

Stygofauna diversity and distribution in Eastern Australian cave and karst areas

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Abstract – This paper reviews the diversity and distribution of the stygofauna of Eastern Australia on a regional basis. Most of the stygofauna is concentrated in the highland karsts of New South Wales and Tasmania. Two hundred and thirty-eight taxa are present and amphipods, syncarids and hydrobiid gastropods are the dominant and most widespread groups. Nearly half of the total fauna are stygobites (82 taxa) and stygophiles (34 taxa). Also present are taxa with Gondwanan and Pangaeian affinities, taxa that are phylogenetic and distributional relicts, and locally endemic taxa. Diversity and distribution at the local karst scale is also discussed using a case study of Wombeyan Caves, one of the richest stygofauna sites in Eastern Australia. The paper concludes with suggestions for further research.

INTRODUCTION

The presence of a diverse global stygofauna (fauna inhabiting groundwater environments) has led to groundwater ecology becoming a major discipline of scientific endeavour (Gibert *et al.*, 1994), particularly in the Northern Hemisphere. In terms of global composition, crustaceans dominate the fauna, there is a paucity of insects, and gastropods are regionally significant (Botosaneanu, 1986; Culver and Sket, 2000; Sket, 1999). The diversity of these groundwater ecosystems was recently highlighted by the identification of stygofauna 'hotspots' in North America and Europe (Culver and Sket, 2000).

Despite considerable continental aridity and a paucity of cave and karst areas by world standards, Australia has been identified as a regional centre of stygofauna diversity (Holsinger, 1993; Knott, 1986; Williams, 1986). Support for this statement arises from research in Western Australia, particularly in Cape Range, Barrow Island and Yanchep (e.g. Humphreys, 2000a; Jasinska and Knott, 2000). The two richest sites in the world for stygal amphipods are the Ethel Gorge calcrete and Barrow Island, both in northwestern Australia (Humphreys, 2001; Bradbury, 2000). There are also more stygal dytiscid beetles in the Yilgarn region (southwestern Australia) than in the remainder of the world combined (Humphreys, 2001). Less attention has been paid to the stygofauna of Eastern Australia (defined herein as east of 138° longitude) but

surveys suggest this is also an important region of stygofauna diversity (Eberhard *et al.*, 1991; Eberhard and Spate, 1995).

This paper synthesises the available information on the stygofauna of Eastern Australia inhabiting karst and cave areas. We describe patterns in composition, diversity and distribution focussing particularly on the crustacean and molluscan fauna of New South Wales and Tasmania. Our intention is to highlight the stygofauna of Eastern Australia, draw attention to what is known of its significance, and encourage further discussion and research.

METHODS AND SOURCES OF INFORMATION

The information presented in this paper is based on several databases, unpublished reports and records of the authors'. Published information is also used for Tasmania (Eberhard *et al.*, 1991; Clarke, 1997), New South Wales (Eberhard and Spate, 1995; Bradbury and Williams, 1997b) and South Australia (Zeidler, 1983; Thurgate, 1995). Details of the locations of specimens and the status of taxonomic determinations are available from the authors.

Most karst and cave areas in Eastern Australia have been cursorily sampled, although a few selected areas in Tasmania (e.g. Ida Bay, Mole Creek) and New South Wales (e.g. Wombeyan, Jenolan) have been more intensively surveyed. Surveys have employed a mixture of techniques

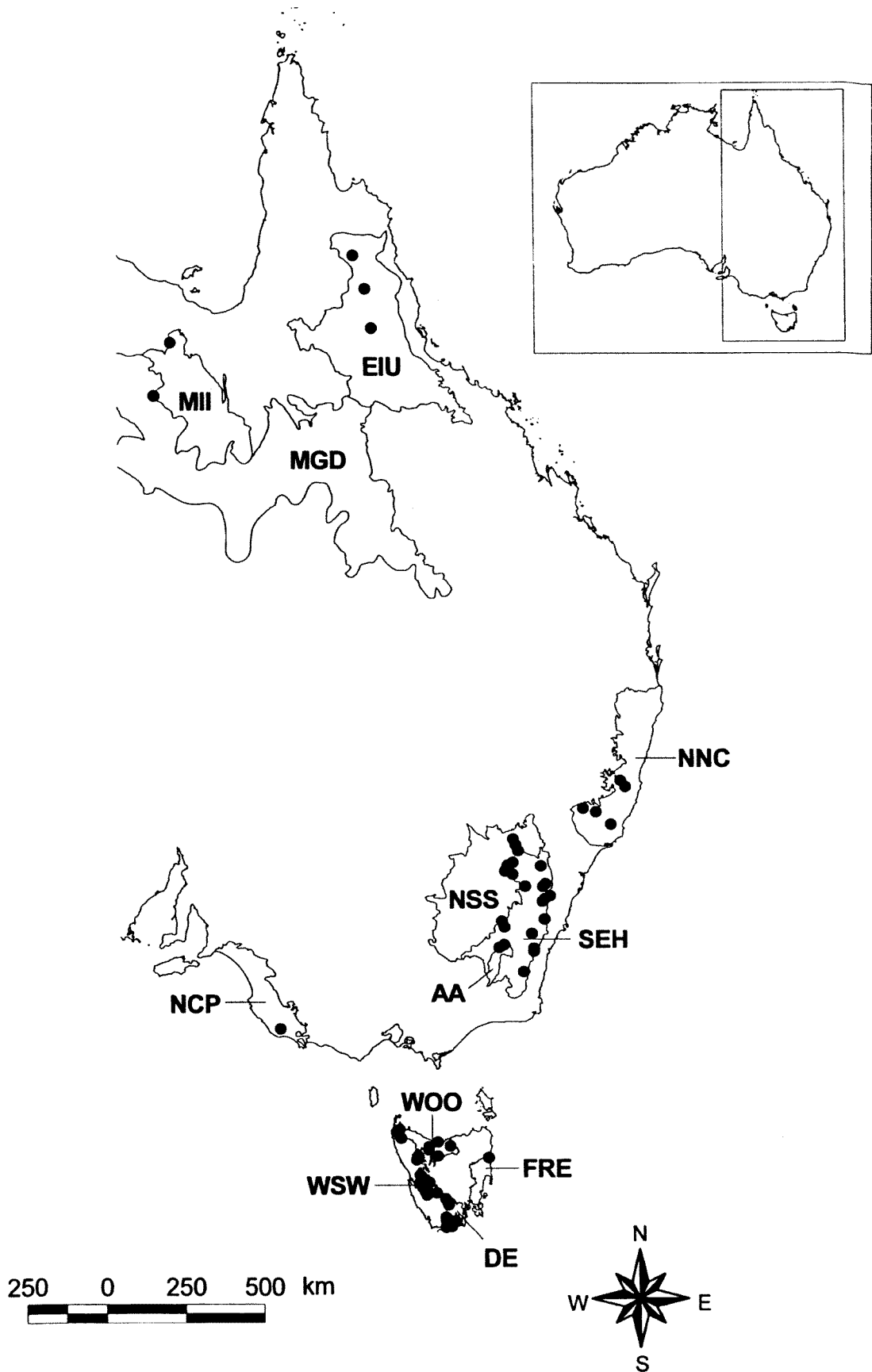


Figure 1 Distribution of stygofauna sites in Eastern Australia. Each dot on the map represents one or more karst areas. Boundaries for IBRA regions are also shown and follow Thackway and Cresswell (1995). Codes for IBRA regions are given in Table 1, except for MII (Mount Isa Inlier) and MGD (Mitchell Grass Downs). These latter two regions are not included in Table 1 as the diversity and composition of their stygofauna is completely undetermined.

including active searching, nets and aspirators, and trapping with modified baited 'yabbie' pots (Eberhard *et al.*, 1991; Eberhard and Spate, 1995; Clarke, 1997).

Much of the stygofauna is undetermined, but we have included information on these taxa to give a more complete indication of the diversity of these ecosystems. Where multiple specimens have not been clearly assigned to a particular genus or species, we have treated these as belonging to a single taxon. Given the distribution patterns discussed below (i.e. highly localised with many endemics), improved taxonomic information will undoubtedly result in an overall increase in diversity.

Nature and Extent of Karst Areas

The karsts of Eastern Australia are not uniformly distributed (Figure 1). Instead, they form a series of scattered outcrops that are concentrated in the southeast of Eastern Australia. The distribution of karst styles broadly corresponds to the biogeographic region boundaries developed under the Interim Biogeographic Regionalisation for Australia (IBRA: Thackway and Cresswell, 1995). These regions (Figure 1) are based on similarities in surface climate, geology, landform and biological attributes. We use the IBRA regions as an organisational framework for discussing the biogeography of the stygofauna, and it is not our intention to infer causality.

Most of the Eastern Australian karsts are of small size with limited surface expression (Table 1). Exceptions to this pattern are found in the extensive Mitchell Grass Downs and Naracoorte Coastal Plain Regions (Figure 1) where the karsts form broad, undulating plains in flat-bedded rock. Many of the caves in these regions have deep open shafts or sinkholes at their entrance. Most caves at Camooweal (Mitchell Grass Downs Region) are

relictual and are perched above the water table for much of the year. In the Mount Gambier karst (Naracoorte Coastal Plain Region) groundwater is present at shallow depths in many caves.

In the Einasleigh Uplands Region, the karsts are residual tropical forms (karst towers) rising above the surrounding plains. They formed during the wetter conditions of the Tertiary (Jennings, 1982). Numerous individual towers are distributed over several hundred kilometres. Subdued tower karsts are also found in the North Coast Region, and these developed in the Cretaceous (Osborne and Branagan, 1988). This region is a transition zone between the tropical karsts described above and temperate karsts described below. Few caves extend to groundwater in either of these regions.

At least 90 small karst areas are widely scattered in the South Western Slopes, South East Highlands and Australian Alps Regions of New South Wales (Figure 1). Often these are ancient karsts, some of which developed in the Permian (Osborne and Branagan, 1988; Osborne, 1993, 1999). These karst areas are impounded, that is, surrounded by higher-lying non-carbonate terrains so groundwater systems are generally small and discontinuous. Approximately 80 small karst areas are located in the Woolnorth, West and South West and D'Entrecasteaux Regions of Tasmania, and are of a similar age and style to those of southeast New South Wales, but are more extensive and deeper systems (Kiernan, 1995). In both states, the karsts are found throughout a range of climatic and altitudinal gradients.

The impounded karsts of New South Wales and Tasmania are complex systems, and many of them have experienced multiple phases of karstification interspersed with periods of marine transgression, burial, infilling and exhumation (Osborne and Branagan, 1988; Osborne, 1993, 1999; Clarke, 1995). In addition, many karst areas of Tasmania lie

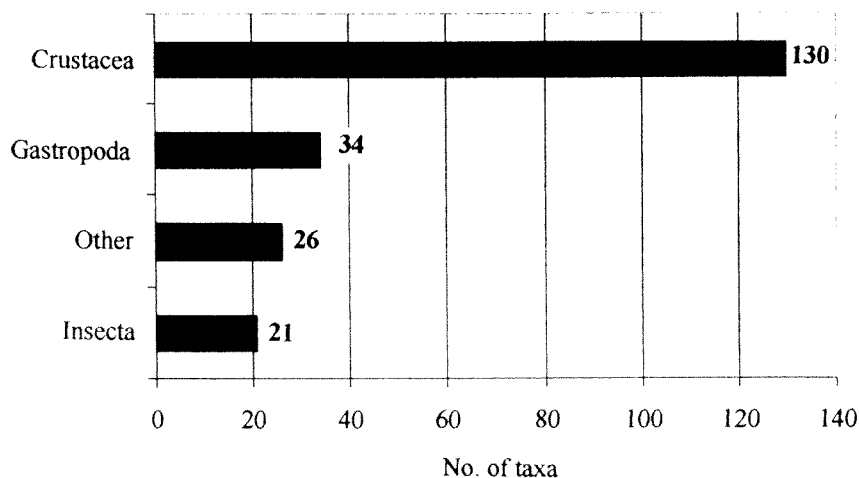


Figure 2 Composition of stygofauna in Eastern Australia. The group designated as 'other' includes protozoans, turbellarians, oligochaetes, nematomorphans, arachnids and bivalves.

Table 1 Karst area characteristics and associated stygofauna families occurring within IBRA regions as defined by Thackway and Cresswell (1995). Representative sites include locations in New South Wales and Tasmania with a high stygofauna diversity (ie more than 10 taxa present). Families with five or more taxa present in a given IBRA region are also indicated.

IBRA Region (IBRA Code)	Location, karst styles and climatic regime ¹	Representative sites ² (Total no. taxa)	Characteristic faunal elements
Einasleigh Uplands (EIU)	QLD: Numerous bluffs (tower karst) over several hundred kilometres. Watertable below caves during dry season except for a few limited sites. Extensive lava tube complex with subterranean groundwater pools and springs. Tropical, seasonally moist/arid.	Mitchell-Palmer (1), Chillagoe (1), Undara Lava Tubes (1)	Paramelitidae
North Coast (NNC)	NSW: Impounded karsts throughout landscape – most relictual and dry. A few caves reach to groundwater, some small stream systems. Warm temperate, summer rainfall.	Stockyard Creek (4), Timor (3), Pigna Barney (3), Willi Willi (1)	Family nov. (Anaspidaceae), Eusiridae, Neoniphargidae
South Western Slopes (NSS)	NSW: Impounded (sometimes extensive) karsts with both relictual caves and groundwater systems. Cool to warm temperate, uniform but highly variable rainfall.	Bowan Park (4), Wellington (3), Bakers Swamp (2), Canomodine (1)	Neoniphargidae (5), Psammaspididae (5), Janiridae
South Eastern Highlands (SEH)	NSW/VIC: Impounded karsts with both relictual caves and active stream/groundwater systems. Cool temperate, highly variable winter rainfall.	Wombeyan (40), Jenolan (15) Wee Jasper (6), Colong (3)	Neoniphargidae (14), Eusiridae, Psammaspididae (5), Phreatoicidae, Glacidorbidae, Hydrobiidae
Australian Alps (AA)	NSW/VIC: Impounded karsts with both relictual caves and active stream/groundwater systems. Cool/cold temperate, variable rainfall regime. Possibly influenced by periglacial conditions during glacial maxima.	Coolman Plains (10), Yarrangobilly (7)	Eusiridae, Neoniphargidae, Psammaspididae, Janiridae, Ancyliidae, Glacidorbidae
Naracoorte Coastal Plain (NCP)	SA/VIC: Flat bedded karst with many “windows” reaching down to regional groundwater. Subject to major water level change through glacial/non-glacial cycles. Cool temperate, moist to semi-arid rainfall regime.	Mount Gambier area (>40, majority epigeal species in springs and cenotes)	Ceinidae, Paramelitidae, Koonungidae, Hydrobiidae, Planorbidae
Woolnorth (WOO)	TAS: Many areas of impounded karsts with active stream/groundwater systems. Cool temperate, moist. Some influenced by periglacial conditions during glacial maxima.	Mole Creek (19), Gunns Plains (16), Loongana (16), Trowutta (9)	Paramelitidae (11), Neoniphargidae, Koonungidae, Amphisopidae, Phreatoicidae, Hydrobiidae (7)
West and South West (WSW)	TAS: Many areas of impounded karsts with active stream/groundwater systems. Cool/cold temperate, very moist. Many karsts influenced by periglacial conditions during glacial maxima.	Franklin (14), Bubs Hill (12), Lower Andrew (10), Precipitous Bluff (10)	Paramelitidae (15), Eusiridae, Neoniphargidae, Koonungidae, Phreatoicidae, Janiridae, Hydrobiidae (15)
D’Entrecasteaux (DE)	TAS: Many areas of impounded karsts with active stream/groundwater systems. Cool/cold temperate, very moist. Some influenced by periglacial conditions during glacial maxima.	Ida Bay (33), Juneë-Florentine (19), Hastings (9), Cracroft (6)	Paramelitidae (13), Eusiridae, Anaspididae, Janiridae, Hydrobiidae (11)
Freycinet (FRE)	TAS: A few small impounded karsts with active stream/groundwater systems. Cool temperate, variable winter rainfall.	Gray (3)	Paramelitidae, Psammaspididae

¹ Karst styles and climatic regimes were compiled by Andy Spate.

² Representative sites and characteristic fauna were determined from an analysis of the New South Wales Cave Invertebrate database (Eberhard and Spate, 1995), Tasmanian RFA database (Clarke, 1997), and recent unpublished records.

Table 2 Composition of major stygofauna groups in Eastern Australia¹. Figures in brackets indicate undetermined taxa that are probably stygobites or stygophiles. Species that have only been collected from a single karst area or single cave are considered endemic.

Taxa	Total No. Genera	Total No. Species	No. Stygobites	No. Stygophiles	Total No. Endemics
Amphipoda ²					
Paramelitidae	10	35	21	9 (5)	18
Neoniphargidae	10	23	20	3	21
Other families	5	8	1	3	3
Syncarida					
Psammaspididae	2	13	13	–	11
Koonungidae	4	5	3	(2)	3
Anaspididae	1	3	1	2	1
Other families	2	3	3	–	3
Decapoda					
Parastacidae	7	17	–	3	6
Other families	2	2	–	1	1
Isopoda					
Phreatoicidae	3	5	3	(2)	1
Janiridae	2	5	4	1	1
Amphisopidae	1	1	1	–	1
Other Crustacea	6	10	2 (5)	(1)	–
Gastropoda ³					
Hydrobiidae	7	25	6 (2)	9	12
Other families	8	9	–	–	6
Coleoptera					
Dytiscidae	2	4	–	2 (1)	–
Other families	2	5	–	–	–
Trichoptera					
Philopotamidae	1	2	–	1	–
Other families	2	2	–	–	–
Other Insecta	11	15	–	–	–
Other taxa	16	38	4 (1)	(2)	10
Totals	104	230	82–90	34–47	98

¹ Based on the New South Wales Cave Invertebrate database (Eberhard and Spate, 1995), Tasmanian RFA database (Clarke, 1997), Thurgate (1995) and unpublished records.

² Additional information from Barnard and Williams (1995), Williams and Barnard (1988) and J. Bradbury (personal communication, 2000).

³ Additional information from W. Ponder (personal communication, 1999).

marginal to or within areas that were covered by glaciers and infilled by glacial sediments during the late Cainozoic (Eberhard *et al.*, 1991; Kiernan, 1990; Clarke, 1995).

COMPOSITION AND DIVERSITY OF STYGOFAUNA

Composition

Table 2 summarises the overall composition of the main stygal orders and families across Eastern Australia. Crustaceans are the dominant and most widespread group (Figure 2), and are composed

primarily of amphipods. The remainder of the crustacean fauna includes syncarids, decapods, isopods, copepods and ostracods. Gastropods, an important component of the stygofauna (Figure 2), are dominated by Hydrobiidae, and also include Ancyliidae and Glacidorbidae. Insects are of minor significance in the stygofaunas of individual karst areas. Less well represented taxa include turbellarians, oligochaetes, arachnids, hydrozoans, nematomorphans and protozoans.

The stygofauna of Eastern Australia includes taxa with varying degrees of dependence on the subterranean habitat (Table 2). Stygobites are obligate and specialised subterranean forms that

often display some degree of troglomorphy (adaptation to subterranean life). Stygophiles are facultative forms that seek out and utilise groundwater environments. Finally, stygoxenes are epigeal forms that occur accidentally and that show no particular affinity to groundwaters (all based on Humphreys, 2000b).

Most stygobites are crustaceans, with amphipods and syncarids having the highest diversity, while amphipods and hydrobiid snails (Table 2) dominate the stygophiles. The decapods and insects also include some stygophiles but most appear to be stygoxenes. The high proportions of stygobites amongst some families (eg. Paramelitidae, Neoniphargidae and Psammaspididae), as well as high proportions of local endemism (Table 2) suggests strong selection pressures or long periods of isolation in subterranean waters for this fauna.

A component of the Eastern Australian stygofauna is composed of taxa with Gondwanan and Pangaeian affinities (Barnard and Karaman, 1984; Williams and Barnard, 1988; Wilson and Wägele, 1994; Bradbury and Williams, 1997a; Wilson and Johnson, 1999). These are found mostly within the higher Crustacea (Table 3). A number of these crustaceans are phylogenetic and distributional relicts, as are the hydrobiid gastropods (Hamilton-Smith and Eberhard, 2000), and so are valuable for biogeographical and evolutionary research. The presence of these families in the cave waters of Eastern Australia suggests some karst areas have acted as refuges (*sensu* Humphreys, 2000c) for stygofauna.

Diversity

Two hundred and thirty stygal species have been recorded from Eastern Australia, and crustaceans comprise up to 57% of the total. Within the crustaceans, 130 species from 55 genera have been recorded. The most diverse crustacean families are the paramelitid, neoniphargid and psammaspid amphipods (Table 2). The hydrobiid snails are also a rich group (25 species from 7 genera) with a diversity that is only surpassed by the paramelitid amphipods (35 species from 10 genera).

Over one third of the stygofauna from Eastern Australia are obligate groundwater animals. At least 82 stygobite taxa have been recorded and they occur in 46 of the 71 karst areas that contain stygofauna (Table 2). Most of these taxa are found within the four families mentioned above. A further 15–20% of the stygofauna are stygophiles, the remainder of the fauna are stygoxenes.

Most cave and karst areas in Eastern Australia have a low richness and abundance of stygofauna by world standards (Culver and Sket, 2000). Few mainland karsts support more than 10 stygal taxa. Wombeyan (40 taxa), Jenolan (15 taxa) and Cooleman Plain (10 taxa) are the exceptions in New South Wales. The Mount Gambier area in South Australia contains over 40 stygal taxa. Tasmania has nine karst areas (Table 1) with this level of diversity including Ida Bay (33 taxa), Juneeflorentine (19 taxa) and Mole Creek (19 taxa).

In mainland karsts, diversity at the level of individual caves is low. Most caves support less than five taxa, and it is rare for more than two obligate taxa to be present in the same cave. In contrast, at least 13 Tasmanian caves contain five or

Table 3 The origins and present global distribution of major stygal crustacean families collected from Eastern Australia. Data based on Banareescu (1990a and 1990b) unless otherwise indicated.

Order and Family	Affinities	Present Distribution
Amphipoda		
Neoniphargidae	East Pangaea ¹	Australia
Paramelitidae	East Gondwana	Australia, South Africa, South America
Ceinidae	East Gondwana ²	Australia, New Zealand, South Africa
Syncarida		
Psammaspididae	Gondwana	Australia
Koonungidae	Gondwana	Australia
Anaspididae	Gondwana	Australia
Stygocarididae	Gondwana	Australia, New Zealand, South America
Parabathynellidae	Gondwana	Cosmopolitan
Isopoda		
Phreatoicidae	East Gondwana	Australia, New Zealand, South Africa, India
Janiridae	Gondwana ³	Australia, South America
Amphisopidae	East Gondwana	Australia, New Zealand, South Africa, India

¹ Bradbury and Williams (1997a).

² Barnard and Karaman (1984).

³ Wilson and Wägele (1994)

Table 4 Distribution of stygofauna in New South Wales and Tasmanian karsts¹. The stygobite category excludes possible stygobites or taxa with an uncertain ecological classification. Highest totals for each category are shown in bold. Region names for the IBRA codes are given in Table 1.

Category	IBRA regions	New South Wales				Tasmania			
		NNC	NSS	SEH	AA	WOO	WSW	DE	FRE
No. karst areas per region containing stygofauna		6	5	15	2	9	13	9	1
Total no. species per region		13	10	56	12	46	55	45	3
No. stygobites		3	9	21	3	14	19	16	2

¹ Data based on the New South Wales Cave Invertebrate database (Eberhard and Spate, 1995) and Tasmanian RFA database (Clarke, 1997), and recent unpublished records.

more stygobitic taxa. This includes Exit Cave (10 stygobites) and Arthur's Folly Cave (14 stygobites) at Ida Bay and Hardy Cave (13 stygobites) at Loongana (Clarke, 1997).

A low abundance of stygofauna is also typical of most Eastern Australian caves, and may relate to limited food supplies (Jasinska and Knott, 2000). However, high abundances have been reported from those caves that contain aquatic root mats, a substantial and reliable food source. This includes caves from Stockyard Creek, Timor, Wellington, Abercrombie and Wombeyan in New South Wales, and Mole Creek in Tasmania (Eberhard and Spate, 1995; Jasinska and Knott, 2000).

DISTRIBUTION PATTERNS OF STYGOFAUNA

Geographic distribution patterns

The broad distribution patterns of stygofauna across the IBRA regions is summarised in Table 1. Most taxa are concentrated in regions in New South Wales and Tasmania. Biases in research effort may have resulted in the apparent focus of diversity within these two States. The karsts of Victoria and southeastern South Australia have only been sparsely surveyed (Hamilton-Smith and Eberhard, 2000). The stygofauna of Queensland is also poorly known, although intensive surveys at Chillagoe and Undara in the Einasleigh Uplands have located several amphipods (Barnard and Williams 1995; J. Bradbury, personal communication, 2000).

Table 4 shows that the distribution of stygofauna in New South Wales and Tasmania is concentrated in the highland areas where karst development is greatest. In Tasmania this includes karsts in the Woolnorth, West and South West and D'Entrecasteaux Regions, all of which support similar levels of stygobite richness. In New South Wales, the stygofauna is concentrated in karsts of the South East Highlands Region.

The overall diversity of stygofauna in New South Wales (83 taxa) is lower than that of Tasmania (98 taxa). Tasmania also has a greater diversity amongst the higher order Crustacea, with 49 taxa from 18 genera and 11 families, while New South Wales contains 36 taxa from 15

genera and seven families. The composition of the Tasmanian stygofauna is also distinct from that of New South Wales at both the generic and species level (Table 1). The number of confirmed stygobites is similar (32 versus 33 taxa respectively) between these States. Stygobites, stygophiles and epigeal species each make up one third of the groundwater fauna in Tasmania, while in New South Wales, stygobites account for 43% of the fauna.

Taxonomic distribution patterns

Amphipoda

Amphipods have the broadest distribution pattern of all crustacean stygofauna in Eastern Australia (J. Bradbury, personal communication, 1999). They are well represented in the karsts of New South Wales and Tasmania and are the only described stygofauna from North Queensland. Overall, Paramelitidae dominates the amphipods and includes 35 stygobite species from eight genera (Table 5). The highest diversity (77% of taxa) of paramelitids are found in Tasmania.

Several paramelitids have a very localised distribution and are only known from hypogean forms. This includes *Uronyctus longicaudus* Stock and Iliffe, 1990 from the Naracoorte Coastal Plain and *Chillagoe thea* Barnard and Williams, 1995 from the Einasleigh Uplands. *Antipodeus* is restricted to Tasmania but is widespread in the surface and hypogean waters of that State. The remaining described paramelitids (Table 5) have a broadly scattered distribution in the surface waters of southeastern Australia, but it is only in Tasmania that they form part of the stygofauna.

Neoniphargid amphipods are endemic to Australia (Bradbury and Williams, 1997a), and the stygofauna includes nine genera and 23 species. Eighty-seven percent of stygal species are restricted to the karsts of New South Wales, the rest occurring in Tasmania. In New South Wales the family occurs in all four IBRA regions but the greatest diversity is found in the South East Highlands (Table 5), where most genera and species have an extremely localised distribution. In Tasmania they occur in the Woolnorth, West and South West Regions.

Table 5 Regional distribution of stygal paramelitid and neoniphargid amphipod genera from Eastern Australia¹. Region codes are provided in Table 1.

IBRA region TAXA	Queensland	New South Wales			South Australia	Tasmania				
	EIU	NNC	NSS	SEH	AA	NCP	WOO	WSW	DE	FRE
Paramelitidae²										
<i>Chillagoe</i>	•									
<i>Uronyctus</i>						•				
<i>Austrogammarus</i>						•	•	•		
<i>Antipodeus</i>							•	•	•	
<i>Austrocrangonyx</i>							•		•	
<i>Giniphargus</i>								•		
<i>Austrochiltonia</i>							•			
Genus near <i>Hurleya</i>							•	•	•	•
Genus near <i>Giniphargus</i>								•		
Neoniphargidae³										
<i>Neoniphargus</i>				•	•		•	•		
<i>Neocrypta</i>		•		•						
<i>Jasptorus</i>				•						
<i>Wombeyanus</i>				•						
<i>Gen. nov. 1</i>				•						
<i>Gen. nov. 2</i>		•		•						
<i>Gen. nov. 3</i>				•						
<i>Gen. nov. 4</i>				•						
<i>Gen. nov. 5</i>				•						
Genus undetermined		•		•						

¹ Based on the New South Wales Cave Invertebrate database (Eberhard and Spate, 1995), Tasmanian RFA database (Clarke, 1997), and recent unpublished records.

² Tasmanian paramelitid stygofauna are currently being revised by J. Bradbury.

³ The undescribed neoniphargid genera were identified by J. Bradbury (personal communication, 1995).

Neoniphargus is the most widely distributed neoniphargid genus in Eastern Australia, but this distribution pattern is highly disjunct. Most are stygobitic species endemic to a single karst area occurring in the South East Highlands, Australian Alps, or West and South West Regions. *N. obrieni* Nicholls, 1926b is the only described stygophile and has been collected from surface waters at Mount Buffalo in Victoria (Bradbury and Williams, 1997b). There are two significant enterable caves at Mount Buffalo, so it is possible that this genus also occurs in hypogean waters (E. Hamilton-Smith, personal communication, 2000). Apart from *Neoniphargus*, all other neoniphargid genera are restricted to New South Wales (Table 5), and most of these are only found at Wombeyan Caves.

Syncarida

Syncarids consist of two extant orders, the Bathynellacea and the Anaspidacea. Bathynellaceans are present in interstitial waters across Eastern Australia but have been largely overlooked in hypogean waters (P. Serov, unpublished data). Three families of Anaspidacea have been recorded from Eastern Australia and all are endemic to the south east of the continent (Table 6), having not been found north of New South Wales (P. Serov, unpublished data).

Tasmania contains the greatest taxonomic

diversity of anaspids, with five genera and up to nine species. Included are a mixture of stygobites and stygophiles, half of which are local endemics, the remainder occurring across two or more karst areas. *Eucrenonaspides*, *Micraspides* and *Anaspides* do not occur in groundwaters of the mainland, and in Tasmanian karsts they are often syntopic (Eberhard *et al.*, 1991). *Anaspides tasmaniae* Thomson, 1893 is widespread with a predominantly surface distribution. Subterranean populations are found mostly in the D'Entrecasteaux and West and South West Regions. The cave taxa form a complex of morphospecies containing both stygophiles and stygobites (A. Clarke, unpublished data). Caves may have been glacial refuges for this species as it occurs in areas formerly subjected to repeated cycles of glaciation (Kiernan, 1990).

Koonunga is the only syncarid genus found both in Tasmania and on the mainland. Epigeal forms of *Koonunga* are scattered widely in surface waters of New South Wales, South Australia and Victoria. Hypogean species are restricted to single karst areas in both the Woolnorth Region of Tasmania and the South East Highlands of New South Wales (A. Clarke, unpublished data; P. Serov, unpublished data).

The stygobite *K. crenarum* Zeidler, 1985 is widespread in the waters of the southern

Table 6 Regional distribution of stygal anaspid syncarid genera from Eastern Australia¹. For region codes see Table 1.

IBRA region TAXA	Queensland		New South Wales				South Australia		Tasmania		
	EIU		NNC	NSS	SEH	AA	NCP	WOO	WSW	DE	FRE
Anaspididae											
<i>Anaspides</i>								•	•	•	
Koonungidae											
<i>Micraspides</i>									•		
<i>Koonunga</i>					•		•	•			
<i>Gen. nov.</i> ²									•		
Family nov. ³											
<i>Gen. nov.</i>			•								
Psammaspididae											
<i>Eucrenonaspides</i>								•	•	•	•
<i>Psammaspides</i>			•	•	•	•					

¹ Based on the New South Wales Cave Invertebrate database (Eberhard and Spate, 1995), Tasmanian RFA database (Clarke, 1997), and P. Serov (unpublished data).

² Eberhard *et al.* (1991).

³ Determined by P. Serov.

Naracoorte Coastal Plain. This Region has been subjected to many marine transgressions, both during the Cretaceous and throughout the Quaternary (Schwebel, 1983). Preferring cool, permanent freshwater environments (P. Serov, unpublished data), *K. crenarum* may have avoided the marine transgressions by inhabiting groundwaters in the north of the region, later dispersing to its present southern distribution by following surface groundwater discharges. Subterranean dispersal is unlikely as there are no continuous fracture systems between the northern and southern karsts, and *K. crenarum* is too large for interstitial travel (Zeidler, 1985).

Two congeneric species of an undescribed anaspid family occur in caves and interstitial waters of the North Coast Region in New South Wales and they are considered to have close affinities with Koonungidae (P. Serov, unpublished data). Both species possess specialised raptorial grasping appendages and are probably active predators (Eberhard and Spate, 1995), in contrast to most other syncarids that are omnivorous detritivores (P. Serov and S. Eberhard, unpublished data).

The dominant syncarid genus in New South Wales is *Psammaspides*, which occurs in five karst areas in the South East Highlands, four areas in the West and South West and one in the Australian Alps. Each species occurs in a single karst area, and often only in one cave. All are stygobites (all undescribed), and are considered phylogenetic and distributional relicts (Eberhard and Spate, 1995). In addition, *P. williamsi* Schminke, 1974, an interstitial species, occurs in the North Coast Region of New South Wales.

Isopoda

Eastern Australian subterranean isopods are less speciose than the amphipods and syncarids, and are more restricted in distribution. The Janiridae and Phreatoicidae dominate the isopod stygofauna of Tasmania and New South Wales. The majority of the stygal isopods from Eastern Australia are completely undetermined.

The janirids are represented by the genus *Heterias* and are found in the Australian Alps and South Western Slopes in New South Wales, and all regions in Tasmania except Freycinet. The phreatoicids include at least three genera and five species. In Tasmania, phreatoicids have a patchy distribution and are found in karst groundwaters on the western side of the State. Stygal phreatoicids in New South Wales all belong to the genus *Crenoicus*, which has a broad distribution in epigeal environments (Wilson and Ho, 1996). Hypogean populations of *Crenoicus* are restricted to two karst areas in the South East Highlands Region.

Mollusca

Tasmania has an outstandingly rich subterranean molluscan fauna (25 taxa), especially of hydrobiid gastropods. Twenty-two hydrobiid species from six genera are found in karst areas of the Woolnorth, West and South West and D'Entrecasteaux Regions, of which seven are probably stygobites. Recent research suggests that 12 stygobitic hydrobiids from Precipitous Bluff may be added to the current total (W. Ponder, personal communication, 1999). This combined level of diversity compares favourably with 28 species of obligate subterranean molluscs known from the much larger landmass of the 48 contiguous United States (Culver *et al.*, 2000).

The molluscan stygal diversity in mainland karsts is very low and probably reflects a more variable moisture and climate regime than is present in Tasmania. At least four genera from three families occur in groundwaters of the Naracoorte Coastal Plain Region but there are no obligate species present. Two genera from this region, *Angrobia* and *Miselaoma* are shared with Tasmania. The fauna of New South Wales includes at least one obligate species of *Austropyrgus* (W. Ponder, personal communication, 1999). Other stygal molluscs from New South Wales are concentrated into several karsts in the South East Highlands and Australian Alps Regions.

Overall distribution patterns

From an examination of the molluscs and higher crustaceans of Tasmania and New South Wales, several dominant distribution patterns are evident. The Tasmanian stygofauna includes species with both localised and broad distribution patterns, and roughly equal proportions of stygobites and stygophiles are present. Taxonomic diversity is high overall in Tasmania and there is considerable speciation across the Paramelitidae and Hydrobiidae (Eberhard *et al.*, 1991; Eberhard and Spate, 1995).

In New South Wales the stygofauna are highly localised in distribution (most species are stygobites endemic to one karst area), and few stygophiles are present. The Neoniphargidae and Psammaspididae comprise the bulk of the taxonomic diversity displaying high generic and species diversity. These differences in distribution patterns between the two States may relate to differences in available habitat, present climate and past vicariant events.

DIVERSITY AND DISTRIBUTION OF STYGOFAUNA AT WOMBEYAN CAVES

We now present a case study of the stygofauna at Wombeyan Caves, New South Wales to more closely examine diversity and distribution patterns within a single karst area. In the context of mainland Eastern Australia, the stygofaunal diversity at Wombeyan is very high. The South Eastern Highlands Region supports two-thirds of the stygofauna of New South Wales, and half of this total is concentrated at Wombeyan Caves. This includes 43% of the stygal neoniphargid taxa of Eastern Australia, most of these being endemic to Wombeyan.

Wombeyan Caves are described in detail in Dyson *et al.* (1982). Most of the karst is contained within the boundaries of the Wombeyan Karst Conservation Reserve. The karst originated as a single lens of Silurian limestone, and in the early Devonian period the limestone was covered by volcanic rocks and modified into a fractured

crystalline marble (James *et al.*, 1982). The karst has a surface extent of 4.13 km² and is surrounded by igneous rocks. The reserve boundaries, major surface streams, and location of sites containing stygofauna are shown in Figure 3.

The hydrology of the Reserve is complex and comprises a number of subterranean catchments (James *et al.*, 1982; T. Dennis, personal communication, 1993) as shown in Figure 3. On the southern side of Mares Forest Creek, Fred Cave and Marble Sewer Spring may be part of the Gap Creek catchment, but hydrological connections have not been clearly established (T. Dennis, personal communication, 1993). The waters within Basin Cave appear to form a perched water table (M. Chalker, personal communication, 1999).

The northern side of Mares Forest Creek is more complex. Glass, River and Gu-rang-atch Caves form part of the subterranean drainage for Oakey Range Creek catchment. All other sites shown in Figure 3 are part of the Wombeyan Creek catchment, which includes a number of drainage systems. Bullio Cave and Mares Forest Creek Cave form part of the Right Bank Drainage Complex, while the Junction-Figtree system, Grants Cave and W78 are part of the Left Bank Drainage Complex.

Table 7 provides a summary of taxa that have been collected from 14 caves at Wombeyan. Half of the stygofauna are crustaceans comprising neoniphargid amphipods (10 taxa, all stygobites), as well as syncarids, decapods and copepods. In addition, gastropods, insects, nemertineans, oligochaetes and turbellarians are present. Recently protozoans have been collected from Wombeyan Caves, and as many as 20 ciliate forms may be present (M.E. Thurgate and J.S. Gough, unpublished).

Each of the catchments contains a distinctive fauna (Table 7). The Basin Cave 'catchment' is the only location where syncarids have been found. Stygobitic amphipods occur in all catchments, but each cave contains one or two species endemic to that cave (Eberhard and Spate, 1995; J. Bradbury, personal communication, 1999). The Oakey Range Creek catchment is particularly rich in this fauna (five taxa). Gastropods (three taxa) occur in four catchments, and are concentrated in caves closest to Mares Forest Creek, the only perennial watercourse on the Reserve (Figure 3).

The distribution of stygofauna in the Left Bank Drainage Complex is interesting because it reflects the presence of two drainage systems within the complex (T. Dennis, personal communication, 1993). Stygoxenes (insects and gastropods) dominate the drainage system containing the Junction-Figtree system, and no stygobites are present. In contrast, stygobitic amphipods dominate Grants Cave and W78, which are found in the second drainage system.

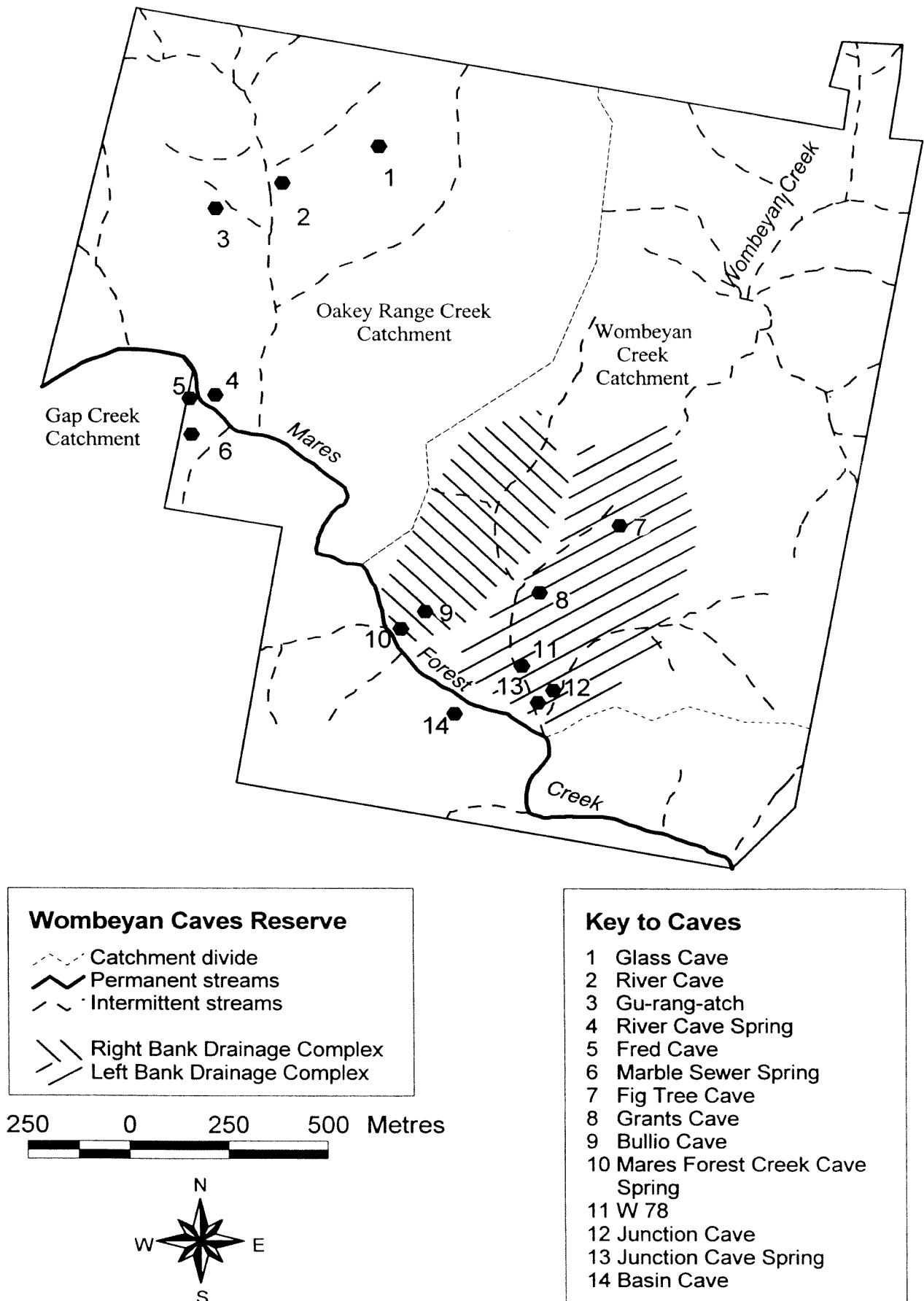


Figure 3 Map of Wombeyan Karst Conservation Reserve showing the location of subterranean catchments (as determined by T. Dennis, personal communication, 1993) and sites containing stygofauna. The shaded sections represent subterranean drainage systems of Wombeyan Creek.

information suggests that New Guinea Ridge, Limestone Creek, Buchan and Murrindal in Victoria; Indi and many places in the Central West of New South Wales; Camooweal and Mitchell-Palmer in Queensland, and Naracoorte in South Australia should be targeted in future survey efforts. The hyporheic fauna of Victorian and South Australian peat swamps (adjacent to or overlying karst) and alluvial aquifers deserve attention, particularly where syncarids are already known. Epigeal and hypogean habitats should be surveyed simultaneously to assist in determining which of the stygofauna are obligate to groundwaters.

Finally, improved management and conservation can only be achieved with better understanding of whole ecosystems. More information is needed about the environments in which stygofauna occur, and the interactions of species within these environments. Collecting data about the physiochemistry of different sites, the fine-scale distribution patterns of stygofauna, the dietary preferences of species and the sensitivity of taxa to disturbance or degradation is vitally important for gaining a better understanding of stygal ecosystems.

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