



Machaeridian locomotion

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The discovery that machaeridians (class Machaeridia Withers, 1926) are annelids allows their mode of locomotion to be interpreted in the context of the body plan of this phylum. The Plumulitidae were errant epibenthic forms, moving with parapodia. The body of Turrilepadidae and Lepidocoleidae, however, was enclosed largely within the mineralized plates that make up the skeleton. Articulated specimens indicate that these machaeridians were able to burrow like other annelids using peristaltic locomotion. A lepidocoleid specimen indicates that multiple waves of shortened and contracted regions moved over the body. This is in contrast to the mode of locomotion in earthworms and most polychaetes, but similar to peristaltic progression in *Polyphysia* (Scalibregmidae). Either the rugose sculpture (turrilepadids) and/or the margins of the overlapping shell plates functioned as a burrowing sculpture, allowing forward movement but preventing backwards slipping. A trace from the Devonian Hunsrück Slate associated with a lepidocoleid indicates that considerable flexing of the skeleton was possible, but this is an escape trace and does not represent normal locomotion. Features of the skeleton of machaeridians are convergent on those of molluscs where the shells likewise function in protection and burrowing. □ *Annelid, polychaete, convergence, hydrostatic skeleton, molluscs, peristalsis.*

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Machaeridians (class Machaeridia) are a group of Palaeozoic armoured annelids (Vinther *et al.* 2008) ranging from Early Ordovician to Permian in age (Cooper & Grant 1972; Hoare *et al.* 1996) that are common constituents of marine fossil assemblages. Until recently their systematic position has been a matter of controversy due to their unusual morphology and the absence of an obvious modern counterpart. Machaeridians had been assigned variously to molluscs (de Koninck 1857; Wolburg 1938; Dzik 1986; Herringshaw *et al.* 2004; Sigwart & Sutton 2007), barnacles (Woodward 1865; Moberg 1914; Bischoff 1975), echinoderms (Withers 1926; Pope 1975) and annelids (Bengtson 1970; Jell 1979; Dzik 1986). However, a plumulitid machaeridian with soft part preservation was discovered recently in the Lower Ordovician (uppermost Tremadoc) of Morocco (Vinther *et al.* 2008). The presence of serially arranged paired parapodia with chaetae in this specimen indicates an annelid affinity for the machaeridians. Their exact place within the annelids is still unresolved, but machaeridians appear to form a monophyletic group based on the characters of the shell plates (Vinther *et al.* 2008).

There are three machaeridian families. The Plumulitidae Jell, 1979 are flattened dorsoventrally with well-developed parapodia and were presumably epibenthic. The Turrilepadidae Clarke, 1896 and Lepidocoleidae Clarke, 1896 are laterally compressed

with shell plates enclosing the body and preventing parapodial locomotion. The parapodia may have been reduced in these groups. These machaeridians are more streamlined in form than the plumulitids and they have been interpreted as burrowers (Dzik 1986; Hints *et al.* 2004). As both turrilepadids and lepidocoleids are almost completely enclosed within their armour it should be possible to interpret their mode of locomotion by analysing the functional morphology of the skeleton even in the absence of evidence of the soft-part morphology.

The machaeridian skeleton

Plumulitids are dorsoventrally flattened with four longitudinal series of shell plates, two inner and two outer. The plates are borne by narrow extensions of the base of the parapodia on either side of the trunk where the inner and outer shell plates are attached to alternate segments (Vinther *et al.* 2008). The inner shell plates are smaller than the outer and they project inwards obliquely in a posterior direction. The outer plates are more elongate and project outwards posteriorly in an orientation roughly normal to the inner shell plates. This arrangement has been reported in articulated plumulitids from a range of localities (Withers 1926; Jell 1979; Rudkin 2001; Vinther *et al.* 2008). The structures to which the shell plates are

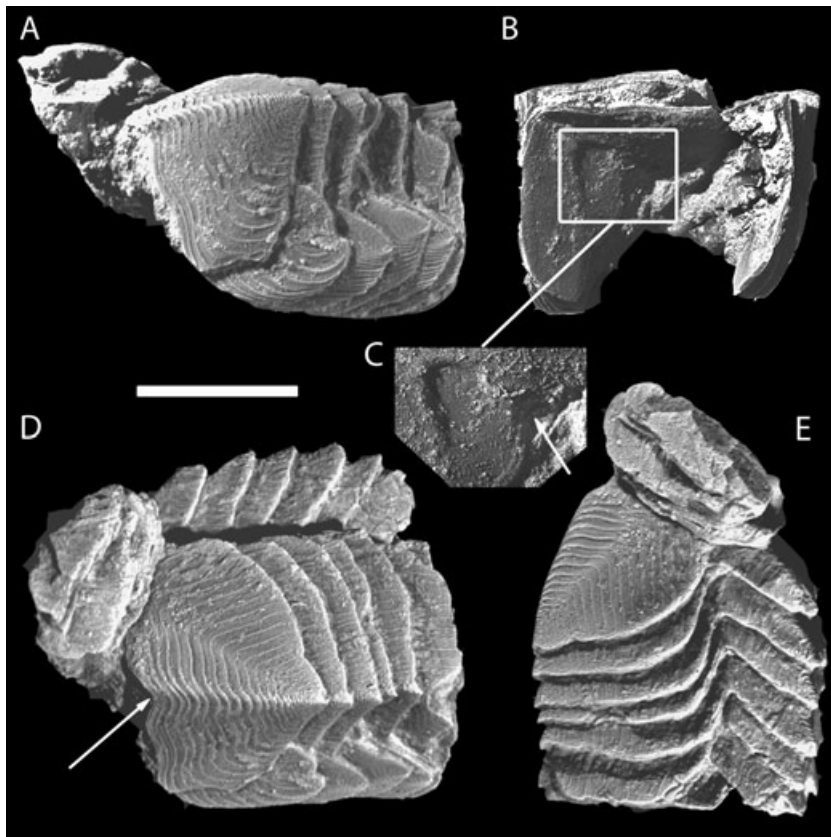


Fig. 1. *Turrilepas wrightiana* (de Koninck, 1857) from the Hemse marl, Gotland, Sweden, Naturhistoriska Riksmuseet $\times 3852$. Scale bar is 5 mm for all images, except for C, in which it is 3 mm. A, lateral view, anterior is to the left. Notice the asymmetric rugose ornamentation. B, transverse view and the square outline of the body (outlined area is the one depicted in C). C, muscle scar and proximal notch on lower surface of inner shell plate. Notice the granular texture on surface. D, oblique view from the upper lateral side, arrow marks notch on the inner shell plate. E, view from above.

attached are similar to the elytra (modified cirri) in aphroditacean annelids. Elytra are developed on every other segment in aphroditaceans (the intervening segments bear smaller cirri) and therefore exhibit a similar kind of segmental alternation to that in plumulitids, but unlike the plates in the latter, they are not mineralized (Rouse & Pleijel 2001).

Dorsal cirri of variable morphology occur on alternate segments in only some phyllocidans (Glasby *et al.* 2008). Machaeridians may belong to this clade, possibly as a stem group aphroditacean. A number of other characters of this group (e.g. aciculae, jaws, ventral cirri, compound chaetae, median and lateral antennae) might be found in new exceptionally preserved machaeridian fossils. The only known specimen preserving soft parts (*Plumulites bengtsoni* Vinther *et al.* 2008) lacks the head, does not show details of the chaetae and only exposes the dorsal side.

Plumulitids are the only machaeridians that lack prominent muscle-scars on the shell plates and the shells are thin (even centimetre-sized shell plates in plumulitids may be only 0.1 mm in thickness, much

thinner than in other machaeridian families). The arrangement of the rugae on the external surface of the shell plates is concentric except in the anterior shell plates of some examples (e.g. *Plumulites tafennaensis*, *P. canadiensis* and *P. richorum*, personal observations) where radial ornamentation occurs (Vinther and Rudkin in press).

Only a small number of articulated turrilepadids have been reported (Adrain *et al.* 1991). Turrilepadids, like plumulitids, have both inner and outer rows of shell plates but, in contrast to plumulitids, the plates have muscle scars. The inner plates bend through about 90° along their midline (the longitudinal fold) giving the body a squarish transverse section (Fig. 1B). The anterior margin of these plates is notched in a position corresponding to the muscle scar (Fig. 1C, D, arrowed). The anteriormost outer shell plates are absent in some taxa, as they are in plumulitids (Adrain *et al.* 1991). The steep slope of the rugae of the inner shell plates faces in a nearly posterior direction on both the dorsal and the lateral surfaces (Fig. 1A, C, D). The exact orientation of the

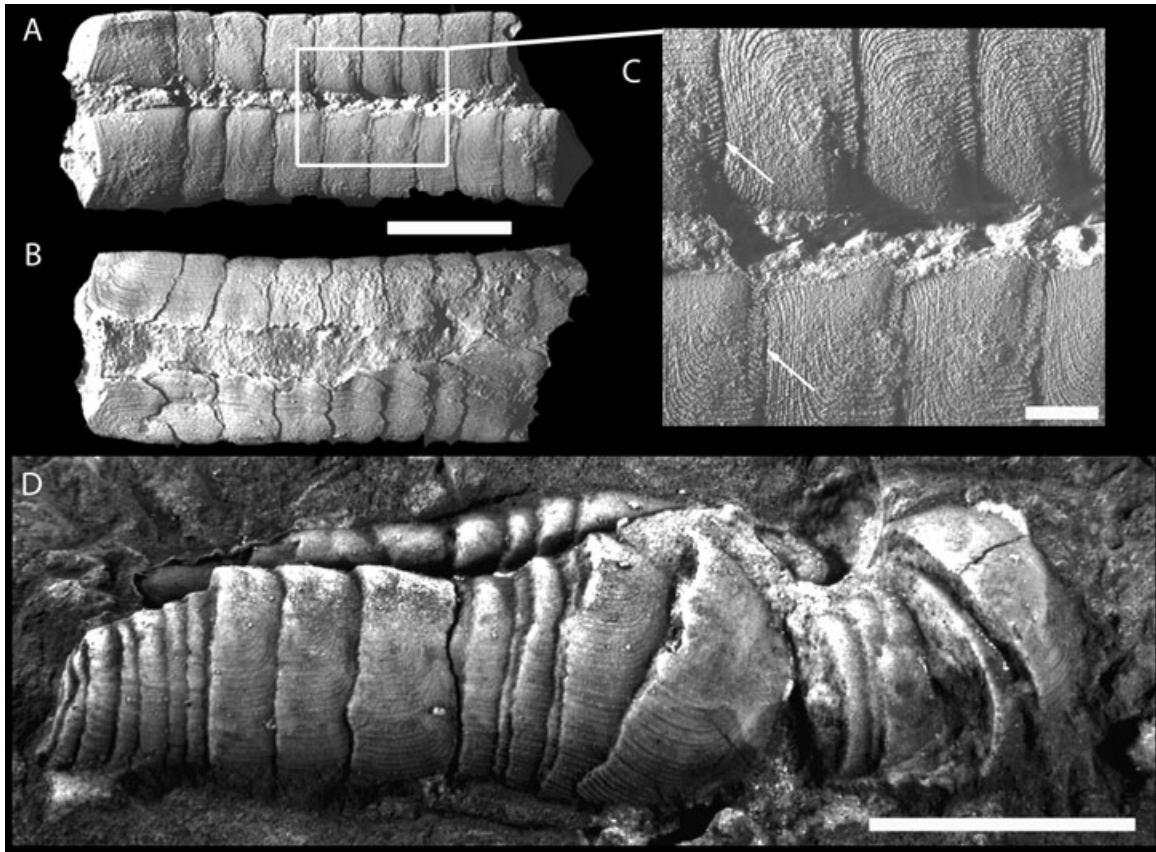


Fig. 2. *Lepidocoleus* sp. from Bois d'Arc Formation, Cravat Member, Lower Devonian, Helderbergian, Coal County, Oklahoma. Scale bars are 5 mm in all images, except for C, in which it is 1 mm. A, B, C, Yale Peabody Museum 222284, dorsoventrally compressed specimen. A, dorsal view (outlined area is the one depicted in C). B, ventral view. C, dorsal median area showing the posterior marginal denticles in juvenile part of shell (arrowed). D, Yale Peabody Museum 222283, specimen showing different degrees of longitudinal contraction along body evident in different sets of overlapping shell plates.

rugae varies between species (e.g. *Turrilepas wrightiana* and *T. modzalevskae* in Adrain *et al.* 1991). A specimen from the Silurian of Gotland, Sweden, illustrated here for the first time (Fig. 1) shows extensive overlap between the plates. Given the completeness of the specimen and consistent arrangement of the plates, this overlap is unlikely to be a taphonomic artefact; we interpret the fossil to represent a result of natural contraction (compare with an extended specimen: Adrain *et al.* 1991, pl. 1, fig. 5).

Some lepidocoleids retain the quadriseriate morphology of the other two families of machaeridians (Dzik 1986; Högström 1997), but most are biseriata with only inner shell plates (Adrain 1992; Högström 2000; Högström and Taylor 2001). The shell plates enclose the body completely ventrally and sometimes articulate dorsally along a tongue and groove hinge (Adrain 1992). Like turrilepadids they show pronounced muscle scars. The number of shell plates in lepidocoleids varies from 14 (*Lepidocoleus sarlei*) to more than 60 (*L. ketleyanus*) in contrast to plumulitids and

turrilepadids where the known range is between 13 and 26 shell plates in a row (Adrain *et al.* 1991 and personal observations). A partially articulated lepidocoleid from the Devonian of Oklahoma, illustrated here for the first time, shows three sets of about three plates overlapping normally followed by four to six strongly overlapping plates (YPM 222283, Fig. 2D). This indicates an ability to contract sections of the body independently. Lepidocoleids with single sets of highly overlapping plates have also been reported from the Silurian of Gotland (*Lepidocoleus* sp. B and C, Högström 2000, fig. 6C–E).

Locomotion in machaeridians

Living annelids crawl in two main ways. Epibenthic errant polychaetes use the parapodia as limbs, swinging them forward and back in waves that run along the body, the parapodia on opposite sides of a segment out of phase. Faster crawling is achieved by undulating

the body; flexure of the longitudinal muscles increases the efficiency of the force generated by the parapodia (Clark 1964). Oligochaetes, such as the earthworm *Lumbricus*, lack parapodia and move by peristalsis, a method of burrowing also found in some polychaetes with reduced parapodia, and in nemerteans like *Lineus* (Clark 1964). Earthworms move by propagating peristaltic waves backwards along the body. Contraction of the longitudinal muscles and relaxation of the circular muscles result in short fat expanded segments which anchor the animal while contraction of the circular muscles and relaxation of the longitudinal muscles allow segments to become long and slender to extend forwards (Gray & Lissman 1938). Posteriorly oriented bundles of chaetae prevent the animal from slipping backwards.

Plumulitids presumably crawled like most polychaetes, using the parapodia. The shell plates probably limited lateral flexibility (articulated fossils are almost always straight apart from a little flexure in the anterior region) and locomotion may have been similar to that in the polychaete *Aphrodite* (Mettam 1971). This polychaete is rather short and wide and has limited ability to flex its body laterally, making its locomotion slow. The absence of muscle scars on the plates in plumulitids suggests that the plates in this family functioned as a passive dorsal armour. The parapodia in turrilepadids and lepidocoleids, in contrast, were enclosed within the shell plates and these forms moved by peristalsis, burrowing in sediment by dynamic changes in the shape of the hydrostatic skeleton and by gaining purchase on the sediment with the shell plates. Höglström (1997) argued that the skeleton of lepidocoleids was opened by hydrostatic pressure and contracted by the muscles attached to the shell plates. She considered that peristaltic waves must have propagated posteriorly as in most annelids, based on the overlap of the shell plates. The examples of turrilepadids and lepidocoleids with different degrees of shell overlap described here and in the literature demonstrate an ability to elongate and shorten the body.

Figure 3A, B illustrates schematically how the posteriorly propagating peristaltic waves typical of annelids could have given rise to locomotion in turrilepadids and lepidocoleids. The Devonian lepidocoleid from Oklahoma (Fig. 2D) indicates that multiple waves could propagate along the trunk simultaneously at least in longer forms, as in earthworms (Gray & Lissman 1938). In this fossil, however, in contrast to earthworms and many polychaetes, the greatest lateral expansion occurs where there is less rather than more shortening of successive segments (Fig. 2D). This indicates a different peristaltic move-

ment to that in earthworms. Earthworms have almost complete septa whereas most polychaete groups have incomplete septa that allow coelomic fluid to flow freely between segments (Clark 1964). Nonetheless the peristalsis performed by the majority of polychaetes is very similar to that in earthworms. Locomotion in the polychaete *Polyphysia*, however, involves *simultaneous* shortening and contraction of sections of the body in waves that move forward (Elder 1973). This is combined with side-to-side movements of the anterior end. The nature of the overlap in the lepidocoleids described here (Fig. 2D) suggests that they may have moved in a similar fashion (Fig. 3C, D), in contrast to the mechanism suggested by Höglström (1997).

Modern scaleworms (Aphroditidae) have muscular insertions in the elytra which allow the gap between the elytron and the dorsal body wall to be reduced, forcing a current in a posterior direction (Mettam 1971). Hydrostatic pressure forces the elytron away from the body wall again and allows inflow of water. The resulting water flow facilitates respiration. Movement of the shells of machaeridians appears to have functioned in a similar way.

A feature of many infaunal molluscs, particularly bivalves, is the evolution of burrowing sculptures (Seilacher 1984). These take the form of ribs aligned near normal to the burrowing direction, asymmetric in section so that their slopes are gentle in the direction of movement and steep in the opposite direction, thus preventing the animal from sliding backwards. The concentric rugae on the inner shell plates of turrilepadids, which are aligned approximately normal to the axis of the trunk and presumed direction of movement, served a similar function in anchoring expanded regions of the body. The spacing between the rugae on the inner shell plates of *Turrilepas wrightiana* is fairly regular (Adrain *et al.* 1991, pl. 1, figs 5, 11; Fig. 1A, D, E). The steep posterior slope would have prevented sliding in a posterior direction but would not have inhibited movement anteriorly. The rugae of the outer shell plates and parts of the inner shell plates, in contrast, which run parallel to the axis of the trunk (and presumed direction of movement) are usually less pronounced and lack asymmetric ratcheting (see for example Adrain *et al.* 1991, pl. 2, fig. 10).

The rugae in lepidocoleids are aligned mostly parallel to the trunk axis and presumed direction of movement. Thus they could not have performed any obvious function in burrowing, although, like those in the plates of turrilepadids, they would have added strength. The orientation of the rugae in lepidocoleids may reflect the extensive growth of the plates in a lateral direction in order to enclose the body fully.

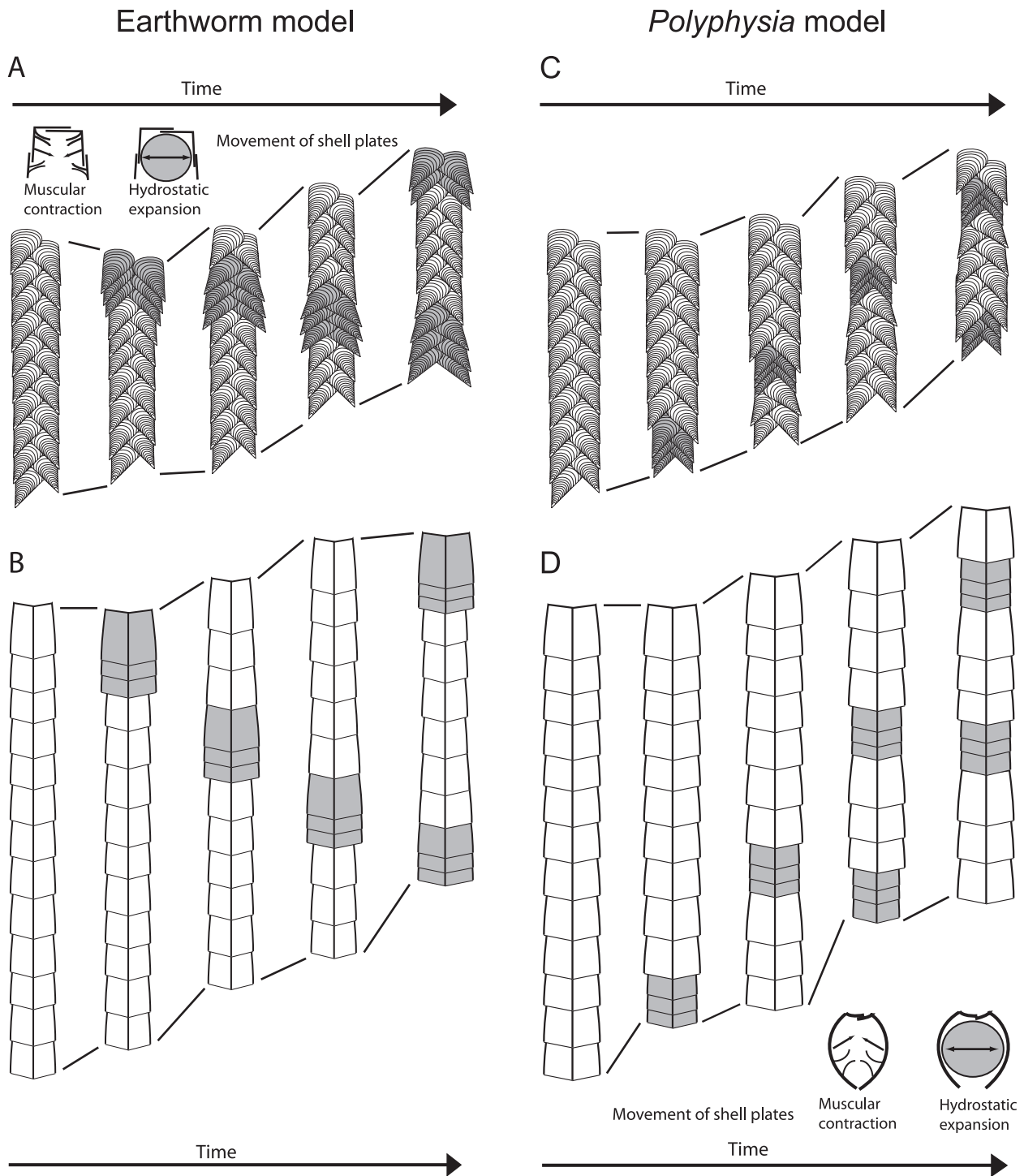


Fig. 3. Schematic model of burrowing modes in turrelpadids (A, C) and lepidocoleids (B, D) depicting the movement of the skeleton under two different models of peristaltic motion. A, B are based on the burrowing mode described in the earthworm *Lumbricus* (Gray & Lissman 1938), and C, D on the burrowing mode described for *Polyphysia* (Elder 1973).

The relief and asymmetry of the rugae in lepidocoleids typically are less pronounced than in the two other machaeridian families. However, the imbricated nature of the armour allowed the posterior margin of

the shell plates to function in a similar manner to the rugae in other machaeridians, although their spacing clearly did not correspond to the grain size of the sediment. The shell plates in some lepidocoleids bear

prominent denticles or spines (Fig. 2C) like those in some turrilepadids (Adrain *et al.* 1991) and plumulitids (Vinther *et al.* 2008). These structures, which form on the posterior facing margin of the juvenile shell, would also have increased purchase on the sediment. The plates in some lepidocoleids were attached dorsally by a tongue and groove hinge (Adrain 1992), and lateral expansion was presumably confined to the ventro-lateral regions for these hinged forms. Other lepidocoleids likewise appear to have had limited ability to separate the shells dorsally.

The shell plates in plumulitids were not inserted directly into the trunk integument, but attached by elytra-like structures with a narrow base as inferred from the soft bodied specimen of *Plumulites bengtsoni* (Vinther *et al.* 2008). This presumably also applied to the turrilepadids and lepidocoleids; their shell plates overlap extensively as in plumulitids allowing only a limited area of attachment to the body. A narrow attachment appears to have been necessary to allow shortening of the trunk; the plates could overlap until the anterior edge of one met the attachment of the plate overlapping it anteriorly. The notch situated centrally on the anterior margin of the inner plates of turrilepadids (Fig. 1C, arrowed) facilitated overlap during contraction of the longitudinal muscles. The plates of turrilepadids and some lepidocoleids overlapped dorsally which presumably allowed them to slide laterally during contraction of the circular and lateral muscles. The lower surface of each plate was lined by a layer of soft tissue evidenced by the decoupled secretion of mineral at the margin and at the base, which shows that there must have been mineral secreting tissue lining at least part of the lower surface. This underlying layer of soft tissue would have prevented sediment from invading the space between the body and shell plates.

We are aware of just one example of a machaeridian associated with a burrowing trace: a lepidocoleid (HS 735) from the Devonian Hunsrück Slate of Germany (Fig. 4). The trace is sinusoidal, but the wavelength is too long to be compatible with movement by flexure of the body. The wavelength of the lepidocoleid trace is about the same as the length of the fossil and does not indicate such a mode of locomotion. This lepidocoleid trace is probably an escape trace made by an animal buried in an unconsolidated turbidite with a different consistency to its normal environment. The trace shows that the animal could flex laterally to a significant degree. Other machaeridian trace fossils no doubt await discovery; the burrows of turrilepadids, for example, should have a squarish cross-section. The lepidocoleid trace would leave a dorsal groove and the ratcheting should also leave regular superimposed imprints.

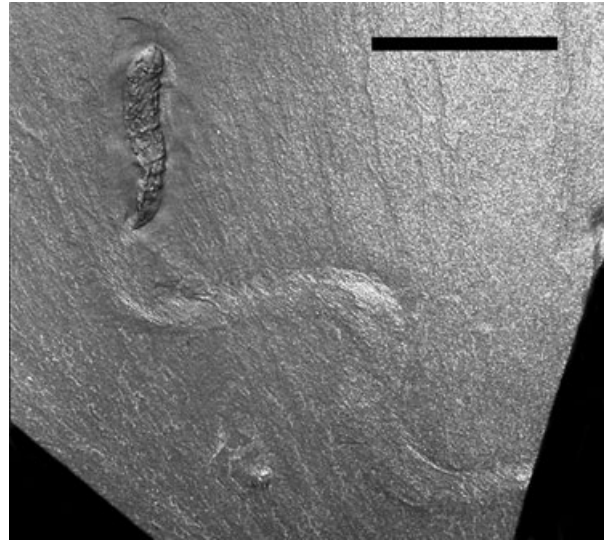


Fig. 4. Lepidocoleid (Deutsches Bergbau Museum, Bochum, HS 735) from the Devonian Hunsrück Slate associated with a burrowing trace. Scale bar 20 mm.

Machaeridian evolution

The oldest known annelids are Cambrian, the polychaete *Phragmochaeta canicularis* from the Early Cambrian Sirius Passet (Conway Morris & Peel 2008) and a diversity of polychaetes from the Middle Cambrian Burgess Shale (Conway Morris 1979). The morphology of these annelids indicates that they were epibenthic errant forms. A cladistic analysis (Eibye-Jacobsen 2004) suggested that they belong to the polychaete stem group indicating that the most basal annelids were epibenthic (Westheide 1997; Rouse & Pleijel 2001) in contrast to the traditional view that the segmented body plan of annelids evolved as an adaptation for burrowing (Fauchald 1974). The clitellates (earthworms, leeches), which were previously assumed to be basal, are probably derived and have lost polychaete characters such as nuchal organs and parapodia (Rouse & Pleijel 2007). It appears that many polychaetes became infaunal burrowers independently.

The oldest known machaeridians are Tremadocian in age (Kobayashi & Hamada 1976; Vinther *et al.* 2008). Plumulitids, which are known from the Upper Tremadoc of Morocco (Vinther *et al.* 2008), are considered to be the most basal or earliest diverging machaeridians (Dzik 1986, Herringshaw & Raine 2007), a position supported by phylogenetic analysis (Vinther *et al.* 2008). A turrilepadid outer shell plate has been recorded from older strata, in the Mid-Tremadoc of Scotland (Herringshaw & Raine 2007).

This fossil, which is poorly preserved as a silicified mould, is identified as a turrilepadid outer shell plate on the basis of five presumed inflections at the shell margin. Even if the affinities of this plate were confirmed by the discovery of additional material, this earlier stratigraphic occurrence does not outweigh other evidence that the epifaunal mode of life of plumulitids was primitive for machaeridians. Thus it is most likely that machaeridians gave rise to infaunal forms independently of other polychaetes. This functional transition is unique among annelids in that it involved the use of mineralized shell plates in burrowing, plates that were presumably retained even in infaunal forms as a protection from predators.

Adrain (1992) regarded the plumulitids and turrilepadids as sister families which he grouped in the order Turrilepadomorpha Pilsbry, 1916 due, in part, to their quadriseriate skeleton. He diagnosed lepidocoleids (order Lepidocoleomorpha Schallreuter, 1985) as biseriata. Dzik (1986) and Högström (1997), however, demonstrated that some lepidocoleids were quadriseriate. Turrilepadids and lepidocoleids share a number of characters, particularly in shell plate morphology: lateral compression, scars for muscle attachment and thicker shell plates. This suggests that these two families form a natural group, and that Turrilepadomorpha (Plumulitidae plus Turrilepadidae) should be abandoned.

Some of the features of plumulitids served as pre-adaptations to burrowing in more derived machaeridians: the asymmetric rugose ornamentation on the inner shell plates served as burrowing sculpture in turrilepadids, the overlapping shell plates attached by a narrow base allowed successive shortening and elongation of sections of the trunk and provided additional burrowing sculpture. The outer shell plates are displaced laterally in both turrilepadids and quadriseriate lepidocoleids relative to their position in plumulitids. This allowed much greater contraction of the body as the inner shell plates could overlap to a greater extent once the attachment of the intervening outer plates had migrated out of the way. This required a different orientation of the integumental extensions carrying the shell plates: while the attachment of the inner shell plates remained dorsolateral, that of the outer became lateral. The ability to contract reached an extreme in some lepidocoleids which lost the outer shell plates (becoming biseriata) leaving just inner shell plates on every other segment.

The discovery that machaeridians are polychaete annelids (Vinther *et al.* 2008) provides a template for interpreting how machaeridians used their skeleton and reveals a striking convergence with the molluscs. The plumulitids are similar to polyplacophoran molluscs (chitons) in being dorsoventrally flattened

with a passive dorsal armour of posteriorly overlapping dorsal plates. The evolution of a dorsal hinge in some lepidocoleids, which joins shell plates that enclose the body, recalls the bivalve body plan. Locomotion in machaeridians, however, was effected by parapodia or peristalsis in a mode characteristic of the hydrostatic skeleton in annelids while the precise mode varied in machaeridians with different morphologies.

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