

Ancient endemism among freshwater isopods (Crustacea, Phreatoicidea)

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Ancient clades with restricted geographic distributions have been found in the isopod crustacean suborder Phreatoicidea. These isopods colonized fresh water in Gondwana by the Triassic Era and today are restricted to permanent groundwaters. A phylogenetic analysis of 21 exemplar species showed that major cladogenic events took place prior to the fragmentation of Gondwana. *Nichollisia*, a genus restricted to India, was deeply nested within a Western Australian and Victorian clade. The Phreatoicidae branched off early in all cladograms, with Australian and New Zealand sister clades. Some clades may be closely associated with Gondwanan landmasses that were subdivided by shallow Cretaceous seas.

INTRODUCTION

The Phreatoicidea are the earliest derived isopod Crustacea (Brusca and Wilson 1991), appearing in the marine fossil record during the Carboniferous (~325 mybp: Hessler 1969; Schram 1970, 1974). Phreatoicideans invaded fresh waters of the Gondwanan supercontinent by the Triassic (*Protamphisopus wianamattensis* (Chilton 1918), see Nicholls 1943) and subsequently became extinct in the oceans. Today, phreatoicideans are restricted to permanent fresh waters and occur in Australia as well as on a few other continental fragments derived from Gondwana (Bănărescu 1990; Wilson and Keable, in press). The distribution of phreatoicideans within Australia shows much endemism at the level of genus and higher (Fig. 1). This paper examines phreatoicidean phylogeny and biogeography in Australia in relation to taxa that occur in other Gondwanan localities. The distributions evident today may reflect the biogeography of clades derived during the Mesozoic.

MATERIALS AND METHODS

Distributional data in this paper comes from localities where we have inspected specimens, either in the collections of the Australian Museum or from other sources. Some records from the literature were not included because the specimens have not been examined. Figure 1 shows this distribution of phreatoicidean taxa within Australia, based on the taxonomy of Nicholls (1943, 1944) but including several new genera. Undescribed species included in this analysis are: *Eophreatoicus* sp., one of >5 new species from Kakadu, Northern Territory and distinct from *E. kershawi* Nicholls 1926; *Phreatomerus* sp., possibly conspecific with *P. latipes* (Chilton 1922) but one of several

distinct genetic forms known from the South Australian artesian springs of the Lake Eyre supergroup (M. Adams, Environmental Report, Kinhill Engineers Pty Ltd); *Hypsometopus* sp. from near Zeehan, Tasmania, possibly conspecific with *H. intrusor* Sayce 1902 but variation has not been fully evaluated; cf. *Hyperoedesipus* sp. from the Pilbara region of Western Australia, a new genus with presumed affinities to *H. plumosus* Nicholls and Milner 1923. The Tasmanian genera are poorly defined but are labelled in Figure 1 to indicate the possible phreatoicidean diversity of this area.

A taxonomic database in the DELTA format (Dallwitz 1980; Dallwitz *et al.* 1993) was used to generate the phylogenetic data (as in Wilson and Keable, in press). As of October 1997, the database contained 21 species, including representatives of non-Australian genera and several undescribed species. Data on some taxa were derived from the literature (e.g., *Nichollisia* Chopra and Tiwari 1950 and *Neophreatoicus* Nicholls 1944) or were not fully dissected because specimens were type material (e.g., adult *Hyperoedesipus plumosus*). Because congeners typically formed single clades (e.g., the Victorian and New South Wales genus *Crenoicus* Nicholls 1944), only one species from each genus was used to simplify the resulting cladograms. The data, therefore, comprised only 17 taxa. The phylogenetic data (135 unordered morphological characters, 98 of which were informative) were analysed using the computer program PAUP version 3.1.1 (Swofford 1993; parsimony analysis settings TBR, Mulpars, addseq = random, 10 iterations). Space constraints preclude the presentation of our primary data in this paper, but they may be obtained on request from the first author. Although the current analysis yielded

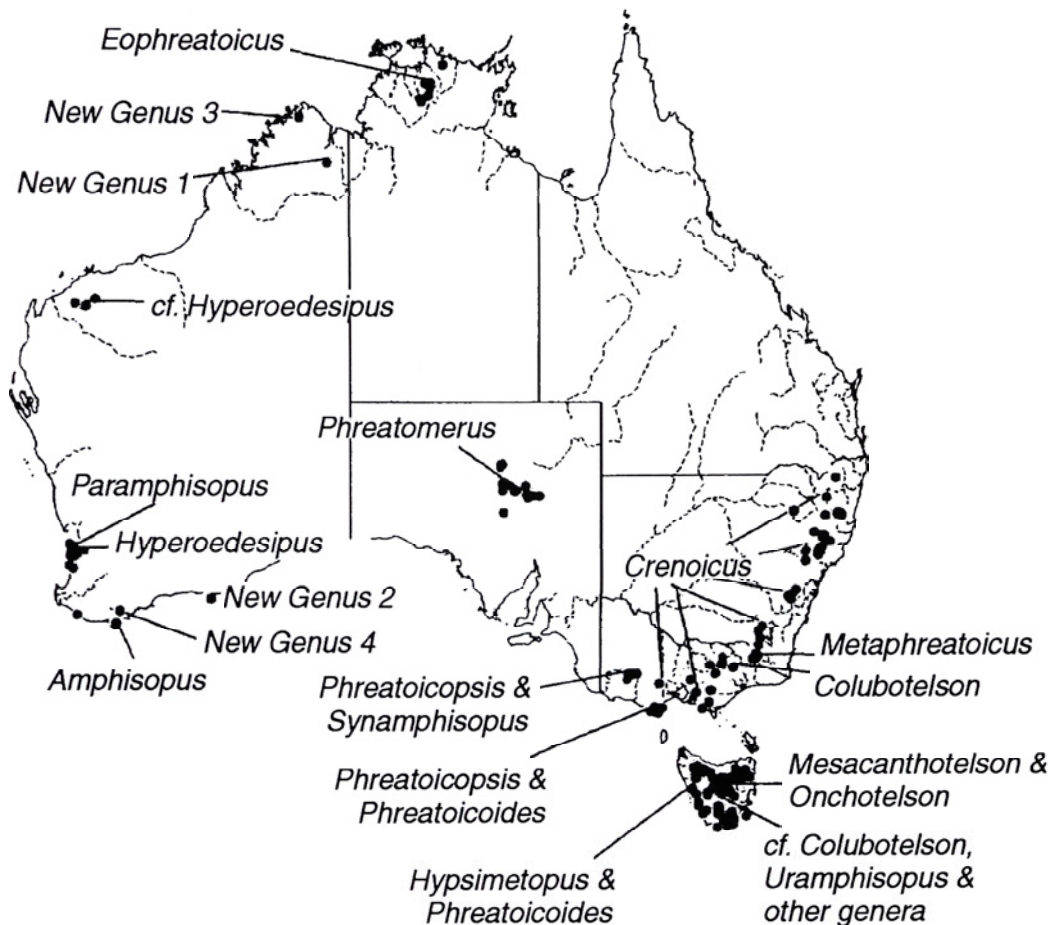


Figure 1. Isopoda Phreatoicida: distribution of genus-level taxa in Australia, based on material that we have examined (filled circles) and using the taxonomy of Nicholls (1943, 1944). Several new genera but not all nominal genera are shown. "New Genus 1" is described in Wilson and Keable (in press) and "cf. *Hyperoedesipus*" is under description. Other new genera are not yet described, and therefore do not appear in the cladistic analysis.

unrooted trees, we orientated the resulting topologies by placing the South African species *Mesamphisopus capensis* (Barnard 1914) as the "outgroup" because this genus may be derived basally (Wilson and Keable, in press). These cladistic estimates should be considered preliminary because some clades may change position after the addition of new taxa. The data are not complete, because several undescribed genera (noted in Fig. 1) and many taxa from Tasmania, New Zealand and other areas are not included. Relationships between areas of endemism were evaluated by replacing phreatoicidean names with their areas on the strict consensus of the trees obtained in the parsimony analysis.

RESULTS AND DISCUSSION

Figure 1 demonstrates that most super-specific taxa consist of geographically restricted clades. *Crenoicicus* is an exception to this pattern, with a distribution that spans the Great Dividing Range through New South Wales and Victoria (Wilson and Ho 1996). The apparent distribution of *Colubotelson*

Nicholls 1944 from Victoria to Tasmania may be a taxonomic artifact. All other genera appear to be localized to relatively small regions. For example, *Eophreatoicus* species are found only on and around the Arnhem Plateau of the Northern Territory, and *Paramphisopus* Nicholls 1944 species, despite being good swimmers and presumably capable of active dispersal, is found only in the coastal ponds of the Perth region, Western Australia.

Are these distributions recent, being established during the times when Australia became arid, or are they older? If older, how old? The phylogenetic analysis (Fig. 2) allows this issue to be addressed as well as to test the effectiveness of the existing classification. The family Amphisopodidae is paraphyletic, with the Phreatoicidae and the Nicholssiidae nested within it. In Nicholls' (1943) conception, the Amphisopodidae was based on what he regarded as primitive characters, so the paraphyly of this family is no surprise. The monophyly of the Phreatoicidae is supported (Wilson and Keable,

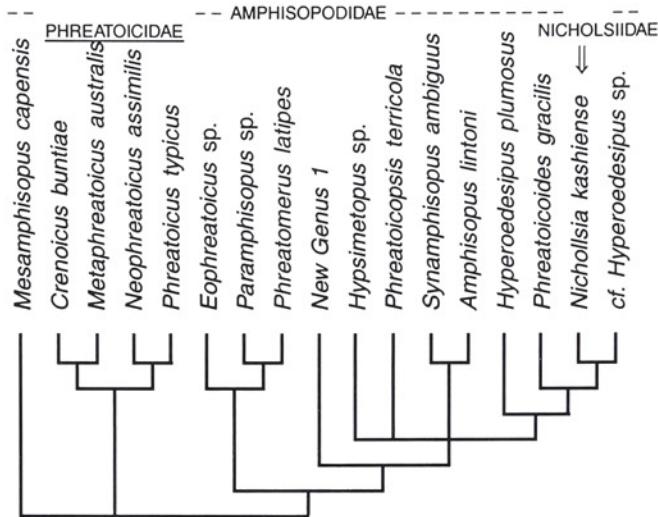


Figure 2. Strict consensus of 3 trees (length 416, consistency index 0.44) resulting from a parsimony analysis of data derived from the DELTA database. Extent of the families in the current classification of the Phreatoicidea (Nicholls 1943; Chopra and Tiwari 1950) are indicated by horizontal lines for the Phreatoicidae (beneath) and the Amphisopodidae (extending laterally, dashed), and by an arrow for the Nicholssiidae.

in press), although this clade has proven to be unstable with the addition of more taxa.

Although the existing classification does not adequately describe these preliminary phylogenetic estimates, named clades (genera) show clear relationships with geography. The major cladogenic events in the phreatoicideans appear to have taken place prior to the fragmentation of Gondwana, in agreement with the fossil record. *Nichollisia*, a genus today restricted to the Indian subcontinent, is deeply nested within a clade including taxa from Western Australia and Victoria. The family Phreatoicidae branched off early in all cladograms, showing distinct Australian and New Zealand sister clades.

By replacing taxon names in the consensus from Figure 2 with general localities of the taxa and their related congeners (Fig. 3), a picture of ancient endemism emerges. The pattern does not match the pattern of fragmentation of Gondwana (reviewed in Storey 1995), because Africa and India should show basal branches in the tree if this were the source of biogeographic vicariance. Because India is nested high in the tree but separated early during the fragmentation of East Gondwana (approximately 120 mybp: Storey 1995), we can infer that many of the basal events represented on the area consensus are at least as old as this. The close association of the Pilbara in Western Australia and the Ganges Plains of India in reconstructions of Gondwana as well as in the consensus (Fig. 3) suggests that traces of ancient geographic vicariance remain in

the modern distribution of phreatoicideans. Because phreatoicidean isopods were present in Gondwanan fresh waters by the Triassic (Chilton 1918), many of the cladogenic events must have pre-dated the supercontinent's breakup.

Some phreatoicidean clades within Australia may also reflect the association of Gondwanan landmasses that were subdivided by shallow Mesozoic seas. Figure 4 overlays the approximate distribution of dry landmasses during the mid-Cretaceous (BMR Palaeogeographic Group 1990) and the current distribution of phreatoicidean localities in Australia. During this period, shallow seas largely divided Australia into a western and an elongate southeast to northwest part. Two distal clades in the taxon-area consensus show a vicariant pattern that may be influenced by this inundation event, the *Paramphisopus* — *Phreatomerus* clade and the *Amphisopus* Nicholls 1926 — *Synamphisopus* Nicholls 1943 clade, both suggesting relationships between Victoria and Western Australia.

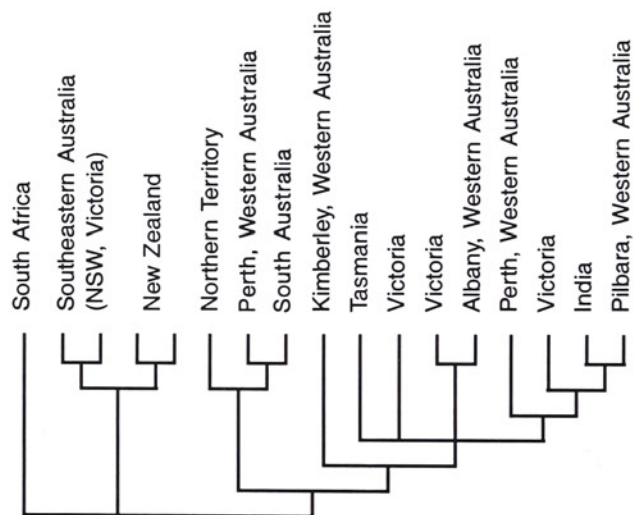


Figure 3. Taxon-area relationships, derived from Figure 2 but with taxa replaced by general localities.

A single phylogenetic estimate (with several possible topologies) is not adequate to identify general biogeographic patterns in ancient taxa. Scientists at the Australian Museum have begun to evaluate these ancient biogeographic patterns by collecting data from a diverse set of arthropods and molluscs, both terrestrial and fresh water, that show phylogenetic patterns that predate the fragmentation of Gondwana. Congruence in the area relationships of these taxa will provide a better picture of the biogeography and evolution of Gondwana and its biota.

The data presented here suggest that phreatoicidean isopods should rank highly in conservation issues. Many of these taxa



Figure 4. Approximate maximum extent of dry land (hatched area) during the middle Cretaceous (119–114 mybp), after BMR Palaeogeographic Group (1990). Modern phreatoicidean localities (from Figure 1) are shown as filled circles.

are historically unique and, because of their high endemism, may be under considerable threat from human activities. Habitats of phreatoicidean species have been damaged or lost owing to urban development (e.g., *Paramphisopus palustris* (Glauert 1924) in the Perth region: unpubl. data) or use of groundwater (e.g., Hergott Bore, South Australia, the type locality of *Phreatomerus latipes*, no longer has isopods: W. Ponder, pers. comm.). Other taxa, such as the poorly known new genera indicated in Figure 1, may be under considerable threat from regional development of groundwater. Such taxa require careful documentation of their distribution and phylogenetic relationships for conservation measures to be effective in protecting Australia's unique biodiversity.

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