Constructional morphology of cerithiform gastropods

Authors: SÄLGEBACK, JENNY, and SAVAZZI, ENRICO

Source: Paleontological Research, 10(3) : 233-259

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/prpsj.10.233

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Paleontological-Research on 15 Jul 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Paleontological Research, vol. 10, no. 3, pp. 233–259, September 30, 2006

Constructional morphology of cerithiform gastropods

JENNY SÄLGEBACK[1] AND ENRICO SAVAZZI[2]

[1]*Department of Earth Sciences, Uppsala University, Norbyvägen 22, 75236 Uppsala, Sweden*

[2]*Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, 10405 Stockholm, Sweden. Present address: The Kyoto University Museum, Yoshida Honmachi, Sakyo-ku, Kyoto 606-8501, Japan (email: enrico5@savazzi.net)*

Received December 19, 2005; Revised manuscript accepted May 26, 2006

Abstract. Cerithiform gastropods possess high-spired shells with small apertures, anterior canals or sinuses, and usually one or more spiral rows of tubercles, spines or nodes. This shell morphology occurs mostly within the superfamily Cerithioidea. Several morphologic characters of cerithiform shells are adaptive within five broad functional areas: (1) defence from shell-peeling predators (external sculpture, preadult internal barriers, preadult varices, adult aperture) (2) burrowing and infaunal life (burrowing sculptures, bent and elongated inhalant adult siphon, plough-like adult outer lip, flattened dorsal region of last whorl), (3) clamping of the aperture onto a solid substrate (broad tangential adult aperture), (4) stabilisation of the shell when epifaunal (broad adult outer lip and at least three types of swellings located on the left ventrolateral side of the last whorl in the adult stage), and (5) righting after accidental overturning (projecting dorsal tubercles or varix on the last or penultimate whorl, in one instance accompanied by hollow ventral tubercles that are removed by abrasion against the substrate in the adult stage). Most of these characters are made feasible by determinate growth and a countdown ontogenetic programme. These varied adaptations often have evolved independently among different taxonomic groups of cerithiforms, and multiple times within the same group.

Key words: Gastropoda, Cerithioidea, cerithiform, functional morphology, ontogeny, evolution, shell, epifaunal, infaunal

Introduction

Gastropods are among the most common shell-bearing invertebrates in shallow-water environments, but the adaptive features of gastropod shells have not been studied to the same extent as those of other invertebrates (e.g., the Bivalvia; see discussion in Stanley, 1970; Savazzi, 1989a, 1994a, 1994b, and references therein). Nonetheless, the literature shows that gastropod shells are amenable to this type of investigation (e.g., Vermeij, 1971, 1979, 1981, 1993, 2001; Palmer, 1977, 1979; Linsley, 1978; Kohn *et al.*, 1979; Bertness and Cunningham, 1981; Signor, 1982a, 1982b, 1983, 1994; Savazzi, 1988, 1989a, 1989b, 1991a, 1991b, 1994a, 1994b, 1996, 1999a; Paul, 1991; Donovan *et al.*, 1999; Kohn, 1999; Savazzi and Sasaki, 2004). Studies that compare the functional morphology of the shell within a broad range of gastropods and of functions are especially infrequent.

The present study aims at surveying the morphologic adaptations of the shell in representatives of the Cerithioidea, as well as selected taxa in the past included in this superfamily but at present placed in separate superfamilies. The common features of these forms are a high-spired, regularly coiled shell with a small aperture not markedly elongated in the antero-posterior direction, a well-developed anterior canal, sinus or notch, and often strong spiral rows of knobs and tubercles, or axial ridges. Within the Cerithioidea in a traditional sense (e.g., see Wenz, 1940), this morphology is characteristic of the Cerithiidae, but is widespread also among taxa at present placed in the Procerithiidae, Potamididae, Diastomidae, Cerithiopsidae, Campanilidae, Thiaridae, Melanopsidae and other families.

Rather than restricting this study to the Cerithiidae, which would exclude at least half of these shell shapes, or expand it to the Cerithioidea, which would include a variety of other shell geometries but still leave out several taxa of potential interest, we prefer to concentrate on all taxa possessing the shell geometry in question, irrespective of their current taxonomic placement. In the lack of a suitable taxonomic grouping, we use the morphologic term *cerithiform*, by which we denote gastropods that are similar in shell shape to the cerithiid genus *Cerithium* (see below). We give this term no taxonomic connotation.

Other families historically or presently included within the Cerithioidea are substantially different from cerithiforms in one or more respects. For instance, the Turritellidae and Mathildidae usually lack a well defined anterior canal and a specialised adult aperture, are suspension feeders and tend to be sedentary or sessile (Alastair, 1938; Yonge, 1946; Morton, 1953; Andrews, 1974; Savazzi, 1996, 1999a, and references therein). The Planaxidae are less high-spired than the large majority of cerithiforms. The Vermetidae and Siliquariidae are sessile and uncoiled or irregularly coiled (Savazzi, 1996, 1999a, and references therein). The Architectonicidae possess very short-spired shells.

The morphologic term turritelliform was used by Signor (1982a, 1982b, 1982c, 1983, 1994; Savazzi *et al.*, 1982) to denote high-spired gastropods in a broader sense than our definition of cerithiform and including representatives of the Cerithiidae, Turritellidae, Terebridae and other families. Therefore, this term is not suited to the scope of our study.

This paper discusses the morphologic features of the cerithiform shell within the conceptual framework of constructional morphology (*sensu* Seilacher, 1970; see also Schmidt-Kittler and Vogel, 1991; Seilacher and Chinzei, 1993; Savazzi, 1999b). Studies of constructional morphology almost invariably profit from the comparison of taxonomically unrelated but morphologically comparable organisms (cf. Savazzi, 1999b). Thus, adaptations of the cerithiform shell are compared with morphologically comparable characters in other taxa. It may be noted that the subject of the present study is in itself of a comparative nature, given that our definition of cerithiform shells encompasses several families currently placed in a few separate superfamilies (see below), which provide the possibility of comparing the results of independent evolution.

Material and methods

Field and laboratory observations on living cerithiforms were carried out by both authors in Iriomote Island, Japan, in May 2004. J. Sälgeback carried out observations in Port Hacking, New South Wales, Australia, in 2003. E. Savazzi carried out observations in NE Italy in 1981 and 1987, in Cebu Island and nearby islands, the Philippines, at several times between 1987 and 1990, near Xiamen, People's Republic of China, in 1991 and near Shizuoka, Japan, in 2004. Localities and environments for each of the observed species are given in the following section.

The repositories of material studied in collections are abbreviated as follows in the Figure captions: UMUT: University Museum, University of Tokyo, Japan. NSM: National Science Museum, Tokyo, Japan. NHM: Natural History Museum, London, UK. SMNH: Swedish Museum of Natural History, Stockholm, Sweden. MNHN: Muséum National d'Histoire Naturelle, Paris, France. Inventory numbers are specified if available. Repositories of illustrated material stored at other locations are spelled out in full in the Figure captions. Material the repository of which is not indicated is in the possession of the authors.

Taxonomic summary

The following table lists the taxonomic position of the cerithiform families and genera discussed in the present paper (with the exception of a few taxa only mentioned in passing). This taxonomic outline follows Healy and Wells (1998a, 1998b), with additions for other taxa (e.g., Houbrick, 1978, 1986, 1992; Kiel, unpublished; Kiel *et al.*, 2000). Our placement of a few Palaeogene genera (e.g., *Bezanconia*, *Bellatara*, *Serratocerithium*) may be questionable. Superfamilies are not included in this summary. The Triforidae are cerithiform, but we exclude them from this study because we do not have sufficient data to assess their functional morphology.

Family Cerithiidae, Subfamily Cerithiinae, Genera *Cerithium*, *Clypeomorus*, *Colina*, *Rhinoclavis*, *Ochetoclava*, *Pseudovertagus*, *Bezanconia*, *Bellatara*, *Gourmya*, *Cerithioclava*

Subfamily Bittiinae, Genus *Bittium*

Family Procerithiidae, Genera *Rhabdocolpus*, *Diatinostoma*, *Cryptaulax*, *Rhynchocerithium*, *Exelissa*

Family Diastomatidae, Genus *Diastoma*

Family Batillariidae, Genera *Batillaria*, *Rhinocoryne*, *Pyrazus*

Family Potamididae, Genera *Potamides*, *Tympanotonus*, *Cerithideopsilla*, *Telescopium*, *Terebralia*, *Serratocerithium*, *Vicarya*

Family Thiaridae, Genera *Faunus*, *Pseudobellardia*

Family Campanilidae, Genera *Campanile*, *Metacerithium*

Family Cerithiopsidae, Genus *Cerithiopsis*

Observations on life habits and behaviour

Cerithium nodulosum (Bruguière)

Locality. Cebu Island, the Philippines. *Environment*. On gravel, coral rubble and stone rubble. *Behaviour*. Always epifaunal, preferentially on hard substrates, sometimes leaving a trail on gravel, but not truly ploughing through the sediment.

***Cerithium vulgatum* (Bruguière)**

Locality. Sea coast in localities along the islands enclosing the lagoon of Venice, NE Italy, and surrounding areas. *Environment*. Preferentially found in artificial intertidal and shallow subtidal rock pools sheltered from direct waves, less commonly on rock piers. *Behaviour*. Always epifaunal on rock surfaces. *Notes*. This species is alternatively placed in *Cerithium* or *Thericium*.

***Cerithium echinatum* Lamarck**

Locality. Iriomote Island, Japan. *Environment*. Beaches and back-reef, on stones and coral rubble. *Behaviour*. Always seen adhering by the foot to a solid substrate.

***Clypeomorus petrosa chemnitziana* (Pilsbry)**

Locality. Iriomote Island, Japan. *Environment*. Sandy sea shore, intertidal on clean coarse foraminiferan sand. *Behaviour*. Always epifaunal, slightly ploughing through the top layer of sediment and leaving a trail.

***Clypeomorus irrorata* (Gould)**

Locality. Iriomote Island, Japan. *Environment*. Rocky shores, intertidal on rock surfaces and stone rubble. *Behaviour*. This species shows a preference for solid substrates.

***Clypeomorus pellucida* (Hambron and Jacquinot)**

Locality. Iriomote Island, Japan. *Environment*. Tidal flat at river mouth, near mangroves, on muddy sand. *Behaviour*. Crawling on the sand surface. The foot and head move gradually forward to a point where they begin to project from beneath the shell. Simultaneously, the anterior portion of the shell lowers itself toward the substrate and the ventrolateral varix (see below) comes to rest on the surface of the sediment. The shell is subsequently pulled forward and upward, with the aperture coming to lay directly above the foot and head. At this point, the shell touches the sediment only in correspondence of its central ventral surfaces. The apex remains slightly lifted from the sediment.

***Clypeomorus subbrevicula* (Oostingh)**

Locality. Iriomote Island, Japan. *Environment*. Tidal flat at river mouth, near mangroves, on rock rubble and muddy sand. *Behaviour*. Both adhering to rock surfaces and crawling on soft sediment at low tide.

***Rhinoclavis vertagus* (Bruguière)**

Localities. Iriomote Island, Japan, Bantayan Island, the Philippines, and several localities along the eastern coast of Cebu Island, the Philippines. *Environments*. sandy shores, intertidal or shallow subtidal. The sediment ranges from medium to coarse, clean biogenic sand. *Ecological notes*. Most specimens collected in Iriomote Island carried a small anemone attached to the dorsal region of the shell immediately posterior to the inhalant siphon. A dark patch on the shell periostracum marks the attachment region of the anemone, which suggests that the latter spent a substantial amount of time attached to the same area. Occasional individuals without anemone, with two anemones, or with a single anemone on the dorsal central region of the shell were also observed. *Behaviour*. Most specimens in Bantayan Island, N of Cebu Island, the Philippines, were ploughing semi-infaunally and leaving a deep trail. In Iriomote Island, Japan, this species was almost always infaunal. Adult specimens (4–6 cm long) plough by periodically dragging the shell forward in "steps" of 5–8 mm, while the foot appears to move forward at a steady rate. Ploughing is a behaviour separate from epifaunal creeping, which takes place with the foot exposed at the surface of the sediment or slightly buried, and produces a shallower trail. *R. vertagus* is capable of both types of locomotion on the same sediment. Surface creeping is generally used to cover short distances (from 0.1 to 0.5 m). Unlike creeping, ploughing is usually accompanied by continuous probing movements of the proboscis (this term is used herein in a general morphological sense rather than anatomical/phylogenetic, because Simone (2001) argued that cerithioids do not possess a true proboscis).

The burrowing process is characterised by several differences with ploughing:

(1) The foot is buried deeper within the sediment (10–15 mm below the shell aperture, as observed in specimens burrowing alongside the aquarium glass).

(2) The head is lifted upward each time the shell is about to be dragged forward. This forms a cavity in the sediment ahead of the shell, and allows its movement forward.

(3) Burrowing is much slower than ploughing, and after an initial phase the shell is completely covered by sediment, and the organism continues to burrow in a horizontal direction.

In the laboratory, *R. vertagus* from Iriomote Island begins burrowing by extending the foot obliquely downward and to the right, anchors it within the sediment, then pulls the shell downward and rotates it so that the siphon points upwards. The first 3–4 burrowing sequences (cf. Trueman and Ansell, 1969, Seilacher, 1982) are accompanied by sideways rocking, which causes the shell apex to move in the left direction. Afterwards, the shell penetrates forward and obliquely downward with each sequence, without rocking. No backslippage was visible at any stage during the burrowing process. The burrowing process from its beginning to the point when the shell is completely covered with sediment takes 9–16 burrowing sequences and approximately 6 minutes.

Rhinoclavis sinensis (Gmelin)

Localities. Iriomote Island, Japan, several localities along the eastern coast of Cebu Island, the Philippines, and Xiamen, People's Republic of China. *Environments*. Sandy shores, intertidal on clean coarse biogenic sand. *Behaviour. R. sinensis* burrows in a way comparable to *R. vertagus*, but without rocking laterally. The siphon is held vertical. There is no visible backslippage during the burrowing process. Unlike in other species of *Rhinoclavis*, the dorsal region of adult *R. sinensis* often remains exposed, and often is marked by a patch of partially abraded periostracum and/or covered by algal filaments. *Notes*. The behaviour of this species is not noticeably different among localities, but the coarseness of its sculpture is much variable.

Rhinoclavis kochi (Philippi)

Localities. Tayud (eastern coast of Cebu Island, the Philippines) and Ibo (Mactan Island, the Philippines. *Environment*. Intertidal banks of clean, coarse biogenic sand. *Behaviour*. Essentially identical to *R. sinensis*.

Rhinoclavis aspera (Linnaeus)

Locality. Iriomote Island, Japan. *Environment*. Sandy shores, burrowing in clean coarse sand. *Behaviour*. The burrowing process is comparable to that of *R. sinensis* and *R. vertagus*. There is no observable rocking or backslipping.

Pseudovertagus aluco (Linnaeus)

Localities. several localities along the eastern coast of Cebu Island, the Philippines. *Environment*. Tidal flats, on clean, very coarse biogenic sand and coral rubble. *Behaviour. P. aluco* is typically epifaunal or semi-infaunal. Often it extends its proboscis and foot deep into the sediment and expands the foot in a way that suggests anchoring it within the sediment. However, it only ploughs through the sediment in a semi-infaunal position, rather than burrowing below its surface. It is slower than *Rhinoclavis*. Living specimens in the field possess an algal coating on the dorsal and lateral regions of the posterior half of the shell that is absent on the sides of the anterior half of the shell. This suggests that the organism typically is semi-infaunal in the field.

Bittium reticulatum (Da Costa)

Locality. NE Italy, near the southern tip of the Venice Lagoon, Italy. *Environment*. intertidal and shallow subtidal on fine sand in a large, slightly brackish lagoon (see Savazzi, 1989a). *Behaviour. Bittium reticulatum* burrows inclined 10–15° forward, rocking the shell about its coiling axis. No backslipping was observed. Burrowing takes 10–15 minutes and 20–30 burrowing sequences or more. Surface locomotion is by periodic dragging of the shell, without rocking.

Batillaria zonalis (Bruguière)

Locality. Iriomote Island, Japan. *Environment*. Estuarine intertidal flats near mangrove swamps, on muddy sand. *Behaviour*. At low tide, it congregates in large clusters on the surface of the sediment, often near the edge of the water or of tidal pools.

Batillaria multiformis (Lischke)

Locality. Hamana Lake, Shizuoka Prefecture, Japan. *Environment*. brackish water, intertidal on muddy sand along the sides of channels. *Behaviour. B. multiformis* is shallowly buried in sand at high tide, and emerges to feed when the bottom is exposed subaerially at low tide. It drags the shell on the surface of the sand, leaving a shallow, irregularly meandering track. It tends to congregate in clusters of tens to hundreds of individuals not far from the water line.

Pyrazus ebeninus (Bruguière)

Locality. Port Hacking, New South Wales, Australia. *Environment*. Tidal flat near mangroves, on muddy sand. *Behaviour*. Moving on the surface of the sediment at low tide, leaving a trail behind the shell.

Cerithideopsilla cingulata (Gmelin)

Localities. Iriomote Island, Japan, and Xiamen, People's Republic of China. *Environments*. Upper portion of tidal flats near mangrove swamps in Iriomote Island, on coarse muddy sand, and upper portion of tidal flats in a lagoon delimited by landfills near Xiamen, on muddy silt and muddy sand. *Behaviour*. Epifaunal on soft sediments at low tide.

Telescopium telescopium (Linnaeus)

Locality. Consolacion, Cebu Island, the Philippines. *Environment*. Intertidal mud flats near mangrove roots, as well as in localities in which mangroves were present until cleared out artificially in the recent past. *Behaviour*. Epifaunal in the field, leaving a deep trail on soft sediment. *T. telescopium* is capable of climbing aquarium walls. However, in tanks it was observed to spend most of the time on native sediment, with its foot shallowly buried, either immobile or ploughing semi-infaunally. Small individuals (25–35 mm) plough with the dorsal regions of the shell horizontal and level with the surrounding sediments, and most of their shell surfaces are covered by sediment. Intermediate specimens are buried to about half of the diameter of the last whorl, while the largest observed individuals (50–60 mm) lie mostly above the surface of the sediment. Ploughing is much slower than burrowing in *Rhinoclavis* (see above), and often alternates with immobility.

Terebralia palustris (Linnaeus)

Locality. Iriomote Island, Japan. *Environment*. Between the roots of mangroves and at the edge of mangrove thickets, occasionally on tidal flats near mangroves. *Behaviour*. It occurs in large numbers in the thickest portions of the vegetation. At low tide it lays immobile and exposed to the air in the shadow. During surface locomotion, it gradually extends the foot and head in the forward direction, approximately to a point directly below the anterior siphon, and at this point pulls the shell forward and upward with a rapid movement. The apex and posterior region of the shell are not lifted and glide on the surface of the substrate, contributing to the formation of a rather deep furrow. During locomotion, *T. palustris* performs side-to side flexing of the proboscis, which suggests sensory probing.

Terebralia sulcata (Born)

Locality. Cebu Island, the Philippines. *Environment*. Brackish water, on stones and mangrove roots. *Behaviour*. This species prefers solid substrates. When placed in tanks with sand or muddy sand at the bottom, it moved quickly to the walls or other solid objects, and was never observed to abandon them afterwards.

Observations on shell morphology

Traces of predation

Several live-collected individuals of *Rhinoclavis* display evident repaired damage by peeling crabs (Figures 1A–E). A few species of the brachyuran crab *Calappa* were observed in the collection localities in the Philippines, and are a likely candidate as the origin of this damage. *Calappa* often probes the sediment with the tip of its chelae (E. Savazzi, pers. obs.), so this type of damage can be expected in both epifaunal and shallow-infaunal gastropods. Essentially identical sublethal damage is common in small to medium-sized cerithiforms since the Eocene (Figures 1F–G).

Naticid boreholes are frequent in empty shells of Recent *Rhinoclavis* (Figure 1H). This agrees well with

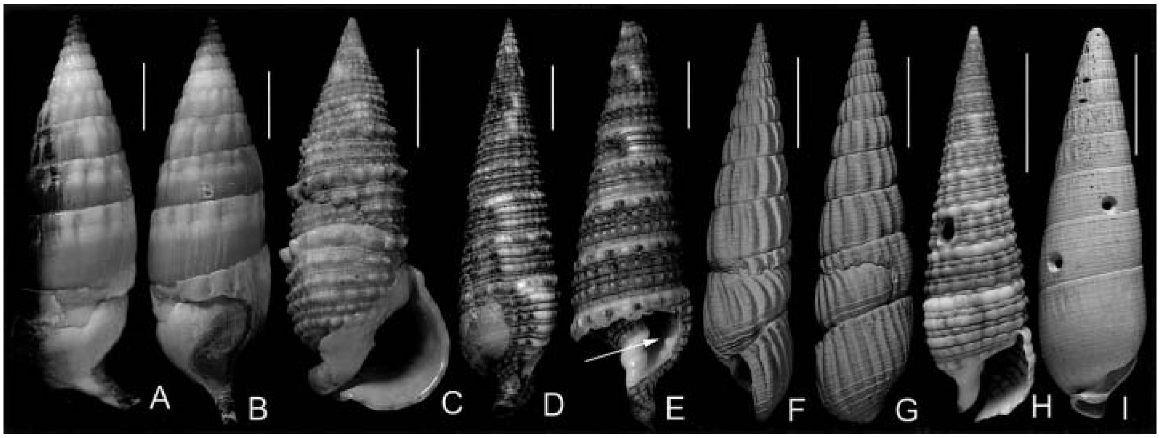

Figure 1. Traces of predation. Sublethal (A–G; E was alive when collected) damage by peeling crabs, and probably lethal damage by naticid gastropods (H–I). **A–B.** *Rhinoclavis vertagus*, Recent, Iriomote Island, Japan. **C.** *Rhinoclavis sinensis*, Recent, Iriomote Island, Japan. **D–E, H.** *R. kochi*, Recent, Tayud, Cebu Island, the Philippines. Arrow indicates the internal barrier. **F–G.** *Diastoma costellatum*, Middle Eocene, Grignon, Paris Basin, France (NHM 32070-1). **I.** *Semivertagus striatus*, Middle Eocene, Chambors, Paris Basin, France (NHM 3251). Scale bars represent 10 mm.

its infaunal habits described above. The Recent *Cerithium salebrosum* and *C. tenellum* are infaunal in soft sediments and are often bored by naticids (Houbrick, 1992). Naticid boreholes are also frequent in a few cerithiforms from the Eocene of the Paris Basin. In particular, *Semivertagus* shells frequently displays naticid boreholes (Figure 1I).

General shell morphology

Cerithiform shells are medium- to high-spired, with an anterior siphon or notch. The aperture is round to slightly elongated antero-posteriorly. The external sculpture ranges from essentially smooth to coarse knobs, ridges and tubercles. A spiral component of the sculpture is very frequent, and consists of prominent lines and/or ridges, often changing in strength among adjacent ridges. Frequently, there is also a periodic component to the sculptures, consisting of knobs and/or axial or collabral ridges. Often, one of the posteriormost spiral ridges or lines of tubercles (i.e., located in proximity of the suture) and/or one or more spiral lines located at the anterior shoulder of the whorl (i.e., in correspondence to the suture of the following whorl) are especially well developed.

Typically, spiral threads uninterrupted by beads or tubercles, like those of turritellids, are absent. The largest cerithiforms tend to possess a single row of rounded knobs or axial or oblique folds, rather than multiple sets of spiral features. A few completely or largely smooth cerithiforms also occur, especially among large species.

The sculpture of cerithiform shells (especially in the Cerithiidae, Potamididae and Batillariidae) often displays an extreme amount of intraspecific variability, which has complicated taxonomic studies (e.g., see Houbrick, 1978, 1981).

Cerithiidae

Cerithium (Figure 2) and *Clypeomorus* (Figure 3) possess anterior siphons straight or slightly bent dorsally, and often strong nodes, tubercles or ribs. The adult outer lip is usually flared and thickened, and

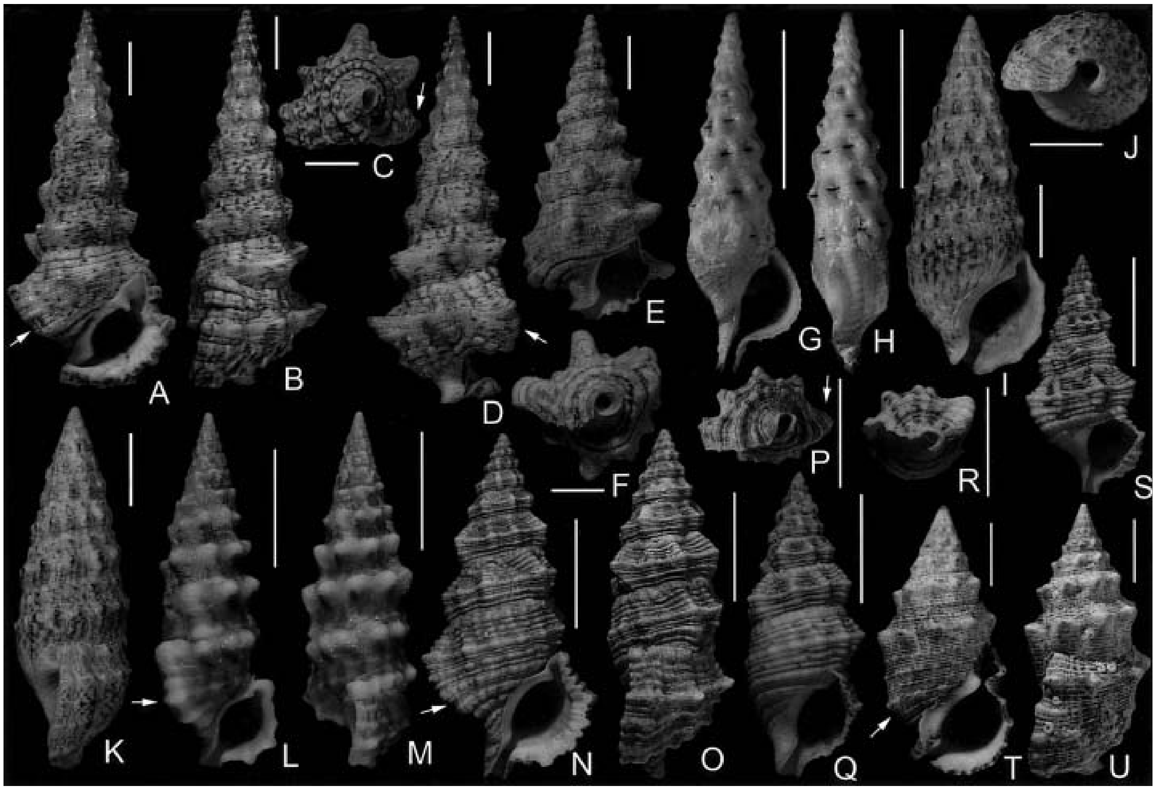

Figure 2. Recent *Cerithium*. Arrows indicate the ventrolateral swelling or varix. **A–F.** *C. nodulosum*, Indo-Pacific (UMUT). Adult (A–D) and subadult (E–F). **G–H.** *C. rostratum*, Mactan Island, the Philippines. **I–K.** *C. vulgatum*, sea-side coast of lagoon islands, Venice, Italy. **L–M.** *Cerithium munitum*, Mactan Island, the Philippines. **N–S.** *C. echinatum*, Iriomote Island, Japan. Adult (N–P) and subadults (Q–S). **T–U.** *C. adustum*, Gulf of California, Mexico (NRM). Scale bars represent 10 mm.

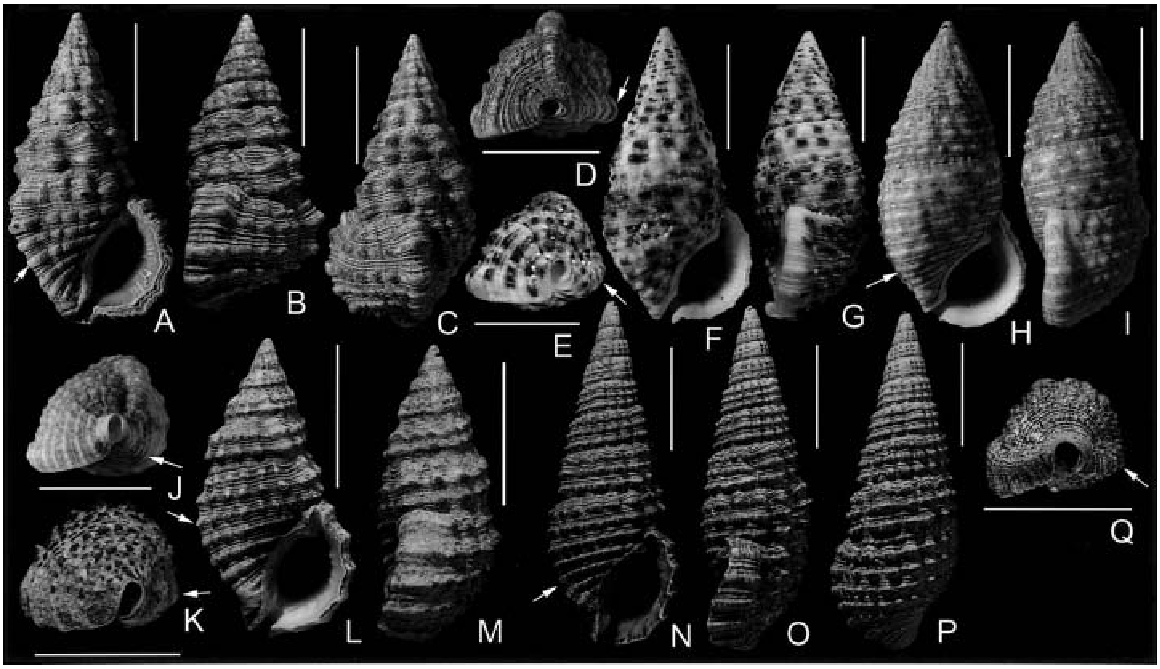

Figure 3. Recent *Clypeomorus*, Iriomote Island, Japan. Arrows indicate the ventrolateral swelling or varix. **A–D.** *C. bifasciata*. **E–G.** *C. brevis*. **H–J.** *C. petrosa*. **K–M.** *C. subbrevicula*. **N–Q.** *C. pellucida*. Scale bars represent 10 mm.

the aperture orthocline to opisthocline. This general morphology is found also in other taxa, e.g., *Colina* (Figure 4) (which, however, is much smaller).

Several representatives of all three genera possess a varix or swelling (hereby referred to as *ventrolateral*) on the left side of the ventral region of the last whorl (arrows in Figures 2–4). Recent species of *Clypeomorus* differ widely in the position of the penultimate varix with respect to the adult aperture (which constitutes the last varix):

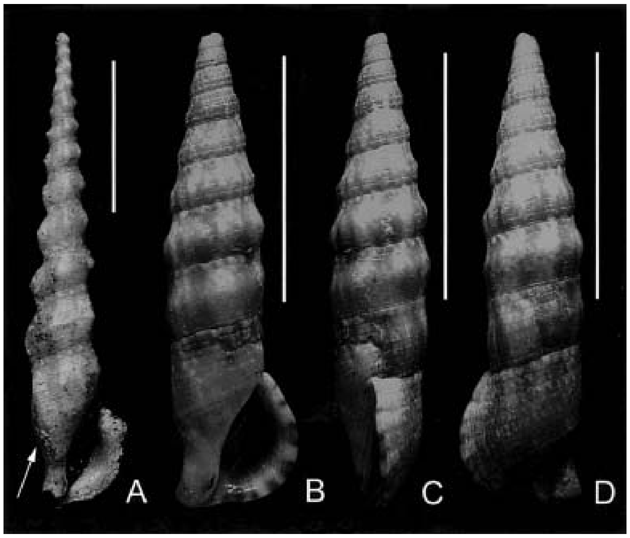

Figure 4. **A.** *Colina* sp., Eocene, Cava Albanello, Vicenza, Italy (Cracco private collection, Vicenza, Italy). Arrow indicates the ventrolateral swelling. **B–D.** *C. macrostoma*, Recent, Indo-Pacific (UMUT). Scale bars represent 10 mm.

C. admirabilis, *C. bifasciata* (Figures 3A–D), *C. brevis* (Figures 3E–G): almost ventrolateral (about 180° around the last whorl from the aperture), but slightly lifted from the substrate.

C. batillariaeformis, *C. petrosa* (Figures 3H–J), *C. purpurastoma*, *C. nympha*: dorsolateral (less than 180° but substantially more than 90°).

C. adunca, *C. irrorata*, *C. subbrevicula* (Figures 3K–M), *C. verbeeki*: ventrolateral (approximately 240°).

C. inflata, *C. pellucida* (Figures 3N–Q): dorsal (approximately 90–100°) and accompanied by an additional varix or swelling in a ventrolateral position.

Rhinoclavis (Figure 5) generally is smoother than *Cerithium* and related taxa, or has asymmetrical ridges or tubercles with steeper faces directed toward the shell apex. The aperture is orthocline to prosocline, with an adult siphon markedly bent in an (anatomically) oblique dorsolateral direction (Figures 5A–B, F–H, J, L, O, Q–T). The anterior canal of juveniles is much shorter and straighter (Figures 5D–E, M, P). The last whorl often has a reduced diameter (especially on the dorsal side), which gives a pupiform aspect to the shell.

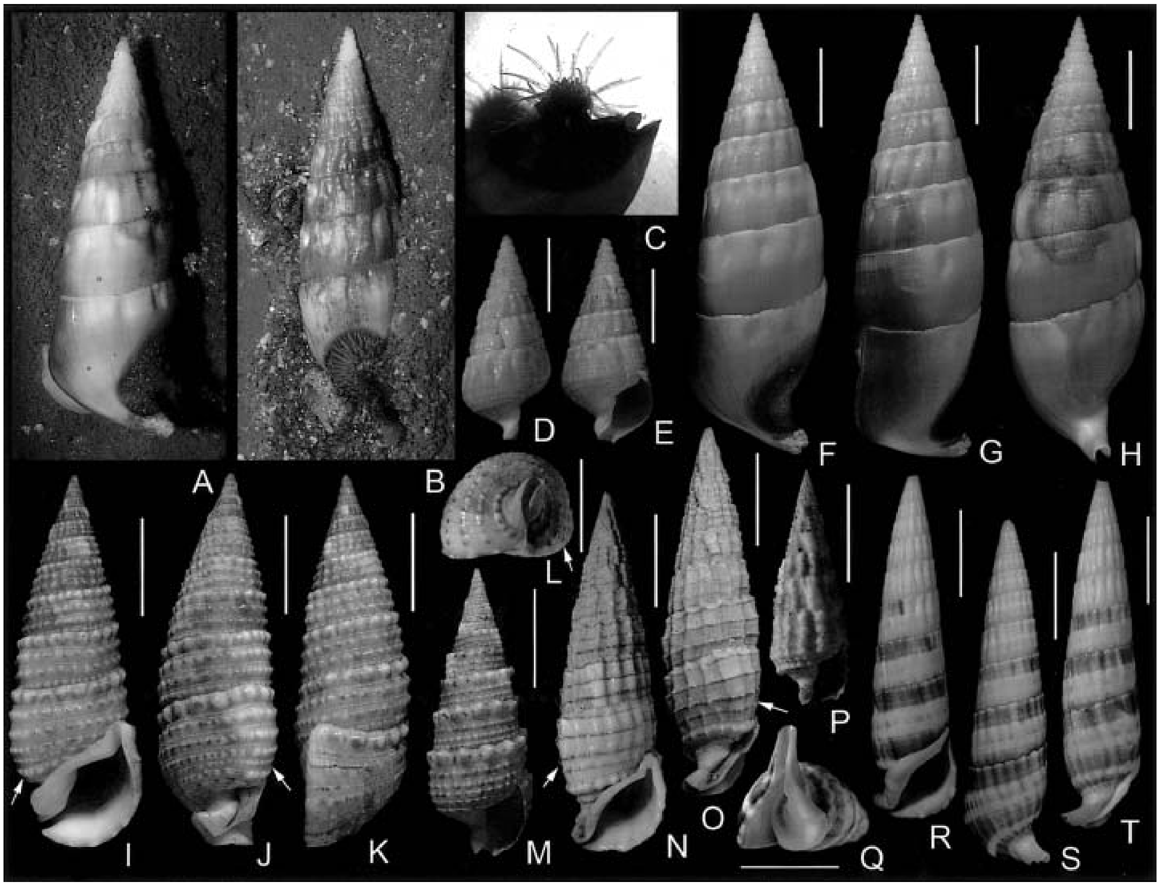

Figure 5. Recent *Rhinoclavis*. Arrows indicate the ventrolateral varix or swelling. **A–H.** *R. vertagus*, Iriomote Island, Japan. Living individual on the surface of the sediment (A) and burrowing (B), detail of symbiotic actinian (C), subadult (D–E) and adult (F–H) shells. **I–M.** *R. sinensis*, Recent, Iriomote Island, Japan. Adult (I–L) and subadult (M) shells. **N–P.** *R. aspera*, Iriomote Island, Japan. Adult (N–O) and subadult (P) shells. **Q–T.** *R. fasciata*, the Philippines. Scale bars represent 10 mm.

The aperture plane of *Rhinoclavis* is not perpendicular to the anterior canal. Since the latter is held vertical in infaunal individuals, the aperture plane forms an angle of up to 45° to the surface of the sediment. This is especially evident in *R. vertagus* and *R. fasciata* (Figures 5F–H, Q–T). During ploughing and burrowing, the outer shell lip functions like the blade of a plough, and shelters the visceral sac and the upper portion of the foot stalk from direct contact with the sediment. When *Rhinoclavis* is epifaunal, it keeps the aperture plane roughly parallel to the sediment surface, and therefore the siphon points obliquely sideways.

The Palaeogene *Semivertagus* (Figure 6) is comparable in general morphology to *Rhinoclavis*. The adult siphon in *Semivertagus* is shorter than in *Rhinoclavis*, but is bent to the same degree and in the same direction.

Pseudovertagus (Figures 7A–J), *Cerithioclava* (Figures 7K–M), *Bezanconia* (Figures 7N–P) and *Bella-*

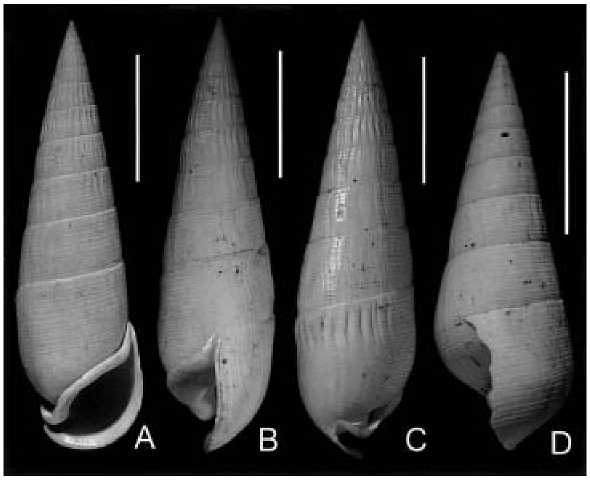

Figure 6. *Semivertagus striatus*, Middle Eocene, Paris Basin, France (NHM). Adult (A–C) and subadult (D). Scale bars represent 10 mm.

Figure 7. Cerithiidae. Arrows indicate the ventrolateral varix or swelling. **A–C, Q.** *Pseudovertagus aluco*, Recent, Tayud, Cebu Island, the Philippines. **D–E, R.** *P. varicosum*, Pliocene, Castell'Arquato, Italy. **F–G, S–T.** *P. nobilis*, Cebu Island, the Philippines. **H–J, U.** *P. clava*, Tahiti, French Polynesia (NSM). **K–M, V.** *Cerithioclava caloosaensis*, Pliocene, Florida, USA (NHM). **N–P.** *Bezanconia spirata*, Paris Basin, France (NHM). Scale bars represent 10 mm.

tara (Figures 8A–H) display general affinities with *Rhinoclavis* and *Semivertagus*, but differ in the orientation of the aperture (almost tangential) and the siphon (long and oblique, but to a lesser extent than *Rhinoclavis*). Also in these genera the juvenile siphon is much shorter and straighter than in the adult. Recent *Pseudovertagus* (Figures 7A–C) displays a behaviour and a distribution of epibionts (see above) consistent with facultative semi-infaunal burrowing, but is not constantly infaunal.

The Pliocene *P. varicosum* has a rather smooth shell and an unusually long siphon, which is not bent obliquely dorsally but sideways (Figures 7D–E). Palaeogene *Bezanconia* (Figures 7N–P) is comparable with *Pseudovertagus*, but differs mainly in its smooth and thicker shell, a deep sutural furrow and a shorter and less curved anterior canal.

Rhinoclavis possess a columellar fold, albeit not very distinct. The species of *Cerithium*, *Clypeomorus*, *Colina* and *Pseudovertagus* we inspected have none.

Palaeogene cerithiids display a broader range of sculpture than subsequent forms. In addition to the spiral rows of knobs, tubercles and beads displayed by most Neogene to recent taxa, Eocene species display also sharp denticulated carinae (e.g., *Serratocerithium serratum*, Figures 8I–J), axially or obliquely elongated nodes (e.g., *Tenuicerithium fragile*), essentially smooth forms except for one or few spiral furrows (e.g., *Bezanconia spirata*; Figures 7N–P) or broad rounded knobs on part of the shell (e.g., *Bellatara palaeochroma*, Figures 8A–H). *Ptychocerithium* is characterised by a few very strong smooth spiral lines on the basis (Figure 9A). A reticulate sculpture is also observed (e.g., *Orthochetus*).

The tubercles on the penultimate whorl of *Bellatara* (Figures 8A–H) are unique in that the earlier ones in

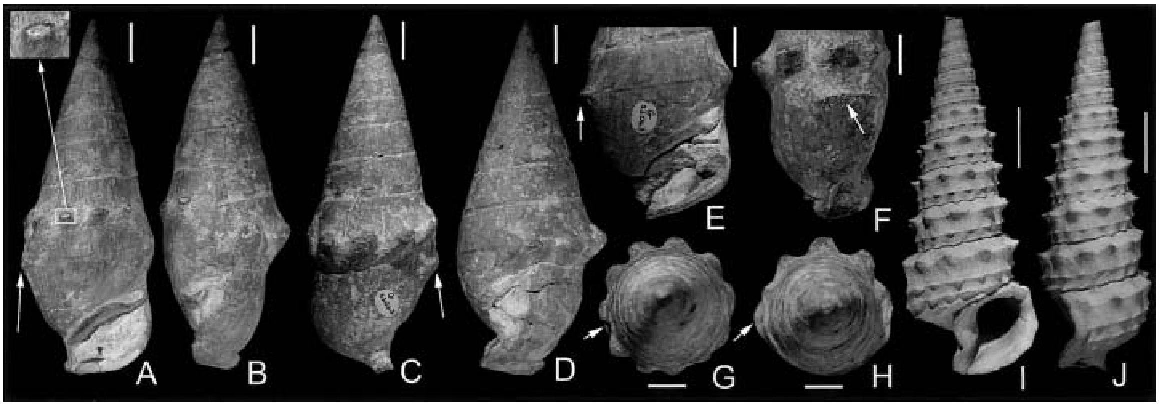

Figure 8. Cerithiidae. Thicker arrows indicate the ventrolateral swelling. **A–H.** *Bellatara palaeochroma*, Eocene, Monte Postale, Italy (NHM). Inset in (A) shows an enlargement of one of the cratered tubercles. **I–J.** *Serratocerithium serratum*, Middle Eocene, Paris Basin. Scale bars represent 10 mm.

ontogeny, which are smaller in size and located ventrally in the adult, have a crater-like appearance, with an oval or eye-shaped thin rim and a hollow center (Figures 8A–B). An examination of the growth lines on the shell surface shows no trace of a closed selenizone in the region between adjacent craters. Unfortunately, no material was available to prepare sections.

Typically, the larger tubercles on the dorsal surface of the penultimate whorl of *Bellatara* are large, apparently not hollow, and do not display craters (Figures 8B–D). However, rare specimens display craters also in this region. Conversely, in exceptional individuals, the tubercles are large and lack craters also on the ventral region of the penultimate whorl (Figure 8G).

Bellatara possesses a sideways-elongated ventrolateral tubercle (thicker arrows in Figure 8) in a position roughly corresponding to the ventrolateral varix or swelling of other cerithiids.

In a number of cerithiid species scattered among several genera, the adult aperture is elongated in the posterior direction, and this region is set off from the main (i.e., pedal) region by a constriction in the outer shell lip and a facing tubercle on the inner lip (e.g., Figures 2A, I, T–U; Figures 3F–I; Figures 5I, R; Figure 6A; Figures 7F–I, K–M). The elongation of the aperture always develops in proximity of the adult aperture, and is a part of determinate growth. Species of *Cerithium* (Figures 2T–U) and *Cerithioclava* (Figures 7K–M) are the most extreme examples of this character.

Campanilidae

The shell consists of a large number of whorls and typically is high-spired (Figures 9B–J). The aperture is opisthocline, with a marked notch near its posterior extremity (Figure 9F, and growth lines in Figure 9J) and usually a flared and thickened adult outer lip. The basis of the shell is relatively flat. These characters result in a round or subrectangular aperture, proportionally shorter antero-posteriorly than in the Cerithiidae. The anterior canal is short but well differentiated.

The external surface typically bears a prominent sculpture of spiral threads and/or knobs (Figures 9B, D, I, J). A gradual ontogenetic change in sculpture is often observed, especially in large species, with spiral threads (Figure 9D) disappearing except for the most adapical one, which changes into a row of large knobs (Figures 9B, I–J).

The subadult shell surface of the Eocene *Campanile cornucopiae* bears a fine sculpture pattern which is spiral near the suture, but apparently growth-unconformable between large knobs (Figures 9H–I; see also Wrigley, 1940).

The internal shell surface in most species of *Campanile* carries two well-developed columellar folds that appear a short distance within the aperture (Figure 9C). In *C. giganteum*, fine spiral threads are observed inside the early whorls. A substantial portion of the early whorls is secondarily thickened and sealed off by septa. Because of this, internal moulds of large campanilids are substantially shorter than the original shells (e.g., Figure 9E), and their apices are rounded into an unusually large (up to 20 mm in diameter) ‘‘protoconch’’-like hemisphere (which corresponds to the adoral surface of the last septum). Cretaceous campanilids have one to three columellar folds, which often decrease in number or disappear during growth (Kiel, unpublished; Kiel *et al.*, 2000). The Cretaceous *Metacerithium* is distinguished by a strong external

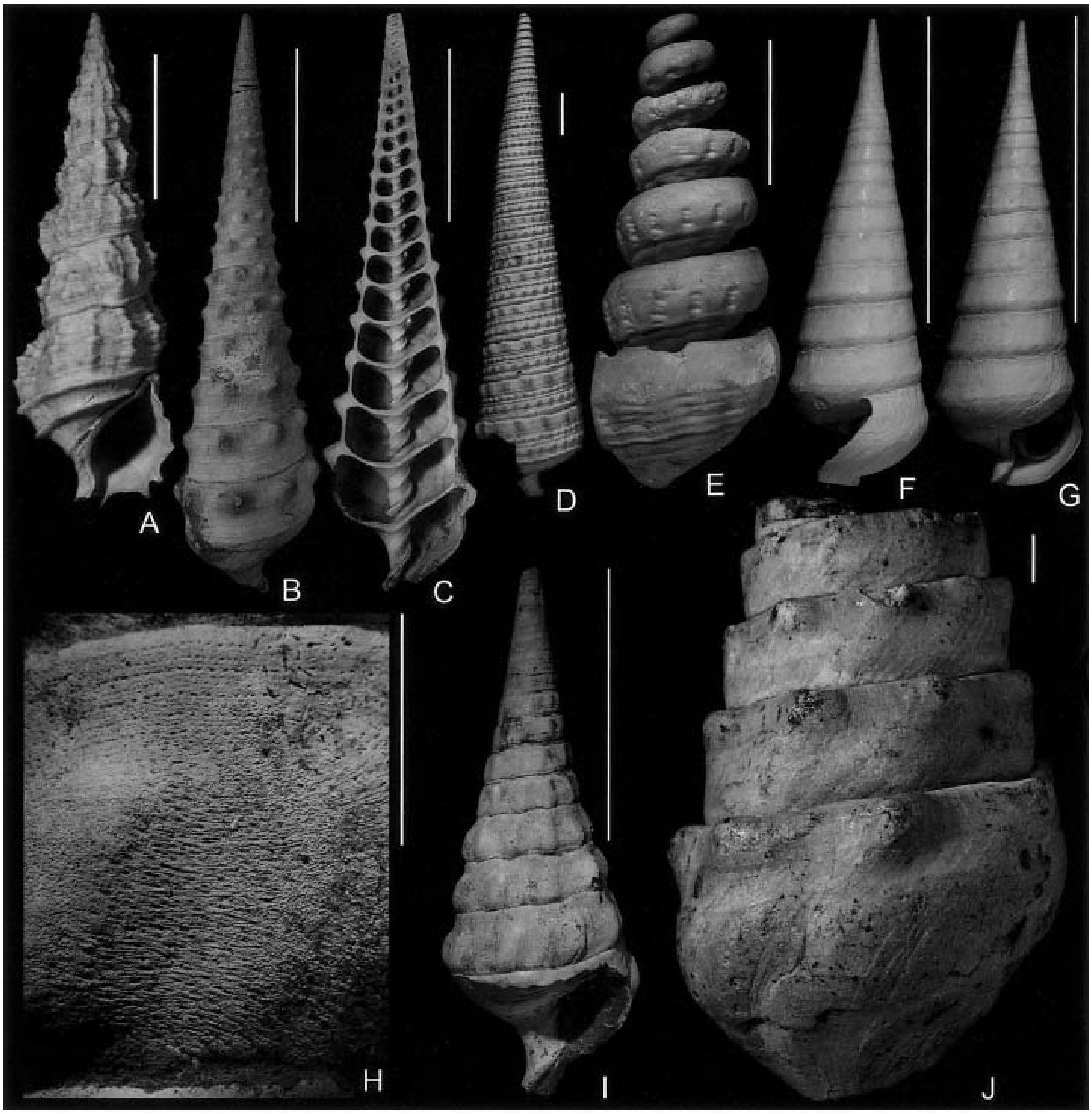

Figure 9. Cerithiidae (A) and Campanilidae (B–J). **A.** *Ptychocerithium lamellosum*, Middle Eocene, Paris Basin, France. **B–C.** *Campanile giganteum* (Lamarck), Middle Eocene, Paris Basin, France (NHM G73778). **D.** *Campanile* cf. *giganteum* (Lamarck), Cotentin, France, Middle Eocene (NHM G58560). **E.** Mould of *Campanile* sp., Easington, St. David's, Jamaica, Eocene (Yellow Limestone), (NHM 36459). **F–G.** *Campanile symbolicum* Tate, Rottnest Island, SW Australia, NSM. **H–I.** *Campanile cornucopiae* (Sowerby), Upper Eocene, Stubbington, UK (NHM C66400). **J.** *Campanile* sp., Portland, Jamaica, Tertiary (NHM G10990). Scale bars represent 10 mm (A, D, H, J) or 100 mm (B–C, E–G, I).

basal keel with denticles or tubercles, and no columellar folds (Kiel, unpublished; Kiel *et al.*, 2000).

Moulds of an Eocene species (Figure 9E) possess numerous internal knobs as well as spiral ridges. The knobs are arranged in sets of internal barriers, each consisting of several teeth projecting inward from the periphery of the whorl. They show a complex ontogenetic pattern, with the number of knobs in each barrier increasing during growth, their height decreasing, and the corresponding knobs on successive barriers gradually merging together to form spiral ridges.

Campanile symbolicum (Figures 9F–G), the only Recent species of this genus, has an essentially smooth shell, no columellar folds (Houbrick, 1981, 1984) and (at least in the material we were able to observe) no visibly specialised adult aperture. However, the sculp-

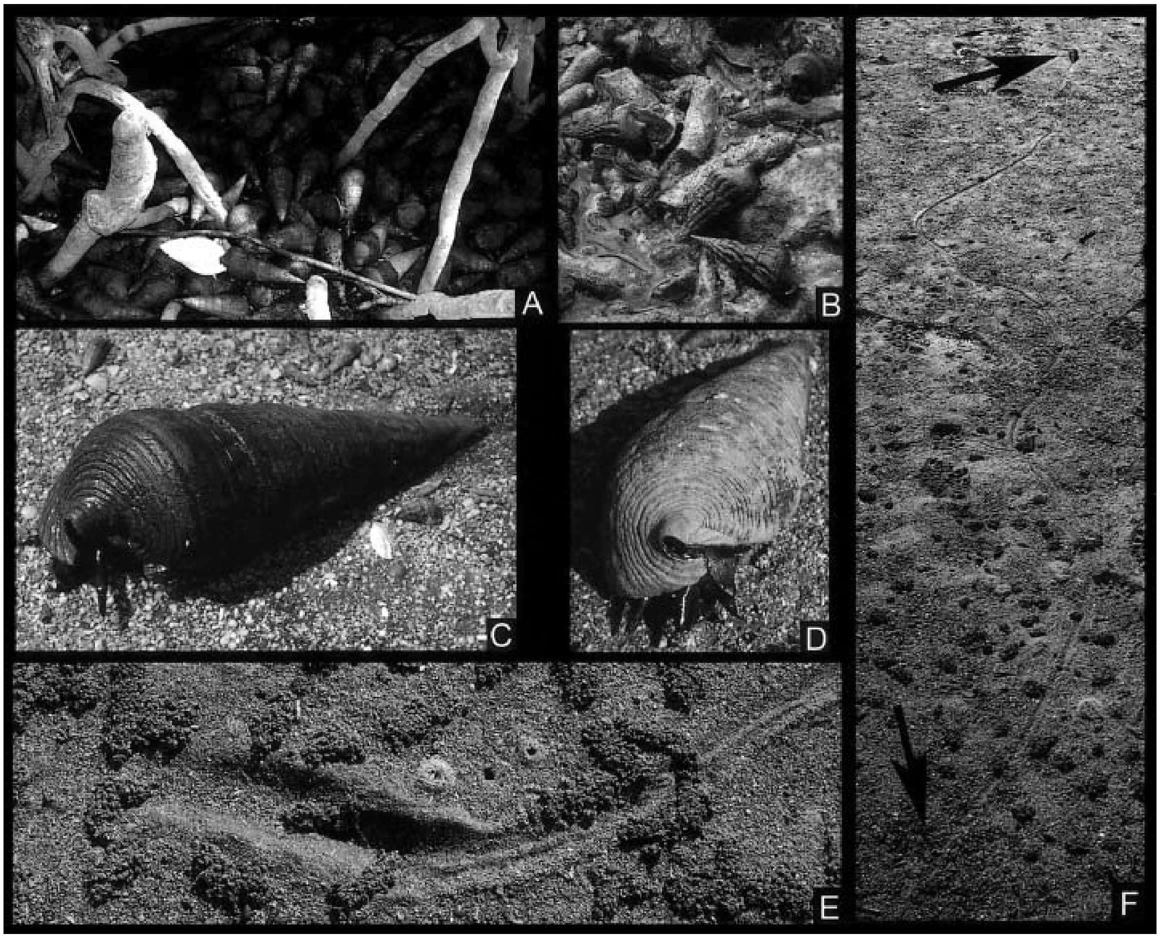

Figure 10. Living *Terebralia palustris*, Recent, Iriomote Island, Japan. Adults clustering among mangrove roots (A), subadults on coral rubble (B), adults crawling on muddy sand (C, D), track left by a buried individual emerging from the sediment (E), and complete track (F) from emergence from the sediment (bottom arrow) to the current epifaunal position of the individual (top arrow).

ture of its early teleoconch is comparable to that of fossil representatives (Wrigley, 1940), and its shell geometry (in particular the shape and inclination of the aperture) fully agrees with that of other campanilids. The literature (e.g., Houbrick, 1984) mentions that a slight change in the profile of the whorl (which possibly refers to the increase in sutural concavity visible in Figures 9F–G) occurs in the last couple of whorls in adult specimens, which suggests a determinate growth pattern.

Species of *Campanile* from the European and Caribbean Eocene are among the largest gastropods, with shell lengths reaching 90–100 cm (e.g., Jung, 1987).

Diastomatidae

The shell of *Diastoma* (Figures 1F–G) lacks a true anterior canal, and instead has an indistinct notch at the basis of the columella. Its sculpture is typically spiral or reticulated.

Potamididae and Batillariidae

The aperture of the Potamididae (Figures 10–12) is rounder than that of the Cerithiidae, and the anterior canal shorter, but well differentiated.

Terebralia (Figures 10, 11A–M) possesses a set of very narrow and deep spiral furrows on the outer surface. The sides of the furrows are in contact with each other near the top of the furrow, leaving a cavity in their innermost portion. In unthickened shells, the furrows correspond to rounded ridges on the interior of the aperture. Secondary thickening gradually smoothens out the inner surface, but the furrows still extend through most of the shell thickness.

In *Terebralia palustris*, (Figures 10, 11A–I) the interior shell surface always possesses an internal barrier

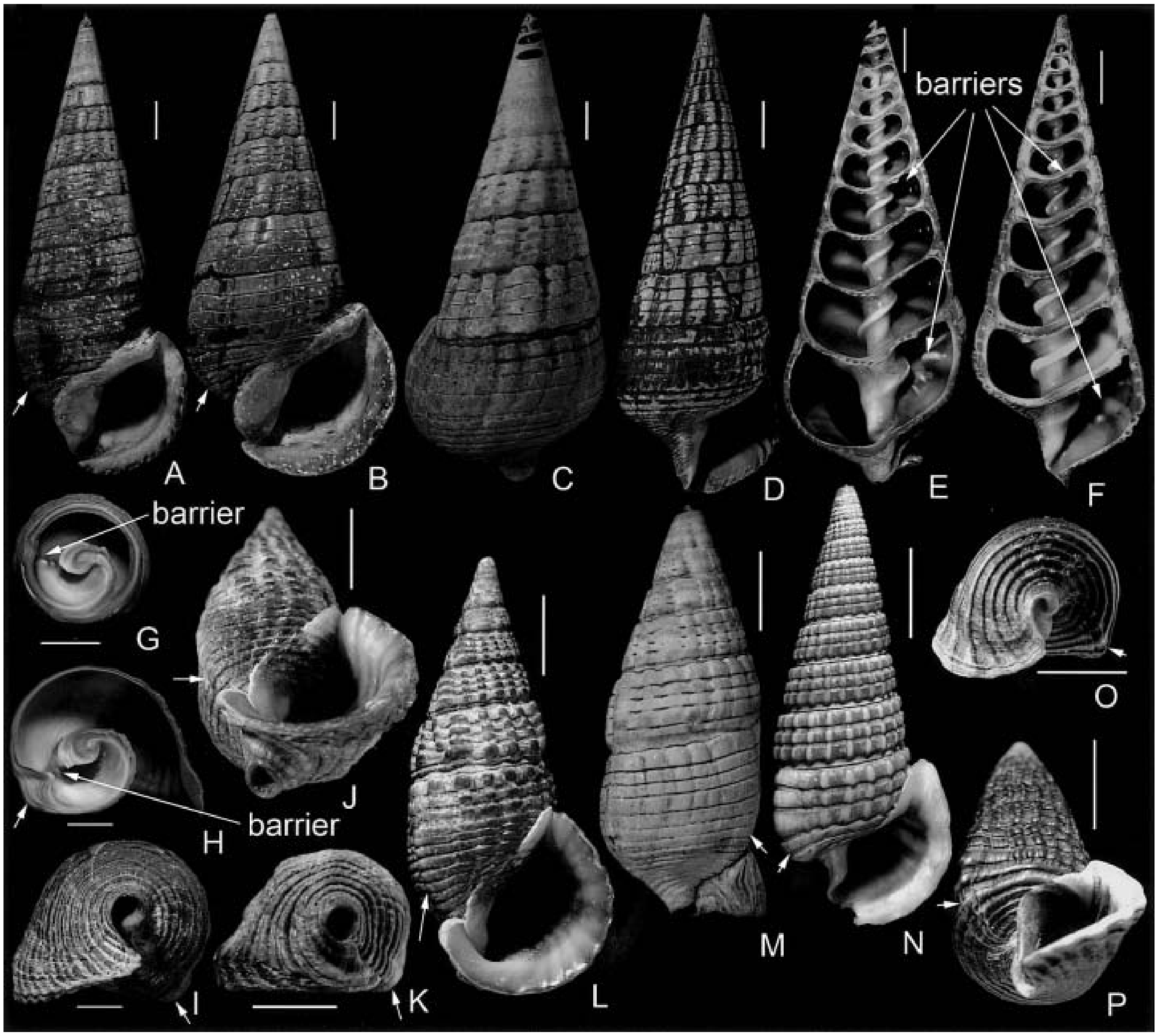

Figure 11. Recent Potamididae. Short arrows indicate the ventrolateral swelling or varix. **A–I.** *Terebralia palustris*, Recent, Iriomote Island, Japan. Adult morphs from the same population (A–C, I), subadult (D), tangential sections through adult (E) and subadult (F) showing internal barriers (long arrows), transversal sections of one adult showing internal barriers (arrows in G–H). **J–M.** *T. sulcata*, Tayud, Cebu Island, the Philippines (J–L) and Moluccas (M, UMUT). **N–P.** *Cerithideopsilla cingulata*, Iriomote Island, Japan. Scale bars represent 10 mm.

in correspondence of the ventrolateral swelling (Figures 11F, H). The barrier consists of a row of teeth projecting from the outer and posterior regions of the whorl and arranged approximately parallel to the swelling and to the growth lines on the shell surface. This is not an apertural barrier, because it is never observed at the aperture of subadult individuals. Instead, it is a secondary feature and accretes gradually within the ventrolateral swelling.

Most specimens of *T. palustris* also display a variable number of internal barriers at earlier growth stages (Figures 11E–G). Each of these barriers is placed within a slight swelling of the outer shell lip, which is secondarily thickened into a varix. The number and spacing of these barriers are extremely variable.

T. sulcata (Figures 11J–M) differs from other species discussed herein for its tangential aperture well suited to clamping. In addition, the anterior region of the outer lip wraps around the siphon, completely surrounding and protecting it except at the tip (Figures 11J, L, M). The epifaunal life habits of this species on mangrove roots (see above) are unusual among the Potamididae.

Cerithideopsilla (Figures 11N–P) is smaller than *Terebralia* and has a proportionally more flared aper-

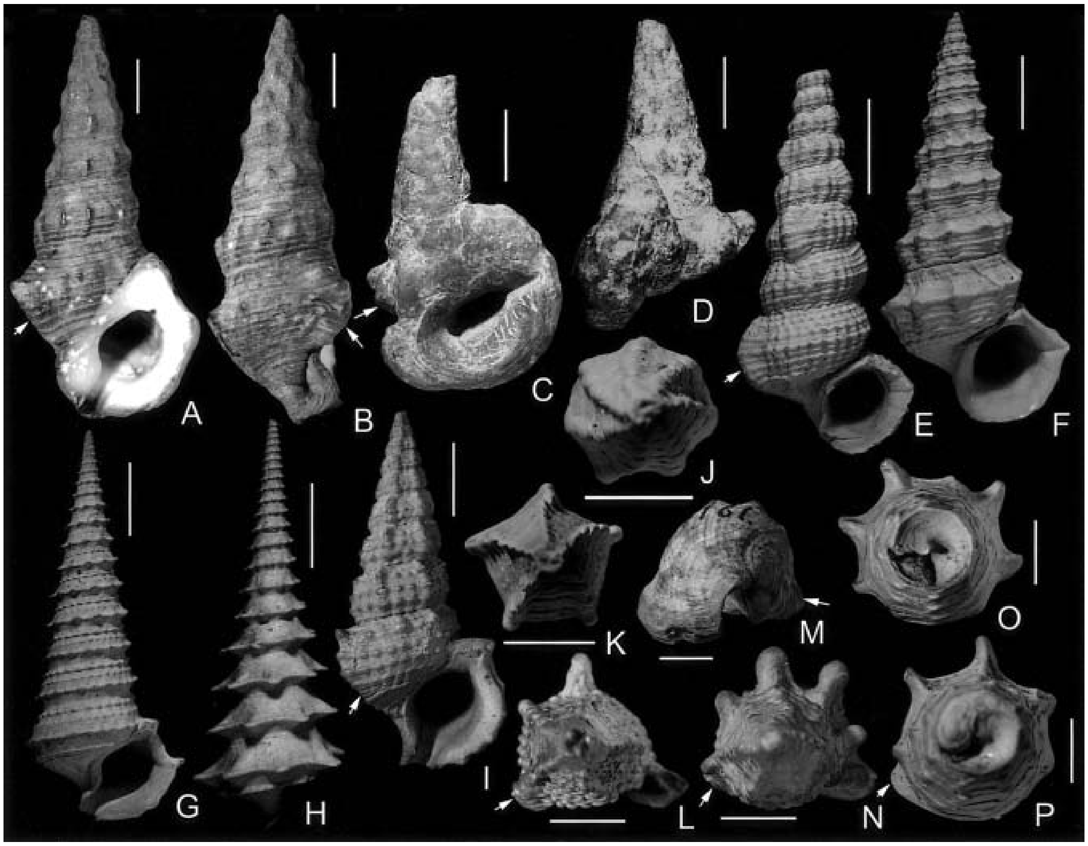

Figure 12. Batillariidae (A–D, I–P) and Potamididae (E–H). **A–B, M.** *Pyrazus ebeninus*, Recent, Australia (UMUT). **C–D.** *Pyrazus cochlear*, Oligocene, Castelgomberto, Italy (MNHN). **E.** *Potamides cf. lapidum*, Middle Eocene, Grignon, Paris Basin (NHM). **F.** *P. angulosus*, Eocene, Paris Basin, France (NHM). **G–H.** *P. tricarinatus*, Eocene, Paris Basin, France. Typical morph (G) and a morph with extremely developed peripheral spines and basal thread but otherwise smooth (H) (G: NHM). **I, L.** *Pyrazus angulatus*, Middle Eocene, Damery, Marne, France (I) and Upper Bracklesham Beds, Brook, UK (L) (NHM). **J, N.** *P. heptagonum*, Middle Eocene, Roncá, Italy (J) and Paris basin, France (N: NHM). **K.** *P. pentagonatus*, Middle Eocene, Roncá, Italy. **O–P.** *P. hexagonum*, Cuisian, Eocene, Gan, France (NHM G82647-9). Scale bars represent 10 mm.

ture, but is otherwise comparable in morphology to *T. palustris* and other soft-bottom potamidids.

Telescopium possesses two columellar folds, and one is present near the aperture of *Terebralia palustris*. In this species, a second fold is gradually built on the posterior side of the whorl (rather than on the columella) over the span up to one whorl (Figures 11E–F). *Telescopium* seems to lack a specialized adult aperture.

Several potamidids possess a ventrolateral varix (short arrows in Figures 11–12). In Recent genera, shell sculpture often consists of either spiral furrows or spiral rows of rounded beads. Tertiary taxa were very varied (e.g., Figures 12C–P; see also Cossmann, 1906), and additionally display rounded oblique ridges reminiscent of Eocene Campanilidae (e.g., in Pliocene *Terebralia scalata*) or sets of prominent, smooth spiral keels (e.g., in Oligocene *Tympanotonos trochlearis*). A single thread may develop into a row of spines on the shoulder (e.g., several Palaeogene *Tympanotonos*), or a crenellated carina (e.g., the Eocene *Potamides angulosus*). A few Palaeogene *Pyrazus* possess strong axial varices that are juxtaposed among adjacent whorls (Figures 12I–L, N–P). A recurrent theme, especially in the Tertiary, is the presence of a peripheral or sutural row of large knobs (Figures 12A–D, F, 13A–D, 14A–D). This parallels the sculpture of the Campanilidae (see above).

In *Rhinocoryne*, a ventrolateral swelling (arrows in Figures 14A–D) is located anteriorly to the peripheral row of tubercles, which continues uninterrupted past the swelling. The latter is a primary feature bearing the same fine sculpture as the surrounding regions, not a secondary apertural callus.

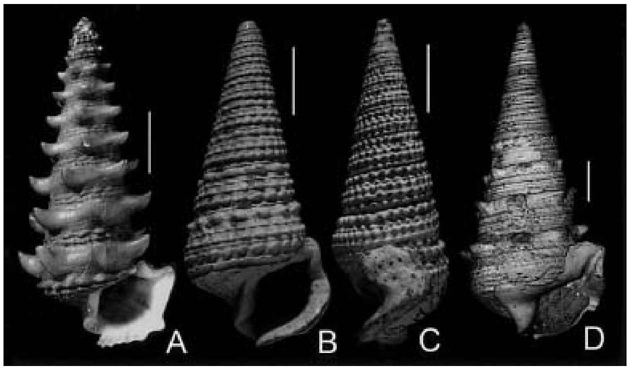

Figure 13. Potamididae. **A.** *Tympanotonos fuscatus*, Recent, West Africa (UMUT). **B–C.** *T. submargaritaceus*, Miocene, Kleinkarben, Mainz Basin, Germany (NHM G22617). **D.** *Vicarya yokoyamai*, Early Miocene, Mizunami City, Gifu Prefecture, Japan (Mizunami Fossil Museum, Mizunami, Japan). Scale bars represent 10 mm.

Batillariidae

The shell aperture (Figures 14E–H) is typically oval and elongated in the antero-posterior direction, slightly opisthocline and with an anterior notch and a small sinus or inflection of the outer lip. Sculpture is variable. This family does not display evident evolutionary trends, and Eocene species of *Batillaria* (e.g., *B. pleurotomoides*) are similar to Recent ones.

Thiaridae *sensu lato*

This section includes with the Thiaridae also genera, like *Brotia*, assigned to other families in recent literature (e.g., see Köhler and Glaubrecht, 2003, and references therein). Most Thiaridae *s.l.* are not cerithiform. In particular, their aperture often is proportionally much larger and higher, and the pleural angle is higher. However, a few taxa have secondarily evolved a cerithiform shell morphology, albeit lacking a true anterior canal. These include species of *Pachychilus*, *Doryssa*, *Brotia*, *Melanotria*, *Glauconia* and *Melanoides* (Figures 14I–J). Several of these forms are difficult to distinguish from Batillariidae. The Recent *Faunus ater* (Figures 15A–B) and a few fossil species

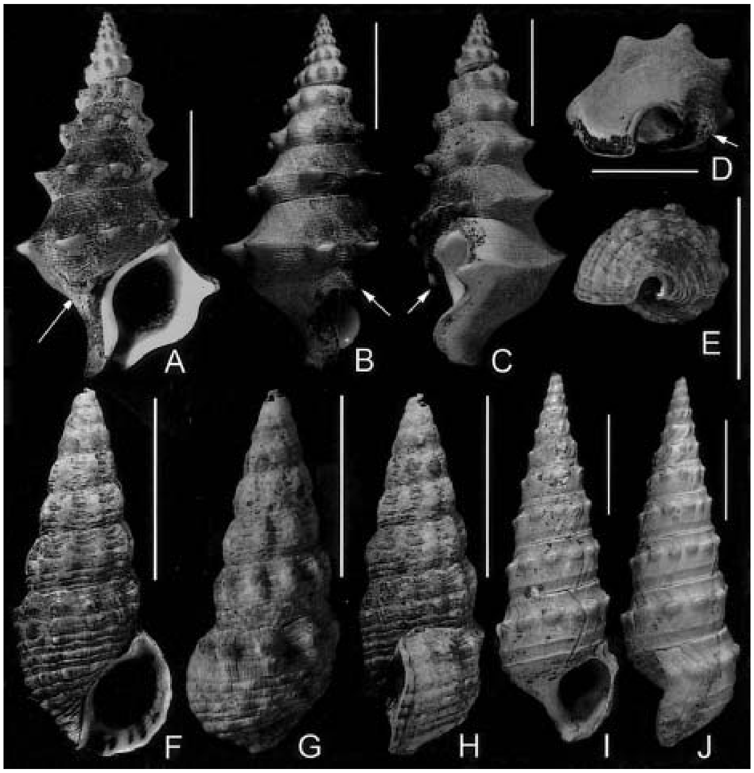

Figure 14. Potamididae (A–D), Batillariidae (E–H) and Thiaridae (I–J). **A–D.** *Rhinocoryne humboldti*, Recent, Costa Rica (National Museum, Tokyo). Arrows indicate the ventrolateral swelling. **E–H.** *Batillaria multiformis*, Hamana Lake, Shizuoka Prefecture, Japan. **I–J.** *Melanoides inquinata*, Eocene, Eparnay, France (NHM32052-4). Scale bars represent 10 mm.

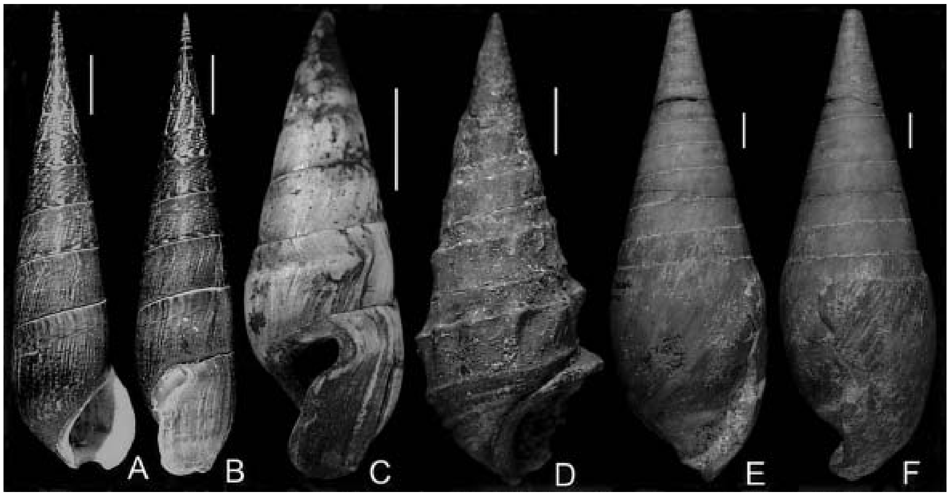

Figure 15. Thiaridae. **A–B.** *Faunus ater*, Recent, Cebu Island, the Philippines. **C.** *F. rigidus*, Upper Eocene, Highcliff, Hants, UK (NHM 72059A). **D.** *F. auriculatus*, Middle Eocene, Roncá, Italy (NHM). **E–F.** *Pseudobellardia gomphoceras*, Eocene, Monte Postale, Italy (NHM). Scale bars represent 10 mm.

of *Faunus* (Figure 15C) are smooth, but the Eocene *F. auriculatus* (Figure 15D) possesses both axial (in the juvenile) and spiral ridges and knobs, and is more typically cerithiform than the former species. *F. auriculatus* often is placed in the genus or subgenus *Pseudobellardia*. However, Palaeogene species traditionally referred to *Pseudobellardia* include also large, smooth Thiaridae (e.g., Figures 15E–F).

A rounded anterior notch and an additional notch of the outer lip are constant features in this family, but the development of the notch on the outer lip ranges from barely noticeable (Figures 14I–J) to very obvious (Figure 15C), and its placement from sutural (Figures 15A–B) or subsutural (Figure 15C) to more anterior (Figures 14I–J).

Pachymelania is probably unique among Recent Thiaridae in possessing a spiral row of very large tubercles. In this respect, it parallels the most heavily sculptured Cerithiidae and Potamididae.

Procerithiidae

Shell morphology in this family (Figure 16) is rather difficult to categorize. It contains taxa superficially similar to *Cerithium* and *Pseudovertagus*, as well as taxa closely reminiscent of *Pyrazus* and *Terebralia* (Figures 16A–D). Some procerithiids also display smooth shells or numerous, weak and smooth spiral lines (Figure 16E), which remind one of the Loxonematidae. Although several procerithiids display a determinate growth, a differentiated adult aperture is not always visible. Nonetheless, examples like Figure 16A are remarkably ''modern'' in appearance, and morphologically closer to the Potamididae than Cerithiidae. In fact, some of these taxa could prove to be early potamidids.

Discussion

Life habits and ecology

Recent cerithiforms are primarily grazers or detritus feeders (Morton, 1967, and therein), mobile, largely marine in shallow water (especially the Cerithiidae), or brackish-water forms (Batillariidae, Potamididae). They are often the most common molluscs in salt marshes and mangrove swamps (Healy and Wells, 1998a, and therein). Many representatives are intertidal or shallow-subtidal. A few (e.g., Melanopsidae) are freshwater forms.

The Potamididae are amphibious (Morton, 1967). *Telescopium*, *Pyrazus*, *Terebralia* and a few species of *Potamides* can be considered semi-terrestrial. These genera have replaced the gill with a pallial lung (Morton, 1967, and therein). Life in intertidal environments has been proved in the Miocene potamidid *Vicarya* (Tojo and Masuda, 1999) and was likely also in Palaeogene potamidids.

Adult and subadult *Terebralia palustris* cluster among mangrove roots at low tide (Figure 10A), while juveniles are common among coral rubble (Figure 10B). The few adults we observed on exposed tidal flats (Figures 10C–D) were at the end of meandering tracks several metres long, which start with a depression where the organism emerged from the sediment (Figure 10E, bottom of Figure 10F). The mollusc itself

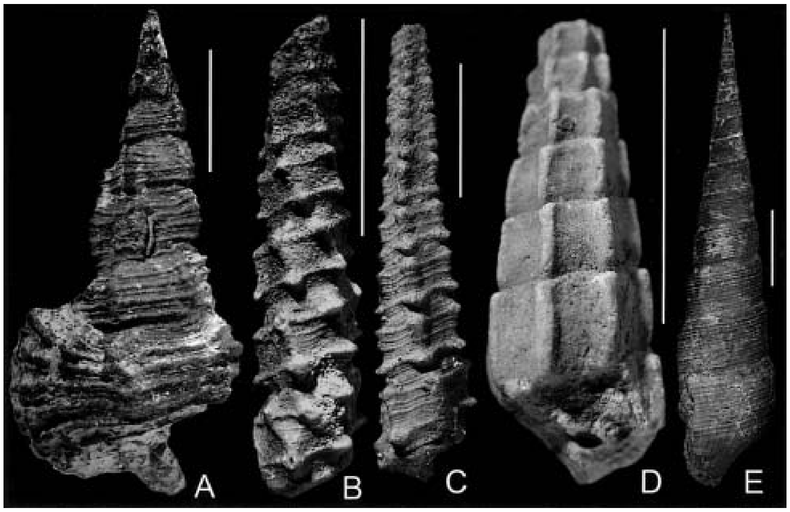

Figure 16. Procerithiidae. **A.** *?Diatinostoma* sp., Cretaceous, Syria (SMNH Moll3872). **B–C.** *Cryptaulax contorta*, Bajocian, Jurassic, Sully (B) and Les Moutiers (C), Bayeux, Calvados, France (NHM G618764 and 81454). **D.** *Rhabdocolpus scalariformis*, Bajocian, Jurassic, St. Vigor, Bayeux, Calvados, France (NHM 81440). **E.** *"Cerithium" abbas*, Middle Jurassic, Bradford Abbas, Dorset, UK (NHM G11282). Scale bars represent 10 mm.

is at the top of Figure 10F. Most adults show a slight selective wear on the ventral apical region (Figures 11A–B) and a higher wear on the dorsal apical region (Figure 11C). While the former is consistent with epifaunal shell dragging, the latter instead suggests that the apex lies exposed at the surface of the sediment when the organism is infaunal and stationary.

In the literature, *Cerithium* is almost always reported as epifaunal on a variety of substrates, with the notable exceptions of *C. salebrosum* (infaunal in sand; Houbrick, 1992), *C. tenellum* and *C. munitum* (Figures 2L–M) (both facultatively infaunal; Houbrick, 1992). Many other species of *Cerithium* burrow shallowly for temporary shelter (e.g., Taylor, 1968; Houbrick, 1974, 1992). *C. coralium* is the only Recent species that lives on muddy sand near mangroves, together with Potamididae (Houbrick, 1992).

Many other cerithiforms are recorded as epifaunal (e.g., *Proclava*; Houbrick, 1978). *Ochetoclava* lives both on sandy and rocky bottoms (Houbrick, 1978). Small taxa like *Colina* are typically epifaunal, as shown by epibiont encrustation of their shells.

Rhinoclavis is consistently reported as a sand burrower. Houbrick (1978) reported infaunal habits in *R. diadema*, *R. bituberculata* and *R. brettinghami*. Our observations of other *Rhinoclavis* species (see above) confirm this. *Pseudovertagus* is a facultative semi-infaunal burrower, but is frequently epifaunal (observations herein). It is often observed on or in coarser sediments than *Rhinoclavis* (herein, and Houbrick, 1978).

Potamididae and Batillariidae prefer muddy sand. Several representatives of these two families burrow for temporary shelter at high tide (see above).

The Recent *Campanile symbolicum* is a subtidal algal feeder creeping on both rock and soft sediments. When on sand, often it lies half-buried or drags the shell through the topmost layer of sediment, leaving a deep furrow (e.g., Houbrick, 1981, 1984). The largest species of *Campanile* from the southern European Eocene generally are found in mixed boulders and loose rubble environments, in shallow water and probably close to the shore (E. Savazzi, pers. obs.). Literature records of fossil campanilids are consistent with an environment comparable to that recorded for *C. symbolicum* (Donovan and Blissett, 1998; Darragh, 2002, and references therein).

Feeding. Most cerithiforms are algal grazers or detritus feeders (Morton, 1967; Houbrick, 1978, 1981, 1985, 1992; Healy and Wells, 1998a, 1998b; references therein), but a few exceptions are known. *Bittium* selects and eats Foraminifera from bottom sediments (Fretter, 1951). *Cerithiopsis* grazes on sponges (Fretter, 1951). *Batillaria zonalis* is a facultative suspension feeder in addition to detritivore (Kamimura and Tsuchiya, 2003). Cerithiforms in mangrove swamps (e.g., *Terebralia*) typically feed on fallen leaves at low tide (Fratini *et al.*, 2001, 2004; albeit *Terebralia* was described as a grazer on the algal coating of soft sediments by Taylor, 1968).

Shell growth

The shells of cerithiform gastropods are characterised by a determinate growth pattern (Vermeij and Signor, 1992; Savazzi *et al.*, in prep.), as clearly shown by their usually specialised adult apertures. After growth stops, shell secretion is restricted to the thickening of internal and/or external surfaces.

Numerous cerithiform taxa also display a countdown growth pattern (Seilacher and Gunji, 1993), in which the construction of the adult aperture is preceded by other specialisations of the shell. This implies that there is a morphogenetic programme at work, which consists of a series of orderly steps preceding the end of the growth process.

Since virtually all gastropods display ontogenetic changes in shell morphology, a useful definition of countdown cannot include all changes preceding the end of the growth process. In the case of cerithiforms, three morphologic categories of changes in shell sculpture and/or geometry are concentrated in separate shell regions. The first change is sudden and located between the larval and post-larval stages. A second change is usually gradual and located within the topmost 1/3 to 1/2 of the adult shell length. This is a transition between the juvenile and subadult stages. A third change begins with the onset of features not present at earlier stages and usually located at fixed angular distances from the adult aperture. In the present paper, the term countdown refers exclusively to this third category of changes. The terms juvenile, subadult and adult are used herein only in a morphologic sense.

Once the external shell surface has been built, it is never secondarily modified in cerithiforms. The internal shell surfaces and apertural callus, on the other hand, are often secondarily thickened.

The countdown process in several cerithiforms begins with the construction of a varix, or swelling, placed at a fixed angular distance (most often about 2/3 of a whorl) from the adult aperture (i.e., ventrolaterally; see above). The adult aperture usually is the most conspicuous ontogenetic change in shell morphology subsequent to the juvenile stage.

Houbrick (1974) reported that species of *Cerithium* from Florida (USA) with a lifespan of about one year grow from juveniles to adults in 3 to 12 months. Observations on other species (Houbrick, 1974; Ayal and Safriel, 1982; Yamaguchi, 1977) indicate a life span of a few years. Thus, in several of these species, individuals spend a large portion of their lifespans as adults. This is particularly important because an extended duration of the adult stage can be expected to play a role in the tradeoffs between characters that can be optimized either in the adult or in the juvenile, but not in both.

Evolution

Procerithiidae. The family Procerithiidae appears to constitute the earliest stock attributable with confidence to the Cerithioidea (Nützel, 2002, and references therein). With the exception of one or a few Late Triassic species assigned to *Cryptaulax* (e.g., by Haas, 1953 and Nützel, 2002), the earliest well established occurrence of the Procerithiidae dates from the Lower Jurassic (Nützel, 2002, and references therein).

Jurassic and Cretaceous Procerithiidae like *Cryptaulax*, *Rhynchocerithium* and *Exelissa* are cerithiform in general aspect and in the presence of an anterior canal, and at least some of them display a differentiated adult aperture not unlike those of Caenozoic cerithiforms (Figure 16A). Likely, these Procerithiidae constitute the ancestors of later cerithioidean stocks like the Cerithiidae. Some Jurassic Procerithiidae display possible affinities with the Loxonematacea.

Cerithiidae. Cretaceous cerithiids are scarce and, probably, some of these taxa are more properly assigned to the Potamididae (see below). "Modern" cerithiids became common first in the Eocene. At that time, cerithiids were already differentiated into two morphologic groups, one related to *Cerithium* and *Clypeomorus*, the other leading to *Rhinoclavis*, *Pseudovertagus* and *Ochetoclava*. Several peculiar taxa from the Eocene appear to be related to, or convergent with, *Pseudovertagus* and *Ochetoclava*. True *Rhinoclavis* evolved later (probably in the Neogene), and represents one of the few evolutionary innovations in cerithiforms after the Palaeogene.

Semivertagus from the Middle Eocene (Figure 6) is similar to Recent *Rhinoclavis* (Figure 5) in shell proportions and sculpture, but the anterior canal and aperture of the former are closer to *Pseudovertagus* (Figures 7A–J, Q–V). *Semivertagus* is the most likely Palaeogene ancestor of *Rhinoclavis*. Eocene *Colina* (Figure 4A) are already fully differentiated from the above lineages and similar to Recent ones (Figures 4B–D).

Potamididae. Turonian species of *Pyrazus* and *Tympanotonus* illustrated by Cossmann (1906) are similar to Tertiary species in shell proportions and strong sculpture. Their anterior canal seems less differentiated than in Caeonozoic taxa. Taxonomic and morphologic diversity within this family apparently peaked in the Eocene of the western Tethys, and has steadily declined since.

Batillariidae. Eocene and later representatives are similar to Recent ones. This family never approached the diversity displayed by the Cerithiidae and Potamididae.

Thiaridae s.l. This family was morphologically extremely diversified in the Palaeogene. In the Neogene, shell geometries with large and antero-posteriorly elongated apertures became predominant, a trend that, with few exceptions, continued to the Recent.

Campanilidae. The Campanilidae are variously placed in the Cerithioidea or Campaniloidea (above references). Several campanilids are known from the Cretaceous of Europe and the Americas (Kiel *et al.*, 2000). *Campanile* became widespread in the Tethys during the Eocene, with numerous records from North and South America, the Caribbean, Europe, Africa, and Asia as far east as Japan (see review in Darragh, 2002). Since the early Miocene *Campanile* is documented in Southeast Asia, Australia and New Zealand, and since the Pliocene it has been exclusively found in Australia (Darragh, 2002, and therein).

As a whole, cerithiform gastropods had a diversity explosion in the Lower to Middle Eocene, and subsequently declined in both number of taxa and variety of shell morphologies. This trend is common to other gastropod lineages (e.g., the Strombidae; see Savazzi, 1991b). The emergence of cerithioidean taxa in the Mesozoic and their reciprocal relationships are not satisfactorily documented in the fossil record.

Recurrent morphologic characters

This section discusses characters, or sets of associated characters, that recur in different cerithiform taxa, but are displayed by only a minority of species within each group. Therefore, a morphologic approach is more suitable to the discussion of these characters than one based on taxonomic ordering.

Columellar folds. From the above description of columellar folds, it appears that this character is present in unrelated lineages. Among genera with this feature, *Rhinoclavis* is an active infaunal burrower, but *Terebralia* is only a facultative burrower, and large *Campanile* are or were epifaunal or, at most, semi-infaunal. *Telescopium* is a facultative burrower, but it tends to cluster epifaunally and subaerially under bushes when inactive for extended periods at low tide (Lasiak and Dye, 1986). Other cerithiforms known to have infaunal habits (see above) do not possess columellar folds.

Thus, this character is not consistently present in burrowing forms, and is also found in prevalently epifaunal forms. It has been stated in the literature (e.g., Signor and Kat, 1984, and references therein) that columellar folds often are associated with burrowing (at least in gastropods with elongated shells). As pointed out by Price (2003), columellar folds have evolved multiple times in gastropods (and among cerithiforms). Several hypotheses have been proposed about their function (see review in Price, 2003), but none have been satisfactorily proven, and the adaptive value of these features in general must be regarded as not understood (Price, 2003). Our observations do not support their use as a reliable indicator of burrowing in cerithiforms.

Siphon. The upward-bent anterior canal of adult *Rhinoclavis* (Figures 5F–H, J, L, Q–T) allows the organism to inhale water when buried, and is an obvious adaptation to infaunal life. Together with the lack of cemented epibionts, the consistent placement of symbiotic actinians at the basis of the siphon in *R. vertagus* confirms our observations that this species is constantly or almost constantly infaunal. Namely, the basis of the siphon (and, to a lesser degree, the dorsal surface, on which actinians are also occasionally observed) allows an epibiont to reach above the sediment surface when the host is buried, and at the same time shelters it from abrasion against the substrate while the gastropod is burrowing.

Among the Strombidae, *Strombus* (*Euprotomus*) possesses a remarkable convergent canal with a similar function (Savazzi, 1988, 1991b, 1994b). In juveniles of both *Euprotomus* and *Rhinoclavis*, the anterior canal must be located along the coiling axis of the shell, where it does not prevent shell growth because it is enveloped by subsequent shell whorls. This constraint is removed in adults, which in turn allows the adult siphon to be better optimized for its respiratory function.

The adult siphon of *Semivertagus* (Figures 6A–D), the likely Palaeogene ancestor of *Rhinoclavis*, is shorter, but still optimized for a comparable function. For this reason, *Semivertagus* is likely to have been a burrower. *Bezanconia* (Figures 7N–P) is probably related to *Pseudovertagus*. Facultative burrowing has been observed in Recent *Pseudovertagus*, and, based on the morphology of the siphon, is likely in fossil species and related genera.

The siphon of *Pseudovertagus varicosum* (Figures 7D–E) is less curved than usual for the genus, and morphologically closer to *Cerithium*, but still oriented obliquely. The reasons for this unusual siphon are unclear.

Aperture plane. According to our observations, infaunal *Rhinoclavis* keep the aperture plane oblique with respect to the sediment surface, and the siphon vertical.

The apertures of *Rhinoclavis*, *Semivertagus*, *Bezanconia*, *Cerithioclava*, most species of *Pseudovertagus* and *Bellatara* (Figures 5–7, 8A–H) are not suitable for effective clamping onto a solid substrate. This agrees well with their documented or inferred life habits on or in soft sediments. In particular, clamping is obviously impossible in most species of *Rhinoclavis*.

Flared apertures as observed in most cerithiforms provide a broad "footprint" and make accidental overturning of the shell less likely. A flared aperture may also shelter the extended soft parts against predators when the organism is epifaunal.

The tangential and very broad aperture of *Terebralia sulcata* (Figures 11J–M) allows efficient clamping onto flat surfaces, and agrees well with the observed preference for solid substrates. When clamped, this semi-terrestrial species communicates with the external environment only through the tip of the siphon (Figures 11J–M), likely as an adaptation against desiccation.

According to Houbrick (1985), *Clypeomorus pellucida* differs from other *Clypeomorus* in living on the aerial roots of mangroves. This is reflected in the tangential adult aperture, the plane of which passes through the shell apex and allows the entire shell to clamp against the substrate (Houbrick, 1985). In most of the other species, clamping on flat surfaces is partly prevented by the projecting ventral region of the penultimate whorl. In these species, the problem is probably lessened by a covering of soft sediment and/or algae on the rock substrates preferred by most *Clypeomorus* (see above), which makes desiccation less of a problem than on mangrove roots. Thus, *C. pellucida* may be regarded as convergent with *T. sulcata*.

Mud-dwelling Potamididae also have adult apertures not well suited to clamping (e.g., *T. palustris*, and to a higher extent *Telescopium telescopium*).

Posteriorly elongated aperture and apertural sinus. A posteriorly elongated aperture with a posterior region separated from the pedal one by a tooth on the inner lip and/or a constriction of the outer lip seems optimized to provide a better separation of the inhalant and exhalant currents (the latter of which exits from the posterior region of the aperture). It occurs in scattered epifaunal as well as infaunal species of the Cerithiidae (e.g., Figures 2A, T–U, 3F, H, 5R, 7K–M), albeit not in the most efficient burrowers. In fact, this adaptation would be ineffective when the aperture is deeply buried.

An exhalant sinus located in the posterior half of the aperture, as observed in the Campanilidae (Figure 9F, growth lines in Figure 9J), Batillariidae (Figure 14H) and Thiaridae (Figures 14J, 15B–C, growth lines in Figure 15F) may also enhance the respiratory activity, and allow the exhalant current to flow unimpeded when the outer lip lies on the surface of the sediment. Thus, it may be related to sedentary, epifaunal or semi-infaunal habits. It is found mostly in freshwater, estuarine and semiterrestrial forms (with the remarkable exception of the Campanilidae, in which it may be related to the large and heavy shell, in addition to scarce mobility).

Ventrolateral varix or swelling. The ventrolateral swelling is optimally placed to enhance the stability of the shell, by analogy with the flared aperture on the opposite side of the shell. This is equally advantageous in soft-bottom and hard-bottom forms, and accordingly it is frequently found in both.

The penultimate varix in *Clypeomorus* is placed in a variety of positions (see observations). When ventrolateral (Figures 3K, Q), it provides a stabilising platform on the opposite side of the flared aperture. When dorsolateral (Figure 3J), it is possibly still functional as a stabiliser, to some extent, by providing a counterweight to the adult aperture and to stop a shell from being completely overturned, but normally does not touch the substrate. This position is uncommon, and a dorsolateral varix is often accompanied by an additional slight swelling (which may not be a true varix) in a ventrolateral position (Figures 3H, J). A dorsal penultimate varix (Figures 3D–E), on the other hand, is positioned to function like a righting dorsal tubercle (see below). In this case, the penultimate varix is virtually always accompanied by an additional, ventrolateral varix positioned as a stabiliser (Figures 3D–E).

The ventrolateral swelling of *Rhinocoryne* (Figures 14A–D) is constructionally unrelated to the peripheral tubercles, as shown by its placement. Likely, it has the same function of a ventrolateral varix as a stabiliser. In *Bellatara*, instead, both the ventrolateral swelling and a spiral row of tubercles are located along a pigmented line that is visible just above the whorl suture of the last couple of whorls (Figures 8D–E). Thus, the swelling in this genus probably is a modified tubercle, and is only convergent with the swelling of *Rhinocoryne* and the ventrolateral varix of other cerithiforms. Thus, the occurrence of at least three constructionally distinct but morphologically convergent structures in similar locations reinforces the functional interpretation given above.

Dorsal righting projections. Knobs, tubercles or swellings located on the dorsal surface of the last or penultimate whorl are optimally positioned to facilitate righting by preventing an overturned shell from laying with the aperture pointing straight upwards. An aperture that is forced to be inclined toward either side is closer to the substrate, and also reduces the risk that the organism will be attacked by a predator while attempting to right itself. Comparable features have been described in other gastropods (e.g., Savazzi, 1991b; Savazzi and Sasaki, 2004).

These features are common on the last whorl of epifaunal or presumed epifaunal cerithiforms (e.g., Figures 2C, O, U; 3K–M; 12D, L–P; 14D), but are located on the penultimate whorl in burrowing forms (Figures 3N–Q; 7C, Q, U; 8H). A similar situation occurs in epifaunal versus burrowing strombids (Savazzi, 1991b). This can be explained as a tradeoff with the necessity of shallow burrowers to prevent portions of the shell from projecting above the surface of the sediment, which is easier to achieve if dorsal projections are not located on the last whorl.

In this context, the slightly dorsolateral varix of some *Clypeomorus* (Figure 3J) may represent a compromise between the advantage in righting provided by a dorsal projection, and its disadvantage in projecting above the substrate when shallowly buried (which is lessened by a dorsolateral, rather than dorsal, placement).

Partly hollow tubercles. The ventral crater-like tubercles of *Bellatara* are superficially similar to the respiratory holes of the Haliotidae, which become plugged secondarily with shell material. However, adult and subadult haliotids display a suture-like line joining adjacent holes, marking a corresponding permanent slit in the mantle edge. No such feature is present in *Bellatara*, and no cerithiforms possess a selenizone, unless one considers the exhalant respiratory tube of the Triforidae or the exhalant notch of *Faunus* (Figures 15B–C) as analogous. The former, however, is present only near the adult aperture. The latter is most developed in the adult.

This suggests that the craters in *Bellatara* do not represent secondarily plugged apertures in the shell surface. We propose that the cratered tubercles were originally covered by a thin canopy of shell material. Secondary shell thickening, instead of filling these tubercles, bridged across their bases, leaving a hollow space within the tubercles. Erosion of the shell surface at a subsequent growth stage (i.e., when the tubercles were located ventrally), caused by friction of the shell being dragged against the substrate, destroyed the canopy, leaving its sharp margin as the edge of the craters.

On the dorsal region, these tubercles are optimally positioned to facilitate righting (see above). Accordingly, these tubercles usually are larger and not cratered.

The ventral region of the last whorl is flat and recessed with respect to the preceding whorl (Figures 8A–D, F, H). Together with a similarly flattened dorsal portion of the last half-whorl (Figures 8B, D, F), this gives the adult shell a pupiform profile when viewed from the side, suggesting that this species was infaunal or semi-infaunal like *Rhinoclavis*. Savazzi (1991b) described a comparable morphology in burrowing strombids.

The tubercles of *Bellatara* likely evolved from antipredatory features comparable with those of many other cerithiforms. They possessed a stiffening function also if not secondarily filled with shell material, especially while located near the thin aperture of a growing shell (it is useful to remember that even non-thickened undulations of the shell surface increase its stiffness). Once growth brought them to a ventral position, however, they became an obstacle to shell dragging. Selective pressure to secondarily remove the tubercles from the ventral region of the adult may have favoured the evolution of hollow tubercles preprogrammed to wear down. This may appear as an ''awkward'' solution (from the point of view of a technological design), but many such examples are known in evolutionary biology. Occasional individuals with large and massive ventral tubercles (Figure 8G) suggest that the morphogenetic program of these features was not yet fully stable in this species.

Internal barriers. These features in *Terebralia palustris* are not apertural, because they are built well within the aperture. Thus, their function is not comparable to the superficially similar apertural barriers observed in other gastropods (e.g., Ranellidae, Nassariidae, several pulmonate families). In the latter gastropods, the barrier is an integral part of the aperture, built at the same time as other apertural features. The principal function of apertural barriers is restricting access to the shell interior by predators, or defending against shell peelers, by making it difficult to position correctly the peeling organs, as well as by increasing the aperture stiffness.

The internal barriers of *T. palustris* become effective against peelers only once the portion of shell between the barrier and the aperture is peeled off. Thus, the barrier constitutes a second line of defence. Until the flaring adult aperture has been built and thickened (and possibly even afterwards), its outer lip is vulnerable to breakage, as documented by frequent instances of shell repair in this region. This sublethal breakage was never observed to cross an internal barrier. In the latter event, the attack invariably seems to be lethal, because the thin shell past the barrier allows a predator to continue peeling.

Internal barriers located within the penultimate varix are observed also in *Rhinoclavis kochi* (Figure 1E). Frequent sublethal attacks by peeling crabs (Figures 1D–E) show its effectiveness as an antipredatory adaptation. Vermeij (1982) found that varices in several Indo-Pacific species of *Rhinoclavis* deter predation by *Calappa* crabs, and prevent the spreading of cracks. In this context, it should be noted also that high-spired shells in general allow the mollusc to retract deeply within the shell, which forces a peeling predator to expend a large amount of energy to reach the soft parts, and thus are in themselves a defence against predators (Vermeij, 1993). Thus, even broadly spaced varices (like those often observed in juvenile cerithiforms) are an effective antipredator device.

The presence of deep furrows that cross most of the shell thickness in *Terebralia* is surprising, considering that the furrows interrupt the shell structure across the whorl, making it presumably less stiff than a uniformly thickened structure. In fact, the whorls in these forms effectively consist of a rib cage of thick spiral stripes joined by a thin coating of shell material bridging the shell interior between adjacent stripes.

In other gastropods (e.g., the Conidae; Kohn, 1999, and references therein) the shell microstructure favours breakage of the shell in a direction parallel to the outer lip. This has been interpreted (Kohn, 1999, and therein) as a defence against predators, effective in increasing the amount of time and energy spent by shell peelers to gain access to the soft parts. In *Terebralia*, it could be expected that the spiral furrows in a secondarily thickened shell have the opposite effect (i.e., favouring cracks to follow a spiral direction). However, repaired damage of this type was not observed in our material. Instead, all sublethal damage in *Terebralia* seems to have occurred when the shell was very thin, and did not display a marked tendency to break in any specific direction. This type of unsuccessful attack almost always stops in proximity of an internal barrier.

These characteristics suggest that the primary adaptive significance of the furrows is of stiffening the shell against peeling (by the corrugated iron paradigm) when the shell is thinnest. Once secondarily thickened, these regions of the shell become effectively protected by their increased stiffness, even though the thickened shell is made less than optimal by the presence of external furrows (which cannot be filled secondarily). This appears to be a tradeoff between mechanical performance in the growing versus adult stages, and its inherent risks to the subadult and adult are also lowered by the internal barrier.

Synchronised sculpture. This is a periodic sculpture with elements juxtaposed from one whorl to the next. It is relatively frequent among gastropods (albeit not cerithiforms), and has been interpreted as possessing a variety of functions (Savazzi and Sasaki, 2004). In *Pyrazus*, synchronised sculpture (Figures 12I–K) likely plays a dual role in stabilizing the shell against overturning, and providing a mechanical stiffening (Savazzi and Sasaki, 2004). In some *Pyrazus* with synchronised sculpture, the sculpture on the last whorl differs from earlier stages (Figures 12I, L, N), and its elements are modified in shape and position to form a ventrolateral varix and/or one or more dorsal righting projections. Synchronised sculpture is also displayed by several Mesozoic Procerithiidae (Figures 16A–D). This is an unusually modern feature among Mesozoic gastropods.

Terraces. The orientation of terraces in *Rhinoclavis* is consistent with a burrowing function for these sculptures (see Savazzi, 1994a, 1994b, and references therein, for a review of burrowing terraces and other frictional sculptures). In fact, Signor (1982a) experimentally demonstrated a burrowing function for the terraces in living *R. aspera*. Comparable asymmetrical sculptures occur in several other cerithiids, including *Bittium* (which does indeed burrow; Savazzi, 1989a) and *Argyropeza* (Kohn, 1986). Houbrick (1991), however, disagreed with a burrowing function for sculptures in the latter genus.

Other cerithiids (e.g., *Pseudovertagus aluco*) possess an asymmetric sculpture superficially similar to burrowing terraces. However, this sculpture is much coarser than burrowing terraces (Figures 7B–C; see discussion in Savazzi, 1994a, 1994b). In addition, often it occurs in species that do not seem to burrow, or that do not do so often and/or quickly.

There may be another explanation for these asymmetric sculptures. These species periodically drag the shell along the surface of the substrate during locomotion. Once the shell is pulled forward and above the cephalopedal mass of the mollusc, it may tend to slip backwards after the columellar muscle is relaxed. In fact, a moderate amount of shell backslippage is observed, e.g., in the epifaunal locomotion of *Batillaria* (Savazzi, unpublished), especially when moving slightly uphill on mud. Under these conditions, backslippage may be reduced by asymmetrical sculptures, in a way not unlike the function of burrowing sculptures. In fossil species, such sculptures could erroneously be interpreted as burrowing terraces if attention is not paid to their coarseness.

Comparison with the Strombidae

Savazzi (1991b, and references therein) studied the constructional morphology of the Strombidae. Although obviously different from cerithiforms in general shape, behaviour and evolutionary history, strombids share with cerithiforms a determinate growth pattern with specialised adult apertures and, frequently, a countdown ontogenetic pattern. Savazzi (1991b) proposed several criteria for the functional interpretation of morphology in strombids. A comparison of the two groups is carried out in this section.

Anterior siphonal canal. The anterior canal of adult *Rhinoclavis* is essentially identical to the one of *Strombus* (*Euprotomus*). Both taxa are sand burrowers, and their anterior canal houses the inhalant respiratory current (Savazzi, 1988). Unlike in *Rhinoclavis*, the anterior canal of *Euprotomus* is bent perpendicularly to the aperture plane (as a consequence of the latter being held horizontal, not oblique like in *Rhinoclavis*). In both taxa, different species show a different length of the anterior canal.

Anterior region of outer lip. A few burrowing strombids (e.g., *Strombus dentatus*) have the anterior portion of the outer lip modified into an oblique plough, which shelters the footstalk from being directly pressed against the substrate (Savazzi, 1988). These strombids also have a slightly prosocline aperture, which presumably facilitates dragging the shell forward through the sediment by contracting the columellar muscle. Both characters are observed also in *Rhinoclavis. Strombus dentatus* possesses three blunt teeth on the portion of the outer teeth that slices through the sediment. These projections may be involved in burrowing (e.g., compare with the teeth along the digging edge of mechanical excavators). Cerithiforms, however, do not possess comparable projections, with the notable exception of the Eocene *Ptychocerithium lamellosum* (Figure 9A), in which two large teeth on the outer lip are located in correspondence of prominent spiral keels on the shell exterior.

In this context, it can be noted that material of this species from the Paris Basin (France) is generally small-sized and lacks any visible asymmetry of the keels, while larger specimens from other localities (e.g., Savazzi, 1989a, Figure 9F) have distinctly terrace-shaped keels. Strombids lack terrace sculptures (Savazzi, 1991b).

Ventrolateral swelling. A ventrolateral varix, swelling or projecting secondary callus is common in strombids. In this family, it acts as a stabiliser to reduce the risk of overturning during surface locomotion. The closely comparable ventrolateral swelling or varix of cerithiforms is discussed above.

Flattened dorsum of last whorl. In the Strombidae, this adaptation is related to burrowing, and prevents the dorsal portion of the last whorl from projecting above the surface of the sediment when infaunal. It is found also in Recent infaunal or semi-infaunal Cerithiidae (e.g., *Rhinoclavis*, Figures 5G, J, O, T; *Pseudovertagus*, Figure 7C) as well as fossil taxa likely to have been burrowers (e.g., *Cerithioclava*, Figure 7L; *Bezanconia*, Figure 7O; *Bellatara*, Figures 8B, D), but also in taxa that are only occasional burrowers (e.g., *Cerithium rostratum*; Figures 2G–H, species of *Clypeomorus*; Figure 3O) or probably epifaunal (e.g., *Colina*, Figure 4C).

Dorsal righting knobs or varices. This character is common among the Strombidae, with most genera displaying examples. These features are essentially identical to those observed in cerithiforms. In both cerithiforms and strombids, dorsal righting projections are typically found on the last whorl in epifaunal forms, and on the penultimate whorl in infaunal ones (see also above).

Concluding remarks. All characters discussed in this comparison between strombids and cerithiforms result from a determinate growth pattern (albeit a few of them may also be achieved, to some extent, by a periodic growth pattern). A few adaptations of strombids (e.g., long posterior canals to inform the organism whether the dorsal portion of the shell is buried; selective weighting of the ventral shell regions; extensive secondary apertural calluses that modify the shape of the aperture or whole shell) do not have counterparts in cerithiforms. Nonetheless, we regard it as remarkable that gastropod groups with such different modes of locomotion (leaping in strombids *versus* shell dragging in cerithiforms) and evolutionary histories share several morphologic adaptations that are the result of parallel evolution. In both groups, many of these functional characters have evolved multiple times in separate lineages.

Functional contexts

This section summarizes the above discussion by arranging the adaptive significance of morphologic characters in general functional contexts.

Defence from shell-peeling predators. Most types of sculpture, and especially spiral rows of tubercles and knobs, increase shell stiffness (by analogy with the paradigm of a corrugated or ribbed iron sheet). Preadult internal barriers, preadult varices and flared and thickened adult apertures are also functional in this context.

Burrowing and infaunal life. Burrowing sculptures, a bent and elongated inhalant adult siphon, a plough-like adult outer lip and/or a flattened dorsal region of the last whorl accompany this life habit.

Caution should be exercised when using the presence of naticid boreholes as indirect evidence of infaunal habits in cerithiforms. Although most naticids hunt and drill infaunally (e.g., Kabat, 1990, and references therein), exceptions are known (e.g., Guerrero and Reyment, 1988; Savazzi and Reyment, 1989; Dietl, 2002). In addition, it is well known that naticids sometimes drill empty buried shells (above references, and therein). Nonetheless, a high frequency of naticid borings in certain species, together with additional evidence, can weight in favour of a burrowing hypothesis. This is the case, for instance, of a few cerithiid and potamidid species from the European Palaeogene, including taxa, like *Semivertagus*, that are regarded as very likely infaunal on the basis of shell morphology.

Clamping of the aperture onto a solid substrate. A broad tangential adult aperture provides this function in a few convergent taxa. The adult siphon in *Terebralia sulcata* wraps completely around the mantle tissues, leaving only the tip open for respiration. This appears to be an extreme adaptation to prevent desiccation.

Stabilisation of the shell when epifaunal. A flared adult outer lip, accompanied by a ventrolateral varix or swelling on the opposite side of the shell, increases the width of its "footprint", and makes it less likely to overturn. This applies to both hard bottom and soft bottom forms. While a flared aperture is almost ubiquitous among cerithiforms, and therefore likely a shared character of the cerithiform *Bauplan*, there are three distinct types of ventrolateral swellings or varices located on the opposite side of the last whorl. Their construction follows different principles, and this allows us to recognize them as a result of convergent evolution triggered by a highly adaptive premium of this character.

Righting after accidental overturning. One or more projecting dorsal tubercles, or a dorsal varix, facilitate righting by preventing the aperture of an overturned shell from facing directly upwards. This reduces the efforts of the organism in righting, and the risk of being attacked by a predator in the process. These characters are located on the last whorl in prevalently epifaunal forms, but on the penultimate whorl in burrowers, in which the surface of the last whorl would project above the surface of the sediment when infaunal. In *Bellatara*, secondarily thickened (and therefore permanent) dorsal tubercles are accompanied by hollow ventral tubercles that are removed by abrasion against the substrate in the adult stage. This removes the conflict between a stiffening function of these tubercles, advantageous to the subadult, and the hindrance caused to the adult, at a subsequent time, by their additional friction when dragging the shell against the substrate.

Conclusions

Several morphological characters of cerithiforms are observed, or inferred, to be adaptive. While some of these characters are widespread, and therefore provide little clue as to their evolutionary patterns, a few display unique constructional differences, which are the telltale sign of convergent evolution. The adaptations occur within a few broad functional areas.

Defence from shell-peeling predators

External relief increases shell stiffness, especially when the shell is thin. A thickened and flared adult aperture is also functional in this context. The multiple evolution of comparable sculptures has resulted in a high degree of convergence among unrelated cerithiform lineages. The coarsest sculpture is found among epifaunal taxa, or taxa that burrow only for temporary shelter.

The very deep and narrow furrows of *Terebralia* are interpreted as increasing stiffness during growth, by folding the shell surface perpendicularly to the aperture at a time when the most recent portion of the shell is very thin. Once the shell is secondarily thickened, the relief is secondarily filled and smoothened interiorly, but the corresponding external furrows cannot be filled. They appear to lose their advantage as stiffeners in the adult, and may even lower the overall strength of the shell. This sculpture is interpreted as a tradeoff between the optimizations of a growing and a fully developed shell.

Internal barriers, effective in stopping shell peelers, are found in at least two families. They occur at apparently random intervals during growth, but in the adult the last barrier is located at an angular distance from the aperture that is constant in each species. The barriers are built secondarily within the shell, not at its aperture.

Burrowing and infaunal life

Burrowing sculptures are present in some species of *Rhinoclavis*. Superficially similar, but coarser sculptures are found in both epifaunal forms and facultative burrowers. It is proposed that the frictional properties of these sculptures may reduce backslippage of the shell also during epifaunal shell dragging, in a manner similar to burrowing.

Rhinoclavis has a very curved and elongated inhalant adult siphon, functional in reaching the surface of the sediment when infaunal. Other taxa have a similar, albeit shorter siphon that probably functions in the same way.

Rhinoclavis also possesses a distinctive plough-like adult outer lip, which shelters the head and foot stalk from abrasion against the sediment.

The dorsal region of the last whorl is flattened and its profile is often recessed with respect to the penultimate whorl in burrowing forms. This allows the last whorl to lie at or below the surface the sediment.

Clamping of the aperture onto a solid substrate

A broad tangential adult aperture, suitable for clamping, is observed in hard-bottom species, especially among *Clypeomorus* and *Terebralia*. Soft-bottom forms, conversely, have apertures poorly suited to clamping.

Specialised exhalant regions

A posteriorly elongated adult aperture in a few Cerithiidae is likely to provide a better separation between inhalant and exhalant currents. An exhalant notch in the Potamididae, Campanilidae and Thiaridae provides a similar function.

Stabilisation of the shell

A broad, usually flaring adult outer lip increases the ventral "footprint" of the shell on the substrate.

In numerous taxa, a swelling or varix is located on the left ventrolateral side of the last whorl in the adult stage. This projection increases the footprint of the shell on the side opposite the aperture. This projection sometimes houses an internal barrier (see above). In these cases, a concurrent function as antipredator defence is involved. However, the latter function alone does not explain the preferential placement of the swelling/varix. At least three nonhomologous and constructionally different types of ventrolateral projections, some of which have no apparent antipredatory value, but all of which fit the stabilizing paradigm, have evolved in cerithiforms, as a result of functional convergence.

Righting after accidental overturning

Projecting dorsal tubercles or a varix on the last or penultimate whorl are common. They make an overturned shell unstable, and force its aperture to lean toward either side instead of pointing straight up. Like in other gastropods, this facilitates righting.

In *Bellatara*, secondarily filled dorsal tubercles are accompanied by hollow ventral tubercles that are removed by abrasion against the substrate in the adult stage.

Epifaunal forms tend to have dorsal projections on the last whorl, while burrowers often build them on the penultimate whorl, where they project to a lesser extent above the surface of the sediment when the organism is infaunal or semi-infaunal.

Growth pattern

Most of the adaptive characters discussed in this paper are allowed by determinate growth and a countdown ontogenetic programme. In particular, the latter is essential to features, like dorsal tubercles and ventrolateral projections, that must be placed at a precise angular distance from the adult aperture in order to function.

Acknowledgements

Travel and research grants were provided by the Japan Society for the Promotion of Science, the Sys:Resource programme at the Natural History Museum, London, UK, the Chinese Academy of Science, the Swedish Foundation for International Cooperation in Research and Higher Education, the Swedish Royal Society of Science, the Sweden-Japan Foundation, the Swedish Natural Sciences Research Council, the Sederholm travel fund from Uppsala University and the Sonderforschungsbereich 53 "Palökologie" at Tübingen University, Germany.

References

Alastair, G., 1938: On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. *Proceedings of the Zoological Society of London*, vol. 108, p. 453–463.

Andrews, H. E., 1974: Morphometrics and functional morphology of *Turritella mortoni. Journal of Paleontology*, vol. 48, p. 1126–1140.

Ayal, Y. and Safriel, U. N., 1982: Role of competition and predation in determining habitat occupancy of Cerithiidae (Gastropoda: Prosobranchia) on the rocky, intertidal, Red Sea coasts of Sinai. *Marine Biology*, vol. 70, p. 305–316.

Bertness, M. D. and Cunningham, C., 1981: Crab shell-crushing predation and gastropod architectural defense. *Journal of Experimental Marine Biology and Ecology*, vol. 50, p. 213–230.

Cossmann, M. 1906. *Essais de Paléoconchologie Comparée*. Vol. 7, 261 p., De Rudeval, Paris.

Darragh, T. A., 2002: *Campanile* (Mollusca: Gastropoda): a new record from the early Miocene of Victoria, Australia. *Alcheringa*, vol. 26, p. 501–506.

Dietl, G. P., 2002: Traces of naticid predation on the gryphaeid oyster *Pycnodonte dissimilaris*: epifaunal drilling of prey in the Paleocene. *Historical Biology*, vol. 16, p. 13–19.

Donovan, D. A., Danko, J. P. and Carefoot, T. H., 1999: Functional significance of shell sculpture in gastropod molluscs: test of a predator-deterrent hypothesis in *Ceratostoma fo-*

liatum (Gmelin). Journal of Experimental Marine Biology and Ecology, vol. 236, p. 235–251.

Donovan, S. K. and Blissett, D. J., 1998: Palaeoecology of the giant Eocene gastropod *Campanile. Eclogae Geologicae Helvetiae*, vol. 91(3), p. 453–456.

Fratini, S., Cannicci, S. and Vannini, M., 2001: Feeding clusters and olfaction in the mangrove snail *Terebralia palustris* (Linnaeus) (Potamididae: Gastropoda). *Journal of Experimental Marine Biology and Ecology*, 261: 173–183.

Fratini, S., Vigiani, V., Vannini, M. and Cannicci, S., 2004: *Terebralia palustris* (Gastropoda; Potamididae) in a Kenyan mangal: size structure, distribution and impact on the consumption of leaf litter. *Marine Biology*, vol. 144, p. 1173–1182.

Fretter, V., 1951: Observations on the life history and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L). *Journal of the Marine Biological Association of the United Kingdom*, vol. 29, p. 567–586.

Guerrero, S. and Reyment, R. A., 1988: Predation and feeding in the naticid gastropod *Naticarius intricatoides* (Hidalgo). *Palaeogeography Palaeoclimatology Palaeoecology*, vol. 68, p. 49–52.

Haas, O., 1953: Mesozoic invertebrate faunas of Peru. *Bulletin of the American Museum of Natural History*, vol. 101, p. 1–328.

Healy, J. M. and Wells, F. E., 1998a: Superfamily Cerithioidea. *In*, Beesley, P. L., Ross, G. J. B. and Wells, A. *eds*., *Mollusca, the Southern Synthesis*, p. 707–733, ABRS and CSIRO Publishing; Collingwood.

Healy, J. M. and Wells, F. E., 1998b: Superfamily Campaniloidea. *In*, Beesley, P. L., Ross, G. J. B. and Wells, A. *eds*., *Mollusca, the Southern Synthesis*, p. 733–737, ABRS and CSIRO Publishing; Collingwood.

Houbrick, R. S., 1974: Growth studies on the genus *Cerithium* (Gastropoda: Prosobranchia) with notes on ecology and microhabitats. *Nautilus*, vol. 88, p. 14–27.

Houbrick, R. S., 1978: The family Cerithiidae in the Indo-Pacific, part 1: The genera *Rhinoclavis*, *Pseudovertagus* and *Clavocerithium. Monographs of Marine Mollusca*: vol. 1, p. 1–125.

Houbrick, R. S., 1981: Anatomy, biology and systematics of *Campanile symbolicum* with reference to adaptive radiation of the Cerithiacea (Gastropoda: Prosobranchia). *Malacologia*, vol. 21, p. 263–289.

Houbrick, R. S., 1984: The giant creeper, *Campanile symbolicum* Iredale, an Australian relict marine snail. *In*, Eldridge, N. and Stanley, S. *eds*., *Living Fossils*, p. 232–235, Springer-Verlag, Berlin.

Houbrick, R. S., 1985: Genus *Clypeomorus* Jousseaume (Cerithiidae: Prosobranchia). *Smithsonian Contributions to Zoology*, vol. 403, p. 1–131.

Houbrick, R. S., 1986: Discovery of a new living *Cerithioclava* species in the Caribbean (Mollusca: Prosobranchia: Cerithiidae). *Proceedings of the Biological Society of Washington*, vol. 99, p. 257–260.

Houbrick, R. S., 1991: Functional inference from gastropod shell morphology—some caveats, *Lethaia*, vol. 24, p. 265–270.

Houbrick, R. S., 1992: Monograph of the genus *Cerithium* Bruguière in the Indo-Pacific (Cerithiidae: Prosobranchia). *Smithsonian Contributions to Zoology*, vol. 510, p. 1–211.

Jung, P., 1987: Giant gastropods of the genus *Campanile* from the Caribbean Eocene. *Eclogae Geologicae Helveticae*, vol. 80, p. 889–896.

Kabat, A. R., 1990: Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia*, vol. 32, p. 155–193.

Kamimura, S. and Tsuchiya, M., 2003: The effect of feeding behavior of the gastropods *Batillaria zonalis* and *Cerithideopsilla cingulata* on their ambient environment. *Marine Biology*, vol. 144, p. 705–712.

Kiel, S., Bandel, K., Banjac, N. & Perrilliat, M. C., 2000: On Cretaceous Campanilidae (Caenogastropoda, Mollusca). *Freiberger Forschungshefte*, vol. C 490, p. 15–26.

Köhler, F. and Glaubrecht, M., 2003: Morphology, reproductive biology and molecular genetics of ovoviviparous freshwater gastropods (Cerithioidea, Pachychilidae) from the Philippines, with description of a new genus *Jagora. Zoologica Scripta*, vol. 32, p. 35–59.

Kohn, A. J., 1986: Slip-resistant silver-feet: shell form and mode of life in Lower Pleistocene *Argyropeza* from Fiji. *Journal of Paleontology*, vol. 60, p. 1066–1074.

Kohn, A. J., 1999: Anti-predator defences of shelled gastropods. *In*, Savazzi, E. *ed*., *Functional morphology of the invertebrate skeleton*, pp. 169–181, John Wiley and Sons, Chichester.

Kohn, A. J., Myers, E. R. and Meenakshi, V. R., 1979: Interior remodeling of the shell by a gastropod mollusc. *Proceedings of the National Academy of Science of the United States*, vol. 76, p. 3406–3410.

Lasiak, T. and Dye, A. H., 1986: Behavioural adaptations of the mangrove whelk, *Telescopium telescopium* (L.), to life in a semi-terrestrial environment. *Journal of Molluscan Studies*, vol. 52, p. 174–179.

Linsley, R. M., 1978: Shell form and the evolution of gastropods. *American Naturalist*, vol. 66, p. 432–441.

Morton, J. E., 1953: *Vermicularia* and the turritellids. *Proceedings of the Malacological Society of London*, vol. 30, p. 80–86.

Morton, J. E., 1967: *Molluscs*. 244 p., Hutchinson University Library, London.

Nützel, A., 2002: The Late Triassic species *Cryptaulax? bittneri* (Mollusca: Gastropoda: Procerithiidae) and remarks on early aspects of the Mesozoic marine revolution. *Paläontologische Zeitschrift*, vol. 76, p. 57–63.

Palmer, A. R., 1977: Function of shell sculpture in marine gastropods: hydrodynamic destabilization in *Ceratostoma foliatum*. Science, vol. 197, p. 1293–1295.

Palmer, A. R., 1979: Fish predation and the evolution of gastropod shell sculpture; experimental and geographic evidence. *Evolution*, vol. 33, p. 697–719.

Paul, C. R. C., 1991: The functional morphology of gastropod apertures. *In*, Schmidt-Kittler, N. and Vogel, K., *eds*., *Constructional Morphology and Evolution*, p. 127–140, Springer-Verlag, Berlin.

Price, R. M., 2003: Columellar muscle of neogastropods: muscle attachment and the function of columellar folds. *Biological Bulletin*, vol. 205: p. 351–366.

Savazzi, E., 1988: Burrowing behavior in Recent Indo-Pacific strombid gastropods. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, vol. 1988, p. 415–430.

Savazzi, E., 1989a: Burrowing mechanisms and sculptures in Recent gastropods. *Lethaia*, vol. 22, p. 31–48.

Savazzi, E., 1989b: New observations on burrowing in strombid gastropods. *Stuttgarter Beiträge zur Naturkunde Serie A* (*Biologie*), vol. 434, p. 1–10.

Savazzi, E., 1991a: Burrowing sculptures as an example in functional morphology. *Terra Nova*, vol. 3, p. 242–250.

Savazzi, E., 1991b: Constructional morphology of strombid gastropods. *Lethaia*, vol. 24, p. 311–331.

Savazzi, E., 1994a: Adaptations to burrowing in a few Recent gastropods. *Historical Biology*, vol. 7, p. 291–311.

Savazzi, E., 1994b: Functional morphology of burrowing and boring organisms. *In*, Donovan, S. K. *ed.*, *The Palaeobiology of Trace Fossils*, p. 43–82, Wiley & Sons, London.

Savazzi, E., 1996: Adaptations of vermetid and siliquariid gastropods. *Palaeontology*, vol. 39, p. 157–177.

Savazzi, E., 1999a: Cemented and embedded gastropods. *In*, Savazzi, E. *ed.*, *Functional Morphology of the Invertebrate Skeleton*, p. 183–195, John Wiley & Sons, Chichester.

Savazzi, E., 1999b: Introduction to functional morphology. *In*, Savazzi, E. *ed.*, *Functional Morphology of the Invertebrate Skeleton*, p. 3–13, John Wiley & Sons, Chichester.

Savazzi, E., Jefferies, R. P. S. and Signor, P. W. III, 1982: Modification of the paradigm for burrowing ribs in various gastropods, crustaceans and calcichordates. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 164, p. 206–217.

Savazzi, E. and Reyment, R. A., 1989: Subaerial hunting behaviour in *Natica gualteriana* (naticid gastropod). *Palaeogeography Palaeoclimatology Palaeoecology*, vol. 74, p. 355–364.

Savazzi, E. and Sasaki, T., 2004: Synchronized sculpture in gastropods. American Malacological Bulletin, vol. 18, p. 87–114.

Schmidt-Kittler, N. and Vogel, K., 1991: Introduction: a new look at morphology. *In*, Schmidt-Kittler, N. and Vogel, K., *eds.*, *Constructional morphology and evolution*, p. 1–6, Springer-Verlag, Berlin.

Seilacher, A., 1970: Arbeitskonzept zur Konstruktions-Morphologie. *Lethaia*, vol. 3, p. 393–396.

Seilacher, A., 1982: Introduction: burrowing strategies. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 164, p. 205–206.

Seilacher, A. and Chinzei, K., 1993: Progress in constructional morphology. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 190, p. 165–167.

Seilacher, A. and Gunji, P.-Y., 1993: Morphogenetic countdowns in heteromorph shells. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 190, p. 237–265.

Signor, P. W. III, 1982a: Constructional morphology of gastropod ratchet sculptures. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 163, p. 349–368.

Signor, P. W. III, 1982b: Influence of shell shape on burrowing rates in infaunal turritelliform snails. *Third North American Paleontological Convention Proceedings*, vol. 2, p. 483–487.

Signor, P. W. III, 1982c: Resolution of life habits using multiple morphologic criteria: shell form and life-mode in turritelliform gastropods. *Paleobiology*, vol. 8, p. 378–388.

Signor, P. W. III, 1983: Burrowing and the functional significance of ratchet sculpture in turritelliform gastropods. *Malacologia*, vol. 23, p. 313–320.

Signor, P. W., 1994: Ratchet riposte: more on gastropod burrowing sculpture. *Lethaia*, vol. 26, p. 379–383.

Signor, P. W. III and Kat, P. W., 1984: Functional significance of columellar folds in turritelliform gastropods. *Journal of Paleontology*, vol. 58, p. 210–216.

Simone, L. R. L., 2001: Phylogenetic analyses of Cerithioidea (Mollusca Caenogastropoda) based on comparative morphology. Arquivos de Zoología, vol. 36, p. 147–263.

Stanley, S. M., 1970: Relation of shell form to life habits of the Bivalvia. *Geological Society of America Memoir*, vol. 125, p. 1–296.

Taylor, J. D., 1968: Coral reefs and associated invertebrate communities (mainly molluscan) around Mahé, Seychelles. *Transactions of the Royal Society of London Series B*, vol. 254, p. 129–206.

Tojo, B. and Masuda, F., 1999: Tidal growth patterns and growth curves of the Miocene potamidid gastropod *Vicarya yokoyamai. Paleontological Research*, vol. 3, p. 193–201.

Trueman, E. R. and Ansell, A. D., 1969: The mechanisms of burrowing into soft substrata by marine animals. *Oceanography and Marine Biology an Annual Review*, vol. 7, p. 315–366.

Vermeij, G. J., 1971: Gastropod evolution and morphological diversity in relation to shell geometry. *Journal of Zoology*, vol. 163, p. 15–23.

Vermeij, G. J., 1979: Shell architecture and causes of death of Micronesian reef snails. *Evolution*, vol. 33, p. 686–696.

Vermeij, G. J., 1981: Apertural form in gastropods. *Lethaia*, vol. 14, p. 104.

Vermeij, G. J., 1982: Gastropod shell form, repair, and breakage in relation to predation by the crab *Calappa*. Malacologia, vol. 23, p. 1–12.

Vermeij, G. J., 1993: *A Natural History of Shells*. 216 p., Princeton University Press, Princeton, NJ.

Vermeij, G. J., 2001: Innovation and evolution at the edge: origins and fates of gastropods with a labral tooth. *Biological Journal of the Linnean Society*, vol. 72, p. 461–508.

Vermeij, G. J. and Signor, P. W., 1992: The geographic, taxonomic and temporal distribution of determinate growth in marine gastropods. *Biological Journal of the Linnean Society*, vol. 47, p. 233–247.

Wenz, W., 1940: Gastropoda, Allgemeiner Teil und Prosobranchia. *In*, Schindewolf, O. H. *ed.*, *Handbuch der Paläozoologie*, vol. 6(1), p. 721–960.

Wrigley, A., 1940: The English Eocene *Campanile. Proceedings of the Malacological Society of London*, vol. 24, p. 97–112.

Yamaguchi, M., 1977: Shell growth and mortality rates in the coral reef gastropod *Cerithium nodulosum* in Pago Bay, Guam, Mariana Islands. *Marine Biology*, vol. 44, p. 249–263.

Yonge, C. M., 1946: On the habits of *Turritella communis* Risso. *Journal of the Marine Biologists' Association of the United Kingdom*, vol. 26, p. 377–380.