NEW PHREATOICIDEA (CRUSTACEA: ISOPODA) FROM GRAMPIANS NATIONAL PARK, WITH REVISIONS OF SYNAMPHISOPUS AND PHREATOICOPSIS

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Abstract

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The Grampians National Park, Victoria, has substantial environmental significance owing to the diversity of endemic species restricted to this reserve. We reinforce this observation by reporting six new species and two new genera of isopod crustaceans endemic to the Grampians, and redescribe two previously known Victorian species representing formerly monotypic genera. These isopods are members of the ancient suborder Phreatoicidea, and show diverse morphologies. To demonstrate the basis for the classification of these species, we present a phylogenetic analysis of exemplar species of most extant genera of Phreatoicidea. Our analysis supports the sister group relationship of Phreatoicopsis and Synamphisopus. We observe a rudimentary accessory flagellum on the antennulae of both genera, but this isopod plesiomorphy optimises on the cladograms as a reversal. Two new genera, Naiopegia gen. nov. and Gariwerdeus gen. nov., are members of the Phreatoicidae, but are distinct from any described taxa in this family. Various metazoan and protist epibionts are commonly encountered on these isopods. These species are described using detailed scanning electron microscopy and inked drawings: family Amphisopodidae, Phreatoicopsis raffae sp. nov., Phreatoicopsis terricola Spencer and Hall, 1897, Synamphisopus doegi sp. nov., Synamphisopus ambiguus (Sheard, 1936); family Phreatoicidae, Naiopegia xiphagrostis gen. nov., sp. nov., Gariwerdeus turretensis gen. nov., sp. nov., Gariwerdeus beehivensis sp. nov. and Gariwerdeus ingletonensis sp. nov.

Table of Contents

Introduction	458
Phylogenetic analysis	
Epibionts	
Systematics	
Amphisopodidae Nicholls	
Phreatoicopsis Spencer and Hall	
Phreatoicopsis raffae sp. nov	
Phreatoicopsis terricola Spencer and Hall	
Synamphisopus Nicholls	
Synamphisopus doegi sp. nov	478
Synamphisopus ambiguus (Sheard)	
Phreatoicidae Chilton	496
Naiopegia gen. nov	497
Naiopegia xiphagrostis sp. nov	
Gariwerdeus gen. nov	
Gariwerdeus turretensis sp. nov	506
Gariwerdeus beehivensis sp. nov	
Gariwerdeus ingletonensis sp. nov	
Acknowledgments	
References	

Introduction

We report six new endemic phreatoicidean isopod crustacean species from The Grampians National Park, in western Victoria, Australia. These isopods are possibly threatened by human use of their ecosystems because The Grampians, despite containing unique landforms, flora and fauna, has a long history of degradation. Anthropogenic impacts include water impoundments, in-stream structures, timber harvesting, grazing and tourism. Although the Park would not ordinarily achieve a high conservation rating owing to this history of human disturbance, it has much natural significance (LCC, 1991; Doeg, 1997). A recent study of invertebrates inhabiting riffle zones of streams in the Grampians (Doeg, 1997) identified at least 20 sites with conservation significance, based on their content of rare or endemic species. Standard limnological methods used in that study collected only relatively large phreatoicidean specimens of the genus Synamphisopus Nicholls, 1943 (Doeg, pers. comm.), and are unlikely to collect the smaller groundwater-dependent taxa reported in this paper. Taking account of this groundwater component, the endemic aquatic fauna of the Grampians National Park is more diverse than previously documented.

A phylogenetic analysis combining the Grampians phreatoicidean fauna with representatives of all other extant genera delimits the systematic relationships of these taxa. This analysis justifies the creation of two new genera for the family Phreatoicidae, *Naiopegia* gen. nov. (monotypic) and *Gariwerdeus* gen. nov. (three new species), as well as new species for the Amphisopodidae genera *Synamphisopus* and *Phreatoicopsis* Spencer and Hall, 1897. These taxa contribute to an understanding of the phylogenetic diversity of the Grampians, owing to their ancient derivation (Wilson and Keable, 2001) and apparently long isolation in this region.

Methods. Isopods described in this paper were collected during a 3-day visit to the Grampians National Park during September 1999. In all cases, samples were taken from substrates on the edges of streams or in springs and seeps using

small plastic hand sieves (~1 mm mesh), and field sorted into small plastic containers. Specimens were preserved in either sodium bicarbonate neutralised 10% formalin solution or 95% ethanol. Preparation of this material for scanning electron microscopy (SEM) included dissection and isolation of individual limbs, ultrasonic cleaning and CO2 critical point drying. Images were obtained using a Leo 435VP SEM equipped with a Robinson backscatter detector, and then saved as digital TIF files. The images were placed into digital image plates with the background removed. The pleopods, which often become distorted during drying, and holotypes were illustrated using light microscopy. Descriptions were generated using the taxonomic database system DELTA (Dallwitz, 1980; Dallwitz et al., 2000a, b; Wilson and Keable, 1999, 2001, 2002). The diagnoses and descriptions below contain only those characters that are diagnostic or that differ among species of the same genus. Descriptions are based on the male holotype or paratypes; female characters are those features that differ from the male and differ among species in the same genus. In the case of the monotypic new genus Naiopegia, we have compared this species with members of *Gariwerdeus* gen. nov. Methods for creating figures and collecting morphological data are described in Wilson and Keable (2002). Phylogenetic analyses used PAUP* (ver.4b8, Swofford, 2001), with the following commands to search for shortest length trees: "hs addseq = random nchuck = 3 chuckscore = 1 nreps = 200randomize = trees; hs start = current nchuck = 0chuckscore = 0;". Successive weighting (commands repeated three times: "reweight; hs") was used to assess the topology based on the least homoplastic characters. Table 1 provides the taxonomic data for the species in this analysis; the data and results are reported in supplementary information (see http://www.museum.vic.gov.au/ memoirs/index.html). Because internal structures of the major clades are uncertain, we do not discuss the characters and results other than as a background for the classification of the new taxa described below.

Table 1. Taxa used for phylogenetic analysis.

Taxa Outgroups	Source of Data
Spelaeogriphus lepidops (Spelaeogriphacea)	Gordon, 1957
Kalliapseudes obtusifrons (Tanaidacea)	AM P26099
Tainisopus fontinalis (Isopoda)	Wilson and Ponder, 1992
Stenasellus virei (Isopoda Asellota)	Magniez, 1975

Table 1. Continued

Taxa Phreatoicidea	Source of Data
Amphisopus annectans	AM P61300
Amphisopus lintoni	AM P8795
Colubotelson joyneri	AM P8796
Colubotelson searli	AM P54098
Colubotelson sp. 1 (Penstock Lagoon, Tas.)	AM P54096
Colubotelson sp. 2 (Uni. Tas.)	AM P54097
Crenisopus acinifer	Wilson and Keable, 1999
Crenoicus buntiae	Wilson and Ho, 1996
Crenoicus harrisoni	NMV J13924, AM P4076, AM P4081
Crenoicus sp. nov.	AM P61301
Eophreatoicus sp. nov. 4	AM P61302
<i>Eophreatoicus</i> sp. nov. 6	AM P54099
Hyperoedesipus plumosus	WAM 10665/6, AM P8799
<i>Hypsimetopus</i> sp. nov. (near Zeehan, Tas.)	AM P54100
Mesacanthotelson setosus	TMH G634/18979
Mesacanthotelson tasmaniae	AM P8767
Mesamphisopus abbreviatus	TMH G681, TMH G682
Mesamphisopus capensis	TMH G678
Metaphreatoicus australis	AM P3347
Metaphreatoicus lacustris	AM G5502
Metaphreatoicus sp.	AM P52667
Neophreatoicus assimilis	Chilton, 1894
Notamphisopus dunedinensis	USNM 54755, Acc.No. 66824; USNM 99567
	Acc.No. 45995
Nichollsia kashiense	Zoological Survey of India C4516/1, C4517/1
Onchotelson brevicaudatus	TMH G3274
Paramphisopus palustris	AM P44487
Paraphreatoicus relictus	TMH G593/18930
Phreatoicoides sp. A	QVM 10: 12377
Phreatoicoides sp. B	QVM 10: 12267
Phreatoicoides gracilis	AM P3348
Phreatoicopsis terricola	this paper
Phreatoicopsis raffae sp. nov.	this paper
Phreatoicus orarii	Nicholls, 1944
Phreatoicus orarn Phreatoicus typicus	AM P52733, AM P52734
Phreatomerus latipes	AM P52755, AM P52754 AM P54102
Pilbarophreatoicus sp. 1	AM P54102 AM P54104
Pilbarophreatoicus sp. 1 Pilbarophreatoicus platyarthricus	
	Knott and Halse, 1999 this paper
Synamphisopus ambiguus Synamphisopus doggi sp. poy	this paper
Synamphisopus doegi sp. nov.	this paper TMH G725
Uramphisopus pearsoni Paluda paraliatus Wilson and Kaabla, 2002	
Peludo paraliotus Wilson and Keable, 2002	WAM C 25051–25052; AM P60532–60533 WAM C 25040, 25050, AM P60527, 60531
Eremisopus beei Wilson and Keable, 2002	WAM C 25049–25050, AM P60527–60531
<i>Platypyga subpetrae</i> Wilson and Keable, 2002	
Naiopegia xiphagrostis gen. nov., sp. nov.	this paper
Gariwerdeus turretensis gen. nov., sp. nov.	this paper
Gariwerdeus beehivensis sp. nov.	this paper
Gariwerdeus ingletonensis sp. nov.	this paper

Abbreviations. NMV, Museum Victoria, Melbourne; AM, Australian Museum, Sydney; QVM, Queen Victoria Museum, Launceston; SAM, South Australian Museum, Adelaide; TMH, Tasmanian Museum and Art Gallery, Hobart; USNM, United States National Museum, Washington, DC; WAM, Western Australian Museum, Perth; bl, body length; GPS, global positioning satellite fix; ind., individuals, specimen or specimens.

Phylogenetic analysis

Parsimony analysis of the data found 84 trees of length 694 (see supplementary information).

When subjected to successive weighting, only three trees result from the analysis. Figure 1 shows the strict consensus of both the parsimony and weighted parsimony analyses. The parsimony consensus shows large polytomies for the taxa of the Amphisopodidae, the Western Australia and Indian species of the Hypsimetopodidae and various clade levels within the Phreatoicidae. Polytomies also appear in both consenses within the genera *Mesamphisopus, Crenoicus* and *Gariwerdeus* gen. nov. because the analysis does not include features that are diagnostic at a species level within those taxa. The presence of *Platypyga subpetrae* Wilson and Keable, 2002 appears to cause most of the discordance among



Figure 1. A, strict consensus of parsimony analysis. B, strict consensus of successive weighted parsimony analysis.

equally parsimonious trees. In an Adams consensus of the 84 trees (see supplementary information), Platypyga appears in a polytomy with two resolved Amphisopodidae clades, indicating that this species causes the collapse of the amphisopodid clades in the strict consensus tree. Deleting this taxon reduces the tree set from 84 trees to only 9 much more resolved trees (length 679) (see supplementary information). In the trees from all of these analyses (parsimony, weighted parsimony, Platypyga removed), general features appear consistently - two major clades corresponding to the families Hypsimetopodidae (sensu Wilson and Keable, 2001) and Phreatoicidae, with Crenisopus Wilson and Keable, 1999 emerging on the branch between Amphisopodidae and Hypsimetopodidae. Stable superspecific clades occur within the families:

Hypsimetopus + *Phreatoicoides*;

Amphisopus + Phreatomerus + Paramphisopus; Phreatoicopsis + Synamphisopus;

Eremisopus + Eophreatoicus;

Crenoicus + New Zealand taxa *Phreatoicus* and *Neophreatoicus*;

Gariwerdeus + Naiopegia.

The positions of these stable clades vary within the major clades depending on the composition of the analysis; additional species or new characters often change the relationships. For the purposes of this paper, however, these results are stable among all trees. Species of *Gariwerdeus* gen. nov. are monophyletic, with *Naiopegia* gen. nov. as its sister group within the Phreatoicidae. The genera *Phreatoicopsis* and *Synamphisopus* are monophyletic, and together form a monophyletic clade within a less well-defined amphisopodid clade.

This latter result is surprising because *Phreato*icopsis superficially resembles no other phreatoicidean genus. Nevertheless, Nicholls (1943) originally assigned the genera Synamphisopus and Phreatoicopsis, with Eophreatoicus Nicholls, 1926, Protamphisopus Nicholls, 1943 (a Triassic fossil) and Uramphisopus Nicholls, 1943 to the heterogeneous amphisopodid subfamily "Phreatoicopsinae" [sic]. The relationships of P. rotamphisopus are under study (research in progress), but *Eophreatoicus* is the sister group to Eremisopus Wilson and Keable, 2002 (fig. 1A), and clearly not as closely related to Synamphisopus and Phreatoicopsis. Uramphisopus is a member of the Phreatoicidae (Wilson and Keable, 2001). Moreover, analyses of 12S and 16S rDNA by Wetzer et al. (2001) also support the sister group relationship of Phreatoicopsis and Synamphisopus. Character states shared by the two genera, other than those discussed below

(Phreatoicopsis remarks), include a large spine on the propodal palm of the male first pereopod, but variation among the species weakens the support of the relationship. The rudimentary second flagellum on the antennula is observed in both genera (Phreatoicopsis: figs. 3C, 10F; Synamphisopus: 18D), but this isopod plesiomorphy optimises on the cladograms as a reversal supporting the sister relationship of the two genera. Our previous analysis of the Phreatoicidea (e.g., Wilson and Johnson, 1999; Wilson and Keable, 2001) did not find this sister relationship because several synapomorphies of Synamphisopus and *Phreatoicopsis* were omitted from the analysis. and one feature (depth of pleonite pleurae) was incorrectly scored. The relative uncertainty of within-family relationships that remain in our analyses prevents the use of Nicholls' (1943, 1944) subfamily categories in the current classification.

Epibionts

Practically all large specimens of Phreatoicopsis are found with Temnocephala (Platyhelminthes) crawling on their sternites and ostracodes on their pleopods, as in many Australian crayfish (Parastacidae). All species of Gariwerdeus gen. nov., Naiopegia gen. nov. and to a lesser extent Synamphisopus and Phreatoicopsis have substantial populations of protozoan epibionts growing on their limbs and somites. In some body positions, the protist epibiont burden is substantial (e.g., percopods - fig. 54A, or mouthparts fig. 44E). Other phreatoicideans have been recorded with various types of sessile protists (Kane, 1969; Clamp, 1991; Fernandez-Leborans and Tato-Porto, 2000; O'Donoghue and Adlard, 2000; Wilson and Keable, 2002). Clamp (pers. comm.) has recorded lagenophryid peritrichs on all phreatoicidean families: Metaphreatoicus australis (Chilton, 1891), Colubotelson searli Nicholls, 1944, C. joyneri (Nicholls, 1926), C. chiltoni (Sheppard, 1927), Mesacanthotelson tasmaniae (Thomson, 1894), Phreatoicoides longicollis Nicholls, 1943, and Phreatoicopsis terricola Spencer and Hall, 1897. Some epibionts may have preferences for host attachment sites, as has been observed in the unrelated Asellus aquaticus (Cook et al., 1998), and two different genera may occur on different locations on the body. Dome-shaped Lagenophryidae peritrichs are found on the pleopods and others on the legs, while the stalked peritrich Vorticella (fig. 43G) and the suctorian ciliates (fig. 49E) appear to prefer the external surfaces of the limbs and body. How these epibionts affect their hosts is unknown.

Systematics

Amphisopodidae Nicholls

Amphisopidae Nicholls, 1943: 25.

Remarks. Our analyses of character distributions among the Phreatoicidea (results above, Wilson and Keable, 2002) has identified an assemblage of taxa that may be assigned to the family Amphisopodidae. The unweighted analyses do not provide strong support for the family, and some taxa do not match the familial characters discussed in Wilson and Keable, 2002. Platypyga Wilson and Keable, 2002 is only weakly associated with the Amphisopodidae, although most character weighted analyses of the data find that it belongs to this clade (e.g., successive weighting results outlined above). Therefore, we do not provide a new classification or diagnosis of the Amphisopidae at this time because the status of this family may be questioned. Although eyes frequently are not expressed in phreatoicideans and thus are homoplasious for phylogenetic analyses, all species currently assigned to this family have eyes, if only small spots as in Phreatoicopsis. While we do not regard this presumed plesiomorphy as significant, this feature may assist in identification (i.e., blind species probably belong to another family).

Phreatoicopsis Spencer and Hall

Phreatoicopsis Spencer and Hall, 1897: 12.— Sheppard, 1927: 117.—Nicholls, 1943: 112.

Type species. Phreatoicopsis terricola Spencer and Hall, 1897, by monotypy.

Diagnosis. Typhlosole well developed, ventral invagination forming double spiral in cross section. Pleotelson posterior margin truncate, circular in posterior view, with terminal anus, not reflexed; lateral lobes absent; dorsal uropodal ridge curving strongly and extending posteriorly from uropods on pleotelson margin. Antennula article 3 rudimentary second flagellum present. Mandible spine row on round pedunculate projection. Maxillula lateral lobe distal margin with many (24-25) robust setae, distal setal row separated by gap from other setal rows; inner lobe narrow and tapering, with 3 pappose setae distally. Pereopod I dactylus ventral margin proximal tooth present; merus dorsal margin projection spine-like and pointed. Pereopods II-VII propodus without articular plate; pereopod IV of male simple, not prehensile; pereopods V-VII basis dorsal ridge not distinctly separated from basis shaft. Pleopods protopods I-II lateral

epipod linear; pleopod II endopod appendix masculina proximal half of shaft solid and rod-like, indented in ventral cross section, with several large subterminal denticles around lateral to medial and dorsal surfaces. *Uropod* rami distal tips pointed.

Remarks. Phreatoicopsis species, in addition to being among the largest of the phreatoicideans and living in semiterrestrial habitats, have other unusual features. Live animals have a light, sometimes pearly cuticle, with bands or patches of bright yellow on some dorsal surfaces, most obviously the head. The legs of *Phreatoicopsis* are unusually thin, lacking the typical amphisopodidan dorsal margin plates on the pereopodal bases, and the large pleonal pleurae possibly form a respiratory chamber for pleopods. Setae on the body and limbs are few, short and typically robust. The small setae on the margins of the pleopods are minutely plumose. The pleotelson lacks any of the typical embellishments seen in aquatic phreatoicideans; it is smooth, simply constructed and opens posteriorly, with a fringe of setae on the posterior margin. Interestingly, the lateral outline of the Phreatoicopsis pleotelson (e.g., figs 2, 9C, 16B) resembles that of Protamphisopus, which Nicholls (1943) placed in his rather heterogeneous subfamily Phreatoicopsinae. Hermaphroditism may be an important feature of the *Phreatoicopsis* reproductive system, although the reasons for the apparently varying proportions of intersexes remain to be determined.

As discussed above, Phreatoicopsis is the sister group to Synamphisopus. This relationship is based on the following putative synapomorphies: the highly developed typhlosole in the hindgut; an unusually high number of robust setae on the maxillula lateral lobes (Phreatoicopsis - fig. 5B; Synamphisopus - figs 20B-C); blunt denticles on the distal tip of the appendix masculina (Phreatoicopsis – fig. 16D; Synamphisopus – figs 23C-E, 31I-J); and a pedunculate mandibular spine row (Phreatoicopsis - figs 4D-E, H, J; Synamphisopus – figs 19B, H, J). The spine row structure is distinct from that of the Phreatoicidae because the bifurcate spines are fused basally so that the two rami of each spine appear to be independent, giving an open appearance to the centre of the spine row. The spine row of Synamphisopus is somewhat less modified than in Phreatoicopsis and flattened dorsoventrally, appearing more simlar to the typical spine row of other amphisopodids.

Phreatoicopsis specimens from the Grampians were previously identified as *P. terricola* Spencer

and Hall (first noted by Raff, 1912). Our examination of this morphologically conservative genus indicates that populations from the Grampians represent a new species, as suggested by Nicholls (1943).

Phreatoicopsis raffae sp. nov.

Figures 2–9

Phreatoicopsis terricola.—Raff, 1912: 70, pl. 5.— Nicholls, 1943: 113, figs 27, 28 (part, material from vicinity of the Grampians is not *Phreatoicopsis terricola* Spencer and Hall, 1897).

Material examined. Holotype. Victoria (Vic.), Flatrock Crossing, Glenelg River Road, Grampians National Park, 37°09.77'S 142°26.59'E (GPS), soil among roots of ferns and under sphagnum moss on side of seep, collected by hand and spoon, R. Wetzer, S. Keable and G. Wilson, 20 Sep 1999, VIC-87, NMV J40730 (male bl 51.9 mm, ethanol preserved).

Paratypes. All lots collection details as for holotype. AM P61250 (1 male bl 32.5 mm, 2 females bl 45.7/51.4 mm, 1 juvenile female bl 29.1 mm, 1 hermaphrodite (with penes, no appendix masculina, with oostegite buds) bl 32.7 mm, 1 indeterminate juvenile bl 19.6 mm), AM P61436 (1 male bl 40.7 mm, dissected for illustration, description and SEM), AM P61437 (1 female bl 46.8 mm, dissected for description and SEM).

Other material. Vic., The Grampians, no other data, AM P61251 (9 ind. ex NMV). Vic., The Grampians: N of the Divide (37°17'S, 142°33'E), 21 Dec 1934, NMV J44871 (>30); Vic., S of the Divide (37°17'S, 142°33'E), I. Mitchell (Stawell, Vic.) per A. Chisolm, 25 Dec 1934, NMV J44873 (>30); Vic., Bellfields, 37°17'S, 142°33'E, J. Clark, 14 Aug 1935, NMV J44882 (5); Vic., Swamp at head of Wannon R. (37°19'S, 142°31'E), J. Clark, 14 Aug 1935, NMV J44892 (7); Vic., Swamp at head of Wannon R. (37°19'S, 142°31'E), J. Dawson, 04 Sep 1935, NMV J44893 (9); Vic., N. McCance, Jul 1961, NMV J21805 (1); Vic., Glenelg R. (37°11'S, 141°43'E), A. Neboiss, 16 Dec 1966, NMV J44885 (1); Vic., 37°17'S, 142°33'E, R. Veerman, December 1968, NMV J44898 (1); Vic., Mt William (37°13'S, 144°48'E), C. McCubbin, 28 Apr 1971, NMV J44883 (1); Vic., Glenisla Range (37°14'S, 142°11'E), A. A. Calder, 04 Mar 1976, NMV J44896 (3) and NMV J44895 (2); Vic., Mt William, 100 m S. of summit, 27 Aug 1978, M.S. Harvey, NMV J48353 (1 female); Vic., Jimmys Creek, 25 Aug 1983, J. Baldwin. NMV J48354 (2); Vic., near Jimmys Creek and Dunkeld Road (37°22'S, 142°31'E), R. Duggan, 26 Jan 1987, NMV J44868 (5); Vic., 37°17'S, 142°33'E, H. Clark, NMV J44869 (57).



Figure 2. Phreatoicopsis raffae, sp. nov. Holotype (NMV J40730), lateral view. Scale bar 5 mm.



Figure 3. *Phreatoicopsis raffae*, sp. nov. Paratype male (AM P61436). A, head, dorsal view. B, antennula, antenna proximal articles, dorsal view. C, antennula article 3 rudimentary second flagellum. D, head, lateral view with antennula and antenna proximal articles. E, antennula, distal tip. F–G, antenna flagellum, distal and proximal articles. Scale bar 1 mm.

Vic., (Vial label gives locality as "From Groener, West Australia", A second label in the vial says "The locality of these specimens is doubtful! Probably Western Victoria") I.R. McCann, 9 November 1982, NMV J44890 (19). No label data: J44782 (2), J44888 (3)

Etymology. This species is named after Janet W. Raff, who first recorded it from the Grampians (Raff, 1912).

Diagnosis. Pleotelson length subequal to width in dorsal view, dorsal length 0.96 width. *Left mandible* incisor process dorsal margin with fourth sloping cusp. *Maxillula* lateral lobe with 4

robust setae in distal row. *Pereopod* VII basis dorsal ridge with robust setae. *Uropod* protopod dorsomedial ridge not projecting beyond distal margin, linear.

Description, including all adult forms. Coloration in life head with large patch of yellow, posterior margins of pereonites 6–7, pleonites 1–2 or 2–3 with yellow transverse stripe, body otherwise grayish, white pereopods, tiny black eye; in 95% ethanol uniform cream, eye black.

Head (figs 3A, D) width 0.73 perconite 1 width. Eyes maximum diameter 0.12 head depth.

Pleonites (fig. 2) 1–4 width 0.78 composite length in dorsal view.



Figure 4. *Phreatoicopsis raffae*, sp. nov. Paratype male (AM P61436). A, paragnaths. B–G, left mandible. H–J, right mandible. Scale bar 0.5 mm.



Figure 5. *Phreatoicopsis raffae*, sp. nov. Paratype male (AM P61436). A–C, maxillula. D–E, maxilla. F–G, maxilliped. Scale bar 1 mm.

Pleotelson (figs 9A, C) lateral length 0.14 body length; depth 1.95 pereonite 7 depth; posterior margin with 72 setae (approximately, including anterior ventral margin near insertion of uropod); ventral margin anterior to uropods with 6 setae.

Antennula (figs 3B–C) length 0.07–0.1 body length, with 13–14 articles. Article 5 length 1.5 width. Article 6 length 1.2 width. Several tiny aesthetascs on article 11 to terminal article. Terminal article length 0.8 width. Antenna (figs 2, 3F–G) length 0.38 body length. Flagel-lum length 0.43–0.62 total antenna length, with 18–22 articles.

Mouthfield clypeus width 0.52 head width. *Mandible* (figs 4B–J) palp length 1.12 mandible length; article 3 with 7 setae, setae denticulate (minutely). Left spine row with 17 spines (basally fused, therefore total probably representing count of both sides of approximately 8 bifurcate spines), additional spines between pedunculate projection and molar absent. Molar process length subequal to width; fine simple spines forming posterior row (short). *Maxillula* (figs 5A–C) medial lobe width 0.5 lateral lobe width; with 8 'accessory setae'. Lateral lobe distal margin with 24 smooth robust setae.



Figure 6. *Phreatoicopsis raffae*, sp. nov. Paratype female (AM P61437), paratype male (AM P61436). A–B, female pereopod I. C–D, male pereopod I. Scale bar 1 mm.

Maxilla (figs 5D–E) medial lobe width 1.33 outer lateral lobe width. Outer lateral lobe length subequal to inner lateral lobe (ratio 1.02). *Maxilliped* (figs 5F–G) endite distal tip with approximately 20 subdistal biserrate setae on ventral surface; medial margin with 6 coupling hooks on left side; dorsal ridge with 17 large distally not noticeably denticulate plumose setae. Palp article 4 length 0.73 width; article 5 length 1.75 width, length 0.75 article 4 length.

Pereopod I (fig. 6) dactylus length subequal to palm length. Propodus length 0.88 width; dorsal margin with 8 minute setae (excluding distal group). Propodal palm with 6–8 broad based setae. Basis length 2.0 width, dorsal ridge with approximately 13 minute setae scattered along ridge. *Pereopod* IV (figs 7A–B) length 0.38 body length. Propodus length 4.5 width, with 4 broad based setae on ventral margin (5 submarginally). Carpus length 0.16 pereopod length, with 4 broad based setae on ventral margin in male (7 submarginally, 1 distinctly larger than others). Ischium posterodistal margin with 4 setae in male (8 submarginally). Basis length 3.25 width.

Penes length 0.37 body width at pereonite 7.

Pleopod (fig. 8) I endopod length 0.65 exopod length. *Pleopod* II endopod length 0.65 exopod length. *Pleopod* III exopod distal article length 0.32 exopod length; endopod length 2.04 width, 0.68 exopod length. *Pleopod* IV exopod length of distal article 0.33 exopod length; endopod length 1.75 width. *Pleopod* V endopod length 1.72 width. *Pleopods* protopod I with 16 simple and minutely serrate setae along length of lateral margin; protopod II with 8 simple and minutely serrate setae along length of lateral margin; 2 submarginally. *Pleopod* I exopod medial margin convex – divergent from lateral margin (weakly concave proximally). *Pleopod* II endopod appendix masculina with 8 minute setae on margin.

Uropod (figs 9B, D, E–G) total length 0.72 pleotelson length. Protopod length 1.89 width, 0.31–0.44 uropod total length; dorsomedial ridge length 0.84 endopod length. Endopod with 3–5 robust setae. Exopod length 0.62–0.67 endopod length, with 3 setae.

Distribution. Central and southern parts of The Grampians National Park, in wetlands or swamps associated with the Wannon and Glenelg Rivers, Victoria.

Remarks. The male and female character states do not appear to be correlated with body size possibly owing to hermaphroditism in this species, so we have not distinguished the sexes in the above



Figure 7. *Phreatoicopsis raffae*, sp. nov. Paratype male (AM P61436), paratype female (AM P61437). A, male pereopod IV. B, female pereopod IV. C, male pereopod VII. D, male pleopod II appendix masculina. E, male pereopod VII proximal articles, with penes. Scale bar 1 mm.



Figure 8. *Phreatoicopsis raffae*, sp. nov. Paratype male (AM P61436). A–E, pleopods I–V. Setae on margins are minutely plumose. Scale bar 1 mm.

description. Species of *Phreatoicopsis* can be identified using the shape of the uropod protopod dorsomedial margin: straight or only slightly curving dorsally and not projecting beyond insertions of rami (*P. raffae*, figs 9D, G) versus curving dorsally and projecting beyond insertions of

rami (*P. terricola*, figs 16C, F). Robust setae on dorsal margin on the basis of pereopod VII in *Phreatoicopsis raffae* sp. nov. (fig.7C) as opposed to fine setae in *P. terricola* will distinguish adults of the two species, but this feature may not be useful for specimens of 35 mm or less.



Figure 9. *Phreatoicopsis raffae*, sp. nov. Paratype male (AM P61436). A–D, pleotelson and uropod, dorsal, posterior and lateral views. E–G, uropod ventral and medial views. Scale bar 1 mm.

Phreatoicopsis terricola Spencer and Hall

Figures 10-16

Phreatoicopsis terricola Spencer and Hall, 1897: 12, pls. 3–4.—Raff, 1912: 70, pl.5 (part, material from vicinity of Otway Range).—Nicholls, 1924: 98.—Nicholls, 1926: 203.—Sheppard, 1927: 117.—Barnard, 1927: 160.—Nicholls, 1943: 113, figs 27, 28 (part, material from vicinity of Otway Range).

Not *Phreatoicopsis terricola*.—Raff, J.W., 1912: 70, pl.5.—Nicholls, 1943: 113, figs 27, 28 (part, material from vicinity of The Grampians is *Phreatoicopsis raffae* sp. nov.).

Type material. Probable syntypes. Victoria, "Banks of Upper Gellibrand River, in burrows (W.H.F. Hill)" (Spencer and Hall, 1897: 13), 38°33'S 143°39'E (estimated from map), specimens lost. Nicholls (1943) reported examining specimens from "Museums of



Figure 10. *Phreatoicopsis terricola*. Hermaphrodite (AM P61438). A, antenna. B–C, antenna flagellum, distal and proximal articles. D, antennula, antenna proximal articles, dorsal view. E, antennula distal articles. F, antennula article 3 rudimentary second flagellum. Scale bar 1 mm.

Melbourne and Adelaide" but apparent types have not been found. Museum Victoria (G. Poore, pers. comm.) has specimens of *P. raffae* sp. nov. (see above), that account for some but not all specimens reported by Nicholls.

Material examined. Vic., Otway Range, 200 m west of Benwerrin–Mount Sabine Track, 0.5 km N of Delaney Road, 38°31.90'S 143°50.76'E (GPS), from soil 20cm deep under fern tree root mat in bank of stream, shovel and hand, G. Wilson, R. Wetzer and S. Keable, 25 Sep 1999, preserved in 95% ethanol, VIC-101, AM P61252 (4 hermaphrodites bl 26 (no appendix masculina, pene bud only on one side)/26 (with appendix masculina)/ 30.5 (no appendix masculina)/40.5 (no appendix masculina) guivenile female bl 24.2/29.8/30.2/50.9 mm, 1 juvenile female bl 24.7 mm), AM P61438 (hermaphrodite bl 46.6 mm, dissected for illustration, description and SEM, collection details as for P61252), AM P61439 (hermaphrodite bl 50.2 mm partially dissected for description and SEM, collection details as for P61252); Vic., Otway Range, from 900 m SW of Cowley Track, 38°33.36'S, 143°50.48'E (map), dug from oval burrows in damp sediment under tree fern roots, no free water observed in substrate, W.F. Ponder and G.D.F. Wilson, 15 Jul 1991, Stn V19, AM P54101 (4 juveniles possibly males (pene buds but no appendix masculina) bl 16.6/18.2/25/25.9 mm, 9 males bl 21.1 (penes and appendix masculina not fully developed)/25.5/25.7/27.5/28.2/28.6/35.7/41.2 (dissected for description)/53.8 mm, 1 hermaphrodite (small penes, no appendix masculina, oostegite buds on anterior pereopods) bl 25 mm, 2 hermaphrodites bl 36 (dissected for description)/46.6 (no appendix masculina) mm); Vic., near Lavers Hill, Otway Range, 38°41'S 143°24'E (estimate), pit trap, A. Fraser, 10 Feb 1972,



Figure 11. *Phreatoicopsis terricola*. Hermaphrodite (AM P61439) A–B, G–I, hermaphrodite (AM P61438) C–F. A, paragnaths. B, left mandible. C–E, left mandible. F, right mandible. G–I, right mandible. Scale bar 1 mm.



Figure 12. *Phreatoicopsis terricola*. Hermaphrodite (AM P61438) A–E, hermaphrodite (AM P61439) F–G. A–C, maxillula. D–E, maxilla. F–G, maxilliped. Scale bar 1 mm.

AM P31004 (1 ind.); Vic., Forrest (38°31'S, 143°43'E), Davey, HW, 26 Feb 1925, NMV J44880 (1); Vic., Upper Gellibrand Gorge, near Forrest (38°33'S, 143°39'E), 'CWB', 17 Dec 1946, NMV J44894 (8); Vic., Otway, Beech Forest (38°27'S, 143°58'E), W.H.F. Hill, 14 Sep 1897, NMV J44875 (4); Vic., Cape Otway, Beech Forest (38°52'S, 143°31'E), H.P. Ashworth, Apr 1897, NMV J44877 (3 degraded, possibly dried at one time); Vic., Beech Forest (this record included "Grampians" in place name) W.H.F. Hill (collector of the syntypes), 11 Nov 1897, J44884 (16 tanned colour); Beech Forest NMV J44876 (1); Vic., Otway Ranges, G. Milledge, 11 Apr–14 Jun 1995: Phillips Track 0.5 km N of Triplet Falls (38°40'S 143°29'E), pitfall traps, G. Milledge, *Nothofagus cunninghamii* forest, J48355, (32); Vic., Young Creek Rd 0.4 km NW of Triplet Falls, (38°40'S 143°29'E), pitfall traps, *Eucalyptus* sp. forest, J48356 (6); Vic., Cobden (38°20'S, 143°04'E), N. McCance, Sep 1963, NMV J44886 (1); Vic., Apollo Bay (38°46'S, 143°40'E), Field Naturalists Club of Victoria, Dec 1904, NMV J44874 (28); Vic., Maits Rest, 10 km W of Apollo Bay, Otway Ranges (38°45'S, 143°34'E), in *Nothofagus cunnighamii* forest, Pitfall Trap, G. Milledge, P. Lillywhite and C. McPhee, 30 Oct 1991, NMV J44878 (1), NMV J44879 (1), NMV J44848 (1 damaged specimen).

P. terricola variant (see Remarks). Vic., Upper



Figure 13. Phreatoicopsis terricola. Hermaphrodite (AM P61438). A-C, pereopod I. Scale bar 5 mm.

Gellibrand Gorge, near Forrest (38°33'S, 143°39'E), 'CWB', 17 Dec 1941, NMV J44891 (22, largest is ~30 mm); Vic., Forrest (38°31'S, 143°43'E), Wilhelms, Jul 1948, NMV J44887 (10, largest is ~40 mm).

Diagnosis. Pleotelson length greater than width in dorsal view, dorsal length 1.22 width. Left mandible incisor process dorsal margin lacking fourth sloping cusp. Maxillula lateral lobe with 5 robust setae in distal row. Pereopod VII basis dorsal ridge lacking robust setae. Uropod protopod dorsomedial ridge distinctly projecting posteriorly beyond distal margin, concave.

Description based on hermaphrodite. Coloration in life, head with patch of yellow, posterior margins of pereonites 6–7, pleonites 1–3 with yellow transverse stripes, body otherwise grayish, white pereopods, tiny black eye; in 95% ethanol uniform cream, eye black.

Head width 0.82 perconite 1 width. Eyes maximum diameter 0.09 head depth.

Pleonites 1–4 width 0.60 composite length in dorsal view.

Pleotelson (figs 16A–C, F) lateral length 0.11 body length; depth 1.88 pereonite 7 depth; posterior margin with 66 setae (approximately, including anterior ventral margin near insertion of uropod); ventral margin anterior to uropods with 10 setae.

Antennula (figs 10D–E, F) length 0.10–0.14 body length, with 12–13 articles. Article 5 length 1.2 width. Article 6 length 1.0 width. Several tiny aesthetascs on article 9 to terminal article. Terminal article length 0.55 width. Antenna (figs 10 A–C) length 0.3 body length. Flagellum length 0.43–0.46 total antenna length, with 24–26 articles.

Mouthfield clypeus width 0.48 head width. *Mandible* (fig. 11) palp length 1.06 mandible length; article 3 with 8 setae, setae smooth. Left spine row with 21 spines (basally fused, total probably representing count on

both sides of approximately 10 bifurcate spines), total count including 1 spine on margin between pedunculate projection and molar. Molar process longer than wide; spines absent. *Maxillula* (figs 12A–C) medial lobe width 0.39 lateral lobe width; with 7 'accessory setae'. Lateral lobe distal margin with 25 smooth robust setae. Lateral lobe width. Outer lateral lobe width 1.64 outer lateral lobe. *Maxilliped* (figs 12F–G) endite distal tip with 38 subdistal biserrate setae on ventral surface (approximately); medial margin with 26 large distally denticulate plumose setae (approximately, not noticeably denticulate). Palp article 4 length 0.66 width; article 5 length 1.67 width, 1.0 article 4 length.

Pereopod I (fig. 13) dactylus length 0.9 palm length. Propodus length 0.97 width; dorsal margin with 12 setae (excluding minute distal group). Propodal palm with 7–8 broad based setae. Basis length 1.86 width, dorsal ridge with 3 minute setae proximally. *Pereopod* IV (figs 14C–D) length 0.31 body length. Propodus length 3.0 width, with 8 broad based setae on ventral margin. Carpus length 0.13 pereopod length, with 8 broad based setae on ventral margin, 2 distinctly larger than others. Ischium posterodistal margin with 7 setae. Basis length 3.83 width.

Penes (fig. 14F) length 0.17 body width at pereonite 7. Pleopods (figs 15, 16d–E) I endopod length 0.79 exopod length. Pleopod II endopod length 0.7 exopod length. Pleopod III exopod length of distal article 0.28 exopod length; endopod length 2.21 width, 0.58 exopod length. Pleopod IV exopod length of distal article 0.29 exopod length; endopod length 1.97 width. Pleopod V endopod length 1.48 width. Pleopod protopods I with 10 simple and minutely serrate setae along length of lateral margin; protopod II with 18 simple and minutely



Figure 14. *Phreatoicopsis terricola*. Hermaphrodite (AM P61438) A–B, F, hermaphrodite (AM P61439) C–E. A–B, pereopod II. C–D, pereopod IV. E–F, pereopod VII with penes, including proximal articles, some setae missing from basis dorsal margin. Scale bar 1 mm.



Figure 15. *Phreatoicopsis terricola*. Hermaphrodite (AM P61438). A-E, pleopods I-V. Setae on margins are minutely plumose. Scale bar 2 mm.



Figure 16. *Phreatoicopsis terricola*. Hermaphrodite (AM P61438). A–C, F, pleotelson and uropod, dorsal, lateral and posterior views. D, pleopod II appendix masculina and endopod. E, pleopod I. G. uropod protopod distal margin, ventral view. Scale bar 1 mm.

serrate setae along length of lateral margin, 1 submarginally. *Pleopod* I exopod medial margin straight – divergent from lateral margin only proximally. *Pleopod* II endopod appendix masculina with 16 setae on margin.

Uropod (figs 16A–C, F–G) total length 0.64 pleotelson length. Protopod length 2.57 width, 0.46–0.5 uropod total length; dorsomedial ridge length 1.15 endopod length. Endopod with 4–6 robust setae (including 3 small dorsolateral setae). Exopod length 0.62–0.78 endopod length; distoventral margin with 2 robust setae. *Distribution.* Wetlands of the Otway Range, including Gellibrand Gorge and Cobden, Victoria.

Remarks. See Remarks under *P. raffae* sp. nov. for distinguishing the two known species of this genus. Nicholls (1943) remarked upon the apparent hermaphroditism observed in this species. In the material that we examined, the distribution of male and female characteristics does not appear to be correlated with body size.

Smaller specimens show some differences from adults that might cause difficulty in identification. In particular, the dorsomedial ridge of the uropodal protopod of small specimens does not project significantly beyond the distal margin of the protopod, and may lack the ventral-most of the three setae on the projection (figs 16F,G). These smaller specimens, however, retain the concave margin of the dorsomedial ridge. The pleotelson ventral margin typically has two robust setae anterior to the uropodal insertion, but smaller specimens may only have a single large seta. Two lots of specimens (NMV J44891, J44887) retain these features in larger individuals (up to 4cm); these have been listed separately as variants of P. terricola.

Synamphisopus Nicholls

Synamphisopus Nicholls, 1943: 95.

Type species. Amphisopus ambiguus Sheard, 1936 by original designation.

Diagnosis. Typhlosole well developed, ventral invagination forming double spiral in cross section. Pleotelson posterior margin cleft, reflexed dorsally; lateral lobes forming vertical plates; dorsal uropodal ridge curving strongly and extending posteriorly from uropods on pleotelson. Antennula article 3 rudimentary second flagellum present. Mandible spine row on round pedunculate projection. Maxillula lateral lobe distal margin with 20-29 smooth robust setae, inner lobe narrow and tapering. Pereopod I dactylus dorsal margin with dense group of elongate setae. Pereopods propodus II-IV without articular plate, V–VII with articular plate; pereopod IV sexually dimorphic, prehensile in male. Pleopods II endopod appendix masculina proximal half of shaft broadly concave in ventral cross section, forming tube at distal tip; with large subterminal denticles around lateral to medial and dorsal surfaces. Uropodal rami distal tips rounded.

Remarks. The synapomorphies of the clade *Phreatoicopsis* + *Synamphisopus* are discussed above in the *Phreatoicopsis* generic remarks. Features of *Synamphisopus* species that differ from *Phreatoicopsis* include limited sexual dimorphism in the fourth pereopod, rounded tips of the uropods, small dorsal plates of the basis on the posterior three pereopods and shape of the pleotelson. Our phylogenetic analysis identifies these features as plesiomorphic character states within the Amphisopodidae. The dense group of elongate setae on the medial side of the pereopod I dactylus, however, are unique to species of

Synamphisopus. These setae (fig. 21H) are bipinnate with two rows of tiny curved, equal length spinules on the distal third of the setal shaft.

Although *Synamphisopus ambiguus* is a large species, easily found and examined, it has not been studied in detail since Sheard's (1936) original description and Nicholls' (1943) treatment. Our redescription of this species revealed a second species of *Synamphisopus* from the Grampians, which we describe below.

Synamphisopus doegi sp. nov.

Figures 17-25

Material examined. Holotype. Victoria, small tributary of Glenelg R. crossing Sawmill Track, Grampians National Park, 37°21.44'S 142°17.79'E (GPS), sand under rocks and submerged wood, hand sieves, pH 5.5, 10.0°C, G. Wilson, R. Wetzer and S. Keable, 21 Sep 1999, VIC-96, NMV J40731 (male bl 23.3 mm, ethanol preserved).

Paratypes. As for holotype. AM P61253 (8 males, 5 females, 1 indeterminate ind.), AM P61434 (male bl 21.4 mm, dissected for illustration, SEM and description), AM P61435 (female bl 17.5 mm, dissected for SEM and description).

Other material. Vic., creek crossing Sawmill Track, tributary of Glenelg R., Grampians, 37°20.22'S 142°19.62'E (GPS), sand under rocks and leaf litter in stream, hand sieves, pH 6.45, 10.8°C, G. Wilson, R. Wetzer and S. Keable, 21 Sep 1999, VIC-95, AM P61254 (male, female, preserved in 95% ethanol); Vic., Sawmill Track, Glenelg R., Grampians, 37°21.75'S 142°16.90'E (map), T. Doeg, 17 Nov 1994, Gr1, AM P61255–6 (2 juvenile ind.); Vic., off Goat Road, tributary of Billimina Creek, Grampians, 37°14.22'S 142°19.07'E (map), T. Doeg, 15 Nov 1994, Gr49, AM P61257 (1 juvenile ind.); Vic., 50 m below The Fortress, Grampians, 37°18.80'S 142°18.00'E (estimate), J.E. Aslin, 26 Apr 1973, SAM C6027 (2 females).

Etymology. This species name honours Tim Doeg (Flora and Fauna Branch, Department of Natural Resources and Environment, Victoria, now at Northcote, Victoria) who sent us fresh specimens of *Synamphisopus* early in our project.

Diagnosis. Pleotelson medial dorsal ridge smoothly arcing, low, in lateral view projecting ventrally to form setose lobe below level of widely cleft medial lobe. *Mandible* palp article 2 with ventrolateral row of elongate setae, most longer than distal article; spine row shaft anterior margin with two separate dentate spines. *Maxillula* medial lobe rounded and broader distally than more proximally. *Maxilliped* palp article 5 suboval, short, length 1.6 width, lateral margin rounded. *Pereopod* I of adult male dactylus



Figure 17. Synamphisopus doegi, sp. nov. Holotype (NMV J40731), lateral view. Scale bar 2 mm.

ventral margin convex, lateral face without pits but with ventrolateral row of setal groups; propodal palm heavily setose on medial margin, lacking large projecting spine. *Pereopods* II–IV basis proximal dorsal margin with row of simple setae, shorter than setal row in male, longer than setal row in female; male pereopod IV propodus ventral margin linear; pereopod VII propodus distomedial margin with setae longer than articular plate or dactylar claw. *Pleopod* II appendix masculina projecting beyond margin of proximal exopod article, with only 1 flattened tubercle on distomedial margin. *Uropod* protopod distoventral margin with 2 robust smooth setae and 1 additional small seta.

Description based on male. Coloration in 95% ethanol white legs, body slate gray-brown, head with black eyespot.

Eyes (figs 17, 18B, I) maximum diameter 0.18 head depth.

Pleonites (fig. 17) 1–4 relative lengths unequal, increasing in length from anterior to posterior, width 0.31 composite length in dorsal view.

Pleotelson (figs 17, 25A–E) lateral length 0.90 depth; dorsal length 1.65 width; depth 1.71 pereonite 7 depth. Medial lobe width 0.58 pleotelson width, greatest length 0.08 pleotelson total length.

Antennula (figs 18C–E) length 0.07 body length, with 9–10 articles. Article 5 length 1.0 width. Article 6 length 1.13 width. Numerous tiny aesthetascs on article 5 to terminal article. Terminal article length 0.75 width.

Antenna (figs 18F–H) length 0.47 body length. Flagellum length 0.71 total antenna length, with 43–46 articles.

Mouthfield clypeus width 0.52 head width. Mandible (fig. 19) palp length 0.82 mandible length; article 3 with 14 setae; cuticular combs present; separate distal group of setae absent; articles 1-2 with groups of long setae (longer than half article length) on ventral lateral margins (along entire length of article 2). Left spine row with 25-27 spines (approximately but basally fused so how many bifurcate unclear), additional spines between pedunculate projection and molar absent, first spine not separated from remaining spines. Right spine row with 19-25 spines (approximately but basally fused so how many bifurcate unclear), additional spines between pedunculate projection and molar absent. Molar process with complex setulate spines forming posterior row. Maxillula (figs 20B-D) medial lobe length 0.8 lateral lobe length, width 0.73 lateral lobe width, with 3 pappose setae; with 2 'accessory' setae, one between distolateral pappose setae and one between distomedial pappose setae, 'accessory' setae distally denticulate. Lateral lobe distal margin with 20 smooth robust setae, distal setal row with 5 robust setae; ventral face with 3 plumose setae. Maxilla (figs 20E-G) medial lobe width 1.29 outer lateral lobe width. Outer lateral lobe width subequal to inner lateral lobe. Maxilliped (figs 20H-I) endite with 7 coupling hooks on right side; dorsal ridge with 25-27 large distally denticulate plumose setae (approximately). Palp article 4 subcircular, article 5 length 0.7 article 4 length.

Pereopod I (figs 21D–H) dactylus projecting beyond palm, length 1.1 palm length; distoventral margin



Figure 18. *Synamphisopus doegi*, sp. nov. Paratype male (AM P61434), paratype female (AM P61435). A–B, male head, dorsal and lateral views. C, male antennula. D, male antennula article 3 rudimentary second flagellum. E, male antennula distal articles. F–H, male antenna. I, female head lateral view. J–K, female antennula. Scale bar 0.5 mm.



Figure 19. *Synamphisopus doegi*, sp. nov. Paratype male (AM P61434). A–E, right mandible. F–J, left mandible. Scale bar 0.5 mm.



Figure 20. *Synamphisopus doegi*, sp. nov. Paratype male (AM P61434). A, paragnaths. B–D, maxillula. E–G, maxilla. H–I, maxilliped. Scale bar 0.5 mm.



Figure 21. *Synamphisopus doegi*, sp. nov. Paratype female (AM P61435), paratype male (AM P61434). A–C, female pereopod I. D–H, male pereopod I. Scale bar 1 mm.



Figure 22. *Synamphisopus doegi*, sp. nov. Paratype male (AM P61434), paratype female (AM P61435). A, male pereopod II. B–C, male pereopod IV. D, female pereopod IV. E–G, male pereopod VII, including proximal articles, with penes. Scale bar 1 mm.

spines positioned along 0.59 total length. Propodus dorsal margin setae present in several groups between proximal and distal margin. Propodal palm without stout denticulate setae. Basis ventrodistal margin with 1 elongate seta. *Pereopod* IV (figs 22B–C) propodus ventral margin with 2 robust setae distinctly larger than others. *Penes* (fig. 22G) length 0.37 body width at pereonite 7, with setae on tip.

Pleopod I length 0.11 body length; exopod length 2.25 width; endopod length 2.28 width, 0.82 exopod length. *Pleopod* II exopod length 2.25 width; exopod distal article length 0.37 exopod length; endopod length 1.91 width, 0.63 exopod length. *Pleopod* III exopod



Figure 23. *Synamphisopus doegi*, sp. nov. Paratype male (AM P61434). A, pleopod I. B–E, pleopod II appendix masculina and endopod. Scale bar 0.5 mm.

length 1.75 width; exopod distal article length 0.35 exopod length; endopod length 0.78 exopod length. *Pleopod* IV exopod length 1.6 width; endopod length 2.03 width, 0.85 exopod length. *Pleopod* V exopod length 1.67 width; exopod distal article length 0.33 exopod length; endopod length 1.66 width, 0.61 exopod length. *Pleopod* II endopod appendix masculina with 48 setae on medial margin; length 0.59 pleopod length.

Uropod (fig. 25) total length 1.2 pleotelson length. Protopod length 2.73 width, 0.42 uropod total length. Endopod with 7–8 robust setae. Exopod length 0.69 endopod length; dorsal margin with 5 robust setae.

Sexual dimorphism and female characters. Antenna length 0.4 body length; flagellum with 39–40 articles. *Pereopod* I (figs 21A–C) propodal palm with 9 stout denticulate setae; robust simple setae basally inflated (difficult to see behind lateral plumes of setae). *Pereopod* IV (fig. 22D) propodus ventral margin with 3 broad based setae on ventral margin (with additional 4 submarginally). *Pleopod* protopod II lateral margin with 8 simple setae proximally. *Uropod* endopod dorsal margin with 5 robust setae. *Distribution.* Glenelg R. drainage, Grampians National Park.

Remarks. Synamphisopus doegi sp. nov. differs from S. ambiguus in several features, making the two species easy to distinguish. The pleotelson medial ridge of *S. doegi* extends ventrally and is produced in a setose lobe, rather than terminating dorsally. The uropod protopod distoventral margin robust setae are smooth rather than spinose. The appendix masculina medial margin setae tend to form two rows basally, although a remnant (or precursor) of these setae can be seen in the S. ambiguus. The pereopod I propodal palm of S. doegi males lacks a spine. This new species also lacks punctae on the dactylus of pereopod I that are distinctive in S. ambiguus. The two species differ in the degree of setation on the body, S. doegi generally being more setose than S. ambiguus in homologous positions.



Figure 24. Synamphisopus doegi, sp. nov. Paratype male (AM P61434). A-E, pleopods I-V. Scale bar 1 mm.



Figure 25. *Synamphisopus doegi*, sp. nov. Paratype male (AM P61434). A–E, pleotelson and uropod, ventral, dorsal, lateral and posterior views. F, uropod protopod distal margin, ventral view. G, uropod, medial view. Scale bar 0.5 mm.

Synamphisopus ambiguus (Sheard)

Figures 26-33

Amphisopus ambiguus Sheard, 1936: p.469, figs 1–18.

Synamphisopus ambiguus. Nicholls, 1943: 96, fig. 24.

Type material. Holotype. Victoria, Fish Falls, Mackenzie R., Grampians, 37°07′S, 142°26′E (estimate), SAM C 2115 (carcass), C 2116 (slides lost).

Material examined. Series from Vic., Grampians, collected G. Wilson, R. Wetzer and S. Keable, Sep 1999, preserved in 95% ethanol – top of Mackenzie Falls, Mackenzie R., 37°06.70'S 142°24.58'E (GPS), seep at side of path, hand sieve, pH 6.9, 8.9°C, 20 Sep, VIC-84, AM P61258 (1 ind.); Vic., base of Mackenzie Falls, Mackenzie R., 37°06.74'S 142°24.52'E (GPS), gravel, sand, mud under rocks in seeps, hand sieves, 20 Sep, VIC-85, AM P61259 (8 ind.); Vic., base of Fish Falls, Mackenzie R., 37°06.59'S 142°24.01'E (GPS), sand under roots of ferns in seeps to side of main falls near seep sources, hand sieves, hand and spoon, pH 6.6, 10.6°C, 20 Sep, VIC-86, AM P61260 (5 males, 3 females), AM P61440 (male bl 24.1 mm, dissected for illustration, SEM and description, collection details as



Figure 26. *Synamphisopus ambiguus*. Female (AM P61441), male (AM P61440). A–B, female head, lateral and ventral views. C–F, male antenna. G–H, male antennule. Scale bar 1 mm.

for P61260), AM P61441 (female bl 26.6 mm, dissected for SEM and description, collection details as for P61260), AM P61442 (male bl 28.2 mm, dissected for SEM and description, collection details as for P61260), AM P61443 (female bl 25.5 mm, dissected for SEM and description, collection details as for P61260); Vic., Stony Creek below Turret Falls on Twin Falls Trail, 37°09.41'S 142°29.90'E (GPS), from gravel under rocks, hand sieves, pH 6.7, 7.2°C, 21 Sep, VIC-89, AM P61261 (16 ind.); Vic., Stony Creek below Turret Falls on Twin Falls Trail, 37°07.93'S 142°30.26'E (GPS), fern roots at stream side, hand sieves, 21 Sep, VIC-90, AM P61262 (1 ind.); Vic., Stony Creek directly below Turret Falls on Twin Falls Trail, 37°09.66'S 142°29.83'E (GPS), from water weed, hand sieves, 21 Sep, VIC-92, AM P61268 (1 ind. and 1 carcass); Vic., base of Beehive Falls near Roses Gap, 36°58.54'S 142°27.01'E (GPS), under rocks in pool and leaf litter in stream, hand sieves, pH 4.6, 10.3°C, 22 Sep, VIC-97, AM P61269 (2 ind.). Vic., off Silverbrand Road, Stony Creek, Grampians, 37°09.20'S 142°29.67'E (map), T. Doeg and J. Read, 15 Nov 1994, site GR19, AM P54103 (1 male bl 26.2 mm, dissected); Vic., Stony Creek, near



Figure 27. Synamphisopus ambiguus. Male (AM P61440). A-C, left mandible. D-H, right mandible. Scale bar 0.5 mm.



Figure 28. *Synamphisopus ambiguus*. Male (AM P61440). A, paragnaths. B–C, maxillula. D–E, maxilla. F–H, maxilliped. I, left mandible molar. J, right mandible molar. Scale bar 0.5 mm.



Figure 29. Synamphisopus ambiguus. Male (AM P61440). A-F, pereopod I. Scale bar 1 mm.

Halls Gap, Grampians, 37°09.72′S 142°29.74′E (map), altitude 510 metres, kick sample, D. Crowther, 10 Dec 1998, 98-220 Site 87, AM P61294 (1 ind.), AM P61295 (2 ind., collection details as for AM P61294 but not kick sample); Vic., 2 km from Zumsteins along road to Halls Gap, Grampians, 37°05′S 142°25′E (estimate), under rocks in fine sand sprayed with water from small trickle over cliff (on uphill side of road) onto rock ledge below, J.H. Bradbury, 29 Mar 1995, JHB VIC#24, AM P53150 (11 ind.); Vic., The Grampians (37°17′S, 142°33′E), A. Neboiss, 1 Oct 1954, NMV J44897 (3, labelled as *Phreatoicopsis terricola*); Vic., Briggs Bluff, Mt Rosea (36°59′S, 142°28′E), I.R. McCann, March 1957, NMV J44889 (1, labelled as *Phreatoicopsis terricola*).

Diagnosis. Pleotelson medial dorsal ridge with posterior obtuse angle, in lateral view projecting

only to posterior margin above level of widely cleft medial lobe. Mandible palp article 2 with ventrolateral setae shorter than distal article; spine row shaft anterior margin without separate dentate spines. Maxillula medial lobe tapering distally. *Maxilliped* palp article 5 elongate, length 2.4 width, lateral margin linear. Pereopod I of adult male dactylus ventral margin sinuous, lateral face with regularly spaced setal pits; propodal palm with setal rows on proximal medial and lateral surfaces, with large spine midlength. Pereopods II-IV basis proximal dorsal margin with single robust seta; pereopod IV propodus ventral margin convex; pereopod VII propodus distomedial margin with setae shorter than articular plate or dactylar claw. Pleopod II appendix



Figure 30. Synamphisopus ambiguus. Female (AM P61441). A-D, pereopod I. Scale bar 1 mm.

masculina not projecting beyond margin of proximal exopod article, with 2 flattened tubercles on distomedial margin. *Uropod* protopod distoventral margin with 3 robust spinose setae.

Description based on male. Coloration in life white (colourless) legs, body slate gray-brown, head with tiny white eyespot; similar in 95% ethanol but eyespot black.

Eyes (fig. 26A) maximum diameter 0.12 head depth.

Pleonites 1–4 relative lengths subequal, width 0.55 composite length in dorsal view.

Pleotelson (figs 33A–E, G) lateral length 0.94 depth; dorsal length 1.46 width; depth 1.64 pereonite 7 depth. Medial lobe width 0.54 pleotelson width, greatest length 0.02 pleotelson total length.

Antennula (figs 26G–H) length 0.09 body length, with 11 articles. Article 5 length 1.29 width. Article 6 length 0.75 width. Numerous tiny aesthetascs on article 8 to terminal article. Terminal article length subequal to


Figure 31. *Synamphisopus ambiguus*. Male (AM P61440), female (AM P61441). A–B, male pereopod II. C–D, male pereopod IV. E, female pereopod IV. F–H, male pereopod VII, including proximal articles, with penes. I–J, male pleopod II appendix masculina and endopod. Scale bar 1 mm.



Figure 32. Synamphisopus ambiguus. Male (AM P61440). A-E, pleopods I-V. Scale bar 1 mm.

penultimate article length, 1.36 width. *Antenna* (figs 26C–F) length 0.51 body length. Flagellum length 0.67 total antenna length, with 54 articles (40 articles in illustration: Sheard, 1936).

Mouthfield clypeus width 0.46 head width. *Mandible* (figs 27, 28I–J) palp length 0.88 mandible length, article 3 with 23 setae, cuticular combs absent; separate

distal group of setae present; articles 1–2 with groups of long setae (longer than half article length) on ventral lateral margins. Left spine row with 36 spines (approximately but basally fused so how many bifurcate unclear), first spine separated from remaining spines. Right spine row with 33 spines (approximately, basally fused so how many bifurcate unclear). Molar process



Figure 33. *Synamphisopus ambiguus*. Male (AM P61440). A–C, G, pleotelson, dorsal, lateral and ventral views. D–E, pleotelson and uropod, lateral view. F, uropod protopod distal margin, ventral view. H, pleopod I. Scale bar 1 mm.

spines absent. *Maxillula* (figs 28B–C) medial lobe length 0.76 lateral lobe length, width 0.5 lateral lobe width, with 4 pappose setae, with 1 'accessory' seta between central pappose setae, 'accessory' setae simple. Lateral lobe distal margin with 29 smooth robust setae, distal setal row with 4 robust setae; ventral face with 4 plumose setae. *Maxilla* (figs 28D–E) medial lobe width 1.86 outer lateral lobe width. Outer lateral lobe wider than inner lateral lobe. *Maxilliped* (figs 28F–H) endite with 5 coupling hooks on right side; dorsal ridge with at least 20 large distally-denticulate plumose setae. Palp article 4 elongate-distally expanded, article 5 length 1.09 article 4 length.

Pereopod I (figs 29A–F) dactylus only slightly shorter than palm, length 0.94 palm length. Propodus dorsal margin setae confined to single group at distal margin. Propodal palm with stout denticulate serrate setae. Basis ventrodistal margin lacking elongate setae. *Pereopod* IV (figs 31C–D) propodus ventral margin with 3 robust setae distinctly larger than others, central seta largest.

Penes (fig. 31H) length 0.5 body width at pereonite 7; setae absent.

Pleopods (figs 31I–J, 32) I length 0.15 body length; exopod length 2.88 width; endopod length 2.0 width, 0.61 exopod length. *Pleopod* II exopod length 2.79 width; exopod distal article length 0.3 exopod length; endopod length 2.98 width, 0.69 exopod length. *Pleopod* III exopod length 2.12 width; exopod distal article length 0.33 exopod length; endopod length 0.72 exopod length. *Pleopod* IV exopod length 2.4 width; endopod length 2.34 width, 0.75 exopod length. *Pleopod* V exopod length 1.83 width; exopod length of distal article 0.38 exopod length; endopod length 1.78 width, 0.67 exopod length. *Pleopod* II endopod appendix masculina with 23 setae on medial margin; length 0.38 pleopod length.

Uropod (figs 33D–E) total length 1.06 pleotelson length. Protopod length 3.46 width, 0.38 uropod total length. Endopod with 12 robust setae (including 5 at distal tip). Exopod length 0.76 endopod length; dorsal margin with 6 robust setae (including 3 at distal tip).

Sexual dimorphism and female characters. Antenna length 0.45 body length; flagellum with 42 articles. *Pereopod I* propodal palm with 20 stout robust conical setae. *Pereopod IV* propodus ventral margin with 5–6 broad based setae on ventral margin (and additional 3–5 submarginally); robust simple setae absent. *Pleopod* protopod II lateral margin with 4 simple setae proximally. *Uropod* endopod dorsal margin with 13 robust setae

Distribution. Stony Creek and Mackenzie R. drainages, and Beehive Falls, Grampians National Park, Victoria.

Remarks. Synamphisopus ambiguus populations vary in at least one feature. Specimens from Fish Falls on Mackenzie R. (the type locality) all have 3–4 robust setae on each side of the cleft pleotelson tip, while specimens from other locations

sometimes have more. Specimens from Stony Creek and from Mackenzie Falls (Mackenzie R. above Fish Falls) have 5–6 setae in this position, while most other specimens, including that from Beehive Falls to the north of the type locality, have 3–4 setae. Sheard (1936) states that the coxae of all legs are fused, that the fourth pereopod is not sexually differentiated and that appendix masculina lacks setae; our material does not support these observations.

Phreatoicidae Chilton

Phreatoicidae Chilton, 1891: 151.

Diagnosis. Head tubercles absent; antennal notch shallow, without posterior extension. Pleonite 1 pleura distinctly shallower than pleurae of pleonites 2–5. *Pleotelson* posterior margin entire, reflexed dorsally, produced. Antennal article 3 rudimentary second flagellum absent. Mandible right lacinia mobilis reduced, incorporated into spine row, with tooth or denticulated scale on anterior face; spine rows linear on pedunculate projection. Pereopod I merus dorsal projection shelf-like and U-shaped. Pereopods II-III propodus with articular plate on posterior side of limb; pereopod IV sexually dimorphic, prehensile in adult males. Pleopod exopods II-V with lateral proximal lobes; protopods medial margin without coupling hooks; protopods I-II lateral epipod absent, III-V lateral epipods lobe-like. Uropod rami distal tips pointed.

Remarks. The Phreatoicidae includes a diverse group of taxa, united by reduction of the right lacinia mobilis, which is fused into the distal member of the spine row. Additionally, the spine rows on both mandibles are pedunculate. The phreatoicid spine rows are notably different from fused spines found in the Synamphisopus + Phreatoicopsis clade (discussed above) because the individual bifurcate spines in the Phreatoicidae are distinct and aligned parallel in a dorsoventral plane. Other features that define the Phreatoicidae are homoplastic, being shared with members of the Amphisopodidae and Hypsimetopodidae. Material from the Grampians contains four species of Phreatoicidae that could not be assigned to any existing genera. The phylogenetic analysis shows that these species are monophyletic, but we cannot diagnose this clade with unambiguous apomorphic features, although three of the species have several synapomorphies. Accordingly, we introduce the genera Naiopegia gen. nov. and Gariwerdeus gen. nov. to accommodate these species.

Naiopegia gen. nov.

Type Species. Naiopegia xiphagrostis sp. nov.

Etymology. The genus name is compounded from the Greek words "Naio", meaning to dwell or inhabit, and "Pege" (f.) for spring.

Diagnosis. Cephalon without eyes, cuticle rugose with cuticular hairs, with elongate setae (longer than basal 2 articles of antennula), especially at ventrolateral margins; clypeal notch present (but weak). Typhlosole minimal, ventral invagination forming laminar projection in cross section. Pleotelson dorsal surface rugose with cuticular hairs, without abundant long setae; medial and lateral lobes distinct; lateral lobes rounded; medial lobe reflexed, projecting beyond lateral lobes, with 4 robust setae. Antennula with 6 (rarely 7) articles, penultimate article elongate and inflated, terminal article shorter than broad, not compound, much shorter than article 5. Antenna basal articles of flagellum with dense cuticular hairs. Mandible palp articles 1 and 2 with row of elongate setae (longer than distal article); right lacinia mobilis anterior scale with 4 robust denticles. Maxilliped basis distal margin adjacent to palp insertion with elongate setae (longer than palp articles 1-3). Pereopod I not strongly dimorphic, propodus of male only somewhat broader than female and dorsal margin not produced proximally; propodal palm concave, spines absent, with stout conical robust setae in male, denticulate robust setae in female, cuticular fringe weakly developed, setal ridge absent. Pereopods I-VII proximal portions (basis, merus, ischium) with numerous elongate setae (many longer than ischium) on dorsal and ventral margins; basis dorsal ridge in cross section rounded on pereopod V, angular on pereopods VI-VII. Pleopod II endopod appendix masculina proximal half of shaft solid and rodlike, indented in ventral cross section, lacking setae on lateral or medial margins. Uropod protopod distoventral margin with 1 robust spinose seta and several simple setae.

Remarks. We introduce a monotypic genus because *Naiopegia xiphagrostis* gen. nov., sp. nov. shares no unambiguous synapomorphies with other genera of the Phreatoicidae. This species has a typical phreatoicid body and limb form, but no species of this family have cuticular hairs on the basal articles of the antennae. Its "reduced" antennule, another diagnostic and apomorphic character, is broadly homoplastic, being found in taxa outside of the Phreatoicidae, such as *Crenisopus* and some species of *Mesamphisopus*. Species of *Gariwerdeus* gen. nov. also

have similar six-articled antennulae (see below), but with a differing composition of the distal two articles. *Naiopegia* lacks the distinctively formed pleotelson of *Gariwerdeus* and is similar in this regard to other phreatoicids. Of the blind, but more typical phreatoicids, the cross sectional shape of the appendix masculina as well as the cuticular hairs on the antennula would separate *Naiopegia* gen. nov. from *Crenoicus*.

Naiopegia xiphagrostis sp. nov.

Figures 34-41

Material examined. Holotype. Victoria, tiny spring-fed tributary of Stony Creek below Turret Falls, at bridge on Twin Falls Trail, Grampians National Park, 37°07.93'S 142°30.26'E (GPS), sand with mud and detritus in minimal seep flow among thicket of sword grass, hand sieve, S. Keable, 21 Sep 1999, VIC-91, NMV J40732 (male bl 12.0 mm, ethanol preserved).

Paratypes. As for holotype. AM P61270 (4 males), AM P61424 (1 male bl 11.7 mm, dissected for illustration, SEM and description), AM P61425 (1 female bl 7.4 mm, dissected for SEM and description), AM P61426 (male bl 11.1 mm, used to supplement description and SEM).

Etymology. The species name is a noun in apposition from the Greek compound name for sword grass, "xiphagrostis", and refers to the vegetation found at the type locality.

Description based on male. Coloration in life with white patches on head in eye region, gray dorsum darker at edges; in 95% ethanol, uniform gray-white.

Head (figs 35B–C) length subequal to width in dorsal view; width 0.81 pereonite 1 width; surface with dense cuticular hairs; setae sparse but forming dense row along ventral margin.

Pereon broad, width 1.2 head width; with scattered roughness (cuticular hairs).

Pleonites in dorsal view 2–4 respective lengths more than half length of pleonite 5; *pleonites* 1–4 relative lengths subequal, width 1.0 composite length in dorsal view.

Pleotelson (figs 41A–D) lateral length 0.12 body length, 0.77 depth; dorsal length 1.22 width; depth 1.5 pereonite 7 depth. Dorsal surface without abundant long setae. Medial lobe width 0.36 pleotelson width, greatest length 0.22 pleotelson total length. Lateral lobes in lateral view curving dorsally, in dorsal view rounded, not extending posteriorly to level of medial lobe, medial length 0.08 pleotelson total length, with 1 robust setae. Ventral margin anterior to uropods with 8 smooth setae, posterior seta subequal to anterior adjacent setae.

Antennula (figs 35B, D) length 0.07 body length, with 6 articles. 2–3 tiny aesthetascs on articles 5–6. Articles 5 and 6 width subequal to article 4. Antenna (figs 35C, E, F–G) length 0.27 body length. Flagellum length 0.66 total antenna length, with 20 articles.



Figure 34. Naiopegia xiphagrostis gen. nov., sp. nov. Holotype male (NMV J40732), lateral view. Scale bar 1 mm.

Mouthfield clypeus width 0.56 head width. Mandible (fig. 36) palp length 0.74 mandible length; article 3 with 7 setae; separate distal group of setae absent; articles 1-2 with elongate setal row. Left incisor process with 2 distal cusps and 1 on dorsal margin (shoulder for fourth cusp apparent but not forming full cusp). Left spine row with 7 bifurcate spines, without additional spines between pedunculate projection and molar. Right spine row with 7 bifurcate spines in addition to lacinia mobilis, without additional spines between pedunculate projection and molar. Molar process longer than wide; 3-4 setulate spines forming posterior row. Maxillula (figs 37B-C) medial lobe length 0.83 lateral lobe length; width 0.65 lateral lobe width. Lateral lobe distal margin with 3 denticulate robust setae, 7 smooth robust setae. Maxilla (figs 37D-F) medial lobe width 0.71 outer lateral lobe width. Maxilliped (figs 37G-H) endite with 3 receptaculi on right side; dorsal ridge with 10-13 large distally denticulate plumose setae (merging with subdistal biserrate setae). Palp insertion on basis ventral surface with 10 subdistal smooth setae (some forming row).

Pereopod I (figs 38A–B) dactylus length 0.9 palm length; ventrodistal margin with row of sharp spines along 0.37 total length. Propodus dorsal margin with 21 setae in several groups between proximal and distal margin (excluding distal group); proximal region not protruding. Propodal palm concave; stout denticulate setae absent; with 9 stout robust simple conical setae; elongate broad based setae absent. Basis ventrodistal margin with 10 elongate setae. *Pereopod* IV (figs 39C–D) dactylus shorter than propodal palm. Propodus with 7 broad based setae on ventral margin, 2 distinctly larger than others; articular plate subequal in length to dactylar claw. *Pereopods* V–VII (figs 39F–G) basis dorsal ridge in cross section rounded on pereopod V, angular on pereopods VI–VII.

Penes (fig. 39I) length 0.25 body width at pereonite 7, distally tapering.

Pleopod I (figs 40, 39H) exopod distal margin rounded, medial margin concave from proximal to distal half, subparallel to lateral margin, dorsal surface lacking setae. *Pleopod* II endopod appendix masculina length 0.61 pleopod length, distal tip truncate; with 5 setae on margin.

Uropod (figs 41A–E) total length 1.08 pleotelson length. Protopod length 0.42 uropod total length; ventral margin with anteriorly-projecting somewhat rigid long setae, forming dense longitudinal row, setae medially robust and distally spinose; distoventral margin with 1 robust spinose seta and 2 simple setae. Exopod length 0.87 endopod length.

Sexual dimorphism, female differences. Antennula length 0.06 body length, with 6–7 articles, article 5 length greater than article 6. Antenna length 0.34 body length, flagellum 0.61 total antenna length, with 16 articles (incomplete, distal most articles missing). Pereopod I (figs 38C–E) dactylus length 0.95 palm length; ventrodistal margin with row of 8 sharp spines, along 0.33 total length; propodal palm with 7 stout robust



Figure 35. *Naiopegia xiphagrostis* gen. nov., sp. nov. Paratype male (AM P61424). A–B, head, antennula, antenna proximal articles, dorsal view. C, head, ventral view. D, antennula distal articles. E, antenna proximal articles, antennula distal articles. F–G, antenna flagellum distal and proximal articles. Scale bar 0.5 mm.

simple conical setae; basis ventrodistal margin with 8 elongate setae. *Pereopod* IV (fig. 39E) propodus articular plate shorter than dactylar claw. *Uropod* length 0.9 pleotelson length, 0.47 uropod total length, exopod length 0.74 endopod length.

Distribution. Known only from small spring-fed tributary of Stony Creek below Turret Falls, at bridge on Twin Falls Trail, Grampians National Park.

Remarks. This species is similar to most other phreatoicids, save for a few distinctive features and the lack of eyes. The elongate setae on all limbs and the inflated, distally-broadened antennular article 5 with a tiny, but distinct article 6 are diagnostic for this species. The antennular details and the plesiomorphic retention of a large reflexed medial lobe on the pleotelson also distinguish it from species of *Gariwerdeus* gen. nov.



Figure 36. *Naiopegia xiphagrostis* gen. nov., sp. nov. Paratype male (AM P61426). A–C, left mandible. D–H, right mandible. Scale bar 0.1 mm.



Figure 37. *Naiopegia xiphagrostis* gen. nov., sp. nov. Paratype male (AM P61424) A, G–H, paratype male (AM P61426) B–F. A, paragnaths. B–C, maxillula. D–F, maxilla. G–H, maxilliped. Scale bar 0.2 mm.



Figure 38. *Naiopegia xiphagrostis* gen. nov., sp. nov. Paratype male (AM P61424), paratype female (AM P61425). A–B, male pereopod I. C–E, female pereopod I. Scale bar 0.5 mm.

The number of distal antennulae articles may be variable among adults of *N. xiphagrostis* sp. nov. – one female has 6 on one side and 7 on the other.

Gariwerdeus gen. nov.

Type Species. Gariwerdeus turretensis sp. nov.

Etymology. The Grampians (an English name deriving from a mountain range in Scotland) National Park is given the name "Gariwerd" by the indigenous Jardwadjali and Djab Wurrung people. The species of this genus appear to be ubiquitious in streams, springs or groundwater seeps within the Park, and thus should bear the original name for this region. *Gariwerdeus* is treated as a masculine noun.

Diagnosis. Cephalon without eyes; clypeal notch absent. Typhlosole minimal, ventral invagination simple (either laminar or 'u' shaped in cross section). Pleotelson dorsal surface with abundant long setae and rugose with dense cuticular hairs; medial and lateral lobes distinct; posterior margin reflexed dorsally, medial lobe compressed anteriorly, shorter than lateral lobes; lateral lobes acutely angular in dorsal or ventral view, in lateral view depressed ventrally, protruding posteriorly from insertion of uropods. Antennula with 6 or fewer articles, distal articles inflated. Antenna flagellum proximal articles without dense cover of cuticular hairs. Mandible palp article 2 with elongate setal row (setae longer than distal article). Pereopod I propodal palm concave,



Figure 39. *Naiopegia xiphagrostis* gen. nov., sp. nov. Paratype male (AM P61424), paratype female (AM P61425). A–B, male percopod II. C–D, male percopod IV. E, female percopod IV. F–G, male percopod VII. H, male pleopod II appendix masculina. I, male percopod VII proximal articles, with penes. Scale bar 0.5 mm.



Figure 40. *Naiopegia xiphagrostis* gen. nov., sp. nov. Paratype male (AM P61424). A–E, pleopods I–V. Scale bar 0.5 mm.



Figure 41. *Naiopegia xiphagrostis* gen. nov., sp. nov. Paratype male (AM P61424). A–D, pleotelson and uropod, lateral, medial and ventral views. E, uropod protopod distoventral margin robust setae. F, pleotelson distal margin, dorsal view. Scale bar 0.5 mm.

spines absent, with stout conical robust, elongate or denticulate setae, setal ridge absent. *Pereopods* I–VII proximal portions (basis, merus, ischium) with numerous elongate setae (many longer than ischium) on dorsal and ventral margins; pereopod VII basis dorsal ridge in cross section angular. *Pleopod* II endopod appendix masculina proximal half of shaft solid and rod-like, indented in ventral cross section, lacking setae on lateral or medial margins. *Uropod* protopod distoventral margin with 1–2 robust spinose seta and several simple setae.

Remarks. In addition to having a setose, light coloured and rugose cuticle, species of *Gariwerdeus* gen. nov. can be recognised most readily by their greatly reduced pleotelson tip, giving an almost truncate appearance to the end of the body. This feature can be seen when collecting specimens in the field. All species of *Gariwerdeus* are also blind. The antennula is pauciarticulate, similar to that of *Naiopegia* gen. nov., but the distal articles differ in all of the *Gariwerdeus* species. Our cursory investigation of the Grampians has detected three species in this genus.

Gariwerdeus turretensis sp. nov.

Figures 42-49

Material examined. Holotype. Victoria, Stony Creek directly above Turret Falls on Twin Falls Trail, Grampians National Park, 37°09.62'S 142°29.82'E (GPS), sand, silt and fern roots at edge of creek, hand sieve, S. Keable, 21 Sep 1999, VIC-93, NMV J40733 (male bl 7.4 mm).

Paratypes. As for holotype. AM P61271 (20 ind.), AM P61427 (male bl 8.6 mm, dissected for illustration, SEM and description), AM P61428 (female bl 8.4 mm, dissected for SEM and description), AM P61429 (male bl 8.3 mm, used to supplement description and SEM).

Other material. Series from Vic., Stony Creek, Grampians, hand sieves, collected G. Wilson, R. Wetzer and S. Keable, 21 Sep 1999, preserved in 95% ethanol - below Turret Falls on Twin Falls Trail, 37°09.41'S 142°29.90'E (GPS), from vegetation at edge of stream in sand, pH 6.7 (out of calibration), 7.2°C, VIC-89, AM P61273 (12 ind.); below Turret Falls on Twin Falls Trail, 37°07.93'S 142°30.26'E (GPS), fern roots at stream side, VIC-90, AM P61274 (male, female); directly below Turret Falls on Twin Falls Trail, 37°09.66'S 142°29.83'E (GPS), from sphagnum at waters edge, hand sieves, VIC-92, AM P61272 (12 ind.) and NMV J40734 (male, 2 females). Vic., Creek, Grampians, 37°09.72'S Stony 142°29.74'E (map), stream riffles, altitude 510 metres, kick sampling, D. Crowther, 10 Dec 1998, 98-220 Site 87, AM P61257 (male).

Etymology. The name refers to Turret Falls on Stony Creek in The Grampians National Park, around which this species was collected.

Diagnosis. Pleotelson tip medial lobe lacking robust sensillate setae but with 8 fine simple setae. Antennula article 6 inflated and bulbous, terminal two segments with one aesthetasc each, article 5 length subequal to article 6 length. Mandible right lacinia mobilis with 1 row of denticles. Pereopod I of male dactylus posterodistal margin smooth; propodus dorsal margin proximally produced, greatly expanded beyond dorsal margin of carpus; propodal palm cuticular fringe weakly developed. *Pereopods* II-IV basis dorsal margin elongate setae in row, not clustered. Pleopod II endopod appendix masculina distal tip truncate, with 3 setae on margin. Uropodal protopod distoventral margin with 1 robust spinose seta and 7 simple setae.



Figure 42. Gariwerdeus turretensis gen. nov., sp. nov. Holotype male (NMV J 40733), lateral view. Scale bar 1 mm.



Figure 43. *Gariwerdeus turretensis* gen. nov., sp. nov. Paratype male (AM P61427) A–D, H, paratype female (AM P61428) E–G. A–B, H, male head, antenna, antennule, lateral, dorsal and ventral views. C–D, male antenna flagellum, distal and proximal articles. E, female head, antenna, antennula, dorsal view. F, female antennula, distal articles. G, ciliate protozoan epibiont (*Vorticella* sp.) on female antenna. Scale bar 0.5 mm.

Description based on male. Coloration in life translucent with dark patches on posterior pleonites, white dorsum anteriorly, head white in eye region; in 95% ethanol eye region lacking colour, gray-white head to pereonite 6, pereonite 7 to pleotelson light brown.

Head (fig. 43B) length subequal to width in dorsal view; width 0.85 pereonite 1 width; surface smooth and shiny (with scattered cuticular combs), dorsal setae sparse.

Pereon narrow, width near head width (1.18 head width); smooth. Typhlosole minimal, ventral



Figure 44. *Gariwerdeus turretensis* gen. nov., sp. nov. Paratype male (AM P61429), paratype female (AM P61428). A–B, male left mandible. C, male paragnaths. D, male right mandible. E–F, female right mandible palp. Scale bar 0.05 mm.

invagination forming laminar projection in cross section.

Pleonites in dorsal view 2–3 respective lengths less than half length of pleonite 5, *pleonite* 4 length more than half length of pleonite 5; *pleonites* 1–4 relative lengths unequal, increasing in length from anterior to posterior, width 0.88 composite length in dorsal view.

Pleotelson (figs 49A–D, G) lateral length 0.13 body length, 0.93 depth; dorsal length 1.3 width; depth 1.47

pereonite 7 depth. Dorsal surface with abundant long setae. Medial lobe width 0.27 pleotelson width, greatest length 0.04 pleotelson total length. Lateral lobes medial length 0.04 pleotelson total length, without robust sensillate setae. Ventral margin anterior to uropods with 4–6 denticulate and smooth setae (posterior seta smooth, anterior setae weakly denticulate), posterior seta smaller than anterior adjacent setae (thicker but shorter).



Figure 45. *Gariwerdeus turretensis* gen. nov., sp. nov. Paratype male (AM P61429). A, maxillula. B–C, maxilla. D–E, maxilliped. Scale bar 0.2 mm.



Figure 46. *Gariwerdeus turretensis* gen. nov., sp. nov. Paratype male (AM P61427) A, paratype female (AM P61428), paratype male (AM P61429) B. A, B, male pereopod I. C–E, female pereopod I. Scale bar 0.5 mm.

Antennula (figs 43E–F) length 0.11 body length, with 6 articles. Single tiny aesthetasc on article 5 to terminal article. Antenna (figs 43B–D) length 0.34 body length. Flagellum length 0.57 total antenna length, with 16 articles.

Mouthfield clypeus broader medially, width 0.65 head width. Mandible (fig. 44) palp length 0.8 mandible length; article 3 with 11 setae; separate distal group of setae present; articles 1-2 with elongate setal row. Left spine row with 7-8 bifurcate spines, without additional spines between pedunculate projection and molar. Right spine row with 8 bifurcate spines, without additional spines between pedunculate projection and molar. Molar process setulate spines forming posterior row (2 tiny on right). Maxillula (fig. 45A) medial lobe length 0.86 lateral lobe length; width 0.67 lateral lobe width. Lateral lobe distal margin with 5 denticulate robust setae, 7 smooth robust setae. Maxilla (figs 45B-C) medial lobe width 0.56 outer lateral lobe width. Maxilliped (figs 45D-E) endite with 2 receptaculi on right side; dorsal ridge with 12 large distally denticulate plumose setae. Palp insertion on basis ventral surface without subdistal smooth setae.

Pereopod I (figs 46A–B) dactylus length 1.07 palm length. Propodus dorsal margin setae confined to single group at distal margin. Propodal palm convex to straight; stout denticulate setae absent; with 4 basally inflated stout robust simple setae; with 3 elongate broad based setae. Basis ventrodistal margin with 7 elongate setae. *Pereopod* IV (figs 47B–C) dactylus length subequal to propodal palm. Propodus with 3 broad based setae on ventral margin, none distinctly larger than others; articular plate shorter than dactylar claw. *Pereopods* V–VII (fig. 47E) basis dorsal ridge in cross section angular.

Penes (fig. 47F) length 0.26 body width at pereonite 7, distally tubular.

Pleopod (figs 48, 47G, 49H) I exopod distal margin rounded; medial margin concave from proximal to distal half, subparallel to lateral margin; dorsal surface lacking setae. *Pleopod* II endopod appendix masculina length 0.59 pleopod length.



Figure 47. *Gariwerdeus turretensis* gen. nov., sp. nov. Paratype male (AM P61429), paratype female (AM P61428). A, male pereopod II. B–C, male pereopod IV. D, female pereopod IV. E–F, male pereopod VII, including proximal articles, with penes. G, male pleopod II appendix masculina and endopod. Scale bar 0.5 mm.

Uropod (figs 49C–D, F–G) total length 1.04 pleotelson length. Protopod length 0.36 uropod total length; dorsomedial margin in dorsal view strongly concave laterally, margin setae absent. Exopod length 0.63 endopod length.

Sexual dimorphism, female differences. Antenna length 0.31 body length, flagellum length 0.63 total antenna length, with 17 articles. *Pereopod* I (figs 46C–E) dactylus length 1.13 palm length; propodal palm with 5 stout denticulate serate setae, 2 stout robust conical simple setae and 3 elongate broad based setae. *Uropod* length 1.06 pleotelson length, protopod length 0.44 uropod total length, exopod length 0.8 endopod length.

Distribution. Stony Creek, above and below Turret Falls, Grampians National Park.

Remarks. Gariwerdeus turretensis sp. nov. is easily distinguished from other species in the genus and from *Naiopegia xiphagrostis* sp. nov. by the enlarged male pereopod I propodus, much larger than males of the other species where the first pereopods of males resemble those of females. A short, almost truncate pleotelson with a highly abbreviated medial lobe that lacks robust setae, and an inflated article 6 on the antennula, also serve to identify this species.



Figure 48. *Gariwerdeus turretensis* gen. nov., sp. nov. Paratype male (AM P61427). A-E, pleopods I-V. Scale bar 0.5 mm.

Gariwerdeus beehivensis sp. nov.

Figures 50-57

Material examined. Holotype. Victoria, among roots of treefern at the base of Beehive Falls, Mud Hut Creek, near Roses Gap, Grampians National Park, 36°58.54'S 142°27.01'E (GPS), hand sieves, pH 4.6, 10.3°C, G. Wilson, R. Wetzer and S. Keable, 22 Sep 1999, VIC-97, NMV J40735 (male bl 7.3 mm).

Paratypes. All lots collection details as for holotype. AM P61276 (39 ind., including male bl 7.8 mm, female bl 5.4 mm used to supplement description), AM P61430 (male bl 8.7 mm, dissected for illustration, SEM and description), AM P61431 (female bl 5.9 mm, dissected for SEM and description).

Other material. Series from Vic., Grampians, collected hand sieves, G. Wilson, R. Wetzer and S. Keable, Sep 1999, preserved in 95% ethanol – base of Fish



Figure 49. *Gariwerdeus turretensis* gen. nov., sp. nov. Paratype male (AM P61429), paratype female (AM P61428). A–D, G, male pleotelson and uropod, dorsal, ventral and lateral views. E, suctorian ciliate protozoan epibiont on male uropod. F, male uropod protopod distal margin, ventral view. H, female pleopod II. Scale bar 0.5 mm.



Figure 50. Gariwerdeus beehivensis gen. nov., sp. nov. Holotype male (NMV J40735), lateral view. Scale bar 1 mm.



Figure 51. *Gariwerdeus beehivensis* gen. nov., sp. nov. Paratype male (AM P61430), paratype female (AM P61431). A, male head, dorsal view. B, female antennula distal articles. C, male antenna proximal articles. D, male antenna flagellum articles. E, female antennula, dorsal view. Scale bar 0.5 mm.



Figure 52. *Gariwerdeus beehivensis* gen. nov., sp. nov. Paratype male (AM P61430). A, D–E, left mandible. B–C, right mandible. Scale bar 0.1 mm.

Falls, Mackenzie R., 37°06.59'S 142°24.01'E (GPS), from reedy pool close to main falls, pH 6.6, 10.6°C, 20 Sep, VIC-86, AM P61277 (male, female); S side of Goulton Gorge, 36°55.89'S 142°25.09'E (GPS), gravel from roots of trees and grasses half way up steep water course, pH 6.7, 14.3°C, 22 Sep, VIC-98, AM P61278 (30 ind.); Goulton Creek on west side of Pohlner Road, 36°58.35'S 142°24.83'E (GPS), roots and sediment, pH 6.1, 17.1°C, 22 Sep, VIC-99, AM P61279 (18 ind.) and NMV J40736 (male, 2 females).

Etymology. This species name is derived from the type locality, Beehive Falls (on Mud Hut Creek) in The Grampians National Park.

Diagnosis. Pleotelson medial lobe with 2 robust smooth setae and several small simple setae. *Antennula* terminal segment inflated and bulbous; article 5 distal articulation rudimentary, length less than article 6 length, lacking aesthetasc. *Mandible* right lacinia mobilis with 1 row of denticles. *Pereopod* I of male dactylus ventrodistal margin with row of thin scale-like spines; propodus dorsal margin not produced proximally; propodal palm cuticular fringe strongly developed, extending along length of setal row. *Pereopods* II–IV basis dorsal margin elongate setae in row, not clustered. *Pleopod* II endopod appendix masculina distal tip broadly rounded, with 3 setae on margin. *Uropod* distoventral margin with 2 robust distally spinose setae, simple setae absent.

Description based on male. Coloration in life brown mottled (although brown colour mostly appears to be fine sediment) with white head, white patch in eye region.

Head (fig. 51A) length subequal to width in dorsal view; width 0.83 pereonite 1 width; dorsal surface with dense cuticular hairs, setae sparse.



Figure 53. *Gariwerdeus beehivensis* gen. nov., sp. nov. Paratype male (AM P61430). A, paragnaths. B–C, maxillula. D–E, maxilla. F–G, maxilliped. Scale bar 0.2 mm.

Pereon broad, smooth, width exceeding head width (1.55 head width). Typhlosole minimal, ventral invagination forming inverted 'u' shape in cross section.

Pleonites 2 length less than half length of 5 in dorsal view, 3–4 respective lengths more than half length of 5; 1–4 relative lengths unequal, increasing in length from anterior to posterior, width 1.44 composite length in dorsal view.

Pleotelson (figs 57A–D) lateral length 0.1 body length, 0.61 depth; dorsal length 1.03 width; depth 1.38 pereonite 7 depth. Dorsal surface with abundant long setae. Medial lobe width 0.33 pleotelson width, greatest length 0.07 pleotelson total length. Lateral lobes medial length 0.1 pleotelson total length. Ventral margin anterior to uropods with 5–9 denticulate setae (anterior 5 setae large and robust, posterior 4 less robust, interspersed with fine setae), posterior seta subequal to anterior adjacent setae.

Antennula (figs 51B, E) length 0.07 body length, with 6 articles, 1–2 tiny aesthetascs on terminal article. Antenna (figs 51A, D) length 0.21 body length. Flagellum length 0.57 total antenna length, with 12 articles.

Mouthfield clypeus broader on left side, width 0.44 head width. *Mandible* (fig. 52) palp length 0.64 mandible length; article 3 with 6 setae; separate distal group of setae present; articles 1–2 with elongate setal row. Right incisor process with 3 cusps. Left spine row with 8 spines, 6 bifurcate, total count includes 2 on margin between pedunculate projection and molar. Right spine row with 10 spines, 8 bifurcate, total count including 2 on margin between pedunculate projection and molar. Molar process length subequal to width;



Figure 54. *Gariwerdeus beehivensis* gen. nov., sp. nov. Paratype male (AM P61430), paratype female (AM P61431). A–B, E, male pereopod I. C–D, female pereopod I. Scale bar 0.5 mm.

complex setulate spines forming posterior row (left) or ciliated spines forming posterior row (right, 2). Maxillula (figs 53B–C) medial lobe length 0.82 lateral lobe length; width 0.73 lateral lobe width. Lateral lobe distal margin with 3 denticulate robust setae, 9 smooth robust setae. Maxilla (figs 53D–E) medial lobe width 1.0 outer lateral lobe width. Maxilliped (figs 53F–G) endite with 3 receptaculi on right side; dorsal ridge with 10 large distally denticulate plumose setae. Palp insertion on basis ventral surface with 1 subdistal smooth seta.

Pereopod I (figs 54A–B, E) dactylus length subequal to palm, length 1.03 palm length; ventrodistal margin thin scale-like spines along 0.28 total length of margin. Propodus dorsal margin with 10 setae in several groups between proximal and distal margin (excluding distal group). Propodal palm sinuate; cuticular fringe weakly developed; stout denticulate setae absent; with 12 stout robust simple conical setae; elongate broad based setae absent. Basis ventrodistal margin with 9 elongate setae in male. *Pereopod* IV (figs 55B–C) dactylus length subequal to propodal palm; distal accessory claw-spines absent. Propodus with 5 broad based setae on ventral margin, 3 distinctly larger than others; articular plate shorter than dactylar claw. *Pereopods* V–VII (fig. 55E) basis dorsal ridge in cross section rounded on pereopod V, angular on pereopods VI–VII.

Penes (fig. 55F) length 0.33 body width at pereonite 7, distally tapering.

Pleopod (figs 56, 57G–I) I exopod distal margin pointed, medial margin sinuate – divergent from lateral margin along most of length, dorsal surface with setae. *Pleopod* II endopod appendix masculina length 0.55 pleopod length.

Uropod (figs 57D–F) total length 1.11 pleotelson length. Protopod length 0.39 uropod total length; dorso-medial margin in dorsal view parallel to lateral margin, margin setae present distally. Exopod length 0.68 endopod length.

Sexual dimorphism, female differences. Antenna length 0.25 body length. Flagellum length 0.52 total antenna length, with 11 articles. *Pereopod* I (figs 54C–D) dacty-lus length 0.93 palm length, ventrodistal margin with 6 narrow scale-like spines, along 0.37 total length;



Figure 55. *Gariwerdeus beehivensis* gen. nov., sp. nov. Paratype male (AM P61430), paratype female (AM P61431). A, male pereopod II. B–C, male pereopod IV. D, female pereopod IV. E–F, male pereopod VII, including proximal articles, with penes. Scale bar 0.5 mm.

propodal palm with 9 stout robust conical simple setae; basis ventrodistal margin with 7 elongate setae. *Uropod* protopod length 0.46 uropod total length; exopod length 0.83 endopod length.

Distribution. Beehive Falls, Mud Hut and Goulton Creek drainages and Fish Falls (Mackenzie R.), Grampians National Park.

Remarks. Several characters distinguish *Gariwerdeus beehivensis* sp. nov. from other species of the genus: the 2 inflated distal antennular segments have only a rudimentary articulation with article 5 lacking aesthetascs, the head is rugose with many fine cuticular hairs, and the medial lobe of the pleotelson has 2–4 robust setae.

The specimens from Goulton Gorge and Goulton Creek (AM P61278–9) contains larger specimens than found in the types (males reaching a length of 11.8 mm versus 8.7 mm in type material). These larger specimens have more prominent medial and lateral lobes on the pleotelson, and have more robust setae on the medial lobe (4 versus 2). The same samples, however, have specimens of similar size to, and indistinguishable from, the type material. The male and female specimens from Fish Falls (AM P61277) are of similar size to the type material and have similar posterior pleotelson lobes; the male from this sample has four robust setae on the medial lobe and the female has three.



Figure 56. *Gariwerdeus beehivensis* gen. nov., sp. nov. Paratype male (AM P61430). A–E, pleopods I–V. Scale bar 0.5 mm.

Gariwerdeus ingletonensis sp. nov.

Figures 58-65

Material examined. Holotype. Vic., Ingleton Spring at picnic ground off Syphon Road, Grampians National Park, 37°18.17'S 142°22.01'E (GPS), in white sand at point where spring flows from under a rock, hand sieves, pH 4.7, 12.7°C, G. Wilson, R. Wetzer and S. Keable, 21 Sep 1999, VIC-94, NMV J40737 (male bl 7.2 mm).

Paratypes. All lots collection details as for holotype. AM P61280 (26 ind., including female bl 6.6 mm used to supplement description), AM P61432 (male bl 8.3 mm, dissected for SEM and description), AM P61433 (female bl 6.7 mm, dissected for SEM and description), AM P61444 (male bl 7.9 mm, dissected for pleopod illustrations), NMV J40738 (male, female, juvenile female).

Etymology. As in other species of Gariwerdeus,



Figure 57. *Gariwerdeus beehivensis* gen. nov., sp. nov. Paratype male (AM P61430), paratype female (AM P61431). A–D, male pleotelson and uropod, dorsal and lateral views. E, male uropod lateral view. F, male uropod protopod distal margin, ventral view. G, female pleopod I. H, male pleopod I. I, male pleopod II appendix masculina and endopod. Scale bar 0.25 mm.

this species is named after the type locality, Ingleton Spring, The Grampians National Park, in this case.

Diagnosis. Pleotelson medial lobe robust sensillate setae absent (but with 6 fine simple setae). Antennula with 5 free articles, articles 5 and 6 inflated, each with 1 aesthetasc, terminal segment with unexpressed articulation. *Mandible* right lacinia mobilis with 2 rows of denticles. *Pereopod* I dactylus ventrodistal margin with thin



Figure 58. *Gariwerdeus ingletonensis* gen. nov., sp. nov. Holotype male (NMV J40737), lateral view. Scale bar 1 mm.

truncate spines; propodus dorsal margin not produced proximally, palm cuticular fringe weakly developed. *Pereopods* II–IV basis dorsal margin elongate setae divided into proximal and distal cluster. *Pleopod* II endopod appendix masculina distal tip truncate, with 6 setae on margin. *Uropod* protopod distoventral margin with 2 robust distally spinose setae and 2 robust simple setae.

Description based on male. Coloration in life creamy white, head with bright white patch in eye region; in 95% ethanol, cream with lighter white patch in eye region.

Head (fig. 59D) length shorter than width in dorsal view; width 0.82 pereonite 1 width; surface with dense cuticular hairs and scattered setae.

Pereon broad, width exceeding head width (1.32 head width); smooth. Typhlosole minimal, ventral invagination forming laminar projection in cross section.

Pleonites 2–4 respective lengths more than half length of pleonite 5 in dorsal view; *pleonites* 1–4 relative lengths unequal, increasing in length from anterior to posterior, width 0.84 composite length in dorsal view.

Pleotelson (figs 65A–B) lateral length 0.11 body length, 0.7 depth; dorsal length 1.06 width; depth 1.5 pereonite 7 depth. Dorsal surface with abundant long setae. Medial lobe width 0.35 pleotelson width, greatest length 0.06 pleotelson total length. Lateral lobes medial length 0.14 pleotelson total length; lateral lobes robust sensillate setae absent. Ventral margin anterior to uropods with 5 denticulate and smooth setae (posterior setae weakly denticulate), posterior seta subequal to anterior adjacent setae (length subequal posterior seta slightly thicker). Antennula (figs 59E–H) length 0.1 body length, with 5 articles, 2 tiny aesthetascs on terminal article. *Antenna* (figs 59A–B) length 0.32 body length. Flagellum length 0.61 total antenna length, with 14–15 articles.

Mouthfield clypeus projecting anteriorly in medial region, width 0.48 head width. Mandible (fig. 60) palp length 0.64 mandible length; article 3 with 6 setae; articles 1-2 with elongate setal row. Left spine row with 11 spines, 8 bifurcate, total count including 3 on margin between pedunculate projection and molar. Right spine row with 15 spines, 9 bifurcate, including 6 on margin between pedunculate projection and molar. Molar process length subequal to width; complex setulate spines forming posterior row (both sides). Maxillula (figs 61B-D) medial lobe length 0.85 lateral lobe length; width 0.73 lateral lobe width. Lateral lobe distal margin with 4 denticulate robust setae, 8 smooth robust setae. Maxilla (figs 61E-F) medial lobe width 0.8 outer lateral lobe width. Maxilliped (figs 61G-H) endite with 4 receptaculi on right side; dorsal ridge with 13 large distally denticulate plumose setae. Palp insertion on basis ventral surface with 9 subdistal smooth setae (forming row).

Pereopod I (fig. 62A) dactylus length subequal to palm; ventrodistal margin thin denticulate spines along 0.51 total length. Propodus dorsal margin with 5 setae in several groups between proximal and distal margin (excluding distal group). Propodal palm concave, with 6 stout serrate setae and 4 elongate broad based setae. Basis ventrodistal proximal margin with 8–14 elongate setae. *Pereopod* IV (fig. 63B) dactylus length subequal to propodal palm. Propodus with 4 broad based setae on ventral margin, 1 distinctly larger than others; articular plate longer than dactylar claw. *Pereopods* V–VII (fig. 63C) basis dorsal ridge in cross section angular.



Figure 59. *Gariwerdeus ingletonensis* gen. nov., sp. nov. Paratype female (AM P61433), paratype male (AM P61432). A–B, female antennula and antenna. C–D, male head, antennula and antenna, dorsal view. E–F, male antennula distal articles. G, female antennula, dorsal view. H, female antennula distal articles. Scale bar 0.5 mm.



Figure 60. *Gariwerdeus ingletonensis* gen. nov., sp. nov. Paratype male (AM P61432). A–C, G, left mandible. D–F, right mandible. Scale bar 0.1 mm.

Penes (fig. 63F) length 0.19 body width at pereonite 7, distally tapering.

Pleopod I (figs 64, 63D–E) exopod distal margin rounded, medial margin concave from proximal to distal half, subparallel to lateral margin, dorsal surface lacking setae. *Pleopod* II endopod appendix masculina length 0.54 pleopod length.

Uropod (figs 65A, C–D) total length 1.22 pleotelson length. Protopod length 0.46 uropod total length; dorso-medial margin in dorsal view concave laterally, margin setae present distally. Exopod length 0.8 endopod length.

Sexual dimorphism, female differences. Antenna flagellum length 0.63 total antenna length, with 12–14 articles. Pereopod I (figs 62B–D) dactylus ventrodistal margin with 8 broad cuticular fringe spines. *Pereopod IV* propodus with 1 broad based seta on ventral margin. *Uropod* total length 1.1 pleotelson length; exopod length 0.89 endopod length.

Distribution. Ingleton Spring, Grampians National Park.

Remarks. An abbreviated antennule, consisting of only 5 segments, is the most distinctive feature of *Gariwerdeus ingletonensis* sp. nov. The inflated, distally expanding distal antennular segment is a composite of two segments with their articulation being unexpressed, but with two separate aesthetascs present. This morphology is similar to



Figure 61. *Gariwerdeus ingletonensis* gen. nov., sp. nov. Paratype male (AM P61432). A, paragnaths. B–D, maxillula. E–F, maxilla. G–H, maxilliped. Scale bar 0.2 mm.



Figure 62. *Gariwerdeus ingletonensis* gen. nov., sp. nov. Paratype male (AM P61432), paratype female (AM P61433). A, male pereopod I. B–D, female pereopod I. Scale bar 0.5 mm.

that seen in amphisopodid species, where the terminal antennular segment is also composite. Of the two species of *Gariwerdeus* that lack robust setae on the medial lobe of the pleotelson, *G. ingletonensis* has a more rounded posterodorsal margin of the pleotelson in lateral view than *G. turretensis* where the pleotelson appears almost truncate in lateral view.

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Figure 63. *Gariwerdeus ingletonensis* gen. nov., sp. nov. Paratype male (AM P61432). **A**, pereopod II. B, pereopod IV. C, F, pereopod VII, including proximal articles, with penes. D–E, pleopod II appendix masculina. Scale bar 0.5 mm.

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Figure 64. *Gariwerdeus ingletonensis* gen. nov., sp. nov. Paratype male (AM P61444). A–E, pleopods I–V. Scale bar 0.5 mm.



Figure 65. *Gariwerdeus ingletonensis* gen. nov., sp. nov. Paratype male (AM P61432). A–B, pleotelson and uropod, lateral and dorsal views. C, uropod, medial view. D, uropod protopod distal margin, ventral view. Scale bar 0.5 mm.

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