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EMERGING KNOWLEDGE OF DIVERSITY, DISTRIBUTION AND ORIGINS OF SOME AUSTRALIAN STYGOFAUNA

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The last decade has transformed understanding of the diversity, distribution and affinities of Australian stygofauna, especially in the more arid parts. Western Australia, in particular, is emerging as having an exceptional diversity of often unexpected lineages. These studies are still in their early stages, in terms of both geographic coverage, and taxonomic and systematic knowledge. However, published species plus information from specialists in certain taxa places the total recognised number of stygal taxa recognised in Australia at 515 species (Dytiscidae, 80; Ostracoda, 29; Copepoda, 109; Isopoda, 40; Amphipoda, 65; Syncarida, 32; Acarina, 150; Gastropoda, 10). This is known to be a considerable underestimate as in numerous higher taxa many undescribed species, not included in figure 1 are known to occur from molecular (R. Leys, pers. comm.) or morphological evidence, especially from the Copepoda (T. Karanovic, pers. comm. 2004), Ostacoda (I. Karanovic, pers. comm. 2004), Bathynellacea (J-L Cho, pers. comm. 2004) and Amphipoda. Stygobiont amphipod species yet to be described are known from Queensland (*Chillagoe* sp.), New South Wales (Neoniphargidae), South Australia (north-western, east-central, and south-eastern - Melitidae and Paramelitidae), Tasmania (Paramelitidae), and Western Australia (Ashburton River, Pilbara region, Yilgarn region - Bogidiellidae, Melitidae and Paramelitidae).The state of flux of this estimate can be gained when it is realised that 54% of this number (including both described and recognised species) have been formally described in the last five years. This value represents 15% of the 3,410 described species in 13 large higher taxa of freshwater stygobites that were enumerated by Scarsbrook *et al.* (2003) from the world synopsis (Botosaneanu 1986). While these world figures are now dated, Australia, which comprises ~7% of the Earth's land area, would appear to greatly exceed the world average of stygal species per area. This is unexpected in a continent where two-thirds of the land mass lies within the arid zone, and it is in the arid zone where much of the stygal diversity occurs. Examination of the proportional distribution of eight higher taxonomic groups within Australia compared with the world average proportional distribution of those taxa (from Scarsbrook *et al.* 2003) reveals that the Australian fauna is probably deficient in isopods and molluscs (9% and 18% world average) but that beetles are greatly over represented (3,100% world average) amongst the Australian stygofauna. The remaining groups considered (Acari, Amphipoda, Syncarida, Ostracoda, Copepoda) have between 61% and 159% world average). Further research may alter this picture, as has occurred recently with the Dytiscidae.

Australian amphipods are diverse and predominently stygal, containing representatives of ancient freshwater lineages, of which the crangonyctoids are the most ubiquitous (Bradbury 1999), and those of relatively recent marine origin (Hadziidae, Melitidae). The distributions match that of land areas supposedly not submerged—as also does the distribution of other freshwater lineages, the Phreatoicidea and Tainisopidea (Humphreys 2004)—and submerged, respectively, in the ocean since the Cretaceous. Crangonyctoid amphipoda have hitherto, with few exceptions, been regarded as confined by the cool fresh waters of the south east and south west of the continent and Tasmania (Barnard and Williams 1995). Calcrete deposits have developed extensively in the Pilbara and Yilgarn Cratons, tectonically stable regions which have been emergent above the sea since the Precambrian. Where these ground waters have remained fresh, especially in the extensive palaeochannels (Humphreys 1999, 2001), they have been found to contain diverse crangonyctoid species as well as bogidiellids; where more saline, to contain hadziid species. It is already clear the knowledge of the diversity of hypogean amphipods in Australia confirms Holsinger's (1993) view that southern Australia is

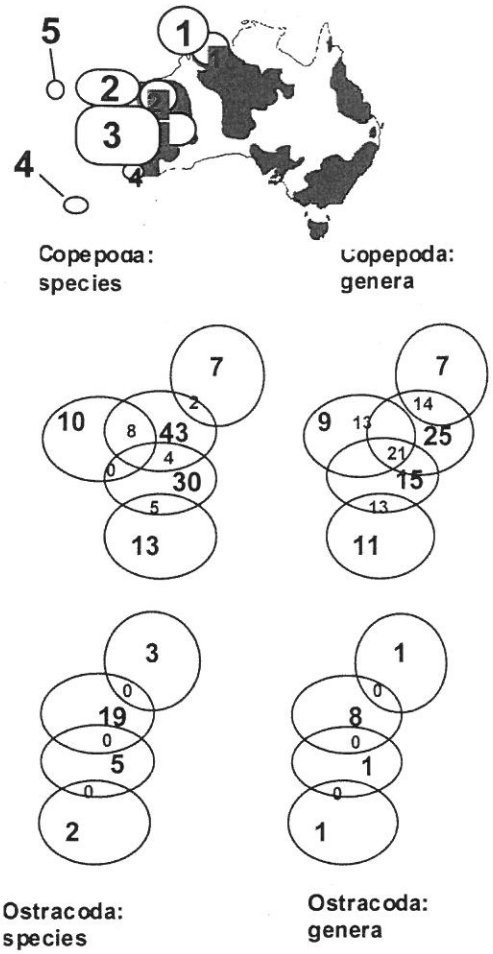

Figure 1 : Venn diagrams showing the number of species (large numerals) and percentage overlap between adjacent regions of Western Australia for stygal Copepoda (upper) and and Ostracoda (lower) species (left) and genera (right). Regions (denoted by number or writing on map): 1, Kimberley; 2, Pilbara; 3,Yilgarn; 4, Leeuwin-Naturaliste, 5, Cape Range/Barrow I.. Date from Ivana Karanovic (pers. comm. 2004) and Tomislav Karanovic (pers. comm. 2004).

a region of significant diversity for this group. However, description of Paramelitidae from the Pilbara region of Western Australia and work underway on species from the Yilgarn Craton contradicts findings elsewhere which predict "only in subtropical areas where freshwater stygobionts have been derived from marine ancestors by stranding ..... have significant stygobiont amphipod faunas evolved in limnic waters" (Holsinger 1993).

Stygal copepods have been recorded from about 500 sites, 112 species of representing four orders, 15 families and subfamilies, and 44 genera. These are distributed amongst regions as follows: in Western Australia, Margaret River, 12; Yilgarn, 31 (T. Karanovic 2004); Pilbara, 43; Kimberley, 8; Queensland: Pioneer Valley, 15; New South Wales, 3 stygoxenes, mainly from caves. Generally, most forms of ancient freshwater origin show Gondwana or Eastern Gondwana connections on global scale, while those of marine origin have Tethyan connections. Of the 112 species, 84% have been described from aquifers in Western Australia (T. Karanovic pers. comm. 2004).

The ostracod fauna of Western Australian continental subterranean waters almost exclusively comprises representatives of the subfamily Candonidae (Podocopida). A total of 29 species has been recorded, 28 of which have been described recently (Karanovic & Marmonier 2002, 2003; I. Karanovic 2003a, b; 2004, 2005, in press). They comprise 11 genera in three distinct tribes: Humphreyscandonini Karanovic, in press; Candonopsini Karanovic, 2004 and a third yet to be formalized (Karanovic in prep). All these tribes are very old lineages within the subfamily Candoninae. The first tribe has eight genera in Australia (19 species) found only in the Pilbara region of Western Australia, and three genera elsewhere (subterranean waters of India and Europe). The Candonopsini contains four genera, two in Australia and the other two in Central and South America, and the third tribe will contains two genera. In addition to the Candoninae, two species of the family Darwinulidae occcur in the interstitial waters and wells (Martens & Rossetti, 2002). Stygal species in anchialine waters are known from the Cytheruridae (Namiotko *et al.* 2004) and

Thaumatocypridae (Myodocopida) (Danielopol *et al.*, 2000) (I. Karanovic, pers. comm. 2004).

There is an exceptional number of Dytiscidae species in the stygofauna of the Australian arid zone, with so far ~80 species known, an order of magnitude greater than elsewhere in the world. It includes stygal species in both the tribes Bidissini (*Limbodessus* and *Bidessodes*) and Hydroporini (*Nirripirti* which may include *Kintingka*) within the subfamily Hydroporinae (Watts and Humphreys 2004), as well as the first stygal diving beetle not belonging to the subfamily Hydroporinae, namely in the Copelatinae (*Copelatus*: Balke *et al.* 2004). The Hyphydrinae and family Noteridae, which have stygal representatives in other parts of the world, are not known as stygofauna in Australia. They occur in the northern and central Yilgarn of Western Australia, and in the Ngalia Basin in the Northern Territory. Up to four species are found in the same calcrete (13 cases of sympatric sister species pairs; Leys *et al.* 2003; Leys *et al.* pers. comm.) and are well separated by size. They exhibit a small range of stygomorphies (reduced or absent eyes, wings, colour and increased mobility of prothorax) which stands in contrast to the large range of unusual morphologies in comparison to epigean close relatives that seem to be a result of relaxation of selection pressures.

The chains of salt lakes (playas) in arid Australia are the base level of groundwater flow along the course of palaeodrainages constrained by Permian palaeovalleys. Groundwater calcretes form near salt lakes and contain diverse stygal communities (Dytiscidae, Amphipoda, Oniscidea, Gastropoda, Ostracoda, Copepoda, Bathynellacea: Humphreys 2001) endemic to a given deposit. The fauna is best known from the Oniscidea (Scyphacidae: *Haloniscus:* Taiti and Humphreys 2001; S. Taiti *et al.* unpublished) and Dytiscidae (80 species of Copelatinae, Hydroporinae: Bidessini, Hydroporini: e.g. Watts and Humphreys 2004) for which both morphological and molecular data are available (Cooper *et al.* 2002; Leys *et al.* 2003) and, contrary to the initial hypothesis about their origin (Humphreys 2001), their phylogenies do not map the palaeodrainage channels. Conversely, ancient lineages, such as crangonyctoids, also represented by discrete populations in the calcretes (R. Leys, pers. comm.), do tend to map the palaeodrainages in the Pilbara (T. Finston and M. Johnson pers. comm. 2004).

There is increasing evidence from arid Australia that elements of both terrestrial and aquatic subterranean fauna are refugial in origin (troglobitic Schizomida, stygal Oniscidea, stygal Dytiscidae). In each case, despite wide distribution of close relatives outside the arid zone (Schizomida: northern monsoonal rainforest, Harvey 1992, 2000, pers. comm. 2004); Oniscidea, *Haloniscus*: south of arid zone, Taiti & Humphreys 2001, S. Taiti *et al.* unpublished; Dysticidae: widely outside arid zone, CHS Watts, data), troglobitic and stygobitic species are confined to the arid zone; there is evidence, also, of a southward progression through time of the isolation of dytiscids in groundwater calcrete aquifers (Leys *et al.* 2003), mapping the southward spread of aridity.

The Western Shield contains a number of ancient (crangonyctoid amphipods, bathynellacean syncarids, phreatoicidean isopoda) as well as Tertiary stygal lineages (Dytiscidae, Oniscidea) but the northern region (Pilbara) has a stygofauna distinct from the southern part (Yilgarn) despite having supposedly been a single land mass since at least the Palaeozoic. This distinction applies to those presumably ancient lineages above, as well as to Tertiary invaders such as the dytiscids and oniscideans. In Figure 1 the diversity (to 2004) of stygal Copepoda and Ostracoda species in Australia and the general lack of overlap, in the ostracods a total lack of overlap between adjacent regions even at the generic level. It is more remarkable that this distinction holds even in the contiguous and long emergent parts of the Western Shield, a distinction that remains enigmatic.

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