Groundwater calcrete aquifers in the Australian arid zone: the context to an unfolding plethora of stygal biodiversity

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Abstract – The Western Shield of Australia has been above sea level since the Palaeozoic. It is incised by ancient palaeovalleys now containing groundwater calcretes that are found throughout much of arid Australia. The calcretes are deposited, owing to surface evaporation, from a groundwater flow path that increases in salinity from fresh to hypersaline groundwater each terminating at a salt lake (playa). The calcrete aquifers contain a diverse obligate groundwater fauna (stygofauna: predominantly Crustacea) in one of the oldest non-marine landscapes on Earth. Each of the 11 calcrete areas examined so far contains a unique fauna; there are over 210 large discrete calcrete bodies in the Western Australian arid zone. This paper examines a working hypothesis that the stygofauna became isolated in the upper tributaries of the palaeodrainage systems by the progressive upstream movement of salinity from the Eocene onwards. Although each calcrete body does have a unique fauna, as predicted by the hypothesis, the hypothesis has proved too simple because the hydrochemical cycles are repeated along the length of the palaeochannels, each terminating in a saltlake immediately downflow of the calcrete. A new hypothesis has to incorporate these intervals of hypersaline groundwater/calcrete discontinuities acting as barriers to dispersal of the stygofauna. The paper focuses on the geological and landscape setting, and the hydrochemical and groundwater context in which this stygal diversity is found. It is intended to serve as a background resource for further work on this diverse stygofauna. A synopsis is provided of the knowledge of this stygofauna. The presence of such highly diverse and locally endemic stygofauna, often ancient relictual lineages, in a major economic resource within arid Australia poses delicate and challenging conservation issues. At the same time the scientific challenge is considerable to understand the development and functioning of these systems in order that they can be managed sustainably.

INTRODUCTION

The magnitude of the biodiversity present in subterranean waters has only recently been given prominence (Marmonier *et al.*, 1993). In a global context, the groundwater fauna of Australia (along with that of Africa) is especially poorly known (Marmonier *et al.*, 1997); and that mostly from the investigation of cave faunas (Eberhard *et al.* 1991; Eberhard and Spate, 1995; Humphreys, 1993, 2000a; Thurgate *et al.*, this volume). Nonetheless, Australia, especially the northwestern part, has unexpectedly come to the attention of stygobiol-ogists and systematists on account of the diverse obligate groundwater fauna (stygofauna) that is being found in the region (e.g. Humphreys, 1993, 1999a, 1999b; Wilson and Keable, 1999; Wilson and Johnson, 1999; Bradbury and Williams, 1996a, 1996b, 1997a, 1997b; Pesce *et al.*, 1996a, 1996b; Pesce and De Laurentiis, 1996; De Laurentiis *et al.*, 1999). This includes a number of higher order taxa variously new to science (undescribed family of flabelliferan

Isopoda: Wilson and Ponder, 1992), new to the southern hemisphere (Thermosbaenacea: Poore and Humphreys, 1992; Remipedia: Yager and Humphreys, 1996; *Danielopolina*: Danielopol *et al.* 2000; Epacteriscidae: Jaume and Humphreys, 2001), or new to Australia (Spelaeogriphacea: Poore and Humphreys, 1998; *Stygocyclopia*: Pseudocyclopiidae, Jaume *et al.* 2001). Many of these taxa occur in near coastal and anchialine waters and are interpreted as comprising a relictual tethyan fauna, several lineages of which have congeneric species known elsewhere only from subterranean waters on either side of the North Atlantic – the northern Caribbean region and the Balearic and Canary archipelagos (Humphreys, 1993, 1999a; 2000a; Jaume and Humphreys, 2001; Jaume *et al.* 2001).

The history of these anchialine ecosystems, mostly in Tertiary rocks, stands in marked contrast to that of inland aquifers on the elevated Precambrian shield. Areas presently land that were ever covered by the
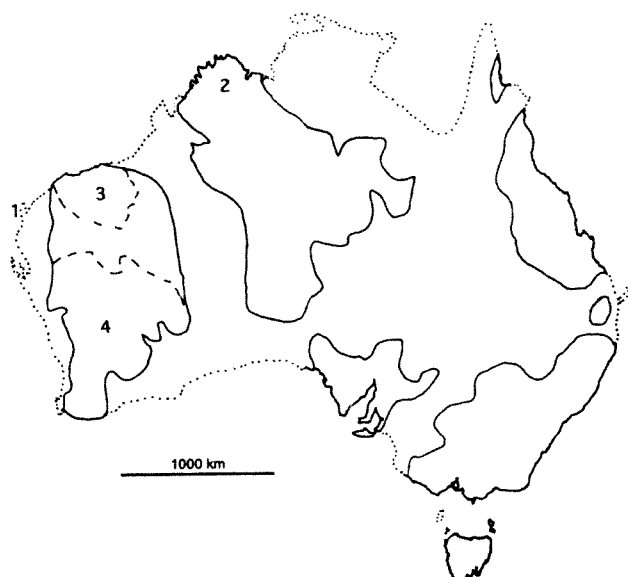
Figure 1 The current outline of Australia superimposed on the areas continually emergent since the Proterozoic. 1. Cape Range; 2. Kimberley; 3. Pilbara; 4, Yilgarn. The solid line encircling the numbers 3 and 4 encompasses much of the Western Shield. Derived from data in BMR Palaeogeographic Group (1990).

sea, even as far back as the Mesozoic, often contain communities of obligate subterranean aquatic species of formerly marine lineages 'stranded' inland by marine recession (Stock, 1980; Boutin and Coineau, 1990; Notenboom, 1991; Holsinger, 1994), particularly in karst areas. This is especially notable in regions that have undergone substantial orogenesis (Messouli *et al.*, 1991; Boutin, 1993). While such areas occur in Australia (orogenic: Humphreys, 1993; stranded: Bradbury and Eberhard, 2000), large parts of Australia have not been inundated by the sea since at least the Palaeozoic (Figure 1), including the Pilbara and Yilgarn Cratons of Western Australia and their associated orogens that collectively may be referred to as the Western Shield (Beard, 1998). These regions of Precambrian rocks are covered by only a thin regolith and seem, on first principles, to proffer poor prospects for the exploration of stygal biodiversity.

This stable, truly continental area of Australia has a non-marine, presumably freshwater history extending though several geological eras. Here, I present a synopsis of the geological and tectonic history of the area and provide the geological and hydrogeochemical context pertinent to the interpretation of biogeographical hypotheses relating to stygofauna. The stygofauna of this region is discussed in general terms, showing the pattern of its distribution and processes that could cause vicariance in stygal lineages.

BIOGEOGRAPHIC HYPOTHESES

The following hypotheses developed progressively.

1. The occurrence of diverse stygofaunas in the Australian arid zone (Humphreys, 1993, 2000a) suggest that other arid regions of Australia should contain stygofaunas relictual from more humid periods.

2. On areas not covered by the sea since the Palaeozoic the stygofauna will include ancient freshwater lineages.

3. Headwater aquifers within single palaeodrainage channels are likely to contain distinct but related faunas. Owing to the progressive onset of aridity such stygofauna will likely be isolated in the fresh groundwater aquifers in the upper tributaries of the palaeodrainage systems. The inland (easterly) draining palaeodrainage channels of the Western Shield are generally saline but the upper tributaries contain fresh groundwater in places (D.P. Commander, personal communication, 1997). This fresh groundwater in the upper reaches would have been progressively isolated from adjacent freshwaters due to the upstream encroachment of salinity following the onset of arid conditions in the Eocene. Hence, the groundwater fauna that may inhabit such an aquifer would likely be distinct from those in other headwater aquifers, even within the same palaeodrainage channel (developed below).

4. The numerous groundwater calcrete aquifers in the Australian arid zone may contain separate faunas. This was suggested by the finding of a rich stygofauna, with Gondwanan affinities, in a single calcrete aquifer in the Pilbara isolated by groundwater divides and water gaps from adjacent aquifers (Poore and Humphreys, 1998). Hence, these aquifers had the potential to contain substantial biodiversity (Humphreys, 1999b) of both macroinvertebrates and meiofauna, including higher order taxa of a relictual nature (Poore and Humphreys, 1998).

5. Stygofauna may be 'older' than the matrix in which they occur (cf. Cape Range anchialine system where the community composition comprises lineages in which global scale vicariance is likely to have occurred long before the formation of the Tertiary strata in which they occur: Humphreys, 2000a, 2000b).

POTENTIAL ISOLATING FACTORS

The hyporheic zone (the underflow and bankflow of rivers) serves both to protect its inhabitants from extremes of temperature, desiccation and discharge (Ward, 1992), and as an aquatic refuge

during droughts (Williams, 1977; discussion in Brunke and Gonser, 1997: 16). Furthermore, it includes the ecotone between surface and groundwaters and thus provides a window between the two ecosystems (Gibert *et al.*, 1997) for the movement of nutrients, organic matter, pollutants and biota, either from groundwater to surface water, or vice versa depending on the relative piezometric (water pressure) heads.

The major river systems that incised their valleys into the Precambrian basement to form the current palaeodrainage system of the Australian arid zone, by analogy with other modern major drainages, would have been freshwater systems containing a suite of epigean and hyporheic communities having some coherence along the length of the drainage (Dole-Olivier *et al.*, 1994; Ward and Voelz, 1994). This results from the connectivity of the hyporheic corridor providing a dispersal route for

meiobenthic taxa along a continuous alluvial aquifer system (Stanford and Ward, 1993), which in the long term is probably interconnected with other catchments (Ward and Palmer, 1994).

With the onset of aridity a waterway would have become progressively more saline, with the salinity being greater downstream owing to cumulative effect of evaporation along the length of the river. With this developing salinity, communities comprising freshwater lineages would have contracted upstream eventually being confined to the headwaters, which remained fresh (e.g. crangonyctoid and bogidiellid amphipods). Meanwhile marine lineages (e.g. melitid and ceinid amphipods) may have moved upstream from the coast (Figure 2), assuming no insurmountable barriers to migration, such as water gaps (Poore and Humphreys, 1998). As the aridity deepened, groundwater would have become the principal
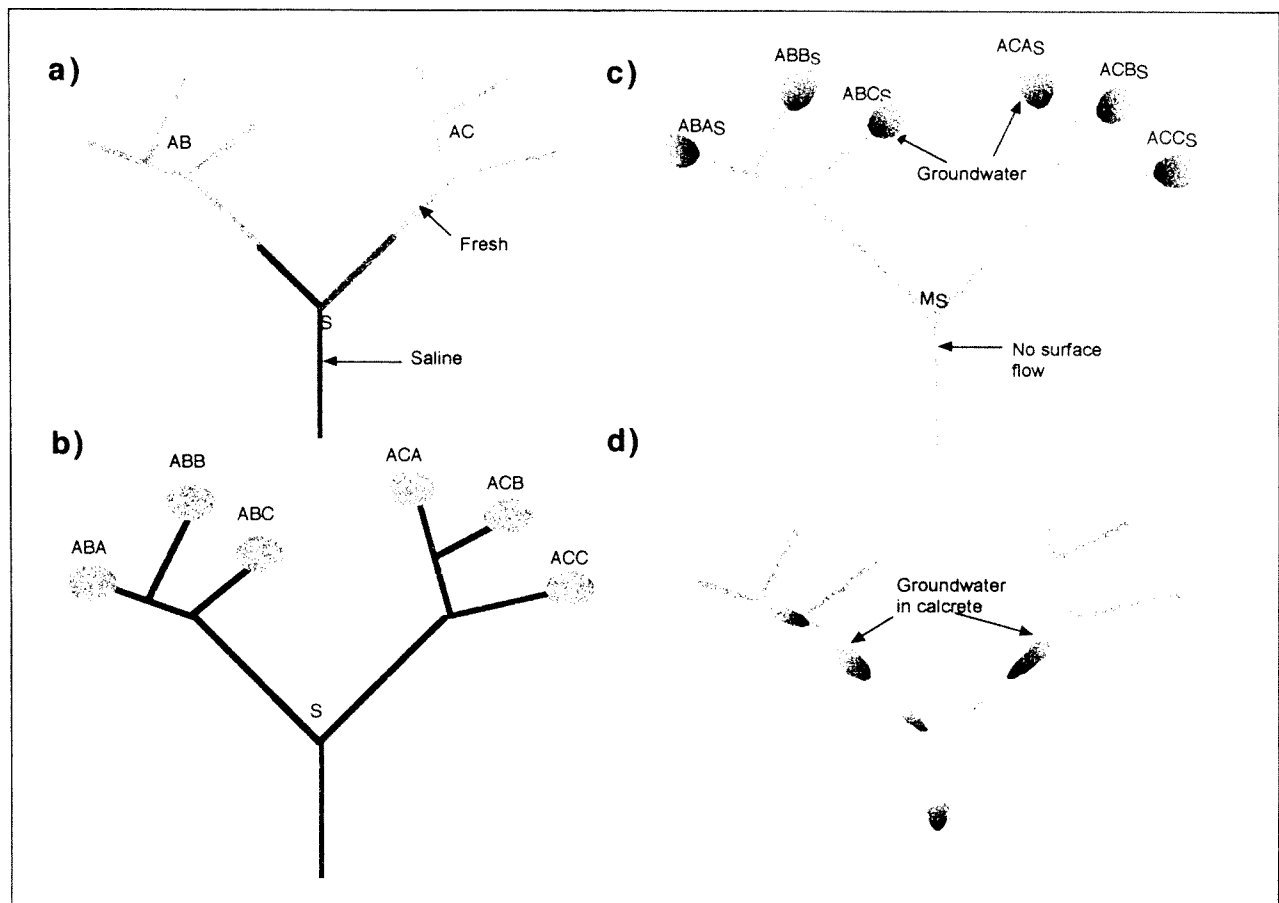

Figure 2   Hypothetical model showing the distribution of fresh and saline waters in a catchment with the progressive onset of arid conditions on a formerly humid system and the isolation of faunistic lineages: a) the onset of salinity (darker shading) in a catchment containing freshwater fauna lineage A (e.g. crangonyctoid Amphipoda or Bathynellacea) isolated into two tributaries giving AB and AC, a marine lineage M invades saline waters (e.g. ceinid Amphipoda); b) salinity progresses upstream restricting freshwater to the headwaters of tributaries further isolating lineage A producing gene pools ABA, ABB .... ACC; c) with increasing salinity surface flow ceases and perennial fresh water is principally underground in the upper tributaries producing isolated gene pools in stygofauna (ABA$_S$, ABB$_S$ .... ACC$_S$ and marine lineage M$_S$); d) the current situation with a series of hydrogeochemical cycles in groundwater repeating down the length of the palaeodrainage system – Morgan's Model– forming groundwater calcrete bodies within which there is a gradient of salinity both vertically and along the flow line.

permanent waters remaining throughout the region. Repeated invasion of groundwater habitats (Culver et al., 1995) can be expected to have accompanied this process. In such a model (Figure 2 a–c) the sequence of isolation (vicariance) should be identifiable from the cladogenic events in the stygofauna.

Geology

Playas and palaeodrainage

The strings of salt lakes, or playas, that form such a prominent part of the landscape in the more arid parts of Australia mostly occur on Precambrian basement rocks (Figure 4 in van de Graaff et al., 1977) and in areas of internal drainage (Figure 1 in ibid.). The playas are the surface manifestation of palaeodrainage channels, rivers that largely stopped flowing when the climate changed from humid to arid in the Palaeocene (Bowler, 1976). The palaeodrainage channels in the Yilgarn were deeply incised into a plateau of Precambrian rocks prior to the break-up of Gondwana, perhaps as early as the Permian. Towards the south, minor palaeodrainage lines probably formed after the uplift of the Darling Plateau, and marine transgressions in the Eocene deeply penetrated the palaeovalleys along the western margin of the Eucla basin (Jones, 1990; L. Worrall, CRCAMET, CSIRO, personal communication 1998) when conditions were

tropical. While the development of these palaeodrainage lines has considerable antiquity, the overall drainage system seen today probably developed in the Late Cretaceous (Morgan, 1993; BMR Palaeogeographic Group, 1990: 82).

Calcrete formation, occurrence and age

The long period of emergence and the ensuing prolonged erosion down to the Precambrian basement has resulted in classical karst terrain being absent from the Western Shield. However, carbonate deposits are widespread throughout the arid zone both as soil and groundwater calcretes (Arakel, 1996). Groundwater or valley calcretes (hereafter termed calcrete) are carbonate deposits whose formation is directly associated with groundwater, rather than with soil development (pedogenic calcrete). These carbonate deposits, generally in the order of 10 m thick, form near the water table of shallow aquifers in arid lands as a result of concentration processes by near-surface evaporation (Jacobson and Arakel, 1986). They are especially important in the Australian context (Figure 3) as they form in arid climates (annual rainfall <200 mm) with high potential evaporation (>3000 mm per year: Mann and Horwitz, 1979). They occur where the movement of the groundwater is slow and where the rainfall is episodic resulting in substantial fluctuations in the water table. Groundwater calcretes often develop

Table 1   Calcrete aquifers containing stygofauna sampled in the Western Shield and adjacent regions. Information on the aquifers is contained in the references cited. The numbers denote locations shown in Figure 3. • denotes calcretes that overlie Proterozoic Wittenoom Dolomite containing solution channels in the upper horizons.

Pilbara

Fortescue Catchment
    1. • Western Fortescue Plain[1]   Millstream Dolomite (Barnett and Commander, 1985)
    2. • Ethel Gorge   Woodward-Clyde, 1997b; BHP, 1997.
    3. • Weeli Wolli   Woodward-Clyde, 1997a
    4. • South Fortescue   Hamersley Iron, unpublished reports Tom Price Water Supply

Ashburton Catchment
    4. Hardey River   Hamersley Iron, unpublished reports Tom Price Water Supply

Ashburton Plain
    5. Robe River[1]   Commander, 1994a
    6. Fortescue River[1]   Commander, 1994b

Yilgarn

Western drainage
    7. Austin Downs   Big Bell Mine, unpublished reports
    8. Cue   personal observation

Eastern drainage
    9. Paroo   Sanders, 1973
    10. Lake Violet   Wiluna Gold Mine, unpublished reports
    11. NE Lake Way   EPA, 1981; Passmore, 1983.
    12. Hinkler Well   Mann and Deutscher, 1978; Mann and Horwitz, 1979
    13. Windarra   Maczurad and Murphy, 1997.

[1] The Western Fortescue Plain catchment, previously draining down the Robe River, was captured from the northwest by the Fortescue River at the end of the Pleistocene or Holocene (Barnett and Commander, 1985).
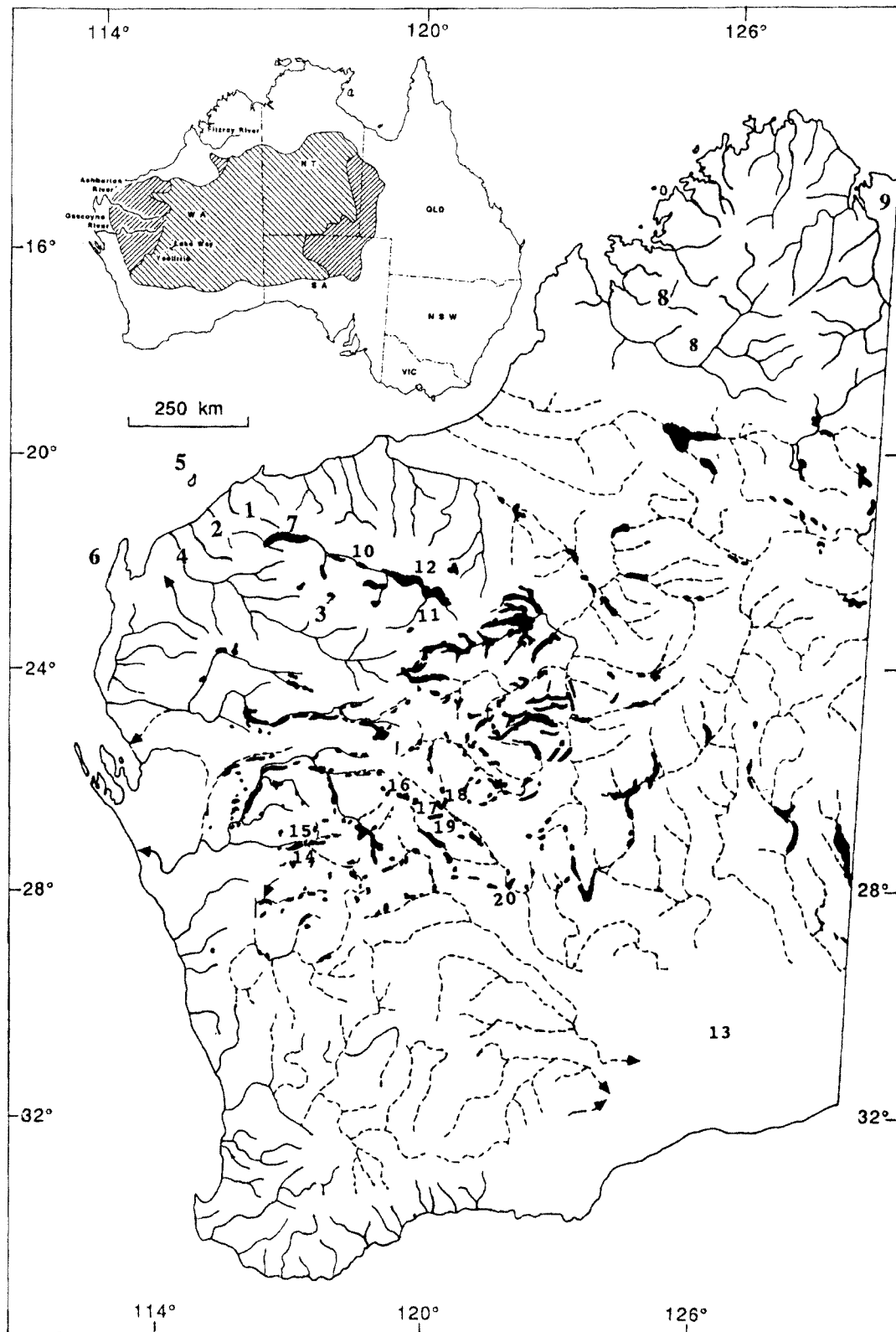
Figure 3   The distribution of groundwater calcrete aquifers in Western Australia. Modern and palaeo- drainage (respectively continuous and dashed lines) and calcrete areas (black) are shown. Derived from data in Geological Survey (1989, 1990), drawn by Julianne Waldock on a base map provided by Philip Commander. Inset: general distribution of groundwater calcretes in mainland Australia, adapted from Mann and Horwitz (1979). 1, Fortescue River; 2, Robe River; 3, Hardey River; 4, Ashburton River; 5, Barrow Island; 6, Cape Range; 7, Millstream (northern edge of the Western Fortescue Plain aquifer; 8, Kimberley Devonian reef system between the 8's; 9, Ningbing Range, an outlier of 8; 10, Mulga Downs; 11, Ethel Gorge near Newman; 12, Fortescue Marsh; 13, Eucla Basin; 14, Lake Austin; 15, Cue; 16, Paroo; 17, Lake Violet; 18, NE Lake Way; 19, Hinkler Well; 20, Windarra, The Carey palaeodrainage channel lies between Paroo and Windarra.

typical karst features (Sanders, 1974; Barnett and Commander, 1985) with sinkholes serving as major recharge zones for the aquifers. Well developed karst has interconnected phreatic conduits providing attributes that make the aquifer suitable both for the exploitation for groundwater and as potential stygofauna habitat. The calcrete bodies considered in this paper are shown in Table 1 with sources of information as to their characteristics.

In the Lake Way and Lake Miranda areas, shallow aquifers occur in lacustrine, aeolian and alluvial/colluvial clay sand deposits, often incorporating gypsum and calcrete deposited by the groundwater (Arakel et al., 1990). The deep aquifers that occur in older calcretes beneath the playa lake facies appear to be interconnected and truncate into Tertiary lateritized terrain (Arakel et al., 1990). The sediments infilling the palaeochannels are mostly Eocene or later but the age of the calcretes is unknown. The extensive alluvial fan calcretes and some of the river valley calcretes formed in the Oligocene (37–30 million years ago) may have following the onset of the continental aridity (Morgan, 1993). Many of the calcrete areas, especially those north of 31°S, are being actively deposited and the others have probably been remobilized and redeposited (Morgan, 1993), attributes that make the dating of calcrete deposits using standard radiometric methods problematic.

Hydrology

There are a number of processes and events which have impinged at various times on the hydrology of the Western Shield and which may have affected the hydrological continuity within the region. These may have permanently isolated some stygal lineages or else permitted faunas to coalesce: these factors are discussed in the following sections.

The Western Shield has been tectonically stable and continuously emergent above the sea since at least the Palaeozoic. At times of high sea level, such as the Eocene (52–37 million years), a relative sea level rise of about 300 m flooded the downstream ends of the palaeorivers. The region was penetrated deeply along the south-western palaeochannels, as far north as c. 30° south. The inland distribution of Thermosbaenacea, which in the Robe River stops at c. 300 m altitude, may reflect this marine incursion. Hence, processes and events occurring throughout the Eocene that may have facilitated or caused the isolation or merging of gene pools are pertinent to the distribution and evolution of the stygofauna within the Western Shield. These processes and events are distinct from the plate tectonic events, such as the progressive fragmentation of Pangaea and Gondwana, factors which together with the Cretaceous and Tertiary marine incursions, more broadly delineated the distribution and composition of the ancient freshwater stygal lineages of Western

Australia. These events are reflected, for example, in the distribution of the Phreatoicidea (Wilson and Keable, 1999), Spelaeogriphacea (Poore and Humphreys, 1998), Amphipoda (Bradbury and Williams 1997a), and the anchialine fauna of the northwest coast (Humphreys, 2000a; Jaume et al., 2001).

Water gaps and groundwater divides

The Robe and Fortescue, which together drain the Western Fortescue Plain (Millstream), flow through one or more water gaps to the west due to incision of a superimposed drainage (Kriewaldt and Ryan, 1967) into the Precambrian basement, as do other rivers draining the western Pilbara. The Proterozoic bedrock at the water gaps is effectively a groundwater hydrological boundary to the west. A groundwater divide within the Western Fortescue Plain occurs between the Robe and Fortescue Rivers, while upstream, the groundwater of the Fortescue River flows towards the Fortescue Marsh (Barnett and Commander, 1985). In consequence, the stygal ecosystem in the Western Fortescue Plain is currently probaly a groundwater island, the age of which is unknown. However, in more humid times, the water balance could well have resulted in unidirectional groundwater drainage in the Fortescue Valley.

The Western Shield is divided from north to south by a drainage divide that separates those catchments draining to the Indian Ocean, some still active rivers, from those draining to the east which are now largely inactive and disorganised (Beard, 1998). The present drainage is superimposed on a much larger palaeodrainage system incised into Precambrian rocks and formed during the Mesozoic when the Western Shield was attached to Antarctica (van de Graaff et al., 1977; Morgan, 1993; Beard, 1998).

The central watershed traverses a palaeosurface barely modified since the Cretaceous (Beard, 1998). This central watershed is of fairly uniform elevation traversed only by a few minor gaps or low points that may be indicative of a change to the drainage patterns in the distant past. On Killara Station, a col 50–100 m below the level of the adjacent watershed, which separates the Murchison and Carey palaeodrainage systems, is the most prominent of these (Beard, 1998). All Australian stygal diving beetles (Dytiscidae: see below) known to date are from these two adjacent palaeodrainage systems but no others drainages have been examined in the Yilgarn. While invoking some significance of this geomorphological gap to the biogeography of the beetles is tempting, this minor gap may merely reflect the trend of less resistant Proterozoic rocks (Beard, 1998). Examination of sympatric taxa from ancient freshwater lineages, for example crangonyctoid amphipods or bathynellid syncarids,
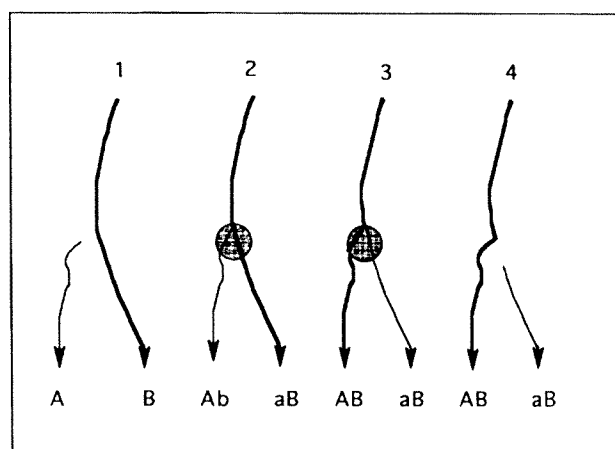
Figure 4 Hypothetical fauna mixing by river capture through times 1 to 4. The initial faunal assemblages A and B in the separate rivers partially merge during the process of river capture (circle); whereas the capturing river becomes a complete mix of A and B. The beheaded river remains predominantly B with a fraction of A (denoted 'a').

would make a substantial contribution to this discussion.

Groundwater faunas may merge or become isolated by long term fluviogenic processes. The lower reaches of a river, or the groundwater aquifers, may become isolated from the original catchment by river capture. This occurred in the lower Robe River, the former drainage of which was captured by the Fortescue River at the end of the Pleistocene or early Holocene (Barnett and Commander, 1985). Alternatively, isolation may result from the redirection of river flow such as occurred in the lower Ord River (Carroll, 1947) where the main flow through the Cave Spring Gap was diverted to its present course. In such cases, the fauna of the captured and capturing sections of the river should mix so that the now isolated lower section of the captured river will contain a representation of the original main stream. The faunal integrity of this will depend on the temporal and spatial extent of the window of opportunity for faunal mixing provided during the process of river capture (Figure 4).

Hydrogeological model

In the Yilgarn, groundwater calcretes form along a hydrogeological gradient, originally characterized from the Hinkler Well calcrete to the west of Lake Way, along the drainage line of which there is a succession of chemical precipitations associated with increasing salinity (Mann and Deutscher, 1978; Mann and Horwitz, 1979). Carbonate is deposited in the mid-line of the drainage with associated silcrete and celestite. Downstream, aeolian deposits

of gypsum occur with sepiolite and aragonite on the shores of the salt lake and on the bed of which halite is found. Upstream of the 'chemical delta', the calcrete is underlain in places by ferricrete and laterite, thought to have formed in more humid climates during the Miocene (Mann and Horwitz, 1979).

Morgan (1993) generalising from the studies of Mann and Deutscher (1978) and Mann and Horwitz (1979) on the Hinkler calcrete. described a model for the development of repeated groundwater calcretes and salt lakes along the length of the palaeodrainage systems. The processes involved differ on either side of the Menzies line, where northern acacia scrub (mulga: *Acacia aneura* F. Muell. ex Benth.) gives way to *Eucalyptus* spp. scrub (also known as the mulga/eucalypt line: Butt *et al.*, 1977), which marks the change of climate from winter dominant rainfall to a more semi-arid mixed winter and summer rainfall region. In the Yilgarn, this latitude (c. 29°30'S) approximates the southern limit of valley calcretes (Morgan, 1965).

In the Oligocene (37–30 mybp) valley calcretes extended further south but they retreated as a result of later geochemical conditions that affected the reactions between groundwater and river channel sediments. North of latitude 30°S, the palaeorivers are characterised by the development along their length of separate hydrogeochemical systems associated with the formation of each salt lake or playa. As salinity increases there is a well defined change in groundwater chemistry (Figure 5). The changes take place between widely separate intake and outflow locations and is also related to the duration of flow of the groundwater. Hence, this increase in salinity of the groundwater and the relative change in chloride: sulphate has both a spatial and temporal dimension.

This hydrochemical trend is initiated at the headwaters of each recharge system, such as a large alluvial fan, and the cycle is terminated at the evaporation outlet marked by the lower boundary of the calcrete with a salt lake. The low salinity waters (500–2000 mg L^{-1} TDS: total dissolved solids) near the intake are alkaline and rich in bicarbonates. The groundwater interacts with the sediments along its flow path and as a result becomes less alkaline, increases markedly in salinity, and changes to a chloride-sulphate type. In the groundwater, a well defined change in common ion ratios develops with increasing salinity, marked especially by a relative increase in chloride and sulphate with respect to other ions. This, in itself, may contribute to the heterogeneity in stygofauna distribution within a given calcrete area reported by Poore and Humphreys (1998). The calcretes pass downstream into dolomites then into gypsum and halites in waters from 20,000 to over 200,000 mg L^{-1} TDS. The main channel calcretes are formed at the

R

Laterite cap mostly removed

Groundwater outflow evaporite

S S

E E E

I

G

G

Remobilised

G

Salt lake

G

Older

G

G G

UNLEACHED BEDROCK

OXIDISING		REDUCING
BICARBONATE WATER	CHLORIDE	SULPHATE WATER
FRESH-BRACKISH ALKALINE 500-5000 ppm	SALINE ALKALINE 5000-20000 ppm	HYPERSALINE NEUTRAL-ACID 20000-200000(+) ppm

SOLUTION CA MG HCO3 FE MN FIXING SIO2	FIXING Fe Mn	surface replacement of Ca with SiO2	Dolomite	
		DEPOSITION OF CALCRETE carbonates replace iron hydroxide		Colloidal clay evaporites

Saprolite and rock

Leached ferruginous sandstone fan and valley fill. Abundant cemented laterine debris

Opaline silica

Contemporary salt pan clay

Granite

Contemporary alluvial fan with ferricrete layer

Calcrete

Trunk valley clay and sandy alluvium

G - Groundwater flow   R - Rainfall   S - Surface runoff   I - Intake   E - Evaporation
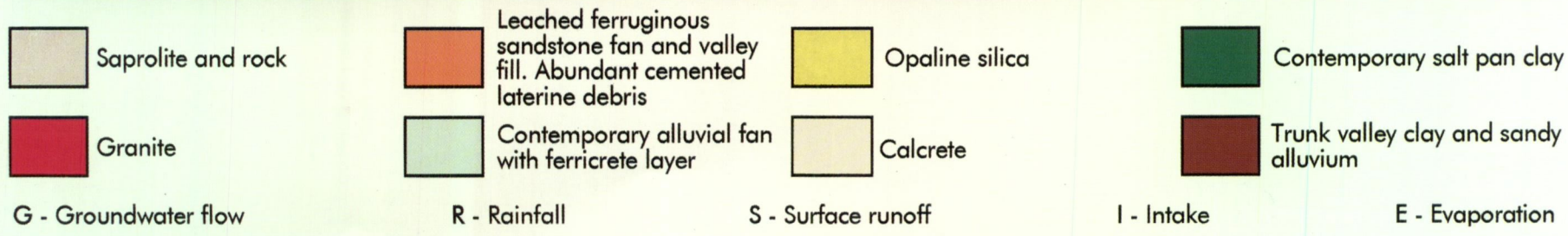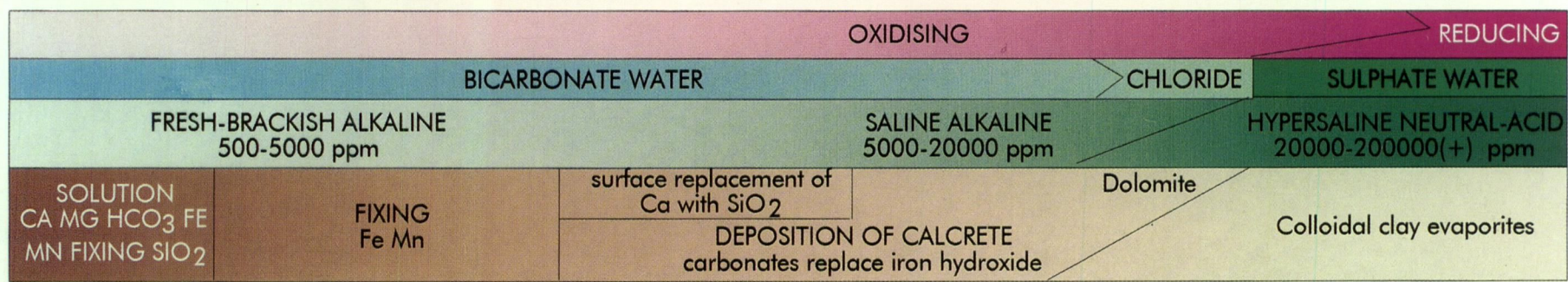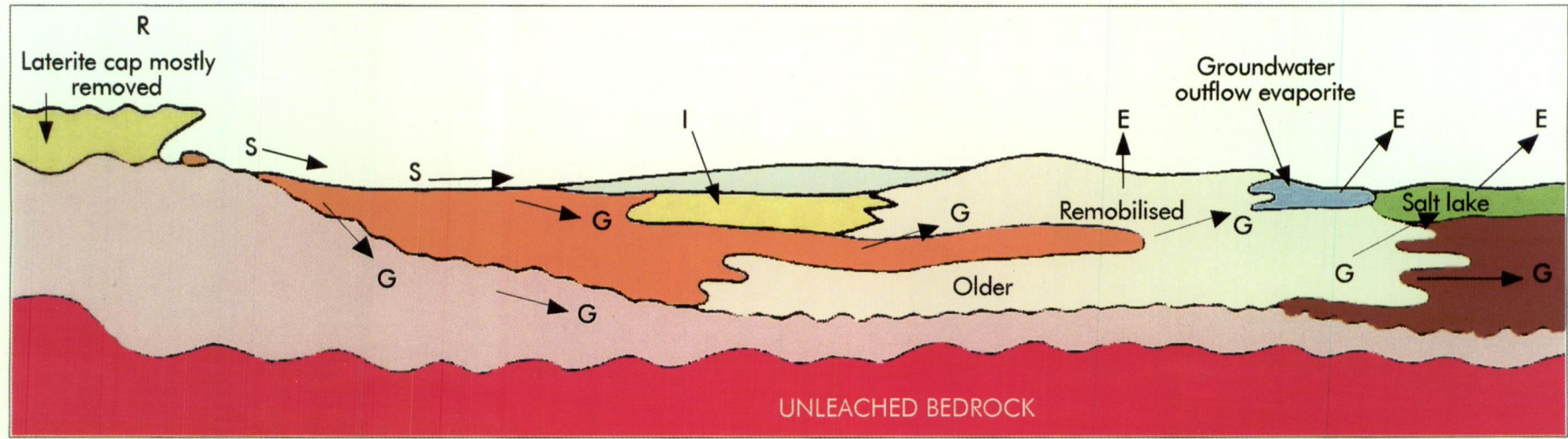
Figure 5   Generalised longitudinal section of the northern part of the Raeside and Carey Palaeorivers showing dissected regolith to the north (left side) with a south facing erosion escarpment and accompanying pediment eroded into the saprolite layer. This feature is followed southwards (right side) by a sedimentary facies of ferricrete-cemented colluvial/alluvial fan, entering the palaeochannel sequence of calcrete, silica, lake basin clay, overlain by evaporites at the groundwater outflow at the salt lake. At the base are shown the changes to the physico-chemical conditions along the groundwater flowpath. This represents a single cycle of a series of hydrochemical cycles that occur along the length of the palaeochannel and which are associated with the saltlakes. Redrawn after Morgan (1993), with permission.

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downstream end of an individual hydrochemical system and immediately upstream of an evaporation outflow area forming a salt lake. This hydrochemical cycle may occur repeatedly along the length of a single palaeodrainage system (e.g., the Carey palaeodrainage system in Figure 1 in Watts and Humphreys, 1999, and Figure 40 in Watts and Humphreys 2000), giving rise to a string of salt lakes that are characteristic of the landscape of the Australian arid zone.

South of 29°S, no such trend occurs in the hydrochemistry of the groundwater; little calcrete is deposited and the common ion ratio shows little alteration with increasing salinity. The groundwaters are typically acid, with sulphur reduction under anoxic conditions possibly associated with the carbonaceous deposits deep in the sediment channels.

The Morgan (1993) model of repeated hydrogeochemical cycles along the length of the palaeodrainage channel (Figure 2 a–c), initiated by

foci of major groundwater recharge, does not lead to easy prediction of the hierarchy of cladogenic events in the stygofauna restricted to the calcrete bodies. Resolution of the sequence of cladogenesis in conjunction with molecular clock estimates may contribute to our understanding of the evolution of these salt lake systems and the development of this arid-zone landscape.

FAUNA

Faunal assemblages, distribution and regional differences

The Western Shield is an area of large geographical extent (c. 10^6 km^2). Stygofaunal sampling, generally of low intensity, has been undertaken recently (since 1996) in the arid zone. The sampling sites are sparsely distributed but from widespread localities (Figure 6). In the context of a large scale faunal survey, some sites
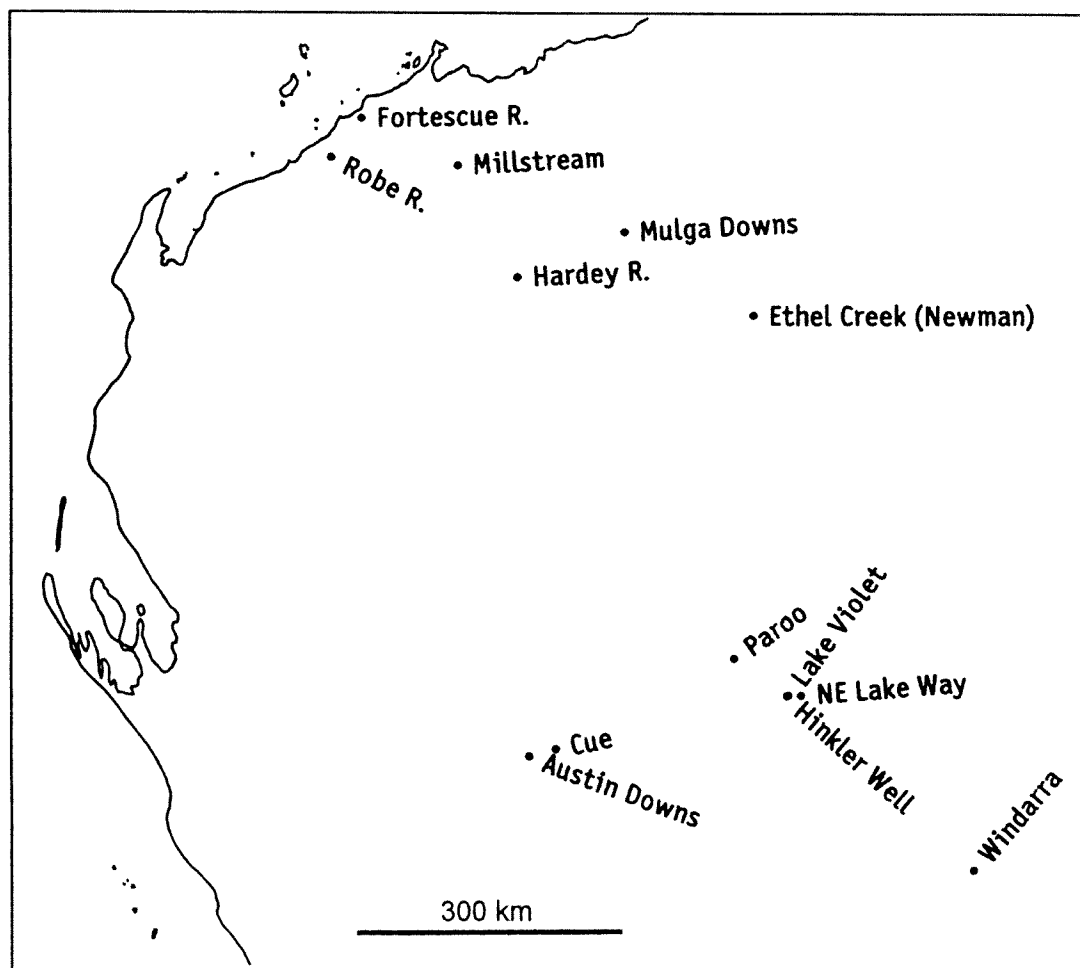

Figure 6   Fauna sampling sites and significant stygal aquifers on the Western Shield. Millstream is on the north central border of the Western Fortescue Plain. Ethel Creek is immediately to the east of Newman. The Hinkler Well label follows the approximate course of the Carey palaeodrainage between Paroo and Windarra. The separate Raeside palaeodrainage (between the labels for Austin Downs and Hinkler Well) has a separate fauna (June 2000), as do Roy Hill (north of Ethel Creek in the Fortescue Valley), and Savory and Ngarari Creek palaeochannels (south of Ethel Creek) that drain inland to Lake Disappointment (September 2000).

have been adequately sampled (Western Fortescue Plain and Ethel Gorge) but others have received only passing attention (e.g. Mt Windarra, Cue).

Few of the taxonomic groups of stygofauna collected have been identified to species or generic-level. Nonetheless, this process has allowed tentative recognition of local and regional differences in the composition and distribution of the stygal assemblages. Further, each discrete calcrete body examined thus far contains not only a unique stygal assemblage, but also comprises species apparently unique to that aquifer (Table 2).

In the following paragraphs, a synopsis of the stygal diversity of the Western Shield is given, together with the current state of taxonomic knowledge.

Pilbara

Stygofauna found initially on the Western Shield in the calcrete aquifers of the Western Fortescue Plain (the Millstream aquifer) had clear Gondwanan affinities (Harvey, 1998; Poore and Humphreys, 1998). This aquifer contains Spelaeogriphacea, an order previously only known from two caves in South Africa and Brazil (Poore and Humphreys, 1998). The associated stygofauna includes other taxa with Gondwanan affinities, such as Phreodrilidae (Oligochaeta: generally with a cool climate Gondwanan distribution: A. Pinder, personal communication 1997), Phreatoicidea (*Pilbarophreatoicus* Knott and Halse, 1999, Wilson and Johnson, 1999: Isopoda), crangonyctoid amphipods (gen. nov., J.H. Bradbury, personal communication 1999; Gondwanan Williams, 1986),

Table 2 Sundry taxa and their distribution on the 'Western Shield'.

Area	Major taxon	Minor taxon
Pilbara		
Fortescue Drainage		
Ethel Gorge	Crangonyctoid amphipod[2]	Gen. A sp. 1 to sp.14
Mulga Downs	Crangonyctoid amphipod	Gen. A sp 15
Millstream	Crangonyctoid amphipod[2]	Gen. B. sp. 1
Ethel Gorge	[1]Flabelliferan isopod	Taxon A sp. 1
Weeli Wolli	[1]Flabelliferan isopod	Taxon A sp. 2
Mulga Downs	Ostracoda	Taxon B sp. 3
Millstream	Ostracoda	Taxon B sp. 2
Millstream	Ostracoda	Taxon B sp. 1
Ethel Gorge	Ostracoda	Taxon C sp. 1
Ethel Gorge	Ostracoda	Taxon C sp. 2
Weeli Wolli	Ostracoda	Taxon C sp. 3
Weeli Wolli	Ostracoda	Taxon C sp. 4
Coastal Plain	Copepoda: Cyclopidae	*Halicyclops rochai* De Laurentiis *et al.*
Coastal Plain + Millstream	Copepoda: Cyclopidae	*Diacyclops humphreysi* Pesce *et al.*
Millstream	Copepoda: Cyclopidae	*Diacyclops reidae* De Laurentiis *et al.*
Millstream	Copepoda: Cyclopidae	*Diacyclops einslei* De Laurentiis *et al.*
Coastal Plain + Millstream	Copepoda: Cyclopidae	*Mesocyclops brooksi* Pesce *et al.*
Coastal Plain + Robe[3]	Thermosbaenacea	*Halosbaena tulki* Poore & Humphreys
Ashburton Drainage		
Hardey River	[1]Flabelliferan isopod	Taxon A sp. 3
Ashburton	Copepoda: Cyclopidae	*Mesocyclops brooksi* Pesce *et al.*
Yigarn		
Western drainage		
Cue	Isopoda: Oniscidea	[4]*Haloniscus* sp. 1
Cue	Ostracoda	Taxon D sp. 1
Eastern drainage		
NE Lake Way	Isopoda: Oniscidea	*Haloniscus* sp. 2
NE Lake Way	Isopoda: Oniscidea	*Haloniscus* sp. 3
NE Lake Way	Isopoda: Oniscidea	*Haloniscus* sp. 4
Paroo	Ostracoda	Taxon D sp. 3
Lake Violet	Ostracoda	Taxon D sp. 2

[1] Second clade of an undescribed family of flabelliferan isopod known elsewhere from the Kimberley (Wilson and Ponder, 1992); [2] crangonyctoids belong to an ancient freshwater lineage (J.H. Bradbury, personal communication); Ceinidae (Amphipoda), a family of marine ancestry (Barnard and Karaman, 1984), are also present but have not been examined. [3] See footote to Table 1. [4]*Haloniscus* is elsewhere known from salt lakes in Australia (Bayly and Ellis, 1969; Williams, 1983) and anchialine systems in New Caledonia (Taiti *et al.*, 1995).

Table 3 Synopsis of the amphipod stygofauna of the northern Pilbara. The assessment was made by J.H. Bradbury from a broadscale screening of available material except that denoted that is in manuscript. A preliminary examination of further new material (101 specimens) from the Pilbara, predominantly in the Ashburton catchment, is estimated to contain an additional 15 species in 8 genera from three families, Paramelitidae, Melitidae and Bogidiellidae (J.H. Bradbury, personal communication, 20 February 2000).

	Genus	Species	Region
A	Paramelitidae:		
	New genus A	14 new species	Ethel Gorge borefield Bradbury 2000.
		new species c	Fortescue Valley Bradbury submitted.
		new species d	Hardey River
	New genus B	new species a	Millstream Bradbury submitted.
		new species f	Weeli Wolli
B	Melitidae		
	Nedsia	new species a	Fortescue River bridge
		new species b	Upper Ashburton
		new species c	Millstream
		new species d	Millstream/Robe River aquifer
		new species e	Old Yaleen Well
C	New genus C	new species a	Millstream
D	New genus D	new species a	Millstream
E	New genus E	new species a	Wiluna
F	New genus F	new species a	Upper Ashburton

and *Tiramideopsis* (Acari: genus previously known only from India: Harvey, 1998). Other stygofauna include a new hydrobiid (Gastropoda: W.F. Ponder, personal communication 1997), Bathynellacea (Syncarida), cyclopoid and harpacticoid Copepoda, Ostracoda (3+ species), and ceinid and melitid amphipods. Several of these also probably have Pangaean affinities, including the Spelaeogriphacea (Poore and Humphreys, 1998), Syncarida (Schminke, 1974; Boutin and Coineau, 1987) and Crangonyctoidea (Barnard and Karaman, 1983).

This aquifer is isolated by a water gap downstream and a groundwater divide upstream (see *Water gaps and groundwater divides*), hence, the fauna is possibly confined to the western Fortescue plain (Poore and Humphreys, 1998). Downstream the stygofauna in the Robe River and Fortescue River alluvial aquifers on the coastal plain (Figure 6) is related to the Cape Range/Barrow Island anchialine fauna (Humphreys, 1999b, 2000a) having tethyan affinities (see Introduction). Upstream the fauna differs at the closest point sampled (upstream of the groundwater divide at Mulga Downs, the calcrete deposit second removed along the Fortescue River). At Ethel Gorge (Figures 6 and 7), a rich stygofauna occurs in calcrete (Eberhard and Humphreys, 1999) comprising numerous taxa of amphipods (Table 3: Ceinidae and 14 species of a new genus of crangonyctoids not known from Millstream Bradbury, 2000) and a second clade (G.D.F. Wilson, personal communication 1998) of an undescribed family of flabelliferan isopods (Wilson and Ponder, 1992), a family known from throughout the Kimberley Devonian Reef system

(Humphreys, 1995; Limestone Billy Hills, W.F. Humphreys, unpublished; Ningbing Range, S.M. Eberhard, unpublished).

Other calcrete areas in the Pilbara that have been sampled for stygofauna, including the upper reaches of the next major drainage basin to the south, the Ashburton River, may be characterised by the presence of the flabelliferan isopod. This most distinctive stygal animal, uncharacteristically robust, clinging and opaque, is represented by a different taxon at all sites so far investigated in the Pilbara (G.D.F. Wilson, personal communication 1998). In addition, all sites contain diverse amphipods, ostracods (especially Candoninae), and copepods (especially Cyclopoidea).

Thus the Pilbara appears to have three types of stygal assemblages distributed in discrete regions:

1, the coastal plain comprising the alluvial fan aquifers of the lower Robe and Fortescue Rivers which has a tethyan community characterised by *Stygiocaris* (Atyidae), *Haptolana* (Cirolanidae) and *Halosbaena* (Thermosbaenacea), of which the latter intrude to an altitude of 300 m on the Robe River, the approximate level of the Late Eocene sealevel high on the Yilgarn (G.W. Kendrick, personal communication, 1999),

2, the Western Fortescue Plain characterised by Spelaeogriphacea and the associated fauna with Gondwanan affinities, and

3, sites upstream of the Western Fortescue Plain and the upper Ashburton catchment characterised by flabelliferan isopods.

Each of these assemblages also has an array of Amphipoda, Ostracoda, Copepoda, Syncarida (Bathynellacea) and Oligochaeta (Phreodrilidae)

Table 4   The distribution of stygal species of dytiscids amongst discrete calcrete bodies in the Yilgarn district of
Western Australia. From Watts and Humphreys (1999[i], 2000). Superscripts between 2–4 in common denote
sympatric species. A new genus and five new species of stygal Dytiscidae were collected (June 2000) in the
separate easterly trending Raeside palaeodrainage (see caption Figure 6) and one new species from a separate
calcrete in the Austin palaeodrainage (Watts and Humphreys, unpublished). Thus, 18 stygal dytiscid species
occur in the Yilgarn compared with the world total recorded by Spangler and Decu (1999) of 17 species in 12
(9 monotypic) genera.

Genus Calcrete body	*Tjirtudessus* W & H[1]	*Nirridessus* W & H	*Kintingka* W & H
Western drainage			
Austin Downs	–	*bigbellensis*	–
Cue	*magnificus*[4]	*cueensis*[4]	–
Eastern drainage			
Paroo	*eberhardi* [2]	*pulpa* [2]	*kurutjutu*[2]
Lake Violet	–	undescribed sp.	–
NE Lake Way	*hahni*	*morgani*	–
Hinkler Well	–	*hinkleri*	–
Windarra	–	*windarraensis*[3]	–
–	–	*lapostaae*[3]	–

which have mostly yet to be taxonomically worked
in any detail.

Yilgarn

Stygal assemblages inhabiting groundwater
calcretes in the Murchison district of the Yilgarn
(Figure 6) are distinguished by the presence of
diving beetles (Coleoptera: Dytiscidae), with up to
three genera occurring sympatrically (Table 4).
Different species of dytiscid are found in each
separate calcrete body examined to date (Watts and
Humphreys, 1999, 2000). Congeneric species of the
dytiscids are found on either side of the drainage
divide that separates the drainage to the Indian
Ocean from that draining to the interior of the
continent. Because groundwater connections across
this ancient water divide on Precambrian rocks are
unlikely, the beetles may have evolved from a
widespread epigean ancestor. The dytiscids are
associated with a diversity of Bathynellacea,
Amphipoda (Crangonyctoidea and Ceinidae: J.H.
Bradbury, personal communication, 1999),
Ostracoda, Copepoda (Harpacticoidea and
Cyclopoidea), Oligochaeta (Phreodrilidae: A.
Pinder, personal communication, 1999) and
Isopoda: Oniscidea (*Haloniscus* spp.: S. Taiti,
personal communication, 1999).

AQUIFER CHARACTERISTICS

Water quality and stratification

The characteristics and quality of groundwater
flowing alongside (parafluvial) and beneath
(hyporheic) surface waters change with distance
from the groundwater/surface water ecotone and
with the relative water pressure which determine
whether the water is flowing into or out of the

groundwater system. These interactions and
properties influence both the river fauna (Boulton,
1993, 2001) and the interstitial and stygofauna along
the course of a river (Danielopol *et al.*, 2000; Dole-
Olivier *et al.*, 1994; Ward *et al.*, 2000).

In the Australian arid zone, large spatial and
temporal changes in water quality occur that result
from the hydrogeochemical processes in the
groundwater flow (see Morgan's model above). The
unpredictable and highly episodic rainfall,
characteristic of the arid zone (Sanders, 1973),
recharges calcrete aquifers through porous, often
karstic surfaces (Barnett and Commander, 1985;
Arakel *et al.*, 1990). These large but episodic recharge
events may cause the groundwater table to fluctuate
widely in height (Jacobson and Arakel, 1986; Morgan,
1993), accompanied by large changes in salinity,
especially near the groundwater surface (Morgan,
1993; Watts and Humphreys, 1999). Quite subtle
changes, such as to the height of the water table, or in
the direction of groundwater flow, may have
profound effects on the location of stygal populations.

Stygofauna occurs in calcretes where the
groundwater surface is only 2 m below the surface
(Windarra), and up to 27 m below the surface in the
Western Fortescue Plain where the calcrete aquifer
itself is up to 30 m thick (Barnett and Commander,
1985). Elsewhere in Australia stygofauna is known
from water tables 59 m below the surface and in
water up to 33 m deep. For comparison, the artesian
Edwards Aquifer in Texas, USA, supports a diverse
stygofauna 415–615 m below the surface in an
artesian system (Longley, 1992), while amphipods
and molluscs, *inter alia*, occur from one kilometre
depth in Morocco (Essafi *et al.*, 1998).

Fresh to saline groundwaters occur widely in
calcretes of the palaeodrainage channels of the
Western Shield and often, perhaps typically, have

fresher water overlying saline deeper water. Such salinity stratified systems may be damaged by the underlying saline layers intruding into the overlying fresh water as a result of excessive pumping. The stygofauna from the Pilbara has been found in fresh waters (salinity <1 g L^{-1} TDS) but in the Yilgarn, stygofauna has been found widely in waters of salinity 1–5 g L^{-1} TDS. Northeast of Lake Way, stygofauna occurs in waters with a salinity stratified from 23 to 41 g L^{-1} (Figure 39 in Watts and Humphreys, 2000) but the salinity zone occupied by the fauna is unknown. This record may be the first stygofauna known from highly saline mid-continental waters.

Williams *et al.* (1990) sampled invertebrates from 79 salt lakes in western Victoria, Australia. Twenty-nine percent of the 142 species examined were found in waters with salinity greater than 23 g L^{-1}. Higher taxa were differentially represented in water with salinity greater than 23 g L^{-1}, ranging from total absence of species (Hydracarina, Odonata, Lepidoptera, Trichoptera), from 20–40% of species (Hemiptera, Mollusca, Ostracoda), to more than 40% of species (Malacostraca, Copepoda, Diptera); only 12% of Coleoptera species were found in these high salinity waters. Species richness from saline lakes (3 to 100 g L^{-1}) was not markedly lower than that of freshwater lakes, and they concluded that salinity may not be an important determinant of species occurrence over most of the salinity range occupied by the fauna of salt lakes.

These findings (Williams *et al.*, 1990) are of particular interest in the context of the calcrete aquifers which may exhibit strong salinity stratification (Figure 39 in Watts and Humphreys, 2000) or fluctuate markedly in salinity at the surface (e.g. annual range between 5–22 g L^{-1}: footnote Table 2 in Watts and Humphreys, 2000). Thus, not only is a wide range of salinity tolerant species available to colonise stygal habitats in Australia, but, once adapted to subterranean life, the particular salinity, over a wide range, may not be a prime determinant of their occurrence.

Such strong salinity gradients in groundwater are often associated with ecotones, as found, for example, in anchialine waters in Mexico (Pohlman *et al.*, 1997, 2000) and on the Cape Range peninsula of Western Australia (Humphreys, 1999a). In the latter, a complex physico-chemical stratification occurred associated with the halocline in which the salinity changed from 19 to 32 g L^{-1} through a depth change of 8.5 m. A diverse microbial assemblage was associated with the resulting oxic/anoxic boundary and, not surprisingly, the stygofauna varied with depth within this system (Humphreys, 1999a), as found elsewhere (Sket, 1986). An analogous chemoautotrophic system may occur associated with the marked salinity stratification found in calcretes of the Western Shield. The plausibility of such a

mechanism in the calcretes is enhanced because groundwaters in desert regions typically have high nitrate and sulphate contents (K.H. Morgan, personal communication, 1999) which, under reducing conditions, could support chemoautotrophic sulphur bacteria (Schulz *et al.*, 1999). In addition, this ecosystem and its fauna may segregate around the halocline, as found in anchialine ecosystems (Sket, 1986; Humphreys, 1999a).

Limits in time and space

An absence of sediment (unconformity) between the Permian and Eocene, throughout the Yilgarn and Pilbara cratons and in much of the intervening Proterozoic basins (L. Worrall, CRCAMET, CSIRO, personal communication, 1998), largely constrains the distribution and timing of colonisation and vicariant events of fauna confined to groundwaters; it could also have disrupted the hyporheic corridor.

The Wittenoom Dolomite, of Proterozoic age, is widespread in the Pilbara. Its upper parts are often karstic and in contact with Tertiary deposits (Barnett and Commander, 1985). This formation may have provided a long term refuge for stygofauna throughout the Mesozoic and account for the presence of an apparently much older fauna in Tertiary aquifers (Poore and Humphreys, 1998; Humphreys, 1999b). This process has also been argued for other taxa in different formations at other localities (Humphreys, 1993, 2000b, 2000c).

Such profound geomorphological constraints are likely to have had a large influence on the composition and distribution of stygofaunal assemblages. The constraints imposed by the erosional landscape on existent and putative stygofauna throughout the Mesozoic may have been released with the onset of a depositional environment in the palaeochannels during the Tertiary.

Although the stygofauna of the Western Shield differs regionally, as well as between the various calcrete bodies within a region, from first principles the stygofauna may be expected to occur widely within a given calcrete body. This is because karst development is widespread near the water table in such aquifers and the resulting open conduit flow should permit wide dissemination of any contained stygofauna. However, no evidence supports this contention of widespread distribution of stygal species within a given calcrete aquifer. Two examples can be given:

During the initial examination of the Western Shield aquifers in 1996, a total of 46 bores was sampled in the central regions of the Western Fortescue Plain aquifer (Millstream). Spelaeogriph-aceans were collected from eight of the sites. The following year 24 additional bores were sampled (plus 20 of the original bores) and together these samples encompassed almost the entire aquifer,
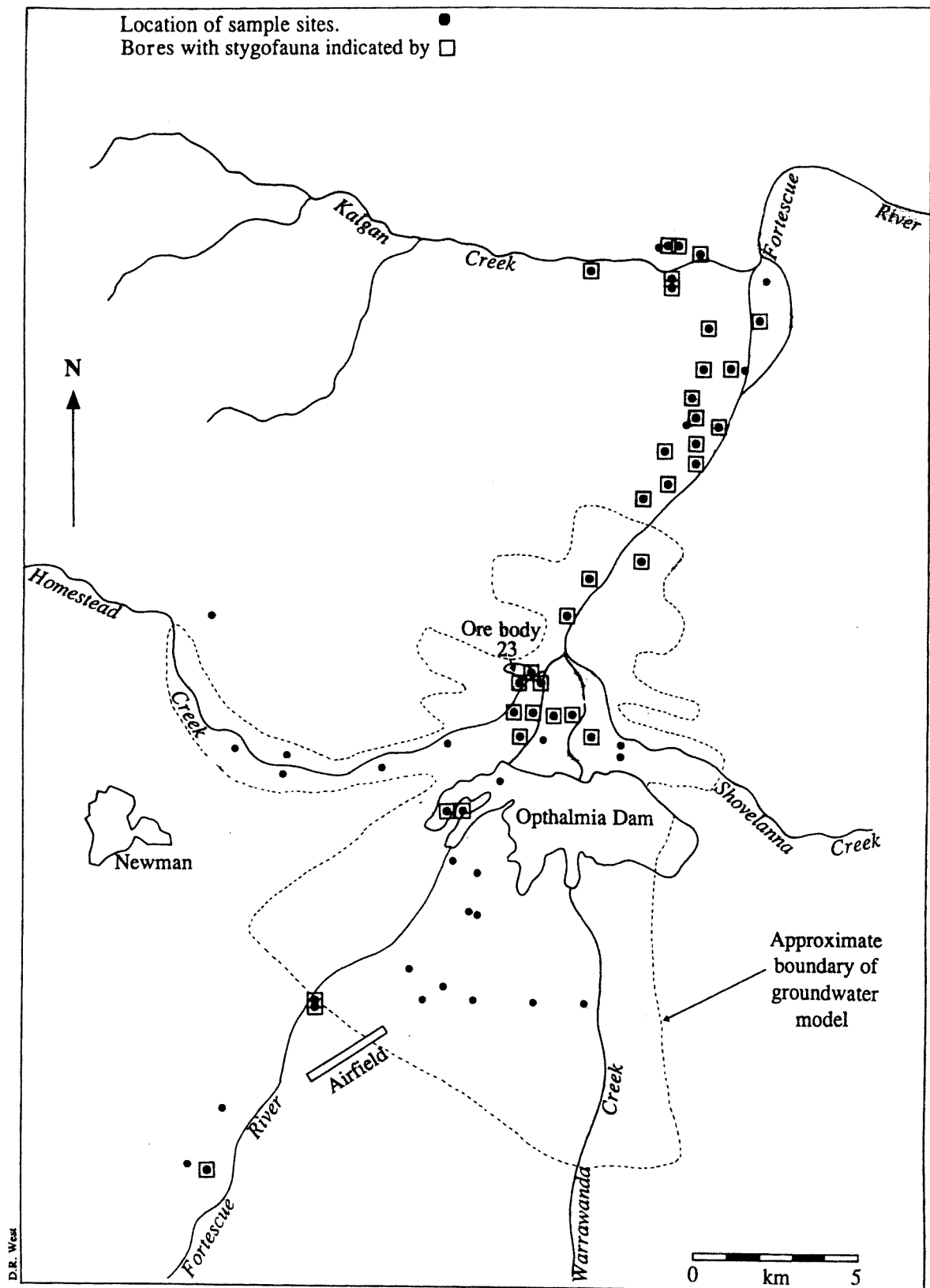
Figure 7 Calcrete aquifer at the junction of the Fortescue River with Homestead, Warrawanda and Shovelanna Creeks near Ethel Gorge, Upper Fortescue. The dotted line represents the limits to the drawdown model (BHP, 1997) for a proposed mining operation involving dewatering below the calcrete (after Eberhard and Humphreys, 1999). This is the most specious stygal amphipod site known globally, containing 14 *Chydeakata* (Bradbury) species (Paramelitidae), largely known only from the central area of the proposed drawdown. The next most specious sites, though taxonomically more diverse, are Barrow Island, W.A. (3, 3, 12 family, general, species minimum), Edwards Aquifer, Texas (4, 7, 10; J.R. Holsinger, personal communication, 2000), Pecina Vjetrenica (Dinaric karst, 3, 3, 10) and Sava River at Dovjez, Slovenia: interstitial, 2, 2, 9; B. Sket, personal cummunication, 2000).

including both sides of the groundwater divide between the Robe and Fortescue drainages. No additional sites produced spelaeogriphaceans (Figure 8; Poore and Humphreys, 1998). Furthermore, some taxa collected from the Millstream aquifer in 1996 were not collected again in 1997, either at the same sites or elsewhere, suggesting that some taxa may be sparse, even rare (e.g. the Phreodrilidae), while others seem to be restricted to discharge areas (e.g. Phreatoicidea). The failure of additional sampling to locate more spelaeogriphacean sites on the Western Fortescue Plain (Poore and Humphreys, 1998) suggests that a given calcrete body cannot be considered as an homogeneous stygal habitat.

In this context, bores may produce artefacts that change the apparent density, composition and distribution of the stygofauna by:

1, acting as conduits for organic carbon from the surface thus providing a superabundance of food energy to an otherwise typically low energy system; depending on the amount, this additional energy may be expected either to attract, thus concentrate the stygofauna in the bore, or else permit epigean taxa to displace stygofauna (Malard, 1995). In this respect hand-dug wells of large diameter (1–3 m) often do not contain stygofauna while adjacent narrow bore wells (bores) commonly do.

2, providing sampling access though water physico-chemically stratified thereby mixing the natural vertically separated faunas;

3, permit faunas from normally unconnected aquifers at different depths to mix;

4, providing an artificial substrate and gaseous exchange interface (changing the redox profile) permitting otherwise separated communities to coexist; and

5, introducing iron (steel pipes) as substrate on which iron bacteria could act (see Fenchel and Finlay, 1995).

The calcrete and neighbouring alluvial and fractured rock aquifers associated with the confluence of several creeks at Ethel Gorge calcrete on the upper Fortescue were sampled for stygofauna at 79 locations (Eberhard and Humphreys, 1999). Stygofauna was recovered from 43 bores and included bathynellids, phreatoicidean and flabelliferan isopods, amphipods, copepods and ostracods. Just one family (crangonytoid amphipods) has been examined taxonomically in detail from the Ethel Gorge calcrete. Despite the widespread sampling in the area, most species of amphipod (10 of 13 undescribed species) are known from only a very small part (<4 %) of this calcrete (Figure 7), in an area planned to be dewatered to a projected depth of 140 m below the surface for a short term mining operation (BHP, 1997). This

calcrete aquifer was repeatedly drawn-down to a moderate extent at Ethel Gorge in the 1970s (G.B. Clark, personal communication, 1999), possibly sufficient to affect phreatophytic vegetation.

DISCUSSION

In recent years stygofauna, groundwater and aquifer ecosystems, have become the focus of much attention on account of the biodiversity and functions therein (Botosaneanu, 1986; Gibert et al., 1994; Juberthie and Decu, 1994, 1998; Culver et al., 1995; Wilkens et al., 2000). There is an increasing realisation that they represent a major component of biodiversity, sometimes greater than the diversity in surface waters (Rouch and Danielopol, 1997), and that they comprise complex ecosystems interacting with surface systems in a manner pertinent both to groundwater and surface water quality (Gibert et al., 1994). Recently the major part of an entire issue of an international journal was devoted to the biodiversity of Crustacea in subterranean waters [*Crustaceana* **72**(8) (1999)].

Much work is needed to start to understand the distribution and distinctiveness of the stygofauna of the groundwater calcrete aquifers of the Western Shield. The initial hypothesis proposed for the development of fresh groundwater refugia at the head of the tributaries of the palaeodrainage systems (section **Potential isolating factors**) at this stage seems too simplistic, and the development is at least more complex and perhaps fundamentally different from that proposed. The presence of distinct faunas in each calcrete area is consistent with the evolution of the hydrogeological system in the palaeodrainage channels (Mann and Deutscher, 1978) as interpreted by Morgan (1993). Namely, the hydrogeological cycles repeated along the length of the palaeodrainage line. The age and stability of the palaeodrainage systems and the suitability for stygofauna of calcrete aquifers, coupled with the repeated cycles of fresh to hypersaline (>200 g L^{-1}) groundwaters along the length of each palaeodrainage system would effectively isolate each stygal assemblage within the region where groundwater characteristics are suitable for their development. Of species found in salt lakes 97% were excluded in such hypersaline waters (Williams et al., 1990).

Conservation

Groundwater calcretes are a major source of potable, stock and industrial water in the arid zone. Furthermore, calcretes are used extensively as a limestone resource, predominantly for neutralising acids resulting from mining operations or mineral processing, and for construction. While the impact of a well managed water abstraction borefield on stygofauna is unknown, a poorly managed system
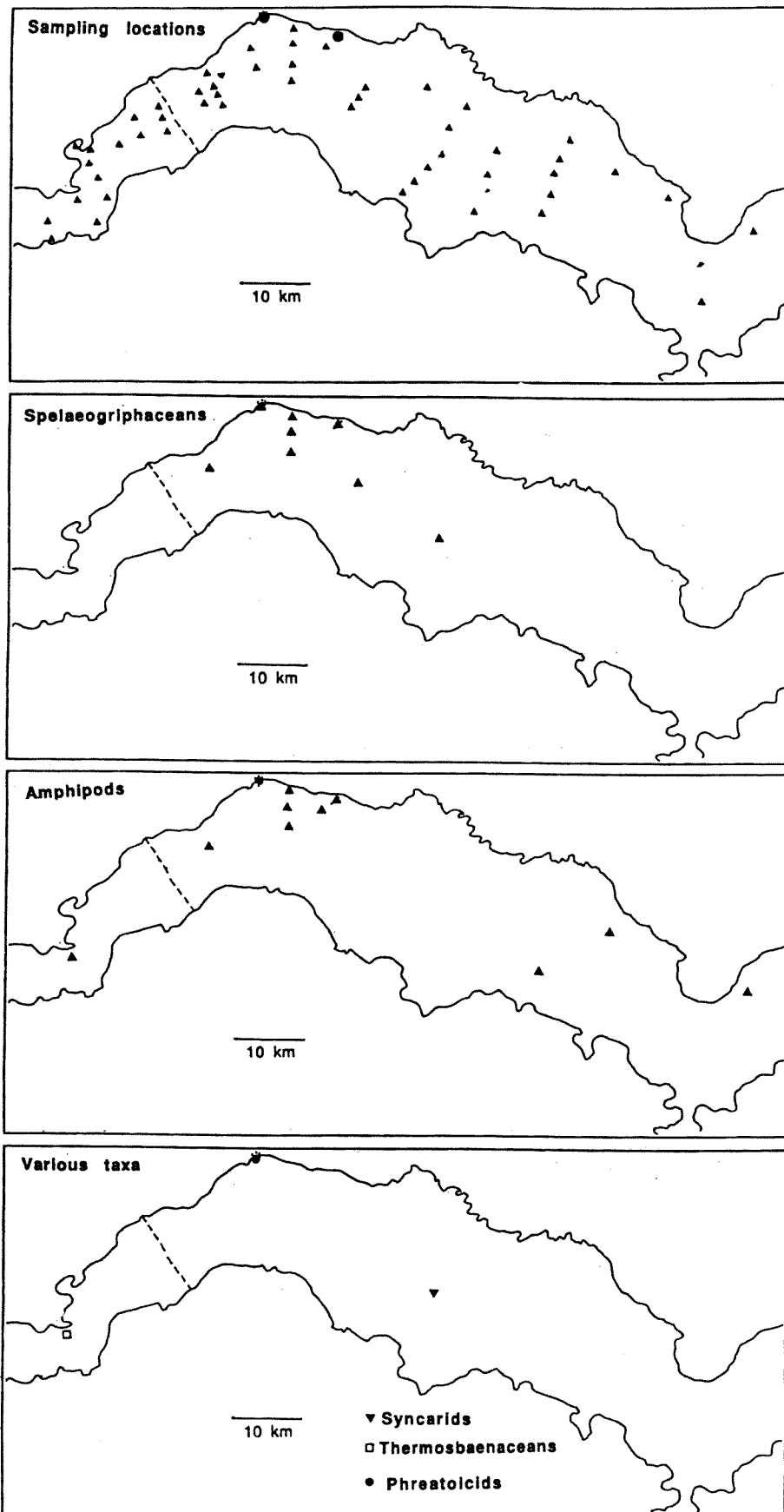
Figure 8   Western Fortescue Plain aquifer (based on Barnett and Commander, 1985) showing sampling locations (triangles in upper map: circles denote multiple sampling points at Palm Springs and Millstream), and the distribution of selected stygofauna taxa in the aquifer of the Western Fortescue Plain. The groundwater divide between the Fortescue and Robe River drainages is denoted by a broken line.

may result in the upward intrusion of salt water within the aquifer. The quarrying of calcretes may remove habitat for stygofauna and expose the water table to greater evaporation, thereby foreshortening the temporal and physical development of the typical groundwater flow envisaged in Morgans model. While the effect of these impacts is uncertain, even quite subtle changes in groundwater quality and quantity, as well as their temporal expression, may have profound effects on the location of stygal populations, for example in the Dytiscidae (Richoux and Reygrobellet, 1986). Unique stygal assemblages may be lost if groundwater pollution occurs (Uéno, 1996).

These ecosystems may face significant risks resulting from the lowering of the water table below ecologically appropriate levels as a result of surface operations (sealing or clearing), as well as those below ground (water abstraction, mine dewatering). In addition, such processes may result in the physical modification or loss of subterranean environments through general surface slumping in floodplain calcrete aquifers resulting from the withdrawal of supporting water.

The discovery that groundwater calcrete aquifers in the Australian arid zone contain rich relictual faunas (Poore and Humphreys, 1998; Humphreys, 1999b; Watts and Humphreys, 1999, 2000), and that these faunas differ between even closely adjacent sites, poses challenging management issues for both operators and regulators.

Hatton and Evans (1998) review of groundwater dependent ecosystems recognised the groundwater dependence of aquifer ecosystems and that it is to be expected these ecosystems represent a key part of the food chain and ecological processes which emerge as river base flow and flow into wetlands. However, they failed to appreciate the diversity of Australia's subterranean fauna, the amount of the information available, or the range in types and extent of aquifer ecosystems present in Australia. As a consequence, they severely underestimated (at 1%) the proportion of Australia covered by groundwater dependent ecosystems, especially those arid zone aquifers within groundwater calcretes. While the authors have subsequently recognized this (T. Hatton and R. Evans, in litt. 1999), the timing was unfortunate as it coincided with policy development by the States and Territories on groundwater dependent ecosystems.

Conclusions

Of the hypotheses suggested earlier:

1) Other arid regions do contain relictual stygofauna.
2) The stygofauna includes ancient freshwater lineages (Syncarida, Crangonyctoidea), probably more recent ones (Dytiscidae), and some ambivalent (Oniscidea).
3) Headwater aquifers do contain distinct but related faunas (Paroo, Hinkler Well: Table 4, Figure 6). In addition, however, non-headwater aquifers — those in line along a given palaeodrainage channel — also contain distinct but related faunas (Paroo, Lake Violet, Windarra: Table 4, Figure 6).
4) Calcrete aquifers do each contain separate faunas comprising significant biodiversity.
5) The Gondwanan affinities of much of the stygofauna of the Western Fortescue Plain suggests an earlier origin than the lacustrine calcrete of Tertiary age in which the fauna occurs; as it is karstic in places the underlying Wittenoom Dolomite, of Proterozoic age, is a prime candidate, although no stygofauna has definitively been recovered from it to date.

The fauna of the calcrete aquifers of the Australian arid zone has barely been examined. Already, some taxonomic groups of the stygofauna comprise the most diverse of any in the world. As with other ecosystems, these complex aquifer ecosystems — of which only the macroinvertebrate section is discussed in this paper — may be expected to provide 'ecosystem services', the nature and extent of which we are largely ignorant. It is to maintain these ecosystem functions that is the thrust of biodiversity debate. In this state of blissful ignorance these ecosystems are being impacted by human activities at an increasing rate. Notwithstanding, these aquifer ecosystems offer exciting opportunities for research into the evolution of subterranean lineages, as well as on the progressive impact of aridity in Australia. The presence of such highly diverse and locally endemic stygofauna, often ancient relictual lineages, in a major economic resource within arid Australia poses delicate and challenging conservation issues. At the same time the scientific challenge is considerable to understand the development and functioning of these systems in order that they can be managed sustainably.

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