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# Micrometric detail in palaeoscolecid worms from Late Ordovician sandstones of the Tafilalt Konservat-Lagerstätte, Morocco

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## ABSTRACT

The late Ordovician Tafilalt Biota of Morocco is a recently discovered Konservat-Lagerstätte that provides abundant paropsonemid eldonioids –resembling those from the Cambrian Burgess Shale and Chengjiang biotas, or other paropsonemid occurrences from the Ordovician to Silurian of the US and Australia–, large discoidal ?holdfasts, non-biomineralised cheloniellid arthropods, rare vermiform fossils and articulated skeletons of echinoderms and trilobites. Exceptional preservation of soft-bodied organisms occurs in medium- to coarse-grained sandstones, in a style reminiscent of the soft-bodied Ediacaran fossils of the White Sea Assemblage. Here, we describe the first articulated scleritomes of a large palaeoscolecid worm from Africa. In addition to the mineralised sclerites, the specimens also exhibit extensive soft-tissue preservation down to micron-scale, including fine detail of annuli with their plate, platelet and microplate arrangement on a reticulate cuticle. Compression fossils of the new species *Gamascolex vanroyi* are represented by external moulds with remains of phosphatised cuticular structure, secondarily weathered into strontian crandallite. Partial foregut fossilization is seen in one specimen, and phosphatised digestive structures are also reported in three co-occurring trilobite genera at the Bou-Nemrou locality. From a palaeogeographic point of view, these North African palaeoscolecids represent the highest palaeolatitudinal occurrence of this Palaeozoic group in Gondwana, describing them for the first time in cold-water areas adjacent to the Late Ordovician South Pole. It also provides a palaeobiogeographic link to the original distribution of the genus *Gamascolex* in a central European Peri-Gondwanan terrane.

*Keywords:* Soft-bodied preservation, Sandbian, First Bani Group, north Africa, South Gondwana.

## 1. Introduction

Exceptionally preserved soft-bodied faunas, belonging to the Fezouata and Tafilalt biotas, were recently discovered from the Early and Late Ordovician of Morocco. Both show that analogues of the Cambrian Burgess Shale (i.e. Fezouata) and terminal Neoproterozoic Ediacaran (Tafilalt) taphonomic windows were still open in the Ordovician (Van Roy, 2006 and 2011; Van Roy et al., 2010). One of the most prominent fossil sites of the Tafilalt Konservat-Lagerstätten occurs in the Jbel Tijarfaïouine area of the eastern Anti-Atlas, halfway between the town of Mecissi (Msissi) and the city of Erfoud (Fig. 1B). Although a number of early Sandbian to late Katian echinoderm localities showing exceptional preservation were reported from this area (Hunter et al., 2010; Lefebvre et al., 2010), Ediacara-style preservation of soft-bodied metazoans mainly occurs in the early Late Ordovician sandstones. This is the case of a locality with abundant paropsonemid eldonioids (Fig. 2C) and large discoidal fossils, also yielding lightly sclerotised cheloniellid arthropods (Fig. 2D) and the rare palaeoscolecid worms described here (Figs. 2A–B and 4). These beds also provide an assemblage of articulated skeletons of benthic echinoderms and trilobites (Figs. 2E–G).

Palaeoscolecids are a group of Cambrian to late Silurian worms characterised by an annulated cuticle with rows of organo-phosphatic plates, an evertible proboscis and spines or nipples at the posterior end. They are widely recorded in the famous Cambrian sites with exceptional preservation, such as Chengjiang (Han et al., 2007), Guanshan (Hu et al., 2012), Zhongbao (Zhang and Pratt, 1996) and Wangcun (Duan et al., 2012) in South China, Spence (Conway Morris and Robison, 1986), Latham and Kinzers shales (Conway Morris and Peel, 2010) in the USA, Sirius Passet (Conway Morris and Peel, 2010) in Greenland, Sinsk (Ivantsov and Wrona, 2004) in Russia and Emu Bay Shale (Glaessner, 1979; García-Bellido et al., 2013) in Australia. However, post-Cambrian records are very sparse, and articulated palaeoscolecid scleritomes (other than cuticle fragments possibly derived from moults) were so far only known from some Ordovician localities of Britain, Bohemia, Peru, USA and China (see Botting et al., 2012; Muir et al., 2014). The material shown here thus represents the first description of Ordovician palaeoscolecids from the African continent, their presence in the older Fezouata Biota so far only mentioned in passing (Van Roy et al., 2010; Martin et al., 2013).

## 2. Geologic setting

The studied fossils come from the main sandstone quarry made for commercial exploitation of fossils at the site of Bou Nemrou (Lat. 31º 19’ 35” N, Long. 04º 31’ 35” W), located east of the El Qaid Erami (El Caïd Rami) valley near Ksar (village) Tamarna, and 9.8 kilometres to the north of the Alnif–Rissani road (Fig. 1C). The site was first mentioned and studied in some detail by Van Roy (2006), who found large paropsonemid specimens (closely resembling “*Eldonia*” *berbera* of Alessandrello and Bracchi, 2003), problematic discoidal fossils, the non-biomineralised cheloniellid arthropod *Duslia insignis* Jahn, 1893 (*D.* cf. *insignis* according to Alessandrello and Bracchi, 2006), diverse trilobites and “a new, enigmatic vermiform fossil” represented by a single specimen (Van Roy, 2006, fig. 3.7; Lefebvre et al., 2011, fig. 3A). The rich echinoderm fauna collected from the locality (labeled as KR-1, CRF-4 or ECR-F4 by previous authors) comprises about 14 genera of eocrinoids, ophiuroids, stylophorans, edrioasteroids, crinoids and a single cyclocystoid (Regnault, 2007; Hunter et al., 2010; Lefebvre et al., 2010, 2011; Sumrall and Zamora, 2011). Trilobites are represented by seven poorly described species (Vela and Corbacho, 2009; Corbacho, 2011). None of the identified taxa allows for precise dating, and no graptolites or microfossils have yet been found at the locality.

From a stratigraphic point of view, the assemblage is restricted to several sandstone beds located close to the top of the lateral equivalent of the First Bani Group, which in the western Tafilalt area cannot be subdivided into formations. In particular, the fossiliferous beds have often been correlated with the Izegguirene Formation of the central Anti-Atlas, which has been dated as early Sandbian (basal “Caradoc”). Gutiérrez-Marco et al. (2003) assigned the top of the First Bani Group to the upper Dobrotivian, a regional stage division that spans the Darriwilian/Sandbian boundary of the global scale (Bergström et al., 2009). This correlation is reinforced by the first Moroccan record of *Gamascolex* Kraft and Mergl, 1989, a palaeoscolecid genus that so far has been restricted to the type Dobrotivian (Dobrotivá Formation) of Bohemia (Kraft and Mergl, 1989).

## 3. Preservation and palaeoecology

Articulated palaeoscolecid scleritomes are delicately preserved as compression fossils in fine- to medium-grained micaceous sandstone, co-occurring on the same slabs with complete and articulated thecae of the eocrinoid *Ascocystites* Barrande, 1887. From consideration of the echinoderm taphonomy, the lithology and sedimentary structures, previous studies suggest a rapid, storm-influenced burial, in a relatively shallow-water environment, with specimens undergoing no significant transportation: burial is estimated to have taken place within two days to one week (Hunter et al., 2010). Palaeoscolecid preservation includes fine details of the dorsal and ventral plates and their original arrangement in transverse rows, intercalary dorsal platelets and the extensive areas covered by microplates, arranged on a cuticle with polygonal to subquadrate reticulation (Figs. 4E–S). From the seven studied palaeoscolecid specimens, five are preserved stretched and the others are partially contracted, with annuli having a slightly concave forward shape in the anterior part of the body (Figs. 2B and 4B). In the dorsal part of each annulus, the contraction is shown by the out-folding of the central band of microplates into a crest, accentuated by the in-folding of the intercalary region between consecutive annuli (Fig. 4C), in an originally elastic body. This flexible, sclerite-covered cuticle has often been related with an infaunal mode of life (Kraft and Mergl, 1989), with occasional epifaunal excursions (Conway Morris and Peel, 2010), with alternating phases of muscular contraction and extension in which the plates grip onto the sediment while burrowing in a weakly cohesive substrate.

Preservation of palaeoscolecids is usually associated with mud-sized sediments from relatively deep-water or restricted environments, as is the case in most Cambrian and Ordovician Konservat-Lagerstätten around the world, but until now the group had never been recorded in shallow-water sandstones. In the Moroccan locality, the specimens range between dorso-ventrally to laterally compressed, and there is no evidence for sediment infilling between the body layers. The preservation of fine details of the soft cuticle in such coarse sediment has been explained by a microbial mat covering the decaying carcass prior to burial and compaction, which favoured an early-diagenetic phosphate precipitation. Microbial activity has been invariably implicated in the calcium phosphate replication of the palaeoscolecid original soft cuticle (Botting et al., 2012; Duan et al., 2012). Our best-preserved material usually occurs as simple external moulds in sandstone, where secondary phosphate minerals were dissolved or partly replaced by a different phosphatic cast (Figs. 4A and D). Its nature has been investigated using EDS-SEM (Fig. 3), which reveals that the mineral coating is composed predominantly of Al, P, Ca, O, Sr, K and Fe, with traces of rare-earth elements (La, Ce, Nd). This aluminium phosphate has been identified as a strontian crandallite –$(Ca,Sr)Al_3(PO_4)_2(OH)_5 \cdot H_2O$–, probably derived by weathering of calcium phosphate, with aluminium released by the clay minerals also present in the rock. In those parts where the phosphatic cast has been lost either mechanically or through weathering, both inner and outer surfaces of the mould show the same composition of the rock matrix, which differs from the cuticular cast mainly by a higher content of Si and Al, a much lower trace element content, and an absence of P.

Phosphatisation in the Tafilalt Biota is not restricted to the palaeoscolecids, but probably extends to the digestive structures preserved in some trilobites. They are recognizable on the dorsal side of the internal moulds of certain genera by a three-dimensionally preserved dark band (Fig. 2E), which in other specimens has been weathered away leaving an axial tube (Figs. 2F–G), very obvious in some of the asaphid specimens illustrated by Van Roy (2006), Corbacho (2011) and Fatka et al. (2013). Whereas in ?*Birmanites calzadai* (Corbacho, 2011) the simple digestive tract runs from the posterior part of the cephalon to the end of the pygidial axis, in ?*Uralichas tardus* Vela and Corbacho, 2009 a wide axial black band runs from the anterior part of the glabella to the fourth thoracic ring, with limonitised lateral indications of probable digestive caeca. A single specimen of *Selenopeltis longispina* Vela and Corbacho, 2009 (Fig. 2G) has a gut running sagittally from the posterior part of the cephalon to the anterior part of the fifth thoracic segment, showing remains of metamerically placed digestive caeca. The latter closely resembles those present in a specimen of *Selenopeltis buchi* (Barrande, 1846) illustrated by Fatka et al. (2013, fig. 3). According to Lerosey-Aubril et al. (2012), a somewhat similar gut phosphatization has almost exclusively been observed in trilobites and other early arthropods, and has been explained by their uncommon ability to store ions (including phosphorus) in their digestive tissues, perhaps related to the moulting of their heavily-mineralised carapace. The restriction of the mineralization to the gut indicates a closed chemical system leading to a confined phosphate precipitation within the digestive lumen soon after death.

## 4. Materials and methods

Uncoated specimens were photographed with a Canon EOS 5D digital camera with a Canon Compact-Macro EF 50 mm (Figs. 2, 4A–D). Scanning electron microscopy was done on very thin, carbon coated, latex peels at 20 kV with a JEOL JSM-6400 (Fig. 4E–S), providing resolution down to the micron-scale of cuticular details. Energy Dispersive X-ray Spectroscopy was carried out with an Oxford X-Max$^{N}$ detector incorporated to the above-mentioned electron-microscope (Fig. 3).

## 5. Systematic palaeontology

Class Palaeoscolecida Conway Morris and Robison, 1986

Family Palaeoscolecidae Whittard, 1953

Genus *Gamascolex* Kraft and Mergl, 1989

*Type species. Gamascolex herodes* Kraft and Mergl, 1989

***Gamascolex vanroyi* sp. nov.** (Figs. 2A–B and 4)

*Type material.* Holotype MGM-6502-X, part and counterpart of an external mould showing dorsal and ventral sides. Six paratypes (MGM-6503-X to MGM-6508-X), all from the type locality, deposited at the Museo Geominero (Madrid, Spain).

*Locality and Horizon.* Uppermost part of the First Bani Group (beds equivalent to the Izegguirene Formation) at the Bou Nemrou locality, western Tafilalt region, Eastern Anti-Atlas, Morocco. Basal Sandbian global stage (= Uppermost Dobrotivian regional stage).

*Etymology.* After Peter Van Roy, researcher of Ordovician soft-bodied fossils who first drew attention to the presence of vermiform fossils at this Moroccan locality.

*Diagnosis.* A large species of *Gamascolex* (> 300 mm long and up to 18.5 mm wide) characterized by a body composed of more than 4,000 sub-equal annuli, ranging between 14–15 annuli per 10 mm (up to 20–24 per 10 mm in contracted specimens). Dorsal ornamentation of each annulus consists of two rows of elongated marginal plates (up to 190 µm long and 72 µm wide) bearing a maximum of 12–14 paired nodes, which are separated by an unarmed band occupied by numerous microplates of globular aspect. About 95–110 dorsal plates in half-circumference; average of 7–7.8 plates per 1 mm transverse (range: 6.5–9 per mm). Small platelets (30 µm wide) with 3–4 nodes, sporadically occur near the interannular area. Ventral ornamentation is usually formed by four rows of rounded plates, smaller (61–80 µm in diametre) than the dorsal plates and more irregularly arranged, also surrounded by microplates on a densely reticulate cuticle.

*Description.* The studied material consists of seven partial specimens of a large palaeoscolecid worm occurring in micaceous sandstone, with soft-tissues replicated in a light-coloured phosphatic mineralisation, or preserved as natural external moulds as a result of weathering removing the phosphatised soft-tissues. The maximum length of the body, measured in the most complete specimen which only lacks the anterior end (Fig. 2A), is 290 mm. Its width remains approximately constant along much of the body, being 9–10 mm in the compressed state, but widens anteriorly to 11 mm. The maximum observed width is 18.5 mm, measured at 44 mm from the anterior end in another specimen (Fig. 2B). The anterior end shows a pronounced tapering, its width rapidly increasing posteriorly to 10 mm within the first 13 mm in the holotype (Figs. 4A–B). Another specimen (Fig. 2B) shows a central structure 2 mm wide and at least 19 mm long, with faint traces of longitudinal strands, which are best interpreted as the retracted introvert. The posterior end shows a rounded termination (Fig. 2A), but its orientation does not allow the recognition of neither the paired nipple-like structures nor the spines or hooks that have been described in some other palaeoscolecids (García-Bellido et al., 2013 and references therein). Annuli of the scleritome are well recognized in most studied specimens. The number of annuli per 10 mm is 14 to15 in fully-stretched specimens (up to 20–24 per 10 mm in contracted individuals), decreasing to 11 annuli per 10 mm in the widest recorded specimen (Fig. 2B). Each annulus is defined dorsally by two rows of large marginal plates, oriented longitudinally to the body axis, and separated by a median zone of microplates (Figs. 4E–G). Each plate is elongate, with maximum dimensions of 190 µm long and 72 µm wide, and bears up to 12–14 paired nodes, subequal in size and about 20–40 µm in diameter (Figs. 4F–H). More rarely, some anterior plates also bear 2–3 central nodes towards the intersegmental area, which are less prominent than lateral-ones (Figs. 4I–J). The dorsal plates are regularly spaced (95–110 per half-circumference; with a range of 6.5–9 plates per transverse millimetre, but averaging 7–7.8) and only sporadically show smaller platelets (30 µm wide) with 3–4 nodes, which are intercalated near the interannular area (Fig. 4H). The space between the two rows of dorsal plates, as well as between adjacent plates, is occupied by numerous papillae-like microplates (Figs. 4J, P, Q).

Diameter of these microplates often decreases slightly close to the main plates and ranges between 2 and 7 µm (average 5–6 µm). The cuticle shows a polygonal pattern wherever the microplates have been lost (Fig. 4R). The dorsal boundary between two consecutive annuli is defined by an intercalary zone with fine microplates, with a somewhat transverse orientation. The plates do not reach the annuli boundary in stretched specimens, and occasionally vary in position between opposing and alternating between consecutive rings (Figs. 4E–F). On the ventral side of each annulus, there are usually four rows of rounded plates (Figs. 4K–N), more irregularly arranged than dorsal plates and of smaller size (61–80 µm in diameter). Each plate bears 4–7 marginal nodes, a central node is never present (Fig. 4O). Apparently there are no platelets, and the numerous microplates, about 3.4–9 µm in diameter, also show transverse arrangement in the intercalary region between consecutive annuli, following a sub-quadrate pattern (Fig. 4S). The transition from the dorsal to the ventral sides of each annulus is gradual, with each band of dorsal plates splitting into two rows of shorter ventral plates (Fig. 4L).

*Discussion.* The studied specimens can be assigned to *Gamascolex* Kraft and Mergl, 1989, due to the large size of the body, the differentiated ornament on dorsal and ventral sides of the cuticle, and by the elongate shape of the dorsal plates with two well defined rows of nodes. As in *Palaeoscolex* Whittard, 1953 and other genera like *Milaculum* Müller, 1973 (= *Plasmuscolex* Kraft and Mergl, 1989), *Shergoldiscolex* Müller and Hinz-Schallreuter, 1993 or *Murrayscolex* Müller and Hinz-Schallreuter, 1993, the plates form regular bands, separated by unarmed zones (Conway Morris, 1997), but *Gamascolex* is the only known genus that combines a ventral ornamentation strikingly different from the dorsal side. However, the Moroccan form differs from the Czech type species *G. herodes* Kraft and Mergl by its larger size (maximum preserved length of 290 mm compared with specimens of over 145 mm), more dense and regular annulation (> 4,500 instead of >500 annuli: average of 14–15 vs. 9–25 annuli in 10 mm), longer dorsal plates and comparatively smaller, more numerous and irregularly arranged ventral plates. The distinct two rows of ventral plates, characteristic of *G. herodes*, are never seen among our material. No evidence of longitudinal ridges were observed neither on the dorsal nor ventral sides of the Moroccan palaeoscolecid. All these differences justify the erection of a new species.

*Occurrence.* Only know from the type locality, top of the First Bani Group (basal Sandbian), Eastern Anti-Atlas, Morocco.

## 6. Conclusions

Articulated scleritomes of a large palaeoscolecid worm, showing exceptional *in situ* preservation both of the sclerites (30–190 µm) and microplates of the connecting cuticle (about 2–9 µm in diameter), are described for the first time from the Late Ordovician of North Africa. Older articulated material from a different organism, though not described or figured, was already reported from the Lower Ordovician shales of the Fezouata Biota by Van Roy *et al.* (2010) and Martin et al. (2013). Fossilization in shallow-water sandstones of the studied specimens, coming from the Tafilalt Biota, may have involved microbial mats covering the carcass, which could have favoured phosphate precipitation prior to extensive decay. The Moroccan material, and in particular the new species *Gamascolex vanroyi* here described, represents the highest palaeolatitudinal record for palaeoscolecids, which in the Upper Cambrian moved to cold-temperate waters off Gondwana (García-Bellido et al., 2013).

The occurrence of –probably phosphatized– digestive structures in some trilobites provides an additional example of soft-part preservation in this Konservat-Lagerstätte, in agreement with the central role that the arthropod gut played in its own phosphatization (Lerosey-Aubril et al., 2012).

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## FIGURE CAPTIONS

Figure 1. A, Map indicating the position of the studied region in Africa. B, Geological sketch map of the central and eastern Anti-Atlas of Morocco, showing the position (star) of the Jbel Tijarfaïouine area (modified from Gutiérrez-Marco et al., 2003). C, Sketch map of the area around the Bou Nemrou locality.

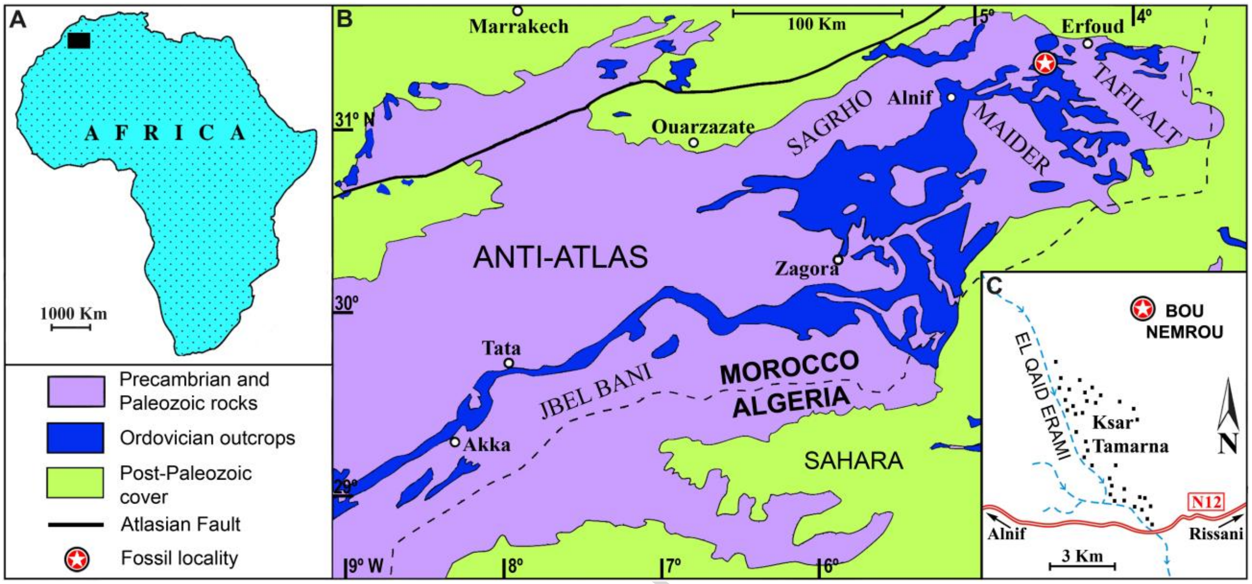
Figure 2. Soft-bodied preservation in sandstone from the Bou Nemrou assemblage (earliest Late Ordovician), Tafilalt Biota. A–B, *Gamascolex vanroyi* sp. nov. (paratypes), a large specimen with slightly coiled posterior end (A), and anterior part of a wide individual with contracted proboscis (arrow, B), MGM-6503-X and MGM-6504-X, respectively; C, "*Eldonia*" cf. *berbera* Alessandrello and Bracchi, paropsonemid disc showing trace of gut (arrow, 'coiled sac' in Alessandrello and Bracchi, 2003), MGM-6509-X; D, *Duslia* cf. *insignis* Jahn, non-biomineralised cheloniellid arthropod, MGM-6510-X –left– and MGM-6511-X –right–; E, ?*Uralichas tardus* (Vela and Corbacho), articulated cephalon and thorax showing dark,

phosphatised gut –unnumbered specimen in exhibit at the Tahiri Museum of Palaeontology of Erfoud (Morocco); F, ?*Birmanites calzadai* (Corbacho), asaphid trilobite showing longitudinal trace of the gut (arrows) –unnumbered specimen in the same exhibit as E–; G, *Selenopeltis longispina* Vela and Corbacho, odontopleurid trilobite with preserved gut (arrow) –specimen in the private collection of Luis Villa (Azuqueca de Henares, Spain)–. Scale bars: A, 20 mm; B, 10 mm; C–G, 30 mm.

Figure 3. One of the Energy Dispersive X-ray Spectroscopy (EDS) analyses performed on the dorsal plates of *Gamascolex vanroyi* sp. nov., which reveal casting by strontian crandallite, with some aluminum released by the clay minerals of the rock, whereas the original non-biomineralised cuticle has been completely lost. The composition of the natural moulds enclosing the phosphatic cast is the same as the rock matrix, and mainly differs by a higher content in aluminum silicates, absence of phosphorous and by a much lower content in rare-earth trace elements.

Figure 4. Holotype specimen and details of trunk ornamentation of *Gamascolex vanroyi* sp. nov., Tafilalt Biota, earliest Late Ordovician of Morocco. A, MGM-6502-X preserved in sandstone, showing light-coloured phosphatic replacement of dorsal surface, compressed over the natural external mould of the ventral surface; B, counterpart of the anterior portion of the same specimen seen by the dorsal side; C, detail of B, external mould showing contracted annuli and rows of dorsal plates; D, detail of framed area in A, with dorsal surface (positive relief) cast over the external mould of the ventral side; E, Dorsal details of two consecutive annuli (arrows) showing

the pair of transverse rows of plates separated by the central band of microplates in each annulus; F, dorsal view of a slightly contracted annulus; G, dorsal view of extended annulus; H–J, elongated dorsal plates, some with central nodes, and intercalatory platelet (arrow in H); K–M, consecutive annuli in ventral view, showing irregular rows of plates, in L grading into dorsal plates (to the left); N–O, general arrangement an detail of a ventral plate; P–Q, microplates arranged in dorsal area and between plates; R, polygonal pattern of the cuticle after the loss of microplates; S, sub-quadrate pattern of the microplates in the intercalary region between consecutive annuli. A to D are natural moulds of holotype specimen preserved in sandstone; E to S are SEM images of latex peels from the external ornament of the holotype (figs. E–K and M–S) and paratype MGM- 6507-X (fig. L). Scale bars: A–B, 10 mm; C, 1 mm; D, 2 mm; E and K–M, 300 µm; F–J, N and P, 100 µm; O and Q, 50 µm; R, 10 µm; S, 30 µm.


A
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1000 Km
Precambrian and Paleozoic rocks
Ordovician outcrops
Post-Paleozoic cover
Atlasian Fault
Fossil locality
B
Marrakech
100 Km
5°
Erfoud
4°
31° N
Ouarzazate
SAGRHO
Alnif
MAIDER
TAFILALT
ANTI-ATLAS
Zagora
30°
Tata
JBEL BANI
MOROCCO
ALGERIA
Akka
SAHARA
29°
9° W
8°
7°
6°
C
BOU NEMROU
EL QAID ERAMI
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N
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3 Km

Figure 1

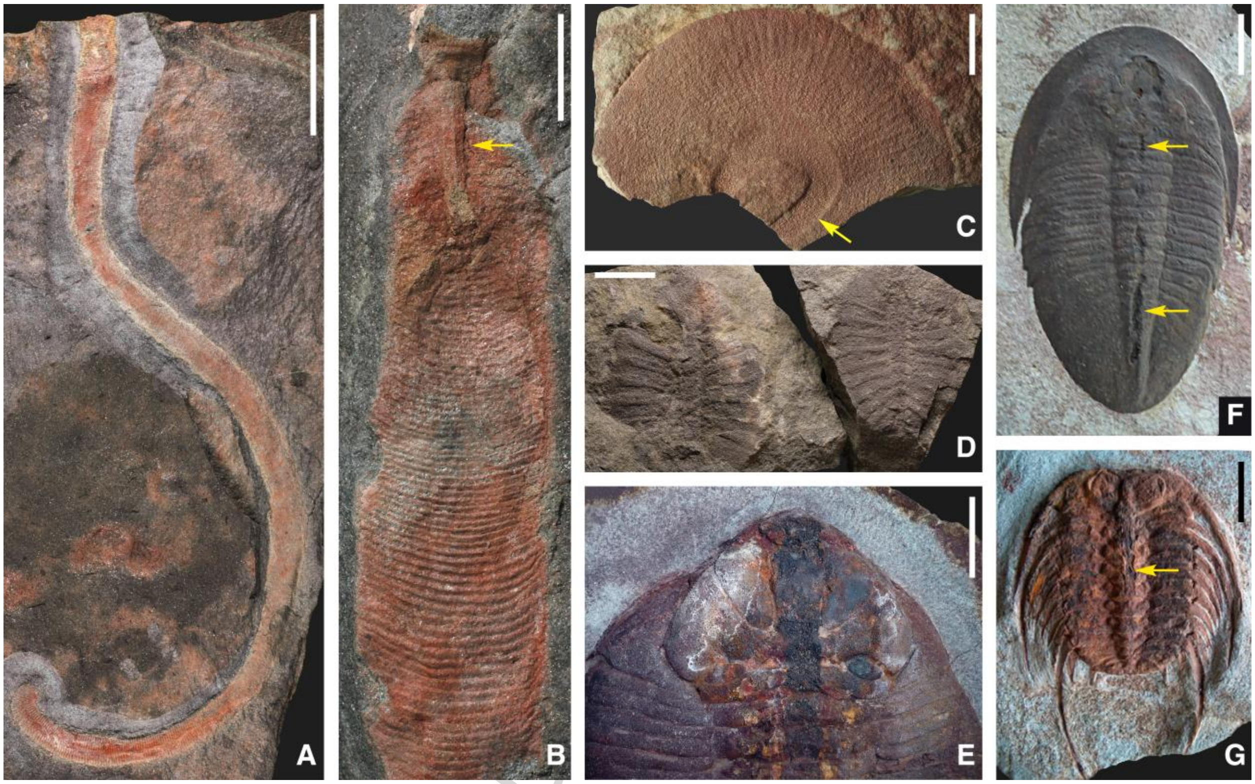

Figure 2

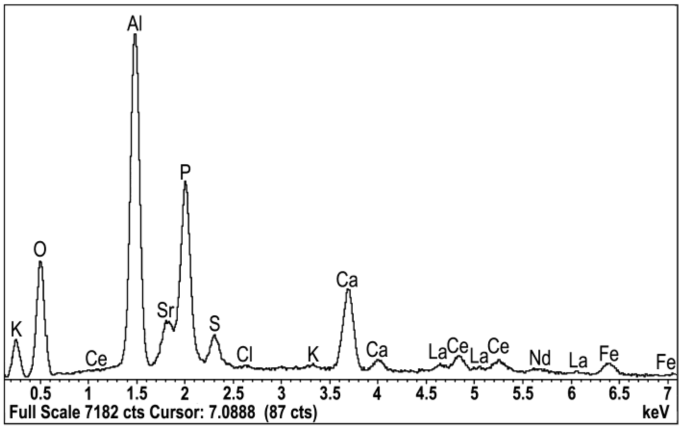
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Figure 3

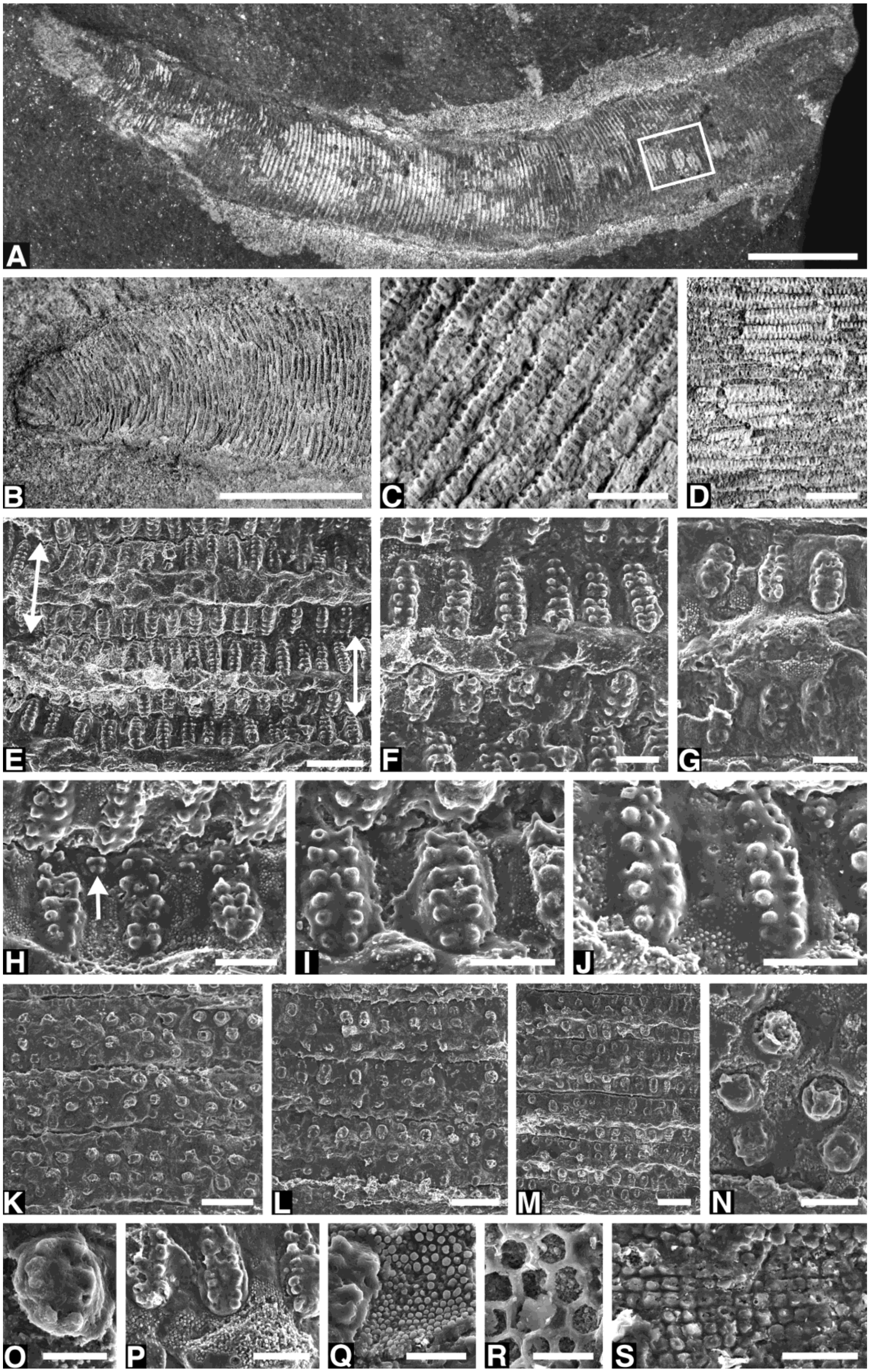
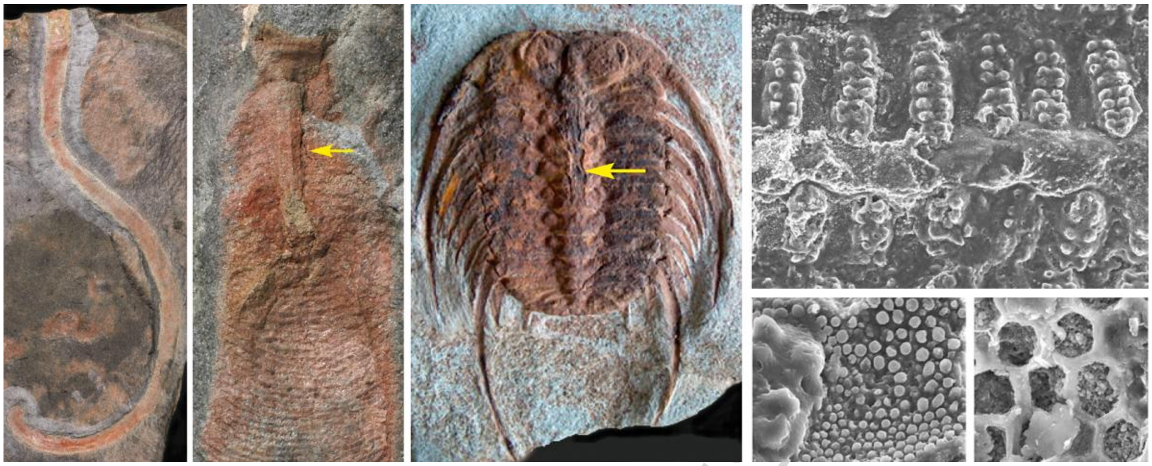


Figure 4



Graphical abstract

Highlights

- Coarse-sandstone can replicate micron-scale soft-body details.
- Diverse assemblage in a high-latitude Upper Ordovician Lagerstätte.
- First articulated palaeoscolecid worm in Africa extends European range.