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Source: American Malacological Bulletin, 33(2):204-211.

Published By: American Malacological Society

DOI: <http://dx.doi.org/10.4003/006.033.0214>

URL: <http://www.bioone.org/doi/full/10.4003/006.033.0214>

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The Anatinellidae and Kymatoxinae: A reassessment of their affinities within the superfamily Mactroidea (Mollusca, Bivalvia)

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Abstract: Morphological phylogenetic analysis of the mactrid subfamilies Mactrinae and Kymatoxinae, plus the mactroidean family, Anatinellidae, indicate that the Kymatoxinae shares closer common ancestry with the Anatinellidae than with the Mactridae. Kymatoxinae is, therefore, reassigned from Mactridae to subfamily rank within Anatinellidae. The lack of a pallial sinus in *Anatinella* G. B. Sowerby I, 1833 suggests that its family was derived from anatomically plesiomorphic members of Mactroidea with at best only weakly developed siphons.

Key words: *Anatinella*, *Raeta*, taxonomy, *Anatina*, phylogeny

The mactroidean family Anatinellidae Deshayes in Gray, 1853 was introduced to distinguish the genus *Anatinella*, previously introduced by Sowerby I (1833a), from *Lutraria* Lamarck, 1799. It was considered a subfamily of Mactridae by Dall (1895). However, it was placed in the superfamily Mactroidea as a valid family by several authors (Keen in Cox *et al.* 1969, Vokes 1980, Lamprell and Whitehead 1992, Nevesskaja 2009, Carter and Campbell. 2011, among others). Anatinellidae contains only one, monotypic genus, *Anatinella*. This genus resembles members of the small mactrid subfamily Kymatoxinae in having tooth-like but non-articulating shell lamellae near the hinge plate, yet the latter family is traditionally assigned to the family Mactridae. The present study evaluates whether the Anatinellidae and Kymatoxinae should be regarded as distinct at the family or subfamily level.

MATERIALS AND METHODS

Type materials for species of *Anatina* Schumacher, 1817 and several Kymatoxinae were examined from the following institutions: Muséum National d'Histoire Naturelle (MNHN), Paris; the Natural History Museum (NHMUK), London; the National Museum of Natural History, Smithsonian Institution (USNM), Washington DC, U.S.A., and the Zoologisk Museum (ZMUC), Copenhagen. All type material of type species of each valid genus was illustrated (Figs. 1–2).

Characters of shell morphology, hinge and ligament structure, shell sculpture, and shell muscle scars were scored for *Anatinella*, members of Kymatoxinae, and members of Mactrinae. Cladistic analysis was performed for selected

members of Mactrinae, *Anatinella*, and Kymatoxinae to provide an objective basis for apomorphies. In this way a phylogenetic analysis using a matrix of morphological characters was performed with the program Tree Analysis using New Technologies (TNT), ver. 1.1 (Goloboff *et al.* 2003). A 'traditional' search based on 1000 replicates using TBR branch swapping was done.

RESULTS

Morphological observations

Anatinella

Anatinella has small, thin, fragile, equivalve, slightly inequilateral, inflated, posteriorly extended, oblong-ovate, slightly posteriorly gaping shells that are anteriorly ovate, posteriorly ovate except for a dorsoposterior, oblique truncation, dorsally slightly downwardly sloping anteriorly and posteriorly, and ventrally broadly ovate (Figs. 1A–D). A low, umbonal-posterior carina separates the flanks from the flattened, posterior area (Figs. 1A–B). Shell sculpture consists of growth lines or commarginal striae and fine, radial lines. Inner shell margins are smooth. The umbos are low, positioned slightly anterior of the midline, and the beaks are prosogyrate. The hinge plate is very narrow except near the ligamental chondrophore, is slightly dorsally arched, and has two divergent cardinal teeth in the right valve (not fused) and a single, inverted V-shaped cardinal tooth in the left valve. There are no true lateral teeth, but a narrow, tooth-like cardinal and accessory shell lamella is present in each valve. The pallial line is continuous, positioned close to the ventral shell

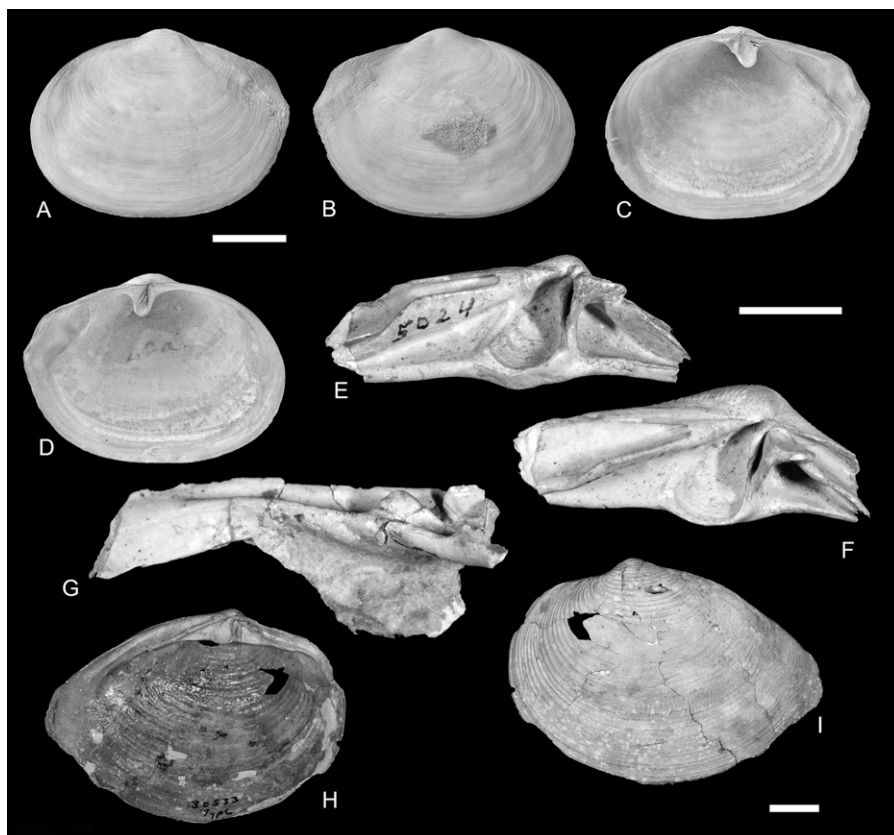


Figure 1. A–D, *Anatinella sibbaldii* G. B. Sowerby I, 1833 (= *Mya nicobarica* Gmelin, 1791, p. 3221), holotype, NHMUK 1996448; E–I, *Pteropsella papyria* (Conrad, 1833), E–F, Syntype ANSP 5024, G, Syntype ANSP 5025, H–I, Lectotype, ANSP 30533. Scale Bar A–D = 1 cm; E–G = 5 mm; H–I = 2 cm.

margin, without a pallial sinus. The anterior adductor muscle scar is very narrow and elongate, positioned close to the anterior shell margin, and occupies much of its length; the posterior adductor muscle scar is subovate, positioned just below posterior hinge, and is flanked anteriorly by a slight thickening of the shell. The periostracum is thin. The dorsal part of the ligament is entirely lamellar, short, opisthodontic, submarginal, and separated from the underlying resilium by a shelly lamina. The resilium is deeply submarginal, inserting on very narrow, tear-drop shaped resilifer extending onto a very narrow, strongly posteroventrally projecting chondrophore (Figs. 1C–D). Soft anatomy is not known in detail, but the absence of pallial sinus suggests at most only very short siphons. The shells are internally porcelainous.

Kymatoxinae

Members of *Kymatoxinae* have small to medium size, very thin, fragile, equivalve, subequilateral, medially inflated but posteriorly compressed, slightly posteriorly or slightly anteriorly or anteroventrally extended, elongate-ovate to subtrigonal shells that are anteriorly narrowly ovate to

roundly ovate, posteriorly ovate to very narrowly ovate (sometimes slightly rostrate and truncate with an umbonal-posterior carina or distinct, radial ridge), dorsally downwardly sloping anteriorly and posteriorly, and ventrally broadly ovate (Figs. 1H–I, 2A–I). The shells gape slightly dorsoposteriorly, with the gape accentuated by an outward reflexion of the adjacent shell margins. The sculpture consists of growth lines or, more typically, narrow to wide, commarginal folds or undulations; the folds may be slightly oblique posteriorly in *Raetella* Dall, 1895 (Fig. 2H). Rarely, minute, radial vermiculate sculpture is present near the umbos and posteroventral area where the periostracum thickens as in *Anatina* (Figs. 2A–B). A lunule may be absent (*Raeta* Gray, 1853) or poorly defined by a slight sulcus (*Anatina*, *Pteropsella* Vokes, 1956); an escutcheon is sometimes present but poorly defined. The umbos are small, rather pointed, only slightly projecting, and are positioned slightly anterior or slightly posterior of the midline; the beaks are prosogyrate. The hinge plate is only slightly thicker than the umbonal part of the shell, and it is slightly arched and generally deeply

longitudinally grooved posteriorly or anteriorly and posteriorly, forming very elongate “shell lamellae” that resemble long pseudocardinal teeth but are symmetrically developed in the two valves and do not articulate. The posterior lateral lamellae may descend distally below the hinge plate. The cardinal teeth are small, with one or two in each valve; one cardinal tooth or its support slightly overlaps the resilifer. The pallial line is narrow and entire, with a short, rounded, to deep, rather narrow sinus.

Soft anatomy is based in part on Harry (1969, for *Raeta*) and Morton (2010) for *Raetellops* Habe, 1952 (= *Raetella*): The siphons are narrow, elongate, about 2/3 as long or as long as the shell, and are comprised of the fused inner and middle mantle folds, including the periostracal groove (siphon type C of Yonge 1957). The siphons are united externally but separated internally for most of their length by an intrasiphonal pallial septum. The siphons are covered with periostracum, but are nevertheless wholly retractile within the shell. The siphons have a left and right lateral, elongate groove corresponding with the position of the long, intersiphonal pallial septum. The incurrent siphon has a distal ring of numerous,

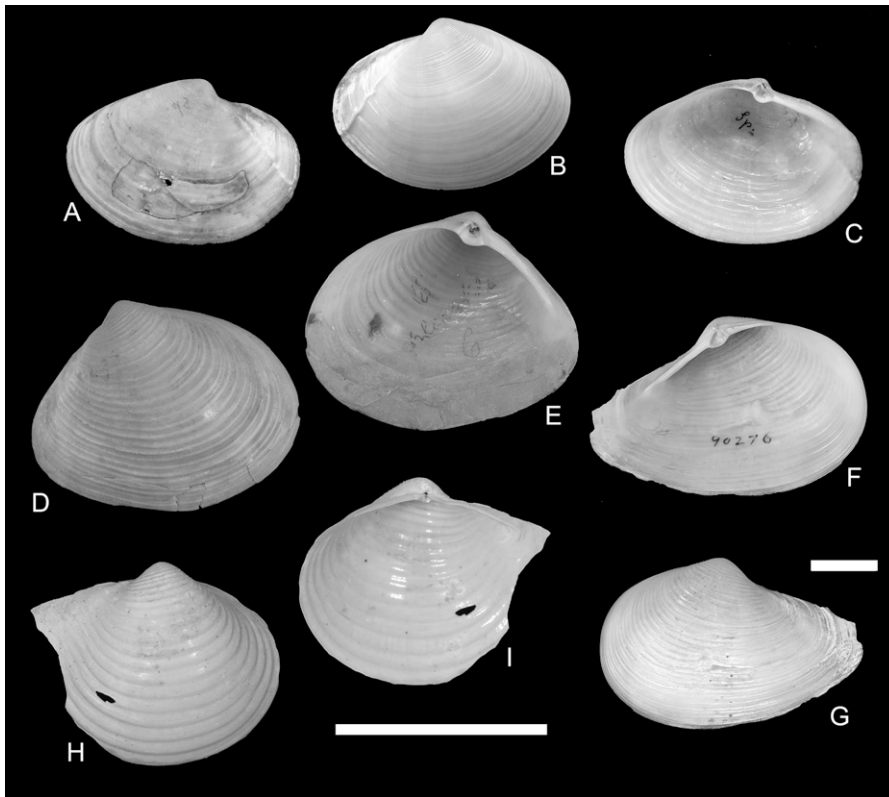


Figure 2. A–C, *Anatina anatina* (Spengler, 1802); A–B, *Mactra anatina*, syntypes, ZMUC unnumbered; C, *A. pellucida* Schumacher, 1817, syntype, ZMUC unnumbered; D–E, *Raeta plicatella* (Lamarck, 1818), Syntype MNHN 5011; F–G, *Raeta (Raetina) indica* (Dall, 1898), Holotype, USNM 90276; H–I, *Raeta (Raetella) tenuis* (Dall, 1898) (ex Hinds MS), Holotype, USNM 519. Scale bar A–G = 1 cm; H–I = 5 mm.

short, simple papillae but no apical, conical diaphragm; the excurrent siphon is non-papillate, but has an apical, conical diaphragm. A narrow, \cap -shaped, membranous valve is present at the base of the incurrent siphon, not developed as a ventrally hanging curtain; or a horizontal, intersiphonal pallial septum is present, with its anterior portion extended as ventrally suspended, lateral lamellae that separate the branchial chambers. The ventral, inner mantle surface has left and right ridges flanking a mantle rejection tract. Left and right sensory organs are present on the upper part of the inner end of the incurrent siphon, each connected by a large nerve to the visceral ganglion. The ventral and anterior mantle margins are united except at a short to long anteroventral pedal mantle aperture by tissue fusion of the inner and middle mantle folds, including the periostracal groove. The pedal mantle aperture is surrounded on its inner margin by a thin, narrow velum from the inner mantle fold. A fourth mantle aperture is absent in *Raeta*, but present in *Raetella*. Orbicular muscles pass from valve to valve ventrally within the fused inner mantle folds, forming an accessory adductor muscle.

The mantle is attached to the inner shell surface proximal to the pallial line at numerous, small spots. The ctenidia are very small, synaptorhabdic, homorhabdic, plicate, with complete outer and inner demibranchs, or with part of the outer demibranchs absent; both ctenidia are fused posteriorly to the pallial septum anterior to the base of the siphons. The outer demibranchs have only slightly shorter filaments than the inner demibranchs medially and posteriorly; the outer and inner demibranchs each have a ventral food groove. The ctenidial axis is slightly oblique to the shell length axis. The ascending lamellae of the outer demibranchs are attached to the visceral mass by ciliary junctions; the ascending lamellae of the inner demibranchs are attached to the visceral mass by tissue fusion; the ascending lamellae are fused medially posterior to the visceral mass, thereby separating the suprabranchial and infrabranchial chambers. The labial palps are very large and broadly triangular. The ctenidium-labial palp association is category II of Stasek (1963). The anterior adductor muscle scar is teardrop-shaped to very elongate and narrow, in the latter case positioned just inside the dorsoanterior shell margin and occupying much of its length. The posterior adductor muscle scar is compact, tear-drop shaped to reniform, or very small, positioned just below the posterior hinge. The anterior pedal retractor muscle scar is minute and slightly removed from the anterior adductor scar on its umbonal side in *Raeta*, or is confluent with the adductor scar in *Anatina*. The posterior pedal retractor muscle scar is also minute, positioned on the umbonal side of the posterior adductor muscle scar, and generally confluent with it. The adult foot is atrophied, small, only slightly elongate, wrinkled, blunt-tipped, and laterally compressed, with the free margin acutely keeled but lacking a medial ventral groove, and with rounded, non-projecting heel. The style sac is separated from the mid gut. The heart has a ventricle penetrated by the rectum, a pair of lateral auricles, and anterior and posterior aortic bulbs.

The lamellar sublayer of the ligament occupies a short or very short, narrow, submarginal fossette, extending postero-ventrally from the beak, ending above and posterior to the resilifer of the internal ligament, and separated from the latter by a prominent to very thin, shelly partition. The fibrous

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sublayer of the ligament occupies a triangular resilifer, vertical to slightly posteriorly inclined, extending from a point below dorsal shell margin and below beaks toward the ventral margin of the hinge plate, or extending ventral to the hinge plate on symmetrical chondrophores. The periostracum is thin, sometimes thickening toward the posterior; some members are described as having “chalky deposits” in their periostracum (Harry 1969).

Maetrinae

Members of *Maetrinae* have medium size, thin to moderately thick, compressed, equivalve, subequilateral, sometimes slightly anteriorly extended or slightly posteriorly extended, rarely posteroventrally extended shells that are subtrigonal to broadly subtrigonal to elongate ovate, rarely obliquely ovate; anteriorly ovate to narrowly ovate, rarely truncate; posteriorly narrowly ovate to nearly pointed, less commonly vertically to obliquely truncate, sometimes attenuated, sometimes with an umbonal-posteroventral carina. The dorsal shell margins slope downward anteriorly and posteriorly; the ventral shell margins are broadly ovate, rarely with a sinus below an umbonal-posteroventral carina or ridge; some members have a blunt to sharp-edged umbonal-posteroventral carina, defining a flat posterior area or marking a strong inward turning inward of the dorsoposterior shell margin. The sculpture is smooth except for growth lines, or consists of narrow to wide commarginal ribs; some members have a single, sharp radial ridge near the dorsoposterior flank. The shell margins are slightly gaping anteriorly and posteriorly. The hinge is moderately wide to wide. The right valve has one deeply bifid cardinal in the right valve, in some cases regarded as two slightly joined cardinals, and single anterior and single posterior, lamellar, lateral teeth. The left valve has one deeply bifid cardinal, sometimes reinforced by a posterior, curved apophysis that extends slightly over proximal anterior part of resilifer. A pallial sinus is present, very shallow to more commonly deep, in the latter case usually rounded apically, and with ventral branch of sinus separate from posteroventral pallial line. The siphons are short to long, united to their tips, with tissue fusion of the inner and entire middle folds and the periostracal grooves, thereby covering the siphons with periostracum (siphon type C of Yonge 1957, 1982). The siphons are generally wholly retractile within the shell. The incurrent siphon has a distal ring of short, simple papillae, with or without an apical, short, conical diaphragm; the excurrent siphon has an apical, conical diaphragm, and either with its own ring of simple papillae, or flanked above and laterally by papillae from a common ring of papillae surrounding the combined ends of the siphons. A basal siphonal diaphragm is absent or present and suspended ventrally from the proximal end of an intrasiphonal pallial septum, over the dorsal part of the incurrent aperture. The

ventral mantle margins near the pedal mantle aperture show only cuticular fusion of the inner surfaces of the middle mantle folds, but tissue grade fusion posterior to this, near the base of the siphons, and anterior to this. The inner surface of the ventral posterior mantle has left and right ridges arching over left and right mantle rejection tracts; these are sometimes accompanied by a smaller, shorter pair of ridges slightly anterior to the larger ridges; or these internal ridges may be absent. A fourth pallial aperture is either absent, or a functional but not tissue-grade fourth pallial aperture may be present. The ctenidia are small to medium-sized, eulamellibranch, homorhabdic, with the upper margins of the ascending lamellae of the inner and outer demibranchs attached to the visceral mass by tissue union or by both cuticular junction and tissue union, respectively. The labial palps are triangular, very long, with ctenidium-palp association category II of Stasek (1963). The stomach is type V of Purchon (1960), with the style sac separated from the mid gut (*Maetra* Linnaeus, 1767) or conjoined. The heart has a ventricle, a pair of lateral auricles, and small anterior and large posterior aortic bulbs. The adductors are isomyarian or with a slightly smaller or slightly larger anterior adductor scar. The anterior and posterior pedal retractor scars are small, positioned adjacent to and on the umbonal side of the respective adductor scars. The foot is large and laterally flattened. The ligament in early members is opisthodontic, parivincular, with prominent nymphs and with very small, subumbonal, fibrous resilium. Typical Cenozoic members have the ancestral parivincular ligament reduced to a slightly to strongly submerged, lamellar sublayer, inserting into a submarginal, elongate fossette in each valve, without nymphs, and separated from an enlarged, fibrous resilium by simple, non-ligamental hinge plate or a shelly partition. The lamellar sublayer of the ligament generally still parallels the dorsoposterior shell margins, and less commonly descends to parallel the posterior margin of the resilifer, rarely sometimes very closely approximating its posterior margin. The resilium is entirely fibrous, triangular to teardrop shaped, ventrally non-projecting or slightly to strongly projecting below the hinge plate on left-right symmetrical chondrophores. The periostracum is thin to thick, two-layered, internally structureless, or with very thin medial zone of minute (mineralized?) granules. The shells are aragonitic and internally porcelaneous. Members are burrowing, mostly marine or estuarine, infaunal deposit feeders, with small ctenidia used for respiration but not feeding, and with enlarged labial palps used to sort sediment entering the incurrent siphon.

Results of cladistic analysis

The subfamily *Maetrinae* is defined by members of *Maetridae* with the apomorphies of the family but lacking the apomorphies of its more derived subfamilies (*Darininae*,

Lutrariinae, Tanysiphoninae). More plesiomorphic members with equivalve, moderately inflated, moderately thick, slightly inequilateral, slightly posteriorly extended shells, broadly ovate ventrally, smooth or with only growth lines, without pedal gapes, with a slightly arched, moderately wide hinge plate with small, bifid to non-bifid cardinal teeth and anterior and posterior lateral teeth, no pallial sinus, very short, tissue grade, incurrent and excurrent siphons (type A+ of Yonge 1982), cuticular but not tissue-grade fusion of the ventral mantle margins adjacent to the pedal mantle aperture, rather small, synaptorhabdic ctenidia with complete inner and outer demibranchs, nearly equal, more or less ovate, adductor

muscle scars, medium size pedal retractor muscle scars, a laterally compressed, anteriorly extended, burrowing foot without a strongly projecting heel, an external, opisthodontic, parivincular ligament with a very small, submarginal subumbonal resilium at its anterior end.

The cladistic analysis of *Anatinella*, Kymatoxinae and Mactrinae species suggests that Kymatoxinae shares closer common ancestry with *Anatinella* than with Mactrinae (Fig. 3). Synapomorphies for the clade of *Anatinella* + Kymatoxinae include the presence of elongate, non-articulating shell lamellae arising from the inner shell surface, plus a very narrow hinge plate, a very narrow, strongly posteroventrally projecting chondrophore, a very narrow, elongate, submarginal/internal resilium, a narrow, elongate, anterior adductor muscle scar, and very thin, fragile shells. The synapomorphy for Kymatoxinae is the presence of a pallial sinus and, by inference, well-developed siphons.

Anatinellinae might be ancestral to the Kymatoxinae. Both subfamilies share apomorphies but *Anatinella* is anatomically more basal than Kymatoxinae in terms of its lack of a pallial sinus. However, *Anatinella* is known only from the Holocene, whereas Kymatoxinae dates from the Eocene. Therefore, until early Cenozoic members of Anatinellidae become known, the possibility must remain open that *Anatinella* reduced the siphons that were present in an ancestor in Kymatoxinae.

If Kymatoxinae shares closer common ancestry with *Anatinella* than with Mactrinae, this should be expressed in the classification of Mactroidea. The Anatinellidae is, therefore, presently enlarged to include the subfamily Kymatoxinae (Table 1). The present revision of Anatinellidae is summarized as follows:

I. Superfamily Mactroidea Lamarck, 1809

A. Family Anatinellidae Deshayes in Gray, 1853.

Family diagnosis: Members of Mactroidea with thin, fragile shells, a slight posterior shell gape, narrow, non-articulating, pseudocardinal-like shell lamellae near the hinge in each valve, with or without a pallial sinus, and commonly with a very narrow, elongate,

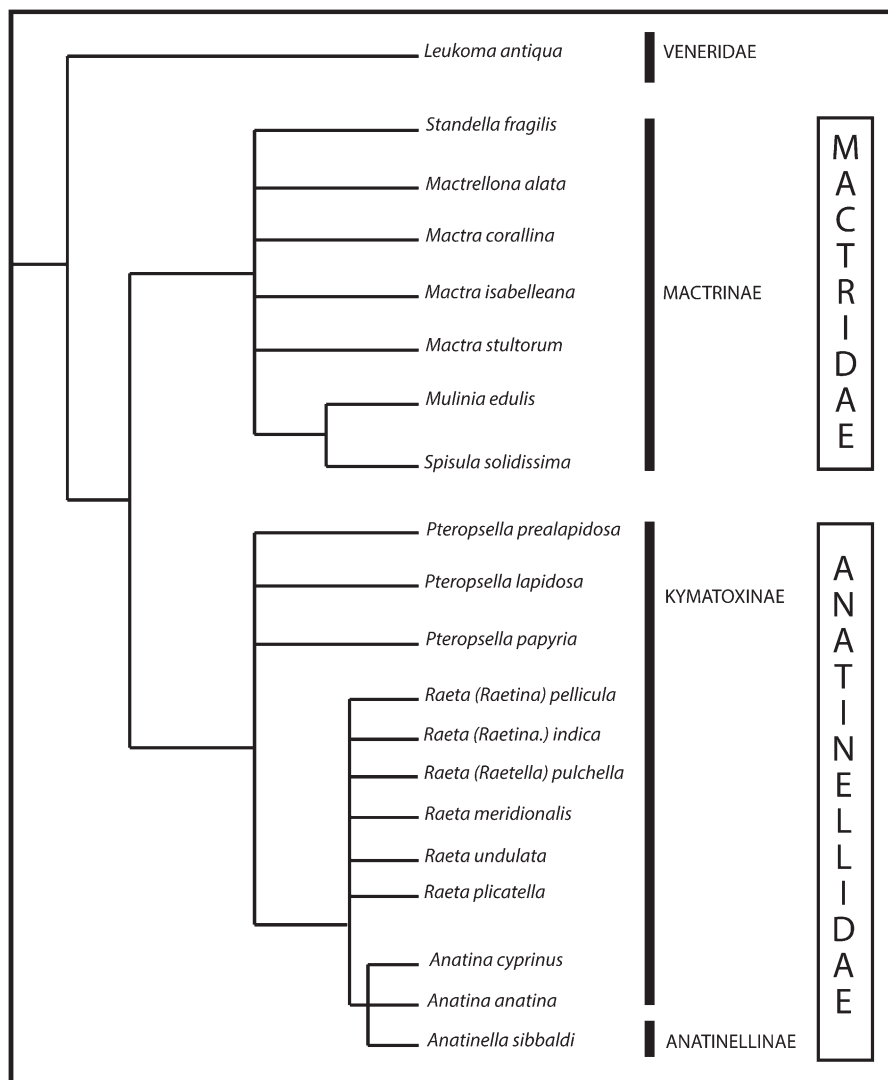


Figure 3. Morphological phylogenetic analysis of Mactrinae and Anatinellidae based on a maximum parsimony heuristic search of the traditional morphological data set (27 characters) and 20 taxa, including the venerid *Leukoma antiqua* King, 1832 as outgroup.

Table 1. Revised suprageneric taxonomy of the superfamily Mactroidea.

Superfamily	Family	Subfamily	Type genus
Mactroidea	Mactridae	Mactrinae Lamarck, 1809	<i>Mactra</i> Linnaeus, 1767
		Lutrariinae J. Gray, 1853	<i>Lutraria</i> Lamarck, 1799
		Darininae Signorelli in Carter <i>et al.</i> 2011	<i>Darina</i> Gray, 1853
		Tanysiphoninae Scarlato and Starobogatov in Nevesskaja <i>et al.</i> 1971	<i>Tanysiphon</i> Benson, 1858
	Anatinellidae	Anatinellinae Deshayes in Gray, 1853	<i>Anatinella</i> G. B. Sowerby I, 1833
		Kymatoxinae Stenzel and Krause in Stenzel, Krause, and Twining 1957	<i>Kymatox</i> Stenzel and Krause in Stenzel, Krause, and Twining 1957
	Cardiliidae		<i>Cardilia</i> Deshayes, 1835
	Mesodesmatidae	Mesodesmatinae J. Gray, 1840	<i>Mesodesma</i> Deshayes, 1831
		Davilinae Dall, 1895	<i>Davila</i> J. Gray, 1853

anterior adductor muscle that occupies much of the anterior shell margin (*Anatinella*, some but not all Kymatoxinae).

1. Subfamily Anatinellinae Deshayes in Gray, 1853 (*nom. transl. et correct.* Dall, 1895: 556, ex family Anatinellidae [sic] Deshayes in Gray, 1853)

Contents: *Anatinella* G. B. Sowerby I, 1833a. Distribution: Indo Pacific, with sole species Holocene *Anatinella nicobarica* (Gmelin, 1791).

Subfamily diagnosis: Members of Anatinellidae lacking a pallial sinus.

2. Subfamily Kymatoxinae Stenzel and Krause, 1957:124, in Stenzel, Krause, and Twining, 1957 [= Pteropsellinae Keen, 1969: N605. According to ICZN Art. 40.1, Kymatoxinae is not to be replaced by Pteropsellinae on account of the synonymy of the type genera.]

Contents: *Pteropsella* Vokes, 1956 [= *Kymatox* Stenzel and Krause, 1957 in Stenzel *et al.*, 1957], East North America, Paleocene-Eocene, with species *Pteropsella papyria* (Conrad, 1833); *P. lapidosa* (Conrad, 1846); *P. prealapidosa* (Stenzel and Krause, 1957). *Anatina* Schumacher, 1817, West Central America, East North, Central and South America, Upper Triassic-Holocene, with species *Anatina anatina* (Spengler, 1802) and *Anatina cyprinus* (Wood and Hanley, 1828), among others (Keen, 1961, Signorelli and Pastorino, 2012). *Raeta* Gray, 1853 (with subgenera *Raeta* s.s., *Raetella* Dall, 1898, and *Raetina* Dall, 1898). *Raeta* (*Raeta*) Gray, 1853, Europe, West North America, Western Atlantic Ocean, East Asia, Upper Cretaceous-Holocene, with species: *Raeta* (*Raeta*) *plicatella* (Lamarck, 1818), *Raeta* (*Raeta*) *undulata* (Gould, 1851), *Raeta* (*Raeta*) *meridionalis* Tate, 1889. *Raeta* (*Raetella*) Dall, 1898 [= *Raetellops* Habe, 1952], East Asia, Australia, Pleistocene-Holocene, with species *Raeta* (*Raetella*) *pulchella* (Adams and Reeve, 1850). *Raeta* (*Raetina*) Dall, 1898, Indian Ocean, Holocene,

with species *Raeta* (*Raetina*) *indica* (Dall, 1898) and *Raeta* (*Raetina*) *pellicula* (Reeve, 1854).

Subfamily diagnosis: Members of Anatinellidae with a pallial sinus. Distinctive features found in some Kymatoxinae but not demonstrably synapomorphies for this subfamily include minute, radial vermiculate sculpture near the umbos and posteroventral area, a poorly defined lunule and escutcheon, left and right sensory organs at the base of the incurrent siphon, orbicular muscles passing from valve to valve ventrally, and a pedal mantle aperture with an annular velum.

DISCUSSION

This work is part of an ongoing revision of superfamily Mactroidea, including all recent and fossil species. For this reason only morphological, but not molecular phylogenetic characters, were considered in the phylogenetic analysis. However, this study does include morphological data both from the literature and from new observations of type materials and non-type specimens.

It remains unknown whether the well-developed siphons in Kymatoxinae are a synapomorphy for that subfamily, developed convergently on Mactrinae, or a plesiomorphy inherited from ancestors in Mactrinae. This is because a pallial sinus is lacking, and well-developed siphons might, therefore, be absent, in the sister (or ancestral?) subfamily Anatinellinae. Molecular phylogenetic data are needed to help resolve the issue of the more basal position of Anatinellinae versus Kymatoxinae.

ACKNOWLEDGMENTS

Special thanks to Paul Callomon (ANSP), Virginie Héros (MNHN), Kathie Way (NHMUK), Ellen Strong and Yolanda

Villacampa (USNM) and Ole Tendall (ZMUC) for their assistance in the revision of the type material and additional examined specimens. JHS acknowledges CONICET of Argentina.

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Submitted: 5 September 2014; **accepted:** 27 January 2015;
final revisions received: 28 April 2015