LETTERS

Machaeridians are Palaeozoic armoured annelids

Jakob Vinther[1], Peter Van Roy[2]† & Derek E. G. Briggs[1]

The systematic affinities of several Palaeozoic skeletal taxa were only resolved when their soft-tissue morphology was revealed by the discovery of exceptionally preserved specimens. The conodonts provide a classic example, their tooth-like elements having been assigned to various invertebrate and vertebrate groups for more than 125 years until the discovery of their soft tissues revealed them to be crown-group vertebrates[1]. Machaeridians, which are virtually ubiquitous as shell plates in benthic marine shelly assemblages ranging from Early Ordovician (Late Tremadoc) to Carboniferous[2], have proved no less enigmatic. The Machaeridia comprise three distinct families of worm-like animals, united by the possession of a dorsal skeleton of calcite plates that is rarely found articulated. Since they were first described 150 years ago[3] machaeridians have been allied with barnacles[4,5], echinoderms[6,7], molluscs[3,8–10] or annelids[9,11,12]. Here we describe a new machaeridian with preserved soft parts, including parapodia and chaetae, from the Upper Tremadoc of Morocco, demonstrating the annelid affinity of the group. This discovery shows that a lineage of annelids evolved a dorsal skeleton of calcareous plates early in their history; it also resolves the affinities of a group of problematic Palaeozoic invertebrates previously known only from isolated elements and occasional skeletal assemblages.

Phylum Annelida
Class Machaeridia
Order Turrilepadomorpha
Family Plumulitidae
Genus ***Plumulites*** Barrande, 1872
Plumulites bengtsoni sp. nov.

Etymology. For Stefan Bengtson, who has made a major contribution to our knowledge of machaeridians and early skeletal fossils.
Holotype. Yale Peabody Museum, YPM 221134 (Figs 1 and 2, and Supplementary Figs 1–3).
Locality and horizon. Twenty-two kilometres north-northeast of Zagora, southeastern Morocco; upper part of the Lower Fezouata formation, Lower Ordovician (Upper Tremadoc)[13]. The exceptionally preserved specimen described here represents the oldest articulated machaeridian (only one other machaeridian of Late Tremadoc age is known, from isolated shell plates[14]). The locality also yields sponges, conulariids, hyolithids, trilobites and other arthropods, echinoderms and graptolites. The lithology is a dark blue–green silty mudstone.
Diagnosis. The outer shell plates possess a relatively wide elevated median area bounded by inflections; the rugae are less prominent where they traverse the median area. Inner shell plates have a much broader median area which is traversed by rugae that show neither inflection nor reduction in relief.
Description. The specimen (Fig. 1) lacks the anterior region and many of the shell plates; decay played a role but some of the shell plates may be concealed within the sediment of the counterpart. The preserved length is about 28 mm. The specimen shows the dorsal surface of the integument. At the anterior right, rotated about 180° relative to its life position, lies a relatively complete outer shell plate showing an umbonal area with circular concentric growth rings (Fig. 1c and Supplementary Fig. 3d). This type of shell plate characterizes the anterior region of plumulitids. Other outer shell plates are evident, two at the anterior left and one at the posterior right; these taper to an angular extremity. The anterior plates are about 1.7 times (Supplementary Fig. 3a) and the posterior 2 times longer than wide. The outer shell plates have denticulate lateral margins, the denticles formed as projections of the underlying shell layer and out of phase with the growth lines and rugae on the dorsal surface (Supplementary Fig. 3a, c, d). One almost complete inner shell plate is present; its shape is close to that of an equilateral triangle (Supplementary Fig. 3b).

The anterior part of the specimen is concealed largely by overlying shell plates. A sediment-filled tube in the anterior part of the fossil is interpreted as the gut. A narrow median linear structure runs along the anteriormost preserved part of the gut (Supplementary Fig. 3e); its nature is unknown. Behind this the trunk tapers posteriorly. Along the length of the trunk, paired lobes extend laterally bearing bundles of long, slender bristles. Up to 18 pairs of these lobes, interpreted as parapodia, are evident. Extrapolation suggests that there must have been at least 25 pairs of parapodia, corresponding to segments, along the length of the trunk. It is difficult to distinguish rami; they may be represented in some cases by two divergent groups of chaetae (Figs 1 and 2a, b). There may be up to 20 chaetae in a bundle on a parapodium. Those parapodia that preserve some original relief show dense transverse wrinkles (Fig. 2a, b). Faint integumental wrinkles are evident on other parapodia and portions of the trunk. There appears to be a dorsal extension of the integument at the base of almost every parapodium (Figs 1 and 2, highlighted as green, and Supplementary Fig. 3f). Owing to the level of splitting, the outline of these extensions is concealed largely within the counterpart.

The soft tissues are preserved in framboids composed of iron oxide (Supplementary Fig. 1), indicating that they were originally pyritic. Red iron oxide, presumably haematite, is concentrated mainly in the parapodia and the chaetae; the specimen is otherwise yellow.
Discussion. The class Machaeridia consists of three families: Turrilepadidae, Plumulitidae and Lepidocoleidae. The body of Plumulitidae was dorso-ventrally flattened[12], whereas that of the other groups was more laterally compressed. Machaeridians are characterized by calcitic shell plates serially arranged in left and right zones with prominent concentric rugae[6]. They appear to have a fixed number of shell plates in the adult[15], but the number in plumulitids is not well documented. The only known complete example, a specimen of *Plumulites richorum* from the Devonian of Australia[12], preserves 20 pairs of inner shell plates. Well-preserved plumulitid skeletons[6,12], such as that of the Upper Ordovician (Caradoc) species *Plumulites tafennaensis*[16] (Fig. 3) from Morocco, show that there are two columns each of posteriorly imbricating inner and outer shell plates. The inner shell plates are smaller than the outer and project

[1]Department of Geology and Geophysics, Yale University, PO Box 208109, New Haven, Connecticut 06520, USA. [2]Department of Geology and Soil Science, Ghent University, Krijgslaan 281/S8, B-9000 Ghent, Belgium. †Present address: School of Geological Sciences, University College Dublin, Belfield, Dublin 4, Ireland.

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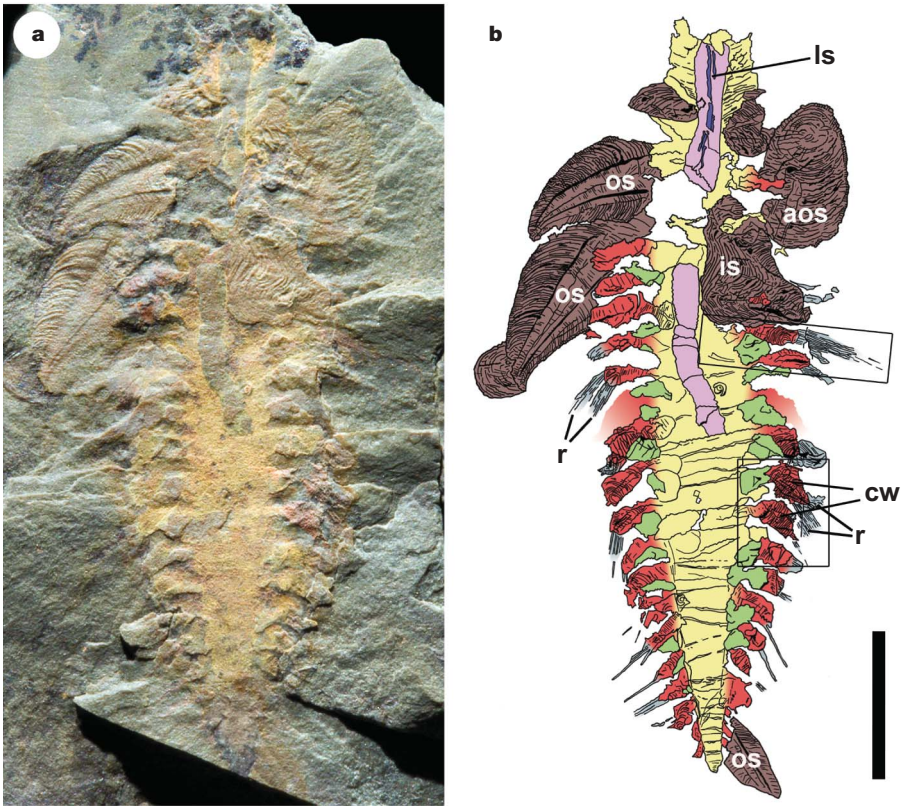

Figure 1 | *Plumulites bengtsoni* sp. nov. from the upper part of the Lower Fezouata formation, Lower Ordovician (Upper Tremadoc), Morocco. **a**, Holotype YPM 221134, part. **b**, Camera lucida drawing of the part. Colours indicate the trunk (yellow), parapodia (red), chaetae (gray), attachment of shell plates (green), gut (purple) and dorsal linear structure (blue). Abbreviations: os, outer shell plate; is, inner shell plate; aos, anterior outer shell plate; ls, linear structure; cw, cuticular wrinkles; r, rami evidenced by divergent bundles of chaetae. Outlines indicate the position of enlarged areas in Fig. 2. Scale bar, 5 mm.

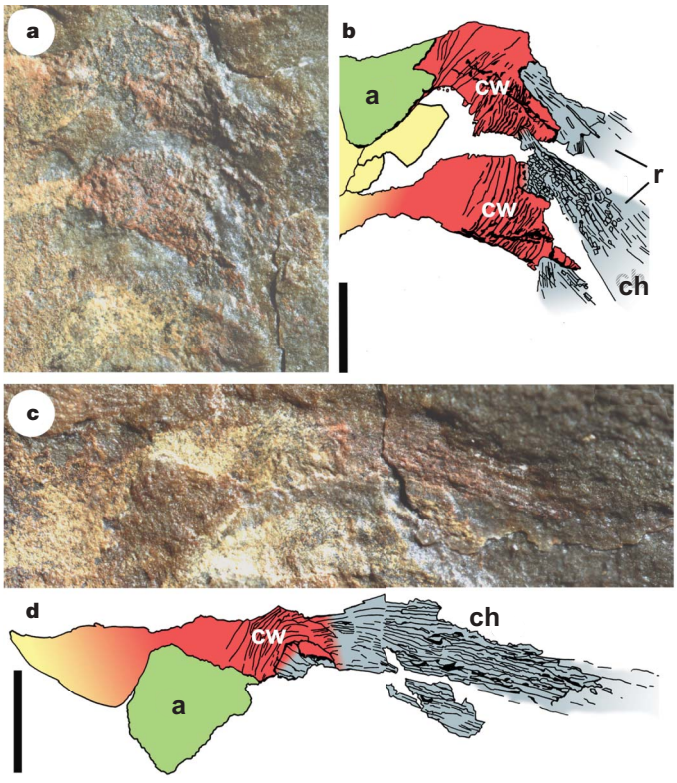

Figure 2 | Details of the parapodia, chaetae and dorsal integumental extensions of *P. bengtsoni*, holotype YPM 221134, part. **a**, Middle right parapodia showing cuticular wrinkles. **b**, Camera lucida drawing of the area in **a**. **c**, More anterior parapodium. **d**, Camera lucida drawing of area in **c**. Colours as in Fig. 1. Abbreviations: cw, cuticular wrinkles; ch, chaetae; a, attachment of shell plates; r, rami evidenced by divergent bundles of chaetae. Scale bar, 1 mm.

inwards obliquely in a posterior direction. The outer plates are more elongate and project outwards posteriorly, perpendicular to the inner shell plates. The anteriormost outer plates, which are sometimes absent, differ in morphology from the remainder[12].

Plumulites bengtsoni shows the morphology characteristic of Plumulitidae with the inner shell plates smaller than the outer and the body dorso-ventrally flattened. Only the anteriormost region of the body appears to be missing, assuming that the differentiated anterior outer plate, although rotated, is approximately in its original position[9,12]. Denticles are present along the lateral margins of the outer shell plates, a feature that may be widespread in this family. The shell plates of *Plumulites kutscheri*[17] (Upper Wenlock, Germany) have denticulate margins, and spinose plumulitid shell plates also have been reported from the Ashgill of Sweden[18]. The morphology of *P. bengtsoni* is very similar otherwise to the type species *Plumulites bohemicus*; it is distinguished by the less pronounced rugae in the elevated median area of the outer plates.

Machaeridians are the only annelids known to have evolved biomineralized dorsal armour. The living Sternaspidae have a pair of chitinous anal plates which are used to cover the burrow entrance[19], but these structures are probably not homologous to machaeridian shell plates. Serpulidae and Spirorbidae secrete biomineralized tubes of calcite and aragonite from glands near the collar[19], but they are sessile and the mode of secretion differs from that in machaeridian shell plates. The overlapping nature and the extent of the growing margin of the shell plates in *P. bengtsoni* indicate that they could not have been attached directly to the trunk or parapodia. The dorsal integumental extensions at the base of each parapodium (Figs 1 and 2, highlighted as green structures) may represent the attachment of the shell plates. Their arrangement corresponds to that in articulated plumulitid skeletons[6,12] in which the inner and outer shell plates alternate in position along a line on each side of the trunk, suggesting that they were attached to successive segments. The integumental extensions must have expanded to accommodate the wide proximal growing margin of the shell plate, in a manner similar to the attachment of elytra (expanded cirri) in living scale worms (Aphroditidae: Phyllodocida).

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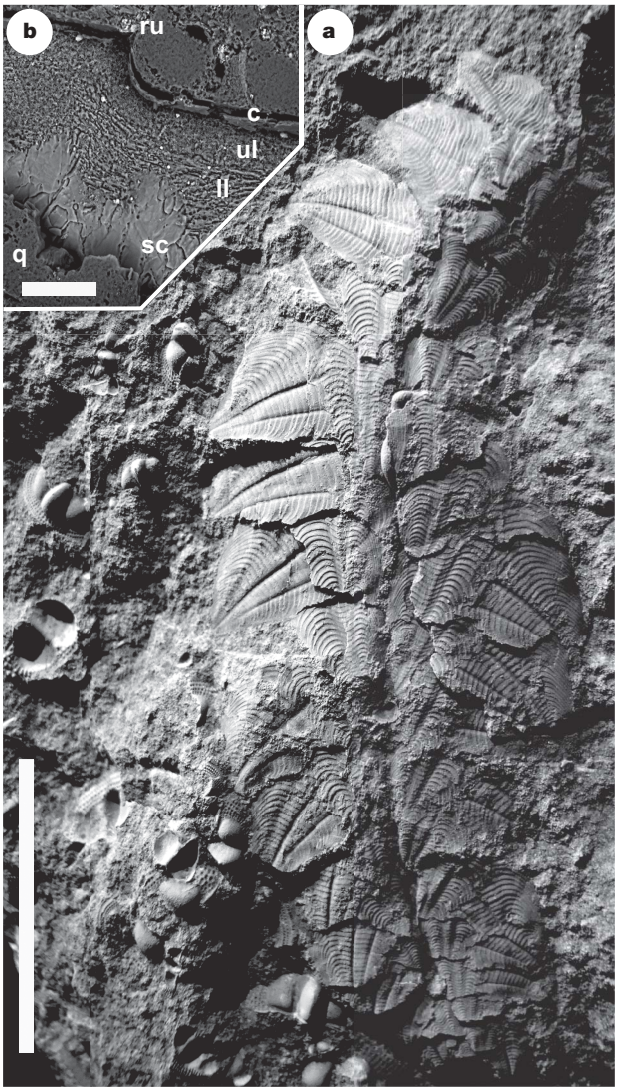

Figure 3 | *Plumulites tafennaensis*[16] from the Upper Ordovician (Caradoc), Morocco. a, YPM 220639 articulated specimen. **b**, Back-scattered electron micrograph of an etched, polished transverse section of a shell plate. The upper part consists of a lower laminated layer (ll) and an upper fine grained layer (ul); a thin separation between the upper shell layer and the matrix is interpreted as evidence of an organic cuticle (c); ru, the site of a ruga. The basal surface is encrusted with quartz (q), and some of the adjacent shell is recrystallized into sparry calcite (sc). Scale bars: **a**, 20 mm; **b**, 50 μm.

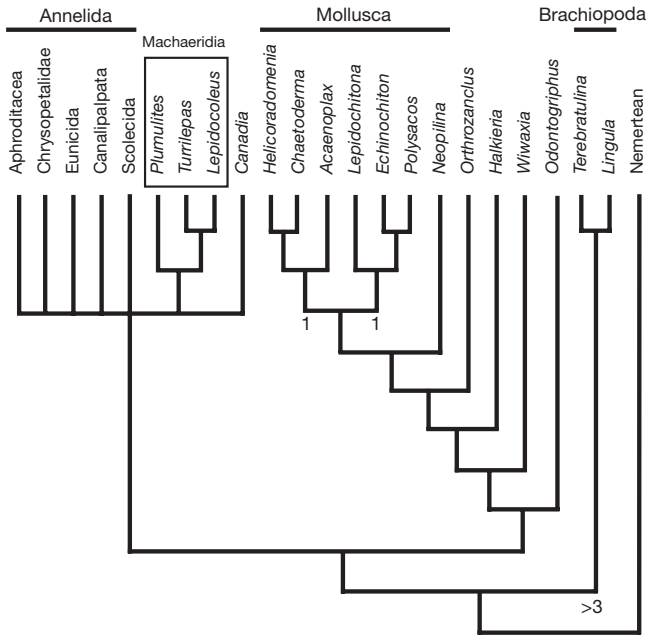

Figure 4 | Strict consensus tree of 66 most parsimonious trees based on a cladistic analysis with 23 taxa and 57 characters (Supplementary Information and Supplementary Fig. 4). Machaeridians resolve with the annelids. Numbers below nodes indicate where the decay index is one or more. Score of best tree, 74; consistency index, 0.811; retention index, 0.897; rescaled consistency index, 0.727; homoplasy index, 0.189.

The position of machaeridians within the annelids is difficult to resolve. A major issue is the homology of the shell plates and of the proximal structures to which they are attached. The inner shell plates in machaeridians are offset and overlap along the median line, as do the elytra of some scale worms. The elytra of scale worms, however, occur only on every other segment, whereas the shell plates of machaeridians appear to be present on every segment. A cladistic analysis (Supplementary Information) resolves the Machaeridia as a member of Annelida, but their position within the group is not resolved when the presence of dorsal cirri in Machaeridia is coded as unknown (Fig. 4). Only when the plumulitids are coded as having cirri and elytra do they resolve as crown-group annelids. They fall in a clade with the living phyllodocidans (Supplementary Fig. 4), which have been interpreted as a paraphyletic basal grade[19,20], in which case machaeridians could still be part of the stem group (see further discussion in Supplementary Information).

Much of the annelid fossil record consists of the elements of the jaw apparatus (scolecodonts), which first appear in the uppermost Cambrian[21]. Soft-bodied fossils are rare: pyrite is also involved in the preservation of whole-body annelids from several other exceptional localities, including the Lower Devonian Hunsrück Slate, Germany[22], the Middle Devonian Arkona Shale, Canada[23], and the Jurassic of La Voulte-sur-Rhône, France[24]. The oldest described examples are from the Middle Cambrian Burgess Shale[25], but occurrences have been reported from the Early Cambrian (Atdabanian) Sirius Passet fauna of Greenland[26]. It has been suggested that machaeridians are related to the older Early Cambrian tommotiids (Mitrosagophora)[9,11], some of which, like *Tommotia*, *Dalyatia* and *Tannuolina*, have left and right shell plates. Tommotiid shell plates are ornamented with prominent concentric rugae and often a median inflected area like that in plumulitid shell plates. Although tommotiids are known only from isolated sclerites, some reconstructions[27,28] imply an organization similar to that in machaeridians. The morphological similarity between the shell plates of machaeridians, tommotiids and brachiopods[11,29] could be interpreted as evidence of a close affinity between annelids and brachiopods. Well-preserved shell plates of *P. tafennaensis* (Fig. 3b) show that they consist of an outer layer formed by marginal accretion and an inner basal layer, as previously recorded in lepidocoleids and turrilepadids[17,30]. An additional external layer probably represents an original organic cuticle (Fig. 3b). Tommotiid shell plates, in contrast, have a characteristic lamellar ultrastructure and phosphatic mineralogy like that in lingulid brachiopods[11,28,29]; as putative stem brachiopods[29] they would have been secreted by a more elaborate mantle. Thus the similarity between shell plates in tommotiids and machaeridians is probably a result of convergent evolution[2].

The discovery of machaeridian soft-tissue morphology resolves the 150-year-old debate about the affinities of this group, and demonstrates that a lineage of annelids developed a distinctive, dorsal, mineralized armour early in their history.

METHODS SUMMARY

The holotype was photographed by using a Canon EOS 350D digital single-lens reflex camera with a Canon EF-S 60 mm f/2.8 Macro USM objective lens stopped down to f32. Details were photographed by using a Leica MZ16 dissecting microscope with Optronics camera using oblique-angled polarized light, and

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combined as a mosaic. Camera lucida drawings were made by using a Wild M5 stereomicroscope. The counterpart was studied in a Philips XL 30 environmental scanning electron microscope (ESEM) equipped with an energy-dispersive X-ray analyser (EDX). Disarticulated shell plates of *P. tafennaensis* in their matrix were embedded in epoxy, and polished sections were etched in 0.5% HCl for 90 s. Back-scattered electron images were taken and the elemental composition analysed in the ESEM.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions P.V.R. performed field work and acquired the specimens. All authors contributed to the interpretation of the fossils and writing the paper.

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