

4-2007

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EDGERLY, J. S., SZUMIK, C. A., & MCCREEDY, C. N. (2007). On new characters of the eggs of Embioptera with the description of a new species of Saussurembia (Anisembiidae). *Systematic Entomology*, 32(2), 387-395

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On new characters of the eggs of Embioptera with the description of a new species of *Saussurembia* (Anisembiidae)

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Abstract. Nine egg characters for eleven species of Embioptera are described for the first time. Egg variability indicates its potential use in taxonomy. Here, we analyse the correlation of this variability with the ordinal classification. In addition, a new species of *Saussurembia* (Anisembiidae) from Trinidad is described, including classical traits in the systematics of Embioptera (adult male and female), as well as general features of the egg and maternal behaviour.

Introduction

The order Embioptera, also called Embiodea or Embiidina, is well defined by numerous morphological, developmental and behavioural traits (see Grimaldi & Engel, 2005 for a discussion of the order's name). Most striking is the presence of silk glands in the foretarsi and the ability of all individuals (juvenile and adult, male and female) to spin silk. Females are juvenile in form, retaining a streamlined, wingless body throughout their life. Embiids also exhibit primitively social behaviour in which adult females provide the maternal care of eggs and nymphs and many species form large colonies of individuals that share silk dwellings. Males, mostly winged, generally die soon after mating and do not contribute to the care of their offspring.

The streamlined, nymphoid form of females allows them to traverse narrow silk passages, tight bark crevices or subterranean tunnels. The apparent constraints imposed by their lifestyle have left female embiids without obvious species-specific, genus- or even family-level traits. As a consequence, taxonomists traditionally concentrate on describing male secondary sexual traits and wings in species diagnoses. Here, we provide a description of a colourful new species whose unusual features allow female diversity and evolution to be brought into sharper focus. The paper is divided into two parts. A species description is provided in Part 1, in which female morphology, eggs and behavioural

traits are added to the male and female traits usually featured in species descriptions (e.g. Szumik, 1998). In Part 2, the informative nature of embiid egg variability in embiid classification is explored.

Part 1. A new species from Trinidad, West Indies

Materials and methods

All measurements are given in millimetres. The ocular ratio (OR) is defined in Szumik (1991). Features of the wing base union are given in Szumik (1996). The following abbreviations have been used: 10Lp1, caudal process of the tenth left hemitergite; 10Rp1, caudal process of the tenth right hemitergite; 10T, tenth tergite; Ep, epiproct; H, hypandrium; Hp, process of the hypandrium; LC1, left basal cercus; LC2, left apical cercus; Lpp, left paraproct; Rpp, right paraproct; Mm, mentum; Sm, submentum; Md, mandible. The terminology used to describe the chaetotaxy of the hind basitarsus involves the number of setae followed by a letter denoting the area in which they are present (P, prolateral; R, retrolateral; V, ventral); two numbers and a letter (A, apical; B, basal) in parentheses indicate the segment ratio. For example, 10P(1:2A) indicates ten setae in the apical half of the prolateral area.

Results and discussion

The character combination of the new species indicates that it is closely related to the anisembiids *Stenembia* Ross

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1972 and *Saussurembia* Davis 1939. Unfortunately, the limits, as well as the concepts, of these genera remain unclear. Many of the diagnostic characters used for *Stenembia* also occur in *Saussurembia*, i.e. Md acute and small, LC1 symmetrical (processes and setae absent), Hp elongate, Ep narrow (stick-like), wing venation (Rs + Ma and Rs are the only veins sclerotized and cross veins are absent except between R1 and Rs) and the general shape of 10Lp1 and 10Rp1 (with small differences in size and degree of sclerotization). Those characters for which these genera differ indicate that one is paraphyletic with respect to the other, and that *Saussurembia* is the autapomorphic form of this group (Szumik *et al.*, 2003). Moreover, the new species has a combination of characters of *Saussurembia* and *Stenembia*. The new species and *Saussurembia* share the presence of a sclerotized line starting from the inner margin of 10Lp1, the ventrally curved 10Rp1 and the basally broad 10Lp1 with acute apex. The new species and *Stenembia* have in common the well-defined Lpp and Rpp, the dorsally curved Lpp and the directed leftward Hp. Because *Saussurembia* was described first and a formal synonymization with *Stenembia* is inevitable, the new species is placed in *Saussurembia*.

Saussurembia calypso new species

Etymology. The specific name derives from the Greek *calyps* meaning 'beautiful nymph' (Borror, 1960). The name refers to the colourful appearance and to the discovery of this species in Trinidad, the home of the popular form of music called 'calypso'.

Diagnosis. *Saussurembia calypso* differs from the other species of *Stenembia* and *Saussurembia* by having Rpp dorsally prolonged, 10Lp1 totally covered by Lpp, Hp elongated and with the acute apex appearing as a second process of 10Rp1 and Md without molar teeth.

Male (holotype). Colour: head dark brown, clypeal region with two small elliptical less pigmented areas. Antenna: first antennite dark brown, the rest lighter brown. Prothorax and basal cerci brownish white; apical cerci lighter brown. Meso, metathorax and legs lighter brown. Abdomen lighter reddish-brown with some reddish pigmentation.

Total length: 7.30. Features of the head, chaetotaxy and terminalia are shown in Fig. 1A–E. Head discoidal: width/length: 0.95. OR: 0.44. Mm + Sm sclerotized, Sm rectangular (Fig. 1E). Wing length: fore, 5.90; hind, 5.10. Wing venation (both wings): type c, Rs + Ma and Rs well developed, first 1/5 of Ma conspicuous, the rest inconspicuous, Mp and Cua inconspicuous. Anal diffuse. Cross veins (both wings): 1 R1–Rs. Hind basitarsus (Fig. 1D): length 0.53, ratio 0.24, chaetotaxy: 5–6P(1:3A); 7–8P(2:3B); 7R(1:5B); 1R(1:4A); 20V(1:2B). Terminalia (Fig. 1B, C): 10Rp1 with the apex lightly expanded and truncate, with many longitudinal carinae. 10Lp1 basally broader with acute apex. Hp longer than H, Hp with apex acute and directed to the left side. H with a depressed area next to the anterior margin of Rpp. Lpp and Rpp well developed, sclerotized and globose; both are prolonged to the dorsal region, hence, conspicuous in the dorsal view. Longitudinal ratio of LC2/LC1: 0.91.

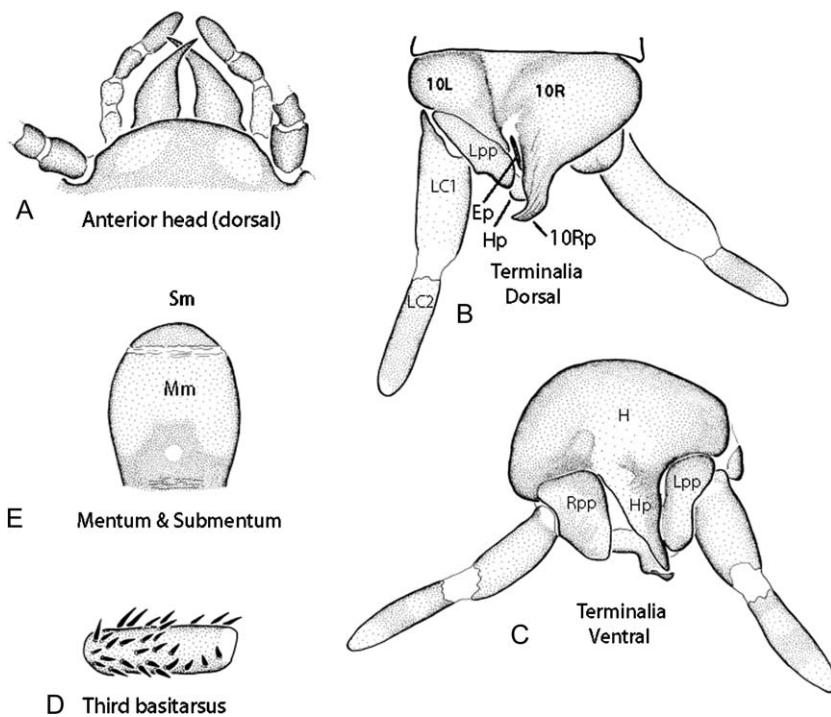


Fig. 1. Traits of male *Saussurembia calypso* sp.n., holotype, type locality: Monas Trinidad. A, Mouthparts; B, C, terminalia; D, hind basitarsus; E, submentum and mentum of labium (see text for abbreviations).

Female (paratype). Colour (Fig. 2): head yellowish-orange. Antenna: antennites 1 and 2 yellowish-white, the rest lighter brown. Prothorax yellowish-white. Mesothorax dark brown. Metathorax and first four tergites light yellowish-brown with two lateral small circular areas (per tergite) whitish and with whitish bands between the sternites; the other abdominal tergites and sternites dark brown with some reddish pigmentation. Basal cerci brownish white (as in males) and apical cerci light brown. Forelegs yellowish-orange; middle and hindlegs light yellowish-brown with the exception of dark brown tibia.

Total length: 9.80. Head: width/length: 0.82; OR: 0.83. Hind basitarsus (Fig. 3C): length: 0.38; width/length: 0.33;



Fig. 2. Female *Saussurembia calypso* sp.n. photographed live at Santa Clara University. She is approximately 9.8 mm.

chaetotaxy: 2R(1:4A); 7A(1:2B); 5P(1:3A); 8P(2:3B) in two rows; 18–22V(2:3B). Terminalia as in Fig. 3B.

Type material. Holotype ♂ *Saussurembia calypso* sp.n. Edgerly 2003, TRINIDAD: Monas Island (61°40'W; 10°42'N), 10.vii.2003 (Edgerly); Deposited in the collection of the Sección de Entomología, Instituto y Fundación Miguel Lillo, Tucumán, Argentina (IFML). Paratypes, TRINIDAD, three males and four females same data as holotype. Matured in culture (iv.2004). All the specimens are in alcohol.

Biology. Specimens were collected from a colony on the bark of an ornamental tree in a manicured lawn area around coastal homes on Monas Island between Trinidad and mainland Venezuela. Nearby palms and fruit trees harboured colonies of the exotic Asian species *Oligotoma saundersii* (Oligotomidae), suggesting that embiids have hitched rides with people to the small island. Therefore, the population of *S. calypso* may also have been introduced there, although natural affiliation with Venezuela is also likely as the genus is South American (Ross, 1972). Their silk is fashioned into tubes that follow the fissures of rough bark. In culture jars at Santa Clara University, they produced layers of tubes affixed to the smooth surface of the jar. Individuals run back and forth through these tubes, and numerous individuals of all ages crowd together in the jumble of tubes. Nymphs and adult females are very active, often wandering outside of their silk. This behaviour is considered to be unusual because embiids generally hide within silk domiciles. Their conspicuous behaviour is intriguing given their banded orange and brown coloration pattern (Fig. 2), suggestive of warning coloration or mimicry known in other insects. Experimentation is needed to confirm the function of their colour pattern.

Eggs and oviposition. Each creamy-white egg (Fig. 3A), approximately 1.05 mm in length, is roughly cylindrical, rounded on one end, and curved slightly along one side (see Fig. 4 for side view of egg). The operculum extends about one-third the length of the egg. The cuticular ridge of the operculum is a distinct white line, smooth with the surface of the egg (unlike the more conspicuously raised ridge seen in *Antipaluria urichi* and others) (see Part 2). The egg of *S. calypso* closely resembles that of congener *S. davisii* (see below) and another anisembiid, *Anisembia texana* (drawings in Melander, 1903).

A 1-day census of laboratory cultures at Santa Clara University revealed that eggs were widely scattered on twenty-three of the fifty pieces of bark used as habitat [bark averaged 53 ± 6.1 cm² (SE) in size]. Of the eighty-eight eggs found, sixty-one (69%) were solitary and fourteen (16%) were in pairs (10% were in groups of three and 4.5% in groups of four). In addition, females ($n = 17$) separated into a group of five and two groups of six, and closely observed for 1 month, showed the same pattern as detected in the cultures. These females laid twenty-two eggs: thirteen eggs were alone, and the others were found in separate groups of

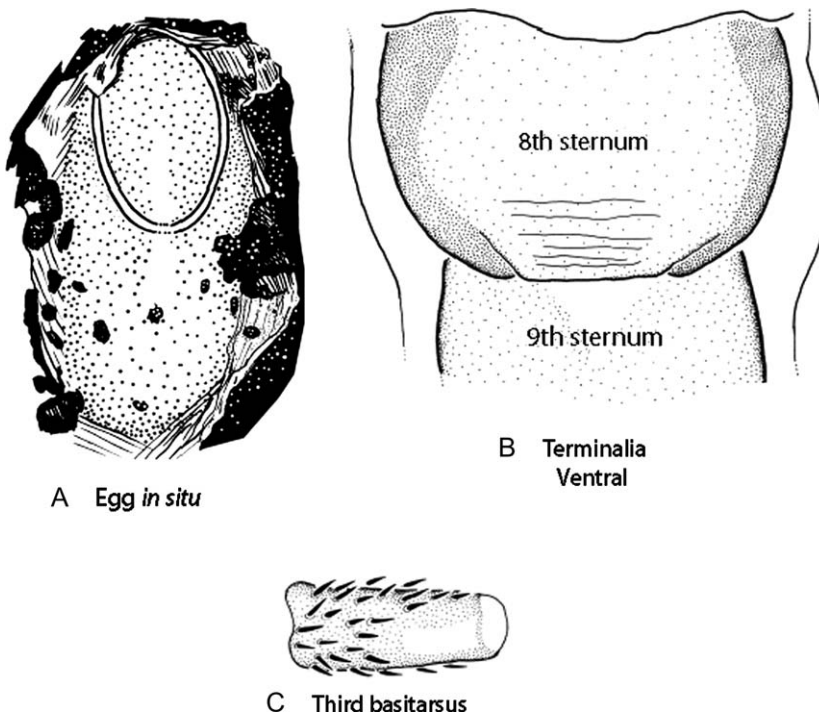


Fig. 3. Traits of female *Saussurembia calypso* sp.n., paratype and an egg. A, Egg (length, 1.05 mm); the egg is shown with a thin silk coating here and there and with patches of macerated material, which are collected by the mother; the egg was traced from a photograph taken through a dissecting microscope with a SonyDFWlink digital camera; B, terminalia (ventral); C, hind basitarsus.

two, three and four. Females were not seen attending the eggs, and when their silk was breached with forceps, none of them returned to repair the silk as other embiids are known to do. These females loosely attached the eggs to bark, stitched them into silk tunnels or buried them within crevices of the bark. Macerated material was sometimes stitched around the egg in the silk (as in Fig. 3A), but when the silk was moved, the macerated material was also easily dislodged. In other species, the treatment of eggs by females is different. For example, females often adhere gathered materials or thick silk to the egg's surface, and assemble them into organized batches, sometimes affixed tightly to the substrate (see references in Edgerly, 1997; Ross, 2000). Interestingly, the treatment of eggs by another anisembiid, *A. texana*, is similar to that of *S. calypso*; Melander (1903) observed captive females fastening single eggs loosely into their silk. Choe (1994) noted that *A. texana* females ($n = 3$) coated their eggs with scraped debris. Each egg was suspended in a silk sheath that separated the egg from the interior of the silk tunnel.

Our observations suggest that *S. calypso* oviposits, nestle the egg into silk or a crevice, but then leave it. Because eggs are scattered, they may not provide an opportunity for egg-guarding by the mother. Embiids are termed subsocial (see references in Edgerly, 1987) because they exhibit maternal care. Indeed, the plesiomorphic *Antipaluria urichi*, the subject of in-depth investigations (for example, Edgerly, 1987, 1988), produces complex egg masses with layers of protective coatings that thwart parasitic wasps. *Antipaluria urichi* lays numerous eggs per batch (mean of fifty-three in the field, up to 117 seen in the laboratory at Santa Clara University), and exhibits a suite of behaviours associated with egg-guarding.

The significance of the maternal trait for the order and the lack of obvious egg-guarding in *S. calypso* warrant further investigation. Choe (1994) investigated this behaviour in *A. texana* and discovered that solitary females with eggs became highly aggressive towards other embiids, suggesting that maternal care exists in this closely related species despite the similar unorganized placement of their eggs.

Part 2. Embiid eggs

Despite Ross's (2000: 13) claim for embiids that 'eggs of all species are remarkably similar', the striking differences between *S. calypso* eggs and those of *Antipaluria urichi*, and the striking similarities to another anisembiid egg (*A. texana*), suggested to us that egg shapes may reflect phylogeny. Ovaries (where the eggs are formed) are adult structures that may express more about phylogeny than is apparent in a female's nymphoid body shape. Therefore, egg morphology may provide clues about a maternal embiid's taxon, which was heretofore almost impossible to determine without access to associated males (often rare or even missing completely from colonies in the field).

Taxon sampling

To conduct our analysis, we collected eggs and adult females from cultures at Santa Clara University and photographed them with a Sony DFWilink digital camera connected to an Olympus dissecting microscope. Measurements were made using ImageJ 1.3 software; the scale was

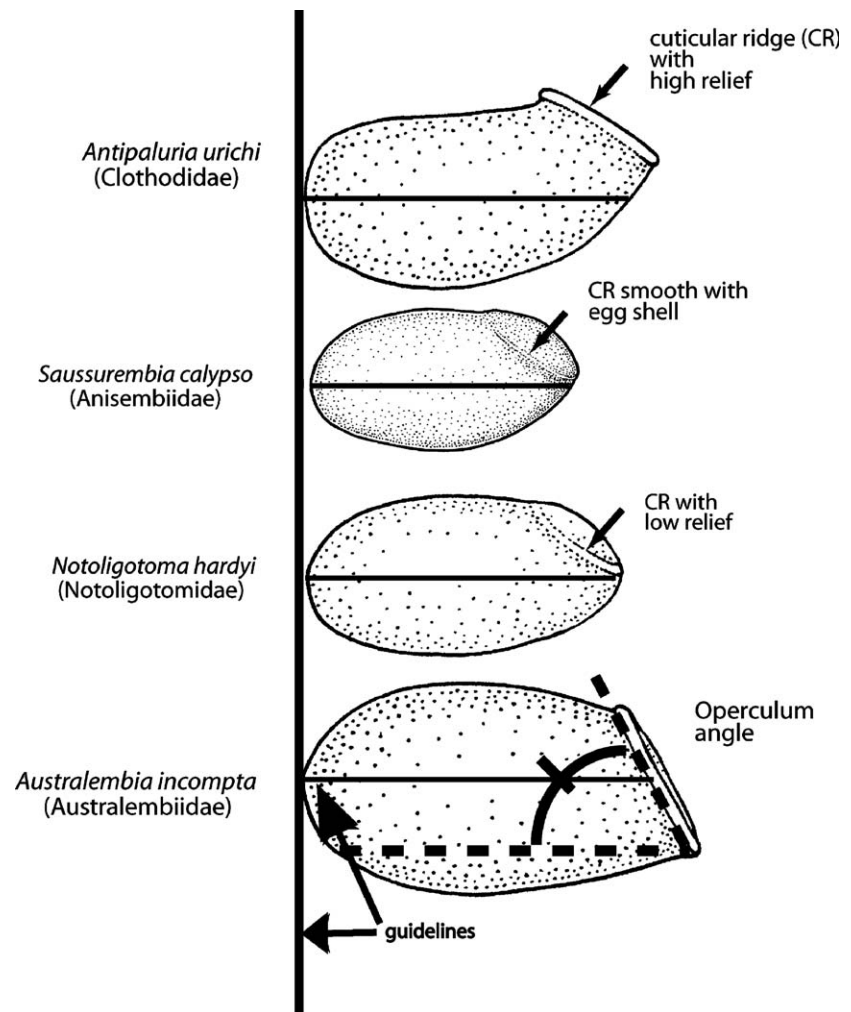


Fig. 4. Eggs (from top to bottom) of *Antipaluria urichi* (Clothodidae), *Saussurembia calypso* sp.n. (Anisembiidae), *Notoligotoma hardyi* (Notoligotomidae) and *Australembia incompta* (Australembiidae). Black lines are guidelines added to highlight the curvature of the upper and lower edges of the egg (characters 1 and 2). The broken line shows the operculum angle (character 8), measured digitally (see text).

calibrated before measurements were taken. Published illustrations of *A. texana* eggs (Melander, 1903) were also measured wherever the character was obvious. This comparative study of eggs was carried out on twelve species of embiids. Our sample is limited because of the difficulty of finding embiids in the field, let alone finding their eggs. Although the taxon sampling may seem small, seven of the nine families that compose the order are represented in this study (Clothodidae, Australembiidae, Notoligotomidae, Archembiidae, Anisembiidae, Teratembidae and Oligotomidae).

Characters

The variation observed in egg shape indicates that these characters are potentially useful in taxonomy. Here, we describe the general features of the egg, as well as details of the operculum, in the following nine characters (see also Figs 4 and 5).

Character 1. Curvature of upper edge (same side as operculum) viewed from the side (Fig. 4). After the initial curve from the bottom of the egg toward the operculum, the

upper curve is: 0, fairly straight line; 1, angled upward gradually then meets operculum with short neck; 2, bowed, curves up and then down again.

Character 2. Curvature of edge viewed from the side (side opposite to operculum) (Fig. 4): 0, fairly straight; 1, slightly bowed; 2, strongly bowed.

Character 3. Height of the cuticular ridge of the operculum (Fig. 4): 0, high relief (the ridge is distinct and raised up); 1, low relief; 2, almost smooth with egg shell.

Character 4. Size of egg relative to female head width; the ratio between the area of the side of the egg and the head width of the female, measured along a line through the widest point of, and including, the eyes.

Character 5. Egg shape: described as the ratio between the width one-quarter of the way down the egg and the width one-quarter of the way up from the bottom (Fig. 5); this measurement depicts a range of forms from oval to cup shaped.

Character 6. Operculum shape (Fig. 5): the ratio between the width at the halfway point and the length. With this measurement, shapes ranging from oval to circular are described.

Character 7. Relative size of the operculum: the ratio between the length of the operculum and the long axis of the egg.

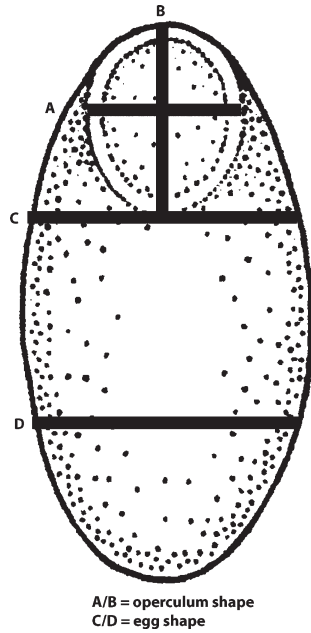


Fig. 5. The egg shape (character 4) was determined by the ratio of lines C to D, and the operculum shape (character 5) was determined by the ratio of lines A to B. Traits were optimized onto the cladogram of adult morphology.

Character 8. Operculum angle (Fig. 4): measured as the angle between a line perpendicular to the base of the egg and the operculum ridge. The opening position of the operculum could be from across to along the long axis of the egg.

Character 9. Surface of the operculum viewed from the side (Fig. 4): 0, convex, it is visible; 1, concave, inconspicuous. Characters 1, 2, 3 and 9 are discrete and codified as additive; the others are continuous characters (see data matrix in Table 1). Measurements include the mean and its standard deviation, except for character 4.

Cladistic analysis

Two very simple means exist to test the extent to which egg features are explained by common ancestry. Most logically, egg characters are optimized onto a phylogeny obtained from another source (i.e. reduced consensus tree of adult morphological data; Szumik *et al.*, 2003). New characters that map well onto the cladogram would be significant. Alternatively, the cladogram obtained from the egg data matrix can be compared with that obtained from adult morphological data. Again, the similarity between the two hypotheses, with evidence analysed separately, indicates concordance. Optimization of the character traits onto the consensus tree of Szumik *et al.* (2003), as well as tree searches for the egg data matrix, were carried out with the program TNT (Goloboff *et al.*, 2004; see reviews of the program in Hovenkamp, 2004 and Meier & Ali, 2005). To check the

Table 1. Data matrix of embiid egg characters.

	Discrete			Continuous ^a					
	1	2	3	9	4	5	6	7	8
<i>Antipaluria urichi</i>	1	2	0	0	0.263	0.783 ± 0.043	0.884 ± 0.102	0.231 ± 0.051	0.853 ± 0.158
<i>Haploembia solieri</i>	1	2	1	1	0.383	0.896 ± 0.072	0.967 ± 0.051	0.267 ± 0.033	0.579 ± 0.111
<i>Oligotoma nigra</i>	0	1	1	1	0.262	0.945 ± 0.094	0.867 ± 0.084	0.280 ± 0.029	0.578 ± 0.048
<i>Oligotoma saundersii</i>	0	1	1	1	0.224	0.911 ± 0.090	1.094 ± 0.064	0.216 ± 0.038	0.699 ± 0.103
<i>Oligotoma hubbardi</i>	0	2	1	1	0.337	1.104	0.416 ± 0.005	0.326 ± 0.048	0.461 ± 0.051
<i>Dinadius nigra</i>	1	2	1	1	0.285	0.880 ± 0.098	0.682 ± 0.050	0.399 ± 0.015	0.424 ± 0.007
<i>Australembia incompta</i>	2	0	0	0	0.421	0.857 ± 0.035	0.976 ± 0.139	0.135 ± 0.046	1.165 ± 0.097
<i>Pararhagadochir trinitatis</i>	0	2	0	1	0.281	0.856 ± 0.072	0.597 ± 0.069	0.382 ± 0.054	0.502 ± 0.085
<i>Notoligotoma hardyi</i>	2	1	1	1	0.383	0.953 ± 0.032	0.859 ± 0.058	0.287 ± 0.015	0.593 ± 0.101
<i>Saussurembia calypso</i>	2	2	2	1	0.332	0.913 ± 0.060	0.825 ± 0.101	0.306 ± 0.060	0.653 ± 0.053
<i>Saussurembia davisi</i>	2	2	1	1	0.453	0.927	0.831	0.304	0.674
<i>Anisembia texana</i>	2	2	1	1	0.332–0.377	?	?	0.38	0.707 ± 0.077

^aMeans shown with standard deviation if available.

(Fig. 7C), eight of the twelve taxa appear, which shows a fairly good concordance.

The traditional classification of the order and the alpha taxonomy, according to Ross (1972), were constructed solely for the male terminalia. Although there have been serious attempts to include other traits of the female terminalia, male and female chaetotaxy, wing traits, and male and female cephalic structures in the higher classi-

fication and alpha taxonomy, because they are potentially useful (Szumik, 1996; Szumik *et al.*, 2003), more comparative studies on new characters of behaviour or nymph instars would be desirable. The promise of this first attempt to analyse the systematic utility of the egg within a phylogenetic framework suggests that a concerted effort to collect and describe embiid eggs would be valuable.

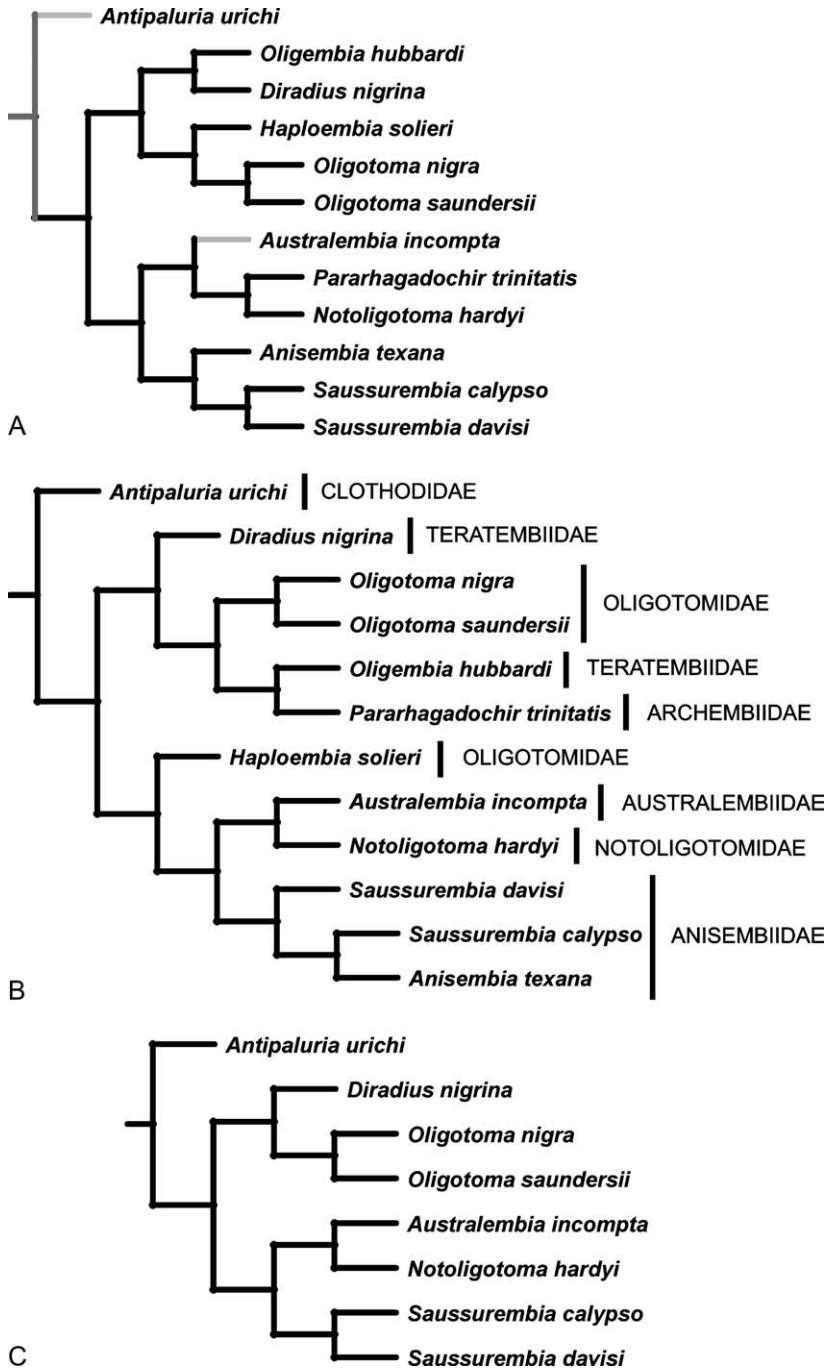


Fig. 7. A, Surface of the operculum viewed from the side (character 9) optimized onto the cladogram of adult morphology. Light grey, convex; black, concave; darker grey, ambiguous. B, Cladogram obtained from egg data matrix. C, Agreement subtree of egg traits and adult morphology.

Acknowledgements

This study was supported by the Agencia de Promoción Científica y Tecnológica PICT2002-01-12605 (CAS) and by a grant from the Howard Hughes Medical Institute to Santa Clara University (Community of Science Scholars Initiative). The authors thank James M. Carpenter, Luisa Montivero and Pablo Goloboff who provided useful comments and criticisms.

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Accepted 22 December 2006

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