



# A new genus of phreatoicidean isopod (Crustacea) from the north Kimberley region, Western Australia

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A new genus and species of phreatoicidean isopod, *Crenisopus acinifer*, has been collected from a freshwater spring in the northern Kimberley region of Western Australia. Empirical cladistic analysis of 10 exemplars of phreatoicidean genera found a single cladogram. The new genus and species assumed a basal position in the Phreatoicidea, placing it within the family Amphisopodidae *sensu lato*. This family, however, was not monophyletic in the preliminary cladogram, suggesting that the taxonomic structure of the suborder must be revised. The cladogram provided evidence for the monophyly of the Phreatoicidae and its New Zealand clade. The analysis suggested that clades of modern phreatoicideans diverged from one another during the Mesozoic Era after they entered fresh water, but prior to the fragmentation of East Gondwana.

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ADDITIONAL KEY WORDS:—Phreatoicidea – Isopoda – taxonomy – phylogeny – biogeography – Gondwana – Southern Hemisphere – fresh water – groundwater.

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## INTRODUCTION

Phreatoicidean isopods are often common in undisturbed freshwater habitats in Australia. The last major treatment of Australian phreatoicidean genera was Nicholls' (1943, 1944) monograph, wherein he divided the suborder into two families, each with several subfamilies. The Amphisopodidae Nicholls, 1943 was partitioned into the following subfamilies: Mesamphisopodinae, Amphisopodinae, Phreatomerinae and Phreatoicopsidinae. The Phreatoicidae Chilton, 1891 was divided into three subfamilies: Phreatoicinae, Mesacanthotelsoninae and Paraphreatoicinae. (The family-level names have been changed to their correct genitive stems; e.g. the stem of '*Amphisopus*' is 'Amphisopod-'.) The composition of these subfamilies must be revised because some genera appear to be misplaced and the subfamily definitions often are not clear (Poore, Knott & Lew-Ton, in press).

Species in these two families occur solely in the Southern Hemisphere (Banareescu, 1990). A third family, the Nicholssiidae Chopra, 1947 from the Ganges Plain of India (Chopra & Tiwari, 1950) is an important exception, indicating Gondwanan biogeographic relationships for the suborder, which can be further illuminated by their fossil record. The Phreatoicidea is the earliest derived of the isopod crustaceans, based on marine fossils (Carboniferous, 325 Myr: Hessler, 1969; Schram, 1970) and on cladistic analyses (Brusca & Wilson, 1991; Wilson, in prep.). Phreatoicideans had colonized fresh water by the Triassic (Chilton, 1918; Nicholls, 1943), and have subsequently been restricted to permanent fresh water habitats, such as ground water bores or springs, as well as spring-fed streams, marshes and lakes. Therefore, the ages of Gondwanan fragmentation, which took place after the Triassic, may have an important bearing on the observed distribution of extant phreatoicidean taxa.

Despite their interest for Southern Hemisphere biogeography and their ongoing endangerment by anthropogenic degradation of fresh waters, surprisingly few taxa of phreatoicideans have been described in the last half of this century, the total count for the suborder being fewer than 50 species (Wilson & Ho, 1996). This paper reports on a new genus and species of phreatoicidean isopod, *Crenisopus acinifer*, collected by W. F. Humphreys and B. Vine (Western Australian Museum) in the northern Kimberley region of Western Australia.

Tropical Western Australia may contain particularly favourable environments for the survival of ancient crustacean relicts, such as the Remipedia (Yager & Humphreys, 1996), the Thermosbaenacea (Poore & Humphreys, 1992), the Spelaeogriphacea (Poore & Humphreys, 1998) and phreatic Isopoda. Recent finds (Wilson, in prep.) of the 'flabelliferan' genus *Tainisopus* Wilson and Ponder, 1992, another new undescribed *Tainisopus*-like genus, and several undescribed phreatoicidean species related to those in the genera *Synamphisopus* Sheard, 1936 and *Hyperoedesopus* Nicholls and Milner, 1923, as well as *Crenisopus acinifer* gen.nov., sp.nov. are notable. These finds demonstrate that more research effort on permanent fresh waters of Western Australia, especially in the Kimberley and the Pilbara regions, may add considerably to our knowledge of crustacean evolution and biogeography. Therefore, conservation of relictual fresh water habitats in these regions, which is negatively impacted by mining, agricultural and pastoral activities (Humphreys, 1994), should have a high priority.

*Crenisopus acinifer* gen.nov., sp.nov. is unlike any other species in the Phreatoicidea, and therefore extends the morphological diversity of the suborder. This paper also marks the first description of a phreatoicidean isopod generated by a taxonomic

database program (the DELTA system: Dallwitz, 1980; Dallwitz, Paine & Zurcher, 1993). This DELTA database is under construction and will contain most described species in the suborder. To explore the affinities of the new species, a computer-assisted cladistic analysis of the phreatoicideans was made directly from a subset of multistate characters in the database. This preliminary analysis contains only nine exemplar species, representing most subfamilies of the Amphisopodidae and the Phreatoicidae. The cladistic analysis indicates an approximate placement for *Crenisopus acinifer*, although definitive inferences on phreatoicidean phylogeny are not warranted at this time.

## METHODS

### *Taxonomic database and cladistic characters*

The DELTA format (Dallwitz, 1980; Dallwitz *et al.*, 1993) was used for building the database, starting from a list of descriptive characters extracted from Wilson and Ho (1996) and an earlier survey of the literature. We conducted extensive evaluations of the range of variation across the suborder, using both illustrations and descriptions from literature and specimens held at the Australian Museum. Because the database was designed to perform multiple roles (taxonomic description, interactive identification, morphometry and cladistic analysis), the assembled data consisted of the full range of characters (multistate, integers, real numbers in the form of ratios, and text). The phylogenetic analysis used only multistate characters, extracted from the database into a NEXUS file format which can be read by MacClade (ver.3.04, Maddison & Maddison, 1992) and PAUP (ver. 3.1.1, Swofford 1993). Characters associated with the eyes, which may be lost independently in different groundwater lineages, and those describing the setal number and position, which are likely to be highly homoplastic, were excluded from the analysis. Some arbitrarily gap-coded characters and invariant or uninformative characters were also excluded. The characters (Appendix 2) were analysed as unordered and multistate.

### *Taxa used and analytical methods*

To establish the relationships of *Crenisopus acinifer* gen.nov., sp.nov., we chose exemplar species from major subfamilial groups established by Nicholls (1943, 1944). At the time of writing, the database contained all species of *Crenoicus* and the additional taxa listed in Appendix 1. Because *Crenisopus acinifer* has a lacinia mobilis on its right mandible, it appears to fit Nicholls' (1943) family definition for the Amphisopodidae, which he divided into five subfamilies (Mesamphisopodinae, Amphisopodinae, Phreatomerinae, Phreatoicopsidinae and Hypsimetopodinae). One species was chosen from each of these subfamilies (Appendix 1) and, where possible, the least modified taxon from each group was chosen. The diverse subfamily Phreatoicopsidinae was represented by *Eophreatoicus* Nicholls, 1926. This genus was chosen because other genera appear to be more specialized: *Synamphisopus* Nicholls, 1943 has an unusual morphology of the tailpiece and uropods, *Phreatoicopsis* Spencer & Hall, 1896 is a highly modified semiterrestrial species, *Protamphisopus* Nicholls,

1943 is a fossil taxon possibly not belonging in this subfamily, and *Uramphisopus* Nicholls, 1943 may be a misclassified Phreatoicidae (Poore *et al.*, in press). Nicholls (1944:4) felt that the subfamilial divisions of the Phreatoicidae were somewhat arbitrary, so species chosen for this analysis were selected to provide a morphological and geographic range. Four members of the Phreatoicidae were also included: *Phreatoicus typicus* Chilton, 1883; *Neophreatoicus assimilis* (Chilton, 1894); *Metaphreatoicus australis* (Chilton, 1891) and *Crenoicus buntiae* Wilson & Ho, 1996.

The choice of outgroup to root the analysis was more difficult. Use of any group within the Phreatoicida is problematical. The Phreatoicidae should not be used for outgroup rooting because the true root may lie somewhere in the Amphisopodidae as currently defined (Nicholls, 1943). The presence of a lacinia mobilis on the right mandible, Nicholls' (1943) defining character of the Amphisopodidae, may be a plesiomorphic feature of the Phreatoicida owing to its presence among other isopods (Brusca & Wilson, 1991) and possibly related non-isopods such as *Spelaeogriphus* Gordon, 1957. Furthermore, some taxa classified by Nicholls (1943) in the Amphisopodidae also lack the right lacinia mobilis, e.g. *Hypsimetopus* (Nicholls, 1943; data herein). Thus, Nicholls' (1943) concept of the Amphisopodidae is questionable. Any isopod taxon external to the Phreatoicida may be derived later than this suborder (Brusca & Wilson, 1991), so presumptive ancestral character states were used instead of an outgroup taxon. A comparison of phreatoicidans with isopods from other suborders, such as *Stenasellus* and *Tainisopus*, allowed the identification of possibly plesiomorphic character states for the Phreatoicida (marked '\*' in Appendix 2). These states were employed as 'ancstates', ancestral state assumptions, to provide a Lundburg rooting of the unrooted trees that resulted from the multistate unordered characters cladistic analysis. MacClade and PAUP were employed to examine the character distributions and to build the most parsimonious unrooted trees, respectively. Preliminary PAUP multiple parsimony analyses were carried out using heuristic searches with 10 iterations of randomised starting trees. The final result was confirmed by a branch and bound search. The generic diagnosis was derived from the characters that changed between the internal nodes of the cladogram.

#### Abbreviations

AM	Australian Museum
TMAG	Tasmanian Museum & Art Gallery
WAM	Western Australian Museum
bl	body length, measured either along the dorsal midline or as segments in lateral view (see Wilson & Ho, 1996)

#### CLADISTIC ANALYSIS RESULTS AND DISCUSSION

##### *Phylogenetic analysis*

Using the data matrix (Table 1) derived from the DELTA database (75 multistate characters, Appendix 2), a PAUP multiple parsimony analysis found a single

TABLE 1. Cladistic data matrix

Character number	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345
<i>Cremisopus acinifer</i>	1?22223321	2125221122	2213212113	2223233213	322122223?	?112221113	1112211241	41233
<i>Crenoicus buntiae</i>	2111121111	3114131231	1112122212	1123231?13	1112122132	3121222311	1111121411	41112
<i>Eophreatoicus</i> sp.	3211121211	32?1121122	1111211213	2122214211	4112123233	2211142213	1221211541	41212
<i>Hypsimetopus</i> sp.	3221221113	2114121222	2122121131	2223131213	112121332?	?112222232	4122212351	41111
<i>Mesamphisopus capensis</i>	1122121321	4125121132	2312212122	2233222212	4211121131	3121222232	1112211541	12233
<i>Metaphreatoicus australis</i>	2311122211	3114131233	2122111113	2122234133	1212113232	3121222133	3111121512	41132
<i>Neophreatoicus assimilis</i>	3221131113	41?43?2233	?1?3211142	?2?2341??	??12121?32	????2223?3	11?221?512	521?1
<i>Paramphisopus palustris</i>	1?22221211	3114131133	2122211212	1233231233	1212222222	2221142211	3211111351	42212
<i>Phreatoicus typicus</i>	3122133323	42?4322232	2123212222	212?234113	1212223?33	3121221313	1113212512	52141
<i>Phreatomerus</i> sp.	1?21223211	3111131122	2223221212	2223214231	4112223232	2211142311	1121211352	41211

Genera of the Phreatoicidea, 10 taxa, 75 characters. All taxa, except *Neophreatoicus assimilis*, were scored directly from specimens in the collection of the Australian Museum, the Western Australian Museum or the Tasmanian Museum and Art Gallery (see Appendix 1). See Appendix 2 for list of characters and character states.

undirected tree (Fig. 1: length 199, CI (consistency index) = 0.538, RC (rescaled consistency index) = 0.234) without rooting by outgroup or presumed ancestral states. With ancstates applied during the heuristic search (marked "\*" in Appendix 2), the analysis generated the same tree (length 202, CI = 0.535, RC = 0.236) but with the root placed on the *Mesamphisopus* branch. The rooted tree is longer because several characters were forced to change by additional steps. For example, character 14 (Appendix 2), a vestigial terminal article on the antennule, found in both basal taxa (*Mesamphisopus* and *Crenisopus*), was forced to change twice on the rooted tree because all potential outgroups for the Phreatoicidea have a tubular or tapering distal article. The mandible of *Mesamphisopus* (Fig. 6F, G) has features in common with *Crenisopus*, especially the spine row, but these states appear more broadly amongst the set of taxa reported here.

A robust estimate of phreatoicidan phylogeny with a revision of the suborder is not yet possible owing to our limited taxonomic sampling. Several hypotheses, however, can be highlighted for further analysis.

The Phreatoicidae may be monophyletic, confirming Nicholls' (1944) classification of this family. This clade was supported by the 'consistent' (meaning that the consistency index is 1.0) character state of short tooth-like setae set on a ridge on the palm of the first pereopod (character 38). Other characters that might define this clade contained more homoplasy. Addition of more taxa to the data may change this topology.

The New Zealand Phreatoicidae may be a monophyletic clade. The New Zealand phreatoicids were defined by the following consistent character states: anteriorly elongate pereonites (char. 6), flattened penultimate antennular article (char. 15), thin spine-like incisor on the mandible (char. 17), subdistal medial bump on uropodal protopod bearing several robust setae (char. 71). This conflicts with Nicholls' (1944) concept for the subfamily Phreatoicinae, which includes the New Zealand taxa, plus *Crenoicus*. The current analysis, however, finds *Crenoicus* to be more closely related to taxa in Nicholls' subfamily Paraphreatoicinae, which includes *Metaphreatoicus*.

The Amphisopodidae is paraphyletic or polyphyletic. *Hypsimetopus* appears to be the sister group of the Phreatoicidae owing to the absence of the lacinia mobilis on the right mandible. This topology is lost, and the character becomes homoplastic if the family Nichollsiidae is added to the tree (preliminary analyses using the same characters), because *Hypsimetopus* and *Nichollisia* Chopra & Tiwari, 1950 share synapomorphies in the form of the pleonites and pleotelson. In either case, however, the monophyly of the Amphisopodidae is lost. The taxonomy may be corrected by raising Nicholls' subfamilies to family status, but with changes to their composition.

*Crenisopus* cannot be classified in any of the existing subfamilies of the Phreatoicidea. *Crenisopus* is the sister group of *Mesamphisopus* in one possible rooting of the undirected tree, thus arguing for its inclusion into the subfamily Mesamphisopodinae. This clade would be supported by character 14, a tiny distal article of the antennule. *Mesamphisopus abbreviatus* (Barnard, 1927) also resembles *Crenisopus* in bearing an unusual inflated penultimate article of the antennula. A constraint forcing the two taxa into a clade results in trees that are one step longer than the unconstrained Lundberg-rooted tree, so this hypothesis is not the most parsimonious topology. Other similarities between *Crenisopus* and *Mesamphisopus* appear to be plesiomorphies, so *Crenisopus* cannot be assigned to the Mesamphisopodinae. *Crenisopus* is tentatively classified amongst the Amphisopodidae *sensu lato* in the current classification established by Nicholls (1943), pending a phylogeny-based division of the family.

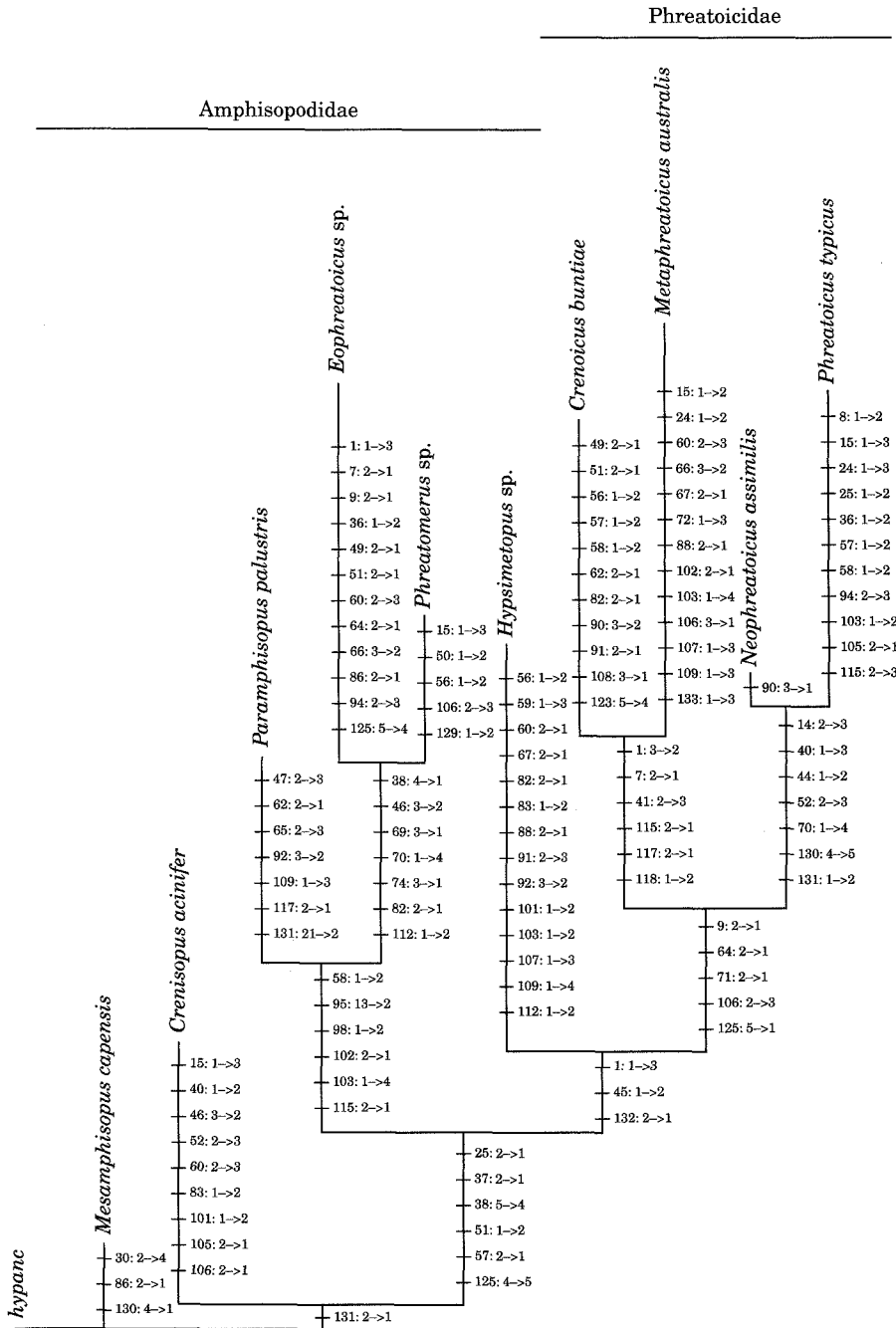


Figure 1. Cladogram of selected phreatoicidae taxa derived from a PAUP 3.0 analysis of the data in Table 1, rooted length 202, consistency index 0.535, rescaled consistency index 0.236. Root determined by a suite of presumptive ancestral states (indicated by artificial taxon 'hypanc'). Branches are marked with the character number and the state changes (see Appendix 2). Nicholls' (1943, 1944) family boundaries indicated at top of figure by horizontal bars. Character transitions with ambiguous optimizations are not shown; e.g. character state 14(2), which could be gained at the terminals, *Mesamphisopus* and *Crenisopus*, or could be gained at the root and lost on the branch leading to the remaining phreatoicidaeans.

*Time of phreatoicidean diversification*

The tentative hypothesis of relationships (Fig. 1) has important implications for the biogeography of the Phreatoicidea. The earliest known fossil phreatoicideans are in Carboniferous marine facies (Schram, 1970, 1974), while the earliest known freshwater phreatoicideans are fossils from Triassic shales of the Sydney region (Chilton, 1918; Hessler, 1969). Whether marine phreatoicideans existed during the Mesozoic Era is not certain, but none have been found after the Permian. We therefore assume that tectonic events, rather than marine dispersal events, influence the distribution of phreatoicidean taxa. Comparing the cladogram in Figure 1 with the assumed ages of continental separation and drift provides information on the ages of the various phreatoicidean clades. *Crenisopus* is derived basally, near *Mesamphisopus*, while the New Zealand phreatoicids branch off much later in the cladogram. This pattern suggests that the major clades of the suborder are extremely ancient, evolving prior to the separation of East Gondwana (Australia, Antarctica, India and New Zealand) from West Gondwana (Africa and South America) (180 Myr; Storey, 1995). The cladogram (Fig. 1) also indicates that the Bassian phreatoicid fauna of Australia (represented by *Crenoicus* and *Metaphreatoicus*) is more closely related to the New Zealand fauna (*Phreatoicus* and *Neophreatoicus*) than to other phreatoicideans. Owing to the estimated times for the separation of New Zealand from Antarctica-Australia (approximately 100 Myr; Storey, 1995), the two clades of the Phreatoicidae may predate the middle Cretaceous. The details of phreatoicidean diversification and biogeography, however, will be clarified by a more extensive phylogenetic analysis of the suborder than presented here.

## TAXONOMY

Suborder Phreatoicidea Stebbing, 1893

Family Amphisopodidae Nicholls, 1943 (*sensu lato*)

***Crenisopus* gen.nov.**

*Type species. Crenisopus acinifer* sp.nov.

*Etymology.* The generic name is derived from the Greek word 'crene' (spring) and the name for isopod 'isopus' (like-foot). Therefore, *Crenisopus* means 'spring isopod'.

*Generic diagnosis.* Head length shorter than width in dorsal view; mandibular notch absent; clypeal notch absent; antennal notch absent. Eyes absent. Pereon narrow, width near head width. Pereonites 2–7 in dorsal view wider than long. Pleonites much deeper than pereonites in lateral view, with large ventrolateral plates (pleurae), basal region of pleopods not visible. Pleonites 1–4 relative lengths in dorsal view unequal, pleonite 4 length greater than pleonites 1–3. Pleotelson lateral length less than depth; telsonic region or tailpiece not distinct, dorsal margin smoothly curved to distal tip, terminal area rounded in dorsal view; pleotelson dorsal uropodal ridge without setae. Antennula terminal article tiny, vestigial; penultimate article inflated, width much greater than proximal article. Antenna propodal article 1 present, forming thin ring. Mandible incisor processes broad, width greater than thickness; right lacinia mobilis present; spine rows on projecting ridges between incisor and



molar processes; spine rows distal part on projection raised above proximal part; molar process triturating surface heavily ridged, with no teeth. Maxilla lateral lobes with bidenticulate setae on distal tips and on medial margin; medial lobe proximal and distal setal rows separated by gap; medial lobe proximal portion distinctly angled to distal portion. Pereopod I dactylus distal accessory spines absent. Pereopod I propodal palm in male and in female lacking stout denticulate setae; stout simple setae present, tooth-like; low conical setae on ridge absent. Pereopods II–VII propodus articular plates absent. Pereopods II–III dactylus spines on ventral margin absent; basis dorsal ridge rounded in cross section. Pereopod IV not sexually dimorphic; dactylus accessory claw one third length of primary claw in male, one third length of primary claw in female; basis dorsal ridge rounded in cross section. Pereopods V–VII dactylus spines present; basis dorsal ridge not distinctly separated from basis shaft, angular in cross section. Penes extending near midline, distally tubular. Pleopods with medial proximal lobes on exopods II–V. Male pleopod I exopod distal margin rounded, lateral margin rounded. Male pleopod II endopod appendix masculina distal tip acutely rounded, marginal setae occurring along lateral and medial margins; endopod lateral margin proximally rounded; basal musculature not pronounced. Uropod protopod dorsomedial ridge not produced, robust spinose setae on distoventral margin present; rami distal tips rounded; rami cross-sectional shape oval or flattened on dorsal surface; endopod longer than protopod.

*Generic remarks.* The following combination of characters make *Crenisopus* unique among the phreatoicideans, disregarding features that relate to its groundwater habitat such as the absence of eyes or cuticular pigment. The telsonic region or tailpiece is not distinct—the dorsal margin curves smoothly to the distal tip; the terminal area is rounded in dorsal view. The antennular terminal article is tiny, vestigial and the penultimate article is inflated, with a width much greater than the proximal article. The male pereopod I propodal palm has multiple composite spine-like projections along its length, as well as stout robust simple setae that are tooth-like. The pereopodal propodi lack an articular plate on the posterior side of the limb. The penes are straight, not curved or directed posteriorly. The male pleopod II endopod appendix masculina basal musculature is not pronounced. The uropodal protopod has robust spinose setae on the dorsomedial margin, and the rami have an oval dorsal cross-sectional shape. As discussed above, *Mesamphisopus* shares the antennular tip form with *Crenisopus*, but the interpretation of this character is ambiguous in the present analysis. Therefore, this genus cannot be placed amongst the existing subfamilies.

### *Crenisopus acinifer* sp.nov.

*Type material.* Holotype male, WAM C23229, bl 4.39 mm; paratype male, WAM C23230, bl 5.25 mm, dissected, 4 slides; paratype male, WAM C23231, bl 4.20 mm, dissected, 1 slide and 1 vial; paratype preparatory female, WAM C23232, bl 4.20 mm, dissected, 1 slide and 1 vial; paratype preparatory female, WAM C23233, bl 4.44 mm, intact; paratype brooding female WAM C23234, bl 3.83 mm, intact; paratype juvenile WAM C23235, bl 2.00 mm, intact; paratype juvenile WAM C23236, bl 2.22 mm, intact; paratype juvenile, WAM C23237, bl 2.16 mm, intact.

*Type locality.* Zebedee Springs, El Questro Station, North Kimberley, Western Australia, lot number BES 3122, 16°00'S 128°01'E, water temperature 35°C. Collected from net placed over spring outlet, 100 cubic meters of water strained; collected by W.F. Humphreys and B. Vine, 13 June 1994.

*Etymology.* The species epithet 'acinifer' comes from the Latin word 'acinus' meaning berry, especially the grape, and the suffix '-fer' meaning bearing or carrying referring to the enlarged penultimate article of the antennules. Therefore, this isopod is the 'berry-carrying spring isopod'.

*Coloration.* Translucent white, cuticle lacking any pigment.

### *Description*

*Head.* (Fig. 3A, E, F) length shorter than width in dorsal view; width 0.9 pereonite 1 width; lateral profile of dorsal surface smoothly curved; cuticle smooth and shiny; tubercles absent; setae sparse. Eyes absent. Cervical groove absent. Mandibular groove absent. Mandibular notch absent. Clypeal notch absent. Antennal notch absent. Frontal process above antennula absent. Mouth field adjacent to the posterior margin of head, maxillipeds inserting at posterior margin of head.

*Pereon.* (Fig. 2) narrow, width near head width; dorsal surface smooth; setae on dorsal surface scattered, length of setae 0.26 body depth. Pereonite 1 in dorsal view wider than medial length, length 0.27 width in male, length 0.11 width in female. Pereonites 2–7 in dorsal view wider than long; respective length-width ratios in male: 0.6, 0.66, 0.55, 0.46, 0.39, 0.23; respective length-width ratios in female: 0.48, 0.48, 0.52, 0.69, 0.44, 0.32. Coxal articulation of pereonites 2–4 fused, 5–7 free. lateral tergal plates of pereonites 2–4 absent, 5–7 absent. Sternal processes absent. Typhlosole absent, gut round in cross section; hindgut caecae absent.

*Pleonites.* (Fig. 2B, D) in lateral view much deeper than pereonites, with large ventrolateral plates, basal region of pleopods not visible; pleonite 1 pleura distinctly shallower than pleurae of pleonites 2–5. Pleonites 2–3 respective lengths less than half the length of pleonite 5. Pleonites 1–4 relative lengths unequal; pleonite 4 length greater than pleonites 1–3 (increasing in length from 1–4), equal to half length of pleonite 5. Pleonites 1–4 width 0.57 composite length in dorsal view. Pleonites 1–5 respective dorsal length ratios relative to maximum width: 0.14, 0.18, 0.26, 0.35, 0.81; depth ratios relative to pereonite 7 depth, respectively 0.87, 1.13, 1.21, 1.23, 1.17. Pleonite 5 lacking dorsal median ridge.

*Pleotelson.* (Fig. 2, 4D) lateral length 0.14 body length, less than depth, 0.86 depth; dorsal length 1.17 width; depth 1.06 pereonite 7 depth. Median dorsal ridge absent; lateral dorsal ridges absent. Telsonic region or tailpiece not distinct—dorsal margin smoothly curved to distal tip, terminal area truncate or rounded in dorsal view; robust sensillate setae absent; elongate pappose setae absent. Dorsal uropodal ridge present (minimally), without setae. Ventral margin anterior to uropods with stout setae, posterior marginal seta larger than anterior adjacent setae, 2–3 setae altogether.

*Antennula.* (Fig. 3B, C) length 0.11 body length in male, 0.09 body length in female, with 6 articles in male, with 6 articles in female. No articles divisible into one large or two small articles. Article 4 shorter than article 3. Article 5 length 1.9 width. Article 6 length 0.40 width. Aesthetascs all tiny, 2–3 on article 5, 1 on article 6.

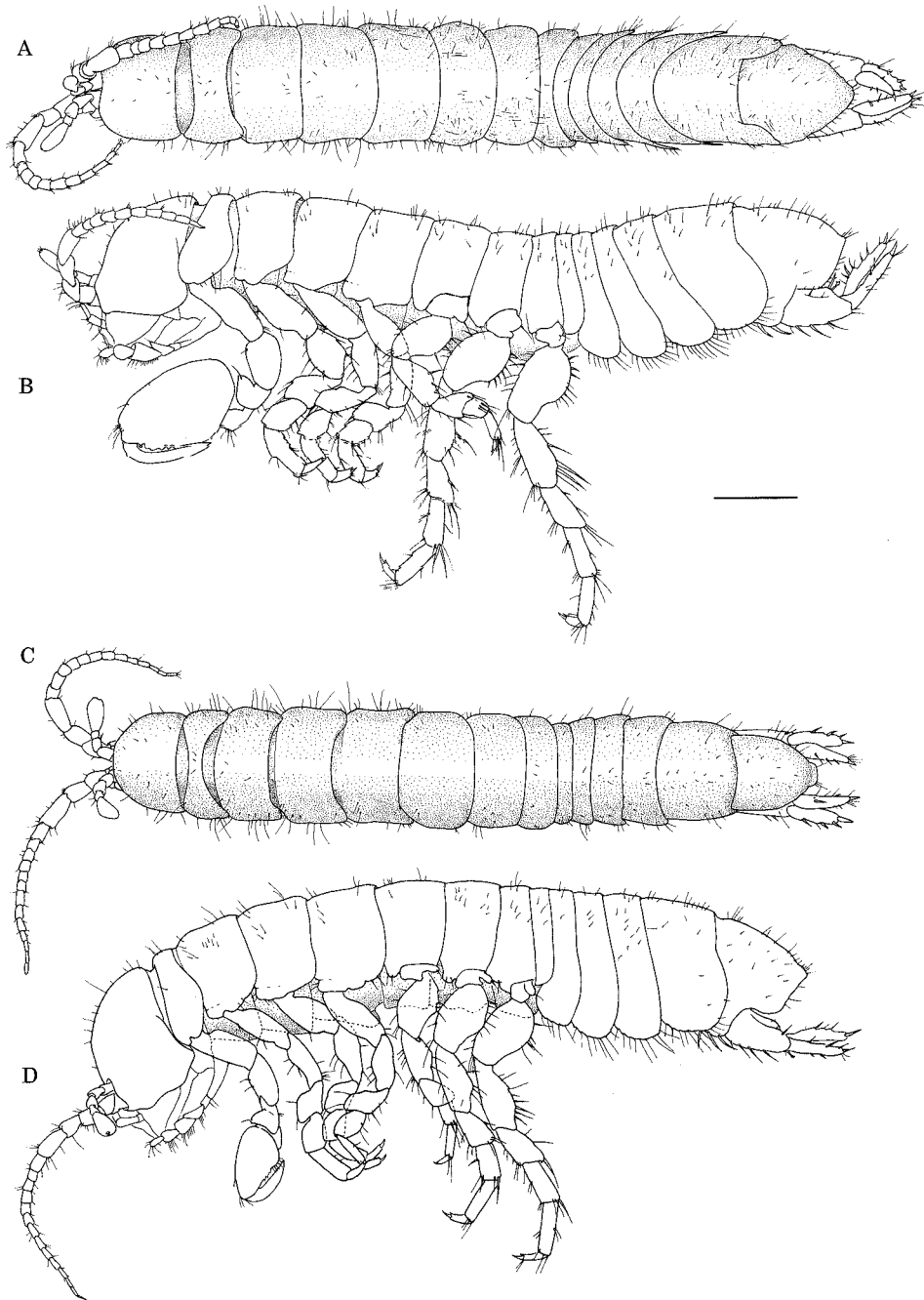


Figure 2. *Crenisopus acinifer* gen.nov., sp.nov., dorsal and lateral views of types. A & B, holotype male, WAM C23229, bl (body length) 4.39 mm C & D, paratype preparatory female, WAM C23232, bl 4.20 mm. Scale bar = 1 mm.

Terminal article tiny, vestigial, shorter than penultimate article, 0.4 width, 0.02 antennular length. Penultimate article inflated, width much greater than proximal article.

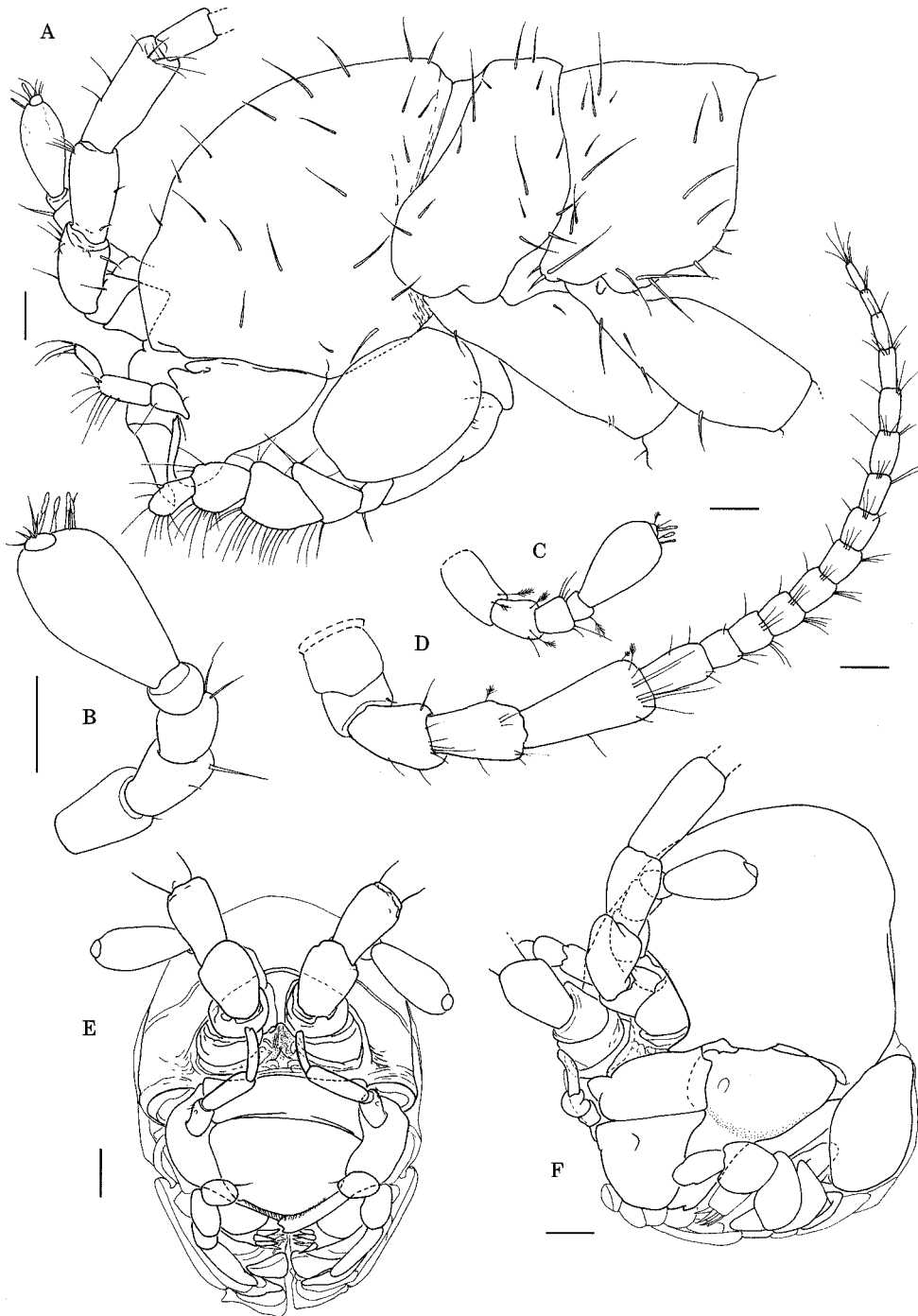


Figure 3. *Crenisopus acinifer* gen.nov., sp.nov. head, antennulae and antennae. A, E, F, head and lateral view with anterior pereonites, frontal and frontal oblique views, respectively. B, C, antennula, lateral and anterior enlarged view. D, right antenna. A, holotype male, WAM C23229, bl 4.39 mm. B–D, paratype male, WAM C23230, bl 5.25 mm. E–F, paratype female, WAM C23232, bl 4.20 mm. Scale bar = 0.1 mm.

*Antenna.* (Fig. 2, 3D) length 0.3 body length in male, 0.33 body length in female. Flagellum length 0.6 total antenna length in male, 0.64 total antenna length in female, with 14 articles in male, with 13 articles in female. Propodal article 1 present, forming thin ring, scale on propodal article 3 absent. Article 5 length subequal to article 4, article 6 longer than articles 4 and 5.

*Mouth field.* (Fig. 3E, F) clypeus consisting of broad bar, rounded laterally at mandibular fossae, width 0.58 head width. Labrum ventrally semicircular in anterior view, approximately same width as clypeus. Paragnaths with distolaterally rounded lobes, having medial setal row and thickened medial base covered with cuticular spines.

*Mandible.* (Figs 5B–E, 6A–E) palp length 0.73 mandible length; article 3 with 4 setae in adults, setae denticulate (in distal half, distal seta without setules); lacking cuticular hairs; combs absent; articles 1 with 1 seta, article 2 with 3–4 simple long slender setae. Incisor processes broad, width greater than thickness. Left incisor process with 4 cusps, cusps all distal. Left lacinia mobilis with 3 cusps. Right incisor process with 4 cusps. Right lacinia mobilis present. Spine rows on projecting ridge between incisor and molar processes, distal part on projection raised above proximal part. Left spine row with 11 spines, 4 of which are bifurcate, first spine not separated from remainder of spine row. Right spine row with 6 spines, 2 of which are bifurcate spines (and fused basally), first spine not separated from remainder of spine row. Molar process stout, heavily keratinised, length subequal to width; triturating surface heavily ridged, with no teeth, complex setulate setae forming a row at posterior.

*Maxillula.* (Fig. 7A, B) medial lobe length 0.82 lateral lobe length; width less than lateral lobe, width 0.71 lateral lobe width; with 3 pappose setae; with 1 'accessory' seta on distolateral margin, 'accessory' seta simple; no short weakly setulate setae on distal tip. Lateral lobe with 7 denticulate robust setae, 4 smooth robust setae, plumose setae on ventral face present, 2 altogether.

*Maxilla.* (Fig. 7C) lateral lobes subequal in length; with bidenticulate setae on distal tips and on medial margin. Inner lateral lobe with 10 long bidenticulate setae. Outer lateral lobe wider than inner lateral lobe; with 10 long bidenticulate setae. Medial lobe width 1 outer lateral lobe width; proximal and distal setal rows separated by gap; setae in ventral basal rows with single row of fine setules; setae in dorsal basal row with distinct base and fine setules; setae in distal row with row of teeth and row of fine setules; proximal portion distinctly angled to distal portion.

*Maxilliped.* (Fig. 8) epipod length 1.37 width; distal tip rounded; distal marginal setae absent; fine cuticular combs absent; ventral surface setae absent. Endite length 0.43 total basis length; distal tip with 4 subdistal biserrate setae on ventral surface; medial margin with 2 coupling hooks on left side, 2 on right side; dorsal ridge with 10 large distally denticulate plumose setae. Palp insertion on basis with no lateral plumose seta, no medial plumose setae, no medial simple setae; ventral surface with no subdistal smooth setae, no subdistal biserrate setae. Palp length 1.03 basis length, width across articles 2–3 1.96 endite width; article 4 length 1 width, shape subcircular; article 5 length 2 width, 0.89 article 4 length.

*Pereopod I.* (Fig. 9) length 0.49 body length in male, 0.35 body length in female. Dactylus shorter than palm in male, length 0.97 palm length, subequal to palm in female, length 1 palm length; ventral margin with no short stout setae in male, with

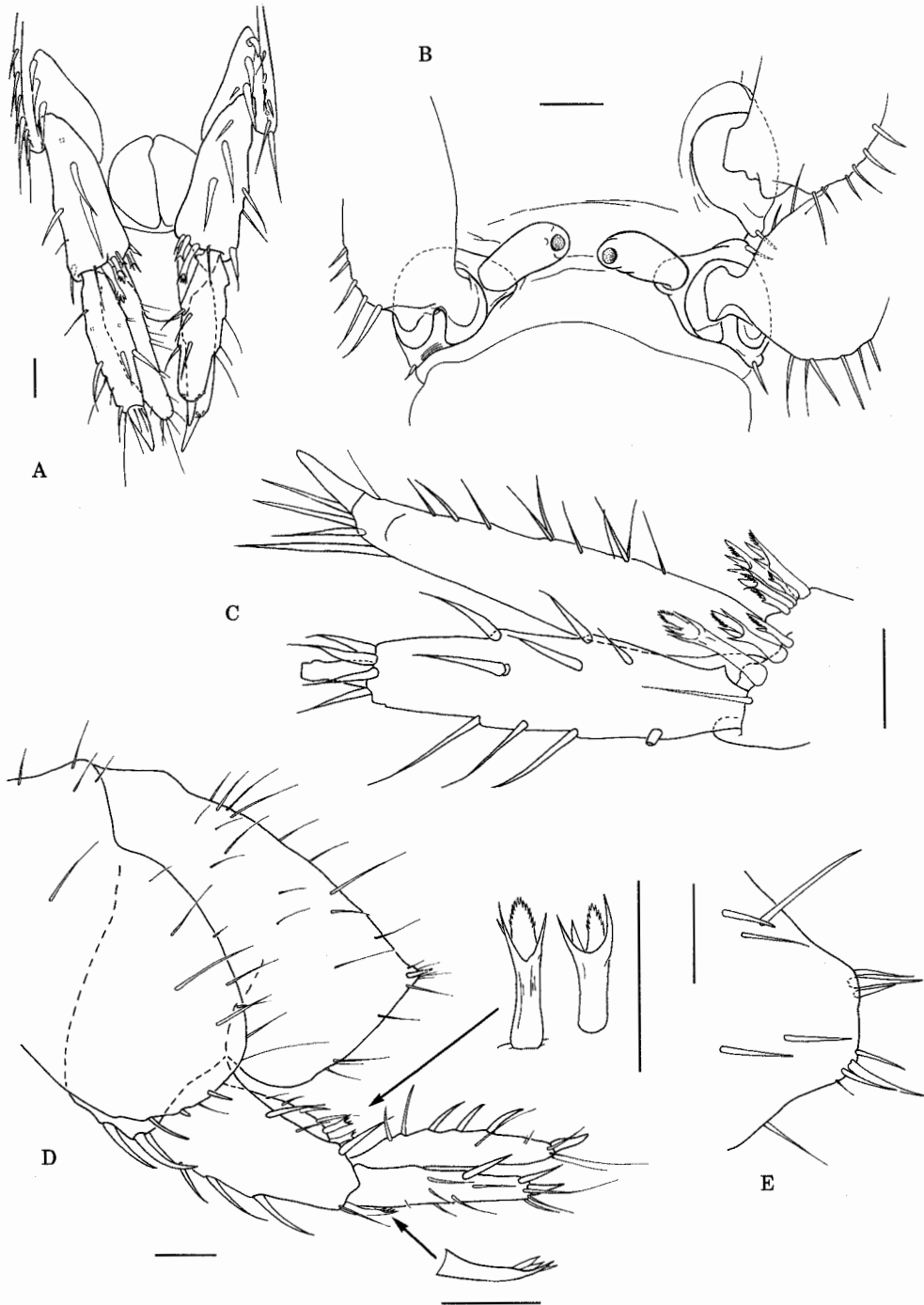


Figure 4. *Crenisopus acinifer* gen.nov., sp.nov. A, D, pleotelson and uropods, ventral and lateral view, B, pereonite 7 and penes, ventral view. C, uropodal rami and protopodal setae, ventral view, E, pleotelson, distal tip, dorsal view. A, C-E, paratype male, WAM C23230, bl 5.25 mm. B, paratype male, WAM C23231, bl 4.20 mm. Scale bar = 0.1 mm.

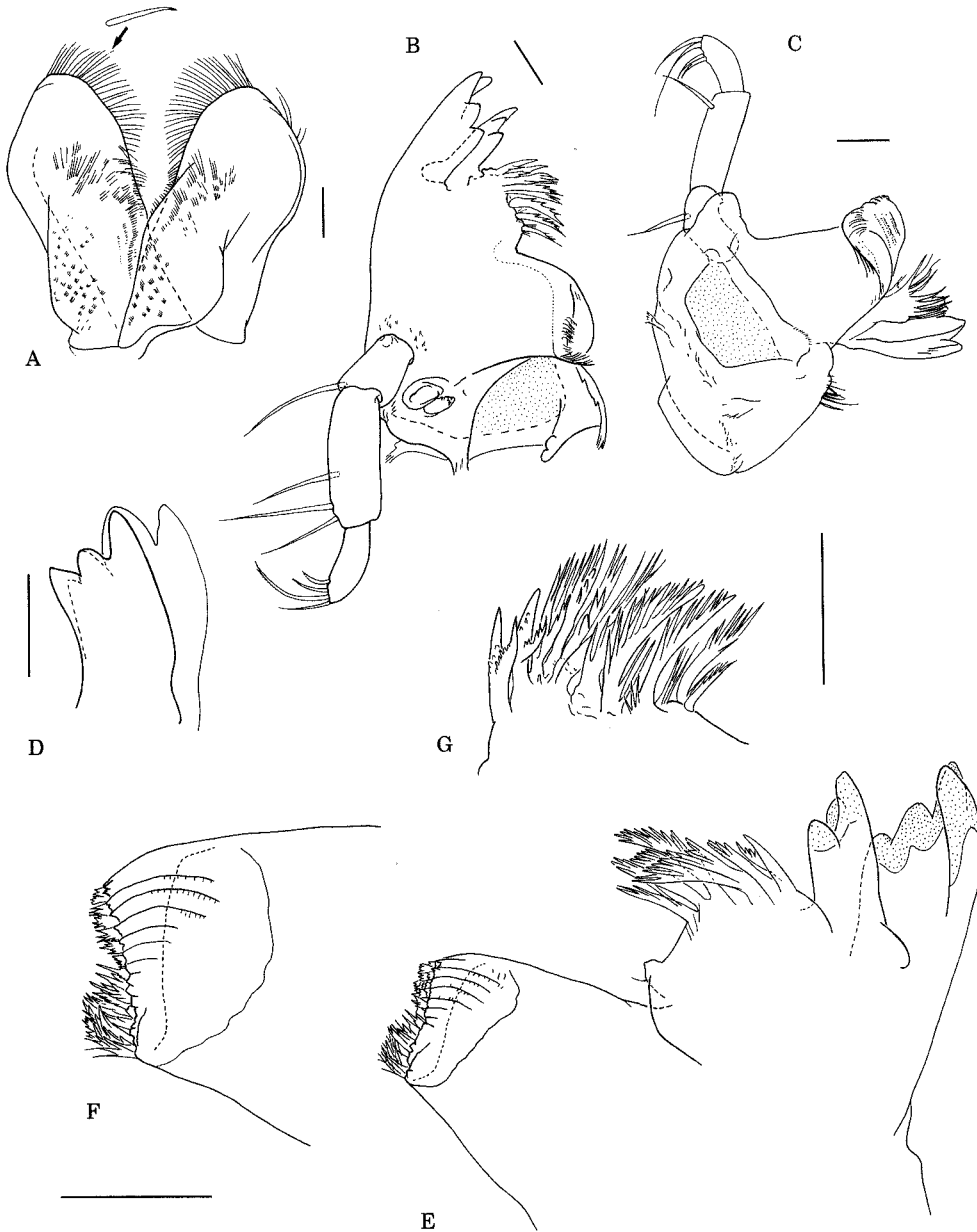


Figure 5. *Crenisopus acinifer* gen.nov., sp.nov. A, paragnaths. B–G, left mandible: B & C dorsal and posterior view; D, lacinia mobilis and incisor process; posterior view; E, distal parts, ventral view; F, molar process, ventral view; G, spine row, dorsal view. A & B, G, paratype male, WAM C23230, bl 5.25 mm. E, F, paratype male, WAM C23231, bl 4.20 mm. Scale bar = 0.05 mm.

no short stout setae in female; distal cuticular fringe absent; claw length 0.18 dactylus length in male, 0.23 dactylus length in female; with 1 distal accessory claw, claw small and ventral; distal accessory spines absent. Propodus length in male 0.25



Figure 6. *Crenisopus acinifer* gen.nov., sp.nov. right mandible. A, B, D, incisor process and spine row, ventral, dorsal and medial views; C, incisor process and lacinia mobilis, posterior view; E, molar process, dorsal view. A–E, paratype male, WAM C23231, bl 4.20 mm. F & G, dorsoposterior view and dorsal view of incisor process and spine row, *Mesamphisopus capensis* (Barnard, 1914), TMAG G678, adult male, bl 10.33 mm. Scale bar = 0.05 mm.

pereopod length, 0.93 width; 0.23 pereopod length, 1.13 width in female. Propodus dorsal margin proximal region in male protruding beyond distodorsal margin of carpus, not protruding in female. Propodal palm in male convex to straight, with multiple composite spine-like projections along length; stout denticulate setae absent;



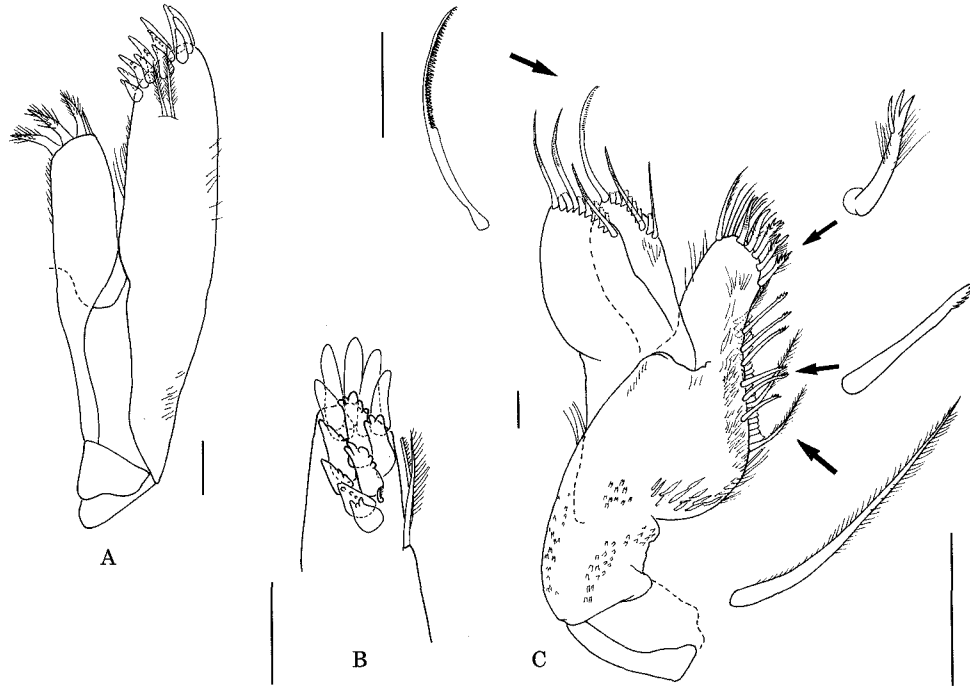


Figure 7. *Crenisopus acinifer* gen.nov., sp.nov. A & B, left maxillula, ventral and medial view. C, right maxilla, ventral view. Paratype male, WAM C23230, bl 5.25 mm. Scale bar = 0.05 mm.

stout robust simple setae present, tooth-like, 8 altogether; low conical setae on ridge absent. Propodal palm in female concave, with multiple composite spine-like projections along length (projections more serrate than in male); stout denticulate setae absent; stout simple setae present, tooth-like, 7 altogether (including 2 distoventral and long); low conical setae on ridge absent. Basis length 2.57 width in male, 2.34 width in female; dorsal setae in male absent, in female positioned proximally, 1 altogether; ventrodistal margin with group of 3 elongate setae in male, with group of 3 elongate setae in female, setae shorter than ischium; anteroproximal surface without dense group of setae.

*Pereopods II-III.* (Fig. 10A, B) respective lengths 0.38, 0.36 body length in male, 0.33, 0.33 body length in female; penicillate setae present (on pereopod III, none on pereopod II). In male dactylus of pereopod II shorter than propodus, dactylus of pereopod III shorter than propodus, dactylus respective lengths 0.59, 0.64 propodus length. In female dactylus of pereopod II shorter than propodus, dactylus of pereopod III shorter than propodus, dactylus respective lengths 0.65, 0.73 propodus length. Dactylus distal accessory claw present, 1 altogether, ventral to primary claw, respective primary claw lengths in male 0.33, 0.37 dactylar length, respective primary claw lengths in female 0.33, 0.33 dactylar length. Dactylus spines on ventral margin absent. Propodus respective lengths 0.15, 0.14 pereopod length in male, 2.14, 2.15 width in male; 0.16, 0.15 pereopod length in female, 2.67, 2.5 width in female; articular plate absent; broad based setae present, respectively 2, 2 altogether in male, respectively 3, 3 altogether in female, on male pereopod II short



Figure 8. *Crenisopus acinifer* gen.nov., sp.nov., maxilliped. A & B, ventral and medial view. C, enlargement of endite, ventral view. Paratype male, WAM C23230, bl 5.25 mm. Scale bar = 0.05 mm.

and thin, sparse, on male pereopod III short, sparse, on female pereopod II short, sparse, on female pereopod III short, sparse. Carpus respective lengths 0.12, 0.13 pereopod length in male, 1.19, 1.46 width in male, 0.15, 0.13 pereopod length in female, 1.5, 1.44 width in female; broad based setae present, respectively 3, 4 altogether in male, respectively 3, 4 altogether in female, on male pereopod II proximal and distal setae approximately half length of middle seta, sparse, on male

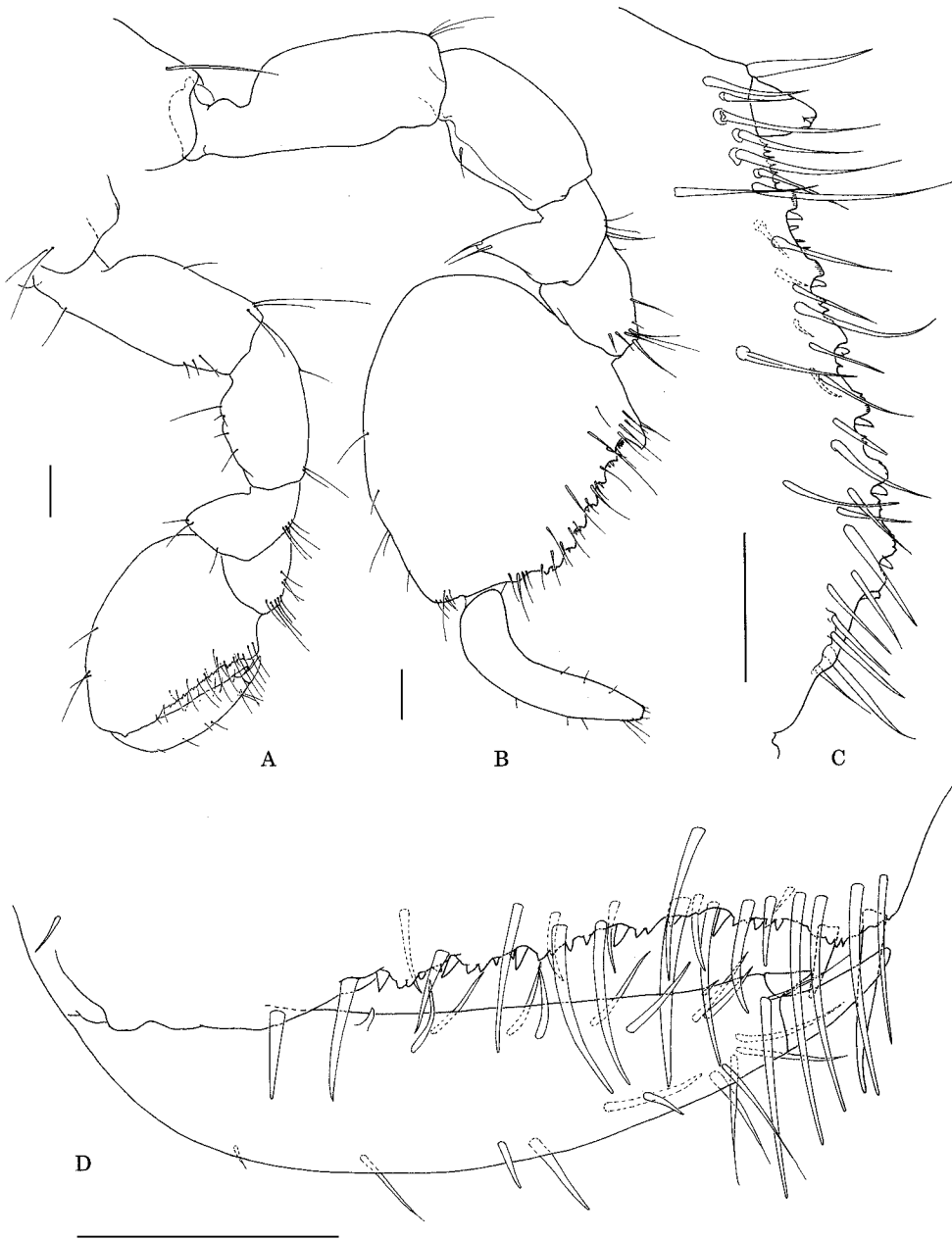


Figure 9. *Crenisopus acinifer* gen.nov., sp.nov., left pereopod I, whole limb with enlargement of palm. A, D, paratype female, WAM C23232, bl 4.20 mm. B & C, paratype male, WAM C23230, bl 5.25 mm. Scale bar = 0.05 mm.

pereopod III proximal and distal setae approximately half length of middle setae, sparse, on female pereopod III proximal seta minute, distal seta about half length of middle seta, sparse, on female pereopod III proximal seta minute, distal seta



Figure 10. *Crenisopus acinifer* gen.nov., sp.nov., anterior pereopods. A-C, left pereopods II-IV, lateral view; E, pereopod II, enlargement of distal tip of dactylus; paratype male WAM C23230, bl 5.25 mm. D, F left pereopod IV, with enlargement of dactylus; paratype female, WAM C23232, bl 4.20 mm. Scale bar = 0.1 mm.

about half length of middle seta, sparse. Basis respective lengths 0.28, 0.28 pereopod length in male, 2.33, 2.21 width in male, 0.25, 0.28 pereopod length in female, 2.5, 2.25 width in female; dorsal ridge in cross section rounded, with 3 long simple and 4 short penicillate setae along ridge, 1 short simple seta medially and distally.

*Pereopod IV.* (Fig. 10C, D) not sexually dimorphic. Length 0.32 body length in male, 0.32 body length in female. Penicillate setae present in both sexes, in male occurring on dorsal margin of basis, in female occurring on dorsal margin of basis. Dactylus subequal to propodal palm; with distal accessory claws or spines in both sexes, one third length of primary claw in male, one third length of primary claw in female. Propodus length in male 0.15 pereopod length, 1.67 width; female 0.14 pereopod length, 2 width; distal width less than palm width, 0.63 palm width; articular plate on posterior side of limb absent; with broad based setae on ventral margin in male present, 2 altogether, with broad based setae on ventral margin in female present, 2 altogether. Carpus length 0.13 pereopod length in male, 0.12 pereopod length in female; with 4 broad based setae on ventral margin in male, 2 distinctly larger than others, with 4 broad based setae on ventral margin in female. Ischium posterodistal margin with 2 setae in male, 3 setae in female. Basis length 1.97 width in male, 2.21 width in female; dorsal ridge in cross section rounded, male with 9 setae (7 simple, 2 penicillate), positioned along ridge, female with 7 setae (5 simple, 2 penicillate), positioned along ridge.

*Pereopods V–VII.* (Fig. 11) respective lengths 0.27, 0.4, 0.42 body length in male, 0.29, 0.37, 0.41 body length in female. Penicillate setae present on dorsal ridge of basis and present dorsodistally on carpus. Dactylus respective claw lengths 0.42, 0.4, 0.39 dactylar length in male, 0.38, 0.41, 0.4 dactylar length in female; distal accessory claws present, 1 altogether, ventral to primary claw, 0.25–0.33 length of primary claw. Propodus respective lengths 0.15, 0.15, 0.16 pereopod length in male, 0.15, 0.16, 0.17 pereopod length in female; articular plate on posterior side of limb absent; distal margins with 5 elongate robust setae. Carpus respective lengths 0.14, 0.15, 0.15 pereopod length in male, 0.11, 0.12, 0.14 pereopod length in female. Basis respective lengths 1.44, 1.55, 1.64 basis width in male, 1.5, 1.47, 1.58 basis width in female; dorsal ridge not distinctly separated from basis shaft, in cross section angular, with 9–11 setae (including 2–3 short, penicillate setae), positioned along ridge.

*Penes.* (Fig. 4B) straight; length 0.23 body width at pereonite 7, extending near midline; shaft smooth, distally tubular; distal tip rounded.

*Pleopods I–V.* (Fig. 12 13) respective lengths 0.14, 0.13, 0.13, 0.12, 0.12 body length in male, 0.13, 0.15, 0.17, 0.16, 0.14 body length in female. Exopods I–V respective lengths 2.02, 1.75, 1.51, 1.54, 1.33 width in male, 2.63, 1.8, 1.43, 1.53, 1.49 width in female; exopod I uniarticulate, exopods II–V biarticulate, II–V proximal article distolateral lobes shorter than distal article, respective lengths of distal articles 0.25, 0.25, 0.31, 0.29 exopod length in male, 0.27, 0.29, 0.29, 0.31 exopod length in female; lateral proximal lobes present on exopods II–V; medial proximal lobes present on exopods II–V. Endopods all unilobed; endopods I–V respective lengths 2.44, 2.21, 1.84, 2.08, 1.74 width in male, 3.3, 2.05, 1.96, 2.09, 1.7 width in female, 0.97, 0.97, 0.89, 0.9, 0.92 exopod length in male, 0.85, 0.98, 0.99, 0.95, 0.92 exopod length in female; male endopods I–V without marginal setae; female endopods I–V without marginal setae. Protopods III–V with lateral epipods. Male pleopod I exopod

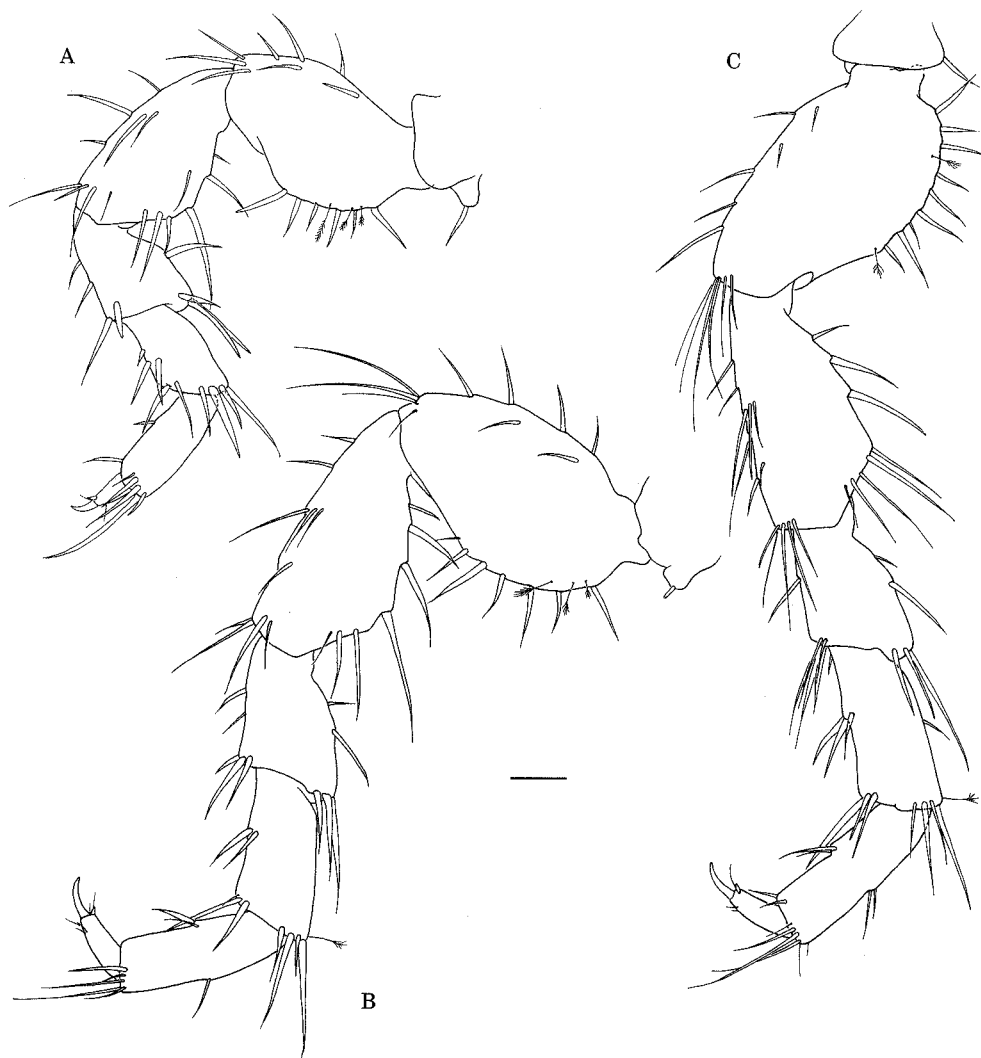


Figure 11. *Crenisopus acinifer* gen.nov., sp.nov., posterior pereopods V–VII. A–C, paratype male, WAM C23230, bl 5.25 mm. Scale bar = 0.1 mm.

broadest proximally, distal margin rounded, lateral margin rounded, dorsal surface with setae. Male pleopod II endopod appendix masculina curved; ventral shape of cross section of proximal half of shaft concave (forming an elongate trough); basal musculature not pronounced; distal tip acutely rounded, without tiny rounded denticles; marginal setae occurring along lateral and medial margins, 18 setae altogether; length 0.58 pleopod length; distal tip extending near to distal margin of endopod. Male pleopod II endopod proximal article distal tip rounded. Male pleopod II exopod distal segment longer than wide, lateral margin proximally rounded.

*Uropod.* (Fig. 4A, C, D) total length 1.37 pleotelson length in male, 1.44 pleotelson length in female. Protopod length 2.48 width in male, 2 width in female, 0.46

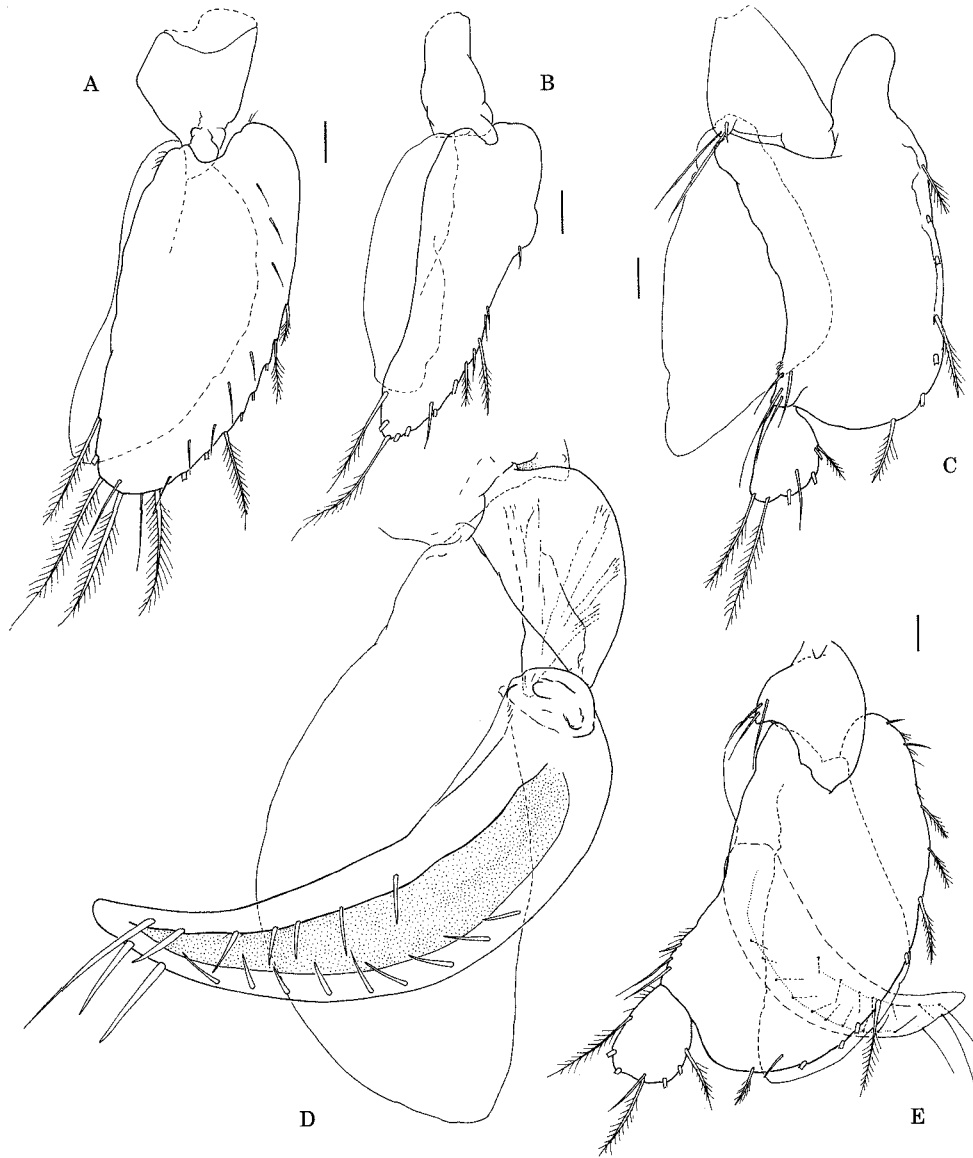


Figure 12. *Crenisopus acinifer* gen.nov., sp.nov., pleopods I-II. A, pleopod I, ventral view; D & E, pleopod II, appendix masculina, dorsal view, and whole limb ventral view; paratype male, WAM C23231, bl 4.20 mm. B & C, female pleopods I-II, paratype female, WAM C23232, bl 4.20 mm. Scale bar = 0.1 mm.

uropod total length in male, 0.39 uropod total length in female; dorsomedial ridge not produced, 0.66 endopod length in male, 0.44 endopod length in female; dorsomedial margin setae robust and spinose distally; dorsolateral margin setae robust and simple; robust spinose setae on distoventral margin present, 9 altogether. Rami distal tips rounded; cross-sectional shape oval or flattened on dorsal surface. Endopod longer than protopod, subequal to or longer than exopod, with robust

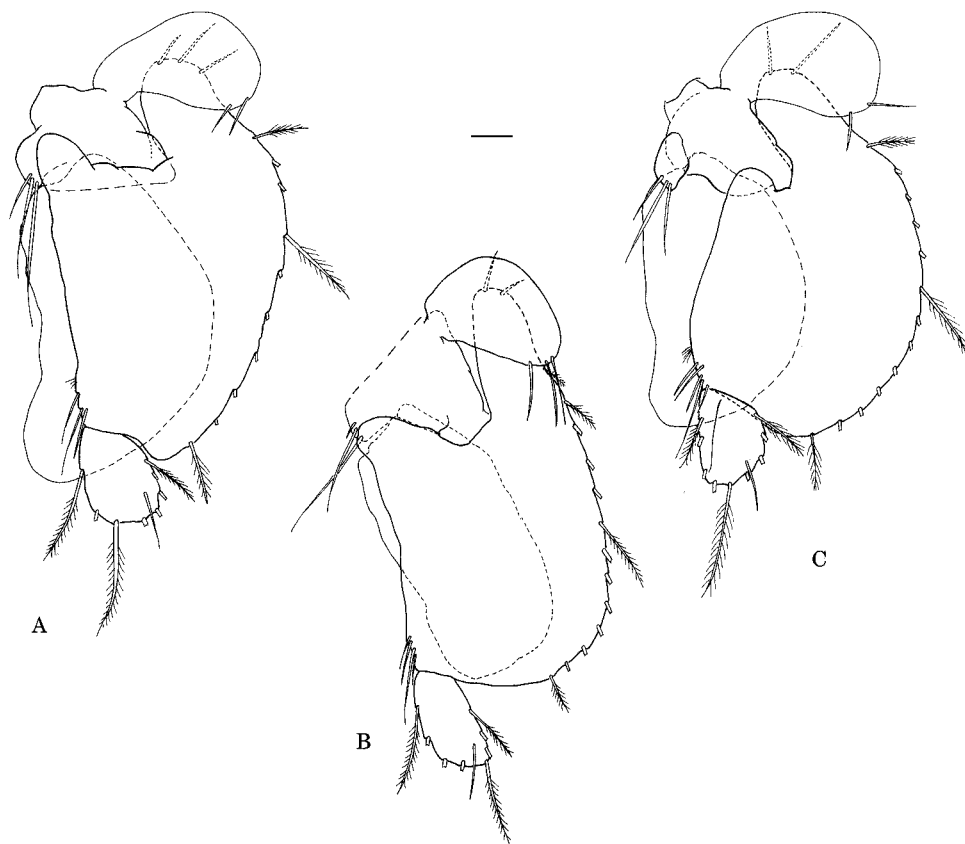


Figure 13. *Crenisopus acinifer* gen.nov. sp.nov. A–C, pleopods III–V, ventral view; paratype male, WAM C23231, bl 4.20 mm. Scale bar = 0.1 mm.

setae on dorsal margin present, with 5 robust setae in male, 5 robust setae in female; spines or spurs on dorsal margin absent. Exopod length 0.93 endopod length in male, 0.97 endopod length in female; not sexually dimorphic; robust setae on dorsal margin present, 4 robust setae in male, 3 robust setae in female.

*General distribution.* Known only from Zebedee Springs, El Questro Station, north Kimberley, Western Australia.

*Species remarks.* The multiple composite spine-like projections along the length of the propodal palm of pereopod I are found both in males and females, but are sexually dimorphic. This dimorphism is not known among other phreatoicideans. In males, they are less acute and fused. In both in males and females, these projections are interspersed with tooth-like, stout, simple setae. Among the phreatoicideans, the multiple spinose setae on the distoventral margin of the uropodal protopod are unique to this species.

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sent us the specimens in 1994, soon after they were collected, and patiently waited for us to finish this description. Lynne Ho prepared some illustrations, inked the line drawings and assembled the plates. Rick Johnson added numerous phreatoicidean taxa and characters to the DELTA data base that were used here for comparison and description. Shane Ahyong (Australian Museum) kindly reviewed an early draft of our manuscript, and two anonymous reviewers provided helpful suggestions for its improvement. We thank the Trust of the Australian Museum and the Australian Biological Resources Survey for their support of this project.

## REFERENCES

- Banarescu P.** 1990. *Zoogeography of fresh waters. General distribution and dispersal of freshwater animals*. Vol. 1. Wiesbaden, Germany: Aula-Verlag.
- Barnard KH.** 1914. Contributions to the crustacean fauna of South Africa. 2. Description of a new species of *Phreatoicus* (Isopoda) from South Africa. *Annals of the South African Museum* **10**: 231–240.
- Barnard KH.** 1927. A study of the freshwater isopod and amphipod Crustacea of South Africa. *Transactions of the Royal Society of South Africa* **14**: 139–215.
- Brusca RC, Wilson GDF.** 1991. A phylogenetic analysis of the Isopoda with some classificatory recommendations. In: Davie PJF, Quinn RH, eds. *Proceedings of the 1990 International Crustacea Conference. Memoirs of the Queensland Museum* **31**: 143–204.
- Chilton C.** 1883. Notes on, and a new species of subterranean Crustacea. *Transactions of the New Zealand Institute* **14**: 87–92, pl. 4.
- Chilton C.** 1891. On a new and peculiar freshwater isopod from Mt. Kosciusko. *Records of the Australian Museum* **1**: 149–171, pls., 23–26.
- Chilton C.** 1894. The subterranean Crustacea of New Zealand: with some general remarks on the fauna of caves and wells. *Transactions of the Linnean Society of London. (2nd Series, Zoology)* **6**: 163–284, pls. 16–23.
- Chilton C.** 1918. A fossil isopod belonging to the fresh-water genus *Phreatoicus*. *Journal and Proceedings of the Royal Society of New South Wales* **51**: 365–388.
- Chilton C.** 1922. A new isopod from Central Australia belonging to the Phreatoicidae. *Transactions of the Royal Society of South Australia* **46**: 23–33.
- Chopra B.** 1947. First record of occurrence in India of the ancient sub-order Phreatoicoidea (Crustacea: Isopoda). *Proceedings of the Indian Science Congress* **34**: 176.
- Chopra B, Tiwari KK.** 1950. On a new genus of phreatoicid isopod from wells in Banaras. *Records of the Indian Museum (Calcutta)* **47**: 277–289, pls. 17–20.
- Dallwitz MJ.** 1980. A general system for coding taxonomic descriptions. *Taxon* **29**: 41–46.
- Dallwitz MJ, Paine TA, Zurcher EJ.** 1993. *User's Guide to the DELTA system. A general system for processing taxonomic descriptions* 4th edition. Canberra: CSIRO Division of Entomology.
- Glauert FGS.** 1924. Contributions to the fauna of Western Australia, No.4. A freshwater isopod. *Phreatoicus palustris* sp.nov. *Journal of the Royal Society of Western Australia*. **10**: 49–57.
- Gordon I.** 1957. On *Spelaeogriphus*, a new cavernicolous crustacean from South Africa. *Bulletin of the British Museum (Natural History) Zoology* **5**: 31–47.
- Helms R.** 1891. Report of a collecting trip to Mount Kosciusko. *Records of the Australian Museum* **1**: 11–16.
- Hessler RR.** 1969. Peracarida. In: Moore RC, ed. *Crustacea (Except Ostracoda)*, Vol. 1. In: Moore RC, series ed. *Treatise of Invertebrate Paleontology*, Part R, Arthropoda 4, Boulder, Colorado and Lawrence, Kansas: The Geological Society of America and University of Kansas, R360–R393.
- Humphreys WF.** 1994. *The subterranean fauna of the Cape Range coastal plain, northwestern Australia*. Unpublished Report to the Australian Heritage Commission and the Western Australia Heritage Committee, Western Australian Museum.
- Maddison WP, Maddison DR.** 1993. *MacClade, Analysis of Phylogeny and Character Evolution*, Version 3. Sunderland, Massachusetts: Sinauer.
- Nicholls GE.** 1926. A description of two genera and species of Phreatoicoidea, with a discussion of the affinities of the members of this family. *Journal of the Royal Society of Western Australia* **12**: 179–210, pls.25–28.

- Nicholls GE. 1943.** The Phreatoicoidea. Part I. The Amphisopidae. *Papers and Proceedings of the Royal Society of Tasmania* **1942**: 1–145.
- Nicholls GE. 1944.** The Phreatoicoidea. Part II. The Phreatoicidae. *Papers and Proceedings of the Royal Society of Tasmania* **1943**: 1–156.
- Nicholls GE, Milner DF. 1923.** A new genus of fresh-water Isopoda, allied to *Phreatoicus*. *Journal of the Royal Society of Western Australia* **10**(6): 23–34.
- Poore GCB, Humphreys WF. 1992.** First record of Thermosbaenacea (Crustacea) from the southern hemisphere: a new species from a cave in tropical Western Australia. *Invertebrate Taxonomy* **6**: 719–725.
- Poore GCB, Humphreys WF. 1998.** First record of Spelaeogriphacea from Australasia: a new genus and species from an aquifer in the arid Pilbara of Western Australia. *Crustaceana* **71**(7): 721–742.
- Poore GCB, Knott B, Lew-Ton H. In press.** Isopoda Phreatoicoidea. In: *Crustacea Peracarida. Zoological Catalogue of Australia*. Canberra: Australian Biological Resources Study.
- Sayce OA. 1902.** A new genus of Phreatoicidae. *Proceedings of the Royal Society of Victoria* **14**: 218–224. pls. 18–19.
- Schram FR. 1970.** Isopods from the Pennsylvanian of Illinois. *Science* **169**: 854–855.
- Schram FR. 1974.** Paleozoic Peracarida of North America. *Fieldiana Geology* **33**: 95–124.
- Sheard K. 1936.** A new phreatoicid from the Grampians, Victoria. *Records of the South Australian Museum* **5**: 469–473.
- Spencer B, Hall TS. 1896.** Description of a new genus of terrestrial Isopoda, allied to the genus *Phreatoicus*. *Proceedings of the Royal Society of Victoria* **9**: 12–21 (pl. III–IV).
- Stebbing TRR. 1893.** *A History of Crustacea – Recent Malacostraca*. In: *The International Scientific Series*, no. 74. London Kegan Paul, Trench, Trübner & Co. Ltd.
- Storey BC. 1995.** The role of mantle plumes in the continental breakup: case histories from Gondwanaland. *Nature* **377**: 301–308.
- Swofford DL. 1993.** *PAUP, phylogenetic analysis using parsimony*, ver. 3.0/Macintosh edition. Champaign: Illinois Natural History Survey.
- Wilson GDF, Ho EL. 1996.** *Crenoicus* Nicholls, 1944, (Crustacea, Isopoda, Phreatoicoidea): Systematics and biology of a new species from New South Wales. *Records of the Australian Museum* **48**: 7–32.
- Wilson GDF, Ponder WF. 1992.** Extraordinary new subterranean isopods (Peracarida, Crustacea) from the Kimberley Region, Western Australia. *Records of the Australian Museum* **44**: 279–298.
- Yager J, Humphreys WF. 1996.** *Lasionectes exleyi* sp. nov., the first remipede crustacean recorded from Australia and the Indian Ocean with key to the world species. *Invertebrate Taxonomy* **10**: 171–187.

## APPENDIX 1

*Taxa used in the phylogenetic analysis*

Some taxa were collected near the type locality of their respective species, but we have not compared our specimens with the types, which in some cases are missing. ('bl' = body length).

*Crenoicus buntiae* Wilson & Ho, 1996. Scored from literature and additional specimens from Mumbedah Swamps, Kanangra-Boyd National Park, New South Wales, Australia, *Sphagnum swamp* at head of Mumbedah Creek, Boyd Plateau: NSW485, 33°53.76'S, 150°3.92'E, 1200 m, collected 18 November 1992 by G. Wilson and party.

*Eophreatoicus* sp. Adult male (bl 21.3 mm) and preparatory female (bl 11.8 mm) specimens scored from a total of 746 individuals, Kakadu National Park, Northern Territory; approximately 1 km upstream of Gubara Pools, near Nourlangie Rock, 12°49.65'S 132°52.96'E (GPS); collected 15 August 1994 by G. Wilson, W. Ponder & V. Kessner.

*Hypsimmelopus* sp. cf. *intrusor* Sayce, 1902. Adult male (bl 9.6 mm) and preparatory female (bl 10.2 mm), from 8 individuals collected near Zeehan, Tasmania, Australia; 41°53'S, 145°21'E; collected 12 July 1990 by A.M.M. Richardson & G.D.F. Wilson. Although collected near the type locality of *H. intrusor*, this species appears to differ from the original description.

*Mesamphisopus capensis* (Barnard, 1914) Tasmanian Museum & Art Gallery G678, adult male, bl 10.33 mm, preparatory female, bl 11.78 mm, Table Mountain, Cape Town, South Africa, collected 1936 by K.H. Barnard (assumed).

*Metaphreaticus australis* (Chilton, 1891) Adult male (bl 17.4 mm) and preparatory female (bl 9.4 mm), from AM P3347, Syntypes, 110 individuals, upper Pipers Creek, Mt. Kosciusko National Park, New South Wales, Australia. 36°25'S, 148°25.5'E (position estimated based on Helms, 1891), collected March 1889 by R. Helms.

*Neophreaticus assimilis* (Chilton, 1894) Scoring is based on descriptions and illustrations provided by Chilton (1894) and Nicholls (1944). Chilton (1894) states that the description is mainly taken from a dissected male specimen and that a few points were also taken from a female specimen that was mounted dry on a slide, bl 10–12 mm (bl of female 10.5 mm). Winchester, South Canterbury New Zealand, in wells.

*Paramphisopus palustris* (Glauert, 1924) Adult male (bl 7.8 mm) and preparatory II female (bl 7.4 mm), from AM P44487, 112 individuals, Lake Monger, Perth, Western Australia. 31°55'S, 115°50'E; collected 22 March 1995 by D. Jones & G.D.F. Wilson.

*Phreaticus typicus* Chilton, 1883. Male (bl 12.8 mm), dissected; preparatory female (bl 13.8 mm). Sample 'Well 2' from sediments at bottom of well, depth approximately 30 m, Templeton, Canterbury Plain, New Zealand, 43°33.11'S, 172°26.38'E, collected 11 June 1986 by G.D. Fenwick. The type locality for *Phreaticus typicus*, Irwell township (43°42.32'S, 172°21.26'E), is 18.9 km SW of Templeton].

*Phreatomerus* sp. cf. *latipes* (Chilton, 1922). Adult male (bl 14.6 mm) and preparatory II female (bl 11.4 mm) from Dead Woman Springs, South Australia. 29°35.37'S, 137°27.28'E, collected 30 August 1983 by W.F. Ponder & B. Jenkins.

## APPENDIX 2

*Character list of phreaticidean taxa analysed in this paper*

Character states marked '\*' were used as ancestral states (ANCSTATES assumptions in PAUP or hypothetical ancestor, 'hypanc', coded in MacClade). All other ancestral states were coded as unknown.

1. Head length: (1) length shorter than width in dorsal view; (2) length subequal to width in dorsal view; (3) length greater than width in dorsal view.
2. Cervical groove length: (1) extending just above the anterolateral margin of pereonite 1; (2) extending nearly to the dorsal margin of head; (3) extending over the dorsal margin of head and connecting medially.
3. Mandibular notch: (1) present; (2) absent.
4. Clypeal notch: (1) present; (2) absent.
5. Antennal notch: (1) present; (2) absent.
6. Pereonites 2–7 in dorsal view: (1) longer than wide; (2) wider than long; (3) anteriorly longer than wide decreasing posteriorly to wider than long.
7. Coxal articulation of pereonites 2–4; (1)\* free; (2) nearly fused; (3) fused.
8. Pleonites 2–5 relative lengths: (1) pleonites 2–4 respective lengths less than half the length of pleonite 5; (2) pleonites 2–4 respective lengths equal to or more than half the length of pleonite 5; (3) pleonites 2–3 respective lengths less than half the length of pleonite 5, pleonite 4 length equal to half the length of pleonite 5.
9. Pleonites 1–4 relative lengths: (1) subequal; (2) unequal, pleonite 4 greater than pleonites 1–3.
10. Pleotelson lateral length: (1) less than depth; (2) subequal to depth; (3) greater than depth.
11. Telsonic region or tailpiece: (1) not distinct, terminal area concave in dorsal view; (2)\* not distinct, dorsal margin smoothly curved to distal tip, terminal area truncate in dorsal view; (3) distinct, reflexed dorsally, trilobed in dorsal or ventral view; (4) distinct, reflexed dorsally, not trilobed, forming medial lobe only.
12. Dorsal uropodal cleft of pleotelson: (1) present; (2) absent.
13. Dorsal uropodal cleft of pleotelson: (1) with several fine setae; (2) without setae.
14. Antennula terminal article shape: (1)\* tubular [sides approximately parallel, length greater than width]; (2) conical; (3) inflated and bulbous [sides curved, width distinctly greater than previous article]; (4) globular [sides curved, length approximates width, subequal or narrower than previous article]; (5) tiny, vestigial.
15. Antennula penultimate article width: (1)\* width subequal to proximal article; (2) inflated, width much greater than proximal article; (3) broad and flattened.

16. Antenna propodal article 1: (2)\* present, forming thin ring; (3) absent.
17. Mandible incisor processes shape: (1)\* broad, width greater than thickness; (2) thin, resembling denticulate spines, width near thickness.
18. Mandible right lacinia mobilis: (1)\* present; (2) absent.
19. Mandible spine row overall shape: (1)\* in smooth low arc between incisor and molar process; (2) on projecting ridge between incisor and molar processes; (3) on pedunculate projection between incisor and molar processes.
20. Mandible shape of spine row ridge: (1)\* distal part in line with proximal parts; (2) distal part on projection raised above proximal part; (3) strongly convex arc, medial part projecting.
21. Mandible right spine row with: (1) first spine separated from remaining members; (2) first spine not separated from remainder of spine row.
22. Mandible molar process length compared to width: (1) wider than long; (2) length subequal to width; (3) longer than wide.
23. Mandible molar process triturating surface: (1) ridged; (2) lightly lineated; (3) smooth.
24. Mandible molar process triturating surface with: (1) several teeth; (2) 1 tooth; (3) no teeth.
25. Maxilla lateral lobes with bidenticulate setae: (1) only on distal tips; (2) on distal tips and on medial margin.
26. Maxilla outer lateral lobe width: (1) wider than inner lateral lobe; (2) width subequal to that of inner lateral lobe; (3) narrower than inner lateral lobe.
27. Maxilla medial lobe proximal and distal setal rows: (1) continuous; (2) separated by gap.
28. Maxilla medial lobe proximal portion: (1) distinctly angled to distal portion; (2) smoothly continuous with distal portion.
29. Maxilliped epipod distal tip shape: (1) rounded; (2) truncate; (3) pointed; (4) medially concave.
30. Pereopod I dactylus length measured along inner margin of dactylus: (1) projecting beyond palm in male; (2) subequal to palm in male; (3) shorter than palm in male.
31. Pereopod I dactylus ventral margin distal cuticular fringe: (1) present; (2) absent.
32. Pereopod I dactylus distal accessory spines: (1) present; (2) absent.
33. Pereopod I propodus dorsal margin proximal region in male: (1) protruding to or beyond distodorsal margin of ischium; (2) protruding beyond distodorsal margin of carpus; (3) not protruding.
34. Pereopod I propodus dorsal margin proximal region in female: (1) protruding to or beyond distodorsal margin of ischium; (2) protruding beyond distodorsal margin of carpus; (3) not protruding.
35. Pereopod I propodal palm in male: (1) concave; (2) convex to straight.
36. Pereopod I palm in male stout denticulate setae: (1) present, serrate, multiple denticulations; (2) present, bifid two spinules only; (3) absent.
37. Pereopod I propodal palm in male stout simple setae not on ridge: (1) present, conical; (2) present, basally inflated; (3) present, tooth-like; (4) absent.
38. Pereopod I propodal palm in male low conical setae on ridge (= keratinized teeth in Wilson and Ho, 1996): (1) present; (2) absent, ridge absent.
39. Pereopod I propodal palm in female: (1) concave; (2) convex; (3) straight.
40. Pereopod I propodal palm in female stout denticulate setae: (1) present, serrate multiple denticulations; (2) present, bifid two spinules only; (3) absent.
41. Pereopod I propodal palm in female stout simple setae: (1) present, conical; (2) present, basally inflated; (3) present, tooth-like; (4) absent.
42. Pereopods II-III dactylus spines on ventral margin: (1) present; (2) absent.
43. Pereopods II-III propodus articular plate found distally on posterior side: (1)\* present; (2) absent.
44. Pereopods II-III basis dorsal ridge in cross section: (1) rounded; (2) angular and produced but not forming distinct plate; (3) produced and forming distinct plate.
45. Pereopod IV: (1) sexually dimorphic; (2)\* not sexually dimorphic.
46. Pereopod IV dactylus: (1) shorter than propodal palm; (2) subequal to propodal palm; (3) longer than propodal palm.
47. Pereopod IV dactylus with distal accessory claws or spines: (1) one-fourth length of primary claw in male; (2) one-third length of primary claw in male; (3) one half-length of primary claw in male.
48. Pereopod IV dactylus with distal accessory claws or spines: (1) one-fourth length of primary claw in female; (2) one-third length of primary claw in female; (3) one half-length of primary claw in female.

49. Pereopod IV propodus distal width: (1) dorsally expanded, greater than palm width; (2) subequal to palm width; (3) less than palm width.
50. Pereopod IV propodus articular plate: (1) longer than dactylar claw in male; (2) length subequal to that of dactylar claw in male; (3) shorter than dactylar claw in male.
51. Pereopod IV propodus articular plate: (1) longer than dactylar claw in female; (2) length subequal to that of dactylar claw in female; (3) shorter than dactylar claw in female.
52. Pereopod IV basis dorsal ridge in cross section: (1) rounded; (2) angular and produced but not forming distinct plate; (3) produced and forming distinct plate.
53. Pereopods V–VII dactylus spines: (1) present; (2) absent.
54. Pereopods V–VII propodus articular plate on posterior side of limb: (1)\* present; (2) absent.
55. Pereopods V–VII basis dorsal ridge: (1) distinctly separated from basis shaft; (2) not distinctly separated from basis shaft.
56. Pereopods V–VII basis dorsal ridge in cross section: (1) rounded; (2) angular; (3) produced but not forming distinct plate; (4) produced and forming distinct plate.
57. Penes form: (1) straight; (2) curved posteriorly.
58. Penes extending: (1) near midline; (2) to midline; (3) past midline and onto pleonite 1.
59. Penes shaft armature: (1) smooth lacking setae; (2) denticulate; (3) with setae.
60. Penes shaft distally overall shape: (1) tapering; (2) broadening; (3) tubular.
61. Penes distal tip shape: (1) rounded; (2) pointed; (3) flattened; (4) truncate.
62. Pleopod exopods I–V lateral proximal lobes: (1) present on exopods II–V; (2) present on exopods I and III–V; (3) absent.
63. Pleopod exopods I–V medial proximal lobes: (1) present on exopods II–V; (2) present on exopods III–V; (3) absent.
64. Pleopod protopod medial epipods: (1) protopods II–V with medial epipods; (2) protopods without medial epipods; (3) protopods II–V with small medial projections.
65. Male pleopod I exopod distal margin: (1) pointed; (2) rounded.
66. Male pleopod I exopod lateral margin: (1) rounded; (2) forming obtuse angle.
67. Male pleopod I exopod dorsal surface setae: (1) with setae; (2) lacking setae.
68. Male pleopod II endopod appendix masculina stylet–distal article distal tip: (1) truncate; (2)\*acutely rounded; (3) sharply pointed and spine-like; (4) pointed and spatulate; (5) broadly rounded.
69. Male pleopod II endopod appendix masculina stylet–distal article marginal setae: (1) only occurring distally; (2) only occurring along lateral margin; (3) only occurring along medial margin; (4) occurring along lateral and medial margins; (5) absent.
70. Male pleopod II exopod distal segment lateral margin: (1) proximally rounded; (2) proximally linear.
71. Uropod protopod dorsomedial ridge: (1) plate-like, not serrate; (2) projecting and spur-like (e.g. ‘third ramus’ in *Uramphisopus*); (3) plate-like, serrate; (4) not produced; (5) with subdistal bump bearing several robust setae.
72. Uropod protopod robust spinose setae (heavy setae with fan of distal spinules) on distoventral margin: (1) present; (2)\* absent.
73. Uropod rami distal tips: (1) pointed; (2) rounded.
74. Uropod rami cross-sectional shape: (1) round; (2) flattened; (3) oval or flattened on dorsal surface; (4) round exopod and dorsally flattened endopod.
75. Uropod endopod: (1) shorter than protopod; (2) subequal to protopod length; (3) longer than protopod.