.l. sp. 1	2
	Mitrella s.l. sp. 2	2
	Mitrella s.l. sp. 3	2
	?*Mitrella* s.l. sp. 4	2
	Mitrella s.l. sp. 5	2
	Mitrella s.l. sp. 6	2
	Mitrella s.l. sp. 7	2
	?*Pyrenoela* sp.	2
	Zafra sp.	2
	Columbellidae indet. sp.	2
	Columbellidae indet. spp.	2
Fasciolariidae	*Fasciolaria suryai* Beets, 1941	2
	Fasciolaria s.l. sp. 1	2
	Fasciolaria s.l. sp. 2	2
	Fusinus sp.	2
	Peristernia beberiana sensu Beets, 1941 non (Martin, 1921)	2
	Peristernia martini Beets, 1941	2
	Peristernia sp.	2
	Fasciolariidae indet. sp. 1	2

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
1	0	0	0	0	0	0	0	0
0	0	6	0	0	0	0	0	0
0	0	0	2	1	0	0	1	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	3	1	1	0	1	0
0	0	0	5	1	0	0	4	0
0	0	4	0	0	0	0	0	0
0	0	17	0	0	0	0	0	0
0	5	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0
0	0	0	10	2	1	1	4	2
0	3	0	0	0	0	0	0	0
0	0	0	17	4	1	1	5	6
0	0	0	4	2	0	0	2	0
0	0	0	1	0	0	0	1	0
0	0	0	1	0	0	0	0	1
0	0	6	1	0	0	0	0	1
0	0	439	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	113	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0
0	0	116	59	14	10	2	23	10
2	0	0	0	0	0	0	0	0
0	0	404	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	3	0	11	2	0	1	7	1
0	3	0	0	0	0	0	0	0
0	0	62	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Family	**Taxon**	**FG**
Nassariidae	*Nassarius mangkalihatensis* Beets, 1941	2
	Nassarius sp. 1 s.l.	2
	Nassarius sp. 2	2
	Nassarius sp. 3	2
	Nassarius sp. 4	2
	Nassarius sp. 5	2
	Nassarius sp. 6	2
	Nassarius sp. 7	2
Melongenidae	*Melongena gigas* (Martin, 1883) *sensu* Beets, 1941	2
	Melongena sp.	2
Muricidae	*Calotrophon* (*Panamurex*) sp. 1	2
	Chicoreus juttingae (Beets, 1941)	2
	Chicoreus microphyllus (Lamarck, 1816)	2
	Chicoreus sp. 1	2
	Chicoreus sp. 2	2
	Chicoreus sp. 3	2
	Chicoreus sp. 4	2
	Haustellum haustellum (Linnaeus, 1758) *sensu* Beets, 1941	2
	Hexaplex ardjunoi (Beets, 1941)	2
	Coralliophila madreporarum (Sowerby, 1822) *sensu* Beets, 1941	3
	Coralliophila aff. *clathrata* (A. Adams, 1854)	3
	Coralliophila spec. nov. [Beets, 1941]	3
	Coralliophila sp. 1	3
	Coralliophila sp. 2	3
	Coralliophila sp. 3	3
	Coralliophila cf. sp. 3	3
	Coralliophila sp. 4	3
	Vitularia cf. *miliaris* (Gmelin, 1791)	2
	Typhina cf. *macropterus* (Martin, 1884)	2
	Typhinae indet. sp.	2
	Tripterotyphis s.l. sp.	2
	Muricidae indet. sp. 1	2
	Muricidae indet. sp. 2	2
	Muricidae indet. sp. 3	2

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	4	0	0	0	0	0	0	0
0	0	627	0	0	0	0	0	0
0	0	0	55	19	9	7	13	7
0	0	18	31	7	5	2	16	1
0	0	0	2	0	0	0	2	0
0	0	0	35	7	4	1	19	4
0	0	7	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	0	0	1	0	0	1	0	0
1	0	0	0	0	0	0	0	0
0	7	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	6	0	2	0	4	0
0	0	0	1	1	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	5	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	2	16	3	3	2	7	1
0	1	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	2	2	0	0	0	0
0	0	0	10	5	1	0	1	3
0	0	1	0	0	0	0	0	0
0	0	8	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Muricidae indet. sp. 4	2
	Muricidae indet. sp. 5	2
	?Muricidae indet. sp.	2
Costellariidae	*Vexillum ardjunoi* (Beets, 1941)	2
	Vexillum cf. *ardjunoi* (Beets, 1941)	2
	Vexillum escheri Beets, 1941	2
	Vexillum aff. *escheri* (Beets, 1941)	2
	Vexillum menkrawitensis Beets, 1941	2
	Vexillum kopenbergae	2
	Vexillum leupoldi Beets	2
	Vexillum sp. 1	2
	Vexillum sp. 2	2
	Vexillum sp. 3	2
	Vexillum sp. 4	2
	Vexillum sp. 5	2
	Vexillum sp. 6	2
	Vexillum sp. 7	2
	Vexillum sp. 8	2
	Vexillum sp. 9	2
	Vexillum sp. 10	2
	Vexillum sp. 11	2
	Vexillum sp. 12	2
	Vexillum sp. 14	2
	Vexillum sp. 15	2
	Vexillum sp. 16	2
	Vexillum sp. 17	2
	Vexillum sp. 18	2
	Vexillum sp. 19	2
	Vexillum sp. 20	2
	Vexillum sp. 21	2
	Vexillum sp. 22	2
	Vexillum sp. 23	2
	Vexillum sp. 24	2
	Vexillum indet. spp.	2

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	2	0	0	0	2	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
0	0	14	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	6	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
0	0	4	16	4	1	1	8	2
0	0	49	0	0	0	0	0	0
0	0	0	21	5	6	1	5	4
0	0	2	9	4	5	0	0	0
0	0	0	11	4	0	1	5	1
0	0	0	1	1	0	0	0	0
0	0	0	1	0	1	0	0	0
0	0	0	1	0	0	0	1	0
0	0	127	0	0	0	0	0	0
0	0	6	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	6	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	29	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	33	11	0	0	0	11	0

Family	**Taxon**	**FG**
Cystiscidae	*Cystiscus* sp. 1	3
	Cystiscus sp. 2	3
	Cystiscus sp. 3	3
	Cystiscus aff. sp. 3	3
	Gibberula sp. 1	3
	Gibberula sp. 2	3
Harpidae	*Harpa muticaeformis* Martin, 1919	2
	*Morum*spec. nov. [Beets, 1941]	2
Marginellidae	*Granulina maduparensis* Beets unpublished	3
	Granulina menkrawitensis (Beets, 1986)	3
	Granulina sp. 1	3
	Granulina sp. 2	3
	Granulina sp. 3	3
	Canalispira indrai (Beets, 1941)	3
	Cryptospira sp. 1	3
	Cryptospira sp. 2	3
	Dentimargo ringicula (Sowerby III, 1901) *sensu* Beets, 1941	3
	Dentimargo sp. 1 s.l.	3
	Dentimargo sp. 2	3
	Dentimargo aff. sp. 2	3
	Dentimargo sp. 3	3
	Dentimargo sp. 4	3
	Dentimargo sp. 5	3
	Mesoginella nangulanensis (Martin, 1916)	3
	Mesoginella cf. *njalindungensis* (Martin, 1916)	3
	Volvarina berauensis (Beets, 1941)	3
	Volvarina sp. 1	3
	Volvarina sp. 2	3
	Volvarina sp. 3	3
	Volvarina sp. 4	3
	Volvarina sp. 5	3
	Volvarina sp. 6	3
	Volvarina sp. 7	3
	Marginella s.l. spec. 1 [Beets, 1941]	3

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
6	0	0	0	0	0	0	0	0
0	0	13	0	0	0	0	0	0
0	0	0	11	2	0	0	9	0
0	0	1	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	9	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1
0	0	108	0	0	0	0	0	0
0	0	16	1	0	0	0	1	0
0	0	4	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	0	0	5	3	0	0	2	0
0	0	0	1	1	0	0	0	0
0	1	0	0	0	0	0	0	0
48	1	309	23	4	6	1	7	5
19	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	6	0	0	0	0	0	0
0	0	7	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
0	0	8	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Marginellidae indet. sp. 1	3
	Marginellidae indet. sp. 2	3
	Marginellidae indet. sp. 3	3
	Marginellidae indet. sp. 4	3
	Marginellidae indet. sp. 5	3
	Marginellidae indet. spp.	3
Mitridae	*Mitra ardjunoi* Beets, 1941	2
	Mitra bayeri Beets, 1941	2
	Mitra cf. *lipaiana* (?) (det. Beets)	2
	Mitra mitrai Beets, 1941	2
	Mitra menkrawitense Beets, 1941	2
	Mitra semari Beets, 1941	2
	Mitra cf. *sokkohensis* Martin, 1916	2
	Mitra vandervlerki Beets, 1941	2
	Mitra sp. 1	2
	Mitra sp. 2	2
	Mitra sp. 4	2
	Mitra sp. 5	2
Volutidae	*Lyria jugosa* Sowerby, 1839 *sensu* Beets	2
	Lyria jugosa Sowerby, 1839 forma spinulosa nov. Beets, 1941	2
Olividae	*Ancilla cinnamomea sensu* Beets, 1941 non Lamarck, 1801	2
	Ancilla aff. *cinnamomea sensu* Beets, 1941 non Lamarck, 1801 s.l.	2
	Ancilla sp. 1	2
	Ancilla sp. 2 s.l.	2
	Oliva australis Duclos, 1835 *sensu* Beets, 1941	2
	Oliva menkrawitensis Beets, 1941	2
	Oliva s.l. sp.	2
Olivellidae	*Olivella* sp. 1	2
	Olivella sp. 2	2
Conidae	*Phasmoconus* aff. *hulshofi* (Martin, 1906)	2
	Phasmoconus menkrawitensis Beets, 1941	2
	Pionoconus achatinus Gmelin, 1791 *sensu* Beets, 1941	2
	Pionoconus magus Linnaeus, 1758 *sensu* Beets, 1941	2
	Asprella sulcata Hwass *in* Bruguière, 1792 *sensu* Beets, 1941	2

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	**L 114**	**TF110**	**TF102**	**SR50**	**SR51**	**SR52**	**SR53**	**SR54**
0	0	2	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	3	0	2	1	0	0
0	1	0	0	0	0	0	0	0
0	10	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
0	0	1	2	0	0	0	1	1
0	0	16	2	2	0	0	0	0
0	0	0	1	0	1	0	0	0
0	0	0	1	0	0	0	1	0
0	3	0	0	0	0	0	0	0
0	10	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
1	1	131	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	10	0	0	0	0	0	0
0	4	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0
0	0	151	8	3	0	0	3	2
1	0	0	0	0	0	0	0	0
0	13	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	6	30	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Dendroconus odengensis s.l. (Martin, 1895)	2
	Dendroconus pamotanensis Martin, 1906 *sensu* Beets, 1941	2
	Rolaniconus tjilonganensis Martin, 1906	2
	Turriconus acutangulus Lamarck, 1810 *sensu* Beets, 1941	2
	Fusiconus spolongensis (Martin, 1916)	2
	?*Fusiconus arntzenii* (Martin, 1916)	2
	?*Fusiconus arntzenii* sensu (Beets, 1941) non (Martin, 1916)	2
	?*Fusiconus* cf. *arntzenii* sensu (Beets, 1941) non (Martin, 1916)	2
	?*Fusiconus* aff. *arntzenii* sensu (Beets, 1941) non (Martin, 1916)	2
	Conus s.l. cf. *mutabilis* Reeve, 1844	2
	Conidae indet. sp. 1	2
	Conidae indet. sp. 2	2
	Conidae indet. sp. 3	2
	Conidae indet. sp. 4	2
	Conidae indet. sp. 5	2
	Conidae indet. sp. 6	2
	Conidae indet. sp. 7	2
	Conidae indet. sp. 8	2
	Conidae indet. sp. 9	2
	Conidae indet. sp. 10	2
	Conidae indet. sp. 11	2
Borsoniidae	*Tomopleura* sp.	2
	Borsoniidae indet. sp. 1	2
Clathurellidae	*Lienardia* sp. 1	2
	Lienardia sp. 2	2
	Lienardia sp. 3	2
	Lienardia sp. 4	2
	?*Lienardia* sp. 5	2
	Clathurellidae indet. sp. 1	2
	Clathurellidae indet. sp. 2	2
	Clathurellidae indet. sp. 3	2
	Clathurellidae indet. sp. 4	2
	Clathurellidae indet. sp. 5	2
Mangellidae	*Benthomangelia vandervlerki* (Beets, 1941)	2

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	46	0	2	0	1	0	1	0
0	1	0	0	0	0	0	0	0
0	13	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0
0	3	2	0	0	0	0	0	0
0	0	7	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	5	2	1	0	2	0
0	0	0	4	1	0	0	3	0
0	0	0	3	3	0	0	0	0
0	0	1	1	1	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	20	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0
0	0	3	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
0	0	0	4	1	0	0	0	3
0	0	18	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	0	0	4	1	1	0	2	0
0	0	6	3	1	0	0	1	1
0	0	5	0	0	0	0	0	0
0	0	4	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Eucithara sawitrae (Beets 1941)	2
	Eucithara aff. *sawitrae* (Beets 1941)	2
	Eucithara sp. 1	2
	Eucithara sp. 2	2
	Eucithara sp. 3	2
	Eucithara sp. 4	2
	Eucithara sp. 5	2
	Eucithara cf. sp. 5	2
	Eucithara sp. 6	2
	Eucithara sp. 7	2
	Mangeliidae indet. sp. 1	2
	Mangeliidae indet. sp. 2	2
Raphitomidae	*Daphnella* sp.	2
	Pseudodaphnella sp. 1	2
	Pseudodaphnella sp. 2	2
	Pseudodaphnella sp. 3	2
	Raphitomidae indet. sp. 1	2
	Raphitomidae indet. sp. 2	2
	Raphitomidae indet. sp. 3	2
	Raphitomidae indet. sp. 4	2
	Raphitomidae indet. sp. 5	2
	Raphitomidae indet. sp. 6	2
	Raphitomidae indet. sp. 7	2
	Raphitomidae indet. sp. 8	2
	Raphitomidae indet. sp. 9	2
Drilliidae	*Iredalea* sp. 1	2
	?*Iredalea* sp. 2	2
	?*Splendrillia* sp. 1	2
	?*Splendrillia* sp. 2	2
	Tylotiella sp. 1	2
	Tylotiella sp. 2	2
	?Drilliidae indet. sp. 1	2
	?Drilliidae indet. sp. 2	2
Pseudomelatomidae	*Crassispira molengraafi* (Martin, 1916)	2

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	1	0	0	0	0	0	0	0
0	0	18	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	12	2	1	1	5	3
0	0	5	0	0	0	0	0	0
0	0	0	13	4	1	2	4	2
0	0	0	1	0	0	0	1	0
0	0	3	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	9	2	1	0	0	1	0
0	0	0	2	0	2	0	0	0
0	0	1	2	0	0	1	0	1
0	0	7	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	38	2	8	5	12	11
0	0	4	1	1	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	18	4	0	0	0	3	1
1	0	0	0	0	0	0	0	0
0	0	0	2	0	0	0	0	2
18	0	0	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Crassispira sp. 1	2
	Inquisitor durgae (Beets, 1941)	2
	Inquisitor cf. *durgae* (Beets, 1941)	2
	Inquisitor sp. 1	2
	?*Inquisitor* sp. 2	2
	Pseudomelatomidae indet. 1	2
	Pseudomelatomidae indet. 2	2
	Pseudomelatomidae indet. 3	2
	Pseudomelatomidae indet. 4	2
	Pseudomelatomidae indet. 5	2
	Pseudomelatomidae indet. 6	2
	Pseudomelatomidae indet. 7	2
	Pseudomelatomidae indet. 8	2
Clavatulidae	?*Turricula kelirensis* (Martin, 1916)	2
	Clavatula s.l. *berauensis* (Beets, 1941)	2
	Clavatula s.l. sp.	2
Strictispiridae	*Strictispira* sp. 1	2
	Strictispira sp. 2	2
	Strictispira sp. 3	2
Turridae	*Gemmula imitatrix* (Martin, 1916) *sensu* Beets, 1941	2
	'*Lophitoma*' sp. 1	2
Terebridae	*Strioterebrum ardjunoi* (Beets, 1941)	2
	Strioterebrum indrai (Beets, 1941)	2
	Strioterebrum mangkalihatensis (Beets, 1941)	2
	Terebra s.l. sp. 1	2
	Terebra s.l. sp. 2	2
	Conoidea indet. sp. 1	2
Cancellariidae	Cancellariidae indet. sp. 1	2
Acteonidae	*Acteon* s.l. sp. 1	2
	Acteon s.l. sp. 2	2
	?Acteonidae indet. sp.	2
	Pupa sp. 2	2
Aplustridae	Aplustridae indet. sp. 1	1
	Aplustridae indet. sp. 2	1

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	0	8	0	0	0	0	0	0
0	0	18	0	0	0	0	0	0
0	0	32	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	1	0	1	0	0	0
0	0	0	1	0	0	0	0	1
0	0	0	1	0	0	0	0	1
0	0	1	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
0	0	0	8	2	0	2	2	2
0	0	2	1	0	0	0	1	0
0	5	0	0	0	0	0	0	0
0	0	68	78	23	15	1	30	9
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	1	0	1	0	0	0
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	1	0	1	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0

Family	**Taxon**	**FG**
Architectonicidae	*Adelphotectonica karikalensis* (Cossmann, 1903) *sensu* (Beets, 1941)	3
	Adelphotectonica sp. 1	3
	Adelphotectonica sp. 2	3
	?*Adelphotectonica* sp. 3	3
	?*Discotectonica* sp.	3
	Heliacus (*Torinista*) *implexus* (Mighels, 1845)	3
	Heliacus sokkohensis (Martin, 1916) *sensu* (Beets, 1941)	3
	Granosolarium mitrai (Beets, 1941)	3
	Psilaxis cf. *radiatus* (Röding, 1798)	3
Odostomiidae	*Odostomia* sp. 1	3
	Odostomia sp. 2	3
	Parodostomia sp. 1	3
	Parodostomia sp. 2	3
	Parodostomia sp. 3	3
	Odostomiinae sp. 1	3
	Odostomiinae sp. 2	3
	Babella sp. 1	3
	Chrysallida sp. 1	3
	?*Chrysallida* sp. 2	3
	Linopyrga sp. 1	3
	Menesthella sp. 1	3
	?*Menesthella* sp. 2	3
	Pyrgulina sp. 1	3
	Pyrgulina sp. 2	3
Pyramidellidae	*Longchaeus* sp.	3
	Pyramidella sp. 1	3
	Pyramidella sp. 2	3
Syrnolidae	*Syrnola* sp.	3
	?*Tibersyrnola* sp.	3
Turbonillidae	*Asmunda* sp.	3
	?*Pyrgiscus* sp.	3
	Turbolidium sp. 1	3
	?*Turbolidium* sp. 2	3
	Turbonilla sp. 1	3

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	1	10	2	0	1	0	0	1
11	0	0	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
1	0	7	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0
0	0	107	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	1	0	0	0	1	0
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	2	0	1	0	1	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1
0	0	1	0	0	0	0	0	0
0	0	0	2	0	1	0	1	0
2	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Turbonilla sp. 2	3
	?*Turbonilla* sp. 3	3
	Eulimella sp.	3
	Bulicingulina sp.	3
	‘Pyramidella’ spec. indet. [Beets, 1941]	3
	Pyramidelloidea indet. sp. 1	3
	Pyramidelloidea indet. sp. 2	3
	Pyramidelloidea indet. sp. 3	3
	Pyramidelloidea indet. sp. 4	3
Ringiculidae	*Ringicula* sp. 1	2
	Ringicula sp. 2	2
	Ringicula sp. 3	2
	Ringicula sp. 4	2
	Ringicula sp. 5	2
Bullidae	*Bulla* sp.	1
Haminoeidae	*Diniatys* aff. d*entifer* (A. Adams, 1850)	1
	Diniatys sp.	1
Cylichnidae	*Acteocina sumatrana* (Thiele, 1925) *sensu* Beets, 1941	2
	Acteocina sp. 1	2
	Acteocina sp. 2	2
	Cylichna durgae Beets, 1941	2
	Cylichna cf. *durgae* Beets, 1942	2
	Cylichna triplicata (Martin, 1916)	2
	Cylichna aff. *triplicata* (Martin, 1916)	2
	Talahabia cf. *dentifera* Martin, 1921	2
	Cylichnidae indet. sp. 1	2
	Cylichnidae indet. sp. 2	2
	Cylichnidae indet. sp. 3	2
	Cylichnidae indet. sp. 4	2
	Cylichnidae indet. sp. 5	2
	Cylichnidae indet. sp. 6	2
	Cylichnidae indet. sp. 7	2
	Cylichnidae indet. sp. 8	2
Retusidae	?*Pyrunculus* sp.	2

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	0	3	0	0	0	0	0	0
0	0	4	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
0	0	41	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0
0	0	0	1	0	0	0	1	0
0	0	0	1	0	0	0	1	0
0	0	6	0	0	0	0	0	0
125	0	0	0	0	0	0	0	0
94	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	12	0	0	0	0	0	0
0	0	36	0	0	0	0	0	0
0	0	4	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	0	17	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
52	8	0	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	68	4	1	1	0	0	2
3	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
0	0	0	2	0	0	0	0	2
0	0	0	1	1	0	0	0	0
0	0	4	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	4	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	5	0	0	0	0	0	0

Family	**Taxon**	**FG**
Cephalaspidea	Cephalaspidea indet. sp.	2
Juliidae	*Berthelinia* sp.	1
	Julia sp.	1
Gastropoda indet. spp.		
Nuculidae	*Leionucula* sp.	5
	Nucula njalindungensis s.l. Martin, 1919	5
	Nucula sp.	5
Mytilidae	*Brachidontes* sp.	4
	Modiolus sp. 1	4
	Modiolus sp. 2	4
	Musculus sp.	4
Arcidae	*Acar* sp.	4
	Anadara antiquata (Linneaus, 1758) *sensu* Beets, 1941	4
	Anadara mangkalihatensis (Beets, 1941)	4
	Anadara nodosa (Martin, 1879) *sensu* Beets, 1941	4
	Anadara sp. 1	4
	Anadara sp. 2	4
	Anadara sp. 3	4
	Arca kelirensis Martin, 1916 *sensu* Beets, 1941	4
	Arca spec. indet. [Beets, 1941]	4
	Barbatia leupoldi spec. nov. [Beets, 1941]	4
	Barbatia wendti (Lamy, 1950) *sensu* Beets, 1941	4
	?*Barbatia* sp.	4
	Scapharca multiformis (Martin, 1879) *sensu* Beets, 1941	4
	Trisidios semitorta (Lamarck, 1819) *sensu* Beets, 1941	4
Glycymerididae	?*Tucetona* sp.	4
Noetiidae	*Arcopsis sculptilis* (Reeve, 1844) sensu *Beets*	4
Pteriidae	*Pteria* s.l. spec indet. Beets, 1941	4
Malleidae	?*Vulsella* sp.	4
	Malleidae indet. sp.	4
Ostreidae	*Dendostrea folia* (Linnaeus, 1758) *sensu* Beets, 1941	4
	Lopha sp.	4
	Ostreidae indet. spp.	4
Pectinidae	*Mimachlamys menkrawitensis* (Beets, 1941)	4

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	11	0	0	0	0	0	0
20	0	58	113	17	20	4	59	13
0	0	15	0	0	0	0	0	0
0	7	52	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1
0	0	4	2	0	0	0	1	1
0	0	0	1	0	0	0	1	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	2	5	2	0	0	1	2
0	5	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	2	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	8	0	0	0	0	0	0
0	0	1	41	13	6	1	13	8
0	2	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	2	2	0	0	0	1	1
0	9	0	0	0	0	0	0	0
0	16	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	3	1	53	18	7	2	19	7
0	2	13	4	1	0	0	2	1
0	0	1	0	0	0	0	0	0
0	0	0	2	0	1	0	1	0
0	2	125	66	11	14	4	26	11
0	0	0	2	0	0	0	0	2
0	1	11	15	1	3	1	5	5
0	3	0	0	0	0	0	0	0

Family	**Taxon**	**FG**
	Mimachlamys aff. *menkrawitensis* (Beets, 1941)	4
	Mimachlamys sp.	4
	Chlamys s.l. sp. 1	4
	Gloripallium cf. *pallium* (Linnaeus, 1758) *sensu* Beets, 1941	4
	Gloripallium sp.	4
Spondylidae	*Spondylus* sp. 1	4
	Spondylus sp. 2	4
Plicatulidae	*Plicatula* sp.	4
Limidae	?*Ctenoides* sp.	4
Lucinidae	*Cardiolucina civica* (Yokoyama, 1927)	5
	Cardiolucina sp. 1	5
	Cardiolucina sp. 2	5
	Linga indrai Beets, 1941	5
	Myrtea spec. nov. [Beets, 1941]	5
	Lucinidae indet. sp.	5
Carditidae	*Cardita* s.l. sp. 1	4
	Cardita s.l. sp. 2	4
	Cardita s.l. sp. 3	4
Corbiculidae	*Corbicula bitruncata* von Martens, 1908 *sensu* Beets, 1941	4
Cardiidae	*Freneixicardia bomasense* (Martin, 1916) *sensu* Beets, 1941	4
	Fragum menkrawitense spec. nov. [Beets, 1941]	4
	Fragum sp. 1	4
	Fragum sp. 2	4
	Fragum sp. 3	4
	Laevicardium njalindungense (Martin, 1922) *sensu* Beets, 1941	4
	Nemocardium sp. 1	4
	Nemocardium sp. 2	4
	?*Acrosterigma* sp.	4
	Vasticardium sp.	4
	Trachycardium denticostulatum (Beets, 1941)	4
	Tridacna (*Camatrachea*) *mbalavuana* Ladd, 1934	4
	Tridacna indet. juvenile	4
	Tridacninae indet. sp. 1	4
	Tridacninae indet. sp. 2	4

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	0	1	13	3	2	1	6	1
1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	0	5	0	1	1	2	1
1	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1
0	0	0	1	0	0	1	0	0
0	0	1	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0
0	0	2	6	2	1	0	1	2
0	1	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
112	0	0	0	0	0	0	0	0
0	0	23	0	0	0	0	0	0
0	0	0	6	2	1	0	2	1
0	2	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
0	0	49	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	1	0	0	0	1	0
0	2	1	2	0	1	0	1	0
0	0	0	1	1	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0

Family	Taxon	FG
	Cardiidae indet. sp. 1	4
	Cardiidae indet. sp. 2	4
	Cardiidae indet. sp. 3	4
	Cardiidae indet. sp. 6	4
	Cardiidae indet. sp. 7	4
	Cardiidae indet. sp. 8	4
	Cardiidae indet. sp. 9	4
	Cardiidae indet. sp. 10	4
	Cardiidae indet. sp. 11	4
Chamidae	*Chama asperella* Lamarck, 1819 *sensu* Beets, 1941	4
	Chama sp. 1	4
	Chama sp. 2	4
	Chama sp. 3	4
Kelliellidae	*Kelliella* sp.	4
Tellinidae	?*Arcopagia* sp. 1	6
	?Eurytellina spec. indet. [Beets, 1941]	6
	Tellina s.l. sp. 1	6
	Tellina s.l. sp. 2	6
	Tellina s.l. sp. 3	6
	Tellina s.l. sp. 4	6
	Tellina s.l. sp. 5	6
	Tellina s.l. sp. 6	6
	Tellina s.l. sp. 7	6
	Tellina s.l. sp. 8	6
	Tellina s.l. sp. 9	6
	Tellina s.l. sp. 10	6
Veneridae	*Atopodonta sawitrae* (Beets, 1941)	4
	Circe ickeae sensu (Beets, 1941) non Martin, 1922	4
	Circe junghuhni Martin, 1917	4
	Circe sp.	4
	Dosinia sp. + juvenils	4
	Gafrarium sp.	4
	Timoclea imbricata (Sowerby II, 1853) *sensu* Beets, 1941	4
	?*Timoclea* sp. 1	4

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	1	2	0	0	1	1	0
0	0	0	11	2	0	3	4	2
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	9	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	3	0	0	0	0	0	0
0	0	0	30	3	3	2	15	7
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	3	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	0	1	0	0	1	0	0
0	0	0	1	0	0	0	0	1
0	0	1	2	0	0	0	1	1
0	0	0	1	0	0	0	1	0
0	0	83	0	0	0	0	0	0
0	0	5	0	0	0	0	0	0
0	0	10	0	0	0	0	0	0
0	0	6	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0
0	7	12	12	2	2	0	4	4
96	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
0	0	10	2	0	0	0	2	0
0	0	0	8	3	1	1	3	0
0	1	0	0	0	0	0	0	0
0	0	1	2	0	1	0	1	0

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Appendix 6.2 (continued): List of all species in samples BA 18, L 114, TF 110, and TF 102 (including subsamples), units containing unidentified taxa included, with feeding guild assignment (FG): 1 = herbivore, 2 = predatory carnivore, 3 = browsing carnivore, 4 = suspension feeder, 5 = chemosymbiotic deposit feeders, 6 = deposit feeders, 7 = boring.

Family	**Taxon**	**FG**
	?*Timoclea* sp. 2	4
	?*Timoclea* sp. 3	4
	Veneridae indet. sp. 1	4
	Veneridae indet. sp. 2	4
	Veneridae indet. sp. 3	4
	Veneridae indet. sp. 4	4
	Veneridae indet. sp. 5	4
Veneroidea	Veneroidea indet. sp. 1	4
	Veneroidea indet. sp. 2	4
Corbulidae	*Corbula solidula* Hinds, 1843 *sensu* Beets, unpublished	4
	Corbula sp. 1	4
	Corbula sp. 2	4
Pholadidae	Pholodidae indet. sp.	7
	Bivalvia indet. sp.	4
Scaphopoda	*Dentalium* (*Dentalium*) *jonkeri* Martin, 1885 sensu Beets, 1941	2
	Dentalium sp. 1	2
	Dentalium sp. 2	2
	Dentalium sp. 3	2
	Dentalium sp. 4	2
	Dentalium sp. 5	2
	Dentalium spec. indet. [Beets, 1941]	2
Acanthochotonidae	*Leptoplax* sp.	1
Crytoplacidae	*Cryptoplax menkrawitensis* Beets, 1941	1
	Cryptoplax sp.	1
Schizochitonidae	*Schizochiton incisus* (Sowerby II, 1841)	1
	Chitonoidea indet. sp. 1	1
	Chitonoidea indet. sp. 2	1
	Chitonoidea indet. sp. 3	1
	Chitonoidea indet. sp. 4	1
	Total specimens	
	Total species	

BA18	L 114	TF110	TF102	SR50	SR51	SR52	SR53	SR54
0	0	0	1	0	0	0	1	0
0	0	1	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
0	0	0	1	1	0	0	0	0
0	0	0	2	0	0	0	2	0
0	0	11	1	0	0	0	1	0
1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	1	1	11	4	2	1	4	0
0	0	0	1	1	0	0	0	0
0	0	0	1	0	0	0	0	1
0	0	0	1	0	0	0	0	1
0	0	1	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
0	0	26	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0
0	0	0	1	0	0	0	0	1
4444	**1410**	**8212**	**1468**	**344**	**232**	**78**	**568**	**246**
185	**188**	**272**	**162**	**84**	**66**	**45**	**97**	**79**

Appendix 6.3: Shared species of all assemblages.

Shared species all samples				
	BA 18	L 114	TF 110	TF 102
Diala semistriata s.l. (Philippi, 1849)	114	4	372	26
Dentimargo sp. 1 s.l.	48	1	309	23
Shared species L 114 , TF 110, TF 102				
	L 114	TF 110	TF 102	
Gibbula leupoldi Beets, 1941	3	89	24	
Smaragdia semari Beets, 1941	13	96	15	
Conomodulus praeangerensis (Martin, 1905)	1	15	5	
Cyclostremiscus novemcarinatus (Melvill, 1906) *sensu* Beets, 1987	1	33	1	
Canarium unifasciatum s.l. Martin, 1984	5	7	33	
Triphora s.l. sp. 3/ *Triphora* spec. indet. [det. Beet]	1	214	15	
Adelphotectonica karikalensis (Cossmann, 1903) *sensu* (Beets, 1941)	1	10	2	
Arcopsis sculptilis (Reeve, 1844) sensu *Beets*	3	1	53	
Dendostrea folia (Linnaeus, 1758) *sensu* Beets, 1941	2	125	66	
Trachycardium denticostulatum (Beets, 1941)	2	1	2	
Circe ickeae sensu (Beets, 1941) non Martin, 1922	7	12	12	
Corbula solida Hinds, 1843 *sensu* Beets, unpublished	1	1	11	
Shared species BA 18, L 114 and TF 110				
	BA 18	L 114	TF 110	
Ancilla aff. *cinnamomea* sensu Beets, 1941 non Lamarck, 1801 s.l.	1	1	131	
Shared species BA 18 and L 114				
	BA 18	L 114		
Cerithium progoense (Martin, 1916)	25	32		
Sassia (*Cymatiella*) *fennemai* (Martin, 1899)	25	1		
Cylichna triplicata (Martin, 1916)	52	8		
Shared species BA 18 and TF 110				
	BA 18	TF 110		
Jujubinus cf. *polychromus* (A. Adams, 1853)	10	13		
Finella cf. *pupoides* A. Adams, 1860	3	322		
Shared species L 114 and TF 110				
	L 114	TF 110		
Hemitoma tricarinata (Born, 1778) *sensu* Beets, 1941	1	1		

Appendix 6.3 (continued)

Barycypraea spec. nov.	1	1
Erronea aff. *berauensis* Schilder	1	1
Naticarius marochiensis (Gmelin, 1791) *sensu* Beets, 1941	2	165
Triphora maharatai Beets, 1941	3	3
Pionoconus magus Linnaeus, 1758 *sensu* Beets, 1941	6	30
?*Fusiconus arntzenii* sensu (Beets, 1941) non (Martin, 1916)	3	2
Nucula njalindungensis s.l. Martin, 1919	7	52
Pteria s.l. spec indet. Beets, 1941	2	13
Shared species L 114 and TF 102		
	L 114	TF 102
Natica helvacea Lamarck, 1822 *sensu* Beets, 1941	8	18
Peristernia beberiana sensu Beets, 1941 non (Martin, 1921)	3	11
Dendroconus odengensis s.l. (Martin, 1895)	46	2
Shared species TF 110 and TF 102		
	TF 110	TF 102
Diodora sp.	5	9
Angaria aff. *spaerula* (Kiener, 1873) *sensu* Beets, 1942	2	1
Cerithium sp. 3 (morphotype A)	346	25
Cerithium sp. 7	138	107
Colina sp. 1	4	14
Rhinoclavis sp. 1 s.l.	126	1
Ampullospira sp. 1	36	5
Ampullospira sp. 2	8	6
Terebellum spp.	72	3
?*Mitrella* s.l. sp. 4	6	1
Zafra sp.	116	59
Nassarius sp. 3	18	31
Coralliophila aff. *clathrata* (A. Adams, 1854)	2	16
Vexillum sp. 9	4	16
Vexillum sp. 12	2	9
Granulina sp. 2	16	1

Appendix 6.3 (continued): Shared species of all assemblages.

Shared species TF 110 and TF 102 (continued)		
	TF 110	TF 102
Mitra sp. 1	1	2
Mitra sp. 2	16	2
Olivella sp. 2	151	5
Conidae indet. sp. 6	1	1
Clathurellidae indet. sp. 2	6	3
Raphitomidae indet. sp. 3	9	2
Raphitomidae indet. sp. 5	1	2
Iredalea sp. 1	1	38
?*Iredalea* sp. 2	4	1
Tylotiella sp. 2	18	6
Strictispira sp. 3	2	1
'*Lophitoma'* sp. 1	68	101
Talahabia cf. *dentifera* Martin, 1921	68	4
Brachidontes sp.	4	2
Acar sp.	2	5
Anadara sp. 3	1	41
?*Barbatia* sp.	2	2
Ostreidae indet. spp.	11	15
Mimachlamys aff. *menkrawitensis* (Beets, 1941)	1	13
Cardiolucina sp. 2	2	6
Cardiidae indet. sp. 6	1	2
Tellina s.l. sp. 5	1	2
Dosinia sp. + juvenils	10	2
?*Timoclea* sp. 1	1	2

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Samenvatting

De Indo-West Pacific (IWP), waaronder het huidige Maleisië, de Filippijnen, Indonesië en Papua Nieuw Guinea valt, wordt gezien als een belangrijk centrum voor marine biodiversiteit (Hoeksema, 2007; Renema et al., 2010). De enorme soortenrijkdom van mariene organismen in dit gebied wordt gekenmerkt door diverse groepen foraminiferen, weekdieren en koralen (Bellwood et al., 2005; Hoeksema, 2007; Kohn, 1990; Wilson en Rosen, 1998). Er wordt verondersteld dat het ontstaan van deze buitengewone biodiversiteit samen valt met de diversificatie van koraalriffen en geassocieerde biota in het vroeg Neogeen (Wilson en Rosen, 1998; hoofdstuk 6). De fossiele fauna's die deze mariene diversificatie in Zuidoost Azië hebben aangetoond zijn echter zeer schaars. In 2010 werd het daarom het "Throughflow" programma in het kader van het Marie-Curie Initial Training Network (ITN) opgericht om de timing en de context van deze diversificatie, in het bijzonder de Miocene associaties en hun leefomgeving (paleohabitats) van Oost Kalimantan (Indonesië), beter vast te kunnen leggen. Voor dit doel hebben we gezamenlijk nieuwe fauna's verzameld en betere dateringen uitgevoerd tijdens een aantal expedities.

Het oorspronkelijke doel van dit onderzoekproject binnen het "Throughflow" programma was om de biodiversiteit van mariene mollusken in het Mioceen van Indonesië te reconstrueren. Om de veranderingen in soortenrijkdom over geologische tijdschalen goed te kunnen reconstrueren is het echter noodzakelijk dat fauna's van eenzelfde leefomgeving, zgn. paleomilieus, met elkaar worden vergeleken. Er bestaan immers grote diversiteitsverschillen tussen milieus (hoofdstuk 3). Uit mijn onderzoek blijkt dat zeegrasmilieus en hun molluskenfauna's een goede modelgroep en milieutype zijn om veranderingen in soortenrijkdom te reconstrueren, om de volgende redenen:

1. *Belang*. Zeegrasmilieus zijn belangrijke mariene ecosystemen met een wereldwijd voorkomen waarvoor veel wetenschappelijke belangstelling bestaat (hoofdstuk 1). Het gaat om milieus met een hoge productiviteit die een belangrijke rol spelen in de koolstof cyclus van de oceanen. Hun wortels stabiliseren sediment en helpen kusterosie en eutrofiering tegen te gaan en organische vervuiling vast te leggen. Verder biedt de driedimensionale structuur een belangrijke leefomgeving voor een veelheid

aan organismen, inclusief groepen die economisch van belang zijn, en als broedgebied voor diverse vissoorten. Zeegrasmilieus worden bedreigd door menselijk handelen en het is daarom belangrijk dat er wetenschappelijke inzichten worden verkregen over de dynamiek van dit type milieu en gerelateerde biodiversiteit op verschillende tijdschalen.

2. *Abundantie en soortenrijkdom*. Mollusken (weekdieren) zijn een fylum waartoe onder meer slakken, tweekleppigen en inktvisachtigen behoren. Ze dragen fors bij aan de soortenrijkdom van zeegrasmilieus. Ze zijn overvloedig aanwezig en domineren vaak de invertebrata. De soortenrijkdom van mollusken in zeegrasmilieus is niet excessief, zoals dat bijvoorbeeld in koraalriffen wel het geval is. Dit maakt het mogelijk om totale molluskenfauna's van zeegrasmilieus te bestuderen binnen bijvoorbeeld de duur van een promotieonderzoek (hoofdstukken 2, 3, 6).

3. *Biodiversiteit*. De globale patronen van soortenrijkdom van zowel zeegras als van geassocieerde soorten volgen die van andere mariene groepen. De maximale soortenrijkdom is te vinden in de eerdergenoemde IWP (hoofdstuk 6).

4. *Fossilisatie*. Zeegras komt vooral voor op enigszins beschutte plaatsen, waarbij de planten de golven en stromingen afzwakken en sediment vastleggen. Deze sedimenten zijn vaak fijn korreliger dan die in aanliggende onbegroeide gebieden (hoofdstuk 1). De kans op fossilisatie is daardoor ook groter in deze gebieden, terwijl het transport van fossiel materiaal van en naar dit zeegrasmilieu kleiner is dan in de omliggende onbegroeide milieus. Daarnaast kunnen hogere pH waarden in dergelijke milieus bijdragen aan hogere calcificatie snelheden van geassocieerde biota en daarmee tafonomisch verlies van schelpen tegengaan. Zeegras geassocieerde mollusken behoren tot de best geconserveerde molluskenfauna's in de mariene geologische overlevering van de IWP. Rif-geassocieerde faunas in het gebied hebben bijvoorbeeld veel last van diagenese (hoofdstukken 2, 3, 5, 6).

5. *Beschikbaarheid.* In verschillende stratigrafische intervallen van het Mioceen van Indonesië zijn zeegras gerelateerde fauna's goed bewaard gebleven. Deze zijn onderwerp van dit proefschrift (hoofdstukken 2, 5, 6).

De focus op specifieke paleomilieus betekent overigens dat deze overtuigend moet kunnen worden vastgesteld in de geologische overlevering. Zeegrassen en de pollen van zeegrassen vergaan gemakkelijk en hebben derhalve een slechte fossiele overlevering. Om zeegrasmilieus in het geologische verleden te kunnen vaststellen zijn dus betere methoden nodig, waardoor de oorspronkelijk focus van dit onderzoek zich gedeeltelijk heeft verlegd naar de bestudering van die mogelijkheden (hoofdstuk 1). Ik heb hiervoor zowel de molluskenfauna's van zeegras en onbegroeide milieus met elkaar vergeleken (hoofdstukken 2 en 3) en de potentie van molluskenassemblages om zeegrasmilieus te karakteriseren onderzocht (hoofdstukken 4 en 5). Vervolgens heb ik voor het eerst de veranderingen in de biodiversiteit van zeegrasmolluskenfauna's tijdens het Mioceen van Indonesië gedocumenteerd (hoofdstuk 6). Dit laatste hoofdstuk gaat ook in op de uitdagingen die het werken met collectie materiaal met zich meebrengt waarvan de verzamel en analyse methoden niet volledig bekend zijn.

Het opstellen van nieuwe soortbeschrijvingen en gedetailleerde taxonomische revisies is van fundamenteel belang voor ecologische en biodiversiteitsstudies, maar dit vormde niet het hoofddoel van mijn onderzoek. Ik heb echter vier nieuwe slakkensoorten beschreven van vroeg Burdigalien afzettingen (vroeg Mioceen) van Banyunganti van Oost Java (hoofdstuk 2). Een groot deel van de taxa die aan de orde komen in hoofdstukken 2, 3 en 6 zijn tot nu toe nog onbeschreven. Echter, het gebruik van open nomenclatuur leverde een praktische oplossing om binnen afzienbare tijd dit onderzoek aan deze zeer diverse en grotendeels onbekende fauna's te kunnen voltooien en deze te openbaren voor de brede onderzoekgemeenschap.

Zeegrassen fossiliseren zelden en hun voorkomen in het verleden wordt veelal verondersteld aan de hand van indirect indicatoren zoals fossiele groepen, sedimentologische, tafonomische en geochemische proxies. Het succesvol kunnen identificeren van zeegrasmilieus in het geologische verleden bleek een flinke uitdaging. Niet alleen mollusken, maar ook andere groepen van organismen en proxies werden gebruikt voor hun potentieel als "Indirecte Paleo Zeegras Indicatoren" (IPSI: indirect paleo seagrass indicators). **Hoofdstuk 1- Introductie** bevat een revisie van voorheen gebruikte IPSI's wat resulteerde in een catalogus voor identificatie van zeegrasmilieus in de fossiele overlevering voor toekomstig onderzoek. Het hoofdstuk gaat ook in op het ecologisch belang van zeegrasvelden en de belangrijkste kenmerken van dit ecosysteem.

Miocene molluskenfauna's van Indonesië komen aan de orde in het eerste deel van dit proefschrift (hoofdstukken 2 en 3). Fossiele molluskengemeenschappen van twee verschillende paleomilieus worden gedocumenteerd en geven een inzicht in de bijzonder goede conservering en hoge soortenrijkdom. Ook ga ik in deze hoofdstukken in op de vragen hoe bepaalde molluskengemeenschappen kunnen worden gekarakteriseerd en worden toegewezen aan bepaalde paleomilieus. En of er ecologische verschillen tussen associaties kunnen worden herkent die geschikt zijn om paleomilieus te onderscheiden.

Hoofdstuk 2 behandelt een studie van een molluskenfauna uit het vroeg Mioceen van Banyunganti, Java. De fauna wordt op grond van haar taxonomische samenstelling, waaronder de indicator taxon *Smaragdia*, haar ecologische karakter en de samenstelling van de begeleidende foraminiferen fauna beschouwd als een zeegrasfauna. De fauna is uitgebreid bestudeerd en 184 mollusken taxa worden gerapporteerd en afgebeeld, waarvan 159 gastropoden. Het merendeel van de taxa is waarschijnlijk nieuw. Vier nieuwe soorten worden beschreven. De fauna van Banyunganti wordt gekenmerkt door een hoge soortenrijkdom, een hoge abundantie van kleine grazende slakjes en door de uitmuntende conservering van de sculptuur van de schelpen.

Hoofdstuk 3 behandelt een goed-geconserveerde molluskenfauna van het Tortonien (laat Mioceen) van Bontang, Oost Kalimantan. De fauna is geassocieerd met vertakkende koralen en het afzettingsmilieu is geïnterpreteerd als een “coral carpet” milieu (vrij vertaald een koraal tapijt). Soortsamenstelling en abundantie alsmede de voedingsklassen zijn geïnventariseerd. De fauna verschilt van de zeegras fauna van Java uit hoofdstuk 2 door de samenstelling van de voedingsgroepen: predators (rovers) onder de slakken zijn veel algemener in de koraal geassocieerde fauna dan in de zeegras fauna. De inventarisatie van de “coral carpet” fauna ondersteunt de aanname dat voedingsecologie een instrument kan zijn voor het onderscheiden van zeegras milieus van andere ondiep mariene milieus in de fossiele overlevering.

Het tweede deel van het proefschrift (hoofstukken 4 en 5) omvat twee manieren om mollusken associaties te gebruiken als IPSIs (zie hoofdstuk 1). De studies zijn niet gericht op individuele taxa maar op proxies die zijn gebaseerd op de samenstelling van hele assemblages (hoofdstuk 4) en op de geochemische signatuur van schelpen (hoofdstuk 5).

Hoofdstuk 4 gaat in op de vraag of de soortensamenstelling van mollusken associaties van zeegrasmilieus daadwerkelijk verschilt van die van omliggende milieus (in dit geval onbegroeide zandbodems). Hiervoor zijn gastropodenassemblages van de moderne zeebodem rond San Salvador, Bahama’s bestudeerd. Deze studie maakt het mogelijk, anders dan de studie van fossiele fauna’s, controle te verkrijgen over de bemonsterde milieus. De soortensamenstelling van de gastropodenassemblages van de zeegrasmilieus en de zandbodemmilieus vertoont een significant verschil. Ook verschilt de soortensamenstelling van monsters in zeegrasvelden en die van onbegroeide zones direct naast de zeegrasvelden. Tot slot zijn er duidelijke verschillen in de tafonomische kenmerken van mollusken die leven in en op een begroeide en onbegroeide zeebodem. In onbegroeide zeebodems zijn de molluskenschelpen veel slechter geconserveerd.

In **Hoofdstuk 5** is de stabiele isotopen signatuur van meer dan 150 schelpen van verschillende mariene paleomilieus van het Mioceen van Oost Kalimantan bestudeerd en die van zeegrasmilieus op Banyunganti, Java (hoofdstuk 2). Van het Tortoon van Oost Kalimantan zijn verschillende fauna’s bestudeerd: drie locaties met vermoedelijke zeegrasfauna’s, een locatie met schelpen van een “coral carpet” milieu (hoofdstuk 3), een gemengd koraal-zeegrasfauna en een brakwaterestuarienefauna. De $\delta^{18}O$/ $\delta^{13}C$ analyses laten consistent hogere $\delta^{13}C$ ratio’s in schelpen van zeegrasmilieus zien. Koolstof isotopen kunnen mogelijk als een aanvullend gereedschap worden gebruikt om paleomilieu interpretaties op grond van soortenassociaties te onderschrijven wanneer monsters uit een tijdinterval van beperkte geografische herkomst met elkaar worden vergeleken. Tot slot is gekeken naar welke processen in zeegras milieus verantwoordelijk zijn voor de gevonden afwijkende koolstof signaturen.

De synthese bevat een vergelijking van drie zeegras geassocieerde molluskenfauna’s uit het Mioceen van Indonesië. De fauna’s worden gekarakteriseerd op grond van soortenrijkdom, abundantie en trofische gemeenschappen (**hoofdstuk 6**). De fauna’s omvatten Vroeg Mioceen (vroeg Burdigalien, Banyunganti, Java, hoofdstuk 2), Midden Mioceen (Mangkhalihat fauna, Kalimantan, Beets, 1942) en Laat Mioceen (Tortoon) fauna’s van Bontang van hoofdstuk 5. Deze fauna’s zijn vergeleken met de Laat Miocene “coral carpet” fauna van Bontang uit hoofdstuk 3. De synthese is een eerste poging om de biodiversiteitsontwikkeling van zeegrasfauna’s te reconstrueren gedurende het Mioceen om zodoende inzicht te bieden in het ontstaan van de moderne globale mariene biodiversiteitshotspot. Laat Miocene monsters hadden een grotere diversiteit dan de monsters uit het Vroeg Mioceen. Beide intervallen vertonen bovendien een veel grotere diversiteit dan de zeegrasfauna's uit het Midden Miocene van een paratropische Turkse locatie waarin een rijke Paratethys fauna aanwezig is.

Samengevat, verschillende indirecte paleo-zeegras indicatoren (IPSIs) worden voorgesteld waarmee paleozeegrasmilieus kunnen worden onderscheiden van andere ondiep mariene milieus (hoofdstuk 1). De trofische signatuur van de slakken, de $\delta^{13}C$ signatuur van schelpen en het voorkomen van de obligate zeegraseter *Smaragdia* identificeren paleo-zeegrasmilieus (hoofdstukken 1-5). Door de identificatie van paleozeegrasmilieus is het mogelijk geworden de timing en context van de diversificatie van de bijbehorende fauna's te documenteren. Echter, de grote soortenrijkdom en vooral het grote percentage onbeschreven soorten maakt dergelijke studies wel een uitdaging. Het belang van gestandaardiseerd bemonsteringen en analyse technieken is onderstreept waarbij het gebruik van bestaande museumcollecties slechts beperkte inzichten oplevert vanwege onbekende verzamel- en analyse technieken (hoofdstukken 3 en 6).

Om de diversiteit vast te kunnen leggen is aanvullende bemonstering en studie nodig van fauna's uit het Midden Mioceen, Plioceen en Kwartair. Toekomstig onderzoek zal ook de rol van parameters als bijvoorbeeld waterdiepte, in het verklaren van diversiteitsvariatie moeten meenemen (hoofdstuk 6).

Zusammenfassung

Die heutige Region weltweit größter mariner Artenvielfalt, auch Diversitäts-Hotspot oder Zentrum größter Biodiversität genannt, liegt im Indo-West Pazifik (IWP), genauer in der Indo-Malaysischen Region, die Malaysia, die Philippinen, Indonesien und Papua-Neuguinea umfasst (Hoeksma, 2007; Renema et al., 2010). Zahlreiche Gruppen mariner Organismen, zum Beispiel Foraminiferen, Mollusken und Korallen tragen zu dieser großen Artenvielfalt bei (z.B., Bellwood et al., 2005; Hoeksema, 2007; Kohn, 1990; Wilson und Rosen, 1998). Es wird angenommen, dass die außergewöhnliche Biodiversität in der Region ihren Ursprung im frühen Neogen hatte und mit der Verbreitung von Korallenriffen und assoziierter Organismen einherging (z.B. Wilson und Rosen, 1998; Kapitel 6). Verfügbare Datensätze über fossile Organismen, die benötigt werden um Verbreitungsmuster mariner Lebewesen im Känozoikum von Süd-Ost Asien zu dokumentieren, sind allerdings vergleichsweise selten. Aus diesem Grund ist die Beschaffung neuer Daten notwendig, um Zeitpunkt und Zusammenhänge der Artendiversifizierung dokumentieren zu können. Um dieser Aufgabe gerecht zu werden, wurde 2010 das Marie-Curie Initial Training Network (ITN) Throughflow ins Leben gerufen. Der Schwerpunkt des Projektes liegt auf der Untersuchung Miozäner Fossilien und ihrer Paläo-Lebensräume im Osten Kalimantans, Indonesien. Die vorliegende Arbeit stellt eines von insgesamt elf Teilprojekten dar, die im Rahmen des Throughflow Programms durchgeführt wurden.

Das ursprüngliche Hauptziel der vorliegenden Forschung war die Rekonstruktion von Biodiversitätsmustern mariner Mollusken im Miozän von Indonesien. Um aussagekräftige Vergleiche der Artenvielfalt in verschiedenen Zeitabschnitten anstellen zu können, ist es notwendig, Vergesellschaftungen zu vergleichen, die aus dem gleichen Paläo-Habitat stammen, da Artenzahlen in verschiedenen Lebensräumen beträchtlich variieren (Kapitel 3). Seegraswiesen und assoziierte Molluskenvergesellschaftungen wurden aus den nachfolgenden Gründen als Modelhabitat und –gruppe für dieses Forschungsprojekt ausgewählt.

1. *Bedeutung*. Seegraswiesen sind weltweit verbreitete marine Lebensräume mit großer ökologischer Bedeutung und erfahren großes wissenschaftliches Interesse (Kapitel 1). Sie zeichnen sich durch hohe Produktivitätsraten aus und spielen eine

wichtige Rolle im Kohlenstoffkreislauf der Ozeane. Die Wurzeln der Seegräser stabilisieren Sedimente und wirken dadurch Küstenerosion entgegen. Seegraswiesen sind in der Lage die negativen Auswirkungen von Eutrophierung einzudämmen und organische Schadstoffe zu binden. Die dreidimensionale Struktur der Seegräser stellt außerdem einen Lebensraum für zahlreiche assoziierte Organismen bereit, darunter Arten mit ökonomischer Bedeutung. Beispielsweise agieren Seegraswiesen als schützender Lebensraum für juvenile Fische. Wie auch andere Habitate im Flachwasserbereich der Meere sind Seegraswiesen durch menschliche Einflüsse gefährdet. Aus diesem Grund sind Studien über die Reaktionen dieses Ökosystems auf klein- und großskalige Umweltveränderungen in der Vergangenheit von kritischer Bedeutung. Umweltveränderungen können beispielsweise durch Schwankungen in der Diversität assoziierter Lebewesen angezeigt werden.

2. *Häufigkeit und Vielfalt*. Die Mollusca (Weichtiere) repräsentieren einen artenreichen Tierstamm, der unter anderem die Schnecken, Muscheln und Tintenfische umfasst. Mollusken sind von großer Bedeutung in Seegraswiesen, da sie signifikant zur Artenvielfalt in diesem Lebensraum beitragen. Zudem treten sie meist sehr häufig auf oder sind sogar die zahlenmäßig häufigste Organismengruppe in der seegrasassoziierten Gemeinschaft wirbelloser Tiere. Dennoch ist die Vielfalt von Mollusken in Seegraswiesen im Vergleich zu der in anderen Habitaten (z.B. Korallenriffe) nicht übermäßig hoch, so dass eine gute Möglichkeit gegeben ist, diese Gruppe in einem eingeschränkten Zeitrahmen zu studieren, ohne von ihrer Artenvielfalt überwältigt zu werden (Kapitel 2, 3, 6).

3. *Biodiversität.* Seegräser und die mit ihnen assoziierten Lebewesen folgen im Allgemeinen den Mustern globaler Artenvielfalt. Seegräser, wie auch zahlreiche andere flachmarine Lebewesen, erreichen den Höchstwert ihrer Diversität in der Indo-Malaysischen Region. Dies gilt auch für eine hohe Zahl von sehr artenreichen Familien der Mollusken, die häufig in heutigen Seegraswiesen zu finden sind (Kapitel 6).

4. *Erhaltung*. Seegraswiesen sind überwiegend in Bereichen verbreitet, in denen die Pflanzen vor starker Strömung und Wellen geschützt sind. Die Vegetationsdecke verringert Strömungsgeschwindigkeiten noch zusätzlich. Seegräser fangen marine Sedimente ein und stabilisieren diese, weshalb sich Sedimente in Seegraswiesen oftmals durch eine geringere Korngröße auszeichnen, als die in benachbarten

vegetationslosen Gebieten (Kapitel 1). Diese Gegebenheiten erhöhen das Erhaltungspotential assoziierter Lebewesen und verringern die Möglichkeit, dass Material aus dem Habitat transportiert wird. Erhöhte pH-Werte in Seegraswiesen können zusätzlich zu gesteigerten Raten der Kalzifizierung assoziierter Organismen führen und sind deshalb ein weiterer möglicher Faktor für den reduzierten Verlust von Molluskenschalen durch taphonomische Prozesse. Seegrasassoziierte Mollusken gehören zu den am besten erhaltenen Fossilgruppen in Miozänen Sedimenten marinen Ursprungs im Untersuchungsgebiet, während der Fossilbericht von riffassoziierten Mollusken auf Grund vom diagenetischem Verlust der biogenen Karbonate sehr lückenhaft ist (Kapitel 2, 3, 5, 6).

5. *Verfügbarkeit.* Das Vorhandensein von Seegräsern im Miozän von Indonesien, einhergehend mit einem erhöhten Erhaltungspotential für seegrasassoziierte Mollusken, führt dazu, dass mehrere fossile Molluskenvergesellschaftungen aus dem Untersuchungsgebiet vorhanden sind, die verschiedene Zeitabschnitte repräsentieren (Kapitels 2, 5, 6).

Die wissenschaftliche Ausrichtung auf einen bestimmten Paläo-Lebensraum ist nichtdestotrotz mit Herausforderungen verbunden. Insbesondere muss das angesprochene Habitat im geologischen Bericht zuverlässig erkannt werden. Seegräser, ebenso wie ihre Pollen, werden gewöhnlich schnell abgebaut, weshalb ihr Fossilbericht sehr lückenhaft ist. Ihr Vorhandensein in der geologischen Vergangenheit wird deshalb häufig unter der Verwendung anderer Verfahren abgeleitet (Kapitel 1). Diesem Umstand ist es geschuldet, dass sich der Schwerpunkt der vorliegenden Forschung auf die Untersuchung der Möglichkeiten einer erfolgreichen Identifizierung von Paläo-Seegraswiesen verlagert hat. Dies dient als Basis für zukünftige Studien der Biodiversität. Die vorliegende Arbeit beinhaltet Beschreibungen von Molluskengemeinschaften aus Seegraswiesen und aus anderen marinen Habitaten im Untersuchungsgebiet (Kapitel 2 und 3), und Studien des Potenzials von Molluskenvergesellschaftungen als Anzeiger für Paläo-Lebensräume (Kapitel 4 und 5). Infolgedessen wurde ein erster Versuch unternommen die Entwicklung der Diversität seegrasassoziierter Mollusken im Miozän des heutigen Biodiversitäts-Hotspots zu rekonstruieren (Kapitel 6). Letzteres Kapitel beschäftigt sich auch mit den Herausforderungen, die mit derartigen Studien einhergehen, beispielsweise Untersuchungen an Fossilmaterial, das unter Anwendung verschiedener Sammlungsmethoden beschafft wurde und abweichende

Vorgehensweisen in der Behandlung von Proben im Anschluss an die Sammlung.

Obwohl die Taxonomie ein wichtiges Fundament für Studien der Ökologie und der Biodiversität darstellt, waren detaillierte taxonomische Bearbeitungen und die Beschreibung neuer Arten keine grundsätzlichen Ziele der vorliegenden Arbeit. Dennoch wurden vier Arten seegrasassoziierter Gastropoden aus dem frühen Burdigalium (frühes Miozän) von Banyunganti, Java, Indonesien, als neue Arten eingeführt (Kapitel 2). Es wird angenommen, dass ein hoher Anteil der in dieser Arbeit dargestellten Mollusken noch nicht beschrieben wurde (Kapitel 2, 3, und 6). Die Anwendung offener Nomenklatur in den vorliegenden Studien bietet eine pragmatische Herangehensweise an die Untersuchung sehr diverser und größtenteils unbeschriebener Molluskenvergesellschaftungen, während gleichzeitig ein unangemessen hoher Zeitaufwand verhindert wird.

Da Seegräser nur in seltenen Fällen fossil überliefert sind, wird ihr Auftreten in der Erdgeschichte häufig durch das Vorhandensein indirekter Anzeiger, wie fossiler Organismen oder sedimentologischer, taphonomischer und geochemischer Signaturen, nachvollzogen. Die erfolgreiche Identifizierung von Seegraswiesen im Fossilbericht war eine große Herausforderung im Rahmen dieses Projekts. Neben Mollusken wurden auch andere Organismengruppen und weitere Anzeiger auf ihr Potenzial hin untersucht, als indirekte Paläo-Seegrasindikatoren (IPSIs) zu dienen. Das Ergebnis ist eine umfassende Neubearbeitung der wissenschaftlichen Literatur über IPSIs, die in der Vergangenheit Anwendung fanden. Dadurch wird zukünftigen Forschern ein Katalog für die Identifizierung von Seegrashabitaten im Fossilbericht zugänglich gemacht (**Kapitel 1**). Dieses Kapitel beinhaltet außerdem eine Einleitung über die Eigenschaften von Seegraswiesen, in der deren ökologische Bedeutung herausgearbeitet wird.

Das Thema des ersten Abschnitts dieser Arbeit (Kapitel 2 und 3) sind Molluskenvergesellschaftungen aus dem Miozän von Indonesien. In diesem Abschnitt werden zwei fossile Vergesellschaftungen vorgestellt, um einen Einblick in den hervorragenden Erhaltungszustand und die große Artenvielfalt der Mollusken, insbesondere der Gastropoden, zu bieten. Außerdem werden in den zwei Kapiteln die folgenden Fragen aufgeworfen: Wie können Molluskenvergesellschaftungen charakterisiert und einem bestimmten Paläohabitat zugeordnet werden? Wie unterscheiden sie sich in ihrer Ökologie und können solche Unterschiede zur

Abgrenzung verschiedener Lebensräume verwendet werden?

In **Kapitel 2** wird eine fossile Molluskenvergesellschaftung aus dem frühen Miozän von Banyunganti, Java, Indonesien, eingeführt. Diese wurde auf Grund ihrer taxonomischen und ökologischen Zusammensetzung, des Vorkommens des Seegrasindikators *Smaragdia* und auf Grund der Zusammensetzung der begleitenden Foraminiferenfauna, als eine seegrasassoziierte Vergesellschaftung identifiziert. Die gründliche Untersuchung der Molluskenvergesellschaftung bietet einen Überblick über alle vorkommenden Arten, und schließt auch seltene Arten und Schalenfragmente mit ein. Die Vergesellschaftung umfasst 184 Arten von Mollusken, von denen 159 Arten von Gastropoden repräsentiert werden. Ein Großteil der vorgestellten Arten wird als unbeschrieben erachtet. Vier häufig auftretende Arten werden als neue Arten eingeführt. Sämtliche Arten werden abgebildet. Die Banyunganti-Vergesellschaftung zeichnet sich durch eine große Artenvielfalt, ein große Häufigkeit kleiner Weidegänger unter den Gastropoden, und eine hervorragende Erhaltung von Schalenornamenten aus.

In **Kapitel 3** wird eine gut erhaltene Molluskenvergesellschaftung aus dem Tortonium (spätes Miozän) von Bontang, Ost-Kalimantan, Indonesien vorgestellt. Die Mollusken treten zusammen mit häufig vorkommenden verzweigten Korallen auf, weshalb ihr Lebensraum als sogenannter Korallenteppich interpretiert wurde. Häufigkeiten von Arten, Artenreichtum und Fraßstrategien dienen als Grundlage, um die Vergesellschaftung zu charakterisieren. Im Vergleich mit der seegrasassoziierten Mollukenvergesellschaftung von Java (Kapitel 2) unterscheidet sich diese Vergesellschaftung in der Zusammensetzung der Mollusken, die unterschiedliche Fraßstrategien verfolgen: In der Korallen-Vergesellschaftung treten räuberische Gastropoden deutlich gehäuft auf. Somit dient die vorliegende Auswertung einer Molluskenvergesellschaftung von einen Korallenteppich zur Unterstützung der Annahme, dass ökologische Vergleiche unter Umständen ein Instrument für die Unterscheidung von Seegraswiesen von anderen marinen Flachwasserhabitaten im Fossilbericht bieten könnte.

Im zweiten Abschnitt dieser Arbeit (Kapitel 4 und 5) werden zwei Anwendungsmöglichkeiten von Molluskenvergesellschaftungen als IPSIs behandelt (siehe auch Kapitel 1). Die dargelegten Studien befassen sich nicht mit einzelnen Arten, sondern versuchen Proxies zu finden, die auf der Artenzusammensetzung von gesamten Vergesellschaftungen (Kapitel 4) und auf der geochemischen Signatur von Molluskenschalen beruhen (Kapitel 5).

Kapitel 4 beschäftigt sich mit der Frage, ob die Artenzusammensetzung von Molluskenvergesellschaftungen aus Seegraswiesen sich von der in angrenzenden Habitaten (in diesem Falle vegetationsloser Sand) unterscheidet. In dieser Studie kommen Thanatozönosen (Totengemeinschaften) mariner Schnecken, die in heutigen Ökosystemen auf San Salvador, Bahamas gesammelt wurden, zur Anwendung. Im Gegensatz zu Untersuchungen an fossilem Material bietet diese Vorgehensweise eine zuverlässige Kontrolle über die Beschaffenheit des beprobten Lebensraums. Die vorliegenden Ergebnisse bezeugen einen hochwertig signifikanten Unterschied zwischen der Artenzusammensetzung von Gastropodenthanatozönosen, die aus Seegraswiesen stammen, und denen, die auf vegetationslosem Sand gesammelt wurden. Zusätzlich unterscheidet sich die Artenzusammensetzung der Thanatozönosen, die innerhalb von Seegraswiesen gesammelt wurden, von derjenigen der Vergesellschaftungen, die vom vegetationslosen Gebiet direkt vor den beprobten Seegraswiesen stammen. Auch die taphonomische Signatur der Schalenvergesellschaftungen zeigt augenfällige Unterschiede im Vergleich von Seegraswiesen und vegetationslosen Gebieten: Schlecht erhaltenes Schalenmaterial tritt häufiger an vegetationslosen Probenstellen auf.

In **Kapitel 5** wird die Zusammensetzung stabiler Isotope, die an mehr als 150 Molluskenschalen von unterschiedlichen Paläohabitaten im Miozän von Java und Ost-Kalimantan gemessen wurden, untersucht. Das untersuchte Material umfasst seegrasassoziierte Mollusken von Banyunganti (Kapitel 2) und von drei weiteren Lokalitäten im Tortonium von Ost-Kalimantan, die ebenfalls als Seegraswiesen interpretiert wurden. Zusätzlich findet Material aus einem Korallenteppich (Kapitel 3), aus einem gemischten Seegras-Korallen-Habitat und aus einem estuarinen Brackwasser-Lebensraum Anwendung. Die Ergebnisse der δ^{18}O- und δ^{13}C-Untersuchungen zeigen gleichbleibend höhere δ^{13}C-Werte für Molluskenschalen, die aus Seegraswiesen stammen. Dies führt zu der Schlussfolgerung, dass Kohlenstoffisotope eine zusätzliche Möglichkeit bieten, um Interpretationen von Paläohabitaten, die auf Grund der Zusammensetzung fossiler Vergesellschaftungen getroffen wurden, in derselben Region und in eingeschränkten stratigraphischen Zeitintervallen zu bestätigen. Es wurde zusätzlich untersucht welche Prozesse in

Seegraswiesen die Isotopenzusammensetzung assoziierter Mollusken wahrscheinlich beeinflussen.

Die Synthese dieser Arbeit führt zu einer vergleichenden Untersuchung von drei seegrasassoziierten Molluskenvergesellschaftungen aus dem Miozän von Indonesien. Diese werden auf Grund von Fraßstrategien, Häufigkeiten von Arten und Artenvielfalt charakterisiert (**Kapitel 6**). Jede dieser Vergesellschaftungen tritt in einer anderen stratigraphischen Einheit auf; sie umfassen damit das frühe Burdigalium (frühes Miozän; Bayunganti-Fauna, Kapitel 2), das mittlere Miozän und das Tortonium (spätes Miozän, Kapitel 5). Zum Vergleich wird außerdem die Korallenteppich-Vergesellschaftung aus dem frühen Tortonium (spätes Miozän; Kapitel 3) herangezogen. Die vorliegende Studie legt einen ersten Versuch vor, die erdgeschichtliche Entwicklung der Biodiversität seegrasassoziierter Mollusken im Gebiet des heutigen Diversitäts-Hotspots während des Miozäns zu rekonstruieren. Proben aus dem späten Miozän scheinen eine höhere Artenvielfalt aufzuweisen als Proben aus dem frühen Miozän, und beide sind erheblich diverser als eine paratropische Molluskenvergesellschaftung aus dem mittleren Miozän der Paratethys (Kapitel 6).

Zusammenfassend wurde eine Reihe indirekter Paläo-Seegras Anzeiger eingeführt, um eine Unterscheidung von Seegraswiesen von anderen marinen Flachwasserhabitaten im geologischen Bericht zu ermöglichen (Kapitel 1). Auswertungen von Fraßstrategien, δ^{13}C-Werte von Molluskenschalen und das Vorkommen des Seegrasfressers *Smaragdia* zeigen sich insbesondere als wertvoll, um Paläo-Seegraswiesen zu identifizieren (Kapitel 1 bis 5). Unter Verwendung dieser Indikatoren können Paläo-Seegraswiesen erfasst werden, was Studien der zeitlichen Abfolge und der Zusammenhänge von Diversitätsmustern der assoziierten Mollusken erst möglich macht. Solche Studien werden durch einen großen Artenreichtum und hohe Zahlen taxonomisch nicht erfasster Arten erschwert, deshalb sind standardisierte Untersuchungsmethoden notwendig. Material aus bereits existierenden Museumssammlungen stellt sich dabei als nur eingeschränkt nützlich heraus, da sein Bericht unter Umständen unbekannte Lücken, beispielsweise auf Grund der angewandten Sammlungsmethode, aufweist (Kapitel 3 und 6).

Großangelegte zusätzliche Sammlungen, insbesondere aus Miozänen, Pliozänen und Quartären Schichten, sind notwendig um die vorliegende Forschung weiterführen und Diversitätsmuster in Zeit und Raum erkennen zu können. Außerdem sollten zukünftige Forschungsvorhaben eine Beurteilung der Rolle beinhalten, die verschiedene Umweltfaktoren (z.B. Wassertiefe) bei der Kontrolle von Schwankungen der Biodiversität in verschiedenen Seegrashabitaten spielen (Kapitel 6).

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Curriculum Vitae

I was born the 3rd of October 1981 in Kiel, Germany where I spent my childhood, went to school and finally finished my degree in geology/paleontology at the Christian-Albrechts-University of Kiel. For my diploma thesis my supervisor at the time, Sven Nielsen, gave me the great opportunity to perform my geological mapping (which was part of my graduate research) on Mocha Island, Chile, and write my thesis on the fossil mollusks from this beautyful place. I cannot thank him enough for opening the door to mollusk wonderland!

He was also the one who asked me one day via skype if he should send me a description of a PhD-position about bryozoans at the Natural History Museum in London. Honestly, I was not very interested, but you shall not refuse potential job opportunities when you are just about to finish your degree. That was a small decision at the time, but what a lucky one! Then this is how I found out about the Throughflow Project and learned that there was a position far more suitable for me: the one about mollusks.

I left Kiel and moved to Leiden, the Netherlands some months later and started my research on seagrass-associated mollusks in the Miocene of Indonesia. The results are many great new friends and colleagues, a bag full of wonderful experiences, including searching for shells in Indonesia and snorkeling in seagrass meadows at the Bahamas, and of course this thesis.

I hope the future will provide me with more beautiful shells, seagrass meadows, and glimpses of the past!

List of Papers

Reich, S., Wesselingh, F.P., and Renema, W. (2014) A highly diverse molluscan seagrass fauna from the early Burdigalian (early Miocene) of Banyunganti (south-central Java, Indonesia). *Annalen des Naturhistorischen Museums in Wien, Serie A* 116: 5-126.

Reich S. (accepted) Gastropod associations as a proxy for seagrass vegetation in a tropical, carbonate setting (San Salvador, Bahamas). *Palaios*.

Reich, S., Warter, V., Wesselingh, F.P., Zwaan, J.C., Lourens, L., Renema, W. (in review) Paleoecological significance of stable isotope ratios in Miocene tropical shallow marine habitats (Indonesia). *Palaios*.

Reich, S., Di Martino, E., Wesselingh, F.P., Todd, J.A., Renema, W. (in review) Indirect paleo-seagrass indicators (IPSIs): a review. *Earth Science Reviews*.

Santodomingo, N., Novak, V., Pretković, V., Marshall, N., Di Martino, E., Lo Giudice Capelli, E., Rösler, A., **Reich, S.**, Braga, J.C., Renema, W., Johnson, K.G. (accepted) A diverse patch reef from turbid habitats in the middle Miocene (East Kalimantan, Indonesia). *Palaios*.

Kusworo, A., **Reich, S.**, Wesselingh, F.P., Santodomingo, N., Johnson, K.G., Todd, J.A., Renema, W. (in review) Diversity and paleoecology of Miocene coral-associated mollusks from East Kalimantan (Indonesia). *Palaios*.

Landau, B., Vermeij, G.J., **Reich, S.** (in review) Classification of the Modulidae (Caenogastropoda: Cerithioidea), with new genera and new fossil species from the Neogene of tropical America and Indonesia. *Basteria*.