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ANATOMICAL SYSTEMATICS OF *ETHERIA ELLIPTICA* (PELECYPODA: MYCETOPODIDAE)

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ABSTRACT

Gross dissection and histological examination of preserved *Etheria elliptica* from Africa revealed this species to be most closely related to the Neotropical Mutelacea: Mycetopodidae, and not to the Unionacea or to the Ethiopean Mutelacea: Mutelidae with which it was hitherto customarily classified. Etheriidae Swainson 1840, for which *E. elliptica* is the type, is placed in synonymy of Mycetopodidae Gray 1840. This is the first interpretation of a species of one mutelacean family occurring in a disjunct biogeographic region to which members of the other family are restricted.

INTRODUCTION

The nominal family Etheriidae Swainson 1840 is generally considered to comprise 4 monotypic nominal genera: (1) *Etheria* Lamarck 1807 [type species by subsequent designation by Gray (1847): *E. semilunata* Lamarck 1807: 404 (= *E. elliptica* Lamarck 1807: 401)], in the Senegal, Niger, Congo and Nile drainages in continental Africa and also from the Malagasy Republic (Madagascar), (2) *Acostaea* d'Orbigny 1851 [type by monotypy: *A. guaduasana* d'Orbigny 1851 (= *Mulleria rivoli* Deshayes 1827)], in the Rio Magdalena in Colombia, (3) *Bartlettia* H. Adams 1866 [type by monotypy: *Etheria stefanensis* Moricand 1856], in the Amazon drainage in Brazil, Peru and Ecuador, and the Paraguay basin in Paraguay, and (4) *Pseudomulleria* Anthony 1907 [type by monotypy: *Mulleria dalyi* E.A. Smith 1898], in the Budra drainage in the State of Mysore in southwestern India.

Whereas some authors (e.g., Pilsbry & Bequaert, 1927; Thiele, 1935; Haas, 1936, 1969a, 1969b; Pain & Woodward, 1961; Yonge, 1962; Parodiz & Bonetto, 1963) have recognized these freshwater bivalves as a distinct, natural family with affinities to the Unionacea: Unionidae s.l., others have considered this assemblage to represent groups in the Mutelacea: Mutelidae s.l. Modell (1942) placed *Bartlettia* and *Acostaea*, and *Etheria* and *Pseudomulleria* in his new mutelid subfamilies Bartlettiinae and Etheriinae, respectively, and Mandahl-Barth (1954, 1968) considered *Etheria* to be a monotypic but highly variable, transformed mutelid genus. In a recent classification, Morrison (1973) created the new familial taxa Acostaeidae and Pseudomulleriidae; *Etheria* was retained in the Etheriidae. He considered *Acostaea*, *Bartlettia* and *Etheria* to be mutelaceans and included *Pseudomulleria* with the Unionacea. Morrison's views are in contrast to those of Haas (1969a, 1969b), who recorded *Pseudomulleria* as a subgenus of *Acostaea* and recognized Unionacea as the sole superfamily of freshwater mussels.

Etheriids were originally grouped together on the basis of their peculiar shell forms, which in adults are unlike those of other naiades. Yonge (1962) subsequently recorded that they share another feature unique among naiades: owing to a localized transverse "pinching," the posterior outer ligament layer is compressed and extended to a corresponding extent laterally into the valves. Petit de la Saussaye (1853), Anthony (1905, 1907), Pain & Woodward (1961), Yonge (1962) and Haas (1969a) provided detailed shell descriptions and/or taxonomic characterizations of these

naiades. Differences between the 4 species, both in shell and animal features, are listed in Table 1.

TABLE 1. Characterization of adult and larval etheriid and other naiades.[1]

Feature	"Etheriidae"				Mutelacea	Unionacea
	Acostaea[2]	*Bartlettia*[2]	*Etheria*	*Pseudomulleria*		
Inequivalved	+	-	+	+	-	-
Adults sessile	+	-	+	+	-	-
Adductor muscles						
Monomyarian	+	-	-	+	-	-
Dimyarian	-	+	+	-	+	+
Posterior mantle						
"Openings"	?	?	+	+	+	+
True siphons	?	?	-	-	+	-
Foot present	?	?	-	-	+	+
Demibranchs						
Plicate	?	?	+	-	-	-
Non-plicate	?	?	-	+	+	+
Marsupium						
Endobranchous	?	?	+	?	+	-
Exobranchous	?	?	-	-	-	+
Tetragenous	?	?	-	-	-	+
Larval type						
Glochidium	?	?	?	?	-	+
Lasidium or lasidium-like	?	?	?	?	+	-

[1] + indicates presence of a feature, - indicates its lack.
[2] Animal unknown.

According to Heard & Guckert (1970) and Heard (1974), different anatomical organizations offer significant characters for interpretation of phylogenetic affinities of naiades at the subfamilial and familial levels. The anatomy of *Etheria elliptica* was previously described by Rang & Cailliaud (1834), Anthony (1905, 1907), Sassi (1910) and Yonge (1962), and that of *Pseudomulleria dalyi* by M.F. Woodward (1898), but the animals of *Acostaea rivoli* and *Bartlettia stefanensis* are as yet unknown.

Several significant features were overlooked in previous anatomical accounts of *Etheria elliptica*. The purposes of this report are the description of those features, confirmation of other attributes already noted, and a revised higher classification of this species.

MATERIAL EXAMINED

In this section is detailed the date, locality and other information on the *Etheria elliptica*

studied here. Shells of these animals have been deposited in the Museum of Zoology, University of Michigan (UMMZ). A list of other taxa whose animal anatomies have personally been studied for comparison is included.

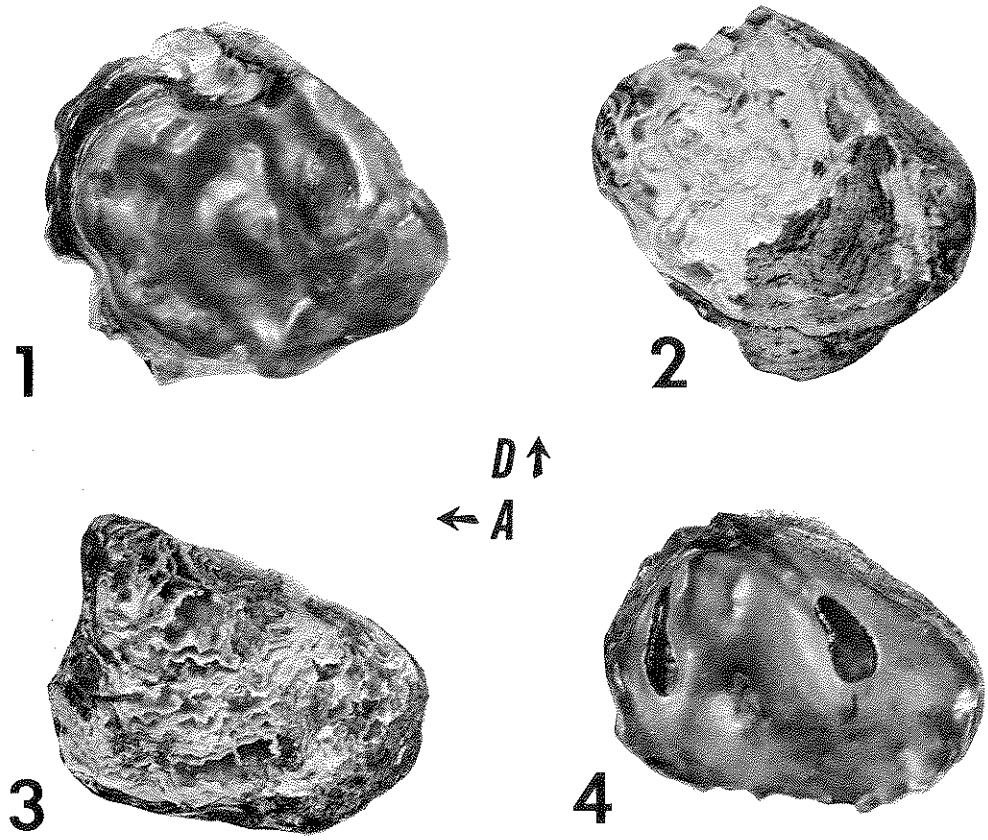
Etheria elliptica

(1) One male from Lake Victoria at Entebbe, Uganda; 26 January 1951. UMMZ 234708. Right valve (Fig. 1) concave, larger: 38.6 mm long x 36.2 mm high; left valve (Fig. 2) convex, smaller (35.3 x 35.3 mm), formerly attached to a solid substrate across its anterior half. (2) One gravid female from the Laupula River above Johnston Falls, Katanga Province, Zaire; 22 December 1959. UMMZ 234709. Left valve (Fig. 3) convex, 76.2 x 60.7 mm, with a prominent "beak" directed dorsoanteriad; right valve (Fig. 4) flattened, 77.7 x 58.3 mm, formerly narrowly attached to a solid substrate at the anterior end, lacking a "beak."

Other Naiades Examined

Mutelacea: Mutelidae Gray 1847 (restricted to the Ethiopian Region by Parodiz & Bonetto, 1963). *Aspatharia* (*Spathopsis*) *petersi* (von Martens), *A.* (*S.*) *wahlbergi* (Krauss), *Mutela alata* (Lea), *M. bourguignati* Bourguignat and *M. nyassaensis* (Lea).

Mutelacea: Mycetopodidae Gray 1840 (Neotropical Region, *fide* Parodiz & Bonetto, 1963). *Anodontites trapesialis* form *exotica* (Lamarck).



FIGS. 1–4. Shells of *Etheria elliptica*. FIG. 1. Inner surface of right valve of Lake Victoria male. FIG. 2. Outer surface of left valve of Lake Victoria male. FIG. 3. Outer surface of left valve of Laupula River female. FIG. 4. Inner surface of right valve of Laupula River female. A, anterior; D, dorsal. See text page 17 for sizes.

Unionacea: Amblemidae Rafinesque (Palearctic, Ethiopian, Oriental and Nearctic regions, *fide* Heard, 1974). *Caelatura framesi* (Connolly) and *C. hypsipryma* (von Martens) from Africa, *Pilsbryoconcha exilis* (Lea) and *Pseudodon cambodjensis* (Petit de la Saussaye) from southeastern Asia, and *Megalonaias boykiniana* (Lea) and *Plectomerus dombeyanus* (Valenciennes) from North America.

Unionacea: Hyriidae Swainson (Australian and Neotropical regions, *fide* Parodiz & Bonetto, 1963). *Hyridella australis* (Lamarck) from Australia.

Unionacea: Margaritiferidae Haas (Palearctic and Nearctic regions, *fide* Heard & Guckert, 1970; Heard, 1974). *Margaritifera falcata* (Gould) from North America.

Unionacea: Unionidae Rafinesque (Palearctic, Ethiopian, Oriental and Nearctic regions, *fide* Heard, 1974). *Anodonta* spp. (cf. Heard, 1975), *Elliptio crassidens* (Lamarck), *Lampsilis claibornensis* (Lea) and *Villosa vibex* (Conrad) from North America, *Cafferia caffra* (Krauss) from Africa, and *Physunio eximius* (Lea) and *Uniandra contradens tumidulus* (Lea) from southeastern Asia.

METHODS

Gross dissection provided for the description of general anatomical features. Histological examination (material prepared as by Heard, 1975) was employed to ascertain the sex of the individuals and to determine the structural details of the demibranchs.

ANATOMICAL FINDINGS

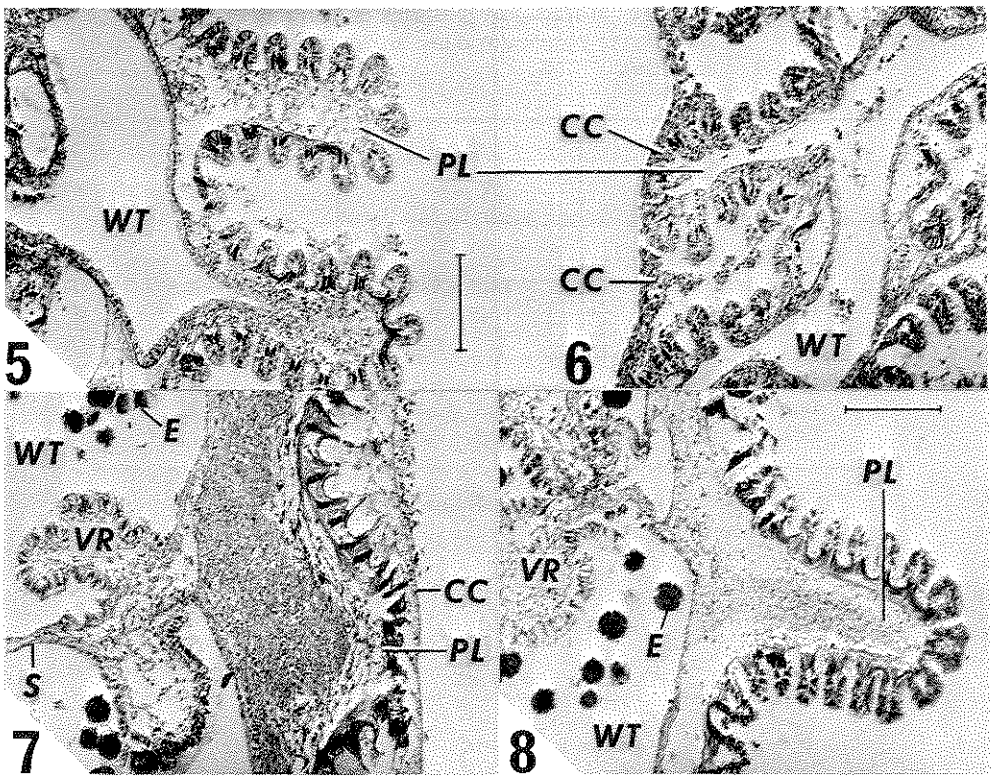
General features

Animals conspicuously dimyarian (cf. Yonge, 1962: fig. 3 on p 428). Mantle sheets united posteriorly only directly behind the ctenidia. True siphons absent, with only an excurrent (anal) and an incurrent (branchial) opening present above and below the mantle fusion, respectively; excurrent opening unclosed above (i.e., pallial suture separating the excurrent opening from a distinct supra-excurrent opening is lacking), and pedal slit continuous with the incurrent opening. Foot entirely lacking. Labial palpi relatively short and of low height for the size of the animal, with their base nearly contiguous with the anterior end of the inner demibranchs. Two ctenidia present, each comprising an outer and an inner demibranch. Outer demibranchs of equal size in each animal, and up to 2 mm shorter than the inner demibranchs which are also of equal size. Diaphragm formed by the dorsal margins of the ctenidia and the mantle fusion between the excurrent and incurrent openings, complete and entirely separating the branchial and suprabranchial chambers.

Both specimens with a narrow band of densely concentrated melanin pigment along the inner edge of the mantle. Male with a single row of short, conical papillae at the apical margin of the inner edge of the mantle from the level of the anterior adductor muscle through the upper 2/3 of the excurrent opening; female similar, but lacking papillae along the excurrent opening. Other, more striking and significant sexually dimorphic features occur in the demibranchs.

Demibranchs

Outer demibranchs in both specimens with the outer (ascending) lamella dorsally attached to the inner surface of the mantle for its entire length, and with the inner (descending) lamella dorsally joined to the dorsal margin of the outer (descending) lamella of the inner demibranchs. Dorsal margin of the inner (ascending) lamella of the inner demibranchs united to the visceral mass along the length of the latter and, posterior to the visceral mass, to the dorsal margin of the inner lamella of the apposing inner demibranch. Outer and inner lamella of each demibranch of



FIGS. 5–8. Photomicrographs of frontal sections of lamellae of *Etheria elliptica*. FIG. 5. Exposed plicae of outer lamella of male inner demibranch. FIG. 6. Protected plica of inner lamella of male outer demibranch. FIG. 7. Protected plica of dorsal region of outer lamella of female inner demibranch. FIG. 8. Exposed plica of ventral region of outer lamella of female inner demibranch. CC, cellular covering; E, embryo; PL, plica; S, septum; VR, vertical ridge; WT, water-tube. Scale for all figures: 200 μ.

equal height, with those of the inner demibranchs higher than those of the outer demibranchs.

All 4 demibranchs in each specimen vertically plicated. Plicae of male inner demibranchs (Fig. 5) and of female outer demibranchs exposed; inner lamella plicae of male outer demibranchs protected by a cellular covering (Fig. 6), as dorsally (Fig. 7) but not ventrally (Fig. 8) are the outer lamella plicae of female inner demibranchs. All 4 demibranchs in each sex with 2 plicae on either side of every water-tube, and interlamellar junctions (i.e., septa) at alternate interplicate positions (Fig. 9). Male inner demibranch lamellae with a few more filaments per plica than in the outer demibranchs (Table 2). Female with about the same number of filaments per plica in both lamellae of the outer demibranchs, in the inner lamella of the inner demibranchs and in the ventral, exposed region of the outer lamella of the inner demibranchs; latter with significantly fewer filaments per plica in the dorsal, protected region.

Each demibranch in both sexes with ordinary (Fig. 9: OF) and principal filaments (PF). All filaments possessing fine frontal (Figs. 10, 11: FFC), coarse frontal (CFC) and latero-frontal cilia (LFC).

TABLE 2. Numbers of filaments per plica of different lamellae of *Etheria elliptica* (values based on 10 plicae per lamella).

Lamella	Male $\bar{x} \pm \sigma$	Female $\bar{x} \pm \sigma$
Inner demibranch		
Inner lamella	14.3 ± 0.9	15.4 ± 1.6
Outer lamella	13.5 ± 2.0	9.5 ± 1.6*
		15.0 ± 0.8†
Outer demibranch		
Inner lamella	11.7 ± 1.8	15.0 ± 1.3
Outer lamella	12.1 ± 0.7	14.7 ± 1.1

*Dorsal region, protected by a cellular membrane.
†Ventral, exposed region.

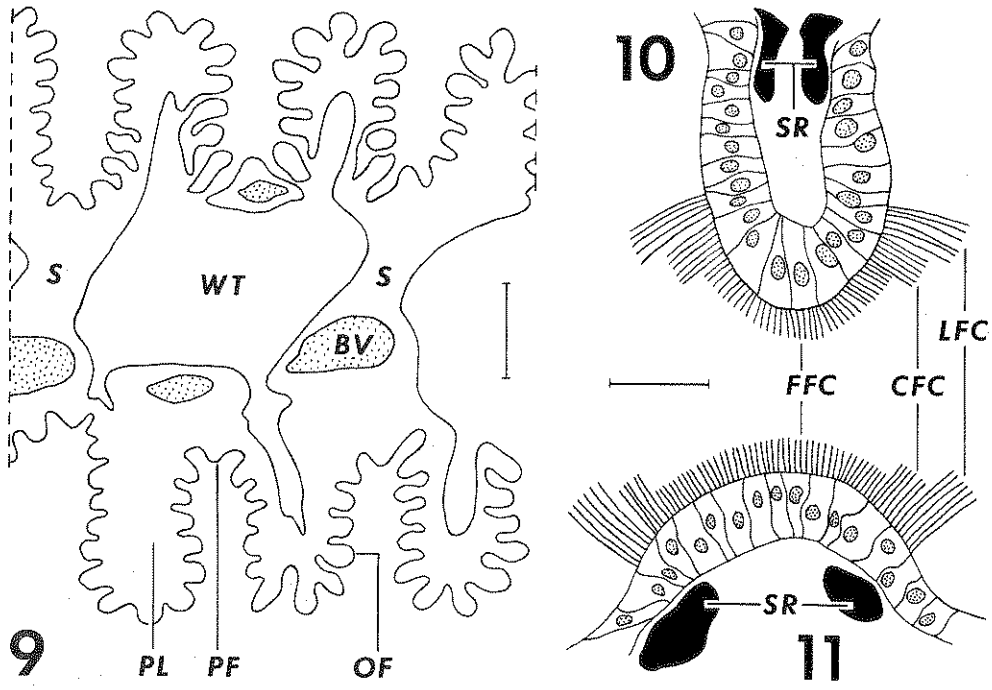


FIG. 9. Frontal aspect of part of a non-marsupial demibranch. BV, blood vessel; OF, ordinary filament; PF, principal filament; PL, plica; S, septum; WT, water-tube. Scale: 250 μ.

FIGS. 10, 11. Transverse views of an ordinary (Fig. 10) and a principal filament (Fig. 11). CFC, coarse frontal cilia; FFC, fine frontal cilia; LFC, latero-frontal cilia; SR, supporting rod. Scale: 25 μ.

Interlamellar junctions developed as continuous, uninterrupted primary septa (Fig. 9: S), with those in the male outer demibranchs only 4/5 as high as the lamellae; septa in the male inner demibranchs and in all female demibranchs of the same height as the lamellae. Primary septa in female inner demibranchs with faint traces of 3 possibly fused perforations. Inner demibranchs of female also possessing, adjacent to the outer lamella, a vertical ridge of tissue projecting into consecutive water-tubes from each surface of the primary septa (Figs. 7, 8: VR).

Endobranchous, i.e., only the inner demibranchs marsupial, and in these the developing young in the gravid female occurred just in the central 3/5 of the length of the demibranchs. Only embryos present. Diameter of fertilization membrane: 77 μ; diameter of embryos: 65 μ.

DISCUSSION

The present findings agree with those of prior accounts on *Etheria elliptica*, except that (1) Rang & Cailliaud (1834) failed to record a posterior mantle union behind the ctenidia, described the ctenidial plicae as tubes and noted the presence of a large foot, (2) Anthony (1905, 1907) illustrated perforated septa in all 4 demibranchs of a non-gravid animal of unstated sex but did not mention these perforations in the text description, and (3) Yonge (1962: 432) stated that the ctenidial "axes are free for the posterior quarter of their length." In addition, Sassi's (1910: 30) contention that "Ausserdem sind grosse Teile der beiden Mantellappen mit Gonaden erfüllt," and his suggestion of the presence of a reduced anterior byssal gland, were not confirmed in this study. Finally, all prior workers overlooked the cellular cover protecting the plicae of certain lamellae, and none noted the presence of what may be incipient secondary septa emanating from each primary marsupial septum. In fact, Anthony's (1905, 1907) illustration of a frontal section of a gravid marsupial demibranch does not include those vertical ridges of tissue.

Etheria elliptica is endobranchous, a feature common to the Unionacea: Hyriidae and to the Mutelacea: Mutelidae and Mycetopodidae. Its mature larvae are unknown, and direct evidence of its superfamilial membership is lacking. However, indirect evidence is provided by comparisons of anatomical attributes, i.e., evidence of familial membership.

All 4 demibranchs in each sex of *Etheria elliptica* contain comparatively distantly spaced and at least sometimes (seasonally?) imperforate interlamellar septa. That condition is known elsewhere among naiades only in mutelaceans, although Germain (1909) illustrated perforated septa in the mutelid *Chelidonopsis arietina* (Rochebrune) [= *Mutela* (*Chelidonopsis*) *hirundo* (von Martens), *fide* Haas (1969a: 584)].

Distantly spaced but perforated septa occur in primitive, tetragenous Unionacea: Amblemidae, and both sexes of hyriids also contain perforated septa in all 4 demibranchs (Ortmann, 1912a, 1920, 1921; pers. observ.). However, hyriids, like unionids, display a dimorphic septal spacing: dense in the region of the marsupium and distant elsewhere (cf. Heard, 1974). Hyriids also differ from *Etheria elliptica* in possessing a continuous pallial suture without a supra-excurrent opening above the excurrent opening (South America) or siphon (Australia) (see Ortmann, 1912a, 1920, 1921; McMichael & Hiscock, 1958; Parodiz & Bonetto, 1963; pers. observ.).

Mutelids are distinguished from *Etheria elliptica* by the presence of true excurrent and usually also incurrent siphons, absence of branchial papillae except in the pseudotaxodont *Iridina spekii* (Woodward), attachment of the inner lamella of the inner demibranchs to the visceral mass only anteriorly, presence of a continuous pallial suture above the excurrent siphon, and the absence of vertical ridges on

marsupial septa (cf. Pelseneer, 1886; Germain, 1909; Ortmann, 1910a, 1918; Bloomer, 1932; Leloup, 1950; Pain & Woodward, 1968; also verified here).

Etheria elliptica shares with mycetopodids those anatomical features by which it is distinguished from mutelids: absence of true siphons and a pallial suture above the excurrent opening, presence of pallial papillae (but not true branchial papillae of other mycetopodids and all unionaceans) and also the vertical septal ridges in the marsupial demibranchs, and greater extent of attachment of the inner demibranchs to the visceral mass (cf. Ortmann, 1911, 1921; Parodiz & Bonetto, 1963; also personally verified).

Of special interest are the vertical septal ridges near the outer lamella of the marsupial demibranchs of *Etheria elliptica*. As noted, true mutelids lack them, whereas Ortmann (1921: 458, 566) recorded their widespread occurrence, also near the outer lamella of the inner demibranchs, in "female" mycetopodids. These ridges were also found in the present study in both inner and outer demibranchs of 6 animals of the mycetopodid *Anodontites trapesialis* f. *exotica* [= *A. exoticus* (Lamarck), *fide* Haas (1969a: 570)], each of which was a non-gravid hermaphrodite. Such ridges are unknown in the Unionacea (see Ortmann, 1910b, 1912b), although female and female-hermaphrodite Unionidae: Anodontinae possess a secondary septum adjacent to each lamella of the outer, marsupial demibranchs (Heard, 1975), and at least some Hyriidae possess several ridge-like projections on each side of marsupial septa (cf. McMichael & Hiscock, 1958: fig. 6 on p 379; Ortmann, 1921: fig. 2a in pl. 48).

Parodiz & Bonetto (1963) characterized the mutelacean Mycetopodidae and Mutelidae as distinct familial groups in part on the basis of larval type. The Neotropical mycetopodids produce lasidia (cf. von Ihering, 1891; Bonetto, 1951; Parodiz & Bonetto, 1963), and the Ethiopian mutelids generate lasidia-like larvae (viz., haustoria, *fide* Fryer, 1959, 1961). Although the mature larval type of the Ethiopian *Etheria elliptica* remains unknown, the adult anatomy of this species recommends its classification with the Neotropical Mutelacea: Mycetopodidae.

This action treats Etheriidae Swainson 1840 and Mycetopodidae Gray 1840 as synonyms. Acting as "first reviser" (Art. 24a, ICZN), we select Mycetopodidae Gray as the senior synonym.

Parodiz & Bonetto (1963) considered the Mutelidae and Mycetopodidae to be mutually exclusive geographically. The present findings indicate an exception, but such an intrafamilial disjunction may not be unique inasmuch as Bonetto (1963) and Parodiz & Bonetto (1963: 206-207) noted that the Neotropical "mycetopodid" *Leila blainvilleanus* (Lea) has siphons, several dorsal muscle scars in the shell and a *Mutela*-like (i.e., haustorium-like) larva; all are features of Ethiopian mutelids.

Whether the remaining 3 "etheriids" constitute a monophyletic group (disputed by Morrison, 1973; 1975, pers. comm.) is presently unknown because the animal of only *Pseudomulleria dalyi* has been described. Judged from Woodward's (1898) anatomical account, it appears to be a monomyarian mutelid and not a unionacean as suggested by Morrison (1973) on conchological grounds. In addition, the animal of *Bartlettia stefanensis* is as yet unknown, although Parodiz & Bonetto (1963) and Morrison (1973) considered the species to be a member of the mycetopodid genus *Anodontites* Bruguière.

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