ORIGINAL ARTICLE

Modern bivalve shell assemblages on three atolls offshore Belize (Central America, Caribbean Sea)

Ilona Hauser · Wolfgang Oschmann · Eberhard Gischler

Abstract The Belize atolls—Glovers Reef, Lighthouse Reef and Turneffe Islands—show differences in geomorphology, lagoonal depth, bottom sediment, growth of mangroves and sea-grass, exposure to waves and currents as well as in their sedimentation rates and their age. Bivalve shell assemblages in lagoonal areas reflect these geomorphological differences. On each atoll, 32 to 44 recent sediment samples were taken (total number of samples 111) and bivalve shells subsequently identified. The resulting database (32,122 bivalve shells in total) was analysed using Q-mode cluster analyses. Both the distribution of species characteristic of different lagoonal habitats and the distribution of bivalves with different life and feeding habits were investigated. Epifaunal suspension feeders were found particularly on hard-bottom along the reef-crests or clinging to mangrove roots. Infaunal suspension feeders show a more diverse distribution. Deeper lagoonal parts and areas with mangrove growth are often inhabited by chemosymbiont-carrying bivalves, indicating locations of reduced sediment. Deep burrowing detritus feeders are very abundant in shallow-water areas with moderate to high water agitation and were seldom found in *Halimeda*-rich sediments.

Keywords Belize · Atolls · Bivalve assemblages · Life habits · Feeding habits · Cluster analyses · Time-averaging

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Introduction

Bivalve assemblages are indicators for lagoonal habitats in the Caribbean. For instance, Robertson (1963) and Purdy et al. (1975) investigated the bivalve fauna of the Belize shelf and Ekdale (1974, 1977) studied the fauna of the Yucatán shelf. Other studies on bivalves in the Caribbean and adjacent areas are available from MacKinnon and Jones (2001) on Grand Cayman, Hoskins (1964) in the Gulf of Batabano (Cuba) and Turney and Perkins (1972) in Florida Bay.

Vermeij (1978), Petuch (1982) and Vermeij and Petuch (1986) described the development of the molluscan provinces in the Eastern Pacific and the Western Atlantic (particularly in the Gulf of Mexico and Caribbean Sea) from the Late Miocene to the Modern, with regard to changing conditions in sea-water exchange, upwelling and sea-level variation during the formation of the Central American Isthmus. Their investigations are solely based on gastropods, whereas bivalves, serving as excellent facies indicators, remained entirely neglected.

However, there are several advantages of using bivalves instead of gastropods for studies dealing with environmental change. Many bivalve species are of great interest for palaeoecological studies, because taxa have comparatively long stratigraphic ranges. Form and concavity of their shells or the existence or non-existence of a pallial sinus allows conclusions regarding their life habit (epifaunal, infaunal, shallow or deep burrowing) to be drawn. The classification of bivalves into ecotype groups, describing their life and feeding habits, provides information about their habitat.

Glovers Reef, Lighthouse Reef and Turneffe Islands are particularly suitable for an investigation of bivalve assemblages, because they represent three comparatively small ecosystems comprising various ecological environments with sediments rich in bivalve shells.

Study area

Climate and oceanography

Glovers Reef, Lighthouse Reef and Turneffe Islands are located east of the Belize Barrier Reef fringing the eastern Yucatán peninsula in the Gulf of Honduras (Caribbean Sea, Central America). Belize climate is subtropical with air temperatures between 27°C in summer and 24°C in winter (Purdy et al. 1975). Most of the year, winds blow from E and NE with average speeds between 7 knots in October and 13 knots in March (Fig. 1). Hurricanes mainly approach from E and SE (Gischler and Hudson 1998). During the time of investigation, tropical storm Chantal and hurricane Iris hit Belize. The microtidal range amounts to 30 cm (Stoddart 1962). Rainfall on the atolls averages 175 cm/year (Stoddart 1962; Purdy et al. 1975) and is highest from May to November and lowest from February to April (Gischler et al. 2003).

During 2001, water temperature and salinity variation were measured at high resolution in atoll lagoons using

Fig. 1 Map of the study area with locations of the box-core samples and positions of conductivity-temperature (*CT*) stations. Note that loggers in the northern lagoonal parts of Glovers Reef and Lighthouse Reef were lost and measured only incomplete data, respectively. *Wind rose* shows the main wind direction and average speed from 1971 to 1981 (data from Belize Weather Bureau)
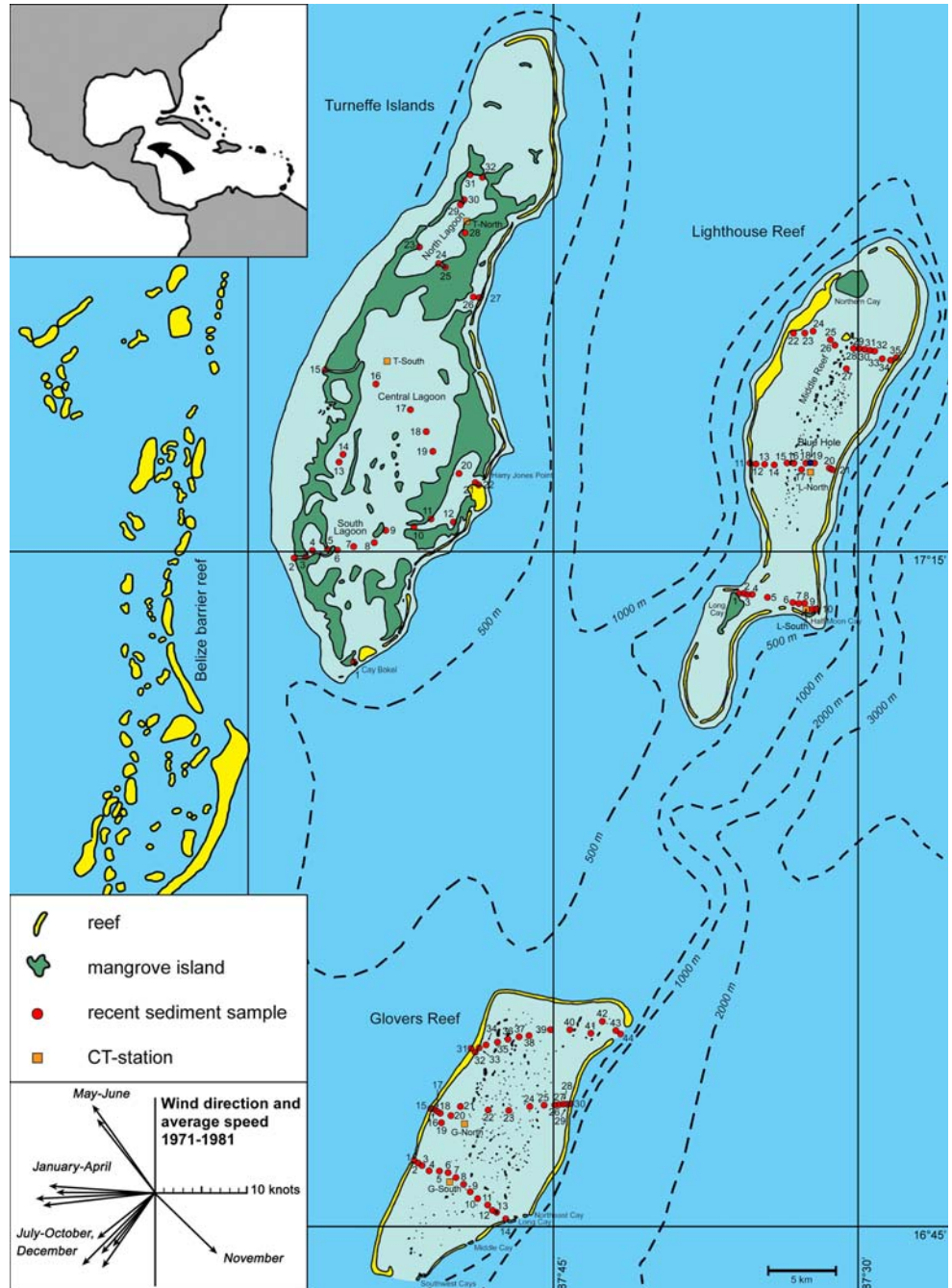
conductivity–temperature (CT) loggers located in the southern lagoonal parts of Glovers Reef and Lighthouse Reef (G-South, L-South) and in the North and South lagoons of Turneffe Islands (T-North, T-South; Fig. 1; Table 1). The highest fluctuations in water temperature and salinity were measured in the North Lagoon of Turneffe Islands ($\Delta T=10.10°C$; $\Delta S=8.07$ psu); the lowest fluctuations were observed in the deep lagoon of Glovers Reef ($\Delta T=6.87°C$; $\Delta S=3.37$ psu).

While water temperatures in the lagoons follow the seasons without any significant differences between Glovers Reef, Lighthouse Reef and Turneffe Islands, salinity profiles in the lagoons vary significantly (Fig. 2). Salinity curves reflect the geomorphology of the atolls, the water depths of the inner lagoons and the water exchange with the open ocean. Salinity is largely controlled by rainfall and evaporation. Precipitation is highest during the rainy season between May/June and November (Fig. 3). In the restricted lagoons of Glovers Reef and Turneffe Islands, lower salinities were measured during this season. On 21 August and 9 October 2001, tropical storm Chantal and hurricane Iris, respectively, caused a noticeable decrease in salinity. This decrease is expressed in the CT-data of Turneffe Islands North Lagoon and only slightly visible in the South Lagoon data. The inner lagoons of Glovers Reef and Lighthouse Reef in contrast do not show any significant decrease in salinity during these months. In the dry season between February and April, only in the North Lagoon of Turneffe Islands was an increasing salinity observed; in the other lagoons, salinity remained largely constant.

The influence of rainfall and evaporation on the salinity becomes especially visible in the shallow North Lagoon of Turneffe Islands, representing a comparably small, restricted system, which is easily controlled by external

Table 1 Water temperature and salinity data from the CT-stations measured from December 2000 to December 2001

CT-station	Average water temperature (°C)	Fluctuations in water temperature (°C)	ΔT (°C)	Average salinity (psu)	Fluctuations in salinity (psu)	ΔS (psu)
G-South	27.70	23.51–30.38	6.87	40.49	38.64–42.01	3.37
L-South	27.84	23.92–31.36	7.44	39.98	37.70–41.64	3.94
T-North	27.98	21.71–31.81	10.10	39.48	34.08–42.15	8.07
T-South	27.72	22.51–30.75	8.24	40.81	37.51–42.55	5.04

Loggers located in the southern lagoonal parts of Glovers Reef and Lighthouse Reef are labelled as G-South and L-South, respectively; those in the North and South Lagoons of Turneffe Islands as T-North and T-South, respectively
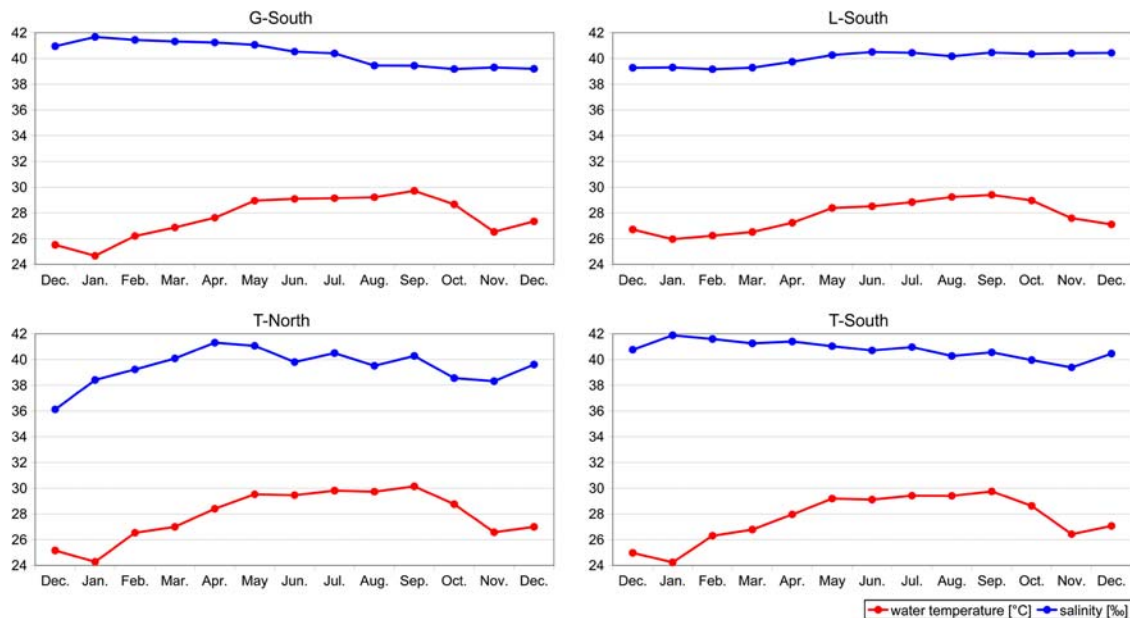

Fig. 2 Lagoonal water temperature and salinity on the three atolls during 1 year (December 2000-December 2001). Loggers located in the southern lagoonal parts of Glovers Reef and Lighthouse Reef are labelled as *G-South* and *L-South*, respectively, those in the North and South Lagoons of Turneffe Islands as *T-North* and *T-South*, respectively

Fig. 3 Precipitation at Carrie Bow Cay, Central Belize Barrier Reef, Smithsonian Field Station. Monthly mean (in mm) for 1995 and 1996 (CARICOMP) compared to monthly mean from 1976 to 1980 (Rützler and Ferraris 1982). Note, precipitation during May 1995 was 0 mm. No data were collected in February and December 1976–1980
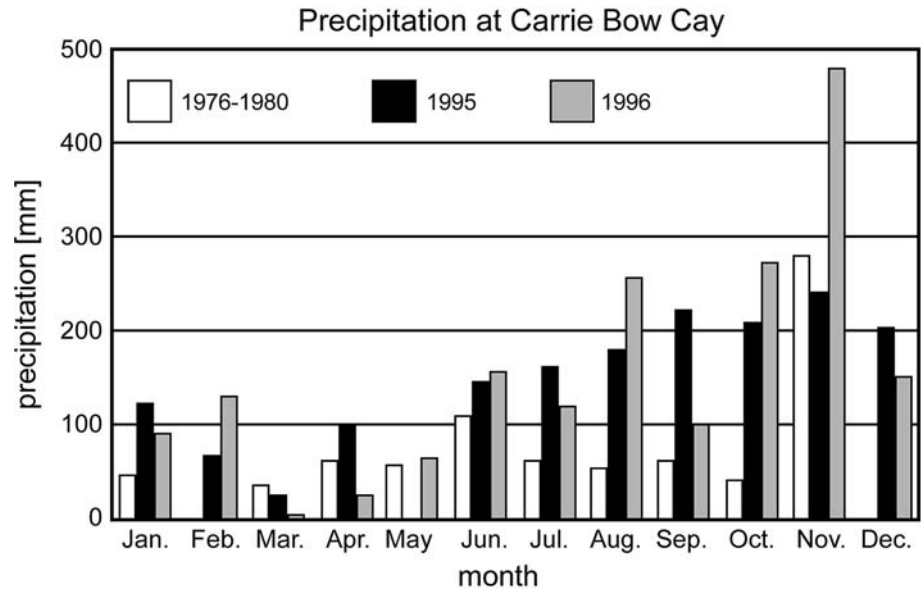
factors. With increasing water depth (T-South: 7.8 m; G-South: 10.5 m), this influence becomes less apparent in the salinity curves. Because of the continuous sea-water exchange, no correlation between salinity and rainfall/evaporation was observed in the open Lighthouse Reef Lagoon.

Geomorphology and environment

The Belize atolls show significant differences with regard to their geomorphology, sediment composition and Holocene development (Gischler and Hudson 1998; Gischler and Lomando 1999). Glovers Reef is 260 km^2 in size, 0.6 km^2 of which are represented by six islands located along the southern windward reef margin. The 20 m deep inner lagoon is covered with ~860 patch reefs. It flattens to the margin and is surrounded by a reef-crest with three tidal channels on the eastern side (Gischler 2003). The shallow margin zones are loosely covered with sea-grass meadows of *Thalassia testudinum*. In the deeper part of the lagoon, sea-grass growth is sparse.

Lighthouse Reef is the smallest atoll and covers an area of 200 km^2, with five islands making up 7.5 km^2. The leeward reef-crest is broken by numerous channels, the windward reef only shows one opening in the south. Middle Reef—a N-S trend of patch reefs (~20 km long)—divides the inner lagoon into a shallow western and a deeper eastern part (water depths down to 3 and 9 m, respectively). Grass cover is more dense in the eastern lagoon, where the Blue Hole, a collapsed karst cave of 140 m depth, is located (Gischler 1994).

Turneffe Islands is the biggest atoll with an area of 525 km^2. Of these, 125 km^2 are represented by islands, which are mainly grown over by red mangrove (*Rhizophora mangle*). On the eastern side of the atoll, a narrow reef-crest with over 20 channels has developed. In the

north, the reef is wider and not interrupted by channels. Two lagoons—a small one in the north and a bigger one, divided into a central and a southern part—are surrounded by mangrove rims with numerous channels (bogues) and ponds. Lagoonal depths reach 6 m (Gischler 1994). Coral patch reefs are rare and found only in the North Lagoon. The bottom of the lagoons is covered with dense sea-grass meadows and the calcareous alga *Halimeda*.

Materials and methods

During March and April 2000, 111 surficial sediment samples were collected along E–W transects in the lagoons of Glovers Reef, Lighthouse Reef and Turneffe Islands (Fig. 1) using a grab sampler (Hydro-Bios, Kiel; volume: 2.25 L). Samples, comprising two grab sampler volumes each (4.5 L), were taken from the boat or by snorkelling when taken along the reef-crests. Bottom-water temperature was measured at each station by holding a contact thermometer into the fresh grab sample. Water depths were measured using a rope with a metrical scale. Exact positioning was achieved by GPS (model MAGELLAN 2000; accuracy 30.8 m).

Two conductivity-temperature probes (CT-probes, type R. Brancker, model XL210) were positioned in the lagoons of each atoll measuring water temperature and conductivity eight times a day, every 3 h, during 1 year (December 2000-December 2001). Four probes measured the entire 1 year-period, one probe from Lighthouse Reef only measured temperature due to malfunction of the conductivity-sensor, and one probe from Glovers Reef was lost. Conductivity (C) was converted into salinity (S) using the practical salinity scale of 1978 (Dauphinee et al. 1980; Perkin and Lewis 1980).

Samples were washed, sieved in the field over a 1-mm mesh, later rinsed in freshwater and oven-dried at 50°C. The volumetric contents were measured using a 250 ml graduated cylinder. Mollusc shells were picked from each fraction under a binocular (type Leica, model MZ6; maximum magnification: 40×) differentiating bivalves, bivalve fragments, gastropods and gastropod fragments, and their volumetric contents were measured again. Animals living at the time of sampling were not distinguished from dead ones. Mollusc fragments consisting of >50% of the valve or showing characteristic features as hinge teeth, pallial line (bivalves) or apex, aperture (gastropods) were regarded as complete valves or individuals, respectively, because such fragments can clearly be assigned to one valve or individual. Fractions containing >300 bivalve shells were divided using a sample splitter. According to Patterson and Fishbein (1989), the statistical error depends on the number of individuals in a sample. It ranges from 1 to 6% for samples containing 300 shells, which is sufficiently significant for statistical studies.

Taxonomic identification of bivalves (for species list see Appendix 1; for photographs of bivalve species see Appendix 2) was based on Warmke and Abbott (1961), Meinkoth (1981), Rehder (1981), Abbott (1986) and Redfern (2001). Q-mode cluster analyses were made using MVSP (version 3.1) to distinguish between different bivalve shell assemblages in diverse lagoonal zones. Only valves identified at species level were included in the analyses. The clustering method ''unweighted pair-group average'' and the Euclidean distance coefficient were used because they showed the most reasonable results, and there are no criteria for the use of any method or coefficient (Swan and Sandilands 1995; Middleton 2000).

Diversity (H'), richness (R) and evenness (E) are indicators for the stability of an ecosystem (Oschmann 1988, 1994a) and were evaluated for the atolls and their lagoonal zones, regarding all bivalves taken in each lagoon, and in each lagoonal zone respectively, as one sample. Each data set of an atoll contains over 8,000 individuals, wherefore statistical significance is given. Diversity was calculated after Shannon and Weaver (1949), richness after Margalef (1958) and evenness after Pielou (1966):

$$H' = -\sum \frac{n_i}{N} \ln\left(\frac{n_i}{N}\right)$$

$$R = \frac{S-1}{\ln(N)}$$

$$E = \frac{H'}{\ln(S)}$$

Table 2 Classification of ecotypes (feeding mechanism and life habit) of the most abundant bivalves

	Ecotypes									burrowing depth of infaunal bivalves
	epifaunal				infaunal siphonate	nestling	infaunal asiphonate			
	cemented	byssally attached	unattached				burrowing	predatory carnivores	chemosymbiotic feeders	
			suspension feeders				detritus feeders			
Chama macerophylla	Modiolus americanus Modiolus sp. Crenella divaricata Barbatia cancellaria Barbatia candida Arcopsis adamsi Ctenoides scabra Argopecten nucleus Lindapecten exasperatus	Glycymeris pectinata	Erycina periscopiana	Diplodonta notata Pleuromeris tridentata Crassinella lunulata	Cardiopsis smithii Americardia guppyi Laevicardium laevigatum Chione cancellata Chione paphia Chione sp. Gouldia cerina Transennella cubaniana Transennella stimpsoni Pitar simpsoni Pitar fulminatus	Ervilla concentrica Ervilla nitens	Semelina nuculoides Cumingia coarctata Cumingia vanhyningi Tellina mera Tellina lintea Tellina gouldii Tellina aegistriata Tellina candeana Tellina similis Tellina sybaritica Tellina listeri	Cardiomya costellata	Anodontia alba Divalinga quadrisulcata[a] Lucina beliziana Parvilucina sp. A Parvilucina costata Here sombrerensis[a] Codakia orbiculata Codakia orbicularis	very shallow burrowing / shallow burrowing / moderately deep burrowing / deep burrowing / very deep burrowing

Lucinids with chemosymbionts were described by Taylor and Glover (2000) and by Arruda et al. (2003).

[a] For these species, a real evidence for chemosymbionts was not found in the literature

where

n_i = number of individuals of species i
N = total number of individuals
S = number of species

Results

Bivalve ecotypes

Shell morphology of bivalves gives information about their life and feeding habits (Stanley 1970). Therefore, both the distribution of species and that of different ecotypes were investigated in this work. The bivalves forming the trophic nucleus of a sample (≥80%; Walker 1972) were divided into the ecotype groups shown in Table 2.

Free-living epifaunal bivalves were distinguished from those attached to the sediment surface. The latter cling to the substrate, either with byssus threads or with a glutinous fluid, which is secreted from the byssus and hardens afterwards. Infaunal bivalves were divided into forms with and without a sipho. Their pallial sinus gives information on the length of the sipho and their burrowing depth, respectively. Nestling forms were rarely found in the sediment samples.

Most epifaunal and infaunal bivalve species found in the samples are suspension feeders. Many deep burrowing forms, like tellinids and some semelids, feed on herbal detritus. In some few samples, predatory carnivores were observed. Nearly all lucinids live in symbiosis with sulphide-oxidising bacteria, sitting in the gill filaments of the bivalve (Taylor and Glover 2006). Chemosymbiosis is a synapomorphy of the Lucinidae and is secondarily lost in only few species. Lucinids occur close to the redox boundary and are able to live temporarily under anoxic conditions (Taylor and Glover 2000; Arruda et al. 2003). Through their pseudo-siphos, they receive oxygen from the sediment surface and H_2S from below the redox boundary (Oschmann 1994a, b).

Bivalve distribution

The bivalve faunas of Glovers Reef, Lighthouse Reef and Turneffe Islands exhibit significant differences. On Glovers Reef, high amounts of *Chione cancellata* and *Parvilucina* sp. A were observed (Fig. 4); tellinids are also very abundant. On Lighthouse Reef, *Tellina* spp. and *Chione cancellata* show similar abundance. *Gouldia cerina* is very common on Turneffe Islands followed in abundance by *Parvilucina* sp. A and *Chione cancellata*.

The distribution of the most common bivalve species (≥5% in at least one sample) along the transects is shown in Fig. 5a–c. It shows a distinct zonation within the lagoons of the three atolls including, firstly, shallow-water areas, exposed to waves and currents, which are generally characterised by the abundance of *Chione cancellata*, *Tellina* spp., *Americardia guppyi*, *Lucina beliziana* and *Pitar* spp.; secondly, highly exposed shallow lagoonal zones which are also inhabited by *Ervilia* spp.; thirdly, slightly exposed shallow-water areas that, furthermore, show high amounts of *Parvilucina costata*, *Codakia orbiculata*, *Glycymeris pectinata* and *Transennella* spp.; fourthly, restricted lagoonal zones, in sediments with a redox boundary close to the sediment–water interface and probable temporarily anoxic conditions, which are locations where *Parvilucina* sp. A and *Gouldia cerina* predominate. Their occurrence is independent from the bathymetry. The zonation within the lagoons also includes, fifthly, deep lagoonal areas, which have the characteristic species *Laevicardium laevigatum* and representatives of the family Pectinidae; sixthly, shallow restricted areas showing temporarily anoxic conditions in the surface sediment, which are the only locations where *Chione* sp. is found, although this venerid is not known to stand anoxic conditions; and, lastly, the restricted environment of mangroves inhabited by *Crassinella lunulata* and *Arcopsis adamsi*, which are only found there.
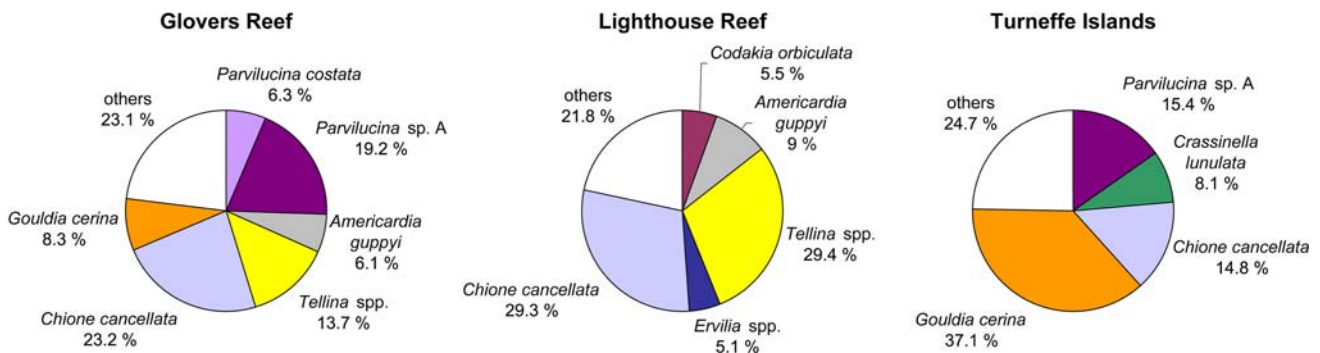

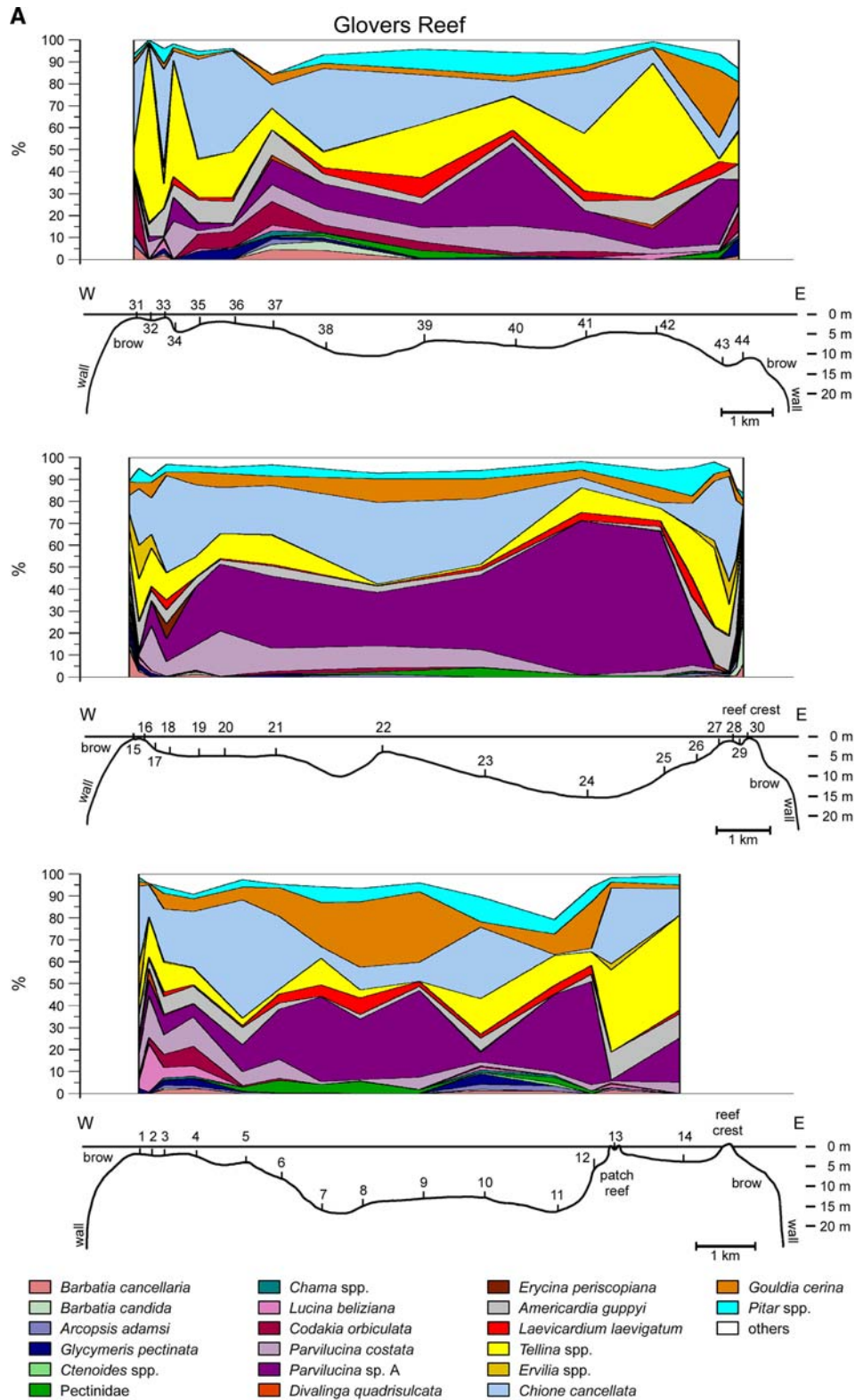**Fig. 4** Most abundant bivalves (>5%) on Glovers Reef, Lighthouse Reef and Turneffe Islands

Fig. 5 Distribution of the most abundant bivalves (>5%) from W to E on Glovers Reef (**a**), Lighthouse Reef (**b**) and Turneffe Islands (**c**). Closely related species of the same morphotype were combined under their genus name. Sample locations are labelled with *numbers* along the transects
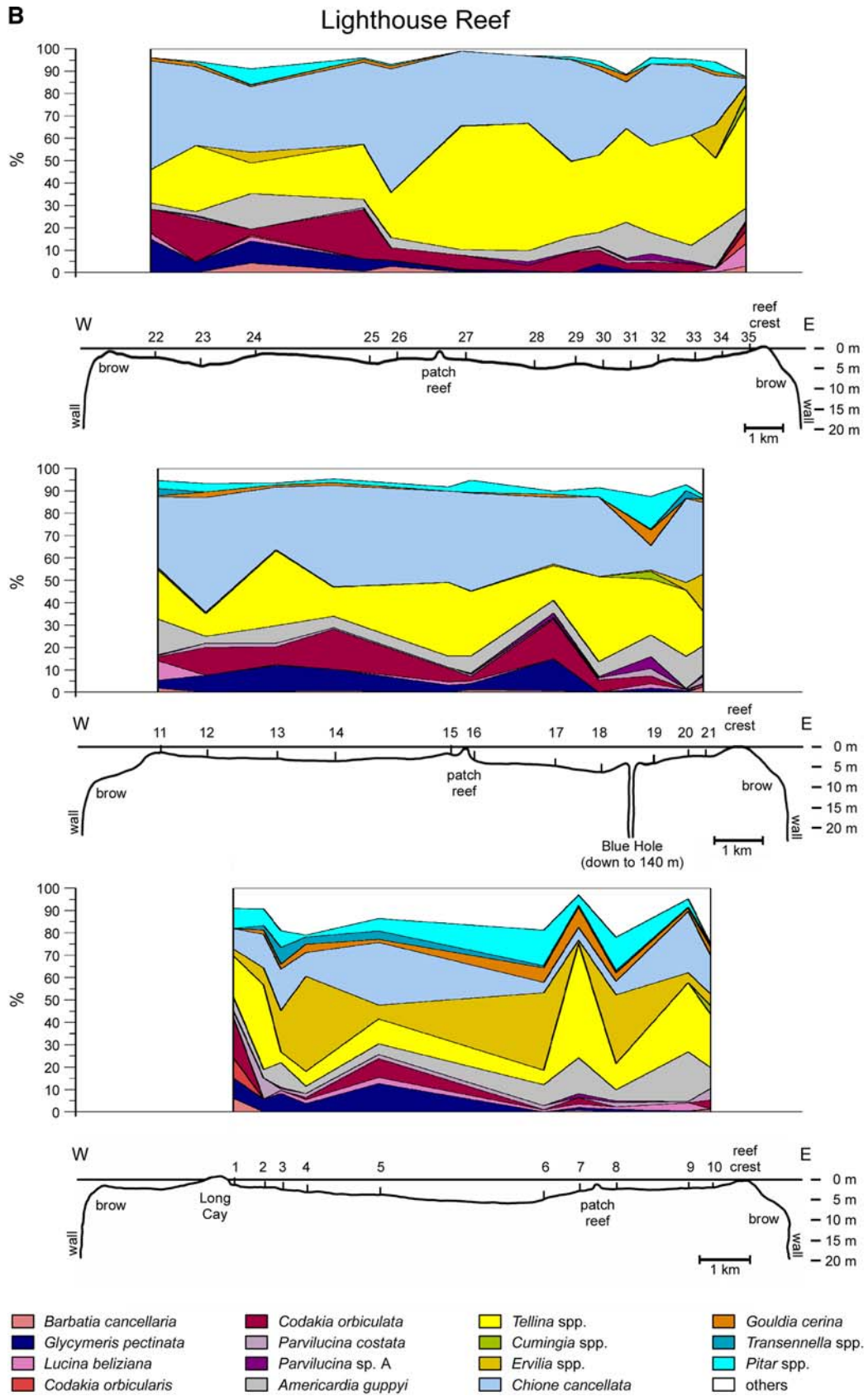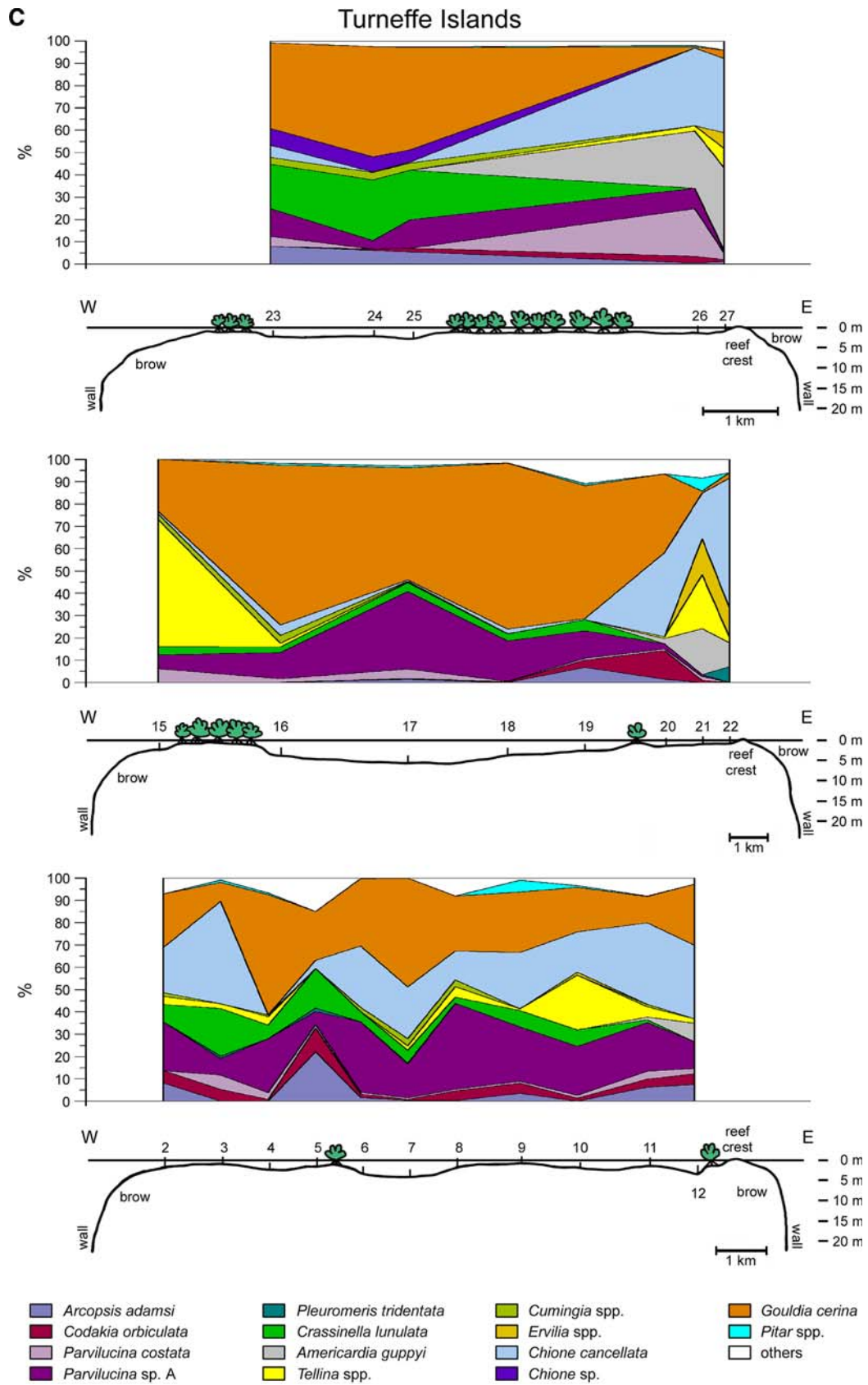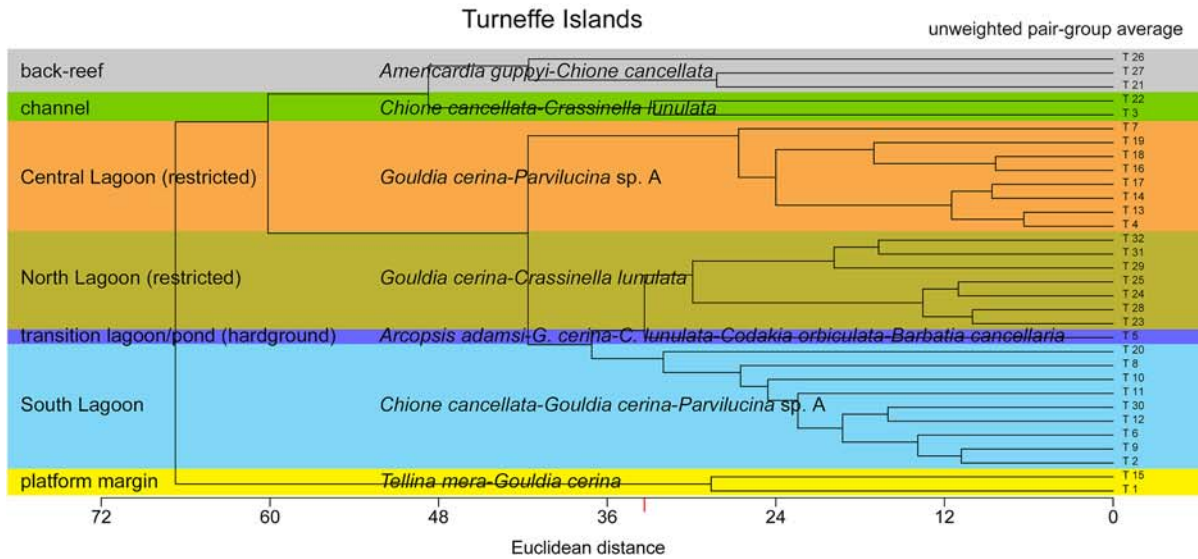
Fig. 5 continued

Fig. 5 continued

Glovers Reef

unweighted pair-group average

restricted deep lagoon — *Parvilucina* sp. A

back-reef — *Tellina similis-Tellina candeana-Parvilucina* sp. A

reef crest (hardground) — *Barbatia candida*

deep lagoon — *Parvilucina* sp. A-*Chione cancellata-Gouldia cerina*

shallow lagoon — *Chione cancellata*

Euclidean distance

Lighthouse Reef

unweighted pair-group average

reef crest (hardground) — *Tellina lintea-Lucina beliziana*

shallow lagoon — *Chione cancellata-Tellina similis*

open lagoon — *Chione cancellata-Ervilia concentrica-Pitar fulminatus-Americardia guppyi-Tellina gouldii-Ervilia nitens*

Euclidean distance

Turneffe Islands

unweighted pair-group average

back-reef — *Americardia guppyi-Chione cancellata*

channel — *Chione cancellata-Crassinella lunulata*

Central Lagoon (restricted) — *Gouldia cerina-Parvilucina* sp. A

North Lagoon (restricted) — *Gouldia cerina-Crassinella lunulata*

transition lagoon/pond (hardground) — *Arcopsis adamsi-G. cerina-C. lunulata-Codakia orbiculata-Barbatia cancellaria*

South Lagoon — *Chione cancellata-Gouldia cerina-Parvilucina* sp. A

platform margin — *Tellina mera-Gouldia cerina*

Euclidean distance
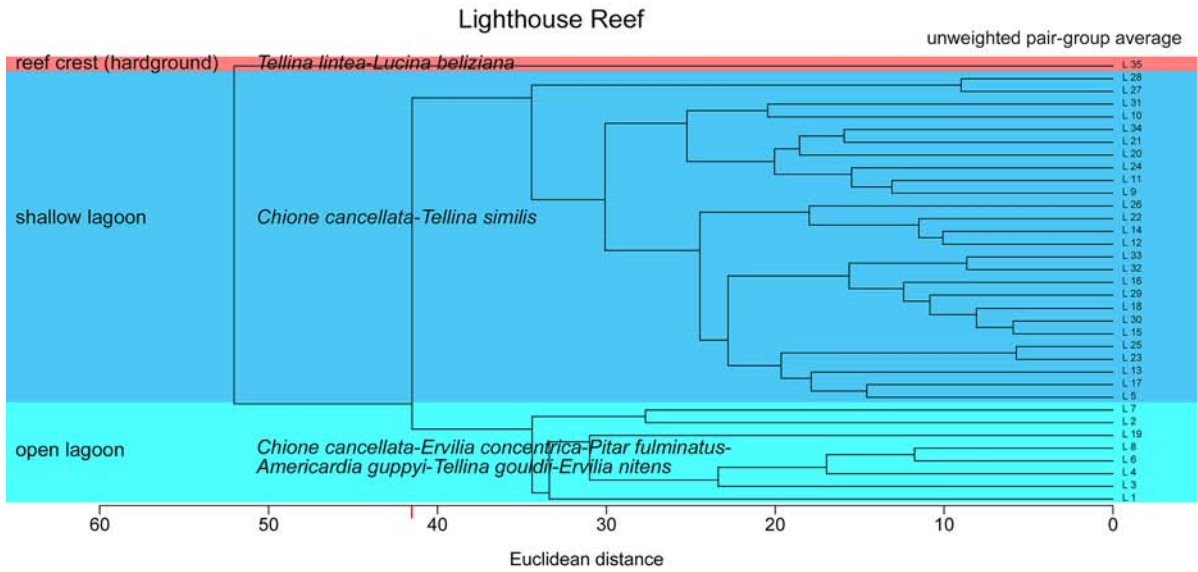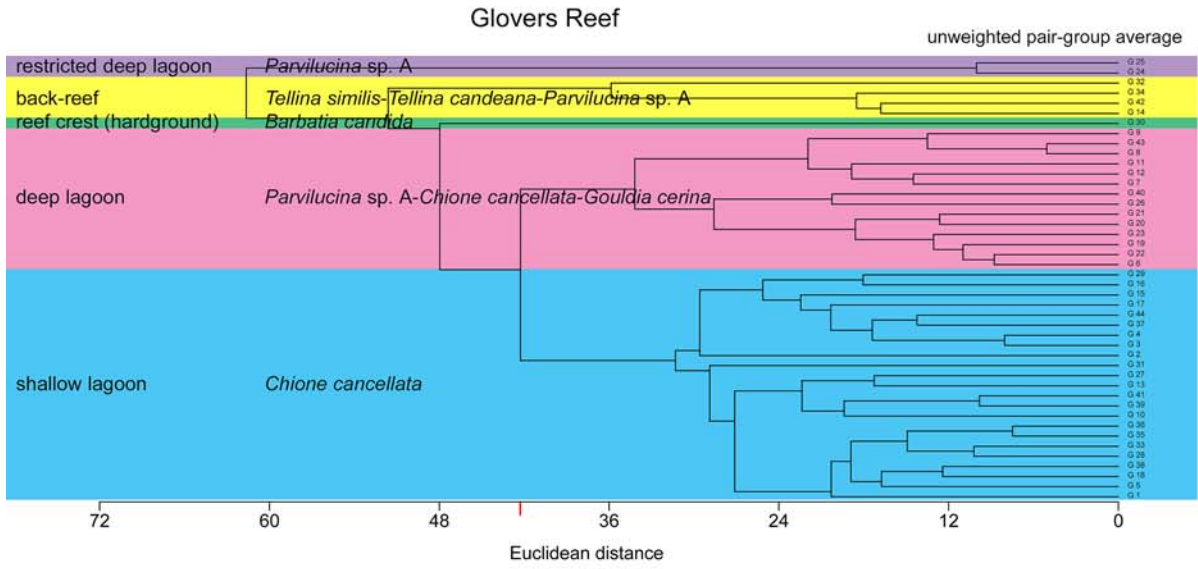
Fig. 6 Q-mode cluster analyses of all clearly identified bivalve species from each atoll. Clustering method: unweighted pair-group average; distance coefficient: Euclidean distance. Note different positions of distance coefficient in individual tree diagrams of the atolls (*red mark* on *x*-axis)

Cluster analyses

Q-mode cluster analyses were performed on our data set in order to characterise lagoonal environments based upon bivalve shell assemblages (Fig. 6). Cluster analyses serve as a tool for describing similarities or dissimilarities between samples. They do not claim to yield absolute results, but rather illustrate similar qualities. The shell assemblages shown in Fig. 6 only specify the corresponding environments. Because of gradual environmental transitions, a few samples assigned to an assemblage derive from different lagoonal zones (G 10, L 19, T 30).

Several observations support the contention that shell transport due to waves and currents can be largely excluded. First, sorting of foraminifera in the lagoons indicates some sediment transport from E–W (Gischler et al. 2003). However, it is largely restricted to the eastern marginal zones of the atolls. Second, the small thin-shelled foraminiferal tests examined are easier to move than the bigger and heavier bivalve shells. Third, the distribution of different bivalve shell sizes as well as that of right, left and articulated valves also gives only little evidence for some sediment transport in the eastern marginal zones (Hauser 2006). We therefore conclude, that the investigated sediments are largely autochthonous deposits containing bivalve assemblages which inhabited the corresponding environment.

Environmental zonation

The distinction of clusters does not result from equal Euclidean distances on each atoll, but was chosen to obtain a clearly visible environmental zonation characterised by different bivalve assemblages. On Glovers Reef and Lighthouse Reef, an Euclidean distance of ~42 was used to differentiate the clusters. On Turneffe Islands, a lower Euclidean distance of ~33 was necessary in order to distinguish the North and South Lagoon environments (Fig. 6). Thus, a total of five lagoonal zones were distinguished on Glovers Reef (restricted deep lagoon, deep lagoon, shallow lagoon, back-reef, reef-crest), three on Lighthouse Reef (shallow lagoon, open lagoon, reef-crest) and seven on Turneffe Islands (North Lagoon, Central Lagoon, South Lagoon, transition lagoon/pond, channel, back-reef, platform margin).

The classification of lagoonal environments by bivalves often shows only blurred boundaries. Differences between environmental zones are particularly small in Lighthouse

Reef Lagoon. On Glovers Reef and Turneffe Islands, the zonations are more distinct. At the same Euclidean distance of ~42, the lagoons of both atolls can be divided into five environments; and, at a Euclidean distance of ~33, Turneffe Islands lagoons can even be divided into seven. The distance coefficient, therefore, functions as a proxy for the heterogeneity of an environment.

Bivalve shell assemblages and distribution of bivalve ecotypes

The bivalve shell assemblages in Table 3 are based on Q-mode cluster analyses (Fig. 6). Even though the distribution of bivalves does not depend on sediment transport, we use the term ''assemblage'', because of the effect of time-averaging. The distribution of bivalve ecotypes in the lagoonal environments is illustrated in Figure 7a–c.

The reef-crest assemblage of Glovers Reef predominantly consists of epifaunal, byssally attached suspension feeders (' candida, *Ctenoides scabra*, *Arcopsis adamsi*, *B. cancellaria*, *Modiolus* sp., *Lindapecten exasperatus*). This assemblage was only found in sample G 30 taken along the eastern reef-crest on hard substrate covered with patches of sand. The back-reef assemblage largely comprises deep burrowing detritus feeders (*Tellina similis*, *Tellina candeana*). The more restricted shallow lagoon is predominantly inhabited by shallow burrowing suspension feeders (*Chione cancellata*, *Americardia guppyi*). *Chione cancellata* also colonises the deep lagoon of Glovers Reef, but the chemosymbiont-carrying *Parvilucina* sp. A is more abundant in this assemblage. This species lives at the redox boundary, which is situated close to the sediment surface. In the restricted deep lagoon, *Parvilucina* sp. A clearly predominates the assemblage.

The reef-crest assemblage of Lighthouse Reef was only found in sample L 35 along the back-reef of the eastern reef-crest. Here, as on Glovers Reef, the reef-crest largely consists of hard substrate normally colonised by epifaunal bivalves clinging to the substrate with their byssus. However, the reef-crest assemblage of Lighthouse Reef predominantly consists of the deep burrowing *Tellina lintea* and other burrowing forms. The sediment fraction >5 mm of this sample composes 92.7% of the total volume and consists of bivalves at 89.6% by volume (Hauser 2006). The bivalve fauna of this fraction is mainly composed of completely encrusted valves of the infaunal *Tellina lintea* (65.3%). Epifaunal, byssate attached genera (*Arca, Barbatia, Arcopsis, Limaria*), expected to live on hard substrate, were only observed in the smaller fraction 1–5 mm. In the open lagoon in the south of Lighthouse Reef, shallow to deep burrowing suspension and detritus feeders (*Chione cancellata*, *Ervilia concentrica*, *Pitar fulminatus*, *Americardia guppyi*, *Tellina gouldii*, *Ervilia nitens*) are distrib-

Table 3 Bivalve assemblages based on the Q-mode cluster analyses shown in Fig. 6

Glovers Reef			Lighthouse Reef			Turneffe Islands		
Lagoonal zone	Bivalve assemblage	%	Lagoonal zone	Bivalve assemblage	%	Lagoonal zone	Bivalve assemblage	%
Reef-crest	*Barbatia candida*	22.4	Reef-crest	*Tellina lintea*	34.1	Platform margin	*Tellina mera*	53.4
	Ctenoides scabra	8.6		*Lucina beliziana*	10.1		*Gouldia cerina*	13.0
	Arcopsis adamsi	7.8		*Codakia orbicularis*	5.8		*Parvilucina costata*	5.0
	Codakia orbiculata	7.8		*Americardia guppyi*	5.8		*Parvilucina* sp. A	5.0
	Barbatia cancellaria	6.0		*Cumingia coarctata*	5.1	Back-reef	*Americardia guppyi*	27.7
	Modiolus sp.	5.2	Open lagoon	*Chione cancellata* Type A	9.4		*Chione cancellata* type A	21.8
	Lindapecten exasperatus	5.2		*Ervilia concentrica*	9.2		*Parvilucina costata*	8.7
Back-reef	*Tellina similis*	42.8		*Pitar fulminatus*	8.7		*Tellina gouldii*	8.6
	Tellina candeana	12.5		*Americardia guppyi*	8.0		*Chione cancellata* type B	7.7
	Parvilucina sp. A	10.7		*Tellina gouldii*	8.0		*Ervilia nitens*	7.5
	Americardia guppyi	8.4		*Ervilia nitens*	6.5	Channel	*Chione cancellata* type A	51.5
	Parvilucina costata	8.3	Shallow lagoon	*Chione cancellata* Type A	34.4		*Crassinella lunulata*	10.7
	Chione cancellata Type A	5.7		*Tellina similis*	16.5		*Gouldia cerina*	5.5
Shallow lagoon	*Chione cancellata* Type A	30.5		*Americardia guppyi*	8.4		*Americardia guppyi*	5.4
	Americardia guppyi	9.1		*Codakia orbiculata*	6.9	Transition lagoon/pond	*Arcopsis adamsi*	22.1
	Tellina similis	8.7		*Tellina candeana*	5.0		*Gouldia cerina*	21.8
	Parvilucina costata	6.1					*Crassinella lunulata*	17.7
	Parvilucina sp. A	5.7					*Codakia orbiculata*	10.7
Deep lagoon	*Parvilucina* sp. A	32.1					*Barbatia cancellaria*	10.3
	Chione cancellata type A	16.4					*Parvilucina* sp. A	5.9
	Gouldia cerina	14.2				South Lagoon (open)	*Chione cancellata* Type A	26.0
	Parvilucina costata	7.1					*Gouldia cerina*	25.1
	Pitar fulminatus	5.3					*Parvilucina* sp. A	20.8
Restricted deep lagoon	*Parvilucina* sp. A	66.8					*Codakia orbiculata*	5.0
	Pitar fulminatus	5.9				Central Lagoon (restricted)	*Gouldia cerina*	57.8
	Gouldia cerina	5.2					*Parvilucina* sp. A	21.4
						North Lagoon (restricted)	*Gouldia cerina*	36.7
							Crassinella lunulata	17.1
							Parvilucina sp. A	8.9
							Chione cancellata Type A	8.1
							Cumingia vanhyningi	7.0
							Chione sp.	6.0
							Arcopsis adamsi	5.4

Note that only the most abundant species composing >5% of an assemblage are listed
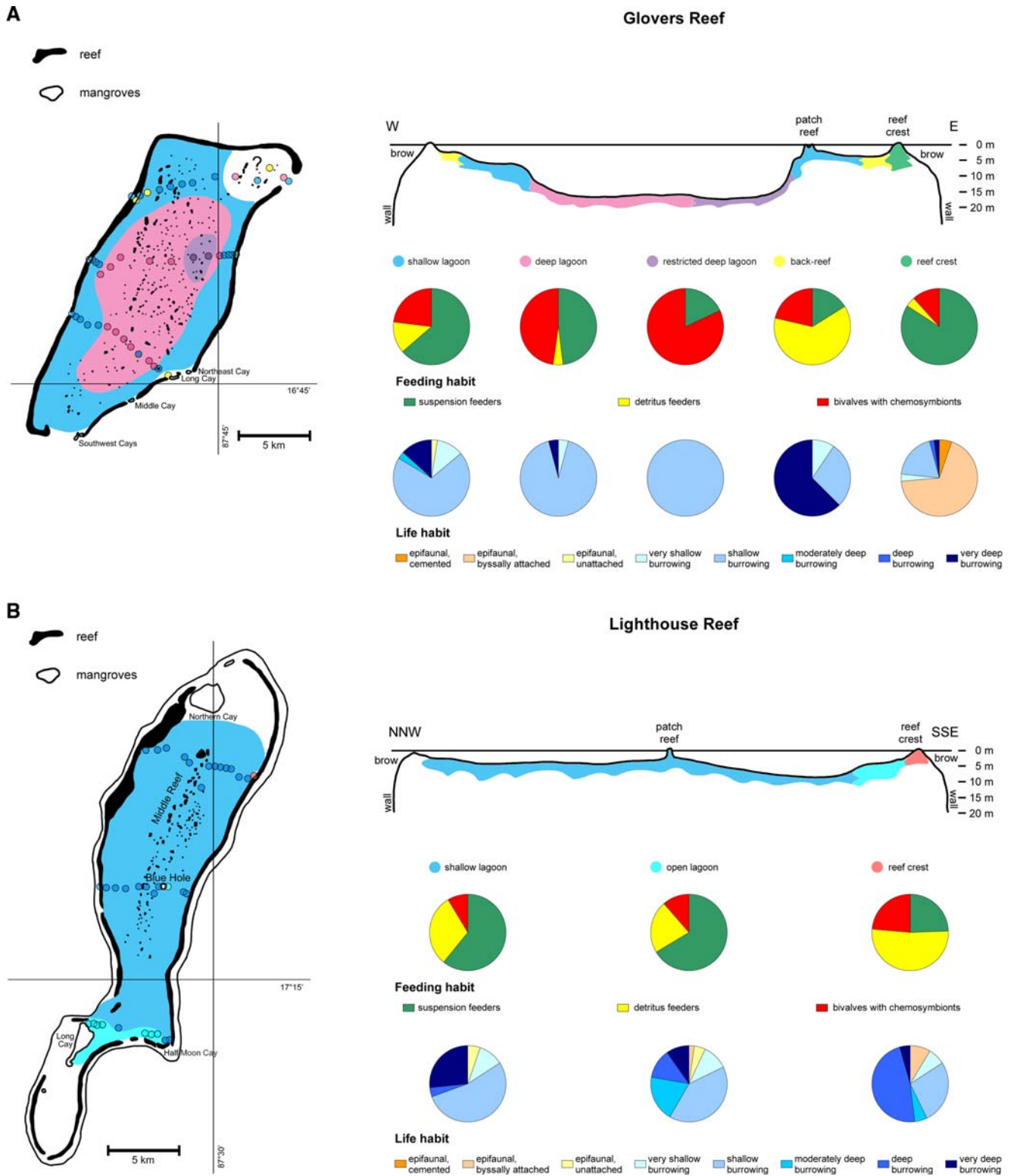
Fig. 7 Bivalve ecotype assemblages in lagoonal zones and along idealised transects on Glovers Reef (a), Lighthouse Reef (b) and Turneffe Islands (c). The area marked with a *question mark on Glovers Reef* is probably characterised by redeposition; the one with the *question mark on Turneffe Islands* is comparable with the open lagoon on Lighthouse Reef and probably encloses an equal bivalve assemblage
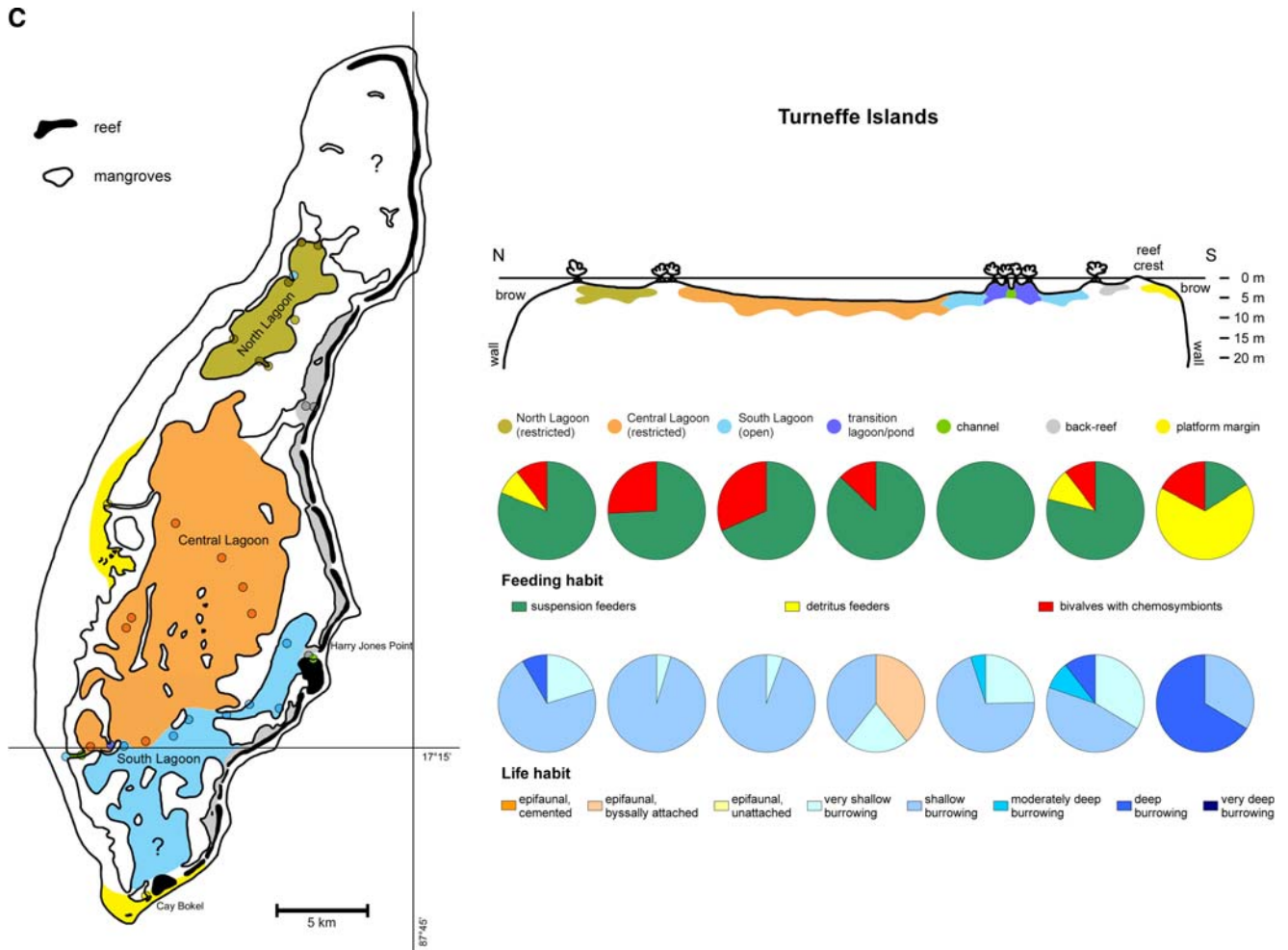
Fig. 7 continued

uted quite evenly. The slightly restricted part of the shallow lagoon is inhabited by *Chione cancellata* and also contains high amounts of *Tellina similis*.

The margin of Turneffe Islands predominantly consists of *Tellina mera*—a deep burrowing species inhabiting the fine grained, less *Halimeda*-rich sediments on the seaward side of the mangrove rim. In the coarse grained sediments of the back-reef area, the shallow burrowing suspension feeders *Americardia guppyi* and *Chione cancellata* were observed. The channels breaking through the mangrove rim are primarily inhabited by *Chione cancellata*. Another characteristic species of this assemblage, living in mangrove environments, is the very shallow burrowing, suspension-feeding *Crassinella lunulata*. This species is also abundant in the transition between the lagoon and the mangrove-surrounded ponds. The predominating species of this environment, however, is *Arcopsis adamsi*, preferably living byssally attached to mangrove roots. Its related species *B. cancellaria* is also characteristic in this assemblage. Besides these forms, the shallow burrowing suspension feeder *Gouldia cerina* and the shallow bur-

rowing, chemosymbiont-carrying species *Codakia orbiculata* and *Parvilucina* sp. A inhabit the transition between lagoon and pond. Compared to the Central and North Lagoon, the South Lagoon of Turneffe Islands is relatively open. Its bivalve assemblage consists of *Chione cancellata* as well as of *Gouldia cerina* and *Parvilucina* sp. A. These two species predominate the restricted Central and North Lagoon of the atoll. The North Lagoon, which is surrounded by mangroves, is also inhabited by *Crassinella lunulata*.

Diversity, evenness and richness

The bivalve faunas of the atolls show diversities between 1.44 in the restricted Central Lagoon of Turneffe Islands and 2.87 along the eastern reef-crest of Glovers Reef (Table 4). On Glovers Reef, diversity (H'), evenness (E) and richness (R) increase from the restricted deep lagoon towards the marginal shallow lagoon. Diversity and evenness also show higher values in the open southern part of Lighthouse Reef Lagoon than in its more restricted

Table 4 Diversity, evenness and richness of bivalve faunas in the lagoonal zones of each atoll

Atoll	Lagoonal zone	Diversity (H′)	Evenness (E)	Richness (R)
Glovers Reef	Reef-crest	2.87	0.83	31.79
	Back-reef	1.84	0.65	16.84
	Shallow lagoon	2.59	0.59	83.89
	Deep lagoon	2.33	0.55	69.88
	Restricted deep lagoon	1.47	0.47	22.85
Lighthouse Reef	Reef-crest	2.28	0.75	20.80
	Open lagoon	2.74	0.69	51.87
	Shallow lagoon	2.22	0.53	66.89
Turneffe Islands	Platform margin	1.77	0.62	16.80
	Back-reef	2.22	0.71	22.84
	Channel	1.91	0.65	18.81
	Transition lagoon/ pond	2.04	0.82	11.82
	South Lagoon (open)	2.12	0.59	35.87
	Central Lagoon (restricted)	1.44	0.44	26.87
	North Lagoon (restricted)	2.01	0.58	31.87

parts in the north. On Turneffe Islands, no such trend is visible.

Comparing the atoll lagoons, diversity, evenness and richness reach their highest values on Glovers Reef, are lower on Lighthouse Reef and lowest on Turneffe Islands (Table 5).

Discussion

Environmental zonation

On the three atolls, boundaries of different lagoonal environments characterised by bivalve shell assemblages are somewhat blurred—partly because of the gradual changes in geomorphology and partly because of the multiple factors (waves, currents, sediment composition and sea-grass cover) influencing the distribution of bivalves. Because of its shallow water depth, Lighthouse Reef Lagoon as a

Table 5 Diversity, evenness and richness of bivalve faunas on the three atolls

|	Diversity (H′)	Evenness (E)	Richness (R)
Glovers Reef	2.661	0.573	103.896
Lighthouse Reef	2.485	0.570	77.889
Turneffe Islands	2.221	0.568	49.890

whole is relatively open compared to the lagoons of Glovers Reef and Turneffe Islands. In the area of the southern transect, Lighthouse Reef is even more exposed to waves and currents. Therefore, this lagoon can only be divided into the two main environmental zones ''shallow lagoon'' and ''open lagoon'' shown in Fig. 6. Compared to Lighthouse Reef, the lagoons of Glovers Reef and Turneffe Islands show a large variety of environments—Glovers Reef because of a wide range in water depths in the middle and in its marginal zones, Turneffe Islands because of the mangrove rim surrounding and separating the lagoons and opening up further ecological niches such as ponds and channels.

Distribution of bivalve species and ecotypes

The bivalve shell assemblages found in the lagoonal sediments of the atolls reflect characteristic differences in water depth, exposure to waves and currents, mangrove growth, substrate, water temperature and salinity as well as in their sedimentation rates.

Firstly, shallow lagoonal zones, which are exposed to waves and currents, are mainly inhabited by the shallow burrowing suspension feeders *Chione cancellata* and *Americardia guppyi*. Besides these two species, the moderately deep burrowing and suspension-feeding *Ervilia* spp. is very common in, secondly, high-energetic shallow-water areas. Thirdly, the back-reef areas and atoll margins show very high abundances of deep burrowing tellinids seeking shelter in the sediment from waves and currents and feeding on herbal detritus. Fourthly, restricted shallow-water areas are predominated by *Gouldia cerina*, a shallow burrowing suspension feeder, whereas the also shallow burrowing, chemosymbiont-carrying *Parvilucina* sp. A characterises, fifthly, restricted deep lagoonal zones with a redox boundary located near the sediment surface. The very shallow burrowing suspension feeder *Crassinella lunulata* is a characteristic species inhabiting, sixthly, mangrove environments. Seventhly, the reef-crests and other areas composed of hard-bottoms are predominantly inhabited by epifaunal, byssate forms, such as *Arcopsis adamsi*, *B. candida* and *B. cancellaria*. The reef-crest assemblage of Lighthouse Reef represents an allochthonous deposit that includes a number of taxa sourced from different environments. Completely encrusted valves of the infaunal species *Tellina lintea* found in this assemblage require a long residence time on the sediment surface and therefore indicate redeposition.

The bivalve distribution in the lagoons is controlled by several environmental factors. The distribution of epifaunal, byssally attached suspension feeders is mainly controlled by the sediment substrate (Fig. 8). Mangrove growth serves as an important environmental factor for the colonisation of the very shallow burrowing *Crassinella*
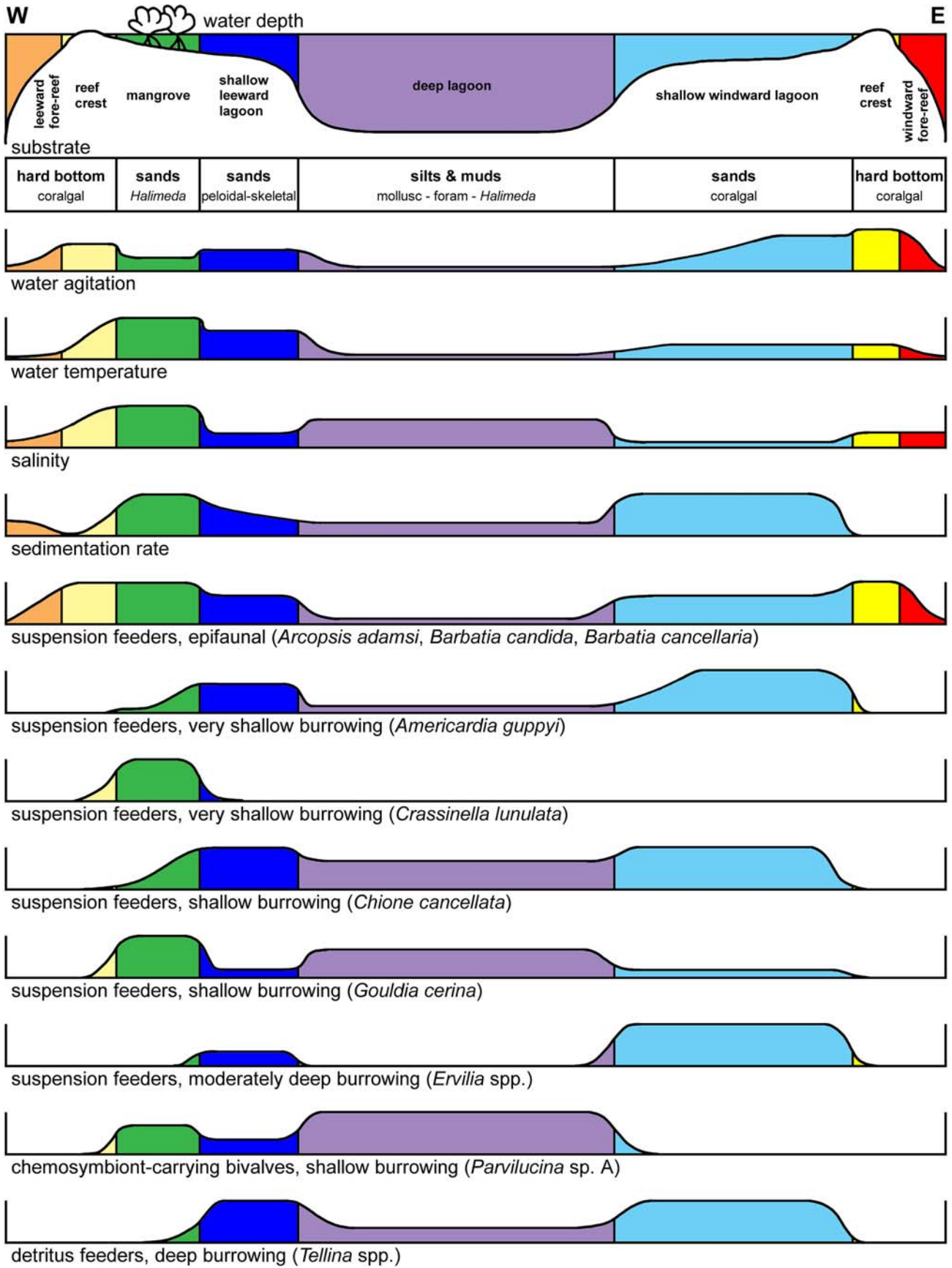
◀ **Fig. 8** Distribution of the most common bivalves depending on different environmental factors along an idealised transect including all environments on *Glovers Reef*, *Lighthouse Reef* and *Turneffe Islands*

lunulata, whereas *Gouldia cerina* is adapted to water agitation and fluctuating salinity. The abundances of *Chione cancellata*, *Americardia guppyi* and *Ervilia* spp. depend on water depth, water agitation and sedimentation rate. Chemosymbiont-carrying forms, indicating a redox boundary near the sediment surface and probably living under temporarily anoxic conditions, only dwell in areas with low water agitation. The distribution of deep burrowing detritus feeders is controlled by water agitation and the amount of fine grained sediment.

Bivalve diversity

The exchange of sea-water and the input of nutrients are sufficient for bivalves in the open lagoons of Glovers Reef and Lighthouse Reef. Due to lower water depths, Lighthouse Reef Lagoon shows a stronger influence of waves and currents as compared to Glovers Reef Lagoon. Therefore, deep burrowing bivalves predominate on Lighthouse Reef adapting to the environmental conditions by taking shelter in the sediment. This predominance of deep burrowing species may cause the lower values of diversity, evenness and richness on Lighthouse Reef in comparison to Glovers Reef. Due to its restricted location and lagoon-surrounding mangroves, only little exchange of sea-water takes place in Turneffe Islands lagoons and the salinity on this atoll is mainly controlled by rainfall and evaporation. The annual fluctuations in salinity support colonisation of only some opportunistic species, which is reflected in low diversity, evenness and richness values.

Additional factors possibly affecting diversity variation among lagoons are their sizes and ages. Habitat size does not seem to be a significant factor as diversity is lowest on Turneffe Islands, the largest of the three investigated habitats. Lighthouse Reef Lagoon, the smallest habitat, shows intermediate diversity. Usually, larger habitats exhibit higher diversity as compared to smaller ones as seen, e.g., in island biography. Lagoon ages show a correlation with diversity. According to core studies (Gischler 2003), Glovers Reef Lagoon is oldest (inundated 8.8 ka BP) whereas Turneffe Islands lagoons are youngest (flooded 6.8 ka BP). Consequently, the mollusc fauna of Glovers Reef Lagoon could be interpreted as being in a late stage of colonisation with high diversity whereas Turneffe Islands lagoons are still in an early stage showing lower diversity.

However, first investigations of mollusc faunas in Holocene lagoon cores show no clear trends in diversity development through time, and therefore do not support this line of argument.

Finally, the observed trend in diversity may also be caused by time-averaging, due to increasing average sedimentation rates from Glovers Reef (0.46 m/ka) towards Lighthouse Reef (0.53 m/ka) and Turneffe Islands (0.82 m/ka; Gischler 2003). Lower sedimentation rates cause a longer residence time of bivalve shells at or close to the sediment surface. This way, species, representing different populations, accumulate during a longer time span, and thus produce higher diversity values. The trend of an increasing time-averaging effect from Turneffe Islands towards Glovers Reef may also be seen in high amounts of bored and encrusted bivalve shells on Glovers Reef and very low amounts on Turneffe Islands (Hauser 2006).

Comparison with bivalve assemblages in the Caribbean and adjacent areas

Bivalve assemblages of the Caribbean and adjacent areas (Gulf of Mexico, Florida Bay) can only be compared in a qualitative way with those described in our study, because of different sampling methods (primarily dredging and drilling) and lower resolution sampling in large areas. Nonetheless, some similarities regarding abundances of species characteristic of certain environments are visible. Akin to our results, Robertson (1963) and Purdy et al. (1975) found high abundances of lucinids in the restricted lagoons of Turneffe Islands. Comparable assemblages to those of Glovers reef-crest and the hard substrates in the transition between lagoon and pond on Turneffe Islands, containing primarily epifaunal species, were described from the Belize Barrier Reef. Purdy et al. (1975) concluded that bivalve diversity is controlled by varying salinity. The lagoonal bivalve mollusc assemblage of the Yucatán shelf described by Ekdale (1974, 1977) shows similarities with the shallow lagoon assemblage on Lighthouse Reef, containing high abundances of *Chione cancellata*, *Tellina candeana*, *T. similis* and *Codakia orbiculata*. *Tellina candeana*, *T. similis* and *Americardia guppyi*, predominating the back-reef assemblage of Glovers Reef, were found as well in the back-reef area of Isla Cancún. Also, *Tellina similis* occurs in the restricted Gulf Subenvironment of the western part of Florida Bay (Turney and Perkins 1972). Wave- and current-influenced environments of the Yucatán shelf and the Gulf of Batabano are mainly characterised by *Ervilia nitens* (Hoskins 1964; Ekdale 1974, 1977).

Conclusions

Bivalves serve as important indicators for lagoonal environments in actuo-palaeontological studies. Their distribution is mainly controlled by lagoonal depth, water agitation, temperature, salinity, substrate, mangrove growth and sedimentation rate.

The three Caribbean atolls—Glovers Reef, Lighthouse Reef and Turneffe Islands—give detailed information about the distribution of bivalve shells, because they represent small ecosystems with a variety of ecological environments.

Epifaunal, byssally attached species characterise hard substrates, e.g. reef-crests, mangrove roots, etc. Shallow burrowing suspension feeders (*Chione cancellata*, *Americardia guppyi*, *Ervilia* spp.) are adapted to low water depths and high water agitation, with exception of *Gouldia cerina* occurring in restricted shallow lagoons. Fine grained sediments in shallow back-reef areas exposed to waves and currents are mainly inhabited by deep burrowing tellinids, whereas chemosymbiont-carrying lucinids (*Parvilucina* sp. A) characterise restricted deep lagoonal environments. The very shallow burrowing *Crassinella lunulata* is adapted to areas with mangrove growth.

Diversity, evenness and richness are highest on Glovers Reef, lower on Lighthouse Reef and lowest on Turneffe Islands. The sedimentation rates on the three atolls resemble this trend, implicating a more pronounced time-averaging effect on Glovers Reef than on Lighthouse Reef and Turneffe Islands. Glovers lagoonal sediments, therefore, presumably comprise faunal elements from several colonial phases being deposited during a longer period, maybe causing higher diversity values on this atoll as compared to Lighthouse Reef and Turneffe Islands. Living conditions for bivalves may be best in Glovers Reef Lagoon, due to intermediate nutrient input and energy conditions. In contrast, Turneffe Islands is controlled by high nutrient input, causing partial oxygen deficiency, and Lighthouse Reef by high energy levels.

Appendix 1: taxonomy

Appendix 1 Taxonomy of the most abundant bivalve species found on the three atolls

Subclass	Order	Suborder	Superfamily	Family	Subfamily	Genus	Subgenus	Species
Pteriomorphia	Mytiloida		Mytiloidea	Mytilidae	Modiolinae	*Modiolus* Lamarck, 1799		*Modiolus americanus* (Leach, 1815)
Pteriomorphia	Mytiloida		Mytiloidea	Mytilidae	Modiolinae	*Modiolus* Lamarck, 1799		*Modiolus* sp.
Pteriomorphia	Mytiloida		Mytiloidea	Mytilidae	Crenellinae	*Crenella* Brown, 1827		*Crenella divaricata* (d'Orbigny, 1842)
Pteriomorphia	Arcoida		Arcoidea	Arcidae	Arcinae	*Barbatia* Gray, 1842	*Barbatia* s.s.	*Barbatia cancellaria* (Lamarck, 1819)
Pteriomorphia	Arcoida		Arcoidea	Arcidae	Arcinae	*Barbatia* Gray, 1842	*Barbatia* s.s.	*Barbatia candida* (Helbling, 1779)
Pteriomorphia	Arcoida		Arcoidea	Noetiidae	Striarcinae	*Arcopsis* Koenen, 1885		*Arcopsis adamsi* (Dall, 1886)
Pteriomorphia	Arcoida		Glycymeridoidea	Glycymerididae	Glycymeridinae	*Glycymeris* Da Costa, 1778	*Tucetona* Iredale, 1931	*Glycymeris pectinata* (Gmelin, 1791)
Pteriomorphia	Limoida		Limoidea	Limidae		*Ctenoides* Mörch, 1853		*Ctenoides scabra* (Born, 1778)
Pteriomorphia	Ostreoida	Pectinina	Pectinoidea	Pectinidae	Chlamydinae	*Argopecten* Monterosato, 1889		*Argopecten nucleus* (Born, 1778)
Pteriomorphia	Ostreoida	Pectinina	Pectinoidea	Pectinidae	Chlamydinae	*Lindapecten* Petuch, 1995		*Lindapecten exasperatus* (G. B. Sowerby II, 1842)
Heterodonta	Veneroida		Chamoidea	Chamidae		*Chama* Linné, 1758		*Chama macerophylla* Gmelin, 1791
Heterodonta	Veneroida		Lucinoidea	Lucinidae	Lucininae	*Lucina* Bruguière, 1797		*Lucina beliziana* J. D. Taylor, 1998
Heterodonta	Veneroida		Lucinoidea	Lucinidae	Lucininae	*Codakia* Scopoli, 1777		*Codakia orbicularis* (Linné, 1758)
Heterodonta	Veneroida		Lucinoidea	Lucinidae	Lucininae	*Codakia* Scopoli, 1777		*Codakia orbiculata* (Montagu, 1808)
Heterodonta	Veneroida		Lucinoidea	Lucinidae	Lucininae	*Parvilucina* Dall, 1901		*Parvilucina costata* (d'Orbigny, 1842)

Appendix 1 continued

| Subclass	Order	Suborder	Superfamily	Family	Subfamily	Genus	Subgenus	Species
Heterodonta	Veneroida		Lucinoidea	Lucinidae	Lucininae	Parvilucina Dall, 1901		Parvilucina sp. A
Heterodonta	Veneroida		Lucinoidea	Lucinidae	Lucininae	Here Gabb, 1866		Here sombrerensis (Dall, 1886)
Heterodonta	Veneroida		Lucinoidea	Lucinidae	Milthinae	Anodontia Link, 1807	Pegophysema Stewart, 1930	Anodontia alba Link, 1807
Heterodonta	Veneroida		Lucinoidea	Lucinidae	Divaricellinae	Divalinga Chavan, 1951		Divalinga quadrisulcata (d'Orbigny, 1842)
Heterodonta	Veneroida		Lucinoidea	Ungulinidae		Diplodonta Bronn, 1831		Diplodonta notata Dall & Simpson, 1901
Heterodonta	Veneroida		Galeommatoidea	Galeommatidae		Erycina Lamarck, 1805		Erycina periscopiana Dall, 1899
Heterodonta	Veneroida		Carditoidea	Carditidae	Carditamerinae	Pleuromeris Conrad, 1867		Pleuromeris tridentata (Say, 1826)
Heterodonta	Veneroida		Carditoidea	Condylocardiidae	Condylocardiinae	Carditopsis E. A. Smith, 1881		Carditopsis smithii (Dall, 1896)
Heterodonta	Veneroida		Crassatelloidea	Crassatellidae	Scambulinae	Crassinella Guppy, 1874		Crassinella lunulata (Conrad, 1834)
Heterodonta	Veneroida		Cardioidea	Cardiidae	Fraginae	Americardia Stewart, 1930		Americardia guppyi (Thiele, 1910)
Heterodonta	Veneroida		Cardioidea	Cardiidae	Laevicardiinae	Laevicardium Swainson, 1840		Laevicardium laevigatum (Linné, 1758)
Heterodonta	Veneroida		Tellinoidea	Tellinidae	Tellininae	Tellina Linné, 1758	Acorylus Olsson & Harbison, 1953	Tellina gouldii Hanley, 1846
Heterodonta	Veneroida		Tellinoidea	Tellinidae	Tellininae	Tellina Linné, 1758	Angulus Mühlfeld 1811	Tellina mera Say, 1834
Heterodonta	Veneroida		Tellinoidea	Tellinidae	Tellininae	Tellina Linné, 1758	Angulus Mühlfeld, 1811	Tellina sybaritica Dall, 1881
Heterodonta	Veneroida		Tellinoidea	Tellinidae	Tellininae	Tellina Linné, 1758	Merisca Dall, 1900	Tellina aequistriata Say, 1824
Heterodonta	Veneroida		Tellinoidea	Tellinidae	Tellininae	Tellina Linné, 1758	Merisca Dall, 1900	Tellina lintea Conrad, 1837
Heterodonta	Veneroida		Tellinoidea	Tellinidae	Tellininae	Tellina Linné, 1758	Scissula Dall, 1900	Tellina candeana d'Orbigny, 1842
Heterodonta	Veneroida		Tellinoidea	Tellinidae	Tellininae	Tellina Linné, 1758	Scissula Dall, 1900	Tellina similis J. Sowerby, 1806
Heterodonta	Veneroida		Tellinoidea	Tellinidae	Tellininae	Tellina Linné, 1758	Tellinella Gray, 1853	Tellina listeri Röding, 1798
Heterodonta	Veneroida		Tellinoidea	Semelidae		Semelina Dall, 1900		Semelina nuculoides (Conrad, 1841)
Heterodonta	Veneroida		Tellinoidea	Semelidae		Cumingia G. B. Sowerby I, 1833		Cumingia coarctata G. B. Sowerby I, 1833
Heterodonta	Veneroida		Tellinoidea	Semelidae		Cumingia G. B. Sowerby I, 1833		Cumingia vanhyningi Rehder, 1939
Heterodonta	Veneroida		Tellinoidea	Semelidae		Ervilia Turton, 1822		Ervilia concentrica (Holmes, 1860)
Heterodonta	Veneroida		Tellinoidea	Semelidae		Ervilia Turton, 1822		Ervilia nitens (Montagu, 1808)
Heterodonta	Veneroida		Veneroidea	Veneridae	Venerinae	Chione Mühlfeld, 1811		Chione cancellata (Linné, 1767)
Heterodonta	Veneroida		Veneroidea	Veneridae	Venerinae	Chione Mühlfeld, 1811		Chione cancellata type A
Heterodonta	Veneroida		Veneroidea	Veneridae	Venerinae	Chione Mühlfeld, 1811		Chione cancellata type B
Heterodonta	Veneroida		Veneroidea	Veneridae	Venerinae	Chione Mühlfeld, 1811		Chione sp.
Heterodonta	Veneroida		Veneroidea	Veneridae	Circinae	Gouldia C. B. Adams, 1847		Gouldia cerina (C. B. Adams, 1845)
Heterodonta	Veneroida		Veneroidea	Veneridae	Meretricinae	Transennella Dall, 1883		Transennella cubaniana (d'Orbigny, 1842)
Heterodonta	Veneroida		Veneroidea	Veneridae	Meretricinae	Transennella Dall, 1883		Transennella stimpsoni Dall, 1902
Heterodonta	Veneroida		Veneroidea	Veneridae	Pitarinae	Pitar Römer, 1857		Pitar fulminatus (Menke, 1828)
Heterodonta	Veneroida		Veneroidea	Veneridae	Pitarinae	Pitar Römer, 1857		Pitar simpsoni (Dall, 1895)

Appendix 2

1 *Modiolus americanus* (Leach, 1815), exterior of right valve, halftone; 2 *Modiolus* sp., exterior of left valve, SEM photograph; 3 *Crenella divaricata* (d'Orbigny, 1842), 3A exterior of left valve, 3B interior of right valve, SEM photographs; 4 *B. cancellaria* (Lamarck, 1819), 4A exterior of right valve, SEM photograph, 4B exterior of right valve with *Homotrema rubrum*, reflex photograph, 4C interior of right valve, SEM photograph; 5 *B. candida* (Helbling, 1779), 5A exterior of right valve, 5B interior of left valve, SEM photographs; 6 *Arcopsis adamsi* (Dall, 1886), 6A exterior of left valve, 6B interior of right valve, SEM photographs; 7 *Glycymeris pectinata* (Gmelin, 1791), exterior (7A) and interior (7B) of right valve, SEM photographs; 8 *Ctenoides scabra* (Born, 1778), exterior (8A) and interior (8B) of left valve, SEM photographs; 9 *Argopecten nucleus* (Born, 1778), exterior of right (9A) and left valve (9B), SEM photographs; 10 *Lindapecten exasperatus* (G. B. Sowerby II, 1842), exterior of right (10A) and left valve (10B), interior of right (10C) and left valve (10D), reflex photographs; 11 *Chama macerophylla* Gmelin, 1791, exterior of right valve, SEM photograph; 12 *Lucina beliziana* J. D. Taylor, 1998, 12A exterior of right valve, 12B interior of left valve, SEM photographs; 13 *Codakia orbicularis* (Linné, 1758), exterior (13A) and interior (13B) of left valve, SEM photographs; 14 *Codakia orbiculata* (Montagu, 1808), 14A exterior of right valve, 14B interior of left valve, SEM photographs; 15 *Parvilucina costata* (d'Orbigny, 1842), exterior (15A) and interior (15B) of right valve, SEM photographs; 16 *Parvilucina* sp. A, 16A exterior of right valve, 16B interior of right valve with *Oichnus* isp., 16C interior of left valve, SEM photographs; 17 *Here sombrerensis* (Dall, 1886), 17A exterior of right valve, 17B interior of right valve, fragmented, SEM photographs; 18 *Anodontia alba* Link, 1807, 18A exterior of left valve, 18B interior of right valve with *Oichnus* isp., SEM photographs; 19 *Divalinga quadrisulcata* (d'Orbigny, 1842), exterior (19A) and interior (19B) of right valve, 19C interior of left valve, fragmented, SEM photographs; 20 *Diplodonta notata* Dall and Simpson, 1901, 20A exterior of left valve with *Oichnus paraboloides*, 20B interior of right valve, SEM photographs; 21 *Erycina periscopiana* Dall, 1899, exterior (21A) and interior (21B) of right valve, 21C interior of left valve, SEM photographs; 22 *Pleuromeris tridentata* (Say, 1826), exterior of right valve, halftone; 23 *Carditopsis smithii* (Dall, 1896), exterior of right (23A) and left valve (23B), interior of right (23C) and left valve (23D), SEM photographs; 24 *Crassinella lunulata* (Conrad, 1834), exterior (24A) and interior (24B) of right valve, 24C interior of left valve, SEM photographs; 25 *Americardia guppyi* (Thiele, 1910), exterior (25A) and interior (25B) of right valve, 25C interior of left valve, SEM photographs; 26 *Laevicardium laevigatum* (Linné, 1758), 26A exterior of left valve, interior of right (26B) and left valve (26C), SEM photographs; 27 *Tellina gouldii* Hanley, 1846, 27A exterior of left valve, interior of right (27B) and left valve (27C), SEM photographs; 28 *Tellina mera* Say, 1834, exterior (28A) and interior (28B) of right valve, 28C interior of left valve, SEM photographs; 29 *Tellina sybaritica* Dall, 1881, 29A exterior of right valve, 29B articulated preservation, interior views, SEM photographs; 30 *Tellina aequistriata* Say, 1824, 30A exterior of left valve with *Oichnus paraboloides*, 30B interior of right valve with algal growth, SEM photographs; 31 *Tellina lintea* Conrad, 1837, exterior (31A) and interior (31B) of right valve, 31C interior of left valve with *Oichnus* isp., SEM photograph; 32 *Tellina candeana* d'Orbigny, 1842, articulated preservation, exterior (32A) and interior views (32B), SEM photographs; 33 *Tellina similis* J. Sowerby, 1806, articulated preservation, exterior (33A) and interior views (33B), SEM photographs; 34 *Tellina listeri* Röding, 1798, 34A exterior of left valve, interior of right (34B) and left valve (34C), SEM photographs; 35 *Semelina nuculoides* (Conrad, 1841), exterior of right valve, halftone; 36 *Cumingia coarctata* G. B. Sowerby I, 1833, 36A exterior of left valve, 36B interior of right valve, SEM photographs; 37 *Cumingia vanhyningi* Rehder, 1939, 37A exterior of left valve, interior of right (37B) and left valve (37C), SEM photographs; 38 *Ervilia concentrica* (Holmes, 1860), exterior (38A) and interior (38B) of right valve, 38C interior of left valve, SEM photographs; 39 *Ervilia nitens* (Montagu, 1808), 39A exterior of left valve, interior of right (39B) and left valve (39C), SEM photographs; 40 *Chione cancellata* type A, exterior (40A) and interior (40B) of right valve, 40C interior of left valve, SEM photographs; 41 *Chione cancellata* type B, exterior (41A) and interior (41B) of right valve, 41C interior of left valve, SEM photographs; 42 *Chione* sp., 42A exterior of left valve, interior of right (42B) and left valve (42C), SEM photographs; 43 *Gouldia cerina* (C. B. Adams, 1845), 43A exterior of left valve, 43B interior of right valve with *Oichnus* isp., SEM photographs; 44 *Transennella cubaniana* (d'Orbigny, 1842), exterior of left valve, SEM photograph; 45 *Transennella stimpsoni* Dall, 1902, exterior of left valve, SEM photograph; 46 *Pitar fulminatus* (Menke, 1828), 46A exterior of right valve, 46B interior of left valve, SEM photographs; 47 *Pitar simpsoni* (Dall, 1895), exterior of left valve, SEM photograph
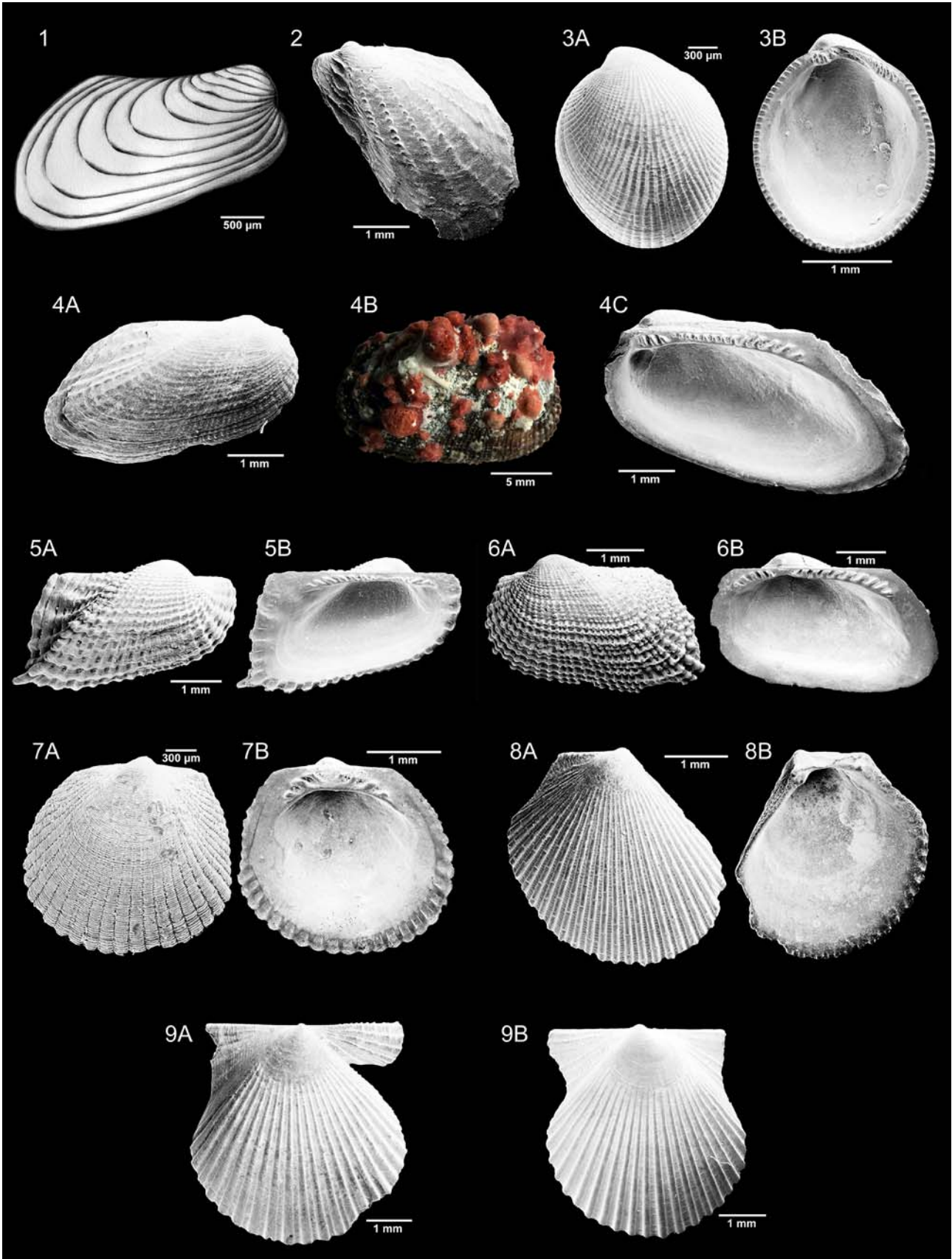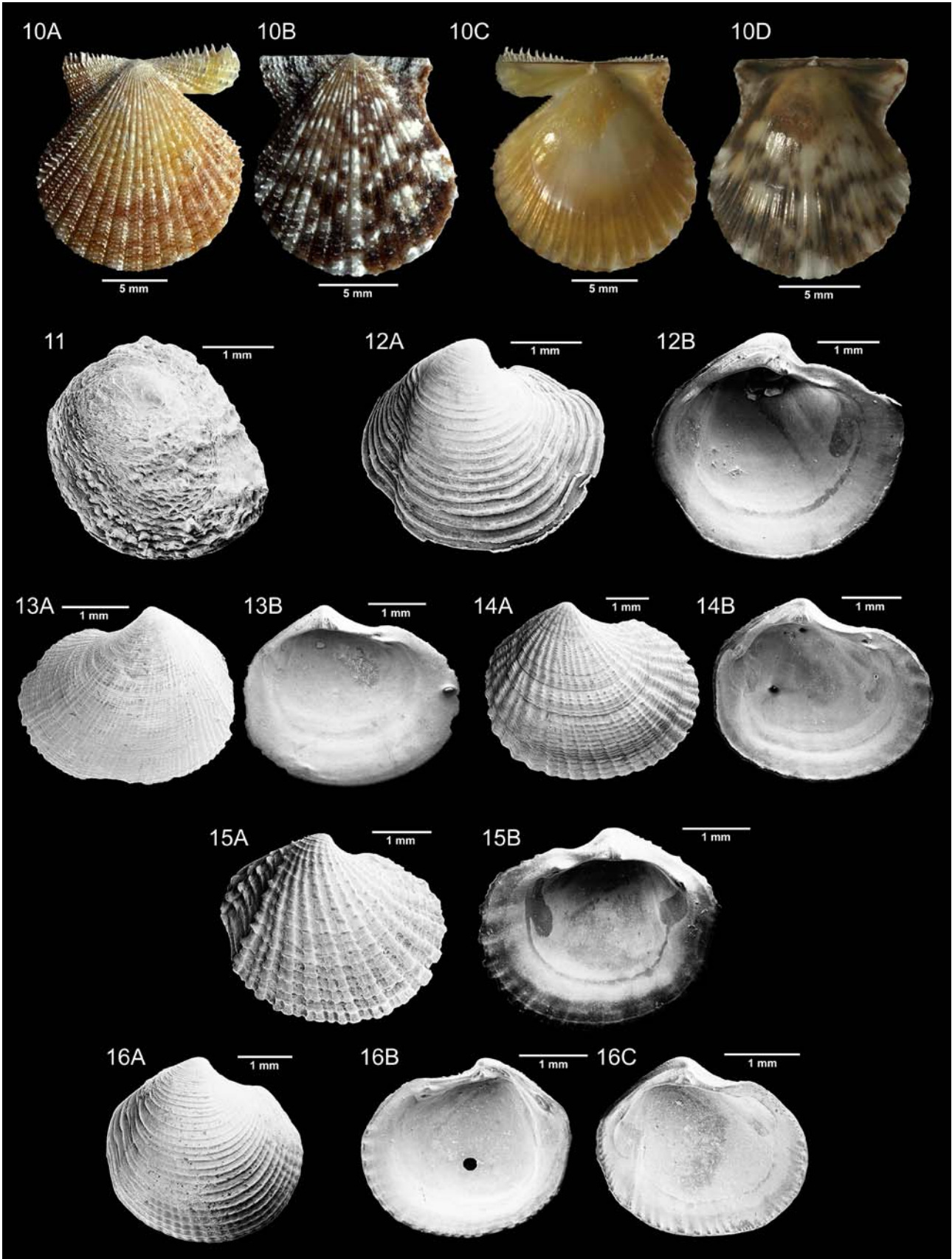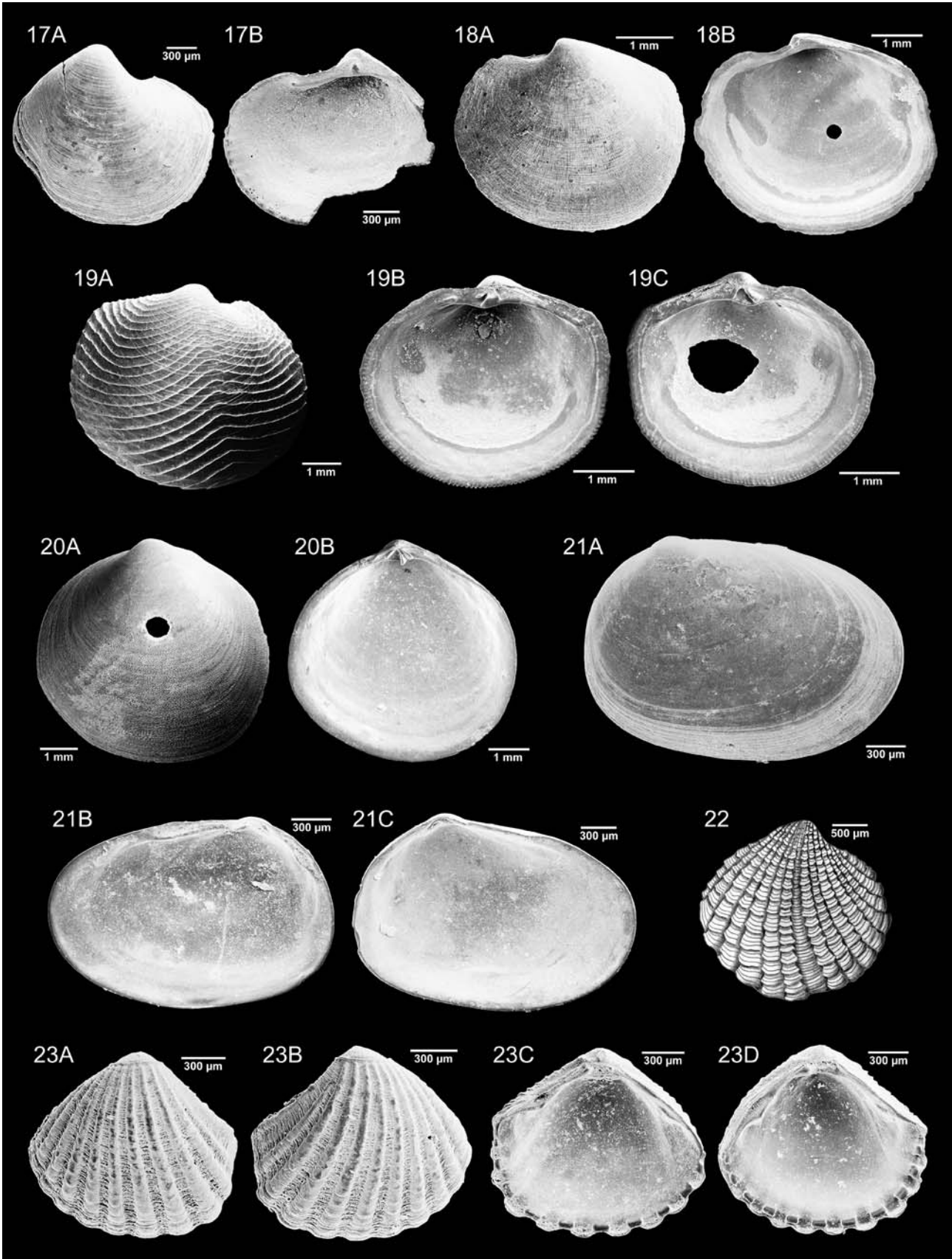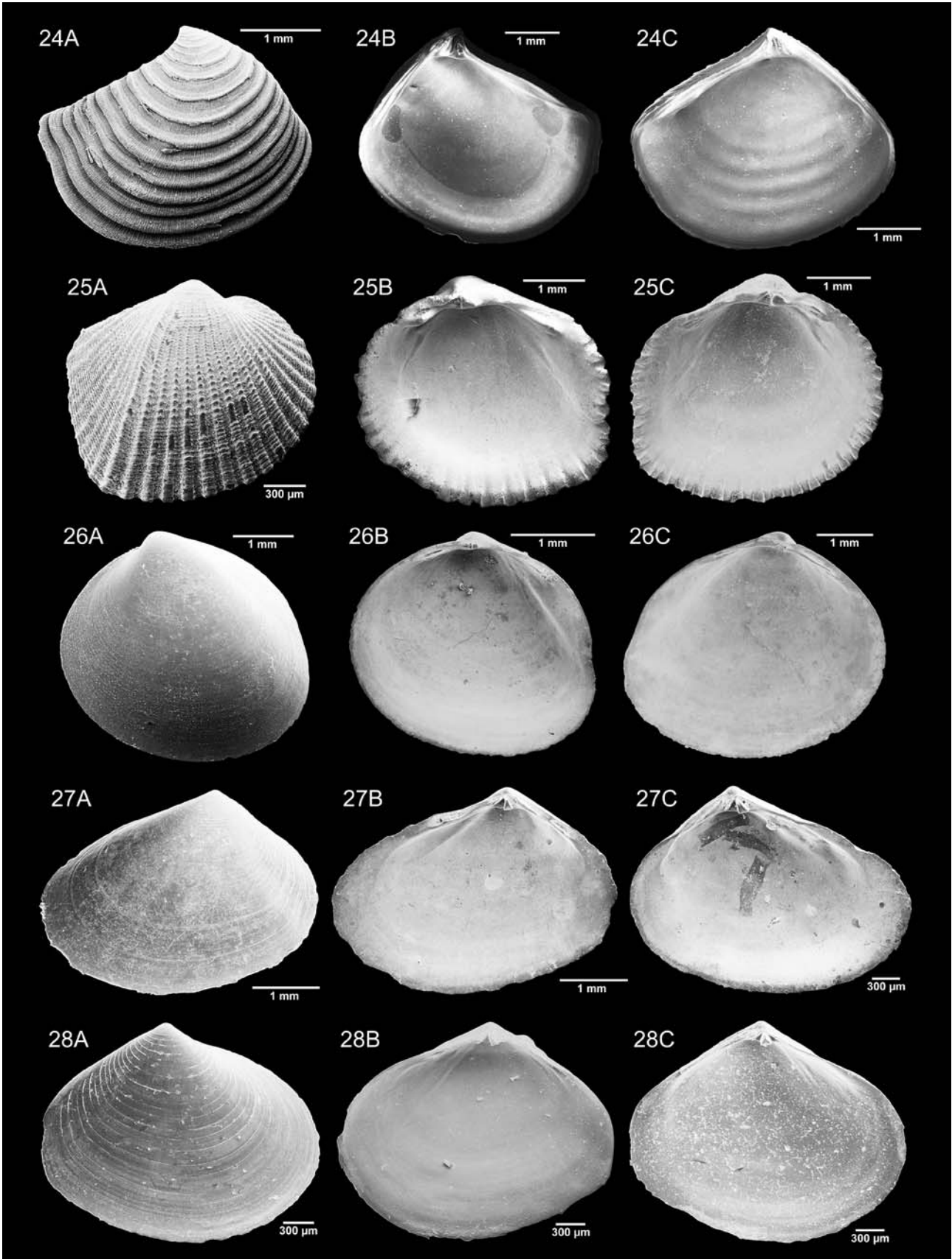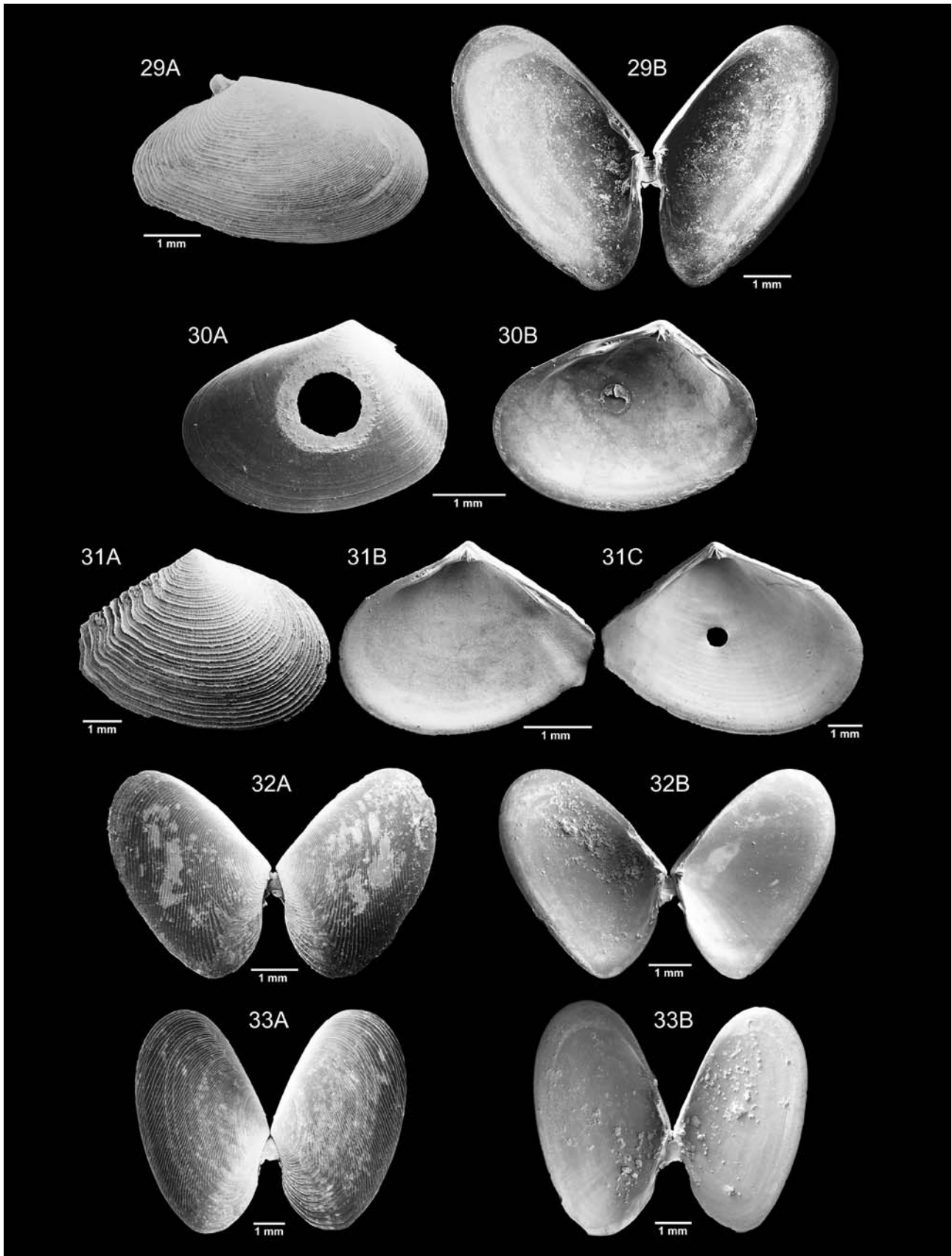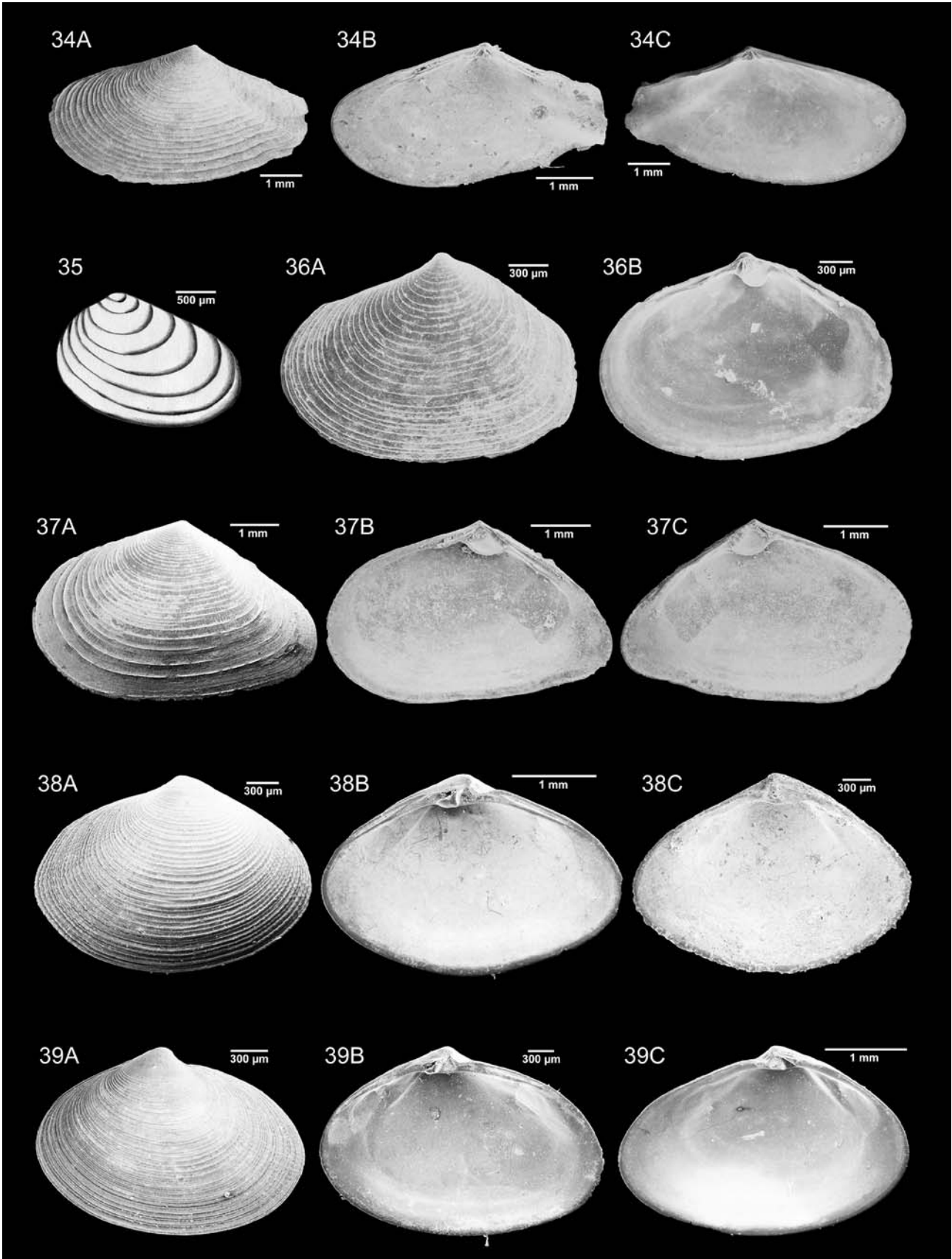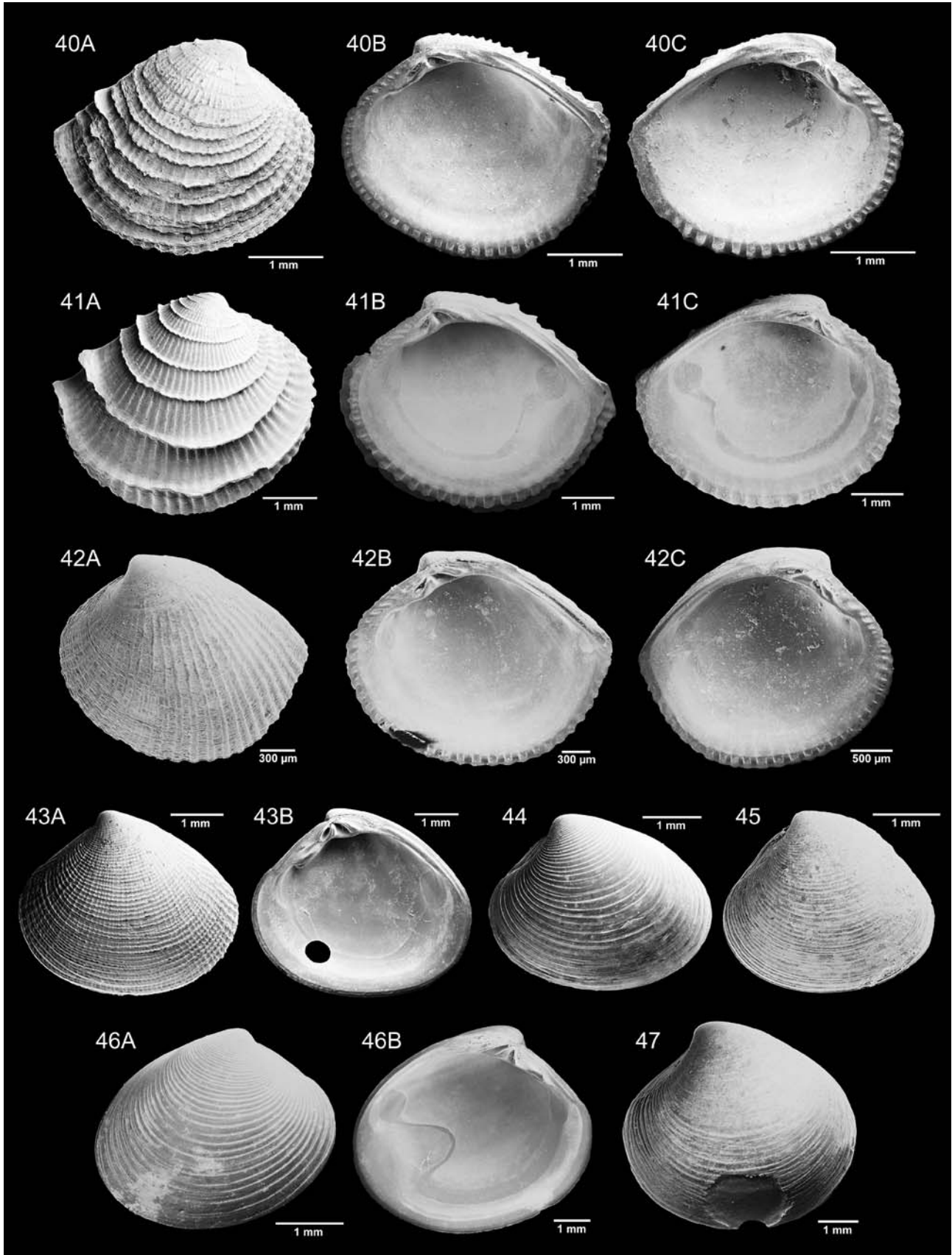
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