Anatomy and relationships of the Early Cambrian worm *Myoscolex*

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Numerous fossil specimens of *Myoscolex ateles* Glaessner, 1979 from the late Early Cambrian Emu Bay shale of Kangaroo Island, South Australia with phosphatized organic matter-rich tissues show its muscular body wall penetrated by rows of rod-like structures — possible chaetae. The body wall was composed of an external layer with transverse (circular) fibres. This layer was thickest in lateral parts of the body and very thin dorsally. In the ventro-lateral quarter of the body circumference, a belt of longitudinal fibres extended along the body. Longitudinal fibres also occurred in the dorsal region of the body. Along the venter extended a narrow longitudinal belt of probably oblique cords, crossing themselves perpendicularly. In having a virtually smooth, laterally flattened body, *Myoscolex* closely resembles the slightly geologically younger *Pikaia* from the Burgess shale of British Columbia, generally believed to be one of the oldest chordates. Being the oldest probable annelid, at least superficially similar to the opheliid polychaetes, *Myoscolex* may appear not too distant from the ancestor of the phylum. The lateral body flattening of *Myoscolex* was apparently an adaptation to swimming by undulation of the body in transverse plane, similar to today's errant polychaetes but without using chaetae or appendages in propulsion.

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Introduction

An ancient geological age of an organism does not guarantee that its anatomy is primitive. However, this increases the probability that a fossil would show a morphological proximity to the ancestor of its clade. This is an unavoidable implication from the basic assumption of any phylogenetic inference: that there is a correspondence between time which passed since the divergence of lineages and their morphological difference. From this point of view the oldest known anatomically preserved worms of once proposed polychaete or echiurid affinities are of special importance, even if their systematic affiliations largely remain controversial. *Myoscolex ateles* Glaessner, 1979 from the late Early Cambrian Emu Bay shale of Kangaroo Island, South Australia is the most informative of them, owing to numerous specimens with phosphatized soft tissues (Glaessner 1979; Briggs & Nedin 1997; Nedin 1997).

The oldest fossils attributable to the Annelida are also important in the context of the recent progress in molecular phylogenetics. Some of the ideas forwarded by molecular biology pose a challenge to palaeontology as it is expected that the fossil record can potentially be used to test various phylogenetic trees based on molecular evidence. At least the fossil data should not be incompatible with those offered by the analysis of the genome. In the case of the high rank taxonomic groupings of animal phyla proposed on the basis of molecular evidence (e.g. De Rosa *et al.* 1999), the Deuterostomia and Ecdysozoa are well supported by the palaeontological evidence (the latter was in fact first inferred from fossils; Dzik & Krumbiegel 1989). To the contrary, the superphylum Lophotrochozoa to which the Annelida belong, remains controversial. Despite some physiological affinities, for instance the use of haemerythrin as an oxygen transport protein (van Holde 1998) or intermediate filament protein sequences (Erber *et al.* 1998), as well as support from embryology (Bartolomaeus 2001), the lophotrochozoan phyla are dramatically different from each other in their anatomies. There were attempts to connect phylogenetically brachiopods, molluscs, and polychaetes via the extinct Cambrian halkieriids (Conway Morris & Peel 1995), but this requires a series of transitional stages which have not yet been found in the fossil record. These controversies make any information on the anatomy of Cambrian annelids of crucial importance.

In the present paper, the anatomy of *Myoscolex*, the oldest putative annelid worm represented in the fossil record, is reconstructed and its evolutionary relationships are discussed.

Materials and methods

Myoscolex is an abundant fossil in the Big Gully fossil assemblage of the Emu Bay shale of Kangaroo Island, South Australia, with several hundred specimens having been collected from there. The rock is a dark fine-grained silty shale with mica flakes. Associated trilobites indicate a late Early Cambrian age (Briggs & Nedin 1997).

The specimens of *Myoscolex* are phosphatized, the phosphate-replaced tissues being especially thick in the middle length of the body. A pink fibrous calcite layer usually developed above the phosphatized tissues marks the surface of the late diagenetic split of the rock laminae. Virtually all specimens are flattened laterally, with the margin without appendages being more convex (Nedin 1997; Briggs & Nedin 1997).

Much of this study was carried out on specimens collected by Martin Glaessner and housed in the South Australian Museum, Adelaide, and specimens of the collection assembled by Christopher Nedin in the Department of Geology and Geophysics of the University of Adelaide. More precise mechanical and chemical preparation has been performed on specimens which have been obtained by the Institute of Palaeobiology of the Polish Academy of Sciences (ZPAL) on the basis of scientific exchange with these institutions. A rock slab that appeared to be crowded with *Myoscolex* phosphatized bodies was split to expose additional specimens. All these specimens were photographed with low angle light and under ethanol, and an Olympus microscope drawing apparatus was used to make drawings.

Part of specimen ZPAL A 6/1 represents phosphatized tissues of the middle part of the body flattened almost precisely laterally (Fig. 1). Its counterpart (Fig. 2) is mostly an external imprint with pieces of phosphatic tissue exfoliated from elevated areas and rods. In some areas the phosphatic tissue was covered by sediment. By removing it with a sharp needle and cleaning the surface with dilute formic acid, details of the external surface of the body were exposed. This is the most informative of the specimens studied.

Specimen ZPAL A 6/2 is an incomplete body slightly twisted while flattened with the venter being covered in its presumably anterior part and exposed in the posterior part (Fig. 3). It was covered with calcite which was removed with a needle and formic acid to expose the surface. It appears to have been partially split before the calcite developed, with the split coming very close to the surface near the venter (some rods are cut along their length), going slightly deeper in lateral and dorsal areas where it crosses the central cavity of the body. In a few places the phosphatized body wall tissues were removed completely to show the other side of the specimen and to expose rods imbedded in the sediment. A much more fragmentary specimen, ZPAL A 6/4, was preserved in a similar way (Fig. 4D,F).

The only dorsally flattened specimen among the material newly described here is ZPAL A 6/3. Although rather poorly preserved, it shows some remnants of phosphatized tissues of the venter and imprints of the rest of the body with ventral and lateral rows of rods in the pink fibrous calcite layer below (Fig. 4A,C). In the anterior-most part of the body, the calcite cover delineates a parabolic outline of a probable head structure, which posteriorly goes a little above the level of the trunk.

To enable a scanning electron microscope study of the internal structure, a piece of a ventral chaeta was removed from specimen ZPAL A 6/1, embedded in plastic, polished and etched in 0.5% phosphoric acid for 15 min.

Description of preserved anatomical structures

Specimens of *Myoscolex* from the Big Gully fossil assemblage of Emu Bay shale show surprisingly stable modes of preservation, with the same set of internal structures being preserved in virtually all known specimens. Thus, the phosphatized body wall layer shows transverse wrinkles at its surface, closely resembling those in recent polychaetes or onychophorans. No stiff cuticle was present. The wrinkles apparently reproduce a fibrous internal organization of the exterior-most body wall layer. The fibres were strictly circular in their arrangement. This can be seen in any specimen with the external surface of the body exposed well enough. Body segmentation is expressed only in the distribution of serial appendages, otherwise the body surface is rather uniform. The wall is penetrated with three series of rod-like structures along both sides of the body. The rods were originally strongly sclerotized. The most prominent rods are attached somewhat above the body axis pointing ventrally. Because the rod-like structures were apparently secreted within the soft tissue and their morphology conforms to annelidan chaetae, they are here referred to as such. Oval bodies located in proximity to their ventral ends may be of a similar nature. Two rows of short ventral chaetae emerge from the body along both sides of a narrow ventral belt, the surface of which is irregularly tuberculated (Briggs & Nedin 1997). In specimens split along deeper layers of the phosphatized tissue of the body wall, longitudinal bands with wrinkles parallel to the body axis emerge. Close to the ventral margin of the thin dorsal longitudinally fibrous belt, a series of oval structures with tubular prolongations can be seen in at least some specimens. All these structures are described below in some detail.

Circular fibres

The original body surface (or at least the surface of its phosphatized wall) is well represented in the ventro-lateral part of specimen ZPAL A 6/1a, where it was preserved intact under soft sediment (Fig. 1). It is finely wrinkled and striated, with the striation being somewhat irregular in its course. No doubt this corresponds to the fibrous nature of the wall. The

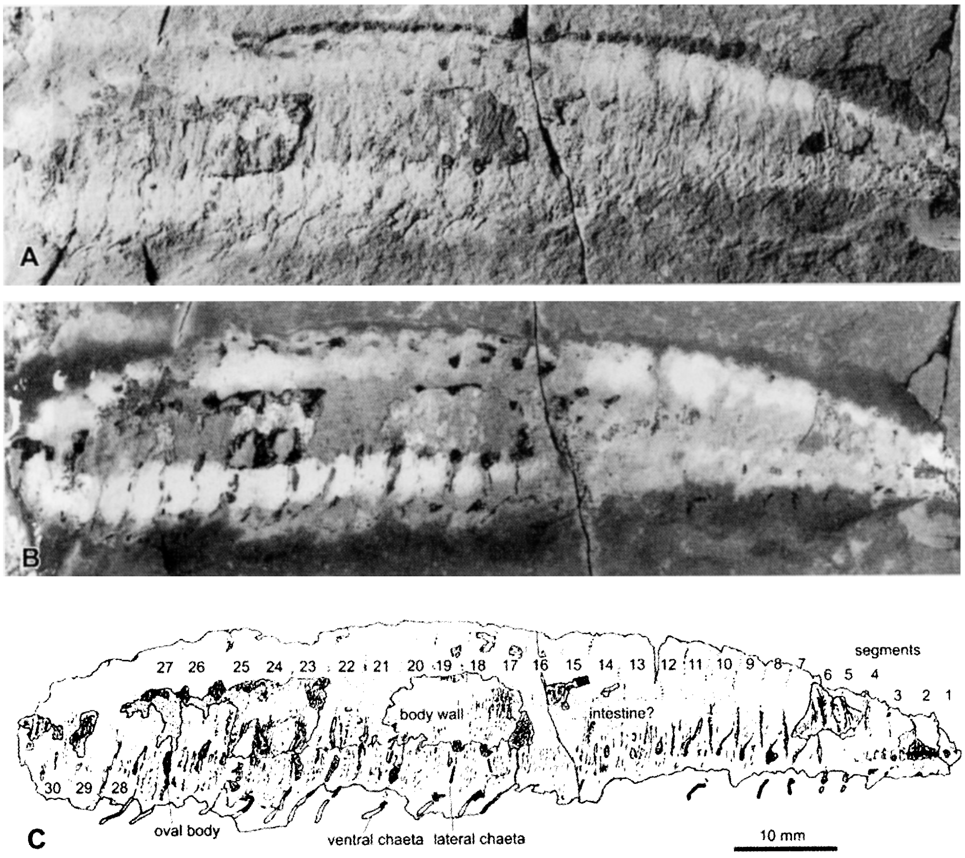

Fig. 1 A–C. *Myoscolex ateles* Glaessner, 1979 from the late Early Cambrian Emu Bay shale of Kangaroo Island, South Australia; laterally compressed specimen ZPAL A 6/1a (part). —A. A low angle light photograph. —B. The specimen submerged in alcohol. —C. An interpretative sketch made with a microscope drawing apparatus using high angle light. Note that the body surface is preserved in the ventro-lateral part of the specimen. All × 2.

fibres were rich in organic matter as they very efficiently worked as nucleation centres for calcium phosphate. Whether these were muscles, as proposed by Briggs & Nedin (1997), or collagenous cords, is more difficult to decide, but this does not matter so much as collagenous fibres had to develop in connection with muscles. The body wall was thus muscularized, with a circular arrangement of muscle fibres.

Some of the more prominent wrinkles show a V-shaped arrangement, merging at ridges where the lateral chaetae are attached. This may be an effect of contraction of muscle fibres operating some organs connected with the chaetae. However, there are no direct signs of the muscles being arranged in discrete sets which could operate appendages.

The wrinkles are most prominent in lateral and ventrolateral parts of the body, and less discernible in its dorsal part. Near the venter, the body wall with circular muscles is delimited by a straight margin, as shown well by specimen ZPAL A 6/2, with the ventral band being of a different structure.

Longitudinal fibrous bands

When exfoliated, for instance in specimen ZPAL A 6/2, the circular layer exposes another layer in the ventro-lateral part

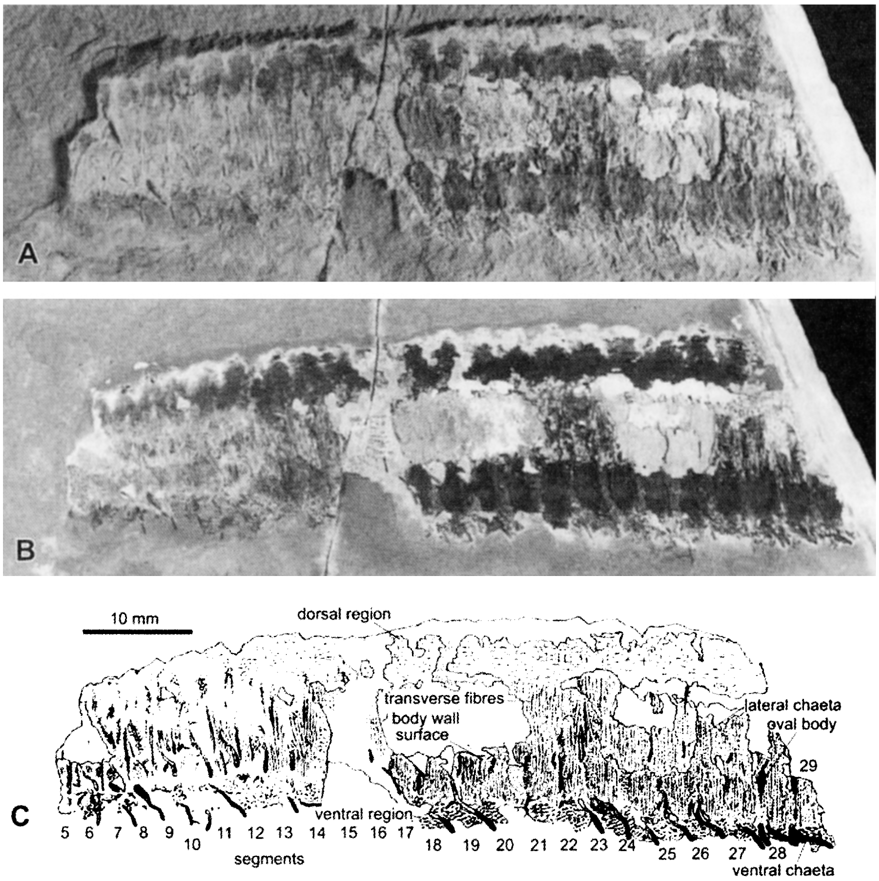

Fig. 2 A–C. *Myoscolex ateles* Glaessner, 1979 from the late Early Cambrian Emu Bay shale of Kangaroo Island, South Australia; specimen ZPAL A 6/1b (counterpart). —A. A low angle light photograph. —B. The specimen submerged in alcohol. —C. An interpretative sketch made with a microscope drawing apparatus using high angle light. Note the stain in the axial part of the body possibly caused by the intestinal content. All × 2.

of the body, with longitudinal wrinkles (Fig. 3). The dorsal margin of this layer is rather clearly demarcated and it does not seem to extend above the middle lateral line of the body. There were thus discrete ventro-lateral bands of longitudinal muscles.

Longitudinal wrinkles, although less apparent, also emerge in the dorsal part of the body; in places they form a network together with equally weak transverse wrinkles.

Ventral band

In some, but not too many, specimens, a rather narrow ventral belt represented by tubercle-like protuberances, irregularly distributed or in oblique rows, is exposed. These are not sclerites, but rather an expression of a somewhat more robust and irregular internal organization of the body wall in this area. The tubercles were nicely illustrated by Briggs & Nedin (1997: fig. 8:6) and are well represented in specimen ZPAL A

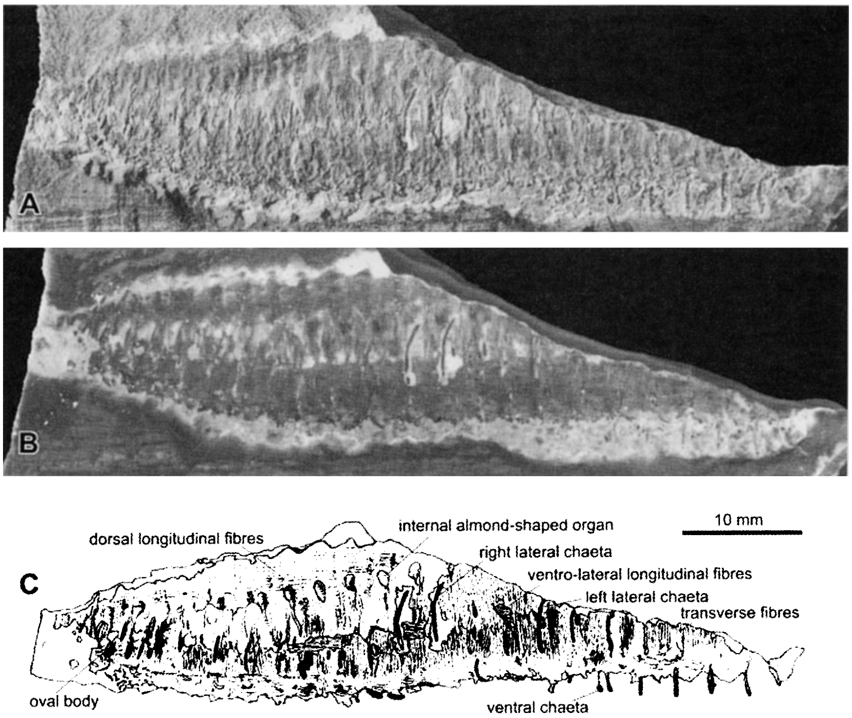

Fig. 3 A–C. *Myoscolex ateles* Glaessner, 1979 from the late Early Cambrian Emu Bay shale of Kangaroo Island, South Australia; slightly twisted along the axis, laterally compressed specimen ZPAL A 6/2. —A. A low angle light photograph. —B. The specimen submerged in alcohol. —C. An interpretative sketch made with a microscope drawing apparatus using high angle light. Note the almost complete lateral chaetae of the right side imbedded in the sediment, exposed by removing part of the phosphatized body covers, and the belt of longitudinal fibres visible partially under an exfoliated external layer with transverse fibres. Oval bodies attached to the surface of the body wall show great variability in size in this specimen. All × 2.

6/1a (Fig. 2). They seem to reproduce more or less oblique (perhaps longitudinal) cords and cords transverse to them. The exact arrangement of structures is unclear and difficult to trace. The boundary of this belt is clear-cut and the circular fibres of the lateral parts of the body do not pass this boundary. The ventral chaetae seem to penetrate the body cover at this boundary.

It thus appears that the muscular body wall of *Myoscolex* was composed of a layer with transverse (circular) fibres. This layer was thickest in lateral parts of the body and probably very thin dorsally. In the ventro-lateral quarter of the body circumference, a belt of longitudinal fibres extended along the body. Longitudinal fibres were also developed in the dorsal region of the body. Along the venter extended a narrow longitudinal belt with thicker probably oblique cords, crossing themselves perpendicularly (Fig. 5G).

Ventral chaetae

A series of ventral rod-like phosphatized structures emerges from the body wall at the boundary between the ventral 'tuberculated' belt and the ventro-lateral zone of longitudinal fibres. They are discernible in virtually all studied specimens, usually orientated oblique to the body axis, posteriorly directed (Fig. 2). They are usually sinuous in appearance, although in the presumably posterior part of specimen ZPAL A 6/2 they are straight (Fig. 3). The sinuosity was thus apparently in one plane. They seem to increase in length posteriorly. Because of their shape and basal imbedding in the body

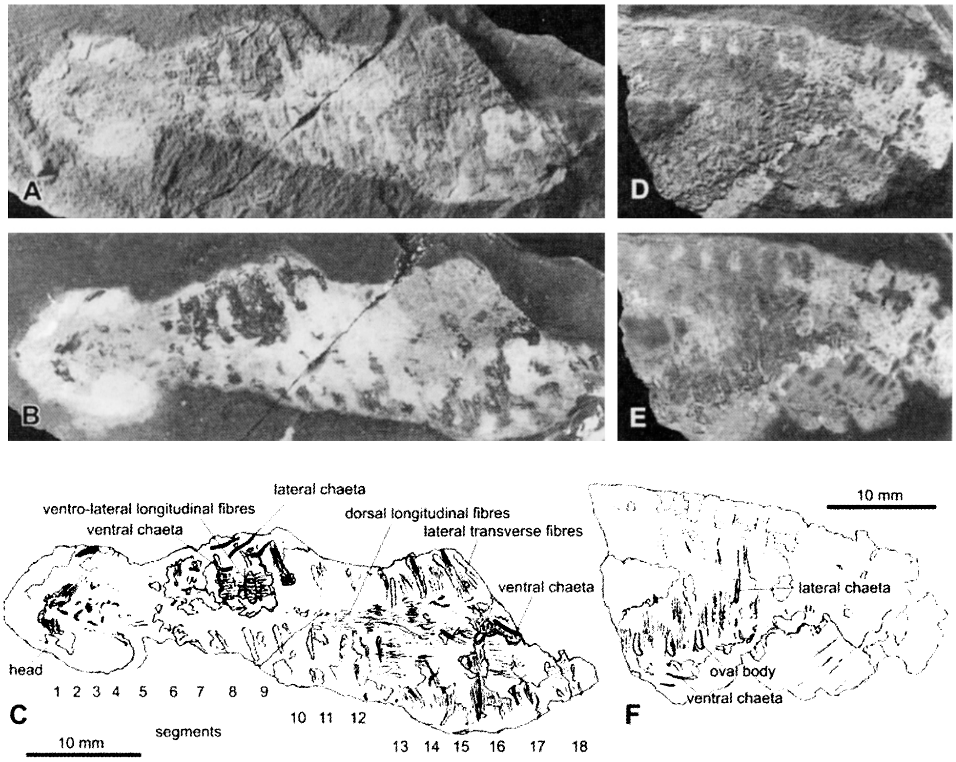

Fig. 4 A–F. *Myoscolex ateles* Glaessner, 1979 from the late Early Cambrian Emu Bay shale of Kangaroo Island, South Australia; dorso-ventrally compressed specimen ZPAL A 6/3 (A–C) and laterally compressed fragmentary specimen ZPAL A 6/4 (D–F). —A, D. Low angle light photographs. —B, E. Specimens submerged in alcohol. —C, F. Interpretative sketches made with a microscope drawing apparatus using high angle light. Note the outline of the head in specimen ZPAL A 6/3 and the well-represented oval bodies in specimen ZPAL A 6/4. All × 2.

tissue, these structures are tentatively referred to as chaetae, following Glaessner (1979), although this remains a rather weakly supported interpretation.

Both ends of the ventral chaetae are blunt. Quite commonly the chaetae show narrowings, giving them a sausage-like appearance (Fig. 5E). This is probably, at least partially, an effect of secondary phosphatization. The end imbedded in soft tissues of the body bulged when collapsed (for instance that on segment 8 in specimen ZPAL A 6/1a; Figs 1, 5E) which suggests that its interior was hollow before phosphatization. This seems to represent the basal portion of the chaeta penetrated with microvilli. In the Recent polychaete *Aphrodite*, the chaetae with a diameter similar to those of *Myoscolex* are filled with microvilli for 2 mm and this part of the chaeta collapses when desiccating. A possibility that this was a kind of bladder originally filled with a secretion cannot be excluded. The latter is suggested by the similarity in size and shape to the lateral almond-like organs (see Fig. 5C,E).

A piece of ventral chaeta was removed to study under the scanning electron microscope, but etching of polished surfaces did not reveal any internal structure, which may not be discernible even in chaetae of recent polychaetes (e.g. Gardiner 1992: fig. 41).

Lateral chaetae

These are elongated strongly phosphatized rods with their ventral ends parabolically blunt and flattened. They had to be rather compact and rich in organic matter to promote such strong phosphatization. Although no internal structure is visible and the calcium phosphate seems homogeneous there,

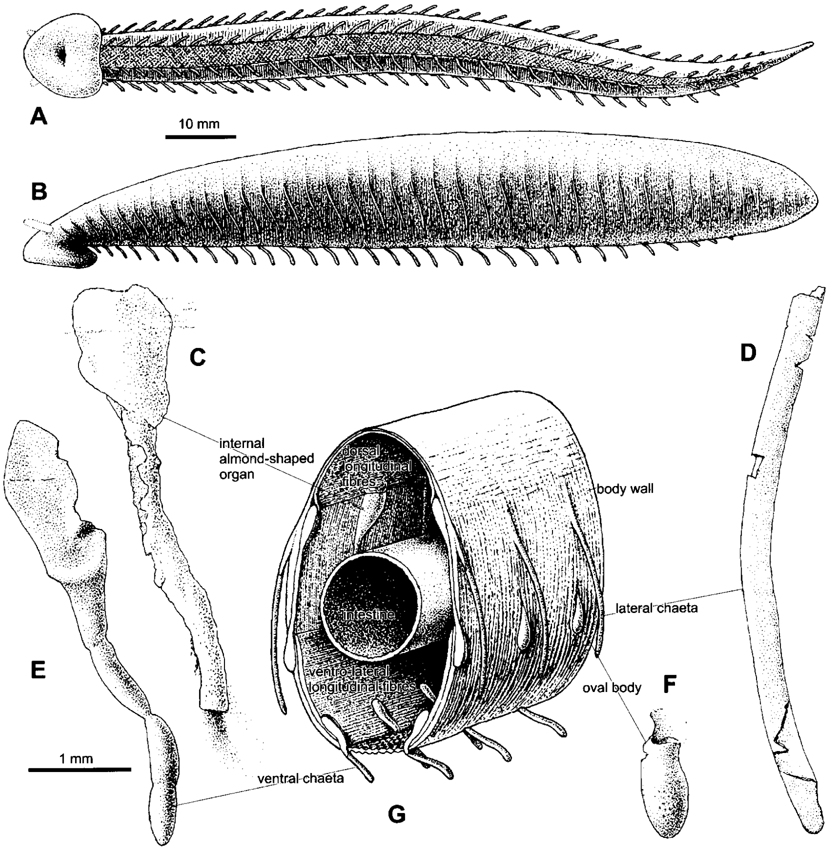

Fig. 5 *Myoscolex ateles* Glaessner, 1979 and internal anatomy based on phosphatized specimens from the late Early Cambrian Emu Bay shale of Kangaroo Island, South Australia. —A, B. Restoration of the external body shape in ventral and left lateral views. —C, D, F. An almond-shaped organ, lateral chaeta and oval organ from specimen ZPAL A 6/2. —E. A ventral chaeta with collapsed proximal part from specimen ZPAL A 6/1. —G. Restoration of a section of the body showing the proposed position of these organs relative to transverse and longitudinal muscle layers in the body wall; diameter of the intestine conjectural.

their homology with annelid chaetae is likely. They emerge from the body wall dorso-laterally and reach in length about a quarter of the body circumference, running almost parallel to its surface, as shown by specimens ZPAL A 6/2 (Fig. 3). In the anterior part of specimen ZPAL A 6/1 (Figs 1, 2), the chaetae are oblique to the segmental boundaries, pointing postero-ventrally. A similar arrangement can be observed in the dorso-ventrally compressed specimen ZPAL A 6/3 (Fig. 4A–C). There the lateral chaetae also generally remain parallel to the body segment boundaries, but in its anterior part some of them are displaced to be almost perpendicular to the segments. In contrast to the former specimen, they point anterior-ward. This suggests that they were rather firmly attached to the body cover along their basal parts but the rest of the chaeta was free.

Lateral oval bodies

These are heavily phosphatized oval structures with a strongly convex external surface and a flattened base which seems to be firmly attached to the body wall. When exfoliated, they leave a smooth shallow impression in the body wall. The external surface is not smooth but with minute depressions, as if punctured with a needle (Fig. 5F). Their size is very variable. In specimen ZPAL A 6/4 they are unusually large, 2.5 mm in dorso-ventral diameter. In specimen ZPAL A 6/4, they show at least three series with the diameter increasing posterior-ward in each of them (Fig. 3), ranging from less than 0.3 mm to 1.5 mm. This may suggest that their content was periodically released.

Dorso-lateral almond-like bodies

In many specimens, series of indistinct elevations are developed near the dorsal area. Specimen ZPAL A 6/2 shows that these are almond-shaped bodies attached to the interior surface of the body wall (Figs 3, 5C). They seem to be partially covered by the dorsal longitudinally striated layer of the body wall, thus inserted between the circular and longitudinal muscular layers (Fig. 5G). Some of them are more elevated, others almost indistinct, which suggests that some were filled with a content while others were empty. In a few of them, the lower, pointed end extends into an indistinct canal. The canal itself continues up to the dorsal margin of the ventro-lateral longitudinal muscle belts. The ends of the canals cannot be precisely traced, but approximately at this level the dorsal margins of the lateral oval organs are located. It is possible that the canals penetrate the body to join the oval organs. If a secretion of the almond-like organs is transferred to the oval bodies via the canals, this would explain the variable shape and size of both of them. The proposedly contractile almond-like organs would have muscular walls thick enough to promote phosphatization but not so dense as the chaetae and oval organs. An alternative, suggested by the similarity to the ventral chaetae (see Fig. 5C,E), is that these are modified chaetae. Being deeply imbedded in the body wall they are unlikely to represent any external appendages.

Head lobe

Very rarely, indistinct traces of some organs at the ends of the body are discernible. In specimen ZPAL A 6/3, the pink calcite cover delimits a parabolically outlined terminal structure (Fig. 4A–C). In places, remnants of phosphatized tissue are preserved with wrinkles oblique to the axis and curved posterior-ward marginally. The outlined structure seems to reflect a true body structure. Its proximal (apparently posterior) margin is elevated in respect to the body axis.

There are some difficulties with determining the relationships of particular layers in this fossil. In its central part there is a field of relatively well-preserved phosphatized body wall which shows two separate layers. The facing layer is covered with lateral chaetae and a few fragmentary ventral chaetae closer to the body axis. This was thus the ventral surface of the body, whereas the deeper layer represents the dorsum. This means that the parabolic terminal structure was posteriorly located more above the venter than anteriorly.

Similar structures were earlier identified as eye remnants by Briggs & Nedin (1997). In the part of specimen AUGD 1046–611 they referred to, the lobe has a very indistinct margin. The counterpart, 611b, also examined by myself, shows phosphatized chaetae only on its right side, so the specimen was apparently laterally compressed. Chaetae are orientated at an angle to the axis, towards the tip of the body. Specimen AUGD 1046–6646b is much more informative, although it also shows chaetae only along one margin, where they are arranged parallel to the body axis. As the body in this case also appears to be laterally compressed, the 'head' itself may be somewhat twisted to be compressed in an oblique dorso-ventral direction. The lobe is broken in the middle but originally it was probably of parabolic outline, as in specimen ZPAL A 6/3. Posteriorly, the lobe penetrates the sediment to a level a little below the rest of the body. Possibly, the two narrow structures interpreted as the right eye by Briggs & Nedin (1997) may represent a pair of tentacles.

The evidence thus seems consistent with the idea that in these few specimens of *Myoscolex* there are remnants of an organ which shows a parabolic outline and was somewhat oblique to the frontal plane of the animal. This suggests that it was a kind of cephalic lobe, everted pharynx, or even a sucker (Fig. 5A,B). The radically different interpretation that this is a pygidial structure cannot be excluded but seems less likely — in early animals it was the head that differentiated structurally first.

Intestine

No truly internal organs are structurally preserved in the studied material of *Myoscolex*. However, there is some indirect evidence suggesting that in the centre of the body there was a voluminous, cylindrical gut. Namely, in some specimens which are split between the left and right halves of the collapsed body wall, among others ZPAL A 6/1, the central zone of the fossil, one third of its total width, behaves differently than the remaining dorsal and ventral parts. The left and right walls separate there easily and the phosphatized tissue differs in coloration (Figs 1, 2). The space between the walls is stained red with oxidized iron minerals. This may reflect the presence of additional internal fill at the time of early diagenesis. Most likely this was the gut with its content.

Body shape

Virtually all of the several hundred specimens of *Myoscolex* are preserved laterally compressed, with just a few being dorso-ventrally compressed (Briggs & Nedin 1997), in some cases the body wall possibly split along the venter (e.g. Briggs & Nedin 1997: fig. 4.4). The original body compression was thus certainly lateral. Most surprisingly, the width of the dorso-ventrally compressed specimen ZPAL A 6/3 (Fig. 4A–C) is the same as the laterally compressed specimens (compare segment 16 with that in specimen ZPAL A 6/1; Fig. 2A–C). This means that the body wall deflation was prediagenetic and that its shape was not controlled by any resistant mesenteria or similar internal structures. A question thus emerges: what kept the body flat if the pressure of internal fluids tended to make it cylindrical? One may speculate that there were internal transverse muscles, similar to those in chaetognaths (see Bone & Duvert 1991: fig. 4.9A) which were strong enough to keep the lateral sides of the body in proximity, but did not provide enough organic matter to enable their phosphatization. The thick, double-layered ventro-lateral zone and thin wall at the dorsum may have also contributed to the flattening.

The body contour of *Myoscolex* was fusiform but seems to narrow more strongly posteriorly. The posterior end of the body is never well preserved, and only a couple of specimens reviewed above show the anterior end with recognizable head structures (Briggs & Nedin 1997). This means that the musculature was best developed in the middle length of the body, the end interpreted as posterior being possibly compressed into a kind of fin.

Anatomical interpretation of the fossils

Briggs & Nedin (1997) proposed that specimens of *Myoscolex* represent the muscular trunk of an arthropod related to the derived anomalocaridid *Opabinia*. The main foundation for this claim was the morphology of specimen AUGD 932–239a. Indistinct impressions, probably representing gill-like appendages, are visible along the convex side of the body; this side thus being apparently ventral. This contrasts with invariable ventral-ward curvature of virtually all specimens of *Myoscolex*. Unlike all specimens undoubtedly belonging to *Myoscolex*, this specimen shows clear segmental boundaries. Most importantly, no rods have been found in association with it, as admitted by Briggs & Nedin (1997). The specimen thus lacks the specific characters of *Myoscolex*. Most probably, this is truly an anomalocaridid, as proposed by Briggs & Nedin (1997), but with no relationship to *Myoscolex*.

To support the idea of a relationship to *Opabinia*, Briggs & Nedin (1997) also used an alleged proboscis in specimen AUGD 1046–756 (part and counterpart). However, the base of the structure interpreted as a proboscis is on a different level from the rest of the body and may not be directly connected with it. It seems to be composed of two separate bands of pink calcite. They are of a rather indifferent morphology and it cannot be excluded that this is a pair of trilobite carapace pleurae or a fragmented *Myoscolex* specimen. Whatever the case, the structure is not specific enough to contradict or support any affinities of *Myoscolex*. The identification of eyes by Briggs & Nedin (1997) was based on the structureless staining which above is interpreted as representing an incomplete cephalic lobe.

The body wall of *Myoscolex* was obviously strongly muscular but without any apparent internal compartmentalization into segments. This implies that the body interior was filled with a fluid which worked as a hydraulic device, stiffening the body. The natural shape of animals with such a body plan is cylindrical, with a round cross-section, as pointed out above. Thus, a question immediately emerges how the lateral body compression was achieved in the evolution of *Myoscolex* and for what. Any anatomical interpretation of *Myoscolex* must include its lateral compression of the body and the presence of paired ventral and lateral rods. Such a derived anatomy in the Early Cambrian is a surprise. However, it had to develop from something less complex and less advanced. No recent or fossil organisms known to me show such a combination of characters. Comparison with *Opabinia*, proposed by Briggs & Nedin (1997), is hardly helpful. Instead, some Cambrian fossil worms and problematic animals may offer insight into the problem of the phylogenetic relationships of *Myoscolex*.

The ventro-dorsal differentiation of the body and its lateral compression seem to be the basic aspects of the body plan which constrain the search for relatives.

Possible fossil relatives of *Myoscolex*

The presumably primitive aspects of the anatomy of *Myoscolex*, represented in the structure of its body wall and intestine, make it somewhat similar to the nemathelminthan worms, very diverse in the Cambrian seas (Conway Morris 1977; Sun & Hou 1987; Hou & Bergström 1994). The apparently derived feature is its body shape, which makes *Myoscolex* at least analogous to the chordates. These two phyla are extremely distant to each other, so the lines of reasoning leading to them are obviously contradictory. Below they are discussed using the scarce evidence on fossils of early worm-like organisms.

Cambrian worms with differentiated venter

Atalotaenia from the Early Cambrian Kinzers Formation of Pennsylvania had an annulated elongated body with a narrow 'ribbon' along the venter (Garcia-Bellido Capdevila & Conway Morris 1999). The ribbon shows transverse wrinkles resembling those on the lateral sides of the body of *Myoscolex*. The only known specimen is coiled, which makes it similar in appearance to palaeoscolecid worms (Garcia-Bellido Capdevila & Conway Morris 1999). It is unlikely that the body was not round in cross-section and no appendages are preserved. Other Cambrian nemathelminthan worms with a differentiated venter were undoubted priapulids with a well-developed proboscis, armed with hooks (Conway Morris 1977; Sun & Hou 1987; Hou & Bergström 1994).

Cambrian animals with laterally compressed bodies

Yunnanozoon is the best known early chordate, owing to hundreds of excellently preserved specimens from the Early Cambrian Chengjiang fauna of China [Chen *et al.* 1995, 1999; Dzik 1995; for a different interpretation of it and related forms from the same fauna see Shu *et al.* (1996a, 1999)]. The general shape and compression of the body of *Yunnanozoon* are similar to *Myoscolex*, but this seems to complete the list of similarities. The dorsal fusiform body unit of *Yunnanozoon* was probably strongly muscular, like the muscular body wall of *Myoscolex*, but it is clearly segmented (probably internally compartmentalized into chambers; Dzik 1995). The transverse lateral structures interpreted as chaetae in *Myoscolex* remotely resemble branchial arches of *Yunnanozoon* in their serial arrangement, but their location at the surface of the muscular body wall makes their correspondence to branchial slits completely unlikely. The lateral oval bodies of *Myoscolex* are a little similar to the gonads of *Yunnanozoon* but serial gonads or other organs occur widely in completely unrelated organisms. At the present state of knowledge of these organisms, any direct relationship of *Myoscolex* to *Yunnanozoon* has thus to be excluded.

More meaningful may be the similarity of *Myoscolex* to the alleged chordate *Pikaia gracilens* Walcott, 1911 from the Middle Cambrian Burgess shale of Canada. Originally it was attributed to the Annelida by Walcott (1911), based on the presence of a pair of sensory tentacles on the head and a series of short appendages along its presumably ventral margin at least in the anterior part of the body (Walcott 1911; Conway Morris & Whittington 1979; Conway Morris 1985, 1998: 104; Shu *et al.* 1996b). Its interpretation as a chordate by Conway Morris (1979b) was based on the lateral compression of the body with a wider caudal end, the presence of transverse muscular bands, and a non-segmented belt above them (interpreted as the notochord) — all features also present in *Myoscolex*.

As the body plan of *Yunnanozoon* is incomparable with that of *Pikaia* they cannot belong to the same phylum. Admittedly, any interpretation of *Pikaia* suffers from poor knowledge of this organism, which is still awaiting detailed palaeontological study and description. Not consistent with the chordate interpretation of *Pikaia* is the presence of two sensory tentacles and a series of ventral appendages, too numerous to represent amphioxus-like oral tentacles. The tentacles are shared by *Pikaia* with the Burgess shale polychaetes, whereas the appendages, although apparently not sclerotized, are comparable in their shape and distribution with the proposed ventral chaetae of *Myoscolex*. Butterfield (1990: 282) pointed out that the fossil specimens of *Pikaia* are preserved in a way suggestive of the presence of a thick cuticle-like body cover. A possibility emerges that the transverse bands correspond to the serial arrangement of superficial structures in the ventro-lateral part of the body wall of *Myoscolex*, whereas the alleged dorsally located notochord corresponds to the thin dorsal region with longitudinal muscles.

In fact, there is little evidence for chordate affinities of *Pikaia*. Its relationship with *Myoscolex* appears a much better solution. Both were initially identified as polychaetes and this line of inference perhaps deserves confrontation with more recent evidence than that available to the authors who proposed these genera.

Zoological relationships of *Myoscolex*

The main aspects of organization of the muscular body wall of *Myoscolex* do not seem specific enough to help in taxonomic affiliation of the organism. Two sets of longitudinal muscle blocks, two located ventro-laterally and two dorsally, can be found in such dissimilar invertebrates as polychaetes (e.g. Gardiner 1992: figs 1, 2) and chaetognaths (e.g. Bone & Duvert 1991; fig. 4.9). The clear dorso-ventral differentiation of the body of *Myoscolex*, the presence of two lateral rows of possible chaetae imbedded proximally into the body wall, probably a wide central intestine, and possible peri-oral lobes, may help in its more specific taxonomic affiliation. They seem to fit the annelid body plan, with only one chaeta represented in each branch of the parapodium.

Alleged echiurid affinities of Myoscolex

Because of the distribution and robustness of chaetae in *Myoscolex*, Glaessner (1979) proposed its relationship to echiurids, but the lateral body flattening, together with the lack of structural similarity between rods and chaetae or aciculae, was used by Conway Morris (1979a) and Briggs & Nedin (1997) to question both echiurid and polychaete affinities.

The unsegmented echiurids are derived annelids (McHugh 1997, 2000; Purschke *et al.* 2000) and the anatomy of *Myoscolex*, if assumed to be echiurid, would appear even more derived, which does not seem consistent with its geologically early age. Aciculae, to which the rods of *Myoscolex* are similar, 'are formed in exactly the same manner as the projecting chaetae; they differ in that much or all of the chaeta remains internalised' (Fauchald & Rouse 1997: 87). These are apparently derived structures (Rouse & Fauchald 1997; Bartolomaeus 1998); the known Cambrian polychaetes did not have aciculae (Conway Morris 1979a), and it seems unlikely that the phosphatized rods of *Myoscolex* correspond to aciculae.

Possible affinities of Myoscolex *to opheliid polychaetes*

The polychaete affinities of *Myoscolex* have been made more specific by Wills (1993), who classified it in the family Opheliidae. The opheliids are similar to *Myoscolex* in having fusiform bodies without any head appendages and bearing only minute parapodia. These polychaetes burrow head downwards in sand or mud and usually a deep ventral groove brings down respiratory current which then escapes along the lateral grooves with gills (Day 1967). The gills are composed of single filaments and closely resemble in shape and size the structures in *Myoscolex* here interpreted as chaetae (it is unlikely for gills to be so heavily phosphatized, however). The simple capillary chaetae of the Opheliidae are arranged in fan-shaped bundles and no comparable structures are preserved in fossils of *Myoscolex*.

According to recent phylogenetic interpretations, the Opheliidae are members of the clade Scolecida, which is deeply rooted in the annelid phylogeny (Fauchald & Rouse 1997; Rouse & Fauchald 1998). Their similarities to *Myoscolex* may thus truly be primitive (plesiomorphic), although some interpretations of the phylogeny of Opheliidae (Bellan *et al.* 1990) place genera with prominent parapodia close to the roots of the family. However, the lateral flattening of the body (without any apparent furrows) and rows of robust chaetae (instead of bunches) in *Myoscolex* are the main differences in its body plan in respect to the Opheliidae.

Early polychaetes in the fossil record

There is no evidence for the presence of annelids in the Precambrian and recent findings of extraordinarily preserved segmented Ediacaran metazoans show that their anatomy is different from annelids [reviewed in Dzik (2002)]. No convincing polychaete fossil is known from the extremely abundant Early Cambrian fauna of Chengjiang, China. Only the Middle Cambrian Burgess shale fauna offers a few species of vagile polychaetes with parapodia armed with numerous chaetae but lacking jaws or aciculae (Conway Morris 1979a). Polychaete affinities have also been proposed by Butterfield (1990, 1994) for *Wiwaxia* of the Burgess shale, based on the similarity of its scales to chaetae of the co-occurring polychaete *Canadia* and *Burgessochaeta*, and some recent polychaetes.

Aciculate polychaetes are known at least from the Early Ordovician. The evolutionary diversification of eunicid polychaetes is well documented by their fossilized jaw apparatuses beginning from the Ordovician (Kielan-Jaworowska 1966). In the Early Devonian Hunsrück slate of Germany, typical vagile polychaetes with aciculae are represented (Bartels & Blind 1995), the oldest pelagic form documented with fossils being *Eotomopteris* from the Early Carboniferous of Scotland (Briggs & Clarkson 1987). In fact, by the Carboniferous, most of the vagile polychaete groups seem to be represented in the fossil record (Schram 1979; Thompson 1979).

The fossil records of infaunal and sessile polychaetes are quite different. Most of the Palaeozoic fossils with oligochaete aspects, preserved well enough to be identifiable, have appeared to be palaeoscolecids. The calcareous tubes from the Palaeozoic and Triassic commonly attributed to sedentary polychaetes represent extinct organisms of probably lophophorate affinities (Dzik 1991; Weedon 1994); the true serpulids are documented from the Jurassic onwards, spirorbids being unknown before the Cretaceous. Organic or agglutinated tubes are usually not specific enough to determine affinities of their builders, but their phylogenetically late origin was inferred by Bartolomaeus (1998: fig. 8).

This suggests that the infaunal and sessile polychaetes diversified much later than the vagile forms. The latter are thus closer to the ancestral annelids, as proposed on a different basis by Westheide (1997). The hypothesis on the origins of polychaetes, depicting the last common ancestor of recent annelids as errant and epibenthic, appears more consistent with the fossil evidence than those implying their oligochaetoid or meiobenthic adaptations (e.g. Giangrande & Gambi 1998).

In any case, the lack of prominent parapodia in *Myoscolex* does not need to be secondary. *Myoscolex* is the oldest known annelid and there is no direct or indirect evidence that anatomically more complex annelids preceded it. The geologically younger *Pikaia*, with its even more chordate-like body appearance and lacking strongly sclerotized chaetae, may represent a further step in improving locomotion by lateral undulations of the body.

Conclusions

In having a virtually smooth, laterally flattened body, *Myoscolex* resembles the Middle Cambrian *Pikaia* and may be related to it. Laterally compressed bodies used to swim by undulation are extremely rare among primitive metazoans. In the form characteristic of *Myoscolex* and *Pikaia* they are, in fact, otherwise exclusive to chordates. Yet, *Myoscolex* cannot be a chordate because of its fundamentally different body plan with a muscular body wall not showing any subdivision into myomeres and encapsulating virtually all internal organs. The vagile polychaete body plan and their way of propulsion seem closer, although usually prominent parapodia and numerous chaetae are also involved in their swimming (Clark & Tritton 1970). Judging from their fossil record, this is an ancient trait of the annelids. This may even be their first distinction from the lobopodian–arthropod lineage, where synchronous contraction of appendages on both sides of the body is the original mode of locomotion (see Manton 1977). *Myoscolex* and *Pikaia* seem thus to represent a Cambrian clade of early annelids, which evolved parallel to the chordates in developing a fish-like locomotion.

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