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THE FIRST ARTICULATED SPECIMEN OF *PLUMULITES CANADENSIS* (WOODWARD, 1889) FROM THE UPPER ORDOVICIAN OF ONTARIO, WITH A REVIEW OF THE ANTERIOR REGION OF PLUMULITIDAE (ANNELIDA: MACHAERIDIA)

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Abstract. Articulated plumulitid machaeridians are rarely preserved intact. Here, we describe a complete specimen of *Plumulites canadensis* (Woodward, 1889) retaining much of the head region. The two anteriormost pairs of shell plates are quite distinct from the rest in outline, density of concentric rugae, and especially the radial ornamentation of the second pair. We demonstrate that the latter condition is present in other complete plumulitids and therefore widespread, which elucidates a larger diversity in morphology of plumulitids than realized previously.

Key words: machaeridians, plumulitids, segmentation, head region, exceptional preservation.

MACHAERIDIANS comprise a group of generally little-known skeletal marine fossils ranging from Ordovician to Permian in age. Until recently, their phylum-level affinities remained controversial, but the discovery of a plumulitid machaeridian with soft parts from the Early Ordovician (Tremadocian) of Morocco (Vinther *et al.* 2008) showed that these organisms were armoured annelid worms. The monophyly of the Machaeridia (Withers, 1926) is well established on the basis of shared morphological characters associated with a calcitic skeleton made up fundamentally of four posteriorly overlapping longitudinal rows of shell plates, distinguishable into inner and outer sets, ornamented by prominent concentric rugae. The three machaeridian families – Plumulitidae (Jell, 1979), Turrilepadidae (Clarke, 1896) and Lepidocoleidae (Clarke, 1896) – are defined by intergrading variations on this morphological groundplan. Most lepidocoleids, for example, have lost the outer shell plates, likely as a consequence of evolving a more efficient burrowing capability (Vinther and Briggs 2009), but others, like *Lepidocoleus ketleyanus* ((Reed, 1901) ex Salter 1873), retained the primitive complement of four rows (Bengtson 1977; Dzik 1986; Högström 1997).

Plumulitid machaeridians were dorsoventrally flattened and presumably lived as epibenthic animals (Vinther and Briggs 2009). The unique specimen of *Plumulites bengtsoni* Vinther, Van Roy and Briggs, 2008 preserved with soft parts demonstrates that the inner and outer shell plates were attached to successive segments along the body and emerged from elytra-like extensions at the dorsal parapodial base. Thus, the number of body segments approximates the total number of inner plus outer shell plate pairs; except for biseriate lepidocoleids, in which outer shell plate rows are lost and every other segment is plateless (Högström *et al.* 2009). Very few complete plumulitid fossils have been described; however, and the anterior region was especially prone to loss prior to burial. The articulated and/or partially complete plumulitid specimens known to the authors are as follows: *Plumulites bohemicus* Barrande, 1872 (Barrande 1872, figs 1, 1a, 1b, pl. 35, figs 15–20; Withers 1926, pl. 8, fig. 1; Dzik 1986, fig. 3); *P. folliculum* Barrande, 1872 (Barrande 1872, pl. 20, figs. 13–17); *P. peachi* (Nicholson and Etheridge, 1880), (Nicholson and Etheridge 1880, pl. 20, figs 18–20; Withers 1926, pl. 7, figs 1–3); *P. trentonensis* Withers, 1926 (Withers 1926; partially complete specimen figured by Ruedemann 1942, fig. 7, 1–4); *P. richorum* Jell, 1979 (Jell 1979, figs 3, 4; Text-fig. 2B, C); *P. xuanheensis* Wu, 1990 (Wu 1990, pl. 1, fig. 1); *P. tafennaensis* Chauvel, 1967 (Chauvel 1967; Vinther *et al.* 2008, fig. 3, complete specimen, but lacking anterior region; Text-fig. 3, another complete specimen);

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P. bengtsoni Vinther, Van Roy and Briggs, 2008 (Vinther *et al.* 2008, figs 1, 2 and suppl. 1, 2; the specimen lacks the anterior region).

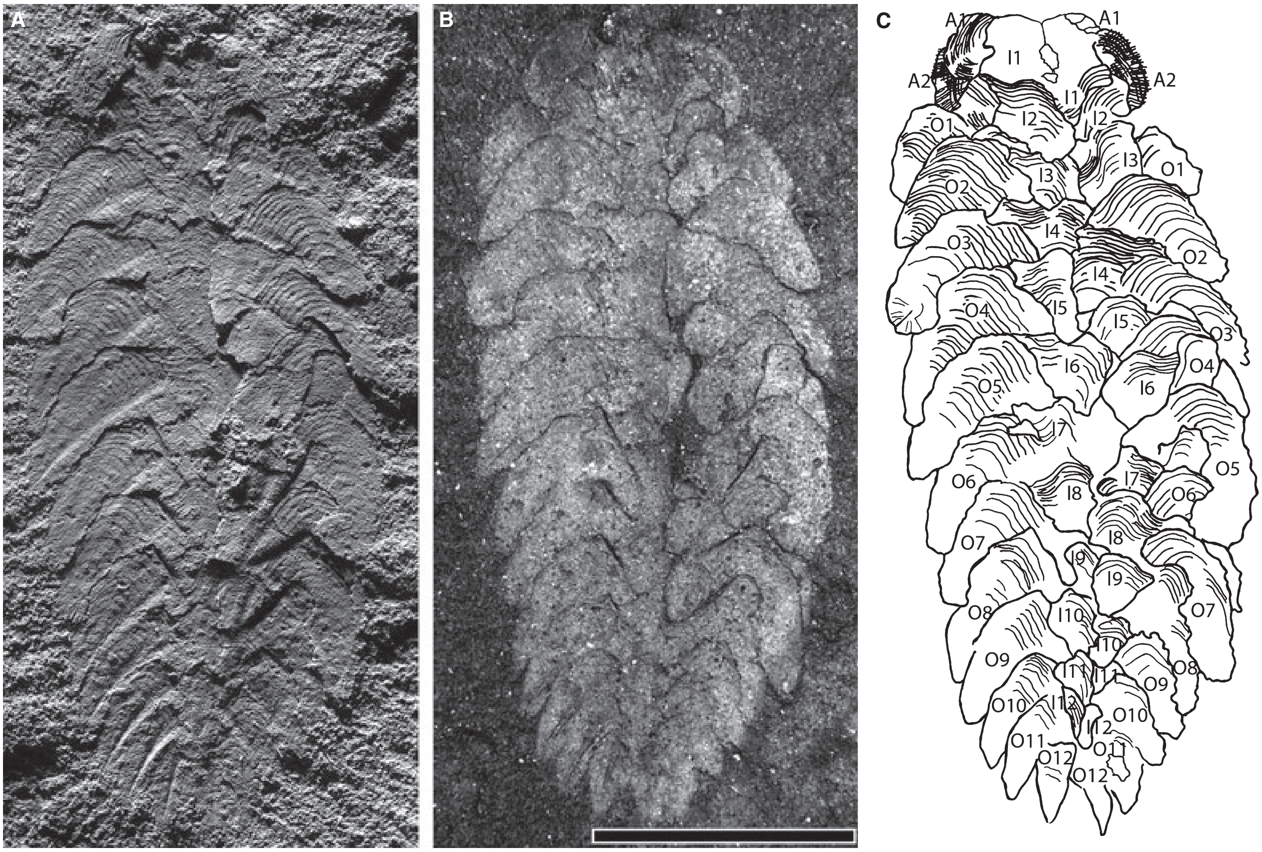
In plumulitid machaeridians, as well as turrilepadids, the anterior region seems to be morphologically distinct (tagmatized) from the rest of the body. Intact, fully articulated specimens are thus particularly important for revealing the morphological variability within the groups as well as for characterizing the segment number of individual species. Modern aphroditacean scale worms show anterior modification (Glasby *et al.* 2008) in the alternation pattern of the elytra as well as in general morphology. Thus, further investigation into the modified anterior region of plumulitids might eventually provide some insight into the condition observed in modern groups and how it evolved, as machaeridians appear to be stem group aphroditaceans (Vinther *et al.* 2008; Vinther and Briggs 2009).

Here, we describe a fully articulated specimen of a plumulitid that we assign to *Plumulites canadensis* (Woodward, 1889), from the Upper Ordovician (Katian) of Ontario, Canada. The specimen preserves most of the anterior region and possesses some features also recognized in plate assemblages of other plumulitid species. These general features are discussed below, accompanied by a review of current knowledge of the anterior region of plumulitids and other machaeridians.

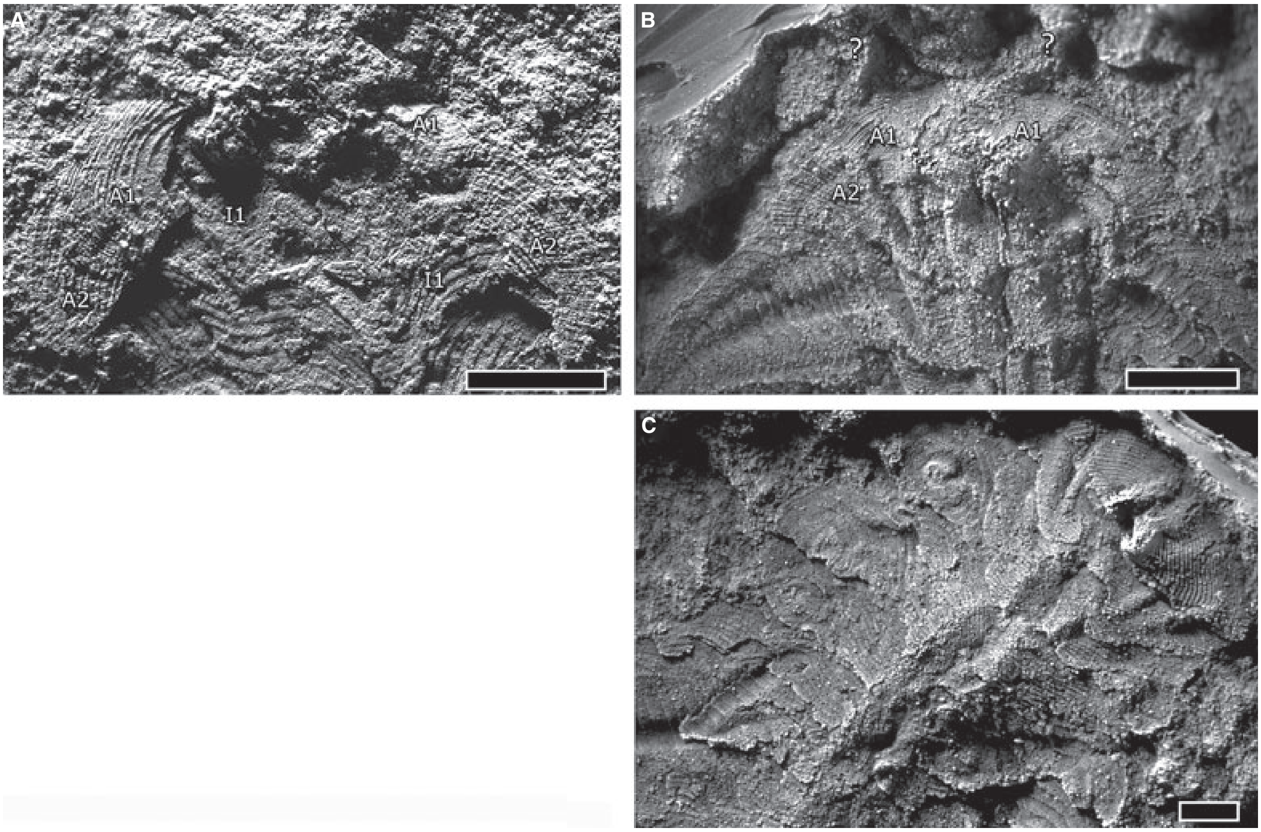
MATERIAL, LOCALITY, STRATIGRAPHIC HORIZON AND AGE

The unique specimen (Text-figs 1, 2A), lacking a counterpart, is catalogued in the Invertebrate Paleontology collections of the Royal Ontario Museum as ROM 53381. It was acquired by exchange with Mr. James A. Sherwood of Ottawa in November 1998. Associated on the same small block of dark, organic-rich, fissile limestone is a complete dorsal exoskeleton of the distinctive isoteline trilobite, *Pseudogygites latimarginatus* (Hall, 1847) (see Ludvigsen 1979).

Locality. Temporary building excavation (underground parking lot of the World Exchange Plaza) between Queen Street and



TEXT-FIG. 1. *Plumulites canadensis* (Woodward, 1889) (ROM 53381). A, specimen photographed in low angle light and coated with ammonium chloride sublimate. B, specimen in high angle light. C, camera lucida drawing. A1–2, anterior shell plates; I1–12, inner shell plates; O1–12, outer shell plates. Scale bar represents 5 mm.



TEXT-FIG. 2. A, Anterior region of *Plumulites canadensis*, ROM 53381, A1 and A2 mark the anterior shell plates as indicated in Text-figure 1C; I1 identifies the first set of inner shell plates. B, *P. richorum* (latex peel of paratype P54265), A1 and A2 are the anterior shell plates; question marks indicate anterior structures discussed in the text referred to as palps by Jell (1979). C, *P. richorum* (latex peel of holotype P54266). Scale bars in all images represent 1 mm.

Slater Street in downtown Ottawa, Ontario; excavated rock was dumped at a landfill site on Innis Road at Cyrville Road on the outskirts of Ottawa in 1992 or 1993; specimen was obtained from landfill prior to 1997.

Stratigraphic horizon and age. Lindsay Formation, Eastview Member (Upper Ordovician, Katian (equivalent of Edenian); probably *pygmaeus* North American Graptolite Zone; Sharma *et al.* 2003).

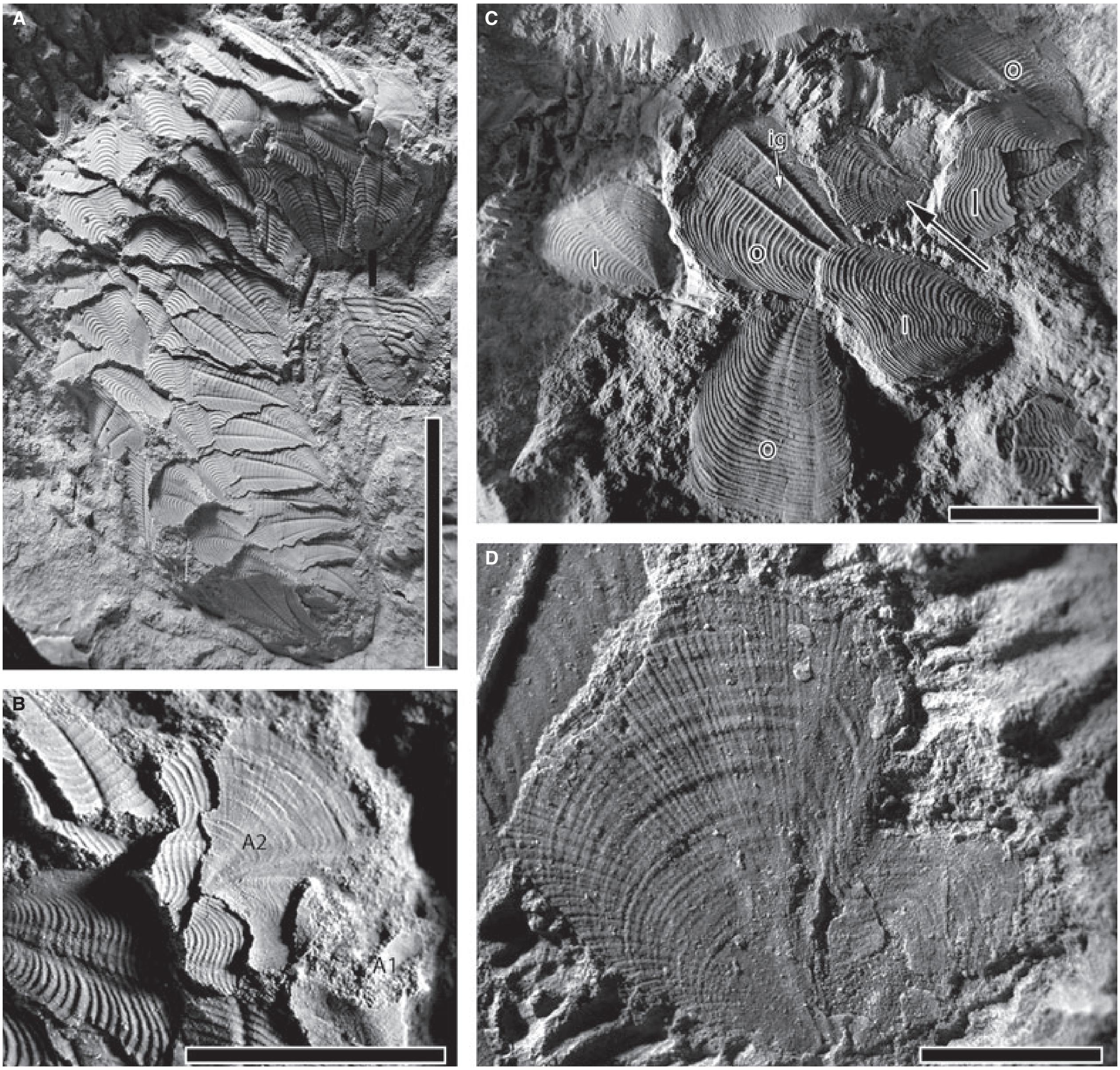
PLUMULITES CANADENSIS (WOODWARD, 1889)

Description and comparison. The specimen (Text-fig. 1) is about 16.5 mm long and 6.8 mm wide and preserves the skeleton in dorsal aspect. It is somewhat compressed overall, and the original shell material has been partially dissolved, especially in the posterior region which retains very little relief.

The anteriormost shell plates are modified compared to those of the remaining trunk. This makes it difficult to assign the first two shell plates to inner or outer rows, and they are referred to here as anterior shell plates one and two (A1 and A2 in Text-fig. 1C). In total, 12 pairs of inner (I1–I12) and outer (O1–O12) shell plates are present on the remaining trunk. The outlines of all the shell plates are obscured because of marginal breakage, but some general morphological features can be discerned.

The exact outline of the first anterior shell plate (A1) (Text-figs 1A, C, 2A) cannot be determined, as only part of the accreting margin (*sensu* Adrain *et al.* 1991; Adrain 1992) is visible. It is distinct from all others, however, in having denser rugae that become more closely spaced towards the accreting margin. The rugae are asymmetric with the steep face oriented in a distal direction. The second shell plate (A2) is distinguished by possession of dense ribs perpendicular to the accreting margin; these appear to have a roughly radial arrangement.

The ribs are distinguished from what are referred to as denticles in plumulitids (Vinther *et al.* 2008) and spines in turrilepadids (Adrain *et al.* 1991) as these latter features are present only at the fringe of the non-accreting margins (radial ribs discussed here can terminate on the accreting margin as well as the non-accreting margin; see Text-fig. 3D). Superimposed on the ribs is a series of concentric symmetrical rugae.



TEXT-FIG. 3. *Plumulites taffenaensis* Chauvel, 1967 from the Caradoc Lower Ktaoua Fm., Morocco. A, cast (Yale Peabody Museum 221701) of original specimen displayed in the private museum owned by Brahim Tahiri, Erfoud, Morocco. Exaggerated region is the first outer shell plate with juvenile concentric growth rings. B, detail of the anterior region, lighting is from the right. A1 denotes the position of the poorly prepared first anterior left shell plate, A2 denotes the second anterior shell plate with radial ornamentation. C, disarticulated shell plate assemblage (YPM 221702) of both inner (I) and outer (O) trunk shell plates and a second anterior shell plate (arrowed). Note the difference in morphology of the upper and lower surfaces of the outer shell plates (O); the lower surface also shows an inner groove (ig) which is observed in other machaeridians. D, close-up of second anterior shell plate in (C). Scale bars represent A, 20 mm; B, 7 mm; C, 10 mm and D, 3 mm.

Outer shell plates exhibit minute denticles like those observed in *Plumulites bengtsoni* by Vinther *et al.* (2008), but they are difficult to illustrate. At least one outer shell plate (O3) shows an area of initial growth with circular concentric growth lines near the apex (Text-fig. 1). Evidence from specimens such as *P. richorum* (Text-fig. 2B) indicates that anterior outer shell plates (O1 and O2) could have had a similar morphology (Jell 1979). Plates posterior to this (e.g. O5, O10–12 left side) appear to taper to a point. Outer shell plates possess a broad elevated median area bounded by gently sloping grooves or furrows; they may have been relatively wide, but no outer shell plate is sufficiently complete to assess the aspect ratio in detail. The same issue pertains to inner shell plates, but the course of the rugae is similar in the holotype specimen of *P. canadensis*, as discussed below.

Remarks. The surface of the fossil appears as a highly reflective film (Text-fig. 1B), similar to that associated with many Burgess Shale organisms. The nature of this film is unknown pending further investigation, but it could represent preservation of an organic sheath or have been formed by diagenetic silicate replacement (Butterfield *et al.* 2007; Orr *et al.* 1998).

DISCUSSION

Although all shell plates in the articulated specimen described herein are marginally incomplete as a result of breakage, there are clear similarities between it and *Plumulites canadensis* (Woodward, 1889), primarily in the pattern of inner shell plate rugae. The holotype of the latter species is an isolated inner shell plate recovered from a lithology identical to that of ROM 53381, in the same Upper Ordovician succession at Ottawa (Woodward 1889). In both specimens, the field between the median area and the medial margin is very broad, making up more than one-third of the width of the inner shell plate, and there is a prominent kink in the inflection of the rugae separating the lateral marginal area and the median area (Text-fig. 1: I4, I8, I9 on the right side). Withers (1926) commented on a distinctive reticulate micro-ornamentation on the type specimen of *P. canadensis,* and a similar ornamentation is evident on the new specimen described herein. This is a feature seen in other machaeridians (Adrain 1992), but its pronounced expression in these two fossils, combined with their closely comparable inner shell plate configuration and occurrence within the same formation in geographical proximity, leads us to assign the complete specimen to *P. canadensis*.

The articulated individual of *Plumulites canadensis* described herein is one of very few complete specimens preserving evidence of the anteriormost region. Other known examples include two individuals from the Devonian of Australia, both referred to *Plumulites richorum* (Text-fig. 2B, C; see Jell 1979). Apparent morphological differences between the two Devonian specimens were ascribed by Jell (1979) to sexual dimorphism. This could be the case, as many extant annelids exhibit dimorphic traits related to reproductive modifications, such as male dwarfism or smaller size, along with the presence of copulatory organs (Glover *et al.* 2005; Vortsepneva *et al.* 2008). No modern annelid, however, exhibits sexually dimorphic traits of the dorsal cirri. Alternatively, the differences between the Devonian specimens might reflect the presence of more than one species at the same locality. The paratype of *Plumulites richorum* (P54265) shows anterior shell tagmatization very similar to that in the specimen of *P. canadensis* described here, having an inner shell plate with dense concentric rugae followed by a shell plate with radial ornamentation (Text-fig. 2B). Two anterior triangular structures on this specimen of *P. richorum*, originally interpreted as soft palps (Jell 1979), were later regarded as a set of anteriorly projecting shell plates (Dzik 1986), thus suggesting the presence of two sets of shell plates anterior to the one with radial ornamentation. The triangular structures, however, show no features such as imprints of rugae or smooth areas to indicate that they are anything other than rock fractures following irregularities caused by the adjacent fossil (Text-fig. 2B). This is our preferred hypothesis. Thus, the morphology of the paratype of *P. richorum* corresponds to that of *P. canadensis* as well as to other examples discussed below. The more posterior shell plates resemble the remaining trunk plates. The holotype specimen (P54266) of *P. richorum* appears to be better preserved and does not show the same morphology (Text-fig. 2C; Jell 1979, fig. 4b–d). Here, three pairs of inner shell plates are present at the anterior end with no complementary outer shell plates, followed by at least three pairs of outer shell plates with juvenile circular concentric growth at the apex (Text-fig. 2C, as observed for at least one shell plate in the articulated specimen of *P. canadensis,* O3; Text-fig. 1) along with intervening inner shell plates.

Plumulites tafennaensis Chauvel, 1967 from the Caradoc (Upper Ordovician) of Morocco also exhibits differentiated anterior shell plates. Text-figure 3A and B shows a cast (YPM 221701) of a specimen in a private collection in Morocco. The specimen is highly contracted compared to another individual of this species (Vinther *et al.* 2008, fig. 3; YPM 220639), but it preserves much of the anterior region. Here, a second shell plate with radial ornamentation and an inflected median area is present as in *P. canadensis* and *P. richorum* (Text-fig. 2A, B). The anteriormost shell plate is obscured because of preparation. The first outer shell plate behind the modified anterior shell plates has juvenile circular concentric growth lines. A disarticulated shell assemblage (YPM 221702) of the same species preserves the second anterior shell plate (Text-fig. 3C, D). It is apparent from this assemblage that the outer shell plates are quite different in structure on the upper and lower surfaces (Text-fig. 3C), which means that caution must be exercised in describing new species based only on features visible on a single plate surface.

Plumulites xuanheensis (Wu, 1990) from China also shows a second shell plate with radial ornamentation (pers. obs. by JV on new images of the holotype).

Turrilepadid machaeridians showing tagmatization of the anterior region similar to that of *P. richorum* have been recognized (Adrain *et al.* 1991). One example (Adrain *et al.* 1991, pl. 2, fig. 6) reveals a frontal region with two anteriormost inner shell plates, but lacking intervening outer plates. Their morphology, with a wide accreting margin and rugae of the first shell plate much denser than on remaining trunk plates, is also seen in the few known plumulitids. It has further been noted that some of the anterior outer shell plates in turrilepadids can have concentric rugae at the apex (Högström 1997), as in plumulitids. Significantly, no shell plates with pronounced radial ornamentation have been recognized in turrilepadids, and this character therefore seems to be exclusive to plumulitids.

It is uncertain whether tetraseriate lepidocoleids also possess a tagmatized anterior region lacking outer shell plates, and with the first subsequent outer plate pairs having circular concentric rugae; no lepidocoleid fossils are known that are complete enough to assess this condition. Anterior shell plates that are modified with denser rugae are seen in the short biseriate *Lepidocoleus sarlei* (Högström and Taylor 2001), but the body is otherwise more or less homogenous. This shows that the anteriormost shell plate (A1) in plumulitids is homologous to the first inner shell plate of turrilepadids and lepidocoleids. The radial ornamentation of the second shell plate appears confined to plumulitids, and it is still uncertain whether it can be homologized with either anterior inner or outer shell plates. Given the uncertainties raised by the two specimens of *P. richorum*, we cannot specifically determine whether this is a unique trait of some plumulitids (a distinct genus) or a sexually dimorphic feature of the whole family.

It is interesting that the anterior region of most tetraseriate machaeridians appears to lack outer shell plates, which are completely lost along the entire trunk in typical lepidocoleids. This evolution of this condition could be of importance in understanding segmental body patterning in annelids as a whole and should be investigated further.

Machaeridians share some distinctive characters with the aphroditacean polychaetes. These include dorsal integumental extensions at the base of the parapodia (dorsal cirri – an aciculate character *sensu* Rouse and Fauchald 1997), which expand out to form larger scale-shaped structures (elytra – an aphroditacean character *sensu* Rouse and Fauchald (1997), although in modern forms the elytra do not carry mineralized plates). Inner and outer shell plates of different morphology attach to alternating segments (a phyllodocidan character; reviewed recently *in* Glasby *et al.* 2008). Thus, machaeridians possess specific characters seen only within some members of the annelid crown group. Caron (2008) argued that machaeridians should be considered stem group annelids based on their derived characters, but stem group relationships of fossil taxa should be established on the basis of plesiomorphies or a subset thereof, and not on the basis of derived characters, as they would not be phylogenetically informative in this sense. Machaeridians are most similar to the aphroditaceans, in which elytra only appear on every other segment along most of the trunk. Lepidocoleid machaeridians lost the outer shell plates rows and were therefore assumed to have plates only on every other segment as well (Vinther and Briggs 2009). This was recently confirmed by the description of a pyritized lepidocoleid with soft parts from the Lower Devonian Hunsrückschiefer (Högström *et al.* 2009), but the condition is presumably an independent derivation from the aphroditacean crown group, as the lepidocoleids have completely reduced parapodia (Högström *et al.* 2009) adapted for an infaunal lifemode (Vinther and Briggs 2009). Aphroditaceans, in contrast, possess well-developed parapodia. Plumulitids, given their epifaunal lifemode and well-developed parapodia, presumably represent the most plesiomorphic morphology for the group.

Although machaeridians have features that suggest they could be an aphroditacean stem group (and thus with the annelid crown), their distinctive calcitic skeletal array demonstrates their monophyly (Adrain 1992; Vinther *et al.* 2008). Inner and outer shell plates are homologous within the three machaeridian families and were present in the common machaeridian ancestor. A differentiated anterior region lacking outer shell plates in the first few segments is homologous between the last common ancestor of plumulitids and turrilepadids and presumably lepidocoleids as they appear derived together with turrilepadids (see Vinther and Briggs 2009). Additional features i.e. ventral cirri, aciculae, lateral and median antennae, palps, compound chaetae and jaws characterize the broader group Aciculata (Rouse and Fauchald, 1997). With the discovery of more exceptional machaeridian fossils, these features are expected to be revealed. The polarity of annelid relationships has not been resolved by molecular phylogenetics (Rousset *et al.* 2007), and the ancestral plesiomorphic traits of the crown group remains to be fully assessed. We cannot categorically reject the hypothesis that machaeridians are stem annelids, but this would require secondary loss of dorsal cirri and segmental alternation in a significant number of the remaining crown group members. Stem-group annelids from the Burgess Shale (Eibye-Jacobsen 2004) do not show any machaeridian or aphroditacean-like features, but were clearly epibenthic with well-developed parapodia as in plumulitids, which suggest that this morphology is the plesiomorphic state for the annelids.

CONCLUSION

Plumulites canadensis is a comparatively short machaeridian with only about 12 shell plates in either of the inner or of the outer rows in addition to two morphologically distinctive anterior shell plate pairs, corresponding to a minimum of 26 body segments. A number of other plumulitid species also possess anterior shell plates that are quite different in shape and ornamentation compared to the more homogeneous trunk plates. Although visible in a figure of the paratype of *P. richorum* published by Jell (1979), the presence of a second anterior shell plate with dense radial ornamentation has not been previously recognized. The total number of shell plates, the extent of their modification in the anterior region (including outline, density of concentric rugae and radial ornamentation) and the presence of juvenile circular growth lines at the apex of the first outer shell plates vary between plumulitid species.

It would be premature to utilize characters of the anterior region to construct any classificatory distinction of plumulitids, as some are present in turrilepadids as well (Adrain *et al.* 1991; Högström 1997). As far as we can discern, the radial ornamentation of the second anterior shell plate pair appears to be unique to some plumulitids. Other variable characters of skeletal morphology, such as the median area of the outer shell plates, may hold some promise for distinguishing among plumulitids at the generic level.

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