

The large branchiopods (Crustacea: Branchiopoda) of gnammas (rock holes) in Australia

B V Timms

School of Environmental and Life Sciences,
University of Newcastle, Callaghan, NSW, 2308

Manuscript received June 2006; accepted July 2006

Abstract

Small water-filled hollows in exposed rock masses occur across Australia and are particularly common in south-western Australia on granite. Sixteen species of large branchiopods, comprising six anostracans, eight conchostracans and two notostracans occur in these gnammas, with at least *Branchinella longirostris*, *Limnadia badia* and *Caenestheriella maraie* in south-western Australia and *Limnadia urukhai* in south-eastern Queensland obligate inhabitants. In Western Australia five common species (the three above plus *Lynceus maclayeanus* and *Eulimnadia dahlia*) are ecologically separated by differences in seasonal occurrence, habitat and feeding requirements. The high diversity in south-western Australia is explained by its great age, rock pools acting as refugia in dry climatic periods, and separation from eastern Australia.

Key words: *Branchinella longirostris*, *Limnadia badia*, *Caenestheriella maraie*, *Lynceus maclayeanus*, niche separation, co-occurrences, south-western Australia.

Introduction

Rock holes, or gnammas as they are known throughout Western Australia and beyond (Bayly 1999), are common and widespread landscape features in Australia. This is particularly so on granitic rocks and in arid/semiarid regions (Carnegie 1898; Bayly 2002). They are semantically equivalent to 'weather pits,' 'solution pits,' 'granite pits,' 'rock basins,' 'pot holes,' 'pits,' and 'pans' (in context, not clay pans or playas) (Smith 1941; Twidale & Campbell 1993; Brendonck *et al.* 2000, Graham in press).

The few studies on Australian gnammas have focused on their geomorphology (Twidale & Corbin 1963; Campbell & Twidale 1995) and community ecology (Bayly 1982, 1997; Bishop 1974; Pinder *et al.* 2000), though Bishop (1967a, 1967b, 1969) considered the autoecology of the conchostracan *Limnadia stanleyana*. Early taxonomical studies by Wolf (1911) described the anostracan *Branchinella longirostris* and the conchostracan *Limnadia badia* from granitic gnammas in south-western Australia, and more recently Webb & Bell (1979) described *Limnadia urukhai* from similar pools in south-eastern Queensland. Otherwise references to large branchiopods of Australian gnammas are little more than species lists, sometimes incompletely identified (Main 1967; Jones 1971; Pinder *et al.* 2000; Bayly 2001, Timms 2002; Timms & Geddes 2003).

The above studies point to a much richer fauna in south-western Western Australia than elsewhere in Australia. Therefore the aim of this paper is to systematically investigate the composition and biogeography of the large branchiopod fauna of gnammas in southwestern Australia, but in a context of Australia as a whole.

Methods

Fifty-two granitic outcrops throughout south-western Western Australia, bounded by Cue in the north, near Balladonia in the east, Holland Rocks in the south and near Perth in the west (Fig. 1) were visited between July and September 2003. The northern, eastern and western limits are near the edge of major outcrops of granitic rocks (Myers 1997); in the south there are many more significant outcrops south of Wagin-Pingrup, but previous studies (Bayly 1982, 1997; Pinder *et al.* 2000) have not recorded large branchiopods on them.

My previous field experience and that of Bayly (1997) suggested larger gnammas had more invertebrate species, and that pools > 10–20 cm deep when full and one to two metres diameter were large enough to contain most species. Stochastic events and different seasonal development strategies may limit the fauna actually present at anyone time. For maximum diversity, pools were visited when full or nearly so and only those deeper than 10 cm and larger than 50 cm diameter were targeted, with an emphasis, if possible, on larger pools. To simplify fieldwork and analysis, gnammas were divided into four types:

- Small shallow pan gnammas generally 0.5 to 1 m in diameter, and 10–20 cm deep when full.
- Larger, deeper pan gnammas generally 2–5 m in diameter and 20–40 cm deep when full.
- Pit gnammas which although of small diameter (50 cm to 1–2 m), were deeper than 0.25 m, often up to 1–2 m deep.
- A variety of other contact pools adjacent to the base of the rock or artificially dammed on the rock. Most had significant contact with soil and were > 2 m diameter.

At each granitic outcrop up to 10 smaller pans and up



Figure 1. Map of localities sampled for large branchiopods in south-western Australia.

to 10 larger pans, if available, were sampled together with any pit gnammas and associated pools that were found on the rock (some pit gnammas are hidden by capping stones and difficult to locate). A round household sieve, 17 cm in diameter, 7 cm deep and of mesh size 1.4 mm, was moved to and fro through each pool for 1–3 minutes depending on numbers caught and any large branchiopods caught transferred to a sorting tray, and then preserved in 80 % ethanol. Species were recorded on a presence-absence basis for each pool.

I adopted a similar approach for some granitic outcrops (Mt Wudinna, Turtle Rock, Poldo Rock, Pooncarra Rock, Pildappa Rock and Peella Rocks) near Wudinna and Minnipa in the Upper Eyre Peninsula, South Australia. Only a summary of this work is presented here. In the winter of 2004, I revisited some of the Western Australian sites studied in 2003 plus many others. This time only a general assessment was made of species present on each granite outcrop and the data used to fill out the species distribution maps.

Some material from other rock pools, or collected at

other times of the year from gnammas in Western Australia were made available to this study by colleagues (see Appendix 1). Other data were gleaned from the literature and from collections in the Western Australian Museum (WAM).

Results

Four species (*Branchinella longirostris*, *Limnadia badia*, *Caenestheriella mariae* and *Lynceus macleayanus*) were collected commonly from most of the 52 granite outcrops studied in Western Australia (Table 1). The first three are obligate inhabitants of gnammas and probably do not occur much beyond the distributions shown in Figures 2–4. The core area for these three species is an irregular oval area bounded by Kalgoorlie, Balladonia, Ravensthorpe, Wagin, Northam, Dallwallinu and Mt Magnet, with minor deviations for each species. *Caenestheriella mariae* is the most limited with no populations found in the southwest, *B. longirostris* also is apparently absent from the southwest and the far

Table 1

Distribution and numbers of large branchiopods in granitic rock pools in Western Australia as determined by field work in 2003.

Rock No.	Outcrops Name	Deep pans					Shallow pans				Pits		Other pools					
		No.	Bl	Lb	Cm	Lm	Tr	No.	Bl	Lm	Cm	No.	Lm	No.	Bl	Lm	Cm	Cp
1	Newmans Rks	2	1		1			10		1								
2	Disappointment Rks	10	3	7				10		4								
3	McDermid Rks	10	7	8	1			10		6								
4	Bushfire Rks	2	1	2	1			10		4								
5	King Rks	5		5	2			10		6								
6	Graham Rks	4						5										
7	Wave Rk	10	2	6				10		1								
8	Anderson Rks	10	5	7				10		4		3						
9	Frog Rk	10	2	4				10		1								
10	Jilbadgie Rk	10	4	6				10		3								
11	Strawberry Rks	1	1	1				5		4								
12	Moorine Rk	2	2	2				5		3								
13	Coarin Rk	2		2				5		2								
14	Bulgin Rk							2										
15	Yorakine Rk	5	3	4				10		4								
16	Yarragin Rks	5	3	3				10		3								
17	Elachbutting Rks	10	3	6	2			10		2								
18	Baladjie Rks	1	1	1	1			10	1	3								
19	Weowannie Rks	5	4	4				5		1								
20	Sanford Rks	10	3	4				5		2								
21	Corrigin Rk							10		1								
22	Boyagen Rk	2						5										
23	Sullivan Rk							2		2								
24	Petrudor Rk							10		4				2*		2		1
25	Cleary Rk							10		5				1^		1		
26	Scotsmans Road'							10		5		2	1					
27	Washington Rks							10		4		2	1					
28	Remlap old hstead'	6	2	2	1			10		2								
29	Paynes Find Rks	10	7	4	2			10		3				1*		1		
30	Wanarra Rks	10	3	1	2			10			1			1^	1	1	1	
31	Green Rk	0						10						1*		1		
32	Wardagga Rk	10	6	2	4			10		1	1			5*		1		
33	Daggar Hills	10	3	1				10										
34	Walga Rk	4	2		4		1	10										
35	Afghan Rk	0						8										
36	Barlongi Rk	0						0										
37	Trainer Rks							10								1		
38	Rainy Rks							10								2		
39	Old Rainy Rks	5	1	3				10				1	1					
40	Hospital Rks	10	4	2				10		1								
41	25 Mile Rks							10		4								
42	Buldanian Rk	3		1				10		2		5	3					
43	McPherson Rk	10	2	6		1		10		1								
44	Lilian Stokes Rks	10	1	4	1	1		10		2								
45	Mt Madden	10	1	3		1		10										
46	Dingo Rk							10		7								
47	Jilakin Rk							10		1								
48	Puntapin Rk							10		2								
49	Yillamining Rk	0						0										
50	Boulder Rk	0						2										
51	Holland Rks	10		9	1	1		10		3		2	2					
52	Xantippe Rks	6	5	6				10#										

No = number of pools sampled; Bl = *Branchinella longirostris*, Lb = *Limnadia badia*, Cm = *Caenestheriella mariaae* (recorded as *Cyzicus* sp. by Bayly (1997) and Pinder (2000)); Cp = *Caenestheriella packardii*; Lm = *Lynceus macleayanus*, Tr = *Triops* near *australiensis*

southeast, while *Limnadia badia* penetrates further south and southeast than other species (Figures 2–4). *Lynceus macleayanus* occurs within this area (Fig. 5), and elsewhere in the state and in South Australia, but almost always in gnammas or pools adjacent to rock outcrops (M. Zofkova, pers. comm.). A fifth species, *Triops* sp. near *australiensis* occurred rarely in one pool on Walga

Rock in 2003 and 2004 (it was also there in 2001, author's unpubl.data), and also in many pools on Ballan Rock in 2004. In addition this species is known from a pan in the Pilbara (northwestern WA) (A. Pinder, pers. comm.).

Detailed analysis of occurrence data on each granite outcrop showed each of the common species had different habitat preferences (Table 1). *Branchinella*



Figure 3. Distribution of *Limnadia badia* in south-western Australia.

Figure 2. Distribution of *Branchinella longirostris* in south-western Australia.



Figure 4. Distribution of *Caenesthericella mariae* in gnammas in south-western Australia.



Figure 5. Distribution of *Lynceus macleayanus* in gnammas in south-western Australia.

longirostris lived almost exclusively in deeper pans (41% of deeper pans on rocks contained the species – range 20–100% of pools on any one rock), and hardly ever was found in shallower pans (< 1% of shallower pans on rocks with the species), never in deep pit gnammas, and only once in a large contact pool. *Caenestheriella mariae* had similar narrow habitat requirements to *Branchinella longirostris* but was not as common – 10% occurrence in deeper pans, and << 1% of shallower pans. It did not occur in deep pits and only once in a contact pool. *Limnadia badia* also was not found in deep pits and larger contact pools, but was much more common overall and more tolerant of shallower conditions [57.0% of deeper pans (range 10–100% on individual rocks), and 31.8% of shallower pools (range 10–100% on individual rocks)]. In contrast to these three species, *Lynceus macleayanus* is a deeper water specialist, being almost confined to deeper pits and larger contact pools (55.5 % of pits and 54.5% of contact pools and not in shallower pans and found in only one deeper pan).

Of the 330 occurrences of large branchiopods in 679 pools in the study area, there were 63 pools with multiple species. The most common co-occurrence (42 sites) was between *B. longirostris* and *L. badia*, and the next (7 sites) between *L. badia* and *Caenestheriella mariae*. There were seven sites with three species co-occurring. The mean number of species per pool was 0.5. Field observations suggest that the three most common species, and the ones most likely to co-occur, feed differently – *B. longirostris* filter feeds in the water column, *L. badia* feeds mainly on bottom debris and *Caenestheriella mariae* feed largely by scraping algae from hard rock surfaces.

The study of a few granite outcrops on Eyre Peninsula, South Australia, yielded only three populations of *Lynceus macleayanus* in deep gnamma pits (two on Pildappa Rock and one on Pooncarra Rock). Pans on these and the other rocks were rarely deeper than 20 cm and larger than 2 m diameter, and did not yield any large branchiopods in winter.

The above data were based on the 2003 study. The 2004 visit to many of the Western Australian sites reaffirmed occurrences, but provided a slightly different impression of relative abundance and distribution of the different species. There were more records of *Caenestheriella mariae* than in 2003 and *Triops* near *australiensis* was common on Walga and Ballan Rocks. *Branchinella longirostris* was often found in shallower pools than in 2003, explained by the pools drying because of evaporation. *B. affinis*, and occasionally *B. wellardi*, occurred in pools at the base of rocks, and at Dunn Rock, south of Newdegate, *B. affinis* occurred in gnammas well away from the base, but elevated only a few metres. Contrawise, *B. longirostris* occurred only in gnammas.

Summer collections from gnammas in both Western Australia and Upper Eyre Peninsula in South Australia, have occasionally yielded *Eulimnadia dahli*. After summer storms in March 2003, some pan gnammas in the northern Wheatbelt (Appendix 1) had this species, but no other large branchiopods (M. Zofkova, pers. comm.). Pans on Corrobinnie, Peella and Pildappa Rocks on Eyre Peninsula also had populations of *E. dahli* after a storm filled pans in November 2003 (author, unpubl.

data). Indicative lengths of *Eulimnadia dahli* are ca.4–6 mm. One population of *Lynceus macleayanus* also continued to exist in November, 2003 in a large pit gnamma on Pildappa Rock, which apparently had water continuously since winter. All Eyre Peninsula pools were dry in February 2004. Following a storm in mid April, 2004, *Eulimnadia dahli* (and *B. longirostris*) were found in gnammas on King Rock (J. Hill, pers. comm.). *Eulimnadia dahli* has also been collected from Karratha Rock Hole in the Pilbara (A. Pinder, pers. comm.), and from Mt Samuel (WAM), in the far northwest and remote inland respectively, of Western Australia (Fig. 1; Appendix 1).

Other WAM records of gnamma species pertain mainly to *Lynceus* n.sp. at various sites in the central deserts of WA (including at Mt Samuel) and *Lynceus* sp. in gnammas in the limestone of the Nullabor Plain. The Mt Samuel site also harboured the anostracan *Streptocephalus* sp.

Searching by the author during 2000–2004 in selected gnammas in eastern Australia (Fig. 1) uncovered no species in granitic pans at Kooyoorra State Park, via Bendigo, Victoria; *Limnadia stanleyana* in pools on sandstone at Kanangra Walls in the Blue Mountains, NSW; *Streptocephalus* sp. from a pool adjacent to granite at Byrock, NSW; *Lynceus* sp. from a rock pool in metamorphic rock at Hood Range, Currawinya National Park, southwestern Queensland; *Caenestheriella packardi* from a deep gnamma (= rockwell) on Rockwell Station, southwestern Queensland, and *Limnadia urukhai* in granitic pans near Stanthorpe, Queensland. *Limnadia stanleyana* also has been found in sandstone pools in the Budawang Mountains west of Ulladulla, NSW (M. Fielder, pers. comm.).

Discussion

Across Australia, sixteen species of large branchiopods have been recorded from gnammas (Table 2). Eleven are judged to be of low or very low frequency of occurrence, but given the right conditions some can become common at one or a few sites, e.g., *Branchinella latzi* on Uluru, NT, *Branchinella basispina* on pools adjacent to granite outcrops on the western edge of the Nullabor, WA, *Lynceus* n. sp. in deep non-granitic gnammas of the central deserts in WA, *Limnadia stanleyana* in pools sandstone mountains west and south of Sydney, NSW and *Branchinella urukhai* in the Stanthorpe area of Queensland. Others occur at more sites and are seen more often so are judged as being 'moderately frequent' in occurrence e.g., *Eulimnadia dahli* in Western Australia and South Australia, *Caenestheriella mariae* in Western Australia, *Lynceus macleayanus* mainly in granitic gnammas throughout the western inland. Two are judged as being of 'high' frequency as they are often encountered in the right season over a large area, e.g., both *Branchinella longirostris* and *Limnadia badia* in the Wheatbelt and Goldfields of Western Australia.

Many of these species are obligate gnamma inhabitants. These include *Limnadia urukhai* in Queensland/New South Wales, *Branchinella longirostris*, *Limnadia badia*, and *Caenestheriella mariae* in Western Australia. It is possible that *Branchinella basispina*, *Limnadia stanleyana*, the new species of *Lynceus* in deep

Table 2

Large branchiopods in gnammas in Australia.

Species	Distribution in rock pools	Frequency of occurrence	Source
<i>Branchinella affinis</i>	Southern WA and southern NT	Very low	Pinder <i>et al.</i> 2000; Timms & Geddes 2003
<i>Branchinella basispina</i>	western edge of Nullabor Plain, WA	Low, localized	Timms & Geddes 2003
<i>Branchinella latzi</i>	Southern NT	Low, localized	Timms & Geddes 2003
<i>Branchinella longirostris</i>	Wheatbelt and Goldfields of WA	High	This study; Timms 2003
<i>Branchinella lyrifera</i>	NE edge of WA Wheatbelt	Very low	Pinder <i>et al.</i> 2000
<i>Streptocephalus</i> spp.	Cent. Australia, west. Murray-Darling Basin	Low, widespread	Bayly, 2001; Author, unpublished
<i>Lynceus macleayanus</i>	WA, SA, west Qld	Moderate	M. Zofkova, unpubl. data; This study; Bayly 1991
<i>Lynceus</i> n.sp.	Central deserts of WA	Low, localized	M. Zofkova Unpubl.data
<i>Eulimnadia dahli</i>	WA, Eyre Peninsula, SA	Moderate	This study
<i>Limnadia badia</i>	Wheatbelt and Goldfields of WA	High	This study.
<i>Limnadia stanleyana</i>	Sydney Basin	Low, localized	Bishop 1974
<i>Limnadia urukhai</i>	Granite belt of southern Qld and adjacent NSW.	Low, localized	Webb & Bell, 1979
<i>Caenestheriella mariae</i>	Wheatbelt & Goldfields of WA	Moderate	This study
<i>Caenestheriella packardi</i>	A pit gnamma Rockwell Station; southwest Qld.	Very low, localized	Author, unpublished data
<i>Lepidurus apus viridus</i>	Southwest WA	Very low	Jones 1971
<i>Triops</i> sp near <i>australiensis</i>	Northwestern WA	Very low	This study

non-granitic gnammas of the remote inland, and the species of *Triops* in pools on Walga Rock, Ballan Rock and Karratha Rock may also qualify, but more data are needed for a confident classification. *Lynceus macleayanus* is also a gnamma specialist but not an obligate inhabitant as there are many old records in other habitats (Richter & Timms, 2005). It lives almost exclusively in deeper pools as shown in Table 1 and noted in Bayly (1997). Many species, while commonly utilizing gnamma habitat, are abundant in other habitats, including *Eulimnadia dahli*, *Branchinella latzi* and *B. affinis*. *Branchinella lyrifera* and *Lepidurus apus viridis* appear to be accidental occurrences as there is only one occurrence of each and both are common in a wide range of habitat types. Not enough is known on *Streptocephalus* spp. to know their habitat specificity. Finally, as shown by Timms and Geddes (2003), there seems to be a recent change in the dominant species on Uluru, from *Branchinella latzi* to *B. affinis*.

Western Australia has by far the most species of large branchiopods in gnammas (12) compared with the Northern Territory (3), New South Wales (3), Queensland (3), South Australia (2), Victoria and Tasmania (0). As for other aquatic invertebrates that are more speciose in southwestern WA than elsewhere *e.g.*, *Parartemia* (Remigio *et al.* 2001), *Branchinella* (Timms 2002), cladocerans (Frey 1991; Hebert & Wilson 2000), ostracods (Halse & McRae 2004), the explanation for the west of Western Australia lies in the great age of a stable landscape. There has been no catastrophic impacts of marine inundation, little volcanism affecting the bulk of the Yilgarn Craton, or glaciation since the Permian. Other contributing factors include adaptation to refugia in times of climatic stress (in this case the more reliable gnammas) and genetic isolation from eastern Australia (Pinder *et al.* 2004).

In concert with the less diverse branchiopod fauna in

Australia than in similar places worldwide (Bănărescu 1995; Williams 1981), few species occur in most Australian gnammas except those in Western Australia. By contrast southern Africa has at least six species of *Branchiopodopsis* living in rock pools (Hamer & Appleton 1996) and *Leptestheriella ineremis* (L. Brendonck, pers. com.), while in western USA and adjacent Mexico *Branchinecta lindahli*, *B. packardi*, *B. lynchi*, *B. coloradensis*, *Eubranchipus oregonus*, *Streptocephalus texanus*, *S. dorotheae*, *Thamnocephalus platyurus*, *Eulimnadia texana*, *Leptestheria compleximanus* and *Triops longicaudatus* occur in rock pools (Baron *et al.* 1998; Belk 1991; Eng *et al.* 1990; Eriksen & Belk 1999; Graham in press; C. Rogers pers. comm.). At least some of these are gnamma specialists, including *Branchiopodopsis wolfi* in southern Africa (Brendonck *et al.* 2000) but none in USA (C. Rogers pers. comm.). It is feasible that south-western Australia may have more species restricted to gnammas than elsewhere, which again probably is a reflection of the geological stability, climate variability and continuous existence of inselbergs and their gnammas over long periods of geologic time (Twidale & Campbell 1993). I emphasise geological stability because in fact the climate has been quite variable and it is probably a combination of a stable geology but instable climate that has led to high diversity – *i.e.* each climatic phase may have led to diversification but there hasn't been events like glaciation, volcanism and marine inundation (other than around the coast) to reset the fauna.

At the recent International Large Branchiopod Symposium, held in Toodyay, Western Australia, in 2004 (where this paper was originally presented), a participant criticised my comment about the great age of the Yilgarn being a cause of high diversity because 'it is instability that causes speciation not stability' but I think in the case of ancient geological stability it could help preserve

diversity caused by repeated climatic variation by protecting the resulting diversity from extinction-causing catastrophic events.

It is noteworthy that among large branchiopods throughout the world, anostracans tend to dominate rock pools and notostracans are particularly scarce, despite the later's adaptations for living in such temporary environments. The contention by Main (1997, 2000) that *Triops* is a characteristic inhabitant of rock pools in Western Australia is not supported by the present data or work by Bayly (1982, 1997) and Pinder *et al.* (2000). Nevertheless, there are persistent populations of *Triops* on three rocks in the north of the state, and B. Knott (pers. comm.) contends the presence of notostracans on granite outcrops in southwest Western Australia twenty years ago.

Spinicaudatan clam shrimps seem to be particularly common and diverse in Australian rock pools compared with those in southern Africa and western USA (Hamer & Appleton 1996; Baron *et al.* 1998; Brendonck *et al.* 2000; Graham in press), though this seems to contradict the statement above about relatively low diversity of large branchiopods in Australian rock pools. Six species, as well as two laevicaudatan clam shrimps are known, with differentiation across Australia. By contrast there is only one specialist anostracan (*B. longirostris*) which is restricted to an apparent centre of speciation in southwestern Australia (Timms 2002), though a few other anostracans occasionally live in gnammas. This species never occurs in nearby mud pools, and if these contain an anostracan it is likely to be the closely related *B. affinis*.

Resources in gnammas are limited and there is intense competition for them, *e.g.*, Brendonck *et al.* (2002). Co-occurrences of branchiopods seem to be less common in gnammas compared with those in other waters. Studies on North American and African gnammas rarely report co-occurrences and do not quantify them (Baron *et al.* 1998; Brendonck & Riddoch 1997; Brendonck *et al.* 2000; Eng *et al.* 1990; Eriksen & Belk 1999; Hamer & Appleton 1996). In eastern Australia no co-occurrences have been noted, but in south-western Australia 24% of pools with at least one large branchiopod had additional species. Comparative figures for all types of freshwater waterbodies with at least one large branchiopod in the wheatbelt and Carnarvon basin are 24% and 76% respectively (A. Pinder, pers. comm.). For anostracans alone there are no recorded co-occurrences in gnammas, compared with 4.9% in all wetlands of the WA Wheatbelt, 31.8% in all wetlands of the Carnarvon basin (A. Pinder, pers. comm.) and 51% of all wetlands in the Paroo in eastern Australia (Timms & Sanders 2002). For clam shrimps, there are 3.8% of gnamma sites with co-occurrences, compared with 48% among other wheatbelt sites, 11.1% of other Carnarvon sites (A. Pinder, pers. comm.) and 20.4% of other sites in the Paroo (Timms & Richter 2002).

When there are co-occurrences in south-western Australia, the participants feed differently. Moreover there is some seasonal separation of species, with *Eulimnadia dahli* a summer species and the remainder winter-spring species. Interestingly a parallel situation is known among Chironomidae in these gnammas –

Paraborniola sp occurs in summer and *Allotrissocladus* spp. are active in winter (Bayly 1999).

Acknowledgements: I appreciate Brenton Knott hosting me in his laboratory at University of Western Australia during July-September 2003. I thank Magdalena Zofkova for identifying *Lynceus macleayanus*, Ian Bayly, Michael Fielder, Adrian Pinder, Darcy Pirotta, Judy Hill and Magdalena Zofkova for provision of specimens, Stephen Weeks for accompanying me to Kanangra Walls, NSW, to collect *Limnadia stanleyana* from the most scenic site occupied by any clam shrimp, Christopher Rogers for information and Olivier Rey-Lescure for drawing the figures. I am also grateful to Ian Bayly, Merlijn Jocqué, and Adrian Pinder for helpful comments on the manuscript.

References

- Bănărescu P 1995 Zoogeography of Fresh Waters Vol 3 Distribution and Dispersal of Freshwater Animals in Africa, Pacific Areas and South America. AULA-Verlag Weisbaden. 1617 pp.
- Baron J.S, La Francois T & Kondratieff B C 1998 Chemical and biological characteristics of desert rock pools in intermittent stream of Capital Reef National Park, Utah. Great Basin Naturalist 58: 250–264.
- Bayly I A E 1982 Invertebrates of temporary waters on granite outcrops in Southern Western Australia. Australian Journal of Marine and Freshwater Research 33: 599–606.
- Bayly I A E 1997 Invertebrates of temporary waters in gnammas on granite outcrops in Western Australia. Journal of the Royal Society of Western Australia 80: 167–172.
- Bayly I A E 1999 Rock of Ages: Human Use and Natural History of Australian Granites. University of W.A. Press, Nedlands, 132pp.
- Bayly I A E 2001 Invertebrate occurrence and succession after episodic flooding of a central Australian rock hole. Journal of the Royal Society of Western Australia 84: 29–32.
- Bayly, I A E 2002 The life of temporary waters in Australian gnammas (rock-holes). Verhandlungen Internationale Vereinigung Limnologie 28: 41–48.
- Belk D 1991 Why only one of two common Central Texas Anostraca atop Enchanted Rock? Hydrobiologia 212: 83–86.
- Bishop J A 1967a Seasonal occurrence of a branchiopod crustacean, *Limnadia stanleyana* King, in eastern Australia. Journal Animal Ecology 36: 77–95.
- Bishop J A 1967b Some adaptations of *Limnadia stanleyana* King (Crustacea: Branchiopoda: Conchostraca) to a temporary freshwater environment. Journal Animal Ecology 36: 599–609.
- Bishop J A 1969 Feeding behaviour of larval and post-larval *Limnadia stanleyana* King, 1985 (Branchiopoda, Crustacea). Crustaceana 17: 108–109.
- Bishop J A 1974 The fauna of temporary rain pools in eastern New South Wales. Hydrobiologia 44: 319–323.
- Brendonck L & Riddoch B 1997 Anostracans ((Branchiopoda) of Botswana: Morphology, Distribution, Diversity and Endemicity. Journal of Crustacean Biology 17: 111–134.
- Brendonck L, Hamer M L, Riddoch B J & Seaman M T 2000 *Branchiopodopsis* species – specialists of ephemeral rock pools. African Journal of Aquatic Science 25: 98–104.
- Brendonck L, Michels E, De Meester L & Riddoch B 2002 Temporary pools are not 'enemy-free.' Hydrobiologia 486: 147–169.
- Campbell E M & Twidale C R 1995 The various origins of minor granite landforms. Caderno Laboratorio Xeológico de Laxe (Coruna) 20: 381–403.
- Carnegie D W 1898 Spinifex and Sand. C.Arthur Pearson, London, 292pp.
- Eng L L, Belk D & Eriksen C H 1990 Californian Anostraca: distribution, habitat and status. Journal of Crustacean Biology 10: 247–277.

- Eriksen C H & Belk D 1999 The Fairy shrimp of California's Pools, Puddles and Playas. Mad River Press, Eureka, California. 196pp.
- Frey D G 1991 The Species of *Pleuroxus* and of three Related Genera (Anomopoda, Chydoridae) in Southern Australia and New Zealand. Records of the Australian Museum 43: 291–372.
- Graham T (in press). Pothole communities on the Colorado Plateau: Biological and physical correlates to large branchiopod occurrences. *Hydrobiologia*
- Hamer M L & Appleton C C 1996 The *Branchiopodopsis* (Crustacea: Branchiopoda: Anostraca) of Southern Africa. *Annals of the South African Museum* 104: 311–377.
- Halse S A & McRae J M 2004 New genera and species of giant ostracods (Crustacea: Cyprididae) from Australia. *Hydrobiologia* 524: 1–52.
- Hebert P D N & Wilson C C 2000. Diversity of the genus *Daphniopsis* in the saline waters of Australia. *Canadian Journal of Zoology* 78: 794–808.
- Jones R E 1971 The ecology of some species of Diptera on granite outcrops. Ph D Thesis, University of Western Australia, Perth.
- Main B Y 1967 Between Wodjil and Tor. Jaracanda Press, Brisbane. 161pp.
- Main B Y 1997 Granite outcrops: A collective ecosystem. *Journal Royal Society of Western Australia* 80: 113–122.
- Main B Y 2000 Habitat template for invertebrates on granite outcrops. *Journal Royal Society of Western Australia* 83: 139–147.
- Myers J S 1997 Geology of granite. *Journal Royal Society of Western Australia* 80: 87–100.
- Pinder A M, Halse S A, McRae J M & Shiel, R J 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.
- Pinder A M, Halse S A, Shiel R J & McRae J M 2000 Granite outcrop pools in south-western Australia: foci of diversification and refugia for aquatic invertebrates. *Journal Royal Society of Western Australia* 83: 149–161.
- Remigio E A, Hebert P D N & Savage A 2001 Phylogenetic relationships and remarkable radiation in *Parartemia* (Crustacea: Anostraca), the endemic brine shrimp of Australia: evidence from mitochondrial DNA sequences. *Biological Journal of the Linnean Society* 74: 59–71.
- Richter S & Timms B V 2005 A list of the Recent clam shrimps (Crustacea: Laevicaudata, Spinicaudata, Cyclestherida) of Australia, including a description of a new species of *Eocyclus* Records of the Australian Museum 57: 341–354.
- Smith L L 1941 Weatherpits in granite of the southern Piedmont. *Journal of Geomorphology* 4: 117–127.
- Timms B V 2002 The fairy shrimp genus *Branchinella* Sayce (Crustacea: Anostraca: Thamnocephalidae) in Western Australia, including a description of four new species. *Hydrobiologia* 486: 71–89.
- Timms B V & Geddes M C 2003. The fairy shrimp genus *Branchinella* Sayce 1903 (Crustacea: Anostraca: Thamnocephalidae) in South Australia and the Northern Territory, including descriptions of three new species. *Transactions of the Royal Society of South Australia*. 127: 53–68.
- Timms B V & Sanders P R 2002 Biogeography and ecology of Anostraca (Crustacea) in middle Paroo catchment of the Australian arid-zone. *Hydrobiologia* 486: 225–238.
- Twidale C R & Corbin E M 1963 Gnammas. *Revue de Géomorphologie Dynamique* 14: 1–20.
- Twidale C R & Campbell E M 1993 *Australian Landforms: Structure, process and time*. Gleneagles Publishing, Adelaide. 569pp.
- Webb J A & Bell G D 1979 A new species of *Limnadia* (Crustacea: conchostraca) from the granite belt in southern Queensland and north New South Wales. *Proceedings Linnean Society of New South Wales* 103: 237–245.
- Williams W D 1981 The Crustacea of Australian inland waters. pp. 1101–1138 in: *Ecological Biogeography of Australia* (Ed. A. Keast) Junk, Dordrecht. 2142pp.
- Wolf E 1911 Phyllopora. In: *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905, Bd 3:253–276*. W. Michaelsen und R. Hartmeyer (eds). G. Fisher, Jena.

Appendix

Sites where species of large branchiopods have been found in Western Australia

Name	nearest town/ locality	latitude	longitude	<i>Branchinella longirostris</i> *	<i>Limnadia badia</i> *	<i>Caenestheriella mariae</i> *	<i>Lynceus macleayanus</i> *	Other Species
Karratha Rock	Karratha	20 55	116 42					<i>Eulimnadia dahlia</i> and <i>Triops</i> near <i>australiensis</i> -A. Pinder.
Mt Samuel	Warburton	25° 54'	125 58					<i>Lynceus</i> n. sp., <i>E. dahlia</i> , <i>Streptocephalus</i> sp.- WAM <i>Lynceus</i> n.sp.- WAM <i>Lynceus</i> n.sp.- WAM
170 km SE Warburton	Warburton	27 00	125 05	2004	2004	2003/4		<i>Triops</i> near <i>australiensis</i>
Ryans Bluff	Warburton	27 14	126 25	2003/4	2004	2004		
Walloo Hill	Cue	27 15	117 26	2004	2004	2004		
Walga Rock	Cue	27 24	117 28	2004	2004	2004		
Dalgaranga Rocks	Cue	27 46	117 01	2004	2004	2004		
Chinaman Rock	Yalgoo	28 00	116 49	2004	2004	2004		
Goolthan Hill	Yalgoo	28 07	116 44	2003	2003	2004		
Daggar Hill	Mt Magnet	28 08	117 36	2003	2003	2004		<i>Triops</i> near <i>australiensis</i>
Ballan Rock	Mt Magnet	28 11	117 25	2004	2004	2004		
Bilya Rock	Mingenew	29 00	115 08		M.Zofkova			
Mt East	Laverton	29 03	122 40					<i>Lynceus</i> n.sp.- WAM
Paynes Find Rocks	Paynes Find	29 10	117 40	2003/4	2003/4	2003	2003	
Yendanga Rocks	Menzies	29 19	120 19	2004	2004	2004	2004	
Wardagga Rock	Paynes Find	29 23	117 30	2003	2003	2003		
Camel Soak	Perenjori	29 24	116 38	2004	2004	2004		
Wanarra Rock	Perenjori	29 31	116 48	2003/4	2003/4	2003/4	2003	<i>Eulimnadia dahlia</i> - M.Zofkova
Green Rock	Perenjori	29 37	116 46	2004	2003/4	2004	2003	<i>Eulimnadia dahlia</i> - M.Zofkova
Old Rainy Rocks	Menzies	29 44	119 37	2003	2003		2003	
Hospital Rocks	Menzies	29 50	120 07	2003	2003			
25 Mile Rocks	Menzies	29 57	121 29	2004	2004	2004		
Old Remlap Rocks	Beacon	30 02	117 38	2003/4	2003/4	2003/4		
Washington Rocks	Beacon	30 09	117 34	2003/4	2003/4	2003/4	2003	
Xantippe Rocks	Dallwallinu	30 17	116 58	2003/4	2003/4			
Yellari Rocks	Beacon	30 20	117 50	2003/4	2003/4			
Cleary Rocks	Beacon	30 23	117 39	2003/4	2003/4			
Petudor Rock	Dallwallinu	30 26	116 58	2003/4	2003/4			
Elachbutting Rock	Beacon	30 36	118 37	2003/4	2003/4	2003	2003	
Yannemooning Rocks	Beacon	30 40	118 33	2003/4	2003/4	2003	2003	<i>Eulimnadia dahlia</i> - M.Zofkova
Newcarlbeon Rock	Kalannie	30 40	117 25	A. Pinder	A. Pinder	2003		<i>Eulimnadia dahlia</i> - M.Zofkova
Baladjie Rock	Bullfinch	30 57	118 53	2003/4	2003/4	2003/4		
Uberin Rock	Dowerin	30 59	116 59	2004	2004	2004		
Yarragin Rock	Trayning	31 02	117 57	2003	2003	2003/4		
Weowannie Rocks	Yellowdine	31 08	119 45	2003/4	2003/4	2004		
Gnarbine Rocks	Coolgardie	31 08	120 57	2003	2003	2004		
Boorabbin Rocks	Yellowdine	31 12	120 17	2003	2003	2003		
Moorine Rock	Westonia	31 13	118 59	2003/4	2003/4	2003		
Sandford Rock	Westonia	31 14	118 46	2003	2003	2003		
Quamine Rocks	Coolgardie	31 16	121 04	M. Zofkova				
Victoria Rock	Coolgardie	31 17	120 56	2003	2003			

Burra Rock	31 22	121 11	2004	2004	2004	
Burracoppin Rock	31 24	118 27	2004	2004	2004	
Yorkrakine Rock	31 25	117 30	2003/4	2003/4	2003/4	
Strawberry Rock	31 27	119 17	2003	2003	2003	
Merridan Rock	31 28	118 18	2004	2004	2004	
Jillbadgie Rock	31 29	119 14	2003/4	2003/4	2003/4	
Frog Rock	31 30	119 14	2003	2003	2003	
Dulyalbin Rock	31 34	118 59	2004	2004	2004	
Cave Hill Rock	31 39	121 14	2004	2004	2004	
Sunday Soak	31 43	121 27	2004	2004	2004	
Mt Hampton	31 45	119 04	I. Bayly	I. Bayly	I. Bayly	
near Madura	31 55	127 04				<i>Lynceus</i> sp.- WAM
Cairn Rock	31 51	118 50		I. Bayly		
Coarin Rocks	31 56	117 45		2003		
25 Mile Rocks	31 57	121 37		2003		
McDermid Rock	32 02	120 43	2003/4	2003/4	2003/4	
Nutysland Nature Res.	32 03	126 06				
Mt Walker	32 04	118 45	2004	2004	2004	
Buldania Rocks	32 04	122 02		2003/4	2003/4	
Newmans Rocks	32 07	123 10	2003	2003	2003	
Disappointment Rock	32 08	120 56	2003/4	2003/4	2003	
Anderson Rocks	32 10	118 51	2003/4	2003/4	2003	
The Humps	32 17	118 57	2004	2004	2004	
King Rock	32 19	119 09	2004	2004	2003/4	2004
Corrigin Rock	32 20	117 53		2003	2003	
Afghan Rock	32 21	123 40		2003	2003	
Sullivan Rock	32 22	116 15		2003	2003	
Bushfire Rks	32 26	119 20	2003/4	2003/4	2003	
Wave Rk	32 27	118 54	2003	2003/4	2003	
McPherson Rks	32 27	121 40	2003/4	2003/4	2004	
Graham Rocks	32 28	119 03	2004	2003/4	2003	
Emu Rock	32 28	119 25	2004	2003/4	2004	
Balladonia Rock	32 28	123 52		2003	2003	
Boyagin Rock	32 29	116 55		2003	2003	
Moir Rock	32 39	121 25	2004	2003/4	2004	
Jilakin Rock	32 40	118 20		2003	2003	
Sugg Rock	32 58	119 39	2004	2004	2004	
Dingo Rock	33 01	118 36		2003	2003	
Lilian Stokes Rocks	33 04	120 06	2003	2004	2003	
Mt Madden	33 15	119 51	2003/4	2003/4	2004	
Mt Ridley	33 17	122 07		2004	2004	
Puntipin Rock	33 20	117 24		2003	2003	
Dunn Rock	33 21	119 30		2004	2004	
Holland Rocks	33 22	118 45		2003/4	2003	2003
Boyatup Hill	33 44	123 02		2004	2004	
Peak Head	35 07	117 56		D.Pirotta		

* Years in these columns refers to dated collections made by the author