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PALEOECOLOGICAL SIGNIFICANCE OF STABLE ISOTOPE RATIOS IN MIOCENE TROPICAL SHALLOW MARINE HABITATS (INDONESIA)

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ABSTRACT: Seagrass meadows are important shallow-water ecosystems that provide habitat for numerous associated organisms and play a crucial role in nutrient cycling, but their detection in the fossil record is problematic. Indirect indicators are often needed to discriminate seagrass beds from other shallow marine paleohabitats. Here, the stable isotope signatures of mollusk shells are examined to determine if they might provide such an indicator in addition to the faunal composition of mollusk assemblages. Aragonitic shells of 167 gastropods and bivalves from Burdigalian and Tortonian deposits in Java and East Kalimantan (Indonesia) are analyzed for their $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ ratios. The faunas represent fully marine to brackish water environments and include seagrass meadows (with dispersed corals), mixed seagrass-coral, and coral-dominated habitats (with dispersed seagrass). We assess processes and settings that shape inorganic isotope signals in the Miocene ambient waters and fractionation processes occurring at the time of shell deposition. Depleted $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ ratios are shown in brackish water samples. Furthermore, chemosymbiotic species show depleted $\delta^{13}\text{C}$ ratios. A significant difference is found between the carbon isotopic signatures of coral- and seagrass-dominated environments within a stratigraphic interval. Seagrass communities consistently yield comparatively enriched $\delta^{13}\text{C}$ ratios. Hence, stable isotope ratios may provide additional evidence for distinguishing paleoenvironments and are helpful in identifying ecological processes and settings within these environments.

INTRODUCTION

The successful recognition of different habitats in the geological past is an indispensable basis for studies on climate history, sea-level changes, and biodiversity. In order to evaluate marine biodiversity through time it is necessary to reliably discriminate habitats, because species richness varies considerably among environments (Gray 2001). A good example is the challenge of recognizing seagrass vegetation in the fossil record. Seagrass meadows are highly productive ecosystems that play an important role in coastal nutrient cycling and yield a diverse community of associated organisms (Duarte and Chiscano 1999; Hemminga and Duarte 2000), but marine angiosperms rarely fossilize. Therefore, independent indicators such as associations of benthic foraminifera and mollusks are often used to infer their presence in the geological past (e.g., Brasier 1975; Eva 1980; James and Bone 2007). In most cases these indicators are indirect and not exclusive. For mollusks, the high abundance of small herbivorous gastropods and the occurrence of the neritid gastropod genus *Smaragdia* may be useful indicators (Moulinier and Picard 1952; Davies 1970; Unabia 1980; Reuter et al. 2010; Reich et al. 2014). Furthermore, seagrass meadows and coral environments are difficult to distinguish if not indistinguishable, because marine angiosperms and scleractinian corals often occur in the same habitat. Patches of corals are common in tropical seagrass beds and compound seagrass-coral associations occur in the transition zone between coral reefs and seagrass meadows (Brasier 1975; Nienhuis et al. 1989). Patches of seagrass can also be present in coral-carpet environments (*sensu* Riegl and Piller 1999).

In this study we aim to test whether stable carbon and oxygen isotope signatures of mollusk shells provide an additional tool for the discrimination of paleohabitats ranging from seagrass meadows to coral carpets. Habitat assignments are based on the abundance of coral remains and on the species and ecological composition of mollusk assemblages, and in one case on the fossilized remains of probable seagrass. We examine whether isotope signatures correspond with *a priori* habitat assignments and whether or not a discrete seagrass signature exists. In addition, we aim to investigate which processes in seagrass meadows influence the isotopic composition of associated shells including the influence of different ecologies of mollusks on the carbon isotope signals of their shells.

Stable isotope signatures of mollusk shells are widely used to reconstruct paleoenvironmental conditions (e.g., Latal et al. 2006a, 2006b; McConnaughey and Gillikin 2008). They precipitate near ^{18}O equilibrium with ambient seawater, therefore kinetic isotopic effects are likely to be small (Epstein et al. 1953; McConnaughey 1989; McConnaughey et al. 1997). However, carbon signals of marine mollusk shells are difficult to interpret. They largely reflect ambient DIC (dissolved inorganic carbon), but can be influenced by other factors as well. These include, for instance, salinity or physiologic processes (McConnaughey and Gillikin 2008). The animal's former diet has relatively little influence on $\delta^{13}\text{C}$ in marine shells compared to those of landsnails (McConnaughey et al. 1997; McConnaughey and Gillikin 2008, and references therein). Furthermore, $\delta^{13}\text{C}$ provides a record of seasonality during bivalve growth and commonly becomes depleted in later growth stages of the shell (e.g., Kennedy et al. 2001; McConnaughey and Gillikin 2008, and references therein).

TABLE 1.—Sampling localities, estimated ages, sample set indications, and preliminary paleoenvironmental interpretations based on associated fossil assemblages. Banyunganti is located on Java; all other localities are located on East Kalimantan.

Locality	Age	Sample set	Paleoenvironment
Banyunganti	early Burdigalian	BA18	seagrass meadow
Bontang	early Tortonian	TF102	coral carpet
Bontang	early Tortonian	TF110	seagrass meadow
Bontang	early Tortonian	TF508_FW1	sandflat, sparse seagrass vegetation
Bontang	early Tortonian	TF508_FW6	estuarine, brackish
Bontang	early Tortonian	TF508_FW7	mixed seagrass-coral
Sangatta	early Tortonian	TF517	seagrass meadow

LOCALITIES AND PALEOENVIRONMENTS

An overview of sampling localities, their age, and paleoenvironmental interpretation is provided in Table 1.

Banyunganti, Java, Indonesia (Sample BA18)—Early Burdigalian (Early Miocene)

The sample locality (-7.760731° S, 110.128372° E) is situated near the village of Banyunganti (province Yogyakarta, Java, Indonesia; Fig. 1A). The shells used in this study derive from a bulk sample collected from marine, early Burdigalian deposits of the Jonggrangan Formation west of the city of Yogyakarta. The locality is described in detail by Reich et al. (2014).

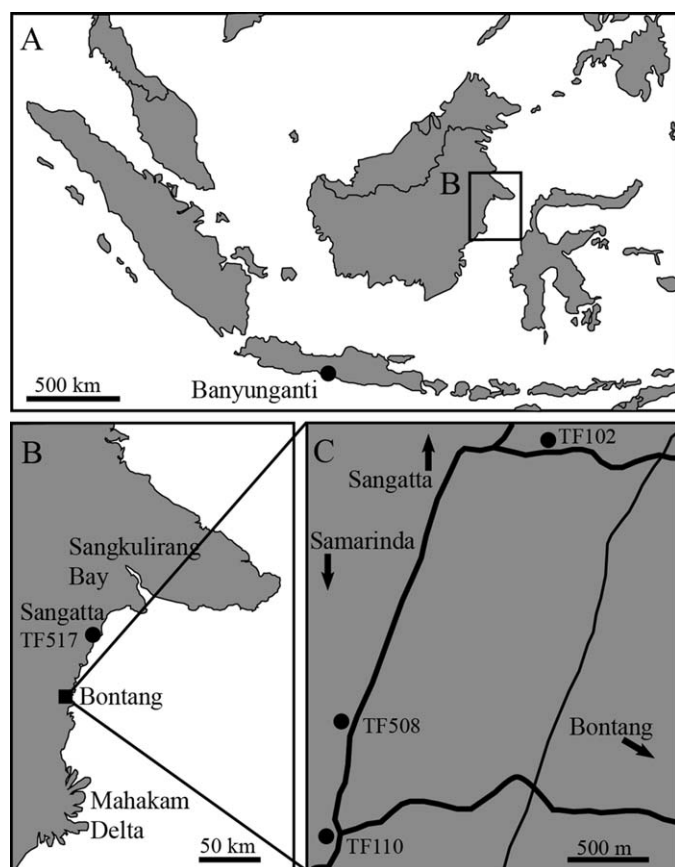


FIG. 1.—Locality map. A) Overview map of Indonesia including the locality of Banyunganti. B) Overview map of the coast of central East Kalimantan including the localities Sangatta (TF517) and Bontang. C) Map of the Bontang area showing the TF-localities 102, 110, and 508.

The excellently preserved mollusk fauna was interpreted as a seagrass-associated assemblage based on the high dominance of small grazing gastropods (69% abundance; e.g., *Rissoina*, *Cerithidium*, *Bothropoma*, Figs 2A–C) and the occurrence of the indicator genus *Smaragdia* (Fig. 2D). The associated assemblage of benthic foraminifera, including the large benthic genus *Pseudotaberina*, hints at seagrass vegetation as well (Renema 2008; Reuter et al. 2010). The associated branching coral fragments are dominated by *Seriatopora* sp. (N. Santodomingo, personal communication 2012). The paleoenvironment is considered to be a seagrass meadow with dispersed intergrowing corals.

Bontang, East Kalimantan, Indonesia (Localities TF102, TF110, TF508)—Early Tortonian (Late Miocene)

The city of Bontang is located at the coast of central East Kalimantan (Fig. 1B), within the Kutai Basin, the largest Cenozoic sedimentary basin of Kalimantan (Moss and Chambers 1999). The Bontang area has recently witnessed a surge in construction work leading to the temporary availability of outcrops at building sites, most of which are located along roads. The outcropping sediments are predominantly marine clay-, silt-, and fine sandstone beds occasionally interbedded with carbonates and lignites. Fluvial deposits occur to the east, stratigraphically above the marine successions. The Bontang marine interval is underlain by older (early–middle Miocene) fluvial, swamp, and shallow marine sediments outcropping to the west in the area of the Indominco coal mine. Samples used in this study were collected at three localities within the Bontang area (Fig. 1C): TF102 (0.16821° N, 117.44350° E; visited in 2010), TF110 (0.14048° N, 117.42692° E; visited in 2010) and TF508 (0.14870° N, 117.42908° E, visited in 2011). Based on benthic foraminifera the age has been estimated as Tortonian (late Miocene) for all localities in the Bontang area referred to in this study. Strontium isotope stratigraphy analysis on mollusks and corals from Bontang (including TF102, TF110, and other localities) results in an age of $9.8 (\pm 0.2)$ Ma, and thus confirms an early Tortonian age (see Renema et al. 2015 for the stratigraphy of the Bontang area).

TF102.—The locality represents the upper part of a marine interval of fossiliferous coarsening-upward silty clay to fine sandy silt with abundant mollusks and corals. Those sediments are covered by nonfossiliferous clay and fine sandstone beds likely representing the lowest deposits of a fluvial series. The locality is described in detail by Kusworo et al. (2015). The shells used in this study were collected from patches of branching corals found on a bedding plane of marine silty clay (hand-collected sample SR45) and a bulk sample taken from the same bed (sample SR50). Shells from both samples were combined and hereafter referred to as TF102. The fossil assemblage is dominated by corals of the genus *Dictyariaea*. The associated mollusk fauna is dominated by carnivorous gastropod species including abundant “*Lophiotoma*” sp. (Fig. 2E) and the coral-feeder *Coralliophila* (Fig. 2F). In total, carnivores make up 48% of the fauna based on specimen numbers. Herbivores make up only 28% of the fauna in terms of abundance. They are mainly represented by medium-sized

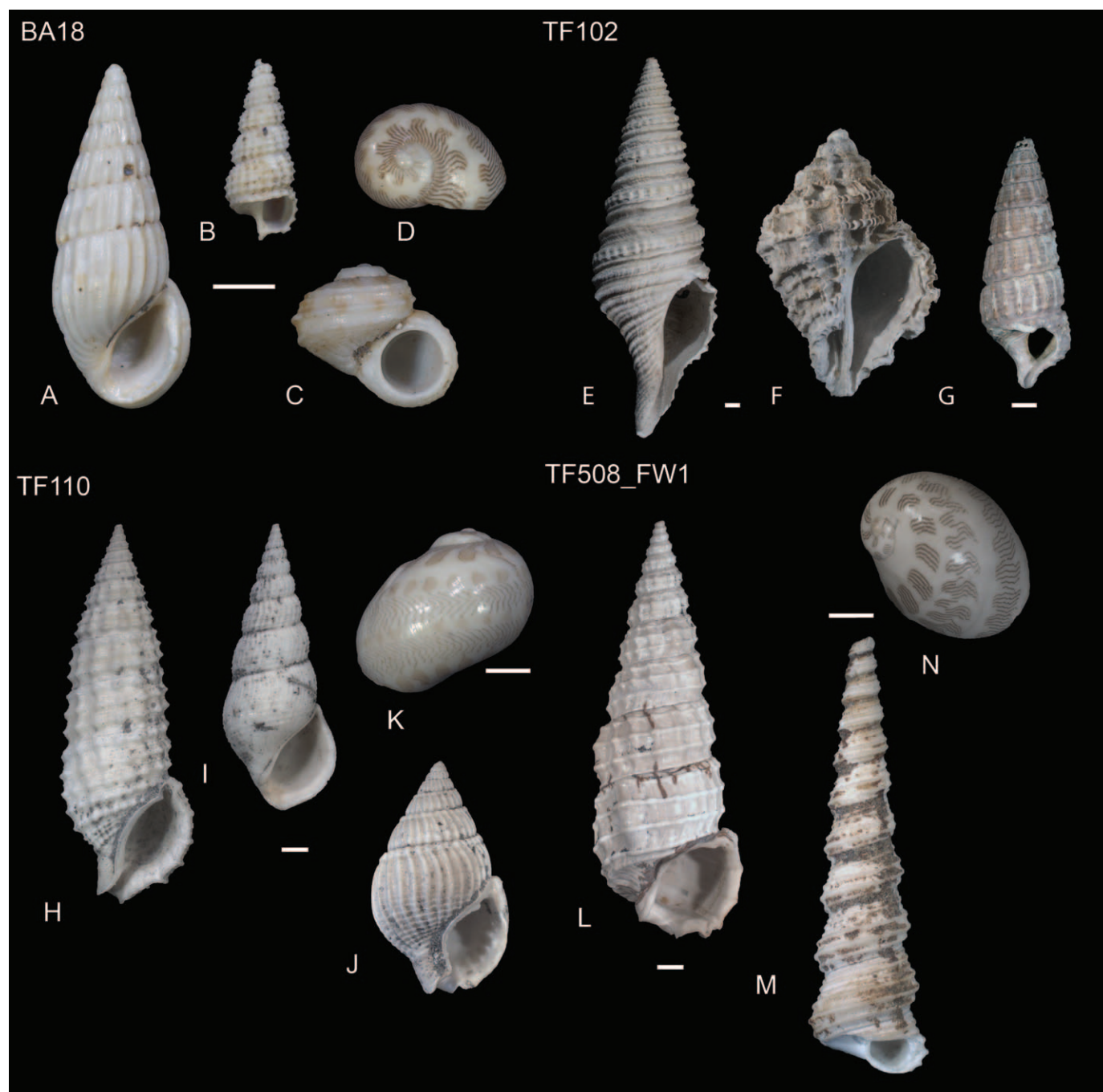


FIG. 2.—Some common and/or indicative gastropods from samples BA18, TF102, TF110, and TF508_1. Scale bars equal 1 mm. **A)** *Rissoina* (*Rissoina*) *banyungantiensis* (RGM 784.843). **B)** *Cerithidium* cf. *perparvulum* (RGM 784.758). **C)** *Bothropoma* *mediocarinata* (RGM 784.746). **D)** *Smaragdia* *jogjacartensis* (RGM 784.754). **E)** “*Lophiotoma*” sp. (RGM 793.968; not analyzed). **F)** *Coralliophila* aff. *clathrata* (RGM 793.969). **G)** *Cerithium* sp. 7 (RGM 793.966). **H)** *Rhinoclavis* sp. 2 (RGM 793.996). **I)** *Rissoina* (*Phosinella*) sp. 1 (RGM 793.997). **J)** *Nassarius* sp. 1 (RGM 793.998; not analyzed). **K)** *Smaragdia* *gelingsehensis* (RGM 793.999). **L)** *Cerithium* sp. 4 (RGM 794.000). **M)** “*Turritella*” sp. (RGM 794.001; not analyzed). **N)** *Smaragdia* *semari* (RGM 794.002).

species (e.g., *Cerithium*, Fig. 2G). However, six specimens of *Smaragdia semari* were found in sample SR50. Their number is very low, but considering that mollusk shells are rarely transported out of their original environment, we can assume they reflect the original life assemblage on a spatial scale (e.g., Kidwell and Bosence 1991; Kidwell and Flessa 1996; Kidwell 2008). This leads us to assume that seagrasses might have been present as well. Therefore, the paleoenvironment is considered to be a coral-carpet environment with dispersed seagrasses.

TF110.—Bulk sample TF110_SR38 (hereafter referred to as TF110) was collected from fossiliferous dark-gray silty clays. The sampled mollusk fauna is diverse and excellently preserved. Herbivorous gastropods are species rich and numerous, including species of *Rhinoclavis*, *Rissoina* (Figs 2H, I), and *Cerithium*. Carnivorous gastropods are abundant as well with *Nassarius* sp. (Fig. 2J) being the most common species in the assemblage; Costellariidae and omnivorous Columbellidae are likewise very abundant. Two species of the seagrass

indicator *Smaragdia* are present in high numbers (*S. gelingsehensis*, 114 specimens, Fig. 2K; *S. semari*, 96 specimens). Coral remains are present in the sample. The locality is inferred to represent a paleo-seagrass meadow with dispersed intergrowing corals.

TF508.—The locality provides a 25 m-long stratigraphic succession of clastic marine and brackish sediments with variable content of mollusks and branching coral fragments. Three samples from different intervals representing different habitats were selected for this study.

Bulk sample TF508_FW1 was collected at ~ 8 m from the base of the succession from a bed of clayey siltstone. The sample contains a well-preserved mollusk fauna characterized by the gastropods *Cerithium* (Fig. 2L) and “*Turritella*” (Fig. 2M) and the bivalve *Placuna*. *Smaragdia semari* (Fig. 2N) is present and indicates the former presence of seagrass vegetation. Fragments of branching corals are rare, but the free-living coral genus *Heterocyathus* is common. The genus indicates a flat undisturbed sandflat probably in a reef-base or interreef environment. Its occurrence points to sparse to moderate seagrass vegetation rather than to the presence of a dense meadow (Fisk 1983; Hoeksema and Best 1991; B.W. Hoeksema, personal communication 2013). The paleohabitat is therefore interpreted as a sandflat with seagrass vegetation present in low density.

Bulk sample TF508_FW6 was collected ~ 20 m from the base of the succession from the upper level of a calcareous siltstone bed. The fossil material is rust colored and the sample contains gypsum crystals. The latter is likely a postdepositional product of partial carbonate dissolution. The associated mollusk fauna is less diverse, with more evenly distributed species abundances than the other faunas used in this study. Bivalves are dominated by *Corbula* sp. and *Anadara nodosa* (Figs 3A, B), both are often preserved articulated. Common gastropod genera are *Nassarius* (Fig. 3C) and medium-sized *Cerithium*. Furthermore, the brackish-water gastropod *Iravadia* is present (Fig. 3D). This faunal composition is comparable to that of recent estuarine faunas reported from the Philippines (Lozouet and Plaziat 2008). Therefore, the sample likely represents a brackish environment.

Bulk sample TF508_FW7 was collected ~ 21.5 m from the base of the succession from organic-rich marls. It is dominated by fragments of branching corals and contains well-preserved mollusk shells. Abundant genera are the gastropods *Cerithium*, *Rissoina*, and *Nassarius* (Figs 3E–G) and the bivalves *Nucula* and *Dendostrea*. The mollusk fauna shares common species with locality TF110. Sample TF508_FW7 contains abundant corals but at the same time four *Smaragdia* species (including e.g., *S. semari*, Fig. 3H), indicating a mixed coral-seagrass habitat.

Sangatta, East Kalimantan, Indonesia (Locality TF517, Sample TF517_FW3)—Early Tortonian (Late Miocene)

Locality TF517 (00.56780° N, 117.63420° E; Fig. 1B) is an artisanal limestone quarry located about 16 km east of the Sangatta coal mine and about 1.3 km northwest of the Tanjung Bara airport. The succession is poorly exposed due to the nature of the excavation process. The base of the succession consists of one meter of lignite with abundant gypsum crystals. A sharp contact exists with the overlying dark-gray clayey silt that contains abundant mollusks and coral fragments. Bulk sample TF517_FW3 (hereafter referred to as TF517) was collected from a clay block dug by an excavator; the exact position within the clay layer is therefore unknown. Strontium isotope stratigraphy analysis on corals and mollusk shells from TF517 indicates an early Tortonian age of $9.2 (\pm 0.2)$ Ma, therefore the locality is younger than localities in the Bontang area (Renema et al. 2015).

The sample contains a diverse and excellently preserved mollusk assemblage interpreted as a seagrass-associated fauna. This is based on the high abundance of small herbivorous gastropods (e.g., *Cerithium*,

Rissoina, *Bothropoma*; Figs 3I–K). Furthermore, plant remains found at the locality show resemblance to marine angiosperms and might therefore be direct evidence for seagrass vegetation, although confirmation is needed. The paleoenvironment is interpreted as a seagrass meadow with dispersed intergrowing corals.

MATERIAL AND METHODS

Samples

Gastropod and bivalve shells representing 43 species in 31 genera and eight different feeding guilds were chosen from the seven fossil samples. In total 167 shells were analyzed. All selected individuals represent species that are common in the original bulk samples. Attention was also paid to choosing taxa that occur in several samples, such as the gastropod species *Diala semistriata* s.l. and the bivalve “*Arcopsis sculptilis*” and the gastropod genera *Rissoina*, *Cerithium*, and *Cylichna*. Shells and shell fragments were first cleaned in an ultrasonic bath to remove adherent sediment and thereafter manually ground to a visually homogenous fine powder. Weights of prepared samples ranged between 540 and 20 µg with an average weight of about 300 µg. Remaining sample material is stored at Naturalis Biodiversity Center, Leiden, The Netherlands (indicated by RGM numbers). A list of samples, including species identifications with taxon authorities and feeding guild assignments, and results for oxygen and carbon stable isotope analyses is provided as Supplementary Data 1.

Species Identification and Feeding Guild Assignment

The mollusk fauna from Banyunganti, Java (BA18) is described by Reich et al. (2014). Species identifications of mollusks from other localities are based on the paleofaunal papers of Beets (1941, 1986), on taxonomic revisions (Laseron 1957; Ponder 1984; Houbriek 1990, 1992; Ponder and De Keyser 1992), and on the taxonomic compendia of Poppe (2008a, 2008b, 2010a, 2010b).

The selected mollusk shells represent eight different feeding guilds; herbivores (including grazers as well as detritivorous gastropods, e.g., *Cerithium* and *Rissoina*), seagrass feeders (*Smaragdia*; Rueda and Salas 2007; Rueda et al. 2009; Unabia 2011), predators on invertebrates (e.g., *Naticarius*), predators on foraminifera (*Cylichna*), browsing carnivores (*Dentimargo*), suspension feeders (e.g., *Circe*), deposit-feeding bivalves (Tellinidae), and chemosymbiotic deposit feeders (Lucinidae; Williams et al. 2004). Assignments to feeding guilds are based on the Neogene Marine Biota of Tropical America molluscan life habits database (Todd 2001) and the comprehensive ecological information provided by Beesley et al. (1998). Assignments based on Todd (2001) concern mollusk families with a worldwide distribution that represent a single feeding guild or genera that occur in tropical America as well as in the Indo-Pacific.

Preservation State

Shell mineralogy was analyzed by Raman spectroscopy using a Thermo DXR Raman microscope with 532 nm laser excitation at Naturalis. Raman spectra were collected at room temperature in the confocal mode which is necessary for analysis of individual layers of a sample on a micron scale (1–2 µm). A grating of 1800 grooves/mm and a pinhole size of 25 µm was used which, combined with the optical path length, yields a spectral resolution of 1.0 cm^{-1} . Spectra were collected in the range of 100–1800 cm^{-1} . In this range, the vibrations of the carbonate anion (CO_3^{2-}) can be detected. The most intense signals of symmetric stretching and in-plane bending of this anion can be used to distinguish aragonite and calcite (e.g., Wehrmeister et al. 2010). Measurements were performed on the outside as well as on the inside of shells. The analysis is nondestructive, therefore the same specimens could be used for Raman testing and stable isotope analysis.

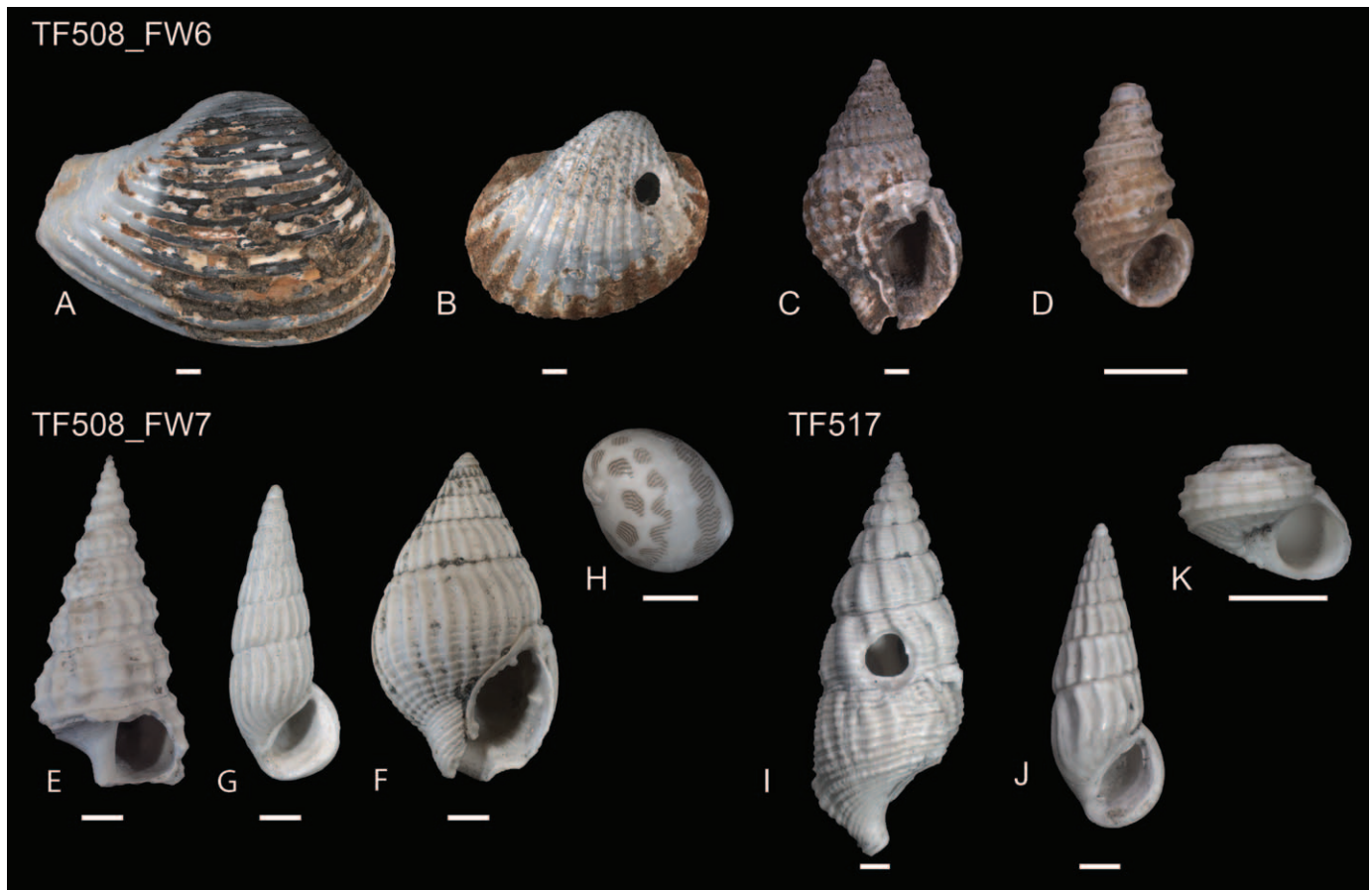


FIG. 3.—Some common and/or indicative gastropods and bivalves from samples TF508-6, TF508_7 and TF517. Scale bars equal 1 mm. A) *Corbula* sp. 2 (RGM 794.003). B) *Anadara nodosa* (RGM 794.004). C) *Nassarius* sp. 6 (RGM 794.005). D) *Iradia* sp. (RGM 794.006; not analyzed). E) *Cerithium* sp. 4 (RGM 794.007). F) *Rissoina* (*Rissoina*) sp. 2 (RGM 794.008; not analyzed). G) *Nassarius* sp. 1 (RGM 794.009; not analyzed). H) *Smaragdia semari* (RGM 794.010). I) *Cerithium* sp. 5 (RGM 794.011). J) *Rissoina* (*Rissoina*) sp. 5 (RGM 794.012). K) *Bothropoma* sp. 2 (RGM 794.013).

Stable Isotope Analyses

Analyses were performed on entire shells of very small specimens and shell fragments of small- to medium-sized individuals. All samples were digested in 103% orthophosphoric acid. Samples (70–400 μg) from Banyunganti, TF110, TF517, TF508_7, and TF102 were analyzed using a Micromass Multiflow head space system connected to a GV Instruments Isoprime IRMS at Royal Holloway University of London, UK. The samples reacted with the acid at 90 °C. After a minimum of four hours, the evolved CO_2 was expanded into the sample loop, and then delivered to the Isoprime mass spectrometer within continuous He-carrier gas flow. Duplicate analyses were performed for each sample and standard, and averaged. Averaged precision (1SD) of duplicates was 0.03‰ for $\delta^{13}\text{C}$ and 0.06‰ for $\delta^{18}\text{O}$. Isotopic ratios are calibrated against the Vienna Pee Dee belemnite (VPDB) through NBS-19 and LSVEC international standards and an in-house standard (RHBNC calcite).

Samples TF508_FW1 and TF508_FW6 and two additional specimens of *Smaragdia* from TF110 (all > 350 μg) were analyzed at Faculty of Earth Sciences at Utrecht University, The Netherlands, using an ISOCARB common bath system directly coupled to a VG SIRA 24 mass spectrometer. Prior to the analysis, each sample was roasted for 30 minutes at 380 °C under vacuum to remove any organic remains. To exclude the possibility that roasting affected the isotopic signals, we reanalyzed the same material without roasting it. The isotopic values of roasted versus unroasted samples display no significant differences and

correlate with linear $R = 0.996$ (Supplementary Data 2). During one run, 40 samples were measured, including one international (IAEA-CO-1) and nine in-house (NAXOS) standards. The samples reacted with the acid for 7.5 minutes at 90 °C. After (linear) correction of the samples using the NAXOS standard as reference, the analytical precision and accuracy were determined by the comparison with international (IAEA-CO-1 and NBS-19) standards. The relative standard deviations, analytical precision and accuracy were better than 0.05‰ and 0.1‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ respectively. Three samples (each from TF110, TF508, and TF517) yielded an amount of < 70 μg ; therefore, they were too small for the requirements of the above described machines. Those samples were analyzed using a Finnigan MAT Kiel III individual acid bath carbonate system coupled to a Finnigan MAT 253 mass spectrometer. Each sample reacted with the acid for 7 minutes at 70 °C. Calibration using the international standard NBS-19 and the in-house standard Naxos revealed an analytical precision better than 0.03‰ and 0.09‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively. The same method was applied for an additional analysis of 9 shell samples from a modern seagrass habitat from Sulawesi, Indonesia.

All isotopic ratios are expressed in conventional delta notation per mil values.

Statistical Analyses

Statistical analyses were performed using PAST 2.16 (Hammer et al. 2001). One-way ANOVA analyses were used to test whether isotope

TABLE 2.—Summary of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ratios of mollusks according to sampling locality; * outlier *Strombus* additionally removed.

Paleo- environment	Seagrass				Coral carpet	Mixed coral-seagrass	Brackish
Sample set	BA18	TF110	TF517	TF508_FW1	TF102	TF508_FW7	TF508_FW6
n	37	37	30	9	9	25	20
$\delta^{18}\text{O}$ mean	−3.02	−2.66	−2.86	−2.79	−2.61	−2.82	−3.97
std	0.29	0.34	0.36	0.2	0.28	0.47	0.4
$\delta^{18}\text{O}$ min	−3.72	−3.41	−3.64	−2.97	−3.09	−3.60	−4.66
$\delta^{18}\text{O}$ max	−2.48	−1.88	−2.22	−2.38	−2.27	−1.95	−3.09
$\delta^{13}\text{C}$ mean	1.46	2.03	1.63	1.03	−0.33	0.16	−1.19
std	1.0	0.55	1.19	1.10	0.95	1.30	0.89
$\delta^{13}\text{C}$ min	−1.32	0.65	−1.93	−0.75	−1.86	−3.35	−2.42
$\delta^{13}\text{C}$ max	3.65	3.66	2.94	2.38	0.91	1.33	0.43
$\delta^{13}\text{C}$ mean, lucinids removed	1.82	2.08	2.04	1.47	0.10*	0.62	-
std	0.61	0.52	0.57	0.76	0.52	0.36	-

ratios from different localities or attributed to different feeding guilds display significant differences. Ratios from localities and guilds were subsequently compared pairwise using Tukey's HSD (Honestly Significant Difference). Significant differences between localities or feeding guilds are expressed by q-values > 4 and p-values < 0.05.

RESULTS

Preservation

Only specimens of *Smaragdia* display a mixed aragonite-calcite signal on the outer shell surface. This represents their original shell mineralogy (Bandel 2008) and is therefore almost certainly not a sign of diagenesis. All other shells are entirely aragonitic. Additional specimens from the same localities were investigated by scanning electron microscopy and showed the original shell microstructure.

ANOVA Analyses

Significant differences were found for oxygen isotope ratios grouped by localities ($F = 34.82$, $p = 1.002\text{E-}26$), carbon isotope ratios grouped by feeding guilds ($F = 22.58$, $p = 3.289\text{E-}20$), carbon isotope ratios grouped by localities ($F = 31.89$, $p = 4.738\text{E-}25$), and are enhanced when using a reduced dataset for $\delta^{13}\text{C}$ ratios grouped by localities (chemosymbiotic deposit feeders removed; $F = 82.85$; $p = 6.626\text{E-}44$). Tukey's HSD furthermore reveals pairwise differences between localities or feeding guilds (see below).

Oxygen and Carbon Values Grouped by Localities

Stable isotope ratios of samples from seven investigated localities are shown in Table 2, Figure 4, and are provided as Supplementary Data 1. Samples (apart from TF508_FW6) yield similar $\delta^{18}\text{O}$ ratios ranging from −1.88 to −3.72. Shells from TF508_FW6 have depleted oxygen isotope ratios which significantly differ from all other localities (Tukey's HSD: $q > 11$, $p = 2.569\text{E-}5$). Also samples from BA18 are slightly depleted in oxygen; significant differences are seen between BA18 and TF102 (Tukey's HSD: $q = 4.88$; $p = 0.01$) and BA18 and TF110 (Tukey's HSD: $q = 4.27$, $p = 0.04$).

Delta ^{13}C ratios are scattered over a wider range than $\delta^{18}\text{O}$ ratios (−3.35 to 3.66). Some samples, mostly lucinid bivalves, show depleted $\delta^{13}\text{C}$ ratios compared to the rest (Fig. 4A, C–F). The depleted carbon isotopic ratios from TF508_FW6 differ significantly from all other localities (Tukey's HSD: $q > 5$; $p < 0.001$), apart from TF102. No significant differences of $\delta^{13}\text{C}$ ratios occur between samples interpreted as seagrass-associated (BA18, TF110, TF508_FW1, and TF517; Tukey's

HSD: $q < 2$; $p > 0.7$). Furthermore, the $\delta^{13}\text{C}$ signals of samples TF102, TF508_FW1, and TF508_FW7 display no significant variation (Tukey's HSD: $q < 4$; $p > 0.1$).

Carbon and Oxygen Values Grouped by Feeding Guilds

Stable isotope ratios grouped by feeding guilds are shown in Table 3 and Figure 5. Feeding guild assignments for each taxon are provided as Supplementary Data 1.

Herbivores and predators on invertebrates yield a wide range of isotope signatures (−4.23 to −2.09 $\delta^{18}\text{O}$ and −0.49 to +2.94 $\delta^{13}\text{C}$). The depleted carbon isotope ratio of −1.86 in a single herbivorous *Strombus* is considered to be an outlier.

Predators on foraminifera (Cylichnidae), browsing carnivores (*Dentimargo*, Marginellidae), and suspension feeders have very similar ratios ranging from −3.72 to −2.27 $\delta^{18}\text{O}$ and −0.36 to +2.45 $\delta^{13}\text{C}$. These ranges are therefore narrower than those of herbivores or predators on invertebrates.

Carbon ratios of seagrass feeders (*Smaragdia*) differ significantly from those of predators on foraminifera (Tukey's HSD: $q = 4.46$, $p = 0.034$) and suspension feeders (TF508_FW 6 excluded; Tukey's HSD: $q = 6.04$, $p = 0.00053$) by being comparatively enriched.

Chemosymbiotic deposit feeders (Lucinidae) from all localities, apart from TF508_FW6 where the family is not present, show a wide range of relatively depleted $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signals. Their carbon isotope ratios differ significantly from those attributed to other feeding guilds (Tukey's HSD: $q > 9$; $p = 3.222\text{E-}5$). Only three of four specimens from TF110 show enriched $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values compared to other lucinids, and plot together with the deposit-feeding tellinids from the same locality (Fig. 5F).

Specimens from sample TF508_FW6 have depleted isotope ratios regardless of their feeding ecology (Fig. 5A, C, E). However, the most striking difference appears between the isotope ratios of infaunal suspension feeders from TF508_FW6 compared to those from other localities (Fig. 5E).

Stable Isotope Ratios and Inferred Paleoenvironments

The stable isotope ratios of mollusks from different paleoenvironments are shown in Figure 6. In order to compare between inferred paleoenvironments we exclude chemosymbiotic lucinids, as their stable isotope signature differs significantly from that of all other feeding guilds.

The brackish water sample TF508_FW6 has depleted oxygen and carbon isotope ratios compared to other samples (see also Discussion below). After removal of isotope ratios from lucinid bivalves the sample

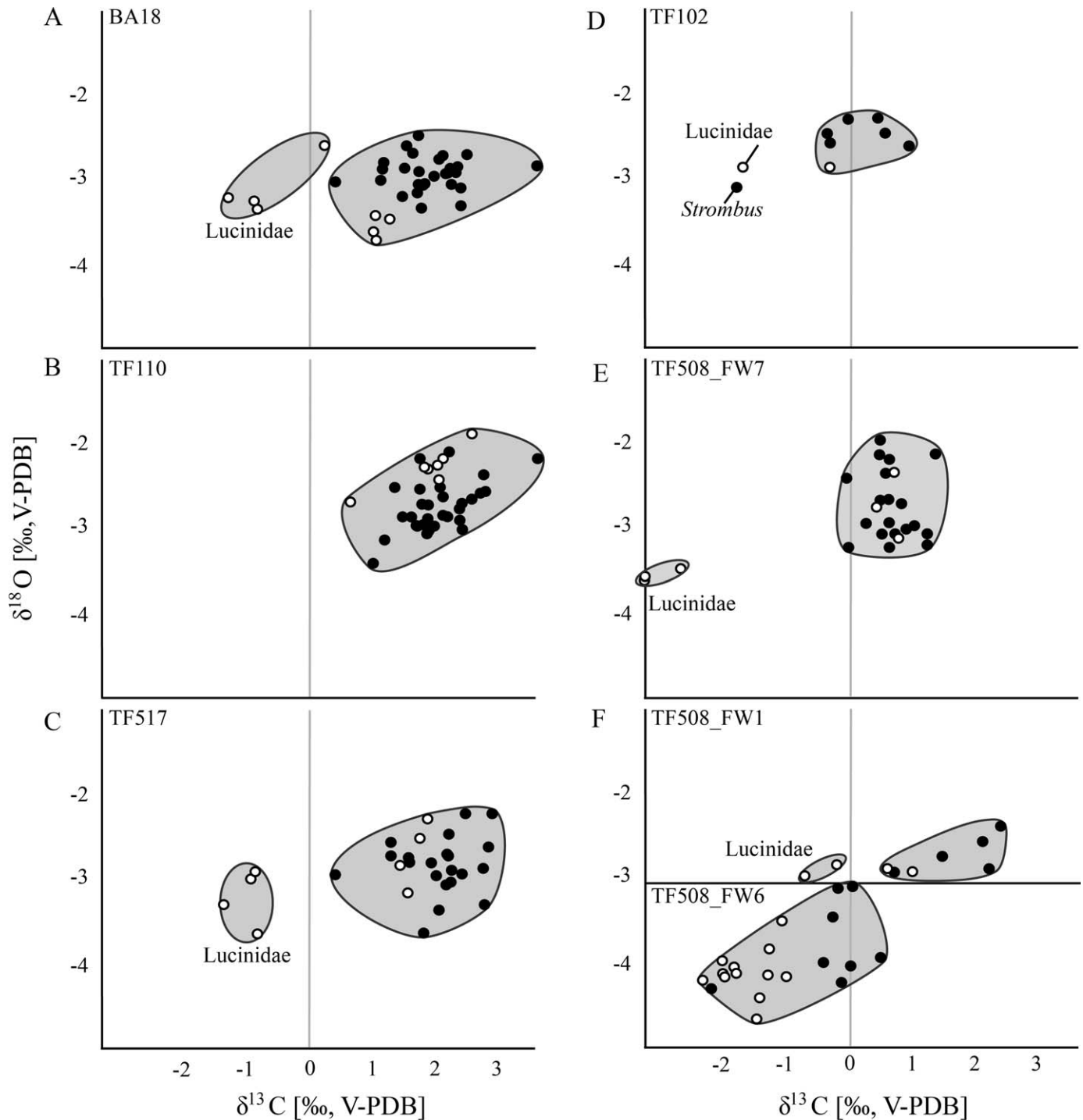


FIG. 4.— $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ratios of gastropods (indicated by black dots) and bivalves (indicated by open circles) arranged according to sampling locality. A) BA18. B) TF110. C) TF517. D) TF102. E) TF508_7. F) TF508_1 and TF508_6.

also differs from TF102 (Tukey's HSD: $q = 6.49$; $p = 0.0001$), whereas no difference between the two localities was seen before.

The carbon isotope ratios of the six marine localities distinguish between coral carpet (depleted $\delta^{13}\text{C}$), mixed coral seagrass (intermediate $\delta^{13}\text{C}$ in TF508_FW7), and seagrass (enriched $\delta^{13}\text{C}$ ratios). The seagrass localities BA18, TF110, TF517, and TF508_FW1 show significantly different carbon isotopic ratios than samples from the

mixed coral-seagrass habitat TF508_FW7 (Tukey's HSD: $q > 4$, $p < 0.01$) and the coral-carpet environment TF102 (Tukey's HSD: $q > 4$, $p < 0.01$).

When including carbon isotope ratios of lucinids, TF508_FW1 (with presumably sparse seagrass vegetation) differs slightly from TF110 (Tukey's HSD: $q = 4.18$, $p = 0.049$), whereas no difference is seen compared to TF508_FW7 (Tukey's HSD: $q = 3.64$, $p = 0.13$).

TABLE 3.—Summary of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ratios of mollusks according to feeding guild (FG): 1 = herbivore, 2 = seagrass feeder, 3 = predator on invertebrates, 4 = predator on foraminifera, 5 = browsing carnivore, 6 = infaunal suspension feeder, 7 = infaunal deposit feeder, 8 = chemosymbiotic deposit feeder. * One outlier removed, ** three outliers removed.

FG	FG 1 (all data*)	FG 2 (all data)	FG 3 (all data*)	FG 4 (all data)	FG 5 (all data)	FG 6 (TF508_FW6)	FG 6 (all data excl. TF508_FW6)	FG 7 (all data)	FG 8 (all data **)
n	65	9	17	15	11	12	12	6	15
$\delta^{18}\text{O}$ mean	-2.86	-2.71	-2.94	-2.81	-2.73	-4.11	-3.00	-2.44	-3.15
std	0.41	0.26	0.54	0.17	0.24	0.28	0.49	0.40	0.34
$\delta^{18}\text{O}$ min	-4.23	-3.06	-4.03	-3.06	-3.01	-4.66	-3.72	-2.91	-3.64
$\delta^{18}\text{O}$ max	-1.95	-2.17	-2.09	-2.51	-2.27	-3.50	-2.28	-1.88	-2.60
$\delta^{13}\text{C}$ mean	1.48	2.56	1.42	1.44	1.59	-1.71	1.05	1.65	-1.23
std	0.84	0.26	1.17	0.78	0.90	0.43	0.63	0.76	1.17
$\delta^{13}\text{C}$ min	-0.35	1.20	-0.49	0.40	0.22	-2.42	-0.36	0.56	-3.35
$\delta^{13}\text{C}$ max	2.94	3.66	2.88	2.44	2.45	-1.08	1.90	2.60	0.65

DISCUSSION

In order to understand processes and factors involved in the isotope signature of the shells we distinguish between processes affecting the composition of the ambient waters and fractionation processes that may occur between the water and the deposition of the shell. We assess factors in order to identify paleoecological processes and settings.

Factors Controlling the Isotopic Composition of Miocene Seawater

Global Ice Volume.—The increase of global ice volume during the middle Miocene generally results in enriched oxygen isotope ratios of lower Miocene carbonates compared to upper Miocene carbonates (Prentice and Matthews 1988; Lear et al. 2000). In this study, the Kalimantan samples are of a Tortonian (late Miocene) age while the material from Banyunganti, Java has a Burdigalian (early Miocene) age. The latter has the most depleted $\delta^{18}\text{O}$ signals of samples assigned to fully marine environments. This likely reflects a different seawater composition at the time of shell formation due to a lower global ice volume in the early Miocene.

Temperature and Salinity.—Temperature and salinity are major factors controlling stable isotope composition of ambient waters; temperature is also known to affect kinetic processes (e.g., Dettman et al. 1999; McConnaughey and Gillikin 2008). The narrow range of $\delta^{18}\text{O}$ ratios implies very similar temperature/salinity settings for the six marine samples of this study. Shells from sample TF508_FW6 are on average 1‰ more depleted in $\delta^{18}\text{O}$ (and $\delta^{13}\text{C}$; Table 2), in this case indicating reduced salinities in a brackish environment (e.g., Eisma et al. 1976). The assemblage composition confirms the paleoenvironmental interpretation. We assume that the samples represent an environment with relatively low residence times (estuarine, see Eisma et al. 1976) and we assume an averaged salinity of 35‰ for marine waters. In comparison to isotope ratios of *Tridacna* shells from the Miocene of Indonesia (-2.3 to -2.2 $\delta^{18}\text{O}$ and 1.4 to 2.4 $\delta^{13}\text{C}$; Batenburg et al. 2011; Warter et al. 2015) and freshwater ratios of -4.6 $\delta^{18}\text{O}$ and -10.5 $\delta^{13}\text{C}$ in the Mahakam river south of the sample sites (S. Troelstra, personal communication 2011), we extrapolate that TF508_FW6 (-3.97 $\delta^{18}\text{O}$ and -1.19 $\delta^{13}\text{C}$) was deposited in water with mesohaline conditions (9‰ based on $\delta^{18}\text{O}$ and 17‰–20‰ based on $\delta^{13}\text{C}$, conservative mixing assumed).

Air-Sea Exchange.—Air-sea exchange is a controlling factor for oceanic $\delta^{13}\text{C}$, because atmospheric and oceanic carbon reservoirs tend toward isotopic equilibrium. Today's equatorial regions have a net transfer of isotopic light CO_2 from the ocean to the atmosphere resulting in ^{13}C enriched surface waters (Lynch-Stieglitz et al. 1995). All samples used in this study, apart from BA18, derive from the same region and

time frame, therefore air-sea exchange is not considered to be a contributing factor to isotope differences among those localities. Samples from BA18 seem slightly depleted in ^{13}C compared to other seagrass associated samples, but no significant difference between carbon ratios of seagrass localities is revealed by Tukey's HSD. Regarding the statistical insignificance, the observed depletion might be just a chance occurrence and cannot be attributed to a process without doubt. If further sampling shows the depletion to be a robust signal, it could be caused by differences of the isotopic composition of atmospheric CO_2 and/or the mode of air-sea exchange in early Miocene compared to late Miocene times, or by environmental differences between localities, such as the influence of ^{13}C -depleted organic matter from other sources (see section on Productivity and Organic Matter below).

Factors and Fractionation Processes Controlling the Isotope Signatures in Shell Formation

Mineralogy.—Members of the seagrass feeding genus *Smaragdia* have slightly enriched $\delta^{13}\text{C}$ ratios compared to other mollusks from the same localities. Most likely this is a result of their calcitic outer shell layer (confirmed by Raman testing), because $\delta^{13}\text{C}$ of calcite is generally enriched compared to coprecipitated aragonite (Krantz et al. 1987).

Feeding Ecology.—Numerous previous studies have attempted to identify food sources and reconstruct food webs in seagrass meadows using carbon isotopes, based on the assumption that a close similarity exists between the carbon signal of organisms and their diet (e.g., DeNiro and Epstein 1978; Thayer et al. 1978; Fry et al. 1982). However, marine mollusks use largely ambient DIC to build their shells rather than respired CO_2 derived from dietary organic carbon (McConnaughey and Gillikin 2008, and references therein). Several studies estimated parts of respired carbon in aquatic (marine and freshwater) mollusk shells at around 10% or less (McConnaughey et al. 1997; Lorrain et al. 2004; Gillikin et al. 2006).

In this study, isotope ratios grouped by feeding guilds overlap considerably and largely group according to localities (Fig. 5). Therefore, different feeding habits seem to have very little influence on the isotope composition of the shells, with a single exception. Lucinid bivalves differ in their isotopic composition from other mollusks in almost all samples (apart from TF110) by their comparatively depleted $\delta^{13}\text{C}$ ratios. This is thought to be a result of bacteria-induced carbon fractionation during carbon fixation, and therefore reflects their chemosymbiotic mode of life (CoBabe 1991). Depleted $\delta^{13}\text{C}$ ratios of oxygen-depleted sediments might also result in ^{13}C depletion of infaunal lucinids (Latal et al. 2006a). In this study nonlucinid infaunal bivalves from the marine sites BA18, TF102, TF508_1, TF508_FW7, and TF517 display an enriched $\delta^{13}\text{C}$ signal

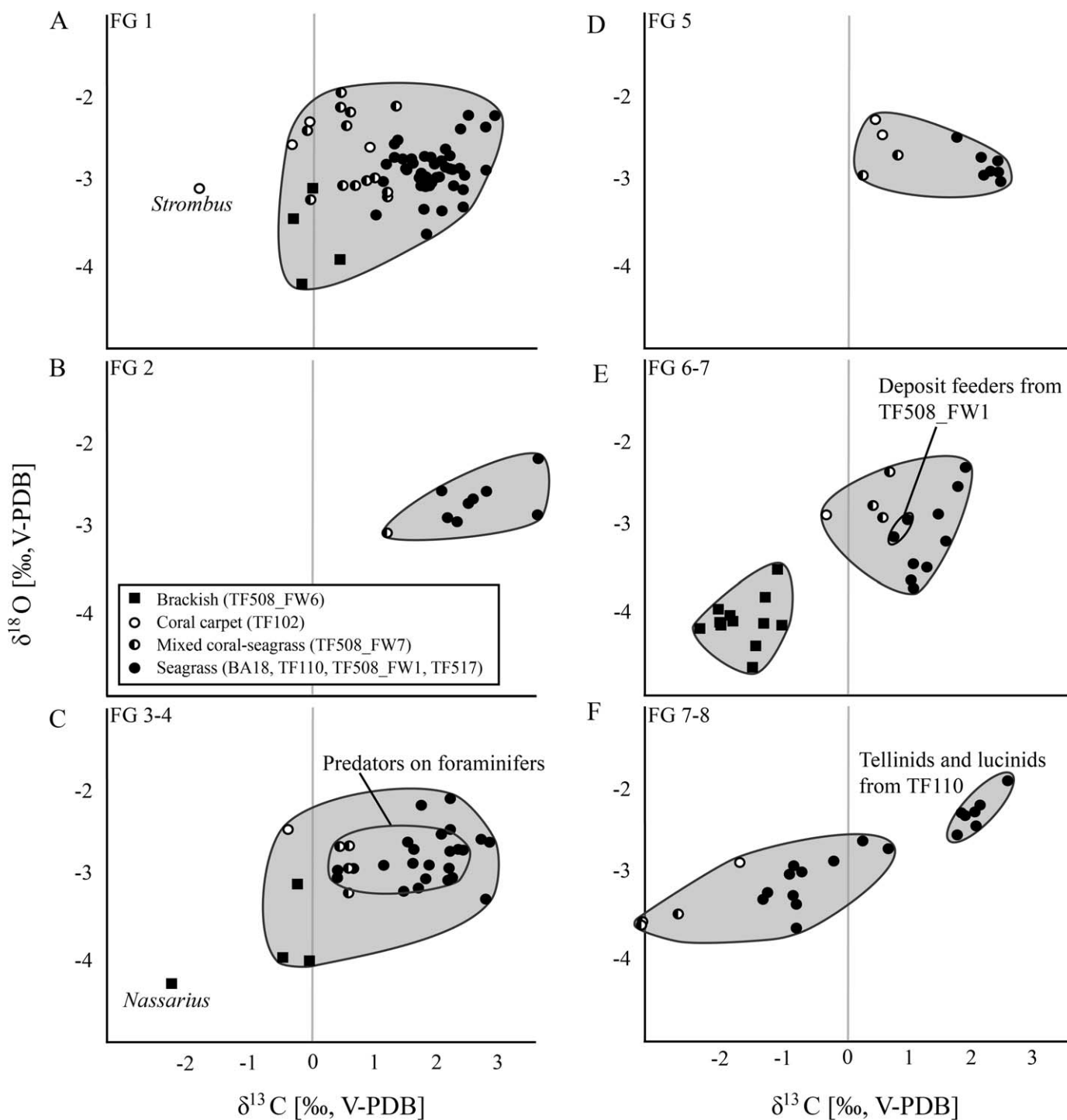


FIG. 5.— $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ratios of mollusks arranged according to feeding guilds (FG 1–8) and paleoenvironmental interpretation (see legend). **A)** FG 1 (herbivores). **B)** FG 2 (seagrass feeders). **C)** FG 3–4 (predators on invertebrates and feeders on foraminifera). **D)** FG 5 (browsing carnivores). **E)** FG 6–7 (suspension feeders, including deposit feeders from TF508_FW1). **F)** FG 7–8 (chemosymbiotic deposit-feeding lucinids, including deposit-feeding tellinids from TF110).

compared to lucinids from the same localities, indicating that the physiology of lucinids is the very likely cause of the depleted $\delta^{13}\text{C}$ ratios in their shells. The relatively enriched $\delta^{13}\text{C}$ ratios of three lucinid specimens from TF110, and possibly also of the fourth specimen and in one *Cardiolucina* from BA18, may reflect deposit feeding. In case of limited supply with reduced sulfur, lucinids can compensate the nutritional limitations by feeding on particles, or additional deposit feeding might

provide an advantage in highly productive depositional environments (Duplessis et al. 2004).

Infaunal versus Epifaunal Habitat.—Previous studies found that infaunal bivalves are depleted in $\delta^{13}\text{C}$ compared to epifaunal bivalves from the same locality (Stevens and Vella 1981; Krantz et al. 1987), whereas in other studies no differences were seen (Tanaka et al. 1986).

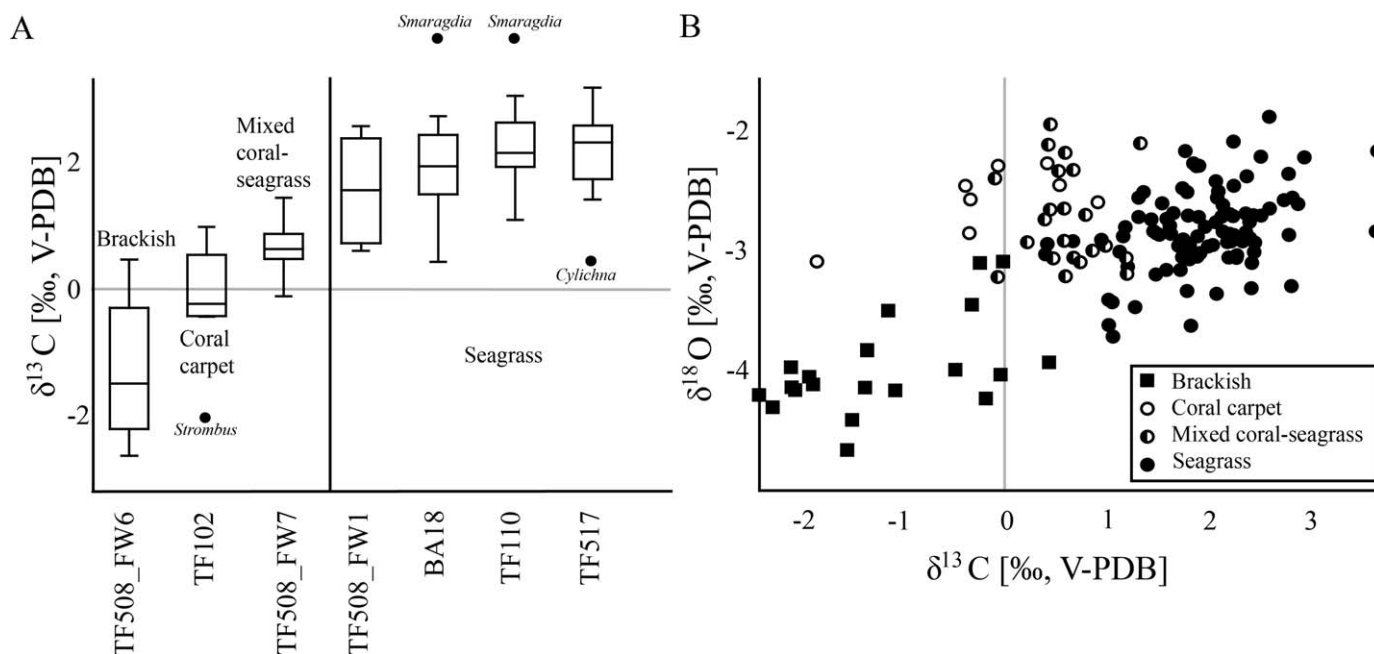


FIG. 6.—Comparison of all isotopic ratios. **A**) Interpolated box plots of $\delta^{13}\text{C}$ values of all localities, outliers indicated by black dots. **B**) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ratios of all samples (including outliers); see legend for paleoenvironmental assignment.

Comparatively depleted $\delta^{13}\text{C}$ values of infaunal bivalves are attributed to ^{13}C -depleted pore water due to the decomposition of ^{13}C -depleted organic matter in the sediment (Krantz et al. 1987, and references therein). Likewise, depleted $\delta^{18}\text{O}$ values may result from the degradation of organic matter by sulfate ions in oxygen-depleted pore waters (Sass et al. 1991). However, none of the above-mentioned studies included material from seagrass meadows.

Seagrass beds store a high amount of organic carbon and generally have high rates of sulfate reduction (Duarte and Cebrián 1996; Holmer et al. 2003, 2009), therefore depleted isotopic values in infaunal bivalves could be expected. However, $\delta^{13}\text{C}$ values of sedimentary organic carbon from modern seagrass beds are often comparatively enriched (−9.8 to −14, rather than −20 in other marine sediments; Fry et al. 1977, and references therein). This reflects the comparatively enriched $\delta^{13}\text{C}$ values of marine angiosperms, especially those in the tropics (typically −10 to −11; Smith and Epstein 1971; Hemminga and Mateo 1996).

In our study, four specimens of the infaunal venerid *Circe junghuhnii* from BA18 show comparatively depleted $\delta^{18}\text{O}$ values (Fig. 4A), whereas infaunal bivalves (excluding lucinids) from other localities (seagrass localities and TF508_FW7) do not show such a depletion in oxygen compared to epifaunal species. A depletion of oxygen in infaunal bivalves might be prevented in some seagrass environments due to the release of oxygen through seagrass roots and rhizomes (Fisher and Hand 1984; Pedersen et al. 1998).

The infaunal bivalves from TF508_FW6, where indications for seagrass vegetation are lacking, show a depletion of ^{13}C compared to epifaunal gastropods. This likely reflects the decomposition of ^{13}C -depleted organic matter in the sediment. Infaunal bivalves (excluding lucinids) from coral carpets and the sparsely vegetated sandflat habitat of TF508_FW1 also display rather depleted isotopic values, but data points are too few to make a clear statement.

However, $\delta^{13}\text{C}$ values of infaunal mollusks from seagrass habitats are mostly as enriched as the $\delta^{13}\text{C}$ values of epifaunal taxa, indicating that sedimentary organic matter in seagrass meadows displays enriched carbon isotope ratios compared to other marine environments as outlined above. Only two specimens of the shallow infaunal *Cylichna* from BA18

and TF517 are depleted in ^{13}C compared to other seagrass-associated cylichnids (Fig. 5C). This probably reflects the presence of depleted pore water over a very small spatial or temporal scale.

Furthermore, infaunal deposit feeders from site TF110 (including Lucinidae) and Veneridae from BA18 show very low variability in their isotope ratios, possibly reflecting very similar environmental conditions in the sediment. At other localities (TF517, TF508_FW7) the isotopic ratios of infaunal bivalves are found scattered between those of epifaunal gastropods, probably reflecting more variable parameters in the sediment, or a negligible difference between the conditions above and below the sediment-water interface. In addition, we cannot rule out that the variation of isotope values in the bivalve material results from the use of shell fragments in our analyses. The use of bivalve shell fragments representing different growth increments may result in an isotope record biased toward a fraction of some years, because carbon isotope values often become more depleted in later growth stages of a bivalve shell (e.g., McConnaughey and Gillikin 2008, and references therein).

Productivity and Organic Matter.—Photosynthetic organisms, such as seagrasses, preferably incorporate the lighter ^{12}C leading to ^{13}C -enriched ambient seawater when productivity is high (e.g., Lynch-Stieglitz et al. 1995). Epifaunal mollusk shells with comparatively enriched $\delta^{13}\text{C}$ values from seagrass localities (BA18, TF110, TF508_FW1, TF517) therefore may indicate a high primary production as known for modern seagrass environments (Duarte and Chiscano 1999). As outlined in the section above on Infaunal versus Epifaunal Habitat, the organic matter stored in seagrass meadows is relatively enriched in ^{13}C , resulting in enriched $\delta^{13}\text{C}$ values for infaunal mollusks; however, $\delta^{13}\text{C}$ measured in modern habitats varies between different seagrass environments. For example, shells from seagrass beds adjacent to mangroves show depleted $\delta^{13}\text{C}$ ratios due to the input of ^{13}C -depleted mangrove carbon (McMillan et al. 1980; Lin et al. 1991; Hemminga et al. 1994). Samples from mangrove areas have carbon isotope values ranging from −0.8 to −3.7, whereas shells from seagrass meadows where mangroves were lacking display enriched values of +0.0 to +1.0 (Lin et al. 1991). Estuarine seagrasses display a more depleted $\delta^{13}\text{C}$ signal than those lacking riverine influence (Simenstad and Wissmar

TABLE 4.—Stable isotope values of recent mollusk shells from a seagrass-vegetated reef-flat (Lankadea, Spermonde, Indonesia).

Sample	Species	^{13}C V-PDB	^{18}O V-PDB
UPG16_1	<i>Bothropoma</i> sp.	1.94	-1.99
UPG16_1.2	<i>Bothropoma</i> sp.	2.52	-2.16
UPG16_2	<i>Smaragdia rangiana</i>	2.26	-1.69
UPG16_4	Conidae indet.	1.98	-3.13
UPG16_4.2	Conidae indet.	1.45	-2.98
UPG16_5.2	<i>Diala semistriata</i>	1.61	-2.49
UPG16_7.2	<i>Euplica</i> sp.	2.68	-1.55
UPG16_8.2	<i>Euplica</i> sp.	2.58	-1.65
UPG16_9.2	<i>Ervillea biscalpata</i>	2.39	-1.37
Mean		2.14	-2.12
Min		1.45	-3.13
Max		2.68	-1.37

1985), likely resulting in comparatively depleted shells in these environments.

Stable Isotope Signatures as Paleoenvironmental Indicators

The similar $\delta^{18}\text{O}$ ratios occurring in our samples suggest that $\delta^{13}\text{C}$ ratios are more likely to discriminate between different habitats. However, $\delta^{18}\text{O}$ records are useful to exclude the possibility that variations in $\delta^{13}\text{C}$ are based on temperature or salinity differences. In coastal settings the influence of freshwater and/or depleted organic carbon, for instance, from mangroves, often leads to depleted carbon isotope values of mollusk shells (Simenstad and Wissmar 1985; Lin et al. 1991; this study: sample TF508_FW6). Depleted $\delta^{18}\text{O}$ values can indicate such depressed salinities.

It is presumed that mollusks in recent open marine conditions precipitate their shells close to seawater-atmosphere equilibrium, therefore the $\delta^{13}\text{C}$ values of their shells should be around 0 (Hoefs 1987). However, in our study, the mollusk shells from seagrass settings are significantly enriched compared to the expected $\delta^{13}\text{C}$ value for marine conditions and compared to contemporaneous samples from coral-dominated environments. This suggests that it is possible to distinguish seagrass from nonseagrass marine environments by the carbon isotope signal of mollusk shells, at least within the same region and time frame. Therefore carbon isotope signals may serve as a control over paleohabitat assignments based on the composition of fossil assemblages. Carbon isotope ratios of mollusk shells show a positive correlation with carbon values of seagrass tissue (Lin et al. 1991); therefore, use of this method might be restricted to (sub)tropical environments because of the relative depletion of $\delta^{13}\text{C}$ of seagrasses in temperate areas (Hemminga and Mateo 1996). When considering just tropical, marine settings, it is unlikely that a specific carbon signature for seagrass meadows exists, as shown by the wide range of carbon isotope values of seagrass-associated shells presented by Lin et al (1991). Although shells from the seagrass meadow far from mangrove influence were comparatively enriched, their carbon isotope values of max. +1.0 are still significantly depleted compared to values for seagrass-associated shells found in our study. Keith et al. (1964) presented stable isotope signatures of recent mollusk shells derived from various marine and freshwater environments. Carbon isotope values of marine mollusks ranged from -1.7 to +4.2. Highest values were found in shells from shallow waters on the Pacific coast of Mexico, including three samples with a value > +2. Although no environmental indications are given in that work, all three samples derived from localities where seagrass meadows were most likely absent (Green and Short 2003). Further studies on the isotope signals of mollusk shells from different modern shallow marine habitats, including seagrass meadows, are necessary to confirm a

general trend of enrichment of shell carbon in seagrass habitats. Unfortunately for our comparisons, many studies on isotope ratios displayed by organisms in modern seagrass habitats are performed on organic material/tissue and not on shells (e.g., Fry et al. 1982). A death assemblage of recent epifaunal gastropod shells collected in 2009 by F.P. Wesselingh from a seagrass-vegetated reef flat (depth = ~ 1 m) off the island of Lankadea (Spermonde, Sulawesi, Indonesia) has enriched carbon isotope values ranging from +1.45 to +2.68 (mean = +2.14) comparable to those from our fossil seagrass assemblages (Table 4). However, the wide range of oxygen isotope ratios present (-1.37 to -3.13, Table 4) may suggest that the stable isotope composition of the shells was additionally influenced by varying salinities, possibly indicating that they were partly transported from different environments. At least for *Smaragdia rangiana* ($\delta^{13}\text{C}$ = +2.26) a seagrass habitat can be safely assumed. More studies of recent material from the region are needed for comparison.

CONCLUSIONS

The shell isotope composition in the studied samples reflects a number of paleoecological conditions and processes. The following conclusions can be made based on our results:

1. Feeding ecology, in most cases, has very little to no influence on the isotopic values of mollusk shells in this study, with the exception of chemosymbiotic taxa. The life mode of most lucinids analyzed seems to be well preserved in their distinctively depleted $\delta^{13}\text{C}$ signature. We conclude that chemosymbiotic taxa should be removed from datasets when aiming for a paleoenvironmental comparison among samples.
2. An ability to switch to deposit feeding by chemosymbiotic lucinids is possibly documented in the stable isotope record of samples from TF110.
3. Infaunal taxa in seagrass meadows are more likely to have shells enriched in ^{13}C compared to infaunal shells from other habitats due to the enriched $\delta^{13}\text{C}$ values of sedimentary organic seagrass carbon.
4. High rates of productivity in seagrass meadows likely cause the enriched $\delta^{13}\text{C}$ values of epifaunal mollusk shells from seagrass habitats.
5. Shells from tropical paleo-seagrass meadows do not display a unique isotope signal that can serve as an independent indicator for the biotope, but in comparison with contemporary samples from nonseagrass environments they have enriched $\delta^{13}\text{C}$ ratios. Therefore, the carbon isotopic ratios of shells can be used to confirm habitat assignments based on the taxonomy and ecology of fossil mollusks within regions and limited stratigraphic time intervals. A control over the context is indispensable.

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SUPPLEMENTAL MATERIAL

Data is available from the PALAIOS Data Archive:
<http://www.sepm.org/pages.aspx?pageid=332>.

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