Stuttgarter Beiträge zur Naturkunde Serie A (Biologie)

Herausgeber:

Staatliches Museum für Naturkunde, Schloss Rosenstein, 7000 Stuttgart 1

Stuttgarter Beitr. Naturk. Ser. A Nr. 353 12 S. Stuttgart, 30. 4. 1982

Shell Sculpture and Burrowing in the Bivalves Scapharca inaequivalvis and Acanthocardia tuberculata*)

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With 5 figures

Summary

The radial ribs in the arcid Scapharca inaequivalvis and the cardiid Acanthocardia tuberculata do not conform to the paradigm for burrowing sculptures, as they are not terrace-shaped, but symmetrical in cross-section. Laboratory experiments with live animals, however, show that the ribs are functional in burrowing. This is attributed to a combination of mechanical and hydraulic effects. The functional morphology of burrowing sculptures cannot be fully understood, unless all aspects of the burrowing process are taken into account.

Zusammenfassung

Die radialen Rippen der Arcide Scapharca inaequivalvis und der Cardiide Acanthocardia tuberculata entsprechen nicht dem Paradigma für Grabskulpturen, da sie nicht terrassenförmig, sondern symmetrisch im Querschnitt sind. Laborexperimente mit lebenden Muscheln zeigen jedoch, daß diese Rippen eine Funktion beim Graben besitzen. Ihr Funktionieren beruht auf einer Kombination mit mechanischen und hydraulischen Effekten. Die Funktion von Grabskulpturen kann nur unvollständig ermittelt werden, wenn nicht alle Aspekte des Grabverhaltens in die Betrachtung einbezogen werden.

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*) Konstruktions-Morphologie Nr. 140.

1. Introduction

Sculptural patterns in hard shelled invertebrates are both well preserved in fossils and amenable to functional analysis. Surface reliefs that aid in burrowing, or burrowing sculptures, have particularly attracted the attention of paleobiologists. Usually, these sculptures are checked against a theoretical model designed to provide the hypothesized function with maximum efficiency, or paradigm (RUDWICK 1964). Transversal ridges with one side consistently steeper than the other are the most obvious model for a burrowing sculpture, as the asymmetry provides low friction in the burrowing direction, but reduces backslippage in the opposite direction when the actively burrowing organ probes forward into the sediment (frictional asymmetry of SEILACHER 1973), like the scaly undersurface of cross-country skis. Other features of the paradigm are perpendicularity of the ridges, or terraces, to the burrowing direction (cross orientation of SEILACHER 1973) and maintaining a constant size of the sculpture during ontogeny (as it is keyed to the unchanging grain size of the sediment). As a result, new terraces should be introduced during ontogeny (allometric densing of SEIL-ACHER 1973).

Terrace shaped sculptures fulfilling most or all the requirements of the paradigm were found in several invertebrate groups (SEILACHER 1961, 1972, 1973, 1976; STANLEY 1969, 1970, 1977; SCHMALFUSS 1976, 1978a, 1978b; SAVAZZI 1981; Jefferies, Schmalfuss, Seilacher & Signor 1981; Savazzi, Jefferies & SIGNOR in press). However, many burrowing invertebrates have smooth skeletons, and a majority of sculptural patterns, especially in the bivalves, are apparently not ideally designed to aid in burrowing. In several cases, trade offs with other functions (for instance, mechanical reinforcement), constructional constraints (a partial cross orientation resulting from a radial or commarginal pattern) and phylogenetic limitations (the unavailability of preadaptive characters favouring the entrance into a new adaptive zone) may be invoked for the poor match to the paradigm. One cannot exclude a priori, however, that different feasible morphologies can exist, unrelated to the paradigm under consideration. Characters not observable in fossils (for instance the movements employed in burrowing or the morphology of the soft parts) may render a terrace sculpture less suitable for burrowing than a smooth surface or a different sculptural pattern, or selective pressure favouring the mechanically optimal sculpture may not be strong enough for it to evolve. Among the bivalves, sculptures complying only in part with the paradigm were actually shown to be func-

<sup>Figs. 1 a-g. Scapharca (S.) inaequivalvis (Bruguière), Northern Adriatic Sea. –
a. live specimen with byssus (arrow), 0.7 x. Note the periostracum naturally worn away over the umbonal region. – b. S. E. M. photograph of the periostracal shingles in the central region of the right valve, 20 x; – c-d. right and left valve, 1 x; – e-f. same, without periostracum, 1 x; – g. anterior view, without periostracum, 1 x; – h-i. Acanthocardia (Rudicardium) tuberculata (Linnaeus), Northern Adriatic Sea, right and anterior views, 1 x. The shells in figs. c-i were covered with magnesium oxide to emphasize the surface relief.</sup>



tional in burrowing (STANLEY 1977 and personal communication), and a variety of other functions were hypothesized or demonstrated for sculptural traits (see review in KAUFMANN 1969).

To determine whether or not sculptures not complying with the paradigm are effective in burrowing, two recent burrowing bivalve species with strong radial ribbing were chosen, the arcoid Scapharca inaequivalvis (Bruguière 1789) and the cardiid Acanthocardia tuberculata (Linnaeus 1758). Their radial ribs are oriented perpendicular to the burrowing direction only in the central region of the shell. They show no visible frictional asymmetry and grow almost isometrically. These bivalves possess also asymmetrical surface features (tubercles, periostracal shingles) whose effects will be discussed below. Strong radial ribs are effective as mechanical reinforcement of the shell, and their interlocking along the commissure supplements the hinge teeth in resisting shear forces (KAUFMANN 1969). Radial sculpture, moreover, is a very common feature in the Arcoida and the Cardiidae. The evolution of asymmetrical burrowing sculptures did take place in these groups (terrace-shaped radial ribs in Cardium (Bucardium), divaricate terraces in Nemocardium (Lyrocardium), N. (Discors), N. (Divaricardium), slightly asymmetrical ribs in very large Scapharca; personal observations). Hence, one cannot argue that constructional or phylogenetic constraints prevent the development of such features in members of these families.

Scapharca inaequivalvis is a rather slow burrower, taking about half an hour to burrow completely beneath the sediment. Unlike many species of the closely related genus Anadara, in this species the posterior slope of the shell is not left exposed. Originally from Japan, this species became naturalized in the northern Adriatic a few years ago and it is now collected for commercial purposes. Acanthocardia tuberculata, a native Mediterranean and Atlantic species, is a faster burrower (1-3 minutes) and possesses a more strongly developed foot. The choice of two species belonging to distantly related families but living in the same biotopes renders the conclusions more reliable and of more general significance.

2. Materials and methods

Freshly collected specimens of Scapharca inaequivalvis and Acanthocardia tuberculata were obtained from the C. A. M. wholesale mollusc market in Chioggia (northeastern Italy). The two species are collected by commercial dredging boats in the sea facing the Venetian lagoon, at a depth of 2-4 m, on sand shoals 1 to 2 km from the coast. Additional juvenile specimens of S. inaequivalvis were found byssally attached to asbestos-filled concrete slabs, immersed in the lagoon near the Istituto di Idrobiologia in Chioggia to observe the settlement of epizoans. A. tuberculata was also dredged in considerable numbers from clean sand in water 15 m deep, about 15 km from the coast off Venice.

Some of the bivalves were kept in running water tanks fed with unfiltered water from the lagoon, at an average temperature of 20–22 °C. Other individuals were kept in a closed circulation system containing continuously filtered and oxygenated sea water, held at a constant temperature of 20 °C. These individuals were fed by pe-

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riodically introducing planktic green algae into the circulation system. This controlled environment approached more closely the natural conditions of the open Adriatic Sea. No significant differences were observed in the burrowing activity of bivalves in the two circulation systems, so data from the two groups are presented together. Some individuals were kept in sand filled buckets submerged in 1.5—2.0 m of water in the lagoon near the Istituto di Idrobiologia. The burrowing depth and orientation of these individuals were found to be consistent with those of the laboratory-kept individuals. A total of 48 individuals of Acanthocardia tuberculata and 65 of Scapharca inaequivalvis was used in the experiments.

After a rest of a few days in clean sand, the bivalves were extracted from the sediment, allowed to reburrow, and the burrowing time and number of burrowing sequences were monitored. Individuals refusing to burrow or showing an unusually long burrowing process were discarded. These individuals, representing less than $5 \, 0/0$ of the total number of bivalves available, had a high mortality rate. Close examination showed that most of them had been injured while being dredged. The mortality rate of individuals showing a normal burrowing activity, on the other hand, dropped rapidly from $3 \, 0/0$ per day in the first days to less than $0,1 \, 0/0$ per day after about one month. No detectable change in burrowing activity occured during this period.

Clean sand from the open sea and washed sand from the beach of Sottomarina di Chioggia, which turned out to have closely similar granulometric compositions (mostly 2-3 phi, or 0.125-0.250 mm dia.), were used in the experiments. The bivalves were placed on an artificially compacted substrate (see BOTTIER & CARTER 1980) underwater, in their erect probing orientation (STANLEY 1970, p. 46) and allowed to burrow. Both species were found to react to water currents produced by other individuals in the same tank and to changes in the light level by momentarily suspending the burrowing process and partly or totally retracting the foot. The number of burrowing sequences (TRUEMAN, BRAND & DAVIS 1966, p. 104) needed to burrow, until the posterior margin of the shell was level with the surrounding sediment, was found to be a measure of the burrowing activity much less susceptible to external disturbances than the burrowing rate index (STANLEY 1970, p. 57), which is a function of burrowing time. The burrowing activity of the two species showed no detectable daily or tidal pattern, and in general the number of burrowing sequences remained relatively constant for each individual. Detailed data for these statements are not supplied in the present paper, but the diagrams in figs. 2 and 5 give a good idea of the overall consistency of the burrowing performance. The interval of inactivity between being placed on the substrate and beginning to burrow was rather variable, but it too tended to be an individual character. A long period of inactivity did not necessarily coincide with a slow subsequent burrowing process.

The periostracum in Scapharca inaequivalvis was removed from the shell with a stiff brush. The radial ribs in both species were covered with atoxic, water insoluble "Pongo" brand modeling wax. This wax can be easily modeled at body temperature, but at 20 °C it is stiff enough to resist abrasion, and sand does not stick to its surface underwater. Care was taken that the wax did not come into contact with the mantle. The changes in burrowing performance of the wax-covered specimens were immediate, and lasted as long as the shell was left covered. Removal of the wax after up to four weeks, on the other hand, immediately restored the original performance (fig. 2). Therefore, it can be concluded that the wax had an exclusively mechanical action on the molluscs. The laboratory controls were manipulated for the same length of time necessary to perform the required modifications of the shell on the specimens to be monitored. The molluscs showed no reaction to prolonged manipulation, other than a temporary decrease in burrowing "readiness" (but not in burrowing performance).

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3. Results and discussion

BOTTJER & CARTER (1980) showed that both the periostracal shingles and the radial ribs of *Anadara ovalis* (Bruguière) reduce sediment scour, as water currents pass around the posterior region of the shell. In addition, they found that the periostracal shingles significantly increase the force necessary to extract the shell from the sediment. *Anadara ovalis* is similar enough to *Scapharca inaequivalvis* that their conclusions are likely to apply to the latter species as well. The periostracal shingles in both species are directed posteriorly and away from the umbones (fig. 1 b). Their asymmetry renders them likely burrowing structures. Moreover, THOMAS (1975 and personal communication) already suggested that the periostracal shingles aid in burrowing in glycymerids.

3.1. Scapharca inaequivalvis

Removal of the periostracum on the posterior slope of *S. inaequivalvis* did not appreciably increase the number of burrowing sequences needed for complete shell burial (fig. 2a). Removal of the periostracum on the anterior or central region caused a detectable increase in the number of burrowing sequences. When



Figs. 2 a—b. Burrowing performance of Scapharca inaequivalvis. — a. The diagrams show the performance of individual specimens during four weeks. The shaded area represents the period during which the shells were left covered with wax. The obliquely ruled area represents removal of the periostracum. — b. The burrowing performance is shown for shells 40—45 mm long, the usual adult size. The average number of burrowing sequences needed to attain complete burial was 9.7 for the unaltered controls, 12.8 for specimens without periostracum, and 14.8 for specimens with the anterior and central ribs covered with wax. Diagram b shows data obtained from simultaneous observations on control and altered individuals, and is not a composite of the diagrams a.

the periostracum was removed from both regions, the average number of burrowing sequences increased by 33% with respect to the unaltered controls (fig. 2b). As already noted by Bottjer & CARTER (1980), the volume and buoyancy of the periostracum is too low for its removal to make any detectable physical difference. The periostracal shingles are therefore likely only to have a mechanical effect on the surrounding sediment. When the shell is incompletely buried in the sediment, it tends to be partly pushed back as the foot probes downward, initiating the burrowing sequence. It is at this time that the posteriorly directed shingles act to increase resistance to backward movement of the shell. When the periostracum was removed, backslippage of the shell increased accordingly. It can therefore be concluded that the anterior and central shingles act as a burrowing structure. On the posterior slope they seem to have no significant effect on the burrowing process. Their main function here, as suggested by BOTTJER & CARTER (1980), may be to reduce scour around the posterior end of the shell or to discourage the settlement of epizoans on the often exposed posterior slope. In spite of the fact that this species of Scapharca burrows more deeply than most species of Anadara, it happens quite commonly that moderate erosion exposes the posterior margins of the shell. In the laboratory as well as in the field, the mollusc does not readjust continuously its life position (as Acanthocardia tuberculata does). Readjusting is possibly rendered difficult by the substantial byssus (fig. 1 a).

Covering the posterior slope of the shell with wax to smooth out the radial ribs, as expected, did not appreciably alter the burrowing performance. Covering the anterior and central regions of the shell, instead, resulted in a marked increase (53 %) in the number of burrowing sequences needed to achieve complete burial (fig. 2b). Smoothening the shell surface with wax has a similar (but greater) effect on the burrowing process, compared with the removal of the periostracal shingles, in spite of the fact that the first operation slightly increases the total mass of the shell (by $2-3 \frac{0}{0}$) and the second decreases it. While the periostracal shingles are asymmetrical, clearly providing frictional asymmetry, the radial ribs are almost symmetrical in cross-section. Actually, in the oldest individuals of Scapharca, the anterior edge of the ribs is more rounded than the posterior. It was already suggested (KAUFMANN 1969, THOMAS 1975, Bottjer & CARTER 1980) that a prominent shell sculpture stabilizes a bivalve shell within the sediment by increasing friction. However, one would expect that a symmetrical sculptural pattern is indifferent or detrimental to burrowing, since it also increases friction in the burrowing direction. The interpretation of the function of the radial ribs must be preceded by a detailed analysis of the burrowing process.

Like most of the burrowing bivalves so far studied, Scapharca inaequivalvis loosens the sediment surrounding its shell with a jet of water, which it ejects antero-ventrally, just prior to pulling on the pedal retractor muscles. This hydraulic action is achieved by adducting the valves with the posterior mantle margins closed. At the same time, blood is forced into the foot, increasing its volume and anchoring it within the sediment (fig. 3 c). Unlike other bivalves, which pull first on the anterior pedal retractor muscles (STANLEY 1970, 1975), download Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

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Figs. 3 a—f. Shell movements of Scapharca inaequivalvis during a typical burrowing sequence. — a—b. The foot probes into the sediment and the shell is consequently partly pushed out (the dotted line in b represents the previous rest position). — c. Water is subsequently expelled antero-ventrally, suspending a considerable amount of sediment, and the shell is pulled straight downward. — d. After about one second the shell rocks forward. — e. It returns to the erect orientation. — f. Comparison of the initial (a) and final (e) positions (respectively, dotted and shaded outlines in f) reveals that progress has been essentially downward, with only a negligible component in the dorsal direction, and not along the longer axis of the shell. The drawings are based on timelapse photographs.

S. inaequivalvis appears to pull first on both the anterior and posterior pairs of pedal retractors. The shell is therefore lowered straight down into the temporary cavity formed in the sediment by the water jet. The symmetrical radial ribs do not hinder the downward movement of the shell, because it takes place in a loosened sediment, and because the cross-section of the shell is reduced by adducting the valves. After a short pause (about one second), during which the sediment begins to settle, the pull is exerted only on the anterior pedal retractors, so that the shell rocks forward (fig. 3d). The ribs now act to prevent backslippage of the shell, while the umbones are pushed downward. The pull is then transferred to the posterior pedal retractors, and the shell rocks backward to the erect orientation (fig. 3 e). When the posterior pedal retractors are contracted, the umbones act as an anchor, as shown by STANLEY (1975) in Mercenaria mercenaria (Linnaeus). Comparison of time-lapse photographs of burrowing sequences of the unaltered controls with those of wax-covered individuals suggest that the ribs reduce backslippage of the shell at two distinct times: when the foot probes downward at beginning of the burrowing sequence, and while

the shell rocks forward. The first effect seems to contribute more substantially to the overall efficiency of the burrowing process.

3.2. Acanthocardia tuberculata

This species has a more typical burrowing sequence, as retraction of the foot and rocking forward are simultaneous (fig. 4). The effect of the radial ribs on the burrowing efficiency is however equally conspicuous (fig. 5). In this species the ribs appear to reduce backslippage mainly while the foot probes downward.



Figs. 4 a-d. Shell movements of Acanthocardia tuberculata (Linnaeus) during a typical burrowing sequence. — b. After probing with the foot into the sediment, — c. water is ejected antero-ventrally and the anterior pedal retractor muscles are contracted, simultaneously lowering the shell and causing it to rotate forward; — d. pulling on the posterior pedal retractor muscles subsequently restores the erect orientation. During this last phase, water may still be rising through the sediment around the shell. The drawings are based on time-lapse photographs.

It is interesting to note that in the first burrowing sequences, while the shell is still mostly exposed, it takes a longer time for the mollusc to dig with the foot to a suitable depth. In these first probing movements, the foot penetrates into the sediment mainly by means of peristaltic waves at the tip of the foot, aided by mucus secretion. Only when the shell is partly buried and provides a suitable friction against the sediment, can the foot be pushed downward while the shell acts as a penetration anchor. This renders the penetration of the foot into the sediment much faster and probably energy-saving with respect to penetration by peristaltic waves alone. The shift from one mode of penetration of the foot to the other seems to be a constant feature in shallowly burrowing bivalves.

In addition to the ribs, Acanthocardia tuberculata also possesses tubercles, or knobs, which in the anterior region are asymmetrical and oriented so as to provide the maximum friction (figs. 1 h—i). The tubercles were left projecting through the wax used to fill the grooves between the radial ribs. The effect of these sculptures on the burrowing process was not checked, as they are little developed in this speceis. Observations on Acanthocardia aculeata and A. echinata, which possess more developed and differentiated tubercles, show that also these structures are functional in reducing backslippage of the shell.



Figs. 5 a—b. Burrowing performance of Acanthocardia tuberculata. — a. The diagrams show the performance of individual specimens during four weeks. The shaded area represents the period during which the shells were left covered with wax. — b. The burrowing performance is shown for shells 35-40 mmlong. This was the commonest size interval in the sample. Diagram b shows data obtained from simultaneous observations on control and altered individuals, and is not a composite of the data shown in diagrams a.

4. Conclusions

Radial ribs in bivalves can be functional in the burrowing process, although they usually lack an asymmetrical cross-section. This is possible because the mechanical properties of the sediment are periodically changed by the hydraulic emission of water, and the cross-sectional area of the shell is reduced by adduction of the valves. It is interesting that, among shallowly burrowing bivalves from the same biotope, a powerful hydraulic action appears to be consistently associated with a marked radial sculpture and umbones not substantially prosogyrate (cf. STANLEY 1975). Thus Scapharca inaequivalvis, Acanthocardia tuberculata, A. aculeata (Linnaeus) and A. echinata (Linnaeus) produce much more powerful jets of water, judging from their effect in suspending sediment particles, than Callista chione (Linnaeus), Mactra stultorum (Linnaeus), Tapes decussata (Linnaeus) and Venerupis pullastra (Montagu), which possess smooth or almost smooth shells. Cerastoderma edule (Linnaeus) and Laevicardium oblongum (Gmelin) have a less marked ribbing pattern, and their hydraulic pumping is intermediate in strength between the other two groups.

The weak fit of radial ribs to the paradigm for burrowing sculptures does not, in itself, invalidate the paradigm approach to the study of the functional morphology of these features. Rather, it may reflect a failure to consider the burrowing sculpture as one character in a set of coadaptations to burrowing. As more examples become available, it may be found that different sets of such characters are associated with different sculptural patterns. For the moment, it must be remembered that a good fit to the paradigm for burrowing sculptures in an organism is a strong indication of an efficient burrowing habit, but the lack of such a fit does not necessarily imply the opposite thing.

In a paper published when the present work had already been accepted for publication, STANLEY (1982) experimentally demonstrated, among other things, that the symmetrical commarginal ribs of the venerid bivalve Chione cancellata (Linnaeus) are functional in reducing scour by water currents, and actually slow down the burrowing process. Since venerid species from the Adriatic sea systematically display a considerably less powerful hydraulic water pumping action than similarly sized cardiids (personal observations), one can assume that this is the case also of Chione cancellata. The high average number of burrowing sequences required for burial computed from STANLEY's data (17. 1) agrees with this hypothesis. Therefore, STANLEY's results are not in contrast with the conclusions of the present paper. Rather, they further show the necessity of taking into account all coadaptive aspects of the burrowing process in the study of the functional morphology of burrowing sculptures.

5. Acknowledgements

The author wishes to thank R. D. K. THOMAS (Lancaster, Pennsylvania) for thoroughly reviewing the manuscript, and K. CHINZEI (Tokyo) for identifying shells of *Scapharca inaequivalvis*. The C. A. M. mollusc wholesale market, the staff and collaborators of the Istituto di Idrobiologia in Chioggia, of the Museo Civico di Storia Naturale in Venice, of the Consorzio per lo Sviluppo della Pesca e dell'Acquicoltura del Veneto (Co. S. P. A. V.) and fishermen in Chioggia supplied material and facilities or helped in various ways. The field work was carried out in May-June and August-September 1981 at the Istituto di Idrobiologia in Chioggia and financially supported by the Sonderforschungsbereich 53 "Palökologie", Tübingen. The present publication is No. 140 in the series *"Konstruktions-Morphologie*".

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Zeitschrift/Journal: Stuttgarter Beiträge Naturkunde Serie A [Biologie]

Jahr/Year: 1982

Band/Volume: 353_A

Autor(en)/Author(s): Savazzi Enrico

Artikel/Article: <u>Shell Sculpture and Burrowing in the Bivalves Scapbarca</u> inaequivalvis and Acanthocardia tuberculata). 1-12