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Morphology of Skeletal Cortex in the Arms of Crinoids (Echinodermata: Crinoidea)

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ABSTRACT—The endoskeleton of echinoderms consists of a meshwork of calcite. Using light and electron microscopy, this study investigates a cortex covering the arms of crinoids. In *Metacrinus rotundus*, it consists of massive calcite and has a regular pattern of ridges and holes. The cortex is covered by thin extensions of epidermal cells whose cell bodies are located in the holes. The cells carry intracuticular cilia and seem to have contact with axons connecting to the central nervous system. The cilia probably have sensory function. We compared three other species of living stalked crinoids and two species of stalkless crinoids and found that they have a similar cortex with varying surface patterns, possibly due to various modes of life. The cortex of arms with its pattern seems to be a species-specific characteristic of crinoids. The ridges of the cortex might influence drag caused by currents or serve to facilitate current detection.

INTRODUCTION

Echinoderms possess a mesodermal endoskeleton that is subdivided into ossicles. Most ossicles consist of a three dimensional, regular or irregular meshwork of calcite trabeculae, called the stereom. The liquid-filled pore space in between the trabeculae can be occupied by cells or extracellular fibrils. The skeleton grows by apposition of new trabeculae onto the surface of the ossicle. Internal growth of an ossicle can occur in echinoderms but such cases are rare (Smith, 1990). Crinoid arms, stalks, and cirri consist of ossicles interconnected by ligaments or muscles. During our studies of the stalked crinoid *Metacrinus rotundus* we found that arms, stalk, and cirri are covered by a dense calcitic layer. The literature gives only brief accounts: Ubaghs (1978) reports that columnals, i.e., cirri and stalk, of fossil stalked crinoids are covered by a cortex characterized by "a dense calcitic microstructure". Arms are not mentioned, however. Macurda and Meyer (1975) showed pores on the surface of arms of extant crinoids that have some regular arrangement but gave no details.

This study tries to replace the insufficient data with a thorough description of the cortex covering the arms of extant crinoids. We report the fine structure of the cortex in the arm of the stalked crinoids *Metacrinus rotundus*, *Saracrinus nobilis*, *Endoxocrinus alternicirrus*, and *Hypalocrinus naresianus* and the stalkless crinoids *Oxycomanthus japonicus* and *Tropiometra afra*. We also investigated the ultrastructure of the tissues associated with the cortex in the arms and cirri of *Metacrinus rotundus*. The data indicated an innervation of the epidermal cells. We therefore also studied the nervous tissues with special regards to their connection with the epidermis. Finally we discuss the morphological data and speculate about the function of the cortex.

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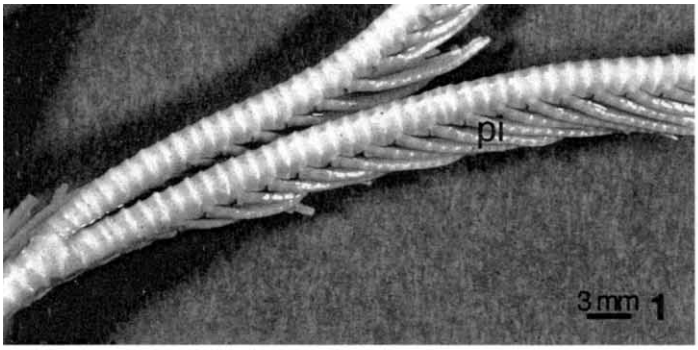
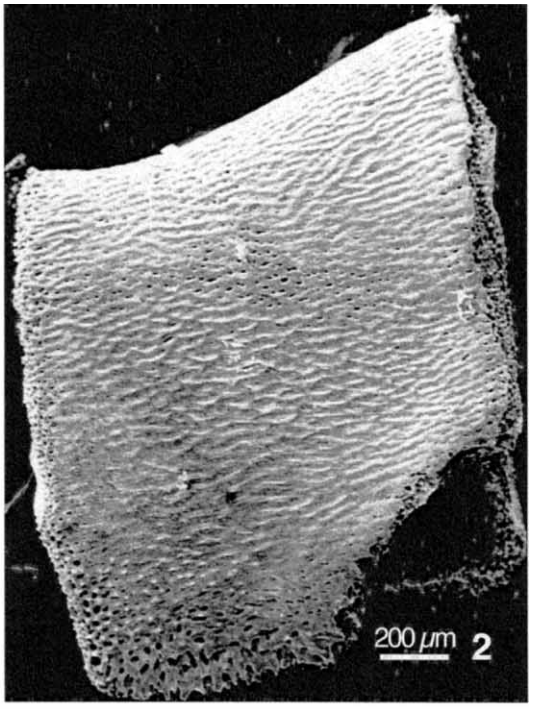
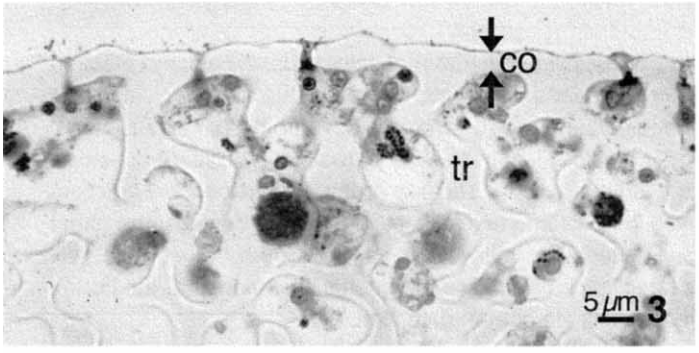
MATERIALS AND METHODS

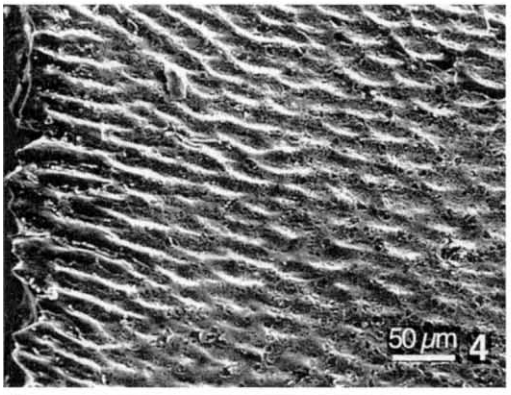
For our study we used specimens of *Metacrinus rotundus* that were dredged from ca. 130 m depth off Numazu, Suruga Bay, Japan. Whole alcohol fixed specimens of *Saracrinus nobilis*, *Endoxocrinus alternicirrus*, and *Hypalocrinus naresianus* were provided by Prof. T. Oji, University of Tokyo. Specimens of *Oxycomanthus japonicus* were collected near Kominato, Chiba Prefecture, and specimens of *Tropiometra afra* were collected in Sagami Bay, Japan.

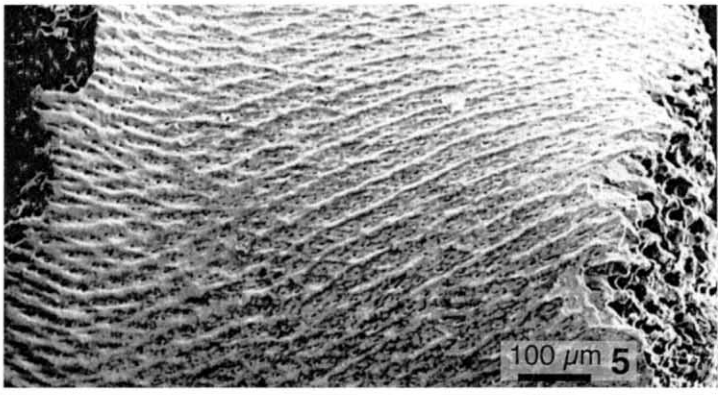
For scanning electron microscopy pieces of arm, stalk, or cirri from fresh or fixed animals were immersed in diluted commercial kitchen bleach until all organic matter was dissolved. Then they were rinsed with distilled water repeatedly and air dried. Samples for critical point drying were not bleached, but fixed in 3.5% glutaraldehyde in 0.05 M cacodylate buffer pH 7.2 for 4 hr, rinsed in buffer and postfixed in 1% osmium tetroxide in the same buffer for 1 hr. Thorough rinse in buffer was followed by an ethanol series and a final step of amyl acetate. Then the samples were dried in a critical point drying apparatus using CO_2 as medium. Both bleached and critical point dried samples were mounted on holders, coated with gold or platinum and observed in a scanning electron microscope JEOL JSM-T220. For light and transmission electron microscopy, pieces of ossicles of freshly caught specimens were fixed in 3% glutaraldehyde in 0.1 M cacodylate buffer containing 0.05% ruthenium red for 1.5 hr. Then the samples were immersed in 1% glutaraldehyde in the same buffer for several hours. Postfixation was in 1% osmium tetroxide in cacodylate buffer. Dehydration with an ethanol series was followed by embedding in araldite or Spurr's resin. After the blocks were polymerized, suitable pieces were cut out and abraded with emery paper to expose the mineral phase. These pieces were decalcified in 1% ethylene diamine tetraacetic acid (EDTA) for several days. Subsequently they were rinsed in distilled water, air dried and reembedded

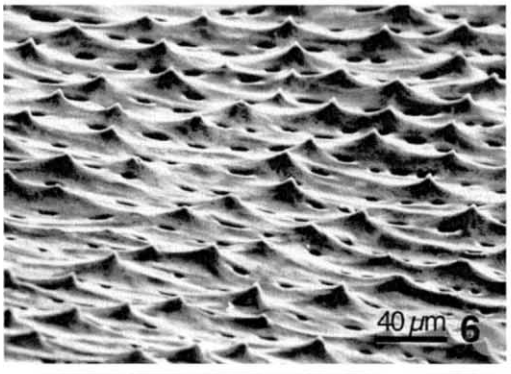


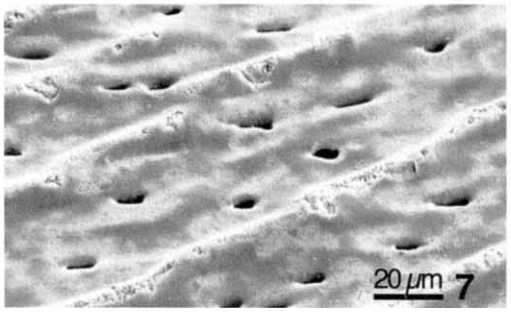


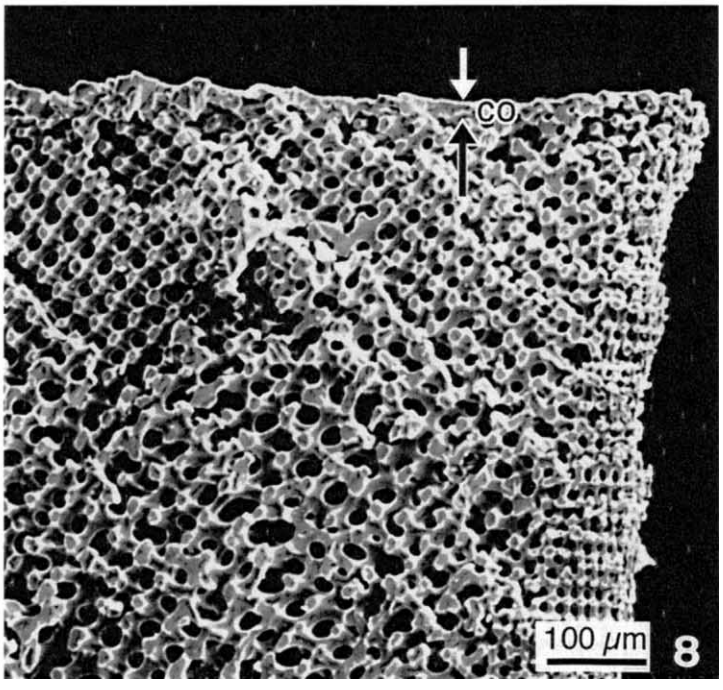












in a second phase of resin. With this method we could ensure that the three-dimensional structure of the skeleton was retained. Semithin sections were cut with glass knives, stained with 1% crystal violet at 60°C, and observed in a light microscope NIKON Labophot 2. For transmission electron microscopy, ultrathin sections were cut with a diamond knife and stained with uranyl acetate and lead citrate. They were observed in a HITACHI H-300 transmission electron microscope. For staining of nervous tissue formaldehyde fixed ossicles were decalcified with EDTA and embedded in paraffine or in Technovit (KULZER) according to the manufacturer's instructions. Semithin sections and paraffine sections were stained with Glees' silver stain (Humason, 1979).

RESULTS

Morphology of the arm skeleton of *Metacrinus rotundus*

The arm of *M. rotundus* (Fig. 1) consists of a row of ossicles. On the oral side of the arm the ossicles are covered by soft tissue containing the radial water canal, coelomic channels and connective tissue. On the aboral and lateral sides the ossicles have a skeletal cortex that displays a geometrical pattern (Figs. 2 to 7).

The cortex is thin (between ca. 3 μm and 10 μm) (Fig. 3) and covers the entire aboral and lateral sides of the arms. It is continuous with the underlying stereom. Ridges on its surface run in various directions (Fig. 2) and create patterns that can be roughly subdivided into two types. On the aboral side and at the oral end of the lateral side the ridges are often curved and irregular (Fig. 4). They are of a more or less constant height. On the lateral sides ridges of the second type are found. They run parallel to each other at an angle of ca. 30° to the long axis of the arm (Fig. 5). They carry small hillocks at regular intervals (Fig. 6). Between the ridges of both types holes of ovoid shape connect to the pore space of the underlying stereom (Fig. 7). The underlying stereom is arranged regularly and is thus a galleried stereom (Fig. 8). There are no layers discernible. Young and thus small arm ossicles are covered only by irregular ridges and lack hillocks. Their cortex has the same thickness as that of older, bigger ossicles.

Ultrastructure of arm cortex

The cortex is covered by an epidermis, and an overlying cuticle (Figs. 9, 10). The basement membrane, although not well defined, underlies the epidermis. In some places we could not follow its course, especially around the cell bodies of the epidermis. The epidermis consists of a single layer of cells whose cell bodies are located in the holes of the cortex. Above the massive calcite of the cortex the cells make up a thin layer that contains variously shaped clear vesicles and a few mitochondria. The bulk of organelles, e.g., nucleus, Golgi apparatus, mitochondria, and various types of vesicles, are located in the cell body in the holes of the cortex. Microvilli extend into the overlying cuticle. Short, single cilia project from the epidermal cells into the cuticle (Fig. 11). By scanning electron microscopy of critical point dried ossicles and by serial sectioning we confirmed that the cilia do not penetrate through the cuticle to the outside. Each cilium is surrounded by a collar of microvilli (Fig. 12). The cuticle is ca. 0.25 μm thick and consists of a single layer of fine granular material. After fixation in fixative containing ruthenium red particles of ruthenium red often adhered to the cuticle (Fig. 9).

The cell bodies of the epidermal cells extend deep into the holes of the cortex. The basement membrane around the cell bodies was often invisible. The pore space of the stereom underlying the epidermis contains cells that make contact with the epidermal cells (Fig. 10). One cell type contains bullet shaped electron dense organelles (BSO-cells, Fig. 13) that have been described before in the stalk of *M. rotundus* (Grimmer *et al.*, 1985). BSO-cells make up a network throughout the stereom of arm and of cirri and also a layer around the nerve running in the center of the arm. The strands of BSO-cells running through the stereom are associated with profiles of small cell processes that might be axons. The processes contain sometimes small vesicles and in some sections they show varicosities (Fig. 13).

In ground sections of decalcified arm pieces and in semithin sections we observed branches of the central nerve extending through the stereom towards the surface (Fig. 14). Silver staining after Glees revealed nerve cell bodies and axons located immediately below the epidermis (Figs. 15, 16).

Fig. 1. Arm of *Metacrinus rotundus*. The construction from a long row of ossicles is clearly visible. Each ossicle carries one small pinnule (pi) at each side. In this and all following photographs of the arm the aboral side is at the upper side.

Fig. 2. Scanning electron micrograph of single ossicle of an arm of *M. rotundus*. The pattern of the skeletal cortex covers the entire aboral and lateral surface.

Fig. 3. Light micrograph of a semithin section of a double embedded arm ossicle of *M. rotundus*. The mineral phase of the ossicle is filled with featureless araldite, whereas the pore space is filled with cells and extracellular material. Note that the cortex (co) has about the same thickness as the trabeculae (tr) of the underlying skeleton.

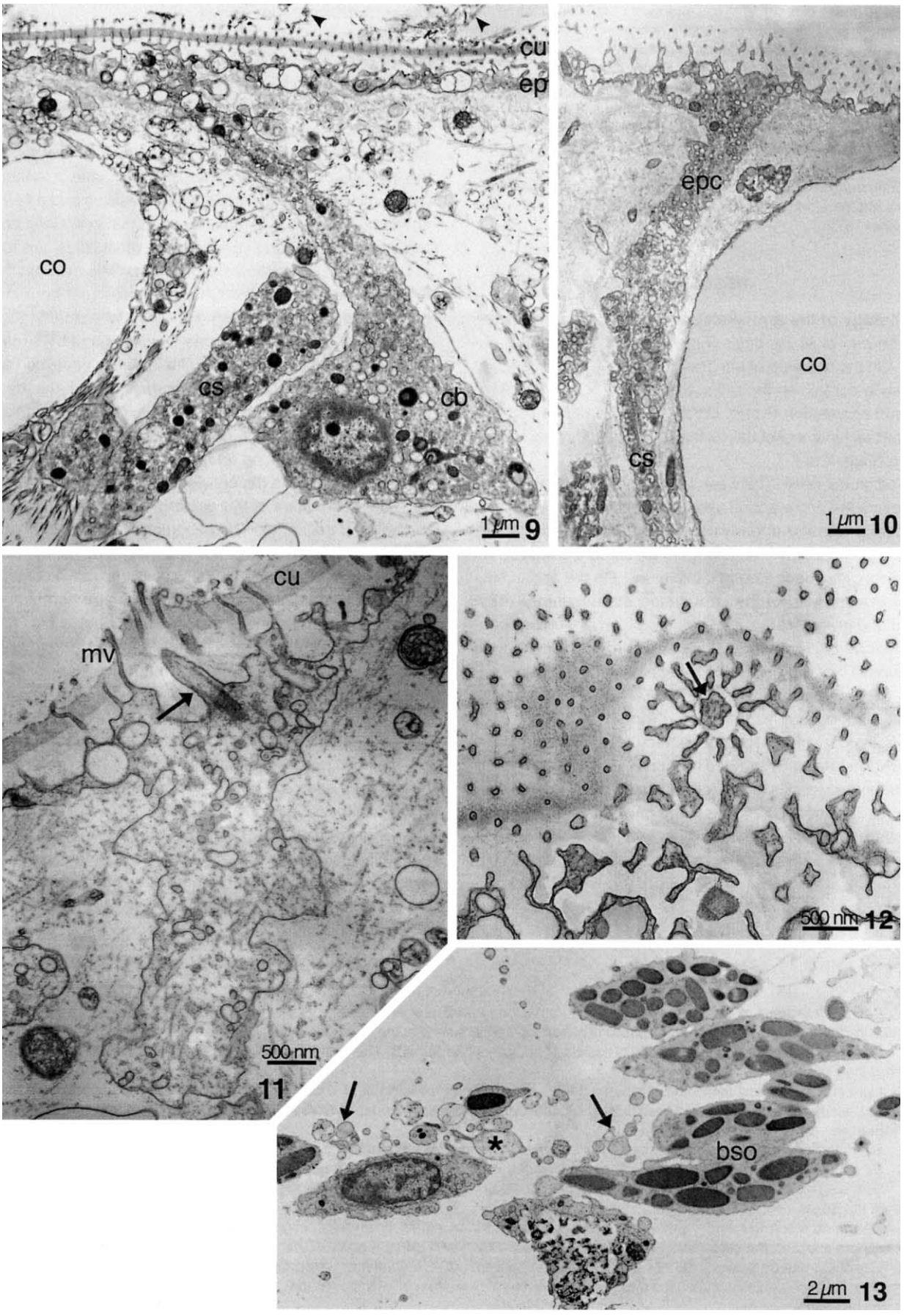
Fig. 4. Scanning electron micrograph of the aboral cortex of the arm of *M. rotundus*. Ridges are curved and irregular.

Fig. 5. Scanning electron micrograph of the lateral cortex of the arm of *M. rotundus*. Ridges are straight and run parallel to each other.

Fig. 6. Scanning electron micrograph of the lateral cortex of the arm of *M. rotundus*. This micrograph was taken from a low angle to show small hillocks on the ridges.

Fig. 7. Scanning electron micrograph of the lateral cortex of the arm of *M. rotundus* showing the holes in the cortex that connect to the underlying pore space of the skeleton.

Fig. 8. Scanning electron micrograph of a piece of arm ossicle of *M. rotundus* that was broken to reveal the inside. The right side of the micrograph is the joint surface whereas the upper side is the aboral side. Note the thin cortex (co) covering a uniformly regular (galleried) stereom without any layering.



Cortex pattern of stalk and cirri

Stalk and cirri of *Metacrinus rotundus* are covered with a similar cortex as the arms. However, its surface pattern lacks ridges, but is smooth. The holes in the cortex of the cirri are round and arranged rather irregularly (Fig. 17). The holes in the cortex of the stalk are elongated and aligned along the longitudinal axis of the stalk (Fig. 18).

Cortex pattern of other stalked crinoids

Saracrinus nobilis. The surface pattern of the arm ossicles of *S. nobilis* is less elaborated than that of *M. rotundus*. At the lateral side the big roundish holes are arranged in parallel lines oblique to the oral/aboral axis of the arm (Fig. 19). On the aboral side of the arm the lines are curved and less orderly arranged (Fig. 20). Ridges are not so prominent, but still clearly visible, especially on the aboral side (Fig. 21).

Endoxocrinus alternicirrus. The pattern of the arm ossicles of *E. alternicirrus* (Fig. 22) is similar to that of *S. nobilis*. The arrangement of the holes is more or less irregular all over the aboral and lateral sides of the arm, and ridges are not developed.

Hypalocrinus naresianus. The surface pattern of *H. naresianus* has holes elongated along the length axis of the arm (Fig. 23). Ridges were not observed. Micrographs of the joint surface between two ossicles show that the cortex of *H. naresianus is* very thick (up to 100 μm) compared to the other species studied (Fig. 24).

Cortex pattern of stalkless crinoids

We studied comparatively the arm ossicles of *Oxycomanthus japonicus* and *Tropiometra afra*. In *O. japonicus* the surface does not resemble a massive cortex, but displays an irregular array of pores similar to the usual irregular pattern of echinoderm stereom. However, the size of the pores and trabeculae are much bigger than that of the underlying stereom (Fig. 25) so that the cortex has a different structure than the stereom.

The surface of the arm ossicles of *Tropiometra afra* is characterized by numerous prominent ridges that run roughly parallel to the length axis of the arm (Fig. 26). In between the ridges the irregular stereom of the underlying skeleton is visible (Fig. 27).

DISCUSSION

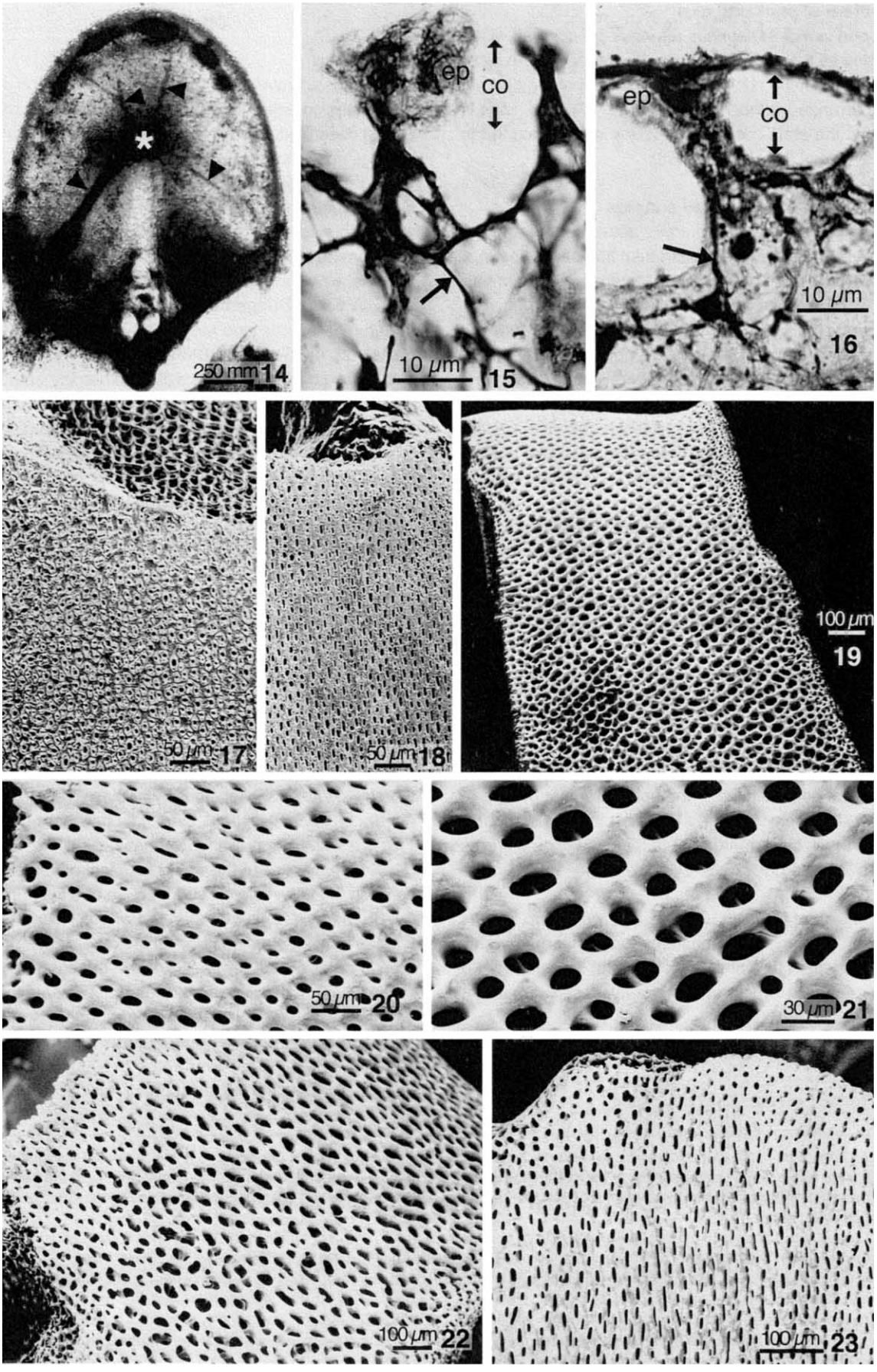
Morphology

Our data provide the first detailed description of the skeletal cortex covering the ossicles of extant crinoids. Ubaghs (1978) described a cortex in the columnals, i.e., stalk and cirri in fossil specimens. However, he gave only a brief account without morphological details, probably because details of skeletal patterns are rarely conserved in fossils. Our data allow for the first time to compare patterns of various species. The comparison shows a high variability of pattern between species, which might provide a useful tool in crinoid systematics. A pore arrangement on the surface of arms is mentioned by Macurda and Meyer (1975), who reported "linear patterns" in the comatulids *Nemaster rubiginosa* and *Comactinia echinoptera* var. *valida*. Since the authors did not mention anything about the underlying skeleton, we cannot judge whether the linear patterns are part of a similar cortex as described in the present study. However, the patterns in the micrographs of Macurda and Meyer (1975) are different from those we describe thus supporting our hypothesis that patterns might indeed be species-specific.

Echinoderm skeleton grows in most cases by accretion (Smith, 1990) with only few exceptions. Growth lines caused by layering of denser skeleton ("perforate skeleton", Smith, 1990) and looser stereom has been observed in the isocrinid *Neocrinus decorus* (Smith, 1990). In *M. rotundus* we did not find any growth lines but only galleried stereom covered by the thin cortex consisting of perforate stereom. The constant thickness of the cortex in small and large ossicles in combination with the lack of layering suggests that skeletal material is rebuilt during growth. The perforate skeleton of the cortex is thereby resorbed and replaced by galleried stereom. The newly generated surface is then covered by new perforate stereom. This is the first finestructural evidence of skeletal resorption in crinoids, and adds to the macroscopical observations of resorption of stalk skeleton by Amemiya and Oji (1992).

In the epidermis of the arm of *M. rotundus* we could not find the conventional basiepithelial nerve plexus that is common in other echinoderms. However, the connection to neuron-like cells in the underlying stereom indicates that the epidermis is innervated. In other echinoderms it is usually easy to tell whether a tissue is of epidermal origin by following its basement membrane, even if the tissue is sunken into the stereom (Märkel and Röser, 1985). In the case of *M. rotundus*,

Fig. 9. The cortex (co) is covered by cuticle (cu) and epidermis (ep). The cell body (cb) of the epidermal cell is located inside the hole of the cortex and is near to a cell (cs) in the stroma of the underlying stereom. Particles of ruthenium red (arrowheads) adhere to the cuticle.
Fig. 10. Transmission electron micrograph of the cortex (co) of the arm of *M. rotundus*. An epidermis cell (epc) is making close contact to a cell (cs) of the underlying stereom.
Fig. 11. Transmission electron micrograph of the epidermis of the arm of *M. rotundus*. Epidermal cell carrying a short cilium (arrow). Serial sections of this area revealed that the cilium did not extend into the free water. Microvilli (mv) extend into the cuticle (cu).
Fig. 12. Transmission electron micrograph of the epidermis of the arm of *M. rotundus*. Grazing section of the cuticle shows a cilium in cross section (arrow) surrounded by a ring of microvilli.
Fig. 13. Transmission electron micrograph of an arm ossicle of *M. rotundus*. Bundles of cells filled with bullet-shaped organelles (bso) run through the pore space of the ossicle from the nerve in the center of the arm to the surface. They are accompanied by small cell processes that might represent axons (arrows). Some of the processes show varicosities (asterisk).



however, the basement membrane looks poorly defined and is even lacking in many places, so that it is impossible to decide whether the neuron-like elements connecting to the epidermal cells are of epidermal origin. We can therefore neither support nor refuse the statement of Heinzeller and Welsch (1994) that the epidermal nerve plexus "is largely confined to the food grooves". Our finding adds to the perception of crinoids as "the odd group out" among echinoderms in terms of their nervous system (Cobb, 1995). It can be speculated that the neuron-like cells in the stereom of *M. rotundus* are nothing else than the basiepithelial plexus of the epidermis deeply sunken into the stereom with the basement membrane no longer separating the plexus from the surrounding connective tissue space.

Another new finding are the subcuticular cilia of the epidermis of *M. rotundus*, which do not protrude beyond the cuticle into the free water. All cilia found in *M. rotundus* were entirely subcuticular, and it seems improbable that they create currents. They could, however, work as pressure or chemical sensors. Considering this observation in context with the innervation we described, it seems justified to say that the ciliated cells probably sense mechanical or chemical stimuli which are then transmitted via the nervous system. In comatulids, Heinzeller and Welsch (1994) have described epidermal cells supposed to be sensory cells. The cilia of these cells protrude through the cuticle into the free sea water, and the cells possess a basal axon-like projection, although a connection to the nervous system was not reported. The cells we found in *M. rotundus* seem more specialized for a sensory function than these comatulid cells.

Function

The function of the cortex cannot be understood without physiological data, which are beyond the focus of this study. However, our morphological data allow some speculations. Smith (1990) mentioned that a cortex can be developed as a protection against abrasion in high-energy environments. This might well be true for crinoids; especially stalked forms are known to be rheophilic spreading their arms into a filtration fan with the aboral side facing the current (Macurda and Meyer, 1975; Baumiller *et al.*, 1991; Birenheide and Motokawa, 1994). The cortex on the aboral side can serve as protection against abrasion by particles swept along with the current. The pattern of ridges and holes is more difficult to explain. The height of the ridges is so small that an influence on the macroscopic current regime cannot be expected (Vogel, 1994). However, small ridges can influence the flow pattern close to the surface. Fast swimming sharks possess a pattern of riblets on their scales. The drag reduction mechanism of this system was investigated in a series of papers (Bechert *et al.*, 1986; Reif, 1985). Basically the riblets of the shark skin are similar to the ridges of the crinoid cortex: not only is their size in the same order of magnitude, but also the maximal swimming speeds of the sharks are similar to the maximal flow speeds crinoids experience. Therefore it seems possible that the ridges of the crinoid cortex reduce drag. However, neither in sharks nor in crinoids has this been shown experimentally. Another possible function of the ridges could be to direct flow to certain areas, where ciliated cells of the epidermis could detect flow speed and direction. The system would thus function as a current detector, which has never been identified in crinoids.

The arms of the comatulid species of this investigation have a less developed cortex. Among them, *Tropiometra afra* has the denser cortex. This species can be found clinging to rocks swept by "abundant, strong currents" (Meyer, 1979) whereas *Oxycomanthus japonicus*, according to local divers, hides in rocks and crevices and is less exposed to currents. Stalked forms generally seem to be rheophilic (Baumiller *et al.*, 1991) and have a well developed cortex. Our data thus seem to indicate a connection between flow regime of the

Fig. 14. Photograph of glutaraldehyde-osmium fixed, double-embedded arm ossicle of *M. rotundus*. This cross ground section reveals nerve branches (arrowheads) running from the central nerve (asterisk) towards the surface of the ossicle. The branch on the lower left runs into the pinnule of that side (not visible).

Fig. 15. Light micrograph of a paraffine section of the cortex in the arm of *M. rotundus*. The sample was decalcified before embedding and thus the position of the calcitic cortex (co) can only be approximated. Silver staining of this section revealed a network of black stained nerve cells whose extensions (arrow) make contact with the cells of the epidermis (ep), which stained brown in the original section.

Fig. 16. Light micrograph of a semithin section of the cirral cortex (co) of *M. rotundus*. Here double embedding method allows precise localization of the cortex but makes staining more difficult. Nevertheless, nerve cell bodies with axons (arrow) can be easily distinguished after silver staining. They make contact with cells of the epidermis (ep).

Fig. 17. Scanning electron micrograph of the cortex of a cirrus of *M. rotundus*. The cirri are covered with a cortex with small round holes. Note the difference to the usual skeletal pattern visible at the upper right. This and the following scanning electron micrographs, except Fig. 24, are surface views of the cortex.

Fig. 18. Scanning electron micrograph of the cortex of the stalk of *M. rotundus*. The cortex of the stalk has small ovoid holes oriented along the longitudinal axis of the stalk (oriented here from top to bottom).

Fig. 19. Scanning electron micrograph of the lateral cortex of the arm of *Saracrinus nobilis*. Big holes are arranged in parallel lines.

Fig. 20. Scanning electron micrograph of the aboral cortex of the arm of *S. nobilis*. On the aboral side the lines are curved and irregular.

Fig. 21. Scanning electron micrograph of the aboral cortex of the arm of *S. nobilis*. The big holes in the cortex allow to see the trabeculae of the underlying skeleton.

Fig. 22. Scanning electron micrograph of the cortex of the arm of *Endoxocrinus alternicirrus*. Roundish holes are spread more or less irregularly over the cortex.

Fig. 23. Scanning electron micrograph of the aboral cortex of the arm of *Hypalocrinus naresianus*. The holes of the cortex are arranged parallel to the longitudinal axis of the arm (here oriented from top to bottom of the Fig.).

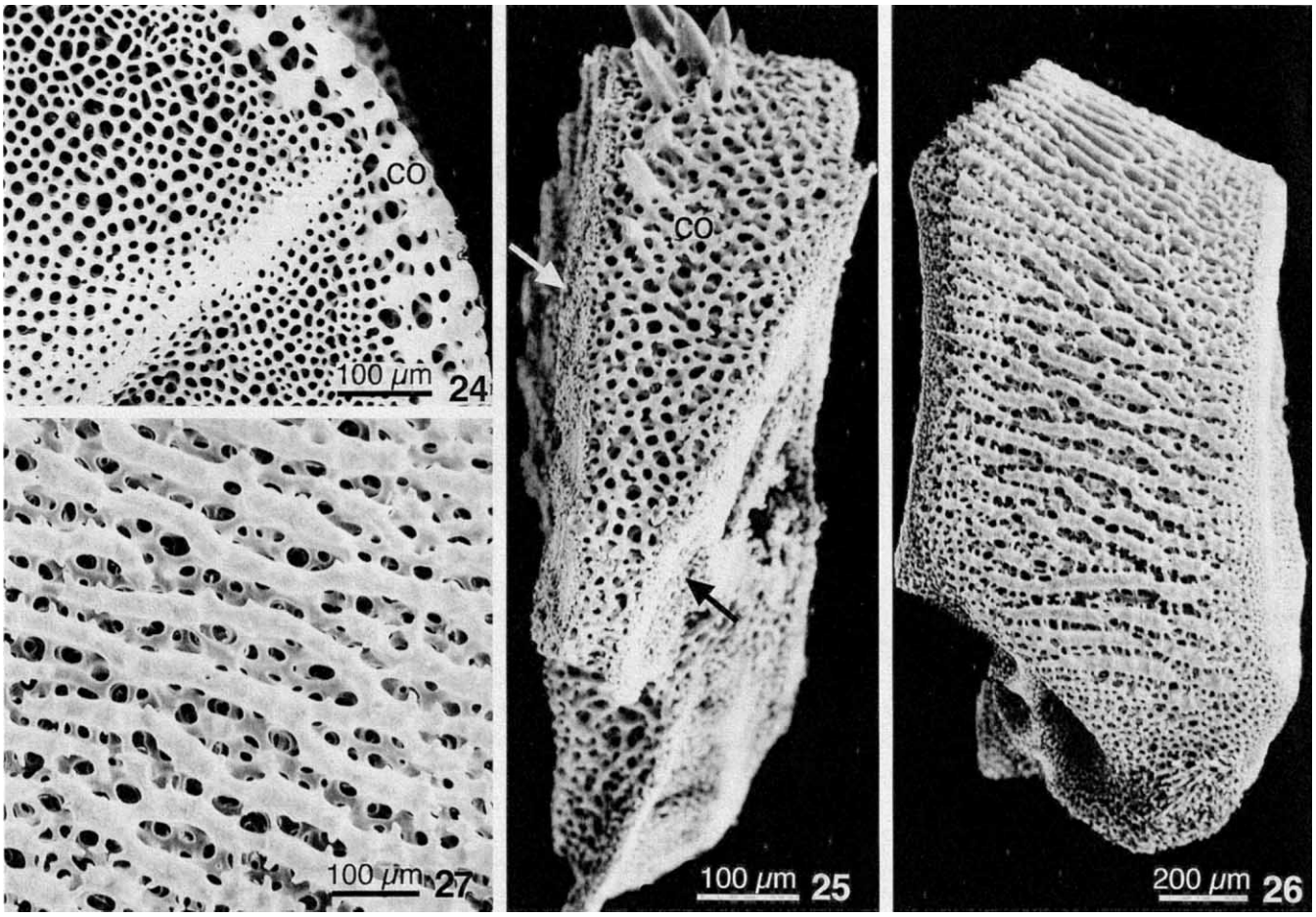


Fig. 24. Scanning electron micrograph of the cortex of the arm of *H. naresianus* (side view). This micrograph from the joint between two ossicles shows the thick cortex (co).
Fig. 25. Scanning electron micrograph of an arm ossicle of *Oxycomanthus japonicus*. The cortex (co) has an irregular pattern of holes that are bigger than those of the underlying stereom (arrows).
Fig. 26. Scanning electron micrograph of an arm ossicle of *Tropiometra afra*. The arm carries numerous thick ridges instead of a continuos cortex.
Fig. 27. Scanning electron micrograph of an arm ossicle of *Tropiometra afra*. This detail shows the underlying irregular stereom visible between the thick ridges.

habitat and the density of the cortex covering the arms of crinoids. However, most data on habitat and life conditions of crinoids are anecdotal and conclusions about morphological adaptions to mode of life need further ecological research.

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