A Redescription of *Paralimnadia urukhai* Webb and Bell 1979 with the Description of a New Species *P. minyspinosa* (Crustacea: Branchiopoda: Limnadiidae)

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Clam shrimps of the genus *Paralimnadia* living in small pools of the eastern highlands are particularly variable between populations. A detailed study of many populations of *P. urukhai* in the northern New England Tablelands revealed almost random variation in normally conservative characters such as egg morphology and cercopod setae as well as wide variation in other less defining characters. This necessitates a revised description of this species. This redescription focuses only on the Stanthorpe group of populations as previous genetic analysis suggests the Bald Rock populations could represent a separate species, but the two cannot be separated presently based on morphological features. However, two populations 100 km to the south are morphologically and genetically distinct enough to constitute a new species which we describe herein. All these populations live in isolated rock pools within forests where dispersal is difficult, so that retained founder effects and local adaptation are probably directing interpopulation variability.

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Key words: founder effect, metamerisation, monopolization theory, New England, *Paralimnadia minyspinosa* n. sp., Spinicaudata, variable morphology.

INTRODUCTION

Several closely related species of *Paralimnadia* inhabit small temporary habitats throughout the Great Dividing Range in eastern Australia. Presently known species include (from north to south), *P. urukhai* (Webb and Bell, 1979) (Stanthorpe area), *P. montana* Timms (New England Tablelands), *P. stanleyana* (King) (Blue Mountains and Sydney Basin), and *P. monaro* Timms (Monaro Tablelands). These and other species are described in Timms (2016) but *P. urukhai* was only mentioned briefly as large variation between populations indicated that it might be composed of more than one species. Many populations of these *Paralimnadia* species, with the exception of *P. montana*, were studied genetically and six lineages were indicated with COI distances ranging from 1.5 – 6.7% (see Fig. 2, Schwentner et al. 2020). These included two lineages each within *P. monaro* and *P. urukhai* and one unassigned lineage near Haystack Mountain. While the latter and all known species were morphologically clearly differentiated (Schwentner et al., in press), the two *P. monaro* and *P. urukhai* lineages were each morphologically indistinguishable.

The taxonomy of Spinicaudata has been hampered by the lack of clear-cut diagnosable characters for many taxa. Many commonly used characteristics are variable within species and this intraspecific variability often overlaps with interspecific variation (e.g., Straškraba, 1965; Schwentner et al., 2012). Recent molecular and morphological studies have established which limnadiid clam shrimp characters are more reliable than others for discriminating between species and genera (Rabet, 2010; Rabet et al., 2015; Rogers et al., 2012, Timms, 2016; Timms and Rogers, in press). In essence for *Paralimnadia*,

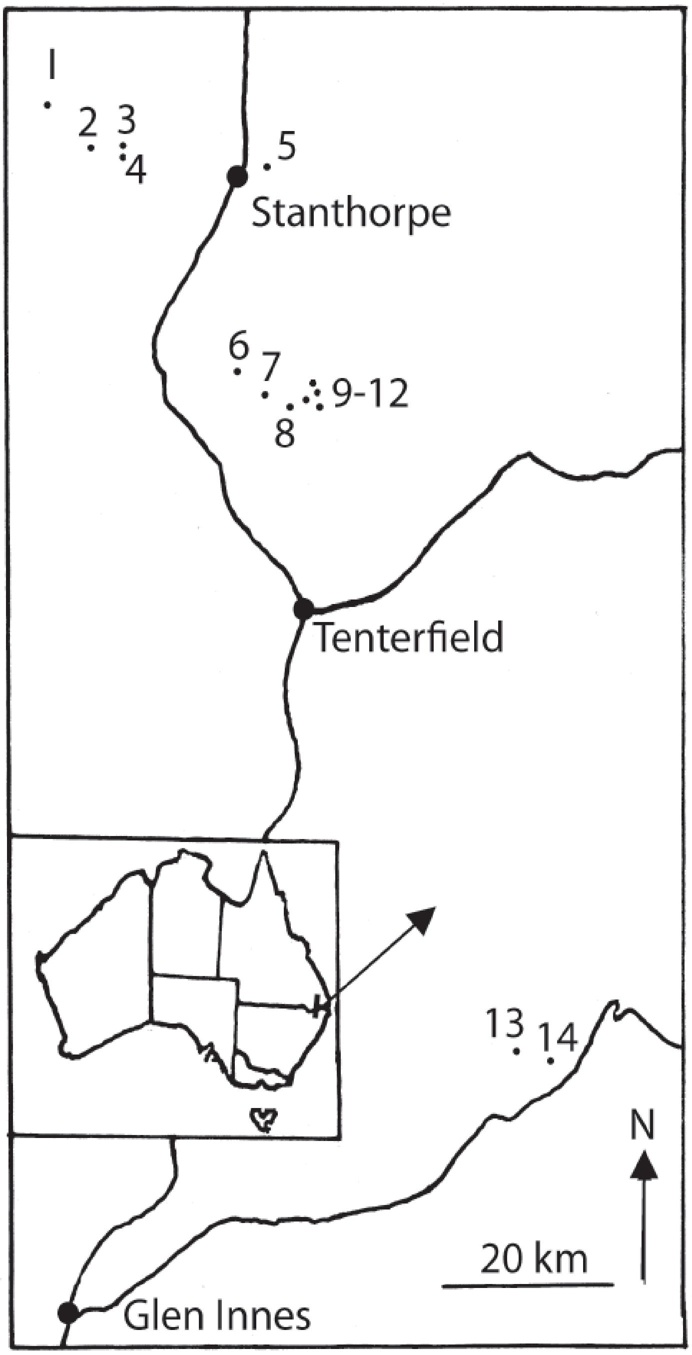


Figure 1. Map of New South Wales showing locations for mountain clam shrimps. Key: 1 Sow and Pigs, 2 Tumbledown, 3 Ergenia, 4 Dragonwyer, 5 Blue Moon Mountain, 6 Bald Rock Creek, 7, Mt Norman, 8 Billy Goat Hill, 9 Bald Rock #3, 10 Bald Rock #5, 11 Bald Rock #1, 12 Bald Rock #6, 13 Mount Haystack, 14, Waratah Trig.

egg morphology and the number, size and distribution of cercopod setae are the most reliable characters. It is not known how natural selection works on these features, except for limited cases of the influence of egg predation (e.g., Dumont et al., 2002, Timms and Lindsay, 2012). Other characters of lesser reliability include telsonic spines (dorsal and posterioventral), antennomeres, and male rostrum and claspers.

With this understanding and based on the genetic analysis of Schwentner et al. (2020), it appeared that *P. urukhai* is much more variable than indicated by its original description and moreover a species new to science lives in similar pools 100 km to the southeast. It is the aim of this paper to revise the description of *P. urukhai* and to describe the species from Haystack Mountain. The morphologically cryptic lineages of *P. urukhai* and *P. monaro* are not formally described due to the lack of diagnostic morphological characters.

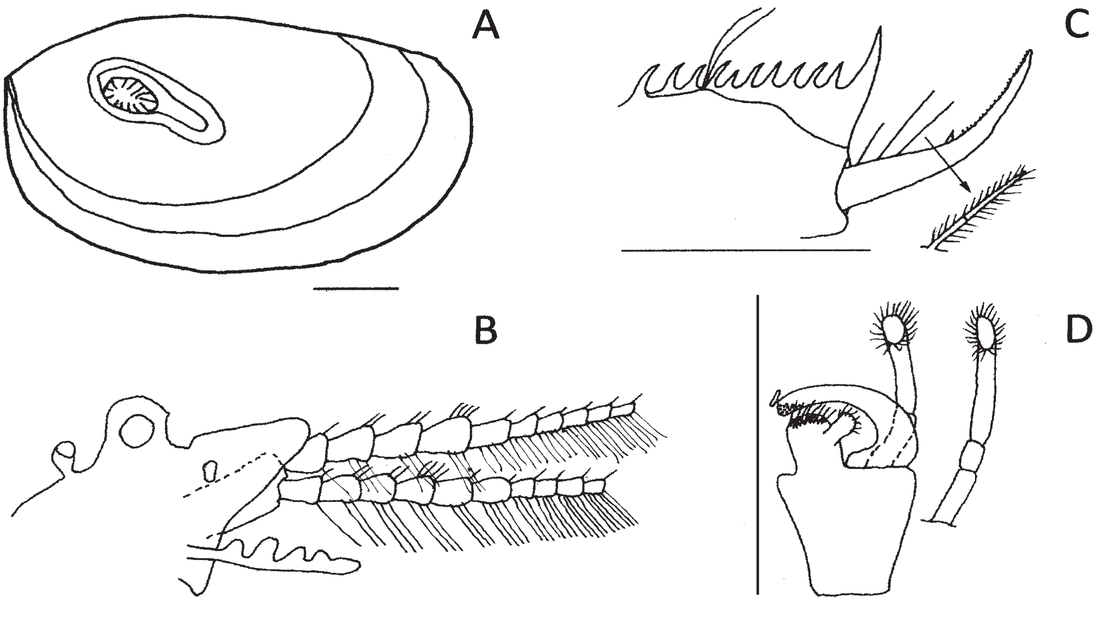
MATERIALS AND METHODS

Specimens, both the holotypes and paratypes of *Paralimnadia urukhai* and numerous individuals of *P. urukhai*-like individuals from various gnammas (rock holes) in the Stanthorpe area and Gibraltar Range National Park, were studied using a Wild M5 dissection microscope equipped with a camera lucida. Some details were observed under magnifications of 100x on an Olympus BHA microscope. Body measurements were made by placing a template marked in 0.5 mm spacings underneath the specimen at magnifications of 10-40x and distance estimated to the nearest half division. Accuracy is deemed to be ± 0.25 mm. A map of the localities is provided in Fig 1.

Eggs were prepared as detailed in Timms and Lindsay (2011) and studied on a Zeiss Evo LS15 Scanning Electron Microscope using a Robinson Backscatter Detector.

Terminology of the claspers follow Kaji et al. (2014) in which the palm (=hand) incorporates parts of limb portions IV and V, the apical club is endite IV, the small palp is an outgrowth of endite IV, the large palp is endite V and its outgrowth, and the moveable finger is the endopod.

Abbreviations used in the text: AM, Australian Museum; BVT, Brian V Timms; MS, Martin Schwentner; NSW, New South Wales; Qld, Queensland; QM, Queensland Museum.



Fugure 2. *P. urukhai* hototype QM W7499. A, carapace; B, head and antennae; C, telson; D, first clasper with detached large palp of second clasper by its right side. Scale bars 1 mm.

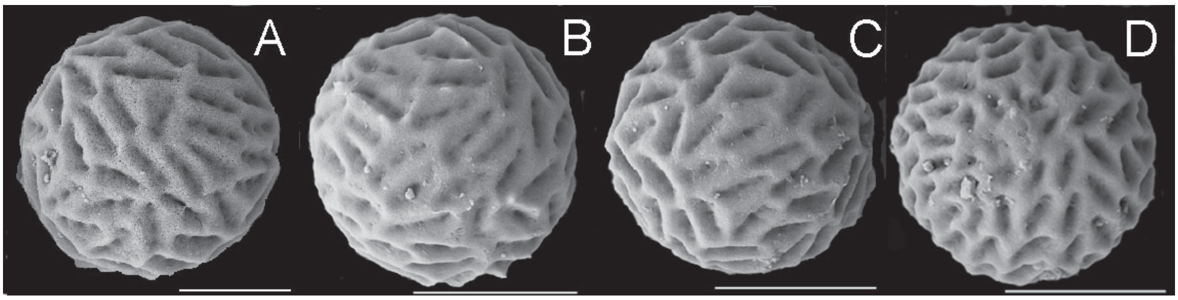


Figure 3. SEM of four eggs of *P. urukhai* from the type locality, AM P103397. Scale bars 0.1 mm.

RESULTS

Redescription of *Paralimnadia urukhai sensu stricto*

Webb and Bell's (1979) description of *Paralimnadia urukhai* is adequate for most purposes, but a renewed focus is needed on some characters in a context of a wider view of the species, so its essential features are redescribed here from the original holotype. Given that genetic analyses suggest a separate species in the Bald Rock area (Schwentner et al. 2020) this description is of *Paralimandia urukhai sensu stricto*.

Diplostraca Gerstraecker, 1866
Spinicaudata Linder, 1945
Limnadiidae Baird, 1849
***Paralimnadia* Sars, 1896**
***Paralimnadia urukhai sensu stricto* Webb and Bell, 1979**
(Fig. 2, 3)

Limnadia urukhai Webb & Bell, 1979: 239–244; Brtek, 1997: 58 (list).
Paralimnadia urukhai —Rogers et al., 2012: 838 (list); Timms, 2016: 471.

Type material

Holotype:
Queensland, near Stanthorpe, Amiens, Sow and Pigs Rocks, 28° 35’ 23”S, 151° 46’ 15”, 26 March 1978. J.A. Webb & G.D. Bell, male, QM W7499.

Paratypes.
Queensland, near Stanthorpe, Amiens, Sow and Pigs Rocks, 28° 35’ 23”S, 151° 46’ 15”, 26 March 1978. J.A. Webb & G.D. Bell, 5 males, 9 females, QM W7499; near Stanthorpe, November, 1929, H. Jarvis, 4 males, 2 females, QM W268;

Description

Holotype (male)

Head (Fig. 2B) with ocular tubercle prominent, the compound eye occupying about 50% of its diameter. Rostrum length close to twice the ocular tubercle, with a straight dorsal surface at an angle of ca. 80° to the frons, apex rounded and with an almost symmetric triangular shape. Ocellus oval at rostrum base. Dorsal organ posterior to the eye by about its height, pedunculate and asymmetrical and about half the height of the ocular tubercle.

First antennae (Fig. 2C) almost twice length of peduncle of second antenna, and with five non-setose lobes of various sizes, the distal one poorly differentiated from the others. Second antennae (Fig. 2C) with a spinose peduncle a little shorter than the rostrum and with both dorsal and ventral flagella with 10 antennomeres. These more robust basally and with terminal antennomeres not well differentiated; dorsal spines 1-4 per antennomere, most numerous mid length, and ventral setae variously 1-7 per antennomere, most numerous distally.

Carapace missing but Webb and Bell's original Fig 3 (reproduced here as Fig. 2A) shows it to be oval and with distinct anterior and posterior dorsal angles and just two growth lines.

Sixteen pairs of thoracopods. Claspers (Fig. 2D) with palm trapezoidal, with a distinct asymmetrical and rounded expansion distomedially. Apical club spherical with distal gripping area bearing spines and denticles and mediolaterally the small palp with many thin spines apically. Finger arcuate with a blunt rounded apex and many rounded pits ventrally. Long palp of claspers I and II inserted on apical edge of palm, with the first palp with two palpomeres and the second palp with three palpomeres; junctions of these palpomeres inerm. Long palp of first clasper about 1.5 x length of palm and in second palp, 2 x length. Other thoracopods of typical structure for *Paralimnadia*, decreasing in size and complexity posteriorly. Last ten abdominal segments dorsally with a short medial spine.

Telson (Fig. 2C) with spine rows bearing about 11 pairs of spines, the anterior 10 of similar size (except for the smaller 5th), each about three times longer than the basal diameter and the distal spine about three times larger than other spines. Spines inerm. Telsonic filaments inserted on a slight mound between the third and fourth spine. Dorsal floor of telson posterior to this mound slopes slightly to the base of the cercopod, but with a slight swelling mid length. Cercopod about as long as the posterior margin of the telson; basal 50% narrowing a little to a small dorsal spine then rapidly narrowing and curved to an acute apex. Three spaced setae on basal half, with the basal seta about the same diameter as the basal cercopod, but the next two distinctly longer, about twice the basal cercopod diameter. Setae geniculate and plumed. Distal half of cercopod with denticular row dorsally. Ventroposterior corner of telson rounded and hardly protruding.

Description of the egg

Webb and Bell (1979) did not examine the egg of this species in detail, though they did provide sketches of the surface morphology of three eggs (from undisclosed collections) showing regular or semi-regular ridges and a size range of 0.14 to 0.20 mm. Given the importance of the detailed morphology of eggs in species delimitation since 1990s (e.g., Belk, 1989; Rabet, 2010; Timms, 2016), eggs from the type locality (not from the original collection but from AM P103397) were studied by SEM (Fig. 3).

Egg. Spherical, average 229 µm (range 222 -231 µm, n = 10). Surface adorned with about 70 roughly rectangular shallow depressions with rounded ends and rounded edges. Most depressions about 56 x 27 µm, but much smaller (30 x 20 µm) and slightly bigger ones (58 x 34 µm) present. Central groove within the depressions about 30 µm long and with mostly three pits (range three to five) in each. Minor variations in surface elevations.

Comments.

This description differs from the original in at least four significant ways, in order of importance: (a) The setae on the basal half of the cercopod are shown in Webb and Bell's Fig 14 being much shorter than the cercopod basal diameter and clumped at about one third of the cercopod length, whereas in reality their length is similar to or longer than the cercopod basal diameter (Fig. 2C), and these setae are actually more spaced and nearer the cercopod base than shown in their Fig. 14, (b) although Webb and Bell mention three to six lobes on antenna 1 (their description is not specifically of the holotype, but an amalgam of all the material they examined), their diagram of the holotype (W7499; Fig. 8) shows no lobes, whereas there are five distinct lobes; (c) The long palp of clasper II has three palpomeres, not two as indicated in their description and illustrated in Fig. 10 from W7502, and (d) Webb and Bell's diagram of telsonic spines (Fig. 14) show all, except the last one, as broadly based (i.e. length about twice basal width) whereas they are finger shaped, about three times longer than basal diameter. Some other differences between the original description and the present redescription, such as the relative diameter of the eye could be better explained by shrinkage in the holotype over the years in the preservative rather than to any misinterpretation.

The female is not redescribed as no allotype was designated and is not possible to allocate any particular individual to the diagrams pertaining to

Table 1 Morphometric variation at 5 Stanthorpe and 7 Bald Rock sites

Character	Stan-thorpe	Bald Rock
Cercopod setae number	3 to 8	3 to 9
Length of these cf cercopod	> diam-eter	< or > diam-eter
Position of spine on cercopod	40-50 %	50 to 60%
Setae distribution on cercopod	basal 20-50%	basal 10-50%
number of telson spines	11 to 19	9 to 18
Number of these that are short	2 to 7	0 to 6
position of telson setae	4th and 5th	3rd and 6th
antennomeres dorsal	8 to 11	8 to 11
antennomeres ventral	8 to 11	9 to 12
number of trunk segments	16 to 18	16 to 18
clasper II palp palpomeres	2 to 3	2 to 3
antenna 1 lobes male	4 to 6	4 to 6

females (Webb and Bell's Figs. 15-24). Their amalgam description is adequate for present purposes.

Variability in *Paralimnadia urukhai sensu stricto*

Webb and Bell (1979) examined a number of collections of this clam shrimp, all from the Stanthorpe area (Sow & Pig Rocks and one collection labelled simply as Stanthorpe) and from their text and diagrams it is apparent that there is variation in many characters normally used to define limnadiid clam shrimps. We also examined eight individuals from each of five sites in the Stanthorpe area (sites 1-5 in Fig 1 and listed below) to ascertain variation in these populations all believed to be *P. urukhai sensu stricto* (Table 1). Individuals had been studied genetically from all of these populations (Schwentner et al. 2020) and were clearly assigned to *P. urukhai*.

Queensland: Blue Moon Mountain, 4.2 km NE of Stanthorpe, 28° 36'11.2"S, 151° 58' 14.5"E, 11 October, 2016, BVT & I.A.E. Bayly, 17 ♂ 18 ♀, AM P103393; Ergenia Property, 12 km W of Stanthorpe in Greenlands, 28° 37'56.1"S, 151° 48' 48.2"E, 23 June 2015, BVT, 17 juveniles, AM P103394; Dragonweyr Property, 12 km W of Stanthorpe in Greenlands, 28° 38'05.7"S, 151° 48' 48.6"E, 23 June 2015, 2♂ 2♀, BVT, AM P103395; Tumbledown Property, 13 km W of Stanthorpe in Greenlands, 28° 38'08.9"S, 151° 48' 10.1"E, 23 June 2015, 3♀, BVT, AM P103396; Sow and Pig Rocks, Harslet Farm, 3.5 km W of Amiens, 28° 35'23"S, 151° 46' 15"E, 18 October 2003, BVT, 8♂ 8♀, AM P103397.

The most significant of observed variations, in order of their value in taxonomic analysis (Timms, 2016) follow:

(a) Cercopod setae. There are usually 3-4 setae a little longer than the diameter of the cercopod, placed anywhere on the basal half of the cercopod, usually clumped, sometimes spaced. Those on the holotype are longer and more spaced than usual.

(b) Telsonic spines. These number 10-19 and vary irregularly in size. The near equality of all the spines except the most posterior spine in the redescribed holotype is unusual.

(c) Antennomeres vary between seven and ten, though ten as in the holotype is typical.

(d) The first antennal lobes vary between three and six, though five as in the holotype is the usual number. Sometimes there is little differentiation in the lobes at all.

(e) Claspers. The relative development of the dorsomedial expansion and its asymmetry varies, with that in the revised holotype description typical. Generally the long palps of clasper I and II are divided into two palpomeres, with the three segmented second palp of the holotype being unusual.

(f) Male rostrum. This is normally large at about twice the length of the ocular tubercle and rounded distally, but is sometimes narrower and pointed. The rostrum of the holotype is a little more massive than usual.

(g) Carapace colour varies generally with ontogeny, becoming darker with age. Re-examination of the collections available to Webb and Bell revealed carapace colours from light brown to very dark brown/black. The supposed clear window through which the claspers are visible (Webb and Bell, 1979, Fig 5) is not universally present in populations.

Identification of *Paralimnadia urukhai* remains possible using Webb and Bell's diagnosis and considering the variability itemised above. These authors gave credence to synonymising *Eulimnadia* with *Limnadia* (at that time *Paralimnadia* was also

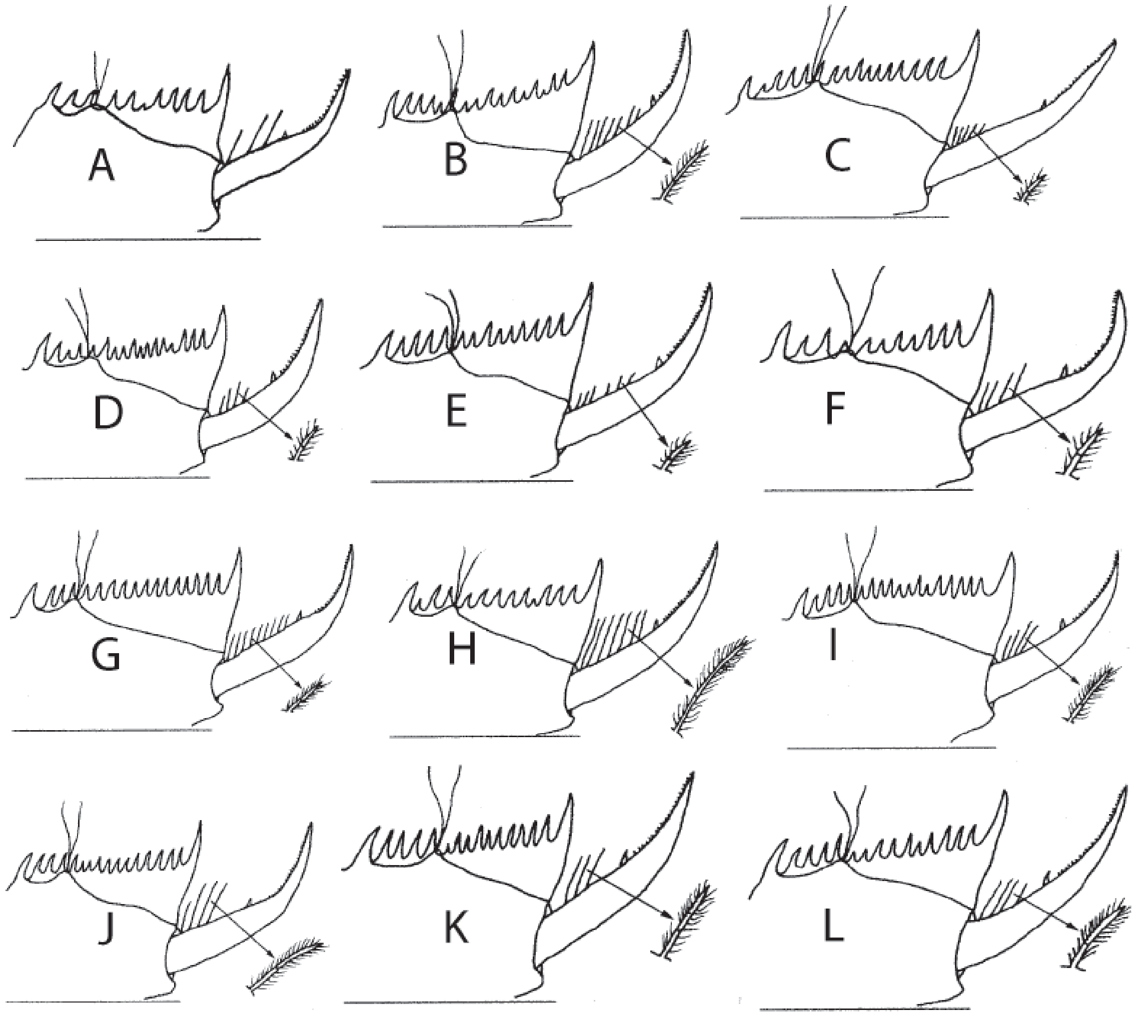


Figure 4. Telsons from 12 populations of *P. urukhai* showing telsonic spines and cercopods. A, Bald Rock Creek; B, Bald Rock #1; C, Bald Rock #2; D, Bald Rock #3; E, Bald Rock #4; F,Bald Rock, #6; G, Billy Goat Hill; H, Blue Moon Mountain; I, Dragonweyr; J, Tumbledown; K, Ergenia; L, Sow and Pigs. Scale bars 1 mm.

treated as a synonym to *Limnadia*, but was resurrected since; Rogers et al, 2012; Timms, 2016), but this was unwarranted as not one specimen available to them had any spine on the ventroposterior corner of the telson, the characteristic feature of all *Eulimnadia* which is totally absent in *Limnadia* and *Paralimnadia* (Timms and Rogers, in Press). One generic character of *Paralimnadia*, unappreciated at the time of Webb and Bell, is the presence of a small spine midlength on the cercopod (Timms, 2016). This is visible on all their diagrams of telsons. They did not however show the distinct mound bearing the telsonic setae, a feature of *Eulimnadia* (Rogers et al., 2012) and *Paralimnadia* (Timms, 2016). It is poorly developed as shown in the revised description of the holotype (Fig 2C), but is easily seen in other specimens that would have been available to them.

***Paralimnadia urukhai* Bald Rock populations**

Schwentner et al. (2020) analysed the genetic differences within and between the five populations studied above and another seven populations in the Bald Rock District. The range of COI distances between them is 4.7 to 6.4%, similar to COI distances observed among other spinicaudatan species (Schwentner et al., 2014, 2015). However, morphological variation within and between both sets of populations was large and the Bald Rock populations could not be morphologically separated from the original *P. urukhai* populations. The basic description of *P. urukhai* given above could be used to identify Bald Rock populations, details of their specific variation are given in Table 1 and Figs 4 and 5.

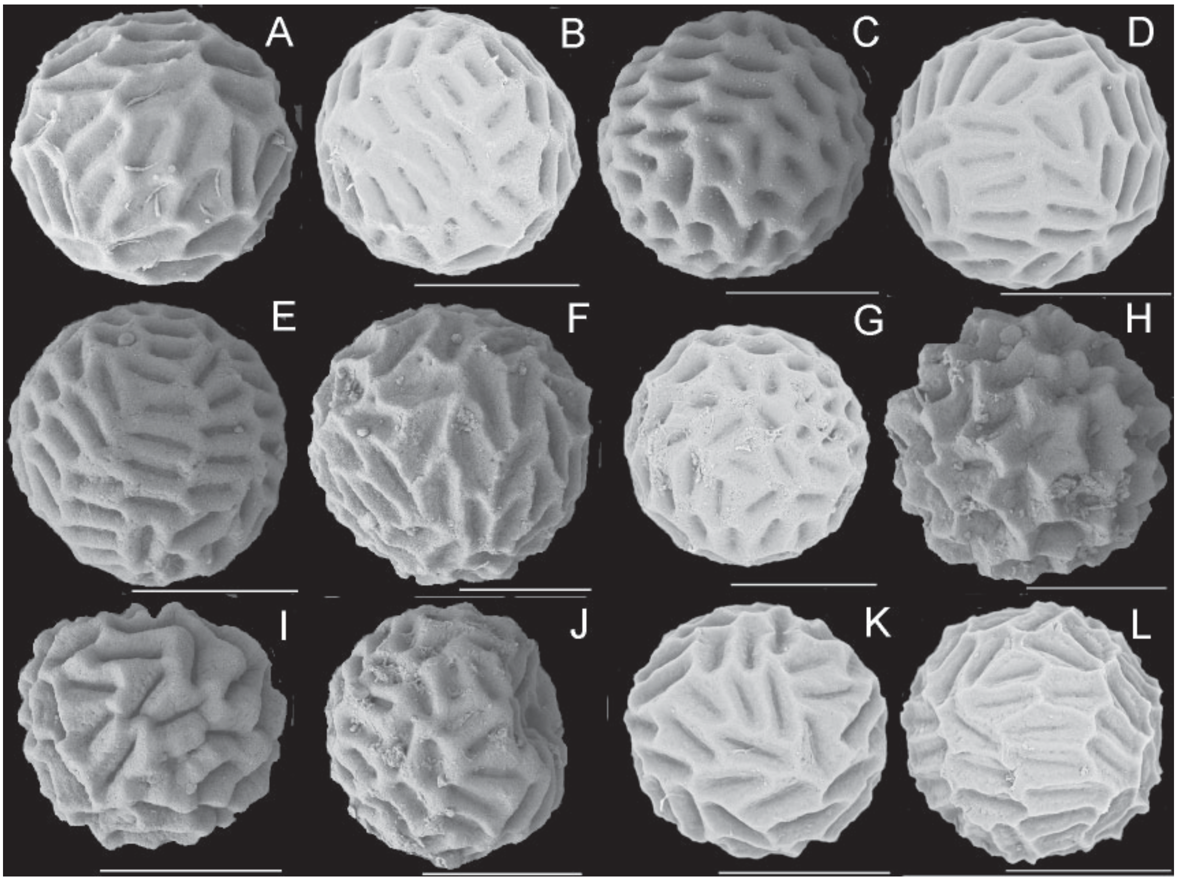


Figure 5. SEM of eggs of the P. urukhai. A, Bald Rock #1; B, Bald Rock #2; C, Bald Rock #3; D, Bald Rock #4; E, Bald Rock #6; F, Bald Rock Ck; G, Billy Goat Hill; H, near Mt Norman, I, Dragonweyr; J, Egernia ; K., Tumbledown; L, Blue Moon Mountain. All scale lines 100 µm.

Populations included (those in which eight individuals examined marked with an *): New South Wales: Bald Rock, 22 km N of Tenterfield, 28º 51' 10.6"S, 152º 02' 28.5"E, A. Ewart, 26 March 1978, 7 males, 1 female, carapaces only, QM W7051; *Mt Norman, Girraween National Park, 28º 51' 30.4"E. 151º 57' 36.9"E, 9 April 1978, J. Surridge and Mr Williamson, 12 males and 15 females, QM 750;*Bald Rock, (BR#1), 22 km N of Tenterfield, 28°51' 10.6"S, 152° 02' 28.5"E, 4 May 2016, I.A.E. Bayly, 12 ♂ 14 ♀, AM P103385; near Bald Rock, (BR#2), 22 km N of Tenterfield, 28° 51' 18.2"S, 152° 01' 54.5"E, 19 January 2016, BVT, 4 ♂ 3♀, AM P103386, 4 May 2016, BVT, 6 specimens, AM P.103387; *South Bald Rock, 19 km N of Tenterfield, (BR#6), 28° 51' 50.3"S, 152° 02' 06.8"E, 24 June 2015, BVT, 10 ♂ 11♀, AM P103388. Queensland: *near Bald Rock, (BR#3) 22 km N of Tenterfield, 28° 51' 28.8"S, 152° 01' 47.9"E, 10 October 2016, BVT, 4♂ 8♀, AM P103389; near Bald Rock, BR#4, 22 km N of Tenterfield, 28° 51' 28.9"S, 152° 01' 47.4"E, BVT, 24 June 2015, 10 ♂ 8♀, AM P103390; *Billy Goat Hill, 9 km NE of Wallangarra, 28° 51' 24.2 "S, 151° 59' 16.5"E, BVT, 15 August 2016, 86 specimens, AM P103391; *Bald Rock Ck, 6.4 km E of Wyberba, 28° 49'51"S, 151° 56' 15"E, BVT, 18 October, 2003, ca 100 individuals, AM P103392.

The most significant of observed variations of the Bald Rock populations, in order of their value in taxonomic analysis (Timms, 2016) follow:

(a) Cercopod setae. Average number per population varied between three and nine. Generally they were shorter than the diameter of the cercopod, but two individuals in two populations were longer. Setae were usually clumped on the basal half of the cercopod, but not always and were sometimes spaced, sometimes clumped.
(b) Telsonic spines number 9-18 with a variable number short.
(c) Antennomeres varied between eight and 12, with usually one more in the ventral ramus.
(d) First antennal lobes as in *P. urukhai sensu stricto*

(e) Claspers as in *P. urukhai sensu stricto*
(f) Male rostrum as in *P. urukhai stricto*
(g) Carapace as in *P. urukhai stricto*
(h) Eggs share the major characters as described for *P. urukhai sensu stricto* but in detail are variable between sites with no features shared within the seven examined populations, indeed between all twelve sites for *P. urukhai sensu lato* (Fig. 5)

Description of the Gibraltar Range species

***Paralimnadia minyspinosa* new species**
(Figs. 6-8)

Etymology.
The most distinctive feature of this species is the row of small spines on the basal half of the cercopod instead of it being clothed with setae. The smallness of the spines suggest the Greek adjective *minys* for small, so the species name is *minyspinosa.*

Holotype.
AM P103361, male, length 6.8 mm, height 3.9 mm, New South Wales, Gibraltar National Park, The Haystack mountain, 29° 58.2"S, 152° 15' 43.6"E, 1120 m asl, 10 October 2016, BVT.

Allotype.
AM P103362, female, length 6.9 mm, height 5.0 mm, collected with the holotype.

Paratypes
AM P103363, 2 males 7.1 x 4.1 mm, 7.0 x 4.0 mm, 2 females 7.3 x 4.8mm, 6.0 x 4.1 mm, collected with the holotype.

Other material**.**
New South Wales*:* six males, six females, Gibraltar National Park, The Haystack mountain, 29° 58.2"S, 152° 15' 43.6"E, 1120 m asl, 10 October 2016, BVT, AM P103364; 6 males, 6 females, Gibraltar National Park,Waratah Trig, 29° 29' 42.8"S, 152°18'27.1"E, 1152m asl, 20 February 2008, BVT, AM P103365.

Diagnosis
Egg spherical with groups of parallel rectangular depressions, sometimes in up to three continuous bands, sometimes in groups of two to many; edge

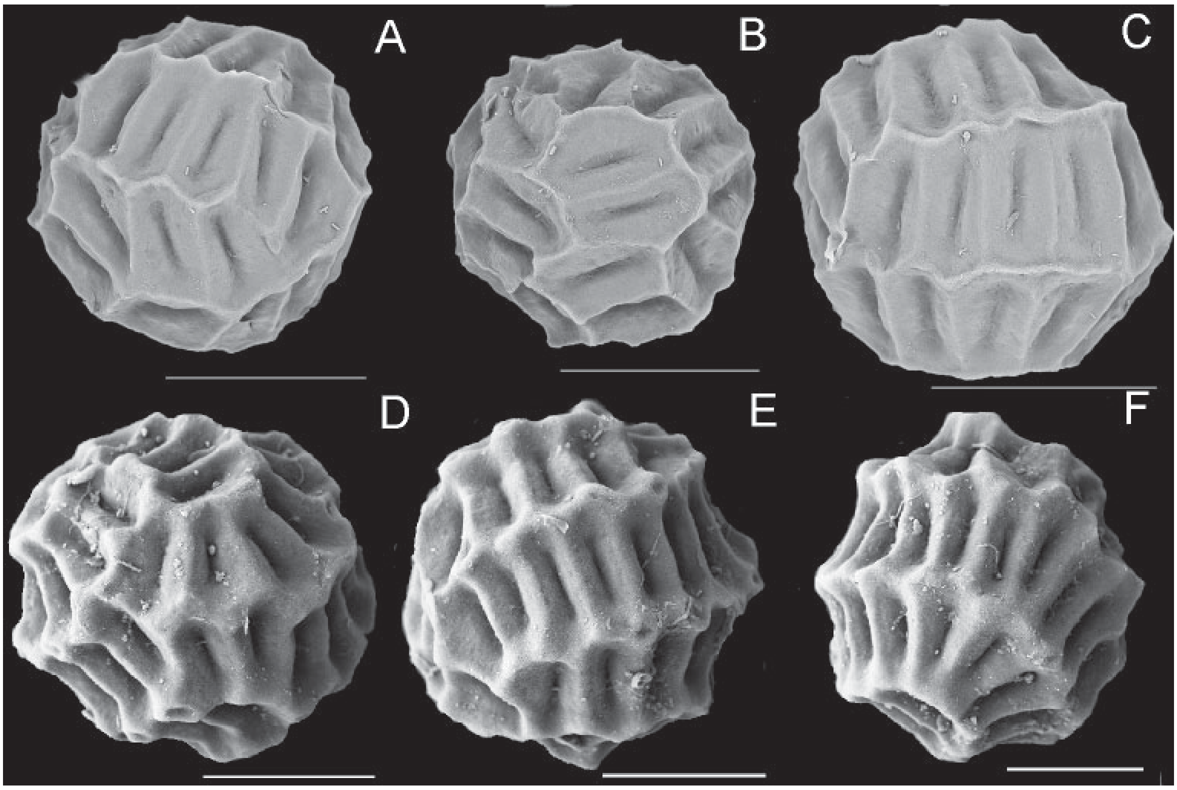


Figure 6. SEM of eggs of *P. minispinosa* n. sp. A,B,C Haystack Mountain, AM P103363. D,E,F Waratah Trig, AM P103365. All scale lines 100 µm.

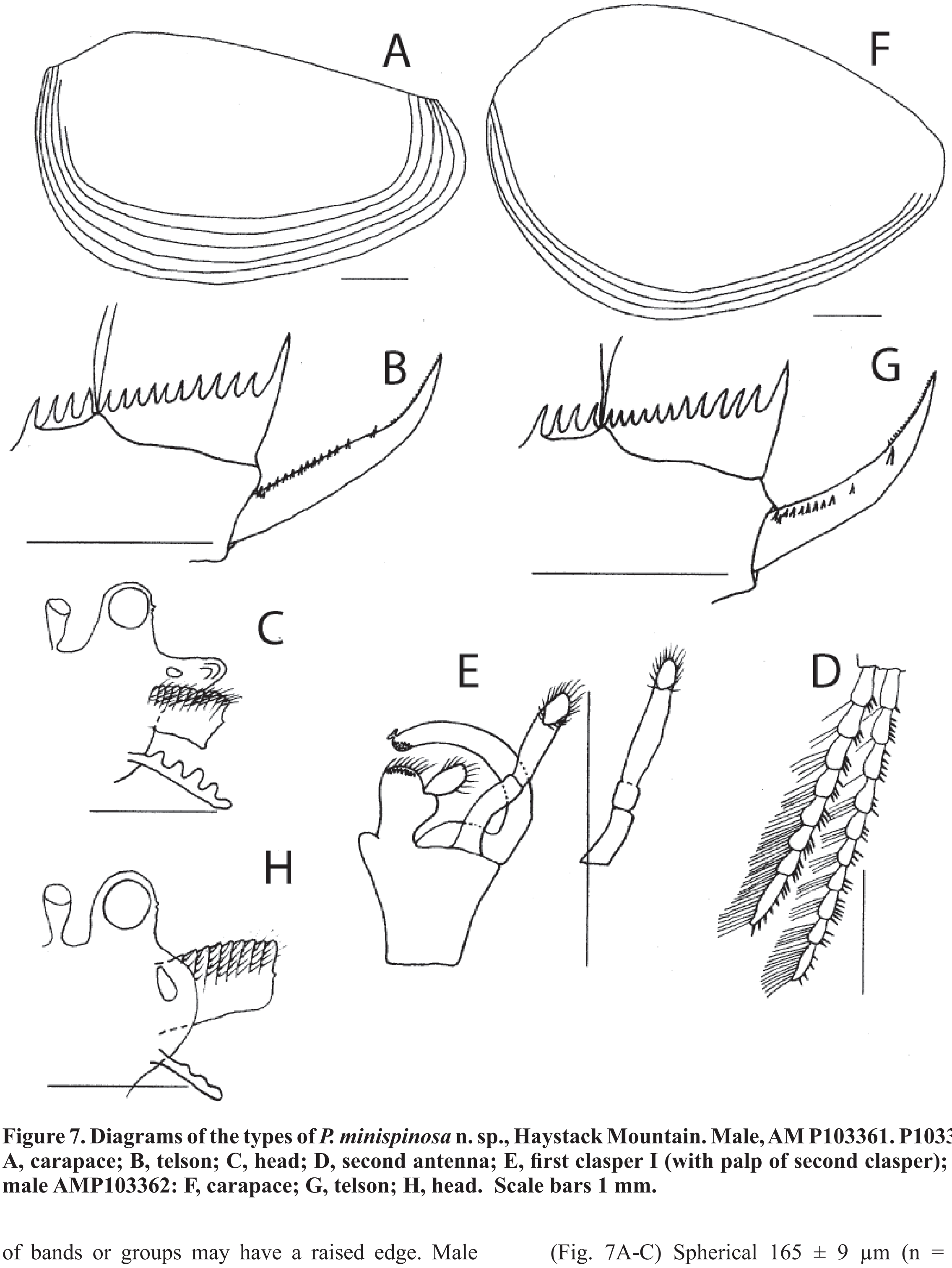


Figure 7. Diagrams of the types of *P. minispinosa* n. sp., Haystack Mountain. Male, AM P103361. P103362. A, carapace; B, telson; C, head; D, second antenna; E, first clasper I (with palp of second clasper); Female AMP103362: F, carapace; G, telson; H, head. Scale bars 1 mm.

of bands or groups may have a raised edge. Male telson with two rows of about 10-16 subequal spines arranged as three groups of different sizes and cercopod with about 9-12 very short spines on basal 60% and terminating in a slightly bigger spine.

Description. Egg

(Fig. 7A-C) Spherical 165 ± 9 µm (n = 10) in diameter, with 33 ± 6 rectangular depressions, average dimensions 31x 62 ± 5µm (n =10), each with a central axial groove and sloping sides and slightly enlarged edges. Depressions often arranged in up to three bands around the egg or in groups of two to many depressions arranged irregularly.

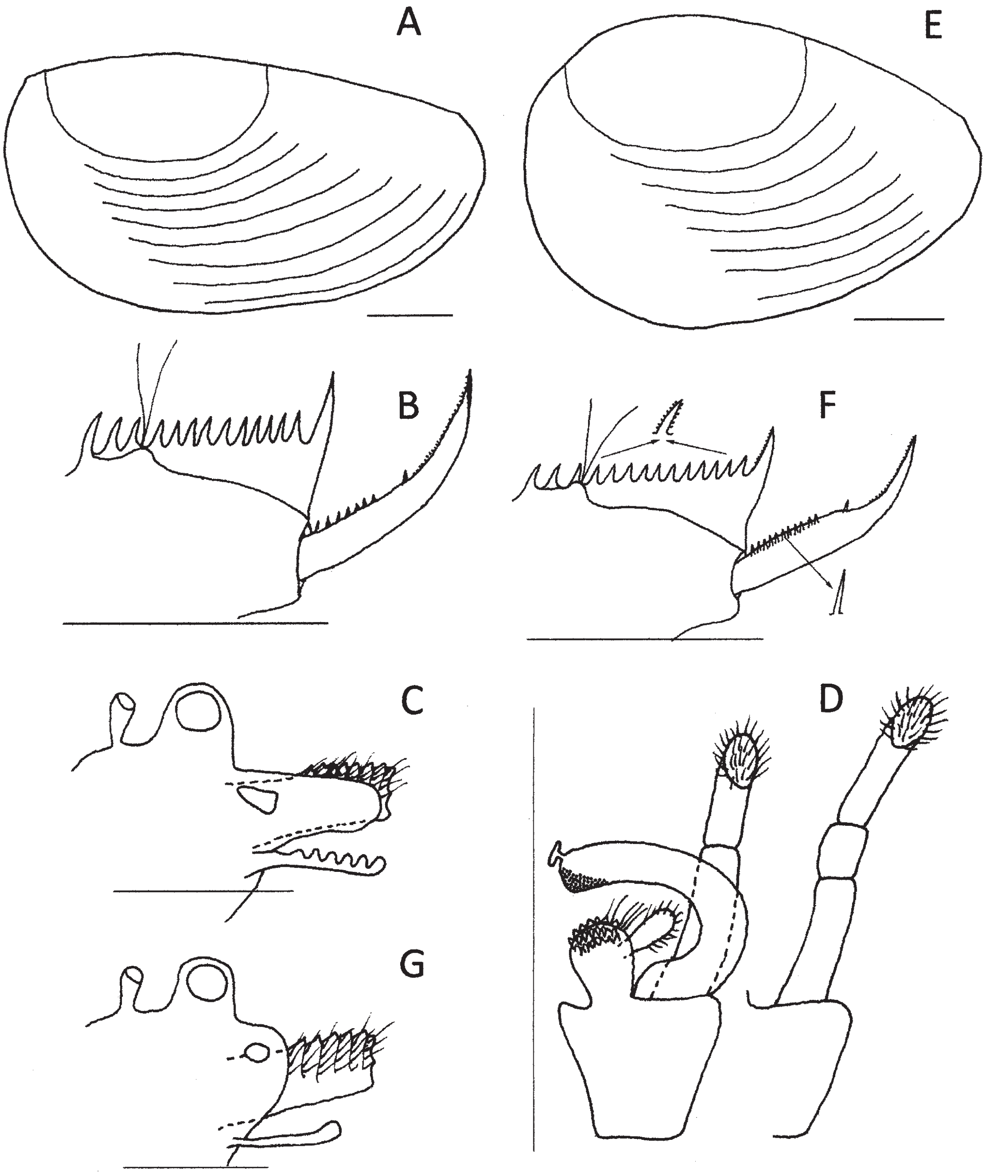


Figure 8. Diagrams of *P. minispinosa* from Warrtah Trig., AM P103365. A, male carapace; B male telson; C, male head; D, male first clasper I (with palp of second clasper); E, female carapace; F, female telson; G, female head. Scale bars 1 mm.

<u>Male:</u>

Head (Fig. 8A) with ocular tubercle prominent, somewhat taller than dorsal organ and with compound eye occupying about 80%. Rostrum protruding a little more than the ocular tubercle and at right angles from its base, with almost parallel upper and lower edges and terminating bluntly. Ocellus about half the volume of the compound eye and lying at base of rostrum.

First antennae (Fig. 8C) almost twice length of peduncle of second antennae; with five lobes, each with numerous short sensory setae. *Second antennae* with spinose peduncle and dorsal flagellum with ten antennomeres and ventral flagellum with one or two antennomeres fewer. Dorsally each antennomere with 1-8 spines, normally about 3-4 and ventrally with 1-10 setae normally about 4-5. Distal antennomere of each flagellum longer than the others and with more setae.

Carapace (Fig. 8A) elongated oval, with peak elevation at about 1/6 along its length. Carapace surface granular and coloured brown, darker dorsally. No window in the pigmentation anterioventrally as in *P. urukhai* (cf. Webb and Bell, 1979). Adductor muscle scar at about 45° to carapace long axis, only visible when animal removed from carapace. Growth lines faint, about five easily visible, and more almost invisible.

Eighteen pairs of thoracopods. Claspers (Fig. 8E) with palm trapezoidal with distinct rounded protruding endite III distomedially. Apical club spherical with many stout spines and longer spines pointing laterally. Small palp with many short, thin setae apically; enlargement in apical club basally to insertion of this palp. Finger arcuate with blunt apex bearing many rounded scales ventrally. Both long palps of claspers inserted on apical edge of palm with first clasper with two palpomeres and second palp incompletely divided into three palpomeres. Long palp of first clasper about 1.3 × length of palm and 1.7 × length in second clasper. Other thoracopods of typical structure for *Paralimnadia*, decreasing in size and complexity posteriorly. Trunk dorsum segments 11-18 with 1-5 small spines medioterminally.

Telson (Fig. 8B) spine ridges with about 15 pairs of spines, all evenly spaced and four groups: anterior group all similar in size and larger than second group of 5-6 spines with the next group of four spines about the size of the first four and the most distal spine about twice the size of all the others. Telsonic filaments originating from mound a little higher than floor of telson and usually positioned between fourth and fifth spine. Floor of telson posterior to mound sloping unevenly posteriorly to base of cercopod. Cercopods almost as long as spinal row of telson, basal 60% hardly narrowing to small spine then tapering to acute apex. About 10-12 short stout spines on basal 60% and many tiny denticles dorsolaterally on apical 40%. These spines one segmented and non-articulated and hence different from setae usually present on the cercopod. Ventroposterior corner of telson, not protruding, rounded and inerm.

<u>Female</u>

Head (Fig. 8H) with ocular tubercle prominent; compound eye occupying about 80%. Rostrum a rounded bulge about half as prominent as the ocular tubercle and with middle basal part occupied by ocellus, about 50% size of compound eye. Dorsal organ posterior to eye by about half its height, pedunculate and asymmetrical and not as high as ocular tubercle

First antennae (Fig. 8H) a little shorter than peduncle of second antennae, with three indistinct lobes each with many short sensory setae. Second antennae as in male.

Carapace (Fig. 8F) as in male, though more vaulted dorsally, and darker dorsally.

Eighteen thoracopods of typical *Paralimnadia* structure. Trunk dorsum with segments 1–9 naked, segments ca ten, 15-18 with 1-5 short spines and segments 11-14 with 5-9 long spines, all mediodistally. Thoracopods 9 and 10 with long flabellum dorsally.

Telson (Fig. 8G) as in male, though with about 15 pairs of telsonic spines, and usually 9-11 smaller spines basally placed on the cercopod.

<u>Variability</u>

Carapace shape is variable with the elongated oval shape for males and more vaulted oval shape in females (Fig. 8A,F; 9A, E). The male rostrum is larger in the Warratah population than in the Haystack population (Fig. 9C cf Fig. 8C). First antenna lobes vary by ±1, as do the number of antennomeres of the second antenna. Growth lines varied in numbers from a few to more than 20 and while indistinct in the Haystack population, were more visible in the Waratah population. A large larval valve is visible in this population. Carapace colouration varied in intensity between populations, but generally darker dorsally than ventrally.

Claspers varied a little between populations, but both had a distinct expansion (a hamulus) on the dorsal distal corner of the trapezoid palm. The first clasper large palp always was of two palpomeres, but the second clasper palp sometimes had two palpomeres, sometimes three. The telsonic spines varied from 13 to 15, rarely with a middle group smaller than the remainder. Cercopods always had numerous small spines, usually numbering 7-12 and terminating in a slightly larger one at about 60% of the length of the cercopod.

Eggs of the Waratah Trig population (Fig. 7D-F) are similar in overall construction, but larger (diameter 224 ± 8, n = 10) with depressions more numerous (40 ± 5, n =10) and more incised.

<u>Differential diagnosis</u>

Of all 15 species of *Paralimnadia*, *P. minyspinosa* n. sp. is most similar to *P. urukhai* and *P. montana* Timms. It differs from *P. urukhai* in (a) having small spines on the basal half of the cercopod instead of setae, (b) the egg surface having similar rectangular depressions, but they are arranged in three bands whereas in *P. urukhai* the depressions are largely random, though in some populations there is some grouping but never into complete bands, (c) these depressions number < 40 in *P. minyspinosa* n. sp. and > 40 in *P. uruhkai*, (d) telsonic setae are usually of similar length, except the most distal one, whereas in almost all populations of *P. urukhai* there are often some that are much shorter, (e) trunk segments number 18 whereas in almost populations of *P. urukhai* there are only 16 trunk segments. Interestingly, there are similar bands of rectangular depressions in the resting eggs of another species inhabiting gnammas, *P. stanleyana* (King) in the Sydney basin (Timms, 2016, Fig.5A-E), but it differs in many characters, including setation of the cercopod, more antennomeres and egg structure (Timms 2016).

Both *P. minyspinosa* n. sp. and *P. montana* have spines on the basal half of the cercopod instead of setae, the only two species of *Paralimnadia* with this character. The spines are different in *P. montana* (Timms, 2016, Fig. 18), being longer (ca. half diameter of cercopod, whereas in *P. minyspinosa* n. sp. they are ca. quarter the diameter) and with about two small spinulae on the spines, whereas in the *P. minyspinosa* n. sp. the spines are inerm. Further differences include (a) the ventroposterior corner of the telson is slightly protruding and denticulated in *P. montana*, but rounded and inerm in *P. minyspinosa* n. sp., (b) there are about seven lobules on the first antenna of males in *P. montana*, but only five in *P. minyspinosa* n. sp. and (c) telsonic setae are shorter and of more variable length in *P. montana* than in *P. minyspinosa* n. sp. Eggs are very different in the two species with those of *P. minyspinosa* n. sp. spherical with two-three bands of rectangular depressions (Fig. 6) but eggs of *P. montana* somewhat irregular cubic with two bands of grooves and ridges with flared marginal lamellae wrapped around each other at right angles (Fig. 11I,J in Timms 2016).

Distribution and ecology

This species is known from only two sites in the Gilbraltar National Park, east of Glen Innes. Both are gnammas (weathering pits) on mountain tops. Their waters are of low conductivity (< 100 µS/cm), high clarity and acid (pH ca. 5-6). Co-occurring invertebrates include dipterans *Paraborniella tonneri* (Edward, 1968), *Dasyhelea* sp. and *Aedes rubrithorax*, the cladocerans *Anthalona* sp. and *Armatalona imitatoria* (Smirnov, 1989) and the ostracods *Cypretta* sp, and *Ilyodromus* sp., all found also in gnammas in the nearby Granite Belt (Timms et al, 2019). *Paralimandia minyspinosa* n. sp. could well occur in similar habitats on other granitic mountain tops in the park.

DISCUSSION

Generic Placement

Recently the generic characters of *Paralimnadia* were revised and enlarged so that now the genus is better defined (Timms and Rogers, In Press). In essence, *Paralimnadia* is characterized by (a) lack of a subcercopod spine, (b) telsonic setae (filaments) on a mound, (c) amplexus during mating in line and (d) gonochoristic reproduction. In addition, there are some secondary diagnostic characters that are less reliable: usually (e) the second antennae have 12 or so antennomeres, (f) the spine at the end of the setal row lies at about 50% of the cercopod length, and (g) the hand of the clasper may have a hamulus (distinct expansion) at the distal medial corner.

These species of mountain clam shrimps of the northern New England bioregion in eastern Australia exhibit these seven diagnostic characters, except for two lineages of *P. urukhai* and *P. minyspinosa* n. sp. which have fewer than the approximately 12 antennomeres of the second antenna. In most populations of these species, the dorsal flagellum has only eight to nine antennomeres with the ventral flagellum having one more. In addition, some populations of both *P. montana* and *P. stanleyana* have only ten antennomeres in the dorsal flagellum, though the usual number is 11 (see also Timms 2016: Table 1). Perhaps living in the unusual habitat of shallow gnammas (rock pools) selects for this condition, as almost all populations with these exceptions live in such pools.

Variability

Paralimnadia urukhai sensu stricto and *P. urukhai* Bald Rock are both even more variable than usual for a clam shrimp (Straškraba 1965). Most unusual is the variation in egg morphology and cercopod setae, generally the two most reliable characters for the differentiation of species (Timms 2016). The variability of eggs and general morphology in *P. stanleyana* has already been examined. (Timms 2016 Fig 3, Table 1). These species live in isolated small rock pools generally in forested country. The explanation for this greater variability than usual may lie in severely restricted dispersal (Brendonck & Riddoch 1999; Schwentner & Richter 2015) combined with founder effects such as priority and monopolization (De Meester et al. 2002; Urban & De Meester 2009).

CONCLUSIONS

Of the six lineages of mountain shrimp in the mideastern uplands of Australia identified by Schwentner et al., (2020), four are now formally described. The other two are morphologically too similar to described species that we hesitate to formally describe. They may represent either morphologically cryptic species or genetically divergent populations. Dispersal restrictions aided by founder effects may have led to this rather high number of species as well as to the strong genetic differentiation observed among populations. These are most evident in the granitic mountains of the Northern New England Biotic Region with its isolated gnammas occupied by *P. urukhai*, but also in the sandstone gnammas of the Blue Mountains and Sydney Basin occupied by *P. stanleyana.* These two regions present different dispersal restrictions: while there are short distances between sites in the Northern New England area forests are dense, whereas in the Sydney basin suitable areas of gnammas are well separated so distance to disperse is probably as important as impositions such as forests. In the Monaro region there is much open grassland, with open forest between the study sites, so dispersal would be less restricted, but suitable wetlands are few and far between and moreover rarely fill (at least during 1980 to 2000; BVT unpublished data).

The rock pool habitats at Stanthorpe often have particularly short hydroperiods (Timms et al. 2019) like those generally inhabited by *Eulimnadia* species which are fast developers (Timms, 2018). Longer lasting rock pools on southern Australia are dominated by various slower developing *Paralimnadia* species (*P. badia* in sw WA, *P. laharum* in western Victoria, *P. stanleyana* in the Sydney Basin, (Timms, 2016, 2018)). For *P. urukhai* senus lato to survive in the Stanthorpe pools maturity at smaller sizes and less metamerisation would be an advantage. This could be achieved by having 16 instead of 18 trunk segments and 8-10 antennomeres instead of 12, both later numbers characteristic of other species of *Paralimnadia.* Having fewer antennomeres is not necessarily a disadvantage as the pools are shallow so extensive swimming away from the substrate is not needed.

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REFERENCES

Belk, D. (1989). Identification of species in the conchostracan genus *Eulimnadia* by egg shell morphology. *Journal of Crustacean Biology* 9(1): 115-125.

Brendonck, L. and Riddoch, B. (1999). Wind-borne short-range dispersal in anostracans (Crustacea: Branchiopoda). *Biological Journal of the Linnean Society* **67**: 87-95.

De Meester, L., Gomez, A., Okamura, B. and Schwenk, K. (2002). The Monopolization Hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecologica* **23**: 121-135.

Dumont, H.J., Nandanim, S. and Sarma, S.S.S. (2002). Cyst ornamination in aquatic invertebrates: a defence against predators. *Hydrobiologia* **486**: 161-167.

Kaji, T., Fritsch, M., Schwentner, M., Olesen, J. and Richter, S. (2014). Male claspers in clam shrimps (Crustacea, Branchiopoda) in the light of evolution: a case study of homology verses analogy. *Journal of Experimental Zoology* **322B**: 269-280.

Rabet, N., 2010. Revision of the egg morphology of *Eulimnadia* (Crustacea, Branchiopoda, Spinicaudata) *Zoosystema* **32**(3): 373-390.

Rabet, N., Clarac, F., Lluch, P., Gallerne, E. and Korn., M. (2015) Review of the *Eulimnadia* (Branchiopoda: Spinicaudata) from north Africa and adjacent regions, with two new species from Mauritania. *Journal of Crustacean Biology* **35**(3): 461-472.

Rogers, D.C., Rabet, N. and Weeks, S.C. (2012). Revision of the extant genera of Limnadiidae (Branchiopoda: Spinicaudata). *Journal of Crustacean Biology* **32**(5): 827-842.

Schwentner, M. & Richter, S. (2015). Stochastic effects associated with resting egg banks lead to genetically differentiated active populations in large branchiopods from temporary water bodies. *Hydrobiologia* **760**: 239-253.

Schwentner, M., Timms, B.V. and Richter, S. (2012). Description of four new species of *Limnadopsis* from Australia (Crustacea: Branchiopoda: Spinicaudata). *Zootaxa* **3315**: 42-64.

Schwentner, M., Timms, B.V. and Richter, S. (2014). Evolutionary systematics of the Australian *Eocyzicus* fauna (Crustacea: Branchiopoda: Spinicaudata) reveals hidden diversity and phylogeographic structure. *Journal of Zoological Systematics and Evolutionary Research* **52**: 15-31.

Schwentner, M., Just, F. & Richter S. (2015). Evolutionary systematics of the Australian Cyzicidae (Crustacea, Branchiopoda, Spinicaudata) with the description of a new genus. *Zoological Journal of the Linnean Society*, 173, 271-295.

Schwentner, M., Giribet, G., Combosch, D. and Timms, B.V. (2020). Genetic differentiation in mountain-dwelling clam shrimp *Paralimnadia* (Crustacea: Branchiopoda: Spinicaudata) in eastern Australia. *Invertebrate Systematics* **34**: 88-100.

Straškraba, M. (1965). Taxonomic studies on Czechoslovak Conchostraca. I. Family Limnadiidae. *Crustaceana* **9**: 263-273.

Timms, B.V. (2016). A review of the Australian endemic clam shrimp *Paralimnadia* Sars 1896 (Crustacea: Branchiopoda: Spinicaudata). *Zootaxa* **4161** (4): 451-508.

Timms, B.V. (2018). Three new species of spinicaudatan clam shrimps from Australia, all from gnammas (rock pools). *Zootaxa* **4418** (2): 136-148.

Timms, B.V. and Lindsay,S. (2011) Morphometrics of the resting eggs of the fairy shrimp *Branchinella* in Australia (Anostraca: Thamnocephalidae). *Proceedings of the Linnean Society of New South Wales* **133**: 51-68.

Timms. B.V. and Rogers, D.C. (In Press). Diagnosing *Eulimnadia* and *Paralimnadia* (Branchiopoda: Spinicaudata: Limnadiidae). *Zoological Studies*

Timms, B.V., Booth, C., Newman, M. and McCann, J. (2020). The ecology of gnammas (weathering pits) on the Stanthorpe Plateau, northern New England Tablelands, with special reference to the clam shrimp *Paralimnadia urukhai* (Webb and Bell) (Crustacea: Branchiopoda: Spinicaudata. *Proceedings of the Royal Society of Queensland* **124**: 1-19.

Urban M.C. and De Meester, L. (2009). Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proceedings Royal Society B.* **276**: 4129-4138.

Webb, J.A. and Bell, G.D. (1979) A new species of *Limnadia* (Crustacea: Conchostraca) from the granite belt in southern Queensland and north New South Wales. *Proceedings of the Linnean Society of New South Wales* **103**: 237-245.