

10. TURRILEPADIDA AND OTHER MACHAERIDIA

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The name Machaeridia was originally proposed (Withers 1926) for Early Paleozoic animals with a bilaterally symmetric body covered with calcitic sclerites arranged in longitudinal rows. Their armors (or strobili; Pope 1975) are only rarely found articulated, and their isolated sclerites are not easily identifiable. Therefore, they do not attract much attention. In calcitic residues from Ordovician limestones treated with dilute acetic acid, however, their remnants frequently dominate in the identifiable skeletal debris, which demonstrates their paleoecologic significance.

The Ordovician–Carboniferous Machaeridia with well-calcified sclerites (genera *Plumulites*, *Mojczalepas* gen. nov., *Turrilepas*, *Deltacoleus*, *Clarkeolepis*, *Plicacoleus* gen. nov., *Lepidocoleus*, *Aulakolepos*, and *Carnicoleus* gen. nov.; see systematic paleontology section below) are here assigned to the order Turrilepadida Pilsbry 1916. There are also many other fossils—in the Cambrian (Tommotiida, Sachitida) and in the Middle Paleozoic (Hercolepadida ord. nov.)—that in several aspects resemble the Ordovician turrilepadids. It is the aim of the present paper to discuss phylogenetic relationships of the Turrilepadida to those groups as well as to other taxa.

BODY PLAN

The genus *Plumulites* is the most primitive known representative of the Turrilepadida. Its body was bilaterally symmetric and dorsoventrally depressed, with four rows of sclerites. The sclerites were thin walled and probably weakly calcified. They developed by mineralization of dorsal covers of leaflike protrusions of the body. Because of their analogy (perhaps also homology; see below) to the annelid elytra, I propose to call these protrusions elytra. Their protective function is self-evident, and hence, I consider as dorsal that side of the body that is covered with elytra.

As judged from the mode of preservation of the articulated strobili of *Plumulites*, its elytra had little mobility in the transverse plane, but the animal may have been able to roll its body in the sagittal plane. Jell (1979) interpreted a specimen of *Plumulites* lacking the anterior part as a heteromorph and reconstructed peculiar palps at its anterior end. The anterior part of that specimen, however, may be tucked under its body, as in the Cambrian *Wiwaxia* (Conway Morris 1982: W).

The “palps” would, then, be posterior tips of elytra.

Mobility in the sagittal plane was strongly restricted in *Turrilepas*. Its body was approximately isometric in cross section, with elytra of the outer (or lateral) rows oriented vertically, as in most Machaeridia. The elytra were mobile in the transverse plane, perhaps up to bringing the lateral elytra in contact along the venter (Fig. 1B). In *Aulakolepos*, in turn, the lateral elytra underwent reduction, and the body was covered nearly exclusively with dorsal elytra (Fig. 1C).

Elytra are metamericly arranged in all machaeridian strobili. The segments of *Plumulites* and other turrilepadids include four elytra each. Two first segments of *Plumulites* (Jell 1979) and *Turrilepas* (Withers 1926), however, bear only two dorsal elytra each; furthermore, the elytra of the first segment are much smaller and more medially located than the others in *Turrilepas* (Withers 1926). The tagma composed of those first segments is here called the head. The subsequent segments bear already four elytra each, but their lateral elytra differ in shape from the more posterior ones. This is the thoracic tagma. In *Plumulites*, the lateral elytra have concentric apical rugae (Figs. 1 and 2; see also Jell 1979). Beginning with the sixth segment, the lateral elytra attain their regular shape and, except for some decrease in size and a slight increase in elongation in the caudal part of the body, the abdominal sclerites are largely uniform (Figs. 2 and 3).

SCLERITE GROWTH AND MORPHOLOGY

In most Turrilepadida, the sclerites grew by secretion of calcitic layers at the base (Fig. 7D; see also Bengtson 1977, 1978). Their marginal increment is indicated by (1) unquestionable growth lines in such genera as *Deltacoleus* and *Plicacoleus* (Fig. 9A), with a complete gradation to typical rugose sclerites (Fig. 6), and (2) morphology of muscle attachment scars at the inner surface of thick machaeridian sclerites (Figs. 5 and 9), with traces of migration from an initially apical position toward the anterior margin, as in brachiopods and bivalves; this would be incompatible with periodic molting of elytra.

In *Plumulites*, however, mineralization probably occurred instantaneously over the entire surface of the elytra. Even large-sized sclerites are

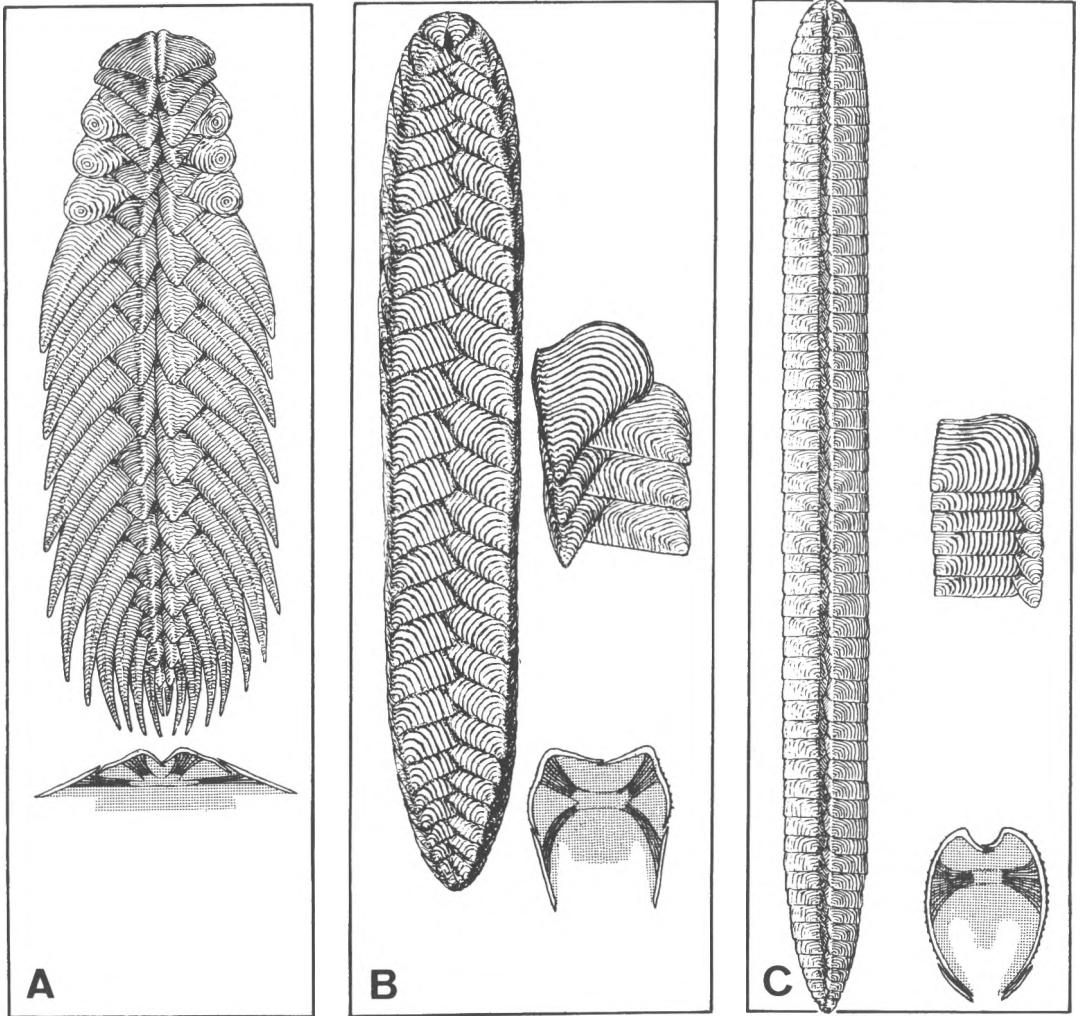


Fig. 1. Body plan of the families of the order Turrilepadida Pilsbry 1916. A. Plumulitidae Jell 1979, based mainly on *Plumulites pieckorum* Jell 1979 (see Jell 1979). B. Turrilepadidae Clarke 1896, based on *Turrilepas wrightiana* (Koninck 1857) (see Withers 1926). C. Lepidocoleidae Clarke 1896, dorsal view based on Ordovician species of *Aulakolepos* (see Withers 1926; Pope 1975), combined with lateral view of *A. kelleyanum* (Reed 1901).

very thin walled and always compressed in *Plumulites*, even those occurring with undistorted calcareous fossils, including other machaeridian sclerites (Fig. 2; see also Withers 1926). They probably were elastic, perhaps organic, and only weakly calcified during life. Their marginal growth is suggested merely by their homology to marginally growing sclerites of the other Turrilepadida.

Dorsal turrilepadid sclerites are always convex and close to isometric in outline. Bengtson (1970) proposed the term sellate for similar sclerites in the Tommotiida. Lateral turrilepadid sclerites are always flat and elongated. They correspond morphologically to mitrate sclerites of the Tommotiida.

In *Plumulites*, lateral sclerites have a medial elevation, semicircular in cross section and separated from the lateral areas by very narrow, shallow depressions. Rugae usually continue over this elevation, though with a decrease in conspicuousness. The semicircular section, morphologic separation, and abrupt appearance of the elevation in the center of thoracic sclerites of *P. bohemicus* Barrande 1872 (Figs. 2A and 3) suggest the presence of a medial canal below the elevation, similar to the central canal in elytra of the Cambrian *Thambetolepis* (Jell 1981).

Lateral margins and tips of the lateral sclerites of *Plumulites* have tubular spines (Schrenk 1978), sometimes laterally branching and always with a suture along their ventral side (Fig. 4B, C). Unlike

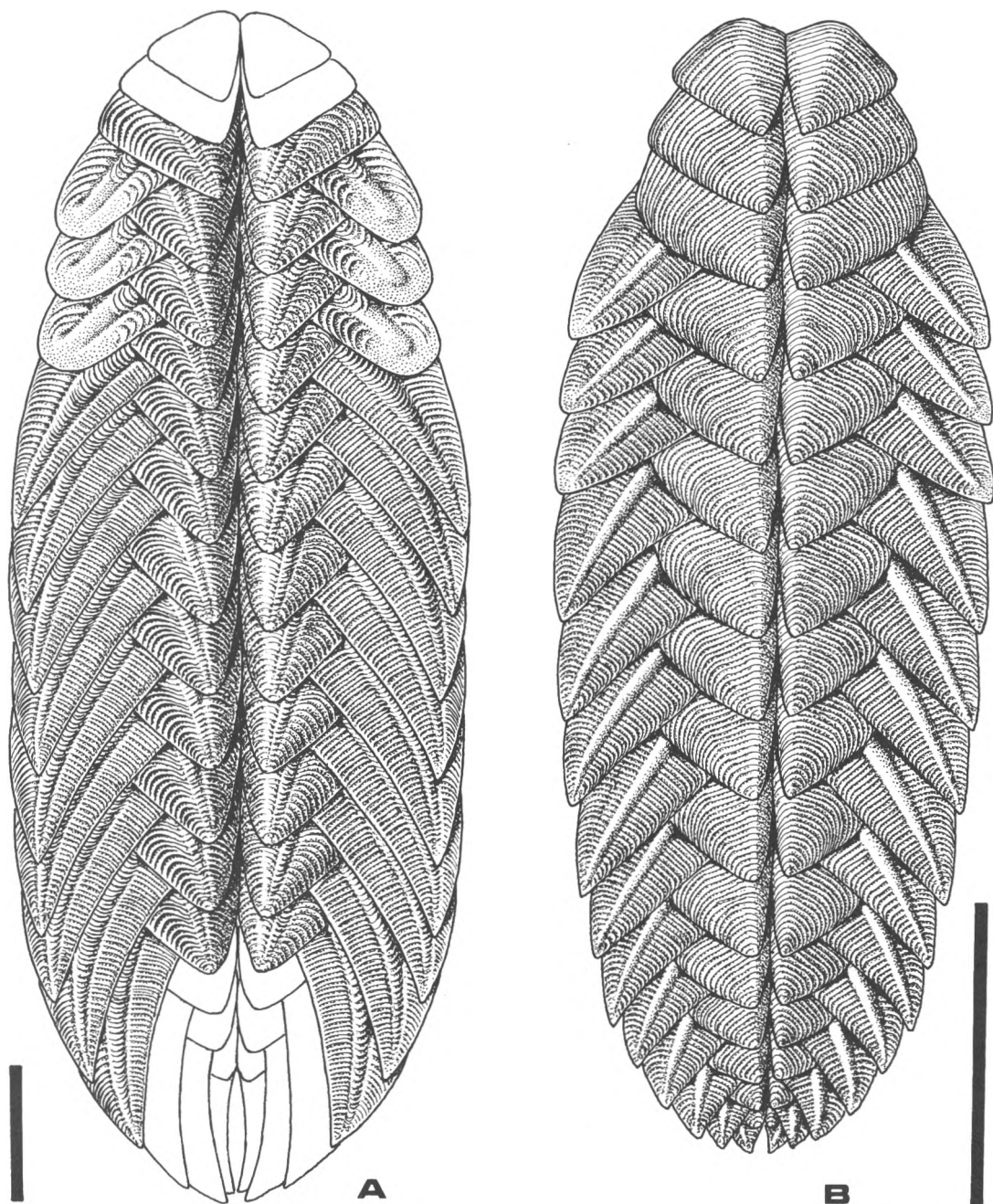


Fig. 2. Reconstruction of *Plumulites* from the Ordovician of Bohemia, based on articulated specimens. Scale bar = 10mm. A. *Plumulites bohemicus* Barrande 1872 from the Šárka Formation (Llanvirnian), Osek (cf. Fig. 3). Perhaps a few more abdominal segments should be added. B. *Plumulites folliculum* Barrande 1872 from the Letna Formation (Caradocian), Trubska. Based mainly on the lectotype NM 1425 (housed at the Narodní Museum, Prague; illustrated by Barrande 1872, pl. XX: 15-15; and Prokop 1965, fig. XIII-42; plasticine cast in Withers 1926, pl. VIII: 2).

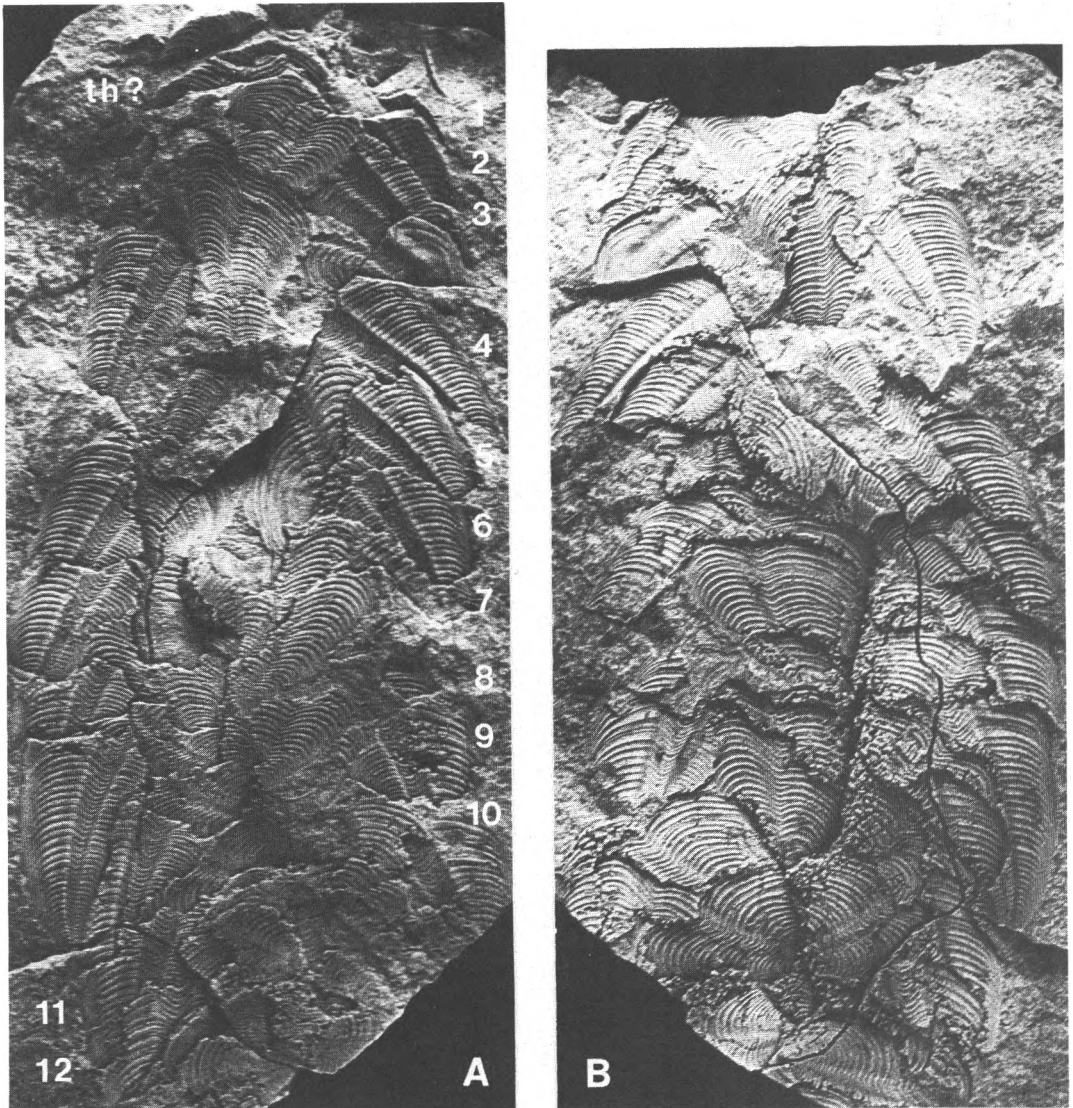


Fig. 3. Part (A) and counterpart (B) of the lectotype of *Plumulites bohemicus* Barrande 1872 from the Šárka Formation (Llanvirnian), Osek, Bohemia (housed at the Narodni Muzeum, Prague; illustrated by Barrande 1872, pl. XX: 1-2; plasticine cast in Withers 1926, pl. VIII: 1). Abdominal segments indicated by consecutive numbers; note displaced thoracic lateral sclerite. $\times 2$.

in other turrelepads, the wall of the elytra was calcified also at the lateral margins in *Plumulites*, and remnants of that layer are preserved ventrally (Fig. 4), but I could not determine if there was a suture at the ventral surface. The tubular spines resemble those found in mollusks and brachiopods, but they might be parallel to the growth front, provided that marginal secretion did indeed occur in *Plumulites*. If, however, the cuticle was secreted and mineralized by the entire surface of elytra, the sutures may be analogous to cuticular border zones separating different fields in elytra of some Recent polychaetes (Pflugfelder 1933).

Notably, the marginal spines are a continuation of rugae (Fig. 4A), which suggests that the latter may reflect presence of pennately arranged internal organs similar to the lateral canals of *Thambetolepis* (see Jell 1981).

Species of *Plumulites* vary in distribution of rugae at the dorsal surface of their sclerites. The main group includes rather uniformly ornamented *P. bohemicus* Barrande 1872 from the Early Llanvirnian Šárka Formation of Bohemia (Fig. 2A), *P. peachi* (Nicholson and Etheridge 1880) from the Late Caradocian Whitehouse Group of England (Withers 1926), and *P. richo-*

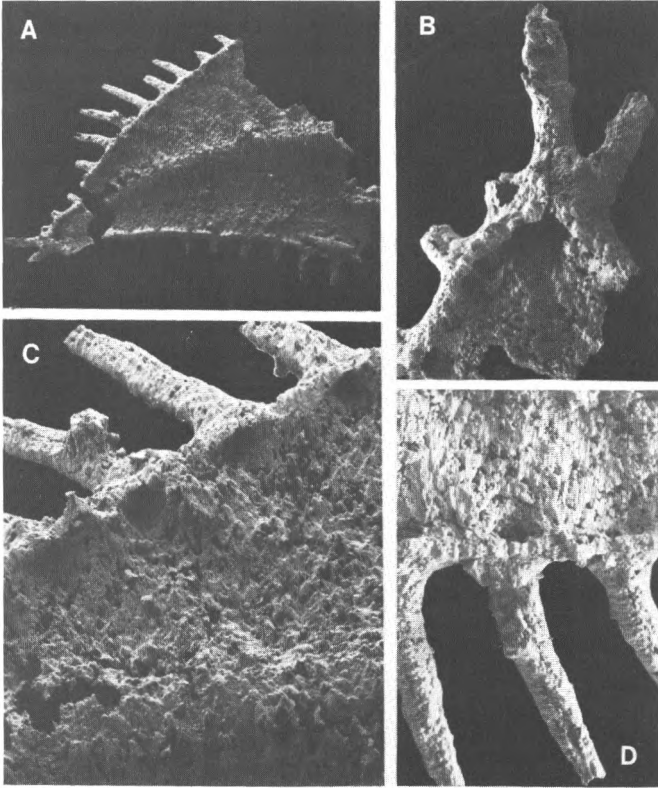


Fig. 4. Isolated lateral sclerite of *Plumulites* sp. from the erratic boulder E-231, *E. robustus* Zone, Llanvirnian (Uhakuan), Garcz, Poland (housed at the Zakład Paleobiologii, Warszawa; ZPAL V.XII/4). A. Internal side. $\times 60$. B. Apical part; note medial ventral suture. $\times 300$. C. Outer margin; note branching tubular spine. $\times 300$. D. Inner margin. $\times 300$.

rum Jell 1979 from the Early Devonian Humevale Formation of Victoria, Australia (Jell 1979). In Bohemia, *P. bohemicus* is replaced in the overlying Dobrotiva Formation by *Compacoleus compar* (Barrande 1872) (= *P. maior* in Prokop 1965, fig. XIII-45), with inner areas of the lateral sclerites having twice as many rugae as the outer areas. *Plumulites folliculum* Barrande 1872 from the Caradocian Libeň and Letna Formations of Bohemia differs from its congeners in its much shorter, densely rugose lateral sclerites (Fig. 2B). A similar ornamentation occurs in the Late Silurian *P. delicatus* Barrande 1872, with only weakly developed medial elevation in the lateral sclerites. Korejwo (1979, pl. 14: 10-11) illustrated two unidentified specimens from the Tournaisian of northern Poland that may represent dorsal and lateral thoracic sclerites of the youngest known plumulitid.

Thick dorsal sclerites of *Mojczalepas* abound in the Llanvirnian of the Baltic area and the Holy Cross Mountains, Poland. They are much thicker than in *Plumulites*, whereas the sinuous outline of rugae makes them different from *Deltacoleus*. The rugae are closely spaced, very high, and lamella shaped in *M. multilamellosa* sp. nov. (Figs. 5A, B, and 6A). In turn, *Mojczalepas* sp. *a* is ornamented with low terraces (Fig. 5C, D), and *Mojczalepas*

sp. *b* has densely spaced rugae resembling growth lines (Fig. 6B). The three species differ also in sclerite cross section. In *M. multilamellosa*, the elytra are almost rectangular in cross section; in *Mojczalepas* sp. *a*, additional angulations developed close to the inner and outer margins; in *Mojczalepas* sp. *b*, the outer area of the sclerite is convex. The paratype of *Deltacoleus crassus* Withers 1926 from the Caradocian Balclatchie Group of England (Withers 1926, pl. VIII: 6) may also belong to *Mojczalepas*, as its rugae are distinctly sinuous in outline.

Only two lateral sclerites have been found that can be attributed to *Mojczalepas*. Their morphology resembles *Plumulites* closely, but their wall is very thick (Fig. 6C, D).

The only species of *Turrilepas* that is known from articulated strobili, *T. wrightiana* (Koninck 1857), is asymmetric; its left dorsal sclerites are not mirror images of the right ones (Withers 1926). Rugae on the left sclerites are straight in the inner area and run obliquely to the inner margin, whereas the corresponding rugae on the right sclerites are gently curved and tangential to the inner margin. Such an asymmetry is unique among turrilepadids. Dorsal sclerites of *T. wrightiana* have a more complex ornamentation pattern than those of *Mojczalepas*. The lateral sclerites,

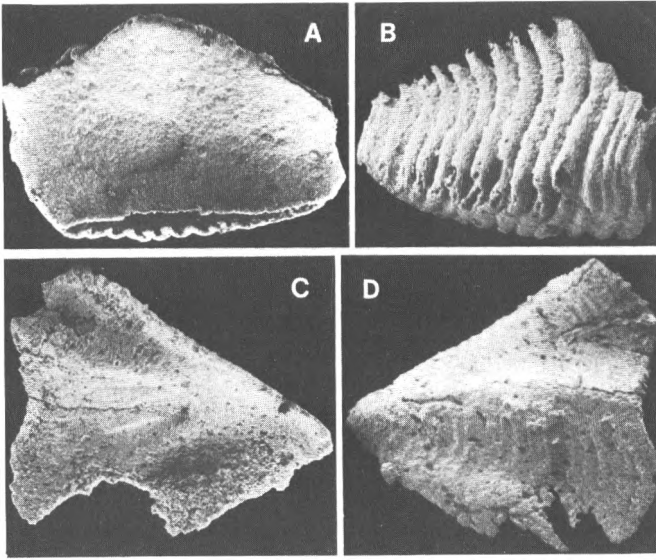


Fig. 5. Dorsal sclerites of *Mojczalepas* gen. nov. A, B. *Mojczalepas multilamellosa* sp. nov., holotype, sample MA-29. *E. reclinatus* Zone, Llanvirnian (Lasnamagian), Mójcza Limestone, Mójcza, Poland (ZPAL V.XII/2). Original calcitic wall covered with thin phosphatic(?) film. $\times 100$. C, D. *Mojczalepas* sp. a, erratic boulder E-297. *E. reclinatus* Zone, Llanvirnian (Lasnamagian), Międzyzdroje, Poland (ZPAL V.XII/5). Preserved calcitic wall. $\times 60$.

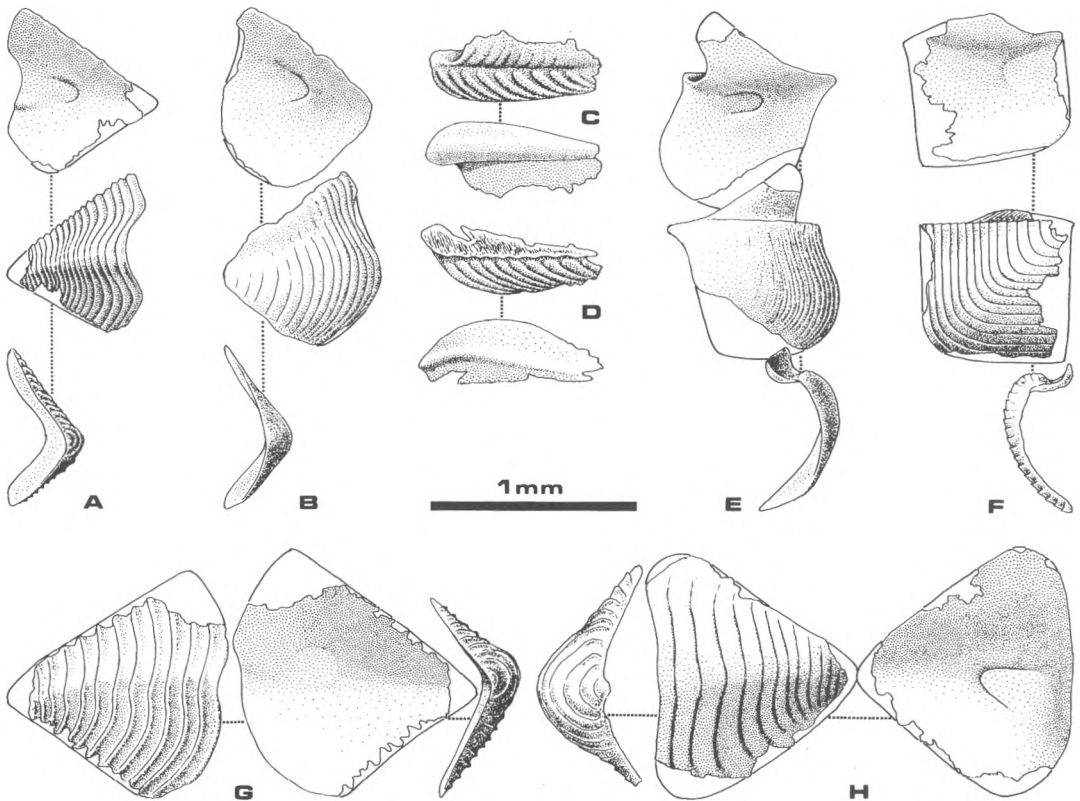


Fig. 6. Sclerites of the most common turrilepadid species from the erratic boulders E-279 and E-323. *E. reclinatus* Zone, Llanvirnian (Lasnamagian). Dorsal sclerites, except for C and D. A. *Mojczalepas multilamellosa* sp. nov. B. *Mojczalepas* sp. b. C, D. Lateral sclerites, perhaps *Mojczalepas* gen. nov. E. *Plicacoleus robustus* sp. nov. F. *Aulakolepos* aff. *suecicum* (Moberg 1914). G. *Deltacoleus* cf. *crassus* Withers 1926. H. *Deltacoleus* sp.

however, are flat, without any medial angulation or elevation, and with a simple pattern of rugae (Withers 1926).

In the Baltic Llanvirnian, machaeridian assemblages are dominated by *Deltacoleus*. Its dorsal sclerites have almost straight rugae, bent only at the high medial angulation. Sometimes the angulation is slightly flattened, with two secondary angulations nearby (Fig. 7A, B). This may reflect either intraspecific variability, or variation along the body, or else (the least likely) asymmetry between the right and left sclerites. There is much variation in conspicuousness and distribution of rugae (Fig. 8), as well as in the pattern of sclerite thickness. The latter character seems to have a bimodal distribution. Some specimens attain the maximum thickness in front of the muscle attachment scar, others in the center of the sclerite. Most likely these are two distinct species of *Deltacoleus*, one of which may be conspecific with *D. crassus* Withers 1926.

In *Clarkeolepis*, originally established for Middle Devonian to Early Carboniferous species, dorsal sclerites are longitudinally ornamented (Elias 1958). I have found turrilepadid dorsal sclerites ornamented with high longitudinal lamellae in an erratic boulder of Baltic origin, earliest Caradocian (Kukrusean) in age. The radially arranged lamellae cross prominent rugae and form fairly deep rectangular cells. Apart from this ornamentation, the sclerites resemble *Deltacoleus*.

Dorsal sclerites of the only known species of *Plicacoleus*, *P. robustus* sp. nov., are widespread but inabundant in the Llanvirnian of the Baltic area and the Holy Cross Mountains, Poland.

They are thick, elongated, convex, and almost smooth, sometimes with growth lines instead of faint rugae; a medial crest separates the convex outer area from the concave inner area (Figs. 6E and 9).

The type species of *Lepidocoleus*, *L. jamesi* (Hall and Whitfield 1875) from the Cincinnati of Ohio, has relatively elongated dorsal sclerites ornamented with prominent rugae (Withers 1926; Pope 1975), which makes it similar to *Deltacoleus* and *Mojczalepas* rather than to the other species assigned by Withers (1926) to *Lepidocoleus*. This impression is reinforced by the thick wall and deeply embedded muscle attachment scar. Nevertheless, the location of the muscle attachment close to the inner side of the sclerite (Withers 1926, pl. II: 5–6) suggests that its inner concave part has been broken off. Under such circumstances, I propose to restrict the genus *Lepidocoleus* to its type species only, and to transfer the other species to the genus *Aulakolepos*.

Contrary to Withers (1926, 1933) and Bengtson (1977), *Aulakolepos ketleyanum* (Reed 1901) from the Wenlockian of England has small but fully developed lateral sclerites (see Bengtson 1977, fig. 3). They are approximately four times narrower than the corresponding dorsal sclerites, triangular in shape, and completely flat. This is indisputable evidence of the machaeridian nature of the Lepidocoleidae.

The oldest known *Aulakolepos* comes from the Late Llanvirnian (Lasnamägian) of the Baltic area (Fig. 6F). Its dorsal sclerites resemble the Ashgillian *A. suecicum* (Moberg 1914) from the same area (Withers 1926). Other Late Ordovician, Sil-

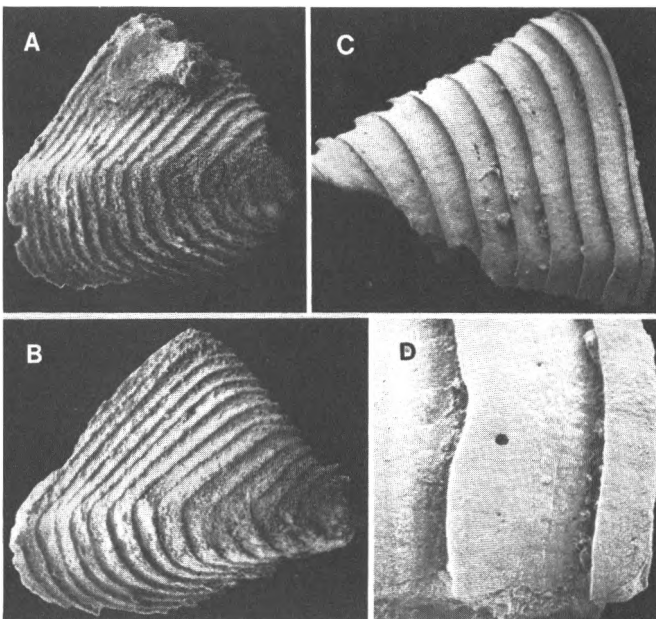


Fig. 7. Dorsal sclerites of *Deltacoleus* cf. *crassus* Withers 1926. A. Specimen ZPAL V.XII/6, erratic boulder E-279. *E. reclinatus* Zone, Llanvirnian (Lasnamägian), Międzyzdroje, Poland. $\times 55$. B. Specimen ZPAL V.XII/7, same boulder. $\times 70$. C. Specimen ZPAL V.XII/8, erratic boulder E-276. *P. originalis* Zone, Arenigian (Volkhovian), Międzyzdroje, Poland. Original calcitic wall replaced by a green, glauconitelike mineral. $\times 100$. D. Same specimen. $\times 450$.

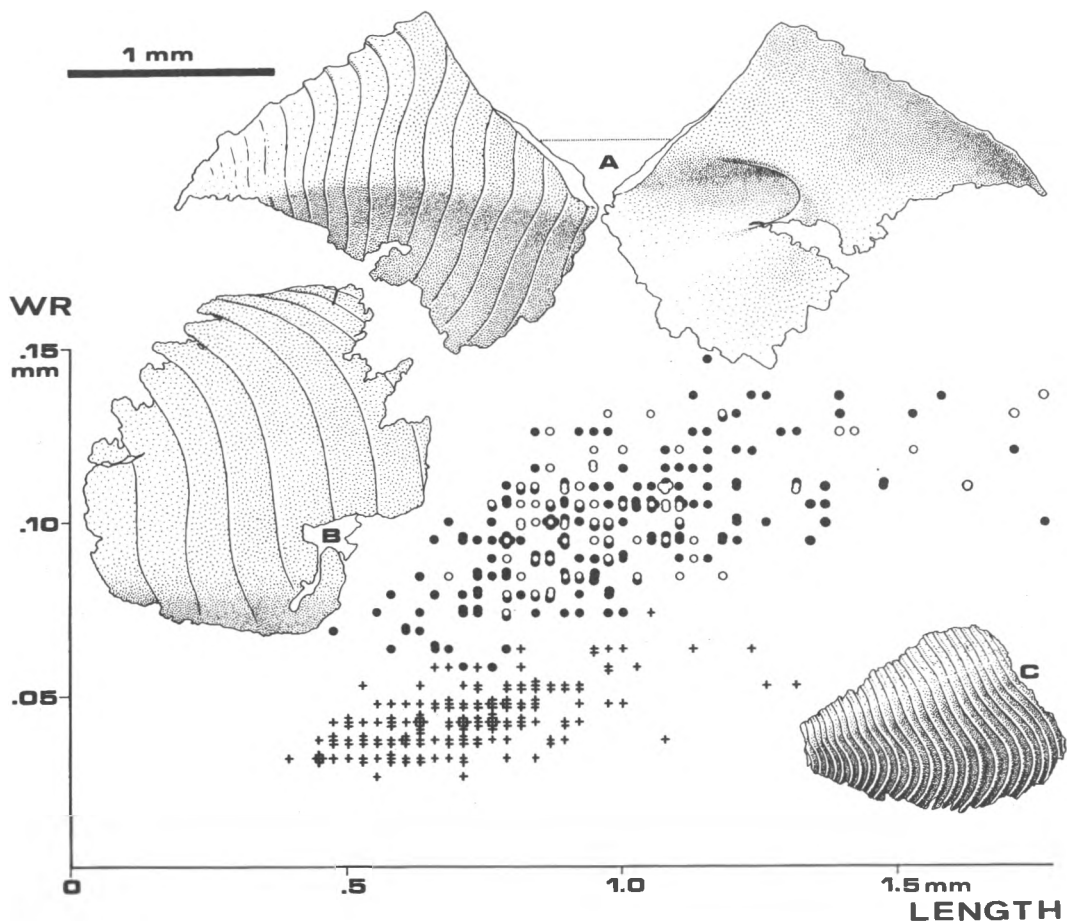


Fig. 8. Density of rugae (WR, average distance between the rugae) versus sclerite length for the most abundant turrellepadid species from the erratic boulder E-323, *E. reclinatus* Zone, Llanvirnian (Lasnamagian), Rozewie, Poland. Circles (and A), *Deltacoleus* sp.; dots (and B), *D. cf. crassus* Withers 1926; crosses (and C), *Mojczalepas multamellosa* sp. nov.

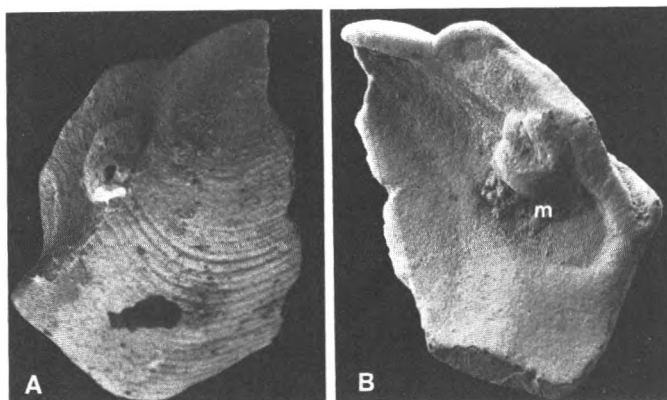


Fig. 9. External (A) and internal (B) views of a dorsal sclerite of *Plicacoleus robustus* sp. nov.. Holotype, sample MA-29, *E. reclinatus* Zone, Llanvirnian (Lasnamagian), Mójcza Limestone, Mójcza, Poland (ZPAL V.XII/3). Note growth lines and muscle attachment scar (m). $\times 100$.

urian, and Devonian species of the genus have much shorter and wider sclerites. Their outer area and medial angulation are ornamented with rugae that continue, sometimes in form of growth lines, in the inner area. There is no evidence of a dorsal ligament, as claimed by Wolburg (1938).

The Ludlowian of the Carnic Alps, Austria, yielded some elongated sclerites with pseudoporous wall and a short posterior duplicature (Fig. 10). They are here described as *Carnicoleus gazdzickii* sp. nov. Their attribution to the Turrilepadida might be disputable, although it is compatible with the available data. Bengtson (1977, 1978) found some tubercles and depressions at the inner surface of Silurian *Aulakolepos*. No duplicature has been reported in *Aulakolepos*, but its presence might be expected because of a significant overlap of sclerites in the strobilus and by analogy to the process of mineralization in *Plumulites*. The pseudopores penetrating the sclerite wall in *Carnicoleus* do not open externally. They resemble muscle attachment scars, especially those left by the pallial muscles of some bivalves. Interpretation of *Carnicoleus* as a *Solen*-like bivalve, however, is contradicted by the absence of adductor muscle scars, presence of duplicature, and development with no indications of metamorphosis, although much change in sclerite shape occurred early in its ontogeny (Fig. 10E). In turn, interpretation of *Carnicoleus* sclerites as *Anatifopsis*-like plates of carpodid echinoderms is

contradicted by their imporous external surface with distinct growth lines and by the mirror-image symmetry.

PALEOCOLOGY

Little is known about the mode of life of the Turrilepadida. Withers (1926) refuted their interpretation as cirripedes but nevertheless envisaged the strobilus attached to the substrate, with its gaping side oriented upward, as in the barnacles. Wolburg (1938) interpreted *Aulakolepos* as a segmented clam with adductor muscles and a dorsal ligament, but this interpretation is incompatible with sclerite morphology. Jell (1979) demonstrated that *Plumulites* was free-living, with dorsoventrally flattened body and elytra confined to its dorsal side. The rugae probably mechanically strengthened the elytra. The body shape and thin sclerite walls of *Plumulites* suggest much mobility of the animal. Its strobilus did not allow for much lateral flexibility, but the body could be rolled up, as in the trilobites. Most probably *Mojczalepas* also belonged to epifauna, as the very high lamellae on its sclerites would be strongly disadvantageous for burrowing.

The majority of turrilepadids, however, have terracelike rugae, with their sharp edges directed posteriorly, which is an adaptation to burrowing in loose sediment. The almost completely smooth surface and clamlike shape of the sclerites of *Pli-*

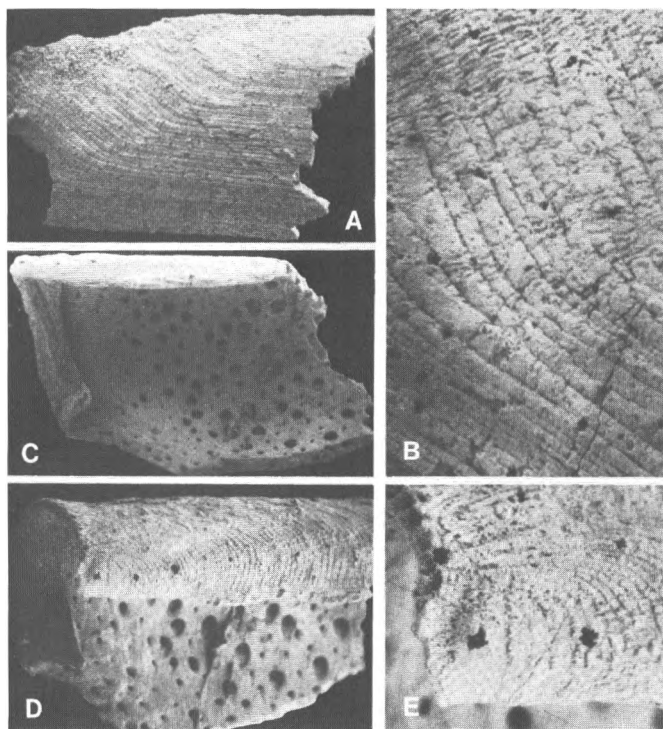


Fig. 10. *Carnicoleus gazdzickii* sp. nov. Ludlowian, Orthoceras Limestone, Valentin Törl, Carnic Alps, Austria. A. Specimen ZPAL V.XII/9. External view. $\times 70$. B. Same specimen. $\times 300$. C. Holotype, ZPAL V.XII/1. Internal view. $\times 70$. D. Holotype. Dorsal view. $\times 100$. E. Holotype. Apex, note ontogenetic changes in shape. $\times 300$.

into account, this implies that in many Early Paleozoic communities the Turrilepadida were not less important than trilobites or gastropods in the vagile benthos.

PHYLOGENETIC RELATIONSHIPS OF THE TURRILEPADIDA

The Turrilepadida range from the Tremadocian (Kobayashi and Hamada 1976) to the Pennsylvanian (Chronis in Bengtson 1978). They did not give origin to any extant animal group. Their possible relatives include the Cambrian Tommotiida and Sachtitida and the Middle Paleozoic Herculepadida.

The order Tommotiida includes animals with body covered with numerous sclerites that are prominently ornamented and lamellar in microstructure. These forms can be arranged into a morphologic series, from high-conical, almost symmetric sclerites of *Lapworthella* through *Kelanella* and *Bengtsonia* and up to low, almost flat, strongly asymmetric and dimorphic sclerites of *Tannuolina* (see Bengtson 1970; Matthews 1973; Matthews and Missarzhevsky 1975; Bischoff 1976; Missarzhevsky and Grigoreva 1981; Yuan and Zhang 1983). The sclerites are composed of calcium phosphatic lamellae, frequently separated by empty spaces; in *Tannuolina*, they are interconnected by tubuli. Such a loose distribution of phosphatic lamellae resembles the pattern observed in some acrotetid brachiopods (Poulsen 1971) and phosphatized arthropod remnants. The spaces between lamellae could have been originally filled with organic tissue. Secondary phosphatization cannot be ruled out, as the majority of tommotiid sclerites are associated with abundant phosphatized fossils or phosphorites (Bengtson 1970). This is in fact suggested by deposition of apatite prismatic layers on lamellae of the tommotiid *Sunnaginia* and subsequent filling of the spaces by loose, coarse apatite crystals (Landing et al. 1980).

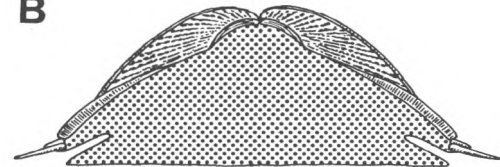
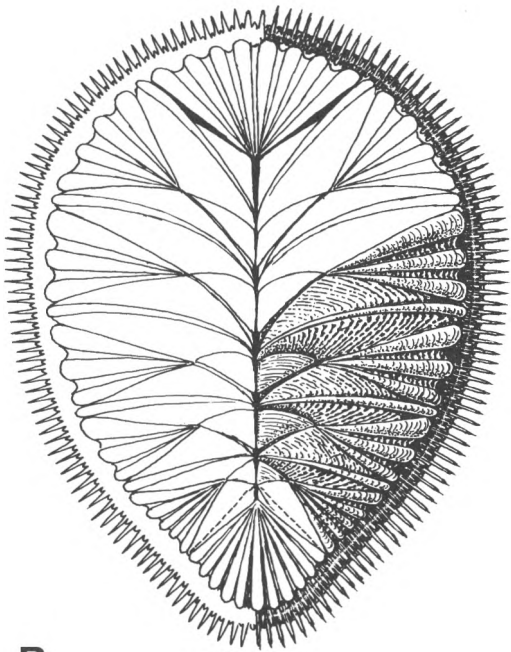
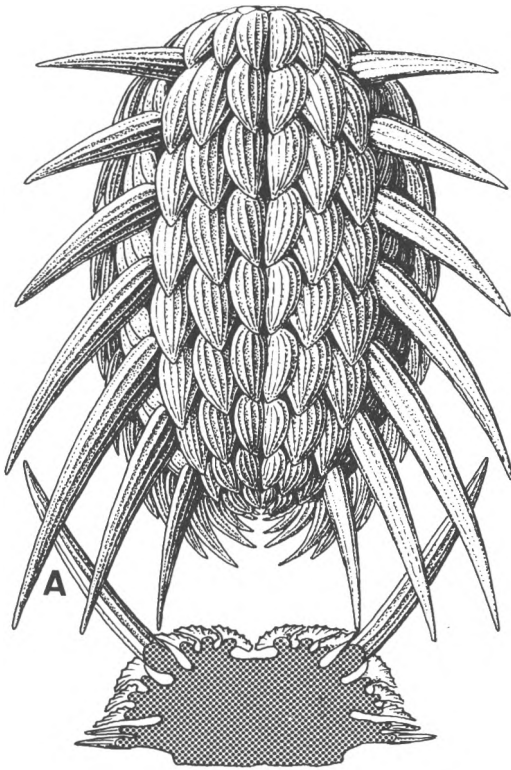
Morphologically, turrilepadid sclerites can be easily derived from the Tommotiida. The tommotiid sclerites supported pyramidal protrusions of the soft body. The animal probably had rows of sclerotized horns along the body. In some species of *Camenella* and *Dailyatia*, however, the sclerites were secreted on flattened protrusions of the body (Bengtson 1970; Matthews and Missarzhevsky 1975; Bischoff 1976), very much like the plumulid elytra. The sclerites are prominently ornamented dorsally but their lower side is almost smooth. In fact, sellate sclerites of *Camenella* closely resemble dorsal sclerites of *Plumulites*, while mitrate sclerites of the former resemble lateral sclerites of the latter (Bengtson 1970). This interpretation is supported by the range of variation in shape and size which is smaller in the sellate than in the mitrate sclerites of *Camenella*, for

the corresponding dorsal sclerites are largely uniform in *Plumulites*, whereas the lateral sclerites are differentiated into thoracic and variable abdominal ones (cf. Jell 1979).

Thus, phylogenetic derivation of the Plumulitidae from the Tommotiidae appears plausible, although the time gap between the early Middle Cambrian (Bischoff 1976) and the Tremadocian (Kobayashi and Hamada 1976) calls for caution.

Another Cambrian group of elytra-bearing animals, the Siphogonuchitidae, is closely related to the Wiwaxiidae (see Bengtson and Missarzhevsky 1981) and included here in the order Sachtitida. The best known sachtitid species is *Wiwaxia corrugata* (Matthew 1899) from the Middle Cambrian Burgess Shale (Conway Morris 1982: W; Chapter 13 by Briggs and Conway Morris, this volume). Its oval body was covered with leaf shaped elytra arranged into 20 longitudinal rows and 8 or 9 segments (Fig. 12A). According to Conway Morris (1982: W), a radulalike organ with two rows of organic teeth occurs in *Wiwaxia*. Wiwaxiid elytra have a very complex internal structure, which is best known in the Early Cambrian *Thambetolepis delicata* Jell 1981 from Australia (Jell 1981). Their external surface is flat, with shallow longitudinal depressions separated by sharp ridges. Internally, they are subdivided into pennately arranged tubular compartments. The axial compartment is wider and opens to the proximal, basal part of the elytron. It seems that the sclerotization proceeded from the elytron surface inward, which resulted in subdivision of the retreating soft body into a featherlike internal organ. This mode of secretion would be rather unusual if mollusk affinities of the wiwaxiids were accepted, as proposed by Conway Morris (1982: W). More primitive sachtitids probably lacked internal compartmentalization of elytra; the arrangement of their elongated, angular sclerites, however, was similar to that in *Wiwaxia* (see Matthews and Missarzhevsky 1975; Bengtson and Missarzhevsky 1981; Bengtson and Conway Morris 1984).

As noted above, the pennate organization of *Thambetolepis* elytra (Jell 1981) resembles the pattern of medial elevation, rugae, and marginal spines in the lateral elytral of *Plumulites*. Of course, this is not conclusive evidence for phylogenetic relationship between the plumulitids and wiwaxiids but, on the other hand, Bengtson's and Missarzhevsky's concept (1981) of Coeloscleritophora including the wiwaxiids and the "hexactinellid sponges" Chancelloriidae is questionable. The "spicules" of *Chancelloria* originated similarly to *Wiwaxia* sclerites (Sdzuy 1969). As judged after the few articulated specimens (Rigby 1978), however, its body plan was different from bilaterally symmetric wiwaxiids. *Chancelloria* was almost certainly sedentary, with radial symmetry of the body and triradiate symmetry of the



“spicules.” This resembles the Early Cambrian *Anabarites* (see Abaimova 1978), which might link the Chancelloriidae to an enigmatic group including *Pirania muricata* Walcott 1920 from the Middle Cambrian Burgess Shale, *Amgaella amgaensis* Korde 1957 and *Yakutina aciculata* (Korde 1957) from the Middle Cambrian of Yakutia. These organisms used to be interpreted as either dasycladacean algae (Korde 1963) or sponges (Conway Morris 1982). The Coeloscleritophora appear thus to be polyphyletic.

Possible relatives of the Turrilepadida include also barnacle-like *Hercolepas signata* (Aurivillius 1892) from the Early Silurian Visby Beds of Gotland, Sweden (Aurivillius 1892). Provided that *Protobalanus hamiltonensis* Hall and Clarke 1888, as described by Van Name (1925), belongs indeed to the same group, which is here proposed as the Hercolepadida ord. nov., their body plan can be tentatively reconstructed (Fig. 12B). The oval body is covered with calcareous dorsal sclerites arranged in four rows, possibly with unpaired, bilaterally symmetric cephalic and caudal sclerites (Van Name 1926). Sclerites of the inner rows are scalloped in shape, with umbones and auricles contacting along the medial commissure. Sclerites of the outer rows are triangular and rather flat. All sclerites are conspicuously ornamented with radial ribs, concentric rugae, and perhaps also punctae. The most peculiar feature of both *Hercolepas* and *Protobalanus* is a corona of small needle shaped spines surrounding the strobilus.

Hercolepadid dorsal sclerites resemble sellate sclerites of *Camenella* in shape, while the lateral sclerites are comparable to tomotiid mitrate sclerites. They resemble plumulitid sclerites in structure, but their orientation in the strobili is different. Sclerite tips are directed posteriorly in the Turrilepadida but almost medially in *Hercolepas*. When taken in conjunction with the corona of marginal spines, this may suggest sessile life habits of the hercolepadids.

I propose to assign the Sachitida, Tommotiida, Turrilepadida, and Hercolepadida to the class Machaeridia Withers 1926.

The most morphologically parsimonious model of machaeridian phylogeny (Fig. 13) suggests that their common ancestor had numerous conical protoelytra with cuticularized surfaces. They

←
Fig. 12. A. Dorsal view and cross section of reconstructed *Wiwaxia corrugata* (Matthew 1899) from the Middle Cambrian Burgess Shale, British Columbia (modified after Bengtson & Conway Morris 1984); enlarged. B. Composite dorsal view of *Hercolepas signata* (Aurivillius 1892) (shaded) fitted into the strobilus of *Protobalanus hamiltonensis* Hall and Clarke 1888 (see Van Name 1925, 1926); also hypothetical cross section, enlarged.

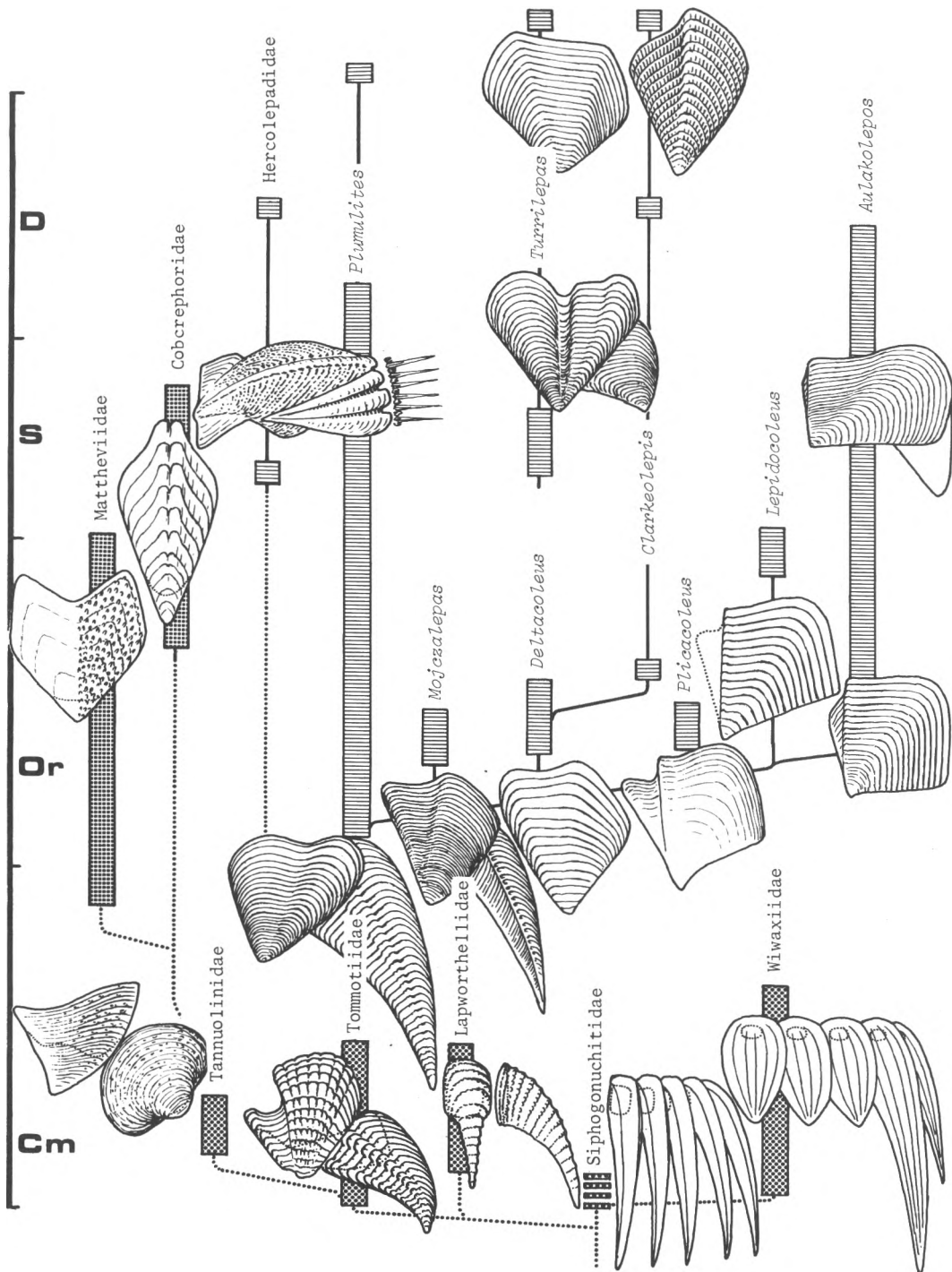


Fig. 13. Proposed relationships among the considered taxa, and their stratigraphic distribution; note that the alleged chitons Cobcrephoridae had phosphatic valves (Bischoff 1981).

could be low, as in *Tannuolina*, or elongated, as in the Siphononuchitidae, but because of considerable sclerite mineralization in *Tannuolina* and *Camennella* and their complex ornamentation and microstructure, the latter interpretation seems more likely. Flattening of protoelytra into typical leaf shaped elytra probably took place independently in the Wiwaxiidae and Tommotiidae. The latter group may have given origin to all the post-Cambrian machaeridians, as indicated by the number of longitudinal rows of elytra. Subsequently, dorsal calcification of elytra replaced scleritization of their entire surface.

PHYLOGENETIC AFFINITIES OF THE MACHAERIDIA

The Machaeridia were originally interpreted as an extinct group of barnacles. This hypothesis was refuted by Withers (1926; but see Bischoff 1976), who suggested their echinoderm affinities. Bather (in Withers 1926) considered carpoids as the closest relatives of the Turrilepadida, while Pope (1975) interpreted lepidocoleid strobili as fragmentary mitrate spines. Microstructural counter-evidence to the latter interpretation was presented by Bengtson (1977, 1978), who proposed earlier a close relationship between the Turrilepadida and Tommotiida, and suggested their annelid affinities (Bengtson 1970). This concept was supported by Jell (1979).

With monophyly of the Machaeridia taken for granted, their typical representative has a bilaterally symmetric body covered by (pseudo)metamerically arranged dorsal protuberances or elytra, each of them with internal canals (known in *Thambetolepis* and inferred in *Plumulites*) that may branch pennately. Metamerically arranged dorsoventral muscles attached to the dorsal wall of each elytron occur in more advanced machaeridians. Body segments tend to differentiate into tagmae. Spines or spicules occur outside the strobilus in the Hercolepadida. Jaw apparatus has been reported in *Wiwaxia*.

The major problem with phylogenetic affinities of the Machaeridia is that the available data allow for more than one coherent interpretation. Potential relatives of the Machaeridia can be sought in the Annelida as well as in the mollusk subphylum Amphineura. A direct phylogenetic relationship of machaeridians to any known representative of those two groups seems unlikely, however. The following speculations are merely aimed at exploring alternative interpretations of the machaeridian body plan within the annelid and mollusk anatomic frameworks.

COMPARISONS TO THE ANNELIDA

Bengtson (1970) compared the Tommotiida to the Early Cambrian onychophore *Xenusion auers-*

waldae Pompeckj 1927 (Jaeger and Martinsson 1967) and suggested that the dorsal humps of *Xenusion* could bear machaeridian-like sclerites. These humps seem to be homologous to tubercles in the cuticular rings of another Cambrian onychophore, *Aysheia pedunculata* Walcott 1911 (Whittington 1978), whereas the latter closely resemble the tubercles of Recent terrestrial onychophores. Cloud and Bever (1973) illustrated, as the trace fossil *Plagiogmus* sp., two Early Cambrian specimens that may represent a connecting link between *Xenusion* and *Aysheia*. They provide evidence for the onychophoran nature of *Xenusion* and also indicate that more than just two longitudinal rows of dorsal humps may occur in marine Onychophora. Still, the morphologic gap between the onychophorans and machaeridians is very wide.

Wiwaxiid and plumulid sclerites do not significantly differ in shape and structure from elytra of the Recent Polychaeta. The elytron originates as a flat extension of dorsal tubercle in the Polychaeta. The tubercle, or elytriphore, contains intestinal caecum of the segment (Pettibone 1953). There are only two longitudinal rows of elytriphores in the Recent amphinomiid polychaetes, with elytra actually present at every second segment. In elytra-bearing segments, the cirri associated with elytriphores are reduced. It is a matter of dispute whether elytra are homologous to cirri (Duncker 1906). If not, there is nothing implausible in a supposition that some extinct polychaetes had more than two rows of elytriphores. Their intestinal caecum might potentially protrude into the elytron to develop into a structure like the internal canal of *Thambetolepis*. The elytriphore has muscles (Duncker 1906) that might be transformed into dorsoventral muscles of the Turrilepadida. Moreover, the jaw structure of *Wiwaxia* (Conway Morris 1982: W) might represent the polychaete jaw apparatus, which may be hardly discernible from the mollusk radula in the fossil record (Kielan-Jaworowska 1966). *Wiwaxia* has no setae that are diagnostic of the Polychaeta. The phyllocid polychaetes, however, also lack setae, while the marginal spines of *Hercolepas* might in fact represent modified setae. The Machaeridia could thus be interpreted as related to the Polychaeta.

Such an interpretation, however, encounters functional problems. With an *Aulakolepos*-like skeleton, parapodia could not function as a locomotory organ. The only mechanism of propulsion available to such an annelid would be snakelike lateral swinging of the body. This mechanism could hardly work in *Lepidocoleus* or *Turrilepas*, with their short bodies. The problem with locomotion could be overcome by the assumption of a footlike crawling and digging organ. The latter concept, however, is incompatible with the body plan of the phylum Annelida.

COMPARISONS TO THE AMPHINEURA

It is now generally accepted that the Mollusca are acoelomate and evolved from crawling flatworms (Salvini-Plawen 1982), while the origin of the Annelida was preceded by development of the coelom in their ancestors, who peristaltically burrowed in soft mud. Thus, the Machaeridia cannot be related to both polychaetes and polyplacophorans, but they might be related to both turbellarians and polyplacophorans (Runnegar et al. 1979).

Leaf shaped protuberances of the body filled with intestinal caeca occur in polyclad flatworms (Hyman 1951). They are not metamerically arranged, but both metamerization and cuticularization are compatible with the body plan of the phylum Platyhelminthes. Fossil record of the flatworms is practically nonexistent. The only fossil that could be related to the Recent *Turbellaria* is the Late Precambrian *Dickinsonia*. With its large, flat, and contractible body, concentric muscular pattern, and medially separated "segments" resembling in their distribution the intestinal caeca and color bands of large-sized polyclad flatworms, *Dickinsonia* fits quite well into the body plan of the Platyhelminthes, perhaps better than into any other phylum (but see Runnegar 1982; see also Chapter 6 by Fedonkin, this volume). If this in-

terpretation were correct, some prototurbellarians would have existed in the Late Precambrian and they could have given origin to the Machaeridia. The Mollusca must also have evolved from Late Precambrian flatworms. It is the Polyplacophora that appear to be the most primitive mollusks (Runnegar et al. 1979). The problem is, then, if the functional analogy between machaeridian elytra and chiton valves reflects their homology. Superficially, there is little similarity between the unpaired, flat valves of Recent chitons, penetrated by numerous aesthetasae, and the paired, imporous, pyramidal sclerites of early machaeridians. This dissimilarity, however, turns out to be less pronounced when the earliest chitons are considered.

As shown by Runnegar et al. (1979), the Late Cambrian *Matthevia variabilis* Walcott 1885 was a chiton. Ventral morphology of the valves of the Early Ordovician *Septemchiton aequivoca* (Robson 1913) from the Šárka Formation of Bohemia very closely resembles *Matthevia* (Fig. 14). The armor of that species is intermediate in morphology between *Matthevia* and other early chitons. *Matthevia*, however, had very thick, conical valves (Fig. 14B), perhaps in response to the high environmental energy. *Septemchiton*, in turn, lived in deeper water (Rolfe 1981) and had roof

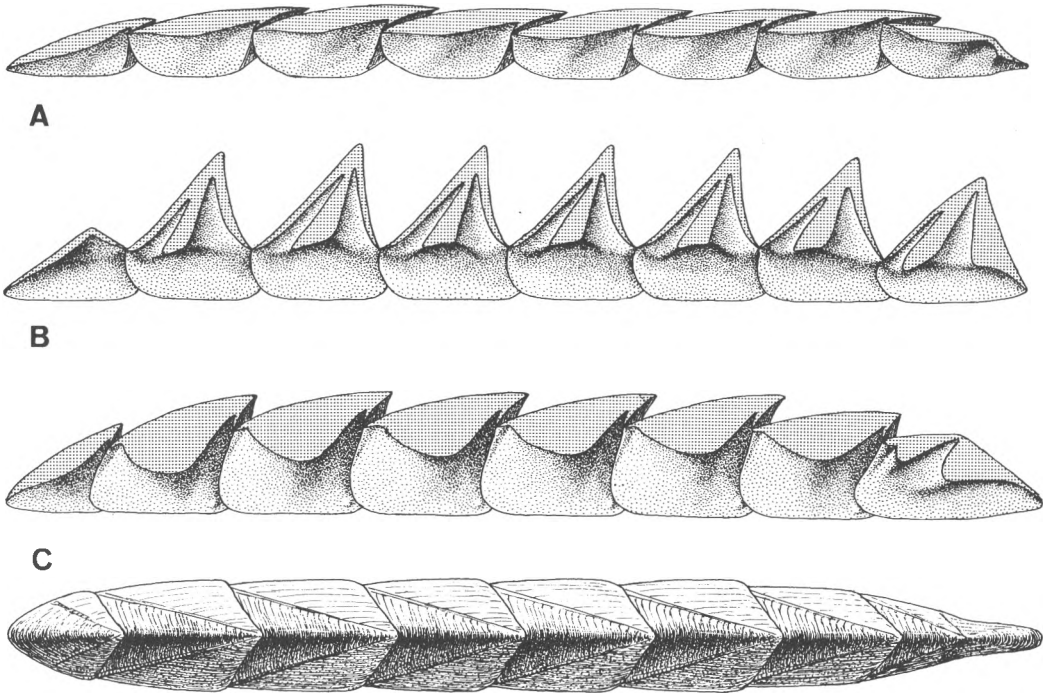


Fig. 14. Reconstruction of the earliest polyplacophorans; not to scale. A. *Chelodes* sp. Based on Runnegar et al. (1979) and specimens from the Mójcza Limestone, Mójcza, Poland. B. *Matthevia variabilis* Walcott 1885. Based on Runnegar et al. (1979). C. *Septemchiton aequivoca* (Robson 1913). Longitudinal section and dorsal view. Based on several articulated but incomplete specimens from the Šárka Formation, Osek, Bohemia (housed at the Národní Museum, Prague).

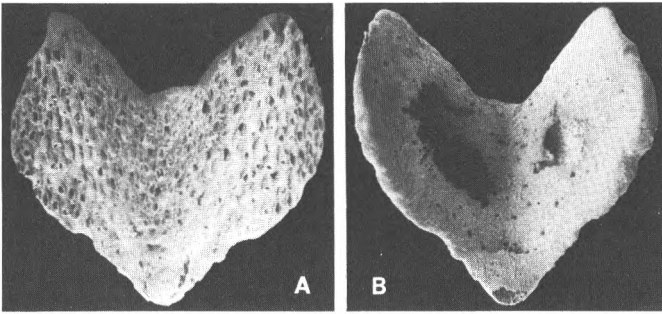


Fig. 15. External A. and internal B. views of an intermediate valve of *Septemchiton* aff. *aequivoca* (Robson 1913), sample MA-4. Late Caradocian, Mójcza Limestone, Mójcza, Poland (ZPAL V.XII/10). Note small duplicature. $\times 100$.

shaped valves with flat lateral areas and narrow posterior duplicature (Fig. 15). The duplicature is homologous to the posterior wall of the pyramidal valves of *Matthevia*. Even the most primitive chitons, such as the Cambrian *Praeacanthochiton* (Runnegar et al. 1979) or the Ordovician *Septemchiton* (Fig. 15), show peculiar microornamentation that, by analogy to Carboniferous chitons (Hoare et al. 1983), may be taken to reflect a system of aesthetae in the external layer of the shell (see Haas and Kristen 1974).

Generally, the plumulitids and most tomotiids had externally smooth sclerites completely lamellar in microstructure. There are, however, at least two exceptions. First, *Tannuolina* had some tubes that penetrated the lamellae and opened at the external surface of the sclerite (Bischoff 1976; Bengtson 1977). Second, *Carnicoleus*, interpreted here as a lepidocoleid machaeridian, had pseudopores (Fig. 10). Its external ornamentation, however, differed from the chitons. The main dorsoventral muscle attachment scars are arranged in two longitudinal rows in the chitons. This is the pattern observed also in the Turrelepadida. One might thus think of the roof shaped valves of *Septemchiton* having originated each by fusion of two dorsal sclerites of *Tannuolina*, although the embryonic development of Recent polyplacophorans (cf. Haas et al. 1979) does not support this hypothesis.

Nevertheless, it is not implausible that the chitons evolved from a machaeridian. Corroborating evidence might in fact be sought in the perinotal(?) spicules of *Hercolepas*, with its otherwise machaeridian strobilus, and in the radula of *Wiwaxia*. But the available data do not allow us to determine if the class Machaeridia is to be placed in the Annelida, parallel to the Polychaeta, or rather in the mollusk subphylum Amphineura, next to the Polyplacophora and Aplacophora.

SYSTEMATIC PALEONTOLOGY

CLASS MACHAERIDIA Withers 1926

Diagnosis: Bilaterally symmetric animals with body covered dorsally with metameric, scleri-

tized elytra arranged into longitudinal rows. Intestinal caeca(?) protruded in elytra in early forms. In later forms, strongly mineralized sclerites propelled by dorsoventral muscles.

ORDER SACHITIDA He 1980

Emended diagnosis: Machaeridians with elongated, usually leaf shaped elytra in about 20 rows; 8 or more segments of the body. Elytra entirely sclerotized; in advanced form, internally subdivided into pennately arranged compartments.

Families: Siphononuchitidae Qian 1977; Wiwaxiidae Walcott 1911.

Distribution: Early to Middle Cambrian.

ORDER TOMMOTIIDA Missarzhevsky 1970

Emended diagnosis: Machaeridians with elytra in four(?) rows, pyramidal in shape, covered with thick mineralized sclerites; elytra of allegedly inner rows sellate, those of outer rows mitrate in shape.

Families: Lapworthellidae Missarzhevsky 1966; Tommotiidae Missarzhevsky 1970; Tannuolinidae Fonin and Smirnova 1967.

Distribution: Early to earliest Middle Cambrian.

ORDER HERCOLEPADIDA ord. nov.

Diagnosis: Machaeridians with oval body covered with four rows of elytra. Elytra calcified dorsally, with complex ornamentation and tips directed medially. Numerous marginal spines around the body.

Family: Hercolepadidae fam. nov.

Diagnosis: As for the order.

Genera: *Hercolepas* Withers 1915; *Protobalanus* Clarke, 1888.

Distribution: Early Wenlockian to Late Eifelian.

ORDER TURRELEPADIDA Pilsbry 1916 nom. corr.

Diagnosis: Machaeridians with elongated body covered with four rows of dorsally calcified ely-

tra. Two first segments of the body have only two inner elytra each; the following three segments have lateral elytra modified. Lateral elytra reduced in advanced forms.

Distribution: Tremadocian to Westfalian.

FAMILY PLUMULITIDAE Jell 1979

Emended diagnosis: Dorsoventrally flattened body with about 20 segments; elytra thin walled; lateral elytra large.

Genera: *Plumulites* Barrande 1872; *Compacoleus* Schallreuter 1985.

Distribution: Tremadocian to Tournaisian.

FAMILY TURRILEPADIDAE Clarke 1896

Emended diagnosis: Box-shaped body with about 30 segments, covered with angular dorsal elytra and smaller, flat lateral elytra; elytra thick walled, each with a distinct muscle scar.

Genera: *Turrilepas* Woodward 1865; *Deltacoleus* Withers 1926; *Clarkeolepis* Elias 1958; *Mojczalepas* gen. nov.; *Spinacoleus* Schallreuter 1985 (-*Rugacoleus* Schallreuter 1985).

Distribution: Arenigian to Namurian.

Mojczalepas gen. nov.

Type species: *M. multilamellosa* sp. nov.

Diagnosis: Elytra similar to *Plumulites* but with thick, calcified dorsal wall. Dorsal elytra have concave inner and convex outer areas, and relatively deep and wide medial sinus at the anterior margin. Lateral elytra have thick, narrow sclerites with prominent medial elevation.

Species included: Type species, *Mojczalepas* sp. a, *Mojczalepas* sp. b.

Distribution: Arenigian to Llanvirnian of Baltic area, Llanvirnian of Holy Cross Mountains, Poland; possibly also Caradocian of England.

Mojczalepas multilamellosa sp. nov. (Figs. 5A, B, 6A, and 8C)

Holotype: ZPAL V.XII/2, Fig. 5A, B.

Type horizon and locality: *E. reclinatus* Zone, Llanvirnian, Mójcza Limestone, Mójcza, Holy Cross Mountains, Poland.

Diagnosis: A species of *Mojczalepas* with sclerites ornamented with densely spaced, high rugae. Outer area of dorsal sclerites with semi-circular lobe at the anterior margin, inner area with medial shallow sinus and marginal narrow lobe.

Remarks: *M. multilamellosa* differs from its congeners in its very prominent and simple pattern of ornamentation. The lateral sclerites (Fig. 6C, D) derived from the erratic boulder E-323 may belong to this species.

Distribution: Llanvirnian of Baltic area and Holy Cross Mountains, Poland.

FAMILY LEPIDOCOLEIDAE Clarke 1896

Emended diagnosis: Laterally compressed body with up to 60 segments, completely covered with large dorsal elytra. Dorsal elytra with large, convex outer area and narrow, concave inner area separated from each other by medial rib. Lateral elytra reduced in size or lacking.

Genera: *Lepidocoleus* Faber 1886; *Aulakolepos* Wolburg 1938; *Plicacoleus* gen. nov.; ?*Carnicoleus* gen. nov.

Distribution: Llanvirnian to Givetian.

Plicacoleus gen. nov.

Type species: *P. robustus* sp. nov.

Diagnosis: Dorsal elytra have thick-walled sclerites with very convex outer area separated by prominent crest from wing shaped inner area. Sclerite width subequal to its length. Sclerites are almost smooth, with indistinct growth lines in the only known species.

Remarks: The peculiar medial crest on dorsal sclerites distinguishes *Plicacoleus* among the machaeridians. The sclerites have sharp posterior margin without any duplicature or marginal spines.

Species included: Type species only.

Distribution: Llanvirnian of Baltic area and Holy Cross Mountains, Poland.

Plicacoleus robustus sp. nov. (Figs. 6E, and 9A, B)

Holotype: ZPAL V.XII/3, Fig. 9A, B.

Type horizon and locality: *E. reclinatus* Zone, Llanvirnian, Mójcza Limestone, Mójcza, Holy Cross Mountains, Poland.

Diagnosis: As for the genus.

Distribution: As for the genus.

Carnicoleus gen. nov.

Type species: *C. gazdzickii* sp. nov.

Diagnosis: Sclerites elongated, semicylindrical in shape, ornamented with growth lines; sclerite wall relatively thin, penetrated with numerous pseudopores. Posterior end of the sclerite sharply truncated, with short duplicature. Inner area of the sclerite narrow, separated by weak angulation from outer area.

Remarks: This is an enigmatic form with uncertain affinities. Though generally lepidocoleid in shape, its sclerites differ from the other Machaeridia in their pseudoporous, perhaps originally aragonitic (now phosphatized) wall and peculiar duplicature.

Species included: Type species only.

***Carnicoleus gazdzickii* sp. nov. (Fig. 10A–D)**

Holotype: ZPAL V.XII/1, Fig. 10C, D.

Type horizon and locality: Ludlowian, Orthocerat Limestone, Valentin Törl, Carnic Alps, Austria.

Diagnosis: As for the genus.

Name derivation: After Dr. Andrzej Gaździcki who collected the sample.

Distribution: Type locality only.

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