Hydrobiologia (2007) 585:99–118
DOI 10.1007/s10750-007-0632-7

OSTRACODA (ISO15)

Groundwater Ostracods from the arid Pilbara region of northwestern Australia: distribution and water chemistry

Jessica M. Reeves · Patrick De Deckker · Stuart A. Halse

Abstract An attempt has been made at a comprehensive study of the diversity and distribution of subterranean ostracods in the Pilbara region, northwestern Australia. The area is a ''hot spot'' for subterranean biodiversity, some of which is currently under threat from extensive mining operations. Both bore and well sites were targeted, totalling 445 sites, to obtain a thorough coverage of the 200,000 km^2. In addition, physical and hydrochemical measurements were obtained for all of the samples (temperature, conductivity, dissolved oxygen, pH, Eh, turbidity, nutrients, major ions). Ostracods were retrieved from approximately 47% of the samples and 56% of the sites. Twenty-one genera and around 110 species of ostracods have been identified. Of these, 72 are new species and a further 10 are currently in open nomenclature, due to the lack of suitable material for formal taxonomic description. The Candoninae are particularly well represented with 12 genera; some, such as *Areacandona* and *Deminutiocandona*, with 25 and 10 species respectively. Most sites (80%) were dominated by only one or two species, with up to six species at some sites. Population density varied from 1–370 individuals/sample. The most abundant and diverse sites occur in fresh, bicarbonate-rich aquifers utilised for water extraction, such as Pannawonica (Robe River), Cane River and Millstream. There is a clear distinction between taxa at the genus level from coastal and low-lying alluvial sites, and upland sites (>300 m altitude). Beyond this, the majority of species are confined within a surface water catchment, or in many cases, a specific aquifer. There are, however, some morphological similarities of the carapaces between different species within similar hydrogeologic settings. Ornate and ridged-valved species are common in the Mg–HCO_3 waters of the Newman and Marillana Creek areas, whereas smooth-shelled, tapered forms are prevalent in alluvial aquifers. The more saline, Na–Cl rich aquifers at the edge of Great Sandy Desert have a particularly distinctive fauna, including one almost triangular species. The distribution of the stygobitic ostracod species in relation to the hydrogeology and water chemistry is discussed.

Guest editors: R. Matzke-Karasz, K. Martens & M. Schudack
Ostracodology – Linking Bio- and Geosciences

Electronic supplementary material The online version of this article (doi:10.1007/s10750-007-0632-7) and accessible for authorized users.

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Keywords Stygofauna · Pilbara · Groundwater · Hydrochemistry · Candoninae · Biogeography

Introduction

The Pilbara region in northwestern Australia is best known for its arid landscape and iron-ore industry. The expansion of mining operations to below the watertable poses several potential problems for the ecology of groundwater, including increased salinisation and contamination of aquifers as well as destruction of habitat. The scarcity of surface water resources in this semi-arid region has lead to groundwater being utilised for town water supplies, mining operations and watering of stock on pastoral leases. In consideration of the threats to groundwater-dwelling organisms, or stygofauna, posed by mining operations and the exploitation of groundwater, the Department of Conservation and Land Management (CALM) is undertaking a survey of stygofauna in the region to provide a framework for the assessment and conservation of groundwater biodiversity. Ostracods have been targeted as a key group for survey, owing to their diversity, abundance and preservation potential in bicarbonate-rich waters, as well as their known response to hydrochemistry (e.g. Forester, 1983, 1986; Radke et al., 2003).

Stygobitic Ostracods

Stygobitic fauna (sensu Gibert et al., 1994) are defined as animals that complete their entire life cycle within subterranean environments. Such animals are known to have slower metabolisms, longer ontogenies and subsequently longer life spans than their surface water counterparts (Culver, 1982). Groundwater-dwelling ostracods share some features that are known to be beneficial to subterranean life, referred to as troglomorphic characters by Christiansen (1962). They are blind, have un-pigmented valves and are comparatively small. Carapace shapes vary from highly elongated to triangular, even with dorsal protuberances (Danielopol & Hartmann, 1986). The majority of taxa within this study are stygobitic. Further studies in the Pilbara region will focus on stygophilic animals, those that live only part of their life in groundwater, such as in hyporheic and spring discharge sites.

Stygofaunal research in Western Australia began in the 1990s with a diverse and unique fauna being found that showed Tethyan affinities at Cape Range Peninsula (Humphreys, 1993a, b, c, 2000; Bradbury & Williams, 1996a; Danielopol et al., 2000; Jaume & Humphreys, 2001) and Barrow Island (Bradbury & Williams, 1996b; Humphreys 2000, 2001a), and Gondwanan affinities in the adjacent arid, cratonic parts of the Pilbara (Poore & Humphreys, 1998; Eberhard & Humphreys, unpublished; Humphreys, unpublished). The Yilgarn to the south (Humphreys, 1999, 2001b; Watts & Humphreys, 1999; De Laurentis et al., 2001) and the tropical Kimberley to the north (Wilson & Ponder, 1992) (Fig. 1) are also rich in stygofauna. Prior to the present study, 23 groundwater ostracod species, 20 candonids and 3 darwinulids, were known to occur in the Pilbara region, all of which were described only recently (Martens & Rossetti, 2002; Halse et al., 2002; Karanovic, 2003, 2005; Karanovic & Marmonier,

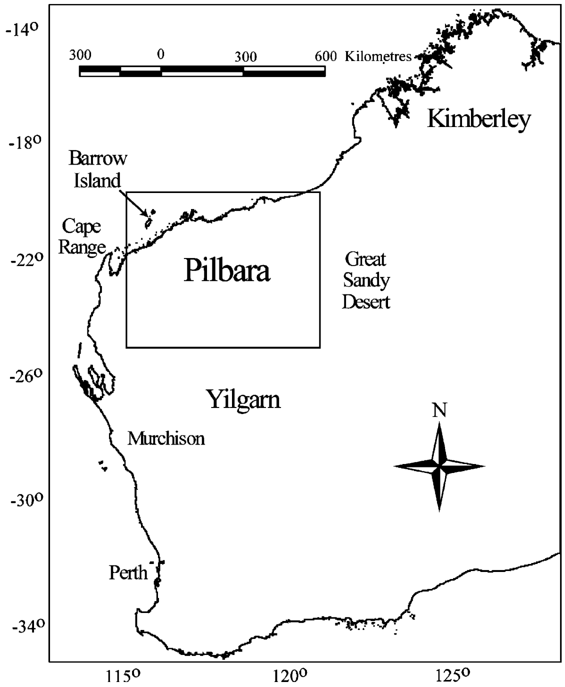

Fig. 1 Locality map of Western Australia. The area in the box represents the Pilbara region

2003). This compares well with the diversity of fauna in the adjacent Murchison (five species, one genus) and Cape Range (one species) regions (Danielopol et al., 2000; Karanovic & Marmonier, 2003).

The groundwater of the Pilbara region provides a refugium for aquatic invertebrates in this arid environment, with a high degree of subterranean biodiversity and endemicity (Humphreys, 1999, 2001, unpublished). The waters are typically rich in bicarbonate, and therefore ostracods are particularly well represented, because of the suitability of such waters for readily forming calcite valves. This study looks at the distribution of the ostracod species in relation to the physical constraints of the aquifers and the hydrochemistry in the Pilbara region.

Study area

The Pilbara region (20–24° S, 115–122° E) of northern Western Australia, covering ~200,000 km^2, is hot and dry. Although climatically regarded as semi-arid, with annual evaporation outweighing precipitation 10:1, the Pilbara is located at the tropical fringe. Seasonality is distinct with hot summers (25–36°C mean summer minimum and maximum) and mild winters (12–27°C mean winter minimum and maximum). Rainfall is erratic and localised, occurring predominantly in the summer months during thunderstorms and cyclonic events (averaging 200–350 mm annually, decreasing inland). Winter rainfall is sometimes significant, particularly in southern areas. There is little permanent surface water and all rivers are ephemeral; however, groundwater is plentiful and mostly fresh.

The region may be divided broadly into three physiographic types: low ranges, wide floodplains and a coastal zone (Fig. 2). The ranges form part of the Pilbara craton which has been emergent since the Palaeozoic. They comprise the Early Proterozoic—Archaean metasedimentary Hamersley Range in the central Pilbara, reaching around 900 m asl, with peaks around 1250 m asl, and the predominantly volcanic Chichester Range to the north, with a more subdued topography of around 600 m asl (Trendall, 1990). These units overlie the Archaean greenstones and granites, which outcrop to the northeast of the region. The regolith comprises a fine red blanket over much of the region, resulting in a very thin vadose zone. The Fortescue and

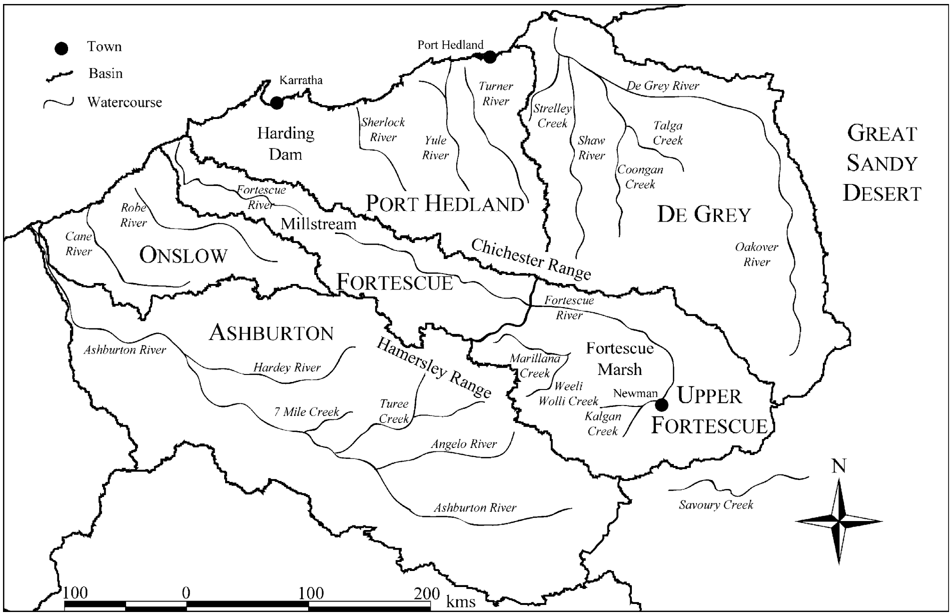

Fig. 2 Map of the Pilbara region, showing key localities within the study. The darker lines represent surface water drainage basins, the finer lines represent major drainage features

Ashburton Rivers form extensive floodplains, draining either side of the Hamersley Ranges. The Robe, Yule and De Grey Rivers extend as broad deltas from the highlands toward the Indian Ocean. Several other minor rivers also traverse this path. The coastal zone comprises broad, flat hummock and tussock grasslands, with scattered woodlands, on cracking clays or sandy soils. Minor Tertiary limestone outcrops occur across the plain.

The current drainage system of the Pilbara is thought to have developed through the Late Cretaceous—Early Tertiary (Beard, 1973, 1998). The calcretes, common to arid regions of Australia, formed from palaeochannels that dried up in the Palaeocene, when the climate switched from humid to arid (Bowler, 1976). Carbonate precipitation is active in the spring discharge regions, such as Millstream and Weeli Wolli.

There are three significant aquifer-types in the Pilbara region (Fig. 3): (1) unconsolidated sedimentary aquifers, including recent valley-fill alluvium and colluvium, and coastal deposits; (2) chemically-deposited calcretes and pisolites within Tertiary drainage channels; and (3) fractured-rock dolomite, banded-iron formations and granite, which form local aquifers (Johnson & Wright, 2001). The Wittenoom Dolomite forms an extensive aquifer, skirting the base of the Hamersley Ranges, commonly with cavernous karst development (Balleau, 1972). There is a noted relationship between the host rock aquifers and the resultant hydrochemistry. Groundwater in the region is typically fresh to low salinity (200–1500 mg l^{-1}) and bicarbonate-dominated, although Na–Cl-rich waters are common in both the coastal and arid eastern margins (Fig. 4). Isotopic analysis (δ^{18}O, δD) of a selection of groundwater samples taken along a transect from the coast to ~300 km inland reveals that the majority of recharge is resultant from cyclonic rains (to be presented elsewhere). There is also a component of seepage through the major waterways to the alluvial aquifers during peak flow times.

The major rivers, including the Ashburton, Fortescue and De Grey systems, all have their

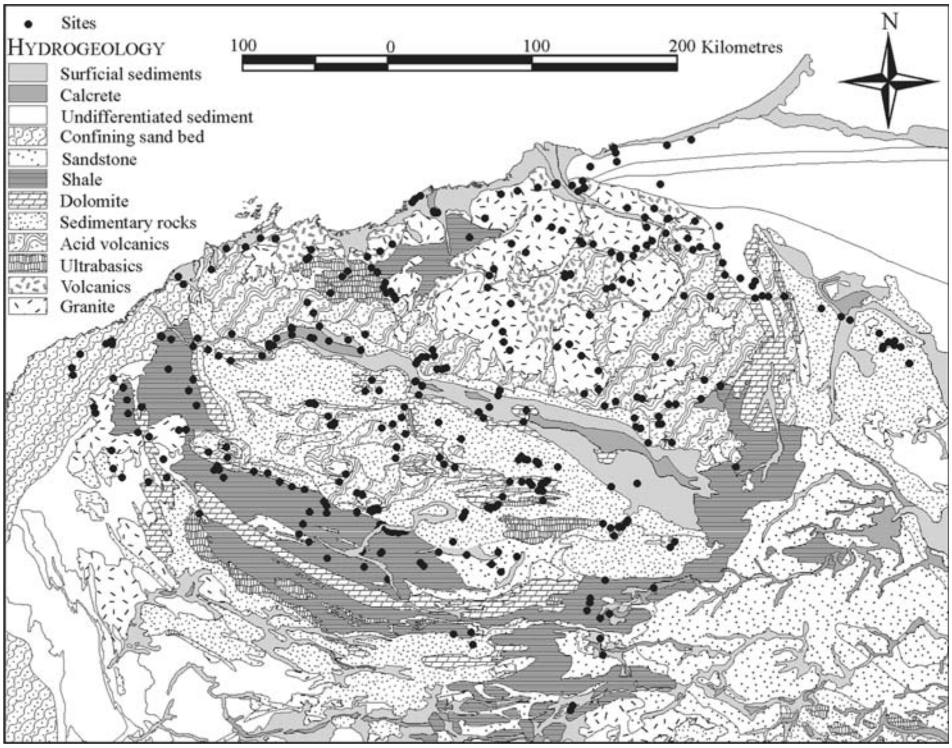

Fig. 3 Hydrogeological map of the Pilbara region, showing the sampling sites of this study (base map courtesy of WA WRC)

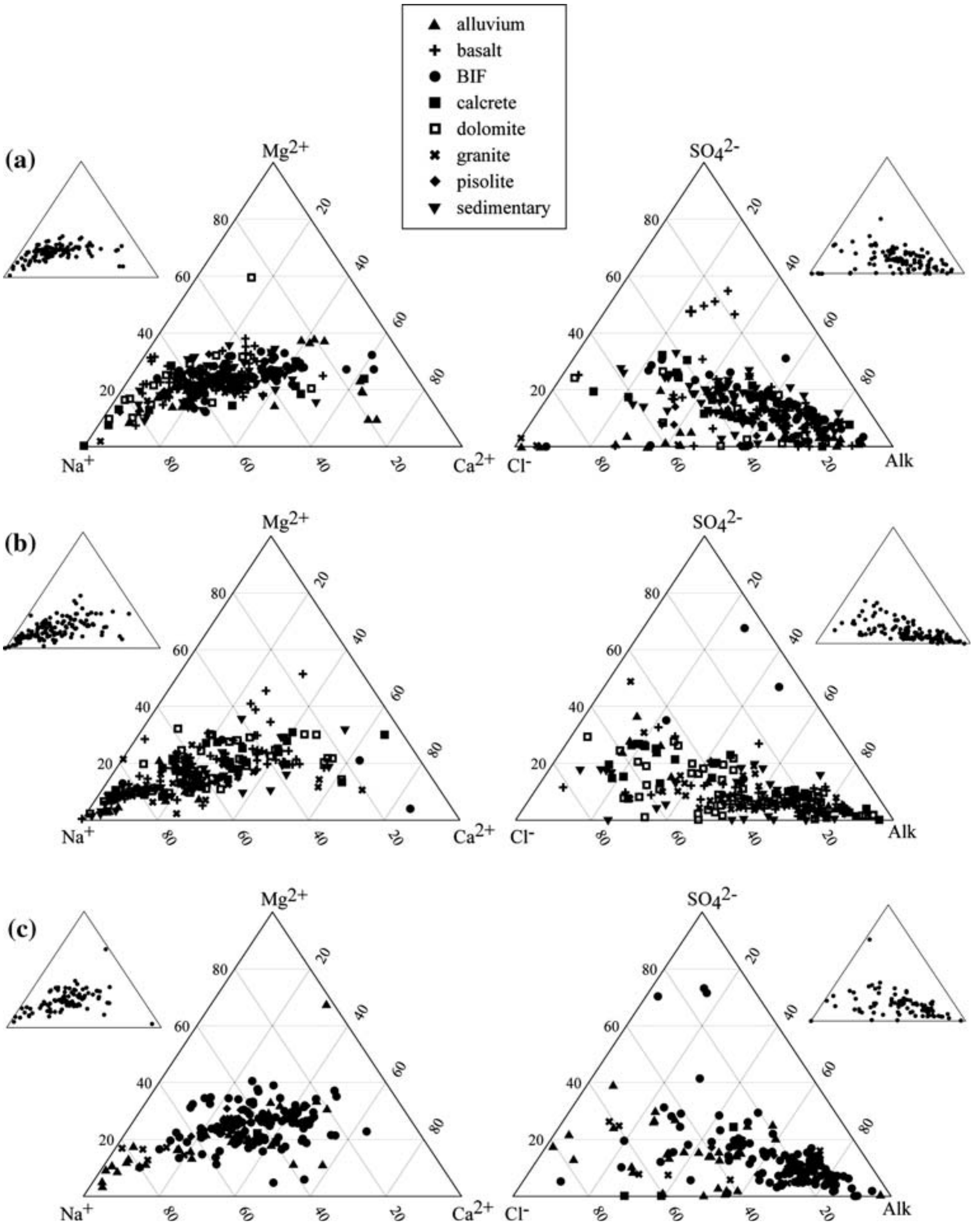

Fig. 4 Ternary plots for major cation (*left*) and anion (*right*) relative concentrations of the groundwaters from (**a**) the Fortescue, (**b**) Ashburton and Onslow and (**c**) De Grey, Port Hedland Coastal and Great Sandy Desert drainage basins. The symbols refer to the hydrogeology of the aquifers from which the samples were taken. The small, inset diagrams refer only to samples containing Ostracods

headwaters in the Proterozoic metasediments and Archaean granites of the Hamersley and Chichester Ranges. Surface waters are largely restricted to drainage lines, with river pools sustained by local bank storage or local water table. Springs are fed by local aquifers, particularly in the karstic areas. Yield from the aquifers is greatest in the calcrete Millstream region and in the Wittenoom Dolomite, producing up to 5,000 Gl/day (Johnson & Wright, 2001). The general direction of flow is from the headwaters in the ranges toward the coast.

There is a groundwater divide within the western Fortescue; the diversion of the lower

Fortescue away from the Robe River is a recent phenomenon, most likely since the Last Glacial Maximum (Barnett & Commander, 1985). Upstream of Mulga Downs, water flows toward the Fortescue Marsh (Barnett & Commander, 1985).

Sampling strategy

Sampling sites were selected to provide broad geographic coverage and to encompass the range of geologic, topographic, physiographic and hydrochemical environments across the Pilbara region. Shallow and deep aquifers were targeted; hyporheic and spring discharge sites were not included in this study. The majority of samples were taken from bores (85%), with the remainder from wells. The sampling area spans latitudes of 19–25° S and longitude of 115–122° E. Samples were taken from a range of altitudes, from the coast to 726 m asl, with a mean height of around 290 m asl. The bore construction differed between sites, in terms of diameter (50–400 mm), casing material (P.V.C or steel) and slotted interval, i.e. the depth along which the bore is open to the aquifer. Several sampled bores were from borefields; clusters of bores used for water extraction for mining and domestic purposes. Wells were all constructed from concrete or wood and between 700–2000 mm in diameter. Environmental attributes recorded for each site include latitude, longitude, altitude, bore/well construction details (including, where available, the depth and geology at the slotted interval), surface geology, vegetation, land-use, and impacts. The covering of the bore/well was also noted. Each bore/well was sampled once in late autumn–early winter (April–July, 2003–2004) and once in late winter–early spring (August–October, 2002–2004) to capture possible seasonal influences on species occurrence (extremely hot summers preclude field sampling at that time of year, with daily temperatures exceeding 40°C).

Materials and methods

Environmental and hydrochemical sampling

Standing water level (SWL, in metres below ground level) and the maximum depth of each bore were measured to the nearest 0.05 m with a Richter Electronic Depth Gauge or weighted Lufkin tape measure. Temperature, pH, Eh, electrical conductivity, dissolved oxygen and turbidity were measured at –1 m SWL using a calibrated Yeo-Kal 611 water quality analyser. Water samples for laboratory analysis (undertaken at Chemistry Centre, Perth, Western Australia) were collected from –1 m SWL using a sterile bailer (Clearwater PVC disposable 38 × 914 mm), and stored in sterile, acidified, 250 ml plastic bottles. One 250 ml water sample was filtered through a 0.45 μm membrane and frozen for analysis of nutrients (total soluble N, total soluble P). Highly turbid samples were pre-filtered though a glass-fibre filter using a hand vacuum pump (Millipore Sterifil Aseptic 47 mm OM041). A second 250 ml water sample was refrigerated for laboratory determination of solute concentrations (Na^+, Ca^{2+}, Mg^{2+}, K^+, Cl^-, HCO_3^-, CO_3^{2-}, SO_4^{2-}, NO_3^-, SiO_2, Fe^{2+}/Fe^{3+}, Mn^{2+}, Sr^{2+}), alkalinity, hardness, colour, turbidity, pH, and total dissolved solids. Laboratory methods followed APHA (1995). Saturation indices and activity coefficients were calculated using PHREEQC (Pankhurst & Appelo, 1999).

Stygofaunal sampling

Bores and wells were sampled for all stygofauna using a plankton net of suitable diameter (47 mm, 97 mm, 147 mm, or 197 mm) to match the bore/well diameter. The net, with a weighted McCartney vial attached, was lowered to the base of the bore/well, then agitated up and down (±1 m, 6 times) to disturb the bottom sediment. Six hauls of the entire water column were made, the first three hauls used a 150 μm net to capture macrofauna, the second three hauls used a 50 μm net to capture microfauna such as rotifers. To minimise loss of fauna through bow-wave effects during hauling, the McCartney vial had the bottom removed and replaced with 50 μm mesh. The entire net haul sample was transferred to a labelled 120 ml polycarbonate container and preserved in 100% ethanol. To maximise preservation for possible DNA analysis, the ethanol was replaced after a few hours by decanting the sample through a 50 μm net and refilling the sample bottle with fresh 100% ethanol. To eliminate the possibility of faunal contamination between sites, the nets were sterilised by washing in a decontaminant (5% solution of Decon 90), then rinsed in distilled water and air-dried.

Ostracod sorting and identification

Preliminary subdivision of fauna was undertaken at CALM's Woodvale laboratory. Prior to sorting, samples were first separated into three size fractions by sieving through 250, 90, and 53 μm Endicott sieves. Ostracods were separated under Leica MZ dissecting microscopes and sent to the senior author and Dr I. Karanovic for further description and counting. Data from both whole specimens with soft parts intact and valves alone were recorded, with the type of record and state of preservation noted. Identification to species level was undertaken using a Leitz binocular microscope. The distinction of new species was based on adult specimens, utilising where possible, soft part and carapace morphology.

Images of each taxon were obtained using a Wild M400 photomicroscope with digital imagery and Cambridge S260 Scanning Electron Microscope (SEM) at the ANU Electron Microscopy Unit. Examples of each new species have been sent to Dr I. Karanovic at the Western Australian Museum for full taxonomic description, to be presented in a forthcoming monograph, and deposition of voucher specimens within the museum's collection.

Statistical analysis

The relationship between ostracod species and ecological variables was investigated using canonical correspondence analysis (CCA) in CANOCO version 4.5 (ter Braak & Smilauer, 2002). Environmental variables that showed strong covariance were omitted from the analysis, leaving a total of fourteen parameters. Scaling was focussed on the inter-species distance, using the bi-plot scaling method and no transformations were made to the species data. Only the 209 samples without missing values were included in the analysis. Samples that had a very strong influence on the analysis and were recognised to be outliers in one or more environmental parameters were classed as supplementary. A total of 89 species, including 81 candonids and 8 *Gomphodella* species, and 1002 occurrences were incorporated into the analysis. The model was evaluated using the Monte-Carlo test with 499 permutations. The significance and the explanatory power of variance for each of the environmental variables were determined by manual forward selection of individual variables. Species abundance data were used in all analyses.

Results

Species composition and distribution

Thus far, 111 species of ostracods have been recovered from bores and wells, 73 of which are new species. Eighteen taxa are referred to here as ''cf'', thus reflecting a close affinity to an already described species, six have been assigned to genera, but not yet species and four are of undetermined genera. In most of these cases, representatives with well-preserved soft parts have not yet been recovered. Only 29 species have previously been described, 14 of these are known only from the Pilbara. The other 15 known species are not restricted to groundwater habitats and have a broader distribution. The distribution and number of occurrences of each of the candonid species recovered are tabulated in Electronic supplementary material.

In total, 56% sites of the 448 sites and 47% of the 751 samples contained ostracod fauna. Of the sites with fauna that were sampled more than once, 63% had fauna on all occasions, 18% only in the wet season and 19% only in the dry season. Many of the samples (60%) with only seasonal occurrence of ostracods had very few animals present, often with only a few valves. In samples with ostracods present on all occasions, the assemblage did not appreciably change between seasons, but in some cases there was a difference in abundance.

Species richness was usually very low (mean = 1.75), the majority of samples (55%) are comprised of only one species (Fig. 5a). Three

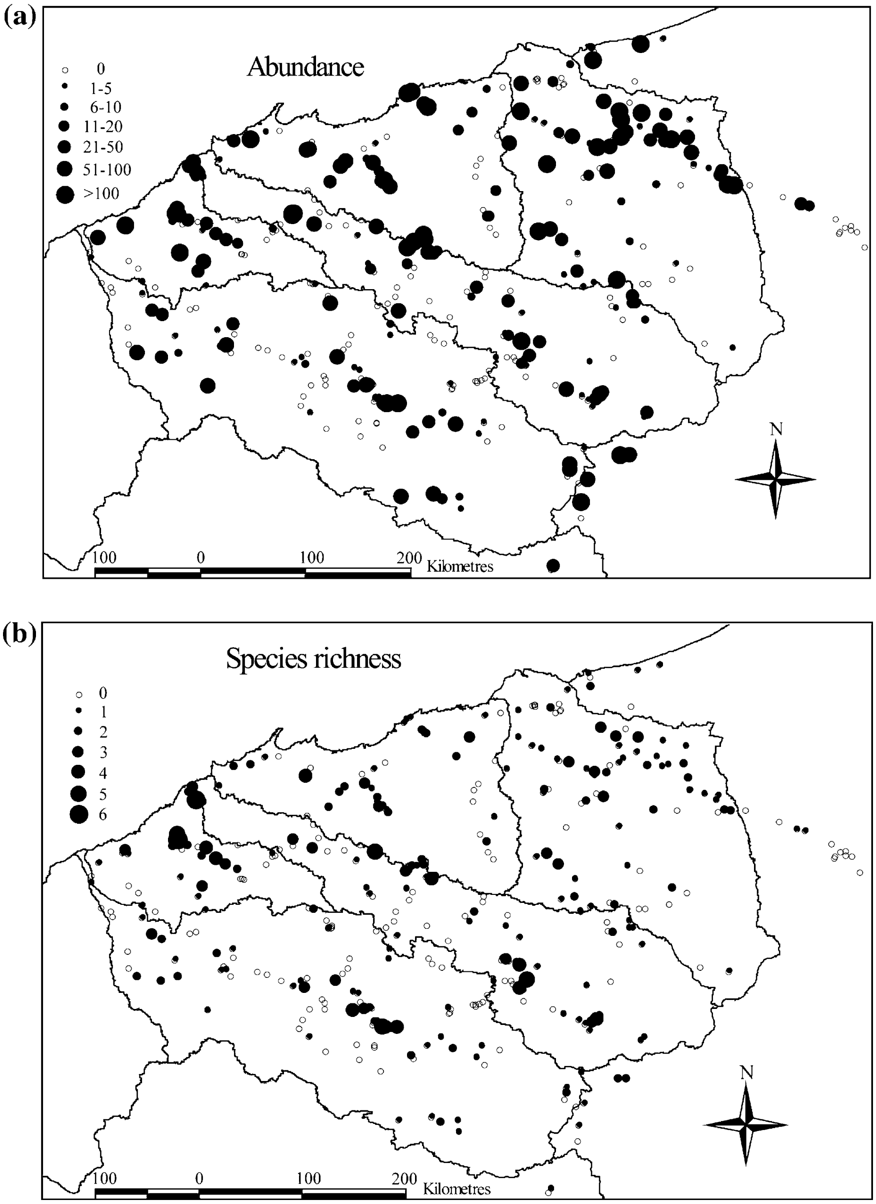

Fig. 5 Maps showing ostracod (**a**) abundances and (**b**) species richness across the Pilbara region. Open circles refer to sites with no recovered ostracods

samples had 6 species present; these were from the Robe River borefield and the Fortescue borefield. Other diverse sites were the Turee Creek and 7 Mile Creek borefields within the Ashburton basin, Weeli Wolli Creek and Marillana Creek in the upper Fortescue area, Cane River borefield in the Onslow basin, Tampathanna Pool, on the southern edge of the Chichester Ranges, and Harding Dam (see Fig. 2).

The abundance of ostracods was highly variable, with a mean number of 40 valves per sample (Fig. 5b), while 42% of samples were found to have less than 10 valves. The most abundant sites were dominated a single species of ostracod. Of the samples containing more than 100 individuals, six were from bore sites containing stygobitic species and four were well sites, with surface-water fauna. Most of the groundwater species

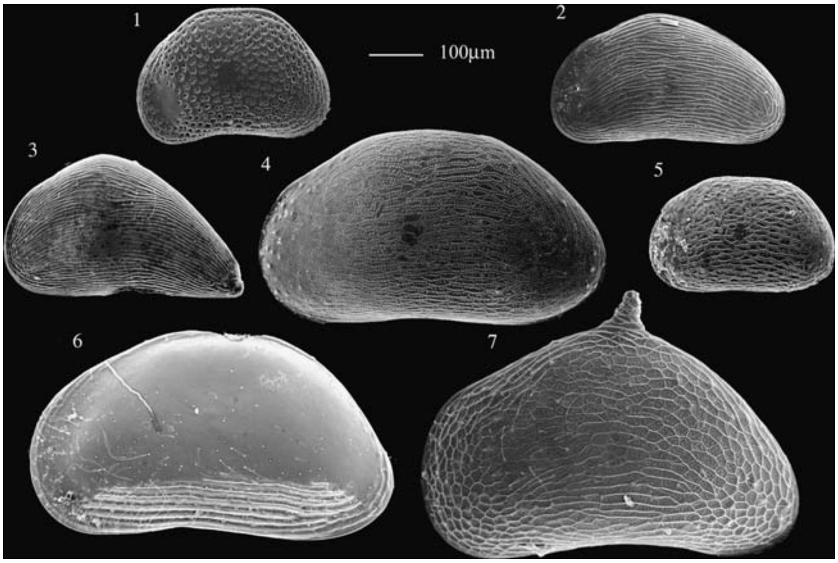

Fig. 6 SEM images of a selection of previously named stygobitic ostracod taxa from the Pilbara, identified in this study. All are left valves of adults; (**1**) *Candonopsis kimberleyi*, (**2**) *Notacandona modesta*, (**3**) *Pilbaracandona eberhardi*, (**4**) *Meridiescandona facies*, (**5**) *Meridiescandona lucerna* (**6**) *Humphreyscandona adorea*, (**7**) *Humphreyscandona fovea*

occurred in high abundance in localised areas, for example: *Humphreyscandona adorea* at Millstream, *Humphreyscandona woutersi* from the Robe River borefield, *Meridiescandona facies* from Marillana Creek and *Deminutiocandona* sp. 4 from the Cane River borefield.

The most broadly distributed fauna consists of surface-water taxa, most commonly found in samples from wells. Species such as *Cypretta seurati* were found in large numbers in such sites from each of the basins. The groundwater fauna was largely restricted to single drainage basins, and in many cases, aquifers. Forty-nine species were recorded from single sites; however, nine of these have been described previously from elsewhere.

By far, the most abundant group was the Candonidae. These included 64 new species and a further 15 that have been described before. Examples of previously described fauna also found in this study are presented in Fig. 6. The Pilbara candonids have been separated into 12 genera, four of which are considered to be new (I. Karanovic, in prep). All genera are represented by a number of species; *Areacandona* and *Deminutiocandona* are the most speciose, having 25 and 10 identified species respectively. Most of these genera are considered endemic to the Pilbara region, with only two species of *Candonopsis* having been previously recorded elsewhere. These include *C. tenuis*, which was described from eastern Australia (Brady, 1886; Sars, 1896) and *C. kimberleyi* (Karanovic & Marmonier, 2002), which was identified from the subterranean waters of the Kimberley region to the north of the Pilbara. All species identified in previous studies in the Pilbara were again collected in this study, with the exceptions of *Humphreyscandona pilbarae* (Karanovic & Marmonier, 2003), *Neocandona novitas*, *N. newmani*, *Areacandona arteria*, *A. mulgae* and *Origocandona gratia* (Karanovic, 2005). The bores from which these species were described were not re-sampled in the present study.

The groundwater ostracod fauna show clear distributional patterns, associated primarily with the extent of the surface water catchment or the aquifer (Fig. 7). Although there are a large number of *Areacandona* species, most were found within the low-lying coastal areas and alluvial aquifers of the Port Hedland, Robe and lower Fortescue basins. One species (*A.* sp. 25), considered to belong to the genus, occurs only to the east of the Oakover River, in the Great Sandy Desert. This is contrast to the previously known

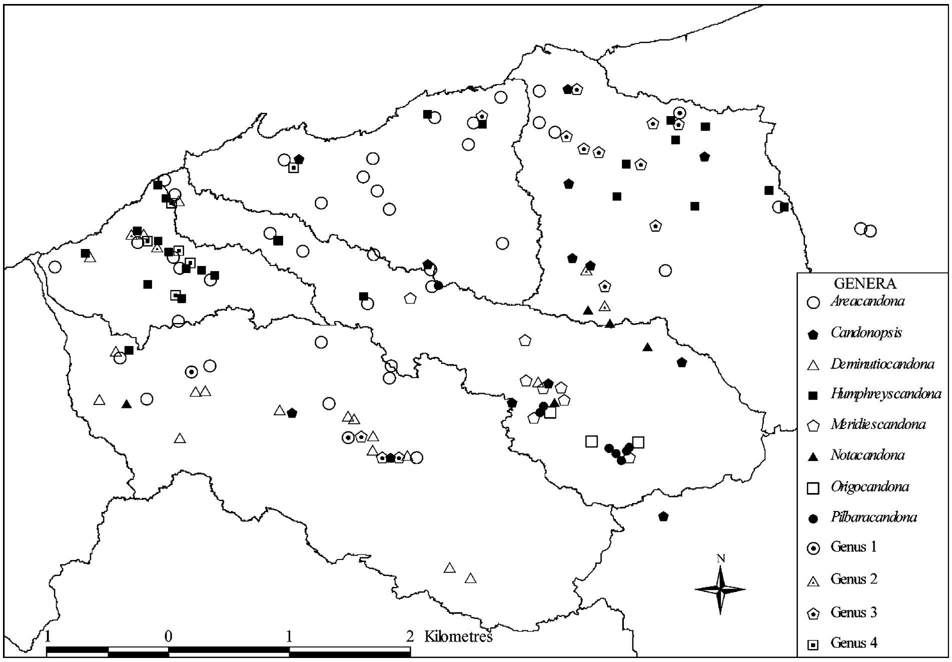

Fig. 7 Map showing the distribution of the genera of Candonidae across the Pilbara region

examples of the genus, *A. mulgae* and *A. arteria*, which were described from the Mulga Downs site in the central Fortescue (Karanovic, 2005). Each species of *Areacandona* occurred over a relatively small area, associated with one or two surface sub-catchments of tributaries flowing into the major rivers. Many species were restricted to single localities. More than one species of *Areacandona* was identified from several well sites. Most species of the genus have smooth, oblong valves, with rounded margins.

Humphreyscandona was associated mainly with the lower Fortescue and Robe River catchments, with each species being geographically distinct. The exceptions were *H.* sp. 2, which occurs in the De Grey/Oakover system and *H.* sp. 1 found around the upper Robe and Cane River region. These distributions were generally consistent with the known extent of the genus (Karanovic & Marmonier, 2003; Karanovic, 2005). *H. waldockae*, which was previously described from Mulga Downs, has now also been found near Port Hedland. Most of these species are comparatively large and well calcified, commonly with ridged or reticulated ornamentation of the valves concentrated around the periphery.

In contrast, *Deminutiocandona* was best represented both in diversity and abundance, in the Ashburton basin, with some species restricted to the Cane River borefield or Robe River borefield of the Onslow basin. Again, individual species showed narrow geographical distributions. Only one species, *D. mica*, has previously been described from the Weeli Wolli area (Karanovic, 2003). This species has been recovered from only one site in this study, and no other species of this genus have been found in Fortescue upland areas.

The unnamed candonid Genus 1, currently comprising two species, has a disparate distribution. Characteristically, species of this genus include valves that are rounded anteriorly and pointed posteriorly with an arched dorsum. The first species, with a heavily ridged carapace, was found in abundance in Eel Ck region of the De Grey basin. The second species, with smooth valves, was recovered from two bore sites in Ashburton basin.

A second unnamed candonid (Genus 2) is also broadly spread, although individual species occur in restricted regions. The genus is characterised by very small, smooth, oblong valves. Two species have been identified; one from the Robe borefield and a second from the upper Shaw River in the De Grey Basin. A third species, thought to belong to the genus, has been identified from a number of sites in the Harding Dam regions, although specimens with soft parts have not yet been recovered to confirm this.

The third open genus (Genus 3) is found largely in the De Grey Basin, from where six species have been differentiated, and a further species from the adjacent Port Hedland region. Species within the genus are characteristically small, with smooth carapaces, clearly differentiated from the other genera on the basis of soft part morphology. Most of the species are restricted to single localities or close regions, however valves of one species (Genus 3 sp. 1) have been located in the Turee Creek region of the Ashburton Basin, more than 200 km from the type locality in the headwaters of the Coongan River. Soft parts of these specimens have not been recovered to confirm identification.

Two species have been tentatively placed in the new candonid Genus 4, their taxonomic affinities are yet to be finalised. They both have smooth valves, tapered anteriorly, and are restricted to the lower Fortescue—Robe River systems.

There was a marked distinction within the Fortescue system between the fauna of the low-lying areas and those of the uplands of the Hamersley Ranges with almost no genera in common. *Meridiescandona* are dominant in the Marillana Creek—Weeli Wolli region, from where the genus was first described (Karanovic, 2003). All upland *Meridiescandona* species were comparatively large and had highly ornamented valves. Two species occurred in the central Fortescue region but these have smooth carapaces.

Pilbaracandona, with clearly ridged valves, also occurs in the uplands, concentrated around the Newman region. This region is particularly diverse, with four species identified. Two species of the genus *Origocandona* were previously described from the Newman region (Karanovic, 2005), only one of which, *O. inanitas*, was collected during this study. In addition, a new species from Kalgan Creek and Weeli Wolli Creek has been identified.

The genus *Notocandona* also showed disparate distribution, with representatives in the uplands

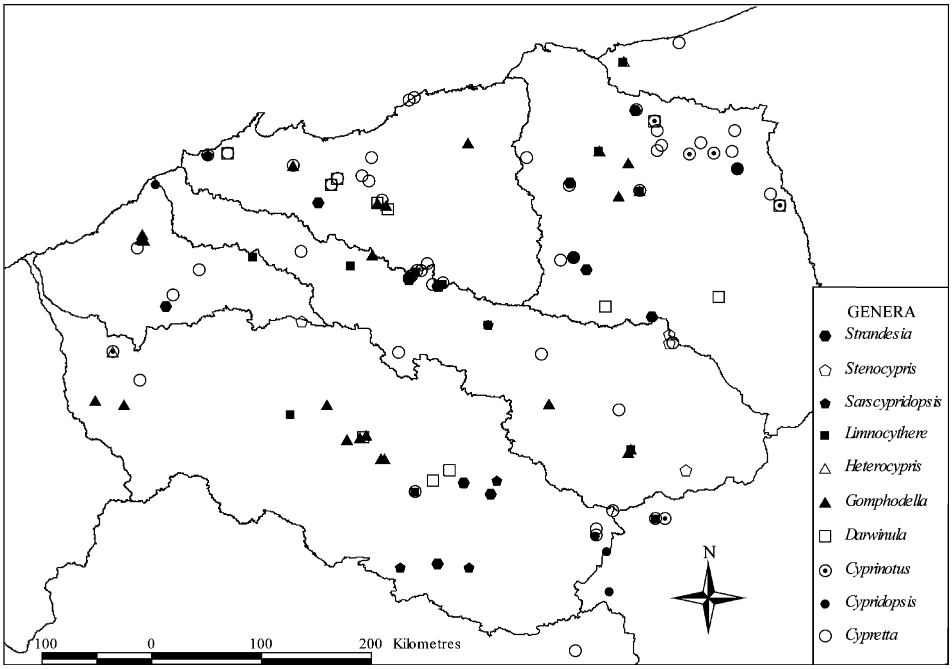

Fig. 8 Map showing the distribution of the genera of non-Candonidae taxa across the Pilbara region

of the Weeli Wolli region, the lower Ashburton, and north of the Chichester Range in the southern De Grey basin, with species unique to each region. Both *Notcandona boultoni* and *N. modesta* have been identified from their type locality, near Weeli Wolli Creek. As for other genera, the species from the upland Weeli Wolli sites have the highest degree of ornamentation, with well-developed ridges across the entire carapace.

Apart from the stygobitic Candonidae, several other stygoxene (sensu Gibert et al., 1994) taxa were recovered. The genus, *Gomphodella*, which is commonly found in springs, thus would best be referred to as crenophilic, was well represented with eight species. Most of the *Gomphodella* species were restricted to the Pilbara region, with several species found at only one locality (Fig. 8). The Ashburton basin was particularly well represented, with five species, each restricted to a separate sub-catchment. The Port Hedland basin had two species, also very localised. The species *Gomphodella hirsuta*, originally described from the Newman borefield (Karanovic, in press), showed a broader distribution, and has now also been identified from the Robe borefield, and two sites in the De Grey basin.

Darwinulids have been found at numerous localities, although have presently not been identified. Three species of Darwinulidae: *Penthesilenula brasilensis, Vestalenula matildae* and *Vestalenula marmonieri* have previously been described from Cape Range and the Pilbara region (Halse et al., 2002; Martens & Rosetti, 2002). In the present study, darwinulids were found in the Port Hedland, De Grey and Ashburton basins, mostly from well sites. There was no clear pattern to their distribution.

Several Cyprididae were found, particularly in the samples taken from uncovered wells, where epigean fauna may have colonised via passive dispersal (Fig. 8). These included *Cypretta* sp., *Cyprinotus kimberleyi*, *C. edwardi*, *Heterocypris kimberleyi*, *Strandesia kimberleyi* and three other unnamed species, *Stenocypris bolieki*, some fragments of *Bennelongia* sp., *Cypridopsis vidua*, *Sarscypridopsis ochracea* and *Limnocythere* sp.. These species showed no clear geographic distribution, and have previously been described from outside the Pilbara region, many in the Kimberley to the north (McKenzie, 1966). Valves of mixed marine origin, including *Xestoleberis*, *Paranesidea*, *Australimoosella* and *Paracytheroma*, were recovered from two coastal sites from within porous aquifers, indicating influence of the proximal seawater. These genera are common in the nearby marine waters (Hartmann, 1978). As these taxa were not the primary concern of this study, they are not considered further here.

Most groundwater species occurred primarily in isolation, as observed by the poor diversity in most sites, but a few associations were noted. These include: *Deminutiocandona* sp. 2, *D*. sp. 9 and *Candonopsis* sp. 2 from the Turee Creek borefield; *D*. sp. 1 and *Humphreyscandona woutersi*, with *Areacandona* sp. 2 also common from the Robe River borefield; and *H*. sp. 2 with either candonid Genus 1 sp. 1 in the Oakover system or *Areacandona* sp. 25 in the Great Sandy Desert. At this stage, it would be premature to assign sympatry to these assemblages and further sampling is required.

In many of the samples from bores sites, in particular, the recovered ostracods were poorly preserved, with soft parts missing. This may be a result of the sampling technique, or an indication that the ostracods were not actually living in the boreholes. For most species, a biocoenosis assemblage was recovered from only one site, or from several boreholes in close proximity. Other sites comprised few well-preserved individuals, empty or disarticulated valves. Species that were dominant in the well sites, such as *Cypretta* sp., *Stenocypris bolieki* and *Cyprinotus kimberleyensis*, were recovered as well preserved, life assemblages from many sites.

Physico-chemistry of the waters

A summary of the data collected from the sites, with and without ostracods, is presented in Electronic Supplementary Material—Appendix 2. The basal depth of bores and wells varied from 3–160 m and depth to groundwater varied from 0–88 m, increasing inland. Coastal and alluvial sites were generally less than 10 m SWL, whereas those on the Hamersley Range exceeded 20 m. Water temperature ranged from 17.3–35.5°C, with a mean of 29.6°C. The highest temperatures were recorded from the lower De Grey River, in the northeast corner of the study area. Temperature variations of up to 5°C were noted between seasons in some of the shallower sites. Turbidity was mostly low, with a mean of less than 6 NTU. Isolated sites with high turbidity were mostly wells in the lower Ashburton. High levels of total nitrogen and phosphorus were also recorded from these sites. Dissolved oxygen (DO) measurements were taken for all sites at the time of sampling. However, several sites selected for profiling of water chemistry were shown to have highly variable values of DO down the core. In some cases changed DO related to a halocline but in others there was no obvious explanation. Routinely collected DO values did not reflect whole of bore conditions reliably and were not used in analyses. Eh values mostly indicated oxidising conditions (mean = 334 mV, ranges = –558–837 mV). Exceptions to this were isolated wells within the lower Ashburton and De Grey basins.

The chemistry of groundwaters of the Pilbara is, at a first glance, relatively predictable (Fig. 4). However, host rock and the aquifer-type primarily determine the composition of the water, and chemical patterns were identified both between and within basins. Most drainage basins showed a clear gradation from characteristically hard, Mg–Ca–Alk-rich headwaters to more Na–Cl dominated lowland water. This was coincident with the change from banded-iron formations (BIF), granite and basaltic fractured rock aquifers in the uplands to the sedimentary and alluvial valley-fill aquifers downstream. Intermediary waters of the Na–Mg–HCO_3-type were also common, particularly in coastal and alluvial sites.

Salinity in Pilbara groundwaters is mostly low, with mean total dissolved solids (TDS) below 1 g l^{-1}, increasing toward the coast. The highest values were recorded at Fortescue Marsh and the remote inland areas of the De Grey basin, both with salinity in excess of 10 g l^{-1}. Some sites within alluvial systems also had increased salinity (~1.5–2 g l^{-1}), reflecting recharge by seepage of evaporated river waters. The freshest waters were recovered from the deeper waters of the fractured rock aquifers. In most cases, there was no appreciable seasonal difference in salinity, although some of the shallow, alluvial sites showed decreased salinity of up to 0.5 g l^{-1} in the wet season. Salinity was found to be generally higher in well sites (mean 1.2 g l^{-1}, range 0.2–5.2 g l^{-1}) than bores (mean 0.9 g l^{-1}, range 0.04–13 g l^{-1}).

Alkalinity varied across the Pilbara, according to the aquifer host-rock. Mean total alkalinity was 284 mg l^{-1}, with a range of 5–3180 mg l^{-1} and the highest values were recorded in the lower Ashburton and the upper De Grey basins, associated with the coastal plain and fractured Proterozoic volcanics, respectively. The lowest values were in the central Fortescue, the Millstream region and in some of the coastal sites, away from areas of active carbonate precipitation.

Carbonate saturation showed a similar distribution to alkalinity, with waters supersaturated with respect to both calcite and dolomite near the upper De Grey and Oakover Rivers, Hooley Creek, around Newman, the Angelo River, the lower Robe and western Port Hedland coastal basin. Undersaturated areas included the upper Robe, the mid-Fortescue and De Grey coastal basins, from where ostracod valves were only rarely recovered.

Chlorinity was highly variable throughout the Pilbara, ranging from 0.2–175 meq L^{-1}, with a mean of 8.8 meq L^{-1}. The pattern of chlorinity across the region was predictable, being highest near the coast and in the alluvial deposits of the mid Fortescue and the lower Ashburton. Wells in the arid inland parts of the upper De Grey, Great Sandy Desert and Ashburton basins also had high chlorinity, probably because of evaporative enrichment. Lowest values were recorded from the upper Fortescue catchments of Weeli Wolli and Marillana Creek.

Most of the Pilbara waters are considered hard to very hard; mean 424 mg l^{-1} and range of 10–6400 mg l^{-1}. There is notable variation in Mg/Ca ratio across the Pilbara; Ca^{2+} dominates waters in the calcrete areas of the De Grey and upper Ashburton basins, whereas Mg^{2+} dominates those in the dolomite-rich parts of the Fortescue, such as Millstream and Weeli Wolli.

With respect to pH, the majority of sites sampled were circum-neutral to moderately alkaline. An exception is the Marillana Creek catchment, where pH as low as 4.4 was recorded.

Oxidation of pyritic shale has been noted in some of the mining lease areas, resulting in acidic, sulphate-rich groundwaters (Johnson & Wright, 2001; Woodward-Clyde, unpublished). Surprisingly, ostracods were identified from these sites, with *Meridiescandona facies* being recovered in large numbers.

Ostracod distribution and water chemistry

The presence of ostracods in Pilbara bores and wells was predominantly determined by the pH ($P < 0.001$) and the carbonate saturation ($P = 0.001$) of the host waters (see Electronic supplementary material for other parameters). Samples with pH below 6 and with Eh values indicating reducing environments or total nitrogen concentrations in excess of 10 mg l^{-1}, rarely contained ostracods.

Among the samples with ostracods, there was a clear distinction between sites with surface water fauna, such as cypridids dominating well sites, and those with a candonid fauna dominant in most bore sites. There was also a significant secondary relationship with salinity and solute composition, with surface water species preferring the more saline waters of higher chlorinity, although the distribution of surface versus groundwater fauna was somewhat distorted by the sampling method, as most samples from the Great Sandy Desert, Oakover River and other remote areas were taken from wells, leading to a larger proportion of surface-water species being present.

The relationship between ostracod species distribution and environmental variables is explored through CCA analysis for samples with only stygobitic ostracods present (Fig. 9). The results of the analysis, incorporating 10 variables, are summarised in Tables 1 and 2. Both the first axis and the model are significant at the 99% level ($P < 0.01$). The first four axes of the CCA combined explained only 5.6% of the variance in species composition, but 54.3% of the variance in species–environment relations. This low explanatory power is due to the very large number of zeroes in the data set, with many species occurring at only one site.

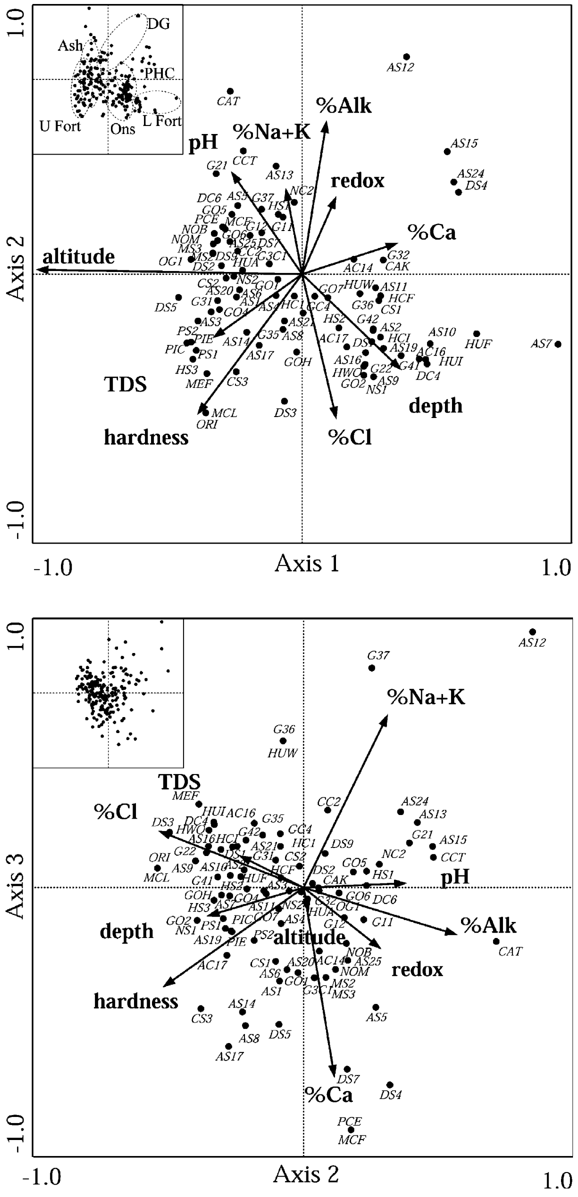

Fig. 9 CCA species–environment biplots for (**a**) axes 1&2 and (**b**) axes 2&3. *Arrows* and *heavy font* refer to environmental variables, species codes, as in Electronic Supplementary Material Appendix Table 3, are in italics. The small inset plots refer to the ordination of samples. See Table 1 for results of the CCA and text for further details. The codes for the surface water basin are Ash—Ashburton, DG—De Grey, PHC—Port Hedland Coastal, L Fort—Lower Fortescue, U Fort—Upper Fortescue

Correlation coefficients for each of the environmental variables incorporated into the CCA with the resulting first four axes are tabulated in Electronic supplementary material. Altitude (–0.95 correlation) was the by far the dominant

Table 1 Percentage of variance explained and significance of each of the environmental variables used in the CCA

Variable	Variance	*P*-value	*F*-value
Altitude	0.91	0.002	3.53
%Na + K	0.65	0.002	2.53
%Alk	0.67	0.002	2.62
%Ca	0.55	0.006	2.13
Hardness	0.55	0.002	2.17
Depth	0.53	0.004	2.12
TDS	0.50	0.002	2.03
%Cl	0.44	0.008	1.79
pH	0.42	0.002	1.72
Eh	0.42	0.002	1.69
Sum	5.64		

environmental factor determining the first axis. Depth to water (0.35) gave a notable positive correlation, which is related primarily to proximity to coast and altitude. Ostracods of the Fortescue system were classified into three main categories; (1) a lowland group, incorporating the coastal and lower floodplain taxa (*Areacandona, Humphreyscandona*), (2) an upland group (*Pilbaracandona*, *Origocandona, Meridiescandona*), focussed around the upper Fortescue and (3) an intermediary group. Very few genera were shared between the upland and lowland groups. Taxa from the midland areas show confluence at generic level but species are restricted to middle elevations. Coincident with changes in altitude are changes in temperature, depth to water and salinity. In addition, aquifer lithology differs from metasedimentary and volcanic rocks in the uplands to predominantly soft sediment, alluvial floodplain and coastal deposits in lowlands.

Position on the second CCA axis was determined by the relative concentrations of alkalinity (0.51) and chloride (–0.48), with hardness also significant (–0.46). This describes a solute evolution, from HCO_3^- rich waters, such as in the dolomite aquifers of the uplands and the spring discharge sites, to Cl^- being the dominant anion in the coastal and central floodplain deposits, where groundwaters are shallow and recharged in part by evaporated stream water. Perhaps associated with a clear relationship between solute evolution and an increasing proportion of surface water species, the stygofaunal ostracod species occurring in Cl^- rich water, such as *Candonopsis* and *Areacandona*, usually have smooth and more poorly calcified valves, indicating a bicarbonate-limited environment. In contrast, those in waters with higher relative bicarbonate, such as *Meridiescandona* and *Notacandona*, have more robust and ornate valves (see Fig. 6 for examples).

The third axis reflected the cations, determined by the relative concentration of $Na^+ + K^+$ (0.54) and Ca^{2+} (–0.59), which is closely related to host-rock lithology, as well as solute evolution. Sites with Ca^{2+}–Mg^{2+}-rich waters in the Newman and Ethel Gorge area, and in calcretes of the upper Ashburton and De Grey basins contained taxa such as *Pilbaracandona* that have large, heavily-ridged valves compared to the small, smooth valves of *Deminutiocandona* and Genus 3 in the more Na^+-dominated waters of the lower De Grey and Ashburton basins. Even the species of *Areacandona* and *Humphreyscandona* that were found in hard waters have heavily calcified valves.

Other significant environmental factors included Eh and pH. Although pH was relatively uniform across the Pilbara, rare sites had low pH (<5) associated with oxidation of pyrite. Only a few taxa, such as *M. facies* and one population of *A.* sp. 12, were found at these sites, although soft parts were not preserved. Eh was shown to be

Table 2 Summary of the results of the CCA performed on 209 active samples and 89 active species (see text for further details)

Axes	1	2	3	4	Total inertia
Eigenvalues	0.930	0.794	0.686	0.628	
Species–environment correlations	0.973	0.900	0.842	0.821	
Cumulative percentage variance					
Of species data	1.7	3.2	4.4	5.6	
Of species–environment relation	16.5	30.6	42.9	53.9	
Sum of all eigenvalues					54.278
Sum of all canonical eigenvalues					5.636

quite variable across the region, with ostracods preferring the oxidised sites. There is no clear relationship between species traits and redox potential, although sites in the lower Robe and De Grey Rivers registered a low Eh.

Discussion

Sampling methods

Preliminary sampling by Halse et al. (2002) of a series of five spring sites in the Pilbara revealed a stygophilic ostracod fauna. These species have been found to not be representative of those recovered from the deeper aquifer itself, contrary to the findings of Gibert et al. (1994). Of the four species identified, *Candonopsis tenuis* and *Limnocythere dorsosicula* have been described from sites across Australia and *Vestalenula marmonieri* from New Caledonia. Only *V. matildae* is thus far considered endemic to the Pilbara (Martens & Rosetti, 2002). Such species have been found in the current sampling program in wells but not bores. *Humphreyscandona adorea* is the only named species currently known from in the hyporheic zone and at depth (S.A. Halse, unpublished data). The hydrochemistry of the groundwater samples is significantly different to that of springs; where the average pH measured was 8.2, conductivity 1700 $\mu S\ cm^{-1}$, and dissolved oxygen in excess of 100%.

The validity of sampling from bores as representatives of aquifers has been questioned, due to potentially increasing DO and dissolved organic carbon, introducing metals to the system via bore casings and permitting mixing of both fauna and water types (Humphreys, 2001b). Although this cannot be categorically ruled out, it is most likely the abundance rather than the diversity of taxa present that would be affected, as supported by this study. There was no observable correlation between bore type and presence, abundance or diversity of ostracod fauna.

The sampling efficiency of the net haul method versus pumping was evaluated in five bores. Sampling by the net haul method collected 34% of the abundance (mean summed proportions for 5 bores) of what was collected by the pumping method (S. Eberhard, pers. commun.). Sampling in subsequent seasons showed variation in the abundance of fauna present in alluvial aquifers, but the taxa present were not greatly altered. This may be in part due to sampling discrepancies between seasons; however, the sites in the alluvial aquifers particularly, are subject to disturbance via scouring of the streambeds during peak flow times during monsoonal and cyclonic rainfall (Davies, 1996; Marmonier et al., 2000).

Pilbara species diversity

Prior to this study, there were published records of 332 species of all stygofaunal taxa from the Pilbara, the majority in the Fortescue basin (Eberhard et al., in press). Fifteen of the seventeen major taxonomic groups of stygofauna have been found in the Pilbara. Even in the preliminary studies, ostracods were particularly well represented, comprising 12.7% of all groundwater taxa, compared with around 3% worldwide (Eberhard et al., in press). The results of this study suggest ostracods represent about 30% of all stygofaunal species in the Pilbara but it should be recognised that ostracods have received more comprehensive examination than many other groups.

High degrees of endemicity are common in groundwater faunal distributions (Gibert et al., 1994). By mid-2004, the PASCALIS (Protocols for the Assessment and Conservation of Aquatic Life in the Subsurface) group had 1239 species of all stygobitic taxa from 11,000 distribution records in France, Italy, Belgium, Slovenia, Spain and the Canary Islands combined (Gibert, 2004). The Pilbara fauna, with more than 70 species of stygobitic ostracods alone, supports the notion of this region being a subterranean biodiversity "hot spot". Szczechura (1980) attributed the genetic isolation of ostracods, and subsequent speciation, to the ability of the group to prosper in a wide range of habitats and withstand or respond to environmental change.

Most previous investigation in the Pilbara was concentrated on groundwater primarily in calcrete deposits (Humphreys, 2001b). However, the alluvial aquifers of the Pilbara are some of the most extensive and contain abundant supplies of freshwater. Alluvial aquifers in Europe, such as in the Rhône, are known to be some of the most abundant and diverse habitats for stygofauna (Marmonier et al., 1993; Rouch & Danielopol, 1997) and also yield well in the Pilbara (Eberhard et al., 2004, in press). Fractured rock aquifers in the Pilbara have previously attracted almost no attention, but have been shown to host ostracods, and other stygofauna (Eberhard et al., 2004).

The regional groundwater ostracod fauna in the Pilbara is extremely large for the size of the region, despite individual sites usually yielding few species. Surrounding regions, such as the Kimberley (Humphreys 1999; Karanovic & Marmonier, 2002) and Murchison (Karanovic & Marmonier, 2002) have not been studied as intensively but clearly have much smaller faunas. Interestingly, there is far greater diversity among stygofaunal ostracods in the Pilbara than among their surface water counterparts (S.A. Halse unpublished data). This has previously been noted only for the stygobitic harpacticoid fauna of Brazil (Rouch & Danielopol, 1997).

Ostracod species distribution

As with most groundwater faunas, distributions in the Pilbara are usually restricted (see Strayer, 1994). Perhaps as a result of the localised distributions and discontinuity of many of the aquifers, particularly in the patchy calcrete regions, many species were collected at only one site. However, a high proportion of singletons are also a feature of surface water studies in Western Australia (Halse et al. 2000; Pinder et al. 2004), suggesting there may be a more general explanation than the nature of groundwater distributions.

Of the truly stygobitic ostracod fauna, no species are shared with the adjacent regions. Furthermore, no Tethys-associated ostracods have been recorded from the Pilbara, unlike within the Tertiary limestones on Cape Range (Danielopol et al., 2000). This region has water of marine origin intersecting with fresh groundwater, forming anchialine systems and was inundated with marine water during the Cainozoic (BMR, 1990).

All stygobitic species in the Pilbara are from freshwater lineages and have Gondwanan affinities (i.e. Candonidae, Darwinulidae). The Candonidae in particular, with their lack of pigmentation, blindness and exaggerated limbs, are considered to have been long adapted to subterranean life. In a climate as arid as Australia's, groundwater provides one of the few permanent freshwater environments suitable for the candonids. In fact, the only known epigean candonids, other than *Candonopsis*, found in Australia from either modern or fossil deposits, are from two dolomitic groundwater-fed swamp sites in Tasmania (De Deckker, 1982). Even *Candonopsis* has been located predominantly in temporary pools, which may also be groundwater fed. In the Pilbara, speciation of the ostracod fauna most likely occurred subsequent to the termination of large surficial conduits during the late Tertiary (van de Graaff et al., 1977), resulting in geographic isolation of fauna within the aquifers. The calcretes that were the focus of the early studies formed in the late Tertiary along the palaeodrainage channels (Bowler, 1976).

Biogeography

There is clear sub-regional differentiation in ostracod fauna, determined primarily by altitude, then surface drainage basin, then aquifer. Altitude does not only reflect height above sea-level, it also affects many secondary factors, such as depth to water, temperature, host-rock chemistry and aquifer type, which may all have an effect on the divergent morphology and taxonomy of ostracods.

The three broad stygofaunal groupings suggested by Humphreys (unpublished) were supported in this study within the Fortescue system: a lowlands group, dominated by *Areacandona* and *Humphreyscandona*, an uplands group comprising *Meridiescandona*, *Notocandona* and *Pilbaracandona*, and an intermediary group. The intermediate group of fauna, centred on the drainage divide between the upper and lower Fortescue, is not as well established in this study because many of the taxa found previously in the Mulga Downs region were not recovered. However, a small suite of ostracods, including species of *Meridiescandona* and *Areacandona*, were found restricted to this central Fortescue region.

There are also shared fauna between lower Fortescue and lower Robe catchments, which reflect the previous course of the Fortescue River that shifted only during the Late Pleistocene. The upper De Grey and Ashburton basins both comprise distinct fauna, each dominated by one genus.

Morphological response to environment

Although belonging to different genera, species can show similarities in morphology in the same or adjacent sites, most likely in response to the ecological/environmental variables. This convergent morphology is in support of Danielopol et al. (1994) who realised common traits in unrelated species from similar environments, both in groundwater and the deep sea and attributed them to adaptive responses. For example, the smooth and tapered forms of *Areacandona* and *Deminutiocandona* are found in alluvial aquifers; the large and well-calcified valves of *Humphreyscandona* in bicarbonate-rich waters and the ornate valves of *Meridiescandona* in Mg^{2+}-rich, lower pH environments. These morphological responses are seen at the generic level, with species of different genera at the same locality showing similar characteristics in the carapace.

Conclusion

This study is the first time that a systematic sampling program for stygobitic ostracods has been undertaken in Australia. A plethora of new species has been discovered and many are currently being described. The restriction of many taxa to single aquifers has great implications for their conservation and management in this economically significant region.

The distribution of species appears to be controlled primarily by historical events that lead to the formation and the extent of the host aquifer, with pre-adaptive colonisation and subsequent speciation. Within an aquifer, alkalinity, salinity (as% Na + K), and pH, together, govern the occurrence of taxa, as determined by canonical correspondence analysis. A combined knowledge of hydrology and hydrochemistry is required to assess the likelihood of ostracod occurrence within aquifers of the Pilbara region. The development of tolerance limits of a wide range of parameters for the known occurrences of each species will assist in the assessment of the effect of any likely impact to the subterranean ecosystem.

The results of the current study confirm and expand upon the predictions of Humphreys (unpublished) that (1) Pilbara stygofauna are restricted to the Pilbara; (2) there are distinct sub-regional patterns of taxonomic groupings; and (3) that not only all undisturbed calcretes, but nearly all local Pilbara aquifers are likely to have ostracods.

Acknowledgements The authors wish to thank M. Scanlon, J. Cocking, and H. Barron for tirelessly undertaking the fieldwork and sorting out the ostracods on which this paper is based. Dr I. Karanovic identified the ostracods in some of the samples on which this paper is based and provided advice on ostracod identification. Jenny McGuire at the Western Australian Chemistry Centre performed the analyses on water chemistry. JMR would also like to thank the Statistical Consulting Unit and the Electron Microscopy Unit of the ANU. Funding for this project was provided by Conservation and Land Management, WA awarded to PDD. We are grateful for comments of two anonymous reviewers that clarified some of the finer points of the manuscript.

References

APHA, 1995. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, Washington.

Balleau, W. P., 1972. Outline of groundwater in the Fortescue River valley: Western Australia Geological Survey Record 1986/8.

Barnett, J. C. & D. P. Commander, 1985. Hydrogeology of the Western Fortescue Valley, Pilbara region, Western Australia. Western Australia Geological Survey Record 1986/8.

Beard, J. S., 1973. The elucidation of palaeodrainage patterns in Western Australia through vegetation mapping. Vegmap Publications, Perth. Vegetation Survey of Western Australia, Occasional Paper 1.

Beard, J. S., 1998. Position and development of the history of the central watershed of the Western Shield, Western Australia. Journal of the Royal Society of Western Australia 81: 157–164.

BMR Paleogeographic Group, 1990. Australia: Evolution of a Continent. Bureau of Mineral Resources, Australia.

Bowler, J. M., 1976. Aridity in Australia: age origins and expression in aeolian landforms and sediments. Earth-Science Reviews 12: 279–310.

Bradbury, J. H. & W. D. Williams, 1996a. Two new species of anchialine amphipod (Crustacea: Hadzzidae:

Liagoceradocus) from Western Australia. Records of the Western Australian Museum 17: 395–409.

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

Brady, G. S., 1886. Notes on the freshwater entomostraca from South Australia. Proceedings of the Scientific Meetings of the Zoological Society of London 1: 82–93.

Culver, D. C., 1982. Cave Life: Evolution and Ecology. Harvard University Press, Cambridge, MA, USA.

Christiansen, K., 1962. Proposition pour la classification des animaux cavernicoles. Spelunca 2: 76–78.

Danielopol, D. L., M. Creuze des Chatelliers, F. Mösslacher, P. Popisil & R. Popa, 1994. Adaptation of Crustacea to interstitial habitats: a practical agenda for ecological studies. In Gibert, J., D. L. Danielopol & J. A. Stanford (eds), Groundwater Ecology. Academic Press, San Diego, USA, 218–243.

Danielopol, D. L., A. Baltanas & W. F. Humphries, 2000. *Danielopolina kornickeri* sp. nov. (Ostracoda, Thaumatocypridoidea) from a Western Australian anchialine cave: morphology and evolution. Zoologica Scripta 29: 1–16.

Danielopol, D. L. & G. Hartmann, 1986. Ostracoda. Part I: stygobiont Ostracoda from inland subterranean waters. In Botosaneanu, L. (ed.), Stygofauna Mundi. A Faunistic Distributional and Ecological Synthesis of the World of Fauna Inhabiting Subterranean Waters. E.J Brill, Leiden, 265–267.

Davies, P. M., 1996. The influence of flow conditions on the structure of the aquatic fauna of streams of the Pilbara, Western Australia. In Noonan, D. (ed.), An Ecological Perspective on Cooper's Creek. Australian Conservation Foundation, Adelaide, 3.

De Deckker, P., 1982. Non-marine Ostracods from two Quaternary profiles at Pulbeena and Mowbray Swamps. Alcheringa 6: 249–274.

De Laurentis, P., G. L. Pesce & W. F. Humphreys, 2001. Copepods from ground waters of Western Australia, VI. Cyclopidae (Crustacea: Copepoda) from Yilgarn region and Swan coastal plain. Records of the Western Australian Museum 19: 243–257.

Eberhard, S. M., S. A. Halse, M. D. Scanlon, J. S. Cocking & H. J. Barron, 2005a. Assessment and conservation of aquatic life in the subsurface of the Pilbara region, Western Australia. In Gibert, J. (ed.), World Subterranean Biodiversity, Proceedings of an International Symposium held 8th–10th December 2004 in Villeurbanne, France, Université Claude Bernard of Lyon 1, PASCALIS European Research Programme, 61–68.

Eberhard, S. M., S. A. Halse & W. F. Humphreys, 2005b. Stygofauna in the Pilbara region, north-west Western Australia: a systematic review. Journal of the Royal Society of Western Australia 88: 167–176.

Forester, R. M., 1983. Relationship of two lacustrine ostracode species to solute composition and salinity: implications for palaeohydrology. Geology 11: 435–438.

Forester, R. M., 1986. Determination of the dissolved anion composition of ancient lakes from fossil ostracodes. Geology 14: 796–798.

Gibert, J., J. A. Stanford, M.-J. Dole-Olivier & J. V. Ward, 1994. Basic attributes of groundwater ecosystems and prospects for research. In Gibert, J., D. L. Danielopol & J. A. Stanford (eds), Groundwater Ecology. Academic Press, San Diego, USA, 8–40.

Gibert, J., 2004. How to assess and conserve groundwater biodiversity. The PASCALIS European project in the international context: main results. Programme and Abstracts of the Symposium of World Subterranean Biodiversity, Lyon, 14.

Halse, S. A., R. J. Shiel, A. W. Storey, D. H. D. Edward, I. Lansbury, D. J. Cale & M. S. Harvey, 2000. Aquatic invertebrates and waterbirds of wetlands and rivers of the southern Carnarvon Basin, Western Australia. Records of the Western Australian Museum Supplement 61: 217–265.

Halse, S. A., M. D. Scanlon & J. S. Cocking, 2002. Do springs provide a window to the groundwater fauna of the Australian arid zone? In International Association of Hydrogeologists (ed.), Balancing the Groundwater Budget, Proceedings of the International Groundwater Conference, Darwin, 2002, 1–12.

Hartmann, G., 1978. Die Ostracoden der Ordnung Podocopida G.W. Müller, 1894 der tropisch-subtropisch Westküste Australiens (zwischen Derby im Norden und Perth im Süden). In Hartmann, G., G. Hartmann-Schröder (eds), Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden, Teil 1. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 75: 64–219.

Humphreys, W. F., 1993a. Patterns of genetic diversity within selected subterranean fauna of the Cape Range Peninsula, Western Australia: systematic and biogeographic implications. Records of the Western Australian Museum Supplement 45: 145–164.

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

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

Humphreys, W. F., 2000. The hypogean fauna of the Cape Range Peninsula and Barrow Island, northwestern Australia. In Wilkens, H., D. C. Culver & W. F. Humphreys (eds), Ecosystems of the World, Vol. 30 – Subterranean Ecoystems. Elsevier, Amsterdam, 581–601.

Humphreys, W. F., 2001a. The subterranean fauna of Barrow Island, Northwestern Australia, and its environment. Mémoire de Biospéléologie 26: 108–127.

Humphreys, W. F., 2001b. Groundwater calcrete aquifers in the Australian arid zone: the context to an unfolding plethora of stygal biodiversity. Records of the Western Australian Museum, Supplement 64: 63–83.

Jaume, D. & W. F. Humphreys, 2001. A new genus of epacteriscid calanoid copepod from an anchialine sinkhole of Northwestern Australia. Journal of Crustacean Biology 21: 157–169.

Johnson, S. L. & A. H. Wright, 2001. Central Pilbara Groundwater Study. Water and Rivers Commission, Perth.

Karanovic, I., 2003. Towards a revision of Candoninae (Crustacea: Ostracoda): description of two new genera from Australian groundwaters. Species Diversity 8: 353–383.

Karanovic, I., 2005. Towards a revision of Candoninae (Crustacea: Ostracoda): Australian representatives of the subfamily, with descriptions of three new genera and seven new species. New Zealand Journal of Marine and Freshwater Research 39: 29–75.

Karanovic, I. & P. Marmonier, 2002. On the genus, *Candonopsis* (Crustacea: Ostracoda: Candoninae) in Australia, with a key to the world recent species. Annuals of Limnology 38: 199–240.

Karanovic, I. & P. Marmonier, 2003. Three new genera and nine new species of the subfamily Candoninae (Crustacea: Ostracoda: Podocopida) from the Pilbara region (Western Australia). Beaufortia 53: 1–51.

Karanovic, I., On the genus *Gomphodella* De Deckker, 1981 (Crustacea, Ostracoda, Limnocytheridae) with descriptions of three new species from Australia and redescription of the type species. Species Diversity (in press).

Marmonier, P., P. Vervier, J. Gibert & M.-J. Dole-Olivier, 1993. Biodiversity in groundwaters. Trends in Ecology and Evolution 8: 392–395.

Marmonier, P., M. Creuzé des Châtelliers, M. J. Dole-Oliver, S. Plenet & J. Gibert, 2000. Rhône groundwater systems. In Wilkins, H., D. C. Culver & W. F. Humphreys (eds), Ecosystems of the World 30 – Subterranean Ecosystems. Elsevier, Amsterdam, 481–512.

Martens, K. & G. Rossetti, 2002. On the Darwinulidae (Crustacea, Ostracoda) from Oceania. Invertebrate Systematics 16: 195–208.

McKenzie, K. G., 1966. Freshwater Ostracoda from northwestern Australia. Australian Journal of Marine and Freshwater Research 17: 259–279.

Pankhurst, D. L. & C. A. J. Appelo, 1999. User's Guide to PHREEQC (version 2) – a computer program for speciation, batch-reaction, one-dimensional transport, and inverse geochemical calculations. US Geological Survey Water-Resources investigation report 99-4259.

Pinder, A. M., S. A. Halse, J. M. McRae & R. J. Shiel, 2004. Aquatic invertebrate assemblages of wetlands and rivers in the wheatbelt region of Western Australia. Records of the Western Australian Museum Supplement 67: 7–37.

Poore, G. C. B. & W. F. Humphreys, 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.

Radke, L. C., S. Juggins, S. A. Halse, P. De Deckker & T. Finston, 2003. Chemical diversity in south-eastern Australian saline lakes II: biotic implications. Marine and Freshwater Research 54: 895–912.

Rouch, R. & D. L. Danielopol, 1997. Species richness of microcrustacea in subterranean freshwater habitats. Comparative analysis and approximate evaluation. Internationale Revue gesamten der Hydrobiologie 82: 121–145.

Sars, G. O., 1896. On fresh-water entomostraca from the neighbourhood of Sydney, partly raised from dried mud. Archiv for Mathematik og Naturvidenskab 18: 1–81.

Szczechura, J., 1980. Causes for speciation in Ostracods. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 7: 439–441.

Strayer, D. L., 1994. Limits to the biological distributions in groundwater. In Gibert, J., D. L. Danielopol & J. A. Stanford (eds), Groundwater Ecology. Academic Press, San Diego, 287–310.

ter Braak, C. J. F. & P. Smilauer, 2002. CANONO Reference manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY, USA.

Trendall, A. F., 1990. Hamersley basin. In geology and mineral resources of Western Australia. Western Australian Geological Survey, Memoir 3: 163–191.

van de Graaff, W. J. E., R. W. A. Crowe, J. A. Bunting & M. J. Jackson, 1977. Relict early Cainozoic drainages in arid Western Australia. Zeitschrift für Geomorphologie 21: 379–400.

Watts, C. H. S. & W. F. Humphreys, 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.

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