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The lobopod *Onychodictyon* from the Lower Cambrian Chengjiang Lagerstätte revisited

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Onychodictyon ferox, from the Lower Cambrian Chengjiang Lagerstätte, is a worm-like armored lobopod with 10 pairs of dorsal plates and a pair of probable sensory appendages ("antennae"). Newly discovered complete specimens show that *Onychodictyon* is represented by two species: *O. ferox* with a "head" bearing a pair of dorsal "antennae" and a trunk with 11 pairs of limbs, whereas *O. gracilis* has a blunt anterior end without any appendages and a trunk with 12 pairs of limbs. Because of the close resemblance of the "antennae" of *O. ferox* and those of the lobopod *Miraluolishania*, they are considered to be homologous structures. The "antennae" of Cambrian lobopodians are proposed to be homologous with the arthropod antennulae.

Key words: Lobopodia, Arthropoda, antennae, Cambrian, Chengjiang Lagerstätte, Yunnan.

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Introduction

The first described lobopodian from the Cambrian was *Aysheaia pedunculata*, reported by Walcott (1911) from the Burgess Shale of Canada. Conway Morris (1977) identified another lobopodian, *Hallucigenia sparsa*, from the same beds. Their morphology and affinities have received broad attention (Whittington 1978; Dzik and Krumbiegel 1989; Hou and Chen 1989; Hou et al. 1991; Ramsköld and Hou 1991; Chen et al. 1995; Budd 1997, 1999; Budd and Peel 1998; Ramsköld and Chen 1998). The Lower Cambrian Chengjiang fauna in Yunnan, south China, has yielded nine further taxa (*Cardiodictyon catenulum*, *Microdictyon sinicum*, *Hallucigenia fortis*, *Onychodictyon ferox*, *Paucipodia inermis*, *Luolishania longicruris*, *Miraluolishania haikouensis*, *Jianshanopodia decora*, and *Megadictyon haikouensis*; Hou and Chen 1989; Hou et al. 1991; Ramsköld and Hou 1991; Chen et al. 1995; Ramsköld and Chen 1998; Luo et al. 1999; Liu et al. 2004, 2006, 2007), adding significantly to the knowledge of the group. Here we reappraise the lobopodian *Onychodictyon*, an armored animal with rigid plates and spines. *O. ferox* was first described by Ramsköld and Hou in 1991, after which there has been some debate about its morphology and affinities (Ramsköld 1992; Ramsköld and Chen 1998; Chen 2004; Hou et al. 2004). The focus of this ongoing debate is whether or not *O. ferox* had antennae. In this paper, we offer some new data on the morphology of this animal and report a new species, or a case of sexual dimorphism, of *Onychodictyon*: *O. gracilis* sp. nov., discovered at Haikou village, Yunnan, from the Qiongzhusi (Chiungchussu) Formation, Yu'anshan Member (*Eoredlichia* Zone), Lower Cambrian.

Institutional abbreviation.—ELI, Early Life Institute, Northwest University, Xi'an, China.

Material and methods

The material described here was recovered from a grayish-green and grayish-yellow mudstone of the Yu'anshan Member (*Eoredlichia* Zone), Helinpu (Chiungchussu) Formation, Lower Cambrian at Haikou, Kunming, Yunnan. Details of the locality and stratigraphy were given in Zhang et al. (2001). More than 70 specimens have been collected from these localities by the working team of the Early Life Institute, Northwest University.

In general, the morphological terms used in the description are those of Ramsköld and Chen (1998) whenever appropriate. The specimens were photographed with an Olympus OM-4 Ti camera. The direction of illumination was varied where necessary to illustrate different features.

Systematic paleontology

Phylum Lobopodia Snodgrass, 1938
Class Xenusia Dzik and Krumbiegel, 1989
Order Xenusiida Dzik and Krumbiegel, 1989

Family Onychodictyidae Hou and Bergström, 1995

Genus *Onychodictyon* Hou, Ramsköld, and Bergström, 1991

Type species: *Onychodictyon ferox* Hou, Ramsköld, and Bergström, 1991 (from Maotianshan, Chengjiang, Lower Cambrian).

Emended diagnosis.—A robust lobopod, subcylindrical in outline, consisting of a "head" and an elongate trunk. The trunk with 10 segments, each segment possessing a pair of dorsal round plates and lobe-like appendages on the ventro-lateral surface.

Remarks.—The genus *Onychodictyon* was first described by Hou et al. (1991) from Chengjiang. Our materials provide new information, indicating different species or sexual dimorphs that differ with respect to the presence or absence of "antennae". Accordingly, the generic diagnosis is revised herein.

Onychodictyon ferox Hou, Ramsköld, and Bergström, 1991

Material.—All specimens came from a grayish-green and grayish-yellow mudstone from the Jianshan section in Haikou village, Haikou County, and the Erjie section in Erjie village, Anning County, Kunming, Yunnan. Helinpu (Chiungchussu) Formation, Yu'anshan Member (*Eoredlichia* Zone), Lower Cambrian.

Diagnosis.—Robustly built lobopod, the body comprises a rounded "head" with "antennae", the trunk with 10 segments and 11 pairs of limbs, long papillae on body and limbs, 10 pairs of plates on the dorsal of the body.

Description.—One complete adult specimen of *Onychodictyon ferox* is about 50–70 mm long (Fig. 1A_1–A_3). It possesses a small head region, which is semi-round in shape. In specimen ELIJSO-013, the "head" is a little convex dorsally, with a semi-elliptical profile and a maximum sagittal length of 2 mm, approximately 50% of its width (Fig. 1A_1–A_5). A pair of flagellum-like structures is about 4 mm long and 0.5 mm wide, protruding from the dorso-lateral side of the "head"; compared with the trunk limbs, the flagellum-like structures are thin and gentle with no annuli or nodes. Therefore, they are most likely sensory appendages ("antennae") (Fig. 1A_1–A_5). Similar appendages also occur in dorso-laterally preserved specimen ELIMF-015B (Fig. 3D). No eyes and head shield are preserved.

The worm-like trunk region is sub-rounded in cross-section. It is composed of 10 segments, with a number of strong and clear annuli (Figs. 1A_1–A_5 and 3C_1, C_2). The anterior portion of the trunk in front of the 3rd segment comprises 2–3 annuli, the 4th, 5th, 6th, and 7th segments of the trunk possesses 5–6 further annuli, the posterior portion of the trunk behind the 7th segment bears 3 annuli (Fig. 1A_1, A_2). Each annulus has a vertical row of "tubercles"; there are usually 10 tubercles in one row observed around the circumference (Fig. 1A_1, A_2). Long, finely annulated appendicules extend from these "tubercles". In each annulus, the appendicules are symmetrically placed relative to the dorsal midline. As in the trunk limbs, fine canals can be observed in these protrusions (Fig. 1B_1, B_2).

Ten pairs of plates are located dorsally in turn in the 10 segments. Each plate is sub-rounded, shows three-dimensional structures (convexity, ridges, rims), with a central broad-based spine directed obliquely upward and out (Figs. 1A_1–A_3, B_1 and 2B).

There are 11 pairs of limbs, the anterior 10 attach at a circular area beneath each plate, the last pair located at the end of the trunk (Fig. 1B_1). The limbs are cylindrical, protruding ventro-laterally from the trunk, all possessing thin, transverse annuli, about 30 in number from the base to the tip (Fig. 1A_1, A_2, B_2). Each limb carries along its length at least two rows of tubercles, similar to those of the trunk (Fig. 1A_1, A_2, B_2). The number of tubercles in each row is at least 10, probably up to 20, and small appendicules can be observed protruding from these tubercles, as in specimen ELIJSO-002A (Fig. 2C), Compared to those of the trunk, the appendicules of the limbs are shorter and thinner. A pair of claws occurs at the end of each limb (Fig. 3E), the direction of each claw varies depending on the preservation of the specimens, except for the claws of limb 11, where the direction is usually bent anteriorly (Fig. 1B_1). The posture further underlines the adaptation of the posterior limb pair to an anchoring function, as suggested by Chen et al. (1995) and Ramsköld and Chen (1998).

The gut is straight and simple (Fig. 1A_1–A_3), usually preserved in a flattened black band, which lies near the ventral margin. No anus has been found.

Onychodictyon gracilis sp. nov.

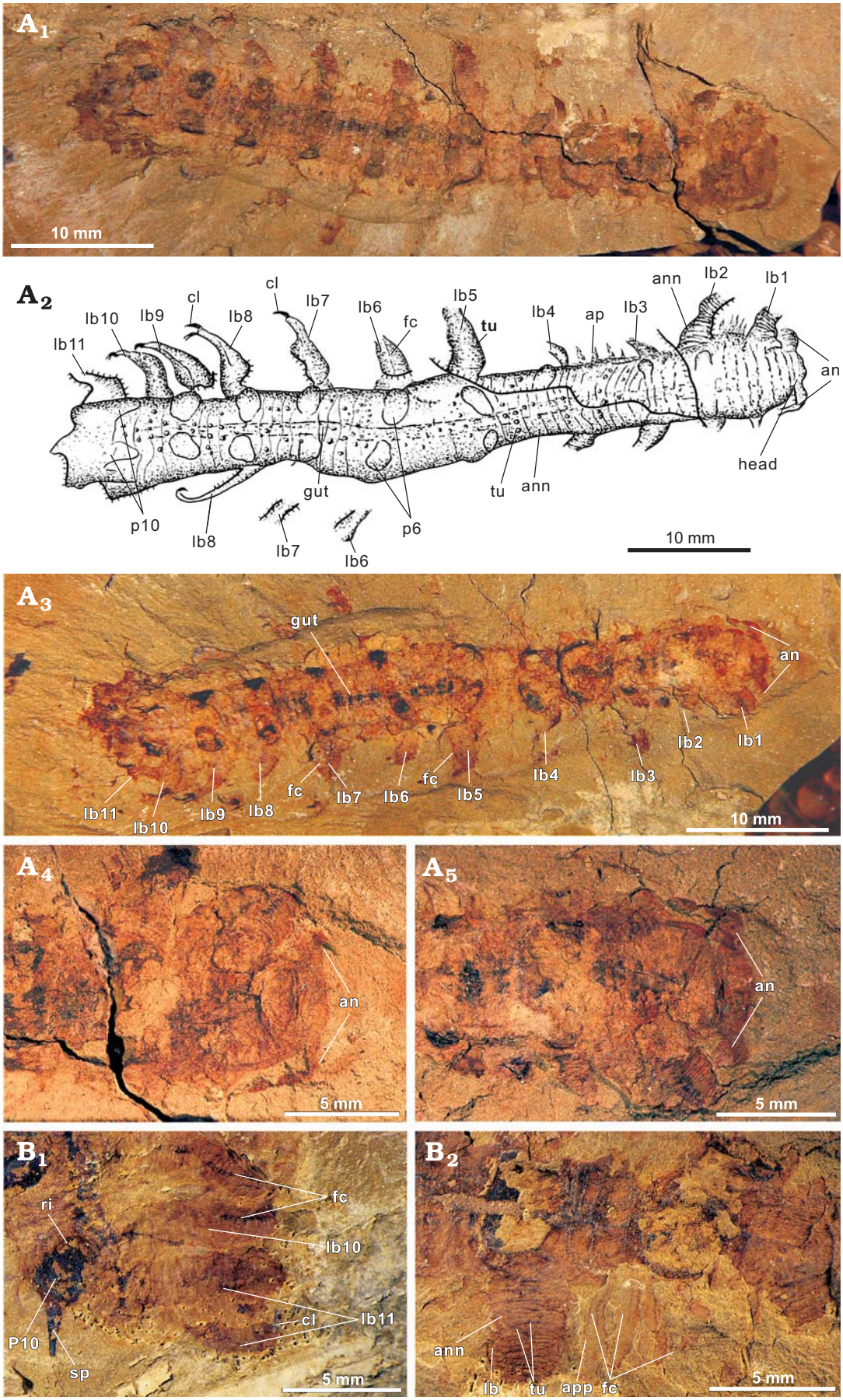
Figs. 2A_1–A_7, 3A_1–C_2.

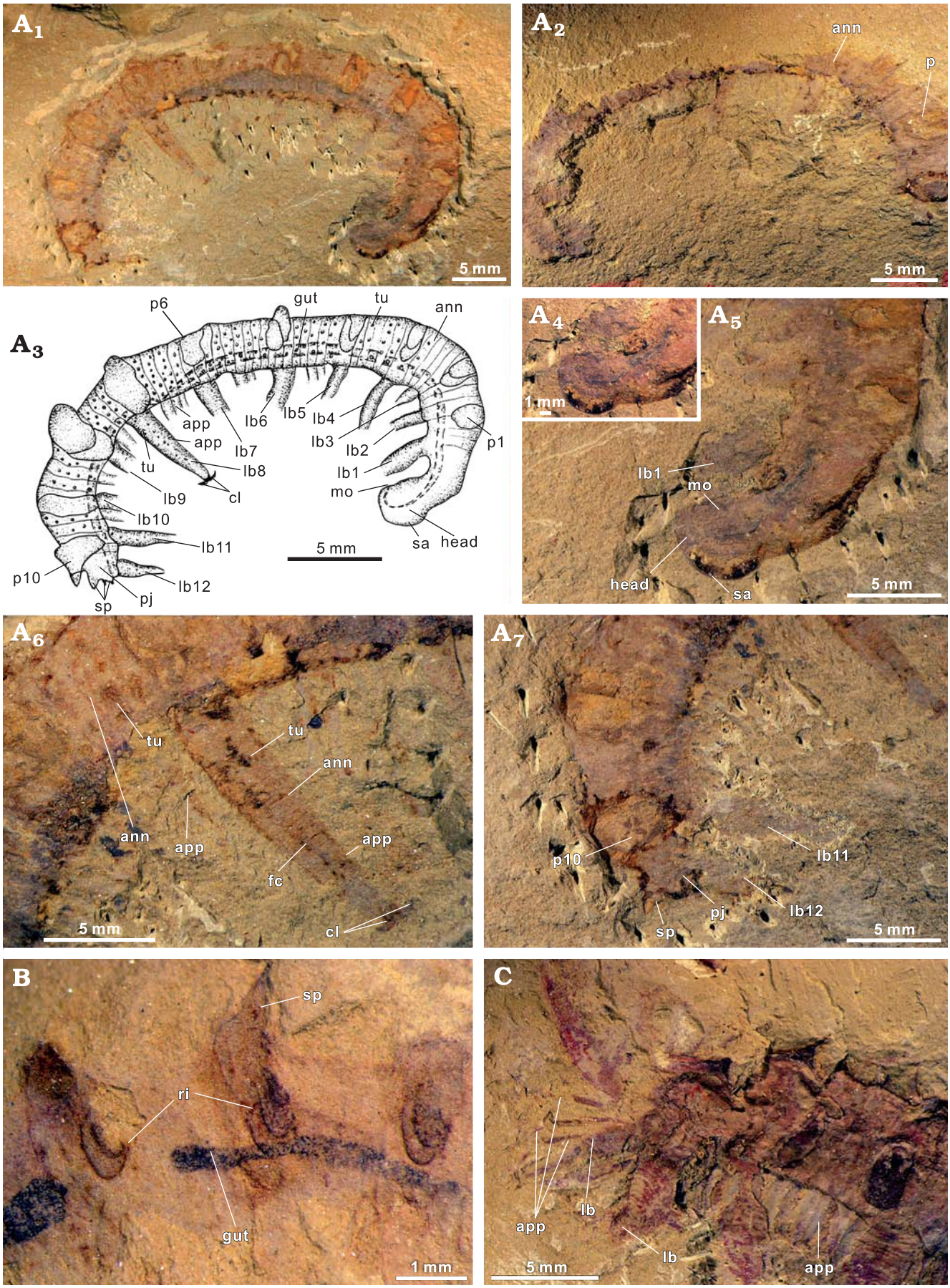
Holotype: ELIJSO-0003 (Fig. 2A_1–A_7); from the Jianshan section, Haikou county, Lower Cambrian.

Derivation of the name: *Gracilis* refers to its delicate appearance.

Diagnosis.—Relatively small to up to 50 mm, the body comprises a rounded "head" without "antennae", the trunk with 10 segments and 12 pairs of limbs, the posterior of the trunk bear-

Fig.1. Early Cambrian lobopod *Onychodictyon ferox* Hou, Ramsköld, and Bergström, 1991, from Haikou, Kunming, Yunnan, China. **A**. Specimen ELIJSO-013; A_1, part ELIJSO-013A, a nearly complete specimen, dorso-ventrally preserved; A_2, Camera lucida drawings of A_1, showing nearly all the main features of *Onychodictyon ferox*, note the paired "antennae", 10 pairs of plates, 11 pairs of limbs, the annuli and tubercles of both the trunk and limbs, the fine canal and claws of limbs; A_3, counterpart ELIJSO-013B showing the paired "antennae", 10 pairs of plates, 11 pairs of limbs and the gut; A_4, enlargement of the head area of A_1, note the paired "antennae"; A_5, enlargement of the head area of A_3, note the paired "antennae". **B**. Specimen ELIJSO-001; B_1, enlargement of the posterior area of ELIJSO-001A, showing the trunk end with the last pair of limbs and the limbs with fine canals; B_2, enlargement of the limbs and appendicula of *Onychodictyon ferox* ELIJSO-001B, note the annuli and tubercles of the limb and appendiculae with fine canal of the trunk. Abbreviations: an, "antennae"; app, appedicules; ann, annuli; cl, claws; fc, fine canal; lb, limb, lb1, the first pair of limb, lb2, the second pair of limb, and so on; p, plate, p1, plate 1, p6, plate 6, and so on; ri, rim of the plate; sp, spines; tu, tubercles. →





ing a short projection. Compared to *Onychodictyon ferox*, *O. gracilis* is smaller, more fragile-looking with more pairs of limbs.

Description.—Three complete specimens (ELIJSO-0003, ELIJSO-0005, and ELIEJO-0017) are known. All three were laterally compressed. The body can be divided into a well-defined head area, a trunk with 10 segments and a small posterior projection. The maximum length (sagittal) of the three specimens is 50 mm (ELIJSO-0003) (Fig. $2A_1$), 35 mm (ELIEJO-0017) (Fig. $3B_1$) and 12mm (ELIJSO-0005) (Fig. $3A_1$), transverse width amounts to 5 mm (ELIJSO-0003) (Fig. $2A_1$), 3.5 mm (ELIEJO-0017) (Fig. $3B_1$) and 1.5 mm (ELIJSO-0005) (Fig. $3A_1$).

The head area is clearly differentiated from the trunk, the ridge on the "head" is very smooth on the antero-ventral side, and a little sclerotized on the dorsal side of specimens ELIJSO-0003 (Fig. $2A_1$, A_3–A_5) and ELIEJO-0017 (Fig. $3B_1$–B_3). However, there is no sign of "antennae" or any other structures on the "head" (Figs. $2A_1$, A_3–A_5, $3A_1$–A_3, B_1–B_3). According to the black trace interpreted as the gut, the mouth is located on the antero-ventral side of the "head" (Figs. $2A_1$, A_3–A_5, $3A_1$–A_3, B_1–B_3).

The trunk region comprises 10 segments, each bearing a number of strong annuli (Figs. $2A_1$–A_3, A_6, $3B_1$, B_3, C_1, C_2), which range between 1 and 6 in number (Fig. $2A_1$, A_3). The number of annuli is in direct proportion to the longitudinal length of the segments. There are only 1–2 in the first segment, increasing to 4 in the 5th segment. The 6th, 7th, 8th segments have 4–6 annuli. The remainder, except for the small projection, all have annuli, the number decreasing from 5 to 2 (Fig. $2A_1$, A_3). As in *Onychodictyon ferox*, each annulus has a vertical row of "tubercles", and long, finely annulated appendicules extend from these (Figs. $2A_1$, A_3, A_6, $3A_1$, A_2, B_1, B_3, C_1, C_2). Similar to those of *O. ferox*, the plates are rounded, dorso-ventrally elongate, convex outward, with a ridge near the edge, with the structure of plates showing the same pattern (convexity, ridges, rims) (Figs. $2A_1$, A_3, $3A_1$–A_3). A pointed spine protrudes from each plate (Fig. $3A_1$–A_3, B_1, B_3, C_2), according to preservation, in some cases only the basal plate of the spines is observable (Fig. $2A_1$–A_3).

Twelve pairs of limbs are observed in *Onychodictyon gracilis*, the first pair located anterior to the first plate pair, and, compared to the other limbs of the trunk, this pair of limbs is fat and strong (Figs. $2A_1$, A_3–A_5, $3B_1$–B_3). As Ramsköld and Chen noted, this pair of anterior limbs is set at a greater distance from Limb1 than Limb1 is from Limb2 (Fig. $2A_1$, A_3). The limb-pairs 2 to 10 are located ventro-laterally of the plate-pairs 1 to 9, respectively (Figs. $2A_1$, A_3, $3B_1$, B_3); limb-pairs 11 and 12 are based anteriorly and posteriorly below plate-pair 10 (Fig. $2A_1$, A_3). As in the limbs of *O. ferox*, there are about 30 rows of thin, transverse annuli from the base to the tip (Fig. $2A_1$, A_3, A_6). Tubercles are present in two rows along the lengths of the limbs, similar to those of the trunk (Fig. $2A_1$, A_3, A_6), the number of series being about 10 to 20, and small appendicules are observed protruding from these tubercles (Fig. $2A_1$, A_3, A_6). A pair of claws occurs at the tip of Limb 8, and these two claws point in the opposite directions (Fig. $2A_1$, A_3, A_6).

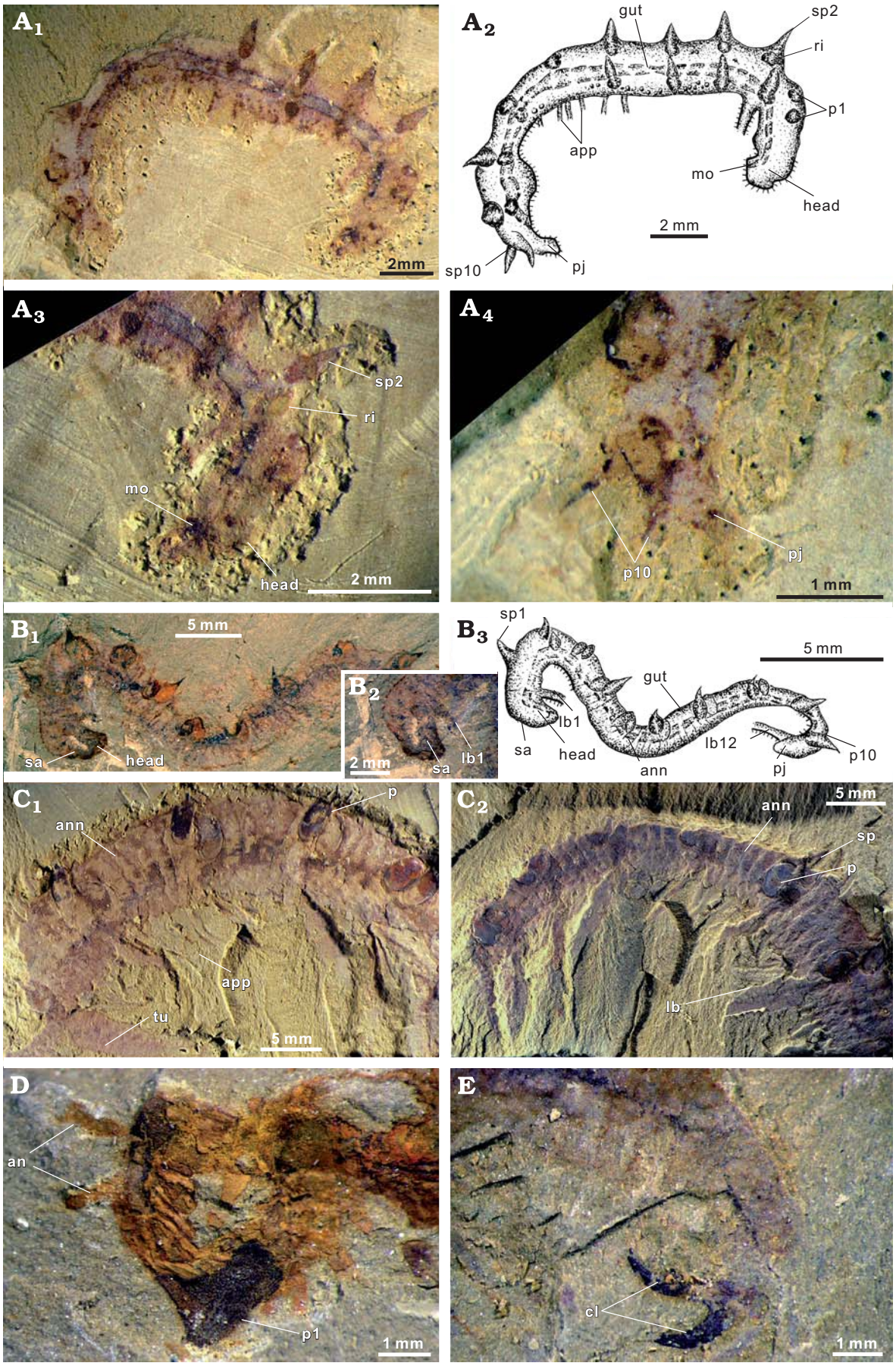
A short posterior projection is well preserved in specimens ELIJSO-0003 (Fig. $2A_1$, A_3) and ELIJSO-0005 (Fig. $3A_1$, A_2, A_4), and is similar to that in *Microdictyon*. The projection of *Onychodictyon gracilis* protrudes postero-ventrally from the margin, slightly ventral to the posterior end of the body, and is about 2.5 mm long by 2 mm wide in specimen ELIJSO-0003 (Figs. $2A_1$, A_3). Probably because of the state of preservation, the ridge of the projection in ELIJSO-0003 shows some signs of small spines (Fig. $2A_1$, A_3), but that of the projection in ELIJSO-0005 is smooth (Fig. $3A_1$, A_4).

The alimentary canal is expressed as a trace with a dark band about 1mm wide. It is simple and straight and extends through much of the body, mostly in a subventral position (Figs. $2A_1$, A_3, $3A_1$, A_2, B_1, B_3). No anus is apparent.

Comparison

The similarites of both *Onychodictyon ferox* and *O. gracilis* are clear, implying a close relationship for the two species of *Onychodictyon*: (1) both are subcylindrical in outline; (2) there are similar dorsal plates and appendicules; (3) both bear lobe-like limbs with tubercles and appendicules; and (4) two claws are present in these two species. However, there are also significant differences between them: (1) *O. ferox* possesses a pair of "antennae" on the "head", while *O. gracilis* does not; (2) 11 pairs of limbs occur on the trunk of *O. ferox*, with 12 pairs of limbs only observed in *O. gracilis* with the first pair of limbs located anterior to the first plate pair; (3) the last limbs of *O. ferox* are located at the end of the trunk with the claws usually bent and directed anteriorly, while in *O. gracilis* the direction of the claws of last limb bent according to the posture of the trunk; and (4) *O. gracilis* bear a small projection on the trunk, while *O. ferox* does not. Accordingly, we interpret

← Fig. 2. Early Cambrian lobopod *Onychodictyon gracilis* sp. nov. and *Onychodictyon ferox* Hou, Ramsköld, and Bergström, 1991, from Haikou, Kunming, Yunnan, China. **A**. Holotype ELIJSO-0003 of *Onychodictyon gracilis* sp. nov.; A_1, part ELIJSO-0003A is well preserved, showing a complete animal; A_2, counterpart ELIJSO-0003B is partly preserved; A_3, Camera lucida drawings of A_1, showing the principal features of *Onychodictyon gracilis* sp. nov.; note the smooth head, 10 pairs of plates, 12 pairs of limbs, the annuli and tubercles of both the trunk and limbs, the gut and claws of the limbs; A_4 and A_5, enlargement of the head area of A_1; note the rounded head with an antero-ventrally located mouth, a little sclerotized area and the following, the first pair of limbs; A_6, enlargement of part of the trunk and limb of A_1, showing the trunk with tubercles, annuli and appendicules, the limbs with tubercles, annuli and two claws; A_7, enlargement of the posterior region of A_1; note the limb11, limb12 and the small projection with spines. **B**. *Onychodictyon ferox* ELIJSO-019A, note the plate in detail. **C**. *Onychodictyon ferox* ELIJSO-002A, showing the appendicules of both the trunk and limbs. Abbreviations: app, appedicules; ann, annuli; cl, claws; fc, fine canal; lb, limb, lb1, the first pair of limb, lb2, the second pair of limb, and so on; p, plate, p1, plate 1, p6, plate 6, and so on; pj, projection; ri, rim of the plate; sa, sclerotized area; sp, spines; tu, tubercles.



Onychodictyon ferox and *O. gracilis* as two different species. However, because different sexes within the same species probably had different morphologies, there is the alternative possibility that the two species represent sexual dimorphs of *Onychodictyon*.

Discussion

Onychodictyon were first described, based on two specimens, as a caterpillar-like animal with "papillae" surrounding the mouth and a pair of "antennae" on the "head" (Ramsköld and Hou 1991; Hou et al. 1991). Later, these "papillae" were regarded as jaws (Ramsköld 1992; Hou and Bergström 1995) and the pair of "antennae" was thought to be a misinterpretation (Bergström and Hou 2001; Hou et al. 2004). Then, Ramsköld and Chen (1998) and Chen et al. (2004) observed 10 new specimens and interpreted the "jaw" structure as a head shield with a pair of appendages anterior to the pair beneath the first plate pair. Based on this information, we can see that the focus of the debate is: (1) whether *Onychodictyon* possessed "antennae" or not; (2) is there a jaw, a head shield, or anything else; (3) is there a pair of anterior appendages? After examination of 70 specimens, we consider that there indeed exists a pair of "antennae" on the "head" of *Onychodictyon ferox* (Fig. $1A_1$–A_5), which is quite similar to that of the coexisting lobopod *Miraluolishania haikouensis* in both its location and morphology (Liu et al. 2004; Xiao 2004; Brigitte et al. in press), both of them located on the dorsal of the "head" and flagellum-like in shape. Furthermore, the "antennae" of *Miraluolishania* are regarded as quite similar to those of arthropods, such as *Fuxianhuia* (Hou and Bergström 1997). Thus, this pair of "antennae" is not only an homologous structure in both *O. ferox* and *Miraluolishania*, but also suggests that such "antennae" might be a primitive link between lobopods and arthropods. Arthropod researchers generally agree that the antennules, or first antennae, of crustaceans are homologous to the antennae of other arthropod groups. Moreover, the antennae of all arthropods seem to be associated with the unfused anterior-most monosegments (Edgecombe 1998; Schram and Hof 1998). Besides, it is virtually certain that antennae of all arthropods were originally uniramous (Hou and Bergström 1997; Dzik 2003). New data indicate that onychophoran antennae are not homologous with those of arthropods; they are innervated by protocerebral and deutocerebral nerves respectively (Scholtz and Edgecombe 2005, 2006). Evaluation of which part of the cerebrum innervated the antennae of *O. ferox* and *Miraluolishania* is beyond the scope of this paper, but considering other distinct differences between *Onychodictyon* and onychophorans, such as no jaw or oral papillae in *Onychodictyon*, we are inclined to believe that the antennae of lobopods are closely implicated in the origin of antennae in arthropods. Concerning the "jaw" or "head shield" we think that both phenomena are artifacts of preservation. Although the dorsal cephalic ridge of *O. gracilis* is a little sclerotized, the head area of both *O. ferox* and *O. gracilis* shows no sign of jaw-like structures or a head shield (Figs. $1A_1$–A_5, $2A_1$–A_5, $3A_1$–A_3, B_1–B_3), and this is a typical character of most lobopods, such as *Cardiodictyon* and *Hallucigenia* (Ramsköld and Chen 1998). A pair of anterior appendages occurs on the trunk of *O. gracilis*, and it appears that these appendages, which are based laterally on the trunk, and also anterior appendages in the same are present in *Aysheaia* (Ramsköld and Chen 1998).

We conclude that, thus far, the common features of *O. ferox* and *O. gracilis* strongly indicate that they belong to the same genus. However, the significant differences between them show that they are likely to be different species or possibly sexual dimorphs. Together with *Miraluolishania*, the "antennae" of these species are crucial to any exploration of the origin of antennae in arthropods.

Acknowledgments

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← Fig. 3. Early Cambrian lobopod *Onychodictyon gracilis* sp. nov. and *Onychodictyon ferox* Hou, Ramsköld, and Bergström, 1991, from Haikou and Erjie, Kunming, Yunnan, China. **A**. Specimen ELIJSO-0005; A_1, a complete specimen of *Onychodictyon gracilis*, from the Jianshan Section, Haikou.; A_2, camera lucida drawings of A_1, note the smooth head area, the antero-ventrally located mouth, 10 pairs of plates and the small posterior projection; A_3, enlargement of the head area of A_1, showing the "head" with an antero-ventrally located mouth; A_4, enlargement of the posterior area of A_1, note the small projection. **B**. Another complete specimen of ELIEJO-0017, from the Erjie Section, Erjie; B_1, a complete specimen of Onychodictyon gracilis; B_2, enlargement of the "head" of ELIEJO-0017, showing the "head" without any structures except a small region of sclerotization on the dorsal margin; B_3, camera lucida drawings of B_1, showing nearly all the main features of *Onychodictyon gracilis* sp. nov.; note the smooth "head", 10 pairs of plates, 12 pairs of limbs, the annuli of the trunk, the gut and the small projection. **C**. Specimen ELIJSO-0011; C_1, enlargement of the trunk of *Onychodictyon* ELIJSO-0011A; C_2, enlargement of the trunk of *Onychodictyon* ELIJSO-0011B, note the annuli similar to the typical segmentation of arthropods, the plate with spine, the tubercles of the limb, and the appendicules of the trunk. **D**. The head of dorso-laterally preserved specimen *Onychodictyon ferox* ELIMFO-015B, note the paired "antennae". **E**. *Onychodictyon ferox* ELIJSO-0008, showing the paired claw. Abbreviations: app, appedicules; ann, annuli; cl, claws; fc, fine canal; lb, limb, lb1, the first pair of limb, lb2, the second pair of limb, and so on; p, plate, p1, plate 1, p6, plate 6, and so on; pj, projection; ri, rim of the plate; sa, sclerotized area; sp, spines; tu, tubercles.

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Supplementary

Synonymies.—Based on the distinct differences between *Onychodictyon ferox* and *O. gracilis*, here we give remarks to help the reader to distinguish them. The material in Ramsköld and Hou (1991), Hou et al. (1991), and Hou and Bergström (1995) is the same specimen NIGPAS 115271 and is *O. ferox*. Ramsköld and Chen (1998) show another three specimens, of which ELRC 33011 possesses 11 pairs of limbs and no projection at the end of the trunk, here considered to be *O. ferox*. The other two specimens, ELRC 33022 and ELRC 33009, are partly shown in their figure; it is hard to decide to which species they belong. The specimen RCCBYU10250 in Hou et al. (2004) is incomplete and, as we have not studied this fossil personally, we cannot make a decision about it. The specimens in Ramsköld (1992) and Bergström and Hou (2001) are all reproduced from Ramsköld and Hou (1991) and should be *O. ferox*.