KARST WETLANDS BIODIVERSITY AND CONTINUITY THROUGH MAJOR CLIMATIC CHANGE: AN EXAMPLE FROM ARID TROPICAL WESTERN AUSTRALIA

W.F. Humphreys
Terrestrial Invertebrate Zoology, Museum of Natural Science, Western Australian Museum, Francis Street, Perth, WA 6000, Australia;
E-mail: bill.humphreys@museum.wa.gov.au

Abstract

Subterranean karst wetlands, recently included as a wetland type under the Ramsar classification, are introduced here to the wetlands biodiversity literature. The general characteristics of karst landscapes explain the connections with non-karstic wetlands, the often diffuse limits to karst wetlands and their vulnerability to exploitation and pollution. Less than 10% of the Earth shows distinctive karst landforms but on a global basis karst wetlands support the greater part of subterranean biodiversity. This introduction is amplified by a detailed account of a single karst wetland, Cape Range peninsula, Western Australia.

Cape Range, the only orogenic Tertiary limestone in Australia, occurs on a continent relatively devoid of karst. It lies in the arid tropics where surface water flows are mostly episodic and frequently saline. The Cape Range karst wetlands contain both freshwater and anchialine wetlands whose natural access is through a few karst windows and caves. The anchialine system shows marked stratification of their physico-chemical and biological profiles. The lack of surface waters and the particular geographical context means that much of the groundwater fauna represents ancient geographical or phyletic relicts. A general case is made supporting the persistence of groundwater fauna in karstic systems through geological eras.

Introduction

The 6th Conference of Contracting Parties to the Ramsar Convention[1] (Brisbane 1996) voted to include subterranean karst wetlands as a wetland type under the Ramsar classification system. This inclusion has far reaching implications, not only for karst regions, but also for a wide range of wetlands, and for groundwater conservation generally. Karst hydrological systems are extensive, occur in many guises, are vulnerable, and frequently support unique phyletic and distributional relictual faunas (see Humphreys. in press a). In addition, they have drainage characteristics (Ford and Williams 1989) that serve to influence the hydrological changes experienced by wetlands remote from the karst systems themselves.

[1] Convention on Wetlands of International Importance especially as Waterfowl Habitat (Ramsar, Iran 1971).

Biodiversity in wetlands: assessment, function and conservation, volume 1
edited by B. Gopal, W.J. Junk and J.A. Davis, pp. 227–258

The biota of karstlands comprise a wide range of epigean taxa, including calciphytes and calciphile lineages such as molluscs – which can be both highly diverse and locally endemic (Solem 1981a, 1981b, 1984, 1985, 1997, Woodruff and Solem 1990) – and, in karst wetlands, phreatophytic vegetation that makes direct use of the groundwater and which can have a major influence on the local hydrology (Tromble 1977). But it also includes the specialised fauna restricted to subterranean aquatic systems – these will be referred to generally as stygobites or stygofauna (Gibert et al. 1994) in contradistinction to troglobites which are essentially terrestrial fauna restricted to subterranean air-filled voids (the term troglobites is sometimes used *sensu lato* to encompass all hypogean environments). Stygofauna can also be both highly diverse and locally endemic (e.g. Holsinger 1978, Longley 1981, Holsinger and Culver. 1988, Wilson and Ponder 1992, Stoch 1995, Bradbury and Williams 1996a, 1996b, 1997a, 1997b, Knott and Jasinska 1998, Humphreys 1999a, Humphreys, in press b, Wilson and Keable 1999).

What is Karst

The unusual geomorphic features of the Kras – known as Karst in the period of the Austro-Hungarian empire – region on the Italo-Slovenian border have become known as 'karst phenomena'. The term karst denotes the distinctive style of terrain resulting predominantly from the dissolution of rock by natural waters, hence the term 'soluble rock landscape' is sometimes used. Owing to their solubility karst is most fully developed in carbonate rocks such as limestone and dolomite, and evaporate rocks such as gypsum. Such areas are characterized by sinking streams, caves, enclosed depressions, fluted rock outcrops and large springs (Fig. 1, Ford and Williams 1989). The integrity of such landscapes is dependent upon the maintenance of the natural hydrological system and they are potentially highly sensitive, comparable in this respect to deserts or coastal margins. Whether the coincidence of karst, desert and coastal systems, as in the Cape Range karst discussed below, makes the area extraordinarily vulnerable is a moot point.

The Limits to Karst Wetlands

The dissolution of carbonate rocks occurs most rapidly with running water and at the interfaces between waters of differing chemical composition, and especially between freshwater and saltwater (Ford and Williams 1989). In most regions water tables, at some stage, have been lower than at present owing, inter alia, to previously drier climate or lower sea level, hence, for this reason alone, karst formations are found commonly well below the current water table. Even in arid zones the lower parts of karst are usually below the water table (phreatic zone) and may contain both lentic (groundwater) and lotic (pressure tubes) wetland systems. Even in those parts of the karst above the local water table (vadose zone) there may be lotic wetlands, as found, for example, in underground stream passages.

Where surface exposures of water occur in karstlands, the normal range of wetland features is produced but, in addition, a number of distinctive features – sometimes with specialized faunas – may also occur associated with karst. Amongst these are anchialine pools (Maciolek 1986, Brock et al. 1987, Thomas et al. 1991,

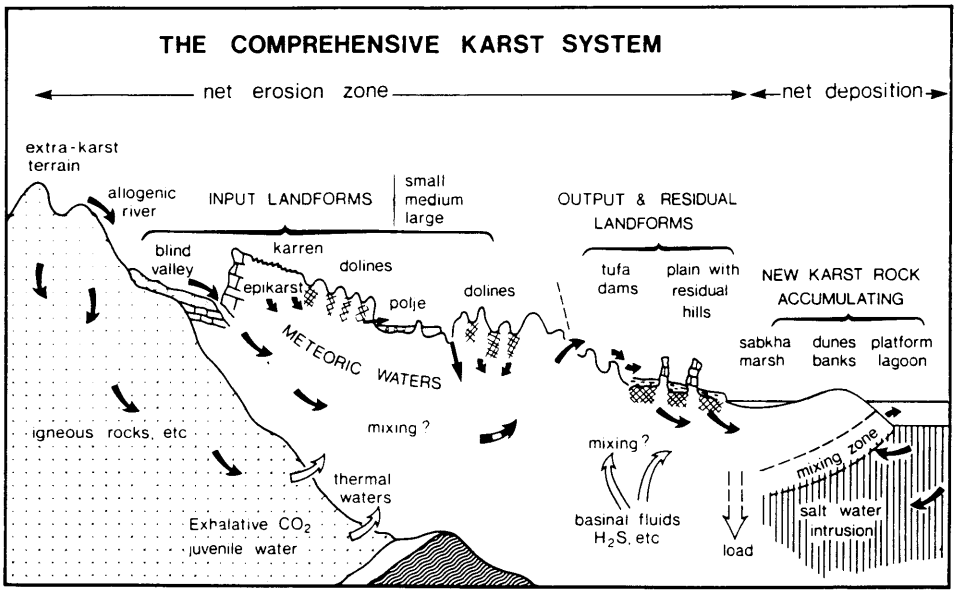

Fig. 1. The comprehensive karst system. (Fig 1.1 of Ford and Williams 1989; with permission).

1992, Iliffe 1992, in press, Sket 1996), springs and spring brooks (Botosaneanu 1998), mound springs (Williams 1965, Harris 1992, Ponder et al. 1995, Knott and Jasinska 1998), tufa (travertine) dams (Julia 1983, Marias 1990, Pentecost 1992, Drysdale and Head 1994, Humphreys, Awramik and Jebb 1995), calcretes (Humphreys 1999a) and blue holes (Stock 1986b, Iliffe 1992), details of which will be presented only where they are relevant to the example presented later in this chapter.

Furthermore, open conduit flow permits large-scale movements within karst which may facilitate dynamical processes – which may themselves be extrinsic to the karst system – supporting the fauna associated with the karst. For example, in the Edwards Aquifer (artesian), Texas (Kuehn and Koehn 1988, Longley 1981, 1992), and in Movile Cave (karstic) in Romania (Sarbu and Popa 1992, Sarbu, in press, Sarbu et al. 1996), sulphides, respectively of petroleum and magmatic origin, support chemoautotrophic ecosystems (Poulson and Lavoie, in press). Analagous systems are found associated with both hydrothermal (Childress and Fisher 1992) and cold deep sea vents (Arp and Fisher 1995, Scott and Fisher 1995), with fauna in the latter also utilising methane harvesting bacteria (MacDonald et al. 1989). Chemoautotropy has also been demonstrated in Frasassi Cave (Sarbu et al., in press), and strongly indicated in anchialine systems (Pohlman et al., in press, Humphreys 1999b).

Karst wetlands merge imperceptibly into groundwater – water which does not interact in the short term with surface waters – and with flow paths beneath (hyporheic) and alongside (epirheic zone) surface water courses with which short-term interactions take place through upwellings and downwellings (Stanford and Ward 1988, Gibert et al. 1994, Ward et al., in press) which have profound effects on

stygal ecology (e.g. Dole-Olivier et. al. 1994, Danielopol et al., in press). The fauna typical of karst wetlands may extend into lava tubes (Wilkens et al.1986), riverine gravels (Boulton 1993), and into immediately sub-littoral systems such as submarine springs (Danielopol and Bonaduce 1990). In addition, through Gyben-Hetzberg systems – in which freshwater lens overlie sea water intrusions (Ford and Williams 1989) – they merge with the marine systems especially in coasts exhibiting anchialine (var. anchihaline) waters which may support extremely diverse, often relictual faunas (Thomas et al. 1991, Iliffe 1992, in press, Thomas et al. 1992, Sket 1996, Yager and Humphreys 1996). Anchialine systems are near coastal subterranean mixohaline waters that are under tidal influence but have only subterranean connections with the sea; they typically occur in volcanic or limestone bedrock and have limited surface exposure (Stock et al. 1986). Such waters typically exhibit marked changes in the depth profiles of numerous physico-chemical parameters (Iliffe, in press, Yager and Humphreys 1996, Humphreys 1999b).

Karst wetlands include two distinct processes that integrate to produce the characteristic karst landscapes. For, in addition to the dissolution processes defining karst, there are also constructional karst features involving the accumulation of new carbonate masses that range in scale from minor speleothem deposition to massive tufa deposits on hillsides. Such depositions may involve both biogenic and physicochemical processes (Humphreys, Awrwnik and Jebb 1995). Associated coral reef complexes may be considered an integral part of the karst system (Hamilton-Smith et al. 1998), as, for example, the large Ningaloo reef fringing the Cape Range peninsula.

Calcretes are a form of carbonate rock generally omitted from discussions of karst. Calcretes occur as soil calcretes and groundwater calcretes and are especially important in the Australian context as they form under arid climates (annual rainfall < 200 mm) with high potential evaporation (>3000 mm per year; Mann and Horwitz 1979). Groundwater calcretes often develop solution features and exhibit the extremely high hydraulic transmissivity showing that the voids and cavities form a conduit system typical of karst aquifers; for example, the Millstream aquifer on the Pilbara craton of Western Australia (Bamett and Commander 1985), and in calcretes associated with the palaeodrainage basins of inland Australia (Sanders 1974, Mann and Deutscher 1978, Jacobson and Arakel 1986, Humphreys 1999a). Groundwater caleretes in the Pilbara and the Yilgarn have recently yielded a rich relict freshwater groundwater fauna with Gondwanan (Harvey 1998, W.F. Humphreys, unpublished), and Pangaean affinities, including the crustacean order Spelaeogriphacea, previously known only from caves in South Africa and Brazil (Poore and Humphreys 1998) and diving beetles (Dytiscidae: Watts and Humphreys 1999, in press).

Global Significance of Karst Wetlands

About 12% of the earth's dry ice-free land comprises carbonate rocks (Fig. 2), which are the principle karst rocks, and between 7-10% shows distinctive karst landforms and/or significant karst groundwater circulation (Ford and Wilhams 1989). The global distribution of karst is uneven (Table 1) – karst regions are mainly distributed on the continents (North America, Asia and Europe) and on seamount islands (Antilles, Oceania), and are less well represented in Africa and Australia (Juberthie and Decu 1994b) and the other Gondwanan fragments.

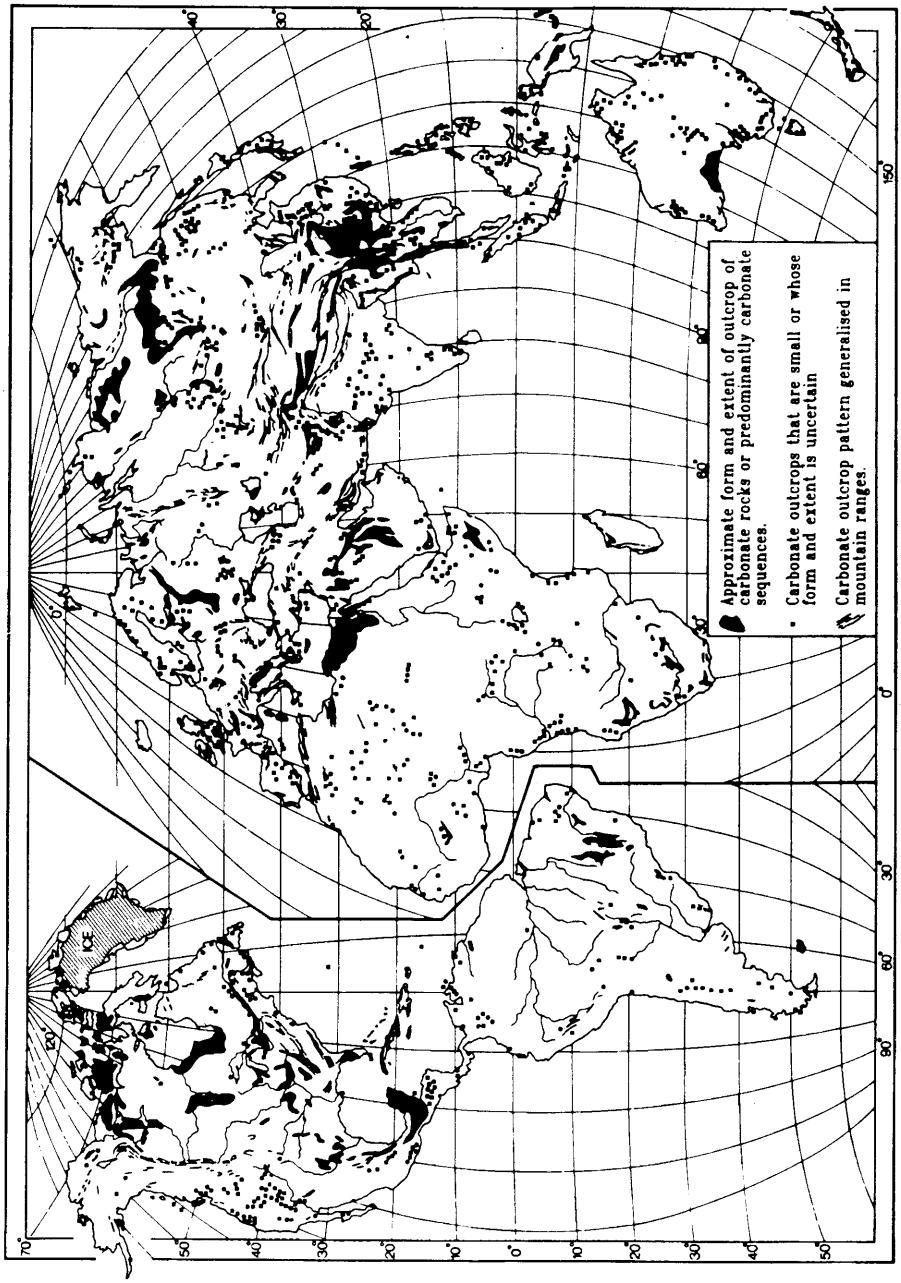

Fig. 2. Major outcrops of carbonate rocks on Earth. (Fig 1.2 of Ford and Williams 1989; with permission).

Table 1. Proportion of the land surface of various countries that are karstic. Data from Juberthie and Decu (1994b).

Country	% Karst
Malta	100.0
Lesser Antilles (many of)	100.0
Cuba	75.0
Slovenia	40.0
Panama	30.0
France	25.0
Italy	25.0
Albania	25.0
Puerto Rico	25.0
Bulgaria	22.5
Spain	22.0
Yugoslavia (formerly)	20.0
China	20.0
Austria	17.0
USA	15.0
Canada	12.0
Belize	8.0
Czechoslovakia (formerly)	2.5
Hungary	1.5
Romania	1.4
Poland	1.3

Ninety-seven percent of the world's freshwater is contained in the groundwater of alluvial aquifers and karstic systems, compared with a mere two percent in rivers and lakes (L'Volich 1974). In many parts of the world groundwater is the source of most potable water and often of the major part of industrial and agricultural water. About 25% of the world's population is supplied largely or entirely by karst waters (Ford and Wifliams 1989).

This enormously important resource – even ignoring the other numerous and varied values of karstic systems (e.g. see Ford and Williams 1989, Davey 1984) – is both heavily exploited and vulnerable to pollution. The surface of karst is often sparsely covered by soil and the undergound drainage with its characteristic open conduit flow, makes karst susceptible to the ingress of pollutants which, for the same reasons, are difficult to contain once they have entered the system (Notenboom et al. 1994).

The management of karst areas requires special knowledge – particularly because surface geomorphology and groundwater drainage are frequently discordant – and management typically needs to extend well outside the karst area itself (Kiernan 1988). The flow characteristics in karst often preclude the simple application of Darcian hygrological models, especially as the hydraulic conductivity of karst systems is markedly scale dependent (Ford and Williams 1989). For the same reasons monitoring wells in karst terrains generally do not work (Quinlan, Davies and Worthington 1992), nonetheless, both are frequently misapplied to karst systems.

Two recent volumes provide a valuable insight into the significance of karst wetlands to stygofauna. The first is the 'Encyclopedia Biospeleologica' (Juberthie and Decu 1994a, 1998) which provides global coverage of both terrestrial and aquatic

hypogean fauna from both a systematic and biogeographical perspective, and deals with the hypogean environments nation by nation, including karst systems. These volumes provide more detailed information on the distribution of karst within each country and the characteristics of its hypogean fauna. The second is 'Stygofauna Mundi' (Botosaneanu 1986) which is a compilation of the world's stygofauna to that date. I have used it to obtain an estimate of the significance of karst wetlands to stygofauna globally, despite the inevitable bias resulting from the concentration of work on stygofauna in Europe and North America. Conservatively, I estimate that about 58% of the worlds stygofauna are associated with karst wetlands (Table 2). The nearly 2000 records involved in these chapters, which comprise only about a fifth of the chapters in the book, are indicative of the biodiversity contained in the stygofauna. Although stygofauna has been sparsely sampled and little researched, it is clear that karst systems harbour a major part of the hypogean wetlands biodiversity. Within them, karst windows between epigean and hypogean environments offer a fascinating glimpse at the subtle selective pressures leading to the evolution of the morphological, behavioural and physiological adaptations to subterranean life (Culver et al. 1995).

Table 2. The distribution of stygofauna species in karst and non-karst hypogean habitats. Amongst the 19 major taxa a conservative average of 58% (±31.7) are found in karst wetlands. Data were extracted from chapters taken at random – excluding predominantly marine groups – from Botosaneanu (1986) and classified according to the habitat description given in the endpapers. Karst categories include habitats A-G, I, T and U; non-karst include habitats H, K-S,V and Z; habitats denoted a and b were excluded as they could not be thus categorised. This is a conservative estimate as some of the non-karst classifications may actually be from karst (e.g. artesian springs). The combined number does not equal the number of species in each group because in many cases a species is found in both karst and non-karst habitats. A species is included even if the habitat is denoted as probable.

Chapter	**Karst**	**Non-Karst**	**% Karst**
5. Porifera	3	0	100
8. Microturbellaria – sub.fw.[1]	26	50	34
9. Turbellaria: tricladida	79	81	49
11. Rotatoria	3	87	3
16. Nematoda – continental sub. aquatic	13	22	37
23. Mollusca – continental sub. aquatic	249	85	75
33. Copepoda: Cyclopoda – continental sub. fw.	93	57	62
35. Copepoda: Harpacticoida – Continental sub. fw.	170	255	40
39. Syncarida	27	131	17
40. Mysidacea	25	1	96
49. Isopoda: Oniscidea	16	0	100
50. Isopoda: Phreatoicidea	1	6	14
54. Amphipoda: Melitid grouping	37	59	39
55. Amphipoda: Niphargus group	117	183	39
56. Amphipoda: Crangonyctid – Holarctic	82	61	57
61. Amphipoda: Liljeborgiidae	1	0	100
62. Amphipoda: Pardaliscidae	1	1	50
63. Amphipoda: Sebidae	1	0	100
86. Pisces	37	9	80

[1] sub. fw. = subterranean freshwater.

Protection

The potential and realised impacts of human activities on groundwater fauna are summarised primarily from the latest authoritative review by Notenboom et al. (1994). Groundwater management includes the need to protect its ecological integrity but this is difficult in karst areas because the dispersivity of pollutants can be very high, and the "filter" phenomena can be deficient or even totally absent (Notenboom et al. 1994). Once pollutants have reached aquifers, sorption and degradation processes are generally low and residence times long. Together these make groundwater environments vulnerable and difficult to rehabilitate. Organic pollution can change groundwater foodwebs because it creates favourable conditions for colonisation by detritivorous epigean organisms. Under these conditions, the unique adaptations of many stygobites to oligotrophic conditions is overridden by pollution and they are replaced by epigean species (Notenboom et al. 1994, Malard 1995).

Anchialine systems, such as much of the coastal area of the Cape Range peninsula discussed in the following example, which often contain endemic fauna, are extraordinarily vulnerable to even slight organic pollution (Iliffe et al. 1984), while being tolerant of a wide range of physico-chemical conditions (Sket 1996, Humphreys 1999b). The terrestrial fauna (troglobites), which provides some food for aquatic biota in the limestone aquifer, also reflects changes in the percolation input of increasing pollution by wastes, fertilizers, and toxic chemicals (Notenboom et al. 1994).

Cape Range peninsula, Western Australia: an example

In this chapter no attempt is made to review karst wetlands on a global basis. On the contrary, owing to the novelty of their inclusion in the Ramsar wetland classification system, one structurally quite diverse system will be examined in some detail to flesh out some of the essential characteristics of such systems. Some comment will be made on the relative diversity of this system vis-à-vis other systems globally. The system in question is the Cape Range peninsula of northwestern Australia, one of the world's more diverse karst fauna provinces. As an example it serves both to emphasise the diversity of the associated fauna and its diverse origins, as well as the diversity of wetland types contained within the karst itself. The example serves to indicate that such systems may have continuity in both space and time throughout long periods of geological time.

Australia

Although areas of carbonate rock occur less frequently in Australia when compared with the world average, about 500 discreet localities are documented (Hamilton Smith and Eberhard, in press). In Australia eight of the 698 wetlands rated as nationally significant (ANCA 1996) comprise inland subterranean karst but only three include obligate subterranean fauna – Loch McNess (ANCA 1996: p. 891) in southwestern Australia, the Spring Tower Complex (ANCA 1996: p. 311) in northern Queensland, and the Cape Range Subterranean Waterways (ANCA 1996: p. 774) in northwestern Australia. The latter, despite being in an arid region, is the only wetland listed principally for its subterranean aquatic fauna.

The listing, as nationally significant, of only eight karst wetlands in Australia belies the significance there of karst wetlands. Although recent work has shown that groundwater fauna is both diverse and widespread in Europe and North America (Marinonier et al. 1993, Gibert et al. 1994), it is poorly known in Australia. It is moderately diverse in Tasmania (Eberhard et al 1991), New South Wales (Eberhard and Spate 1995), and in the Kimberley, Western Australia (Humphreys 1995a). Elsewhere in Western Australia the stygofauna is highly diverse in the Pilbara (Poore and Humphreys 1998, Humphreys, 1999a) and in parts of the Camarvon Basin (Cape Range peninsula and Barrow Island: Humphreys 1993b 1994, 1999a, Bradbury and Williams 1997b). Owing to the novelty of the inclusion of karst wetlands under the Ramsar Convention, it may be expected that many significant areas of karst wetland will be recognised worldwide as they are assessed and as knowledge of their stygofauna improves.

As will be shown below, a karst region of moderate size may support not only a great deal of genetic diversity within taxa, but species swarms and diverse communities within habitats, as well as diverse habitats. One karst area may support an intermixed array of hypogean systems – terrestrial, freshwater, marine and anchialine.

Cape Range peninsula

Arid zones are considered to be sparsely populated with troglobites *sensu lato* owing both to a lack of water (Howarth 1980) and the low food input from xeric plant communities (Peck 1978). Hence, *a priori*, the arid northwest of Australia might be thought peripheral to debate on specialised subterranean animals, as well as to discussion on both wetlands biodiversity and persistence. Yet the subterranean fauna of the Cape Range peninsula in northwestern Australia is amongst the more diverse in the world and is recognized to contain relict fauna of the highest conservation status (Morton et al. 1995).

The diversity of the subterranean fauna of the Cape Range peninsula is partly a result of the juxtaposition of terrestrial, freshwater and anchialine systems. Within the composition of this fauna are echoes of orogenic and eustatic events, climatic change, and of past connections with other parts of Australia, eastern Gondwana and even Pangaea (Harvey 1993, Harvey et al. 1993, Humphreys 1993a-d, Poore and Humphreys 1992, Yager and Humphreys 1996). While I deal here only with the aquatic component of the fauna, it should be borne in mind that this rich aquatic fauna occurs immediately beneath a diverse terrestrial fauna of obligate cave dwellers (Humphreys 1993a 1993d, in press b) which will, in part at least, form part of the food web (Humphreys 1999b, Humphreys and Feinberg 1995).

Here, I discuss the diversity of both the hypogean biota and the habitats of this arid zone subterranean wetland, the affinities of its fauna and its ancient origins. The thesis is developed that these subterranean wetlands, being well buffered from the vicissitudes of most types of surface change, can survive little altered through eras of geological time. Such communities may be expected to be very resilient to the perturbations resulting from Recent climatic change, despite their apparent vulnerability to other anthropogenic changes (Iliffe et al. 1984) and the wide variety of physico-chemical environments that they may inhabit (Humphreys 1994, Yager and Humphreys 1996, Sket 1996, Humphreys 1999b).

Regional Setting

To appreciate the area it is necessary to place it in regional and geological context. The Cape Range peninsula projects northwards into the Indian Ocean on the western shoulder of Australia just within the tropics (Fig. 3). The west coast is fringed by the Ningaloo coral reef lying on Australia's narrowest continental shelf (Kendrick et al. 1991). Barrow Island lies 170 km northeast, on the shallow North West Shelf, part of a continuous series of shelves extending around northern Australia to New Guinea. Cape Range and Barrow Island are anticlines of Tertiary marine limestones of Oligocene to Miocene age (Wyrwoll et al. 1993, McNamara and Kendrick 1994). The Cape Range anticline, rising to an altitude of 310 m, started to fold in the Late Miocene (Malcolm et al. 1991) and has been fully emergent since at least the Pliocene (Wyrwoll et al. 1993), possibly earlier (Humphreys 1993c). Cape Range is the only Tertiary orogenic limestone in Australia; limestones of this type are the host rocks for much of the most biologically interesting karst in the world (Spate and Little 1997). The emergent marine terraces and the coastal plain, cut into the Miocene limestones, are covered by Pliocene and Quaternary deposits of alluvial and colluvial materials including carbonate based conglomerates, calcarenites, siliceous dunes and sand plains (Wyrwoll et al. 1993).

The Cape Range Subterranean Waterways (hereafter 'the waterways') occupy the entire coastal plain and the lower foothills of the Cape Range peninsula northward of a line joining Norwegian Bay on the west coast and the Bay of Rest on Exmouth Gulf (ANCA 1996). A closely related system occurs on Barrow island (Fig. 3). They occur in the Quaternary deposits of the coastal plain and extend into the underlying Tertiary limestones and those of the foothills of Cape Range.

In the waterways fresh water overlays sea water that has penetrated the aquifer at depth and the watertable declines towards sea level near the coast (Allen 1993). It is a Ghyben-Herzberg system in which a freshwater lens floats on a wedge of sea water (Fig. 4). In a perfect Ghyben-Herzberg system under hydrostatic equilibrium, the layer of freshwater is about 40 times as thick as the height of the water table above sea level (Ford and Williams 1989). In practice, as in Cape Range, there is a zone of mixing where the water is variously brackish and this zone may be very thick, up to 30 m in the waterways (Yager and Humphreys 1996, Humphreys 1999b). If the groundwater flow is intercepted, for example by a borefield, then it will cause the saltwater interface to move inland and upward (Davidson 1995).

The coastal plain waters are, in places, anchialine, that is they have no surface connection with the sea but fluctuate with marine tides, contain sea-derived species, have limited exposure to the open air, and have noticeable marine and terrestrial influences (Stock et al. 1986). Anchialine waters, to which access is gained through karst windows, are typically highly stratified, with fresh water – brackish water in arid areas – overlying sea water at depth (Fig. 5). This stratification is commonly associated with major changes in other physico-chemical parameters such as oxygen concentration (becoming less oxic with depth; Sket 1996, Yager and Humphreys 1996, Humphreys 1999b), and redox potential.

Consequently the near coastal sections of the waterways grade from marine near the coast and at depth, to freshwater inland and near the surface, with a variable

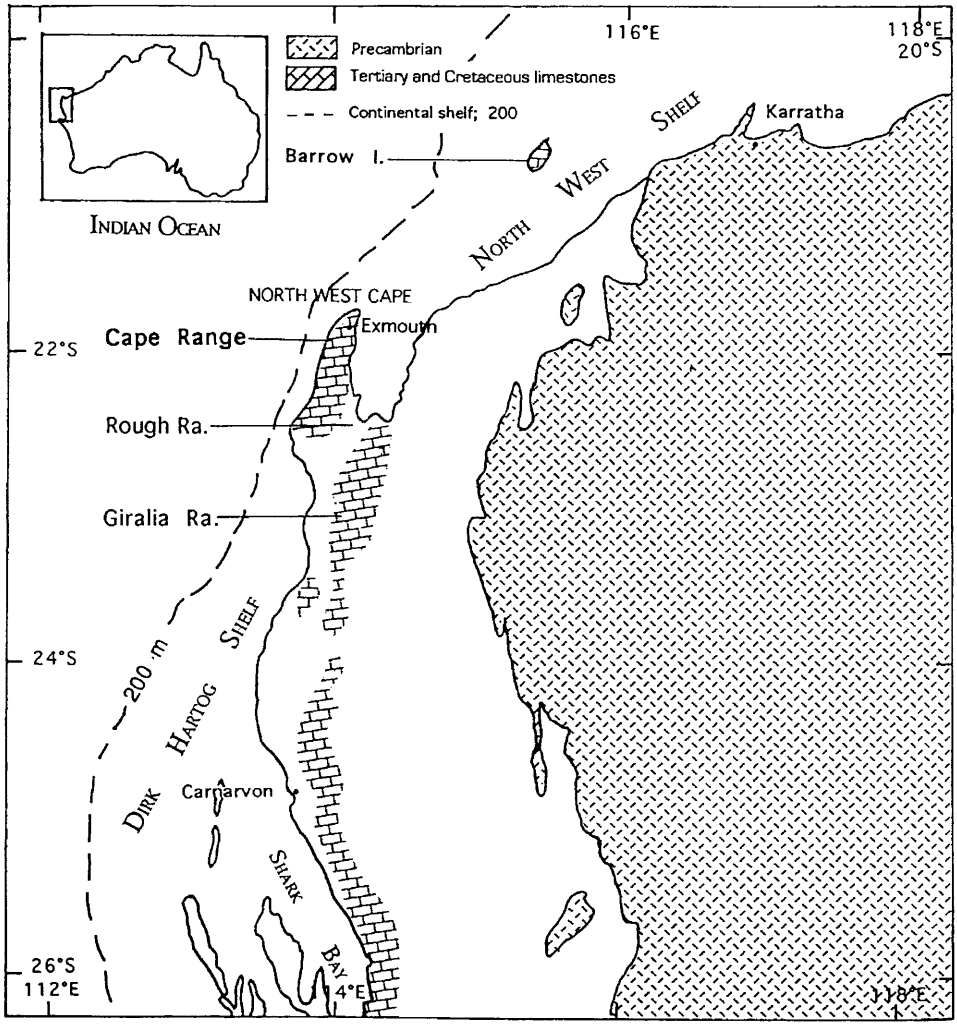

Fig. 3. The regional setting of the Cape Range Peninsula and Barrow Island. The Precambrian Pilbara Craton has not undergone major regional deformation since 2400 Ma (Trendall 1990) and has been, emergent continuously for >600 Ma. This is fringed to the west by middle Mesozoic deposits (c. 100 Ma). A series of anticlines of Cretaceous and Tertiary limestones occurs further to the west. Compiled from Hocldng et al. (1987) and Wyrwoll et al. (1993). Drawn by C. Lawrence.

zone of mixing in between. Such anchialine systems are noted both for their relict faunas and their species richness (Sket 1981 1996), and they are the subject of widespread conservation assessment (Sket 1981, Maciolek 1986, Brock et al. 1987, Ridgley and Chai 1990, Martin et al. 1991, Thomas et al. 1991, Iliffe 1992, Martin et al. 1992, Thomas et al. 1992, Bailey-Brock and Brock 1993).

The waterways occur beneath a diverse arid zone vegetation comprising mostly *Eucalyptus* scrub and *Ficus*, and, on the plain, principally *Triodia* grassland and

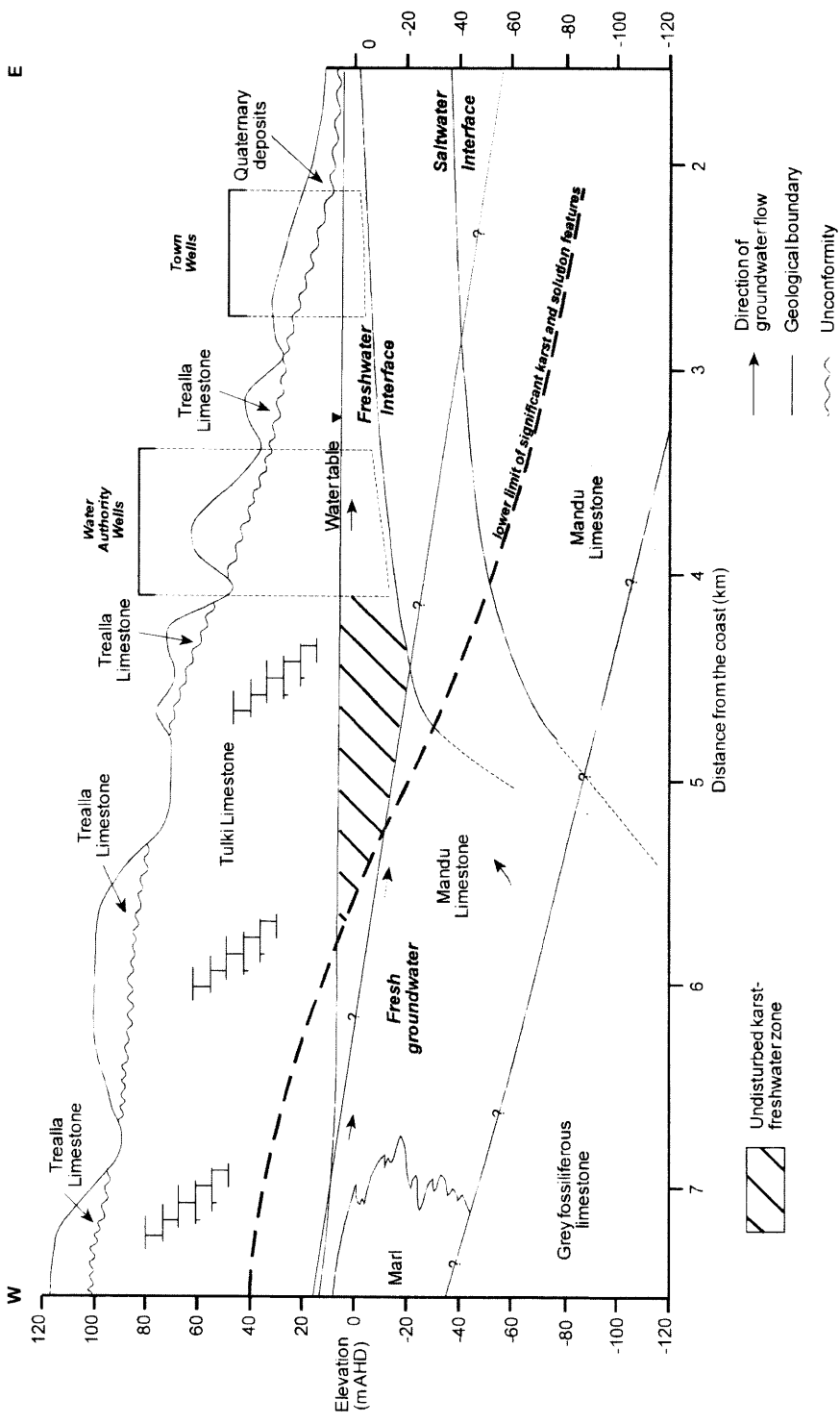

Fig. 4. Generalised hydrogeological cross-section of the Exmouth groundwater area as a representation of the aquifer on the Cape Range peninsula. The hatched line is the lower limit of significant karst and solution features. (With permission of the Water Corporation).

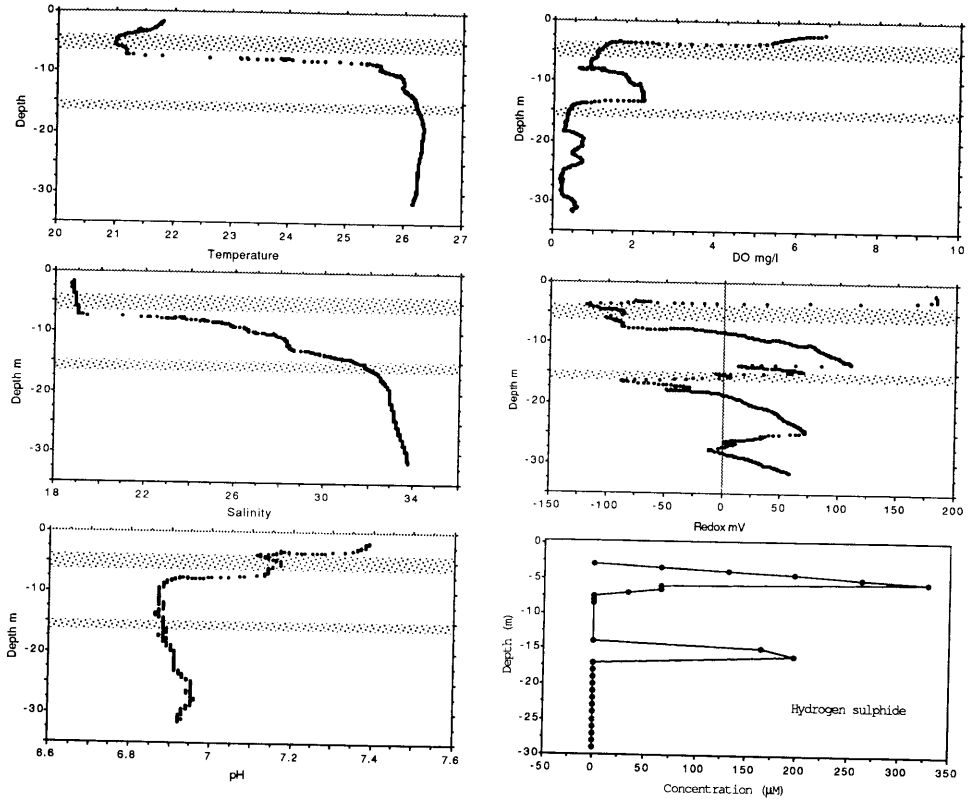

Fig. 5. Depth profile of the physico-chemical environment of cave C-28 in the Cape Range Subterranean Waterways.

chenopods (Keighery and Gibson 1993). Stable isotope composition shows that the energy utilized by the fauna in one eastern part of the range is predominantly from deeper rooting C-3 plants but with a significant contribution from C-4 plants (Davies 1996). While both the terrestrial and aquatic components feed on the specialised subterranean fauna, they also make opportunistic use of epigean fauna entering the stygal realm through surface openings, both natural and artificial (Humphreys and Feinberg 1995, W.F. Humphreys, unpublished).

Access to water within Cape Range proper is limited to five caves in which the water surface is at an altitude of about 180 m. These caves contain a melitid amphipod showing marked genetic discontinuity across gorges (Humphreys and Adams 1991, Adams and Humphreys 1993). It was probably once part of (Humphreys 1993c) the speciose melitid community on the coastal plains (Bradbury and Williams 1996a) but from which it is now disjunct.

The subterranean realm above the water table contains a very rich, endemic troglobite community which comprises at least 41 species (31 genera) and constitutes mostly a relict rainforest-floor fauna, with both temperate and tropical elements (Harvey et al. 1993, Humphreys 1993a 1993c). This attests to a much wetter

past, probably in the late Miocene (Humphreys 1993c). Together with the stygofauna of at least 22 species (12 genera) they make the Cape Range/Barrow Island system one of the worlds richer assemblages of subterranean fauna. This is especially the case as the area has been the subject of very little research effort compared with other areas recognised for the diversity of their hypogean fauna, such as the Appalachian Mountains in the United States (e.g. Holsinger and Culver 1988), or Mexico (e.g. Reddell and Mitchell 1971). It contains 11.2% of the described specialised subterranean fauna of the World's tropics, 15. 1% of the aquatic and 8.6% of the terrestrial fauna (based on data from Peck and Finston 1993).

Methods

Sampling and descriptive effort has focused on the subterranean fauna and so characterisation of the biota of the few open pools is poor. Sampling has been conducted from the surface and by cave diving, using nets of various types (mesh size 125-350 μm), baited traps and by hand from open anchialine pools, caves, traditional wells (human occupation of the area extends to 33,000 years BP; Morse 1993), pastoral wells and bores constructed for other purposes (water abstraction, piezometers, exploration, monitoring and shot holes), rarely by filtering the output of pumps. The physico-chemical environment was determined as described elsewhere (Humphreys 1994, 1999b, Yager and Humphreys 1996).

For the purpose of this paper, it is convenient to consider the Cape Range Subterranean Waterways together with Barrow Island, despite the lack there of karst windows and where access to the stygofauna is mainly through 40 to 50 m deep boreholes. The shallow North West Shelf would have been exposed through much of the Pleistocene and into the early the Holocene. There are both terrestrial and aquatic subterranean species in common between Barrow Island and the east coast of the Cape Range peninsula (Adams and Humphreys 1993, Harvey and Humphreys 1996) suggesting that the emergent shelf was suitable habitat for the troglobites *sensu lato* (Humphreys 1993c).

Biodiversity in an Arid Zone Wetland

The waterway should be discussed against the background that the area is both arid and hot, and made effectively more arid owing to the karst terrain. The mean daily temperature is c. 27°C with the mean monthly maximum temperature exceeding 35°C for four months and the mean relative humidity is persistently low (Vine et al. 1988). Consequently the annual evaporation (3219 mm) exceeds the sparse precipitation (median = 280 mm) by more than an order of magnitude (Vine et al. 1988). Rainfall in the region results from at least four processes (Gentilli 1972) resulting in very low predictability between both seasons and years (Humphreys et al. 1989). The fixed red sand dunes of Pleistocene age (Wyrwoll et al. 1993) that overlie parts of the north and south parts of the range, and beneath which both troglobites and stygobites are found (W.F. Humphreys, unpublished), attest that previously the area has been even more arid. Conversely, at other times the area has been substantially wetter, supporting rainforest, as is evident from the lowland rainforest affinities (Harvey et al. 1993, Humphreys 1993a 1993c, in press b) of the terrestrial troglobite fauna in both Cape Range itself and on the adjacent coastal plain.

Stygofauna

A minimum of 26 stygofaunal taxa occur in the wetlands (Table 3) including the only two species of blind fish in Australia. The remaining species are mainly crustaceans and the fauna appears predominantly to be endemic to the Cape Range and Barrow Island systems. The fauna includes a great diversity of amphipods (Bradbury and Williams 1996a, 1996b, 1997a, 1997b) – the only known representatives in the southern hemisphere of the class Remipedia (Yager and Humphreys 1996), the order Thermosbaenacea (Poore and Humphreys 1992), and the genera *Haptolana* (Bruce and Humphreys 1993) and *Danielopolina* (Baltanas and Danielopol 1995). The crustacean fauna includes marine (melitid and hadziid amphipods), euryhaline (bogidiellid amphipods) and freshwater (syncarids, which probably evolved before the break-up of Pangaea) lineages, as well as major stygobiont lineages that are widely disjunct from congeneric species found on either side of the North Atlantic (e.g. Remipedia and Thermosbaenacea) and/or which belong to lineages clearly Tethyan in origin (thaumatocypridid ostracods, *Haptolana*). Six genera are apparently endemic to the region (Humphreys 1993b, 1994, Knott 1993, Bradbury and Williams 1996a 1997b, Yager and Humphreys 1996).

The anchialine fauna consists of the same groups of crustaceans as recorded from anchialine caves of the Caribbean region (Bahamas, the Yucatan Peninsula of Mexico, and Cuba; Yager 1987a, 1987b, 1994) and the Canary Islands (Lanzarote; Wilkens et al. 1986, 1993). It comprises, amongst others, remipedes, cirolanid isopods, atyid shrimp, ostracods, gammarid amphipods and thermosbaenaceans.

Table 3. The composition of the stygofauna of northwestern Australia. About half of the fauna has been found since 1991. The fauna is found variously in caves in Cape Range itself (R), on the coastal plain bordering Cape Range (P), and on Barrow Island (I). * denotes highly stygomorphic species.

Major taxon	**Genus and Species**	**Locality**
Turbellaria	Microturbellaria	PI
Polychaeta: Spionidae	Gen. nov. et sp. nov. R. Wilson, pers. comm. 1996	P
Ostracoda: Halocyprida	* *Danielopolina* sp.nov. Baltanas & Danielopol, 1995	P
Ostracoda: Cypridacea	*Aglaiella* sp.nov. K. Wouters, pers. Comm. 1995	PI
Ostracoda: Cytheracea	*Darwinula* sp. K. Wouters, pers. Comm. 1995	P
Remipedia: Nectiopoda	* *Lasionectes exleyi* Yager & Humphreys	P
Syncarida: Bathynellacea	*Atopobathynella* sp. nov. H.K. Sminke, pers. comm. 1994	IP
Isopoda: Cirolanidae	* *Haptolana pholeta* Bruce & Humphreys	PI
Amphipoda: Melitidae	* *Norcapensis mandibulis* Bradbury & Williams	R
	* *Nedsia douglasi* Barnard & Williams	P
	* *N. strakraba, N. hurlberti, N. humphreysi, N. urifimbriata, N. fragilis, N. macrosculptilis, N. culptilis* all Bradbury & Williams	I
Amphipoda: Hadziidae	* *Liagoceradocus subthalassicus* Bradbury & Williams	I
	* *Liagoceradocus branchialis* Bradbury & Williams	P
Amphipoda: Bogidiellidae	* *Bogidomma australis* Bradbury & Williams	I
Thermosbaenacea	* *Halosbaena tulki* Poore & Humphreys	PI
Decapoda: Atyidae	* *Stygiocaris lancifera* Holthuis	P
	* *Stygiocaris stylifera* Holthuis	PI
Pisces: Eleotridae	* *Milyeringa veritas* Whitley	P
Pisces: Synbranchiformes	* *Ophisternon candidum* (Mees)	P

This aquatic community composition has become predictable in anchialine habitats (Holsinger 1989, 1992, Poore and Humphreys 1992, Humphreys 1993b, Yager and Humphreys 1996) despite the great disjunction from congeners that are mostly found in subterranean habitats on either side of the North Atlantic (e.g., Poore and Humphreys 1992, Bruce and Humphreys 1993, Yager and Humphreys 1996). The affinities of the fauna are considered predominantly to lie with the Tethys ocean (Table 4; Humphreys 1993b, Knott 1993) that opened between the continents of Gondwana and Laurasia and which persisted from the Triassic until the late Eocene (200-40 Ma; Smith and Briden 1977). It will be argued later that this may represent a surviving Jurassic community.

The stygofauna occupies waters with a wide range of physico-chemical characteristics. While some species appear to be restricted to waters beneath a strong pycnocline (*Lasionectes exleyi, Danielopolina* sp. nov., *Liagoceradocus branchialis*; Yager and Humphreys 1996), others, such as *Stygiocaris stylifera* and *Milyeringa veritas*, are variously found in habitats ranging from open anchialine pools in full sunlight, in canals in freshwater caves, and beneath a strong pycnocline at a depth of 32 m in seawater beneath several layers of hydrogen sulphide in almost anoxic waters. The range of physico-chemical characteristics of the water from which various species have been collected is given elsewhere (Humphreys 1999b). The fauna is predominantly euryhaline. The mean salinity (total filterable solids, mg L^{-1}) of the water at sites where *O. candidum* was sampled, was 3520 (range 710-7700; n = 8 sample sites), *M. veritas* 8168 (250-26500; n = 20), *Stygiocaris* spp. 2859 (370-20000; n = 25), *H. tulki* 2577 (610-7700; n = 19), *H. pholeta* 1783 (660-3300; n = 6), *Norcapensis mandibulis* in Cape Range s.s. 437 (390-500; n = 3), melitid amphipod, coastal plain 3622 (660-11000; n = 19).

Surface Fauna

The waterways have very restricted surface expression, limited to one substantial drowned sinkhole (cenote: Yager and Humphreys 1996) and perhaps 15 karst windows, no more than 2 m across, into the anchialine system. The stygofaunal diversity, high by world standards, is complemented by an epigean fauna which inhabits these karst windows and also contains some disjunct species (see Appendix).

Although only two algae have been characterised, these karst windows support substantial primary production from green plants in the photic zone. The nitrification and sulphur bacteria, which occur near the pycnocline (Yager and Humphreys 1996, Humphreys 1999b), may make some chemoautotrophic contribution to the energy supply for this anchialine fauna (Humphreys 1999b) as occurs in a similar system in Yucatán (Pohlman et al., in press). Anchialine atyids on Hawaii, in addition to filter feeding like their freshwater relatives (Fryer 1977), also scrape the benthic algal/cyanobacterial crust ingesting diatoms, cyanobacteria and algae (Bailey-Brock and Brock 1993). Hence, it is likely that such systems are more complex than currently appreciated.

The faunal diversity in the karst windows includes strictly marine forms, such as the circumtropical syllid polychaete *Sphaerosyllis centroamericana*, and estuarine elements, such as the mollusc *Iravadia* sp. and possibly the amphipod *Grandidierella* sp., elsewhere known only from the saltings at Dampier, Western Australia (J. Lowry.

Table 4. The affinities of genera from the stygofauna of northwestern Australia. T = Tethyan, G = Gondwanan, P = Pangean

Taxon	Genus	Distribution	Affinities
Ostracoda: Cypridacea	*Aglaiella*	?G	Egypt, Mozambique, Sri Lanka (K. Wouters, pers. comm. 1995)
Halocyprida	*Danielopolina*	T	West Indies, Canary Is., Galapagos, Atlantic abyssal
Syncarida: Bathynellacea	*Atopobathynella*	G	SE Australia, New Zealand, Chile
Thermosbaenacea	*Halosbaena*	T	West Indies, Colombia, Canary Is. (Poore & Humphreys 1992)
Amphipoda: Melitidae*	*Nedsia* spp.	T	(Knott 1993)
Hadziidae	*Liagoceradocus*	T	W. Pacific, Madagascar, Canary Is.
Bogidellidae	*Bogidomma*	P	Endemic genus
Isopoda: Cirolanidae	*Haptolana*	T	Cuba, Somalia (Bruce & Humphreys 1993)
Decapoda: Atyidae	*Stygiocaris*	T	Madagascar (Banarescu 1990)
Remipedia: Nectiopoda	*Lasionectes*	T	Turks & Caicos, West Indies (Yager & Humphreys 1996)
Pisces:			
Perciformes: Eleotridae	*Milyeringa*	–	Endemic genus, affinities unknown
Synbranchiformes	*Ophisternon*	?T	Circum tropical (Mexican caves)

*Melitids are possibly ancestral to the Hadziids (Barnard and Barnard 1983), almost all of which are blind stygobionts with a Tethyan distribution.

pers. comm. 1994). Freshwater elements are also represented such as thiarid molluscs, water mites, dragonflies, gerrids and dytiscids and feral tropical aquarium fish. The meiofauna of the area is essentially unknown.

One substantial surface waterway, Yardie Creek, crosses the coastal plain and extends as a short gorge, less than two kilometre long, extending into Cape Range. This overdeepened gorge – the only extensive permanent inland water within c. 100 km – cuts through the waterways and must be in hydrological continuity with them. However, the nature of this connection has not been characterized although tidal fluctuations, as is generally found in the anchialine system (W.F. Humphreys and R.D. Brooks, unpublished), do occur in the creek when the bar is closed (N. McGregor, pers. comm. 1996). The creek, which is generally closed by a sandbar that is breached by exceptional tides and/or rainfall – and when dugong, *Dugong dugon* (Müller), may feed there (N. McGregor, pers. comm. 1996) – is a mixohaline system that ranges from fully marine to freshwater.

Despite the large extent of this waterway within an arid zone, no systematic sampling has been undertaken there. The biota is predominantly marine, including a remnant of a formerly more extensive mangal (Kendrick and Morse 1990), and fish, at least one species, *Craterocephalus capreoli* Rendahl (Atherinidae), having populations in the creek that are genetically divergent from those in the adjacent sea (R. Watts, pers. comm. 1996).

In the less saline upper reaches, and at a small spring-fed freshwater pool raised above the general level of the creek, there is a fringing vegetation of emergent aquatics, chiefly *Typha domingensis* Pers. (Typhaceae) and *Schoenoplectus litoralis* Schrader (Cyperaceae). Both are disjunct by several hundred kilometres from their

respective main range (Keighery and Gibson 1993). There is also a disjunct population of *Melanoides* sp., a freshwater thiarid gastropod (Slack-Smith 1993).

Age and Persistence of the Stygofaunal Community

Here I discuss the age and persistence of the subterranean community now inhabiting the waterways and show that they could have existed in this habitat for very long periods despite great climatic changes (Quilty 1994). The general stability of the area has attributes favouring long-term persistence of a subterranean fauna. It is in close proximity to the Pilbara Craton, emergent since the Silurian at least. Additionally, it has been in continual juxtaposition, since the Cretaceous, to both an emergent shoreline and to the continental shelf, and throughout this period has had a carbonate depositional environment (Hocking et al. 1987).

I argue that the composition of the anchialine fauna from Australia to the Caribbean, and the presence of obligate stygal species widely disjunct from their congeners, supports an early vicariance as a result of seafloor spreading and suggests the survival to the present of a Triassic or Jurassic community. This community was protected in its stygal realm from changes at the surface. I go on to discuss the general significance of groundwater fauna regionally in permitting the persistence of biota through climatic and other changes at the surface.

Tethyan Affinities and Age of the Fauna

A number of crustaceans occur as congeneric species on either side of the North Atlantic which belong to higher taxonomic ranks (e.g. *Remipedia, Thermosbaenacea*) whose biological characteristics are such that they that were considered to be especially convincing examples of Tethyan relictual distributions (Newman 1991). These taxa are restricted to a range of hypogean habitats, have few young and the free-living larval stages have been suppressed. They are extreme K-strategists (Stock 1986a) – the species have very limited power of dispersal, a potential further limited by their restriction to a range of hypogean habitats and often specialised environmental requirements. For example, remipeds have only been collected by cave divers in anchialine caves below a density interface (Yager and Humphreys 1996). These specialised requirements enhance the already high potential of troglofauna *sensu lato* to be discriminating palaeogeographical monitors (Danielopol 1980, Sbordoni 1982).

Furthermore, the presence on either side of the North Atlantic of congeneric species such as *Halosbaena* and *Monodella* (Thermosbaenacea), *Stygogidiella, Pseudoniphargus, Psammogammarus, Gevgeliella* and *Spelaeonicippe* (Amphipoda), *Curassanthura* (Isopoda) and *Speleonectes* (Remipedia), which have the same stygal lifestyles, provides support for the hypothesis that the vicariance was due to the opening of the Atlantic. The hypothesis is more convincing because their distribution on a reconstructed Jurassic landmass is relatively modest (Fig. 6).

A number of species congeneric with members of the classically Tethyan relict fauna found on either side of the North Atlantic, or with otherwise widely disjunct distributions, are also known from the Cape Range system of northwestern Australia (Fig. 3); for example, *Halosbaena* (Canaries and Caribbean), *Haptolana* (Cuba, Somalia), *Lasionectes* (Turks and Caicos), *Liagoceradocus* (Canaries and

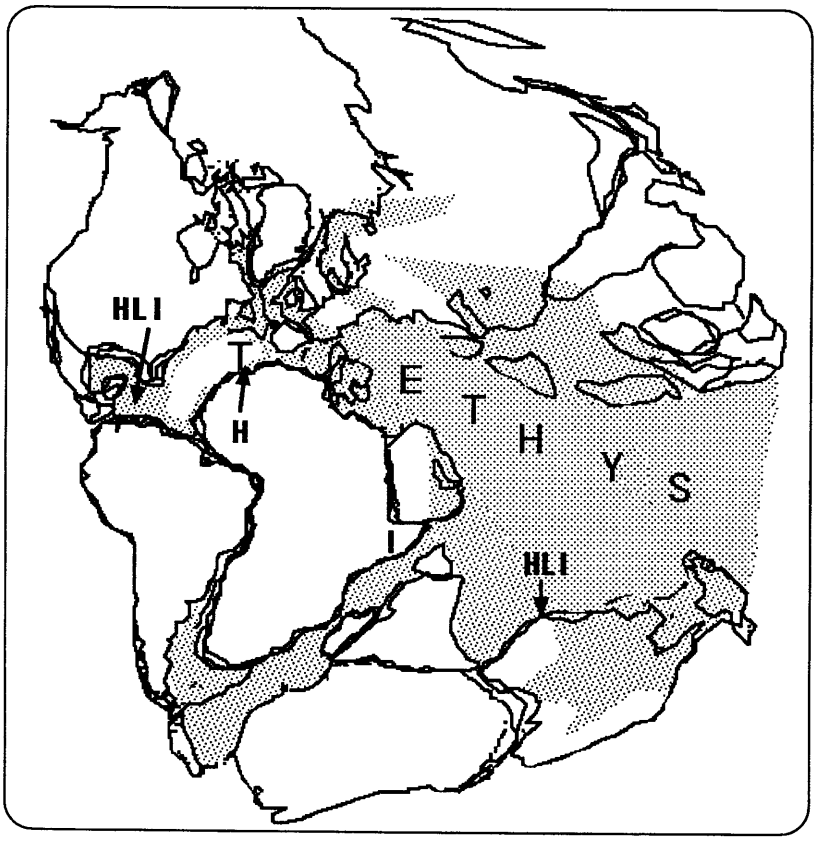

Fig. 6. The relative location of the continental plates and the extent of the epicontinental seas in the Jurassic (151 Ma) when the Tethys Sea first connected the present Caribbean, Mediterranean and Indian Ocean regions. Even with this reconstruction the genera *Halosbaena* (Thermosbaenacea; H), *Haptolana* (Isopoda: Cirolanidae; I) and *Lasionectes* (*Remipedia;* L), known from northwest Australia have widely disjunct distributions variously including Somalia, the Canary and Caribbean islands. The plate map was produced using Scotese and Denham (1988) and simplified.

Pacific) and *Danielopolina* (North Atlantic and eastern Pacific; Baltanas and Danielopol 1995). Being obligate stygofauna, the genera are likely to have been present as stygofauna before the isolation of the Australian plate. At least one of these lineages is known to have been present in marine caves at this time. Fossil ancestors of *Danielopolina* occur in submarine fissure and cave fills showing that they had already colonised para-anchialine systems by the Late Jurassic (Aubrecht and Kozur 1995). Should these five independent lineages prove to be monophyletic, then the age of vicariance of these widely disjunct congeneric species may, perhaps, be sought in the congruence of area cladograms. Attempts are currently in progress to test this hypothesis using molecular clocks.

The distribution of remipeds and their associated fauna can be explained by cave colonization along the shores of Tethys during the Triassic and Jurassic (225-160

Ma BP; Cals and Boutin 1985), and subsequent dispersal after the break-up of Pangaea in the Mesozoic (Wilkens et al. 1986) through sea floor spreading and continental drift (Stock and Longley 1981, Iliffe et al. 1984, Hart et al. 1985, Wägele and Brandt 1985). During the early Cretaceous the plate that is now Western Australia formed the eastern shore of Greater Tethys (Howarth 1981).

For both *Halosbaena* (Wagner 1994, H.P. Wagner, pers. comm.) and *Danielopolina* (Baltanas and Danielopol 1995) cladistic analysis suggests that the Australian populations were isolated from those in the Atlantic region prior to the vicariance resulting from the opening of the Atlantic itself. This sequence is consistent with that of the break-up of Pangaea proposed by Howarth (1981) and the dissolution of Gondwana during which the separation of Africa from Antarctica (i.e. of West from East Gondwana, 142-133 Ma BP) predated the opening of the Atlantic Basin between Africa and South America (127 Ma BP; Partridge and Maud 1987). By the Upper Cretaceous (c. 80 Ma BP, probably even by the Middle Cretaceous, 100 Ma BP; Cande and Mutter 1982) Australia was not even joined by epicontinental seas to landmasses other than Antarctica (Howarth 1981). This concordance is consistent with the hypothesis that the genera rafted on the tectonic plates and in which case there has been remarkable morphological conservatism (cf. Poore and Humphreys 1992, Bruce and Humphreys 1993, Yager and Humphreys 1996) following an early vicariant event.

The very predictability of the higher taxonomic composition of this community (see above), with widely vicariant common genera, coupled with the clear Tethyan affinities of the fauna, suggest that the community has survived since the opening of the Atlantic and that we are dealing with a surviving Jurassic community.

Under this hypothesis, the fauna is much too old to have colonised the Tertiary limestones of Cape Range, and they would have to have colonised older substrates and subsequently migrated to their present location. Being obligate stygofauna, they must perforce have migrated within a matrix that was of necessity continuous in space and time. What factors favour this route?

Inland from Cape Range, the Pilbara Craton – continuously emergent since the Precambrian (Hocking 1990) – is fringed with Mesozoic rocks which initially could have been colonised by the fauna and from which subsequent migration within the matrix could have populated the developing Cainozoic rocks (Humphreys 1993b 1993c). That the area seems to be suitable for such migration – across the emergent North West Shelf in the Pleistocene – is supported by the current distribution of both terrestrial and aquatic troglobites (see above) as well as the genetic affinities of *Stygiocaris stylifera* (Adams and Humphreys 1993). However, the area also has other attributes making it especially favourable for the survival of an ancient relict fauna.

Tectonic Context and Palaeo-environment

The Exmouth Sub-basin, in which Cape Range lies, was initiated in the Early Jurassic (c. 200 Ma BP) and was in contact with the waters of the Neotethys (Apthorpe 1994) and has remained predominantly a marginal marine environment. It has been continuously in close proximity to the continental margin since Greater India broke away in the Early Cretaceous (c. 140 Ma BP). By the middle Cretaceous (c. 85 Ma BP) the separation of the tectonic plates had advanced sufficiently to permit full oceanic circulation, which, combined with the warmer water resulting

from the northward movement of Australia Plate, led to the domination of reef and platform carbonates for the remainder of the Cretaceous. This marine carbonate depositional environment continued throughout the Cainozoic (Malcolm et al. 1991). An eastwest compressional phase of tectonism in the Late Miocene, that resulted from the subduction of the Australian plate beneath the Asian plate, led to the formation of the Cape Range and Rough Range anticlines by inversion and thrusting along the basin margin (Malcolm et al. 1991).

A fault trending north-east across the base of the peninsula (roughly from Point Cloates to the Bay of Rest; Fig. 3) marks the boundary between the Gascoyne sub-basin and the Exmouth sub-basin (Hocking et al. 1987). The Cretaceous and Cainozoic deposits in the latter are underlain by Carboniferous and earlier rocks, whereas in the former they are underlain by Jurassic rocks, as are those in the Barrow sub-basin and the Dampier sub-basin. This boundary closely approximates the known southern distribution of the Cape Range stygofauna.

Longevity

The parsimonious explanation, then, is that we are dealing with a surviving Jurassic community that has gradually separated from the Atlantic province through sea-floor spreading and rafting on the tectonic plates. Even were the fauna Miocene in origin – proposed by some theories on the origin of anchialine faunas (Por 1986, Stock 1986a, 1990) that do not incorporate the highly disjunct distributions of obligate stygofauna (Humphreys, in press a) – the longevity of these aquatic systems is still considerable.

To account for the presence of a clearly old fauna in Tertiary Cape Range, I considered the community to have migrated across the North West Shelf during the Miocene from adjacent to the Pilbara Craton (Humphreys 1993b, 1993c). However it now seems possible that this phase could have occurred much earlier, in the middle Cretaceous, and that the community could subsequently have remained more or less in situ staying within the matrix near the surface as the carbonate sediments accumulated. Nonetheless, several elements of the stygofauna have recently been found, as predicted (Humphreys 1993b, 1993c), in aquifers of the Carnarvon Basin where they abut the Pilbara Craton (W.F. Humphreys, unpublished). There they (*Haptolana, Stygiocaris, Halosbaena)* are found in alluvial aquifers overlying Miocene limestone, in the cobble beds deposited by rivers entering the coastal plain from the Pilbara Craton, and even penetrating river gravels onto the craton itself as far as groundwater divides (W.F. Humphreys, unpublished).

At present elements of the stygofauna are known from an altitude of c.300 m to 31 m below sea level. The fauna is sampled particularly from the crystalline Tulki Limestone and, as the range is an anticline, it dips beneath the sea around the periphery of the peninsula. Marine tides are apparent in the caves 1.5 km inland (Fig. 7; W.F. Humphreys and R.D. Brooks, unpublished) and in water bores up to 3.5 km inland (Forth 1973) indicating open conduit flow of the groundwater within the coastal plain. This tidal movement will serve to expand the zone of mixing at the saltwater interface and transport nutrients and energy though the coastal anchialine aquifer. The latter is demonstrated by the transport of heat associated with the tidal movement in a cave (Fig. 8), such heat transport may in itself have ecological consequences (Shepherd et al. 1986). This movement is thought to occur in karsti-

fied Tulki Limestone as it dips beneath sea level. Owing to Pleistocene sea level changes, the limestone is likely to be karstic to greater than 100 m below sea level, channels having formed at the changing water table, especially by mixture corrosion. Divers have penetrated caves to 31 m below sea level, deeper than the present depth of the sea over much of the North West Shelf.

Some of the more recent surface changes impinging upon the area are evident. During the Quaternary oceans were lowered by 120-140 m during maximum glacials and elevated by 5 to 8 m in the warmest interglacials. Thus for most of the Pleistocene the North West Shelf would have been exposed above sea level and had a similar geomorphology to the present coastal plain. The distribution and genetic composition of the present fauna indicates that this extensive coastal plain provided suitable habitat for both the terrestrial and aquatic subterranean fauna. Such eustatic changes would have altered the geographic extent of this wetland which is now pushed against the foothills of Cape Range and is about as constrained as it has ever been. The fixed red dunes and the relict rainforest troglofauna provide evidence of both wetter and drier climates in the past (see above).

It is hypothesised that the elements of this community have survived, by virtue of its subterranean existence, owing to the amelioration of the vagaries of the surface, geomorphological and geological changes, and due to their being able to move through the matrix of the rock while remaining protected in the hypogean realm, successively adjusting to vertical and lateral shifts in the location of its habitat.

General Case

There is wide supporting evidence from other taxa and areas that troglobites survive in their protected underground ecosystems with remarkably little morphological

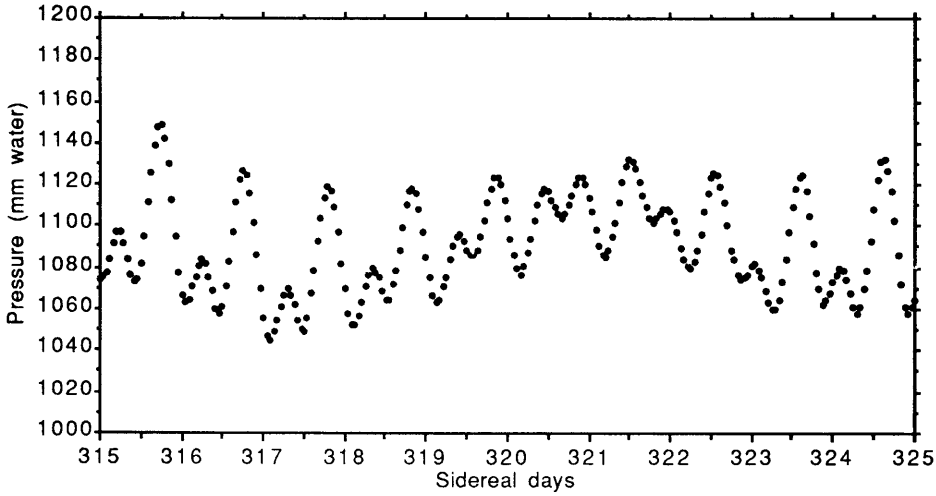

Fig. 7. Semidiurnal tidal movements in cave C-28, an anchialine cenote on the Cape Range peninsula, 1.5 km inland from the Indian Ocean. Data were recorded hourly using pressure transducer and data logger for 10 days in 1996 [DataFlow, Noosaville, Queensland] (W.F. Humphreys and R.D. Brooks, unpublished data).

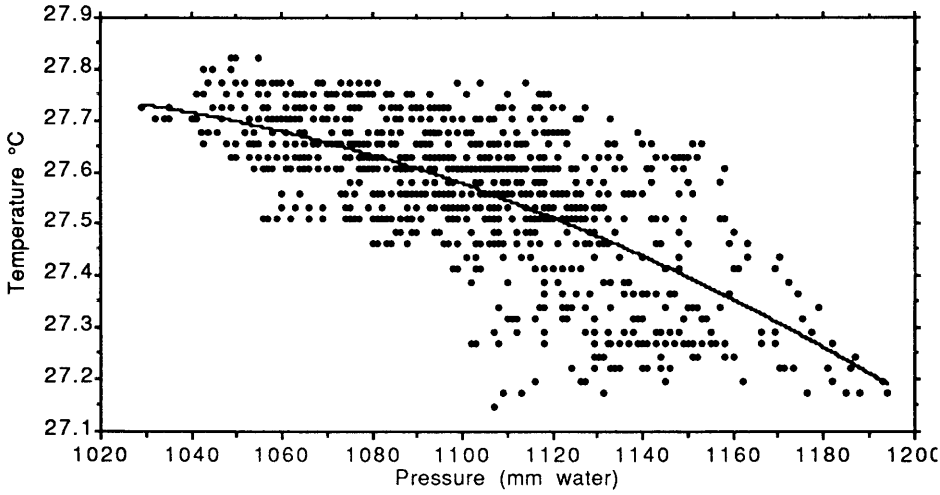

Fig. 8. The relationship between relative water level (X mm) and water temperature (°C) in C-215, a strongly tidal cave, for the period 300-339 sidereal days 1996. The water is 23.8 m below ground level and would, in the absence of tidal action, be expected to have a stable water temperature on a daily basis. The tidal cycle is about half that shown in Figure 7 but of similar form. Temperature = $0.023X, - 1.18 \times 10^{-5} X^2 + 16.58$ ($r^2 = 0.46$, Fs 2,934 = 403.1, $P<0.0001$) (W.F. Humphreys and R.D. Brooks, unpublished data).

change through long periods of geological time. As no ordinal taxon of terrestrial troglobites is restricted to the hypogean, the most compelling evidence comes from aquatic taxa.

A range of widely distributed freshwater lineages is known whose biogeography is explicable if they entered freshwater and were subsequently dispersed by tectonic plate rafting, for example the syncarids (Schmink 1974, Boutin and Coineau 1987), spelaeogriphaceans (Poore and Humphreys 1998), and bogidiellid (Karaman 1982, Stock 1977 1983) and crangonyctid amphipods (Holsinger 1986), plus at least four orders of isopods (phreatoicids, aselloids, calabozoids and ?protojaniroids: Wägele 1990).

It appears that such hypogean animals and even, as suggested here, the communities in which they occur, can survive the myriad perturbations that would have impinged on a given locale through geological time – tectonic, orogenic and eustatic events, climatic, atmospheric and oceanic changes, and of past connections with other parts of Australia, eastern Gondwana and even Pangaea. As such, anthropogenic global warming and its consequences is unlikely to cause any serious problems to these hypogean wetlands, in sharp contrast to the epigean wetlands. Nonetheless, these hypogean wetlands are highly vulnerable to more direct anthropogenic changes (e.g. Notenboom et al. 1994), having a low capacity to cope with disturbance, and which are difficult, if not impossible, to restore once degraded (Yuan 1988). Owing to the characteristics of karst regions, and where the surface and groundwater drainage are often discordant (Kieman 1988, Ford and Williams 1989, European Commission 1995), management has to be holistic and often to extend beyond the confines of the karst itself.

Acknowledgements

I thank the numerous people who have supported me in the field and the laboratory and who have provided information, taxonomic expertise and encouragement. The work has been variously funded by Federal and State agencies, private trusts and companies. All are acknowledged fully in more appropriate publications.

Appendix

High level taxonomic groupings of taxa collected in open water bodies that do not comprise part of the stygofauna. The references denote the source of determinations other than the author.

Rhizoclonium ?tortuosum (Dillw.) Kuetz. (Chlorophyta: Cladophoraceae); *Lamprothamnium papulosum* (Wallr.) J. Gr. (Charophyta: Characeae); *Euplotes* sp. and *Paramecium* sp. et al. (Protista, Knott 1993); various undetermined foraminifera (D. Haig, pers. comm. 1995), microturbellaria, rotifers, nematodes, oligochaetes, ostracods and harpacticoid copepods; molluscs *Iravadia* (*Iravadia*) sp. ?*I. ornata* (Iravadiidae: status ambiguous: Slack-Smith 1993) and *Melanoides* sp. (Thiaridae; Slack-Smith 1993); polychaetes *Sphaerosyllis centroamericana* Hartmann-Schröder 1959 and *Typosyllus* (Ehlersia) cf. *broomensis* Hartmann-Schröder 1979 (Syllidae); ostracod *Aglaiella* Daday 1910 sp. nov. (K. Wouters, pers. comm. 1995); the cyclopoid copepods *Metacyclops mortoni* Pesce, De Laurentiis and Humphreys 1996, *Microcyclops varicans* G.O. Sars, *Apocyclops dengizicus* (Lepechkine), *Halicyclops longifurcatus* Pesce, De Laurentiis and Humphreys 1996, and *Halicyclops spinifer* Kiefer 1935; aorid amphipod *Grandidierella* sp. nov. (elsewhere known only from saltworks concentration pools in Dampier; J. Lowry, pers. comm. 1994); water mite *Coaustraliobates longipalpis* (Lundblad) (Acarina: Hydracharina: Hygrobatidae); fragments of trichoptera and odonata (Humphreys and Feinberg 1995); girrid bug *Limnogonus* sp. (nymph, from distributions it is probably *Limnogonusfossarum gilguy* Andersen and Weir, in press: T.A. Weir, pers. comm. 1996); chironomid *Chironomus* (*Kiefferulus*) *intertinctus* Skuse; dytiscid beetle *Copelatus irregularis* Macl.; feral guppies *Poecilia reticulata* Peters 1859 (Pisces: Poeciliidae). The latter are in an overflow pool in the borefield supplying Kailis Fisheries (conductivity 335 mS m^{-1}) and in the tank at Upper Bulbarli Well (conductivity 110 mS m^{-1}). The former is maintained as a stock watering point and the guppies were reportedly introduced to control mosquitos at the recommendation of the W.A. Water Authority (G. Passmore; pers comm.). The guppies clearly thrive under these conditions and the population density is immense. The populations could be spread by people or by flooding of the natural drainage line. If they enter natural freshwater or brackish waters they are likely to eliminate the native fauna (G. Allen, pers. comm. 1993). Several other species of feral tropical aquarium fish have recently been seen in the anchialine system, including cyclids (W.F. Humphreys and D.B. Noltie, unpublished) but they do not seem to have become established (pers. obs. 1999).

References

Adams, M. and Humphreys, W.F. 1993. Pattems of genetic diversity within selected subterranean fauna of the North West Cape peninsula, Westem Australia: systematic and biogeographic implications. Records of the Western Australian Museum, Supplement 45: 145-164.

Allen, A.D. 1993. Outline of the geology and hydrogeology of Cape Range, Camarvon Basin, Western Australia. Records of the Western Australian Museum, Supplement No. 45: 25-38.

ANCA. 1996. A Directory of Important Wetlands in Australia. Second Edition. Australian Nature Conservation Agency, Canberra, Australia. 964 pages.

Apthorpe, M. 1994. Towards an Early to Middle Jurassic palaeogeography for the North West Shelf: a marine perspective. Pages. 201-210. In: Purcell, P.G. and Purcell, R.R. (Editors), The Sedimentary Basins of Western Australia. Proceedings of Petroleum Exploration Society Australia Symposium, Perth, 1994. Petroleum Exploration Society, Perth

Arp, A.J. and Fisher, C.R. 1995. Introduction to the symposium: Life with sulfide. American Zoologist 35: 81- 82.

Aubrecht, R. and Kozur, H. 1995. *Pokornyopsis* (Ostracoda) from submarine fissure fillings and cavities in the Late Jurassic of Czorsztyn Unit and the possible origin of the Recent anchialine faunas. Neuesjahrbuchfür Geologie und Paläontologie 196: 117.

Bailey-Brock, J.H.and Brock, R.E. 1993. Feeding, reproduction, and sense organs of the Hawaiian anchialine shrimp *Halocaridina rubra* (Atyidae). Pacific Science 47: 338-355.

Baltanas, A. and Danielopol, D. 1995. Cladistic analysis of *Danielopolina* species (Ostracoda: Itaumatocyprididae) and the origin of anchialine fauna. Mitteilungen Hamburgisches Zoologische Museum und Institut 92: 315-324.

Banarescu, P. 1990. Zoogeography of Fresh Waters, 1. General Distibution and Dispersal of Freshwater Animals. AULA-Verlag, Wiesbaden.511 pages.

Barnard, J.L. and Barnard, C.M. 1983. Freshwater Amphipoda of the World. I. Evolutionary Patterns. Hayfield Associates, Virginia, USA. 830 pages.

Bamett, J.C. and Commander, D.P. 1985. Hydrogeology of the Western Fortescue Valley, Pilbara Region, Western Australia. Geological Survey Record 1986-18. Western Australia Geological Survey, Perth. 89 pages.

Botosaneanu, L., (Editor) 1986. Stygofauna Mundi: A Faunistic, Distributional, and Ecological Synthesis of the World Fauna Inhabiting Subterranean Waters (including the marine interstitial). E.J. Brill, Leiden, The Netherlands. 740 pages.

Botosaneanu, L. (Editor). 1998. Studies in Crenobiology: The Biology of Springs and Springbrooks. Backhuys Publishers, Leiden, The Netherlands. 261 pages.

Boulton, A.J. 1993. Stream ecology and surface-hyporheic hydrologic exchange: implications, techniques and limitations. Australain Journal of Marine and Freshwater Research, 44: 553-564.

Boutin, C. and Coineau, N. 1987. *Iberobathynella* (Crustacea, Syncarida, Bathynellacea) sur le continent africain. Implications paléobiogéographiques. Comptes Rendus de l'Academie des Sciences, Paris, 304 (Sér. III) (13): 355-357.

Bradbury, J.H., and Williams, W.D. 1996a. Freshwater amphipods from Barrow Island, Western Australia. Records of the Australian Museum 48: 33-74.

Bradbury, J.H., and Williams, W.D. 1996b. Two new species of anchialine amphipod (Crustacea: Hadziidae: *Liagoceradocus*) from Western Australia. Records of the Western Australian Musewn, 17: 395-409.

Bradbury, J.H. and Williams, W.D. 1997a. Amphipod (Crustacea) diversity in underground waters in Australia: an Aladdin's Cave. Memoirs of the Museum of Victoria 56: 513-519.

Bradbury, J.H. and Williams, W.D. 1997b. The amphipod (Crustacea) stygofauna of Australia: description of new taxa (Melitidae, Neoniphargidae, Paramelitidae), and a synopsis of known species. Records of the Australian Museum 49: 249-341.

Brock. R.E., Norris, J., Zeimann, D. and Lee, M.T. 1987. Characteristics of water quality in anchialine pools of the Kona, Hawaii, coast. Pacific Science 41: 200-208.

Bruce, N.L. and Humphreys, W.F. 1993. *Haptolana pholeta* sp. nov., the first subterranean flabelliferan isopod crustacean (Cirolanidae) from Australia. Invertebrate Taxonomy 7: 875-884.

Cals, P. and Boutin, C. 1985. Découverte au Cambodge, domaine ancien de la Tethys orientale, d'un nouveau "Fossil vivant" *Theosbaena cambodjiana*, n. g., n. sp. (Crustacea, Thermosbaenacea). Comptes Rendus Hebdomadaire des Seances de l'Academie des Sciences, Paris, série D, 300: 337-340.

Cand,e, S.C. and Mutter, J.C. 1982. A revised identification of the oldest sea-floor spreading anomalies between Australia and Antarctica. Earth and Planetary Science Letters 58: 151-160.
Childress, J.J. and Fisher, C.R. 1992. The biology of hydrotherrnal vent animals: physiology, biochemistry and autotrophic symbioses. Oceanography and Marine Biology: An Annual Review 30: 337-442.
Culver, D.C., Kane, T.C. and Fong, D.W. 1995. Adaptation and natural selection in caves: the evolution of *Gammarus minus*. Harvard University Press, Cambridge, Massachusetts. 223 pages.
Danielopol, D.L. 1980. An essay to assess the age of the freshwater interstitial ostracods of Europe. Bijdragen tot de Dierkunde 50: 243-291.
Danielopol, D.L. and Bonaduce, G. 1990. The colonisation of subsurface habitats by *Loxoconchidae* Sars and *Psammocytheridae* Klie. Pages 437-453. In: Whatley, R. and Maybury, C. (Editors), Ostracoda and Global Events. Chapman and Hall, London.
Danielopol, D.L., Pospisil, P., and Dreher, J., in press. Danube wetland groundwater system. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors), Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.
Davey, A.G. (Editor) 1984. Evaluation criteria for the cave and karst heritage of Australia. Report of the ASF National Heritage Assessment Study. Helictite 15(2): 1-40.
Davidson, W.A. 1995. Hydrogeology and groundwater resources of the Perth Basin Region, Western Australia. Geological Survey of Western Australia, Bulletin 142: 1-257.
Davies, P.M. 1996. Appendix 1: Stable isotope analyses of food-webs associated with stygofauna of Exmouth borefield. In Supplementary investigation of the effect of public water supply abstraction on the stygofauna and aquifer of the Cape Range. An addendum to Extensions to Exmouth Water Supply Borefield, CER, June 1995. Water Authority of Western Australia, Perth. 13 pages.
Dole-Olivier, M-J., Marmonier, P., Creuzé des Châtelliers, M. and Martin, D. 1994. Interstitial fauna associated with the floodplains of the Rhône River (France). Pages 313-346. In: Gibert, J., Danielopol, D.L., and Stanford, J.A. (Editors). Groundwater Ecology. Academic Press, London.
Drysdale, R. and Head, J. 1994. Geomorphology, stratigraphy and C^{14}-chronology of ancient tufas at Louie Creek, northwest Queensland, Australia. Geographie physique et Quaternaire 48 (3): 285-295.
Eberhard, S. and Spate, A. 1995. Cave Invertebrate Survey: toward an atlas of NSW cave fauna. Report for the NSW Heritage Assistance Program, Nov. 1995. 112 pages.
Eberhard, S.M., Richardson, A.M.M. and Swain, R. 1991. The Invertebrate Cave Fauna of Tasmania. Zoology Department, University of Tasmania, Hobart, Australia. 174 pages.
European Commission. 1995. COST action 65: Hydrogeological Aspects of Groundwater Protection in Karstic Area Guidelines. Directorate General XII, European Commission, Luxembourg. 15 pages.
Ford, D.C. and Williams, P.W. 1989. Karst Geomorphology and Hydrology. Unwin Hyman, London. 601 pages.
Forth, J.R. 1973. Exmouth water supply. Geological Survey of Western Australia, Annual Report 1972: 11-15.
Fryer, G. 1977. Studies on the functional morphology and ecology of the atyid prawns of Dominica. Philosophical Transactions of the Royal Society, London, B, Biological Science 277: 57-128.
Gentilli, J. 1972. Australian Climatic Patterns. Nelson, Melbourne. 285 pages.
Gibert, J., Stanford, J.A., Dole-Olivier, M-J. and Ward, J.V. 1994. Basic attributes of groundwater ecosystems and prospects for research. Pages. 7-40. In: Gibert, J., Danielopol, D.L., and Stanford, J.A. (Editors). Groundwater Ecology. Academic Press, London.
Hamilton-Smith, E. and Eberhard, S.M., in press. Conservation of cave communities in Australasia. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors). Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.
Hamilton-Smith, E., Kieman, K. and Spate, A. 1998. Karst management considerations for the Cape Range karst province, Western Australia. A report prepared for the Department of Environmental Protection, Perth. 80 pages.
Harris, C.R. 1992. Mound springs: South Australian conservation initiatives. Rangelands Journal 14: 157-173.
Hart, C.W., Manning, R.B., and Iliffe, T.M. 1985. The fauna of Atlantic marine caves: evidence of dispersal by sea floor spreading while maintaining ties to deep waters. Proceedings of the Biological Society of Washington 98: 288-292.
Harvey, M.S. 1993. The systematics of the Hyidae (Pseudoscoipionida). Invertebrate Taxonomy 7: 1-32.

Harvey, M.S. 1998. Unusual new water mites (Acari: Hydracarina) from Australia, Part 1. Records of the Western Australian Museum 19: 91-106.

Harvey, M.S. and Humphreys, W.F. 1996. Notes on the genus *Draculoides* Harvey (Schizomida: Hubbardiidae), with the description of a new troglobitic species. Records of the Western Australian Museum, Supplement 52: 183-189.

Harvey, M.S., Gray, M.R., Hunt, G.S. and Lee, D.C. 1993. The cavernicolous Arachnida and Myriapoda of Cape Range, Western Australia. Records of the Western Australian Museum, Supplement 45: 129-144.

Hocking, R.M. 1990. Camarvon Basin, in Geology and mineral resources of Western Australia: Geological Survey of Western Australia, Memoir 3: 457-495.

Hocking, R.M, Moors, H.T. and van de Graaff, W.J.E. 1987. Geology of the Carnarvon Basin, Western Australia. Geological Survey of Western Australia, Bulletin 133: 1-289.

Holsinger, J.R. 1978. Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae). II. Species of the eastern United States. Smithsonian Contributions to Zoology No. 266: 1-144.

Holsinger, J.R. 1986. Holarctic crangonyctid amphipods. Pages 535-549. In: Botosaneanu, L. (Editor), Stygofauna Mundi: A Faunistic, distributional and Ecological Synthesis of the World Fauna Inhabiting Subterranean Waters (including the Marine Interstitial). E.J. Brill, Leiden, The Netherlands.

Holsinger, J.R 1989. Preliminary zoogeographic analysis of five groups of crustaceans from anchialine caves in the West Indian region. Proceedings of the 10th International Congress of Speleology, Budapest 13-20 August 1989. Kósa, A. (Editor), Magyar Karszt- és Barlangkutató Társulat 2: 25-26.

Holsinger, J.R. 1992. Two new species of the subterranean amphipod genus *Bahadzia* (Hadziidae) from the Yucatan Peninsula region of southern Mexico, with an analysis of phylogeny and biogeography of the genus. Stygologia 7: 85-105.

Holsinger, J.R. and Culver, D.C. 1988. The invertebrate cave fauna of Virginia and a part of eastern Tennessee: zoogeography and ecology. Brimleyana 14: 1-164.

Howarth, F.G. 1980. The zoogeography of specialized cave animals: a bioclimatic model. Evolution 34: 394-406.

Howarth, M.K. 198 1. Palaeogeography of the Mesozoic. Pages 197-220. In: Cooks, L.M.R. (Editor), The Evolving Earth. Oxford University Press, Oxford.

Humphreys, W.F. 1993a. Cave fauna in semi-arid tropical Western Australia: a diverse relict wet-forest litter fauna. Mémoires de Biospéologie, 20: 105-110.

Humphreys, W.F. 1993b. Stygofauna in semi-arid tropical Western Australia: a Tethyan connection? Mémoires de Biospéologie, 20: 111-116.

Humphreys, W.F. 1993c. The significance of the subterranean fauna in biogeographical reconstruction: examples from Cape Range peninsula, Western Australia. Records of the Western Australian Museum, Supplement 45: 165-192

Humphreys, W.F. (Editor) 1993d. The Biogeography of Cape Range, Western Australia. Records of the Western Australian Museum, Supplement 45. Western Australian Museum, Perth. 248 pages.

Humphreys, W.F. 1994. The subterranean fauna of the Cape Range coastal plain, northwestern Australia. Report to the Australian Heritage Commission and the Western Australian Heritage Committee. Western Australian Museum, Perth. 202 pages. Unpublished.

Humphreys, W.F. 1995a. Limestone of the east Kimberley, Western Australia: karst and cave fauna. Report to the Australian Heritage Commission and the Western Australian Heritage Committee. Western Australian Museum, Perth. xix + 190 pages. Unpublished.

Humphreys, W.F. 1995b. Subterranean fauna. In: Consultative Environmental Review: Extensions to Exmouth Water Supply Borefield, CER, June 1995. Water Authority of Western Australia, Perth. 23 pages.

Humphreys, W.F., 1999a. Relict stygofaunas living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages. Pages 219-227. In: Ponder, W. and Lunney, D. (Editors) The Other 99%. The Conservation and Biodiversity of Invertebrates. Transactions of the Royal Zoological Society of New South Wales, Mosman 2088, Australia.

Humphreys, W.F., 1999b. Physico-chemical profile and energy fixation in Bundera Sinkhole, an anchialine remiped habitat in north-western Australia. Journal of the Royal Society of Western Australia 82: 89-98.

Humphreys, W.F., in press a. Relict faunas and their derivation. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors), Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.
Humphreys, W.F., in press b. The hypogean fauna of the Cape Range peninsula and Barrow Island, north-west Australia. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors). Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.
Humphreys, W.F., and Adams, M. 1991. The subterranean aquatic fauna of the North West Cape Peninsula, Western Australia. Records of the Western Australia Museum 15: 383-41 1.
Humphreys, W.F., Adams, M. and Vine, B. 1989. The biology of *Schizomus vinei* (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. Journal of Zoology, London 217: 177-20 1.
Humphreys, W.F., Awramik, S.M. and Jebb, M.H.P. 1995. Freshwater biogenic tufa dams in Madang Province, Papua New Guinea. Journal of the Royal Society of Western Australia 78: 43-54.
Humphreys, W.F. and Feinberg, M.N. 1995. Food of the blind cave fishes of northwestern Australia. Records of the Western Australian Museum 17: 29-33.
Iliffe, T.M. 1992. Anchialine cave biology. Pages 614-636. In: Camacho, A.I. (Editor) The Natural History of Biospeleology. Monografias Museo Nacional de Ciencias Naturales, Madrid.
Iliffe, T.M., in press. Anchilaine cave ecology. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors), Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.
Iliffe, T.M., Jickells, T.D. and Brewer, M.S. 1984. Organic pollution of an inland marine cave from Bermuda. Marine Environment Research 12: 173-189.
Jacobson, G. and Arakel, A.V. 1986. Calcrete aquifers in the Australian arid zone. Pages 515-523. In: Proceedings of the International Conference on Groundwater Systems Under Stress, Brisbane. Australian Water Resources Council, Melbourne.
Jasinska, E.J., Knott, B. and McComb, A.J. 1996. Root mats in ground water: a fauna-rich cave habitat. Journal of the North American Benthological Society 15: 508-519.
Jennings, J. N. 1983. The disregarded karst of the and and semi-arid domain. Karstalogia 1: 61-73.
Juberthie, C. and Decu, V. (Editors) 1994a. Encyclopedia Biospeleologica, volume 1. Société de Biospéologie, Moulis, and Bucharest. 834 pages.
Juberthie, C. and Decu, V. 1994b. Structure et diversité du domaine souterrain: particularities des habitats et adaptations des especes. Pages 5-22. In: Juberthie, C. and Decu, V. (Editors), Encyclopedia Biospeleologica, Vol. 1. Société de Biospéologie, Moulis and Bucharest.
Juberthie, C. and Decu, V. (Editors) 1998. Encyclopedia Biospeleologica, volume 2. Société de Biospéologie, Moulis and Bucharest. 834 pages.
Julia, R. 1983. Travertines. Pages 64-72. In: Scholle, P.A., Bebout, D.G. and Moore, C.H. (Editors). Carbonate Depositional Environments. American Association of Petroleum Geologists Memoir 33. Tulsa, Oklahoma.
Karaman, G.S. 1982. Critical remarks to the recent revisions of the *Bogidiella* group of genera with some study of some taxa (Fam. Gammaridae). Poljoprivreda I. Sumarstvo, Titograd 28: 31-57.
Keighery, G. and Gibson, N. 1993. Biogeography and composition of the flora of the Cape Range peninsula, Western Australia. Records of the Western Australian Museum, Supplement 45: 51-85.
Kendrick, G.W. and Morse, K. 1990. Evidence of recent mangrove decline from an archaeological site in Western Australia. Australian Journal of Ecology 15: 349-353.
Kendrick, G.W., Wyrwoll, K-H. and Szabo, B.J. 1991. Plio-Pleistocene coastal events and history along the western margin of Australia. Quaternary Science Reviews 10: 419-439.
Kiernan, K. 1988. The Management of Soluble Rock Landscapes: An Australian Perspective. The Speleological Research Council Ltd., Sydney. 61 pages.
Knott, B. 1993. Stygofauna from Cape Range peninsula, Western Australia: Tethyan relicts. Records of the Western Australian Museum, Supplement 45: 109-127.
Knott, B and Jasinska, E.J. 1998. Mound springs of Australia. Pages. 23-38. In: Botosaneanu, L. (Editor). 1998. Studies in Crenobiology: The Biology of Springs and Springbrooks. Backhuys Publishers, Leiden, The Netherlands.
Kuehn, K.A. and Koehn, R.D. 1988. A mycofloral survey of an artesian community within the Edwards Aquifer of Central Texas. Mycologia 80: 646-652.
Longley, G. 1981. The Edwards Aquifer: earth's most diverse groundwater ecosystem? International Journal of Speleology 11: 123-128.
Longley, G. 1992. The subterranean aquatic ecosystem of the Balcones Fault Zone Edwards Aquifer in Texas – threats from overpumping. Pages. 291-300. In: Stanford, J.A. and Simons, J.J. (Editors). Proceedings of the First International Conference on Groundwater Ecology. American Water Resources Association, Bethesda, Maryland.

L'Volich, M.I. 1974. World Water Resources and Their Future. (English translation A.G. U.). Mysl' P.H., Moscow.

MacDonald, I.R, Boland, G.S. and Baker, J.S. 1989. Gulf of Mexico hydrocarbon seep communities. II. Spatial distribution of seep organisms and hydrocarbons at Bush Hill. Marine Biology 101: 235-248.

Maciolek, J.A. 1986. Environmental features and biota of anchialine pools on Cape Kinau, Maui, Hawaii. Stygologia 2: 119-129.

Malard, F. 1995. Contribution à l'étude biologique de la qualité des eaux souterraines karstiques: application à un site atelier Nord-Montpelliérain (bassin de la source du Lez). Thesis, Université Claude Bemard, Lyon.

Malcolm, R.J., Pott, M.C. and Delfos, E. 1991. A new tectono-stratigraphic synthesis of the North West Cape area. APEA Journal 1991: 154-176.

Mann, A. W., and Deutscher, R. L. 1978. Hydrogeochemistry of a calcrete containing aquifer near Lake Way, Western Australia: Journal of Hydrology 38: 357-377.

Mann, A.W. and Horwitz, R.C. 1979. Groundwater calerete deposits in Australia: some observations from Western Australia. Journal of the Geological Society of Australia, 26: 293-303.

Marias, D.J.D. 1990. Microbial mats and the early evolution of life. Trends in Ecology and Evolution 5: 140-144.

Marrnonier, P., Vervier, P., Gibert, J. and Dole-Olivier, M-J. 1993. Biodiversity in ground waters. Trends in Ecology and Evolution 8: 392-395.

Martin, L.H., Eakins, K.E. and Logan, A. 1991. Physical characteristics of the anchialine ponds of Bermuda. Bulletin of Marine Science 48: 125-136.

Martin, L.H., Logan, A. and Eakins, K.E. 1992. Biotic characteristics of the anchialine ponds of Bermuda. Bulletin of Marine Science 50: 133-157.

Martin, M.W. 1990. Exmouth town water supply investigation report and recommendations for future work.. Geological Survey of Western Australia, Perth. Hydrogeology Report No 1990-136. Unpublished. 11 pages.

McNamara, K.J. and Kendrick, G.W. 1994. Cenozoic molluscs and echinoids of Barrow Island, Westem Australia. Records of the Western Australian Museum, Supplement 51: 1-50.

Morse, K. 1993. Who can see the sea? Prehistoric Aboriginal occupation of the Cape Range peninsula. Records of the Western Australian Museum, Supplement 45: 227-242.

Morton, S.R., Short, J. and Barker, R.D. 1995. Refugia for biological diversity in arid and semi-arid Australia. Biological Diversity series, Paper No. 4. Biological Diversity Unit, Department of the Environment, Sport and Territories, Canberra. 171 Pages.

Newman, W.A. 1991. Origins of Southern Hemisphere endemism, especially among marine crustacea. Memoirs of the Queensland Museum 31: 51-76.

Notenboom, J., Plénet, S., and Turquin, M.-J. 1994. Groundwater contamination and its impact on groundwater animals and ecosystems. Pages 477-504. In: Gibert, J., Danielopol, D.L., and Stanford, J.A. (Editors). Groundwater Ecology. Academic Press, London.

Peck, S.B. 1978. New montane *Ptomaphagus* beetles from New Mexico and zoogeography of southwestern caves (Coleoptera; Lciodidae; Catopinae). Southwestern Naturalist 23: 227-238.

Peck, S.B. and Finston, T.L. 1993. Galapagos Island troglobites: the question of tropical troglobites, parapatric distributions with eyed sister species, and their origin by parapatric speciation. Mémoires de Biospéologie 20: 19-37.

Pentecost, A. 1992. Travertine: life inside the rock. Biologist 39: 161-164.

Pohlman, J.W., Cifuentes L.A., and Iliffe, T.M. in press. Food web dynamics and biogeochemistry of anchialine caves: a stable isotope approach. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors), Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.

Ponder, W.F., Eggler, P. and Colgan, D.J. 1995. Genetic differentiation of aquatic snails (Gastropoda: Hydrobiidae) from artesian springs in and Australia. Biological Journal of the Linnean Society 56: 553-596.

Poore, G.C.B., and Humphreys, W.F. 1992. First record of Thermosbaenacea (Crustacea) from the Southern Hemisphere: a new species from a cave in tropical Western Australia. Invertebrate Taxonomy 6: 719-725.

Poore, G.C.B. and Humphreys, W.F. 1998. The first record of the Spelaeogriphacea (Crustacea) from Australasia: a new genus and species from an aquifer in the arid Pilbara of Western Australia. Crustaceana 71: 721-742.

Por, F.D. 1986. Crustacean biogeography of the Late Middle Miocene Middle Eastern landbridge. Pages 69-84. In: Gore, R.H. and Heck, K.L. (Editors) Crustacean Biogeography. A.A. Balkema, Rotterdam and Boston.

Poulson, T.L. and Lavoie, K.H., in press. The trophic basis of subsurface ecosystems. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors), Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.

Quilty, P.G. 1994. The background: 144 million years of Australian palaeoclimate and palaeogeography. Pages 14-43. In: Hill, R.S. (Editor), History of the Australian vegetation: Cretaceous to Recent. Cambridge University Press, Cambridge.

Quinlan, J.F., Davies, G.J. and Worthington, S.R.H. 1992. Rationale for the design of cost-effective ground-water monitoring systems in limestone and dolomite terranes: cost-effective as conceived is not cost-effective as built if the system design and sampling frequency inadequately consider site hydrogeology. Proceedings of the 8th Waste Testing and Quality Assurance Symposium: 552-570. U.S. Environmental Protection Agency, Washington, D.C., USA.

Reddell, J.R. and Mitchell, R.W. 1971. A checklist of the cave fauna of Mexico. II. Sierra de Guatemala. Tamaulipas. Bulletin of the Association for Mexican Cave Studies 4:181-215.

Ridgley, M.A. and Chai, D.K. 1990. Evaluating potential biotic benefits from conservation: anchialine ponds in Hawaii. The Environmental Professional 12: 214-228.

Sanders, C.C. 1974. Calcrete in Western Australia. Western Australian Geological Survey Annual Report 1973, 12-14.

Sarbu, S.M., in press. A chemoautotrophically based groundwater system. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors), Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.

Sarbu, M.S., Galdenzi, S., Menichetti, M. and Gentile, G. in press. Geology and biology of the Frasassi Caves in central Italy, an ecological multi-disciplinary study of a hypogenic underground karst system. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors), Ecosystems of the World, vol. 30. Subterranean Ecosystems Elsevier, Amsterdam.

Sarbu, S.M., Kane, T.C. and Kinkle, B.K. 1996. A chemoautotrophically based cave ecosystem. Science 272 (5270): 1953.

Sarbu, S.M. and Popa, R. 1992. A unique chemoautotrophically based cave ecosystem. Pages 641-666. In: Camacho, A.I. (Editor) The Natural History of Biospeleology. Monografias Museo Nacional de Ciencias Naturales, Madrid.

Sbordoni, V. 1982. Advances in speciation of cave animals. Pages 219-240. In: Barrigozzi, C. (Editor). Mechanisms of Speciation. A.R.Liss Inc., New York, USA.

Schminke, H.K. 1974. Mesozoic intercontinental relationships as evidenced by bathynellid crustacea (Syncarida: Malacostraca). Systematic Zoology 23: 157-164.

Scotese, C.R. and Denham, C.R. 1988. Terra Mobilis: Plate Tectonics for the Macintosh. Earth in Motion Technologies, Houston, Texas.

Scott, K.M. and Fisher, C.R. 1995. Physiological ecology of sulfide metabolism in hydrothermal vent and cold seep vesicomyid clams and vestimentiferan tube worms. American Zoologist 35: 102-111.

Shepherd, B.G., Hartrnan, G.F. and Wilson, W.J. 1986. Relationships between stream and intergravel temperatures in coastal drainages, and some implications for fisheries workers. Canadian Journal of Fisheries and Aquatic Sciences 432: 1818-1822.

Sket,. B. 1981. Fauna of anchialine (coastal) cave waters, its origin and importance. Proceedings 8th International Congress of Speleology: 646-647.

Sket, B. 1996. The Ecology of anchihaline caves. Trends in Ecology and Evolution 11: 221-255.

Slack-Smith, S.M. 1993. The non-marine molluscs of the Cape Range peninsula, Western Australia. Records of the Western Australian Museum, Supplement 45: 87-107.

Smith, A.G., and Briden, J.C. 1977. Mesozoic and Cenozoic Paleocontinental Maps. Cambridge University Press, Cambridge. 46 pages.

Solem, A. 1981a. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). II. Taxa from the Kimberley, *Amplirhagada* Iredale 1933. Records of the Western Australian Museum, Supplement 11: 147-320.

Solem, A. 198lb. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). III. Taxa from the Ningbing Ranges and nearby areas. Records of the Western Australian Museum, Supplement 11: 321-425.

Solem, A. 1984. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). IV. Taxa from the Kimberley, *Westraltrachia* Iredale 1933 and related genera. Records of the Western Australian Museum, Supplement 17: 426-705.

Solem, A. 1985. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining Kimberley genera and addendum to the Kimberley. Records of the Western Australian Museum, Supplement 20: 707-981.

Solem, A. 1997. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). VII. Taxa from Dampierland through the Nullarbor. Records of the Western Australian Museum, Supplement 50: 1461-1906.

Spate, A.P. and Little, L. 1997. Is the conventional approach to karst area management appropriate to tropical Australia? Proceedings of the Eleventh Conference on Australasian Cave Tourism And Management, May 1995: 68-84, Australasian Cave and Karst Management Association, Melbourne.

Stanford, J.A., and Ward, J.V. 1988. The hyporheic habitat of river ecosystems. Nature 335: 64-66.

Stoch, J.H. 1995. The ecological and historical determinants of crustacean biodiversity in groundwaters, or: why are there so many species? Mémoires de biospéologie 22: 139-160.

Stock, J.H. 1977. The taxonomy and zoogeography of the Hadziid Amphipoda, with emphasis on the West Indian taxa. Studies on the Fauna of Curaçao, Amsterdam 55: 1-130.

Stock, J.H. 1983. Discovery of a Bogidiellid amphipod crustacean in inland waters of the East Indian Archipelago: *Bogidiella* (*Medigidiella*) *sarawacensis* n. sp. Crustaceana 44: 198-204.

Stock, J.H. 1986a. Caribbean biogeography and a biological calendar of geological events. In: Gore, R.H. and Heck, K.L. (Editors) Crustacean Biogeography. Crustacean Issues 4: 195-203.

Stock, J.H. 1986b. Two new amphipod crustaceans of the genus *Bahadzia* from 'blue holes' in the Bahamas and some remarks on the origin of the insular stygofaunas of the Atlantic. Journal of Natural History 20: 921-933.

Stock, J.H. 1990. Insular groundwater biotas in the (sub)tropical Atlantic: a biogeographical synthesis. Atti. Convegni Lincei, Accademia nazionale dei Lincei, Roma 85: 695-713.

Stock, J.H., Iliffe, T.M. and Williams, D. 1986. The concept 'anchialine' reconsidered. Stygologia 2: 90-92.

Stock, J.H., and Longley, G. 1981. The generic status and distribution of *Monodella texana* Maguire, the only known North American Thermosbaenacean. Proceedings of the Biological Society of Washington 94: 569-578.

Thomas, M.L.H., Eakins, K.E. and Logan, A. 1991. Physical characteristics of the anchialine ponds of Bermuda. Bulletin of Marine Science 48: 125-136.

Thomas, M.L.H., Logan, A., Eakins, K.E. and Mathers, S.M. 1992. Biotic characteristics of the anchialine ponds of Bermuda. Bulletin of Marine Science 50: 133-157.

Tromble, J.M. 1977. Water requirements of mesquite (*Prosopis juliflora*). Journal of Hydrology 34: 171-179.

Vine, B., Knott, B. and Humphreys, W.F. 1988. Observations on the environment and biology of *Schizomus vinei* (Chelicerata: Schizomida) from Cape Range, Western Australia. Records of the Western Australian Museum 14: 21-34.

Wägele, J.W. 1990. Aspects of the evolution and biogeography of stygobiontic Isopoda (Crustacea, Peracarida). Bijdragen tot de Dierkunde 60: 145- 150.

Wägele, J.W. and Brandt, A. 1985. New west Atlantic localities for the stygobiont panthurid *Curassanthura* (Crustacea, Isopoda, Anthuridae) with descriptions of *C. bermudensis* n. sp. Bijdragen tot de Dierkunde 55: 324-330.

Wagner, H.P. 1994. A monographic rerview of the Thermosbaenacea (Crustacea: Peracarida). Zoologische Verhandelingen No. 291: 1-338.

Ward, J.V., Malard, F., Stanford, J.A. and Gonser, T., in press. Interstitial aquatic fauna of shallow unconsolidated sediments, particularly hyporheic biotopes. In: Wilkens, H., Culver, D.C. and Humphreys, W.F. (Editors). Ecosystems of the World, vol. 30. Subterranean Ecosystems. Elsevier, Amsterdam.

Water Corporation. 1996. Supplementary investigation of the effect of public water supply abstraction on the stygofauna and aquifer of the Cape Range. An addendum to Extensions to Exmouth Water Supply Borefield, CER, June 1995. Water Authority of Western Australia, Perth. 12 pages.

Watts, C.H.S. and Humphreys, W.F. 1999. Three new genera and five new species of Dytiscidae (Coleoptera) from underground waters in Australia. Records of the South Australian Museum 32: 121-142.

Watts, C.H.S. and Humphreys, W.F. in press. Six new species of *Nirridessus* and *Tjirtudessus* (Dytiscidae; Coleoptera) from underground waters in Australia. Records of the South Australian Museum.

Wilkens, H., Parzefall, J. and Iliffe, T.M. 1986. Origin and age of the marine stygofauna of Lanzarote, Canary Islands. Mitteilungen. Hamburgisches Zoologische Museum und Institut 83: 223-230.

Wilkens, H., Parzefall, J., Ocaña, O. and Medina, A.L. 1993. La fauna de unos biotopos anquialinos en Lanzarote (I. Canarias). Mémoires de Biospéologie 20: 283-285.

Williams, I.R. 1965. Notes on a mound spring on Mardie Station, near Cape Preston. Geological Survey of Western Australia, Perth. Annual Report 1964. 36 pages.

Wilson, G.D.F. and Keable, S.J., 1999. A new genus of phreatoicidean isopod (Crustacea) from the north Kimberley Region, Western Australia. Zoological Journal of the Linnean Society, 126: 51-79.

Wilson, G.D.F. and Ponder, W.F. 1992. Extraordinary new subterranean isopods (Peracarida: Crustacea) from the Kimberley Region, Western Australia. Records of the Australian Museum 44: 279-298.

Woodruff, D.S., and Solem, A. 1990. Allozyme variation in the Australian camaenid land snail *Cristilabrum primum*: a prolegomenon for a molecular phylogeny of an extraordinary radiation in an isolated habitat. The Veliger 33: 129-139.

Wyrwoll, K-H., Kendrick, G.W. and Long, J.A. 1993. The geomorphology and Late Cenozoic geological evolution of the Cape Range – Exmouth Gulf region. Records of the Western Australian Museum, Supplement 45: 1-23.

Yager, J. 1987a. *Cryptocorynetes haptodiscus*, new genus, new species, and *Speleonectes benjamini*, new species, of Remipede crustaceans from anchialine caves in the Bahamas, with remarks on distribution and ecology. Proceedings of the Biological Society of Washington 100: 302-320.

Yager, J. 1987b. *Speleonectes tulumensis*, n. sp. (Crustacea: Remipedia) from two anchialine cenotes of the Yucatan Peninsula, Mexico. Stygologia 3: 160-166.

Yager, J. 1994. *Speleonectes gironensis*, new species (Remipedia: Speleonectidae), from anchialine caves in Cuba, with remarks on biogeography and ecology. Journal of Crustacean Biology 14: 752-762.

Yager, J. and Humphreys, W.F. 1996. *Lasionectes exleyi*, sp. nov., the first remipede crustacean recorded from Australia and the Indian Ocean, with a key to the world species. Invertebrate Taxonomy 10: 171-187.

Yuan Daoxian 1988. On the karst environmental system. Pages 30-46. In: Yuan, D. (Editor). Karst Hydrogeology and Karst Environment Protection. 2 vols. Geological Publishing House, Beijing, China.