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AMPHIPOD (CRUSTACEA) DIVERSITY IN UNDERGROUND WATERS IN AUSTRALIA: AN ALADDIN'S CAVE

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Abstract

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The presently known troglobitic and troglophilic (stygobiont) species of Australian aquatic amphipods are listed and discussed, and their geographical distributions are indicated. The 26 species known are predominantly in crangonyctoid and hadzioid families. Further undescribed species are referred to. The diversity is high and confirms Australia as a centre of stygobiont amphipod speciation. Explanations for the diversity include the considerable extent of karst, the frequent occurrence and extensive areas of former marine transgressions, and palaeoclimatic fluctuations. Attention is drawn to the usefulness of stygobiont amphipods as biogeographical tools, and to the need for their diversity in Australia to be noted in discussions, legislation and actions to conserve Australian biodiversity.

Introduction

Until relatively recently, our knowledge of the taxonomy of Australian freshwater amphipods (Crustacea: Amphipoda) was limited. Few species had been described, the extent of diversity was unrecognized, and most available species descriptions were in need of revision. Williams and Barnard (1988) began the initial revision needed with redescriptions of all known species and added descriptions of a few new species. Their efforts were continued in a second paper (Barnard and Williams, 1995). Both papers referred to subsurface as well as surface forms.

Taxonomic studies of the Australian freshwater amphipods are a long way from completion but the papers of Barnard and Williams and other recent studies have pointed to the existence of much greater diversity amongst surface forms than had been realised. They also point to the existence of greater biodiversity amongst subsurface forms than had been realised (Williams, 1986). The diversity of subsurface forms is confirmed by the studies of Knott (1983) and Bradbury and Williams (1995, 1996 a, b) and unpublished work on recent collections from caves and other underground waters in Western Australia, New South Wales and Tasmania. This diversity amongst subsurface forms is not surprising given both the paucity of previous studies and, more importantly, the fact that amphipods are known worldwide to be amongst the most widespread, abundant and diverse of subsurface aquatic invertebrates (Holsinger, 1991).

In this paper, our immediate intentions are to summarize the present status of our knowledge of the taxonomy of hypogean amphipods in Australia on the basis of described species, to provide some indication of the extent of diversity based on described species and undescribed material, and to offer some explanation for this diversity. Thus this paper provides a basis for discussion and should help achieve two, more general aims, namely:

1. to focus attention upon the usefulness of hypogean amphipods as biogeographical tools (given the nature of their ecology and environments) within an Australian context, and
2. to draw attention to the significant diversity of Australian hypogean amphipods at a time when considerable discussion is taking place at a variety of levels — State, Federal and international — on the conservation of biodiversity.

In these discussions, the diversity of hypogean amphipods should not be forgotten; whilst caves and other subsurface waters do not have the faunal diversity of surface waters, and of course lack plants, within the animal groups that do occur there (see, for example, Culver, 1982, and Barr and Holsinger, 1985), much speciation has taken place. Holsinger (1991, 1994a) has previously noted the global importance of hypogean amphipods for biogeographical studies, and Knott (1985) has noted their interest in Australia. Australian speleologists have long recognized the need for caves to be conserved and their fauna protected on the basis of both biological and geomorphological criteria. Governments have generally acted sympathetically to this need for cave protection and conservation.

In passing, we also mention the recent recognition of much higher diversity than expected in other bodies of inland water in Australia that — like underground waters — have generally received less attention from biologists than permanent fresh waters near major metropolises. These waters include salt lakes, temporary streams and freshwater lakes, and other bodies of surface water in arid and semi-arid regions. Recent work has indicated that considerable biodiversity occurs within such localities (e.g., see Frey, 1991; Timms, 1993; Comin and Williams, 1994). Their fauna, however, does not usually involve amphipods as these crustaceans are more or less confined to permanent, fresh waters. It does involve a comprehensive range of other invertebrate groups.

Present status of the hypogean (stygobiont) amphipod fauna

Table 1 lists all described species recorded thus far from either underground waters (caves, boreholes) or springs near their source. It lists two principal sorts of taxa: those which have been recorded from underground waters (including springs) and nowhere else (obligate stygobionts or troglobites *sensu* Barr and Holsinger, 1985); and those recorded from both underground and surface waters (facultative stygobionts or troglophiles). In total, the table lists over 30 species of which half can be regarded as troglobites and half, troglophiles. All are endemic. On the basis of described species, therefore, approximately 60 per cent of the total amphipod diversity of Australian inland waters can be found in subsurface waters. This figure is far higher than the global figure of 13 per cent given by Holsinger (1993) for the approximate fraction of all described amphipod species that are stygobionts. Our percentage is undoubtedly inflated by our concentration on stygobionts during recent studies. It seems likely that more balanced and comprehensive studies of both hypogean and epigean species will lead to some correction of this high figure towards a lower value.

With regard to the systematic positions of the species listed in the table, it is immediately obvious that most belong to the three groups identified by Holsinger (1993) as those of most importance so far as hypogean amphipod diversity is concerned worldwide, namely, the crangonyctoids, the hadzioids *s. l.* and the bogidiellids.

The geographical distribution of the species listed in Table 1 is indicated in Fig. 1. An obvious point to emerge from this figure is the large number of stygobiont species recorded from Western Australia. Of particular note in this respect is the extraordinarily large number described from Barrow Island, a relatively small offshore island. Species recorded from this island comprise those collected from boreholes (species of *Nedsia* and *Bogadomma australis*), and two species from an anchialine cave — that is, a coastal cave under marine influence — (*Liagoceradocus* spp.). None of the *Nedsia* species was found co-existing with another (but note paucity of specimens available), and all at present are known only from one locality each, the type locality. Apart from the facultatively subterranean *Austrochiltonia australis,* which is also a common and widespread surface form, other species listed in the table and figured in the map are likewise recorded from either a single locality or a restricted area. An absence of sympatry appears to be generally characteristic of stygobiont amphipods elsewhere too.

A less obvious point shown by Fig. 1 is that the distributions of hypogean amphipods extend more to the north in Australia than do those of

Figure 1. Geographical distribution of stygobiont amphipods in Australia. 1–12, hadzioids; 13, *Bogadomma*; 14–28, crangonyctoids. *Austrochiltonia australis*, *Phreatochiltonia anapthalma* and *Pseudomoera fontana* omitted.

Table 1. Systematic position and geographic distribution of Australian subterranean amphipods. The index numbers relate to Fig. 1.

Taxon	Distribution	Habit	Index no.
HADZIOIDS			
Melitidae			
Nedsia straskraba Bradbury & Williams	Barrow Island	troglobite	1
N. fragilis Bradbury & Williams	Barrow Island	troglobite	2
N.humphreysi Bradbury & Williams	Barrow Island	troglobite	3
N.hurlberti Bradbury & Williams	Barrow Island	troglobite	4
N.urifimbriata Bradbury & Williams	Barrow Island	troglobite	5
N.macrosculptilis Bradbury & Williams	Barrow Island	troglobite	6
N.sculptilis Bradbury & Williams	Barrow Island	troglobite	7
Liagoceradocus subthalassicus Bradbury & Williams	Barrow Island	anchialine troglobite	8
Liagoceradocus branchialis Bradbury & Williams	North West Cape	anchialine troglobite	9
Nedsia douglasi Barnard & Williams	North West Cape	troglobite	10
Brachina invasa Barnard & Williams	Flinders Ranges	hyporheic interstitial	11
Nurinna Cave *Melita* like	Nullabor Plain	troglobite	12
BOGIDIELLIDS			
Bogidiellidae			
Bogadomma australis Bradbury & Williams	Barrow Island	troglobite	13
CRANGONYCTOIDS			
Paramelitidae			
Hurleya kalamundae Straskraba	SW Australia	troglobite	14
Protocrangonyx fontinalis Nicholls	Darling Range, WA	troglophile	15
Uroctena westralis (Chilton)	nr Perth W A	troglophile	16
Totgammarus eximius Bradbury & Williams	SW Australia	troglophile	17
Chillagoe thea Barnard & Williams	N Queensland	troglobite	18
Giniphargus pulchellus Karaman & Barnard	Gippsland Vic	troglobite	19
Austrogammarus species Barnard & Karaman	Tasmania	troglophile	20
Austrogammarus smithi Williams & Barnard	Tasmania	troglophile	24
Antipodeus antipodeus (G.W.Smith)	Tasmania	troglophile	21
Antipodeus wellingtoni (G.W.Smith)	Tasmania	troglophile	22
Antipodeus franklini Williams & Barnard	Tasmania	troglophile	23
Uronyctus longicaudus Stock & Iliffe	SE South Australia	troglobite	25
Perthiidae			
Perthia acutitelson Straskraba	SW Australia	troglophile	26
Neoniphargidae			
Neoniphargus obrieni Nicholls	Mt Buffalo, Vic.	possible troglophile	27
Neoniphargus spp. Stebbing	Tasmania	troglophile	28
CEINIDS			
Ceinidae			
Phreatochiltonia anapthalma Zeidler	Mound spring, SA	poss troglobite	29
Austrochiltonia australis (Sayce)	cosmopolitan	troglophile	30
EUSIRIDS			
Eusiridae			
Pseudomoera fontana (Sayce)	SE Australia	troglophile	31

any surface aquatic amphipod. Thus, those from Barrow Island in Western Australia and *Chillagoe thea* in Queensland lie many hundreds of kilometres north of areas where surface amphipods occur. It is not difficult to provide an explanation of this; freshwater amphipods are not common in subtropical and tropical waters and only subterranean waters in these regions provide the lower temperatures and more stable environmental conditions required to support amphipod populations. It may be noted that not all northern and apparently suitable subtropical subsurface waters in Australia contain amphipods. The Cutta Cutta caves near Katherine, Northern Territory, for example, do not appear to be inhabited by amphipods; a recent and diligent search for them by one of us (WDW) failed to locate any specimens although considerable material of the atyid shrimp which do inhabit the caves was collected (*Parisia* spp.; see Williams, 1964). Perhaps the water in this cave system is too warm, the atyids too powerful a competitor, or there was no available ancestral surface form. No amphipods, likewise, have been collected from caves in the Kimberly region of Western Australia (Humphreys, 1995).

As for geographical patterns, three are obvious and accord with the broad biogeographical patterns postulated by Holsinger (1994a) for all subterranean amphipods and perhaps other malacostracans. These patterns are:

1. that shown by stygobionts derived from old freshwater ancestors (limnostygobionts);
2. that shown by stygobionts derived from marine ancestors, and
3. that shown by stygobionts inhabiting coastal waters with marine affinities and clearly derived from closely allied marine ancestors (thalassostygobionts or 'crawl-outs').

The process involved in pattern 3 is often referred to as 'stranding'. Crangonyctoid species clearly exhibit pattern 1, hadzioid species, pattern 2, and *Liagoceradocus* species, pattern 3. Other Australian stygobionts are less easily assigned to a particular pattern, but *Pseudomoera fontana* at least, given its marine taxonomic affinities and despite its entirely freshwater distribution, would appear to exhibit pattern 3. Fig. 2 indicates how close the correlation between distribution of stygobiont amphipods derived from hadziid ancestors is with areas of marine transgression and, conversely, of those with crangonyctoid ancestors and areas not inundated before or during the Cretaceous.

Figure 2. Marine transgressions in Australia during the Cretaceous (119–114 million years ago). Redrawn from Paine (1990). Areas free of inundation shaded.

The ecological nature of subsurface waters inhabited by species here considered as stygobionts covers a considerable range in type. Avoiding the plethora of technical terms that have been applied to subsurface waters, included are freshwater streams and lakes in inland caves in calcareous karst, coastal anchialine caves containing marine or brackish water, springs, mud or plant detritus on the bottom of surface waters which are in obvious continuity with the water table in unconsolidated substrata, and interstitial (hyporheic) water associated with streams. The collection of material from such a diversity of habitats itself demands diversity. For example, cave forms have been collected from open water by sweep nets or by baiting, forms in interstitial waters by pumping, and spring species by placing nets over surface outlets for extended periods (collections of *Brachina invasa* were made by placing a collecting net over the outlet of a spring for 12 hr).

The diversity of the hypogean amphipod fauna

On the basis of described species alone (Table 1), it is obvious that significant diversity exists amongst amphipods found in subsurface waters in Australia. How much more diverse will this fauna prove to be when further investigations have taken place? We have reason to believe that the answer is that it will prove to be substantially more diverse. This response is based in part on our possession of further undescribed material from underground waters and including at least three new species from Western Australia, two from Queensland, and three from New South Wales (see also Eberhard et al., 1991). We believe it doubtful, however, that the number of species of hypogean amphipods in Australia will ever reach the numbers found in the two most diverse regions of the world in so far as this group is concerned, that is, the central-southern European — Mediterranean region and the eastern and southern North American — West Indian region. Even so, it is already clear that our increased knowledge of the diversity of hypogean amphipods in Australia confirms, as indicated, Holsinger's (1993) view that southern Australia is a region of significant diversity for this group. However, unlike the genera:species ratios found in the two regions of highest diversity mentioned, where the usual pattern is one of many species per crangonyctoid genus and few species per hadzioid genus, the pattern in Australia appears to be different, with many species per genus an obvious pattern for at least some hadzioid genera, and few species per genus for most crangonyctoid genera.

The causes of diversity

Two issues are involved in considering this matter. First, the factors that have led to the evolution of styobiont amphipods in Australia, and second, those factors responsible for the high diversity.

The first set of factors are of relatively little interest in the present context; it may be presumed that the evolutionary routes followed by stygobiont amphipods in Australia are similar to those followed elsewhere by such organisms. Thus, all originated from surface forms by regressive evolution — irrespective of whether selection, the accumulation of neutral mutations, or genetic drift was the more important in this process (Culver, 1982) — after isolation from surface forms had occurred following sea-level change, the onset of climatic aridity, or a given geomorphological event. A number of evolutionary steps have been proposed through which populations pass as stygobiont species evolve. As a general rule, three broad ones can be recognized to accommodate the evolution of stygobionts from both inland and marine ancestors (Holsinger, 1994a). The first is inclusive of troglophiles with few if any troglomorphic features. *Neoniphargus obrieni* provides an example. The second also include troglophiles but these do exhibit some troglomorphic features. Various species of *Antipodeus* provide examples. The third step includes troglobites with clear troglomorphy. *Hurleya kalamundae*, *Nedsia* species, and *Protocrangonyx fontinalis* are some examples.

Of much greater interest are those factors responsible for the high diversity. In this connection it is instructive to determine those features held in common by the two regions of greatest stygobiont amphipod diversity, the central-southern European — circum Mediterranean region and the eastern and southern North American — West Indian region. In both regions, the following features are both held in common and regarded as significant in promoting the development of high diversity (Holsinger, 1994a): a former proximity to the Tethys Sea, the lack of extensive glaciation during the Pleistocene, large areas of karst, and widespread marine transgressions in the late Mesozoic and Cainozoic. To a not inconsiderable degree, *these features also characterise large parts of the Australian continent.* Over much of the Mesozoic, the Tethys Sea lay west of Australia; apart from the highlands of Tasmania and small areas of the highest mountains in the south-east of the mainland, the Australian continent was free of ice during the Pleistocene; and marine transgressions covered large areas of the Australian continent during the early Cretaceous (Fig. 2). The only difference, and one of degree not kind, is the extent of karst in Australia. Karst does occur widely in Australia (Jennings, 1985; Mathews, 1985), but continuously extensive areas are confined to the Nullabor Plain and the lower Murray Valley, with only relatively minor occurrences elsewhere (included here is the Fitzroy Basin of Western Australia, the Cooleman Plain, Jenolan and Wee Jasper areas of New South Wales, the Buchan caves area of Victoria, the Mole Creek area of northern Tasmania, and the Barkly Basin of Queensland).

The evolution of stygobionts does not depend entirely upon the presence of karst, but there is little doubt that it does promote their evolution and the development of diversity. In any event, we believe that the features listed above, including the occurrence of karst — albeit it to an extent more limited than in the southern Europe — Mediterranean and North American — West Indian regions — have been important in producing the observed diversity of the Australian stygobiont amphipod fauna. Also important, we believe, has been both:

1. *continental drift* during which Australia first broke free from Gondwana and then passed through a series of quite distinct climatic zones during the Cainozoic, and
2. *palaeoclimatic fluctuations* including periods of aridity which, in conjunction with allied sea-level changes for coastal populations, would have served to isolate surface and subsurface populations of a species and have led to the development of discrete drainage basins.

A succession of favourable (wetter and colder) and unfavourable (drier and warmer) climates could easily have provided mechanisms promoting stygobiont speciation as epigean populations were driven to seek subterranean refugia. It may also be that some troglomorphic forms (lacking eyes) now found in surface waters actually represent the return to epigean conditions of hypogean forms in the absence of surface competitors, the latter having become extinct during former unfavourable conditions. It is not possible, for eyes, once lost, to be regained.

Finally, some explanation should be offered for the extraordinary diversity of stygobionts on Barrow Island. The most likely one is that after stranding, ancestral populations were isolated in a series of small and discrete subterranean basins where genetic drift led to the evolution of separate species from the original founder population.

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