Freshwater molluscs in the Australian arid zone

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ABSTRACT

Important freshwater systems found in arid areas range from springs to waterholes and rivers. Periods of extreme aridity in the Pleistocene, especially during the last glacial period, resulted in the drying of most freshwater systems apart from a few permanent water holes and artesian springs. The present composition of the freshwater molluscan fauna reflects this history and is a mix of recent recolonisers and relictual taxa. A database of 5,047 records of freshwater molluscs was compiled from museum records for continental Australia and interrogated for the purposes of examining distributional trends for inland arid and semi-arid Australia. Endemism and species richness were examined at species, genus and family level. Of the 125 species-group taxa included in the analysis, 42 (33.6%) are narrow-range endemics (occupying three or fewer 10 km^2 grid squares. Of these endemics, 33 (78.6% of the narrow range endemics and 26.4% of the remaining taxa are found only in artesian springs associated with the Great Artesian Basin. In addition to molluscs, these springs contain many other indigenous aquatic invertebrates and fishes and several rare or indigenous plants. A few large permanent waterholes also contain endemic taxa. Most molluscs found in intermittent waters adopt strategies to avoid desiccation or to facilitate dispersal and are generally widely distributed. The presence of molluscan and other (fishes, turtles) endemics in some large arid zone waterholes suggests that those habitats may have persisted through the last glacial. The continued existence of many of these habitats, and thus their inhabitants, is under threat from human activities relating to water use and modification of habitats.

Key words: Artesian springs, Great Artesian Basin, narrow range endemics, refugia; waterholes; species richness; biodiversity; aquatic; invertebrates; museum records.

Introduction

Arid zones and freshwater habitats are intuitively incompatible. Nevertheless, important freshwater systems are found in arid areas – these ranging from springs, including oases to waterholes and rivers. Because of the often wide separation of the permanent to semi-permanent aquatic habitats, the potential for speciation is present, especially in poorly dispersing groups such as molluscs. However, such diversification (resulting from absent to low gene flow) also requires long-term stability of habitats. Such small areas of habitat, whether they are originally small or secondarily small due to contraction, are generally referred to as refugia (e.g., Morton *et al.* 1995).

Much of the inland was endowed with lush vegetation and was well watered until the late Pliocene (e.g., Bowler 1976; Alley 1998; White 1994). The last glacial resulted in a massive onset of aridity (Bowler 1976; Nanson *et al.*, 1992; Kershaw and Nanson 1993; White 1994; Hesse *et al.* 2004) which commenced about 25,000 BP and reached its peak between 18,000 and 16,000 BP. DeDeckker (1986) argued that during the most severe part of the aridity event most inland lakes and rivers dried necessitating recolonisation of the aquatic fauna from near coastal areas and refugia such as permanent water holes and artesian (mound) springs. In this paper we examine the arid-zone freshwater molluscan fauna to ascertain what elements conform to the recent recolonisation model and those that may be relictual. While important relictual faunas are present in ground waters in arid areas, notably in NW Australia (e.g., Humphreys 1999; Humphreys and Harvey 2001), we restrict this review to surface waters.

The distribution and extent of temporary wetlands in the Australian arid zone are highly variable and dependent mainly on tropical weather systems (Roshier *et al.* 2001). Because most freshwater habitats in the arid zone are ephemeral, at least in the long term, aquatic animals living in these habitats must have strategies to survive desiccation. Long-term embryo or larval survival (equivalent to desiccation resistant spores or seeds) is not a strategy employed by freshwater molluscs. Instead, various behavioural adaptations enable those that inhabit ephemeral water bodies to survive.

The Australian freshwater molluscan fauna is becoming rather well-known. Most groups have either been recently revised or are in the process of being revised. Consequently, it is possible to make general statements about the fauna as a whole.

There are three main strategies adopted by freshwater molluscs to enable them to live in the arid-zone. These are:

(1) Physiological and behavioural adaptations that enable survival in extreme conditions. These include:-

- Desiccation survivors – these taxa avoid desiccation in temporary water bodies by behavioural adaptations (e.g., burrowing in mud or attaching tightly to rocks or logs partly embedded in the mud prior to drying).
- Reproductive modifications enabling rapid breeding on reflooding.
- Ability to withstand major fluctuations in temperature, pH, salinity etc. An extreme modification is the ability of *Coxiella* to survive in saline pools and lakes.

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(2) Ability to disperse and colonize – these taxa have behavioural or physiological adaptations that facilitate dispersal (e.g., by birds, floods, wind etc.) and, upon reaching a suitable habitat, the ability to successfully colonize it. These animals must recolonize from local or distant aquatic arid zone refugia, or from areas bordering the arid zone. Adaptations include:-

- Living in microhabitats (e.g. on macrophytes), which are likely to increase the likelihood of the snails becoming caught up on bird's feet.
- Rapid growth and achievement of reproductive maturity.
- Hermaphroditism (and the ability to self fertilize) or parthenogenesis, enabling a single immature individual to successfully colonise.

(3) Refuge inhabitants – taxa that inhabit long-term permanent water. These taxa are typically endemics and usually do not inhabit areas outside their habitats.

Methods

We used a database of 5,047 records of Australian freshwater molluscs compiled by the Department of the Environment and Heritage from available digital specimen records of freshwater molluscs primarily from the Australian Museum collections. We use these data with the same caveats given for similar studies involving museum records (see Slayter *et al.* 2006). The dataset was updated to minimise taxonomic and spatial errors. Records dated pre-1950 were excluded from the analyses, as previous experience indicates that early historical records rarely have sufficient spatial accuracy for this type of analysis. Records with a spatial error range >20km were also excluded. All records in the database were corrected to a standard taxonomy (Smith *et al.* 2002; 2004) supplemented by expert opinion and any clear anomalies removed. The result of this is a dataset of 1898 records, comprising 125 taxa, by far the most comprehensive yet compiled for Australia.

These records were loaded into the Australian Natural Heritage Assessment Tool (ANHAT), a custom-designed analysis tool built on Microsoft Access (Microsoft 2000) and ArcGIS geographic information system (ESRI 1999). ANHAT is designed to perform basic comparative analyses on the presence or absence of taxa across multiple genera, families or orders. It displays the result in a geographic information system (ArcGIS) as a simple shaded map of Australia where each grid cell represents a 1:100,000 map sheet that corresponds approximately to a 50 kilometre square.

Observational data were transferred to 10 x 10 km grid cells, generating species lists for every cell within Australia within ANHAT. Use of a grid measured in kilometres rather than degrees ensured a consistent sample area across the continent. The analysis was run on these 10 x 10 km grids, but generalised to 1:100,000 map sheets, i.e. 50 x 50 km grids, for reporting.

Species Richness: A score was allocated to each 10km grid cell representing the total number of species recorded in that cell and the eight surrounding grid cells, providing an estimate of the number of species present within a 30 km x 30 km area. This method, known as a neighbourhood analysis (Prendergast and Eversham 1997; ESRI 1999), minimises the effect of arbitrary boundaries caused by grid analysis. The richness score for each map sheet was the score of the highest scoring 10km grid cell within it.

Endemism: We calculated weighted endemism following Crisp *et al.* (2001). Weighted endemism (WE) seeks to avoid the traditional problem in endemism studies, where an arbitrary region or range-size threshold is used to define what constitutes an endemic species. WE avoids a threshold for endemism by applying a simple continuous weighting function, assigning high weights to species with small ranges, and progressively smaller weights to species with larger ranges (Laffan and Crisp 2003). We calculated WE by counting all species in each 30km x 30km area of nine adjacent cells, but weighting each by the inverse of its range-size. In the current study, species ranges were estimated by summing the number of 10 kilometre grid cells that contained observation records. A species recorded in only one grid cell, would thus contribute to the cell's endemism score 1000 times as much as a widespread species recorded in 1000 cells, but widespread species still contribute to the score.

There are a range of definitions for the arid and semi-arid zone of Australia. We have broadly followed the definition given in Morton *et al* (1995), being the 250mm rainfall zone in southern Australia and in northern Australia, where evaporation is higher, the 500mm rainfall zone. For the purposes of display in the maps, we have used the approximate line of the 550mm rainfall zone. Although this falls well outside the arid and semi-arid zone proper, it helps to provide a context for analysis.

Brief overview of river systems in the arid zone

The arid zone encompasses several of the drainage divisions recognised in Australia (Bureau of Meteorology 2006). These are:- Murray-Darling, South Australian Gulf (in part), South-west coast (inland part), Indian Ocean (encompassing the mid Western Australian area including the Pilbara), Lake Eyre, Bulloo-Bancannia and Western Plateau. It excludes the well-watered coastal drainages of the North-east and South-east Coast Divisions and the Tasmanian Division, as well as the monsoon-fed coastal rivers of the Timor Sea Division (including the Kimberley) and the Gulf of Carpentaria Division (Fig. 1H).

Some rivers are ancient, such as the Finke River (Pickup *et al.* 1988), others exhibit more recent drainage patterns. The main Lake Eyre drainages (such as the Georgina, Diamantina and Thomson Rivers and Cooper Creek) have intermittent flows but there are some large, permanent waterholes (e.g., Hamilton *et al.* 2005). The main drainage channels of arid and semi-arid rivers are characteristically intermittent in flow, with flow regimes highly variable (Walker *et al.* 1995; Puckridge *et al.* 1998). Associated flood plain habitats (billabongs (Fig. 1G), pools, swamps) are similarly variable and typically short-term. These water bodies can be filled following flooding resulting from significant rain in remote areas of the catchment. Similarly, arid-zone lakes are intermittent, filling only occasionally (Kotwicki 1986; Bowler *et al.* 2001; Timms 2001).

Some water bodies (e.g. many claypans) are independent of flood plains and fill only during significant local rain. They occur in small depressions in gibber country and between sand dunes. They have clay soils which retain shallow surface water until it evaporates, usually within a few days following rain. Larger claypans can have one or a few species of molluscs living in them.

Ancient palaeochannels in Western Australia are not associated with significant surface water (Van De Graaff *et al.* 1977). However, several subsurface water bodies have interesting stygobiont faunas associated with them (e.g., Humphreys 1999; Humphreys and Harvey 2001), including significant faunas of crustaceans, water beetles (Cooper *et al.* 2002; Leys *et al.* 2003) and some unnamed hydrobiid gastropods. However, it is not our intention to review these faunas here. Similarly, cave systems on the Nullabor contain troglobitic species but no molluscs have been recorded to date (Davey *et al.* 1992)

Faunal elements

Only two families of freshwater molluscs are absent from the arid zone –the gastropod families Glacidorbidae (review by Ponder and Avern 2000), and Neritidae (Smith et al. 2004). In addition, there are many genera in the families represented in the arid zone that are restricted to the non-arid parts of Australia (including Tasmania). A brief overview of the families present in the arid zone is given below.

Hyriidae (freshwater mussels). The only genera present in the arid zone are *Velesunio* Iredale, 1934 and *Alathyria* Iredale, 1934 which are rather widely distributed (McMichael and Hiscock 1958; Walker *et al.* 2001). Genetic and phylogenetic work on this family is currently being undertaken. Findings to date include the discovery of cryptic freshwater mussel taxa in the Lake Eyre drainages (Baker *et al.* 2003; Hughes *et al.* 2004), suggesting that further previously unrecognised diversity will be revealed, and that *Alathyria* is nested within *Velesunio.*

Survival strategies involve adults burying in mud. Like nearly all bivalves, hyriids are suspension feeders and have separate sexes. Glochidia larvae are released from brood pouches in the gills and attach to fishes for a period enabling dispersal.

Populations of freshwater mussels are under threat in many rivers probably due to altered flow regimes, introduction of exotic fishes, pollution etc. (Walker *et al.* 2001; Ponder and Walker 2003).

Corbiculidae. This small family contains a single freshwater genus (*Corbicula* Mühlfeld, 1811 – previously *Corbiculina* Dall, 1903) in arid Australia. The taxa are very poorly understood but some genetic studies are currently being undertaken. There is often thought to be one widespread species in Australia (*Corbicula australis* (Deshayes, 1830)) but it is likely that several are present. Work on *Corbicula* elsewhere has revealed the existence of clonal species (Park *et al.* 2002; Lee *et al.* 2005). Populations have been severely reduced in the Murray-Darling system (Ponder and Walker 2003). Cite reproduction paper by Byrne et al. 2000) Their survival strategy is burying in sediment but they tend to be found in rivers with permanent or semi-permanent water holes. Corbiculids are hermaphrodites and their shelled larvae are retained in brood pouch to be released as benthic crawling post larvae.

Sphaeriidae. These small, fragile bivalves were reviewed by Korniushin (2000). He described one species (*Pisidium* (*Euglesa*) *centrale* Korniushin, 2000 from two localities in the George Gill Range, central Australia. Three species are also found in the Murray-Darling drainages but none are endemics. Most species are in coastal drainages.

Viviparidae. This family of large to medium sized snails with two recognised genera (*Notopala* Cotton, 1935 and *Larina* A. Adams, 1854 (Smith *et al.* 2004: Ponder in prep.) is being extensively revised by one of us (WFP). *Larina* (previously *Centrapalia*) *lirata* (Tate, 1887), an arid-zone riverine endemic, lives beneath rocks in large permanent waterholes. The only living relative is *Larina strangei* Adams, 1854 known from a few eastern coastal Queensland rivers. *Notopala waterhousii* (Adams and Angas, 1864) and a similar undescribed species live in a few large permanent waterholes on the Barkly (= Barkley) Tablelands. While these endemics persist in areas that have long-term permanent water there are also several widespread species. The two most common and widespread viviparids in the arid zone are *Notopala kingi* (Adams and Angas, 1864) and *N. alisoni* (Brazier 1879), the latter occurring sympatrically with the former in the Lake Eyre drainages and also occurring in a few Queensland coastal rivers.

Viviparids feed by a combination of filter feeding and benthic grazing. Adults bury themselves in mud when waterholes and ponds dry. Young are retained in a pallial brood pouch to post larval stage.

Notopala species were once widespread and abundant in the Murray Darling system but are now extinct in the wild, surviving only inside a few irrigation pipelines as a result of river regulation (Sheldon and Walker 1993, 1997; Ponder and Walker 2003).

Thiaridae. The Australian taxa in this group are currently being revised by M. Glaubrecht and his students. *Plotiopsis balonnensis* (Conrad 1850) is very widespread in inland rivers although numbers have markedly declined in the Murray Darling system (Ponder and Walker 2003). Other members of this family are found in coastal rivers in the north-west, north and north-eastern parts of the mainland. In *Plotiopsis* Brot, 1874 and the related genus *Thiara* Bolten, 1798, larvae are released from a brood pouch in the head.

Hydrobiidae. Hydrobiids have undergone extensive radiations in streams and rivers in SE Australia and Tasmania (e.g., Ponder *et al.* 1993; Clark *et al.* 2003) but in the arid zone are nearly all confined to artesian springs. Here they have undergone extensive diversification within five genera (three endemic to these springs) (Ponder *et al.* 1989, 1996; Ponder and Clark 1990; Ponder 2004b; Perez *et al.* 2005). An exception is a species of *Austropyrgus* Cotton, 1942 that lives in springs fed from local ground water in the Flinders Ranges and is otherwise widespread in SE Australia with many taxa (Clark *et al.* 2003). Hydrobiids are not desiccation resistant and neither are their eggs, which are small, single and benthic.

Figure 1. Some arid zone aquatic snail habitats. **A.** One of the large pools, Dalhousie Springs, northern South Australia. Photo: W Zeidler. **B.** Kewson Hill, a spring-formed hill in the Lake Eyre Supergroup, South Australia. Photo: W Ponder. **C.** Blanche Cup Spring, Lake Eyre Supergroup. Photo: W Ponder. **D.** Big Spring, Edgbaston Station, western Queensland. Photo: J. Ponder. **E.** cattle damaged spring in far western Queensland. Photo: J. Ponder. **F.** spring on Bundoona Station. Photo: J. Ponder. **G.** billabong, northern South Australia. Photo: W Ponder. **H.** Burke River, western Queensland. Photo: J. Ponder.

Bithyniidae. This family has been recently revised (Ponder 2004a). There are a few species of *Gabbia* Tryon, 1865 known from the arid zone, one in central Australia, one widespread in western Queensland and New South Wales, one found in the Indian Ocean Division and three artesian spring endemics found in western Queensland. Those living in temporary pools appear to survive either by burying or attaching to solid objects buried in the mud. These animals feed by a combination of filter feeding and benthic grazing. Sexes are separate and eggs are laid in small clusters encased in firm jelly.

Pomatiopsidae. The genus *Coxiella* Smith, 1894 contains several species found in salt lakes mainly in the western and southern parts of the continent (Macpherson 1957). *Coxielladda gilesi* (Angas, 1877), originally described from Lake Eyre, is found scattered around the eastern half of the arid zone. Some details of the ecology of *Coxiella* are provided by Berger (1988) and Williams and Mellor (1991).

Assimineidae. *Aviassiminea palitans* Fukuda and Ponder, 2003 is found in springs in the Great Sandy Desert, Western Australia, as well as in springs in non-arid parts of the Kimberley and the Northern Territory. The only other freshwater assimineid known from mainland Australia is found in a few coastal springs in south Western Australia (Fukuda and Ponder 2003).

Planorbidae (including Ancylinae). This diverse family of pulmonate snails are represented in the arid zone by the "buliniform" genera *Glyptophysa* Crosse, 1872 and *Isidorella* Tate, 1896, the planate *Gyraulus* Charpentier, 1837 and the limpet *Ferrissia* Walker, 1903. The systematics of the buliniform genera of this family were reviewed by Walker (1988) and the species are currently being investigated (WFP and J. Walker). There are several highly variable taxa and the diversity is higher than previously thought. There is an undescribed endemic species of *Glyptophysa* from springs on Edgbaston Station near Aramac in western Queensland (which we refer to as Edgbaston Springs below). *Gyraulus* was recently revised by Brown (2001) including the description of an endemic species from Edgbaston Springs. No recent studies have been done on the freshwater limpets (*Ferrissia*). Planorbids are hermaphrodite and capable of self-fertilization. Their jelly-encased egg masses are often laid on aquatic vegetation.

Lymnaeidae. Australasian lymnaeids are currently being investigated by L. Puslednik. There are two species that are presently collectively called *Austropeplea lessonii* (Deshayes, 1830) (Boray and McMichael 1961; Smith 1992; Smith *et al.* 2002), one of which is found in northern Australia and the other through the eastern half of the mainland. The taxon currently known as *Austropeplea tomentosa* (Pfeiffer, 1855) has a range extending through New Zealand, SE Australia and Tasmania. It may actually represent a species complex with taxa mainly found in well-watered areas but some populations are found in semi-arid areas in the eastern half of the southern parts of Australia. Lymnaeids are hermaphrodites capable of self-fertilization and lay jelly-encased egg masses, often on vegetation.

Artesian springs

Artesian springs have long been recognised as important habitats in arid lands in many parts of the world (e.g., Cole 1968), but the recognition of their importance in Australia has been slow. By far the most significant Australian artesian spring system is that associated with the Great Artesian Basin (GAB) underling about a fifth of mainland Australia including much of the arid or semi-arid zones (Habermehl 1980; Cox and Barron 1998).

Water enters the basin through recharge zones formed from outcropping aquifer mainly on the eastern margin of the basin, on the western slopes of the Great Dividing Range. Smaller recharge areas occur on the western margin in northern South Australia. Groundwater flows mainly westward towards the southwest and to the northwest and north in the northern part at around one to five metres per year, with some of the GAB water shown to be about one million years old (Torgersen *et al.* 1991; Habermehl 2001).

Often artesian water is the only reliable source of potable water, historically via springs. Prior to the 1870s, there were around 3,000 flowing springs ringing the GAB (Habermehl 1982, 2000). The springs were a vital source of water for Aborigines as well as early explorers, workers and pastoralists (Harris 1981, 1992; Harris *et al.* 2002). The drilling of thousands of bores led to the extinction of about a third of the springs and reduced flows for the remainder (Ponder 1986; Harris 1992; Fairfax and Fensham 2002, 2003; Fensham and Fairfax 2003). Extant springs are clustered in 13 major spring "supergroups" (Habermehl 1982; Ponder 1986; Fensham and Fairfax 2003) mostly in South Australia (Ponder 1986; Zeidler and Ponder 1989) (Fig 1A - 1C) and Queensland (Fig 1D - 1F) (Fensham and Fairfax 2003) while those in New South Wales are mostly extinct (Pickard 1992). Biological studies were late in coming. Fishes were not properly sampled in South Australian springs until the 1970s (Glover and Sim 1978) and in Queensland the 1990s (Wager 1995; Wager and Unmack 2000; Unmack 2001a, b). The first report on aquatic invertebrates in South Australian springs was in the 1970s (Greenslade *et al.* 1985) and the first report on an invertebrate group (hydrobiid snails) from Queensland springs was in 1990 (Ponder and Clark 1990).

The GAB springs are now known to be home to many indigenous aquatic invertebrates and fishes (Ponder 1986, 2004b), most with restricted distributions and several rare or indigenous plants (Fensham and Fairfax 2003). Some higher taxa are unique to certain springs or spring group (Ponder 2004b; Wilson and Keable 2004).

The radiation of hydrobiid gastropods in these springs comprises about 35 species-group taxa (several undescribed and a few in non-arid-zone springs) and has been rather well studied (Colgan and Ponder 1994, 2000, 2001; Ponder 1995, 2004b; Ponder *et al.* 1989, 1996; Ponder and Clark 1990; Perez *et al.* 2005). Molecular studies have shown that hydrobiids have undergone monophyletic radiations in each of the major spring complexes in which they occur (Perez *et al.* 2005). A few hydrobiids related to those in the Queensland artesian springs have recently been found in springs just off the GAB (WFP and CS, pers. observ.) and other congeners occur in a few eastern coastal rivers (Ponder 1991). Similar radiations of other aquatic animals endemic to the springs do not appear to have occurred on this scale but there are some significant endemic species of fishes and species and even higher taxa amongst groups such as Crustacea and Platyhelminthes (see Ponder 2004b for overview) suggesting that these habitats may also be very significant relictual habitats for groups that may have been more widespread in the inland during the Tertiary.

Other important aquatic habitats

Other important arid zone aquatic habitats including several permanent springs and waterholes in the Great Sandy Desert, Western Australia (Graham 2001; Kendrick 2001a) and the Millstream Springs in the Pilbara (Kendrick 2001b), some of which have endemic aquatic taxa although there are no known endemic molluscs. Numerous springs and small waterholes are associated with hills and gorges in Central Australia – well known examples being Palm Valley and various locations in the MacDonnell Ranges (Morton *et al.* 1995) - but none of these are known to contain endemic aquatic molluscs, suggesting that these aquatic habitats may not have survived the more arid periods during the Pleistocene.

A few large permanent waterholes occur in rivers or on flood plains. Of particular significance are those associated with the Newcastle Creek drainage between Newcastle Waters and Lake Woods and Anthony Lagoon on Creswell Creek, about 260 km east of Newcastle Waters on the Barkly Tableland, Northern Territory. Both of these water-courses terminate in dry lakes (Lake Woods and Tarrabool Lake respectively). Lake Woods was much larger and up to six metres deeper about 22,000 years ago (Hutton *et al.* 1984). The largest on the Newcastle Creek, Longreach Waterhole, is best studied. It is permanent because of its depth and its water is highly turbid with a very high 473-1150 mg/L total solids (Townsend 2002). These waterholes each contain two species of *Notopala*, one of which (*N. waterhousii*) is endemic to the Newcastle Creek waterholes and another, *N.* n.sp., to Anthony Lagoon. These two endemics are the largest of Australia's viviparids. The other smaller species, *N. kingi*, found in both systems, is widespread in western Queensland and the arid areas of the Northern Territory. *Larina lirata*, another viviparid with a somewhat restricted distribution, lives beneath rocks in large waterholes in rivers in the north western part of the Lake Eyre Basin.

Bore drains and swamplands associated with free-flowing bores also often provide habitat for aquatic and other water dependant biota (James *et al.* 1999; Noble *et al.* 1998) including freshwater molluscs. However, given that their existence creates drawdown affecting artesian springs, in our opinion, creation or maintenance of these artificial habitats has a deleterious impact. Similarly, bores and wells can have adverse impacts on local groundwater systems so that natural seepages and springs are adversely affected.

Distribution and endemism

The analyses showed species richness focused in the Pilbara and across the northern border of the arid zone with moderately high richness in the Lake Eyre and the Murray-Darling drainages (Fig. 2). Areas of endemism are shown in figures 3 and 4.

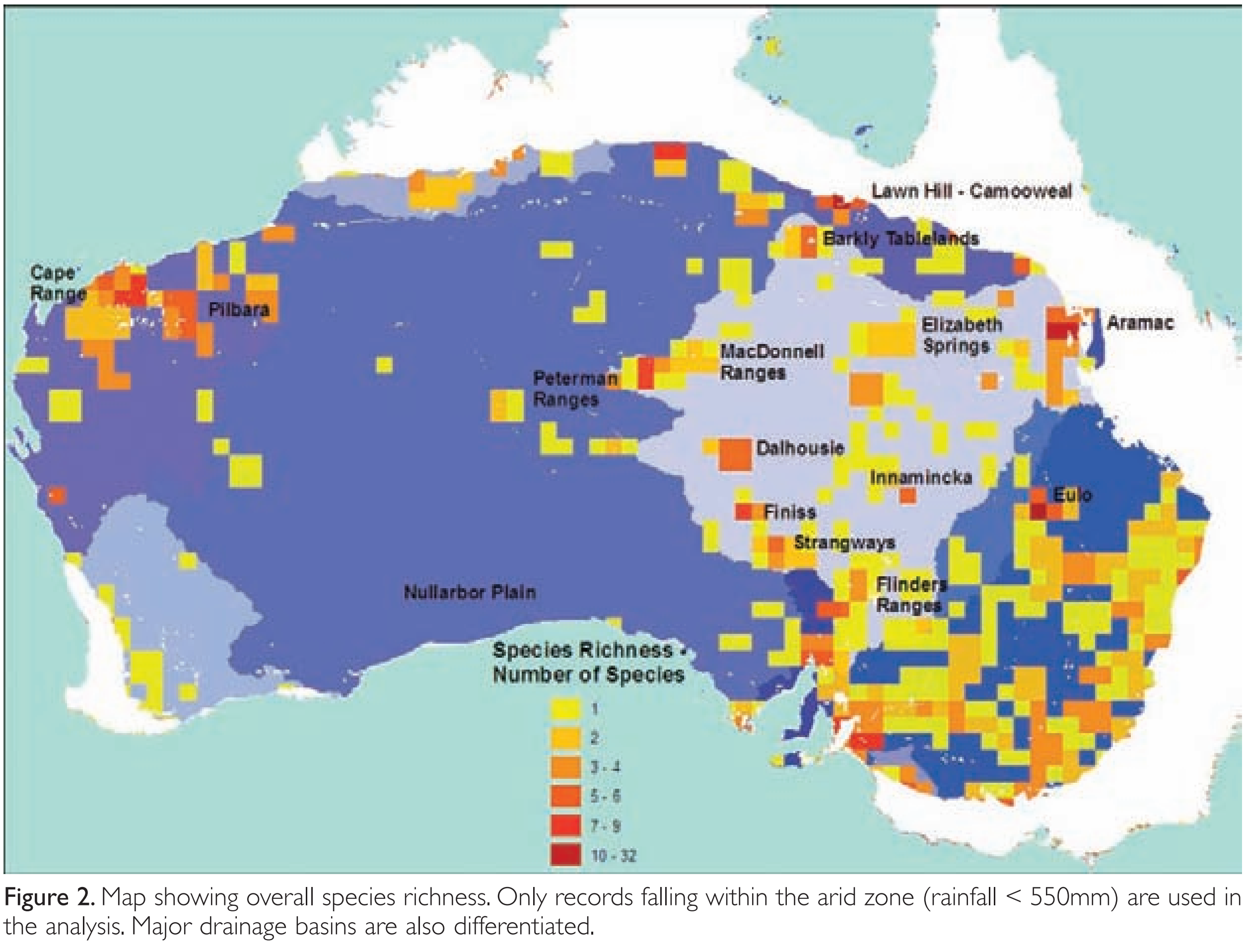

Figure 2. Map showing overall species richness. Only records falling within the arid zone (rainfall < 550mm) are used in the analysis. Major drainage basins are also differentiated.

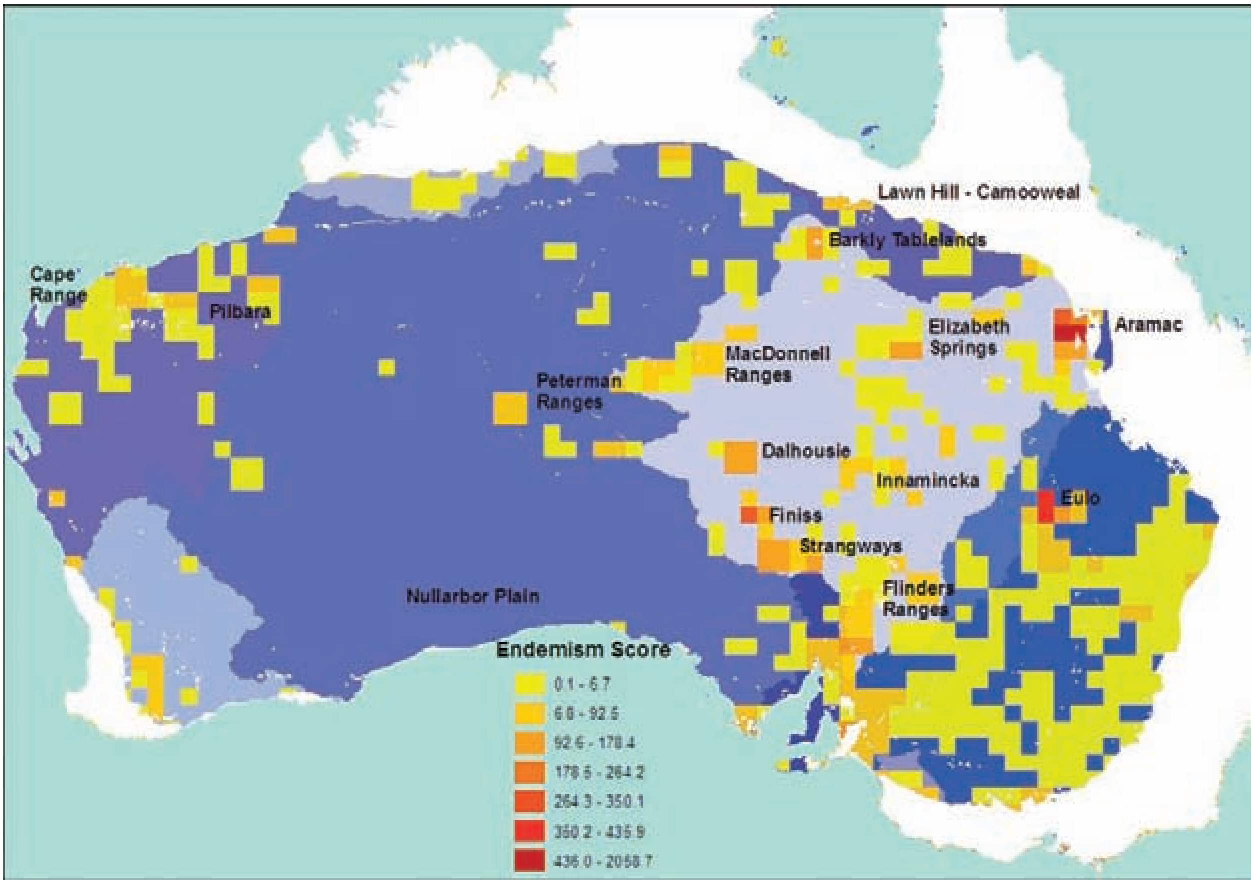

Figure 3. Map of areas of endemism. Only records falling within the arid zone (rainfall < 550mm) are used in the analysis. Major drainage basins are also differentiated.

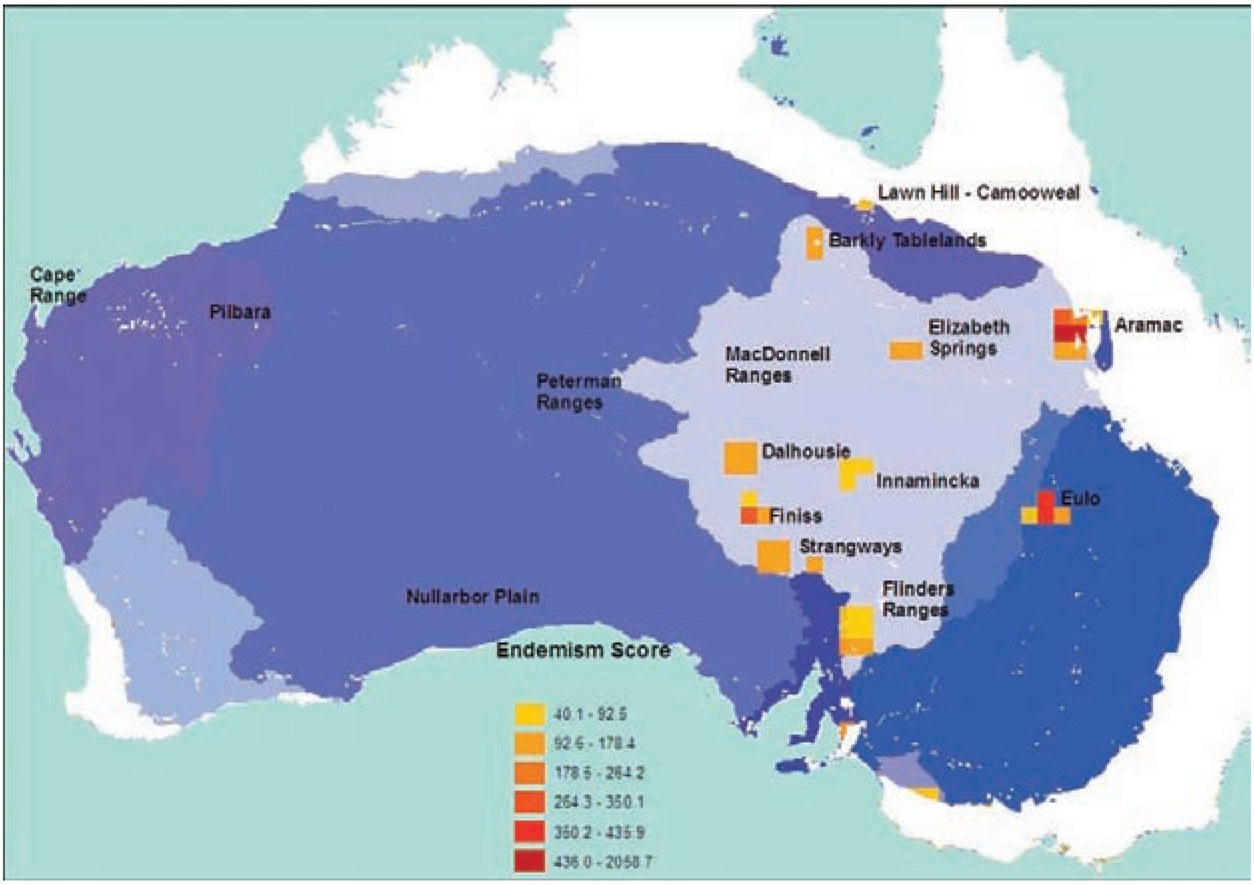

Figure 4. Map of areas of high endemism. Only records falling within the arid zone (rainfall < 550mm) are used in the analysis. Major drainage basins are also differentiated.

Of particular interest in the inland areas of western Queensland is the hot-spot of endemism in the springs on Edgbaston (Fig. 1D) and the nearby Myross Stations near Aramac, which largely reflects the high number of endemics (12 species). Similarly, the artesian spring faunas of the Lake Eyre Supergroup springs (Fig. 1A) in northern South Australia, which have 10 endemic hydrobiid species, although over a wider area. Dalhousie Springs, also in northern South Australia, have three endemic hydrobiids. Other areas of significance are the springs on Bundoona Station (Fig. 1F) in the Eulo area (SW Queensland - four endemics), and another three areas which each have a highly restricted taxon and one or more localised taxa: the Great Darling Anabranch (NSW - one endemic), the Barkly Tablelands (NT - one endemic), and the Hammersley Ranges in the Pilbara (WA - one endemic).

Although there is good correlation with richness and endemism (compare figs 2 and 3), some areas, such as the Lawn Hill - Gregory River area (Qld), the Innamincka area (SA) and the Burrup area (WA) have high species richness (>8 taxa) but little or no endemism. Conversely, the Hammersley Ranges have one endemic and comparatively low species richness (4 taxa). In general species richness is focused in the Pilbara and across the northern border of the arid zone but there is also moderately high richness (5-7 taxa) in the Lake Eyre and the Murray-Darling drainages (Fig. 3).

Discussion

On the assumption that very significant extinction occurred with the onset of aridity in the Pliocene and subsequently during arid periods during the Pleistocene (see Introduction), much of the fauna is arguably the result of relatively recent recolonisation. This recently derived fauna appears to largely occupy intermittent waters in the arid zone and has strategies to avoid desiccation and/or to facilitate dispersal. These taxa are generally widely distributed, although a few have narrow ranges.

Narrow range endemic taxa can arise in a number of different ways (Ponder and Colgan 2002). The contraction of a previously wide ranging species to a small area of available habitat as a result of increasing aridity; a local speciation events in increasingly isolated peripheral habitat and persistence of small areas of suitable habitat over long periods of time. In the later case, such habitats, for example, large, permanent water holes, are presumably remnants of a much more expansive area of suitable riverine habitat and speciation may be relatively recent. Although a few narrowly-endemic species live in long-term permanent water holes, most are found only in artesian springs associated with the Great Artesian Basin. These permanent springs are typically relatively small in extent and taxa associated with them probably never have had a wide range. The GAB springs have apparently remained rather constant, at least until Europeans commenced large scale extraction of artesian water.

There is good evidence of an "ancient" Australian freshwater molluscan fauna, including viviparids (Hamilton-Bruce *et al.* 2002; Kear *et al.* 2003) and a thiarid (Hamilton-Bruce *et al.* 2004), from the Cretaceous of north western NSW. Hyriids are also present in the Australian Mesozoic dating from the Triassic (Hocknull 2000) providing evidence of the antiquity of at least these elements of the Australian freshwater fauna, as does DNA evidence (Graf and O'Foighil 2000). Tertiary freshwater mollusc faunas from inland Australia are poorly known but from the scant fossil material available, there were at least a few taxa present in the Miocene unlike any living today (e.g., Ludbrook 1980).

Of the 125 species-group taxa included in the analysis, 42 (33.6%) are narrow-range endemics (occupying three or fewer grid squares – 19 occupy 1, 14 occupy 2 and 9 occupy 3). Of these endemics, 33 (78.6% of the narrow range endemics and 26.4% of total taxa) are found only in artesian springs. The relative paucity of non-artesian spring molluscan endemics may be because, in even recently reviewed groups, the taxonomy is morphologically based, while a few lack any modern revision.

In the current analysis, the wide-ranging taxa (>250 grid squares) are all problematic (*Corbicula* and some species of Planorbidae). In these cases, the broad-based taxa that are currently recognised are not soundly based because detailed studies on an adequate range of material have not been carried out. When such studies are forthcoming, finer taxonomic discrimination may result. For example, one of us (WFP) has been studying viviparids of which there are six taxa recognised by Smith (1992). With careful morphological discrimination more than 20 species-group taxa can be recognised. In this group, as in others, further cryptic diversity will probably also be uncovered using molecular studies, especially in areas with relictual aquatic habitats, as with the recognition of cryptic hyriid taxa in what was considered to be a single morphological species (Baker *et al.* 2003).

The artesian spring hydrobiid fauna is unlike that found in other aquatic systems (Perez *et al.* 2005) and attests to the uniqueness and prolonged existence of these habitats. Comparisons with most other aquatic habitats and invertebrate groups are difficult, either because they are insufficiently collected at a continental scale or because they are largely represented by widely distributed, readily dispersed species. Available species richness and endemism data on groups such as water beetles, dragonflies and damselflies suggests that major permanent water refugia such as the Finke River and the Barkly Tablelands may still be important centres for richness, but not endemism (Slatyer unpublished data 2005).

Fishes have been recently reviewed (Unmack 2001a, b) and the following summary is from Unmack 1995, 2001a, b, 2005. Endemics in the arid zone other than those found in artesian springs and the Murray Darling Drainage are: *Neosilurus* sp. - Bulloo River, closely related to other taxa in coastal drainages to the north; *Neosiluroides cooperensis* Allen and Feinberg 1998 – Cooper Creek; *Porochilus argenteus* Zietz, 1896 – Diamantina and Georgina Rivers, Cooper Creek and parts of Barkly Tablelands; *Craterocephalus centralis* Crowley and Ivantsoff, 1990 - Finke River and tributaries; *C. eyresii* Steindachner, 1884 - Drainages associated with Lake Eyre, Lake Frome and Lake Torrens; *Macquaria* sp. - two undescribed subspecies of this species are known, one in the Lake Eyre drainage system and one in the Bulloo River; *Hypseleotris* sp. - Upper Barcoo and Thompson Rivers (Cooper Creek Drainage); *Mogurnda clivicola* Allen and Jenkins, 1999. "couple of creeks in Flinders Ranges", also Barcoo and Bulloo Rivers; M. *larapintae* Allen and Jenkins, 1999 - Finke River; M. sp. - two rivers in Barkly Drainage; *Chlamydogobius japalpa* Larson, 1995 - Upper Finke River. There are at least nine additional fishes endemic to GAB artesian springs, notably Dalhousie Springs and some of the Lake Eyre Supergroup springs in South Australia and Edgbaston Springs and Elizabeth Springs in Queensland. The existence of these fishes, including additional species that are more widely distributed in arid zone rivers, add weight to the idea that aquatic refugia did exist in large ground-water fed water holes during the last glacial.

This pattern is not supported by frogs or freshwater turtles, even though fossil turtles are found in the arid-zone (Gaffney 1981; Thomson 2000). Three species of turtle, *Chelodina expansa* Gray, 1857, *C. longicollis* Shaw, 1794 and *Emydura macquarii macquarii* Gray, 1830 are found in the Murray-Darling system, although both former species are also found in coastal rivers. Another species, *Chelodina steindachneri* Siebenrock, 1914 is restricted to the Indian Ocean Division in Western Australia while the subspecies *Emydura macquarii emmottii* Cann *et al.*, 2003 is found only in Cooper Creek (Georges *et al.* 2003). The fossil species *Elseya lavarackorum* White and Archer, 1994 was described from fossil material in travertine deposits from northern Queensland and subsequently was found alive in the catchment of the Nicholson River on the Barkly Tablelands (Thompson *et al.* 1997). The distribution of this taxon would seem to provide some support for the Barkly Tablelands being important as a refugia across several taxa: endemic molluscs (e.g., *Notopala*), fish, as well as for turtles and this is in keeping with previous identification of the Gregory and Nicholson Rivers as significant refugia (e.g., Morton *et al.* 1995).

A recent review of the continental distribution of frogs is available (Slatyer *et al.* 2006) and the following summary is derived from that analysis. Anurans are generally poorly represented in the arid and semi—arid zone, although they have been successful at occupying most of the continent. Most species typically occupy broad areas of inland Australia and are burrowing species not dependent on permanent water. There are comparatively few species with even a relatively limited distribution, however the survey record for amphibians is poor. The genus *Uperoleia*, Gray 1841 contains most of the species with relatively restricted distributions. *Uperoleia capitulata* Davies, McDonald and Corben, 1986, *Uperoleia micromeles* Tyler, Davies and Martin 1981 and *Uperoleia trachyderma* Andersson, 1916 are the only currently recognised of limited range extent. *U. micromeles* is associated with the Tanami desert and *U. trachyderma* is only known from near Elliott in the Northern Territory. *Uperoleia capitulata* is associated with the channel country of western Queensland and New South Wales and, interestingly, this same area appears to represent the main concentration of species richness and endemism in the arid and semi-arid zone (Slatyer *et al.* 2006). The absence of any relict anurans in the arid and semi-arid zone and the general dependence of frogs in this region on strategies other than permanent refugia is interesting. Both the Myobatrachidae and Hylidae are commonly regarded as Gondwanan in origin (e.g., Tyler 1999) and absence of endemic anurans dependent on permanent aquatic refugia in the arid zone may suggest either that such Pleistocene refugia were inadequate or that the phylogeography of anurans in Australia may be more complex than previously accepted (Slatyer *et al.* 2006), with the need for more molecular work to establish the boundaries of known and possible species in inland Australia (e.g., Tyler 1999).

Thus, the evidence suggests that whatever refugia may have existed during the past two million years, available aquatic habitats were generally not extensive enough to support surface water-dependent frogs or reptiles. The same picture is even more apparent with mammals and birds, with no arid zone endemics that are fully water dependent.

Future studies on the genetic structure of various molluscan (and other aquatic) taxa in the Australian arid zone by Jane Hughes and her group at Griffith University (summaries in CRCFWE 2001, 2002) will no doubt reveal greater diversity than is currently recognised using morphospecies concepts. Their current studies include work on Hyriidae (see above) and Viviparidae (Hughes *et al.* 2001) and studies have commenced on *Corbicula*. These studies, together with work on freshwater prawns (Cook *et al.* 2002; Carini and Hughes 2004) have demonstrated considerable genetic differentiation between drainages.

Conservation

Water resources are, by definition, scarce commodities in arid and semi-arid areas, especially with the inevitability of global warming, and are thus placed under considerable stress by demands from agriculture, domestic and industrial (mainly mining) use (e.g., Walker *et al.* 1995; White 2000; Kingsford 2000; Australia State of the Environment Report 2001). Their relative scarcity means that each water source can also sustain considerable damage from stock and feral animals.

Water extraction for agricultural or other use could have significant or even devastating impacts on ground water and thus the permanence of water holes used as refugia. Studies improving our understanding the role of permanent and semi-permanent waterholes in the sustainability of arid-zone aquatic fauna (the Dryland River Refugia Project) are being undertaken by a team in the CRC for Freshwater Ecology and involves researchers from several institutions (CRCFWE 2002, 2003).

River regulation through damming and other modifications is a significant threat to inland rivers and their biota (e.g., Walker *et al.* 1995; Puckridge *et al.* 1998; Kingsford 1999, 2000; Puckridge 1999; Boulton 1999; White 2000). This is well demonstrated with the extreme regulation of the rivers of the Murray-Darling Basin that has had profound impacts on wetlands and the riverine environment resulting in the decline of many species and the extinction of some taxa (Gehrke *et al.* 2003). Consequently, plans to modify some of the few remaining largely unmodified arid-zone rivers so that (probably unsustainable) irrigation farming can be carried out (e.g., Walker *et al.* 1995; Kingsford 1999) are of considerable concern.

Other human modifications including the introduction of exotic fishes, particularly the Common Carp (*Cyprinus carpio* Linnaeus, 1758) (Harris 1994), excessive water extraction for irrigation, pollution from agricultural chemicals, stock and townships, toxic algal blooms and the destruction of riparian vegetation have all had major impacts on many of the Murray-Darling rivers in particular.

While the above threats apply to the habitats and all their inhabitants, freshwater molluscs are particularly vulnerable to extinction (e.g., Ponder 1997; Ponder and Walker 2003; Lydeard *et al.* 2004) as demonstrated by the extinction or near extinction of several freshwater molluscs in the Murray-Darling system, largely resulting from flow regulation (Ponder and Walker 2003).

The GAB springs: GAB springs are important aquatic habitats and land forms in their own right but are also the home of significant endemic biota. While South Australian springs are relatively well studied, with some significant springs protected (Harris *et al.* 2002), these habitats in Queensland remain rather poorly known and mostly unprotected (Ponder 1986, 2004; Fensham and Fairfax 2003). The GAB springs have been recognised as 'threatened' for some time (e.g. Harris, 1981, 1992; Ponder, 1986, 1995; DEST, 1994; Morton *et al.* 1995; Noble *et al.*, 1998) and the discharge springs were listed as an endangered ecological community under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* in 2001.

Conservation problems encountered in Australian artesian systems are similar to those in other parts of the world. They include the over-extraction of water leading to drawdown and excessive modification of natural spring habitats (e.g., Ponder 1986; Jensen *et al.* 1998; Fairfax and Fensham 2002, 2003). The most immediate conservation issue is to reduce drawdown in the GAB. About 88-90% of current usage is by pastoralists and much is wasted through evaporation and soakage (Cox and Barron 1998). Government-sponsored bore capping and control programs are reducing wastage, but major mining ventures are using increasingly larger amounts of GAB water, resulting in problems with local drawdown. Other significant threats include spring modification, trampling by stock and feral animals, and the introduction of exotic plants and animals. In the latter category, the spread of cane toads (*Bufo marinus* Linnaeus, 1758) and mosquito fish (*Gambusia holbrooki* Girard, 1859) is of particular concern because of their known impact on small aquatic native animals.

In the last decade, GAB water usage and spring conservation have become increasingly significant issues. Programs such as those facilitating bore rehabilitation and capping to reduce the wastage from previously free flowing bores (e.g., Reyenga *et al.* 1998), provide hope for the future of at least some of these unique habitats.

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