

Upper Palaeozoic Anomalodesmatan Bivalvia

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SYNOPSIS. The systematics of the Late Palaeozoic Anomalodesmata (Bivalvia) are considered. Two families, the Sanguinolitidae and Permophoridae, are recognized which are considered to include the ancestors of most of the post-Palaeozoic taxa. They are united by the presence of periostracal spicules in many species of both families, which we regard as a synapomorphy. The new genus *Gilbertsonia* is recognized in the Sanguinolitidae and the two new genera *Siliquimya* and *Bowlandia* are described in the Permophoridae. The Grammysiidae are considered to be a paraphylum which includes the stem group of the Sanguinolitidae. The new Subfamily Cuneamyinae is recognized within the Grammysiidae. We retain three other family group taxa in the Anomalodesmata, the Orthonotidae, the Solenomorphidae (tentatively including a new Subfamily Promacrinae) and the Edmondicea, which are better placed there than elsewhere, but we have difficulty finding reliable synapomorphies linking them to mainstream forms. Of these three families, we only have evidence that the Solenomorphidae survived beyond the Palaeozoic. Various Upper Palaeozoic Anomalodesmata demonstrate development of a posterior gape, a deep pallial sinus or elongation of the shell, which (by analogy with living taxa) indicate the development of deep sessile burrowing, while other taxa are interpreted as shallow infaunal, slightly mobile burrowers or infaunal nestlers. Some we interpret as crevice dwellers, cavicolous or even epifaunal. The Anomalodesmata reached a high degree of species diversity in the Upper Palaeozoic, with the result that among infaunal bivalves they were commonly the most species numerous bivalve subclass. This species diversity has subsequently increased only gradually, at a much slower rate than other infaunal bivalves. They are now commonly outnumbered by the Lucinacea, Mactracea, Veneracea and Tellinacea in many shallow marine habitats. All Upper Palaeozoic Anomalodesmata have a parivincular, opisthodontic ligament mounted on nymphs which, in conjunction with elongation of the animals posterior to the umbones, leaves the distal part of the dorsal shell margin joined only by periostracum, best interpreted as primitively present rather than the result of secondary fusion. The hinge systems have few or no hinge teeth. No Palaeozoic anomalodesmatan has as yet been discovered with an internal ligament, typical of a number of Mesozoic and surviving lineages.

INTRODUCTION

During the last two decades understanding of the morphology and ecology of Upper Palaeozoic bivalves (pelecypods) has developed rapidly and, in particular, the understanding of the adaptation of form to burrowing habits and the ancestral relationship of Mesozoic forms. An early analysis by Newell (1956) was followed by the work of Runnegar (1965, 1966, 1967, 1968, 1974), Waterhouse (1965, 1966, 1969a, 1969b) and Runnegar & Newell (1974). Astafieva-Urbaitis has extensively examined the morphology and relationships of Carboniferous forms (1962, 1964, 1970, 1973, 1974a, 1974b), and Muromzeva has described both Carboniferous and Permian taxa from the Soviet Arctic (1974, 1984).

The present paper examines the morphology and relation-

ships of forms which have been referred to *Sanguinolites* M'Coy 1844, and *Allorisma* King 1844, and their relationships to each other and to younger forms are considered. (Hind (1900: 311) referred these genera to the Family Coelonotidae M'Coy 1855. The family name Coelonotidae (not Coelonotidae) was used by M'Coy (1852: 275). The name Coelonotidae is apparently unavailable as it is not based on a valid generic name (I.C.Z.N. Art. 11 (e)), as observed by Runnegar (1967: 27)). Our work should be considered within the overall framework presented by Runnegar & Newell (1974) and Runnegar (1974). One group of species, which for the present is referred to *Pleurophorella* Girty (1904), is shown to be readily separable and should be placed in the Family Permophoridae. Hitherto, this family has been placed in the Superfamily Carditacea; in this paper its position there is regarded as unlikely as is also its relationship with the heterodonts. Other forms are placed in the

Edmondiidae and Sanguinolitidae and their family relationships are discussed.

Astafieva-Urbaitis (1974a) has investigated the relationships of species placed in *Sanguinolites*. She concluded that a number of distinct groups have been included in the genus *Sanguinolites*. We agree with her conclusions, and we make further proposals to help in resolving this problem, based on the examination of the extensive collections in the British Museum (Natural History), London, including Hind's material. Astafieva-Urbaitis (1974b) also discussed the characters and relationships of *Praeundulomya*, which she concluded was related to *Wilkingia*, and she placed it within the Family Sanguinolitidae. In 1973 she had proposed the Subfamily Undulomyiinae (of the Sanguinolitidae) for *Wilkingia*, *Praeundulomya*, and *Undulomya*. In 1983 with Dickins she introduced a new name *Dulunomya* for species which they regarded as morphologically intermediate between *Wilkingia* and *Praeundulomya*. Here we reassess these genera based on their type species and include *Exochorhynchus*. We consider a taxon in this subfamily to be ancestral to *Pholadomya*.

SHELL STRUCTURE

In common with the living Anomalodesmata, the shell thickness of the Sanguinolitidae is variable: it is thin in *Sanguinolites* and *Wilkingia* and rather thicker in *Pleurophorella*. Most species of these genera have a pustulose surface. In the more spectacular forms the pustules are calcareous spikes (Aller 1974), which occur in *Wilkingia*, *Praeundulomya*, *Pholadella*, *Cimitaria* and *Chaenomya* where they are arranged in prominent radial rows. In *Pleurophorella striatogranulatus* they are better described as pustules.

Periostracal calcareous structures occur in several groups of bivalves (Carter & Aller 1975) but are not clearly present in all the taxa we consider to belong to the Anomalodesmata; this may sometimes be due to lack of preservation or sometimes their real absence. Where they do occur, however, in spike-like form, we consider that they indicate that the taxa possessing them do belong to the subclass. We consider the absence of periostracal calcareous structures in certain Anomalodesmata to be a character of taxonomic value at a level lower than subclass.

Periostracal calcareous structures are very uncommonly preserved in the Edmondiacea. Their presence in one species of the Family Megadesmidae (Runnegar 1965) and in Russian specimens of the genus *Allorisma* (Astafieva-Urbaitis & Dickins, personal observation) leads us to accept the inclusion of the superfamily within the Anomalodesmata. Other records of calcareous surface spicules that we have checked in the Edmondiacea have proved to be spurious. Pustules are also unknown in the Orthonotidae, a fact which supports the view that they should not be included within the Pholadomyoidea.

Spicules are clearly preserved in *Pachymyonia* cf. *occidentalis* Dickins (1963: pl. 5, fig. 20) from the Permian Fossil Cliff Formation of Irwin River, West Australia, but this species may be related to *Sanguinolites argutus* Phillips, from the Viséan of Britain, rather than the Megadesmidae. Wilson (1960: 111) recorded fine, close-set striae radiating from the umbones of *Edmondia sulcata* (i.e. *Allorisma sulcata* of this paper). He considered these to be internal representatives of the rows of minute tubercles on the exterior of the shell

illustrated by Hind (1899: pl. 35, fig. 11a). Hind's piece of shell, however, is apparently a *Wilkingia* and the radiating striae seem to be concerned with the attachment of the mantle to the shell and not connected with external pustules.

We have been able to study the shell structure in just one species, *Myofossa costellata* (M'Coy, 1851a) where an internal nacreous layer is perfectly preserved (Fig. 1). A very thin

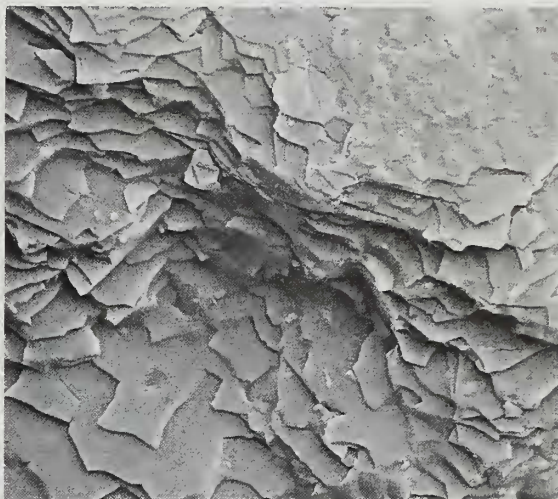


Fig. 1 Nacreous shell structure of the inner ostracum of *Myofossa costellata* (M'Coy); BM L46425, oblique stereoscan view of broken shell, $\times 720$; see also Fig. 12d.

outer layer is less well preserved and is in a blocky, recrystallized form, but we have been able to interpret it by its general appearance as a thin prismatic outer layer that was originally aragonite. A simple thin myostracal layer of short aragonite prisms was identified, as in other Mollusca.

We suspect that the calcareous shell of the Sanguinolitidae consists of an outer layer of aragonite prisms, usually with a pustulose surface, and an inner layer of nacreous structure subdivided by a sheet of myostracum. This combination of aragonite prisms with an inner nacreous layer is generally considered primitive for the Mollusca (Taylor 1973), and we believe it to be the primitive condition of the Anomalodesmata. We consider that non-nacreoprismatic shells have evolved on several separate occasions in the descendants of the Palaeozoic Anomalodesmata. Intermediate stages are recognized in the Myopholadidae which we interpret as early representatives of the Pholadidacea (Taylor, Kennedy & Hall 1973). The nacreous layer may have given rise to homogeneous structure in the Ceratomyidae, although this structure could already have been present in the Edmondiidae and the Solenomorphidae, one species of which may have been their ancestor. This may also have happened in the Pleuromyiidae and their descendants such as *Panopea*, and in *Gastrochaena* and *Myoconcha*. It may also have evolved later into cross lamellar structure in the Myopholadidae and Myidae.

In the Corbulacea, crossed and complex crossed-lamellar structure may also have evolved from the primitive anomalodesmatid shell, but an alternative possible derivation of this group is from the heteroconchs via the Myophoricardiidae. *Myopholas* and some species of *Panopea* retain the outer layer of aragonite prisms complete with pustules, at least in

their early growth stages, but these are lost in the later Pholadacea, the Myidae and *Hiatella*.

HINGES

We have examined well-preserved hinges in several species of *Sanguinolites*, *Pleurophorella*, *Myofossa*, *Wilkingia* and *Chaenomya* and have compared them with the better known hinges of the Edmondiidae, Permophoridae, Megadesmidae and the post-Palaeozoic Anomalodesmata. The sanguinolitid dorsal margin is usually straight and long, the valves being in juxtaposition from just in front of the umbones to a point above or just posterior to the posterior adductor scar. Nymphs are present, but are normally not well developed; their anterior point is immediately below the umbones, and posterior to this point (Figs 6, 9, 12, 13, 32) they vary from short to long.

We have observed ligament material only in *Pleurophorella* sp., *Sanguinolites costatus*, *Chaenomya leavenworthensis* and *Edmondia* sp. Ligaments have previously been described in the Megadesmidae (Runnegar, 1968). In that family the ligament does not extend posteriorly very far from the nymph. Runnegar recognized a small extension to the ligament beyond the partly fibrous 'C spring' ligament mounted on the nymphs. In his text-figure 1a he calls this the 'fusion(?) layer', following the interpretation of modern ligaments by Yonge (1957), Owen, Trueman & Yonge (1953) and others. In the Edmondiidae (Waterhouse 1966, Runnegar & Newell 1974) the ligament nymph is relatively more elongate.

The Upper Palaeozoic taxa here included in the Pholadomyacea have a limited range of ligament types. All have structures which are properly described as nymphs; a number of species have the remains of ligament attached to these nymphs. In what we interpret as the more primitive forms, the nymph is set in a clearly defined escutcheon, usually set between dorsal carinae, which extends from the initial growth point between the umbones to the posterior dorsal corner of the shell. In most of these taxa the dorsal margins within the escutcheon are straight and come into close contact with each

other, whether the valves are preserved in the live open or closed position. In such forms we consider that the periostracal covering of the ligament continued beyond the distal end of the nymphs, joining the shells as periostracal ligament. This type of ligament has been termed 'fusion layer' by Yonge (1957). However, in the case of these Upper Palaeozoic anomalodesmatans we consider the term to be inappropriate. We consider that this periostracum was not formed by fused mantle edges but was more likely to have been laid down by the original, primitive dorsal skin of the animal. It may have been deposited initially by the inner surface of the outer mantle fold at the posterior of the shell and then thickened by the outer surface of the skin along the dorsum. The dorsum and the periostracal ligament may have been extended from a more primitive shorter state by posterior hypertrophy of these elongate infaunal animals.

Modifications of the primitive ligament pattern that occur in the Upper Palaeozoic Anomalodesmata include the presence of nymphs where the lamellar and fibrous ligament layers are attached. In a hypothetical, simplest form, all the layers of the ligament would extend approximately the same distance distally along the dorsum. This arrangement occurs today only in the Mytilacea, where it is modified by the peculiar nature of the calcareous material joining the ligament to the shell. In all the Pholadomyacea we have studied, the distinct nymph does not run to the end of the escutcheon. The nymph is usually relatively short in the taxa we interpret as having been entirely infaunal; this condition occurs in *Grammysioidea*, *Sedgwickia*, and *Chaenomya*. It is slightly longer in the Undulomyiinae, longer still in *Sanguinolites*, and quite long in many of the Permophoridae, which include species we would interpret as only semi-infaunal, byssally attached nestlers. Some Gastrochaenacea have reduced the length of the nymph from that of their permophorid ancestors. *Spengleria rostrata* (Spengler), from St Thomas, has a broad short nymph, whereas *Gastrochaena mytiloides* (Lamarck) from Mauritius has an elongate ligament set in a notch along the top of the hinge, suggesting that the length of the ligament may be highly adapted to slight differences in life style and might not always reflect phylogeny.

The Edmondiacea also have a relatively long ligament nymph (Runnegar & Newell 1974) which may be a primitive

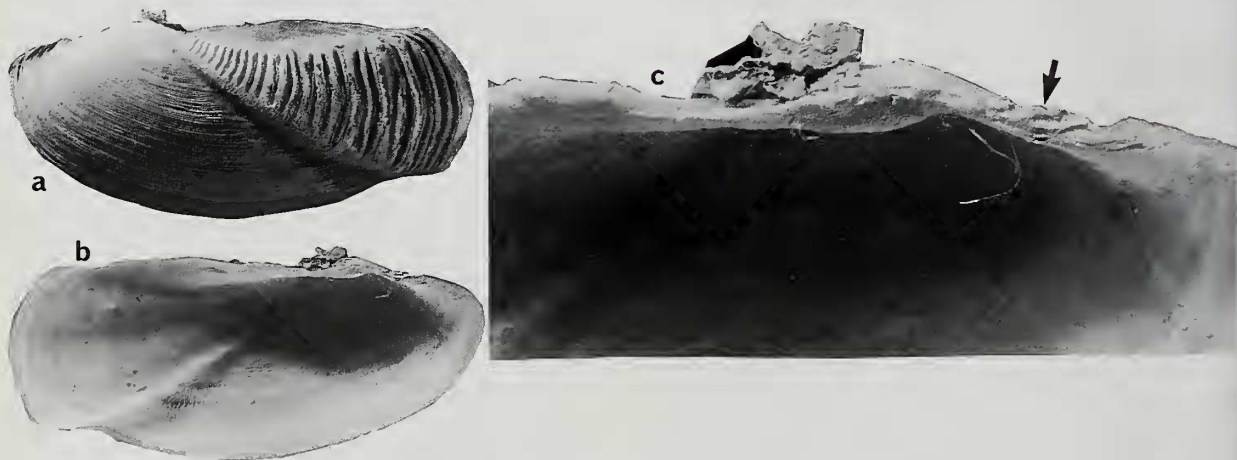


Fig. 2. *Spengleria rostrata* (Spengler). Recent, St Thomas I., Caribbean. BM (ZD) unnumbered (Cuming Collection, ex Dr Hornbeck). Figs 2a, 2b, exterior and interior view of left valve, slightly enlarged. Fig. 2c, interior view of dorsal margin of left valve, showing the development of ridges anterior to the umbones due to the emplacement of anterior fused periostracum (arrowed), $\times 6$.

character for that superfamily. Some Sanguinolitidae, as well as the majority of species of *Pholadomya*, develop a marked permanent posterior gape for the siphons. By comparison with living taxa, such large gapes are invariably accompanied by fused siphons of type 'C' (Yonge, 1957). In *Chaenomya* the gape extends along the posterior part of the dorsal margin. The escutcheon is partly lost and it is clear that the dorsal margins behind the nymphs were not continuously joined by periostracal ligament. We take this to be an advanced character, associated with largely or at least partly retractile siphons.

In *Spengleria rostrata* the valves are joined by periostracum anterior to the umbones. In dead shells the anterior dorsal margin has a chalky texture with layers of periostracum along the shell margin (Fig. 2). This clearly resembles, and we consider it to be analogous to, the structure figured by one of us (Astafieva-Urbaitis 1964) in a species of *Allorisma*, where it was suggested that they may be anterior teeth.

SYSTEMATIC DESCRIPTIONS

Abbreviations. Specimens in the following institutions are referred to in the text and figure captions with the following abbreviations:

- BGS – British Geological Survey, Keyworth, Nottingham.
 BM – The Natural History Museum, Cromwell Road, London (formerly the British Museum (Natural History)).
 BMR – Bureau of Mineral Resources and Mines, Canberra.
 EMP – École des Mines, Paris (now at Université de Lyon, France).
 GSI – Geological Survey of India, Calcutta.
 NMI – National Museum of Ireland, Dublin.
 SM – Sedgwick Museum, Cambridge.
 USNM – United States National Museum, Washington.
 MNHN – Musée Nationale d'Histoire Naturelle, Brussels.

Subclass ANOMALODESMATA Dall, 1889

The Upper Palaeozoic taxa included in this subclass are listed on p. 92. We describe here representatives of the Edmondiacea and Pholadomyacea. What we interpret as primitive characters within the subclass include an equivalve nacreoprismatic shell composed entirely of organic material and aragonite, joined across the dorsum by a three-layered, opisthodontic, parivincular ligament mounted on narrow but distinctive nymphs. More or less isomyarian adductor muscles are joined by an entire pallial line. We are uncertain whether the most primitive Anomalodesmata possess simple hinge teeth or have none. We regard the possession of spicules of aragonite on the shell surface set within the periostracum as a synapomorphy of the Anomalodesmata, but we are prepared to modify this view if a sister group of the extant representatives is recognized which did not develop this feature. We consider it unlikely that the view expressed by Carter & Aller (1975), that these periostracal spicules are the homologue of similar structures in chitons and therefore a primitive character of the Mollusca, is correct. Most Anomalodesmata have somewhat elongate shells, which we consider to be primitively infaunal, often with modification of the form of the posterior margin, which suggests that the inhalant water current of the mantle cavity was posteriorly placed. This may not be the case in primitive edmondiaceans. A subumbonal sulcus is present in many anomalodesmatans and may indicate the anterior limit of ventral mantle fusion.

Pojeta (1971) has excluded the family Orthonotidae from the Anomalodesmata, suggesting first that they should be allotted to a separate Order Orthonotoida (Pojeta 1978), but he later suggested an affinity with the Mytiloida (Pojeta, Zhang & Yang 1986). On all occasions, and with support from Runnegar (1974), the similarity between the Orthonotidae and the living Solenacea was stressed by these authors. A separate (unpublished) study (N.J.M. *in litt.*) supports an alternative view that the Solenacea are more closely related to the Tellinacea, and both superfamilies probably arose from an ancestor currently classified with the Tancrediidae. We suggest that the *Solen*-like shape has arisen at least four times throughout bivalve evolution; once within primitive Ordovician forms of uncertain affinity, once in the Orthonotidae, once in the Quenstedtiidae and at least once in the Solenacea. We consider all these cases to be due to convergence. The significance of the Orthonotidae to the classification relates to our inability to decide, on the presently available evidence, whether the Devonian to Triassic family Solenomorphidae is more closely related to early Devonian Sanguinolitidae such as '*Leptodomus acutirostris*' (Sandberger) (Beushausen, 1895: pl. 24, figs 8–10) or to *Orthonota*. Bittner (1895: pl. 1) illustrated a series of species of *Solenomorpha* from the Carnian of northern Italy which grade insensibly into what seem to be the earliest representatives of the Cuspidariidae. Interpretation of their ancestry will indicate whether or not the Cuspidariidae are properly placed in the Anomalodesmata. The shell shape, differentiation of a corselet and subumbonal sulcus, all typical of species of *Orthonota*, are not characters of the Mytilacea. However, until a well-preserved hinge is described for that genus, its systematic position remains debatable.

We include provisionally a new Subfamily Promacrinae (p. 93) within the Solenomorphidae. *Promacrus* is superficially similar to the living aracean *Litharca*, but apparently does not have an arcid hinge. Many of the species have an opisthodontic parivincular ligament with the umbones well to the posterior, and are similar in this respect to the Solemyidae. However, a specimen of *Promacrus* in the United States National Museum labelled *Promacrus undatus* Ulrich MS, from the Lower Cuyahoga Shale of northern Ohio, has a clearly preserved anterior adductor scar, which does not impinge upon the body attachment scars in the way peculiar to the Solemyidae. In addition we take the condition of *Promacrus websterensis* as originally illustrated by Weller (1899; 34, pl. 2, figs 2–7; pl. 3, fig. 1), where the umbones are more medially placed, as primitive for the genus and subfamily, and therefore less similar to the solemyid shape. We provisionally place the Promacrinae in the Solenomorphidae but feel this view may have to be modified when the hinge of *Promacrus* is adequately described.

The Prothyridae are another difficult family to place with certainty, but in Driscoll's illustration of the surface sculpture (Driscoll, 1965: pl. 11, figs 1–9), the fine radial striae resemble similar structures in a number of Mesozoic Anomalodesmata. Although carbonate spicules are not preserved in *Prothyris* a relationship to the Anomalodesmata is indicated.

Superfamily EDMONDIACEA King, 1850

The Edmondiidae include three oval genera, *Edmondia*, *Scaldia* and *Cardiomorpha*, which are more or less isomyarian with an entire pallial line, and a more elongate genus *Allorisma*. *Edmondia*, *Scaldia* and *Allorisma* share an internal rib below the hinge plate which is not usually well developed in species

of *Cardiomorpha*. The Edmondiacea share only primitive characters with the other Anomalodesmata, except for the rare occurrence of periostracal spicules. All the other characters we are able to recognize, we would expect to be primitive in early members of the Heteroconchia. The superfamily is placed within the Anomalodesmata largely by tradition. However, by assuming the periostracal spicules are a synapomorphy for the Anomalodesmata as a whole we support their inclusion in this subclass. At present we find no irrefutable evidence for the occurrence of edmondiaceans before the latest Silurian, but we suspect that earlier representatives will be either recognized or confirmed.

The rounded edmondiid shell with its regularly curved pallial line is consistent with a mantle cavity lacking a specialized channelling for the inhalant current. We consider the more elongate form and more intricate musculature of *Allorisma* to be advanced features. This lack of channelling of the inhalant current might have been similar to that of primitive living Veneroida such as *Astarte* and nuculoids such as *Nucula*, and may well have been primitive for the Lucinoida. Unlike representatives of the latter order, no edmondiid or conceivable relative discussed below, megadesmid, mactromyid or poromyid, has the hypertrophied anterior adductor scar of the Lucinacea, which is clearly visible in the earliest certain lucinacean, *Ilionia* (from the Silurian of northern Europe).

We include two Palaeozoic families in the Edmondiacea, the Edmondiidae and the Megadesmidae. The Edmondiidae are found mainly in strata of Devonian to Permian age, laid down in temperate and warm seas, now in the northern hemisphere, whereas the Megadesmidae mainly occur in the cold and cold-temperate waters of the southern hemisphere of Permian times. De Koninck (1877–8) distributed his new species from the Permian of Australia, now recognized as belonging to *Megadesmus*, among his own genera *Edmondia* and *Cardiomorpha*. Although the megadesmid genera from Australia have a characteristic shape, a relatively larger size, immensely thicker shells and more robust ligaments than Carboniferous species of *Edmondia* and *Cardiomorpha*, the similarity implied by de Koninck is real. The relationship has been widely discussed and has been summarized by Runnegar (1967: 29). We have compared the shell shape and hinge structure of a young specimen of *Megadesmus grandis* (Dana) and the musculature of several specimens of *Astartila intrepida* (Dana), both from the Illawara District of New South Wales, Australia, with the same features of a well-preserved Lower Namurian English specimen of *Cardiomorpha obliqua* Hind, and find no significant differences. Unlike *Edmondia*, *Scaldia* and *Allorisma*, *Astartila* and *Megadesmus* have no significant internal rib on the hinge plate. We know of no taxon more similar to these megadesmids than *Cardiomorpha obliqua*, and interpret that species as the closest known relative to the Megadesmidae. We have noted the superficial similarity in shape and sculpture between *Cardiomorpha* and the Jurassic genus *Ceratomya*. Both have a similar size, globose form and comarginal ribs, which has led Runnegar to speculate (1974: text-fig. 3) that *Ceratomya* evolved from the edmondiids and occupied a deeper burrowing habitat, signified by the acquisition of a pallial sinus. *Ceratomya* also developed an internal ligament by overlap of the left nymph by the right valve, and further has homogeneous rather than nacreoprismatic shell structure. Our greatest misgiving, however, is in the shell morphology of the oldest genus we attribute to the Ceratomyidae and which we would interpret as the primitive

morphology of that family. This is the Rhaetian to Hettangian genus *Pteromya*, which is more elongate and less gibbous than any *Cardiomorpha* or *Edmondia*. At present we are impressed by the external similarity between the sculpture of *Pteromya* and that of Middle Jurassic species of Cuspidariidae, and we conclude that the similarity between the gibbous shells of *Ceratomya* and *Cardiomorpha* is a consequence of convergence.

The question still arises as to whether the Edmondiacea survived beyond the end of the Palaeozoic. At an early stage we thought that the Corbulacea (Mesozoic to Recent) were derived from the Megadesmidae (outlined in Taylor *et al.* 1973, final chapter). However, we now favour a relationship between the Corbulacea and the Crassatellacea, particularly the Triassic family Myophoricardiidae. We consider the similarity of hinge structure between the Corbulidae and the Myidae to be best interpreted as a case of convergence. It is hoped to enlarge on this hypothesis in a later paper.

It has been suggested by Runnegar & Newell (1974) that the late Triassic genus *Ochotomya* Kiparisova *et al.* 1966 may have evolved from a megadesmid ancestor. It is possible that *Ochotomya* is an early representative of the Poromyacea. We can find no authentic poromyacean earlier than the Late Campanian; we include the *Liopistha* group in the Cardiacea on the basis of their cardinal teeth, shell structure and muscle scars. In spite of the considerable time gap between the Late Triassic and the Campanian we have so far been able to suggest no more plausible relationship for the Poromyacea. However, *Bowlandia* sp. (Fig. 45) is an equally plausible relative for *Ochotomya*. The basis for separation of the Edmondiacea is discussed under Pholadomyacea. Here we note the considerable convergence between the genus *Allorisma* of the Edmondiidae and genera of the sanguinolitid Subfamily Undulomyiinae. They are distinguished by the pattern of the accessory musculature and the presence of the hinge plate rib which appears to be a synapomorphic character of a number of Edmondiidae, although it may be lost during the course of later evolution. The possibility arises that the Mesozoic genus *Mactromya* and its relatives are descendants of the genus *Edmondia*, and that the Edmondiacea as a whole are better placed in the Heteroconchia. We are uncertain whether the subumbonal hinge teeth present in the edmondiid genus *Scaldia* and the Mesozoic genera *Sphaera* and *Schafhaeutlia* are an advanced or primitive character for the group. We have been unable to ascertain the shell structure of Palaeozoic Edmondiacea. In the Upper Pennsylvanian of Texas an unnamed species occurs in a preservation similar to that which has yielded shell structure information in some other taxa; only the growth laminae were clearly preserved. It is possible that the inner layer was nacreous but it is not sufficiently well preserved for us to be certain. Runnegar (1967: pl. 6, fig. 12) has illustrated what appears to be the nacreo-prismatic shell of the genus *Megadesmus*. The Lower Jurassic *Mactromya cardioides* (Phillips), from the Lower Pliensbachian, Luridum Subzone of Blockly, Gloucestershire, England, shows clear aragonite crossed lamellae and some finer structure that was apparently of amorphous type. This shell structure does not conflict with our view that the Mactromyidae may be closely related to the Lucinacea. Further work is necessary to decide whether the similarity of the Edmondiidae to the Mactromyidae is the result of convergence or descent.

Family EDMONDIIDAE King, 1850

Genera referred here to this family are *Edmondia*, *Allorisma*, *Scaldia* and *Cardiomorpha*, which all possess a hinge plate reinforced internally by a ridge or lamellar plate projecting into the shell cavity; it is equivalent to the 'internal cartilage plate or ossicle' (Wilson 1960, Waterhouse 1969a, Runnegar & Newell 1974). Earlier, one of us (Dickins 1963) had suggested that the Megadesmidae might be included in the family Edmondiidae, but this relationship has been discussed by Runnegar & Newell (1974), who showed that *Allorisma*, *Scaldia* and *Cardiomorpha* also had an internal lamellar plate as well as having other characters in common with *Edmondia*. On the basis of this information and further data presented here we also conclude that the Edmondiidae and the Megadesmidae should be recognized as separate families. Edmondiids from western Europe such as *Cardiomorpha obliqua* Hind (1898: 263) and *Edmondia lyellii* Hind (1899: 300) are the most similar to typical Australasian genera *Megadesmus*, *Pyramus* and *Astartila*. We imagine the ancestry of the Megadesmidae to have been from taxa such as these. *Cardiomorpha obliqua* in particular is thick-shelled for an edmondiid. Although its hinge margin is quite thick, the internal rib is only just distinct and its adductor and accessory muscle scars are rather similar to those of the megadesmids. We suspect that the species of *Vacunella*, *Australomya* and *Myonia* from eastern Australia are true anomalodesmatids, which are not

necessarily closely related to the megadesmids. Periostacial spicules are not usually preserved on the shell surface of Edmondiacea, but Runnegar (1965: pl. 13, fig. 9) clearly illustrates their presence in *Megadesmus gryphoides* (de Koninck). We are unable to say whether they originally occurred on other taxa within this superfamily.

We follow Astafieva-Urbaitis (1964) and Runnegar & Newell (1974) in separating *Allorisma* from *Edmondia* and add some further information on the musculature of *Allorisma*. *Scaldia* can be separated, as it possesses a hinge tooth, and *Cardiomorpha* includes slender to inflated circular shells with inrolled umbones. The Edmondiidae were apparently shallow burrowers and did not develop in the same area as the Megadesmidae. The Edmondiidae are found mainly in strata laid down in temperate and warm seas of the northern hemisphere, whereas the Megadesmidae mainly occur in the cold and cold temperate waters of the southern hemisphere.

Genus *ALLORISMA* King, 1844: 315

Fig. 3

TYPE SPECIES. *Hiatella sulcata* Fleming (1828: 462) by subsequent designation of King (1850: 196, footnote 6) (not *Cardiomorpha sulcata* de Koninck, 1842, which is not an *Allorisma*).

Wilson (1960: 114) and Newell (1969: N818) considered

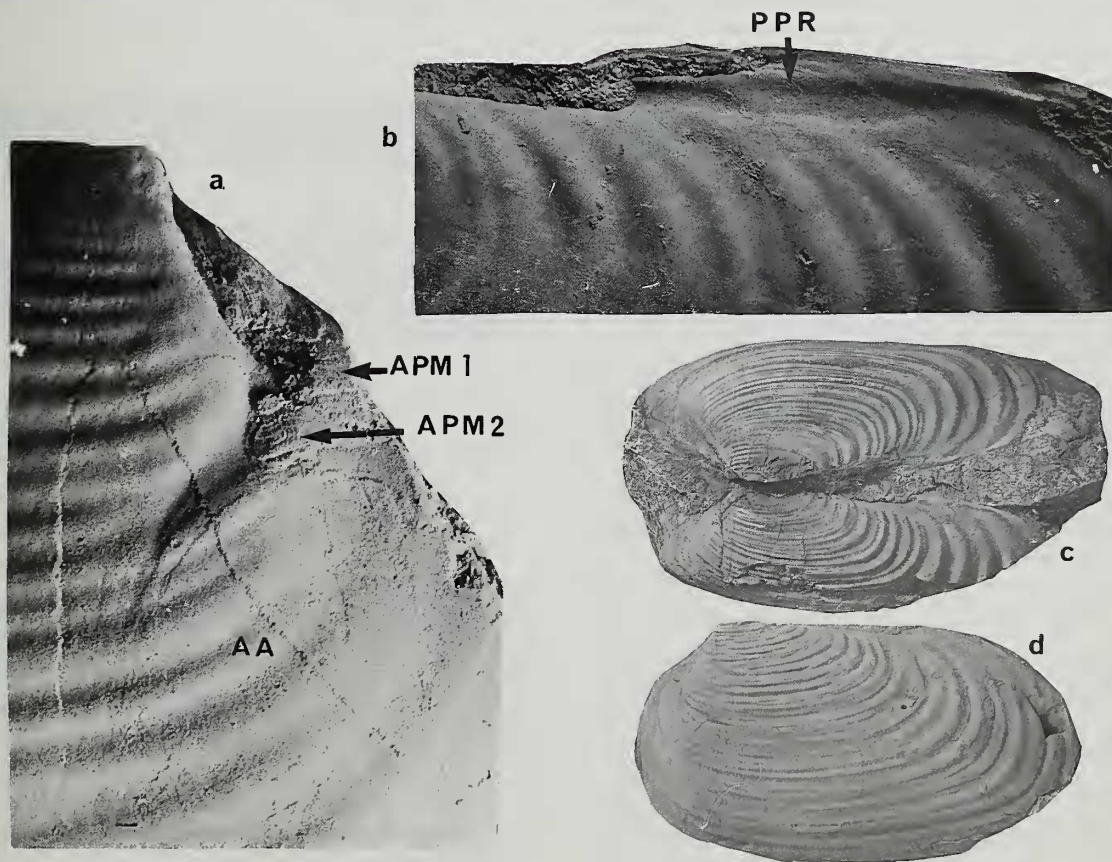


Fig. 3 *Allorisma sulcata* (Fleming). Carboniferous. Figs 3a-b, Lower Namurian, Main Limestone, Stanhope, Northumberland; BM PL5000, Trechmann Collection. Fig. 3a, anterior of right valve with anterior adductor AA, and two anterior pedal-body attachment scars APM1 and APM2; Fig. 3b, posterior dorsal area of left valve with attachment scar or posterior pedal retractor PPR. Figs 3c-d, Viséan, Ballasalla, Isle of Man; BM L45456, dorsal and side views, $\times 1$.

Sanguinolaria sulcata Phillips 1836 to be the type species of *Allorisma* by original designation of King (1844: 313). In his original description of *Allorisma*, however, King mentions several species and only in the letter of introduction to his paper does he refer to the new genus '*Allorisma* for species represented by *Sanguinolaria sulcata*. Ph'. This does not seem to represent an explicit designation of type species, whereas in 1850 King made a definite designation. Wilson (1960: 112) chose a lectotype for *Hiatella sulcata* Fleming from amongst Fleming's specimens, and presented evidence that *Sanguinolaria sulcata* Phillips 1836 should be regarded as a synonym of *Hiatella sulcata* Fleming 1828.

SYNONYMS. *Edmondiella* Chernychev, 1950: 74 (type species, *Sanguinolaria sulcata* Phillips 1836 by original designation). *Edmondia* King 1850 *pars* (1850: pl. 20, figs 1-2) (not *Edmondia* de Koninck, 1844).

DESCRIPTION. Thin-shelled, elongate oval, with umbones situated distinctly towards the front. Rather evenly rounded over the surface of the shell and lacking a distinct escutcheon or lunule. Ornament of well developed rounded rugae more or less parallel to the external margin. In internal impressions a smooth area is marked off by the anterior adductor. Has a distinct internal ridge or lamellar plate as in other Edmondiidae. Hinge lacks teeth and apparently with an external opisthodontic ligament. Anterior adductor muscle scar moderately well marked at right angles to margin in front of umbones rather than vertical. Two other separate muscle attachment marks are associated with the adductor (Fig. 3). The longer scar runs parallel to the front part of the dorsal margin and behind has a distinct buttress (clavicle). At the dorsal end of the buttress is the rounded mark of another muscle. The two smaller muscles perhaps represent the pedal protractor and retractor. The posterior adductor muscle is poorly marked but a posterior pedal retractor is visible towards the back of the dorsal margin. Delicate lines radiate from the umbones of external impressions.

REMARKS. The description is largely based on the type species. The elongate shape seems sufficient to distinguish *Allorisma* from *Edmondia*, which, in addition, commonly has lamellate shell ornament not so far recorded in *Allorisma*. Although the anterior accessory muscles are similar in *Edmondia* (Runnegar & Newell 1974) and *Allorisma*, a distinct buttress is not recorded in *Edmondia* nor the muscle impression at the dorsal end of the buttress.

[Note: *Allorisma regularis* de Verneuil (1845: 298; pl. 19, figs 6a-b; pl. 21, figs 11a-b) was attributed by de Verneuil to King out of courtesy. It was, however, never described by King but is referred to by him (King 1850: 196) as described by de Verneuil. The two specimens figured by de Verneuil represent two species. We here designate the specimen figured in de Verneuil, 1845: pl. 19, figs 6a-b as the lectotype, to safeguard the usage of Astafieva-Urbaitis (1962), who was apparently the first revising author. This specimen belongs to the genus *Wilkingia*. The other specimen (de Verneuil 1845: pl. 21, figs 12a-b) has a lamellar plate and belongs to *Allorisma* as used in this paper, and as appreciated by King in his footnote. It is here considered to be a synonym of *Allorisma sulcata*.]

Superfamily PHOLADOMYACEA King, 1844

Although the family name Pholadomyidae was used by Gray (1847: 194) (Newell 1969: N818, Runnegar 1974: 425), it was used earlier by King (1844: 315). The name Pholadomyacea is assigned by Newell (1965: 21) to Fleming (1828), but this is apparently an error because Fleming (1828: 424) referred *Pholadomya* to the Cardiadae (*sic*).

In the *Treatise*, Newell (1969) separated the Edmondiidae as a single family in the superfamily Edmondiacea, but Runnegar & Newell (1974) place the family in the Pholadomyacea. In the latter case the name Edmondiacea would become redundant, as also would Grammysiacea, the Grammysiidae being placed in the Pholadomyacea, which has priority over both names. The superfamily has thus become very broad and we have misgivings about including some Palaeozoic genera, which, although generally related to *Pholadomya*, are rather distinctive. Runnegar & Newell and our present work emphasize the significance of the lamellar plate in the Edmondiidae. We consider the muscle attachment associated with the plate would give greater stability and strength to the valves in burrowing. Apparently this feature is a long-standing one, as the lamellar plate is also developed in a Welsh Lower Devonian species, ?*Edmondia* sp. from the Tilestones at Capel Horeb (BM LL31477). We propose to emphasize the significance of this feature by recognizing the Superfamily Edmondiacea to include the Family Edmondiidae.



Fig. 4 *Solenomorpha minor* (M'Coy). Lower Carboniferous, Viséan, Yeat House Quarry, Cumberland. BM L47699, Hind Collection (figd Hind, 1904: 159; pl. 22, fig. 3); views of steinkern from the top and left side, showing anterior adductor AA, and anterior pedal retractor APR. $\times 1$.

We place the Sanguinolitidae and the Permophoridae in the Superfamily Pholadomyacea, although this is not altogether satisfactory because these two families are distinct from the rest of the superfamily. Alternatively, to separate a Superfamily Grammysiacea for these two families would seem even less satisfactory. The later representatives of *Grammysia* itself appear to be a group of round-shelled, non-siphonate species for which we can find no evidence of survival beyond the end of the Devonian. We would be reluctant to propose another superfamily without further work and review of pre-Carboniferous and post-Permian bivalve faunas, because the lineages we are discussing and using as a basis of family taxonomy occur in the Carboniferous and later faunas, and this information will allow the establishment of more satisfactory systematics.

Family SANGUINOLITIDAE Miller, 1877

SYNONYM. *Caelonotidae* M'Coy, 1855, an invalid name according to ICZN Art. 11c (not *Coelonotidae*).

REMARKS. On the basis of a better understanding of *Sanguinolites* and the assignment of species hitherto placed in *Sanguinolites* to *Myofossa*, *Pleurophorella* and *Gilbertsonia*, a more satisfactory definition of *Sanguinolites* is possible. The family contains more or less transversely elongate shells with a lunule and a distinct, flattish escutcheon. The ligament is lodged in an opisthodontic groove at the front point of the escutcheon, with a small slender nymph. Earlier, Dickens (1963) considered that the flattish elongated area (escutcheon) behind the umbones was a ligament area, but fresh work has shown that the bulk of the ligament, the spring part, is lodged in a groove at the front end of the area (Fig. 11d). It is possible, however, that the periostracal ligament was continuous with that covering the shell surface in this region and that it continued posteriorly to the distal end of the escutcheon (Yonge's (1957) fusion layer, see p. 54, discussion on hinges). Shells with granular surface spicules are found in this family. We divide the family into Subfamilies *Sanguinolitinae*, *Undulomyiinae*, *Pholadellinae*, *Alulinae*, *Chaenomyiinae* and *Vacunculinae*. The similarity of escutcheon and posterior area or corselet exhibited between the *Sanguinolitidae* and the permophorid *Pleurophorella*, which led Hind (1900) to include both in his interpretation of the genus *Sanguinolites*, has suggested to us a common origin for the two.

Subfamily SANGUINOLITINAE Miller, 1877

[*nom. trans.* herein, *ex Sanguinolitidae* Miller]

In this subfamily are placed the genera *Sanguinolites*, *Myofossa* and *Gilbertsonia* along with the several genera listed on p. 94. These forms were apparently adapted to a shallow infaunal environment. *Sanguinolites* especially retained unspecialized features. *Myofossa*, on the other hand, has characteristic features of the escutcheon which at some future time may serve as the basis for recognizing a separate subfamily. The family Permophoridae, to which *Sanguinolites* seems closely related, has specialized by the development of subumbonal hinge teeth for a shallow infaunal environment, and from time to time species became specialized for an endobysate habitat.

Genus SANGUINOLITES M'Coy, 1844: 47

TYPE SPECIES. *S. discors* M'Coy (1844: 49; pl. 8, fig. 4), subsequently designated by Stolizcka (1871: xix, 270) (= *S. angustatus* (Phillips) (1836: 208; pl. 5, fig. 2)). Hind (1900: 367) concluded that M'Coy's type of *S. discors* was a young specimen of *S. angustatus* (Phillips, 1836), and our examination of the type specimens and other material confirms that *S. discors* is a junior subjective synonym of *S. angustatus* (Phillips) 1836.

DESCRIPTION. Elongate with umbones well anterior of mid-point. Well differentiated posterior dorsal area, with three radiating ribs present. The top one delimits an elongate marked escutcheon, there is a medially placed one, and a third, running to the posterior ventral margin, delimits the area itself and also the subvertical siphonal margin. The area

is ornamented with comarginal growth laminae, some of which may form thin ribs. Ventral margin curved, flank ornamented with distinct rounded ribs separated by wider interspaces. Dorsal margin long and straight behind umbones set in a distinct escutcheon. A ligament groove extends behind the umbones, separating a slender but distinct nymph. The straight dorsal margins behind the nymph were probably joined by periostracal ligament (Fig. 6). Moderately impressed anterior adductor scar, rounded, with a deeply inset anterior pedal retractor at its dorsal umbonal edge extended more or less parallel to the anterior umbonal ridge, at about 45° to the cardinal margin and not at right angles as in the Permophoridae. No buttress visible.

Posterior adductor scar barely discerned. Pustules visible above ribs towards the anterior ventral margin in *S. costatus* Meek & Worthen 1869 (Upper Pennsylvanian, Texas). There are few records of pre-Carboniferous species of *Sanguinolites*, although we consider '*Leptodomus acutirostris* Sandberger as illustrated by Beushausen (1895: pl. 24, figs 8-10) from the L. Devonian of the Rheinland to belong here or to a very closely related genus.

Sanguinolites angustatus (Phillips, 1836) Figs 5a-d

- 1836 *Sanguinolaria angustata* Phillips: 208; pl. 5, fig. 2.
 1844 *Sanguinolites angustatus* (Phillips); M'Coy: 48.
 1844 *Sanguinolites discors* M'Coy: 49; pl. 8, fig. 4.
 1900 *Sanguinolites angustatus* (Phillips); Hind: 366-8; pl. 40, figs 1-6.
 ?1910 *Sanguinolites simulans* Girty: 224.
 ?1969 *Sanguinolites simulans* Girty; Pojeta: 16; pl. 3, figs 3-5.

TYPES. BM PL4272, the lectotype of *Sanguinolaria angustata* Phillips, from 'Bolland', Yorkshire/Lancashire border, Lower Carboniferous, Viséan. National Museum of Ireland, the lectotype (selected herein) of *Sanguinolites discors* M'Coy (1844: pl. 5, fig. 2). USNM 155895 is the holotype of *Sanguinolites simulans* Girty; Pojeta (1969: 16) stated that this is the only original specimen of Girty.

OTHER MATERIAL. BM 97184 and BM L47471, 2 paralectotypes of *S. angustata* from Poolvash, Isle of Man. BM 52029 from Clifton, near Bristol. One paralectotype (Nat. Mus. Ireland, not numbered) of *Sanguinolites discors*, from the Arenaceous Shales at Bruckless, Dunkinelly, N.W. Ireland.

REMARKS. We have examined and refigured (Fig. 5c) Phillips' type specimen of *Sanguinolaria? angustata* and M'Coy's type specimen of *Sanguinolites discors*. Our examination confirms the conclusion of Hind (1900: 366) that *S. discors* is a synonym of *S. angustatus*.

Sanguinolites costatus (Meek & Worthen, 1869) Fig. 6

- 1869 *Allorisma costata* Meek & Worthen: 171.
 1873 *Allorisma costata* Meek & Worthen; Meek: 585-6; pl. 26, fig. 15.

MATERIAL EXAMINED. USNM 1506, two specimens from the Upper Carboniferous, Pennsylvanian Cisco Formation, near Jacksboro, Texas.

REMARKS. This Upper Carboniferous species is very similar to *S. angustatus* in both shape and sculpture. It may be distinguished by its wider-spaced comarginal ribs. Small numbers

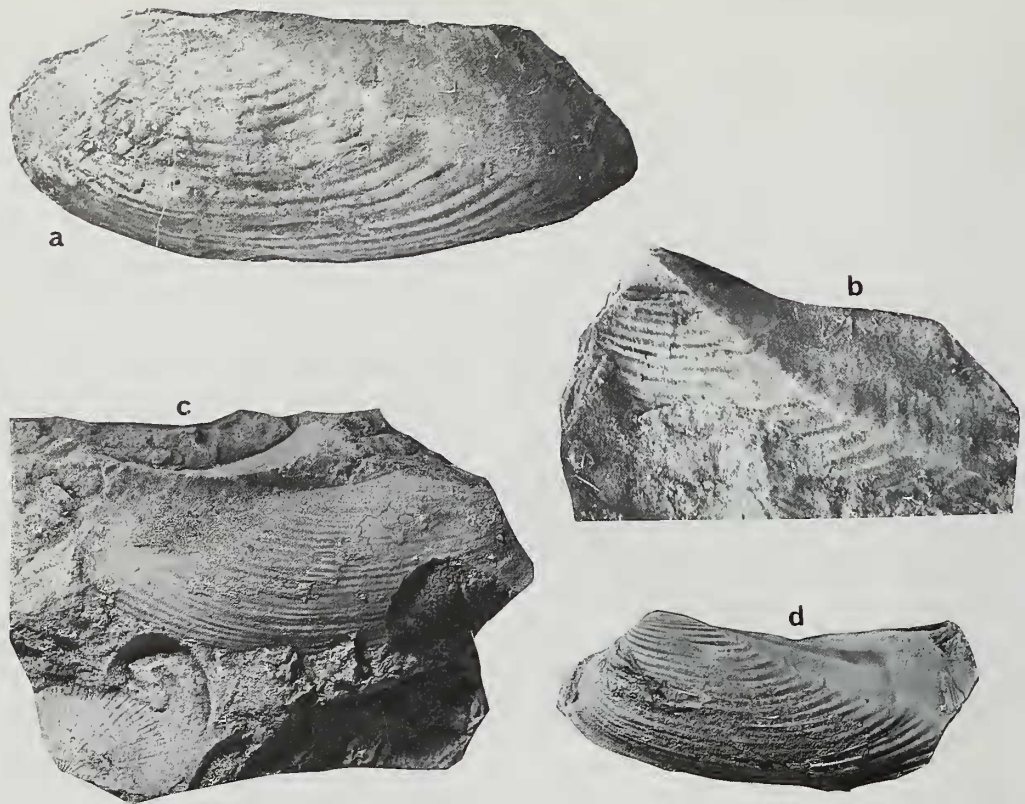


Fig. 5 *Sanguinolites angustatus* (Phillips). Figs 5a–b, Arenaceous shale, Bruckless, Dunkineely, County Donegal, Ireland: NMI, Griffiths Collection; Fig. 5a, **lectotype** (selected herein), and Fig. 5b, **paralectotype** (on same piece of rock), of *S. discors* M'Coy, both $\times 3$. Fig. 5c, Lower Carboniferous, Viséan, Bolland, Yorkshire; BM PL4272, Gilbertson Collection, **lectotype** of *Sanguinolites angustatus*, side view, $\times 1.5$. Fig. 5d, Lower Carboniferous, Clifton, Bristol; BM 52029, $\times 1.3$.



Fig. 6 *Sanguinolites costatus* Meek & Worthen. Locality *24827, Upper Carboniferous, Pennsylvanian, Cisco Formation, near Jacksboro, Texas; USNM Dr* 1506, Renfro Collection; Fig. 6a, top view; Fig. 6b, oblique dorsal view; Fig. 6c, slightly oblique view of left side showing the ligament nymph of the right valve; all approx. $\times 2$.

of periostracal spicules were observed on the lower anterior part of the flank below the comarginal ribs. Our interpretation of this is that their function of maintaining the position of the shell in the sediment had been taken over by the comarginal ribs. The value of this species relates to its ligament attachment area being unequivocally well preserved. It has relatively long, low, slender nymphs separated from the outer escutcheon surface by a deep ligament groove.

?*Sanguinolites argutus* (Phillips, 1836) Figs 7a–b

1836 *Cucullaea arguta* Phillips: 210; pl. 5, fig. 20.

1897 *Cucullaea arguta* Phillips; Hind: 174.

1900 *Sanguinolites argutus* (Phillips) Hind: 368–9; pl. 40, figs 15–16.

HOLOTYPE. BM 97155, Lower Carboniferous, Viséan, 'Bolland', Yorkshire/Lancashire Border, England; Gilbertson Collection.

DISCUSSION. ?*Sanguinolites argutus* is a much more tumid shell than *S. angustatus*. The posterior area or corselet is marked by a very sharp angularity, almost a carina; this leaves the area diverging from the plane of commissure at a fairly high angle until it approaches the siphonal margins. Hind described this species as one of the rarest in the Carboniferous. It may, however, prove to be an important species because it resembles *Myonia carinata* from the Permian of eastern Australia in its morphology. As yet we are uncertain whether this is due to convergence or whether it indicates a natural relationship.

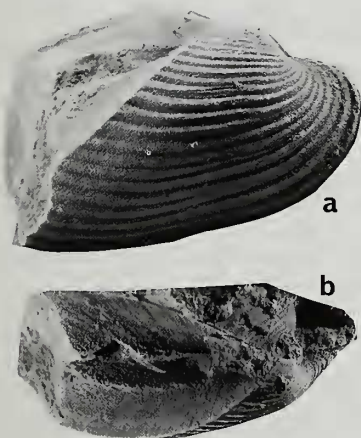


Fig. 7 *Sanguinolites argutus* (Phillips). Lower Carboniferous, Viséan, Bolland, Yorkshire, England; BM 97155, Gilbertson Collection, holotype; Fig. 7a, right side, Fig. 7b, dorsal view; both $\times 3$.

Genus *MYOFOSSA* Waterhouse, 1969b

TYPE SPECIES. *Myonia subarbitrata* Dickins, 1963 (p. 48; pl. 5, figs 2–12) by original designation.

REMARKS. In attempting to decide on the correct generic name for this taxon we have considered the following nominal genera in addition to *Myofossa*:

Sedgwickia M'Coy, 1844, type species *S. attenuata* M'Coy, 1844, by subsequent designation of Stoliczka, 1871 (Fig. 8).

Palaeocorbula Cowper Reed, 1932, type species *P. difficilis* Cowper Reed, 1932, by monotypy (Fig. 15).

Grammysiopsis Chernychev, 1950, type species *Grammysiopsis irregularis* Chernychev, 1950, by original designation.

Ragozinia Muromzeva 1984; type species, *Ragozinia dembskajae* Muromzeva & Guskov in Muromzeva, 1984, by original designation.

DISCUSSION. The type specimen of *Sedgwickia attenuata* M'Coy (1844: 62; pl. 11, fig. 39; refigured by Hind, 1899: pl. 27, fig. 8) has been kindly lent by Dr Colm E. O'Riordan, formerly of the Natural History Division of the National Museum of Ireland, Dublin. It is refigured here (Fig. 8). *S. attenuata* is the type species of *Sedgwickia* by subsequent designation of Stoliczka (1871: xix, 271); Chernychev's (1950: 33) designation of *Sedgwickia gigantea* M'Coy is invalid. The generic name was used by Hind (1899) and Runnegar (1974: 932), and the species to which Runnegar refers are included here in *Myofossa*. However, Hind included a variety of species, including some that we would ascribe to the trigoniacean family Schizodidae. We are unable to interpret the type species, *S. attenuata*, from its holotype (Fig. 8), which is small and badly crushed. The ribbing is poorly preserved and there are no details of the hinge or musculature. In particular the characteristic form of the escutcheon which would allow us to refer it in the present genus is absent or not preserved. Recollecting from the type locality might show that M'Coy's species is a synonym of *Sanguinolites variabilis* M'Coy of Hind (not *Cosmomya variabilis* (M'Coy)). This species is described here as *Myofossa hindi* sp. nov. With the present state of knowledge the binomen *Sedgwickia attenuata* M'Coy, 1844 should be rejected as a *nomen dubium*.



Fig. 8 '*Sedgwickia attenuata*' M'Coy (*nomen dubium*). Lower Viséan, Arenaceous Shale [of Yellow Sandstone Group], River Bannagh, Drumcurren (near Kesh, County Fermanagh), Northern Ireland; NMI, Griffiths Collection, holotype; view of crushed composite mould of left valve, $\times 3$.

Chernychev (1950) included two species in his new genus *Grammysiopsis*: the type species, *G. difficilis*, and *G. kazakhstanensis* n. sp. His own '*Grammysioides*' *welleroides* (Chernychev, 1950: pl. 7, fig. 68 only) may be a synonym of the latter. His type species is rather poorly illustrated and we were unable to say with certainty whether this is a *Myofossa*. The peculiar grouping and turning of the comarginal ribs towards the posterior area suggest to us that this should be

considered as a separate genus, at present not described outside the USSR. However, the second species, *G. kazakhstanensis* (Cherychev, 1950: pl. 6, figs 53a–d, 54a–b) is almost identical to *Myofossa hindi* described here. Other species doubtfully included by Chernychev, *G. donaica* and *G. obscura*, may be synonyms of *Cosmomya variabilis* (M'Coy). The problem appears to have been solved by Muromzeva (1974), who illustrated a number of species of *Grammysiopsis*, ranging from the Viséan to the Carboniferous–Permian boundary, that have the same characteristic twist to the ribs as Chernychev's type species. From this material from Kazakhstan and the Soviet Arctic we can see that *Grammysiopsis* may be easily distinguished from *Myofossa* by the enormous size of its posterior gape. *Grammysiopsis* appears to be a distinct offshoot of *Myofossa* which has developed much more substantial siphons, presumably of type 'C', that has so far not been recognized outside the Soviet Union.

Cowper Reed's (1932) genus *Palaeocorbula* is based on a single specimen (Figs 14a–c). It is smaller than most species of *Myofossa* and shows no sign of the posterior attenuation. This marked difference in shape leads us to accept it as a distinct genus. It is possible, however, that the specimen is deformed and the similar pattern of ribbing on the anterior and central part of the flank may necessitate the future synonymizing of the two taxa when more material becomes available.

SUBDIVISIONS OF *Myofossa*. At present we recognize two subgenera of *Myofossa*: *Myofossa* s. str. and *Ragozinia*. Species of *Myofossa* from the British Lower Carboniferous have been described as *Sanguinolites* by Hind (1900). All species of *Myofossa* are more convex, relatively shorter and do not have the distinctly delimited and sculptured coelete possessed by *Sanguinolites*. Driscoll (1965) included the species *Myofossa omaliana* (de Koninck), which occurs in both NW Europe and the U.S.A., in *Grammysia*. However, the latter genus has a less attenuate posterior shell, a less well defined siphonal area, usually no gape and a completely simple pallial line.

DIAGNOSIS. Oval in shape. Distinguished mainly by the features of the escutcheon. This consists of an internal heart-shaped area in which the ligament is lodged in a groove immediately below the umbo; in turn this is bound externally by a distinctly marked-off escutcheon which is again bounded externally by the umbonal ridge. Shell generally gaping at the rear with a more or less well developed sulcus running from the umbo towards the mid-part of the ventral margin. Flank usually bearing distinct, low, comarginal ribs, often fewer in number in a distinct anterior area, and more on the main part of the flank.

REMARKS. A number of Carboniferous species share the characteristic features of *Myofossa*. The Carboniferous species have a small ligament nymph, but this hardly seems sufficient to place them in a different genus. They include *Sanguinolites omalianus* de Koninck, 1842, *S. costellatus* M'Coy, 1851a, and *Myofossa hindi*, which can be distinguished from *Sanguinolites* proper, as well as some other genera, by their more oval shape. From other Megadesmidae and Edmondiidae they are distinguished by the distinctive features of their escutcheon.

During the course of this work we first thought that *Myofossa* might be placed with the Megadesmidae. However, the nature of the escutcheon and the persistence of this

feature in bivalves from the middle of the Palaeozoic to the Mesozoic has caused us to regard this feature as of considerable importance. We have, therefore, assigned *Myofossa* to the Sanguinolitidae which have similar characteristics of the escutcheon.

Species of *Myofossa* have a variety of shell form comparable with living species of *Laternula* Röding, 1798. At present it does not seem to us that the earlier species of the Laternulidae and the Thraciacea as a whole are derived from them; we consider it more likely that the similarity between Upper Palaeozoic *Myofossa* and Recent Laternulidae is a matter of partial convergence.

Subgenus **MYOFFOSSA** (**MYOFFOSSA**)

Myofossa (**Myofossa**) **subarbitrata** (Dickins, 1963)

Figs 9a–f

1963 *Myonia subarbitrata* Dickins: 48–9; pl. 5, figs 2–12, 22.

1969b *Myofossa subarbitrata* (Dickins) Waterhouse: 32, 66.

MATERIAL. The type material from the Lower Permian, Nura Nura Member of the Poole Sandstone Formation, of the Canning Basin, Western Australia, all in the Bureau of Mineral Resources and Mines, Canberra, Australia.

DISCUSSION. New illustrations are given here (Figs 9a–f) to show the striking similarity between the present species and British Carboniferous species of *Myofossa*.

Myofossa (**Myofossa**) **hindi** sp. nov.

Figs 10a–e

1851a *Sanguinolites variabilis* M'Coy: 174 (pars).

1855 *Sanguinolites variabilis* M'Coy; M'Coy: 508; pl. 3f, fig. 7 only.

1900 *Sanguinolites variabilis* M'Coy; Hind: 379; pl. 44, figs 3–8 only.

?1900 *Sanguinolites variabilis* M'Coy; Hind: 379; pl. 44, fig. 1 only.

?1900 *Sanguinolites v-scriptus* Hind: 382; pl. 42, figs 5, 5a only.

HOLOTYPE. BM L47511, from the Viséan Redesdale Ironstone (Figs 10a–d) (also figured by Hind, 1900: pl. 44, fig. 3.)

PARATYPES. BM L47512–47516, the specimens figured by Hind (1900: pl. 44, figs 4, 4a, 5, 6, 7 & 8) and BM L3231 (Fig. 10e here), all from the Redesdale Ironstone; Sedgwick Museum, Cambridge, the type of M'Coy's ovate variety of *Sanguinolites variabilis*, from the Carboniferous Limestone of Lowick, Northumberland.

DIAGNOSIS. Broadest towards front part of shell, fairly evenly rounded from front to back, not tumid. Umbones not especially raised above dorsal part of shell. Carina rounded. Rapid increase in number of ribs towards the rear along line of greatest tumidity.

DESCRIPTION. Features of the genus are well shown in the material from the Redesdale Ironstone. The lunule and the escutcheon are distinct. A groove is present on either side of the carina outside of which there is an area between the groove and the rounded carina which has ribs less well developed than in front of the carina. The posterior has a

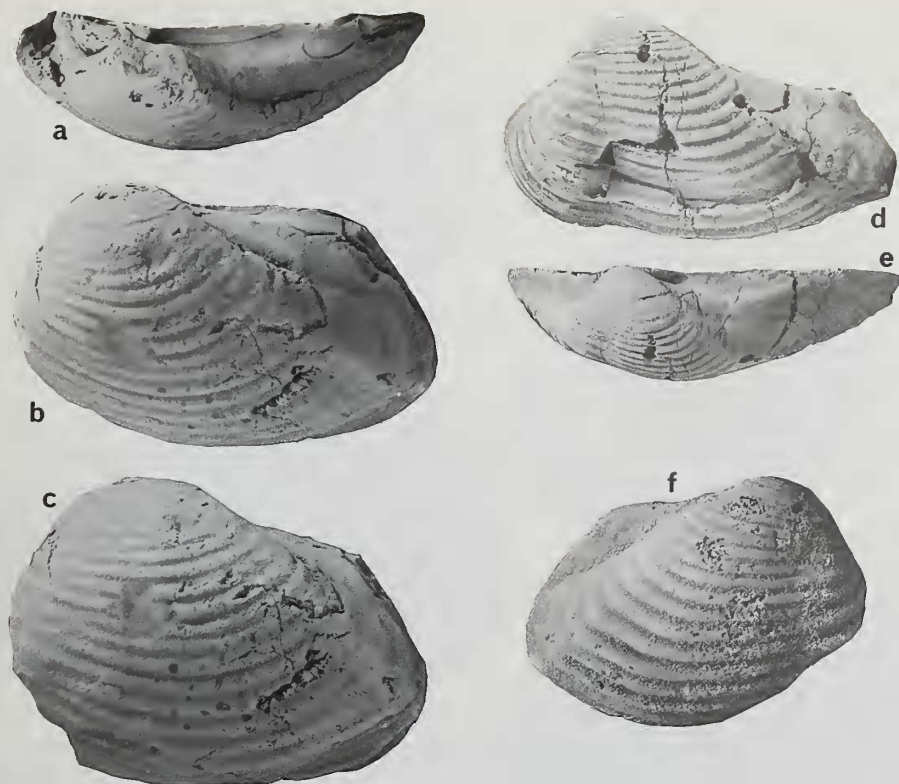


Fig. 9 *Myofossa (Myofossa) subarbitrata* (Dickins). Lower Permian, Nura Nura Member of Poole Sandstone Formation, 1.6 miles SW of Paradise Homestead, Canning Basin, Western Australia. Figs 9a-c, BMR CPC 3885, holotype; Fig. 9a, top view; Fig. 9b, oblique view showing siphonal area; Fig. 9c, view of left side; all $\times 3$. Figs 9d-e, BMR CPC 3886, paratype A; Fig. 9d, view of left valve; Fig. 9e, top view; both $\times 2$. Fig. 9f, BMR CPC 3887, paratype B, side view showing slight subumbonal sulcus, $\times 3$.

significant gape. A narrow ligament groove is shown behind the umbo in BM L47314 and the hinge appears to be edentulous. The ribbing is distinctive. In the holotype, 16 ribs can be counted in the front part of the shell which are more or less concentric. The rib number increases rapidly by interpolation and 39 are present in the most tumid part of the shell; some of the added ribs make a distinct Y-like bifurcation with ribs at the front. A rounded posterior adductor muscle scar is shown in BM L3231 and the back part of the pallial line has a shallow sinus.

BM L47515, from Redesdale, has a well-preserved short nymph with a narrow, lunate ligament groove separating it from the escutcheon. Its inner surface is juxtaposed to the other nymph and does not project inwards from the remaining part of the posterior dorsal shell margin.

REMARKS. Hind (1900: 381) recognized that M'Coy (1851a: 174; 1855: 508; pl. 3f, figs 6, 6a, 7, 7a) had included two distinct shells in *Sanguinolites variabilis*. Elsewhere (p. 69) we have pointed out that the specimen in M'Coy, 1855: pl. 3f, fig. 5, 6a, is the lectotype of *Cosmomya variabilis* (M'Coy), selected by Hind (1900), and a new name is now required for the other specimen. Driscoll (1965: 91) included this species as a synonym of *Myofossa [Grammysia] omaliana* (de Koninck) in his redescription of that species. However, although *Myofossa hindi* has a similar shape to *M. omaliana*, the ornament, particularly the density and style of splitting of the ribs, is quite distinctive. Both species occur in the British Isles, but in rather different lithologies and apparently never together.

M. hindi is known only from the Carboniferous Limestone at Lowick and from the shell band in the Redesdale Ironstone, D₂ Zone, both in Northumberland. *M. omaliana*, on the other hand, occurs in Viséan limestone in Kildare and Limerick, commonly at Thorpe Cloud, Derbyshire, and in the lowest Namurian Great Limestone at Stanhope, Northumberland.

Myofossa (Myofossa) omaliana (de Koninck, 1842)

Figs 11a-d

- 1842 *Pholadomia omaliana* de Koninck: 65; pl. 5, fig. 4a-b.
 1885 *Chaenomys omaliana* (de Koninck); de Koninck: 6; pl. 1, figs 12-15.
 1900 *Sanguinolites omalianus* (de Koninck); Hind: 372-4; pl. 40, figs 17-24.

TYPE MATERIAL. Not seen, lent to de Koninck by M. Puy, from 'l'argile de Tournay', Tournaisian, Belgium.

REMARKS. This seems to be a very widespread species, occurring throughout the Lower Carboniferous and the base of the Upper Carboniferous, in Belgium, the British Isles and the United States. It has been extensively discussed by Driscoll (1965), but does not include *Sanguinolites variabilis* M'Coy, *pars* (= *Myofossa hindi* sp. nov.), see above.

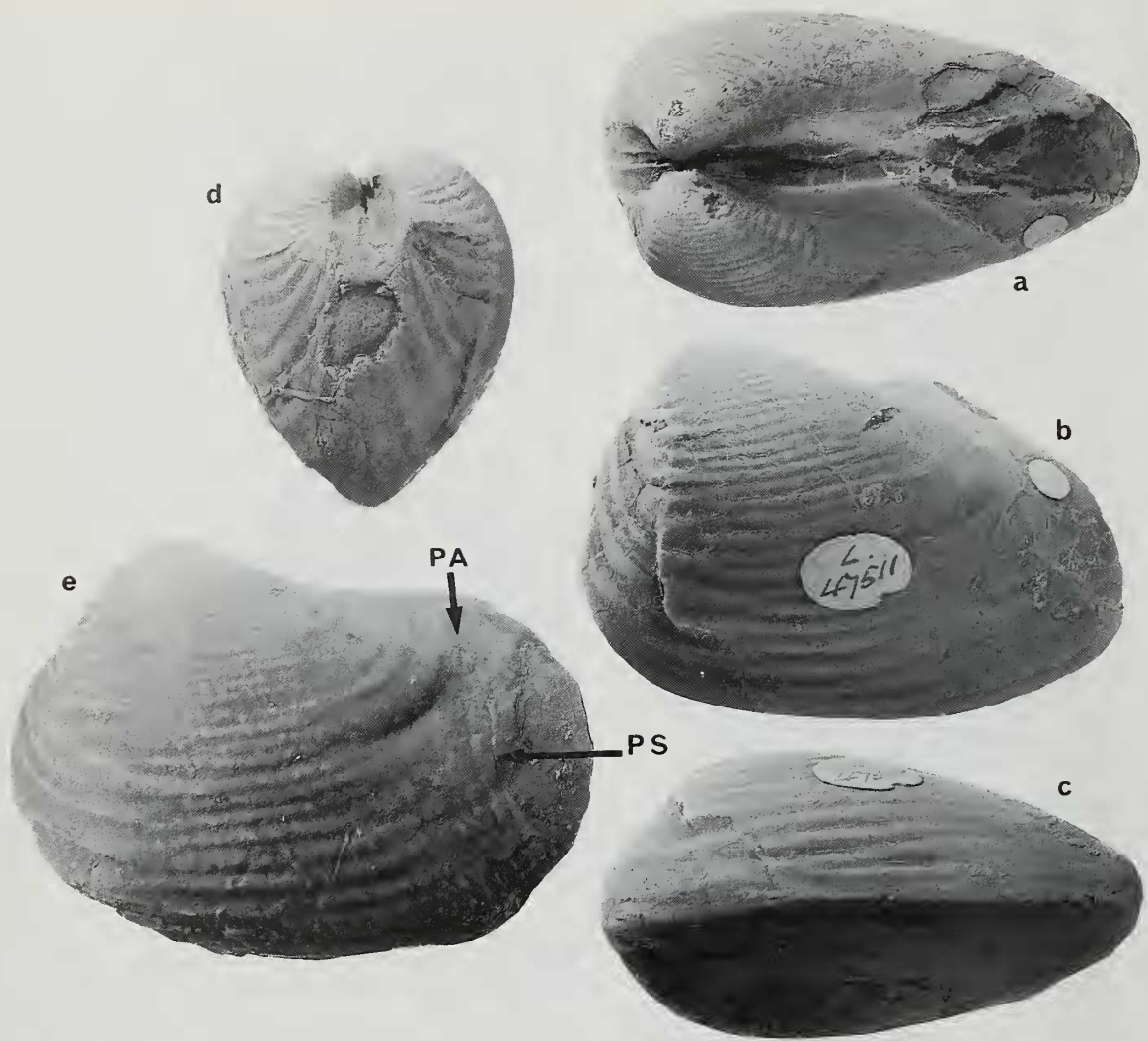


Fig. 10 *Myofossa hindi* sp. nov. Lower Carboniferous, Viséan, Asbian, Redesdale Ironstone, Redesdale, Northumberland. Figs 10a–d, BM L47511, holotype, bivalved specimen (Hind, 1900: pl. 44, fig. 3); Fig. 10a, dorsal view; Fig. 10b, view of left side; Fig. 10c, ventral view; Fig. 10d, anterior view. Fig. 10e, BM L3231, paratype, view of left valve of steinkern; PA — posterior adductor, PS — pallial sinus. All $\times 2$.

***Myofossa (Myofossa) costellata* (M'Coy, 1851)**

Figs 1, 12a–d

- 1851a *Leptodomus costellatus* M'Coy: 174.
 1855 *Leptodomus costellatus* M'Coy; M'Coy: 508; pl. 3f, fig. 5.
 1900 *Sanguinolites costellatus* M'Coy; Hind: 377–9; pl. 41, figs 8–10.

SYNTYPES. SM E13273 (M'Coy, 1855: pl. 3f, fig. 5), and four unfigured syntypes, SM E9319–22, all from the Lower Limestone Series (Viséan) of Craige, Kilmarnock, Ayrshire, Scotland.

REMARKS ON NOMENCLATURE. *Myofossa costellata* is a junior secondary homonym of *Sanguinolites costellatus* M'Coy, 1844, considered by Hind (1900: 379) to be the posterior end of an internal cast of *Solemya costellata*.

DISCUSSION. *Myofossa costellata* is evenly ribbed, and has 50% more ribs per unit distance from the umbones than *M.*

hindi. Like *M. hindi*, it also occurs in very fine-grained facies. It is more elongate than the other species described here. It has not been found to occur with either *M. omaliana* or *M. hindi*. The fine ribbing recalls that of *Ragozinia*, but it does not have the smoother sub-umbonal part of the flank.

Subgenus **RAGOZINIA** Muromzeva, 1984

TYPE SPECIES. *Myofossa (Ragozinia) dembskajae* (Muromzeva & Guskov, in Muromzeva 1984) (? = *Myofossa (Ragozinia) amatopensis* (Thomas, 1928)).

***Myofossa (Ragozinia) amatopensis* (Thomas, 1928)**

Figs 13a–e

- 1928 ?*Sanguinolites amatopensis* Thomas: 224–5; pl. 6, figs 10, 10a.
 1963 *Chaenomya* sp. Dickins: 51; pl. 8, figs 12–16.

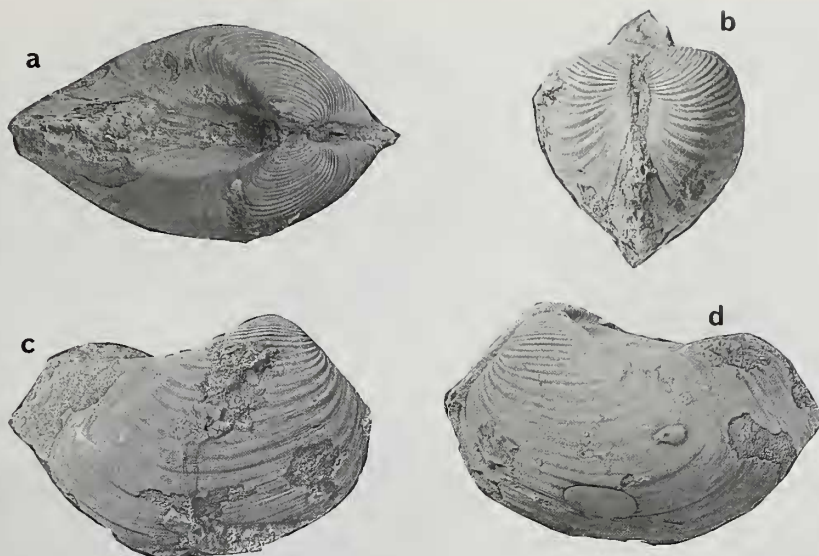


Fig. 11 *Myofossa omaliana* (de Koninck). Lower Carboniferous, Kildare, Ireland; BM 26327; Fig. 11a, top view; Fig. 11b, anterior view; Fig. 11c, view of right side; Fig. 11d, view of left side. All $\times 1$.

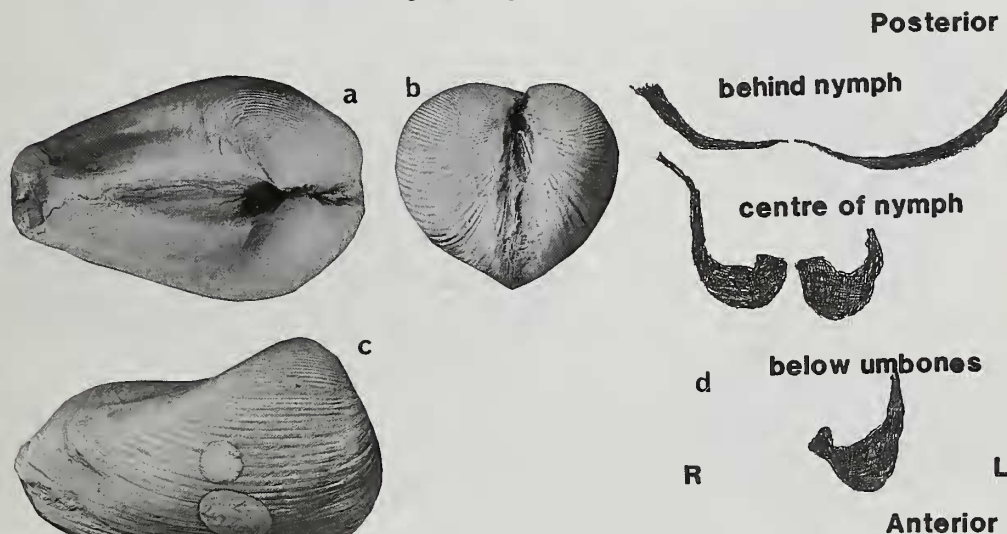


Fig. 12 *Myofossa costellata* (M'Coy). Lower Limestone Shale, Lower Carboniferous, Gurdy railway cutting, Gurdy, near Beith, Ayrshire, Scotland; BM L47489; Fig. 12a, top view; Fig. 12b, anterior view; Fig. 12c, view of right side; all $\times 1.25$. Fig. 12d, BM L46425, transverse sections through ligament nymph, with detached nymph of right valve re-orientated to original position; approx. $\times 13$; see also Fig. 1.

- ?1976 *Myonia* (*Myonia*) *gorskyi* Astafieva-Urbaitis: 32; pl. 3, fig. 5.
 f. 1984 *Ragozinia gorskyi* (Astafieva-Urbaitis); Muromzeva: 113-14; pl. 41, figs 6-8.
 ?1984 *Ragozinia dembskajae* Muromzeva & Guskov, in Muromzeva: 114; pl. 41, figs 2, 4, 5.

HOLOTYPE. SM A4971, from the 'Goniatite Bed', Parinas Quebrada, Peru, Permian (not Upper Carboniferous as interpreted by Thomas); Barrington-Brown collection. The type material of this species was apparently mistakenly associated with Pennsylvanian ammonoids when collected.

OTHER MATERIAL. BM L9448, Irwin District, Perth Basin, Western Australia, no horizon recorded, but almost certainly

Fossil Cliff Formation, Late Sakmarian; University of Western Australia, type no. 45374 (Dickins 1963: pl. 8, figs 12-13), from the Fossil Cliff Formation, Fossil Cliff, Perth Basin; Commonwealth Palaeontological Collection (C.P.C.) No. 3881, from the Callytharra Formation, Carnarvon Basin; C.P.C. No. 3882, from the Nura Nura Member of the Canning Basin. These are all thought to be of Lower Permian, Late Sakmarian age.

DIMENSIONS. BM L9498: length 84mm, height 48mm, width (two valves) 35mm, gape c. 9mm.

DISCUSSION. During reorganization of the collections at the British Museum (Natural History) BM L9498 was found with Mesozoic specimens. It was recognized as specifically identical

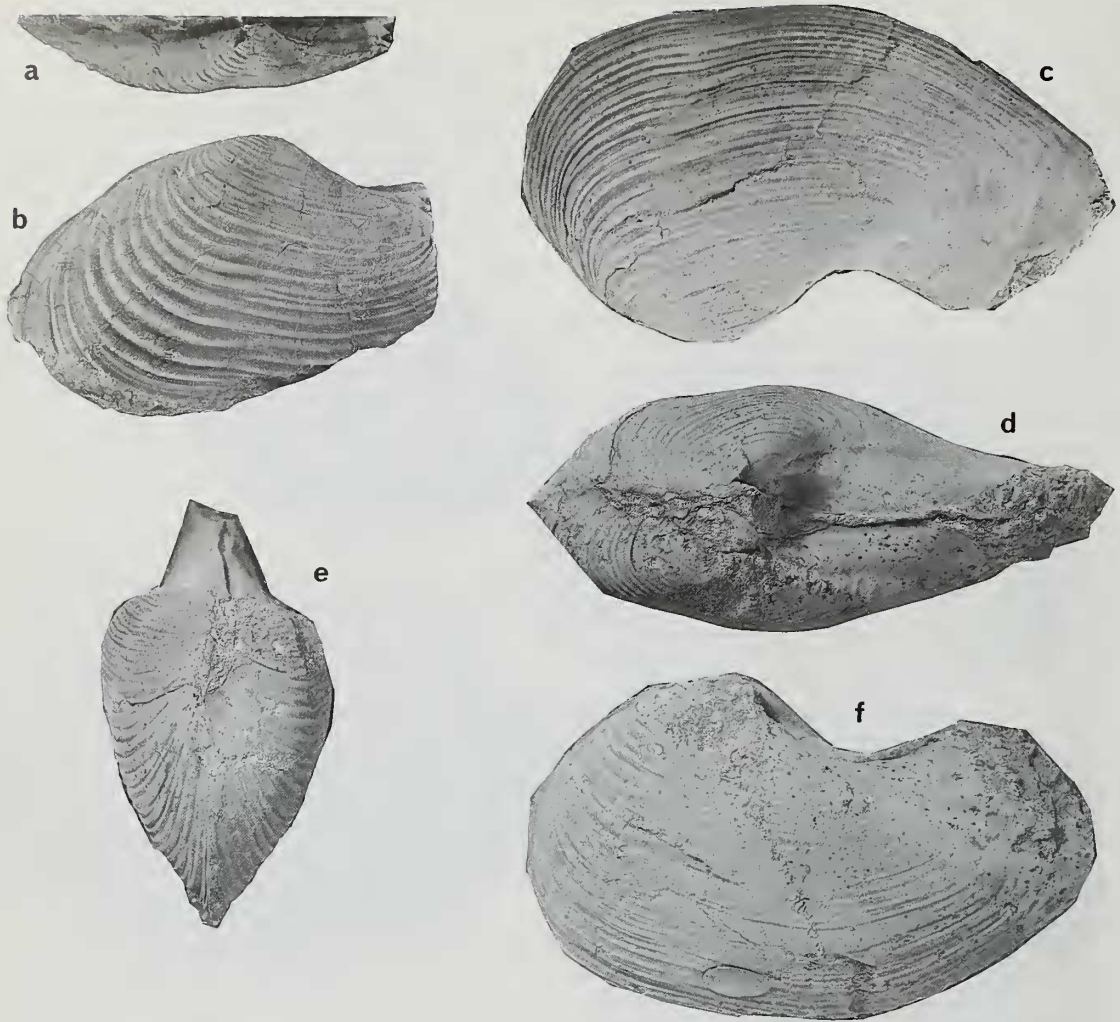


Fig. 13 *Myofossa (Ragozinia) amatopensis* (Thomas). Figs 13a–b, Permian, 'Goniatite' bed, Parinas Quebrada, Amatope Mountains, north-west Peru; SM A4971, Barrington Brown Collection, holotype; Fig. 13a, top view; Fig. 13b, left side. Figs 13c–f, Lower Permian, Sakmarian, Fossil Cliff Formation, Irwin District, Western Australia; BM L9498; Fig. 13c, right side; Fig. 13d, top view; Fig. 13e, anterior view; Fig. 13f, left side. All $\times 1$.

with the specimens described by Dickins and there is now adequate material to indicate that this is a very widespread species. The matrix of the newly discovered Australian specimen, BM L9498, is that of the Fossil Cliff Formation. The label with the specimen reads 'Irwin District, Western Australia. Presented H. P. Woodward, May 1892'. The specimen apparently came from Fossil Cliff.

Although Runnegar (1969: 285) has suggested this species belongs to *Australomya*, the features of the escutcheon show that it belongs to *Myofossa*. When we compared the Australian material with Thomas' Peruvian holotype we were unable to find any significant differences. The Western Australian specimens and the holotype show considerable similarity to the Carboniferous species assigned in this paper to *Myofossa*, and especially to *S. (Ragozinia) gorskyi* from the Kungurian of the USSR, though the specimens from Western Australia are rather larger. Muromzeva (1984) distinguished a separate species, *M. (R.) dembskajae*, which had a much more attenuated posterior. We have not been able to examine any

of her material, but we suspect the differences may be due to crushing. The posterior part of the shell, however, is more upturned in *M. (R.) amatopensis* than in the Carboniferous species, probably reflecting adaptation to deeper burrowing. *M. (R.) amatopensis* differs from its contemporary, *M. subarbitrata*, in lacking a concave anterior margin, its much finer ribbing and in being upturned at the back.

Myofossa sp. subgenus undetermined

Fig. 14

MATERIAL. USNM Ass 161469, Graham (top of Jacksboro), Old Gunter Road, 0.5 miles south of Texas 24, 5 miles NE of Jacksboro, Texas. USNM DR II 1506, Renfro Collection, loc. 1506, similar horizon, Upper Pennsylvanian, Texas.

DESCRIPTION. This apparently undescribed species has sculpture of the same general pattern as *Myofossa*, s. str., but much more exaggerated. There is an anterior field of prominent comarginal ribs with obvious radiating pustulose striae.

These striae are more randomly arranged within the ill-defined lunule, which is terminated at the sub-umbonal sulcus where it meets the ventral margin anterior to the umbones at a distinct sinus in the shell margins. The larger, main area of the flank is an area of low comarginal ribs and radial striae. These pustulose radial striae stop abruptly at the posterior area, which has strong transverse ridges parallel to the siphonal margins. There is no carina to the escutcheon which has periostracal creases on the shell surface and an ill-defined lunule.

REMARKS. *Myofossa* sp. has a wider central field of comarginal ribs, extending well anterior to the umbones, than *Grammysiopsis maria* (Worthen; Runnegar 1974: pl. 3, figs 1, 2, 11). The species may eventually prove to belong to *Grammysiopsis*.

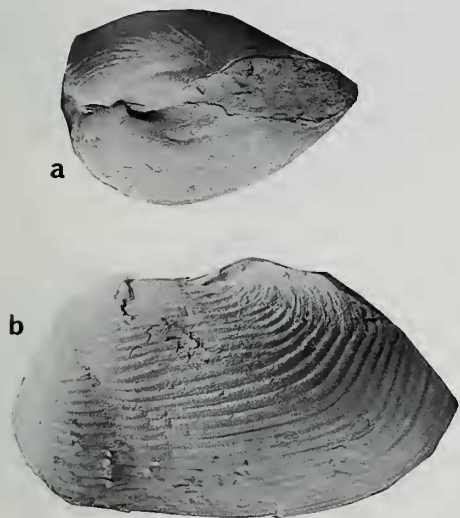


Fig. 14 *Myofossa* sp. nov. Upper Pennsylvanian, Graham Formation (top of Jacksboro Member), Old Gunter Road, 0.5 mile south of Texas 24, 5 miles NE of Jacksboro, Texas; USNM Ass 161469; Fig. 14a, top view, with posterior end tilted upwards; Fig. 14b, left side; both $\times 1.7$.

Genus *PALAEOCORBULA* Cowper Reed, 1932

Figs 15a-c

TYPE SPECIES. *Palaeocorbula difficilis* (Cowper Reed, 1932), by monotypy.

DISCUSSION. There are strong similarities between the shape and sculpture of *Myofossa* and *Palaeocorbula*. This latter genus is based on a single specimen of *P. difficilis* from Middle Horizon One, of the Lower Permian Agglomerate Slates of Kashmir. The specimen is housed in the collections of the Geological Survey of India, Calcutta; we have been kindly supplied with photographs of the type by S. C. Shah, Director of Palaeontology and Stratigraphy at the Geological Survey of India, which are reproduced here (Fig. 15). In our interpretation the short, coarse comarginal ribs are anterior and they bifurcate at a short distance from the anterior margin, in a similar manner to most other species of *Myofossa*. The posterior siphonal area is nearly smooth. In the holotype the valves are mutually displaced and much of the corselet of

the two valves is apparently missing (Fig. 15). It appears to us that the posterior of the left valve has been somewhat foreshortened by diagenetic or tectonic deformation. These vagaries of preservation apparently led Cowper Reed to interpret the animal as inequivalve and place the genus in the Corbulidae. It is the strong similarity in style of ribbing between *Palaeocorbula* and *Myofossa subarbitrata* (Fig. 9), and a number of other species belonging to the genus, that allows us to interpret *Palaeocorbula* as a close relative of *Myofossa*.

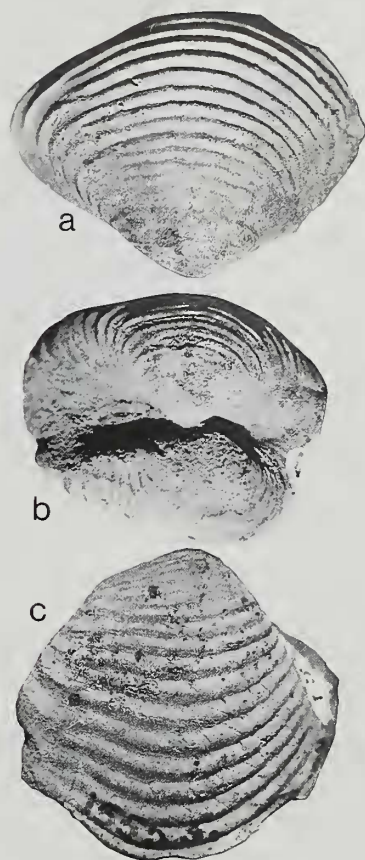


Fig. 15 *Palaeocorbula difficilis* (Cowper Reed). Upper Permian, Kashmir, India; GSI 15553, holotype; Fig. 15a, right side; Fig. 15b, top view; Fig. 15c, left side; all $\times 1.5$.

Genus *COSMOMYA* Holdhaus, 1913

TYPE SPECIES. *Cosmomya egraria* Holdhaus (1913: 446; pl. 94, fig. 3a-c), by monotypy. A plaster cast of the type specimen in the GSI has been figured by Dickins & Shah (1965: pl. 17, fig. 13-14).

SYNONYMY. *Palaeocosmomya* Fletcher, 1946 (type species, *P. teichertii* Fletcher, 1946 by original designation (? = *Cosmomya egraria* Holdhaus, 1913; ? = *Cosmomya artiensis* (Krotova, 1885: 255; pl. 3, fig. 20)).

DISCUSSION. The relationship between *Cosmomya* and *Palaeocosmomya* has been discussed by Dickins & Shah (1965). At that time the family relationships of the genus were obscure but the early species from the British Lower

Carboniferous, particularly the material in the British Museum (Natural History) described by Hind (1900) as *Sanguinolites v-scriptus*, show a transition between early species of *Myofossa* to *Cosmomya* by the gradual acquisition of typical eccentric zig-zagging ribs. This has led us to place *Cosmomya* in the Sanguinolitidae. *Cosmomya* differs from *Grammysiopsis* Chernychev, 1950 and *Pentagrammysia* Chernychev, 1950 by the position of these ribs, and it differs from *Praeundulomya* Dickens, 1957, by the shell shape and by lacking the posterior elongate shell thickenings that run close to the hinge in that genus. *Pentagrammysia*, a genus that has developed the ribbing style of the Mesozoic genus *Goniomya* independently, seems to have evolved in central or eastern Asia separately from *Cosmomya*, but we suggest that it also has common ancestry with a species of *Myofossa*. Several species of *Pentagrammysia* are illustrated in Muromzeva's publications (particularly 1974: pls 21–23). In the British species described below, ascending stratigraphical position reflects increasing complexity of ribbing pattern. Early species of the Mesozoic genus *Goniomya* differ from the type species of *Cosmomya*, *Pentagrammysia* and *Siphogrammysia* in having a sub-umbonal V in the ribbing which slopes downwards and backwards, and is horizontally truncated at least in the umbonal area. We have not been able to decide whether *Goniomya* is directly descended from one of these Upper Palaeozoic genera with V ribbing, or whether *Goniomya* has developed this style of ribbing independently. The material figured by Runnegar (1974: pl. 3, figs 1, 2, 11) as *Cosmomya maria* (Worthen) is better placed in *Grammysiopsis*, and if both fragments do in fact belong to the same species, they do not differ significantly from *G. bisulcatiformis* Muromzeva & Kagarmanov (in Muromzeva 1974: 108; pl. 23, figs 21–22).

***Cosmomya v-scripta* (Hind, 1900)**

Figs 16a–b

1900 *Sanguinolites v-scriptus* Hind: 382; pl. 42, figs 6, 6a, 7, 7a only.

LECTOTYPE. BM L47495 (BM L46533 is the counterpart), here designated, is Hind's (1900: pl. 42, figs 7, 7a) figured specimen; it is from a marine sand approximately 500ft. below the third bed of Millstone Grit, probably E2 Zone, Congleton Edge, Cheshire, England. Fig. 16.

PARALECTOTYPES. BM L47494, the specimen figured by Hind (1900: pl. 42, figs 6, 6a), the same horizon and locality as the lectotype. The second paralectotype, BM L47493 also figured by Hind (1900: pl. 42, figs 5, 5a), should be referred to *Myofossa hindi*; it is from the Redesdale Ironstone. We have found no other material.

DIAGNOSIS. Escutcheon and groove inside rounded posterior carina developed as in *Myofossa*. Posterior V of ribbing distinct, but only a slight anterior V. A slight sulcus runs from the umbo to the anterior part of the dorsal margin in the position of the slight anterior V of the ribbing.

DESCRIPTION. Little can be added to Hind's description and to the diagnosis. The three specimens are deformed in different directions, and measurements are not meaningful. The lectotype is compressed laterally, and the paralectotype BM L47494 is elongated front to back. Despite this the principal characteristics of the species seem clear enough. The prominent umbo of BM L47493 from the Redesdale Ironstone is apparently an artefact, and although this specimen is quite small, it is clearly a different species.

DISCUSSION. The relationship of this species to *Myofossa* on the one hand and to the type species of *Cosmomya* on the other hand seems well established. The characters associated with the escutcheon are essentially those of *Myofossa*. The anterior sulcus and ribbing represent the basic pattern of *Cosmomya*. The anterior V in the ribbing, however, is only slightly developed and the posterior V is less distinct. The pattern, however, is so close that there is little doubt that *Cosmomya v-scripta* is an ancestral species of the genus.

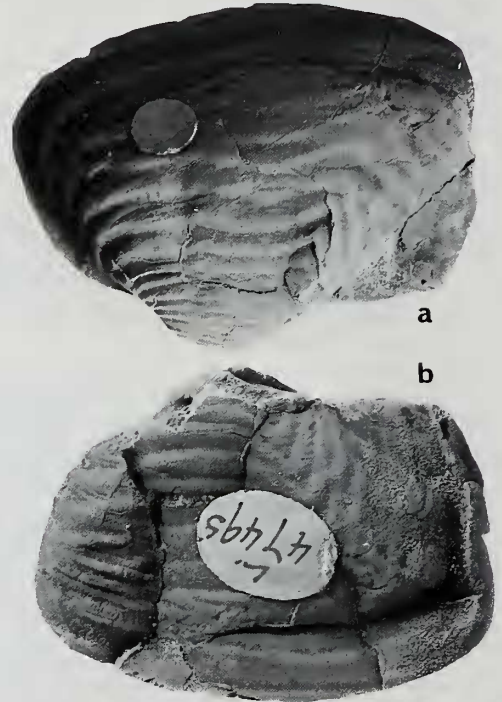


Fig. 16 *Cosmomya v-scripta* (Hind). Namurian (probably E2), marine sand c. 500 ft below third Millstone Grit, Congleton Edge, Cheshire; BM L47495, lectotype (selected herein); Fig. 16a, right valve; Fig. 16b, left valve; both $\times 2.5$.

C. v-scripta resembles '*Grammysiopsis*' *omolonicus* Muromzeva (1974: 108; pl. 21, figs 1–3), which comes from near the Permo-Carboniferous boundary in the Omolonsk Massif, Irbichan, U.S.S.R. It does not, however, have such an extensive posterior gape and area. '*G.*' *bisulcatiformis* Muromzeva & Kazamanov (in Muromzeva 1974: 108; pl. 22, fig. 21) is difficult to distinguish from '*G.*' *omolonicus*; both species differ in having a considerably deeper V in the ribbing.

***Cosmomya variabilis* (M'Coy, 1851)**

Figs 17a–d

- 1851a *Sanguinolites variabilis* M'Coy: 174, *pars*.
 1854 *Sanguinolites variabilis* Morris: 223.
 1855 *Sanguinolites variabilis* M'Coy: 508; pl. 3f, figs 6, 6a only.
 1900 *Allorisma variabilis* (M'Coy); Hind: 424; pl. 44, fig. 2.
 1900 *Sanguinolites interruptus* Hind: 383; pl. 42, figs 8, 9, 10; pl. 49, fig. 10.

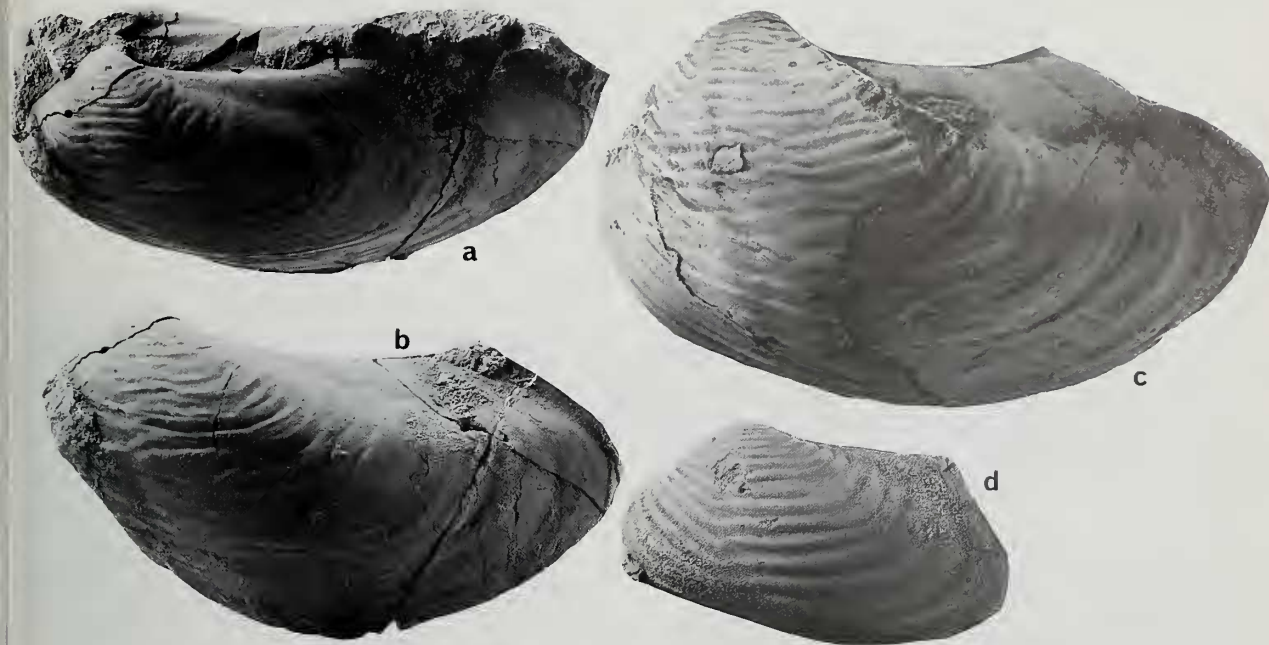


Fig. 17 *Cosmomya variabilis* (M'Coy). Figs 17a–b, High Viséan, Lowick, Northumberland; SM E1100, lectotype; Fig. 17a, angled top view; Fig. 17b, side view (note that the anterior ventral part of the shell is missing). Fig. 17c, Lowest Namurian, Main Limestone, Stanhope, Weardale, Northumberland; BM PL1598, left valve. Fig. 17d, Lower Carboniferous, Viséan, Thorpe Cloud; BM L47497, syntype of *Sanguinolites interruptus* Hind, left side. All $\times 1.5$.

LECTOTYPE. SM E1100 (M'Coy, 1855: pl. 3f, figs 6, 6a), subsequently designated by Hind (1900: description of pl. 44, fig. 2).

SYNTYPES OF *Sanguinolites interruptus*. These are BM L47496 (Hind, 1900: pl. 42, fig. 8), BM L47497 (Hind, 1900: pl. 42, fig. 10), BM L47538 (Hind, 1900: pl. 49, fig. 10), and one specimen from the same locality said by Hind to be in the collection of Mr Holroyd of Manchester; all are from the Lower Carboniferous, Viséan of Thorpe Cloud, Derbyshire, England.

OTHER MATERIAL. BM L46434–40, 7 specimens from Castleton or Thorpe Cloud in the Hind Collection; BM L43637, from Narrowdale, and BM L46433 from Gateham, between Wetton Hall and Narrowdale; all Lower Carboniferous, Viséan.

DESCRIPTION. Oval, tumid shell with distinct rugae, which are straight or slightly curved and comarginal in the mid part of the flank, but diverge across the growth lines in the anterior part forming a slight V. There is an indistinct V in the posterior part before they curve round with the siphonal margin. The greatest tumidity is posterior to the umbones. Umbo moderately distinct, pointed towards the front. The lunule is obscure and the escutcheon is typical for *Cosmomya* and *Myofossa*. There is a rounded carina ventrally, and above this a groove running to the posterior margin of the posterior flattened area; above this the escutcheon proper is an elongated flat area bordering the external margin of the shell. From comparison with similar shells, a ligament groove and nymph might be expected at the anterior part of this flat area. A slight posterior gape was probably present. A shallow sulcus runs from the umbo to the ventral margin.

DIMENSIONS (mm):	Length	Height	Width
BM L47497, LV	39	23	9
BM L47496, LV	31	19	8

DISCUSSION. Two distinct species are represented in M'Coy's (1855) illustrations: i.e. his pl. 3f, figs 6 and 6a, and his pl. 3f, figs 7 and 7a. The identity of his third specimen (pl. 3f, fig. 8) is not clear, but it may be the same as his pl. 3f, figs 6 and 6a, as suggested by M'Coy himself when he described it as an oblong variety.

Hind (1900: 381) recognized these two different species and he referred them to two genera, *Sanguinolites* and *Allorisma*, both with the specific name *variabilis* attributed to M'Coy. Hind's choice of lectotype is in accordance with I.C.Z.N. Article 74 (a) (v), which states that a specimen that was not originally described as a syntype, i.e. was described as a variety, is not available for choice as lectotype. He incorrectly determined the specimen as an *Allorisma* (*Wilkingia* in terms of present usage), apparently failing to notice the incipient Vs of the discordant ribbing present on the lectotype; he included specimens of *Wilkingia regularis* de Verneuil in the same species. The lectotype, although damaged in the anterior region, is clearly the same species as BM PL1598, from the Lower Namurian Main Limestone of Stanhope near Durham, see Fig. 17c.

The V in the ribbing of this species is the only apparent difference from the genus *Myofossa*, but we consider this sufficient to allow us to recognize it as an early species of *Cosmomya*. It differs from *Cosmomya v-scripta* in having a less well marked posterior V in its ribbing. BM L46433 has more steeply dipping anterior transcurrent ribs than the other

specimens and is in this way similar to the anterior flank of *Pentagrammysia*.

Genus *SIPHOGRAMMYSIA* Chernychev, 1950

TYPE SPECIES. *Pholadomya kasanensis* Geinitz 1880. Permian. ?Kazanian, Kazan, U.S.S.R.

DISCUSSION. *Siphogrammysia* resembles some other sanguinolitids in shape and has divergent ribs forming Vs in a similar way to *Cosmomya* and *Pentagrammysia* (Chernychev 1950; ?=*Manankovia* Astafieva-Urbaitis, 1983), but the discordant ribs are much bolder in design and more prominent. They are convergent in pattern with ribs of the trigoniacean, *Iotrigonia*, and a number of Unionacea including *Trigonioides*. A number of *Siphogrammysia* species have been described from the Upper Permian of Kazan and the Taimyr Peninsula. Here (Fig. 18) we illustrate some material from Malaysia which may be the same age.

Siphogrammysia cf. *kasanensis* (Geinitz, 1880) Fig. 18

cf. 1880 *Pholadomya kasanensis* Geinitz: 38-9; pl. 6, figs 23, 23a.

cf. 1894 ?*Goniomya kasanensis* (Geinitz); Nechaev: 314-16; pl. 10, figs 22, 26.

1950 *Siphogrammysia kasanensis* (Geinitz); Chernychev: 26-7; pl. 7, figs 61-3.

MATERIAL. BM PL5001 and BM PL5009, from Geological Survey of Malaysia locs. 106/RF/15 and 116/F/9; Labis area of Johore, Malaysia; in weathered silty shales associated with poorly preserved Ammonoidea, possibly mid-Permian *Agathiceras* sp.



Fig. 18 *Siphogrammysia* cf. *kasanensis* (Geinitz). ?Upper Permian, Kazanian, Malaysia, locality 116/F/9B; BM PL5001; $\times 2.4$.

DISCUSSION. The anterior flank of this species has prominent, broad transcurrent ribs which 'V' sharply, and near-vertical less prominent ribs below the umbones. A second V delimits the siphonal margin at its ventral point, with the V opening to the posterior. Yet a third V runs close to the dorsal part of the dorsal or siphonal area, again open to the posterior. This species differs from *Sanguinolites inordinata* Thomas (1928:

226-7; pl. 6, figs 8, 8b; pl. 8, fig. 7), which appears to be conspecific with *Goniomya kasanensis*, as interpreted by Lutkevich & Lobanova (1960: 86; pl. 11, figs 1, 2), in having no break in the transcurrent ribs of the anterior flank. The latter two species clearly belong to *Cosmomya* rather than to *Siphogrammysia*, and are probably conspecific with *C. egraria* Holdhaus.

Genus *GILBERTSONIA* nov.

TYPE SPECIES. *Sanguinolaria gibbosa* J. de C. Sowerby, 1827 here designated.

DESCRIPTION. Nearly smooth, with comarginal growth lines and obscure comarginal ribs. No surface pustules observed. Umbones forward of mid-point, rounded and opisthogyrally. A wide posterior dorsal area between the umbones and the siphonal margins joins the flank with a gentle change in shell slope, not defined by any feature of the ornament. Shell thin, inflated and elongate; striations on the inner shell surface possibly represent migrating points of mantle attachment. Anterior margin rounded and protruding; ventral margin sinuous, following a shallow, near vertical ventrolateral sulcus, sub-parallel to the hinge. Lunule distinct but not carinate, smooth; escutcheon long, narrow and carinate. The adductors are apparently sub-equal although the anterior one is not well preserved on any specimen we have examined. The posterior adductor is large, sub-rounded and spans the wide posterior dorsal area. The pallial line is without a sinus; it passes ventrally and posteriorly from the lower posterior edge of the posterior adductor parallel to the sloping posterior shell margins. The hinge plate is moderately thick, with a moderately long, very narrow, barely protruding nymph. The dorsal margins are opposed (adpressed) in a straight line well to the posterior. This indicates that they were joined by periostracal ligament.

OTHER SPECIES. *Unio ansticei* J. de C. Sowerby (1840: pl. 39), and two apparently unnamed species from the Upper Carboniferous, Fort Jackson area, Texas.

REMARKS. *Gilbertsonia* resembles *Pachymya*, but that Mesozoic genus does not have a clearly defined lunule and has a much more robust ligament nymph and particularly prominent lines of shell surface pustules. Species of *Pachymya* are usually more thick-shelled than *Gilbertsonia*. The position of the posterior part of the pallial line also differs, and *Pachymya* has a shallow but distinct pallial sinus.

Eopleurophorus [*Sanguinolites*] *hibernicus* Hind has a very similar shell shape but a less sinuous ventral margin; it also has a posterior dorsal area with low ribs.

Gilbertsonia gibbosa (J. de C. Sowerby, 1827)

Fig. 19a-g

- 1827 *Sanguinolaria gibbosa* J. de C. Sowerby: 6: 92; pl. 548, fig. 3.
 1836 *Sanguinolaria tumida* Phillips: 209; pl. V, fig. 3.
 1844 *Allorisma gibbosa* (J. de C. Sowerby); King: 315.
 ?1844 *Sanguinolites contortus* M'Coy: pl. 19, fig. 3.
 ?1885 *Sanguinolites luxurians* de Koninck: 73; pl. 16, figs 1-3.
 ?1885 *Sanguinolites tumidus* (Phillips); de Koninck: 81; pl. 16, fig. 6.

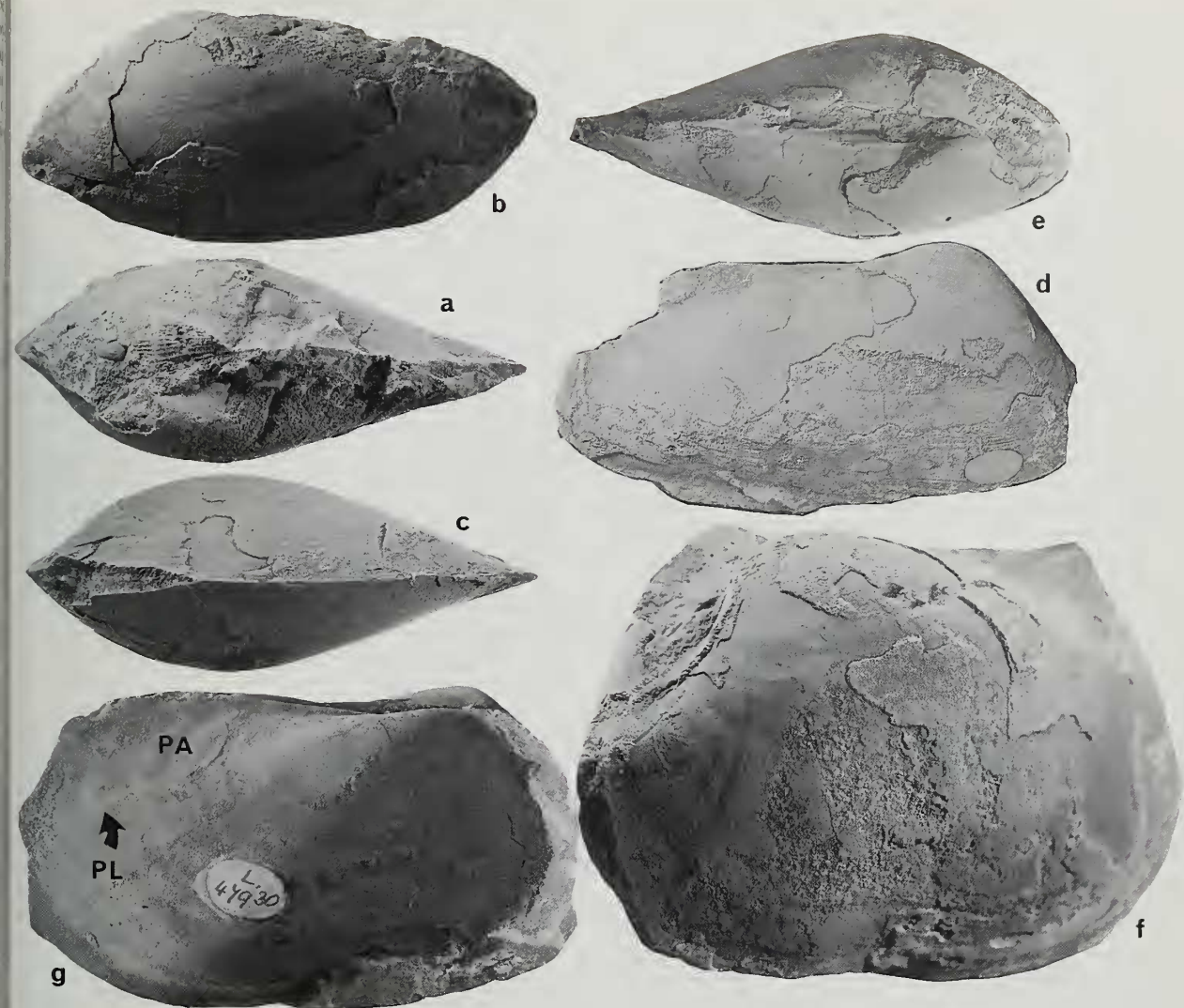


Fig. 19 *Gilbertsonia gibbosa* (J. de C. Sowerby). Lower Carboniferous, Viséan. Figs 19a–c, 'Queen's County' (= County Laois), Ireland; BM 43056, holotype; Fig. 19a, top; Fig. 19b, left side; Fig. 19c, bottom; all $\times 1.1$. Figs 19d–e, Kildare, Ireland; BM L231, Tennant Collection; Fig. 19d, right side; Fig. 19e, top; both $\times 1$. Fig. 19f, ?Bolland, Yorkshire; BM 97200, Gilbertson Collection, slightly oblique view of anterior of left valve showing anterior adductor; $\times 1.5$. Fig. 19g, Kildare, Ireland, BM L47930, right side, with posterior adductor PA, and pallial line without pallial sinus PL.

1885 *Sanguinolites portlocki* de Koninck: 82; pl. 16, fig. 11.

1885 *Chaenomya requiana* (de Rychholdt); de Koninck: 7; pl. 1, fig. 11.

1900 *Sanguinolites luxurians* de Koninck; Hind: 402–4; pl. 46, figs 3–5.

HOLOTYPE. BM 43056 is the figured and only known type specimen; from the Lower Carboniferous of 'Queen's County' (= County Laois), Ireland.

TYPES OF *Sanguinolites tumida* PHILLIPS. The specimen figured by Phillips (1836: pl. V, fig. 3) has not been discovered in the Phillips collection at Oxford nor in the Gilbertson collection at the BM(NH). Phillips said his figure was deduced from a large Irish specimen. Specimens from the Gilbertson collection listed as *S. tumida* in the Gilbertson

Catalogue, but not labelled as such by Phillips and not belonging to the species as here understood (that is, not belonging to the same species as illustrated by Phillips), are not accepted here as syntypes. These include BM 97164 belonging to the species here recognized as *Myofossa omaliana* de Koninck (p. 63).

OTHER MATERIAL:

BM L231 from the Carboniferous Limestone of Kildare, Ireland; Tennant Collection, Fig. 19d–e (Hind identified this specimen as *S. luxurians*).

BM 97187 (41.6.7.132 in Gray Catalogue; 92g in Gilbertson Catalogue; *Isocardia* sp.; Phillips MS: pl. 5b, fig. 34; see below).

BM 36937, Carboniferous Limestone, Clane, Kildare, Ireland, Pratt Collection.

BM L13486, Carboniferous Limestone, Derbyshire, England.
 BM L47930, Lower Carboniferous, Kildare, no other details.
 BM L45242, Lower Carboniferous, St. Doolaghs, Co. Dublin, Ireland (labelled *Allorisma ansticei* Sowerby); Hind Collection.
 BM(NH). Bancroft Collection no. 786, Clane, Kildare, Ireland.

REMARKS. Phillips' species *Sanguinolaria tumida* has to be interpreted from his figure (Phillips, 1836: pl. 5, fig. 3). Although we have been able to examine the mock-ups for the original plate (with kind help from Mr P. Powell of the Oxford University Museum) we have not been able to locate a type specimen, either in Phillips' own collection at the Oxford University Museum, or in the Gilbertson Collection at the BM(NH). The original manuscript and published figures seem to portray a species which may be considered to be a synonym of *Gilbertsonia gibbosa*. Unfortunately, the specimens in the Gilbertson Collection which we attribute to this species are not named as such in Gilbertson's manuscript catalogue, housed in the Palaeontology Library at the BM(NH). A further difficulty is that a specimen labelled no. 85 in the Gilbertson Catalogue, and there identified as *S. tumida*, is clearly not the specimen or species figured by Phillips; it is a *Myofossa omaliana* (p. 63). Hind apparently thought that the specimen BM 97200 was Phillips' figured specimen of *S. tumida*, but it does not have any individual features in common with the figure. We are therefore unable to identify any type material of *Sanguinolaria tumida* Phillips. Because we consider that species to be a junior subjective synonym of *Sanguinolaria gibbosa* J. de C. Sowerby, by identification of Phillips' figure with that species, we do not think it would be advantageous to create a neotype for Phillips' species. It is possible that *Sanguinolites luxurians* de Koninck, from the slightly older Calcschiste de Tournai, is the same species; but in de Koninck's figure the umbones are closer to the anterior. *S. luxurians* seems to have been based on only one specimen. De Koninck grouped his *S. luxurians* with species that have two diagonal folds (ribs?); if such ribs are present at all in *G. gibbosa* they are very indistinct. They are not at all comparable with the radiating sculpture that occurs on the corselet in some *Sanguinolites* and Permophoridae.

Sanguinolites contortus M'Coy may be a distorted specimen of the present species; we have not been able to examine the holotype. At present we treat *S. contortus* as a *nomen dubium*.

Subfamily UNDULOMYINAE Astafieva-Urbaitis, 1984

In this subfamily are placed *Wilkingia*, *Praeundulomya*, *Undulomya*, *Exechorhynchus*, *Dyasmya* gen. nov. and probably *Manankovia*. The subfamily contains elongate forms progressively adapted for deep burrowing. A lunule and escutcheon are present, with the ligament lodged in a groove at the front end of the escutcheon area on a narrow ligament nymph. The external shell surface is granular, except for the escutcheon, with aligned periostracal spicules. Species of *Wilkingia* are known to have a deep pallial sinus. Runnegar (1969: 287, fig. 53c) records a pallial sinus in a specimen from the topmost Carboniferous or lowermost Permian of the U.S.A. The other characters of *Praeundulomya* and *Undulomya* link them to *Wilkingia*, from which we infer that they may also have had a deep pallial sinus. Just

noticeable in *Wilkingia regularis*, but better developed in *W. maxima*, is a low, rounded, elongate rib present on the internal shell surface, running from the umbones towards the posterior margin. In *Praeundulomya* and *Undulomya* a second rib occurs, a little lower, which reaches the posterior margin at a point where the division between the two siphons would be expected. This feature also occurs in *Siliquimya*? Permophoridae.

The genera of this subfamily do not have the deeply inset anterior adductor, with a shell thickening immediately behind it, characteristic of *Siliquimya*. *Undulomya* has prominent V-shaped ribs, very similar to those in *Pentagrammysia* Chernychev, 1950, but that Carboniferous genus does not have the posterior interior radiating ribs that link it with *Praeundulomya* and *Wilkingia*. We therefore conclude that the V ribs have developed independently in this case. Astafieva-Urbaitis (1974b: fig. 1) illustrates a species from Kazakhstan with transcurrent ribs on the anterior only intermediate between *Undulomya* and *Praeundulomya*. The *Undulomyinae* may be distinguished from *Vacunella* Waterhouse 1965 by the form of the escutcheon; in *Vacunella* the escutcheon does not have a sharp carinate edge and it is ill-defined distally where the dorsal margins pass evenly into the posterior siphonal gape. *Vacunella* also has much broader nymphs. *Myonia* Dana 1847, here also included in the *Vacunellinae*, has no pallial sinus.

Genus UNDULOMYA Fletcher, 1946

TYPE SPECIES. *U. pleioleura* Fletcher, by original designation, = *Goniomya singaporensis* Newton, 1906.

Undulomya singaporensis Newton, 1906

- 21906 *Goniomya scrivenori* Newton, 49: pl. 25, fig. 1.
- 1906 *Goniomya singaporensis* Newton: 493; pl. 25, figs 2-3.
- 1913 *Goniomya uhligi* Holdhaus: 450; pl. 94, fig. 2.
- 21928 *Sanguinolites deportatus* Thomas: 229; pl. 6, figs 6.
- 21928 *Sanguinolites insolitus* Thomas: 228-9; pl. 6, figs 11-12.
- 1946 *Undulomya pleioleura* Fletcher: 399-400; pl. 34, figs 1-5; pl. 35, fig. 1.
- 1956 *Undulomya pleioleura* Fletcher; Dickins: 29; pl. 4, figs 6-8.

TYPE MATERIAL. The two syntypes of *Goniomya singaporensis* are BM L19154, from the Permian, possibly Artinskian Singapore (J. B. Scrivenor collection, ex Mr Guthrie) mistakenly described by Newton as Middle Jurassic; and BM L19173, part and counterpart of a fragment (Mr Hanitch collection). BM L19153 (apparently missing) is the holotype of *Goniomya scrivenori*. The holotype of *Goniomya uhligi* from a geode in black shales below the Werfen Beds, NW of Kunplong, SW of the Niti Pass (horizon mistakenly doubted by Holdhaus (1913) and changed to Spiti Shales), is in the museum of the Geological Survey of India, Calcutta, and is from the same locality as *Cosmomya egraria* Holdhaus 1913. The type material of *Sanguinolites deportatus* and *S. insolitus* from the 'Goniatite Bed' and Steel Hill, Parinas Quebrada Amatope Mountains, Peru, is in the Sedgwick Museum Cambridge; it is probably Lower Permian in age, but is

apparently associated in the collections with Pennsylvanian ammonoids.

REMARKS. This species has been well described and illustrated by Fletcher (1946), but examination of material from Singapore and Peru convinces us that it has a wide geographical range outside Australia and that there are a number of older names available for it. While the species has almost exactly the same shape as *Praeundulomya maxima*, with identical escutcheon and posterior internal ribs, it has developed a very pronounced V pattern of ribs with the line bisecting the angle of V sloping slightly backwards below the umbones. It is the similarities, coupled with what appears to be a good intermediate discovered by one of us (Astafieva-Urbaitis 1974b), which lead us to suggest the close relationship between the two genera. We have been unable to discover the posterior part of the pallial line in any of the material we have examined, but assume that the species would have been siphonate with a deep pallial sinus because that feature is present in the presumed ancestor and other members of the subfamily.

Genus *WILKINGIA* Wilson, 1959

TYPE SPECIES. *Venus elliptica* Phillips, 1836 (*non V. elliptica* Lamarck 1818), by original designation (as interpreted by Wilson, 1959; = *Allorisma regularis* King, *in de Verneuil*, 1845).

SYNONYMS. *Allorismiella* Astafieva-Urbaitis, 1962: 36 (type species by original designation, *Allorisma sulcata* Hind (1900: 42; pl. 48, figs 3–11), wrongly quoted as '*Allorisma sulcata* Hind, 1896'; this is not *Hiatella sulcata* Fleming, 1828 (see p. 57) and not *Allorisma sulcata* King, 1844: 316. We consider *Allorisma sulcata* as interpreted by Hind and Astafieva-Urbaitis to be a junior subjective synonym of *Allorisma regularis* King, *in de Verneuil* 1845 (see below), and a junior objective synonym of *Venus elliptica* Phillips, *non* Lamarck.

Dulunomya Astafieva-Urbaitis & Dickins, 1984; type species by original designation *Dulunomya serpuhovensis* Astafieva-Urbaitis & Dickins. We consider *Dulunomya serpuhovensis* to be a junior subjective synonym of *Allorisma regularis* King, *in de Verneuil* 1845.

REMARKS. In order to establish the identity of the nominal subgenera *Wilkingia* and *Allorisma* we have had to overcome a series of compounded errors and misinterpretations. King (1850: 196–9; pls 16, 20) clearly distinguished the characters of these taxa but unfortunately, by reference to misidentified type species, applied the names in reverse. From his footnote 1 on p. 196, however, it is clear that in his first publication (King 1844) he used the name *Allorisma* both for members of the family Edmondiidae and for forms with a deep pallial sinus here included in the Undulomyiinae. Indeed the internal rib below the hinge is described as occurring in *Allorisma sulcata* (Fleming) (King 1844: 316). In 1850, King in effect changed his mind over the identification of *Allorisma* when he discovered that the characters of *Sanguinolaria sulcata* of both Fleming and Phillips resembled those of *Edmondia*, and differed from the siphonate forms here included in the Undulomyiinae. His intention was to use *Allorisma* for the siphonate species (King 1850: pl. 20, fig. 5 only), but unfortunately he misidentified his material with the non-siphonate species *Allorisma sulcata* (Fleming, 1828) which he

wrongly regarded as different from *Sanguinolaria sulcata* Phillips 1836 (see p. 58).

DIAGNOSIS. Lunule present and distinct escutcheon made up of an elongated flat area. Evenly rounded from front to back. Ribs constant in number. Pallial sinus deep.

DISCUSSION. In the Viséan and Namurian rocks, from the Moscow Basin to England and the U.S.A., there is a close knit group of species, which may only be distinguished in well-preserved specimens when subtle differences of shell shape and the form of the pallial sinus can be observed. These make up the genera *Wilkingia*, and *Praeundulomya* as here recognized. *Wilkingia* is of moderate size with sinuous ventral margins, and this group includes *W. regularis* and *W. ?transversa*. Species of *Praeundulomya* are large and include *P. maxima*, which has sub-parallel ventral and dorsal margins. The Permian *P. concentrica* also has this shape but is not so large.

It may prove in the future better to join *Wilkingia* with *Praeundulomya* as a junior subjective synonym, but at present we retain the two genera separated by the characters mentioned here.

Wilkingia regularis (King, *in de Verneuil* 1845)

Figs 20–24

- ?1836 *Venus elliptica* Phillips: pl. 2, fig. 7 (*non* Lamarck 1818).
- 1845 *Allorisma regularis* King, *in de Verneuil*: 298; pl. 19, fig. 6 only.
- 1850 *Allorisma sulcata* (Fleming); King: pl. 20, fig. 5.
- 1900 *Allorisma sulcata* (Fleming); Hind: 320, 422–4; pl. 48, figs 3, 5, 6, 9–11.
- ?1900 *Allorisma sulcata* (Fleming); Hind: pl. 48, fig. 8 only.
- 1900 *Allorisma variabilis* (M'Coy); Hind: pl. 48, figs. 1, 2 only.
- ?1950 *Tellinomorpha sarytschevae* Chernychev: 42; pl. 11, fig. 90.
- ?1950 ?*Tellinomorpha* sp. Chernychev: 43, fig. 92.
- 1959 *Wilkingia elliptica* (Phillips); Wilson: 402–4; pl. 71, figs 1, 3–6.
- ?1959 *Wilkingia elliptica* (Phillips); Wilson: pl. 71, fig. 2 only.
- 1962 *Allorismiella sulcata* (Hind) Astafieva-Urbaitis: 36.
- ?1962 *Allorismiella sulcata* (Hind); Astafieva-Urbaitis: 36–7, fig. 2.
- 1962 *Allorismiella regulariformis* Astafieva-Urbaitis: 39–40, fig. 2.
- 1984 *Dulunomya serpuhovensis* Astafieva-Urbaitis & Dickins: 38–9; pl. 2, figs 1–3.

TYPES. There are 12 syntypes in the de Verneuil Collection of the École des Mines (stored at present at the University of Lyon). Four of them are associated on a board bearing the register number 1743, and labelled '*Allorisma regularis* King, Sloboda, gouv. de Toula, Carbonifère. Coll. de Verneuil'; one of these is here selected lectotype (Fig. 20a–d), and the other three become paralectotypes. Other paralectotypes with similar locality labels are two specimens numbered 1744 and three specimens numbered 1745. Three more paralectotypes are on blocks numbered 1742 (two specimens; one of them was figured by de Verneuil (1845: pl. 21, fig. 11)) and 1746, labelled '*A. regularis* King, Valdai, Coll. de Verneuil'; we identify these three paralectotypes with the genus

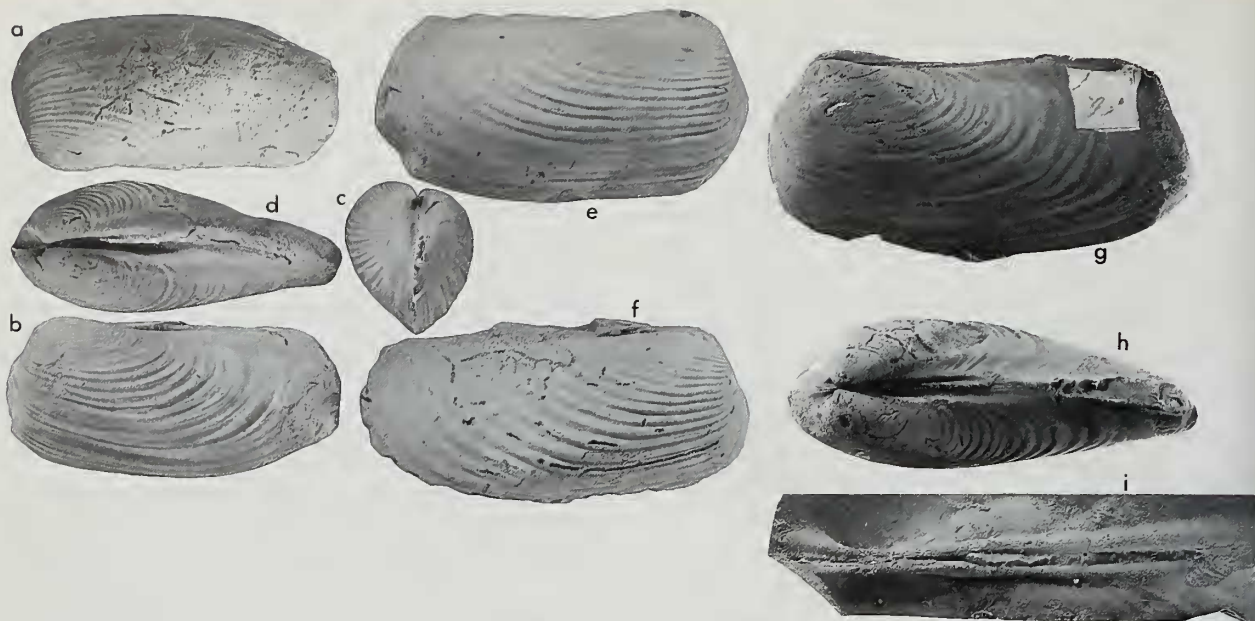


Fig. 20 *Wilkingia regularis* (King, in de Verneuil). Lower Carboniferous, Viséan; Sloboda, Gouv. de Toula, Russia. Figs 20a–d, EMP 1743 (1 of 4), de Verneuil Collection, lectotype (selected herein), a silicified steinkern; Fig. 20a, right side; Fig. 20b, left side; Fig. 20c, anterior; Fig. 20d, dorsum. Figs 20e–f, EMP 1744, paralectotypes, views of right sides. Figs 20g–i, BM L18, ? ex de Verneuil Collection, ? paralectotype; Fig. 20g, left side; Fig. 20h, dorsum; Fig. 20i, latex cast of hinge area seen from the inside to show inner surface of nymphs. All $\times 0.88$, except Fig. 20i, $\times 1.5$.

Allorisma King. Finally, two specimens (BM L18) in the BM (NH) that have the collectors' number 50, in similar handwriting to one of the Valdai specimens, may also be original syntypes that now become paralectotypes.

SYNONYMS. Although under normal circumstances we consider it inadvisable to designate types for junior synonyms or other invalid names, we feel that it is necessary to do this in the present case in order to preserve the stability of the generic name *Wilkingia*.

1. *Venus elliptica* Phillips, 1836 (*non* Lamarck, 1818). **Neotype**, here designated, is BM L47526, the specimen figured by Hind (1900: pl. 48, fig. 4). Wilson (1959: 402) designated the figure in Phillips (1836: pl. 2, fig. 7) as the lectotype of this species. In the same publication, however, he stated that the original specimen could not be found in the collections of the Yorkshire Philosophical Society (at the Yorkshire Museum, York) where it might be expected to be stored, nor in the Hancock Museum, Newcastle-upon-Tyne, nor in the University College Galway, Ireland. We have also been unsuccessful in finding the specimen in the Gilbertson Collection in the BM(NH) (it is not listed in Gilbertson's manuscript catalogue). We have also searched in vain in Leeds City Museum and in the Phillips Collection at Oxford University Museum. In a series of Phillips' original drawings and mock-up plates for the *Geology of the Yorkshire Coast* kindly made available to us by Mr P. Powell of the Oxford University Museum, an original drawing of *Venus elliptica* is preserved together with the information that this specimen came from Harelaw, Northumberland and was in the collection of the Rev. C. V. Harcourt. These Harcourt specimens should be in the York Museum, and we would like to thank Dr Pyrrah

of that Museum for carrying out a further unsuccessful search.

Unfortunately it is very difficult to determine the taxonomic position of Phillips' lost specimen from his figure. Its characters include the elliptical shape with a rounded, non-sinuuous venter, small size, indication of a lunule and broad, regular, distinct comarginal rugae. If indeed it was an anomalodesmatid it could be a synonym of one of four taxa, *Sanguinolaria sulcata* Fleming, *Sanguinolaria maxima* Portlock, *Allorisma regularis* King or *Pholadomya omaliana* de Koninck. *Siliquimya plicata* (Portlock), even if this small size, has a distinctly more elongate shape and a sharper increase in curvature at the posterior ventral margin. In 1845, King (*in de Verneuil*) identified Phillips' species with one from Russia and indicated that it occurred in northern England. He used the name *Cardiomorpha sulcata* de Koninck 1842 for this species. In order to avoid further difficulty, the neotype chosen here makes *Venus elliptica* Phillips 1836 (*non* Lamarck, 1818) a subjective synonym of *Wilkingia regularis* (King, *in de Verneuil* 1845).

2. *Allorismiella sulcata* Astafieva-Urbaitis, 1962. In her original description of *Allorismiella*, Astafieva-Urbaitis designated *Allorismiella sulcata* Hind as type species. Under ICZN Article 70c this must be construed as a deliberate misapplication of the name which Hind (1900) himself correctly attributed to Fleming 1828, but then misidentified. Following the provisions of this Article, the type species fixed by that action is deemed to be a new nominal species. In her original description, Astafieva-Urbaitis (1962: 40) referred to the specimens figured by Hind (1900: pl. 48 [pl. 18 cited in error], figs 3–11), the specimen figured by Fedotov (1932: pl. 10, fig. 5), and other specimens she had

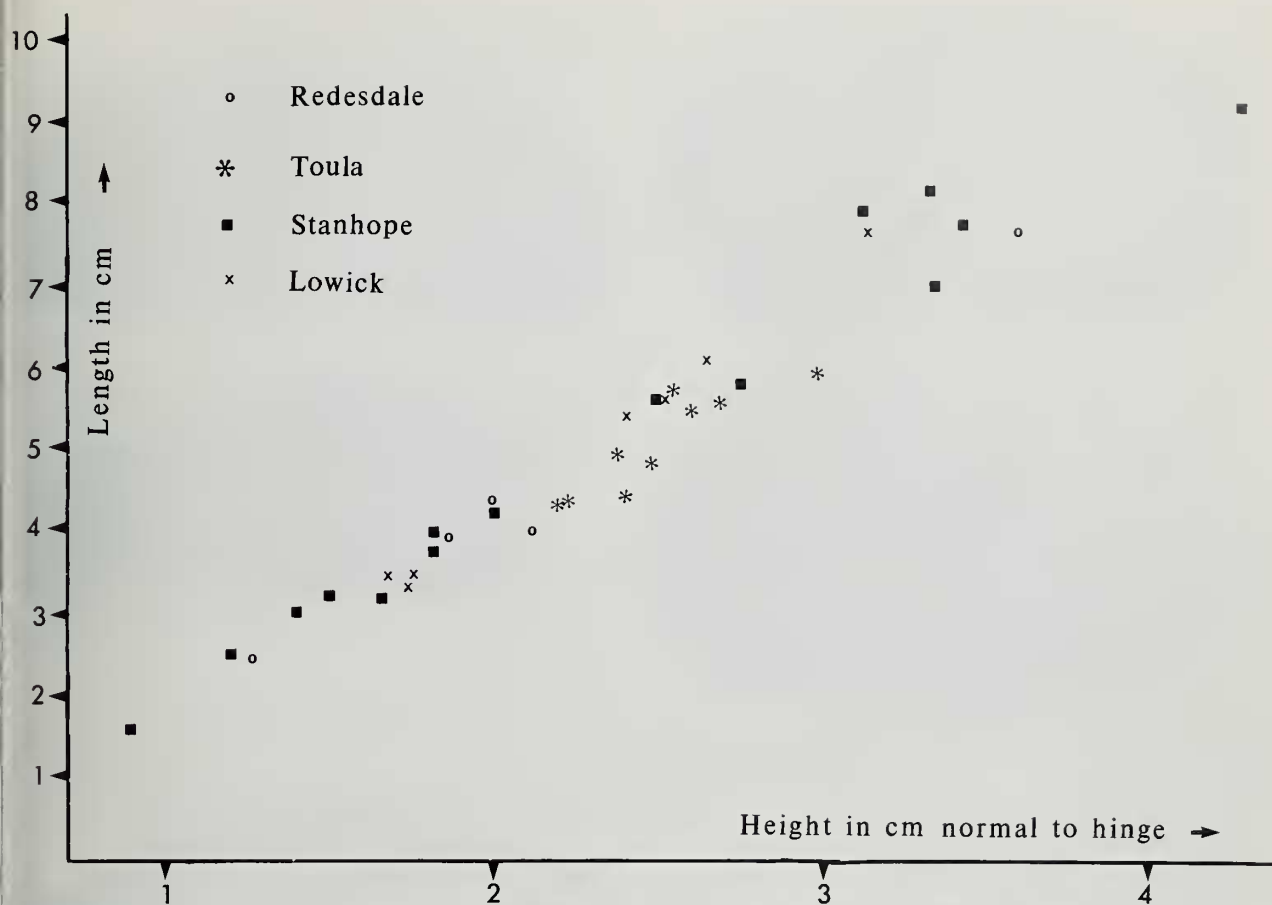


Fig. 21 *Wilkingia regularis* (King, in de Verneuil). Scatter diagram of height/length ratios of the four samples: (1) Redesdale Ironstone (Viséan) and (2) Main Limestone (Lower Namurian), both from Stanhope, Weardale; (3) Upper Viséan or Lowest Namurian, Lowick; (4) the type series from Sloboda (Viséan) (excluding specimens of *Allorismiella*); this shows that the Redesdale material does not have a different height/length ratio from the other samples.

in front of her; all must be considered to be the type series of her new species. BM L47526, the specimen figured by Hind (1900: pl. 48, fig. 4), is here designated lectotype. By this action BM L47526 becomes the type specimen of both *Venus elliptica* Phillips (*non* Lamarck) and *Allorismiella sulcata* Astafieva-Urbaitis, so they are objective synonyms. Consequently the genera *Wilkingia* and *Allorismiella* become objective synonyms. In our opinion the valid name for the type species of *Wilkingia* Wilson is the oldest available subjective synonym, *Wilkingia regularis* (King, in de Verneuil, 1845).

MATERIAL. BM(NH): Hind Collection: Lower Limestone series, top Viséan (P2, D2 or D3, Brigantian); and Redesdale Limestone, L.-M. Viséan (B2 = D1, Asbian); Trechmann Collection: Main Limestone, Lowest Namurian, Stanhope, near Durham; and Viséan, Four Laws Limestone, Redesdale, Northumberland. EMP: de Verneuil Collection: mid-Viséan (said to be pre-Asbian), Sloboda, Toula, S. of Moscow. BGS: Redesdale Limestone, Northumberland (specimens figured by Wilson, 1959). SM: Lowick, Northumberland, Viséan.

DESCRIPTION. The shell is of medium size and very thin, resembling species of *Pleuromya* and early species of

Panopeidae except that the dorsal margins extend in a straight line further towards the posterior. It is elongate with the umbones well towards the anterior. The ventral margin is sinuous, marking an obvious but gentle subumbonal sulcus. The maximum height is at about the mid-point, well to the posterior of the umbones. The umbones are slightly tumid and only slightly raised above the hinge line. The nymphs are relatively long and very slender, barely protruding from the long, straight, adpressed posterior dorsal margins, which themselves indicate that they were joined by periostracal ligament well towards the posterior margins. The hinge is edentulous. The musculature, including the pallial sinus, is illustrated in Fig. 22.

The comarginal rugae or ribs are a little irregular, but rather constant in number from front to back. They are in the form of shell corrugations, and apart from the barely discernible growth lines are equally well preserved on the steinkern and the shell surface. There are almost imperceptible radiating ridges on the steinkerns possibly reflecting lines of surface pustules that occur across the complete shell surface except within the escutcheon. The shell has a small lunule which has no carina, instead curving imperceptibly into the anterior part of the flank. The long narrow escutcheon is limited by a sharp carina, and there is a slight shell thickening, in the form of a

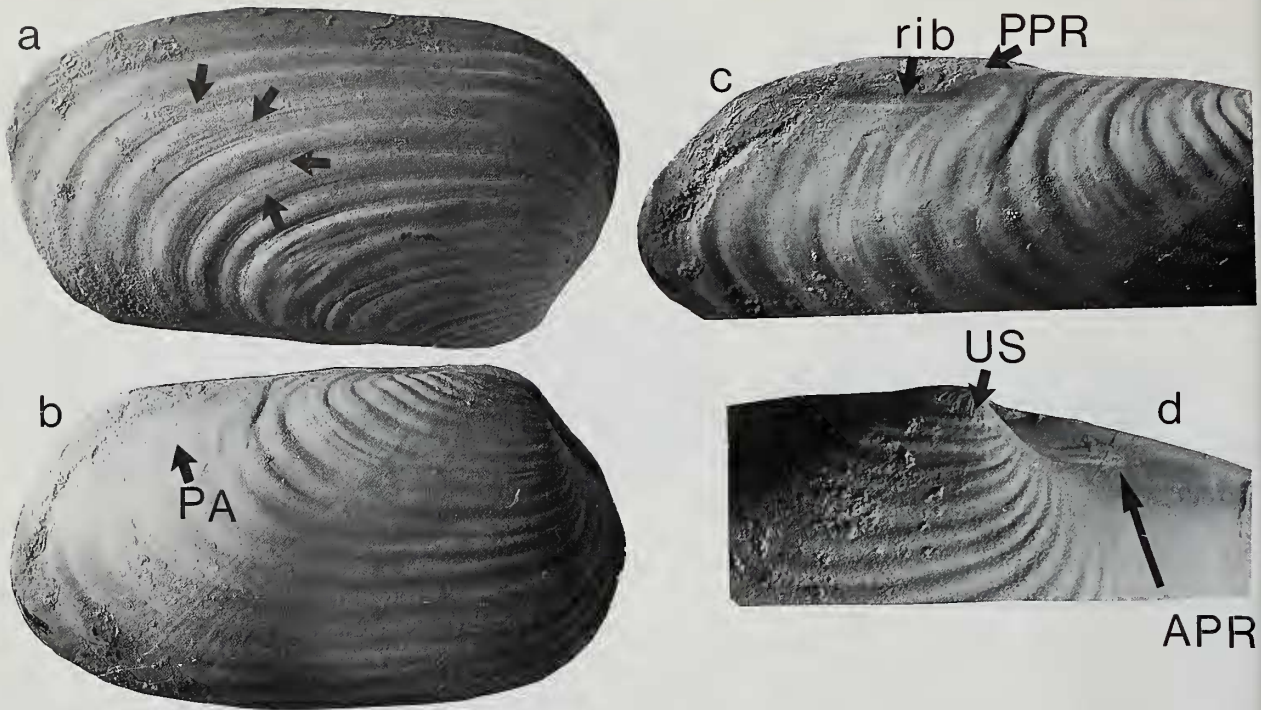


Fig. 22 *Wilkingia regularis* (King, in de Verneuil). Lower Carboniferous, Viséan (Asbian), Redesdale Ironstone, Redesdale, Northumberland. BM PL5002; Fig. 22a, left side, position of pallial sinus arrowed, periostracal pustules visible in postero-dorsal area, $\times 2$; Fig. 22b, right side with posterior adductor (PA), $\times 2$; Fig. 22c, oblique view of siphonal area of right side, showing posterior pedal retractor scar (PPR) and internal dorsal rib, approx. $\times 3$; Fig. 22d, umbonal area viewed obliquely from top, showing scars of anterior pedal retractor (APR) and accessory umbonal scars (US), approx. $\times 4$.

low internal rib, running at a very low angle from the umbo towards the posterior margin.

REMARKS. Hind included *Posidonomya transversa* Portlock (1843: 174; pl. 38, fig. 9) in the synonymy of this species without comment. There is no indication from Portlock's figure that it belongs to this superfamily and we consider that Hind made a mistake. Another early nominal species that belongs in *Wilkingia*, *Lutraria primaeva* Portlock (1843: 441; pl. 34, fig. 5), was curiously interpreted by Hind (1900: 307) as an *Edmondia*. Hind went so far as to claim that another specimen had been substituted for the original, but it is clear that this is not so, from both Portlock's drawing and from his measurements. However, the measurements and the figure suggest that this species falls outside the variation of *W. regularis*, and it is probably a senior synonym of *Allorisma monensis* Hind. *Wilkingia regularis* differs from *W. primaeva* in being more elongate and having a differently shaped pallial sinus.

Hind (1900: 424; pl. 48, figs 1–2) described specimens of this species from Lowick and Calderwood as *Allorisma variabilis* (M'Coy). The lectotype of that nominal species (Fig. 17, p. 69) is, however, a crushed specimen of *Cosmomya*, also from Lowick. Amongst Hind's specimens, the ribbing on the umbonal area is only significantly irregular in the lectotype, and this is characteristic of *Cosmomya*. Most of the specimens of the present species, recognized by Hind as *Allorisma sulcata*, by Wilson as *Wilkingia elliptica* and by Astafieva-Urbaitis as *Allorismiella sulcata*, come from the Redesdale Ironstone, of high Viséan, Asbian, age, in

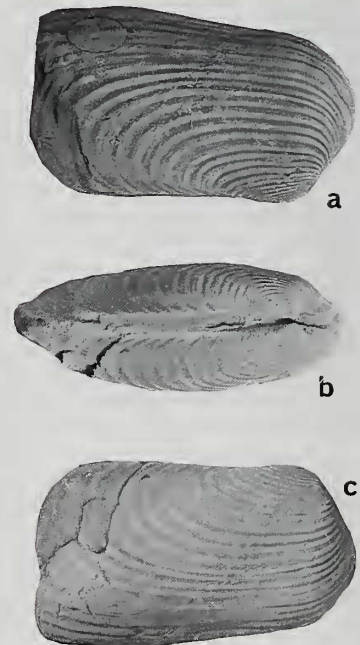


Fig. 23 *Wilkingia regularis* (King, in de Verneuil). Lower Carboniferous, Viséan (Asbian), Redesdale Ironstone, Redesdale, Northumberland. BM L45252, Hind Collection, **neotype** (selected herein) of *Venus elliptica* Phillips, 1836 (*non* Lamarck, 1818). Fig. 23a, left valve; Fig. 23b, dorsal view; Fig. 23c, right valve; all $\times 1$.

Northumberland. The material available from this locality is often a little crushed, many of the specimens have eroded anterior and posterior margins, and many of the specimens are of small size. The limestone specimens from Lowick and Stanhope are better preserved and larger, as are the specimens from Sloboda in what used to be the 'Gouvernement de Toula', south of the Moscow Basin. The difference in preservation and size led Astafieva-Urbaitis to identify smaller gaping specimens as *A. sulcata*, distinct from *A. regularis* (1962: 36). We are uncertain whether or not these smaller Russian specimens belong to the same species. However, simple measurements of shell length and height (Fig. 21) suggest that the British specimens do not differ in these parameters, and they are also very close to the type material from the type locality of *Wilkingia regularis*. When Astafieva-Urbaitis introduced the name *Allorismiella* she was unaware that Wilson had at the same time been working on similar species and had introduced a new name three years earlier; she also had no opportunity to examine either Hind's material or the type series of *W. regularis*, which are the types of *Allorismiella* and *Dulunomya* respectively. She was working only with undescribed Russian specimens. Her holotype of *Dulunomya serpukhovensis* (Astafieva-Urbaitis & Dickins 1984: pl. 2, figs 1a-d) is identical in shape and sculpture to two of the paralectotypes of *Wilkingia regularis* (Figs 20e, 20f; those numbered 1744). Other specimens she refers to (Astafieva-Urbaitis, 1962: pl. 39, fig. 1) are apparently more closely related to the species described here as *Praeundulomya maxima* Portlock.

Wilkingia. Subumbonal sulcus negligible or absent. Umbones more prominent than in other members of the subfamily. Anterior of shell prominent. The flatish posterior-dorsal or siphonal area is set off by a marked change in surface, forming a low rounded angle from the umbones to the posterior ventral margin, subcarinate. The shell structure of the type species is unknown but the outer surface bears very dense, close rows of small periostracal spicules. *Dyasmya* has a small but sharp pallial sinus, not much differing from that of a young *Wilkingia*. A small posterior gape is present. The comarginal rugae are less regular than those of *Wilkingia*, and in some specimens of the type species are barely present. The ligament is external, opisthodontic, parivincular, of medium length, mounted on narrow nymphs. The hinge plates are slender and parallel when viewed from above and without any teeth.

REMARKS. Beside the type species, the genus may include *Allorisma baldryi* Thomas, 1928, apparently from the Lower Permian of Peru; *Thracia longa* and possibly the more rounded *Thracia alta*, both of Lutkevich & Lobanova, 1960, from the Lower Permian of the Taimyr peninsular; and *Sanguinolites lunulatus* (Keyserling) as interpreted by those authors. Unfortunately the hinges of none of these species are known.

The more quadrate species of *Dyasmya* are very similar in outline to the Mesozoic genus *Pleuromya*, while the more rounded *Dyasmya alta* (particularly those individuals figured by Lutkevich & Lobanova (1960: pl. 11, figs 3-7)) resembles the Jurassic genus *Gresslya*. Both the Mesozoic genera have more advanced hinge types and a homogeneous inner ostracum, but they could have descended from *Dyasmya*.

The Jurassic species '*Pleuromya*' *angusta* Agassiz, 1843, commonly attributed to *Arcomya*, is very similar in shape but has many fewer rows of periostracal spicules. At present this seems to be the most suitable genus for Agassiz' species. We have observed a nacreoprismatic aragonite shell in specimens of this species in the BM(NH) from the Lias of southern England. *Arcomya* has an Upper Jurassic type species and is relatively longer and narrower, with a wide subumbonal sulcus sloping down and back below the umbones; it does not have the prominent umbones of *Dyasmya*.

Dyasmya elegans (King, 1850)

Figs 25a-b

1850 *Allorisma elegans* King: 198; pl. 16, figs 3-5.

1967 *Wilkingia elegans* (King) Logan: 63-4; pl. 10, figs 6-10.

REMARKS. The shell has very dense, closely-packed lines of small, periostracal spicules, apparently over the total exterior surface of the shell. There is clear but fragmentary confirmation of the position of the pallial line as illustrated by Logan (1967: pl. 10, fig. 6a-b) in two of our rather poorly preserved internal moulds (BM PL96 and BM PL5006). These are from the lower part of the shell limestone of the Magnesian Limestone of Claxheugh Quarry, County Durham, England, and are apparently of Kazanian age.

We have no further information concerning this species beyond that available to Logan (1967) when he was preparing his monograph. We note, however, that it may well be intermediate between Carboniferous *Wilkingia* and the Mesozoic genus *Pleuromya*. *Pleuromya* has a form of pallial line and accessory muscle scars suggesting that it had a similar form of mantle fusion and siphon formation to the living

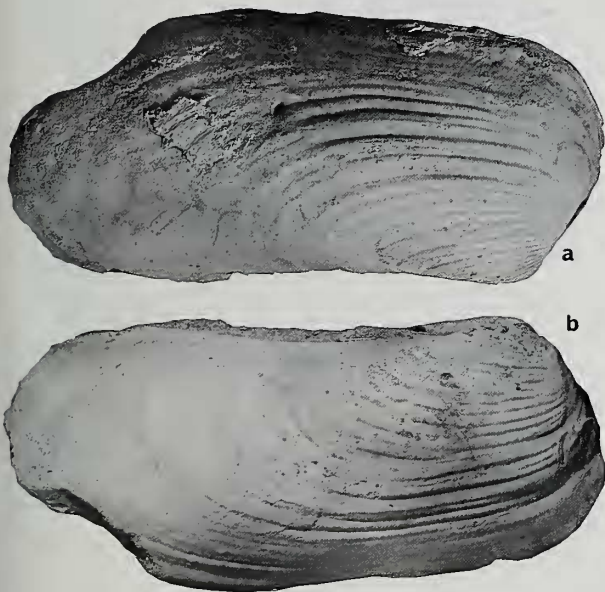


Fig. 24 *Wilkingia regularis* (King, in de Verneuil). Upper Carboniferous, Lower Namurian, Main Limestone, Stanhope, Weardale, Northumberland. BM PL5003; Fig. 24a, left side; Fig. 24b, right side; both $\times 0.9$.

Genus *DYASMYA* nov.

TYPE SPECIES. *Allorisma elegans* King, 1850.

DESCRIPTION. Small to medium-sized undulomyine with sharp escutcheon and lunule. Escutcheon relatively wider than in

of the dorsal shell margins typical of *Pleuromya* and other Myacea.

Genus *PRAEUNDULOMYA* Dickins, 1957

TYPE SPECIES. *Praeundulomya concentrica* Dickins 1957, by original designation.

DESCRIPTION. Transversely elongate, with well-developed escutcheon behind umbones in the form of a flat marginal area. The ligament proper was apparently lodged in a relatively short groove on the proximal edge of narrow nymphs close behind the umbones. The flat marginal area was probably covered and joined by periostracum, continuous with the ligament (see p. 54). The muscle scars are very shallowly impressed and a deep pallial sinus is visible in *P. maxima* and *P. subcuneata* (but not the type species). There are one or two ribs running below the hinge posterior to the umbones. These appear as grooves on the steinkern or composite mould, and are better developed than in *Wilkingia*. In the Permian species *P. concentrica*, the two posterior grooves are as well developed as they are in *Undulomya*. In outline from above, bivalved specimens have a distinctive tapering shape.

Praeundulomya is distinguished from *Wilkingia* essentially by the shape; in *Praeundulomya* the ventral and dorsal margins are sub-parallel with only a very slight subumbonal sulcus, whereas *Wilkingia* has a much more sinuous ventral margin. This difference is less obvious in young specimens.

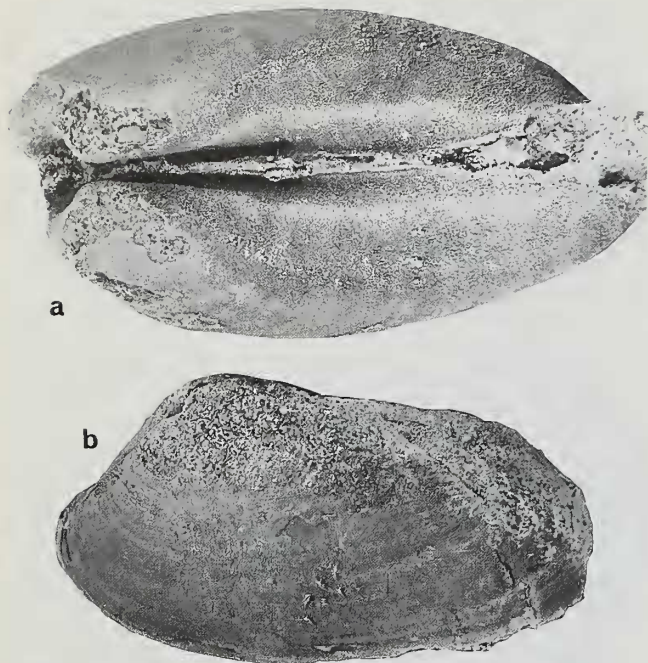


Fig. 25 *Dyasmya elegans* (King). Upper Permian, Magnesian Limestone, Claxheugh Quarry, Durham; C. T. Trechmann collection. Fig. 25a, BM PL5004, top view; Fig. 25b, BM PL5005, left side; both $\times 2$.

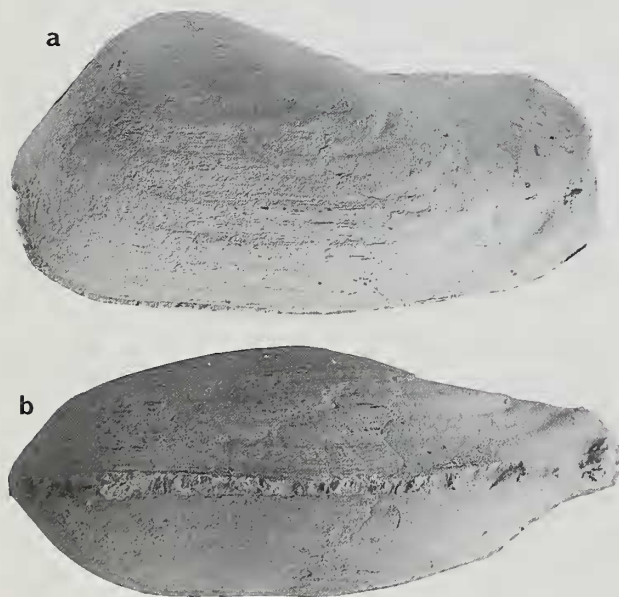


Fig. 26 *Wilkingia* sp. Lower Carboniferous, Kansas. USNM, no register number; Fig. 26a, left side; Fig. 26b, ventral view; both approx. $\times 0.8$.

genera *Mya* and *Panopea*, differing somewhat in these features from the type species of *Wilkingia*. We have been unable to find additional material with these important details preserved. It may be important that the form of the escutcheon resembles that of *W. regularis* without the lateral separation



Fig. 27 *Wilkingia granosa* (Shumard). Upper Carboniferous, Pennsylvanian, 'Cisco, Graham', Young County, Texas. USNM Acc. 27130 (1 of 9), left side; the right valve is raised and shows the anterior part of the ligament nymph (the posterior part of the right valve is considerably eroded); $\times 1.3$.

REMARKS. Species here included as *Praeundulomya* have mostly been attributed to *Wilkingia* or *Dulunomya* by other recent authors. In the Gondwana area *Praeundulomya* seems to have been replaced by *Undulomya* and *Exochorhynchus* early in Permian time, before the beginning of the Kazanian. The transition between *Praeundulomya* and *Undulomya* was demonstrated by Dickins (1957). Transitional species such as *U. insolitus* (Thomas, 1928) therefore indicate an age somewhere in the Upper Artinskian, following the correlation of Dickins (1963: 21). In the Amatope Mountains, Peru, Permian bivalves and Pennsylvanian ammonoids seem to be associated; this might be due to mixing during collection.

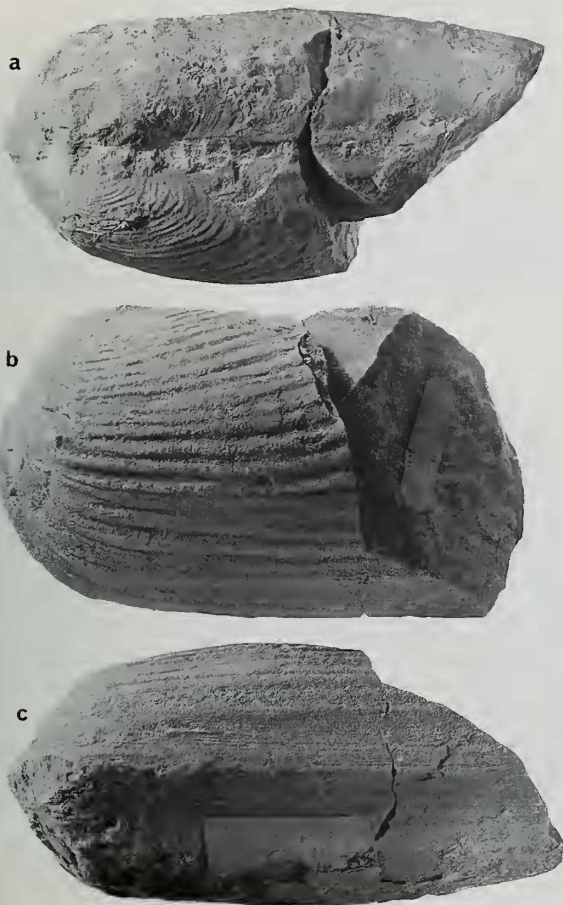


Fig. 28 *Praeundulomya maxima* (Portlock). Lower Carboniferous, Viséan, Donaghenny, Co. Tyrone, Ireland; BGS 6561, holotype; Fig. 28a, top view; Fig. 28b, left valve; Fig. 28c, ventral view; all $\times 0.88$.

***Praeundulomya maxima* (Portlock, 1843) Figs 28–29**

- 1843 *Sanguinolaria maxima* Portlock: 434; pl. 36, figs 1a, 1b.
 1851a *Sanguinolites clava* M'Coy: 172.
 1852 *Allorisma terminalis* Hall: 413; pl. 2, fig. 4a–b.
 ?1859 *Allorisma subcuneata* Meek & Hayden: 37; pl. 1, figs 10a–b.
 1898 *Allorisma subcuneata* Meek & Hayden; Weller: 79–80.
 1900 *Allorisma maxima* (Portlock); Hind: 419; pl. 47, fig. 5.
 ?1900 *Allorisma maxima* (Portlock); Hind: 419; pl. 47, figs 6, 7a, 7b.
 1962 *Allorismiella regularis* (King); Astafieva-Urbaitis: 39, fig. 1.
 ?1974 *Wilkingia terminale* (Hall); Runnegar: pl. 1, fig. 31.
 ?1984 *Dulunomya maxima* (Portlock); Astafieva-Urbaitis & Dickins: 39.

HOLOTYPE. BGS (Leeds) 6561 (figured Portlock (1843: 434; pl. 36, figs 1a, 1b) and Hind (1900: pl. 47, fig. 5)), preserved

in a light grey Carboniferous Limestone (possibly early Viséan), from Tyrone, Donaghenny, Co. Tyrone, Ireland.

OTHER MATERIAL. SM E1089, the type of *Sanguinolites clava* M'Coy 1851, and SM E1090, both from the Upper Grey Limestone, Upper Viséan, D2 (lower part of the Brigantian), at Llangollen, north Wales. SM E1090 is apparently slightly younger than the holotype.

DIAGNOSIS. Robust subquadrate species, with thin shell, ventral margin more or less parallel to the dorsal. Ornament of coarse, evenly rounded rugae parallel to the exterior, anterior and most of the ventral margins, but thicker and non-parallel at the posterior margin.

DESCRIPTION. Lunule and escutcheon present. Escutcheon made up of an elongate flattened area. Below the escutcheon there is a well-marked groove. The adductor muscles and the rear part of the pallial line are clearly visible in BM L47524. The anterior adductor muscle is rounded and slightly ovoid in a dorsoventral direction. Above is a small rounded scar, apparently of the anterior pedal retractor. The posterior adductor is high, rounded, but lightly marked. A deep pallial sinus is visible below the muscle scar. Thin shell is preserved in a few places. A small posterior gape was apparently present.

COMPARISONS. The specimens figured by Hind (1900: pl. 47, figs 6, 7) from the Viséan of Llangollen, north Wales, can be seen to have a slightly more sinuous posterior shell outline and have slightly less regular ribs than the holotype, even though the latter is not a complete specimen. At present we do not regard this as a specific difference. In fact specimens from the Upper Pennsylvanian of Texas named *Allorisma subcuneata* by Meek & Hayden (1858) more closely resemble the holotype. These younger specimens are usually a little smaller than *P. maxima*, but it is difficult to pick out any specific difference even in the best-preserved individuals. Also *Allorisma terminalis* Hall (1852) is probably a synonym of *P. subcuneata*. At present we do not have enough material on which to make measurements that might confirm our view that these species are similar in shape, and we tentatively include both as synonyms of *P. maxima*. Likewise we are unable to distinguish the two specimens from the Viséan of the Moscow Basin listed in the synonymy.

Praeundulomya maxima is very similar to the Permian type species *P. concentrica* Dickins 1957, but the latter has broader radiating internal posterior shell ribs. It also has comarginal low ribs that are more broadly spaced, which undergo low angular changes of direction in the lower part of the posterior or siphonal area. The pallial sinus of *P. concentrica* has not been observed although it is assumed to have been present, as an advanced character shared with *Wilkingia* and other species of *Praeundulomya*.

Genus **EXOCHORHYNCHUS** Meek & Hayden, 1865

TYPE SPECIES. ?*Allorisma altirostrata* Meek & Hayden, 1858, by original designation.

REMARKS. Examination of the type material of *E. altirostrata* in the United States National Museum led us to reject the use of this generic name, because all of the specimens were crushed and apparently foreshortened along their long axis, making it impossible to compare them with *Praeundulomya*.

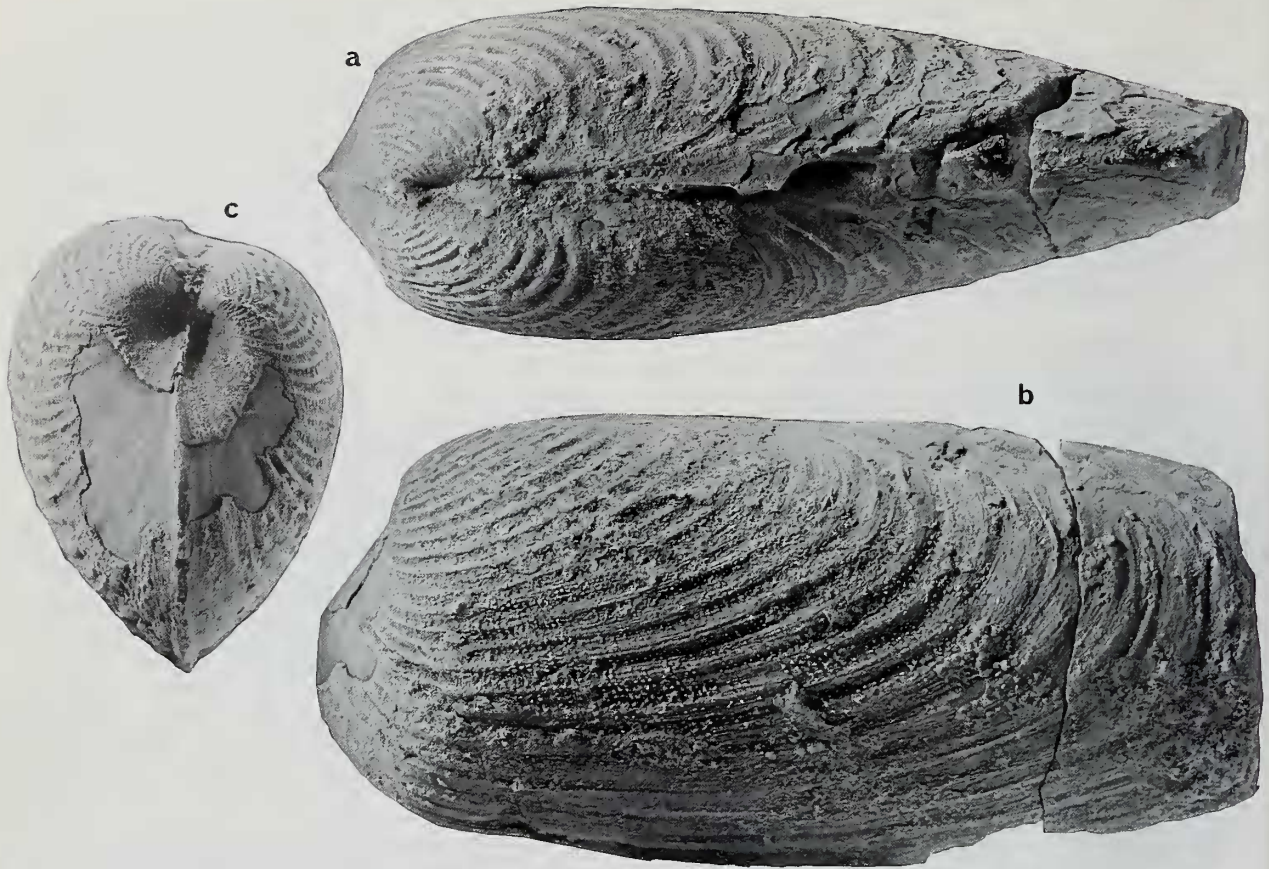


Fig. 29 *Praeundulomya maxima* (Portlock). Upper Carboniferous, Upper Pennsylvanian, Cisco Formation, near Jacksboro, Texas. BM PL5012. C. H. C. Brunton Collection (previously identified as *subcuneatus* Hall); Fig. 29a, dorsal view; Fig. 29b, side view; Fig. 29c, anterior view; all $\times 1.5$.

Runnegar (1974) also took this view and rejected the name as a *nomen dubium*. However, our more recent examination of the type material of *Allorisma barringtoni* Thomas, 1928, first described as Carboniferous but here reinterpreted as Upper Artinskian, has shown us that there really are some species that have shells much shorter than *Undulomya maxima*, and which seem to be intermediate in form between Undulomyiinae and the Mesozoic species of *Homomya* and *Pholadomya*. They also show no trace of the internal dorsal posterior ribs that are typical of *Undulomya* and *Praeundulomya*. For these reasons we resurrect the generic name *Exochorhynchus*.

Exochorhynchus barringtoni (Thomas, 1928)

Figs 30a–b

- 1928 *Allorisma barringtoni* Thomas: 221–2; pl. 7, figs 5, 6.
 ?1960 *Allorisma similis* Lutkevich & Lobanova: 83; pl. 10, figs 6–8.

MATERIAL. The holotype is SM A4948 (Fig. 30), and SM A4971 is one of several paratypes in the same collection; all are apparently from the Permian, probably the Upper Artinskian, of Sullana Rd., 1.5 miles south of El Muerto and Steel Hill, Parinas Quebrada, NW Peru, but (?wrongly) associated with mid-Pennsylvanian ammonoids when they were collected.

DESCRIPTION. A medium-sized species with rounded posterior

and anterior margins and the ventral margin sub-parallel to the hinge line. The regular, low comarginal rugae are very similar to those of *Praeundulomya*. The posterior gape is very narrow and the narrow escutcheon is defined by a low, but distinct, carina. The umbones are well to the anterior, and the shell is apparently very thin.

REMARKS. *Exochorhynchus barringtoni* resembles the concentrically ribbed Pholadomyidae in the Triassic and it may be ancestral to them. There is also a considerable similarity to the Australian genus *Vacunella*. For the present, however, we follow the view of Runnegar and others that *Vacunella* developed independently in the Australasian area from some species of *Myonia* lacking a pallial sinus.

A number of similar species of *Exochorhynchus* have been described from Mongolia by Astafieva-Urbaitis (1981). The species described by Lutkevich & Lobanova (1960) from the Taimyr Peninsula of arctic Russia is somewhat distorted but has no features to distinguish it from the present species.

Subfamily **CHAENOMYINAE** Waterhouse, 1966

Genus **CHAENOMYA** Meek, 1865

TYPE SPECIES. ?*Allorisma leavenworthensis* Meek & Hayden, 1859, by monotypy.

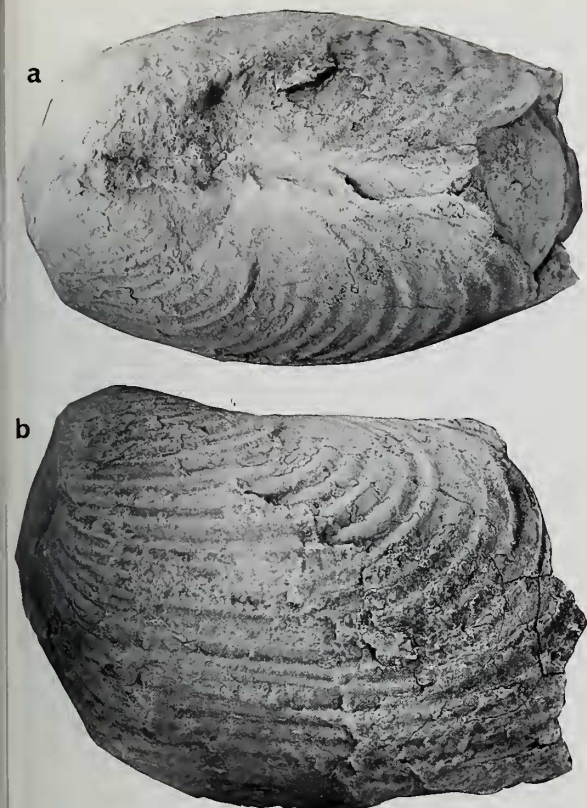


Fig. 30 *Exochorhynchus barringtoni* (Thomas). ?Lower Permian, ?Upper Artinskian, Sullana Road, 1.5 miles south of El Muerta Steel Hill, Parinas Quebrada, Amotape Mountains, NW Peru. SM A4971, paratype; Fig. 30a, dorsal view; Fig. 30b, left valve; both $\times 1.5$.

DESCRIPTION. Medium-sized, elongate shells with the umbones about half-way between the mid-point and the anterior margins. Prominent rounded posterior gape present, of almost the full shell height. Hinge without teeth; a well-developed ligament nymph extends for a short distance behind the umbones which supports a stout short C-spring ligament (see Fig. 31). The rounded edges of the escutcheon fade half-way to the posterior margins, which diverge in a gentle curve to form the top of the siphonal gape. The shell is thin and covered with regular rows of periostracal spicules.

COMPARISONS. *Chaenomya* Meek, 1865, has a broad posterior gape and hence, by comparison with living taxa, probably had long, conjoined, periostracum-covered siphons. It does not, however, have a deep pallial sinus, a feature we take to be a synapomorphy of the Undulomyiinae, and we therefore consider that it lies on a separate line of descent from *Pholadomya* and that subfamily. *Chaenomya* is very similar to the Jurassic genus *Osteomya* but we think that this is a case of convergence; *Osteomya* shares the transcurrent rugae on the anterior flank with the partly contemporaneous genus *Plectomya*, which differs only in having a narrow posterior gape. *Chaenomya* has more prosogyral umbones than either *Osteomya* or *Plectomya*. There are comparable dense pustulose striae on the flank but these are much more prominent on the siphonal area of *Chaenomya* than either of the two Jurassic genera. The convergence probably reflects

comparable increase in the development of the siphons. *Chaenomya* also shows convergence, in characters we associate with deep burrowing, with the Undulomyiinae and the East Australian Permian genus *Vacunella*. Both of these taxa have a prominent inflexed pallial sinus and only a very modest posterior gape, which leads us to believe they belong to a different line of descent. It is possible that *Chaenomya* evolved from a species of similar shape and with a similar pallial line but without the wide posterior gape, such as the species described by de Koninck (1885) as *Chaenomya jacunda* (see p. 82 below). The wide posterior gape seems to be an alternative strategy of siphon formation to that of *Wilkingia* and *Pholadomya*, where in the living genus at least type 'C' siphons are developed with only a modest posterior gape. *Australomya* Runnegar (1969) is more compressed, lacks the distinct posterior or siphonal area and has a tendency towards opisthocline umbones. In this last character it resembles later genera such as *Thracia* and *Plectomya*. At present we are unable to ascribe more than this one species to the subfamily. Runnegar (1974: 928-9) also included *Cosmomya* in the Chaenomyiinae, because he rejected the use of the name Sanguinolitidae, following his inclusion of *Sanguinolites* in the Grammysiidae.

***Chaenomya leavenworthensis* (Meek & Hayden, 1859)**
Fig. 31

- 1859 ?*Allorisma leavenworthensis* Meek & Hayden: 263-4.
1865 *Chaenomya leavenworthensis* (Meek & Hayden); Meek: 42.
1967 *Chaenomya leavenworthensis* (Meek & Hayden); Runnegar: 63; pl. 11, figs 12-13.
1969b *Chaenomya leavenworthensis* (Meek & Hayden); Waterhouse: 38-9, figs 7J, 8I, 13; pl. 1, fig. 4; pl. 2, figs 5-9; pl. 3, figs 1-4, 7.
1974 *Chaenomya leavenworthensis* (Meek & Hayden); Runnegar: 929, text-fig. 5g; pl. 3, figs 5, 7.

MATERIAL. One specimen, USNM collection, from the Upper Carboniferous, at loc. 515g, Lower Graham Formation, 0.5 miles north of Texas 24, 6.5 miles west of Jacksboro, Texas.

REMARKS. This beautifully preserved specimen shows the distribution of spicules and the form of the ligament in perfect detail. The internal characters were well illustrated by Runnegar (1974: text-fig. 5g).



Fig. 31 *Chaenomya leavenworthensis* (Meek & Hayden). Upper Carboniferous, Lower Graham Formation, locality 515g, 0.5 miles north of Texas 24, 6.5 miles west of Jacksboro, Texas. USNM; with ligament and periostracal spicules preserved; dorsal view, approx. $\times 1$.

Subfamily ALULINAE Maillieux, 1937

REMARKS. These are elongate shells with an extended posterior. The shell surface bears rows of prominent periostracal pustules, which we interpret as a synapomorphy of the majority of the Anomalodesmata. The ligament is external, borne on a well-defined nymph and, most importantly, a well-formed cardinal tooth is present. The hinge of *Alula* is well illustrated by Runnegar & Newell (1971).

Genus *TELLINOMORPHA* de Koninck, 1885

TYPE SPECIES. *Tellinomorpha cuneiformis* de Koninck, 1885, by monotypy.

COMMENTS. The elongate form and rudimentary cardinal tooth in the right valve link *Tellinomorpha* with the Alulinae.

Tellinomorpha cuneiformis de Koninck, 1885 Figs 32a-b

1885 *Tellinomorpha cuneiformis* de Koninck: 90-1, pl. 21, figs 1, 2.

1900 *Tellinomorpha cuneiformis* de Koninck; Hind: 433, pl. 49, figs 5-9.

HOLOTYPE. Musée nationale d'Histoire naturelle de Belgique, Brussels, no. 1698, from the Lower Carboniferous, Viséan, at Argenteau, near Visé, Belgium; this is the only known specimen.

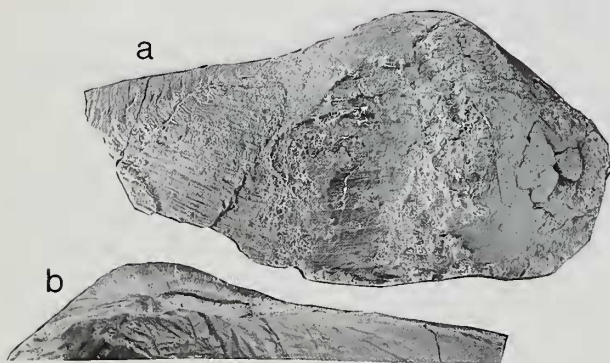


Fig. 32 *Tellinomorpha cuneiformis* de Koninck. Lower Carboniferous, Viséan, Argenteau, near Visé, Belgium. MNHN 1698, holotype; Fig. 32a, exterior of right valve; Fig. 32b, hinge area of interior of same valve, $\times 1$.

DESCRIPTION. The holotype has the characteristic shape of a sanguinolitid, with a broad subumbonal sulcus and a sinuous ventral margin. The posterior part of the shell is attenuated, with the narrow siphonal area demarcated by the upturn of the growth lines. The siphonal margin has a slight median sulcus shaped so that two siphonal orifices are formed. The central surface of the flank has fine radiating striae which are, however, eroded and it is not certain whether or not they bore surface pustules. Irregular surface rugae are present indicating wrinkles in the periostracum. The hinge of the right valve (the only one known) has teeth below the umbo resembling those of some heterodonts and other groups where weak 'cardinal' teeth are present. The formula is RV

(1) 0 1 0 N, which resembles some found in the trigoniacean family Schizodidae, but the arched gap or hiatus typical of the schizodids (Newell & Boyd, 1975: fig. 2) is not present, and *Tellinomorpha* has a very typical anomalodesmatid shape. The hinge is similar in the disposition of the teeth to that of *Alula* (figured by Runnegar & Newell, 1971: fig. 270) although they are less prominent, more like those of the Permophoridae. Simple teeth of this nature have apparently developed independently in a number of closely and distantly related stocks. *Tellinomorpha* does not have the elongate escutcheon typical of most Sanguinolitidae. The dorsal margin is apparently not parallel to the plane of commissure, indicating that there may have been both anterior and posterior shell gaps. There is a short, moderately stout ligament nymph behind the umbo, separated from the dorsal shell surface by a well-formed, narrow ligament groove.

REMARKS. *Tellinomorpha* may be compared with '*Sanguinolites clavatus* Etheridge 1877 (non *Allorisma clavata* McChesney 1860), but that species has an elongate, carina-bound escutcheon, indicating that the periostracal ligament joined the two valves back to the dorsal posterior margin, whereas the dorsal margins of *Tellinomorpha* apparently diverged posteriorly in a similar fashion to *Chaenomya* (Fig. 31). Examination of specimens from the Viséan Limestones of the Derbyshire Dome, England, attributed to *Tellinomorpha* by Hind (1900), show that these do not have the attenuated siphonal area of this genus and belong, in fact, to *Wilkingia*.

Subfamily Uncertain

An unnamed genus, intermediate in form between *Gilbertsonia* of the Sanguinolitinae and *Chaenomya*, is described here. It is possibly ancestral to *Chaenomya* or *Vacunella* or to both, and it includes the species '*Chaenomya jacunda* de Koninck. Without further details of its characters we are uncertain in which subfamily it should be included.

Genus Uncertain

'*Chaenomya jacunda* de Koninck resembles *Gilbertsonia* in shape but has a broad, shallow pallial sinus, somewhat resembling that of several species of *Myofossa* and *Cosmomya*. A narrow but obvious siphonal gape is present, which is about two-thirds of the total shell height, and therefore not as extensive as the posterior gape of *Chaenomya leavenworthensis*.

'*Chaenomya jacunda* de Koninck, 1885 Figs 33a-d

1885 *Chaenomya jacunda* de Koninck: 7; pl. 1, figs 1-8.
1974 *Sedgwickia? jacunda* (de Koninck) Runnegar: pl. 3, figs 14-16.

MATERIAL. BM L13446, BM L13481, BM L47500 and BM PL1655, from the Lower Carboniferous, Viséan, at Tournai, Belgium.

DESCRIPTION. Medium-sized anomalodesmatid, gibbous with forward-pointing umbones well to the anterior. A small lunule is present with a subrounded carinate margin. The posterior dorsal margin is relatively long and straight, set in a broad escutcheon which is bounded by subrounded carinae. The siphonal margins are relatively long and straight, forming

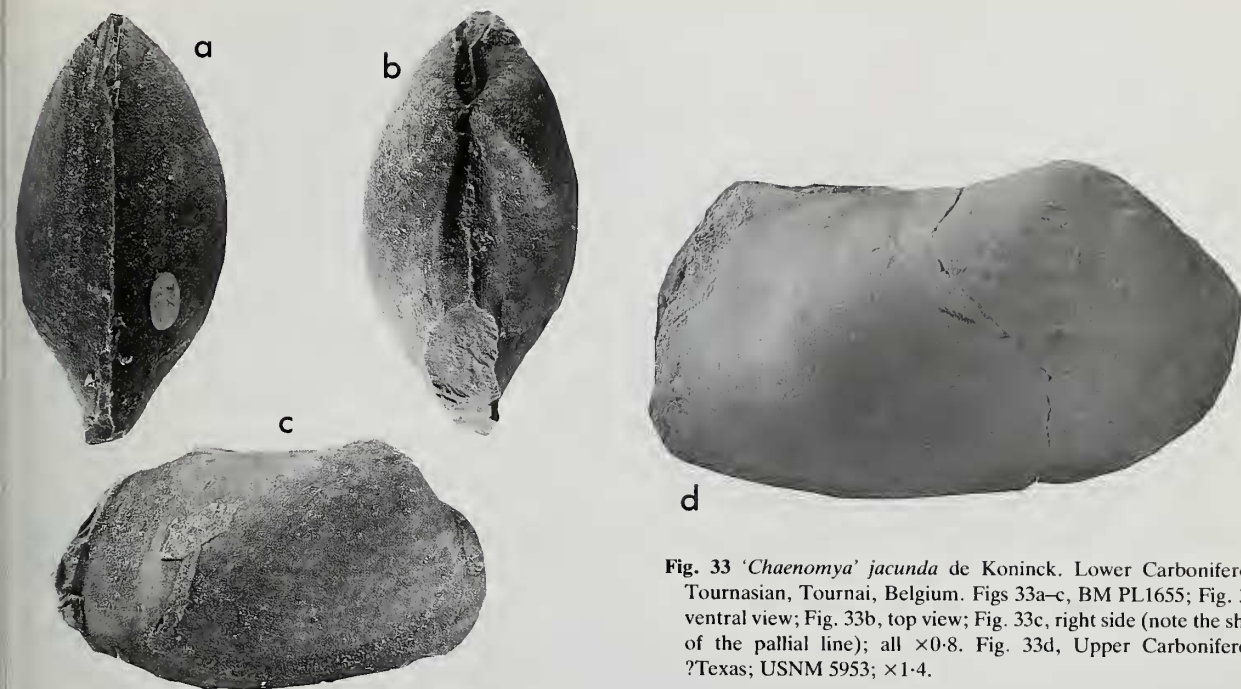


Fig. 33 '*Chaenomya*' *jacunda* de Koninck. Lower Carboniferous, Tournasian, Tournai, Belgium. Figs 33a-c, BM PL1655; Fig. 33a, ventral view; Fig. 33b, top view; Fig. 33c, right side (note the shape of the pallial line); all $\times 0.8$. Fig. 33d, Upper Carboniferous, ?Texas; USNM 5953; $\times 1.4$.

an obtuse angle with the hinge line. There is a moderate siphonal gape. The maximum width lies well to the posterior, but when viewed from above or below the shell at first narrows rapidly then straightens out towards the siphonal gape. There is a wide but shallow pallial sinus sub-parallel to the siphonal margin.

REMARKS. '*C.*' *jacunda* resembles some species of *Myonia* and *Vacunella* in shape and it is one possibility that it is their ancestor. An example (USNM 5952, Fig. 33c), possibly different, from the Upper Pennsylvanian of Texas, suggests that this rather rare taxon may have had a considerable time range. '*C.*' *jacunda* is also closely similar to some species of the Mesozoic genus *Pachymya*, particularly *P. crassiuscula* (Morris & Lycett, 1855) from the Bacocian of Normandy and England. '*C.*' *jacunda* is similar to *Myofossa omaliana* (de Koninck) in general shape and in the form of the pallial line. It is, however, much larger and does not have the opisthodetic imbrones typical of *Myofossa*. The two could share close common ancestry.

Family **PERMOPHORIDAE** van de Poel, 1959
[*Pro* Pleurophoridae Dall, 1895; I.C.Z.N., Art. 40]

In the present paper we propose that the family Permophoridae should be included with the Anomalodesmata rather than with the heterodonts, as in the *Treatise* classification (Chavan, 1969; Moore, 1969: N543). Aspects of the *Treatise* diagnosis of this family are, we suggest, an interpretation, based on its assumed systematic position. The following phrases, quoted from the *Treatise*, are clearly correct if the Permophoridae were properly interpreted as carditaceans; in fact they are an expression of the more obvious differences: 'Cardinals partly obsolete', 'radial ribs tending to be obsolete on anterior part of surface', 'anterior laterals lacking in most' (Chavan,

in Moore, 1969; N543). The similarities between the Permophoridae and the Carditidae and the placing of the Permophoridae in the Carditacea depend upon the interpretation of the dentition. In heterodont terms, the teeth of the Permophoridae may be described as lucinoid when they are present. Bernard's analysis of heterodont teeth (1895), although of immense value in the Veneroidea, is now suspected of supporting false homologies in the lucinoids (MacAlester 1966, Morris 1978). The considerable doubt concerning homologies of teeth between the heterodonts and the Trigoniacea had led Boyd & Newell (1968) to abandon the Bernard-Douvill  system for that superfamily and instead make use of a more objective (i.e. with no presupposition of homology) Steinmann notation. We suggest that the Permophoridae and the Carditidae belong to quite different subclasses of bivalves which separated before or at the very beginning of the Ordovician. If by some chance their cardinal teeth are homologous, which is unlikely on our present evidence, their form would be primitive for the two subclasses and would not indicate a close relationship between the two families. We think that the apparent similarity of tooth pattern in the two families is more likely to be the result of convergence. The number of possible teeth patterns is limited when there are fewer individual teeth. We therefore urge the use of the Steinmann notation for toothed forms of the Permophoridae. The true relationship of the Carditacea, we consider, has been recognized by Yonge (1969), who described the great similarity of 'mantle fingers' between the teeth in both Carditidae and Astartidae. The modioliform shape of some Maastrichtian to Recent Carditidae we would interpret as an advanced character because nearly all the earlier Cretaceous Carditidae are round in shape, resembling *Cyclocardia* and *Venericardia* and similar or more gibbous species of Astartidae, but with radiating ribs.

There is no clear evidence in the fossil record that the Cretaceous to Recent Carditidae are descended from those in

the late Triassic. The fact that the Cretaceous carditids share most of their characters with the Astartidae leads us to believe that the Carditidae as presently recognized (Chavan 1969) are not a single clade. We believe that more than one group descended from ancestors at present classified with the Astartidae. They are, we believe, essentially 'Astartidae' which have developed radial ribs, a phenomenon that probably happened more than once. We therefore support Yonge's view that there is no need for two superfamilial names, Crassatellacea and Carditacea.

Most Permophoridae may be distinguished from most Mytiloidea by the presence of a clearly-marked escutcheon and the fact that the external ligament is mounted on relatively short, upward facing, nymphs although there is considerable overlap between the two taxa in overall shell shape.

Subfamily **PERMOPHORINAE** van de Poel, 1959 (1895)

[*Nom. trans.* Chavan, in Moore 1969]

Genus **PERMOPHORUS** Chavan, 1954

Figs 34–35

TYPE SPECIES. *Arca costata* Brown, 1841, by monotypy.

REMARKS. The nomenclature of this genus is fully dealt with by Chavan in the *Treatise* (Chavan, in Moore 1969: N543). Examples of the type species and a similar species from the Permian of the Glass Mountains are figured here to show clearly the characteristics of the genus.

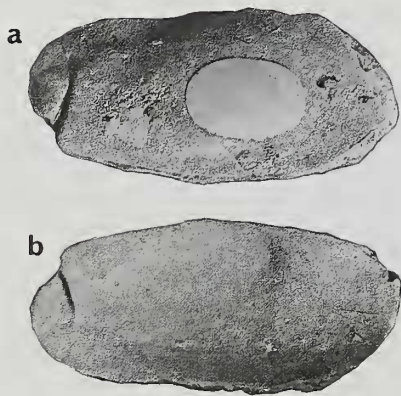


Fig. 34 *Permophorus costatus* (Brown). Upper Permian, Magnesian Limestone, England; BM PL235, steinkern; Fig. 34a, right side; Fig. 34b, left side; both $\times 1.5$.

Licharew (1925: 125) proposed a new name, *Pleurophorina*, in which he included a single species, *Modiola simpla* Keyserling (1846: 28; pl. 10, fig. 22; pl. 14, fig. 1), which must, therefore, be the type of the genus by monotypy. The hinges figured by Licharew (1925: pl. 1, figs 1, 2) are close to *Permophorus* Chavan (1954) (pro *Pleurophorus* King, 1844, non Mulsant, 1842). If Licharew's specimens are correctly referred to *Modiola simpla* Keyserling, and we are not able to check on this, then *Permophorus* may be a synonym of *Pleurophorina*.

The shell is elongate-ovate with the umbones well towards the anterior. The rounded posterior margin and the area from

it to the umbones is separated from the flank by a fine radial rib. There are sometimes further radial ribs on this posterior dorsal area. The flank and anterior are usually smooth. The hinge has an opisthodontic parivincular ligament set on slender short nymphs. Posterior lateral teeth occur, sometimes in each valve. The right valve has a single, moderately large cuneiform tooth which fits between the two subumbonal teeth of the left valve. These may be seen in the rather badly preserved steinkerns (Logan 1964) of *P. costata* but are better observed in *Permophorus* cf. *albequus* (Beede) (Fig. 35). The anterior adductor scar is of small to medium size, and deeply inset leaving a well-formed vertical buttress behind it. The posterior adductor is rounded and of medium size and set below the distal end of the posterior lateral tooth. The pallial line is entire although it is usually very faint towards the posterior of the shell.

Genus **PLEUROPHORELLA** Girty, 1904

TYPE SPECIES. *Pleurophorella papillosa* Girty, 1904, by original designation, from the Graham formation, Pennsylvanian (Cisco), of Young County, Texas.

SYNONYMS. *Eopleurophorus* Elias, 1957: 780 (type species, *Cypricardia? tricostata* Portlock (1843: 441; pl. 34, fig. 17) as interpreted by Hind (1900: 391), by original designation); from Carnteel, County Tyrone and Drumkeeran, County Fermanagh, Ireland.

DIAGNOSIS. Transversely elongate, distinct lunule and escutcheon, radiating ornament fairly well developed, especially in posterior part of shell. Granulation of shell surface by periostracal spicules distinct, apparently absent in some. More or less edentulous. Ligament lodged in a narrow elongated groove in the anterior part of a flat escutcheon which extends well towards the rear. Nymphs slender and low. The anterior adductor scar is well differentiated and bounded at the rear by a distinct buttress.

REMARKS. Chavan (1969: N546) placed *Pleurophorella* in the Permophoridae, though he expressed some doubt. We refer to this genus a number of Carboniferous species which have usually been referred to *Sanguinolites*; these include *Sanguinolites tricostatus* (Portlock, 1843), which is the type species of *Eopleurophorus* Elias (1957: 781), *S. striatolamellosus* (de Koninck, 1842), *S. striatus* Hind, 1900, *S. striatogranulatus* Hind, 1900, *S. visetensis* (de Ryckholt, 1847), *S. oblongus* Hind, 1900, *S. roxburgensis* Hind, 1900, and *S. ovalis* Hind, 1900. Other Carboniferous species are also included here.

Poor development or absence of teeth, together with the granulation of the shell surface, have perhaps hindered recognition of the relationships of this group. Genera of Permophoridae with well-developed lateral and cardinal hinge teeth share with the edentulous Carboniferous forms the distinctive lunule and escutcheon and the distinctly separated anterior adductor scar. The genus *Stuchburia* from the Lower to Upper Permian (see Dickins, 1963: 95) has poorly developed cardinal teeth and variable development of posterior lateral teeth, and occupies an intermediate position. The development of external granulation (pustules—a short rounded form of periostracal spicules) is apparently variable in both edentulous and tooth-bearing forms. Its presence or absence may also reflect preservation. In Permian and



Fig. 35 *Permophorus* cf. *albequus* (Beede). Permian, West Texas; Fig. 35a, inside of left valve, $\times 4$; Fig. 35b, umbonal area inside right valve, *c.* $\times 8$. Photographs kindly provided by Professor N. Newell.

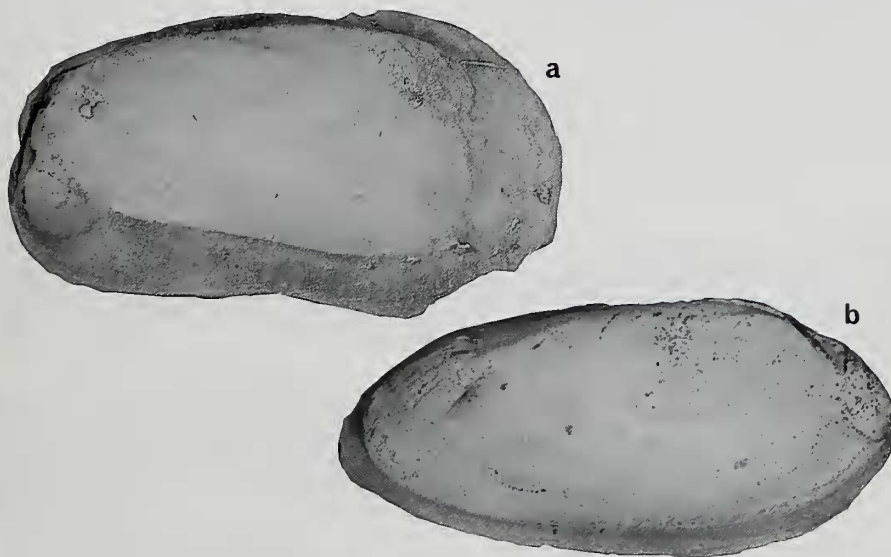


Fig. 36 Two species of *Stutchburia* with normal and unusual pallial muscle attachment. Fig. 36a, *Stutchburia farleyensis* (Etheridge); Lower Permian, Farley, New South Wales, Australia; BM PL603, with deeply inserted adductors and entire pallial line. Fig. 36b, '*Stutchburia*' sp.; Lower Permian, Bowen Coalfield, Queensland, Australia; BM PL539, with similar adductors and pallial line, but with an area of small spots, apparently of muscle attachment, below the posterior adductor, where a pial sinus is found in many other bivalves; both $\times 1.5$.

Triassic forms, granulation has been rarely recorded. Newell (1940: 298; pl. 3, fig. 16), however, described and figured irregularly occurring pustules in *Permophorus albequus* (see Fig. 35) from the Upper Permian of the USA, and Licharew (1925: 125) described granulation in *Pleurophorina* from the Kazanian of the USSR. From these data, it is reasonable to conclude that the forms with heterodont-like dentition are related to edentulous forms, and at present it appears that the edentulous Carboniferous forms are the more primitive in this respect.

Hind (1904) included two British Viséan species in the genus *Spathella* Hall 1885, '*Spathella tumida* Hind and '*Spathella cylindracea* (M'Coy). These seem to us to belong

to *Pleurophorella*. Hinge details of *Spathella* are not well known, but Pojeta, Zhang & Yang (1986: 73) diagnosed the genus based on its type species as a lithophagiform modiomorphid with coarse comarginal ornament. This, and their illustrations of *Spathella typica* Hall, suggest to us that *Spathella* is not an anomalodesmatid and the two species were incorrectly placed in it by Hind.

Pojeta, Zhang & Yang (1986: 86; pl. 57, figs 5-8) also figured topotype material of *Sphenotus arcaiformis* Hall & Whitfield, 1869, the type species of that genus. They also followed Driscoll (1965) and others in ascribing to *Sphenotus* some species that we would attribute to *Pleurophorella*. When the hinge and musculature of *Sphenotus*

arcaeiformis are known it may well prove correct to synonymize *Pleurophorella* with *Sphenotus*; in the meantime we prefer to use *Pleurophorella*, where these characters are now known.

***Pleurophorella papillosa* Girty, 1904** Fig. 37

1904 *Pleurophorella papillosa* Girty: 729-32; pl. 45, figs 4-6; pl. 46, fig. 5.

?1969 *Pleurophorella papillosa* Girty; Chavan: N546.

MATERIAL. A single specimen, USNM G. A. C. Collection, from the Upper Pennsylvanian ('Upper Finis'), hills 0.5-1



Fig. 37 *Pleurophorella papillosa* (Girty). Upper Carboniferous, Upper Pennsylvanian, Upper Finis Shale; hills 0.5-1 mile north of a point 0.3 miles NE of intersection of old Chico Road, 3.2 miles east of Jacksboro, Texas; USNM, G.A.C. Collection; dorsal view with ligament in place; c. $\times 1$.

mile north of a point 0.3 miles north-east of intersection of old Chico road and Wizard Wells Road, 3.2 miles east of Jacksboro, Texas.

DIAGNOSIS. Shell surface with fine, close-packed pustules all over, otherwise without ornament. Nymphs slender and long, nearly half the length of the escutcheon.

REMARKS. We figure a specimen (Fig. 37) that conforms to Girty's original description and comes from the same area and horizon. It shows the nature of the nymph, occupying the anterior part of the escutcheon, and the surface is covered with fine close-packed pustules which seem to us to be merely low rounded periostracal spicules that do not show any particular alignment.

***Pleurophorella tricostata* (Portlock, 1843)** Figs 38a-i

1843 *Cypricardia? tricostata* Portlock: 441; pl. 34, fig. 17.

1900 *Sanguinolites tricostatus* Portlock; Hind: 391-3.

?1900 *Sanguinolites striatogranulatus* Hind: 393-4; pl. 42, figs 16-22.

HOLOTYPE. BGS 14747 (Figs 38a, b).

OTHER MATERIAL. BM L13446, Carboniferous Limestone, Britain (no further details recorded); BM 22545 and BM L13481, J. Wright Collection, Carboniferous Limestone, Little Island, County Cork; BM L47500, Hind Collection, Poolvash, Isle of Man; all are from the Viséan. BM L24821-3 (Gilbertson Collection no. 97) are three syntypes of *Cypricardia glabrata* Phillips, 1836, that could be young

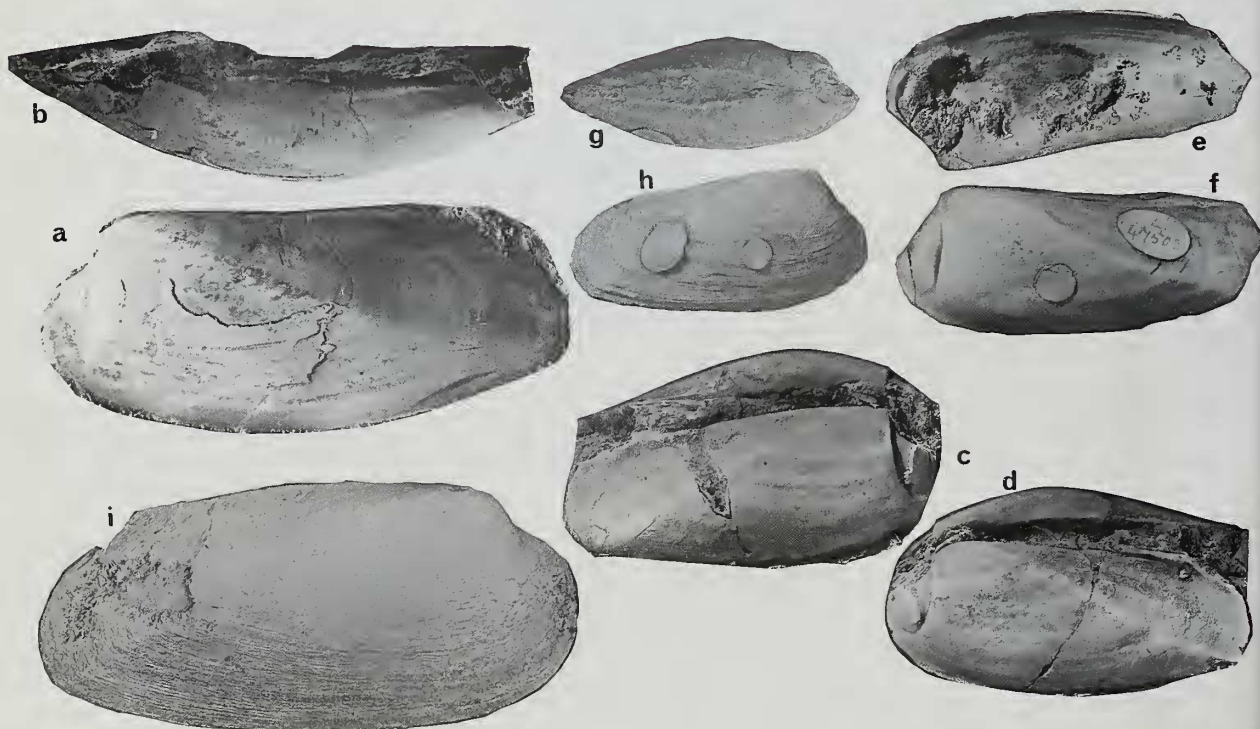


Fig. 38 *Pleurophorella tricostata* (Portlock). Lower Carboniferous, Viséan. Figs 38a-b, County Fermanagh, Northern Ireland; BGS 14717, holotype; Fig. 38a, left valve, side view; Fig. 38b, left valve, dorsal view; both $\times 1.6$. Figs 38c-h, three syntypes of *Sanguinolites striatogranulatus* Hind; Figs 38c-f, Poolvash, Isle of Man; Figs 38c-d, BM L47500; Fig. 38c, right side; Fig. 38d, left side; both $\times 1$; Figs 38e-f, BM L47502; Fig. 38e, right side; Fig. 38f, left side; both $\times 1$; Figs 38g-f, Stebden Hill, Yorkshire, England; BM L47499, with shell preserved; Fig. 38g, dorsal view; Fig. 38h, right valve; both $\times 0.9$. Fig. 38i, Little Island, County Cork, Ireland; BM L24545, $\times 1.8$.

individuals of this or a number of other British species. As we are unable to decide to which of the smoother species they belong, we provisionally reject Phillips' species *Cypricardia glabrata* as a *nomen dubium*.

DESCRIPTION. Both the lunule and the escutcheon are defined by a distinct carina. The escutcheon is two-thirds of the shell length and the distance from the umbones to the posterior margins is five-sixths of the shell length. The dimensions of specimen BM L24545 are: L 42 mm, H 28.5 mm, U-P 35 mm. The umbones are prosogyral and confluent with a convex lorum on both valves, whereas *Sanguinolites* is concave in this area. The ligament nymph is visible in BM L13446 and 3M L13481; it is separated from the dorsal edge of the escutcheon by a distinct narrow groove, and its dorsal margin lies just below the margin of the escutcheon.

The internal surface is visible in BM L47500. The anterior adductor is well impressed into a raised area of the inner shell surface. The pallial line is partly visible in this specimen but is very faint; it does not have a sinus. Two radiating, fine, low ribs are present between the escutcheon and the low radiating line delimiting the corselet, which distinguishes the species from *Pleurophorella visetensis* de Rychholt (*sensu* Hind, 1900) which has three such ribs.

Closely related species which are not thought to be synonyms are: *Sanguinolites striatolamellosus* de Koninck, *sensu* Hind (1900: 398; pl. 43, fig. 11 & 11a) (Fig. 39) (*non* *Cypricardia striatolamellosa* de Koninck, 1842: pl. H, fig. 1a-c); *Isocardia transversa* de Koninck (1842: pl. 1, fig. 3a-b); *Sanguinolites oblongus* Hind (1900: pl. 43, figs 6-7); and possibly *Sanguinolites visetensis* (de Rychholt, 1847) *sensu* Hind (1900: 395; pl. 43, figs 1-4). We consider, however, that *Sanguinolites striatogranulatus* Hind (1900: 393; pl. 42, figs 6-22) may well be a synonym and the differences in shape and granulation may reflect preservation rather than specific differences.



Fig. 39 *Pleurophorella striatolamellosa* (de Koninck). Lower Carboniferous, Viséan, Stebden Hill, Yorkshire; BM L47510; Fig. 39a, left valve; Fig. 39b, dorsal view; Fig. 39c, anterior view; all $\times 1.25$.

Pleurophorella sp.

Fig. 40

MATERIAL. USNM 515g, two specimens from the Lower Graham Formation, Upper Pennsylvanian, 0.5 miles north of Texas 24, 6.5 miles west of Jacksboro, Texas.

DESCRIPTION. Shell ornament consisting of concave-upwards, sharp, comarginal ribs with intervening fine growth laminae. No surface pustules are preserved. Carinate lunule and escutcheon present. The carina bounding the escutcheon is

crenulate with prominent backward-pointing growth lines. The hinge of the right valve is particularly well preserved (Fig. 40); there is a small anterior tooth, parallel to the anterior dorsal margin, and a thin posterior tooth running parallel to and below the ligament nymph. The nymph is moderately long. It is not well preserved at its proximal end, where there may have been an attachment of the outer anterior ligament. The ligament groove is well preserved, and the ligament is present at the distal end; more proximally the upper surface of the nymph is transversely striate where part of the inner ligament layer has broken away. Growth laminae are visible on the inner surface of the nymph just below the attachment area of the inner ligament.



Fig. 40 *Pleurophorella* sp. Upper Carboniferous, Upper Pennsylvanian, Lower Graham formation, 0.5 miles north of Texas 24, 6.5 miles west of Jacksboro, Texas; USNM 515g, external view of left valve together with hinge of right valve; $\times 1.25$.

REMARKS. *Pleurophorella* sp. is closely similar in morphology to *Stutchburia*.

Pleurophorella transversa (de Koninck, 1842) Fig. 41

1842 *Cypricardia transversa* de Koninck: 94; pl. 1, fig. 3; pl. 3, fig. 8.

1842 *Isocardia transversa* de Koninck: pl. 1, fig. 3 only.

1885 *Sanguinolites transversus* (de Koninck); de Koninck: 76; pl. 17, figs 4-5.

MATERIAL. BM 32908, de Koninck Collection, is a single specimen associated with an original label in de Koninck's

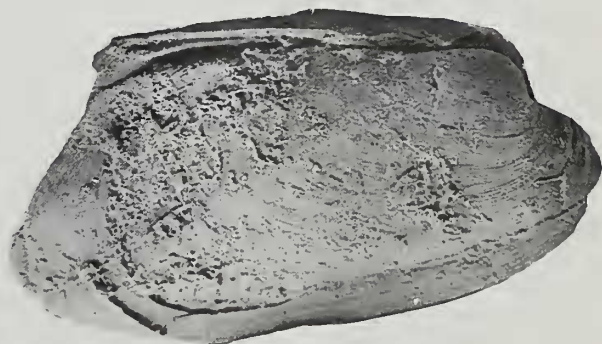


Fig. 41 *Pleurophorella transversa* (de Koninck). Lower Carboniferous, Tournaisian, Tournai, Belgium; BM 32908, de Koninck Collection, ?syntype, slightly oblique view of right side to show posterior lateral tooth of left valve in its correct orientation; $\times 2.5$.

hand reading '*Cypricardia transversa* de Kon.' It is similar in shape and proportions to de Koninck's original figure, but with the valves slightly displaced, and it might be the figured syntype. A second specimen, a steinkern, bearing the same number appears to have been misidentified.

REMARKS. The displacement of the two valves has now exposed part of the hinge of the left valve (Fig. 41), which has a long, narrow hinge plate set into a long narrow carinate escutcheon. There is a slender short 'posterior lateral tooth' that we believe to have developed independently from similar teeth in the heterodonts. There is also a short nymph exposed which runs for a short distance behind the umbones, separated from the shell surface of the escutcheon by a marked ligament groove.

?*Pleurophorella cuneata* (Phillips, 1836) Fig. 42

1836 *Nucula cuneata* Phillips: 210; pl. 5, fig. 14.
1897 '*Nucula*' *cuneata* Phillips; Hind: 205.

HOLOTYPE. BM 97147, Viséan, Bolland, Yorkshire; Gilbertson Collection.

REMARKS. This tiny specimen has umbones at the anterior where it is cordate in section. The dorsal and ventral margins diverge slightly so the greatest height is towards the posterior. The posterior margins are rounded. The shell is very similar in form to a date mussel, except that there is a clearly marked elongate carinate escutcheon, typical of the Permophoridae. The similarity of form to a date mussel raises the possibility that ?*Pleurophorella cuneata* was also a rock borer.



Fig. 42 ?*Pleurophorella cuneata* (Phillips). Lower Carboniferous, Viséan, Bolland, Yorkshire; BM 97147, Gilbertson Collection, holotype; approx. $\times 8$.

Genus **BOWLANDIA** nov.

TYPE SPECIES. *Cypricardia rhombea* Phillips, 1836.

ETYMOLOGY. The generic name is derived from the Forest of Bowland, Yorkshire, an area locally famous for its Carboniferous fossils.

SYNONYM. *Ivanovia* Astafieva-Urbaitis, 1978 (non Dubrolyubova, 1935), type species, *I. slovenica* Astafieva-Urbaitis, 1978, by monotypy. See below.

NOMEN DUBIUM. *Digonomya* Whidborne 1897: 16–17 (type species, *D. elegans*) is superficially similar to the present genus. The type material is in the BGS collections but shows none of the characters of the hinge and is not well preserved; on this account we reject the generic name *Digonomya* as a nomen dubium.

DIAGNOSIS. The new genus resembles *Pleurophorella* but it

has a relatively reduced anterior ventral margin giving it an overall modioliform appearance; we interpret from this that *Bowlandia* had a semi-infaunal byssate to epifaunal byssate habit, much like living *Mytilus edulis*, except that we have no evidence that the genus occurred intertidally. The anterior-ventral margins converge at about 30° in the type species but at a much greater angle, about 150° , in *B. angulata*, suggesting attachment of the latter to harder and more planar substrates. The adductor muscles are somewhat anisomyarian with the anterior one varying from rather small to somewhat reduced. We have only observed the posterior adductor in *B. angulata*; it is medium-sized and rounded, and set close below the distal end of the escutcheon.

REMARKS. *Bowlandia* gen. nov. differs from *Goniophora* Phillips, 1848, in having a thicker shell, a more substantial hinge, and a sharp carinate, elongate escutcheon. It does not have the wide flange delimiting the posterior dorsal area that is present in *Goniophora*, nor the thin diverging internal buttresses that occur behind the umbones of that genus. It is most likely that the two genera belong to different superfamilies. *Goniophora* has recently been under investigation by Dr John Pojeta jr and may not be correctly placed in the Modiomorphidae. There are also no characters yet observed that link *Goniophora* conclusively with the Anomalodesmata.

Hind (1899: 338) proposed the name *Mytilomorpha* as a replacement name for *Goniophora* Phillips, 1848, because *Goniophorus* had been used by Agassiz for a genus of crinoids. This was, however, unnecessary. From Hind's statement *Cypricardia cymbiformis* J. de C. Sowerby is to be regarded as the type species of both *Goniophora* and *Mytilomorpha*, and therefore *Mytilomorpha* is an objective synonym of *Goniophora*.

We consider that the Carboniferous species *Bowlandia rhombea* (Phillips) and *B. angulata* (Hind) should not be placed in *Goniophora*, and belong in fact to the Permophoridae. The similarity is superficial: where *Goniophora cymbiformis* occurs in a badly crushed condition, as in the Upper Silurian of the Ludlow area, it often occurs with a second, apparently unnamed species of similar size and shape but without the considerable flange, which is probably correctly placed in *Cosmogoniophorina* Isberg, 1934. The two have been sometimes thought to be the same species, but in our opinion, this second, Upper Silurian species and the genus *Cosmogoniophorina* itself, belong to the family Permophoridae.

Bowlandia may prove to be closely related to the Upper Permian genus *Naiadopsis* Mendes, 1952 (Runnegar & Newell, 1971: 56–7, fig. 25) from the Parana Basin. *B. rhombea* also closely resembles '*Ivanovia*' *slovenica* Astafieva-Urbaitis (not *Ivanovia* of Dubrolyubova), which is, however, only known from two views of the right side. *Bowlandia slovenica* apparently has a slight flexure of the pallial line, just below the posterior adductor.

***Bowlandia rhombea* (Phillips, 1836)** Figs 43a–h

- 1836 *Cypricardia rhombea* Phillips: 209; pl. 6, fig. 10.
1885 *Sanguinolites rhombea* (Phillips); de Koninck: pl. 15, fig. 28.
1899 *Mytilomorpha rhombea* (Phillips) Hind: 338; pl. 38, figs 6–11.

LECTOTYPE. BM L3480, here designated, is the specimen

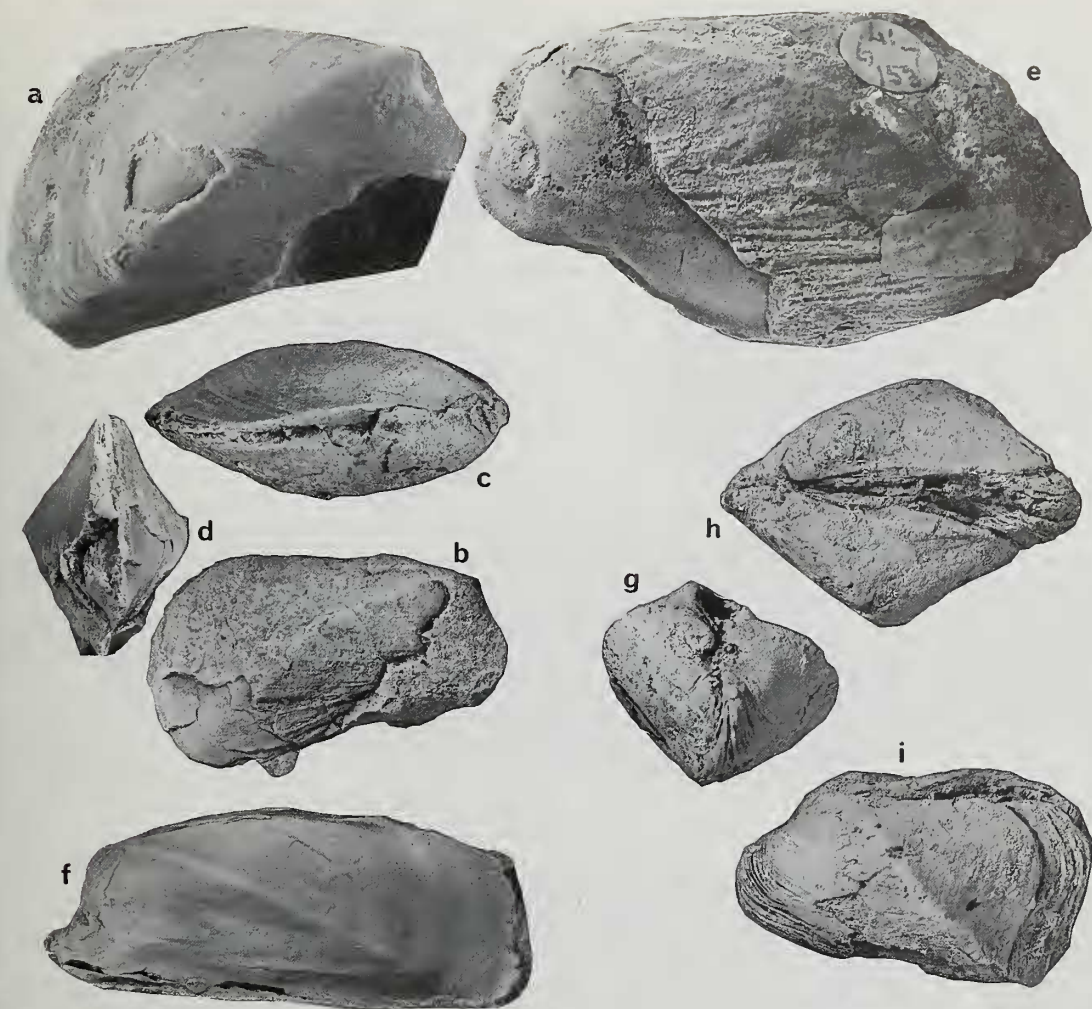


Fig. 43 *Bowlandia rhombea* (Phillips). Figs 43a–e, Lower Carboniferous, Viséan, Bolland, Yorkshire; Fig. 43a, BM L3480, Gilbertson Collection, lectotype, side view of right valve; Figs 43b–d, BM 97182, similar to the lectotype; Fig. 43b, right side; Fig. 43c, dorsal view; Fig. 43d, posterior view; all $\times 1.5$; Fig. 43e, PL5010, probable paralectotype, Gilbertson Collection (no. 97a), view of left side; $\times 2$. Fig. 43f, Lower Carboniferous, Viséan, Poolvash, Isle of Man; BM L47456, large elongate specimen, left side of steinkern; $\times 0.67$. Figs 43g–i, Lower Carboniferous, Tournaisian, Tournai, Belgium; BM PL5011; Fig. 43g, anterior view; Fig. 43h, dorsal view; Fig. 43i, left valve; c. $\times 2$.

gured by Phillips, from the Carboniferous Limestone, Viséan, at Bolland, Yorkshire; Gilbertson collection.

PARALECTOTYPE. BM 97182, from the same horizon and locality as the lectotype. Three further specimens from Bolland in the Gilbertson Collection (no. 97a) are listed as *Cypricardia glabrata* Phillips and therefore are unlikely to be syntypes. (BM L24821–3, Gilbertson Catalogue no. 7, are three syntypes of the true *Cypricardina glabrata*. They are clearly not the same as those of no. 97a; although details of the hinge are not shown, they may belong to *leurophorella*).

OTHER MATERIAL. We refer the following specimens to *B. rhombea*:

Kind Collection: BM L45931–4, Castleton, Derbyshire; BM L45935–7, Elbolten, Yorkshire; BM L47451, Wetton Hill, Leek, Staffordshire; BM L47452–4 and BM L47456, Poolvash, Isle of Man.

Roscoe Collection: BM L43647, Wetton Hill, Leek, Staffordshire; BM L43616–26 and BM L43648, Narrowdale, Hartington, Derbyshire.

Butler Collection: BM L8175, Wetton Hill, Leek, Staffordshire.

Bather Collection: one specimen, Viséan, D₂, Peakhill Farm, Mam Tor, Derbyshire.

OTHER POSSIBLE SYNONYMS. De Koninck (1885) figured many specimens from the Carboniferous of Belgium under many new specific names. All were attributed to *Sanguinolites*, and most are closely similar to *Bowlandia rhombea*, though at the small sizes of most of them it is difficult to distinguish *Bowlandia* from the more carinate species of *Pleurophorella*. The following de Koninck species from the Viséan, étage 3, mostly from Visé, are probably synonyms of *Bowlandia rhombea*: *Sanguinolites apertus* de Koninck (1885: pl. 15, figs 1, 2), *S. solitarius* (pl. 15, figs 16, 17), *S. vexillum* (pl. 15, figs 19, 31, 32), *S. reversus* (pl. 15, fig. 25), *S. bipartitus* (pl. 15,

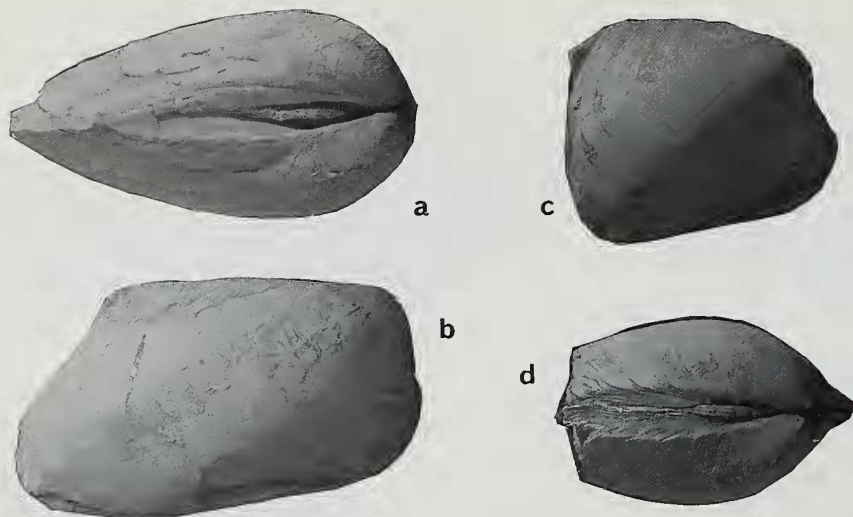


Fig. 44 *Bowlandia* sp. Figs 44a–b, Upper Carboniferous, Pennsylvanian, Missouri Series, Ochelata Group, Wann Formation; old uncompleted railroad cutting, 4 miles north and 2 miles east of Copan, Oklahoma, USA; USNM 6832, Conlin Collection; Fig. 44a, dorsal view; Fig. 44b, right valve. Figs 44c–d, Upper Carboniferous, Pennsylvanian, Canyon Series, Graford Group Shale, above Willow Point Island Member; Bridgeport Clay Pit, Wise County, Texas; USNM 7277, Conlin Collection; Fig. 44c, right valve; Fig. 44d, dorsal view. All slightly enlarged.

fig. 27), *S. quadricostatus* (pl. 15, fig. 34) and *S. reniformis* (pl. 15, figs 45, 46). The first specimen of *S. apertus* (pl. 15, figs 1, 2) is identical to *Bowlandia rhombea* except for the small rounded anterior gape which may have been for a byssus, but a second specimen (de Koninck, 1885: pl. 15, figs 3, 4) is much more elongate and may belong to a separate species. Other specimens from the same horizon and locality figured by de Koninck, but with de Rykholt specific names, that are probably also examples of *Bowlandia rhombea* are: *S. fabalis* (pl. 15, fig. 35), *S. praesectus* (pl. 15, fig. 37), *S. scapha* (pl. 15, fig. 38), *S. lyellianus* (pl. 15, fig. 39) and *S. tabulatus* (pl. 15, figs 41–4). Five more de Koninck (1885) species from other horizons and localities in Belgium that are probably also synonyms of *Bowlandia rhombea* are: *S. cuneatus* (pl. 16, figs 14, 15), *S. constrictus* (pl. 16, fig. 17), *S. angulatus* (pl. 16, fig. 18), *S. deletus* (pl. 16, fig. 19), all from étage 2, and *S. parvulus* (pl. 16, figs 20–3) from the Tournaisian.

COMPARISONS. *B. rhombea* is intermediate in form between *Permophorus* and *B. angulata* (Hind); the carina separates the flank from the posterior dorsal area at an angle of about 110° in *B. rhombea* but at only about 90° in *B. angulata*. The latter species, only recorded from the Viséan of Thorpe Cloud, Derbyshire, is also very much larger in all known examples except one, and has no trace of the radial cord on the posterior dorsal area close above the carina which is usually visible in *B. rhombea*.

Genus *SILIQIMYA* nov.

TYPE SPECIES. *Sanguinolaria plicata* Portlock, 1843.

DESCRIPTION. Elongate, narrow genus of a similar shape to the Recent Solenacea genera *Siliqua* and *Cutellus*. Umbones well towards the anterior, shell thin with a slightly backwards-sloping sulcus in young growth stages only. The ligament and nymphs start between the umbones; they are opisthodontic and

parivincular, long and straight. The dorsal margins are in juxtaposition from the umbones to the posterior margins. The nymphs are narrow and elongate with a narrow ligament groove. The ligament is set in a long, narrow escutcheon limited by sharp carinae.

The shell has a posterior inner rib at a very low angle to the hinge, which appears as a sulcus on the steinkern. The shell surface has low, rounded, comarginal rugae with no clearly defined corselet, although the rugae become irregular between the siphonal margins and the umbones. No surface pustules have been observed. The pallial line is very faint except close to the anterior adductor. The specimen illustrated in Fig. 45a has a relatively small, rounded and very faint posterior adductor scar and has been interpreted by Hind as having an entire pallial line; it is almost impossible to see the posterior part of the pallial line in a number of very well-preserved specimens, but none has a visible pallial sinus. The anterior adductor scar is rounded and slightly truncated towards the umbones. It is well inserted in front of a moderately thick buttress. There is a prominently inserted anterior pedal retractor between the anterior adductor and the umbones, lying close to the hinge. Small accessory muscle scars form a group of short incised striae on the anterior surface of the umbones of the steinkern. The shell appears to have a slight posterior gape (but see Hind, 1900: 389).

DISCUSSION. From M'Coy to the present time, *Siliquimya plicata* has always been placed in *Sanguinolites*. It differs from that genus, however, in having a more gently rounded posterior margin with no clearly defined corselet and in being less gibbous. It resembles a much elongated version of the Devonian genus *Glossites*. We have been influenced by the outline shape of *Pleurophorella striata* (Hind, 1900, 401–2; pl. 46, figs 1–2, & pl. 50, fig. 22), intermediate between *Siliquimya* and *Pleurophorella* of the Permophoridae. This leads us to suggest that *Siliquimya* should be included in the Permophoridae and its similarity to taxa included in the

Sanguinolitinae is partly a result of parallelism. Unfortunately the detailed characters of the accessory musculature of *?Pleurophorella striata* that might corroborate this interpretation are as yet unknown.

***Siliquimya plicata* (Portlock, 1843)** Figs 45a–c

?1842 *Sanguinolaria plicata* M'Coy, in Griffith: 12. *nomen nudum*.

1843 *Sanguinolaria plicata* Portlock: 433; pl. 34, fig. 18.

1843 *Sanguinolaria transversa* Portlock: pl. 34, fig. 21 [see discussion of *Wilkingia*, p. 73]

1844 *Sanguinolites plicatus* (Portlock); M'Coy in Griffith: 49; pl. 10, figs 3a, 3b.

1844 *Sanguinolites iridinoides* M'Coy in Griffith: 49; pl. 12, fig. 1.

1849 *Pholadomya iridinoides* (M'Coy); d'Orbigny: 128.

1900 *Sanguinolites plicatus* (Portlock); Hind: 387–8; pl. 44, figs 9, 11–15; pl. 45, figs 1–4.

?1900 *Sanguinolites striatus* Hind: 401; pl. 50, fig. 22 only. [Fuller synonymies were given by Hind (1900: 387–8) and Paul (1941)].

TYPE MATERIAL. The holotype in the BGS collections, figured by Hind (1900: pl. 44, fig. 11), is a young individual with both valves preserved. The holotype of *Sanguinolaria transversa* Portlock, in the same collection, was also figured by Hind (1900: pl. 45, fig. 1). SM E1045, here designated the lectotype of *Sanguinolites iridinoides* M'Coy, is the specimen figured by M'Coy, and is from the Viséan of Lowick, Northumberland.

OTHER MATERIAL. BM PL2760, from the Viséan near Keswick, Northumberland. BM L5224, BM L28181–8, BM L46457 and BM L46473–6 from the Redesdale Ironstone,

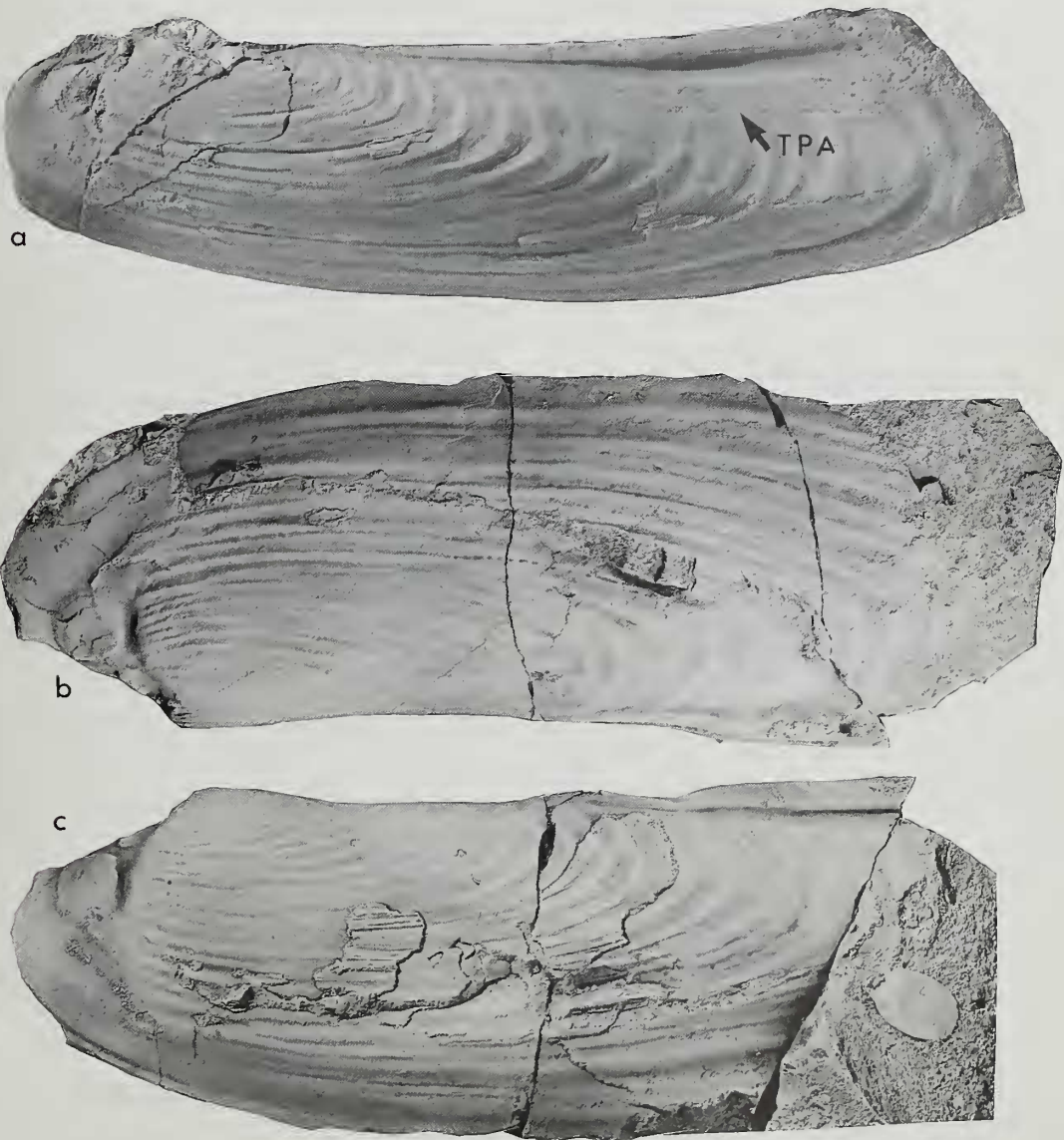


Fig. 45 *Siliquimya plicata* (Portlock). Upper Viséan. Fig. 45a, Lowick, Northumberland; SM E2817, left side, trace of posterior adductor clearly visible (TPA). Figs 45b–c, near Keswick, Cumbria; BM PL2760; Fig. 45b, right side of steinkern; Fig. 45c, left side. All $\times 1$.

Asbian, of Redesdale, Northumberland. BM L8988 from the Viséan, Wardle Shale, near Edinburgh. BM L47507 from the Viséan, Upper Limestone, at Orchard, near Glasgow. BM L46479 from the Viséan, at Lawston Linn, Liddet Water. SM E2816-7, E20863 and E1046 from Lowick, Northumberland.

DESCRIPTION. An elongate, compressed, soleniform species with low umbones well towards the anterior. The anterior margins are subrounded and the posterior margins are obliquely truncated, sloping backwards, and form an angle with the dorsal margins, but are rounded ventrally. Some Redesdale Ironstone specimens have the shell preserved, apparently without periostracal spicules. The ornament consists of comarginal rugae which are offset and broader along a line between the umbo and the posterior ventral margin. The ligament is posterior, set on a long slender nymph. The dorsal margins are linear and contiguous to the posterior margin. The ligament is set down in a long, narrow carinate escutcheon; the carinae are sharp and very gently concave. The anterior adductors are subcircular and relatively small with a considerable thickening of the shell behind them in the form of a low, straight, slightly anterior sloping clavicle. The posterior adductors are hardly visible in most specimens; they lie well towards the posterior margin and close to the dorsum; they are subcircular. The pallial line is moderately incised at the anterior, but it is very difficult to follow towards the posterior. Hind (1900: 388) interpreted it, apparently correctly, as entire.

INCERTAE SEDIS

Genus *SPHENOTUS* Hall, 1885

TYPE SPECIES. *Sphenotus arcaeformis* (Hall & Whitfield, 1869), subsequently designated by Miller, 1889: 513, Middle Devonian, Hamilton, New York State. For a figure see Hall, 1885: pl. 65, figs 7-11. There are no modern illustrations of this species.

The generic name *Sphenotus* has been used by Driscoll (1965) and Pojeta (1969) for species we would include in *Pleurophorella*. Neither author based his opinion on a reconsideration of Hall & Whitfield's type species, which is of Middle Devonian age. Examination of Hall's illustrations suggests that these may be related genera but we do not find sufficient similarity to accept their synonymy. McAlester's Upper Devonian *Sphenotus tiogenesis* may be a thin-shelled mud-dwelling member of this genus (McAlester, 1962: 62; pl. 26, figs 1-14).

Genus **GRAMMYSIOIDEA** Williams & Breger, 1916
(See Runnegar, 1974: 931)

TYPE SPECIES. *G. princiana* Williams & Breger 1916: 133. from the Lower Devonian. Moose River. Miss. We have examined a syntype, USNM 66190, kindly lent by Mr F. Collier, which is badly crushed and distorted, and has no ornament preserved. This species was apparently quite wrongly illustrated in the *Treatise* (Newell 1969: N821). We conclude that at present the species and genus is unrecognizable and should be rejected as a *nomen dubium*.

A CLASSIFICATION OF THE ANOMALODESMATA

This study of Upper Palaeozoic Anomalodesmata has revealed a greater diversity than we previously suspected. It is the documentation of this diversity which we consider furnishes further information for the overall classification of the Anomalodesmata. Below we offer an interim classification of Upper Palaeozoic taxa which is a modification of Cox *et al.* (1969). Runnegar (1974) and Morton (1982). We expect to modify the classification further, when we study the Mesozoic taxa.

Subclass **ANOMALODESMATA** Dall, 1889

We interpret the characters of primitive members to include an aragonitic nacreoprismatic shell with periostracal spicules developed early in their history. The hinge consists of a slender hinge plate with an opisthodontic parivincular ligament set on slender nymphs and few or no hinge teeth. An escutcheon is usually present and the posterior dorsal margins are close and joined by periostracum. Adductors subequal to anisomyarian. Pallial line primitively without sinus. Shapes typical of sessile deep burrowers to byssate nestlers.

?Order **ORTHONOTOIDA** Pojeta, 1978

Superfamily **ORTHONOTACEA** Miller, 1877
[nom. trans. Pojeta, 1978]

Family **ORTHONOTIDAE** Miller, 1877

Elongate shells, apparently without periostracal spicules. Ligament external, opisthodontic.

Orthonota Conrad, 1841.

Palaeosolen Hall, 1885; gross shell characters convergent with the heterodont superfamily Solenacea.

?*Cymatonota* Ulrich, 1893.

Superfamily uncertain

Family **SOLENOMORPHIDAE** Paul, 1941
(=Solenopsidae Neumayr, 1883)

Elongate shells, with external opisthodontic ligament. Shell structure unknown. (The species *Solenomorpha elegantissima* Hayasaka, 1925 which has well preserved periostracal spicules has been better placed in *Alula* by Hayami & Kase 1977). An alternative classification would relate *Solenomorpha* to the elongate M. Devonian Sanguinolitinae with the lack of periostracal spicules interpreted as secondary loss. In that case Solenomorphidae would be closer to the mainstream anomalodesmatids.

Subfamily **SOLENOMORPHINAE** Paul, 1941
[nom. trans. herein]

Umbones towards or at the anterior. Deeper burrowing attained by elongation of the posterior shell.

Solenomorpha Cockerell, 1903; no spicules known.
Enniostra Hajkr, Lukasova, Ruzicka & Rehor, 1975.

?Subfamily **PROMACRINAE** nov.

Radiating striae present, apparently without spicules. Elongation of shell anterior to umbones to give a *Donax*- or *Solemya*-like shape. Shell structure unknown, muscle scars poorly known.

Promacrus Meek, 1871.

?Family **PROTHYRIDAE** Miller, 1889

Dorsal part of anterior margins bear small protrusion.

Prothyris Meek (in Meek & Worthen 1869); fine radiating striae, no periostracal spicules.
Paraprothyris Clarke, 1913.
Amphikoilum Novozilov, 1956.

Order **PHOLADOMYOIDA** Newell, 1965

(?=Myoida Stoliczka, 1870;
 =Desmodontida Neumayr, 1883)

Usually infaunal nestlers to very deep burrowers. Ligament primitively external, opisthodontic, becoming internal in several unrelated post-Palaeozoic lineages. Pallial line primitively without sinus, but developing this feature in several eparate lineages, the most advanced forms in this respect having long siphons of type 'C'. Shell surface bearing periostracal spicules in the primitive forms. Ordovician to Recent. A paraphylum including the ancestors of at least some septibranchs.

?Superfamily **EDMONDIACEA** King, 1850

Without surface spicules, buttressing parallel to hinge commonly present, characteristic pedal muscle scar pattern commonly present. Shell structure unknown. The Edmondiacea share shell shape and simplicity of hinge with the more primitive Pholadomyoidea, characters which cannot be counted as firm synapomorphies. They do not possess the hypertrophied anterior adductor muscle, a synapomorphy of the Lucinoidea, and it would be unreasonable to suggest that *Allorisma* had an anterior inhalent current which we would interpret as a primitive character possessed by most Lucinoidea. Any arrangement of hinge teeth is more simple than that possessed by any of the major groups of Heteroconchia, so the Edmondiacea remain in the Pholadomyoidea rather by default than by sharing any recognized synapomorphy.

Family **EDMONDIIDAE** King, 1850

(?=Cardiomorphidae Miller, 1877;
 =Allorismidae Astafieva-Urbaitis, 1964)

Edmondia de Koninck, 1841.
Allorisma King, 1844.
Scaldia de Ryckholt, 1847.
Cardiomorpha de Koninck, 1841.

Family **MEGADESMIDAE** Vokes, 1967
 (=Pachydomidae Fischer, 1886, nom. inval.)

Megadesmus J. de C. Sowerby, 1839.
Astartila Dana, 1847.
Pyramus Dana, 1847.
Plesiocyprinella Holdhaus, 1918.
Farrazia Cowper Reed, 1932.
 ?*Casterella* Mendes, 1952.

Superfamily **PHOLADOMYACEA** King, 1844
 [nom. trans. Newell, 1965]

(=Grammysiacea Miller, 1877, nom. trans. Dickens, 1963)

Primitively myiform with external, posterior parivincular ligament mounted on paired upward-facing nymphs. Primitive shell structure considered to be nacreo-prismatic aragonite with radiating rows of periostracal spicules. Hinge line with few or no hinge teeth. Usually elongate shells with rounded or sub-rounded ends, often with a subumbonal sulcus. Shallow to deep sessile burrowers. Although a pallial sinus is present in many Upper Palaeozoic taxa, the more primitive lack this feature. We may interpret from this that they were primitively without siphons, but siphons of varying complexity, types 'B' or 'C', apparently develop separately in a number of lineages. The more primitive living forms are eulamellibranch filter feeders. A paraphylum including the Pholadomyidae and their Palaeozoic ancestors, together with the ancestors of the Thraciacea, Pandoracea, Poromyacea, Hiatellacea, Gastrochaenacea, Pholadidacea, Clavagellacea and probably the Myacea.

Family **GRAMMYSIIDAE** Miller, 1877

Sulcate forms with a break in shell ornament, becoming arcticiform. Ligament external, born on narrow nymphs. Shell structure unknown but surface commonly with radiating lines of periostracal spicules.

Subfamily **GRAMMYSIINAE** Miller, 1877

[nom. trans. herein]

Later taxa arcticiform, pallial line without sinus. Sulcus usually present.

Grammysia de Verneuil, 1847.

Subfamily **CUNEAMYINAE** nov.

Elongate, myiform, pallial line incompletely known. Shallow subumbonal sulcus sometimes present.

Cuneamia Hall & Whitfield, 1875.
 ?*Rhytimya* Ulrich, 1884.
 ?*Grammysioidea* Williams & Breger, 1916.
 ?*Protomya* Hall, 1885 (=Palaeomya Hall, non Zittel & Goubert, 1861).

Family **SINODORIDAE** Projeta & Zhang, 1984
 [Elevated to a superfamily by Projeta, Zhang & Yang, 1986.]

Sinodora Projeta & Zhang, 1984.
Palaeodora Fleming, 1957.

Family SANGUINOLITIDAE Miller, 1877

Pallial sinus absent to deep. Ligament external opisthodontic, mounted on nymphs. Non-gaping to widely gaping. Hinge teeth usually absent but 'cardinals' known to be present in Alulinac. Nacreo-prismatic shell structure known in some sanguinolitines, probably occurred throughout the family.

Subfamily SANGUINOLITINAE Miller, 1877

(?=Arcomyidae Fischer, 1886)

Pallial sinus shallow or absent. Shell elongate. No hinge teeth.

- Sanguinolites* M'Coy, 1844.
Myofossa Waterhouse, 1969b.
Palaeocorbula Cowper Reed, 1932.
Ragozinia Muromzeva, 1984.
Cosmomya Holdhaus, 1913.
Grammysiopsis Chernychev, 1950.
Pentagrammysia Chernychev, 1950.
 ?*Siphogrammysia* Chernychev, 1950.
 ?*Glossites* Hall, 1885.
Cimitaria Hall & Whitfield, 1875.
Gilbertsonia gen. nov. (see p. 70).
 ?*Pachymyonia* Dun, 1932.
 ?*Leinzia* Mendes, 1949.

Subfamily PHOLADELLINAE Miller, 1887

Radial ribbing present.

- Pholadella* Hall & Whitfield, 1869.

Subfamily ALULINAE Mailleux, 1937

Median tooth present in RV only. Deeper burrowing attained by elongation of the posterior shell, convergent with Solenomorphidae.

- Alula* Girty, 1912.
Unklesbyella Hoare, Sturgeon & Kindt, 1979.
 ?*Tellinomorpha* de Koninck, 1885.

Subfamily UNDULOMYINAE Astafieva-Urbaitis, 1973

Deep pallial sinus known in some genera. Narrow anterior and or posterior gape sometimes present.

- Wilingia* Wilson, 1959.
Praeundulomya Dickins, 1957.
 ?*Manankovia* Astafieva-Urbaitis, 1984.
Undulomya Fletcher, 1946.
Exochorhynchus Meek & Hayden, 1865.

Subfamily CHAENOMYINAE Waterhouse, 1966

Pallial line truncated by broad shallow sinus parallel to the vertical posterior margins; posterior gape wide and rounded.

- Chaenomya* Meek, 1865.

Subfamily VACUNELLINAE Astafieva-Urbaitis, 1973

Pallial line usually truncated with shallow to medium pallial sinus. Narrow posterior gape often present.

- Vacunella* Waterhouse, 1965.
 ?*Australomya* Runnegar, 1969.
Myonia Dana, 1847.

Family PERMOPHORIDAE van de Poel, 1959

[*nom. nov. pro* Pleurophoridae Dall, 1895]

(?=Kalenteriidae but not including Redoniidae Babin, 1966)

Elongate ovate of modioliform with external opisthodontic ligament usually mounted on narrow nymphs. Periostracal spicules present only in the more primitive forms. Usually not gaping. Cross-lamellar shell structure known in Jurassic taxa.

Subfamily PERMOPHORINAE van de Poel, 1959

- Permophorus* Chavan, 1954.
Pleurophorella Girty, 1904.
 ?*Pleurophorina* Licharew, 1925.
Siliquimya gen. nov. (see p. 90).
Bowlandia gen. nov. (see p. 88).
Ivanovia Astafieva-Urbaitis, 1978.
 ?*Cosmogoniophorina* Isberg, 1934.
 ?*Cosmogoniophora* McLearn, 1918.
 ?*Goniophorina* Isberg, 1934.
 ?*Naiadopsis* Mendes, 1952.
 ?*Jacquesia* Mendes, 1944.
 ?*Macackia* Mendes, 1954.
 ?*Roxoa* Mendes, 1952.

Other genera as listed in the *Treatise*, except for *Redonia* Rouault, 1851 which is unlikely to belong to the Anomalodesmata or the Heteroconchia.

Eager, 1978, discussed the evolutionary origins of the Anthracosiacae. His hypothesis included an ancestor for that superfamily among late Viséan, apparently marine taxa, which he called *Sanguinolites* Hind, non M'Coy. He specifically mentioned two taxa, *Sanguinolites abdenensis* and *Sanguinolites ovalis*. These species, described by Hind (1900), are not well preserved and details of their hinge and musculature are not fully known. One possibility is that they belong to *Pleurophorella* as interpreted in the present work (p. 84); in which case the Anthracosiacae could prove to be a non-marine offshoot of the Permophoridae.

NOMEN DUBIUM

- Sphenotus* Hall, 1885.

CONCLUSIONS

The Anomalodesmata were more prominent during the Upper Palaeozoic than in almost any modern environment, forming more than half of the total infaunal species in the British Viséan for example. However, they have slowly

increased in numbers of species from the late Palaeozoic to the Recent. Their less prominent position today is purely the result of much more rapid diversification of other infaunal groups in the later Mesozoic and Tertiary, particularly the siphonate heterodonts.

Diagnosis of the subclass is difficult; it is recognized by particularly negative characters which include few or no hinge teeth and a generalized myiform shell. The parivincular ligament borne on nymphs, clearly primitive for the group, is shared by the Heteroconchia and the more primitive nuculoids. We recognize periostacal spicules as a primitive character for the mainstream Anomalodesmata that include the Pholadomyoidea. This leaves us with considerable uncertainty as to which bivalves are the closest sister groups of this order.

The traditional inclusion of the Edmondiacea within the subclass and the disputed inclusion of the Orthonotida are neither confirmed nor denied by any evidence we have been able to find. The superficial resemblance between *Allorisma* (Edmondiacea) and the Undulomyiinae is shown to be a case of convergence.

Our classification has made use of more taxa at the family and subfamily level than some recent classifications of this group, e.g. Newell, 1969 and Runnegar, 1974. Although the Upper Palaeozoic anomalodesmatids did not exploit the variety of internal hinges typical of the Mesozoic and Kainozoic, their diversity of shell shape and pallial sinus, both reflecting their life habits and our interpretation of their phyletic relationships necessitate this action.

The Upper Palaeozoic subfamilies within the Sanguinolitidae differ essentially from the non-siphonate Grammysiidae, particularly including *Grammysia* itself, in all developing deeper burrowing siphonate forms. We have been able to establish polarity of characters of the dorsal shell margins and hinge within the Sanguinolitidae. We have related this to the evolution of siphons. We have interpreted an elongate carinate escutcheon and no posterior gape as primitive and loss of carinate escutcheon and acquisition of a posterior gape as advanced. This polarity has guided us in our taxonomic evaluation.

One interesting aspect of the Runnegar schematic view of anomalodesmatid evolution (1974: text-fig. 3) is that it shows absolutely no interruption at the Permo-Triassic boundary except for the demise of the Australasian taxon Megadesmidae. At this time we are uncertain whether or not the Megadesmidae may themselves be ancestral to at least some septibranchs. In the evidence as it is known, we can also show no distinct indication of an extinction event at this time but feel the record close to the boundary, and particularly in the early Triassic, is so poor that at present no reasonable interpretation can be made. The one possibility of an extinction at the family level at this time is the Edmondiidae, but we do not know whether the Mesozoic family Mactromyidae is similar because of common descent or because of convergence.

We have established the broad similarity between the Permophoridae and the Sanguinolitidae which we interpret as reflecting a close phyletic relationship. As byssate nestlers, crevice dwellers and at least one apparent cavicolous taxon, they foreshadow some of the habits of their post-Palaeozoic descendants, which we believe may include the Gastrochaenacea and *Hiatella*.

The present apparent poverty or patchiness of the Devonian record of Anomalodesmata leads to a number of uncertainties; e.g. we are unable to show whether or not the multiplicity of development of siphonate forms which is apparent by the Lower Carboniferous (Viséan) is a result of

an earlier Carboniferous radiation with some convergence of shape to early Palaeozoic taxa or whether the individual clades, subfamilies in this study, have a more ancient history. The earlier Palaeozoic Subfamily Cuneamyinae includes taxa with similar shape to the Upper Palaeozoic siphonate ones but we have been unable to discover the nature of the pallial line, and hence presence or absence of siphons, in this early group, nor whether there were repeated parallel radiations producing convergent forms.

This is of particular importance in considering the tracing of their history from the Palaeozoic through to the Mesozoic. The schematic evolutionary tree outlined by Runnegar (1974) and repeated by Morton (1987) is an over-simplification and is replaced here by a classification that is both rather more complicated and less certain in some details. However, the essential aspect of shallow burrowers giving rise to deeper burrowers, which may be interpreted from a comparison of shell morphology, remains a key insight into their evolution. Our own classification is outlined above.

The stratigraphical distribution within the Upper Palaeozoic of anomalodesmatids has been used for correlation, particularly in the early Permian of eastern Australia. We find further stratigraphical value in the Sanguinolitidae, particularly those with prominent or discordant ornament. We are, however, perplexed by, and unable to resolve without further field collecting, the bivalve fauna from the Upper Palaeozoic shale sequence from Peru, described by Thomas (1928). This has a distinct Upper Artinskian aspect but is accompanied in the collections at Cambridge and in Thomas' description by Pennsylvanian ammonoids. The distinctive part of the fauna includes species of *Ragozinia*, *Undulomya* and *Exochorhynchus*. Does this represent an earlier occurrence of taxa in an as yet unrecognized southern bivalve province, or is it the result of the mixing of two faunas, possibly when they were collected?

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