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Source: Paleontological Research, 8(4) : 221-239

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/prpsj.8.221

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Paleontological Research, vol. 8, no. 4, pp. 221–239, December 31, 2004
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A comparison of morphological adaptations in the cardiid bivalves *Cardium* and *Budmania*

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Received June 2, 2004; Revised manuscript accepted September 14, 2004

Abstract. A comparison of the Neogene lymnocardiine *Budmania* with Neogene to Recent Cardiinae, and especially *Cardium costatum* Linnaeus, shows homoplasy in the relatively low shell thickness, presence of conspicuous, internally hollow keels and overall shell geometry. However, *Budmania* lacks the secondary shell resorption and associated features found in Cardiinae, and an inferential analysis of the adaptive significance of shell morphology reveals further differences between the two taxa. In particular, the keels in *C. costatum* are optimised for a dual function as mechanical strengthening and as anchors within the sediment, but only for the latter function in *Budmania*.

Key words: Mollusca, Bivalvia, Cardiidae, functional morphology, sculpture, behaviour, burrowing

Introduction

A previous study on the morphological adaptations of shells of cardiid bivalves (Savazzi, 1985) showed that the genus *Cardium* Linnaeus, 1758 and, in particular, the Pliocene to Recent *C. costatum* (Linnaeus) display a number of shell characters not found in other marine representatives of the Cardiidae (see below). On the other hand, the Miocene fresh- or brackish water lymnocardiine *Budmania* Brusina, 1897 displays a shell morphology radically different from that of other Lymnocardiinae and superficially similar to that of *C. costatum*. The present paper compares and analyses the constructional and adaptive significance of these characters in the two lineages.

A particular point of interest in this study is that extreme specialisations in shell morphology, of a type unknown in other cardiids, have evolved in parallel in the Cardiinae and Lymnocardiinae, which otherwise display rather conservative morphologies and are not very closely related to each other (see discussion below). This instance of parallel evolution allows the constructional principles, adaptive significance and possible evolutionary pathways of these features to be compared in the two lineages. A further goal of this comparison is to verify whether the inferential methods used to analyse the adaptive significance of morphologic features are reliable, and sufficiently refined to allow the recognition of detailed differences in adaptive strategies that are similar in a general sense.

Since neither living specimens nor preserved soft parts of the Recent species studied in this paper were available to the authors and the information on the life habits of these species in the literature is rather scanty, this study was carried out as an exercise in actuo-palaeontology.

Material and methods

Several Recent specimens of *Cardium costatum* and *C. hians* Brocchi, 1814, mostly represented by beached isolated valves, were observed in the collections of the Swedish Museum of Natural History, Stockholm, Sweden (abbreviated as SMNH in figure captions and appendix), in the University Museum, University of Tokyo (UMUT) and in the Departments of Palaeontology and Invertebrate Zoology, Natural History Museum, London, United Kingdom (NHM-P and NHM-IZ, respectively). A few additional live-collected specimens of both species were purchased for this study from commercial shell dealers. This last material is in the possession of the authors. Several tens of specimens of *Budmania* spp. (Lymnocardiinae) from the late Miocene of the Pannonian Lake (East Europe; see Geary *et al.*, 2000, and references therein) were observed by E. Savazzi in the collections of the

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Natural History Museum in Vienna, Austria (abbreviated NHMW in the figure captions). Additional fossil specimens of *Budmania* spp. and *C. hians* were observed in the collections of the Department of Palaeontology, Natural History Museum, London, United Kingdom (NHM-P).

The generic and subgeneric taxonomic arrangement of the Cardiidae used herein follows Keen (1980). The descriptive terminology used in this paper follows Keen (1969a), with the following exceptions specific to the taxa discussed herein. The term *intercostae* is used to denote the depressed spaces between the radial ribs of cardiids. This term is applied to both external shell features and their corresponding internal regions. The term *keel* is applied to substantial projections located on top of radial ribs and growing steadily without substantial changes in size and profile at the growing edge, thus forming a continuous relief (as opposed to tubercles and spines, which are features built at periodic intervals and absent from intervening shell regions). Keels are present in *Cardium costatum* and *Budmania* spp.

Techniques for the reconstruction of weight and volume *in vivo*

The volume of the internal shell cavity was measured by filling the shells with beach sand. The sand was subsequently weighted and the weight converted to millilitres by the relationship 148 g = 100 ml, determined by averaging the weight of a few samples of the same sand with a volume of 100 ml (measured with a graduated cylinder). The reconstructed volume *in vivo* was computed by adding the volume of shell material (derived from its weight and an experimentally measured specific gravity of cardiid shell material of 2.53) to the volume of the internal shell cavity (measured as described above). Weight of the living animal was computed by assuming a specific gravity of 1.03 for the soft parts, including water filling the shell. The reconstructed weight *in vivo* could then be calculated by adding this to the weight of the shell.

Taxonomy, morphology and life habits

There is no general consensus on the scope of the family Cardiidae. Keen (1969a, 1969b, 1980) regarded the superfamilies ''Cardiacea'', containing the Cardiidae, Lymnocardiidae and other families, and ''Tridacnacea'', containing the Tridacnidae, as distinct. However, other studies, including recent ones, placed the Lymnocardiinae and Tridacninae as subfamilies within the Cardiidae (e.g., Schneider, 1998; Schneider and Ó Foighil, 1999). There is also a disagreement on the ancestry of the Cardiidae and on the relationships of early Cardioidea with this family (e.g., see discussion and references in Schneider and Carter, 2001). This paper adopts the view of these last authors in regarding the Cardiinae, Lymnocardiinae and Tridacninae as subfamilies of the Cardiidae.

Cardium (s. s.) herein is regarded as containing the species *C. costatum* (the type species of *Cardium*) and *C. hians* (plus possibly a few poorly preserved species from the Neogene to Pleistocene of NW Africa and SW Europe; pers. obs.). *Cardium* (*Bucardium*) contains a few Neogene to Recent species characterised by the intercostae forming deep notches along the posterior shell margin rather than a single, large siphonal gape (e.g., see Savazzi, 1985). *C. hians* sometimes is regarded as a member of *C.* (*Bucardium*), but this view is not followed herein because the combination of morphological shell characters of this species (see below) clearly points to a closer affinity with *C. costatum*. In fact, the presence of keels in the latter species is the only substantial difference from *C. hians*, while *C.* (*Bucardium*) does not possess the large siphonal gape, partly hollow hinge structure, secondarily thinned intercostae and associated microtubules, secondary shell pigmentation and external shell encrustation characteristic of both species of *Cardium* (see below).

Lymnocardium Stoliczka, 1871 is the type genus of the subfamily Lymnocardiinae. The spelling *Limnocardium* is a *nomen nullum* according to Keen (1969a), but this spelling is frequently used also in modern literature. *Budmania* is regarded by some authors (e.g., Marinescu, 1973) as a subgenus of *Lymnocardium*, while others regard *Budmania* as a synonym of *Lymnocardium*. *Budmania* is regarded as a genus herein, because of its substantial differences in shell geometry from all species of *Lymnocardium*.

Most infaunal cardiids (with the exception of the partly smooth Protocardiinae and a few lightweight taxa that have secondarily lost their external sculpture) are characterised by a rounded or oval shell outline and a sculpture consisting of prominent radial ribs (Savazzi, 1984, 1985). The radial ribs usually form interlocking denticles along the commissure line that prevent shearing movements of the valves in closed shells. The foot is long, muscular and L-shaped. It is kept bent, with its distal portion located within the anterior or antero-ventral shell region and its tip pointing in the antero-dorsal direction when the shell is closed (Savazzi, 1985).

With the exception of the Tridacninae and some members of the Fraginae, which are epifaunal or semi-infaunal and possess photosymbiotic zooxanthellae

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(Yonge, 1936; Kawaguti, 1950; Watson and Signor, 1986; Jacobs and Jones, 1989; Jones and Jacobs, 1992; Carter and Schneider, 1997; Isaji *et al.*, 2001), the family Cardiidae contains actively burrowing, shallow-infaunal taxa in soft sediments (e.g., Stanley, 1970; Savazzi, 1982, 1985) and displays a broad range of shell geometries and other morphological specialisations (e.g., Keen, 1980; Savazzi, 1985). Infaunal forms display a variety of locomotory patterns, which include burrowing, emerging from an infaunal position, ploughing (with the commissure line and the distal portion of the foot approximately horizontal and the shell mostly or totally exposed above the sediment) and leaping (Stanley, 1970; Savazzi, 1982). When buried, cardiids typically keep the posterior shell margin level with the surface of the sediment or only slightly buried, and the hinge line vertical or slightly oblique.

Observations

Cardium costatum

Distribution.—This species is found in shallow sandy/muddy bottoms along the Atlantic coast of West Africa as far south as Angola (Sabelli, 1980; Gofas *et al.*, 1989) but, unlike *C. hians* (see below), not in the Mediterranean. It is often locally abundant (Gofas *et al.*, 1989), although apparently not collected on a commercial basis. It is recorded from depths of 0 to 50 m (above references). It is also locally common in Pliocene sediments of the same region (Gofas *et al.*, 1989). According to the scarce information in the literature, it occurs in sediments ranging from coarse sand to mud (e.g., Sabelli, 1980).

External features.—The shell is globose and highly inflated, with a long straight hinge line (Figures 1A–E). The posterior commissure has a rather narrow

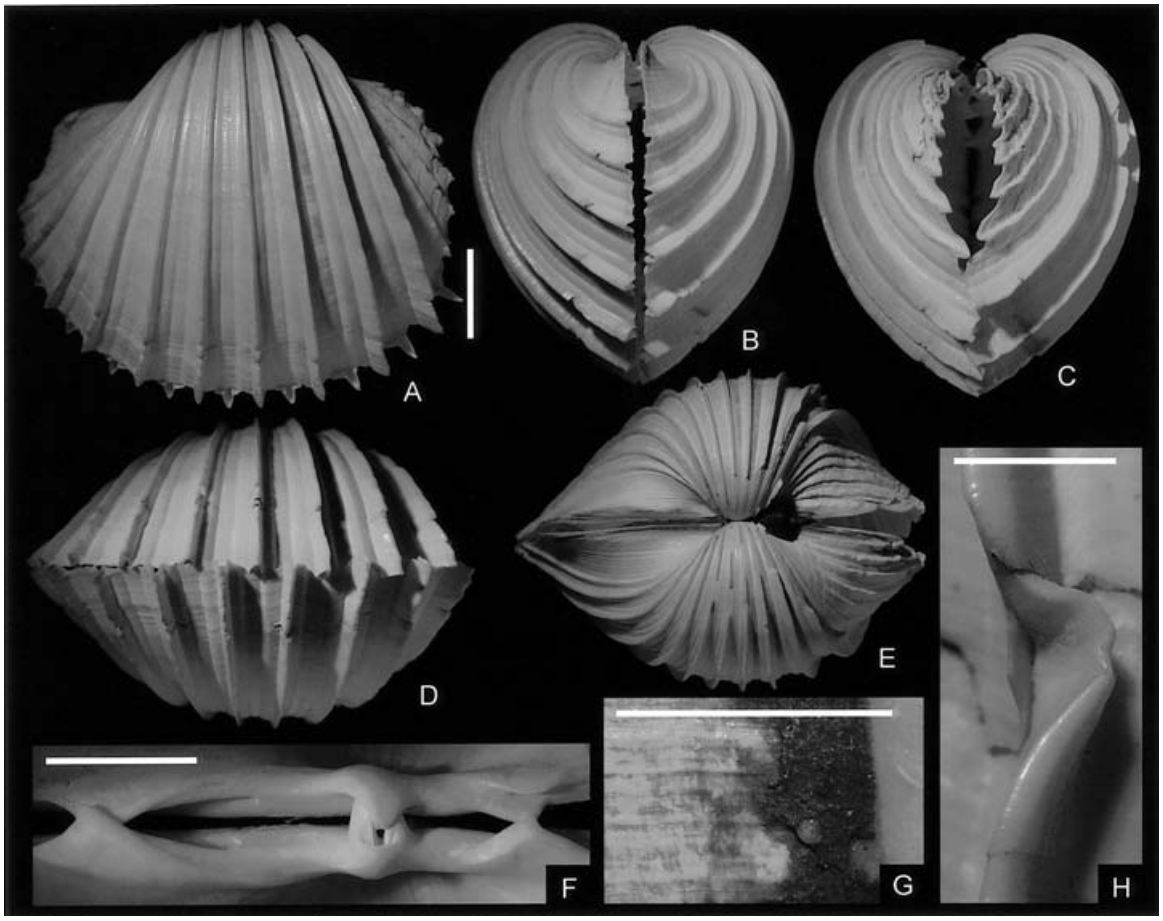


Figure 1. *Cardium costatum* Linnaeus, Recent. A–F. Specimen from Mbour, Senegal. Left lateral (A), anterior (B), posterior (C), ventral (D) and dorsal (E) views. F–H. Specimen from unknown West African locality (SMNH). Internal view of hinge (F, with posterior toward the left), details of crusty deposits on shell exterior (G) and deformed carina on external rib (H).

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permanent gape in the siphonal region (Figure 1C). Each valve bears approximately 15–16 radial ribs, of which those located on the anterior and central slopes bear prominent keels along their crests (Figures 1A–E; see also below). The ribs on the posterior slope (numbering approximately 5 in the available material) bear a much less developed, more irregular ridge along their posterior margin (Figures 1A, C, E). The region of the anterior slope located anteriorly to the first radial rib bears several radial riblets (Figures 1A–B, E).

The radial ribs of opposing valves interlock along the commissure in the posterior half of the central slope. In this region, the commissural extremities of the keels located on the radial ribs project slightly across the commissure plane (Figure 1D). When the shell is viewed in lateral view, the ventral extremities of the keels extend well below the ventral commissure (Figure 1A).

The intercostae are flat and, on the posterior half of the shell, pale brown- or rust-coloured in live-collected specimens. In specimens preserved in their original state, an amorphous or rust-coloured crust covers part or all of the pigmented regions of the intercostae. The pigmented region stops at least 10 mm from the shell-edge. On many specimens, the anteriormost of the pigmented intercostae is pigmented only on roughly its dorsal half.

Internal features.—The keels on the radial ribs are hollow and closed off by very thin septa spaced at irregular intervals. In the observed material, the last of these septa is located at 12 to 32 mm from the ventral extremity of the keels (this distance was measured by inserting a coarse, semi-stiff nylon fishing thread into the keel). The cavity within each keel communicates with the shell interior through a deep notch in the shell margin (Figure 2G). The ventral opening of the cavities within the keels is exposed to the external environment also when the shell is closed (Figure 1A).

The externally pigmented regions of the intercostae correspond to similarly pigmented (albeit devoid of any crusty deposits) areas on the shell interior. These areas are delimited ventrally by an 8–14 mm high region in which the shell appears opaque and visibly reduced in thickness, as compared to the 8–12 mm of height of the intercostae closest to the shell edge. The opaque areas are evidently the site of secondary shell resorption. No resorption is detectable on the interior surfaces of the radial ribs, or in any other region of the shell.

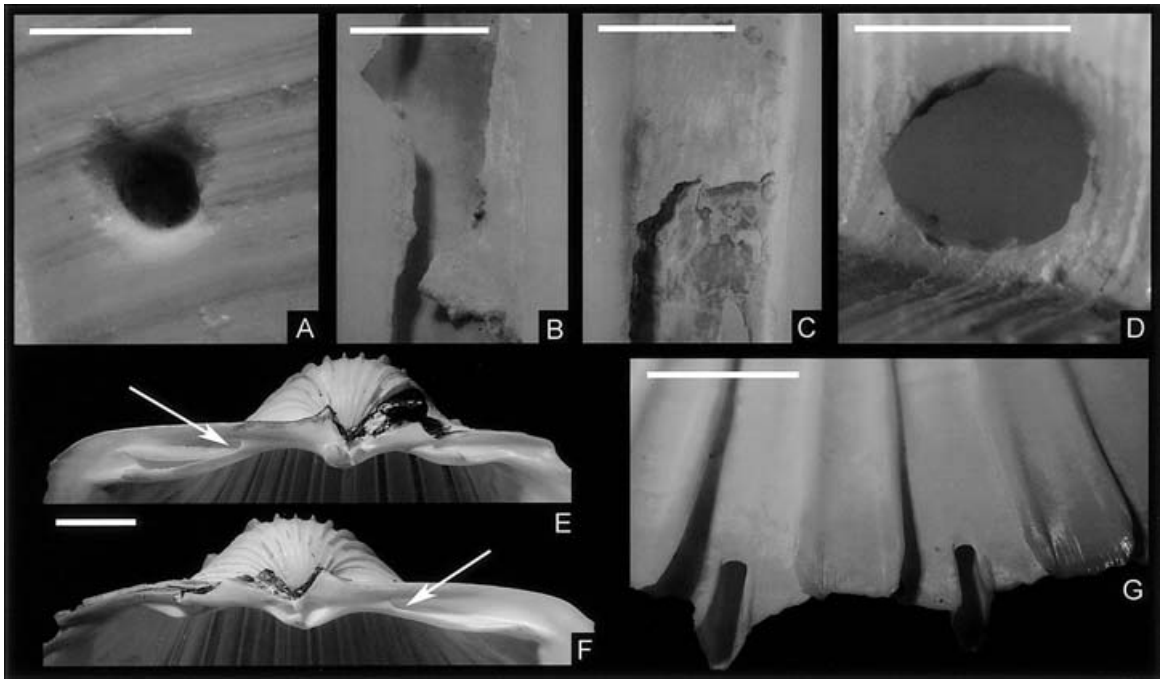


Figure 2. *Cardium costatum* Linnaeus, Recent, West Africa (SMNH). A. External view of borehole located on pigmented intercostal region of central shell slope. B–C. Secondarily deposited layers of shell material on the internal shell surface produced in response to the borehole illustrated in A and D. Smaller, rather irregular borehole on opposite valve of the same specimen illustrated in A–C. In this instance, the bivalve did not react by secreting shell material on the shell interior. E–F. Hinge. Arrows point to hollow sockets. G. Internal view of ventral shell margin, showing notched margins of two keels. Scale bars represent 1 mm (D), 2 mm (A), 5 mm (B, C), 10 mm (E–G).

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In the umbonal region, a thick (2–2.5 mm) layer of secondarily secreted shell material covers both the ribs and their intercostae. In the posterior shell region, the ventral edge of this layer extends ventrally to cover the ribs, but leaves the intercostae exposed.

The anterior hinge sockets of both valves contain rather large cavities which extend up to the beak (arrows in Figures 2E–F). A similar but smaller cavity is present also in the posterior socket of the right valve of most specimens (Figure 2E).

The secondarily etched and the pigmented regions are densely perforated by microtubules reaching the external surface of the shell. These features are absent in other areas of the shell. The microtubules in this species were discussed and illustrated by Seilacher (1990, fig. 4a). The microtubules and their distribution in *C. costatum* are essentially identical to those observed in *C. hians* (Harper and Savazzi, in prep.).

In three specimens, small (0.3–0.7 mm wide) boreholes were observed. One such borehole (Figures 2A–C) was located on the thin, pigmented portion of an intercosta on the posterior shell slope. The bivalve evidently survived the damage, and reacted by depositing an extensive patch of shell material (originally at least 150 mm^2, partly broken off after the specimen was collected) covering most of the region of the intercosta and separated from the original shell surface by a small space. This suggests that the epithelium became detached from the shell interior in this region. The other two boreholes are located on keels well away from the shell margin, and no reaction by the bivalve is visible (Figure 2D).

Cardium hians

Distribution.—This species is recorded from the Pliocene of the Mediterranean (especially Italy; e.g., Rossi Ronchetti, 1952), and the Recent of the southern Mediterranean and the coast of West Africa as far south as Angola (Abbott and Dance, 1983; Bernard, 1984; Gofas *et al.*, 1989). It lives in soft sediments. The depth range provided in the above literature is somewhat inconsistent (intertidal to 30 m according to Abbott and Dance, 1983; 20–50 m according to other authors, see above references). Because of its large siphonal gape (see below), combined with the shallow-infaunal habits typical of cardiids, its contracted siphons would remain largely exposed when the shell is closed, a fact that makes this species unlikely to be typically intertidal.

External surface.—The shell is large, globose and relatively thin, with a broad permanent gape in the posterior region (Figure 3D). The umbones are subcentral and orthogyrate (Figures 3A–B). The sculpture consist of broad radial ribs (Figures 3A–E). Unlike the large majority of cardiids (including *C. costatum*), the ribs in this species do not interlock along the commissure (Fig. 3E), and therefore do not prevent shearing movements of the valves even when the shell is closed. The anterior slope carries rather small fluted spines (Fig. 3A, C, E) comparable with those present in species of *Acanthocardia* (cf. Savazzi, 1985, fig. 12B, F–G). The spines are fragile and easily broken or worn off, and as a consequence they are totally absent on early portions of the shell. These spines are inserted onto the central regions of ribs, and oriented with the concave side facing away from the shell margin. The central slope is devoid of spines, while the ribs on the posterior slope carry moderately long, sharp-tipped spines inserted along the posterior edges of the ribs (Figures 3A–B, D–E). The spines located near the edges of the siphonal gape project from the shell margins and their tips are directed in the posterior direction. As a result, the spines lie obliquely with respect to their insertion surfaces, and almost flat against the shell surface (Figure 3A).

The recessed intercostae have a central secondary, smaller radial riblet. These riblets are rounded in cross-section and never carry spines. In live-collected specimens, the ribs located on the posterior 1/3 to 1/2 of the shell and their surrounding intercostae are covered by a thick, rust-coloured to dark-brown, crusty layer of material (Figure 4A). This material is absent in other regions of the shell, where the periostracum is thin and featureless under visual examination. The encrustation is also absent along a 10–20 mm wide band of shell surface lining the ventral and posterior shell margins. The distribution of the encrustation is also uneven along the midline of the shell, since its distribution varies among intercostal spaces (Figure 3A).

A comparison of specimens of different sizes (60–100 mm in length), which presumably represent different growth stages, shows that the absence of crusty deposits near the shell margin is a constant feature present throughout growth (with the possible exception of specimens shorter than 60 mm, which were not available for this study), and not part of a countdown (Seilacher and Gunji, 1993) morphogenetic programme associated with determinate growth.

In its natural state, the shell is reddish-brown in its central region (i.e., corresponding to the area on the internal shell surface that is enclosed within the pallial line; cf. Figures 3A, B), while a 6 to 15 mm-wide band along the anterior and ventral margins, and a broader band along the posterior margin are much paler in colour (Figure 3A; see also Poppe and Goto, 1993, pl. 16:1a; Matsukuma *et al.*, 1991, pl. 146:11). Speci-

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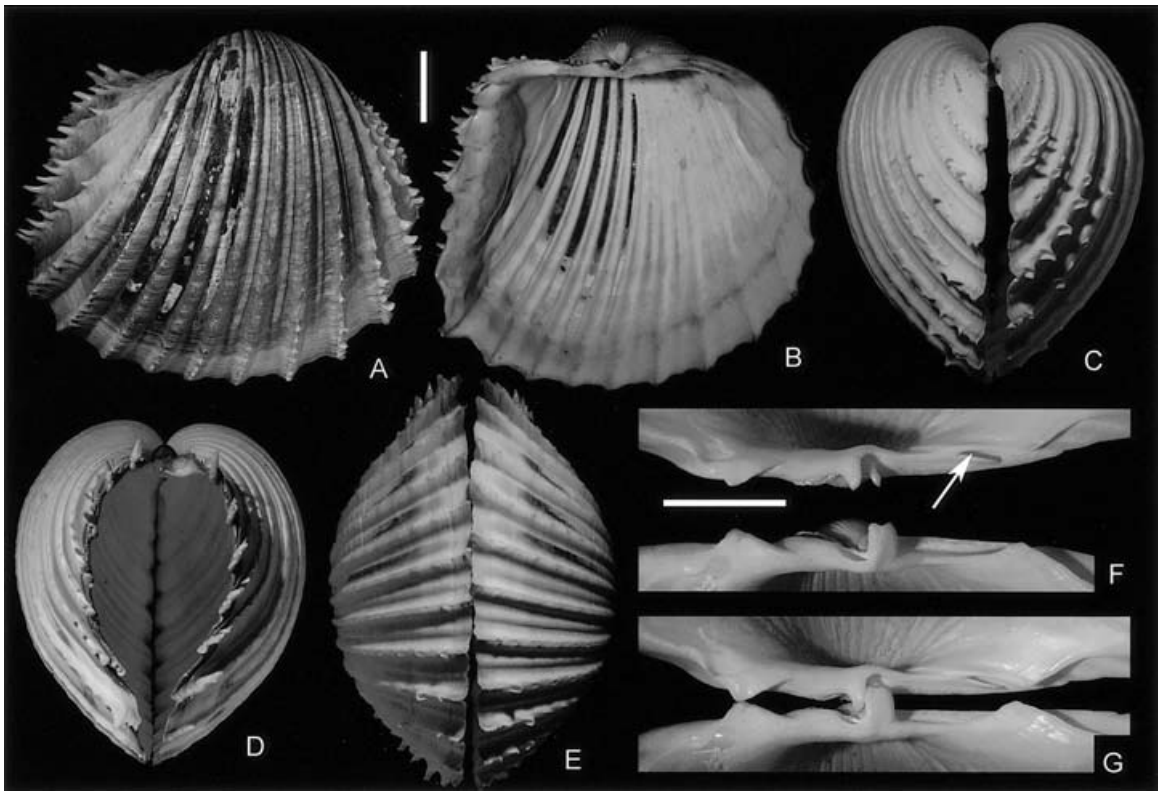


Figure 3. *Cardium hians* Brocchi, Recent. A. Exterior of isolated right valve, Algeria (SMNH). B. Interior of isolated left valve, Algeria (SMNH). C–E. Anterior (C), posterior (D) and ventral (E) views, Dakhla, West Sahara. F–G. Interior view of hinge (with posterior toward the left), Senegal.

mens purchased through shell dealers often have been scrubbed energetically, sometimes bleached with chemicals, and are paler in colour. This applies to several of the Recent specimens illustrated in the modern literature (e.g., Abbott and Dance, 1983; Bernard, 1984, pl. 59, 69). For the same reason, the crusty deposits are often partially or totally absent, but a careful examination often shows that they were originally present.

Boreholes were not observed in *C. hians*.

Internal features.—The muscle scars are large and well developed, and comparable in size and shape with those of large species of *Acanthocardia* (Figure 3B). The pallial line is well marked, and bears a shallow pallial sinus corresponding to the siphonal gape.

There is a rather thick (1.5–2.5 mm) patch of secondarily secreted shell material in the umbonal region. The outline of this patch is uneven and on the posterior half of the shell it is deeply incised in correspondence to the secondary ribs (Figures 3B, 4B–D). The shell in these regions therefore is not secondarily thickened. These incisions are absent on the anterior half of the shell, where the secondary thickening covers the interior of the umbonal region evenly and extends roughly to the middle of the shell height (Figure 3B).

In the posterior half of the shell, the secondary ribs and a narrow surrounding band of shell surface corresponding to the intercostal spaces are dark in colour up to about 20–30 mm from the shell margin (Figure 3B). In the ventral direction, the dark regions are followed by strips where the shell surface appears bleached and eroded (Figures 3B, 4E–F). Erosion markedly decreases the shell thickness in these areas (in adult *C. hians*, roughly from the original 2 mm near the shell margin down to .5 mm well within the pallial line). These strips gradually fade away at a distance of 10–20 mm from the shell margin. Thus, the dark colour and etched regions on the shell interior correspond to the crusty deposits on the outer surface of the shell. Ventrally to the eroded areas, the shell surface on the interior and exterior of the shell appears unaltered.

The hinge line is long and straight, and the anterior socket of the right valve is hollow almost up to the central portion of the hinge in many specimens (arrow

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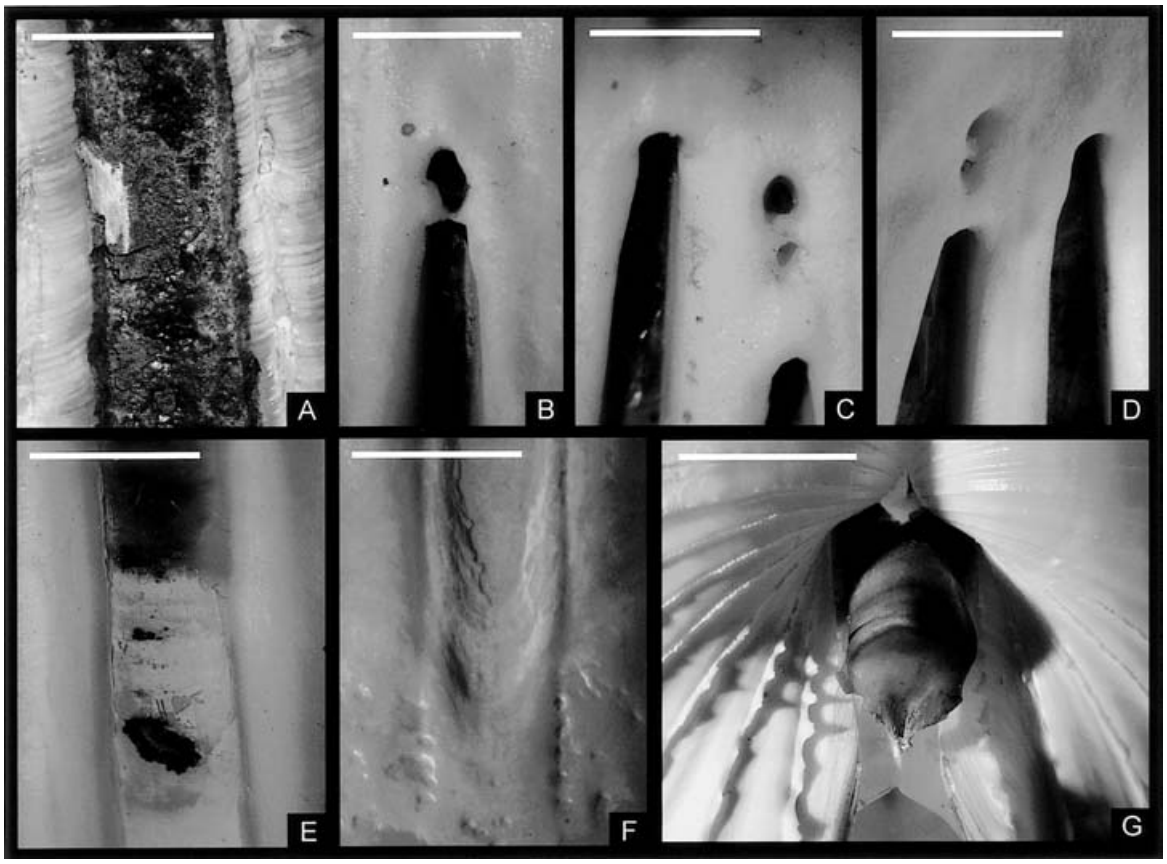


Figure 4. *Cardium hians* Brocchi, Recent, Dakhla, West Sahara. A. Exterior of intercosta with crusty deposits. B–D. Interior of intercostae in umbonal region. E–F. Interior of intercostae in ventral region, showing secondary resorption of shell material (bottom in E, top in F). The scale bar corresponds to 200 μm in A, 50 μm in B–E.

in Figure 3F).

Budmania

Distribution.—The genus *Budmania* is a lymnocardiine exclusive to the Pannonian Lake (Eastern Europe), and is late Miocene in age (Imre Magyar, pers. comm.). It is found prevalently in silt and silty sand, has a patchy occurrence, and often forms an oligotypic association in which other bivalves are scarce or absent (Brusina, 1897, 1902; Marinescu, 1973). The extremely specialised lymnaeid gastropod *Valenciennius* is found with *Budmania*.

External features.—The shell is large and bears a small number of radial ribs, each with a very strong keel. Species and morphs that possess fewer ribs also tend to display stronger keels. The shell displays a permanent siphonal gape (Figures 5D, K). The umbones are typically central and in most species only slightly prosogyrate. Keels are poorly developed or absent around the siphonal gape. The keels are deformed in many specimens (Figures 5A, H). Keels on one valve appear to be deformed independently of those on the opposite valve (Figure 5H).

A few species of *Budmania* have been described, differing mostly in the number and obliquity of radial ribs, and the degree of development of the keels, but there is a considerable intraspecific variability, with superficially similar morphs present in two or more species (Marinescu, 1973).

Internal features.—The hinge is relatively weak compared to other cardiids, but not especially so for a lymnocardiine. The hinge line is long and straight, and typically extends for roughly equal lengths anterior and posterior to the umbo. In these respects it is comparable with that of *Cardium costatum* (see above), but the teeth and sockets are less developed and lack the hollow structure observed in the latter species.

The keels are hollow and contain several parallel cavities that follow the direction of growth, instead of a single cavity as in *C. costatum*. In cross-sections of the keels, each cavity is surrounded by concentric

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Figure 5. A–D, F, H–O. *Budmania semseyi* (Halaváts), Königsgnad, Rumania. Exterior (A), interior (B), dorsal (C) and posterior (D) views of right valve, exterior of right valve of specimen with weaker keels (F), dorsal view of articulated specimen (H), growing extremity (I) of keel, openings of multiple keel cavities in shell interior (J, L), posterior view of closed specimen (K), keels broken obliquely (M) or transversally (N) and showing internal cavities, and diagenedic solution pits on exterior. G. *Budmania* cf. *aequicostata* (Marinescu), Königsgnad, Rumania. Scale bars represent 20 mm (A–K). The picture in K has been processed to lighten the sediment, in order to increase contrast with the shell.

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growth lines (Figure 5N), which indicate that the cavities were occupied by extensions of the mantle that continued to secrete shell material after the external surface of the keel was built. To a lesser extent, a comparable structure is observed in *C. costatum* (Schneider and Carter, 2001, fig. 9.1). Septa were not observed within these cavities in *Budmania*, but occasionally the cavities become suddenly reduced in diameter and a new wall of shell material is built, separated from the old wall by a hollow space (bottom of Fig. 5N). This may be the result of a sudden detachment of the mantle tissues from the walls of the keel cavity and their retraction toward the shell commissure.

The shell edge carries deep notches corresponding to the growing extremities of the keels (Figure 5B). This character is comparable with the similar notches in *C. costatum* (Figure 2G), but in *Budmania* one or more of the cavities within a keel may open directly into the shell cavity, in a position dorsal to the corresponding notch (Figure 5J). Individual cavities near the edge and the base of the keel are subcircular in cross-section, while those in the central region of the keel are compressed laterally in most specimens (Figure 5N). The shell margin along the growing edge of each keel is sharp and rather thin (Figure 5I). In this region, there is a single, elongated cavity within the keel, which subsequently separates into several individual cavities.

The edges of the intercostae along the ventral margin form projecting structures that interlock with the internal side of the ribs of the opposite valve when the shell is closed, thus preventing shearing movements of the valves (see a comparable situation in the case of *Cardium costatum*, above). The construction of the projecting edges of the intercostae results in a folding of the mantle edge against itself on either side of the projection. This, in turn, results in a discontinuity in the shell structure that facilitates diagenetic solution of shell material, evident in Figures 5G and O.

Discussion

Function of keeled ribs

Savazzi (1985) proposed that the keeled ribs of *Cardium costatum* function primarily as mechanical reinforcement, that they impart rigidity to an otherwise fragile shell (because of the secondarily thinned intercostal spaces; see also below), and that, together with the rib onto which they are attached, they are equivalent in mechanical properties to the engineering structures known as T-beams because of their T-shaped cross-section. He further stated that the hollow ''stems'' of the T-beams in *C. costatum* reduce shell weight in comparison with an equivalent massive structure.

In engineering, when the stiffness of a plate is to be increased and the nature and amount of the material cannot be changed, a number of alternative designs can be used, including (1) adding keels perpendicular to the plate, (2) folding the plate into an undulated structure, or folding it in other ways (e.g. into ''bumps''), or (3) building a structure made of two plates separated by a thick layer of spongy (but stiff) material or a set of septa or struts connecting the plates. In all these instances, the goal is to increase stiffness by increasing the effective thickness (i.e., distance between opposite surfaces) of the original plate. All these structures typically are stiffer (i.e., less subjected to deformation by strain) than a flat massive plate built with the same amount of material. The radial ribs of *Cardium* (s. s.) are an example of alternative (2). Because of the presence of keels, the sculpture of *C. costatum* actually is a combination of T-beams with a corrugated plate (structures 1 and 2). The hollow keels of this species are also an example of structure (2), while the multiple keel cavities of *Budmania* are better classified as an example of alternative (3).

All structures involving corrugations and comparable types of folding and/or ribbing display an anisotropic stiffness, which is highest against bending about an axis perpendicular to the folding and ribbing. Excessive strain (i.e., the deformation that results from the application of an external force, or stress) may cause materials to fail by deforming irreversibly and/or by cracking. The latter phenomenon prevails in mollusc shells. In addition, thin sheets and struts of any material are especially sensitive to another type of failure, i.e., buckling, which, in simplified terms, consists of bending sideways when subjected to compressive forces. Thin structures are especially vulnerable to buckling because their reduced thickness allows this sideways deformation. In mollusc shells, buckling results in cracking of the skeletal material. Buckling is especially critical because its onset typically reduces the stiffness of a structure suddenly and drastically, thereby starting a chain reaction with more buckling and ultimately a catastrophic failure of the skeleton as a result.

Bivalve shells are subjected mainly to forces that tend to squeeze the shell. These forces can be external (i.e., predators attempting to crush the shell, waves causing impacts of the shell against other objects, pressure by surrounding loose sediment) or internal (contraction of the adductor and pedal retractor mus-

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cles). All forces perpendicular to a beam result in a corresponding bending of the beam. In turn, this bending causes the surface of the beam facing toward the applied force to become shorter (i.e., to be subjected to compression lengthwise), and the opposite side to become longer (i.e., to be subjected to lengthwise distension). A comparable situation applies to plates. Thus, the material of bivalve shells is subjected mainly to compressive forces in their outer layers, and to distensive forces in their inner layers as a result of stress being applied to the shell.

Consequently, in *C. costatum* the keels are subjected mainly to compressive forces directed along their length. In order to resist buckling, the keels must be as straight as possible, because any pre-existing deformation sideways would be the likely site of initial buckling. Curvature of the shell surface is necessary to provide internal space for the soft parts, and this curvature, in itself, contributes to stiffness (this situation may be compared to a spherical container, which displays the highest resistance against external or internal isotropic pressure).

The maximal strengthening effect of the keels is attained when they are perpendicular to the surrounding shell surface, because this maximises the height between the surrounding shell surface and the edge of the keel (i.e., the thickness of the equivalent plate). A keel that projects obliquely, rather than perpendicularly, from the shell surface would have a lower effective height and would curve sideways (because of the curvature of the underlying shell surface), thereby providing a much lower stiffness and potentially inviting buckling.

Ideally, the keels should be evenly spaced and of a constant size. In a bivalve with a radial sculpture pattern, both characters are prevented by constructional constraints: radial ribs and keels are unavoidably closer to each other in the umbonal region. Their size is also smaller in this region, because the overall size of the shell was correspondingly smaller at the time the ribs were built. Short of secondarily modifying the position and size of the keels (which is not known to happen in any bivalve), there are no ways of avoiding this shortcoming. However, the resulting weakness of the umbonal region is compensated for by secondary thickening on the interior of the shell (Figures 4B–D).

In order to reduce the risk of buckling, it is important that the keels run as straight as possible from the umbo to the shell margin. A small-scale bending or undulation of the keels would likely become the site of incipient buckling. An even bending on a larger scale creates a lesser, but still undesirable weakness. In fact, the keels, being radial features, are constrained to a helicospiral, rather than straight growth path. Also in this case there are no ways to avoid such a constructional constraint. However, this is mitigated by the fact that also the surrounding shell surface follows the same growth path. In conclusion, keels that follow a regular growth path and are rarely deformed can be regarded as a strong indication of a stiffening function, while this function should be excluded for ribs that are frequently deformed.

In *C. costatum*, undulating or otherwise deformed keels are very unusual, and in all observed instances this type of deformity is associated with repaired damage to the shell and/or mantle margins (Figure 1H) or parasite infestation (possibly by polychaetes). It is further observed that such deformities are rapidly repaired and, with few exceptions, a damaged keel subsequently resumes normal growth.

The situation in *Budmania* is very different. A large proportion of the specimens (at least 20% to 35%, depending on how large a deformation of the keels is regarded as significant) possess at least one sideways deviation of a keel that would seem to prevent its function as a mechanical reinforcement. Often, two or more adjacent keels are grossly deformed (Figures 5A, H). This is especially common in species and morphs with prominent keels. Also, deformations of the keels usually are not associated with detectable shell damage, and persist for an extensive length of the keels, often without signs of returning to a regular path. At the same time, it can be noted that the keels in several species of *Budmania* project from the shell surface to a much higher extent than in *C. costatum*, both in absolute height and in height relative to total shell size. In a scenario in which the primary adaptive value of keels is that of mechanical reinforcement, higher keels would impart a higher stiffness to the shell. However, this would also significantly increase the vulnerability of deformed keels to buckling. Therefore, while mechanical stiffening can be regarded as one of the likely principal functions of keels in *C. costatum*, the same cannot be asserted of *Budmania*.

This difference may be related to the different environments of these species. While *Budmania* occurs exclusively in muddy sediments characteristic of a low-energy limnic or brackish environment (above references), *C. costatum*, according to the literature (see above), is found in both muddy and sandy sediments, and thus likely is typical of low- to medium-energy environments, and may even occur in relatively high-energy near-shore sandy bottoms. Thus, the ecological preferences of *C. costatum* seem to make mechanical stiffening more necessary than in *Budmania*. Alternative or concurrent functions of the keels in *Budmania*,

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therefore, should be sought.

Keels or other strong external relief can be expected to oppose movement of the shell within a soft substrate, by increasing friction between shell and sediment. Although this friction is difficult to predict on a quantitative basis (e.g., see Savazzi and Pan, 1994, and discussion in Savazzi, 1985), it is possible to design a qualitative paradigm (Rudwick, 1964; Paul, 1975) for increased friction, and to compare this paradigm with keeled ribs in order to assess whether this sculpture is optimised to provide this function.

Several Recent cardiids are known to burrow shallowly in the sediment in a downward direction. In the life position, most infaunal cardiids keep the hinge axis vertical or slightly oblique (Stanley, 1970; Savazzi, 1982, 1985; references therein). The direction of burrowing is approximately downward with a shell in an orientation similar to the normal life position (e.g., Stanley, 1970; Savazzi, 1985). In keels optimised for anchoring the shell within the sediment, maximum friction would require the keels to be oriented horizontally in the life position. However, since the keels (together with radial ribs) are part of a growth-conformable sculpture pattern, they cannot be oriented parallel to each other, and must diverge away from the umbones and toward the shell margin. Because of additional constraints of mechanical strength (see above) keels tend to be perpendicular to the surrounding shell surface, rather than parallel to each other on adjacent ribs. Finally, keels would be most effective as anchors when placed in regions where the shell has a high cross-sectional area (i.e., on the central slope), while they would be of little use on the anterior and posterior slopes.

Interestingly, this last property of the paradigm is diametrically opposite to ''perimeter smoothening'' (Seilacher, 1973) in burrowing sculptures, i.e., a partial or total flattening of shell relief on the central slope of burrowing bivalves, in order to reduce friction against the sediment in this region.

Thayer (1975) discussed the adaptations of benthic invertebrates to soft substrata, concentrating on epifaunal forms. In particular, he formulated the principle that organisms living on very soft substrates, in order to avoid sinking into the sediment, tend to have a low specific gravity and to distribute their weight onto a broad surface area in contact with the sediment. These epifaunal organisms, consequently, tend to be flattened and to rest onto the surface of the substrate by a broad ''snowshoe''.

The situation of infaunal organisms, not discussed in detail by Thayer (1975), is partly different, because their entire body is surrounded by sediment. Thus, a broad surface area in contact with the substrate does not need to be flat. Therefore, the keels of *C. costatum* and *Budmania* can be interpreted as an alternative way of increasing the surface area in contact with soft sediment. However, the extent of the surface area alone cannot be the only relevant factor. In fact, it is possible to provide the same surface area by substituting the few and large ribs of these cardiids with many very small ribs. This is unlikely to provide the same anchoring properties within a semifluid sediment, because the volume of sediment trapped among these ribs would be very small and the shell, in practice, would behave almost like a smooth one.

At the opposite extreme of hypothetical designs, one may envision building a single, very large keel around the shell, which effectively would become similar to the flattened organisms discussed by Thayer (1975). The latter solution is impractical for infaunal burrowers, because this type of snowshoe would make burrowing impossible or extremely difficult. Thus, the keels of *C. costatum* and *Budmania* may be regarded as a compromise between the contrasting requirements of burrowing and anchoring the shell within the sediment. While a general discussion of organisms on or in very soft sediments lies outside the scope of the present paper, the present instance suggests that emphasis should be shifted from their surface area to the volume of sediment surrounding the organism and affected by the weight of the latter.

The keels in *C. costatum* and *Budmania* comply with the features of the paradigm for anchoring sculpture, except for deviations explained by constructional constraints and by the need to allow burrowing (see above). In conclusion, the keels in *C. costatum* and *Budmania* appear to be reasonably optimised to function as anchors within the sediment. This anchoring function could be interpreted as adaptive in different contexts. In very soft sediment, anchoring sculpture, combined with low shell weight (see above, and below), could effectively prevent sinking within the substrate. Anchoring sculpture could also prevent a shell partly exposed above the surface of the sediment from being dislodged by water movements. Likely, this sculpture would neither unduly hinder the mollusc from burrowing (which in cardiids takes place in a sediment fluidised by injection of water through the pedal gape; Stanley, 1970; Savazzi, 1982, 1985), nor from emerging from the sediment (because the foot is large and strong enough to carry out this action quickly; Savazzi, 1985).

The higher development of keels in *Budmania* may reflect life in an environment in which burrowing took place infrequently, thus lessening the problem posed

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by large keels in this context. It may also reflect the necessity for very effective anchors to prevent the organism from sinking into the sediment, especially since *Budmania* lacks several of the specialisations to reduce shell weight that are observed in *Cardium* (s. s.) (see also below). The frequent diagenetic deformation or crushing of *Budmania* by sediment compaction observed in the available material also suggests life in a water-laden, soupy muddy sediment that, in turn, implies a very low-energy environment.

A significant difference between *C. costatum* and *Budmania* is that, in the former, the ventral ends of the keels (i.e., their growing surfaces) extend below the commissure line when the shell is viewed from the side (Figure 1A). The growing faces of the keels, in fact, are almost parallel to the commissure plane. In *Budmania*, instead, these faces of the keels project obliquely sideways, leaving a ventral region free from keels (Figures 5D, K). This is especially true of species of *Budmania* that possess large keels.

This may find an explanation in behavioural differences. According to verbal reports by West African fishermen collected by A. Seilacher (pers. comm.), *C. costatum* is frequently caught in drag-nets. When the nets are pulled out of the water, this species often is seen leaping about by rapidly extending its foot. This is essentially identical to the behaviour observed in other marine cardiids (Stanley, 1970; Savazzi, 1985). The fishermen further reported that *C. costatum* appears to ''eat'' fish caught in the same nets. This is probably a misunderstanding based on the fact that extension of the foot between the valves forces them to gape considerably (also a common feature in cardiids; above references). Once the foot is retracted, the valves may accidentally close around nearby objects contained in the nets, thus giving the impression that the mollusc is attempting to enclose them within the shell. These reports confirm that *C. costatum* leaps energetically when in distress, and that its foot is well developed.

On the other hand, the Lymnocardiinae may have been adapted primarily to creeping, rather than leaping. Creeping is also observed in Recent marine cardiids (e.g., Savazzi, 1985), but in limnic bivalves it may be especially useful to counteract seasonal changes in water depth by allowing the organisms to migrate. In this context, it may be observed that leaping in cardiids is poorly directed (above references), and more effective for escaping predators than for long-range locomotion.

Several lymnocardiine taxa possess a rectangular shell outline with a straight ventral margin (Fig. 6A), which contrasts with the rounder ventral outline of other cardiids. The straighter ventral region of the

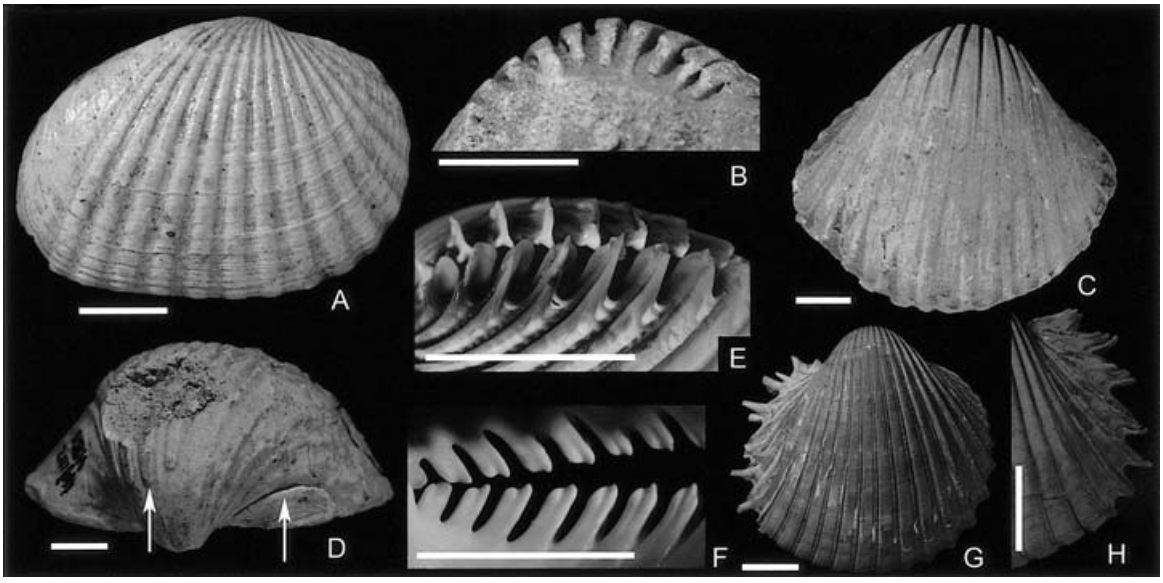


Figure 6. A. *Lymnocardium majeri* Hörnes, Miocene, Agram, Croatia (NHM). B–C. ?*Cardium latisulcatum* Sowerby, Tertiary, Lisbon, Portugal (NHM). Internal mould, dorsal (B) and lateral (C) views of right valve. D. *Cardium* cf. *hians*, Cyrenaica, Libya (NHM RHB 2111A). Internal mould of right valve, dorsal view. Left arrow indicates the change in relief corresponding to secondary thickening of the intercostae. Right arrow indicates sediment infilling of hollow hinge socket. E–F. *Cardium* (*Bucardium*) *ringens* Bruguière, Recent, Senegal (Chiba Prefectural Museum, Chiba, Japan). G–H. *Cardium burdigalinum* Lamarck, Lower Miocene, Aquitaine, France (NHM). Adult right valve (G) and posterior slope of juvenile left valve (H). Scale bars represent 10 mm. See the text for details.

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commissure in the Lymnocardiinae may be an adaptation to stabilise the shell during creeping (Müller and Magyar, 1991). Several lymnocardiines also have subdued ribs on the central shell slope, another feature that can be interpreted as adaptive in the context of creeping. The lack of keels that project ventrally in *Budmania* may be interpreted as functional in facilitating creeping. The lesser height of the keels in *C. costatum* (which is comparable with *B. aequicostata* and weakly sculptured morphs of *B. semseyi*, which also have moderately developed keels that project ventrally from the commissure: Figures 5E–G), together with its capability of leaping, makes the ventral keels a minor problem in this context.

Thinned intercostae

Resorption of shell material from the internal surfaces of the intercostae reduces the overall shell weight. A quantitative estimate of this amount in *C. hians*, based on a reduction of shell thickness from 1.2 to 0.3 mm measured in actual specimens, yields a reduction in the total volume of shell material of about 195 mm^3, i.e., approximately 0.5 g. Together with an overall rather thin shell, hollow hinge sockets and rather broad siphonal gape, secondary resorption yields a significantly lightweight shell.

The Cretaceous subgenus *Granocardium* (*Ethmocardium*) possesses intercostal rows of macroscopic pits on its internal shell surface (Keen, 1980, pl. 2.9). These pits are present only within the pallial line, so they are apparently the result of secondary resorption. They may be convergent with the secondarily resorbed intercostae of *Cardium* (s. s.).

Intercostal microtubules and secondary deposits

Microtubules are known in several bivalves (e.g., see references and discussion in Araujo *et al.*, 1994). Two types have been identified, one built as a primary feature at the shell edge, the other of secondary origin and present only in the area enclosed within the pallial line (above reference, and therein). The microtubules in *Cardium* (see Seilacher, 1990) are evidently of the latter type. It is also visible from Figures 3A–B that the secondary deposition of pigmented material onto the exterior of the shell coincides with the beginning of shell resorption on the inside.

In other bivalves, microtubules have been found to be occupied by either unicellular or multicellular mantle processes. It appears likely that similar processes are responsible for the secretion of secondary deposits on the external surfaces of the intercostae in *Cardium*. Secondary pigmentation of the intercostae probably is due to a similar material deposited on the walls of the tubules and/or permeating the surrounding shell material. This type of secondary deposit on the external shell surfaces is unknown in other bivalve groups, but preliminary observations suggest that the intercostal regions of other cardiids closely related to *Cardium* (s. s.) may possess secondary shell resorption, microtubules and secondary pigmentation within the shell structure (Harper and Savazzi, in prep.). Savazzi (1985) suggested that the microtubules and associated secondary deposits in *Cardium* (s. s.) may deter predation by shell-borers capable of producing small boreholes, conceivably as a result of the chemical nature of the secondary deposits. This can be compared with the conchiolin layer present in the Corbulidae, which has an evident deterrent effect on shell-boring naticids (e.g., Lewy and Samtleben, 1979). The occurrence of very small boreholes that seem to concentrate on the thinnest shell portions in *C. costatum* and the presence of secondary deposits exclusively in these thinnest regions indirectly support this idea. Large boreholes produced by predators that, conceivably, would be able to bore through the thicker shell portions were not observed in *Cardium* (s. s.).

Relationships between shell-weight and volume

A comparison of reconstructed weight versus volume *in vivo* in a range of Recent cardiid species is shown in Fig. 7. In this diagram, each line represents the linear regression of computed values of weight

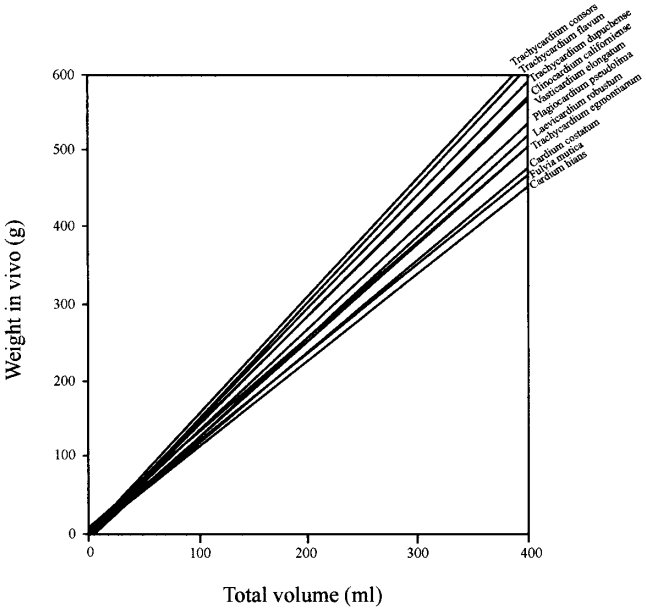


Figure 7. Relationships between reconstructed weight *in vivo* versus total volume in selected cardiid species. See the text for details.

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versus volume *in vivo* (see the section on materials and methods) for two or more specimens of a range of Recent marine cardiid species chosen as representative of different shell thickness and weight. In particular, an effort was made to include the most lightweight forms among the material available for this study (which, aside from *Cardium* (s. s.), turned out to belong consistently to the subfamily Laevicardiinae *sensu* Keen, 1969a). The regression lines were plotted to the same absolute length in order to allow the visual comparison of species of different absolute shell size. The individual data points are omitted for clarity (see the appendix for all measurements). All regression lines pass through, or close to, the origin, thus showing that the ratio between volume and weight grows in an essentially linear fashion in all studied species. In turn, this suggests that the direct comparison of species and specimens of different sizes is not biased by size-related factors.

As visible in Figure 7, *C. hians* is the species with the lowest ratio of weight to volume in the tested sample. The second-lowest is *Fulvia mutica*, which carries a large number of very shallow radial ribs and is uniformly thin-shelled. In this species, as discussed by Savazzi (1985), the cross-section of the radial ribs is terrace-shaped, and their burrowing function is supplemented by a row of periostracal hairs that line the top of each rib and are bent in the posterior direction. This adaptation likely compensates for the shallow height of the terraces. *Cardium costatum* ranks third and is lighter than several smooth, thin-shelled species belonging to the Laevicardiinae (*sensu* Keen, 1969a).

A smooth shell minimizes the use of shell material, and this character was discussed by Thayer (1975) as one of the adaptations frequently occurring in organisms living in or on very soft sediments and being associated with a thin shell. *C. costatum* and *C. hians* are remarkable exceptions to this principle, thanks to their hollow hinges, secondary resorption of shell material and (in *C. costatum*) hollow keels. The function of keels and large ribs as anchors within a semifluid sediment, which partly explains this apparent deviation from the norm, is discussed above.

Since resorption in *Cardium* (s. s.) is concentrated in the posterior half of the shell, this character also displaces the centre of gravity of the shell in the forward (i.e., lowermost in the life position) direction. This can be expected to discourage the accidental rotation of the shell within a semifluid substrate, and may in fact allow an overturned shell to passively regain the proper life orientation within the sediment, a character that may enhance survival in sediments that are frequently fluidised by wave or current action. Savazzi and Yao (1992) described a comparable selective weighting of the anterior portion of the shell in freshwater unionaceans (albeit likely possessing a much higher specific gravity than these cardiids). Selective thickening of the skeletal portions located lowermost in the life position has been described also in other soft-bottom invertebrates, including byssate and sessile reclining bivalves (e.g., Seilacher, 1990; Savazzi, 1999b).

The delicate nature of *Budmania* specimens and the possibility that the specific gravity of their shells has been altered by fossilisation prevent its inclusion in Fig. 7. However, a qualitative assessment shows that this species is relatively thin-shelled but lacks the unusual specialisations of *Cardium* (s. s.) with the exception of its hollow keels (which, however, appear to be more massive than those of *C. costatum*). Although probably *Budmania* would rank among the lightest cardiids in Figure 7, it appears unlikely that it would be as lightweight as *Cardium* (s. s.).

Evolution

The exceptionally prominent external sculpture of *Budmania* is unique among the Lymnocardiinae, which otherwise tend to possess subdued ribs or entirely smooth shells. *Budmania* likely evolved from one of the earlier, weakly sculptured forms in the Miocene or basal Pliocene *Lymnocardium* stock. For instance, *L. pelzelni*, *L. ochetophorum* and *L. secans* (see Marinescu, 1973) are comparable to *Budmania* in shell outline, shape and reduced number of strong radial ribs, and interlocking of the ribs of opposite valves along the ventral margin. They are, however, considerably smaller and less convex, and lack keels. These species are contemporary with *Budmania* and therefore not its likely ancestors, but nonetheless show the probable affinities of *Budmania* with *Lymnocardium*.

The main difference between *Budmania* and *Lymnocardium* is the presence of keels in the former genus. Unlike the Cardiinae, most Lymnocardiinae lack tubercles and spines on their radial ribs. However, a few lymnocardiines possess radial ribs topped by a relatively sharp ridge. For instance, *L. schmidti* possesses ribs bearing ridges with a slightly beaded appearance (Marinescu, 1973, pl. 4, figs. 1–3). It is possible that the keels in *Budmania* have evolved either from this type of ridge or from cardiid-like tubercles. The height of the keels in *B. ferruginosa* undulates periodically (Marinescu, 1973, pl. 6, fig. 2a), a fact that suggests evolution from tubercles or a comparable periodic sculpture.

A few Neogene and/or Quaternary marine species

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belonging to or related to *Cardium* display peculiar adaptations. The internal mould of a species of dubious identification (Figure 6B–C) shows deep incisions in the umbonal region. The corresponding ridges on the shell interior can be followed in the ventral direction, in which the relief becomes inverted (Figure 6C). Thus, these ridges in the umbonal region correspond in position to the external ribs, not intercostae as it might be expected. A thick secondary layer apparently smoothed out all internal relief near the umbones (Figure 6B). These features result from a growth process in which the ribs were secondarily thickened, but apparently not the intercostae. This appears to be a constructional process different from that of *C. costatum* and *C. hians*, although it produces a comparable result on internal shell relief.

An internal mould of a species with clear affinities with *C. hians*, but possibly distinct from it, displays the sediment infilling of a very broad cavity within the posterior region of the hinge (rightmost arrow in Figure 6H). This cavity was much broader than in Recent *C. hians*. This mould also displays secondary shell thickening of the intercostae in the umbonal region (leftmost arrow in Figure 6H), essentially identical to the corresponding feature in *C. costatum* and *C. hians*.

Direct ancestors of *Cardium* apparently are unknown, but this genus may have evolved from *Acanthocardia* or a similar genus. The spines in *C. hians* and the general shell characters (except for those unique to *Cardium*) are similar to those exhibited by several species of *Acanthocardia*. The keels of *C. costatum* likely have evolved from *Acanthocardia*-type spines. A variety of spine types and of their constructional processes exists in the latter genus (see Savazzi, 1985), and these features can be modified into continuous keels by modifying the constructional programme to secrete a continuous structure instead of periodic spines. The modifications required by this new programme are probably minor, since the spines in *Acanthocardia* and several other cardiids are built as secondary additions onto the shell exterior by projections of the mantle that extend outside the shell margin (Savazzi, 1985). In fact, the notched posterior commissure of the Recent *C.* (*Bucardium*) *ringens* (Figures 6E–F) has been interpreted as a feature not functional in itself, but only in allowing the construction of continuous ridges on top of the radial ribs (Savazzi, 1985). The marginal notches in *Bucardium* differ from those of *Cardium* (s. s.) and *Budmania* in being exposed, a consequence of the fact that the ridges in *Bucardium* are built by addition of shell material on their external surfaces, rather than at the margin and internal surfaces as in the former genera.

The Neogene *Cardium* (*Bucardium*) *burdigalinum* has shallower commissural notches in its posterior commissure and, on the posterior slope, radial ribs carry continuous ridges in the juvenile stage, which turn into pointed spines in the adult (Figures 6G–H). As a whole, the posterior shell region of this species is rather similar to that of *C. hians*, but the intercostae of this *Bucardium* are much narrower, a character that further differentiates *Bucardium* from *Cardium* (s. s.). These differences persist throughout the fossil record of *Cardium* (s. s.) and *Bucardium*, and indicate that these are distinct evolutionary lineages that were already separated in the Miocene.

Apparently there are no literature reports of microtubules in cardiids other than *Cardium* (s. s.). The occurrence of comparable structures in several other bivalve families (see above) indicates that they evolved several times. Their occurrence in *Cardium* (s. s.) therefore is not exceptional, although their adaptive value in allowing the secondary secretion of material on the outside of the shell appears to be unique.

The last question to be addressed is the degree of taxonomic affinity between *Cardium* (s. s.) and *Budmania*. Assuming that the fossil record of these and related genera is reasonably complete, it is readily seen that *Cardium* and *Budmania* constitute independent lineages. The cardiine and lymnocardiine stocks were already geographically and ecologically separated before the appearance of either lineage. In particular, the Cardiinae evolved from a marine lineage probably close to *Acanthocardia*, while the Lymnocardiinae were confined to gradually less saline waters of the Pannonian Basin during the Neogene. The remarkable morphological similarity of keeled ribs in *Cardium costatum* and *Budmania* can be attributed to a combination of two factors: (1) parallel evolution favoured by the function of keels as anchors in soft sediment, and (2) the availability of a common cardiid *Bauplan* (see discussion of this term in Savazzi, 1999a). In particular, the constructional mechanism of tubercles and spines on the shell exterior is widespread among cardiids, and its modification into the construction of continuous hollow keels did not require substantial changes in its nature. On the other hand, the internal structure of the hollow keels differs in *C. costatum* and *Budmania*, which further suggests a parallel evolution of this feature in the two taxa.

Conclusions

The hollow keels in *Cardium costatum* and *Budmania*, although comparable in morphology and con-

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struction, are the product of parallel evolution and were absent in common ancestors of the two taxa. This is reflected in the internal structure of the keels, which differs in the two taxa.

The comparable overall shell morphology in these two taxa is also the product of parallel evolution, but a detailed analysis shows significant differences between the two lineages. In *Cardium* (s. s.), secondary resorption on the inner surface of the intercostae and hollow hinge sockets yield lightweight shells in spite of their prominent sculpture, while *Budmania*, although relatively thin-shelled, lacks these optimisations. Except for the presence of keels, *C. costatum* is much more similar to *C. hians* than to *Budmania*. The keels in *C. costatum* are highly regular in shape and regain their regularity quickly, following deformation induced by external factors. Their distribution and orientation on the shell are compatible with a mechanical bracing function. The keels in *Budmania*, instead, are frequently irregular, including numerous examples in which they are not visibly the result of accidents, and their irregularity persists and/or develops over a substantial portion of their ontogeny. This difference supports a functional interpretation of the keels as a combined mechanical reinforcement and as anchors within the sediment in *C. costatum*, while their frequent irregularities in *Budmania* make them vulnerable to breakage by buckling, and therefore they must function only as anchors.

As a whole, shell morphology in both taxa appears to be optimised for life in soft fine-grained sediments, but with important differences: *Cardium* (s. s.) occupies medium-energy marine environments, in which shells are subjected to compressive mechanical stresses and predators capable of drilling small holes are present, whereas *Budmania* occupied low- to very low-energy limnic environments, lacking these additional factors.

Acknowledgements

A Sys:Resource grant from the Natural History Museum, London, UK to E. Savazzi and fellowships from the Japan Society for the Promotion of Science, the Swedish Foundation for International Cooperation in Research and Higher Education, the Swedish Royal Academy of Science and the Sweden-Japan Foundation for visits to Japan by E. Savazzi and J. Sälgeback are gratefully acknowledged.

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Appendix

The following table lists the measurements on which Figure 7 is based. The measurements obtained from empty shells in collections are shell-weight and internal volume. When only isolated valves were available, the total weight and volume were computed by doubling the measurements of the available valve.

Species	Repository	Shell-weight (g)	Volume (ml)
Cardium costatum Linnaeus	SMNH	64	188.4
	UMUT	7.4	37
	authors	40.3	124.2
	authors	57.2	204.1
Cardium hians Brocchi	authors	29.8	155
	authors	14.1	76.8
	authors	20.9	124.1
Achantocardia tuberculata (Linnaeus)	authors	12.9	14
	authors	11.5	14.2
	authors	10.2	11.4
Acanthocardia aculeata (Linnaeus)	UMUT	52.4	100
Plagiocardium setosum (Redfield)	SMNH	6.5	10.9
	SMNH	4.7	6.7
	SMNH	2.3	2.3
Plagiocardium pseudolima (Lamarck)	SMNH	44	73.4
	SMNH	49	68.5
	SMNH	38	61.3

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Species	Repository	Shell-weight (g)	Volume (ml)
	SMNH	37.8	60.3
	SMNH	63.8	100.6
	SMNH	190.3	286
Vepricardium multispinosum (Sowerby)	SMNH	10.3	27
	SMNH	16.2	38.3
	SMNH	3.5	11.9
Vepricardium coronatum (Schröter)	SMNH	7.5	14.7
	SMNH	9.2	17.2
	SMNH	7.8	9.5
Vepricardium fimbriatum (Wood)	SMNH	9.2	17.2
Vepricardium sinense (Sowerby) (1 valve)	SMNH	5.2	11.7
	SMNH	2.5	3.9
	SMNH	1.2	1.6
Vepricardium asiaticum (Bruguière) (1 valve)	SMNH	15.6	28
Trachycardium isocardia (Linnaeus)	SMNH	81.3	62.9
	SMNH	91.8	89.7
Trachycardium consors (Sowerby)	SMNH	123.6	93
	SMNH	92.2	71.3
	SMNH	25.3	19.9
Trachycardium egmontianum Shuttleworth	SMNH	22.8	23.3
	SMNH	21.2	19.3
	SMNH	19.9	22
Trachycardium flavum (Linnaeus)	SMNH	31.3	28.5
	SMNH	15.2	20.2
	SMNH	12.3	12.8
Trachycardium muricatum (Linnaeus)	SMNH	25.6	36.1
	SMNH	14	24.1
	SMNH	8.1	12.2
	SMNH	8.4	9.9
Acrosterigma alternatum (Sowerby)	SMNH	7.6	15.3
	SMNH	10.8	20.1
	SMNH	85.4	110.8
	SMNH	21.1	40.7
Papyridea radiata (Reeve)	SMNH	6.5	21.9
Papyridea bullata (Reeve) (1 valve)	SMNH	1.7	5.923
(1 valve)	SMNH	2.3	8.686
(1 valve)	SMNH	0.6	1.63
Vasticardium assimile (Reeve)	SMNH	23.1	22.5
	SMNH	13.1	12.5
	SMNH	28	26.2
	SMNH	14.4	17.4
Vasticardium flavum dupuchense (Reeve)	SMNH	22	21.8
	SMNH	42.2	39.1
	SMNH	10	9.7
	SMNH	7.5	7.3
Vasticardium elongatum (Bruguière)	SMNH	160.8	183.1
	SMNH	63.1	77.8
	SMNH	19.7	21.2
Laevicardium elatum (Sowerby)	SMNH	21.1	64.4
Laevicardium robustum (Lightfoot)	SMNH	32.1	86.4
	SMNH	45.6	101.9
	SMNH	56.1	111.6
Laevicardium oviputamen (Reeve)	SMNH	8.9	23.1
	SMNH	1.3	3.6
	SMNH	0.4	1.4
Fulvia aperta (Bruguière)	SMNH	42.7	148.7
	SMNH	20.7	67.2
	UMUT	31.8	125

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Species	Repository	Shell-weight (g)	Volume (ml)
Clinocardium corbis (Martyn)	SMNH	94.6	104.2
	SMNH	80.6	118.7
	SMNH	15.8	19.2
Clinocardium californiense (Deshayes)	SMNH	50.4	56.3
	SMNH	4.6	7.4
	SMNH	4.8	7.3
	SMNH	3.6	5.5
Clinocardium sp.	authors	19.9	34.9
	authors	14.2	25.1
	authors	18.5	29.1

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