

New palaeoscolecid plates from the Cambrian Stage 3 of northern Mongolia

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New material of disarticulated paleoscolecid remains have been found in “Small Shelly/Skeletal Fossils” assemblages from Cambrian Stage 3 extracted from a section in the Khubsugul Lake region of northern Mongolia. The current material is composed of isolated phosphatic plates, rendering the whole-body reconstruction and comparisons difficult. However, the morphology of the plates is unique enough to warrant description of a new genus and species *Floraconformis egiinensis*. The new taxon is characterized by a stellate depression network spreading from the middle that separates numerous elevations. *Floraconformis egiinensis* gen. et sp. nov. represents one of the oldest records of isolated palaeoscolecid plates.

Key words: Small Shelly Fossils, biomineralization, palaeoscolecid, Cambrian Explosion, Mongolia.

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Introduction

Palaeoscolecids represent an extinct class of millimetric to decimetric worm-like organisms characterized by an annulated, cylindrical body with a cuticle consisting of numerous individual button-shaped plates or platelets. Recovered as body fossils and isolated phosphatic or phosphatized plates, palaeoscolecids occur widely from Cambrian Series 2/ Stage 3 to the upper Silurian (Müller and Hinz-Schallreuter 1993; Ivantsov and Wrona 2004; Conway Morris and Peel 2010; Topper et al. 2010; Garcia-Bellido et al. 2013; Wang et al. 2014; Smith 2015; Kouraiss et al. 2018; Wendruff et al. 2020; Whitaker et al. 2020; Leibach et al. 2021; Shi et al. 2022). Most studies agree that palaeoscolecids *sensu lato* represent a grade within ecdysozoans, although their precise biological affinity within the Ecdysozoa remains unresolved (Smith 2015). However, palaeoscolecids *sensu stricto* (see Smith 2015; Smith and Dhungana 2022) are more likely to be the stem lineage of either Priapulida or Nematomorpha (Harvey et al. 2010; Wills et al. 2012). Recent studies proposed the creation of a new clade Palaeoscolecidomorpha (Shi et al. 2022), which is equivalent to Palaeoscolecida *sensu lato* in Harvey et al. (2010). Significantly, this clade is introduced as stem-group Priapulida, not as a potential stem lineage of the Nematomorpha.

Here we report fossils found in the form of isolated plates in a SSFs assemblage from the Khubsugul Lake region of northern Mongolia. All names applied to palaeoscolecid plates in SSFs assemblages (for example the common taxon *Hadimopanella* Gedik, 1977) are regarded as form taxa, due to their isolated nature (Topper et al. 2010). Indeed, making the connection between isolated plates and a whole-body taxon is difficult. Different types of plates may co-occur on the same animal (e.g., *Palaeoscolex spinosus* Ivantsov and Wrona, 2004 or *Hadimopanella oezgueli* Gedik, 1977; Barragán et al. 2014b) and morphologically identical plates may occur in different biological species (e.g., *Rhomboscolex chaoticus* Müller and Hinz-

Schallreuter, 1993, and *Corallioscolex gravius* Müller and Hinz-Schallreuter, 1993). Nonetheless, the vast majority of plates described herein are sufficiently different from any previously described palaeoscolecid fossils to merit taxonomic description as a new genus and species, *Floraconformis egiinensis* gen. et sp. nov.

Nomenclatorial acts.—This published work and the nomenclatorial acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:D9B96732-5853-49C5-9AA8-FF-F4A283F85E

Institutional abbreviations.—NRM, Swedish Museum of Natural History, Stockholm, Sweden.

Other abbreviations.—SSFs, Small Shelly Fossils.

Material and methods

The samples were collected during the 2019 field campaign to northern Mongolia. All fossils documented here are from a single measured stratigraphic section, named Khuhtolgoi (Fig. 1; 50°08'31.6" N, 100°04'47.7" E). The section intersects an interval within the Erkhelnuur Formation of the Khubsugul Group. The Erkhelnuur Formation is about 2000 m thick in this region and is composed of alternating limestone and dolostone beds (Anttila et al. 2021). The base of the 131.9 m thick (true thickness) Khuhtolgoi section is characterised by dark-grey limestone and dolostone beds that transitions to dark-grey micritic limestone. Trilobite fragments appear at 87.74 m above the base of the section followed by archaeocyathids at 128.04 m. The presence of trilobites and archaeocyathids suggest correlation with the recently defined Middle Member of the Erkhelnuur Formation (Anttila et al. 2021). However, as the Khuhtolgoi section is fault bounded at both bottom and top, its exact stratigraphic position within the Erkhelnuur Formation cannot be precisely determined.

The isolated palaeoscolecid plates have been recovered from six samples situated 121.84–130 m above the base of the Khuhtolgoi section. The age of the section is likely to represent the unnamed Cambrian Series 2, Stage 3 and can be correlated with the Atdabanian stage of Siberia (Dorjnamjaa and Altanshagai 2015; Korovnikov and Lazarev 2021). The presence of *Rhombocorniculum cancellatum* (Cobbold, 1921) suggests correlation with upper part of Cambrian Stage 3 (Steiner et al. 2007; Topper et al. 2007, 2009; Wotte and Sundberg 2017; Korovnikov et al. 2018; Wallet et al. 2022).

To extract fossils from the rock, limestone samples were washed and placed in a solution of 5% acetic acid for several days. Acetic residues were sieved, dried, and the faunal elements were hand-picked from the residue under a binocular microscope. Selected specimens were set on a stub and gold coated, to be analysed with a Quanta 650 FEG SEM housed at the NRM, using an accelerating voltage of 15 kV.

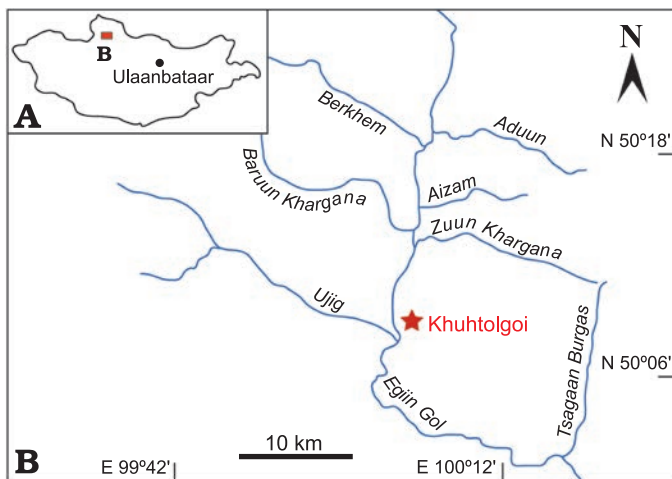


Fig. 1. A. Map of Mongolia showing location of the studied section. B. Precise location of the section Khuhtolgoi.

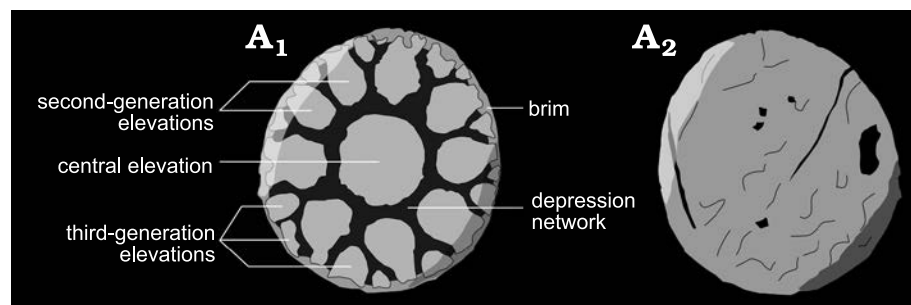


Fig. 2. Schematic drawing of palaeoscolecid *Floraconformis egiinensis* gen. et sp. nov. plate showing the terminology used, based on specimen NRM X11497; outer (A_1) and inner (A_2) side.

In this study, a total of 260 plates were found and 80 were selected for morphological analysis and measurements. Measurements were obtained using the tools available in the SEM during the imaging process. All measurements (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app68-Goni_et_al_SOM.pdf) represent the mean diameter. The material is stored at the NRM, in the Department of Palaeobiology.

The morphological terminology used herein predominantly follows that of Topper et al. (2010) and Whitaker et al. (2020). Palaeoscolecid plates are generally characterized by an ornamented outer side and a smooth inner side. The outer side of the plates are typically ornamented by a series of protuberances, referred to as nodes that can vary widely in morphology and display a range of configurations. The plates of *Floraconformis egiinensis* gen. et sp. nov. however, do not possess nodes, but are instead characterized by a depression network, that covers the outer side. The depression network defines a maximum of three categories of elevations: a large central elevation, smaller second-generation elevations, and third-generation elevations (Fig. 2). A brim represents the peripheral region of the plate but is only present when the network does not reach the edge of the plate.

Systematic palaeontology

Superphylum Ecdysozoa Aguinaldo, Turbeville, Linford, Rivera, Garey, Raff, and Lake, 1997

Phylum uncertain

Clade Palaeoscolecidomorpha Shi, Howard, Edgecombe, Hou, and Ma, 2022

Class Palaeoscolecida Conway Morris and Robison, 1986

Order uncertain

Family ?Palaeoscolecidae Whittard, 1953

Genus *Floraconformis* nov.

ZooBank LSID: um.lsid:zoobank.org:act:C99D6FB6-64A2-49A4-8281-5002BAD9A925

Etymology: From Latin *flora*, flower and *conformis*, like; referring to the flower-like shape of plates.

Type species: *Floraconformis egiinensis* gen. et sp. nov. by monotypy; see below.

Diagnosis.—As for the type species.

Remarks.—The isolated plates described here are referred to the Palaeoscolecida based on the similarities to dermal plates of known palaeoscolecid worms (Müller and Hinz-Schallreuter 1993; Topper et al. 2010; Botting et al. 2012). Typical features of palaeoscolecid plates are present, like a phosphatic composition, circular to elliptical general shape, possessing one ornamented side, a porous core and a hyaline outer layer. As such it is reasonable to include these Mongolian fossils within the Palaeoscolecida.

Because *Floraconformis egiinensis* gen. et sp. nov. plates are not tuberculate it cannot readily be accommodated within the diagnosis of the family Palaeoscolecidae as proposed by Botting et al. (2012). Elevations on *Floraconformis egiinensis* gen. et sp. nov. plates described here are formed from the extension of the depression network. In contrast, plates belonging to the species of *Hadimopanella* Gedik, 1977, *Milaculum* Müller, 1973, *Kaimenella* Märss, 1988, and *Utahphospha* Müller and Miller, 1976, have elevations that are extensions of an otherwise solid surface. However, in other aspects, the plates fit well within the range of plate morphologies documented from the family and *Floraconformis egiinensis* gen. et sp. nov. is here regarded as a likely member of the Palaeoscolecidae. This assignment is supported by the presence of individual plates lacking ornamentation across a number of formally described palaeoscolecid genera, such as *Scathascolex* Smith, 2015, and *Utahscolex* Whitaker, Jamison, Schiffbauer, and Kimmig, 2020, that have been assigned to the Palaeoscolecidae based on the presence of features such as an annulated cuticle, that can only be observed on body fossils. The wide variety of ornamentation (or lack thereof) on the surface of plates seen across members of the family indicates that the definition of the family may need to be revised to better incorporate the morphological variability observed in isolated phosphatic plates.

The plates described herein are morphologically distinct from previously described palaeoscolecid plates, including those belonging to species of *Hadimopanella*, *Milaculum*, *Kaimenella*, or *Utahphospha*. All of these form genera bear nodes on their convex outer surface, whereas the elevations on *Floraconformis egiinensis* gen. et sp. nov. plates are created by the stellate depression network. The top surfaces of elevations are concave. Moreover, plates belonging to species of *Milaculum* and *Kaimenella* are elongated ovals and not circular as in *Floraconformis egiinensis* gen. et sp.

nov. The only known palaeoscolecid plates that bear some resemblance to those of *Floraconformis egiinensis* gen. et sp. nov. are that of a three-dimensionally preserved specimen from Australia (1 km north of Mt Murray, Duchess, Queensland; upper Templetonian stage in the Australian scheme; correlated with upper Wuliuan) described by Müller and Hinz-Schallreuter (1993) as *Palaeoscolecida* gen. et sp. indet. The single published image of this specimen shows a section through the cuticle, parallel to the surface and small plates are visible (Müller and Hinz-Schallreuter 1993: text-fig. 17D). The plates are circular, with a central delineated elevation and smaller elevations arranged around the central one, apparently separated by furrows. Unfortunately, the plates are lacking a detailed description, preventing precise comparison to *Floraconformis egiinensis* gen. et sp. nov. It is difficult to evaluate if this Australian specimen can be accommodated into the newly introduced genus *Floraconformis*. Alternatively, the specimen may represent a related taxon, but the lack of information regarding the Australian material prevents a definitive conclusion.

Floraconformis gen. nov. should be considered as a form genus (like *Hadimopanella*, *Milaculum*, *Kaimenella*, and *Utahphospha*) pending further analyses, as neither articulated material nor microplates have been found in the Mongolian material.

Stratigraphic and geographic range.—Cambrian Series 2, Stage 3; Khuhtolgoi section, northern Mongolia.

Floraconformis egiinensis gen. et sp. nov.

Figs. 3–7.

ZooBank LSID: urn:lsid:zoobank.org:act:7B85B938-9948-490A-B1F5-78649C6076AC

Etymology: For the river Egiin Gol that flows near the section and the type locality.

Holotype: NRM X11462; well preserved plate (Fig. 3).

Type locality: Khuhtolgoi, along the Egiin Gol river, south of Khubsugul Lake, northern Mongolia.

Type horizon: Samples Khu1-141.8 to Khu1-167.2, upper Erkhelnuur Formation, Khubsugul Group, Cambrian Series 2, Stage 3.

Material.—Holotype: NRM X11462; paratypes: NRM 11463, 11465, 11467, 11489–11535, 11554, 11555. Type material only.

Diagnosis.—Circular to slightly elliptical, biconvex, phosphatic plates. The outer side displays a stellate depression network that creates a series of elevations. The outer face of each elevation is slightly concave. The central elevation is the largest elevation and can occupy up to 30% of the entire width of the plate. A second large circular elevation is delimited from the brim of the plate and is typically divided into one or two concentric rings of smaller elevations by the depression network. Small tubercles are present on the brim when the outer hyaline layer is preserved.

Description.—All plates are circular to slightly elliptical in outline (Figs. 3, 4), with a diameter ranging from 98 to 233 μm (mean 147 μm , $n = 80$; see SOM). Both inner and outer sides are convex. The surface of the inner side is usu-

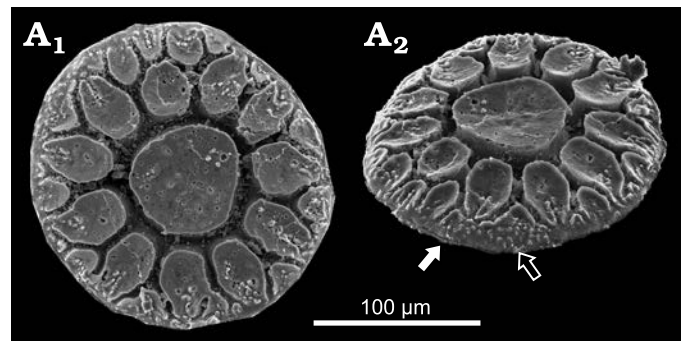


Fig. 3. Palaeoscolecid *Floraconformis egiinensis* gen. et sp. nov., plate from Khuhtolgoi section, northern Mongolia, Cambrian Stage 3. Holotype NRM X11462 in dorsal (A_1) and dorso-lateral (A_2) views. The white arrow shows the small gap present on few plates, at the bound between inner and outer sides. The black arrow shows small tubercles that are present on the brim, when the outer hyaline layer is preserved.

ally smooth, although a fingerprint-like structure can be observed in a few specimens (Fig. 5A). The outer side displays various ornamentations based on the formation of the depression network; a deeply incised network of furrows separates a series of elevations (Figs. 3, 4). This network demarcates a central circle with radiating and bifurcating rays, which result in a stellate appearance. Morphological variation of the stellate pattern depends predominantly on the development of the depression network. In some samples, a wide marginal brim can be observed when the depression network is focused in the middle of the plate (Fig. 4O), but in others, the brim is narrow or absent when the depression network reaches the margin of the plate (Fig. 4A). The depression network defines a variety of elevations that range from circular to oval in shape, with a slightly concave top surface (Figs. 3, 6). The top of the elevations is usually wider than in the middle, giving the impression that the margins of the elevations slightly overhang the depressions (Figs. 3, 6).

There is almost always a single central circular to elliptical elevation that is larger than the surrounding elevations. This central elevation occupies approximately 30% of the entire plate width (see SOM). The central elevation is surrounded by a ring of between 6 and 11 second-generation elevations that are delimited from the brim by a step (Fig. 4J₂; see also Fig. 4O, R). The second-generation elevations are smaller than the central elevation and have two main characteristics: (i) they are disposed radially around and adjacent to the central elevation, forming a ring and (ii) they are usually elongated toward the margin of the plate. Sometimes a third generation of elevations (formed between the second-generation elevations as the depression network bifurcates towards the edge) are visible closer to the edge of the plate (Figs. 3, 4B). These have a similar shape to the other elevations but are smaller. Total number of elevations varies up to 33, depending on the development of the depression network (which may be variable across the plate). The space between the top of the elevations (or the width of the depression network) is also highly variable and ranges 7.6–21.6 μm (measurements in plan view).

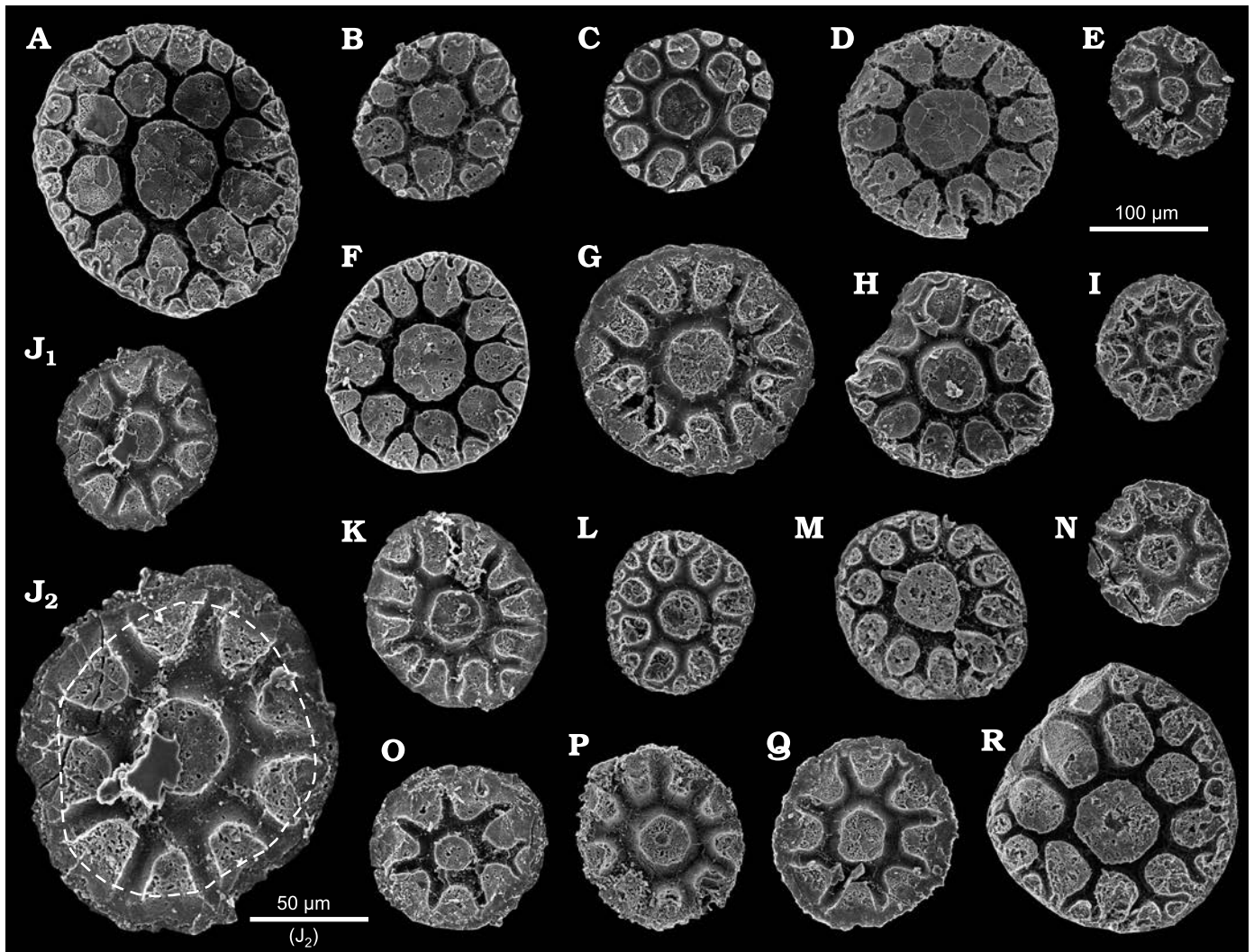


Fig. 4. Palaeoscolecid *Floraconformis egiinensis* gen. et sp. nov., plates (in dorsal view) from Khuhtolgoi section, northern Mongolia, Cambrian Stage 3. A. NRM X11465. B. NRM X11493. C. NRM X11502. D. NRM X11492. E. NRM X11489. F. NRM X11497. G. NRM X11495. H. NRM X11521. I. NRM X11508. J. NRM X11505 in general (J₁) and close-up (J₂) views; the dashed line in J₂ represents the second large elevation delimited from the brim mentioned in the diagnosis. K. NRM X11500. L. NRM X11513. M. NRM X11499. N. NRM X11490. O. NRM X11496. P. MNRM X11491. Q. NRM X11523. R. NRM X11463.

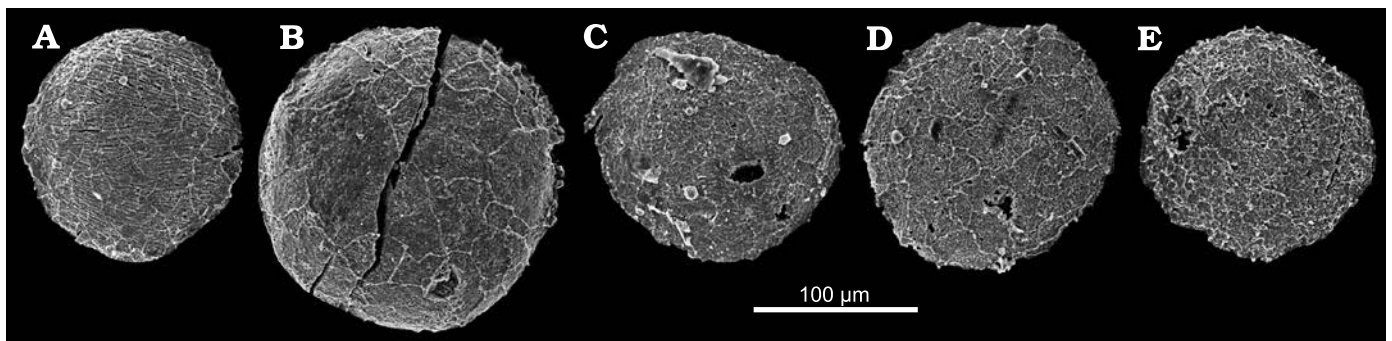


Fig. 5. Palaeoscolecid *Floraconformis egiinensis* gen. et sp. nov., plates (in ventral view) from Khuhtolgoi section, northern Mongolia, Cambrian Stage 3. A. NRM X11516; note the fingerprint-like ornamentation on this plate. B. NRM X11522. C. NRM X11498. D. NRM X11518. E. NRM X11501.

Two kinds of textures can be observed on the plate surface: a thin hyaline outer layer, which covers a porous core. The hyaline external layer is predominantly smooth, but infrequently it bears some small tubercles on the brim (Fig. 3)

or on the most external elevations (Fig. 4A). Generally, the hyaline layer is not preserved, revealing the porous core's fibrous structure (Fig. 6). Around the circumference of the plate at the junction between the inner and the outer sides, a

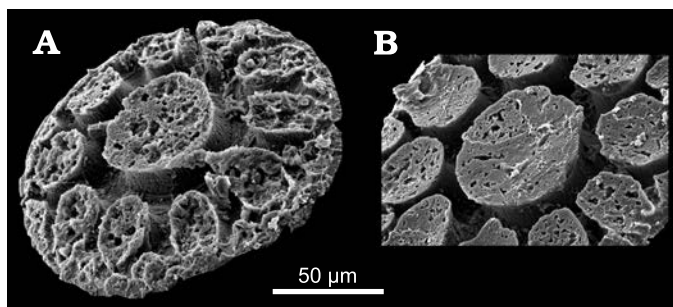


Fig. 6. Fibrous structures observed on elevations on the dorsal sides of palaeoscolecid *Floraconformis egiinensis* gen. et sp. nov., plate from Khuhtolgoi section, northern Mongolia, Cambrian Stage 3. these structures are only visible when the outer hyaline layer is absent. A. NRM X11499. B. NRM X11497.

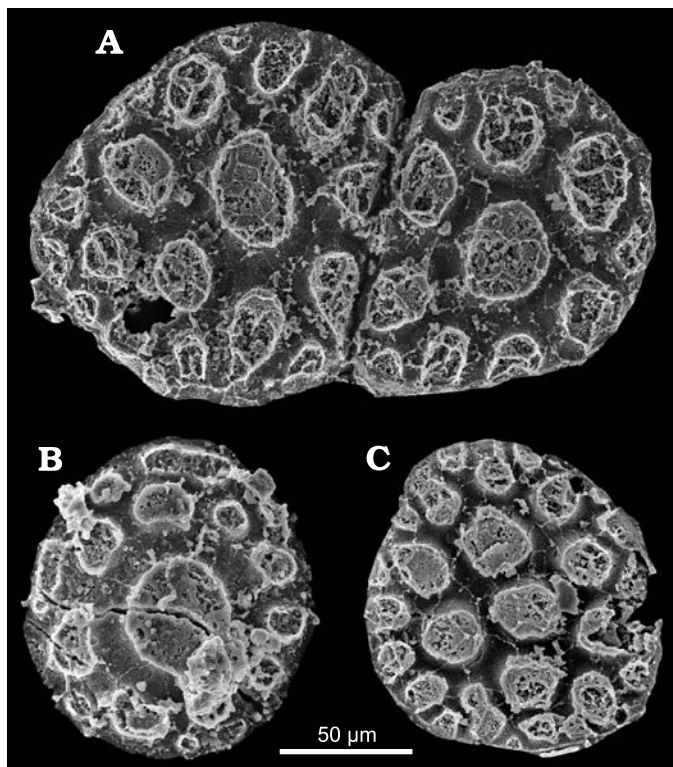


Fig. 7. Unusual plates of palaeoscolecid *Floraconformis egiinensis* gen. et sp. nov. from Khuhtolgoi section, northern Mongolia, Cambrian Stage 3. A. NRM X11467; two merged plates. B. NRM X11524; second and third-generation elevations are not elongated toward the margin but parallel to it. C. NRM X11510; absence of the usual larger central elevation.

furrow of a few micrometres can be observed (Fig. 3: white arrow). This furrow is observed on plates, whether the hyaline layer is preserved or not.

Although most plates conform to the general pattern described above, a few plates in the collection differ slightly. In particular, one specimen consists of two merged plates (Fig. 7A). In this specimen, one plate is slightly larger in diameter (134 vs. 108 μm), but the size of the elevations and the width of the depression network are approximately the same across both plates. The junction between the plates is a straight furrow, narrower but slightly deeper

than the usual depression network. Usually, plates are isolated and circular (Fig. 4), without any deformation along the edge, suggesting that they were not arranged immediately next to each other in the cuticle. Even though this specimen is an isolated case among 260 specimens, it indicates that plates could be formed in direct association with each other within the cuticle. In another unusual specimen (Fig. 7B), second-generation elevations are not elongated radially toward the edge of the plate, but are elongated parallel to the edge around the central elevation. A third unusual type of plate has no well-defined large central elevation (Fig. 7C). In this specimen, there are two approximately central elevations that are slightly larger than the other elevations.

Remarks.—Articulated-body preservation of Cambrian palaeoscolecids reveals that plates across a range of morphologies can occur in the scleritome of a single animal (Müller and Hinz-Schallreuter 1993; Ivantsov and Wrona 2004; Topper et al. 2010; Smith 2015; Streng et al. 2017). The development of different plate morphologies in palaeoscolecid scleritomes may be related to particular locations on the body, environmental influences, or different developmental stages (Brock and Cooper 1993; Müller and Hinz-Schallreuter 1993; Harvey et al. 2010; Barragán et al. 2014a). *Floraconformis egiinensis* gen. et sp. nov. from Mongolia is known exclusively from isolated plates but these show a distinctive type of plate morphology and ornamentation (Fig. 4). The characteristic depression network that defines the concave elevations differentiates *Floraconformis egiinensis* gen. et sp. nov. from all other palaeoscolecid form taxa, and from plate morphologies of articulated taxa, with the possible exception of the plates of *Palaeoscolecida* gen. et sp. indet. from the Templetonian stage of Australia (correlated with Wuliuan; drilling Duchess 18.1 km north of Mt Murray, Queensland; *Triplagnostus gibbus* Zone; Müller and Hinz-Schallreuter 1993: text-fig. 17D). Although the morphology of the plates from Australia bears some similarities to that of *Floraconformis egiinensis* gen. et sp. nov., there are key differences. In particular, the plates from Australia are smaller (maximum diameter 70 μm) than the material from Mongolia described herein (minimum diameter 98 μm), and the elevations do not appear concave as in the Mongolian material.

According to Barragán et al. (2014a), the size of a palaeoscolecid plate is defined and fixed at its inception whilst the external ornamentation is secondary and variable. Articulated palaeoscolecid taxa typically bear plates that are between 20 and 60 μm in diameter (Müller and Hinz-Schallreuter 1993; Topper et al. 2010; Botting et al. 2012; Wang et al. 2014; Streng et al. 2014). However, larger plates comparable to those reported herein have been recovered from acid isolated plate assemblages. Two form species, *Hadimopanella knappologica* (Bengtson 1977) and *Hadimopanella oezguli* Gedik, 1977 have comparable or larger plate diameters of 460 and 400 μm maximum, respectively (Ivantsov and Wrona 2004; Kouchinsky et al.

2015; Barragán et al. 2014a). The size of *Floraconformis egiinensis* gen. et sp. nov. falls within the overall size range of Cambrian palaeoscolecid isolated plates. Further distinguishing characteristics include the presence of third-generation elevations and a brim in *Floraconformis egiinensis* gen. et sp. nov., not seen on the Australian plates. The palaeoscolecid specimen from Australia is also significantly younger (late Templetonian in the Australian scheme; correlated with late Wuliuan) than *Floraconformis egiinensis* gen. et sp. nov. from Mongolia (Atdabanian Stage in the Siberian scheme; correlated with Cambrian Stage 3). Pending additional material from Australia for comparison, we conclude that while Palaeoscolecida gen. et sp. indet. of Müller and Hinz-Schallreuter (1993) may be a closely related taxon, it is unlikely to be conspecific with *Floraconformis egiinensis* gen. et sp. nov. from Mongolia.

Stratigraphic and geographic range.—Type horizon and locality only.

Discussion

In addition to *Floraconformis egiinensis* gen. et sp. nov., two fragmentary fossil specimens (Fig. 8), morphologically sim-

ilar to species of the genus *Stoibostrombus* Conway Morris and Bengtson in Bengtson et al., 1990, are present 167.2 m above the base of the section. Although the biological affinity of *Stoibostrombus* remains unclear, the taxon has tentatively been affiliated with palaeoscolecid worms (Skovsted et al. 2011). The morphology of the Mongolian fragments fits with the diagnosis of the family Stoibostrombidae Conway Morris and Bengtson, 1990, however, the basal ornamentation is distinctive. The basal ornament consists of separate, small, button-shaped elements with concave top surfaces similar to the elevations in *Floraconformis egiinensis* gen. et sp. nov. A thin hyaline layer covers these elements (Fig. 8A₃), under which the support is porous (Fig. 8B₃). The differences in basal ornament indicates that these fragmentary cones from Mongolia do not conform to the type and only species, *Stoibostrombus crenulatus* Conway Morris and Bengtson in Bengtson et al., 1990 (Bengtson et al. 1990: figs. 93–98). We instead suggest that they may be sclerites associated with *Floraconformis egiinensis* gen. et sp. nov. or a similar taxon, possibly representing the aboral spines that are preserved on some palaeoscolecid specimens (Müller and Hinz-Schallreuter 1993: text-fig. 11; Duan et al. 2012: fig. 2).

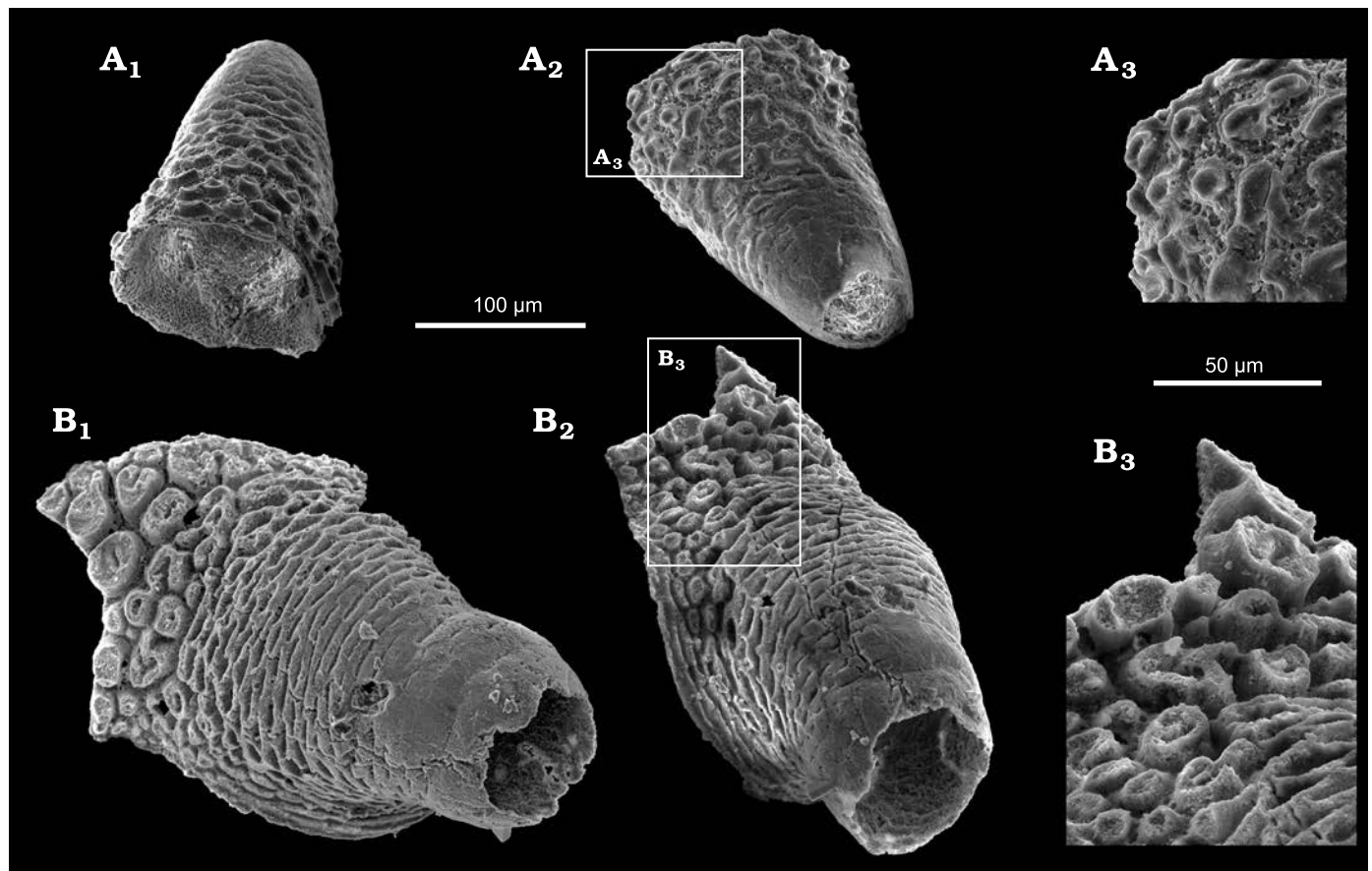


Fig. 8. Two conical fossils regarded as palaeoscolecid fragments from Khuhtolgoi section, northern Mongolia, Cambrian Stage 3. **A.** NRM X11556 in latero-abapical (A₁) and latero-apical (A₂) views, with a close-up on button-shaped elements (A₃). **B.** NRM X11556 in latero-apical (B₁, B₂) views, with a close-up on button-shaped elements (B₃).

Conclusions

Floraconformis egiinensis gen. et sp. nov. is the first palaeoscolecid recorded from northern Mongolia. Despite recovery as isolated plates, specimens of *Floraconformis egiinensis* gen. et sp. nov. are morphologically unique and can therefore be used to designate a new species. This contributes to the diversity of Cambrian palaeoscolecid form taxa, of which only members of four genera have been previously described: *Hadimopanella* Gedik, 1977, *Milaculum* Müller, 1973, *Kaimenella* Märss, 1988, and *Utahphospha* Müller and Miller, 1976. Despite significant faulting in the region, *Floraconformis egiinensis* gen. et sp. nov. can be confidently correlated with Cambrian Stage 3 and therefore represents one of the oldest reports of isolated palaeoscolecid plates in the fossil record.

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