

# Systematics of the Phreatoicoidea

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## ABSTRACT

We provide a new cladistic analysis of the Phreatoicoidea, revising previously employed characters and including additional generic exemplars. This analysis reinforces the conclusion that many currently recognized families and subfamilies are not monophyletic. The 'primitive' family Amphisopodidae is paraphyletic and the Nicholliidae (with species from India) appears to be a clade within the Australian subfamily Hypsimetopodinae. The results also suggest changes to the composition of some subfamilies. By removal of the southeastern Australian genus *Crenoicus*, the Phreatoicinae is restricted to New Zealand taxa. Approximate ages of tectonic rifting of the super-continent Gondwana were used to biogeographically constrain the timing of events in phreatoicoidean phylogeny. Because the Indian genus *Nicholisia* is nested within the Australian Hypsimetopodinae, this clade has a minimum age of 130 million years. Phreatoicoidean isopods were classified into three ecotypes: surface-cryptic, surface-burrower, and groundwater dwelling forms. The phylogenetic distribution of these ecotypes provides evidence for at least two separate colonizations of groundwater habitats. One colonization may be older than the rifting of Indian subcontinent and the other is approximately dated by the separation of New Zealand from East Gondwana. The phylogenetic age, endemism and localized diversity of phreatoicoidean isopods confer a high conservation value upon this group. This phylogenetic and biogeographic knowledge of phreatoicoidean isopod crustaceans may assist informed decisions on their conservation.

## 1 INTRODUCTION

Phreatoicoidean isopod crustaceans are an ancient group, as evident from their fossil record (Schram 1974) and phylogenetic origin as the sister group to all other isopods (Brusca & Wilson 1991). Marine fossil phreatoicoidean isopods are known from the late Carboniferous (Schram 1974), and fresh water fossils of Triassic age in Australia are similar to living taxa (Chilton 1918, Nicholls 1943), indicating that the group is morphologically conservative. Extant taxa have a classic Gondwanan distribution (Banarescu 1990). Recent evaluations of their phylogenetic biogeography (Wilson & Johnson 1999) indicate that ancient relationships emerge at the generic level. For example, *Crenisopus* Wilson & Keable, 1999 appears to be basally derived, and *Pilbarophreatoicus* Knott & Halse, 1999 ('New

Genus X5' in Wilson & Johnson 1999) is related to *Nichollisia* Chopra & Tiwari, 1950 from India.

The classification of the Phreatoicoidea needs revision because the suborder is much more diverse than currently recognized. Currently, fewer than 50 Australian species are described. The monotypic genus *Eophreatoicus* Nicholls, 1943, found in Kakadu National Park and Arnhemland (Northern Territory), contains minimally ten additional undescribed species (unpublished data). Similarly, *Crenoicus* Nicholls, 1943, has two or three undescribed species in each large watershed region in New South Wales above 1000 m (e.g., Kosciusko Plateau, Boyd Plateau, Barrington Tops) (Wilson & Ho 1996, Adlem 1996), possibly reaching a total of 14-16 species in this state alone. A linear extrapolation of these figures for *Crenoicus* yields approximately 200 undescribed species of phreatoicideans in Australia. The recognition of these additional species also suggests that many phreatoicideans are short-range endemics with highly relictual distributions. Where Phreatoicoidea are mentioned in faunal surveys, however, the specimens are rarely identified to species categories (e.g., recent cave surveys of Eberhard et al. 1991 and Eberhard & Spate 1995). Australia has nineteen nominal genera of phreatoicidean isopods (Table 1) and at least three new undescribed genera. Many existing genera are poorly defined and difficult to identify based on the existing monographic works. Because the existing classification of phreatoicideans is not based on phylogenetic relationships (Wilson & Keable 1999, Wilson & Johnson 1999), these problems cannot be adequately treated until a well corroborated phylogeny is estimated. Clearly, new tools to classify and identify phreatoicidean species are needed.

We report a new evaluation of the phylogeny and classification of the phreatoicideans, with evidence for diversification of endemic taxa during the Mesozoic Era in Gondwana. This paper extends the study of Wilson & Johnson (1999), providing a more detailed analysis of phreatoicidean relationships by including additional taxa from Australia and New Zealand, new out-groups and new data on specimens of *Nichollisia* from India. We also use this inferred phylogeny to evaluate the evolution of generalized ecotypes within the Phreatoicoidea.

## 2 MATERIALS AND METHODS

The matrix for phylogenetic analysis was generated from a DELTA database as described by Wilson & Keable (1999) and Wilson & Johnson (1999). The character list (Appendix 1) excludes several multi-state characters in the DELTA database, particularly those involving eyes, owing to the variability in these features. Setal counts and ratios (describing the relative sizes of body parts) are also excluded from the character set. The trimmed character set consists of 79 characters, 77 of which are variable and parsimony informative (Appendix 1). Only taxa for which we have completed data entry have been used in the analysis (Table 1, which should be consulted for authors of phreatoicidean genera; Appendix 2). Some congeneric taxa were omitted (e.g., some *Crenoicus*, species) because preliminary analyses indicate that they cluster together. Several potentially congeneric taxa in *Metaphreatoicus* and *Colubotelson*, however, were included in the analysis to constrain the position of these taxa. Unlike previous analyses of the phreatoicideans, we have included two isopod outgroups, *Tainisopus* Wilson & Ponder, 1992 and *Stenasellus* (Dollfus 1897). All possible living isopod out-groups are 'upstream' taxa – derived later than

Table 1. Genera of the Phreatoicoidea. Key: \* = not Australian; Xn = new genera observed by the authors; # = not in the DELTA database (July 1998). Australian State Abbreviations: NSW, New South Wales; WA, Western Australia; SA, South Australia; NT, Northern Territory; VIC, Victoria; TAS, Tasmania. <sup>1</sup>Based on our evaluation of specimens in hand.

Genus	Described Species (est. new species <sup>1</sup> )	Distribution
* <i>Mesamphisopus</i> Nicholls, 1943	4	South Africa
* <i>Neophreatoicus</i> Nicholls, 1944	1	New Zealand
* <i>Nichollsia</i> Chopra & Tiwari, 1950	2	India
#* <i>Notamphisopus</i> Nicholls, 1944	6	New Zealand
* <i>Phreatoicus</i> Chilton, 1882	2	New Zealand
<i>Amphisopus</i> Nicholls, 1926	2	WA
# <i>Colacanthotelson</i> Nicholls, 1944	1 (1?)	NSW, (TAS?)
<i>Colubotelson</i> Nicholls, 1944	15 (1?)	VIC, NSW, TAS
<i>Crenoicus</i> Nicholls, 1944	4 (>20)	VIC, NSW
<i>Crenisopus</i> Wilson & Keable, 1999	1	NE Kimberleys, WA
<i>Eophreatoicus</i> Nicholls, 1926	1 (>10)	NT
<i>Hyperoedesipus</i> Nicholls & Milner, 1923	1	WA
<i>Hypsimetopus</i> Sayce, 1902	1	TAS
# <i>Mesacanthotelson</i> Nicholls, 1944	4	TAS
<i>Metaphreatoicus</i> Nicholls, 1944	4	NSW, TAS
# <i>Onchotelson</i> Nicholls, 1944	2	TAS
# <i>Paraphreatoicus</i> Nicholls, 1944	1	TAS
<i>Paramphisopus</i> Nicholls, 1943	3	WA
<i>Phreatoicoides</i> Sayce, 1900	3	TAS, VIC
<i>Phreatoicopsis</i> Spencer & Hall, 1896	1 (1?)	VIC
<i>Pilbarophreatoicus</i> Knott & Halse, 1999	1 (1-2)	Pilbara, WA
<i>Phreatomerus</i> Sheppard, 1927	1 (1?)	SA
# <i>Protamphisopus</i> Nicholls, 1943	1	NSW (fossil)
<i>Synamphisopus</i> Nicholls, 1943	1	VIC
# <i>Uramphisopus</i> Nicholls, 1943	1	TAS
# (New Genus X2)	(1)	SE WA
# (New genus X3)	(1)	Kimberleys, WA
# (New genus X4)	(1)	SW WA

the ancestor of the phreatoicoideans (cf. Brusca & Wilson 1991). The chosen outgroup taxa have some possibly plesiomorphic traits, such as a basal article of the antennal protopod and a rudimentary second flagellum on the antennula. Many character states of *Tainisopus* and *Stenasellus* were necessarily inapplicable and were scored as unknowns. We make no claims about the phylogenetic position of these two taxa relative to the phreatoicoideans.

Phylogenetic analysis was performed with 'Portable PAUP\*' (beta version 4.0.0d64 for DOS; Swofford, 1999), applying 10 random addition sequence iterations using MulPars with the characters unordered and equally weighted. Taxa scored as multi-state for particular characters were interpreted as displaying polymorphism. Bremer support (decay values) was obtained using constraint trees generated by AutoDecay (version 4.0; Eriksson 1998) and analysed using PAUP\*. Character distributions were evaluated using MacClade (ver. 3.07; Maddison & Maddison 1992).

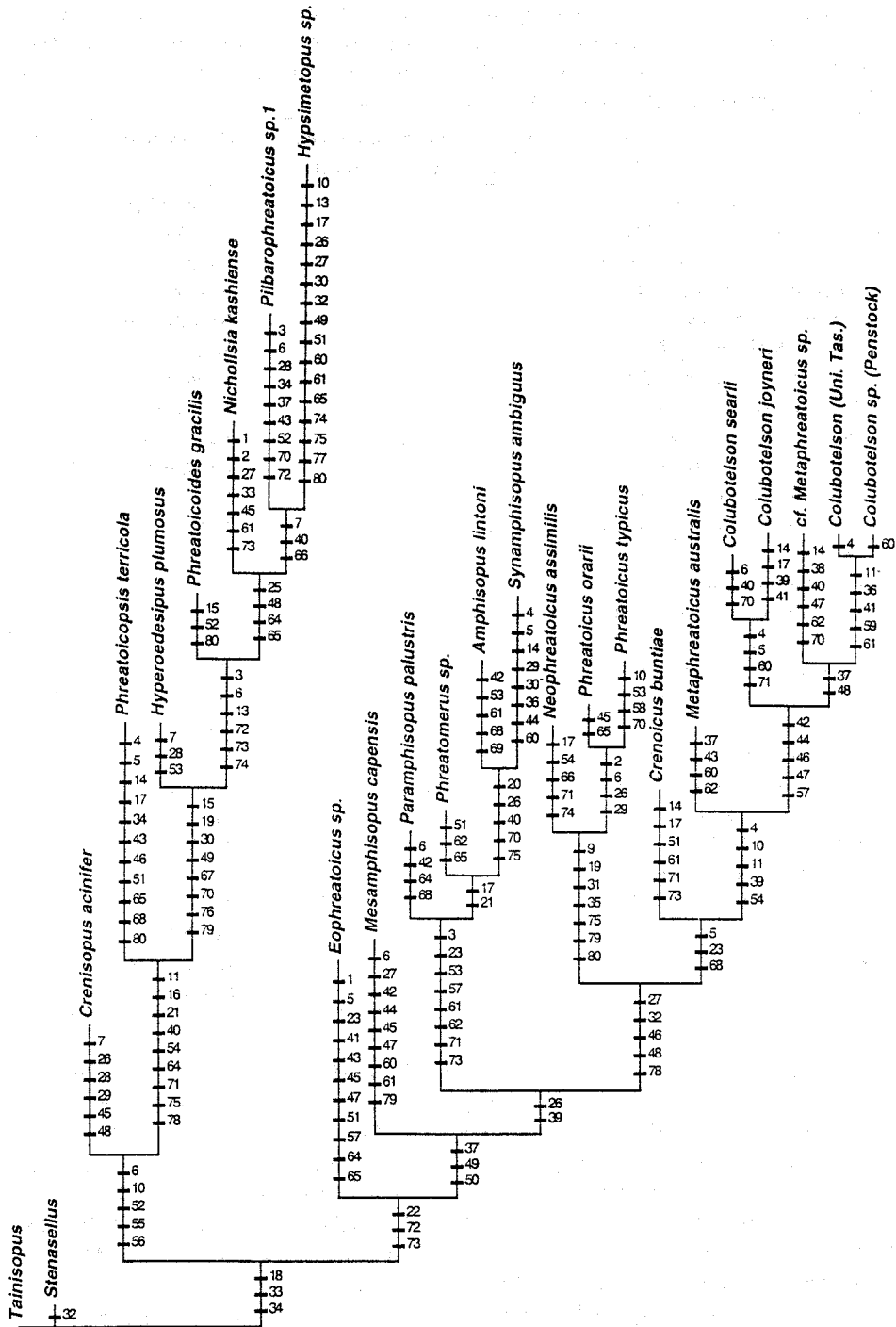


Figure 1. The single tree resulting from a PAUP\* analysis of the data in Table 2: tree length 335, consistency index 0.394, retention index 0.561, rescaled consistency index 0.221. Character 80 is a non phylogenetic eocyte character: see Figure 3.

### 3 RESULTS AND DISCUSSION

#### 3.1 Phylogenetic Analysis

A single tree results from the analysis of the data in Table 2, (length 335, consistency index 0.394, rescaled consistency index 0.221; Fig. 1). Four clades relating to the status of the current classification are well supported, based on their branch or Bremer support (Bremer 1994) values (Fig. 2 with node labels and branch support). An additional clade (node 4) is marked; although it was supported by only three steps because of its correspondence to the family Phreatoicidae and because its position is constrained owing to well-supported clades at nodes 3 and 5. The character changes defining these five nodes are summarized in Table 3. The well supported clade '*Crenisopus*+node 1' is not labeled because it has no implications for the existing classification. After this paper was completed, the coding of uropodal protopodal medial ridge characters (75-76) was revised owing to new observations on Tasmanian taxa not included in this analysis. These changes did not result in new topologies for the well-supported branches, although some Phreatoicidae in-group relationships were changed, owing to low levels of character support in those branches.

#### 3.2 Apomorphies

Consistent characters (character consistency index = 1.0) define well-supported nodes in the single cladogram (Figs 1-2; Table 3). The in-group node for the Phreatoicidea is identified by three apomorphies. A vaulted pleotelson (higher than broad; char. 18) is a synapomorphy of all species of phreatoicideans. Many species have a dorsally reflexed distal tip of the pleotelson (char. 22), but this feature is not universal for the suborder, and is absent in the taxa of nodes 1 and 2 (Fig. 2). The bifurcate spines in the mandibular spine row (char. 33) are found in nearly all phreatoicideans. *Nichollisia* has undivided mandibular spines, an apparent reversion. Phreatoicideans are also basally defined by the projecting ridge of the spine row (char. 34). Most species, however, have a pedunculate spine row.

The subtree including *Crenisopus*, *Phreatoicopsis* and the Hypsimetopodinae Nicholls, 1943 (name corrected from Nicholls' original spelling, Hypsimetopinae) is defined by the absence of a propodal articular plate on most but not all pereopods (chars. 52, 55 and 56). Node 1 (hypsimetopodines + *Phreatoicopsis*) is defined by the consistent characters of an indented distal tip of the pleotelson (char. 21) and a pleonite 1 pleural depth that is similar to pleurae on the more posterior pleonites. Node 2 clade members (hypsimetopodines) have pleopodal exopods with elongate lateral lobes on the proximal article (char. 63) and lack protopodal epipods (char. 67). The partial amphispodine clade (node 3) and the phreatoicid clade (node 4) have no consistent characters defining them. Node 3, however, is strongly supported by at least 6 character changes. An unusually thin mandibular incisor process (char. 31) and a broad maxillular medial lobe (char. 35) define the New Zealand phreatoicine clade (node 5).

#### 3.3 Classification

Nicholls (1943) placed undue influence on the presence of a lacinia mobilis on the right mandible as the defining feature of the Amphispodidae, even though it is absent in *Hyp-*





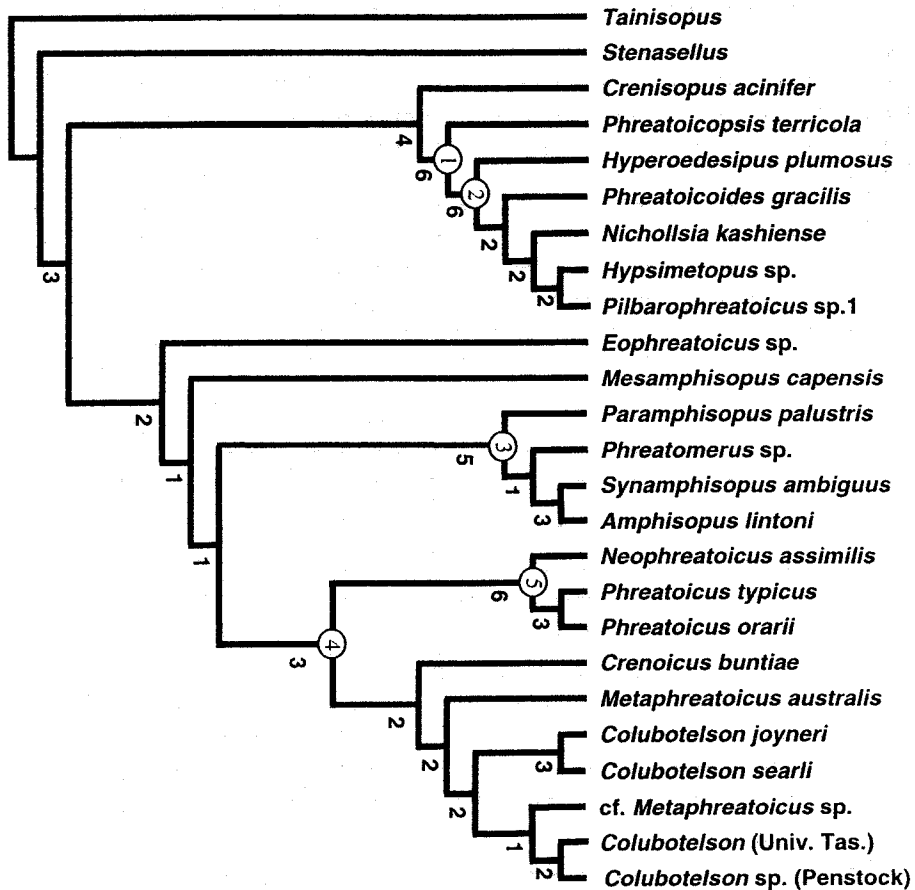


Figure 2. Branch support for cladogram in Figure 1 (Bremer support numbers to the left of the branches), with nodes of well supported clades (numbers in circles). Apomorphies for marked nodes are shown in Table 3.

*simetopus*. The Amphisopodidae, although almost all members have the right lacinia, consists of at least two distinct clades in our analysis and is paraphyletic owing to the nested position of the Phreatoicidae. Moreover, the right lacinia mobilis may be a plesiomorphy, because it occurs in the peracaridan outgroup Spelaeogriffacea as well as in other isopods, such as *Tainisopus*. Such a distribution renders the right lacinia mobilis uninformative for defining clades of Phreatoicida. The remainder of Nicholls' (1943:25) definition of the Amphisopodidae consists of variable features.

The cladogram resulting from the analysis (Figs 1-2) shows that the current family-level classification is not consistent with the phylogenetic relationships of the Phreatoicida (Table 4). These results, however, must be considered preliminary because some genera classified by Nicholls (1943, 1944) have not been evaluated. Therefore, a new arrangement cannot be proposed at this time. Several changes, however, will be necessary because the positions of some taxa are likely to be stable under larger taxon samples. The Indian genus *Nichollsia* is nested in a clade containing the Australian genera *Hypsimeto-*



Table 3. Apomorphies of well-supported branches in Figures 1-2. See appendix 1 for character and character state definitions. Single-lined arrows indicate transitions assigned to a branch in some, but not all, optimisations. Double-lined arrows indicate unambiguous transitions. Consistency indices for each character shown in parantheses.

Branch	Character, state change & (consistency index)
Ingroup node to ( <i>Crenisopus</i> +node 1)	03, 1->2 (0.250); 06, 1=>2 (0.143); 10, 1=>3 (0.333); 27, 1->3 (0.333); 52, 1=>2 (0.333); 53, 1->2 (0.200); 55, 1=>2 (0.333); 56, 1=>2 (1.000).
Branch to node 1	11, 1=>3 (0.286); 16, 1=>2 (1.000); 21, 1=>3 (1.000); 38, 2->3 (0.286); 40, 2=>3 (0.400); 54, 2=>1 (0.400); 62, 1->4 (0.667); 64, 1=>4 (0.500); 71, 1=>3 (0.286); 75, 1=>2 (0.167); 77, 1->2 (0.200); 78, 2=>1 (0.667).
Branch to node 2	01, 1->3 (0.455); 15, 1=>3 (0.667); 19, 1=>2 (0.500); 30, 2=>3 (0.143); 37, 3->1 (0.250); 42, 2->1 (0.286); 49, 2=>1 (0.333); 50, 2->1 (0.500); 63, 1->2 (1.000); 67, 1=>2 (1.000); 70, 1=>2 (0.167); 76, 2=>3 (0.500); 79, 2=>1 (0.286).
Branch to node 3	03, 1=>2 (0.250); 07, 1->2 (0.200); 10, 1->2 (0.333); 11, 1->2 (0.286); 23, 1=>2 (0.667); 34, 3->2 (0.429); 53, 1=>2 (0.200); 57, 2=>4 (0.333); 61, 3=>1 (0.286); 62, 1=>3 (0.667); 71, 1=>3 (0.286); 73, 1=>3 (0.600).
Branch to node 4	01, 1->2 (0.455); 27, 1=>2 (0.333); 32, 1=>2 (0.333); 41, 2->1 (0.200); 46, 2=>1 (0.333); 48, 4=>1 (0.500); 76, 2->1 (0.500); 78, 2=>1 (0.667).
Branch to node 5	01, 2->3 (0.455); 09, 2=>3 (0.750); 14, 3->4 (0.500); 19, 1=>2 (0.500); 30, 3->2 (0.143); 31, 1=>2 (1.000); 35, 1=>2 (1.000); 75, 1=>2 (0.167); 79, 2=>1 (0.286).

*pus*, *Phreatoicoidea*, *Hyperoedesis* and *Pilbarophreatoicus* (node 2 in Fig. 2). Because this clade is strongly supported (Bremer support of six steps), the eventual classification will recognize the junior synonymy of Nichollsiidae. The name of this clade could be based on Hypsimetopodinae although the placement of the more basal genera *Phreatoicopsis* and *Mesamphisopus* is relevant, because Nicholls (1943:28) based a subfamily name on each of these genera (Table 4). These names would have precedence pending their inclusion into the hypsimetopodine clade. The sister group relationship between *Phreatoicopsis* and the hypsimetopodines is well supported (six steps for node 1, Fig. 2), so a revised classification may recognize a monotypic phreatoicopsidine clade and a hypsimetopodine clade.

The composition of the Amphisopodidae (Table 4) may be reduced considerably with only *Amphisopus*, *Synamphisopus*, *Paramphisopus* and *Phreatomerus* included in a well-supported clade (node 3, Fig. 2). The Phreatoicinae (node 5) appears to be confined to those taxa that occur in New Zealand with *Crenoicus* falling outside this clade. Most of the southeastern Australian phreatoicoidean genera may be placed in either the Mesacanthotelsoninae or the Paraphreatoicinae, pending analysis of the mesacanthotelsonine genera. Other available family names, such as the Mesamphisopodinae, have an uncertain status because the basal parts of the cladogram are weakly supported and unstable compared to previous analyses (Wilson & Keable 1999, Wilson & Johnson 1999).

### 3.4 Biogeography and Cladogenic events

The addition of more taxa and characters produced a result that supported the conclusions of Wilson & Johnson (1999). The clade *Nichollisia*+*Hypsimetopus*+*Pilbarophreatoicus* is

Table 4. Family-level phreatoicidean names from Nicholls (1943, 1944) compared to well-supported clades in phylogenetic analysis.

Species	Family name & subfamily	Node Number in Figure 2
	AMPHISOPODIDAE	
<i>Amphisopus lintoni</i>	Amphisopodinae	3
<i>Paramphisopus palustris</i>	Amphisopodinae	3
<i>Hypsimetopus</i> sp.	Hypsimetopodinae	2
<i>Phreatoicoides gracilis</i>	Hypsimetopodinae	2
<i>Hyperoedesis plumosus</i>	Mesamphisopodinae	2
<i>Mesamphisopus capensis</i>	Mesamphisopodinae	–
<i>Eophreatoicus</i> sp.	Phreatoicopsinae	–
<i>Phreatoicopsis terricola</i>	Phreatoicopsinae	1
<i>Synamphisopus ambiguus</i>	Phreatoicopsinae	3
<i>Phreatomerus latipes</i>	Phreatomerinae	3
<i>Crenisopus acinifer</i>	–	–
<i>Pilbarophreatoicus</i> sp. 1	–	2
<i>Nichollisia kashiense</i>	NICHOLLSIIDAE	2
	PHREATOICIDAE	
<i>Colubotelson joyneri</i>	Paraphreatoicinae	4
<i>Colubotelson searli</i>	Paraphreatoicinae	4
<i>Colubotelson</i> sp. (Penstock Lagoon)	Paraphreatoicinae	4
<i>Colubotelson</i> sp. (Univ. Tasmania)	Paraphreatoicinae	4
<i>Metaphreatoicus australis</i>	Paraphreatoicinae	4
cf. <i>Metaphreatoicus</i> sp.	Paraphreatoicinae	4
<i>Crenoicus buntiae</i>	Phreatoicinae	4
<i>Neophreatoicus assimilis</i>	Phreatoicinae	5
<i>Phreatoicus orarii</i>	Phreatoicinae	5
<i>Phreatoicus typicus</i>	Phreatoicinae	5

deeply nested within the resulting cladogram (Figs 1-2) providing a minimum age constraint of ~120mybp (million years before present) on the events depicted by our cladogram (Indian subcontinental rifting; Storey 1995). The South African genus *Mesamphisopus* is no longer derived basally as in previous cladograms (Wilson & Keable 1999, Wilson & Johnson 1999), although the position of the root in the phreatoicidean cladogram is not strongly supported. If this basal topology proves to be better supported with more data, the minimum age of phreatoicidean diversification must be prior to the initial rifting between West and East Gondwana (~180mybp; Storey 1995). This latter age is consistent with ~237mybp age for the fossil phreatoicidean *Protamphisopus wianamattensis* (Chilton, 1918), known from freshwater lacustrine habitats preserved in the Middle Triassic Wianamatta shales of Sydney (Herbert 1997). The freshwater diversification of the phreatoicideans, therefore, may have taken place in Gondwana during the Triassic. Later biogeographic patterns may have been further influenced by later Mesozoic events, such as the inundation of East Gondwana during mid Cretaceous times (Wilson & Johnson 1999).

A more detailed biogeographic picture is somewhat less obvious. Biogeographic paralogy (Nelson & Ladiges 1996), wherein several independently evolving subclades replicate

the same biogeographic patterns, may complicate phreatoicoidean distributions because their relationships may have been established prior to Gondwanan rifting. The hypsimetopodine clade (node 2, Fig. 2) has transoceanic and trans-Australian relationships (Table 1), although the precise sister group relationships within this clade are weak. The amphispodine clade (node 3, Fig. 2) shows several trans-Australian patterns and the large phreatoicid clade (node 4, Fig. 2) has both trans-Tasman and trans-Bassian relationships. The distribution of the Phreatoicoidea may be the only restricted biogeographic pattern, with this family being confined to southeastern Australia, Tasmania and New Zealand. Confirmation of this pattern requires further phylogenetic analysis of the remaining genera in this family. The distributions of taxa in nodes 1-3 overlaps those in node 4, so a better understanding of these patterns may be improved by resolution of the basal phylogenetic relationships.

### 3.5 Evolution of ecotypes

With few exceptions, extant phreatoicoideans are freshwater animals with limited swimming abilities. The earliest known ecotype for these animals is exemplified by *Protamphisopus wianamattensis* (Chilton, 1918), found in shales containing 'fishes, labrithodonts, insects, coprolitic fragments and plants' (Tillyard 1916, quoted in Chilton 1918). This animal probably lived much as *Paramphisopus palustris* or the Tasmanian species of *Uramphisopus*, *Onchotelson*, or *Mesacanthotelson* do today, among vegetation in freshwater lakes and ponds. In more arid environments where permanent lakes and streams are absent, phreatoicoidean species are associated at the surface with spring-fed brooks or seeps. In all cases, they prefer to live among fallen vegetation or aquatic roots and, if the substrate consists of coarse gravel, will live in-faunally as well. Most, but not all, such species have eyes and are pigmented. Species of *Crenoicus*, common denizens of highland *Sphagnum* swamps in New South Wales and Victoria, are exceptions: they are blind but have some color. We designate this ecotype as 'surface-cryptic,' owing to their surface-living habits but with an inclination to hide.

A second ecotype, which we designate as 'surface-burrower', includes species that burrow in fine sediments and are found alongside submerged roots of living vegetation such as button grass or sedges. Species of this ecotype also may be found in the burrows of crayfish (pholeteros: Richardson & Swain 1978, Horwitz 1989). Species of *Phreatoicoides* and *Hypsimetopus* are included in this category. Another 'surface burrower,' *Phreatoicopsis terricola*, creates small oval burrows in the moist soil among tree fern roots but without overlying free-running water. Many 'surface-burrowers' are white and pigmentless, as well as blind, although *Phreatoicopsis* has tiny eyes and some color in the head region.

The third ecotype, designated 'ground water,' includes truly hypogean phreatoicoideans that are found only in permanent ground water, such as wells or springs, and occur in surface pools and spring outflows only during the wet season. All such taxa are translucent, completely without color and blind. The New Zealand phreatoicoideans, *Nichollsia* from India, and *Hyperoedesipus*, *Crenisopus* and *Pilbarophreatoicus* from Western Australia are examples of this ecotype. The richness of Western Australian genera in this ecotype may reflect the relative aridity of this region. Appendix 2 includes observations on living conditions of most species included in this analysis.

The ecotype classification was plotted on the phylogenetic tree (Fig. 3). The majority

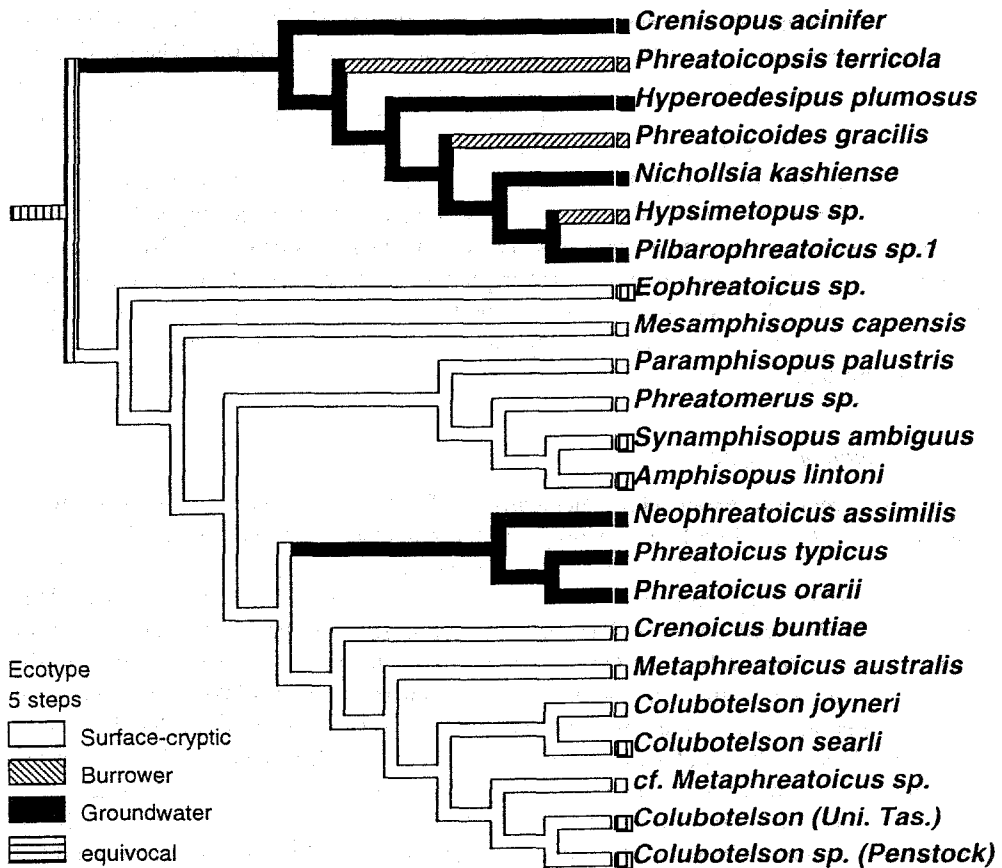


Figure 3. Phylogenetic distribution of ecotypes for in-group phreatoicideans, using the topology shown in Figures 1-2.

of the species are surface-cryptic, which may be the plesiomorphic habit for this suborder. The groundwater ecotype arose at least twice in the evolution of the phreatoicideans, because the clade containing New Zealand representatives of this type (node 5) is well separated from nodes 1 and 2, with surface-cryptic taxa placed basally. The New Zealand genus *Notamphisopus* has not been included in this analysis, although information in Nicholls (1944) indicates that its eyeless species are surface-cryptic. Species of *Crenoicus* occurring in Australia are also surface-cryptic and blind but several undescribed species also occur in the groundwater of caves (Eberhard & Spate 1995, Wilson & Ho 1996, unpublished data). Therefore, both *Crenoicus* and *Notamphisopus* species may represent instances of re-invasion of surface habitats from the groundwater. Emergent adaptation to surface habitats is also supported in the clade *Crenisopus*+node 1, with burrowing ecotype taxa apparently showing multiple derivations from groundwater ancestors. Of the taxa in this clade, only *Phreatoicopsis terricola* has eyes, although they are tiny compared to the large eyes of the basally derived genera *Eophreatoicus* or *Mesamphisopus*.

The timing of phreatoicidean adaptations to groundwater habitats may be addressed us-

ing biogeographic constraints. Because *Nichollisia* is deeply nested into the groundwater/burrowing clade (nodes 1 & 2 in Figs 2 and 3), these taxa adapted to this habitat minimally by ~120mybp, before the rifting of the Indian subcontinent from West Gondwana. The New Zealand phreatoicine clade (node 5, Fig. 2) may have adapted to hypogean habitats after this subcontinent separated from Australia and Antarctica (~90mybp). The adjacent clade position of *Crenoicus*, which includes some cavernicolous species, suggests that the hypogean adaptations of the New Zealand taxa could be older.

#### 4 CONCLUDING REMARKS

Improving our knowledge of the Phreatoicidea requires urgent action owing to continuing degradation of their habitats, especially in areas where ground water is used for mining, agriculture and industry. The existing phreatoicidean classification is inadequate, despite their potential value in biogeography and conservation. As an interim source of information, this paper provides a well-resolved cladistic estimate with immediate applications. The phylogenetic relationships of phreatoicidean ecotypes suggest that these adaptations to ground water habitats are ancient. The phreatoicidean dependence on groundwater may greatly constrain their ability to survive rapid human-induced changes to the ground water environments. Admittedly, this observation is general for hypogean faunas on any continent but in the Australian context, where water is a limited and unpredictable resource, it takes on much more importance. In pre-European times, extensive wetlands associated with forests on the Great Dividing Range in southeastern Australia may have provided many habitats for phreatoicideans and other invertebrates (cf. Mollusca: Ponder 1994, 1997). Over the last 200 years, upland groundwater-fed springs and swamps associated with woodlands has been extensively modified or removed by the activities of graziers and foresters. Cattle, sheep, and feral domestic animals, such as pigs, goats and horses, further degrade remaining freshwater habitats by feeding and trampling on associated wetland vegetation. Many regions of the Great Dividing Range become arid during part of the year owing to vegetation removal, and no longer support surface exposures of ground water. Because *Crenoicus* species appear to have small geographic distributions (Wilson & Ho 1996), many species may have been lost along with these decimated woodlands. Extinct *Crenoicus* species in New South Wales alone may exceed the estimated number of extant species (approximately 20 spp.). The threat of more extinctions continues today owing to extensive logging in some state forests, adding to the exaggerated wet-dry cycles caused by vegetation removal. This example has parallels in other regions, such as in Western Australia where direct use of ancient aquifers for mining and agriculture threatens the groundwater faunas (Humphreys 1994).

The first step in preventing extinctions is informing those in charge of the management of these habitats on the diversity and relevance of their native fauna and flora. Our phreatoicidean research will attempt this first step because conservation choices and priorities could favor those taxa that provide the highest phylogenetic diversity for a region (e.g. Faith 1992). As demonstrated here, phreatoicidean isopods, with their ancient relationships and adaptations to sensitive habitats, provide great potential for defining the phylogenetic diversity of the regions in which they occur.

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## APPENDIX 1 – LIST OF CHARACTERS AND CHARACTER STATES

1. Head length: (1) length shorter than width in dorsal view; (2) length subequal to width in dorsal view; (3) length greater than width in dorsal view.
2. Head lateral profile of dorsal surface: (1) smoothly curved; (2) angularly curved; (3) indented; (4) flattened curve.
3. Cervical groove: (1) straight, or undulating, or smoothly curved; (2) absent.
4. Mandibular genal groove: (1) present, smoothly indented; (2) present, with acute indentation; (3) absent.
5. Mandibular notch: (1) present; (2) absent.
6. Clypeal notch: (1) present; (2) absent.
7. Antennal notch: (1) present; (2) absent.
8. Pereion relative width in dorsal view: (1) narrow, width near head width; (2) broad, width exceeding head width.
9. Pereionites 2-7 in dorsal view: (1) longer than wide; (2) wider than long; (3) anteriorly longer than wide decreasing posteriorly to wider than long; (4) anteriorly and posteriorly wider than long, but longer than wide in the middle.
10. Coxal articulation of pereionites 2-4: (1) free, with a pronounced v-shaped suture; (2) nearly fused, with a u-shaped suture; (3) fused, with no suture.
11. Coxal articulation of pereionites 5-7: (1) free; (2) nearly fused; (3) fused.
12. Lateral tergal plates of pereionites 2-4: (1) absent (coxae visible in lateral view); (2) extending ventrally (coxae not visible in lateral view).
13. Sternal processes: (1) present; (2) absent.
14. Typhlosole form in cross-section: (1) well developed, ventral invagination forming double spiral; (2) minimal, ventral invagination inverted, 'U' shaped; (3) absent, gut round; (4) intermediate, ventral invagination 'Y' shaped
15. Pleonites in lateral view (depth of pleurae/epimera): (1) much deeper than pereionites, with large ventrolateral plates, basal region of pleopods not visible; (2) having depth approximating depth of pereionites, with small ventro-lateral plates, basal region of pleopods visible; (3) having depth equal to depth of pereionites, without ventrolateral plates.
16. Pleonite 1 pleura size: (1) distinctly shallower than pleurae of pleonites 2-5; (2) near depth of pleurae of pleonites 2-5.
17. Pleonites 1-4 relative lengths: (1) subequal; (2) unequal, pleonite 4 length greater than pleonites 1-3.
18. Pleotelson form: (1) broader than high; (2) vaulted, higher than broad.
19. Pleotelson lateral length: (1) less than depth, or subequal to depth; (2) greater than depth.

20. Pleotelson lateral dorsal ridges: (1) absent; (2) continuous with telsonic region.
21. Telsonic region or tail piece median lobe in dorsal view: (1) entire; (2) cleft (i.e. two horizontal projections at posterolateral margins, narrowly separated); (3) broadly indented (i.e. no real horizontal projections); (4) broadly incised (i.e. two horizontal projections at posterolateral margins but more widely separated).
22. Telsonic region median lobe: (1) not reflexed; (2) reflexed dorsally.
23. Telsonic region lateral lobes: (1) absent; (2) forming a vertical plate; (3) forming a rounded setose lobe in dorsal view.
24. Telsonic region (if medial lobe indented) sensillate setae: (1) absent, or fine; (2) robust setae distinctly heavier than setae on dorsal surface.
25. Telsonic region posterior margin of pleotelson irregular denticulations: (1) present; (2) absent.
26. Dorsal uropodal ridge of pleotelson: (1) present; (2) absent.
27. Antennula terminal article shape: (1) tubular (sides approximately parallel, length greater than width), or conical; (2) inflated and bulbous (sides curved, width distinctly greater than previous article), or globular (sides curved, length approximates width, subequal or narrower than previous article); (3) tiny, vestigial.
28. Antennula penultimate article length: (1) distinctly longer than any other article; (2) subequal or shorter than other articles.
29. Antennula penultimate article width: (1) width subequal or narrower than proximal article; (2) inflated, width much greater than proximal article; (3) broad and flattened.
30. Antenna propodal article 1: (1) present, large; (2) present, forming thin ring; (3) absent.
31. Mandible incisor processes shape: (1) broad, width greater than thickness; (2) thin, resembling denticulate spines, width near thickness.
32. Mandible right lacinia mobilis: (1) present; (2) absent.
33. Mandible spine rows bifurcate spines: (1) absent; (2) present.
34. Mandible spine rows shape: (1) in smooth low arc between incisor and molar process; (2) on projecting ridge between incisor and molar processes; (3) on linear pedunculate projection between incisor and molar processes; (4) on round pedunculate projection between incisor and molar processes.
35. Maxillula medial lobe width: (1) less than lateral lobe; (2) subequal to lateral lobe, or greater than lateral lobe.
36. Pereiopods ischium dorsal margin with single elongate robust simple seta: (1) present; (2) absent.
37. Pereiopod I dactylus length measured along inner margin of dactylus: (1) projecting beyond palm in male; (2) subequal to palm in male; (3) shorter than palm in male.
38. Pereiopod I dactylus length: (1) projecting beyond palm in female; (2) subequal to palm in female; (3) shorter than palm in female.
39. Pereiopod I dactylus ventral margin distal cuticular fringe: (1) present; (2) absent.
40. Pereiopod I dactylus accessory claws: (1) with several distal accessory claws; (2) with 1 distal accessory claw; (3) without distal accessory claws.
41. Pereiopod I dactylus distal accessory spines: (1) present; (2) absent.
42. Pereiopod I propodus dorsal margin proximal region in male: (1) protruding to or beyond distodorsal margin of ischium; (2) protruding beyond distodorsal margin of carpus; (3) not protruding.
43. Pereiopod I propodus dorsal margin proximal region in female: (1) protruding to or

- beyond distodorsal margin of ischium; (2) protuding beyond distodorsal margin of carpus; (3) not protuding.
44. Pereiopod I propodal palm in male stout denticulate setae: (1) present, serrate (multiple denticulations); (2) present, bifid (two spinules only); (3) absent.
  45. Pereiopod I propodal palm in male stout robust simple setae not on ridge: (1) present, conical; (2) present, basally inflated; (3) present, tooth-like; (4) absent.
  46. Pereiopod I propodal palm in male low conical setae on ridge: (1) present; (2) absent.
  47. Pereiopod I propodal palm in female stout denticulate setae: (1) present, serrate (multiple denticulations); (2) present, bifid (i.e. two spinules only); (3) absent.
  48. Pereiopod I propodal palm in female stout robust simple setae not on ridge: (1) present, conical; (2) present, basally inflated; (3) present, tooth-like; (4) absent.
  49. Pereiopod I merus dorsal margin projection in anterior-dorsal view: (1) shelf-like and U-shaped in male; (2) spine-like and pointed in male.
  50. Pereiopod I merus dorsal margin projection: (1) with numerous elongate fine simple setae; (2) with 1 or 2 robust simple setae.
  51. Pereiopods II-III dactylus spines on ventral margin: (1) present; (2) absent.
  52. Pereiopods II-III propodus articular plate: (1) present; (2) absent.
  53. Pereiopod IV: (1) sexually dimorphic; (2) not sexually dimorphic.
  54. Pereiopod IV dactylus: (1) shorter than propodal palm; (2) subequal to propodal palm; (3) longer than propodal palm.
  55. Pereiopod IV propodus articular plate on posterior side of limb: (1) present; (2) absent.
  56. Pereiopods V-VII propodus articular plate on posterior side of limb: (1) present; (2) absent.
  57. Pereiopods V-VII basis dorsal ridge in cross section: (1) rounded; (2) angular; (3) produced but not forming distinct plate; (4) produced and forming distinct plate.
  58. Penes form: (1) straight; (2) curved posteriorly.
  59. Penes length: (1) extending near midline; (2) extending past midline and onto pleonite 1.
  60. Penes armature: (1) smooth, lacking setae; (2) shaft denticulate; (3) with setae on shaft; (4) with setae on tip.
  61. Penes shaft distal shape: (1) tapering; (2) broadening; (3) tubular.
  62. Penes distal tip shape: (1) rounded; (2) pointed; (3) flattened; (4) truncate.
  63. Pleopod exopods II-V proximal article distolateral lobes: (1) shorter than distal article; (2) subequal or longer than distal article.
  64. Pleopod exopods I-V lateral proximal lobes: (1) present on exopods II-V; (2) present on exopods I and III-V; (3) absent; (4) present on exopods I-V.
  65. Pleopod exopods I-V medial proximal lobes: (1) present on exopods II-V; (2) present on exopods III-V; (3) absent; (4) present on exopods I-V.
  66. Pleopod protopod medial epipods: (1) with medial epipods or with small medial projections; (2) without medial epipods.
  67. Pleopod protopod lateral epipods: (1) protopods III-V with lateral epipods or protopods I-V with lateral epipods; (2) protopods without lateral epipods.
  68. Male pleopod I exopod distal margin: (1) pointed; (2) rounded.
  69. Male pleopod I exopod lateral margin: (1) rounded; (2) broadly angular.
  70. Male pleopod I exopod dorsal surface setae: (1) with setae; (2) lacking setae.
  71. Male pleopod II endopod appendix masculina ventral shape of cross section of proximal half of shaft: (1) concave (forming an elongate trough); (2) convex (rod-like);



- (3) convex (flattened in cross section).
72. Male pleopod II endopod appendix masculina basal musculature: (1) pronounced; (2) not pronounced.
  73. Male pleopod II endopod appendix masculina distal tip: (1) truncate, or broadly rounded; (2) acutely rounded; (3) sharply pointed and spine-like; (4) pointed and distally spatulate.
  74. Male pleopod II endopod appendix masculina length: (1) distal tip extending near to distal margin of endopod (either laterally or medially extending beyond half length of exopod); (2) distal tip not extending beyond half length of exopod.
  75. Uropod protopod dorsomedial ridge: (1) not produced; (2) produced.
  76. Uropod protopod dorsomedial ridge bump with robust setae: (1) bump with robust setae; (2) plate-like; (3) spur or spine-like.
  77. Uropod protopod robust spinose setae on distoventral margin: (1) present; (2) absent.
  78. Uropod rami distal tips: (1) pointed; (2) rounded.
  79. Uropod endopod: (1) shorter than protopod; (2) subequal to protopod length; (3) longer than protopod.

#### APPENDIX 2 – MATERIAL EXAMINED AND HABITAT

(Abbreviations: AM, Australian Museum; WAM, Western Australian Museum; TMAG, Tasmanian Museum & Art Gallery; ZSIC, Zoological Survey of India Calcutta; bl, body length)

- Amphisopus lintoni* (Nicholls, 1926): AM P8795, 1 primary male (bl 8.7 mm) and 1 preparatory II female (bl 15.3 mm), from 6 males, 15 females, Albany, W.A. 35°00'S, 117°52'E (estimated from map), 'on submerged stakes or snags or under vegetation growing in water' (Nicholls 1943:81), G.E. Nicholls, collected prior to March 1927.
- Colubotelson* sp. (Penstock Lagoon, Tasmania): AM P54096, several males and females from approximately 172 specimens taken from trout gut, Penstock Lagoon, central Tasmania, Australia, 42°06'S 146°46'E, T. Hume, 25 April, 1977.
- Colubotelson* sp. (University of Tasmania, Hobart): AM P54097, male (bl 14.1 mm), female (bl 10.5 mm). Among fallen leaves in stream on University of Tasmania campus, Hobart, Tasmania, Australia, 42°53'S 147°19'E, R. Swain, 14 July 1990.
- Colubotelson joyneri* (Nicholls, 1926): AM P8796, male (bl 12.8 mm), preparatory II female (bl 10.5 mm), from 14 males and 5 females, Mt. Buffalo, Victoria 36°45'S, 146°35'E, 'in black ooze in shallow ditches, and puddles, beneath sphagnum in several boggy areas, and ... in fairly fast-flowing creeks. ... It would seem that it requires a sheltered situation...' (Nicholls 1944:110), G.E. Nicholls, Feb 1925.
- Colubotelson searli* Nicholls, 1944 (originally described as subspecies *C. joyneri searli*): AM P54098, male (bl 14 mm) and preparatory I female (bl 9.6 mm), stn. SC 418, Mt Baw Baw, Victoria 37°50.18'S, 146°15.39'E (GPS), in *Sphagnum* moss, altitude 1460 m, S. Clark, 4 Jan 1997.
- Crenisopus acinifer* Wilson & Keable, 1999: WAM C23229, holotype male (bl 4.39 mm), WAM C23230, paratype male (bl 5.25 mm dissected), WAM C23231 paratype male (bl 4.20 mm), WAM C23232 paratype preparatory female (bl 4.20 mm, dissected), WAM C23233 paratype preparatory female, (bl 4.44 mm), Zebedee Springs, El Questro Station, north Kimberley, W.A., Australia, 16°00'S 128°01'E, collected in net

over spring outlet, 100 cubic meters of water strained, water temperature 35°C, W.F. Humphreys & B. Vine, 13 June 1994.

*Crenoicus buntiae* (Wilson & Ho, 1996): Data from Wilson & Ho (1996). Female characters not included in Wilson & Ho (1996) were scored from AM P44463, preparatory II female (bl 11.7 mm) from Mumbedah Swamp at head of Mumbedah Creek, Kanangra-Boyd National Park, NSW, Australia, at and near 33°53.73'S, 150°4.05'E, altitude 1200 m, in submerged *Sphagnum* moss, G. Wilson & party, 2 April 1992 & 18 Nov 1992.

*Eophreatoicus* 'sp.6': AM P54099, male (bl 21.3 mm) and 1 preparatory II female (bl 11.8 mm), ~1 km upstream of Gubara Pools, 12°49.65'S 132°52.96'E (GPS), Kakadu National Park NT, under leaves and among roots in gravel, G. Wilson, W. Ponder & V. Kessner, 15 August 1994.

*Hyperoedesipus plumosus* Nicholls & Milner, 1923: Combination of literature (Nicholls & Milner 1923, Nicholls 1943), 'cotype' primary male (bl 6.7 mm) and preparatory II female (bl 5.4 mm), WAM 10665/6 and AM P8799 primary male (bl 4.7 mm), spring-fed pool at foot of Lesmurdie Falls, Darling Range, W.A., Nicholls, collection date unknown.

*Hypsimetopus* sp.: AM P54100, 1 primary male (bl 9.6 mm) and 1 preparatory II female (bl 10.2 mm), specimens scored from 8 individuals from near Zeehan, Tasmania, Australia; 41°53'S, 145°21'E (estimated from map), from roots of submerged sedges and button grass, A.M.M. Richardson & G.D.F. Wilson, 12 July 1990.

*Mesamphisopus capensis* (Barnard, 1914): TMAG G678, 1 primary male (bl 10.33 mm) and 1 preparatory female (bl 11.78 mm), near reservoir on Table Mountain, Cape Town, South Africa, altitude approx. 3000 ft., from a swiftly running stream under the moss growing on stones in the river bed, K.H. Barnard, circa 1936.

*Metaphreatoicus australis* (Chilton, 1891): AM P3347 Syntypes: 1 primary male (bl 17.4 mm) and 1 preparatory II female (bl 9.4 mm) specimens scored from 110 individuals from Upper Pipers Creek, Mt Kosciusko National Park upper Pipers Creek, NSW, 36°25'S, 148°25.5'E (estimated from collector's account), in pools under rocks, R. Helms, March 1889.

cf. *Metaphreatoicus* sp. (Thredbo River, NSW): AM P52667, 1 primary male (bl 15.8 mm) and prep II female (bl 14.6 mm) from 5 males, 3 females and 3 juveniles. Stn. NSW 497, Spring-fed tributary of Thredbo River on Cascade Trail, Kosciusko National Park, NSW 36°31.81'S 148°16.07'E, altitude 1620 m and temp 10.1°C, under moss in roots with gravel, G. Wilson & W. Vader, 20 Feb 1993.

*Neophreatoicus assimilis* (Chilton, 1894): Data from literature, Chilton (1894) and Nicholls (1944), Winchester, South Canterbury, New Zealand, in wells and from a spring discharging into Trout Hatchery at Temuka NZ (Nicholls 1944).

*Nichollisia kashiense* Chopra & Tiwari, 1950: ZSIC C4516/1, male (bl 27.7 mm), and supplemented by female (bl ~16.96 mm), male (bl 21.8 mm), female (bl 15.8 mm), male (bl 20.8 mm), ZSIC C4517/1, nontype specimens from type locality, well, Benaras Cant (UP).

*Paramphisopus palustris* (Glauert, 1924): AM P44487, 1 primary male (bl 7.8 mm) and 1 preparatory II female (bl 7.4 mm), from 112 individuals from Lake Monger, Perth, W.A. 31°55'S, 115°50'E (est from map), under fallen reeds and vegetation along shoreline, D. Jones & G.D.F. Wilson, 22 March 1995.

*Phreatoicoides gracilis* Sayce, 1900: AM P3348, 'normal' male (bl 17.7 mm) and brood-

- ing female (bl 12.9 mm), Narracan River, 30 km SE of Warragul, Victoria, Gippsland, Victoria, O.A. Sayce, collected before Sept 1912.
- Phreatoicopsis terricola* Spencer & Hall, 1896: AM P54101, 1 primary male (bl 41.2 mm) and hermaphrodite (bl 36 mm), from 16 individuals [largest male bl 53.8 mm], Stn V19, 900 m south west of Cowley Track, Otway Ranges, Vic, 38°33.36'S, 143°50.48'E (map), dug from oval burrows in damp sediment under tree ferns roots – no free water observed, W.F. Ponder & G.D.F. Wilson, 15 July 1991.
- Phreatoicus orarii* Nicholls, 1944: Data from Nicholls, 1944, Figures 35-36; in wells of the Orari River valley.
- Phreatoicus typicus* Chilton 1883: Lectotype female, Canterbury Museum catalogue number IZ 3550 (bl approximately 18.5 mm), type locality, Templeton, Canterbury Plains, New Zealand. AM P52733, male (bl 12.8 mm). AM P52734, preparatory female (bl 13.8 mm); male (bl 11.5 mm); male (bl 12.8 mm): Templeton, 43°33.11'S, 172°26.38'E (map), from sediments at bottom of well 2, depth approximately 30 m, G.D. Fenwick, 11 June 1986 (detailed data in Wilson & Fenwick 1999).
- Phreatomerus* sp. (cf. *latipes*): AM P54102, 1 primary male (bl 14.6 mm) and 1 preparatory II female (bl 11.4 mm) of possibly undescribed species from Dead Woman Springs, South Australia. 29°35.37'S, 137°27.28'E (map), W.F. Ponder & B. Jenkins, 30 Aug 1983.
- Synamphisopus ambiguus* (Sheard, 1936): AM P54103, male (bl 26.2 mm) and preparatory II female (bl 24.9 mm), site GR19, in Stony Creek, off Silverbrand Rd, the Grampians, Vic, 37°09.20'S 142°29.67'E (map), T. Doeg & J. Read, 15 Nov 1994.
- Pilbarophreatoicus* n.sp.1: AM P54104, male (bl 9.2 mm) and preparatory II female (bl 8.5 mm), Stn BES 4873, Millstream aquifer, Pilbara, Western Australia, 21°35'S, 116°58'E, W.F. Humphreys & S.M. Eberhard, 30 July 1997

## REFERENCES

- Adlem, L.T. 1996. Biogeography of the freshwater Peracarida (Crustacea) from Barrington Tops. Unpublished Honors Thesis, N.S.W. Bachelor of Science. Newcastle: Department of Geography, University of Newcastle.
- Banarescu, P. 1990. *Zoogeography of fresh waters. General distribution and dispersal of freshwater animals*. Vol.1 (with 208 maps). Wiesbaden: Aula-Verlag.
- Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10: 295-304.
- Brusca, R.C. & G. D. F. Wilson 1991. A phylogenetic analysis of the Isopoda with some classificatory recommendations. *Mem. Queensland Mus.* 31: 143-204.
- Chilton, C. 1918. A fossil isopod belonging to the fresh-water genus *Phreatoicus*. *J. Proc. Roy. Soc. New South Wales* 51: 365-388.
- Eberhard, S. & A. Spate 1995. *Cave Invertebrate Survey: Towards an Atlas of NSW Cave Fauna*. A report prepared under NSW Heritage Assistance Program NEP 94 765. Queanbeyan: National Parks & Wildlife Service, NSW.
- Eberhard, S.M., A.M.M. Richardson & R. Swain 1991. *The invertebrate cave fauna of Tasmania*. Hobart: Zoology Department, University of Tasmania.
- Eriksson, T. 1998. *AutoDecay ver. 4.0*. Program distributed by the author. Stockholm: Department of Botany, Stockholm University.
- Faith, D.P. 1992. Systematics and conservation on predicting the feature diversity of subsets of taxa. *Cladistics* 8: 361-373.

- Herbert, C. 1997. Sequence stratigraphic analysis of Early and Middle Triassic alluvial and estuarine facies in the Sydney Basin, Australia. *Austr. J. Earth Sci.* 44: 125-143.
- Horwitz, P.H.J. 1989. The faunal assemblage (or pholeteros) of some freshwater crayfish burrows in southwestern Tasmania. *Bul. Austr. Soc. Limnology* 12: 29-36.
- Humphreys, W.F. 1994. *The subterranean fauna of the Cape Range coastal plain, northwestern Australia*. Report to the Australian Heritage Commission and the Western Australia Heritage Committee. Perth: Western Australian Museum.
- Knott, B. & S.A. Halse 1999. *Pilbarophreatoicus platyarthricus* n.gen., n.sp. (Isopoda: Phreatoicoidea: Amphispodidae) from the Pilbara region of Western Australia. *Records of the Australian Museum* 51(1): 33-42.
- Maddison, W.P. & D.R. Maddison 1992. *MacClade, analysis of phylogeny and character evolution, version 3*. Sunderland, Massachusetts: Sinauer.
- Nelson, G. & P.Y. Ladiges 1996. Paralogy in cladistic biogeography and analysis of paralogy-free subtrees. *Amer. Mus. Novitates* 3167: 1-58.
- Nicholls, G.E. 1943. The Phreatoicoidea. Part I. The Amphispodidae. *Pap. Proc. Roy. Soc. Tasmania* 1942: 1-145.
- Nicholls, G.E. 1944. The Phreatoicoidea. Part II. The Phreatoicoidea. *Pap. Proc. Roy. Soc. Tasmania* 1943: 1-156.
- Ponder, W.F. 1994. Australian freshwater Mollusca: Conservation priorities and indicator species. *Rec. Queensland Mus.* 36: 191-196.
- Ponder, W.F. 1997. Conservation status, threats and habitat requirements of Australian terrestrial and freshwater Mollusca. *Mem. Mus. Victoria*, 56: 421-430.
- Richardson, A.M.M. & R. Swain 1978. The freshwater invertebrates. Lower Gordon River scientific survey, report to the Hydro-Electricity Commission, Tasmania. Hobart: University of Tasmania.
- Schram, F.R. 1974. Paleozoic Peracarida of North America. *Fieldiana, Geology* 33: 95-124.
- Storey, B.C. 1995. The role of mantle plumes in the continental breakup: case histories from Gondwanaland. *Nature* 377: 301-308.
- Swofford, D.L. 1999. *PAUP\* 4.0, Phylogenetic Analysis Using Parsimony (and Other Methods)*. Sunderland, Massachusetts: Sinauer.
- Tillyard, R.J. 1916. Mesozoic and Tertiary Insects of Queensland and New South Wales: Descriptions of the Fossil Insects. *Queensland Geol. Surv. Publ.* 253: 11-60.
- Wilson, G.D.F. & G.D. Fenwick 1999. Taxonomy and Ecology of *Phreatoicus typicus* Chilton, 1883 (Crustacea, Isopoda, Phreatoicoidea). *J. Roy. Soc. New Zealand* 29(1): 41-64.
- Wilson, G.D.F. & E.L. Ho 1996. *Crenoicus* Nicholls, 1944, (Crustacea, Isopoda, Phreatoicoidea): Systematics and biology of a new species from New South Wales. *Rec. Austr. Mus.* 48: 7-32.
- Wilson, G.D.F. & R.T. Johnson 1999. Ancient endemism among freshwater isopods (Crustacea, Phreatoicoidea). In: The Other 99%. The conservation and Biodiversity of Invertebrates, W.F. Ponder & D. Lunney (eds) 264-268. Mosma: *Trans. Roy. Zool. Soc. New South Wales*.
- Wilson, G.D.F. & S.J. Keable 1999. A new genus of phreatoicoidean isopod (Crustacea) from the North Kimberley Region, Western Australia. *Zool. J. Linn. Soc.* 126: 51-79.