New insights into the Devonian sea spiders of the Hunsrück Slate (Arthropoda: Pycnogonida) (#93929)

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New insights into the Devonian sea spiders of the Hunsrück Slate (Arthropoda: Pycnogonida)

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Background. The sea spiders (Pycnogonida) of the Hunsrück Slate (Lower Devonian, ~ 400 million years ago) are iconic in their abundance, exquisite pyritic preservation and, in their distinctive body plan compared to extant sea spiders (Pantopoda). Consequently, the Hunsrück sea spiders are important in understanding Palaeozoic Pycnogonida, yet they remain poorly characterised, impacting upon attempts to establish the timescale pycnogonid evolutionary history.

Methods. Here we investigated previously described and new material representing four of the five Hunsrück pycnogonids: *Flagellopantopus blocki* Poschmann & Dunlop, 2006, *Palaeoisopus problematicus* Broili, 1928, *Palaeopantopus maucheri* Broili, 1929 and *Pentapantopus vogteli* Kühl, Poschmann & Rust, 2013. Using X-ray microtomography and Reflectance Transformation Imaging, we describe new fossils, provide evidence for new anatomical features, and interpret these data in comparison to extant species.

Results. We provide the first detailed description of the cephalic appendages of *Palaeoisopus problematicus* and revise the interpretation of the organisation of its ocular tubercle. Furthermore, we provide new insights into the structure of the legs and the proboscis of *Palaeopantopus maucheri*, the first description of the body of *Flagellopantopus blocki* and describe a new specimen of *Pentapantopus vogteli*, demonstrating that it was octopodous, in contrast to previous interpretations. We also reinterpret the previously published illustration of (the probably lost) *Palaeothea devonica*. We discuss the ecological traits of the Hunsrück pycnogonids based on their morphological adaptations, and finally suggest that contra previous suggestions, there is no compelling evidence of Pantopoda in the Devonian. Through comparative interpretation of the legs as well as general morphology, we suggest that Hunsrück fossils can be divided into two morphological groups.

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ABSTRACT

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INTRODUCTION

Sea spiders (Arthropoda: Pycnogonida) are enigmatic animals, in terms of their extant diversity (Sabroux, Hassanin & Corbari, 2019; Brenneis et al., 2020), biology (Brenneis et al., 2017, 2023; Lehmann, Heß & Melzer, 2017; Brenneis & Wagner, 2023), phylogeny (Arabi et al., 2010; Sabroux et al., 2017; Ballesteros et al., 2021; Sabroux, Corbari & Hassanin, 2023) and their ecology (Dietz et al., 2018). The same is true of their fossil record which is perhaps best described as few and far between (tab. 1). Only of 11 to 13 species (two are still regarded as ambiguous) have been described, representing over 500 Myrs (million years of evolutionary history; Bergström, Stürmer & Winter, 1980; Waloszek & Dunlop, 2002; Poschmann & Dunlop, 2006; Charbonnier, Vannier & Riou, 2007; Kühl, Poschmann & Rust, 2013; Rudkin et al., 2013; Sabroux et al., 2019). There are long fossil hiatuses between the Devonian and Jurassic, and between the Jurassic and the present (see a review of known fossils in Sabroux et al. 2019). The description of the known fossils is also challenging. The few researchers who have conducted research on pycnogonid fossils have produced high quality work, but studies are typically of limited means (primarily based on light microscopy and X-rays) and this has, in turn, limited interpretation.

Sea spiders are integral to understanding the early evolution of arthropods since they branch near the roots of Arthropoda and Chelicerata (Martin et al., 2010; Rehm et al., 2011; Lozano-Fernandez et al., 2016; Ballesteros & Sharma, 2019; Ballesteros et al., 2021; Sabroux, Corbari & Hassanin, 2023). Since extant pycnogonid species (which are united in the order Pantopoda; Hedgpeth, 1954; Bergström, Stürmer & Winter, 1980; Bamber, 2007) are highly derived and hardly comparable to other arthropods, fossil pycnogonids have the potential to inform on the origin of their unique bodyplan and its transformation from the primitive arthropod condition.

Recent years have seen limited work on fossil sea spiders: four fossils species have been described in the last decade (Kühl, Poschmann & Rust, 2013; Rudkin et al., 2013; Sabroux et al., 2019), no comprehensive restudy has been published for more than 40 years (Bergström, Stürmer & Winter, 1980) and there are only two short reviews of their fossil record (Bamber, 2007; Sabroux et al., 2019).

Recently, Ballesteros et al. (2021) used the fossil record of sea spiders to undertake the first molecular clock analysis for Pycnogonida, using Jurassic fossils as well as the Silurian *Haliestes dasos* for calibration. The taxonomic assignment of the fossils used as calibration points has been called into question (Sabroux, Corbari & Hassanin, 2023) highlighting the need for a comprehensive review of the sea spider fossil record. To this end, we recently reviewed the sea spiders of La Voulte-sur-Rhône, providing new observations and interpretations using X-ray microtomography and Reflectance Transformation Imaging (RTI; Sabroux et al., 2023). New material of the exquisite *Haliestes dasos* from the Herefordshire Lagerstätte was also recently reported (Siveter et al., 2023), definitively excluding it from the crown-group Pantopoda (Wolfe et al., 2016; Ballesteros et al., 2021). Following on from these works, we now review what is probably the most remarkable, and in any case the most diverse sea spider fossil fauna known: the fossil pycnogonids of the Hunsrück Slate, Germany (Broili, 1928, 1929, 1930, 1932; Bergström, Stürmer & Winter, 1980; Poschmann & Dunlop, 2006; Kühl, Poschmann & Rust, 2013).

Five species are recorded from the Emsian (c.a. 400 Ma) Hunsrück Slate: *Palaeoisopus problematicus* Broili, 1928; *Palaeopantopus maucheri* Broili, 1929; *Palaeothea devonica* Bergström, Stürmer & Winter, 1980; *Flagellopantopus blocki* Poschmann & Dunlop, 2006; and *Pentapantopus vogteli* Kühl, Poschmann & Rust, 2013. *Palaeoisopus problematicus* was the first described sea spider fossil, first interpreted as an isopod (hence its name) by Broili (1928) who mistook the antero-posterior axis, i.e. interpreted the animal's abdomen as a proboscis, and its chelifores as an abdomen. It was only later that Broili (1932) recognized *P. problematicus* to be a pycnogonid – a surprising intuition, given that he still did not restore the proper antero-posterior axis of the fossil. This taxonomic assignment was subsequently met with scepticism (e.g., Hedgpeth, 1954), but when the antero-posterior axis was revised correctly (Dubinin, 1957; Lehmann, 1959), the pycnogonid affinity of *P. problematicus* was widely accepted (e.g., Hedgpeth, 1978). *P. problematicus* presents the typical features of sea spiders (i.e., the three pairs of cephalic appendages, the proboscis, and the ocular tubercle), but the deviation it shows from the modern Pycnogonida body plan are striking: its legs were flattened, with a variable number of podomeres depending on the body segments, a long, segmented abdomen that bore a terminal telson, and enigmatic ring-like structures associated with the base of its legs.

Palaeopantopus maucheri was discovered at about the same time as *P. problematicus*, but its identification as a sea spider was much less problematic (Broili, 1929): the fossil presents the typical eight cylindrical legs of sea spiders, cephalic appendages, and a characteristic sea spider-like outline; a proboscis was later identified (Bergström, Stürmer & Winter, 1980). Nevertheless, this fossil also shows several unique features, such as the apparent absence of a cephalic segment, a long, segmented abdomen, and similar ring-like structures at its leg bases as in *P. problematicus*. Discovered much later were *Palaeothea devonica*, which has been regarded as the oldest possible evidence of Pantopoda in the fossil record (Bergström, Stürmer & Winter, 1980), the bizarre *Flagellopantopus blocki* with its long flagellum, and *Pentapantopus vogteli*, a purported ten-legged sea spider (Bergström, Stürmer & Winter, 1980; Poschmann & Dunlop, 2006; Kühl, Poschmann & Rust, 2013). As detailed below, the holotype and only specimen known of *Palaeothea devonica* is probably lost.

The sea spiders of the Hunsrück Slate are thus remarkably different from extant sea spiders, *i.e.*, pantopods. In particular, the abdomen of *P. problematicus*, *P. maucheri* and *F. blocki* was clearly developed, segmented and sometimes possessed a conspicuous telson, while a reduced, unsegmented abdomen lacking a telson is arguably the most solid synapomorphy for Pantopoda (Bergström, Stürmer & Winter, 1980; Sabroux et al., 2019, 2023). This differentiates Hunsrück – and Palaeozoic pycnogonids in general – from the sea spiders of the Jurassic, which are all typical pantopods (Charbonnier, Vannier & Riou, 2007; Sabroux et al., 2019, 2023). It was however suggested that *F. blocki*, *P. devonica*, *P. maucheri*, or *P. vogteli* could be possibly related to Pantopoda, relying on some common features of each of these fossils with extant pycnogonids (e.g., structure of the chelifores, of the abdomen or of the legs, polymerous species) or based on phylogenetic analyses (Bergström, Stürmer & Winter, 1980; Siveter et al., 2004; Poschmann & Dunlop, 2006; Bamber, 2007; Kühl, Poschmann & Rust, 2013). If it was demonstrated that at least one of these fossils could be confidently assigned to the crown-group Pantopoda, this would bear significantly on the calibration of the sea spiders evolution to time, providing the oldest calibration point(s) for the minimal age of the group (Sabroux et al., 2023). If not, the Hunsrück pycnogonids remain of considerable importance in informing the taxonomy of fossil sea spiders which is poorly developed. *P. problematicus* and *P. maucheri* were assigned to two orders, Palaeoisopoda and Palaeopantopoda (Broili, 1930, 1932; Hedgpeth, 1978; Bamber, 2007) of which they are the sole representatives. Similarly, the Silurian *Haliestes dasos* was assigned to a third order, Nectopantopoda (Bamber, 2007), while others have not been assigned to any suprageneric group (tab. 1). Deciphering how these fossils are related to each other, to pantopods, and to other arthropods, will provide a clearer understanding of the early evolution of sea spiders during the Palaeozoic and, ultimately, help to resolve where Pycnogonida fit into Arthropoda phylogeny. This work is a first step of such a revision, presenting a new perspective of the Hunsrück sea spiders morphology using X-ray microtomography and RTI.

GEOLOGICAL SETTING AND PALAEOENVIRONMENT

The Hunsrück Slate (Bartels, Briggs & Brassel, 1998; Rust et al., 2016 and references herein), sometimes referred to the German *Hunsrückschiefer*, outcrops between the Mosel and the Rhine, south and west of Koblenz, in the part of the Rhenish Massif that extends into the Rhineland-Palatinate Land (see the map fig. 3 in Bartels, Briggs & Brassel 1998). During the Late Pragian and the Early Emsian (Devonian: 407.7 ± 0.7 Mya; Kaufmann et al., 2005), this region formed a shallow, well oxygenated marine habitat (probably just below the wave base and not deeper than 100 m) along the coastline of the Old Red Sandstone Continent. This environment was inhabited by a large diversity of organisms (more than 260 animal species have been identified) including sponges, arthropods, molluscs, bryozoans, annelids, echinoderms and fishes (Bartels, Briggs & Brassel, 1998; Rust et al., 2016). Continental erosion formed mud and sand that were transported by rivers into the Central Hunsrück Basin. Locally, in the region of Budenbach, mudflows were frequent, facilitating the rapid autochthonous or parautochthonous burial of a few living organisms, and resulting ultimately in exquisitely preserved fossils that qualitify the Hunsrück Slate as a Konservat-Lagerstätte. Part of this material was pyritized. Accumulating deposits of mudstones encasing these specimens progressively metamorphosed the sediments into the modern slates, that were latter exploited by man as early as the Roman period in western Germany (and possibly before), through the Middle Ages until the end of the 20th century.

MATERIALS AND METHODS

Studied material

We accessed and studied in detail 46 plates preserving 64 fossil specimens (listed in supplementary material 1) representing at least four species: *Palaeoisopus problematicus* (52 specimens), *Palaeopantopus maucheri* (four specimens), *Flagellopantopus blocki* (one specimen), and *Pentapantopus vogteli* (three specimens, with possibly an additional one) and some undetermined pycnogonid material (three specimens). We could not locate the holotype and only specimen known of *Palaeothea devonica* and as such, it could not be included in our study. Part of the fossil material described here has already been presented in previous works while some other fossils are figured and described for the first time (refer to supplementary material 1). The fossils are preserved as flattened slates with variable levels of pyritization. They are hosted in the collections of the Museum für Naturkunde, Berlin (collection numbers MB-A-), the Institut für Geowissenschaften, Section Palaeontology, University of Bonn (collection numbers IGBP-), the Naturhistorisches Museum Mainz (collection numbers NHMMZ PWL), and the Bayerische Staatssammlung für Paläontologie und Geologie of Munich (collection numbers SNSB-BSPG-).

X-ray microtomography

Seventeen specimens were selected for X-ray microtomography, scanned either with a Nikon XTH 225ST scanner at the University of Bristol, a Phoenix|x-ray v|tome|xs at the Rheinische Friedrich-Wilhelms-Universität Bonn, or a Yxlon FF85 Modular at the Museum für Naturkunde in Berlin. The current during the scan ranged from 70 to 300 µA, voltage from 30 to 215 kV and exposure time from 1 to 2 s. A tungsten reflection target and copper and tin filters were used in some cases. The voxel sizes obtained ranges from 10 to 126 µm depending primarily on the size of the slab hosting the specimen (see supplementary material 2 for detailed parameters for each scan). Often the poor contrast between the matrix and specimens (where not pyritised) or the resulting streak artefacts (where pyritised) precluded segmentation. As such, we instead present microtomography data using two-dimensional maximum intensity projections over a few slices. The software ORS Dragonfly (build 2021.3.0.1087, Montreal, Canada) was used to reconstruct these projections.

Reflectance transformation Imaging

Reflectance Transformation Imaging (*e.g.*, Béthoux, Llamosi & Toussaint, 2016; Decombeix et al., 2021; Sabroux et al., 2023) was used to image the surface of the fossils. This was performed for 48 fossil specimens, using an RTI-dome, *i.e.*, a hemispheric rig placed over the fossil with an automated lighting series of LEDs evenly spaced around its concave surface. Here, we used a 32-cm diameter light dome equipped with 52 LEDs distributed over three rings. Light orientation was recorded on each image by a reflective metal ball. Photos were taken with a Nikon D850 mounted with NIKKOR 40, 60 and 105 mm lenses or a Canon EOS 700D digital camera, with Canon 50 mm and Canon EF 100 mm macro lenses. (Supplementary material 3).

Images were computed with the software RTIbuilder (Cultural Heritage Imaging, San Francisco) using the Highlight Based (HSH Filter) operation sequence. The resulting models were then visualised using the RTIviewer software (Cultural Heritage Imaging, San Francisco). RTIviewer allows the user to vary the direction of illumination at will. “Specular enhancement” allows the contrast between illuminated and shadowed surfaces of the item to be enhanced by estimating the normal for each pixel and using this to render surfaces using synthetic specular highlights. Finally, “normals visualization” enables visualisation of all normals at once with false colours depending on the position of the light source that most strongly illuminates a given part of the item.

RESULTS

Systematic Palaeontology

The synonymy lists were written following the recommendations of Matthews (1973). The terminal claw of appendages is counted here as one podomere, and podomere nomenclature adopted is the same as in Sabroux et al. (2023) and Siveter et al. (2023).

Class Pycnogonida Latreille, 1810

Palaeoisopus problematicus Broili, 1928

Figs. 1-19, 36A.

v* 1928 *Palaeoisopus problematicus*: Broili, plate 1.

1932 *Palaeoisopus problematicus*: Broili, pp 45-54, figs 1-5.

vp 1932 *Palaeoisopus problematicus*: Helfer, pp70, 71, figs 53, 55.

vp 1933 *Palaeoisopus problematicus*: Broili, pp33-46, plates 1-5.

1944 Palaeoisopus problematicus: Størmer, p. 146 [text], fig. 29a.

1954 Palaeoisopus problematicus: Hedgpeth, 197-199 [text], 201 [text], 202 [text], fig. 3.

1955b Palaeoisopus problematicus: Hedgpeth, pp P171-P173 [text], fig. 123.

1957 Palaeoisopus problematicus: Dubinin, 881, fig. 1A-B.

1958 Palaeoisopus problematicus: Tiegs & Manton, p. 321 [text], fig. 18a.

vp 1959 *Palaeoisopus problematicus*: pp 98-101, Lehmann, tabs 10, 11.

1978 Palaeoisopus problematicus: Hedgpeth, pp 23-25 [text], 30 [text], 33 [text], figs 1, 2B.

vp 1980 *Palaeoisopus problematicus*: Bergström et al., pp 10-31, 32 [text], 33 [text], 47-49 [text], figs 1-23, 34 [affinities].

v 1998 *Palaeoisopus problematicus*: Bartels et al., 153-155, figs 130-132

v 2012a *Palaeoisopus problematicus*: Kühl et al., p. 70 [text], figs 74, 75.

v 2012b *Palaeoisopus problematicus*: Kühl et al., p. 74 [text], figs 74, 75. [cop. Kühl et al. 2012a.]

2017 *Palaeoisopus problematicus*: Südkamp, pp 77-79, figs 118-120.

Examined material: HOLOTYPE: SNSB-BSPG 1928 VII 11: 1 juv. – **OTHERS:** IGPB-AR-339: 1 sp., -AR-340: 1 sp., -M-142: 1 sp., -HS195: 1 juv., -HS206:1 sp., -HS207:1 sp., -HS456: 1 sp., -HS457: 1 sp., -HS582: 2 spp., -HS636: 1 sp., -HS660: 1 sp., -HS694: 1 sp., -HS1039: 3

spp.,– MB-A-46: 1 sp., -47: 1 sp., -288: 1 sp., -313: 1 sp., -3969-1: 1 sp. – NHMMZ PWL 1986/3: 1 juv., 1992/178-LS: 1 sp. 1994/54-LS: 1 juv., 1 sp., 1994/55-LS: 1 sp., 1994/56-LS: 1 sp., 1994/133-LS: 1 sp., 1995/17-LS: 1 sp., 1995/35-LS: 4 spp., 1996/18-LS: 1 sp., 1997/44-45-LS: 3 spp., 1998/122-LS: 2 spp, 1998/155-LS: 1 sp., 2000/46-LS: 1 juv. 2003/272-LS: 2 spp., 1 juv., 2008/141-LS: 1 sp., 2013/8: 1 sp. – SNSB-BSPG 1932 I 63: 1 sp., 1932 I 67: 1 sp., 1967 I 306: 1 sp., 2021 IV 1: 1 sp.

Members of this species are very large for pycnogonids, reaching up to 400 mm in diameter, and are among the best-known fossils in the Hunsrück Slate; more than 80 specimens are known. The investigations of (Bergström, Stürmer & Winter, 1980) detailed the general morphology of *Palaeoisopus problematicus*, with a complete description of the trunk, the abdomen and the legs. We accessed 52 specimens, including new material (supplementary material 1), to compare and revise the descriptions of Bergström, Stürmer & Winter (1980; based on 57 specimens) in the light of new evidence.

The body of *P. problematicus* is composed of four trunk and five abdominal segments (figs 1, 2). The cephalon is fused with the first trunk segment as in modern pycnogonids. The fusion of the cephalon and the first trunk segment confers a roughly square shape. Posteriorly the cephalon carries the lateral processes to which the first pair of walking legs (WL1) articulates. These processes are approximately cylindrical in shape, with lateral thickening and ornamentation composed of rounded tubercles. Anteriorly and ventrally to the lateral processes, the cephalon also carries lateral extensions to which palps articulates, their distal border broadened. Ovigers insert ventrally, at about the same level as the lateral processes of the first trunk segment (fig. 3). The anterior margin of the head on which the chelifores articulates also presents an ornamented thickening. The posterior margin of the cephalon is thickened and ornamented with tubercles.

The proboscis is visible on some ventrally preserved specimens (fig. 3), the tip of it being posteriorly directed. Some specimens preserved laterally (fig. 4) suggest that the proboscis is folded ventrally (its tip directed posteriorly), though the proboscis cannot be unambiguously identified in these specimens. If correct, this position is potentially a resting position and that the proboscis was mobile, as seen in modern species presenting the same orientation of the proboscis (such as many modern Ascorhynchidae). The proboscis is tubular in shape overall, without clear proximal or distal narrowing. According to Bergström, Stürmer & Winter (1980) the dorsal surface of the proboscis is divided into three fields, suggesting that it is composed of three antimeres like extant species: an observation was made based on a single specimen that we could not examine.

The ocular tubercle region (fig. 5) is positioned near the anterior margin of the cephalon. It has six rounded features (fig. 6). The anteriormost is roughly reniform, and there are two positioned postero-laterally to the first, surrounding a third central one. Posterior to these, are two further lateral rounded features with a broader base. These six features are concentrated in a region on the cephalon. More posteriorly, a sixth feature is also visible. Bergström, Stürmer & Winter (1980) proposed that this posteriormost feature is a posterior ocellus; these authors also interpreted the anterior, reniform features as an anterior eye, and two of two posterior features as laterally positioned eyes (fig. 6). If correct, this arrangement would be very different from extant species that instead present anterior and posterior eye pairs, and this interpretation does not explain the identity of the three features directly posterior to the “anterior eye”. It seems unlikely that any of these represent any eye at all, since eyes of modern sea spiders generally protrude from the cuticle as a low convex lens (Brenneis, 2022) which is unlikely to preserve as markedly as the structures here following the dorsoventral compression typical of Hunsrück fossils. We note that many species in the genus *Rhynchothorax* (family Rhynchothoracidae) possess a disposition of more or less elongated tubercles very similar to the features seen in *P. problematicus* (fig. 6; some of them can be absent in some species). We suggest that the features of *P. problematicus* are tubercles, homologous to those in *Rhynchothorax*. The two tubercles postero-lateral to the anteriormost correspond in position to the two lateral sense organs (*sensu* (Lehmann, Heß & Melzer, 2017). These sensory structures have been identified in all sea spider families except for Pycnogonidae (Brenneis, 2022). We cannot address whether these were already functional as lateral sense organs (indeed, their exact function remains unknown even in modern species; (Lehmann, Heß & Melzer, 2017)).

Trunk third and fourth segments have two to three pairs of large tubercles arranged in a V tapering posteriorly (figs 2, 7). These are followed posteriorly by thinner tubercles which are more variable in disposition and/or preservation. The fourth trunk segment carries two pairs of dorsal tubercles, and many thinner tubercles may be present more posteriorly. The distal margin of each trunk segment is thickened and presents additional ornamentation composed of about ten tubercles along its length. The lateral processes are very short on the first trunk segment and are longer posteriorly. Their orientation is almost orthogonal to the trunk axis on the first trunk segment, and increasingly diagonal posteriorly, by the fourth trunk segment the axis of the lateral processes is almost parallel to the trunk. The distal margin of the lateral processes is thickened and ornamented with tubercles.

The abdomen (figs 8, 9) is attached on a posterior thickening of the fourth trunk segment. It carries four rectangular segments that are increasingly elongated distally, and a terminal fifth, lanceolate, very elongated segment (about 40 % of the total abdomen length). The fifth abdominal segment carries a ventrally positioned anus at approximately a quarter of the total segment length (fig. 8I-P). We interpret the terminal three quarters to be a post-anal telson anteriorly fused with the ultimate abdominal segment. At least the four distal abdominal segments and the telson carry short setae along their lateral margin. Thickened ridges are present medioventrally and mediodorsally. Dorsally each trunk segment have an anterior thickened margin. This thickened anterior margin may be present ventrally as well, as observed in specimen IGPB-HS1039 (fig. 8I-L), although it is not visible in specimen IGPB-HS660 (fig. 8M-P). Both ventral and dorsal sides show a free arthrodial membrane. It is larger ventrally, giving the abdomen great ventral mobility (figs 9, 10A); dorsally, the arthrodial membrane is smaller, and provided limited dorsal mobility to the abdomen (fig. 9D-F), except at the abdomen base where mobility seems important (fig. 9A-C). Each abdominal segment has setae along its lateral margins, which in some cases (fig. 9G-I) appear to be relatively long. They are arranged in at least one, possibly several, rows. Low numbers of additional setae can sporadically be found on the ventral or dorsal surface of each abdominal segment, especially (but not exclusively) on the posterior margin (figs 8M-P, 9J-L). In specimen IGPB-HS660 (fig. 8M-P) there is clear evidence of a pair of short setae on the ventroposterior margin of the fourth abdominal segment.

The chelifores (figs 10, 11) have prominent chelae. Despite their often-superb preservation, we are puzzled by their segmentation. Bergström, Stürmer & Winter (1980) counted (with some hesitation) five podomeres, three of which are scapes: this differs significantly from what is observed in any modern pycnogonid, which generally have three podomeres (including one scape), although sometimes one, two or four (with one or two scapes) are present, but never five. From the material we examined, we could not confidently identify five podomeres; four (including two scapes) is the minimal number and seems as likely, if not likelier, than five. The robustness of this interpretation is, however, limited by the ambiguity of the ornamentations of the scapes: it is often very difficult to determine whether ornamentation demarks the margin of a segment, or is in more of a median position (see highlighted margins and lines in figures 10 and 11). The proximal margin of the chelifores' first podomere has a ridge ornamented by tubercles, roughly perpendicular to the segment axis; more distally, iss another, diagonal ridge (the distal margin of the first scape?) that is ornamented with large tubercles, some of which have marks of possible setal insertions (fig. 11 J). This is followed by another ridge (the proximal ridge of the second scape?) roughly perpendicular to the axis of the purported second scape. Still more distally, is another ridge diagonal to the axis of the appendage. This may either represent a median ridge (two scapes) or the joint between the second and the third scapes (three scapes). It is followed distally by one final ridge – the distal margin of the ultimate scape. Because it is not possible to distinguish proximal and distal margins of the purported joints between the second and third scapes, and because it is more conservative (in light of chelifore morphology of extant pycnogonids), we foster the two-scapes hypothesis (fig. 14A).

The palps (figs 10, 12) are preserved laterally and generally directed anteriorly. They are composed of two proximal rings (figs 10, 12D, E) which together form the proximalmost podomere following the interpretation of Siveter *et al.* (2023) for walking legs. The second podomere possesses an angular projection at its distal margin (fig. 12A, B, D). The third and fifth podomeres are about 1.5 times to twice as long as the others. The seventh podomere typically has dorsal spur, its cuticle sometimes appearing coarse (fig. 12G) or bearing short setae (fig. 10). There is no distal claw. The second to fifth podomeres have a thickened distal margin. In total, we count a total of 10 podomeres in the palp of *P. problematicus*. This number differs from the typical (extant) sea spider bodyplan, which has nine podomeres, or a reduction from this fundamental pattern (Sabroux et al., 2023). Even *Haliestes dasos* has nine palpal podomeres, excluding the terminal claw (Siveter et al., 2023). Typically, in modern species, the palps have a first short coxa 1, followed by a longer coxa 2 (Sabroux et al., 2023). Since the ovigers of *P. problematicus* have three coxal rings, and palps only two, we hypothesize that the second podomere of the palp of *P. problematicus* could be the distalmost ring of coxa 1, that is individualised. We therefore propose to apply the nomenclature of Sabroux et al. (2023) and Siveter et al. (2023) as presented in figure 14B, D. Whether this additional podomere was mobile does not seem to be addressable here.

The ovigers (fig. 13) are positioned ventrally, as in extant species. Ovigers are never totally preserved in any studied specimen, making it difficult to count podomeres. The limbs bear a distal claw (fig. 13 A, C, D). In specimen NHMMZ PWL 1995/35-LS (fig. 13A, F, K, P), nine podomeres plus a podomere composed of three proximal rings (the coxa 1) can be counted; a part of the limb (from the seventh proximal podomere) is hidden under a leg. In the hidden part of the oviger, there is room for at least one more podomere, suggesting at least 11 podomeres (in agreement with Bergström, Stürmer & Winter, 1980). Also, the fourth podomere appears slightly larger than more distal ones. In the right oviger of specimen NHMMZ PWL 1994/133-LS (fig. 13B, G, L, Q), a similarly longer podomere is visible as the eighth most distal podomere. This supports the 11 podomeres hypothesis (fig. 14C). Most extant families (Ammotheidae, Ascorhynchidae, Callipallenidae, Colossendeidae, Nymphonidae, Pallenopsidae, Rhynchothoracidae; see, for example (Sabroux et al., 2023) also have 11 podomeres, which has been suggested as the plesiomorphic state among Pantopoda (Bamber 2007). We consider the count herein uncertain, however, due to the absence of any completely preserved and uninterrupted oviger. There is evidence of setae on the purported eighth podomere (fig. 13C, H, M, R), on the fifth and sixth podomeres (fig. 13A, F, K, L), and probably on some of the tarsal podomeres (fig. 13E, J, O, T). The distal margin of the last tarsal podomere (purported tenth podomere) forms a sort of vertical lamella ornamented with spines in at least some specimens (fig. 13C, D), although this is not apparent in all specimens (fig. 13A). Ovigers are one of the appendages in which sexual dimorphism, when present, is the most marked morphologically (*e.g.*, (Sabroux et al., 2023)), and this could be also the case here, although a simple difference in preservation seems as likely.

The first pair of walking legs (WL1; fig. 15) has four proximal rings (see also fig. 1) interpreted in *Haliestes* as coxae 1 (Siveter et al., 2023). These are followed by eight plain podomeres: the next podomere, coxa 2, is roughly trapezoidal, enlarging distally. It carries at least two ornamented ridges extending proximo-distally. Their exact position is difficult to interpret due to the flattening of the fossil that deformed the legs, but these are likely to be dorsal and anterior in position. The distal margin of coxa 2 is thickened. Coxa 3 is roughly cylindrical, with its distal margin thickened markedly, with a dorsal notch probably enabling the levator-depressor swing. The femur is roughly triangular, its broader side ventral, marking a strong geniculation in the legs, and its distal margin thickened. The patella, tibia, tarsus, and propodus are strongly flattened laterally, as made clearly visible in specimens that have their legs preserved dorsally (fig. 15L-Q). The dorsal ridge of these podomeres have one row of short setae. The ventral margin of the patella, tibia and tarsus distally presents a cluster of short setae near the insertion of the arthrodial membrane of the following podomere. Dorsally, these podomeres carry a (single?) row of short setae set on small tubercles. The propodus has at least two rows of denticles on its distal lamellar margin (fig. 15I-K). The claw is subchelate. In modern pycnogonids, the distal claw of legs (generally referred to as the main claw) is movable, so it is very much possible that the distal claw of *P. problematicus* WL1 was able to close on the distal indented margin of the propodus, making it a raptorial and/or cutting appendage.

The walking legs two to four (WL2-4; fig. 16) differ from WL1 in presenting an additional podomere compared to WL1, as seen in *Haliestes dasos* (this additional podomere is referred to as a metatibia; Siveter et al., 2023). We propose that these two “additional” podomeres are homologous, and therefore have followed the same nomenclature. The coxa 1 presents three (WL2) or two (WL3-4) rings; it is shorter than broad. Coxa 2 is distinctly more elongated than in WL1, about 2.5 to 4.5 times as long as broad. It is ornamented like WL1, including rounded tubercles and short setae. Coxa 3 and the femur are short, about as long as broad, and the femur is triangular as seen in WL1. The patella is much more elongated than that of WL1: about twice as long as broad. The tibia, metatibia, tarsus, and propodus are all longer than broad. Podomeres from the patella to the tarsus presents two rows of long ventral setae (fig. 16M-P), as well as short dorsal setae. The propodus also carries setae, but it is unclear whether these are in one or several rows (fig. 16E-H). The terminal claw is subchelate.

Juveniles: a few specimens of much smaller size are regarded as juveniles of this species, including the holotype (figs 1, 17, 18). Besides their smaller size, they differ from the adults in having a larger propodus on WL1, and the WLs are ornamented with only a few ventral setae rather than a dense range of ventral setae like in adults. Ventral setae of WL1 are also much longer than in adults and are disposed in a loose range along the length of WL1 rather than in a distal bouquet.

Palaeopantopus maucheri Broili, 1929

Figures 20-24, 36A

v* 1929 *Palaeopantopus maucheri*: Broili, pp 272-274, 277, fig. 6, plate 5.

v 1930 *Palaeopantopus maucheri*: Broili, pp 209-213, figure.

v 1932 Palaeoisopus problematicus: Helfer, fig. 54.

1954 Palaeopantopus maucheri: Hedgpeth, pp 197 [text], 198 [text], 202 [text], 203 [text], fig. 4.

1955a Palaeopantopus maucheri: Hedgpeth, pp P169 [text], P170 [text], fig. 122.

1957 Palaeoisopus problematicus: Dubinin, 881, fig. 1Г, Д.

1958 Palaeoisopus problematicus: Tiegs & Manton, p. 321 [text].

1978 Palaeopantopus maucheri: Hedgpeth, pp 25 [text], 32 [text], fig. 3.

vp 1980 *Palaeopantopus maucheri*: Bergström et al., pp 33-41, 46-48 [text], figs 24-29.

1998 Palaeopantopus maucheri: Bartels et al., pp 155 [text; pro parte], 156 [text] [non fig. 133.].

v 2017 *Palaeopantopus maucheri*: Südkamp, pp 78, 79, fig. 121.

Examined material. HOLOTYPE. SNSB-BSPG 1929 V 3: 1 sp. – **OTHER.** SNSB-BSPG 1930 I 501: 1 sp., MB-A-45: 1 sp.

We accessed the three specimens described by Broili, (1929; fig. 20), Broili (1930; fig. 21) and Bergström, Stürmer & Winter (1980; fig. 22) and are aware of no additional material for this species. We propose that the specimen identified by Bartels, Briggs & Brassel (1998), IGPD-

HS437, does not belong to *Palaeopantopus maucheri* (see the dedicated paragraph in this section). Bergström, Stürmer & Winter (1980) also suggested that specimen MB-A-45 (fig. 22) could be another species, distinct from *P. maucheri*, but RTI and microtomography reveal a body plan very similar in all well-preserved structures, except for a smaller size that may indicate different sex or life stage. The combination of RTI and X-ray microtomography data allow us to go further into details with the description of this species.

The trunk is compact, four-segmented, and broad. Lateral processes are very short and touching, their distal margin thickened (fig. 20). The posterior margin of each trunk segment is slightly broadened. There is no evidence of a cephalon in dorsal or ventral view (figs 20, 22), though cephalic appendages and proboscis are present (see below).

The abdomen is composed of at least six elements (figs 20, 21), including three short, proximal elements, a median element of medium size, and two longer, distal elements. These two long distal elements are clearly identified as abdominal segments, with their joint visibly bent in the two specimens where the abdomen is visible. The first three or four, proximal elements are reminiscent of the coxal rings of the walking legs (see below). It is not clear if their demarcation represents true segmentation and these four elements may correspond to one to four abdominal segments. Bergström, Stürmer & Winter (1980) suggested that the anus was terminal (hence regarding *P. maucheri* as a telson-less pycnogonid), based on their interpretation of internal pyritization as a trace of the digestive tract. However, this internal pyritization is also present in the palps and ovigers (e.g., fig. 20G), while in extant pycnogonids the digestive tract never extends into these appendages (Frankowski, Miyazaki & Brenneis, 2022). Thus, we do not accept the internal pyritization to represent a digestive tract and so *P. maucheri* could have possessed a non-terminal anus (and thus a telson). The lanceolate tip of the abdomen, starting about after the first proximal fourth of the last abdominal segment length, could correspond in shape to an abdomen quite like the one of *Palaeoisopus problematicus.* To our knowledge there is, instead, no instance of extant pycnogonids (which all show a terminal anus) with a long distal portion of the anus slender and lanceolate.

The proboscis of *P. maucheri* is challenging to delimit. There is little doubt that the roughly pyriform, rounded structure extending posteriorly on the venter (figs 20, 22) is part of this proboscis. However, the slender, tapering structure projecting anteriorly from it (figure 22) puzzled Bergström, Stürmer & Winter (1980) just as it puzzles us. A similar structure can also be observed with RTI on the ventral side of the holotype (fig. 20E, F) and its presence is confirmed by microtomography (fig. 20G). Bergström, Stürmer & Winter (1980) ultimately interpreted this structure as a cephalic appendage, which is consistent with the internal pyritization seen in the holotype (fig. 20G): in this case, it would be the oviger. Under this hypothesis, the proboscis is likely folded ventrally, with its distal mouth oriented posteriorly, and its base probably movable as in *P. problematicus*. However, the striking continuity of this structure with the proboscis cannot be ignored, especially in specimen MB-A-45 (fig. 22A-D). We suggest, as an alternative hypothesis, that this structure could also be the anterior part of the proboscis. If so, the slender, tapering projection is likely the distal part of the proboscis (and the rounded, pyriform part was proximal) as there is no evidence of any articulating petiole (like in *Eurycyde*) or anterior head projection (like in modern *Ascorhynchus*). Under this hypothesis, the round, broad proximal portion of the proboscis would be its base, implying that it inserts very posteriorly on the body, at the level of the third trunk segment (figs 20H, 22F). If correct, this condition is very different to extant species and it could perhaps be linked with the apparent disappearance of the head in this species, which could in turn be linked with a ventralisation of the cephalon. Alternatively, perhaps the proboscis of *P. maucheri* possessed ventral ornamentation that would project posteriorly, as seen in the modern *Anoplodactylus californicus-digitatus* complex (Arango & Maxmen, 2006).

Cephalic appendages are all present. Chelifores are poorly preserved, and do not show any evidence of chelae (figs 20, 22). Palps are identified as such based on their anterior position, but their preservation is too poor to address their segmentation (Begström *et al.* 1980 identified at least seven podomeres) although their base clearly shows annular structures. The tip of the palps does not show any evidence of a terminal claw. The ovigers are positioned posteriorly to the palps. They present a hook distally (a strigilis?) followed by at least two broad podomeres (fig. 22). Bergström, Stürmer & Winter (1980) counted nine podomeres, though we can neither confirm nor reject this assertion. The base of the ovigers is not visible.

Walking legs (fig. 23) have annular structures at their base. Bergström, Stürmer & Winter (1980) suggested that these corresponded to the lateral processes rather than to the appendages in this species (unlike *P. problematicus*) based on the presumed absence of lateral processes. However, as indicated above, we identify the lateral processes as short but present. In addition, it seems unlikely that such similar structures could be convergent between *P. problematicus* and *P. maucheri* (as well as in *Halietes dasos*, and other Hunsrück fossils as demonstrated below). We therefore interpret these rings as coxa 1, as in *P. problematicus*. Due to the potentially high number of podomeres in the legs of *P. maucheri*, we refrain from applying the nomenclature of Sabroux et al. (2023) and Siveter et al. (2023) for WL (but see Discussion). The two podomeres following coxa 1 were relatively short (the second was slightly longer than the third in many cases) and the following fourth and fifth podomeres were always directed on the same axis so that their joint may not have been movable. These two podomeres are up to twice as long as the proximal ones, the fifth longer than the fourth. The sixth podomere is narrower than the fifth, about three to five times as long as wide in the holotype. The seventh podomere is about 10% longer.

Distal podomeres are more difficult to define due to the distal fragmentation which either reflects anatomical segmentation or an artefact due to pyritization; the eighth podomere seems to be shorter, or as long as the seventh. It was followed by at least one, or possibly two, podomeres, which were then followed by a hook-like feature. This hook was variable in shape and its fragmentation suggests that it is composed of several, short podomeres, rather than made of a single curved podomere (such as the propodus of many extant species). Based on the number of fragments that can be counted, it composed at least four podomeres. However, taphonomic artefacts cannot be excluded to explain this fragmentation. These putative podomeres are followed by a terminal claw (fig. 23A-L, S).

Flagellopantopus blocki Poschmann & Dunlop, 2006

Figs 25-27, 36A

v* 2006 *Flagellopantopus blocki*: Poschmann & Dunlop, pp 984-986, text-fig. 1.

V 2017 *Flagellopantopus blocki*: Südkamp, pp 79, 80, fig. 123.

V 2019 *Flagellopantopus blocki*: Sabroux et al., pp 1927 [text], 1929 [text], 1945 [text], Supplementary Material 3.

Material. HOLOTYPE. NHMMZ PWL 2004/5024-LS.

This species described by Poschmann & Dunlop (2006) is, as far as we know, represents by a single specimen (fig. 25; but see discussion). Here, the CT-scan provides interesting insights to the body of *F. blocki*, and RTI helps us to improve our understanding of the structure of the legs relative to the accounts of Poschmann & Dunlop (2006) and Sabroux et al. (2019).

The trunk segments (fig. 25E-F) are individualised rather than fused. The cephalon carries a mediodorsal tubercle interpreted as the ocular tubercle (fig. 25F), which has not been observed before. The distal margin of each segment is inflated, and ornamented with rounded tubercles, including one bigger dorsomedial tubercle on each segment margin. The first lateral processes are about as long as their basal width, the others about twice as long as the width of the base, separated by a distance shorter than their own diameter.

The proboscis is proximally obscured, even to X-ray imaging, but distally, it was pyriform in shape, tapering to a blunt tip. How the proboscis insert on the head is therefore not clear: its proximal part may be missing, or alternatively, the proboscis could have been simply detached during the decay of the specimen.

The abdomen was broad and segmented. It is composed of four large proximal segments about as long together as the last three trunk segments (the third abdominal segment slightly longer than the others), followed by a very long flagellum, more than three times the length of the body (from the head to the abdomen). The flagellum is likely articulated, rather than rigid, as suggested by the curves along its length. Some traces of potential segmentation are also visible. The second abdominal segment carries two dorsolateral extensions near its distal margin that are likely to represent long setae.

Cephalic appendages are all present. Chelifores are long, with their chelae not preserved or absent. Palps reach the tip of the proboscis; their segmentation is poorly preserved. Ovigers (fig. 26) have similarly poor preservation, although they have a strigilis (possibly four-segmented).

This appears to have terminated with a small distal claw that is visible both with RTI and X-ray microtomography data.

Walking legs all shared (fig. 25B) the same structure as far as it is possible to identify from their preservation: the most complete leg in the holotype is the right third leg. Proximally, we suggest coxae 1 carry three rings, contra three podomeres as interpreted by Poschmann & Dunlop (2006), concomitant with the previous interpretation of Sabroux et al. (2019). However, RTI reveals that the remaining organisation of the leg was very different from the interpretation of these two references. The rings were followed by what we propose is a long podomere (about six times as long as wide), that was initially interpreted as two podomeres by Sabroux et al. (2019). This was followed by a smaller podomere at a geniculation. We infer that the fourth and fifth podomeres were interpreted as a single segment by Poschmann & Dunlop (2006) and Sabroux et al. (2019). RTI imaging, however, suggests that they were likely two podomeres sharing a single axis, their joint seemingly immovable (fig. 25B). These were subequal in length, about five to six times as long as wide. The sixth, slightly curved, podomere is much more slender and longer. The seventh podomere is probably only partially preserved. We refrain from using the nomenclature of Sabroux et al. (2023) and Siveter et al. (2023) to assign identities to these podomeres (but see Discussion), as we did for *Palaeopantopus maucheri* with which it shares several structural resemblances. The third ring of the coxae 1 of the WL1 carries a thin projection, probably a seta.

Pentapantopus vogteli Kühl, Poschmann & Rust, 2013

Figs 28, 29, 31, 36A

v* 2013 *Pentapantopus vogteli*: Kühl et al., 557, 558, figs 1, 2 v 2017 *Pentapantopus vogteli*: Südkamp, pp 79, 80 [pro parte], fig. 122c, d.

Material. HOLOTYPE. NHMMZ PWL 2004/5024-LS. – **PARATYPE.** Same plate, 1 specimen. – **OTHER.** Same plate, one specimen.

When first described (presented figure 28), *Pentapantopus vogteli* was considered to be the first 10-legged fossil pycnogonid (Kühl, Poschmann & Rust, 2013). While this condition is found in modern species (which are generically called polymerous, alongside 12-legged species; Arnaud & Bamber, 1987) it is extremely rare. In this description, we include a new specimen (fig. 29), that was hidden together with the holotype and paratype amidst a crinoid (*Parisangulocrinus zeaeformis*). Like *P. vogteli*, this specimen presents molariform indentations on the ventral side of the WL (fig. 29), and presents an overall similar leg structure, justifying its taxonomic assignment. However, it differs from the original description in that this specimen has four rather than five leg pairs, and as many trunk segments. Reinvestigating the holotype and paratype with RTI and X-ray microtomography (fig. 28), we find no evidence of five trunk segments: the paratype (preserved laterally) exhibits four pairs of legs and the holotype (probably preserved ventrally) presents seven legs. It seems more likely that either the supposedly fourth or fifth left leg in the holotype corresponds to the fourth leg of the other pair and is folded on the other side during the burial of the specimen. As such, *P. vogteli* is octopodous.

The trunk of *P. vogteli* is four-segmented, the cephalon fused with the first trunk segment. The lateral processes are about as long as wide, separated by about their diameter.

The proboscis, which is clearly visible in a new specimen (fig. 29), was elongated. It is preserved folded ventrally, suggesting it is either movable or directed vertically.

The abdomen is present, and is relatively short compared to other Devonian species, reaching beyond the lateral processes; it is not possible to determine whether it is segmented.

The cephalic appendages are all present. The chelifores are composed of at least three podomeres, including at least one scape. Palps and ovigers have their segmentation poorly preserved and hardly discriminable in the holotype; the left palp of the new specimen (fig. 29) potentially bear a terminal claw (fig. 28C).

The walking legs have their coxae 1 annulated at least in WL2 and 3 (and very probably also in WL1 and 4), the number of their rings being difficult to determine (beyond a minimum of three in each). WL1 present six other podomeres (claw excluded) after the ringed coxa 1 in the holotype, compared to seven in WL2-4; WL1 of the new specimen appears similar in condition, as the portion of the leg covered by WL2 is not large enough to hide a complete podomere. Given the peculiarity of this assemblage, we refrain here from naming these podomeres following the nomenclature of Sabroux *et al.* (2023) and Siveter *et al.* (2023). WL1 podomeres following coxa 1 included, from proximal to distal: a long second podomere (about five times as long as wide); a short third podomere (about as long as wide); a short fourth podomere (about twice as long as wide) with two or three ventral molariform indentations; the next two podomeres (the fifth and sixth) present ventrally four or five molariform indentations each and a few long setae (apparently organised in pairs) not visible in type material; the seventh and eighth podomeres which also possibly present setae and molariform indentations; and a long terminal claw (the eighth podomere) that is incompletely preserved in the type material. This claw is subchelate, movable (as indicated by the different positions it shows in left WL1-3 of the new specimen; fig. 29) and probably able to close on the sole of the propodus, as observed in many extant species. In WL2-4, one additional podomere relative to WL1 is present somewhere between the fifth and the eight podomeres (probably in seventh position; see Discussion). The fifth to seventh (WL1) and fifth to eighth (WL2-4) podomeres present loosely distributed long setae on the ventral surface that seem to occur in pairs (fig. 29E).

Pentapantopus ? *vogteli* ? Kühl, Poschmann & Rust, 2013

Fig. 30

Material. NHMMZ PWL 2007/29-LS: 1 sp.

The pycnogonid is associated with two specimens of *Budenbachia beneckei* Stuertz, 1886. Itslegs are not preserved and so it is not possible to address the presence of molariform indentations on the ventral margin of legs, as seen in the new specimen (fig. 29). Nevertheless, the two specimens have a very similar trunk outline. The number of annulations at the base of legs can be counted: four in WL1, five in WL2, four or five in WL3, and possibly three in WL4. This morphology is compatible with *Pentapantopus vogteli*. Distal to the rings, is a short structure that we identify as a potential second podomere; but this could equally be an additional disarticulated ring, or arthrodial membrane. The cephalon is remarkably well preserved, bearing a conspicuous ocular tubercle pointing anteriorly, in a very similar fashion to *Haliestes dasos*. Chelifores are present, possibly as well as palps. The segmentation of the abdomen is difficult to determine, its size and shape being very much like *P. vogteli* and *H. dasos*.

Pycnogonida gen. sp.

Figs 32, 33

v . 1998 *Palaeopantopus maucheri*: Bartels et al., p. 155 [text ; pro parte], fig. 133

Material. IGPD-HS437: 1 sp.

This specimen (fig. 32) was originally identified as the fourth representative of *Palaeopantopus maucheri* to be found (Bartels, Briggs & Brassel, 1998). But the two lateral projections inserted on the second abdominal segment suggest otherwise. While this specimen undoubtedly contrasts with other species described from Hunsrück (except, perhaps, *Palaeothea devonica*; see Discussion), its preservation does not allow for a sufficient list of diagnostic characters and, thus, for the description of a new species.

The trunk (fig. 33) is four-segmented. The cephalon potentially has a low, rounded ocular tubercle. The posterior margins of the trunk segments widens, possibly bearing a mediodorsal tubercle each. The lateral processes are present, with a thickened distal margin.

The proboscis does not seem to be preserved.

The abdomen is multisegmented, with the two proximal-most segments being broad, about as long as wide, their posterior margin widening. The third segment is long (at least twice as long as broad), followed by up to three small segments about as long as wide. The second abdominal segment carries laterally two long processes, possibly setae, as in *Flagellopantopus blocki*.

Cephalic appendages: the chelifores are inserted anteriorly on the head, their number of podomeres is unclear. The chelae, if correctly identified, are comparatively large. The palps are either absent or unpreserved. The ovigers are positioned ventrally, with at least one posterior geniculation marking a joint, typically like the femoro-patellar geniculation of extant species (Sabroux et al., 2023).

The four pairs of walking legs consist of at least seven podomeres: three short ones, and four longer ones. The ultimate podomere visible in the right WL1 is either a terminal claw or it carries one. Proximally, we cannot be sure whether the specimen has coxal rings like in other Devonian fossils.

Undetermined pycnogonids

Fig. 34

v 2013 "undetermined pycnogonid": Kühl et al., p. 7, fig. 4

v . 2017 *Pentapantopus vogteli*: Südkamp, pp 79, 80 [pro parte], fig. 122a, b.

Material. IGPB-HS195: 1 sp., NHMMZ PWL 2004/5024-LS: 2 sp.

Three specimens with the typical outline of a sea spider are found associated with crinoids [*Parisangulocrinus zeaeformis* (Follmann, 1887); and *Imitatocrinus gracilior* (Roemer, 1863)], but cannot be confidently assigned to any known taxon, and are not complete enough to be described as a new species. Two of them are already described by Kühl, Poschmann & Rust (2013). There is not any solid evidence to refer these three specimens to the same species, except a general similar outline and size. Two of the three specimens present clear evidence of coxal rings (fig. 34E-L). The rest of the preservation is insufficient to allow any taxonomic assignment or species description.

DISCUSSION

Ecology of the Devonian pycnogonids

The Hunsrück fossils were likely benthic or epibenthic, as underpinned by the fact that most of the fossils are animals that were trapped by mud-flows, from which free-swimming organisms would more easily escape (Rust et al., 2016). This is supported by the fact that *Palaeopantopus maucheri*, *Flagellopantopus blocki*, and specimen IGPD-HS437 share cylindrical legs with extant taxa and, as such, it is very likely the fossil species were benthic. This does not exclude the fossils being able to occasionally “swim” in the water column (e.g., (Morgan, 1972)). *Palaeoisopus problematicus* and *Pentapantopus vogteli*, with their flattened legs and long ventral setae were probably able to swim actively. Adult *P. problematicus* are found in great abundance (Südkamp, 2017) suggesting that they were often caught in Budenbach mud-flows, and thus that they were epibenthic rather than pelagic. Interestingly, *P. vogteli* and juveniles of *P. problematicus* are much rarer, most commonly found associated with crinoids (figs1, 17, 18, 28, 29; *Imitatocrinus gracilior* and *Parisangulocrinus zeaeformis*). It has been suggested that this could signify an association between these two organisms (Bergström, Stürmer & Winter, 1980), however, we note that this never occurs with adult *P. problematicus*. It is also possible that specimens of juveniles of *P. problematicus* and the species *P. vogteli* occasionally rested (or ate?) amidst crinoids arms, and were therefore trapped by mudflows, whilst swimming specimens could generally escape. In other words *P. vogteli* and *P. problematicus* juveniles were maybe living higher in the water column, explaining their rarity relatively to adult *P. problematicus*. Yet, *Palaeopantopus maucheri* and *Flagellopantopus blocki* are even rarer, but undoubtedly benthic. It is therefore possible that some other preservation biases are also at play, such as the preservation of larger specimens.

Was *Palaeothea devonica* a pantopod?

We could not locate the holotype of *Palaeothea devonica*. This specimen belonged to a private collection when described by Bergström, Stürmer & Winter (1980) and it may have been sold, or lost (C. Bartels, pers. comm.). To date, it is the sole specimen attributed to this species with confidence. Given their size, it is possible that the small unidentified sea spiders on the plate NHMMZ PWL 2010/5-LS observed by Kühl, Poschmann & Rust (2013) fig. 34A-H), or the smaller specimen of the plate IGPB-HS195 (fig. 34I-L), are related to this species. However, all of these specimens are only fragmentarily preserved. Besides, the holotype of *P. devonica* was never prepared and was only studied and illustrated based on X-ray projections. The illustrations available of this fossil Bergström, Stürmer & Winter (1980) provide very few informative details. For this reason, it is not possible for us to confidently attribute any specimen to *P. devonica* until the holotype can be identified and redescribed. If the disappearance of the holotype is confirmed, it will be necessary to identify this binomen as a *nomen dubium*.

Based on their observations, Bergström, Stürmer & Winter (1980) concluded that *P. devonica* had no basal leg annulations (= annulated coxae 1) and possessed three short coxae on each leg and chelifores with reduced chelae. Hence they interpretated this species as a pantopod, even suggesting affinities with Ammotheidae *sensu* Stock (1994) [= Ascorhynchoidea *sensu* Bamber 2007] (a group now regarded as paraphyletic; Ballesteros et al., 2021; Bamber, El Nagar & Arango, 2023; Sabroux, Corbari & Hassanin, 2023). This morphological interpretation is questionable. Re-examination of the radiographs published by Bergström, Stürmer & Winter (1980) shows that the so-called coxae are very narrow, more than usual for these podomeres (fig. 35); we could as well interpret these structures as annulated coxae 1. The abdomen is poorly preserved, but its broad base and the outline on the radiographs of Bergström, Stürmer & Winter (1980) indicate it was comparatively large. Affinities of *P. devonica* with Pantopoda are therefore dubious at best.

Interestingly, *P. devonica* shares many characters with *Flagellopantopus blocki* and/or the specimen IGPD-HS437: this includes the thickened posterior margin of the trunk segments, the four dorsomedian tubercles on trunk segments, and the number of annulations at the leg bases (in *F. blocki*). It is also worth noting that the abdomen of *P. devonica* could also have the same dimensions as the massive abdomen of *F. blocki* or the specimen IGPD-HS437, although no unequivocal conclusion can be drawn from available illustrations. Perhaps *P. devonica* was of the same species as either one or the other of these two pycnogonids, though its smaller size would imply it was a juvenile or a different sex. Perhaps it could be another, third species. Unfortunately, these hypotheses cannot be properly addressed in the absence of the holotype of *P. devonica*.

Variability of the Pycnogonida walking leg ground plan

The most emblematic characteristic of modern sea spiders that makes them (almost) unmistakable in the field is their slender morphology with a narrow, often inconspicuous body onto which long legs articulate. This typical aspect has led to the sea spiders being coined as "no-bodies" (e.g., Brenneis et al., 2017), or pantopods (Pantopoda Gerstäcker, 1863; literally "all made of legs"). Therefore, including pantopods within a broader phylogenetic framework among Pycnogonida and Arthropoda in general, involves a thorough comparison of the appendages. In most cases, the Hunsrück sea spiders have poorly preserved cephalic appendages; in contrast walking (or swimming) legs were more massive and therefore often better preserved, sometimes exquisitely.

Leg type 1: Pantopoda

The leg pattern of modern sea spiders (as, presumably, in all pantopods) is very stable (fig. 36), with rare exceptions such as the parasitoid *Nymphonella tapetis*. From proximal to distal, the WL are composed of: three short coxae; three long podomeres: femur, patella, tibia (more often referred to femur, tibia 1 and tibia 2 in taxonomic literature); variably elongated tarsus and propodus; and a terminal claw often flanked by two auxiliary claws. Hunsrück fossils show that this ground plan (to which we will refer to as leg type 1; table 2) has not always been the sole leg pattern for sea spiders.

The most conspicuous and constant feature that differentiates Hunsrück fossils from leg type 1 is the annular structure at the base of legs. It was identified in *Palaeoisopus problematicus* and *Palaeopantopus maucheri* (e.g., (Bergström, Stürmer & Winter, 1980) and we also show clear evidence of its presence in *Flagellopantopus blocki* and *Pentapantopus vogteli*. As explained above, we suspect that *Palaeothea devonica* also had basal annulations. This structure is also observed at the base of legs of *Haliestes dasos* (Siveter et al., 2023). Siveter *et al.* (2023) argued that these rings are likely homologous with the coxae 1 of leg type 1, relying on two arguments: 1) the position of legs in *H. dasos* suggest that the joint between the purported coxa 1 and 2 of this species has a promotor-remotor swing, which is typical of the coxa1-coxa 2 articulation (Manton, 1978) – note that the Hunsrück material does not provide further evidence to support this observation; and 2) that the following podomere could be identified as coxa 2 through a ventrodistal protuberance that is typical of coxa 2 of extant pantopods, where the gonopores open. While Bergström, Stürmer & Winter (1980) interpreted the annulations at the base of legs of *P. problematicus* the same way as Siveter *et al.*, they proposed something different for *P. maucheri*, namely that they were “without doubt” part of the lateral processes seen also in *P.*

maucheri. This hypothesis relies on the absence of lateral processes, an observation which we do not accept, as detailed above. We therefore regard the coxal rings as homologous among all the sea spiders that present it.

Leg type 2: *Palaeoisopus*, *Pentapantopus* and *Haliestes*

We identify two types of legs among the non-pantopod pycnogonids that both share the coxae 1 rings. The second pattern (leg type 2) is observed in *P. problematicus*. It is inappropriate to describe the appendages 4 to 7 of *P. problematicus* as walking legs as their paddle-like morphology suggests they were primarily adapted for swimming. Conveniently, WL1 in *P. problematicus* had the same number of podomeres as pantopods, allowing us to propose an easily drawn podomere-by-podomere homology hypothesis (see also Siveter et al., 2023). Following this hypothesis, the femorae of *P. problematicus* are conspicuously shorter and compact compared to those of Pantopoda. The patella is the most elongated podomere, and the tibia, tarsus and propodus are similar in length and shape. The laterally flattened shape of the patella, tibia, tarsus and propodus in this fossil give the leg its characteristic paddle-like structure. The propodus is followed by a lone, subchelate terminal claw (perhaps closing on the indentations on the opposite margin of the propodus). Siveter et al. (2023) showed a very similar pattern in *H. dasos*, of which WL1 only differs from *P. problematicus* in that i) its transversal section is rather elliptic and not as strongly laterally compressed as in *P. problematicus*, ii) the femorae are more elongated, though they remain short relative to the patella and tibia, and iii) the tarsus is reduced to a small podomere, similar to many of the extant sea spiders.

In WL2-4 of *P. problematicus* (as in *H. dasos*), there is one additional podomere (figs 16, 17, 36). Since this additional podomere is “paddled”, it must be somewhere between the patella and the propodus. Siveter et al. (2023) suggested based on length comparison that this additional podomere is to be found in *H. dasos* between the tibia and the tarsus, naming it the “metatibia”. They suggested that the metatibia was also present in *P. problematicus*.

P. vogteli also presents a different number of podomeres between the WL1, and WL2-4. Like *P. problematicus* and *H. dasos*, the legs were laterally flattened (figs 28, 29, 36), and the terminal claw was subchelate. Finally, these three fossils all had setae on the ventral surface of the legs; the distribution of these setae was sparse in *P. vogteli*, like in *H. dasos*. But a fundamental difference with these two other fossils is that *P. vogteli* had one less podomere on all legs, *i.e.*, eight in WL1, and nine in WL2-4. The fact that the number of podomeres varied between the first and the following pairs of WL suggests that *P. vogteli* also had metatibia in WL2-4; so that a podomere is lacking from the overall count. This could be the tarsus: as this podomere is greatly reduced in *H. dasos* compared to *P. problematicus*, a possible scenario is that this podomere is progressively reduced and then completely lost/incorporated in *P. vogteli*.

Leg type 3: *Palaeopantopus* and *Flagellopantopus* (and *Palaeothea*?)

At first glance, leg type 3 found in *P. maucheri* and *F. blocki* appears to represent an intermediary state between type 1 and type 2, including both annular coxae and cylindrical legs but the situation is actually more complex. It is actually difficult to propose a hypothesis of homology between leg podomeres of type 3 and those of types 1 or 2. In *P. maucheri*, the number of podomeres exceeds ten. The terminal part of the legs seems to be composed of a series of small podomeres, at least five, possibly six (it is unclear whether this number varied in the different pairs of legs), in addition to the terminal claw. More proximally, there was at least one more “long” podomere in comparison to Pantopoda. Two of these long podomeres were most often aligned, with no evidence for mobility at the joint. This characteristic feature is also observed in *F. blocki*, suggesting a podomere-by-podomere homology (fig. 36). The terminal part of the legs of *Flagellopantopus* is lacking, but based on this hypothesis it is possible to estimate the number of missing podomeres in that species.

We have considered two hypotheses of homology between these limbs and the other leg types. The first relies on the homology between the ventral and dorsal geniculations in leg types 1 and 3. The two aligned podomeres formed, in this case, a "divided" femur. It was followed by the patella, the tibia, and an elongated tarsus. The propodus would then have been divided into at least six small podomeres and was followed by a terminal claw.

The second hypothesis of homology is based on inferring these aligned podomeres as two reflecting the plesiomorphic segmentation of the limb articles, and assumes that the small terminal podomeres represent a divided propodus. Under this hypothesis, the number of podomeres in the plesiomorphic limb was the same as the WL of type 2, suggesting the presence of a metatibia. Interestingly, there is no difference in the number of podomeres between WL1 and the other WL, in contrast to leg type 2. This suggests that if there were a metatibia, it might not have been homologous to the one found in *P. problematicus*. This hypothesis is therefore less parsimonious than the first.

The situation found in *Palaeothea devonica* cannot be addressed with certainty given the dearth of information we have on the legs of this species. The presence of annular coxae 1, and legs that appear cylindrical, allow us to speculate that the limbs of this species are most likely to be of type 3. Similarly, the leg of the specimen IGPB-HS437 could correspond to type 3, but there is no clear evidence of the coxal rings nor of the division of the femur/additional WL podomere as observed in other species.

Affinities of the Hunsrück sea spiders

Sea spiders have been classified in up to four orders: Palaeoisopoda, Palaeopantopoda, Nectopantopoda and Pantopoda (see tab 1; Hedgpeth, 1954, 1978; Bamber, 2007). Hedgpeth (1954) included extant species in Pantopoda, a name that was until that time used as a synonym of the class Pycnogonida Latreille, 1810. The order Palaeopantopoda was named some 25 years before by Broili (1930) for the species *Palaeopantopodus maucheri*. Later, when he recognised *Palaeoisopus problematicus* as a sea spider, he also placed this species in the order (Broili, 1932). Hedgpeth (1978) divided Palaeopantopoda into two infraorders, Palaeopantopodina Broili, 1930 and Palaeoisopodina Hedgpeth, 1978, which were much latter raised to the ordinal level (*i.e.*, Palaeopantopoda and Palaeoisopoda) by Bamber (2007). Bamber (2007) also established a fourth, monospecific Order, Nectopantopoda, for *Haliestes dasos*. This classification is still in use (see for example (Bamber, El Nagar & Arango, 2023)), but this reflects more the scarcity of attempts to review it than a real consensus.

This work demonstrates that *P. problematicus*, *P. maucheri* and *Flagellopantopus blocki* all had a long, segmented abdomen, with often (if not always) a terminal telson. We suggest this was also probably the case for *Palaeothea devonica* and *Pentapantopus vogteli*. This character is arguably plesiomorphic as it mirrors the state in all potential fossil outgroups and it is plesiomorphic to arthropods as a whole. Consequently, the reduced, unsegmented, telson-less abdomen of pantopods is a robust autapomorphy for the group. All fossils studied here presents the typical annulated coxae 1 (it not unambiguously observed only in the specimen IGPB-HS437). This also clearly distinguishes these fossils from Pantopoda, which have legs of type 1 (*i.e.*, without annular coxae 1).

Leg morphology allows us to identify two distinct groups among the Devonian fossils. On one hand are sea spiders that had laterally flattened WL with ventral setae and a first leg pair with a reduced number of podomeres, that probably served a raptorial function (leg type 2). This group included *P. problematicus* and *P. vogteli*, to which we can also add the Silurian species *H. dasos*. On the other hand are the sea spiders *P. maucheri*, *F. blocki*, and perhaps *P. devonica*, that had cylindrical legs (leg type 3) and a broad, segmented abdomen.

Whether these two groups represent clades, or whether one or both are grades, remains uncertain. The group of *P. problematicus* had a number of characters that have the potential to be "good" synapomorphies. The paddle-like distal podomeres of legs are potentially one: there is a trend in extant chelicerates to have flattened legs, but in these sea spiders this condition affects the proximal podomeres rather than the distal ones. However, the condition of fossils is often unknown. Another candidate is found in the modified, potentially raptorial first legs, but this is not unique to these sea spiders (*e.g.*, the eurypterid families Megalograptidae and Mixopteridae has such limbs; Schmidt et al., 2022). Similarly, the metatibia has the potential to be a synapomorphy, but the podomere composition and homology of many ancient chelicerates remains poorly understood. The group of *P. maucheri* was unambiguously characterised only by cylindrical legs and the annular coxae 1, which are characters found in the two other Pycnogonida groups. The super-division of the propodus can only be confirmed in *P. maucheri*, and the division of the femur into two immobile podomeres is putative.

CONCLUSION

The pycnogonids of the Hunsrück Slate are a unique testimony of the Palaeozoic diversity among Pycnogonida. The four species we redescribe, *Flagellopantopus blocki*, *Palaeoisopus* *problematicus*, *Palaeopantopus maucheri*, and *Pentapantopus vogteli*, show different morphology within their body and the legs, suggesting two morphological groups (potentially corresponding to two clades) that surely had different biology and ecology. Unidentified specimens leave the possibility of even more diversity. None of these two groups have survived until today, where only pantopod pycnogonids can be observed.

In their tree-dating analysis, Ballesteros et al. (2021) estimated that crown-group Pantopoda diversified in the Silurian (at the latest) and that by the Late Devonian, all extant pantopod super-families listed by Sabroux, Corbari & Hassanin (2023) had already diversified. However, there is no trace of any of these taxa in the Devonian material or before, nor throughout the Devonian-Jurassic gap in the pycnogonid fossil record that ends with the fauna of La Voulte sur Rhône and Solnhofen, in which pantopods are the only representatives of Pycnogonida (Charbonnier, Vannier & Riou, 2007; Sabroux et al., 2019, 2023). It remains uncertain whether the absence of pantopods among the rich Hunsrück material is a consequence of biased preservation (given that this material is primarily represents by the gigantic *P. problematicus*, and smaller forms are rarely found). Alternatively, or additionally, it is possible that pantopods inhabited different environments (e.g., abyssal waters) than the Hunsrück species. Lastly, we must consider that the diversification times calculated by Ballesteros et al. (2021) are based upon the contemporary taxonomy and since then *Haliestes dasos* has been removed from the pantopod crown group (Siveter et al., 2023; Sabroux et al., 2023). This taxonomic revision will, inevitably, impact upon molecular clock estimates, including those of Ballesteros et al. (2021).

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Figure 1

Palaeiosopus problematicus, holotype SNSB-BSPG 1928 VII 11.

(A) Standard view. (B) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C) Normals visualization. (D-E) Maximum intensity views of X-ray microtomography. (F) Interpretative drawing. *ab*: abdomen, *ce*: cephalon, *ov*: oviger. *WL1-4*: walking legs 1-4. Scale bar 5 mm.

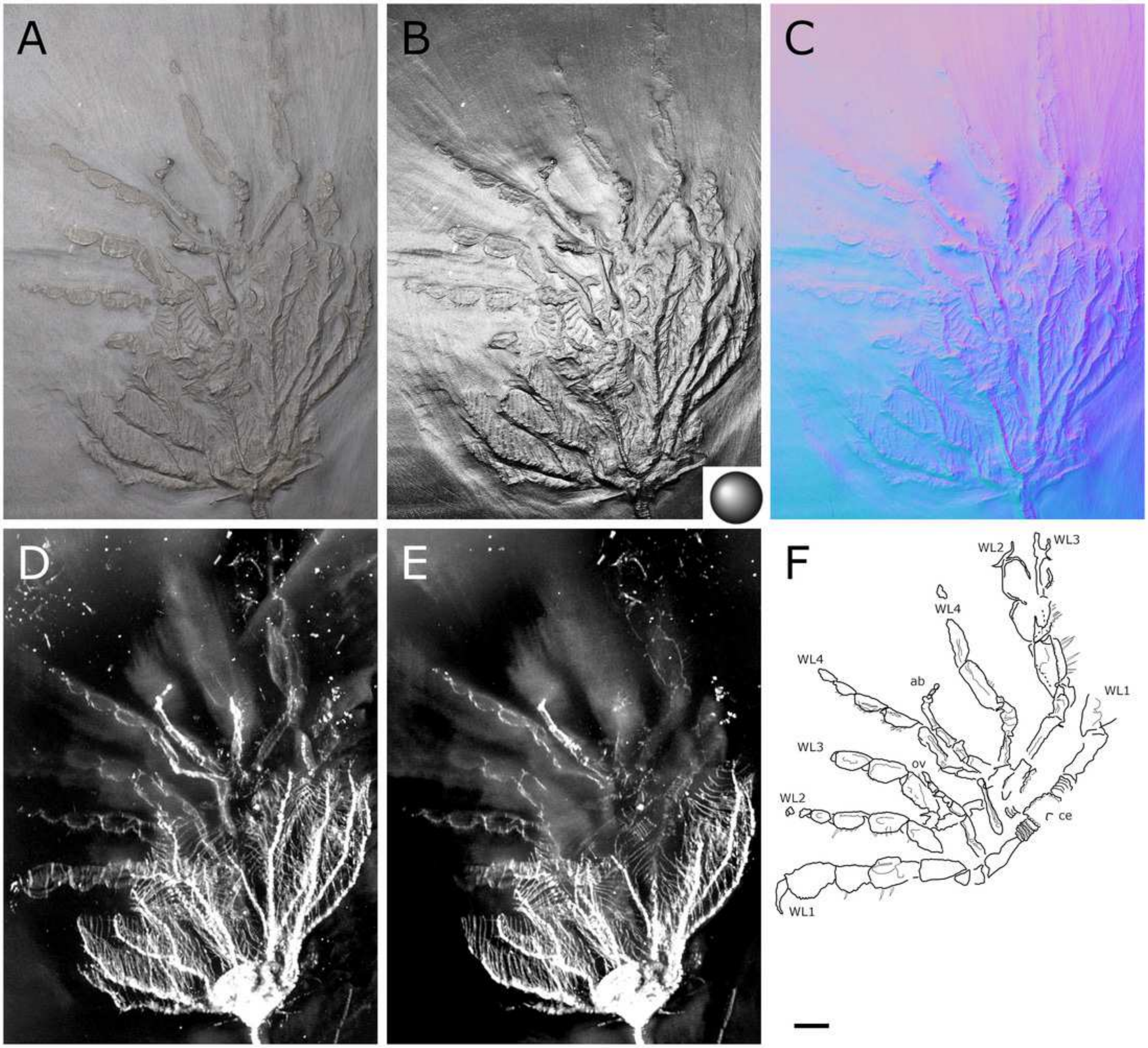

A
B
C
D
E
F
WL2
WL3
WL4
WL4
ab
WL1
WL3
ov
WL2
ce
WL1

Figure 2

Palaeoisopus problematicus, body of specimen NHMMZ PWL 1994/133-LS.

(A) standard view. (B) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C) Normals visualization. (D) Interpretative drawing. Scale bar 5 mm.

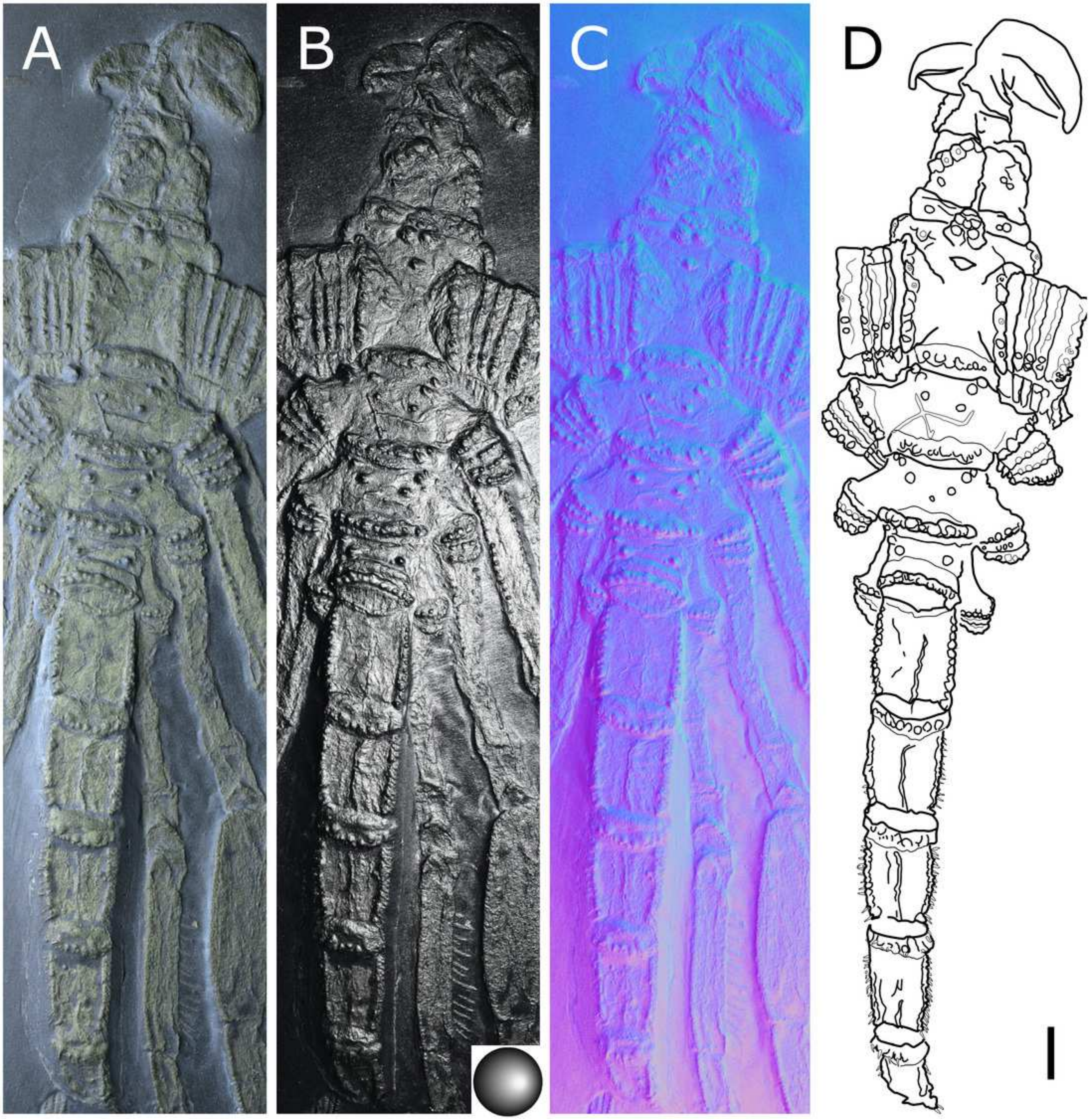
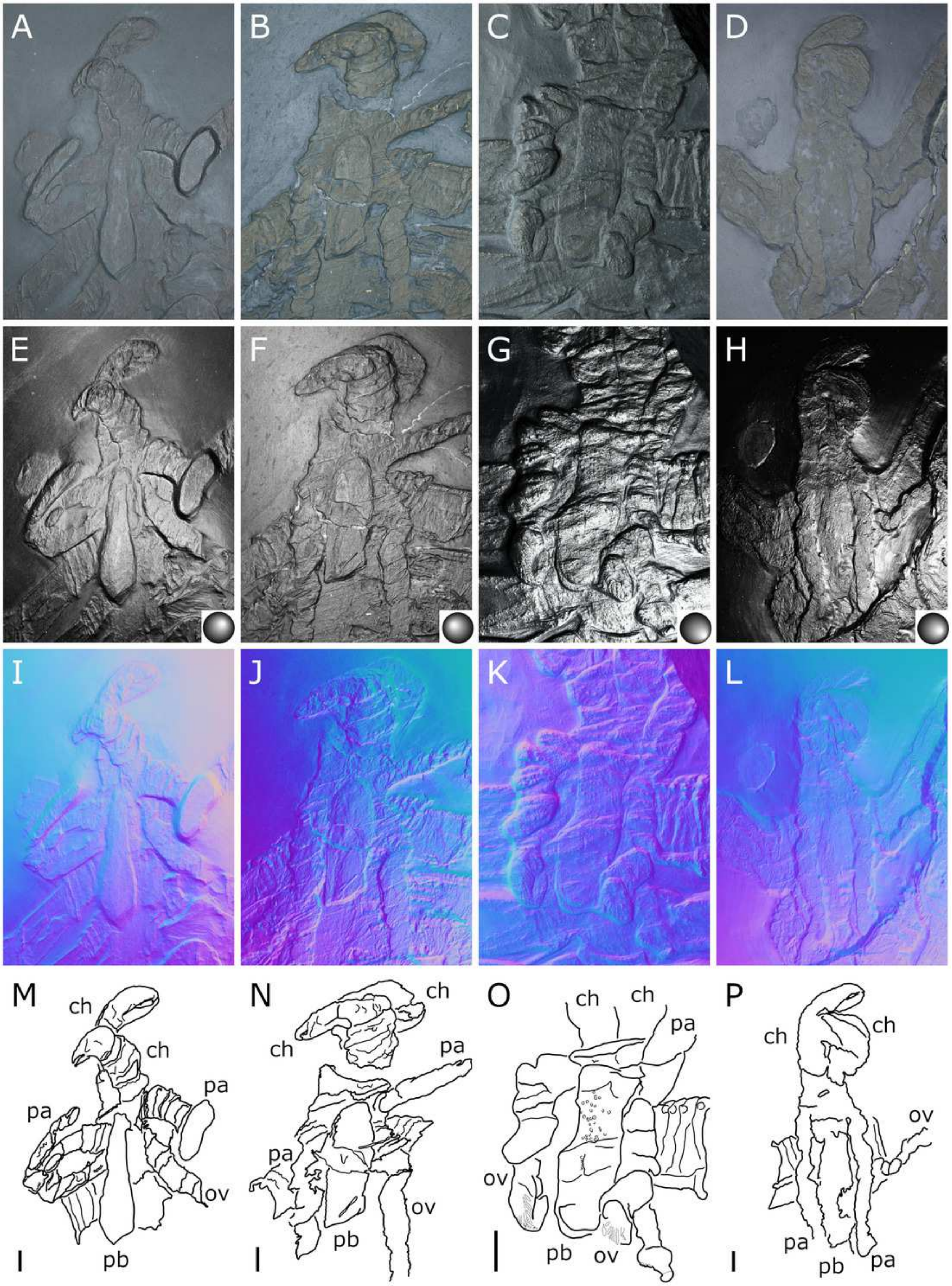

A
B
C
D

Figure 3

Palaeoisopus problematicus, cephalon and proboscis in ventral view.

Specimens IGPB-HS207 (A, F, I, M), IGPB-HS660 (B, F, J, N), SNSB-BSPG 1932 I 67 (C, G, K, O) and NHMMZ PWL 1997/44-45-LS (D, H, L, P). (A-D) Standard view. (E-H) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (I-L) Normals visualization. (M-P) Interpretative drawings. *ch*: chelifore, *pa:* palp, *pb*: proboscis, *ov*: oviger. Scale bars 5 mm.


A
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D
E
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H
I
J
K
L
M
ch
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pa
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ov
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ch
pa
pa
ov
pb
O
ch
ch
pa
ov
pb
ov
P
ch
ch
ov
pa
pb
pa

Figure 4

Palaeoisopus problematicus, lateral view of the body where the proboscis is potentially visible.

Specimens IGPB-HS457 (A, C, E) and NHMMZ PWL 199535-LS (B, D, F). (A-B) Standard view. (C-D) Normals visualization. (E-F) Interpretative drawings. *ch*: chelifore, *pa:* palp, *pb*: proboscis, *ov*: oviger, *WL1-4*: walking legs 1-4. Scale bars 5 mm.

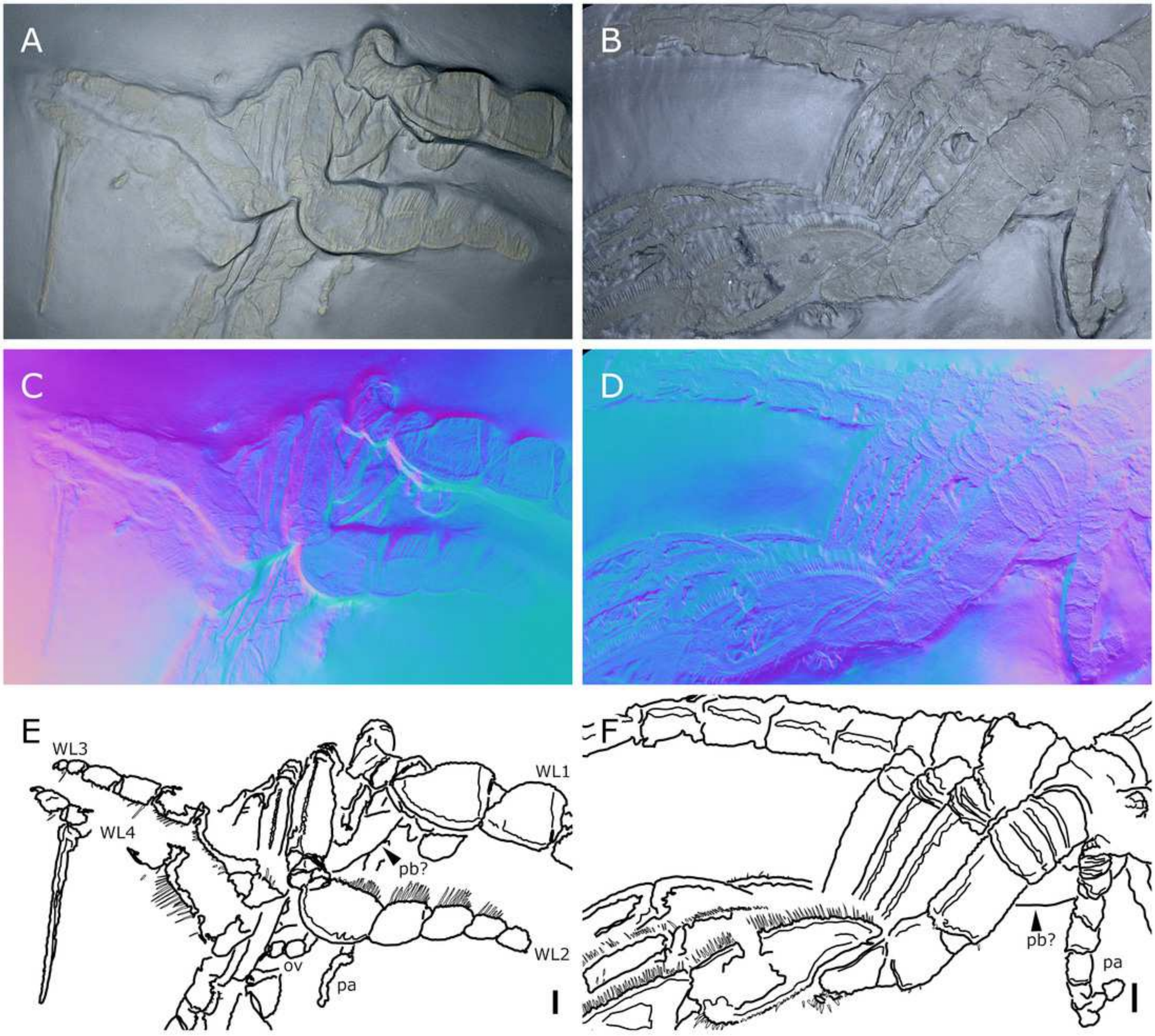
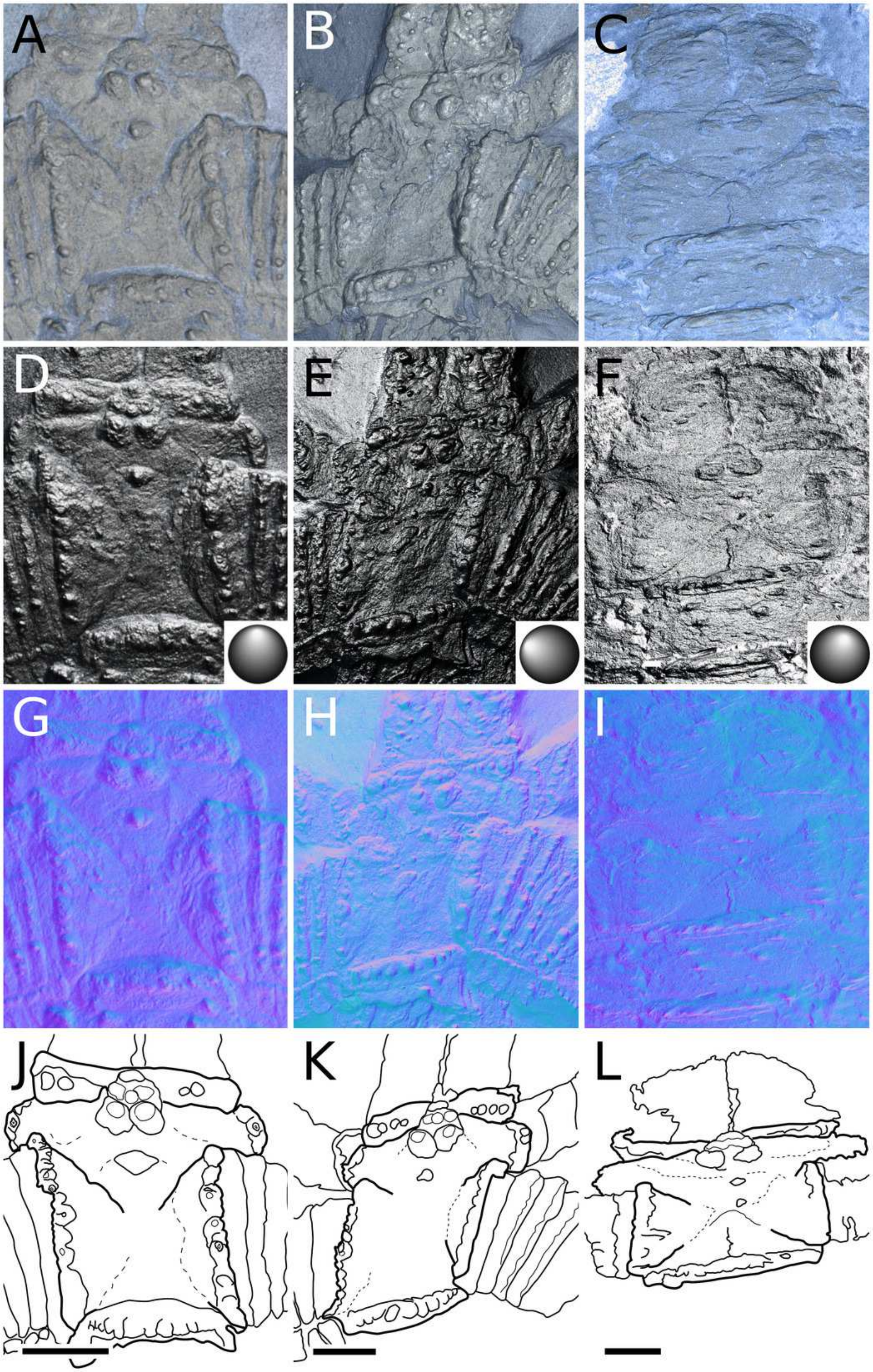


Figure 5

Palaeoisopus problematicus, cephalon and first trunk segment.

Specimens NHMMZ PWL 1994/133-LS (A, D, G, J), NHMMZ PWL 2008/141-LS (B, E, H, K) and IGPB-AR-340 (C, F, I, L). (A-C) Standard view. (D-E Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (D-I) Normals visualization. (J-L) Interpretative drawings. Scale bars 5 mm.


A
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C
D
E
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K
L

Figure 6

Diagram of the organisation of the ocular tubercle ornamenation of *Palaeoisopus problematicus* as well as a few representatives of the modern *Rhynchothorax*.

Colours indicate putative homologies. In the case of the posteriormost dorsal tubercle of *R. coraliensis*, there is no clear evidence of ornamentation, but Staples (2019) represents a low elevation of the tergite around this position which could correspond. Asterisks (*) indicate the tubercles that were interpreted as eyes by Bergström, Stürmer & Winter (1980). *lo*: lateral sense organ (coloured in orange). *Rhynchothorax* ocular tubercles diagrams are based on the illustrations of Arnaud (1974) Child (1979, 1988) and Staples (2019).

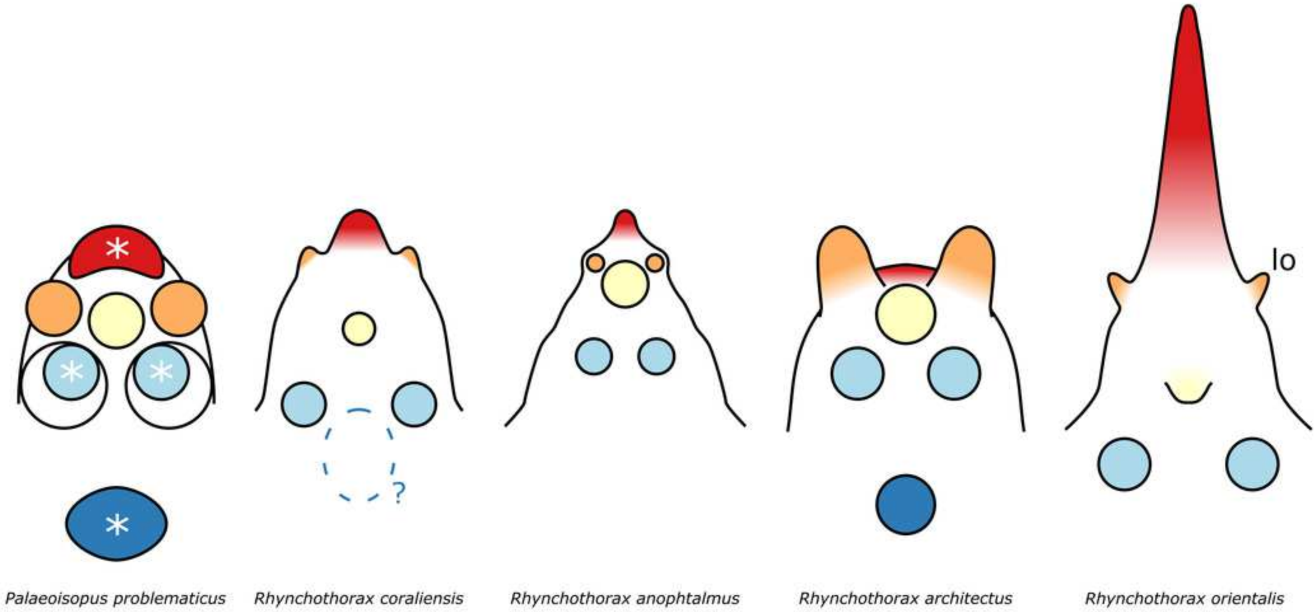


Figure 7

Palaeoisopus problematicus, trunk and cephalon of the specimen IGPB-HS206.

(A) General view of the fossil. (B-D) Zoom on the cephalon region: (B) Standard view. (C) Normals visualization. (D) Interpretative drawing. Scale bar 5 mm.

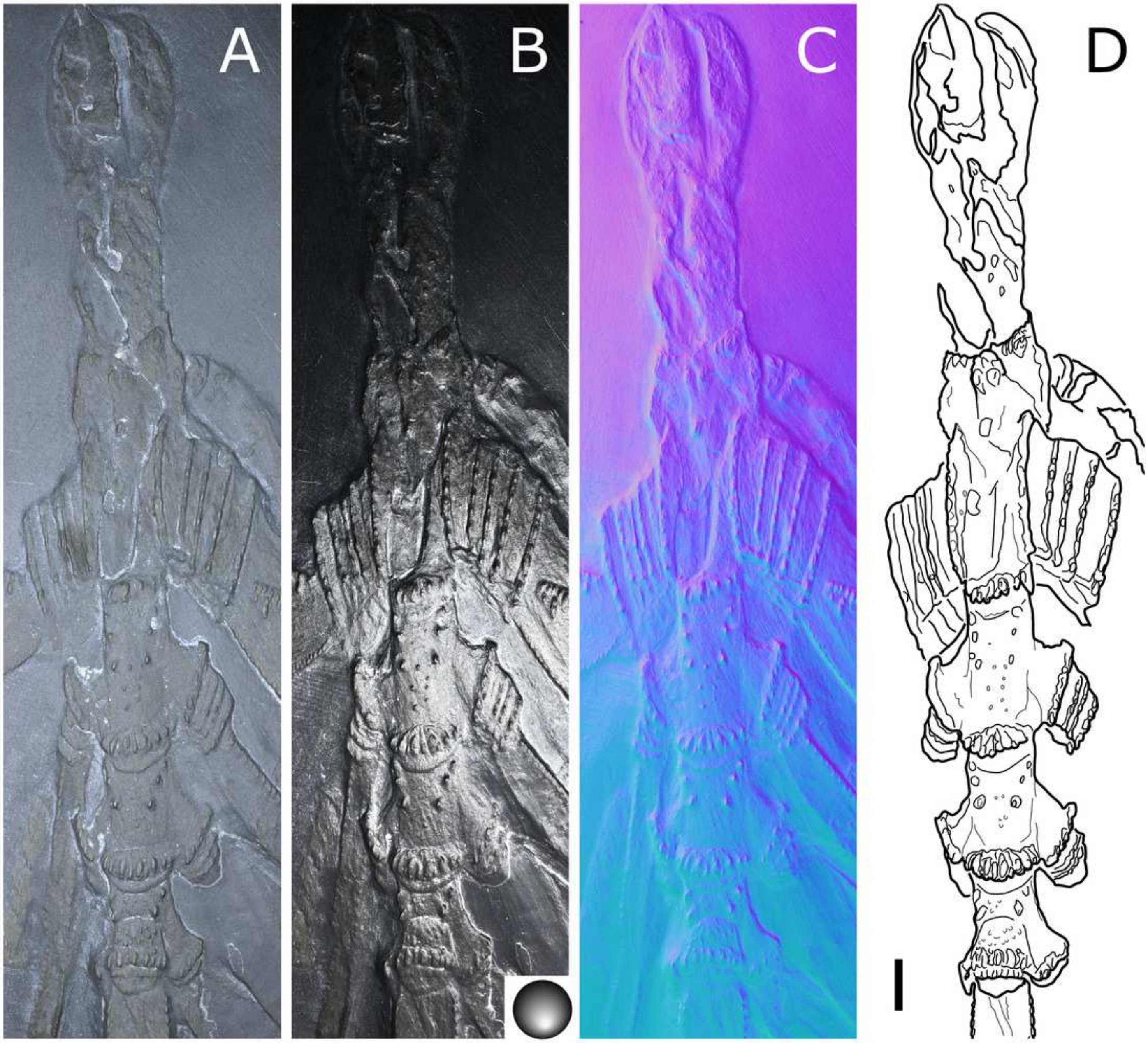
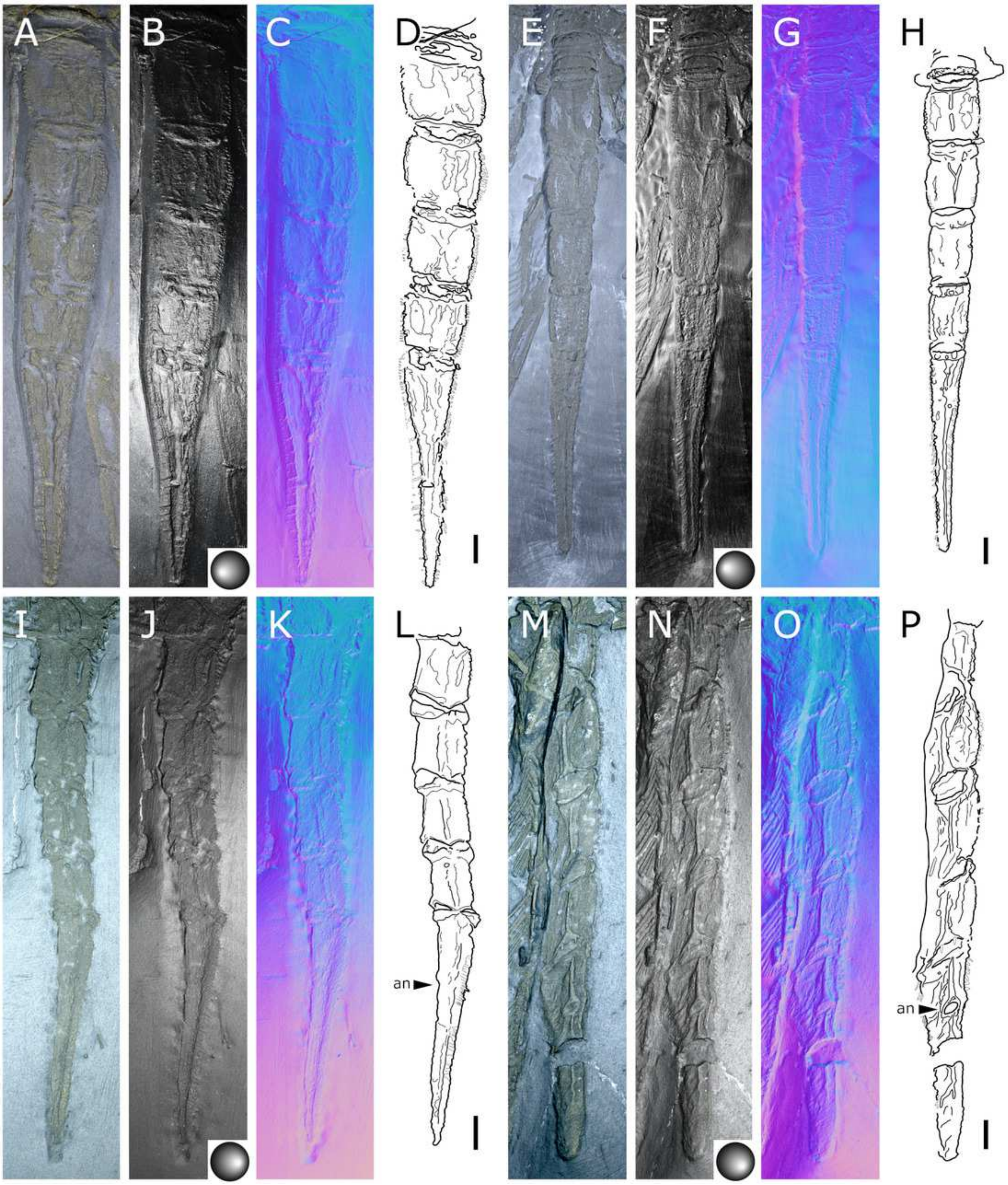


Figure 8

Palaeoisopus problematicus, abdomen.

Specimens MB-A-46 (A-D, dorsal view), NHMMZ PWL 1998/122-LS (E-H, dorsal view), IGPB-HS1039 (I-L, lateral view), IGPB-HS660 (M-P, ventral view). (A, E, I, M) Standard view. (B, F, J, N) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C, G, K, O) Normals visualization. (D, H, L, P) Interpretative drawings. *an*: anus. Scale bars 5 mm.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K
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an
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an

Figure 9

Palaeoisopus problematicus, evidence for the mobility range of the abdomen (in lateral view).

Specimens NHMMZ PWL 1994/56-LS (A-C), NHMMZ PWL 1995/35-LS (D-I) and IGPB-HS694 (J-L). (A, D, G, J) Standard view. (B, E, H, K) Normals visualization. (C, F, I, L) Interpretative drawings (in I, the abdomen was coloured in yellow for better visibility, and the WL1 of another specimen is coloured in green). *an*: anus. Scale bars 5 mm.

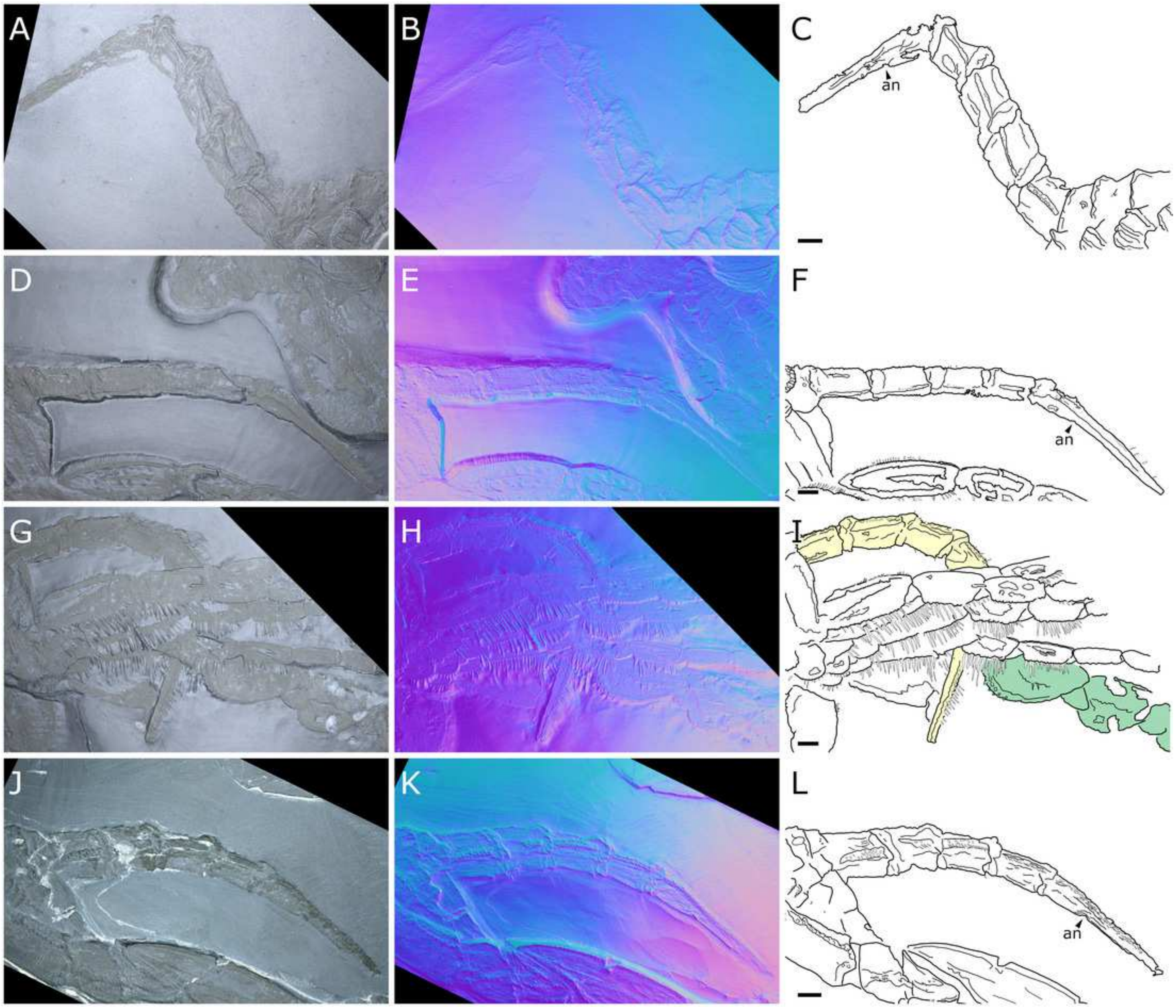
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Figure 10

Palaeoisopus problematicus, specimen IGPB-HS582.

(A) General view of the fossil. (B-D) Zoom on the cephalon region: (B) Standard view. (C) Normals visualization. (D) Interpretative drawing. Margins and lines (see text) are highlighted with different colours according to their position. *ch:* chelifore, *pa:* palp, *ov*: oviger. Scale bars: A: 20 mm, D: 5 mm (B-C same scale as D).

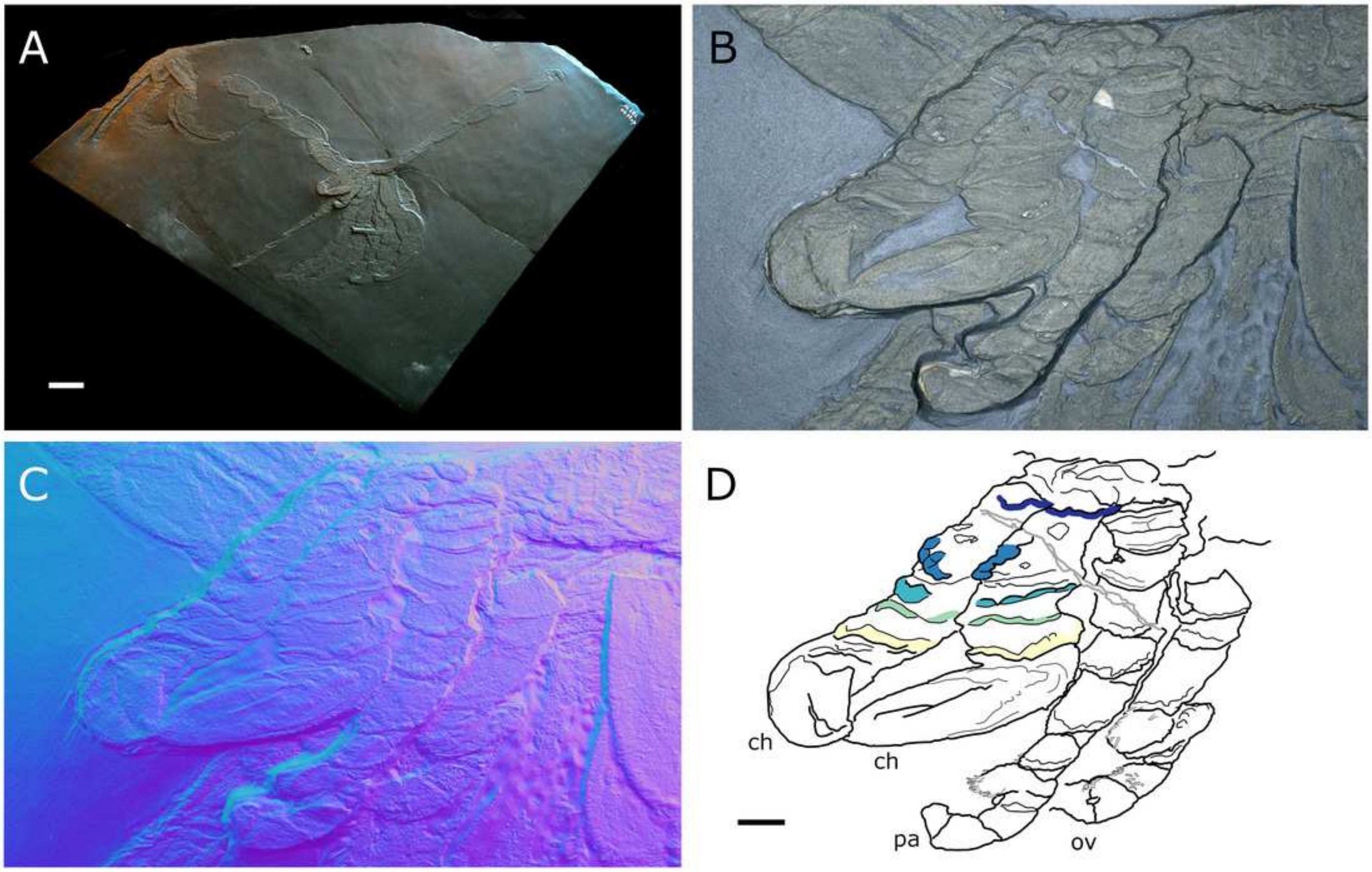

Figure 11

Palaeoisopus problematicus, chelifores.

Specimens NHMMZ PWL 1996/18-LS (A, D, G, J), NHMMZ PWL 2008/141-LS (B, E, H, K) and SNSB-BSPG 1932 I 67 (C, F, I, L). (A-C) Standard view. (D-F) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (G-I) Normals visualization. (J-L) Interpretative drawings. white arrowheads indicate some of the potential setae insertions. Margins and lines (see text) are highlighted with different colours according to their position. Scale bars 5 mm.

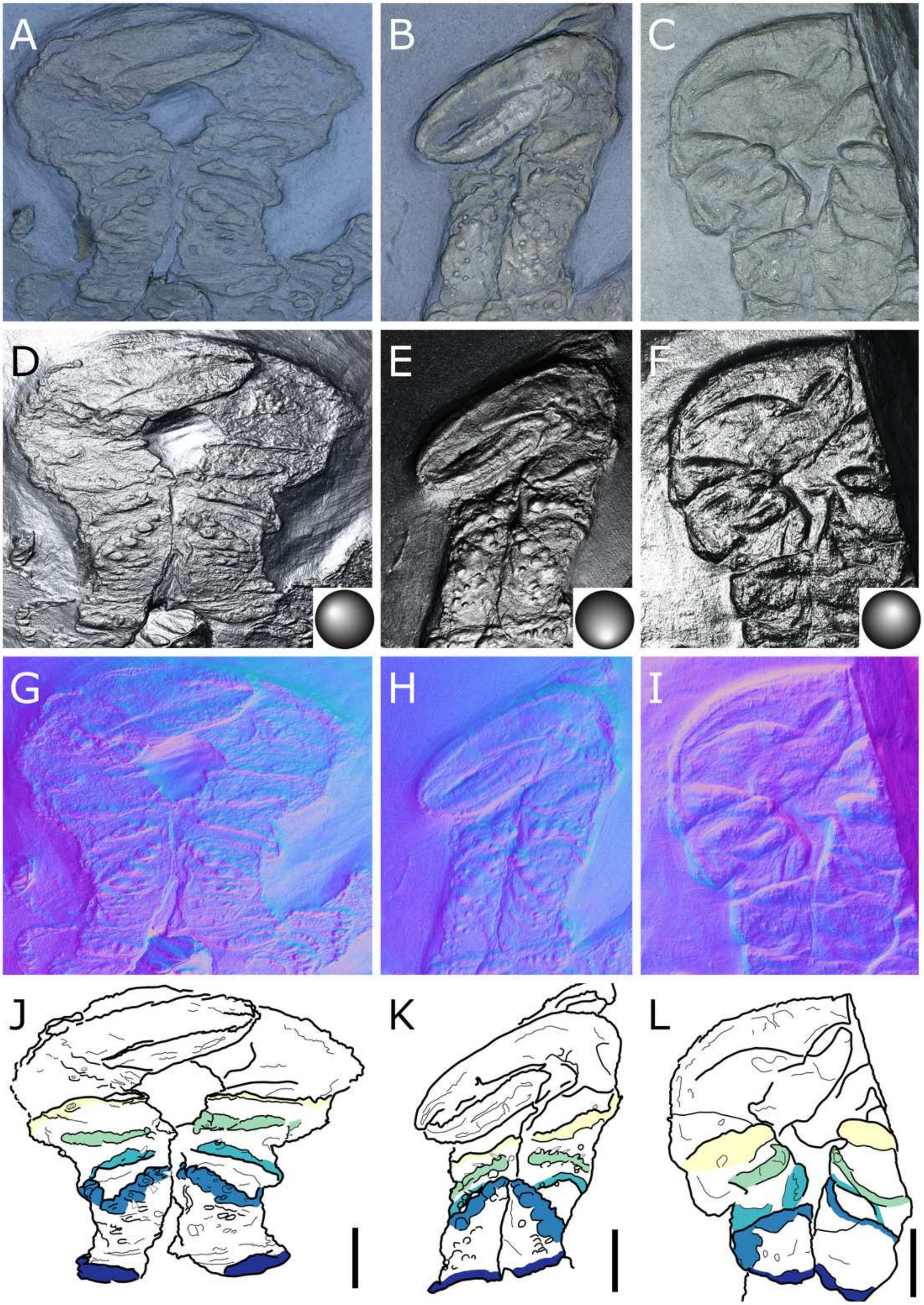
A
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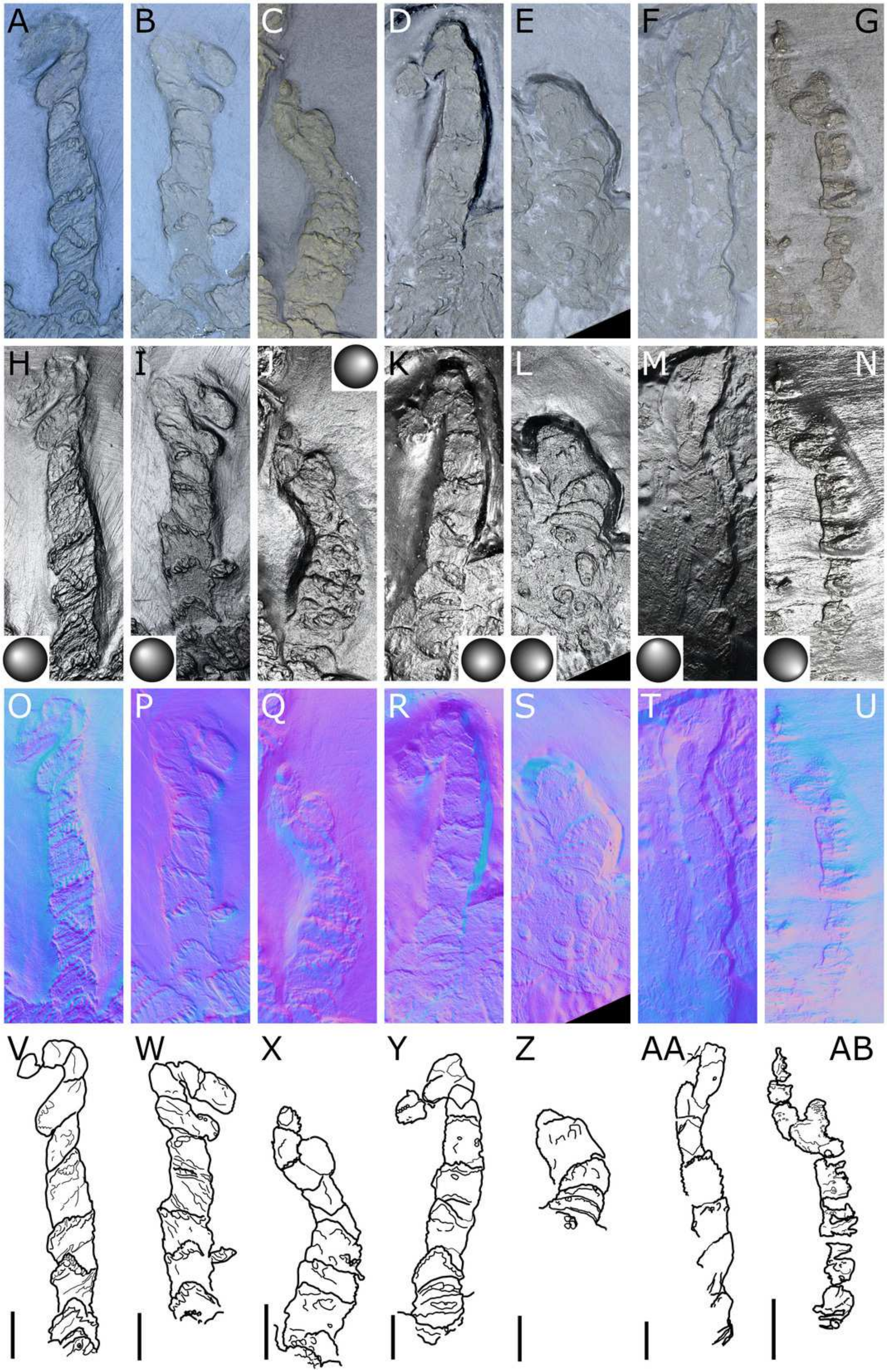
Figure 12

Palaeoisopus problematicus, palps.

Specimens NHMMZ PWL 1996/18-LS (right palp: A, H, O, V; left palp: B, I, P, W), NHMMZ PWL2008/141-LS (left palp: C, J, Q, X), NHMMZ PWL 1995/35-LS specimens 1 (right palp: D, K, R, Y) and 2 (right palp: E, L, S, Z), NHMMZ PWL 1997/44-45-LS (right palp: F, M, T, AA), SNSB-BSPG 1932 I 63 (left palp: G, N, U, AB). (A-G) Standard view. (H-N) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, bottom left or top right; see supplementary material 3 for details). (O-U) Normals visualization. (V-AB) Interpretative drawings. Scale bars 5 mm.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M
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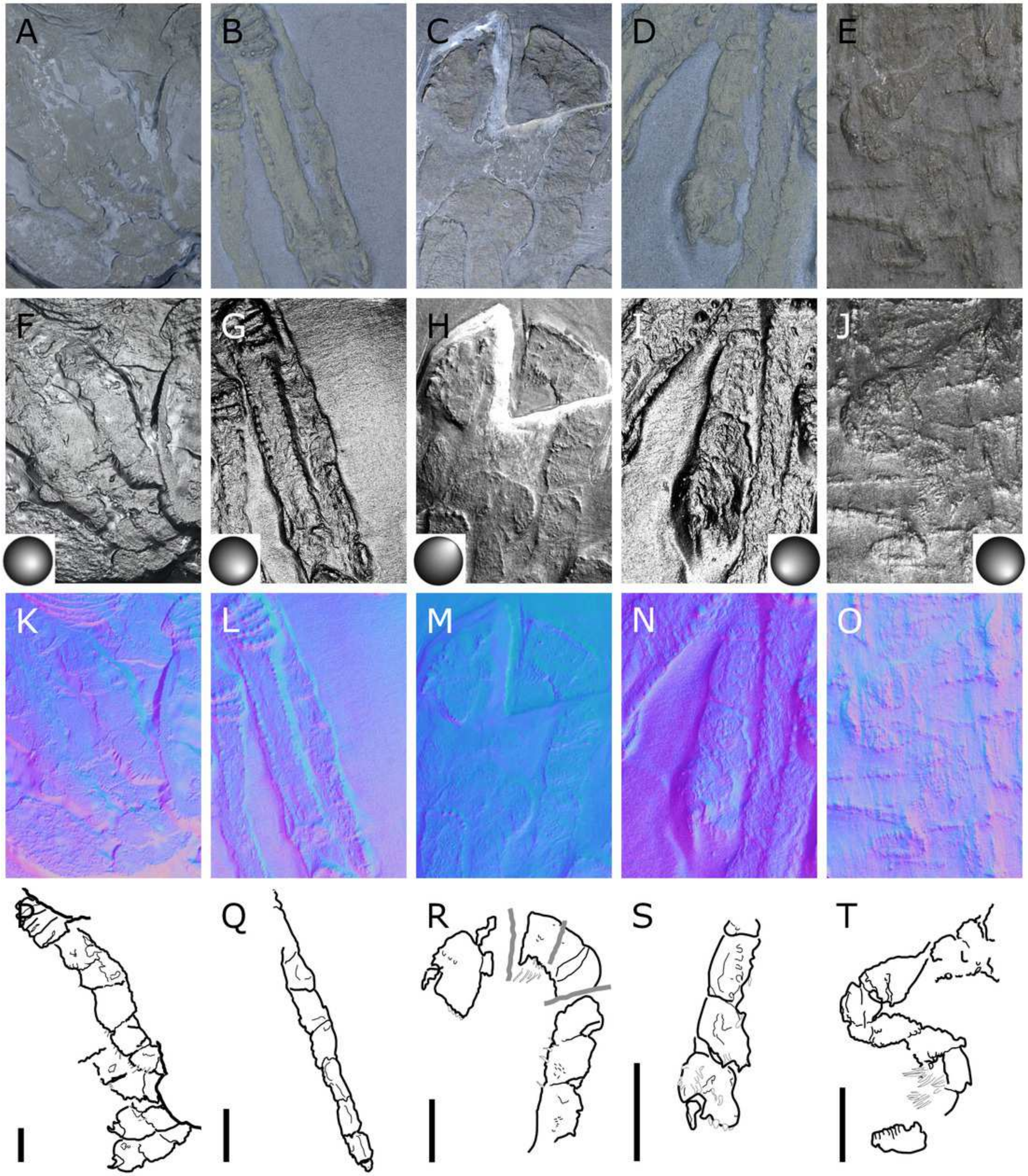
Q
R
S
T
U
V
W
X
Y
Z
AA
AB

Figure 13

Palaeoisopus problematicus, ovigers.

Specimens NHMMZ PWL 1995/35-LS specimen 3 (unidentified oviger: A, F, K, P), NHMMZ PWL 1994/133-LS (right oviger: B, G, L, Q), NHMMZ PWL 1994/56-LS (unidentified oviger: C, H, M, R), NHMMZ PWL 1994/133-LS (right oviger: D, I, N, S) and SNSB-BSPG 1932 I 63 (unidentified oviger: E, J, O, T). (A-E) Standard view. (F-J) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right or bottom left; see supplementary material 3 for details). (K-O) Normals visualization. (P-T) Interpretative drawings. Scale bars 5 mm.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R
S
T

Figure 14

Diagram of the interpreted structure of the cephalic appendages of *Palaeoiospus problematicus.*

(A) Chelifore. (B) Palp. (C) Oviger. (D) Colour code for putative podomeres homology in palps and ovigers, following the nomenclature of Sabroux et al. (2023) and Siveter et al. (2023).

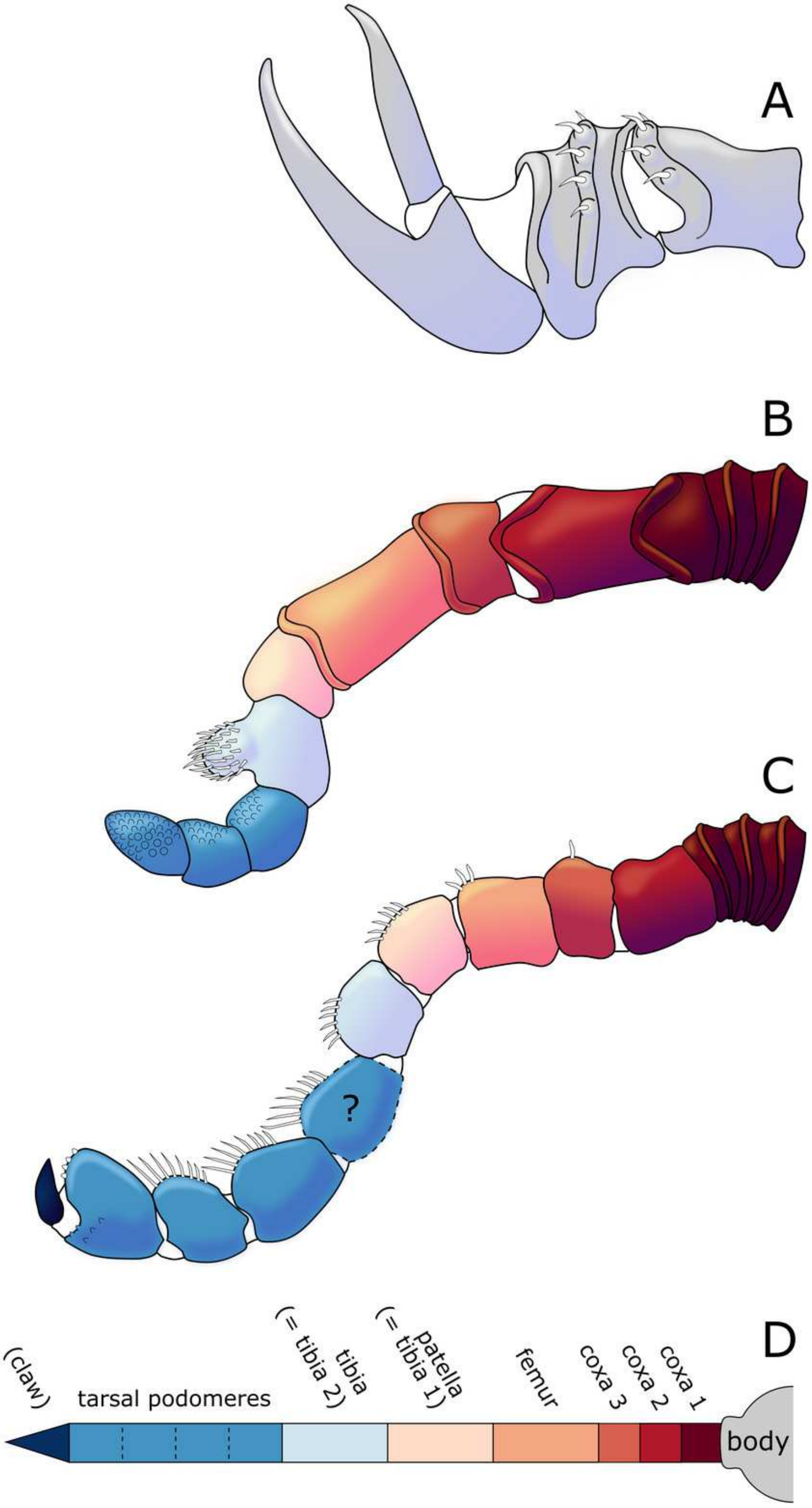

A
B
C
?
D
(claw)
tarsal podomeres
tibia (= tibia 2)
patella (= tibia 1)
femur
coxa 3
coxa 2
coxa 1
body

Figure 15

Palaeoisopus problematicus, first walking pair of legs (WL1).

Specimens NHMMZ PWL 2008/141-LS (left WL1, lateral view: A-D), IGPB-HS636 (left WL1, lateral view: E-H), terminal podomeres of IGPB-HS582 (left WL1, lateral view: I-K; note the ventral spines), IGPB-AR-340 (left WL1, dorsal view: L-N), MB-A-46 (left WL1, dorsal view: O-Q). (A, E, I, L, O) Standard view. (B, F) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right or bottom left; see supplementary material 3 for details). (C, G, J, M, P) Normals visualization. (D, H, K, N, Q) Interpretative drawings. *cx1-3*: coxa 1-3, *cl*: claw, *fe*: femur, *pt*: patella, *pr*: propodus, *ta*: tarsus, *ti*: tibia. Scale bars 5 mm.

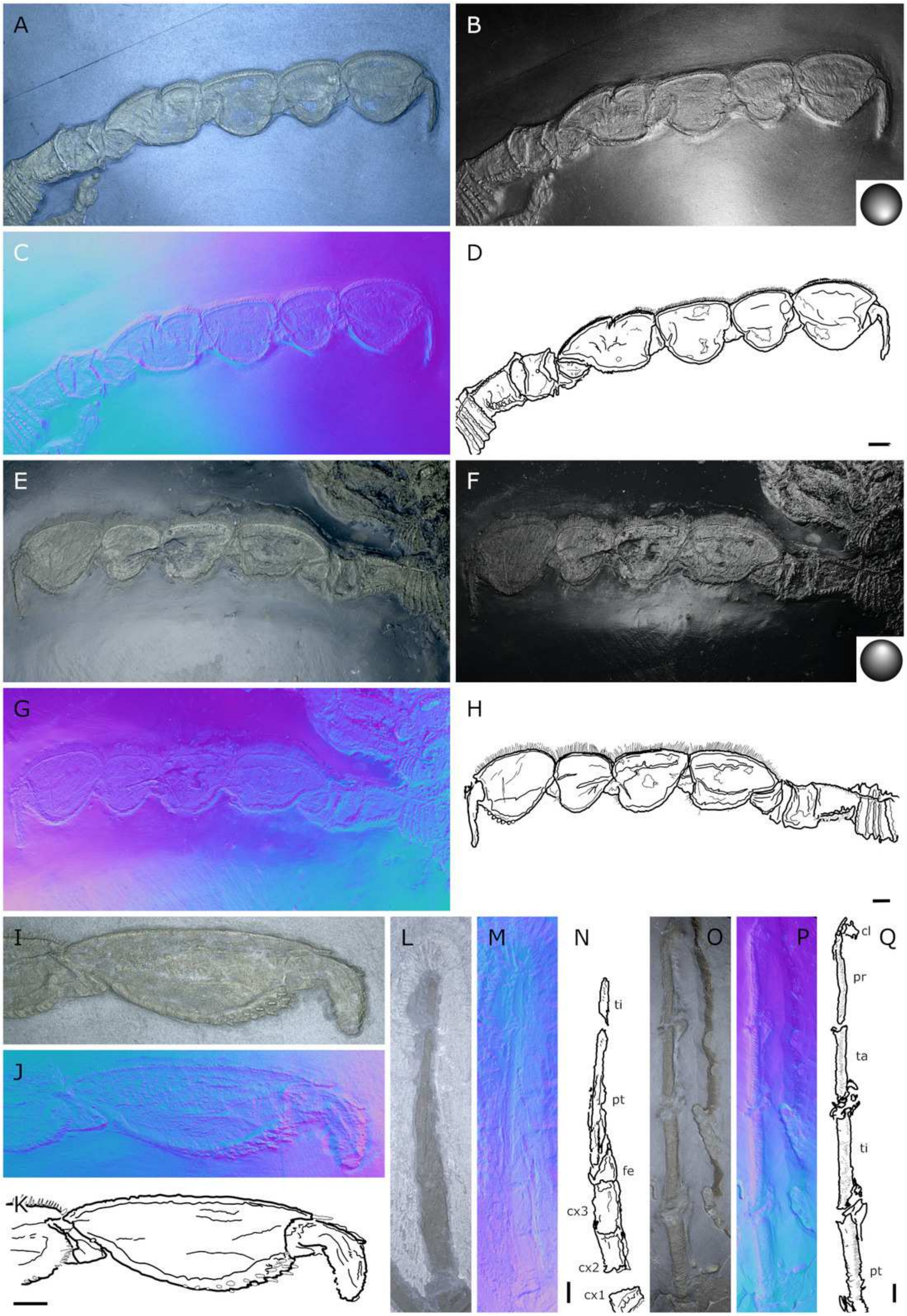

A
B
C
D
E
F
G
H
I
J
K
L
M
N
ti
pt
fe
cx3
cx2
cx1
O
P
Q
cl
pr
ta
ti
pt

Figure 16

Palaeoisopus problematicus, second to fourth walking pairs of legs (WL2-4).

Specimens IGPB-HS1039 (A-D), IGPB-HS582 (specimen 2, right WL: E-H), MB.A.46 (right WL: I-L) and IGPB-HS582 (specimen 1, right WL: M-P). (A, E, I, M) Standard view. (B, F, J, N) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom left, see supplementary material 3 for details). (C, G, K, O) Normals visualization. (D, H, L, P) Interpretative drawings. *WL2-4*: walking legs 2-4. Scale bars 5 mm.

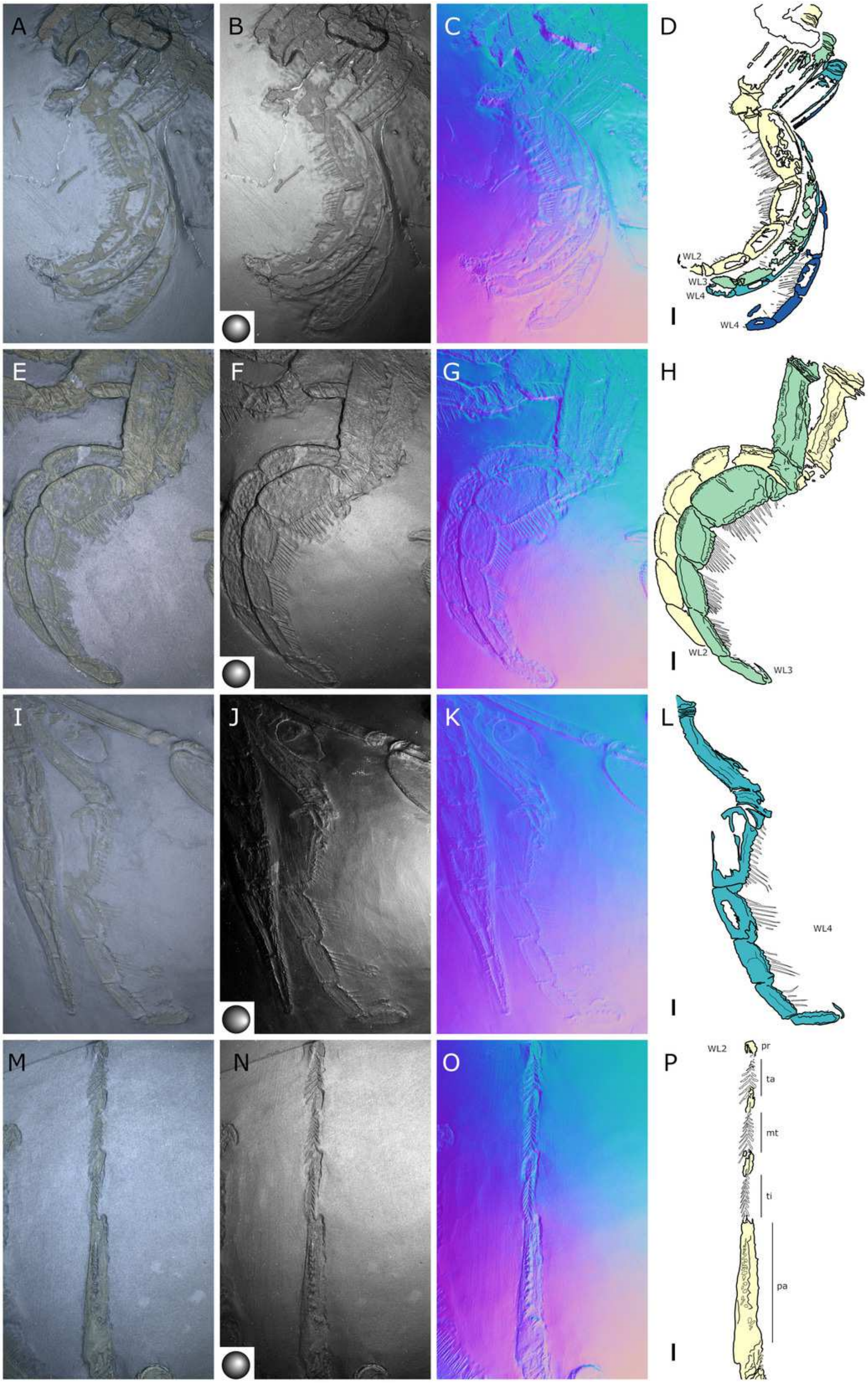
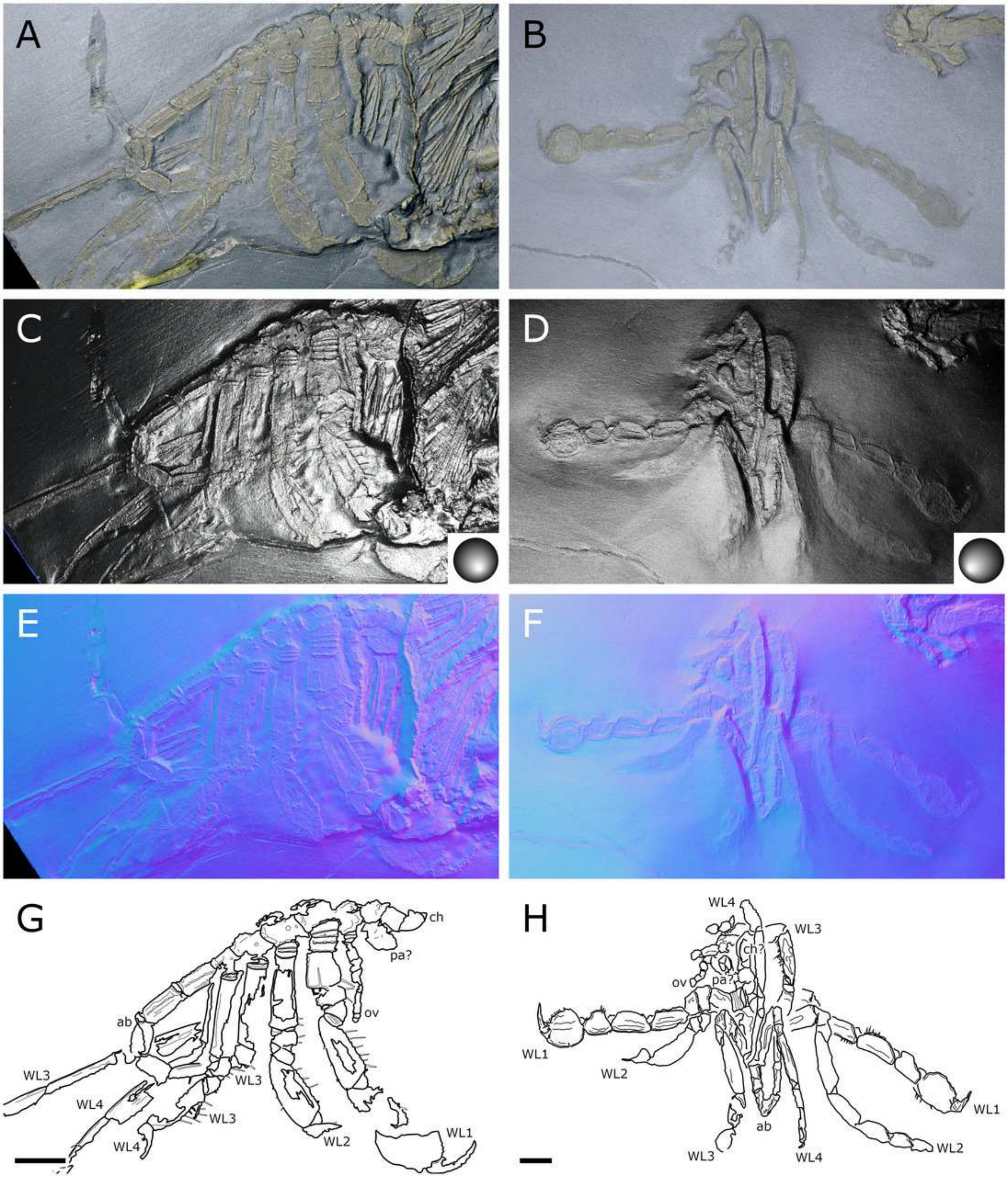

A
B
C
D
WL2
WL3
WL4
WL4
E
F
G
H
WL2
WL3
I
J
K
L
WL4
M
N
O
P
WL2
pr
ta
mt
ti
pa

Figure 17

Juvenile instars of *Palaeoisopus problematicus* (see also following illustration).

Specimens IGPB-HS195 (A, C, E, G) and NHMMZ PWL 2003/272-LS specimen 1 (B, D, F, H). (A, B) Standard view. (C, D) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (E, F) Normals visualization. (G, H) Interpretative drawings. *ab*: abdomen, *ch*: chelifore, *ov*: oviger, *pa*: palp, *WL1-4*: walking legs 1-4. Scale bars 5 mm.


A
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C
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G
ch
pa?
ov
ab
WL3
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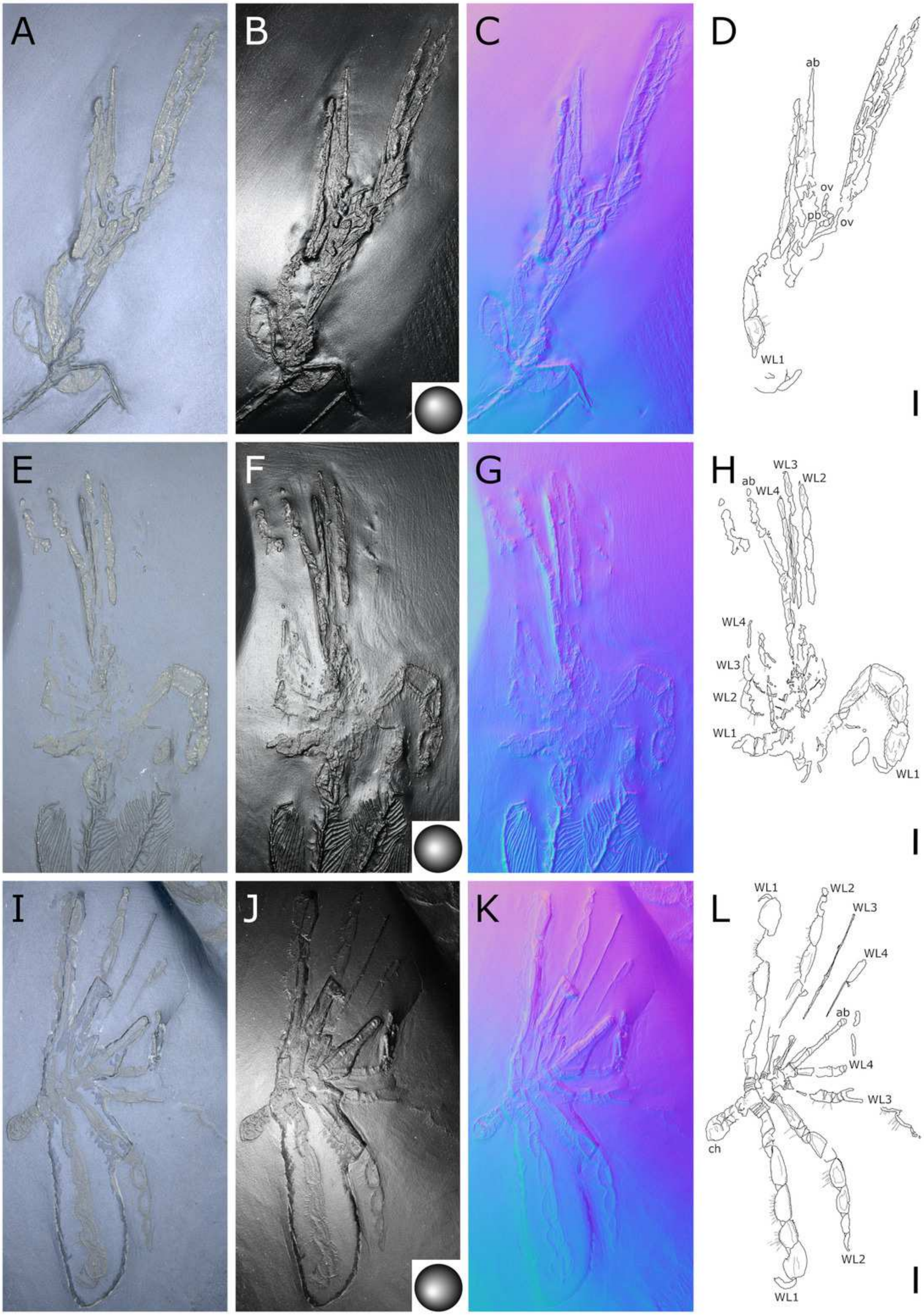
WL3
WL4
WL2
WL1
H
WL4
WL3
ch?
ov
pa?
WL1
WL2
ab
WL3
WL4
WL1
WL2

Figure 18

Juvenile instars of *Palaeoisopus problematicus* (see also previous illustration).

Specimens NHMMZ PWL 1994/54-LS (A, D, G, J), NHMMZ PWL 1986/3 (B, E, H, K) and NHMMZ PWL 2000/46 (C, F, I, L). (A-C) Standard view. (D-F) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom left, see supplementary material 3 for details). (G-I) Normals visualization. (J-L) Interpretative drawings. *ab*: abdomen, *ch*: chelifore, *ov*: oviger, *pb*: proboscis, *WL1-4*: walking legs 1-4. Scale bars 5 mm.


A
B
C
D
ab
ov
pb
ov
WL1
E
F
G
H
ab
WL3
WL4
WL2
WL4
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WL2
WL1
WL1
I
J
K
L
WL1
WL2
WL3
WL4
ab
WL4
WL3
ch
WL2
WL1

Figure 19

Palaeoisopus problematicus reconstruction based on observed material, in dorsal view.

The number of podomeres of the chelifore scapes is speculative (see related section).

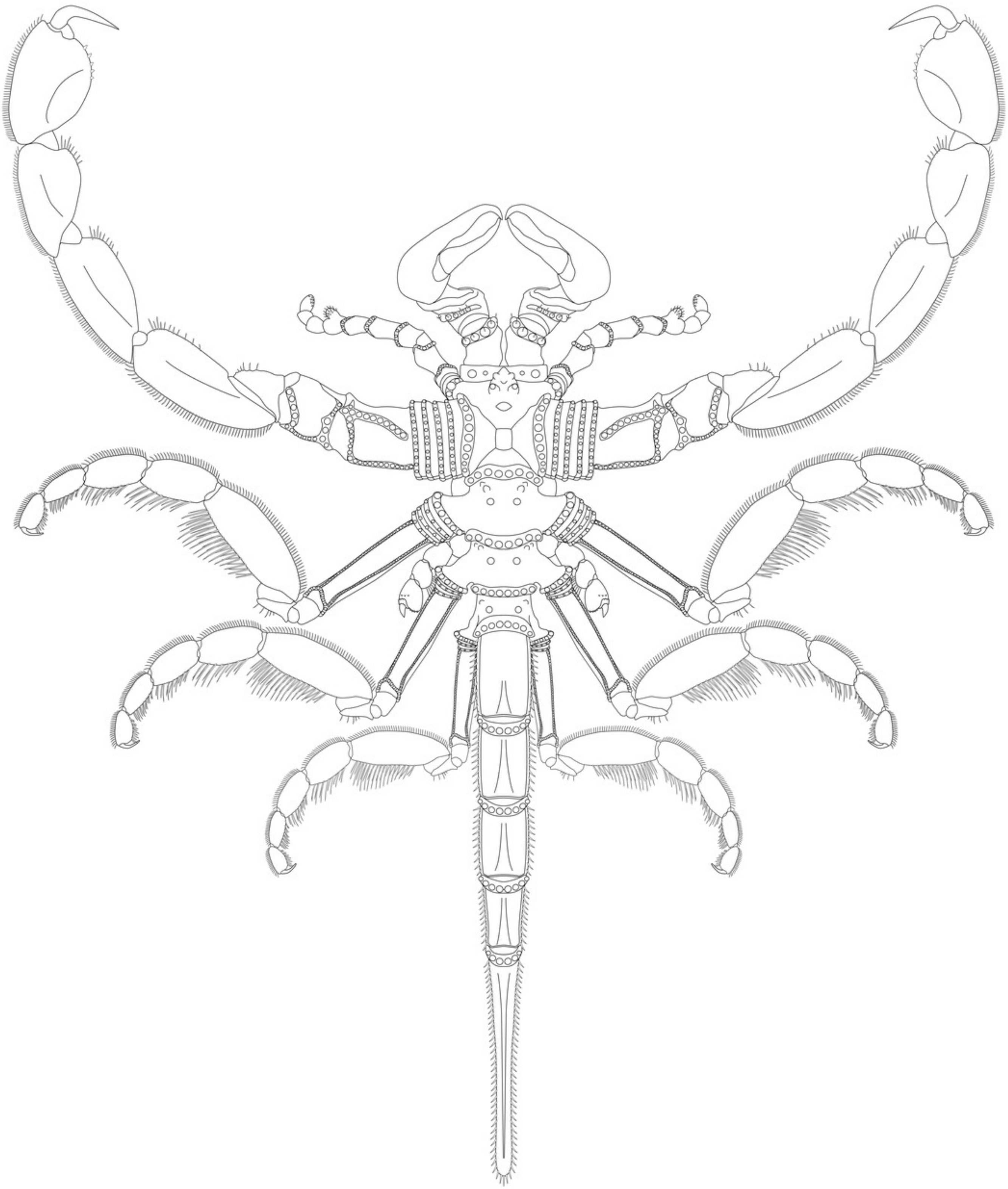

Figure 20

Palaeopantopus maucheri, holotype SNSB-BSPG 1929 V 3.

Dorsal (A-D) and ventral (E-F) views of the body. (A, E) Standard view. (B) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C, F) Normals visualization. (D) Interpretative drawing based of the fossil’s surface. (G) Maximum intensity views of X-ray microtomography. (H) Interpretative drawing of structure revealed with X-ray, overlapped with surface structure (in grey). Pictures E and F were mirrored to correspond to align with A-D, G and H. *ab*: abdomen, *ch*: chelifore, *pa*: palp, *pb*: proboscis, *ov*: oviger, *WL1-4*: walking leg 1-4. Scale bar: 2 mm.

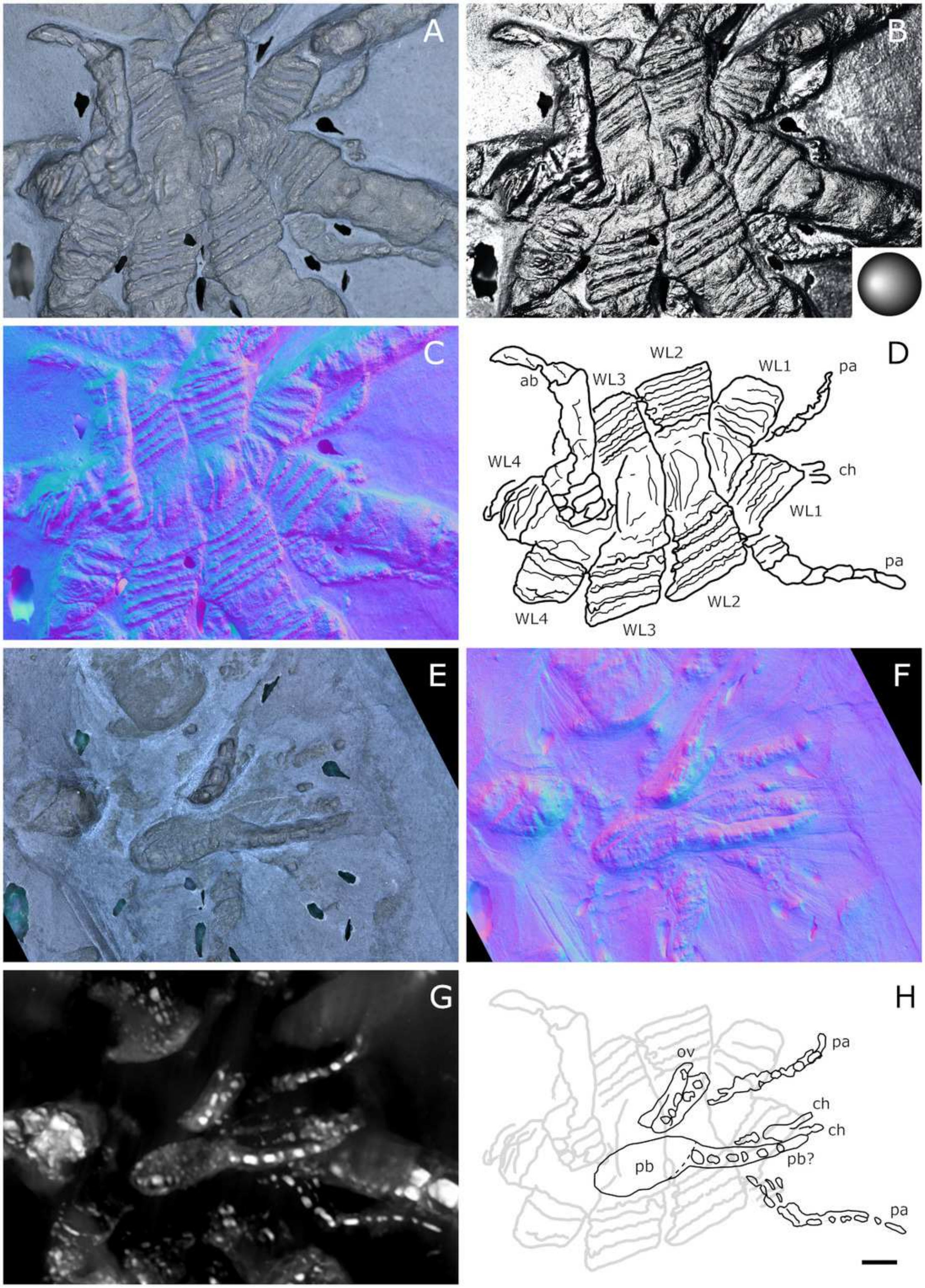
A
B
C
D
ab
WL3
WL2
WL1
pa
WL4
ch
WL1
pa
WL4
WL3
WL2
E
F
G
H
pa
ov
ch
ch
pb
pb?
pa

Figure 21

Palaeopantopus maucheri, specimen SNSB-BSPG 1930 I 501, posterior view of the body.

(A) Standard view. (B) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C) Normals visualization. (D) Interpretative drawing based of the fossil's surface. *ab*: abdomen, *pa*: palp, *ov*: oviger, *WL1-4*: walking leg 1-4. Scale bar: 5 mm.

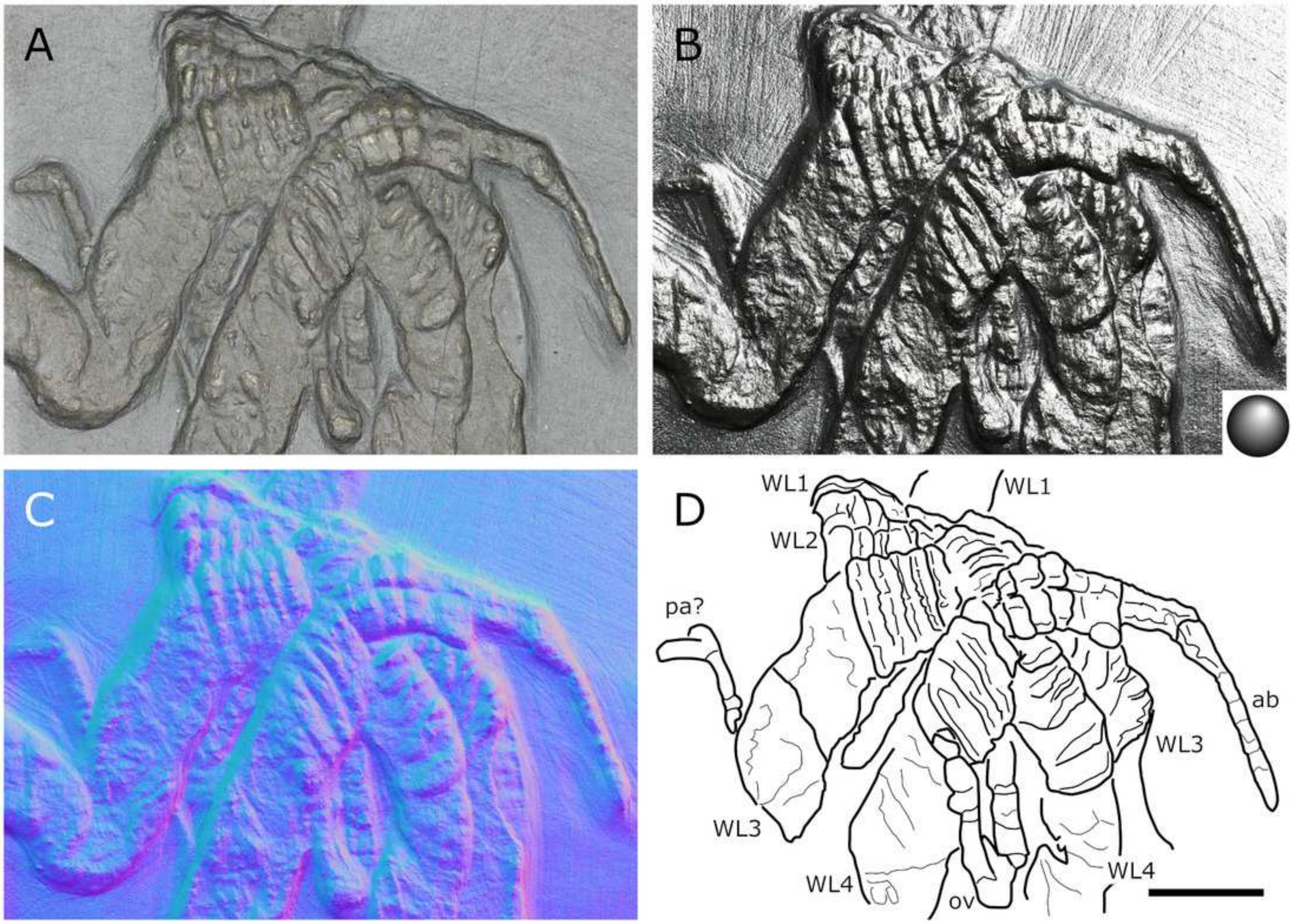

Figure 22

Palaeopantopus maucheri, specimen MB-A-45, ventral view of the body.

(A) Standard view. (B) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C) Normals visualization. (D) Interpretative drawing based of the fossil's surface. (E) Maximum intensity views of X-ray microtomography. (F) Interpretative drawing of structure revealed with X-ray, overlapped with surface structure (in grey). *ab*: abdomen, *ch*: chelifore, *pa*: palp, *pb*: proboscis, *ov*: oviger, *WL1-4*: walking leg 1-4. Scale bar: 5 mm.

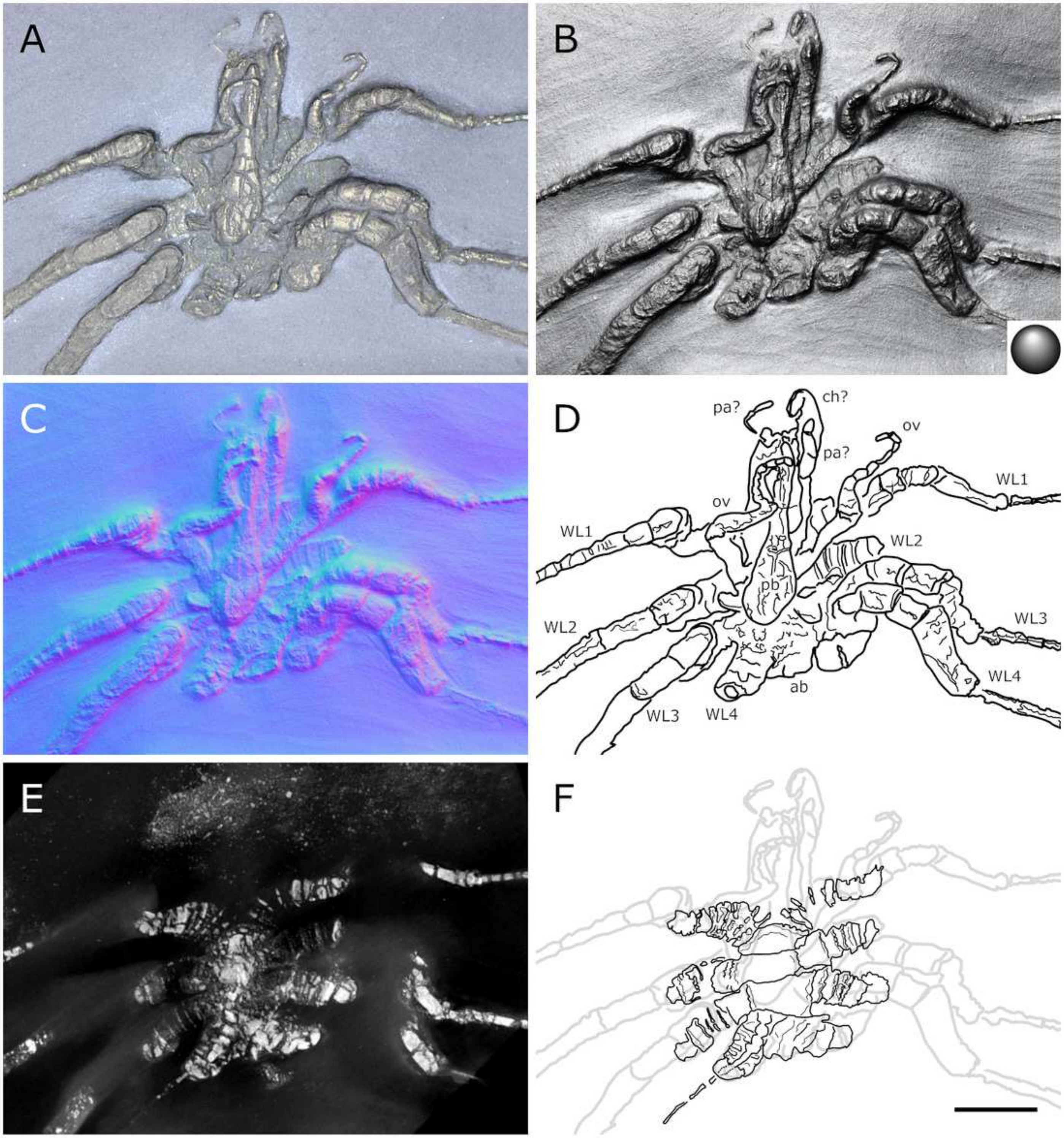
A
B
C
D
pa?
ch?
ov
pa?
WL1
ov
WL1
WL2
pb
WL2
WL3
WL4
ab
WL3
WL4
E
F

Figure 23

Palaeopantopus maucheri, legs.

Holotype SNSB-BSPG 1929 (A-L), specimens MB-A-45 (M-O) and SNSB-BSPG 1930 I 501 (P-R). (A, D, G, J, M, P) Standard view. (B, E, H, K, N, Q) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C, F, I, L, O, R) Normals visualization. (S) Interpretative drawings of all legs, put to the same scale. All scale bars 5 mm, B and C same as A; E, F same as D; H, I same as G; K, L same as J; N, O same as M; Q, R same as P.

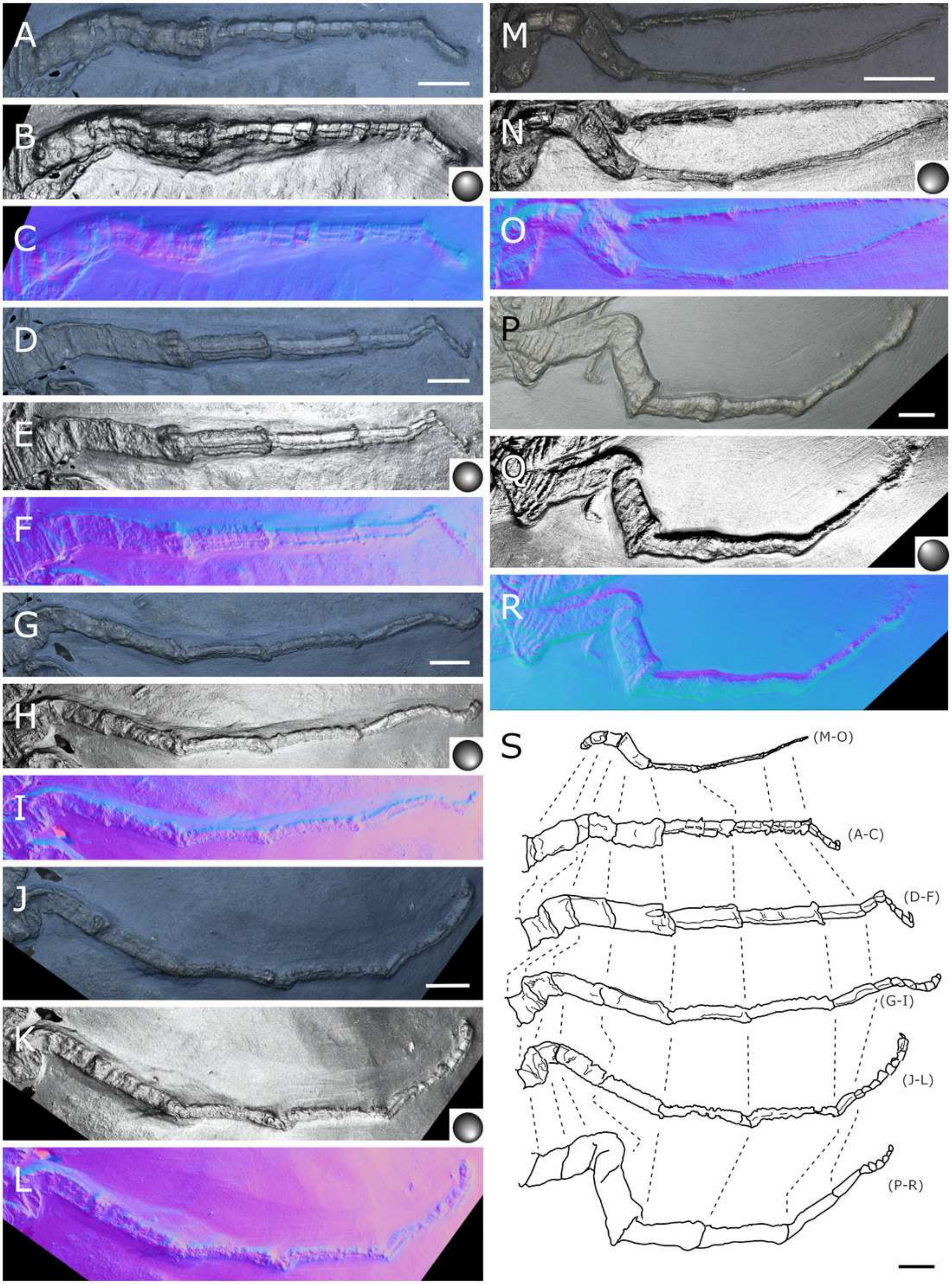
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
(M-O)
(A-C)
(D-F)
(G-I)
(J-L)
(P-R)

Figure 24

Palaeopantopus maucheri reconstruction based on observed material, in dorsal view.

The structure and number of podomeres in the cephalic appendages, as well as the terminal podomeres of the walking legs, are conjectural.

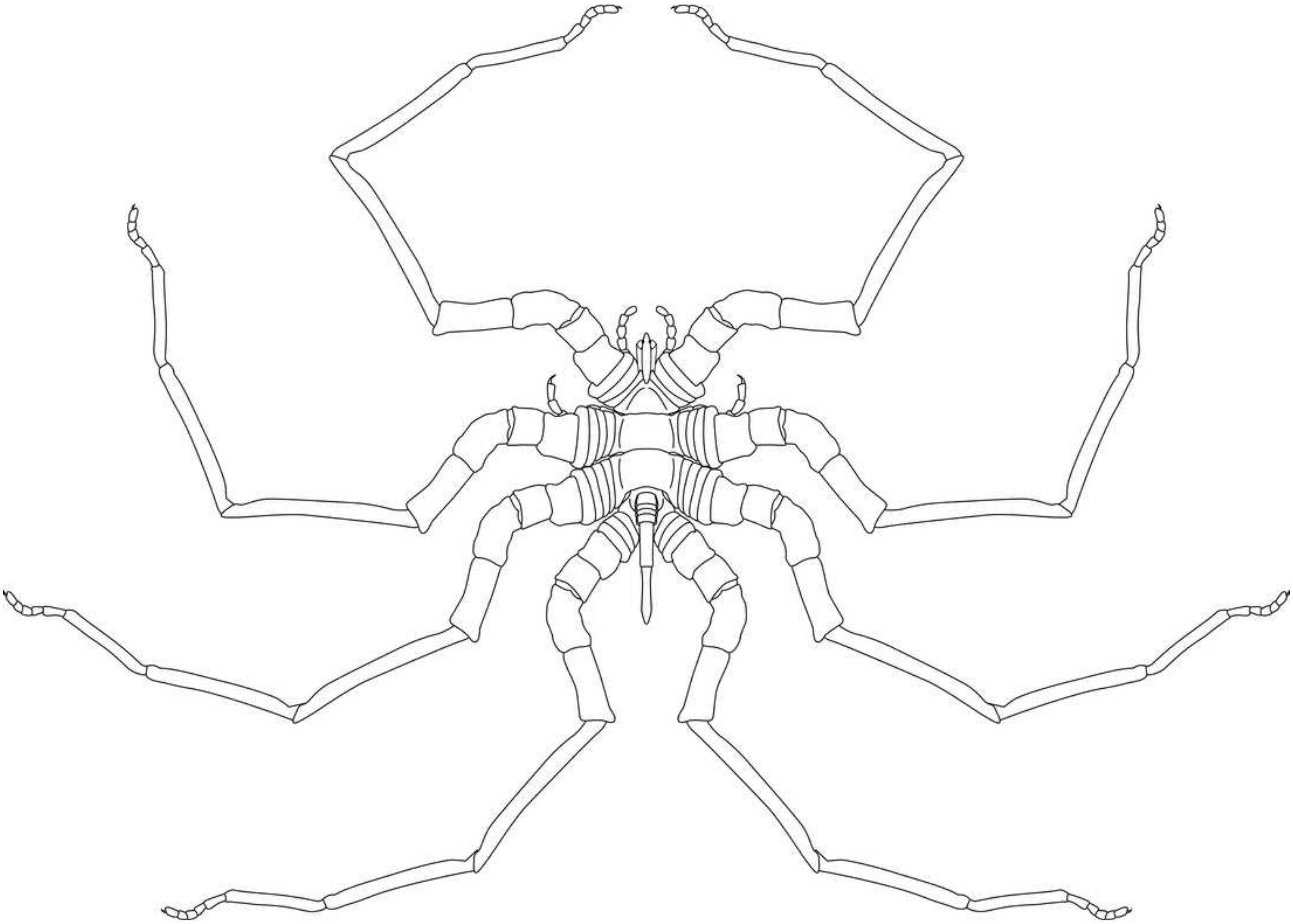

Figure 25

Flagellopantopus blocki, holotype NHMMZ PWL 2004/5024-LS, ventral view.

(A) Standard view. (B) Normals visualization, white arrowheads indicate the immobile joint. (C) Interpretative drawing based of the fossil's surface. (D-E) Maximum intensity views of X-ray microtomography. (F) Interpretative drawing of structure revealed with X-ray, overlapped with surface structure (in grey). *ab*: abdomen, *ch*: chelifore, *fl*: flagellum,*ot*: ocular tubercle, *ov*: oviger, *pa*: palp, *pb*: proboscis; *se*: seta, *WL1-4*: walking leg 1-4. Scale bar: 5 mm.

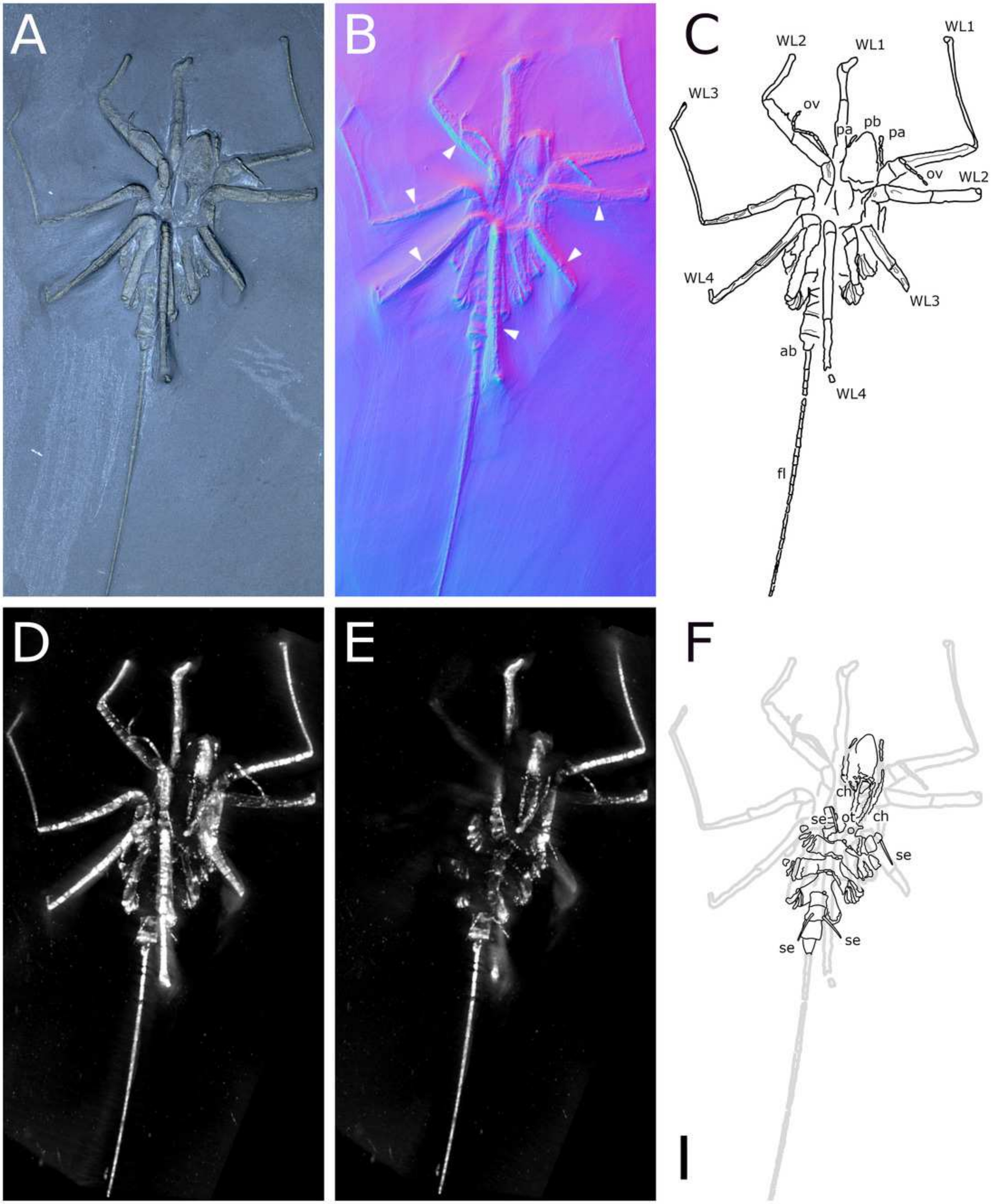
A
B
C
WL2
WL1
WL1
WL3
ov
pa
pb
pa
ov
WL2
WL4
WL3
ab
WL4
fl
D
E
F
ch
se
ot
ch
se
se
se

Figure 26

Flagellopantopus blocki, ovigers of holotype NHMMZ PWL 2004/5024-LS.

Right (A, C, E, G) and left (B, D, F, H) ovigers. (A, B) Standard view. (C, D) Normals visualization. (E, F) Maximum intensity views of X-ray microtomography. (G, H) Interpretative drawing, tentative podomere-per-podomere homology hypothesis indicated by colour codes (refer to figs 15 and 37). Scale bars 2 mm.

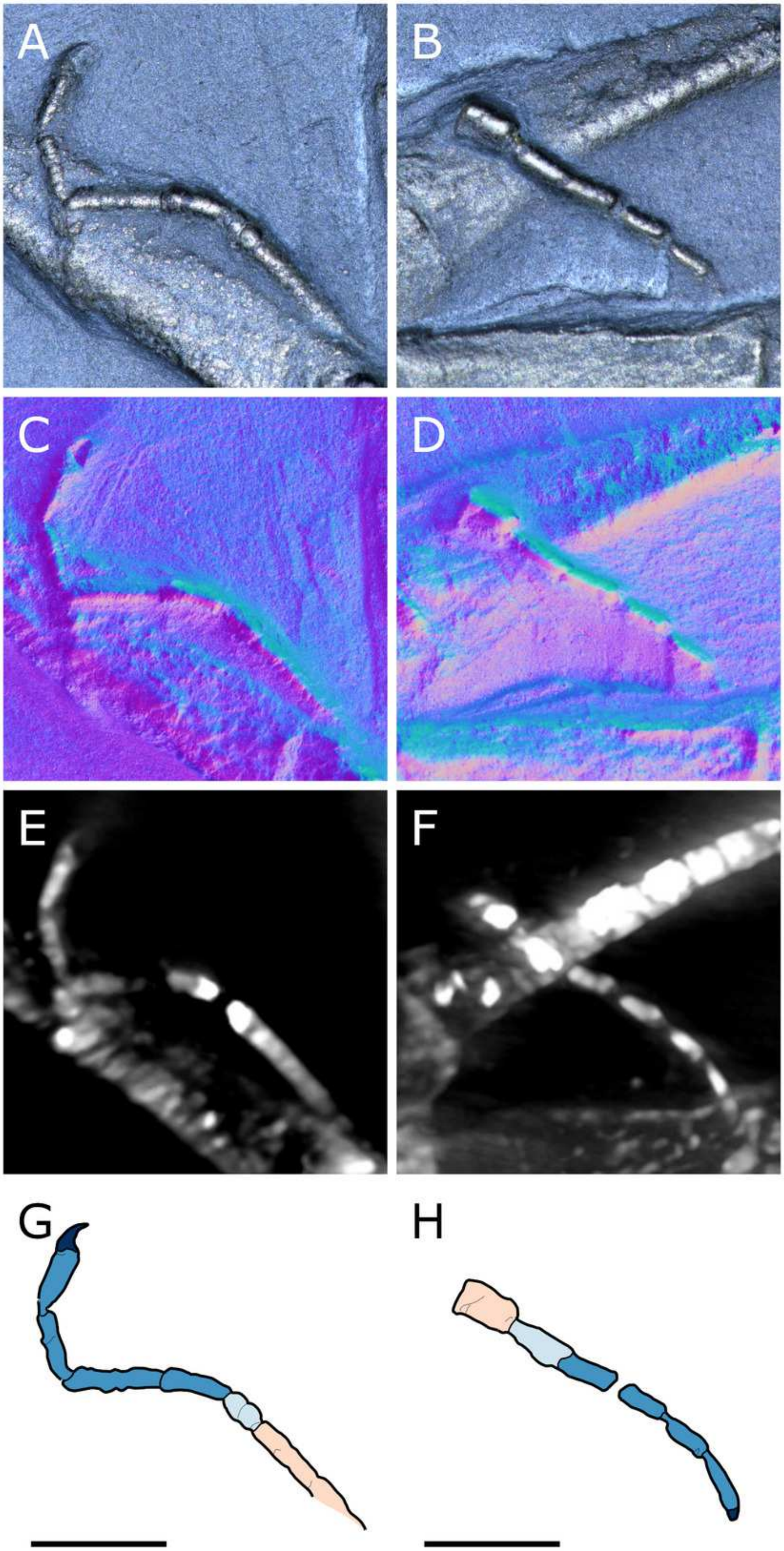
A
B
C
D
E
F
G
H

Figure 27

Flagellopantopus blocki, reconstruction based on observed material, in dorsal view.

The proximal portion of the proboscis, and the structure of the chelifores and the palps are conjectural.

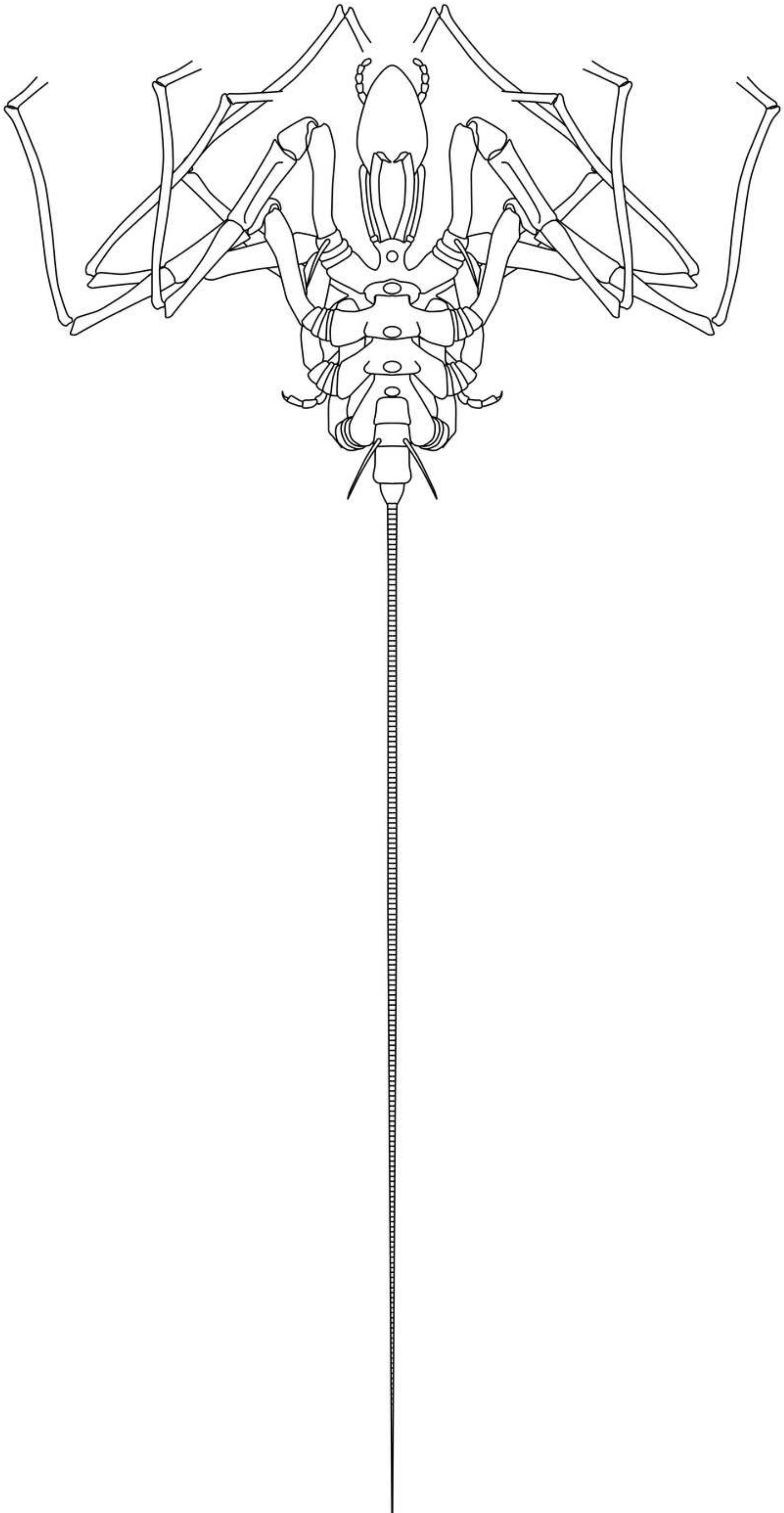

Figure 28

Pentapantopus vogteli holotype and paratype NHMMZ PWL 2010/5-LS.

(A) Standard view. (B) Normals visualization. (C) Maximum intensity views of X-ray microtomography. (D) Interpretative drawing (holotype in yellow, paratype in green). *ch*: chelifore, *ov*: oviger, *pa*: palp, *pb*: proboscis, *WL1-4*: walking leg 1-4. Scale bar: 5 mm.

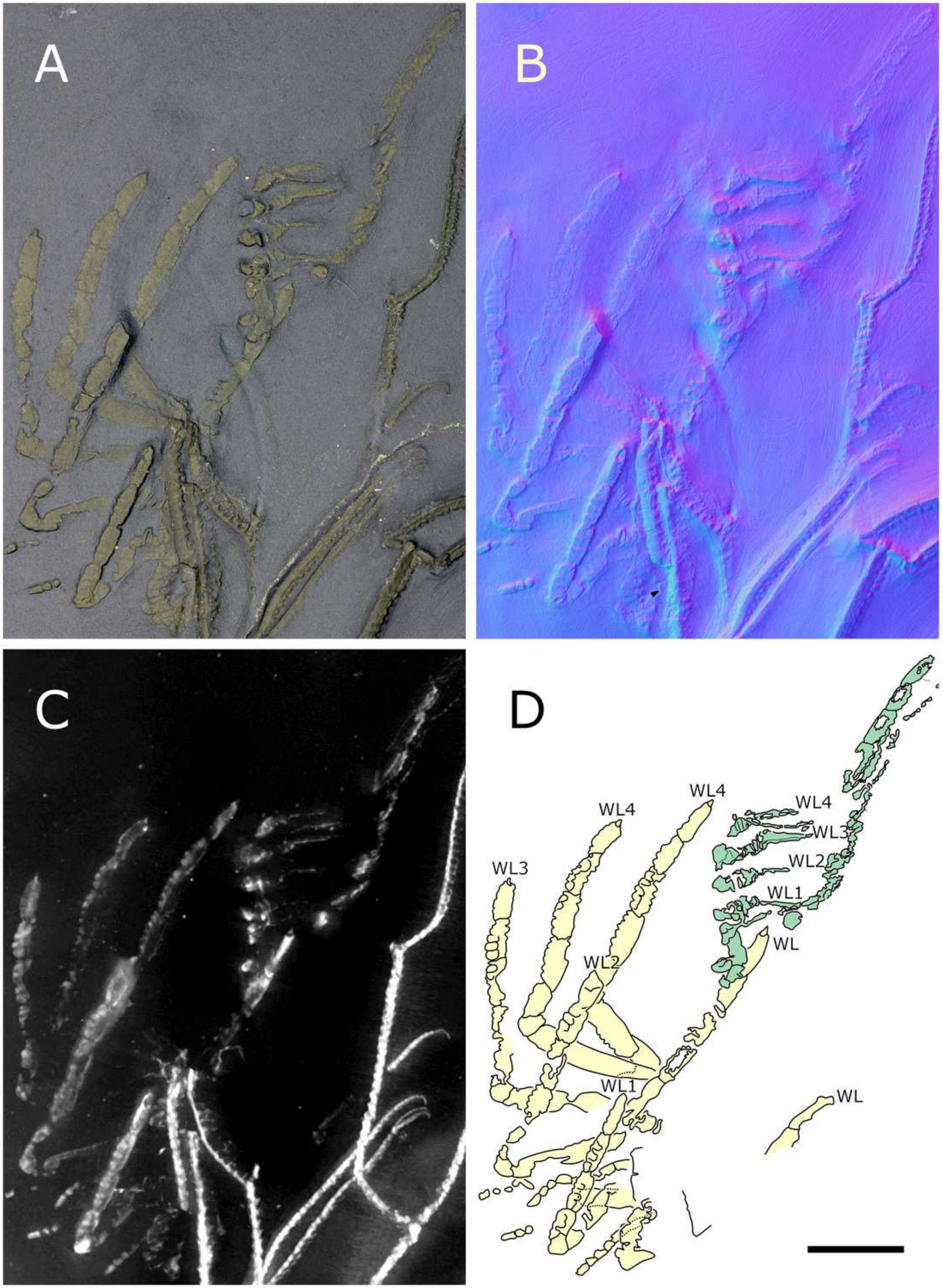
A
B
C
D
WL4
WL4
WL4
WL3
WL3
WL2
WL1
WL
WL2
WL1
WL

Figure 29

Pentapantopus vogteli, NHMMZ PWL 2010/5-LS, specimen 5.

(A, B) Whole specimen. (C) Close-up on the body (arrow: coxal rings, white arrowhead: abdomen, black arrowhead: palpal claw?). (D) Close-up on WL3 (arrow: terminal claw). (E) Close-up on WL2 (arrow: terminal claw, arrowhead: molariform indentations of the ventral side of WL). (A, C, D, E) Maximum intensity views of X-ray microtomography. (B) Interpretative drawing. *ab*: abdomen, *ch*: chelifore, *ov*: oviger, *pa*: palp, *pb*: proboscis, *WL1-4*: walking leg 1-4. Scale bars: 5 mm (A, B), 2 mm (C), 1 mm (D, E).

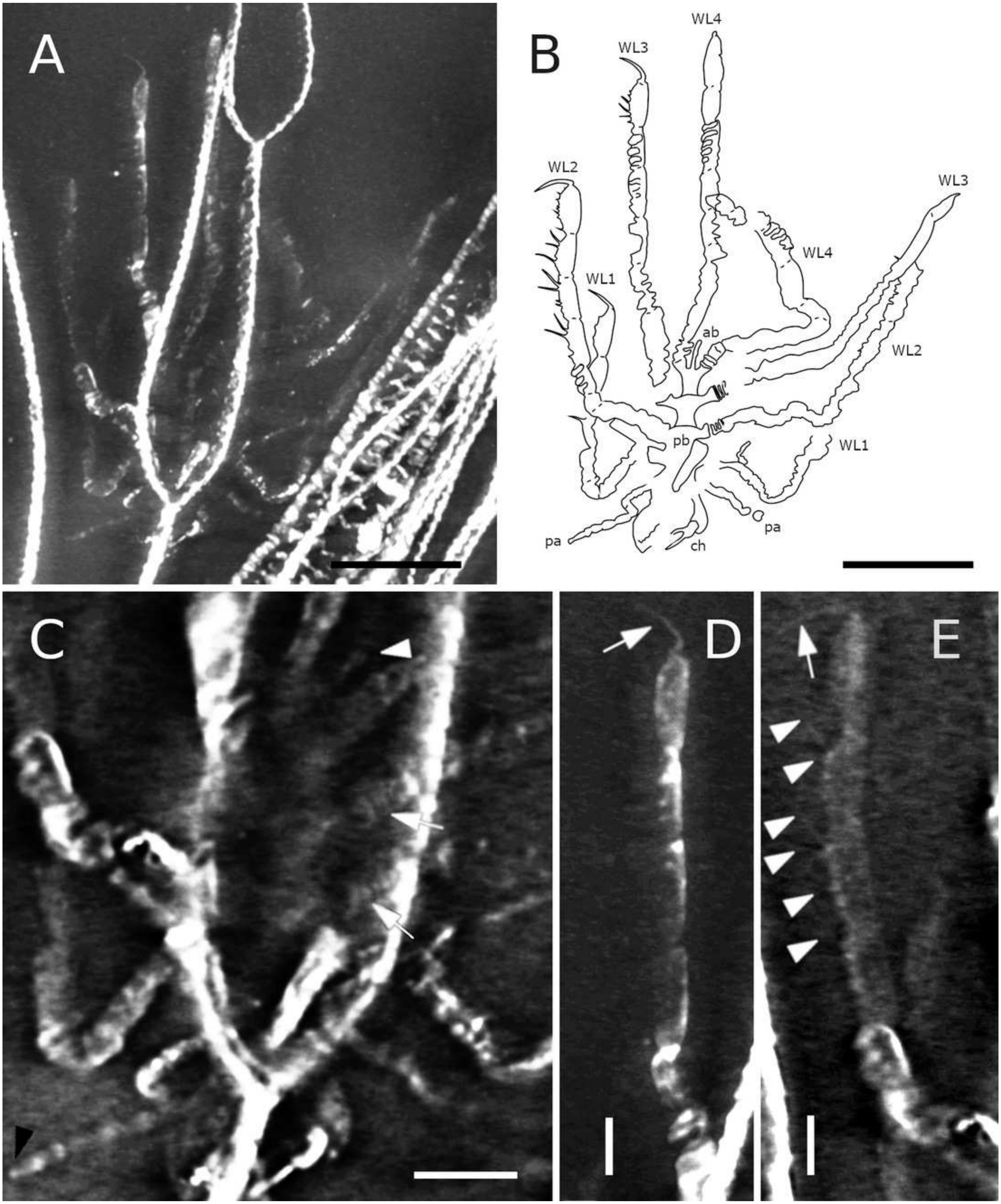
A
B
WL4
WL3
WL2
WL1
WL3
WL4
ab
WL2
pb
WL1
pa
pa
ch
C
D
E

Figure 30

Specimen NHMMZ PWL 2007/29-LS, dorsal view.

(A) Association with ophiuroid (*Budenbachia beneckei* Stuertz, 1886). (B-E) Focus on the specimen. (A, B) Standard view. (C) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (D) Normals visualization. (E) Interpretative drawing. *ab*: abdomen, *ch*: chelifore, *ot*: ocular tubercle, *ov*: oviger, *pa*: palp, *WL1-4*: walking leg 1-4. Scale bar: 10 mm (A), 2 mm (E). B, C, D same scale as E.

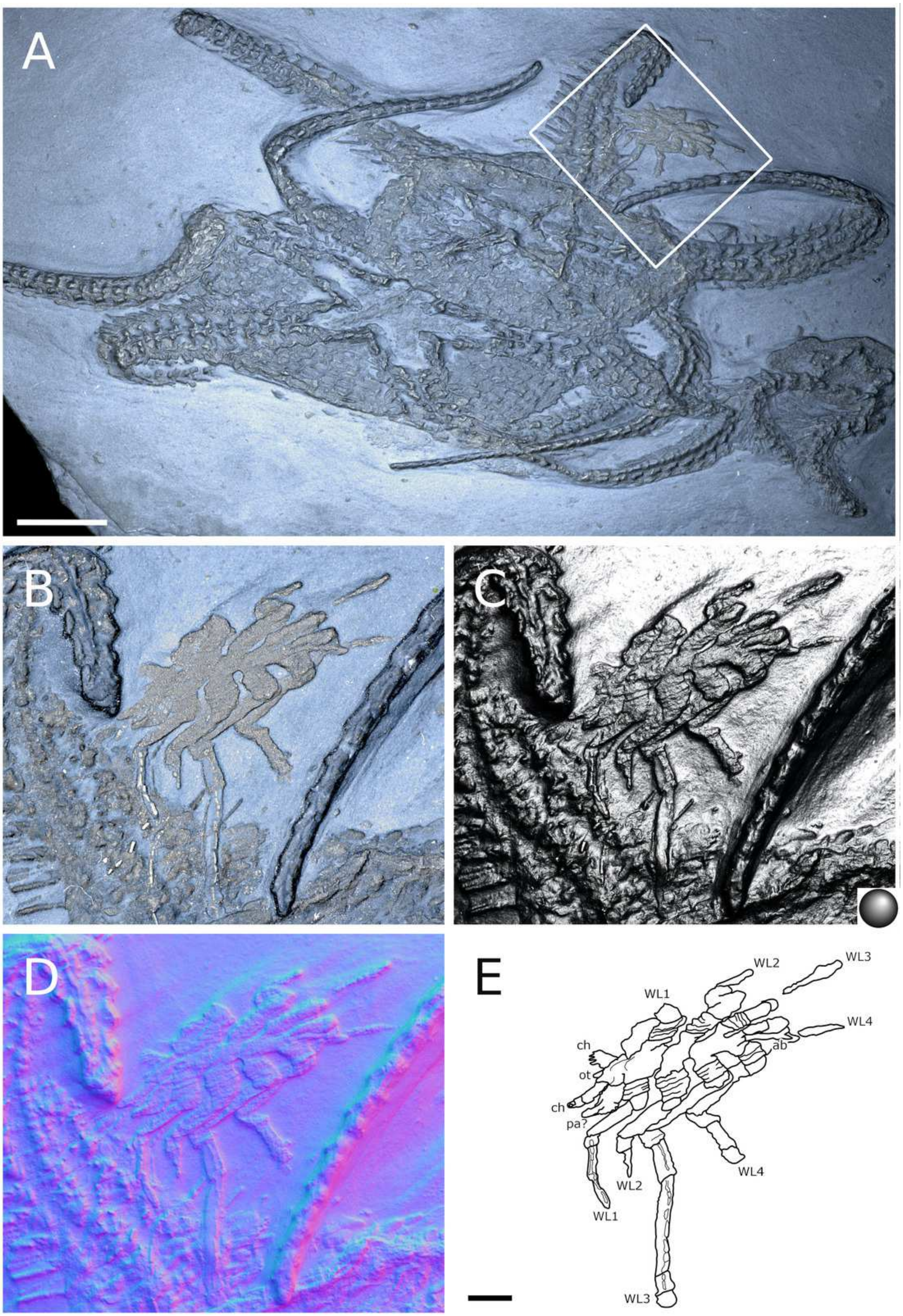
A
B
C
D
E
WL2
WL3
WL1
WL4
ch
ab
ot
ch
pa?
WL4
WL2
WL1
WL3

Figure 31

Pentanpantopus vogteli, reconstruction based on observed material, in dorsal view.

The articulation of the abdomen is conjectural, inspired by the morphologically similar *Haliestes dasos* (Siveter *et al.*, 2004, 2023); so is the presence of a claw at the tip of the palps, the structure of the palps and ovigers. The structure of the chelifores and the number of coxal rings are also speculative. The structure of the cephalon relies on the specimen NHMMZ PWL 2007/29-LS, which is possibly a representative of *Pentapantopus vogteli*.

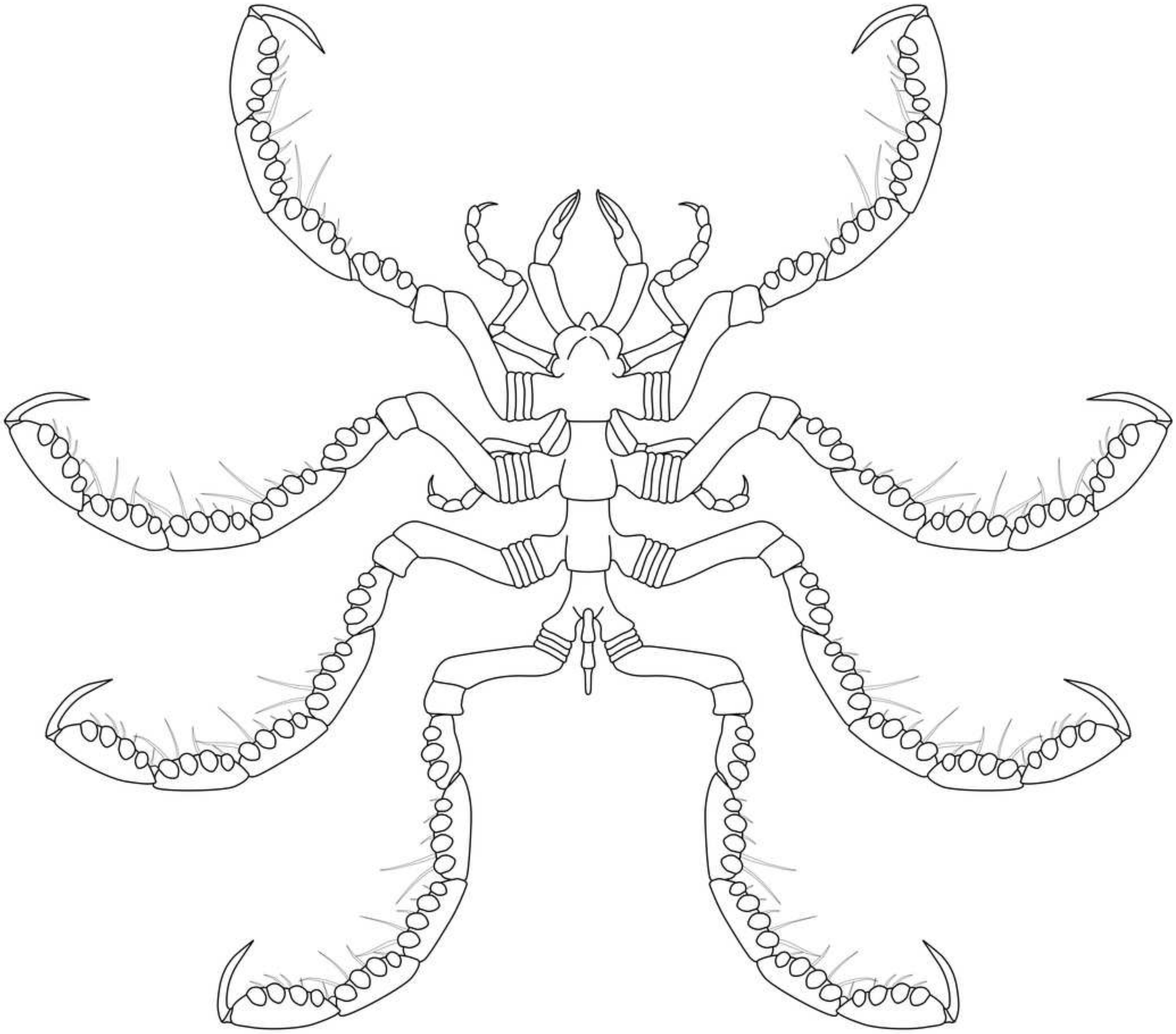

Figure 32

Specimen IGPB-HS437, ventral view.

(A) Standard view. (B) Normals visualization. (C) Maximum intensity views of X-ray microtomography. (D) Interpretative drawing. *ab*: abdomen, *ce*: cephalon, *WL1-4*: walking leg 1-4. Scale bar: 5 mm.

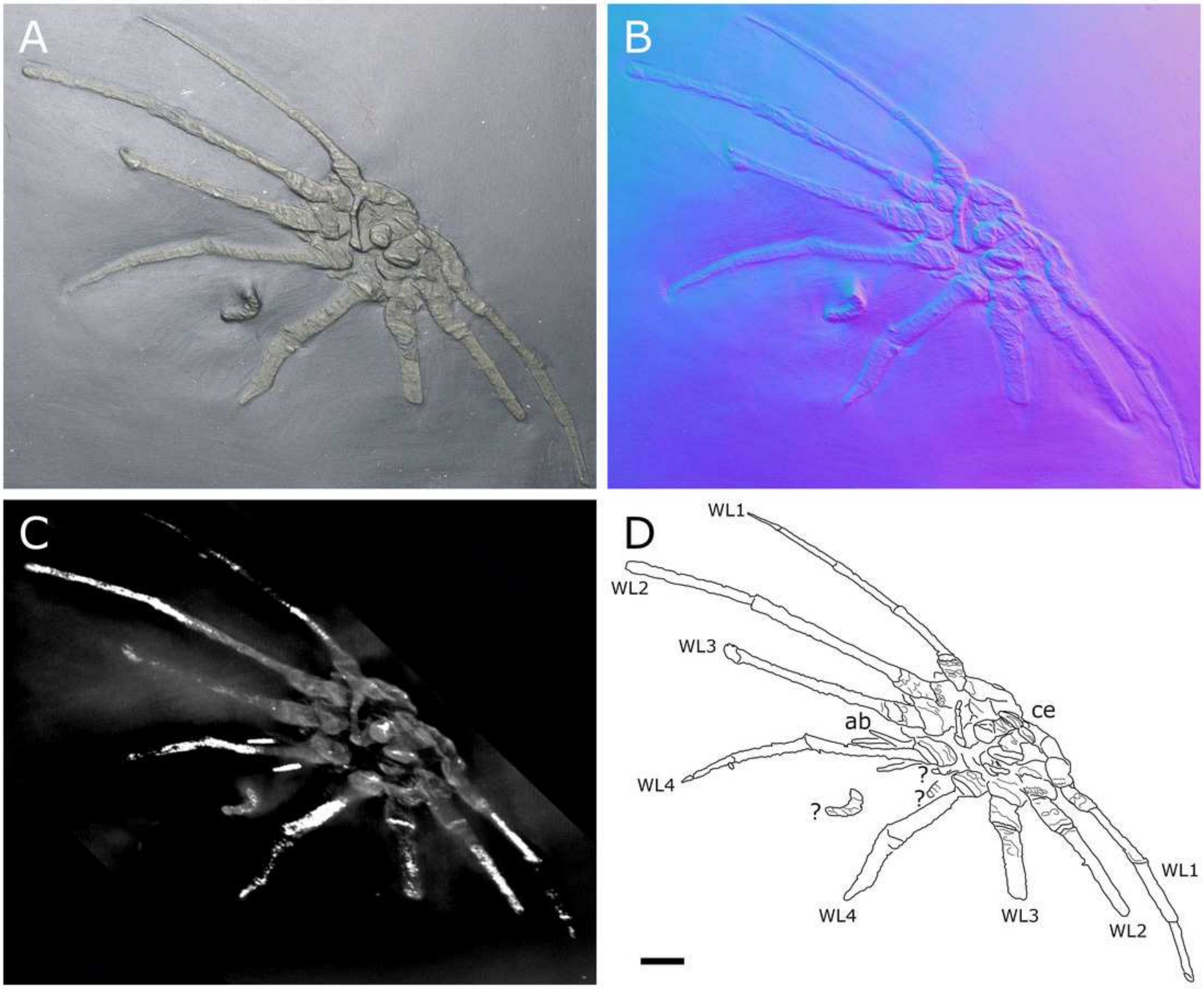

Figure 33

Specimen IGPB-HS437, ventral view of the body.

(A) Standard view. (B) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C) Normals visualization. (D-F) Maximum intensity views of X-ray microtomography. (G) Interpretative drawing based of the fossil’s surface. (H) Interpretative drawing of structure revealed with X-ray, overlapped with surface structure (in grey). *ch*: chelifore, *ot*: ocular tubercle, *ov*: oviger, *WL1-4*: walking leg 1-4. Scale bar: 5 mm.

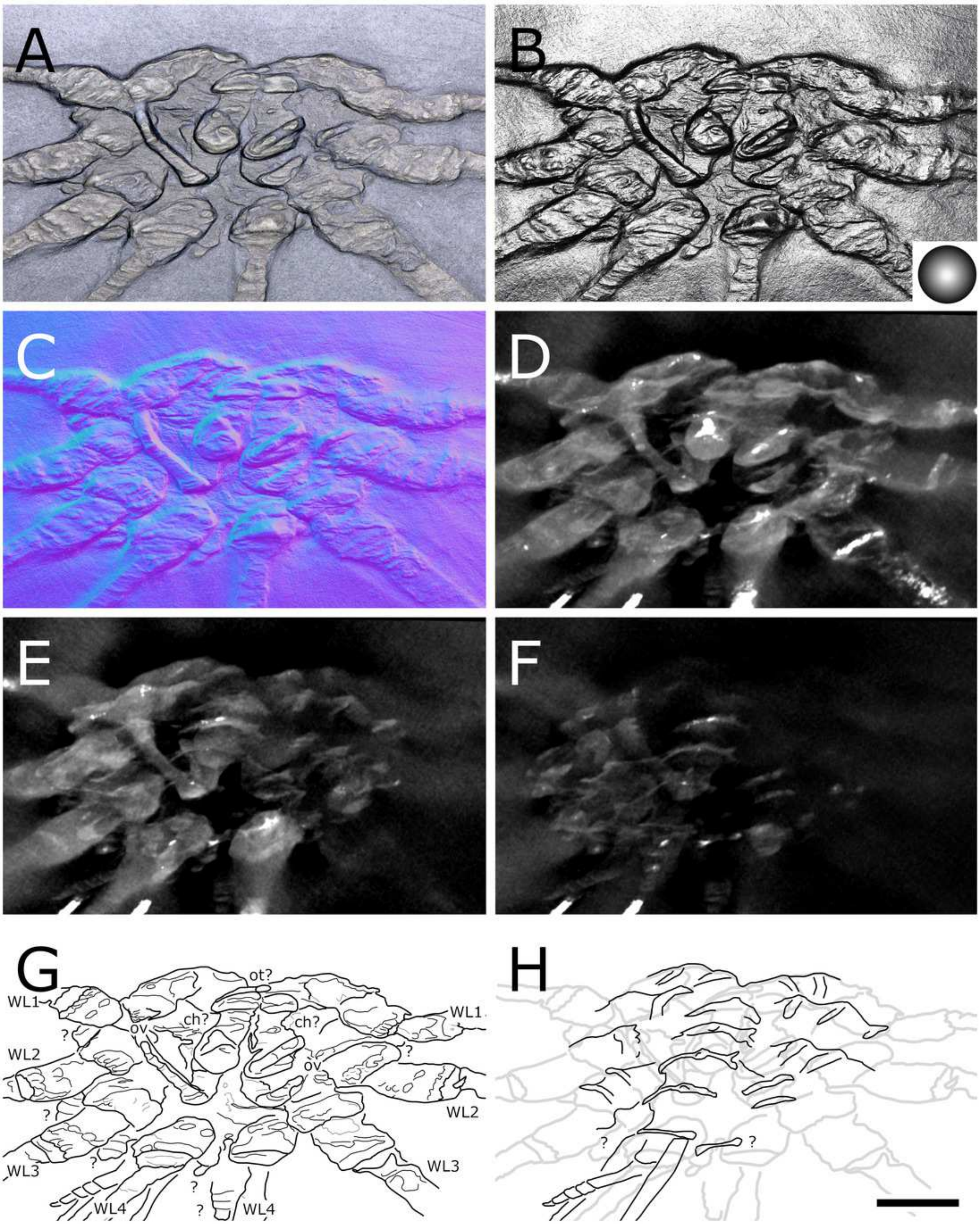
A
B
C
D
E
F
G
ot?
WL1
WL1
ch?
ch?
?
ov
WL2
?
ov
?
WL2
WL3
?
WL3
?
?
WL4
?
WL4
H
?
?

Figure 34

Undetermined pycnogonids.

NHMMZ PWL 2010/5-LS (specimen 3: A, D: specimen 4: E-H) and IGPB-HS195 specimen 2 (I, L). (A, E, I). Standard view. (B, F, J) Specular enhancement (direction of the light is indicated by the hemisphere on the bottom right, see supplementary material 3 for details). (C, G, K) Normals visualization. (D, H, L) Interpretative drawing. Scale bars 5 mm.

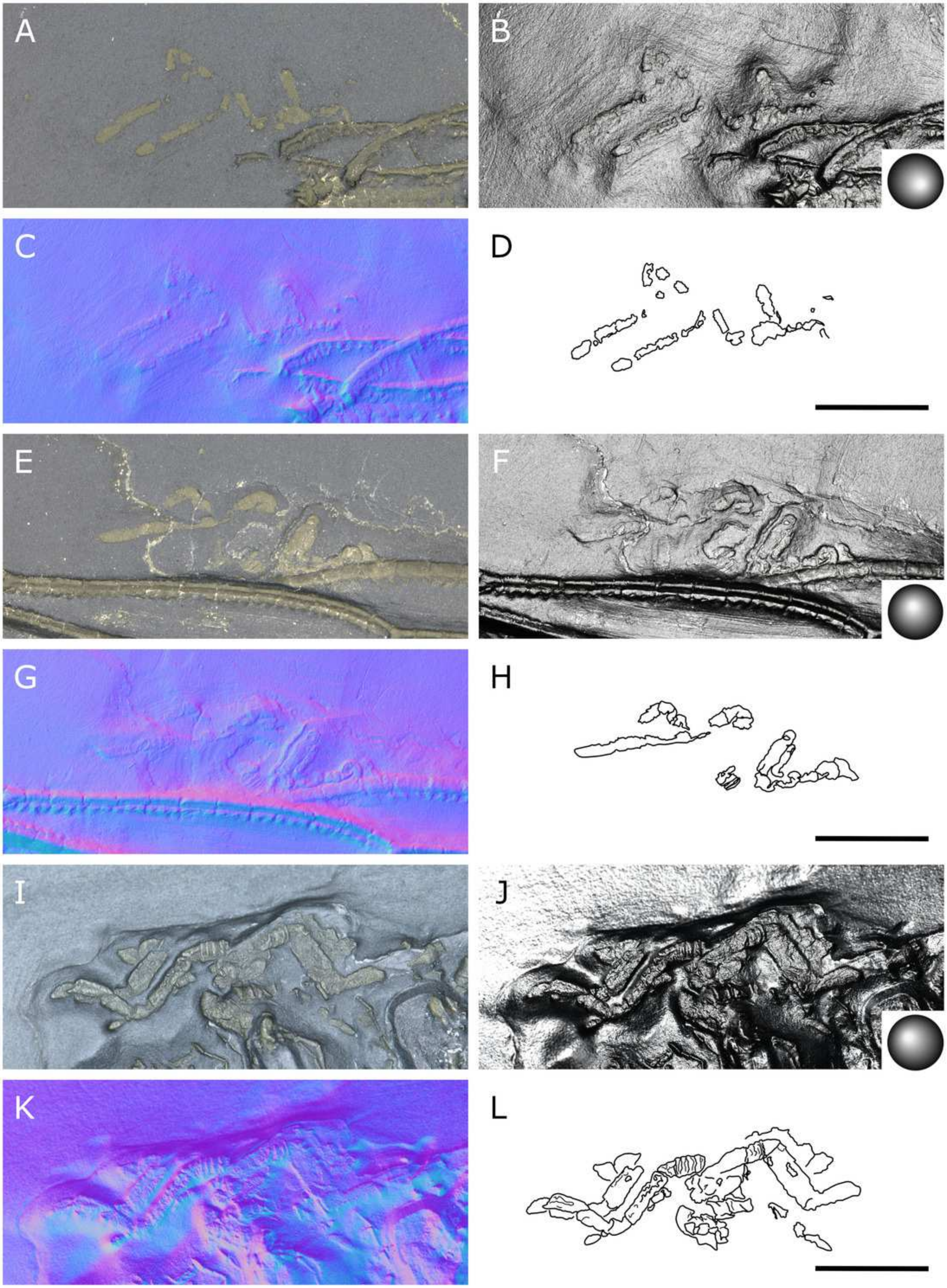
A
B
C
D
E
F
G
H
I
J
K
L

Figure 35

Interpretative drawing of the holotype of *Palaeothea devonica*.

Drawing based on the X-ray images provided by Bergström, Stürmer & Winter (1980). Scale bar 1 mm.

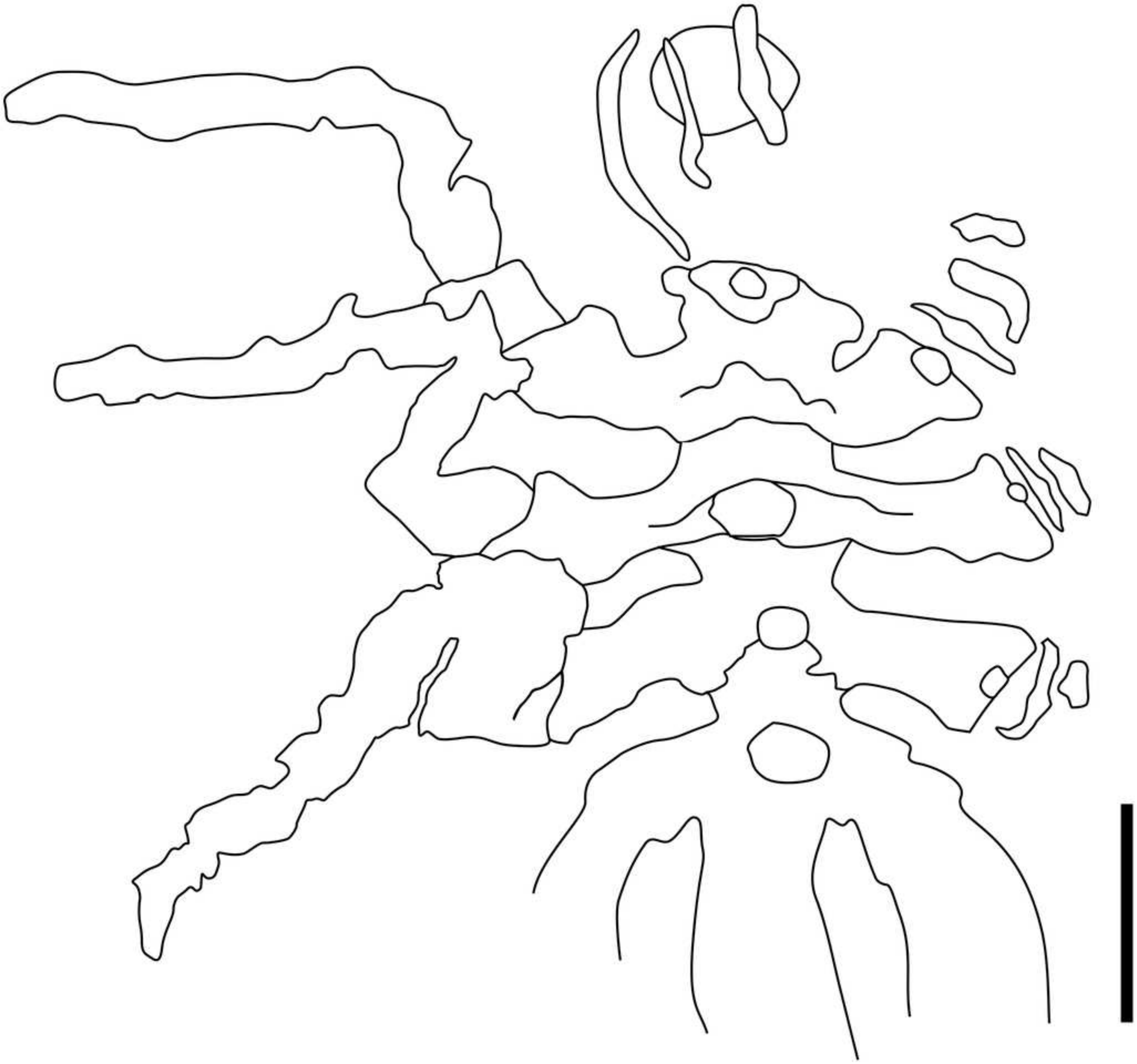

Figure 36

Walking legs of sea spiders and hypothetical homologies among podomeres.

(A) Reconstruction and hypothesised homology (see text and table 2 for explanations). (B) Colour code, following the nomenclature of Sabroux et al. (2023) and Siveter et al. (2023).

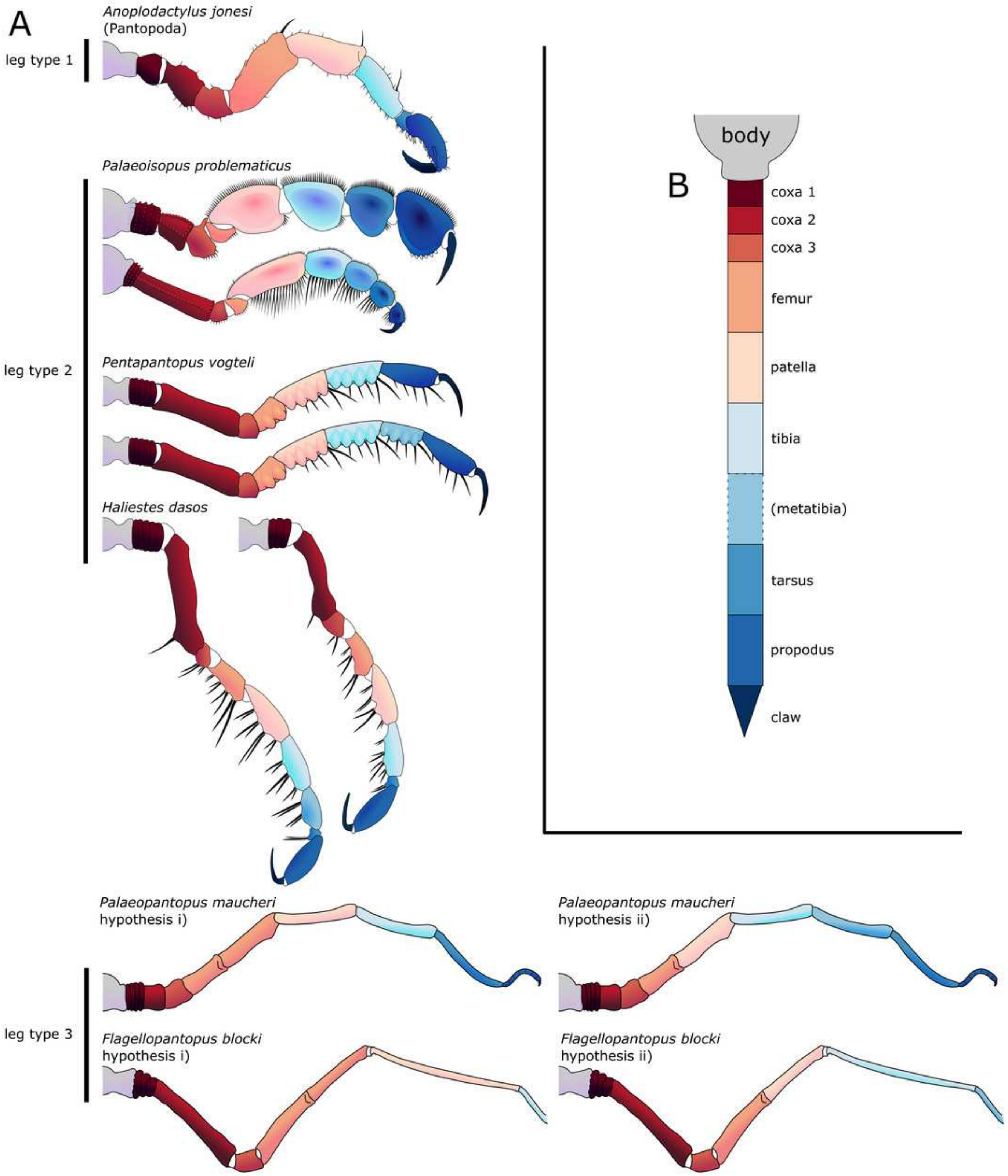
A
leg type 1
Anoplodactylus jonesi
(Pantopoda)
Palaeoisopus problematicus
leg type 2
Pentapantopus vogteli
Haliestes dasos
Palaeopantopus maucheri
hypothesis i)
Palaeopantopus maucheri
hypothesis ii)
leg type 3
Flagellopantopus blocki
hypothesis i)
Flagellopantopus blocki
hypothesis ii)
B
body
coxa 1
coxa 2
coxa 3
femur
patella
tibia
(metatibia)
tarsus
propodus
claw

Table 1(on next page)

List of sea spider fossil species and their current classification.

Asterisks (*) indicate the species for which we could access specimens for this study. See Sabroux *et al.* (2019) for an alternative representation and additional information.

Locality	Species	current classification (see Bamber et al. 2023)	main references
Orsten (Upper Cambrian)	*Cambropycnogon klausmuelleri* Waloszek & Dunlop, 2002	Possibly Pycnogonida (larval stage?)	Waloszek & Dunlop, 2002
Manitoba (Upper Ordovician)	*Palaeomarachne granulata* Rudkin, Cuggy, Young & Thompson, 2013	Possibly Pycnogonida (moult?)	Rudkin *et al.* 2013
Herefordshire (Lower Silurian)	*Haliestes dasos* Siveter, Sutton, Briggs & Siveter, 2004	Nectopantopoda Bamber, 2007	Siveter *et al.* 2004, 2023
Hunsrück Slate (Lower Devonian)	**Flagellopantopus blocki* Poschmann & Dunlop, 2006	Pantopoda *incertae sedis*	Poschmann & Dunlop, 2006
	**Palaeoisopus problematicus* Broili, 1928	Palaeoisopoda Hedgpeth, 1978	Bergström *et al.*, 1980
	**Palaeopantopus maucheri* Broili, 1929	Palaeopantopoda Broili, 1930	Bergström *et al.,* 1980
	Palaeothea devonica Bergström, Stürmer & Winter, 1980	Pantopoda *incertae sedis*	Bergström *et al.,* 1980
	**Pentapantopus vogteli* Kühl, Poschmann & Rust, 2013	Pycnogonida	Kühl *et al.*, 2013
La Voulte-sur-Rhône (Middle Jurassic)	*Colossopantopodus boissinensis* Charbonnier, Vannier & Riou, 2007	Pantopoda Gerstäcker, 1863	Charbonnier *et al.* 2007, Sabroux *et al.*, 2023
	Palaeoendeis elmii Charbonnier, Vannier & Riou, 2007	Pantopoda Gerstäcker, 1863	Charbonnier *et al.* 2007, Sabroux *et al.*, 2023
	Palaeopycnogonides gracilis Charbonnier, Vannier & Riou, 2007	Pantopoda Gerstäcker, 1863	Charbonnier *et al.* 2007, Sabroux *et al.*, 2023
Solnhofen Upper Jurassic)	*Colossopantopodus nanus* Sabroux, Audo, Charbonnier, Corbari & Hassanin, 2019	Pantopoda Gerstäcker, 1863	Sabroux *et al.* 2019
	?*Eurycyde golem* Sabroux, Audo,	Pantopoda Gerstäcker,	Sabroux *et al.* 2019

	Charbonnier, Corbari & Hassanin, 2019	1863

Table 2(on next page)

Characteristics of the three leg types in Pycnogonida.

Leg type 3 is presents following two alternative hypotheses (i) and (ii). See also fig. 36.

Leg characters	leg type 1	leg type 2	leg type 3 (hypothesis i)	leg type 3 (hypothesis ii)
coxa 1	simple	annulated	annulated	annulated
femur	simple	simple	divided	simple
femur and patella	mobile	mobile	mobile	immobile?
metatibia	absent	present in swimming legs 2-4	absent	present in all walking legs
rows of long ventral setae	absent	present	absent	absent
transversal section	cylindrical	laterally flatten	cylindrical	cylindrical

1