

REVIEW OF THE CAENOZOIC HETERODONT BIVALVE SUPERFAMILY DREISSENACEA

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ABSTRACT. The Dreissenacea consists of one family, the Dreissenidae, with subfamilies Dreisseninae for *Dreissena* (with three subgenera), *Congeria* and *Mytilopsis*; and Dreissenomyinae for *Dreissenomya* (two subgenera). Poorly preserved *Prodreissensia* is provisionally placed in the Dreisseninae, but may be wrongly assigned to the superfamily. Dreissenids live in fresh and brackish water. Most are epifaunal and byssally attached but *Dreissenomya* was infaunal and unattached. *Mytilopsis* first appeared in the European Eocene and invaded the Western Hemisphere in the late Oligocene. *Dreissena*, *Congeria* and *Dreissenomya* arose in the late Miocene of the Paratethys. Two genera survive: *Mytilopsis* occurs naturally only in the Western Hemisphere and *Dreissena* in Europe and Western Asia. European Mio-Pliocene boundary extinctions coincide with the break up of Paratethys and the Messinian salinity crisis. Often anomalous increases in the distribution of both Recent genera are attributed to human activity, but some records from eastern Asia are due to confusion with *Sinomytilus* (Mytilacea).

THE largely freshwater, eulamellibranchiate, anisomyarian superfamily Dreissenacea first appears in the Eocene and is still living. It was placed in the Veneroida (Heterodonta) in the classification of Newell (1965) which was adopted by McCormick and Moore *in* Moore (1969). Confirmation of this position was provided by Taylor, Kennedy and Hall (1973) who stressed the strong resemblance between the shell structures of *Dreissena* itself and the Corbiculacea, another largely freshwater superfamily which dates back into the Mesozoic.

Examination of the fossil record and the Recent distribution of the Dreissenacea shows that the generic ranges, geographical distribution and arrangement of the genera given by Keen *in* Moore (1969) (see Table 1) in the Treatise and by Eames *in* Morley Davies (1971) are in need of modification. The Treatise classification (Moore 1969) had some influence on the views of both Morton (1970) and Marelli and Gray (1985) on evolution of the superfamily: in consequence, several of their conclusions also need re-examination.

It is understandable how much of the confusion arose. Firstly for generic determination it is necessary to examine internal features of the shell: one such feature is the presence or absence (pl. 1, figs. 6, 14, 16) of the apophysis which may be hidden under the septum and can easily be overlooked except in good specimens and good illustrations. Secondly, many species were originally described either as *Mytilus* or *Dreissena*. In addition, this situation is further complicated by the almost universal practice of European workers of placing all species possessing an apophysis in *Congeria*, regardless of the fact that most resemble the type species of *Mytilopsis* (pl. 1, figs. 11–14) rather than that of *Congeria* (pl. 3). Thirdly, it is becoming clear that many Recent occurrences of both *Dreissena* and *Mytilopsis* are the result of human introduction.

Oppenheim (1891, pl. 51) gave excellent illustrations of the internal details of several European Eocene species, showing that all whose internal features were known possessed an apophysis (pl. 2, figs. 12–18). These species had been originally described as *Dreissena* and have subsequently been assigned to various subgenera of *Congeria*, but are here regarded as belonging to *Mytilopsis*. Most subsequent European studies, however, have concentrated on the varied dreissenid faunas of the Neogene of the Paratethys, stretching from Austria eastwards through the southern USSR as far as the Aral Sea. The basis of the more recent Russian classifications (Starabogatov 1970; Babak 1983) is the work of Andrussov (1897–8; 1900) whose very comprehensive monograph of fossil and

TABLE 1. Summary of modern classifications of the Dreissenacea

Keen <i>in</i> Moore (1969)	Babak (1983)	Herein
Fam. DREISSENIDAE	Fam. DREISSENIDAE Subfam. DREISSENINAE	Fam. DREISSENIDAE Subfam. DREISSENINAE
<i>Dreissena</i> (<i>Dreissena</i>) — — (<i>Prodreissensia</i>) <i>Dreissenomya</i> (<i>Sinucongeria</i>)	<i>Dreissena</i> (<i>Dreissena</i>) (<i>Pontodreissena</i>) (<i>Modiolodreissena</i>) — —	<i>Dreissena</i> (<i>Dreissena</i>) (<i>Pontodreissena</i>) (<i>Modiolodreissena</i>) <i>Prodreissensia</i>
<i>Congeria</i>	<i>Congeria</i> (<i>Congeria</i>) (<i>Rhombocongeria</i>) (<i>Eocongeria</i>) (<i>Trigonipraxis</i>) (<i>Andrusoviconcha</i>) (<i>Mytilopsis</i>)	<i>Congeria</i> (= <i>Congeria</i>) (= <i>Congeria</i>) (= <i>Mytilopsis</i>) (= <i>Mytilopsis</i>) (= <i>Mytilopsis</i>)
<i>Mytilopsis</i>	(<i>Mytilopsis</i>) Subfam. DREISSENOZYINAE <i>Dreissenomya</i> (<i>Dreissenomya</i>) (<i>Sinucongeria</i>)	<i>Mytilopsis</i> Subfam. DREISSENOZYINAE <i>Dreissenomya</i> (<i>Dreissenomya</i>) (<i>Sinucongeria</i>)

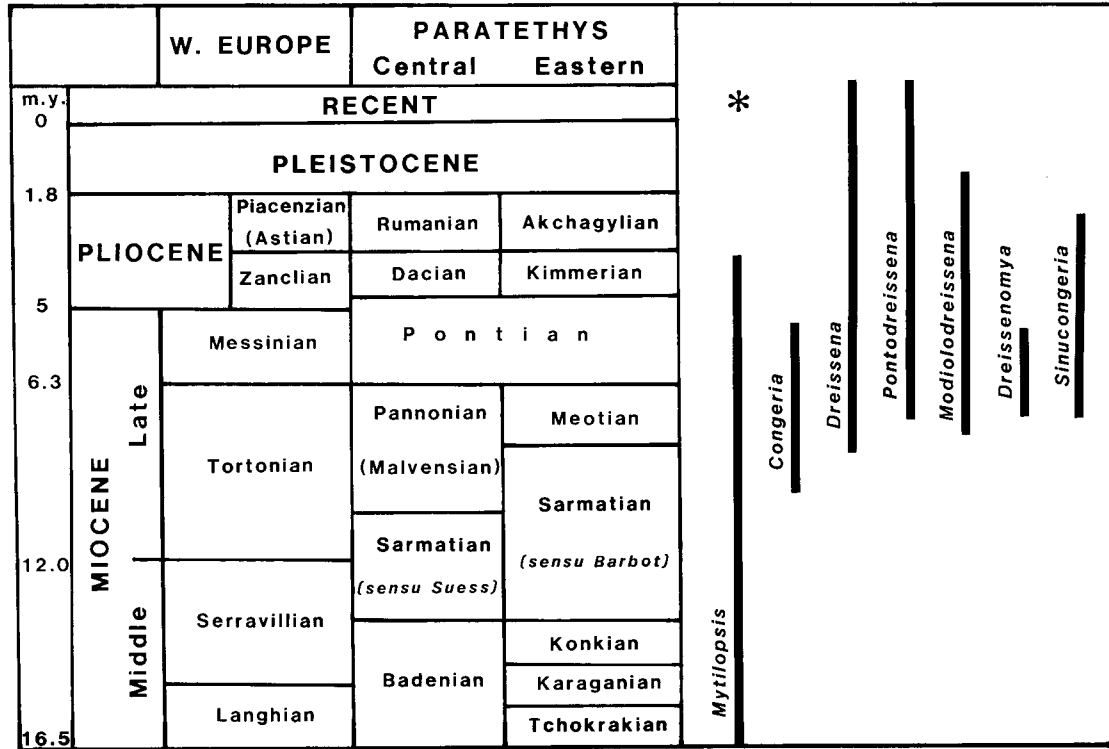
TABLE 2. Relationship between informal groups of the genus *Congeria* proposed by Andrussov (1897–8) and the subgeneric arrangements adopted by Starabogatov (1970) and Marinescu (1973)

Andrussov, 1897–8*	Starabogatov, 1970	Marinescu, 1973
eocena <i>eocena</i> (<i>sic</i>) = <i>eocena</i> Oppenheim	<i>Eocongeria</i> nov. subgen.	
mytiliformes <i>basteroti</i> Deshayes	<i>Mytilopsis</i> Conrad	<i>Mytilia</i> nov. subgen.
modioliformes <i>amygdaloides</i> Dunker	<i>Andrusoviconcha</i> nov. subgen.	<i>Modiola</i> nov. subgen.
subglobosae <i>no type species</i>	<i>Congeria</i> Partsch	<i>Congeria</i> Partsch
rhomboidea <i>no type species</i>	<i>Rhombocongeria</i> nov. subgen.	<i>Rhomboidea</i> nov. subgen.
triangulares <i>triangularis</i> Partsch	<i>Trigonipraxis</i> nov. subgen.	<i>Triangularia</i> nov. subgen.

* Andrussov's informal groups and their 'type species' are shown in this column.

living Dreissenidae of Eurasia also dealt with species from the rest of the world. Andrussov (1898) divided both *Congeria* and *Dreissena* into a number of non-binomial 'groups', and gave 'type species' for some but not all of them (see Table 2). Later authors have subsequently formalized these groups as nomenclatorially valid subgenera, sometimes with type species different to those originally suggested by Andrussov. In the present work all such subgenera of *Congeria* are

synonymized either with *Conger* or *Mytilopsis* (Table 1). The aim of the present study is to revise the stratigraphic and geographic distributions of the various genera and to suggest improvements to the classification adopted by earlier authors. Text-fig. 1 shows the correlation adopted herein for the European post-Lower Miocene.



TEXT-FIG. 1. European post-lower Miocene correlation and generic ranges. *Mytilopsis* first occurs in the Eocene. Key, asterisk, *Mytilopsis* reintroduced after becoming extinct in eastern Hemisphere. Based on Steininger *et al.*, 1985.

The generic synonymies given herein concentrate on names proposed in modern taxonomic works. They omit the numerous variations in the spelling of *Dreissena*. Also omitted are the many nineteenth-century names which have long since fallen into disuse. This information is readily available elsewhere (Keen *in* Moore, 1969; Vokes 1980).

The scope of this study is somewhat limited by the comparatively small collections in the Palaeontology and Zoology departments, British Museum (Natural History) (BMPD; BMZD) and is therefore largely based on reinterpretation of the literature. Probably the most useful source of reliable specific identifications and natural groupings is Andrussov (1897-8). Other important works consulted include the following concerned with classification: Orlov (1960); Keen *in* Moore (1969); Starabogatov (1970); Babak 1983.

Works summarizing regional distribution and containing illustrations and references sufficiently adequate for reinterpretation include: for Europe:- Archambault-Guezou (1976a, b); Iljina *et al.* (1976); Locard (1893); Marinescu (1973, 1975); Oppenheim (1891, 1892); Papp (1953, 1954); Rozanov (1986); Zelinskaya *et al.* (1968); for the Western Hemisphere:- Keen (1971); Marelli and Gray (1983); Olsson (1961); Nuttall (1990, pp. 275-287); for West Africa:- Pilsbry and Becquaert (1927). Anatomy and other aspects of the biology of living *Dreissena* are dealt with by Morton (1970) and by Yonge and Campbell (1968). Escarbassiere and Almeida (1976) and Morton (1981)

dealt similarly with living *Mytilopsis*. Several, mainly early, papers have been largely ignored because it is not possible to interpret the sparse stratigraphical information they contain. For example, among those that have proved too difficult to use is the important study of Yugoslav Miocene dreissenids by Kochansky-Devidé and Slisković (1978). They figured many apparently rather crushed species and introduced (pp. 35, 60) a new informal group, the 'luciniformes'. Their range chart (p. 76) differs from current views in correlating the Tortonian with the Badenian, regarding both as pre-Sarmatian. They placed both the Otnangian and Karpathian within the Helvetian, which they regarded as pre-Badenian. Nowadays the general consensus is to consider the Helvetian as equivalent to the Tortonian.

MORPHOLOGY AND MODE OF LIFE

Inequivalvity

Slight inequivalvity in the Dreissenacea arises from two factors. In all genera except *Dreissenomya*, some articulation, or rather means of relative location between the two valves, is achieved by differences in the ventral shell margin or commissure immediately posterior to the umbones (pl. 1, figs. 2, 3). In the left valve a sinus followed by a broader upswelling is developed just posterior to the umbo. In *Dreissena* (*Pontodreissena*) *rostriformis* (Deshayes 1838) upswelling is very pronounced, forming a strong beak (pl. 1, figs. 8–10). In the right valve, an upward angular projection is present immediately posterior to the umbo. The sinus developed behind this projection is rather weaker than the upswelling in the left view. These structures, which are purely modifications of the commissure, are not true hinge teeth, even though they are concerned with articulation. The other cause of inequivalvity is that the byssal notch is not always developed evenly in both valves. Yonge and Campbell (1968, p. 5) stated that in *Dreissena polymorpha* (Pallas) the umbo of one valve overlaps that of the other ventrally, and this one alone bears the byssal notch. They did not state which valve is which and their observation on the byssal notch cannot be confirmed. This species lives in clusters with the result that both shell shape and also the orientation of the byssal anchorage could well be influenced by crowding against adjacent shells. This habit of living in tight clumps adopted by most dreissenids (text-figs 2A, E) can cause considerable morphological variation due to pressure from adjacent individuals. This has led to the description of numerous unnecessary nominal species, as witnessed by the lengthy synonymies in Marelli and Gray (1983) and in Nuttall (1990, pp. 280, 285) of, respectively, Recent and Neogene *Mytilopsis*. Similar reservations must be expressed about the large number of other fossil species described as occurring either together or at particular horizons. Internal inequivalvity may occur in the septal region. The septa of the two valves are often not mirror-images of each other. Variations occur in the size and shape of the muscle attachments on the septa and also the way in which the septa may, or may not be, supported or buttressed from below.

Anterior muscle attachments

The form of the septum and its muscle attachments have provided the basis not only of generic separation but also much of the evidence of the evolution of the family. The anterior adductor muscle is always attached to the septum. In *Dreissena* (pl. 1, fig. 6) and *Dreissenomya* (pls. 5, 6; text-fig. 3) the pedal/byssal retractor scar occurs on the dorsal part of the septum. In *Mytilopsis* (pl. 1, figs. 14, 16) the pedal/byssal retractor scar is situated on a myophore placed sometimes slightly underneath, sometimes posterior to, the dorsal part of the septum. In *Congeria* (s.s.) this myophore tends to be fused to the dorsal margin of the septum (pl. 3). This fusion may be interpreted as resulting from massive thickening of the septum rather than a fundamental difference between *Congeria* and *Mytilopsis*. The taxonomic usefulness of the septum and apophysis has been questioned (Archambault-Guezou 1982, with further references). Previously (1976a, pl. 9, figs. 16, 17) she had illustrated juvenile valves of the southern French 'infra-Pliocene' (= Messinian) '*Congeria*' *rhodanica* (Fontannes 1882) (here transferred to *Mytilopsis*). In the right valve the

apophysis is fused to the septum and the pedal/byssal scar is deep and oval. In the left valve the apophysis is mounted behind and below the septum.

Archambault-Guezou (1976*b*) was clearly of the opinion that '*C. rhodanica*' was extremely closely related to '*C. subcarinata*' (Deshayes 1838) originally described from the Pliocene of the Crimea. Morton (1970) figured a left valve (BMPD LL18540) of '*C. subcarinata botenica*' Andrussov, 1897 from the Middle Pontian of Rumania in which the apophysis is fused to the septum. Examination of a further sample (BMPD LL9022-4) from another Rumanian locality of Upper Pontian age (pl. 6, figs. 8-10) confirms his observation on the left valve, but also shows that the apophysis in two accompanying right valves is in the normal position for *Mytilopsis*. This is a mirror image of the situation in *M. rhodanica*. Unfortunately, lack of material makes it impossible to discover how constant the difference between valves is in these two species or subspecies. The possibility that the difference is random, caused by the shells living at different attitudes in clumps, cannot be dismissed.

Examples of reduction of the apophysis in apparently different lineages during the late Miocene are illustrated by Papp (1950) and Pana (1962). This suggests that *Dreissena* may be polyphyletic and is, perhaps, some justification for the recognition of its three described subgenera.

All these aberrations in the arrangement of the septum and apophysis are perhaps to be expected at a period during which the Dreissenacea were evolving rapidly. If *Mytilopsis* gave rise to *Congeria* and *Dreissena*, it seems highly likely that the quite good fossil record should reveal fossils, such as those discussed above, which may be interpreted as intermediate forms. I will accept, therefore, the presence of the apophysis, or lack of it, as being a useful taxonomic distinction in most instances. Morton (1981, p. 39), in discussing the anterior pedal retractor in *Dreissena*, *Congeria* and *Mytilopsis*, inferred that the introduction of the apophysis was a progressive improvement, and his fig. 11 certainly supports his view that there is an increase in the mechanical efficiency of the pedal/byssal retractor muscle. It is, however, a reverse of the evolutionary sequence. *Mytilopsis*, with an apophysis, appeared some 40 million years before *Dreissena* dispensed with this structure, and is still successful.

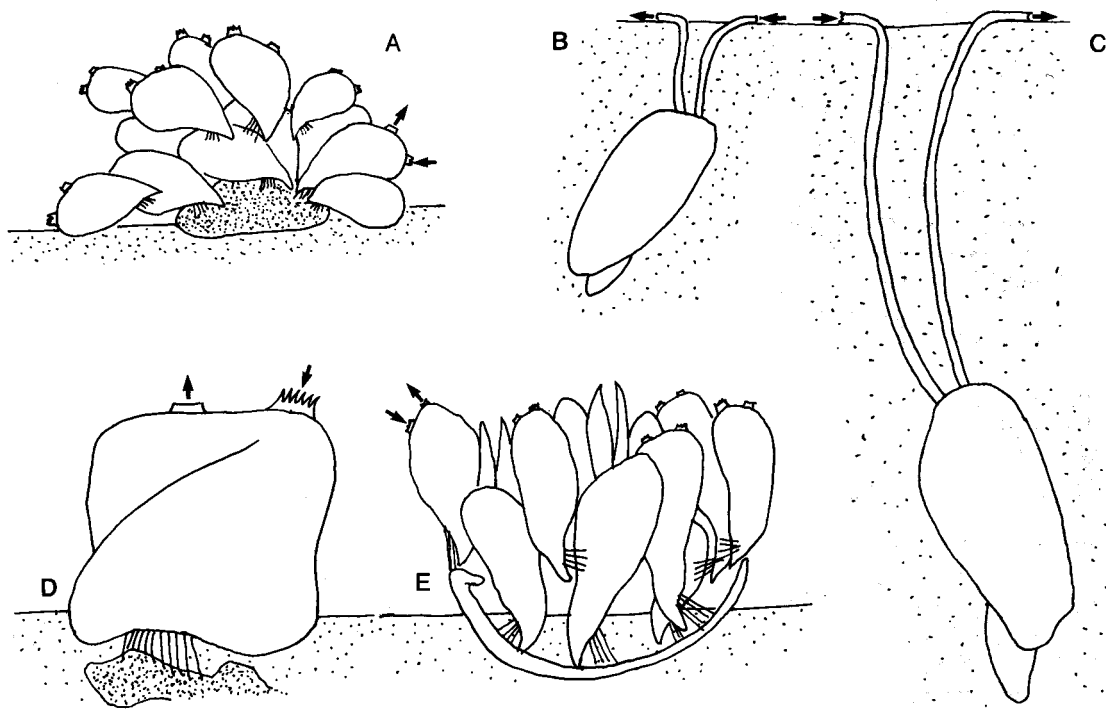
Articulation

The family appears to be edentulous. Morton (1970) described and figured the interiors of left valves of *Dreissenomya* (*Sinucongeria*) *aperta* (Deshayes 1838) (BMPD LL18541) and *Congeria* (*C.*) *subglobosa* Partsch (BMPD LL22134), stating that the former has two rudimentary cardinal teeth and the latter a poorly developed cardinal covered in life by the anterior adductor. In fact, both valves of LL18541 possess a single irregular rugose ridge crossing the hinge plate (pl. 6, figs. 1, 2, 5, 6). These ridges, however, are not only far too low to articulate as teeth, but are also in the wrong position to do so. They are situated more or less opposite each other rather than being offset like true teeth which fit into corresponding sockets in the other valve. Another specimen (BMPD L19502; pl. 6, figs. 3, 4, 7) and numerous illustrations (Archambault-Guezou 1976*a*, pls. 4, 5; Marinescu 1975, pls. 6-8) show wide variation in both size and position of these ridges on the septum of *D. (S.) aperta*. Similar ridges occur in other species of *Sinucongeria*. Examination of LL22134 and other specimens of *Congeria subglobosa* (Pl. 3) shows that no cardinal tooth, however poorly developed, exists. The ridge is not always present, and, as in *Sinucongeria*, cannot have acted as a tooth. These ridges are here interpreted, therefore, as some modification to the adductor muscle attachment area rather than as rudimentary dentition. It is possible that they mark the boundary between the 'catch' and 'quick' components of the anterior adductor muscle. Yonge and Campbell (1968), however, in rather briefly discussing the musculature of *Dreissena polymorpha* (Pallas), do not mention finding these two separate components of the adductor muscle. An alternative explanation is that ridges or corrugations might help to make a more secure anchorage between the muscle and shell.

Marinescu (1975, p. 78, text-figs. 4, 5, 6, 8) stated that there was a rudimentary cardinal tooth in the right valve of *Dreissenomya* (s.s.), in contrast to *D. (Sinucongeria)*, which he described as edentulous. His text-fig. 5 illustrates a series of juvenile shells (0.6-1.3 mm long). The structure,

situated on the commissure just below the umbo, is in the correct position for a tooth, but (his text-fig. 5E) also occurs in the left valve. In adult shells (BMPD L19501, L71745) (pl. 5, figs. 1–5) it appears to match a slight indentation of the commissure below the umbo, and is unlikely to have been an effective form of articulation. This structure could be equivalent to the flexures of the commissure in the umbonal region of more typical members of the family, rather than a cardinal tooth.

The umbones are terminal in the majority of Dreissenacea, including the earliest known. It is only in the late Tertiary *Dreissenomya* (s.s.) that they are situated some distance behind the anterior of the shell, but still well forward. The change in umbonal position can be regarded as a secondary modification connected with adaptation to an epifaunal mode of life (text-fig. 2B, C).



TEXT-FIG. 2. Mode of life of Dreissenacea. Arrows indicate inhalent and exhalent siphons. A, Recent *Dreissena* and *Mytilopsis*, epifaunal, byssally attached to hard object such as pebble or piece of wood. Dead shells at bases of cluster shown without siphons. B, extinct *Dreissenomya* (*Sinucongeria*) and C, *D.* (*Dreissenomya*), both infaunal, powerful burrowers, with foot extended. D, extinct *Congeria subglobosa* Partsch, epifaunal, attached to hard object by massive byssus. E, extinct *Mytilopsis spathulata* (Partsch) epifaunal, byssally attached cluster on dead valve of *Congeria subglobosa*, dead shells shown without siphons, or with valves not closed. Based on LL 28243. Upper Miocene, Pannonian, Hengersdorf Brick Pit, 10 km S. of Vienna. All extinct examples from late Miocene and Pliocene of Paratethys. B and C modified from Marinescu, 1975. All figures approximately $\times 0.5$.

Mode of life

All known Recent species of both *Dreissena* and *Mytilopsis* are epifaunal, living in clusters attached to each other by the byssus (text-fig. 2A). The cluster or colony (text-fig. 2E, BMPD LL28243) of the Austrian Pannonian *Mytilopsis spathulata* (Partsch) on a single valve of *Congeria subglobosa* Partsch is evidence that some fossil dreissenids were adapted to a similar mode of life.

The habit of forming clusters is probably a reflection of the fact that byssally attached epifaunal bivalves, such as many Dreissenacea and Mytilacea, often need to exploit every suitable piece of hard substrate. The pallial line in *Dreissena* (s.l.), *Mytilopsis* and *Congeria* is normally described as being entire, and the siphons of *D. polymorpha* (Pallas) were described as short (Yonge and Campbell 1968; Morton 1969). Such features are indicative of an epifaunal existence. Morton (1970, p. 567, text-fig. 7) described the pallial line of *Mytilopsis sallei* (Recluz 1849) as not being indented by a sinus. Later, on studying living material of the same species, he described it (1981, p. 30) as having a slight pallial sinus, an unusual feature in an epifaunal species (p. 37), and (p. 39) mentioned that its extensible siphons helped it cope with a high sediment load. However, Morton did not state how far the siphons could extend. These interesting observations led him (1981, p. 30) to reconsider his views on *Congeria zsigmondyi* Halavats, from the Pontian of Hungary (1970, p. 565, text-fig. 4), which he had previously described as lacking a pallial sinus and which he had interpreted as being a byssally attached, infaunal species like the quadrate and globose *Congeria subglobosa* Partsch from the Pannonian of the Vienna Basin (1970, p. 565, text-fig. 3). Morton had argued (1970, p. 569) that, in moving water, the size of the latter species would put a great strain on the byssal apparatus. It seems unlikely that *Congeria* was completely infaunal. It has no pallial sinus, so it may be inferred that the siphons were short as in *Dreissena*. It would almost certainly prefer not to be buried sufficiently for the siphons to be permanently covered by sediment, even though Yonge and Campbell (1968) had described the normally epifaunal *D. polymorpha* as being singularly oblivious to the presence of silt because of its ability to expel massive collections of pseudofaeces. The large size of the byssal notch in *C. subglobosa* (pl. 3, fig. 4) and other large species suggests that the byssus may have been extremely well developed and able to cope with bottom currents, which in the muddy clay facies of the Pannonian were probably not strong. It is difficult to imagine that these large, heavy *Congeria* lived in clumps: they were almost certainly solitary and byssally attached to hard objects such as dead shells (text-fig. 2F).

The pallial sinus which Morton (1981) described in *M. sallei* (pl. 1, fig. 19, herein) and in *C. zsigmondyi* is barely noticeable, consisting of a slight truncation of the posterior portion of the pallial line. These pallial lines are not indented, and it is difficult to justify Morton's comparison (1981, pp. 30, 37) between them and the fully sinupalliate *Dreissenomya* (*Sinucongeria*) *aperta* (Deshayes) (pl. 6, figs. 2, 4). By no means all species assigned to *Mytilopsis* possess this weak pallial sinus. Species in which it may be detected include *M. leucophaetus* (Conrad 1831) (pl. 1, fig. 11), the living type species, and *M. basteroti* (Deshayes in Lamarck, 1836) from the Lower Miocene of Aquitaine (pl. 5, fig. 9). It is almost certain that all species of *Mytilopsis*, whether or not this weak pallial sinus is detectable, were basically epifaunal and byssally attached. *Dreissenomya* (s.l.), in which a definite pallial sinus is present, is thought to have been infaunal. Morton (1970, pp. 564, 568, text-fig. 2) suggested that *D. (S.) aperta* was infaunal and byssally attached as it possessed a byssal notch. However, the commissure in this species is so irregular and variable that it is impossible positively to identify a byssal notch as indicated in Morton's figure. Marinescu (1975, p. 90) stated that the gapes in *D. (Sinucongeria)* were either less important than in *Dreissenomya* (s.s.) or absent altogether. He made no mention of the presence of a byssal notch in either subgenus. *Dreissenomya (D.) schroeckingeri* (Fuchs 1870a), on the other hand, possesses pronounced anterior (pedal) and posterior (siphonal) gapes (Marinescu 1975, p. 78, text-fig. 3). Marinescu also (pp. 105–107) discussed the mode of life of these subgenera. Single valves were less common than specimens with both valves together, found nearly perpendicular to the bedding plane, presumably in life position. The indications are that the Pontian *D. (D.) schroeckingeri* lived at depths of up to 30 cms below the sediment surface and that *D. (S.) aperta* at about 5–7 cm (text-fig. 1B, C). He considered that the earlier, Meotian, species of both subgenera were barely covered, as they often occur as isolated valves, and that juveniles, lacking the posterior gape were also surface dwellers. According to Prof. W. Russell-Hunter (*pers. comm. in* Yonge and Campbell, 1968), juveniles of living *Dreissena* use the foot to move about from time to time and produce a weak byssus with only a few threads for temporary attachment. With growth, the foot becomes less important as an organ of locomotion and a much stronger, more permanent byssus is formed. It seems likely that juvenile

fossil dreissenids had similar habits. It is reasonable to suppose that the earlier species of *Dreissenomya* (s.l.) followed this pattern, but the later, more deeply buried species differed in not being byssally attached as adults. They were possibly strong and rapid burrowers, in a manner comparable to members of the Tellinacea.

Other characters

The opisthodontic ligament and soft parts of *D. polymorpha* (Pallas) are described in detail (Yonge and Campbell 1968; Morton 1969). *Mytilopsis sallei* (Recluz 1849), a member of the only other living genus, is similarly dealt with (Escarbassiere and Almeida 1976; Morton 1981). The shell structure of *D. polymorpha* was studied by Taylor, Kennedy and Hall, (1973) who noted its strong resemblance to that found in the Corbiculacea, a predominantly freshwater superfamily, whilst Archambault-Guezou (1982) noted cylindrical perforations which she considered to be tubules in two other living species, which she placed in *Congerina*, but are here assigned to *Mytilopsis* as *M. leucophaetus* (Conrad) and *M. cochleatus* (Kickx in Nyst, 1835).

Planktotrophic larvae are reported in both living genera (Morton 1969, with further references) for *D. polymorpha* (Pallas), and by Escarbassiere and Almeida (1976, p. 167, fig. 14) for *Mytilopsis sallei* (Recluz). As Morton pointed out, the retention of a free-swimming larva is unique among freshwater bivalves. Morton (1969) showed that *D. polymorpha* possessed a very efficient filtering system that enabled it to live in both fast-running and in relatively static freshwaters. *M. sallei* is similar in this respect and, additionally, is extremely tolerant to salinity changes between 0–50‰ (Escarbassiere and Almeida 1976; Morton 1981). This must be an important factor in its ability to be transported across oceans and also in its survival in tropical estuaries and harbours where salinity can vary enormously between wet and dry seasons.

SYSTEMATIC PALAEOLOGY

Repositories. With the exception of figures reproduced from other works, all figures are of specimens in the British Museum (Natural History). Fossils are in the Palaeontology Department (BMPD) and their registration numbers are prefixed by either L or LL. Recent specimens are in the Zoology Department (BMZD), whose registration numbers frequently refer to a whole sample rather than a single specimen.

Subclass HETERODONTA

Order VENEROIDA

Superfamily DREISSENACEA Gray in Turton, 1840

Diagnosis. Normally mytiliform to modioliform; umbones terminal or nearly so; umbonal septum or shelf present, but sometimes vestigial; edentulous; heteromyarian with anterior adductor muscle attached to septum; gills eulamellibranchiate; shell aragonitic, outer layer of simple and crossed lamellae; inner layer of complex crossed lamellae.

Distribution. Lower Eocene to Recent, Europe, Asia Minor and as far east as Kazakhstan (Aral Sea region). Late Oligocene, Central and tropical South America, spreading northwards into southern and Atlantic seaboard areas of United States during the Neogene. Introduced to India, Hong Kong and Japan. Probably introduced to Fiji and West Africa.

Remarks. The characters mentioned in this diagnosis are discussed in the section on morphology and mode of life, whilst the distribution of the family is dealt with under each genus in turn and in the discussion.

Family DREISSENIDAE Gray in Turton, 1840

Diagnosis. As for superfamily.

Subfamily DREISSENINAE, Gray *in* Turton, 1840

Diagnosis. Umbones terminal; pallial sinus absent or weak; byssal gape usually marked.

Remarks. Living Dreisseninae are usually mytiliform, sometimes triangular or quadrate, and have short, separate, siphons. They are epifaunal, byssally attached in clusters. Distinctions between them and the Dreissenomyinae are discussed under the latter.

Distribution. As for superfamily.

Genus DREISSENA van Beneden, 1835a

(text-fig. 2A).

Type species. *Mytilus (sic) polymorphus* Pallas, 1771, by monotypy. Recent, Europe. (pl. 1, figs. 1–6).

Diagnosis. Mytiliform, smooth except for growth lines, with simple septum on which anterior adductor and pedal-byssal retractor muscles are mounted; apophysis lacking; pallial line entire.

Distribution. Late Miocene (Meotian)-Recent, Europe, northern Asia Minor and as far east as the Aral Sea, and the River Euphrates.

Remarks. Numerous fossil species have been recognized particularly in the Paratethys. Many have very restricted distributions both geographically and stratigraphically and the suspicion remains that some are of little more than local significance. Carinate mytiliform *Dreissena* (s.s.) may be easily distinguished from the non-carinate, more modioliform *D. (Pontodreissena)* and *D. (Modiolodreissena)*, but the differences between these do not seem great.

Subgenus DREISSENA van Beneden, 1835a

Plate 1, figs. 1–6.

Diagnosis. *Dreissena* with straight dorsal margin and markedly angular diagonal carina.

Distribution. As for genus (s.l.)

Remarks. *Dreissena* (s.s.) corresponds to the *carinatae*-group of Andrussov (1897–8). The living type species, *D. polymorpha* is long ranging, first occurring in the Meotian of the eastern Paratethys (Iljina *et al.* 1976). Archambault-Guezou (1976b) and Locard (1893) gave useful summaries of its spread from its apparent area of origin. Much of its dispersal through the rivers and canals of western Europe has occurred very recently, being recorded from the Danube in 1769, England in 1824 and the south of France by 1865–6. This rapid spread probably coincided with increasing trade and the interconnections of inland waterways by canals and locks. Locard (1883) described two species from the upper reaches of the Euphrates river system in northern Syria, and later (1893) recorded the genus from above Baghdad. The Holotype (BMZD 1984243) of *Mytilus tenebrosus* Reeve, 1858, described from the Mississippi, is a damaged *D. polymorpha*. It is the only record of the genus from the Western Hemisphere and may be discounted, having either been mislocalized or transported as ballast.

Subgenus PONTODREISSENA Logvinenko and Starabogatov, 1966

Plate 1, figs. 7–10, plate 2, figs. 6–8.

Type species. *Mytilus rostriformis* Deshayes, 1838, by original designation. Pliocene, Crimea, (pl. 1, figs. 7–10, pl. 2, figs. 6–8).

Diagnosis. Dorsal margin convex; ventral margin slightly concave behind umbone; not tumid, diagonal ridge much weaker than in *D. (Dreissena)* and mainly confined to umbonal region; septum broad.

Distribution. Late Miocene (Meotian) to Recent, Paratethys and bordering Mediterranean (see below).

Remarks. The work in which this subgenus was erected has not been seen. *Pontodreissena* is used by Starabogatov (1970), Babak (1983) and Rozanov (1986). *Pontodreissena* corresponds to part of the *modioliformes*-group of Andrussov (1897–8): other members of this group were assigned to *D. (Modiolodreissena)* by Babak (1983). *D. (P.) rostriformis* is first recorded from the Meotian of the eastern Paratethys (Rozanov 1986) though other authors do not recognize it before the Pontian. Archambault-Guezou (1976*b*) summarizes its distribution. In her opinion, it originated in the Dacian Basin during the Lower Pontian and persisted there through the Dacian, invading the eastern Paratethys during the Middle Pontian, continuing there throughout the Pliocene and into the Quaternary, and living now in the Caspian. It invaded the Mediterranean, being found in strata of probable Messinian age from Greece, Italy, Sicily, southern France and southern Spain. Other species are shorter ranging, mainly confined to the eastern Paratethys, and all extinct (Babak 1983).

Subgenus MODIOLODREISSENA Babak, 1983

Plate 2, figs. 3, 4.

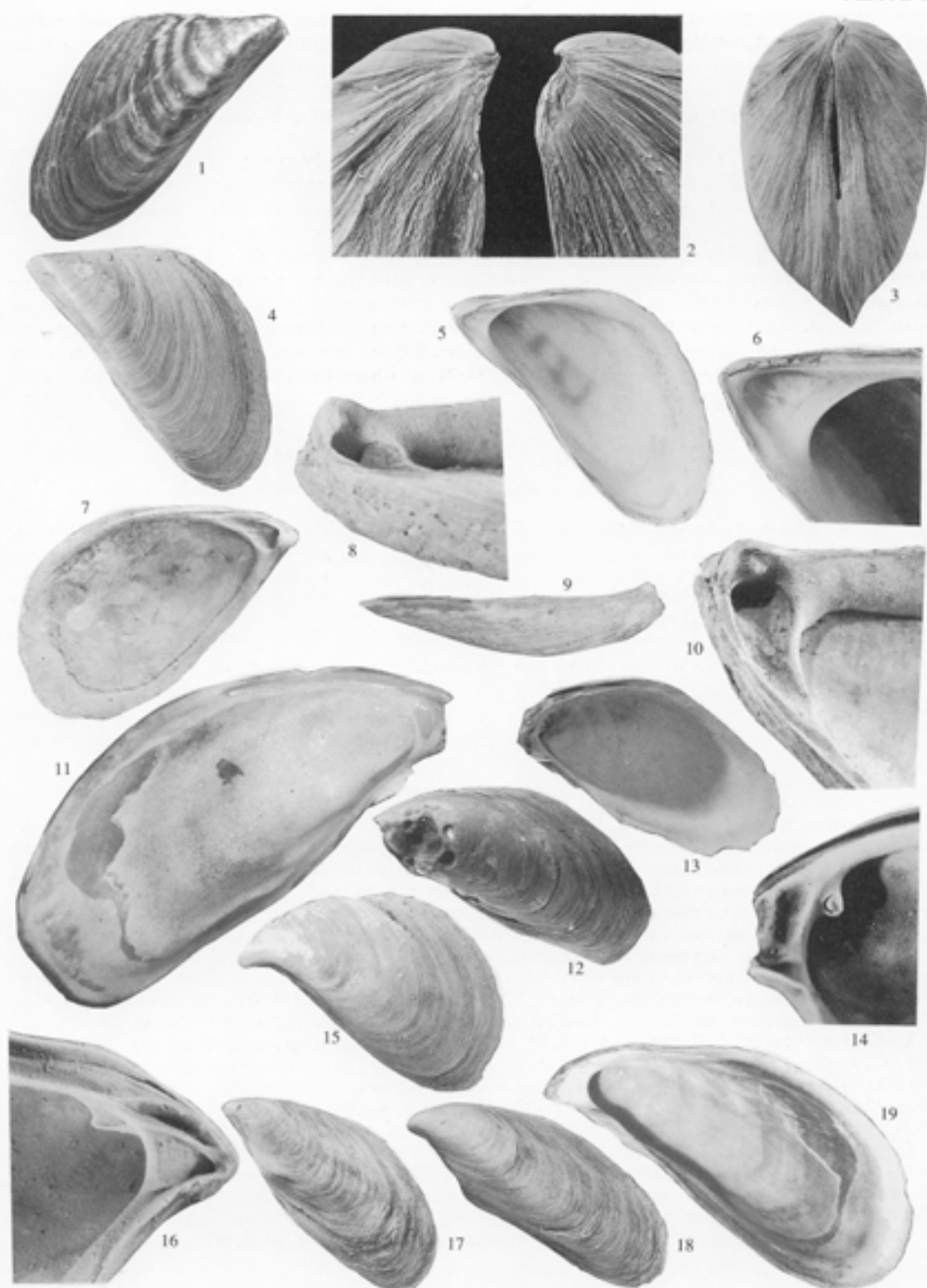
Type species. *Dreissensia theodori* Andrussov, 1893, by original designation, Pliocene, Crimea, (pl. 2, figs. 3, 4).

Diagnosis. Like *D. (Pontodreissena)* but amygdaloidal with both dorsal and ventral margins convexly curved; diagonal ridge lacking.

Distribution. Late Miocene (Meotian) – Late Pliocene (Akchagylian), Paratethys only.

EXPLANATION OF PLATE 1

- Figs. 1–6. *Dreissena (D.) polymorpha* (Pallas), sample BMZD 1984242, Recent, Commercial Docks, London, G.B. Sowerby Colln. 1, right valve. 2, 3, ventral views (left valve on right of figures) to show different profiles of commissures in beak region (compare with fig. 8, below), and also byssal notch in fig. 3. 4, left valve. 5, 6, right valve, internal view showing septum. $\times 2$, except 2, 6, both $\times 5$.
- Figs. 7–10. *Dreissena (Pontodreissena) rostriformis* (Deshayes 1838), LL 28238/1 left valve, Pliocene, exact horizon unknown, Kamych-Burun, Kerch Peninsula, Crimea, U.S.S.R. 7, internal, $\times 1.5$, 8, 10, details of septum and rostrate process from different angles, both $\times 4$. 9, ventral view, showing rostrate process (compare with fig. 2 above), $\times 1.5$.
- Figs. 11–14. *Mytilopsis leucophaetus* (Conrad 1831) sample BMZD 1984239. Recent, Green Cove Springs, Black Creek (tributary of St John's River), Florida, attached to submerged wood, collected live by Messrs D. C. Marelli and M. J. Greenberg. 11, 12, left valve internal, showing slight pallial sinus, $\times 5$, external view $\times 3$. 13, right valve internal, $\times 3$. 14, umbonal area of another right valve, tilted to show apophysis, $\times 10$. (N.B. The umbones of this species invariably seem to be eroded).
- Figs. 15, 16, 18, 19. *Mytilopsis sallei* (Recluz 1849). 15, sample BMZD 1984230, left valve of shell figured as *Mytilus sallei* by Reeve, 1858, pl. 10, fig. 44, Central America, Cuming Colln, $\times 2.5$. 16, left valve of shell from same sample, detail of septum and apophysis, $\times 10$. 18, sample 1984236, left valve of shell figured as *Mytilus domingensis* Recluz (1852) by Reeve, 1858, pl. 100, fig. 44, Dominican Republic, Cuming Colln, $\times 2$. 19, right valve of shell from same sample showing extremely weak pallial sinus, $\times 2.5$.
- Fig. 17. *Mytilopsis africanus* (van Beneden 1835*b*), sample BMZD 1984238, left valve of shell figured as *Mytilus africanus* by Reeve, 1858, pl. 10, fig. 47, Senegal, Cuming Colln, $\times 1.5$, cf. figs. 18 and 19.



NUTTALL, *Dreissena*, *D.* (*Pontodreissena*) and *Mytilopsis*

Remarks. The broad septum often extends some distance along the dorsal margin. The *modioliformes*-group of Andrussov (1897–8) is split between this subgenus and *D. (Pontodreissena)*: the distinctions between them do not seem great, but may be useful in the context of Paratethys geology. Rozanov (1986) records *D. rimestiensis* (Fontannes 1887) from the Meotian, the species survives to the top of the Pontian in Rumania. The type species first occurs in the late Pontian (Kamyschburun, Kertsch Peninsula) and persists into the Akchagylian.

Genus CONGERIA Partsch, 1835

Plate 2, figs. 1–3, Plate 3, figs. 1–6, text-fig. 2D.

Type species. *Congeria subglobosa* Partsch, 1835, subsequent designation by Pilsbry, 1911, Upper Miocene, Pannonian, Vienna Basin, (pl. 3, figs. 1–6). = *Globocongeria* Taktakishvili, 1973, p. 14, (objective synonym), type species *Congeria subglobosa* Partsch, 1835, by original designation, = *Rhombocongeria* Starabogatov, 1970, type species *Congeria rhomboidea* M. Hörnes, 1870, by original designation, Upper Miocene, Pontian, Hungary, (pl. 2, figs. 1–3) = *Rhomboidea* Marinescu, 1973, (objective synonym of *Rhombocongeria*), type species *Congeria rhomboidea* Hörnes, 1870, by original designation.

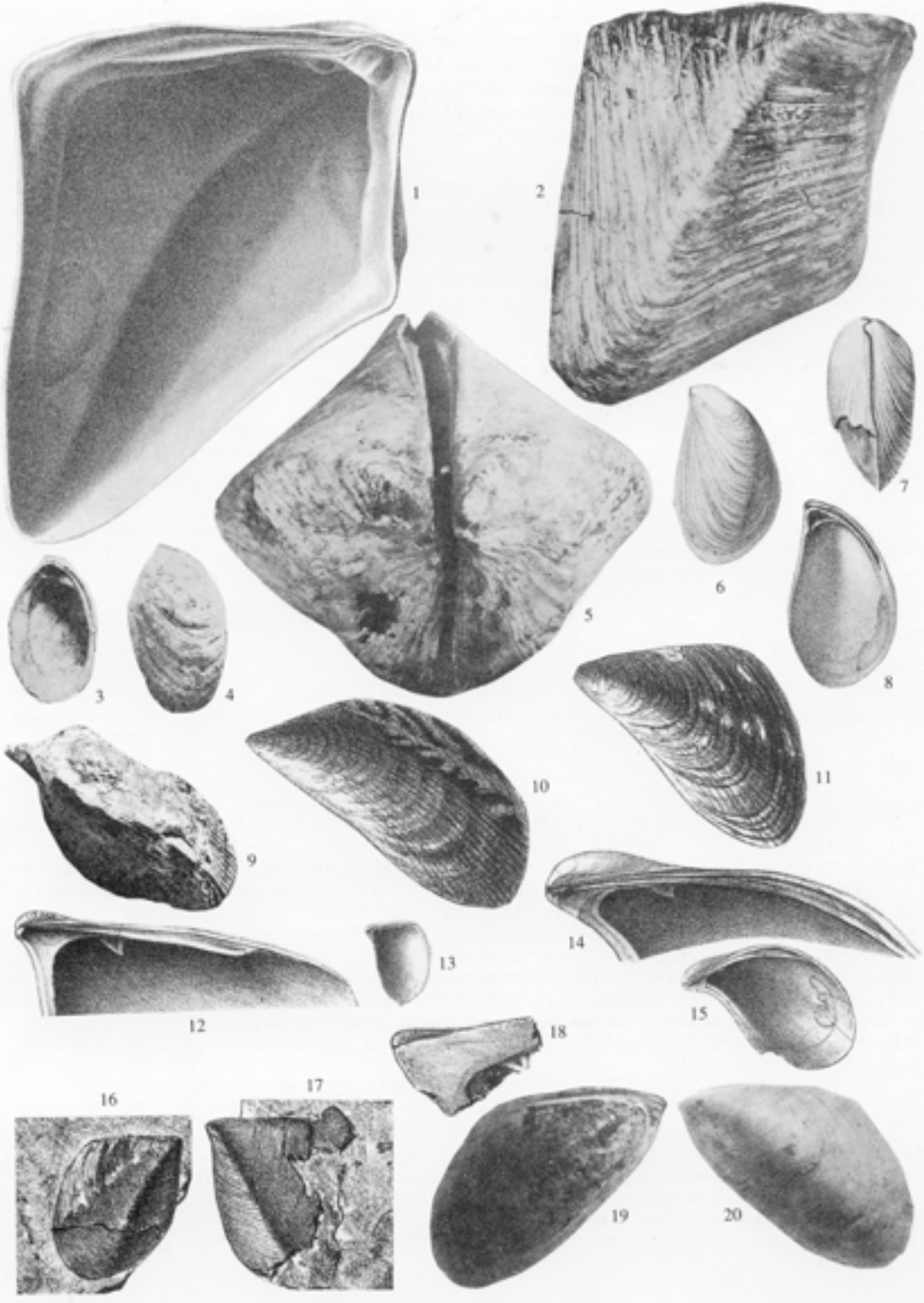
Diagnosis. Quadrate to rhomboidal; smooth except for growth lines; apophysis fused to septum; pallial line entire.

Distribution. Late Miocene (Pannonian to Lower and Middle Pontian), western Paratethys only.

Remarks. There is more than one approach to the classification of dreissenids possessing an apophysis as well as a septum. The first, with variations, adopted by most Eastern Hemisphere authors (Andrussov 1897–8; Orlov 1960; Starabogatov 1970; Taktakishvili 1973; Marinescu 1973;

EXPLANATION OF PLATE 2

- Figs. 1, 2, 5. *Congeria rhomboidea* M. Hörnes, presumed Upper Miocene, Pontian, 1, left valve internal, Arpád, S.E. of Fünfkirchen, southern Hungary, from M. Hörnes, 1867, pl. 48, fig. 4a. 2, 5, right valve and anterior view, from Andrussov, 1897, pl. 10, figs. 8, 10. 2, Ogrugliak, Croatia, Yugoslavia, 5, Arpád, Hungary, all $\times 1$.
- Figs. 3, 4. *Dreissena (Modiolodreissena) theodori* Andrussov (1893), Pliocene, late Kimmerian or early Akchagylian, Eisenerzschichten, Kamych-Burun, Kerch Peninsula, Crimea, U.S.S.R., from Andrussov, 1897, pl. 13, figs. 16, 15. 3, right valve internal. 4, left valve, both $\times 2$.
- Figs. 6–8. *Dreissena (Pontodreissena) rostriformis* (Deshayes 1838), presumed Pliocene, exact horizon and locality unknown, Crimea, U.S.S.R. from Deshayes, 1838, pl. 4, figs. 14–16. 6, left valve. 7, ventral view, with left valve on right of drawing. 8, right valve internal, all $\times 1$.
- Fig. 9. *Prodreissensia perrandoi* Rovereto, Lower Oligocene, Tongrian, Mioglia, Liguria, Italy, left valve of the figured syntype, from Rovereto, 1990, pl. 4, fig. 14, $\times 1.5$.
- Figs. 10, 11. ?*Prodreissensia euchroma* (Oppenheim 1891), Lower Eocene, Mt. Pulli, near Valdagno, Vicentin, Italy, figured syntypes, from Oppenheim, 1891, pl. 51, figs. 5a, 6a. 10, $\times 4$; 11, $\times 2$.
- Figs. 12, 13. *Mytilopsis chonioides* (Cossmann), Upper Eocene, Priabonian, Le Ruel, Seine-et-Oise, France, right valve of Cossmann's (1887, pl. 6, figs. 32, 33) figured syntype, as refigured by Oppenheim, 1891, pl. 51, figs. 1, 1a, approx. $\times 6$, $\times 1$.
- Figs. 14, 15. *Mytilopsis curvirostris* (Cossmann), Eocene, Priabonian, Marines, Seine-et-Oise, France, right valve of Cossmann's (1887, pl. 6, figs. 29, 30) figured syntype, as refigured by Oppenheim, 1891, pl. 51, figs. 2, 2a, approx. $\times 5$, $\times 1.67$.
- Figs. 16, 17, 18. *Mytilopsis eocenica* (Oppenheim, 1891), Lower Eocene, Dorogh, near Gran, northern Hungary, from Oppenheim, 1891, pl. 51, figs. 8b, d, f, 16 internal view of right valve umbonal region; 17, left valve; 18, right valve, magnifications unknown.
- Figs. 19, 20. *Mytilopsis modiolopsis* (Andrussov, 1897–8), Upper Miocene, Meotian, Akmanajsky, Crimea, U.S.S.R., left valve, internal, external, from Andrussov; 1897, pl. 9, figs. 10, 9, $\times 3$.



NUTTALL, *Dreissenidae*

Archambault-Guezou 1976a, b, 1982; Babak 1983) is to place them all in a varying number of subgenera or 'groups' of *Congeria* Partsch, the first valid name available. The second view is that adopted by Keen (in Moore 1969) who recognized *Mytilopsis* as a separate genus with a basically Western Hemisphere distribution. A modification of these two views, along with, in some cases radical, revision of the stratigraphic and geographic ranges of the subgenera concerned is adopted herein. The basic argument for this decision relies on the fact that mytiliform species resembling living *Mytilopsis* are the first dreissenids to appear in the Eocene, being recorded from all provinces in which dreissenids are found at that time. In contrast, the large, heavy and often quadrate rather than mytiliform species, typified by *C. subglobosa*, occur only at about the Miocene-Pliocene boundary in the western Paratethys. *Congeria* is here regarded as a short-lived offshoot of *Mytilopsis*.

Andrussov's (1897-8) divisions of *Congeria* into various non-binomial 'groups', for some of which he designated 'type-species' have been validated subsequently, and some have junior synonyms (see Table 2).

Comparatively few species remain in *Congeria*. Most are illustrated and listed as members of the *subglobosae* and *rhomboidea* groups by Andrussov (1897-8). They are recorded from the Vienna Basin, Yugoslavia, Hungary and Rumania. *C. subglobosa* Partsch was first described from the Plattensee (Lake Balaton) district of Hungary and is common in the Pannonian of the Vienna Basin. *C. rhomboidea* M. Hörnes, was first described from Hungary and, in common with other species assigned to *C. (Rhomboides)* by Marinescu (1973), is confined to the Lower and Middle Pontian (Odessian and Portaferrian).

Some confusion may exist about the status of *Globocongeria*. Taktakishvili (1973, p. 14) designated *C. subglobosa* Partsch as type species, thus making it an objective synonym of *Congeria* (s.s.) itself. Taktakishvili's interpretation of *Congeria* (s.s.) was that it corresponded to the *mytiliformes* and *eocenae* groups of Andrussov, both of which are here placed in *Mytilopsis*. Unfortunately the *Zoological Record (Mollusca)* for 1978, p. 425 quoted the type species of *Globocongeria* as being *Congeria digitifera* Andrussov, 1897-8. This, in fact, was merely the first species dealt with by Taktakishvili (1973, p. 36) in his formal descriptions of the Pliocene dreissenids of western Georgia. All the species assigned by Taktakishvili to *Globocongeria* belong to Andrussov's *subglobosae* group, and thus to *Congeria* (s.s.).

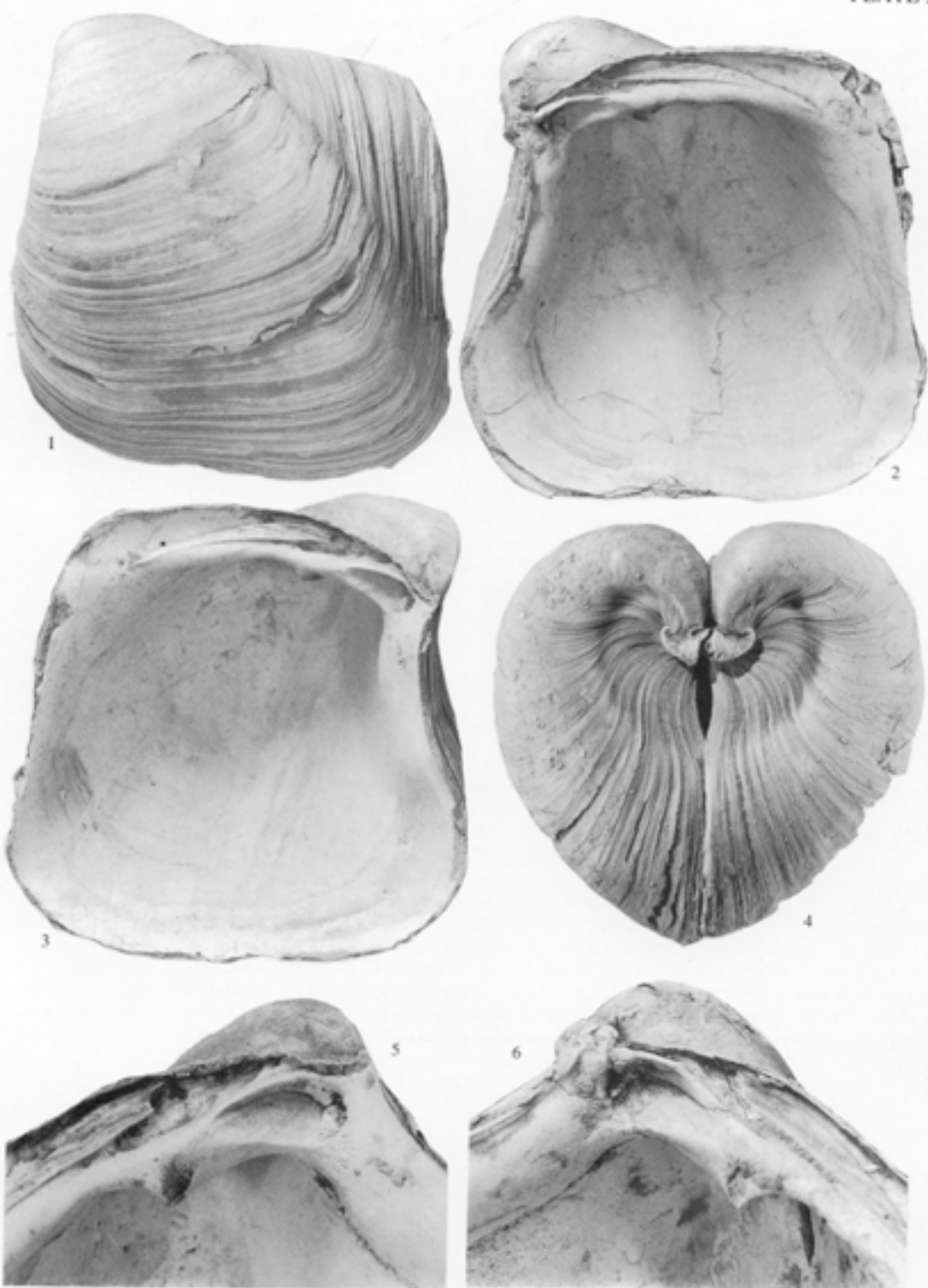
Genus MYTILOPSIS Conrad, 1858

Plate 1, figs. 11-19; Plate 2, figs. 12-20; Plate 4, figs. 1-16; Plate 5, figs. 6-13; Plate 6, figs. 8-10; text-figs. 2A, E.

Type species. *Mytilus leucophaetus* Conrad, 1831, subsequent designation by Dall, 1898, Recent, eastern U.S.A., (pl. 1, figs. 11-14). = *Andrusoviconcha* Starabogatov, 1970, type species *Congeria modiolopsis* Andrussov, 1897-8, by original designation, Upper Miocene, Meotian, Crimea, (pl. 2, figs. 19, 20). = *Eocongeria* Starabogatov, 1970, type species *Tichogonia (Congeria) eocenica* Oppenheim, 1891 (see remarks), by original designation, Lower Eocene, Hungary, (pl. 2, figs. 16-18). = *Mytilia* Marinescu, 1973, type species *Congeria neumayri* Andrussov, 1897-8, by original designation (preoccupied by *Mytilia* Gray, 1858, Reptilia and by *Mytilia* Gosse in Hudson and Gosse, 1886, Rotifera), = *Modiola* Marinescu, 1973, type species *Congeria czizeki* Hörnes, 1867, by original designation (preoccupied by *Modiola* Lamarck, 1801, Mollusca), =

EXPLANATION OF PLATE 3

Figs. 1-6. *Congeria subglobosa* Partsch, Upper Miocene, Pannonian, Austria. 1, 2, 3, 5, 6. LL 28239., Brunn, near Vienna, (ex K.K. Mineralien-Kabinet), 1, left valve, × 1. 2, right valve, internal, × 1. 3, left valve internal, × 1. 5, left valve, tilted, to show apophysis, × 1.5. 6, right valve, tilted to show apophysis, × 1.5. 4, LL 28240/1. Hennersdorf Brick Pit, 10 km S. of Vienna, F. Rögl, B. R. Rosen and J. G. Darrell Colln, front view showing byssal notch, × 1.



NUTTALL, *Congeria subglobosa*

Trigonipraxis Starabogatov, 1970, type species *Congeria triangularis* Partsch, 1835, by original designation, Upper Miocene, Pannonian, Hungary, (pl. 4, figs. 1–5). = *Triangularia* Marinescu, 1973, type species *Congeria ornithopsis* Brusina, 1892, by original designation, (preoccupied by *Triangularia* Frech, 1894, Mollusca).

Diagnosis. Like *Dreissena*, but possessing an apophysis, usually behind, but sometimes partly underneath and partially fused to the septum; pallial sinus, if present, very weak.

Distribution. Lower Eocene – Pliocene, Europe; late Oligocene – Recent, central and northern South America and Caribbean, spreading to North America bordering Gulf of Mexico and Atlantic. Introduced (Recent), southern India, Japan and Hong Kong, probably introduced, Fiji, West Africa and Rhine–Scheldt Delta.

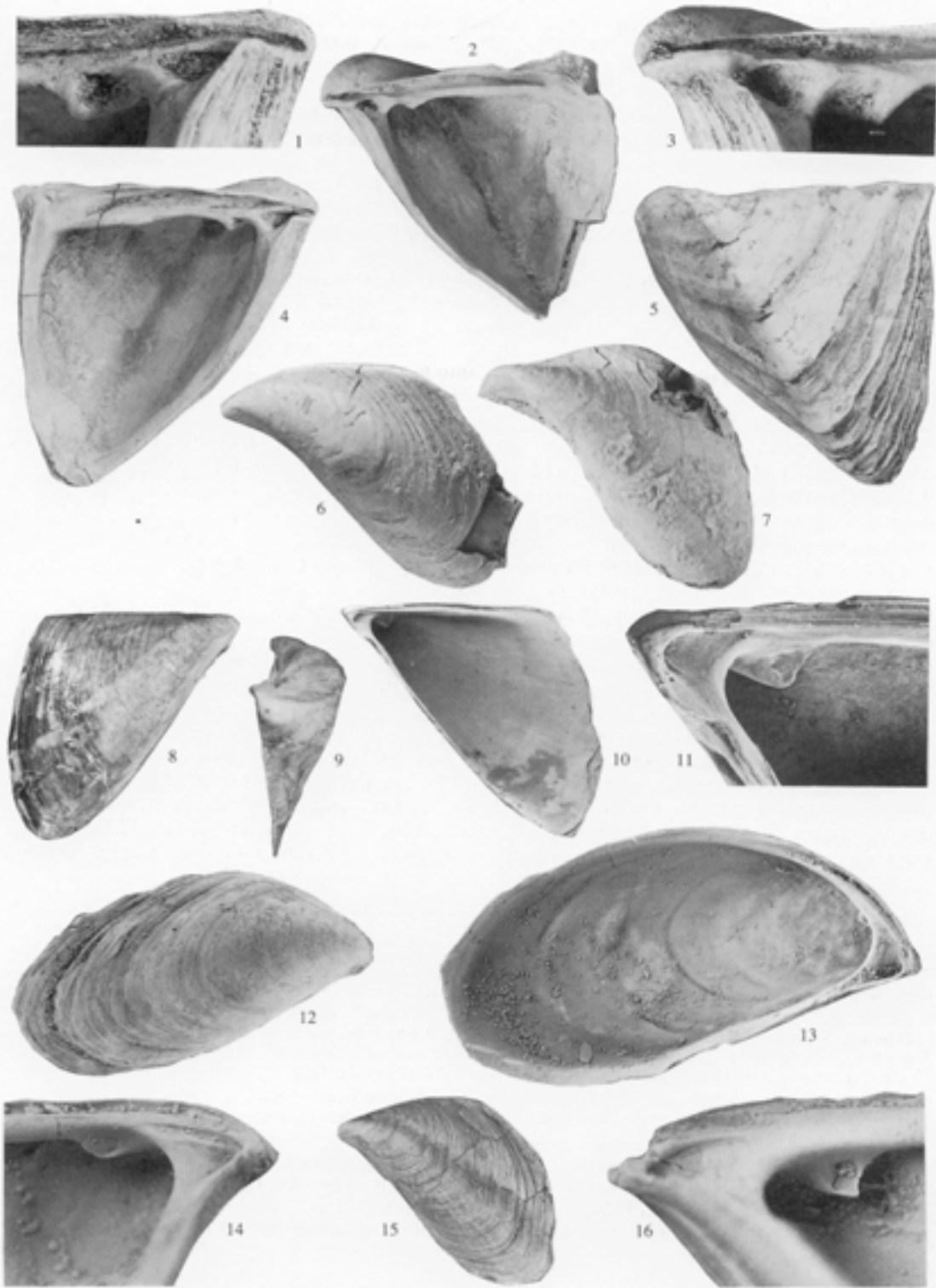
Remarks. The generic synonymy and its relationship to Andrussov's (1897–8) 'groups' is best explained by reference to Table 2, whilst the main reasons for placing these taxa in *Mytilopsis* rather than *Congeria* are given in the remarks on the latter genus. Andrussov (1897–8) placed all the living Western Hemisphere nominal species of *Mytilopsis*, including the type species *M. leucophaetus* and *M. sallei* (Recluz 1849) (pl. 1, figs. 15, 16, 18, 19), into his 'mytiliformes'-group, whilst he placed the living European *M. cochleata* (Kickx in Nyst, 1835) and the West African *M. africanus* (van Beneden 1835b) (pl. 1, fig. 17) into his 'modioliformes'.

It would appear, however, (Nuttall 1990, pp. 282, 284, fig. 335) that *M. africanus* is synonymous with the form of *M. sallei* originally described as *M. domingensis* (Recluz 1852) (pl. 1, fig. 19) from the Dominican Republic. It is suggested (S. Morris, BMZD, *pers. comm.*) that this African occurrence may well be the result of introduction by man, perhaps during the period of the slave trade between West Africa and the West Indies. *M. cochleata* is also likely to have been introduced to the Rhine–Scheldt Delta from the Western Hemisphere. Variation within species is such that there is no apparent reason for the separation of Recent 'mytiliformes' from 'modioliformes'.

Starabogatov (1970, p. 83) designated, as type species of *Eocongeria*, a new subgenus of *Congeria*, *Dreysensia* (*Congeria*) *eocenica* Munier-Chalmas in Hébert and Munier-Chalmas (1877, p. 126), even though the name appears only in a faunal list and is clearly a *nomen nudum*. Oppenheim (1891, p. 953) was the first to describe the species and is here credited with its authorship. Members of the 'eocenes'-group of Andrussov, upon which *Eocongeria* is based, are all of Eocene age and exhibit a wide variation in shell shape, but most are typical of *Mytilopsis*. *D. eocenica* from the Lower Eocene (Eames in Morley Davies, 1975, p. 146) of Dorogh, Hungary, possesses a low angular fold not normally seen in *Mytilopsis*, but the form of its septum and apophysis is indistinguishable from that of modern *Mytilopsis*. Oppenheim (1891, pl. 51) gave excellent illustrations, including the internal characters, of this and three other Eocene species, *C. chonioides* (pl. 2, figs. 12, 13) and *C. curvirostris* (pl. 2, figs. 14, 15) both described by Cossmann (1887) from the French upper Eocene,

EXPLANATION OF PLATE 4

- Figs. 1–5. *Mytilopsis triangularis* (Partsch), Upper Miocene, Pontian, Radmanest, Banate, Hungary. 1, 4, 5, L19499/1, left valve, 1, interior, tilted, showing typical *Mytilopsis* apophysis, $\times 4$. A, 4 interior, $\times 1.5$. 5, exterior, $\times 1.5$. 2, 3, L19499/2, right valve. 2, interior, $\times 1.5$. 3, interior, tilted, $\times 4$.
- Figs. 6–11. All from Miocene, Pebasian, Peru.
- Fig. 6. *Mytilopsis sallei* Recluz (1849), LL 27195, left valve, Panamá, $\times 3$.
- Fig. 7. *Mytilopsis scripta* (Conrad 1874), LL 27956, left valve, Pichana, $\times 2.5$.
- Figs. 8–11. *Mytilopsis* cf. *scripta* (Conrad 1874), LL 27914, right valve, Panamá. 8, external; 9, anterior; 10, internal, all $\times 5$. 11, internal, showing apophysis, $\times 20$.
- Figs. 12–16. *Mytilopsis sowerbyi* d'Orbigny (1850), Upper Eocene, Priabonian, Lower Headon Beds, all Hordwell (except 15, Mead End) Hampshire. 12, LL 28131, Edwards Colln, right valve, $\times 4$. 13, LL 28130, left valve internal $\times 4$. 14, 16, LL 28242/1, 2, Hastings Colln, internal views of umbonal region, tilted to show apophysis lying under septum. 14, left valve; 16, right valve, both $\times 10$. 15, LL 28244, Edwards Colln, left valve, $\times 2$.



NUTTALL, *Mytilopsis*

and of *C. euchroma* Oppenheim, 1891, (pl. 2, figs. 10, 11) from the northern Italian Eocene. Andrussov (1897) recorded *C. curvirostris* as the basal member of his 'mytiliformes'-group (= *Mytilia*) and *C. euchroma* along with the British Priabonian *D. sowerbyi* (d'Orbigny 1850) (pl. 4, figs. 12–16) as one of the earliest 'modioliformes'. In the present work *C. euchroma* is provisionally placed in *Prodreissensia* because it possesses radiating ribbing whilst the other species mentioned above are considered to be typical of *Mytilopsis*. Thus, there seems as little reason for either generic or subgeneric separation of these early members of the family, as there is for separating the living species discussed in the preceding paragraph.

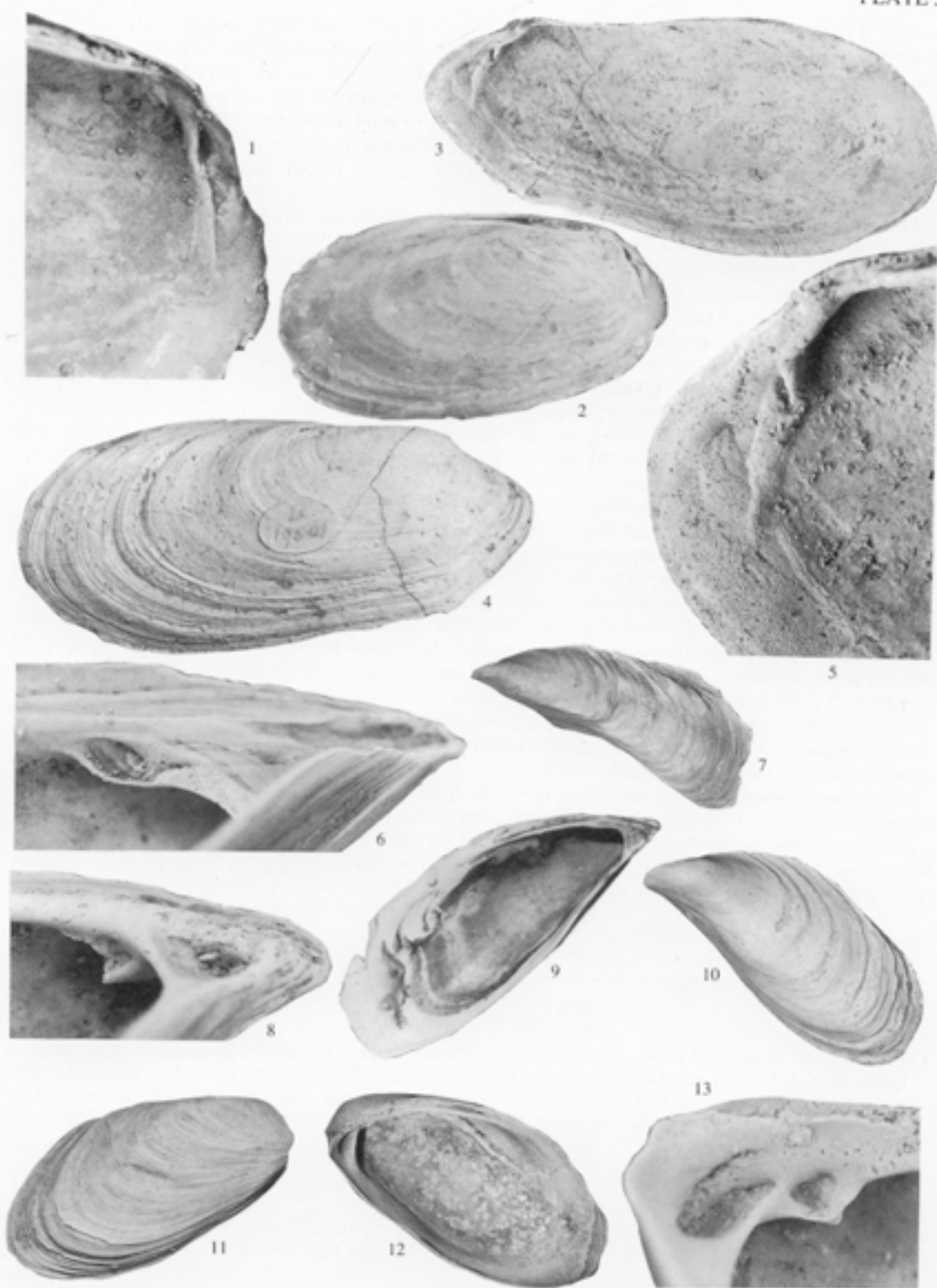
During the Eocene *Mytilopsis* is represented by several species (Oppenheim 1891; Andrussov 1897–8) including *M. eocenica* (Oppenheim 1891), Lower Eocene, Dorogh, Hungary; *M. curvirostris* and *M. chonioides* (both Cossmann 1887) rare in the Sables Moyon (Bartonian = Priabonian) of the Paris Basin (Cossmann and Pissarro 1904–6) and *M. sowerbyi* (d'Orbigny 1850) from the Lower Headon Beds (Priabonian), of Hampshire and the Isle of Wight, England (BMPD).

Oligocene species include *M. nystiana* (d'Orbigny 1852), Tongrian (= Lattorfian), Belgium (Glibert and de Heinzelin 1954 as *Congerina nysti*) and *M. aralensis* (Merklin 1974), Middle Oligocene, Aral Sea Region, USSR. *M. brardi* (Brongniart 1823) was recorded (Wenz 1921) from the Cerithien-schichten of the Mainz Basin, now dated as Chattian (Martini in Steininger *et al.* 1985, p. 334). This species persists into the Miocene, occurring in the Aquitanian *Corbicula*-Schichten and overlying Hydrobien-Schichten (Wenz 1921). Widespread Miocene occurrences include *M. amygdaloides* (Dunker 1848), (pl. 5, figs. 11–13) probably late Lower Miocene, Wurttemberg, Germany (BMPD); *M. alta* (Sandberger 1874), Middle Miocene (Pontilévian), Faluns of Touraine, France (Glibert and van de Poel 1967); several species from the Aquitanian to Helvetian of the Aquitaine Basin, France, including (pl. 5, figs. 8–10) *M. basteroti* (Deshayes in Lamarck, 1836) (see Cossmann and Peyrot 1914; BMPD); *M. sandbergeri* (Andrussov 1897–8), Miocene, Poland (Friedberg 1936); *M. sandbergeri*, Miocene (Konkian and Tortonian), and several species up to the Meotian, of the Ukraine (Zelinskaya *et al.* 1968); *M. soceni* and *M. moesia* (both Jekelius, 1944) Sarmatian, Rumania and also Vienna Basin (Papp 1954; Sieber 1955); *M. spathulata* (Partsch 1835) (pl. 5, figs. 6, 7, text-fig. 2E) and several other species, Pannonian, Vienna Basin (Papp 1951, 1953; Sieber 1955); several species, Meotian, Paratethys (Rozanov 1986); *M. subcarinatus* (Deshayes 1838), Pontian and Lower Kimmerian, Paratethys, and other species of which the last surviving were *M. mirabilis* (Seninsky 1905) and *M. caucasica* (Seninsky 1905) (see Babak 1983, p. 87), both of which died out in the late Kimmerian.

In Western Europe, the last surviving, naturally occurring *Mytilopsis* appears to be *M. rhodanica* (Fontannes 1882) from the 'Infra-Pliocene' (Messinian) of the Rhone Valley. According to Archambault-Guezou (1976b) this species was derived from *M. subcarinatus* (Deshayes 1838) of the Paratethys, having migrated into the Mediterranean in the same way as *Dreissena* (*Pontodreissena*) *rostriformis* (Deshayes 1838) (see above).

EXPLANATION OF PLATE 5

- Figs. 1–5. *Dreissenomya* (*D.*) *schroeckingeri*, (Fuchs, 1870a), Upper Miocene, Pontian, Radmanest, Banate, Hungary. 1, 2, L71745, left valve interior, 1, $\times 4$; 2, $\times 1.5$. 3–5, L19501, right valve, 3, 4, $\times 1.5$; 5, $\times 4$.
 Figs. 6, 7. *Mytilopsis spathulata* (Partsch), L23908/1, left valve, Upper Miocene, Pannonian, Brunn, near Vienna, Austria. 6, detail of internal umbonal region, tilted, apophysis attached to posterior of septum (right valve has similar arrangement), $\times 10$. 7, $\times 2$.
 Figs. 8–10. *Mytilopsis basteroti* (Deshayes 1836), Lower Miocene, Aquitanian or Burdigalian, Dax, Landes, France, Deshayes Colln. 8, 9, LL 28240/1, left valve, 8, internal view of worn umbonal region, $\times 10$. 9, to show weak pallial sinus, $\times 2.5$. 10, LL 28240/2, left valve, $\times 2$.
 Figs. 11–13. *Mytilopsis amygdaloides* (Dunker, 1848), probably late Lower Miocene, Unterkirchberg, Bavaria, L1266/1, left valve, 11, 12, $\times 2.5$. 13, tilted to show apophysis, $\times 10$.



NUTTALL, *Dreissenomya* and *Mytilopsis*

The Western Hemisphere distribution of *Mytilopsis*, the only dreissenid to reach the New World, is discussed in detail by Nuttall (1990, pp. 278–280, figs. 319–325). The first occurrences, some thirty million years later than the appearance of the genus in Europe, are of *M. trigalensis* (Olsson 1931) from the late Oligocene of the Pacific coastal region of Peru and of *M. dalli* (Clerc in Joukowsky, 1906) from rocks of similar age in Western Panama. *M. trigalensis* may well be conspecific with the later (Miocene, but now extinct) *M. scripta* (Conrad 1874) (pl. 4, fig. 7) from the Pebas Beds of the Upper Amazon Valley. Until the appearance of the Panama landbridge in the Pliocene, South America was an island with the result that the Caribbean and tropical eastern Pacific areas formed one faunal province. The presence of the living Caribbean *M. sallei* (Recluz 1849) (pl. 4, fig. 6) in the Pebas Beds and other Miocene occurrences of *M. scripta* in the Magdalena Valley and at La Tagua in the Oriente of Colombia suggest that *Mytilopsis* invaded the Upper Amazon Valley from the Caribbean. *M. dalli* is very similar to *M. sallei* and may be synonymous. *M. sallei* also occurs in the Miocene of the Dominican Republic. The living type species of *Mytilopsis*, *M. leucophaetus* (Conrad) is not known before the Pliocene. It is recorded as *M. jamaicensis* (Woodring 1925) from the Bowden Beds (now known to be Pliocene) of Jamaica. A series of shells (LL28109–29) from the Plio-Pleistocene Caloosahatchee Formation of Florida originally identified as *Congerina lamellata* Dall (1898) appears to be a mixture of *M. sallei* and *M. leucophaetus*. Detailed distribution maps of the two species at the present day are given by Marelli and Gray (1983). They show that they overlap in this region nowadays and that *M. leucophaetus* now occurs as far north as the Hudson River. The apparent lack of fossil records from the eastern seaboard of the United States points to this northward extension of its distribution being the result of introduction.

A distribution map given by Starabogotov (1970, fig. 12) erroneously shows *Mytilopsis* as occurring over much of north-eastern South America including the Amazon Basin and the northern Brazilian coastal strip as far south-east as Recife (Pernambuco). Dunker (1853), who described *Tichogonia rosmaessleri* (a junior synonym of *M. sallei*) from Pernambuco, was himself very dubious about the locality information, and this record can safely be discounted. Although *M. sallei* is widespread on Caribbean islands (Marelli and Gray 1983), it is not encountered further eastward and its presence is not mentioned in the very thorough review of the Surinam fauna (Altena 1971).

On the Pacific coast, *Mytilopsis* is known only from northern South America (Olsson 1961; Keen 1971) at the present day. It is probable that Fijian occurrences (Dall 1898; Hertlein and Hanna 1949) are the result of introduction, though clearly not primarily as a result of the opening of the Panama canal (in 1914) as suggested by Morton (1981). Morton's suggestion that *M. sallei* has been more recently introduced to southern India is supported. The species has subsequently been reported in Victoria Harbour, Hong Kong (Huang and Morton 1983) and in Shimizu Harbour, Honshu, Japan (T. Habe, *pers. comm.* in Huang and Morton), and in Tokyo Bay (Furuse and Hasegawa 1984). There is the possibility, however, that more than one species of *Mytilopsis* has been introduced westwards across the Pacific from the Americas. Marelli and Gray (1985) placed the Fijian *M. alleyniana* Hertlein and Hanna (1949) in the synonymy of *M. adamsi* Morrison (1946), originally described from the Pearl Islands, Panama.

The occurrences of *M. cochleatus* (Kickx in Nyst, 1835) in the Rhine-Scheldt Delta (Adam 1960; Wolff 1969) and of several nominal West African species (Pilsbry and Bequaert 1927, Congo; Binder 1958, 1968, Ivory Coast; Reeve 1857–8, Senegal) are also thought to be the result of introduction.

Records of *Mytilopsis* from the East Indies (Keen in Moore, 1969) and Indonesia (Eames in Morley Davies, 1971) are probably based on the septate *Sinomytilus* Thiele (1934, p. 801), described as a section of *Mytilus* whose type species is *Dreissena crosseana* L. Morlet (1884). Specimens (BMZD 1906.9.19.76–77) of this species and of *D. massiei* L. Morlet (1892) (BMZD 1902.3.22.55), both from Cambodia, confirm Thiele's assignment to the Mytilidae. Their inner shell layer appears to be nacreous.

Trigonipraxis, (pl. 4, figs. 1–5) (the 'triangulares' group of Andrussov 1897–8) is well covered in other literature (Brusina 1892; Jekelius 1944; Papp 1953; Sieber 1955; Marinescu 1973). It is confined to the Pannonian and Pontian of the Pannonian and Dacic Basins. Differences between

nominal species assigned by these authors to this group are mostly slight and there seems to be no compelling reason for subgeneric separation from *Mytilopsis*. This view is supported by the occurrence of rather similar trigonal-shaped *Mytilopsis* (pl. 4, figs. 8–11) in Miocene brackish-water deposits in South America (Nuttall 1990, pp. 285–6, figs. 347, 348).

Genus *PRODREISSENSIA* Rovereto, 1898

Plate 2, fig. 9.

Types species. *Dreissensia (Prodreissensia) perrandoi* Rovereto, 1898, by original designation, Lower Oligocene, Tongrian, northern Italy, (pl. 2, fig. 9).

Diagnosis. Resembling *Dreissena* but with sculpture of radiating costules; septum present, shell interior otherwise unknown.

Distribution. ?Lower Eocene and Lower Oligocene (Tongrian), northern Italy only.

Remarks. Rovereto (1898, pp. 159, 174) described his single, poorly preserved species from the Tongrian of Mioglia (Liguria) as the type of a new 'section' of *Dreissena* characterized by longitudinal ribbing. The only known illustration is Rovereto's later (1900, pl. 4, fig. 14) external view of his type specimen. Both this and the original description were copied by Sacco (1904, p. 152, pl. 29, fig. 12) who was unable to add any new information about this taxon. The illustration clearly shows both the faint traces of radiating ribs and a strong carinate diagonal ridge. The original specific description mentioned the presence of an area (septum), but gave no other details of the interior. Rovereto (1898, p. 159), presumably because of its strong carination, had compared his species with the much younger *Dreissena gnezdai* Brusina, 1884, which was described from near Zagreb and placed by Andrussov (1897–8) in his *Congeria 'triangulares'* group. All other members of Rovereto's rich bivalve fauna are undoubtedly marine, raising the suspicion that this species might be a septate member of the Mytilacea.

Tichogonia (Congeria) euchroma Oppenheim (1891) (pl. 2, figs. 10, 11) from the Lower Eocene, Lignite Marls of Mount Pulli (Vicentin, North Italy) seems to be the only definite species of the Dreissenidae with similar radiating ribbing. Oppenheim's description mentioned the presence of a septum but stated that the Schloss (hinge) and apophysis were as yet unknown. Andrussov (1900, pl. 3, figs. 23, 24) provided photographic illustrations of the exterior of two of Oppenheim's original specimens. The ribs are faint and the diagonal ridge is low and definitely not carinate. The outline is mytiliform as in typical *Mytilopsis* and *Dreissena*. It is possible that *T. (C.) euchroma* and *P. perrandoi* may be related in spite of the differences in shape.

The systematic position of *Prodreissensia perrandoi* cannot be properly assessed because of lack of knowledge of internal details of its shell. Its Palaeogene age, however, would suggest that it is more likely to be an offshoot of *Mytilopsis* rather than *Dreissena*, if it is, in fact, a member of the family. *T. (C.) euchroma*, on the other hand, is definitely a dreissenid.

Subfamily DREISSENOMYINAE Babak, 1983

Diagnosis. Shell modioliform, compressed; umbones not terminal; apophysis lacking; sinupalliate; posterior siphonal gape present.

Distribution. Late Miocene-early Pliocene (Meotian-late Pannonian) to top Pliocene (Rumanian), Paratethys only.

Remarks. In comparison with nearly all Dreisseninae the shell is modioliform rather than mytiliform and is laterally compressed. Exceptions include species such as *Mytilopsis amygdaloides* (Dunker) (pl. 5, figs. 11–13), which is slightly modioliform but not compressed, whilst *Dreissena*

(*Pontodreissena*) (pl. 1, figs. 7–10) and *D. (Modiolodreissena)* (pl. 2, figs. 3, 4), though fairly compressed, are basically mytiliform with terminal umbones. In Dreissenomyinae a byssal notch is lacking and an antero-ventral pedal gape may sometimes be observed. The commissure, however, is so irregular that these features, interpreted as adaptations to an infaunal mode of life, are not always readily apparent in most specimens, particularly separated valves. They are therefore omitted from the subfamilial diagnosis.

Babak (1983, p. 60) referred to Dreissenomyinae Taktakishvili, 1973. I have been unable to find any reference to this new subfamilial name either in Taktakishvili's work, or in the 1978 *Zoological Record* which covers his paper. Authorship is therefore tentatively ascribed to Babak (1983).

Genus DREISSEMYIA Fuchs, 1870b

Types species. *Congeria schroeckingeri* Fuchs, 1870a, by original designation. Upper Miocene, Pontian, Hungary, (pl. 5, figs. 1–5, text-figs. 2B, C; 3A, B, D, E).

Diagnosis. As for subfamily.

Distribution. As for subfamily.

Subgenus DREISSEMYIA Fuchs, 1870b

Plate 5, figs. 1–5, text-figs. 2C, 3A, B, D, E.

Diagnosis. Umbones well back from anterior of shell; thin-shelled; both antero-ventral and posterior gapes marked; septum reduced to strong ridge, with anterior adductor and pedal/byssal scars lying partly on and partly anterior to ridge; pallial sinus deep.

Distribution. Late Miocene – early Pliocene (Meotian – late Pannonian) to late Pontian, Paratethys.

Remarks. See under *D. (Sinucongeria)*.

Subgenus SINUCONGERIA Lorentz, 1894

Plate 6, figs. 1–7, text-fig. 2B, 3C, F.

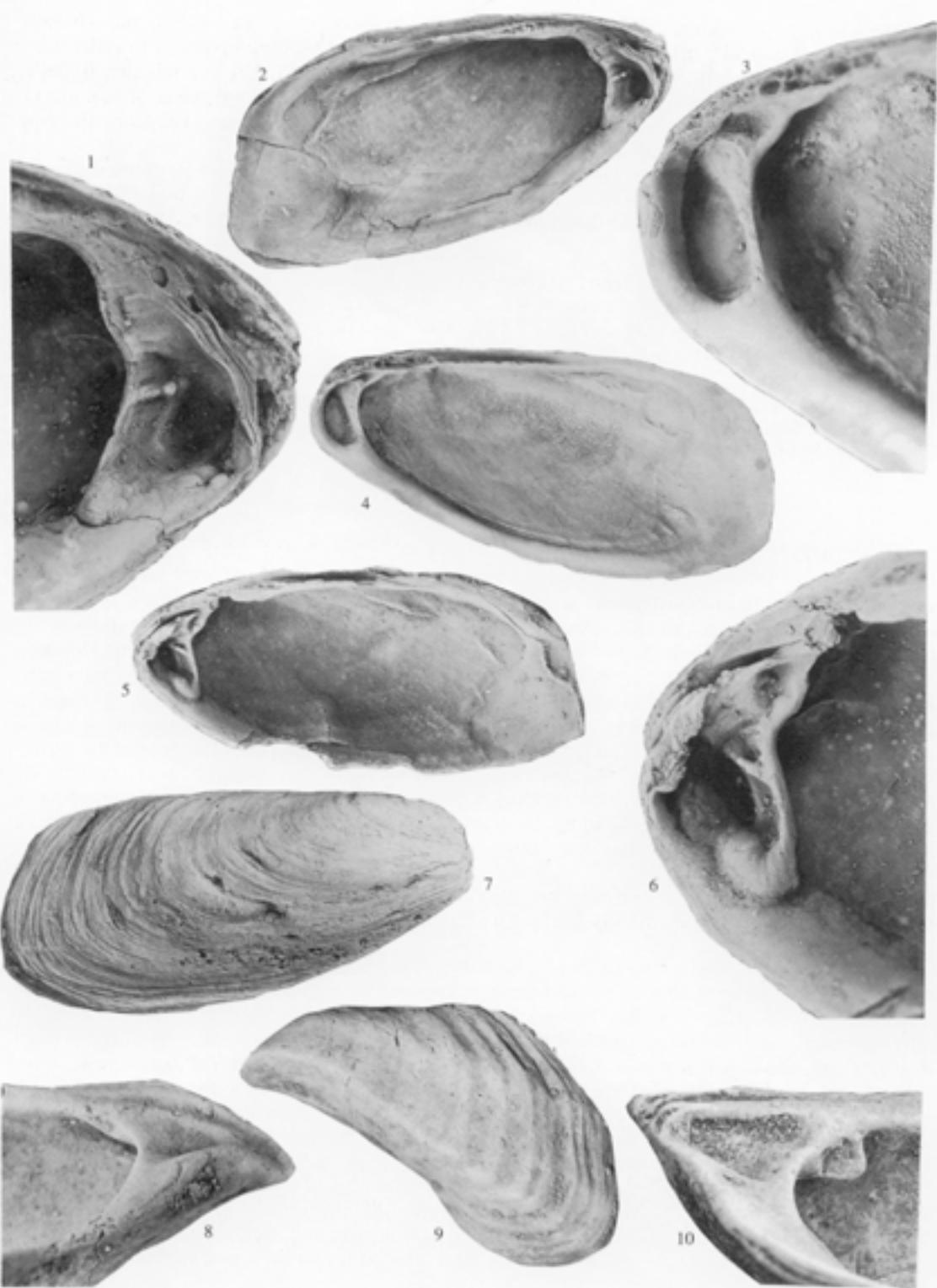
Type species. *Congeria arcuata* Fuchs, 1870a, by monotypy, Upper Miocene, Pontian, Hungary, (text-fig 3C, F).

Diagnosis. Similar to *Dreissenomyia* s.s. but thicker shelled; umbones almost terminal; valves more tumid; true septum present, usually bearing irregular ridges; pallial sinus not very deep.

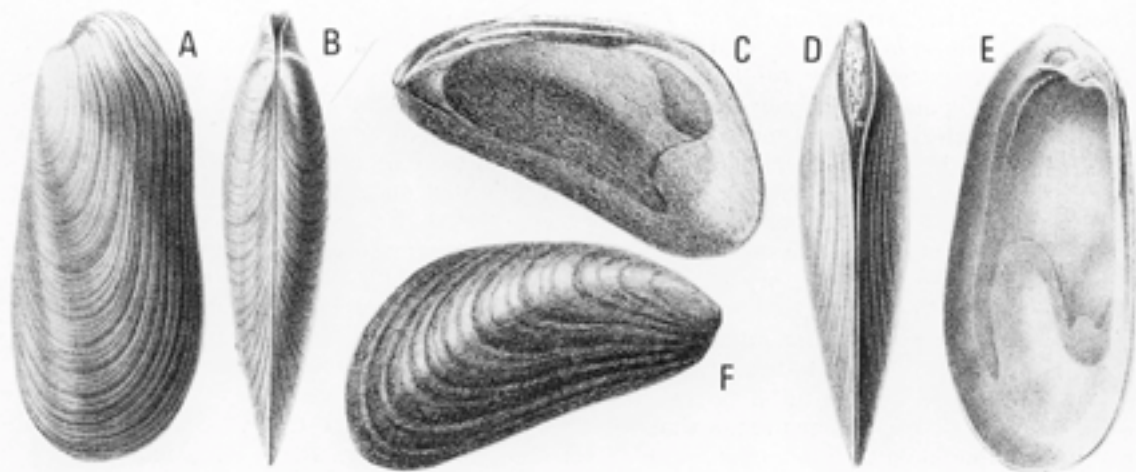
EXPLANATION OF PLATE 6

Figs. 1–7. *Dreissenomyia (Sinucongeria) aperta* (Deshayes 1838). 1, 2, 5, 6, LL 18451, Upper Miocene, Upper Pontian (Bosphorion), Stoichitza Valley, Cocorova-Mehedintzi, Rumania, F. Marinescu Colln, (left valve figured Morton 1970, text-fig. 2). 1, 2, left valve interior, $\times 4$, $\times 1.5$. 5, 6, right valve interior, $\times 4$, $\times 1.5$. 3, 4, 7, L19502, probably Pliocene (Kimmerian or Akchagylian), Crimea, U.S.S.R., right valve. 3, 4, interior $\times 4$, $\times 1.5$. 7, exterior, $\times 1.5$.

Figs. 8–10. *Mytilopsis subcarinata botenica* Andrussov (1897–8), ?Top Miocene-basal Pliocene, Upper Pontian, Basinul Govorei, Rumania, ex Muzel Istoria Naturala "Gr. Antipa", Bucharest, 8, 9, LL 9023, 8, left valve internal, tilted, with anterior pedal/byssal attachment fused to posterior wall of septum as in *Congeria*, $\times 3$. 9, same external, $\times 1.5$. 10, LL 9022, right valve internal, tilted, with 'normal' *Mytilopsis* apophysis, $\times 3$.



NUTTALL, *Dreissenomya* (*Sinucongeria*) and *Mytilopsis*



TEXT-FIG. 3. All from Upper Miocene, Pontian, Radmanest, Banate, Hungary. A, B, D, E. *Dreissenomya* (*D.*) *shroeckingeri* (Fuchs), from Fuchs, 1870*b*, pl. 16, figs. 5–8, $\times 1$. C, F. *Dreissenomya* (*Sinucongeria*) *arcuata* (Fuchs), from Fuchs, 1870*a*, pl. 16, figs. 12, 13, $\times 2$.

Distribution. Late Miocene (Meotian – late Pannonian) to top Pliocene (Rumanian), Paratethys.

Remarks. *Dreissenomya* (s.s.) barely penetrates into the Euxinic Basin, the eastern limit of its distribution being the western Black Sea Coast. *Sinucongeria*, however, is represented there by the long-lived (Pontian-Rumanian), and comparatively widely distributed, *D. (S.) aperta* (Deshayes 1838) (pl. 6, figs. 1–7) which occurs in the Crimea, Kerch Peninsula and as far east as western Georgia, as well as in the Dacian and Pannonian Basins. Marinescu (1975) assigned eight species to *Dreissenomya* (s.s.) and seven to *Sinucongeria*. Although *Dreissenomya* (s.s.) with its markedly non-terminal umbo, greatly reduced septum and deeper pallial sinus, would appear to be further removed from the standard dreissenid pattern than *Sinucongeria*, both subgenera first appear in the Meotian. Marinescu postulated descent from *Congerina* (*Andrussoviconcha*) *novorossica* Sinsow (1877). Archambault-Guezou (1976*a*, pls. 4, 5) provided numerous illustrations of *D. (S.) aperta* (Deshayes) including syntypes, and of *D. (D.) shroeckingeri*.

DISCUSSION

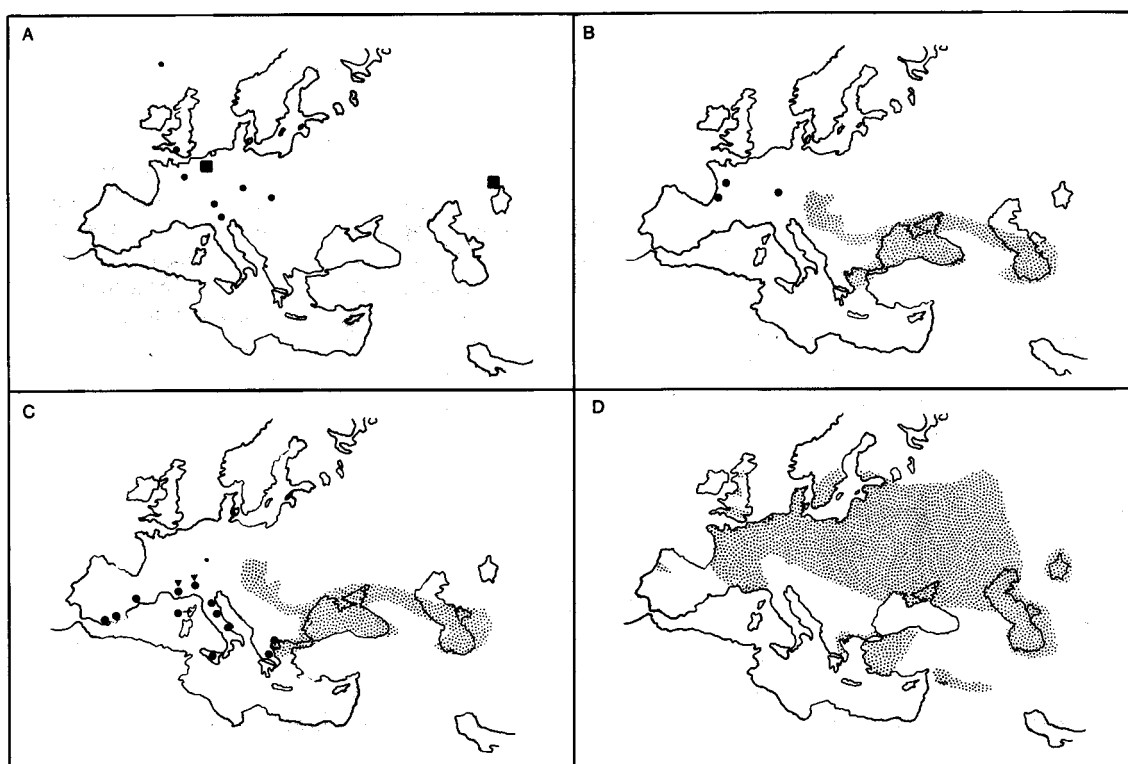
The classifications set out by Keen *in* Moore (1969), by Babak (1983, p. 60) and that proposed herein may be compared in Table 1. So little is known about *Prodreissensia*, based on poorly preserved material, that it is idle to speculate on its relationship with the other genera. Its Palaeogene age, however, does suggest that it is either synonymous with, or an early offshoot from, *Mytilopsis*, if indeed it is a member of the Dreissenidae. Keen's placement of *Dreissenomya* and *Sinucongeria* as subgenera of *Dreissena*, on the grounds that they lack the apophysis, is not accepted. It is, however, worth remembering that all three were probably derived from species of *Mytilopsis* living at more or less the same time and place: the late Miocene of the Paratethys. Babak's classification is an emended version of that proposed by Starabogatov (1970).

The stratigraphic ranges of genera are summarized in Text-fig. 1. Only the two surviving genera, *Mytilopsis* and *Dreissena* are comparatively long-ranging. The remainder are confined to the Paratethys during the Neogene and have short ranges: it is estimated that none survived beyond 5 million years, and that *Dreissenomya* (s.s.) may have existed for as little as 2 million years.

Similarities in shell structures (Taylor, Kennedy and Hall 1973) provide strong evidence that the Corbiculacea and Dreissenacea shared common ancestry. No early Tertiary fossils showing intermediate characters have been found.

There are two possible and inter-related explanations. First, the changes from a shallow infaunal to byssally attached epifaunal mode of life could have occurred quite rapidly. The later sudden radiation shown by the superfamily in the late Miocene of the Paratethys, including re-adaptation to an infaunal mode of life by *Dreissenomya*, suggests that such an explanation is plausible. Although *Mytilus* has small, crenulate, dysodont teeth (Nuttall, fig. 46, 5 in Moore, 1969) situated at the anterior extremity of the shell, loss of dentition in dreissenids may well be connected to the adoption of a heteromyarian, mytiliform shell suitable for epifaunal life. The narrow, pointed, umbonal region allows little space for hinge teeth, whose efficiency would be likely to be very limited in such an anterior position. In addition, the possession of a ligament analogous to that of *Mytilus*, which Trueman (p. N64 in Moore, 1969) described as being among the most powerful known, may also reduce the need for dentition.

The second possible explanation is that, as a general rule, the fossil record of freshwater and marginal marine faunas is far less continuous than those of shelf seas. In the late Cretaceous and Palaeogene of Europe, there were no extensive freshwater basins of comparable extent to the Neogene Paratethys.



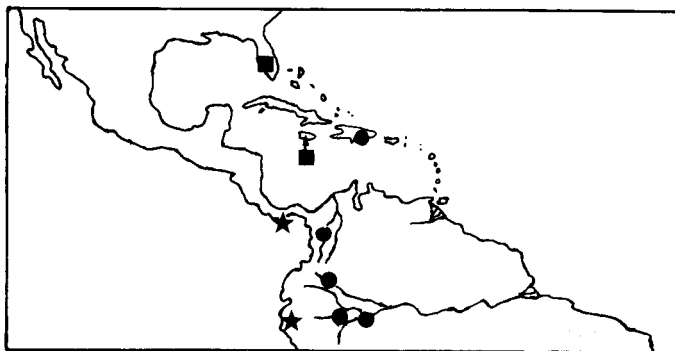
TEXT-FIG. 4. A. Palaeogene distribution of *Mytilopsis*. Key: circles, Eocene, squares, Oligocene. B. Lower and Middle Miocene distribution of *Mytilopsis* in Europe and western Asia. Key: circles, western Europe; stipple, throughout Paratethys. C. Late Miocene (Messinian) distribution of Dreissenacea in Europe and western Asia. Key: circles, *Dreissena*; triangles, *Mytilopsis*; stipple, Paratethys with *Mytilopsis* and *Dreissena* throughout; *Dreissenomya* and *Dreissenomya* (*Sinucongeria*) mainly in western and central areas. D. Recent world distribution of *Dreissena*, shown stippled.

Mytilopsis sowerbyi (d'Orbigny) the only known English Caenozoic species of Dreissenidae occurs quite commonly in freshwater horizons of the English Priabonian Headon Beds, but these beds are confined to comparatively small areas in Hampshire and the Isle of Wight. This sporadic distribution pattern is repeated elsewhere throughout most of the Tertiary (text-fig. 4). *Mytilopsis brardi* (Brongniart), accompanied by small hydrobiid snails, crowd some bedding planes in freshwater Oligo-Miocene deposits of the Mainz Basin of Germany. Glibert and de Heinzelin (1954, pp. 388–9) found only 54 individuals of *M. nystiana* (d'Orbigny) among 90,000 specimens from two marine horizons in the Belgian Lower Oligocene. Most of the other rarities were also non-marine species. Similarly, *M. basteroti* (Deshayes) is a comparatively rare constituent of the rich marine inshore faunas of the Lower Miocene in the Aquitaine Basin, occurring at localities thought to have been situated only a few kilometres from the then shoreline. All the specimens of this species that I have examined are more worn than those of marine species in these faunas, suggesting transport after death (pl. 5, figs. 8–10). The genus occurs in much the same way in the Middle Miocene Faluns of Touraine.

Recognition of chance invasions and local extinctions is of importance in interpreting the history of the superfamily. Such events include:

1. The invasion by *Mytilopsis* of tropical America by the late Oligocene (text-fig. 5), some thirty million years after its first appearance in Europe, probably as adult shells attached to logs, rather than as veliger larvae.

TEXT-FIG. 5. Fossil occurrences of *Mytilopsis* in western Hemisphere. Key: stars, late Oligocene; circles, Miocene; squares, Pliocene.

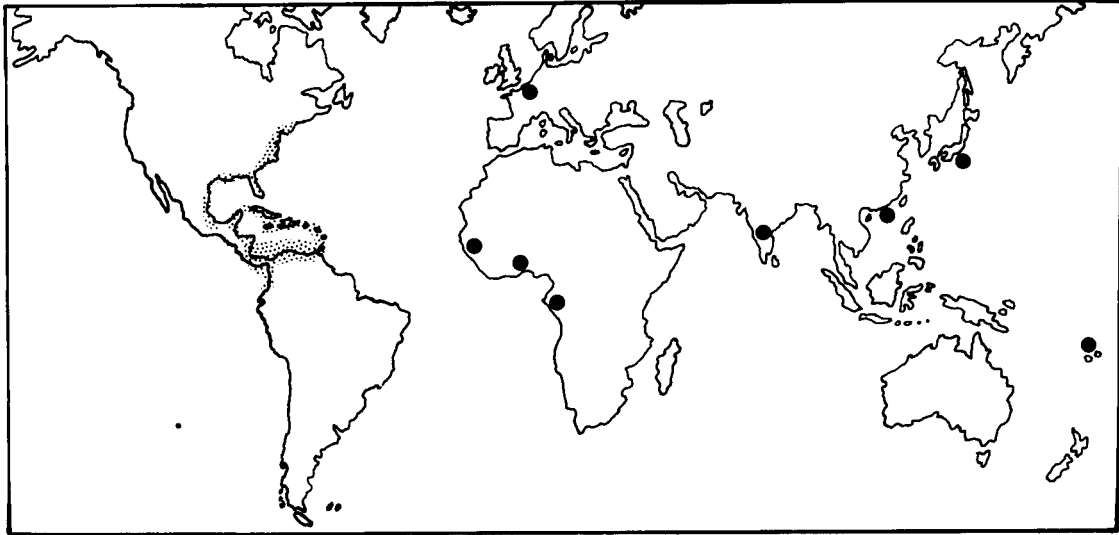


2. The local extinction of *Mytilopsis* in western Europe during the Middle Miocene, preceding its eventual disappearance from the Paratethys.

3. The short-lived invasion, during the Messinian, of the Mediterranean region from the Black Sea, by Paratethyan species of both *Mytilopsis* and *Dreissena* (*Pontodreissena*). Although *Mytilopsis* survived well into the Kimmerian (Lower Pliocene) in the eastern Paratethys and *D. (P.) rostriformis* is still living there, neither is represented by descendants in the western European Pliocene and Pleistocene. As neither genus survived along the borders of the Mediterranean, their disappearance is unlikely to have been due to competition between them. It seems far more likely that their local extinction was due to the removal of suitable fresh and brackish-water habitats.

4. The Recent considerable extension of the geographical distribution of dreissenids as a result of human activity. The industrial revolution, linking of waterways and increase in water-borne trade appears to be responsible for the invasion of much of Europe, via the Danube, since the mid-eighteenth century. It is suggested that *Mytilopsis* probably increased its range from Florida northwards along the United States eastern seaboard in similar fashion, whilst shipping has led to its appearances in Fiji, India, Hong-Kong, Japan, West Africa and the Rhine-Scheldt delta (text-fig. 6).

Offshore marine molluscs occupy an extremely stable environment in comparison to the habitats of freshwater molluscs. The history of the Dreissenidae illustrates the success of the highly



TEXT-FIG. 6. Recent distribution of *Mytilopsis*. Key: stipple, naturally occurring; black circles, presumed introduced.

conservative but, most importantly, salinity-tolerant *Mytilopsis* which has survived since the early Tertiary. Nevertheless, its invasion of the Western Hemisphere during the Oligocene appears to have been chance, whilst its disappearance from Europe (except by re-introduction) shows its vulnerability to changed conditions. The rapid diversification of the family in the Paratethys during the late Miocene when *Dreissena*, *Congeria* and infaunal *Dreissenomya* all appeared, is a startling example of fast evolution. The equally rapid extinction of all but *Dreissena* as conditions changed with the break-up of Paratethys shows how vulnerable freshwater molluscs can be when their habitats are altered. Both *Mytilopsis* and *Dreissena* appeared to colonize new regions very slowly unless influenced by man. This inability to spread quickly in natural freshwater conditions is another source of long-term vulnerability. The veliger larva, which allows rapid dispersal in the sea, and even in estuarine conditions successfully exploited by *Mytilopsis*, is still of some advantage in lakes. However, in stretches of river unaffected by tides, veligers are unlikely to be nearly as successful in migrating upstream as the unionacean glochidian larvae attached to the gills of fish.

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