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A new millipede (Diplopoda: Helminthomorpha) from the Middle Triassic Luoping biota of Yunnan, Southwest China, and a review of Mesozoic millipedes

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Abstract.—A new helminthomorph millipede, *Sinosoma luopingensis* from the Triassic Luoping biota of China, has 39 body segments, metazonites with lateral swellings that bear a pair of posterolateral pits (?insertion pits for spine bases), and sternites that are unfused to the pleurotergites. This millipede shares a number of characters with nematophoran diplopods, but lacks the prominent dorsal suture characteristic of that order. Other "millipede" material from the biota is more problematic. Millipedes are a rare part of the Luoping biota, which is composed mainly of marine and nearshore organisms. Occurrences of fossil millipedes are exceedingly rare in Triassic rocks worldwide, comprising specimens from Europe, Asia, and Africa, and consisting of juliform millipedes and millipedes that are either nematophorans or forms very similar to nematophorans. Millipede diversity only increases in the Cretaceous.

Introduction

Because of their terrestrial habitus, millipedes are rarely preserved as fossils. Fossil millipedes are mainly documented from the Paleozoic, as they are relatively abundant in the extensive coal-forest deposits of the Upper Carboniferous, and amber deposits, particularly those of the Cenozoic. Only rarely have they been described from the Mesozoic (Wilson and Anderson, 2004; Shear et al., 2009; Shear and Edgecombe, 2010; Edgecombe, 2015). Mesozoic occurrences include two described genera from the Triassic, one from France and another from central Siberia, one genus from the Jurassic of Australia, and five genera from the Cretaceous (Mexico, Europe, Mongolia and Myanmar), but additional millipede material is known from the Triassic of Africa and the Cretaceous of Europe. A number of other Mesozoic specimens have been noted, but not formally described, in the literature, however, including specimens from Africa.

Asian occurrences are from the Pleistocene of China (Chia and Liu, 1950), the Cretaceous of Mongolia (Dzik, 1975) and Myanmar (Carlson, 2007; Su and Huang, 2015), and the Triassic of Siberia (Dzik, 1981) and China (Hu et al., 2010). Fossil millipedes have been noted from two localities in China: Zhoukoudian (Choukoutien) in Beijing, and Luoping County in Yunnan Province. Chia and Liu (1950) studied a large number (c. 80) of specimens from the Upper Cave of the famous Pleistocene hominid site Zhoukoudian, assigning this material to *Julus* cf. *terrestris* and the new species *Julus peii*. Their material is clearly juliform, although in need of redescription and reconsideration as to generic and suprageneric placement. More recently, Hu et al. (2010, p. 2277, fig. 5j) have noted the presence of millipedes in the Luoping fauna, illustrating one of those specimens. The purpose of this paper is to describe the specimen illustrated by Hu et al. (2010), to briefly document another specimen with possible millipede affinity in the Luoping biota, and to provide a brief, comprehensive, review of Mesozoic millipedes.

Geological setting

The Luoping fossil *Lagerstätte* is located in Luoping County, Yunnan Province, southwest China (Fig. 1). This is in the southwestern part of the Yangtze Platform between the Nanpanjiang Basin and the Yangtze Platform (Enos et al., 2006). The Luoping biota is part of Member II of the Guanling Formation, of the Anisian stage (Middle Triassic) based upon the conodont *Nicoraella kockeli* zone (Huang et al., 2009; Zhang et al., 2009). Sediments of the Luoping biota comprise five units (Fig. 1). The lower thick-bedded unit consists of muddy and dolomitic limestone, mainly containing bivalves and gastropods. This is overlain by the lower thin-bedded unit, which consists of laminar micritic limestone, containing abundant fossil fish, marine reptiles, arthropods, echinoderms, plants, etc., in rocks bearing siliceous concretions and bentonite layers. Above this is the middle thick-bedded unit, consisting of strongly bioturbated bioclastic limestone, with marine reptiles, bivalves, and gastropods. The following upper thin-bedded sequence consists of laminar argillaceous marl, containing abundant fossil fish, marine reptiles, and arthropods (Hu et al., 2010). These beds typically exhibit sedimentary characters of slump structures, indicating soft-sediment deformation. The upper thick-bedded sequence consists of thick massive limestone with bivalves and gastropod fragments, and rare marine reptile remains.

The Luoping biota comprises a mixture of marine and terrestrial organisms (Hu et al., 2010) deposited in a marine environment. The biota includes marine reptiles, fish, echinoderms (crinoids, sea urchins, sea cucumbers, and sea stars), bivalves, gastropods, belemnoids, ammonoids, brachiopods, conodonts, foraminifers, and marine and nearshore arthropods. Among the thousands of fossils from the Luoping biota, arthropods comprise more than 90%, including lobsters, shrimp, mysidaceans, isopods, cycloids, conchostracans, ostracods, horseshoe crabs, and at least one certain millipede (Hu et al., 2010).

Millipedes, along with conifers, are clear terrestrial components of the predominantly marine Luoping biota. Based on the preservation of conifer remains, Hu et al (2010, p. 2278) hypothesized that conifers were transported c. 10 km into the Luoping Basin. Comparisons can be made with other biotas that have mixed marine and terrestrial components. Fossil millipedes are a small component, for instance, of the Essex fauna of Mazon Creek (Baird and Anderson, 1997; Hannibal, 1997, p. 173; Hannibal, 2000, p. 30), which has been interpreted as being marginal marine, consisting of predominantly marine organisms capable of tolerating changes in salinity (Baird et al., 1985; Baird, 1997). And the Triassic *Hannibaliulus wilsonae* is from a brackish-water facies that have yielded marine or marginal marine organisms including lingulid brachiopods and limulids (Shear et al., 2009, p. 2), two groups that are also found in the Luoping biota. The Luoping biota has a stronger marine influence than have these other facies, however. The assumed transportation distances to the basin are not extreme for millipedes. Distribution of extant millipedes shows that millipedes have been able to colonize land over long distances of open ocean. A premier example is the colonization of the Hawaiian Islands by various millipedes (Shelley and Golovatch, 2011, p. 33, p. 68), presumably by rafting. The paucity of millipedes in the Luoping biota contrasts with the more common occurrence of millipedes in some assemblages with a nonmarine origin, for instance in the Cretaceous site of Las Hoyas, Spain, where millipedes are more numerous (but still only a small proportion of the fauna) (Selden and Shear, in press).

Material

The main specimen described (LPI-61593) is preserved in mostly dorsal view, somewhat rotated to the left, providing lateral views of sternites and legs on some sections of the right side of the millipede. This has also resulted in the left hand side of the millipede being folded over to a small degree. The body is arrayed in a loose, sinuous, relaxed pattern. The specimen has been compressed, with lines of breakage differing on different portions of the body. Some segments are slightly offset at breaks. The mostly dorsal attitude of preservation may be due to the millipede being flattened, or simply due to the lack of strong coiling. Strong coiling, even if partial, results in preservation of fossils millipedes in lateral view.

Systematic paleontology

Class Diplopoda Blainville in Gervais, 1844

Subclass Helminthomorpha Pocock, 1887

Superorder & Order *incertae sedis*

Remarks.—Characters present do not allow confident assignment to any extant or extinct order of millipedes, but the segment number (39), ring structure (sternites not fused to the pleurotergites), large head, simple collum that does not cover the head, and presence of a pair of pits on the lateral swellings of the metazonites that may have been insertion points for setae, suggest a nematophoran affinity, although a colobognath affinity cannot be ruled out. A distinct midline is lacking however; therefore this taxon is not assigned to the Nematophora.

A nematophoran, specifically calipodidan, affinity has been suggested for *Hannibaliulus wilsoniae* (Shear et al., 2009; Edgecombe, 2015, p. 347). That form bears some resemblance to *Sinosoma*. Although *H. wilsonae* does appear to have a distinct midline, the lattermost sides of the pleurotergites are difficult to determine.

Genus *Sinosoma* Huang and Hannibal

Type species.—*Sinosoma luopingensis* new species by original designation and monotypy.

Diagnosis.—Millipedes with 39 body segments, including a small collum. Metazonites divided by furrows into three transverse parts which are flanked laterally by narrow, suboval swellings bearing a pair of posterolateral pits (?spine bases). Sternites free. Legs of medium length, stout.

Etymology.—The generic name is derived from the stem *Sino*-, meaning “pertaining to China,” in reference to the country where the specimen was collected. The ending *–soma* is a common ending for millipedes that has the advantage of not implying membership in a particular millipede order.

Sinosoma luopingensis Huang and Hannibal

Figures 2–3

Diagnosis.—As per genus.

Description.—Medium-sized millipede, approximately 19 mm long, elongate with 39 segments, inclusive of collum and telson (epiproct). Most segments more-or-less uniform in width, widest midbody segments about 1 mm wide as preserved, reconstructed width slightly more than 1 mm; first few body segments at anterior tapering anteriad, last few segments tapering posteriad. Prozonites well exposed, exposed length up to 0.18 mm, metazonites up to 0.38 mm long. Ratio of exposed length of prozonites (excluding anteriormost and posteriormost segments) to length of metazonites ranging from about 34% to 50%, indicating that prozonites were probably well exposed in life (although not quite as exposed in the fossil, since the specimen is relaxed). Penultimate segment reduced in length.

Head medium-sized, difficult to interpret because of twisting from dorsal position and crushing (oval missing area on right side is the result of preparation). Parts of gnathocliarium(?) exposed below head, slightly displaced. Antenna swollen, club-shaped, five antennomers preserved on ?right antennae, the fourth and fifth of which are the largest. Collum small, not covering head, quadrangular, slightly smaller than metazonite of following segment. Prozonites well exposed, depressed, with granular ornamentation. Posterior margin with distinct rim.

Metazonites raised, divided into three subequal parts by two transverse grooves.

Indication of midline lacking (longitudinal cracks on dorsal surface are not aligned along midline).

Longitudinal groove divides short lateral swellings (?paranota) from remainder of pleurotergite dorsally. Anteriormost and posteriormost part of articulation somewhat invaginated. Lateral swellings extend short distance from sides of pleurotergites. Swellings elongately suboval, covered with small tubercles. Pair of prominent pits (?insertion points for setae), located on posterolateral corner of dorsal surface of swelling. Pits are on an irregular, raised area. Pits present at least on segments 7, 8, 15, 18, 19, 20, 21, 24, 28, 29, and 31. Pits in each pair obliquely oriented. Ozopores apparently lacking. Epiproct longer than segment preceding it but subequal in length to segment in front of that segment. Posterior termination of segment smoothly rounded, lacking any projections. Surface coarsely granulate. Cytoscutes (cuticular platelets) polygonal, five-to-six sided, about 10 micrometers wide.

Anal valves not seen (covered by epiproct). Telson small, subrounded. Surface of prozonites and metazonites bearing tiny granules, with relatively larger granules on preanal segment.

Sternites incompletely seen, but disarticulated from pleurotergites, indicating that they were separate in life. Surface more coarsely granulate than preceding segment.

Legs stout, length subequal to the length of body segments (prozonite plus metazonite). Coxae and second segment (presumed prefemur) wide, prefemur longest, with remainder of segments decreasing in length. Two segments preceding epiproct apodous.

Etymology.—The trivial name denotes the location from which the specimen was collected.

Remarks.—The head area is difficult to interpret (Fig. 3.1). It is compressed and there has been some displacement due to compression. Preparation has also removed parts of the integument. There is a possibility that the two antennae may overlap somewhat.

The lateral swellings described here as possible paranota could also be conceivably interpreted as ventral portions of pleurotergites, or even as pleurites. Such an interpretation would be unlikely, however, as pleurites, and ventrolateral parts of pleurotergites, of fossil millipedes are typically seen only when specimens are preserved in ventral or lateral view (e.g., Wilson and Hannibal, 2005, figs. 2–3, 5–6). Furthermore, there is no breakage and displacement along the groove that divides the swellings from the pleurotergites in *Sinosoma* as there is in *Pleurojulus,* which does have separate pleurites. Such breakage has contributed to a longstanding discussion of the nature of the pleurites of *Pleurojulus*, although Wilson and Hannibal (2005) have provided detailed evidence for there being separate pleurites in that taxon. To complicate this picture, paranota have also been confused with pleurites, as with the paranota of "*Pleurojulus" steuri*" Schneider and Werneberg, 1998 described as pleurites (Wilson and Hannibal, 2005, p. 1106).

Paranota here could also be interpreted as the ventral portion of the pleurotergite as what appears to be a border is present on the lateral side of some metazonites. The inflation of the lattermost part of the tergites (that is what are described as swellings here) argues against such an interpretation.

The paired pits on the posterolateral corners of the lateral swellings of the metazonites are here interpreted as spine bases in part because of their being paired. They do not show any internal structure suggestive of their being ozopores. There is a history of confusion between ozopores and spine bases in fossil millipedes, and ozopores have been incorrectly described as spine bases in both fossil euphoberiids and palaeosomatids (Hannibal and Krzeminski, 2005, p. 209). Still, it would be unusual for ozopores to be paired as are the pits of *Sinosoma*.

Comparisons to other taxa

This specimen is similar in a number of ways to the Triassic form *Hannibaliulus wilsonae*, from the Grès à Voltzia (Anisian) of eastern France, which Shear et al. (2009) assigned tentatively to the Callipodida. Edgecombe (2015, p. 347) has subsquently noted the lack of features that would confirm assignment to that order with certainty. *H. wilsonae* has up to 44 segments, a small collum, and probably free sternites. The telson of *H. wilsonae* is also similar in shape to that of *Sinosoma*.

Shear et al. (2009) also noted a general resemblance of *H. wilsonae* to the Paleozoic genus *Pleurojulus*. This is in great part due to the presence of ?crushed ventral flanges on the former.

Division of the dorsal surface of the pleuotergites into transverse sections is not unusual and is found in a number of unrelated taxa, including the archipolypod *Palaeodesmus tuberculata* Wilson and Anderson, 2004, and extant polydesmid *Polydesmus*, which have transverse furrows. In both of those taxa, however, the surface of the metazonite is also subdivided by longitudinal furrows. A single dorsal furrow crosses the pleurotergite of *H. wilsonae*.

The body ring of the Luoping millipede is most like that of callipodids and chordeumatids in that the sterna are not fused to the pleurotergite. The tapering of the anterior and, especially posterior, is like that of chordeumatids. In the presence of spines on the swellings (as interpreted here), the new species is more like a chordeumatid (see for example Shear, 1977, fig. 1), and the segment number of the two forms (39 in the new species; 30 in chordumatids) is also much closer to that of chordeumatids than callipodids. The relatively large head, especially compared to the collum, is also like a chordeumatid. It differs from chordeumatids, however, in its lack of a prominent midline.

Segment number of the new millipede is very close to that of palaeosomatid archipolypods, which have up to 38 segments (Hannibal and Krzeminski, 2005, p. 208). The pleurotergites of palaeosomatids have ozopores born on lateral bosses, however.

Antennae very stout.

Etymology.—*Luoping*, in reference to the location from which the millipede was collected.

Occurrence.—The upper thin-bedded unit of the Luoping biota, Member II of the Guanling Formation, Anisian, Middle Triassic. Luoping County, Yunnan Province, southwest China.

Types.—Holotype LPI-61593.

SECOND SPECIMEN

incertae sedis

Figure 4

Description.—Segmented organism with 21 segments preserved (Specimen LPI-63009). Segments about 1 mm long. Margin(s) rimmed. Larger segment at one end.

Remarks.—This can conceivably be a fossil millipede, as it consists of a series of similar segments. These segments are in the same size range, but are simpler, than those of *Sinosoma*. It does not have sufficient features to be sure of an assignment.

Mesozoic millipedes

Mesozoic millipedes have been described, noted, and/or illustrated in a number of publications, beginning in the mid-1850s. These reported occurrences are reviewed below to put the occurrence of *Sinosoma* into context. This brief review updates the reviews of Mesozoic millipedes in Shear et al. (2009), Shear and Edgecombe (2010), and Edgecombe (2015).

A number of Triassic millipedes have been previously noted, although only two have been named and described in detail. These are *Tomiulus angulatus* Martynov, 1936, and *Hannibaliulus wilsonae* Shear et al., 2009, from France. *Tomiulus angulatus*, found in Siberia, is a julimorph-like millipede. It was diagnosed by Sharov (1962), based on Martynov (1936), and subsequently redescribed by Dzik (1981), who assigned it to the family Xyloiulidae Cook, 1895. This specimen is preserved in lateral view, with only the pleurotergites preserved. Reexamination of the holotype at the Paleontological Institute Moscow shows that its pleurotergites are terminated ventrally by a distinct, rounded rim (personal observation, JTH), a feature indicated in Sharov's (1962, p. 23) diagnosis (see translation by Dzik, 1981, p. 397). This implies that the sternites were not fused to the pleurotergites. Ozopores appear to be lacking. The lack of preserved sternites in the holotype of *Tomiulus* also indicates that the sternites and pleurotergites were unfused. Furthermore, it is likely that the sternites were narrow. The Xyloiulidea, as diagnosed by Wilson (2006, p. 639), include elongate, cylindrical millipedes with ozopores, short legs, and ornamentation composed of longitudinal striations ranging from horizontal striae (longitudinal striae) to oblique ridges and grooves. As Shear et al. (2009) have pointed out, only the lattermost character is present in *Tomiulus*, so its identity as a xyloiulid cannot be confirmed, although it is certainly likely that this form was also elongate, cylindrical, and juliform-like in general configuration.

Additional millipedes have, however, been noted and illustrated, but not formally described or named, from Triassic rocks. These include juliform millipedes from the Lower Triassic of Bethulie and Bergville, South Africa, noted several decades ago by Kitching (1977, p. 9) and Lawrence (1984, p. 134). Lawrence described them as gregarious juvenile juliform millipedes. Reisz and Laurin (1991, fig. 1) identified similar forms found in association with the skeletons of the procolophonid Owenetta as millipede-like arthropods, and interpreted these arthropods as scavengers. Subsequently, Groenewald and Kitching (1995, p. 37) listed millipedes comparable to extant *Gymnostreptus* Brölemann, 1902 (a spirostreptid in the superorder Juliformia) as occurring in the *Lystrosaurus* Assemblage Zone of the Beaufort beds (earliest Triassic) of South Africa. More recent mentions include those of Reisz and Scott (2002, fig. 1) who illustrated what appear to be juliform millipedes. These same millipedes were subsequently illustrated in color by MacRae (1999, p. 195). Retallack et al. (2003, p. 1142), after authors previously cited, noted that the specimens previously noted from Bethulie were comparable to extant *Gymnostreptus*, a spirostreptid. More recently, Abdala et al. (2006, p. 507, fig. 3D) noted and illustrated what they identify as a probable juliform millipede preserved with tetrapods in a carbonate concretion (collected by B. J. Kitching) from the Bethulie area. They did not observe any limbs on the millipede, which they interpreted as sharing a burrow with *Owenetta* (Abdala et al., 2006, p. 511). Based on the published comments and the published illustrations of these forms, it is probably safe to state that these are juliform-like millipedes.

A millipede body-fossil trace has been described from the Triassic of Utah (Mikeldon et al., 2006), but Lerner et al. (2007) have justifiably disputed a myriapod as the trace-maker.

This leaves us with two groups of Triassic millipeds: juliform-like millipeds and millipedes that are at least similar to nematophorans.

The Jurassic record consists of the enigmatic form *Decorotergum warrenae* Jell, 1983. This form, rounded in cross section, with clear prozonites and metazonites, has been accepted by recent authors as a chilognath millipede, although without support of an original assignment as an oniscomorph or a polydesmid (Shear et al., 2009; Edgecombe, 2015). Even its identity as a millipede is in need of confirmation; some of the ventral terminations of the pleurotergites appear to be arched dorsally. There are a number of examples of misidentification of millipedes as other taxa; and vice versa (see Hannibal, 2001).

Cretaceous forms, however, have a decidedly modern look to them. These forms include some polyxenids (Rasnitsyn and Golovatch, 2004; Duy-Jacquemin and Azar, 2004), a colobognath (Carlson, 2007; Wilson, 2006, fig. 4), spirobolids (Dzik, 1975), and a polydesmid (Wilson, 2006, fig. 4). Of these, only the polyxenids and spirobolids have been well studied. The polyxenids (three genera) have been referred to families that include extant forms. The colobognath, noted as a polyzoniid with siphonophorid characters, has not been described in detail. *Globiulus* Dzik, 1975, is a spirobolid that Shelley and Floyd (2014, p. 24–25; but see also Shear et al., 2009, p. 16–17) assigned to an extant subfamily. Recently, a new millipede fauna has been noted by Buscalioni and Poyato-Ariza (2016), and Selden and Shear (in press) have assigned these forms tentatively to the Xyloiuloidae.

Excluded from consideration here is *Julopsois cretacea* Heer, 1874, a Cretaceous form interpreted as a julid by Scudder (1886, p. 18), but which Hoffman (1969, p. R605) excluded from the Diplopoda. Also excluded is *Calciphilus*, a Cenozoic millipede that a number of authors, including Hoffman (1969, R604) correctly included in the Diplopoda, but erroneously listed as being Cretaceous (see McKee [1946] for a description of the deposit). Anton Fritsch (1910, p. 6–7, pl. 4, figs. 9–13) also described Cretaceous myriapods from Bohemia, including specimens he identified as a (?) glomerid and a julid. Fritsch did not name these taxa and these specimens are poorly preserved and difficult to interpret. Of these, the specimen of the supposed glomerid is the most millipede-like. These Cretaceous specimens are more poorly preserved than the specimens he described from the Gaskohle of Bohemia, and Fritch’s illustrations of the Czech material are not as accurate as are those of the material of the Gaskohle, which, in turn, are not very accurate (J.T.H., personal observations). Based on the original description and illustrations, the species ?*Xylobius mexicanus* Mullerried, 1942 from the Upper Cretaceous of Mexico, may be an authentic millipede. The specimen is missing however, and so its identity cannot be confirmed.

It is only in the Cretaceous that very well preserved material is available. This is partly because of the occurrence of amber deposits that preserve very delicate fossils. Based on the sparse fossil record of the Mesozoic, it appears that is was only in the Cretaceous that the Diplopoda took on a modern aspect.

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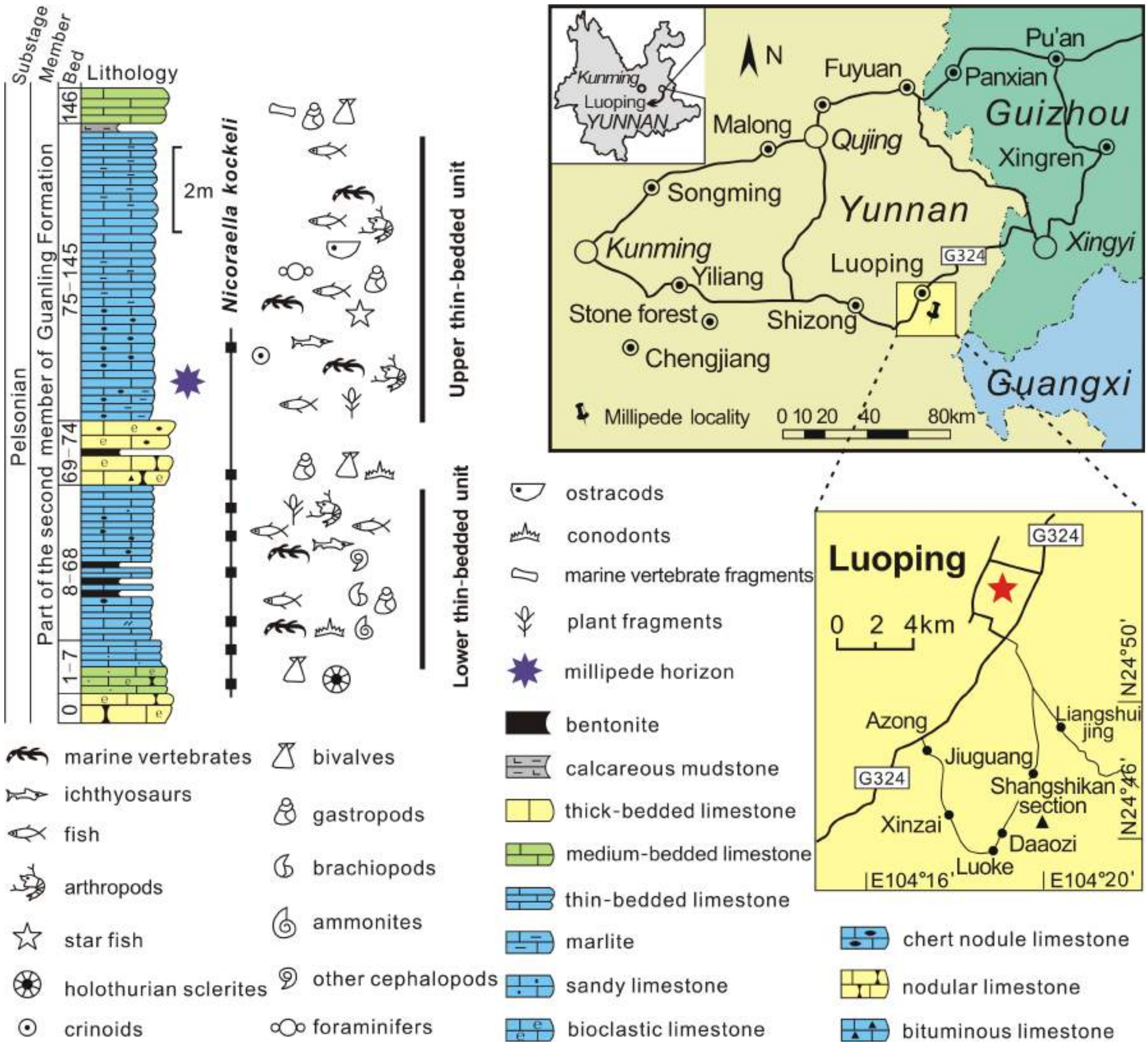
Figure 1. Location map and stratigraphic occurrence of the millipede locality in Luoping County of east Yunnan Province, southwest China.

Figure 2. *Sinosoma luopingensis* gen. et sp. nov., holotype, from the Middle Triassic Guanling Formation. Specimen LPI-61593, mostly in dorsal view. (1) entire millipede after preparation; (2) explanatory drawing of holotype; (3) anterior, showing the antenna, head, collum, metazonite, prozonite, and lateral swelling (?paranotum); (4) segments posterior to the head, the may be sutures, but probably cracks; (5) appendages on the trunks, free sternites below the lateral swelling (?paranotum), and transverse groove; (6) telson, lateral swelling (?paranotum) and transverse groove on the trunks. (an = antenna, ap = appendages, c = collum, cr = crack, ls = lateral swelling (?paranotum), h = head, mz = metazonite, pz = prozonite, st = sternite, t = telson, tg = transverse groove).

Figure 3. Detailed anatomical structures, micro-ornamentation, and appendages of the millipede *Sinosoma luopingensis* gen. et sp. nov., LPI-61593, holotype. (1-2) head structures and ornament of the millipede, the collum upper margin is flexed cephalad, a very short prozonite of the next segment is situated behind the collum, five antennomeres of antenna are visible, head capsule triangle in lateral view, (?)gnahocliarium, numerous fine granules on the collum and head (enlarged in Fig. 2 by SEM, black arrow pointed, corresponding the position in white boxed area of Fig. 3.1); (3) trunk appendages showing the specific structure of legs, with elements labeled, ventral sternites are not fused to dorsal cuticles, and transverse grooves seen on several metazonites; (4, 6) almost parallelogram shaped sternites are not fused to dorsal cuticle, two pits at the posterior of the paranotum, tiny granules on the prozonite and metazonite surface, the cracks clear on the metazonite, lateral swelling (?paranotum) are separate by prominent longitudinal grooves (Fig. 3.11); (5, 7) posterior part, relatively larger granules on the telson than on other trunk rings; enlarged granular ornament on preanal ring surface by SEM pointed in figure 3.5; (8-10) enlarged view of the metazonite and prozonite by SEM, showing the numerous tiny granules on the ring surface. The granules on the prozonite are relative smaller than those on the metazonite The hexagon-shaped ornament figure 3.9 shows cytoscutes (cuticular platelets) polygonal, five-to-six sided (called hexagonal in the MS so far), about 10 micrometers wide on the depressed part of metazonite (in Fig. 3.9, pointed in Fig. 3.10), the cracks and the depression shows it is not a suture (white arrow pointed in Figs. 3.4 and 3.10); (11-12) enlarged view of lateral swelling (?paranotum) on the metazonite, showing two pits (?spine bases) and the granular ornaments. (an =

antenna, ap = appendages, c = collum, cr = crack, (?)g=(?)gnahocliarium, h = head, fe = femur, ls = lateral swelling (?lateral paranotum/paranota), lg= longitudinal groove mz = metazonite, p = pits, pof = postfemur, prfelateral swelling (?paranotum) = prefemur, pz = prozonite, st = sternite, t = telson, ta = tarsus, tg = transverse groove, ti = tibia).

Figure 4. Specimen LPI-63009, specimen with 21 segments (Figs. 4.1-4.4).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ammonites
other cephalopods
foraminifers
ostracods
conodonts
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millipede horizon
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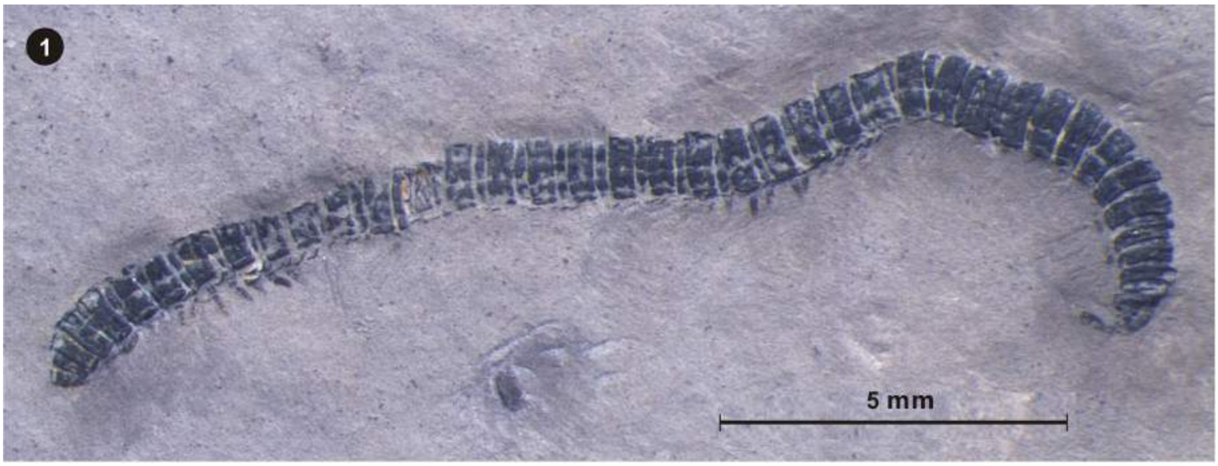
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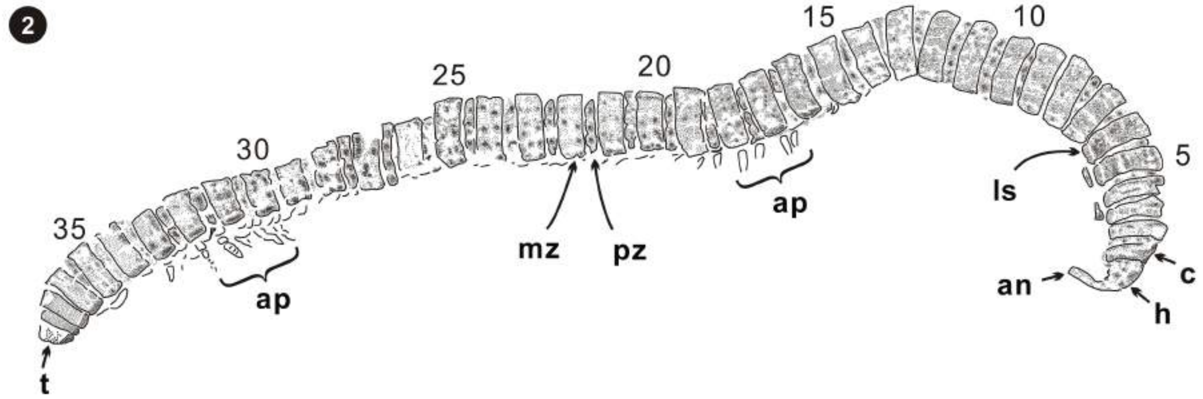
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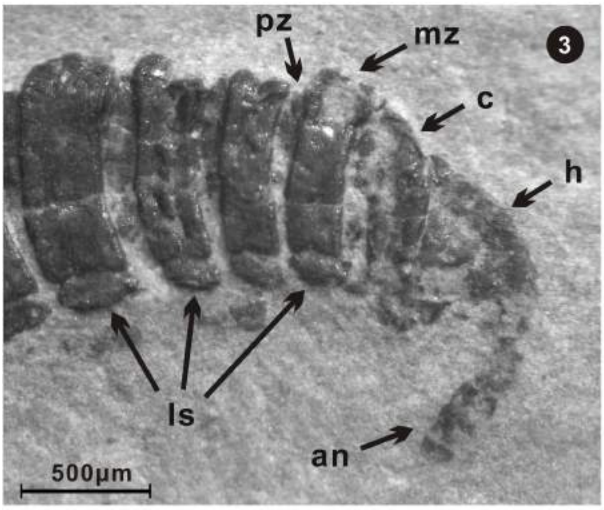
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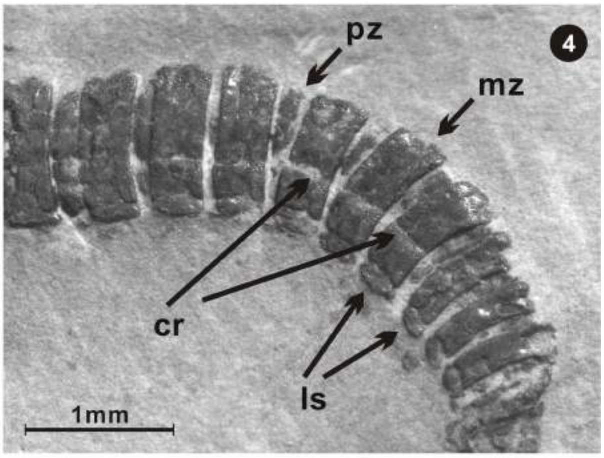
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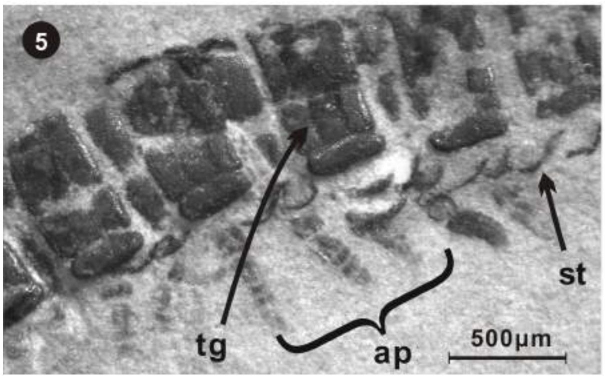
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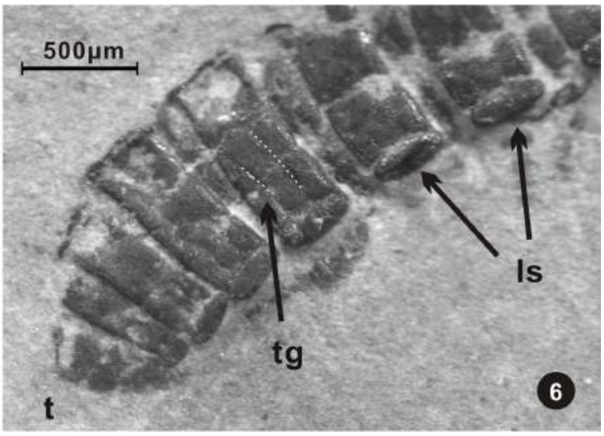
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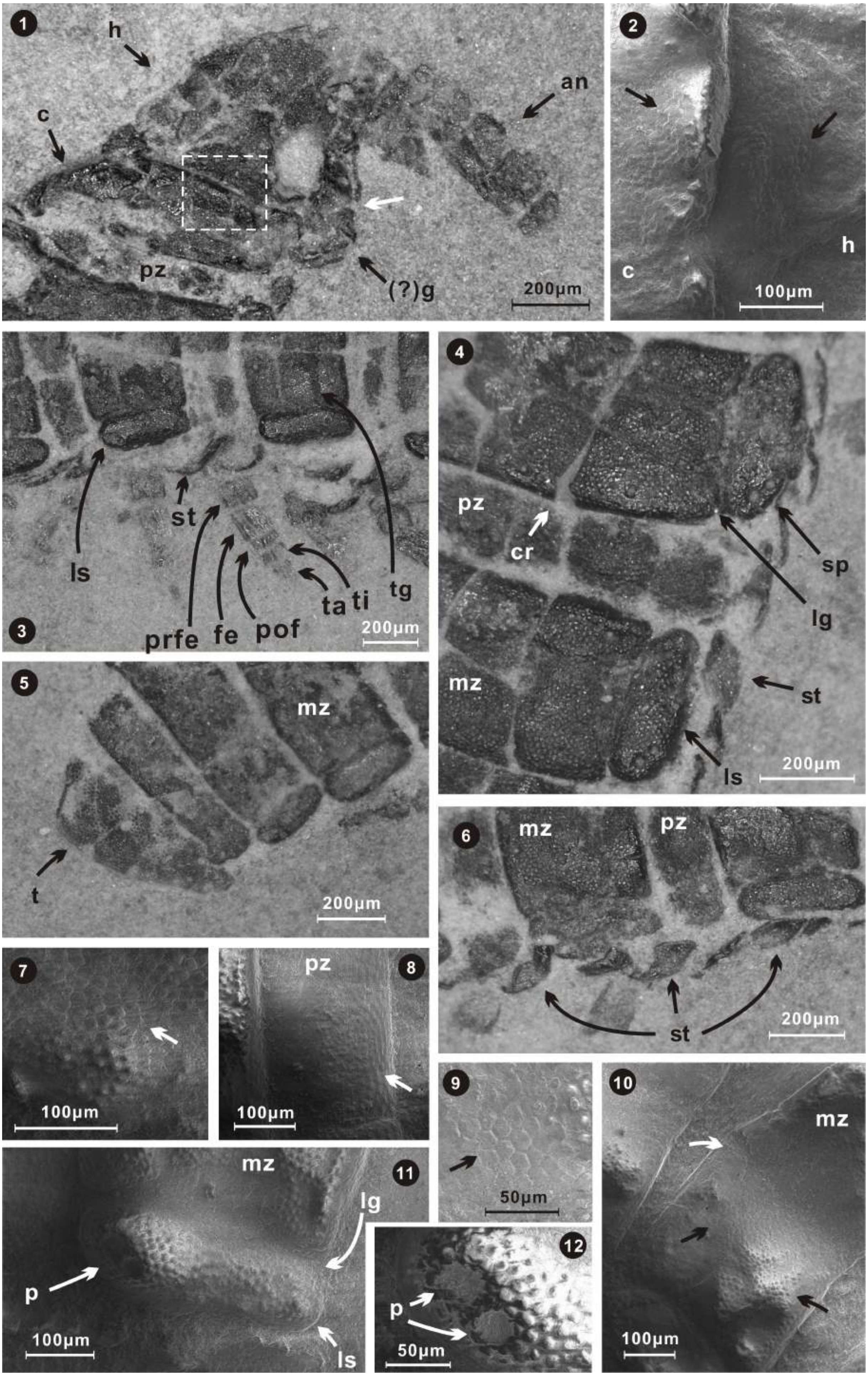
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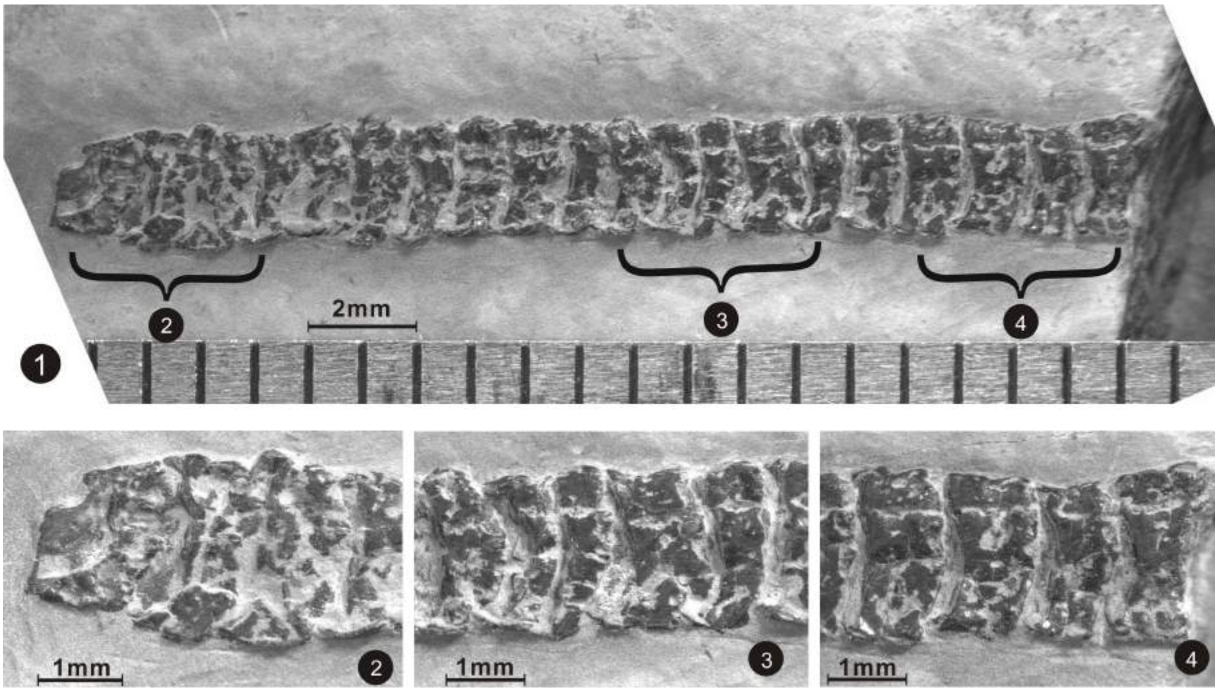
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