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Edmondia and the Edmondiacea Shallow-Burrowing Paleozoic Pelecypods

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ABSTRACT

Edmondia, nominate genus of the family Edmondiidae and the superfamily Edmondiacea, has a deeply furrowed hinge plate on each valve. The furrow contains a row of small suspensory muscle insertions, previously interpreted as a ligament groove. Carboniferous and Permian genera *Scaldia*, *Allorisma*, and *Cardiomorpha* have broadly similar hinges and are grouped with *Edmondia* in the Edmondiidae. The presence of the hinge furrow distinguishes the Edmondiidae from otherwise similar representatives of the families Grammysiidae and Megadesmidae. All three families are here referred to the superfamily Pholadomyacea, and Edmondiacea is dropped.

The oval, equivalved Paleozoic bivalve *Edmondia* de Koninck is distinguished by its hinge plate seen in internal molds as a slot parallel to the dorsal margin (fig. 1). *Edmondia* is the nominate genus of the family Edmondiidae and the superfamily Edmondiacea (King, 1850) of the subclass Anomalodesmata, and the classification of the subclass is influenced by our understanding of the morphology and affinities of this genus. Particular significance has been attributed by many students to the deep furrow of the hinge plate of *Edmondia*, but its function has remained

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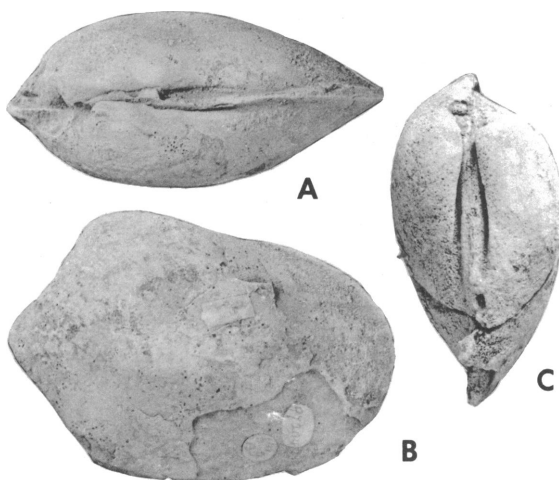


FIG. 1. Calcareous internal molds of *Edmondia*. A, B. *Edmondia primaeva* (Portlock), BM(NH) 97204, Gilbertson Collection, provenance unknown. C. *Edmondia lyelli* Hind, BM(NH) L45517, Viséan, Elbolton, Yorkshire, England. All $\times 0.75$.

unclear. We now can show that the ventral face of this structure has a row of circular muscle insertions (fig. 2C) which, by analogy with living nuculoids and other clams, probably mark muscles supporting the visceral mass. In these shells the posterior pedal retractor muscle normally is inserted on the posterior end of the hinge plate (fig. 3). Consequently, the hinge plate is not, as Waterhouse (1969b) and others have suggested, the site of an internal ligament. Its significance needs to be reassessed.

In the present article we describe the morphology of *Edmondia* and the closely related genera *Scaldia* de Ryckholdt, *Cardiomorpha* de Koninck, and *Allorisma* King, and we review the classification and affinities of the Edmondiidae.

ABBREVIATIONS

AM, Australian Museum

AMNH, the American Museum of Natural History

BM(NH), British Museum (Natural History)

DGP, Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Brazil

GSQ, Geological Survey of Queensland

MCZ, Museum of Comparative Zoology, Harvard University

SMC, Sedgwick Museum, University of Cambridge

UNE, University of New England

UQ, University of Queensland

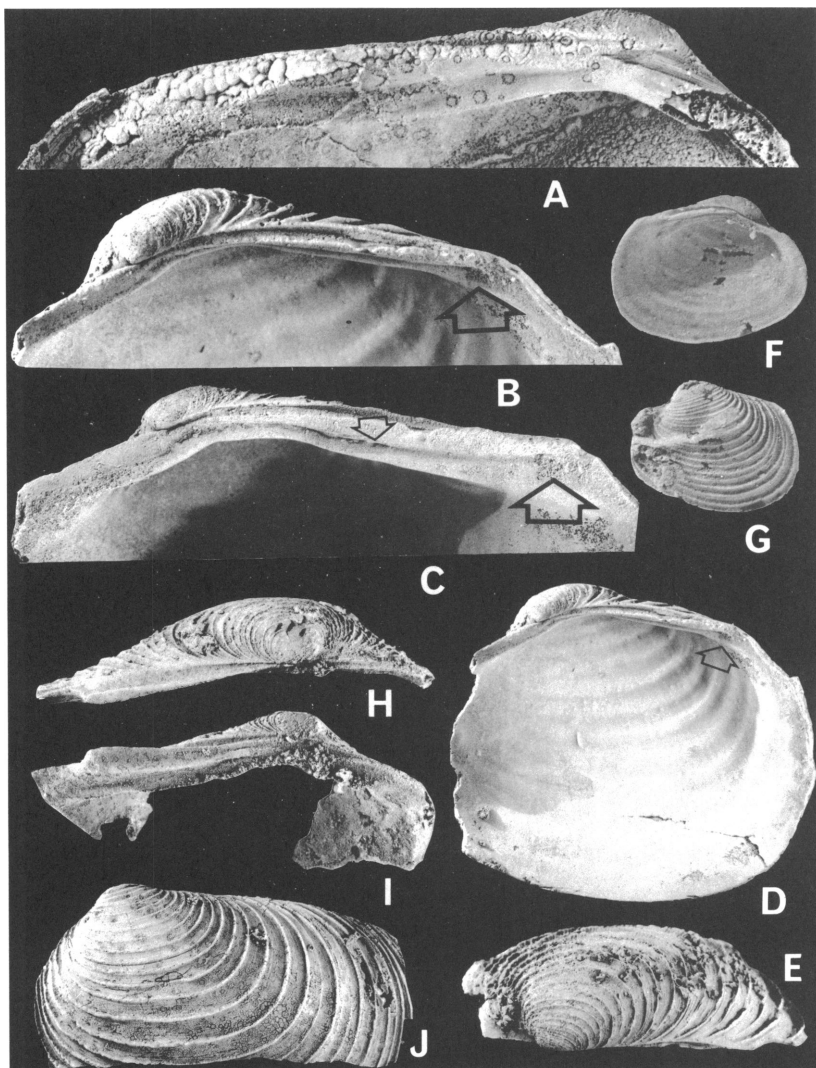


FIG. 2. Silicified *Edmondia* from Permian of Texas and New Mexico. A. AMNH 28997, Getaway Limestone, Guadalupe Mountains, New Mexico. $\times 1.8$. B-E. AMNH 28994, Bone Springs Limestone, Guadalupe Mountains, New Mexico. B, C $\times 1.8$; D, E $\times 0.9$. F, G. USNM 165792, loc. 703a, Road Canyon Formation, Glass Mountains, Texas. $\times 0.9$. H, I. USNM 165798, loc. 702, Glass Mountains, Texas. $\times 0.9$. J. AMNH 28997, Getaway Limestone, Guadalupe Mountains, New Mexico. $\times 0.9$.

Arrows indicate position of posterior pedal retractor muscle insertion and muscle pits on hinge plate.

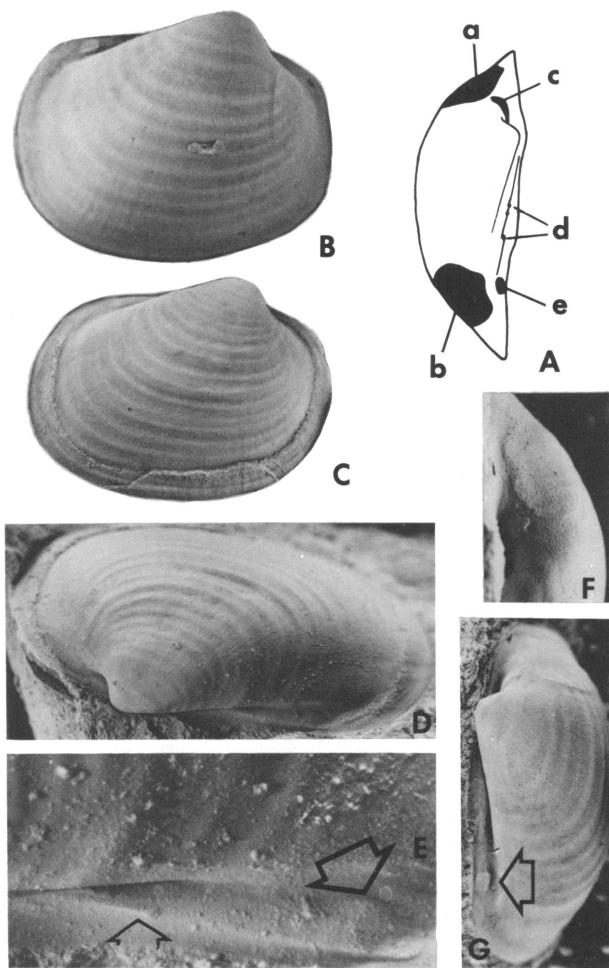


FIG. 3. Calcareous internal molds of *Edmondia aspenwallensis* Meek showing musculature. A. Composite diagram showing muscle insertions in black: a, anterior adductor; b, posterior adductor; c, anterior pedal retractor; d, muscle insertions on hinge plate; e, posterior pedal retractor. B, F, G. USNM 165774, Pennsylvanian, Kansas City, Missouri. C-E. USNM 165775, same locality. B and C $\times 1$.

Arrows indicate posterior pedal retractor muscle insertion area and track of small muscle insertion on hinge plate.

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GENUS *EDMONDIA* DE KONINCK, 1842

TYPE SPECIES: *Isocardia unioniformis* Phillips, 1836, by original designation. We believe that upon further study the following genera will prove to be synonymous with *Edmondia*: *Aediculus* Gistel, 1948 (obj.), *Broeckia* de Koninck, 1885, and *Pseudedmondia* Fischer, 1887.

LECTOTYPE: BM(NH) PL784, Gilbertson Collection, from a Lower Carboniferous limestone knoll near "Bolland" (probably Newton-in-Bowland or Slaidburn), 10–11 km. northwest of Clitheroe, Yorkshire; by subsequent designation of Wilson (1960, p. 113). This specimen, first illustrated by Phillips (1836, pl. 5, fig. 18), has been adequately refigured by Hind (1899 [1896–1900], pl. 28, figs. 1, 1a). It is an uncrushed, articulated, partly decorticated specimen showing part of the hinge plate projection in the left valve, and the posterior part of a small external ligament groove in the right valve. There are no obvious shell gapes. Phillips's specimen was collected by an amateur named Gilbertson and its precise locality is unknown. However, most of Phillips's specimens, which are labeled "Bolland," are believed to have come from the Slaidburn knolls (Parkinson, 1936, p. 296).

OTHER SPECIMENS: Two other specimens from the Gilbertson Collection [BM(NH) Palaeont. Dept. 97204, 97207] from unrecorded localities may belong to *E. unioniformis*. Both are carbonate internal molds that clearly show the inner projections of the hinge plates (fig. 1A, B).

SILICIFIED SPECIMENS OF TEXAS AND NEW MEXICO: The structure of the hinge of *Edmondia* is well shown by a number of excellently preserved shells from mid-Permian limestones of the Glass Mountains, Texas, and the Guadalupe Mountains, New Mexico (fig. 2). The ligament is opisthodontic and parivincular and was attached to broad nymphs which may project dorsally above the posterodorsal edge of the shell. There are no hinge teeth. One well-preserved specimen has a number of linear pits along the furrowed surface of the hinge plate (fig. 2B, C), and the same specimen shows an obscure trace of the insertion area of the posterior pedal retractor muscle. Ornament is variable; some species are smooth, others are orna-

mented with regularly spaced projecting comarginal lamellae which may be radially fluted.

Edmondia aspenwallensis: Two well-preserved internal molds of *Edmondia aspenwallensis* Meek from the Pennsylvanian Kansas City Formation of Missouri (fig. 3) show the position of the anterior and posterior pedal retractor muscle insertions and the insertion area of the anterior adductor muscle. The posterior pedal retractor muscle is situated high on the shell at the posterior end of the hinge plate, in the same position as the obscure scar seen on the silicified Permian specimen from New Mexico. Most importantly, one of the Missouri specimens shows clear evidence of small muscle insertion areas in the center of the hinge plate (fig. 3E). Its function



FIG. 4. Holotype of *Edmondia oblonga* McCoy, 1855, SMC E987, calcareous internal mold from Lower Carboniferous Limestone at Lowick, Northumberland, England. Adductor and pedal muscle insertions are like those of *Edmondia aspenwallensis*, and pallial line is nonsinuate.

is judged by us to be a support for visceral suspensory muscles as in some nukuloid bivalves.

HOLOTYPE: The holotype of *Edmondia oblonga* McCoy from the early Carboniferous limestone at Lowick, Northumberland, England, has adductor and pedal muscle insertions like those of *Edmondia aspenwallensis* and a well-preserved, nonsinuate pallial line (fig. 4).

GENUS *SCALDIA* DE RYCKHOLDT, 1852

TYPE SPECIES: *Scaldia kickxiana* de Ryckholdt, 1852, by original designation.

EUROPEAN SPECIMENS: Waterhouse (1966) has figured several specimens of *Scaldia* from Tournai, Belgium. The shells are smooth and circular, with a ligament like *Edmondia*, and a shallow elongate depression in the posterior part of the hinge. However, all specimens have well-developed hinge teeth in both valves.

SILICIFIED SPECIMENS FROM TEXAS AND NEW MEXICO: Permian specimens of *Scaldia* from the United States are better preserved than the European specimens, and the hinge plate is more clearly visible (fig. 5). As in *Edmondia*, there is a series of small pits in the central depression of the hinge plate (fig. 5G). The ligament is external, opisthodontic, parivincular, and attached to very small elongate nymphs not clearly differentiated from the valve margin. There is a well-defined tooth and socket in each valve; the tooth of the right valve lies ahead of that of the left.

GENUS *CARDIOMORPHA* DE KONINCK, 1852

TYPE SPECIES: *Isocardia oblonga* Sowerby, 1825, through subsequent designation of Woodward (1854, p. 323). We follow Newell (1969, p. N818) with respect to the synonymy of *Cardiomorpha*.

TYPE MATERIAL: According to Hind (1898 [1896–1900], p. 261), the type specimen of *Isocardia oblonga* is lost but the locality is known to be Blackrock, County Dublin. Hind figured a specimen he claimed to have the same provenance (*op. cit.*, pl. 21, figs. 1, 1a-b), but the locality he gave is in County Cork. We base our concept of the type species on this specimen [BM(NH)Palaeont. Dept. L24803], which is obviously conspecific with a number of well-preserved specimens of *Cardiomorpha* housed in British and American museums. It shows small oval anterior adductor muscle insertions in the lunular areas of each valve and a smooth, nonsinuuated pallial line near the growing margin of the shell. These features are visible in other specimens of *C. oblonga* (fig. 6A–D).

OTHER EUROPEAN SPECIMENS: The adductor musculature and pallial line of *Cardiomorpha* are particularly well shown by an unregistered British Museum specimen identified as *Cardiomorpha* cf. *obliqua* Hind. In this specimen the adductors were subequal in size and the anterior muscle is situated lower on the shell than in *C. oblonga*. Another British Museum specimen [BM(NH)Palaeont. Dept. 97209, fig. 6E, F], a carbonate internal mold identified as *C. orbicularis* Hind, shows that the posterior part of the hinge was thickened and projected into the valve in much the same way as the hinge plate of *Edmondia*.

Well-preserved hinges are visible on four valves of *Cardiomorpha* cf. *oblonga* of the de Koninck collection of Harvard University from the Lower Carboniferous Limestone at Visé, Belgium (fig. 7). These specimens show a narrow but distinct groove in the ventral surface of the hinge plate similar to *Edmondia*.

Cardiomorpha corrugata McCoy, 1844, type species of *Isoculia*, is similar in shape and known musculature to other species of *Cardiomorpha* (Hind, 1898 [1896–1900], p. 271), but differs in being ornamented with coarse,

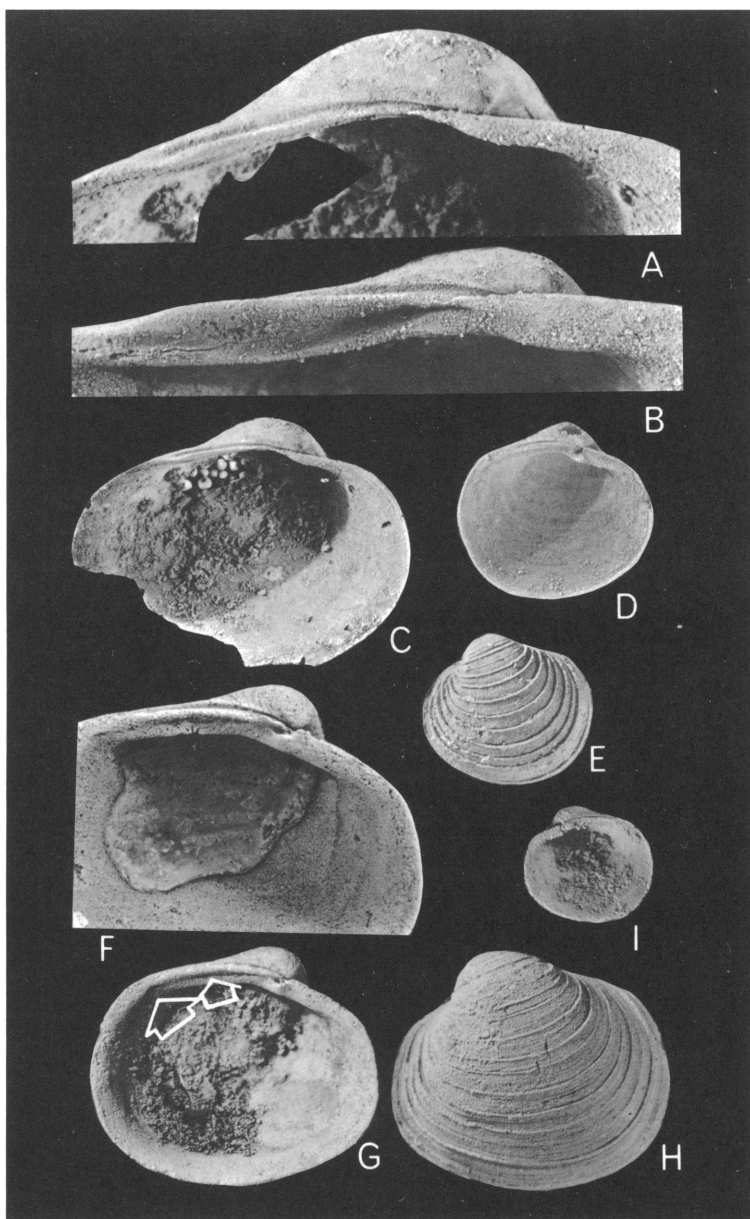


FIG. 5. Silicified *Cardiomorpha* and *Scaldia* from Permian of Texas. A–C. *Cardiomorpha* sp., loc. 703, Road Canyon Formation, Glass Mountains, Texas. A, B $\times 2$; C $\times 1$. D–I. *Scaldia* sp., loc. 703, Road Canyon Formation, Glass Mountains, Texas. F $\times 2$. D, E, G, H, I $\times 1$.

Arrows indicate position of posterior pedal retractor muscle insertion and muscle pits on hinge.

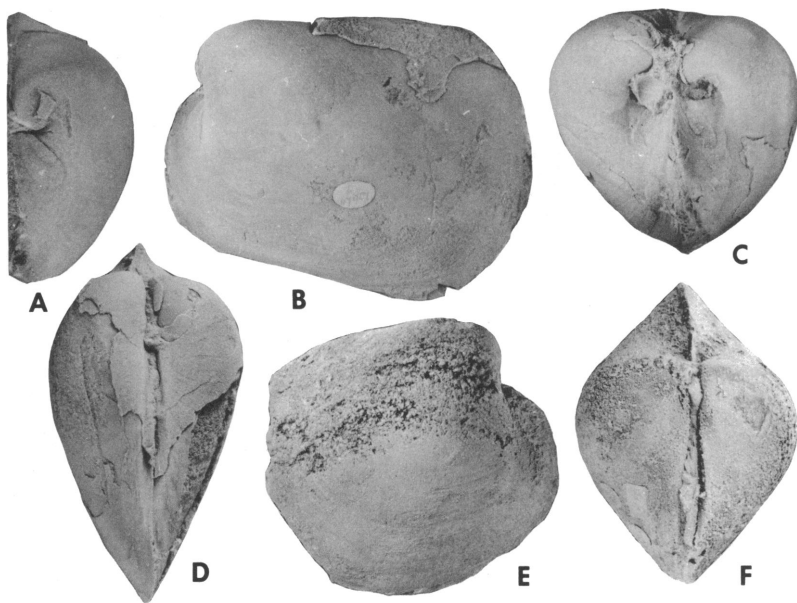


FIG. 6. Calcareous internal molds of *Cardiomorpha*. A, B. *Cardiomorpha oblonga* (Sowerby), BM(NH) L47917, Lower Carboniferous, Ireland. C. *Cardiomorpha oblonga*, MCZ uncatalogued specimen, de Koninck Collection, Kildare, Ireland. D. *Cardiomorpha oblonga*, UNE F12624, Early Carboniferous, Ireland. E, F. *Cardiomorpha orbicularis* McCoy, BM(NH) 97209, Gilbertson Collection, probably Lower Carboniferous of Great Britain, provenance unknown. All $\times 0.68$.

regularly spaced, comarginal rugae. We agree with Hind that *Isoculia* should be regarded as a junior synonym of *Cardiomorpha*.

SILICIFIED SPECIMEN FROM TEXAS: Well-preserved smooth left valves that can be referred to *Cardiomorpha* are shown in figure 5A–C. The hinge plate is clearly visible and is of the kind found in *Edmondia*.

GENUS *ALLORISMA* KING, 1844

TYPE SPECIES: *Sanguinolaria sulcata* Phillips, 1836 (= *Hiatella sulcata* Fleming, 1828) by original designation; probable synonyms would include *Edmondiella* Chernyshev 1950 (obj.) and *Allorismiella* Astafieva-Urbajtis, 1962.

LECTOTYPE: An extended search by Wilson (1960) located only one of Phillips's syntypes, a specimen now kept in the Yorkshire Philosophical Society Collection, Yorkshire Museum, York. It has been figured by Hind (1899 [1896–1900], pl. 34, fig. 3) and Wilson (1960, pl. 8, figs. 3, 3a); it is

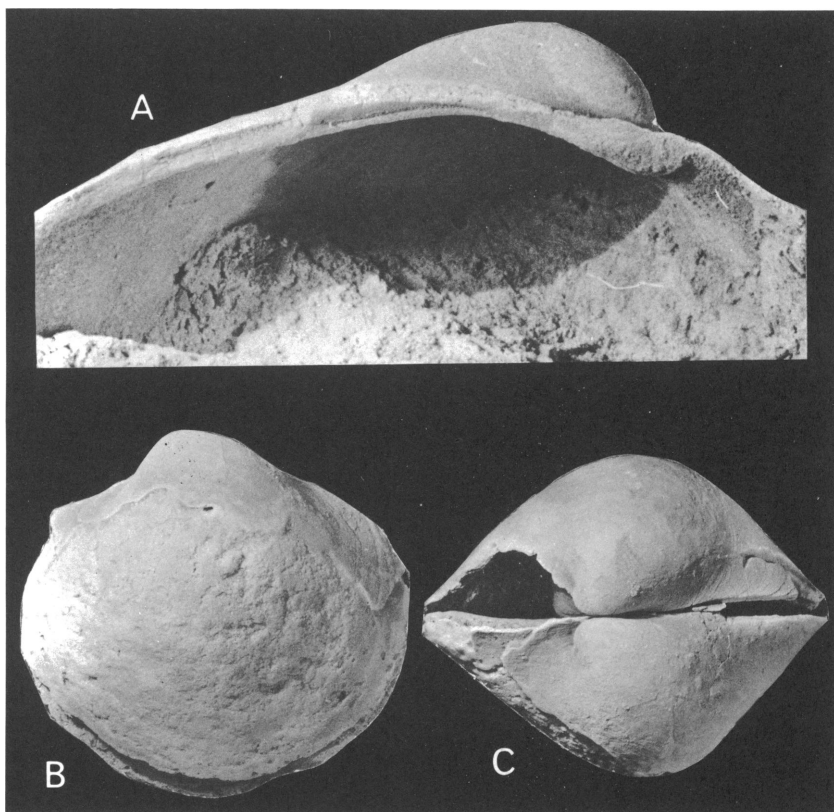


FIG. 7. Calcareous half-grown individual of *Cardiomorpha oblonga* Sowerby, MCZ 18,007, Koninck Collection, Viséan of Belgium. A. Hinge of left valve. $\times 2$. B. Exterior of left valve. C. Dorsal aspect showing strongly twisted prosogyre beaks.

not the specimen figured by Phillips, which is believed to be lost. Wilson implied that he regarded this specimen to be the lectotype of *Sanguinolaria sulcata*. We now designate this specimen as the lectotype of that species.

Wilson's study also showed that *Sanguinolaria sulcata* Phillips, 1836, is a subjective synonym and a secondary homonym of *Hiatella sulcata* Fleming, 1828. The lectotype of *Hiatella sulcata* is at the Royal Scottish Museum, Edinburgh, specimen 1870.14.305a (by subsequent designation, Wilson, 1960, p. 111), and it has been figured by Wilson (1960, pl. 8, figs. 1, 1a). In 1959 Wilson proposed the name *Wilkingia* for elongate shells with a deep pallial sinus previously inappropriately referred to *Allorisma*. Wilson showed that both *Sanguinolaria sulcata* and *Hiatella sulcata* have a shelly

projection attached to the hinge plate and suggested that *Allorisma* is a subjective junior synonym of *Edmondia*. The two are obviously closely related. In addition to having the furrow in the hinge plate, the type species of *Allorisma* has the posterior pedal retractor muscle inserted on the end of the hinge plate (see Waterhouse, 1969a, fig. 7B). However, *Allorisma sulcata* is considerably more elongate than other species of *Edmondia* and it has a well-developed buttress behind a prominent anterior pedal muscle insertion area (Waterhouse, 1969a, fig. 7). These features can probably be used to distinguish *Allorisma* from *Edmondia*, and both are visible in the lectotype of *Sanguinolaria sulcata* (Wilson, 1960, pl. 8, figs. 3, 3a). We therefore diagnose *Allorisma* as an elongate, coarsely rugose shell, with a hinge plate and pedal musculature like *Edmondia*, but having a prominent buttress behind the anterior pedal muscle insertion area.

FAMILY EDMONDIIDAE KING, 1850

Only two genera are referred to this family by Cox et al. (1969): *Edmondia* and *Cardiomorpha*. *Scaldia* is considered to be fimbriid lucinacean and *Allorisma* is synonymized with *Edmondia*. By contrast, Vokes (1967) referred 35 genera to the family, partly because he included all genera of the family Grammysiidae Miller, 1877, and partly because he listed some genera placed elsewhere in the *Treatise*. Dickins (1963) and Waterhouse (1966, 1969b) have included the cool-water Permian bivalves *Megadesmus*, *Myonia*, *Pyramus* and related genera in the Edmondiidae, but we prefer to place these genera in a separate family—Megadesmidae Vokes, 1967 (Runnegar and Newell, 1971; Runnegar, In press a).

PHILOSOPHY OF FAMILY CLASSIFICATION: There is evidence for slow iterative evolution in the bivalve subclass Anomalodesmata (fig. 8; Runnegar, In press, b). Briefly, major evolutionary changes in the nature of the ligament and the shape of the generating curve of the valves are discernible through the last two-thirds of the Phanerozoic. It is assumed that surface-dwelling or shallow-burrowing shells without gapes and completely retractable siphons are less specialized than their contemporaneous moderate- to deep-burrowing counterparts. We envisage a slowly evolving stock of shallow-burrowing species that may periodically and relatively rapidly produce deeper burrowing forms. We assume this process frequently is irreversible, that is, shells adapted for deep-burrowing are unlikely to produce descendants that lack these adaptations. Their lot may be extinction rather than adaptation. When this occurs, new deep-burrowing forms will evolve to fill the vacated niches, and the new forms will be recognizable if sufficient evolutionary change has occurred in the shallow-burrowing stock. For example, the most significant differences

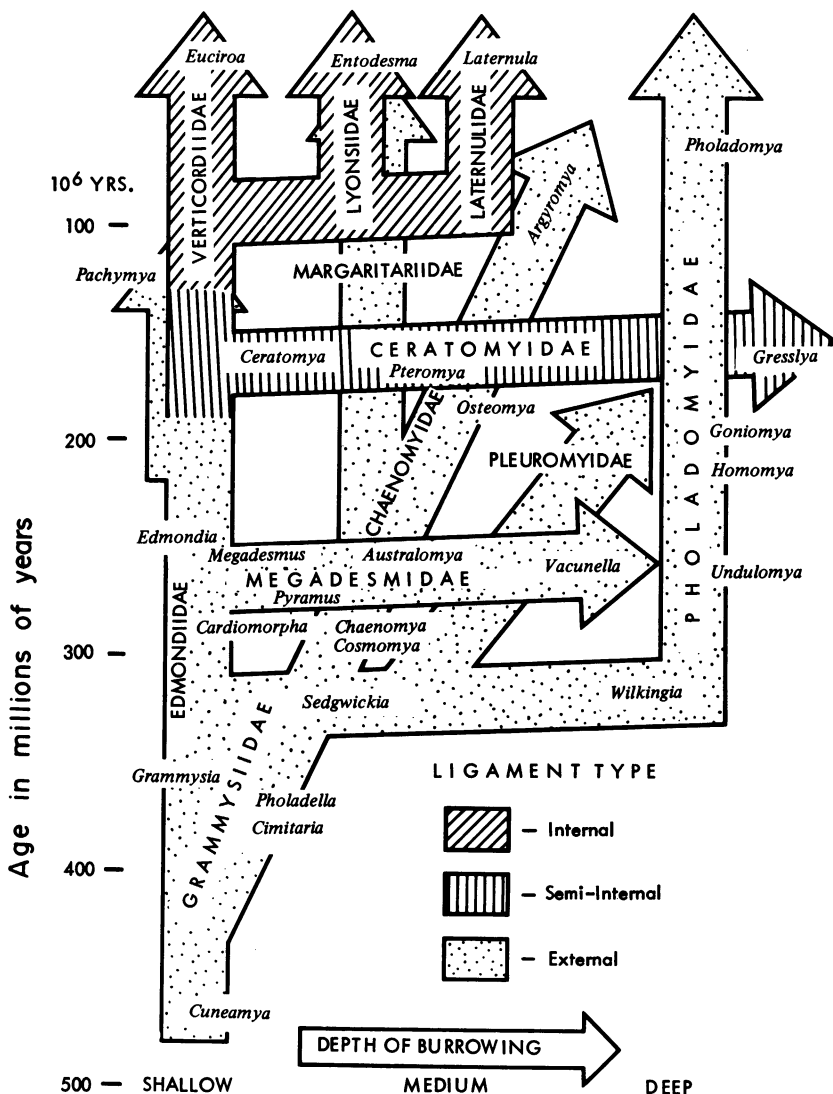


FIG. 8. Schematic view of the evolution of common burrowers of the subclass Anomalodesmata.

among the Permian shallow-burrowing bivalve *Megadesmus* Sowerby, the Jurassic shallow burrower *Ceratomya* Sandberger, and the late Tertiary and living genus *Euciroa* Dall, lie in the structure of the ligament. In

Megadesmus it is totally external, in *Ceratomya* it is attached externally in the left valve and internally in the right valve, and in *Euciroa* it is totally internal. Precisely equivalent structures occur in the deep-burrowing genera *Vacuella* Waterhouse (Permian), *Gresslya* Agassiz (Jurassic), and *Laternula* Röding (living). The close affinity of contemporaneous shallow- and deep-burrowing genera is indicated by other features such as the arrangement of the accessory pedal musculature of *Megadesmus* and *Vacuella* (Runnegar, 1966, 1967). A useful family classification will reflect natural events by separating convergent (homeomorphic) genera and uniting those with closely connected phylogenies. In defining the limits of families one may be influenced by precedent, although this may not always be reliable; *Ceratomya* and *Gresslya* are normally placed in the same family (Ceratomyidae) but *Euciroa* and *Laternula* are referred to different families (Verticordiidae and Laternulidae).

LIMITS OF THE EDMONDIIDAE: *Edmondia*, *Scaldia*, *Allorisma*, and *Cardiomorpha* lived contemporaneously, and their morphology suggests they lived on or just within the surface layers of the sea floor. *Cardiomorpha*, in particular, resembles *Grammysia* de Verneuil, which Bambach (1971) and Stanley (1972) believed lived semi-infaunally attached by a byssus (the endobyssate condition of Stanley, 1972). The only "specialized" feature of these shells is the muscle-bearing furrow of the hinge plate. Two alternatives are open: to restrict the family Edmondiidae to shells having a grooved hinge plate, or to widen the family to include genera like *Grammysia* and *Grammysioidea* (fig. 9), which have similar musculature and ligament but lack a furrowed hinge plate. We prefer the former alternative although we concede it might be acceptable to entertain a wider definition of the family.

The relationships of the Edmondiidae to the Grammysiidae, the Megadesmidae (= Pachydomidae, invalid name), and the Pholadomyidae have been discussed at length in recent literature (Dickins, 1963; Waterhouse, 1965, 1966, 1967, 1969a, 1969b; Runnegar, 1965, 1966, 1967, 1969, 1972, In press b; Astafieva-Urbajtis, 1970; Runnegar and Newell, 1971). There is general agreement that all these families are closely related but Waterhouse presented a view which differs significantly from ours.

Waterhouse is impressed by the similarity of the hinge teeth of *Scaldia* and the Australian Permian megadesmid *Astartila*, and has suggested they should be placed in the same subfamily, Astartilinae, of the Edmondiidae. He supports this decision by arguing that both *Edmondia* and the megadesmids have a depression in the hinge that housed an internal ligament, and suggests that a similar structure in modern examples of the type species of *Pholadomya*, *P. candida*, indicates a close relationship among the edmondiids,

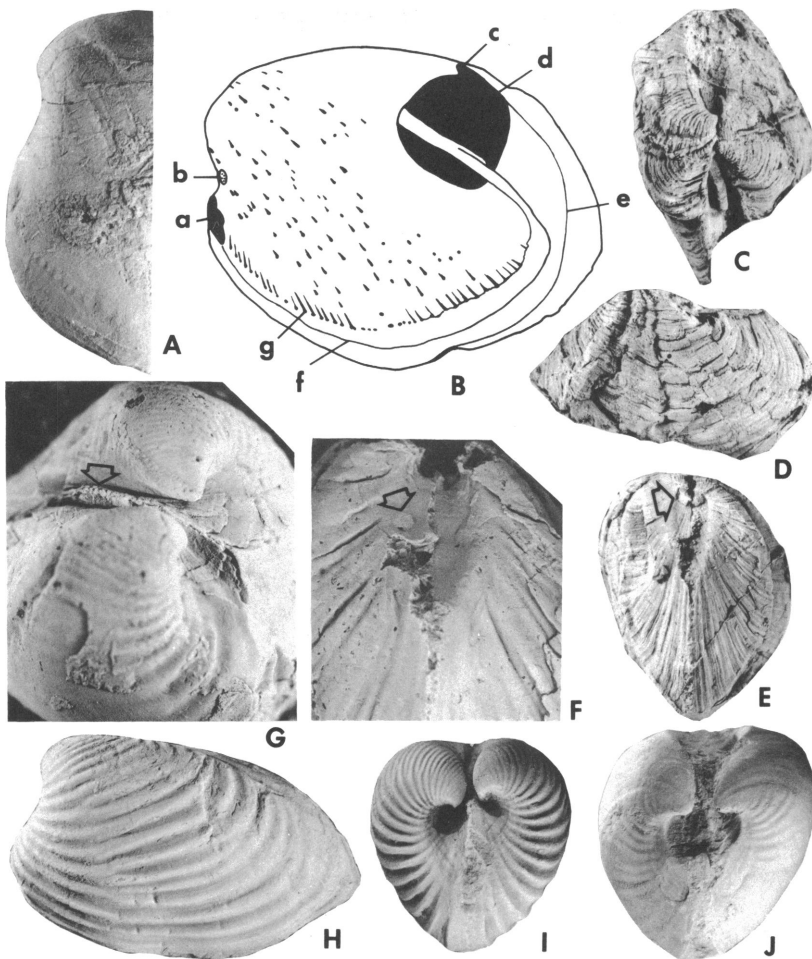


FIG. 9. Calcareous internal molds of *Grammysia* and *Grammysioidea* from the Silurian and Devonian of the United States. A. *Grammysia bisulcata* (Conrad), AMNH 29258, Middle Devonian, Hamilton Group, New York, showing pitted anterior pallial line. $\times 0.9$. B. J. *Grammysia circularis* Hall, AMNH 5335/1 (Hall, 1885, pl. 57, figs. 4–5), Hamilton Group, Blenheim, Schoharie County, New York. B $\times 0.9$; J $\times 0.68$. a, anterior adductor; b, anterior pedal retractor (on commissure side of umbo); c, posterior pedal retractor; d, posterior adductor; e, possibly junction of inner and outer shell layers; f, outer edge of pallial muscle; g, pitted anterior pallial line. C, D. *Grammysia rugosa* Williams, USNM 101174b, Silurian, Edmunds Formation, Burnt Cove, Washington County, Maine. $\times 0.9$. Note well-defined lunule and escutcheon and external ligament. E, F. *Grammysia rugosa*, USNM 101174a, same locality as C. E $\times 0.9$; F $\times 1.8$. Anterior pedal retractor (arrow) on ventral surface of lunule. G. *Grammysioidea* sp., AMNH 28996, Devonian, Marcellus Formation, Bridgewater Shale or Solsville Member, AMNH loc. 3012, Swamp Road, 2 mi. N of Morrisville, New York, showing edentulous hinge and small external ligament (arrow) which has split anteriorly as umbones enroll. $\times 1.8$. H, I. *Grammysioidea* sp., YPM 77, Braun-Schuchert Coll., locality unknown. $\times 0.68$.

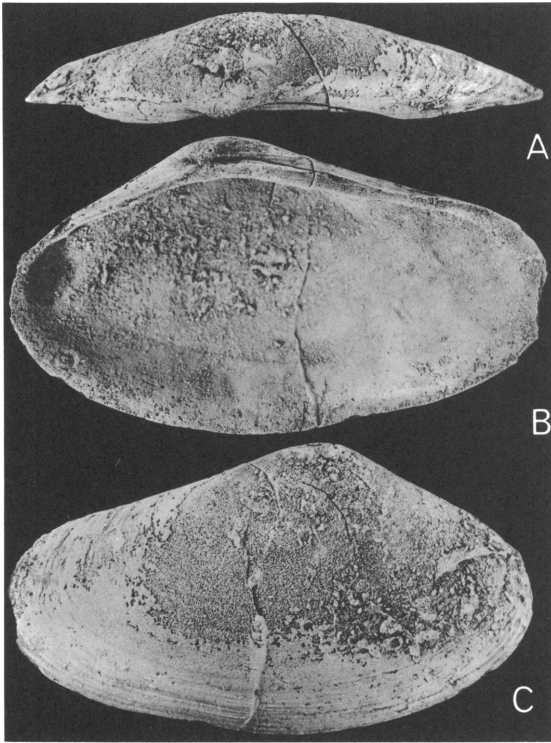


FIG. 10. Rare megadesmid from Permian of United States. ?*Australomya*, new species, AMNH 28998, Bone Springs Limestone, Guadalupe Mountains, New Mexico. $\times 0.75$.

megadesmids, and *Pholadomya*. He presents an elaborate classification of the Paleozoic genera that separates the common megadesmid genera into four subfamilies; Edmondiinae, Chaenomyinae, Pachydominae (= Megadesminae), and Astartilinae (Waterhouse, 1969b). As the "ligamental" hinge depression of *Edmondia* is a muscle support structure and the hinge depression of *Pholadomya* did not house any part of the ligament (Runnegar, 1972), Waterhouse's arguments are not acceptable to us.

PALEOGEOGRAPHIC IMPLICATIONS: Runnegar (In press a) has suggested that the Megadesmidae are a provincial group, largely confined to the cool temperate seas of the Late Carboniferous and Permian. (Only one very rare and questionable megadesmid has been discovered in the diverse silicified bivalve assemblages of the western United States; see fig. 10.) Some genera are even more restricted, found only in the Paraná lake-sea

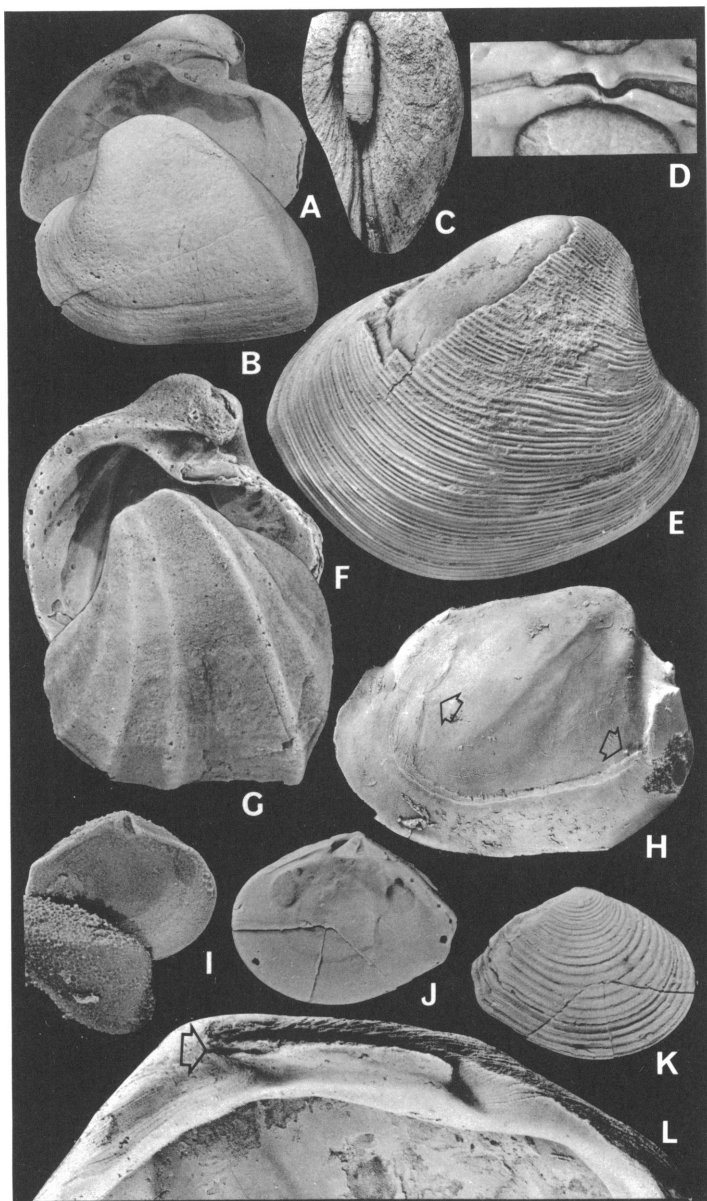


FIG. 11. Morphology of Megadesmidae. A, B. *Plesiocyprinella carinata* Holdhaus, AMNH 28976, Permian, Estrada Nova Formation, Brazil. $\times 1.5$. C. *Pyramus laevis* (Sowerby), UQ F49664, Permian, Wasp Head Formation, New South Wales. $\times 0.75$. D. Hinge of *Megadesmus gryphoides* (de Koninck), GSQ F9583, Permian, Tiverton Formation, Queensland. $\times 0.75$. E. *Megadesmus gryphoides* (de Koninck), AM F27392, Permian, Dalwood Group, New South Wales. $\times 0.75$. F, G. *Ferrazia cardinalis* Reef, AMNH 28980, Permian, Estrada Nova Formation, Brazil. $\times 1.5$. H, L. *Pyramus laevis* (Sowerby), UQ F47931, Permian, Wasp Head Formation, New South Wales. H $\times 0.56$; L $\times 1.5$. Arrows indicate accessory muscles. Note groove for anterior outer layer of ligament at anterior end of nymph. I–K. *Pyramus anceps* (Reed). I. USNM 165746, Permian, Estrada Nova Formation, Brazil. J, K. DGP 7-52, Permian, Estrada Nova Formation, Brazil. $\times 1.8$.

of eastern South America (Runnegar and Newell, 1971). By contrast, edmondiid genera are widely distributed in warm temperate and tropical late Paleozoic deposits. We regard the megadesmids (fig. 11) as a morphologically parallel group which probably diversified separately from an edmondiid or grammysiid stock in the late Carboniferous. They are united by close morphological gradations (Runnegar, 1966; Runnegar and Newell, 1971). All lack the distinctive hinge plate of the edmondiids.

SUPERFAMILY EDMONDIACEA: Edmondiacea King, 1850 (nom. transl. Newell, 1965), takes precedence over Grammysiacea Miller, 1877, if the Edmondiidae and Grammysiidae are referred to the same superfamily, but Pholadomyacea Gray, 1847 (nom. transl. Newell, 1965), is an older superfamily name which should also be considered.

The classification used by Cox et al. (1969) referred the Grammysiidae, Orthonotidae, Megadesmidae, and Pholadomyidae to the Pholadomyacea, but leaves the Edmondiidae in the Edmondiacea. Waterhouse (1969b) and Astafieva-Urbajtis (1970) grouped the Megadesmidae and Edmondiidae in the Edmondiacea, but only Waterhouse referred deeper burrowing shells (*Chaenomya* and *Vacunella*) to this superfamily. All authors agree that the Carboniferous bivalve *Wilkingia* belongs in the Pholadomyidae (Waterhouse, 1969b; Astafieva-Urbajtis, 1970; Cox et al., 1969; Runnegar, 1972).

The taxonomic solution we suggest is summarized in figure 8. Because of close morphological gradations between shallow- and deep-burrowing Paleozoic genera, Runnegar (In press b) referred all these forms with an external ligament to the Pholadomyacea. Mesozoic and Cenozoic genera with semi-internal or internal ligaments are placed in two superfamilies, Ceratomyacea and Pandoracea. The superfamily name Edmondiacea is thus no longer needed and can be suppressed in favor of the older name Pholadomyacea.

PALEOECOLOGY: Craig (1956) reported life-oriented specimens of *Edmondia* in inclined burrows in an ash bed. His reconstruction of the situation since informed us (personal commun.) that Craig's shells are *Wilkingia*, not *Edmondia*. We know of no instance where life-oriented specimens of *Edmondia* have been recorded, but assume from the shell morphology that it was a sluggish, shallow burrower.

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