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A EUCRUSTACEAN FROM THE CAMBRIAN ‘ORSTEN’ OF SWEDEN WITH EPIPODS AND A MAXILLARY EXCRETORY OPENING

by DIETER WALOSZEK[1], ANDREAS MAAS[1]*, JØRGEN OLESEN[2], CAROLIN HAUG[3] *and* JOACHIM T. HAUG[3]

[1]WG Biosystematic Documentation, University of Ulm, Helmholtzstrasse 20, D-89081, Ulm, Germany; e-mails: dieter.waloszek@uni-ulm.de, andreas.maas@uni-ulm.de
[2]Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Universitetsparken 15, 2100, Copenhagen Ø, Denmark; e-mail: jolesen@snm.ku.dk
[3]Department of Biology II, Functional Morphology Group, University of Munich (LMU), Großhaderner Straße 2, D-82152, Planegg-Martinsried, Germany; e-mails: carolin.haug@palaeo-evo-devo.info, joachim.haug@palaeo-evo-devo.info
*Corresponding author

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Abstract: The Cambrian species *Paulinecaris siveterae* n. gen. n. sp., known from two trunk fragments, represents the first record of epipods (serving as gills and osmoregulatory structures) in a crustacean from the Swedish ‘Orsten’. Moreover, it is the first report of the maxillary excretory opening of a crustacean based on Cambrian material of ‘Orsten’-type preservation. One specimen comprises the maxillary segment with an appendage and several thoracic segments with parts of their limbs; a second specimen is a fragment possibly of a more posterior part of the trunk. As in other known small eucrustaceans, the tergites of the new species lack prominent tergopleurae, so that the limbs insert directly ventral to the tergal margins. Limb preservation includes the maxilla and several thoracopods, all possessing a prominent, fleshy basipod with six setose endites along their median rim distally to the proximal endite. The presence of long and prominent limbs of *P. siveterae* suggests that it had good swimming ability, while the slight C-like curvature of their basal limb part, basipod, indicates involvement of the limbs also in so-called ‘sucking chambers’ for suspension feeding coupled with locomotion. The estimated total length of *P. siveterae*, 2–3 mm, is comparable to that of extant cephalocarids, but its appendages are twice as long and wide. The limbs of *P. siveterae* also differ in size and armature from extant eucrustaceans as well as early representatives of this group known from the ‘Orsten’ assemblages. The general morphology of the limbs, for example in having a fleshy and C-shaped basipod with several setae-bearing endites medially, identifies *P. siveterae* as an entomostracan eucrustacean, but a lack of further details precludes its affinity with any of the in-group taxa. Three epipods on the outer edge of the basipod, as in *P. siveterae*, are also known from the Cambrian eucrustacean *Yicaris dianensis* from China and early ontogenetic stages of extant fairy shrimps (Anostraca); their adult stages have two epipods. This hints at an original number of three epipods in the ground pattern of Entomostraca, but some uncertainty remains with regard to the eucrustacean ground pattern because Malacostraca possess a maximum number of two.

Key words: Eucrustacea, Entomostraca, basipod, endite, epipod, excretory gland opening.

EPIPODS are structures that occur laterally on the post-maxillulary appendages of eucrustaceans and serve for respiration and osmoregulation. They vary in number and morphology (Fig. 1; Boxshall 2004; Boxshall and Jaume 2009; Maas *et al.* 2009), occurring, for example as single elements (diplostracans, notostracans, Fig. 1A; phyllocarids, Fig. 1B, C), or as pairs (anaspidaceans, Fig. 1D; adult anostracans). Larval anostracans (brine shrimps) have two epipods. The proximal epipod is subdivided into two lobes, which are still separate in larvae, pointing to a possibly original number of three epipods (Fig. 1E). The shape of epipods also varies as follows: in embryonic leptostracans and bathynellaceans, they are bottle- or club-shaped with a more or less circular circumference occur; in anaspidaceans and anostracans (Fig. 1D, E), they are leaf-shaped and flattened; in phyllocarids (Fig. 1C), they are subtriangular or plate-like and drawn out distally. Another type of structure often referred to as epipods is the branched ‘gill’ occurring in stomatopods at the medio-anterior side of the exopods of their pleopods 1–5 (Boxshall and Jaume 2009; Maas *et al.* 2009). However, the homology of these ‘gills’ to epipodial

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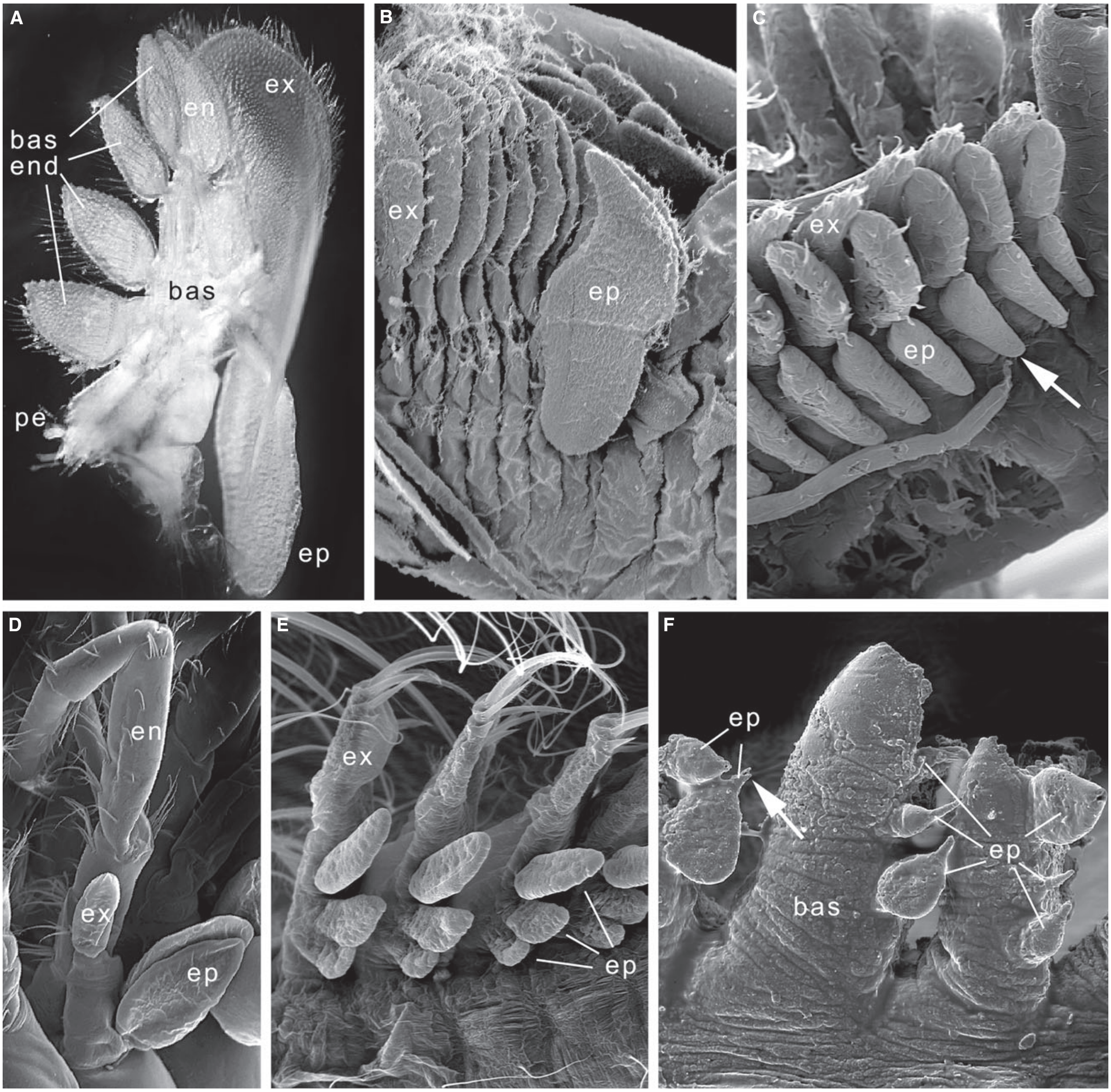


FIG. 1. Examples of thoracopodal epipods of selected eucrustacean species; images not to scale. All limbs orientated in the same direction, with body–appendage joint down and distal ends up. A, light microscopy image of a thoracopod of an adult *Triops cancriformis* (Linné, 1758) (Phyllopoda, Branchiopoda, Entomostraca) with one club-shaped epipod. B, SEM image of adult *Nebalia brucei* Olesen, 1999 (Leptostraca, Malacostraca) with one leaf-shaped, '2-divided' epipod. C, SEM of larval specimen of *Nebalia longicornis* Thomson, 1879 with one lobate, subtriangular (nonflattened) epipod; arrow points to an elongated tip (see also F). D, SEM of *Anaspides tasmaniae* Thompson, 1893 (Caridoida, Eumalacostraca, Malacostraca) with two leaf-shaped epipods. E, SEM of a late larval stage of *Eubranchipus grubii* (Dybowski, 1860) (Anostraca, Branchiopoda, Entomostraca; from Møller *et al.* 2004), with three epipods, the distal one club-shaped and the middle epipod more subrectangular. F, SEM of the Cambrian *Yicaris dianensis* Zhang, Siveter, Waloszek and Maas, 2007 (Entomostraca) with three epipods, not yet fully developed in this specimen (subtriangular, as in C; arrow points to an elongated tip, similar to that in C; epipod becomes subrectangular later in ontogeny). Abbreviations: bas, basipod; bas end, basipodal endite; en, endopod; ep, epipod; ex, exopod; pe, proximal endite.

structures of other eucrustaceans remains to be demonstrated. Decapod eumalacostracans also exhibit several types of branched outgrowths that serve as gills but which differ from the aforementioned types.

Transitions between different epipod morphologies occur in both time and space: ontogenetically, as the morphology of a single epipod changes during growth and/or sequentially, from anterior to posterior along the body axis and/or from proximal to distal within a single appendage (phyllocarids, Fig. 1B; anostracans, Fig. 1E). Ontogenetic and sequential changes can be coupled, because heterochronic evolution has played a major role in the evolution of crustacean appendages and their substructures (Haug *et al.* 2010*a*, *b*).

The two different functions of epipods, namely osmoregulation and respiration, may be spatially decoupled (Alberti and Kils 1983; McMahon and Wilkens 1983; Pequeux 1995; Freire *et al.* 2008). Osmoregulation often takes place in the proximal epipods (if more than one is developed along an appendage); respiration usually takes place in the distal epipods. In decapod eumalacostracans, only the posterior gills seem to function for respiration and osmoregulation, while the anterior ones serve only for respiration (cf. Cieluch *et al.* 2004, 2007).

For both functions, plate-like epithelia of a superficially similar morphology are involved, but osmoregulation takes place in cells having a folded basal part and many mitochondria, serving as an energy supply for active sodium–potassium pumps. Respiratory epithelia, on the other hand, allow passive O_2 transport through the cell interspaces. There appears to be frequent confusion of these functions, especially in the older literature, due to the lack of particular histological studies, improper discrimination or simply because of technological problems (Rieder *et al.* 1984; Boxshall and Jaume 2009; Maas *et al.* 2009). In addition, the softer cuticle underneath arthropod shields or tergopleural areas is often assumed to serve as a respiratory surface (Olesen 2013). In most ostracodes, the epithelium underneath the shield cuticle serves for osmoregulation (Keyser 1990).

Epipods are seemingly restricted to Eucrustacea (cf. Maas *et al.* 2009), but there is little detailed documented morphological information about them. Comparable structures do not seem to be part of the ground pattern of any other euarthropod group, such as Insecta, Myriapoda, Chelicerata or the extinct Trilobita. It has long remained unclear whether epipods evolved in the ancestor of Eucrustacea or were present earlier, possibly even in the ground pattern of Crustacea *s. l.* (see Stein *et al.* 2008), most likely also including myriapods and insects (cf. Glenner *et al.* 2006; Zhang *et al.* 2007; Haug *et al.* 2010*a*; Reumont *et al.* 2012).

The most informative source of early crustacean fossils is the exceptionally preserved three-dimensional Cambrian microfossils of the Swedish 'Orsten'. This material contains representatives of different evolutionary levels, derivatives of the evolutionary lineage towards Eucrustacea as well as early representatives of modern in-groups and is known from several countries and a wide stratigraphical range (Maas *et al.* 2006). However, the best preserved known fossil groups of the 'Orsten', namely the exclusively Cambrian Phosphatocopina (sister group to Eucrustacea; see Maas *et al.* 2003), and the 'Orsten' eucrustacean representatives *Skara* Müller, 1983, *Bredocaris admirabilis* Müller, 1983, *Dala peilertae* Müller, 1982, *Walossekia quinquespinosa* Müller, 1983, and *Rehbachiella kinnekullensis* Müller, 1983, all lack epipods or comparable structures (Müller 1983; Müller and Walossek 1985*a*, *b*, 1988; Walossek 1993, 1999; Walossek and Müller 1998). Thus, the discovery of epipods in an 'Orsten'-type preserved species in the early Cambrian of China, *Yicaris dianensis* Zhang, Siveter, Waloszek and Maas, 2007, stratigraphically the oldest eucrustacean described so far, was a surprise (Zhang *et al.* 2007). Its thoracopods and maxillae each possess three epipods, while the maxillulae have only two setae in a corresponding position (Fig. 1F; for an alternative interpretation see Boxshall and Jaume 2009). Its epipods exhibit some sequential differences in shape along the appendage series, both from proximal to distal and during ontogeny. It appears that they developed from a small seta with a faintly bulged proximal part, became bottle-shaped and grew further into a subtriangular structure and, eventually, into a rectangular plate with short marginal seta-like outgrowths opposite to the attachment edge (Zhang *et al.* 2007; Maas *et al.* 2009). A similar case of oval swellings with distal setae on appendages occurs in only one other Cambrian 'Orsten' arthropod species, on the outer distal edges of endopod portions of the euarthropod *Agnostus pisiformis* (Wahlenberg, 1818) (Müller and Walossek 1987). Due to their unusual position, it is unclear whether these structures represent respiratory organs. Remarkably, in all extant, crustacean taxa epipods develop ontogenetically from as round or slightly flattened lobes, the significance of which needs to be elucidated.

The description of *Y. dianensis* prompted a search for new material in the Swedish 'Orsten' collections from Sweden (housed in Ulm) obtained by the late Klaus J. Müller, Bonn, the discoverer of the 'Orsten', and resulted in the discovery of two specimens with epipods on their trunk appendages (Maas *et al.* 2009, their Fig. 12A–C). Although differing in detail, these specimens are interpreted to represent different body regions of a new taxon, *Paulinecaris siveterae* gen. et sp. nov., which we describe herein and assess its bearing on the origin and evolution of epipods within Eucrustacea.

MATERIAL AND METHODS

The material consists of two incompletely preserved specimens, currently housed in Ulm but to be transferred to the University of Bonn: UB W 418 (specimen 6697) and UB W 419 (specimen 8961), both from the Cambrian of Sweden. Investigations followed the standard techniques of studying 'Orsten' microfossils (Müller 1985; Maas *et al.* 2006). Scanning electron microscopy (SEM) was undertaken in the 1990s in Bonn and recently, using a Zeiss DSM 962 SEM at the University of Ulm. Drawings and other images were processed using standard software, such as Adobe Illustrator and Photoshop CS3 and 4. Measurements taken on the images were adjusted to the nearest 5 μm (Walossek 1993).

The appendages of both specimens were photographed and combined, partly tilted horizontally and size-adjusted in a single image to more readily facilitate comparisons when reconstructing a whole limb (as assembled in Fig. 7A). During the reconstruction, setae and spines were added but kept fairly narrow and short due to the lack of knowledge about their original dimensions. The overall morphology of the animal and head region in particular remains unknown. Accordingly, we reconstructed only a trunk portion viewed from posterolateral aspect; this view could be obtained particularly from UB W 418. This image was overlain by an SEM image from the cephalocarid *Lightiella monniotae* Cals and Delamare Deboutteville, 1970. The latter image, a posterior view of a cross-section, resulted from breakage of a specimen after critical point drying (Olesen *et al.* 2011) and was stretched to fit the size of *P. siveterae*. Terminology follows that introduced in various papers, particularly Walossek 1993, and recently reviewed in Haug *et al.* (2013).

SYSTEMATIC PALAEONTOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank: http://zoobank.org/References/7A0E7023-C257-425E-A6D6-621D4BA999CD.

CRUSTACEA *s. l.* as characterized by Stein *et al.* (2008)
LABROPHORA Siveter, Waloszek and Williams, 2003
EUCRUSTACEA *sensu* Walossek (1999) (= Crustacea Brünnich, 1772 = Eucrustacea Kingsley, 1894)
ENTOMOSTRACA Latreille, 1809 (as characterized by Waloszek 2003*b*)
Genus PAULINECARIS gen. nov.

LSID. urn:lsid:zoobank.org:act:FC76D815-3261-4F10-9564-CEA525EC865E

Type species. Paulinecaris siveterae gen. et sp. nov. from the Cambrian 'Orsten' of Sweden.

Derivation of name. In honour and memory of the late Pauline Siveter, wife of our colleague, Emeritus Professor David J. Siveter.

Paulinecaris siveterae gen. et sp. nov.

2009 'Species I'; Maas *et al.*, p. 268, 269; Fig. 12A, B (UB W 418).
2009 'Species II'; Maas *et al.*, p. 268, 269; Fig. 12C (UB W 419).

LSID. urn:lsid:zoobank.org:act:CD6130FB-7544-400C-9D98-3B0DD4C9C460

Derivation of name. For Pauline Siveter.

Type material. The holotype UB W 418 (specimen 6697; Müller collection sample no. 6760) represents parts of the head and the appendage-bearing postmaxillulary region back to the fifth trunk segment (Fig. 2A, B). The appendages are preserved only on some segments and otherwise indicated by their place of insertion (Fig. 2C). Specimen UB W 419 (specimen 8961; sample no. 6785) is a trunk portion of six segments, but most likely from a more posterior region than that of the holotype. Parts of its appendages are preserved or indicated by areas of insertion.

Type locality. Quarry near the farm Gum at the Kinnekulle, Västergötland, Sweden, which yielded the bulk of the Swedish 'Orsten' material. *A. pisiformis* Biozone (= Zone 1, Upper Cambrian, of traditional usage), latest part of Series 3, Cambrian (approximately 505 Ma).

Correlation of appendage pairs. Because of the fragmentary preservation of the specimens, it is not clear exactly which appendages are preserved. The most anterior appendage of the holotype is interpreted as the maxilla. A more or less half-circular pore located immediately behind the stem of the most anterior appendages of the holotype (Fig. 4H) is interpreted as the opening of the maxillary excretory gland (excretory pores are restricted to the segments of the antenna and maxilla in Eucrustacea), which implies that this limb is the maxilla. This interpretation supports the suggestion that the preserved region comprises the rear part of the head and part of the trunk, and also indicates that, at least with regard to the parts preserved, the maxilla does not significantly deviate in morphology from that of the thoracopods. The maxillula, as first postmandibular limb, would be different from the succeeding limbs already in the ground pattern of Eucrustacea. Excretory openings on the first thoracic segment do not exist in any euarthropod, fossil nor extant. That this first limb in the specimen is considered to be the maxilla is, hence, the most parsimonious interpretation. This is the first record of a maxillary excretory gland opening of a Cambrian 'Orsten' crustacean (a putative antennal gland opening was reported for Skaracarida; Müller and Walossek 1985*a*, *b*).

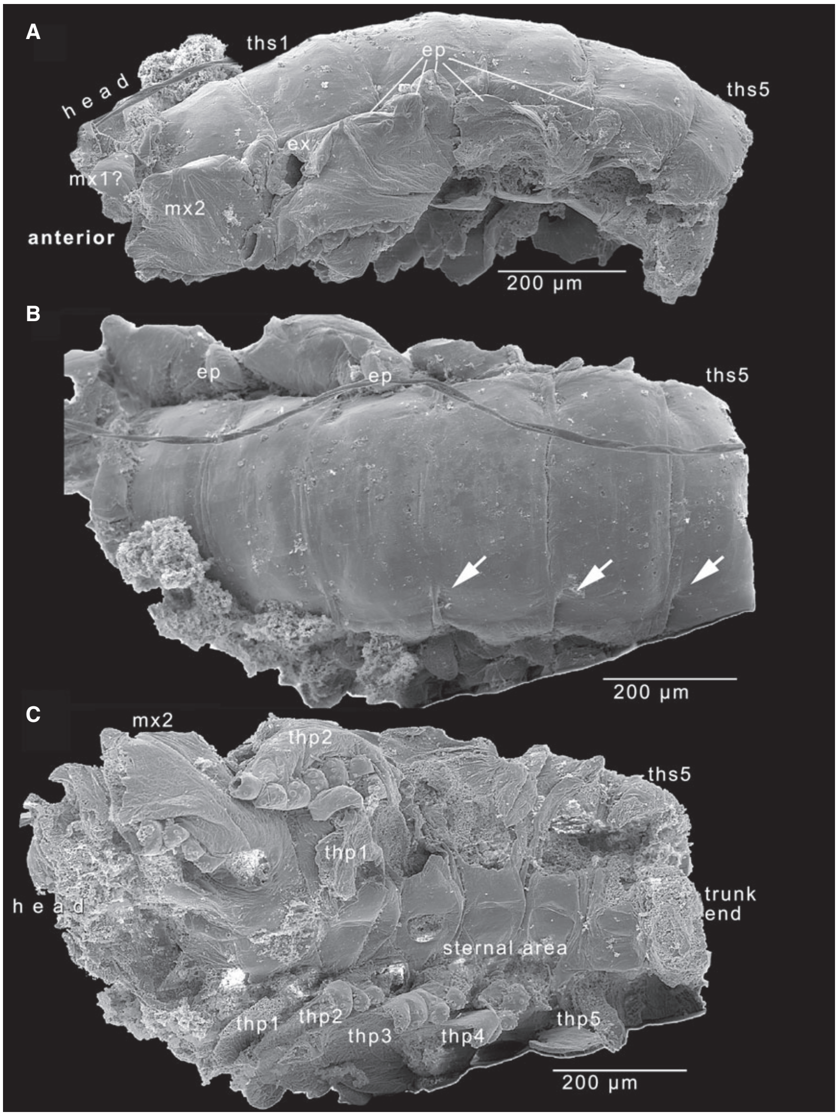


FIG. 2. *Paulinecaris siveterae* gen. et sp. nov; holotype UB W 418. A, view of left side. B, dorsal view; short tergopleural area between pivots marked by arrows. C, ventral view. Abbreviations as in Figure 1, also: mx1?, fragment of the putative maxillula; mx2, maxilla; thp, thoracopod; ths, thoracic segment. Scale bars represent 200 μm.

Diagnosis (based on both specimens; details of head and trunk end unknown). Eucrustacean with appendage-bearing trunk with tergites merging directly into the body proper above the appendages, lacking tergopleurae. Sternites rectangular, slightly raised, medially divided into two halves. All postmaxillulary appendages large relative to the body comprising a basipod that carries the two rami and three lobate epipods laterally. Median edge of limb stem with a proximal endite and six basipodal endites. General armature of at least the five anterior appendages: three anterolateral setae on the basipod, proximal endite and proximal two basipodal endites with a crescent-shaped row of posterior setae, and one central spine. Distal four endites with an oblique row of 3–4 setae and 1–3 prominent central spines, few setae posterodistally.

Description. Based on the only two known specimens representing parts of the posterior head and trunk (UB W 418; Figs 2A–C, 3A–F, 4A–H) or of the trunk only (UB W 419; Figs 5A–C, 6A–G). The two specimens most likely belong to the same developmental stage.

Main body. Head with segments as far posteriorly as the maxilla, trunk with at least seven tergite-bearing segments, caudal end unknown. Trunk tergites rectangular, gently convex. Lengths increasing from approximately 130 μm in first thoracomere to 180 μm in fifth thoracomere; widths increasing from 300 to 400–430 μm and heights being 150–200 μm throughout. Tergal widths decrease in the tergites with fairly constant lengths of about 150 μm; height of these tergites decreasing from about 200 μm anteriorly to about 100 μm in the most posterior known tergite. Tergites appear weakly sclerotized and smooth throughout, lacking pores and ornament such as denticles or hairs. The connecting pivot joints are located on either side of the tergites near the fairly straight lateral margins (Fig. 2B). Laterally, the tergal margin continues into the body proper without formation of a distinct tergopleura overhanging the body–

appendage joints/sockets. Moreover, the cuticle continues directly into the membranous sockets of the appendages without a folding system. Adjacent tergites are separated by narrow membranes that are slightly squeezed out laterally (Figs 2B, 3D).

Ventral surface of each of the maxillary and trunk segments slightly convex to straight, sternitic area between the insertions of the appendages is about 150 μm wide and approximately 100 μm long; maxillary sternite possibly shorter and lengths slightly decreasing progressively from segment to segment (Figs 2C, 3C). Sternites separated medially into two parts by a shallow double furrow running axially, surface of each sternal part slightly convex (Fig. 3C). Sternitic surface smooth, apparently lacking ornament. Ample membranes separate adjacent sternites (Fig. 3C).

Head. No details are known except for the maxillary segment, which seems to be identical to the trunk segments. The maxillary excretory gland opening is located immediately behind the stem of the maxilla (Fig. 4H).

Appendages in general. Maxillae and trunk limbs insert ventrolaterally at a relatively short body–appendage joint area immediately below the lateral tergal margin in an abaxially extending membranous socket (Figs 2C, 3B). They extend ventrolaterally from the body. Body–appendage joint area possibly 100–145 μm long (specimens deformed) in mediolateral axis and 60 μm in anteroposterior direction, with a proximal endite at the proximomedian edge of the membrane and a subrectangular basipod. Endopod arises mediodistally on the basipod; exopod inserts on the sloping laterodistal edge of the basipod. Between exopod and body the fairly slim basipodal rim bears three lobes, interpreted as epipods (Figs 3D–F, 5C, 6D, E).

Basipod. Basipods strictly abaxially oriented, about 150 μm wide in mediolateral aspect and 300–330 μm long, carrying a row of median endites. Basipods appear thin in anteroposterior aspect and C-curved (convex anteriorly and concave posteriorly; Fig. 6B). Basipods possibly weakly subdivided and little sclerotized, as indicated by fine furrows on posterior side of the basipods and the finely wrinkled cuticle (Fig. 3E; softness possibly facilitates the recovery stroke of the limbs, Fig. 3B). Anterior side of the basipods more strongly sclerotized, weakly subdivided horizontally into scleritic parts that lead towards the endites (Fig. 4G). Again, anteriorly at the furrow between such sclerites, two fine setae arise, and one more seta is located slightly more anteriorly on the distal edges of the sclerites (Figs 4, 7A).

Proximal endite, basipodal endites. Proximal endite rounded, ovoid, about 1.5 × larger than the adjacent two proximal basipodal endites 1 and 2 (Fig. 4B). Its convex median side carries two possibly short spine-like setae (Fig. 4C). Around the posterior curvature stem, a row of 10–11 setae, which are larger and finer from distal to anteroproximal end. Basipodal endites 1 and 2 similar to proximal endite but slightly smaller and even more rounded or ball- to drop-shaped. Armature consisting of 7–8 posterior setae and just one major seta or spine medially (Fig. 4A, D). Median surface also gently rounded. In the putatively more posterior appendages of UB W 419, the armature is generally the same, but the setation is less developed, that is, 7–8 posterior setae and just one central spine on the proximal endite and maximally six posterior setae on endites 1 and 2 (Figs 6A, C, 7A).

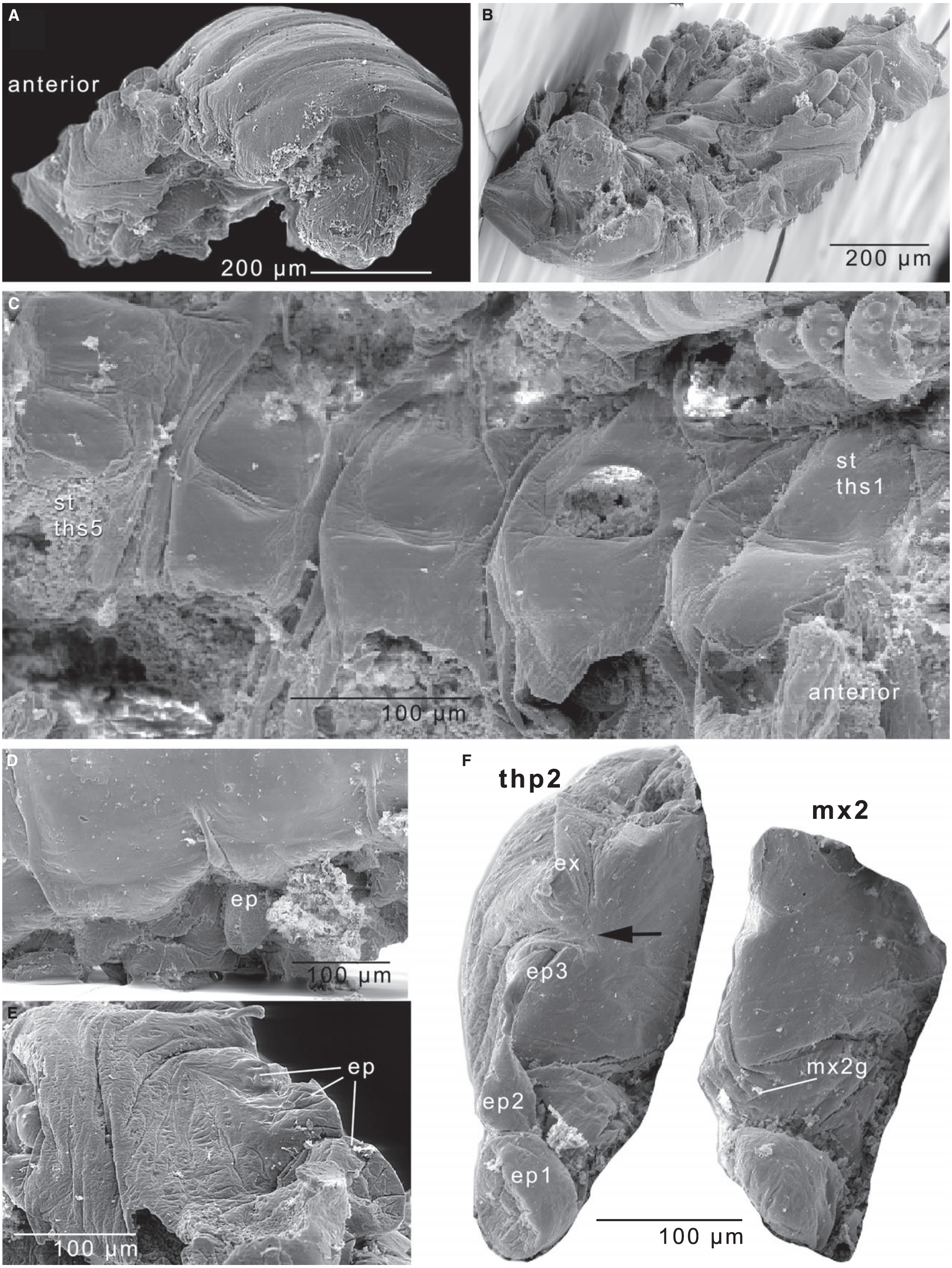
Basipodal endites 3–6 mainly differ from the more proximal endites in being drawn out mediodistally and therefore are more trapezoidal and longer. Accordingly, their less-developed armature (1–3 median spines and a few posterior spines) points more distally (Fig. 4E). The anterior sclerite leading to the third basipodal endite is continuous with the endite, except for a faint vertical line, but already its setae-bearing surface is more mediodistally oriented and much shorter than that of endite 2 (Fig. 4A). Accordingly, the entire endite looks trapezoidal with a median hump bearing the central spine. The 3–4 anterior setae form an oblique row from anterodistally to medioproximally in the anterior appendages, the maximally three in the posterior appendages are located on the plate. Armature of endite 3 changes from two different-sized central spines on the anterior limbs to one on the posterior limbs. Posterodistally, there are up to three more setae on endite 3, which results in a triangular-shaped arrangement in median view on the anterior limbs (Fig. 4E), and less so in the posterior limbs (Fig. 6A).

Endite 4 is continuous with the anterior sclerite. This may also hold true for endite 5, which is known only from its median surface, which is very similar to endite 3 also with regard to its setal pattern and the distal shift of the now slightly humped enditic surface. The distal endite 6 is preserved on the second left thoracopod of the holotype. It is similar to the third and fourth endites in being trapezoidal but is less elevated and even appearing slightly shorter in mediolateral aspect (Fig. 4F). This design indeed leads on to that of the first article of the endopod, as also being preserved in the holotype specimen (Fig. 4F).

Setae of the proximal endite and most likely also all basipodal endites bear fine setulae that are widely and irregularly distributed along the shaft of the setae.

Endopods. Inner rami are only fragmentarily known, and most likely comprise a number of articles. Median surfaces mediodistally protruded, similar to the enditic protrusions of the basipod. The number of setae on the endopodal enditic protrusions is

FIG. 3. *Paulinecaris siveterae* gen. et sp. nov; holotype UB W 418. A, view of the dorsal area from posterior aspect. Note the size of the limbs projecting from the body. B, view of the ventral region from posterolaterally (right side on the stub). C, sternal region (anterior to the right). D, short, soft tergopleural regions with the limbs inserting directly below; epipods inserting close to the limb bases. E, finely wrinkled, weakly sclerotized cuticle of basipod and epipods of left maxilla. F, lateral view of second thoracopod and maxilla of left side; epipods numbered consecutively; proximal epipod discoidal, succeeding epipod smaller and club-like, distal epipod smaller still. Black arrow indicates outer edge of exopod. Anterior surface of basipod (to the right) more firmly sclerotized than posterior side. Abbreviations as in Figures 1, 2, also: mx2 g, putative excretory gland opening of maxilla; st, sternite. Scale bars represent 200 μm (A–B) and 100 μm (C–F).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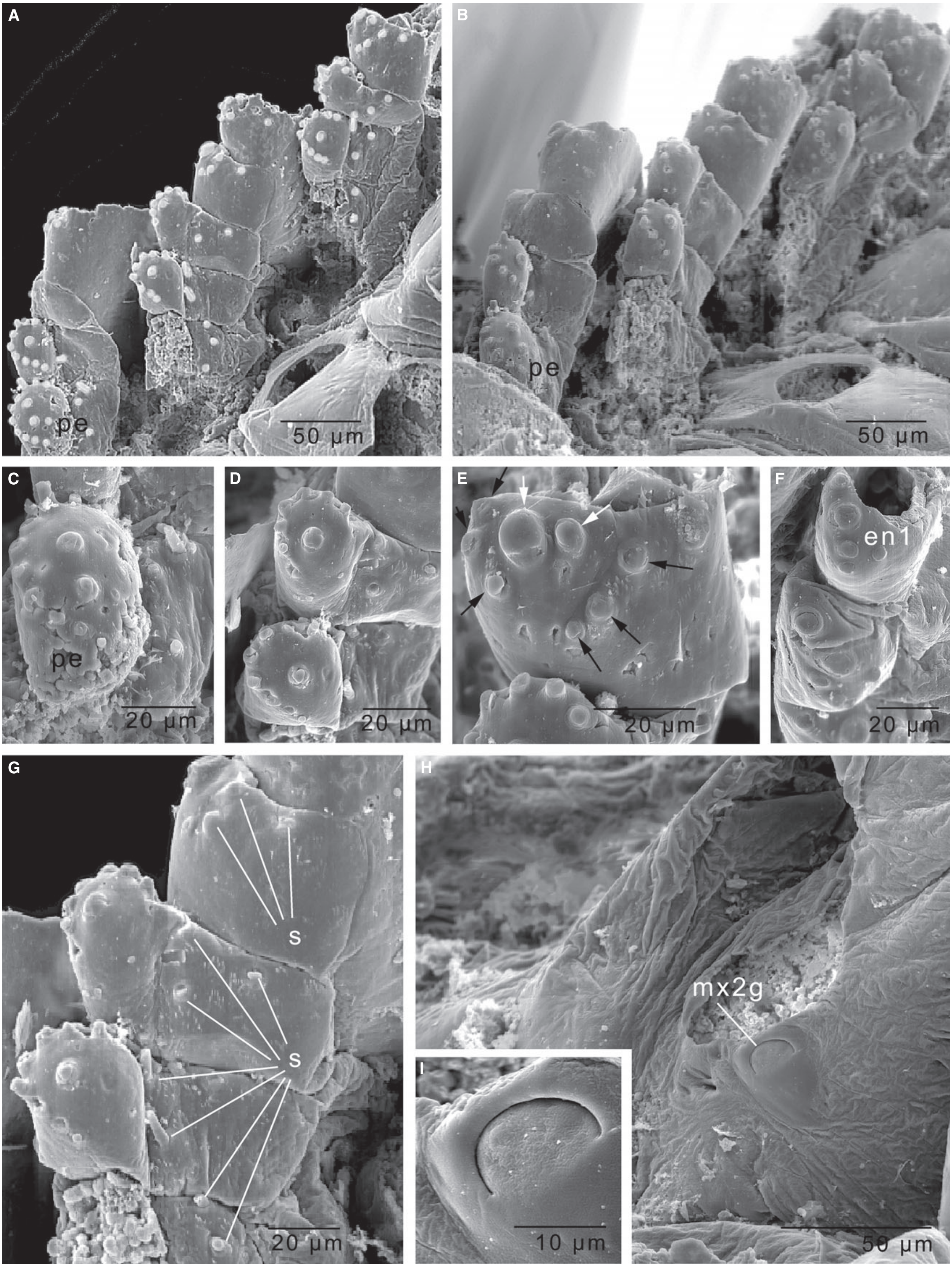
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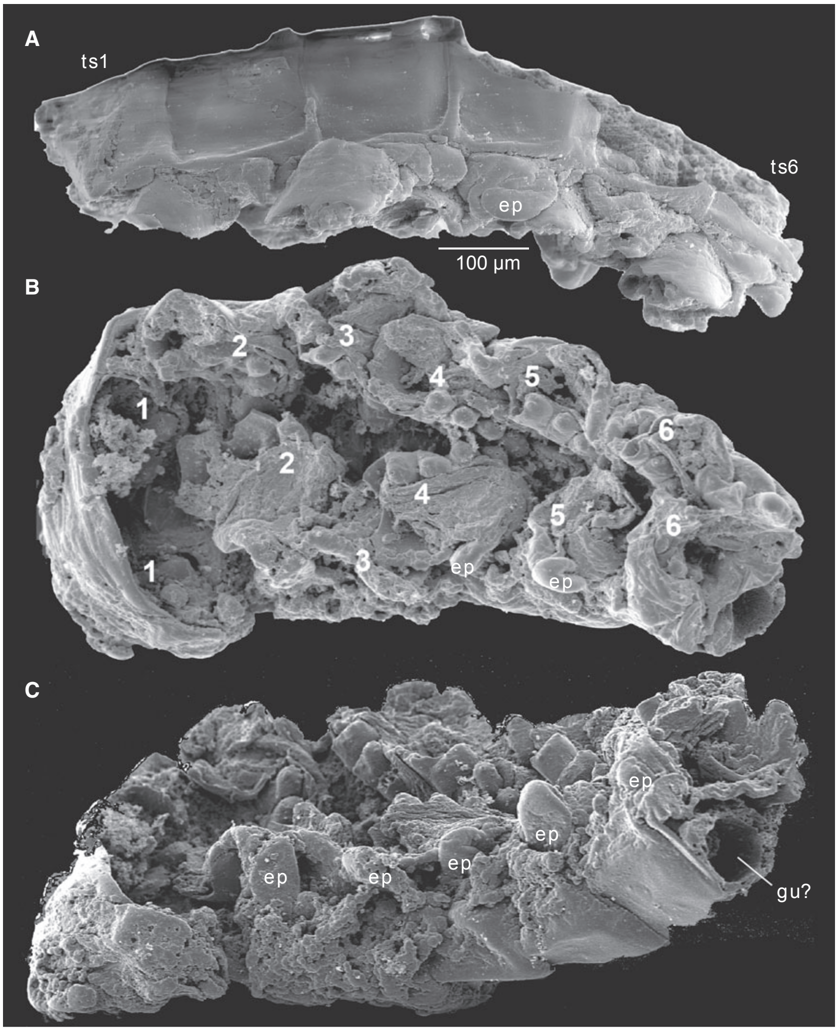


FIG. 5. *Paulinecaris siveterae* gen. et sp. nov., specimen UB W 419. A, lateral view of the trunk fragment comprising six segments with limbs. Cuticle of posterior tergites missing. B, ventral view (segments numbered). C, ventrolateral view showing the epipods and short tergites with their straight margins; limbs inserting directly below margin. Hole at the trunk end may correspond to the gut. Abbreviations as in Figures 1–4, also: gu?, possible gut; ts, trunk segment. Scale bar represents 100 μm.

fewer than on the basipodal endites. The central spine had a generally more robust shape than that of the setae. The spines of the distal endites seem to be stouter than those of the proximal endite and first two basipodal endites. The spine of one of the proximal enditic protrusions is (of the holotype) more than 20 μm long; posterior setae are about 20 μm long. Enditic surfaces and the anterior sclerotizations leading to the endites have fine denticles, some arranged as small groups or short rows (Figs 4G, 6C). The denticles are not as densely distributed or as elongate as in other Cambrian eucrustaceans, where they sometimes appear like brushes on the surface of the endites.

Exopods. Outer rami are known only from the second thoracopod of the holotype, as indicated by a slightly oval insertion at the sloping outer lateral side of the basipod (Fig. 3F). Further details are not known.

Epipods. From the outer proximal side of the basipod, three lobes interpreted as epipods arise in a proximal to distal row (Fig. 3D–F). From proximal to distal, they change from a more loaf-shaped form, about 100 μm long, to a slightly compressed fingertip-like distal-most epipod, possibly 50 μm long, that arises from the outer basipodal edge and is rounded distally

FIG. 4. *Paulinecaris siveterae* gen. et sp. nov. Details of holotype UB W 418. A, view of the three right-side trunk limbs showing their basipodal endites and setation. B, same view as in A from more posterior aspect, displaying the crescentic posterior rows of the proximal endite and proximal two basipodal endites. C, detailed view of proximal endite of the left limb in A and B. D, succeeding two basipodal endites (note the main spine in the centre of the endites). E, succeeding endite with different setation pattern, all shifted medio-distally, appearing like a triangle of three anterior and three posterior setae (black arrows), surrounding two central spines (white arrows). F, sixth basipodal endite and first segment of endopod (en1). G, anterior sclerotizations leading to the endites and bearing three narrow setae. Distally, the sclerotizations continue into the endites. Surfaces with few fine denticles (see Fig. 6C). H, sternal area with proximal part of maxilla exposing the maxillary gland opening, enlarged in I. I, maxillary gland opening, enlarged from H. Abbreviations as in Figures 1–3, also: s, seta. Scale bars represent 50 μm (A–B, H); 20 μm (C–G); and 10 μm (I).

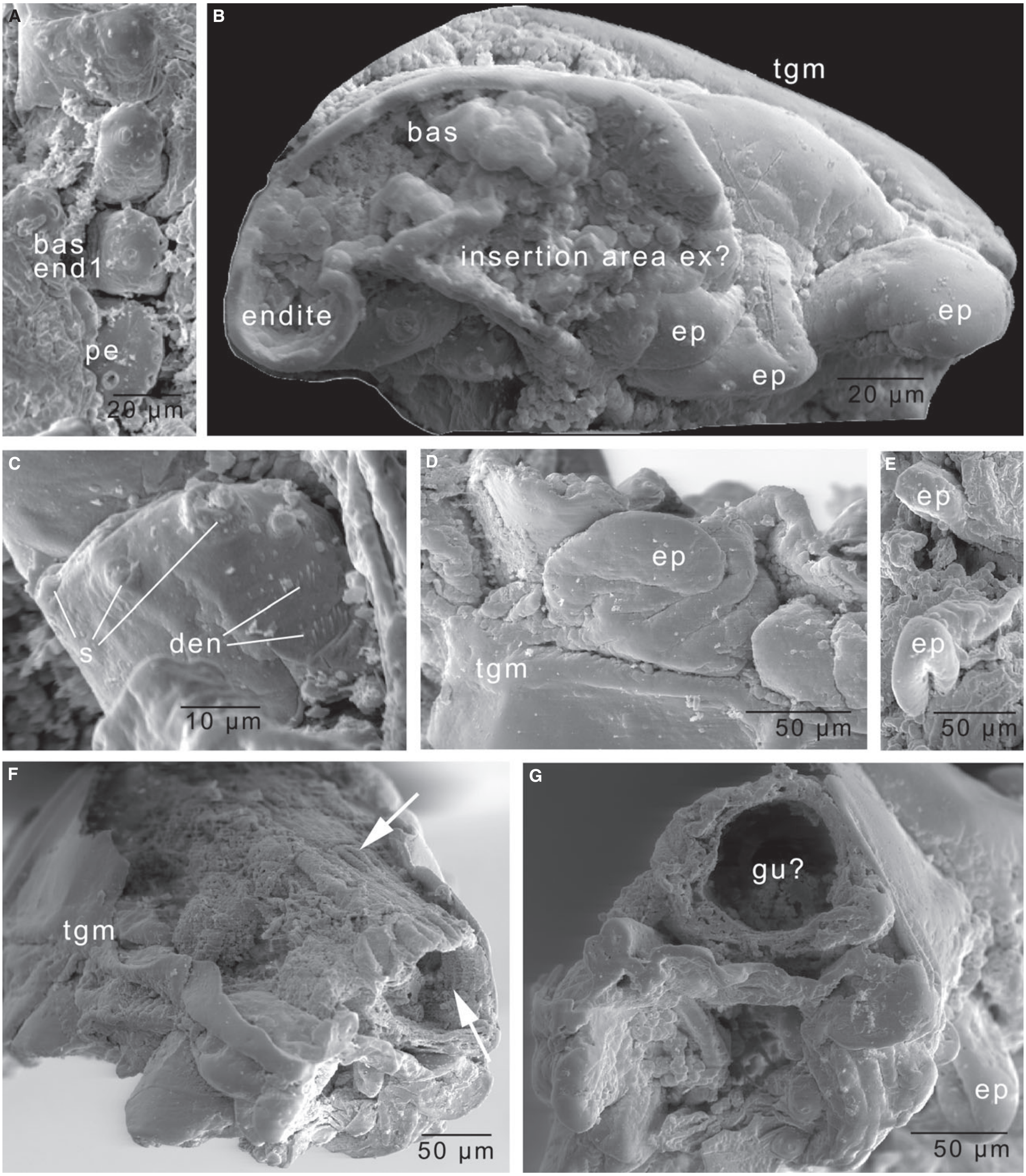


FIG. 6. *Paulinecaris siveterae* gen. et sp. nov. Details of specimen UB W 419. A, median view of proximal endite and succeeding three basipodal endites. Compare with Figure 4. B, broken limb showing the C-curvature of the basipod, with posteriorly turned endite and convex anterior side. C, distal endite with strong central spine and smaller flanking setae, surrounded by several small denticles, some in-groups. D, semidiscoidal basal epipod. E, two of the lobate, more distal epipods. F, posterior end of UB W 419 lacking the cuticular cover, exposing an area of strands resembling musculature (upper arrow). Lower arrow points to putative gut tube at rear, showing fine internal annulation, possibly representing muscle fibres. G, view of the posterior end with the putative gut tube. Abbreviations as in Figures 1–5, also: den, denticles; tgm, tergal margin. Scale bars represent 20 µm (A–B); 10 µm (C); and 50 µm (D–G).

(Fig. 2C). The median epipod is about 80 μm long and 35 μm wide. The surface of the lobes appears to be very soft (Figs 3F, 6D) and lacking ornament or setae.

Hind body. Unknown, but some aspects can be commented on. The surface below the last tergites of UB W 419, exposed possibly due to breakage, has fine parallel stripes that are interrupted at the segment boundaries by transverse strips. This may represent regularly arranged muscle fibres running towards the rear of the trunk as part of the dorsal trunk musculature (Fig. 6F). A large hole in the centre of the broken end, with fine annulations inside, may represent the gut that seems to occupy a large amount of the posterior internal body void (Figs 6G, 7B, for comparison see Fig. 7C).

Preservational aspects and reconstruction. While the dorsal side of the body behind the maxillary segment is fairly undistorted, not much is preserved of the head, except for possibly the mass at the anterior end of the holotype. Accordingly, a reconstruction of the anterior body region is not undertaken. Furthermore, the shield is not preserved. As the cephalic appendages in particular are subject to adaptations to different feeding strategies, it is unwise to speculate on their morphology. Only the maxilla is known in some detail, of which the available parts indicate that it was as prominent as the trunk limbs and similarly equipped (a trunk-limb-shaped maxilla is a plesiomorphy that persists deep into Eucrustacea and especially Entomostraca (retained in Cephalocarida and Ostracoda and a number of 'Orsten' eucrustaceans, e.g.); see Waloszek 2003*b*, Olesen *et al.* 2011).

Knowledge of the endites along the medial edge of the maxilla and the trunk limb morphology is obtained from the preserved limb parts of the two specimens. It also enables recognition of the changes in the shape of the endites in the anterior to posterior appendages and from proximal to distal in each limb, as well as the changes in the armature and position of the individual setae (Fig. 7A). The fifth thoracopod bears a third basipodal endite that is longer than the more posterior ones, which suggests a decrease in the number of endites towards the more posterior appendages. Such a decrease is known also from other eucrustaceans such as extant cephalocarids, in which the appendage series is never really homonymous (Olesen *et al.* 2011).

The posterior end of UB W 419 is squeezed and wrinkled and gives no clues of its continuation (Fig. 5A), but the details of its appendages would favour a slight decrease in all parameters towards the end of trunk. With regard to these data, the body of *P. siveterae* increases slightly in width to decrease again towards the 10th or 11th trunk segment. It is therefore not unlikely that the complete animal had this limited number of segments. Nothing is known of the possibly rather narrow trunk end. However, a telson and furcal rami are predicted to have been present originally because these features belong to the ground pattern of Eucrustacea.

The decrease in the size of the segments and the armature of the appendages can also be interpreted as indicating an immature state for the specimens in hand. However, the specimens seem to represent a metrically large stage, approximately as large as an adult extant cephalocarid (Fig. 7B) or co-existing Cambrian eucrustacean species (as listed in the differential diagnosis).

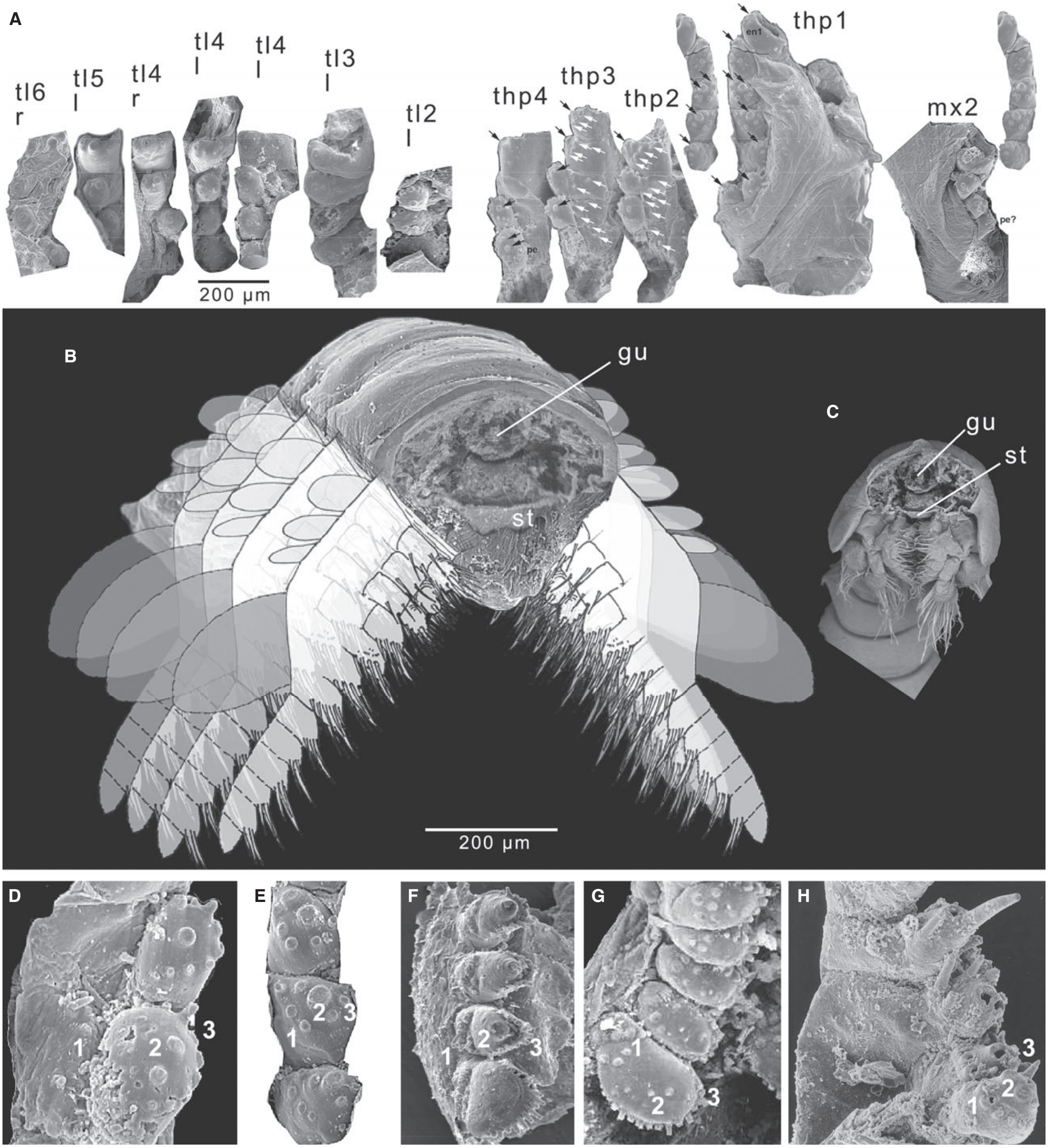
Differential diagnosis. In gross shape, *P. siveterae* resembles various species of Cambrian eucrustaceans of 'Orsten'-type preservation. This holds particularly true for the shape and size of its tergites (Figs 2A, B, 5A), the insignificance of the tergopleurae (Fig. 2B), the bipartite morphology of the sternites (Figs 2C, 3C) and the presence of several basipodal endites on the (postmaxillulary) appendages (Figs 4A, B, 6A).

Paulinecaris siveterae has closest similarities with *R. kinnekullensis* and *Y. dianensis*, and less so with *W. quinquespinosa*, *D. peilertae* and *B. admirabilis* (Müller and Walossek 1988; Walossek 1993; Zhang *et al.* 2007; detailed descriptions of *W. quinquespinosa* and *D. peilertae* are in preparation). However, all these Cambrian species differ from each other in detail. The specific shape of the segment boundaries in *P. siveterae*, having connecting pivot joints and an indication of muscle scars, is similar to that in *R. kinnekullensis*, *Y. dianensis*, *W. quinquespinosa* and *D. peilertae*. The tergal rims are either better developed than in *P. siveterae* (*R. kinnekullensis*, *Y. dianensis*, *W. quinquespinosa and D. peilertae*) or entirely missing (*B. admirabilis*). The cuticular continuation, by fine wrinkles into the membranes of the limb bases, is similar to *Y. dianensis*. *R. kinnekullensis* has, additionally, pronounced bumps on its tergites laterally with an intervening depression and distinctive pivots connecting the tergites. *P. siveterae* and the Cambrian eucrustaceans named above differ also in the specific shape and armature of the basipodal endites of maxillae and thoracopods: *P. siveterae* has six basipodal endites while *R. kinnekullensis* and *Y. dianensis* have at least seven. *P. siveterae* also differs from those two species in the shape of its endites, with *Y. dianensis* having endites that are rather separate from one another, widened distally, with armature comprising vertical rows of setae anteriorly, a central hump for the single central spine and an almost triangular row of posterior setae (Fig. 7F). In early growth stages of *R. kinnekullensis,* the endites are oval-shaped (Fig. 7G), but in more mature growth stages they may also be more triangular posteriorly; in any case, and by contrast to the conditions in *P. siveterae*, the endites always lack a central hump but have many anterior setae. In other species, such as *W. quinquespinosa* and *D. peilertae,* the endites are even more compacted and brick-like, again with a different armature (unpublished information).

DISCUSSION

Towards a systematic position of P. siveterae

Evidence from appendages. Appendages of crustaceans and arthropods are of significance with regard to phylogenetic affiliations because all species differ in details of lifestyle and have modified their appendages accordingly (Haug *et al.* 2013). The maxillae and thoracopods of *P. siveterae* allow comparison with various crustacean taxa and hints at a position within Eucrustacea. With regard to further in-group relationships, *P. siveterae* lacks any of the many autapomorphies of Malacostraca, particularly the coxabasipod subdivision of the maxillae and thoracopods and the shape of the maxillae, which are blade-like in malacostracans, concave in anteroposterior aspect, held against the



anterior mouthparts and have a coxal median edge, which is split into two endites medially, and a basipod that has a two-part median edge (Walossek 1993; Olesen and Walossek 2000; Richter and Scholtz 2001; Haug *et al.* 2013). In *P. siveterae,* the maxilla and the thoracopods have a large fleshy basipod, a proximal endite and several basipodal endites, as occur in various Entomostraca. Several phylogenies have been suggested for nonmalacostracan crustaceans (Regier *et al.* 2010; Reumont *et al.* 2012) but they differ from each other in many respects and, as a rule, do not consider the characters from fossil material, as presented here and elsewhere (Walossek 1993; Maas *et al.* 2003; Haug *et al.* 2010*b*).

We have therefore chosen to base our considerations of the systematic affinities and of the evolution of epipods on phylogenies, such as those of Maas *et al.* (2003), Waloszek (2003*b*) and Haug *et al.* (2010*b*), which include evidence from fossils. Following Waloszek (2003*b*), Entomostraca is characterized by several autapomorphies, some of which are also relevant for the present study:

1. Basipod of all postmaxillulary appendages prominent, fleshy and C-shaped curved to form interappendage sucking chambers;
2. Median edge of basipod drawn out into a series of six or even seven distinct, slightly posteriorly oriented protrusions, the basipodal endites;
3. Endites (basipodal endites and proximal endite) with a specific armature of three sets of setae: an anterior group or row of setae, a central group of spines and a posterior group or row of setae (Fig. 7D–H; Haug *et al.* 2013).

In cephalocarids, the endites, including the proximal endite and the basipodal endites, bear internal muscles that facilitate their movement (Hessler 1964; illustrated for the cephalocarid *Hutchinsoniella macracantha* by Sanders 1963, also including a sketch showing the movement). This system of mobile endites along the limb stem is seen as a complex feature that characterizes the Entomostraca in general (Walossek 1993; Haug *et al.* 2013). Lobate endites suggesting such morphology can also be found in fossils such as *R. kinnekullensis*, *Y. dianensis* or *D. peilertae* and in a modified way in all eubranchiopod taxa. This functional system is quite different from the simpler enditic elongations of the inner margins of basipods and coxae, often also called endites, known from nonentomostracan fossil crustaceans such as the phosphatocopines and derivatives of the stem linage: setae- or spine-bearing humps are known, for example, from the proximal endite and basipod of 'stem-lineage' taxa, as, in *Martinssonia elongata* (Haug *et al.* 2010*b*), but they appear immobile and their armature, including that of the separate proximal endite is simpler and consists only of a few setae or spines. The Cambrian Phosphatocopina, the putative sister group to Eucrustacea, also have a single nonmobile basipodal endite on their postmandibular limbs, similar to that of the stem-lineage derivatives, but the armature of the proximal endite, the basipodal endites and those of the endopod articles are like those in entomostracans and consist of three sets of spines (Fig. 7H; Maas *et al.* 2003; see especially their fig. 66A, in which these three rows are illustrated for different limb parts of the mandible of a phosphatocopine).

Clearly different from such morphology are the blade-like extensions that occur on maxillulae and maxillae of malacostracan taxa, as noted above (e.g. 'inner plate' and 'outer plate' of gammaridean Amphipoda; Mayer *et al.* 2012). Moreover, malacostracans lack basipodal endites on all thoracopods, that is, on thoracopods of set I (thoracopods 1–8) and set II (pleopods 1–6; Walossek and Müller 1998). Furthermore, only extant leptostracan Phyllocarida among Malacostraca have a well-developed median setation on their thoracopods of the first set, because they use

FIG. 7. A, photographic correlation of the preserved limb parts of *Paulinecaris siveterae* gen. et sp. nov. from maxilla (mx2) to fourth thoracopod (thp4) of UB W 418 and from trunk limb 2–6 (tl2–6) of UB W 419; partly mirrored to fit into the series. White arrows point to fine anterior setae, black arrows point to larger spine-like setae at the peaks of each of the enditic surfaces. Sizes adjusted. B, SEM image of a body segment of *P. siveterae* using the size-adjusted cross-section of the cephalocarid *Lightiella monniotae* Cals and Delamare Deboutteville, 1970 (C) and a tentative reconstruction of *P. siveterae* using parts of an SEM micrograph (body and one limb) and adding a schematic drawing of a thoracopod (stippled areas uncertain, mainly endopod and exopod). C, separated cross-section of *L. monniotae;* note that the two animals differ particularly with regard to the size of tergopleurae and limbs. Tergopleurae lacking in the fossil but are well developed in *L. monniotae*. D–H, endites of Cambrian crustaceans; not to scale. D, proximal endite and first basipodal endite of *P. siveterae*, with recessed anterior setae (1), rounded enditic surfaces with 1–2 spine-like setae (2) and crescent of posterior setae (3). E, distal endites of *P. siveterae* with oblique row of anterior setae, median spine-like setae on medio-distal hump and few posterior setae. F, isolated and protruding endites of *Yicaris dianensis*, vertical row of anterior possibly movable setae ('Sperrborsten') along a ridge, conical median hump extending into spine and triangular row of posterior setae; proximal endite lacking median setae or spines (see Zhang *et al.* 2007 for details). G, endites of *Rehbachiella kinnekullensis*, anterior set made of rows and isolated setae ('Sperrborsten'), few fine setae of spines on shallow median surface, and crescent of posterior setae (filter setae with double rows of regularly distributed setulae). H, Cambrian phosphatocopine from Australia lacking an exopod on all known limbs (Walossek *et al.* 1993; specimen 9067); three sets of setae or spines also present here: oblique row of anterior setae, median hump with spines and posterior set of few setae. Abbreviations as in Figures 1–6, also: l, left; r, right. Scale bar in B–C represents 200 μm.

them for food intake (Walossek 1993). Even these have only two parallel rows of setae along the thin median edge of their anteroposteriorly flattened thoracopodal stems faintly subdivided into coxa and basipod. Such an arrangement most likely represents a ground pattern feature of Malacostraca (Walossek 1993). Furthermore, subordinate setulae on the long setae at the median edge of the limb stems of malacostracan taxa point in the opposing direction compared with those in entomostracans such as branchiopods (Walossek 1993). Phyllocarids possess a thoracopodal filtratory system while Eumalacostraca may have undergone much modification from this basic pattern. But even the relatively small and weakly sclerotized extant phyllocarids may not reflect the original system with regard to the large, strongly sclerotized fossil representatives with their stenopodial, possibly nonfiltratory, limbs (Bergström *et al.* 1987). In the light, not least, of the possibility of endites occurring at least in fossil phyllocarids (see below), this requires further investigation.

The single known exception of a thoracopodal basipod with enditic protrusions among the Malacostraca is the Silurian phyllocarid *Cinerocaris magnifica* Briggs, Sutton, Siveter and Siveter, 2004. This species was described as possessing several endites along the limb stems of its thoracopods (Briggs *et al.* 2004), but neither a proximal endite nor a subdivision of the elongated limb stem into a coxa and basipod, or any armature with setae and/or spines can be ascertained due to limitations of resolution. Due to this uncertainty, it is currently difficult to accept that several basipodal endites occurred on thoracopods in the ground pattern of Malacostraca, as in Entomostraca, and furthermore, that several basipodal endites should also be present in the eucrustacean ground pattern.

A proximal endite below the basipodal endites is, in itself, plesiomorphic to all crustaceans in the wider sense, the Crustacea *s. l.* (cf. Walossek and Müller 1990; Haug *et al.* 2010*a*, *b*). It starts as a faint sclerotization within the membrane connecting the body and the third cephalic limb (Stein *et al.* 2005, 2008 for *Oelandocaris oelandica*), eventually growing out into a hump with a median set of spines or setae anteriorly. Because the coxa is simply a modification of this proximal endite below the basipod by enlargement of the sclerotization around the limb stem in a ring-like manner, that is representing the evolutionary as well as ontogenetic successor of the endite (Walossek 1993; Haug *et al.* 2013), the presence of a proximal endite excludes the presence of a coxa. Accordingly, because a division of the limb stem into coxa and basipod occurs in both malacostracan in-groups, Phyllocarida and Eumalacostraca, this morphology should have evolved twice in Malacostraca (in Phyllocarida and Eumalacostraca) if *C. magnifica* truly possesses several endites along its limb stems, which, however, does not appear parsimonious to us.

At the level of Labrophora (†Phosphatocopina and Eucrustacea), the armature of the proximal endite consisted of some setae anteriorly, a central spine and a few setae posteriorly, seemingly ‘copied’ to the single enditic protrusion of the basipod and the endopodal articles too (Fig. 7H; see above). Because all known derivatives of the lineage towards Labrophora (Phosphatocopina + Eucrustacea) have a different arrangement, this specific enditic armature consisting of three sets of spines/setae is considered not only as an autapomorphy of Labrophora (Maas *et al.* 2003; Haug *et al.* 2013), but also a feature that suggests a position of *P. siveterae*, sharing such armature, within the Labrophora. Again the occurrence of this specific arrangement in three sets also on all basipodal endites is developed only in the Entomostraca among Eucrustacea and is therefore considered as an autapomorphy of this taxon (Waloszek 2003*b*; Zhang *et al.* 2007 put the feature into the ground pattern of Eucrustacea, but there are no data for this assumption at present). Because this feature is present in *P. siveterae* and also the adornment of the anteriorly positioned setae with two rows of fine posteriorly pointing setulae, and that of the posterior setae with two rows of anteriorly pointing setulae (Malacostraca have just two rows of setae and differently oriented setulae; Walossek 1993, Haug *et al.* 2013), a position of *P. siveterae* within Eucrustacea and furthermore within Entomostraca is, hence, very likely.

Another feature to consider is the number of endites, that is proximal and six basipodal endites (Fig. 8). This number is well within the range of endites on the appendages of other entomostracan taxa and also in the phyllocarid *C. magnifica,* which has 6–7 endites (Briggs *et al.* 2004). One characteristic used to distinguish between an entomostracan and a malacostracan type of trunk limb(s) is whether a proximal endite (Entomostraca) or a coxa (Malacostraca) is present. According to Briggs *et al.* (2004), a coxa-basipod distinction is impossible to recognize in the material of *C. magnifica*. In their reconstruction of a generalized trunk limb (Briggs *et al.* 2004, Fig. 2i), based on trunk limbs 4–8, seemingly six endites are present. The most proximal of these, which is slightly bent, indeed may be the proximal endite; if so, this would obviously differ from typical malacostracan morphology. Another possibility is that the three proximal median lobes (endites?) in the generalized trunk limb of *C. magnifica* correspond to the coxa as present in other malacostracans, and the three succeeding lobes are basipodal. However, this question has to remain open, as the number of endites of *C. magnifica* is still uncertain. It may be as many as 6–7 (Briggs *et al.* 2004) or it may be that the three proximal lobes represent just one damaged portion, which would yield only four (one coxal and three basipodal) endites.

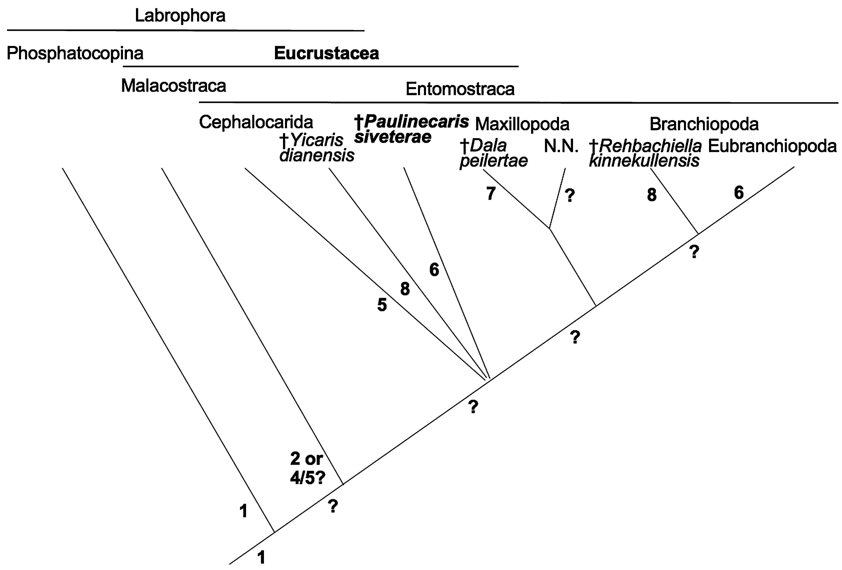


FIG. 8. Hypothesis of relationships within labrophoran Crustacea, including the presumed position of *Paulinecaris siveterae* gen. et sp. nov. Arabic numbers refer to the number of basipodal endites on trunk limbs at the respective nodes; uncertain values marked by question marks. N.N., nomen nominandum.

Among extant entomostracans, Cephalocarida have five basipodal endites and (eu)branchiopods six (Rogers *et al.* 2006) or less due to fusion of the endites (Møller *et al.* 2004). Maxillopods do not use their trunk limbs for feeding so they have no distinct enditic system. Possible Cambrian representatives of Maxillopoda have seven endites (*B. admirabilis*, *D. peilertae*) and Branchiopoda in the wider sense (*R. kinnekullensis)* have eight, as does *Y. dianensis*, which currently cannot be readily assigned to any major entomostracan group. That *P. siveterae* has six basipodal endites would therefore at least distinguish it from those particular species at a low systematic level.

The high number of basipodal endites in the postmaxillulary limbs of especially fossil taxa among Eucrustacea (Fig. 8) appears to represent the plesiomorphic condition at least among Eucrustacea, while only one enditic protrusion may have characterized the labrophoran ground pattern condition. A lower number of endites than six to eight in most extant representatives (Fig. 8) may, consequently, be explained as a derived feature. However, as data on the enditic armature of eucrustaceans are sparse, this question must remain open. It also remains unclear whether the development from an original condition of one setae-bearing protrusion, as in Phosphatocopina, to a higher number of basipodal endites, as in Entomostraca and Malacostraca (if present) occurred in a single step.

In summary, based on the morphology of its maxillae and trunk appendages, *P. siveterae* can be regarded as belonging to the Entomostraca (Fig. 8), but a more definite systematic assignment is not possible at present. A unique feature that distinguishes *P. siveterae* from all other 'Orsten' eucrustaceans (autapomorphy of the taxon) is the enditic armature, which changes along a limb in a specific way: proximally it is similar to other Cambrian eucrustaceans, but distally the arrangement is more like that in phosphatocopines. This mixture of conservative and new elements has not been reported from any other species.

Evidence from tergites and sternites. The lack of distinct tergopleurae has never received detailed consideration in comparative morphological and phylogenetic studies of Crustacea or Arthropoda. Tergites with lateral extensions, called tergopleurae, are an autapomorphy of Arthropoda *s. s.* (Waloszek *et al.* 2005) and have been retained in all descendant taxa of Euarthropoda. Tergopleurae are particularly well known, for example, from trilobites (the name Trilobita even refers to the conspicuous tergopleurae in this taxon although tergopleurae are plesiomorphically retained), but also occur in basal chelicerates (Chen *et al.* 2004; Liu *et al.* 2007) and in malacostracan Crustacea. Euchelicerates, myriapods and hexapods, more or less, lack tergopleurae and in early derivatives of the Crustacea *s. l.*, such as *M. elongata* (Haug *et al.* 2010*b*), *Cambropachycope scutula* and *Goticaris longispinosa* (Haug *et al.* 2009) or the various species of Phosphatocopina tergopleurae are also short to lacking. In *O. oelandica* and in *Henningsmoenicaris scutula* (Walossek and Müller 1990; Haug *et al.* 2010*a*) tergopleurae are present, but they not distinctly set off from the middle part of the tergite. Within entomostracan Eucrustacea, there seem to be only small tergopleurae, the largest being in the thorax region of cephalocarids (Olesen *et al.* 2011), while the occurrence of tergopleurae in several copepodan in-group taxa (see Huys and Boxshall 1991 for all major copepodan groups) most likely represent 'reinventions'. Within Malacostraca, tergopleurae are especially found in the anterior thorax of certain peracarid groups such as isopods and in the posterior thorax or pleon of certain decapods. Short to absent tergopleurae occur in the anterior thorax of most in-group taxa and in the pleon of mysids, and especially in interstitial or stygobiont taxa (e.g. among anaspidaceans, bathynellids, tanaidaceans and others). All this hints at multiple independent loss of this structure among Euarthropoda rather than a multiple reinvention of tergopleurae. The lack of tergopleurae in *P. siveterae* does therefore not contradict its proposed phylogenetic position.

Sternites are the ventral counterparts of tergites and occur as sclerotized cuticular areas between a limb pair. Like tergites, sternites have received relatively scant attention in comparative studies. Sternites might have been rather weakly sclerotized in the ground pattern of the Arthropoda *s. s.*, as they are not really visible in all early derivatives (see, e.g. Hou and Bergström 1997 for *Fuxianhuia protensa* Hou, 1987 and *Chengjiangocaris longiformis* Hou and Bergström, 1991; and Waloszek *et al.* 2005 for *Shankouia zhenghei* Chen, Wang, Maas and Waloszek in Waloszek, Chen, Maas and Wang, 2005). Subsequently, that is in the evolutionary lineage towards Euarthropoda, sternites seem to have become slightly better sclerotized and developed into slightly elevated transverse bars between the appendages, separated from one another by membranous cuticle. Most likely each postoral segment bore one sternite, and this was retained in most representatives of Euarthropoda, as is best seen, for example, in *A. pisiformis*, an exceptionally preserved euarthropod from the late Cambrian 'Orsten' (Müller and Walossek 1987), in trilobites and deep into the chelicerate lineage. Studies of the embryology of web spiders demonstrate that this status is retained not only deep into derived taxa, but also the first appendage (the chelicera, or antennula in crustacean terminology) still has a postoral sternite (cf. Liu *et al.* 2009). This status is lacking in all other euarthropod taxa. While there are no clear data regarding myriapods and insects, early derivatives of Crustacea *s. l.* retained at least the status of separate sternites from the first postantennal segment backwards (cf. Maas *et al.* 2003; Haug *et al.* 2009, 2010*a*, *b*).

Modification of sternites is widespread, often involving their fusion into larger plates. Such modifications often affected the postoral side of the head region. There, the product of fusion has generally been termed 'sternum' to distinguish it from the isolated sternites of the trunk region. Examples are known from euchelicerates (Liu *et al.* 2009), insects (Liu *et al.* 2010) and Labrophora (including Eucrustacea, Maas *et al.* 2003; Haug *et al.* 2013), but the number of fused segments varies and it seems that all major groups acquired their particular situation convergently from the plesiomorphic status of having separate sternites. In certain eumalacostracans, fusion also affected the anterior thorax (anterior 8 segments = thorax I, according to Walossek and Müller 1998). In phyllocarid Malacostraca, all sternites posteriorly to pleon segment 4 are separate, uniform and slightly raised with median elevations in a series forming a keel-like structure (Walossek 1993; Olesen and Walossek 2000). The posterior two pleon segments are ring-shaped and so lack a separate sternite.

The sternites are also separate in the Carboniferous malacostracan *Tealliocaris woodwardi* (Etheridge, 1877) (Briggs and Clarkson 1985), while in other taxa, such as decapod eumalacostracans, thoracic sternites may fuse to form a plate-like structure (Scholtz and Richter 1995; Dixon *et al.* 2003), particularly in achelates (rock and slipper lobsters) and brachyuran crabs. Within the Entomostraca, the pattern is generally poorly known. Cephalocarida have uniform, slightly raised but separate sternites between all thoracopods (Fig. 7C), while Branchiopoda, including the Cambrian *R. kinnekullensis*, have subdivided sternites that are infolded to form a deep V-shaped groove for food transportation towards the mouth (Sanders 1963; Walossek 1993). In other Cambrian taxa such as *Y. dianensis*, *D. peilertae*, *W. quinquespinosa*, as in *P. siveterae*, the sternites are subdivided but simple plates and are not recessed to form a sternitic food groove. External sternite morphology has been little investigated among maxillopods (see Haug *et al.* 2011 for some examples), so cannot be used currently to help determining the systematic position of *P. siveterae*.

Evolution of epipods

The first Cambrian crustacean with epipods that was described is the eucrustacean and probable entomostracan *Y. dianensis* (Zhang *et al.* 2007). Its epipods differ within a single appendage, the proximal and distal ones being leaf-shaped with one or two setae or spines, while the middle epipod is more club-shaped. However, such differences might merely represent an ontogenetically early morphology (later developmental stages are unknown). The presence of setae on the epipods of *Y. dianensis* prompted some authors to conclude that the series of repetitive structures along the outer edge of the maxilla and trunk appendages of *Y. dianensis* could have evolved independently from the 'real' epipods of other crustaceans (Boxshall 2007; Boxshall and Jaume 2009). In our view it is more parsimonious to assume a common origin of all these structures as epipods, most likely in the ancestor of Eucrustacea. As was also previously noted, epipods do not occur in the majority of Cambrian 'Orsten' crustaceans (Boxshall and Jaume 2009). Although true, such absences can be explained and may have more than one reason. The majority of the species in question are early representatives of Crustacea *s. l.* (Haug *et al.* 2009, 2010*a*, *b*) including phosphatocopines (Maas *et al.* 2003), all of which branch off below the evolutionary level of Eucrustacea. Therefore, lack of epipods in these species appears to be merely a plesiomorphic trait. Other known species such as *D. peilertae*, *B. admirabilis* and the three species of *Skara* have been interpreted as Maxillopoda, which generally lack epipods. Indeed most maxillopods, for example in-group thecostracans, such as ascothoracids, facetotectans and cirripedes, and also copepods and mystacocarids, lack epipods and a dorsal organ. Thecostracans have, at a corresponding position of the dorsal organ of branchiopods, the anterior set of four sensorial setae of the so-called lattice organ (Müller and Walossek 1985*b*; Jensen *et al.* 1994*a*, *b*; Høeg *et al.* 1998; Liu and Dong 2007; Haug *et al.* 2011). Only the Cambrian 'Orsten' maxillopod *B. admirabilis* has a dorsal organ similar to that of Branchiopoda in all stages of development including the putative adult with all seven thoracopods developed, but it clearly lacks epipods (Müller and Walossek 1988). At least for some of the extant members of this taxon, such as copepods or cirripedes, it has been assumed that their epipods had been reduced during evolution (Boxshall and Jaume 2009). Within other Entomostraca, the tiny cephalocarids also lack epipods at any developmental stage and also lack a dorsal organ (Sanders 1963; Olesen *et al.* 2011). This lack may be explained by their special benthic life style (the so-called pseudoepipodite of Sanders 1963 is simply part of the exopod).

The absence of epipods in 'Orsten' eucrustaceans, in the Cambrian marine branchiopod *R. kinnekullensis*, which is known from over 100 specimens of numerous developmental stages up to a larva with 13 trunk segments, is remarkable, because most extant branchiopods have epipods (Olesen 2007, 2009). Their early larvae have an osmoregulatory dorsal organ. In anostracans and another branchiopod, the aberrant 'conchostracan' *Cyclestheria hislopi* (Baird, 1859), epipods do not differentiate ontogenetically prior to the development of ten pairs of thoracopods (Fryer 1983; Schrehardt 1986; Olesen 1999). When full differentiation of the epipods is achieved, the early larval dorsal organ disappears, or is reduced or modified (Günzl 1978, 1980; Olesen 1996) before the adult stage is reached (Olesen 1999, 2004). Perhaps the presence of epipods in extant branchiopods can in some way be explained by their occurrence in freshwater habitats. *R. kinnekullensis* also has the early larval organ, and its reduction happens after several instars (Walossek 1993), but epipods do not appear. Small size is always a possible explanation for the lack of epipods, but the reason why they are absent in *R. kinnekullensis* is unclear (Walossek 1993).

In *Y. dianensis,* epipods occur earlier in development than in any extant taxa and are present (at least on the first thoracopods) already in a larval stage with four trunk segments (Zhang *et al.* 2007). As mentioned above, many small-sized crustaceans lack epipods but the occurrence of epipods is not necessarily directly correlated with body size. All of the eucrustaceans mentioned above, extant and fossil, are small, but their epipods appear well before the animals attain a size of about 2 mm. Late appearance of epipods during ontogeny also holds for Malacostraca. In the euphausiid *Euphausia superba* Dana, 1852, for example, the epipod (gill) of the first thoracopod appears as an undifferentiated bud in the Furcilia II stage, in which the animal is already about 1 cm long (Maas and Waloszek 2001). The segmental composition of the adult, that is an individual with 14 trunk segments, is reached two moults earlier in the Calyptopis III stage, at a length of about 7–8 mm. It seems reasonable to assume that the late appearance of epipods during ontogeny is another associated character state in the ground pattern of Eucrustacea. The situation in *Y. dianensis* might therefore be explained as a heterochronic shift (cf. Haug *et al.* 2010*a*, *b*) autapomorphic to this particular species and, likewise, autapomorphic to the morphology of its epipods.

In summary, hitherto the only firm evidence of epipods in known Cambrian Eucrustacea is in *Y. dianensis* and *P. siveterae*. In contrast to *Y. dianensis*, the epipods of *P. siveterae* are distally rounded and lack spines or setae and are either discoidal or tubular lobes (Maas *et al.* 2009). In this respect, *P. siveterae* has epipods, which are more similar to those of extant crustaceans than to those of *Y. dianensis*. A reason for this might simply be that the morphology of the epipods of *Y. dianensis* is either a feature of early immature stages or is autapomorphic. That *P. siveterae* has three epipods supports the suggestion that there were originally three in the ground pattern of Entomostraca (Maas *et al.* 2009), a condition that would then have been retained in the larval stages of some anostracan branchiopods (Fig. 1E; Møller *et al.* 2004).

Gills in other fossil representatives of Arthropoda s. s.*?*

In general, lightly cutinized structures are rarely preserved in fossil arthropods, except when preserved in 'Orsten'-type preservation. The flat, leaf-shaped exopods of the three species of early representatives of Arthropoda *s. s.* (sclerotized arthropods; Waloszek *et al.* 2005) from the early Cambrian of China (*C. longiformis* Hou and Bergström, 1991, *F. protensa* Hou, 1987 and *S. zhenghei* Chen, Wang, Maas and Waloszek *in* Waloszek, Chen, Maas and Wang, 2005) inserting laterally at the basis of a long multiarticulated main rod were possibly rather softly sclerotized (= 'arthropodium'). Because such a design was retained in Euarthropoda, it has been interpreted as a ground pattern feature of Arthropoda *s. s.*, which was modified later by the addition of marginal setae. In the ground pattern of Euarthropoda, all postantennular appendages comprise three elements, a novelty at this level: a flat, plank-like basipod with spines along its median margin; a nine-segmented endopod, with all but the distal segment being slightly drawn out mediodistally, with one or three spines arising from the mediodistal humps; and a paddle-shaped exopod with long marginal setae (Maas *et al.* 2004; Waloszek *et al.* 2005, 2007; Liu *et al.* 2007; Haug *et al.* 2012, 2013). It is very likely that these appendages (the 'euarthropodium') were multifunctional and used mainly for locomotion and feeding.

Of these two limb types, it is probably mainly the exopod that was used for swimming, particularly after the setae appeared. Alternatively, the exopod has also been interpreted as a 'gill branch'. A respiratory and osmoregulatory function has been assumed for the exopods of the euarthropod in-group Trilobita in particular. However, Suzuki and Bergström (2008) demonstrated that trilobite exopods are probably not modified for respiration, a view supported by Maas *et al.* (2009). Furthermore, Suzuki and Bergström (2008) suggested that the trilobite exopods produced a water current that passed over the soft body surface underneath the tergopleurae, which supposedly acted as a respiratory surface. This appears plausible particularly because in all animals, respiration occurs more or less passively over the entire body surface or lightly sclerotized areas, independently of whether there are specific respiratory organs such as gills or lungs (Taylor and Taylor 1992).

Chelicerata *s. l.* most likely originally lacked gills. Their appendages consisted of a basipod carrying a nine-segmented endopod and a paddle-shaped exopod (Liu *et al.* 2007; Haug *et al.* 2012). Fossil members of the Euchelicerata, such as the synziphosurine xiphosurans *Offacolus kingi* Sutton, Briggs, Siveter, Siveter and Orr, 2002 and *Dibasterium durgae* Briggs, Siveter, Siveter, Sutton, Garwood and Legg, 2012 from the Silurian Herefordshire lagerstätte, had exopods (on prosomal and opisthosomal legs) but no epipods (Sutton *et al.* 2002; Briggs *et al.* 2012). The situation in xiphosurine Xiphosura, and possibly all extant representatives of Euchelicerata, is slightly different. There the prosomal appendages are uniramous but their opisthosoma possesses structures for respiration/osmoregulation. Only xiphosurans retained opisthosomal appendages, and there gill structures are located at the posterior side of the leaf-shaped exopods in the form of a large number of fine, horizontally attached blades (Suzuki *et al.* 2008). All other euchelicerates lack true limbs on their opisthosoma. The respiratory structures on the ventral side of the opisthosoma are considered to be modifications of former limbs, although their evolutionary origin remains obscure. Gill structures may have been found in a possibly secondarily aquatic scorpion (Poschmann *et al.* 2008), but this feature does not contradict the basal lack of gills in Chelicerata.

All extent adult myriapods and insects have limb rods mainly serving for locomotion but lack exopods. Even food collection is, at least originally, rarely a function of these limbs (e.g. dragon flies like to hold their prey between their first thoracopods). Epipods or gill-like structures also appear to be lacking in the adults. This holds true at least for the few early fossil representatives of these taxa. Gill-like structures may, however, occur in aquatic larval stages (as also demonstrated from fossil mayfly nymphs; Martins-Neto 1996), which must be considered as a secondary feature due to the terrestrial origin of myriapods and insects. In Crustacea, the exopods basally also served for locomotion, and not for respiration; regardless of whether they were paddle-shaped or multi-annulated. Exceptions are few, the best known being the woodlice among peracarid caridoid eumalacostracans, but their in-group position prevents one from assuming that this is a basal design. Gill structures laterally at the basipods therefore have been found exclusively in eucrustaceans.

Already these few examples make it very likely that no explicit gill structures were present in the ground pattern of Euarthropoda. Within crown-group crustaceans, gill structures have been reported for a few non-'Orsten' fossils, such as in a reptantian decapod from the Jurassic Solnhofen limestones (Schram and Dixon 2004), which is remarkable given their concealed position within a gill chamber. In stomatopods, however, where gills would appear to be easier to access, no such structures have been found, not even in exceptionally preserved material (Haug *et al.* 2010*c*).

CONCLUSIONS

Based mainly on appendage, tergite and sternite morphology, *P. siveterae* is interpreted as an entomostracan eucrustacean. The new species provides additional evidence for the presence of three epipods in the ground pattern of Eucrustacea (Maas *et al.* 2009) and hints at the evolution of epipods not earlier than in the evolutionary lineage towards the Eucrustacea. Morphogenesis of epipods by enlargement of a swelling at the base of a seta at the outer edge of the limb, as seen in *Y. dianensis* (Fig. 1F) and proposed by Maas *et al.* (2009) to be ancestral, however, cannot be clearly confirmed. The epipods of *P. siveterae* are round to slightly anteroposteriorly flattened tubular lobes, appearing more similar to epipods of extant eucrustaceans, particularly those of branchiopods, particularly phyllopods (cf. Fig. 1A). In the ground pattern of Eucrustacea, the maxilla, which looks like a trunk appendage, and the trunk appendages had most likely three epipods. The large diversity in number and shape of the epipods among modern eucrustaceans can be readily derived from this state (Boxshall 2007; Boxshall and Jaume 2009).

The *P. siveterae* material is also important in that the gut (Figs 5C, 6G) and possibly muscle fibres (Fig. 6F) are preserved, a rare occurrence in 'Orsten'-type preservation (cf. Maas *et al.* 2006). Moreover, the opening of the maxillary excretory gland is also preserved, the first time this feature is recorded in a Cambrian arthropod (the structure shown by Müller and Walossek 1985 for the two Swedish species of *Skara* is interpreted as the opening of the antennal segmental excretory gland). Excretory glands were originally present in all segments of arthropods (Arthropoda *s. l.*; Mayer 2006), but only two pairs of segmental excretory glands remain functional in Eucrustacea, the antennal and maxillary glands, so-named after the position of their openings (embryologically even more may occur, such as in anostracan branchiopods and cephalocarids; Benesch 1969; Hessler and Elofsson 1991). Within Malacostraca, the plesiomorphic state is developed in phyllocarid Malacostraca (Cannon 1926). Antennal excretory openings often characterize early larvae (the hatching (ortho)nauplius, with its few segments, is simply too short to have the maxillary openings), and functional antennal glands are also retained in adults of many eumalacostracan taxa. These may have either both antennal and maxillary excretory openings preserved, or just the antennal openings. Most entomostracan taxa, however, switched completely to retain only the maxillary gland as functional. The exceptions are Cephalocarida (Hessler and Elofsson 1991) and some ostracods, which still retain the plesiomorphic state. Accordingly, this may be regarded as a further, but admittedly weak hint of the entomostracan affinities of *P. siveterae*. Outside the Crustacea, the Chelicerata, Myriapoda and Hexapoda, all have very different locations of their excretory glands, which are incompatible with those of Eucrustacea. Thus, hypotheses of the interrelationships of at least the insects to a particular eucrustacean in-group taxon cannot be validated based on this type of evidence.

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