Naturalis Repository

# Indirect paleo-seagrass indicators (IPSIs): A review

S. Reich, E. Di Martino, J.A. Todd, F.P. Wesselingh, W. Renema

Downloaded from
https://doi.org/10.1016/j.earscirev.2015.01.009

Article 25fa Dutch Copyright Act (DCA) - End User Rights
This publication is distributed under the terms of Article 25fa of the Dutch Copyright Act (Auteurswet) with consent from the author. Dutch law entitles the maker of a short scientific work funded either wholly or partially by Dutch public funds to make that work publicly available following a reasonable period after the work was first published, provided that reference is made to the source of the first publication of the work.

This publication is distributed under the Naturalis Biodiversity Center 'Taverne implementation' programme. In this programme, research output of Naturalis researchers and collection managers that complies with the legal requirements of Article 25fa of the Dutch Copyright Act is distributed online and free of barriers in the Naturalis institutional repository. Research output is distributed six months after its first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and copyrights owner(s) of this work. Any use of the publication other than authorized under this license or copyright law is prohibited.

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the department of Collection Information know, stating your reasons. In case of a legitimate complaint, Collection Information will make the material inaccessible. Please contact us through email: collectie.informatie@naturalis.nl. We will contact you as soon as possible.

Earth-Science Reviews 143 (2015) 161–186

Contents lists available at ScienceDirect

Earth-Science Reviews

journal homepage: www.elsevier.com/locate/earscirev

# Indirect paleo-seagrass indicators (IPSIs): A review

S. Reich [a,*], E. Di Martino [b], J.A. Todd [b], F.P. Wesselingh [a,1], W. Renema [a]

[a] Naturalis Biodiversity Center, Department of Geology, P.O. Box 9517, 2300 RA Leiden, the Netherlands
[b] Natural History Museum, Department of Earth Sciences, Cromwell Road, London SW7 5BD, UK

## ARTICLE INFO

*Article history:*
Received 31 January 2014
Accepted 29 January 2015
Available online 7 February 2015

*Keywords:*
Marine angiosperms
Seagrass meadow
Faunal association
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, habitat restriction, and others. 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. 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. The presence/absence of many potentially seagrass-associated taxa cannot serve as a useful indicator due to a lack of habitat restriction, but statistical evaluations of abundance data are promising to discriminate seagrass beds from neighboring areas. However, such studies are available for only a few commonly seagrass-associated organism groups. Furthermore, the applicability of many indicators is confined by latitude, because their occurrence is restricted to (sub)tropical or at most warm temperate regions.

## Contents

---

[*] Corresponding author. Tel.: +31 71 7519663.

*E-mail addresses:* sonja.reich@naturalis.nl (S. Reich), manu.dimartino@hotmail.it (E. Di Martino), j.todd@nhm.ac.uk (J.A. Todd), frank.wesselingh@naturalis.nl (F.P. Wesselingh), willem.renema@naturalis.nl (W. Renema).

[1] Tel.: +31 71 7519663.

http://dx.doi.org/10.1016/j.earscirev.2015.01.009
0012-8252/© 2015 Published by Elsevier B.V.

## 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 changes, 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 (Gray, 2001; Bouchet et al., 2002). Therefore, the successful recognition and discrimination of paleohabitats are 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 (Zuschin and Hohenegger, 1998; Kusworo et al., 2015).

Seagrass meadows are distributed worldwide from Australia and New Zealand to Iceland, Norway and Greenland, spanning the coasts of Africa,

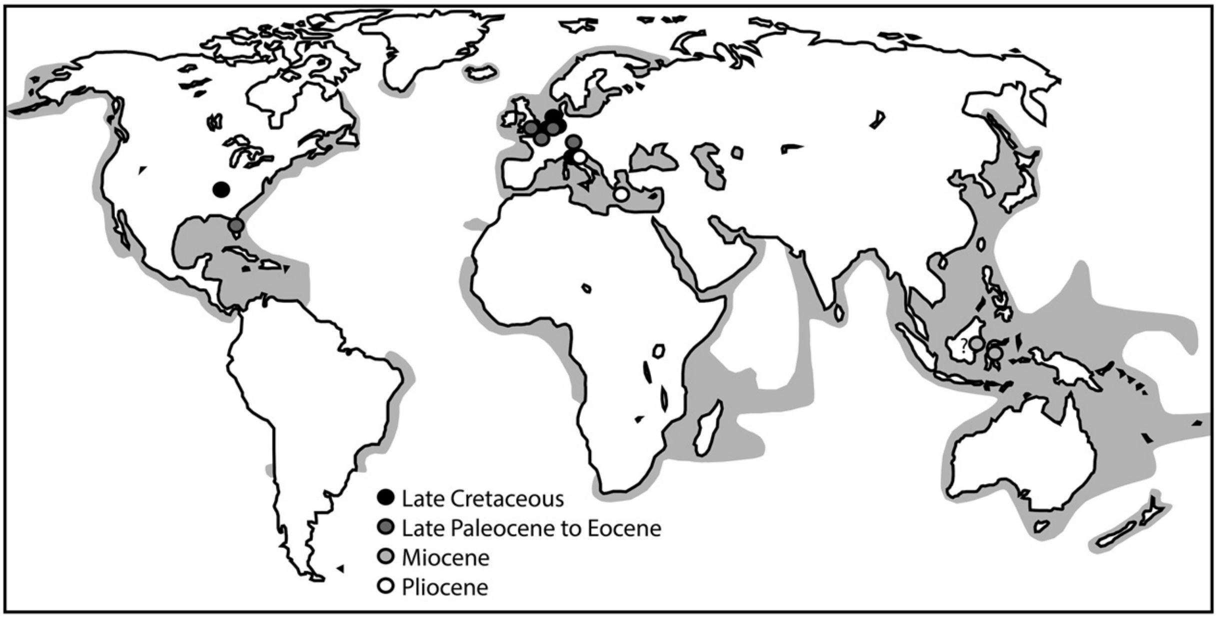

**Fig. 1.** Worldwide occurrences of fossil seagrasses; see legend for stratigraphic assignments. The shaded areas represent the range of modern seagrass distribution. After Green and Short (2003).

India, The Middle East, North and South America and Europe with the exception of Antartica (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 (Mukai, 1993; Green and Short, 2003). Marine angiosperms predominantly occur in the tidal and shallow subtidal zone down to about 15 m, but have also been reported from depths down to 90 m, depending on seagrass species and 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 (Nienhuis et al., 1989; Hoeksema, 2007). In the Caribbean the presence of fringing reefs, which have been 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; Spalding et al., 2001; Johnson et al., 2007). 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 are often higher in seagrass meadows than in adjacent unvegetated areas that lack a three-dimensional structuring (Brasier, 1975; Mikkelsen et al., 1995; Hemminga and Duarte, 2000; Barnes and Barnes, 2012). 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 (Short and Neckles, 1999; Jackson, 2001; Orth et al., 2006; Hughes et al., 2009; Waycott et al., 2009; Rasheed, 2011).

Fundamental to studies of seagrass habitats in deeper time is the assumption that seagrass meadows in the geological past since their Late Cretaceous origin 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 et al., 1989). Other studies focus on the macrobenthic invertebrate community, often combined with an assessment of the infauna (e.g., Boström and Bonsdorff, 1997; Barnes and Barnes, 2012), 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; Eva, 1980; Domning, 2001; Vélez-Juarbe, 2014). 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 sedimentological and taphonomic indicators, and the presence of fossil organisms that are interpreted as typical for seagrass associations (Brasier, 1975; Eva, 1980; Domning, 1981; 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 other 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. Specimens deposited in the Natural History Museum in London, UK are indicated by NHMUK 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 its usefulness (Sections 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. Organisms that occur frequently in modern seagrass environments, but have never been directly applied as IPSI are not treated in this study. This includes for instance sponges, brachiopods, and crustaceans (with the exception of ostracods). Those groups have a reasonably good fossilization potential and future research on their habitat affinities and distribution in the fossil record might reveal additional possibilities to apply them as IPSIs.

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.

Organisms that serve as IPSI may show strong preferences for particular seagrass species, e.g., depending on size, shape, and life span of specific seagrass leaves. In general, long-lived and structurally complex seagrass taxa (e.g., *Posidonia* and *Amphibolis*) appear to host a more abundant and diverse epiphytic community than short-lived taxa such as *Heterozostera* (Borowitzka et al., 2006, and references therein). Although in many cases it is not possible to assign fossil seagrasses to an individual species, and in cases lacking seagrass preservation it is impossible, one should be aware that relations between certain IPSIs and certain (extinct) seagrass species likely existed in the past and may bias the record of paleo-seagrass beds towards environments with a specific seagrass species composition.

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 adjacency. When using assemblage compositions as IPSIs, use of autochthonous assemblages is essential. However, out-of-habitat transport is rare for fossil organisms, especially in level-bottom 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 (Section 3.1). Many IPSIs have a narrower geographic range than that of seagrasses and their use is therefore limited to their region of occurrence. This particularly concerns the latitudinal distribution of IPSIs, because many are restricted to low latitudes. 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

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 those encrusters with fragile skeletons.

#### 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 likely to occur in any seagrass habitat world-wide; 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 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 (see Section 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, USA and France and the Pliocene of Greece (Ivany et al., 1990; Taylor and Todd, 2001; Moisette et al., 2007). 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 and Domke, 1955; Voigt, 1981). 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, England (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, USA (Lumbert et al., 1984; Ivany et al., 1990; Benzecry and Brack-Hanes, 2008). 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, Indonesia. 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).

The following records are not depicted in Fig. 1: a fossil from the late Cretaceous Izumi Sandstone in Japan (Koriba and Mikki, 1958) that was later doubted to represent a marine angiosperm (Brasier, 1975; Kuo and McComb, 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 worm tubes. 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; *Metrarabdotos*, *Adeonellopsis*, *Cigclisula*, and *Gemelliporella* from the Mio-Pliocene of the Cibao Valley, Dominican Republic (Cheetham and Jackson, 1996; see Section 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 *Metrarabdotos* 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 Cheethan and Jackson (1996: Fig. 8.10) that strongly resemble the epidermis of the Recent seagrass *Halodule*. Importantly, when taken together with *Metrarabdotos*' preferred paleo-bathymetries at the present day, this suggested taxonomic affinity allows one to infer the presence of relatively deep-water seagrass assemblages. However, it must be noted that 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 (Harper Layer: Todd, 1993) 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 to 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 (Section 4.1.1; Fig. 2A–C), 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 (Sections 4.1.2–4.1.3; Fig. 2D–G). Interpretations especially based on symbiont-bearing, benthic foraminifera assemblages as seagrass-associated are frequently justified by citing only one or a limited number of publications reporting the occurrence of these taxa in seagrass meadows without considering that they may occur in other environments as well (e.g., Cushman, 1922; Eva, 1980; Steinker and Clem, 1984; Langer, 1993), which is not sufficient for such a general statement. In fact, most taxa that are generally associated with seagrass habitats occur also outside these habitats, either epiphytic on algae or even on other substrates. 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 non-vegetated 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) and Berau shelf (Renema, 2006). 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 a long-lived flat surface and do not necessarily depend on seagrasses. It also has to be accounted for that the groups of seagrass-associated foraminifera discussed in the following share a common issue: Most studies are confined to tropical regions and seagrass-characteristic foraminifer taxa are often larger, photosymbiotic ones that do not occur in temperate and polar climate zones. Therefore, it is unlikely that foraminifer assemblages can perform as IPSIs in high latitudes.

#### *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; Fig. 2A–C). Groups that are commonly reported as associated with seagrasses include soritids (*Marginopora*, *Sorites*, and *Amphisorus*; Fig. 2A–B), planorbulids

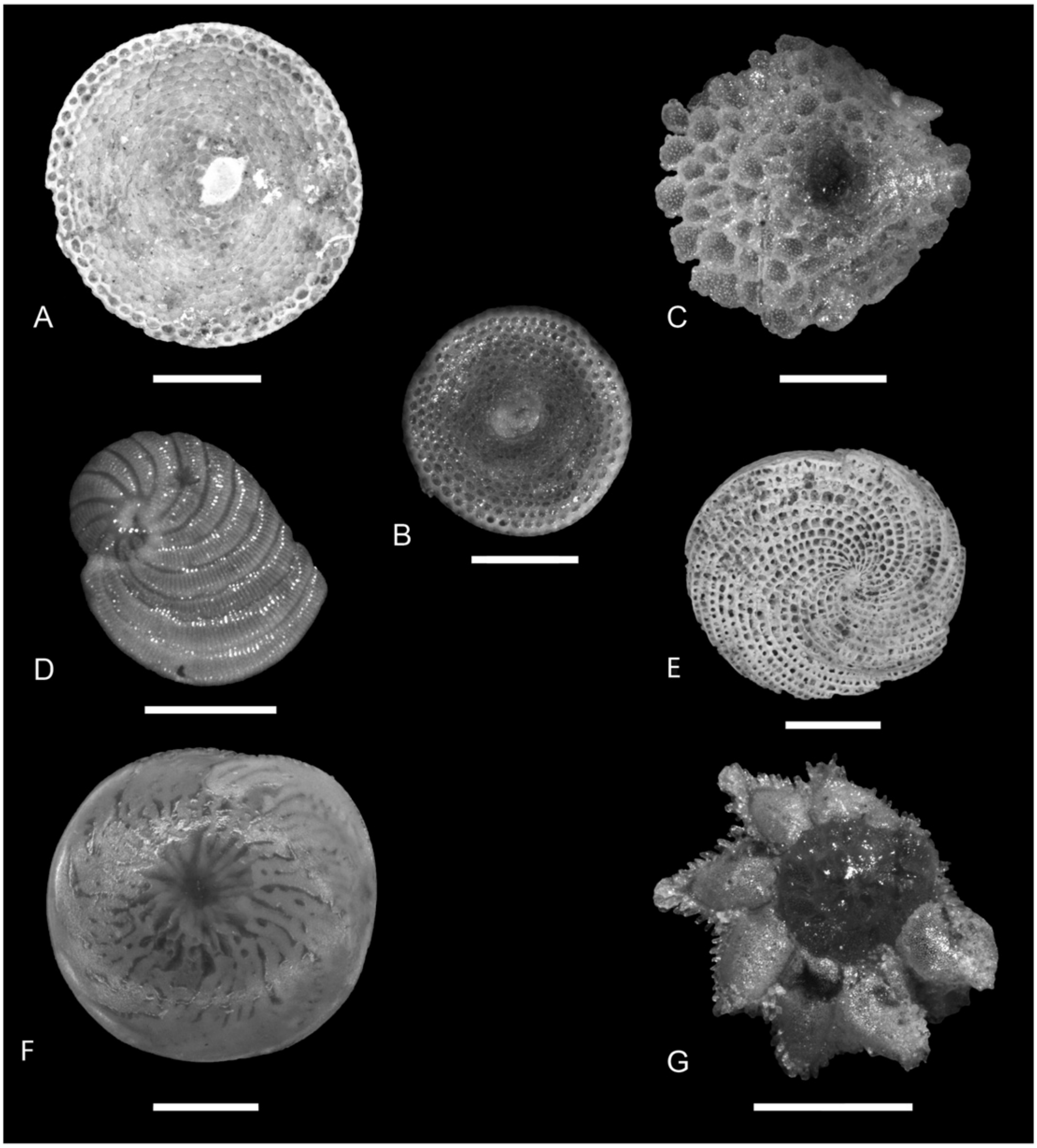

**Fig. 2.** Some common fossil and Recent shallow-water foraminifera from Indonesia. All scale bars equal 0.5 mm. A–C) Permanently attached foraminifera. A) *Sorites* sp. (RGM 3270, Kembang Sokkoh, Java, early Burdigalian). B) *Planorbulina* sp. (UPG 24, Spermonde, Sulawesi, Recent). C) *Amphisorus* sp. (UPG 24, Spermonde, Sulawesi, Recent). D–E) Motile porcelaneous photosymbiotic foraminifera. D) *Peneroplis* sp. (UPG 24, Spermonde, Sulawesi, Recent). E) *Pseudotaberina vandervlerki* (BA 18, Banyunganti, Java, early Burdigalian). F–G) Motile hyaline photosymbiotic foraminifera. F) *Amphistegina lobifera* (UPG 21, Spermonde, Sulawesi, Recent). G) *Calcarina* sp. (UPG 35, Spermonde, Sulawesi, Recent).

(*Planorbulina*, Fig. 2C), 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 one 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. The photosymbiotic taxa included in the group are restricted to the (sub)tropical climate belt.

*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 (Martin, 1986; Martin and Wright, 1988; Buchan and Lewis, 2008).

*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 and Troelstra, 2001; Renema, 2006). Modern *M. vertebralis* has been found on seagrasses, but is more abundant on other shallow marine, exposed substrates (e.g., Maxwell, 1968; Ross, 1972; Lobegeier, 2002), 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 in New Caledonia *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 (W. Renema, pers. obs.).

*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*; Fig. 2D), and archaiasinids (e.g., *Archaias*). The latter group is most frequently associated with seagrasses (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; Cann et al., 2006; Brandano et al., 2009; Reuter et al., 2010; O'Connell et al., 2012). For instance, the high abundance of the extinct archaiasanid genus *Pseudotaberina* in Indonesia and India helped to indicate the presence of seagrass vegetation (Renema, 2008b; Reuter et al., 2010; Fig. 2E). 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 are not dependent on seagrasses.

*Stratigraphic and geographic range*: Archaiasinids in general: Eocene to Recent, circum(sub)tropical, most abundant in the fossil record in the Paleogene of the Middle East and the Pliocene of the Caribbean. *Austrotrillina*: early Oligocene to early Miocene; tropical Pacific, (sub) tropical Africa and Eurasia (Adams, 1968; Renema, 2008b). *Pseudotaberina*: early to middle Miocene; Middle East to Papua New Guinea. 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 (Hallock and Peebles, 1993; Hohenegger, 1994; Fujita and Hallock, 1999; Renema, 2006). Most taxa (e.g., *Borelis*, *Peneroplis*, and *Archais*) have been observed in other environments as or even more frequently than in seagrass meadows (Hallock and Peebles, 1993; Hohenegger, 1994; Fujita and Hallock, 1999; 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 associated with seagrass-facies in the fossil record, 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, due to its close association with seagrass facies. However, its habitat restriction remains unclear and its stratigraphic and geographic range is very restricted (see above). 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 amphisteginids (e.g., *Amphistegina*, Fig. 2F), calcarinids (*Calcarina*; Fig. 2G), 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*: 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 calcarinids which are late Miocene to 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 other seagrasses, but this difference is most likely related to other environmental parameters (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). *Conclusions*: Weak IPSI (taxonomic uncertainty and lacking habitat restriction).

#### *4.1.4. Abundance of motile hyaline foraminifera (genus Elphidium)*

*In modern seagrass meadows*: The group includes elphidiids (*Elphidium*), which can be very abundant in seagrass meadows.

*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).

*Stratigraphic and geographic range*: Cenozoic (incl. Recent), worldwide.

*Fossilization potential*: High.

*Frequency of occurrence*: Frequently occurring in modern environments and fossil associations. Elphidiids are among the most abundant and ubiquitous fossils in shallow marine environments.

*Habitat restriction*: Elphidiids are hard to identify; *Elphidium* itself is one of the most eurytopic genera and their use as IPSI is restricted to cases where they 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 (Fig. 3A–B; Sola et al., 2013). Coralline algae, mainly belonging to the genus *Mesophyllum*, grow attached to *Posidonia* seagrass and 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 also recorded in the Miocene of Spain (Sola et al., 2013). The seagrass-encrusting coralline algae *Synartrophyton patenta* develops flat mushroom-like growth forms (Womersley, 1996; Browne et al., 2013). Furthermore, crustose coralline algae can form tubes around stems and leaf axes of seagrasses (Fig. 3B; Davies, 1970; Sola et al., 2013).

*Stratigraphic and geographic range*: Applicable for all time intervals. Thin talli (e.g., *Hydrolithon* and *Pneophyllum*) that encrust seagrass leaves and may form 'hooked' shapes have a world-wide distribution, as do laminar growth forms (e.g., *Hydrolithon* and *Lithophyllum*) that may form tubes. The distinct growth forms described above for *Mesophyllum* are only known from the Mediterranean. The mushroom-shaped *Synartophyton patenta* is found in the temperate zone of the Southern Hemisphere (Womersley, 1996; Browne et al., 2013).

*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, but abundance varies considerably among different localities also within the same climate zone (J.C. Braga, pers. comm.). 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). The mushroom-shaped *S. patenta* encrusts various substrates besides seagrasses (Womersly, 1996; Browne et al., 2013).

*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 to middle Miocene and in late Pliocene to early Pleistocene seagrass facies in Australia (Lukasik et al., 2000; James and Bone, 2007).

*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 and Babcock, 2002).

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

### 4.4. Occurrence of hydroids (genus Dynamena)

*In modern seagrass meadows*: Hydroids (e.g., genus *Dynamena*) are commonly found in the epiphytic community in seagrass meadows (Den Hartog, 1979; Borowitzka et al., 2006; Ben Brahim et al., 2010). Some hydroid species are reported as obligate seagrass epiphytes (e.g., Hughes et al., 1991).

*Use as IPSI*: Among seagrass-associated hydroids only genus *Dynamena* is recorded as a fossil. 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, preserved as epibiont bioimmurations (sensu Taylor, 1990) in the attachment area of the small ostreid oyster *Cubitostrea cubitus*. This oyster is frequently,

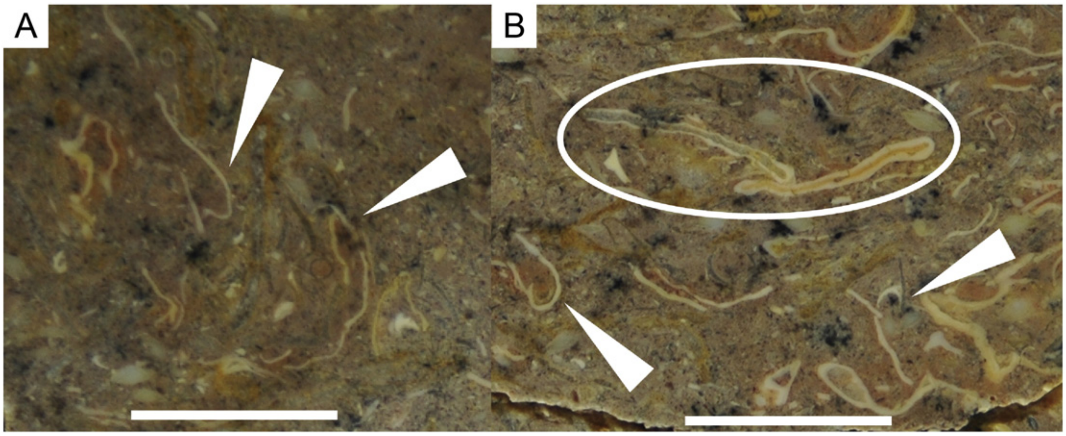

**Fig. 3.** Cut sample of Messinian (late Miocene) limestone containing 'hooked' and tubular coralline red algae (Poniente Basin, Almería, Spain). Scale bars equal 8 mm. Material housed in Facultad de Ciencias, Estratigrafía y Paleontología, Universidad de Granada, Spain. Photos provided by J.C. Braga. A. Hooked coralline red algae (indicated by arrows). B) Tubular coralline red algae (encircled) and some smaller hooked coralline red algae (indicated by arrows).

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. 4; Taylor and Todd, 2001).

*Stratigraphic and geographic range*: *Dynamena* is currently distributed worldwide, but its only fossil records are from a few horizons from a single site in the middle Eocene (Lutetian).

*Fossilization potential*: In general low for soft-bodied hydroids. *Dynamena* is 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*: *Dynamena* is not restricted to seagrass meadows, but abundantly recorded from macroalgae (e.g., Rossi et al., 2000). Other hydroids are obligate seagrass epiphytes, but unknown in the fossil record.

*Conclusion*: The occurrence of bioimmured seagrass epiphytes reported from the Lutetian of the Paris Basin is currently unique. The majority of the substratum bioimmurations at this site (including that in Fig. 4) 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. 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.

**Fig. 4.** Bioimmuration of *Dynamena* hydroid colony attached to a seagrass leaf, preserved by the oyster *Cubitostrea*, middle Eocene, Paris Basin.
From Taylor and Todd (2001).

### 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* (Fig. 5A) and *Siderastrea radians* (Lewis, 1989; Johnson, 1992) 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*, *Placocyathus*, *Thyasanus*, *Trachyphyllia*; Fig. 5B–C) were associated with seagrass vegetation in the Miocene and Pliocene in the

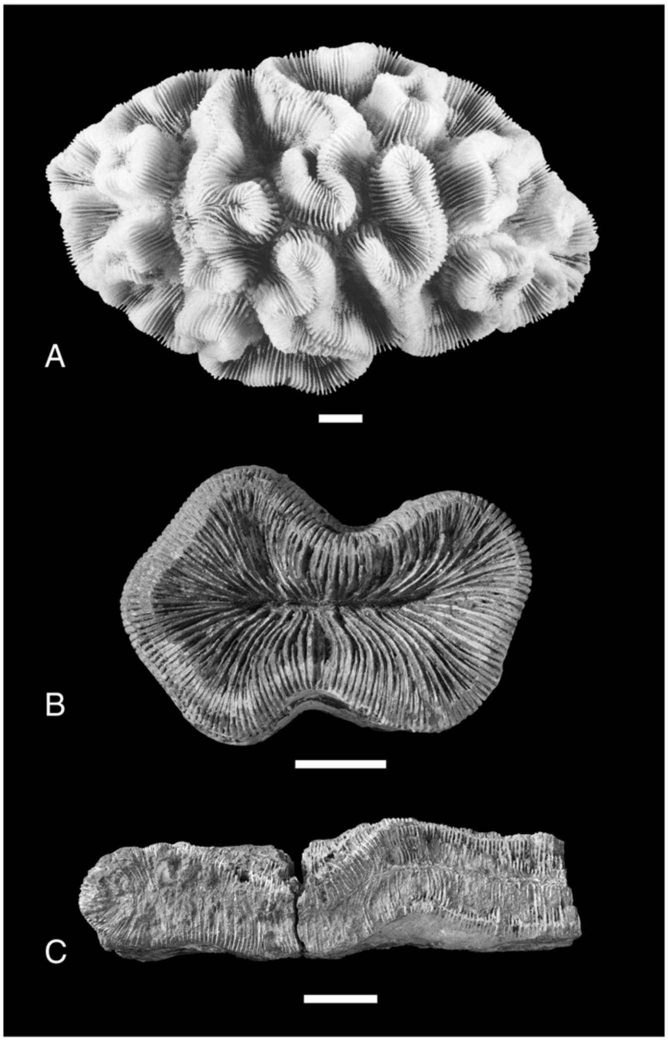

**Fig. 5.** Seagrass-associated Recent and fossil corals (photos by NHM London photo unit, provided by K.G. Johnson). All scale bars equal 2 cm. A) *Manicina areolata* (Carrie Bow Cay, Belize, Recent). B) *Trachyphyllia bilobata* (NHMUK PI CO R28753, Neogene, Dominican Republic). C) *Thyasanus excentricus* (NHMUK PI CO R28754, Jamaica, Neogene).

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 *Metrarabdotos* 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–Placocyathus–Thyasanus–Trachyphyllia* 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.

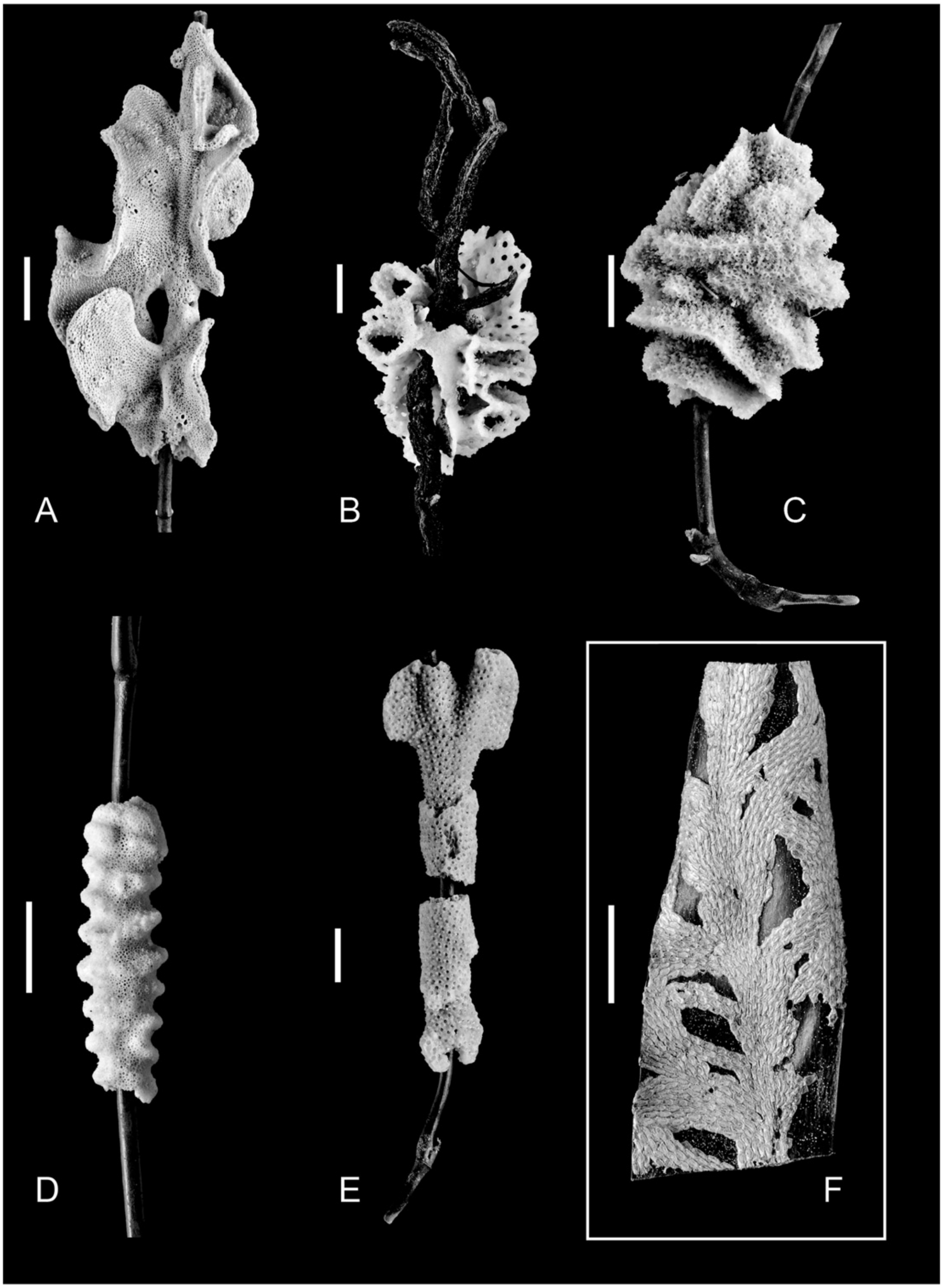

**Fig. 6.** Recent bryozoans associated with seagrass (adapted from Di Martino and Taylor, 2014). All scale bars equal 5 mm. A–E) Bryozoans developing cylindrical colonies wrapping around seagrass stems (Blanche Point, Adelaide, South Australia). A) *Adeonellopsis* sp. (NHMUK 2013.7.12.2). B) *Triphyllozoon* sp. (NHMUK 2013.7.12.5-6). C) *Celleporaria* sp. (NHMUK 2013.7.12.1). D) *Densipora* sp. (NHMUK 2013.7.12.4). E) *Thornelya* sp. (NHMUK 2013.7.12.3). F) *Electra posidoniae* encrusting a seagrass leaf of *Posidonia oceanica* (NHMUK 2013.7.12.7, Ischia, Italy).

*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; Fig. 6). 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; Hayward, 1974; Harmelin, 1976). 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 oriented 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 (Fig. 6A–E; 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*: In general applicable for all time intervals and potentially for all regions. However, due to their limited preservation potential, very few studies have dealt with fossil bryozoan communities unequivocally associated with seagrass. Those are restricted to the Maastrichtian of The Netherlands, the Eocene of Florida, the Oligo-Miocene of Australia, the middle Miocene of India, East Kalimantan (Indonesia), Poland and Czech Republic, and the Pliocene of Greece and tropical America (see above). Recent records have been mainly reported from the intensively investigated Mediterranean Sea. Only a few records exist outside of this area (northern Saudi Arabia, Japan and southern and western Australia; see above).

*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 (Fig. 6F; 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). Additionally, records of Recent and fossil seagrass-associated bryozoans are biased towards (sub)tropical and warm-temperate climate-zones. Therefore, it remains questionable if they can perform as IPSIs in higher latitudes. There are no studies that aim to distinguish seagrass-associated bryozoans from other bryozoan communities based on abundance data using quantitative, multivariate methods. Such studies might also improve the potential of bryozoans to perform as IPSIs. Abundant tube-like bryozoan colonies and holdfast structures perform as highly suggestive IPSIs, but have a comparatively low potential for preservation.

### 4.7. Mollusks

#### 4.7.1. Composition of bivalve assemblages (taxa and functional groups)

*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 (Davies, 1970; Jackson, 1972; Brasier, 1975; Mikkelsen et al.,. 1995; Deehr et al., 2001). 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 (4.7.2). Abundances of specific bivalve taxa may vary significantly among seagrass meadows and neighboring habitats as demonstrated for modern shallow-marine environments in the Red Sea where bivalves characterize the mollusk association with muddy seagrass vegetation (Zuschin and Hohenegger, 1998; Zuschin and Oliver, 2003).

*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; Reich et al., 2014). A higher abundance of deposit feeders such as tellinids and nuculids might be expected in seagrass beds compared to neighboring areas, like those 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 the same region, shallow infaunal venerid bivalves of the genus *Chione* became relatively more abundant following the presumed onset of increasing seagrass coverage (Paul and Herbert, 2014). The genus represents also the most abundant bivalve taxon in the seagrass-associated Banyunganti-assemblage (early Miocene of Java, Indonesia; Reich et al., 2014). Other more specific cases are discussed below, i.e., the occurrence of Pinnidae, 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.

*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. A direct relationship between the abundance of *Chione* and the presence of seagrass meadows is not yet established. The higher abundance of the genus in the late Pliocene of Florida could also represent a time-averaging artifact (Vermeij and Herbert, 2004; Paul and Herbert, 2014).

### *4.7.2. Occurrence of Pinnidae (in life position)*

*In modern seagrass meadows*: Modern Pinnidae (fan-mussels) most frequently occur in seagrass habitats (Lemer et al., 2014).

*Use as IPSI*: The occurrence of fossil Pinnidae in life position has been used, among others, as an IPSI in the middle Miocene of the Styrian Basin, Austria (Reuter and Piller, 2011; Reuter et al., 2012)

*Stratigraphic and geographic range*: Lower Carboniferous — Recent; circumtropical, Mediterranean, and North East Atlantic (Schultz and Huber, 2013).

*Fossilization potential*: High, but lower than for many other bivalves due to comparatively thin shells (Beesley et al., 1998)

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

*Habitat restriction*: Fossil Pinnidae in life position, 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 seagrasses did not yet exist (Davis and Elliot, 1957; Fürsich, 1980).

*Conclusions*: The presence of Pinnidae in general is a weak IPSI due to their lack of habitat restriction. However, if they occur in high abundance it can strengthen the argument for the former presence of seagrasses.

### *4.7.3. Occurrence of lucinids (and other chemosymbiotic bivalves)*

*In modern seagrass meadows*: Lucinidae (e.g., *Anodontia*, *Codakia*, *Lucina* among the larger taxa) can be abundant or may even numerically dominate the deeper infauna in seagrass meadows (Jackson, 1972; Greenway, 1995; Mikkelsen et al., 1995; Zuschin and Hohenegger, 1998; Barnes and Hickman, 1999; Johnson et al., 2002; Nakaoka et al., 2002; Zuschin and Oliver, 2003; Meyer et al., 2008). 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, but only in 56% of temperate seagrass beds investigated by Van der Heide et al. (2012), probably due to the temperature-dependent production of sulfur. Likewise, the statistical evaluation of lucinid abundance data identified seagrass beds in the subtropical Red Sea (Zuschin and Hohenegger, 1998), whereas such evaluations were not able to discriminate seagrass meadows in the temperate northern Adriatic Sea (Weber and Zuschin, 2013). 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*: Shallow-water Lucinidae are common in fossil faunas associated with seagrasses (James and Bone, 2007; Moisette et al., 2007; Reuter et al., 2010; Reich et al., 2014). The evolutionary diversification of the family is closely associated with the origination of mangrove swamps and seagrass meadows at the end of the Cretaceous as shown by its rapid increase in taxonomic diversity and abundance in these habitats after a long period of apparent low diversity extending from the Silurian (Stanley, 2014). 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 known 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. Most useful in the (sub)tropics. Likely not applicable for temperate and polar regions.

*Fossilization potential*: High.

*Frequency of occurrence*: Frequent in modern (sub)tropical seagrass meadows (and likewise in the fossil record), moderately frequent to absent in temperate seagrass beds.

*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; they were abundant components of bivalve faunas before seagrasses even existed (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 (sub)tropical mollusk assemblage it might rather exclude the assemblage from being a seagrass association. The usefulness of lucinid abundance data is strongly influenced by latitude: wheras statistical evaluations of lucinid abundance may serve as a highly suggestive proxy in (sub)tropical settings, this IPSI is probably not applicable in temperate and polar regions.

### *4.7.4. 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 and species-rich in meadows than in other adjacent habitats (e.g., Mikkelsen et al., 1995; Sheridan, 1997; Barnes and Barnes, 2012). Several gastropod families, e.g., Strombidae, Xenophoridae, and Hipponicidae, show strong preferences for seagrass habitats (e.g., Janssen et al., 2011; Stoner and Waite, 1991; Table 1). Furthermore, the benthic gastropod assemblage commonly includes

**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, 2014 |
| | 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) |
| | Hipponicidae | Janssen et al. (2011) |
| | Xenophoridae: *Xenophora* | Janssen et al. (2011) |
| | 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) |
| | Neritidae: *Smaragdia* | see Section 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) |

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 (Jackson, 1972; Marsh, 1973; Boström and Bonsdorff, 1997). Common epiphytic gastropods include small cerithioideans 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 (Marsh, 1976; Morgan and Kitting, 1984; Greenway, 1995; Mikkelsen et al., 1995; Rueda et al., 2009a; Albano and Sabelli, 2011). The shallow-water species of shallow infaunal gastropods of the families Ringiculidae and Cylichnidae occur predominantly close to seagrass beds (Beesley et al, 1998). Zuschin and Hohhenegger (1998) showed that various modern shallow-marine facies, including two different seagrass facies, in the Northern Red Sea are characterized by the composition of mollusk death assemblages. The latter study also identified facies-characteristic gastropod-associations that can serve as indicator taxa for seagrass vegetation in the region. Reich (2014) showed 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 (Fig. 7A–D).

*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 (Mandic et al., 2002; James and Bone, 2007; Zuschin et al., 2007; Reuter et al., 2010; Harzhauser, 2014; Reich et al., 2014). Paleo-environmental interpretations of different seagrass localities in the Miocene of Java and East Kalimantan, Indonesia are likewise largely based on common gastropod taxa (Reich et al., 2015; Fig. 7E–H).

*Stratigraphic and geographic range*: Potentially applicable for all time intervals and regions. However, comparative studies of seagrass versus non-seagrass gastropod associations are confined to (sub)tropical regions. Therefore, it is unknown if gastropods can serve as IPSIs in higher latitudes. *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.

*Habitat restriction*: None of the gastropod taxa listed here (Table 1) is restricted to seagrass meadows. *Bittium*, for instance, also occurs abundantly on macroalgae (Chemello and Milazzo, 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* (Section 4.7.4), occurred at low frequencies. Likewise, all indicator species identified by Reich (2014), apart from *S. viridis*, were also reported from non-seagrass habitats.

*Conclusions*: Presence/absence data of certain gastropod taxa may at most perform as a suggestive IPSI due to a lack of habitat restriction. However, studies on modern death assemblages indicate that the statistical evaluation of abundance data provides clear distinctions between gastropod associations from seagrass meadows and neighboring areas in the investigated regions (Zuschin and Hohenegger, 1998; Reich, 2014), and therefore serves as a highly suggestive IPSI. The ecological composition of gastropod associations should be taken into consideration as well (Section 4.7.5).

### 4.7.5. Occurrence of *Smaragdia*

*In modern seagrass meadows*: The neritiid snail *Smaragdia* is closely associated with seagrass vegetation worldwide (Taylor and Lewis, 1970; Kay, 1979; Higo et al., 1999; Rueda et al., 2009a; Zuschin et al., 2009). Two species, *S. viridis* (Fig. 7D) 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 neritiids, 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 was confirmed by one of us (Reich,2014) 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), the early Miocene of India and Indonesia (Harzhauser, 2014; Reuter et al., 2010; Reich et al., 2014; Fig. 7J), and the middle Miocene of the Paratethys (Zuschin et al., 2007). The genus also occurs at various localities in the late Miocene of Indonesia (Reich et al., 2015; Fig. 7I).

*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).

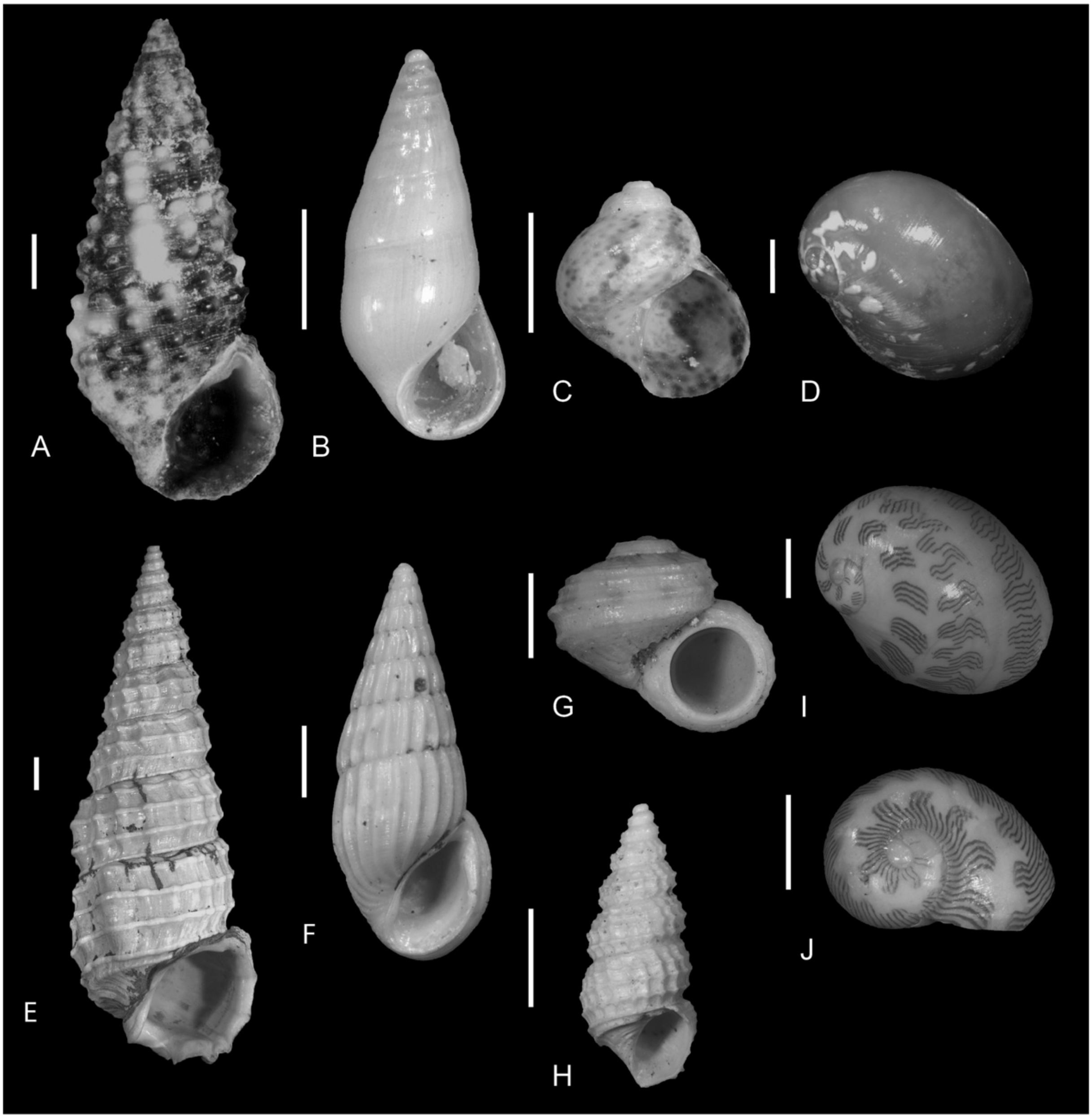

**Fig. 7.** Common Recent and fossil seagrass-associated gastropods. All scale bars equal 1 mm. A–D) Recent gastropods from seagrass beds at San Salvador, Bahamas (Reich, 2014). A) *Cerithium lutosum* (RGM 783.157). B) *Zebina browniana* (RGM 783.159).C) *Eulithidium thalassicolum* (RGM 783.153). D) *Smaragdia viridis* (RGM 783.154). E–J) Fossil gastropods from the Miocene of Indonesia. E) *Cerithium* sp. 4 (RGM 794.000, locality TF 508, East Kalimantan, Tortonian). F) *Rissoina* (*Rissoina*) *banyungantiensis* (RGM 784.843, Java, early Burdigalian). G) *Bothropoma mediocarinata* (RGM 784.746, Java, early Burdigalian). H) *Cerithidium* cf. *perparvulum* (RGM 784.758, Java, early Burdigalian). I) *Smaragdia semari* (RGM 794.002, locality TF 508, East Kalimantan, Tortonian). J) *Smaragdia jogjacartensis* (RGM 784.754, Java, early Burdigalian).

*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 (Kusworo et al., 2015).

### 4.7.6. 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., Nakaoka et al., 2001; Arroyo et al., 2006). Taylor (1978) showed that species richness of predatory gastropods in different habitats at Addu Atoll, Maldives was higher in seagrass beds compared to adjacent algal-dominated habitats, but lower than in reefal environments. The comparatively high diversity of seagrass-associated organisms, 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 (Moulinier and Picard, 1952; Davies, 1970; Brasier, 1975; Ivany et al., 1990; James and Bone, 2007; Moisette et al., 2007; Reuter et al., 2010; Reich et al., 2014). 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

(Section 4.7.7) we suggest that gastropod feeding ecology should be treated seperately when comparing feeding guild compositions. A comparison of patterns in feeding ecology of fossil gastropod assemblages from different shallow marine habitats has been made by Kusworo et al. (2015), 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 in the coral-associated fauna (Fig. 8A–B). This might be a characteristic feature of seagrass-associated gastropod communities. Gastropods from the Miocene of Java, Indonesia (Reich et al., 2014) 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. 8B–C), suggesting that a consistent ecological signature of seagrass-inhabiting mollusks may exist both across regions and over larger time-scales. A paired study of Panamian 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 are also dominated by herbivores, but 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 (Reich, 2014) 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.

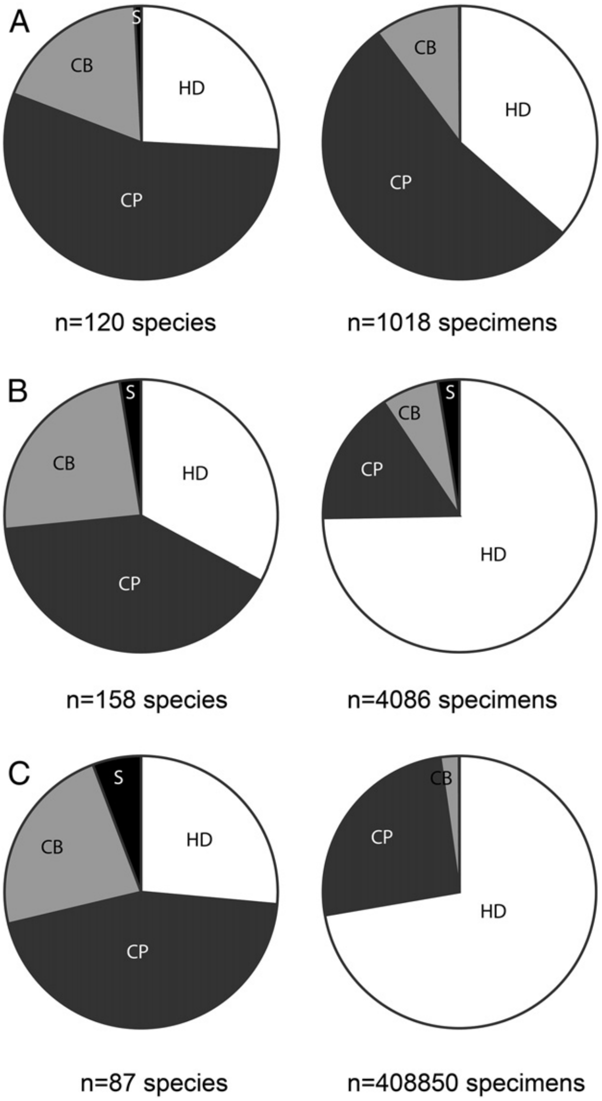

**Fig. 8.** Feeding guild composition of gastropod faunas based on numbers of species (right column) and numbers of specimens (left column); with HD = herbivores and detritivores, CP = predatory carnivores, CB = browsing carnivores, S = suspension feeders. A) Fossil assemblage from a coral-carpet habitat. 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. (2009a; nudibranchs removed).

*Stratigraphic and geographic range*: As for species composition of gastropods (Section 4.7.4).

*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.

*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 (Reich, 2014), and especially in macroalgae assemblages (Chemello and Milazzo, 2002; Leite et al., 2009). 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 (Kusworo et al., 2015; S. Reich, pers. obs.).

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

### 4.7.7. High gastropod/bivalve ratio (epifaunal/infaunal ratios)

*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. However, Paul and Herbert (2014) observed a change in the ratio of infaunal predatory naticid gastropods and epifaunal predatory muricid gastropods in the Pliocene of Florida, with epifaunal muricids becoming relatively more abundant with the presumed expansion of seagrass vegetation after the early Pliocene, due to their better adaption to consolidated substrates.

*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 among different 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. After the early Pliocene when seagrass meadows extended in the Caribbean region, the relative abundance of the shallow infaunal venerid bivalve *Chione* increased (Paul and Herbert, 2014). Although a direct relation between the high abundance of *Chione* and the increase of seagrass vegetation has not been established (Vermeij and Herbert, 2004; Paul and Herbert, 2014), this would likewise lead to comparatively lower gastropod/bivalve ratios in the region.

*Habitat restriction*: Comparatively high gastropod/bivalve ratios are not restricted to seagrass meadows. 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 a mangrove environment, not in a seagrass meadow.

*Conclusions*: Weak IPSI. Probably in some cases 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. The ratio of inaunal naticids versus epifaunal muricids might provide a rather rough IPSI in the Pliocene of Florida, but a general relationship is not yet established.

### 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 as epiphytic species. Epiphytic species can be recognized by carapace morphology (Section 4.9) or known habitat information of each species if available. A study on ostracod assemblages in the Baltic Sea showed that epiphytic taxa were lacking in water with very low salinities and therefore were not able to indicate phytal habitats in the transition zone of fresh to brackish water (Frenzel et al., 2005).

*Stratigraphic and geographic ranges*: *Loxoconcha* and *Xestoleberis*: Cretaceous to Recent; *Paradoxostoma*: ?Cretaceous/Eocene to Recent; *Cythere*: Eocene to Recent; *Aurila* and *Hemicytherura*: Pliocene to Recent (Moore, 1961; Yamaguchi and Goedert, 2010). Each of these genera has 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 (Section 4.9). The composition of ostracods assemblages may yield an IPSI that is applicable in high latitudes, although not in environments with very low salinities.

### 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*: In general as for ostracods assemblages (Section 4.8): 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 (Rosenfeld, 1979; Frenzel et al., 2005).

*Conclusions*: Possibly has potential to be a useful suggestive IPSI, at least for marine macrophyte vegetation. An advantage of carapace morphology over species composition maybe that no detailed taxonomic knowledge is necessary to discriminate the carapaces of epiphytic and benthic species, therefore also non-specialists on ostracod taxonomy perhaps will be able to identify epiphytic assemblages in the fossil record.

### 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*, ophiuroids, and deposit-feeding holothurians (Brasier, 1975; Byrne et al., 2004). Furthermore, seastars, and particularly their juveniles, inhabit seagrass meadows (e.g., Bos et al., 2008). 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 with ophiuroids being the most common motile invertebrate in the seagrass-associated community.

*Stratigraphic and geographic range*: Applicable for all time intervals and regions regarding (juvenile) echinoderm remains in general. For specifically mentioned taxa: *Diadema*: (late Eocene?) early Miocene to Recent; Caribbean, tropical South America, tropical East Atlantic, warm-temperate North Atlantic, Mediterranean, Red Sea, West Indian Ocean, New Zealand. *Echinocyamus*: upper Cretaceous to Recent; worldwide. *Lytechinus*: early Miocene to Recent; Panamian North Pacific, Gulf of Mexico, Caribbean and tropical South America, and fossil from California, Japan and Fiji (with *L. variegatus*: late Miocene to Recent; Gulf of Mexico, Caribbean and tropical South America). *Tripneustes*: early Miocene to Recent; Panamian North Pacific, Caribbean, Red Sea, West Indian Ocean, West Pacific (fossil only); *Toxopneustes*: Pliocene to Recent; Panamian North Pacific, Red, Sea, Indo-Pacific, Japan. *Clypeaster*: fossil since the upper Eocene: circum(sub)tropical (with many species from the Neogene of Cuba) and Europe (with many species from the Miocene of Italy); Recent: circum(sub)tropical, Japan, New Zealand; *Protoreaster nodosus* (see below): Recent only; (sub)tropical West Pacific, West Indian Ocean, Spain. *Antedon*: Miocene to Recent; worldwide with the exception of polar seas (all information from Boxshall et al, 2014 and Kier and Lawson, 1978).

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

*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 (Moore et al., 1963; Greenway, 1995). 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). The juveniles of some modern species of seastars, however, are potentially restricted to seagrass meadows (e.g., *Protoreaster nodosus*: Bos et al., 2008).

*Conclusions*: Weak IPSI (lack of habitat restriction; even taxa characteristic of modern seagrass meadows are in most cases not restricted to the environment). Known obligates, such as juvenile *Protoreaster nodosus*, are unknown in the fossil record. However, the high abundance of juvenile echinoderms in a fossil assemblage can be used to strengthen the argument for paleo-seagrass vegetation if other indicators are present. We are not aware of any quantitative studies that aim to distinguish seagrass-associated echinoderms (or specific groups of echinoderms) from other echinoderm associations. Such studies might be able to improve the potential of echinoderms to perform as IPSIs.

### 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*: To our knowledge the only available study that applied fossil otoliths as IPSI is Green (2002) who used the presence of juvenile sciaenid otoliths as an additional character for the interpretation of the Eocene Moody's Branch Formation, Louisiana and Mississippi, USA, as a seagrass habitat.

*Stratigraphic and geographic range*: For sciaenids: 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. Further studies on the distribution of otoliths of seagrass-associated fish in shallow-marine facies, preferably using abundance data, might reveal a higher potential of otoliths as IPSIs.

### 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 (Domning, 1982; Ames et al., 1996). 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; Vélez-Juarbe et al., 2012; Vélez-Juarbe, 2014). 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 to Recent. The distribution of prorastomid, protosirenid and dugongid fossils is shown in Fig. 9. It should be noted that their fossil occurrences are concentrated in the Caribbean and Europe and are comparatively scarce around the Indo-Pacific. This 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, 2014).

*Frequency of occurrence in the fossil record*: Moderately frequent to rare, depending on region.

*Habitat restriction*: Although dugongids and probably also prorastomid and protosirenids 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, 2014).

## 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 resuspension 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 non-vegetated 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 resuspension (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

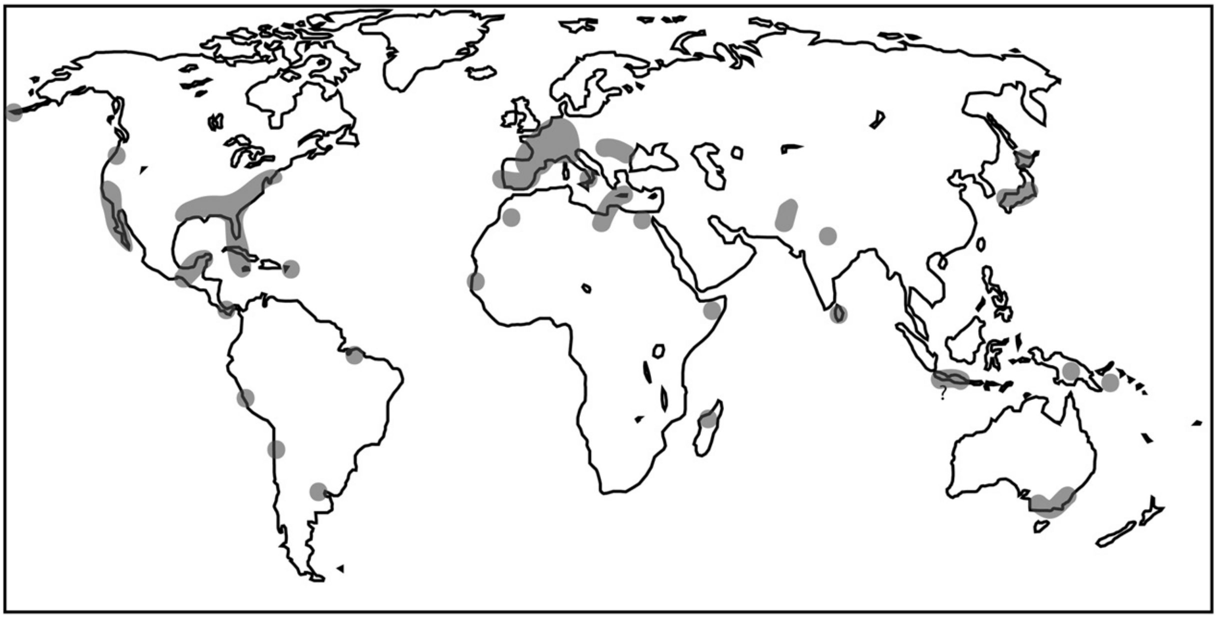

**Fig. 9.** Worldwide distribution of fossil prorastomid, protosirenid and dugongid occurrences. After Domning (1996).

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, which are generated by the seaward migration of blowout structures (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 considerd 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 in 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. Reich (2014) 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 her 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. 7E–H; Reich et al., 2014).

*Fossilization potential*: High.

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

*Habitat restriction*: A specific taphonomic signature that is restricted to seagrass meadows does not exist (Leonard-Pingel, 2005).

*Conclusions*: Weak IPSI; 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 that 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 (middle Eocene) Calcaire Grossier 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 middle 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, USA 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, 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 $\delta^{13}C$ values of typically −10 to −11‰ (Smith and Epstein, 1971; Hemminga and Mateo, 1996), 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 $\delta^{13}C$ 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 (Reich et al., 2015). 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. The method is likely to be restricted to (sub)tropical regions because of a relative depletion of $\delta^{13}C$ of seagrasses in temeperate areas (Hemminga and Mateo, 1996).

*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 (Simenstad and Wissmar, 1985; Lin et al., 1991).

*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 $\delta^{13}C$ 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 (Eglinton and Hamilton, 1967; Frewin, 1993 in De Leeuw et al., 1995). Because seagrass meadows may cover large areas of 100 s 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 (De Leeuw et al., 1995; Duarte and Cebrián, 1996).

*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 $\alpha,\omega$-dicarboxylic acids ($C_{26}$–$C_{28}$), and in the case of *Zostera marina* from temperate regions a specific series of $\alpha,\beta$-diOH-fatty acids (Nichols et al., 1982; Nichols and Johns, 1985; Frewin, 1993; De Leeuw et al., 1995). 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. Geographic range congruent with that of seagrasses.

*Fossilization potential*: Higher-plant long-chain acids found in leaf waxes appear to remain constant over time (Logan et al., 1995; Huang et al., 1996; 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 (Logan et al., 1995; Huang et al., 1996). 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., Eglinton and Hamilton, 1967, 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. In addition, our characterization of IPSIs is based on perfectly preserved material and poorer preservation will hamper the use of individual IPSIs by differing amounts.

The record of paleo-seagrass facies is strongly biased towards the (sub)tropics and warm-temperate regions (e.g., the Mediterranean). Paleo-seagrass meadows from warm climate zones are easier to identify than those occurring in cold-temperate and polar regions, because various IPSIs (e.g., photosymbiotic foraminifers, corals, and 'constructive' micrite envelopes) are restricted to lower latitudes. This relation can be well illustrated by the example of lucinid bivalves (4.7.3). The frequency of occurrence as well as the abundance in seagrass meadows of those chemosymbiotic bivalves considerably decreases from (sub) tropical to temperate regions (Van der Heide et al., 2012). Large-scale studies like the one conducted by Van der Heide et al. (2012) do not exist for other seagrass-associated taxa. Studies on occurrences, abundance and species richness of seagrass-associated organisms in high latitudes are scarce in general. Therefore, it is unclear whether and to what extent many of the associations between seagrass and higher taxa that exist in the tropics are present in temperate and polar regions. In conclusion, it is likely that paleo-seagrass beds in temperate and polar regions remain unidentified in the paleontological record. Possibly, ostracod assemblages are useful IPSIs for low-latitude seagrass meadows, because genera typically associated with marine vegetation do have a worldwide distribution. However, it might be difficult to distinguish seagrass assemblages from other epiphytic ostracods assemblages (4.8–9.).

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, various foraminifera (e.g., *Elphidium*), mollusks and echinoids. The mere presence of such taxa is not able to distinguish paleo-seagrass from non-seagrass environments and exceptions of obligate seagrass-associated organisms with a good preservation potential that can serve as indicator taxa are scarce. Therefore, the community structure of fossil assemblages in terms of abundance of taxa and functional groups (e.g., feeding guilds) provides more reliable IPSIs. Comparative studies of modern-day mollusk death assemblages from (sub)tropical shallow-marine habitats showed that multivariate statistical evaluations of abundance data are able to clearly discriminate seagrass and non-seagrass associated assemblages (Zuschin and Hohenegger, 1998; Reich, 2014). Such studies are comparatively time-consuming and require in-situ assemblages that are rich in specimens, and a profound taxonomic knowledge of the studied organism group. This might explain why such studies are relatively rare compared to evaluations using the presence of only one or a few taxa as IPSI. In addition, the characteristics for mollusk death assemblages from modern environments (e.g., indicator taxa) might not be necessarily transferable to fossil assemblages, particularly those from other geographic regions. In addition, some shallow-marine habitats might be more easily distinguishable from seagrass meadows than others. Whereas seagrass-associated mollusk assemblages differ from those found on unvegetated sand or in coral-dominated environments in specific regions (Zuschin and Hohenegger, 1998; Reich, 2014; Kusworo et al., 2015), differentiation may be more challenging when it comes to other vegetal marine habitats with a three-dimensional structuring, such as macroalgae-dominated environments. 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, one should be cautious in inferring that strap-shaped 'vegetal' substrates are 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 our proposed classification of IPSIs, divided into strong (conclusive or highly suggestive), suggestive, and weak indicators. This classification is only intended to be a simple and practical guide to their use.

Conclusive IPSIs are those that document the presence of seagrasses by preserving imprints, etchings, or casts of roots, rhizomes, stems, or leaves. These IPSIs are both rare in the fossil record and represent structures that can be difficult to distinguish from those related to other plants and algae. 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; and abundant lucinid bivalves and comparatively high carbon isotope ratios point to a high sedimentary organic content.

Naturally, the more numerous the IPSIs present, 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 by 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 (Reich

**Table 2**
Classification of IPSIs.

Direct seagrass indicators
Plant fossils
High-resolution bioimmurations of seagrasses

Strong IPSIs
Conclusive IPSIs
Rhizome imprints preserved by oysters
Root casts
Root etchings on shells
Seagrass specific biomolecules

Highly suggestive IPSIs
Abundance of tube-like encrustations of coralline algae and bryozoans
Abundance of 'hooked' crustose coralline red algae
Gastropod abundance data
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
Presence of gastropod taxa
Feeding guild composition of gastropod assemblages
Species composition of ostracod assemblages
Carapace morphology of ostracods

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)
High relative abundance of *s*
Pinnidae in life position
Occurrence of lucinids (and other chemosymbiotic bivalves)
High gastropod/bivalve ratio (epifaunal/infaunal 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

et al., 2014, 2015). 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). Such integrative approaches using sedimentology, paleontology, paleoecology, taphonomy, and (if possible) geochemistry are clearly preferable for characterizing potential seagrass facies and fossil associations.

Among higher taxa, mollusks provide the widest variety of 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. However, as discussed before, these IPSIs serve well for (sub)tropical and warm-temperate regions, but are probably not applicable in cold-temperate and polar climatic zones.

## Acknowledgments

This research was funded by the Marie Curie Actions Plan, Seventh Framework Program of the European Union (Throughflow, grant no. 237922). Many colleagues helpfully provided their knowledge on various aspects of this study. We thank J. Cottrell, A. Cutler, J.W. de Leeuw, S. Donovan, R. van der Ham, R.D. Pancost, G. Stringer, P.D. Taylor, and M. Yasuhara. Special thanks go to J.C. Braga and K.G. Johnson for their helpful comments and the additional provision of photographs. Furthermore, we would like to acknowledge the work of D.P. Domning, M. Zuschin and an anonymous reviewer who helped considerably to improve the manuscript.

## References

Adams, C.G., 1968. A revision of the foraminifer genus *Austrotrillina* Parr. Bull. Br. Mus. Nat. Hist. Geol. 16, 71–97.
Aguirre, J., Riding, R., Braga, J.C., 2000. Diversity of coralline red algae: origination and extinction patterns from the Early Cretaceous to the Pleistocene. Paleobiology 26, 651–667.
Albano, P.G., Sabelli, B., 2011. Comparison between death and living mollusc assemblages in a Mediterranean infralittoral off-shore reef. Palaeogeogr. Palaeoclimatol. Palaeoecol. 310, 206–215.
Ames, A.L., Van Vleet, E.S., Sackett, W.M., 1996. The use of stable carbon isotope analysis for determining the dietary habits of the Florida manatee, *Trichechus manatus latirostris*. Mar. Mamm. Sci. 12, 555–563.
Arroyo, M.C., Salas, C., Rueda, J.L., Gofas, S., 2006. Temporal changes of mollusc populations from a *Zostera marina* bed in southern Spain (Alboran Sea), with biogeographic considerations. Mar. Ecol. 27, 417–430.

Balata, D., Nesti, U., Piazzi, L., Cinell, F., 2007. Patterns of spatial variability of seagrass epiphytes in the north-west Mediterranean Sea. Mar. Biol. 151, 2025–2035.

Ball, M., Shinn, E.A., Stockmann, K., 1967. The geologic effects of Hurricane Donna in south Florida. J. Geol. 75, 583–597.

Bałuk, W., Radwański, A., 1977. Organic communities and facies development of the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). Acta Geol. Pol. 27, 85–123.

Barnes, R.S.K., Barnes, M.K.S., 2012. Shore height and differentials between macrobenthic assemblages in vegetated and unvegetated areas of an intertidal sandflat. Estuar. Coast. Shelf Sci. 106, 112–120.

Barnes, P.A.G., Hickman, C.S., 1999. Lucinid bivalves and marine angiosperms: a search for causal relationships. In: Walker, D.I., Wells, F.E. (Eds.), The Seagrass Flora and Fauna of Rottnest Island. Western Australia Museum, Perth, pp. 215–238.

Beavington-Penney, S.J., Wright, V.P., Woelkerling, W.J., 2004. Recognising macrophyte-vegetated environments in the rock record: a new criterion using 'hooked' forms of crustose coralline red algae. Sediment. Geol. 166, 1–9.

Beesley, P.L., Ross, G.J.B., Wells, A., 1998. Mollusca: The Southern Synthesis. Fauna of Australia. Volume 5, Part A–B. CSIRO Publishing, Melbourne.

Ben Brahim, M., Hamza, A., Hannachi, I., Rebai, A., Jarboui, O., Bouain, A., et al., 2010. Variability in the structure of epiphytic assemblages of *Posidonia oceanica* in relation to human interferences in the Gulf of Gabes, Tunisia. Mar. Environ. Res. 70, 411–421.

Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Mar. Ecol. Prog. Ser. 215, 79–92.

Benson, R.H., 1961. Ecology of ostracode assemlgaes, Treatise on Invertebrate Paleontology, Part Q, Arthropoda 3. In: Moore, H.B. (Ed.), Boulder: Geological Society of America. University of Kansas Press, Lawrence, pp. Q56–Q63.

Benzecry, A., Brack-Hanes, S.D., 2008. A new hydrocharitacean seagrass from the Eocene of Florida. Bot. J. Linn. Soc. 157, 19–30.

Betzler, C., Martín, J.M., Braga, J.C., 2000. Non-tropical carbonates related to rocky submarine cliffs (Miocene, Almería, southern Spain). Sediment. Geol. 131, 51–65.

Bone, Y., James, N.P., 1993. Bryozoans as carbonate sediment producers on the cool-water Lacepede Shelf, southern Australia. Sediment. Geol. 86, 247–271.

Borowitzka, M.A., Lavery, P.S., van Keulen, M., 2006. Epiphytes on seagrasses. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, pp. 441–461.

Bos, A.R., Gumanao, G.S., Alipoyo, J.C.E., Cardona, L.T., 2008. Population dynamics, reproduction and growth of the Indo-Pacific horned sea star, *Protoreaster nodosus* (Echinodermata; Asteroidea). Mar. Biol. 156, 55–63.

Boström, C., Bonsdorff, E., 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. J. Sea Res. 37, 153–166.

Bouchet, P., Lozout, P., Maestrati, P., Heros, V., 2002. Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. Biol. J. Linn. Soc. 75, 421–436.

Boxshall, G.A., Mees, J., Costello, M.J., Hernandez, F., Gofas, S., et al., . World Register of Marine Species. Available from, http://www.marinespecies.org (at VLIZ. Accessed 2014-11-07).

Brachert, T.C., Betzler, C., Braga, J.C., Martin, J.M., 1998. Microtaphofacies of a warm-temperate carbonate ramp (uppermost Tortonian/lowermost Messinian, southern Spain). Palaios 13, 459–475.

Brandano, M., Frezza, V., Tomassetti, L., Pedley, M., Matteucci, R., 2009. Facies analysis and palaeoenvironmental interpretation of the Late Oligocene Attard Member (Lower Coralline Limestone Formation), Malta. Sedimentology 56, 1138–1158.

Brasier, M.D., 1975. An outline history of seagrass communities. Palaeontology 18, 681–702.

Bretsky, S.S., 1978. Marine grass banks—a possible explanation for carbonate lenses, Pierre Shale (Cretaceous), Colorado. J. Sediment. Petrol. 48, 999–1000.

Brouns, J.J.W.M., Heijs, F.M.L., 1985. Tropical seagrass ecosystems in Papua New Guinea. A general account of the environment, marine flora and fauna. Mar. Biol. 88, 145–182.

Browne, C.M., Maneveldt, G.W., Bolton, J.J., Anderson, R.J., 2013. Abundance and species composition of non-geniculate coralline red algae epiphytic on the South African populations of the rocky shore seagrass *Thalassodendron leptocaule* M.C. Duarte, Bandeira & Romeiras. S. Afr. J. Bot. 86, 101–110.

Buchan, O.C., Lewis, R.D., 2008. Recent benthic Foraminifera as indicators of seagrass-bed characteristics, San Salvador, Bahamas: the addition of taphonomy. Geologic Problem Solving with Microfossils: a Volume in Honor of Garry D Jones. SEPM Spec. Publ. 83–92.

Budd, A.F., Johnson, K.G., Stemann, T.A., 1996. Plio-Pleistocene turnover and extinctions in the Caribbean reef-coral fauna. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), Evolution and Environment in Tropical America. The University of Chicago Press, pp. 169–204.

Byrne, M., Smoothey, A., Hogget, A., Uthicke, S., 2004. Population biology of shallow water holothuroids and ophiuroids from Rain Island and Moulter Cay, Northern Great Barrier Reef. In: Heizeller, T., Nebelsick, J.H. (Eds.), Proceedings of the 11th International Echinoderm Conference, Munich. Taylor & Francis, London, pp. 25–38.

Cann, J.H., Clarke, J.D., 1993. The significance of *Marginopora vertebralis* (Foraminifera) in surficial sediments at Esperance, Western Australia, and in last interglacial sediments in northern Spencer Gulf, South Australia. Mar. Geol. 111, 171–187.

Cann, J.H., Murray-Wallace, C.V., Riggs, N.J., Belperio, A., 2006. Successive foraminiferal faunas and inferred palaeoenvironments associated with the postglacial (Holocene) marine transgression, Gulf St Vincent, South Australia. The Holocene 16, 224–234.

Chandler, M.E.J., 1961. The Lower Tertiary Floras of Southern England. I. Palaeocene Floras, London Clay Flora (Supplement). British Museum of Natural History, London.

Cheetham, A.H., Jackson, J.B.C., 1996. Speciation, extinction, and the decline of arborescent growth in Neogene and Quaternary Cheilostome Bryozoa of tropical America. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), Evolution and Environment in Tropical America. The University of Chicago Press, pp. 205–233.

Chemello, R., Milazzo, M., 2002. Effect of algal architecture on associated fauna: some evidence from phytal molluscs. Mar. Biol. 140, 981–990.

Chesters, K.I.M., Gnauck, F.R., Hughes, N.F., 1967. Angiospermae. In: Harland, W.B., Holland, C.H., House, M.R., et al. (Eds.), The Fossil Record—A Symposium with Documentation. Geol Soc Lond, pp. 269–389.

Clementz, M.T., Goswami, A., Gingerich, P.D., Koch, P.L., 2006. Isotopic records from early whales and sea cows: contrasting patterns of ecological transition. J. Vertebr. Paleontol. 26, 355–370.

Clementz, M.T., Sorbi, S., Domning, D.P., 2009. Evidence of Cenozoic environmental and ecological change from stable isotope analysis of sirenian remains from the Tethys–Mediterranean region. Geology 37, 307–310.

Collinson, M.E., 1983. Fossil Plants of the London Clay. Palaeontological Association Field Guides No 1. Palaeontological Association, London.

Collinson, M.E., 1996. Plant macrofossils from the Bracklesham Group (Early & Middle Eocene), Bracklesham Bay, West Sussex, England: review and significance in the context of coeval British Tertiary faunas. Tertiary Res. 16, 175–202.

Costa, F.H.A., Nehm, R.H., Hickman, C.S., 2001. Neogene paleontology in the northern Dominican Republic; 22, The family Neritidae (Mollusca: Gastropoda). Bull. Am. Paleontol. 359, 47–69.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., et al., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260.

Cramer, M.D., Hawkins, H.J., 2009. A physiological mechanism for the formation of root casts. Palaeogeogr. Palaeoclimatol. Palaeoecol. 274, 125–133.

Cronin, T.M., Holmes, C., Wingard, L., Ishman, S.E., Dowsett, H.J., Waibel, N., 2001. Historical trends in epiphytal ostracodes from Florida Bay: implications for seagrass and macrobenthic algal variability. Bull. Am. Paleontol. 361, 159–197.

Cummins, R.H., Boardman, M., Miller, A., 1995. Sedimentology and taphonomy of a Holocene carbonate lagoon: Pigeon Creek, San Salvador, Bahamas. In: Boardman, M. (Ed.), Proceedings of the Seventh Symposium on the Geology of the Bahamas. Bahamian Field Station, Ltd., San Salvador, Bahamas, pp. 25–40.

Curry, D., 1965. Palaeogene beds of south-east England. Proc. Geol. Assoc. 76, 151–173.

Cushman, J.A., 1922. Shallow water foraminifera of the Tortuga region. Carnegie Inst. Wash. 17, 1–85.

Cutler, A.H., 1995. Taphonomic implications of shell surface textures in Bahia la Choya, northern Gulf of California. Palaeogeogr. Palaeoclimatol. Palaeoecol. 114, 219–240.

Davies, G.R., 1970. Carbonate bank sedimentation, eastern Shark Bay, Western Australia. Mem. Am. Assoc. Pet. Geol. 13, 85–168.

Davis, A.G., Elliot, G.F., 1957. The palaeogeography of the London Clay Sea. Proc. Geol. Assoc. 68, 255–277.

De Leeuw, J.W., Frewin, N.L., Van Bergen, P.F., Sinninghe Damsté, J.S., Colinson, M.E., 1995. Organic carbon as a palaeoenvironmental indicator in the marine realm. Geol. Soc. Lond. Spec. Publ. 83, 43–71.

De Saporta, G., Marion, A.F., 1878. Révision de la flore Heersienne de Gelinden d'après une collectionappartenant au comte G. de Looz. Mém Acad R Belg, Cour Sav Étrang. 41 pp. 1–112.

Debenay, J.P., Payri, C.E., 2010. Epiphytic foraminiferal assemblages on macroalgae in reefal environments of New Caledonia. J. Foraminifer. Res. 40, 36–60.

Debey, M.H., 1848. Übersicht der urweltlichen Pflanzen des Kreidegebirges überhaupt und der Aachener Kreideschichten insbesondere. Verh. Nat. Hist. Ver. Preuss. Rheinl. 5, 113–125.

Debey, M.H., 1851. Beitrag zur fossilen Fauna der holländischen Kreide (Vaels bei Aachen, Kunraed, Maastricht). Verh. Nat. Hist. Ver. Preuss. Rheinl. 8, 568–569.

Deehr, R.A., Cummins, H., Boardman, M.R., Zimmerman, R.A., 2001. Paleocommuninity reconstruction of a tropical carbonate lagoon, Graham's Harbor, San Salvador, Bahamas. In: Greenstein, B.J., Carney, C.K. (Eds.), Proceedings of the 10th Symposium of the Geology of the Bahamas and Other Carbonate Regions. Gerace Research Center, San Salvador, Bahamas, pp. 187–200.

Dekker, H., 2000. The Neritidae (Gastropoda) from the circumarabian seas, with the description of two new species, a new subgenus and a new genus. Vita Marina 47, 29–64.

Den Hartog, C., 1979. Seagrasses and seagrass ecosystems, an appraisal of the research approach. Aquat. Bot. 7, 105–107.

Di Martino, E., Taylor, P.D., 2014. A brief review of seagrass-associated bryozoans, recent and fossil. Stud Tridentini. Sci. Nat. Acta Geol. 94, 79–94 (IBA Conference 2013 Volume).

Diedrich, C.G., 2008. The food of the miosiren *Anomotherium langenwieschei* (Siegfried)—indirect proof of seaweed or seagrass by xenomorphic oyster fixation structures in the Upper Oligocene (Neogene) of the Doberg, Bünde (NW Germany) and comparisons to modern *Dugong dugon* (Müller) feeding strategies. Senckenberg. Marit. 38, 59–73.

Dilcher, D., 2015. Fossil plants from the Coon Creek Formation. Tenn. Div. Geol. Bull. (in press).

Domning, D.P., 1977. An ecological model for late Tertiary sirenian evolution in the North Pacific Ocean. Syst. Zool. 25, 352–362.

Domning, D.P., 1981. Sea cows and seagrasses. Paleobiology 7, 417–420.

Domning, D.P., 1982. Evolution of manatees: a speculative history. J. Paleontol. 56, 599–619.

Domning, D.P., 1996. Bibliography and index of the Sirenia and Desmostylia. Smithson. Contrib. Paleobiol. 80, 1–611.

Domning, D.P., 2001. Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. Palaeogeogr. Palaeoclimatol. Palaeoecol. 166, 27–50.

Domning, D.P., Beatty, B.L., 2007. Use of tusks in feeding by dugongid sirenians: observations and tests of hypotheses. Anat. Rec. 290, 523–538.

Domning, D.P., Morgan, G.S., Ray, C.E., 1982. North American Eocene sea cows (Mammalia: Sirenia). Smithson. Contrib. Paleobiol. 52, 1–69.

Duarte, C.M., 1991. Seagrass depth limits. Aquat. Bot. 40, 363–377.

Duarte, C.M., Cebrián, J., 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41, 1758–1766.

Duarte, C.M., Chiscano, C.L., 1999. Seagrass biomass and production: a reassessment. Aquat. Bot. 65, 159–174.

Eglinton, G., Hamilton, R.J., 1967. Leaf epicuticular waxes. Science 156, 1322–1335.

Eva, A.N., 1980. Pre-Miocene seagrass communities in the Caribbean. Palaeontology 23, 231–236.

Fishelson, L., 1974. Ecology of the northern Red Sea crinoids and their epi- and endozoic fauna. Mar. Biol. 26, 183–192.

Fisher, M.R., Hand, S.C., 1984. Chemoautotrophic symbionts in the bivalve *Lucina floridana* from seagrass beds. Biol. Bull. 167, 445–459.

Fisk, D.A., 1983. Free-living corals: distributions according to plant cover, sediments, hydrodynamics, depth and biological factors. Mar. Biol. 74, 287–294.

Fornos, J.J., Ahr, W.M., 1997. Temperate carbonates on a modern, low-energy, isolated ramp: the Balearic Platform, Spain. J. Sediment. Res.B. 67, 364–373.

Fredston-Herman, A.L., O'Dea, A., Rodriguez, F., Thomas, W.G., Todd, J.A., 2013. Marked ecological shifts in seagrass and reef molluscan communities since the Mid-Holocene in the southwestern Caribbean. Bull. Mar. Sci. 89. http://dx.doi.org/10.5343/bms.2012.1077.

Frenzel, P., Henkel, D., Siccha, M., Tschendel, L., 2005. Do ostracod associations reflect macrophyte communities? A case study from the brackish water of the southern Baltic Sea coast. Aquat. Sci. 67, 142–155.

Frewin, N.L., 1993. The Distribution and Preservation of Organic Matter in Recent Lagoonal Carbonate Sediments, Florida Bay, USA. PhD Thesis. University of London.

Froede jr., C.R., 2012. Rhizolith evidence in support of a late Holocene sea-level highstand at least 0.5 m higher than present at Key Biscayne, Florida. Geology 30, 203–206.

Fry, B., Scalan, R.S., Parker, P.L., 1977. Stable carbon isotope evidence for two sources of organic matter in coastal sediments: seagrasses and plankton. Geochim. Cosmochim. Acta 41, 1875–1877.

Fujita, K., Hallock, P., 1999. A comparison of phytal substrate preferences of Archaias angulatus and *Sorites orbiculus* in mixed macroalgal-seagrass beds in Florida Bay. J. Foraminifer. Res. 29, 143–151.

Fürsich, F.T., 1980. Preserved life positions of some Jurassic bivalves. Palaeontol. Z. 54, 289–300.

Gautier, Y., 1952. Note sur la faune bryozoologique de la région de Villefranche-sur-Mer. Bull. Inst. Oceanogr. 1008, 1–18.

Geraci, S., 1974. I briozoi di Punta Manara (Sestri Levante—Golfo di Genova). Ann. Mus. Civ. Stor. Nat. Giacomo. Doria, Genova 80, 33–57.

Geraci, S., Cattaneo, R., 1980. Il popolamento a briozoi (Cheilostomata) della prateria a Posidonia di Procchio (Isola d'Elba). Ann. Mus. Civ. Stor. Nat. Giacomo. Doria, Genova 83, 107–125.

Glover, E.A., Taylor, J.D., 2007. Diversity of chemosymbiotic bivalves on coral reefs: Lucinidae (Mollusca, Bivalvia) of New Caledonia and Lifou. Zoosystema 29, 109–181.

Goreau, T.F., 1959. The ecology of Jamaican coral reefs I. Species composition and zonation. Ecology 40, 67–90.

Gray, J.S., 2001. Marine diversity: the paradigms in patterns of species richness examined. Sci. Mar. 65, 41–56.

Green, T.M., 2002. A Comparison of Paleoecological Determinations Based on Vertebrate Faunas From the Moodys Branch Formation (Upper Eocene) of Louisiana and Mississippi. M.S. Thesis.. The University of Louisiana, Monroe.

Green, E.P., Short, F.T., 2003. World Atlas of Seagrasses. University of California Press, Berkeley.

Greenstein, B.J., 1991. An integrated study of echinoid taphonomy: predictions for the fossil record of four echinoid families. Palaios 6, 519–540.

Greenway, M., 1995. Trophic relationships of macrofauna within a Jamaican seagrass meadow and the role of the echinoid *Lytechinus variegatus* (Lamarck). Bull. Mar. Sci. 56, 719–736.

Gregor, H.-J., 1991. Ein neues fossiles Seegras—Posidocea frickhingeri nov. gen. et spec. im Paläogen Oberitaliens (Verona). Doc. Nat. 65, 1–11.

Gregor, H.-J., 2003. Erstnachweis von Seegras-Resten (Posidonia) im Oberen Eozän der nördlichen Kalkalpen bei Hallthurm. Doc. Nat. 148, 1–19.

Gudmundson, G., 1994. Phylogeny, ontogeny, and systematics of recent Soritacea Ehrenberg, 1839 (Foraminiferida). Micropaleontology 40, 101–155.

Hallock, P., Peebles, M.W., 1993. Foraminifera with chlorophyte endosymbionts: habitats of six species in the Florida Keys. Mar. Micropaleontol. 20, 277–292.

Harmelin, J.-G., 1976. Le sous-ordre des Tubuliporina (Bryozoaires Cyclostomes) en Méditerranée: écologie et systématique. Mém. Inst. Océanogr. 10, 1–326.

Harzhauser, M., 2014. A seagrass-associated early Miocene Indo-Pacific gastropod fauna from South-West India (Kerala). Palaeontogr. Abt. A 302, 73–178.

Hayward, P.J., 1974. Observations on the bryozoan epiphytes of Posidonia oceanica from the island of Chios (Aegean Sea). In: Pouyet, S. (Ed.), Bryozoa 1974 Documents Laboratoire de Géologie Faculté de Sciences de Lyon. 3, pp. 347–356.

Heck, K.L., Able, K.W., Fahay, M.P., Roman, C.T., 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition, seasonal abundance patterns and comparison with unvegetated substrates. Estuaries 12, 59–65.

Hemminga, M.A., Duarte, C.M., 2000. Seagrass Ecology. Cambridge University Press.

Hemminga, M.A., Mateo, M.A., 1996. Stable carbon isotopes in seagrasses; variability in ratios and use in ecological studies. Mar. Ecol. Prog. Ser. 140, 285–298.

Hernandez, M.E., Mead, R., Peralba, M.C., Jaffé, R., 2001. Origin and transport of n-alkane-2-ones in a subtropical estuary: potential biomarkers for seagrass-derived organic matter. Org. Geochem. 32, 21–32.

Hesse, M., Weber, M., Halbritter, H.M., 1999. Pollen walls of Araceae, with special reference to their fossilization potential. Grana 38, 203–209.

Higo, S., Calloman, P., Goto, Y., 1999. Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan. Elle Scientific Publications, Osaka.

Hoeksema, B.W., 2007. Delineation of the Indo-Malayan centre of maximum biodiversity: the coral triangle. In: Renema, W. (Ed.), Biogeography, Time and Place: Distributions, Barriers, and Islands. Springer, Dordrecht, pp. 117–178.

Hoeksema, B.W., Best, M.B., 1991. New observations on scleractinian corals from Indonesia: 2. Sipunculan-associated species belonging to the genera Heterocyathus and Heteropsammia. Zool. Meded. 65, 221–245.

Hohenegger, J., 1994. Distribution of living larger foraminifera NW of Sesoko-Jima, Okinawa, Japan. Mar. Ecol. 15, 291–334.

Hohenegger, J., 1996. Remarks on the distribution of larger foraminifera (Protozoa) from Belau (Western Carolines). Occas. Pap. Kagoshima University Res. Cent. S. Pac. 85–90.

Hosius, A., von der Marck, W., 1880. Die Flora der Westfälischen Kreideformation. Palaeontographica 26, 125–236.

Houbrick, R.S., 1980. Observations on the anatomy and life history of *Modulus modulus* (Prosobranchia: Modulidae). Malacologia 20, 117–142.

Houbrick, R.S., 1981. Anatomy of *Diastoma melanioides* (Reeve, 1849) with remarks on the systematic position of the family Diastomatidae (Prosobranchia: Gastropoda). Proc. Biol. Soc. Wash. 94, 598–621.

Houbrick, R.S., 1984. *Diastoma melanioides* (Reeve), a relict snail from South Australia. In: Eldridge, N., Stanley, S. (Eds.), Living Fossils. Springer Verlag, Berlin.

Houbrick, R.S., 1992. Monograph of the Genus Cerithium Bruguière in the Indo-Pacific (Cerithiidae: Prosobranchia). Smithson. Contrib. Zool. 510, 1–211.

Houbrick, R.S., 1993. Phylogenetic relationships and generic review of the Bittiinae (Prosobranchia: Cerithiodea). Malacologia 35, 261–313.

Huang, Y., Lockheart, M.J., Logan, G.A., Eglington, G., 1996. Isotope and molecular evidence for the diverse origins of carboxylic acids in fossils and sediments from the Miocene Lake Clarkia deposits, Idaho, U.S.A. Org. Geochem. 24, 289–299.

Hughes, R.G., Johnson, S., Smith, I.D., 1991. The growth patterns of some hydroids that are obligate epiphytes of seagrass leaves. Hydrobiologia 216, 205–210.

Hughes, A.R., Williams, S.L., Duarte, C.M., Heck, K.L., Waycott, M., 2009. Associations of concern: declining seagrasses and threatened dependent species. Front. Ecol. Environ. 7, 242–246.

Ivany, L.C., Portell, R.W., Jones, D.S., 1990. Animal–plant relationships and paleobiogeography of an Eocene seagrass community from Florida. Palaios 5, 244–258.

Jackson, J.B.C., 1972. The ecology of the molluscs of *Thalassia* communities, Jamaica, West Indies. II. Molluscan populaton variability along an environmental stress gradient. Mar. Biol. 14, 304–337.

Jackson, J.B.C., 2001. What was natural in the coastal oceans? PNAS 98, 5411–5418.

James, N.P., Bone, Y., 2007. A late Pliocene–early Pleistocene, inner shelf, subtropical, seagrass-dominated carbonate: Roe Calcarenite, Great Australien Bight, Western Australia. Palaios 22, 343–359.

Janssen, R., Zuschin, M., Baal, C., 2011. Gastropods and their habitats from the northern Red Sea (Egypt, Safaga) Part 2: Caenogastropoda: Sorbeoconcho and Littorinimorpha. Ann. Nat. Hist. Mus. Wien. Ser. A. 113, 373–509.

Jarochowska, E., 2012. High-resolution microtaphofacies analysis of a carbonate tidal channel and tidally influenced lagoon, Pigeon Creek, San Salvador Island, Bahamas. Palaios 27, 151–170.

Jernakoff, P., Nielsen, J., 1998. Plant–animal associations in two species of seagrasses in Western Australia. Aquat. Bot. 60, 359–376.

Johnson, K.G., 1992. Population dynamics of a free-living coral: recruitment, growth, and survivorship of *Manicina areolata* on the Caribbean coast of Panamá. J. Exp. Mar. Biol. Ecol. 164, 171–191.

Johnson, K.G., Budd, A.F., Stemann, T.A., 1995. Extinction selectivity and ecology of Neogene Caribbean reef corals. Paleobiology 21, 52–73.

Johnson, M.A., Fernandez, C., Pergent, G., 2002. The ecological importance of an invertebrate chemoautotrophic symbiosis to phanerogam seagrass beds. Bull. Mar. Sci. 7, 1343–1351.

Johnson, K.G., Todd, J.A., Jackson, J.B.C., 2007. Coral reef development drives molluscan diversity increase at local and regional scales in the late Neogene and Quaternary of the southwestern Caribbean. Paleobiology 33, 24–52.

Johnson, K.G., Jackson, J.B.C., Budd, A.F., 2008. Caribbean reef development was independent of coral diversity over 28 million years. Science 319, 1521–1522.

Kamiya, T., 1988. Morphological and ethological adaptions of Ostracoda to microhabitats in *Zostera* beds. In: Hanai, N., Ikeya, N., Ishizaki, K. (Eds.), Evolutionary Biology of Ostracoda. Kodansha Ltd., Tokyo, Japan.

Kauffman, E.G., Arthur, M.A., Howe, B., Scholle, P.A., 1996. Widespread venting of methane-rich fluids in Late Cretaceous (Campanian) submarine springs (Tepee Buttes), Western Interior seaway, U.S.A. Geology 24, 799–802.

Kay, E.A., 1979. Hawaiian marine shells. Reef and Shore Fauna of Hawaii, Section 4, Bernice P Bishop Museum Special Publication. 64. Bishop Museum Press, Honolulu, pp. 539–633.

Keith, M.L., Anderson, G.M., Eichler, R., 1964. Carbon and oxygen isotopic composition of mollusk shells from marine and fresh-water environments. Geochim. Cosmochim. Acta 28, 1757–1786.

Kennedy, H., Beggins, J., Duarte, C.M., Fourqurean, J.W., Holmer, M., Marbá, N., et al., 2010. Seagrass sediments as a global carbon sink: Isotopic constraints. Glob. Biogeochem. Cycles 24. http://dx.doi.org/10.1029/2010GB003848.

Kidwell, S.M., Bosence, D.W.J., 1991. Taphonomy and time-averaging of marine shelly faunas. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy. Releasing the Data Locked in the Fossil Record. Plenum, New York, pp. 115–209.

Kidwell, S.M., Flessa, K.W., 1996. The quality of the fossil record: populations, species, and communities. Annu. Rev. Ecol. Syst. 26, 269–299.

Kier, P.M., 1977. The poor fossil record of the regular echinoid. Paleobiology 3, 168–174.

Kier, P.M., Lawson, M.H., 1978. Index of living and fossil echinoids 1924–1970. Smithson. Contrib. Paleobiol. 34, 1–182.

Kloos, D.P., 1984. Studies on the Recent Foraminifer *Sorites orbiculus* (Forskal) From Curacao (Netherlands Antilles). Doctoral dissertation. University of Amsterdam.

Koriba, K., Mikki, S., 1958. *Archeozostera*, a new genus from the Upper Cretaceous of Japan. Palaeobotanist 1960 (7), 107–110.

Kouchi, N., Nakaoka, M., Mukai, H., 2006. Effects of temporal dynamics and vertical structure of the seagrass *Zostera caulescens* on distribution and recruitment of the epifaunal encrusting bryozoan *Microporella trigonellata*. Mar. Ecol. 27, 145–153.

Kuo, J., McComb, A.J., 1989. Seagrass taxonomy, structure and development. In: Larkum, A.W.D., McComb, A.J., Shepard, S.A. (Eds.), Biology of Seagrasses. Elsevier, Amsterdam, pp. 6–73.

Kusworo, A., Reich, S., Wesselingh, F.P., Santodomingo, N., Johnson, K.G., Todd, J.A., et al., 2015. Diversity and paleoecology of Miocene coral-associated mollusks from East Kalimantan (Indonesia). Palaios 30, 116–127.

Laborel, L., 1967. A revised list of Brazilian scleractinian corals and description of a new species. Postilla 107, 1–14.

Langer, M.R., 1993. Epiphytic foraminifera. Mar. Micropaleontol. 20, 235–265.

Larkum, A.W.D., West, R.J., 1990. Long-term changes of seagrass meadows in Botany Bay, Australia. Aquat. Bot. 37, 55–70.

Laurent, L., Laurent, J., 1926. Étude sur une plante fossile des dépôts du Tertiaire marin du sud de Célèbes. Jaarb. Mijnwez. Ned. Oost-Indië 54, 169–190.

Lee, J.J., Burnham, B., Cevasco, M.E., 2004. A new modern soritid foraminifer, *Amphisorus saurensis* n. sp., from the Lizard Island Group (Great Barrier Reef, Australia). Micropaleontology 50, 357–368.

Leite, F.P.P., Tambourgi, M.R.S., Cunha, C.M., 2009. Gastropods associated with the green seaweed *Caulerpa racemosa*, on two beaches of the northern coast of the state of São Paulo, Brazil. Strombus 16, 1–10.

Lemer, S., Buge, B., Bernis, A., Giribet, G., 2014. First molecular phylogeny of the circumtropical bivalve family Pinnidae (Mollusca, Bivalvia): evidence for high levels of cryptic species diversity. Mol. Phylogenet. Evol. 75, 11–23.

Leonard-Pingel, J.S., 2005. Molluscan Taphonomy as a Proxy for Recognyzing Fossil Seagrass Beds. M.S. Thesis. Louisina State University, Baton Rouge.

Leonard-Pingel, J.S., Jackson, J.B.C., O'Dea, A., 2012. Changes in bivalve functional and assemblage ecology in response to environmental change in the Caribbean Neogene. Paleobiology 38, 509–524.

Les, D.H., Cleland, M.A., Waycott, M., 1997. Phylogenetic studies in Alismatidae, II: evolution of marine angiosperms (seagrasses) and hydrophyly. Syst. Bot. 22, 443–463.

Lewis, J.B., 1989. Spherical growth in the Caribbean coral *Siderastrea radians* (Pallas) and its survival in disturbed habitats. Coral Reefs 7, 161–167.

Lin, G., Banks, T., Sternberg, L.O., 1991. Variation in delta 13C values for the seagrass *Thalassia testudinum* and its relation to mangrove carbon. Aquat. Bot. 40, 333–341.

Lobegeier, M.K., 2002. Benthic foraminifera of the family Calcarinidae from Green Island Reef, Great Barrier Reef Province. J. Foraminifer. Res. 32, 201–216.

Logan, G.A., Smiley, C.J., Eglinton, G., 1995. Preservation of fossil leaf waxes in association with their source tissues, Clarkia, northern Idaho, USA. Geochim. Cosmochim. Acta 59, 751–763.

Lozouet, P., Plaziat, J.-C., 2008. Mangrove Environments and Molluscs—Abatan River, Bohol and Panglao Islands, Central Philippines. Conchbooks, Hackenheim.

Lukasik, J.J., James, N.P., McGowran, B., Bone, Y., 2000. An empeiric ramp: low-energy, cool-water carbonate facies in a Tertiary inland sea, Murray Basin, South Australia. Sedimentology 47, 851–881.

Lumbert, S.H., den Hartog, C., Phillips, R.C., Olsen, F.S., 1984. The occurrence of fossil seagrasses in the Avon Park Formation (late Middle Eocene), Levy County, Florida (U.S.A.). Aquat. Bot. 20, 121–129.

MacFadden, B.J., Higgins, P., Clementz, M.T., Jones, D.S., 2004. Diets, habitat preferences, and niche differentiation of Cenozoic sirenians from Florida: evidence from stable isotopes. Palaebiology 30, 297–324.

Mandic, O., Harzhauser, M., Spezzaferri, S., Zuschin, M., 2002. The paleoenvironment of an early Middle Miocene Paratethys sequence in the NE Austria with special emphasis on paleoecology of mollusks and foraminifera. Geobios. Mem. Spec. 24, 193–206.

Marsh, G.A., 1973. The *Zostera* epifaunal community in the York River, Virginia. Chesap. Sci. 14, 87–97.

Marsh, G.A., 1976. Ecology of the gastropod epifauna of eelgrass in a Virginia estuary. Chesap. Sci. 17, 182–187.

Marsh, H., O'Shea, T.J., Reynolds III, J.E., 2011. Ecology and Conservation of the Sirenia: Dugongs and Manatees. Cambridge University Press.

Martin, R.E., 1986. Habitat and distribution of the foraminifer *Archais angulatus* (Fichtel and Moll) (Miliolina, Soritidae), northern Florida Keys. J. Foraminifer. Res. 16, 201–206.

Martin, R.E., Wright, R.C., 1988. Information loss in the transition from life to death assemblages of foraminifera in back reef environments, Key Largo, Florida. J. Paleontol. 62, 399–410.

Mateu-Vicens, G., Box, A., Deudero, S., Rodríguez, B., 2010. Comparative analysis of epiphytic foraminifera in sediments colonized by seagrass *Posidonia oceanica* and invasive macroalgae *Caulerpa* spp. J. Foraminifer. Res. 40, 134–147.

Maxwell, W.G.H., 1968. Areas of the Great Barrier Reef. Elsevier, Amsterdam.

McCoy, E.D., Heck Jr., K.L., 1976. Biogeography of corals, seagrasses and mangroves: an alternative to the center of origin concept. Syst. Zool. 25, 201–210.

Meyer, E., Nilkerd, B., Glover, E.A., Taylor, J.D., 2008. Ecological importance of chemoautotrophic lucinid bivalves in a peri-mangrove community in eastern Thailand. Raffles Bull. Zool. 18, 41–55.

Mikkelsen, P.M., Mikkelsen, P.S., Karlen, D.J., 1995. Molluscan biodiversity in the Indian River lagoon, Florida. Bull. Mar. Sci. 57, 94–127.

Miller, A.I., Cummins, H., 1990. A numerical model for the formation of fossil assemblages: estimating post-mortem transport along environmental gradients. Palaios 5, 303–316.

Moissette, P., 2012. Seagrass-associated bryozoan communities from the Late Pliocene of the Island of Rhodes (Greece). In: Ernst, A., Schäfer, P., Scholz, J. (Eds.), Bryozoan Studies 2010, Lecture Notes in Earth System Sciences, 143. Springer, Berlin, pp. 187–201.

Moissette, P., Koskeridou, E., Corneé, J.-J., Guillocheau, F., Lécuyer, C., 2007. Spectacular preservation of seagrasses and seagrass-associated communities from the Pliocene of Rhodes, Greece. Palaios 22, 200–211.

Moore, R.C., 1961. Treatise on Invertebrate Paleontology, Part Q, Arthropoda 3: Geological Society of America. Boulder and University of Kansas Press, Lawrence.

Moore, H.B., Jutare, T., Bauer, J.C., Jones, J.A., 1963. The biology of *Lytechinus variegatus*. Bull. Mar. Sci. 13, 23–53.

Morgan, M.D., Kitting, C.L., 1984. Productivity and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. Limnol. Oceanogr. 29, 1066–1076.

Moulinier, R., Picard, J., 1952. Recherches sur les herbiers de phanérogames marines du littoral méditerranéen français. Ann. Inst. Oceanogr. Paris 27, 157–243.

Mukai, H., 1993. Biogeography of the tropical seagrasses in the western Pacific. Mar. Freshw. Res. 44, 1–17.

Murray, J.W., 1970. The foraminifera of the hypersaline Abu Dhabi lagoon, Persian Gulf. Lethaia 3, 51–68.

Nakaoka, M., Toyohara, T., Matsumasa, M., 2001. Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuchi Bay, Japan. PSZN. Mar. Ecol. 22, 379–395.

Nakaoka, M., Mukai, H., Chunhabundit, S., 2002. Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed. Ecol. Res. 17, 625–638.

Neahr, T.A., Stunz, G.W., Minello, T.J., 2010. Habitat use patterns of newly settled spotted seatrout in estuaries of the north-western Gulf of Mexico. Fish. Manag. Ecol. 17, 404–413.

Nebelsick, J.H., Kowalewski, M., 1999. Drilling predation on recent clypeasteroid echinoids from the Red Sea. Palaios 127–44.

Nelsen, J.E., Ginsburg, R.N., 1986. Calcium carbonate production by epibionts on *Thalassia* in Florida Bay. J. Sediment. Petrol. 56, 622–628.

Nesti, U., Piazzi, L., Balata, D., 2009. Variability in the structure of epiphytic assemblages of the Mediterranean seagrass *Posidonia oceanica* in relation to depth. Mar. Ecol. 30, 276–287.

Nichols, P.D., Johns, R.B., 1985. Lipids of the seagrass *Thalassia hemprichii*. Phytochemistry 24, 81–84.

Nichols, P.D., Klumpf, D.W., Johns, R.B., 1982. Lipid components of the seagrasses, *Posidonia australis* and *Heterozostera tasmanica* as indicators of carbon source. Phytochemistry 21, 1613–1621.

Nienhuis, P.H., Coosen, J., Kiswara, W., 1989. Community structure and biomass distribution of seagrasses and macrofauna in the Flores Sea, Indonesia. J. Sea Res. 23, 197–214.

O'Connell, L.G., James, N.P., Bone, Y., 2012. The Miocene Nullarbor Limestone, southern Australia; deposition on a vast subtropical epeiric platform. Sediment. Geol. 253, 1–16.

Ogden, J.C., 1980. Faunal relationships in Caribbean seagrass beds. In: Phillips, R.C., McRoy, C.P. (Eds.), Handbook of Seagrass Biology: An Ecosystem Approach. Garland Pub., Inc., New York, pp. 173–198.

Ogden, J.C., 1997. Marine managers look upstream for connections. Science 278, 1414–1415.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., et al., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987–996.

Pancost, R.D., Pagani, M., 2006. Controls on the carbon isotopic compositions of lipids in marine environments. In: Volkman, J.K. (Ed.), Marine Organic Matter: Biomarkers, Isotopes and DNA. The Handbook of Environmental Chemistry Volume 2 N. Springer-Verlag, Berlin, pp. 209–249.

Parsons, K.M., Brett, C.E., 1991. Taphonomic processes and biases in modern marine environments: an actualistic perpective on fossil assemblage preservation. In: Donovan, S.K. (Ed.), The Processes of Fossilization. Columbia University Press, New York, pp. 22–65.

Patriquin, D.G., 1975. "Migration" of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. Aquat. Bot. 1, 163–189.

Paul, S., Herbert, G.S., 2014. Plio-Pleistocene drilling predation in Florida bivalves: predator identity, competition, and biotic change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 404, 67–77.

Pérès, J.M., Picard, J., 1964. Nouveau manuel de bionomie bentique de la Mer Méditerranée. Rec. Trav. Stat. Mar. Endoume. 31, 1–137.

Perry, C.T., 1999. Biofilm-related calcification, sediment trapping and constructive micrite envelopes: a criterion for the recognition of ancient grass-bed environments? Sedimentology 46, 33–45.

Perry, C.T., Beavington-Penney, S.J., 2005. Epiphytic calcium carbonate production and facies development within sub-tropical seagrass beds, Inhaca Island, Mozambique. Sediment. Geol. 174, 161–176.

Petta, T.J., Gerhard, L.C., 1977. Marine grass banks—a possible explanation for carbonate lenses, Tepee Zone, Pierre Shale (Cretaceous), Colorado. J. Sediment. Petrol. 47, 1018–1026.

Phillips, R.C., Meñez, E.G., 1988. Seagrasses. Smithson. Contrib. Mar. Sci. 34.

Pomar, L., 2001. Ecological control of sedimentary accommodation: evolution from a carbonate ramp to rimmed shelf, upper Miocene, Balearic Islands. Palaeogeogr. Palaeoclimatol. Palaeoecol. 175, 249–272.

Pomel, A., 1849. Matériaux pour servir à la flore fossile des terrains jurassiques de la France. Amt Ber 25ste Versamm Deutsch Naturf Ärzte, Aachenpp. 331–354.

Ponder, W.F., de Keyzer, R.G., 1992. A revision of the genus *Diala* (Gastropoda: Cerithiodea: Dialidae). Invertebr. Taxon. 6, 1019–1075.

Puga-Bernabéu, Á., Braga, J.C., Martín, J.M., 2007. High-frequency cycles in Upper-Miocene ramp-temperate carbonates (Sorbas Basin, SE Spain). Facies 53, 329–345.

Pusey, W.C., 1975. Holocene carbonate sedimentation on northern Belize Shelf. In: Wantland, K.F., Pusey, W.C. (Eds.), Belize Shelf-Carbonate Sediments, Clastic Sediments, and Ecology. Am Assoc Pet Geol, Stud Geol 2, pp. 131–233.

Rasheed, M.A., Unsworth, K.F., 2011. Long-term climate-associated dynamics of a tropical seagrass meadow: implications for the future. Mar. Ecol. Prog. Ser. 422, 93–103.

Reich, S., 2014. Gastropod associations as a proxy for seagrass vegetation in a tropical, carbonate setting (San Salvador, Bahamas). Palaios 29, 467–482.

Reich, S., Wesselingh, F.P., Renema, W., 2014. A highly diverse molluscan seagrass fauna from the early Burdigalian (early Miocene) of Banyunganti (south-central Java, Indonesia). Ann. Nat. Hist. Mus. Wien. Ser. A 116, 5–129.

Reich, S., Warter, V., Wesselingh, F.P., Zwaan, H., Renema, W., Lourens, L., 2015. Paleoecological significance of stable isotope ratios in Miocene tropical shallow marine habitats (Indonesia). Palaios 30, 53–65.

Renema, W., 2006. Large benthic foraminifera from the deep photic zone of a mixed siliciclastic-carbonate shelf off East Kalimantan, Indonesia. Mar. Micropaleontol. 58, 73–82.

Renema, W., 2008a. Habitat selective factors influencing the distribution of large benthic foraminifera assemblages over the Kepulauan Seribu. Mar. Micropaleontol. 68, 286–298.

Renema, W., 2008b. Internal architecture of Miocene *Pseudotaberina* and its relation to Caribbean archaiasins. Palaeontology 51, 71–79.

Renema, W., 2010. Is increased calcarinid (foraminifera) abundance indicating a larger role for macro-algae in Indonesian Plio-Pleistocene coral reefs? Coral Reefs 29, 165–173.

Renema, W., Hohenegger, J., 2005. On the identity of *Calcarina spengleri* (Gmelin 1791). J. Foraminifer. Res. 35, 15–21.

Renema, W., Troelstra, S.R., 2001. Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 175, 125–146.

Reuter, M., Piller, W.E., 2011. Volcanoclastic events in coral reef and seagrass environments: evidence for disturbance and recovery (Middle Miocene, Styrian Basin, Austria). Coral Reefs 30, 889–899.

Reuter, M., Piller, W.E., Harzhauser, M., Kroh, A., Roegl, F., Coric, S., 2010. The Quilon Limestone, Kerala Basin, India: an archive for Miocene Indo-Pacific seagrass beds. Lethaia 44, 76–86.

Reuter, M., Piller, W.E., Erhart, C., 2012. A Middle Miocene carbonate platform under silici-volcanoclastic sedimentation stress (Leitha Limestone, Styrian Basin, Austria)—depositional environments, sedimentary evolution and palaeoecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 350–352, 198–211.

Reymond, C.E., Uthicke, S., Pandolfi, J.M., 2011. Inhibited growth in the photosymbiont-bearing foraminifer *Marginopora vertebralis* from the nearshore Great Barrier Reef, Australia. Mar. Ecol. Prog. Ser. 435, 97–109.

Ribes, T., Salvadó, H., Romero, J., del Pilar, Gracia M., 2000. Foraminiferal colonization on artificial seagrass leaves. J. Foraminifer. Res. 30, 192–201.

Richardson, S.L., 2000. Epiphytic foraminifera of the Pelican Cays, Belize: diversity and distribution. Atoll Res. Bull. 475, 209–230.

Richardson, S.L., 2004. 2004. Seasonal variation in epiphytic foraminiferal biotas from *Thalassia* seagrass habitats, Twin Cays, Belize. In: Macintyre IG, Rützler K, Felle IC, editors. The Twin Cays Mangrove Ecosystem, Belize: Biodiversity, Geological History, and Two Decades of Change. Atoll Res. Bull. 517, 1–39.

Riordan, N.K., James, N.P., Bone, Y., 2012. Oligo-Miocene seagrass-influenced carbonate sedimentation along a temperate marine palaeoarchipelago, Padthaway Ridge, South Australia. Sedimentology 59, 393–418.

Rosenfeld, A., 1979. Seasonal distributions of recent ostracodes from Kiel Bay, western Baltic Sea. Meyniana 31, 59–82.

Ross, C.A., 1972. Biology and ecology of *Marginopora vertebralis* (Foraminiferida), Great Barrier Reef. J. Eukaryot. Microbiol. 19, 181–192.

Rossi, S., Gili, J.M., Hugues, R.G., 2000. The effects of exposure to wave action on the distribution and morphology of the epiphytic hydrozoans *Clava multicornis* and *Dynamena pumila*. Sci. Mar. 64, 135–140.

Rueda, J.L., Salas, C., 2007. Trophic dependence of the emerald neritid *Smaragdia viridis* (Linnaeus, 1758) on two seagrasses from European coasts. J. Molluscan Stud. 211–214.

Rueda, J.L., Gofas, S., Urra, J., Salas, C., 2009a. A highly diverse molluscan assemblage associated with eelgrass beds (*Zostera marina* L.) in the Alboran Sea: microhabitat preference, feeding guilds and biogeographical distribution. Sci. Mar. 73, 679–700.

Rueda, J.L., Salas, C., Urra, J., Marina, P., 2009b. Herbivory on *Zostera marina* by the gastropod *Smaragdia viridis*. Aquat. Bot. 90, 253–260.

Schultz, P.W.W., Huber, M., 2013. Revision of the Worldwide Recent Pinnidae and Some Remarks on Fossil European Species. Öhringen, Germany, Acta Conchyliorium.

Scoffin, T.P., 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. J. Sediment. Petrol. 40, 249–273.

Semeniuk, T.A., 2001. Epiphytic foraminifera along a climatic gradient, Western Australia. J. Foraminifer. Res. 31, 191–200.

Shears, N., Babcock, R., 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132, 131–142.

Sheridan, P., 1997. Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, U.S.A. Estuar. Coast. Shelf Sci. 44, 455–469.

Short, F.T., Neckles, H.A., 1999. The effects of global climate change on seagrasses. Aquat. Bot. 63, 169–196.

Simenstad, C.A., Wissmar, R.C., 1985. δ13C evidence of the origins and fates of organic carbon in estuarine and nearshore food webs. Mar. Ecol. Prog. Ser. 22, 141–152.

Smith, B.N., Epstein, S., 1971. Two categories of $^{13}$C/$^{12}$C ratios for higher plants. Plant Physiol. 47, 380–384.

Sola, F., Braga, J.C., Aguirre, J., 2013. Hooked and tubular coralline algae indicate seagrass beds associated to Mediterranean Messinian reefs (Poniente Basin, Almería, SE Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 374, 218–229.

Sonshine, E.E., 2012. The Characterization of Organic Carbon From Sedimentary Cores From Zostera Marina Beds, Maquoit Bay, Casco Bay, Maine. Geology Theses, (Paper 4).

Spalding, M.D., Ravilious, C., Green, E.P., 2001. World Atlas of Coral Reefs. University of California Press, Berkeley.

Spalding, M.D., Taylor, M., Ravilious, C., Short, F., Green, E., 2003. Global overview. The distribution and status of seagrasses. In: Green, E.P., Short, F.T. (Eds.), World Atlas of Seagrasses. University of California Press, Berkeley, pp. 5–26.

Stanley, M.S., 2014. Evolutionary radiation of shallow-water Lucinidae (Bivalvia with endosymbionts) as a result of the rise of seagrasses and mangroves. Geology 42, 803–806.

Steinker, D.C., Clem, K.V., 1984. Some nearshore foraminiferal assemblages from phytal substrates and bottom sediments, Bermuda. The Compass 61, 98–115.

Steinker, P., Steinker, D.C., 1976. Shallow-water foraminifera, Jewfish City, Bahamas. Mar. Sedimentol. Spec. Publ. 1, 171–180.

Stockmans, F., 1936. Végètaux éocènes des environs de Bruxelles. Bull. Mus. R. Hist. Nat. Belg. 76, 1–56.

Stoner, A.W., Waite, J.M., 1991. Trophic biology of Strombus gigas in nursery habitats: diets and food sources in seagrass meadows. J. Molluscan Stud. 1991, 451–460.

Taylor, J.D., 1971. Reef associated molluscan assemblages in the Western Indian Ocean. Symp. Zool. Soc. Lond. 28, 501–534.

Taylor, J.D., 1978. Habitats and diet of predatory gastropods at Addu Atoll, Maldives. J. Exp. Mar. Biol. Ecol. 31, 83–103.

Taylor, P.D., 1990. Preservation of soft-bodied and other organisms by bioimmuration—a review. Palaeontology 33, 1–17.

Taylor, P.D., James, N.P., 2013. Secular changes in colony-forms and bryozoan carbonate sediments through geological history. Sedimentology 60, 1184–1212.

Taylor, J.D., Lewis, M.S., 1970. The flora, fauna and sediments of the marine grass beds of Mahé, Seychelles. J. Nat. Hist. 4, 199–220.

Taylor, P.D., Todd, J.A., 2001. Bioimmuration. In: Briggs, D.E.G., Crowther, P.R. (Eds.), Palaeobiology II. Blackwell Science, Oxford, pp. 285–289.

Taylor, J.D., Glover, E.A., Smith, L., Dyal, P., Williams, S.T., 2011. Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). Zool. J. Linn. Soc. 163, 15–49.

Telford, M., Harold, A.S., Mooi, R., 1983. Feeding structures, behaviour, and microhabitat of *Echinocyamus pusillus* (Echinoidea: Clypeasteroida). Biol. Bull. 165, 745–757.

Todd, J.A., 1993. The bivalve shell as a preservation trap, as illustrated by the Late Jurassic gryphaeid, *Deltoideum delta* (Smith). Scr. Geol.Spec. Issue 2, 417–433.

Todd, J.A., 1994. The role of bioimmuration in the exceptional preservation of fossil ctenostomates, including a new Jurassic species of *Buskia*. In: Hayward, P.J., Ryland, J.S., Taylor, P.D. (Eds.), Biology and Palaeobiology of Bryozoans. Olsen & Olsen, Fredensborg, Denmark, pp. 187–192.

Todd, J.A., Taylor, P.D., 1992. The first entoproct. Naturwissenschaften 79, 311–314.

Touchette, B.W., Burkholder, J.M., 2000. Overview of the physiological ecology of carbon metabolism in seagrasses. J. Exp. Mar. Biol. Ecol. 250, 169–205.

Tracey, S., Todd, J.A., Le Renard, J., King, C., Goodchild, M., 1996. Distribution of Mollusca in units S1 to S9 of the Selsey Formation (middle Lutetian), Selsey Peninsula, West Sussex. Tertiary Res. 16, 97–139.

Unabia, C.C., 1980. *Smaragdia* (Gastropoda: Neritidae), a seagrass animal. Pac. Sci. 34, 340.

Unabia, C.R.C., 2011. The snail Smaragdia bryanae (Neritopsina, Neritidae) is a specialist herbivore of seagrass *Halophila hawaiiana* (Alismatidae, Hydrocharitaceae). Invertebr. Biol. 130, 100–114.

Valentine, J.F., Heck Jr., K.L., 1991. The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. 154, 215–230.

Van der Ham, R.W.J.M., van Konijnenburg-van Cittert, J.H.A., Indeherberge, L., 2007. Seagrass foliage from the Maastrichtian type areas (Maastrichtian, Danian, NE Belgium, SE Netherlands). Rev. Palaeobot. Palynol. 144, 301–321.

Van der Heide, T., Govers, L.L., Fouw, Jd, Olff, H., van der Geest, M., van Katwijk, M.M., et al., 2012. A three-stage symbiosis forms the foundation of seagrass ecosystems. Science 336, 1423–1434.

Vávra, N., 1979. Bryozoa from the Miocene of Styria (Austria). In: Larwood, G.P., Abbott, M.B. (Eds.), Advances in Bryozoology. Academic Press, London, pp. 585–609.

Vávra, N., 1984. A littoral bryozoan assemblage from the Korytnica Clays (Middle Miocene: Holy Cross Mountains, Central Poland). Acta Geol. Pol. 34, 223–237.

Vélez-Juarbe, J., 2014. Ghost of seagrasses past: using sirenians as a proxy for historical distribution of seagrasses. Palaeogeogr. Palaeoclimatol. Palaeoecol. 400, 41–49.

Vélez-Juarbe, J., Domning, D.P., Pyenson, N.D., 2012. Iterative evolution of sympatric seacow (Dungongidae, Sirenia) assemblages during the past ~26 million years. PLoS ONE 7, e31294.

Vermeij, G.J., Herbert, G.S., 2004. Measuring relative abundance in fossil and living assemblages. Paleobiology 30, 1–4.

Voigt, E., 1956. Der Nachweis des Phytals durch Epizoen als Kriterium der Tiefe vorzeitlicher Meere. Geogr. Rundsch. (Sonderdruck) 45, 97–119.

Voigt, E., 1979. The preservation of slightly or non-calcified fossil Bryozoa (Ctenostomata and Cheilostomata) by bioimmuration. In: Larwood, G.P., Abbott, M.B. (Eds.), Advances in Byozoology. Systematics Association Spec 13. Academic Press, London, pp. 541–564.

Voigt, E., 1981. Upper Cretaceous bryozoan-seagrass association in the Maastrichtian of the Netherlands. In: Larwood, G.P., Nielsen, C. (Eds.), Recent and Fossil Bryozoa. Olsen & Olsen, Fredensborg, pp. 281–298.

Voigt, E., Domke, W., 1955. *Thalassocharis bosqueti* Debey ex Miquel, ein strukturell erhaltenes Seegras aus der holländischen Kreide. Mitt. Geol. Staatsinst. Hambg. 24, 87–102.

Wanless, H.R., 1981. Fining-upwards sedimentary sequences generated in seagrass beds. J. Sediment. Res. 51, 445–454.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., et al., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. U. S. A. 106, 12377–12381.

Weber, K., Zuschin, M., 2013. Delta-associated molluscan life and death assemblages in the northern Adriatic Sea: implications for paleoecology, regional diversity and conservation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 370, 77–91.

Wilson, B., 1998. Epiphytal foraminiferal assemblages on the leaves of the seagrasses *Thalassia testudinum* and *Syringodium filiforme*. Caribb. J. Sci. 34, 131–132.

Wilson, B., 2008. Population structures among epiphytal foraminiferal communities, Nevis, West Indies. J. Micropalaeontol. 27, 63–73.

Woelkerling, W.J., Irvine, L.M., Harvey, A.S., 1993. Growth-forms in non-geniculate coralline red algae (Caorallinales, Rhodophyta). Aust. Syst. Bot. 6, 277–293.

Womersley, H.B.S., 1996. The Marine Benthic Flora of Southern Australia. Part IIIB. Gracilariales,Rhodymeniales, Corallinales and Bonnemaisoniales. Australian BiologicalResources Study, Canberra.

Yamaguchi, T., Goedert, J.L., 2010. A new species of *Cythere* (Ostracoda) from the middle Eocene McIntosh Formation, Doty Hills, Washington State, USA, and its significance for the evolutionary history of the genus. J. Paleontol. 84, 709–719.

Zabala, M., 1986. Fauna dels briozous dels Països Catalans, vol 84. Arx Sec Ciénc Inst d'Estud Catalans, Barcelona.

Zuschin, M., Hohenegger, J., 1998. Subtropical coral-reef associated sedimentary facies characterized by molluscs (Northern Bay of Safaga, Red Sea, Egypt). Facies 38, 229–254.

Zuschin, M., Oliver, G., 2003. Bivalves and Bivalve Habitats in the Northern Red Sea: The Northern Bay of Safaga (Red Sea, Egypt): An Actopaleontological Approach. Vienna Natural History Museum.

Zuschin, M., Harzhauser, M., Mandic, O., 2007. The stratigraphic and sedimentologic framework of fine-scale faunal replacements in the Middle Miocene of the Vienna Basin (Austria). Palaios 22, 285–295.

Zuschin, M., Janssen, R., Baal, C., 2009. Gastropods and their habitats from the northern Red Sea (Egypt: Safaga). Part 1: Patellogastropoda, Vetigastropoda and Cycloneritimorpha. Ann. Nat. Hist. Mus. Wien. Ser. A. 111, 73–158.