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### FIMBRIA AND ITS LUCINOID AFFINITIES (MOLLUSCA; BIVALVIA)

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ABSTRACT. *Fimbria* is the only surviving genus of the Fimbriidae, a family of bivalve mollusks that flourished during the Mesozoic. The conchological and anatomical features of *Fimbria* show that the family belongs to the superfamily Lucinacea and that it is closely allied to the Lucinidae. The systematic position of the Fimbriidae in relation to other lucinoid families is discussed, and a possible phylogeny for the superfamily is re-constructed.

#### INTRODUCTION

The relationship of the Fimbriidae with other lucinoid bivalves has been questioned by McAlester (1966), who suggested that additional anatomical and morphological data would be necessary before certain families, the Fimbriidae included, could be unequivocally assigned to the Lucinacea. It has been usual to include *Fimbria* and its fossil relatives in the Lucinacea (Dall, 1895; Thiele, 1935; Franc in Grassé, 1960; Eberzin in Orlov, 1960; Newell, 1965; Moore, 1969). Dall in Zittel (1900) considered the Fimbriidae an offshoot of the Lucinidae. The reason for this assignation was conchological, based on the structure of the dental and ligamental elements of the hinge of *Fimbria*. Anatomical characteristics supplementing the features of the shell allow the definite inclusion of the Fimbriidae in the Lucinacea.

The species of Recent *Fimbria* were reviewed by Lamy (1921) and Nicol (1950), and according to the latter there are only two living species, both distributed in the Indo-Pacific area. During the Mesozoic, particularly the Jurassic and Cretaceous, the genus *Fimbria* was rich in number of species and was widely distributed throughout warm and temperate seas (Pictet, 1855; Stoliczka, 1871). Both species-number and distribution dwindled during the Tertiary.

THE ANATOMY OF *FIMBRIA FIMBRIATA*

*Mantle.* The mantle is thin, translucent over much of its surface and open ventrally in an extensive pedal gape. Its edge is fringed with two rows of tentacles. It is fused anteriorly above the anterodorsal surface of the anterior adductor muscle (Fig. 1) and posteriorly, ventral to the incumbent aperture (Fig. 2). The fusion of the mantle lobes anteriorly is much like that in *Myrtea spinifera* (Montagu) as figured by Allen (1958, fig. 7c) and provides a broad anterior incumbent pathway by which water and suspended matter are drawn into the mantle cavity.

*Muscles.* The adductor muscles are large and are differentiated into 'quick' and 'catch' fibers. The posterior adductor muscle is irregularly oblong and rounded, whereas the anterior adductor is larger and subsemilunate, with the ventral portion wider or more extensive.

*Siphons.* Incurrent and excurrent apertures are developed posteriorly (Fig. 2). The incurrent opening consists of a simple rounded aperture, laterally flanked by two ridges of tentacles; ventrally, the muscular lobes of the mantle are fused to form a narrow

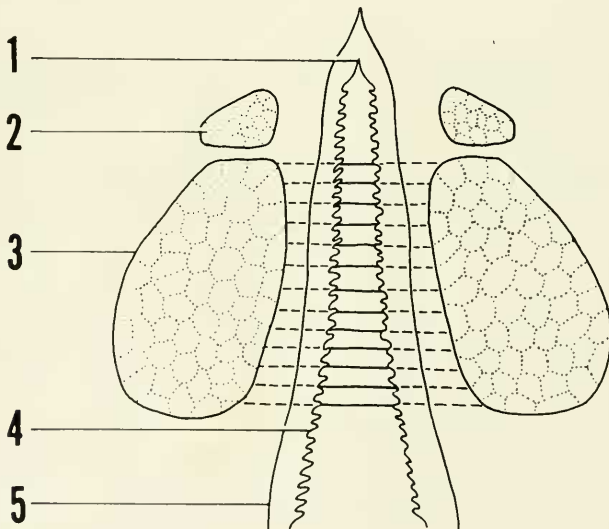


Figure 1. Diagrammatic view of anterior portion of *Fimbria*. 1. Point of anterior mantle fusion. 2. Anterior pedal retractor muscle. 3. Anterior adductor muscle. 4. Inner mantle fold. 5. Outer mantle fold.

isthmus, and dorsally they are joined in a broad union, which separates the excurrent siphon. The excurrent siphon consists of a large muscular tube which is capable of being invaginated and lies, when turned inside out, in the suprabranchial chamber. The siphonal retractor muscles are not developed, and the orifice of

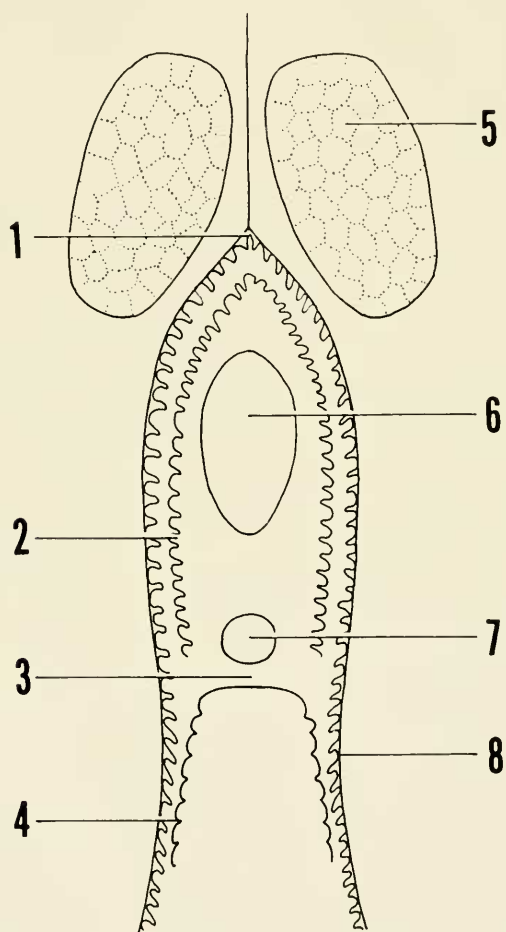


Figure 2. Diagrammatic view of posterior portion of *Fimbria*. 1. Point of fusion of outer mantle fold. 2. Secondary papillate fold. 3. Extent of tissue grade mantle fusion. 4. Inner mantle fold. 5. Posterior adductor muscle. 6. Excurrent invaginable siphon. 7. Incurrent aperture. 8. Outer mantle fold.

the aperture is flanked by two rows of papillae. The posterior aspect of *Fimbria* (Fig. 2) is similar to that of *Codakia orbicularis* (Linnaeus) as is illustrated by Allen (1958, fig. 9b).

*Foot.* The foot in *Lucina* has been studied by Barrois (1885). In *Fimbria*, it is large, subtrigonal, somewhat laterally compressed, longitudinally grooved or creased, heeled posteriorly, and pointed anteriorly (Fig. 3). In addition to its strong intrinsic longitudinal and circular muscles which surround a central sinusoidal lumen, the foot has a pair of anterior pedal retractors that attach to the shell just posterodorsal to the anterior adductor muscle and a pair of posterior pedal retractors that insert just anterodorsal to the posterior adductor muscle.

*Gills and palps.* The true gills or ctenidia consist of single, bilateral, inner demibranchs that are fused to the visceral mass dorsally and to each other posteriorly. They also attach to the muscular portion of the edge of the mantle between the ventral incurrent and dorsal excurrent apertures, thus effectively forming a septum that creates the dorsal suprabranchial chamber, into which empty the reproductive, excretory and faecal products.

Although longitudinally wrinkled, the gills are non-plicate, smooth or flat and apparently homorhabdic. They are thus similar to other lucinoids (Ridewood, 1903). In the specimens dissected, the demibranchs were retracted and thin, not thick and turgescient as are the gills in *Lucina* (Ménégaux, 1889). The filaments are interconnected, and the inner ascending lamella is shorter than the outer descending lamella, so that the latter appears to be a supra-axial extension of the demibranch. Unlike certain other lucinoids (Read, 1962; Hartman and Boss, 1966), the gills are not distinctively colored by hemoglobin.

As in other lucinoids (Thiele, 1886), the labial palps of *Fimbria* are very much reduced and consist of narrow flaplike lips bordering the mouth that accept, at their distal ends, the anteriormost portion of the demibranchs (Fig. 4). The reduction of labial palps is probably related to the increased efficiency of the ciliary mechanisms of the anterior incurrent canal and permits the ingestion of relatively large food particles (Allen, 1958).

The relation between the labial palps and ctenidia has been studied by Stasek (1963). Lucinoids, *Fimbria* included, exhibit a pattern, the category III of Stasek, in which the ventral tips of the anterior filaments of the inner demibranch are not inserted into a distal oral groove. Further, the inner demibranch may be fused to the inner palp lamella. Although the demibranch inserts

between the palp lamellae in *Fimbria*, there is no fusion (Fig. 4).

*Mantle gills.* The reduction of the true gills to only a single demibranch and the existence of the anterior incurrent canal probably were preadaptive anatomical features that aided in the development of another unusual character in lucinoids, namely, the mantle gill, noted by Duvernoy (1854: 115, pl. 5, f. 3) and Semper (1880).

Pelseneer (1911) discerned three different types of mantle gills and these have been discussed by Allen (1958). *Fimbria* is somewhat unusual in the development of two large flaps on the posteroventral surface of the anterior adductor muscle (Fig. 3). A large pallial vessel courses through the mantle diagonally from the mantle gill to the auricles. The flaplike structures of the mantle gills lie on either side of the channel of the anterior incurrent canal on the ventral surface of the anterior adductor muscle.

*Intestine.* The morphology of the alimentary canal was not studied in detail. A short esophagus enters the rather large stomach anteroventrally and the combined style-sac and midgut leaves it posteroventrally; the stomach is of the Type IV category of Purchon (1958). The digestive glands surround the stomach and are not developed into external visceral pouches. The intestine forms a simple loop in the visceral mass and enters the pericardium slightly to the right of the midline; the rectum passes over the dorsal surface of the posterior adductor muscle and empties into the suprabranchial chamber near the nephroprocts.

*Heart and kidney.* The complex of the heart and kidney is located posterodorsally and does not vary significantly from the typical eulamellibranch pattern (Ménégaux, 1890; Odhner, 1912). The heart is simple and lies in an expansive, somewhat triangular pericardium; two extremely large, thin-walled auricles receive blood from the large pallial vessel and the ctenidia. The ventricle is thick-walled and does not completely encircle the rectum; a dorsal aorta extends anteriorly. Pericardial glands (White, 1942) were not detected.

The kidney lies between the heart and the posterior adductor muscle and consists of two bilateral portions. The anteroventral reno-pericardial funnels collect fluid from the pericardial cavity; the posterior saclike parts of the kidney are broadly connected medially. The posterior portion of the kidney encircles the posterior retractor muscles. The kidneys open via bilateral nephroprocts to the suprabranchial chamber posterior to the gonadial aperture near the excurrent invaginable siphon.

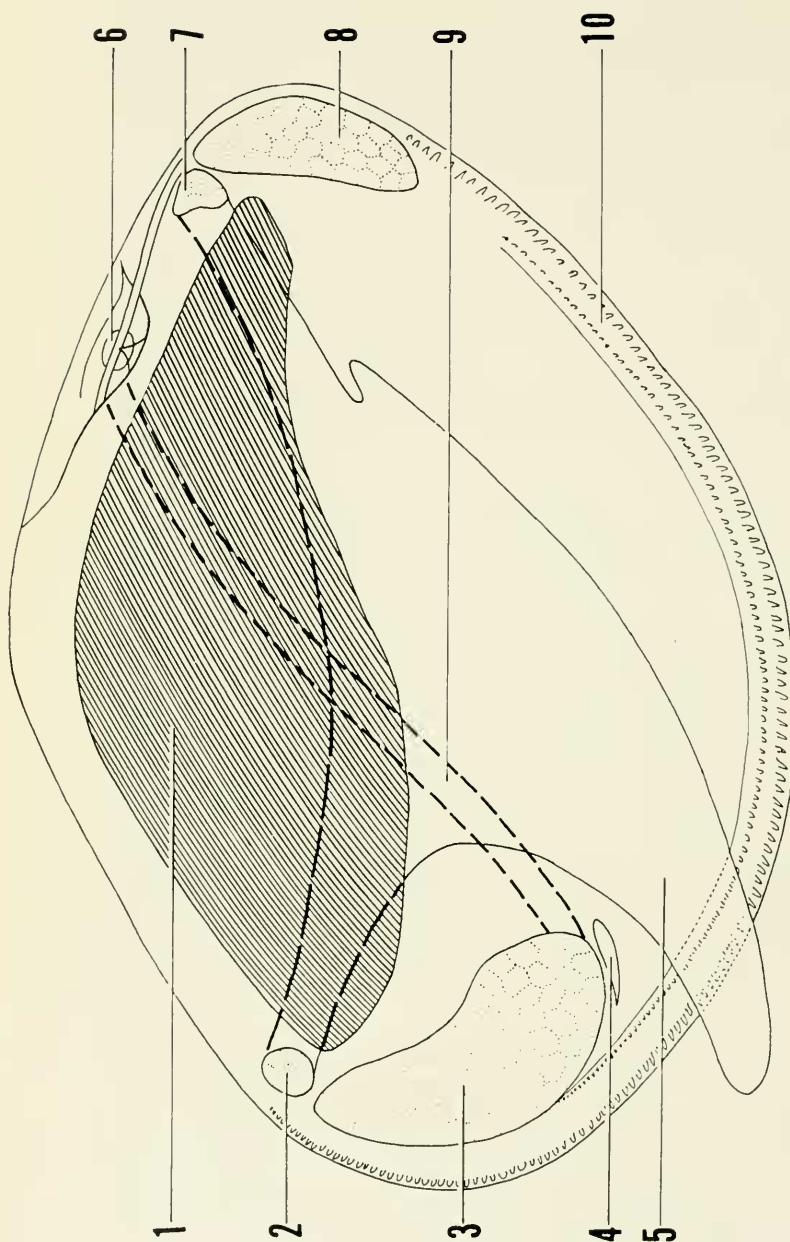


Figure 3. Diagrammatic illustration of the anatomy of *Fimbria*. Specimen viewed from left side with the mantle removed. 1. Ctenidium. 2. Anterior pedal retractor muscle. 3. Anterior adductor muscle. 4. Mantle gills. 5. Foot. 6. Pericardial area with rectum traversing the ventricle, lateral auricle and pericardium. 7. Posterior pedal retractor muscle. 8. Posterior adductor muscle. 9. Position of pallial vessel from the mantle vessel to the heart. 10. Mantle edge with rows of tentacles.

*Nervous system.* The general pattern of the nervous system of *Fimbria* is not significantly different from that of other lucinoids or eulamellibranchs (Duvernoy, 1854). There are three main ganglionic centers: cerebropleural, pedal, and visceral. The cerebropleural ganglia are located on the inner surface of the anterior adductor muscle, just over the labial palps on either side of the mouth; they are united via a medial cerebropleural commissure (Fig. 4). Anteriorly, the ganglia give rise to nerves which supply

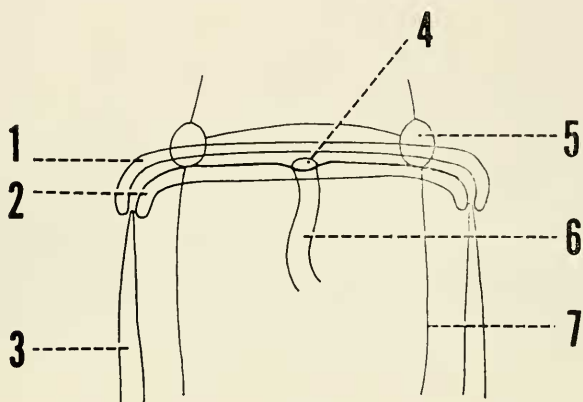


Figure 4. Diagrammatic view of the buccal area. 1. Outer labial palp. 2. Inner labial palp. 3. Ctenidium. 4. Mouth. 5. Cerebropleural ganglion with cerebropleural commissure. 6. Esophagus. 7. Cerebropleural-visceral connective.

the anterior adductor muscle and the anterior pallial musculature. Anterolaterally are branches to the labial palps, while extending ventrally from the ganglia are the cerebropleural-pedal connectives and posteriorly the cerebropleural-visceral connectives. Both pedal and visceral ganglia are closely juxtaposed and fused; the pedal ganglion gives rise to branches that innervate the intrinsic pedal musculature as well as portions of the viscera. The visceral ganglion is located on the inner surface of the posterior adductor muscle. Rather large branchial nerves arise laterally from the ganglion. The posterodorsal surface of the ganglion gives rise to small, short renal nerves, whereas the large posterior pallial nerve splays out over the ventral surface of the adductor muscle.

*Specimens examined.* (All *Fimbria fimbriata* (Linnaeus 1758)): Ifaluk Atoll, Caroline Ids. (USNM 616497); Bikini

Lagoon, Bikini Atoll, Marshall Ids. (USNM 584711); NE side of Ngaloa Ids., Fiji Ids. (USNM 674578); E of Mathuvata, N coast of Vanua Levu, Fiji Ids. (USNM 674577); Yanutha Id., N Coast of Viti Levu, Fiji Ids. (USNM 674576).

## DISCUSSION

The unusual anatomical features in the Lucinacea were noted long ago by the famous naturalist Poli (1791), who figured the Mediterranean *Tellina* [*Lucina*] *lactea* with its elongate, cylindrical foot and single demibranch. Some of the anatomical characters of *Fimbria* were described by Valenciennes (1845a and b), who noted the reduction of the ctenidia to single demibranchs and the smallness of the labial palps. He showed that the foot of *Fimbria* differed in shape from that of other lucinoids. Thiele (1935), following Dall, remarked that in *Fimbria*, the mantle was fringed by two rows of papillae and the excurrent siphon was retractile. Allen (1958) studied a number of species of lucinoids and distinguished the Ungulinidae [Diplodontidae], Thyasiridae, and Lucinidae anatomically.

Table 1 contrasts the living families of the Lucinacea. The Fimbriidae are most closely allied to the Lucinidae. Both families have in common: 1) an excurrent siphon consisting of a unique invaginable tube; 2) an anterior point of fusion of the mantle edges that is dorsal to the anterior adductor muscle; 3) the ctenidia, consisting of a single inner demibranch on each side of the animal; 4) greatly reduced palps; 5) a tissue-grade fusion of the muscular lobes of the mantle ventral to the posterior incurrent aperture. Some species of the Lucinidae also develop accessory respiratory organs or mantle gills and have a foot which is differentiated posteriorly into a heel for digging. Fimbriids differ from lucinids in the development of a bilaterally compressed subtrigonal and pointed foot, thin demibranchs without large amounts of subfilamentar tissue, a double row of papillae along the mantle margin, and the confluence of the ventral surface of the anterior adductor muscle with the pallial musculature.

In addition, the shell of *Fimbria* is strong and heavy with thickened dentition, elongately-ovate in shape and cancellately sculptured (Fig. 5). The scar of the anterior adductor muscle is contiguous with the pallial line, a configuration unlike that of lucinids, in which the anterior adductor scar protrudes inwardly and is separated from the pallial line.



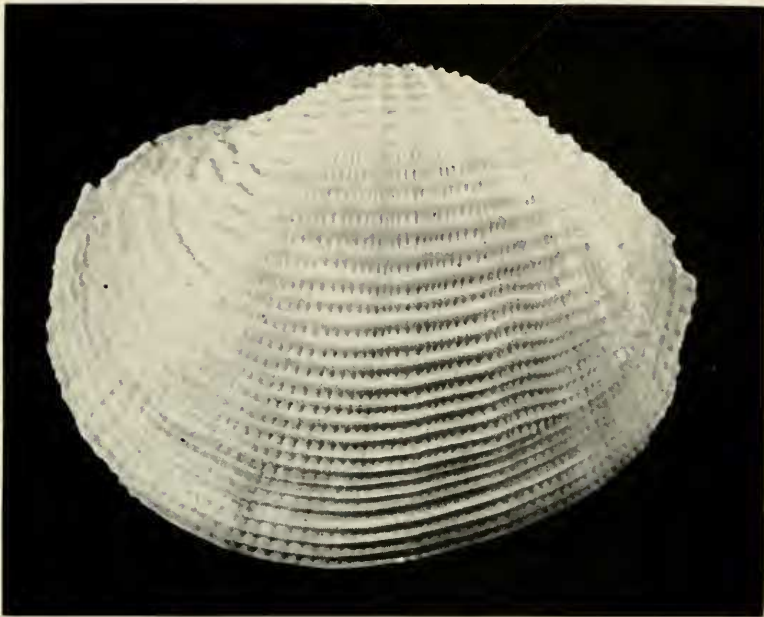


Figure 5. External view of left valve of *Fimbria fimbriata*, length = 30.5 mm, from Yanutha Id., N Coast of Viti Levu (USNM 674576).

Although the ecology of living *Fimbria* was not studied in the field, it is known that the species are reef-dwellers, preferring relatively shallow water in coralline sand (Nicol, 1950). The heavy, strongly ribbed shell is an adaptation to the coarse substrate which the species inhabits. Further, *Fimbria* probably lives near the sand-sea interface, for it possesses the anterior-posterior water-flow mechanisms of other lucinoids but lacks the vermiform foot to construct a long anterior incurrent mucus tube.

In addition to the family-level characteristics, *Fimbria* may be included in the Lucinacea because of the following anatomical features: 1) an extensive pedal gape; 2) the enlargement of the ventral surface of the anterior adductor muscle to facilitate an anterior inhalant current; and, 3) the relatively poorly differentiated and simple posterior incurrent aperture.

Table 1. Comparison of some anatomical features of four living families of the Lucinacea.  
EMF=Extent of mantle fusion beneath the incurrent aperture.

	Fimbridae	Lucinidae	Thyasiridae	Ungulinidae
Anterior incurrent aperture	no fusion over anterior adductor muscle	no fusion over anterior adductor muscle	fusion $1/4-1/3$ surface of anterior adductor muscle	fusion $1/2-3/4$ surface of anterior adductor muscle
Posterior apertures	1) invaginable incurrent siphon 2) incurrent aperture rounded 3) papillate 4) EMF tissue grade	1) invaginable incurrent siphon 2) incurrent aperture rounded 3) usually papillate 4) EMF tissue grade	1) no siphon 2) incurrent aperture slitlike 3) no sensory papillae; sensory "buttons" 4) EMF not tissue grade	1) no siphon 2) incurrent aperture slitlike 3) papillate 4) EMF tissue grade
Foot	subtriangular, heeled	subvermiform, heeled	vermiform, not heeled	semipedunculate
Gills	inner demibranch only; not thick	inner demibranch only; thick	both outer and inner demibranchs; moderately thick	both outer and inner demibranchs; thin
Palps	much reduced	much reduced	reduced, but with maximum of seven folds	moderate, subtriangular
Digestive Diverticula	internal	internal	produced into external grapelike pouches	internal

The Fimbriidae are more distantly related to other lucinoid families. The Thyasiridae are unique in having a highly differentiated vermiform foot, external pouches for the digestive diverticula, both outer and inner demibranchs, a posterior incurrent slit without differentiated papillae, and a nontissue grade connection of the muscular folds of the mantle beneath the incurrent slit (Allen, 1958; Nakazima, 1958; Kauffman, 1967). The Ungulinidae [=Diplodontidae] possess posterior sensory papillae, both inner and outer demibranchs (Duvernoy, 1842), moderately sized labial palps, and a fusion of the mantle musculature over one-half the surface of the anterior adductor muscle.

Working with the Thyasiridae, Ungulinidae [=Diplodontidae], and Lucinidae, Allen (1958) suggested that these families were related in an evolutionary series, starting with the Ungulinidae [=Diplodontidae], which were considered the most 'primitive' family, and progressing through the Thyasiridae to the more 'specialized' Lucinidae. McAlester (1966) postulated that the relationship was actually reversed and that the Ungulinidae [=Diplodontidae] and Thyasiridae were convergent with 'typical heterodont' bivalves. The single important heterodont feature referred to by McAlester is the presence of both inner and outer demibranches in thyasirids and unguinids; however, it is now known that this feature may not be as important as previously thought, since different species in the same genus (e.g., *Astarte*) may either have a full complement of demibranchs or have only a single demibranch. Nevertheless, if the Paleozoic stock of lucinoids had only a single demibranch, then the Ungulinidae [=Diplodontidae] and Thyasiridae, which branched from them in the late Paleozoic or early Mesozoic, had to re-acquire this morphological feature. Thus, McAlester's interpretation of the phylogenetic relationship among these lucinoid families is essentially correct. However, the geological record itself provides a better clue to phylogeny than do inferences based on supposed anatomical features of fossil lineages.

The Lucinidae and Fimbriidae are geologically older than the Thyasiridae and Ungulinidae [=Diplodontidae] (Moore, 1969) (Fig. 6). The lucinids may date from the Silurian; *Ilionia* Billings, a Middle to Upper Silurian genus from Sweden and eastern Canada is the first known member of the Lucinidae. However, if *Babinka* Barrande is considered a lucinoid (McAlester, 1965), the superfamily is traceable to the Middle Ordovician. *Fimbria* von Mühlfeld appeared in the Bathonian of the Middle Jurassic and radiated in the Cretaceous while other fimbriids were present earlier in the



Figure 6. Proposed evolutionary relationships of four living families of the Lucinacea. Question marks indicate possible derivations of families. Solid lines denote known lineages: the Lucinidae, from the Silurian (*Ilionia* Billings); the Fimbriidae, from the Upper Triassic (*Schafhaeutlia* Cossmann); the Thyasiridae, from the Middle Triassic (*Storhodon* Giebel), and the Ungulinidae from the Upper Cretaceous (*Brachymeris* Conrad).

The diagrams indicate anatomical features: in the fimbriid-lucinid lineage, invaginable excurrent siphon, rounded incurrent aperture and inner demibranch only; in the thyasirid-ungulinid lineage, no excurrent invaginable siphon; slitlike incurrent aperture and both outer and inner demibranchs.

Upper Triassic (*Schafhaentlia* Cossmann) and even in the Carboniferous (*Scaldia* de Ryckholt) (Eberzin *in* Orlov, 1960; Moore, 1969).<sup>1</sup>

The Ungulinidae [=Diplodontidae] probably arose in the Upper Cretaceous (*Brachymeris* Conrad and *Felaniella* Dall) and were certainly present in the Paleocene, whereas the Thyasiridae are known positively from the Cretaceous and probably from the Middle Triassic (*Storthodon* Giebel). Thus, the phylogenetic diagram presented by McAlester (1966) can be extended and augmented with the insertion of the Fimbridiidae near to the Lucinidae, from which stem they diverged in the early Mesozoic or late Paleozoic (Fig. 6).

#### ACKNOWLEDGMENTS

Dr. J. Rosewater of the United States National Museum (USNM) loaned preserved specimens for dissection. The manuscript was critically read by Professor B. Kummel, Dr. R. D. Turner, and Mr. R. I. Johnson.

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<sup>1</sup> *Scaldia* de Ryckholt from the Viséan and Tournaisian Dinantian of the Lower Carboniferous has only recently been placed in the Fimbridiidae by Chavan *in* Moore (1969). Previously it was considered in the Edmondiidae (Vokes, 1967). Ryckholt's original figures indicate that *Scaldia* has a pallial sinus, a characteristic which prevents the genus from being considered Lucinacean and which removes it from the Fimbridiidae.

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ADDENDUM: While this paper was in press, J. A. Allen and J. F. Turner (1970. *Pacific Science*, **24**(2): 147-154) published 'The morphology of *Fimbria fimbriata* (Linné) (Bivalvia; Lucinidae)' in which they proposed placing the genus *Fimbria* in the family Lucinidae.