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Keys to the Australian clam shrimps (Crustacea: Branchiopoda: Laevicaudata, Spinicaudata, Cyclestherida)

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Abstract The morphology and systematics of clam shrimps is described followed by a key to genera. Each genus is treated, including diagnostic features, list of species with distributions, and references provided to papers with keys or if these are not available preliminary keys to species within that genus are included.

Keywords gnammas, freshwater, crustaceans, morphology

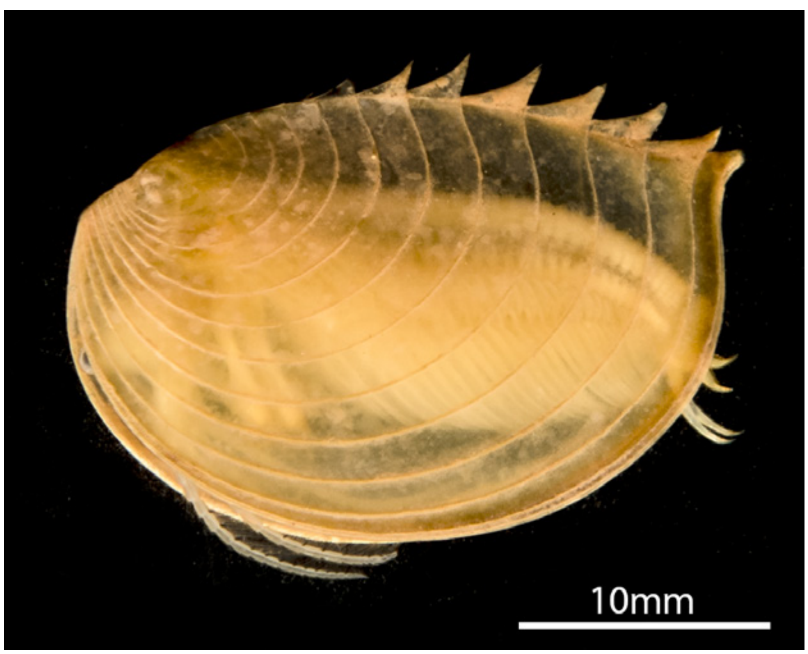


Figure 1: *Limnadopsis birchii* – Worlds largest clam shrimp.

Introduction

Australia has a diverse clam shrimp fauna with about 78 species in nine genera recognised in 2017 (Rogers *et al.*, 2012; Timms, 2012, 2013; Schwentner *et al.*, 2012a,b, 2013a,b, 2015b,a; Timms & Schwentner, 2017; Tippelt & Schwentner, 2018) . This is an explosion from 26 species in 2008 (Richter & Timms, 2005; Brendonck *et al.*, 2008) when Australia's proportion of the world fauna was about 15%; now it is about 30%. It is anticipated another five species will be described before 2020.

There have been two periods of active research on Australian clam shrimps, the first from 1855 to 1927 with a peak around the turn of century and then recently from 2005 to the present with a peak in 2015-6 (Figure 2).

Only one species was added to Australia's fauna in the period 1928 to 2004. The early period was dominated by European taxonomists, many of whom relied on local collectors. Initially species were described from around Sydney (e.g. what is now known as *Paralimnadia stanleyana* – the first clam shrimp described from Australia), Melbourne, Perth and south-east South Australia, but soon attention was turned to the inland where cyzicid shrimp inhabiting turbid waters were encountered. The second peak is due to two factors – my work on two species-rich genera which had earlier been almost ignored (Timms, 2016a,b) and species differentiated by molecular means by visiting researcher Martin Schwentner in a series of publications (Schwentner *et al.*, 2012a,b, 2013b,a, 2015b,a; Tippelt & Schwentner, 2018). Actually there was a fore-runner to Schwentner's works: another German researcher, Stefan Richter, came to Australia in 2004 and together with me, restarted work on Australian clam shrimps by assessing what had been described over the years and adding one new species to the list (Richter & Timms, 2005).

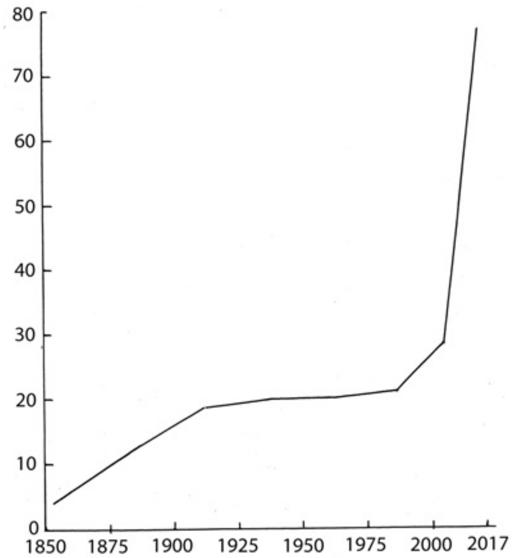


Figure 2: Number of known species of Australian clam shrimps over time.

Systematics

Ideas on the relationships between the branchiopod groups and their classification have changed markedly over the decades, though for the last few years the scheme shown in Figure 3 has been widely accepted for a decade now. It is clear clam shrimps are polyphyletic, so that the old term for them, the Conchostraca, is no longer valid, and has not been since the 1980s.There are three separate groups in two orders, the pea shrimps (Order Laevicaudata), and the remaining taxa in the order Diplostraca with the spiny clam shrimps (suborder Spinicaudata) and the little *Cyclestheria* (suborder Cyclestherida) with the last group closely related to the numerous cladocerans (suborder Cladocera). The term Diplostraca is used to encompass all these groups, except the Laevicaudata. The old term Phyllopoda is also no longer used; it used to include the fairy shrimps (Anostraca), the shield shrimps (Notostraca) and the clam shrimps (Conchostraca).

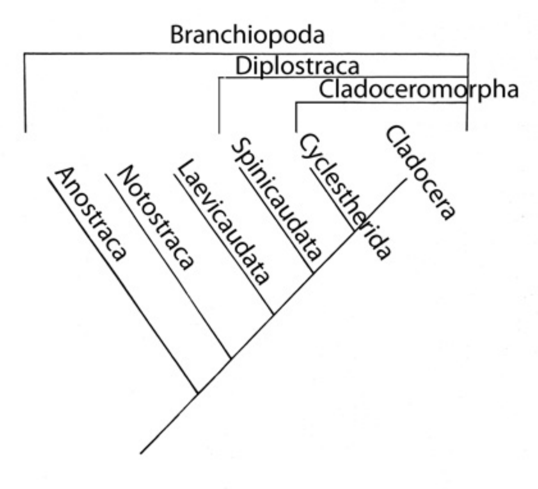


Figure 3: Phylogeny of the Branchiopoda (after Richter *et al.* 2007; Olesen 2009).

Morphology of clam shrimps

Branchiopods are primitive crustaceans characterised by: similar larval morphology; foliacious limbs; a body of a head, trunk and telson; and almost all living in temporary waters and having eggs resistant to desiccation. Those with a bivalved carapace and using one or two pairs of claspers are the clam shrimps and cladocerans, which are contained within the orders Laevicaudata and Diplostraca.

The head consists of a few segments which encompass a rostrum, compound eyes (usually completely fused into one in clam shrimps), an ocellus, two pairs of antennae and various mouthparts including a mandible and one or two pairs of maxillae (figure 4). Detailed structure of the head is different in each of the families. The trunk is composed of many similar segments, common segment numbers are 10, 16, 18, and 22-26, with just a few *Limnadopsis* having more (*eg* 32 segments in *L. birchii*). Each trunk segment bears a pair of foliacious limbs, the thoracopods. Typically the thoracopods vary in complexity and are smaller and less complex posteriorly. The telson usually has two rows of spines on the functionally dorsal side (really the posterior edges) and a moveable claw, the cercopod, the most posterior body part. The body is enclosed in a bivalve carapace attached by muscles originating just behind the head. This carapace is of standard shape for each major group and usually has growth lines and perhaps its surface is marked in various patterns.

Clam shrimps are notoriously variable, especially in the details of the rostrum, number of spines on the telson, and number of growth lines, but also the number of lobes on the first antenna and antennomeres of the second antenna. If such features are used in the keys be prepared for 10-20% variation.

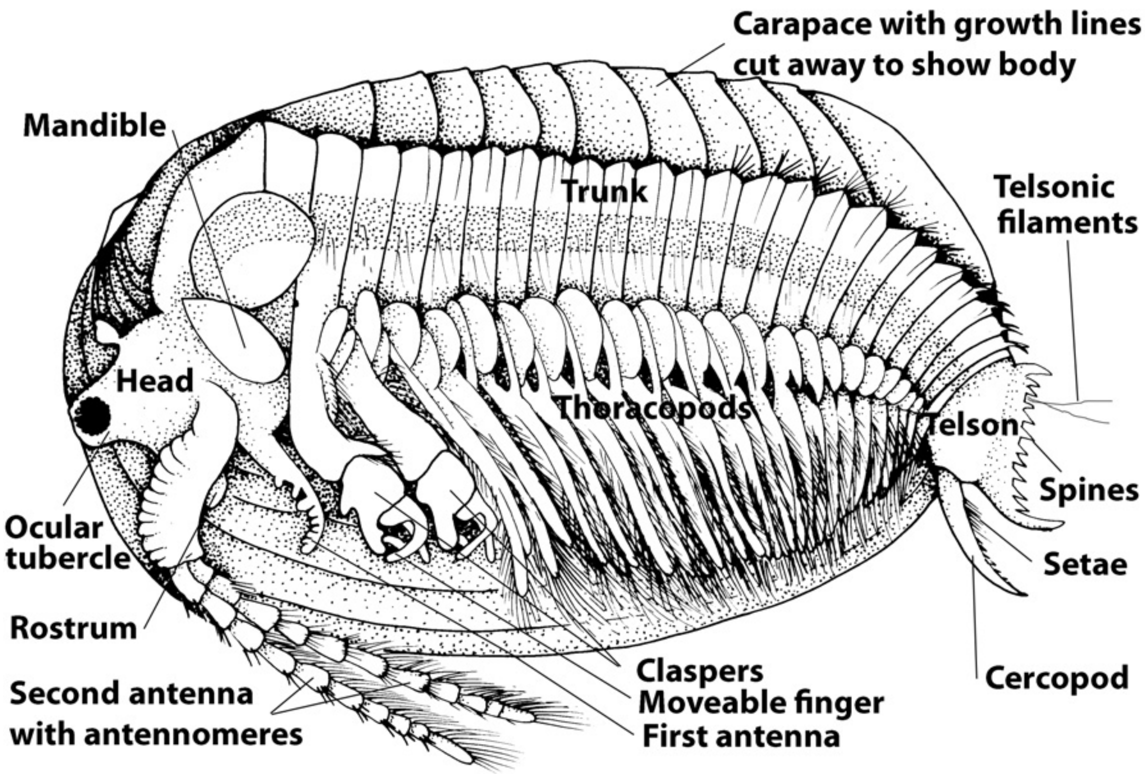
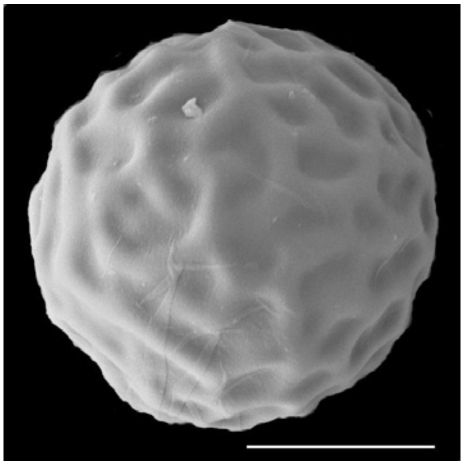
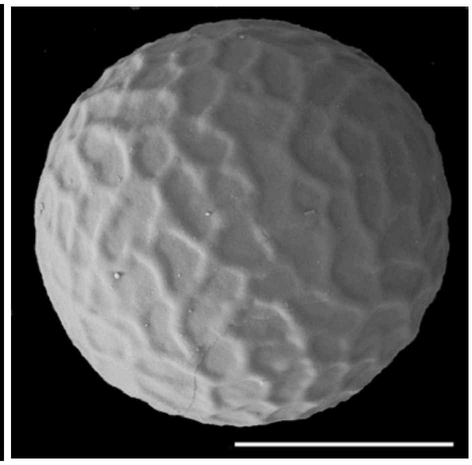


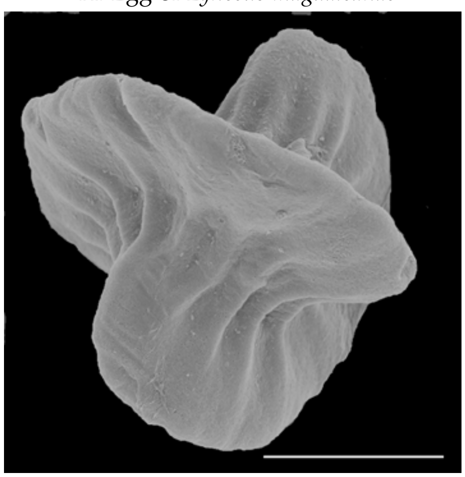
Figure 4: Clam shrimp (*Limnadopsis pilbarensis*) with parts labelled. Image courtesy Jane McRae.



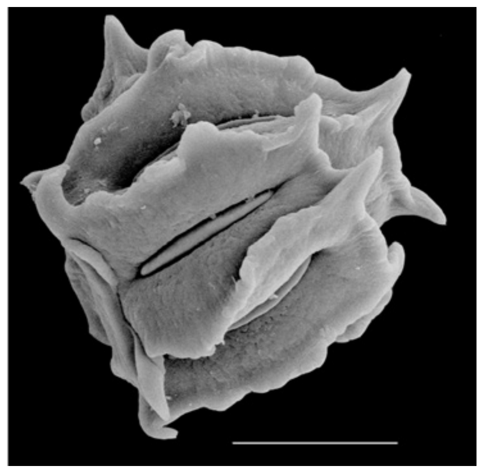
A: Egg of *Lynceus magdaleanae*



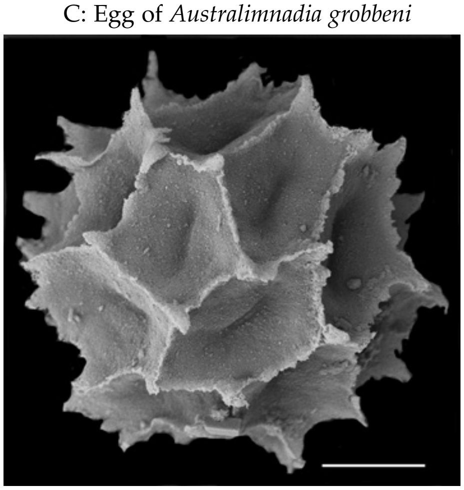
B: Egg of *Ozestheria lutraria*



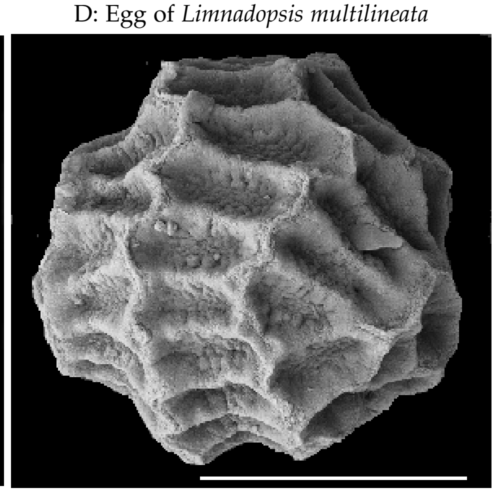
C: Egg of *Australimnadia grobbeni*



D: Egg of *Limnadopsis multilineata*



E: Egg of *Eulimnadia dahli*



F: Egg of *Paralimnadia stanleyana*

Figure 5: Eggs of representative species of clam shrimp. SEM scale bars 0.1 mm.

Keys to Families and Genera of clam shrimp

1. Carapace laterally compressed with few to many growth lines 2
   Carapace spherical .. **Lynceidae** *Lynceus*

2. Carapace lateral outline roughly rectangular, oblong, or oval (never circular); telson with many short spines except the last one; when mature > 4mm; found in temporary waters 3
   Carapace lateral outline circular; telson with a few long spines, decreasing in length anteriorly; mature specimens < 4 mm; generally in vegetation in permanent waters **Cyclestheridae** *Cycthestheria*

3. No spine on the rostrum; telson with coarse dorsal spines, usually unequal; length:height ratio of carapace about 1:1.5 4
   Spine protruding anteriorly from rostrum; telson with many fine subequal dorsal spines; carapace length:height about 1:2 ... **Leptestheriidae** *Leptestheria*
   [Rarely *Eocyzicus* may have a rostral spine, but the other two characters put it in the correct couplet]

4. Clam shrimp head elongated and with an occipital notch; rostrum with a dorsal groove; valves thick and swollen with umbone well developed; mate amplexing venter to venter .... **Cyzicidae** 5
   Clam shrimp with a head sub-spherical and without an occipital notch; rostrum midline the highest part; valves thin with no or limited umbone ... **Limnadiidae** 6
   [3 of the 4 genera in the Limnadiidae in Australia amplex in line, the exception being *Eulimnadia*]

5. Males with a triangular rostrum; posterior trunk segments with several dorsal spines .... *Ozestheria*
   Males with broad hatchet-like rostrum (*ie* subrectangular to spatulate); posterior trunk segments with one dorsal spine .... *Eocyzicus*

6. Scaliform setae on the apex of the finger of the clasper; setal row on cercopod terminates in 1-6 spines .... *Limnadopsis*
   A small suction disc on the apex of the clasper finger; setal row on cercopod terminates in 0-1 spines 7

7. Telsonic spine row heteromorphic between anterior and posterior of telsonic filaments; 18 to 24 trunk segments; carapace 9-18 mm; usually > 8 growth lines .... *Australimnadia*
   Little difference of telsonic spines from anterior to posterior of telsonic filaments; 15-20 trunk segments, usually 16-18; carapace 5-10 mm; usually < 8 growth lines 8

8. Posteriorly directed projection under the cercopod base; setal row on cercopod on basal 75% or more (some exceptions mainly in WA); second antennae usually with 8 antennomeres (again some exceptions, mainly in WA) .... *Eulimnadia*
   No projection beneath the cercopod base; setal row extends < 65% (usually ca 50%) along cercopod ; second antennae usually with 10-12 antennomeres (one exception in SE Qld) .... *Paralimnadia*

The Genera of clam shrimps

Laevicaudata: Lynceidae

Lynceus Müller, 1776

Lynceus tends to be found in temporary pools with longer hydrological cycles, about six weeks. This is because they are usually about the slowest growing of all clam shrimps. Though typically the carapace is a dull yellow colour, it can be brown, reddish, and rarely white. Size ranges from 4-9 mm.

Other distinctive features: the head is large (subequal to the body size) and convexly curved with a distinct rostrum, which in males is truncated while in females it is usually rounded. The first antennae is short and generally consists of two antennomeres. The second antenna is large and consists of a peduncle of about 3 antennomeres and two rami, of 25-30 antennomeres Generally there are 10 pairs of thoracopods, decreasing in size and complexity posteriorly. In males the first thoracopod is modified as a clasper; its finger (the endopod) varies in the different species and is a useful specific character. The telson is much reduced and almost invisible. Females have a lamellar process (= lamina abdominalis) on the sides of the last few segments, which help to hold the eggs. Its shape is useful taxonomically.

Most species feed by scraping algae off hard surfaces, e.g., sides of rock pools, off plants. *Lynceus* is a worldwide genus with about 35 species. There are six described species in Australia and there may be another in northern Queensland. A key to these six species is available in Timms 2013. Recently a new species with Australian affinities was described from nearby New Caledonia (Olesen *et al.*, 2016).

All six Australian species of *Lynceus* have round dimpled eggs, reminiscent of golf balls (Figure 5A). The dimples vary in shape and size according to species though there is some variability so that specific surface configurations are not too characteristic.

Australian species

Lynceus argillaphilus Timms, 2013

Lives in a few pools in the coastal Pilbara, WA. It is the only *Lynceus* living in ultra-turbid sites.
Distribution WA.

Lynceus baylyi Timms, 2013

The largest *Lynceus*, reaching 9 mm. Always found in rock pools (pit and pipe gnammas).
Distribution Southern and central inland of WA, southwestern NT and northwestern SA

Lynceus macleayanus (King, 1855)

Sometimes occurs in gnammas, but is the common species of ordinary pools.
Distribution Qld, NSW, Vic, Tas, rarely in SA and patchily in WA.

Lynceus magdaleanae Timms, 2013

Lynceus magdaleanae is common in the pit gnammas of southwestern WA. Also recorded (or more likely a closely related, undescribed species) from non-rock pools in north Qld.
Distribution SW WA, Qld(?).

Figure 6: Clam shrimp (*Lynceus susanneae*) frontal view. From a limestone gnamma on Nullarbor Plain, WA. Image courtesy Jane McRae.

***Lynceus susanneae* Timms, 2013**
Figure 6

Lynceus susanneae occurs in limestone gnammas on the Nullarbor Plain, WA.
Distribution WA.

***Lynceus tatei* (Brady, 1886)**

Lynceus tatei is the smallest of the species of *Lynceus* and seems to be most at home in shallow seasonal ponds, *eg* in vernal pools at Parafield Airport, SA.
Distribution SA, patchily in southern Qld, NSW, Vic, Tas and sw WA.

Cyclestherida

Cyclestheria Sars, 1887

Until recently it was thought *Cyclestheria* included just one circumtropical species, *C. hislopi*, but work by Schwentner *et al.* 2013a showed each continent has distinct species with 2 or 3 species found in Australia. Separation is by molecular means; all our species are undescribed.

Other distinctive features (see Olesen *et al.* 1997): Head small roughly 1/4 of whole animal. Single compound eye and ocellus (naupliar eye) close together. First antenna a short tubular structure, second antenna biramous with 7 antennomeres each. One pair of claspers in male. 15-16 pairs of thoracopods. Telson dorsal edge with 6 pairs of spines increasing in length posteriorly. Cercopods even longer than last telsonic spines and without setae.

Males are uncommon at most sites. Usually females carry many embryos of developing young within the carapace between their body and the dorsal edge.

Figure 7: *Cyclestheria* sp. North Queensland. Image courtesy Claire Sives.

***Cyclestheria* sp.**
Figure 7

Cyclestheria sp. is an algal feeder and no doubt is eaten by a variety of invertebrate and bird predators. It is usually found in the vegetated littoral of permanent waterbodies, but can occur in temporary sites as well. See Timms 1986; Schwentner *et al.* 2013a.
Distribution Northern Australia down the east coast to about southern Qld; also sw Qld and nw NSW. (One species Top End, NT, another ne Qld and another sw Qld; nw WA not tested genetically).

Spinicaudata: Leptestheriidae

Eoleptestheria Daday, 1914

This genus has only recently been recorded from Australia and was thought at the time to be a very recent invader (Timms 2009b), but some unpublished work suggests this is not so.

Although the spine at the rostrum apex is diagnostic, some cyzicids may have similar spine. The carapace is almost rectangular with rounded corners and has a length: height ratio of about two. In adult specimens there are many growth lines (ca 7-10). The male head has a spatulate (= hatchet-like) rostrum as does *Eocyzicus* in the Cycizidae. There are usually 22-32 body segments, and a telson with numerous fine telsonic denticles and a cercopod generally without long setae, just short denticles basally and longer denticles distally. Males have the first two thoracopods modified as claspers and females generally have two thoracopods with dorsal extensions (exopods) for holding eggs.

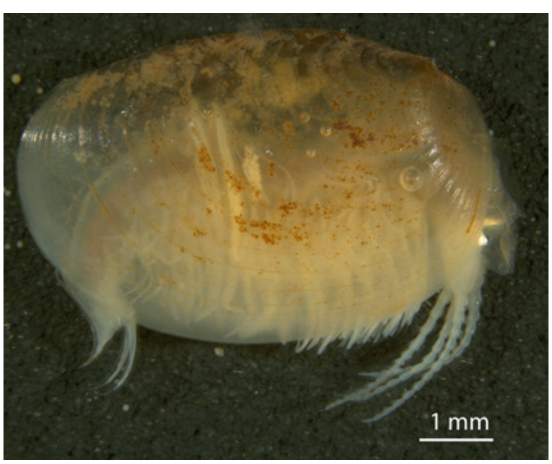


Figure 8: *Eoleptestheria* cf. *ticinensis*. From a swamp on Bloodwood station, Paroo, NSW. Image courtesy Claire Sives.

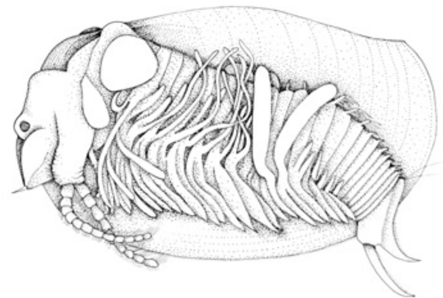


Figure 9: *Eoleptestheria* cf. *ticinensis*. Drawing by Jane MacRae.

Eoleptestheria cf. *ticinensis*

Our species is morphologically indistinguishable from the widespread European species, *Eoleptestheria ticinensis* (figures 8, 9) but DNA analysis when done may prove otherwise.

Distribution To date occurrences are spasmodic in the northern half of Australia: North Qld, inland sw Qld and adjacent nw NSW, Pilbara coast in WA.

Spinicaudata: Cyzicidae

Ozestheria Schwentner, Just and Richter, 2015

The generic name for this group of species has varied over time (in approximate order) between *Estheria*, *Cyzicus*, *Caenestheria* and *Caenestheriella*, with a brief excursion into *Eocyzicus* by one totally misguided author, and finally into *Ozestheria* when Schwentner *et al.* (2015a) in an exhaustive study by molecular analysis placed all the Australian species into an endemic genus.

Data on the eggs of only two species are available. Both have round eggs with flat surfaces between low walled polygons (Figure 5B). The polygons are about as numerous as the dimples of *Lynceus* eggs, but are flat floored instead of saucer-shaped. This egg sculpturing is found in some fairy shrimp eggs as well.

Diagnostic features: *Ozestheria* are spincaudatans with valves thick and swollen, more or less oval, with distinct growth lines. The umbone is well developed and nor far beyond the anterior of the carapace. Rostrum triangular in both sexes and without a posterior margin. No rostral spine. Head may or may not have an occipital condyle (backward extension). Male clasper with narrow claw-like scales at moveable finger apex. Posterior trunk segments dorsally with many spines. Telson with few spines of variable size. All species mate-guard venter to venter.

Almost all species are coloured brown or reddish brown with some yellowish and a new one black. It seems that species commonly encountered (*O. lutraria* and *O. parkardi*) develop slowly. For an account of mate guarding and amplexus see Sigvardt *et al.* (2017) who studied mating in *Ozestheria*.

Ozestheria presently contains 9 described species (Richter & Timms, 2005), but their taxonomy has not yet been studied so the actual number may be fewer, as many are poorly described and their variability is unknown. Schwentner *et al.* (2015a) confirmed *O. berneyi*, *O. lutraria*, *O. rubra*, *O. sarsi*, *O. mariae* and 13 'species' of *O. packardi* based on molecular evidence. The latter does not include a new undescribed species from Nth Qld, despite it keying out near *O. packardi*.

The following preliminary key to Australian *Ozestheria* species is based on original descriptions and experience with some species.

1. Head with an occipital condyle (=backward extension); dorsum of posterior trunk segments with large forked vertical spines 2
   Head without an occipital condyle; back of head meets hind margin at right angles; dorsum of posterior trunk segments with a few individual spines, not forked or rigidly vertical. 4

2. About 8 antennomeres; about 10 telsonic spines; only dorsum of carapace pigmented; <2 cercopod setae . . . . *O. mariae*
   Antennomeres number >12; >20 telsonic spines, all of carapace pigmented; >10 cercopod setae on basal 20 to 40% 3

3. Almost black in colour; 18 antennomeres; about 24 telsonic spines . . . .
   Ozestheria n. sp. A of north inland Qld.
   Brown in colour; 12-14 antennomeres, about 20 telsonic spines . . . .
   O. packardi sensu lato

4. Cercopod with no or only a few setae on and near base 5
   Cercopod with many (about 8-12) setae on basal 50% 7
   (Fig. 8)
5. Eyes separated; 25 trunk segments . . . . .
   O. dictyon
   Eyes confluent; 23-24 trunk segments . 6

6. Growth line intervals with striae and punctae; 2-3 pairs of setae on basal 25% of cercopod . . . . *O. berneyi*
   Growth line intervals with reticulated hexagons; no setae on cercopod . . . . . . *O. elliptica*

7. Carapace length: height ratio > 2; Carapace quadrangular with a central straight portion ventrally and subequally rounded anterior and posterior surface
   O. rufa
   Carapace length: height ratio < 1.7; Carapace oval with ventral edge all curved and anterior and posterior edges with markedly different curvatures 8

8. Telson dorsal surface with 4-5 pairs of small but robust spines 9
   Telson dorsal surface with 18-20 thin spines . . . . *O. rubra*

9. Carapace sloping dorsal margin meets posterior margin smoothly, i.e. no posterior angle 10
   Carapace with an angle between dorsum and posterior curvature ....*O. sarsii*

10. Carapace red-brown; polygonal sculpturing between growth lines ....*O. lutraria*
    Carapace colourless; granulated sculpturing between growth lines ...*O. pellucida*

The Australian species are listed below.

***Ozestheria berneyi* (Gurney, 1927)**

Gurney gives a length of 5mm, but recently collected specimens reached 8 mm.
Distribution Described from Longreach, Qld, but occurs throughout western Qld, nw NSW and northern SA (Mt Isa, Boulia, Thargomindah, Paroo, Enngonia and Marla).

***Ozestheria dictyon* (Spencer and Hall, 1896)**

Length 8 mm. Sayce 1903 thinks *Ozestheria dictyon* could be synonymous with *O. lutraria*.
Distribution Originally found in Palm Creek, central Australia, but has not been recognised since.

***Ozestheria elliptica* (Sars, 1897)**

Based on one female and has not been recognised since. Length only 5 mm.
Distribution Roebuck Bay, northern WA.

Figure 10: *Ozestheria lutraria*. From a claypan on Bloodwood Station, Paroo. Image courtesy Claire Sives.

***Ozestheria lutraria* (Brady, 1886)**
Figure 10

Australia's largest cyzicid at 14 mm, and is the second most common *Ozestheria* in the Paroo.
Distribution Occurs across Australia in a variety of turbid waters, particularly in claypans.

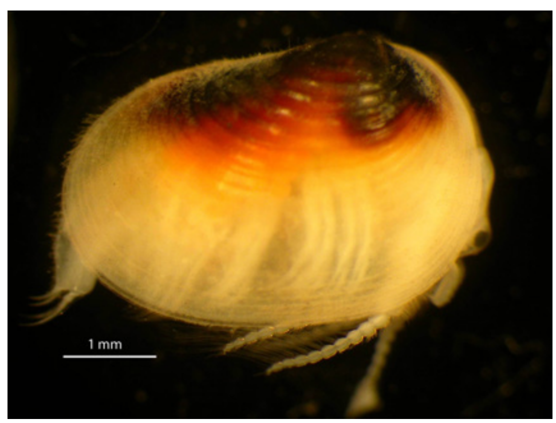


Figure 11: *Ozestheria mariae*. From King Rocks, WA. Image by Jane MacRae.

***Ozestheria mariae* (Olesen and Timms, 2005)**
Figure 11

Colouration distinctive: brown to dull red dorsally, but clear ventrally. *Ozestheria mariae* is a small species, reaching 5 mm.

Distribution Occurs throughout the WA wheatbelt and nearby goldfields in granitic gnammas.

Figure 12: *Ozestheria packardi*. From Paroo, NSW. Image by Jane MacRae.

Ozestheria packardi **(Brady, 1886) Figure 12)**

Schwentner *et al.* 2015a showed that this taxon represents a species complex with at least 13 forms in eastern Australia. As yet no attempt has been made to distinguish morphologically between these, but it will be difficult. Spencer and Hall (1896) tried and noted three subspecies but with intergrades. Length 5 to 9 mm.
Distribution Apparently occurs across Australia and is our most common species.

Ozestheria pellucida **(Timms, 2018)**

This species has a similar ecological niche as *O. mariae*, eating algae on the walls of gnammas in WA. The carapace of *O. mariae* is coloured red-brown at least dorsally whereas *O. pellucida* it is colourless.
Distribution In sandstone gnammas of the central Kimberley, WA.

Ozestheria rubra **(Henry, 1924)**

Henry (1924) gave the length as 6 mm, but specimens collected recently reached 9 mm.
Distribution Described from a single female from the lower Darling and Paroo Rivers in western NSW. Schwentner *et al.* 2015a has confirmed its presence in waterbodies around Eridunda, southern NT, Algebuckina, Lake Erye basin, SA, Lake Galilee, Qld, and the central Paroo, nw NSW, thus showing it has a wide distribution in inland eastern and central Australia. Many of the Paroo sites were just hyposaline (3-5 g/L) when specimens were collected.

Ozestheria rufa **(Dakin, 1914)**

Brtek 1997 thinks *Ozestheria rufa* is synonymous with *O. sarsii* but Dakin 1914 argues some differences. Size is not given.
Distribution Known only from two females from Boulder City near Kalgoorlie, WA.

Ozestheria sarsii **(Sayce, 1903)**

The validity of this species has been confirmed by molecular analysis based on a specimen from the riverland of South Australia (Schwentner *et al.*, 2015a). Length 8 mm.
Distribution Described from one male from Lake Aurean in the Murchinson catchment of mid WA; also known from the Pilbara.

Other known species of *Ozestheria*

A new undescribed species of *Ozestheria* occurs in seasonal waterbodies in north Qld in drainages to the eastern Gulf of Carpentaria. It is identifiable using the key above.

Spinicaudata: Cyzicidae

Eocyzicus Daday, 1914

The worldwide genus *Eocyzicus* was not recognised in Australia until *E. parooensis* was described in 2005 (Richter & Timms, 2005). Presently 11 species have been described, all endemic, with the likelihood of a few more being discovered. Overseas, 19 species are known with most species found in southeast Asia (Rogers *et al.*, 2017). Most of these later species are poorly described and many synonyms exist. Locally, most species are well described but nevertheless are hard to distinguish, so much so, the latest review paper (Tippelt & Schwentner, 2018) did not include a key.

Overseas, species tend to be brown or black, but Australian species are cream coloured. Australian species are 5-12 mm long with valves thick and inflated, more or less oval, with distinct growth rings. The umbone is well developed and nor far beyond the anterior of the carapace. Males have a subquadrate rostrum, females a triangular one, both with a posterior margin and rarely with an apical spine. Dorsum of posterior trunk segments with one spine per segment. Male claspers with moveable finger apex slightly expanded and with a few scales. Many telsonic spines, telsonic filaments on a raised mound, cercopod with basal setae and a short spine after the most posterior one. All species mate venter to venter. The presence of *Eocyzicus* in Australia has only been recognised only since 2005 (Richter & Timms, 2005). Its hidden diversity was revealed by Schwentner *et al.* 2013b with the delineation of 11 species based on molecular evidence. These have many overlapping morphological characteristics so that their recognition is difficult. Nevertheless a provisional key is provided here.

Key to male *Eocyzicus* species

It is essential to have mature specimens and helpful to have a few specimens rather than one. *Eocyzicus careyensis* is not included as no males are known. Its females are similar to *E. parooensis*, from which they can be distinguished by having only 8 thoracic segments with dorsal spines compared with 9 or more in *E. paroonesis*. Also see distinguishing features of the distribution of both species.

1. Cercopod setae >14 2
   Cercopod setae <12 3

2. Telsonic spines $\geq$16 (usually 16); growth lines >20 (usually 24) . . . .
   E. armatus Tippelt and Schwentner, 2018
   Telsonic spines <15 (usually 11); growth lines <20.(usually 16) . . . .
   E. parooensis Richter and Timms, 2005
   [A few *E. armatus* have as few as 11 telsonic spines and as few as 15 growth lines. *E. parooensis* almost invariably lives in hyposaline waters and *E. armatus* only rarely does.]

3. Growth lines >30; in WA only . . . .
   E. occidentalis Tippelt and Schwentner, 2018
   Growth lines <30; not in WA 4
   [But *E. richteri* and *E. timmsi* sometimes have >30 growth lines. If so *E. occidentalis* has > 14 antennomeres (unless specimens damaged) and *E. richteri* has 11-13 antennomeres. Also if so, *E. occidentalis* has >16 telsonic spines and *E. timmsi* <15 spines.]

4. Growth lines > 12; antennomeres >11 . 5
   Growth lines <12; antennomeres 10 . . . .
   E. parvus Tippelt and Schwentner, 2018
   [*Eocyzicus parvus* lives in vegetated sites as does *E. phytophilus* (and often *E. parooensis* in hyposaline waters); all other species live in essentially unvegetated often turbid sites.]

5. Average number of growth lines >19 . . 7
   Average number of growth lines <18 . . 6
   [Individual *E. richteri*, *E. timmsi* and *E. ubiquus* may occasionally have 17-18 growth lines, but averages always higher. Also rare individuals of *E. phytophilus* may have 19 or 20 growth lines, but averages always <18.]

6. Carapace length <4 mm; trunk segments with dorsal spines <13 (usually 12) . . . .
   E. breviantennus Tippelt and Schwentner, 2018
   Carapace length >4.5 mm; trunk segments with dorsal spines >13 (usually 14) . . . .
   E. phytophilus Tippelt and Schwentner, 2018

7. Average number of telsonic spines >15 . *E. argillaquus* Timms and Richter, 2009 and *E. richteri* Tippelt amd Schwentner, 2018
   Average number of telsonic spines<13 . . *E. timmsi* Tippelt and Schwentner, 2017 and *E. ubiquus* Tippelt and Schwentner, 2018
   [The four species in the final couplet are difficult to distinguish from one another. *Eocyzicus timmsi* is geographicallly separable by occurring allopatrically in central inland Qld, whereas the remaining three are sympatric particularly in southwest Qld and northwest NSW.]

The Australian species of *Eocyzicus* are listed below.

Eocyzicus argillaquus Timms and Richter, 2009

Lives in very turbid claypans, also other turbid pools. Sympatric with *E. armatus*, *E. parooensis*, *E. parvus*, *E. phytophilus*, *E. richteri*; co-occurs rarely with *Eocyzicus phytophilus*.
Distribution sw Qld, middle Paroo, NSW, L. Eyre catchment, SA.

Eocyzicus armatus Tippelt and Schwentner 2018

Lives in clear fresh and hyposaline waters. Sympatric with *E. argillaquus*, *E. parooensis*, *E. phytophilus*, *E. richteri*, *E. ubiquus*; co-occurs rarely with *E. ubiquus*.
Distribution Middle Paroo, NSW, southern NT, coastal Pilbara, WA.

Eocyzicus breviantennus Tippelt and Schwentner 2018

Lives in fresh turbid waters. Sympatric with *E. argillaquus*.
Distribution Western Lake Eyre basin, SA.

Eocyzicus careyensis Tippelt and Schwentner 2018

Lives in saline water, salinity not recorded. Not sympatric with other *Eocyzicus* spp.
Distribution Lake Carey, WA.

Eocyzicus occidentalis Tippelt and Schwentner 2018

Lives in turbid claypans. Not sympatric with other *Eocyzicus* spp.
Distribution Carnarvon basin, WA.

Figure 13: *Eocyzicus parooensis*. From Gidgee Lake, Bloodwood Station, Paroo, NSW. Image courtesy Sue Lindsay.

Eocyzicus parooensis Richter and Timms, 2005

Lives in clear hyposaline waters to about 15 g/L. Sympatric with *E. argillaquus*, *E. armatus*, *E. phytophilus*, *E. richteri*, *E. ubiquus*.
Distribution Middle Paroo, NSW.

Eocyzicus parvus Tippelt and Schwentner 2018

Lives in clear freshwaters with vegetation. Sympatric with *E. argillaquus*, *E. phytophilus*, *E. ubiquus*.
Distribution Middle Bulloo catchment, sw Qld.

***Eocyzicus phytophilus* Tippelt and Schwentner 2018**

Lives in clear or turbid freshwaters with vegetation. Sympatric with *E. argillaquus*, *E. armata*, *E. parooensis*, *E. parvus*, *E. richteri*, *E. ubiquus*; co-occurs rarely with *E. argillaquus*.
Distribution Middle Paroo, nw NSW, sw Qld, western Lake Eyre basin, SA.

***Eocyzicus richteri* Tippelt and Schwentner 2018**

Lives in fresh turbid waterbodies. Sympatric with *E. argillaquus*, *E. armata*, *E. parooensis*, *E. parvus*, *E. ubiquus*; co-occurs rarely with *E. argillaquus*.
Distribution Middle Paroo, nw NSW, sw Qld, Lake Eyre catchment, SA.

***Eocyzicus timmsi* Tippelt and Schwentner 2018**

Lives mainly in turbid waters, occasionally in clear waters. Not sympatric with other *Eocyzicus* species.
Distribution Vicinity of Lakes Galilee and Buchanan (but NOT in saline Lake Buchanan), central inland Qld.

***Eocyzicus ubiquus* Tippelt and Schwentner 2018**

Lives in a large variety of waters: ponds to lakes, clear to turbid, fresh to hyposaline. Sympatric with *E. argillaquus*, *E. armata*, *E. parooensis*, *E. parvus*, *E. phytophilus*, *E. richter*; co-occurs rarely with *E. armata*.
Distribution nw NSW, sw Qld, coastal Pilbara, WA.

Spinicaudata: Limnadiidae

Limnadopsis Spencer and Hall, 1896

Limnadopsis is an endemic genus of relatively large clam shrimps (to 30mm), some of which are very distinctive in that their growth lines protrude as serrations (=carinae) dorsally on the carapace. *Limnadopsis birchii* is the world's largest clam shrimp (see Figure 1).

Other features of *Limnadopsis* (see Figure 4): Rostrum variable, but typically elongated triangular, sometimes truncated. Occipital notch and condyle absent. Weak umbone or none. 8-24 growth lines, usually distinct. Telson with many (11-45) dorsal spines; cercopod with a setal row on basal 30-70% and terminating in 1-6 spines. Setae plumose, simple or setaform spines.

Like other limnadiid genera, eggs are species specific, but with some variation between species so that most are round with grooves, but some are odd shaped like cupcakes, bells, tops (Figure 5D). In *Limnadopsis* the grooves are often widened with a filling of apparently different structured material. In most species the grooves are elongated but in some they small and round with a surrounding funnel-shaped wall.

There are twelve described species of *Limnadopsis*, which are listed below. Only 8 of these are included in the key of Timms 2009a.

***Limnadopsis birchi* (Baird, 1860)**

Distribution Almost Australia wide but absent in Vic and Tas, generally in the semiarid inland.

***Limnadopsis bloodwoodensis* Schwentner, Timms & Richter, 2012**

Distribution Occurs in the central Paroo catchment in sw Qld and nw NSW in slightly saline shallow lakes. Eggs have been found in central western NSW.

***Limnadopsis brevirostris* Schwentner, Timms & Richter, 2012**

Distribution Known only from its type locality near Taroom, central Qld.

***Limnadopsis centralensis* Schwentner, Timms & Richter, 2012**

Distribution Found so far in the Eridunda-Curtin Springs area south of Alice Springs.

***Limnadopsis minuta* Timms, 2009**

Distribution Known only from its type locality in far nw NT.

***Limnadopsis multilineata* Timms, 2009**

Distribution Known from Kimberley area, WA. Most collections are from gnammas (rock pools).

***Limnadopsis occidentalis* Timms, 2009**

Distribution Northwestern and central WA, mainly in claypans and floodplain pools.

***Limnadopsis paradoxa* Timms, 2009**

Distribution Mainly in somewhat humic seasonal ponds and episodic lakes in southeastern wheatbelt of WA. Like many clam shrimps it is only present for a few weeks after filling.

***Limnadopsis paratatei* Schwentner, Timms & Richter, 2012**

Distribution Occurs in a variety of freshwater pools in the central Paroo catchment and adjacent Bulloo catchment of sw Qld and nw NSW.

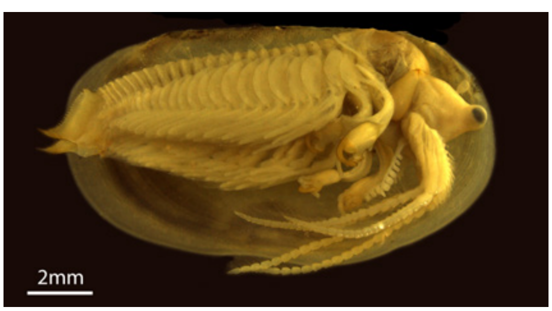


Figure 14: *Limnadopsis parvispinus*. From Paroo, NSW. Image courtesy Claire Sives.

***Limnadopsis parvispinus* Henry, 1924**
Figure 14

Distribution Inland NSW and southern inland Qld with a possible subspecies in the Lake Buchanan area of northern Qld.

***Limnadopsis pilbarensis* Timms, 2009**

Distribution Occurs in a variety of temporary pools in the Pilbara, WA.

***Limnadopsis tatei* Spencer and Hall, 1896**

Distribution Almost Australia wide but not yet recorded from southern NSW, Vic, Tas, southern SA or southern WA. Again mainly a semiarid species.

Spinicaudata: Limnadiidae

Australimnadia Timms and Schwenter, 2012

This genus was erected by Timms and Schwenter in 2012 to accommodate a large (about 15 mm) clam shrimp sparsely distributed in the north and east of Australia. Since then two smaller species have been found in WA.

Diagnostic features of the genus: Carapace generally more rounded than in other limnadiids, with a length: height ratio of <1.5. Growth lines numerous, always >8 in adults, and often many more and hence like *Limnadopsis*. Head characteristically limnadiid; second antennae with 12 or more antennomeres. Two species have 23-24 trunk segments, the other only 18. The claspers as in other limnadiids, each with a small suctorial disc on the finger apex. The spinal row on the telson is distinctly heteromorphic with ca 8-11 spines anterior to the telsonic setae distinctively different from the 10-12 posterior spines in two species, less so and with fewer numbers anteriorly in *A. torqueova*. Cercopod with numerous long setae and without a projection under its base.

No *Australimnadia* are common, indeed *A. torqueova* has not been collected since 1954. All species are relatively large and more oval than most other limnadiid clam shrimps. *Australimnadia grobbeni* at up to 15 mm challenges some *Limnadopsis* species for being comparatively large. All have unusually shaped eggs, with two species having eggs shaped as two discs at right angles (in fact two are named for this feature). The genus is endemic to Australia, but the type species, *A. grobbeni* is named after an Austrian professor and its types are in Vienna. Originally this species was called *A. gigantea* to celebrate its size, until the first specimens collected and described were found in a small museum in Vienna.

Two of the three species of *Australimnadia* have distinctive double discoid eggs (Figure 5C). Presumably this shape makes it difficult for egg predators to manipulate such eggs and hence devour them. The remaining species has eggs of many facets, like a polygonal dice.

The three species of *Australimnadia* are listed below and can be distinguished using the key of Timms & Schwentner 2017.

Figure 15: *Australimnadia grobbeni*. From a gilgai at Moonie, Qld. Image courtesy Sue Lindsay.

***Australimnadia grobbeni* (Daday, 1926)**
Figure 15

Distribution Occurs sparsely in NT, Qld, NSW and also in the early days in Vic in a variety of pools, but presently the most reliable sites are the gilgai of the Moonie area of inland Qld.

***Australimnadia multifasciata* Timms and Schwentner, 2017**

Distribution Has been found only once in pools of the Ashburton floodplain near Onslow, WA. This area has since been extensively modified for the Wheatstone gas development and so could be extinct.

***Australimnadia torqueova* Timms and Schwentner, 2017**

Distribution Used to occur on the coastal sand plain in sw WA, from at least Perth to Mandurah, but has probably been lost to urbanisation.

Spinicaudata: Limnadiidae

Eulimnadia Packard, 1874

This is a world-wide genus and until recently Australia had three valid described species. Now there are 16 and the number is still rising. The most common mode of reproduction is androdioecy where males are few and putative females (=hermaphrodites) are abundant. This leads to isolated genetic lineages so that molecularly there are many species with limited distributions (e.g. 13 in northern NSW and Qld, Schwentner *et al.* 2015b. These are not easy to define morphologically.

A favourite habitat for many *Eulimnadia* species is in gnammas (rockholes). Of the 22 spinicaudatans species in gnammas in Australia, seven belong to *Eulimnadia* (Timms, unpublished data.) Such are favoured as their development time is short (1-2 weeks) and hence in tune with the short hydroperiods in many gnammas.

Intra-specific variability in species of *Eulimnadia* is high even for notoriously variable clam shrimps (Straâskaba, 1965). The most reliable character for identification of the genus is the so called spine, really a narrow protrusion, underneath the base of the cercopod. (In species occurring outside of Australia this protrusion is more spine-like.) Generally, but not universally, *Eulimnadia* has 8 (range 6-9) antennomeres in second antenna, and a setal row on the cercopod occupying the basal 80% or thereabouts. This setal row ends a short spine.

Otherwise they are of general limnadiid characteristics, and without an umbone or occipital notch. Carapace length: height ratio is usually > 1.55 in males and > 1.5 in hermaphrodites and growth lines number <8 (sometimes <5) in adults. Trunk segments usually number 18 (range 16-18). These figures apply to Australian species only. Species are separated on the basis of their cercopod setae (length, number) and to a much lesser extent on their telsonic spines, details of the rostrum, and clasper morphology. Actually eggs are species specific in *Eulimnadia* (and also in many other limnadiids), but because of the unreliably of other characters, characters based on egg morphology assume great importance in *Eulimnadia*.

Eggs of *Eulimnadia* are usually round with many grooves, sometimes within a polygon, and in other species grouped together in 2-5s (Figure 5E). A couple are not round, but cylindrical or star-shaped, and hence form a continuum with eggs of *Limnadopsis* and *Paralimnadia*.

Keys to 10 species are provided in Timms 2016a. The best key is based entirely on eggs, the male key is incomplete, but the key using hermaphrodites separates all 10 species. The other species occur mainly in WA and have characters a little different to those of the east (*eg* 12 antennomeres, shorter setal rows on the cercopods).

***Eulimnadia australiensis* Timms, 2016**

Distribution occurs in the northern half of NSW and throughout Qld. *Eulimnadia australiensis* has been found in a variety of pools, including gnammas.

Figure 16: *Eulimnadia beverleyae*. From a freshwater pool at Bloodwood, Paroo, NSW. Image courtesy Claire Sives.

***Eulimnadia beverleyae* Timms, 2016**
Figure 16

Distribution Occurs in mainly clear water pools in the central Paroo (nw NSW and sw Qld) and possibly could be more widespread in the eastern inland.

***Eulimnadia canalis* Timms, 2016**

Distribution So far has been found only in the Paroo and Bulloo catchments in nw NSW and sw Qld.

***Eulimnadia centenaria* Timms, 2016**

Distribution Known only from gnammas near Katherine in the NT.

***Eulimnadia contraria* Timms, 2016**

Distribution Known only from its type locality near Aramac in central Qld.

***Eulimnadia dahli* Sars, 1896**

Eulimnadia dahli is possibly a species complex.
Distribution Occurs across northern Australia with little variation but as one collects southwards towards middle Australia variation becomes greater.

Eulimnadia datsonae Timms, 2015

Eulimnadia datsonae has many features of *Paralimnadia* and could belong in that genus rather than in *Eulimnadia*.
Distribution Lives in clear water pools in coastal WA from about Geraldton to somewhat south of Perth and somewhat inland into the Wheatbelt where it can be found in the clear pools at the base of granite outcrops, but not in gnammas on them, which are occupied by *Paralimnadia badia*.

Eulimnadia feriensis Dakin, 1914

The clasper of *Eulimnadia feriensis* is so different from normal *Eulimnadia* claspers, the body extension under the cercopod base is different from usual, there are 12 antennomeres and only about 40% of cercopod has setae, that it may not be a *Eulimnadia*.
Distribution Known from just a couple of sites in sw WA.

Eulimnadia gnammaphila Timms, 2016

Further work may show it is species group, with separate species in WA, SA and Vic. It occurs only after summer rains, so is not in competition with the typical *P. badia*, a winter-spring shrimp.
Distribution A gnamma specialist across southern Australia.

Eulimnadia hansoni Timms, 2016

Distribution Known from pools in the central Paroo and Bulloo River systems, but could occur more widespread in the eastern inland.

Eulimnadia kimberleyensis Timms, 2018

Distribution Lives in remote pools in sandstone in the Kimberley in WA.

Eulimnadia pinocchionis Timms, 2016

Distribution Another gnamma specialist, this time from the Pilbara, WA.

Eulimnadia rivolensis Brady 1886

Eulimnadia rivolensis is the first *Eulimnadia* described from Australia. For a long it time it was treated as a junior synonym of *Limnadia* (=*Paralimandia*) *sordida* but it should be restored to its original status with *E. palustera* Timms as a junior synonym.
Distribution Occurs in southern WA, southern SA, southern Vic and Tas.

Eulimnadia taroomensis Timms, 2016

Distribution A limited distribution, in the middle Dawson valley round Taroom. Probably it is limited to the lateral riverine lagoons which flood only following unusually heavy rainfall.

Eulimnadia uluruensis Timms, 2016

Distribution Known from gnammas on top of Uluru and from pools among the tors of Kata Tjuta in central Australia.

Eulimnadia vinculuma Timms, 2015

Eulimnadia vinculuma is aberrant in that it has 12 antennomeres and a setal row occupying only 55% of the cercopod. Such characters suggest a placement in *Paralimnadia*.
Distribution Occurs in pools in sandy coastal lowlands and pools in the Darling Range in sw WA.

Spinicaudata: Limnadiidae

Paralimnadia Sars, 1896

Paralimnadia was first proposed by Sars in 1896 to house *Limnadia stanleyana* King, 1855, the first clam shrimp species described from Australia. The genus was resurrected by Rogers *et al.* 2012 to contain a few Australian species all then in *Limnadia*. *Paralimnadia* is endemic to Australia and presently contains 15 species and it is likely that this number will increase soon.

Paralimnadia has all the classical characteristics of the Limnadiidae, such as the head with an ocular tubercle and without an occipital notch or condyle. The rostrum is variable, but often triangular in males. Second antennae usually have 12 antennomeres (range 7-13). The carapace length: height ratio is usually >1.55 in males and > 1.45 in females and hermaphrodites and it has <8 growth lines in adults. Trunk segments usually number 18, though there are species with 16 and 20. Male claspers are normal for the Limnadiidae. Telsonic spines average 15, but vary between 2-25. There is no narrow protrustion below the cercopod base as in Eulimnadia. Setae on the cercopod clothe the basal 40-63% (*P. badia* has an inerm (=bare) cercopod).

Keys to 15 species are given in Timms 2016b. One key uses only eggs, as again egg morphology is species specific, and the other key uses males. (Males and females usually are in equal numbers in *Paralimnadia*.) Like *Eulimnadia*, eggs of *Paralimnadia* are often round with many grooves (Figure 5F). However many are distorted either as barrels, astroform, and are flared to various degrees. *Paralimnadia* and *Eulimnadia* eggs are often not characteristic for genera but nevertheless in all cases species are distinctive.

The 15 Australian species of *Paralimnadia* are listed below.

***Paralimnadia ammolophus* Timms, 2016**

Distribution lives in two pools in coastal sand dunes in northern NSW. It was once far more common than it presently is because mineral sand mining in the 1970-80s destroyed its habitat.

***Paralimnadia badia* (Wolf, 1911)**
Figure 17

Information on the biology of *P. badia* is provided by Benvenuto *et al.* 2009 and Calabrese *et al.* 2016.

Distribution *Paralimnadia badia* is the common and widespread clam shrimp in the numerous gnammas on granite outcrops of the Wheatbelt and adjacent areas of sw WA, plus one record from the Eyre Peninsula, SA.

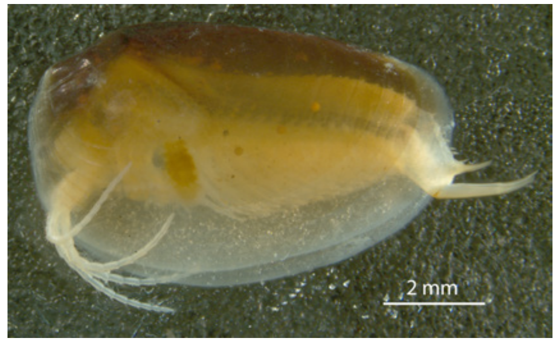


Figure 17: *Paralimnadia badia*. From a gnamma on King Rocks. Image courtesy Sue Lindsay.

***Paralimnadia bishopi* Timms, 2016**

Distribution Occurs in coastal sand dunes on the east coast of Cape York, Qld.

***Paralimnadia cygnorum* (Dakin, 1914)**

Distribution Occurs in pools on sandy coastal locations Perth to Esperance, WA.

***Paralimnadia flavia* Timms, 2016**

Distribution Known from three widely spaced sites in the Top End of the NT.

Figure 18: *Paralimnadia hyposalina*. From a lake near Moora, WA. Image courtesy Sue Lindsay.

***Paralimnadia hyposalina* Timms, 2016**
Figure 18

Distribution Lives in hyposaline lakes to about 14g/L, coastal plain around Moora, WA.

***Paralimnadia laharum* Timms, 2018**

Like many species of *Paralimnadia*, *P. laharum* lives in rock pools when they hold water, usually from May to October.
Distribution Grampians, Victoria. Most common in pools at higher elevations in the north.

***Paralimnadia monaro* Timms, 2016**

Paralimnadia monaro is allied morphologically to *P. stanleyana*, *P. montana* and *P. urukhai*.
Distribution Has been seen found in a few pools, mainly in granite, on the Monaro Tableland, NSW.

***Paralimnadia montana* Timms, 2016**

Paralimnadia montana is now not as common as it once was, due to the conversion of the lagoons to pasture or permanent waters.
Distribution Shallow pools on the New England tablelands, NSW, often in the iconic lagoons there, and occasionally in granitic gnammas nearby.

***Paralimnadia multispinosa* Timms, 2016**

Distribution Found in a turbid roadside burrow pit near Paynes Find, WA. This is an unusual habitat for a *Paralimnadia* (being turbid and not clear water) so its natural habitat and true distribution is unknown.

***Paralimnadia queenlandicus* Timms, 2016**

Paralimnadia queenlandicus exhibits minimal variability from north to south and from east to west, in contrast with that of *Eulimnadia* species in the same area, thus highlighting the difference in reproduction between the two genera (Schwentner *et al.*, 2015b).
Distribution Occurs in a variety of pools throughout inland Qld and northern NSW.

***Paralimnadia saxilatis* Timms, 2016**

Distribution Another species of gnammas, this time of Uluru, NT and Mt Kaputar in the midwest of NSW.

***Paralimnadia sordida* (King, 1855)**

Distribution Once common in the Botany swamps, NSW, and thereabouts, as well as in pools on the sandy lowlands of Port Phillip, Vic. However *Paralimnadia sordida* can now only be found in NSW, in temporary pools along Stockton Bight, Newcastle and possibly in sand dune pools south of Sydney.

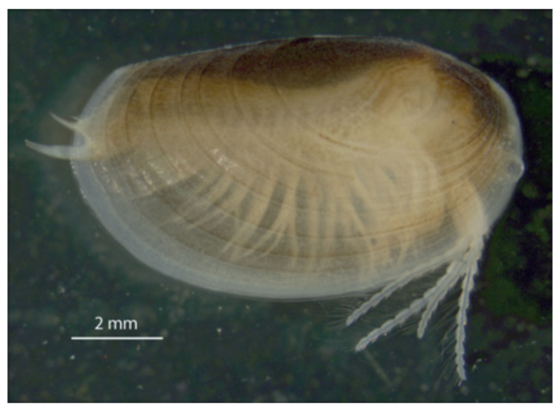


Figure 19: *Paralimnadia stanleyana*. From a gnamma near Bundeena, NSW. Image courtesy Sue Lindsay.

***Paralimnadia stanleyana* (King, 1855)**
Figure 19

Jim Bishop studied the biology of *Paralimnadia stanleyana* (see Bishop (1967, 1968)).
Distribution Sandstone gnammas in the Sydney basin, NSW. The most accessible place to see them is in the Royal National Park, 15 minutes' walk to the coast from Bundeena. They can be found at any time of year except June to September.

Figure 20: *Paralimnadia urukhai*. From a gnamma near Stanthorpe, Qld. Image courtesy Claire Sives.

Paralimnadia urukhai (Webb and Bell, 1979) Figure 20

Basic biological information is available in Webb & Bell 1979, but further details will be added later as its biology is presently being studied.
Distribution Lives in gnammas of the granite belt in southern Qld and far northern NSW.

Paralimnadia westraliensis Timms, 2016

Distribution Possibly once occurred throughout the WA Wheatbelt but presently restricted to a few outliers (probably due to salinisation of wheatbelt waters). Still common in the Esperance hinterland, WA, as this area as yet is hardly affected by salinisation.

Other known species of _Paralimnadia_

A gnammaphile similar to *P. urukhai* occurs in granite pools in the Gilbraltar Range National Park, northern NSW.

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