



A new species of *Eulimnadia* (Crustacea; Branchiopoda; Diplostraca; Spinicaudata) from North America

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Abstract

Eulimnadia graniticola n. sp. from Stone Mountain, Georgia, and the Florida Keys, USA, is defined primarily on molecular characters and egg morphology. Ecological, reproductive and life history data are provided. This species is the second species of branchiopod crustacean reported from Stone Mountain more closely related to the South American fauna than to its North American congeners.

Key words: Clam shrimp, eggs, vernal pools, rock outcrop pools, Georgia, Florida

Introduction

During a study of the higher taxonomy of the world Spinicaudata, we encountered a previously undescribed species of limnadiidan clam shrimp of the genus *Eulimnadia*. This new species is known from the depressional pools on Stone Mountain, in the state of Georgia and from seasonal wetlands in the Florida Keys, USA. The Stone Mountain site is particularly interesting in that it is the largest granitic pluton in North America. The depressional pool is also the type locality for the anostracan *Dendrocephalinus lithaca* (Creaser, 1940) (Rogers 2006).

Material and methods

Eggs from the Georgia locality were cultured to adult stage at the University of Akron, in Akron, Ohio, USA.

Morphological Analyses

The material was examined using a Wild M8 dissection stereomicroscope, and was sketched freehand. The specimens were compared with congeners:

Eulimnadia africana Brauer, 1877 KENYA: Kalif District: Malindi, Mombasa Road, 3 km south of Watamu Junction, 1 km west on dirt road in flooded sand quarry, 27 August 1987, R. C. Drewes, CAS 165159, Det. D. C. Rogers, DCR-535.

Eulimnadia agassizi Packard, 1874 USA: FLORIDA: Munsen Sand Hills, south of Tallahassee, 4 October 2000, T. Spears, Det. D.C. Rogers, DCR-405.

Eulimnadia brasiliensis Sars, 1902 BRAZIL: MINAS GERAIS: CODEVASF fish ponds at Tres Marias, 1998, A. Ferreira, Det. D.C. Rogers, DCR-365.

Eulimnadia colombiensis Roessler, 1990 BRAZIL: MINAS GERAIS: Nova Lima, temporary pool at Capão Xavier, 8 September 2001, reared from soil, D.C. Rogers, DCR-406.

Eulimnadia cylindrova Belk, 1989 USA: LOUISIANA: Jefferson County: Grand Isle, 10 July 1940, G. H.

Penn Jr., Det. D. C. Rogers, DCR-538. NEW MEXICO: Luna County: Stock tank dug into a playa on BLM land, 22.5 km east of Columbus, T29S, R6E, S12, 1200 meters elevation, 26 September 1999, R. Worthington, Det. D.C. Rogers, DCR-404. ECUADOR: GALAPAGOS ISLANDS: Isla Santa Cruz: Table Mountain, 440 meters elevation, 16 April 1964, D. Q. Cavagnero, Det. D. C. Rogers, DCR-537.

Eulimnadia diversa Mattox, 1953 USA: GEORGIA: DeKalb County: Lithonia Rock, 21 April 2001, S. Cammack, Det. D. C. Rogers, DCR-351. 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.

Eulimnadia near *follisimilis* Ferreira & Garcia, 2001 USA: NEW MEXICO: San Juan County: ~29 km west of Shiprock on County Road 364, 22 August 2001, B. K. Lang, Det. D. C. Rogers, DCR-453. Socorro County: Stock Tank ~3.7 road km 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.

Eulimnadia magdalensis Roessler, 1990 BRAZIL: PARAIBA: Cabo Branco, Mare #1, 18 July 1993, N. Rabet, DCR-444.

Eulimnadia sp., 1837 MAURITIUS ISLAND: Cap Malheureux, Mare temporaire (la mort), 19 April 2001, N. Rabet & V. Rabet, DCR-438.

Eulimnadia ovata Nayar, 1965 INDIA: Bharathidasan University Campus, September 2003, C. Amutha, Det. D. C. Rogers, DCR-545.

Eulimnadia texana Packard, 1871 USA: CALIFORNIA: Shasta County: Palo Cedro, Spanish Oaks Drive Pond, September 1991, DC Rogers, DCR-14. Palo Cedro, Redbud Lane, irrigation ditch, July 1993, DC Rogers. NEW MEXICO: Luna County: Stock tank, 14.3 road km east of Columbus, T29S, R6W, S6, 1210 meters elevation, 26 September 1999, R. Worthington, Det. D.C. Rogers.

Molecular Analyses

Total DNA was isolated and partial 28S DNA sequences generated from a total of 118 *Eulimnadia* specimens representing 10 nominal species [i.e., *africana*, *agassizii*, *brasiliensis*, *colombiensis*, *cylindrova*, *diversa*, *follisimilis*, *magdalensis*, *michaeli*, and *texana*,] from North America, South America, Africa and Asia. Protocols for DNA isolation, PCR and DNA sequencing are from Hoeh et al. (2006) and Weeks et al. (2006).

Reproductive Analyses

Determining the mating system in clam shrimp is a multi-step process of culturing and isolating "female" (herein, "female" is used to denote that we do not yet know whether the individuals are females or hermaphrodites) clam shrimp, culturing their offspring, determining sex ratios, and if need be examining the gonad to confirm the presence of ovotestes (Weeks *et al.* 2005, 2008). If the "females" produce viable offspring in isolation, then they are either parthenogenetic females or self-compatible hermaphrodites. To distinguish between these alternatives, one notes whether there are two classes of "females": ones that have no males among their unisexually produced offspring (monogenics) and ones that have ~25% males among their unisexually produced offspring (amphigenics; Sassaman and Weeks 1993). The relative proportion of these two hermaphroditic types depends on the rate of outcrossing in the source population (Otto *et al.* 1993). Because no other "female" organism has been described that produces 25% males when raised in isolation (Bull 1983; Bell 1985), finding any amphigenic hermaphrodites among the surveyed clam shrimp is most parsimoniously explained by assuming the species is androdioecious (Weeks *et al.* 2005, 2008). However, a lack of amphigenics can either be because the species is androdioecious but the population surveyed is comprises only monogenic hermaphrodites, or because the species reproduces parthenogenetically. Determining between these last two alternatives can be accomplished via sectioning of the gonad (Weeks *et al.* 2005).

Culturing and Isolating Methods

Approximately 100 ml, by volume, of field-collected soil containing clam shrimp eggs was placed in the bottom of a three liter plastic tank and hydrated with deionized water. The tank was maintained under

“standard conditions” (Weeks *et al.* 1997; 1999; 2001) of 25°C, low aeration, constant light, and fed a mixture of baker’s yeast and ground Tetramin™ flake fish food.

Directly before sexual maturity, 50 “females” were isolated in 500 ml plastic cups containing approximately 5 ml of soil taken from a New Mexico site known to be free of any branchiopod eggs. Isolated “females” were allowed to lay eggs for 7 days. Eggs in the cups were then allowed to dry naturally, the cups were sealed with lids, and then placed in the dark for >30 days.

Development of Laboratory Egg Banks

After storing, 47 egg banks were hydrated using the methods above. The cups were checked daily for a period of two weeks for signs of hatching. Eleven of the 47 egg banks hatched, and the resulting nauplii were transferred to 10 l rearing tanks containing 100 ml of soil and deionized water. Tanks were maintained under standard conditions. Upon sexual maturity, the clam shrimp were counted and sexed.

Results

Eulimnadia graniticola species novae

(Figure 1)

Etymology: The name “*graniticola*” comes from the word “granite”, referring to the rock type that the type locality is situated in, and the Latin suffix “-cola”, which means “dweller”.

Types: Holotype: female/ hermaphrodite, data: USA: Georgia: Dekalb County: Stone Mountain: rock outcrop depressional temporary wetland, ~500m elevation, 29 August 2005, T. Sanderson, R. Posgai and S. Weeks, deposited Los Angeles County Museum, LACM type number CR 2005-038.1. Allotype: same data as holotype, deposited LACM CR 2005-038.2. Paratypes: same data as holotype, 9 female/hermaphrodites, 3 males, deposited LACM CR 2005-038.3. Paratypes: same data as holotype, 5 females/ hermaphrodites, deposited D. C. Roger’s collections (DCR accession number 707).

Additional Material Examined: USA: Florida: Monroe County: Upper Matecumbe Key, rainwater pool, 11 female/ hermaphrodites, 17 April 2007, L. Hribar. Lower Matecumbe Key, rainwater pool, 1 female/ hermaphrodite, 17 April 2007, L. Hribar. Windley Key, rainwater pool, 14 female/ hermaphrodites, 1 male, 17 April 2007, L. Hribar. Vaca Key rainwater pool, 2 female/ hermaphrodite, 31 October 2007, L. Hribar. All additional material deposited at Virginia Museum of Natural History.

Description. Female: Head with ocular tubercle prominent, overreaching rostrum (Figure 1A). Head broader than ocular tubercle. Contiguous compound eyes large, subcircular to reniform, 0.75 times the width of the ocular tubercle. Ocular angle smoothly arcuate to rostrum. Naupliar ocellus subtriangular, lying just posterior to, or slightly above and posterior to rostrum. Rostrum pronounced, broadly rounded to truncated, 0.5 to 0.3 times the width of the ocular tubercle (Figure 1 C, D). Ventral surface of rostrum even with ventral surface of head. Dorsal organ prominent, slightly pedunculate, directed anteriorly, hemispherical, with anterior face flat and circular.

First antennae well below and posterior to rostrum, pedunculate, and 0.5 times as long as second antennal peduncle (Figure 1A). Second antennae 2 to 2.5 times as long as head. Second antennal peduncle subequal in length to head, slightly geniculate, and bearing dorsal transverse rows of spiniform setae. Second antennal anterior flagellum (exopod) with six (right) or seven (left) annulations, each dorsally with a transverse row of spiniform setae. Posterior flagellum (endopod) with four (right) or five (left) such annulations, and about 0.17 times longer than anterior flagellum. Both flagellae with a ventral, longitudinal row of long plumose natatory setae, about 0.6 times the length of the peduncle.

Carapace broadly oval, with three or four well separated, shallowly impressed, obscure growth lines, with the subapical growth line most salient (Figure 1F). Adductor muscle scar broad, oblong, about twice as long as wide.

Fourteen to sixteen pairs of thoracopods, with tenth and eleventh pairs bearing dorsally elongated flabellae for carrying the eggs (Figure 1B).

Telson with ten to thirteen pairs of posterior spines borne on the posteriolateral ridges (Figure 1B). Caudal filaments originating on the posterior surface between the ridges at or about the fourth pair of spines. Telson posteriolateral ridges each terminating in an elongated spiniform projection, 2.5 to 3.0 times as long as the nearest spines. Cercopods projecting posteriorly from the ventral surface of the telson, each subtended by an anteriobasal spiniform projection, directed posteriolaterally over the base of the cercus. Cerci are subequal in length to the telson, and are margined medially with a longitudinal row of long plumose setae that extends from the base distally to the point where the cercus abruptly tapers to the apex.

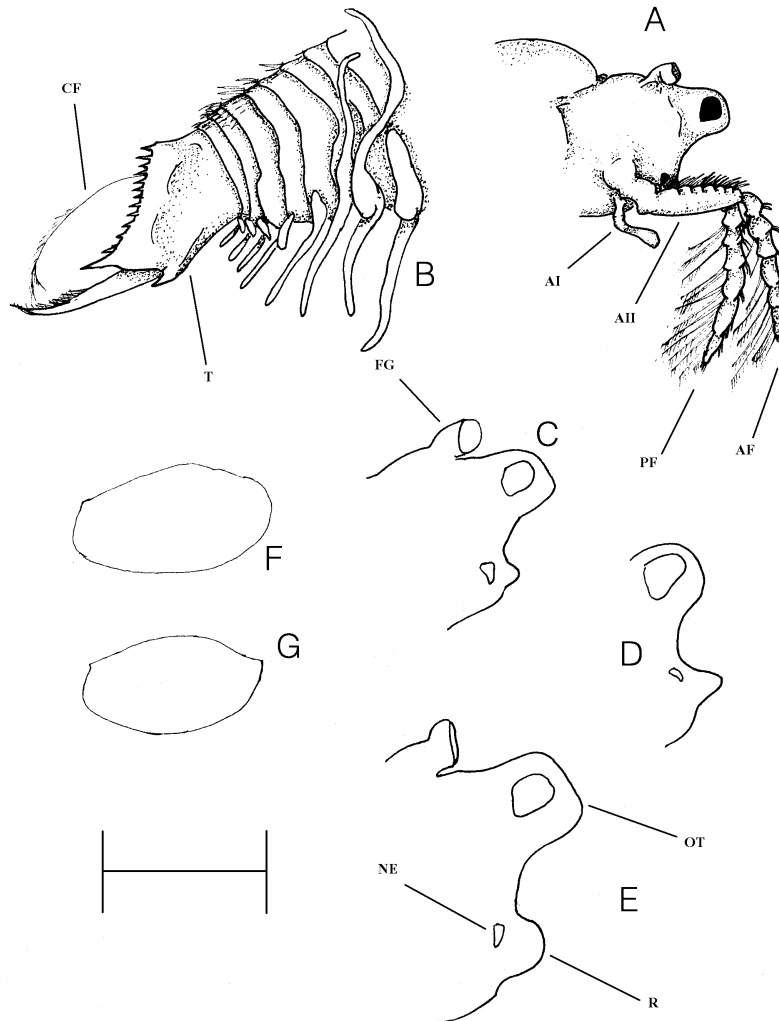


FIGURE 1. *Eulimnadia graniticola* n. sp. A) Holotype: head, right lateral view, scale bar = 2mm. B) Holotype: posterior trunk and telson, right lateral view, scale bar = 2.9mm. C & D) variation in female/hermaphrodite head morphology. E) Allotype: head, right lateral view. F) Holotype: carapace outline, right lateral view, scale bar = 5.8mm. G) Allotype: carapace outline, right lateral view, scale bar = 5.8mm. CF = caudal filament; T = telson; AI = first antenna; AII = second antenna; AF = anterior flagellum; PF = posterior flagellum; FG = frontal organ; OT = ocular tubercle; NE = naupliar eye; R = rostrum.

Male: Head as in female, except rostrum pronounced, truncated, 0.3 to 0.2 times the width of the ocular tubercle (Figure 1 E). Ventral surface of rostrum even with ventral surface of head. First antennae well below and posterior to rostrum, pedunculate, and subequal in length to second antennal peduncle. antennae approximately 2.5 times as long as head, and otherwise as in female. Carapace broadly oval (although maybe slightly acute anteriorly, Figure 1G) and otherwise as in female.

Sixteen pairs of thoracopods, with first and second pairs modified as claspers to amplex the female. First thoracopod (terminology follows McLaughlin, 1980) with endite I and II each bearing a longitudinal row of aciculate setae. Endite III without setae. All three endites slope out to the endite from the thoracopod, with an abrupt declivity distally. Endite IV broad, transverse, grasping surface with numerous flat topped denticles, and a distal fringe of spiniform setae. Endite IV with palp pedunculate, slightly longer than endite, and bearing a few short apical spiniform setae. Endite V broadly arcuate proximally, distal portion parallel to basal portion, grasping surface with numerous ventral flat topped denticles, and a subapical, suctorial organ on posterior side of endite apex. Endite VI elongate, slightly arcuate in proximal segment, and straight in distal segment. Proximal segment attaining the distal most portion of the arc of endite V, and bearing an anterior apical transverse row of spines. Endite VI distal segment apex broader than remainder of endite, and bearing several short aciculate setae apically, and three to five arcuate spines subapically posteriorly. Exopod filiform, not attaining endite IV. Epipod broadly ovate. Second thoracopod similar to first. Last seven to nine thoracic segments each with a dorsal transverse row of spines, directed posteriorly, and originating submarginally.

Thoracic segments and telson as in female.

Egg: Subspherical, ~200 μm in diameter. Surface with numerous, narrow, rectilinear paired polygons, ~ 100 μm in length, ~10 μm wide, with truncated ends. Spaces between polygons produced as rounded ridges. Spines or other projections absent.

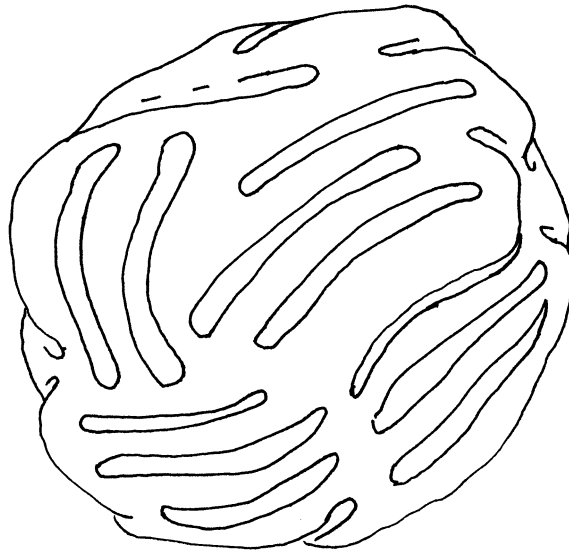


FIGURE 2. *Eulimnadia graniticola* n. sp. Egg. (egg is 210 microns in diameter).

Differential Diagnosis: *Eulimnadia graniticola* n. sp. is a typical member of the genus *Eulimnadia* as defined by Rogers, et al. (in review). Specifically it is a typical limnadiid clam shrimp, with the occipital notch and condyle absent; frontal organ present and pedunculate; first antennae not segmented; carapace with dorsal margin smooth, lacking carinae, with an arcuate hinge line, rarely sinuate, umbone absent; male first two thoracopods with endite five bearing an apical suctorial organ; telson with a posteriorly directed spiniform projection present on the ventroposterior angle, anterior of the cercopod base; caudal filament borne on a projecting mound; eggs spherical to subspherical or cylindrical to cylindrical with one end larger than the other, with large rectilinear polygonal depressions separated by ridges, occasionally with lamellar or setiform spines at polygon ridge line confluences (Belk, 1989; Martin, 1989; Martin and Belk, 1989; Rogers et al., in review; Rabet, in press).

Unfortunately due to the tremendous morphological plasticity in the genus *Eulimnadia*, an adequate differential diagnosis of the adults is not possible at this time. This inherent plasticity in the Spinicaudata has frustrated many workers (Straškraba 1966; Sissom 1971; Belk 1989; Martin and Belk 1989; Martin 1989),

however a certain amount of morphological stability in the eggs has been shown to be useful in defining *Eulimnadia* species (Belk 1989; Martin and Belk 1989), or at least species groups (Brendonck *et al.* 1990). With this in mind, based on egg morphology, we can say that *E. graniticola* is most similar to *E. follisimilis*. Both species bear subspherical, spineless eggs, with linear, often paired, polygons, however the linear polygons in *E. follisimilis* are simple slits, whereas in *E. graniticola* the polygons are rectilinear, about one tenth as wide as long. All other American *Eulimnadia* species with subspherical eggs have subcircular, unpaired polygons (i.e.; *E. brasiliensis*, *E. ovilunata*, *E. ovisimilis*, *E. diversa*), or if paired rectilinear polygonal depressions are present, the eggs are much more angular, with the angles produced as spiniform structures (i.e.; *E. astrova*).

Eulimnadia graniticola is separated from all other *Eulimnadia* species by the basic subspherical form of the egg. All remaining *Eulimnadia* species have a strongly angular, cylindrical or subcylindrical egg form (Belk, 1989; Martin, 1989; Martin and Belk, 1989; Rogers *et al.*, in review; Rabet, in press).

Reproduction: Among the 11 families that successfully hatched, both all “female” and mixed cohorts were noted (Table 1). Because these families were produced by isolated “females,” there was no possibility of male parentage, and thus these isolated “females” were either parthenogenetic females or self-compatible hermaphrodites. To distinguish between these alternatives, we examined the sex ratios among the families with males: these families produced an average of 18% males and 82% “females.” The sex-determining mechanism found in *Eulimnadia texana* predicts that selfing hermaphrodites that are “amphigenic” will produce 75% hermaphrodites and 25% males (Sassaman and Weeks 1993). The male-producing “females” in the current comparisons did not significantly deviate from this expectation ($\chi^2_{(2)} = 2.45$; $0.3 < P < 0.2$), and thus we inferred that *E. graniticola* is androdioecious, with mixtures of males, monogenic (M) hermaphrodites and amphigenic (A) hermaphrodites (Table 1). Among the 11 isolated hermaphrodites, 4 (36%) were found to be monogenic and 7 (64%) were found to be amphigenic (Table 1).

TABLE 1. Offspring sex ratios in cohorts reared from 11 isolated hermaphrodites. “Type” refers to hermaphroditic mating type: A = amphigenic and M = monogenic.

Family	Hermaphrodites	Males	Total	%Hermaphrodite	%Male	Type
A7	1	0	1	100.0%	0.0%	M
A11	2	0	2	100.0%	0.0%	M
A13	7	0	7	100.0%	0.0%	M
A14	4	2	6	66.7%	33.3%	A
A18	15	1	16	93.8%	6.3%	A
A24	1	2	3	33.3%	66.7%	A
A33	23	7	30	76.7%	23.3%	A
A35	8	0	8	100.0%	0.0%	M
A36	12	1	13	92.3%	7.7%	A
A43	13	3	16	81.3%	18.8%	A
A47	13	2	15	86.7%	13.3%	A
Total	99	18	117	84.6%	15.4%	
A-only	81	18	99	81.8%	18.2%	

Discussion

Morphological definition of Spinicaudatan clam shrimp species is difficult. Compared to other branchiopod crustaceans, like the laevicaudatan clam shrimp and the Anostraca, which have separate sexes, the Spinicaudata are morphologically plastic in the fine details, and uniform in the gross characters. Unlike the spinicaudatans, the laevicaudatans and the anostracans typically have clearly defined separate sexes, thus their morphology has been subjected to sexual as well as natural selection. This has resulted in species-specific, ornamental morphology driven by cöadapted mate recognition systems in anostracans and laevicaudatans (Martin and Belk 1988; Rogers 2002). In the anostracan genus *Artemia* where parthenogenesis is common (Baird, 1964; Browne and Spencer 1987; Yaneng 1987), the secondary sexual characters are far more uniform, and like the spinicaudatans, species are difficult to define morphologically. Consequently, since the Spinicaudata have widespread hermaphroditism, sexual selection would necessarily be circumscribed or absent, with the direct result that the animals are adapted for and adapting to their environment, truncating morphological adaptation, but (speculatively) probably diversifying more in adaptations towards water chemistry, temperature, and salinity regimes.

E. graniticola and *E. follisimilis* eggs form a morphological “group” that appears to be distinct from other *Eulimnadia* taxa with a subspherical egg. The fact that egg morphology seems stable at least for species “groups” if not species (Belk 1980; Martin and Belk 1989; Brendonck *et al.* 1990) provides us with at least one morphological tool for describing taxa. It may be that each morphological “group” comprises a single species, especially where there is overlap in egg characters (Brendonck *et al.* 1990).

Molecular Analyses

A 28S *Eulimnadia* DNA sequence matrix was constructed that contains 1023 nucleotide characters. Four of the 118 sequences in this matrix are from *E. graniticola* individuals. In three non-contiguous nucleotide characters, the four *E. graniticola* individuals were fixed for a cytosine residue while all other sequenced *Eulimnadia* specimens possessed a thymine residue at these positions. The presence of three unique 28S apomorphies in the *E. graniticola* specimens examined is consistent with the hypothesis that they represent a distinct species.

Determination of Mating System

Androdioecy in the Spinicaudata was originally described in *Eulimnadia texana* (Sassaman and Weeks 1993), by conducting a series of “progeny tests”: collecting eggs from isolated “females” and rearing the resulting offspring to note egg viability and offspring sex ratios. Sassaman and Weeks (1993) used these methods to conclude that *E. texana* populations were actually mixtures of males and two types of hermaphrodites: those that produced no male offspring (monogenics) and those that produced 25% male offspring (amphigenics). Using these same methods, Weeks and colleagues have documented this same mating system in an additional 12 species of *Eulimnadia* (Weeks *et al.* 2005, 2006, 2008).

Herein we have evidence that *Eulimnadia graniticola* is also androdioecious. Seven out of 11 isolated hermaphrodites produced males among their offspring, and the observed sex ratio (18% male) was not significantly different than that expected (25%) under the sex-determining mechanism outlined for congeneric species (Sassaman and Weeks 1993; Weeks *et al.* 2008). Additionally, the observed proportion of amphigenic hermaphrodites (64%) is similar to that reported for 12 species of *Eulimnadia* (58%, Weeks *et al.*, 2008) and for *E. texana* (63%, Weeks *et al.*, 1999). Thus, the best explanation of the current results is that *E. graniticola* has the same sex determining mechanism as the previously described *Eulimnadia* species, and is therefore an androdioecious mix of males and two types of hermaphrodites (monogenics and amphigenics).

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