REVISION OF THE EXTANT GENERA OF LIMNADIIDAE (BRANCHIOPODA: SPINICAUDATA)

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A B S T R A C T

The extant genera of the spinicaudatan clam shrimp family Limnadiidae are revised using morphological criteria built on previously published molecular analyses. The combined analyses demonstrate the presence of eight well defined genera, two of which are new to science and one (*Paralimnadia*) that is resurrected. We present the description of the new genus *Afrolimnadia* and the new genus and species *Calalimnadia mahei* n. sp. described from Mauritius Island. Both molecular and morphological data strongly support eight genera: *Afrolimnadia* n. gen., *Calalimnadia* n. gen., *Eulimnadia*, *Imnadia*, *Limnadia*, *Limnadopsis*, *Metalimnadia* and *Paralimnadia*.

KEY WORDS: *Afrolimnadia*, *Calalimnadia*, *Eulimnadia*, *Imnadia*, *Limnadia*, *Limnadopsis*, *Metalimnadia*, *Paralimnadia*

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INTRODUCTION

The spiny clam shrimp (Branchiopoda) comprise three distinct suborders in order Diplostraca: Laevicaudata, Spinicaudata, and Cyclestherida. Cyclestherida is a sister group to the remaining diplostracan suborder Cladocera (water fleas) (Olesen et al., 1997; Olesen, 1998; Taylor et al., 1999; Spears and Abele, 2000; Brabrand et al., 2002; deWaard et al., 2006). The monophyly of Branchiopoda has been strongly supported by recent phylogenetic analyses (Spears and Abele, 2000; Giribet et al., 2001; Regier et al., 2005, 2010; Richter et al., 2007; Olesen, 2007, 2009), but interordinal relationships within the class (as well as many evolutionary relationships at lower taxonomic levels throughout the class) have not been clearly elucidated (Braband et al., 2002; deWaard et al., 2006; Olesen, 2007; Schwentner et al., 2009). The latter situation limits our ability to test fundamental hypotheses concerning arthropod body plan, limb morphology, and breeding system evolution.

Spinicaudata has been supported as a monophyletic group in multiple studies (Spears and Abele, 2000; Braband et al., 2002; deWaard et al., 2006; Weeks et al., 2009). However, spinicaudatan interfamilial and generic relationships are not well resolved and strong evidence for monophyly is available for only one of the three spinicaudatan families (Limnadiidae: Hoeh et al., 2006). Herein, we examine the evolutionary relationships among genera of Limnadiidae *sensu lato*.

The systematics within Spinicaudata has been problematic and the principal difficulties are still far from being resolved. The spinicaudatans are known from as far back as the Devonian (Tasch, 1969) and currently occur on all conti-

nents except Antarctica (Belk, 1982; Brendonck et al., 2008; Rogers, 2009). The recent forms occur in the same general habitats as other large branchiopods: seasonally astatic wetlands, and inland saline pools and lakes (Brendonck et al., 2008; Rogers, 2009). Although spinicaudatans are common worldwide, they have been poorly studied: a few studies have assessed their morphology on a regional level (Straskraba, 1962, 1964; Belk, 1989; Marinček and Petrov, 1991b; Roessler, 1995; Pereira and Garcia, 2001; Brtek, 2005; Schwentner et al., 2011), genetics (Sassaman, 1989; Weeks and Zucker, 1999; Duff et al., 2004; Weeks, 2004; Weeks et al., 2005b; Weeks et al., 2009), phylogeny and biogeography (Richter and Timms, 2005; Hoeh et al., 2006; Weeks et al., 2006; Weeks et al., 2009; Schwentner et al., 2011). However, their reproductive biology has been examined extensively (Scanabissi-Sabelli and Tommasini, 1990; Weeks et al., 1999; Scanabissi and Mondini, 2000; Weeks et al., 2000; Scanabissi et al., 2006; Weeks et al., 2008; Weeks et al., 2009). Most attention has been devoted to the limited analysis of spinicaudatan morphological systematics; ~150 species are recognised world-wide (Brtek, 1997). There are severe uncertainties at almost all taxonomic levels. Presently, Spinicaudata is subdivided into three families (Martin and Davis, 2001; Rogers, 2009; Ahyong et al., 2011), but the monophyly of two of these (Cyzicidae and Leptestheriidae) is uncertain, as Leptestheriidae is presented as a monophyletic lineage within Cyzicidae in the analyses of Hoeh et al. (2006), or with Cyzicidae paraphyletic (Schwentner et al., 2009). However, the Hoeh et al. (2006) phylogenetic analyses/trees were not designed to estimate evolutionary relationships among the three spinicaudatan families but rather to assess the relationships among

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limnadiid genera using cyzicids + leptestheriids as the out-group. The monophyly of the third family, Limnadiidae, is strongly supported (Hoeh et al., 2006; Schwentner et al., 2009).

Morphological diagnosis of spinicaudatan clam shrimp species is difficult, the members being morphologically plastic in the fine details and generally uniform in gross morphology. Generally, Spinicaudata are branchiopod crustaceans (sensu Olesen, 2007) with laterally compressed bodies enclosed by a laterally compressed, bivalved carapace, which is capable of closing around the animal. It has been postulated that many spinicaudatans from distinct higher taxa, e.g., *Eulimnadia* and *Limnadia*, often appear strongly similar in morphology due to the retention of ancestral character states rather than from convergence or parallelism (Hoeh et al., 2006). Coupled with this, other large branchiopod groups (such as Laevicaudata and Anostraca) typically have clearly defined separate sexes, and thus their morphology has been subjected to sexual as well as natural selection. This sexual selection has resulted in species specific, ornamental morphology driven by coadapted mate recognition systems in anostracans and laevicaudatans (Martin and Belk, 1988; Rogers, 2002). As a result, since Spinicaudata have widespread hermaphroditism (in all but one Limnadiid genus) (Sassaman, 1995; Weeks et al., 2008), sexual selection would necessarily be circumscribed or absent, with the direct result that the animals are adapted for and to their environment, truncating morphological diversification (Rogers et al., 2010). Schwentner et al. (2011) have suggested that the form and number of scaliform setae on the male's clasping endites are sexually selected and may represent part of a mate recognition system. However, the clasping endites are used to grip a portion of the female carapace margin, not a particular reciprocal structure as in Anostraca (Rogers, 2002). Furthermore, the clasping endites are not visually inspected (as in Anostraca) (Rogers, 2002) or palpated by the female. Thus, it is unlikely that these structures have been shaped by a mate recognition system as opposed to the need of the male to hang on.

The molecular analyses of Weeks et al. (2009) demonstrated the presence of eight well-defined limnadiid genera. Herein, building from Weeks et al. (2009), we provide stable morphological characters unique to these clades, providing morphological definitions for these genera. We describe two of these clades as new genera and resurrect the genus *Paralimnadia*, which comprises the Australian species previously referred to *Limnadia*.

METHODS AND MATERIALS

We examined the morphology of 228 male and 388 female/hermaphrodite limnadiid clam shrimp collected from around the world from all described genera (631 individuals total). From these specimens came the 173 individuals sequenced for the molecular study presented in Weeks et al. (2009). The specific collecting data of the material used in this study were not presented in Weeks et al. (2009), so the material examined is presented in an on-line Appendix I, with all available collection data and the number of individuals examined.

Specimens were either adults preserved in 95% ethyl alcohol or were reared from eggs in the laboratory. *Calalimnadia mahei* n. gen, n. sp. used for the description were collected in 10% formalin and preserved in 70% ethanol. Samples were either collected by us or sent to us by colleagues. For each of the populations that were reared from eggs, we collected soil from natural, dried field sites. We made soil collections by sampling at many locations across each dried habitat and then homogenizing the soil in plastic bags. Approximately 500 mL of this field-collected soil was placed in the bottom of a 37 L aquarium and hydrated with deionized water. The aquarium was maintained under "standard conditions" (Weeks et al., 1997, 1999, 2001) of 25-28°C, low aeration, constant light, and fed a mixture of baker's yeast and ground Tetramin™ flake fish food (2.5 g of each suspended in 500 mL of water).

A separate set of "food limited" *Eulimnadia texana* cultures were maintained using the methods described above, except as relates to feeding. One set of cultures (Cultures A1, A2, and A3) was fed only baker's yeast, a second culture fed baker's yeast and ground Tetramin™ flake fish food (Cultures B1 and B2), and a third set of cultures fed a mixture of baker's yeast and ground Tetramin™ flake fish food described above, coupled with the alga *Selenastrum capricornutum* (Cultures C1, C2 and C3).

Shrimp were reared to sexual maturity (based on the presence of eggs in the brood chamber for females/hermaphrodites and presence of claspers in males) and then preserved in 95% ethanol or frozen in a −80°C freezer for morphological analyses.

Preserved specimens were examined using a Wild M8 dissection stereomicroscope. To separate males from females/hermaphrodites, each specimen was examined for presence of eggs and elongated epipodites (females/hermaphrodites) or claspers (males). Because there are no recent keys for this family, species diagnostic characters were identified using descriptions from peer reviewed scientific literature, original descriptions, older keys and direct comparisons with previously identified material in public and private collections.

Some living specimens had specific appendages removed in order to examine the regenerated form of the structures.

RESULTS

Tremendous variation of characters typically used for spinicaudatan diagnoses was found within cultures during our study. The specific results of one culture are presented in Table 1. Within a single species culture, growth lines could vary from 2 to 7 in females/hermaphrodites and 1 to 6 in males. The form of the naupliar eye varied from oval to triangular. Animals with algal or diatom colonies on the carapace tended to have punctate surfaces between the growth lines, whereas siblings without the algal or diatom colonies were smooth.

Two separated side by side cultures of *E. texana* originally derived from a single clutch cultured from a female cultured from a New Mexico pool were found to react differently to perceived predatory pressure. In one culture a single clam shrimp was crushed in the culture tank twice per week for three weeks. No animals were harmed in the other tank.

Table 1. Results from a single culture of *Eulimnadia texana*. M = male, H = hermaphrodite.

Specimen	Gender	# Growth lines	Carapace length × breadth	Rostral shape	AII antennomeres flagellomeres (anterior/posterior)	Telson spines (right/left)
1	H	3	0.73	Rounded	12/14	10/12
2	H	2	0.67	Angular	11/11	14/13
3	M	2	0.60	Rounded	17/17	11/13
4	H	3	0.69	Rounded	9/9	21/19
5	M	2	0.58	Angular	14/16	16/16
6	M	1	0.67	Rounded	8/14	6/26
7	H	4	0.65	Angular	10/19	15/18
8	M	6	0.59	Rounded	12/12	10/10
9	M	4	0.57	Angular	14/19	9/9
10	H	4	0.61	Rounded	11/11	18/17
11	H	7	0.66	Rounded	11/9	19/13
12	H	3	0.70	Rounded	17/18	10/10
13	M	3	0.61	Rounded	15/13	12/16

The remaining specimens in the tank with crushed animals grew transverse spiny ridges on the dorsum of the posterior most thoracic segments and the females/hermaphrodites rostrums became more angular or acute. The individuals in the other tank did not develop any such ridges and the female/hermaphrodite rostra were rounded. These preliminary results presented here will be more fully presented in another paper.

The preliminary specific results of the food limited cultures are presented in Table 2. Animals kept to a limited diet matured at a slower rate, had fewer growth lines, smaller clutch size and smaller body length. Conversely, cultures fed a more varied diet had larger body length, a faster maturation rate, more growth lines, growth lines more clearly defined, and larger clutch size.

Specimens with the antennae removed regenerated them over successive molts. However, regenerated antennae tended to be spiny instead of setose, had fewer annulations, were shorter than the originals and were thicker in diameter. Males that had one or more claspers removed also regenerated the appendages over several molts, but often with fewer and shorter setae and more spines. Regenerated cercopods

tended to be more arcuate and more chitinized, but no variation in the medial setal pattern was detected.

SYSTEMATICS

Limnadiidae Burmeister, 1843

Limniadiidae Burmeister, 1843 nom. null. fide Tasch, 1969
Limnadiidae Burmeister, 1843 nom. correct. Fide Tasch, 1969; Sars, 1896a; Simon, 1886 (in part); Daday, 1913, 1925; Botnariuc and Orghidan, 1953 (in part); Keilhack, 1961 (in part); Straškraba, 1962, 1964; Tasch, 1969; Belk, 1982; Marinček and Petrov, 1991b; Sassaman, 1995; Thiéry, 1996; Brtek, 1997 (in part), 2005; Olesen et al., 1997; Defaye et al., 1998; Olesen, 1998, 2000; Brendonck, 1999; Martin and Davis, 2001; Pereira and Garcia, 2001; Pabst and Richter, 2004; Brtek, 2005; Richter and Timms, 2005; Weeks et al., 2005b; Hoeh et al., 2006; Schwentner et al., 2009; Weeks et al., 2009; Rabet, 2010
Limnadiadae Baird, 1849 nom. imperf.
Limnadidae Girard, 1854 nom. imperf.
Imnadiidae Botnariuc and Orghidan, 1941, 1953; Marinček and Petrov, 1991b; Miličić and Petrov, 2007
Estheriinidae (Kobayashi, 1954), Novojilov, 1958 (not 1957 as per Tasch, 1969)
Limnadopseidae Novojilov, 1958; Brtek, 1997; Naganawa, 2001
Limnadopsioidea Novojilov, 1958
Limnadopsidae Tasch, 1969
Paraimnadiidae Roessler, 1991b
Metalimnadiidae Roessler, 1995
Limnadopsinae Dumont and Negrea, 2002

Diagnosis.—Cephalic forniciés not extending anteriorly. Rostrum variable, blunt to acute, long or short. Compound eyes fused medially, projecting in ocular tubercle. Frontal organ present, typically pyriform, produced on a stalk, sometimes sessile (*Metalimnadia* and *Imnadia*). Carapace thin, laterally compressed, umbone present (*Limnadopsis*), lacking (*Limnadia*) or obscure (*Metalimnadia*). Carapace with or without melanistic pigmentation, growth lines often obscured. Male first two thoracopods with endopod (sensu Olesen, 2007) bearing apical suctorial organ or modified tactile setae (absent in *Metalimnadia*). Telson with paired caudal filaments. Eggs 170-250 μm in diameter, varying in shape and ornamentation.

Table 2. Results from "food limited" *Eulimnadia texana* cultures. First twenty animals captured per culture examined. Culture set A reared on baker's yeast. Culture set B: baker's yeast and ground Tetramin™ flake fish food. Culture set C: baker's yeast, ground Tetramin™ flake fish food and the alga *Selenastrum capricornutum*. Values in parentheses represent standard deviations.

Culture	Days to first clutch	Average clutch size	Average body length (mm)	Average # growth lines
A1	18	51	2.9	2 (0.58)
A2	17	84	2.9	2 (0.05)
A3	19	99	2.6	3 (0.5)
B1	14	104	2.9	2 (1.53)
B2	16	138	3.4	3 (0.82)
C1	8	171	5.2	4 (1.53)
C2	11	230	4.8	3 (0.05)
C3	10	199	5.0	4 (0.01)

Geography.—Worldwide distribution except Antarctica.

Remarks.—Limnadiidae is separated from the other spini-caudatan families by the cephalic fornicies not extending anteriorly. Tasch (1969) retained Kobayashi's (1954) limnadiid subfamilies, Limnadiinae and Estheriininae. All extant limnadiid taxa are in Limnadiinae. We recognize eight extant limnadiid genera, two of which are new and one is resurrected from synonymy. Naganawa (2001) created a new genus *Uenia* to accommodate *Eulimnadia kobai* Uéno, 1940, which Naganawa based, in part, on Brtek's (1997) comment in his checklist concerning this species "...probably gen. nov." and that the frontal organ is expanded larger than in other limnadiids. Naganawa (2001) stated that he did not examine any material, just the figures in the original species description (Uéno, 1940). Until formal analyses and descriptions are made with specimens in hand and published in the peer-reviewed literature, it is prudent to take a more conservative approach and not accept the generic name *Uenia* at this time. However, should this taxon prove to be valid, the name *Uenia* Naganawa, 2001 is available and would have priority.

Afrolimnadia n. gen.

Limnadia. Brauer, 1877; Brtek, 1997
Eulimnadia (in part). Hoeh et al., 2006; Weeks et al., 2009; Rabet, 2010

Etymology.—From the Greek: "Afro-" referring to Africa, "limn" meaning "lake" or "marsh" and "dia" meaning "goddess." Literally, the name means "African lake goddess." "*Limnadia*" is the first genus name of the family created by Brongniart (1820) for *L. lenticularis*.

Diagnosis.—(Figs. 4J, 5E) Rostrum variable, typically rounded in females, acute to aciculate in males. Rostrum lacking spine. Angle between rostrum and frons from 100° to 80°. Occipital notch and condyle absent. Naupliar eye variable, typically triangular. Frontal organ pedunculate, length 0.7 to 2.5 times distance of organ from ocular tubercle. First antennae not segmented. Female first antennae 0.6-1 times second antennal peduncle length. Male first antenna length 1.2-2.0 times second antennal peduncle length. Carapace dorsal margin smooth, lacking carinae, hinge line arcuate, rarely sinuate. Carapace surface between growth lines slightly to strongly malleate. Umbone absent. Carapace unpigmented. Females average two growth lines (n = 7, range 2-3, SD = 0.90), males average four growth lines (n = 4, range 2-4, SD = 0.50). Carapace height divided by length averages 0.75 in females (range 0.68-0.90, SD = 0.22), 0.7 in males (range 0.56-0.80, SD = 0.05). Muscle scar angle 35 to 40 degrees from normal, i.e., body horizontal axis.

Male first two thoracopods, endite V bearing an apical suctorial organ. Endite IV typical for family, with apical dense field of long spines.

Eggs attaching to prolonged exopods of thoracopods IX and X.

Thoracic segments smooth. Telson with posteriorly directed spiniform projection present at ventroposterior angle, anteriad of cercopod base. Telson posterior margins each with posteriolateral spine row, confluent dorsally, confluence not projecting. Each row averaging 13 spines (n = 14,

range 10-15, SD = 0.37). Caudal filament originating between spine rows at third spine pair from confluence. Caudal filament never borne on mound.

Cercopods dorsal margin sinuate, longer than ventral telson margin. Cercopod medial surface with single basal spine and longitudinal row of plumose setae along proximal 80%. Cercopod with subapical, dorsal cirri, extending 5% of the cercopod length.

Egg diameter 100-150 μm, Spherical to subspherical. Eggs with narrow slit shaped depressions separated by narrow ridges.

Males amplex females venter to venter, at right angles to female's body.

Remarks.—This genus most closely resembles *Eulimnadia*, but is readily separated by the presence of a single medio-proximal spine on the cercopod, proximal to the medial setal row. In *Eulimnadia*, this spine is distal to the setal row.

This genus comprises the material originally referred to in Weeks et al. (2009) as "Undescribed eulimnadioid sp. 1." Based on our morphological definition for *Afrolimnadia* and the molecular diagnoses provided by Weeks et al. (2009), we refer *Eulimnadia alluaudi* Daday de Deés, 1926 to this genus. Thirty-five species of *Eulimnadia* have been described and another four undescribed species have been provisionally reported (Rabet, 2010), but only seventeen species were available for this study. Further study may demonstrate that other species currently ascribed to *Eulimnadia* belong in this genus, and that other morphological characters are diagnostic as well. Until *Eulimnadia* can be properly revised, only one species can be ascribed to this new genus: *Afrolimnadia alluaudi* (Daday de Deés, 1926) n. comb.

The material that we have of this species was collected from Republic of South Africa, although the taxon was originally described from Madagascar, and there are inconsistencies in the egg morphology (Rabet, 2010). We identified our material based upon the original description (Brauer, 1877) and other references to the South African fauna (Brendonck, 1999). At this time our material cannot be ascribed to *E. alluaudi* with complete confidence until a complete revision of the African limnadiid species can be conducted (Rabet, 2010).

Calalimnadia n. gen., Rabet and Rogers

"Undescribed limnadiid." Hoeh et al., 2006
"Undescribed eulimnadoid NS74." Weeks et al., 2009

Etymology.—From the Greek: "cal-" is a prefix meaning "beautiful," plus "limnadia." Literally the name means "beautiful lake goddess." See etymology section under *Afrolimnadia* for further explanation.

Diagnosis.—(Figs. 1-3, 4H) Hermaphrodites only. Rostrum rounded, without spine. Angle between rostrum and frons 100° to 120°. Occipital notch and condyle absent. Naupliar eye shape variable from oval to triangular. Frontal organ pedunculate, length approximately 1.5 times distance of organ from ocular tubercle. First antennae not segmented. First antennae length 0.7-1.0 length of second antennal peduncle. Carapace dorsal margin smooth, lacking carinae, hinge line arcuate, rarely sinuate. Carapace surface between growth lines smooth. Umbone absent. Carapace without

pigmentation. Growth lines average 3.5 (n = 38, range 2-5, SD = 1.35). Carapace height divided by length averages 0.73 (range 0.70-0.78, SD = 0.04). Muscle scar angle 35 to 40 degrees from normal.

Eggs attaching to prolonged exopods of thoracopods IX and X.

Thoracic segments smooth or with dorsoposterior ridge margined with spines or setae. Telson with posteriorly directed spiniform projection present on ventroposterior angle, anteriad of cercopod base. Telson posterior margin posteriolateral spine rows confluent dorsally, with confluence not projecting. Each row with average of 22.62 spines (n = 21, range 19-24, SD = 1.20). Caudal filament originating between spine rows at third or fifth spines from confluence. Caudal filament never borne on mound.

Cercopods straight, elongate, ~3 times length of telson ventral margin, each medially with longitudinal row of setae on proximal 80-90%, with apex beyond the cirrus bent dorsally. Setae long and plumose. Setal row terminates with single spine. Cercopod with subapical, dorsal cirrus, extending from 4-15% of cercopod length.

Egg averages 169.2 μm in diameter (n = 6, range = 159.8-180.4, SD = 7). Shape spherical to subspherical. Eggs with broad, round ridges, with narrow slits between ridges.

Comments.—*Calalimnadia* most closely resembles *Eulimnadia*, as both genera share the ventroposterior spiniform projection on the telson. However, *Calalimnadia* is readily separated by having straight, elongated cercopods (with the apex after the cirrus bent dorsally). In *Eulimnadia* the cercopods are arcuate or sinuate. Additionally, the average number of telson spines is greater than in *Eulimnadia*.

To date, this genus is known only from the island nation of Mauritius. Further study may demonstrate that other species currently treated as *Eulimnadia* belong in this genus, and that other morphological characters are diagnostic as well.

One species is attributed to this genus.

Calalimnadia mahei n. sp., Rabet and Rogers
(Figs. 1-3)

"Undesrcribed eulimnadoid." Weeks et al., 2009
"Undesrcribed limnadiid." Hoeh et al., 2006

Material Examined.—Holotype deposited in MNHN-IU-2009-1713; paratypes deposited in MNHN-IU-2009-1714, personal collection of the authors. Mauritius Island, Cap Malheureux, pool called "La Mort" (death in French) (Fig. 1), 19 April 2001. Additional specimens collected in
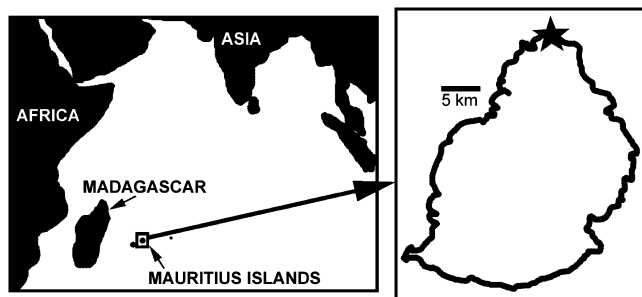
the vicinity are clearly immature. Complementary material deposited in author's collection are obtained from animals cultured from resting eggs collected from type locality.

Etymology.—The specific epithet is given in homage to Bertrand-François Mahé de La Bourdonnais (1699-1753) who was a French naval officer and an important administrator of Mauritius Island where the new species was collected.

Description.—Cephalic region as for genus (Figs. 2A, B and 3A). Second antennae natatory with peduncle bearing 10 to 12 indistinct segments (average = 11.35, n = 27, SD = 0.52) on both flagella. Flagella bearing plumose setae on ventral margin and spines on dorsal margin. Maxillary gland elongate, surrounding adductor muscle.

Carapace as for genus (Fig. 2A). Average length 9.52 mm (n = 38, range = 7.83-10.82, SD = 0.72), average height 6.85 mm (range = 5.6-7.83, SD = 0.57) and height divided by length average is 0.72 (range = 0.68-0.77, SD = 0.02).

Thoracic segments (Figs. 2A, 3A) average 22.19 in number (range 20-24, SD = 0.98). Posterior thoracic segments may have a dorsoposterior ridge margined with spines or setae or be smooth.

Telson (Figs. 2A, C and 3A) with posteriorly directed spiniform projection, sometimes short, present on ventroposterior angle, anteriad of cercopod base. Projection length subequal to basal width. Telson posteriolateral spines sometimes ornamented by minute setae except largest, distal most spine. Cercopods straight, elongate with curved extremity. Cercopod spinulae arranged in several rows with one terminal row of spinules.

Egg (Fig. 3B-E) shell surface with broad round ridges, with narrow slits between the ridges. Four layers in cross section (Fig. 3E), shell thickness varying from 30.1 μm (n = 8, average = 25.3 μm, SD = 4.3 μm) under the ridges to 9.3 μm (average = 11.5 μm, SD = 2.4 μm) under the slits. Shell alveolar layer (layer 4 in Fig. 3E) with vesicles of variable shape and size from 0.66 to 2.54 μm. Largest vesicles more frequent in cortical crest. Strut thickness variable from 0.24 to 0.72 μm. Alveolar layer border with small pores from 0.15 to 0.99 μm in diameter.

Live animals vary from yellow to white with no melanin pigment outside eyes.

Development.—The progressive development of this species comprises at least six naupliar stages and a succession of bivalved juvenile stages. The larval development will be described in detail elsewhere, however it is similar to other Limnadiids (see Olesen and Grygier, 2003; Eder, 2002; Pabst and Richter, 2004).

Ecology.—*Calalimnadia mahei* live in temporary pools with a variety of surface areas and depths (from 15 cm to more than 1 m). This species co-occurs with the anostracan *Streptocephalus reunionensis* Thiéry and Champeau, 1994 (reported here for the first time in Mauritius island) only in the deepest pool. Other associated fauna were not specifically collected, but young tadpoles, ostracodes, and culicid larvae were observed.

In culture, hatching began 16 hours after immersion and the first juveniles stages appeared 24 hours after hatching. First egg production occurred between 7 and 10 days after hatching. The maximum longevity in the laboratory
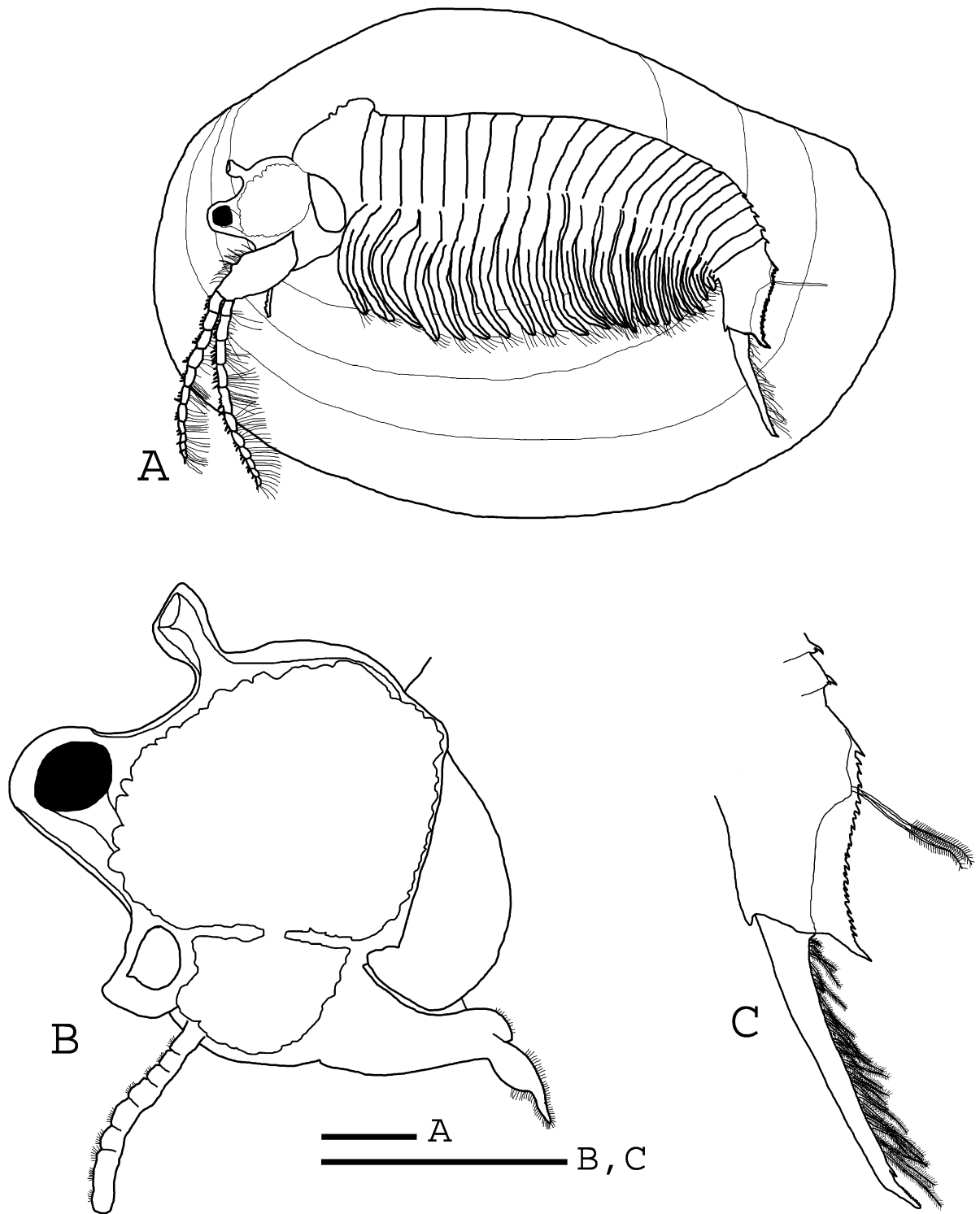

Fig. 1. Map of Indian Ocean with Mauritius Island indicated and detail showing study area locality where *Calalimnadia mahei* were collected.

Fig. 2. *Calalimnadia mahei* n. gen., n. sp. A, young adult, left lateral view; B, head, left lateral view; C, telson, left lateral view. Scale bars = 1 mm.

was 40 days at 28°C. We also found *C. mahei* to be less tolerant to low temperatures than *Streptocephalus reunionensis*. We observed mortality in culture when nocturnal temperatures dropped below 20°C verses 15°C for *S. reunionensis*. The life cycle of *Streptocephalus* is also much longer, which would explain its distribution in the deepest pool.

Remarks.—The only other spinicaudatan species known from Mauritius Island is the atypical *Eulimnadia mauritiana* (Guérin, 1837) described from Mauritius Island and not reported since. Initially this species was identified as *E. mauritiana* by the collector (NR). However, the species was included in phylogenetic studies and was referred to as an undescribed limnadiid due to its phylogenetic position as a
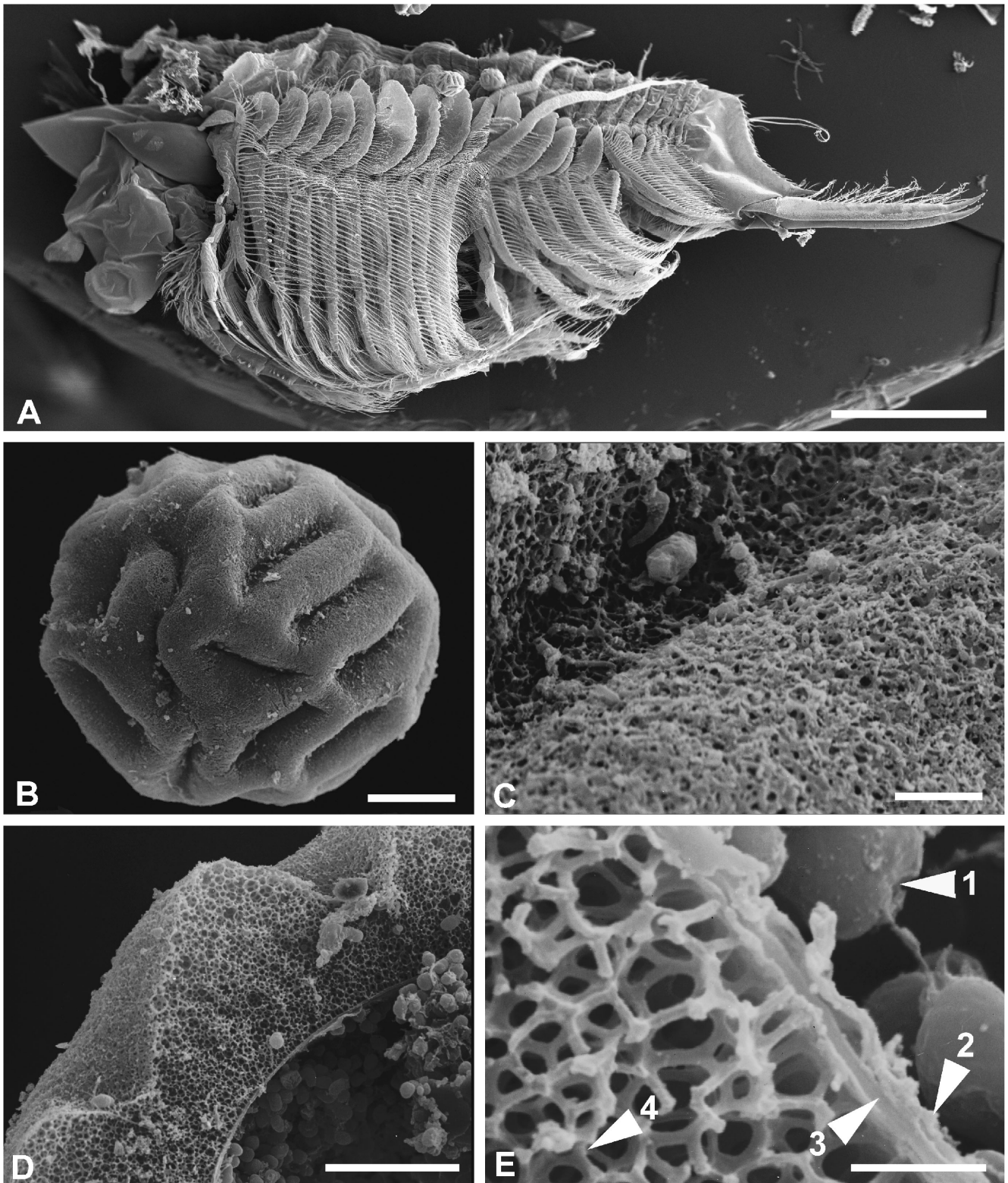
Fig. 3. *Calalimnadia mahei* n. gen., n. sp. A, young adult, left lateral view; B, egg; C, egg, surface detail; D, egg shell, cross section; E, egg shell, cross section, detail. Scale bar: A = 1 mm; B = 40 μm; C = 4 μm; D = 20 μm; E = 2 μm.

sister group to *Eulimnadia* and *Metalimnadia* (Hoeh et al., 2006). These two species are very similar as adults, other than the genus level differences, but have very different egg morphology. *Calalimnadia mahei* have spherical eggs, whereas *Eulimnadia mauritiana* have twisted eggs (Rabet, 2010).

As mentioned above, the naupliar stages are similar in all limnadiid genera previously studied. However, because the generic characters appeared later during the juveniles stages, we recommend a future comparison of the development of these stages in order to find other genus level characters.

This species was initially selected by NR for laboratory study because it has a longer life cycle and is more prolific than species of *Eulimnadia*, which reach sexual maturity after 4 to 6 days relative to 7 to 10 days for *C. mahei*. Also, *Eulimnadia* spp. Typically live 15 to 20 days (this study and unpublished data) verses 40 days for *Calalimnadia*.

Eulimnadia Packard, 1874

Eulimnadia. Mattox, 1954; Tasch, 1969; Belk, 1989; Martin, 1989; Martin and Belk, 1989; Pereira and Garcia, 2001; Weeks and Duff, 2002; Olesen and Grygier, 2003; Hoeh et al., 2006; Schwentner et al., 2009; Rabet, 2010

Limnadia. Webb and Bell, 1979; Brtek, 1997; Naganawa, 2001

Uenia Naganawa, 2001

Diagnosis.—(Figs. 4B, E, F, K, and 5D) Rostrum variable, blunt to acute, long or short. Rostrum rarely with spine. Angle between rostrum and frons 100° to 80°. Occipital notch and condyle absent. Naupliar eye variable, from oval to triangular. Frontal organ pedunculate, length approximately 1.55 times distance of organ from ocular tubercle. First antennae not segmented. Hermaphrodite first antennae length 0.6-1 times length of second antennal peduncle. Male first antenna length 1.2-2.0 times length of second antennal peduncle. Carapace dorsal margin smooth, lacking carinae, hinge line arcuate, rarely sinuate. Carapace surface between growth lines smooth. Umbone absent. Carapace occasionally pigmented. Hermaphrodites average 3.5 growth lines (n = 67, range 1-11, SD = 0.69) males average 4 growth lines (n = 45, range 2-10, SD = 0.91). (272 hermaphrodites and 127 males were examined, however most had the carapace damaged or covered in algae such that carapace characters were obscured or obliterated.) Carapace height divided by length averages 0.67 in hermaphrodites (range 0.55-0.73, SD = 0.06) and 0.62 in males (range 0.50-0.70, SD = 0.04). Muscle scar angle from 0° to 90° from normal.

Male first two thoracopods with endite V bearing apical suctorial organ. Endite IV typical for family, may be broadly transverse or bear dense apical field of short setae, or a few long setae or spines.

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.

Thoracic segments smooth or with dorsoposterior ridge rimmed with spines or setae. Telson with posteriorly directed spiniform projection on ventroposterior angle, anteriad of cercopod base. Telson posterior margin posteriolateral spine rows confluent dorsally, with confluence not projecting. Each row averages 15.2 spines (n = 117, range 6-22, SD = 1.3). Caudal filament originating between spine rows at second, third, fourth, fifth, or seventh spines from confluence. Caudal filament borne on projecting mound.

Cercopods arcuate, occasionally sinuate. Cercopod with medial longitudinal setal row on proximal 20-90%. Setae plumose and either long or short. 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 cylindrical 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).

Males amplex hermaphrodites venter to venter, at right angles to hermaphrodite's body, or in same plane.

Remarks.—Webb and Bell (1979) synonymized *Eulimnadia* with *Limnadia* based on their interpretation of various descriptions of species in both genera. Their opinion was that the character Daday (1925) employed to separate the genera (presence or absence of a spiniform projection at the telson distoposterior angle) was gradated through various taxa. However, Belk (1989), Martin (1989), and Martin and Belk (1989) argued that the presence or absence of the spine (regardless of its size) was a discrete character, and they furthermore demonstrated other characters that separate the genera (position of the caudal filaments above or below the telson ridge confluence, and the presence or absence of a spine anterior to the cercopod insertion point).

A single hermaphrodite specimen we examined from Thailand had a rostral spine. This is the only record of a rostral spine in Limnadiidae.

Eulimnadia is reported from all continents except Antarctica.

Eulimnadia has been inferred to be ancestrally androdioecious, i.e., males + hermaphrodites, with some derived all-hermaphroditic populations and species (Weeks et al., 2006, 2009). Only one species, to date, has had no males observed in any population surveyed: *E. agassizii* (Packard, 1874) (Smith, 1992; Weeks et al., 2005b, 2008). The remaining species have a bimodal distribution of sex ratios among populations, with two peaks: one at 0% males and one at ~18% males (Weeks et al., 2008).

Imnadia Hertzog, 1935

Imnadia. Botnariuc and Orghidian, 1941; Straškraba, 1964; Marinček and Petrov, 1991b; Eder, 2002

Diagnosis.—(Figs. 4A and 5C) Rostrum projecting, without spine. Angle between rostrum and frons 100° to 80°. Occipital notch broad and shallow, twice as broad as deep. Occipital condyle conical. Naupliar eye triangular. Frontal organ sessile. Carapace with dorsal margin smooth, lacking carinae, hinge line arcuate. Carapace surface between growth lines smooth. Umbone absent. Carapace without pigmentation. Females average three growth lines (n = 2, range 2-4, SD = 1.14); males average five growth lines (n = 2, range 4-5, SD = 0.05). Carapace height divided by length averages 0.67 in females (range 0.65-0.71, SD =0.06) and 0.60 in males (range 0.59-0.63, SD = 0.03). Muscle scar angle 30° from normal.

Male first two thoracopods with endite V bearing apical suctorial organ. Endite IV typical for family.

Eggs attaching to prolonged exopods of thoracopods IX and X.

Thoracic segments smooth. Telson with posteriorly directed spiniform projection present on ventroposterior angle. Telson posterior margin spine rows confluent dorsally, not

Fig. 4. Representative structures from limnadiid genera. A, *Imnadia yeyetta*, head, left lateral view; B, *Eulimnadia* sp., head, left lateral view; C, *Metalimnadia* sp., head, lateral view; D, *Limnadopsis birchii*, left cercopod, dorsal view, plumose setae not shown; E, *Eulimnadia* sp. left cercopod, dorsal view, plumose setae not shown; F, *Eulimnadia* sp., telson left lateral view; G, *Paralimnadia* sp., telson, left lateral view; H, *Calalimnadia* n. gen., distal end of telson and cercopod, right lateral view; I, *Limnadopsis* sp., telson, left lateral view; J, *Afrolimnadia*, distal end of telson and cercopod, left lateral view; K, *Eulimnadia* sp., distal end of telson and cercopod, left lateral view.
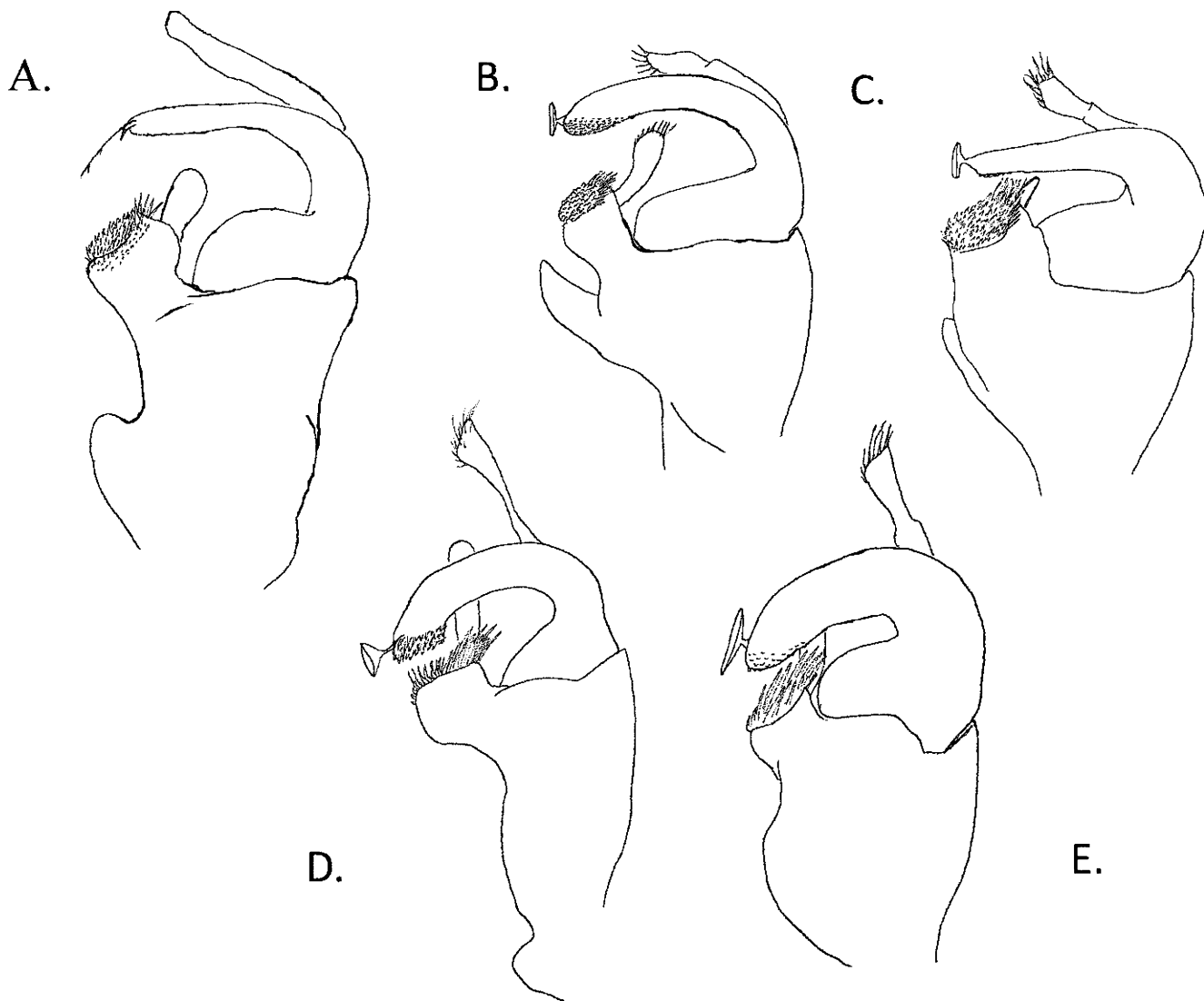
Fig. 5. Representative limnadiid male right first clasper. A, *Limnadopsis tatei*; B, *Paralimnadia badia*; C, *Imnadia yeyetta*; D, *Eulimnadia follisimilis*; E, *Afrolimnadia* "*alluadi*."

projecting. Each row averaging 14 spines (n = 4, range 11-19, SD = 3.77). Caudal filament originating between spine rows at fifth spines from confluence.

Cercopods slightly sinuate, each medially with longitudinal row of long plumose setae on proximal 60%. Setal row terminates with a single spine. Cercopod with subapical dorsal cirrus, extending 35% of cercopod length.

Eggs 100-150 μm in diameter, subspherical with slit shaped polygonal depressions separated by lamellar ridges (Thiéry and Gasc, 1991).

Males amplex females venter to venter, at right angles to female's body. Populations are gonochoristic and male-biased, ranging from 50-65% males (Sassaman, 1995; Weeks et al., 2008).

Remarks.—This genus is endemic to the western Palaearctic and contains the single species *Imnadia yeyetta* Hertzog, 1935. Straškraba (1964) and Brtek (1997) provide synonymies.

Limnadia Brongniart, 1820

Monoculus Linnaeus, 1761
Limnadia. Broginart, 1820; Simon, 1886; Daday, 1913, 1925; Straškraba, 1964; Tasch, 1969; Belk, 1989; Martin, 1989; Martin and Belk, 1989; Roessler, 1991a, b, 1995; Brtek, 1997; Eder et al., 2000; Schwentner et al., 2009
Daphnia Herman, 1804
Limnadella Girard, 1854
Estheria Baird, 1860

Diagnosis.—Rostrum variable; typically blunt in hermaphrodites and acute in males. Rostral apical spine absent. Angle between rostrum and frons 100° to 80°. Occipital notch and condyle absent. Naupliar eye oval to triangular. Frontal organ pedunculate. Frontal organ length 2-2.5 times distance between base of frontal organ and ocular tubercle. Carapace dorsal margin smooth, lacking carinae, hinge line arcuate. Carapace surface between growth lines smooth or faintly malleate. Umbone absent. Carapace with-

out pigmentation. Carapace growth lines frequently absent. Hermaphrodites average one growth line (n = 9, range 0-2, SD = 1.41); males average eight growth lines (n = 2, range 7-9, SD = 0.84). Carapace height divided by length averages 0.69 in hermaphrodites (range 0.67-0.71, SD = 0.03) and averages 0.62 in males (range 0.59-0.66, SD = 0.03). Muscle scar angle 20 to 40° from normal.

Male first two thoracopods with endite V bearing apical suctorial organ. Endite IV typical for family.

Eggs attaching to prolonged exopods of thoracopods X and XI.

Thoracic segments smooth or with dorsoposterior ridge margined with spines or setae. Telson without spiniform projection on ventroposterior angle, anteriad of cercopod base. Telson posterior spine rows confluent dorsally, confluence not projecting. Each row averaging 14 spines (n = 11, range 11-19, SD = 3.611). Caudal filament originating at or above apex of dorsal spine row confluence. Caudal filament never borne on mound.

Cercopods arcuate, with or without a medial longitudinal row of setae along proximal 30-40%. Setae simple, short, sometimes spiniform. Setal row terminates with 0-9 spines. Cercopod with subapical, dorsal cirrus, extending from 10-50% of cercopod length.

Eggs 120-170 μm in diameter, double discoidal in shape. Eggs with narrow slit shaped depressions separated by low ridges [eggs figured in Thiéry and Gasc (1991) and Shen and Huang (2008)].

Males amplex hermaphrodites venter to venter, at right angles to hermaphrodite's body. Populations consists of nearly 100% hermaphrodites, with males rarely collected in only a few locations (Sassaman, 1995; Eder et al., 2000; Weeks et al., 2008).

Remarks.—*Limnadia orinoquiensis* Roessler, 1991a needs further examination; it may not be a species of *Limnadia*. Otherwise, under our definition of *Limnadia*, there is only one recognized species: *Limnadia lenticularis* (Linnaeus, 1758).

Limnadopsis Spencer and Hall, 1896

Estheria. Baird, 1860 (in part)
Limnadopsis. Sayce, 1903; Wolf, 1911; Dakin, 1914; Henry, 1924; Tasch, 1969; Brtek, 1997; Richter and Timms, 2005; Timms, 2009; Schwentner et al., 2009; Schwentner et al., 2011
Limnadiopsis. Daday, 1925 nom. imperf.; Schneider and Sissom, 1982 nom. imperf.
Limnadiopsium Novojilov, 1958; Brtek, 1997

Diagnosis.—(Figs. 4D, I and 5A) Rostrum variable, blunt to acute, triangular or truncated, long or short, lacking apical spine. Angle between rostrum and frons 100° to 50°. Occipital notch and condyle absent. Naupliar eye variable, typically triangular. Frontal organ pedunculate. Frontal organ length 1.0 to 3.5 times distance between base of frontal organ and base of ocular tubercle. Carapace dorsal margin growth lines expanded dorsally into carinae or smooth. Carapace hinge line arcuate or straight. Carapace surface between growth lines smooth. Umbone typically present, rarely absent. Carapace with or without some pigmentation. Females average 13.4 growth lines (n = 14, range 8-24, SD = 3.98); males average 11.86 growth lines

(n = 12, range 8-14, SD = 2.19). Carapace height divided by length averages 0.67 in females (range 0.51-0.97, SD = 0.14) and averages 0.65 in males (range 0.54-0.94, SD = 0.15). Muscle scar angle ranges from 40 to 90 degrees from normal.

Male first two thoracopods with endopod with scaliform setae, lacking a suctorial organ. Endite IV typical for family.

Eggs attaching to prolonged exopods of thoracopods IV to XII, VI to XI, or IX, X and XI.

Thoracic segments may have a dorsoposterior ridge or a dorsoposterior projection margined with spines or setae. Telson with or without a spiniform projection on ventroposterior angle anteriad of cercopod base. Telson posterior margin spine rows confluent dorsally, with confluence projecting dorsoposteriorly or with spines at confluence larger in diameter than subsequent spines. Each row averaging 22.3 spines (n = 26, range 11-45, SD = 15.75). Caudal filament originating between spine rows at either third or fourth, or fourteenth and fifteenth spines from confluence.

Cercopods arcuate, each medially with longitudinal setal row along proximal 30-70%. Setae plumose, simple or setaform spines, long or short. Setal row terminates in 1-6 spines. Cercopod with subapical, dorsal cirrus, extending 5-40% cercopod length.

Eggs 150-200 μm in diameter, varying greatly in shape, with species specific morphology. Eggs with large rectilinear polygonal depressions separated by ridges, occasionally with lamellar or setaform spines at polygon ridge line confluences (Timms, 2009).

Male amplexes female on posterior carapace margin, keeping body in line, single file, behind female.

Remarks.—Species are all gonochorisitic, with sex ratios ranging from 32-88% males (Sassaman, 1995; Weeks et al., 2008). The genus *Limnadopsis* was revised by Timms (2009), with keys to species provided; however, additional undescribed species have been discovered (Weeks et al., 2009; Schwentner et al., 2011).

Metalimnadia Mattox, 1952

Metalimnadia. Pereira and Garcia, 2001
Paraimnadia Roessler, 1991b

Diagnosis.—(Based on two specimens in hand and from the literature descriptions cited above.) (Fig. 4C) Rostrum acute or truncated in both sexes. Angle between rostrum and frons 110° to 80°. Occipital notch and condyle absent. Naupliar eye oblong or triangular. Frontal organ sessile. Carapace dorsal margin smooth, without carinae or with (one specimen) one pair of carinae on anterior margin. Hinge line straight or arcuate, anterior end may project anteriorly. Carapace surface between growth lines smooth or punctate. Umbone present. Carapace often with heavy pigmentation. Females and males average 7-13 growth lines. Carapace height divided by length ranges 0.59-0.61 in females and ranges from 0.60-0.65 in males. [Muscle scar circular in our specimen, but in literature the angle depicted at 20 degrees from normal.]

Male first two thoracopods with endite V bearing apical suctorial organ. Endite IV typical for family.

Eggs attaching to prolonged exopods of thoracopods IX and X.

Thoracic segments sometimes with dorsoposterior ridge margined with spines or setae. Telson with spiniform projection on ventroposterior angle, anteriad of cercopod base. Telson posterior spine rows confluent dorsally, with confluence not projecting. Each row with 9-16 spines. Caudal filament originating between spine rows at second, third, or fourth spines from confluence.

Cercopods slightly arcuate apically, otherwise straight. Cercopods each medially with longitudinal row of short or long plumose setae along proximal 60%. Setal row terminates with short spine. Cercopod with subapical dorsal cirrus.

Eggs 130-160 μm in diameter, subcylindrical in shape and appearing tumid. Eggs with thin ridges, with regularly spaced spinules.

Male amplexes female venter to venter, at a right angle to female's body.

Remarks.—This is a gonochorisitic taxon with even male: female ratio (Sassaman, 1995).

One described species, *Metalimnadia serratura* Mattox, 1952, and at least one undescribed species.

Paralimnadia Sars, 1896b n. status

Limnadia. King, 1855, 1864; Claus, 1872; Brady, 1886; Simon, 1886; Whitelegge, 1889; Daday, 1925; Bishop, 1967; Webb and Bell, 1979; Brtek, 1997; Timms and Richter, 2002; Richter and Timms, 2005; Weeks et al., 2009; Schwentner et al., 2009

Eulimnadia. Sars, 1896b; Brady, 1886; Simon, 1886; Whitelegge, 1889; Sayce, 1903; Wolf, 1911; Dakin, 1914; Glauert, 1924; Henry, 1924; Gurney, 1927

Paralimnadia. Sars, 1896b; Sayce, 1903; Wolf, 1911; Dakin, 1914; Henry, 1924

Diagnosis.—(Figs. 4G and 5B) 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. Naupliar eye oval to triangular. Frontal organ pedunculate. Frontal organ length 0.5 to 1.5 times distance between base of frontal organ and base of ocular tubercle. Carapace dorsal margin smooth, lacking carinae, hinge line arcuate, rarely sinuate. Carapace surface between growth lines smooth. Umbone absent. Carapace with or without pigmentation. Females average 4.5 growth lines (n = 42, range 1-11, SD = 0.92); males average 4 growth lines (n = 52, range 1-13, SD = 0.64). Carapace height divided by length averages 0.70 in females (range 0.6-0.8, SD = 0.92) and averages 0.61 in males (range 0.5-0.7, SD = 0.03). Muscle scar angle 10 to 80 degrees from normal.

Male first two thoracopods with endite V bearing apical suctorial organ. Endite IV typical for family, although soometimes 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.

Thoracic segments with dorsoposterior ridge margined with spines or setae. 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 15 spines (n = 94, range 5-25, SD = 1.75). Caudal filament originating between spine rows at third, fourth, or fifth spines from confluence. Caudal filament never borne on mound.

Cercopods arcuate, occasionally sinuate. Cercopod medial surface with longitudinal row of setae along proximal 20-70%, occasionally absent, or reduced to two or three setae. Setae plumose, sometimes long or short. Setal row terminates with 0-4 spines. 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.

Male amplexes female on posterior carapace margin, keeping body in line, single file, behind female.

Remarks.—The genus *Paralimnadia* most closely resembles the genus *Limnadia*. It is readily separated by the form of the eggs, which are spherical to subspherical in *Paralimnadia*, and double discoid in *Limnadia*. In *Paralimnadia*, the cercopod setae are plumose, whereas in *Limnadia* they are short and setaform. The sex ratio in *Paralimnadia* is 50:50 (range = 30-67%; Weeks et al., 2008), whereas in *Limnadia* populations are almost entirely hermaphroditic and rarely have males. Furthermore, like the genus *Limnadopsis*, mating occurs with the male amplexing the female from behind, his body in line with the female, rather than amplexing ventrally, as occurs in all other limnadiid genera and spinicaudatan families. This amplexial behavior appears to be limited to these two genera, and is not known in clam shrimp outside Limnadiidae.

Other less reliable characters can be used secondarily to separate the genera. The carapace of *Paralimnadia* is smooth (unless it is scarified by algae or diatoms) between the growth lines, and often is pigmented with brown, especially near the brood chamber. In *Limnadia*, the carapace interspaces are sometimes malleate, and never pigmented. The rostrum in *Paralimnadia* is highly variable, being angulate or rounded in females and acute, obtuse, or elongated and rounded in males. Hermaphrodites in *Limnadia* have a rounded rostrum, whereas males have an acute rostrum. The distance from the base of the ocular tubercle to the base of the frontal organ tends to be 0.5-1.5 times the length of the frontal organ in *Paralimnadia*, versus 2.0-2.5 times in *Limnadia*.

Sars (1896b) first proposed the genus name *Paralimnadia* for King's (1855) species *Limnadia stanleyana*. Based on our morphological and molecular diagnoses for the genus *Paralimnadia*, the following examined species are placed herein (following Richter and Timms, 2005):

P. badia (Wolf, 1911)
P. cygnorum (Dakin, 1914)
P. stanleyana (King, 1855)
P. sordida (King, 1855)
P. urukhai (Webb and Bell, 1979)

At this time, we have not examined *Limnadia grobbeni* Daday, 1925 or *L. victoriensis* (Sayce, 1903), but it is likely that they belong in *Paralimnadia* as well. These species should be examined to determine their proper generic placement. With the genus *Paralimnadia* resurrected, and defined according to modern standards, the genus needs a proper review, with all the species redescribed and an identification key developed. Considering the size of Australia, and the number of new crustacean species described from astatic

aquatic habitats (Timms, 2004) and the suggested presence of several undescribed species (Weeks et al., 2009), it is probable that more species of *Paralimnadia* remain to be discovered.

To date, all species in the genus, suspected or otherwise, are limited to Australia, as is their sister genus *Limnadopsis* (Weeks et al., 2009; Schwentner et al., 2009). However, little work has been done in South America or Africa and species of *Paralimnadia* may be found there. *Paralimnadia* and *Limnadopsis* share the large range of egg bearing epipods and the inline amplexial mating behavior. These two character states are unique to these Australian endemic genera.

DISCUSSION

Quantification of morphological characters in spinicaudatan clam shrimp has always been problematic (Straškraba, 1965; Marinček and Petrov, 1991a, b). These animals are morphologically plastic in the fine details and uniform in gross morphology (Straškraba, 1964, 1965; Belk, 1989; Martin, 1989; Martin and Belk, 1989; Marinček and Petrov, 1991a, b; Petrov and Marinček, 1995; Pereira and Garcia, 2001). The polymorphism of many structures, even within populations (Marinček and Petrov, 1991a, b), among siblings (Rogers, unpublished; Marinček and Petrov, 1991b) or based on age (Marinček and Petrov, 1991a), makes the definition and diagnosis of families, genera and species quite difficult. As a result, this tremendous plasticity of the finer morphological details has yielded numerous described taxa that later were found to be variations of the same species (Straškraba, 1964, 1965; Belk, 1989; Petrov and Marinček, 1995).

In the preliminary results from our cultures we found that many characteristics traditionally used to separate limnadiid species were inconsistent and varied based upon age, regeneration, predator response, algal growth and scarring, and food quality, thus reducing their value as diagnostic structures as has been reported for other branchiopods (Rogers, 2001). These results and others will be presented elsewhere. However even within cultures, where variables were constant to all individuals tremendous variation in traditional characters occurred. Due to the amount of variation in these characters, we used only those characters that appeared stable within the generic clades generated in Weeks et al. (2009) and avoided any attempt to define limnadiid species.

In Limnadiidae *sensu lato*, there has been great disagreement on the relationships of the genera. The taxonomic status of *Eulimnadia* (as well as that of the "Australian" *Limnadia* [= *Paralimnadia* herein]) has been an ongoing controversy in limnadiid systematics since its description by A. S. Packard in 1874 (Sars, 1895a, b; Sayce, 1903; Daday, 1925; Ueno, 1940; Barnard, 1929; Mattox, 1954; Brehm, 1958; Straskraba, 1965; Webb and Bell, 1979; Brtek, 1997; Pereira and Garcia, 2001). The disagreement was founded on differing opinions regarding the ability to morphologically differentiate specimens of *Eulimnadia* from those of *Limnadia*. However, based on quantitative morphological characters (Belk, 1989; Martin, 1989; Martin and Belk, 1989), and on molecular analyses (Hoeh et al., 2006; Weeks et al., 2009; Schwentner et al., 2009) *Eulimnadia* has been demonstrated to be a valid genus.

KEY TO THE GENERA OF LIMNADIIDAE

1 Frontal organ sessile (Fig. 4A) 2
1′ Frontal organ pedunculate (Fig. 4B) 3
2 Occipital condyle absent (Fig. 4C) . . . . *Metalimnadia*
2′ Occipital condyle present (Fig. 4A) . . . . *Imnadia*
3 Male suctorial organ present, obvious (Fig. 5B-E); in all sexes telson posterior margin spine rows with dorsal confluence not produced (Fig. 4F); carapace not carinate 4
3′ Male suctorial organ reduced to a few scales (Fig. 5A); all sexes with telson posterior margin spine rows with dorsal confluence produced (Fig. 4I), or at least dorsal most spine longer or stouter than subsequent spines; carapace may be carinate dorsally at growth lines . . . *Limnadopsis*
4 Telson without a ventral spiniform projection (Fig. 4G, I) 5
4′ Telson with a ventral spiniform projection just anteriad of cercopod base (Fig. 4F, H, J, K) 6
5 Eggs double discoid or subcylindrical; cercopod setae short, sometimes spiniform; mating pairs with partners at right angles to each other . . . . *Limnadia*
5′ Eggs subspherical; cercopod setae variable, sometimes absent; mating pairs with partners in single file . . . . *Paralimnadia*
6 Cercopods sinuate or arcuate at least on dorsal margin, subequal or slightly longer than telson ventral margin (Fig. 4K, J) 7
6′ Cercopods straight, >2.5 times as long as telson ventral margin (Figs. 2, 4H) . . . . *Calalimnadia*
7 Caudal filament borne on a projecting mound (Fig. 3F); carapace smooth between growth lines; male endite 4 on first and second thoracopods with a field of short spines, sometimes with setae, spines length less than width of endite (Fig. 5D); cercopods with medial long plumose setae and with or without a single spine at distal end of setal row, never with a medial proximal spine (Fig. 4E, K) . . . . *Eulimnadia*
7′ Caudal filament never borne on a mound (Fig. 5G); carapace slightly malleate between growth lines; male endite 4 on first and second thoracopods with a field of long spines, spines length at least width of endite (Fig. 5E); cercopods with medial proximal spine, and a longitudinal row of long plumose setae (Fig. 4J) . . . . *Afrolimnadia*

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APPENDIX I. MATERIAL EXAMINED

The following (Table A.1) material was examined for our study. Collection data provided by the collectors was not always complete. All identifications were made by us using existing keys and descriptions and direct comparison with identified reference material. All material used in the morphological examination prior to being processed for the Weeks et al. (2009) molecular analyses is indicated by an ID number. Material without an ID number was not used in the molecular analyses of Weeks et al. (2009). F = female, H = hermaphrodite, M = male.

Table A.1.

Taxon	Locality data	ID number used in Weeks et al., 2009	Number of specimens examined
Afrolimnadia n. gen.	REPUBLIC OF SOUTH AFRICA: KWA ZULU NATAL: Natal Phinda Game Preserve, M. Hammer	W285	7F, 4M
	BOTSWANA: Thamaga, M. Hammer	W261	2M
	BOTSWANA: Thamaga, M. Hammer	W320	2M
Calalimnadia mahei n. gen., n. sp.	REPUBLIC OF MAURITIUS: Cap Malheureux, La Mort temporary pool, 19 April 2001, N. Rabet and V. Rabet, DCR-438	NS74	40H

Table A.1.   (Continued.)

Taxon	Locality data	ID number used in Weeks et al., 2009	Number of specimens examined
Eulimnadia agassizi Packard, 1874	USA: FLORIDA: Munsen Sand Hills, south of Tallahassee, 4 October 2000, T. Spears		4H, 4M
	USA: MARYLAND	W272	5H, 2M
	USA: MARYLAND	W278	3H, 4M
Eulimnadia brasiliensis Sars, 1902	BRAZIL: MINAS GERIAS: CODEVASF fish ponds at Tres Marias, 1998, A. Ferreira	W229	10H
Eulimnadia braueriana Ishikawa, 1895	JAPAN: Otsu Shiga at Mitsu 2-Chome, M. J. Grygier	W274	6H, 2M
	JAPAN: Sakai Cho 3-Chome 9, M. J. Grygier	NS41	3H, 3M
Eulimnadia colombiensis Roessler, 1990	BRAZIL: MINAS GERIAS: Nova Lima, temporary pool at Capão Xavier, 8 September 2001, reared from soil, A. Ferreira	NS105	14H
Eulimnadia cylindrova/ texana/belki	BRAZIL: UTM #06072767/7765859		7H, 5M
	MEXICO: BAJA CALIFORNIA SUR: Km 76.5	NS16	4H, 4M
Eulimnadia cylindrova Belk, 1989	USA: LOUISIANA: Jefferson County: Grand Isle, 10 July 1940, G. H. Penn Jr., Det. D. C. Rogers, DCR-538.		6H, 1M
	USA: NEBRASKA		3H, 3M
	ECUADOR: Galapagos Islands	NS65	4H, 6M
	USA: NEW MEXICO: Luna County: Stock tank dug into a playa on BLM land, 14 miles east of Columbus, T29S, R6E, S12, 1200 meters elevation, 26 September 1999, R. Worthington, Det. D. C. Rogers, DCR-404		21H, 19M
	ECUADOR: GALAPAGOS ISLANDS: Isla Santa Cruz: Table Mountain, 440 meters elevation, 16 April 1964, D. Q. Cavagnero, Det. D. C. Rogers, DCR-537		4H
	ECUADOR: GALAPAGOS ISLANDS		1H
Eulimnadia dahli Sars, 1896	AUSTRALIA: WESTERN AUSTRALIA: Pabellup Swamp, S. Weeks	W101	3H, 3M
	AUSTRALIA: WESTERN AUSTRALIA: Pilbara, S. Weeks	W102	1M
	AUSTRALIA: WESTERN AUSTRALIA: Pygery Rocks	W106	3H, 3M
	AUSTRALIA: WESTERN AUSTRALIA: Green Roc	W113	4M
	AUSTRALIA: WESTERN AUSTRALIA: The Humps Bag #1	W231	1M
	AUSTRALIA: WESTERN AUSTRALIA: Bunjil	W240	10H
Eulimnadia diversa Mattox, 1937	USA: GEORGIA: DeKalb County: Lithonia Rock, 21 April 2001, S. Cammack, Det. D. C. Rogers, DCR-351		4H, 4M
	USA: NEW MEXICO: Sandoval County: roadside pools on CR313, N35° 19′ 31.17″, W106° 32′ 13.66″, 12 August 2002, B. K. Lang, Det. D. C. Rogers, DCR-494		8H, 8M
	USA: FLORIDA: Blake Pond, 30 June 2002, S. Weeks	W276	2H
	USA: MISSISSIPPI	W317	3H
	USA: WASHINGTON: Othello, M. Hill		18H, 2M

Table A.1.   (Continued.)

Taxon	Locality data	ID number used in Weeks et al., 2009	Number of specimens examined
Eulimnadia feriensis Dakin, 1914	AUSTRALIA: WESTERN AUSTRALIA: Kadji-Kadji, S. Weeks		10H
	AUSTRALIA: WESTERN AUSTRALIA: Wanarra Rock		2H, 1M
	AUSTRALIA: WESTERN AUSTRALIA: TAM Pool		3H
Eulimnadia follisimilis Pereira and Garcia, 2001	USA: NEW MEXICO: San Juan County: ~18 miles west of Shiprock on County Road 364, 22 August 2001, B. K. Lang, Det. D. C. Rogers, DCR-453	W321	4H, 4M
	USA: NEW MEXICO: Socorro County: Stock Tank ~2.3 road miles east of Forest Route 549 and US Route 60, south of Route 60, N34° 04′ 38.22″, W107° 24′ 43.73″, ~2166 meters elevation, 26 August 2002, B. K. Lang, Det. D. C. Rogers, DCR-455	W322	5H, 8M
Eulimnadia magdalensis Roessler, 1990	BRAZIL: PARAIBA: Cabo Branco, Mare #1, 18 July 1993, N. Rabet, DCR-444		4H
	VENZUELA	NS99	1H
Eulimnadia michaeli Nayar and Nair, 1968	THAILAND: Khoen Kaen: L. Sanoamuang	W348	1H
	THAILAND: Khoen Kaen: L. Sanoamuang	W349	1H, 2M
	THAILAND: Khoen Kaen: L. Sanoamuang		2 H, 2M
Eulimnadia ovata Nayar, 1965	INDIA: Bharathidasan University Campus, September 2003, C. Amutha, Det. D. C. Rogers, DCR-545		6H
Eulimnadia texana (Packard, 1871)	MEXICO: BAJA CALIFORNIA SUR		4H, 4M
	USA: CALIFORNIA: Shasta County: Palo Cedro, Spanish Oaks Drive Pond, September 1991, DC Rogers, DCR-14		17H, 9M
	USA: CALIFORNIA: Shasta County: Palo Cedro, Redbud Lane, irrgation ditch, July 1993, D. C. Rogers		11H, 10M
	USA: NEW MEXICO: Luna County: Stock tank, 8.9 road miles east of Columbus, T29S, R6W, S6, 1210 meters elevation, 26 September 1999, R. Worthington, Det. D. C. Rogers	W280	5H, 5M
	USA: NEW MEXICO	W281	4H, 7M
Eulimnadia graniticola Rogers, Weeks and Hoeh, 2010	USA: GEORGIA: DeKalb County: Stone Mountain	W170	11H, 6M
Imnadia yeyetta Hertzog, 1935	FRANCE: BOUCHES du RHŌNE: Cerisière Nord, Tour du Vallat, Arles, 27 September 2000, N. Rabet, DCR-440		2F
	AUSTRIA	W128	2F/H, 2M
Limnadia sp. 1	USA: FLORIDA: Red Hills north of Tallahassee, 8 October 2000, T. Spears, Det. D. C. Rogers, DCR-407		8H

Table A.1. (Continued.)

Taxon	Locality data	ID number used in Weeks et al., 2009	Number of specimens examined
Limnadia lenticularis (L., 1761)	USA: FLORIDA: Leon County: Leon City, Lake Manson area, past intersection of Road 305 and 303, in small pool, 28 August 2001, T. Spears, Det. D. C. Rogers, DCR-392	NS25	3H
	USA: GEORGIA: Early County: Shackleford-William's Bluff Preserve (TNC), 21 March 2003, J. Jensen and T. Floyd, Det. D. C. Rogers, DCR-515		8H
	USA: GEORGIA: Newton County: 2 April 1998, J. Battle, Det. D. C. Rogers, DCR-389		16H
	JAPAN: Aomori	W216	1M
	ITALY: Ferrara, 10 May 2003, Cesari	W154	1H
	AUSTRIA: Hermas	W254	9H
Limnadopsis sp.	AUSTRALIA: NEW SOUTH WALES: 37 km west of Coonable, pond , 22 February 1992, G. Challet, Det. D. C. Rogers, DCR-480		1F
Limnadopsis birchii (Baird, 1860)	AUSTRALIA: WESTERN AUSTRALIA: Great Central Road Swamp		1F, 1M
	AUSTRALIA: New South Wales: Paroo, Bloodwood Station, 2000, S. Richter, DCR-292		1F
	AUSTRALIA: New South Wales:		1F, 1M
Limnadopsis occidentalis (Timms, 2009)	AUSTRALIA: WESTERN AUSTRALIA: Kadji Kadji Clay Pan	W116	2M
	AUSTRALIA: WESTERN AUSTRALIA: Tardun CBC Dam	W127	3F, 1M
	AUSTRALIA: WESTERN AUSTRALIA	W109	1F, 1M
Limnadopsis tatei Spencer and Hall, 1896	AUSTRALIA: WESTERN AUSTRALIA: Lasseter Highway	W201	1M
	AUSTRALIA: WESTERN AUSTRALIA: 7J Creek	W290	3F, 3M
Metalimnadia serratura Mattox, 1952	GUYANA: Morawhanna: Brakish canal south of Morawhanna, 23 May 1952, K. A. L. Reading, Det. D. C. Rogers, DCR-346		1M
Metalimnadia sp.	BRAZIL: Paraiba, N. Rabet	NS109	1F
Paralimnadia badia	AUSTRALIA: WESTERN AUSTRALIA: Wanarra Rock, Gnamma 5	W136	4F, 2M
	AUSTRALIA: WESTERN AUSTRALIA: Wanarra Rock, Gnamma 2	W144	2F, 1M
	AUSTRALIA: WESTERN AUSTRALIA: Dunn Rock	W251	1F, 3M
Paralimnadia cygnorum	AUSTRALIA: WESTERN AUSTRALIA: Dingo	W194	3M
Paralimnadia sordida	AUSTRALIA: WESTERN AUSTRALIA: Mettler's Road	W197	16F, 8M
	AUSTRALIA: WESTERN AUSTRALIA: Wannara Clay Pan	W110	4M
	AUSTRALIA: WESTERN AUSTRALIA: Armadale Road	W137	1M
Paralimnadia stanleyana	AUSTRALIA: WESTERN AUSTRALIA: Kanagra Walls	W180	5M

Table A.1.   (Continued.)

Taxon	Locality data	ID number used in Weeks et al., 2009	Number of specimens examined
Paralimnadia sp.	AUSTRALIA: WESTERN AUSTRALIA: B. V. Timms	W121	11F, 19M
	AUSTRALIA: WESTERN AUSTRALIA: Tardun CBC Dam	W119	1F, 2M
Paralimnadia urukhai (Webb and Bell)	AUSTRALIA: NEW SOUTH WALES: B. V. Timms	W169	11F, 19M