



# Urstylidae – a new family of abyssal isopods (Crustacea: Asellota) and its phylogenetic implications

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We report three new species of isopod crustaceans that belong to a rare higher taxon of asellote Isopoda. This taxon does not fit into current classifications. The isopods occurred in abyssal soft sediments, near manganese nodules, and in the vicinity of hydrothermal vents. Given their wide spatial occurrence across the Atlantic and Pacific Oceans, a cosmopolitan distribution is assumed. A cladistic analysis revealed a close relationship with the Macrostylidae, a common representative of the deep-sea macrofauna. Analyses of character evolution across the Janiroidea showed sufficient synapomorphies to justify the erection of *Urstylis* **gen. nov.** and the new family Urstylidae based on the three new species. All taxa are described in this paper. Urstylidae is characterized, amongst other apomorphies, by an elongate habitus with spade-like head; uropods are long, styliform; one pleonite is free; antennal merus and carpus are relatively short; the first pereopod is carpo-propodosubchelate, and more robust and shorter than pereopod II. Several characters, such as the pereopods' posterior scale-like claw that basally encloses the distal sensilla may be interpreted as ancestral when compared to the situation in the highly derived Macrostylidae.

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## INTRODUCTION

The asellote isopod superfamily Janiroidea Sars, 1897, is the most speciose superfamily amongst isopods. It currently comprises 22 accepted families (Schotte *et al.*, 2013) plus seven genera with uncertain affinities (Wilson, 2013). Janiroidea gave rise to the oldest of isopod lineages in the deep sea (Raupach, Held & Wägele, 2004; Raupach *et al.*, 2009), probably before the advent of the Triassic (Lins *et al.*, 2012). Today, most deep-sea janiroid families have a wide or cosmopolitan distribution, and are commonly encountered in abyssal soft sediments (Hessler & Thistle, 1975; Hessler, Wilson & Thistle, 1979). Despite decades of sampling the deep sea, however,

only a small fraction of the deep-sea floor has been studied (Ramirez-Llodra *et al.*, 2010) and rare taxa continue to be revealed that do not fit in any of the currently established groups (see e.g. Just, 2005; Osborn, Madin & Rouse, 2011).

Isopods that did not fit into current classifications were encountered during the Woods Hole Oceanographic Institution programs (Rex *et al.*, 1993; Wilson, 1998). They were not treated taxonomically owing to uncertainty about their affinities. Subsequently, this same type of isopod has appeared in samples from the Pacific Ocean, both the Clarion-Clipperton Fracture Zone (CCFZ; Thistle & Wilson, 1987, 1996; Wilson, 1987a); and the Galapagos Rift Zone (Grassle *et al.*, 1985); and were more recently collected again in the CCFZ by the Russian scientific centre 'Yuzhmorgeologia', the Federal State Unitary Geological

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Enterprise, Southern Scientific & Production Association for Marine Geological Operations, Gelendzhik. These new species had a habitus that resembled Macrostylidae Hansen, 1916. One was marked as 'Macrostylidae new genus' in publications that listed this species (Thistle & Wilson, 1987).

A careful account of their morphology showed that they had none of the apomorphic characters of macrostylids, so a more detailed analysis of the three species was undertaken. The culmination of evidence has convinced us that sufficient information was available to add another family to the Janiroidea, Urstylidae fam. nov., comprising one new genus and three species. The potential relationships of this new family amongst Janiroidea are discussed, with a consideration of apomorphic features of both the Macrostylidae and the new family.

## MATERIAL AND METHODS

### SAMPLING

Sampling was conducted during various US and Russian cruises by different institutions. Samplers employed were box corers (Hessler & Jumars, 1974) or epibenthic sled (Sanders, Hessler & Hampson, 1965). Please refer to the type localities and further records of the respective new species for detailed information.

### TERMINOLOGY

Terminology is largely based on previous work on Janiroidea (Wilson, 1989; Riehl & Brandt, 2010, 2013). Ratios described as 'near' or 'subequal' are defined as being  $\pm 5\%$  of the second measurement (Kavanagh & Wilson, 2007).

For reasons of comparability, the podomeres of the antenna are named in this paper instead of numbering them. The close relationship between the new taxa and Macrostylidae makes assumptions of homologies necessary and given the difference in article numbers between them, consecutive numbering of the articles would lead to confusion. The presence or absence of the antenna first article is obscured by simply counting the basal podomeres owing to its transformations across the entire order (Wilson, 2009). We hence adopted the nomenclature used by Hansen (1893) for Malacostraca: the first three articles are named 'precoxa', 'coxa', and 'basis'. The antennal scale (i.e. rudimentary exopod or squama) is located at the basis and allows the antennal articles to be homologized across all isopod taxa.

### CHARACTER MATRICES AND CLADISTIC ANALYSIS

The data were assembled and analysed following Wirkner & Richter's (2010) approach. For the taxon

sampling, an exemplar approach (Yeates, 1995; Prendini, 2001) was chosen. A character matrix was assembled in MESQUITE (Maddison & Maddison, 2011) starting with the data from Wilson (2009). All major asellotan groups and all families of the Janiroidea were covered; the non-asellotan taxa were removed. The character set was subsequently expanded to address many derived features found in the Janiroidea, with synapomorphies of all families of this group. From the available taxonomic-systematic literature, species were selected according to the following rationale: (1) wherever possible, we used the type species of the type genus for each family so that the resulting classification is unambiguous. Types were chosen wherever the available descriptions fulfilled certain quality standards (completeness and detail of description and illustrations, availability of type material). In some cases, we used nontype species owing to incomplete descriptions. (2) Species for which DNA was available to the authors from online repositories or otherwise were chosen because this will allow a combined analysis of morphological and molecular data sets. (3) Species with exceptionally detailed descriptions were chosen in some cases where neither (1) nor (2) applied. The exemplar character coding was not followed when a character state was not known for the exemplar species but the state had a consistent condition across all other species of the genus or family.

The evolution of the entire clade Janiroidea is beyond the scope of this publication and will be addressed separately (T. Riehl & G. D. F. Wilson, unpubl. data). To evaluate the phylogenetic position of the three new species, we reduced the set of exemplar taxa to those that are potentially (or at least superficially) related. The exemplars chosen belong to the families Desmosomatidae Sars, 1897, Janirellidae Menzies, 1956, Katianiridae Svavarsson, 1987, Macrostylidae Hansen, 1916, Mesosignidae Schultz, 1969, Nannoniscidae Hansen, 1916, and Thambematidae Stebbing, 1913. We excluded many families owing to their fundamentally different morphologies (e.g. Munnopsidae Lilljeborg, 1864, Munnidae Sars, 1897, Santiidae Wilson, 1987b, Dendrotionidae Vanhöffen, 1914, Haplomunnidae Wilson, 1976) or because of significant differences in copulatory structures: Ischnomesidae Hansen, 1916 and Haplomiscidae Hansen, 1916 have a dorsal opening to the spermathecal duct ('cuticular organ'), whereas the families considered here have lateral openings. Our selection was also based on previous analyses which showed that this suite of families at least has proximity to Macrostylidae (Wägele, 1989; Raupach *et al.*, 2009).

After the sister-group relationship with macrostylids was established in a preliminary analysis with limited taxon number, the macrostylid taxon

sampling was broadened so that the terminals cover the morphological diversity currently known for this family. All currently known species of *Macrostylis* were studied for this purpose as well as recently collected and undescribed material. The selection of macrostylid terminals was made to represent the fundamental range of morphological variability across this family. The terminals represent clades within this family that have been identified by morphological and molecular means (Riehl & Brandt, 2013; T. Riehl, unpubl. data). This approach was taken to test whether both groups are reciprocally monophyletic. Our interpretation is restricted to establishing the position of the new taxa.

The morphology of the three new species was analysed using light microscopy and scanning electron microscopy (SEM; see taxonomy section below). Comparative analysis with the other Janiroidea led to character conceptualization where characters were defined and explained and assumptions of homology were made. States of 407 characters were newly defined or in some cases adopted from previous studies (e.g. Wilson, 1985, 2009; Brusca & Wilson, 1991). All were used in the analysis but states for only those 75 characters relevant for the new taxa and their systematic relationships are outlined, defined, and discussed in detail. Characters are constructed to be independent from each other. Our aim was to decompose morphologies into the smallest homologous characters with consistent states that are real alternatives (i.e. distal margin rounded vs. acute, rather than round vs. not round). We separated independent features into different characters to avoid mixing nonhomologous states (i.e. presence/absence features are separate from structural features of the present state).

A cladistic analysis was used to infer the most parsimonious relationship scenarios amongst the terminals and to test the homology hypotheses defined in the character concepts. The character matrix was evaluated using TNT (Goloboff, Farris & Nixon, 2008), in a thorough analysis with the following settings: the root was forced to *Janira maculosa* Leach, 1814 based on previous studies suggesting a basal position of Janiridae in the Janiroidea (Wägele, 1989); a 'new technology' analysis was conducted with sectorial search, ratchet, drift, and tree fusing (all at standard settings); seed was set to 12345 and the minimum tree length was found 100 times. A strict consensus tree was generated from the four equally shortest trees retained. The consensus tree was resampled following the jackknife algorithm with a removal probability of 25% and 10 000 replicates. Relative and absolute Bremer support values were derived from tree-bisection-reconnection (TBR; Goloboff & Farris, 2001). The complete data set has been deposited in

TREEBASE under the following URL: <http://purl.org/phylo/treebase/phyloids/study/TB2:S14396>.

Finally, the evolutionary interpretation of the character changes was carried out.

#### TAXONOMY

Whole specimens were transferred from 70–96% ethanol to an ethanol-glycerine solution (1:1) and subsequently to glycerine. For illustration of appendages in standard views, dissected parts were temporarily mounted on slides following Wilson (2008) and stained with methyl green or chlorazol black. Dissected appendages were mounted on permanent slides using Euparal following Riehl & Kaiser (2012) in the cases of the specimens archived in Hamburg (ZMH K) and Vladivostok (MIMB). The specimens deposited in Sydney (AM P.) and Washington D.C. (USNM) were mounted as follows: the parts were transferred from glycerine to a 50:50 pure ethanol and turpeneol solution in a relatively deep and straight-sided dish. The turpeneol-ethanol mixture is turbulent because the ethanol evaporates quickly, and the solution thus will tend to run over flat or curved surfaces. After approximately 5 min, the parts were transferred to Euparal. A Carl Zeiss Leo 1525 microscope was used for SEM and the specimen was mounted on a specimen holder after Pohl (2010).

Character states were coded using the computer software DELTA (Dallwitz, 1980, 1993; Dallwitz, Paine & Zurcher, 2010) to generate descriptions. A database previously used for Macrostylidae (Riehl & Kaiser, 2012; Riehl, Wilson & Hessler, 2012; Riehl & Brandt, 2013) was adopted. An identification key and species' diagnoses were prepared using KEY (Dallwitz, 1974) as implemented in DELTA. The key was manually complemented with further characters to allow more exact identification. Measurements were taken from line drawings using either the distance-measurement tool embedded in Adobe Acrobat Professional or ImageJ and in accordance with the methods described by Hessler (1970). A stage micrometer was used for calibration. All appendages' article-length ratios are given in proximal to distal order, excluding setae. Many ratios are used for descriptions in this paper. To avoid multiple repetition of the word 'times,' these are reported as a multiplier of an object of a telegraphic phrase to indicate the size of the subject of the phrase (see Wilson, 1989). For example, 'endopod length 2.2 width' means 'the length of the endopod is 2.2 times its width.' This example is mathematically equivalent to the equation 'L = 2.2W'. Dependent object clauses, separated off by a comma, do not repeat the subject. Descriptions of pereopod setae are provided in proximal to distal and lateral to medial order of description

in accordance with Riehl *et al.* (2012). Line drawings were created with the programs Inkscape and Adobe Illustrator following Coleman (2003, 2009).

## RESULTS

### CHARACTER CONCEPTUALIZATION

In the following section, we discuss the concepts for the characters that appear synapomorphies for the Macrostylidae and Urstylidae, relative to a selected set of outgroup taxa. This reduced character set does not discuss all characters in the matrix used in the analysis, although we provide the complete matrix as Supporting Information Appendix S1. This data set is too limited to infer relationships within or between the other taxa used.

#### *Antennula and antenna articulation position on the cephalothorax*

Anteriorly inserting first antennula or antenna articles are widely distributed in Janiroidea. The articulations sit in a transverse plane. In Macrostylidae, the articulation sockets are positioned on the dorsolateral surface of the cephalothorax. In this case, the plane of the articulation is tilted lateroventrally resulting in a dorsolateral orientation (see e.g. Riehl *et al.*, 2012: fig. 7). Another distinct direction of the articulation of the antennula can be found in Echinothambematidae, where it is tilted slightly anteroventrally and laterally resulting in a dorsal and anterolateral orientation. The antennal articulation is in the transverse plane. In Haplomunnidae (not treated here), the lateral aspect found in Echinothambematidae is absent. Here, the antennular and antennal articulations are orientated anterodorsally.

Character 1. Antennula articulation position: 0 = anteriorly; 1 = dorsolaterally; 2 = anterodorsally.

Character 2. Antenna articulation position: 0 = anteriorly; 1 = dorsolaterally.

#### *Antennula basal article orientation*

In most species, the first article projects anteriorly. In Macrostylidae a posterodorsal projection can be found. Echinothambematidae have a highly flexible first article that can occupy every orientation from anterolaterally to dorsally; and in Haplomunnidae and some Dendrotonidae (not treated here), the first article projects anterodorsally.

Character 3. Antennula basal article orientation: 0 = anteriorly; 1 = posterodorsally; 2 = anterodorsally; 3 = anterolaterally to dorsally.

#### *Antennula flagellum aesthetasc number per article in adult male*

Most Janiroidea have one aesthetasc per flagellar segment in the male. Several taxa, mostly with a small

flagellum, have more aesthetascs per antennular segment (two to five); in some cases, substantially more than five aesthetascs per segment are present.

Character 4. Antennula flagellum aesthetasc number in adult male per article: 0 = one; 1 = two to five; 2 = six or more.

#### *Antennula hypertrophy in adult males*

Whereas the lengths and widths of antennulae are similar in both sexes in many Janiridae and 'munnooid' taxa (Wägele, 1989), some groups, such as Macrostylidae have a thicker antennula in adult males (article width increased relative to length) than in the females, also referred to as hypertrophy.

Character 5. Antennula hypertrophy in adult males: 0 = absent; 1 = present.

#### *Antenna axis*

In most Isopoda, the antenna in relaxed position has a curved axis. Basal podomeres that are cuneiform (wedge-shaped) provide the basis for this as the articular planes are not parallel. Although the first article is usually positioned and projecting anteriorly, the antenna on the whole can thus be directed posteriorly. In some groups, all podomeres are approximately cylindrical with proximal and distal articulations aligned. In these cases, bending of the axis is the result of articulation only.

Character 6. Antenna axis: 0 = curved; 1 = straight.

#### *Antenna article 3 (basis) scale*

The exopod of the crustacean antenna is called the squama, scale, or scaphocerite (McLaughlin, 1980). It is located on the basis of the limb (Wägele, 1989). In Asellota, this exopod is rudimentary, or completely absent.

Character 7. Antenna article 3 (basis) scale (presence): 0 = present; 1 = absent.

#### *Antennal basal article 1 (precoxa)*

We consider two distinct states in which the first podomere of the antenna is either present and fully articulated, or absent (Wägele, 1983; Brusca & Wilson, 1991).

Character 8. Antennal basal article 1 (precoxa): 0 = present; 1 = absent.

#### *Antenna article 3 (basis) length relative to articles 2 and 4*

The antenna basis is either longer than coxa and ischium or at most subsimilar in length.

Character 9. Antenna article 3 (basis) length (vs. articles 2 and 4): 0 = longer; 1 = subsimilar or shorter.

*Antenna article 6 (carpus) length relative to the combined lengths of podomeres 1–4*

The carpus of the antenna occurs in two states in the Janiroidea: distinctly longer than the preceding articles (precoxa–ischium) combined or relatively short in comparison to articles 1–4.

Character 10. Antenna article 6 length (vs. podomeres 1–4): 0 = longer; 1 = subsimilar or shorter.

*Mandibular lateral seta*

A seta is present laterally on the mandible body in Macrostylidae, approximately at the location of the palp articulation in other groups. Seta-like objects occurring in *Mexicope* are located more ventrally and occur next to the mandible palp. These are considered analogous because of differences in structure and location.

Character 11. Mandibular lateral seta: 0 = absent; 1 = present.

*Differentiation of the lacinia mobilis on the right mandible*

The right lacinia mobilis may be either indistinguishable from the remainder of the spine row or differentiated to form a heavily calcified and movable tooth-like structure (Richter, Edgecombe & Wilson, 2002).

Character 12. Mandibular right lacinia mobilis: 0 = indistinguishable; 1 = differentiated.

*Mandibular palp*

In Janiroidea, the palp is plesiomorphically present and apomorphically absent across various groups.

Character 13. Mandibular palp: 0 = present; 1 = absent.

*Maxilliped palp article 2 width and length ratios*

Three distinct conditions are recognized with respect to the width relationships of the first (ischium) and second (merus) palp articles of the maxilliped. Maximal widths are measured perpendicularly to the palp axis (character 14). The maxilliped article 2 (merus) shows considerable variability in the relationship between lateral length (LL) and medial length (ML) as well as between LL and width. Here, we define three states for the LL-width relationship: the LL is either subsimilar to the width, distinctly smaller, or distinctly greater (character 15). Further, we distinguish the state in which the lateral length is subequal to or exceeds the medial length from the state in which the lateral length is distinctly shorter than the medial length (character 16).

Character 14. Maxilliped palp article 2 width (vs. article 1 width): 0 = wider; 1 = subsimilar; 2 = narrower.

Character 15. Maxilliped palp article 2 lateral length vs. width: 0 = LL  $\approx$  width; 1 = LL < width; 1 = LL > width.

Character 16. Maxilliped palp article 2 lateral vs. medial length: 0 = LL  $\geq$  ML; 1 = LL < ML.

*Maxilliped palp article 4 length–width ratio*

Articles with a length that clearly exceeds the width are considered elongate. Where length and width are subsimilar, the article is short. Maximum width and length of the maxilliped article 4 (propodus) are used.

Character 17. Maxilliped palp article 4 L/W ratio: 0 = L  $\approx$  W; 1 = L > W.

*Posterolateral setae on pereonites*

Posterolateral setae are defined as those robust setae that are located on or near the apex of posterolateral tergite projections, and are clearly directed posteriorly. Such setae are usually prominent in that they are the only setae on an otherwise asetose cuticle or because they exceed other setae in close proximity in length, width, and/or robustness.

Character 18. Posterolateral setae on pereonites: 0 = absent; 1 = present.

*Pereonite tagmosis and functional groupings*

Throughout the Isopoda, the body has functional groupings or tagmata wherein limbs within a group have similar morphological construction and orientation.

Character 19. Pereonal tagmosis, functional groupings: 0 = 4:3; 1 = 3:1:3.

*Anterior pereonites' size relative to posterior pereonites*

Width and depth of the anterior pereonites (tagma) may be increased significantly in comparison to posterior body segments, resulting in an overall posteriorly narrowing body shape.

Character 20. Anterior vs. posterior pereonites size: 0 = subsimilar; 1 = wider, deeper.

*Anterior pereonites' integration relative to posterior pereonites*

Different levels of integration are defined by the expression of the intersegment articulation. Integration is low when segments are freely articulated, spaced, and movable against each other. Highly integrated segments form a compact subsection of the body with confluent outlines and tight articulations.

Character 21. Anterior pereonites integration: 0 = low; 1 = high.

*Anterior pereonites lateral margins (transition between segments)*

Whereas in most Asellota the lateral outline is notched between the segments, in Macrostyliidae the segments of the anterior pereonites have a seamless transition creating an entire outline.

Character 22. Anterior pereonites' transition between segments: 0 = notched; 1 = entire.

*Anterior pereonites' sternite margins (fusion)*

The cuticular membrane at segment borders allows the segments to move against each other. Where segments are highly integrated; movability may be lost, the segment margins may fuse.

Character 23. Anterior pereonites' sternite margins: 0 = expressed; 1 = (partly) fused.

*Tergal projections laterally on anterior pereonites 2–4 and posterior pereonites 6–7 (presence)*

This character differentiates between the condition in which the tergites project laterally beyond the lateral margin of the coxae and the condition in which the coxae are aligned with the tergites or project beyond. Anterior and posterior segments are treated separately.

Character 24. Tergal projections laterally on anterior pereonites 2–4: 0 = absent; 1 = present.

Character 25. Tergal projections laterally on anterior pereonites 5–7: 0 = absent; 1 = present.

*Oostegites on pereopods 1 and 2*

The number of oostegites and the legs involved in creating the pouch can vary across the Janiroidea.

Character 26. Pereopod 1 oostegite: 0 = present; 1 = absent.

Character 27. Pereopod 2 oostegite: 0 = present; 1 = absent.

*Pereonite 4 anterior collum*

The presence of a collum in pereonite 4 is apomorphic for the Macrostyliidae (Riehl *et al.*, 2012).

Character 28. Pereonite 4 anterior collum: 0 = absent; 1 = present.

*Position of the coxa insertion on pereonite 4*

The coxal insertion on pereonite 4 is located either anteriorly or medially on the lateral margin.

Character 29. Pereonite 4 coxa insertions: 0 = anterolateral; 1 = mediolateral.

*Ventral spines on pereonites 1 and 2*

In pereonite 1, a clear distinction can be made when the spine either assumes a ventral-posterior orientation or is directed anteriorly and projects ventrally

to the cephalothorax. As species groups show considerable variation, we have treated each pereonite individually.

Character 30. Pereonite 1 ventral spine orientation (if present): 0 = anteriorly; 1 = ventrally and posteriorly.

Character 31. Pereonite 2 ventral spine: 0 = absent; 1 = present.

*Anterior pereopods' coxae shape*

The coxae of the anterior pereopods are either ring-like projections with clear coxa–body articulations or they are embedded into the ventral pereonal cuticle, which is referred to as 'disc-like'.

Character 32. Anterior pereopods coxae: 0 = ring-like; 1 = disc-like.

*Coxa setation of anterior and posterior pereopods*

The degree of setation on the coxae varies considerably across the Janiroidea, although those taxa that have the coxa in a more ventral position or reduced typically have unadorned coxae.

Character 33. Anterior pereopods' coxae setation: 0 = present; 1 = absent.

Character 34. Posterior pereopods' coxae setation: 0 = present; 1 = absent.

*Pereopod I–IV orientation*

The anterior locomotory appendages of Janiroidea are either orientated anteriorly and held in a ventrolateral position, or their orientation is somewhat dorsal and held in a lateral position.

Character 35. Pereopod I orientation: 0 = ventrolateral; 1 = dorsolateral.

Character 36. Pereopod II orientation: 0 = ventrolateral; 1 = dorsolateral.

Character 37. Pereopod III orientation: 0 = ventrolateral; 1 = dorsolateral.

Character 38. Pereopod IV orientation: 0 = ventrolateral; 1 = dorsolateral.

*Shape of dactylus posterior (ventral) claw of the anterior and posterior pereopods*

The diversely modified setae that form the ventral dactylar claws (Wilson, 1985) appear in diverse shapes. They are often claw-shaped similar to the dorsal claw. Further forms of modification are flattened, scale-like claws; elongate structures that are dorsally concave and ventrally keeled; straight, unarticulated spines; hand-shaped, serrate claws (see Wilson, 1985). In the posterior pereopods, claws may have retained (or regained) a simple seta-like appearance. Anterior and posterior claws show considerable differences in some taxa, these have been coded separately.

Character 39. Shape of the anterior pereopod dactylus posterior claw (if present): 0 = claw-like; 1 = scale-like; 2 = thin elongate, with ventral carina, distally tapering, clinging to distal sensilla, 3 = thin, unarticulated spine; 4 = broad, serrate.

Character 40. Posterior pereonites' dactylus posterior claw (if present) shape: 0 = claw-like; 1 = scale-like; 2 = seta-like.

*Position of the dactylus distal sensillae in the anterior and posterior pereopods relative to the claws*

Distally on janiroidean dactyli and adjacent to the dorsal claw, small modified setae can be found that have a probable sensory function and are commonly referred to as sensillae (Wilson, 1989; Riehl & Brandt, 2010). Their number is variable, usually up to three. Their shape resembles a thin, flexible tube, often with fringe-like microstructure (Riehl & Brandt, 2010). The positional relationship of the dorsal and ventral claws to the distal sensillae (Wilson, 1985) can be sorted into three different categories: the sensilla(e) may be located between the claws in close proximity, basally enclosed by a large dorsal and a short scale-like ventral claw, or the two claws form a canal within which the sensilla is enclosed.

Character 41. Anterior pereopods' dactylus distal sensillae: 0 = not enclosed; 1 = enclosed; 2 = basally enclosed.

Character 42. Posterior pereopods' dactylus distal sensillae: 0 = not enclosed; 1 = basally enclosed.

*Pereopod I dactylus distal sensillae*

In most families, these sensillae are short and do not project beyond the dorsal claw. In Urstylidae, these sensillae are elongate and project beyond the claws. In Macrostylidae, one distal sensilla is thick and immovable and is enclosed by dorsal and medial claws.

Character 43. Pereopod I dactylus distal sensillae: 0 = short, slender; 1 = long; 2 = thick, robust.

*Length of the anterior pereopods' dactylus medial sensillae*

Medially on the dactylus of Janiroidea, a single or small clutch of sensillae is present. These can either be rather short in a way that they do not distally project beyond the claws, or they are enlarged and project distally.

Character 44. Anterior pereopods' dactylus medial sensillae: 0 = short, thin; 1 = elongate, swollen.

*Pereopod I ischium dorsal margin*

A dorsally projecting ischium of the first pereopod can be distinguished from an ischium with subparallel dorsal and lateral margins (character 45). The pro-

jections differ largely in their extent (character 46). Where the projection is small, it has a rounded or triangular appearance; the width of the article is smaller than its length. A large projection is defined by a tapering shape and an article width that exceeds its length.

Character 45. Pereopod I ischium dorsal margin: 0 = subparallel; 1 = projecting.

Character 46. Pereopod I ischium dorsal margin projection: 0 = small; 1 = large.

*Pereopod I merus shape*

Measurement of the dorsal length (taking into account also distodorsal processes) in relation to the article's maximal width allows short and elongate merus to be distinguished. A short merus is characterized by having a dorsal length subequal to or shorter than its width. Usually, a distinct distodorsal projection is present. Long merus have a dorsal length exceeding their width. Distodorsal projections are absent or minute in this case.

Character 47. Pereopod I merus shape: 0 = short; 1 = long.

*Pereopod I carpus shape*

Five shapes of the first pereopod carpus are defined (Just & Wilson, 2004, 2007; Wilson, 1987b): a triangular carpus has a short dorsal margin and a much longer ventral margin; trapezoid means that the segment is proximally slender and distally widening, dorsal and ventral margins have subsimilar lengths; an elongate carpus has parallel dorsal and ventral margins, is slender and multiple times longer than wide; quadrate refers to a short carpus with length subsimilar to width and parallel margins; a sickle shape is present when dorsal and ventral margins are parallel, with the ventral margin concave and the dorsal margin convex.

Character 48. Pereopod I carpus shape: 0 = triangular; 1 = trapezoid; 2 = elongate; 3 = quadrate; 4 = sickle-shaped.

*Pereopod I opposition between carpus and propodus*

This character addresses whether the carpus and propodus are involved to form a subchela. Subchelae can vary a lot in their degree of opposition, whereas the opposition alone does not define a chela. To identify a subchela as such, structures associated in grasping need to be present as well: ventral projections, spine-like setae, or rows of spinules.

Character 49. Pereopod I opposition between carpus and propodus: 0 = absent; 1 = present.

*Pereopod I length in relation to pereopod II*

Three categories of length can be distinguished in pereopod I compared to pereopod II. These patterns

were recognized by Hessler (1970) for Desmosomatidae and we extend their generality. Regarding the length, the categories shorter and subsimilar or longer are discriminated.

Character 50. Pereopod I length vs. pereopod II: 0 = distinctly shorter; 1 = subsimilar or longer.

*Pereopods II and III merus, carpus, and propodus form and setation*

Fundamental transformations to pereopods II and III occur amongst the janiroideans, although defining these changes should avoid sole reference to assumed habits, such as ‘ambulatory’ or ‘fossorial’. Limited information on approximate functions of the limbs is available from behavioural observations (Hessler & Strömberg, 1989) and so we have added parenthetical comments, but the characters are defined on morphology. The ‘ambulatory’ state is defined by a short paucisetose merus, and carpus and propodus without or with only ventral robust setae and subparallel margins. Two distinct ‘fossorial’ states are defined and considered analogous rather than homologous because of fundamental structural differences: the first can be recognized by its short, paucisetose merus, and multiple rows of robust setae on the carpus and propodus, both with broadened margins. The second ‘fossorial’ state is characterized by an elongate ischium, merus, and carpus, all with broadened margins and dorsal and ventral rows of robust setae, propodus slender and paucisetose.

Character 51. Pereopod II form: 0 = ‘ambulatory’; 1 = ‘fossorial I’; 2 = ‘fossorial II’.

Character 52. Pereopod III form: 0 = ‘ambulatory’; 1 = ‘fossorial I’; 2 = ‘fossorial II’.

*Pereopod III carpo-propodal joint rotation*

A rotation of the third pereopod at the carpo-propodal joint is one of the synapomorphies for Macrostylidae (see Riehl & Kaiser, 2012: fig. 4c). As a consequence, the propodus and dactylus angle dorsolaterally instead of ventrally in relation to the limb, or posteriorly along the body axis. The articular plate at the propodo-dactylar joint, usually positioned laterally on the limb, has a dorsomedial position and the medial sensillae of the dactylus assume a dorsal position.

Character 53. Pereopod III carpo-propodal joint rotation: 0 = absent; 1 = present.

*Pereopod III ischium form*

The presence of a strong projection of the pereopod III ischium dorsal margin is apomorphic for Macrostylidae. Most other janiroideans have only a distal increase in width if anything, but never have a distinctive bulge midlength on the ischium.

Character 54. Pereopod III ischium form: 0 = straight or slightly vaulted; 1 = with dorsal lobe.

*Pereopod III ischium dorsal setation*

The ischial projection of the Macrostylidae is furnished with robust and fine setae that are especially useful for species group delimitation (but see Riehl & Kaiser, 2012). Most species have one or two robust setae at the apex of the projection. Other janiroideans have few, if any, ischial setae in a dorsal midlength position.

Character 55. Pereopod III ischium dorsal setation: 0 = setation minor or absent; 1 = setation prominent.

*Pereopod IV*

Several conditions of the fourth pereopod can be distinguished regarding its overall length and its carpus length. The leg-length categories (character 56) are highly elongate when the length exceeds the body length, in extreme cases up to several times; subsimilar to preceding and subsequent pereopods; or distinctly shorter than pereopods III and V. For the carpus, the following length categories (character 57) are recognized: clearly longer than merus and near propodus length; subsimilar merus length, longer propodus; subsimilar to merus and propodus.

Character 56. Pereopod IV length: 0 = elongate; 1 = subsimilar; 2 = shorter.

Character 57. Pereopod IV carpus (elongation): 0 = longer merus, subsimilar propodus; 1 = subsimilar merus, longer propodus; 2 = subsimilar merus and propodus.

*Paired sensory organ dorsally on pleotelson*

The paired sensory organs present on the pleotelson of Macrostylidae (Hansen, 1916; Wägele, 1989) and two of the *Urstylis* species are homologized based on similarity in position and underlying anatomy. They are located dorsally in the posterior half of the pleotelson, either as broom setae (= penicillate setae) or in cavities that contain crystalline structures and are interpreted as statocysts.

Character 58. Pleotelson dorsal paired sensory organ (type; if present): 0 = statocyst; 1 = broom seta.

*Pleopodal cavity posterior form*

The margin of the pleopodal cavity is usually defined by the opercular pleopods. It is considered closed when the opercular pleopods seal off the cavity with the ventrally emerging posterior wall of the pleopodal cavity. It is open when a preanal trough extends the pleopodal cavity to the posterior apex of the pleotelson. In the latter case, the opercular pleopods may or may not extend caudally to the pleotelson apex.

Character 59. Pleopodal cavity posteriorly: 0 = closed; 1 = open.

*Pleotelson lateroventral setal rows and ridges*

Ventrally on the pleotelson of Macrostylidae, ridges follow the margin of the pleopodal cavity (character



60). They extend from the posterior end of the preanal trough to the anterior region of the pleotelson where in some species they divide from the pleopodal cavity and continue along the lateral cuticle of the pleotelson. Alongside these rows, macrostylids have rows of long and relatively robust setae (character 61). These also occur in janiroideans that do not feature the ridges, such as Urstylidae, or other taxa not treated here such as Pleurocopidae, Santidae, some Paramunnidae, and some Munnopsidae (Syneurycopinae, *Microcope* Malyutina, 2008). Setae and ridges are thus considered independent and have been separately coded.

Character 60. Pleotelson lateroventral ridges: 0 = absent; 1 = present.

Character 61. Pleotelson lateroventral setal rows: 0 = absent; 1 = present.

#### *Anus position with regard to pleopodal cavity*

Typically, the anus is either covered by the opercular pleopods and thus inside the pleopodal cavity, or it is exposed and outside the cavity. Where the opercular pleopods are shorter than the pleopodal cavity the anus is situated within the cavity but still exposed.

Character 62. Anus position with regard to pleopodal cavity: 0 = inside; 1 = outside.

#### *Male pleopod I medial & lateral lobe arrangement*

The first pleopod in Janiroidea has grooves distally on the dorsal surface that guide the second pleopod stylet motion during copulation (Wilson, 1987b). The position of these grooves determines the border between medial and lateral lobes of the pleopod distal apex. The position of the lobes with regard to each other is often group-specific. The lateral and medial lobes can, for instance, be either arranged lateral to each other and in the same plane or the medial lobes override the lateral lobes ventrally.

Character 63. Male pleopod I medial and lateral lobes arrangement: 0 = lateral; 1 = medial lobes ventrally 'overriding' lateral lobes.

#### *Type of setae distally on the female pleopod II*

Using a light microscope, the setae on the distal margin of the female opercular pleopod appear to be asetulate in most Janiroidea. *Macrostylis* species are special in having pappose setae, whereas *Urstylis thiotyntlus* has apically sensillate setae.

Character 64. Female pleopod II distal setae (type): 0 = simple; 1 = pappose; 2 = sensillate.

#### *Length of setae distally on the female pleopod II*

Whereas most taxa with an apical row of setae on the operculum feature only relatively short setae, in Urstylidae, Macrostylidae, and Mesosignidae, these setae are distinctly longer, partly covering the anus.

We define short as being subequal or less than one-quarter of the operculum length and long as significantly larger than this.

Character 65. Female pleopod II distal setae (length): 0 = short; 1 = long.

#### *Female pleopod II lateral fringe of fine setae*

The opercular pleopod II of the female janiroideans has marginal setae, either distally that may or may not cover the anus, or laterally. Amongst the taxa studied here, most species had a fringe of setae laterally, although *Urstylis zapiola*, *Janirella*, *Echinothambema*, *Desmosoma*, and *Pseudomesus* lacked the setae.

Character 66. Female pleopod II lateral fringe of fine setae (presence): 0 = absent; 1 = present.

#### *Length of the male pleopod II stylet*

The Janiroidea show substantial variability in the length of the male pleopod II endopodal stylet, so this feature is likely to be more useful for defining subgroups rather than being distinctive at the family level. The stylet is basally a relatively short straight (e.g. *Janirella*) or curved (e.g. *Janira*) structure and both forms can be seen amongst the Macrostylidae and Urstylidae. Amongst other taxa not included in this analysis, the stylet may be also sinusoidal (e.g. *Munella*) or coiled (e.g. *Dendromunna*, some Munnopsidae). We consider the stylet to be short when it does not project beyond the distal tip of the protopod; it is intermediate when it projects distinctly beyond the protopod tip but is shorter than 1.5 times the protopod length; otherwise it is long.

Character 67. Male pleopod II stylet length: 0 = short; 1 = intermediate; 2 = long.

#### *Male pleopod II exopod form*

The pleopod II exopod in Janiroidea is a short, unarticulate ramus, often with a distal hook (Wilson, 1987b). We find it either to be short and stout with its length not exceeding its width, or elongate when clearly longer than wide.

Character 68. Male pleopod II exopod form: 0 = stout; 1 = elongate.

#### *Pleopod III exopod*

The third pleopod shows consistent patterns across the families of the Janiroidea (Wilson, 1985, 1989: figs 36, 37) so that length, width, and expression of segmentation are useful apomorphic features. The plesiomorphic form is a broadly operculate, biarticulate exopod with a fringe of short plumose setae. The exopod becomes less important and undergoes a variety of independent reductions amongst the families of Janiroidea. As these shape and setation characters appear to be independent, they are divided

into relative length and width features. The exopod occurs as either mono- or biarticulate (character 69). Three different width categories are distinguished: significantly broader than the endopod, subsimilar to the endopod width, distinctly narrower (character 70). Distally on the exopod, single or multiple conspicuous setae are situated either apically, subapically on the dorsal surface, or distributed along the apical margin (character 71).

Character 69. Pleopod III exopod: 0 = biarticulate; 1 = monoarticulate.

Character 70. Pleopod III exopod width (vs. endopod): 0 = subsimilar; 1 = narrower.

Character 71. Pleopod III exopod distal setae (position): 0 = apically; 1 = subapically; 2 = apical and lateral margins.

*Uropod position in relation to anus position, in taxa in which the uropods insert posterolaterally*

In the Asellota, Microcerberidae, and Phreatoicoidea, the uropods insert near the posterior pleotelson margin, either on the ventral margin or below it, although some Janiroidea have the uropods inserting well above the pleotelson margin on the dorsal surface (e.g. Paramunnidae and Munnidae; not treated here). For those taxa that have the uropods placed posteriorly at the posterolateral margin (above the pleopodal cavity margin but typically below the pleotelson dorsal surface), the uropods are located in direct proximity to the anus in many taxa (Desmosomatidae, Nannoniscidae, some Munnopsidae) and in the cases of the Joeropsididae, some Munnopsidae (Ilyarachninae and Lipomerinae), and some undescribed Desmosomatidae (not treated here) even cover the anus. Plesiomorphically (Asellidae, Janiridae), the uropods insert adjacent to the anus but typically with a small separation. In Macrostylidae, Urstylidae, and several other taxa with long, styliform uropods, the latter insert some distance laterally to the anus.

Character 72. Uropod insertion (where posterolateral) relative to anus: 0 = adjacent; 1 = separate.

*Presence of uropod exopod*

The uropod exopod is absent across several groups of Janiroidea independently of the position or overall size of the uropod.

Character 73. Uropod exopod (presence): 0 = present; 1 = absent.

*Uropod exopod length relative to endopod length and shape*

Where the uropod exopod is present, three length categories are distinguished in comparison with the endopod length: Both rami are either subsimilar, the exopod is distinctly shorter but a recognizable elongate ramus, or the exopod may be vestigial, squat,

shorter than long, and immovable because of its small size, although full articulation may be present.

Character 74. Uropod rami relative length: 0 = subsimilar; 1 = exopod smaller; 2 = exopod vestigial.

*Uropod endopod length in relation to the protopod length*

Depending on the length of the uropod protopod, the length of the endopod can be relatively long or short. Macrostylidae and Urstylidae have extremely elongate uropods; in the majority of species most of the length consists of the protopod. Other families were included in our analysis because they also have elongate uropods, and small or vestigial endopods.

Character 75. Uropod endopod length vs. protopod length: 0 = longer; 1 = subsimilar or shorter.

## SYSTEMATICS

ASELLOTA LATREILLE, 1802

JANIROIDEA SARS, 1897

**URSTYLIDAE FAM. NOV.**

*Zoobank registration*

urn:lsid:zoobank.org:act:5FAFBD95-32CB-4C73-B904-3DA4C73447B5

*Type genus*

*Urstylis* gen. nov., designated here.

*Composition*

*Urstylis* gen. nov.

*Family diagnosis*

Cephalothorax spatulate, widening posteriorly, prognathous. Pleotelson anterior margin 'stalked', not directly adjacent to preceding pereonites. Antenna merus and carpus both subsimilar or shorter than podomeres 1–4 together; merus shorter than carpus. Antennal scale present as rudimentary, unarticulated spine. Maxilliped palp article 2 width subequal to article 1 width. Pereopodal coxae setose. Pereopod I carposubchelate, more robust and shorter than pereopod II; ischium with dorsal setose lobe, carpus trapezoidal, widening distally, with dorsal and ventral margin lengths subsimilar. Pereopods II–VII similar in size and shape. Posterior pereopods dactylus posterior (ventral) claw scale-like, flattened in cross-section; distal sensillae basally enclosed between dorsal and ventral claws. Male pleopod I medial lobes ventrally 'overriding' lateral lobes. Male pleopod II exopod thick and slightly longer than wide. Pleopod III exopod bisegmented with clear articulation; distal article much narrower than proximal article, inserting distomedially; projecting near distal tip of endopod. Uropod insertions at posterolateral pleotelson margin;

uropods long, styliiform, exopod rudimentary (assumed for *Urstyliis thiotyntlus* gen. et sp. nov.).

#### Family description

Body elongate, more slender in male than in female (assumed for *U. thiotyntlus*). Cephalothorax spatulate, with anterolateral insertions of antennulae and antennae; lateral margins setose. Pereonal tagmosis 4:3. Pereonites 1–4 lateral margins subparallel, anteriorly rounded, and posteriorly abruptly narrowing (fossosome absent); articulations fully expressed, movable; lateral margins setose, pereonal collum absent. Coxae inserting lateroventrally, visible in lateral view. Posterolateral margins of pereonites 5–7 rounded, lateral margins setose. Pleonite 1 tergal and sternal articulations with pleotelson present, dorsally with two setae at posterior tergite margin. Pleotelson subrectangular, elongate, lateral outline with weak waist separating longer anterior and shorter posterior convex margin, posterior margin concave at uropod insertions; apex convex, broadly rounded, ventrally with setal ridges absent; longitudinal trough absent. Anal opening parallel to frontal plane. Marsupium with four pairs of oostegites (pereopods I–IV), oopore lateroventrally (Fig. 1). Antennula and antenna orientated anteriorly. Antennula of six articles, axis inflected at articulation of elongate articles 1 and 2, article 1 longest and widest; aesthetascs simple, tubular. Antenna with six podomeres, precoxaischium squat, ischium elbow joint, article insertions at right angles, basis with unarticulated small spine (probably homologous with scale), flagellar articles each with several thin, tubular aesthetascs, more in male than in female. Mandible without palp, incisor process multidentate, gracile, much thinner than basal region; lacinia mobilis grinding or crushing, multidentate, right lacinia clearly smaller than left lacinia, left mandible incisor with dorsal cusps forming right angle to distal and ventral cusps. Maxilliped basis medioventrally with seta absent; palp narrower than basis, wider than endite, first article distolateral lobe present, fourth article distomedial lobe present. Pereopodal coxae ring-shaped, setose; dactyli with two claws inserted terminally; ventral claw much smaller than dorsal claw, scale-like, basally enclosing distal sensillae.

Pereopod I modified, shortest and broadest, ischium with dorsal setose lobe, carpus broader distally, laterally flattened; pereopods II–VII similar in size, shape, and setation, getting slightly more slender from II to VII, carpus-propodus elongate, cylindrical, lengthening from pereopods II to VI. Opercular pleopods distally setose; setae asetulate. Male pleopod I proximally with subparallel lateral margins, distally widening, with no distolateral horns, lateral lobes not extending distally beyond medial lobes. Male pleopod

II protopod slender, tapering distally, narrower than pleopod I. Female operculum stout, ovoid, without keel, broadly rounded distally, ventrally overlapping the lateral margins of the pleopodal cavity, distally not reaching anus. Pleopod III protopod and endopod subequal in length and width, endopod with three plumose distal setae, setae longer than endopod; exopod biarticulate, with distinct articulation, lateral outline not continuous, with lateral fringe of fine setae mostly restricted to proximal article, distal article length approximately 0.33 times proximal article length, approximately 0.5 times proximal article width, with conspicuous subterminal seta shorter than distal article. Pleopod IV exopod subequal in length to endopod, elongate, flat, with lateral fringe of fine setae, setae longer than exopod width, distally with plumose seta, seta slightly smaller than exopod. Pleopod V uniramous. Uropod long, styliiform, biramous, exopod squat, minute, wider than long, with one or few setae; protopod exceeding the length of the pleotelson (known only in *Urstyliis zapiola* and *Urstyliis solycopia manca*).

#### Distribution

Species of Urstyliidae have been found exclusively on abyssal soft sediments. They are known to occur in the western South Atlantic, near manganese nodules in the tropical North Pacific, and in the vicinity of hydrothermal vents near the Galapagos.

#### URSTYLIS GEN. NOV.

##### Zoobank registration

urn:lsid:zoobank.org:act:E046CF0B-5DBA-4077-8C54-0F206467EE8C

##### Gender

The ending ‘-is’ is nominative singular feminine, as in *Macrostyliis*.

##### Type species

*Urstyliis zapiola* sp. nov., designated here.

##### Etymology

Based on the likely basal position of this genus to Macrostyliidae and supposedly primitive character states, the Old High German prefix ‘Ur-’, meaning ‘thoroughly’ was chosen. It adds the meaning proto-, primitive, or original to nouns with which it is combined. This prefix was especially chosen in honour of Robert R. Hessler, who employed this prefix for naming ancestral character states or modelled ancestral species. The root ‘-styliis’ refers to the shape of the uropods that characterize species of *Urstyliis* and the related Macrostyliidae. It is based on the Greek  $\zeta\tau\upsilon\lambda\acute{\iota}\varsigma$  which is the complementary feminine form of  $\zeta\tau\upsilon\lambda\omicron\varsigma$  (stylos; masculine), meaning column or pillar.

*Composition*

*Urstylis zapiola* sp. nov., *U. solicopia* sp. nov.,  
*U. thiotyntlus* sp. nov.

*Generic diagnosis*

Pereon without sternal spines, not keeled. Pereonites 1–4 not tightly packed with anterior submarginal row of setae and lateral margin setose, posterolateral margin without prominent spine-like seta. Long setae on pedestal (uncalcified) articulations along lateral and anterior tergite margins. Pleotelson waist well pronounced, paired dorsal sensory organ present. Pereopod I positioned ventrally, orientated anteriorly, ischium dorsal lobe not longer than merus dorsal lobe.

*URSTYLIS ZAPIOLA GEN. ET SP. NOV.*

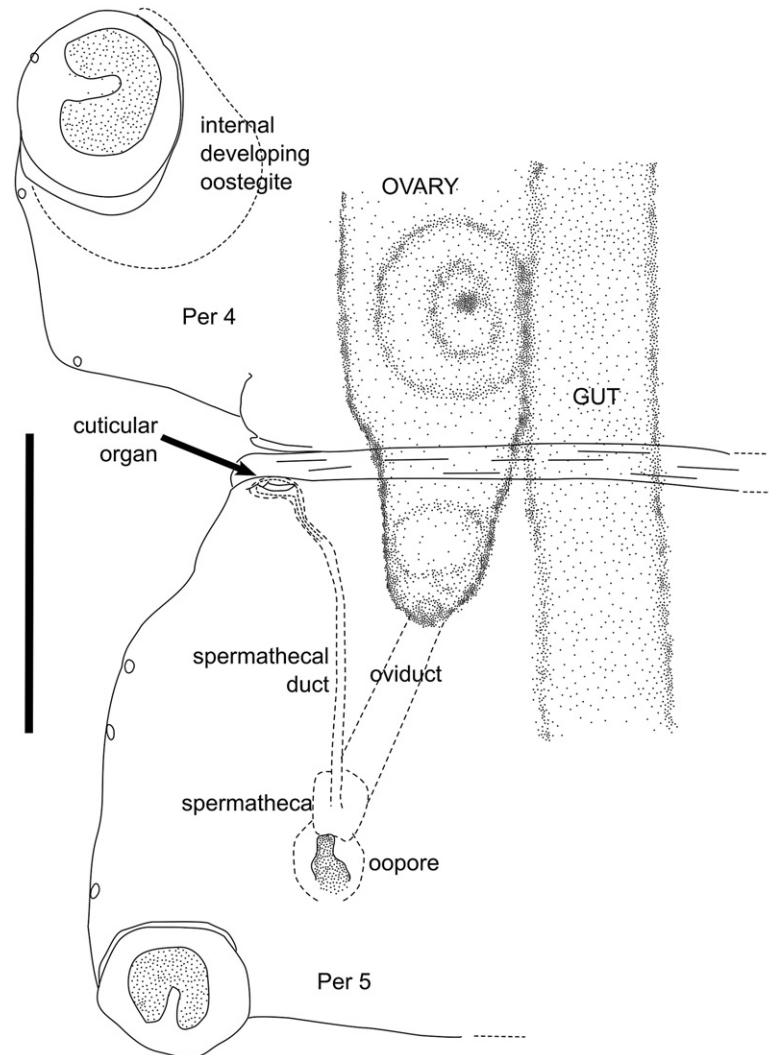
FIGURES 1–9

*Zoobank registration*

urn:lsid:zoobank.org:act:3948B113-52B4-4CF5-93B7-710C67C9EA25

*Etymology*

This name refers to the type locality on the Zapiola Drift, a topographical feature in the Argentine Basin underlying a deep-sea current strongly influencing the deep Argentine Basin sediments (Flood, Shor & Manley, 1993) called the Zapiola Anticyclone (de Miranda, Barnier & Dewar, 1999). It is a feminine noun in apposition.



**Figure 1.** *Urstylis zapiola* gen. et sp. nov., adult female paratype USNM 1208014, ventral view of pereonites (Per) 4, 5, showing arrangement of reproductive organs, internal oostegite and gut; legs omitted for clarity. Scale bar = 0.1 mm.

*Type fixation*

Adult male holotype USNM 1208013, designated here.

*Type material examined*

USNM 1208013: adult male holotype, 1.9 mm. USNM 1208014: adult female paratype, 1.8 mm. AM P.90631: adult male paratype [dissected, parts on two slides (AM P.90631.001)]. USNM 1208015: adult male, 1.9 mm, head damaged, uropod ~0.8 mm; adult male 1.9 mm. AM P.67340: four brooding females, 1.7 mm; two brooding females, 1.6 and 1.8 mm; four females, 1.6, 1.8, 1.9 mm (twice); three adult males, 1.5 mm (twice), 1.7 mm; three individuals fragmented, two females, male. George D. F. Wilson (GDFW) collection: male paratype (sectioned on four slides), 1.6 mm.

*Type locality*

Argentine Basin, 43°33.0'S, 48°58.1'W, 5208–5223 m, Woods Hole Oceanographic Institution Research Vessel (R/V) Atlantis II cruise 60, benthic station 247A, 17.iii.1971, epibenthic sled. *Urstylis zapiola* was collected in a particularly large epibenthic sample. The isopod composition of this sample is provided in Supporting Information Appendix S2.

*Further records*

Known only from the type locality.

*Type material – remarks*

Only two specimens, both male, retained uropods and so the least damaged specimen was used for the holotype. Of the brooding females, two had embryos in the brood pouch, only three each. The males were typically heavily calcified whereas the females were not.

*Diagnosis*

Body subcylindrical; pleotelson length/width ratio 1.5, waist well pronounced, paired dorsal sensory organ located in tergal cuticular tubercles; pereonites 4 and 5 subequal; pereonite 6 slightly longer than pereonite 5; pereonite 7 posterolateral margins not projecting posteriorly; pereopod I ischium dorsal lobe with one seta. Pereopods V–VII ischium and carpus without strong seta mid-dorsally.

*Description of female*

Body (Fig. 2C) length 1.8 mm, 4.0 width. Ventral spines on pereonites 1–7 absent. Cephalothorax–pleotelson with imbricate ornamentation covering all tergites, sternites, and opercular pleopods.

Cephalothorax (Figs 2C, 6C) length 0.80 width, 0.18 body length; frons in dorsal view convex, smooth, frontal furrow present, convex anterior margin adjacent to clypeus, not projecting; antennal articulations

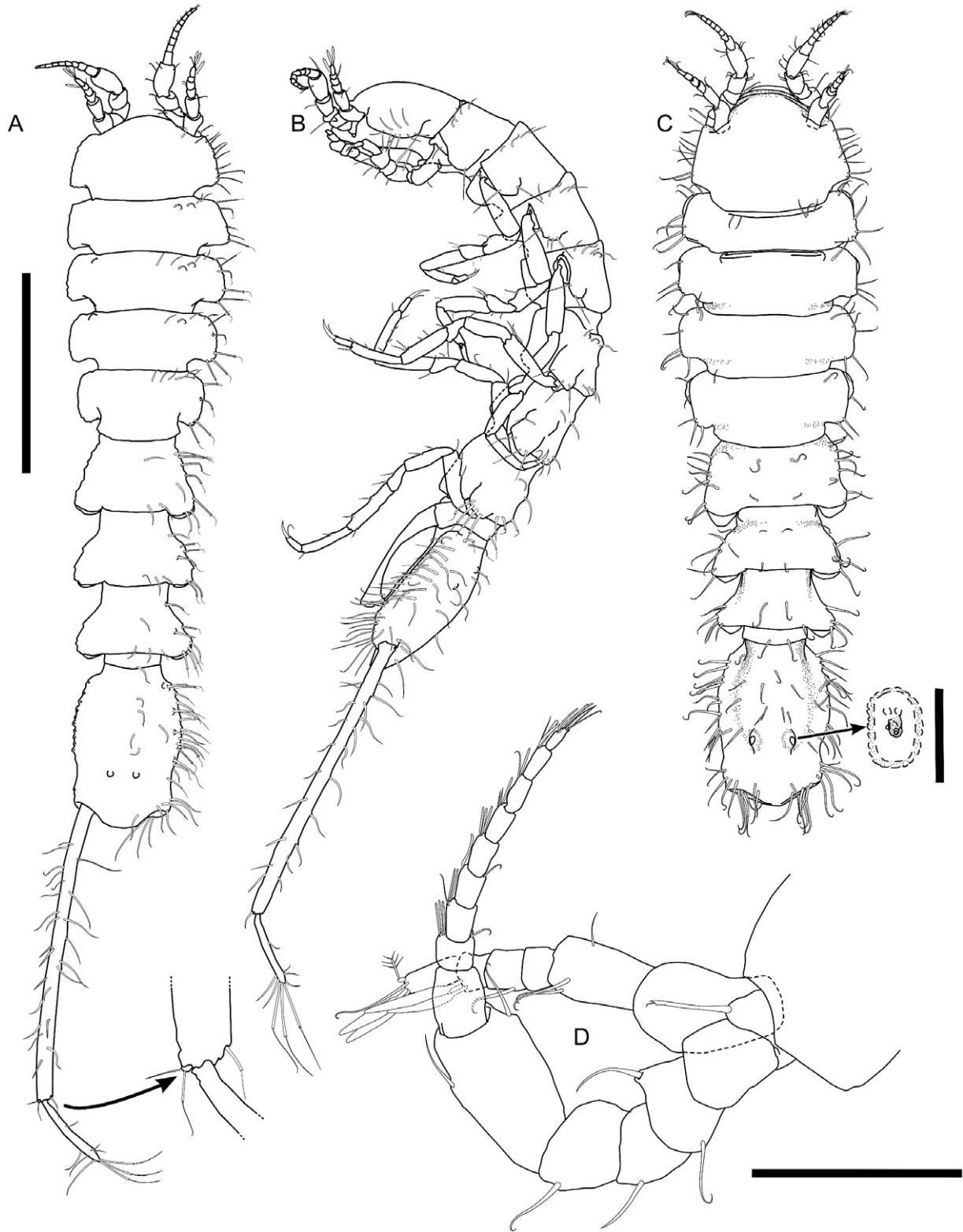
anteriorly. Posterolateral margins angular, blunt (angle > 90°). Posterolateral setae on cephalothorax and pereonites 1–7 asensillate, simple. Pereonites 1–3 with row of setae on anterior tergite margin. Pereonite 1 length 0.2 width, 0.05 body length, anterior margin concave. Pereonite 2 length 0.36 width, 0.09 body length. Pereonite 3 length 0.35 width, 0.09 body length. Pereonite 4 width 1.2, pereonite 5 width, length 0.42 width, 0.10 body length; lateral margins anteriorly and posteriorly convex with medial concavity. Posterolateral margins rounded.

Pereonites 5–7 length subequal, each 0.08–0.09 body length, narrowing from 5 to 7. Posterior margins setose; setae asensillate, simple, flexibly articulating, short. Posterolateral margins produced posteriorly, rounded. Pereonite 5 length 0.42 width, 0.85 pereonite 4 length. Posterior margin with four setae. Pereonite 6 length 0.49 width, 1.1 pereonite 5 length. Posterior margin with six setae. Pereonite 7 length 0.51 width. Posterior margin with six setae.

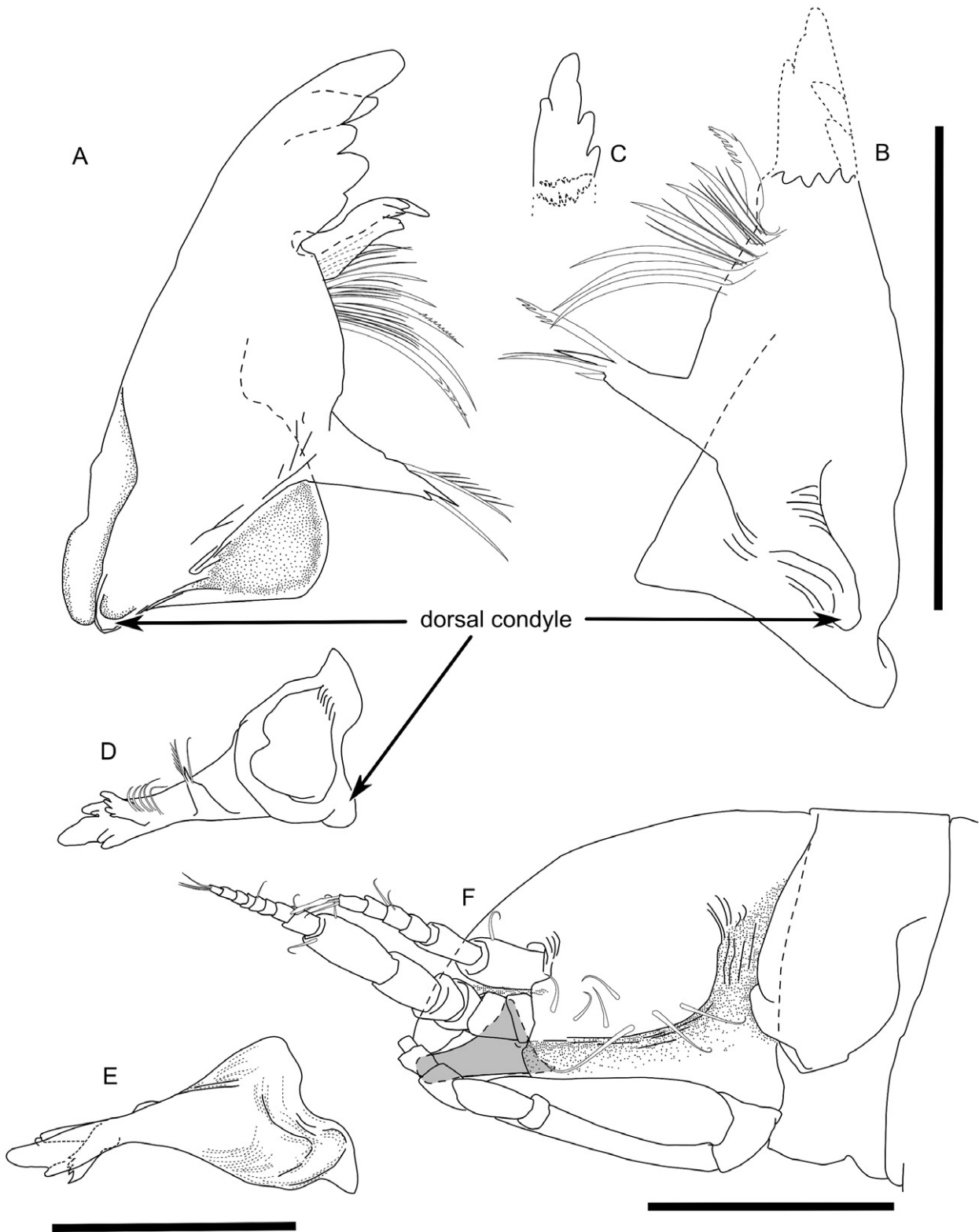
Pereonite 1 length 0.25 pereonite 7 length, width 0.52 pereonite 7 width. Pleotelson length 0.22 body length, 1.5 width, width 0.95 pereonite 7 width; paired dorsal organ on the tergal surface in cuticular tubercles; apex length 0.13 pleotelson length, laterally with four simple setae. Pleopodal cavity width 0.79 pleotelson width.

Antennula (Fig. 3F) relative length ratios of articles 1.0, 0.70, 0.33, 0.33, 0.33, 0.33, L/W ratios of articles 1.5, 2.0, 1.0, 1.0, 2.0, 2.0. Article 1 with one simple seta. Article 2 with one simple seta. Article 4 with two simple setae. Article 6 with two aesthetascs, aesthetascs simple, tubular. Antenna (Fig. 3F) length 0.18 body length. Ischium angular with medial projection, about as long as coxa. Merus about as long as coxa, basis, and ischium together, articulating distolaterally on ischium, antennal proximodistal axis with distinctly sharp bend. Carpus longer than merus, articulating distolaterally on merus, antennal proximodistal axis with distinctly sharp bend between merus and carpus. Flagellum with eight articles and two to six short setae distally on each article.

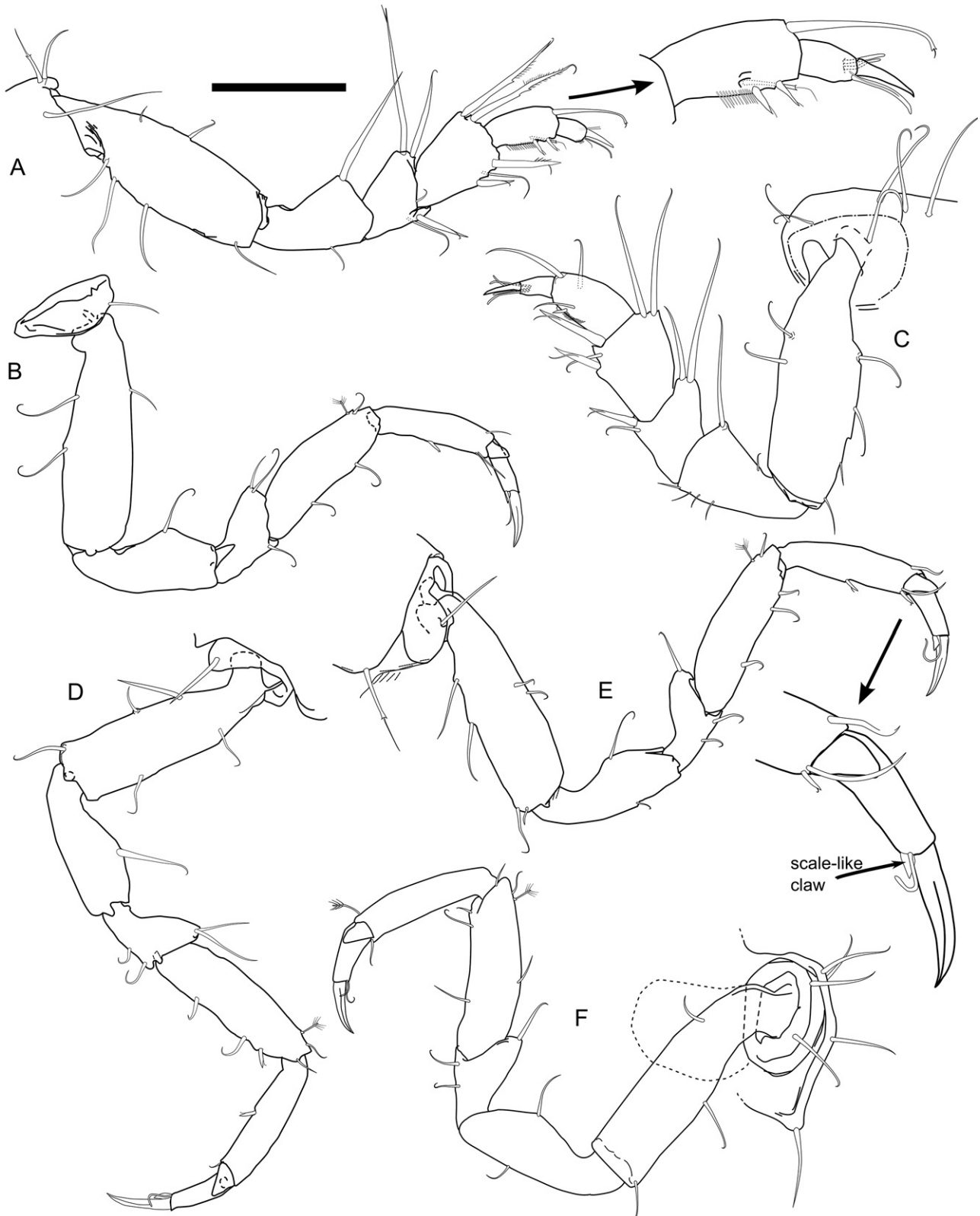
Pereopod I (Fig. 4) length 0.26 body length; article L/W ratios 3.3, 1.3, 0.67, 1.2, 1.5, 1.0; relative article length ratios 1.0, 0.40, 0.20, 0.35, 0.30, 0.10. Ischium longer than wide, dorsal margin with two setae: one long, simple on dorsal lobe apex and one short, simple proximally. Merus dorsal margin with two long, simple setae, ventral margin with two setae: one simple, one robust, bifid. Carpus distodorsally with two long, simple setae, ventrally with three setae: one short, robust, bifid, one long, slender, one monoserrate, robust, bifid. Propodus dorsally with two simple setae: one long distally and one small, more proximally; ventrally with two setae: one simple, slender, one bifid,



**Figure 2.** *Urstylis zapiola* gen. et sp. nov. A, B, adult male holotype USNM 1208013. C, adult female paratype USNM 1208014. D, adult male paratype, AM P. 90631. A, dorsal habitus with enlargement of uropodal exopod. B, lateral habitus. C, dorsal habitus with enlargement of structure on pleotelson. D, antennula and antenna, *in situ*, lateral view. Scale bars = 0.5 mm, (A–C); 0.1 mm (D); 0.05 mm (C enlargement).



**Figure 3.** *Urstylis zapiola* gen. et sp. nov., mandibles. A–E, adult male paratype AM P. 90631, F, adult female paratype USNM 120801. A, left mandible, dorsal view. B, right mandible, dorsal view. C, right incisor process. D, E, left mandible, medial view and lateral view, respectively. F, head, left lateral view, showing position of mandible (darkened). Scale bars = 0.1 mm (A–C); 0.1 mm (D, E); 0.2 mm (F).



**Figure 4.** *Urstylis zapiola* gen. et sp. nov., anterior pereopods. A, B, D, E, adult male paratype AM P. 90631. C, F, adult female paratype USNM 120801. A, C, pereopod I. B, D, E, pereopods II–IV; E, pereopod IV with enlargement of dactylus and claws (arrow). F, pereopod III. Scale bar = 0.1 mm.



robust; with row of setules proximally to bifid seta. Dactylus distally with three sensillae, dorsal claw length 1.0 dactylus length, robust.

Pereopod II slightly longer than pereopod I. Ischium dorsally with one simple seta on dorsal lobe apex. Merus dorsally with two simple setae distally on apex, ventrally with one simple seta distally. Carpus with one distodorsal and two ventral simple setae.

Pereopod III (Fig. 4F) length 0.34 body length; article L/W ratios 3.6, 2.2, 1.0, 3.0, 3.3, 2.5; relative article length ratios 1.0, 0.61, 0.28, 0.67, 0.56, 0.28. Ischium dorsal lobe flat and rounded; proximally and on apex without seta; distally with one simple seta. Merus dorsally on apex with one simple seta, ventrally with two simple setae. Carpus dorsally with four setae: one simple medially, one broom seta and two simple distally, ventrally with three simple setae. Dactylus distally with two sensillae.

Operculum (Fig. 5C) length 1.5 width, 0.82 pleotelson dorsal length. Apical width 0.82 operculum maximal width. Lateral fringe of setae absent. With 14 pappose setae on apex, completely covering anal opening. Uropod broken in female.

*Female genital system:* Female copulatory duct (cuticular organ) (Fig. 1). The opening for the spermathecal duct is located ventrally adjacent to the articular membrane at the anterior corner of pereonite 5. The spermathecal duct extends medially toward the posterior margin of the ovary and then has a sharp turn posteriorly. Rather than intersecting the oviduct midway, the duct ends in an indistinctly demarcated region just inside the oopore; the position of this structure is consistent with it being the spermatheca, although no sperm were observed in that region. The duct was highly reflective in the preparatory female specimen studied (USNM 1208014), so it may have contained sperm from a prior mating encounter as insemination in janiroideans occurs well before the parturial moult (Veuille, 1980; Wilson, 1987b, 1991). The oopore was medial and anterior to the coxa of pereopod V, and the oviduct continued in a dorsomedial direction to the ovary, which terminated just beyond the anterior margin of pereonite 5. The ovae were indistinct and did not fill the lumen of the ovary, indicating that the female was not fully in reproductive condition. The female was at least in preparatory condition because developing oostegites were observed on pereonites 1–4 beneath the cuticle adjacent to the coxae (Fig. 1).

#### *Description of adult male*

Body (Figs 2, 6) length 2.0 mm, 4.5 width. Cephalothorax (Fig. 6) frontal ridge absent; length/width ratio subequal to female, length 0.83 width, 0.16 body

length; without setae dorsally, posterolateral corners rounded, posterolateral setae present. Pereonite 1 length 0.31 width, 0.06 body length. Pereonite 2 length 0.37 width, 0.07 body length. Pereonite 3 length 0.41 width, 0.08 body length. Pereonite 4 width 1.1 pereonite 5 width, length 0.56 width.

Pereonites 5–7 similar in shape, size and setation, subequal in length to pereonite 4. Length 0.6 width. Pleonite 1 length 0.23 pereonite 7 length, with two simple setae. Pleotelson in dorsal view similar to female. Length 1.4 width, 0.22 body length, width 0.95 pereonite 7 width. Posterior apex length 0.13 pleotelson length, pleopodal cavity width 0.81 pleotelson width.

Antennula (Figs 2D, 6C) length 0.48 head width, 0.50 antenna length, width 1.0 antenna width; article L/W ratios 1.8, 1.3, 0.5, 1.0, 0.5, 3.0; relative article length ratios 1.0, 0.57, 0.14, 0.29, 0.14, 0.43; of six articles; terminal and penultimate articles with two tubular aesthetascs, respectively.

Antenna (Fig. 2D) length 0.18 body length, basal articles slightly more stout than in female, flagellum of nine articles, precoxa–ischium squat, globular, coxa–ischium longer than precoxa; ischium distally with one simple seta. Merus longer than ischium, distally with one simple seta. Carpus slightly stouter than in female, with two subdistal setae.

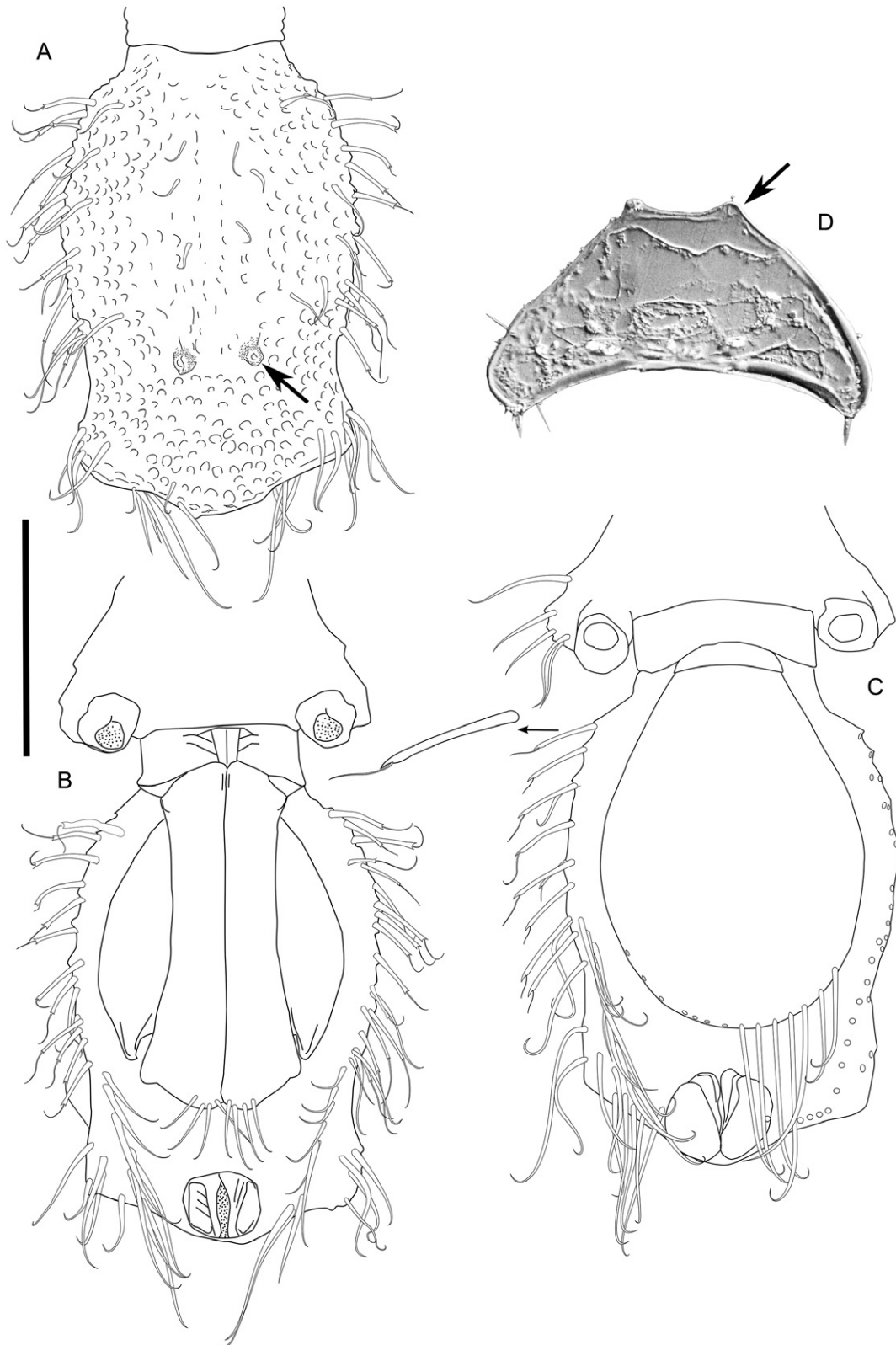
Mandibles (Fig. 3) molar with two spines and two to three setulate spines; left mandible incisor process with five cusps, lacinia mobilis with four denticles; right mandible incisor process with four cusps, lacinia mobilis spine-like, with eight denticles.

Maxillula (Fig. 7B, C) lateral lobe terminally with 11 robust and three slender setae. Maxilla (Fig. 7D) lateral lobe length subsimilar to middle lobe length, with six setae terminally, four long, two shorter distomedially; middle lobe with five setae terminally, four long, one short distomedially; medial lobe terminally with seven setae, medially with a setal row.

Maxilliped (Figs 6C, 7E, F) basis length 3.9 width, with two coupling hooks; endite distally truncate, with three fan setae, eight slender setae, and one spine-like seta distomedially, lateral margin with row of setae; epipod length 2.8 width, 0.81 basis length. Palp article 1 shorter than article 3, distomedially with one seta, distolateral extension short, length 0.21 article 1 length, rounded; article 2 wider than articles 1 and 3, with two distomedial setae; article 3 with five medial setae; article 4 distomedial extension minute, with four setae; article 5 terminally with four setae.

Pereopods' I–VII (Figs 4, 5) dactylus dorsal claw subequal to dactylus in length with one sensilla inserting terminally.

Pereopod I (Fig. 4A) length 0.22 body length; article L/W ratios 3.0, 1.8, 0.80, 1.4, 1.7, 2.0; relative article



**Figure 5.** *Urstylis zapiola* gen. et sp. nov., pleotelson. A, B, adult male paratype AM P. 90631, dorsal and ventral views, respectively. C, adult female paratype USNM 120801, ventral view. D, section through transversal plane of the pleotelson at the location of the paired dorsal cuticular tubercles (arrow). Scale bar = 0.2 mm.

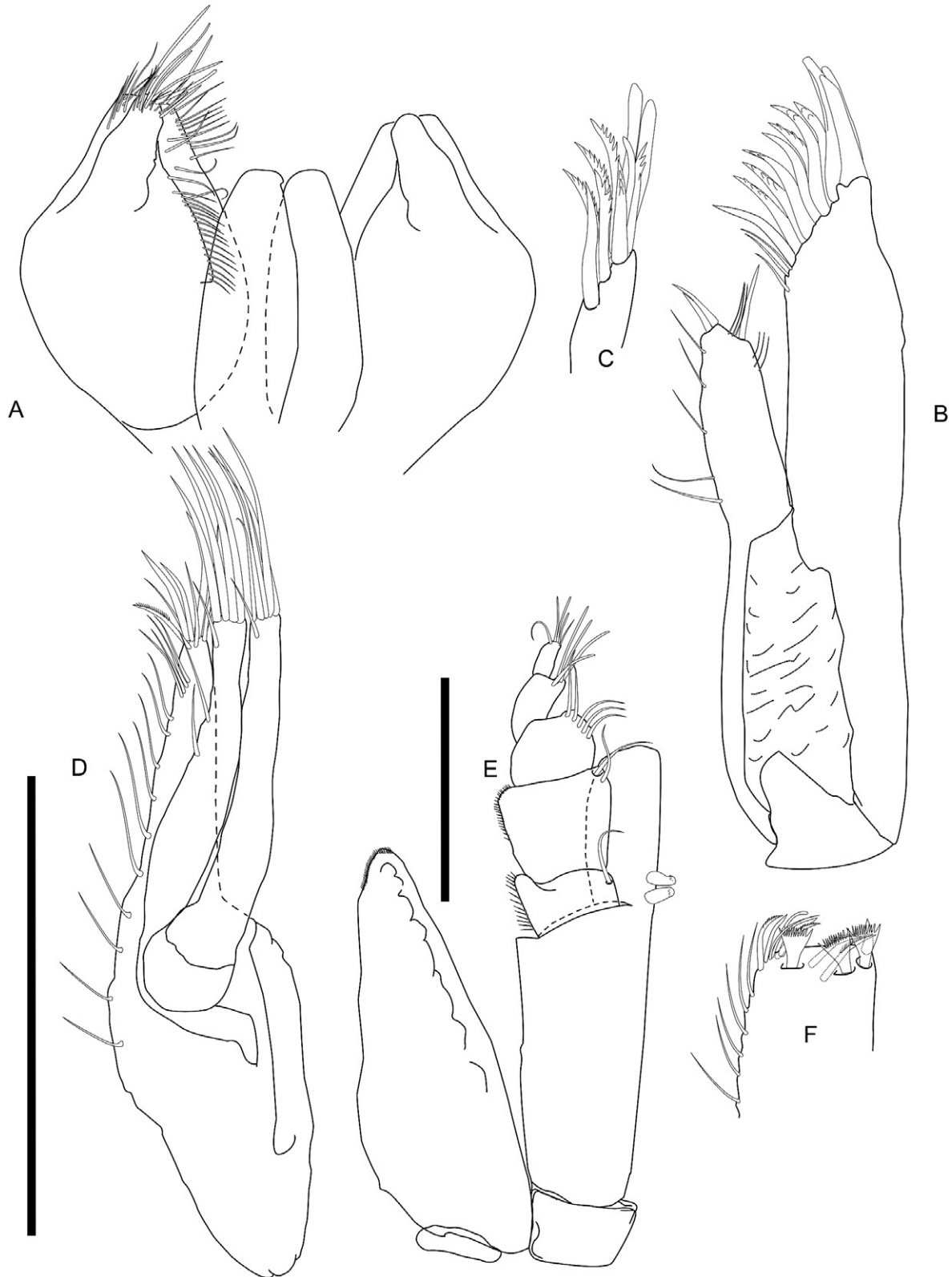


**Figure 6.** *Urstylis zapiola* gen. et sp. nov., views of head. A–C, adult male paratype, AM P. 90631. A, dorsal view, dotted structures showing internal attachment of mandibular muscles. B, C, ventral view, without and with maxilliped, respectively. Scale bar = 0.2 mm.

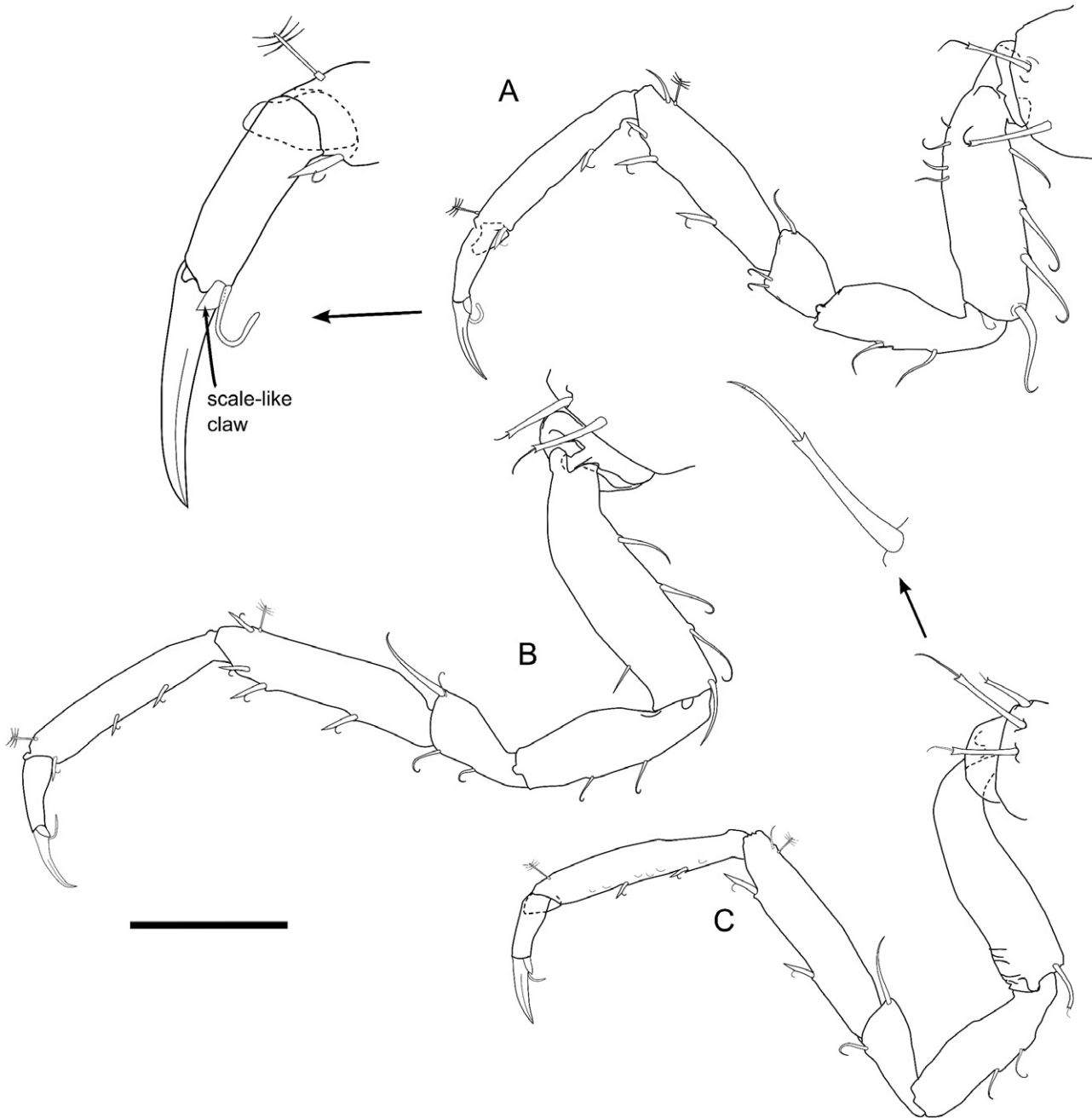
length ratios 1.0, 0.5, 0.22, 0.39, 0.28, 0.11. Ischium dorsally with one simple seta. Merus dorsally with one simple seta. Merus dorsally with two long, bifid setae, ventrally with three setae: one thin, one robust, bifid distally and one small more laterally at mero-carpal articulation. Carpus with two distodorsal long setulate, bifid setae, ventrally with three setae: one thin, two robust,

bifid. Propodus with one long distodorsal seta and two short, ventral setae.

Pereopod II (Fig. 4B) length 0.27 body length; article L/W ratios 3.4, 2.0, 1.0, 2.8, 4.0, 4.0; relative article length ratios 1.0, 0.59, 0.29, 0.65, 0.47, 0.24. Ischium dorsally with one simple seta on apex. Merus dorsally with two simple setae on apex, ventrodorsally



**Figure 7.** *Urstylis zapiola* gen. et sp. nov., mouthparts in ventral view. A–F, adult male paratype AM P. 90631. A, paragnaths. B, maxillula. C, maxillula lateral lobe, medial view. D, maxilla. E, maxilliped. F, maxilliped endite, distal margin, enlargement of E. Scale bars = 0.1 mm (A–D); 0.1 mm (E).



**Figure 8.** *Urstylis zapiola* gen. et sp. nov., posterior pereopods. A–C, adult male paratype AM P. 90631, pereopods V–VII. Scale bar = 0.1 mm.

with one simple seta. Carpus dorsodistally with one small, simple seta, ventrally with two setae.

Pereopod III (Fig. 4D) length 0.30 body length; article L/W ratios 3.6, 2.5, 0.80, 3.0, 3.3, 2.5; relative article length ratios 1.0, 0.56, 0.22, 0.67, 0.56, 0.28. Setation as in female.

Pereopod IV (Fig. 4E) length 0.3 body length; article L/W ratios 3.4, 2.8, 1.0, 3.3, 3.3, 2.5; relative article length ratios 1.0, 0.65, 0.29, 0.76, 0.59, 0.29.

Pereopods V–VII (Fig. 8) similar to pereopods II–IV in size, carpi and propodi slightly more elongate; setation similar: ischium dorsally without seta; midventrally with two simple setae. Merus distodorsally with two setae: one minute, one long, prominent; midventrally and distoventrally with one simple seta; distodorsally with one bifid seta; midventrally with two robust, bifid setae; distoventrally with one robust, bifid seta.

Pereopod V (Fig. 8A) 0.31 body length; article L/W ratios 3.0, 2.75, 1.25, 3.25, 6.5, 2.5; relative article length ratios 1.0, 0.73, 0.33, 0.87, 0.87, 0.33.

Pereopod VI (Fig. 8B) length 0.34 body length; article L/W ratios 3.4, 3.0, 1.5, 3.5, 4.3, 2.0; relative article length ratios 1.0, 0.71, 0.35, 0.82, 0.76, 0.24.

Pereopod VII (Fig. 8C) length 0.31 body length, slightly smaller pereopod VI length; article L/W ratios 3.5, 2.5, 2.0, 4.7, 6.5, 2.0 relative article length ratios 1.0, 0.71, 0.43, 1.0, 0.93, 0.29.

Pleopod I (Figs 5B, 9A, B) length 0.73 pleotelson length, 2.5 width, distal width 1.3 proximal width. Distomedial lobes with ten long, simple setae altogether; distoventrally with minute, simple setae present, in semicircular arrangement on both sides.

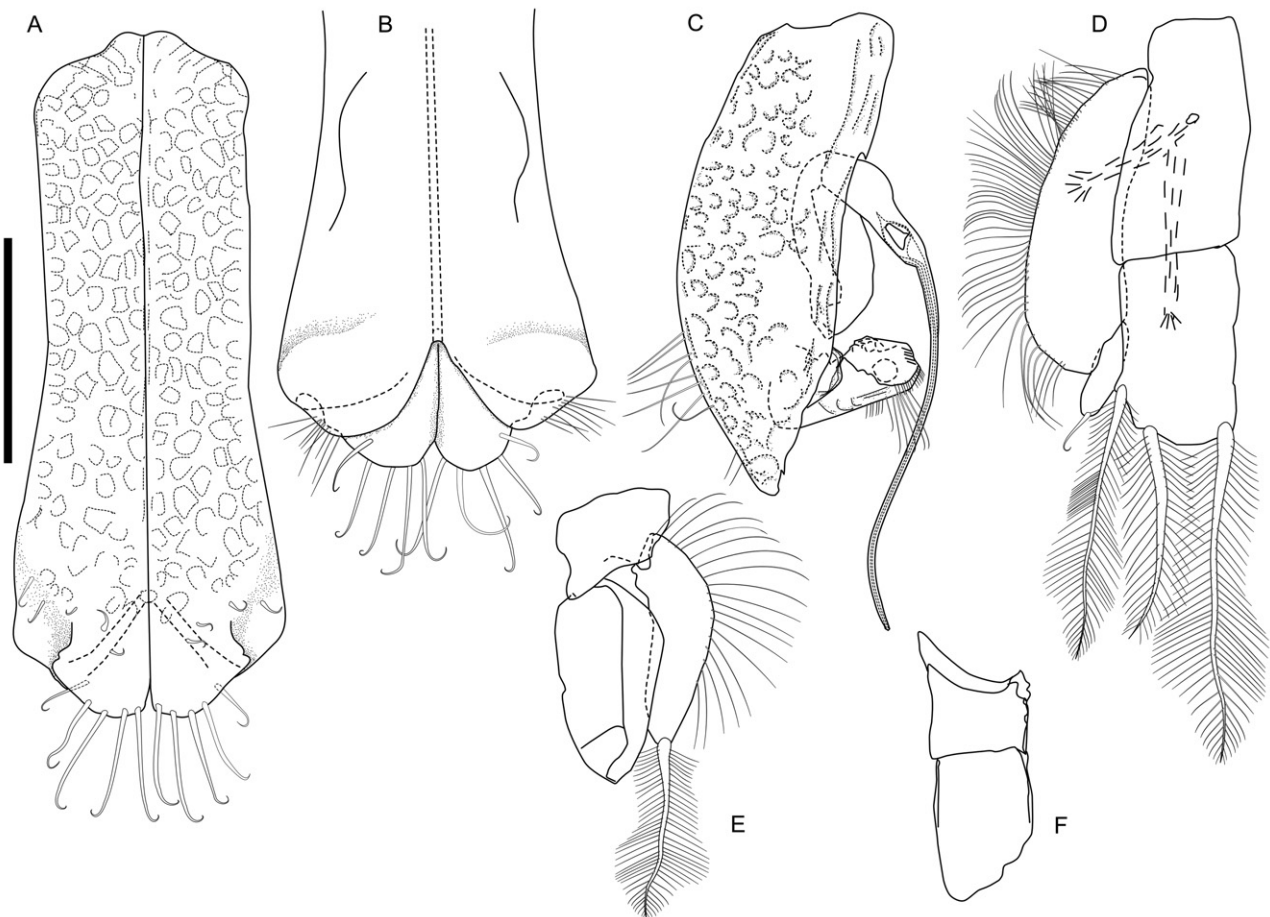
Pleopod II (Fig. 9C) protopod apex tapering, with rounded tip, distolateral margin with ten thin setae. Endopod distance of insertion from protopod distal margin 0.36 protopod length. Stylet sinuous, narrowing distally to sperm-duct opening, extending beyond

distal margin of protopod, length 0.95 protopod length; sperm-duct opening located 0.17 stylet length from stylet proximal margin. Exopod length 0.32 protopod length, with rows of fine and minute setae laterodistally.

Pleopod III (Fig. 9D) length 2.1 width, protopod length 1.7 width, 0.53 pleopod III length; endopod plumose terminal setae longer than endopod, medial seta longest, 0.80 pleopod III length. Exopod length 0.84 pleopod III length, proximal article broadened distally, width 0.85 endopod width; distal article length 0.30 proximal article length, width 0.30 proximal article width, subterminally with one seta; lateral fine setae about as long as exopod width.

Pleopod IV (Fig. 9E) length 1.9 width, endopod length 1.8 width, about twice as long as protopod. Exopod length 3.3 width, 1.1 endopod length; terminal plumose seta length 0.88 exopod length. Pleopod V (Fig. 9F) length 2.4 width.

Uropod (Fig. 2A, B) length 2.4 pleotelson length; protopod length 17.6 width; with numerous scattered



**Figure 9.** *Urstyliis zapiola* gen. et sp. nov., pleopods, adult male paratype AM P. 90631. A, B, pleopod I, ventral and dorsal view, respectively. C–E, pleopods II–V, ventral view. Scale bar = 0.1 mm (A, C–F).

simple setae. Endopod inserting terminally, length 0.28 protopod length, 8.6 width, width narrower than protopod. Exopod minute, length about 0.05 endopod length, globular, with two setae.

#### Remarks

*Urstylis zapiola* was collected in a particularly large epibenthic sample (WHOI 247) from the abyssal plain of the Argentine Basin: 1316 individuals and 72 species of isopods. This locality is below 5200 m, showing that isopod species richness can be high, even at the greatest abyssal depths, contra the source-sink theory of Rex *et al.* (2005) that abyssal diversity should be a subset of and therefore smaller than bathyal diversity. For a detailed taxa list see also Supporting Information Appendix S2.

### URSTYLIS SOLICOPIA SP. ET GEN. NOV.

FIGURES 11–21

#### Zoobank registration

urn:lsid:zoobank.org:act:8BCACEA0-2180-4CB8-ACF5-0F36DE73A3B8

#### Etymology

The species name refers to the type locality in the Pacific Ocean (Clarion-Clipperton Fracture Zone; CCFZ) being rich in manganese nodules (Fig. 10). The

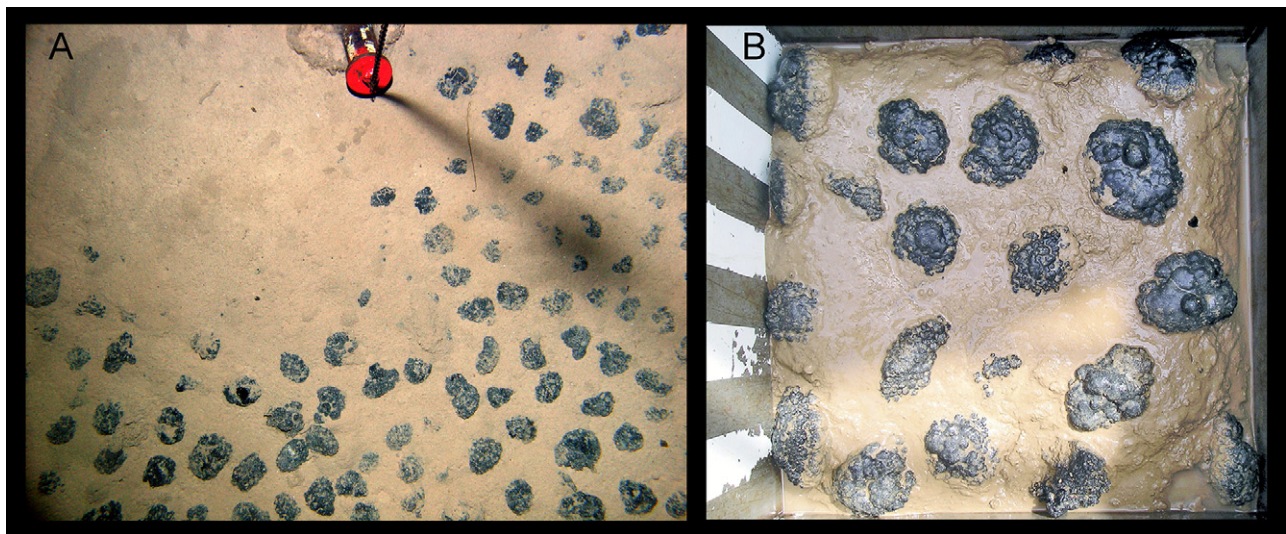
epithet *solicopia* is derived from the Latin words *solis*, singular genitive of *solum* earth, bottom, and *copia* meaning plentiful translating into *of plentiful bottom*. It is a feminine adjective.

#### Type fixation

Ovigerous female holotype, 2.0 mm, ZMH K-43070, designated here.

#### Type material examined

ZMH K-43070: ovigerous female holotype, 2.0 mm, station (st.) 8717. ZMH K-43052: non-ovigerous female paratype, 2.0 mm, st. 8581, greatly damaged; ZMH K-43053: one non-ovigerous female anterior fragment, sputter-coated for SEM, st. 8687; ZMH K-43054: juvenile female paratype, 1.7 mm, st. 8698; ZMH K-43055: adult male paratype, 2.1 mm, st. 8581, dissected for illustrations; MIMB 28178: adult male paratype, 1.7 mm, st. 8719; ZMH K-43057: juvenile female paratype, 1.2 mm, st. 8670; ZMH K-43058, juvenile female paratype, 1.6 mm, st. 8571; ZMH K-43059: non-ovigerous female paratype, 2.0 mm, st. 8615, greatly damaged; ZMH K-43060: juvenile male paratype, 1.1 mm and juvenile female paratype, 1.2 mm; st. 8660; MIMB 28178: one juvenile female, 1.6 mm, and two mancae paratypes, 1.1 mm, st. 8717; ZMH K-43062: juvenile female paratype, 1.5 mm, st. 8721; ZMH K-43069: ovigerous female paratype, 2.0 mm, st. 213.



**Figure 10.** Bottom characteristics in the Russian claim in the Clarion-Clipperton Fracture Zone manganese-nodule area at the type locality of *Urstylis solycopia* gen. et sp. nov. Station 90, R/V Yuzhmorgeologia cruise 4–06; 13°13.11780'N, 134°29.49900'W; 4804 m. A, photograph taken by autonomous camera mounted on giant box corer before impact. B, box core sample, size of sample 0.25 m<sup>2</sup>, scale: one interval on left inner wall of the box = 5 cm. Courtesy of Slava Melnik, State Scientific Center Yuzhmorgeologia.

**Table 1.** *Urstylis solycopia* gen. et sp. nov. type locality. Details of sampling locations and dates

R/V name	Project #	Station #	Latitude	Longitude	Depth (m)	Date
Yuzhmorgeologia	4-06	90	13° 13.11780' N	134° 29.49900' W	4804	15.viii.2006
Yuzhmorgeologia	18-01	213	13° 53.24598' N	129° 06.48198' W	4750	27.vii.2003
Gelendzhik	4-08	8571	12° 59.67060' N	133° 46.29540' W	4790	22.vii.2009
Gelendzhik	4-08	8581	13° 04.77720' N	133° 57.27540' W	4840	24.vii.2009
Gelendzhik	4-08	8615	13° 22.21440' N	133° 55.15320' W	4905	28.vii.2009
Gelendzhik	4-09	8660	12° 50.52120' N	133° 23.60700' W	4824	19.xii.2010
Gelendzhik	4-09	8670	12° 55.36980' N	133° 37.71120' W	5031	24.xii.2010
Gelendzhik	4-09	8687	13° 09.42720' N	133° 21.59220' W	4882	06.i.2011
Gelendzhik	4-09	8698	13° 16.17480' N	133° 25.06380' W	4947	05.i.2011
Gelendzhik	4-09	8717	13° 28.17420' N	133° 30.07080' W	4889	02.i.2011
Gelendzhik	4-09	8719	13° 29.02080' N	133° 32.77380' W	4860	30.xii.2010
Gelendzhik	4-09	8721	13° 30.13380' N	133° 30.50220' W	4859	30.xii.2010

R/V, Research Vessel.

#### Type locality

Collected with box corer from the Russian claim in the Clarion-Clipperton Fracture Zone manganese-nodule area during several expeditions by the Russian Scientific Centre 'Yuzhmorgeologia' (Federal State Unitary Geological Enterprise, Southern Scientific & Production Association for Marine Geological Operations), Gelendzhik (Table 1). The locality is characterized by soft sediment with manganese nodules of varying size and density (Fig. 10).

#### Type material – remarks

The holotype ovigerous female and several paratypes show some shrinking artefacts possibly caused by treatment with ethanol and low degree of calcification. These caused the depressions shown in the habitus illustrations of the female. The natural condition is shown in the SEM figures. Uropods are broken and missing in the complete type series except in one manca, which is extremely damaged and therefore not illustrated.

#### Further records

GDFW collection: USA National Oceanic and Atmospheric Administration (NOAA) Deep Ocean Mining Study (DOMES), 0.25 m<sup>2</sup> box corer samples: DJ08, manca, DJ08 24.xi.1977 9°25.23'N, 151°4.46'W, 5205 m; DJ32, manca, 30.xi.1977, 9°16.00'N, 151°56.10'W, 5043 m; DJ39, manca, 03.xii.1977, 9°35.80'N, 151°6.80'W, 5117 m; GDFW collection, DJ46, brooding female, five mancae, 19.v.1978, 9°28.00'N, 151°27.60'W, 5216 m; DJ49, manca, 20.v.1978, 9°23.40'N, 151°25.30'W, 5171 m; DJ73, manca, 27.v.1978, 9°28.10'N, 151°15.60'W, 5107 m.

#### Diagnosis

Body dorsoventrally flattened, tergite surfaces rather hirsute; pereonite 4 width subequal to pereonite 5

width, pereonite 6 shorter pereonite 5; pereonite 7 posterolateral margins projecting posteriorly. Pleotelson length/width ratio 1.3, paired dorsal organ expressed as pedestal broom setae articulating on flat conical elevations. Pereopod I ischium dorsal lobe with two setae; pereopods V–VII ischium and carpus mid-dorsally with seta present.

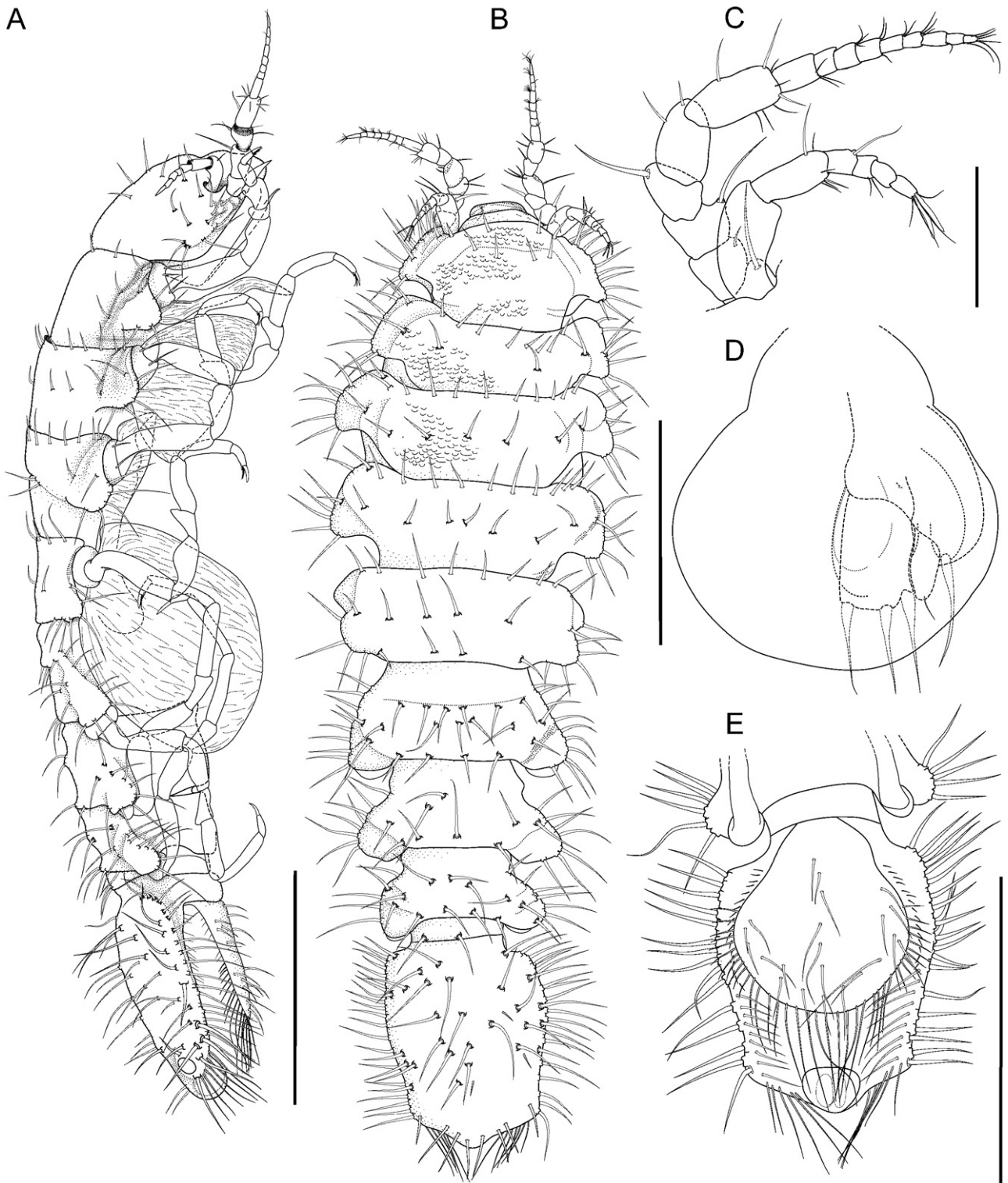
#### Description of female

Body (Figs 11A, B, 12A, C, E) length 2.0 mm, 3.4 width, dorsoventrally slightly flattened, tergite surfaces hirsute, with long setae on pedestal (calcified) articulations along lateral and anterior tergite margins. Ventral spines on pereonites 1–7 absent. Imbricate ornamentation on cephalothorax–pleotelson covering whole tergite. Cephalothorax–pereonite VII posterolateral setae simple, asensillate.

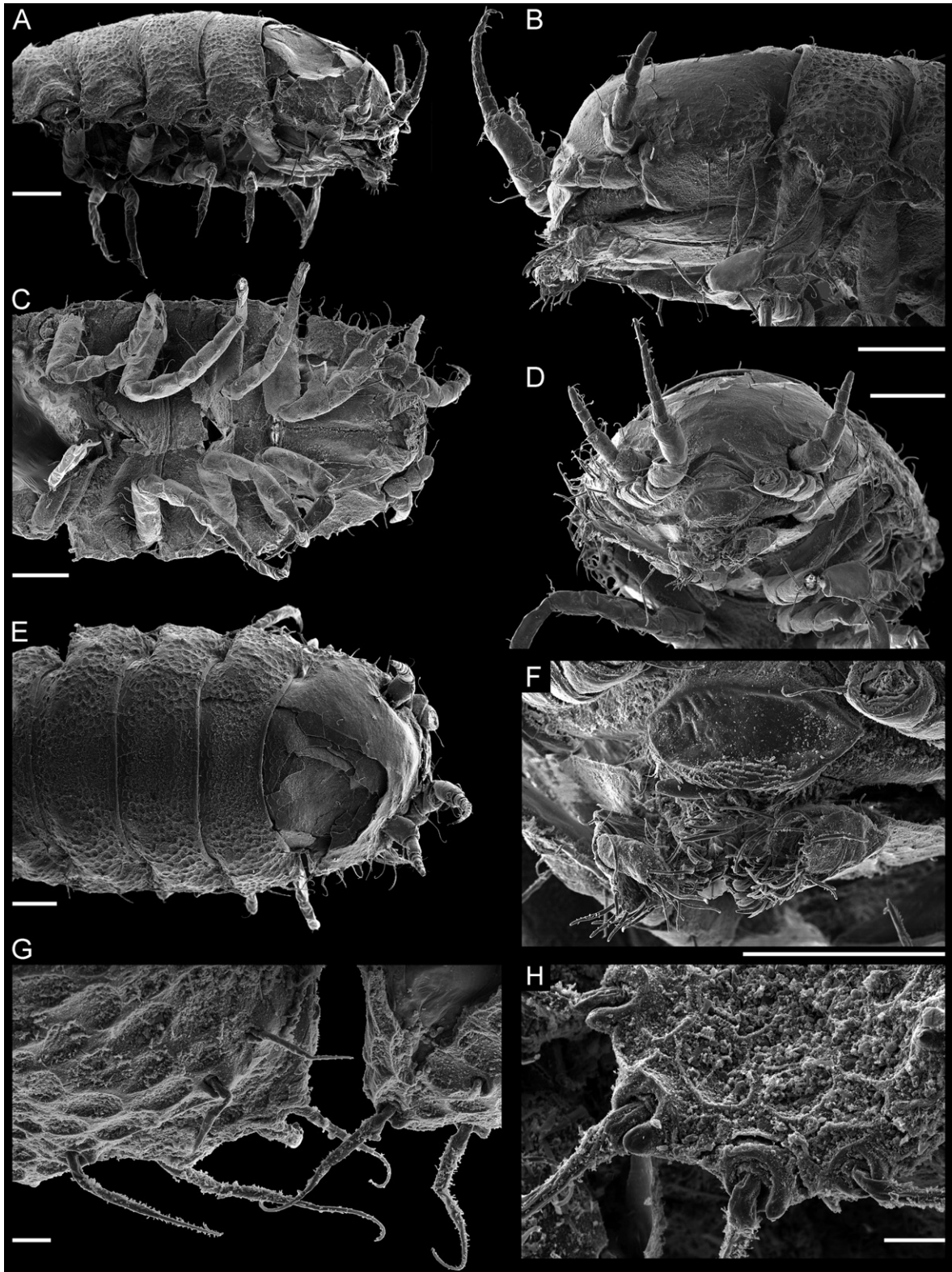
Cephalothorax (Figs 11A, B, 12A–E) length 0.61 width, 0.13 body length; frons in dorsal view convex, smooth, frontal ridge present, slightly convex; dorsal surface with array of setae. Posterolateral margins angular, blunt; posterolateral setae asensillate, simple, flexibly articulated on calcified pedestal articulations. Pereonite 1 length 0.24–0.29 width, 0.07 body length, anterior margin straight. Pereonite 2 length 0.28–0.32 width, 0.08–0.09 body length. Pereonite 3 length 0.32–0.37 width, 0.09–0.10 body length. Pereonite 4 width 1.1 pereonite 5 width, length 0.37–0.38 width; lateral margins in dorsal view convex, almost parallel; posterolateral margins rounded.

Pereonites 5–7 (Fig. 11A, B) of similar shape, diminishing in length and width from 5 to 7. Posterior tergite margins with four simple, asensillate, flexibly articulating setae; setae long, extending beyond posterolateral margin. Posterolateral margins rounded. Coxae setose, setae simple, asensillate, on





**Figure 11.** *Urstylis solicipia* gen. et sp. nov., ovigerous female holotype ZMH K-43070. A, habitus, lateral. B, habitus, dorsal. C, antennula and antenna, dorsomedial, *in situ*. D, pleopods, ventral, *in situ*. E, pleotelson, ventral. Scale bars = 0.5 mm (A, B, E); 0.1 mm (C); 0.2 mm (D).



**Figure 12.** *Urstylis solicopia* gen. et sp. nov., paratype female fragment ZMH K-43053. A, lateral habitus. B, lateral cephalothorax. C, ventral habitus. D, frontal head. E, dorsal habitus. F, mouthfield. G, cephalothorax right posterolateral margin and pereonite anterolateral margin. H, pereonite 2 posterolateral margin, lateral view. Scale bars = 0.1 mm (A–F); 10 µm (G, H).

pedestals. Pereonite 5 length 0.45 width, 1.1 pereonite 4 length. Pereonite 6 length 0.44 width, 0.91 pereonite 5 length. Pereonite 7 length 0.43–0.75 width.

Pleonite 1 length 0.32 pereonite 7 length, dorsally with two setae. Pleotelson length 0.22–0.24 body length, 1.25–1.32 width, slightly wider than or as wide as pereonite 7; paired dorsal organ expressed as pedestal broom setae. Posterior margin straight or slightly concave laterally at uropod insertions, apex convex, length 0.13–0.18 pleotelson length, posterolaterally with four simple setae. Pleopodal cavity width 0.80 pleotelson width.

Antennula (Fig. 11C) length 0.45 head width, 0.54 antenna length; width 0.90 antenna width. Article 1 without setae. Article 2 with six simple setae. Article 3 length subequal width, with one simple seta. Article 4 length subequal width, with two simple setae. Article 5 distinctly longer than wide, cylindrical. Article 6 with two aesthetascs.

Antenna (Fig. 11C) length 0.18 body length; relative length ratios of articles 1.0, 1.3, 1.3, 1.3, 2.0, 2.3, L/W ratios of articles 0.75, 1.0, 0.80, 1.0, 2.5, 2.3. Basis angular with dorsolateral projection; longer than coxa. Ischium angular with medial projection, longer than coxa. Merus shorter than articles 1–3 together, distally with one simple seta. Merus articulating distolaterally on ischium, antennal proximodistal axis with distinctly sharp bend. Carpus longer than merus, distally with seven simple setae. Flagellum with nine articles. Mouthparts as in female.

Pereopod I–VII (Figs 13–15) dactyli with two claws and two sensillae inserting terminally and two sensillae subdistally, pereopod I dorsal claw subequal to dactylus in length, ventral claw length 0.5 dorsal claw length, pereopods' II–VII dorsal claw length about 0.6 dactylus length, ventral claw scale-like, tiny, length 0.23–0.25 dorsal claw length.

Pereopod I (Figs 13A, 14A–E) length 0.24 body length; article L/W ratios 2.9, 1.5, 0.67, 1.3, 2.0, 2.0; relative article length ratios 1.0, 0.45, 0.20, 0.40, 0.30, 0.10. Ischium dorsal margin with two simple setae, dorsal lobe projecting near basal width of article. Merus dorsal margin with two simple setae, one long, one short, ventral margin with two setae, one small, simple, one long, bifid, monoserrate. Carpus dorsally with two simple setae. Articular plate on propodus absent; dactylus distally with two sensillae, dactylus dorsal claw length 1.0 dactylus length.

Pereopod II (Figs 13B, 14G) length 0.30 body length; article L/W ratios 3.5, 1.0, 2.0, 2.5, 3.3, 2.5; relative article length ratios 1.0, 0.48, 0.24, 0.48, 0.48, 0.24. Ischium dorsally with two simple setae, one long medially, one short distally, with dorsal setae on dorsal margin. Merus dorsally with two simple setae, one long, one short and slender, with dorsal setae on dorsal margin, ventrally with two simple

setae: one short medially, one long distally. Carpus distodorsally with one simple seta, ventrally with three bifid setae. Pereopod III (Fig. 13C) length 0.31 body length; article L/W ratios 3.5, 2.2, 1.0, 2.8, 3.7, 2.0; relative article length ratios 1.0, 0.52, 0.24, 0.52, 0.52, 0.19. Ischium with one simple, not prominent seta on apex. Merus dorsally with two long, simple setae, ventrally with two short, simple setae. Carpus distodorsally with one broom seta and one short simple seta; ventrally with three setae: one bifid medially, one simple and one bifid subdistally. Pereopod IV length 0.31 body length, about as long as neighbouring pereopods; article L/W ratios 3.0, 2.2, 1.0, 3.3, 3.7, 2.0; relative article length ratios 1.0, 0.61, 0.28, 0.72, 0.61, 0.22.

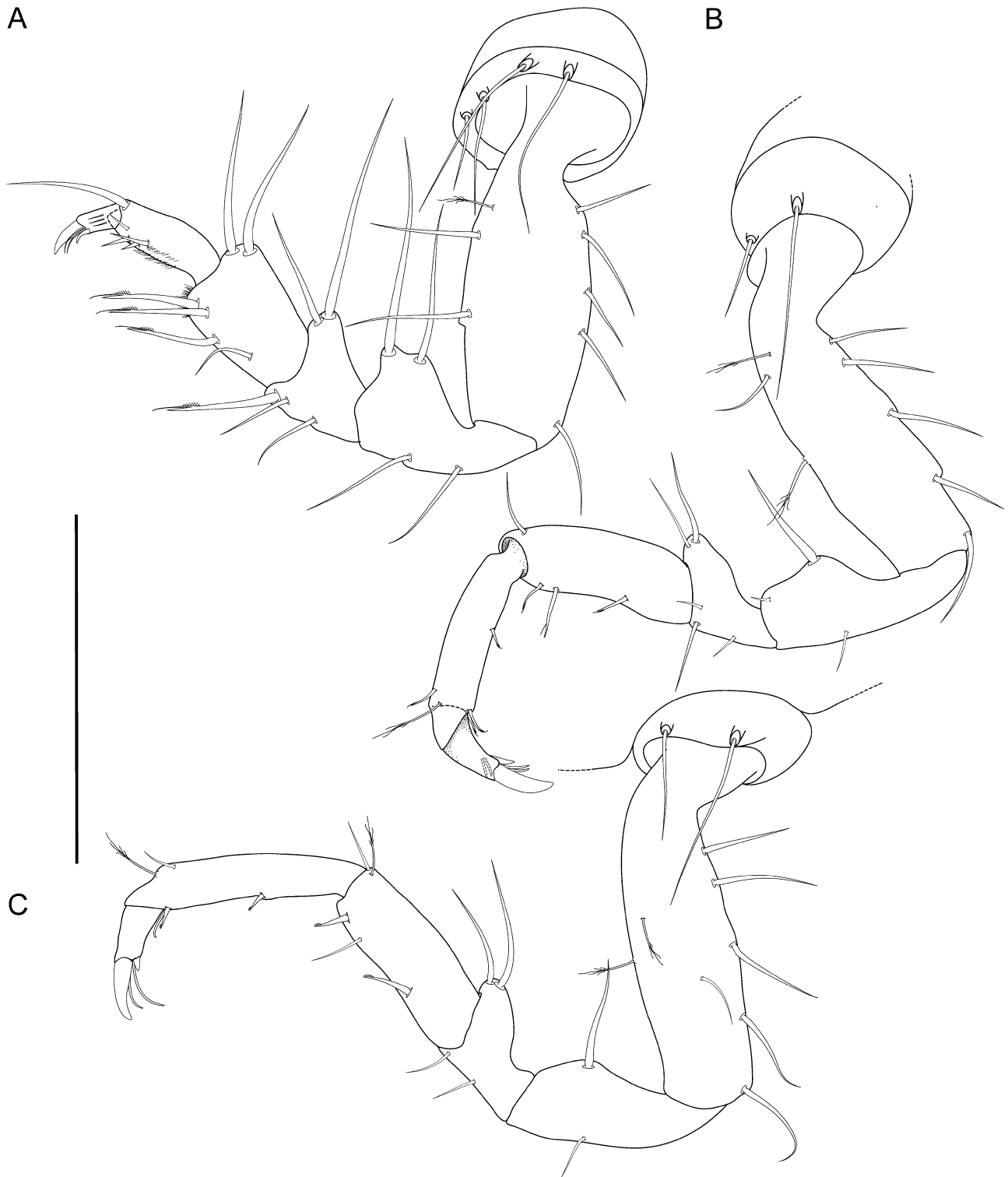
Pereopods V–VII (Fig. 15) similar in setation. Ischium mid-dorsally with one simple seta, distodorsally with setae absent, midventrally with two simple setae. Merus distodorsally with two setae, one simple, slender, one bifid, midventrally with one simple, small seta, distoventrally with two setae, one simple, long, one simple, small. Carpus mid-dorsally and distodorsally with one bifid seta respectively, distoventrally with three bifid setae. Pereopod V length 0.33 body length; article L/W ratios 3.4, 2.2, 1.8, 3.3, 6.5, 2.5; relative article length ratios 1.0, 0.65, 0.41, 0.76, 0.76, 0.29. Pereopod VI length 0.35 body length; article L/W ratios 4.3, 2.8, 2.0, 5.0, 7.5, 2.5; relative article length ratios 1.0, 0.65, 0.47, 0.88, 0.88, 0.29. Pereopod VII length 0.37 body length; relative article length ratios 1.0, 0.61, 0.50, 0.83, 0.89, 0.28; article L/W ratios 3.6, 2.8, 2.3, 5.0, 8.0, 2.5.

Operculum (Fig. 11D, E) ovoid, length 1.1 width, 0.69 pleotelson dorsal length; apical width 0.82 operculum maximal width. Lateral fringe consisting of ten to 11 setae, with fluent transition to row of 17 asetulate apical setae. Apical setae completely covering anal opening.

Uropod (measured from other material) length 2.8 pleotelson length; protopod length 23.3 width, 2.1 pleotelson length, protopod distal margin blunt, endopod insertion terminal; endopod length 12.1 width, 0.37 protopod length, endopod width; exopod length 0.05 endopod length.

#### *Description of adult male*

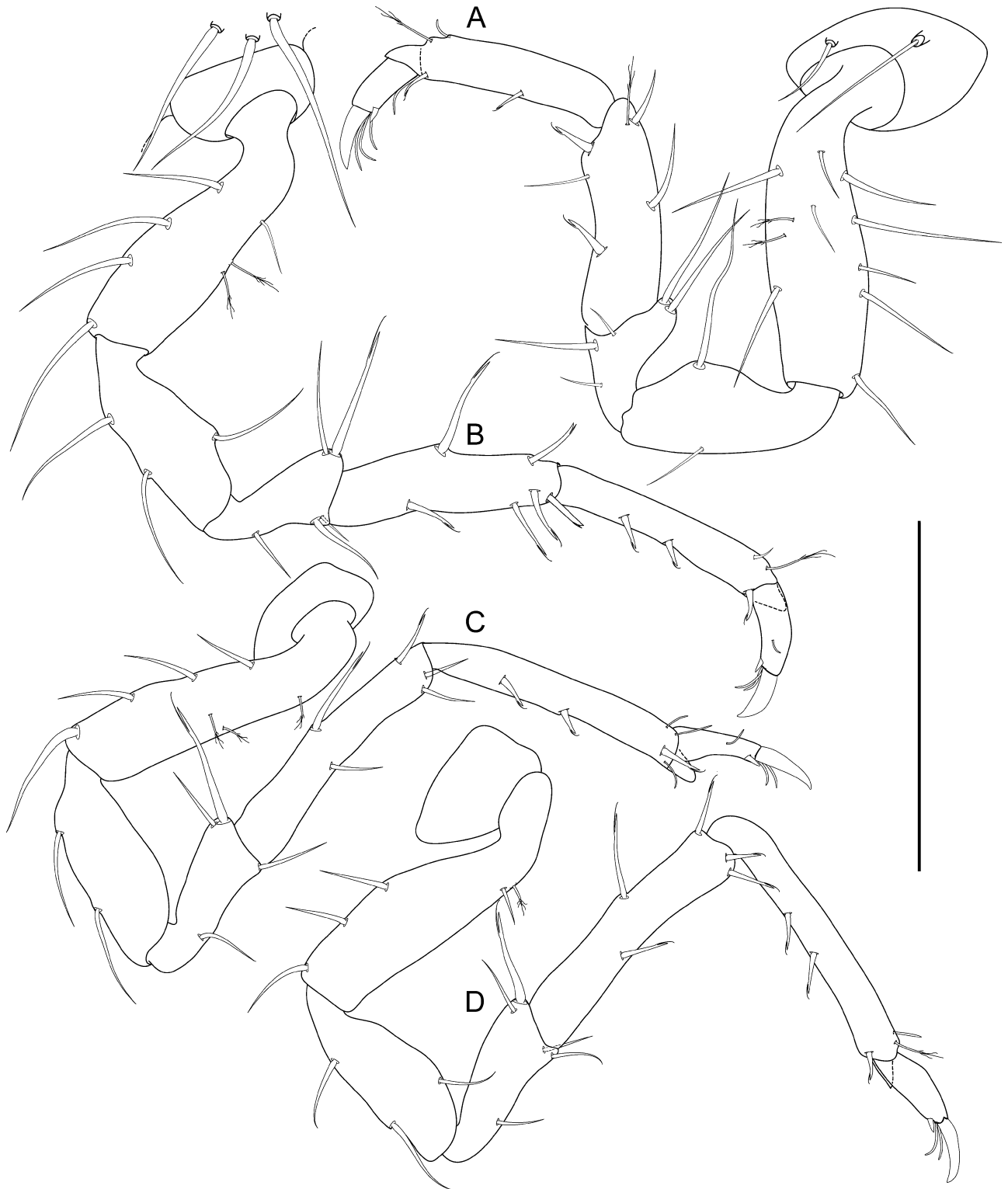
Body (Fig. 16A, C) length 2.1 mm, 4.0 width. Cephalothorax frontal ridge present, slightly convex; length/width ratio larger than in female, length 0.74 width, 0.15 body length; with conspicuous dorsal array of setae: four simple setae in a quadrate arrangement, posterolateral setae absent, posterior margins setulose. Pereonite 1 length 0.20 width, 0.05 body length. Pereonite 2 length 0.36 width, 0.09 body length. Pereonite 3 length 0.34 width, 0.09 body length. Pereonite 4 posterolateral margins not produced posteriorly.



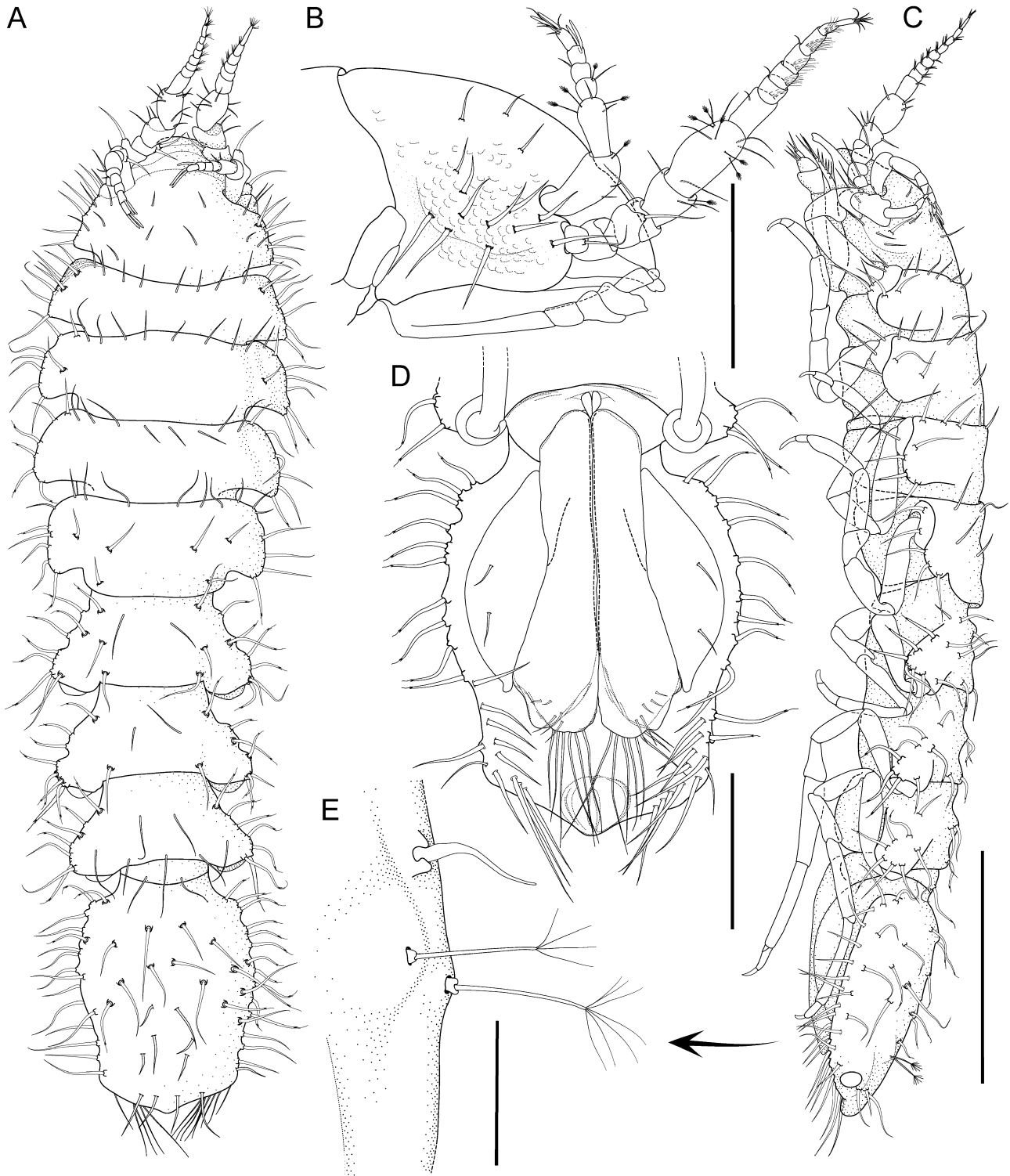
**Figure 13.** *Urstylis solicopia* gen. et sp. nov., ovigerous female holotype ZMH K-43070. A, pereopod I. B, pereopod II. C, pereopod III. Scale bar = 0.2 mm.



**Figure 14.** *Urstylis solicipia* gen. et sp. nov., paratype female fragment ZMH K-43053. A, pereopod I propodus distodorsal margin bisetulate seta. B, medial pereopod I propodus, dactylus. C, lateral pereopod I. D, pereopod I carpus distoventral margin robust seta with subdistal fringe-like sensilla. E, pereopod I ventral dactylus. F, pereopod II dorsal dactylus. G, pereopod II medial dactylus. H, close-up of G. I, pereonite 2 lateral dactylus. Scale bars = 10 µm (A, B, D–I); 0.1 mm (C).



**Figure 15.** *Urstylis solicipia* gen. et sp. nov., ovigerous female holotype ZMH K-43070. A, pereopod IV. B, pereopod V. C, pereopod VI. D, pereopod VII. Scale bar = 0.2 mm.



**Figure 16.** *Urstylis solicopia* gen. et sp. nov., adult male paratype ZMH K-43055. A, habitus, dorsal. B, cephalothorax, lateral. C, habitus, lateral. D, pleotelson, ventral. Scale bars = 0.5 mm (A, C); 0.3 mm (B); 0.2 mm (D); 0.05 mm (E).

Pleotelson (Fig. 16A, C, D) in dorsal view similar to female, constricted anteriorly to uropod articulation, width maximum anterior to waist, setal ridges not visible in dorsal view; length/width ratio in male subequal to female, 0.23 body length, width subequal pereonite 7 width, tergite with several projecting and calcified pedestals with setal articulations. Posterior apex length 0.14 pleotelson length, pleopodal cavity width 0.87 pleotelson width.

Antennula (Fig. 16B) length 0.81 head width, 0.57 antenna length, width 0.88 antenna width; article L/W ratios 1.7, 2.0, 1.0, 1.0, 1.0, 2.0; relative article length ratios 1.0, 0.83, 0.25, 0.25, 0.25, 0.30; terminal and penultimate articles with two aesthetascs respectively. Article 1 with two simple setae and one broom seta. Article 2 with five setae: two simple, three broom. Article 3 with one simple seta and one broom seta. Article 4–5 both with one simple seta. Article 6 elongate, distinctly longer than article 5. Antenna (Fig. 16B) length 0.29 body length, flagellum of six to nine articles, article length–width ratios subsimilar in males and females. Merus distally with four simple setae and one broom seta. Carpus distally with ten setae: five simple, five broom.

Mandible (Fig. 17) molar process apex with two spines and three setulate setae; left mandible incisor process with five cusps, lacinia mobilis with four denticles; right mandible incisor process with four cusps, lacinia mobilis with six denticles. Maxillula (Fig. 18A) lateral lobe terminally with 11 robust and three slender setae. Maxilla (Fig. 18B) lateral lobe with five setae terminally: one robust, serrate, two simple, two slender, simple; middle lobe with five setae terminally: three robust, serrate, two slender, simple; medial lobe terminally with six setae: two short, robust, laterally, two long, robust, two slender, simple. Maxilliped (Fig. 18C, D) basis length 3.9 width; endite distally with two fan setae; with two coupling hooks; palp articles 1 and 2 subsimilar in width, article 1 distomedially with one seta, distolateral lobe length 0.35 article 1 length, article 2 wider than article 3, article 1 shorter than article 3, article 4 distomedial extension with three setae, article 5 with five distal setae; epipod length 2.6 width, 0.85 basis length, distolaterally fringed with setulae.

Pereopods I–VI (Figs 19, 20) similar to those in female in size, proportions and setation. Pereopod VII length 0.42 body length, shorter than pereopod VI; relative article length ratios 1.0, 0.74, 0.58, 1.1, 1.1, 0.26. Article L/W ratios: 3.8, 2.8, 2.8, 6.7, 6.7, 2.5. Pleopod I (Figs 16D, 21A) length 0.84 pleotelson length, distal width 1.6 proximal width, distomedial lobes rounded, distally with six to eight long setae, distolateral lobes with five to seven small setae, ventral surface subdistally with five short setae

on each side. Pleopod II (Fig. 21B) protopod with fringe of > 32 thin setae on distolateral margin; apex projected, narrowly rounded. Endopod distance of insertion from protopod distal margin 0.35 protopod length. Stylet sublinear, extending beyond distal margin of protopod, length 0.88 protopod length.

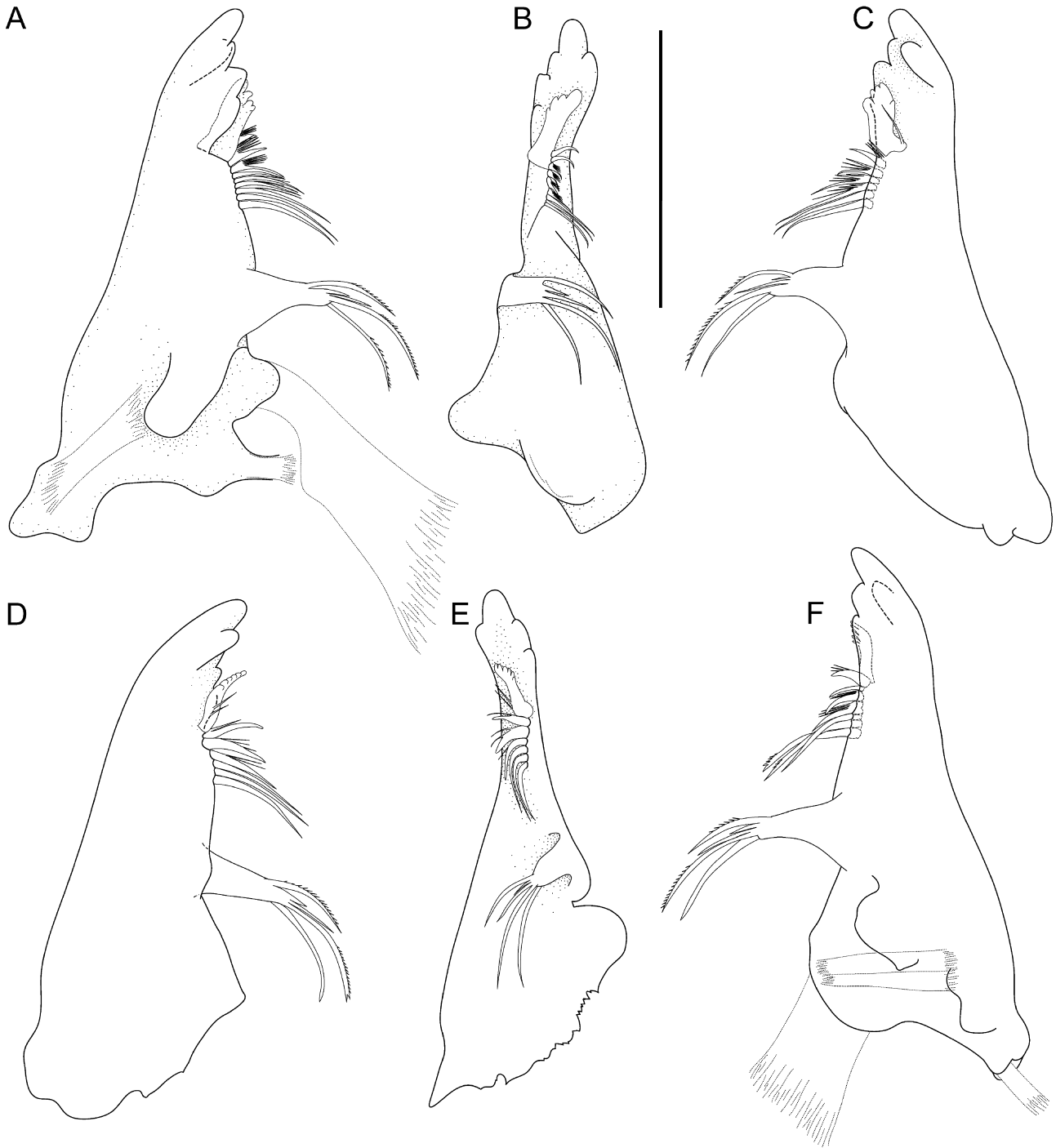
Pleopod III (Fig. 21C) length 1.8 width, protopod length 2.0 width, 0.56 pleopod III length, endopod terminal plumose setae longer than endopod. Exopod length 0.84 pleopod III length, proximal article as wide as endopod, with fringe of fine setae; seta length subsimilar to pleopod III exopod width; distal article length 0.36 proximal article length, width 0.47 proximal article width, conspicuous subterminal seta present. Pleopod IV (Fig. 21D) length 2.0 width, endopod length 1.7 width, exopod length 4.7 width, exopod length 0.78 endopod length, lateral fringe of setae present. Pleopod V (Fig. 21E) length 2.4 width.

#### Remarks

*Urstylis solicipia* gen. et sp. nov. is the most setose species currently known for this genus. The anterior tergites bear rows of setae along their anterior margin as well as medially across the segments. The posterior tergites have medial and posterior rows of simple setae. Another distinguishing feature is that all pereon and pleonal tergites of *U. solicipia* are covered with imbricate ornamentation and to a lesser degree the sternites, too. Dorsally on the pleotelson, a pair of broom setae on flat, cone-shaped elevations is located in approximately the same position as the tubercles in *U. zapiola* or the statocysts in *Macrostylis*. The operculum of this species has a lower length–width ratio than in *U. zapiola*.

The 0.25 m<sup>2</sup> box corer samples from the USA National Oceanic and Atmospheric Administration (NOAA) Deep Ocean Mining Study (DOMES) collected by GDFW and colleagues in 1977–1978 provide data on the population of this species at DOMES site A. The species appeared in six out of 55 samples with a total of 11 individuals. As the samples were open box corers with no partitions, the total area sampled is 13.75 m<sup>2</sup>, which gives a population density of this species of 0.8 individuals per m<sup>2</sup>, based on random expectations. As most species do not occur randomly but show patchy (under-dispersed) distributions (Kaiser & Barnes, 2008), the effective density can be expected to be much higher. Despite the large number of samples collected at DOMES site A, no males were found, suggesting that, as observed in haploniscids (Brökeland, 2010), macrostylids (Riehl & Kaiser, 2012), and tanaids, the males occur at a lower density than females or juveniles. The expectation that juveniles should be the most frequent size class is borne out by these samples.





**Figure 17.** *Urstylis solicipia* gen. et sp. nov., adult male paratype ZMH K-43055. A–C, left mandible. D–F, right mandible. Scale bar = 0.1 mm.

***URSTYLIS THIOTYNTLUS* GEN. ET SP. NOV.**

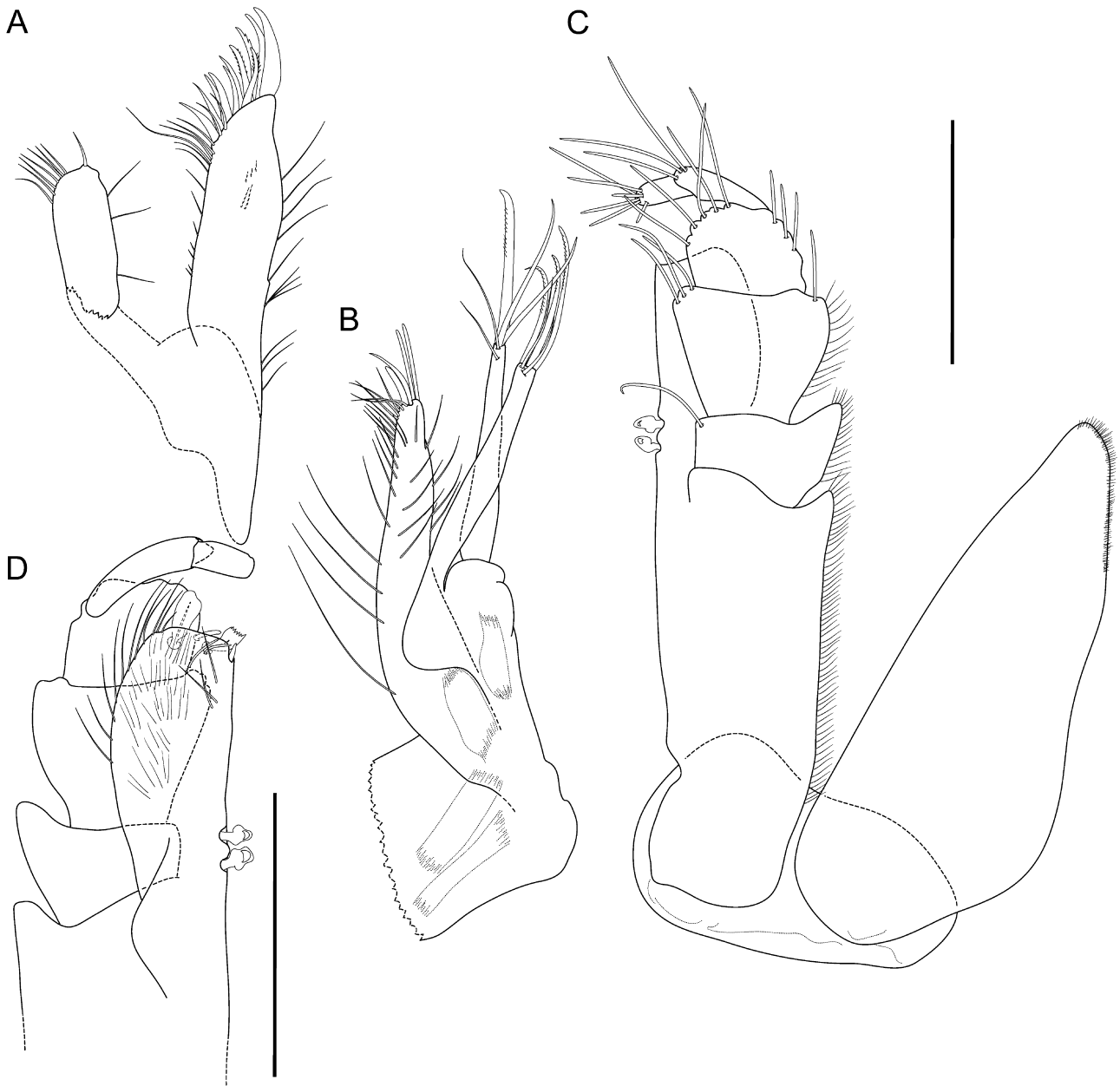
FIGURES 22–25

*Zoobank registration*

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*Diagnosis*

Body subcylindrical; anterior pereonites medioventrally keeled; all sternites with projecting spines; spines directed posteriorly; without dorsal setae, posterolateral margins of all pereonites with prominent, robust spine-like seta; pereonites 1–4 tightly



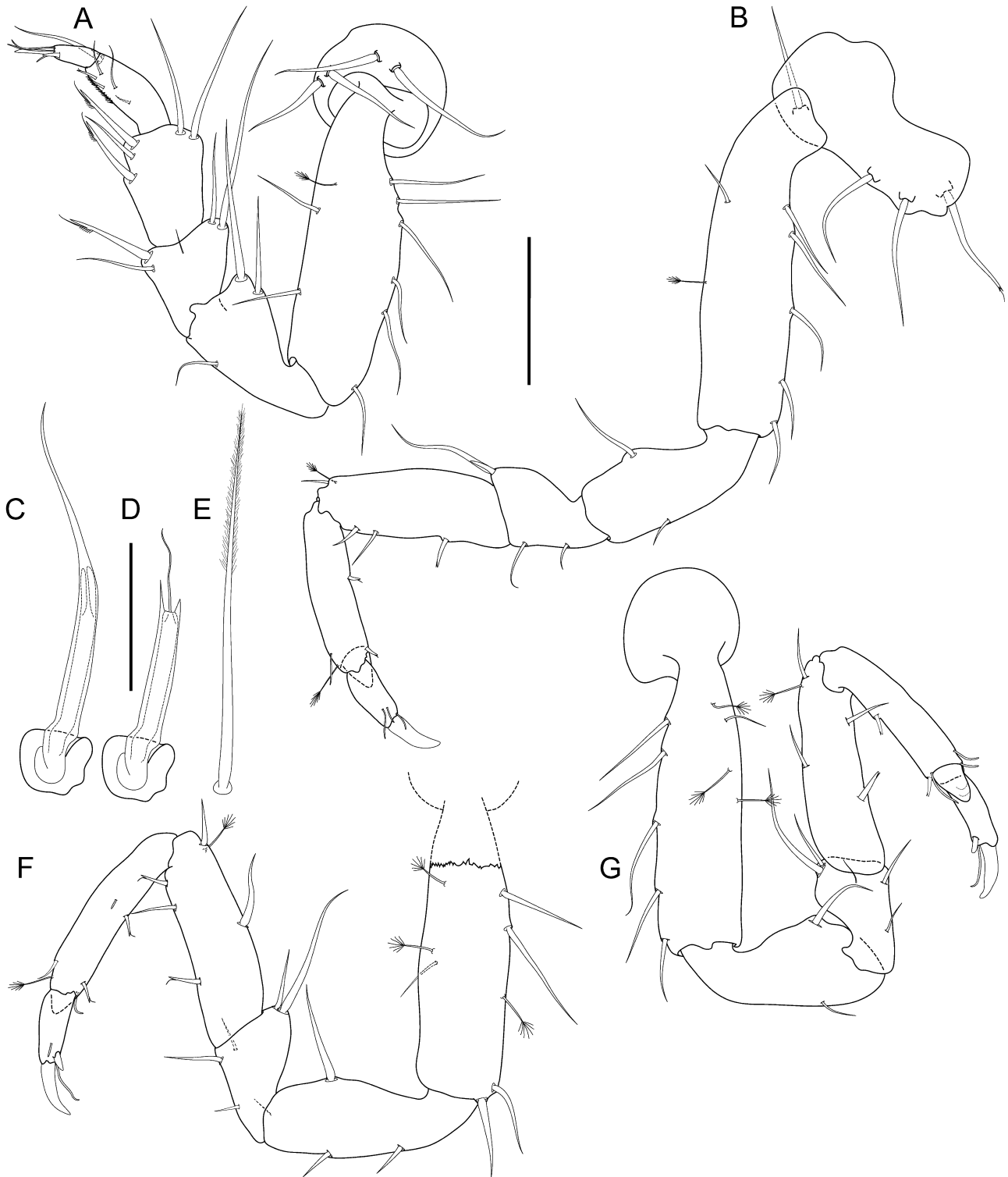
**Figure 18.** *Urstylis solycopia* gen. et sp. nov., adult male paratype ZMH K-43055. A, maxillula. B, maxilla. C, maxilliped, ventral, endite setation omitted. D, maxilliped endite close-up, dorsal. Scale bars = 0.1 mm.

packed, pereonite 4 wider than pereonite 5, posterolateral margin with prominent, spine-like seta and simple setae; pereonite 6 shorter than pereonite 5; pereonite 7 posterolateral margins not projecting posteriorly. Pleotelson rectangular, length 2.0 width, waist weakly pronounced; paired dorsal sensory organ absent. Pereopod I projecting laterally and dorsally, ischium dorsal setose lobe longer than merus dorsal lobe, with three enlarged setae;

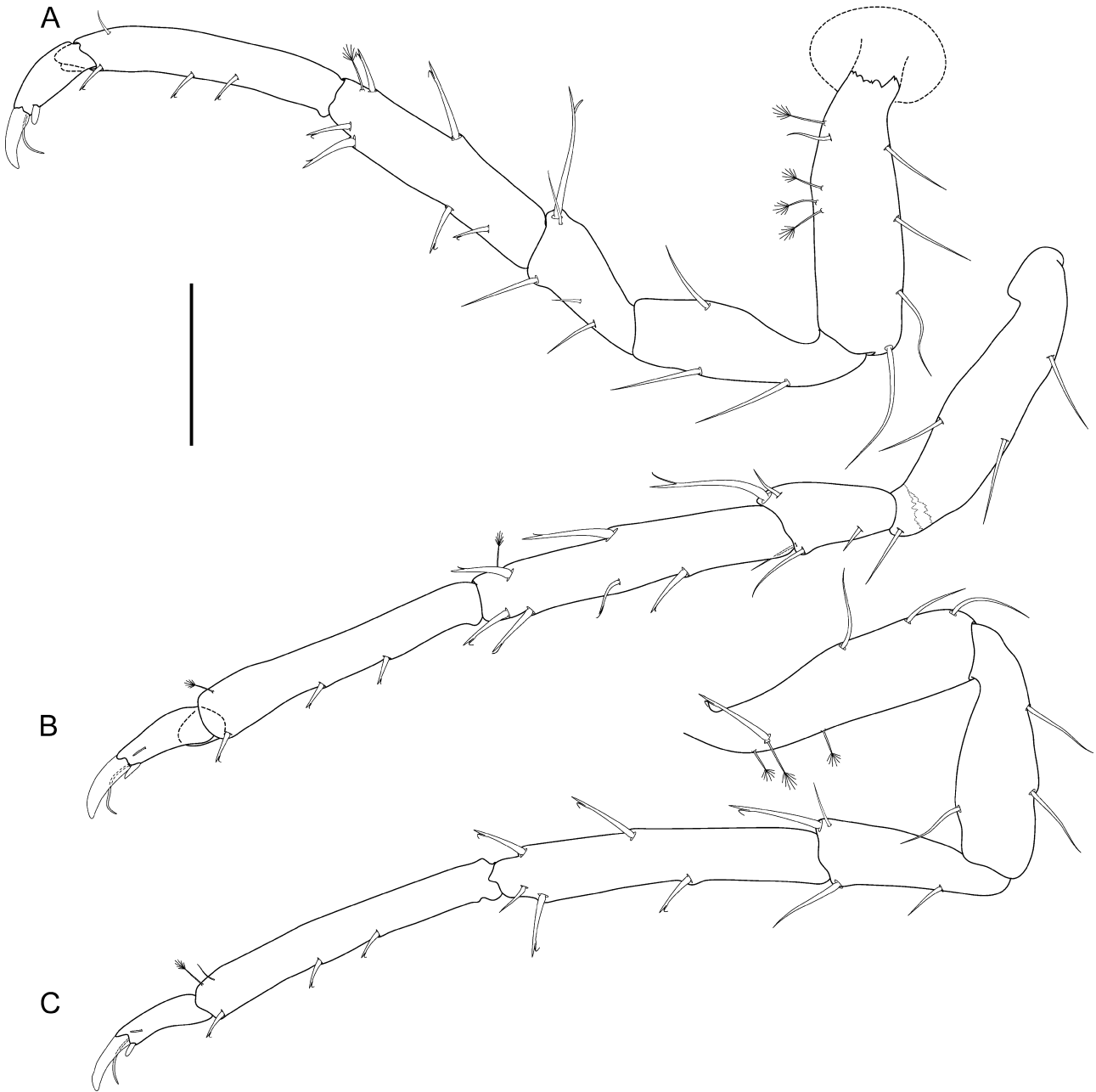
pereopods V–VI ischium with seta mid-dorsally, carpus mid-dorsally with no seta. Female pleopod II distal setae apically sensillate.

#### *Etymology*

This name, derived from the Greek words *theiodes* meaning sulphur-like and *tyntlos* mud, refers to the sulphide-rich sediments around the hydrothermal



**Figure 19.** *Urstylis solicipia* gen. et sp. nov., adult male paratype ZMH K-43055. A, pereopod I. B, pereopod II. C, simple seta as found on the trunk cuticle and pereopods with indicated internal structures. D, simple seta with cuticle broken and internal tissue exposed distally. E, bisetulate seta. F, pereopod III. G, pereopod IV. Scale bars = 0.1 mm (A, B, F, G); 0.025 mm (C–E).



**Figure 20.** *Urstylis solicipia* gen. et sp. nov., adult male paratype ZMH K-43055. A, pereopod V. B, pereopod VI, basis broken and lost, ischium damaged. C, pereopod VII. Scale bar = 0.1 mm.

mounds of the Galapagos mid-ocean ridge system. It is a masculine noun in apposition.

*Type fixation*

Adult female holotype, 1.6 mm, USNM 1208016, designated here.

*Type material examined*

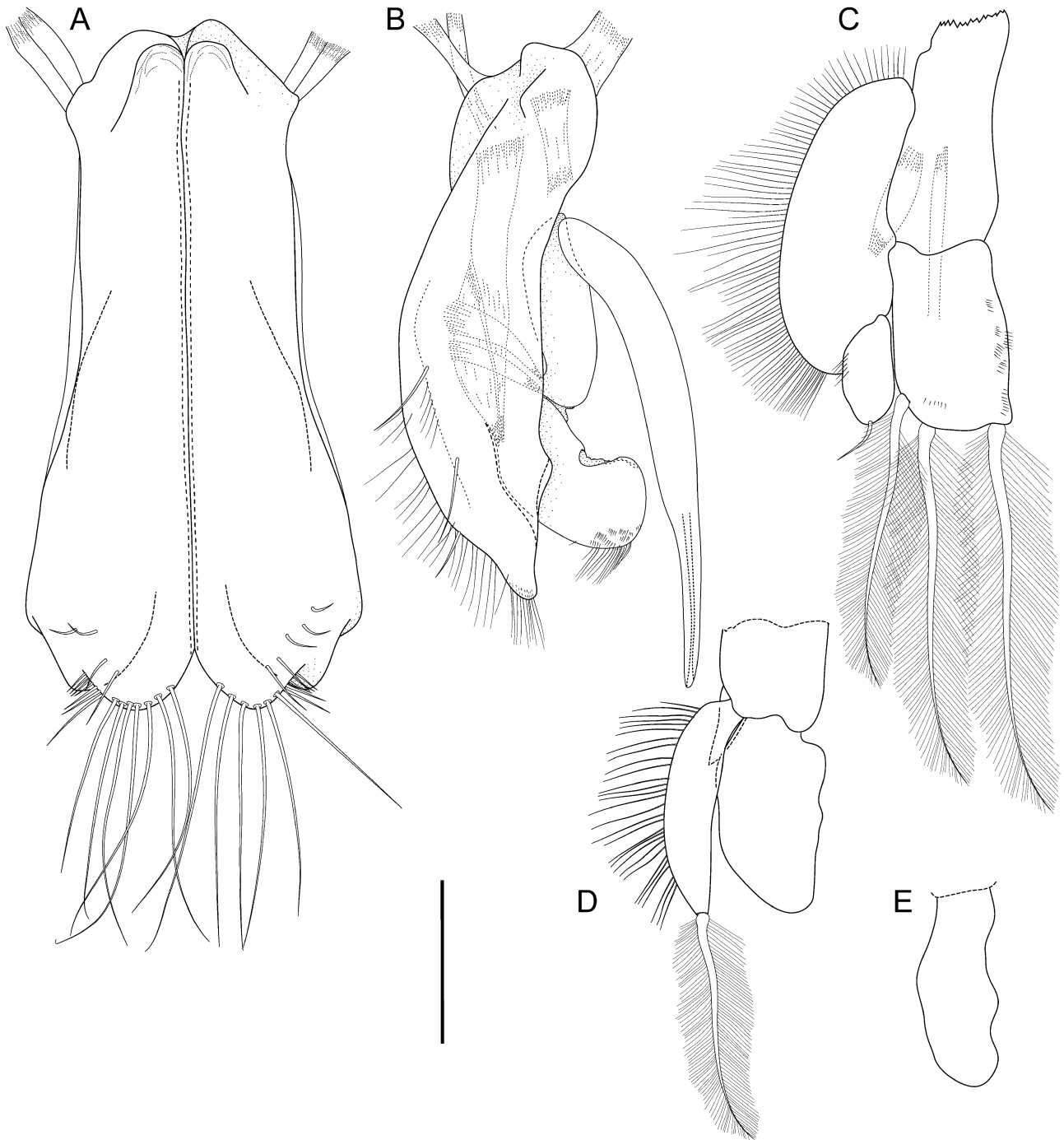
USNM 1208016: adult female holotype. USNM 1208017: manca stage 1 paratype.

*Type locality*

Galapagos Hydrothermal Mounds region, R/V Gillis st. 301 ('away from mounds' – see Grassle *et al.*, 1985), 0°35.0'N, 86°05.7'W, 2730 m, box core (one of 25 subcores).

*Type material – remarks*

Holotype female missing antennal flagellum and uropods; several pereopods broken at basis; pleopod II



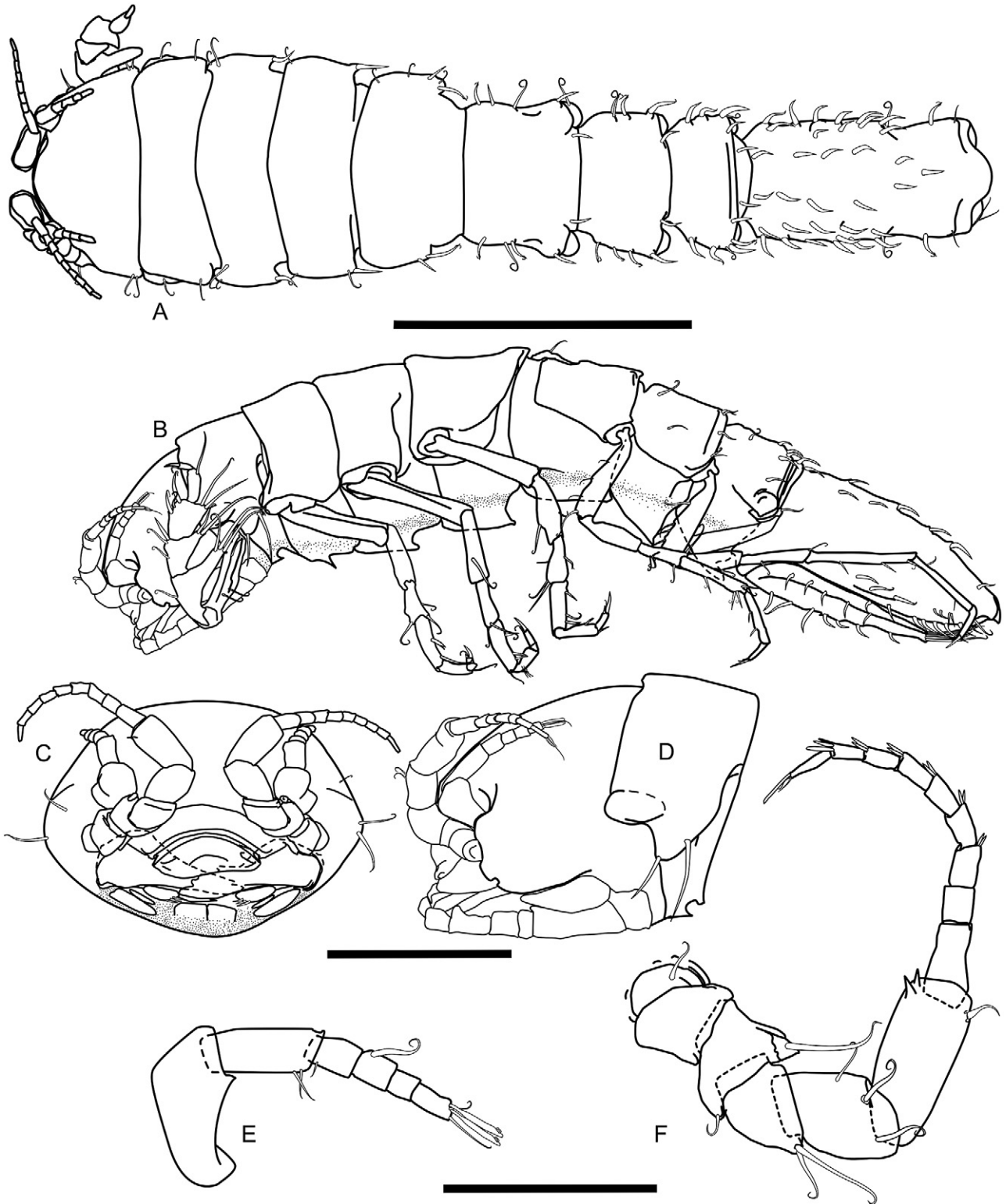
**Figure 21.** *Urstylis solicopia* gen. et sp. nov., adult male paratype ZMH K-43055. A, pleopod I. B, pleopod II, ventral. C, pleopod III. D, pleopod IV. E, pleopod V. Scale bar = 0.1 mm.

(operculum) removed and mounted on slide. Manca stage 1 specimen missing antennae and uropods.

*Description of female*

Body (Fig. 22) subcylindrical, length 1.6 mm, 4.0 width, tergite surfaces hirsute, setation of lateral

tergal margins present, with long setae along lateral margins of pereonites; posterior pereonites and pleotelson with dorsal robust setae. Ventral spines acute, keel-like, directed posteriorly. Pereonite 1 spine small. Pereonite 2 spine small, placed midway on midline. Pereonites 3 and 4 spines small, closer to



**Figure 22.** *Urstylis thiotyntlus* gen. et sp. nov., holotype female USNM 1208016. A, dorsal habitus. B, ventral habitus. C, D, head anterior and left lateral view, respectively. E, antennula, lateral view. F, antenna, medial view. Scale bars = 0.5 mm (A, B); 0.2 mm (C, D); 0.1 mm (E, F).

posterior segment border. Pereonite 5 spine absent. Pereonite 6 spine prominent, triangular in lateral view, closer to posterior segment border. Pereonite 7 spine prominent. Imbricate ornamentation absent on all pereonites. Cephalothorax length 0.61 width, 0.14 body length; frons in dorsal view convex, smooth, frontal furrow present, convex anterior margin adjacent to clypeus, not projecting. Posterolateral setae present. Posterolateral margins angular, blunt.

Pereonite 1 length 0.35 width, 0.08 body length, anterior margin straight. Posterolateral setae asensillate, simple. Pereonite 2 length 0.33 width, 0.08 body length. Posterolateral setae robust. Pereonite 3 length 0.42 width, 0.10 body length; posterolateral setae asensillate, robust, flexibly articulated. Pereonite 4 width 1.04 pereonite 5 width, length 0.63 width; lateral margins curved, in dorsal view lateral margins narrowing posteriorly to coxae, with distinct indentation posterior to coxa. Posterolateral margins tapering. Posterolateral setae sensillate, robust, flexibly articulated.

Pereonites 5–7 posterior tergite margin with two sensillate, robust, flexibly articulated setae; setae extending beyond posterolateral margin. Posterolateral margins not produced posteriorly. Tergite posterolateral setae sensillate, robust. Pereonite 5 length 0.75 width, 0.80 pereonite 4 length. Pereonite 6 length 0.59 width, 0.94 pereonite 5 length. Pereonite 7 length 0.56 width.

Pleotelson (Fig. 22A, B) length 0.26 body length, 2.0 width, narrower than pereonite 7; paired dorsal sensory organ absent. Posterior margin apex length 0.11 pleotelson length. Posterior apex setae absent. Pleopodal cavity width 0.85 pleotelson width.

Labrum anterior margin in dorsal view concave. Concavity on left side, margin sinusoid, no distal cuticular spinules.

Antennula (Fig. 22E) length 0.51 head width, length 0.46 antenna length, width 0.69 antenna width; relative length ratios of articles 1.0, 0.75, 0.34, 0.28, 0.18, 0.34; L/W ratios of articles 1.8, 2.3, 1.4, 1.2, 1.1, 2.2. Article 1 distinctly longer than wide, dorsally flattened, ventrally semicircular, longest and widest. Articles 2–4 distinctly longer than wide. Article 3 with one asensillate seta. Article 4 with one asensillate large, distally curled seta. Article 5 length subequal to width. Terminal article with two simple tubular aesthetascs.

Antenna (Fig. 22F) length 0.25 body length. Basis angular with dorsolateral projection, shorter than coxa, rudimentary scale present. Ischium longer than coxa. Merus longer than coxa, basis, and ischium combined, distally with two asensillate setae, articulating distolaterally on ischium, antennal proximodistal axis with distinctly sharp bend. Carpus longer than merus, distally with one asensillate seta. Flagellum with nine articles.

Mandibles (Figs 22C, D, 23A): left mandible incisor process simplified, mono- or bidentate rounded, blunt; right mandible incisor process multidentate with dorsal and ventral subdistal teeth that partly enclose lacinia.

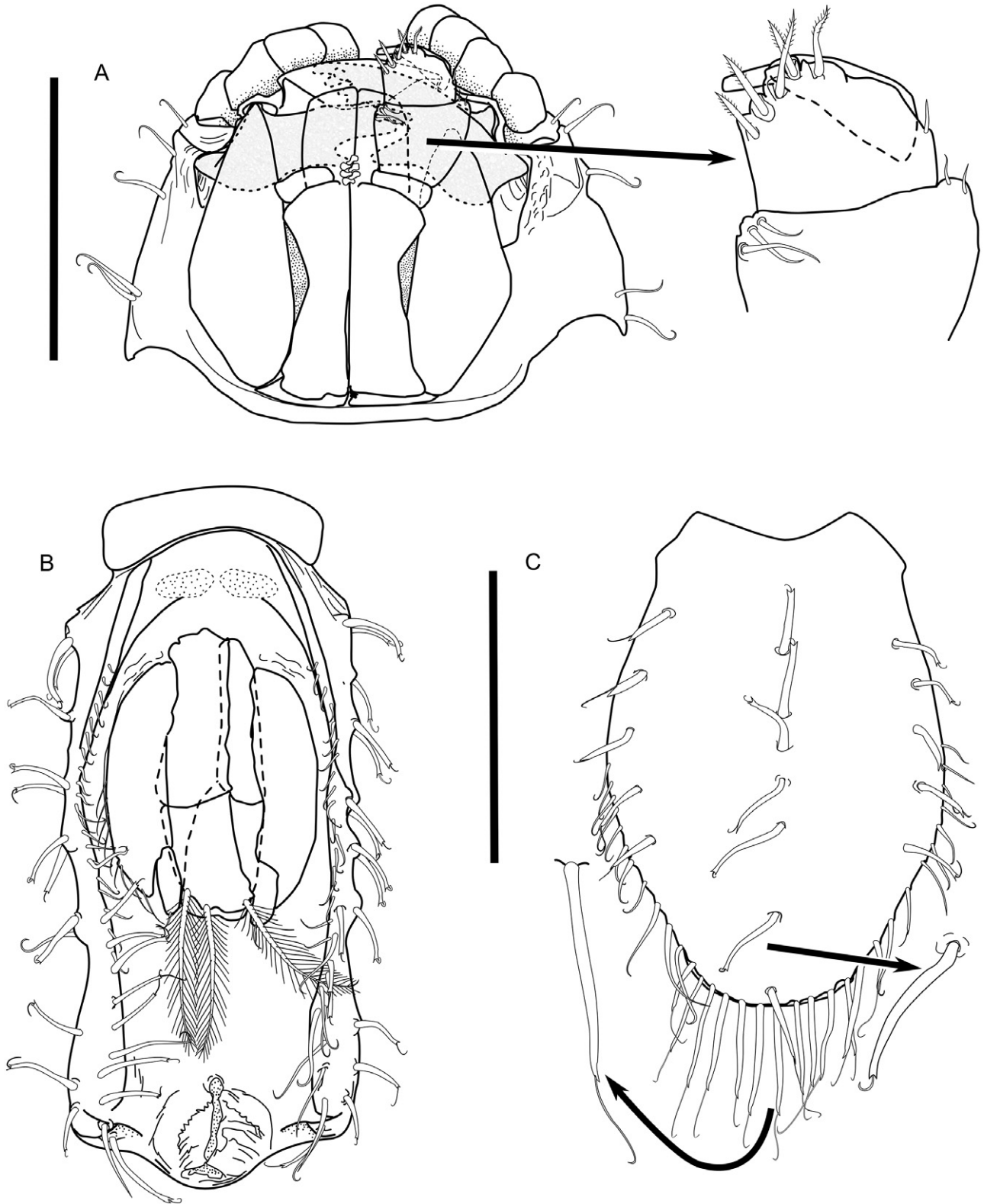
Maxilliped (Fig. 23A) with three coupling hooks, article 2 wider than articles 1 and 3, article 1 shorter than article 3, article 4 distomedial extension present; epipod length 2.8 width, 0.87 basis length.

Anterior pereopodal coxae ring-shaped, coxal setation present. Pereopod I (Fig. 24A) positioned laterally and dorsally; length 0.28 body length; article L/W ratios 1.96, 0.83, 0.90, 1.64, 2.43, 4.27; relative article length ratios 1.00, 0.62, 0.41, 0.55, 0.35, 0.30; ischium dorsal margin with lobe projecting much greater than basal width of segment, with three enlarged setae: one simple seta, two distally biserrate. Merus dorsal margin with two setae: one simple, one distally bidentate; ventral margin with three setae: two distally curled, one robust subdistally sensillate. Carpus dorsally with two distally biserrate setae. Propodus with one long distodorsal seta and one short ventral seta, articular plate on propodus absent; dactylus distally with two sensillae, dorsal claw length slightly shorter than dactylus.

Pereopod II (Fig. 24B) longer than pereopod I, length 0.37 body length; article L/W ratios 4.0, 2.3, 1.3, 2.6, 3.3, 4.0; relative article length ratios 1.0, 0.50, 0.31 0.46, 0.30, 0.26. Ischium dorsally with 1 distally curled simple seta. Merus dorsally with two setae, ventrally with one seta; setae distally curled simple. Carpus dorsally with one broom seta, ventrally with three setae: one distally curled, simple and two robust, subdistally sensillate. Dactylus distally with one sensilla, dorsal claw length similar to dactylus length.

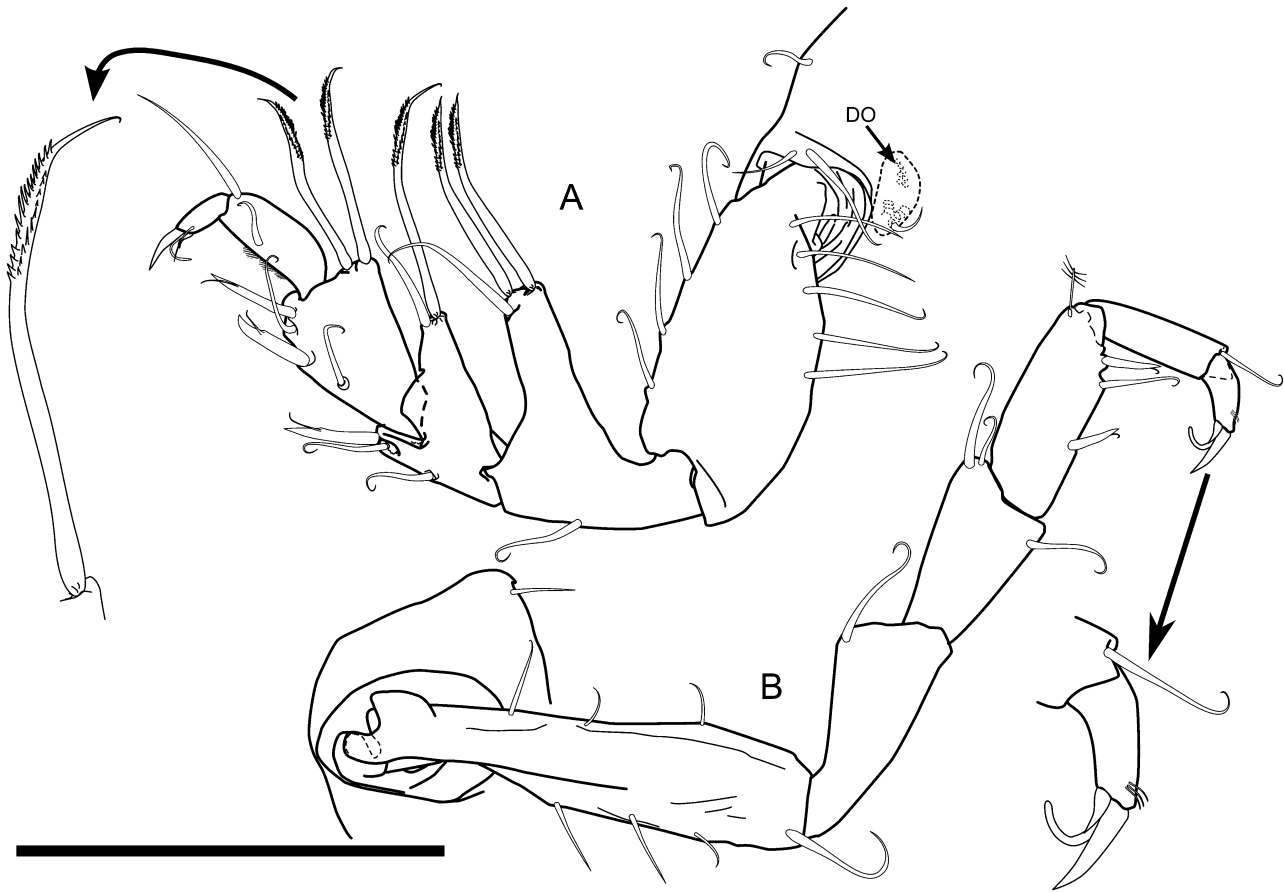
Pereopod III (Fig. 25A) length 0.39 body length; article L/W ratios 3.4, 2.0, 1.8, 2.5, 3.0, 4.0; relative article length ratios 1.00, 0.48, 0.44, 0.50, 0.36, 0.34. Ischium with no seta proximodorsally, dorsal lobe flat, rounded; proximally with one seta. Merus dorsally with two simple, distally curled setae, at dorsodistal margin, ventrally with two simple, distally curled setae, along ventral margin. Carpus dorsally with two simple setae, ventrally with three setae: two simple marginally, one sensillate robust distally. Dactylus with one sensilla.

Pereopod IV (Fig. 25B) length 0.48 body length, more robust and longer than pereopod III (~43% longer); article L/W ratios 4.7, 2.9, 1.6, 3.0, 3.7, 5.9; relative article length ratios 1.0, 0.63, 0.36, 0.48, 0.32, 0.30. Pereopod V (Fig. 25C) length 0.39 body length; article L/W ratios 5.8, 2.9, 3.4, 5.5, 7.3, 6.3; relative article length ratios 1.0, 0.61, 0.51, 0.65, 0.65, 0.41. Ischium mid-dorsally with one small simple seta,



**Figure 23.** *Urstylis thiotyntlus* gen. et sp. nov., holotype female USNM 1208016. A, maxilliped, ventral view, with enlargement of palp articles 2–3. B, pleotelson, ventral view, operculum removed to show pleopod III. C, operculum ventral view. Scale bars = 0.2 mm (A); 0.2 mm (B, C).





**Figure 24.** *Urstylis thiotyntlus* gen. et sp. nov., holotype female USNM 1208016. A, pereopod I, lateral view. B, pereopod II, lateral view, with enlargement of dactylus and claws (arrow). Scale bar = 0.2 mm.

midventrally with two simple distally curled setae. Merus distoventrally with one simple distally curled seta. Carpus distodorsally with two setae: one simple, one penicillate; midventrally with one seta; distoventrally with two elongate, robust, sensillate setae.

Pereopod VI (Fig. 25D) length 0.48 body length; article L/W ratios 4.7, 3.8, 4.5, 9.1, 8.5, 2.9; relative article length ratios 1.0, 0.73, 0.75, 1.12, 0.93, 0.52. Ischium dorsally with one seta, midventrally with two distally curled simple setae. Merus distodorsally with one distally curled simple seta; midventrally with one distally curled simple seta; distoventrally with one simple seta. Distodorsally with two simple setae; midventrally with two thin robust sensillate setae; distoventrally with two thin robust sensillate setae.

Pereopod VII basis ventral margin with row of three elongate setae; setae shorter than basis width.

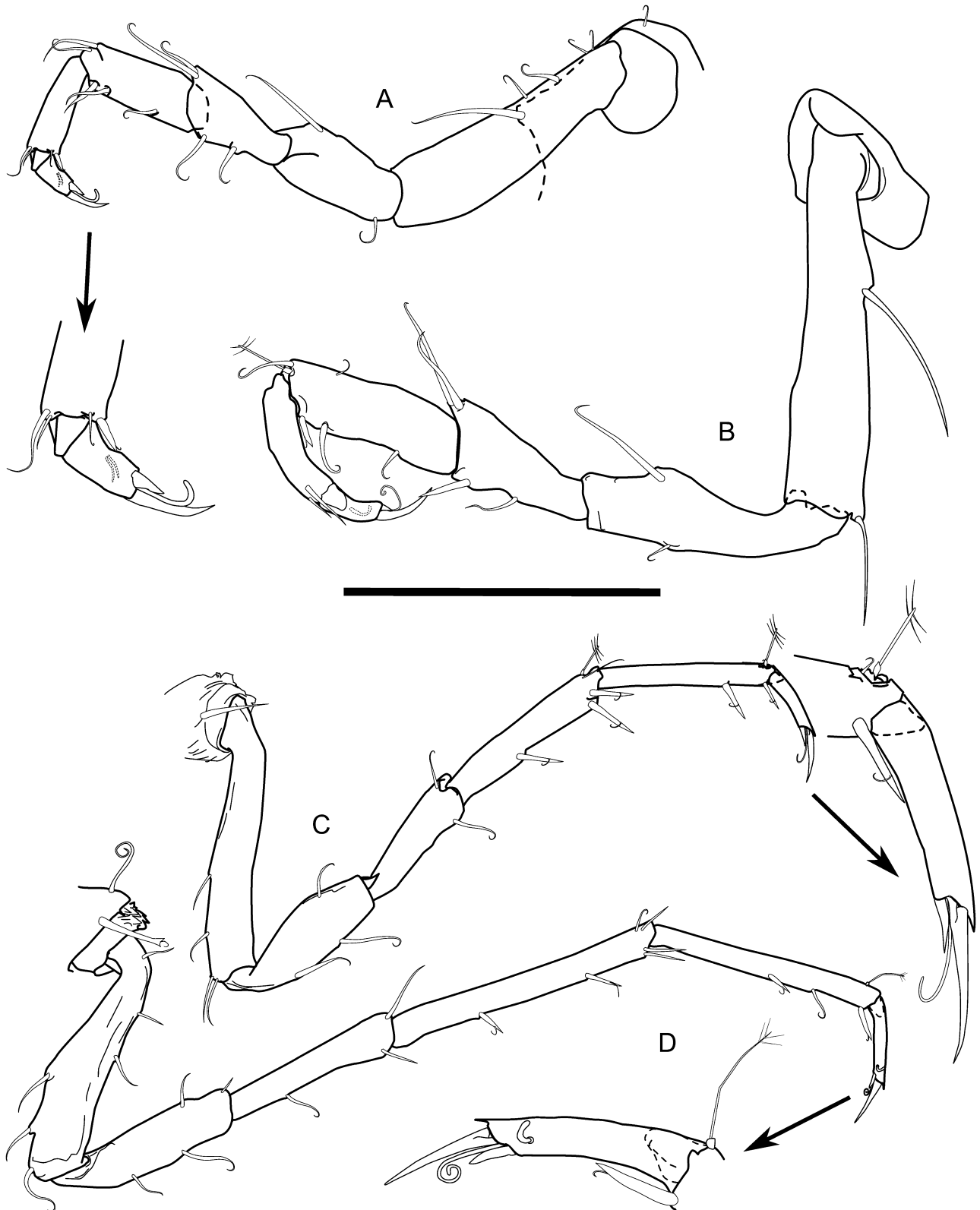
Operculum (Fig. 23C) length 1.4 width, 0.82 pleotelson dorsal length; apical width 0.50 operculum width; distally tapering. With lateral fringe consisting of eight bifurcate distally sensillate setae, with con-

tinuous transition to apical row of 17 setae; apical setae asetulate, distally sensillate, extending to anal opening.

Pleopod III (Fig. 23B) length 2.3 width; protopod length 2.4 width, 0.61 pleopod III length. Uropod broken.

#### Remarks

*Urstylis thiotyntlus* gen. et sp. nov. differs from the other two species in the genus by its laterally positioned pereopod I. This limb is further modified by being more robust and having distinctive dorsal projections on the ischium, merus, and carpus, all of which bear large distally denticulate setae. The attitude of the first pereopod is reminiscent of that seen in macrostylids and the Desmosomatidae although, in these taxa, the relevant limbs are pereopods II–III. Given that this limb position is common amongst desmosomatid and macrostylid species known to be fossorial (Hessler & Strömberg, 1989), we infer that this species may also be fossorial. Differences between pereopods II–IV and V–VI are more pronounced and



**Figure 25.** *Urstylis thiotyntlus* gen. et sp. nov., holotype female USNM 1208016. A–D, pereopods III–VI, left side, lateral view. A, C, showing enlargement of dactylus. D, pereopod VI dactylus, right side, lateral view. Scale bar = 0.2 mm (A–D).

## KEY TO THE SPECIES OF URSTYLIDAE

1. Body without sternal spines, (females) not keeled; pereonite 4 posterolateral margins rounded, with simple setae; pereonite 6 posterolateral margins produced posteriorly, rounded; pleotelson rather stout ( $L/W < 1.5$ ), with anterior and posterior convex outline separated by concave waist; pereopod I positioned ventrally and orientated anteriorly, ischium dorsal margin projecting near basal width of segment.....2
- Body with sternal spines, partly keeled; pereonite 4 posterolateral margins acutely tapering, with robust, spine-like setae; pereonite 6 posterolateral margins not produced; pleotelson elongate ( $L/W > 1.5$ ), subrectangular, waist only weakly pronounced, lateral margins subparallel; pereopod I positioned lateroventrally and orientated dorsolaterally, ischium dorsal margin projection much greater than basal width of segment.....*Urstylis thiotyntlus* sp. nov.
2. Body subcylindrical; pereonite 7 without posterolateral protrusions; pereopod VII shorter than pereopod VI; operculum with lateral setal fringe absent.....*Urstylis zapiola* sp. nov.
- Body dorsoventrally flattened; pereonite 7 with posterolateral protrusions similar to pereonite 6; pereopod VII length subsimilar pereopod VI length; operculum with lateral setal fringe present...*Urstylis solicipia* sp. nov.

pereopod I is more derived than in *U. zapiola* and *U. solicipia*. *Urstylis thiotyntlus* presages the robust midventral spines seen in *Macrostylis* species with the possession of keel-like spines on most sternites, which only occur amongst other species of *Urstylis* as v-shaped midline keels of *U. zapiola* sp. nov. males. *Urstylis thiotyntlus* also lacks the distinctive dorsal organs occurring on the pleotelson of *U. zapiola*, but has a distinctively narrow pleotelson. Of the three species, *U. thiotyntlus* has the least number of setae on the dorsal surfaces, and these setae are shorter and more robust. Pereonites 1–4 are more integrated and relatively wide relative to the posterior body part in comparison to the other *Urstylis* species.

This species was collected as part of a study of the Galapagos hydrothermal sedimentary community by Grassle *et al.* (1985). Although the Gillis sample 301 (containing this species) was taken away from hydrothermal mounds, it is still within a nautical mile of the mounds. As such, this background sedimentary community probably is still influenced by nearby hydrothermal activity. Gillis 301, however, is somewhat more diverse than samples taken amongst the hydrothermal mounds (Grassle *et al.*, 1985). Overall, the isopod diversity of the Galapagos hydrothermal mounds region is high. The appearance of this species in one single sample thus concurs with the rare appearance of *Urstylis* in the high isopod diversities observed for the CCFZ (Thistle & Wilson, 1987, 1996) and Argentine Basin (see above).

## PHYLOGENETIC RESULTS

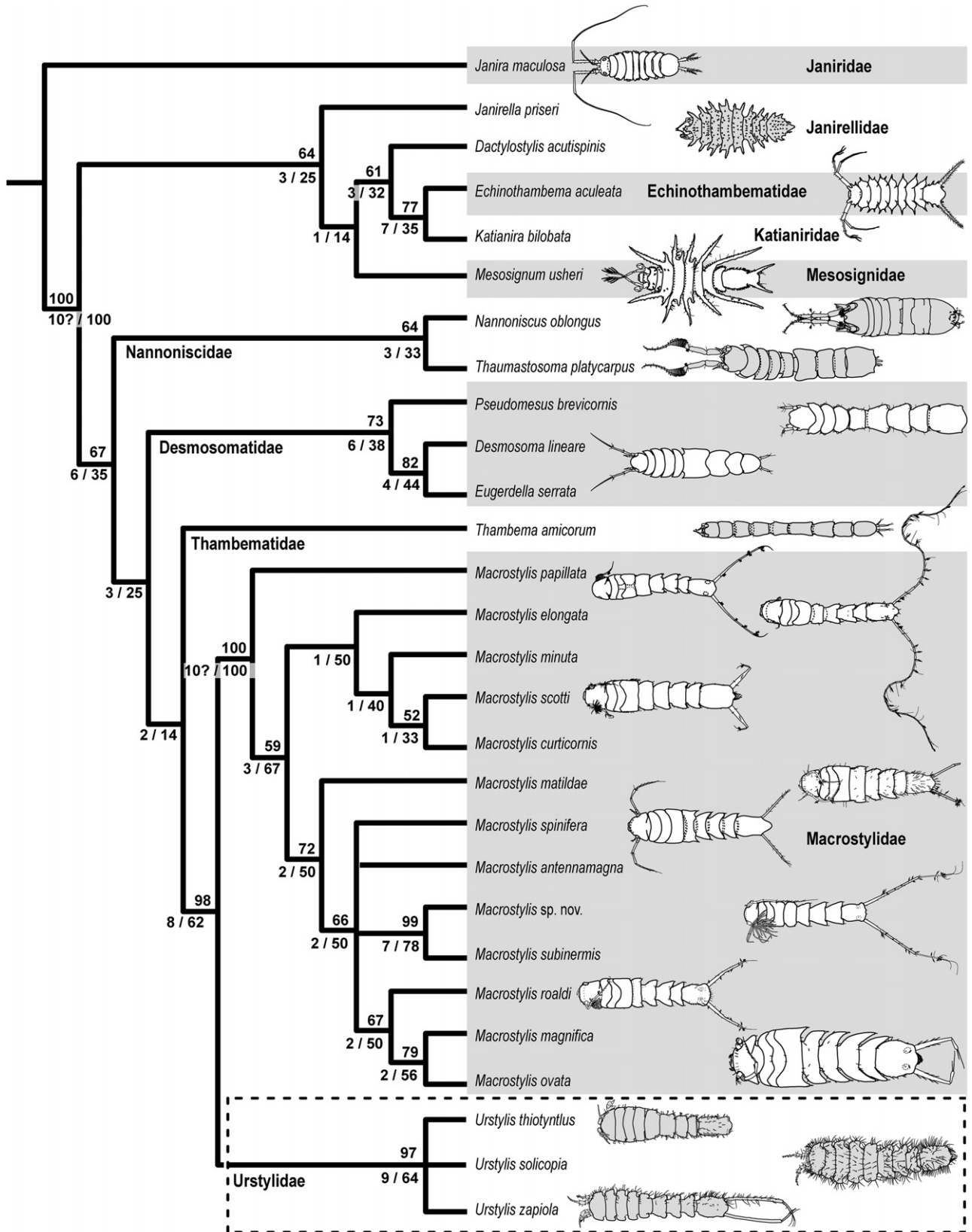
Both TNT analyses, thorough and fast, retained four shortest trees with a best score of 677 (Fig. 26). The three new species form a monophyletic group, henceforward referred to as Urstylidae. It is supported by 14 synapomorphies, a jackknife value of 97, Bremer support of 9, and relative (rel.) Bremer value of 64 (Fig. 27; see also Discussion). Macrostylidae were found to be the closest related to Urstylidae with ten

synapomorphies supporting this clade (jackknife 98, Bremer 8, rel. Bremer 62). Macrostylidae are nevertheless distinctly separated by 43 synapomorphies (jackknife 100, Bremer > 10, rel. Bremer 100). The most basally derived clade comprises Echinothambematidae, Janirellidae, Katianiridae, and Mesosignidae. The sister clade to Macrostylidae and Urstylidae is Thambematidae. Desmosomatidae and Nannoniscidae have separate positions respectively basally to Thambematidae.

## DISCUSSION

The three new species are placed within the 'higher Janiroidea' because of the typical, highly derived janiroid opercular pleopods of the males (Wilson, 1987b). Their bodies are elongate and slender, lateral tergal projections are absent, and the anterior pereopods feature rows of relatively robust setae on both ventral and dorsal margins that are typical features of a fossorial lifestyle as seen, e.g. in *Eugerdella* and Macrostylidae (Hessler & Strömberg, 1989). A close relationship to the 'munoid' taxa *sensu* Wägele (1989) can thus be excluded. Consequently, those taxa were not considered in the analyses presented here.

A reduction in the length of the antennula, flattened triangular molar processes, and a long mandibular spine row are characteristic for the desmosomatid–nannoniscid–macrostylid clade as inferred by Wägele (1989) and the new species share these character states. They furthermore share a distomedial process on the maxilliped carpus (palp article 3). Analogous conditions, however, occur in Janirellidae Munnidae, Paramunnidae, Munnopsidae, *Xostylus*, and Katianiridae. Further inter- or intrafamiliar relationships are beyond the scope of this work and will be addressed separately (T. Riehl & G. D. F. Wilson, unpubl. data). The data set used for this study is reduced with regard to the taxa



**Figure 26.** Strict consensus of four most parsimonious trees, based on morphological characters, analysed under equal weights, showing the position of Urstylidae amongst potentially related Janiroidea. The terminal taxa are exemplars representing families (bold font; not to scale): *J. maculosa* Leach, 1814; *J. priseri* Chardy, 1972; *D. acutispinis* Richardson, 1911; *E. aculeata* Mezhov, 1981; *K. bilobata* Gurjanova, 1930; *M. usheri* Menzies, 1962a; *N. oblongus* Sars, 1870; *T. platycarpus* Hessler, 1970; *P. brevicornis* Hansen, 1916; *D. lineare* Sars, 1864; *E. serrata* Brix, 2006; *T. amicorum* Stebbing, 1912; *M. papillata* Riehl, Wilson & Hessler, 2012; *M. elongata* Hansen, 1916; *M. minuta* Menzies, 1962b; *M. scotti* Riehl & Brandt, 2013; *M. curticornis* Birstein, 1973; *M. matildae* Riehl & Brandt, 2013; *M. spinifera* Sars, 1864; *M. antennamagna* Riehl & Brandt, 2010; *M. subinermis* Hansen, 1916; *M. roaldi* Riehl & Kaiser, 2012; *M. magnifica* Wolff, 1962; *M. ovata* Birstein, 1970; *U. thiotyntlus* sp. nov.; *U. solycopia* sp. nov.; *U. zapiola* sp. nov. Support values above branches are derived from jackknife resampling (10 000 repetitions; removal probability = 25; group frequencies). Below the branches, Bremer support (from 3758 trees, cut 0) and relative Bremer support (from 2344 trees, cut 0) are given. In cases for which absolute Bremer supports are followed with a question mark (?), the respective groups are supported by a value of 10 or higher. Jackknife values below 50 are not shown.

used and therefore, relationships within clades other than the macrostylid–urstylid clade have to be treated with care.

#### THE PHYLOGENETIC RELATIONSHIP BETWEEN URSTYLIDAE AND MACROSTYLIDAE

Affinity between the new species and Macrostylidae was validated by the parsimony analyses (Fig. 26), depicted by a long list of synapomorphies (Fig. 27). Superficially close groups such as Echinothambematidae, *Dactylostylis*, and Katianiridae have a fundamentally different underlying morphology. The broad pleotelson with elongate styliform uropods articulating distinctly separate from the anus has thus evolved at least twice independently.

The prognathous, spade-like head that is posteriorly widened and fits into the anterior margin of pereonite 1 is an important homology. In taxa that have a presumed burrowing lifestyle, such as Macrostylidae and Urstylidae, some Desmosomatidae and Nannoniscidae (Hessler & Strömberg, 1989), the anterior pereonites (1–3) are often broader and deeper than the posterior pereonites, giving the body a posteriorly tapering shape. The enlarged dimensions of the anterior pereonites may reflect increased musculature. Although this is a synapomorphy for Urstylidae and Macrostylidae, it has independently evolved in some desmosomatids and nannoniscids (character 20).

The results are inconclusive about the sternal spines that are present in *U. thiotyntlus*, most (but not all) macrostylids, some Nannoniscidae, and rarely in Desmosomatidae (characters 30, 31). These may have a common origin in the *Urstylis*–*Macrostylis* clade but an independent origin is equally as parsimonious.

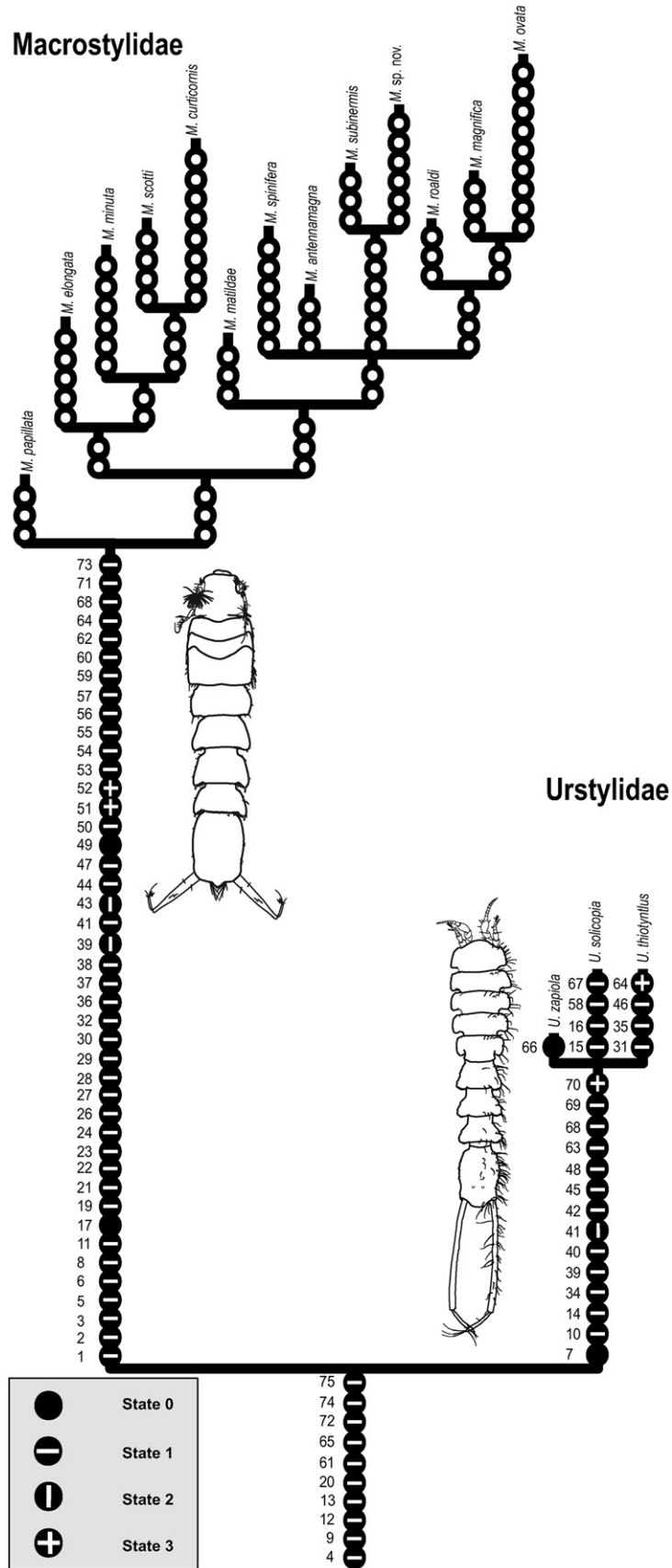
Although basally derived taxa, especially those with long antennular flagellae, have one aesthetasc per flagellar segment in the male (character 4),

Macrostylidae and the new species have several of these chemosensory setae on the distal segments. This can be interpreted as a chemosensory enhancement for sexual purposes (females typically have only one to two aesthetascs) and possibly as compensation for the reduction of aesthetasc-bearing segments.

Within Asellota, the antennal basis length (character 9) often exceeds the length of coxa and ischium respectively, especially in taxa of the ‘munnopsoid radiation’. Urstylids and macrostylids, however, have subsimilar length relationships of the basal antenna podomeres. Our analyses also suggest independent reduction of this segment in *Pseudomesus* and in some of the basally derived taxa.

Several mandibular characters support a macrostylid–urstylid relationship. The right lacinia mobilis (character 12) evolved from a spine-row member to a heavily calcified structure independently in *Echinothambema*, *Dactylostylis*, and in the last common ancestor of the macrostylid–urstylid clade. A mandibular palp is plesiomorphically present in most groups of Janiroidea, although reduced multiple times across this monophyletic group (character 13), such as in Munnidae, *Pleurocope*, some Paramunnidae, Nannoniscidae, Haplomunnidae, Desmosomatidae, and some Munnopsidae. Its absence is an apomorphic character for the macrostylid–urstylid clade.

More similarities between the two families are found on the body segments. Specialized setae are present on posterolateral tergite margins of the pereonites in Macrostylidae and *U. thiotyntlus* (character 18). In other taxa, although setae might be generally present, such specialized configuration is absent. The setal distribution and robustness varies across the species of *Macrostylis*: most commonly they are spine-like in pereonites 5–7. Our data suggest either independent origins or a secondary reduction in *U. solycopia* and *U. zapiola*.



**Figure 27.** Synapomorphies for Urstylidae and subtaxa, as well as for Macrostylidae and their joint clade common to all four shortest trees mapped on the phylogenetic tree (Fig. 26). The number of synapomorphies is translated into branch length. Apomorphies for Macrostylidae are indicated but detailed information is omitted as these exceed the scope of this paper. **Urstylidae fam. nov.** is defined by 14 unique synapomorphies. Macrostylidae are highly derived and their large number (43) of synapomorphies is the main argument against the inclusion of **Urstylis gen. nov.** in this family. A sister-group relationship of both families is supported by ten shared apomorphies. *M.*, *Macrostylis*; *U.*, *Urstylis*.

Further evidence for their close relationship is present on the pleotelson. Elongate setae constituting the apical setal row on the operculum (character 65) are rather uncommon amongst Janiroidea. This state is synapomorphic for the macrostylid–urstylid clade and a homoplasy in mesosignids and katianirids.

*Urstylis thiotyntlus* is clearly distinguished from the other new species but similar to some macrostylids, for example with regard to robust, spine-like posterolateral setae (character 18). These are present in the majority of macrostylids but missing in other species of *Urstylis* and all of the outgroup taxa. A common origin can thus be neither verified nor excluded.

Other features of *U. thiotyntlus* must be considered derived. The ischium dorsal margin of pereopod I is dorsally expanded as in most Janiroidea (character 45). This lobe is usually located on the distodorsal region of the article and is simply rounded or almost triangular. The condition present in *U. solicipia* and *U. zapiola* is thus plesiomorphic. The subparallel margins found in Macrostylidae, several Paramunnidae, Nannoniscidae, and Munnopsidae (not treated here), as well as the extremely expanded dorsal lobe found in *U. thiotyntlus* (character 46), must be considered as (multiple independent) derivations.

#### NEW INSIGHTS ON THE EVOLUTION OF THE HIGHLY DERIVED MACROSTYLIDAE

Urstylidae show many plesiomorphic character states indicating a more basal derivation than the Macrostylidae. This is depicted by translating unique synapomorphies into branch length (Fig. 27). The free pleonite expressed in all three species is one example of a plesiomorphic character. A pleon with five freely articulated pleonites is present in most malacostracan crustaceans. Throughout the isopods, many groups show tendencies for the integration of the posterior pleonites into a pleotelson. Thus, the pleotelson has differing compositions amongst the major groupings of Isopoda (Wägele, 1989; Brusca & Wilson, 1991; Brandt & Poore, 2003; Wilson, 2009). The pattern of articulation loss between pleonite 1 and the pleotelson defines clusters of taxa within the Janiroidea. Macrostylidae are variable in this regard but mostly show a loss of articulation (Kussakin, 1999; Riehl *et al.*, 2012).

More evidence that Urstylidae is not as highly derived as Macrostylidae or, for example, many Nannoniscidae or Desmosomatidae, can be seen in the lower degree of tagmosis (character 19). Although Macrostylidae can be considered to have the most-derived tagmosis amongst the before-mentioned taxa, Desmosomatidae and Nannoniscidae often have a clear distinction in form and setation of the anterior and posterior pereopods. In Urstylidae, pereopods II–VII are fairly similar. Additionally, the integration of the segments (characters 21–23) is less derived than in Macrostylidae: the segments appear to be movable against each other and are laterally equally spaced.

Several morphological features of Urstylidae seem to represent intermediate conditions assuming an evolutionary trajectory from a primitive janirid-like ancestor (Wägele, 1989) to the highly derived Macrostylidae. The relatively strong anterior habitus, also present in *Eugerdella* for example, may have a common origin in all three groups (character 20). The specific organization and shape of the pereopodal claws and dactylar sensillae (characters 39–44) is incompletely studied but nevertheless, evolutionary patterns can be observed across all the Janiroidea, based on the few species that have been studied in detail (Wilson, 1985). The ventral claw on the dactylus of most janiroideans is typically either seta-like or more robustly claw-like, although several groups, such as Haploniscidae (not treated here), and Urstylidae have distinctly flattened or scale-like ventral claws (character 39). In Macrostylidae, this claw is thin and elongate, dorsally concave, often with a ventral carina, distally tapering and bending upwards, clinging to the distal sensilla. Whereas in most taxa, the anterior and posterior pereopods have similar claws, in Urstylidae for example, the Macrostylidae show substantial differences. Here, the posterior claws are shaped like simple or serrate setae, generally subcircular in cross-section (character 40).

The shape of the ventral claw by itself does not provide sufficient information regarding a potential evolutionary trajectory. The basal inclusion of the distal sensilla by the claws (characters 41, 42), however, may be interpreted as an intermediate state in Urstylidae. The macrostylid anterior dactylus is furnished with claws that cover the distal sensilla along its entire dorsal and ventral margins. Distal sensillae plesiomorphically sit between the dorsal

and ventral claws and are fully exposed. This claw apomorphy is probably not homologous to the enclosed claws of the Munnopsidae (Wilson, 1989). That is because, unlike the Munnopsidae, the distal sensilla in *Macrostylis* is uniquely thick and has lost the fringe-like microstructure (character 43). The elongate, rod-like uropods inserting at the posterolateral margin in distinct separation from the anus (character 87) was one of the characters that initially led to allocation of the new taxa to Macrostylidae (Thistle & Wilson, 1987) and seems indeed to be of common origin. Interestingly, detailed study of the uropods revealed the presence of a vestigial exopod (character 73). Again, this situation may represent the ancestral condition from the macrostylid perspective. In the latter taxon, the uropod exopod is completely reduced.

The interpretation of the paired sensory organ (character 58) on the pleotelson is problematic. The subcuticular organ of Macrostylidae discovered by Hansen (1916) has never been analysed anatomically or physiologically. In *U. zapiola*, we identified a pair of cuticular tubercles that seem to house a cavity, which resembles the macrostylid organ as it is filled with some sort of crystalline structure (Fig. 2C). Given this agreement in position and form, we assume a homology between the structures in Macrostylidae and *U. zapiola*. In *U. solicopia*, a pair of broom setae (= penicillate setae) was found in a similar position and arising from cuticular elevations. Although anatomical studies are needed, such as on the innervation of both structures, we hypothesize a common origin of both types of sensory organs. Indeed, these tubercles and broom setae can be found in a wide range of Janiroidea including many Haploniscidae (e.g. Brökeland & Wägele, 2004: fig. 26), some Munnopsidae (e.g. Malyutina, 2003: electronic supplement fig. 1), and in the nannoniscid genus *Austroniscus* (S. Kaiser, pers. comm.), which may indicate a fundamental synapomorphy rooted deep within the whole superfamily. Unfortunately, not much attention has been paid to these structures in the taxonomic literature. Owing to their small size, they may have been overlooked in many cases. Consequently this character was left unscored in our database for most taxa; confirmation of the homology of these structures in urstylids and macrostylids remains to be found.

#### CLASSIFICATORY CONSEQUENCES

According to our results, Macrostylidae is the sister group to the new species but the *Urstylis* species share numerous derived character states. One example is the relatively short carpus (character 10) of the antenna. This podomere is elongate throughout

the Asellota and, because this is also found in phreatoicids, it probably represents the plesiomorphic condition. In Janiroidea, however, this article is often distinctly longer than the combined length of the preceding articles, such as many Janiridae, Macrostylidae, Janirellidae, and Munnopsidae.

Other group-specific characters lie in the proportions of the maxilliped (characters 14–17): the length–width ratio of the maxilliped palp article 2 (merus) is highly variable across Janiroidea. Some groups, such as Mesosignidae and *Dactylostylis*, show a consistently narrow article 2. Across the other families, both merus that are as long as wide and merus that are wider than long commonly occur.

The carposubchelate first pereopod (character 49) and the ventral comb of spinules are plesiomorphic, as seen in the Asellidae and Phreatoicoidea. The inclusion of the dactylus, however, to form a carpopodiosubchela furnished with ventral robust setae participating in grasping are evolutionary novelties that independently arose in Urstylidae, Desmosomatidae, and Nannoniscidae. The first pereopod undergoes multiple other transformations throughout the Asellota. Plesiomorphically (e.g. amongst Phreatoicoidea, Asellidae, Stenetriidae, and other basal asellotans) the first pereopods are shorter than more posterior pereopods (character 50). In the Janiridae, males have a larger first pereopod than females, but this is complicated by the second pereopod also being sexually dimorphic in the species *Janira maculosa*. In Macrostylidae, pereopod I is subsimilar in length to the second pereopod, whereas in the Urstylidae, it is always shorter – plesiomorphically according to our analyses. Amongst basally derived asellotes, the limb is plesiomorphically propodosubchelate (Wilson, 1987b, 2009), and it appears as a more leg-like structure in the basally derived janiroideans such as Janiridae, possibly via intermediate states (Wilson, 1986) in which both the carpus and propodus become enlarged (e.g. Munnidae and Paramunnidae). Amongst the more derived janiroideans, a subchelate state occurs but with the palm being the carpus and the movable finger being the propodus and dactylus together. This pattern is complicated by several taxa having the propodosubchelate state amongst apparently more derived taxa (e.g. *Pleurocope* or *Torwolia*). To capture the transformations, many of which seem to be independent, the shapes of the carpus (character 48) and propodus as well as the degree to which they oppose one another (character 49) are treated here as separate characters. In the plesiomorphic propodosubchelate state, the carpus is triangular, but it is trapezoidal (unique in Urstylidae and analogous to *Thaumastosoma* in the context of our analysis) or rectangular, and elongate in the walking-leg-like pereopods.



Other unique features can be found in the pleopods. The short and stout male pleopod II exopod found in Janiroidea (character 68) is remarkably elongate in Urstylidae. A rather large number of complex synapomorphies for the three new species as well as for Macrostylidae was accumulated. These outnumber the joint synapomorphies multiple times, so including the new taxa in Macrostylidae would result in a less definable group. Additionally, within the genus *Macrostylis* more (morphological) diversity is present than suggested by the monotypy of the family (Fig. 27). Macrostylids have never been revised systematically and the absence of generic diversity is owing to a lack of taxonomic effort rather than a lack of morphological variability (Riehl & Brandt, 2013). Riehl & Brandt (2013) found relatively large genetic divergence within macrostylids and hypothesized that thorough analyses are likely to reveal substantial morphological diversity within *Macrostylis*. Although all currently known macrostylids were studied, only a small subset was chosen here for practical reasons to represent the family. Nevertheless, because these represent distinct major clades within the monotypic family (T. Riehl, unpubl. data), the basal synapomorphies are likely to be fundamental for this taxon as a whole and the reciprocal monophyly can be generalized. As Macrostylidae internal relationships are beyond the scope of this paper, such characters have mostly been omitted in the analyses and character conceptualization.

Considering the clear distinction of the new species from macrostylids overall, inclusion within this family would have negative practical effects on the concept of Macrostylidae. We thus are justified in the erection of a new family-level taxon: Urstylidae. We argue that this decision provides a more conservative and durable nomenclature.

#### BIOGEOGRAPHICAL CONSIDERATIONS

The phylogenetic analysis has another outcome that combines with other research on the age of deep-sea isopod groups. The low average density (approximately one individual in every 1.25 m) at which these isopods occur shows that they are rare in the fauna, but apparently the species are extremely widespread geographically. As we can conceive of no mechanism that would rapidly transport populations between the South Atlantic and the North Pacific, we conclude that their ancestors came to the two regions by crawling or perhaps movement by occasional erosive currents. The results of Lins *et al.* (2012) centre the branch leading to the Macrostylidae in the mid-Permian around 275 Mya (credibility interval ranges from the Upper Carboniferous to the upper Triassic). Our analyses place the Urstylidae on this branch. The

geographical distance (~14 350 km) separating the *Urstylis* localities implies that the ancestral population began spreading several hundred million years ago. Thus, we believe the application of the prefix 'Ur' to the family name to be apt.

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#### REFERENCES

- Birstein YA. 1970.** New Crustacea Isopoda from the Kurile-Kamchatka Trench area. In: Bogorov VG, ed. *Fauna of the Kurile-Kamchatka Trench and its environment*. Proceedings of the Shirshov Institute of Oceanology (Vols 1–2, Vol. 86: 1). Moscow: Academy of Sciences of the USSR, 308–356.
- Birstein YA. 1973.** Deep water isopods (Crustacea. Isopoda) of the north-western part of the Pacific Ocean. *Akademiya Nauk, SSSR: Moscow*, 1–213.
- Brandt A, Poore GCB. 2003.** Higher classification of the flabelliferan and related Isopoda based on a reappraisal of relationships. *Invertebrate Systematics* **17**: 893–923.
- Brix S. 2006.** A new species of Desmosomatidae (Isopoda: Crustacea) from the deep Southern Ocean: *Eugerdella serrata* sp. nov. including remarks to the morphological variability within *Eugerdella* Hessler, 1970. *Mitteilungen aus dem hamburgener zoologischen Museum und Institut*, 69–84.
- Brökeland W. 2010.** Description of four new species from the *Haplomisiscus unicornis* Menzies, 1956 complex (Isopoda: Asellota: Haplomisiscidae). *Zootaxa* **2536**: 1–35.

- Brökeland W, Wägele J-W. 2004.** Redescription of three species of *Haploniscus* Richardson, 1908 (Isopoda, Asellota, Haploniscidae) from the Angola Basin. *Organisms Diversity & Evolution* **4**: 237–239.
- Brusca RC, Wilson GDF. 1991.** A phylogenetic analysis of the Isopoda with some classificatory recommendations. *Memoirs of the Queensland Museum* **31**: 143–204.
- Chardy P. 1972.** *Janirella priseri* sp. n., Isopode abyssal de l'Atlantique nord. *Crustaceana. Supplement* **3**: 11–18.
- Coleman CO. 2003.** “Digital inking”: how to make perfect line drawings on computers. *Organisms Diversity & Evolution* **3**: 303–304.
- Coleman CO. 2009.** Drawing setae the digital way. *Zoosystematics and Evolution* **85**: 305–310.
- Dallwitz MJ. 1974.** A flexible computer program for generating identification keys. *Systematic Biology* **23**: 50–57.
- Dallwitz MJ. 1980.** A general system for coding taxonomic descriptions. *Taxon* **29**: 41–46.
- Dallwitz MJ. 1993.** DELTA and INTKEY. In: Fortuner R, ed. *Advances in computer methods for systematic biology: artificial intelligence, databases, computer vision*. Baltimore, MD: Johns Hopkins University Press, 287–296. Available at: <http://delta-intkey.com>
- Dallwitz MJ, Paine TA, Zurcher EJ. 2010.** *User's guide to the DELTA editor*. Available at: <http://delta-intkey.com>
- De Miranda AP, Barnier B, Dewar WK. 1999.** On the dynamics of the Zapiola Anticyclone. *Journal of Geophysical Research* **104** (C9): 21137–21149.
- Flood RD, Shor AN, Manley PL. 1993.** Morphology of abyssal mudwaves at project MUDWAVES sites in the Argentine Basin. *Deep Sea Research Part II: Topical Studies in Oceanography* **40**: 859–888.
- Goloboff PA, Farris JS. 2001.** Methods for quick consensus estimation. *Cladistics* **17**: S26–S34.
- Goloboff PA, Farris JS, Nixon KC. 2008.** TNT, a free program for phylogenetic analysis. *Cladistics* **24**: 774–786.
- Grassle JF, Brown-Leger LS, Morse-Porteous L, Petrecca RF, Williams I. 1985.** Deep-sea fauna in the vicinity of hydrothermal vents. *Bulletin of the Biological Society of Washington* **6**: 443–452.
- Gurjanova E. 1930.** Beiträge zur Fauna der Crustacea-Malacostraca des arktischen Gebietes. *Zoologischer Anzeiger* **86**: 231–248.
- Hansen HJ. 1893.** Zur Morphologie der Gliedmassen und Mundtheile bei Crustaceen und Insekten. *Zoologischer Anzeiger* **16**: 193–212.
- Hansen HJ. 1916.** Crustacea Malacostraca: the order Isopoda. *Danish Ingolf Expedition* **3**: 1–262.
- Hessler RR. 1970.** *The Desmosomatidae (Isopoda, Asellota) of the Gay Head-Bermuda Transect*. Bulletin of the Scripps Institution of Oceanography (Vol. 15). Berkeley, Los Angeles, CA, London: University of California Press.
- Hessler RR, Jumars PA. 1974.** Abyssal community analysis from replicate box cores in the central North Pacific. *Deep Sea Research and Oceanographic Abstracts* **21**: 185–209.
- Hessler RR, Strömberg JO. 1989.** Behavior of janiroidean isopods (Asellota), with special reference to deep sea genera. *Sarsia* **74**: 145–159.
- Hessler RR, Thistle D. 1975.** On the place of origin of deep-sea isopods. *Marine Biology* **32**: 155–165.
- Hessler RR, Wilson GDF, Thistle D. 1979.** The deep-sea isopods: a biogeographic and phylogenetic overview. *Sarsia* **64**: 67–75.
- Just J. 2005.** Xenosellidae, a new family of Janiroidea (Asellota: Isopoda: Crustacea), for *Xenosella coxospinosa* gen. nov., sp. nov., from the marine bathyal of eastern Australia. *Zootaxa* **1085**: 21–32.
- Just J, Wilson GDF. 2004.** Revision of the *Paramunna* complex (Isopoda: Asellota: Paramunnidae). *Invertebrate Systematics* **18**: 377–466.
- Just J, Wilson GDF. 2007.** Revision of *Austrosignum* Hodgson and *Munnogonium* George & Strömberg (Paramunnidae) with descriptions of eight new genera and two new species, (Crustacea: Isopoda: Asellota). *Zootaxa* **1515**: 1–29.
- Kaiser S, Barnes DKA. 2008.** Southern Ocean deep-sea biodiversity: sampling strategies and predicting responses to climate change. *Climate Research* **37**: 165–179.
- Kavanagh FA, Wilson GDF. 2007.** Revision of the genus *Haplomesus* (Isopoda: Asellota: Ischnomesidae) with erection of four new genera. *Invertebrate Systematics* **21**: 487–535.
- Kussakin OG. 1999.** Marine and brackish-water isopods from cold and temperate waters of the Northern Hemisphere suborder Asellota. Part 2. Families Joeropsididae, Nannoniscidae, Desmosomatidae, Macrostylidae. *Keys to the fauna of the SSSR, Vol. 3*. St. Petersburg: A. F. Alimov, Publication of the Zoological Institute of the Russian Academy of Sciences.
- Latreille PA. 1802.** Histoire naturelle générale et particulière des Crustacés et des Insectes. *Histoire Naturelle generale et particuliere, nouvelle edition, accompagnée des notes, Vol. 3*. Paris: G. L. L. Buffon, Dufart.
- Leach WE. 1814.** Crustaceology. In: Brewster D, ed. *The Edinburgh Encyclopædia*. Edinburgh: A. Balfour, 383–437.
- Lilljeborg W. 1864.** Bidrag til kändedommen om de inom Sverige och Norrige förekommande Crustaceer af Isopodernas underordning och Tanaidernas familj. *Inbjudningsskrift till Åhörande af de Offentliga Föreläsningar*. Upsala: CA. Leffler, Konglige Academie Boktryckare, 31 pp.
- Lins LSF, Ho SYW, Wilson GDF, Lo N. 2012.** Evidence for Permo-Triassic colonization of the deep sea by isopods. *Biology Letters* **8**: 979–982.
- Maddison WP, Maddison DR. 2011.** *Mesquite: a modular system for evolutionary analysis*. Available at: <http://mesquiteproject.org>
- Malyutina MV. 2003.** Revision of *Storthyngura* Vanhöffen, 1914 (Crustacea: Isopoda: Munnopsididae) with descriptions of three new genera and four new species from the deep South Atlantic. *Organisms Diversity & Evolution* **3**: 245–252.
- Malyutina MV. 2008.** *Microcope* gen. nov.—a new deep-sea genus of Munnopsidae (Crustacea, Isopoda, Asellota), with

- description of two new species from the Southern Hemisphere. *Zootaxa* **1866**: 555–574.
- McLaughlin PA. 1980.** *Comparative morphology of recent crustacea*. San Francisco, CA: W. H. Freeman.
- Menzies RJ. 1956.** New abyssal tropical Atlantic isopods with observations on their biology. *American Museum Novitates* **1798**: 1–16.
- Menzies RJ. 1962a.** The zoogeography, ecology, and systematics of the Chilean marine isopods. *Reports of the Lund University Chile Expedition 1948–1949, Vol. 42*. Lund: CWK Gleerup.
- Menzies RJ. 1962b.** The isopods of abyssal depths in the Atlantic Ocean. In: Barnard JL, Menzies RJ, Bacescu MC, eds. *Abyssal Crustacea, Vema Research Series, Vol. 1*. New York: Columbia University Press, 79–206.
- Mezhov BV. 1981.** Isopoda. In: Kuznetsov AP, Mironov AN, eds. *Benthos of the Submarine mountains Marcus-Necker and adjacent Pacific regions*. Moscow: Academy of Sciences of the U.S.S.R. P. P. Shirshov Institute of Oceanology, 62–82.
- Osborn KJ, Madin LP, Rouse GW. 2011.** The remarkable squidworm is an example of discoveries that await in deep-pelagic habitats. *Biology Letters* **7**: 449–453.
- Pohl H. 2010.** A scanning electron microscopy specimen holder for viewing different angles of a single specimen. *Microscopy Research and Technique* **73**: 1073–1076.
- Prendini L. 2001.** Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. *Systematic Biology* **50**: 290–300.
- Ramirez-Llodra E, Brand A, Danovaro R, De Mol B, Escobar E, German CR, Levin LA, Martinez Arbizu P, Menot L, Buhl-Mortensen P, Narayanaswamy BE, Smith CR, Tittensor DP, Tyler PA, Vanreusel A, Vecchione M. 2010.** Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Bioessences* **7**: 2851–2899.
- Raupach MJ, Held C, Wägele J-W. 2004.** Multiple colonization of the deep sea by the Asellota (Crustacea: Peracarida: Isopoda). *Deep Sea Research Part II: Topical Studies in Oceanography* **51**: 1787–1795.
- Raupach MJ, Mayer C, Malyutina MV, Wägele J-W. 2009.** Multiple origins of deep-sea Asellota (Crustacea: Isopoda) from shallow waters revealed by molecular data. *Proceedings of the Royal Society B: Biological Sciences* **276**: 799–808.
- Rex MA, McClain CR, Johnson NA, Etter RJ, Allen JA, Bouchet P, Warén A. 2005.** A source-sink hypothesis for abyssal biodiversity. *The American Naturalist* **165**: 163–178.
- Rex MA, Stuart CT, Hessler RR, Allen JA, Sanders HL, Wilson GDF. 1993.** Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* **365**: 636–639.
- Richardson H. 1911.** Les crustacés isopodes du Travailleur et du Talisman: formes nouvelles. *Bulletin du Museum National d'Histoire Naturelle* **17**: 518–534.
- Richter S, Edgecombe GD, Wilson GDF. 2002.** The lacinia mobilis and similar structures—a valuable character in arthropod phylogenetics? *Zoologischer Anzeiger – A Journal of Comparative Zoology* **241**: 339–361.
- Riehl T, Brandt A. 2010.** Descriptions of two new species in the genus *Macrostylis* Sars, 1864 (Isopoda, Asellota, Macrostylidae) from the Weddell Sea (Southern Ocean), with a synonymisation of the genus *Desmostylis* Brandt, 1992 with *Macrostylis*. *Zookeys* **57**: 9–49.
- Riehl T, Brandt A. 2013.** Southern Ocean Macrostylidae reviewed with a key to the species and new descriptions from Maud Rise. *Zootaxa* **3692**: 160–203.
- Riehl T, Kaiser S. 2012.** Conquered from the deep sea? A new deep-sea isopod species from the Antarctic shelf shows pattern of recent colonization. *PLoS ONE* **7**: e49354.
- Riehl T, Wilson GDF, Hessler RR. 2012.** New Macrostylidae Hansen, 1916 (Crustacea: Isopoda) from the Gay Head-Bermuda transect with special consideration of sexual dimorphism. *Zootaxa* **3277**: 1–26.
- Sanders HL, Hessler RR, Hampson GR. 1965.** An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. *Deep Sea Research and Oceanographic Abstracts* **12**: 845–867.
- Sars GO. 1864.** Om en anomal Gruppe af Isopoder. *Forhandlingene Videnskaps-Selskapet, Anar 1863*. Christiania, 205–221.
- Sars GO. 1870.** Nye Dybvandscrustaceer fra Lofoten. *Særskilt aftrykt af Videnskaps-Selskapet, Forhandlingene for 1869*. Christiania, 147–174.
- Sars GO. 1897.** On some additional Crustacea from the Caspian Sea. *Annales du Musée Zoologique Academie Imperiale des Sciences St. Petersburg* **2**: 273–305.
- Schotte M, Boyko CB, Bruce NL, Poore GCB, Taiti S, Wilson GDF. 2013.** Isopoda, Janiroidea. *World marine, freshwater and terrestrial isopod crustaceans database*. Available at: <http://www.marinespecies.org/Isopoda/aphia.php?p=taxdetails&id=155716>
- Schultz GA. 1969.** *The marine isopod crustaceans*. Hampton, NJ: William C. Brown Company.
- Stebbing TRR. 1912.** On the Crustacea Isopoda of the 'Porcupine' expedition – abstract. *Proceedings of the Zoological Society of London* **4**: 42.
- Stebbing TRR. 1913.** On the Crustacea Isopoda from the 'Porcupine' expedition. *Transactions of the Zoological Society of London* **20**: 231–246.
- Svavarsson J. 1987.** Reevaluation of *Katianira* in Arctic waters and erection of a new family, Katianiridae (Isopoda: Asellota). *Journal of Crustacean Biology* **7**: 704–720.
- Thistle D, Wilson GDF. 1987.** A hydrodynamically modified, abyssal isopod fauna. *Deep-Sea Research. Part A. Oceanographic Research Papers* **34**: 73–87.
- Thistle D, Wilson GDF. 1996.** Is the HEBBLE isopod fauna hydrodynamically modified? A second test. *Deep-Sea Research Part I* **43**: 545–554.
- Vanhöffen E. 1914.** Die Isopoden der Deutschen Südpolar-Expedition 1901–1903. In: Drygalsky E, ed. *Deutsche Südpolarexpedition 1901–1903*. Zoologie (Vol. 7). Berlin: Georg Reimer, 449–598.
- Veuille M. 1980.** Sexual behaviour and evolution of sexual dimorphism in body size in *Jaera* (Isopoda

- Asellota). *Biological Journal of the Linnean Society* **13**: 89–100.
- Wägele J-W. 1983.** On the homology of antennal articles in Isopoda. *Crustaceana* **45**: 31–37.
- Wägele J-W. 1989.** *Evolution und phylogenetisches System der Isopoda: Stand der Forschung und neue Erkenntnisse*. Zoologica (Vol. 140). Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.
- Wilson GDF. 1976.** The systematics and evolution of *Haplomunna* and its relatives (Isopoda, Haplomunnidae, new family). *Journal of Natural History* **10**: 569–580.
- Wilson GDF. 1985.** The systematic position of the Ilyarachnoid Eurycopidae (Crustacea, Isopoda, Asellota). Unpublished PhD dissertation, University of California, San Diego.
- Wilson GDF. 1986.** Evolution of the female cuticular organ in the Asellota (Crustacea, Isopoda). *Journal of Morphology* **190**: 297–305.
- Wilson GDF. 1987a.** *Crustacean communities of the manganese nodule province (DOMES site A compared with DOMES site C)*. Report for the National Oceanic and Atmospheric Administration Office of Ocean and Coastal Resource Management (Ocean Minerals and Energy) no. NA-84-ABH-0030 (p. 44). La Jolla, California 92093: Scripps Institution of Oceanography.
- Wilson GDF. 1987b.** The road to the Janiroidea: comparative morphology and evolution of the asellote isopod crustaceans. *Journal of Zoological Systematics & Evolutionary Research* **25**: 257–280.
- Wilson GDF. 1989.** *A systematic revision of the deep-sea subfamily Lipomerinae of the isopod crustacean family Munnopsidae*. Bulletin of the Scripps Institution of Oceanography (Vol. 27). Berkeley, Los Angeles, CA, London: University of California Press.
- Wilson GDF. 1991.** Functional morphology and evolution of isopod genitalia. In: Bauer RT, Martin JW, eds. *Crustacean sexual biology*. New York: Columbia University Press, 228–245.
- Wilson GDF. 1998.** Historical influences on deep-sea isopod diversity in the Atlantic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* **45**: 279–301.
- Wilson GDF. 2008.** A review of taxonomic concepts in the Nannoniscidae (Isopoda, Asellota), with a key to the genera and a description of *Nannoniscus oblongus* Sars. *Zootaxa* **1680**: 1–24.
- Wilson GDF. 2009.** The phylogenetic position of the Isopoda in the Peracarida (Crustacea: Malacostraca). *Arthropod Systematics & Phylogeny* **67**: 159–198.
- Wilson GDF. 2013.** Janiroidea incertae sedis. In: Schotte M, Boyko CB, Bruce NL, Poore GCB, Taiti S, Wilson GDF, eds. *World marine, freshwater and terrestrial isopod crustaceans database*. Available at: <http://www.marinespecies.org/Isopoda/aphia.php?p=taxdetails&id=268172> on 18 September 2013.
- Wirkner CS, Richter S. 2010.** Evolutionary morphology of the circulatory system in Peracarida (Malacostraca; Crustacea). *Cladistics* **26**: 143–167.
- Wolff T. 1962.** The systematics and biology of bathyal and abyssal Isopoda Asellota. *Galathea Report* **6**: 1–320.
- Yeates DK. 1995.** Groundplans and exemplars: paths to the tree of life. *Cladistics* **11**: 343–357.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Urstylidae matrix trees.

**Appendix S2.** Information on isopod diversity at type locality of *Urstylis zapiola*.