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A STUDY OF THE GNAMMAS (ROCK POOLS) IN SOME GRANITIC OUTCROPS IN CENTRAL VICTORIA, WITH A COMPARISON OF THEIR INVERTEBRATE COMMUNITIES ACROSS SOUTHERN AUSTRALIA

Brian V. Timms[1]

[1]Centre for Ecosystem Science, School of Biology, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2256, Australia

Correspondence: brian.timms @unsw.edu.au

ABSTRACT: Gnammas in central Victoria occur at Kooyoora, Terrick Terrick, Mt Pilot near Chiltern and Bald Rock near Euroa. Though similar structurally and with similar hydroperiods to those in the Western Australian Wheatbelt and on Eyre Peninsula (EP), South Australia, many are smaller and all have fresher waters. Momentary species richness in pan gnammas range from 2.7 at Bald Rock to 9.3 at Terrick Terrick and in pit gnammas from 7.6 at Kooyoora to 15.3 at Terrick Terrick. These figures are significantly lower than figures of *ca* 30 for WA pans and *ca* 10 for EP pans, but ambivalent for pits, *cf* 12 in WA, and 9 on EP. Central Victorian gnammas have only one endemic species compared with many in WA and a few on EP. Species seem to have few special adaptations for life in Victorian gnammas, compared to many in WA. Factors thought to be influencing these differences include habitat size (a function of site age), number of gnammas per rock exposure (habitat variability and availability), and past climatic fluctuations (promotion of speciation). All these factors enhance diversity in WA, but mostly inhibit it in central Victoria, with Eyre Peninsula being intermediate.

Keywords: species richness, endemism, adaptations, metacommunities**,** *Aedes alboannulatus, Sarscypridopsis, Eulimnadia gnammaphila*

Granite is a hard and durable rock, yet under the right conditions it can corrode to form hollows which may contain water. Such hollows are termed gnammas, an Indigenous term from the Nyungar people of southwest Western Australia, and now applied to such rock pools throughout Australia and even beyond (Twidale & Vidal Romaní 2005). Gnammas can occur in other rock types too, such as sandstone and limestone. Together, their most iconic inhabitants are various species of fairy and clam shrimps (Jocqué et al. 2010) and many such shrimps are known from gnammas across Australia (Timms 2006, 2012a, 2012b, 2014a, 2016a, 2016b).

Gnammas of southern Western Australia are well studied and claimed to be the most diverse in the world (Brendonck et al. 2016). At least 230 species of invertebrates have been identified from these gnammas, including many endemic species (Pinder et al. 2000), among which are two fairy shrimps and at least four clam shrimps (Timms 2006). This diversity is a biogeographic function of the presence of numerous pools providing various habitats over a wide area, many partially isolated on inselbergs, and of past climatic fluctuations promoting speciation in isolated groups of pools (Pinder et al. 2000). A more limited area of granitic inselbergs on northwest Eyre Peninsula, South Australia, and isolated from the Western Australian series by the extensive dry Nullarbor plain, has many gnammas, but with an invertebrate fauna not as diverse and with few endemic species compared with western fauna (Timms 2014a). The sandstone gnammas of the Sydney Basin are depauperate (Bishop 1974), but there could be reasons for this other than biogeographical.

Gnammas are of two basic types: pans are shallow (20 cm, often much less), flat floored and usually roughly circular and often <3 m in diameter (Twidale & Corbin 1963; Timms & Rankin 2015), while pits are much deeper (50 cm to *ca* 2 m), any shape but largely hemispherical in cross-section (Twidale & Romani 2005; Timms 2013). In essence these geomorphic differences bestow much shorter hydroperiods on pans than on pits. The pan gnammas in Western Australia are most diverse and with many unique faunal components (Pinder et al. 2000). The pit gnammas are far less diverse and not too different from ordinary pools in the landscape (Timms 2014b). The distinction between pan and pit gnammas is maintained on Eyre Peninsula but to a lesser degree (Timms 2014a). Sydney sandstones lack pit gnammas so the role of gnamma depth in eastern Australia is unknown.

Special adaptations are needed for living in pan gnammas (Bayly 2011). Branchiopods (fairy, clam, shield shrimps and cladocerans), ostracods and copepods are preadapted by having resistant eggs able to withstand the rigours of pool dryness. Many species are pigmented to counteract strong UV rays in the clear waters, some copepods and beetles have life cycle adaptations to

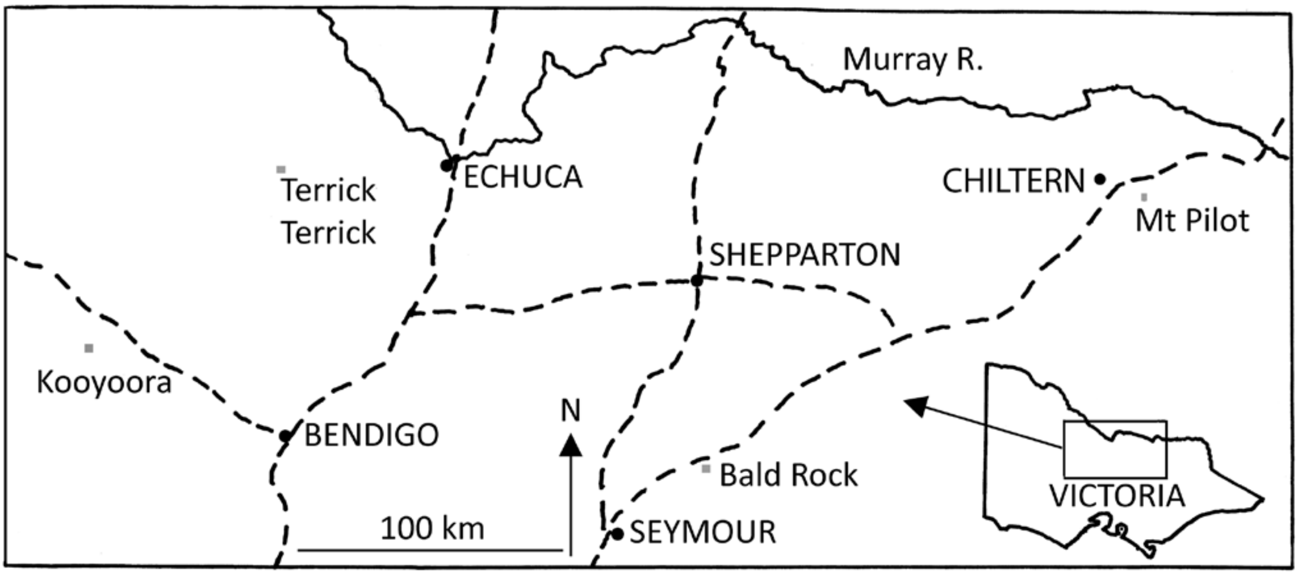

Figure 1: Map of north-central Victoria showing the four study sites with reference to major cities and roads (dashed).

advantage their populations, and some dipteran larvae are cryptobiotic to survive the dry periods (Jones 1971, 1974; Bayly 2011; Timms 2012a).

Victoria has many areas where granitic rocks outcrop, though inselbergs are uncommon (Hills 1940). These granites have different mineralogy to those of the cratons of Western Australia and South Australia and have very different ages (*ca* 400–450 Ma in Victoria and *ca* 3000 Ma in Western Australia, though surface exposures are much younger) (Johnson 2009). Bayly (2011) depicted a few Victorian gnammas and commented on their biology, but otherwise little is known of either the presence of gnammas or of their fauna and flora. Some granites are extensive but fractured and with isolated exposed bare rock surfaces (e.g. Kooyoora State Park, northwest of Bendigo); some have a few outcrops in a sea of granitic grus (e.g. Terrick Terrick National Park, west of Echuca); a few granites appear as isolated exposed surfaces on mountain tops (e.g. Mt Pilot near Chiltern); and an example of an inselberg is Bald Rock in the Strathbogie Ranges near Euroa (Figure 1).

The author has studied the gnammas in north-central Victoria, firstly to find as many as possible, and then to systematically study their biology. The following knowledge gaps for these gnammas have been addressed: (a) what habitat is provided, (b) how diverse are their fauna and flora, (c) what is the level of endemicity, (d) are there differences between shallow pans and deeper pits, and (e) is there evidence of adaptations to life in these temporary environments?

METHODS

Searching revealed 17 pan gnammas in five groups and 11 pit gnammas in Kooyoora State Park, five pan and five pit gnammas at Terrick Terrick, four pan gnammas on Mt Pilot and eight pan gnammas at Bald Rock, making 50 sites altogether (Figures 2–5) (Appendix 1). At Terrick Terrick, there were many nearby manmade artificial pools, decades old, whereas at all other sites the gnammas were the only water bodies in the vicinity. Other granite exposures in the Strathbogie Ranges and on Mt Buffalo had hardly any gnammas, and if present, they were so sparsely spaced to be accessed inefficiently for regular visits. The northwest flank of Mt Korong (near Wedderburn) had many gnammas but these were on private property and not accessible for this study.

Previous studies had shown five visits over two to three years were sufficient for species accumulation curves to plateau (Timms 2014a), but while this also applied to the present pan gnammas, most of the present pit gnammas needed eight visits for the curves to plateau. Field trips were held in June 2013, September 2013, April 2014, June 2014, September 2014, January 2015, June 2015, August 2015, October 2015 and February 2016. Visits were concentrated in the April to September period when almost all sites were likely to hold water. Late-spring and summer trips were uncommon as the pans were likely to be dry, though many pits still held water. The January 2015 trip was held to record the response to unusual summer rains.

On each visit to each pool, a water sample was taken to determine conductivity in µS/cm using an ADWA332 conductivity meter, while turbidity was measured in a Secchi disc tube calibrated in Nephelometric Turbidity Units (NTU). This tube does not measure turbidity lower than 5 NTU, so very clear waters are not accurately noted. Depth was determined with a stout tape measure and, when a pool was deemed full, its length and width were measured and volume calculated. Almost all gnammas at cross-section were shaped roughly like a parabola — the

Figure 2: Kooyoora pan 3, maximum diameter 2.85 m.

Figure 3: Mt Pilot pan 24, maximum diameter 4.1 m.

Figure 4: Bald Rock pan 28, maximum diameter 3.8 m.

pans a flattened parabola, and the pits a more typical hairpin parabola — and the same formula ($V = 2/3 \pi r^2 z$) was used to calculate their volume, where V = volume, r = average radius and z = depth. Site 10 was more like a rectangular box, so V = lwz was used, where l = length, w = width. Most pits, when discovered, were severely sedimented (probably due in part to the absence of Indigenous custodians), so on a preliminary trip in March 2012 they were excavated in part or in full (but not # 38, 46 and 48, as they were too big), with the proviso that superficial sediment likely to have resting crustacean eggs and plant stages was returned immediately afterwards (Anon, undated). This was done to restore the pits back to their more natural condition and hence to emphasise the difference in hydrology from the shallow pans.

To sample the microfauna in both types of gnammas, a small plankton net (opening 10 cm by 8 cm, length 50 cm, net mesh 159 µm) was used for one minute in areas in which the bottom sediment was stirred in order to catch benthic species as well as planktonic species. Microfauna smaller than *ca*150 µm were not studied. In the pans, macroinvertebrates were caught with a 12 cm diameter household sieve of 1 mm mesh, whereas in pits a pond net of 1 mm mesh and with an opening 25 cm wide, 20 cm high and 30 cm deep supported on a D frame and with a handle 1.8 m long was used. Both nets were swept through the water for two minutes. Experimental macroinvertebrate sweeps for shorter and longer periods suggested that 80–90% of species present were caught within two minutes. Macroinvertebrates were sorted alive in a white tray, and representatives of all species caught were preserved in alcohol for later identification, and the remainder returned alive to the pools, together with all tadpoles. The entire microfauna collection was preserved in alcohol for later study. Abundances were estimated on a log scale, the macrofauna from numbers in the sorting trays in the field and the microfauna from numbers as seen in petri dishes under the microscope. The same methods were used to create the WA and EP datasets used in comparative analyses.

To test questions of faunal relationships between these groups of gnammas, multivariate analyses calculated using PRIMER (v6) (Clarke & Gorley 2006) were used. The Victorian datasets included the four sets of pan gnammas and two sets of pit gnammas, with abundance values averaged over five visits for pans and eight visits for pits. In addition, the fauna of the selected pans and pits of the Western Australian Wheatbelt and Eyre Peninsula (Timms

Figure 5: Terrick Terrick pit 46, length 9.2 m.

2012a, 2012b, 2014a, 2014b) were compared using data from 30 pans on three inselbergs in each state. Averages over five visits were used for the three EP inselbergs and two WA inselbergs, but for one WA inselberg data from only three visits were available. For pit gnammas data from two of the five sets of ten pits in WA (Timms 2014b) and just ten pits from EP (Timms 2014a) were used. Field and laboratory counts were all log-transformed ($\log_{10}(x+1)$) and a similarity matrix constructed using the Bray–Curtis similarity coefficient. Non-metric multidimensional scaling (NMDS) ordination was then performed to visualise patterns in assemblage composition among the datasets. Where appropriate, one-way analyses of similarity (ANOSIMs) were used to test for differences among groups followed by SIMPER (similarity percentages) analysis of the species contributing to group similarities and differences. The correlation coefficient was used to test a possible relationship between gnamma size and momentary species richness (MSR) and a student's t-test to look for significant differences between MSR means.

RESULTS

Physicochemical features

Studied pans ranged in size from average diameters of 105–595 cm and 5–22 cm deep, with many in the range of 200–300 cm diameter and 7–10 cm deep (Table 1). Some

Table 1: Some physicochemical features of central Victorian gnammas.

Sites	Depth (cm) mean ± SE	Volume (L) mean ± SE	Conductivity (µS/cm) mean ± SE	Turbidity (NTU) mean ± SE
Kooyoora pans	10.1 ± 1.0	219 ± 35	67 ± 5	19.9 ± 3.5
Terrick Terrick pans	9.8 ± 1.7	551 ± 227	65 ± 11	8.3 ±2.2
Mt Pilot pans	9.2 ± 1.1	320 ± 133	37 ± 3	10.4 ± 2.6
Bald Rock pans	7.1 ± 0.6	111 ± 13	74 ± 7	11.7 ± 0.9
Kooyoora pits	34.0 ± 3.6	748 ± 351	42 ± 10	17.5 ± 2.0
Terrick pits	72.6 ± 12.6	14593 ± 8431	90 ± 20	29.5 ± 8.7

pans were omitted at Kooyoora, Mt Pilot and Bald Rock due to their small size (<100 cm largest diameter) and shallowness (<4 cm deep). The smallest and shallowest pans occurred on Bald Rock, the largest at Terrick Terrick and the deepest at Kooyoora. The Kooyoora averages were inflated by one relatively deep pan, which featured a deeper area associated with an opened vertical joint — in a sense it had some features of a pit gnamma.

Pan conductivities ranged from 13–326 µS/cm with means in the 37–74 µS/cm range (Table 1). Lowest values were recorded at Mt Pilot and highest values at Bald Rock. Pan turbidity ranged from 5–100 NTU (but note values of less than 5 probably occurred, constrained by the measuring device) with averages between about 8 and 20 NTU. Terrick Terrick waters were slightly clearer than elsewhere, while Kooyoora waters were on average slightly more opaque. In all pools, the lowest conductivities and clearest waters occurred after major infills and generally higher values were recorded when water levels were low. High turbidity in the large Terrick Terrick pits was due to algal blooms.

Pit gnammas were found only at Kooyoora and Terrick Terrick (Appendix 1). Those at Kooyoora were generally smaller than the pans, but on average three times deeper, while average size and depths were much greater at Terrick Terrick due to three very large pits (see sites 46, 48 and 49 in Appendix 1) (Table 1). These could be deeper than measured because accumulated bottom sediments were not removed before the study; similarly for Kooyoora pits 38, 43, 44 and 45.

Almost all sites overflowed during the study, probably many times for most pans. All pans dried in September–

Table 2: Number of gnammas with various plants.

	Pans				Pits	
	Kooyoora	Terrick	Mt Pilot	Bald Rock	Kooyoora	Terrick
Species No. of sites	17	5	4	8	11	5
Callitriche stagnalis Scop.	17	5	4	8	7	1
Nitella sp.					1	
Crasulla nr *natans* Thunb.		1			2	2
Glossostigma sp.	9	3			1	2
unidentified grammaceae	3	2				1
Isoetes pusilla Marsden & Chinnock	9		4		1	1
Limnosella curdieana F. Meull.	1		1			
Eleocharis acuta R. Br.					1	2
Elatine gratioloides A. Cunn.					3	
Lemna sp.						4
Lepileana australis Drumm. ex Harvey						2
Myrophyllum nr *verrucosum* Lindl.						2
Otellia ovalifolia (L.) Pers.						3
Potomogeton tricarinatus F. Muell. & A. Benn, ex A. Benn.						2
Vallisneria sp.						3

Table 3: Species richness.

Sites	Number	Momentary SR		Cumulative SR	
	of sites	mean	range	mean	total
Kooyoora pans	17	6.5	4.8 - 7.8	13.3	42
East Track	6	7.0	5.4 - 8.0	21.5	
Caves and Leaches Rd	4	6.7	5.2 - 7.8	12.2	
Kirwan Rd	3	6.7	5.8 - 7.8	11.7	
Brenanah Rd	4	5.5	4.8 - 7.0	13.2	
Terrick Terrick pans	5	9.3	7.0 - 12.4	20.2	32
Mt Pilot pans	4	5.1	4.2 - 5.9	14.2	21
Bald Rock pans	8	2.7	1.2 - 3.2	6.1	13
Kooyoora pits	11	7.6	4.5 - 10.0	20.0	43
Terrick pits	5	15.3	11.4 - 18.7	40.6	69

October each year and usually did not fill till April–May, though summer rains caused brief partial fillings. The pits also filled at the same time as the pans, but persisted longer each spring and some into summer. The three large pits at Terrick Terrick were not observed to overflow, though water could have seeped out through adjoining soils in sites 48 and 49. Both of these dried in some summers, but their bottom muds remained moist; site 46 never dried during the study.

Aquatic plants

Typically the study gnammas supported swards of aquatic plants (Table 2), most numerous each July to September, and seasonally later in the deep pits of Terrick Terrick. *Callitriche stagnalis* was by far the most common species and was recorded in all pans and many pits. *Isoetes pusilla* occurred commonly in the Mt Pilot and Koorooya pans, but hardy elsewhere. Otherwise the pans had few species: five at Kooyoora, four at Terrick Terrick, three at Mt Pilot and two at Bald Rock. In contrast, the pits were species rich, especially the larger pits (seven species in Kooyoora and thirteen at Terrick Terrick). Except for *C. stagnalis* at Kooyoora, pit species were largely different from those in pans, not dominant, ubiquitous, or persistently present.

During winter and spring (and onwards into summer in the deep pits), filamentous algae enshrouded the higher plants: *Spirogyra* sp. and the filamentous diatom *Aulacoseira* sp. were the most common.

Invertebrate species richness

Mean momentary species richness (MSR) for the 34 pans ranged from 1.2 to 12.4, with a grand mean of 5.9 (Table 3). Terrick Terrick pans were the richest (mean 9.3) and the Bald Rock pans by far the poorest (mean 2.7). The largest group of pans at Kooyoora had a value of 6.7. Cumulative species lists for these pans were 2.4 to 3.3 times higher and reached 30 in one large pan at Terrick Terrick, 28 and 26 taxa in two large pans at Kooyoora, but otherwise maximal values were rarely more than 21 taxa. The pan metacommunity at Kooyoora numbered 42 taxa, at Terrick Terrick 32 taxa, at Mt Pilot 21 taxa and at Bald Rock 13 taxa, with a grand total of 50 taxa for pans in north-central Victoria (Table 3).

Table 4: Characteristic species in central Victorian gnammas.*

Gnammas	Per cent explained	Taxa in order
Kooyoora pans	78%	*Sarscypridopsis, Aedes, Heterocypris, Dasyhelea*
Terrick Terrick pans	87%	*Sarscypridopsis, Heterocypris, Aedes, Armatalona*
Mt Pilot pans	86%	*Dasyhelea, Sarscypridopsis*, nematodes, *Aedes*
Bald Rock pans	87%	*Sarscypridopsis,* nematodes, *Armatalona*
Kooyoora pits	75%	*Sarscypridopsis, Aedes, Heterocypris, Ceriodaphnia*
Terrick Terrick pits	54%	*Sarscypridopsis, Heterocypris, Mesocyclops, Boeckella, Moina, Daphnia*

*As determined by PRIMER and SIMPER

Despite the variability in species richness across the area, the dominant species were almost uniform in each set of pans: the ostracod *Sarscypridopsis* sp., followed by the mosquito *Aedes alboannulatus* (Macquart) *sensu lato*, then perhaps the ostracod *Heterocypris* sp. or the chydorid cladoceran *Armatalona imitatoria* (Smirnov) or the ceratopogonid *Dasyhelia* sp. (Table 4). The Bald Rock pans deviated the most from this hierarchy as they lacked mosquitoes, while at Mt Pilot, *Dasyhelea* sp. was particularly common.

Species richness in the two sets of pit gnammas was quite different, though their dominant invertebrates were similar (Table 3). For the Kooyoora pits, mean MSR ranged from 4.5–10.0, with a mean of 7.0, which matches the values for their pan gnammas in the same region. Dominant species were almost the same in pits and pans, with *Ceriodaphnia* sp. an extra in the pits. Richness, however expressed, was about twice as great in the larger Terrick Terrick pits, in which there were many isolated occurrences of beetles and true bugs and a few extra species e.g. molluscs and leeches (Table 3), perhaps facilitated by their permanence or semi-permanence. As in most other gnamma groupings, *Sarscypridopsis* sp. was dominant and *Heterocypris* sp. common, though *Mesocyclops notius* Keifer was abundant in most Terrick Terrick pits, as were a number of species common in ordinary ponds, e.g. *Moina* spp., *Ceriodaphnia* sp., *Daphnia carinata* King, *Boeckella triarticulata* Thomson, *Agraptocorixa* spp., *Micronecta* sp., *Anisops*, spp., *Chironomus* spp., odonatans, and mayflies, while some common pan species such as *Aedes alboannulatus* and *Dasyhelea* sp. were also present, but not common. Overall 73 taxa were encountered in the pit gnammas, and given the similarly of pan fauna when their species were added, the grand total was 81 taxa (Figure 6, Appendix 2).

Endemism

Of the taxa fully identified, only one is endemic to gnammas. The clam shrimp, *Eulimnadia gnammaphila* Timms, has been found so far only in pan gnammas across southern Australia (Timms 2016a), including a few at Kooyoora. The ostracod species near *Tonnacypris* in two Bald Rock pans is certainly a local endemic species and may be an undescribed genus (S. Halse, pers. comm.). The copepod *Mesocyclops notius* and the cladoceran *Armatalona imititoria* are most common in gnammas, but also occur in other habitats (Russ Shiels, pers. comm.). There could be endemic species among the unidentified ostracods, perhaps among *Cypretta* and *Heterocypris,* which have multiple species in Western Australian gnammas (S. Halse, pers. comm.; K. Martens, pers. comm.). All insect inhabitants were of widespread eurytopic species.

Biology

Eulimnadia gnammaphila occurred only briefly soon after the pans first filled from dryness, usually in April–May, but also following significant summer rains. It was found only in a few pans (sites 1, 4, 5 and 12), grew quickly with adults appearing in about a week and persisting only a couple of weeks (K. Lee, pers. comm.), so that it was not present from May–June onwards. On field trips early in the season, emerging chironomids, ceratopogonids and mosquitoes were commonly observed, but they also emerged throughout the year (except in winter) and especially if the weather was calm. The chironomid *Paraborniella tonnoiri* Freeman and the ceratopogonid *Dasyhelea,* if found in dried sediments, could be revived by wetting. The same microcrustaceans occurred throughout the yearly cycle, suggesting little seasonal or successional replacement of populations. Except for a few dipterans, notably *Aedes, Paraborniella* and *Dasyhelea*, the beetle *Sternopriscus multimaculatus* (Clark) and the boatman *Agraptocorixa hirtifrons* (Hale), most insect appearances were sparse and sporadic. Many bugs and beetles bred in small numbers in the gnammas, most obviously in the large pits at Terrick Terrick.

Distributions

While many active dispersers such as beetles, bugs and water mites were of limited occurrences, even some of the more common species were not found throughout the area (see Appendix 2). Most striking was the absence of the almost ubiquitous mosquito *Aedes alboannulatus* from the exposed Bald Rock. This rock and Mt Pilot lacked other supposed active dispersers, e.g. *Cloeon* sp. on Bald Rock and *Paraborniella tonnoiri* on both. Less surprising is the patchy distribution of some passive crustacean dispersers: (i) *Eulimnadia gnammaphila* was found only in a few Kooyoora pans, even absent in pans adjacent to ones with it; (ii) *Moina micrura* Kurz occurred in just one group of Kooyoora pans and was apparently absent in all other pans; (iii) *Neothrix* sp. was absent in one group of Kooyoora pans but present in all others; (iv) *Cypretta* sp. was widespread, even in some Bald Rock pans, but was absent from two Kooyoora groups; (v) *Limnocythere* sp. occurred in just two groups of pans, Terrick Terrick and Mt Pilot; (vi) the widespread *Heterocypris* sp. was absent on one Kooyoora group and also Mt Pilot and Bald Rock, and (vii) the apparent endemic and new ostracod near *Tonnacypris* occurred (S. Halse, pers. comm.) in only two pans at Bald Rock.

In almost all instances, the study gnammas were well removed from other waterbodies, but the Terrick Terrick sites were among many other temporary waters,

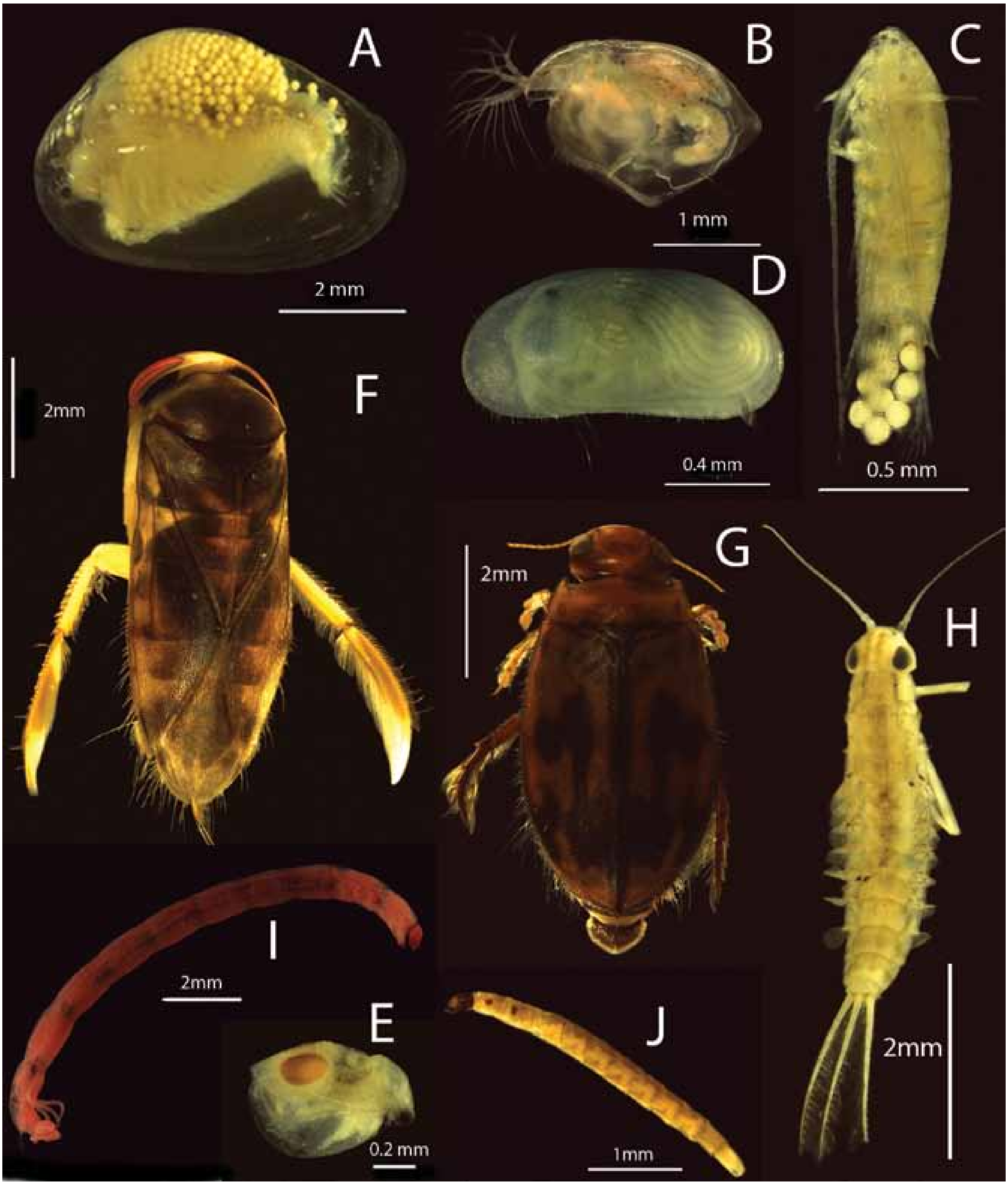

Figure 6: A few invertebrates of Victorian gnammas. A, clam shrimp *Eulimnadia gnammaphila*; B, cladoceran *Simocephalus acutiroistratus*; C, copepod *Boeckella triarticulata*; D, ostracod *Candoncypris* sp.; E, cladoceran *Ceriodaphnia* sp. with ephippial resting egg; F, boatman *Agraptocorixa hirtifrons*; G, diving beetle *Megaporus howitti*; H, mayfly *Cloeon* sp.; I, chironomid *Chironomus alternans*; J, ceratopogonid *Dasyhelea* sp. Note the various scales. Images courtesy of Claire Sives.

as explained earlier. The Terrick Terrick pans had many species not found elsewhere, perhaps influenced by these sources. Among the species found only in these pans were *Triops australiensis* (Spencer & Hall), *Simocephalus acutirostratus* (King), *Alona rigidicaudis* (Smirnov), and *Newnhamia* sp.; these all occurred in the artificial sites as well (author, unpublished data). The pits at Terrick Terrick had an even greater number of unique species, but many of these (e.g. snails, leeches, limpets) rarely occurred in the artificial sites, so there may be other reasons for their presence, such as the semi-permance/permanence of two Terrick Terrick pits.

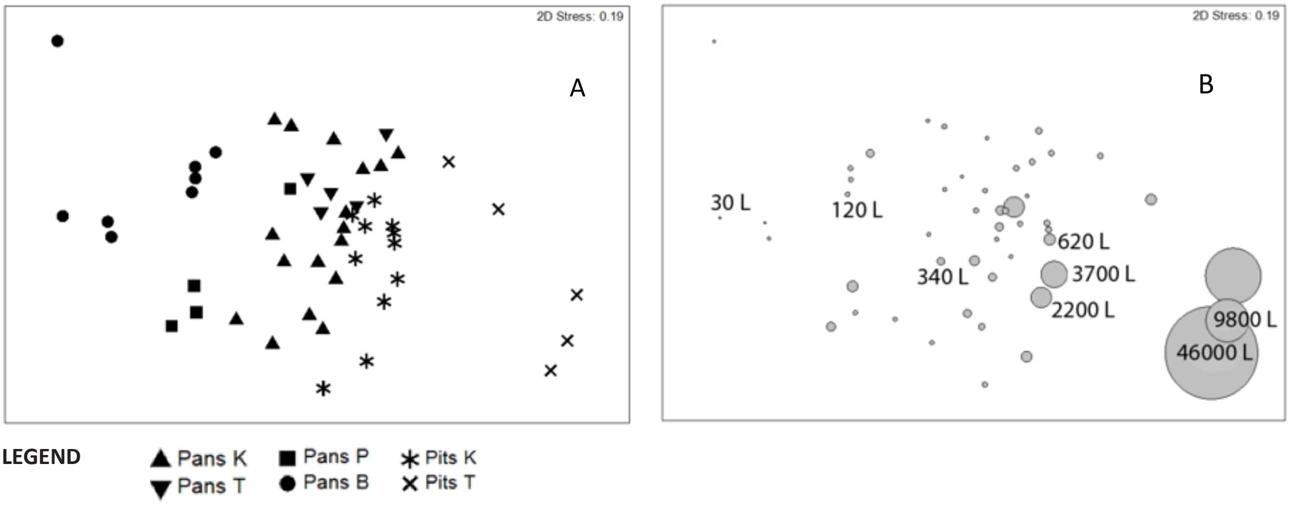

Figure 7: A, ordination of the north-central Victorian pan and pit gnammas; B, ordination of the same gnammas, but showing each gnamma according to its volume in litres.

Community relationships

Multivariate analyses of the pans and pits by district (the Kooyoora pans from the four sub-areas at Kooyoora were considered as one) (Figure 7) show no distinct groupings but a gradation from the small pans of Bald Rock and Mt Pilot on the far left of the plot to the larger pans of Kooyoora and Terrick Terrick, to the pits of Kooyoora and Terrick Terrick, with the three large Terrick Terrick pits forming a subgroup to the far right of the ordination. However, when Victorian pans and pits are compared with those in WA and SA (Figure 8) there are distinct groupings by state for pans, but much less so for pits. For the latter, the smaller Victorian pits at Kooyoora separate to the lower right of the ordination while the larger Terrick Terrick pits lie with the WA pits (which also tend to be relatively large (Timms 2014b)). Also, Figure 8 shows the SA pits are placed adjacent to the WA pits and removed somewhat from the Victorian pits.

Habitat size, a surrogate for hydroperiod in these temporary habitats, is an important factor influencing diversity. For pans, the correlation coefficient between volume and MSR is r = 0.519 (df = 33) and for pits r = 0.769 (df = 15), both significant at P = 0.001. For both habitats combined, Figure 7 illustrates the role of habitat size in similarities and differences between the six entities.

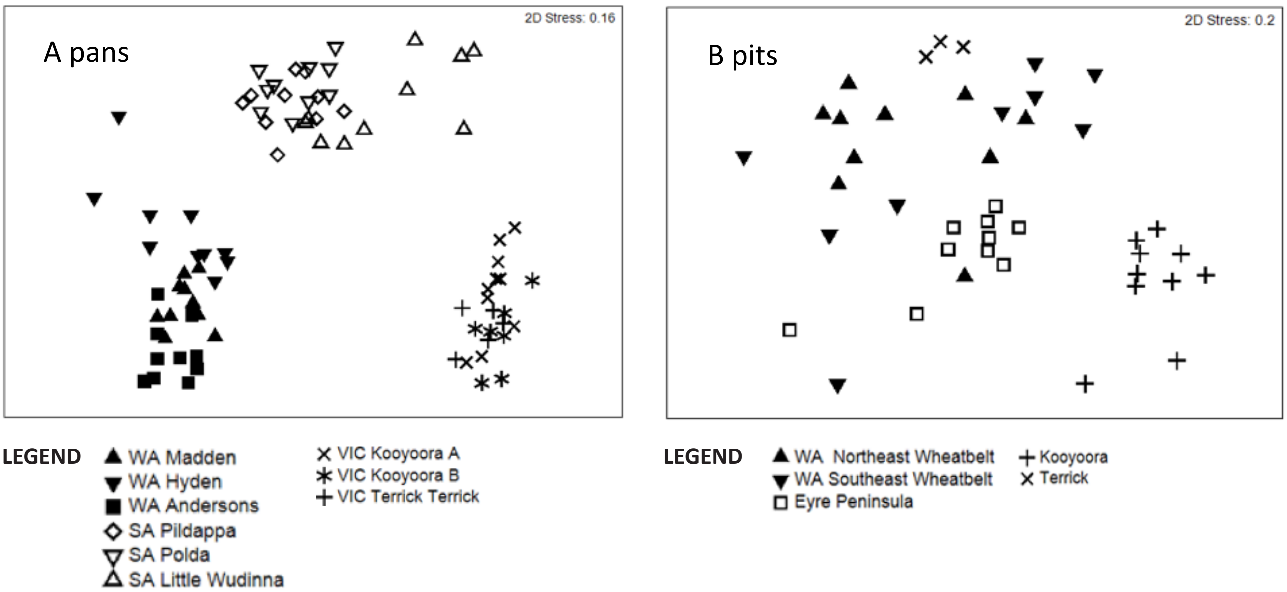

Figure 8: A, ordination of nine groups of pan gnammas from across southern Australia showing distinct organisation by state; B, ordination of five groups of pit gnammas from across southern Australia showing hardly any organisation by state.

DISCUSSION

Despite some differences between the four areas and two types of gnammas, the central theme is one of low species richness, dominance by just a few widespread species, only one endemic species and few special adaptations for life in these Victorian gnammas. Of course the crustaceans have the general adaption of producing resistant eggs and the same cryptobiotic species (*P. tonnoiri* and *Dasyhelea* sp.) occur in Victoria too, but there are no other life cycle adaptations (e.g. early emergence of cyclopoid copepods) or UV protective pigmentation in Victorian species.

Habitat size, a surrogate for hydroperiod in these temporary habitats, is an important factor influencing diversity as the above correlations and Figure 7 illustrates. This is an expression of the permanency gradient theory enunciated by Wellborn et al. (1996) and has been shown previously in Australia for pit gnammas in Western Australia (Timms 2014b). Habitat size and related hydro-regime are key features of temporary habitats worldwide (Vanschoenwinkel et al. 2009).

The pan gnammas studied in Victoria are about as diverse as the Sydney Basin rock pools (Bishop 1974) and a few granitic pools at Moonbi on the southern edge of the New England Tableland (Timms 2016c). Exact comparisons cannot be made due to the different methodologies used in these studies, but the meta-communities at Kanangra Walls and North Head (both Sydney Basin) have about twenty species, including a clam shrimp, copepods, ostracods and insects such as *Paraborniella tonnoiri* and *Dasyhelea* sp., while the larger Moonbi pools have 41 species, again with largely the same components as in the Sydney Basin rock pools.

These Victorian pan gnammas (and other gnammas in southeastern Australia as noted above), are less diverse than those on Eyre Peninsula, though the meta-community (as measured by cumulative species richness) is similar in each state. It is the individual pan gnammas in Western Australia that are particularly diverse (about three times that in Victoria) (Table 5). The meta-community on each WA inselberg is about a third more diverse than in Victoria and Eyre Peninsula, while the total regional fauna in WA is far more diverse (260 species versus 50 species in Victoria, but protistians and rotifers are poorly studied in this work; without them the comparison is 221: 49). The state and inselberg figures for Western Australia are inflated by pan gnammas occurring over a much wider area and being more numerous per rock outcrop compared to those studied in central Victoria (Pinder et al. 2000; Timms 2012a, 2012b). Pinder et al. (2000) explained the unusual high diversity in the WA pans as being a product of speciation during past climate changes. In addition there are hundreds of pan gnammas on some rocks (Timms 2012b) and thousands across the Wheatbelt and Goldfields that add habitat heterogeneity and hence more niches, both tending to enhance meta-community diversity (Pinder et al. 2000). Also there is some regionalisation in faunal composition across southern WA (Bayly 1982, 1997; Pinder et al. 2000; Timms 2012b). Pan conductivity and turbidity, while a little different between states, are of no consequence.

Table 5: Comparisons of gnammas in southern Australia.

State	Central Wheatbelt, West. Aust.*			Eyre Peninsula, Sth Aust.*			Central Victoria	
Pans	Madden	Hyden	Yanney	Pildappa	Polda	L Wudinna	Kooyoora	T. Terrick
Number	10	10	10	10	10	10	10	5
Maximum depths (cms)^	17.0 ± 2.0	18.9 ± 1.6	15.8 ± 2.4	15.6 ± 1.3	18.1 ± 1.6	17.7 ± 1.9	11.5 ± 1.4	9.8 ± 1.7
Volume (litres)^	5544 ± 3352	2094 ± 655	2039 ± 768	540 ± 99	1900 ± 652	1130 ± 270	194 ± 42	551 ± 227
Conductivity (µS/cm)^				522 ± 41	734 ± 53	436 ± 115	65 ± 7	65 ± 11
Turbidity (NTU)^				11.8 ± 2.3	5.9 ± 0.7	12.4 ± 2.7	18.2 ± 39.4	8.3 ±2.2
CSR	51	41	41	29	33	32	33	32
MSR^	30.7 ± 1.0	26.6 ± 4.1	29.5 ± 3.0	9.0 ± 0.3	11.0 ± 0.4	9.0 ± 0.5	6.9 ± 0.3	9.3 ± 1.0
Pits	Pits NE	Pits Mid			all areas		Kooyoora	T. Terrick
Number	10	10			`10		11	3 biggest
Maximum depths (cms)^	78.0 ± 13.6	63.0 ± 8.3			46.2 ± 4.5		34.0 ± 3.6	76
Volume (litres)^	20020 ±10488	1062 ± 383			1318 ± 307		748 ± 351	23924
Conductivity (µS/cm)^	154 ± 49	154 ± 39			331 ± 67		42 ± 10	84
Turbidity (NTU)^	19.3 ± 5.0	20.2 ± 3.9			73.9 ± 32.2		17.5 ± 2.0	39
CSR	58	57			42		43	69
MSR^	12.1 ± 1.6	7.5 ± 0.7			9.1 ± 0.6		7.6 ± 0.5	17.3

* Based on data in Timms 2012a, 2014a, 2014b; ^ values given as means ± SE, except only mean for Terrick Terrick pits.

While there are differences in diversity in the pit gnammas in each state, there is little biogeographical difference — the dominant insects in each are the same widespread eurytopic species, though the crustaceans vary a little (Timms 2014a, 2014b). Instead, the difference in diversity between states in the pit gnammas (Table 5) is explained by habitat-size differences (r = 0.931, df = 4, P = 0.01). The above state-based differences in pan gnammas influence the contrast between pans and pits in the three states; multivariate analyses of differences between pan and pit gnammas in each state show a vast difference in Western Australia (Timms 2014b), a small difference in Eyre Peninsula (Timms 2014a) and little difference in the Kooyoora group (gnammas roughly the same size), but a large difference in the Terrick Terrick series (gnammas very different is size) (Figure 7, Table 5). Different species dominate in the comparison of pans and pits in Western Australia and Eyre Peninsula, but the dominants (namely *Sarscypridopsis* and *Aedes*) are similar in pans and pits in Victoria, with some addition of common species in the large Terrick Terrick pits (Table 4).

The above difference in pan gnammas between states is further revealed by a limited multivariate analysis of communities for a few areas in each, all except one with ten gnammas per group studied in the same way (Figure 8). Pan gnammas in each study area group together, and moreover they group together by state, so that state biogeographical differences are more influential in determining community structure than other factors studied. This has previously been shown by continent, but not within a large land mass (Jocqué et al. 2010).

However, in contrast, pit gnammas show little differentiation between states (Figure 8B), as might be expected by the strong influence of size on their species diversity. Again, local groups of pit gnammas had similar communities, but these overlapped across the continent. The separation of the two Victorian groups so that the large Terrick Terrick pits lay near the equally large northeast Wheatbelt pits of WA, with the small Kooyoora pits well away, proved state relationships were overshadowed by the influence of habitat size. Differences in pit species richness were not aligned with minor differences in community structure between pit groups.

Two basic dispersal modes are exhibited in these gnammas — active and passive dispersal (*cf.* Jocqué et al. 2010). The active dispersers include all the insects, though many of these are restricted in these gnammas by small habitat size, as seen in the contrast between 43 species in the large pits at Terrick Terrick and just five species in the small pans at Bald Rock (Appendix 2). Even the ubiquitous *Aedes abloannulatus* is absent in the Bald Rock sites, though in this case it is thought the exposed position may be inimical to weak-flying dispersers. By contrast the passive dispersing crustaceans — e.g. *Sarscypridopsis, Heterocypris, Cypretta, Ilyodromus, Armatalona* and *Neothrix* — are more widely represented (Appendix 2), though there are some curious omissions and concentrations, as cited above, possibly due to inferior dispersal mechanisms. Molluscs are restricted to the most permanent sites at Terrick Terrick, as most have little ability to withstand dryness, whereas this is not a problem for the crustaceans with their drought-resistant eggs.

CONCLUSIONS

Gnammas in central Victoria occur in scattered small groups and except for some at Terrick Terrick are relatively small. Both pan and pit gnammas are dominated by the ostracod *Sarscypridopsis* and the mosquito *Aedes* and have an overall average of less than ten species momentarily, though the large Terrick Terrick pits are almost twice as speciose. Cumulative species richness is higher at *ca* 30 in pans and 40–70 in pits, and with 81 species recognised in the meta-community. Habitat size is particularly important in differentiating taxon richness between gnamma groups.

Compared with gnammas across southern Australia, pits and pans are little different from each other in central Victoria as against the marked difference in Western Australia. This is due largely to the extremely rich and distinct fauna in pans of *c*a 30 taxa momentarily and a community across the vast Wheatbelt of *ca* 230 taxa. The central Victorian gnammas have just one endemic and few special adaptations for survival, other than resting eggs in the crustaceans, in contrast to the situation in Western Australia. The differences are associated with speciation in gnammas in isolated rock outcrops during past climate changes in Western Australia, coupled with widespread occurrence and abundance of gnammas and their generally larger size in Western Australia. All three factors promote diversity in the west.

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