Conference Paper

The Machaeridia — a square peg in a pentagonal hole

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The Machaeridia are a group of enigmatic Palaeozoic fossils, occurring in rocks of Ordovician to Carboniferous age. They consist of bilaterally arranged, characteristically sculptured calcitic plates, which form an elongated composite skeleton. In 1926, on the basis of investigations by T. H. Withers, F. A. Bather suggested that they were an aberrant stock of echinoderms, and this suggestion, based mostly on conflicting observations regarding fine structure, has since had a strong influence on discussions about the affinity of the group. However, new investigations of the microstructure of machaeridian plates show that it differs completely from that of all known echinoderms. Internal, as well as external structures of the plates suggest that they were exoskeletal and grew by successive deposition from an epithelium.

INTRODUCTION

In the early part of this century, T. H. Withers studied some enigmatic Palaeozoic fossils then referred to the Cirripedia, and found that in a number of specimens of the genus Lepidocoleus broken calcitic plates showed cleavage surfaces similar to those characteristic of fossil echinoderms. In 1926, Withers published his monograph on the Machaeridia¹ — a new fossil group encompassing the genera Lepidocoleus, Turrilepas, Plumulites and Deltacoleus. Discussion of the affinities of the group gave considerable significance to the echinoderm--like structure of the *Lepidocoleus* plates, for Withers could show convincingly that the machaeridians had nothing to do with cirripedes, and no other affinities were apparent from morphological considerations alone. The possibility that the machaeridians were echinoderms was, however, presented with much reservation. Not only were the cleavage surfaces seen in only a few species of one genus, but the animal that Withers reconstructed also seemed to have very little in common with any known echinoderm. It was an elongated flexible animal, covered with two (Lepidocoleidae) or four (Turrilepadidae) longitudinal rows of imbricating plates with a characteristic sculpture of what appeared to be well marked growth lines. The plate rows were joined along a hinge in the median plane. Each of the hinged plates commonly carried a shallow impression, probably a muscle scar, on the inside.

The impact of these observations on the crystal structure of some representatives of *Lepidocoleus* may not have become so great had it not been enhanced by F. A. Bather's authoritative support for the echinoderm hypothesis in the preface to Withers' monograph. Although again with some basic reserva-

tions, he speculated on the Machaeridia being an early offshoot from the echinoderm stock that branched off before the echinoderms had developed pentameral symmetry. In 1930, Bather² again suggested this hypothesis (»... it seems to me that *Lepidocoleus* and *Turrilepas* have just such a skeleton as may be imagined to have clothed a *Dipleurula* when that creature began to feel the need of some external protection for its soft, flexible, vermiform body...«) and proposed the branch *Echinoderma bilateralia* to include Machaeridia and Heterostelea. In contrast, Withers, in a short paper on a Silurian *Lepidocoleus* a few years later³, did not even mention echinoderms.

During the 50 years since the concept of Machaeridia was established, they have received only sporadic attention in basic studies, and Withers' monograph still stands as the only comprehensive treatment of the group. They are now known to range from the Lower Ordovician to the Upper Carboniferous (Lower Pennsylvanian⁴). The concept of machaeridians as echinoderms has been adopted in a number of systematic accounts⁵⁻⁷, and various solutions have been advocated to the problem of fitting them into an echinoderm frame^{8, 9}. In the echinoderm part of the Treatise on Invertebrate Paleontology, Ubaghs¹⁰ accepts them with a question mark. However, there have also been dissenting views¹¹⁻¹⁵, and there seems to be a growing reluctance to accept these elusive animals as echinoderms, even though Withers' assertion that some machaeridian plates have echinoderm structure has remained unchallenged.

The present study is intended to scrutinize the microstructural evidence for echinoderm affinity of the machaeridians. It is part of a larger project aimed at a revision of the systematic concepts of the Machaeridia and an understanding of their biology. The microstructural results presented here are thus in a way preliminary, but for the present purpose they are sufficient, since they show unambiguously that any similarity between specimens described in this paper and living or fossil echinoderms is purely coincidental, and that echinodermatologists constructing phylogenetic schemes for their phylum can omit the Machaeridia with clear consciences.

THE ALLEGED ECHINODERM-LIKE STRUCTURE OF MACHAERIDIAN PLATES

The elements in a composite echinoderm skeleton consist of a fine meshwork of magnesium-rich calcite with a high degree of continuity within the crystal lattice. Each element thus consists of a single calcite crystal¹⁶; exceptions to this rule are exceedingly rare. However, in curved plates of some echinoids¹⁷ and blastoids¹⁸ the direction of the crystal axes may change from one part of the plate to the other, following the curvature of the plate. This would be due to dislocations within the lattice.

This unique structure of the skeleton provides good criteria for recognizing fossil echinoderms. In most instances a fossilized echinoderm plate consists of a solid calcite crystal in which the pores in the meshwork, originally occupied by soft tissue, have been filled with secondary calcite precipitated in crystallographic continuity with the existing calcite. If any trace of the meshwork remains it is usually only at the surface of the plate, where the pores have been filled with sediment before the in-crystallization started. Thus, if a calcitic fossil fragment breaks along well-defined cleavage surfaces, and especially if it extinguishes uniformly and simultaneously between crossed nicols in a polarizing microscope, it can be considered with confidence to belong to an echinoderm, even if no morphological evidence is present. If the fragment shows a finely reticulated surface pattern, the matter is usually settled.

Withers'¹ comparison of machaeridian plates with echinoderm skeleton was based on the following observations:

1) Plates of *Lepidocoleus*, *Plumulites*, and *Turrilepas* all showed a fine reticulate ornament on their inner surfaces.

2) In five species of *Lepidocoleus*, he had seen more or less well-developed cleavage surfaces similar to those in fossil echinoderms.

3) A thin section of a plate of *Lepidocoleus squamatula* from the Upper Ordovician of Bohemia showed complete extinction between crossed nicols. Such extinction was also observed in fragments of plates of this species and of *L. suecicus*.

I have not been able to confirm any of these observations on the material that I have studied. The fine surface pattern on the inside of machaeridian plates is a characteristic feature in most, if not all, members of the group, but everywhere I have observed this pattern it has been distinctly granulated, not reticulated (Pl. I:2, 3).

Well developed, glossy cleavage surfaces occur in my material in specimens of *Lepidocoleus*, *e. g.* in a species from the Upper Ordovician of the Koängen borehole, Scania (material kindly provided by Ragnar Nilsson, Lund), and in several species from different parts of the Silurian of Gotland (Pl. I:1). In all these cases the similarity with echinoderm-type cleavage is only superficial, for the cleavage surfaces are usually strongly curved; there may be a tangential difference of up to 45° from the inner to the outer part of the plate. If the cleavage surfaces represent planes within a crystal lattice, then the lattice must be strongly warped.

As for the thin section of a plate of *L. squamatula* studied by Withers¹ (pp. 31 and 84), re-investigation of the specimen shows that the extinction, far from being simultaneous, passes along the plate through a rotation of the microscope stage of about 40° (Pl. I: 4—6). Again, if it is a single crystal, it must be strongly warped.

The evidence presented so far has considerably decreased the likelihood of a structural relationship between the machaeridian and echinoderm skeleton, but has not altogether excluded it. As mentioned earlier, the crystal lattice of echinoderm plates may also be warped, and this could produce an effect such as that shown in the *Lepidocoleus* plate in Pl. I : 4—6, and theoretically it could also account for the curved cleavage planes. To clear up this uncertainty, a microstructural investigation was made on plates of one species of *Lepidocoleus* showing well developed cleavage surfaces, and of one species each of *Lepidocoleus* and *Turrilepas* not showing such surfaces. All specimens are from the Silurian of Gotland. The localities are given with their code-names, as used in Gotland geology since 1974^{19} .

METHODS

The plates were studied optically in thin section and by SEM microscopy of natural and broken surfaces, both fresh and etched, and of polished and etched sections.

The thin sections were prepared by embedding the oriented specimens in an epoxy resin and grinding them from both sides to a thickness of $25-30~\mu m$. The sections

PLATE I

Figured specimens are in the Swedish Museum of Natural History, Stockholm—SMNH—or British Museum (Natural History), London—BM(NH).

1. Fragment of Lepidocoleus sp. a, middle Ludlovian Eke Beds, Petsarve 15, Gotland (sample No. Got 74-23, coll. S. Bengtson), showing well developed glossy cleavage surfaces at angles to exterior growth lines. SMNH No. X 1501. SEM micrograph. x40.

2. Interior side of plate of *Lepidocoleus* sp. a (same sample as in 1), showing granulated surface. SMNH No. X 1502. SEM micrograph. x200.

3. Interior side of keeled plate of *Turrilepas* sp., upper Wenlockian Halla Beds, Hörsne 6, Gotland (sample No. 74–37. coll. S. Bengtson), showing granulated surface. SMNH No. X 1503. SEM micrograph. x200.

4-6. Thin section of plate of *Lepidocoleus squamatula* (Barrande) from Upper Ordovician of Mt. Kosov, Bohemia (coll. J. Barrande). BM(NH) No. In 17507. Transmitted light, crossed nicols. Crosses indicate direction of nicols; ticked bars indicate direction of c axis alignment of the extinguished crystals. This is the section discussed by Withers (1926, pp. 31 and 84) which has been one of the chief pieces of evidence for ascribing an echinoderm stereom to the Machaeridia. Note the undulatory extinction. x30.

7-8. Left plate of *Lepidocoleus* sp. b, upper Wenlockian Slite Beds, Svarvare 3, Gotland (sample No. 75/3C, coll. M. G. Bassett). SMNH No. X 1504. Median fold oriented upward and lateral margin downward. In 7, the proximal margin is to the left and the distal margin to the right. Coated with ammonium chloride. x15.

9-11. Thin section of plate of *Lepidocoleus* sp. a, middle Ludlovian Eke Beds at Petsarve 15, Gotland (sample No. Got 74-23, coll. S. Bengtson). SMNH No. X 1505. Section parallel to median fold; proximal margin (broken) upward, outer side to the left. Transmitted light, crossed nicols. Crosses indicate direction of nicols, with ticked bars indicating general direction in which c axes of most of the extinguished crystals are aligned. Note boundary between inner and outer layer in 9. x60.

Polished and etched section of plate of Lepidocoleus sp. a, same sample as 9-11. SMNH No. X 1506. Orientation of section as in 9-11. Note outer and inner layers, internal growth structures, and curvature and direction of cleavage planes. The object in the lower left corner is an ostracode carapace. Position of 13 indicated. SEM micrograph. x100.

13. Detail of same, showing boundary between outer (left) and inner (right) layer. Note regular crystal faces in outer layer. SEM micrograph. x1500.

14. Polished and etched section of plate of *Lepidocoleus* sp. a, same sample as 9-11. SMNH No. X 1507. Orientation of section as in 9-11 and 12-13. Detail across the plate near distal margin. Note outer (left) and inner (right) layer, and alignment of elements in inner layer according to morphology of granulated inner surface (granulation visible as cast in the embedding medium to the right). Note also longitudinal elements and cleavage plane (lower left) in outer layer. SEM micrograph. x850.

15. Same specimen, detail across plate near proximal margin. Inner layer here absent. Note change in direction of etched out crystal faces through thickness of plate. The deeply etched zones going from lower right to upper left appear to conform to internal growth planes of plate (cf. 12, middle part). x850.

PLATE II

1. Thin section of keeled plate of *Turrilepas* sp., upper Wenlockian Halla Beds, Hörsne 6, Gotland (sample No. Got 74–37, coll. S. Bengtson). SMNH No. X 1508. Section perpendicular to median fold; exterior side upward; median fold, with prominent growth line, to the right (plate broken immediately inside median fold). Transmitted light, crossed nicols. Cross indicates direction of nicols. x60.

2. Polished and etched section of keeled plate of *Turrilepas* sp. (same sample as 1). SMNH No. X 1509. Section perpendicular to median fold; picture shows detail across plate just lateral to fold. Outer side upward. Note alignment of elements in inner part of plate with granulated inner surface, increase in size of elements towards the exterior, and elongation of elements in outer part of plate. SEM micrograph. x1200.

3-5. Thin section of plate of Lepidocoleus sp. b, upper Wenlockian Slite Beds, Svarvare 1, Gotland (sample No. G74-68, coll. K. Larsson). SMNH No. X 1510. Section parallel to median fold; proximal margin to the left, outer side upward. Transmitted light, crossed nicols. Crosses indicate directions of nicols; ticked bars indicate direction of c axis alignment of most of the extinguished crystals. Note finely lamellar structure parallel to plate surfaces and rod-shaped elements perpendicular to them. Position of 6-7 indicated in 3. x60.

6—7. Detail of same, showing thin capping of clear calcite with downward directed pegs. Transmitted light, crossed nicols. Crosses indicate direction of nicols. Note undulatory extinction in discrete units of the clear calcite capping. x300.

8. Polished and etched section of *Lepidocoleus* sp. b (same sample as 3–7). SMNH No. X 1511. Section perpendicular to median fold. Detail across plate at median fold, showing disc-shaped elements aligned parallel to plate surfaces. Exterior side upward (uppermost white zone is edge of embedding epoxy). SEM micrograph x3600.

9. Same specimen, detail across plate near lateral edge, showing structure of rod-shabed elements and capping calcite layer with downward directed pegs (top left; cf. 6-7). SEM micrograph x1800.





were then investigated in a polarizing microscope equipped with a Berek compensator for determining the planes of c axis orientation.

The sections used in SEM investigations were prepared by orienting the specimens on stubs, embedding them in epoxy resin, grinding to the desired level, polishing, etching the surface in $2^{9}/_{0}$ EDTA for 20 minutes, and coating with gold.

Both kinds of sections were cut in different directions through the plates. The ones figured here are either parallel to the median fold or perpendicular to it. The median fold is the sharp fold (oriented upwards in the *Lepidocoleus* plate in Pl. I : 7, 8) in the plate producing the hinge structure at the fixed margin both in *Lepidocoleus* plates and in the keeled (median) plates of *Turrilepas*.

LEPIDOCOLEUS SP. A

The material used is from the middle Ludlovian Eke Beds at the locality Petsarve 15, Gotland. It consists of fragmented plates, isolated through elutriation of weathered marl.

Glossy cleavage surfaces are well developed in fragments of this species, crossing the plate at angles to the lines of growth (Pl. I:1). The cleavage surfaces are usually curved, with an axis of curvature parallel to the surface of the plate. Partly developed cleavage planes can be seen in the specimen in Pl. I:12, which was somewhat fractured during sectioning.

The cleavage surfaces often do not encompass the zone closest to the inside of the plate, where instead a dullish fracture surface is developed.

Optical studies of thin sections

In thin sections perpendicular to the surfaces of the plate, all of the plate except for a zone at the inner surface shows a regular extinction pattern between crossed nicols. If the section is parallel to the median fold, there is a zone of extinction parallel to the plate surface, that moves through the thickness of the plate with rotation of the stage (Pl. I:9—11). The change in crystal direction through the plate seems to conform well to the curvature of one of the cleavage surfaces as observed in the fragments before sectioning (Cf. also the actual cleavage planes in Pl. I:12; this specimen is cut in the same direction as that in Pl. I:9—11). However, sections cut parallel to the surfaces of the plate indicate that there is no exact agreement between the directions of the c axes and the exterior growth lines.

In portions of the plate, there are rod-shaped structures perpendicular to the outer surface which extinguish slightly out of phase with each other (Pl. I : 11, lower part of the specimen). Also, there may be small isolated patches which extinguish out of phase with the surrounding calcite. In sections cut parallel to the surface of the plate, there appear long crystalline elements that cross the exterior growth lines and extinguish out of phase with the surrounding areas. The direction of the c axes in such an element is roughly perpendicular to its long axis.

In contrast to the outer layer, which generally behaves like a strongly warped crystal lattice with few irregularities, the layer closest to the interior side of the plate shows no distinct extinction pattern, or only faint local extinction. It seems to consist of submicroscopic crystallites with little preferred orientation. This zone is thickest near the distal margin, and wedges out short of the proximal margin (Cf. Pl. I: 7 with caption, for the use of the terms »distal«

and »proximal« margin). In Pl. I:9 (upper right) there can be seen a series of wedges towards the proximal margin, apparently formed by successive accretion of matter during growth of the plate.

SEM studies

The two plate layers observed in thin sections can be clearly distinguished also in SEM studies on polished and etched surfaces (Pl. I : 12—14). The outer layer does not show any definite shape of the crystal units, but the etching has proceeded along well aligned crystal faces, suggesting a strict lattice structure (Pl. I : 13 and 14, left, and 15). Moreover, the direction of the exposed crystal faces changes through the thickness of the plate (Pl. I : 15), conforming to the pattern of warping indicated by the direction of the crystallographic c axes (Pl. I : 9—11) and by the planes of cleavage (Pl. I : 12).

The innner layer consists of small elements, a few micrometres in size (e. g. Pl. I: 13 and 14, right). They show no general alignment of crystal faces, as is the case in the outer layer, but the elements themselves are often aligned with structures within the layer. This is most conspicuous in areas where the granular pattern on the inner surface is well developed; the granulation is reflected in the alignment of the elements (Pl. I: 14, right). In the outer layer, there are occasionally rod-shaped elements which might also be connected with this granulation (Pl. I: 14, left; cf. also the rod-shaped structures in Pl. I: 11).

The SEM investigations confirm the presence of internal growth structures in the plates, as shown in Pl. I : 12. Some apparent growth planes can be followed up through the outer layer (e. g. Pl. I : 15). There is no true lamination in the outer layer, but instead the growth planes are visible as cleavage planes. These seem to conform to the planes of the c axes, so it is reasonable to assume that they are formed by one of the crystal faces parallel to the c axis.

LEPIDOCOLEUS SP. B

The material is from the uppermost part of the upper Wenlockian Slite Marl at localities Svarvare 1 and 3. The marl is here rich in plates of *Lepidocoleus*, representing at least two species, differing in plate morphology and fine structure. One is similar in structure to L. sp. a, as described above, and often shows glossy cleavage surfaces. The fine structure of the other species, here referred to as L. sp. b, is described below. In this species, no glossy cleavage surfaces have been observed. The figured example of a whole *Lepidocoleus* plate, Pl. I:7—8, belongs to this species.

Optical studies in thin sections

In thin sections perpendicular to the surfaces, the plate appears to be built up of very fine lamellae running approximately in the direction of the plate (Pl. II : 5). Extinction between crossed nicols is diffuse, irrespective of the direction in which the section is cut. There may be a weak extinction maximum in parts of the plate, particularly near the interior surface; the c axes are here aligned perpendicular to the fine lamellae (Pl. II : 3—5). In areas which show extinction the lamellation is also most regularly developed. The most common disturbance of the lamellation is an undulation marking out rod-shaped elements perpendicular to the plate surfaces. These elements are also visible in the extinction pattern (e. g. Pl. II : 3).

There is a thin (up to ca 5 μ m), clear external layer which shows marked extinction in units. The extinction is not simultaneous even within one unit, but undulates. From this outermost layer there are peg-like processes going down into the finely lamellar layer, influencing the course of the lamellation (Pl. II : 6—7).

SEM studies

The lamellar structure seen in thin sections can be recognized also in SEM studies of etched surfaces. The plate is built up of disc-shaped elements which are generally aligned parallel to the plate surfaces (Pl. II : 8). It has not been possible to see any continuous lamellae along the plate; it may be that the lamellar appearance is produced by the stacking of individual disc-shaped elements, and that there are no lamellae in a strict sense. In most parts of the plate, there is an increase in size of the elements from the interior to the exterior side. The granulated interior side is reflected in the undulating pattern of the internal structure (Pl. II : 9).

The thin external layer with the downward directed pegs can also be identified in SEM studies, as seen in Pl. II:9, top. From this picture, taken where the plate is thin, it appears that the pattern of the pegs may be related to that of the granulation of the interior surface. Both structures apparently join in forming the rod-shaped elements through the plate.

TURRILEPAS SP.

The material is from a sample of weathered marl from the upper Wenlockian Halla Beds at the locality Hörsne 6. The sediments consist of bituminous inter-reef deposits, and are very rich in maccaeridians, mostly *Turrilepas*. This sample contains several hundreds of plates of varying completeness. The investigation is based on the most commonly occurring species, which seems to be close to the type species, *T. wrightiana*. No glossy cleavage surfaces have been observed in this Gotland species.

Optical studies of thin sections

In thin sections the plate substance appears devoid of regular structures. As seen in the section in Pl. II : 1, there may be a thin (about 10 μ m) external finely grainy layer, but this has not been observed in other sections. Some sections may also show an internal dividing plane connected with the thick sculpture of the growth lines (e. g. Pl. II : 1, top right).

The pattern of extinction is patchy, although a compensator reveals a preferred orientation of the c axes perpendicular to the plate surfaces. In some sections the extinction pattern makes out elongated elements perpendicular to the plate surface (Pl. II : 1, middle). These do not extinguish as single crystals, but rather as aggregates of subparallel microcrystals (undulatory extinction).

SEM studies

In a SEM mount, the plate is seen to consist of small elements generally increasing in size towards the exterior side (Pl. II : 2). There is, however, no sharp division between an outer and inner layer. As in *Lepidocoleus* spp. a and b, the elements show an alignment that reflects the fine granulation on the interior surface (Pl. II : 2, lower half). In the figured specimen this effect can be followed in all parts of the plate for about 50 μ m towards the exterior side. The outer portion of the plate has elongated elements in a direction perpendicular to the plate surface (Pl. II : 2, top). Even though there appear to be crystal faces exposed by the etching process, there is no alignment of the faces as in *Lepidocoleus* sp. a (cf. Pl. II : 2 and Pl. I : 15).

DISCUSSION

The three species of machaeridians investigated have a common denominator in possessing an inner layer of densely packed, fine elements in close alignment with the granulated inner surface of the plate. The elements may be discshaped to produce a lamellar appearance and have fairly well aligned crystallographic c axes (*Lepidocoleus* sp. b), or they may be less regular in shape and have more randomly oriented crystal axes (*Lepidocoleus* sp. a, *Turrilepas* sp.). In the *Turrilepas* species there is an outward transition into a more coarsely granulated substance. In *Lepidocoleus* sp. b, the lamellar or pseudolamellar layer makes up almost all of the thickness of the plate, and is capped by a very thin layer of clear calcite with a distinct, but not simultaneous, extinction as seen between crossed nicols. In *Lepidocoleus* sp. a, however, the inner layer is fairly thin, and most of the plate is composed of this seemingly homogenous crystalline calcite in which the crystal axes are rigorously aligned, but in which the general direction of the lattice changes considerably through the plate.

It is this latter structure that has — by its appearance as a homogenous crystal lattice — caused the misconception that machaeridians have a skeleton of echinoderm type. It is clear from the above evidence that they do not; some (or all) representatives of *Lepidocoleus* have a thicker or thinner outer layer in their plates made up of dense calcite (at least in the fossilized state) with a very rigid crystallographic structure, most unusual in appearance and not in any way suggesting an echinoderm stereom. All evidence — the exterior growth lines, the alignment of internal structural elements with the fine morphology of the inner surface of the plates, and the interfingering of the boundary between the interior and exterior layers in *Lepidocoleus* sp. a (cf. PI I : 9—11) — indicates that machaeridian plates grew in the manner normal for most invertebrate exoskeletons, *i. e.* through stepwise deposition of mineralized substance from an epithelium, and not through extension of an endoskeletal calcitic meshwork.

Acknowledgements. A large number of colleagues have been very helpful in obtaining specimens of machaeridians from both museum and personal collections. To all of them I express my deep gratitude.

I am grateful to the staff at the British Museum (Natural History) for access to the collections of machaeridians and for the loan of the important thin section of a *Lepidocoleus* plate (Pl. I: 4-6 herein) discussed, but not figured, by Withers.

The manuscript was kindly read and criticised by Michael G. Bassett, Cardiff. who also improved the English, and by Christina Franzén and Anders Martinsson, Uppsala.

The investigation of the Machaeridia is carried out as a contribution to the IGCP Project Ecostratigraphy.

NOTE ADDED IN PROOF

The recent article by Pope²⁰ on »machaeridian echinoderms« came to my attention after the submission of this manuscript. In his article, Pope elaborates a previously⁹ presented hypothesis that lepidocoleid plates were in fact protective covers for the paired posterior spines of certain »carpoid« echinoderms of the order Mitrata. I find his arguments entirely unconvincing and have discussed them in detail elsewhere²¹.

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IZVOD

Machaeridia — četvrtasti čep u pentagonalnoj rupi

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Machaeridia su skupina zagonetnih paleozojskih fosila koje nalazimo u stijenama od ordovicija do karbona. Sastoje se iz bilateralno poredanih i karakteristično skulpturiranih kalcitnih ploča koje tvore uzduženo sastavljeni skelet. Na osnovu istraživanja T. H. Withersa, F. A. Bather je 1926 godine izrazio mišljenje da Machaeridia pripadaju aberantnoj lozi bodljikaša. Iako je to mišljenje bazirano najviše na protivurječnim opažanjima fine strukture, ono je od tada jako utjecalo na rasprave o srodnosti te skupine. Međutim, nova istraživanja mikrostrukture machaeridnih ploča pokazuju da se potpuno razlikuju od svih poznatih bodljikaša. Unutarnje i vanjske strukture ploča pokazuju da su ploče bile exoskeletne i da su rasle uzastopnim taloženjem iz epitela.