

Constructional morphology of cardiid bivalves: an overview (Konstruktions - Morphologie Nr. 142)

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ABSTRACT — *Within the Cardiidae, extremely varied sculptural patterns contrast with evolutionary conservatism of other morphological characters. Most sculptural features can be interpreted as burrowing sculptures, and this accounts for part of the morphological convergences between different groups. However, there appears to be no univocal relation between particular types of sculptures, burrowing mechanisms and sediment types. In most cases, the microstructure of sculptural features seems to be of better taxonomic value than the general aspect of the sculptural pattern.*

RIASSUNTO — [Morfologia costruzionale dei Cardiidi] — *Nella famiglia Cardiidae (Bivalvia) la varietà dei tratti sculturali contrasta con la relativa costanza di altri caratteri morfologici. Molti tipi di ornamentazione possono essere interpretati come sculture di scavo, ma non esistono evidenti relazioni tra particolari tipi di sculture, meccanismi di scavo e tipi di substrato. In molti casi, la microstruttura dei caratteri sculturali sembra avere maggior valore tassonomico dell'aspetto generale delle sculture.*

INTRODUCTION

The Cardiidae are a relatively compact bivalve family primarily adapted to shallow burrowing in loose sediments. The genus *Corculum* is secondarily adapted to an epifaunal life habit. Following Keen (1980) the Limnocardidae are regarded as a separate family, and are excluded from the following discussion.

Recent cardiids occur worldwide, mostly in neritic and coastal environments, including brackish water lagoons. The life habit of fossil representatives is believed to have been closely comparable with that of Recent species. In spite of the high number of known fossil taxa, the geological history of the Cardiidae is not well documented, and no detailed reconstruction of the evolutionary lineages was so far attempted. Remarkable morphological convergences within the family and iterative evolutionary patterns further complicate the task. The following discussion focuses on the constructional morphology (Seilacher 1970) of a few selected groups. Although this is not intended to be a coverage of the whole family, many of the conclusions are likely to apply to other cardiid taxa. The present contribution summarizes the result of a project on the constructional morphology of cardiid bivalves carried out by the author for the Sonderforschungsbereich 53 « Palökologie », Tübingen (West Germany).

DISCUSSION

Cardiid shells are typically subcircular or ovate in outline, highly inflated, with slightly prosogyrate umbones. A radial ribbing pattern of variable strength is present in virtually all Cenozoic representatives. Even when the ribs are subdued, the corresponding crenulations at the shell margin remain well developed. Interlocking of these crenulations along the ventral commissure increases resistance to shear forces, thus deterring predation by shell-opening organisms (cf. Kauffman 1969). The radial ribbing pattern increases also the mechanical resistance of the shell against crushing. The well developed, L-shaped foot often exceeds half of the total mass of the soft parts. Its bent shape allows emergence from the shell through the ventral commissure, thus reducing the maximum shell gape, while at the same time allowing the mollusc to burrow with the hinge line tilted about 60 degrees from the horizontal. This orientation allows the short siphons to reach to the surface of the sediment. In fully buried animals, the posterior commissure lies just below the sediment surface. The morphology of the soft parts in fossil cardiids, as inferred from the muscle scars, the general shell morphology and the maximum amount of gape allowed by the hinge teeth, seems to have remained essentially unchanged since the Mesozoic. The extremely varied sculptural patterns of Cenozoic

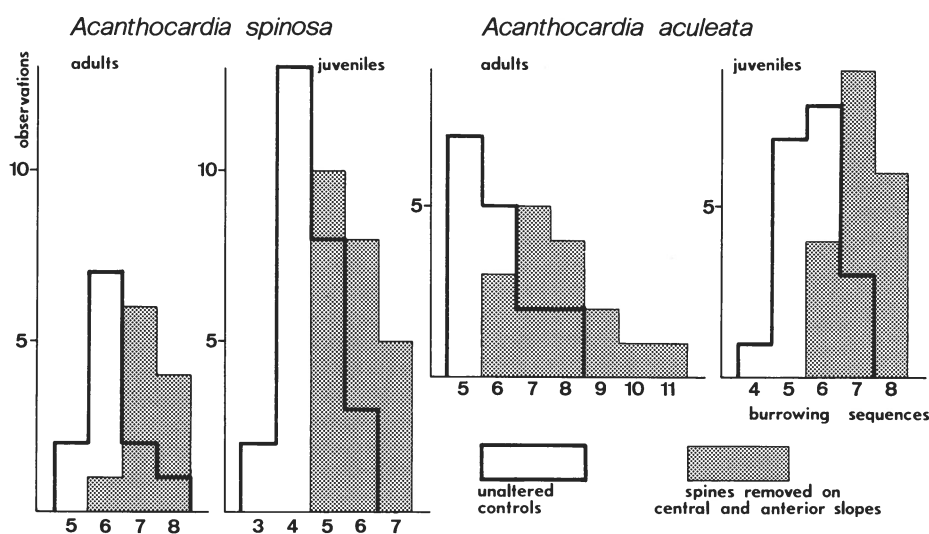
cardiids, however, contrast with the evolutionary conservatism of the other characters mentioned above. Thus, sculptural features must be given primary importance in any reconstruction of phylogenetic lineages. Moreover, sculptural patterns in burrowing bivalves are likely to have a direct relationship with the life habit and the burrowing mechanism, which makes them ideal subjects for studies of functional morphology.

It is useful to deal first with the functional morphology of the radial ribbing pattern, since this is widespread in the family and seems to have become established earlier in evolution than other types of sculptures. The mechanical strengthening effects discussed above are likely the primary function of these features. Since cardiids are efficient burrowers (Stanley 1970, 1981, Savazzi 1982a), it is reasonable to expect that selective pressure favours morphological changes of the ribs to facilitate in burrowing. The functional morphology of burrowing sculptures has been studied in a wide spectrum of organisms (see references in Savazzi 1982b and Signor 1982). The fundamental requirements of the paradigm (Rudwick 1964) for burrowing sculptures, as summarized by Seilacher (1972, 1973), are *cross orientation* (burrowing sculptures should be approximately perpendicular to the burrowing direction), *frictional asymmetry* (they should be asymmetrical in cross-section, so as to facilitate penetration into the substrate, while at the same time reducing backslippage), *perimeter smoothening* (sculptures should be subdued where the cross-sectional area of the organism is higher), and *allometric densing* (burrowing sculptures should remain constant in size during growth of the organism, since their mechanical properties are related to the unchanging grain size of the sediment; new sculptures should therefore be added during growth). Allometric densing can be achieved in different ways, according to the growth pattern of the organism. The marginal accretion of bivalve shells poses no constructional constraint to allometric densing, but certain sculptural patterns may render its introduction difficult or impossible. To achieve allometric densing, radial ribs should periodically bifurcate, or new ribs should be introduced. In most cardiids, neither thing is observed. Other alternative solutions to this problem will be discussed below. The radial ribs of cardiids are approximately perpendicular to the burrowing direction only on the central slope. Since this is also the region of maximum cross-sectional area, it is not possible to achieve cross orientation *and* perimeter smoothening at the same time. This last requirement of the paradigm is sacrificed in favour of cross orientation.

Terrace-shaped ribs are found on the central shell slope in several cardiid lineages, most notably in the Cardiinae (*Bucardium*), Trachycardiinae (*Mexicardia*)

and Laevicardiinae (*Fulvia*). In this last subgenus, frictional asymmetry is enhanced by posteriorly directed periostracal hairs projecting from the top of the terrace-shaped ribs. These hairs are likely a burrowing feature comparable with the periostracal shingles of burrowing anadarinids (Savazzi 1982a). Allometric densing of these asymmetrical ribs is forbidden by the constant number of radial ribs. A comparable lack of allometric densing is found also in the Paleogene brachyuran *Lophoranina* (Savazzi 1981). In this crab, the number of terraces remains constant during growth (unlike other burrowing Crustacea), but their height relative to the body size is progressively reduced, so as to keep their absolute height approximately unchanged. The absolute height of the terraces is a significant parameter, since the mechanical properties of burrowing sculptures are keyed to the sediment grain size. A similar adjustment of the terrace height is found in *Bucardium* and *Mexicardia*, but it is insufficient to keep the absolute terrace height constant. As it will be seen below, this may reflect a different set of coadaptations to burrowing. Evolution of terrace-shaped ribs in different cardiid groups is most probably the result of convergent evolution. This is not surprising, since these functional features improve the burrowing process. Slightly asymmetrical ribs, while not significantly aiding in burrowing in an active way, do nonetheless reduce resistance to penetration through the sediment. Therefore, a gradual evolutionary process from symmetrical ribs to terraces would have to cross no abrupt functional threshold, which makes multiple evolution further likely. In fact, it is rather surprising to see that a majority of cardiids did *not* evolve terrace-shaped ribs. Laboratory experiments with live individuals of *Acanthocardia tuberculata* (Linnaeus) provided a partial answer to this problem (Savazzi 1982a). This species possesses strong radial ribs devoid of any visible frictional asymmetry. Nonetheless, it was shown that artificial smoothening of the shell significantly increases the number of burrowing sequences (Trueman, Brand & Davis 1966) needed to burrow. This contrasted with the expected results, since it was supposed that symmetrical ribs would rather slow down the burrowing process, as they exert the same friction against the sediment in both directions (actually, this is the case with the venerid *Chione cancellata* (Linnaeus), as demonstrated by Stanley 1981). The results with *A. tuberculata* were attributed to the fact that the mechanical properties of the sediment are temporarily changed, at the beginning of each burrowing sequence, by injection of water through the pedal opening in the mantle. In accordance with this interpretation, most species of cardiids from the Northern Adriatic Sea show a water pumping action significantly more powerful than other similarly sized bivalves

EFFECT OF THE SPINES ON THE BURROWING PERFORMANCE



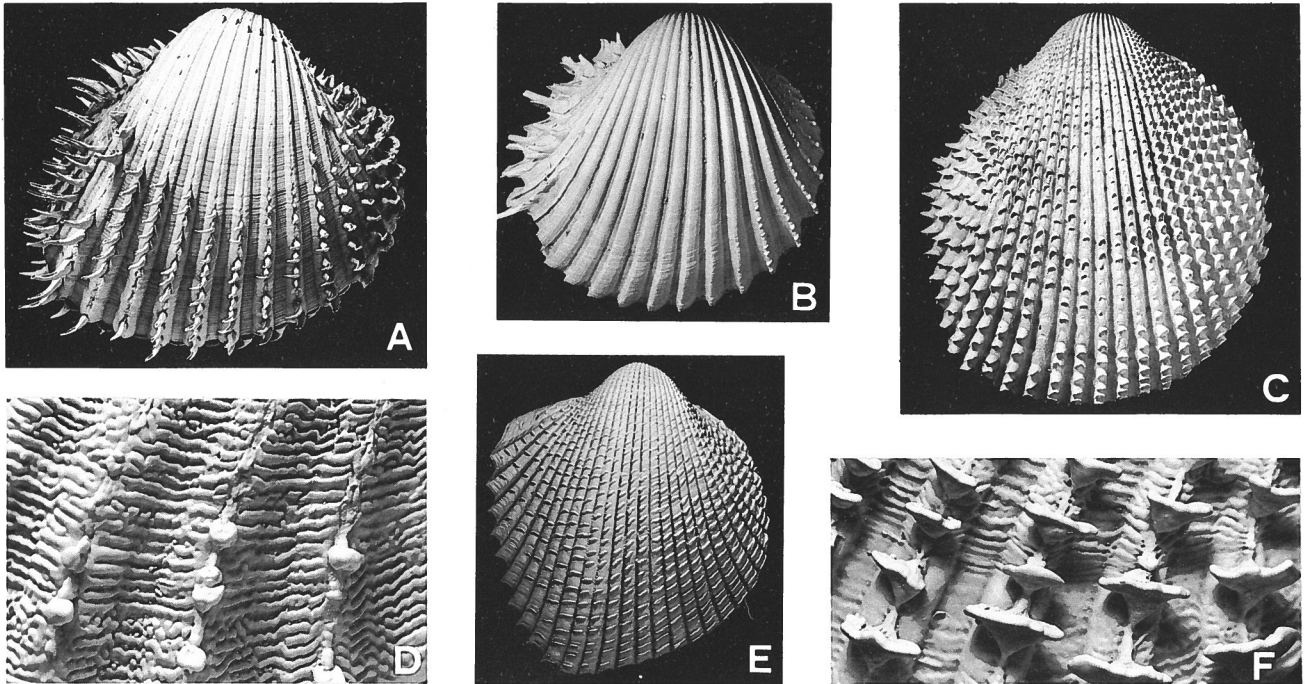
Text-fig. 1 - Live specimens of *Acanthocardia spinosa* and *A. aculeata* whose spines were artificially removed were allowed to burrow, and the burrowing performance was checked against that of unaltered controls. The Kolmogorov-Smirnov one-tailed non-parametric statistical test applied to the results rejects the null hypothesis (spines do not influence the burrowing performance) at $K=1\%$. For details of the laboratory techniques see Savazzi (1982a). « Adults » and « juveniles » refer to shell lengths above 50mm and between 25 and 35mm, respectively.

from the same area. Investigation of a larger sample of species is necessary before general conclusions can be reached, but these preliminary observations suggest that evolution of terrace-shaped ribs is not directly functional in aiding in the burrowing process, but its selective advantage lies rather in allowing a reduction of the energy spent in the water ejecting process. In addition, introduction of features, like terraces, that are optimally suited to a restricted range of sediment types reduces the available choice of exploitable environments. Thus, the evolutionary « choice » between symmetrical and terrace-shaped ribs appears as a choice of different sets of coadaptations to burrowing, rather than the adoption of a « good » burrowing sculpture in place of a « bad » one. Similarly, the growing height of terraces in cardiid bivalves is not a negative factor (as it would probably be in the brachyuran *Lophorina*), since it is allowed by the strong hydraulic pumping action.

In addition to the radial ribbing pattern, two other types of sculpture deserve attention. Tubercles, spines or knobs located on the radial ribs are found in representatives of all subfamilies. On the anterior and central shell slopes these sculptural traits are often asymmetrical and properly oriented to function as burrowing sculptures. Experiments with *Trachycardium egmontianum* (see Stanley 1981), *Acanthocardia spinosa* and *A. aculeata* (Text-fig. 1) show that the spines are burrowing sculptures. The spines in *Acanthocardia* are often well differentiated in shape along the shell (Text-fig. 2, A), and considerably varied among different species (Text-fig. 2, D, F). As for the shape of the radial ribs, it is not possible to link particular types

of spines to characteristics of the burrowing process or of the preferred type of sediment. Rather than fine-tuned adaptations to slightly different ecological niches, the different morphologies of the spines appear as parallel evolution of roughly equivalent burrowing sculptures without particularly stringent requirements. The ontogenetic processes leading to the construction of spines and tubercles reflect the parallel evolutionary pathways: The spines in *Trachycardium* (*Trachycardium*) are growth-conformable features obtained by periodically expanding the mantle outside the shell margin (Text-fig. 2, C). Perpendicularity to the burrowing direction is obtained by appropriately shaping the shell commissure. This results in wide gaps along the commissure between successive ribs. The nodes in *Fragum* (Text-fig. 2, E) are similarly oriented, resulting in comparable gaps along the commissure. However, the growth lines show that the nodes are somewhat resilient over the shell, indicating a different constructional principle. In *Acanthocardia* (Text-fig. 3) the mantle often envelops the tubercle on all sides. The attachment area of the tubercles in most cardiids varies in extension along the commissure, being significantly smaller on the central slope. This facilitates breakage of the spines from early formed parts of the shell, thus achieving perimeter smoothening (see Text-fig. 2, A). Also, the attachment of the tubercles and spines is shaped so as to present maximum resistance against breakage towards the umbones, which roughly coincides with the maximum friction encountered in the burrowing process.

Spines or tubercles are often present also on the posterior slope, where they cannot have a burrowing



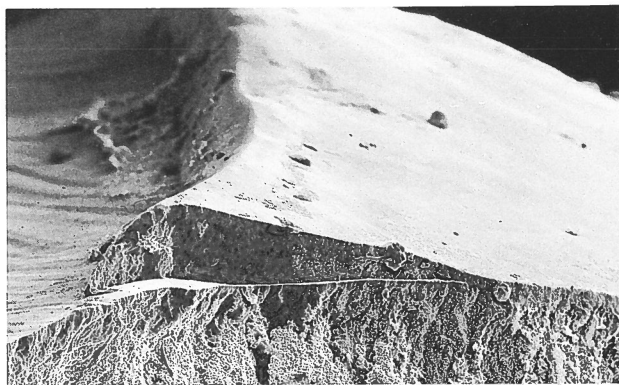
Text-fig. 2 - A: *Acanthocardia aculeata* (Linnaeus), Recent, near Venice, Northern Adriatic Sea (Mediterranean), x 0.5, author's collection. B: *Cardium* (*Bucardium*) sp., Miocene, unknown French locality, x 1, GPIT (GPIT = Geol. Paläont. Institut Tübingen). C: *Trachycardium isocardia* (Linnaeus), Recent, West Indies, x 1, GPIT. D: Detail of the sculpture on the anterior slope of *Acanthocardia paucicostata* (Sowerby), Recent, near Venice, Northern Adriatic Sea (Mediterranean), x 6, author's collection. The shell margin lies at bottom. E: *Fragum fragum* (Linnaeus), Recent, Japan, x 1, courtesy of A. Seilacher. F: Detail of sculpture on the anterior slope of *Acanthocardia echinata mucronata* (Poli), Recent, Adriatic Sea (Mediterranean), x 6, author's collection.



Text-fig. 3 - Newly formed spine at the ventral shell margin of *Acanthocardia aculeata*, Recent, Northern Adriatic Sea (Mediterranean), x 15. The base of an earlier formed, fully grown spine is partly visible at top right. The darker band near the shell margin (lowermost) represents the area of active carbonate secretion by the mantle. Note that the whole spine was enclosed in the mantle during its formation.

function, since they meet the sediment only when most of the shell is already buried. Short spines are functional in reducing scour by water currents around the posterior end of the shell (Stanley 1981), while larger spines are likely a defense against predation (Text-fig. 2, A, B). Very long, defensive posterior spines have likely evolved from smaller, scour-preventing sculptures, thus constituting an exaptation *sensu* Gould & Vrba (1982).

Divaricate terrace patterns are found only in subgenera of *Nemocardium*. These terraces comply to all requirements of the paradigm for burrowing sculptures, except for increasing in height with growth. As seen above, this is likely to have an adaptive value. Unlike divaricate terraces in other burrowing bivalves, which are merely a wrinkling of the outer shell layer, the terraces in *Nemocardium* are resilient over the shell, from which they are separated by a structural discontinuity (Text-fig. 4). This implies that the mantle continues the secretion of the terrace for time, by reflecting over the shell margin. This constructional process reminds those of the spines in *Acanthocardia* and the nodes in *Fragum*. Most subgenera of *Nemocardium*, except for the terraced forms, are devoid of



Text-fig. 4 - Transversal fracture of a terrace line in *Nemocardium* (*Lyrocardium*) *lyratum*, Recent, New Zealand, x 15. Note the discontinuity between the terrace and the underlying shell. The shell margin lies in the right direction. The thick periostracum was removed with hypochlorite before fracturing the specimen.

spines or tubercles. However, the morphogenetic capability of building these structures, present in the family « Bauplan », did not disappear together with the morphological character, and was utilized to evolve a new sculptural pattern. The constructional pattern of the *Nemocardium* terraces appeared in the Paleogene, and has remained unchanged at least since the Middle Eocene. Therefore, it would perhaps be reasonable to separate the terraced *Nemocardium* subgenera from the ones devoid of divaricate sculpture, regarding them as a distinct genus. It is interesting to note that divaricate patterns are widespread in bivalves (Seilacher 1972), and growth-unconformable sculptures are found also in other cardiid subfamilies (Text-fig. 2, D).

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