

FIRST FOSSIL ASELOTTE (ISOPODA: ASELLOTA), FROM THE UPPER TRIASSIC (NORIAN) OF THE CARNIC PREALPS (FRIULI, NORTHEASTERN ITALY)

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ABSTRACT

The first asellote isopod from the fossil record is described here as *Fornicaris calligarisi* Wilson and Selden, n. gen. and sp. The two specimens, both probably males, showing dorsal morphology, come from loose material of the Dolomia di Forni Formation in the bed of the Tagliamento River below the town of Forni di Sotto, Udine Province, Friuli Venezia Giulia Autonomous Region, northeastern Italy. The Dolomia di Forni Formation is Triassic (Norian) in age, and the fossils date from approximately 210-215 Ma. Characters such as narrow, elongate eye stalks, tiny uropods, and enlarged first pereonite (found in terminal males) place the fossil within the Paramunnidae. Parsimony analysis using TNT placed the fossil within the *Austrosignum-Munnogonium* species complex. The robust pereopods with hooked tips, elongate and robust carpus and propodus of pereopod I, axial compression of the pereon, and the large size of the fossils (>2× related extant taxa) are features particular to the fossil genus and species.

KEY WORDS: Dolomia di Forni Formation, Janiroidea, Paramunnidae

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INTRODUCTION

Isopods are common inhabitants of marine, freshwater, and humid terrestrial environments, but not plentiful as fossils. In particular, while fossil isopods are known from numerous suborders (Hessler, 1969; Etter, 2014; Jones et al., 2014; Klompmaker et al., 2014; Broly et al., 2015), until now, no members of the large and diverse suborder Asellota, comprising marine and freshwater forms, have been described from the fossil record. Here, we describe a new genus and species of asellote isopod based on two specimens from the Upper Triassic (Norian) of the Carnic Prealps (Friuli, northeastern Italy).

A cursory examination of these specimens suggested they showed ventral views of the cycloid *Halicynne* von Meyer, 1844, which is not uncommon in the Triassic of Europe (von Meyer, 1847; Trümpfi, 1957; Merki, 1961; Gall and Grauvogel, 1967; Gall, 1971). Even though the ventral appendages of cycloids are poorly preserved, what is known about them is that they have fewer appendages, with fewer podomeres, than the fossil described here, no well-developed anterior grasping appendage. A single, large carapace is always visible (Dzik, 2008). Further investigation proved that the animals from Friuli are isopod crustaceans.

Although isopods appear frequently among Mesozoic strata (Etter, 2014), some groups apparently do not fossilize

well and have been slow to be reported in the literature. The terrestrial isopods described prior to Broly et al. (2015) were known only from Cenozoic facies, although Lins et al. (2012), using molecular dating techniques on modern taxa, asserted that the Oniscidea and other isopod suborders appeared prior to the Mesozoic, perhaps as early as Carboniferous or Late Devonian. The suborder Asellota may fossilize poorly, owing to their thin cuticle, and were currently unreported in the fossil literature, despite Lins et al. (2012) estimating their age in the late Paleozoic. The lack of asellotans in the fossil record is changing, with new fossils known to one of us (GDFW) from the Cenomanian (Cretaceous; N. Morel, pers. comm.) and Early Norian (Late Triassic) strata from Italy (Paolo Schirolli, pers. comm.). This paper is the first report of Asellota from the fossil record, corroborating prior predictions of an early Triassic/late Paleozoic date for the suborder (Wilson, 1999).

Geological Setting

The two specimens described here, MFSN_{gp}44534a-b and MFSN_{gp}44535a-b, were found in debris in the bed of the Tagliamento River, close to the town of Forni di Sotto, Udine Province, Friuli Venezia Giulia Autonomous Region, northeastern Italy (Fig. 1A); they come from two separate slabs, probably close to each other but without any evident stratigraphical and topographical relationship (so

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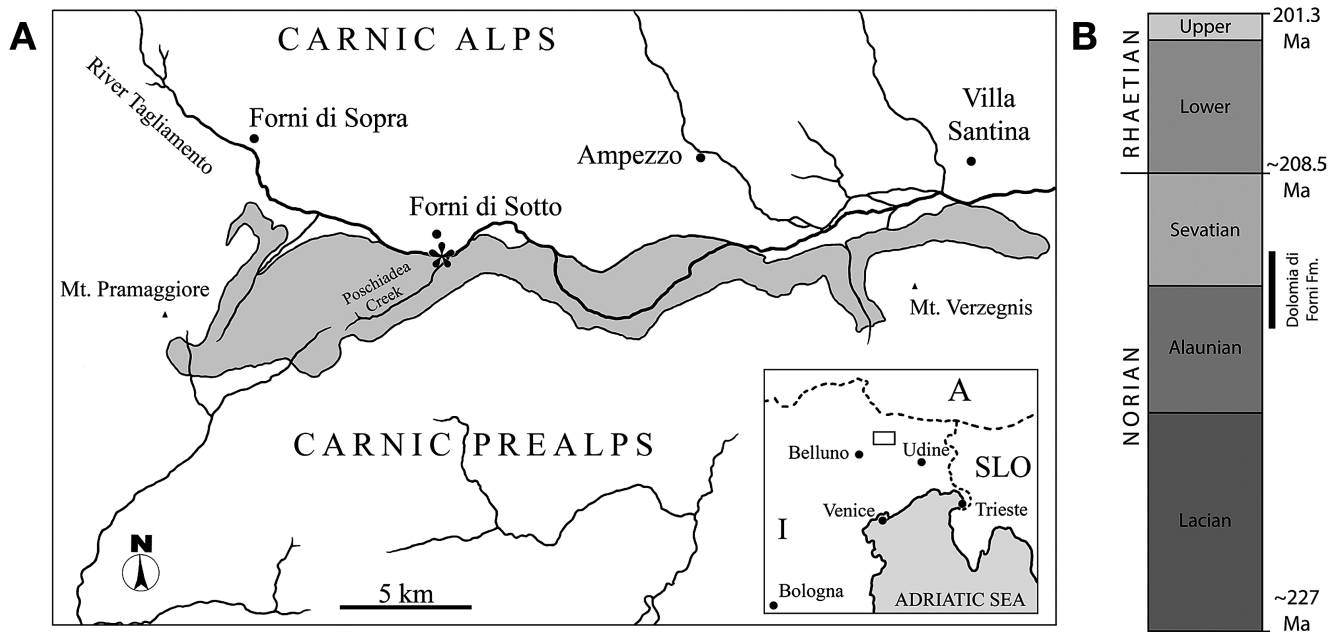


Fig. 1. A, map showing site of the fossil locality (*) in the bed of the Tagliamento River below the village of Forni di Sotto and its location within Italy (inset). B, stratigraphic column showing the position of the Dolomia di Forni Formation within the Norian stage (Upper Triassic).

they possibly come from distinct layers and outcrops). The collector is deceased, so further information is inaccessible.

Upstream from the locality, the Tagliamento River receives tributaries from the Carnic Alps (to the north) and from the Carnic Prealps (to the south). The importance of tributaries and their debris input is higher from the south. Left (north) tributaries of the river mainly cross Early-Middle Triassic and Carnian lithostratigraphic units (Braga et al., 1971; Venturini, 2006), while the Carnian Prealps are locally dominated by the Norian Dolomia di Forni Formation (see Dalla Vecchia and Selden, 2013).

The dark grey to brownish, saccharoid (and laminated) dolostone of the two specimens corresponds with the dominant lithology in the Dolomia di Forni Formation (Mattavelli and Rizzini, 1974; Dalla Vecchia, 2012); dark grey, laminated dolostone is much rarer in the Carnian and Middle Triassic units cropping out along the left bank of the upper Tagliamento valley in the area under examination, and absent in the Lower Triassic (Braga et al., 1971; Venturini, 2006). The lamination of MFSNgp44535a-b resembles the irregular, undulate lamination of stromatolites; Mattavelli and Rizzini (1974) reported the presence of subtidal stromatolite levels in the Dolomia di Forni Formation along Poschiadea Creek, which flows into the Tagliamento River just where the specimens were collected, below Forni di Sotto. Thus, the specimen probably comes from that section of the formation.

The Dolomia di Forni is a sequence of dark grey to black or brown, well-bedded, bituminous dolostone with chert, 700-850 m thick (Carulli et al., 2000, and references therein). It crops out as an east to west band for over 30 km in the Carnic Prealps of the Friuli Venezia Giulia Autonomous Region and is a lateral equivalent of the Dolomia Principale Formation (= Hauptdolomit of German authors). It represents deposition in an anoxic marine basin whose maxi-

mum depth was about 400 m, and was surrounded by the shallow water carbonate platform of the Dolomia Principale Formation (Carulli et al., 1997; Scotti et al., 2002). The basin originated by tensional tectonics at the western end of the Pangean Gulf of Tethys (Gaetani et al., 2000). The age of the Dolomia di Forni Formation is late middle to early late Norian (late Alaunian-early Sevatian), based on its conodont content (Roghi et al., 1995; Moix et al., 2007; Dalla Vecchia, 2012). Since the Norian-Rhaetian boundary falls around 208.5 Ma (International Chronostratigraphic Chart v. 2014/02: Cohen et al., 2013, updated), the specimens described here are somewhat older, possibly 210-215 Ma (Fig. 1B).

Because the specimens were found in loose blocks, their exact provenance is unknown and we cannot report an associated fauna and flora. However, the fossiliferous part of the Dolomia di Forni Formation has yielded a peculiar fossil assemblage composed of arthropods, a polychaete worm, ophiuroids, possible coleoid remains, gastropods, bivalves, several taxa of marine fish (a chondrichthyan, a coelacanthiform crossopterygian, and many osteichthyans), terrestrial tetrapods (including some of the oldest pterosaurs, a protorosaurian, and a drepanosauromorph reptile), and terrestrial plant remains (mainly Coniferales) (see Dalla Vecchia, 2012 for more information).

Arthropods include abundant and diverse decapod crustaceans (*Dusa longipes* (Pinna, 1974), *Acanthochirana triassica* Garassino, Schweigert and Muscio, 2014, *Antrimporus colettoi* Garassino, Schweigert and Muscio, 2014, *A. noricus* Pinna, 1974, *Acanthinopus gibbosus* Pinna, 1974, *Glypheia rigoi* Garassino, 2000, *Glaessnericaris* Garassino and Teruzzi, 1993 sp., *Pseudocoleia mazzolenii* Garassino and Teruzzi, 1993, *Rosenfeldia triassica* Garassino, Teruzzi and Dalla Vecchia, 1996, and *Archaeopalinurus laevis* Pinna, 1974), thylacocephalans (*Microcaris minuta* Pinna, 1974,

Atropicaris rostrata Arduini and Brasca, 1984, and *Clausocaris pinnai* Arduini, 1992), and a spider (*Friularachne rigoi* Dalla Vecchia and Selden, 2013) (Dalla Vecchia and Muscio, 1990; Garassino et al., 1996; Dalla Vecchia, 2012).

MATERIAL AND METHODS

The two specimens, holotype MFSNgp44534a-b and paratype MFSNgp44535a-b, both consisting of part and counterpart, are deposited in the Museo Friulano di Storia Naturale, Udine, Friuli, Italy. MFSNgp44534a-b is the better preserved (Figs. 2, 3) and shows more morphology than MFSNgp44535a-b, which is more of a ghostly outline (Fig. 4) and the more distal parts of which are not preserved. Both specimens show dorsal morphology, on part and counterpart.

The specimens were studied and photographed using a Wild MZ8 stereomicroscope; preliminary pencil drawings were made using a camera lucida attachment on a Wild MZ3 stereomicroscope. Photographs were taken with a Canon EOS 5D Mark III digital camera attached to the MZ8 using DSLR Assistant (<http://www.dslrassistant.com>), and manipulated with Adobe Photoshop on an Apple MacBook Pro computer. Except where stated, photographs were taken under 70% ethanol; when dry, cross-polarized illumination was used. In most cases, sharper focus was achieved by merging a stack of images using Photoshop (see Selden, 2014 for details). Final drawings were made from the photographs and pencil drawings using the open-source vector illustration program Inkscape (inkscape.org) and finished with iDraw (inddeo.com/idraw). All measurements are in mm; \geq indicates an incomplete article and hence a minimum measurement.

Character and measurement data from the photographs were scored into a DELTA taxonomic database (Dallwitz et al., 2000) that was developed by Just and Wilson (2004, 2006, 2007). The database was used to generate the description for the new species, which was edited for clarity in the manuscript. Taxon choice for parsimony analysis: The DELTA database currently contains 126 taxa from the *Paramunna* group, the *Austronanus* group, the *Austrosignum-Munnogonium* complex, and the speciose genus *Pentaceration* (Just and Wilson, 2004, 2006, 2007; Just, 2009). Not all taxa were used: exemplars were chosen from each genus, typically the type species with a few additional species to add to the character range. In addition, three outgroup taxa from the families Santiidae (*Santia*), Xenosellidae (*Xenosella*) and Janiridae (*Austrofilius*) were used. In total, 36 taxa and 136 multistate unordered characters were used for the parsimony analysis. The DELTA directive *tonex* was used to generate a Nexus file, which was read into Mesquite (Maddison and Maddison, 2015). The data were exported to a TNT file, and were analyzed using the following scripted commands in TNT (see Goloboff et al., 2008) “drift: fitd 2 rfitd 0.1; sect:slack 5; xmu = verbose hit 20 drift 10 ratchet 10.” Bremer absolute and relative support were obtained from 9262 trees and from 6554 trees, respectively. The resulting trees and consensus were evaluated and graphics were generated in Mesquite. The tree was edited using Inkscape.

Abbreviations

MFSNgp – Geological and Paleontological Collections of the Museo Friulano di Storia Naturale. Limb segmentation: co – coxa; ba – basis; is – ischium; me – merus; ca – carpus; pr – propodus; da – dactylus.

MORPHOLOGICAL INTERPRETATION

Both specimens reveal dorsal morphology only, with substantial taphonomic flattening, evidenced by the splayed limbs and crushed antennae. The head region is defined by an anterior articulated flap, presumed to be the labrum, and posteriorly is embedded in a large V-shaped, first segment, pereionite 1, from which the robust first leg projects. Laterally the head has thin ocular lobes with 2-3 ocellar lenses at the tip best seen on MFSNgp44534b (Fig. 5A).

The head is assumed to be longer in male than the female, based on modern taxa. Stalked eyes are visible (Fig. 3), with presumed lateral apex rounded. Pereionites 1-2 are fused at the midline, and the articulation is only visible laterally (present in only males in modern species). After the first

pereionite, the divisions of the pereionites are obvious laterally, but the axial part of the segmental boundaries are poorly defined. The segmentation is strongly compressed axially, especially in pereionites 2-4. The pereionite lateral margins vary: 1 angular and projecting, 2-3 centrally concave, 4 rounded, 5 with a rounded anterolateral projection anterior to coxae, and 6-7 are assumed to be linear, but appear concave in the fossil owing to preservational compression. The outline of the pleotelson is most visible on MFSNgp44535a-b (Fig. 4), and is ovoid in outline. Traces of the first pleonite can be seen, at least laterally from the axis of the body. Nine appendages are easily visible, including two antennae. The antennae, presumably antennula and antenna, are preserved as one large and a second smaller proximal podomere, with only traces of the distal flagella and fragments of the other podomeres. The flagellum of the first antenna can just be made out on the left side of MFSNgp44534a (Fig. 4). The antennae do not appear geniculate, although their fragmentary nature makes interpretation difficult. In the antenna, article 2 has an apparently smooth lateral margin: no spines are apparent; article 3 projects anteromedially from article 2; the presence of antennal scales is uncertain; in males of similar modern genera, the antenna is much more robust than female (hence a male fossil is assumed). Of the remaining seven appendages, all presumably pereiopods, the first has a strongly inflated carpus with one or more rows of sharp setae along the anterior edge (Figs. 2, 3). The pereiopod I propodus is not preserved, except as a distal fragment attached to the base of a strongly developed dactyl on the left side of MFSNgp44534a. Because the distal part of the propodus is embedded in the same layer as the proximal part, we infer that the propodus is elongate and curved, being longer than the carpus. The pereiopod I ischium-merus-carpus flexure is recurved (or prehensile); in the more posterior appendages this flexure is procurved. In the posterior six pereiopods, which are all similar, the carpus is not inflated, and the propodus (where preserved) is slender (Fig. 6). A typical peracaridan podomere sequence of coxa, basis, ischium, merus, carpus, propodus and dactyl is visible when preserved (and hence presumed for all) (Fig. 6). On MFSNgp44535a, a thin arc of the pleotelson is preserved, with a discoloration of the matrix projecting from the posterolateral margin. Close inspection of this region reveals that the shadow is two layered and has distal rod-like marks (Fig. 5B); these marks resemble the basal parts of penicillate setae that are common on asellotan uropods. This structure is interpreted as the uropod, with the ventral endopod and a dorsal exopod, found in a group of asellotan families that have the uropod rotated into a vertical plane. No trace of the uropod protopod is present, so the uropod is interpreted to be biramous and lacking the protopod.

The pleonal structures (pleon consisting of a single free pleonite and a large single segment pleotelson) seen in these fossils are present only in janiroidean Asellota, and in particular the munnoid families (Wägele, 1989) that have tiny uropods (Munnidae, Paramunnidae). Of these two families, the enlarged first pereionite and thin, elongate eyestalks are found only among the Paramunnidae. As a result, we classify these fossils in this family.

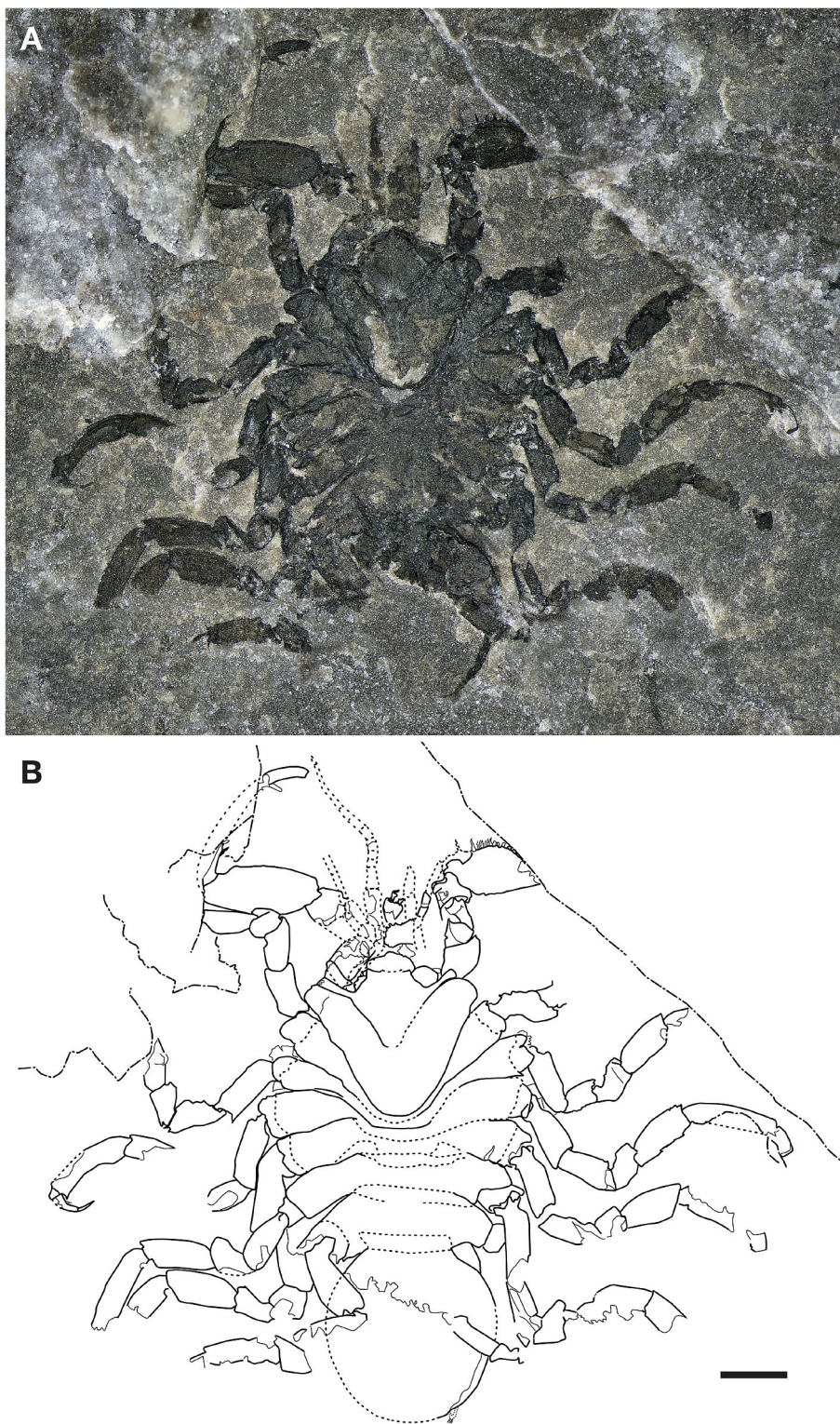


Fig. 2. *Fornicaris calligaris* Wilson and Selden, n. gen. and sp. Holotype MFSNgp44534a, part. A, photograph under ethanol and cross-polarized light. B, interpretative drawing; solid lines = morphology seen in the fossil, fine lines = broken edge of fossil (not corresponding to morphology), dotted lines = interpreted morphology, dash-dot lines = matrix features (cracks, broken edges). Scale bar = 1 mm. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

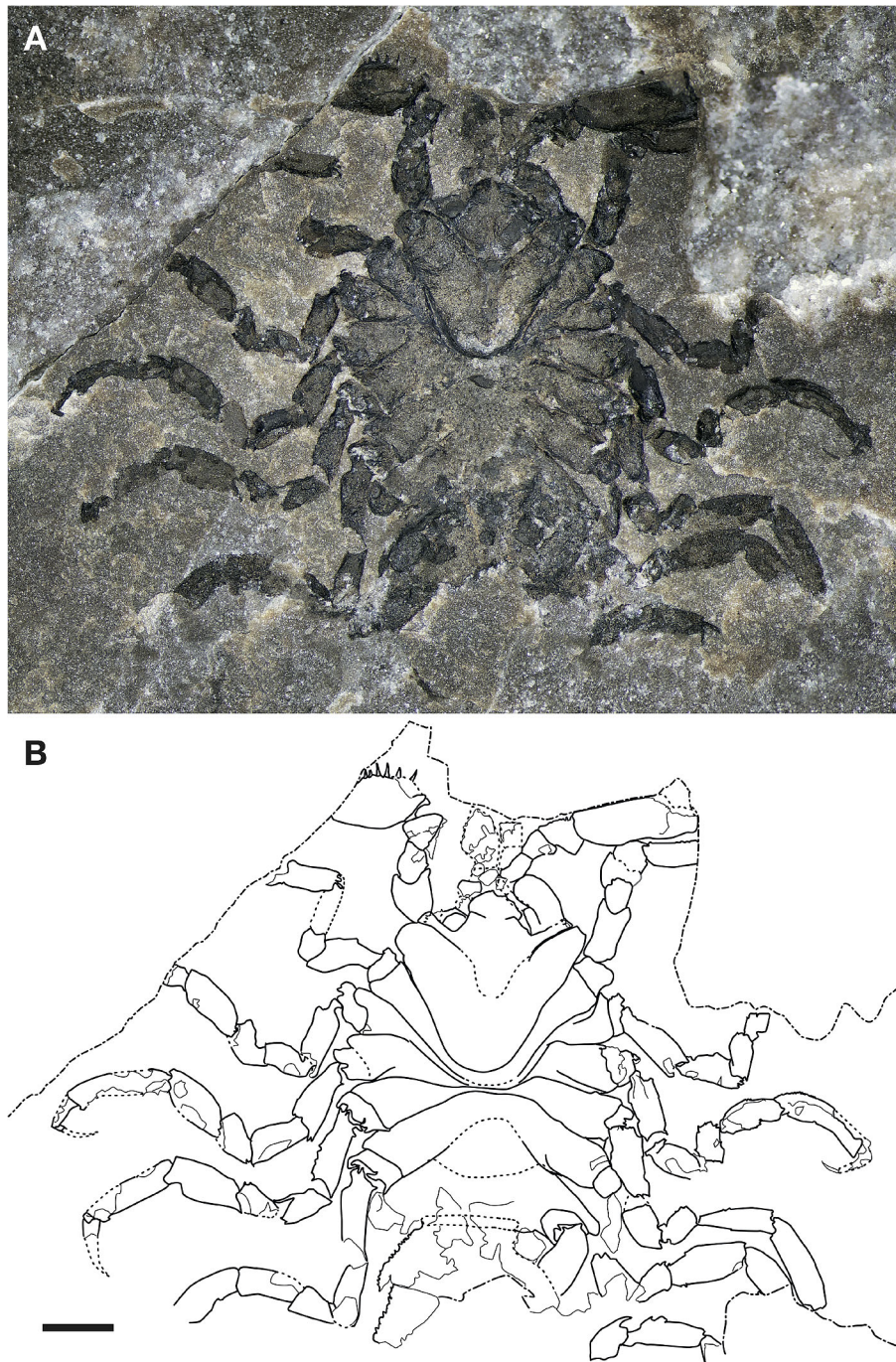


Fig. 3. *Fornicaris calligarisi* Wilson and Selden, n. gen. and sp. Holotype MFSNgp44534b, counterpart. A, photograph under ethanol and cross-polarized light. B, interpretative drawing; solid lines = morphology seen in the fossil, fine lines = broken edge of fossil (not corresponding to morphology), dotted lines = interpreted morphology, dash-dot lines = matrix features (cracks, broken edges). Scale bar = 1 mm. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

SYSTEMATICS

Order Isopoda Latreille, 1817
 Suborder Asellota Latreille, 1802
 Janiroidea Sars, 1897
 Paramunnidae Vanhoeffen, 1914

Diagnosis (revised from Wilson, 1980; see also Kussakin, 1988; characters preserved in the fossil shown in italics).—Janiroidea with *broad ovate body*, often with laterally pro-

jecting tergal plates or coxal processes. *Head often recessed into first pereionite*. Eyes, if present, on lateral projections, eyes and lateral projections often absent. *Pleotelson broad, ovate or shield shaped; pleonite 1 ring-like, narrow, shorter than perionite 7*. Anus covered by opercular pleopods, anal cavity confluent with pleopodal cavity. Antennula short, with six articles, rarely five or seven, with single terminal aesthetasc. Antenna short, never longer than

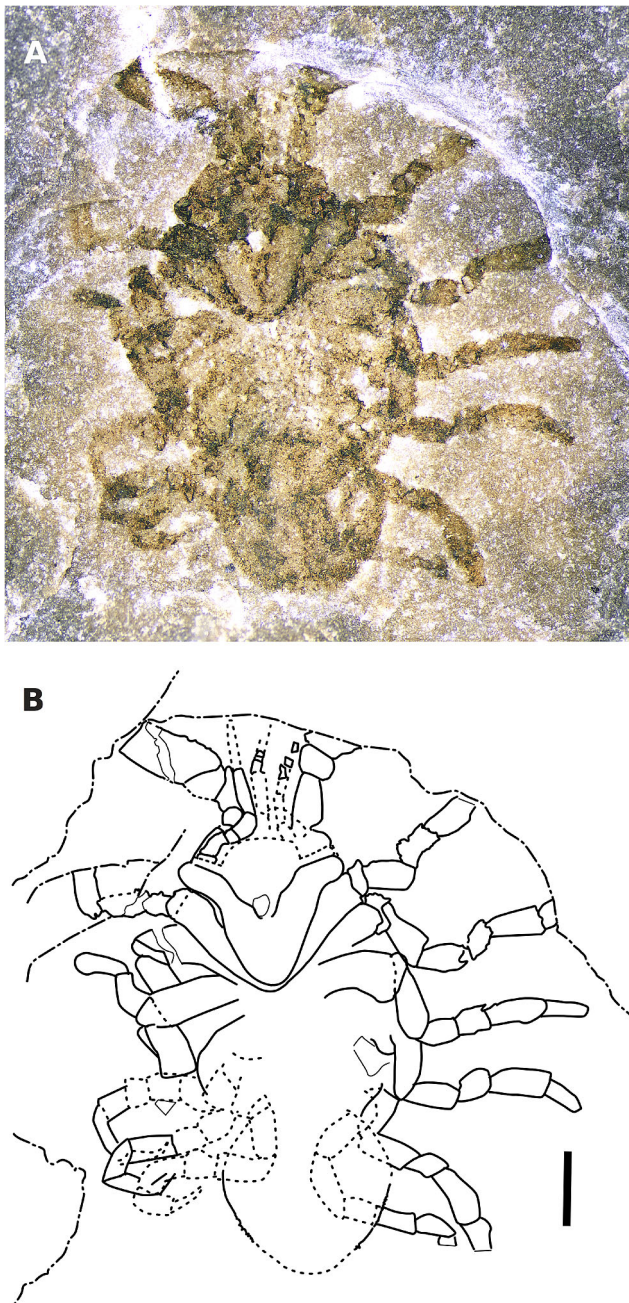


Fig. 4. *Fornicaris calligarisi* Wilson and Selden, n. gen. and sp. Paratype MFSNgp44535a. A, photograph under ethanol and cross-polarized light. B, interpretative drawing; solid lines = morphology seen in the fossil, fine lines = broken edge of fossil (not corresponding to morphology), dotted lines = interpreted morphology, dash-dot lines = matrix features (cracks, broken edges). Scale bar = 1 mm. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

body; with two major bends (geniculations) between article 2-3 medially and articles 3-5 laterally; article 3 elongate (in *Abyssianira*, nearly subequal to other protopodal articles); flagellum typically with seven articles (ranging from 5-15); antennal scale absent or as unarticulated tubercle. Mandible palp never longer than body of mandible or absent, with few setae and cuticular combs. *Pereiopod I* prehensile; remaining *pereiopods* ambulatory. Male pleopod I sagittate distally,

smooth ventrally with tufts of small setae on lateral corners; penile papillae enter pleopodal sperm duct internally. *Uropoda* tiny, biramous or uniramous; if biramous, *exopod* positioned dorsally to *endopod*; protopod present as minute basal joint or absent.

Remarks.—Many characters used to identify Paramunnidae are not preserved in these fossils. The antennae and the male first pleopod, as well as the tiny uropods, are generally diagnostic for this family. Some genera, such as *Abyssianira*, depart from this pattern with an antennal third article that is short and without significant geniculations. In this case, the fragmented antennae and antennulae (Figs. 2-4) provide only a suggestion of their size and configuration. The narrow elongate eye stalks of these fossils, however, are seen in only two families (Paramunnidae and Pleurocopidae). The tiny uropod (Fig. 5B) eliminates from consideration the Pleurocopidae, which has a biramous pleopod with a well developed protopod. Other features place the fossils in a section of Paramunnidae near the genus *Cryosignum* Just and Wilson, 2007 (see phylogenetic section below). The enlarged first pereionite (“shoulders”) found in terminal males (i.e., males in their final instar) is the most immediately recognizable feature. The “shoulders” occur in other genera within the family (e.g., in the type genus and species *Paramunna bilobata*; see Just and Wilson, 2004). In conjunction with the shape of the first pereionite, the eyes of male *Cryosignum* have greatly elongate, narrowed and anterolaterally angled eyestalks relative to the females, similar to the condition seen in these fossils (Fig. 5A; females unknown).

Nevertheless, this fossil differs considerably and, not surprisingly (given the great age), from extant paramunnids. The pereionites are robust and somewhat hook-like distally, and pereiopod I has a carpus and propodus that is substantially more elongate and robust than seen in extant members of this family. The configuration of the pereion is also unusual with substantial axial compression of the pereionites. The fossils are also over twice as large as morphologically similar extant taxa (6-7 mm compared to recent *Cryosignum* that are less than 3 mm long).

Fornicaris Wilson and Selden, n. gen.

Type Species.—*Fornicaris calligarisi* Wilson and Selden, n. sp., here designated.

Etymology.—From the locality, the town of Forni di Sotto, after which the rock strata in which the fossils were found, the Dolomia di Forni, was named; and Latin *caris*: a crab, a common suffix for fossil crustaceans.

Diagnosis.—Head without anterior dorsal projects, frontal margin concave at labrum; eyes stalks much narrower than long, directed anterolaterally to margin of pereionite 1, expanding distally to 2-3 ocelli. Pereion broadly ovate, without dorsal spines or ornamentation; lateral margins lacking spines or plates; adult males (assumed) with robust V-shaped pereionite 1 and highly axially compressed pereionites 2-4; all coxae visible in dorsal view, lacking spines or other projections. Pleonite 1 width greater than length, much narrower than pereionite 7. Pleon ovate, without dorsal or lateral spines or denticles; posterior margin smoothly rounded; uropodal insertions not indented, on posterolateral margin. (Mouthparts unknown.) *Pereiopod I* robust, distally with en-

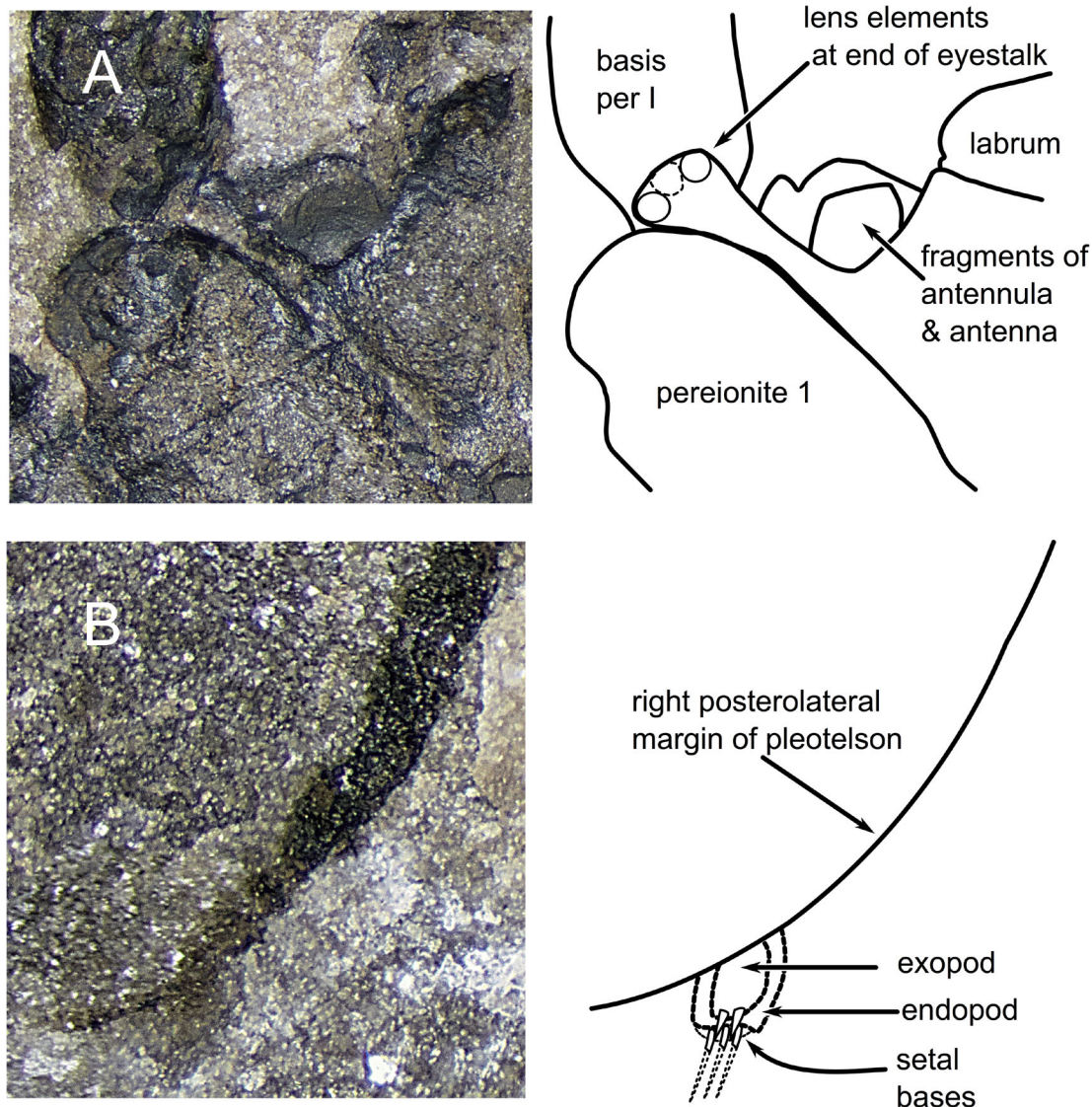


Fig. 5. *Fornicaris calligarisi* Wilson and Selden, n. gen. and sp. Eye and uropod, enlarged detail from holotype MFSNgp 44534, showing specimen on left and interpretation on right. A, left eye from counterpart MFSNgp44534b, with surrounding anatomy of the head and pereopod I. B, uropod from part MFSNgp44534a. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

larged carpus and propodus; carpus ventral margin with multiple robust setae (at least 6); propodus elongate, curved, longer than carpus with ventral row of short robust setae. Pereiopods II-VII shorter than body length, robust with curved dactyli. (Pleopods unknown.) Uropods inserting on posterolateral margin, biramous, protopod absent.

***Fornicaris calligarisi* Wilson and Selden, n. sp.**
Figs. 2-7

Etymology.—In memory of the collector of the specimen, Claudio Calligaris.

Type Fixation.—Holotype MFSNgp44534a-b, here designated.

Material Examined.—Holotype MFSNgp44534a-b, part and counterpart: body length 7.23 mm. *Paratype* MFSNgp 44535a-b, part and counterpart: body length 5.77 mm.

Remarks on Type Material.—MFSNgp44534a-b is preserved on a 4 mm thick layer of thinly laminated, dark grey dolostone at the top or the base (original way up is unknown) of a 25 mm thick, massive, dark grey layer. Measurements in mm: antenna flagellum ≥ 1.52 , basal podomeres 1.75; antennule basal podomeres ≥ 1.42 ; pereopod I ba 0.76, is 0.65, me 0.50, ca 1.80, pr 1.80, da 0.79, total ba-pr 5.47; pereopod II ba 0.79, is 0.73, me 0.43, ca 0.77; pereopod III ba 0.95, is 0.80, me 0.53, ca 1.00; pereopod IV ba 0.95, is 0.80, me 0.58, ca 0.99, pr 1.36, da 0.60, total ba-pr 4.67; pereopod V ba 1.05, is 0.80, me 0.54, ca 1.07, pr 1.38, total ba-pr 4.83; pereopod VI ba 1.08, is 0.92, me 0.59, ca 1.15; pereopod VII is 0.83, me 0.64, ca 0.98.

MFSNgp44534a-b is preserved in dark grey-brownish dolostone with alternating submillimetre, light (thicker) and dark (thinner), slightly undulating laminae. In both specimens, the dolostone has a saccharoidal appearance.

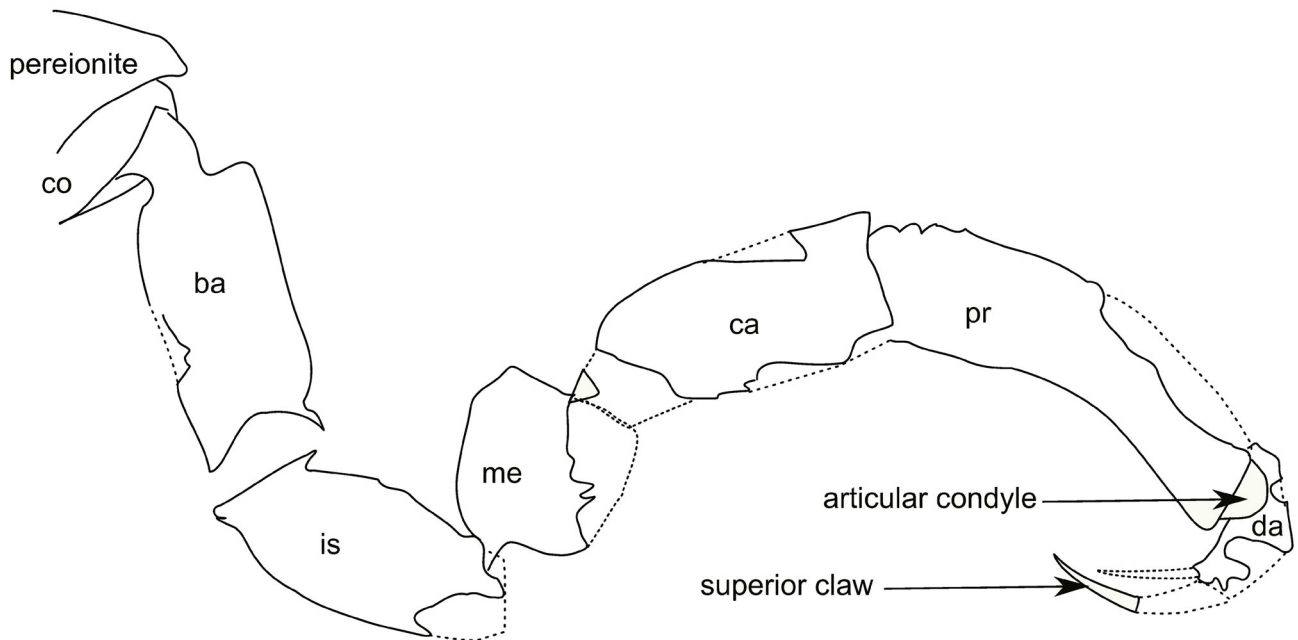
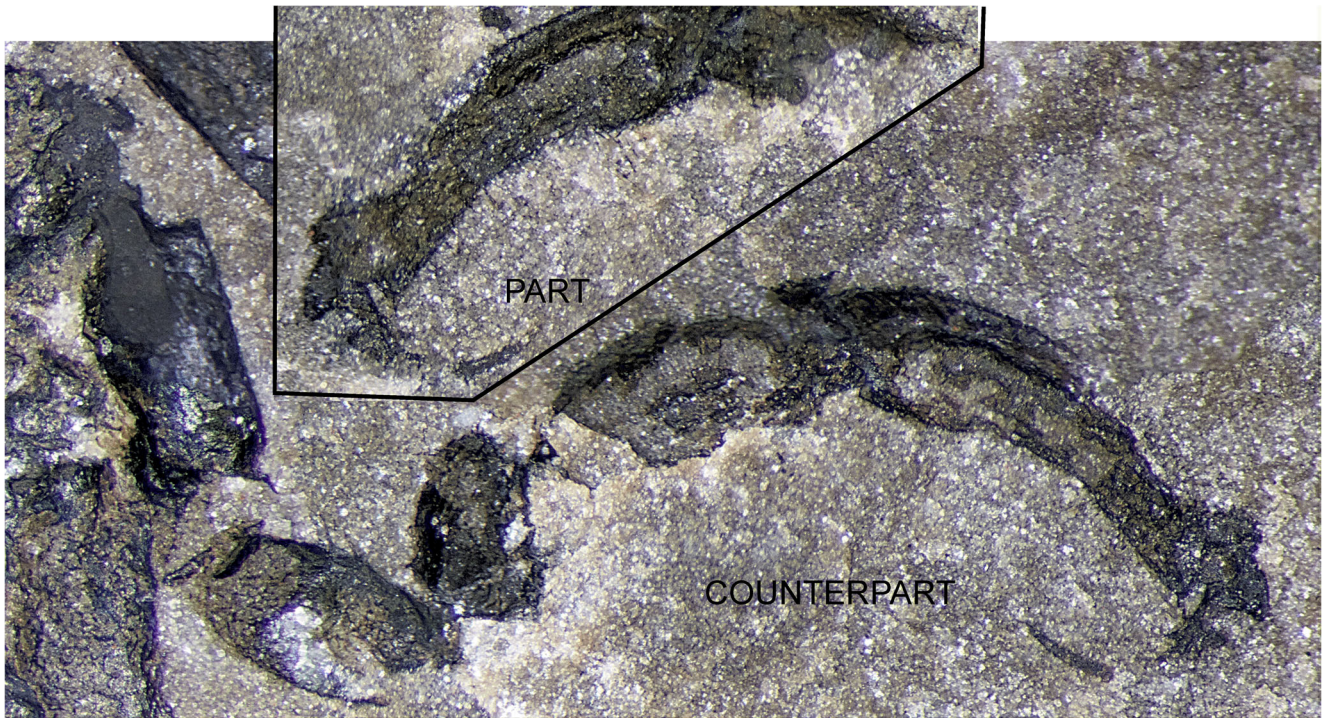


Fig. 6. *Fornicaris calligarisi* Wilson and Selden, n. gen. and sp. Pereiopod IV, enlarged detail from holotype MFSNgp 44534, showing part and counterpart, and interpretation of the limb. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

Measurements in mm: pleotelson length 2.16, width 2.12, ratio 0.98; pereiopod I ba 0.69, is 0.61, me 0.34, ca 1.05; pereiopod II ba 0.55, is 0.47, me 0.24, ca ≥ 0.69 ; pereiopod III ba 0.66, is 0.66, me 0.40, ca ≥ 0.89 ; pereiopod IV ba 0.94, is 0.57, me 0.28, ca 0.85; pereiopod V ba 0.52, is 0.58, me 0.40, ca 0.79.

Description (based mainly on holotype).—Body ovate; width 0.51 length, widest at pereionite 5 (small anterolateral projection on per 5). Head length 0.52 width; length poste-

rior to eyestalks 2.6 anterior length. Frontal margin without projections, with angular lateral margins adjacent to antennae, concave medially; anterodorsal surface smooth, without ornamentation (no spines or tubercles but cuticle with cellular structure); dorsal surface smooth, without projections. Eyes on lobes produced laterally from head. Eyestalks prominent, fixed, length 3.5 width (widest distally), without projection on posterolateral margin, shaft axis axis approximately linear, shaft before apex approximately parallel, long

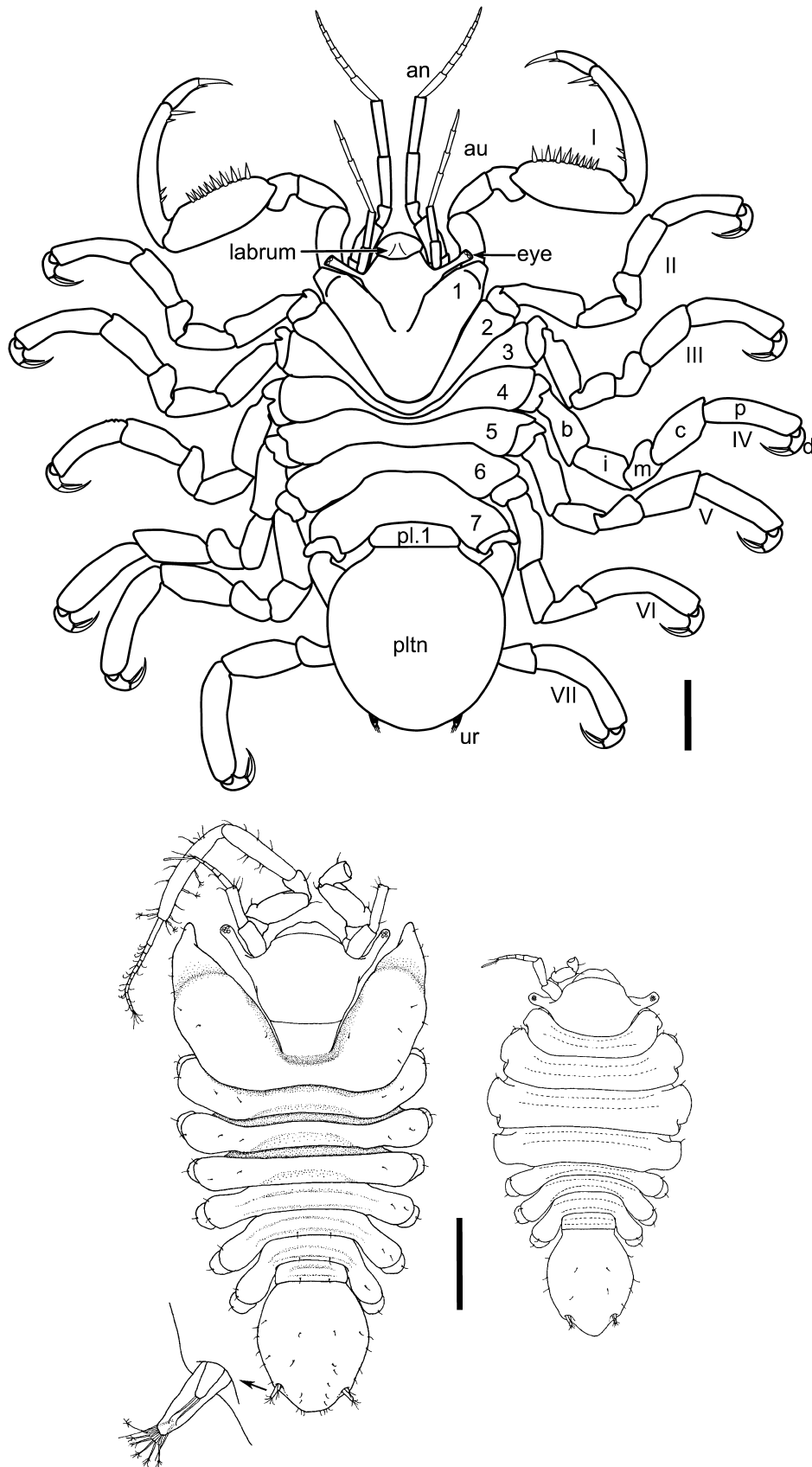


Fig. 7. *Fornicaris calligarisi* Wilson and Selden, n. gen. and sp. Reconstruction (top) based mainly on information from the holotype, with details of pereopod IV and the pleotelson from the paratype; scale bar 1 mm. *Cryosignum lunatum* (Hale, 1937) holotype male and female (bottom), scale bar 0.5 mm.

axis angling forward 25°, margins indistinct in both fossils but show up as changes in matrix surface, ocelli also indistinct but identified by ovoid reflective surfaces. Pereionites 1-2 fused at midline, articulation only visible laterally. Pereionites 1-7 lateral margins not projecting, coxae visible in dorsal view. Pereionites 1-7 dorsal surface smooth, without median projections (no apparent spines or tubercles although cuticle has cellular structure). Pereionite lateral margins: 1 angular and projecting, 2-3 centrally concave, 4 rounded, 5 with rounded anterolateral projection anterior to coxae, 6-7 linear. Pereionite 4 in dorsal view extending to margins of pereionites 3 and 5. Pereionite 5 in dorsal view extending laterally to margins of pereionites 4 or 6. Pereionite lateral margins smooth. Pereionites 5 and 6 proximoposterior margin without denticles. Pereionites medial margins indistinct in fossil but detected as depressions in medial surface; pereionites 2-4 medial margins compressed anteriorly behind strongly posterior projection of pereionite 1.

Pleon length 1.20 width. Pleonite 1 free (medial margins indistinct in matrix), width 1.1 distance between uropods (distance based on assuming bilateral symmetry), length 0.26 width. Pleotelson laterally rounded but lacking inflection between lateral and proximal margins; dorsal surface smooth. Pleotelson lateral margins smooth (hint of denticulation in paratype but not clear). Pleotelson posterior margin evenly curved between uropods and to lateral margin, smooth without denticles, apex broadly rounded (in paratype), without sharp spine-like tip, forming 144° angle from vertex to uropod insertions.

Antennula projecting from head anteriorly (uncertain; may be anterodorsally prior to taphonomic distortion); articles 1-2 combined extending beyond eyestalk apex (longer than eyestalk); article 1 length shorter than 2 (indistinct owing to fragmentation), article 1 not extending beyond pereionite 1 lateral margin, article 1 tubular, article 1 width subequal to 2, article 1 lacking spines; article 2 tubular and rounded distally, distal articles inserting apically, article 2 distal margin difficult to determine, information from darkened places in matrix and several plates; article numbers uncertain.

Antenna article 2 lateral margin smooth, lacking spines, 3 projecting anteromedially from article 2, antennal scale presence uncertain, 4 without spine, 5 approximately tubular, 5 length subequal to article 4; flagellum with at least 9 articles, proximal article distinctly longer than more distal articles, length 2.4 second article length.

Mandible palp not seen.

Pereiopodal coxae I-IV lateral margins rounded, without elongate projections. Pereiopod I coxa with large angular plate fused to pereionite 1; basis anterior margin smooth, length 2.5 width; ischium anterodistal margin smooth, ischium shaft without spines; merus with smooth anterior and posterior margin, posterior margin with no robust setae observed; carpus oval, robust, elongate, multisetulate, distal width 0.41 posterior margin length, posterior margin with 6 robust setae (at least), without crenate ridges absent (or not observed) or denticles; propodus tubular, elongate, without distal spine, with 4 robust setae (possibly more because middle propodus not preserved), smooth; dactylus ventral claw not preserved, dactylus without spines. Pereiopod II basis

anterior margin smooth; ischium posterior margin smooth; dactylus dorsal and ventral claws thin, elongate, dorsal claw longer than dactylus, ventral claw near length of dactylus. Pereiopod V-VII dactylus dorsal and ventral claws similar to those of pereiopod II-IV, coxae extending beyond tergite in dorsal view, lateral margins rounded, without denticles or spines.

Uropods on margin of pleotelson, not covered dorsally with small flap of cuticle or hood. Uropods with two rami; uropod endopod distal margin rounded; insertion assumed to be on margin or perhaps ventrally, uropods show only as discoloration of matrix although putative endopod with multiple linear traces assumed to be setal remnants; protopod if present, not visible.

Size.—Largest male 7.23 mm.

Distribution.—Fossil: Upper Triassic, late middle to early late Norian (late Alaunian-early Sevatian), found in the Carnic Prealps.

DISCUSSION

Phylogeny

A parsimony analysis using TNT (Goloboff et al., 2008) of Paramunnidae type exemplars found two trees that had identical topologies for the in-group taxa (one shown in Fig. 8). Although the Bremer support values are low for all groups (Fig. 8), the analysis at least supports the inference that *Fornicaris calligarisi* belongs within Paramunnidae. In this analysis, character 26 (68) (enlarged male first pereionite) was scored as unmodified for *Fornicaris* because scoring this character as “enlarged” caused instability in the arrangement of the major clades. This observation suggests that enlarged first pereionite might be an ancestral state, so that its current distribution appears highly homoplasious relative to the out-groups. *Fornicaris* was positioned within the *Austrosignum-Munnogonium* complex of species (Just and Wilson, 2007), regardless of how character 26 was scored. *Fornicaris* differed from its putative sister genus *Cryosignum* by 14 unambiguous apomorphies (characters 2, 22, 32, 33, 35, 51, 57, 61, 62, 97, 102, 105, 115, 129; see Appendix), highlighting much divergence in the paramunnid form from Triassic times.

Mode of Life.—Paramunnidae contains marine epibenthic species that can occur on all types of substrates (soft sediments, rocky hard surfaces, or on larger plants or animals), ranging from the intertidal zone to the deep sea (Wilson, 1980). Given the depositional setting of the Dolomia di Forni Formation, an anoxic basin, it is most likely that *Fornicaris calligarisi* lived in relatively shallow water, possibly on the adjacent carbonate platform. Like most Asellota, paramunnids cannot swim, and their pleopods are used for reproduction (in the males) and respiration. They are thought to be detritivores, but some species could also be micropredators that feed on smaller organisms or newly settled larvae. *Fornicaris calligarisi* has enlarged first pereiopods, which could be used for either predating organisms larger than the prey of modern paramunnids or, if the specimens are indeed males, for mating.

Fossil Record.—This is the first asellotan reported from the fossil record, but other studies have inferred the presence of

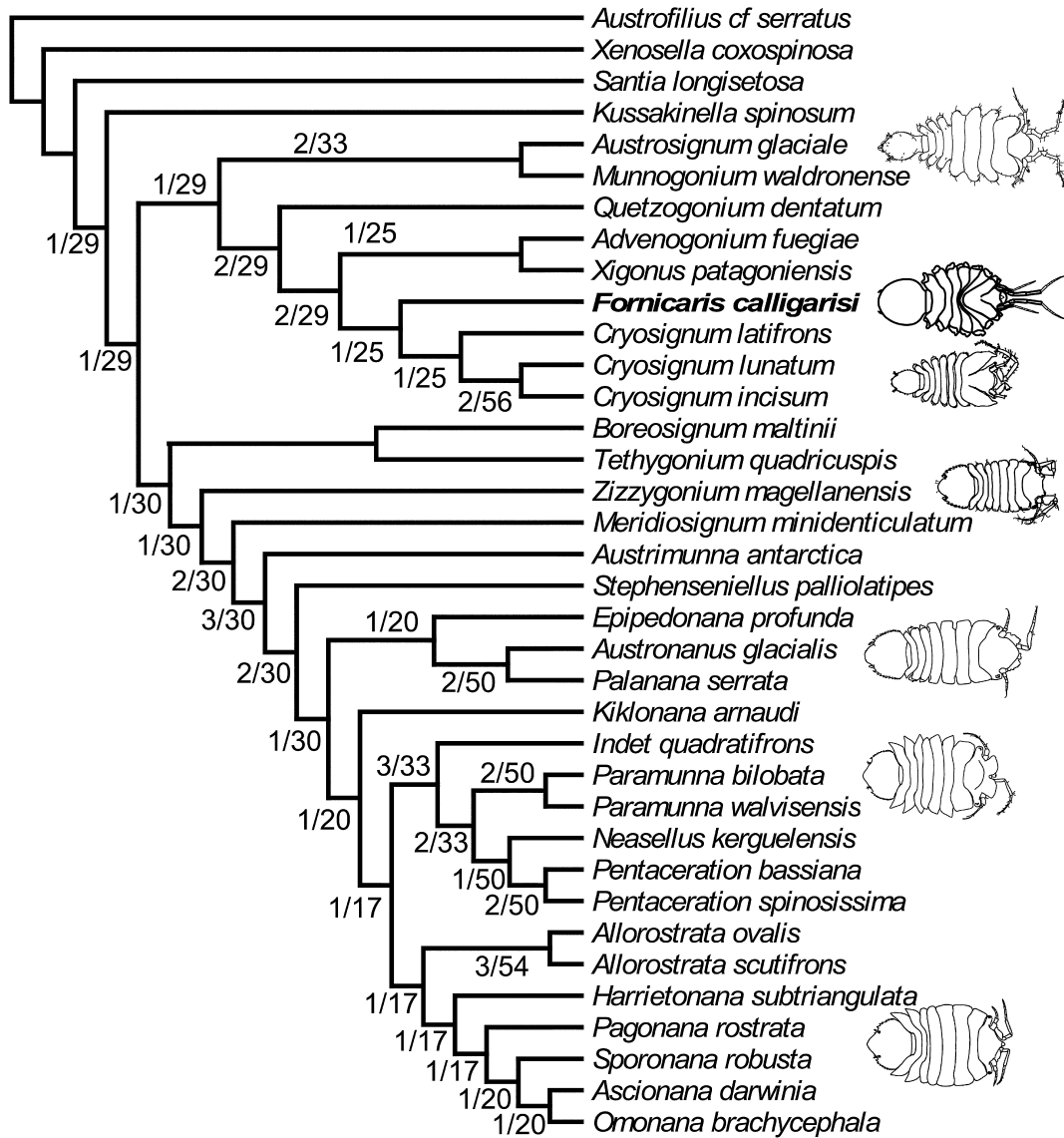


Fig. 8. One of two trees identical for in-group taxa (length 456 steps) resulting from parsimony analysis of Paramunnidae section that contains *Fornicaris calligaris* Wilson and Selden, n. gen. and sp. Each clade is marked with Bremer absolute/relative support values. Example images of Paramunnidae are right of the relevant species name.

Asellota before or during the Permo-Triassic (Wilson, 1999; Lins et al., 2012). That the fossils described here belong to Paramunnidae is significant; unpublished results on the phylogeny of Janiroidea (a subset of which was published in Riehl et al., 2014) found that Paramunnidae occurs distal in the tree to most other families. If this is the case, then fossils of Asellota should be sought in the Carboniferous and Permian, similar to their possible sister group, the Phreatoicoidea (Schram, 1970; Wilson, 2009), which has a growing fossil record (Fu et al., 2010; Etter, 2014).

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Appendix. Description of characters.

Character no.	Description
1(21)	Head (sexual dimorphism); 1. not sexually dimorphic, male head length similar to that of females and juveniles; 2. longer in male than female; 3. shorter in male than female; 4. sexually dimorphic in the shape of the anterior margin, not in the size of the head.
2(26)	(Head) frontal margin (with projection or not); 1. with projection; 2. without projections.
3(27)	(Head) frontal margin (if lacking any frontal projections); 1. without angular lateral margins adjacent to antennae; 2. with angular lateral margins adjacent to antennae.
4(28)	(Head) frontal margin (form, taxa lacking large projections only); 1. broadly rounded (e.g., <i>armaudi</i>); 2. shallow convex, almost straight medially (e.g., simplex), or nearly straight laterally (e.g., <i>antarctica</i>), or concave laterally (e.g., <i>serraticoxa</i>); 3. concave medially (e.g., <i>dentatum</i>).
5(29)	(Head) frontal margin (form, if with projection); 1. with 2 dorsolaterally projecting lobes (e.g., <i>Paramunna bilobata</i>); 2. with one broad anterior lobe, with thick lateral corners (e.g., gen. <i>Incertae sedis</i> ; <i>quadratifrons</i>); 3. with rounded flat anterior projection (e.g., <i>Ascionana bassiana</i>); 4. dorsally upcurving anteriorly, without lateral corners but indented at antennular insertion (e.g., <i>Austrimuna serrata</i> "boathed"); 5. with short blunt median projection (e.g., <i>rostrata</i> or <i>subtriangulata</i>); 6. with broadly rounded narrow rim, lacking lateral corners; 7. weakly convex anteriorly, upcurved with rounded lateral corners; 8. with single middle spine projecting anteriorly and two lateral spines (e.g., <i>Pentaceration</i>); 9. with two lateral spines (e.g., <i>Compoceration</i>).
6(30)	(Head) frontal margin (shape of mid and lateral spines, only for <i>Pentaceration</i> spp.); 1. all spines straight and slender; 2. middle spine straight, lateral ones curved backwards, distally up-curved (e.g., <i>P. curvicornis</i>); 3. mid-spine short pointed triangle, lateral spines long, broad pointed; forward curved (e.g., <i>P. bovicornis</i>); 4. mid spine straight, lateral ones slightly inward-upward curve in distal half (e.g., <i>Pentaceration spinosissima</i>); 5. mid spine straight, lateral ones slightly sinuous; 6. all spines straight and triangular with broad base; 7. all spines with broad base, mid spine straight, lateral ones slightly forward-inward curving; 8. all spines straight and slender, with bifid apex.
7(31)	(Head) frontal margin (relative sizes of mid and lateral spines; <i>Pentaceration</i> spp. only); 1. all spines subequal in size; 2. lateral spines slightly longer and broader than mid spine; 3. lateral spines slightly longer than mid spines; 4. lateral spines clearly longer and broader than mid spine.
8(33)	(Head) above frontal margin (species with anterolateral spines only; <i>Compoceration</i> character); 1. with globose reticulate spine above anterolateral spines (e.g., <i>Compoceration</i>); 2. without globose spine.
9(34)	(Head) frontal margin (taxa with anterodorsally projecting lobes, shape; in dorsal view, all others absent); 1. with 2 dorsolaterally projecting rounded lobes (e.g., <i>capensis</i>); 2. with 2 dorsolaterally projecting quadrate lobes (e.g., <i>bilobata</i>); 3. with 2 dorsolaterally projecting spine-like lobes (e.g., <i>quadricornis</i>); 4. with 2 dorsolaterally projecting conical lobes (e.g., <i>minituberculata</i>); 5. without 2 dorsolaterally projecting lobes.
10(35)	(Head) frontal margin (only taxa with anterodorsally projecting lobes; shape in lateral view); 1. anterior rim dorsoventrally thin in lateral view (anterior projection; length greater than or subequal to thickness); 2. anterior rim dorsoventrally thick in lateral view (anterior projection; length less than thickness).
11(36)	(Head) frontal margin (lobe projection size, only taxa with anterodorsally projecting lobes); 1. prominent, each lobe projecting well beyond anterior apex; 2. low, each lobe not projecting significantly beyond anterior apex.
12(37)	(Head) frontal margin (lobe ornamentation, only taxa with anterodorsally projecting lobes); 1. with thin anterior flange; 2. with small denticles; 3. with denticles; 4. without projecting ornamentation.
13(38)	(Head) frontal margin (ornamentation of the spines, only for species with middle and lateral spines, <i>Pentaceration</i> spp.); 1. with denticles; 2. irregularly denticulate; 3. smooth; 4. smooth with many small marginal setae.
14(48)	(Head) anterodorsal surface (ornamentation); 1. smooth, without ornamentation (most Paramunnidae); 2. with low median bilobed hump (e.g., <i>orientale</i> Shimomura and Mawatari).
15(49)	(Head) dorsal surface (ornamentation); 1. smooth, without projections; 2. with bilateral pair of low broad subconical lobes or convexities; (e.g., <i>A. escandellae</i>).
16(50)	Eyes (configuration); 1. sessile on dorsolateral surface of head (plesiomorphic condition); 2. on lobes produced laterally from head (Paramunnidae condition); 3. absent, without structures in eye region.
17(51)	Eyestalks (approximate length); 1. prominent (projecting to or beyond antennular article 1, but not projecting beyond pereonite 1); 2. elongate (projecting beyond pereonite 1); 3. vestigial (length approximating width, partially covered by base of antennula; e.g., <i>Munnogonium waldronense</i>); 4. short (shorter than antennular article 1, not reaching pereonite 1 lateral margin; e.g., <i>multiniitii</i>).

Character no.	Description
18(54)	Eyestalks (in male, projection on posterolateral margin); 1. of male without projection on posterolateral margin (normally rounded); 2. of male with projection on posterolateral margin (e.g., <i>A. bassiana</i>).
19(56)	Eyestalks (in female, projection on posteroventral margin); 1. of female without projection on posterolateral margin (normally rounded); 2. (of female with projection on posterolateral margin).
20(58)	Eyestalks lateral apex (shape); 1. rounded; 2. rounded with tiny protruding point; 3. rounded with few denticles; 4. rounded distally micro denticulate; 5. tapering, distally rounded; 6. tapering to pointed apex; 7. somewhat flattened; 8. pointed, spine-like; 9. blunt with few denticles.
21(59)	Eyestalks shaft axis (shape); 1. axis approximately linear; 2. curving posteriorly (e.g., <i>Stephenseiellus serraticornis</i>); 3. curving anteriorly; 4. sinuous (e.g., <i>Notoxenoides</i>); 5. curved backwards in distal half (e.g., <i>Neasellus argentinensis</i>).
22(60)	Eyestalks shaft before apex (approximate shape); 1. approximately parallel (many species); 2. constricted proximally; 3. somewhat inflated midlength, margins convex; 4. tapering laterally from broad base (e.g., <i>fuegtae</i>); 5. rounded bump (basically lacking sides; e.g., <i>Mummogonium</i> species).
23(64)	Pereonites 1-2 (articulation between these two pereonites); 1. completed articulated (most paramunids); 2. fused at midline, articulation only visible laterally (e.g., <i>Neasellus</i> spp.).
24(65)	Pereonites 1-4 lateral margins (lateral projection); 1. not projecting, coxae visible in dorsal view; 2. not projecting, coxae not visible in dorsal view; 3. distinctly projecting, coxae not visible in dorsal view; 4. pereonite 1 not projecting, pereonites 2-4 projecting in acute lateral spine, coxae not visible in dorsal view; 5. pereonites 1 and 4 not projecting, pereonites 2 and 3 projecting in acute lateral spine, coxae not visible in dorsal view; 6. pereonite 1 not projecting, pereonites 2-3 projecting in acute lateral spine, pereonite 4 with tiny lateral mid-point, coxae not visible in dorsal view; 7. pereonite 1 not projecting, pereonites 2-3 projecting in triangular spine with broad base, acutely pointed, pereonite 4 projecting in much smaller spine, coxae not visible in dorsal view; 8. pereonite 1 not projecting, pereonite 2-3 projecting in triangular spine with broad base, acutely pointed, pereonite 4 with tiny lateral mid-point, coxae not visible in dorsal view; 9. pereonites 1-3 projecting, pereonite 4 laterally rounded, not projecting; coxae not visible in dorsal view.
25(66)	Pereonites 5-7 lateral margins (projecting and coxae); 1. not projecting, coxae visible in dorsal view; 2. not projecting, coxae not visible in dorsal view; 3. distinctly projecting, coxae not visible in dorsal view; 4. pereonite 5 and 6 distinctly projecting, pereonite 7 slightly projecting, coxae not visible in dorsal view; 5. pereonites 5 and 6 distinctly projecting, pereonite 7 subrectangular (e.g., <i>Pentaceration megalomos</i>); 6. pereonites 5 and 6 distinctly projecting, pereonite 7 rounded (e.g., <i>Paramunna denticulata</i>); 7. projecting in triangular spine with broad base, acutely pointed coxae not visible in dorsal view; 8. projecting in triangular spine with broad base, acutely pointed projection of pereonite 7 much smaller than those of pereonites 5 and 6, coxae not visible in dorsal view; 9. with angular projection, coxae visible in dorsal view posterior to projection (e.g., <i>Meridiosignum undulatum</i>).
26(68)	Pereonite 1 of terminal male (sexual dimorphism in "shoulders"); 1. only slightly enlarged compared to adult females or juveniles; 2. greatly enlarged (lateral margin more than 1.5 that of female).
27(71)	Pereonites 1-4 dorsal surface (ornamentation - ridges); 1. smooth; 2. with transverse medially rounded depressions (pereonites 2-4 only); (e.g., <i>Ascionana notaedorsalis</i>); 3. with transverse ridges (e.g., <i>lanatum</i>).
28(72)	Pereonites 1-4 dorsal surface (ornamentation - median spines); 1. without median projections; 2. each with broad conical median spine (<i>spinotum</i> Kussakin, 1982); 3. each with single middorsal slender upright spine; 4. each with three dorsal slender spines, one on midline and projecting, two on each side of the middorsal spine (e.g., <i>Pentaceration bifficlyro</i>).
29(73)	Pereonites 1-4 dorsal surface (if with ornamentation - median spines); 1. with broad conical median spine (<i>spinotum</i> Kussakin, 1982); 2. elongate.
30(74)	Pereonites 1-4 lateral margins (single elongate seta presence); 1. without single elongate seta (most species); 2. with single elongate seta (e.g., <i>polynesienis</i> Mueller).
31(75)	Pereonites 5-7 dorsal surface (ornamentation - ridges and spines); 1. smooth; 2. with transverse ridges (e.g., <i>lanatum</i> Hale); 3. with median transverse spine-like ridges (e.g., <i>spinotum</i> Kussakin).
32(76)	Pereonites 5-7 dorsal surface (if with ornamentation - median spines); 1. without median projections; 2. with single broad conical median spines on pereonites 5-6 and two spines on pereonite 7 (e.g., <i>spinotum</i> Kussakin, 1982); 3. with single broad conical median spines on pereonites 5-6, smooth on pereonite 7 (e.g., <i>Pentaceration kermadecia</i>); 4. with single middorsal slender upright spine; 5. each with three dorsal slender spines, one on midline and two on each side of middorsal spine (e.g., <i>Pentaceration bifficlyro</i>).

Character no.	Description
33(77)	Pereonite lateral margin 1 (lateral margin shape); 1. rounded (e.g., bilobata males); 2. rounded with short pointed mid spine; 3. rounded with lateral denticles of varying size; 4. rounded widening posteriorly; 5. linear (e.g., bilobata – linear margin, corners may be rounded); 6. concave distally, convex proximally (e.g., <i>Pentacercation rithothalassa</i>); 7. angular and projecting (e.g., <i>polynesiensis</i> Mueller); 8. projecting as rounded spatulate process (e.g., <i>Neaselius</i> spp.); 9. with spine (e.g., <i>Pentacercation lancifera</i>).
34(78)	Pereonite lateral margin 2-3 (shape); 1. rounded; 2. linear (linear margin, corners may be rounded); 3. angular and projecting (e.g., <i>walvisensis</i>); 4. projecting as a rounded spatulate process (e.g., <i>Neaselius</i> spp.); 5. with spines; 6. centrally concave (e.g., <i>kerquelenensis</i>); 7. rounded, with small posteriorly projecting lobes (e.g., <i>latifrons</i>).
35(79)	Pereonite lateral margin 4 (margin shape); 1. rounded; 2. linear (linear margin, corners may be rounded); 3. angular (e.g., <i>walvisensis</i>); 4. with spine (e.g., <i>Pentacercation</i>); 5. with short spine; 6. with tiny spine (e.g., <i>Pentacercation denticornis</i>); 7. with anterior lobe followed by small concavity (e.g., <i>kerquelenensis</i>).
36(80)	Pereonite lateral margin 5 (shape); 1. rounded; 2. linear (linear margin, corners may be rounded); 3. with rounded anterolateral projection anterior to coxae; 4. angular but not projecting over coxae (e.g., <i>Stephenseniellus</i>); 5. with spine (e.g., <i>Pentacercation</i>); 6. angular and projecting over coxae; 7. projecting as long spatulate process, rounded distally (e.g., <i>Neaselius</i> spp.).
37(81)	Pereonite lateral margin 6-7 (shape); 1. rounded (e.g., <i>magnetica</i>), or linear (e.g., <i>notaadorsalis</i>); 2. angular and projecting (e.g., <i>Paramunna bilobata</i> , <i>P. walvisensis</i>); 3. angular but not projecting over coxae (e.g., <i>Stephenseniellus</i>); 4. with spine (e.g., <i>Pentacercation</i>); 5. with spine, that of pereonite 6 much larger than spine on pereonite 7 (e.g., <i>Pentacercation dentifera</i>); 6. with spine and subrectangular shape respectively; 7. rounded and angular, respectively; 8. pereonite 6 projecting as long spatulate process, rounded distally, pereonite 7 slightly projecting (e.g., <i>Neaselius</i> spp.); 9. pereonite 6 projecting as long spatulate process, pereonite 7 rounded (e.g., <i>Paramunna denticulata</i>).
38(82)	Pereonite lateral margin 6-7 (tumaculum presence); 1. tumaculum in pocket on anterolateral margin (e.g., <i>Pentacercation bassiana</i>); 2. without tumaculum.
39(83)	Pereonite 4 in dorsal view (recessed or not); 1. extending to margins of pereonites 3 and 5; 2. recessed from lateral margin of pereonites 3 and 5 (e.g., <i>Pentacercation</i>).
40(84)	Pereonite 5 in dorsal view (constricted or not); 1. extending laterally to margins of pereonites 4 or 6; 2. distinctly narrower than pereonites 4 and 6; 3. distinctly broader than pereonites 4 and 6.
41(85)	Pereonite lateral margins (presence of small robust setae, not fine; setae); 1. without robust setae; 2. with robust setae on pereonites 5-7 only (e.g., <i>Stephenseniellus</i>).
42(86)	Pereonite lateral margins (smooth or denticulate); 1. smooth; 2. denticulate on at least some segments; 3. irregularly denticulate; 4. weakly denticulate; 5. smooth but with slightly rough cuticle (e.g., <i>Pentacercation omalos</i>).
43(88)	Pereonite lateral margins (5 denticulation); 1. 5 smooth; 2. 5 finely denticulate (sometimes broken off in poor specimens); 3. 5 denticulate; 4. irregularly denticulate; 5. weakly denticulate; 6. denticulate on anterior margin; 7. 5 with spinous denticles on posterolateral margin (e.g., <i>quadratifrons</i>); 8. 5 with thin microdenticulate marginal flanges (e.g., <i>Pentacercation bovicornis</i>).
44(89)	Pereonites 5 and 6 proximoposterior margin; 1. with 1 strong denticle (e.g., <i>Pentacercation curvicornis</i>); 2. with lobe; 3. without denticles.
45(90)	Pereonite lateral margins (6-7 denticulation); 1. 6-7 smooth; 2. 6-7 finely denticulate (sometimes broken off in poor specimens); 3. 6-7 denticulate; 4. irregularly denticulate; 5. weakly denticulate; 6. 6-7 with thin microdenticulate marginal flanges (e.g., <i>Pentacercation bovicornis</i>); 7. 6-7 with spinous denticles on posterolateral margin (e.g., <i>quadratifrons</i>); 8. 6 smooth, 7 with denticles on posterolateral margin only; 9. 6 denticulate, 7 smooth.
46(91)	Pereonites 6 and 7 proximoanterior margin; 1. without lobe; 2. with lobe.
47(95)	Pleonite 1 (free pleonite?); 1. free; 2. fused to pleotelson (observations from specimens only).
48(98)	Pleotelson (lateral shape); 1. laterally rounded but with inflection between proximal and lateral margins (<i>Paramunna</i> group taxa); 2. laterally rounded but lacking inflection between lateral and proximal margins (<i>Austrosignum-Munnogonium</i> group taxa); 3. laterally produced, inflection near middle of lateral margin; 4. rounded anteriorly, tapering posteriorly; 5. laterally angular anteriorly, straight sided (e.g., <i>Paramunna walvisensis</i>); 6. with short proximal neck, proximal and lateral margins evenly merging lateral margins nearly straight, diverging distally; 7. with short proximal neck, lateral margin nearly straight, with inflection between proximal and lateral margins; 8. with distinct neck, proximal and lateral margins forming evenly merging curve; 9. with 2 antero-lateral processes curved backwards, lateral margins concave (e.g., <i>Pentacercation pleonartetus</i>).
49(99)	Pleotelson dorsal surface; 1. with several short spines (e.g., <i>P. spinosissima</i>); 2. with 1 single conical spine at neck level (e.g., <i>P. bassiana</i>); 3. with 1 single conical spine on proximal third; 4. smooth; 5. with two dorso-lateral ridges, composed by two rows of denticles each (e.g., <i>Paramunna denticulata</i>).

Character no.	Description
50(100)	Pleotelson proximal margin length (compared to lateral margin length); 1. subequal to lateral margin length (within 5%); 2. shorter than lateral margin length; 3. longer than lateral margin length.
51(104)	Pleotelson lateral margins (position of denticulation); 1. denticulate; 2. denticulate only level with uropods; 3. smooth.
52(107)	Pleotelson posterior margin (general shape); 1. produced (forming rounded angle posteriorly); 2. evenly curved between uropods (e.g., <i>profunda</i>).
53(108)	Pleotelson posterior margin apex (general shape); 1. broadly rounded (typical for many paramunnids); 2. narrowly rounded (rounded just at tip); 3. pointed (may or may not have projecting spine in this position; e.g., <i>Austrosignum</i>); 4. broadly rounded with notch at midline (e.g., <i>Neasellus</i> spp.).
54(109)	Pleotelson posterior margin (apex spine-like or not); 1. without sharp spine-like tip; 2. with sharp spine-like distal tip (e.g., <i>spinotum</i> Kussakin); 3. with elongate spine (e.g., many <i>Pentaceration</i> species – need chars to; describe shape and length).
55(113)	Pleotelson posterior margin (continuation of lateral margin); 1. evenly curving into lateral margin (e.g., <i>bassiana</i>); 2. set apart from lateral margins by concavity at level of uropods (e.g., <i>bilobata</i>).
56(114)	Pleotelson posterior margin (denticle presence); 1. smooth (e.g., <i>Paramunna bilobata</i>); 2. with single denticle each side; 3. with large denticles laterally all of approximately same size (e.g., <i>Epidonana profunda</i>); 4. with large denticles on entire margin all of approximately same size; (e.g., <i>quadrafrons</i>); 5. with denticles on entire margin all of approximately same size, plus 2 large diverging denticles at midlength of posterior margin (e.g., <i>Paramunna denticulata</i>); 6. with fine denticles laterally, grading to smaller denticles posteriorly, none on posterior apex (denticles smaller than lateral denticles, e.g., <i>Palanana serrata</i>); 7. with few denticles laterally, none on posterior apex (e.g., <i>Pentaceration pleonarietis</i>); 8. with large denticles laterally all of approximately same size, none on distal notch (e.g., <i>Neasellus</i> spp.); 9. with uniformly fine denticles laterally (denticles small compared to size of uropod, or lateral margin denticles); 10. irregularly denticulate; 11. smooth but with slightly rough cuticle.
57(116)	Pleotelson posterior margin fringing setae (projecting or not around margin); 1. short, not projecting substantially at pleotelson tip; 2. elongate at pleotelson tip, row projecting well beyond terminal margin.
58(117)	Antennula projecting from head (direction); 1. anteriorly (plesiomorphic); 2. anterodorsally (e.g., <i>Santia</i> , <i>Xenosella</i>); 3. laterally (Paramunnidae).
59(118)	Antennula with (total number of articles; add states as necessary); 1. 5 articles (e.g., <i>Austronanus aucklandensis</i> ; <i>Stephenseiellus</i>); 2. 6 articles (e.g., most Paramunnidae); 3. 7 articles (rare?).
60(120)	Antennula article 1 length (compared to article 2); 1. subequal to 2 (within 5%; many taxa); 2. longer than 2 (e.g., <i>Harrietonana subtriangulata</i>); 3. shorter than 2 (e.g., <i>quadrafrons</i>).
61(121)	Antennula article 1 (length compared to eyestalks and pereonite 1); 1. not extending beyond pereonite 1 lateral margin (length shorter or subequal to eyestalk); 2. reaching to or extending beyond pereonite 1 lateral margin (length longer than twice eyestalk length; e.g., <i>multini</i> Schiecke and Fresi, 1972).
62(122)	Antennula article 1 (general shape, inflated or tubular); 1. tubular; 2. inflated; 3. basally flattened, curving ventrally.
63(123)	Antennula article 1 (general shape, width compared to article 2); 1. width subequal to 2; 2. broader than 2.
64(124)	Antennula article 1 (types of spines present); 1. with distomedial spines; 2. with 2 small denticles distomedially; 3. with midmedial spine; 4. lacking spines; 5. with distolateral spines (outgroups?).
65(125)	Antennula article 2 (distoventral projection present?); 1. with distoventral projection, distal articles inserting dorsally; 2. tubular and rounded distally, distal articles inserting apically.
66(127)	Antennula (distal articles); 1. with 6 articles, articles 5 and 6 with distinct articulation (e.g., most Paramunnidae); 2. with 5 articles, articulation between articles 5 and 6 absent, distal; article 5 distinctly longer than articles 3 or 4; 3. (with more than 6 articles).
67(129)	Antennula articles (comparative lengths of taxa with 6 articles in; antennula only); 1. 5-6 of subequal length, longer than article 3, article 4 slightly shorter than 3 (long short longest longest); 2. 5-6 of subequal length, longer than articles 3-4 (short short long long); 3. 4-6 of subequal length, all longer than article 3 (short long long long); 4. 3-6 all subequal length (short short short short); 5. 4-5 of subequal length, shorter than articles 3 and 6 (long short; short long); 6. 4-5 of subequal length, shorter than articles 3 but longer than 6; (long, short, short, shortest); 7. 4 and 6 shorter than articles 3 and 5 (long short long long); 8. 4-6 of subequal length, all shorter than 3 (long short short short; e.g., <i>robusta</i>); 9. 3 and 5-6 of subequal length, longer than article 4 (long short long long); 10. 3-4 short and subequal in length, 5 longest, 6 somewhat shorter than 5 but longer than 3-4; 11. 3-4 subequal in length, shorter than 5, article 6 the longest (short short long longest); 12. 5 longest, 3 4 6 subequal (short short long short; Outgroups).

Appendix (Continued.)

Character no.	Description
68(130)	Antennula articles (comparative lengths of taxa with 5 articles in antennula only); 1. article 5 length subequal to articles 3-4 combined; 2. article 5 longer than articles 3-4 combined; 3. article 5 shorter than articles 3-4 combined.
69(131)	Antenna article 2 (article 2 spines); 1. lateral margin with more than 2 spines (e.g., <i>Stephenseniellus serraticornis</i>); 2. lateral margin with two spines (e.g., <i>Austronanus glacialis</i> ; <i>Harrietonana</i> , <i>Palana</i>); 3. lateral margin with single spine; 4. lateral margin smooth, lacking spines (e.g., <i>Paramunna</i>); 5. lateral margin smooth but with a medial bulge in proximal half (e.g., <i>Pentaceration omalos</i>).
70(132)	Antenna article 3 (form, angled medially or not); 1. projecting anteriorly from article 2 (plesiomorphic condition); 2. projecting anteromedially from article 2 (Paramunnidae).
71(133)	Antenna (article 3) (presence of antennal scale, paramunnid form or not); 1. distinct dorsolateral scale present (plesiomorphic condition); 2. scale absent, article simple, tubular; 3. scale absent, article with proximolateral bulge having seta (Paramunnidae condition).
72(134)	Antenna (article 3) (length compared to 1-2); 1. short, length subequal to basal articles 1-2 together; 2. elongate, length distinctly longer than articles 1-2 together.
73(135)	Antenna (article 3) (sexually dimorphic or not); 1. male and female similar; 2. male much more robust than female (e.g., <i>affinis</i> Malyutina and; Ushakova).
74(136)	Antenna (article 3) in ventral view (general shape); 1. tubular (e.g., <i>Paramunna walvisensis</i>); 2. inflated midlength, margins curved (e.g., <i>Omonana parasimplex</i>); 3. lateral margin curved, medial margin straight (e.g., <i>Xigonus patagoniensis</i>); 4. distally expanded, distolateral margin angular (e.g., <i>Kiklonana arnauti</i>); 5. quadrate, lateral margin expanded (e.g., <i>Pagonana dilatata</i>); 6. flat and rounded, distolateral margin with concavity beside insertion of article 4 (e.g., <i>Pentaceration pleonarietis</i>); 7. triangular, marginally denticulate, distal margin with deep concavity beside insertion of article 4 (e.g., <i>Paramunna denticulata</i>).
75(138)	Antenna (article 3) presence of lateral crenate flange); 1. without crenate flange on lateral margin; 2. with crenate flange on lateral margin.
76(139)	Antenna (article 3) medial margin crenate flange); 1. without crenate flange on medial margin; 2. with crenate flange on medial margin.
77(141)	Antenna (article 3) medial margin (spines on proximal part); 1. smooth proximally; 2. (proximal part with spines); 3. with denticles along medial margin (e.g., <i>Pentaceration pleonarietis</i>).
78(145)	Antenna article 3 distomedial margin (presence of spine or projection); 1. without projection; 2. (e.g., <i>adensis</i> Muller, 1991).
79(146)	Antenna article 3 distomedial margin with (features of the projection; if present); 1. blunt or broadly rounded (e.g., <i>polynesiensis</i> Muller, 1991); 2. pointed or spine-like projection (e.g., <i>adensis</i> Muller, 1991).
80(148)	Antenna article 4 (presence of distolateral spine); 1. without spine; 2. with distolateral anteriorly curved spine (e.g., <i>quadricuspis</i> n.sp.).
81(149)	Antenna article 5 (shape); 1. approximately tubular (same width distally and proximally); 2. rounded basally and tapering distally.
82(151)	Antenna flagellum with (count articles); 1. up to 5 articles; 2. 6 articles; 3. 7 articles; 4. 8 articles or more.
83(152)	Antenna flagellum proximal article (length compared to next article); 1. shorter than more distal articles; 2. subequal to more distal articles; 3. distinctly longer than more distal articles.
84(154)	Mandible palp (palp present?); 1. present; 2. absent.
85(155)	Mandible palp (palp shape); 1. shorter than incisor process, article 2 inflated, article 3 not curved, with few setae (stubby form); 2. longer than incisor process, article 2 tubular, article 3 curved (not known for <i>Paramunna</i> -group species).
86(156)	Mandible molar process distally; 1. truncate, tritritative surface cylindrical (e.g., <i>Compoceration</i>); 2. wedge-shaped, tritritative surface sloping; 3. flared, tritritative surface oval-shaped (e.g., <i>Pentaceration</i>).
87(157)	Maxilliped palp article 1 (with or without spine); 1. with lateral spine (e.g., <i>Palana serrata</i>); 2. without lateral spine (e.g., <i>Paramunna</i> species).
88(158)	Maxilliped palp article 2 (with or without spine); 1. with lateral spine; 2. without lateral spine (e.g., <i>Paramunna</i> group species).
89(159)	Pereiopodal coxae I-IV lateral margins (shape); 1. rounded (may or may not be visible in dorsal view); 2. angular in dorsal view; 3. projecting into elongate spines in dorsal view; 4. not projecting in dorsal view.
90(162)	Pereiopod I coxa of male (spines or other ornamentation); 1. with short straight anteriorly-directed spine (may vary with maturity); 2. with elongate upcurved anteriorly directed spine (may vary with maturity); 3. with dentate anteriorly-directed plate; 4. with large angular plate fused to pereonite (e.g., <i>Cryosignum lunatum</i> (Hale)); 5. with rounded plate (e.g., <i>Meridiosignum convexum</i>); 6. unelaborated, anterior margin simple.
91(163)	Pereiopod I coxa (articulation in terminal or mature males); 1. distinctly articulated on pereonite 1; 2. in terminal males fully fused to pereonite 1 (e.g., <i>lanata</i> Hale, 1937).

Character no.	Description
92(164)	Pereiopod I basis anterior margin (ornamentation); 1. anterior margin smooth; 2. with crenate ridge, or with smooth ridge (e.g., <i>Paramunna denticulata</i>), or with crenate ridge and also on posterior margin (e.g., <i>mitterbuculata</i>); 3. with row of blunt spines; 4. with row of acute spines; 5. with few broad, rounded spines anterodistally; 6. with single spine (e.g., <i>dentatum</i> Winkler); 7. with 2 diverging spines or with 2 straight spines.
93(166)	Pereiopod I ischium anterodistal margin; 1. smooth; 2. with blunt spines; 3. with small spines; 4. with sharp spine in row; 5. with crenate ridge; 6. with robust bulge (e.g., <i>Xigonus patagoniensis</i>).
94(167)	Pereiopod I ischium shaft (spines present); 1. without spines; 2. with 1 posterior and 1 lateral spines (e.g., <i>quadriscuspis</i>); 3. with row of spines on anterior margin (2 or more spines, e.g., <i>Meridiosignum convexum</i>); 4. with 1 short spine on mid-anterior margin; 5. with 2 short spine on mid-anterior margin; 6. with 1 long spine; 7. with 1 acute spine on anterior margin; 8. with 1 blunt spine on anterior margin.
95(169)	Pereiopod I merus (spines on posterior margin); 1. with smooth posterior margin; 3. with 2 spines on posterior margin; 4. with row of low rounded tubercles on posterior margin (<i>Xigonus patagoniensis</i>); 5. with several thin crenate ridges on posterior margin (e.g., fuegiae).
96(170)	Pereiopod I merus posterior margin (elongate robust setae); 1. with only fine setae; 2. with one robust seta on distal margin; 3. with 2 (or more) robust setae on distal margin (not recorded).
97(171)	Pereiopod I carpus (general shape); 1. oval (type 1); 2. triangular (type 2); 3. quadrate (type 3); 4. irregularly rectangular (e.g., <i>Pentaceraion bovicornis</i>); 5. posterodistally projecting (type 4); 6. tubular (walking leg form of Janiridae and higher Janiroidea).
98(174)	Pereiopod I carpus posterior margin (number of major robust setae); 1. with only one robust seta (no taxa known); 2. with 2 robust setae (e.g., <i>Paramunna</i> complex species, common to many paramunnids); 3. with 2 large robust setae and 1 distal short robust seta (e.g., <i>Austrosignum glaciale</i>); 4. with 3 subequal robust setae (e.g., <i>Austrosignum-Mummogonium</i> complex species); 5. (with more than 3 setae).
99(176)	Pereiopod I (carpus) posterior margin robust setal shafts (shape of major robust setae – curved or straight); 1. straight; 2. curved (e.g., <i>adenensis</i> Muller, 1991).
100(177)	Pereiopod I (carpus) posterior margin crenate ridges (crenate ridges adjacent to robust setae); 1. present (e.g., <i>Austrosignum glaciale</i>); 2. absent.
101(178)	Pereiopod I (carpus) posterior margin (count large denticles proximal to robust setae); 1. with no denticles proximal to robust setae; 2. with 1 denticle proximal to robust setae; 3. with 2 denticles proximal to robust setae; 4. with 3 denticles proximal to robust setae; 5. with translucent flange proximal to robust setae.
102(179)	Pereiopod I (carpus) posterior margin (count large denticles between robust setae); 1. with no denticles between robust setae; 2. with 1 denticle between robust setae; 3. with 2 denticles between robust setae; 4. with 3 denticles between robust setae; 5. with translucent flange between robust setae.
103(181)	Pereiopod I propodus (distally broadening); 1. narrowing distally to insertion of dactylus; 2. distally broad and tapering steeply to insertion of dactylus (may be angular or rounded); 3. tubular, elongate (outgroups, janirid and related taxa).
104(182)	Pereiopod I propodus (distal spine); 1. without distal spine; 2. with distal spine (e.g., <i>Pagonana rostrata</i> , <i>P. hodgsoni</i>).
105(183)	Pereiopod I (propodus) opposing margin (seta type); 1. with simple seta; 2. (with robust seta – see next character); 3. lacking setae.
106(184)	Pereiopod I with propodus opposing margin (count robust setae); 1. 1 robust seta; 2. 2 robust seta; 3. 3 robust seta; 4. 4 robust setae or more.
107(185)	Pereiopod I (propodus) opposing margin (dentate ridge or spines); 1. smooth; 2. with crenate ridge; 3. with distal spine; 4. with translucent flanges.
108(186)	Pereiopod I dactylus ventral claw (gap between dorsal and ventral claw); 1. robust, distinctly separated from dorsal claw, projecting away from dactylar axis (<i>Tethygonium</i> species); 2. thin, positioned directly adjacent to dorsal claw, projecting along dactylar axis (most paramunnids).
109(187)	Pereiopod I dactylus (presence of spines); 1. without spines; 2. with sharp spine on ventral margin proximal to accessory claw (e.g., <i>adenensis</i> Muller, 1991); 3. with translucent flange on posterior margin.
110(188)	Pereiopod II basis (shape); 1. smooth; 2. male with distal indurate lobe; 3. with crenate ridge.
111(189)	Pereiopod II basis anterior margin; 1. smooth; 2. with a single spine; 3. with a row of spines.
112(190)	Pereiopod II ischium posterior margin (projections or spines); 1. smooth (no projections); 2. with crenate ridge; 3. with row of spines (e.g., <i>kerquelenensis</i>); 4. with broadly rounded projection (e.g., <i>polynesiensis</i> Mueller).
113(191)	Pereiopods II and III basis and ischium (shape in males); 1. as in females (most Paramunnids); 2. basis with distoventral projection and ischium with proximoventral projection (e.g., <i>Mummogonium quequensis</i>).
114(192)	Pereiopod II carpus ventral margin (type of robust setae on ventral margin); 1. with (2 or 3) short robust setae (no longer than width of article; 2. with row of elongate stiff robust setae (more than 3, much longer than width of segment; e.g., <i>M. falklandicum</i>); 3. with simple setae only.

Appendix. (Continued.)

Character no.	Description
115(193)	Pereiopod II propodus ventral margin (type of robust setae on ventral margin); 1. with (2 or 3) short robust setae (no longer than width of article); 2. with row of elongate stiff robust setae (more than 3, much longer than width of segment; e.g., <i>M. falklandicum</i>); 3. with 1 distal robust seta; 4. with simple setae only.
116(194)	Pereiopod II dactylus (elongate seta-like distal claws); 1. dorsal claw robust, less than length of dactylus; ventral claw much shorter than dorsal claw (most Paramunnidae); 2. dorsal claw robust, longer than dactylus ventral claw pectinate shorter and much thinner than dorsal claw; 3. dorsal claw thin, longer than dactylus; ventral claw much shorter than dorsal claw; 4. dorsal and ventral claws thin, elongate, dorsal claw longer than dactylus, ventral claw near length of dactylus (e.g., <i>Munnogonium</i> ; slope 1); 5. dorsal and ventral claws thin, elongate and bifid, both claws longer; than dactylus (e.g., <i>Munnogonium diplonychia</i>); 6. dorsal and ventral claws subequal in length, both longer than dactylus; (e.g., <i>Pentaceration bifidylus</i>).
117(195)	Pereiopod V-VII dactylus (type of claws); 1. dorsal and ventral claws similar to those of pereiopod II-IV (most Paramunnids); 2. dorsal and ventral claws thick and robust, dorsal claw near length of dactylus, ventral claw much shorter than dactylus (e.g., <i>Munnogonium diplonychia</i>); 3. dorsal claw thick and robust, subequal in length to dactylus, ventral; claw minute, seta-like.
118(196)	Pereiopod V-VII coxae (visible in dorsal view); 1. not visible in dorsal view, covered by tergite; 2. extending beyond tergite in dorsal view.
119(197)	Pereiopod V-VII coxae lateral margins (marginal shape); 1. rounded; 2. elongate and projecting (e.g., <i>Austronanus dentatus</i>); 3. angular and projecting; 4. forming elongate spines.
120(198)	Pereiopod V-VII coxae (lateral margins setae); 1. without elongate or robust setae; 2. each with single apical robust seta (e.g., <i>Stephenseniellus</i>); 3. each with 2 robust setae; 4. each with several robust setae (more than 2 setae, put number in comment for now); 5. each with single elongate simple seta (e.g., <i>polymnestensis</i> Mueller).
121(199)	Pereiopod V-VII coxae (lateral margins spines or denticles); 1. without denticles or spines; 2. lateral margin denticulate.
122(201)	Male pleopods I (<i>Paramunna sagittate</i> or not); 1. sagittate (Paramunnidae); 2. lateral lobes positioned posteriorly (plesiomorphic condition).
123(205)	Male pleopod lateral sublobe (distal lateral sublobe shape); 1. with rounded distal sublobe; 2. with bluntly triangular distal sublobe; 3. with pointed triangular; 4. with flat-tipped distal sublobe.
124(206)	Male pleopods I lateral lobes distal sublobe (position of stylet groove and distal sublobe); 1. emerging adjacent to proximal lateral sublobe; 2. distinctly separated from enlarged proximal sublobe; 3. completely overlapped by proximal sublobe; 4. partly overlapped by proximal sublobe; 5. overlapping smaller proximal sublobe; 6. partly overlapping proximal sublobe.
125(207)	Male pleopods I lateral lobes distal sublobe; 1. with tuft of simple setae; 2. with robust seta on apex (e.g., <i>Munnogonium globifrons</i>); 3. with tuft of simple setae and 1 thick seta with distal pore (e.g., <i>Munnogonium quequensis</i>).
126(209)	Male pleopods I (distal projection overall shape of posterior margin); 1. forming acute angle, or approximately forming right angle; 2. forming obtuse angle.
127(210)	Male pleopods I (distal projection shape of apices); 1. with pointed apices; 2. with bluntly pointed apices; 3. with rounded apices; 4. with truncate apices.
128(211)	Male pleopods II stylet (shape: simple arc or elongate and curved); 1. simple arc-shaped curve, tapering smoothly to tip, reaching near end of protopod (most Paramunnidae); 2. sinusously curved, distally thin and hair-like, reaching well beyond distal margin of protopod (e.g., <i>affinis</i> Malyutina and Ushakova); 3. arc-shaped, elongate tapering, curving well beyond apex of protopod.
129(212)	Female operculum (shape in ventral view); 1. nearly circular; 2. ovoid; 3. distal part tapering with concave distolateral margins.
130(214)	Uropods (insertion position); 1. on margin of pleotelson; 2. dorsal and directly adjacent to lateral margin of pleotelson; 3. dorsal, well separated from lateral margin of pleotelson; 4. ventral to lateral margin of pleotelson but visible in dorsal view (e.g., <i>Xigonus</i>); 5. ventral to lateral margin of pleotelson, projecting ventrally and not visible in dorsal view (e.g., <i>allorostrata</i>).
131(215)	Uropods (recessed or not); 1. not recessed, protopod visible (e.g., <i>Austrimnum antarctica</i>); 2. recessed, protopod or insertion not exposed (e.g., <i>Paramunna bilobata</i>).
132(216)	Uropods (covered with small hood or not); 1. not covered dorsally with small flap of cuticle or hood; 2. covered by small dorsal cuticular hood (e.g., <i>Palliolatipes</i> sp.nov.); 3. recessed into protruding cuticle tube with large mediolateral projection; 4. recessed into irregular, spinose cuticle tubes; 5. recessed into simple cuticle fold.
133(218)	Uropod protopod; 1. absent; 2. present.
134(219)	Uropod protopod; 1. hidden; 2. exposed.
135(220)	Uropods (number of rami); 1. with two rami (if endopod small, exopod length 0.3-0.5 endopod length); 2. with two rami, exopod vestigial; 3. exopod absent; 4. apparently absent.
136(221)	Uropod endopod distal margin (presence of medial curved spine); 1. rounded; 2. acutely pointed, curving medially (e.g., <i>Austrorognum glaciale</i>).