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Special Issue: Fossil and Modern Clam Shrimp (Branchiopoda: Spinicaudata, Laevicaudata) **Open Access**

Diagnosing *Eulimnadia* and *Paralimnadia* (Branchiopoda: Spinicaudata: Limnadiidae)

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Eulimnadia and *Paralimnadia* are both strongly supported, monophyletic limnadiid lineages based on molecular studies. However, defining the two taxa morphologically relies on the presence/absence of a subcercopodal spiniform projection; otherwise there is considerable overlap and confusion in morphological characters between the two taxa. The most discriminatory of these characters are examined here and applied to Australasian species. As a result, five *Eulimnadia* species are transferred to *Paralimnadia*. These characters are then applied to world *Eulimnadia* species and other limnadiid genera which share key features with *Eulimnadia*.

Key words: Clam shrimp, Cercopods, Antennomeres, Claspers, Amplexus, Reproductive systems.

BACKGROUND

The recent spinicaudatan clam shrimp encompass three extant families; Cyzicidae, Leptestheriidae and Limnadiidae. The Limnadiidae was first established by Burmeister (1843), defined as those spinicaudatan taxa with a pedunculate frontal organ, which at that time was the single genus *Limnadia*. In 1874 and 1896 the genera *Eulimnadia* and *Limnadopsis* were added respectively. *Paralimnadia* was described from Australia by Sars (1896), but was treated as a synonym of *Limnadia* until the revision by Rogers et al. (2012). The fundamental definition of the family did not change until 1935, when *Imnadia* was described by Hertzog. Mattox described *Metalimnadia* in 1952, and then *Gondwanalimnadia*, *Calalimnadia* (Rogers et al. 2012) and *Austrolimnadia* (Timms and Schwentner 2012), were all described in 2012. (For full taxonomic history, see Rogers 2020). Using molecular and morphological data, Weeks et al. (2009) and Rogers et al. (2012) demonstrated that Sars' *Paralimnadia* was a valid genus, distinct from *Eulimnadia*.

A cogent morphological diagnosis for *Eulimnadia* has vexed carcinologists for almost 150 years. Packard (1874) erected the genus in a rambling description but without a specific diagnosis, though he did mention 'a stout conspicuous spine on the lower angle of the telson under the terminal spines' (the subcercopodal spiniform projection on the telson). This structure later (Daday 1925) became the only defining character of *Eulimnadia*, the "terminal spines" determined as homologous to the cercopods in other branchiopods. Then followed a plethora of descriptions of new species of *Eulimnadia* from around the world, all separated from other Limnadiidae on the one character of having a ventroposterior spiniform projection at the base of the cercopod. Webb and Bell (1979) commented on the range of shape of the spiniform projection, and sank *Eulimnadia* into *Limnadia*. They argued that the form was so variable, that it was insufficient to separate the two genera, and this was followed by Brtek (1997). However, Martin and Belk (1989) showed that the form of the structure was an entirely different character state than the presence or absence of the structure, and also

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added the condition of the caudal filaments being borne on a projecting mound for the separation of *Eulimnadia* from *Limnadia*.

Brtek (1997) listed 52 described *Eulimnadia* species, but careful re-examination reduces the number to approximately 35, and 17 species have been described since then to bring the total back to 52 (Pereira and García 2001, Durga Prasad and Simhachalam 2004, Timms and McLay 2005, Babu and Nandan 2010, Rogers et al. 2010, Timms 2015 2016a). Clam shrimp display a wide range of morphological variation within and among species and many morphological characters traditionally used over the last century have been shown to be of little value (Straškaba 1965, Sissom 1971, Fryer 1987, Belk 1989, Rogers et al. 2012).

Rogers et al. (2012) separated *Eulimnadia* from all other limnadiid genera by a combination of characters. *Eulimnadia* was specifically separated from *Paralimnadia* by the presence of a subcercopodal spiniform projection (Fig. 1A, B) and the telsonic filaments borne on a mound, the projection and mound both being absent in *Paralimnadia* (Rogers et al., 2012). However, Timms (2016b) demonstrated that both of these character states could be found in some *Paralimnadia* species. It should also be noted that this spiniform projection is not unique to *Eulimnadia*, but is shared with *Calalimnadia* and *Gondwanalimnadia* (Rogers et al., 2012). Rogers et al. (2012) also separated *Eulimnadia* from *Paralimnadia* by the form of amplexus, which is transverse in *Eulimnadia* and single file in *Paralimnadia* (as well as in *Limnadopsis*). The reproductive system is also different, as *Eulimnadia* is androdioecious, whereas *Paralimnadia* is gonochoristic. Other described character states for the two genera were presented as overlapping ranges (Rogers et al. 2012).

Molecular phylogenetic studies strongly support the monophyly of both *Eulimnadia* and *Paralimnadia*, with *Paralimnadia* and *Limnadopsis* forming a separate clade within the Limnadiidae (Hoeh et al. 2006, Schwentner et al. 2009 2015, Weeks et al. 2009, Reed et al. 2015). With recent updates (Timms 2016a b 2019) there are now in Australia 14 described *Eulimnadia* species and 16 described *Paralimnadia* species, providing a range of species on which to test morphological differences between the two genera. Here, we examine potentially reliable morphological characters for each genus, re-evaluate the generic placement of the Australian taxa, and apply the new possible diagnostic characters to *Eulimnadia* globally.

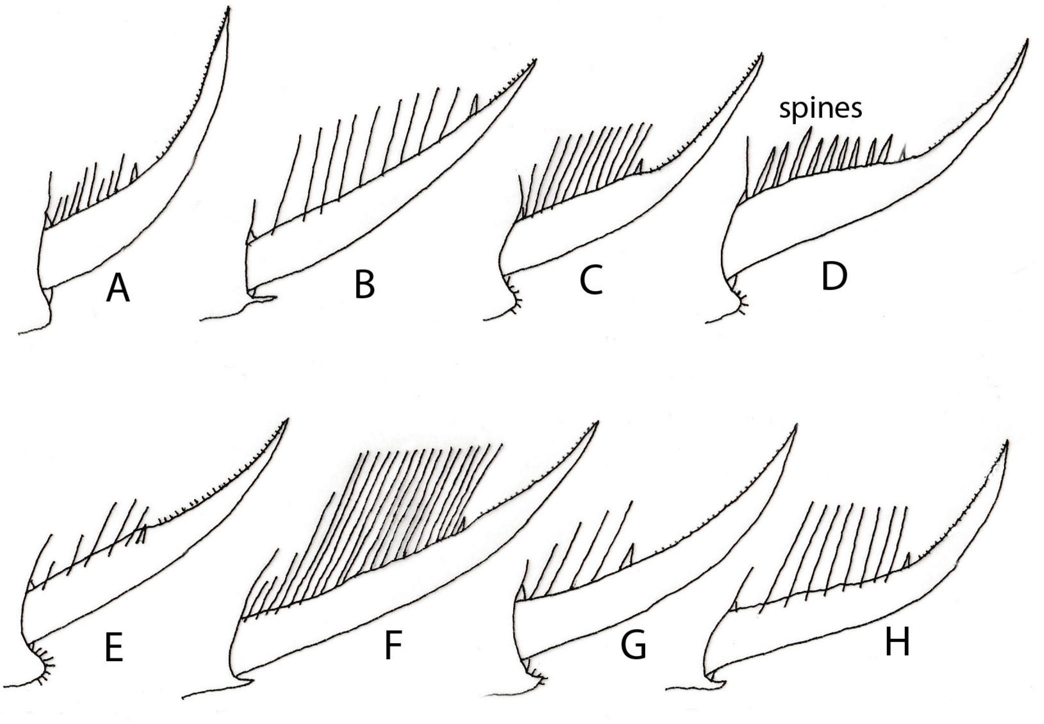

Fig. 1. Representative male cercopods of Australian *Eulimnadia* and *Paralimnadia*. A, *P. stanleyana* (King) (typical sub-basal area of cercopod in *Paralimnadia*); B, *E. gnammaphila* (typical sub-basal cercopod spiniform spine in *Eulimnadia*); C, *P. hyposalina*; D, *P. montana*; E, *E. feriensis*; F, *E. vinculuma*; G, *E. datsonae*; H, *E. palustrea*. Cercopods range in length from 1.2 to 1.5 mm and have plumose setae dorsally except *P. montana* which has spines.

MATERIALS AND METHODS

863 specimens of 25 *Eulimnadia* and 15 *Paralimnadia* species were examined in this study. The specific material examined is presented in appendix 1. Specimens were collected in the wild either during the wet season with a dip net, or collected from the substrate during the dry season and cultured from resting eggs according to Sars' Method (Van Damme and Dumont 2010). Specimens were examined using a Wild M-8 zoom stereoscope. Identifications were made through comparison with material in the collections of the authors and from the literature. All drawings were made by hand. We specifically examined the form of the first antennal lobes and second antennal antennomeres, male rostrum, claspers, telson spine count, insertion of the telsonic filaments, telson subcercopodal spiniform projection, and the cercopods for consistent, measurable morphological differences between *Eulimnadia* and *Paralimnadia*.

RESULTS

Characteristics of Australian and New Zealand species

The form of the subcercopodal ventroposterior projection varies from absent to triangular to acute in Australian species (Timms 2015 2016a). It is described in *Paralimnadia* species such as *P. hyposalina* Timms 2016 (Fig. 1C), *P. montana* Timms, 2016 (Fig. 1D), and *P. urukhai* Webb and Bell 1979, and also in *Eulimnadia datsonae* Timms 2015 (Fig. 1G), *E. palustrea* Timms 2015 (Fig. 1H), and *E. vinculuma* Timms 2015 (Fig. 1F), while *E. feriensis* Dakin 1914 (Fig. 1E) and *E. centenaria* Timms, 2016 have a blunt, robust subcercopodal projection (Tables 1 and 2). The projections in *E. palustera* and *E. vinculuma* (Fig. 1F) are most like a spiniform projection as in such *Eulimnadia* species as *E. belki* Martin 1989, *E. ovilunata* Martin and Belk 1989 and *E. ovimilis* Martin and Belk 1989, making differentiation in these cases problematic. However, if the projections are viewed ventrally (Fig. 2) then there is distinct difference between the acute, spiniform projections of typical *Eulimnadia* and blunt/rounded projections in aberrant *Paralimnadia.* If interpretation of the spiniform projection is strictly applied then at least five Australian species belong in *Paralimnadia*, not *Eulimnadia* (F and J known as *Paralimnadia*, G, H, K known as *Eulimnadia*).

The cercopod form appears to be highly conservative in limnadiid genera and is useful in species recognition in its four Australian genera. In both genera the cercopods are arcuate to sinuate, and medially bear a longitudinal row of plumose setae, which terminates with 0–4 spines. Distally the cercopod has a subapical, dorsal cirrus. Generally, in *Eulimnadia* and *Paralimnadia*, there is a single small spine near the end of the setal row and its position at about 75–80% of the length in *Eulimnadia* but at only 40–65% in *Paralimnadia* (Tables 1 and 2) (Fig. 1). Again there are a few exceptions, but if *E. centenaria*, *E. datsonae*, *E.*

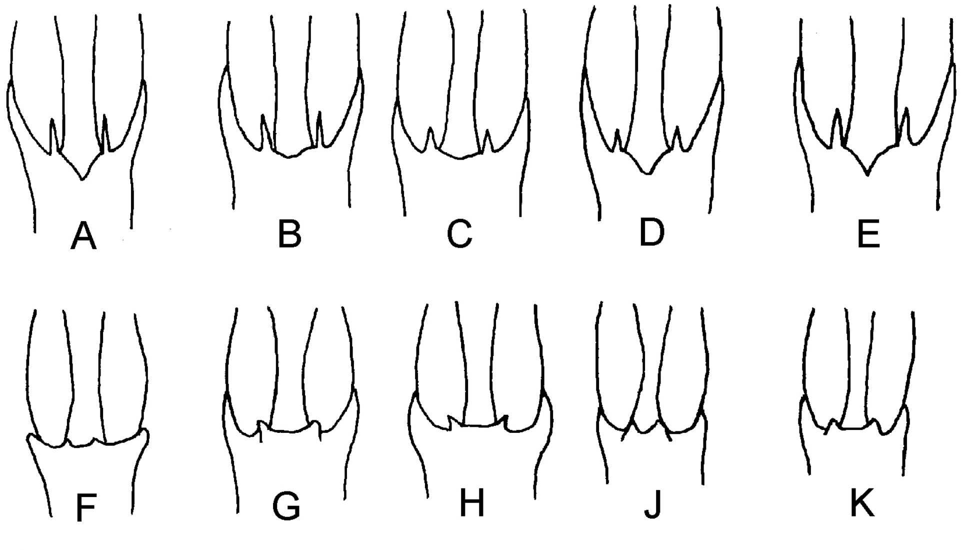

Fig. 2. Ventral views of subcercopod spine /projection of representative Australian *Eulimnadia* and *Paralimnadia*. A, *E. australiensis*; B, *E. beverleyae*; C, *E. gnammaphila*; D, *E. taroomaensis*; E, *E. uruluensis*; F, *P. cygnorum*; G, *E. datsonae*; H, *E. palustera*; J, *P stanleyana*; K, *E. vinculuma*. Scale bars = all about 0.4 to 0.6 mm.

palustrea and *E. vinculuma* are moved to *Paralimnadia* there are none. In cases where the spiniform projection is problematic, this character is more reliable.

The number of antennomeres is not usually a good taxonomic character, as they are easily broken and regrown to give false numbers, and the number of antennomeres is variable. Nevertheless, an attempt in comparing the number of antennomeres in *Eulimnadia* and *Paralimnadia* show a general difference based on ca 8 units in *Eulimnadia* and ca 12 units in *Paralimnadia* (Tables 1 and 2). This shorter flagellum in *Eulimnadia* was noted by Packard (1883) but was subsequently ignored as a possible generic character. There are two exceptions among *Paralimnadia* species, *P. hyposalina* and *P. urukhai*, though neither are too far from the nominated 12 antennomeres listed in Timms 2016b. The situation in *Eulimnadia* is more definitive, with *E. centenaria*, *E. datsonae*, *E. palustera* and *E. vinculuma* with 11–12 antennomeres, the *Paralimnadia* condition. The situation in *E. canalis* Timms 2016 and *E. taroomaensis* Timms 2016 with 9–10 antennomeres is too close to the *Eulimnadia* figure of eight antennomeres

Table 1. Generic characters of Australian species of *Eulimnadia* (based on Timms 2015 2016a)

Species	Subcercopodal spine	Cercopod spine position	Number of antennomeres	Medial edge of clasper palm	Androdiocey
E. australiensis	present	at 66%	8	rounded protrusion	probably
E. beverleyae	present	at 73%	8	minor protrusion	probably
E. canalis	present	at 78%	9–10	no males	unknown
E. dahli	present	at 80%	8	minor protrusion	probably
E. hansoni	usually	at 77%	8	smooth	maybe not
E. gnammaphila	present	at 76%	7–8	minor protrusion	probably
E. pinocchionis	present	at 80%	8	minor protrusion	probably
E. taroomaensis	present	at 78%	9	no males	unknown
E. ulurensis	present	at 74%	7	minor protrusion	probably

Table 2. Generic characters of *Paralimnadia* (based on Timms 2016b)

Species	Subcercopodal spine	Cercopod spine position	Antennomeres	Medial edge of clasper palm	Androdiocey
P. ammolophos	absent	46%	10–12	moderate protrusion	no
P. badia	absent	cercopod inerm	12	long pointed hamulus	no
P. bishopi	absent	58%	13–14	small protrusion	no
P. centenaria	rounded	56%	12	smooth	unknown
P. cygnorum	absent	43%	12	small pointed hamulus	no
P. datsonae	triangular	35%	11	strong hamulus	no
P. feriensis	rounded	38%	13	smooth	unknown
P. flavia	absent	60–66%	12–13	small pointed hamulus	no
P. hyposalina	triangular, with spinulae	43–48%	9–10	small rounded protrusion	no
P. marplesi	triangular	50%	9–12	small rounded protrusion	unknown
P. monaro	absent	44–48%	12–13	rounded protrusion	no
P. montana	triangular, with spinulae	50%	11	minor protrusion	no
P. multispinosa	absent	52%	12	knobby hamulus	no
P. palustera	acute	50%	13	Strong hamulus	no
P. queenslandicus	absent	62–65%	12–13	small sharp hamulus	no
P. saxitalis	absent	46–50%	12	small sharp hamulus	no
P. sordida	absent	60%	10	minor protrusion	no
P. stanleyana	absent	40–55%	10–12	pointed hamulus	no
P. urukhai	absent to triangular	43–58%	7–10	moderate hamulus	no
P. vinculuma	acute	48%	11	strong hamulus	no
P. westraliensis	absent	60–63%	12–13	knobby hamulus	no

to warrant shifting them to *Paralimnadia* based on this character alone.

Many *Paralimandia* and *Eulimnadia* have a protrusion (termed a hamulus when sizeable) on the medial surface of the clasper hand (endite IV corm). In *Paralimnadia* the hamulus can be small or large, while in *Eulimnadia*, except for *E. datsonae*, *E. palustera* and *E. vinculuma*, it is small or non-existent (Table 1 and 2) (Fig. 3). Further, in different populations of *P. rivolensis* Brady 1886 a hamulus is present in two populations, but absent from 14 others (Timms 2019). So this character is not a reliable discriminator, though if the hamulus is large and protruding then *Paralimnadia* is indicated.

As stated above, *Eulimnadia* are androdioecious, with few to no males, while *Paralimnadia* are gonochorisitic, with 1:1 sex ratios. This later feature is already part of the diagnosis for *Paralimnadia* (Rogers et al. 2012; Timms 2016b) but, although Packard (1874) noted his specimens of *E. agassizii* were all female, its significance went unnoticed till Weeks et al. (1997). Androdioecy or gonochoristic reproduction modes are rarely proved histologically, but sex ratios may indicate the reproductive strategy. Again on this criterion, *E. datsonae*, *E. palustera* and *E. vinculuma* seem not to belong to *Eulimnadia*. Furthermore, *Eulimnadia* (when males are present) amplex transversely, and *Paralimnadia* amplex in a single file (Rogers et al. 2012). Of these questionable species (*E. centenaria*, *E. datsonae*, *E. palustrea* and *E. vinculuma*) amplexus has only been observed in *E. datsonae*, and it is single file, suggesting that it belongs in *Paralimnadia*. Other morphological characters such as male rostrum, telson spine numbers, insertion of the telson filaments, number of first antennal lobes, and presence or absence of spines on the clasper palp junctions have been tested but there are no significant differences between the two genera.

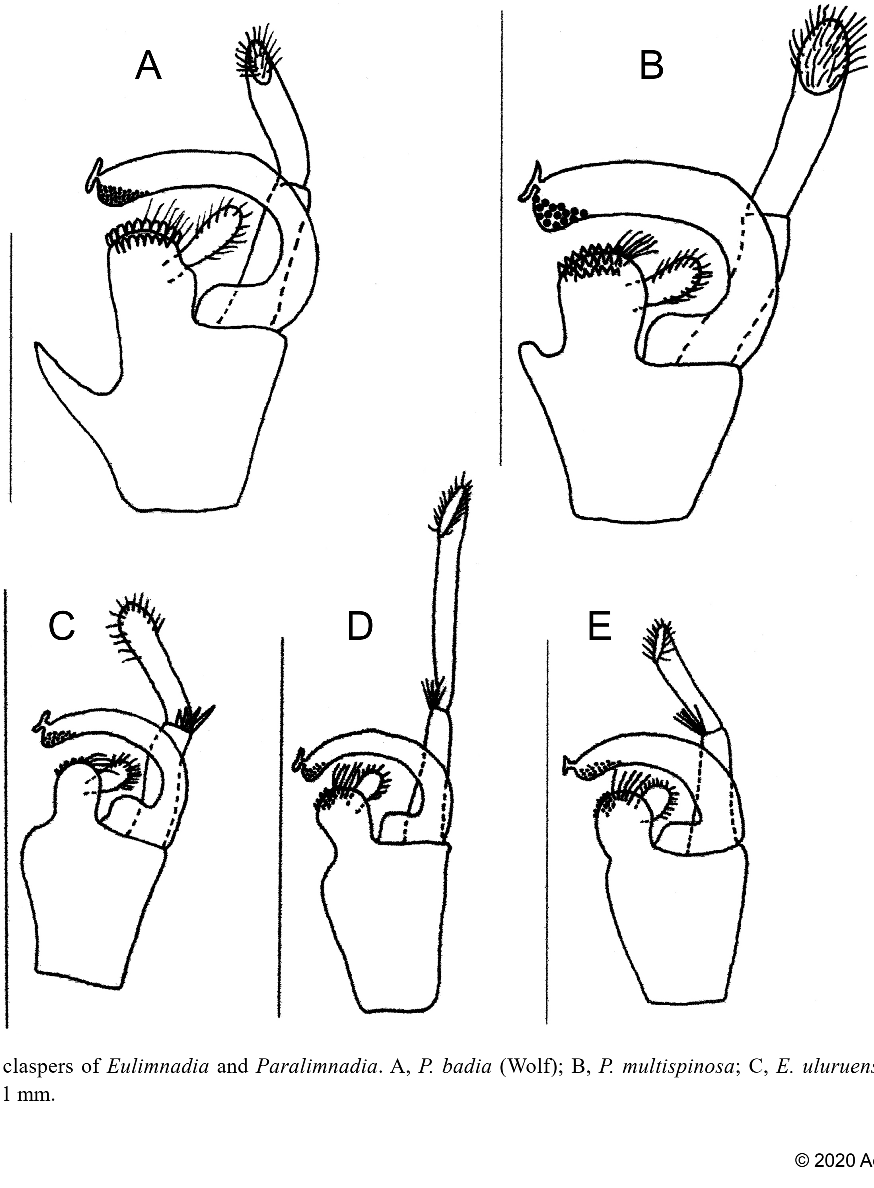

Fig. 3. Representative claspers of *Eulimnadia* and *Paralimnadia*. A, *P. badia* (Wolf); B, *P. multispinosa*; C, *E. uluruensis*; D, *E. dahli*; E, *E. centenaria*. Scale bars = 1 mm.

TAXONOMY

Diplostraca Gerstaecker, 1866
Onychocaudata Olesen and Richter 2013
Spinicaudata Linder, 1945
Limnadiidae Burmeister, 1843

Paralimnadia centenaria comb. nov.

= *Eulimnadia centenaria* Timms 2016a: 365–367, Figs. 3H, I, 8

Comments: This is another species without a true spiniform subcercopodal process, but has a rounded protrusion instead. Among the 11 species of Australian *Eulimnadia* described in Timms (2016a), its metrics are distinctly different with a cercopod spine at 56% of the cercopod length, and 12 antennomeres per flagellum. The sex ratio in the only collection available is 12 males to 26 females, an indeterminate ratio but less likely to characterise *Eulimnadia* than *Paralimnadia*. It lacks a hamulus but this is not diagnostic. Unfortunately, its amplexus position is unknown.

Paralimnadia datsonae comb. nov.

= *Eulimnadia datsonae* Timms, 2015: 445–447, Figs. 4–5

Comments: This species lacks a true spiniform subcercopodal process, instead having a triangular projection covered with denticulae. Furthermore, the cercopod spine is placed at about 35% of the cercopod length, there are 11 antennomeres on each flagellum, mating is in line and sex ratios are approximately 1:1 (Table 1), all *Paralimnadia* characteristics. In addition, there is a robust hamulus projecting at a right angle from the endite corm IV, with its length 0.5x the apical club diameter (Fig. 4D in Timms 2016b). Specimens from Jurien Bay, WA, are slightly different (BVT unpublished data). Significantly, there is variation in the ventroposterior area of the telson, so that it varies from rounded to somewhat triangular and always without denticles, there are 12 antennomeres on each flagellum and the hamulus is even more protruding and is slightly curved distally. The cercopod setae are absent, and the spine is small, placed midlength, and in females the cercopod is apparently geniculated. It is assumed that the nearly inerm geniculate cercopod is aberrant in this population.

Paralimnadia feriensis comb. nov.

= *Eulimnadia feriensis* Dakin, 1914: 300. Pl. 2, Figs. 14–18; Richter and Timms, 2005: 348; Timms, 2015: 441–445, Figs. 1–3
= *Limnadia feriensis* Brtek, 1997: 57 (list)

Comments: This species lacks a true spiniform subcercopodal process, instead having a rounded process covered in short spines, as observed in some juvenile *Eulimnadia* species (DCR personal observation). The cercopod spine is placed at about 40% of the cercopod length, and there are 13 antennomeres on each flagellum (Table 2). Amplexus position and sex ratios are unknown.

Paralimnadia marplesi comb. nov.

= *Eulimnadia marplesi* Timms and McLay, 2005: 409–414, Figs. 1–4

Comments: This New Zealand species also lacks a true subcercopodal spiniform process, instead having a triangular process (Timms and McLay 2005, Figs. 2G, 3C). Moreover, its cercopod spinal position is at 50% of the cercopod length, there are 9–12 antennomeres per flagellum, and in the only collection available there are nine males and two females, hardly a ratio expected for *Eulimnadia*, but indicative that gonochoristic reproduction is likely. There is a small mound on the endite IV corm medial surface, again not definitive. This species has far more affinities with *Paralimnadia* than *Eulimnadia* and so should be shifted to *Paralimnadia.*

Paralimnadia vinculuma comb. nov.

= *Eulimnadia vinculuma* Timms, 2015: 449–451, Figs. 5, 7

Comments: This species has a similar sharp triangular to spiniform subcercopodal process as in *E. palustera* so that differentiation on this character is problematic. However, the cercopod spine position at 48% of the cercopod length is distinctive and there are 11 antennomeres (Table 1) per flagellum. The mating position for this species is unknown, but the sex ratio is very nearly 1:1, and there is a distinct hamulus on the clasper; its length is slightly less than half the apical club diameter.

Eulimnadia gnammaphila Timms, 2016

Comments: Now that *E. feriensis* is considered a *Paralimnadia*, if Reed et al. (2015) had correctly identified their specimens, they would have appeared as *Paralimnadia* and *Eulimnadia* in their phylogenies, but they sequenced them only as *Eulimnadia*. The Gene

Bank accession numbers in their table 1 for *E. dahli* and *E. feriensis*, both misidentified, should be reassigned to *E. gnammaphila.*

Comments on taxonomy

Besides a strict interpretation of the subcercopodal projection, three other characters may be used in distinguishing between *Eulimnadia* and *Paralimnadia*: 1) cercopod setal row terminating with a small spine at or near 75–80% of cercopod length in *Eulimnadia* and at or near 40–65% in *Paralimnadia*; 2) second antenna with entire/unregenerated flagellae with antennomeres numbering ca 8 in *Eulimnadia* and ca 12 in *Paralimnadia*, and; 3) the very few or no males to females ratio suggest androdioecy and probably *Eulimnadia*, while 1:1 ratios indicate gonochory and *Paralimnadia*. It is possible some *Eulimnadia* (*e.g.*, *E. hansoni*) are gonochoristic (Timms 2016a) so this character is not absolute, though there are no known *Paralimnadia* which reproduce androdioeciously.

We have no molecular data to confirm the new generic placements of the species listed above in the results section. However, analyses are in progress. Based on these characters and our associated results, we revise the diagnoses for the two genera.

Eulimnadia Packard, 1874

Diagnosis: (modified from Rogers et al. 2012). Populations composed of males and hermaphrodites or hermaphrodites only; amplexus is transverse (venter to venter). Rostrum variable, blunt to acute, long or short. Angle between rostrum and frons 100° to 80°. Occipital notch and occipital condyle absent. Pedunculate frontal organ length approximately 1.55 x

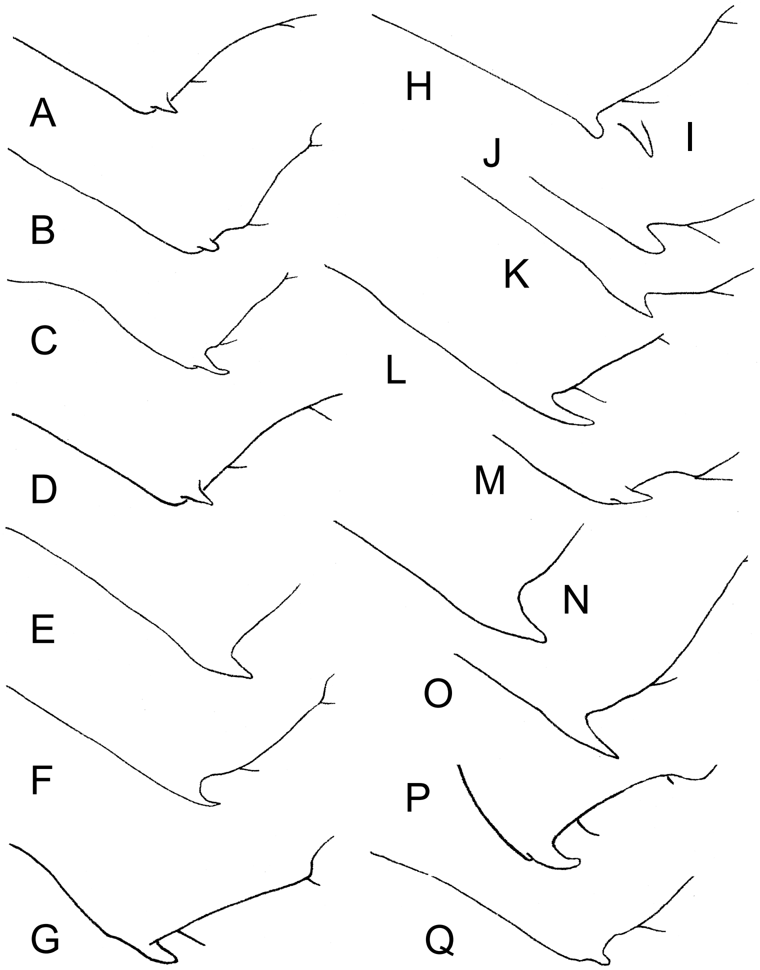

Fig. 4. Subcercopodal projection (and variation), left lateral view, among non-Australian *Eulimnadia* species. A, *E. agassizii*; B, *E. astraova*; C, *E. brasiliensis*; D, *E. braueriana*; E, *E. chaperi*; F, *E. colombiensis*; G, *E. cylindrova*; H and I, *E. diversa*; J and K, *E. folisimilis*; L, *E. geayi*; M, *E. graniticola*; N, *E. michaeli*; O, *E. magdalensis*; P, *E. ovisimilis*; Q, *E. texana*.

distance of organ from ocular tubercle. Second antenna with ~8 antennomeres per flagellum. Carapace dorsal margin smooth, lacking carinae, hinge line arcuate, rarely sinuate. Carapace intervals smooth. Umbone absent. Carapace occasionally pigmented. Muscle scar angle from 0° to 90° from the longitudinal axis of the animal. Clasper endopods each bearing an apical suctorial organ. Endite IV may be broadly transverse or bear dense apical field of short setae, or a few long setae or spines. Thoracic segments smooth or with dorsoposterior ridge rimmed with spines or setae. Eggs attaching to prolonged exopods of thoracopods VII and VIII or VIII, VIII to IX or XII, IX and X, X and XI, or XI and XII. Telson with posteriorly directed subcercopodal spiniform projection on ventroposterior angle, anteriad of cercopod base. Telson posterior margin posteriolateral spine rows confluent dorsally, with confluence not projecting. Each row has from 6 to 22 spines. Caudal filament originating between spine rows at second, third, fourth, fifth, or seventh spine from confluence. Caudal filament borne on projecting mound. Cercopods arcuate, occasionally sinuate. Cercopod with medial longitudinal setal row on proximal 75–80%. Setae plumose and long. Setal row terminates with single spine. Cercopod with subapical, dorsal cirrus, extending from 5–30% of cercopod length. Eggs 170–250 µm in diameter. Shape spherical to subspherical or cylindrical to subcylindrical with one end larger than other. Eggs with large rectilinear polygonal depressions separated by ridges, occasionally with lamellar or setaform spines at polygon ridge line confluences (Belk 1989, Martin 1989, Martin and Belk 1989, Rabet 2010). Australian (Australia), Afrotropical, Nearctic, Neotropical, Oriental, and Palaearctic (North Africa) bioregions.

Paralimnadia **Sars, 1896,** ***sensu*** **Rogers et al., 2012**

Diagnosis: (modified from Rogers et al. 2012). Populations composed of males and females (1:1); male amplexes female on posterior carapace margin, keeping body in line, single file, behind female. Rostrum variable, from blunt to acute, long or short, in both sexes. Angle between rostrum and frons 100° to 80°. Occipital notch and condyle absent. Frontal organ pedunculate. Frontal organ length 0.5 to 1.5 times distance between base of frontal organ and base of ocular tubercle. Second antenna with ~12 antennomeres per flagellum. Carapace dorsal margin smooth, lacking carinae, hinge line arcuate, rarely sinuate. Carapace intervals smooth. Umbone absent. Carapace with or without pigmentation. Muscle scar angle 10° to 80° from normal. Thoracic segments with dorsoposterior ridge margined with spines or setae. Male first two thoracopods with endopod bearing apical suctorial organ. Endite IV typical for family, although sometimes broadly transverse or bearing dense, apical setal field. Eggs attaching to prolonged exopods of thoracopods IX and X, X and XI, or XI and XII. Telson without spiniform projection on ventroposterior angle, anteriad of cercopod base. Telson posterior margin spine rows confluent dorsally, with confluence projecting or not. Each row averaging 5–25 spines. Caudal filament originating between spine rows at third, fourth, or fifth spine from confluence, born on a mound. Cercopod with proximal portion cylindrical, distal portion narrowing. Cercopod medial surface with longitudinal row of setae along proximal 40–60%. Setae plumose, sometimes long or short. Setal row terminates with one spine. Cercopod with subapical, dorsal cirrus, extending 10–50% of cercopod length. Eggs 100–170 µm in diameter, spherical to subspherical in shape. Eggs with large rectilinear polygonal depressions separated by ridges, occasionally with lamellar or setaform spines at polygon ridge line confluences. Australian (Australia, New Zealand) and Oriental (Sulawesi) bioregions.

Many authors, *e.g.*, Martin (1989), Martin and Belk (1989), Rogers et al. (2012), Reed et al. (2015) have proposed that *Eulimnadia* is in need of revision. Major problems centre around variability among individuals within and between populations (*e.g.*, Straškraba 1964, Belk 1989), inadequate description and illustration of species, mainly prior to the 1980s, and problems in the morphological definition of *Eulimnadia* (*e.g.*, Sars 1895, Daday 1925, Mattox 1954, Webb and Bell 1979, Martin 1989, Belk 1989, Brtek 1997, Pereira and García 2001).

Characteristics of *Eulimnadia* globally

Literature descriptions of 34 *Eulimnadia* species were examined for the same features noted as in the Australian study: the form of the telson spiniform projection (Fig. 4), the position of the spine at the distal end of the setal row on the cercopod, the number of antennomeres, the status of the medial surface of the clasper hand, and whether or not androdioecy is indicated by the sex ratio or better still by histology.

There is a large range in the position of the cercopod spine, from 60–90% of the cercopod length, with an average of 81% for the 34 species. According to Rogers et al. (2012) the range is 20–90%, but it seems Timms (2016a) did not encounter the most aberrant species in his survey. So this character is not as definitive outside of Australia, though with only a few exceptions the position is greater than 65% and for most near 80%. Thus this character is useful but not necessarily definitive.

There is also a much larger range for the number of second antennal antennomeres (5–17) globally. Two species, *E. curvirostris* Roen, 1952 and *E. kobai* Uéno, 1940 from China, are clearly outliers with 17 antennomeres, as the next highest number is 10. Although mentioned in the literature (*e.g.*, Rogers et al. 2013; Reed et al. 2015) neither species has been studied since description. Without these two species the average is 7.8 antennomeres. So having ca eight antennomeres is a satisfactory guide to *Eulimnadia* but not necessarily definitive.

For about half (18) of the species in the survey, androdiocecy is indicated by sex ratios but only proved histologically for a few (such as *E. texana*, Weeks et al. 1997). There is no information for the remainder, but it should not be assumed they are gonochoristic. However, if sex ratios are the only guide then gonochoristic reproduction is indicated for *E. indocylindrova*, *E. pulchra*, *E. santiaguensis*, and *E. agassizii*. Of more importance in the form of amplexus, with single file being unique among all clam shrimp to the *Paralimnadia*/*Limnadopsis* clade.

Concerning a distinct hamulus on the male clasper medial surface, where males are known, not one *Eulimnadia* has a distinctly narrow protruding hamulus, though a couple have a sharp angle distally (*E. geayi*, *E. follisimilis*) and a few (10) have a moderate rounded protrusion distally. As in the Australian species this character is useful, but not necessarily definitive.

CONCLUSIONS

For differentiation between *Eulimnadia* and *Paralimnadia* in Australia the extra features of the cercopod setal row extent and the number of antennomeres are indeed useful, with the form of the hamulus and sex ratio sometimes useful. Of course, this assumes the exact form of the spiniform projection is correctly diagnosed.

At a global level, there is more variation in the extent of the setal row and number of antennomeres, as perhaps might be expected with greater number and isolated occurrences of species, so that extreme values detract from the general average of the setal row occupying 80% of the cercopod and there being ca eight antennomeres. However, there is no discriminatory value in noting these characters (and the presence of a spiniform telson process) in *Eulimnadia* as they overlap with the same characters in related *Gondawanalimnadia* and *Calalimnadia* and these two genera are easily distinguished from *Eulimnadia* on other characters (Rogers et al. 2012). There is however, value when describing a new limnadiid or redescribing a species to include the characters studied herewith to be absolutely sure of its proper placement.

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Authors' contributions: The authors contributed equally.

Competing interests: The authors declare that they have no competing of interests.

Availability of data and materials: The original Australian specimens are stored in various museums in Australia (see Timms 2015 2016a b) and the most world *Eulimnadia* examined are kept in the collections of DCR, the while data on the remainder are in the literature. The species examined for this study are listed in appendix 1.

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Ethics approval consent to participate: Not needed for studies on clam shrimps in Australia or the United States of America.

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Supplementary Materials

Appendix 1. Species examined. (download)