Morphogenesis and Ecogenesis of Bivalves in the Phanerozoic

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Abstract—The morphology, systematics, and ecology of bivalves are discussed. Changes in the taxonomic composition and morphogenesis of this group in the Phanerozoic are traced. Several ethological-trophic groups are characterized, and changes in their taxonomic composition over time are revealed. Bivalve communities dominating different geological periods are characterized. In the Phanerozoic, the taxonomic diversity of bivalves gradually increased. This increase was interrupted by a drop in taxonomic diversity in the Early Triassic. The majority of ethological-trophic groups are known to have appeared in the Early Paleozoic, but it is only from the Late Paleozoic onwards that bivalves became dominant or common organisms in all zones of the continental shelf.

INTRODUCTION

Bivalves are one of the most widespread and diverse marine benthic groups, including nearly 2300 genera in 263 families.

Bivalves became especially abundant and diverse (in familial and generic composition) from the beginning of the Mesozoic, although they played a significant part in benthic communities as early as the mid-Ordovician.

The majority of bivalves are bottom dwelling, not particularly mobile animals, that are associated with specific environments.

The study of the taxonomic and ethological-trophic composition and morphology of the genera in communities allows for the reconstruction of the environment, i.e., the character of basins and their constituents, the reconstruction of evolution and change of benthic faunas, and the changes in the hydrology of the basins inhabited by these faunas at different times. Studies of this kind have been undertaken using bivalves from the Triassic of northern Middle Siberia by Kurushin (1984, 1900a), the Jurassic and Cretaceous of the same regions by Zakharov (1983, 1995) and Zakharov and Shurygin (1978, 1979), the Cretaceous of the *American Midcontinent* by Rouds *et al.* (1972) and Kauffman (1974, 1975), the Cretaceous of the Russian Platform by Sobetskii (1978) and Savchinskaya (1982) and the Caspian Basin by Sobetskii *et al.* (1985), for the Paleogene of the Fergana Valley by Hecker *et al.* (1962), for the Cenozoic of the Paratethys by Merklin, 1950; Hoffman *et al.*, 1978; Nevesskaja *et al.* (1986), for the evolutionary history of the Black Sea by Nevesskaja (1965) and Iljina (1966), and others.

Bivalve studies were very important for marine biocenology. The author of the term *biocenosis* (Mobius, 1877) chose an oyster bank as an example of a biocenosis dominated by bivalves. The further development of biocenological studies allowed recognition of the trophic types of bottom dwelling invertebrates (Turpaeva, 1948, 1949, 1953; Sokolova, 1954), the understanding of the structure of a biocenosis containing various trophic groups (Turpaeva, 1949, 1954; Vorobyev, 1949), the establishment of the trophic zonation of benthic communities and their connection with the hydrological characters of the basins (Savilov, 1957, 1961; Neiman, 1963, 1969, 1977; Kuznetsov, 1963, 1964, 1976, etc.) and was connected to a varying extent with the studies of modern bivalve communities. Many theoretical problems of biology and paleontology were studied based on bivalves, for instance, the importance of abiotic and biotic factors for the evolution, tempo, and periodicity of the development of selected groups within a single higher taxon (Newell, 1952, 1967; Davitashvili, 1969; Valentine, 1969; Nevesskaja, 1972b; Bretsky, 1973), the role of cosmopolitan and endemic taxa in evolution (Bretsky, 1973), the range of variability in connection with speciation, types of speciation and morphogenesis, homeomorphy and parallel evolution (Nevesskaja, 1967, 1972a; Nevesskaja *et al.*, 1986, 1987), etc.

A wide distribution of bivalves and the fact that particular genera and species belong to particular stratigraphic levels make the study of this group very valuable for resolving the problems of biostratigraphy of the Mesozoic and Cenozoic (and to a lesser extent Upper Paleozoic) beds where bivalves are the major component of assemblages.

The understanding of the migrations of bivalves resulting from the merging of previously separated basins is very important for correlations, because it allows parallels to be drawn between the stratigraphic schemes in neighboring regions, and the reconstruction of the paleogeography of the basins of the past.

This study is based on the database of all (ca. 2300) bivalvian genera from the Cambrian to the present day, including data on morphology, ecology, and geographic and stratigraphic ranges (from "*Osnovy paleontologii*," 1960; *Treatise...*, 1969–1971; and many later publications). The study incorporates information on the morphology and systematics of bivalves and on the composition of extinct marine assemblages, which included bivalves, in various periods of Phanerozoic history (see Nevesskaja, 1998, 1999).

Based on these data, the morphogenesis of major shell characters and related soft body structures were studied, and changes in the taxonomic composition and diversity dynamics of bivalves throughout geological time were revealed.

In addition to the studies cited in Chapters I–IX, the following monographs and papers devoted to the systematics of bivalves from various stratigraphic units were included in the list of References. The data from these studies were used for the preparation of Table II. 1 and discussions in other chapters:

Early and Middle Paleozoic: Hicks (1873), Vogel (1962), McAlester (1965), Babin (1966, 1982), Bradshaw (1970, 1978), Bazhenova (1971a, 1971b), Bradshaw and Bradshaw (1971), Carter (1971), Desparmet *et al.* (1971), Nalivkin (1971), Snyder and Bretsky (1971), Babin and Melon (1972), Bretsky (1973), Pojeta *et al.* (1973, 1976, 1987), Pojeta and Runnegar (1974, 1985), Morris and Fortey (1976), Pojeta and Palmer (1976), Runnegar and Jell (1976), Saul (1976), Krasilova (1977, 1979, 1981, 1987, 1990), Pojeta and Glibert-Tomlinson (1977), Stanley (1977a), Pojeta (1978, 1988), Kříž (1979, 1984, 1985, 1995), Jell (1980), Morris (1980), Yochelson (1981), Babin *et al.* (1982), McKinnon (1982, 1985), Tunnicliff (1982, 1987), Liljedahl (1983, 1984a, 1984b, 1985, 1989a, 1989b, 1989c), Bailey (1983), Marsh (1984), Pojeta and Zhang (1984), Babin and Gutiérrez-Marco (1985, 1991), He and Pei (1985), Wen (1985), Ermak (1986), Shu De-Gan (1986), Karczewski (1987), Rehfeld and Mehl (1989), Struve (1989), Bengston *et al.* (1990), Johnston (1991, 1993), Freitas *et al.* (1993), Sánchez and Babin (1993), Desbiens (1994), Elicki (1994), Bogolepova and Kříž (1995), Kříž and Bogolepova (1995), Sánchez (1995a, 1995b, 1999), Esakova and Zhegallo (1996), and Cope (1997);

Late Paleozoic: Amalitzky (1891), Astafieva (1988, 1991a, 1991b, 1993, 1994, 1995, 1997), Astafieva and Astafieva-Urbaitis (1992), Astafyeva and Astafyeva-Urbaytis (1994), Astafieva-Urbaitis and Dikins (1984), Astafieva-Urbaitis and Ramovsh (1985), Astafieva-Urbaitis *et al.* (1976), Astafieva-Urbaitis (1973, 1974a, 1974b, 1981, 1983, 1988, 1990, 1994), Astafieva-Urbaitis and Astafieva (1985), Betekhtina (1966, 1972, 1974, 1998), Betekhtina *et al.* (1987), Dickins (1983, 1989, 1999), Driscoll and Hall (1963), Feng (1988), Gonzalez (1978), Gusev (1963, 1990), Hoare *et al.* (1978), Kanev (1980, 1989, 1994), Logan (1967), Muromtseva (1974), Muromtseva and Gus'kov (1984), Newell (1999), Newell and Boyd (1970, 1975, 1981, 1999), Plotnikov (1945, 1949), Runnegar (1966, 1972a, 1972b, 1983), Runnegar and Newell (1971), Waterhouse (1970a, 1970b, 1979, 1980a, 1980b, 1982, 1988), and Yang Zhi-Rong and Chen Jin-Hua (1985);

Mesozoic: Sobetskii (1960, 1977b), Martinson (1961, 1965, 1982), Jefferies and Minton (1965), Zakharov (1965, 1966b, 1970, 1981a), Andreeva (1966, 1971), Kiparisova *et al.* (1966), Polubotko (1966, 1988), Hallam (1968), Nakano (1970a, 1970b, 1973, 1974, 1977), Speden (1970), Freneix (1971–1972, 1979), Allasinaz (1972), Barsbold (1972), Kolesnikov (1977, 1980), Glibert and van de Poel (1973), Sanin (1973, 1976), Bobkova (1974), Freneix and Sornay (1974), Križ and Cech (1974), Skwarko (1974), Dhondt (1975, 1979, 1984), Marincovich (1975), Martinson *et al.* (1975), Bychkov *et al.* (1976), Martinson and Shuvalov (1976), Milova (1976, 1988), Poyarkova (1976), Dang Vu-Huk (1977), Scott (1978), Heinberg (1979a, 1979b, 1989, 1993), Mordvilko (1979), Kelly (1980, 1988a, 1988b, 1995a, 1995b), La Barbera (1981), Kelly *et al.* (1984), Sanin *et al.* (1984), Trushchelev (1984), Vyalov (1984), Bychkov (1985), Dagis and Kurushin (1985), Kurushin (1985, 1987a, 1987b, 1987c, 1990b, 1992, 1998), Leanza (1985), Romanov (1985), Polubotko and Milova (1986), Sei (1986), Fleming (1987), Dhondt and Dieni (1988, 1993), Cooper (1989), Fürsich and Werner (1989), Kurushin and Trushchelev (1989), Ma Qui-Hong (1989), Yanin (1989), Polubotko *et al.* (1990), Toshimitsu *et al.* (1990), Sha (1992), Skelton and El-Asa'ad (1992), Gili and Skelton (1993), Gou Zong-Hai (1993), Yazikova (1993, 1996a, 1996b, 1998), MacLeod (1994), Crame (1995, 1996), Gavrilova (1995a, 1995b), Aberhan and Fürsich (1996), Aberhan and Hillebrand (1996), Dagis *et al.* (1996), Repin (1996, 2001), Boyd and Newell (1997, 1999), Damborenea (1997), and Silbering *et al.* (1997);

Cenozoic: Gray (1847), Odhner (1919), Kazakova (1952), Masuda (1962), Tolstikova (1964), MacNeil (1967), Wilson (1967), Kalishevich (1969, 1973), Kazakhishvili (1969), D. Moore (1969), Starobogatov (1970), Bayer (1971), Savitskii (1971, 1979a, 1979b), Spaink (1972), Turner (1972), Allen and Sanders (1973), Vokes (1973, 1977, 1980, 1986), Kafanov (1974, 1975, 1976, 1986a, 1986b, 1987, 1991, 1997, 1998a, 1998b), Sinel'nikova (1975), Strougo (1975, 1976a, 1976b), Ward and Blackwelder (1975), Yonge (1975), Allison and Addicott (1976), Berezovskii (1977, 1999), Hayami *et al.* (1977), Hayami and Noda (1977), Kafanov and Popov (1977), Sanders and Allen (1977, 1985), Keen (1980), Allison and Marincovich (1981), Devyatilova and Volobueva (1981), E. Moore (1983, 1987, 1992), Shileiko (1985, 1989), Allen and Hannah (1986), Darragh (1986), Hayami and Hosoda (1988), Corselli and Bernocchi (1991), Lee (1992), Volobueva *et al.* (1994), Kafanov and Savitskii (1995), and Maestrati and Lozouet (1995).

The major ethological-trophic groups are recognized and characterized morphologically. The changes in the taxonomic composition of selected groups throughout the Phanerozoic for the basins studied in general and for various sea zones (coastal shallow waters, shallow and deep shelves, zones of organic buildup, and zones with disaerobic conditions) were traced. The relative abundance of genera representing different trophic groups is evaluated to recognize dominant, abundant, common and rare taxa. This evaluation provided a better understanding of the changes that occurred.

Sections in Chapter I "Development of the Shell" and "Shell Microstructure" were written by S.V. Popov.

CHAPTER I. MORPHOLOGY OF BIVALVES

Bivalves are aquatic animals, usually with a bilaterally symmetrical and laterally compressed body, often elongated in the posterior–anterior direction. The body is enclosed in a shell secreted by the mantle and composed of two valves on the right and left sides of the body. The shell, except in very rare cases, is external.

(1) Structure of the Soft Body

The soft body of a bivalve consists of a main body and a muscular foot. The head, including all of the cephalic sensory organs present in other mollusks, is absent in bivalves. The body is covered by a mantle (Fig. I. 1, *5*), which consists of two lobes connected on the top and often loose at the bottom (Dogel, 1939; Jaekel, 1953; Yonge, 1954, 1978; *Osnovy paleontologii*, 1960; Zatsepin and Filatova, 1968; Kauffman, 1969; Allen, 1985).

The mantle extremity is usually subdivided into three folds, the external (secretory), middle (sensory), and internal (musculature) folds. The external fold is usually responsible for the secretion of the shell (see Popov, 1977). The middle fold usually possesses sensory organs (tentacles, eyes, tactile cells, etc.), whereas the inner fold usually contains mantle (pallial) muscles. These muscles are attached to the shell along the pallial line. The mantle lobes border the mantle cavity, containing the visceral sack, gills, and foot.

The mantle cavity may be completely open along the anterior, ventral, and posterior margins (Fig. I. 2a), or the ends of the mantle may be fused to varying extents. For instance, the mantle ends may be fused only in one place posteriorly, thus forming a single exit, or anal opening (Fig. I. 2b). The flaps of the mantle may be extended to form a short tubelike siphon, conducting fluid to within the mantle cavity. Two openings appear when the mantle flaps merge in two places (passage in and passage out) (Fig. I. 2c), whereas the mantle extremities may form two siphons (Fig. I. 1, *6*), i.e., the exhalant (anal) and inhalant (gill) siphons. The foot, similar to that in the previous case, freely moves out through the open part of the mantle in the anterior of the lower part of the shell. When the mantle is fused in three places (Fig. I. 2d), the foot extends through the anterior of the lower opening. More rarely, the fourth opening develops on the ventral margin of the shell, which is used for the extension of the byssus (Fig. I. 2e).

The margins of the inhalant and, sometimes, of the anal openings may possess tentacles and tactile nodes.

The siphons may be either independent of each other, partly connected (Fig. I. 2d), or completely fused to form a single tube (Fig. I. 2e) subdivided by an internal septum. Sometimes, this septum is continued forward to connect with the gills and separates the anal and gill sections. The length of the siphons widely varies in different taxa. The two siphons may be of the same or of different lengths. In some taxa, the inhalant siphon is longer, while in others, the exhalant siphon is longer. Usually the siphons can be completely withdrawn inside the shell. However, there are exceptional cases when they cannot be withdrawn; in this case, the siphons are covered by the cuticular layer or protected by a calcareous tube or by auxiliary calcareous lamellae. In the case of long siphons, a posterior opening develops for letting them out. Well-developed siphons are usually present in burrowing or boring bivalves.

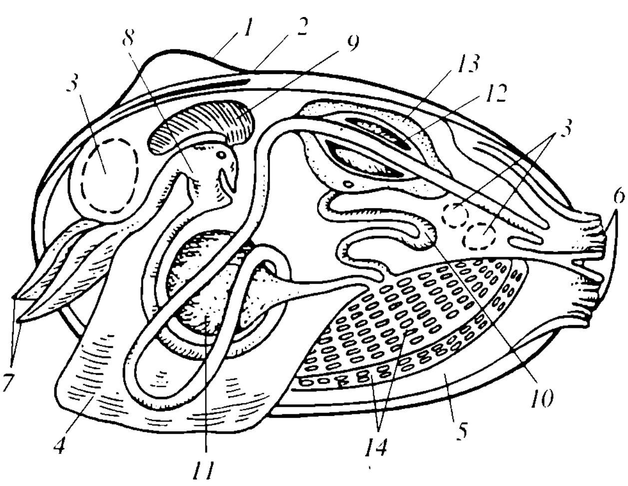


Fig. I. 1. Organization of a bivalve (after *Biologicheskii entsiklopedicheskii slovar'*, 1986, text-fig. from p. 168). Designations: (*1*) shell, (2) ligament, (*3*) adductors, (*4*) foot, (5) mantle, (*6*) siphon, (7) labial palps, (*8*) stomach, (*9*) liver, (*10*) kidney, (*11*) gonad, (*12*) heart, (*13*) pericardium, and (*14*) gills.

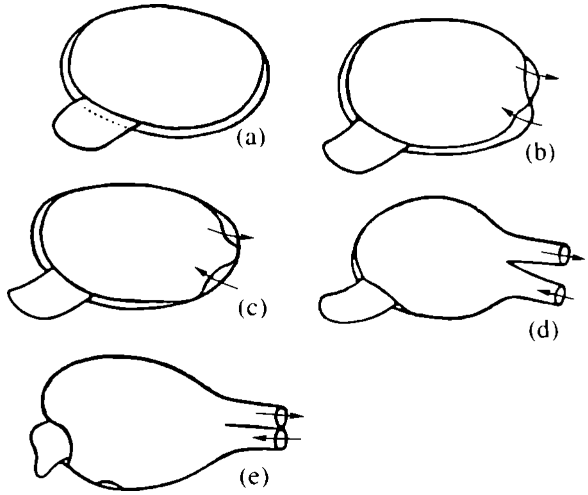


Fig. I. 2. Different types of fusion of the mantle and development of siphons in bivalves (after *Osnovy paleontologii*..., 1960, text-fig. 38): (a) mantle margins (except for dorsal margin) free, (b) singe exhalant (anal) opening is separated, (c) mantle is fused in two places to form three openings (exhalant, inhalant, and for protruding the foot), (d) as above, but with siphons developed, and (e) mantle is fused in three places to form four openings (inhalant, exhalant, for foot, and for byssus).

Because bivalves have no head, they lack a buccal cavity, tongue, jaws, and salivary glands. The mouth opening is in the anterior part of the body. Grooves extend along both sides of the mouth and reach the anterior margin of the gillbase. Lamellar outgrowths develop along the margins of the grooves (upper and bottom lips). The ends of the lips form labial palps (Fig. I. 1, *7*), represented by triangular lamellae that hang into the mantle cavity and are covered by ciliate epithelium. Suspended food particles are conducted along the grooves toward the mouth, and water flow is produced by ciliate movements of the gill epithelium. The food is transported to the mouth by the labial palps. The mouth opening leads to the short esophagus and then to the stomach (Fig. I. 1, *8*), where the digestive gland, or so-called liver, also opens (Fig. I. 1, *9*). The latter consists of several lobes. The posterior part of the stomach contains the exit to the blind sack which contains a gelatinous crystalline style, composed of proteins secreted by the walls of the sack that facilitate digestion. The stomach leads to the narrow intestine, and then to the rectum. The rectum usually penetrates the ventricle of the heart and turns back, terminating in the anus.

The structure of the digestive system is variable. A classification of the types of stomachs was proposed by Purchson (1956, 1957, 1958, 1959, 1960, 1963, 1987a), Dinamani (1967), and, later, by Starobogatov and Skarlato (Nevesskaja *et al.*, 1971; Starobogatov, 1992).

Except for the Teredinidae that feed on wood, and the so-called predators (Septibranchia), bivalves feed on organic debris, phytoplankton, and bacteria.

The nervous system is symmetrical and consists of three pairs of ganglia (cerebral, pedal, and visceroparietal) connected by long connectives. The cerebral ganglia occur near the anterior adductor and innervate the labial palps, anterior adductor, and anterior mantle. The pedal ganglia are at the base of the foot, innervating it. The visceroparietal ganglia lie beneath the rectum, usually near the posterior adductor. They innervate the gills, the posterior mantle, the posterior adductor, and all the inner organs. Mantle nerves extending along the margin of the mantle are responsible for all structures of the mantle margin and siphons.

The sensory cells, responsible for tactile functions, are grouped along the mantle margin, on the labial palps, siphon margins, foot, etc. Osphradia (chemical sense organs) lie at the base of the gills. The function of balance and, possibly, hearing is performed by the paired statocysts located on the foot close to the pedal ganglion. The eyes develop in different parts of the body, most frequently along the mantle margin, or on the ends of the siphons.

The blood system is not completely closed. The heart (Fig. I. 1, *12*) is in the pericardium (Fig. I. 1, *13*) and is composed of a ventricle and two atria. The rectum, with rare exceptions, passes through the heart. Two aortas extend from the ventricle (anterior and posterior). The anterior aorta gives rise to several arteries supplying the intestine, digestive and reproductive glands, foot, the anterior part of the mantle, and mouth lobes. The posterior aorta gives rise to two arteries supplying the rectum, posterior adductor, retractors of the siphons, etc. The arteries branch into small vessels, which conduct the blood in the system of venous lacunas from which the blood is transported to the venous sinus below the pericardium, then, to the kidney canals, and eventually into the gill arteries leading to the gill lamellae. There the blood is oxidized; then, it is collected into the gill veins leading to the atria. However, some of the venous blood goes directly to the gill arteries, while some blood goes from the lacunae and venous canals immediately to the atria. Thus, arterial blood is mixed with venous blood in the heart.

The excretory organs are represented by kidneys, or nephridia (Fig. I. 1, *10*), which are open on one side to the mantle cavity, and on the other, through the ciliate funnel, to the pericardium. The excretory exits lie on the sides of the foot base.

The reproductive system is composed of symmetrical paired gonads (Fig. I. 1, *11*), which open into the mantle cavity near the excretory kidney openings, or in the distal part of the kidneys. Bivalves are usually bisexual; however, some are hermaphrodites. The genital products in some taxa are excreted through the kidney exits, but in the majority of bivalves, the canals of the gonads have independent outer openings lying on the sides of the foot base near the kidneys' openings. Fertilization is either completely or partly external.

The respiratory organs are represented by two pairs of gills, hanging into the mantle cavity on either side of the foot (Fig. I. 1, *14*). The gill structure in bivalves varies widely, and it is one of the major taxonomic criteria. In the Protobranchia, the most primitive forms, the gills are typical ctenidia, i.e., are composed of two rows of short, triangular, and flat lamellae on the axis along which the nerve and gill blood vessels (ascending and descending) run. Each lamella contains a blood cavity. The lower part of the lamella is covered by ciliate epithelium, so that the lower margin of the gill, formed by ciliate parts of-the lamellae, draws a current of water into the mantle cavity. The axis of the gill is attached by a resilient band to the dorsal part of the body and the posterior adductor (Fig. I. 3a).

In the Filibranchia, the gill lamellae are strongly elongated and transformed into gill filaments hanging into the mantle cavity and curved in a looplike manner to form ascending and descending courses. The filaments of the external row are bent outwards, toward the mantle wall, whereas the filaments of the inner row are bent inwards, towards the foot (Fig. I. 3b).

In cases where the gill filaments are connected, a pseudofilibranchiate type develops, which, after further development, leads to the gills of the Eulamellibranchiata type. This type is characterized by the gill lamellae and the filaments of each lamella that form numerous interlamellar and interfilamentary connectives containing blood vessels. As a result, a system composed of the ascending and descending lamellae of the external and internal gill lamellae or half-gills (Fig. I. 3c) is produced. Both types occur in the order Autobranchia.

Behind the foot, the edges of the inner plates occasionally merge to form a septum in the mantle cavity. This septum may be fused with the septum between the siphons, in which case the mantle cavity is subdivided into the lower and upper sections. In the lower section, the water flows from outside through the inhalant siphon, is received in the lower, larger, part of the mantle cavity, flows through the gills, carries the food particles to the mouth, and then turns to the upper part of the mantle cavity to be taken out by the exhalant siphon.

In the Septibranchia, the gills are considerably changed. The septum inside the mantle cavity, which appeared as a result of the fusion of the edges of the inner gill blades, is transformed into the muscle septum, which is fused posteriorly with the septum between the siphons. The septum has slits and openings connecting the upper, or respiratory, and lower sections of the mantle cavity (Fig. I. 3d).

The ventral side of the body possesses a musculature projection, i.e., foot (Fig. I. 1, *4*), the shape of which is very variable depending on the lifestyle of the bivalves. In the most primitive forms, the foot has a discoidal sole. More often, the foot is wedge-shaped, laterally compressed, has a pointed lower edge, and is used for burrowing. In adherent bivalves, the foot is reduced or completely absent (oysters, rudists). In bivalves inhabiting deep holes, the foot is also rudimentary or absent. When the foot is strongly developed, an anterior opening is also developed to allow it to protrude.

The foot often has a byssus gland. This gland excretes byssus, a bundle of organic filaments, used for attachment to a substrate (Figs. I. 4a, I. 4b, *by*). The appearance of byssus varies from a few thin filaments to a complete byssus network (a tangled mass of fibers). The byssus attachment may be permanent, or temporary allowing a mollusk to re-attach and change its habitat. Occasionally, the byssus is present in young mollusks and disappears in adults. The extent of the development of the byssus often depends inversely on the development of the foot. In some taxa (e.g., *Anomia*), the byssus in adults is calcified, and the mollusk remains attached to the end of its life. An opening (byssal notch) often develops for the protruding byssus.

The foot protrudes out of the shell and is pulled inside by the pedal muscles including the protractors (which elongate the foot), anterior and posterior retractors (which contract the foot), and elevators (which elevate the foot). The pedal muscles are attached to the foot base at one end and to the shell surface at another (Fig. I. 4, *pm*). The development of muscles widely varies in different taxa.

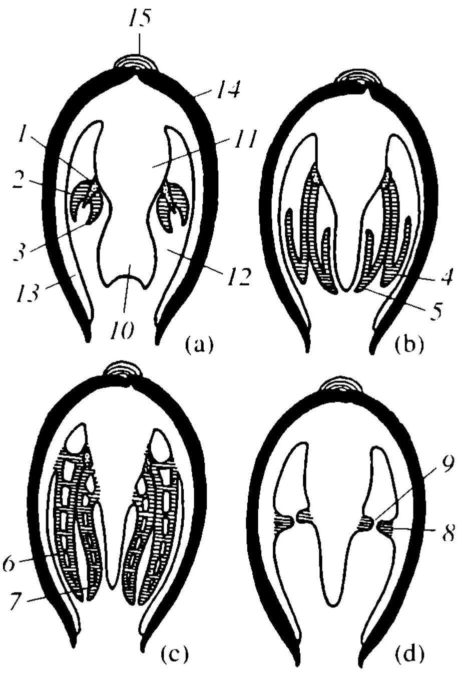


Fig. I. 3. Major types of gill structure in bivalves (after *Zhizn' zhivotnykh*..., 1968, text-fig. 74): (a) Protobranchia, (b) Filibranchia, (c) Eulamellibranchia, and (d) Septibranchia. Designations: (*1*) ctenidium axis, (*2*) external lamella of ctenidium, (*3*) internal lamella of a ctenidium, (*4*) external gill filament consisting of ascending and descending filaments, (*5*) internal gill filament consisting of ascending and descending filaments, (*6*) external half-gill, (*7*) internal half-gill, (*8*) muscular septum, (*9*) openings in the septum, (*10*) foot, (*11*) body, (*12*) mantle cavity, (*13*) mantle, (*14*) shell, and (*15*) ligament.

In addition to pedal muscles, bivalves also have mantle and siphon muscles, and adductor muscles. The mantle is attached to the valve walls by the mantle muscle, and as they contract, the mantle is pulled into the shell. The siphons are also contracted by the retractor muscles to be pulled into the shell. The valves are pulled together by adductors (thick bunches of muscle fibers extending across from one valve to the other). Usually bivalves have two adductors, anterior and posterior. The anterior adductor is positioned above the mouth near the anterior margin, while the posterior adductor lies below the anus near the upper margin of the posterior end of the body (Fig. I. 5, *aad, pad*). The majority of bivalves have two adductors, more or less similar in size. These forms are called isomyarian, or homomyarian. However, there are also numerous bivalves in which the adductors are dissimilar. For instance, in adherent bivalves, the anterior adductor is usually weakened, displaced under the beak, and virtually looses its function (Fig. I. 4a, *aad*), or disappears completely to leave only the large posterior muscle, shifted toward the middle of the shell (Fig. I. 4b, *pad*). More rarely, the anterior muscle is larger in size than the posterior. Bivalves with prominently uneven adduc-

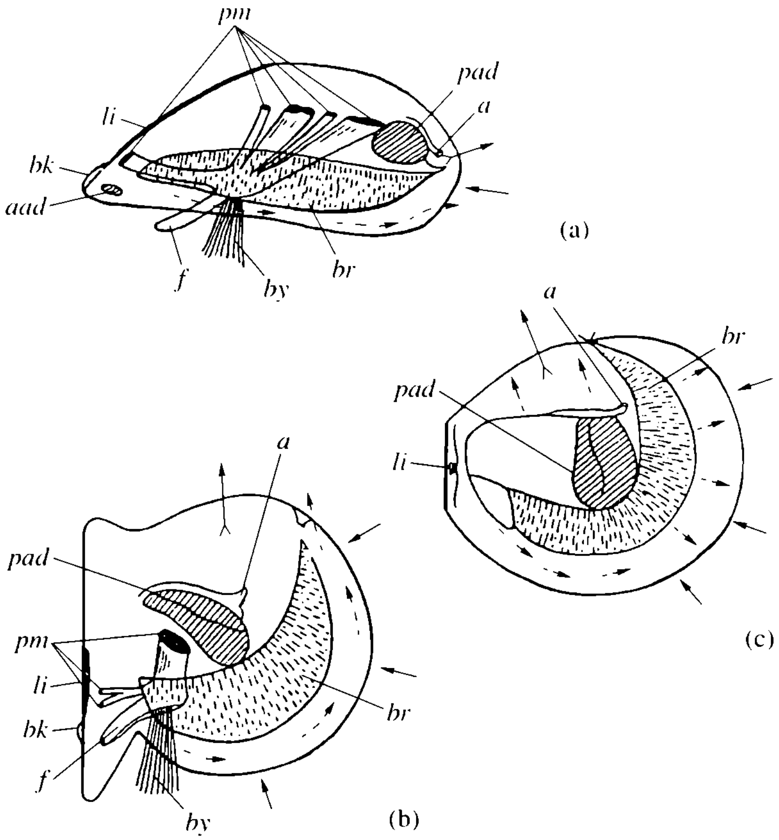


Fig. I. 4. Changes of position of organs in sessile bivalves (after *Osnovy paleontologii*..., 1960, text-fig. 25): (a) *Mytilus*, (b) *Pteria*, and (c) *Ostrea*. Designations: (*a*) anus, (*aad*) anterior adductor, (*bk*) beak, (*br*) gill, (*by*) byssus, (*f*) foot, (*li*) ligament, (*pad*) posterior adductor, (*pm*) pedal muscle, ——► exhalant flow, ◄—— inhalant flow, and – –► flow within the mantle cavity.

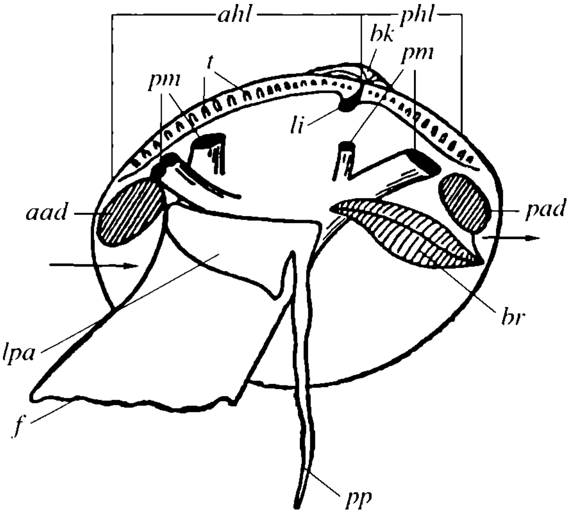


Fig. I. 5. Bivalve shell and soft body (after *Osnovy paleontologii*..., 1960, text-fig. 3). Designations: (*aad*) anterior adductor, (*ahl*) anterior hinge line, (*bk*) beak, (*br*) gills, (*f*) foot, (*li*) ligament, (*lpa*) labial palp, (*pad*) posterior adductor, (*phl*) posterior hinge line, (*pm*) pedal muscles, (*pp*) palp proboscis, and (*t*) teeth.

tors are called anisomyarian. Those bivalves with a single adductor are referred to as monomyarian.

A change in the position and action of the adductor is observed in some burrowing bivalves (in pholadids), in which the anterior adductor assumes the role of the ligament which has disappeared. This adductor lies on the inflexed lip of the anterior margin of the valves, i.e., outside. Its contraction opens the shell.

The shell usually opens using the ligament (a cartilaginous extension of the external conchiolin layer (periostracum) secreted by the mantle). The elastic ligament connects both valves near the hinge margin and acts as an antagonist of the adductors, opening the shell when these muscles are relaxed. The ligament may be external in its position (in this case, it is seen from outside) or internal, i.e., concealed between the upper (hinge) margins of the valves (Fig. I. 5, *li*).

Usually, the ligament is composed of two structurally and mechanically different portions with opposite functions. One portion is composed of fibrous calcified conchiolin, containing calcareous spicules or fibers, which occasionally concentrate to form a lithodesma. This portion can withstand only contracting tensions,

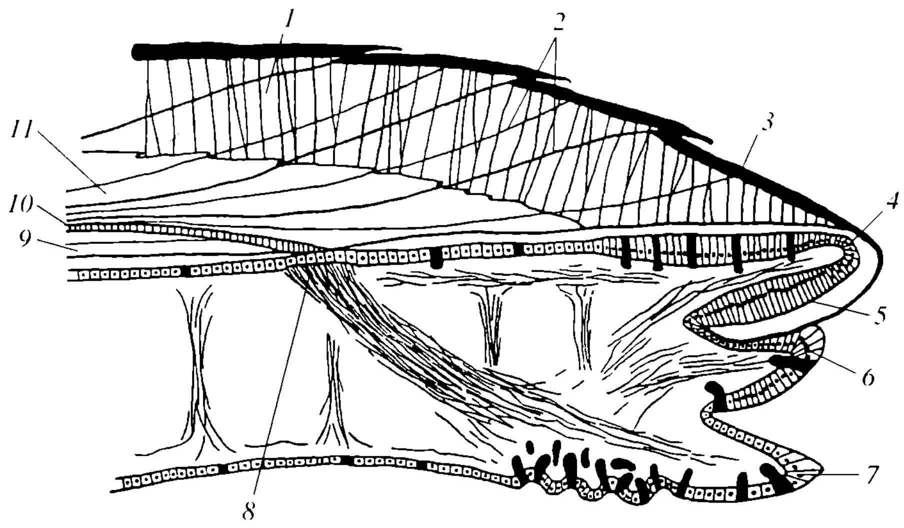


Fig. I. 6. Radial section of shell and mantle in *Anadonta cygnea* (Taylor *et al.*, 1969 after Beedham, 1958). Designations: (*1*) external layer, (*2*) growth line, (*3*) periostracum, (*4*) cells of the epithelium of the external mantle fold, (*5*) periostracum groove, (*6*) middle fold, (*7*) internal fold, (*8*) place of the mantle muscle attachment, (*9*) internal layer, (*10*) pallial myostracum, and (*11*) middle layer.

and is easily torn as a result of stretching tensions. Therefore, this portion of the ligament, or fibrous ligament, may work normally only when it lies below the cardinal (hinge) line (which determines the position and direction of the force when the valve opens) or very close to the cardinal line. As the valves grow, the cardinal axis is lowered, and the fibrous ligament becomes partly above the axis. The upper part of the ligament becomes stretched, fibers tear, and the part of the ligament above the axis ceases to act. Another part of the ligament is composed of a lamellar layer of conchiolin, and is resistant to all kinds of tension. This is a lamellar ligament, which is completely noncalcified and usually lies above the axis. The structure and degree of development of the outer and inner ligaments may be very different even in closely related taxa. Both ligaments can consist of fibrous and lamellar parts, although the outer ligament is more often lamellar, while the inner is more often fibrous; however, the opposite also occurs.

The most primitive ligament (amphidetic) is found in bivalves with a straight hinge line. It is an outer ligament extending along the entire hinge line. More often, the outer ligament lies on the nymph, a special area behind the beak. This is an opisthodetic type of ligament. Some bivalves have an inner ligament (resilium), which lies in a pit (resilifer), or on a ledge (chondrophore). Sometimes, bivalves have both outer and inner ligaments, the development of which can considerably differ. For instance, in the case of a very well developed inner ligament, the outer ligament is usually poorly pronounced. The inner ligament, in rare cases, is subdivided into several parts (multivincular). In burrowing pholadids the ligament is completely reduced, and its function is performed by the anterior adductor.

(2) Development of the Shell (by S.V. Popov)

The shell of bivalves is composed of calcium carbonate and is covered on the outside by a thin organic layer. The shell is secreted by the epithelium of the external surface of the mantle. The secretion of the external organic layer covering the shell (periostracum) begins in the furrow between the middle and external mantle folds and continues by the epithelium of the inner surface of the external mantle fold (Fig. I. 6). The external carbonate layer is produced by the external fold of the mantle. The middle layer is formed by the epithelial cells of the external surface of the mantle up to the point of the muscle attachment. The inner layer is secreted by the mantle surface above the mantle muscle.

The mollusk shell is produced without immediate contact with the cells of the mantle epithelium, because the products of secretion (calcium carbonate and organic compounds) are excreted into the extrapallial fluid. The exceptions are the deposition of the carbonate at the place of muscle attachment (myostracum or hypostracum) and development of the periostracum. The periostracum covering the shell is composed of a chino-binding protein, resistant to both alkaline and acid environments, which protects the carbonate part of the shell from being dissolved. The structure of the carbonate part of the shell depends on the composition and structure of the organic matrix.

Shell growth does not occur evenly throughout the mollusk's life, but depends on the biorhythms of the animal. As a result, shells always possess growth lines, which can be both regularly repetitive and sporadic (produced by damage, illness, etc.). Repetitive growth lines may be of several different orders. The largest correspond to the seasonal cycles and are often seen on the external surface of the shell. The smaller correspond to reproductive seasons, tides, and 24-hour cycles. The daily growth rate depends on the living conditions of the mollusk. It is lower in winter, in the reproductive season, and in older animals.

Ontogenetic changes of structure have been studied in only a few species (in cardiids, in *Cyclocardia*) (Popov, 1977, 1983). At the prodissoconch stage, at a shell size of about 0.5 mm, there are no subdivisions into layers, and the structure appears grainy. On the internal surface, the granules are larger, elongate, and show the beginning of perpendicular orientation. At the stage of early discoconch (ca. 1 mm long), the shell is composed of two layers. The third (external) layer, with a different orientation of elements appears later. In *Acanthocardia*, *Parvicardium*, and *Cerastoderma*, the development of the external layer begins at shell size ca. 1 mm; in *Serripes groenlandicus* (Clinocardiinae), it begins at shell size ca. 5 mm; and in *Pratulum thetidis* and *Nemocardium edwardsi* (Protocardiinae), it begins at 8 mm from the beak. This layer first appears in the intracostal spaces and, only later, on the costae.

In the brackish-water environments inhabited by some cardiids, the ontogenetic development of structure can be even more extended. In *Cerastoderma glaucum* from the sea of Azov and from the limans of the Black and Caspian seas, the external layer often does not develop until a shell size of 8–10 mm is attained, and in some Caspian specimens, it does not develop at all, and the shell remains two-layered.

(3) Shell Microstructure (by S.V. Popov)

Major types of shell microstructure were discovered and described as early as the beginning of the 20th century using the optical microscope. Study of the shell structure in many systematic groups of mollusks showed that their entire diversity may be allocated to several types of microstructure (nacreous, foliated, simple prismatic, composite prismatic, crossed-lamellar, complex crossed-lamellar, and homogeneous (Bøggild, 1930; Taylor *et al.*, 1969, 1973; Popov, 1977, 1980, 1986a, 1986b, etc.). However, the use of electron microscopy has shown that, within these types, the details of microstructure and the relationships between the mineral and organic shell components can be quite different. This has made classification more complex, because it requires the recognition of varieties and textures (Carter, 1980; Popov, 1992). It is noteworthy that these and subsequent attempts at classification are purely morphological. Apparently, superficially similar structures can develop in unrelated groups from different initial structures by different evolutionary processes. On the one hand, this is explained by the limited number of possible structural transformations of the skeleton, and on the other, by limitations in the ability of researchers to discern fine differences in genetically different structures.

Nacreous structure is unique for mollusks. It is composed of aragonite sheets, orientated in parallel to the shell surface. These sheets have a hexagonal (more rarely, rhomboid or square) shape, or are irregular in outline. Calcareous sheets are enclosed in the organic matrix. This matrix is in fact composed of an interlamellar matrix separating one layer of sheets from another, and an intercrystalline matrix separating the sheets of the same layer.

(1) *Sheet nacre*. Sheets are arranged in regular layers parallel to the shell surface. In contrast to gastropods and cephalopods, bivalves form an interlocking brick wall pattern (in radial section), because individual sheets are not located directly one below another, but somewhat displaced. The nacre of this structure is typical of the inner layer of many bivalve superfamilies (Nuculacea, Pinnacea, Unionacea, Pholadomyacea, and Pandoracea), while in Mytilacea and Pteriacea, it forms both the inner and the middle shell layers (Taylor *et al.*, 1969).

(2) *Lenticular nacre* is formed by vertical pillars of sheets arranged one above the other. The height of such pillars may reach 20–30 μm. In the middle part, they are all approximately the same, while toward the margins, the size of the sheets decreases, resulting in the lenticular shape of the pillar. Nacre of this texture is usually developed in the middle layer of a shell. It is observed in Nuculacea, Trigonacea, and Pandoracea (Taylor *et al.*, 1969). It is not unusual for both varieties of the nacreous structure to occur in the same shell (sheet nacre is in the inner layer, while lenticular nacre is in the middle layer).

Foliated structure is similar to nacre, but is composed of calcite sheets. The sheets are hexagonal in shape and occur at an angle to the surface of growth, so that the sheets of the previous layer are partly covered by those of the succeeding layer. Within one layer of simultaneously developed sheets, the direction of their longer axes remains parallel, but in other areas it may change. Because of this, the general view of the foliated structure in the radial section looks irregular. The sheets may lie parallel to the inner surface of the shell, or can be oblique, and even vertical. A change in the sheet arrangement is often observed within the same layer, resulting in zig-zag-shaped structures (Ostreacea and, Pectinacea). A thick interlamellar matrix, characteristic of nacre, is absent in this case, and each sheet is enclosed in the cover of the intracrystalline matrix. The sheet size may vary widely. The length can be 10–15 μm, the width 3–5 μm, and the thickness 0.2–0.5 μm. Foliated structure is observed in the Ostreacea, Pectinacea, Anomiacea, and Limacea (Taylor *et al.*, 1969).

(A) Prismatic structure. The prismatic structure usually forms the external layer of the bivalvian shell. Prisms are oriented vertical to the shell surface and have straight parallel walls, but sometimes branch.

(1) *The simple prismatic structure* is composed of regular large multisided vertical prisms separated from

each other by a thick interprismatic matrix. In the tangential section, the prisms are pentagonal or hexagonal. Calcite prisms are characteristic of the Pteriacea, Mytilacea, Pinnacea, and Ostreacea, while aragonite prisms occur in the Unionacea, Trigoniacea, Pandoracea, Pholadomyacea, and Poromyacea (Taylor *et al.*, 1969).

(2) *The irregular prismatic structure* is composed of irregular prisms varying in thickness (some Lucinidae and Veneridae) (Popov, 1992).

(3) *Fibrous prismatic structure*: (a) thin fibrillar prisms 0.5–1.5 μm in cross section are inclined toward the umbo and often arranged in bunches. A thin prismatic layer (mozaicostracum) is often present on the external surface (some Lucinidae); (b) the mozaicostracum is absent, the prisms are covered by thin transverse hatching (some Tellinidae).

(4) *Acicular prismatic (spherulitic prismatic) structure* (after Carter, 1980): (a) small needle-shaped prisms are arranged in large megaprisms directed toward the external surface (some Lucinidae and Mactridae); (b) megaprisms are absent; sometimes, needle-shaped prisms are collected in bunches (some Psammobiidae).

(5) *Compound prismatic structure*: (a) prisms of the first order are relatively small, multisided, composed of needle-shaped prisms of the second order, and are fan-shaped radiating from the center of the prism. Prisms of the first order are directed toward the external surface and are inclined toward the umbo (some Veneridae); (b) prisms are large (10–20 to 50 μm in cross section), irregular, varying in thickness, and composed of long needle-shaped prisms of the second order radiating at a small angle (some *Anadara*); (c) prisms are smaller (1–4 μm), subquadrate or more irregular in cross section, and composed of small needle-shaped elements (some Cardiidae and Tellinidae).

(B) Composite prismatic structure. The composite prismatic structure always forms the external layer of the shell and is composed of horizontal prisms of the first order, which are formed of smaller needle-shaped prisms of the second order radiating from the center of the layer toward its margin. Small prisms of the second order are rounded or polygonal in cross section, their diameter decreases going from the margin toward the center of prisms of the first order, and is 1–5 μm or even less. Prisms of the first order are directed toward the beak and inside the layer. Prisms of the first order are often absent, and the external layer is formed by thin prisms of the second order, which are arranged in a feather-like way (some Lucinidae, Veneridae, and Donacidae) (Bøggild, 1930; Taylor *et al.*, 1969; Carter, 1980; Popov, 1992).

(1) *Acicular composite prismatic structure*: Megaprisms are composed of small needle-shaped prisms (some Nuculidae).

(2) *Fibrous composite prismatic structure*: (a) Megaprisms are composed of small fibrous prisms (some Cardiidae and Tellinidae); (b) megaprisms are absent. Fibroid prisms either radiate from the middle of the layer or diverge from the upper part of the external layer (some Cardiidae, Tellinidae, Lucinidae, and Donacidae).

(3) *Compound composite prismatic structure*: (a) Megaprisms are composed of complex prisms formed of small acicular prisms (some Donacidae); (b) megaprisms are absent; regular, compound prisms (7–25 μm in cross section) radiate from the upper part, or from the middle of the layer. Prisms may merge to form vertical, radially arranged plates, 10–20 to 50 μm thick (some Veneridae). The same structure, but with irregular prisms with variable thickness occurs in some Veneridae (rare) and some Tellinidae.

(C) Crossed-lamellar structure is the most complex and advanced structure, widely occurring in bivalves and gastropods. It is always composed of aragonite and is built from lamellae of several orders. In the neighboring lamellae of the first order, the plates of the second order are orientated in opposite directions. Large plates are usually directed perpendicular to the shell surface and extend along the growth lines. However, when radial ribbing is present, the lamellae are more complexly curved, although remaining perpendicular to the growth zone at the shell margin. Within the plates of the first order, the orientation of the plates of the second order change their orientation in the way that they cross each other in any section (external and middle layers of the Arcidae, Limopsidae, Glycymeridae, Carditidae, Lucinidae, Cardiidae, most Veneridae, Tellinidae, Donacidae, etc.).

(D) Complex crossed-lamellar structure. This structure is composed of the same lamellae of the second order as in the previously described crossed-lamellar structure, but it is less regular:

(1) *Irregular complex crossed-lamellar structure*: Irregular blocks of plates alternate with blocks where the orientation of the lamellae is opposite (inner layer of the Arcidae, Lucinidae, Tellinidae, etc.).

(2) *Crossed-matted structure*. Lamellae of the second order form irregular branching plates of the first order (some Cardiidae and *Macoma*).

(3) *Cone complex crossed lamellar structure*. Lamellae form vertical pillars of cones, inserted inside each other (inner layer of some Cardiidae).

(E) The homogeneous structure may be characteristic of both the external and internal layers. It is composed of aragonite and built from small granules with similar optical orientation. The granules are variable in size, have long, lenticular, or irregular shape, and are enclosed in organic covers. Granules always lie parallel to the growth lines; therefore, they are horizontal in the inner layer and may be oblique or vertical in the external layer, parallel to the growth zone.

(1) *The granular structure* is composed of small granules, 0.3–4 μm in size (some Veneridae).

(2) *The crossed-matted lineated structure* is composed of elongate crystallites, 0.2–0.3 × 5–10 μm in

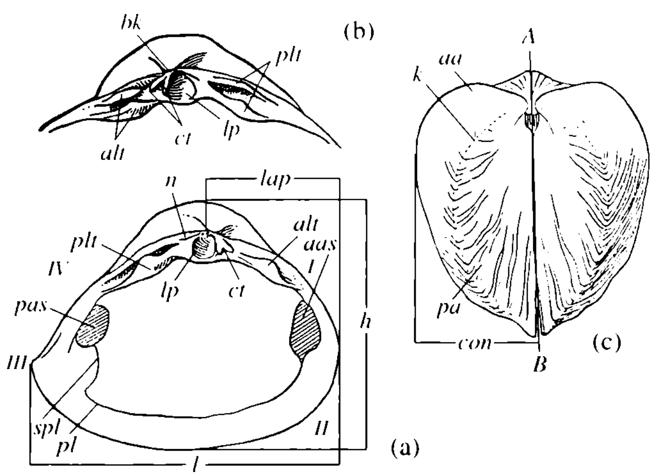


Fig. I. 7. Shell structure in *Mactra* (after Nevesskaja, 1963, text-fig. 1): (a) left valve interior, (b) hinge of the right valve, and (c) shell exterior. Designations: (*aa*) anterior area, (*aas*) anterior adductor scar, (*alt*) anterior lateral teeth, (*bk*) beak, (*ct*) cardinal teeth, (*con*) convexity, (*h*) height, (*k*) keel, (*l*) length, (*lap*) length of the anterior part of the valve, (*lp*) ligament pit, (*n*) nymph, (*pa*) posterior area, (*pas*) posterior adductor scar, (*pl*) pallial line, (*plt*) posterior lateral teeth, and (*spl*) pallial sinus; (*AB*) plane of commissure; (*I–II*) anterior margin; (*I–IV*) hinge, or cardinal, margin; (*II–III*) lower, or ventral, margin; and (*III–IV*) posterior margin.

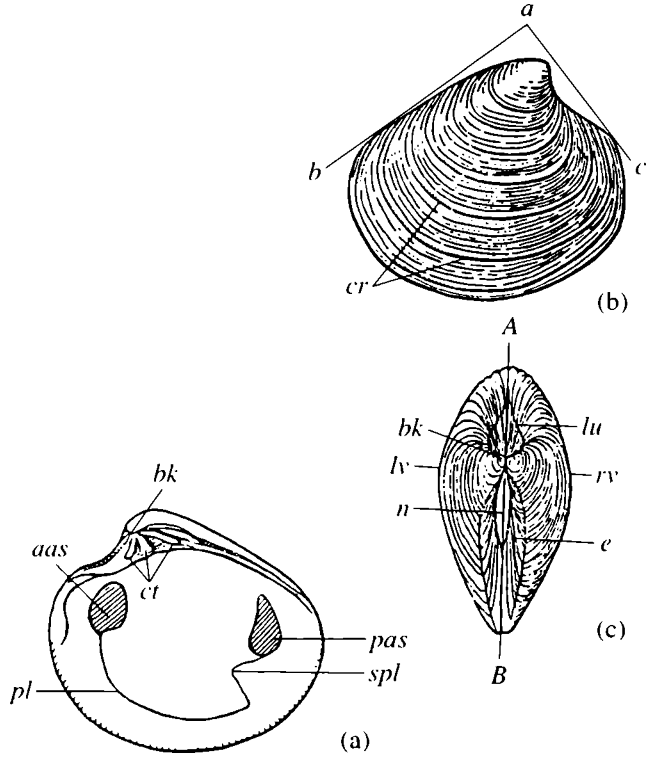


Fig. I. 8. Shell structure in *Chione* (after Nevesskaja, 1963, text-fig. 24): (a) right valve interior, (b) right valve exterior, and (c) lateral view of a shell. Designations: (<*bac*) apical angle, (*cr*) concentric ribs, (*e*) escutcheon, (*lu*) lunule, (*lv*) left valve, and (*rv*) right valve. For other designations, see Fig. I. 7.

size, extended in each section in two major directions (it often shows a gradual transition to the crossed-lamellar structure (some Veneridae, Tellinidae, and Donacidae).

(3) *The irregular homogeneous structure* is composed of elements of complex and irregular shape, 0.5–3.0 μm in size (some Veneridae, Tellinidae, Donacidae, etc.).

Among bivalves, more ancient and primitive groups have a more stable shell structure. For instance, almost all Arcidae, Glycymeridae, and Carditidae have similar microstructure. The Lucinidae also have small variations of structure except for several aberrant groups (*Anodontia*, *Linga*, and *Lucinoma*). In contrast, the evolutionary young and flourishing bivalve groups (Veneridae and Tellinacea) have a highly variable structure. The shell in these groups is often composed of 4 or 5 types of microstructure, which sometimes varies even within the same species.

Microstructural characteristics that can be used in taxonomy are usually related to the structure of the external layer. Apparently, this is due to by the ontogeny of the structure. The external layer, which appears later in ontogeny, is more readily changeable in phylogeny. The microstructure of the inner and middle layers is more stable, while the observed differences in the structure of these layers (transition from the crossed-lamellar structures into the homogeneous and the texture differences of the complex crossed-lamellar structure) often cannot be used as taxonomic criteria, since they occur in different specimens of the same species, or even in the same shell.

In fossil shells, calcareous material (both calcite and aragonite) is preserved for quite a long time because it is protected by the conchiolin cover. The original composition and skeleton structure is frequently preserved in Cenozoic and Mesozoic taxa, and in some cases nonrecrystallized shells may be found even in Paleozoic rocks. However, aragonite often transforms into more stable calcite, or is replaced by other minerals.

(4) Shell Morphology

Because the system of bivalves is largely based on the shell, which greatly reflects the features of the soft body, it is important to discuss shell morphology.

As mentioned above, the body of a mollusk is enclosed within a shell, which consists of two valves (left and right). The shell shape can vary greatly, depending on the mollusk's mode of life. Most often, the valves are oval or oval egg-shaped and flattened from the sides, but they can also be rounded, strongly elongated and flattened, wedge-shaped, etc.

The valves are, for the most part, equally convex and are mirror images of each other. The shell in this case is referred to as equivalve (Figs. I. 7b, I. 8c). In some cases, especially when one of the valves is attached to the substrate, or the shell lies freely on one valve, the

Fig. I. 9. Inequivalve shell of the oyster *Rhynchostron* (after *Treatise*..., 1971, text-fig. J97): (a) complete shell and (b) left valve. Designations: (*lv*) left valve and (*rv*) right valve.

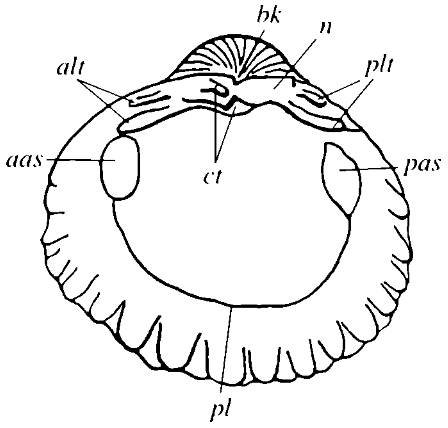


Fig. I. 10. Shell interior of *Cerastoderma* (right valve) (after Nevesskaja, 1963, text-fig. 19). For designations, see Fig. I. 7.

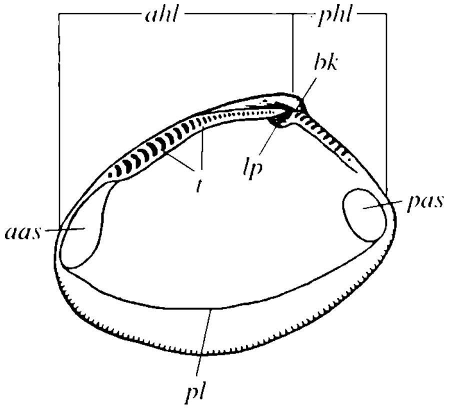


Fig. I. 11. Shell interior of *Nucula* (right valve) (after Nevesskaja, 1963, text-fig. 2). Designations: (*ahl*) anterior hinge line, (*lp*) ligament pit, (*phl*) posterior hinge line, and (*t*) teeth. For other designations, see Fig. I. 7.

shell becomes inequivalve. The attached lower valve becomes more convex, while the free upper valve becomes less convex, and is flattened or even concave (Fig. I. 9a). The plane drawn through the junction of the valves is referred to as the pane of commissure, and in equivalve shells, it is the plane of symmetry (Fig. I. 7, *AB*). In inequivalve shells, this plane is shifted toward the less convex valve.

The shell margin, along which the valves are connected, is referred to as the dorsal, (hinge or upper) margin (Fig. I. 7, *I–IV*). The opposite margin is called the ventral, or lower (Fig. I. 7, *II–III*). The anterior (Fig. I. 7, *I–II*) and posterior (Fig. I. 7, *IV–III*) margins are those near the mouth and anus, respectively.

Along the hinge line, the valves are flexibly connected by the elastic ligament, and are closed together, from inside, by adductor muscles. Along the hinge line, the shell has a hinge reinforcing the junction of the closed valves, which precludes their movement along each other in longitudinal and lateral directions.

Shell growth begins from the umbo (beak) (Figs. I. 7b, 8a, 10, 11, *bk*), which is in the upper part of the shell and is surrounded by concentric growth lines (Fig. I. 12, *gl*). The beak projects above the hinge (dorsal) margin to varying extents and may be curved forward (prosogyre beak) (Fig. I. 7a), backward (opisthogyre beak) (Fig. I. 11), or inward (orthogyre beak) (Fig. I. 10). Sometimes, it is curved spirally (spirogyre beak) (Fig. I. 9b). When the beak is in the middle of the hinge line, the shell is called equilateral. In cases where the beak is shifted anteriorly or posteriorly, the shell is inequilateral. When the beak is strongly shifted forward, the anterior margin is very short and may even disappear completely. In this case, the beak occupies the anteriormost position and is called terminal (Fig. I. 12b). In relation to the hinge line, the projection of the beak can vary. A strongly projecting beak, inclined over the hinge margin, is referred to as a gryphoid beak (Fig. I. 9b).

Usually, the beginning of the beak, which corresponds to the protoconch, is inseparable from the remaining part of the shell, but the protoconch is sometimes clearly delineated. Usually, the shell shape

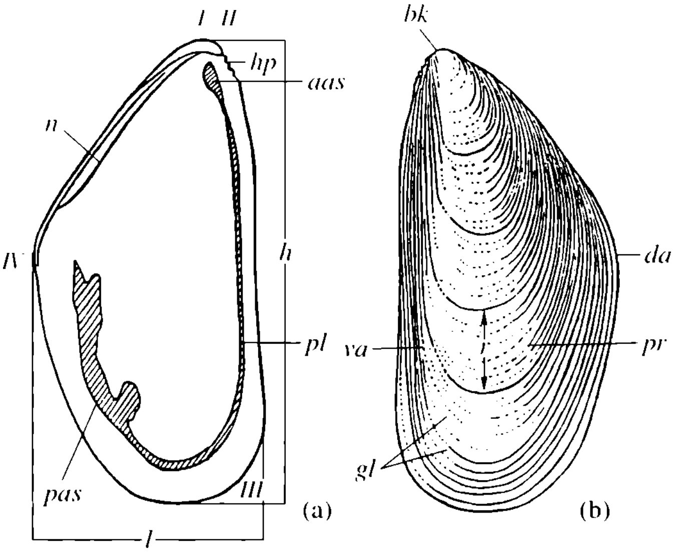


Fig. I. 12. Shell of *Mytilus* (after Nevesskaja, 1963, text-fig. 11): (a) left valve interior and (b) left valve exterior. Designations: (*da*) dorsal area, (*gl*) growth lines, (*hp*) hinge projections, (*pr*) posterior ridge, (*r*) annual rings, and (*va*) ventral area; (*I–III*) ventral margin, (*I–II*) dorsal margin, and (*II–III*) posterior margin. For other designations, see Fig. I. 7.

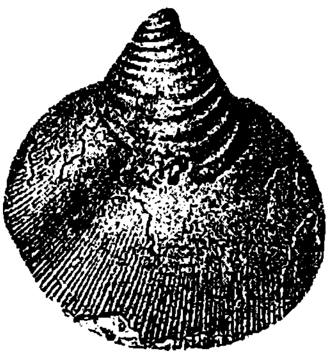


Fig. I. 13. Right valve exterior of *Slava* (after *Treatise*..., 1969, text-fig. B2.4).

changes gradually as the shell grows, and only very rarely does it happen quickly (Fig. I. 13).

The hinge margin consists of two parts, the anterior (to the front of the beak) (Figs. I. 5, *ahl*; I. 7a, 7b, *I*) and the posterior (to the back of the beak) lines (Figs. I. 5, *phl*; I. 7a, 7b *IV*). Therefore, the ratio between these lines depends on the position of the beak. When the beak is central, their length is equal; when the beak is prosogyre, the anterior line is shorter; and when the beak is opisthogyre, it is longer. When the beak is terminal the anterior portion disappears completely (Fig. I. 12).

The external surface of valves can be smooth, i.e., covered only with growth lines. A particular type of growth line reflects traces of interrupted growth called annual rings (Fig. I. 12b). Apart from the growth lines, the shell surface may possess various ornamentation, most frequently radial (Fig. I. 14b, *rr*), or concentric (Fig. I. 8b, *cr*), thin, or prominent ribs, varying in shape, structure, mutual arrangement, and number. The slopes of the ribs may be similar, or different. The shape of the connection of the slopes of the ribs, or ridges, may also be very different. The ribs can be smooth, or have scales, nodes, and various spines. In some taxa, the ornamentation is very complex, resulting from a combination of different kinds of ribbing (reticulate, divaricate, etc.). In some shells, only the umbilical area is ornamented (umbilical ornamentation), or different parts of the shell possess different ornamentation. Sometimes, the left and right valves are ornamented differently. Some shells have a posterior keel (Fig. I. 7c, *k*), which most often subdivides the shell surface into the anterior area (Fig. I. 7c, *aa*) and posterior area (Fig. I. 7c, *pa*). When the anterior hinge line is absent, the posterior keel divides the shell surface into the dorsal area (Fig. 12b, *da*) and ventral area (Fig. 12b, *va*).

The dorsal side often has two areas, one to the front and another to the back of the beak. These are called the lunula (anterior: Fig. I. 8b, *lu*) and escutcheon (Fig. I. 8b, *e*) and are separated from the remaining surface of the shell by a riblet, furrow, etc.

In some taxa, the ends of the hinge margin are attenuated to form auricles anteriorly and/or posteriorly (Fig. I. 14, *au*), which are, to varying extents, separated from the remaining surface of the shell. A byssal notch is often observed under the anterior auricle. Sometimes, the shell exhibits wing-shaped expansion anteriorly and, more rarely, posteriorly.

Shells are mostly closed, but occasionally have a gape for the foot (in the anteroventral part) and for the siphons (posteriorly).

Rarely, shells may be covered by the mantle from the outside, thus resulting in an internal shell. Sometimes the shell is reduced, and in this case, additional tube or additional plates usually develop.

The inner surface of the shell is usually concave and bowl-shaped, with structures negatively reflecting the ornamentation of the external surface (Fig. I. 14a). Independent ornamentation is more rare. Inner edges may be dented, while the external surface is smooth or possesses concentric ribbing.

The interior of the valves has scars of several muscles: adductors, protractors, and retractors of the foot, mantle, siphons, etc. The hinge margin usually has hinge and ligament supports.

A shell usually has two adductors (anterior and posterior). The muscle scars are usually clearly noticeable and are more or less equal in size (Figs. I. 7, 8a, *aas*, *pas*). In some taxa, the anterior adductor is small and shifted under the beak (Fig. I. 12a) or disappears completely. In the latter case, the scar of the posterior adductor is almost in the center of the valve (Fig. I. 14a). More rarely, the anterior adductor is more strongly devel-

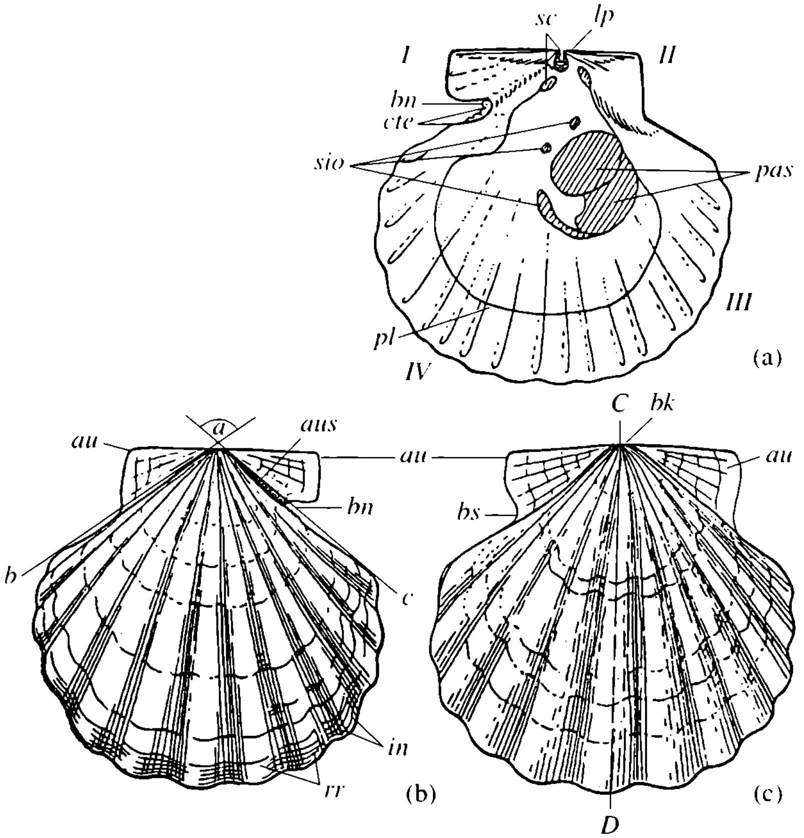


Fig. I. 14. Shell of *Chlamys* (after Nevesskaja, 1963, text-fig. 7): (a) right valve interior, (b) right valve exterior, and (c) left valve exterior. Designations: (*au*) auricles, (*aus*) auricle sinus, (*bac*) apical angle, (*bn*) byssal notch, (*bs*) byssal sinus, (*cte*) ctenolium, (*in*) interrib spaces, (*lp*) ligament pit, (*rr*) radial ribs, (*sc*) scar of the ring muscle, and (*sio*) scars produced by the attachments of internal organs; (*C–D*) median line, (*I–IV*) anterior margin, (*I–II*) hinge margin, (*II–III*) posterior margin, and (*III–IV*) ventral margin. For other designations, see Fig. I. 7.

oped, and, in this case, its scar is larger than the posterior scar. In some anisomyarian taxa, the anterior muscle is attached to a special septum under the beak (Fig. I. 15, *sep*). In pholadids, when the ligaments are reduced, the anterior adductor is located on the upturned anterior margin (Fig. I. 16, *ur*). In the majority of bivalves, the line of attachment of the mantle to the shell looks like a scar line on the inner surface of the valves parallel to the ventral margin called the pallial line (Figs. I. 7a, 8a, *pl*). The pallial line may be simple (or entire) (Fig. I. 10) or with a sinus (Figs. I. 7a, 8a, *spl*), which results from the development of the muscle of the inhalant and exhalant siphons. The sinus may be small, or deep, and may vary in size and position.

Apart from the above muscle scars, the valves sometimes show traces of the attachment of the pedal muscles, and the earlier taxa may have traces of the attachment of the mantle in the umbilical region. Pholadids have a protuberance (apophysis) to accommodate the pedal muscles under the beak (Fig. I. 16, *ap*).

The shell has structures for the attachment of the ligament, which can be, as said above, external, internal, or both. For instance, a narrow plate (called the nymph)

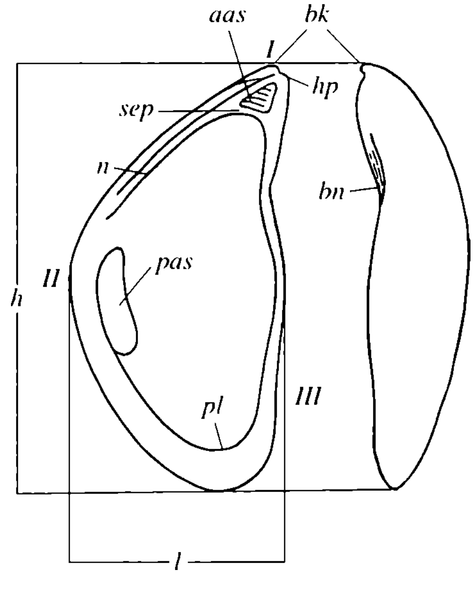


Fig. I. 15. Shell interior of *Dreissena* (left valve) (after Nevesskaja, 1963, text-fig. 42); (*sep*) septum. For other designations, see Figs. I. 7, I. 12, and I. 14.

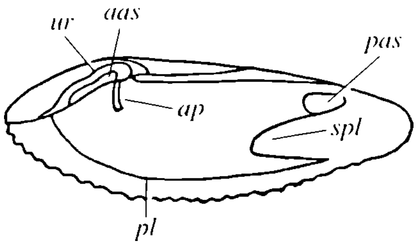


Fig. I. 16. Shell interior of *Barnea* (right valve) (after Nevesskaja, 1963, text-fig. 47). Designations: (*ap*) apophysis and (*ur*) umbilical reflection. For other designations, see Fig. I. 7.

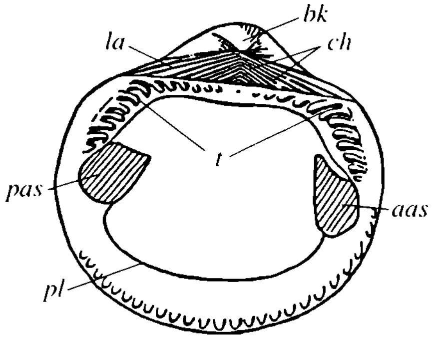


Fig. I. 17. Shell interior in *Glycymeris* (after *Osnovy paleontologii...*, 1960, text-fig. 8). Designations: (*ch*) chevrons, (*la*) ligament area, and (*t*) teeth. For other designations, see Fig. I. 7.

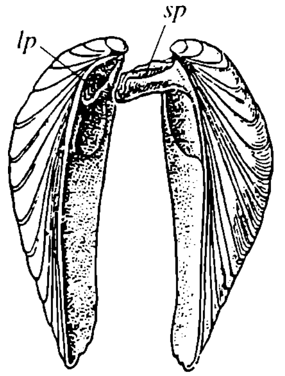


Fig. I. 18. Ligament apparatus in *Mya* (after *Osnovy paleontologii...*, 1960, text-fig. 96). Designations: (*lp*) ligament pit and (*sp*) spoon.

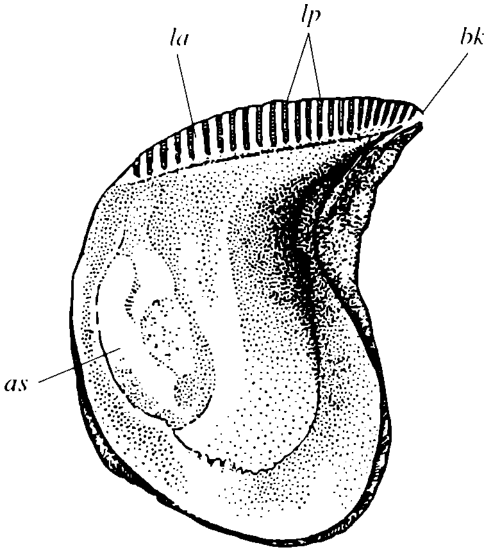


Fig. I. 19. Left valve interior in *Isognomon*. Designations: (*as*) adductor scar, (*bk*) beak, (*la*) ligament area, and (*lp*) ligament pits.

developed behind the beak to attach the external opisthodet ligament (Figs. I. 7a, I. 12a, *n*). When this ligament is located lower between the valves, the nymph also becomes lower. The amphidetic external ligament is usually located on the more or less wide ligament area (Fig. I. 17, *la*), occurring between the beak and the hinge margin and covered by parallel rows of diagonal furrows (chevrons) (Fig. I. 17, *ch*). The latter represent traces of the successive attachments of the lamellar ligament, which moves as the shell grows. The ligament pit is developed to accommodate the internal ligament in the hinge margin under the beak, on both valves, or only on one of them (Figs. I. 7a, I. 14a, *lp*), or on a spoon-shaped ledge (spoon) (Fig. I. 18a, *sp*). These structures supporting the internal ligament are called resilifer or chondrophore. In some taxa having both internal and external ligaments, there is also a nymph and a ligament pit (resilifer) (Fig. I. 7a). The multivincular ligament is located on the ligament area in several ligament pits, the number of which increases as the shell grows (Fig. I. 19).

Shells of most bivalves have a hinge on the inner side of the hinge margin. The hinge is composed of a row of projections, or teeth and corresponding tooth pits. The thickenings of the hinge margin, on which the teeth and tooth pits are located, is called the hinge area.

Hinge structure is one of the most important taxonomic criteria for the classification of bivalves, and for the reconstruction of their phylogeny. It is very different in different groups, resulting in several types of hinges being distinguished.

The types most widely occurring among Recent bivalves include primary and secondary taxodont (ctenodont and neotaxodont, or pseudoctenodont, respectively), heterodont, desmodont, dysodont, and schizodont hinge types. Extinct bivalves also had preheterodont, actinodont, lyrodesmodont, cyrtodont, pachyodont, pterinoid, and some others.

The ctenodont (= primary taxodont) hinge consists of many teeth, usually arranged in one row on either side of the beak, the subumbilical and submarginal teeth being of the same shape (Fig. I. 11). The tooth row is continuous, or interrupted by the ligament pit.

The taxodont (secondary taxodont, neotaxodont, or pseudotaxodont) hinge consists of many teeth aligned in one row on either side of the beak; the subumbilical and submarginal teeth may be of the same shape, or the submarginal teeth are elongated, while the subumbilical teeth are shortened (Fig. I. 17). The tooth row is continuous, or the teeth may be weakened under the beak, or be completely absent. Both types of taxodont hinges are known, beginning from the Ordovician.

The heterodont hinge, first recorded in the Silurian, is composed of a few teeth differing in shape and arrangement. These are subumbilical cardinal teeth (usually not more than three), positioned below the beak and more or less perpendicular to the hinge margin (Figs. I. 7a, I. 8a, *ct*), and lateral teeth, occurring anteriorly (anterior lateral [Fig. I. 7a, *alt*]) and posteriorly (posterior lateral [Fig. I. 7a, *plt*]) of the beak, and lying more or less parallel to the hinge margin. The maximum number of lateral teeth is two anterior and two posterior teeth in either valve. Some teeth may be absent.

The desmodont hinge is characterized by the weak development, or complete absence of teeth, while the internal ligament is developed. To support this ligament the shell has a chondrophore in the shape of a spadelike, or spoonlike shelf (Fig. I. 18, *sp*). This type of dentition is known from one Ordovician genus, but became more widespread only from the Permian.

The hinge margin can completely lack teeth (edentulous), or can possess small toothlike projections (dysodont hinge [Fig. I. 12a, *hp*]). Species with the edentulous hinge are known beginning from the Cambrian, and the dysodont hinge is recorded beginning from the Carboniferous.

The schizodont hinge has two elongated teeth diverging from the beak in the right valve, and three in the left valve. The middle tooth in the left valve is split and enters the space between the teeth of the right valve. The subumbilical teeth of this hinge are usually referred to as pseudocardinal (Fig. I. 20, *pt*). This hinge type first appeared in the Carboniferous, but became widespread from the Triassic, and apparently evolved independently in the Unionidae and Trigoniidae.

The actinodont hinge consists of a row of teeth radiating from the beak. The typical actinodont hinge has short subumbilical teeth (see Fig. V. 3), while the lyrodesmoid hinge lacks them (see Fig. V. 4). Both types of actinodont hinge are known beginning from the Early Ordovician. The true actinodont hinge was only known until the Triassic, while the lyrodesmoid hinge is recorded only in the Ordovician and isolated species with this hinge type are recorded from the Jurassic.

The cyrtodont hinge consists of anterior and posterior submarginal teeth, between which there is an area without teeth (Fig. I. 21). This hinge type is known from the Early Ordovician to the Devonian, inclusive.

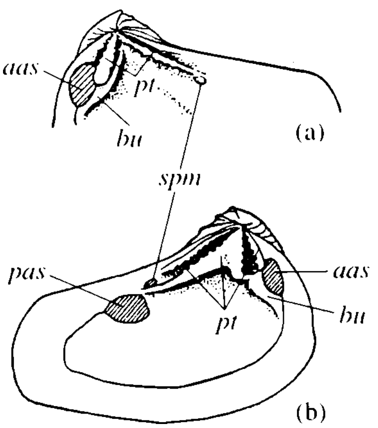


Fig. I. 20. Shell interior in trigoniids (after *Osnovy paleontologii*..., 1960, text-fig. 14): (a) hinge of the right valve and (b) left valve. Designations: (*aas*) anterior adductor scar, (*bu*) buttress, (*pas*) posterior adductor scar, (*pt*) pseudocardinal teeth, and (*spm*) pedal retractor scar.

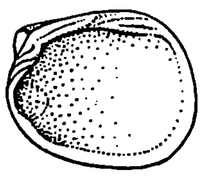


Fig. I. 21. Cyrtodont hinge of the right valve of *Cyrtodonta* (after *Treatise*..., 1969, text-fig. C14b).

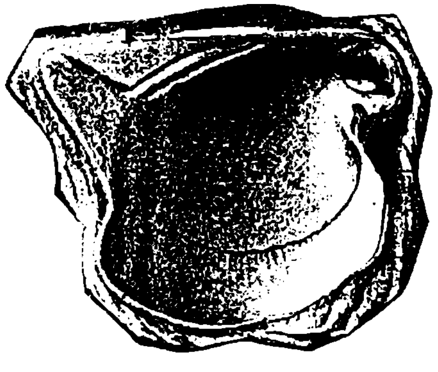


Fig. I. 22. Pterinoid hinge, left valve of *Pterinea* (after *Treatise*..., 1969, text-fig. C34, 8).

The pterinoid hinge is characteristic of taxa with a terminal or almost terminal beak, under which there is a row of short subumbilical teeth, and a few elongated submarginal teeth at some distance (Fig. I. 22). Bivalves with this hinge type are known from the Early Ordovician until the present, but were most widespread from the Devonian to the end of the Cretaceous.

The rarer types include the isodont and pachyodont hinges, along with some hinge types preceding the secondary taxodont and heterodont types (see also the

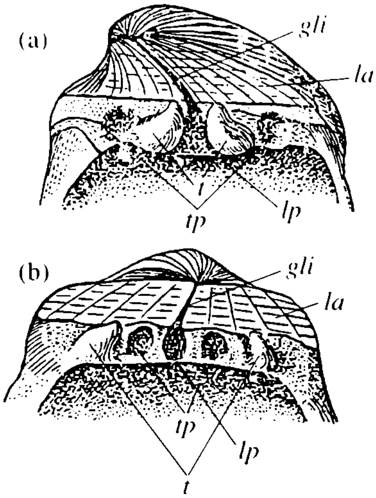


Fig. I. 23. Isodont hinge of *Spondylus* (after *Osnovy paleontologii...*, 1960, text-fig. 13): (a) right valve and (b) left valve. Designations: (*gli*) external ligament gape, (*la*) ligament area, (*lp*) ligament pit, (*t*) teeth, and (*tp*) tooth pits.

chapter "Morphogenesis"). The isodont hinge is composed of teeth and pits arranged symmetrically anteriorly and posteriorly of the ligament pit. Each valve has two teeth and two pits. The teeth on the right valve are positioned closer, while on the left they are shifted to the margins of the ligament area (Fig. I. 23). This hinge type is recorded in bivalves from the beginning of the Mesozoic to the present. The pachyodont hinge is characteristic mainly of rudists, and consists of a few massive, large, asymmetrical, curved or spiny teeth entering the pits on the other valve.

Many Paleozoic (especially Early and Middle Paleozoic) bivalves had a hinge of the preheterodont type, which consisted of only subumbilical teeth (usually one or two), sometimes, only in one valve, while the other valve had a corresponding pit. Sometimes, there were only posterior marginal, usually elongated (one or two) teeth, or one subumbilical tooth and one submarginal tooth (see Fig. V. 1).

Several nonmarine bivalves have a hinge composed of a series of uneven teeth of irregular shape, the type that could be called pseudotaxodont.

Some genera are characterized by the preservation of the larval hinge (provinculum). In these, the hinge margin is dentate, and true teeth do not develop.

It is worth noting that among representatives of the suprageneric taxa with hinges of the above types, there are genera with strongly reduced teeth, and even those lacking teeth completely.

Apart from all the above structures, the inner surface of the shell sometimes possesses ridges or tooth-shaped crests enforcing the shell, especially the hinge area or resilifer.

The shapes and ornamentation of the inner surface often negatively reflect shapes of the external surface (negative ornamentation [Fig. I. 14a]). Some pectinoid taxa have ridges and toothlike projections radiating symmetrically anteriorad and posteriorad of the top of the ligament pit (cardinal crurae) and/or between the main body of the shell and the ears (auricular crurae).

The inner margins of the valves (especially, the lower margin) can sometimes be dentated, although the external surface is smooth, or has concentric ribbing (Fig. I. 8a). In many pectinids, there is a row of denticles on the edge of the byssal notch, called ctenolium (Fig. I. 14a, *cte*).

The most complex shell wall structure is observed in rudists, the group with pallial canals and/or auxiliary cavities, siphonal bands, siphonal pillars, etc.

(5) Reproduction and Ontogenetic Changes of the Soft Body and the Shell

Reproduction of bivalves occurs in various ways. In the majority of bivalves, fertilization is external, with eggs and sperm excreted in the water, where the actual fertilization and subsequent development take place. Eggs usually float freely in the water; more rarely they form accumulations and are attached to substrate (shells, algae, etc.). Some bivalves are viviparous (oysters, carditids, some freshwater species, etc.).

After cleavage, fertilized eggs form a trochoform larva, which has a bunch of long flagellae on the top, close to an equatorial band of cilia. Larvae have a digestive tract, bilobate liver, protonephridia, and sensory organs (apical tegmen and a pair of statocysts), an incipient foot, and an incipient shell represented by a single cuticular plate. This plate grows, becomes calcified, then folds into two parts to form the two valves of the primary shell (prodissoconch). At the fold, the valves are connected by a thin conchiolin film, while the ligament is still undeveloped. The hinge margin is straight. A single (anterior) adductor develops to close the valves. This is the stage of the primary prodissoconch.

After a series of transformations, the trochophore larva is transformed into a veliger, which is very similar to an adult. The nervous system and liver are well developed, the rectum is curved; the pedal, visceral ganglia, incipient gills, and the heart–pericardium complex develop. The upper part of the larva, possessing the equatorial band of cilia, is transformed into a velum (disc covered by cilia) used for movement in the water. The veliger swims with the velum on top, while the cilia of the velum are move constantly, which aids swimming in various directions.

The veliger (free-swimming larva) is a very important living stage of bivalves, which enables their wide distribution. Transformations continue in the veliger. Some larval organs disappear (fore-mouth partition, velum, larval muscles, and protonephridia), while the heart, pericardium, gills, nephridia, gonads, and labial palps develop. The foot is usually well developed even

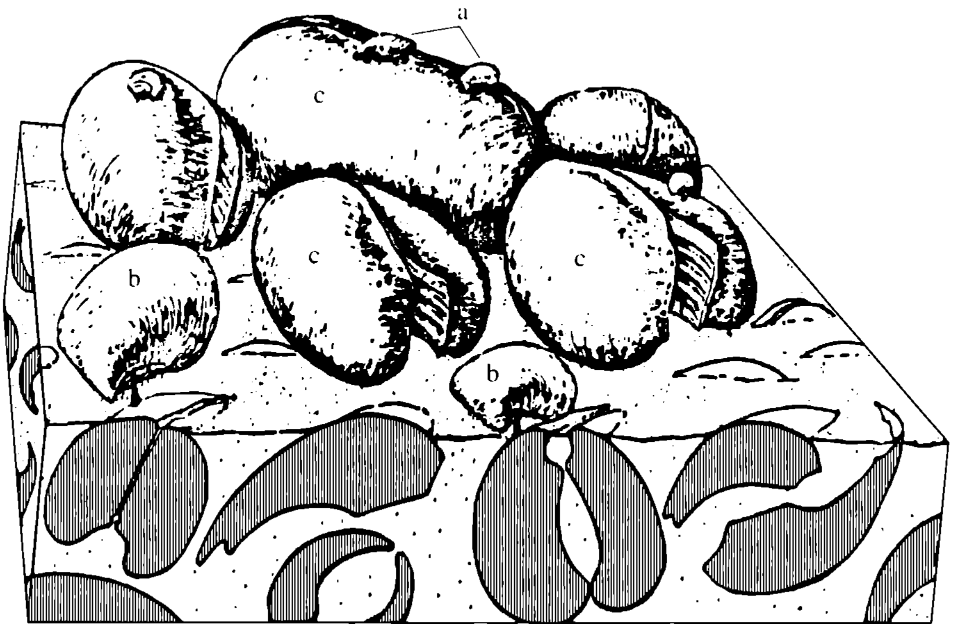


Fig. I. 24. Changes in the shell related to the changing mode of life in the ontogeny of Eocene *Pachyperna* (Isognomonidae) (after Posenato, 1995, text-fig. 8): (a) epibyssal juvenile mollusks attached to the hard substrate; (b) the same, later in ontogeny; and (c) adult recliners on the soft substrate.

in those taxa in which it is absent in adults. An incipient byssal gland appears at the base of the foot.

By the end of the metamorphosis, the larvae approach the bottom and settle to transform into young mollusks. If the appropriate substrate is absent, development may be delayed until the larvae come into contact with an appropriate region of the sea bottom.

By this time, the shell passes from the stage of the primary prodissoconch to the stage of a complete dissoconch. The previously straight hinge margin becomes arched. The shell is equivalve, with equilateral smooth valves. The second (posterior) adductor develops. Even those taxa which have only one adductor in the adult state, at this stage have two. A complete prodissoconch has a hinge that differs from that of adults and is composed of a series of small transverse denticles (provinculum), or of several tooth-shaped projections. The ligament appears. Later in ontogeny, the soft body of the mollusk acquires adult features, and the prodissoconch is replaced by the dissoconch.

As mentioned above, most bivalves have a free-swimming larval stage. However, there are species in which this stage is absent. In this case, the animal lays a few large eggs with a large amount of nutrients, which allow the eggs to develop irrespective of the presence of food in the surrounding water. This is particularly important for deep-water species, since the amount of food suitable for juveniles at the bottom is very restricted (*Osnovy paleontologii...*, 1960; Zatsepin and Filatova, 1968).

The dissoconch (the shell of mollusks that settled on substrate) can transform in ontogeny and differs considerably in juveniles and adults (Werner, 1939). This difference concerns the shape of the valves, ornamentation, hinge, ligament, degree of development of the sinus of the pallial line, and other characters.

Examples of such ontogenetic changes were obtained by studying a series of shells of different sizes belonging to the same species beginning from 0.5 mm, in some Miocene and Holocene species (Nevesskaja, 1962, 1967, 1975).

A sharp change in the shell shape (differences in inequivalve and inequilateral appearances, elongation, convexity, etc.) is particularly noticeable in species in which the adults are attached (mytilids, dreissenids, oysters, etc.) and/or in species, which are attached at early stages, and later become free lying (recliners) (Posenato, 1995) (Fig. I. 24). Ornamentation may be different in juvenile and adult shells (Tellinidae, Cardiidae, Lucinidae, etc.). The development of the ligament and hinge has been thoroughly studied in heterodont taxa. The nymph at the early stages may be absent (Veneridae, Cardiidae, and *Donax*), submerged (Carditidae), or weakly developed and short (Lucinidae, *Angulus*). Later in ontogeny, it grows and becomes longer. The ligament pit is also not developed at early stages. When it appears, it is shallow and narrow, but later gradually becomes deeper and wider (*Abra* and *Spisula*) (Fig. I. 25).

The pallial line is entire in juveniles of the species that have a sinus in adults, while the sinus appears and becomes deeper as the shell grows (Figs. I. 26A, 26B).

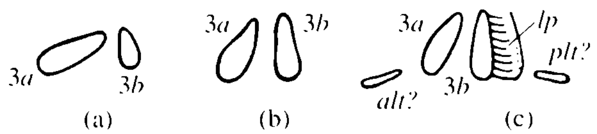


Fig. I. 25. Changes in the hinge and development of the pit to accommodate the internal ligament in the right valve of *Abra tellinoides* (Sinz.) in ontogeny, at the shell length of (a) 0.5–0.6, (b) 0.8, and (c) 2.5–3.0 (after Nevesskaja, 1975, text-fig. 9). For designations, see Fig. I. 7.

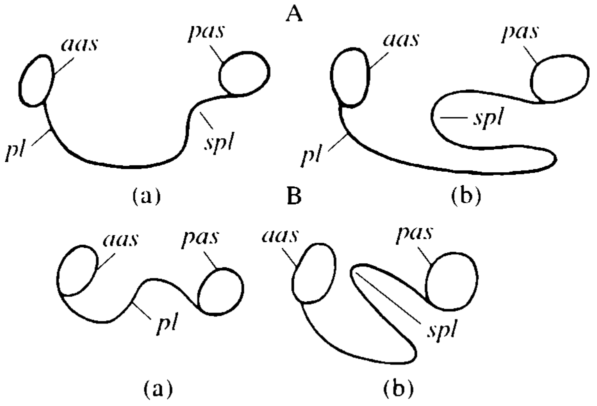


Fig. I. 26. Changes in the shape and depth of the pallial sinus as the shell grows (in mm). (A) in *Venerupis curta* (Andrus.): (a) 0.8 long and (b) in adults (after Nevesskaja, 1975, text-fig. 6); (B) in *Dosinia maeotica* (Andrus.): (a) 0.9–1.2 and (b) over 3–4 (after Nevesskaja, 1975, text-fig. 3). For designations, see Fig. I. 7.

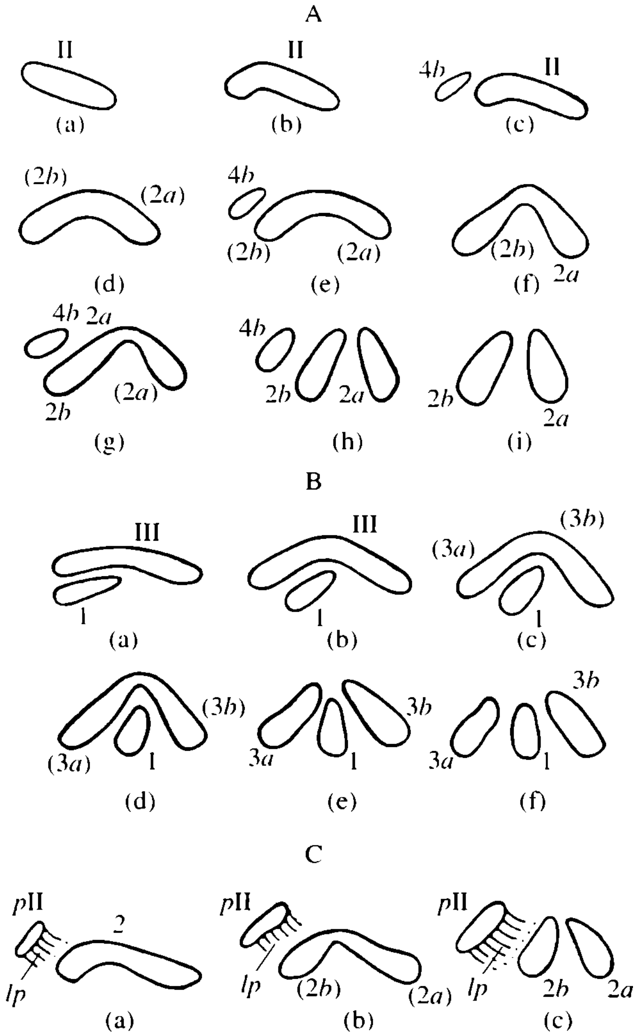


Fig. I. 27. Changes in the hinge corresponding to the increasing length of the shell (in mm): (A) left valve of *Venerupis abichi* (Andrus.): (a) 0.5–0.6, (b, c) 1, (d, e) 2–3, (f, g) 4.0–4.5, and (h, i) 5; (B) right valve of the same species: (a) 0.5–0.6, (b) 0.9–1.2, (c) 1.6–1.7, (d) 3.0–3.2, (e) 3.5–4.0, and (f) 4.2–4.5 (after Nevesskaja, 1975, text-figs. 7 and 8); and (C) left valve of *Ervilia pisilla minuta* (Sinz.): (a) 0.6–0.7, (b) 0.8–1.0, and (c) 1.2 and more (ibid., text-fig. 11). Designations: (*lp*) ligament pit.

The hinge is the structure that transforms the most. The ontogenetic development of hinges was extensively studied by Bernard (1895, 1896, 1897a, 1897b, 1897c, 1898) in a number of bivalve groups and, in some other species, by Werner (1939), Jørgensen (1946), Rees (1950), and Nevesskaja (1962, 1967, 1975).

Differences in the ontogenetic development of the hinge in Miocene and Holocene bivalves were studied in species belonging to different families of the orders Venerida (Veneridae, Cardiidae, Tellinidae, Mactridae, Donacidae, and Scrobiculariidae) and Astartida (Lucinidae), which have a heterodont hinge. In all the taxa studied, teeth appeared early in ontogeny (from 0.4 mm of body length, the hinge was composed of primary dental plates (Veneridae), or separate lateral and cardinal teeth, or was of mixed type (plates later developing in teeth, and teeth themselves). The provinculum, in all species studied, was developed only at very early stages (before 0.4 mm). The stage of primary plates in heterodont taxa was observed in the hinge of the Veneridae (Figs. I. 27A, 27B), the genera *Monodacna* and *Adacna* (Cardiidae), *Loripes* (Lucinidae), *Spisula* and *Ervilla* (Fig. I. 27C) (Matcroidea). Sometimes, this stage may be absent, and the cardinal and lateral teeth appear in ontogeny as new formations and are independent of each other.

Among mytilids (order Cyrtodontida), the provinculum stage in some species (*Mytilus galloprovincialis* and *Mytilaster volhynicus*) was observed when the shell was 0.4 mm high. Later, the teeth of the provinculum disappear to be replaced by tooth-shaped projections at a shell height of 1 mm. In *Modiolus phaseolinus*, *M. adriaticus*, and *Mytilaster lineatus*, the stage of the provinculum is preceded by the stage of a smooth hinge line. The provinculum appears in shells when those become 0.6–0.8 mm high. It disappears at a height of

1 mm, and is often retained even in adults (Nevesskaja, 1962, 1975).

CHAPTER II. SYSTEM OF BIVALVES

The name *bivalves* (in Greek script) was first used by Aristotle in the 4th century B.C. Linnaeus (1758, p. 645) used this name (in Latin script) and defined the group as a subdivision Bivalvia of the group Testacea of the Class Vermes (Vermes: Testacea: Bivalvia). Linnaeus did not subdivide the group further.

Later, various researchers used a broad variety of characters as a basis for classification of this group. This included the hinge (Martini, 1773), the symmetry of the shell (Bruguiere, 1792), differences between the valves (Lamarck, 1799, 1801), the number of adductors (Lamarck, 1818), the degree of the openness of the mantle (Latreille, 1825), the development of the siphons (Fleming, 1828; Orbigny, 1843; Woodward, 1851–1856; 1875; Hoernes, 1884), morphology of the foot (Gray, 1847), and the gill structure (Fischer, 1897).

The most popular systems from the end of the 19th century were those of Neumayr (1833, 1891) based on the hinge and Pelseneer (1889, 1891, 1906) based on the gills. According to Neumayr, bivalves included six orders: Paleoconcha (Cryptodonta), Desmodonta, Taxodonta, Heterodonta, Dysodonta (or Anisomyaria), and Schizodonta. According to Pelseneer, they included five orders (Protobranchia, Filibranchia, Eulamellibranchia, Pseudolamellibranchia, and Septibranchia).

Most paleontologists (e.g., Zittel, 1881–1885; Borissyak, 1899; Yakovlev, 1925; Pavlova, 1927; Davitashvili, 1949; Dechaseaux, 1952; Korobkov, 1954) accepted Neumayr's system. Thiele (1925, 1935), dealing with both extinct and modern bivalves, tried to unify Neumayr's and Pelseneer's systems and proposed three orders, Taxodonta, Anisomyaria, and Eulamellibranchia. The last order was subdivided into four suborders (Schizodonta, Heterodonta, Adapedonta, and Anomalodesmata). Thus, Thiele's system was based on both the structure of the hinge and the characters of the soft body (development of adductors, structure of gills, etc.).

In 1960 two systems were published (one in *Osnovy paleontologii...*, 1960) and one by Cox (1960).

The system used in *Osnovy paleontologii...* (1960) was based on the hinge and on the evolutionary history of bivalves. The class was subdivided into six orders (Taxodonta, Anisomyaria, Schizodonta, Heterodonta, Desmodonta, and Rudistae). The order Taxodonta includes bivalves with the taxodont hinge, i.e., with numerous, usually identical, teeth arranged in a single row. The order includes two suborders (Palaeotaxodonta (= Ctenodonta) and Neotaxodonta (= Pseudoctenodonta). The order Anisomyaria includes bivalves with a weakly developed anterior adductor, and usually with the edentulous hinge. The order Schizodonta is characterized by the schizodont hinge. The order Heterodonta includes bivalves with the heterodont hinge composed of cardinal and lateral teeth. The order Desmodonta includes bivalves with weakly developed teeth, but with a well-developed internal ligament lying on special protrusions. The order Rudista includes distinctive, usually attached bivalves with the pachyodont hinge.

The system of Cox (1960) was based on the hypothesis of Douvillé (1912) of three primary directions of adaptive radiation of bivalves that led to three lineages: (1) normal, i.e., retaining active movement; (2) sessile; and (3) burrowing. In this system, the class includes three subclasses. The subclass Protobranchia comprises the most primitive and probably ancestral bivalve group with the taxodont and cryptodont hinges (including a large portion of the so-called normal lineage after Douvillé). The second subclass Pteriomorphia includes the representatives of the sessile group sensu Douvillé, and the third subclass Heteroconchia includes the burrowing lineage and the remaining part of the normal lineage recognized by Douvillé. Merklin (1962, 1965) made several changes to the system. For instance, he suggested that the burrowing group Desmodonta (Eudesmodontida and Asthenodontida after Cox) and the sessile Pachyodontida of the class Heteronchia be assigned to separate subclasses, so that the organization of the higher taxa would reflect phylogeny.

Newell (1965a) and Vokes (1967) proposed a new Bivalvia system for the *Treatise on Invertebrate Paleontology*. This system was accepted in *Treatise...* (1969). These authors proposed the subdivision of Bivalvia into six subclasses (Palaeotaxodonta, Cryptodonta, Pteriomorphia, Palaeoheterodonta, Heterodonta, and Anomalodesmata), which were represented by 15 orders. This system is also based primarily on the hinge structure; however, it takes into account the morphology of the shell wall and the soft body (gills, siphons, and mantle). Because of this, the polyphyletic orders Taxodonta and Desmodonta, which had been established based on the hinge in *Osnovy paleontologii...*, were subdivided. Taxa belonging to the Taxodonta were transferred to the Palaeotaxodonta and Pteriomorpha, while those belonging to the Desmodonta were transferred to the Heterodonta (Myoida), Anomalodesmata (Pholadomyoida), and Cryptodonta (Solemyoida).

The bivalve system proposed by the zoologist Purchon is based on characters of the digestive system. The first variant of the system (Purchon, 1963) was considerably different from that published later (Purchon, 1987b). According to the latter system, the class bivalvia consists of two subclasses: Protobranchia, including the orders Nuculoida and Solemyoida, and Lamellibranchia with the orders Pteriomorpha, Mesosyntheta (suborders Trigonoida and Unionoida), Anomalodesmata (suborders Pholadomyoida and Septibranchia), and Gastropemta (suborders Pholadomyoida and

Septibranchia), and Gastropempta (suborders Veneroida and Myoida).

A review of the above data shows that, right back to the period of Cuvier and Lamark, the classification of bivalves was based on a wide variety of characters, including the shape and relative position of the valves, extent of the fusion of the mantle lobes, structure of the siphons, number of adductors, presence or absence of the sinus of the pallial line, shape of the foot, type and position of the ligament, type of the hinge, gill structure, and the structure of the digestive system.

It is noteworthy that systems based on soft body anatomy (Pelseneer, 1906; Purchon, 1959, 1963, etc.) differed considerably from the systems based on the shell (Neumayr, 1883; *Osnovy paleontologii...*, 1960; etc.). This may be because the characters on which these systems are based developed at different rates, resulting in a mosaic type of evolution. The presence of many parallel lineages has also complicated natural systematics (Newell, 1965a; Purchon and Brown, 1969).

Attempts to use ecological characters in bivalve taxonomy (Douvillé, 1912; Cox, 1960; Merklin, 1962, 1965) have provided correct recognition of major evolutionary trends, but could not provide reliable criteria for the separation of parallel lineages.

Systems presently used by malacologists and published in major reference books (Thiele, 1935; Dechaseaux in Pivetaux, 1952; Korobkov, 1954; *Osnovy paleontologii...*, 1960; Fedotov, 1960; *Zhizn' zhivotnykh*, vol. 2, 1968; *Treatise...*, 1969) mainly belong to the so-called conchological systematics, although there are some meeting points with the so-called anatomical systems. The only way to resolve the contradictions between these two approaches and to produce an integrated system for both extinct and extant bivalves is to incorporate all features in phylogenetic reconstructions. This may reveal instances of parallel and convergent evolution of similar characters of the soft body and the shell.

An attempt at such a synthesized study of all important morphological traits of the gills, digestive system, and hinge, taking into account the phylogeny of particular bivalvian groups, was undertaken by the zoologists O.A. Skarlato and Ya.I. Starobogatov and the paleontologists A.G. Eberzin and L.A. Nevesskaja (Nevesskaja *et al.*, 1971; Skarlato and Starobogatov, 1975, 1979).

As a result of this revision, three superorders were recognized within the class Bivalvia (Protobranchia, Autobranchia, and Septibranchia).

The superorder Protobranchia (= Nuculiformii Starobogatov, 1992) is characterized by the following features: the gills are represented by a primitive bifoliate ctenidium, with relatively short gill lamellae; the labial palps are adapted for conducting food; a primitive stomach has a few (two or three) liver ducts, large and small tiflosoles not entering the stomach, numerous and intensely branching diverticles; the foot has a flat sole and lacks a byssus. The pelagic larva is of the endolarval type, i.e., its body is surrounded by expanded outgrowths of the upper hemisphere with several bands of cilia. The hinge is primary taxodont (ctenodont) or edentate. This group includes debris-feeders (scavengers and substrate-feeders).

The superorder Autobranchia (= Mytiliformii Starobogatov, 1992) including Flibranchia and Eulamellibranchia, is characterized by the following set of characters. The gills are transformed into a filtering sieve with strongly elongated lamellae composed of ascending and descending branches. The labial palps conduct the food particles from the gills into the mouth. The sorting structures of the stomach are well developed. The tiflosole is large and extends deep into the stomach. The liver has many ducts. The foot is wedge-shaped without a flat platform. The byssal gland is often present. The larval stage is represented by the trochophore and veliger. The hinge is preheterodont, heterodont, dysodont, and desmodont. The group includes suspension-feeders and scavengers–substrate-feeders. In the latter case, in contrast to the previous suborder, the food particles are filtered in the gills.

In the representatives of the suborder Septibranchia (= Conocardiiformii Starobogatov, 1992) the gills are transformed into a septum, i.e., a membranous pump powered by muscle contractions. The labial palps conduct relatively large food particles from the subseptal space to the mouth. The stomach is covered by a chitinous film, which also covers the sorting field. The liver is composed of a few diverticles and has two exits into the stomach. The foot is wedge-shaped and has a longitudinal groove. The larva is throchophore and veliger. The hinge is desmodont and reduced. The group is predatory.

These three superorders are readily distinguished, although they should not be regarded as subclasses, because of the similar organization typical of all Bivalvia.

Thirteen orders are distinguished within these three superorders. Protobranchia includes Ctenodontida (= Nuculida) and Solemyida. Autobranchia includes Actinodontida (= Unionida), Cyrtodontida (= Mytilida), Pectinida, Pholadomyida, Hippuritida, Astartida (= Lucinida), Carditida, and Venerida. Septibranchia includes Verticardiida, Poromyida, and Cuspidariida (Fig. II. 1).

Unlike in *Osnovy paleontologii...* (1960), the orders Ctenodontida (suborder Palaeotaxodonta of the order Taxodonta after *Osnovy...*) and Solemyida (= superfamily Solemyacea of the order Desmodonta after *Osnovy...*) are assigned to the superorder Protobranchia. The necessity of such assignment was clearly outlined by Cox, whereas an extensive study of modern Protobranchia, both with a ctenodont hinge (*Nuculoidea*, Malletioidea, and Nuculanoidea) and without it (Solemyoidea and Manzenelloidea) showed that these groups are similar in the structure of the gills and stomach. Some Solemyida (Manzenelloidea) are similar to

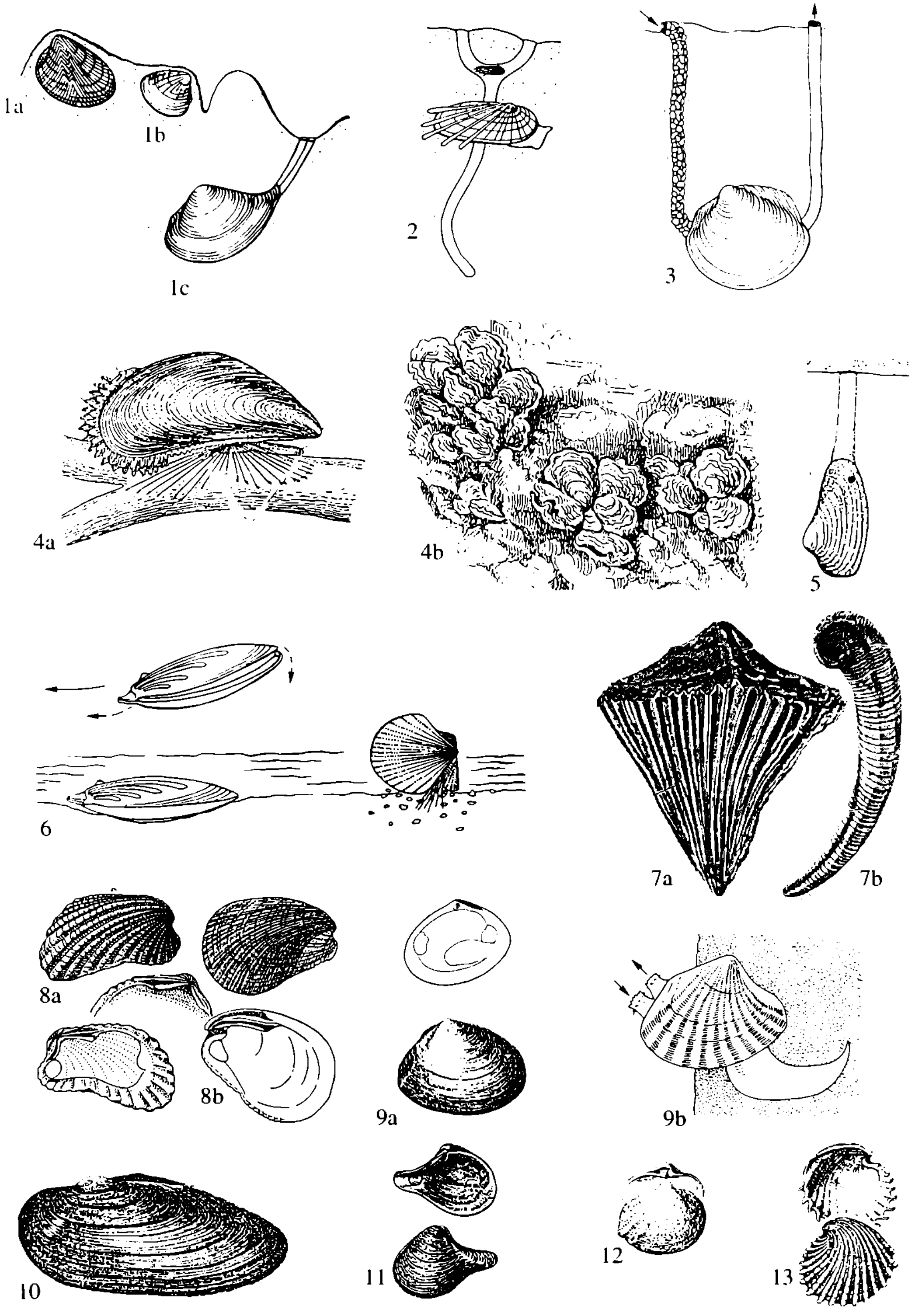


Fig. II. 1. Representatives of different orders of Bivalvia: (1) order Ctenodontida: (a) *Acila*, (b) *Nucula*, and (c) *Nuculana*; (2) order Solemyida: *Solemya*; (3) order Astartida: *Lucinoma*; (4) order Cyrtodontida: (a) *Mytilus* and (b) *Ostrea*; (5) order Pholadomyida: *Pleuromya*; (6) order Pectinida: Pectinidae; (7) order Hippuritida: (a) *Radiolites* and (b) *Caprinuloidea*; (8) order Carditida: (a) *Cardita* and (b) *Beguina*; (9) order Venerida: (a) *Macoma* and (b) *Didacna*; (10) order Actinodontida: *Unio*; (11) order Cuspidariida: *Cuspidaria*; (12) order Poromyida: *Poromya*; and (13) order Verticordiida: *Vericordia*.

Table II. 1. Classification of bivalves and quantitative distribution of the number of genera in the families throughout time

	€	O$_1$	O$_{2-3}$	S	D	C	P	T$_1$	T$_{2-3}$	J	K$_1$	K$_2$	Ꝑ$_1$	Ꝑ$_2$	Ꝑ$_3$	N$_1$	N$_2$	Q	Recent	Total number of genera
Superorder indet.																				
Order indet.																				
Family Arhouriellidae Geyer et Streng, 1998	1																			1
Superorder Protobranchia																				
Order Ctenodontida (=Nuculida, Nuculoida)																				
Superfamily Ctenodontoidea Wörmann, 1893																				
Family Praenuculidae McAllester, 1969	?1–2	6	13	3	2															20
Family Ctenodontidae Wörmann, 1893		1	4	1	5	1	1				?1	?1	?1	?1	?1					9–10
? Family Isoarcidae Keen, 1962										1	1	1								1
? Family Tindariidae Scarlato et Starobogatov, 1979													1	1	1	1	1	1	1	1
Superfamily Glyptarcoidea Cope, 1996																				
Family Glyptarcidae Cope, 1996		1	1																	
Superfamily Nuculoidea Gray, 1824																				
Family Tironuculidae Babin, 1982		3	1																	3
Family Nuculidae Gray, 1824			1	1	2	1	1	3	3	3	3	3	3	4	5	6	6	6	6	13
Superfamily Malletioidea H. et A. Adams, 1857																				
Family Malletiidae H. et A. Adams, 1857			10	7	5	1	2	3	6	6	3	3	4	4	4	4	4	4	8	33
Family Cadomiidae Scarlato et Starobogatov, 1979			2	2																4
? Family Thoraliidae Morris, 1980		1																		1
Superfamily Nuculanoidea H. et A. Adams, 1858																				
Family Nuculanidea H. et A. Adams, 1858					1	2	2	4	3	4	4	8	7	14	16	15	16	14	24	37
Family Saturnidae Allen et Hannah, 1986													1	1	1	1	1	1	4	4
Family Adranidae Scarlato et Starobogatov, 1979														1	1	1	1	1	1	1
Family Poroledidae Scarlato et Starobogatov, 1979																			2	2
Superfamily Sareptoidea A. Adams, 1860																				
Family Sareptidea A. Adams, 1860								1	1	1	1	1	1	1	1	1	1	1	1	1
Family Zealedidae Scarlato et Starobogatov, 1979															1	1	1	1	1	1

Table II. 1. (Contd.)

	€	O$_1$	O$_{2-3}$	S	D	C	P	T$_1$	T$_{2-3}$	J	K$_1$	K$_2$	₽$_1$	₽$_2$	₽$_3$	N$_1$	N$_2$	Q	Recent	Total number of genera
Family Pristiglomidae Sanders et Allen, 1973																			3	3
Superfamily Phaseoloidea Scarlato et Starobogatov, 1971																				
Family Phaseolidae Scarlato et Starobo-gatov, 1971																			1	1
Family Siliculidae Allen et Sanders, 1973																			2	2
Family Lametilidae Allen et Sanders, 1973																			1–2	1–2
Superfamily Radiidentoidea Egorova et Starobogatov, 1975																				
Family Radiidentidae Egorova et Starobogatov, 1975																			1	1
Order Solemyida																				
Superfamily Solemyoidea H. et A. Adams, 1857																				
Family Solemyidae H. et A. Adams, 1857		1	2	4	3	3	6	2	2	?	?	?	1	1	1	2	2	2	2	7–8
Superfamily Acharacoidea Scarlato et Starobogatov, 1979																				
Family Acharacidae Scarlato et Starobogatov, 1979					1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Superfamily Manzanelloidea Chronic, 1952																				
Family Manzanellidae Chronic, 1952							1													1
Family Nucinellidae Vokes, 1956										1	1	1	1	2	2	2	2	2	2	3
Superorder Autobranchia																				
Order Fordilloida																				
Superfamily Fordilloidea Pojeta, 1975																				
Family Fordillidae Pojeta, 1975	1	?	1																	2
Order Actinodontida (=Unionida)																				
Superfamily Lyrodesmatoidea Ulrich, 1894																				
Family Lyrodesmatidae Ulrich, 1894		4	3																	4
Superfamily Cycloconchoidea Ulrich, 1884 (=Actinodontoidea Douvillé, 1912)																				
Family Cycloconchidae Ulrich, 1884		6–8	3–4	1																8
Family Babinkidae Horny, 1960		1	1																	1

Table II. 1. (Contd.)

	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q	Recent	Total number of genera
Family Redoniidae Babin, 1966		2	2																	3
Family Allodesmatidae Dall, 1895			2	1																3
Family Ischirodontidae Scarlato et Starobogatov, 1979			1																	1
Superfamily Modiomorphoidea Miller, 1977																				
Family Modiomorphidae Miller, 1977		5–7	20–26	10–13	10–14	4	5													32–42
Family Coxiconchidae Babin, 1977		1	1																	1
?Family Kinerkaellidae Betekhtina, 1972						2–3	3–5													5–7
?Family Abiellidae Starobogatov, 1970						3	5	1	1	1										7
?Family Prilukiellidae Starobogatov, 1970 (=Microdontidae Weir, 1969)							6													6
Superfamily Palaeoanodontoidea Modell, 1964																				
Family Palaeoanodontidae Modell, 1964 (=Palaeomutelidae Weir, 1967)						?1	5	1												6–7
Family Sinomyidae Scarlato et Starobogatov, 1979							1													1
Superfamily Actinodontophoidea Newell, 1969																				
Family Actinodontophidae Newell, 1969							1	1	1											1
Family Tanaodontidae Scarlato et Starobogatov, 1979					1															1
Superfamily Anthracosioidea Amalizki, 1842 (=Nyassoidea Hall, 1885)																				
Family Nyassidae Hall, 1885					1															1
Family Anthracosiidae Amalitzki, 1842						3–7	2–4													5–8
Family Archanodontidae Modell, 1942							1													1
Superfamily Trigonoidea Lamarck, 1819																				
Family Schizodidae Newell et Boyd, 1975				1	1	1	1													2
Family Myophoriidae Brown, 1849					4–5	1	4	4	6	1?										13–15
Family Trigoniidae Lamarck, 1819							1	?	9	18	21	21	1	1	2	2	2	1	1	~50
Family Scaphellinidae Newell et Ciriack, 1962							1													1

Table II. 1. (Contd.)

	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	Ꝑ_1	Ꝑ_2	Ꝑ_3	N_1	N_2	Q	Recent	Total number of genera
Superfamily Carydiodea Haffer, 1959																				
Family Carydiidae Haffer, 1959					1															1
Superfamily Trigonodoidea Modell, 1942																				
Family Trigonodoidae Modell, 1942 (=Pachycardiidae Cox, 1961)							1	2	5–6	2										8–9
Family Desertellidae Deshaseaux, 1946											1									1
Superfamily Unionoidea Rafinesque, 1820																				
Family Unionidae Rafinesque, 1820									1	4	8	13	13	11	23	24	27	43	108	130
Family Margaritiferiidae Henderson, 1929									1	2	3	3	1	1	1	1	1	1	1	4
Family Trigonioididae Cox, 1952											3	6								6
Family Pseudohyriidae Kobayashi, 1968											2	3								3
Superfamily Etherioidea Deshayes, 1830																				
Family Mutelidae Swainson, 1840												1	3	3	3	3	4	5	14	14
Family Etheridae Deshayes, 1830																	1	1	3	3
Superfamily Gastrochaenoidea Gray, 1840																				
Family Gastrochaenidae Gray, 1840										2	1	1	1	3	2	2	2	2	2	4
Order Cyrtodontida (=Mytilida)																				
Superfamily Ambonychioidea Miller, 1877																				
Family Ambonychiidae Miller, 1877		1	13	3–4	6–10	2–4														20–26
Family Monopteriidae Newell, 1969						1														1
Family Naiaditidae Scarlato et Starobogatov, 1979						2	3													3
Family Myaliniidae Frech, 1891					?	8–10	8–9	3	2–3	1–2										14–20
Family Eurydesmatidae Reed, 1932							1													1
Family Atomodesmatidae Waterhouse, 1976							6	1												6
Family Procopievskiidae Ragozin, 1933							2													2
Superfamily Falcatodontoidea Cope, 1996																				
Family Falcatodontidae Cope, 1996		1																		1
Superfamily Pterioidea Gray, 1847																				
Family Pterineidae Miller, 1877		?2	5–8	10–12	12	5	4–5													22–29

Table II. 1. (Contd.)

	€	O$_1$	O$_{2-3}$	S	D	C	P	T$_1$	T$_{2-3}$	J	K$_1$	K$_2$	₽$_1$	₽$_2$	₽$_3$	N$_1$	N$_2$	Q	Recent	Total number of genera
?Family Kochiidae Mailieux, 1931				1																1
Family Kolymiidae Kuznezov, 1973							1													1
Family Pteriidae Gray, 1847									4–6	3	2	3	2	2	2	3	3	3	3	9–11
Superfamily Arcoidea Lamarck, 1809																				
Family Parallelodontidae Dall, 1898		1	1	1	1	3–4	1	1	4	5–6	3	5	?	2	1	1	1	1	2	14–16
Family Frejidae Ratter et Cope, 1998				4																4
Family Arcidae Lamarck, 1809										2	2	4	4	5	7	7	7	7	11	11–12
Family Cucullaeidae Stewart, 1930										4	4	1	1	2	2	2	2	2	2	4
Family Noetiidae Stewart, 1930											2	6	4	8	4	4	4	4	4	13
Superfamily Praecardioidea Hoernes, 1884																				
Family Praecardiidae Hoernes, 1884			1	5	2	1														5
Family Cardiolidae Fischer, 1886				12–13	1–2															12–13
?Family Palaeocardiidae Scarlato et Starobogatov, 1979				2																2
Superfamily Cyrtodontoidea Ulrich, 1894																				
Family Cyrtodontidae Ulrich, 1894		3	8	3–4	1															10–11
Family Matheriidae Scarlato et Starobogatov, 1979			2	1	2															2
Superfamily Antipleuridoidea Neumayr, 1891																				
Family Antipleuridae Neumayr, 1891			3	5	3															8
Family Dexiobiidae Newell et La Rocque, 1969				?1		1														1–2
Superfamily Myodacryotoidea Tunnecliff, 1987																				
Family Myodakryotidae Tunnecliff, 1987			1																	1
Superfamily Lunulacardioidea Fischer, 1887																				
Family Lunulacardiidae Fischer, 1887			3	8	3	1														10
Superfamily Leiopectinoidea Krasilova, 1952 (=Rhombopterioidea Korobkov, 1960)																				
Family Rhombopteriidae Korobkov, 1960*			1	1																1

*Johnson (1993) assigned this form to the Osteidae; however, the presence of two adductors is in conflict with this assignment.

Table II. 1. (Contd.)

	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	Ꝑ$_1$	Ꝑ$_2$	Ꝑ$_3$	N_1	N_2	Q	Recent	Total number of genera
Family Leiopectinidae Krasilova, 1952				3	3															3
Superfamily Posidonioidea Frech, 1909																				
Family Pterinopectinidae Newell, 1938				1	5	4	3	4												9
Family Posidoniidae Frech, 1909						1	1	2	12	6	1	1								18
Family Deltopectinidae Dickins, 1957						2	4													6
Family Oxytomidae Ichikawa, 1958							1	?	2	4	4	1								7–8
?Superfamily Umburroidea Johnston, 1991																				
Family Umburridae Johnston, 1991				1																1
Superfamily Aviculopectinoidea Meek et Hayden, 1864																				
Family Aviculopectinidae Meek et Hayden, 1864					3	20	17	3	8	1										30
Family Crenopectinidae Scarlato et Starobogatov, 1979					1															1
Family Pseudomonotidae Newell, 1938						2	3	?	2											6
?Family Chaenocardiidae Miller, 1889						7	3	1	2											8
Family Monotidae Fischer, 1887								1	1–2											2–3
Superfamily Mytiloidea Rafinesque, 1815																				
Family Mytilidae Rafinesque, 1815					1–3	3	3–4	2	6	15	11	11	13	20	18	22	20	21	40	55–58
Superfamily Pinnoidea Leach, 1819																				
Family Pinnidae Leach, 1819						?1	?1	?1	?1	4	4	3	3	3	3	3	3	3	4	7
Superfamily Isognomonoidea Woodring, 1825 (=Bakevellioidea King, 1850)																				
Family Cassianellidae Ichikawa, 1958							1	2	7	1										7
Family Isognomonidae Woodring, 1825							1	1	3–4	4	3	1	1	2	1	2	2	2	2	7–8
Family Bakevellidae King, 1850							?1	2	8	10	12	10–11	?	1						17–18
Family Dattidae Healey, 1908									1											1
Superfamily Mysidielloidea Cox, 1964																				
Family Mysidiellidae Cox, 1964								2	4											4
Family Pergamiidae Cox, 1964									3	2	1									4
Superfamily Inoceramoidea Giebel, 1852																				
Family Inoceramidae Giebel, 1852							3	2	10	3–4	8				?					16–18

Table II. 1. (Contd.)

	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q	Recent	Total number of genera
Superfamily Buchioidea Cox, 1953																				
Family Buchiidae Cox, 1953								1	2–3	5	2	3								9–10
Superfamily Limopsoidea Dall, 1895																				
Family Limopsidae Dall, 1895									2	1	1	1	1–2	1–2	1–2	1–2	2–3	2	6	5–6
Family Phylobryidae Bernard, 1897														2	1	2	3	4	4	5
Family Aupouriidae Scarlato et Starobogatov, 1979																	1	1	1	1
Superfamily Ostreoidea Rafinesque, 1815																				
Family Ostreidae Rafinesque, 1815									2	3	2	10	7	13–14	10–11	6	6	6	6	21–22
Superfamily Gryphaeoidea Vialov, 1936																				
Family Gryphaeidae Vialov, 1936										5	9	12	4–5	4–5	4–5	4	2	2	2	21–22
Superfamily Malleoidea Lamarck, 1819																				
Family Malleidae Lamarck, 1819										1	?	8	5	8	3	3	1	1	2	14
Family Pulvinitidae Stephenson, 1941										3	2	2	2	?	?	?	?	?	1	3
Superfamily Glycymeroidea Newton, 1922																				
Family Glycymeridae Newton, 1922											2	7	1	1	1	2	3	3	5	10
Superfamily Limarcoidea Scarlato et Starobogatov, 1979																				
Family Limarcidae Scarlato et Starobogatov, 1979														1	?	?1	?1	?1	?1	1–2
?Superfamily Antactinodontoidea Guo, 1980																				
Family Antactinodontidae Guo, 1980					3															3
Order Pectinida																				
Superfamily Pernopectinoidea Newell, 1938																				
Family Entoliidae Korobkov, 1960 (=Pernopectinidae Newell, 1938)						1	1	3	5	5–6	1	3–4								9–11
Family Propeamussiidae Abbot, 1954										1	1	1	1	1	1	1	1	1	1	1
Superfamily Limoidea (=Limarioidea) Rafinesque, 1815																				
Family Limidae (=Limariidae) Rafinesque, 1815						1	3–4	4–5	10–12	10	5	6	6	6–7	6	6	6	6	7	18–20
Family Terquemiidae Cox, 1964							1	1	4–5	1–2	?1	?1								4–6

Table II. 1. (Contd.)

	Є	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q	Recent	Total number of genera
Family Dianchoridae Sobetski, 1977									1	1	1	2								2
?Family Chondrodontidae Freneix, 1959											1	1								1
Superfamily Anomioidea Rafinesque, 1815																				
Family Anomiidae Rafinesque, 1815							1	?	?	2	1	2	1	3–5	4	5	4	4	5–6	9–12
Family Placunidae Gray, 1840														1	1	1	1	1	1	1
Superfamily Pectinoidea Rafinesque, 1815																				
Family Pectinidae Rafinesque, 1815						?		2	11–12	18	8	7	5	8	10	24	23	17	19	56–58
Superfamily Plicatuloidea Watson, 1930																				
Family Atretidae Scarlato et Starobogatov, 1979								1	1	1	1	1								1
Family Plicatulidae Watson, 1930									2	2	2	2	1	1	1	1	2	1	2	3
Superfamily Dimyoidea Fischer, 1886																				
Family Dimyidae Fischer, 1886									1	1	1	1	1	2	2	1	2	1	3	5
Superfamily Spondyloidea Gray, 1826																				
Family Spondylidae Gray, 1826										1	1	1	1	1	1	1	1	1	1	1
Order Pholadomyida																				
Superfamily Grammysioidea Miller, 1877																				
Family Grammysiidae Miller, 1877		1	1	2–3	6–10	6–9	9–13	1	1–2											13–21
Superfamily Orthonotoidea Miller, 1877																				
Family Orthonotidae Miller, 1877			4	1	2															4
Superfamily Edmondioidea King, 1850																				
Family Edmondiidae King, 1850					2	6	3													7
Family Megadesmidae Vokes, 1967						1	4–5	1												4–5
Superfamily Pholadomyoidea Gray, 1847																				
Family Pholadellidae Miller, 1877					1	1														1
Family Pholadomyidae Gray, 1847						8	11–12	1	5–6	11	4	4	3	4–5	1	1	1	1	3	28–31
Superfamily Pleuromyoidea Zittel, 1881																				
Family Ceratomyidae Arkell, 1934								1	3	3–4						?				4–6
Family Pleuromyidae Zitell, 1887									1	1	1	1	1	1	1	1	1	1	1	1

Table II. 1. (Contd.)

	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₱$_1$	₱$_2$	₱$_3$	N_1	N_2	Q	Recent	Total number of genera
Family Burmesiidae Healey, 1908									3	1										3
Family Myopholadidae Cox, 1964										1	1									1
Superfamily Cercomyoidea Crickmay, 1936																				
Family Cercomyidae Crickmay, 1936									1	1	1	1								1
Superfamily Myochamoidea Bronn, 1862																				
Family Laternulidae Hedley, 1918										3	3	4	1	1	2	2	2	2	5	9
Family Periplomatidae Dall, 1895												2	2	2	2	2	2	2	2	3
Family Lyonsiidae Fischer, 1877														2	1	1	1	1	2	3
Family Myochamidae Bronn, 1862																2	2	2	2	2
Family Margaritariidae Vokes, 1964																1				1
Superfamily Thracioidea Stolizka, 1870																				
Family Thraciidae Stolizka, 1870										1	1	1	1	1	2	3	3	4	8	8
Superfamily Pandoroidea Rafinesque, 1815																				
Family Pandoridae Rafinesque, 1815												1	1	1	1	1	1	1	1	1
Family Cleidothaeriidae Hedley, 1918												?1	1	1	1	1	1	1	1	1
Superfamily Clavagelloidea Orbigny, 1843																				
Family Clavagellidae Orbigny, 1843												1	1	1	1	2	2	2	5	5
Superfamily Penicilloidea Scarlato et Starobogatov, 1971																				
Family Penicillidae Scarlato et Starobogatov, 1971																1	1	1	1	1
Family Humphreyidae Scarlato et Starobogatov, 1979																			1	1
Order Hippuritida																				
Superfamily Megalodontoidea Morris et Lycett, 1853																				
Family Megalodontidae Morris et Lycett, 1853		1	1	1	3	1	1	1	7–8	3										13–15
Family Tusayanidae Scarlato et Starobogatov, 1979					1															1
Family Dicerocarditidae Kutassy, 1934									3	2	2	3								9
?Family Pterocardiidae Scarlato et Starobogatov, 1979										1	1									1

Table II. 1. (Contd.)

	€	O$_1$	O$_{2-3}$	S	D	C	P	T$_1$	T$_{2-3}$	J	K$_1$	K$_2$	₽$_1$	₽$_2$	₽$_3$	N$_1$	N$_2$	Q	Recent	Total number of genera
Superfamily Caprotinoidea Gray, 1848																				
Family Diceratidae Dall, 1895										6	1	1								6
Family Monopleuridae Munier-Chalmas, 1873										1	3	7								8–9
?Family Lithiotidae Reis, 1903										1										1
Family Caprotinidae Gray, 1848											8	6								8
Family Caprinidae Orbigny, 1850											10	18								24
Superfamily Requienioidea Douvillé, 1814																				
Family Requieniidae Douvillé, 1814										1	4	7								8
Family Epidiceratidae Rengarten, 1950											3	3								3
Superfamily Hippuritoidea Gray, 1848																				
?Family Plicatostilidae Lupher et Packard, 1930											1									1
Family Radiolitidae Gray, 1848											6	38								38
Family Hippuritidae Gray, 1848												16								16
Superfamily Arcinelloidea Scarlato et Starobogatov, 1971																				
Family Arcinellidae Scarlato et Starobogatov, 1971																1	1	1	1	1
Order Astartida																				
Superfamily Astartoidea Orbigny, 1844																				
Family Cardiniidae Zittel, 1881			1	1	1	1	1	1	5–6	4										11–12
Family Astartidae Orbigny, 1844					3	2	5	1	4	18	12	15	7	7	5	5	5	6	6	40
Family Opidae Chavan, 1952					1	?	?	1	?	5	3									7
Family Myophoricardiidae Chavan, 1867								1	3											3
Superfamily Mactromyoidea Cox, 1929																				
Family Mactromyidae Cox, 1929				1	1	1–2	1	?	?	4	2	4	?	?	1	?	?	?	1	11–12
Family Montanariidae Scarlato et Starobogatov, 1979					1															1
Family Fimbriidae Nicol, 1950						1	?	?	1	4	2	2	1	2	1	1	1	1	1	9
Superfamily Lucinoidea Fleming, 1828																				
Family Ilionidae Scarlato et Starobogatov, 1979				1	1															2

Table II. 1. (Contd.)

	€	O$_1$	O$_{2-3}$	S	D	C	P	T$_1$	T$_{2-3}$	J	K$_1$	K$_2$	Ꝑ$_1$	Ꝑ$_2$	Ꝑ$_3$	N$_1$	N$_2$	Q	Recent	Total number of genera
Family Thyasiridae Dall, 1901									1	?	1	1	1	1	1	2	5	7	8	10
Family Lucinidae Fleming, 1828										8–9	9	9	19	34	34	38	31	33	35	51–52
Superfamily Crassatelloidea Férussak, 1822																				
Family Crassatellidae Férussac, 1822					1	2	1	?	?	?	4	4	4	5	5	6	6	6	9	9
Superfamily Hiatelloidea Gray, 1824																				
Family Hippopodidae Cox, 1969					?1					1										1–2
Family Hiatellidae Gray, 1824										2	2	2	4	4	5	5	5	4	4	5
Superfamily Pseudocardinioidea Martinson, 1961																				
Family Pseudocardiniidae Martinson, 1961									1	10–16										11–17
Family Ferganoconchidae Martinson, 1961										1										1
Superfamily Donacoidea Fleming, 1828																				
Family Tancrediidae Meek, 1864									2	3	4	1								5
Family Sowerbyidae Cox, 1929									?1	1										1–2
Family Donacidae Fleming, 1828												1–2	1	2	1	2	2	2	4	5–6
Superfamily Cycladoidea Rafinesque, 1820																				
Family Neomiodontidae Casey, 1955										5	6	1								7
Family Cycladidae Rafinesque, 1820 (=Sphaeriidae Jeffreys, 1862)										?1	1	1	1	1	1	1	1	1	1	1
Family Pisidiidae Gray, 1857											2	2	2	3	3	3	3	3	4	5
Family Euperidae Heard, 1965														1	1	1	1	1	1	1
Superfamily Cyamoidea Philippi, 1845																				
Family Sportellidae Dall, 1899										1	?	?	6	7	5	8	7	4	6	13
Family Cyamidae Philippi, 1845																1	1	3	8	9
Family Turtoniidae Clarck, 1855																2	1	1	1	2
Family Neoleptonidae Thiele, 1934																	2	3	10	10
Family Perrierinidae Soot-Ryen, 1959																		1	1	1
Superfamily Kellioidea Forbes et Henley, 1848																				
Family Kelliidae Forbes et Henley, 1848													1	4	3	10	8	8	17	17
Family Erycinidae Deshayes, 1850													2	6	6	11	12	13	10–17	15–17

Table II. 1. (Contd.)

	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	Ꝑ$_1$	Ꝑ$_2$	Ꝑ$_3$	N_1	N_2	Q	Recent	Total number of genera
Superfamily Leptonoidea Gray, 1847																				
Family Leptonidae Gray, 1847													2	3	3	3	4	4	6	6
Family Montacutidae Clark, 1855														6	2	7	9	9	26	31–34
Superfamily Galeommatoidea Gray, 1840																				
Family Galeommatidae Gray, 1840													1	1–2	1	2	2	1	17–21	19–24
Family Ephippiodontidae Scarlato et Starobogatov, 1979																			1	1
Superfamily Cyrenoidoidea H. et A. Adams, 1857																				
Family Cyrenoididae H. et A. Adams, 1857																			1	1
Superfamily Chlamydoconchoidea Dall, 1884																				
Family Chlamydoconchidae Dall, 1884																			1	1
Order Carditida																				
Superfamily Carditoidea Fleming, 1828																				
Family Archaeocardiidae Khalfin, 1940				1	1															1
Family Carditidae Fleming, 1828					1	?	?	?	4	2	4	8	12	17	14	19	16	16	16	42
Family Terraiidae Scarlato et Starobogatov, 1979							1–2	1–2	1–2											1–2
Family Aenigmoconchidae Betekhtina, 1968							1													1
Superfamily Kalenteroidea Marwick, 1953																				
?Family Butovicellidae Kříž, 1965				1																1
Family Mecynodontidae Haffer, 1959					1															1
Family Kalenteridae Marwick, 1953 (=Permophoridae van Poel, 1959)					?1	1–2	5	2	2	2	1	1								9
Family Myoconchidae Newell, 1957					?1	?	2–3	?	1	2–3	1	1								4–7
Superfamily Condylocardioidea Bernard, 1897																				
Family Condylocardiidae Bernard, 1897														3	4	7	11	11	15	16
Order Venerida																				
Superfamily Cardioidea Lamarck, 1809																				
Family Cardiidae Lamarck, 1809									2	4	7	11	9	19	27	64	52	46	34	102
?Family Lahiliidae Finlay et Marwick, 1937												1	1	1	1	1				1
Superfamily Arcticoidea Newton, 1891																				
Family Arcticidae Newton, 1891									2	15	14	10–12	1	3–5	3	2	2	1	1	28–32
Family Ptychomyidae Keen, 1969										1	1									1
Family Trapeziidae Lamy, 1920											?	2	?	3–4	2	2	2	2	3–4	7–10
Family Pollicidae Srephenson, 1953												2								2
Family Euloxidae Gardner, 1943																2				2
Family Bernardinidae Keen, 1963																			2	2

Table II. 1. (Contd.)

	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	Ꝑ$_1$	Ꝑ$_2$	Ꝑ$_3$	N_1	N_2	Q	Recent	Total number of genera
Superfamily Tellinoidea Blainville, 1814																				
Family Unicardiopsidae Vokes, 1967										1										1
Family Quenstedtiidae Cox, 1929										1										1
Family Tellinidae Blainville, 1814											1	11	9	9	11	15	16	15	22	33
Family Icanotiidae Casey, 1961											2	1								2
Family Psammobiidae Fleming, 1928												1	3	5	4	4	6	7	8	12
Family Solecurtidae Orbigny, 1846												3	3	4	4	4	4	4	6	6
Family Pharellidae Tryon, 1884																	1	1	1	1
Superfamily Glossoidea Gray, 1847																				
Family Ceratomyopsidae Cox, 1964										2										2
Family Glossidae Gray, 1847											1	1	1	1–2	1	1	1	1	2	2–3
Superfamily Corbiculoidea Gray, 1847																				
Family Corbiculidae Gray, 1847										6–7	10	7–8	3	5	3	4	4	3	3–4	18–22
Superfamily Pleurodesmatoidea Cossmann et Peyrot, 1909																				
Family Corbulidae Lamark, 1818 (=Aloididae Thiele, 1935)										1	3	4	3	4	3	4	4	2	4	13
Family Erodontidae Winckworth, 1932														1	1	1	1	1	1	1
Family Spheniopsidae Gardner, 1928														1	1	1	1	1	2	2
Family Pleurodesmatidae Cossmann et Peyrot, 1909																1				1
Superfamily Pholadoidea Lamarck, 1809																				
Family Pholadidae Lamarck, 1809										4	7	13	11	15	13	14	15	15	18	29
Family Teredinidae Rafinesque, 1815,													2	3	3	3	3	3	16	16
Superfamily Solenoidea Lamarxk, 1809																				
Family Cultellidae Davies, 1935											1	3–4	1	4	4	4	5	5	6–7	8–10
Family Solenidae Lamarck, 1809													2	2	2	2	2	2	2	4
Superfamily Veneroidea Rafinesque, 1815																				
Family Veneridae Rafinesque, 1815											8	18	11	44	48	56	60	53	56	100
Family Petricolidae Deshayes, 1839														1	1	3	2	2	2	3
Family Lutetidae Davidaschvili, 1930														2	2	4	1	1	1	4
Family Vesicomyidae Dall, 1908															2	5	3	3	3	6
Family Rzehakiidae Korobkov, 1954															2	2				3
Family Cooperellidae Dall, 1900																1	1	1	1	1
Family Glauconomidae Gray, 1853																			1	1
Superfamily Mactroidea Lamarck, 1809																				
Family Mactridae Lamarck, 1809												5	2	6	6	11	16	11	18	35
Family Mesodesmatidae Gray, 1839														1–2	?1	3–4	3–4	3	12–13	13–15
Family Cardiliidae Fischer, 1887														?1	1–2	1–2	1–2	1	1	3

Table II. 1. (Contd.)

	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q	Recent	Total number of genera
Family Anatinellidae Gray, 1853																			1	1
Family Tanysiphonidae Scarlato et Starobogatov, 1971																			1	1
Superfamily Ungulinoidea H. et A. Adams, 1857																				
Family Ungulinidae H. et A. Adams, 1857												2	3	6	6	8	8	8	9–10	12–13
Superfamily Tridacnoidea Lamarck, 1819																				
Family Tridacnidae Lamarck, 1819													1	5	4	4	2	2	2	6
Family Goniocardiidae Scarlato et Starobogatov, 1979														1						1
Superfamily Chamoidea Lamarck, 1809																				
Family Chamidae Lamarck, 1809													1	1	2	3	3	3	3	3
Superfamily Scrobicularioidea H. et A. Adams, 1856																				
Family Scrobiculariidae H. et A. Adams, 1856														2	2	2	1	2	2	2
Family Semelidae Stolizka, 1870													1	4	3	4	4	4	6	6
Superfamily Kellielloidea Fischer, 1887																				
Family Kelliellidae Fischer, 1887													1	2–3	1	1	1	1	3	6–7
Superfamily Myoidea Lamarck, 1809																				
Family Myidae Lamarck, 1809													1	2	3	5	5	5	5	9
Family Raetomyidae Newton, 1919														2						2
Superfamily Dreissenoidea Gray, 1840																				
Family Dreissenidae Gray, 1840															2	3	4	3	3	4
Superfamily Gaimardioidea Hedley, 1916																				
Family Gaimardiidae Hedley, 1916																1	1	4	4–5	4–5
Superorder Septibranchia														3	2	2	3	3	9	9
Order Verticordiida																				
Superfamily Verticordioidea Stolizka, 1870																				
Family Verticordiidae Stolizka, 1870													1	3	2	2	3	3	9	9
Order Poromyidea																				
Superfamily Poromyoidea Dall, 1886																				
Family Poromyidae Dall, 1886												3	1	3	1	1	1	1	2	6
Order Cuspidariida																				
Superfamily Cuspidarioidea Dall, 1886																				
Family Cuspidariidae Dall, 1886										1	1	2	3	2–3	2	2	3	3	5	6–7
?Order Conocardioida																				
Superfamily Conocardioidea Miller, 1889																				
Family Conocardiidae Miller, 1889			1	1	1	1	1													1

Ctenodontida in hinge structure (data of Skarlato and Starobogatov, see Nevesskaja *et al.*, 1971). Skarlato and Starobogatov (1979) proposed assigning the order Praecardiida to Autobranchia, rather than to Protobranchia, although there is no clear evidence for such an assignment of this extinct order.

The order Cyrtodontida (= Mytilida) is similar to other Autobranchia in the structure of the gills and stomach, the type of feeding, and the development of the hinge. This order includes representatives of the suborder Neotaxodonta of the order Taxodonta (accepted in *Osnovy...*) and some anisomyarian taxa from the order Anisomyaria (accepted in *Osnovy...*). The other members of the latter order are assigned to the order Pectinida based on the specific structure of the digestive system and, to some extent, the hinge.

The order Actinodontida (=Unionida) almost entirely corresponds to the order Schizodonta accepted in *Osnovy paleontologii...* The superfamily Gastrochaenoidea, which in *Osnovy paleontologii...* was assigned to the order Desmodonta, is also transferred to the order Actinodontida because it is similar in digestive system to other actinodontids (Dinamani, 1967).

The order Heterodonta of *Osnovy paleontologii...* is subdivided into three orders: Astartida, Carditida, and Venerida, according to the morphological differences and origin of these groups, although the latter is not always clear. The superfamily Dreissenoidea, which in *Osnovy paleontologii...* was assigned to the order Anisomyaria, is presently assigned to the order Venerida. The order Hippuritida corresponds to the order Rudistae accepted in *Osnovy paleontologii...*, except for the family Arcinelloidea (Odhner, 1919), members of which were previously assigned to the superfamilies Chamoidea and Megalodontoidea.

The order Pholadomyida, accepted in Newell's interpretation, includes part of the order Desmodonta from *Osnovy paleontologii...* Based on the anatomy of the stomach and gills, the remaining part of the order Desmodonta is assigned to the order Venerida (Solenoidea, Myoidea, Pholadoidea) and to the superorder Septibranchia (Poromyoidea and Cuspidariodea). As mentioned above, the superfamily Gastrochaenoidea is assigned to Actinodontida.

Thus, the order Taxodonta, Desmodonta, and Heterodonta from *Osnovy paleontologii...* have been shown to be the most polyphyletic.

The main differences between this system and that used in *Treatise...* (1969) are (1) the separation of the superorder Septibranchia, whose members are considerably different from all other bivalves in the structure of gills, the digestive system, and feeding strategy; (2) interpretation of Autobranchia as an integral group, which is not subdivided into subclasses or superorders (in *Treatise...*, this group is subdivided into Pteriomorphia, Palaeoheterodonta, Heterodonta, and Anomalodesmata); (3) the establishment of the order Pectinida characterized by a distinctive type of digestive system; (4) a different order-level grouping of taxa with the heterodont hinge. In the classification accepted in the present paper, there are three orders (Astartida, Carditida, and Venerida) corresponding to two recognized in *Treatise...* (Venerida and Myoida). The assignments of the superfamilies between the orders is also different in that the members of the order Veneroida are assigned to all three orders, whereas the majority of Myioida are assigned to Venerida.

After *Treatise...* was published, Vokes (1980) published a systematic and bibliographic catalogue of the bivalvian genera and, later, (Vokes, 1990) emended it.

Recently, Amler (1999) proposed a combined classification of bivalves. According to his classification, the class Bivalvia is subdivided into two subclasses (Protobranchia and Autobranchia), the composition of which corresponds to the superorders accepted in the classification of Nevesskaja, Skarlato, Starobogatov, and Eberzin. The only difference is the assignment of Septibranchia as an order of Autobranchia. The number of subdivisions of the infraclasses (subclasses, superorders, and orders) is larger than that proposed by the above authors.

The classification of bivalves accepted in the present study is shown in Table II. 1, which also shows the number of genera in the families throughout geological periods, and the general number of genera in each family.

In addition to the 13 orders of the scheme by Nevesskaja *et al.* (1971) and Skarlato and Starobogatov (1979), the order Fordilliida is accepted here as a separate taxon within the superorder Autobranchia. This order includes the single superfamily Fordilloidea, ranging from the Cambrian to the Early Ordovician and having the most primitive hinge, ligament, and muscles.

Thus, approximately 2300 genera belonging to 263 families, 110 superfamilies, and 14 orders span the Phanerozoic (Table II. 1).

The taxonomic position of the Rostroconchia remains debatable. This group was proposed as a new class by Pojeta *et al.* (1972), a proposal that was supported by Pojeta and Runnegar (1976, 1985), Runnegar (1978), Karczewski (1987), and Babin *et al.* (1999). The main difference between this group and the true bivalves is the presence of a shell with a single valve in larvae and subadults.

Branson, La Rock, and Newell (see *Treatise...*, 1969) regarded Rostroconchia as the order Conocardioida (subclass indet.) with one superfamily and one family Conocardiidae. Starobogatov (1977) and Skarlato and Starobogatov (1979) regarded this group as an order assigned to the superorder Septibranchia that includes two suborders: (1) Conocardiina (superfamilies Eupterioidea, Euchasmatoidea, and Conocardioidea) and (2) Ribeiriina (Technophoroidea and Ischyrinioidea). Starobogatov (1992) recognized five orders within the superorder Conocardiiformii: Verticordiiformes, Dallicordiiformes, Conocardiiformes (including the suborders Eopterioidei, Ribeirioides, and Conocardioides), Cuspidariiformes, and Poromyiformes.

A detailed study of the development of a genus of the Conocardiidae showed that the earliest stage (prodissoconch) has a bivalvian shell similar to that of bivalves (particularly, venerids), while specific conocardiid features are acquired later, although it retains a functioning hinge of a few teeth and a ligament occupying a wide area. Thus, the Conocardioidea and, possibly, the entire order should be assigned to bivalves rather than to Rostroconchia. Apparently, in this case, conocardiids are homeomorphic to Rostroconchia (Heanley III and Yancey, 1998; Yancey and Heanley III, 1998). Conocardiida are known from the Middle Ordovician to the Permian.

CHAPTER III. CHANGES IN THE TAXONOMIC COMPOSITION OF BIVALVES IN THE PHANEROZOIC

The three superorders of Bivalvia are unequal in their diversity and distribution. The superorder Protobranchia is represented by two orders, Ctenodontida and Solemyida, of which the first was more diverse (20 families and ca. 140 genera). The generic diversity of the Ctenodontida was moderately high (ca. 30 genera) in the second half of the Ordovician; then, it maintained at a constant level (around 15 genera, or slightly fewer) from the Silurian to the terminal Cretaceous; in the Cenozoic, it somewhat increased (30 genera) and reached approximately 60 genera at present time (Fig. III. 2, *1*). The Solemyida contained slightly more than 10 genera, known from the Early Ordovician to the present day.

The superorder Autobranchia is most taxonomically diverse. It contains nine orders, over 230 families, and more than 2200 genera.

Representatives of various orders of the Autobranchia differ in distribution throughout the Phanerozoic, with different families and genera dominating in different periods. The order Fordilloida is known only from the Cambrian–Ordovician (two genera). The order Actinodonta displays the peaks of generic diversity in the second half of the Ordovician (41 genera), Permian (41 genera), Early Cretaceous (39 genera), Late Cretaceous (48 genera), Oligocene and Neogene (31–37 genera), and Recent (ca. 130 genera) (Fig. III. 1, *1*). The order Cyrtodontida was dominant throughout the Phanerozoic beginning with the Mid-Ordovician (from 40 to 100 genera) (Fig. III. 1, *2*). The order Pectinida reached peaks of diversity in the second half of the Triassic and Jurassic (40 and 45 genera, respectively) and in the Pleistocene until the present (Fig. III. 2, *2*). The order Pholadomyida played a significant role in the Late Paleozoic (25 genera in the Carboniferous and 33 in the Permian), Jurassic (22 genera), and Recent (32 genera) (Fig. III. 2, *3*). The order Hippuritida was only well represented in the Cretaceous (ca. 40 genera in the Early Cretaceous and ca. 100 genera in the Late Cretaceous). The order Astartida played an important role in the Jurassic (70 genera), and beginning from the Eocene to the present day (90 genera in the Eocene, 78 in the Oligocene, over 100 in the Neogene, and 200 in the Recent) (Fig. III. 1, *3*). Representatives of the order Carditida played a moderately important role and became more diverse in the Neogene (up to 10 genera in the Paleozoic and Mesozoic, 12–20 in the Paleogene, and 20–30 in the Neogene). The order Venerida, which appeared in the Middle Triassic, became important from the Cretaceous (four genera in the second half of the Triassic, 20 in the Jurassic, 55 in the Early Cretaceous, ca. 100 in the Late Cretaceous and Paleocene, more than 180 in the Eocene, 170 in the Oligocene, ca. 240 in the Neogene, and 270 genera at present) (Fig. III. 1, *4*).

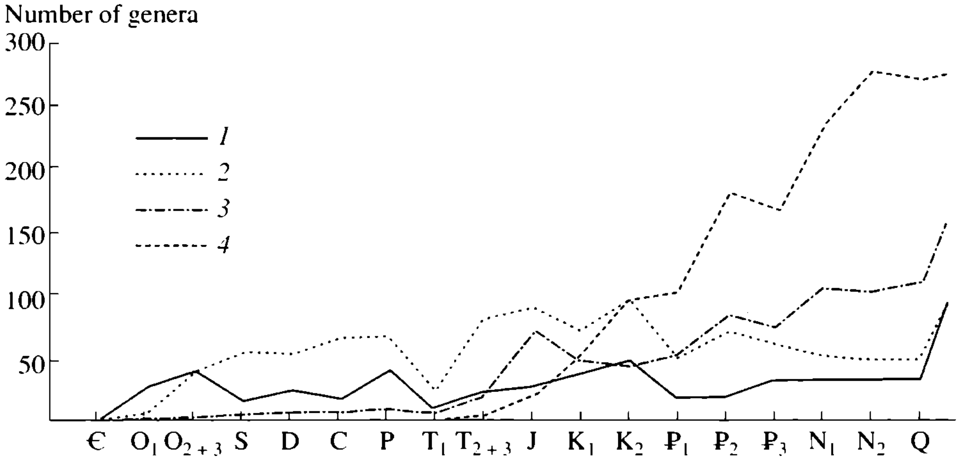


Fig. III. 1. The number of genera in the orders (*1*) Actinodontida, (*2*) Cyrtodontida, (*3*) Astartida, and (*4*) Venerida in different periods of the Phanerozoic.

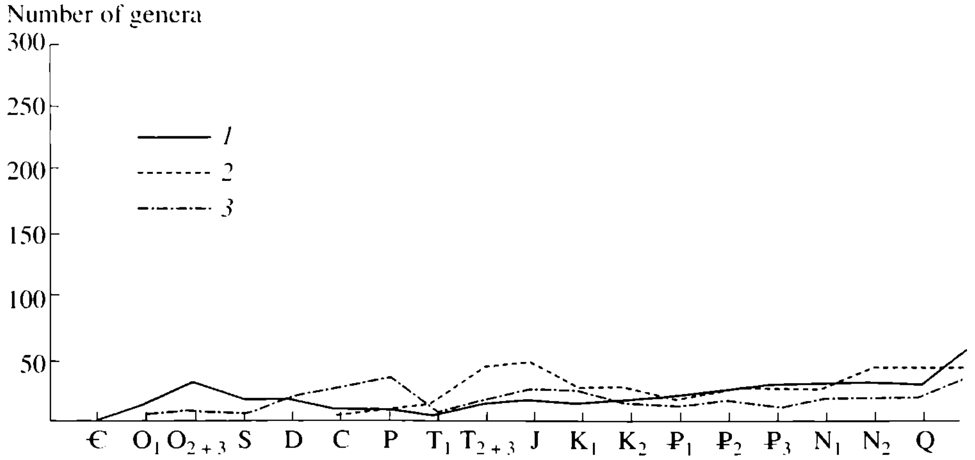


Fig. III. 2. The number of genera in the orders (*1*) Ctenodontida, (*2*) Pectinida, and (*3*) Pholadomyida in different periods of the Phanerozoic.

The superorder Septibranchia includes three orders and only three families and about 25 genera (Table II. 1). These orders are Vericordiida (Paleocene–Recent), Poromyida (Late Cretaceous–Recent), and Cuspidariida (Jurassic–Recent), each was represented by at least ten genera.

The changes in the families dominating different Phanerozoic periods are discussed below.

In the Cambrian seas, bivalves were small in size and extremely scarce. They were represented by genera belonging to a few families. These were *Pojetaia* Jell, 1980 (? family Praenuculidae, order Ctenodontida), *Fordilla* Barrande, 1881 (family Fordillidae, order Fordilloida), *Arhouriella* Geyer et Streng, 1998 (family Arhouriellidae Geyer et Streng, 1998, ord. indet.), and very doubtfully *Afghanodesma* Desparet, G. et H. Termier, 1971 (family Praenuculidae, order Ctenodontida).

Other genera allegedly occurring in the Cambrian are junior synonyms (*Jellia* Li et Zhou, 1986 and *Buluniella* Ermak, 1986), invalid taxa (*Camya* Hinz-Schallreuter, 1995 and *Oryzoconcha* He et Pei, 1985), or apparently belong to other classes (*Lamellodonta* Vogel, 1962; *Praelamellodonta* Zhang, 1980; Xianfengoconcha Zhang, 1980; *Cycloconchoides* Zhang, 1980; *Hubeinella*, Zhang, 1980; *Tuarangia* Mac Kinnon, 1982; and *Yangtzedonta* Yu, 1985) (Havliček and Křiž, 1978; Geyer and Streng, 1998).

Fordilla is found in the Lower Cambrian, *Pojetaia* is found in the Lower Cambrian and the basal beds of the Middle Cambrian, *Arhouriella* is found in the Middle Cambrian, and *Afghanodesma* is found in the Upper Cambrian–Lower Ordovician (Tremadocian).

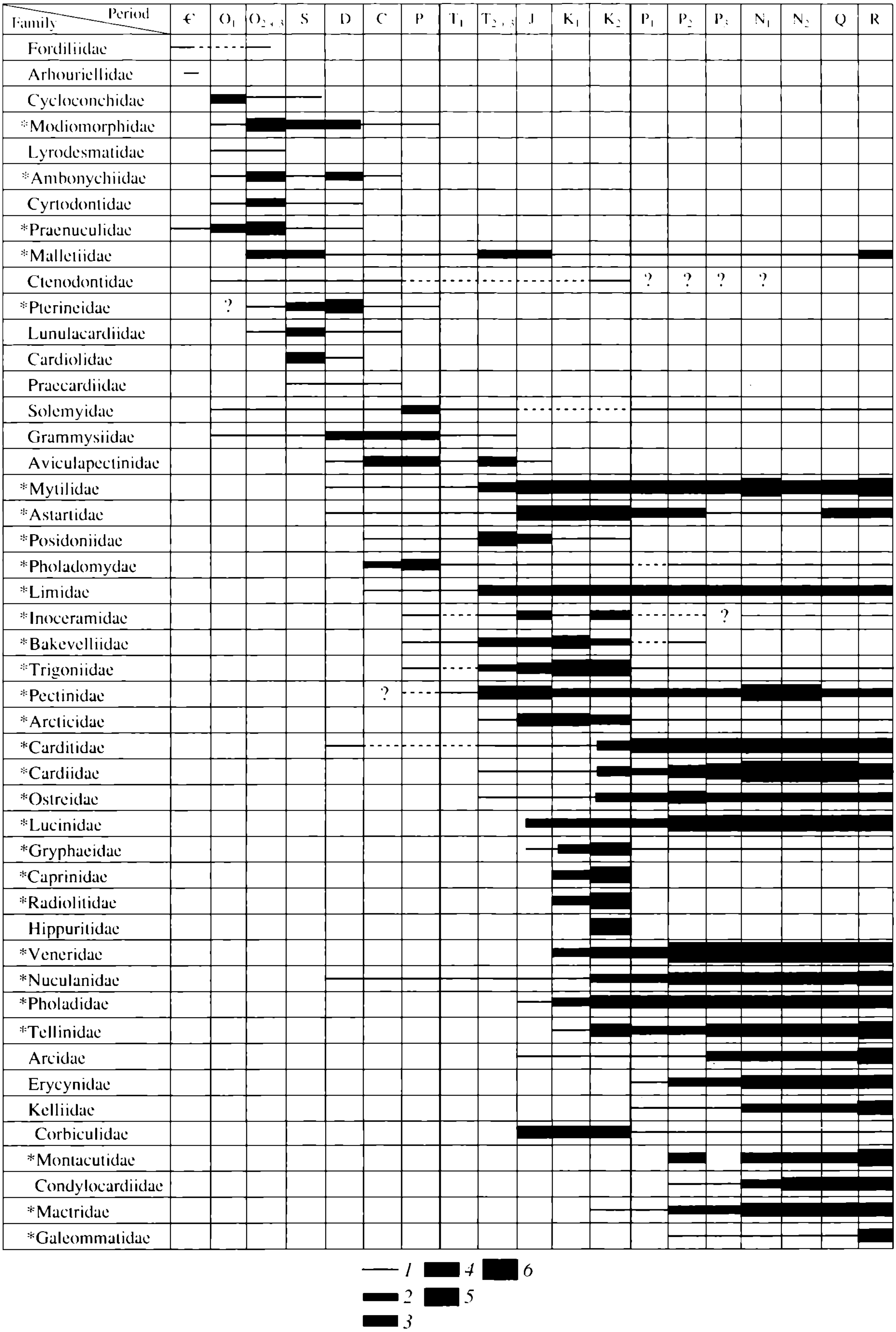
In the Early Ordovician, the taxonomic diversity of bivalves sharply increased (42–48 genera of 19–20 families). The genera of the families Cycloconchidae and Praenuculidae (each is represented by six genera, i.e., 14% of the total number of genera), Modiomorphidae (5 genera, 12%), Lyrodesmatidae (4 genera, 10%), Tironuculidae (3 genera, 7%), Cyrtodontidae (3 genera, 7%), and Redoniidae (2 genera, 5%).

Only one or two families are recorded from the Cambrian (Praenuculidae and, possibly, Fordillidae), whereas other families first appeared at the beginning of the Ordovician. Three families were confined to the Early Ordovician, while the remainder continued into later epochs (Fig. III. 3).

In the Middle and Late Ordovician, the familial and generic composition of bivalves broadened. The seas at that time were inhabited by members of 115–124 genera belonging to 31 families. The assemblages were dominated by the Modiomorphidae (20 genera, 17%), Praenuculidae (13, 11%), Ambonychiidae (13 genera, 11%), Malletiidae (10 genera, 9%), and Cyrtodontidae (8 genera, 7%). The generic composition of the Pterineidae was rather diverse: (5 genera, 4.5%), Ctenodontidae (4 genera, 3.5%), Orthodontidae (4 genera, 3.5%), Cycloconchidae, Lyrodesmatidae, Lunulacardiidae, and Antipleuridae (each represented by 3 genera, or 3%). Three families were restricted to the Middle–Late Ordovician.

In the Silurian, the number of genera decreased somewhat (99–106), whereas the number of families increased (37); three families were confine to this period. The composition of the dominant families was similar to that of the Middle–Late Ordovician, although

Fig. III. 3. Distribution and generic diversity of families dominating at different stages of the Phanerozoic: (*1*–*6*) number of genera in a family; (*1*) from 1 to 5, (*2*) from 6 to 10, (*3*) from 11 to 20, (*4*) from 21 to 30, (*5*) from 31 to 40, and (*6*) over 40. Asterisks mark families containing 20 and more genera in total.


Period
Family
Є
O1
O2+3
S
D
C
P
T1
T2+3
J
K1
K2
P1
P2
P3
N1
N2
Q
R
Fordiliidae
Arhouriellidae
Cycloconchidae
*Modiomorphidae
Lyrodesmatidae
*Ambonychiidae
Cyrtodontidae
*Praenuculidae
*Malletiidae
Ctenodontidae
*Pterineidae
Lunulacardiidae
Cardiolidae
Praecardiidae
Solemyidae
Grammysiidae
Aviculapectinidae
*Mytilidae
*Astartidae
*Posidoniidae
*Pholadomydae
*Limidae
*Inoceramidae
*Bakevelliidae
*Trigoniidae
*Pectinidae
*Arcticidae
*Carditidae
*Cardiidae
*Ostreidae
*Lucinidae
*Gryphaeidae
*Caprinidae
*Radiolitidae
Hippuritidae
*Veneridae
*Nuculanidae
*Pholadidae
*Tellinidae
Arcidae
Erycynidae
Kelliidae
Corbiculidae
*Montacutidae
Condylocardiidae
*Mactridae
*Galeommatidae
?
1
2
3
4
5
6

the role of some families changed. The number of dominant families increased, they included the Cardiolidae (represented by the largest number of genera 12–15, 13%), Pterineidae and Modiomorphidae (each represented by 10 genera, 10%), Lunulacardiidae (8 genera, 8%), Malletiidae (7 genera, 7%), Antipleuridae (5 genera, 5%), Praecardiidae (5 genera, 5%), Solemyidae (4 genera, 4%), Praenuculidae, and Ambonychiidae (each represented by 3 genera, 3%).

In the Devonian, the families Pterineidae (12 genera, 11%), Modiomorphidae (10 genera, 9%), Ambonychiidae and Grammysiidae (each represented by 6 genera, 5%) dominat. The families Ctenodontidae, Malletiidae, and Pterinopectinidae were less diverse (each was represented by 5 genera, 4.5%). The family Myophoridae was slightly less diverse (4 genera, 3.5%). In total, the Devonian marine assemblages included 112–130 bivalvian genera belonging to 44 families. Eight families were confined to the Devonian.

In the Carboniferous, bivalvian assemblages included 119–139 genera of 40 families; only one family was confined to the Carboniferous. In this time, the families Aviculopectinidae (20 genera, 17%), Pholadomyidae (8 genera, 7%), Chaenocardiidae (7 genera, 6%), and Edmondiidae (6 genera, 5%) became dominant. Of the families, which previously dominated, the Grammysiidae (6 genera, 5%) retained their importance, while the diversity of Pterineidae (5 genera, 4%) and Modiomorphidae (4 genera, 3.5%) sharply decreased. Among nonmarine bivalves, the Unionidae and Myalinidae (10 genera each, 8.5%) played an important role.

In the Permian, the assemblages included 170–187 genera of 55 families; six were confined to the Carboniferous. The composition of the dominant families remained similar to that of the Carboniferous; they included the Aviculopectinidae (represented by 17 genera, 10%), Pholadomyidae (11 genera, 6.5%), Grammysiidae (9 genera, 5%), Megadesmidae (8 genera, 5%), Solemyidae (6 genera, 3.5%), and Astartidae (5 genera, 3%). The three last families were not previously among the most diverse families. Among nonmarine taxa, the Myalinidae and Unionidae (11 genera, 6.5%) continued to dominate.

In the Early Triassic seas, the familial and generic composition of bivalves was impoverished compared to the Permian. The assemblages included 73–76 genera of 38 families; two families are confined to the Early Triassic. The genera of the families Limidae, Myophoridae, Nuculanidae, and Pterinopectinidae dominated (4 genera each, 5.5%). The families Malletiidae, Myalinidae, Nuculidae, and Entoliidae contained three genera each (4%). More than half of these families did not dominate in other periods in the Phanerozoic (Fig. III. 3).

In the Middle and Late Triassic, the taxonomic composition became considerably more diverse. The assemblages included 205–222 genera of 63 families; three families were confined to the Middle and Late Triassic. The families Posidoniidae (12 genera, 6%), Pectinidae (11 genera, 5.5%), Limidae (10 genera, 5%), and Trigoniidae (9 genera, 4.5%) were especially diverse. The families Aviculopectinidae (8 genera, 4%), Cassianellidae (7 genera, 3.5%), Malletiidae, Myophoridae, and Mytilidae (6 genera in each, 3%) were less diverse.

In the Jurassic, marine bivalves were represented by 335–352 genera of 87–89 families; six or seven families were confined to the Jurassic. The families Trigoniidae, Pectinidae, and Astartidae (each represented by 18 genera, 5.5%), Mytilidae and Arcticidae (15 genera each, or 4.5%), Pholadomyidae (11 genera, or 3.5%), Limidae, Inoceramidae, and Bakevellidae (10 genera, 3%) were most diverse.

In the Early Cretaceous, marine bivalves were represented by 316–321 genera of 88–91 families, of which 4–6 were confine to this period. The group of dominant families was similar to that of the Jurassic, although a few new families appeared and some families became less important. The group of the most diverse families included the Trigoniidae (21 genera, 6.5%), Arcticidae (14 genera, 4.5%), Bakevellidae and Astartidae (12 genera, 4%), Mytilidae (11 genera, 3.5%), Gryphaeidae, Caprinidae, and Lucinidae (9–10 genera, 3%).

In the Late Cretaceous, the number of families somewhat increased, and the generic composition became considerably more diverse. Altogether, there were 460–472 genera of 97–99 families. The most diverse families were the rudists Radiolitidae (38 genera, 8%), Caprinidae (18 genera, 4%), and Hippuritidae (16 genera, 3.5%). The families Trigoniidae (21 genera, 4.5%) Veneridae (18 genera, 4%), Astartidae (15 genera, 3.5%), Pholadidae (13 genera, 3%), and some others dominated. The freshwater Unionidae (13 genera, 3%) became more diverse.

In the Early Paleogene (Paleocene), the rudists disappeared, while the familial and generic composition was considerably impoverished. Marine bivalves were represented by 250–253 genera of 67–69 families. The families Lucinidae (19 genera, 8%), Mytilidae (13 genera, 5%), Carditidae (12 genera, 5%), Pholadidae and Veneridae (11 genera, 4.5%), Cardiidae (9 genera, 3.5%), Astartidae and Nuculanidae (7 genera, 3%) were most diverse. The freshwater Unionidae were also diverse, similar to that in the Late Cretaceous (13 genera, 5%).

In subsequent Oligocene and Eocene time, the group of dominant families remained almost unchanged, although the Pectinidae joined in. In the Eocene, the number of families and genera sharply increased compared to the Paleocene and remained almost the same in the Oligocene. In the Eocene, there were 98–100 families (two were confined to this period) and 433–451 genera; in the Oligocene, 99–102 families and 434–439 genera were registered. The dominant role belonged to the genera of the families Veneridae (44 and 48 genera, 10 and 11% in the Eocene and Oligocene, respectively). This was followed by the families Lucinidae (34 genera, 8%), Mytilidae (20 and 18 genera, 4.5 and 5.5% in the Eocene and Oligocene, respectively), Cardiidae (19 and 27 genera, 4.5 and 6%), Carditidae (17 and 14 genera, 4 and 3%), Pholadidae (15 and 13 genera, 3.5 and 3%), and Nuculanidae (14 and 16 genera, 3 and 4%). The Pectinidae were represented by 8 genera (2%) in the Eocene and by 10 genera (3%) in the Oligocene. The Unionidae were dominant in freshwater habitats (11 genera in the Eocene, and 23 genera in the Oligocene).

In the Neogene, the number of families and genera, and the group of dominant families were very similar to those of the Paleogene. In the Miocene, there were 574–580 genera of 109–111 families (three families are restricted to this epoch), while in the Pliocene, there were 568–573 genera of 110–111 families. The families Veneridae (56 and 60 genera, 10% in the Miocene and Pliocene, respectively) and Cardiidae (64 and 52 genera, 11 and 9%) dominated. They were followed by the Lucinidae (38 and 31 genera, 7 and 5.5%), Pectinidae and Mytilidae (24 and 23 genera of pectinids and 22 and 20 of mytilids, 4% each), Carditidae (19 and 16 genera, 3%). The role of Tellinidae and Mactridae (15 and 16, 11 and 16 genera, 2.5–3 and 2–3%, respectively) increased. The diversity of the freshwater Unionidae remained high (24 and 27 genera, 4 and 5% in the Miocene and Pliocene, respectively).

In the Quaternary seas, the number of families and genera was almost the same as in the Neogene (568–569 genera of 108–109 families). The dominant families included the Veneridae (53 genera, 9.5%), Cardiidae (46 genera, 6%), Lucinidae (33 genera, 6%), Mytilidae (21 genera, 3.5%), and Pectinidae (17 genera, 3%). Freshwater bivalves were dominated by the Unionidae (43 genera, 7.5% of the total number).

The Recent bivalvian fauna shows a sharp increase in the number of families (123, of which 14 are confined to this period) and, especially, of genera (850–867), i.e., about 300 of 850–867 presently extant genera are found only in modern basins. Apparently, this does not indicate an increased diversification in the Recent, but results from the fact that the modern fauna is more completely studied, including taxa from habitat types that are not usually well represented in the fossil record. It is noteworthy that the proportion of small-sized genera sharply increased (the family Montacutidae is represented by 24 genera; the Erycynidae, Kelliidae, and Galeommatidae include 17 genera each; the Neoleptonidae includes ten genera; etc.). A number of families from the deep-water faunas, unknown from the ancient seas, also contributes to the difference. The increase in the total number of genera of the freshwater Unionidae (up to 108, i.e., 13% of the total number) is also attributable to the more intense study of modern bivalves.

Therefore, the special task for paleontologists studying bivalves from the younger beds is to extensively compare fossils with modern representatives of similar surviving genera to emend the taxonomic positions of extinct (primarily Neogene) bivalves. Apparently, after such a revision, the number of genera and families restricted to the modern basins will be reduced. In any event, the group of dominant families in modern fauna changed insignificantly. The Veneridae currently include 56 genera (6.5%); the other dominant families are the Mytilidae (40 genera, 4.5%), Lucinidae and Cardiidae (34 genera, 4%), Nuculanidae and Montacutidae (25 genera, 3%) Tellinidae (22 genera, 2.5%), Pectinidae (19 genera, 2.2%), Mactridae and Pholadidae (18 genera, 2%). The proportion of other families is less than 2% of the total number of genera.

CHAPTER IV. DYNAMICS OF THE TAXONOMIC DIVERSITY OF BIVALVES IN THE PHANEROZOIC

Studies of the taxonomic diversity of marine biota in the Phanerozoic showed that the largest changes occurred at the Lower and Middle Cambrian boundary, Middle and Upper Cambrian boundary, and the Cambrian–Ordovician, Lower–Middle Ordovician, Ordovician–Silurian, Permian–Triassic, and Triassic–Jurassic boundaries. These crises are seen in taxa of several ranks, whereas the Cretaceous–Tertiary crisis was only observed in families and genera and affected the taxa of higher taxonomic ranks far less profoundly (Newell, 1963, 1967; Valentine, 1969; Boucot, 1975, 1990; Sepkoski, 1978, 1979, 1990; *Razvitie i smena...*, 1981; Alekseev, 1989a, 1989b; Nevesskaja, 1999; etc.).

It was also shown that different groups of extinct invertebrates responded differently to global critical events (for references, see Nevesskaja, 1999).

Nevesskaja (1972b) was the first to discuss the changes in the taxonomic diversity of the bivalvian orders, superfamilies, families and genera. Subsequently, Afanasjeva and Nevesskaja (1994), Afanasjeva *et al.* (1998), in the course of the Research Program "Ecosystem Turnovers and the Evolution of the Biosphere" studied the changes in the taxonomic diversity of bivalves at the critical events of the Permian and Triassic, while Nevesskaja and Amitrov (1995) studied the changes in the Cenozoic, after the Cretaceous–Tertiary crisis. Afanasjeva and Nevesskaja (1994) and Afanasjeva *et al.* (1998) compared the response of bivalves, brachiopods, and bryozoans to the crises, whereas Nevesskaja and Amitrov (1995) compared the response of bivalves and gastropods.

It is interesting to study the dynamics of the taxonomic diversity in the Phanerozoic, using new data accumulated after *Osnovy paleontologii...* (1960) and *Treatise...* (1969) were published and taking into account changes in the geochronological dating.

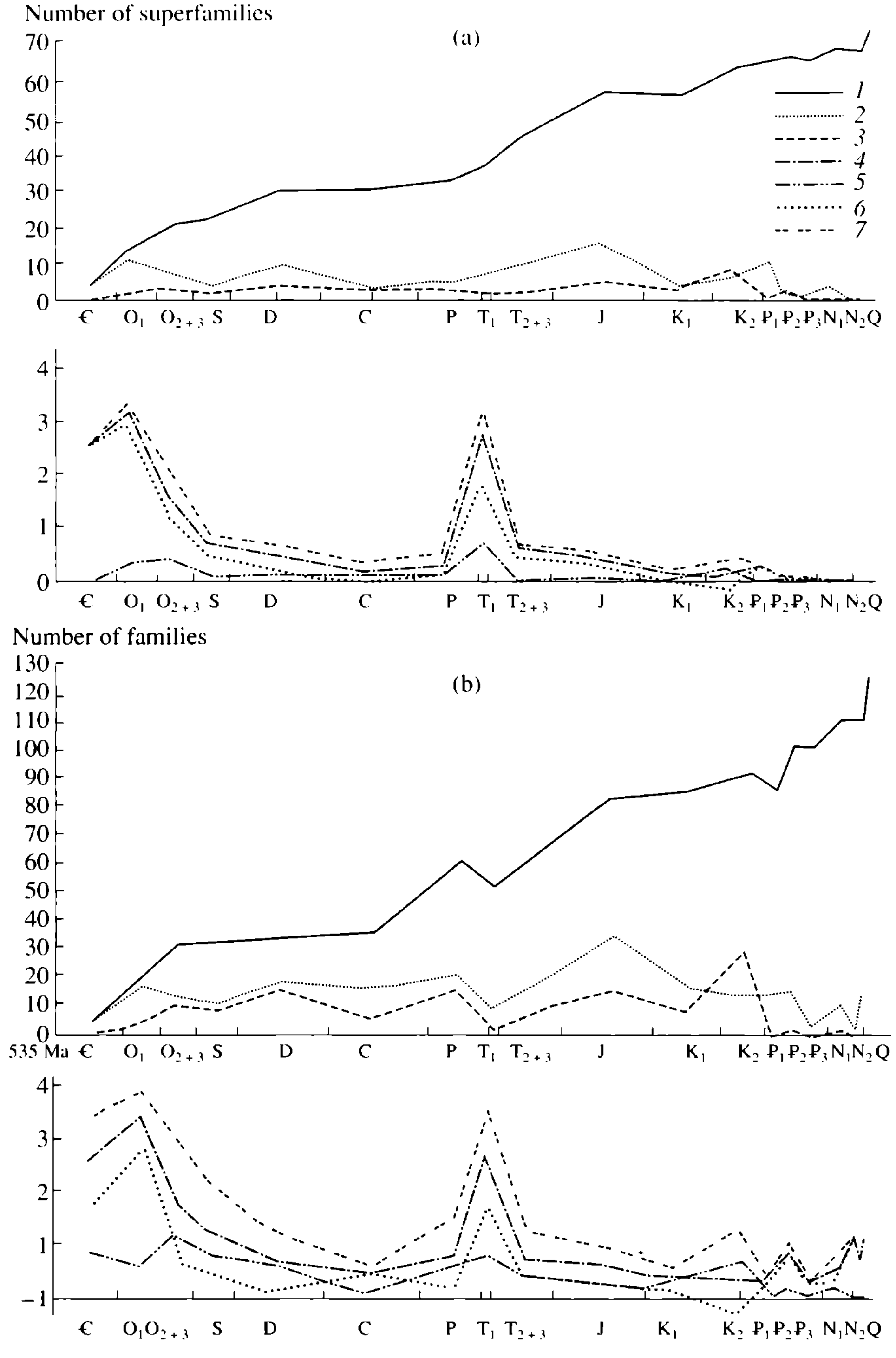


Fig. IV. 1. Changes in the total number of (a) superfamilies, (b) families, and (c) genera: (*1*) total number, (*2*) first appeared, (*3*) became extinct, (*4*) rate of appearance, (*5*) rate of extinction, (*6*) rate of diversification, and (*7*) rate of total change in composition.

As was mentioned in the previous chapter, the first bivalves appeared in the Early Cambrian and belonged to two–three genera of two superorders (Protobranchia and Autobranchia), whereas the taxonomic position of one more genus remains uncertain.

The third order (Septibranchia) is known only from the beginning of the Jurassic. Of 11 orders belonging to the Protobranchia and Autobranchia, two, as mentioned above, are known from the Early Cambrian onwards, five from the Early Ordovician, one from the Middle

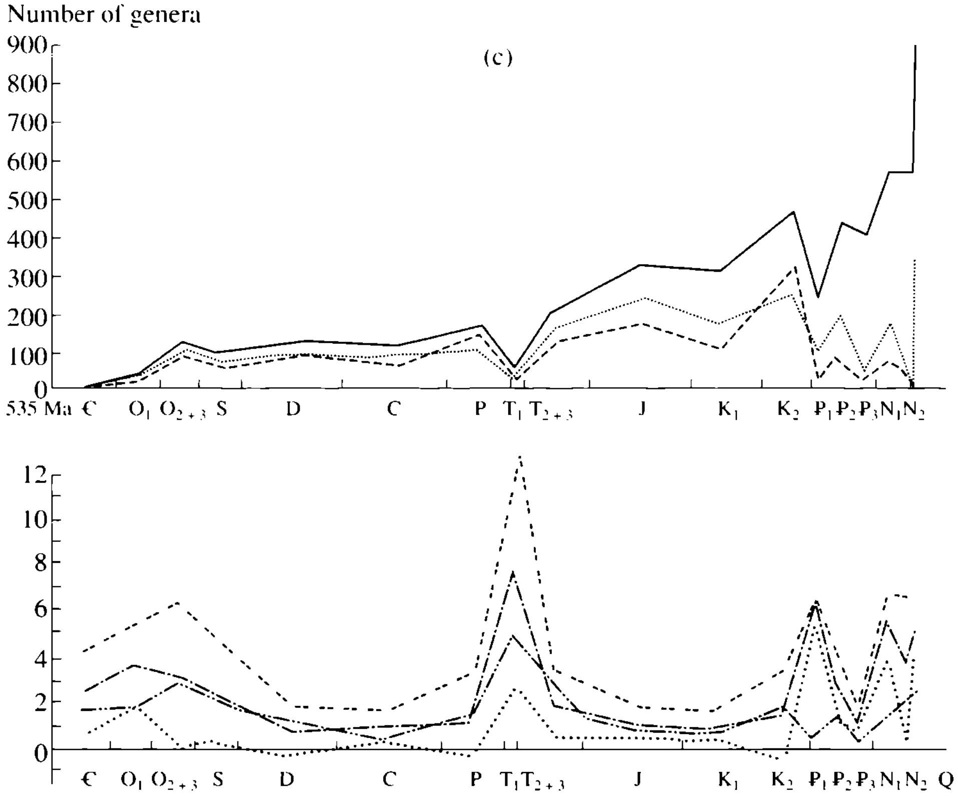


Fig. IV. 1. (Contd.)

Ordovician, and one order from the Silurian, Carboniferous, and Middle Triassic.

Three orders of the superorder Septibranchia originated in the Jurassic, Late Cretaceous, and Early Paleogene.

The analysis of the absolute numbers of orders in total, and of the numbers of the orders, which appeared and became extinct in the interval considered, shows a gradual increase in the number of orders from two in the Cambrian to 12 from the basal Paleogene to the Recent. A significant increase in the number of the newly appearing orders occurred in the Early Ordovician. Lesser peaks are recorded in the Carboniferous, Triassic, and Late Cretaceous. Representatives of only two orders became extinct (Fordilloida in the second half of the Ordovician and Hippuritida in the Late Cretaceous (Table. IV. 1).

The total number of taxa of lower rank (superfamilies, families, and genera) also increased throughout the Phanerozoic. This process continued almost uninterrupted for the superfamilies (Fig. IV. 1a), while the development of the diversity of the families and especially genera (Figs. IV. 1b, IV. 1c) shows several peaks and troughs. The peaks coincide with the second half of the Ordovician, Permian, Jurassic, Late Cretaceous, Eocene, and Miocene (for genera), Paleocene and Oligocene. These peaks and troughs had different intensities. The Mid-Ordovician and Permian peaks and the Early Triassic and Paleocene troughs were especially pronounced.

The largest number of new superfamilies and families appeared in the Early Ordovician, Devonian, Permian (only for families), Jurassic, Paleocene (for superfamilies), Eocene (for families), and Miocene. The largest number of new genera appeared in the Middle Ordovician, Permian, Jurassic, Late Cretaceous, Eocene, and Miocene.

A considerable number of extinct families and genera were recorded in the second half of the Ordovician, of families and superfamilies in the Devonian, of families and genera in the Permian, and of all taxa of this rank in the Jurassic and Late Cretaceous.

Somewhat different data can be obtained if the number of taxa appearing and becoming extinct are counted as percentage over the duration of time interval and as a proportion of all the taxa existing in the interval studied. This gives more information than the absolute numbers. Using this technique, the rate of appearances interpreted as $S/D \times 100$ and the rate of extinction estimated as $E/D \times t \times 100$ were counted (S is the number of newly emerging taxa, D is the total number known from the interval, E is the number of extinct taxa, t is the duration of the interval in myr). A rate of diversification equal to the differences between the rate of appearance and extinction, and the coefficient of the total change in the taxonomic composition equal to the sum of the rates

Table IV. 1. Number of orders, rates of their appearance, extinction, diversification and total change in the Phanerozoic

Parameter	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q	R
Total number	2	7	8	8	8	9	9	9	10	11	11	11	12	12	12	12?	12?	12?	12?
Number of appearing orders	2	5	1	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	0
Number of extinct orders	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Rate of appearance	2.5	2.64	0.50	0.48	0	0.17	0	0	0.28	0.14	0	0.28	1.06	0	0	0	0	0	0
Rate of extinction	0	0	0.50	0	0	0	0	0	0	0	0	0.28	0	0	0	0	0	0	0
Rate of diversification	2.5	2.64	0	0.48	0	0.17	0	0	0.28	0.14	0	0	1.06	0	0	0	0	0	0
Total change	2.5	2.64	1.0	0.48	0	0.17	0	0	0.28	0.14	0	0.56	1.06	0	0	0	0	0	0

of radiation and extinction were also calculated. The diversification rate is positive when appearances exceed extinctions and negative when extinctions exceed appearances. The rate of change in the total composition is greatest when both the rates of appearances and extinctions are high.

For the orders, superfamilies, and families the rates of appearances and diversification and coefficient of the total change of the composition were the highest in the Early Ordovician, i.e., soon after the appearance of bivalves in the Cambrian. The rates of appearance and diversification of bivalvian genera in the Early Ordovician were also high, whereas the peak of generic diversity was shifted to the second half of the Ordovician. The following peak of all above parameters for all taxa, except orders, occurred in the Early Triassic. For genera, the Early Triassic peak was even greater than the Early Ordovician peak (Fig. IV 1). In the subsequent periods, peaks in the rate of appearance, diversification, and general change in the composition did not coincide for taxa of different rank. For superfamilies and families (Figs. IV. 1a, IV. 1b), a small peak of the total change occurred in the Late Cretaceous due to the fact that the extinction rate exceeded the appearance rate, which resulted in a negative value of the diversification rate. For families, small peaks of the appearance and diversification rates and of the total change in the diversity are recorded in the Eocene and Miocene. Peaks of the above parameters calculated for genera in the Cenozoic occurred in the Paleocene and Miocene (Fig. IV. 1c). An increase in the above parameters for orders is recorded in the Eocene (Table IV. 1).

The rate of extinction and appearance of different taxa in different time were different. Thus, a high appearance rate of new taxa in the Early Ordovician was associated with the relatively low extinction rate, whereas in the Early Triassic, peaks of the appearance and extinction rates were similar for all taxa (except orders). In the Late Cretaceous, the extinction rate was higher than the appearance rate for superfamilies, families, and genera, whereas in the Paleocene, the ratio was reversed, especially clearly for genera. In the Eocene, both rates were relatively high, whereas in the Oligocene, they were low, especially, the appearance rate. In the Miocene, the appearance and extinction rates increased, while in the Pliocene, the extinction rate decreased for families (down to zero) and the appearance rate increased. For genera, in the Pliocene, the appearance rate dropped, while the extinction rate increased. This shows that there is no regular pattern in the changes of the appearance and extinction rates.

Thus, in the Paleozoic, there was one clear peak in the appearance of new taxa (from orders to families), which occurred in the Early Ordovician (see also Stanley, 1968). This peak was responsible for the maximum diversification rate and for the maximum change in the taxonomic composition, except for genera, for which most peaks were shifted to the second half of the Ordovician because of the increased appearance and extinction rates.

The taxa below order rank show a peak of all relative values of appearance, extinction, and diversification rates, and of the total change in the Early Triassic, although the absolute values (total number of species, number of appearing and extinct genera and families) are highest in the Permian, while they dropped in the Early Triassic, especially for genera. Thus, the drop in diversity in the Early Triassic was due to the considerable extinction at the Permian–Triassic boundary, and subsequent rapid appearance of new taxa in a short interval of 7 myr. Therefore, despite the decrease in the absolute number of families and genera in the Early Triassic, the total change in the taxonomic composition and diversification rate were highest, for families slightly lower than in the Early Ordovician, and for genera they were highest in the Phanerozoic.

The crisis at the Cretaceous–Tertiary boundary affected taxa from superfamily to the generic ranks, and led to increased extinction in the Late Cretaceous. This resulted in a decrease in the total number of families and especially genera in the Paleocene, negative values of diversification in the Late Cretaceous, and a sharp increase in the rate of appearance of new genera, diversification rate, and coefficient of the total change in the generic composition in the Paleocene (Nevesskaja and

Amitrov, 1995), whereas for families these events are shifted to the Eocene.

At the level of families and genera, small peaks of the appearances of new genera, rates of diversification, and the coefficient of total change were in the Neogene, although they were not very expressed because the intervals (e.g., Pliocene) were short (Nevesskaja and Amitrov, 1995).

The comparison of the dynamics of taxonomic diversity of bivalves with that of other marine animals (see Alekseev *et al.*, 2001) showed significant differences. First of all, the number of bivalve orders, after a sharp increase in the Early Ordovician, increased gradually up to the present, without any drops at the Ordovician–Silurian boundary, Devonian–Carboniferous boundary, Permian–Triassic boundary, Triassic–Jurassic boundary, and Cretaceous–Tertiary boundary, as opposed to other marine organisms (Alekseev *et al.*, 2001, text-fig. 6). Thus, only the peaks in the number of orders in the Ordovician are shared by all groups.

Regarding families and genera, shared events included a sharp increase in their number in the Ordovician, especially, at the end of this period, and a subsequent considerable drop in the appearance of new taxa. Right up to the Permian, bivalves show stable diversity, which is not interrupted by a noticeable drop at the Silurian–Devonian boundary or at the Devonian–Carboniferous boundary, as opposed to other groups. In the Permian, diversity increased, which did not occur in the majority of other groups. A sharp decrease in the number of families and genera at the Permian–Triassic boundary was shown by all marine organisms. From the Early Triassic to the Late Cretaceous, the number of families and genera gradually increased without being interrupted at the Triassic–Jurassic boundary. The increase of the number of taxa in the Late Cretaceous, followed by a sharp decrease at the Cretaceous–Tertiary boundary, were the same in all marine groups. The same applies to the sharp increase in diversity from the Paleozoic to the Recent with a small drop in the Oligocene.

Thus, only the Ordovician events, which displayed a sharp increase in the number of all taxa followed by a drop, and the Permian–Triassic events which displayed an interval of low rates of appearance and diversification (up to a negative rate for genera) in the Early Triassic followed by a maximum increase of these rates and of the coefficient of total change in taxonomic composition, were shared by other groups. Nevertheless, this crisis was considerably less pronounced than in other invertebrate groups (Nevesskaja, 1999, text-fig. II. 3, *1*; Alekseev *et al.*, 2001, text-fig. 6) and was seen only at the level of lower-rank taxa, while taxa of the order level were not affected.

The Cretaceous–Tertiary event was even less significant, because it affected only families and genera. From the beginning of the Paleogene, modern genera became dominant (Paramonova, 1975), while from the Oligocene, the generic composition was almost identical to the present day (only species within the genera were replaced).

The crises at the Ordovician–Silurian, Silurian–Devonian, Devonian–Carboniferous, and Triassic–Jurassic boundaries seen in other invertebrate classes did not affect bivalves to a noticeable extent.

The critical Permian–Triassic and Cretaceous–Tertiary events, which also affected other benthic groups, could have been caused by the global changes in sea level, which resulted in changes in depths, substrates, anoxies, climatic fluctuations, and other abiotic factors (including food resources) (for references, see Nevesskaja, 1999). However, synchronic extinctions in the sea and on the continents could have been a consequence of other global events (Alekseev *et al.*, 2001; Dmitriev, 2002).

CHAPTER V. MORPHOGENESIS OF BIVALVE SHELLS IN THE PHANEROZOIC

This chapter describes the changes in the shell as an entire structure in the Phanerozoic, and the establishment and development of all taxonomic characters.

A few Cambrian taxa had an equivalve shell without a gape, which could be equilateral or inequilateral. The anterior end was usually shorter, less commonly longer, than the posterior. The shell usually had a prosogyral and weakly projecting beak.

The external surface was smooth, or, more rarely, ribbed posteriorly (*Pojetaia*). The hinge was preheterodont, comprising 1 to 3 toothlike projections under the beak. More rarely, teeth were absent. There was only one adductor imprint (or two, but the anterior was smaller). Additional (visceral) muscle imprints were present. The ligament was external and opisthodetic (*Fordilla* and *Pojetaia*) or amphidetic (*Arhouriella*). The pallial line was entire.

In the Early Ordovician, shell elements became more diverse. The shell was equivalve, usually without a gape, inequilateral (90%). Shells with a shorter anterior part prevailed (over 70%), but shells with a longer anterior part were also rather common (ca. 20%). The beak was most often prosogyral (60%) and, more rarely, orthogyral or opisthogyral. The external surface was usually smooth (60%), often, concentrically ribbed (ca. 20%), more rarely, radially ribbed, or striated. Even more rarely, it had a composite ornamentation. Some taxa had shells with auricles and a byssal notch.

The hinge of Early Ordovician bivalves was extremely diverse, which is an example of so-called archaic diversity. Along with the preheterodont type of hinge consisting of only one or two subumbilical teeth (*Colpantix, Miquelana, Pharcidoconcha, Babinka*, and *Coxiconcha*), or together with one or two posterior submarginal teeth (*Moridunia, Redonia*, and *Xestoconcha*) (Fig. V. 1), there were also edentate taxa (*Solemya, Corallidomus*, some *Arenigomya, Cleionychia*, and *Gomophora*), taxa with a ctenodont or primary taxodont hinge (*Paulinea, Pensarinia, Ctenodonta, Praenucula*, and *Decepterix*) (Figs. V. 2a, V. 2b), actinodont hinge (*Actinodonta, Palaeopteria, Cycloconcha, Celtoconcha, Carminodonta*, and *Fortewensia*) (Figs. V. 3a–3e),

Fig. V. 1. Preheterodont hinge in *Moridunia simplicidens* Cope, 1996 (family Redoniidae), ×3, Lower Ordovician (after Cope, 1996, Fig. 6c).

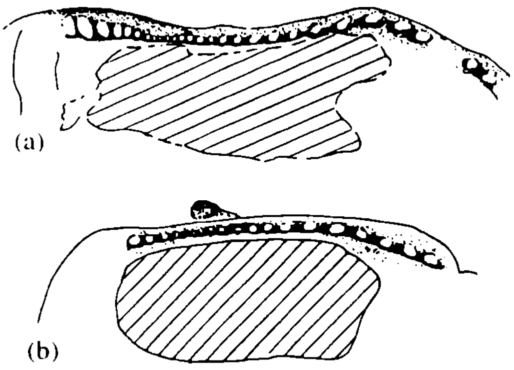


Fig. V. 2. Ctenodont hinge of the Early Ordovician members of the family Praenuculidae: (a) *Pensarinia laeviformis* Cope and (b) *Paulinea parva* Cope, ×10 (after Cope, 1996, text-figs. 2 and 3).

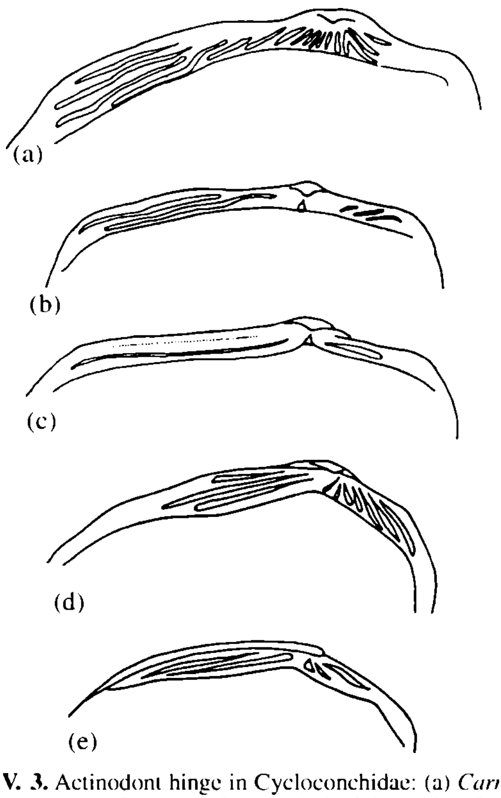


Fig. V. 3. Actinodont hinge in Cycloconchidae: (a) *Carminodonta crassa* Cope, ×4, Lower Ordovician (after Cope, 1996, text-fig. 6A); (b) *Celtoconcha foveata* Cope, ×4, Lower Ordovician (after Cope, 1996, text-fig. 6B); (c) *Fortowensia grandis* Cope, ×2, Lower Ordovician (after Cope, 1996, text-fig. 6D); (d) *Actinodonta cuneata* Phillips, Lower Silurian (after Babin and Gutiérrez-Marco, 1985, text-fig. 3f); and (e) *Cycloconcha ovata* Ulrich, Ordovician (after Babin and Gutiérrez-Marco, 1985).

Fig. V. 4. Lyrodesmoid hinge in *Lyrodesma acuminata* (Ulrich) (family Lyrodesmatidae), Middle Ordovician (after *Treatise*..., 1969, text-fig. D 62, 1a).

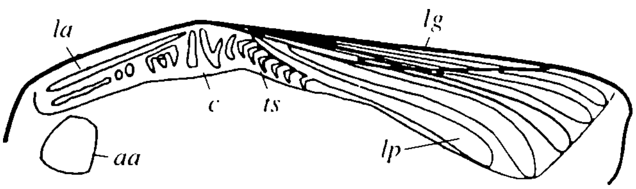


Fig. V. 5. Ctenodont-actinodont hinge in *Catamarcaia* (fam. indet.), Lower Ordovician (after Sánchez, 1995, text-fig. 1). Designations: (*aa*) anterior adductor, (*c*) umbilical teeth, (*la*) lamellar anterior tooth, (*lg*) ligament grooves, (*lp*) posterior lateral teeth, and (*ts*) series of taxodont teeth.

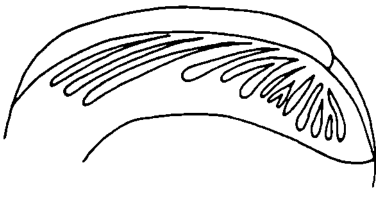


Fig. V. 6. Lyrodesmoid-actinodont hinge of *Copidens* (family Cycloconchidae), Ordovician (after Babin and Gutiérrez-Marco, 1985, text-fig. 3e).

Fig. V. 7. Preheterodont-actinodont hinge in *Ananterodonta* (family Cycloconchidae), Lower Ordovician–lower part of the Middle Ordovician (after Babin and Gutiérrez-Marco, 1985, text-fig. 3c).

cyrtodont hinge (*Cyrtodonta, Cyrtodontula*, and *Falcatodesma*), lyrodesmoid hinge (*Lyrodesma*) (Fig. V. 4), and with a combined hinge. The latter included ctenodont-actinodont, or ctenodont-neotaxodont (*Natasia, Ekaterinodonta*, and *Catamarcaia*) (Fig. V. 5), lyrodesmoid-actinodont (*Copidens*) (Fig. V. 6), and preheterodont-actinodont (*Ananterodonta*) hinges (Fig. V. 7). This time was marked by the appearance of rare taxa with hinge types that became more widespread later, including the pterinoid hinge (*Tromelinodonta* and *Noradonta*), desmodont hinge (*Arenigomya*), and neotaxodont, or the secondary taxodont hinge (*Parallelodon*). There was also a variety of the ctenodont hinge (glyptarcid), which consisted of anterior and posterior hinge lines composed of numerous teeth. Some anterior

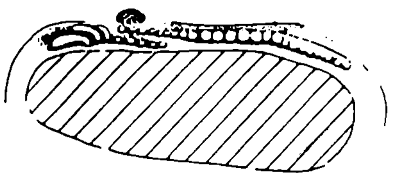


Fig. V. 8. Glyptacid hinge of *Glyptarca* (family Glyptarcidae), Lower Ordovician (after Cope, 1996, text-fig. 5): hinge of the left valve and hinge of the right valve.

teeth in the anterior hinge line were elongated and arched, and almost parallel to each other and the hinge line, while the small posterior teeth of this hinge line were overlapped by the anterior part of the posterior hinge line composed of small teeth, the number of which was greater than in the anterior hinge line (Fig. V. 8).

The extreme variability of the hinge, and the presence of many intermediate types in Early Paleozoic genera were noted by Babin and Le Pennec (1982).

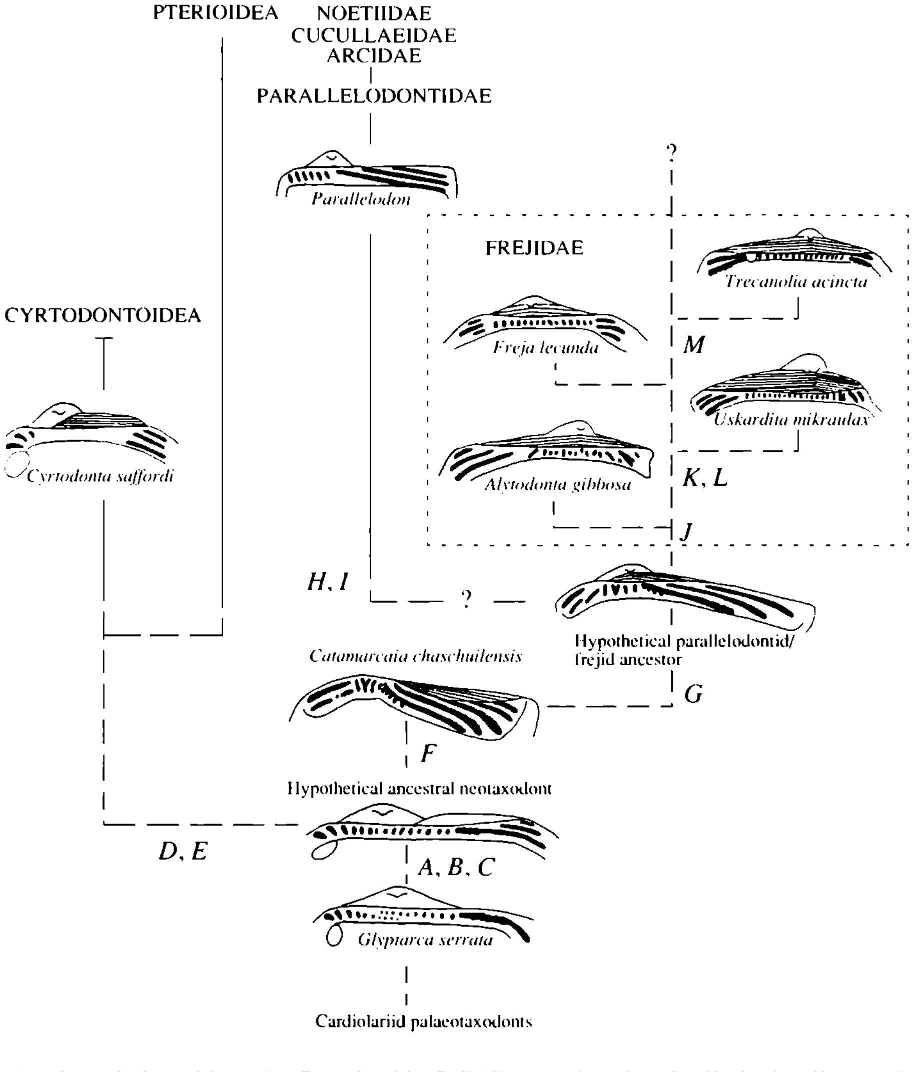


Fig. V. 9. Origin and early evolution of the order Cyrtodontida. Solid lines are based on fossils, broken lines are hypothesized. Cardiolariid paleotaxodonts are assigned to the family Praenuculidae (order Ctenodontida); *Glyptarca*, to the family Glyptarcidae in the same order. (*A*) loss of the subumbilical overlap of the branches of the hingeline, (*B*) appearance of the opisthodetic preduplivincular ligament, and (*C*) appearance of the crossed-lamellar middle layer and composite crossed-lamellar inner layer of the shell; characters *A*, *B*, and *C* are evidence of the formation of the order Cyrtodontida; (*D*) loss of the subumbilical teeth and (*E*) appearance of the prismatic calcite external shell layer; characters *D* and *E* led to the emergence of the Cyrtodontoidea; (*F*) appearance of the opisthodetic duplivincular ligament; (*G*) development of the amphidetic duplivincular ligament, and possibly, emergence of the hypothetical common ancestor of the Parallelodontidae and Frejidae, i.e., the first representatives of the superfamily Arcoidea; (*H*) shift of beaks anteriorly; (*I*) turn of the anterior teeth in the ventral-convergent position; characters H and I indicate the transition to the Parallelodontidae; (*J*) an increase in the number of the pseudocardinal teeth, leading to the emergence of the family Frejidae in the superfamily Arcoidea; (*K*, *L*, *M*) changes within the Frejidae: (*K*) further increase in the number of the pseudocardinal teeth and shortening of the pseudolateral teeth, (*L*) expansion of the hinge area and duplivincular ligament, and (*M*) development of denticles on the lateral teeth (after Ratter and Cope, 1998, text-fig. 7).

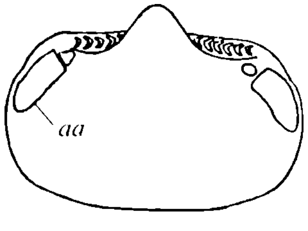


Fig. V. 10. Left valve interior of *Cuyopsis* (family Praenuculidae). Upper Ordovician (after Sánchez, 1999, text-fig. 3): (*aa*) anterior adductor scar.

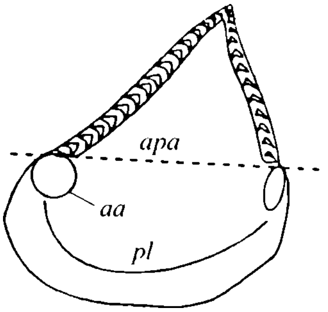


Fig. V. 11. Right valve interior of *Trigonoconcha* (family Praenuculidae), Upper Ordovician (after Sánchez, 1999, text-fig. 5). Designations: (*aa*) anterior adductor scar; (*apa*) anteroposterior axis; and (*pl*) pallial line.

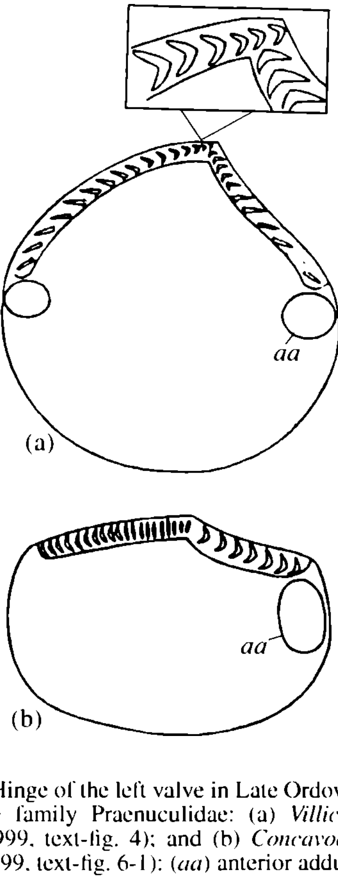


Fig. V. 12. Hinge of the left valve in Late Ordovician members of the family Praenuculidae: (a) *Villicumia* (after Sánchez, 1999, text-fig. 4); and (b) *Concavodonta* (after Sánchez, 1999, text-fig. 6-1): (*aa*) anterior adductor scar.

The hypothetical morphogenesis of the transition from the primary taxodont (ctenodont) to the secondary taxodont (neotaxodont, or pseudotaxodont) hinge was suggested by Ratter and Cope (1988) (Fig. V. 9).

Usually, there were two almost identical muscular scars (70%). More rarely, they were different (the anterior scar was larger than the posterior). Very rarely, the shell had only one posterior scar. Some taxa, along with these adductor scars and pedal scars, possessed visceral muscular scars. The ligament was external, apparently, opisthodetic. Taxa with an entire pallial line dominated, whereas the sinus was developed only in *Lyrodesma* and was short.

In the second half of the Ordovician (Middle–Late Ordovician), the first rare inequivalve shells appeared (less than 10%). Smooth shells without a gape dominated, concentrically ribbed shells became more frequent (30%), whereas other types of ornamentation were rare. Inequivalve shells with a shorter anterior part dominated. For the first time genera with a terminal beak were recorded from this level. The beak is usually prosogyral (70%); more rarely, orthogyral; or opisthogyral. Taxa with auricles and a byssal notch became somewhat more frequent (ca. 10%). The hinge was represented by a smaller number of types than in the Early Ordovician. The majority of genera had a ctenodont (primary taxodont) hinge (ca. 30%). Usually the hinge of this type had two hinge lines meeting at the beak and consisting of straight or chevron-like teeth, with the apices turned toward the beak (*Praenucula, Tancredi-opsis, Cuyopsis*, and *Trigonoconcha*) (Figs. V. 10, V. 11). There were also shells with a hinge, in which the posterior line overlapped the anterior line (*Villicumia* and *Cardiolaria*) (Fig. V. 12a), and with differently directed apices of the chevrons: either (1) in both lines from the beak (*Concavodonta* and *Emiliania*) (Figs. V. 12b and V. 13a), or (2) in the anterior line directed toward the beak, and in the posterior line from the beak (*Hemiconcavodonta*) (Fig. V. 13b). Edentate shells were common (20%), the preheterodont hinge occurred in approximately 15%); the actinodont hinge (ca. 10%) and cyrtodont hinge were common, while the lyrodesmoid, pterinoid, and neotaxodont hinges were are (Fig. V. 14). Shells with an intermediate hinge were scarce. The proportions of bivalves with different adductor scars were similar to those in the Early Ordovician. Genera with a reduced or absent anterior scar became more common. Additional muscular scars were observed in only a few genera. Taxa with an external ligament (usually, opisthodetic) dominated, although some genera had an internal ligament, or combined internal and external ligaments. The pallial line was entire in almost all genera. Only two genera had a shallow sinus.

Silurian and Devonian bivalves had similar proportions of various characters, although there were some differences. The proportion of inequivalve shells increased compared to that in the Ordovician (ca. 20%). Shells usually lacked a gape. Shells with a smooth surface were no longer dominant. They occurred in equivalent numbers to those with concentric and radial ribs, whereas genera with concentric, radial striae, and composite ornamentation were less frequent. Inequilateral shells with a shorter anterior part continued to dominate (ca. 70%). Taxa with a reduced anterior part and terminal beak (ca. 10% in the Silurian and 15% in the Devonian) were relatively common. The beak in the majority of genera was prosogyral (70%); more rarely, it was orthogyral and opisthogyral. Bivalves with auricles, a byssal notch, and with a gape were rare. Edentate shells prevailed (35–45%), genera with a ctenodont hinge were common (16–20%), shells with a preheterodont hinge were rarer (less than 10%). The actinodont, cyrtodont, and neotaxodont hinges were rare. Genera with a heterodont hinge appeared in the Silurian (*Paracyclas* and *Illionia*) and Devonian (*Cypricardella* and *Eodon*) as well as genera with a schizodont hinge (*Schizodus*). Genera with a pterinoid hinge became more common (ca. 10%). Bivalves with two almost equal adductor scars dominated (ca. 60%). Shells with a larger posterior scar (15–25%) and with a single posterior scar (15–20%) were common. Shells with a larger anterior scar were rare. Auxiliary muscular scars occurred rarely (6% of genera in the Silurian and 3% in the Devonian). Genera with an external ligament were dominant. These included shells with an opisthodetic ligament (30% in the Silurian and 45% in the Devonian) and amphidetic ligament (22% in the Silurian and 15% in the Devonian). The internal ligament was observed in a few genera (less than 5%), and a combination of external and internal ligaments was also observed in rare Devonian taxa. Bivalves lacking a ligament were recorded for the first time from this period. The pallial line was entire in most genera (90%), only 10% possessed a shallow sinus.

In the Late Paleozoic, the proportion of genera with an inequivalve shell increased to 25–30%. Smooth shells, and those with concentric ribs, were most common (25–30%), while shells with radial ribs occurred more rarely (ca. 20%). Shells with composite ornamentation constituted ca. 15%, while those with radial and concentric striae constituted less than 10%. The majority of shells lacked a gape, although the proportion of genera with a gape increased (10%). Inequilateral shells with a shorter anterior part predominated (ca. 70%), whereas there were also shells with a reduced anterior part and a terminal beak (ca. 10%), equilateral (ca. 20%), and rare taxa had inequivalve shells with a longer anterior part (less than 5%). Beaks were mostly prosogyral (ca. 70%), whereas orthogyral and opisthogyral beaks were observed in 20 and 10%, respectively. The proportion of genera with auricles and a byssal notch (25–40%) considerably increased. Genera with an edentate hinge dominated (55–60%), while taxa with a heterodont hinge (ca. 10%), dysodont hinge (7–8%), neotaxodont hinge (6% in the Carboniferous and 3% in the Permian), pterinoid hinge (3–4%), ctenodont hinge (1–2%), and actinodont hinge (1.5%) were less widespread. Genera with a desmodont hinge appeared in the Permian (5%), whereas the cyrtodont and heterodont hinges were absent beginning with the Carboniferous. Approximately half of all taxa had two equal adductor scars, 30–40% had a single posterior scar, and less than 20% had scars of different sizes, with a smaller anterior scar in most cases. Auxiliary scars were present in 1–2% of all taxa. Genera with an external opisthodetic ligament dominated (45%), while taxa with both types of ligament were frequent, especially in the Permian (up to 25%). The external amphidetic ligament was developed in 10% of the Carboniferous genera and 4.5% of the Permian genera, while the internal ligament was present in 6 and 3%, respectively. The external ligament placed in the pits in the ligament area appeared in the Permian. Shells lacking a ligament were scarce (at most 1%). Genera with an entire pallial line dominated (ca. 85–90%), while 13% of the Carboniferous genera and 6% of the Permian genera had a shallow sinus. A deep sinus was developed in 2 and 3% of the genera, respectively.

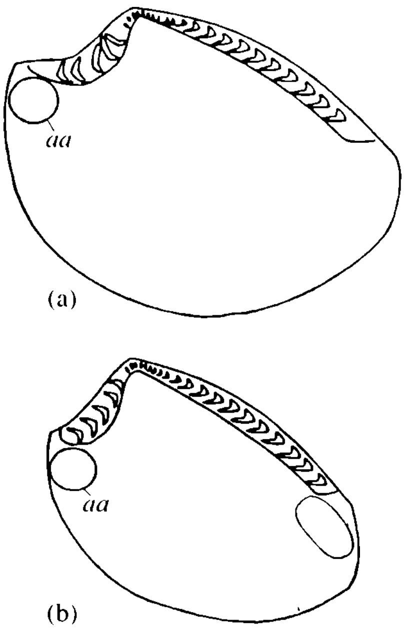


Fig. V. 13. Hinge of the right valve in Late Ordovician members of the family Praenuculidae: (a) *Emiliania* (after Sánchez, 1999, text-fig. 8); and (b) *Hemiconcavodonta* (after Sánchez, 1999, text-fig. 6-2). For designations, see Fig. V. 11.

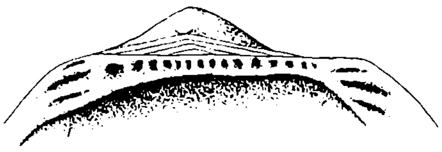


Fig. V. 14. Hinge of the right valve in *Freja* (family Frejidae). Lower Silurian (after Ratter and Cope, 1998, text-fig. 1C).

In the Mesozoic, inequivalve shells became even more abundant (a third or more of all genera), and also did genera with composite ornamentation (20–23%).

Smooth shells also became more common. The same number of genera had concentric and radial ribbing; 6–8% of all genera had a gape. In the Cretaceous, bivalves with a reduced shell first appeared. This was compensated for by the development of the calcareous tubule and auxiliary plates. In the Triassic and Jurassic, taxa with auricles and a byssal notch were numerous (20–30%), whereas in the Cretaceous, their number decreased to less than 10%. Inequilateral shells with a shorter anterior part continued to dominate (65–70%), although the proportion of equilateral shells increased to 20–25%. In the Triassic and Jurassic, genera with the reduced anterior part and the terminal umbo were common (10–15%). Very few taxa had a shorter posterior part. In the majority of genera, the beaks were prosogyral (ca. 70% in the Triassic and Jurassic and ca. 60% in the Cretaceous); more rarely, orthogyral (10–20%) and opisthogyral (ca. 10%) beaks occurred. Shells with the spirogyral beak appeared for the first time (4, 10, and 16% in the Triassic, Jurassic, and Cretaceous, respectively). The proportion of edentate genera gradually decreased (42% in the Triassic, 33% in the Jurassic, and 22% in the Cretaceous), while the proportion of heterodont taxa increased (15% in the Triassic, 25% in the Jurassic, and 32% in the Cretaceous). Genera with the schizodont hinge became more common (10%), whereas in the Cretaceous, genera with a pachyodont hinge were common (18%). Beginning with the Jurassic, shells with the actinodont hinge completely disappeared, while the importance of the genera with a pterinoid hinge decreased (9% in the Triassic, 4% in the Jurassic, and 1.5% in the Cretaceous). The proportions of shells with the taxodont hinge [including the ctenodont (4–6%) and neotaxodont hinge (4–6%)], desmodont hinge (3–4%), and dysodont (2–4%) hinge were small, but stable. The genera with the isodont hinge first appeared, although their proportion remained low (1–2.5%). Similar to in the Late Paleozoic, half of all genera in the Triassic and Jurassic had almost two equal adductor scars, whereas in the Cretaceous, the number of such genera increased (to 70%). They were followed by the genera with a singe posterior muscular scar (44% in the Triassic, 33% in the Jurassic, and 20% in the Cretaceous). The anisomyrian taxa were less common (6–12% with a smaller anterior scar and 2–3% with a larger anterior scar). Taxa in which the anterior muscular scar was on the umbilical reflection appeared in the Triassic. Auxiliary scars were rarely present. The majority of genera had only the external ligament (from 55 to 70%), of which 4% had the ligament in the pits of the ligament area; 14 to 21% of all genera had only the internal ligament, 5–15% had both external and internal ligaments, while 5–8% lacked a ligament completely. As before, taxa with an entire pallial line dominated (88% in the Triassic and 75% in the Cretaceous); however, the proportion of genera with a sinus on the pallial line increased from the Triassic (12%) to the Cretaceous (25%). The proportion of taxa with a deep sinus also increased (from 2 to 6%, respectively).

In the Cenozoic, equivalve shells sharply dominated (85–88%). The ornamentation was diverse. Genera with a smooth shell, concentric and radial ribs, and with a composite ornamentation existed in almost equal proportions (20–25%). The proportion of shells possessing auricles and a byssal notch, as in the Cretaceous, was small (4–7%). Most genera had a shell without a gape. The gape was present in 8–10% of all genera. The proportion of taxa with a reduced shell increased compared to the Cretaceous. In these taxa, the calcareous tubule (ca. 0.5%) or auxiliary plates were sometimes developed (1–1.5%). As before, inequilateral shells with a shorter anterior part dominated (65%); of these, in 3–4% of genera, the anterior margin was completely absent. Approximately a third of all genera had an equilateral shell (27–30%), while genera with a shorter posterior part were rare (5–6%). Genera with the prosogyral beak were dominant (70–75%), while the beak was opisthogyral in 13–18%, orthogyral in 8–12%, and spirogyral in 2–3% of all genera. In the Cenozoic genera, the heterodont hinge dominated (45–55%), whereas 17–22% of all genera had the edentate hinge; 11–12% of the Paleogene and 8–9% of the Neogene–Quaternary genera had the taxodont hinge. The primary taxodont, or ctenodont, hinge was present in 6–7% of the Paleogene genera and in 5% of the Neogene-Quaternary genera, while the secondary taxodont, or neotaxodont, was present in 4–5% and 3–4% of all genera, respectively. The dysodont, desmodont, and schizodont hinges were present in 3–5% each. Very few bivalves had isodont or pterinoid hinges. Approximately 70% of all Paleogene and 80% of Neogene genera had two almost equal muscular scars, while 16–18% of Paleogene and 11–12% of Neogene genera were anisomyarian. Among the latter, most shells had a larger anterior scar (11–12% of Paleogene and 9% of Neogene–Quaternary genera). Genera with a single posterior muscular scar constituted 12–15% of all the Paleogene and 10–12% of Neogene and Quaternary genera. Virtually no shells had auxiliary muscle scars. Shells with the external ligament dominated (ca. 60%), and among those only 3–5% had the amphidetic ligament, while others had the opisthodetic ligament. Shells in which the external ligament was located in the pits on the ligament area were very rare. The internal ligament was present in 16–22% of all genera, whereas the internal and external ligaments were in 9–12%. The ligament was absent in 5–10% of all genera. The majority of genera had an entire pallial line (ca. 65%). Among shells with a sinus, most had a shallow sinus, whereas a deep sinus was present in 10–13%.

The appearance and development of particular morphological characters are discussed below (Fig. V. 15).

Degree of inequivalvity. The first bivalves had an equivalve shell, whereas the first inequivalve genera appeared in the second half of the Ordovician (less than 10%). Later, the proportion of inequivalve bivalves increased during the terminal Early Paleozoic and the Late Paleozoic (from 20 to 30%) to reach a maximum in the Mesozoic (up to 30–35%). In the Cenozoic, the proportion of these shells decreased to 12–17%.

Ornamentation. In the Cambrian and Early Ordovician, shells with a smooth surface prevailed. From the mid-Ordovician, their number decreased and remained at a level of 25–30% until the end of the Mesozoic and then maintained a level of about 25% in the Cenozoic and the Recent. Genera with concentric ornamentation appeared in the Early Ordovician and remained at a level of 30%, more rarely, 40% (second half of the Ordovician, Devonian, Permian, and Jurassic), to the present day. Shells with radial striae and ribs in the Ordovician constituted about 15% of the total number of genera. Later, the proportion of genera with such ornamentation ranged from 20 to 30%. The proportion of genera with composite ornamentation gradually increased from the Ordovician to the Permian (from 2 to 15%), and in the Mesozoic and Cenozoic, it was at a level of 20%.

Degree of inequilaterality. The extent of the inequilaterality of the shell also fluctuated in geological time. The first bivalves were equilateral or slightly inequilateral; later, shells in which the anterior part was shorter became dominant (60–70%). The proportion of equilateral shells somewhat increased (15–20% in the Paleozoic, 20–25% in the Mesozoic, and ca. 30% in the Cenozoic and Recent). Genera in which the anterior part was reduced and the umbo became terminal were absent in the Cambrian and Early Ordovician and first appeared in the Middle Ordovician; however, they were not very common, and nor were shells with a shorter posterior part, first recorded in the Cambrian (usually, less than 10%).

Beak. Genera with the prosogyral, opisthogyral, and orthogyral beak were known from the Early Ordovician, and their percentage was more or less stable over the whole of the Phanerozoic (60–70% of genera had prosogyral beaks, while 10–20% had opisthogyral and orthogyral beaks). Shells with spirogyral beaks appeared beginning with the Triassic, but constituted only 5% of all genera. Only in the Jurassic and Cretaceous, their proportion increased to 10 and 16%, respectively. Subsequently, it sharply dropped and has not risen above 2–3% since.

Presence of auricles and a byssal notch. Genera with auricles and a byssal notch became especially numerous in the Late Paleozoic and in the first half of the Mesozoic (in the Triassic and Jurassic, they constituted up to 20–30% of all genera). Beginning with the Cretaceous, their percentage somewhat dropped. Winglike shells are known beginning with the Silurian and usually present in a few genera (2–3%). Only in the Triassic and Jurassic, their proportion increases to 8%.

Hinge. The most noticeable changes in the Phanerozoic occurred in the hinge structure and in the proportions of different hinge types. As mentioned above, in the Cambrian, a few recorded genera had primitive hinges, i.e., the preheterodont (or, possibly, so-called pretaxodont) hinge composed of one to three subumbilical teeth (Hprg). In the Ordovician, the diversity of hinge types considerably increased. Shells with the preheterodont hinge continued to exist, but many genera with the actinodont hinge (Ha) appeared; edentate genera (Htl) and those with the ctenodont (Hc) (primary taxodont) hinge were common. Rare genera had the cyrtodont (Hcyr), pterinoid (Hpt), lyrodesmoid (Hl), secondary taxodont (pseudoctenodont) (Ht), pachyodont (Hpa), and desmodont (Hdes) hinges. The Ordovician archaic diversity gradually decreased throughout the Paleozoic. At the same time, the hinge types that became widespread in the Mesozoic and Cenozoic began to develop.

In the Silurian, shells with the lyrodesmoid hinge almost disappeared, and the first few genera with the heterodont hinge appeared. In the Devonian, no major changes happened, except for the appearance of the first genera with the schizodont (Hs) hinge. In the Carboniferous, shells with the cyrtodont and preheterodont hinge types were absent, whereas the dysodont (Hdys) hinge appeared. In the Permian, shells with desmodont hinges became widespread.

Thus, in the Early and Middle Paleozoic, genera with the edentate (12–20% in the Ordovician and 35–45% in the Silurian and Devonian), ctenodont (16–30%), and preheterodont (at least 60% in the Cambrian and ca. 10–15% in the Ordovician and Devonian) hinges dominated; in addition, the actinodont hinge was common in the Ordovician (15–20%).

In the Late Paleozoic, genera with the toothless hinge (55–60%) were dominant, while the proportion of shells with the heterodont hinge considerably increased (up to 10%). Other hinge types occurred more rarely.

In the Mesozoic, shells with the toothless (42% in the Triassic, 33% in the Jurassic, and 22% in the Cretaceous) and heterodont hinges (15% in the Triassic, 25% in the Jurassic, and 32% in the Cretaceous) dominated, while in the Cretaceous, the genera with the pachyodont hinge (ca. 20%) became common. The last shells with the actinodont hinge were recorded in the Triassic (less than 1%). For the first time genera with the isodont hinge (His) appeared, although they were rare. Other hinge types, known in Mesozoic genera, were rather uncommon, with only those shells with a schizodont hinge constituting up to 10%.

In the Cenozoic, genera with the heterodont hinge became dominant. The proportion of these genera fluctuated around 50%. The toothless hinge was rather common (ca. 20%), whereas other hinge types were less common. The ctenodont hinge was present in 5–7% of genera, the schizodont, desmodont, and neotaxodont were in 3–5% (genera with the schizodont hinge increased in number in the Quaternary and Recent up to 7–12% due to the development of freshwater unionids). The dysodont hinge was present in 3–4% of genera, while the isodont, pterinoid, pachyodont, and provinculum hinges were present in less than 1% of all genera (or even less). In the Neogene (Miocene), the limopsid hinge (Hli) appeared, but it was present in only 0.2–0.3% of all genera.

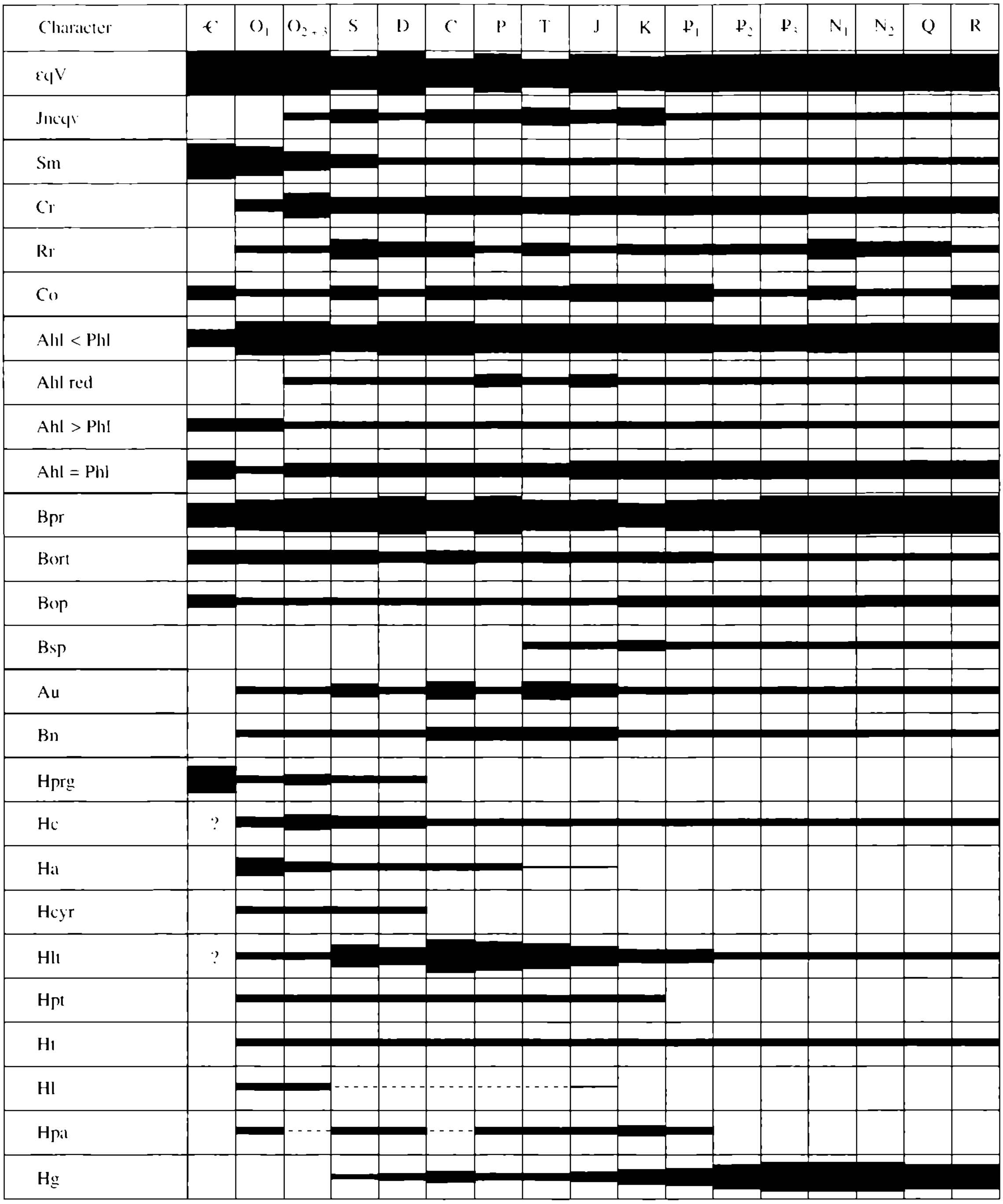


Fig. V. 15. Change in proportions of bivalvian genera with a certain set of morphological characters in the Phanerozoic. Characters: relation between valves: (Eqv) equivalve and (Ineqv) inequivalve shells; ornamentation: (Sm) smooth, (Cr) concentrically ribbed and striate, (Rr) radially striate and ribbed; and (Co) composite; degree of inequilaterality: (Ahl = Phl) anterior part is equal to the posterior part, i.e., equilateral shell; (Ahl < Phl) anterior part is shorter than the posterior part; (Ahl > Phl) anterior part is longer than the posterior part; (Ahlred) anterior part is reduced; beak: (Bop) opisthogyral, (Bort) orthogyral, (Bpr) prosogyral, and (Bsp) spirogyral; hinge: (Ha) actinodont, (Hg) heterodont, (Hdes) desmodont, (Hdys) dysodont, (His) isodont, (Hc) ctenodont, (Hl) lyrodesmoid, (Hli) limopsid, (Htl) toothless, (Hpr) provinculum, (Hprg) preheterodont, (Hpt) pterinoid, (Hpa) pachyodont, (Hs) schizodont, (Ht) taxodont (secondarily taxodont), and (Hcyr) cyrtodont; arrangement of adductor scars: [2As] two equal scars; [2As (Aas>)] two scars, anterior is larger than the posterior; [2As (Aas<)] two scars, anterior smaller than the posterior; and [1As] one scar; ligament: (Lin) internal, (Lin+ex) internal and external, (Lex) external, and (Ll) ligament is lost; pallial sinus: (Si) present, (Sid) deep, and (Sil) absent; (Au) presence of auricles; (Bp) presence of byssal notch; (Hy) presence of gape; and (Ct) calcareous tube is present; percentage of genera: (*1*) less that 1%, (*2*) 1 to 10%, (*3*) 11 to 20%, (*4*) 21 to 30%, (*5*) 31 to 40%, (*6*) 41 to 50%, (*7*) 51 to 60%, (*8*) 61 to 70%, (*9*) 71 to 80%, (*10*) 81 to 90%, and (*11*) 91 to 100%.

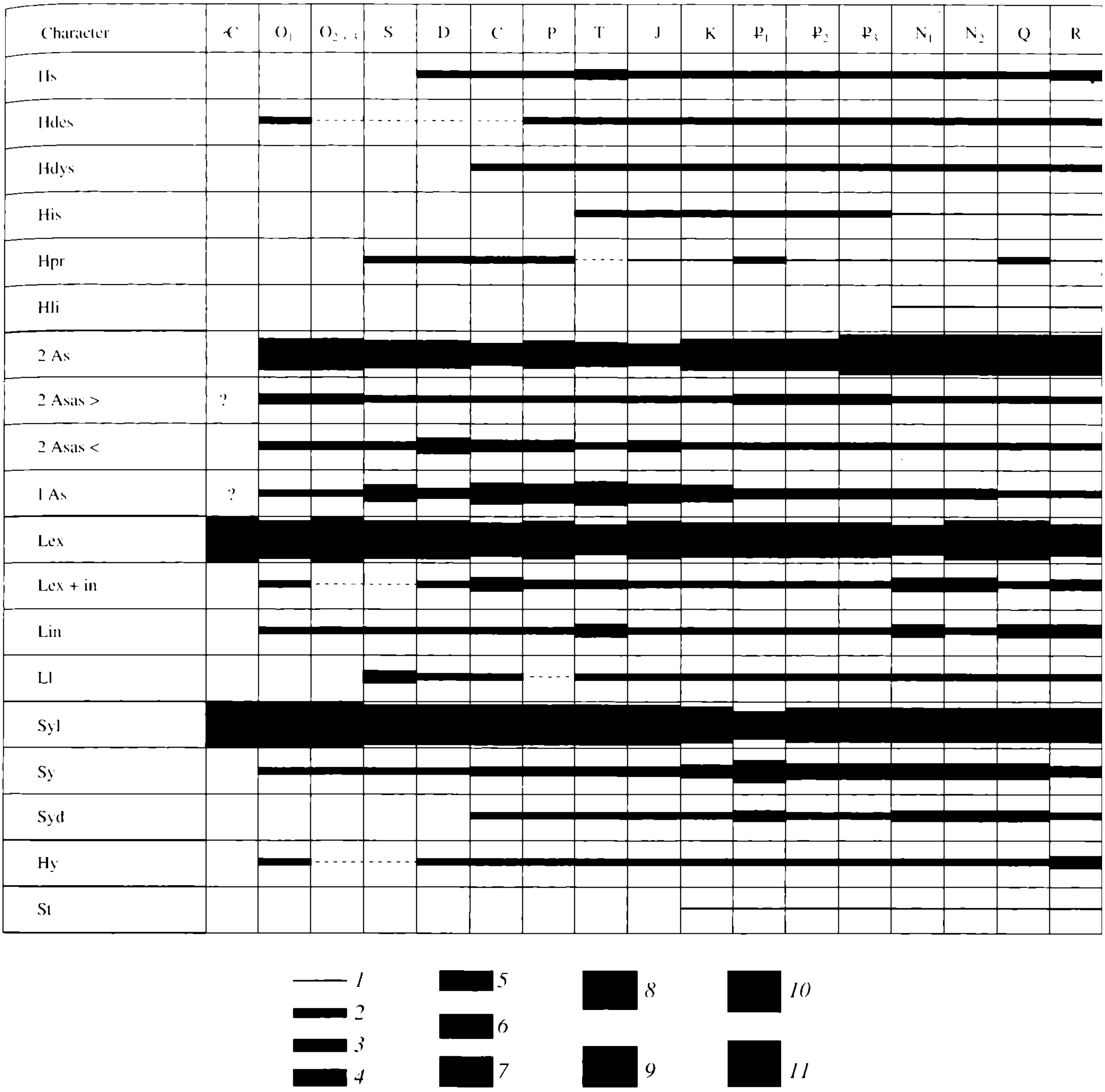


Fig. V. 15. (Contd.)

Muscular scars. In the Cambrian genera, only the posterior muscular scar was developed well, while the anterior scar was small (if it was present at all). Beginning from the Early Ordovician, genera with two almost equal adductor scars were dominant (45 to 80%). Anisomyarian taxa were less common. A smaller anterior muscular scar was present in 13–25% of Paleozoic genera, 6–12% of Mesozoic genera, and 3–7% of Cenozoic genera, whereas the better developed anterior scar was present in only 1–4% of Paleozoic and Mesozoic genera, and only in the Early Ordovician were there more than 10% of such genera. In the Cenozoic, 9–12% of all genera had a larger anterior scar. One (posterior) adductor scar was present in less than 10% of Ordovician genera, whereas in the Silurian and Devonian, it was present in 21 and 15% of genera, respectively. In the Late Paleozoic, Triassic, and Jurassic, it was present in 30–45%; in the Cretaceous, it was in 20%; and in 10–15% of all genera in the Cenozoic, i.e., the shells with a single muscle were most common from the Late Paleozoic to the Jurassic.

Shells in which the anterior muscular scar was placed on the valve of the anterior hinge line first appeared in the Triassic, and were present in 0.5% of genera in the Triassic and Jurassic and in 3% of genera from the Cretaceous to the present.

Auxiliary muscular scars, which were possibly left by the muscles, which fixed the mantle in the subumbilical region (Kříž, 1995), were characteristic of all Cambrian genera and many Early Ordovician genera (12%). Later, their proportion decreased to 1–2% in the Late Paleozoic and Triassic and was less than 1% in the Jurassic and Cretaceous. No taxa with auxiliary scars are recorded from the Cenozoic.

Ligament. The Cambrian genera had only the external ligament, which could be opisthodetic, or amphidetic. Taxa with the external opisthodetic ligament dominated throughout the Phanerozoic, whereas the amphidetic ligament was present in 5–25% of Paleozoic genera, and less than 5% of Mesozoic and Cenozoic genera. Shells in which the external ligament was situated in the pits on the ligament area appeared in the Permian and were moderately common throughout the Mesozoic (5–8%), whereas their proportion decreased in the Cenozoic. A combination of the external and internal ligaments was recorded beginning from the Early Ordovician, but it became common only from the Devonian. In the Late Paleozoic and Triassic, the proportion of such genera reached 15–25%. From the Jurassic to the present, the proportion of such genera was approximately 10%, more rarely, slightly more. Genera with the internal ligament appeared in the Early Ordovician, although in the Paleozoic, their proportion did not exceed 7%, and from the Triassic increased to 15–20%.

Pallial line. During the entire Phanerozoic, genera with a complete pallial line were dominant; they strongly prevailed in the Paleozoic and Triassic (100% in the Cambrian and 84–93% from the Ordovician to the Triassic), while from the Jurassic, their role gradually decreased (75–80% in the Jurassic and Cretaceous and 50–65% in the Cenozoic). The proportion of genera with the pallial sinus increased (8–10% in the Ordovician, ca. 15% in the Late Paleozoic and Triassic, 20–25% in the Jurassic and Cretaceous, and ca. 35% in the Cenozoic). Genera with a deep sinus appeared only from the Late Paleozoic and constituted 2–3% from the Carboniferous to Jurassic, 6% in the Cretaceous, and slightly over 10% in the Cenozoic.

Gape. The gape was developed in a small number of bivalve genera. More than half of boring bivalves had a shell opening from behind. This feature was also present in many deeply burrowing and crevice-dwelling suspension-feeders. The first opened shells are recorded from the Early Ordovician, and their proportion remained constant throughout the Phanerozoic (ca. 10%).

In the majority of boring bivalves, the shell was reduced. This was compensated for by either the development of the auxiliary plates (Pholadidae) or the calcareous tubule (Clavagellidae). The reduction is observed from the Jurassic (0.5 of genera had a reduced shell). From the Cretaceous until the present, the proportion of these taxa has been 3–3.5%.

CHAPTER VI. ECOLOGY OF BIVALVES

(1) Factors Responsible for the Distribution of Bivalves

(a) Abiotic Factors

Bivalves are important organisms in the marine benthos. They depend on many physical parameters (temperature, salinity, gas regime, water turbulence, substrate, depth, and food resources) (Turpaeva, 1948, 1953, 1954, 1957; Sokolova, 1954; Pérès, 1961; Neiman, 1963, 1969, 1977, 1985; Kuznetsov, 1964, 1969, 1976, 1980; Harper and Palmer, 1997; etc.).

Based on temperature affinity, the following groups are recognized: thermophilic, cryophilic, stenothermal, and eurythermal. The distribution of these groups depended on climatic zonation, which existed in different time intervals and on local conditions. It is noteworthy that the Paleozoic was dominated by eurythermal bivalves, a group that was not subdivided into thermophilic and cryophilic forms. Apparently, this resulted from the fact that bivalves in the Early and Middle Paleozoic seas were mainly distributed in marginal and coastal areas, where temperatures were unstable. In the Late Paleozoic, they were abundant in all zones of boreal and notal seas, while in the tropical realm, they were restricted to the marginal and coastal zones. In the Mesozoic and Cenozoic, especially beginning with the Jurassic period, the differences in the boreal-notal and tropical malacofaunas became noticeable at generic and familial levels (see Chapter IX). These differences became especially prominent in the second half of the Mesozoic and at present (Gladenkov, 1978, 1987; Kafanov, 1979; Stevens, 1989; Gladenkov and Sinel'nikova, 1990, 1991; Clarke, 1992; Rex *et al.*, 1993; etc.).

The effect of fluctuations of salinity and ion content of the water was significant in the epicontinental basins, while the open seas may have had reduced salinity near river mouths. In such freshwater regions, the composition of bivalves was impoverished and dominated by euryhaline taxa (Hecker *et al.*, 1962; Hudson, 1963, 1980; Dzhalilov, 1983; Poyarkova, 1984; Fürsich and Werner, 1984, 1986; Fürsich and Kauffman, 1984). Almost closed basins with reduced salinity and modified ion content contained endemic brackish-water faunas (Nevesskaja, 1971; Runnegar and Newell, 1971; Nevesskaja *et al.*, 1986).

The changes in the oxygen content in the bottom water layers and in the sediment, i.e., the formation of disaerobic conditions, caused the disappearance of oxyphilic species and the dominance of taxa tolerant to such conditions.

Benthic bivalves are greatly dependent on the hydrodynamics of surrounding waters, because the latter determine the distribution of temperatures, salinity, gas content, character of the substrate, degree of turbidity, and amount and quality of food. Zones of increased hydrodynamics were usually inhabited by bivalves with large and massive shells and were dominated by suspension-feeders, especially, those which were cemented. Zones of reduced hydrodynamics with fine-grained sediment and increased content of organic matter were dominated by debris-feeders (Kuznetsov, 1976, 1980; Stanton and Dodd, 1976; etc.). A good example of the dependence of the composition of bivalves on the fluctuation of the hydrodynamics of marine basins is the change in the communities in the Late Jurassic Lusitanian Basin (Fürsich and Werner, 1986). In the periods characterized by high hydrodynamics, this basin was inhabited by the shallowly burrowing eurybiontic suspension-feeders *Eomiodon*. In the environment of moderately high hydrodynamics, this basin was inhabited by communities of the endobyssal semi-infaunal suspension-feeders *Modiolus*, the epifaunal cemented *Praeexogyra* and *Nanogyra*, and a community of the semi-infaunal *Stegoconcha* and cemented *Lopha* settled on the fine-grained sands and carbonate mudstones. In the environment of low hydrodynamics, muddy substrates were inhabited by the infaunal debris-feeder *Palaeonucula* accompanied by some infaunal suspension-feeders.

With reference to the sea depth, shallowwater and deepwater species are commonly recognized. These species constituted shallow-water and deep-water communities, respectively. For the shallow shelf, the depth was not very important; more important were the hydrodynamics, substrate, salinity, etc. In the deep zones, in the environment of low hydrodynamics, low temperatures, muddy substrates, and frequent oxygen deficiency, the composition of bivalves was considerably more uniform than at lesser depths. It was also noted that shallow-water species are usually adapted to a broader range of environmental factors and are evolutionarily more flexible than deep-water species (Jackson, 1974).

The distribution of bivalves was largely affected by the substrate, which was one of the major factors. The type of substrate was determined by the hydrodynamics, material brought from land, rate of sedimentation, bioturbation by infaunal organisms, development of marine vegetation, etc. The major features of the substrate include the degree of stability, consolidation, sorting, aeration, size of grains, content of organic matter, and the presence of skeletal remains in the sediment. These remains could be a substrate for epibionts, objects for boring, a recess for epibionts, and could inhibit infaunal organisms from burrowing in the sediment. Trueman *et al.* (1966), Alexander (1993), Alexander *et al.* (1993) showed the correlation of the rate of burrowing of the semi-infaunal and infaunal bivalves and the grain size of the sediment; bivalve species were referred to different groups depending on the specialization to substrate, which was reflected in the shell morphology.

Hard substrates were usually inhabited by the eurybiont taxa, both firmly and flexibly attached, and boring bivalves, while the loose and soft substrates were inhabited by free-lying and burrowing bivalves, and soft and dense substrates were inhabited by free-lying and creeping bivalves.

In terms of feeding, all bivalves are consumers, or heterotrophs, i.e., they feed on other organisms. They feed on (1) seston, mostly consisting of phyto- and microzooplankton suspended in bottom water layers, corpuscular dead debris, detritobacterial and mineral organic bacterial complexes and dissolved organic matter, (2) settled debris with bacteria and microphyto- and microzoobenthos, (3) debris buried in the sediment, (4) living and dead organisms, (5) products of metabolism of symbionts (microscopic algae and chemiautotrophic bacteria (Newell, 1965b; Nicol, 1972; Kuznetsov, 1980, 1986; Neiman, 1985; Zezina, 1986; Reid and Brandt, 1986; Kuznetsov *et al.*, 1987, 1988; Fiala-Medioni and Felbeck, 1989; McDonald *et al.*, 1990; Chassard-Bouchaud *et al.*, 1990; Seilacher, 1990; Ohno *et al.*, 1995).

(b) Biotic Factors

Benthic organisms usually compete for habitats and food. To overcome this competition, the epifaunal suspension-feeding bivalves, like other invertebrates, fed in different layers of bottom waters (multi-storey distribution). The majority of genera were confined to 0–5 cm over the bottom, although from the second half of the Carboniferous, representatives of some genera moved into higher stories (5–10 and 10–20 cm).

Differentiation of depth of burrowing was also characteristic of the infaunal taxa. For instance, the suspension-feeders of the orders Praecardiida, Actinodontida, Cyrtodontida, and Pholadomyida occupied the storey from 0 to –6 cm. The storey from –6 to –12 cm was inhabited by certain genera of the orders Pholadomyida (from the end of the Silurian), Venerida (from the Devonian), Cyrtodontida (from the end of the Early Carboniferous), and Actinodontida (from the middle of the Triassic), whereas the storey from –12 to –100 cm was inhabited only by the representatives of two orders, Pholadomyida (from the middle of the Early Carboniferous) and Venerida (from the Triassic) (Ausich and Bottjer, 1990, 1991). Because all these suspension-feeders fed only in the water layer immediately above the surface of the sediment, the storey distribution was not caused by competition for food resources, but more likely facilitated a more rational spatial distribution, serving as an adaptation precluding predation by gastropods and arthropods. At the same time, the storey distribution of debris-feeders also developed as a result of competition for food.

Bioturbation of the sediment caused by the activity of the infaunal debris-feeders and predators and responsible for the development of the amenalism of the trophic group was unfavorable for bivalves (Thayer, 1979, 1983; Jablonski *et al.*, 1983). The bioturbation in the Mesozoic became high enough to preclude sessile suspension-feeders from inhabiting the soft grounds. This resulted in some epifaunal forms becoming infaunal (Thayer, 1983).

Predation, which increased beginning with the Mesozoic, greatly affected the distribution of bivalves (Vermeij, 1977). Adaptation against predation included heavily ornamented and thickened shells and a strong conchiolin layer, decreased inner space, secretion of the ability to close the shell, fast escape, concealment, and the development of poisons (Vermeij, 1983; Harper and Skelton, 1993; Harper, 1994; Kelley *et al.*, 1995; Stone, 1998). The increase in predation was also responsible for a decrease in the proportion of epibiontic bivalves and for the distribution of infaunal taxa.

The relationships between bivalves and brachiopods occupying similar niches are noteworthy. Brachiopods played a major role in the communities of epifaunal invertebrates during the entire Paleozoic. However, after the Permian–Triassic crisis, they lost their importance. However, it is unlikely that they were displaced by bivalves (Afanasjeva and Nevesskaja, 1994; Afanasjeva *et al.*, 1998). More likely, brachiopods failed to recover after the crisis at the end of the Permian and to adapt to new conditions in the Meso-Cenozoic. Brachiopods had nonplanktontrophic larvae, could not reattach after they were pulled off the substrate as a result of the increased bioturbation, did not have adaptations to resist the increased pressure of predation, could not burrow in the substrate, and were generally less capable of surviving unfavorable conditions (Stanley, 1968; Thayer, 1985, 1986; Miller and Sepkoski, 1988; Rhoads and Thompson, 1993; Aberhan, 1994; Shubert and Bottjer, 1995).

In contrast, bivalves had several advantages allowing their wide and rapid distribution in the Meso-Cenozoic seas. These included the presence of a long planktonic stage, which could continue at times of stressed (in particular, anoxic) conditions, or until the animal reached a substrate suitable for settlement, high tolerance of postlarval stages and adults to the habitats, including various substrate and temporary high-stress environments (reduced salinity, disaerobic conditions, etc.), effective mobility of adults in some genera (some species could float above the substrate in an unfavorable environment and become pseudoplanktonic, being attached by the byssus to floating objects), development of strong foot and siphons, which allowed burrowing and escape from the environment of high bioturbation, and the appearance of adaptations against predators (Stanley, 1968; Kauffman, 1975; Thayer, 1983, 1985, 1986; Aberhan, 1994).

(c) Environment and Composition of Benthos in Different Zones in the Sea

The above abiotic and biotic factors had different effects in different sea zones. This resulted in the difference in the composition of benthos, including bivalves. Therefore, it is more useful not only to discuss the taxonomic and ecological composition of bivalves, but also to consider the characteristic features of bivalvian communities in different sea zones and their changes throughout time.

The following zones are recognized: (1) marginal (lagoons, bays, and deltas), (2) tidal and coastal (intertidal), (3) shallow shelf (upper part of the sublittoral zone), (4) organic buildups and (5) deep shelf (lower part of the sublittoral and pseudoabyssal zones). The comparative characterization of the zones is cited from the literature (for references see Nevesskaja, 1998, table II. 2).

The marginal zone shows reduced or increased salinity or its strong fluctuations, low water turbulence, occasional oxygen deficiency, muddy, sandy, and carbonate–muddy substrates, high bioturbation, development of cyanobacterial mats, and moderately diverse benthos usually consisting of eurybiontic taxa.

The coastal zone has active hydrodynamics, unstable regime because of the sea level fluctuations, changes of the land material influx, etc. The substrates are coarse-clastic and coarse-grained, more rarely, muddy and carbonate–muddy, often, shellstones, usually with spot distribution of sediments of various types. The bioturbation is high. The concentration of the suspension near the bottom is relatively high, while the quantity of the organic matter in the sediment is low. The benthos is the same as in the marginal zone.

In the zone of the shallow shelf the salinity is normal, the hydrodynamics are moderately high, but the shallowest regions are affected by storm waves. The aeration is good. The substrates are sandy, silty, and bioclastic. The bioturbation is high. The bottom water layer contains a high quantity of food particles, whereas the quantity of the organic matter in the sediment is low. Benthos is diverse. Dense algal vegetation is typical.

The zone of organic buildups is usually confined to shoals. The salinity is normal, the hydrodynamics are high, the aeration is good. The grounds between the bioherms and biostromes are detrital and bioclastic, more rarely, quartzitic-sandy. The benthos is diverse, dominated by epifaunal sessile reef-builders and calcareous algae.

The deepwater zone shows normal salinity, reduced hydrodynamics, possible oxygen deficiency, and muddy substrates. The quantity of suspended matter is relatively low in the bottom water layers, whereas the quantity of the organic matter in the sediment is high. The benthos is impoverished and weakly variable. Vegetation is absent.

(2) Ethological-Trophic Groups of Bivalves and Their Distribution in the Phanerozoic

(a) Ethological-Trophic Groups

Of all factors affecting the distribution of bivalves, the type of feeding and mode of life (preferred substrates and degree of mobility) are the most important.

Of the major trophic groups of benthic organisms (suspension-feeders, sorting and nonsorting debris-feeders, predators, and herbivores, see Turpaeva, 1948, 1953, 1957; Savilov, 1957, 1961; Scott, 1972, 1976; Walker and Bambach, 1974; Kuznetsov, 1976, 1980) bivalves do not include only nonsorting debris-feeders and herbivores. Passive predators are represented by a small group of genera assigned to the superorder Septibranchia. Representatives of this group have gills transformed into a muscle septum. Small organisms conducted by the inhalant siphon are crushed by the crests on this septum. The Septibranchia are known only beginning with the Jurassic, but their absence in older rocks can be explained by their low numbers and rarity in all epochs of their existence.

Suspension-feeders were the most diverse bivalves. Sorting debris-feeders were more restricted in taxonomic composition, while predators belonging to the Septibranchia played an insignificant role.

One group of bivalves feeds on the products of metabolism of the chemiautotrophic bacteria and microscopic algae (symbionts of mollusks). This feeding type was characteristic of some unrelated taxa, including vesicomyids (*Vesicomya* and *Calyptogena*), solemyids (*Solemya* and *Acharax*), lucinids (*Epilucina, Lucinoma*, and *Myrtea*), thyasirids (*Thyasira, Conchocele, Axinopsida*, and *Axinulus*), mytilids (*Bathymodiolus* and *Amygdalum*). This type was typical near hydrotherms and other vents, where feeding is based on bacterial autochemosynthesis, and mollusks were bacteriosymbiotrophs, while also retaining the original suspension feeding strategy (Kuznetsov *et al.*, 1987; Squires and Goedert, 1991; Kochevar *et al.*, 1992; Conway *et al.*, 1992; Campbell and Bottjer, 1995; Squires and Gring, 1996; Kuznetsov and Maslennikov, 2000; Krylova, 2002).

Some bivalves inhabiting completely different environments (mainly reef buildups) were symbionts of microscopic photosynthetic algae (zooxanthellae). These bivalves belonged to rudists, tridacnids, some solemyids, cardiids, etc.

The majority genera and families maintained their trophological features throughout their existence and belonged to one of the above trophic groups. Only in a few taxa did feeding strategies vary. For instance, representatives of the family Tellinidae, mostly feeding on debris, could occasionally become suspension-feeders (Kuznetsov, 1986). Some brackish-water Cardiidae, in environments with an insufficient quantity of suspended matter, whisked the sediment with siphons and fed like debris-feeders (Romanova, 1963). As mentioned above, some families of suspension-feeders (Lucinidae, Cardiidae, Mytilidae, etc.), include species, which along with suspension feeding use products of metabolism of symbiotic chemoautotrophic bacteria and microscopic algae. This was the major feeding type of the Vesicomyidae, many rudists, and the Tridacnidae.

Various ethological classifications of bivalves in relation to the substrates and mobility were proposed by both marine biologists (Thorson, 1957; Pérès, 1961) and paleontologists (Kudrin, 1957, 1966; Markovsky, 1966; Kauffman, 1969; Stanley, 1968; Kojumdgieva, 1976a, 1977).

Two main groups are recognized in relation to the substrates, infaunal (or endobiontic, i.e., bivalves living inside the substrate) and epifaunal (epibiontic), i.e., living on the substrate (Thorson, 1957). There is an intermediate group of semi-infaunal bivalves, which are only partly submerged in the substrate, while the posterior part of the shell is above the surface of the substrate.

In relation to mobility, the endobiontic bivalves include groups burrowing shallowly and deeply, boring bivalves, bivalves inhabiting cracks, cavities, etc., while the epibiontic bivalves include cemented species, byssal forms, and nonattached (lying, crawling, and swimming) taxa.

A combination of trophological and ethological features resulted in the recognition of several ethological-trophic groups (Stanley, 1968; Pojeta, 1971; Runnegar, 1974; MacKenzie and Pojeta, 1975; Nevesskaja, 1981; Thayer, 1983; Wake *et al.*, 1986; Aberhan, 1994). Taking into account some morphological criteria (presence or absence of byssus and siphons), the following system of ecological (ethological-trophic) groups is proposed (Fig. VI. 1).

I. Suspension-feeders

I.1. Infaunal (endobiontic):

I.1.1. Shallowly burrowing bivalves lacking byssus and siphons;

I.1.2. Shallowly burrowing bivalves with byssus and lacking siphons;

I.1.3. Shallowly burrowing bivalves, lacking byssus, but with two siphons;

I.1.3a. The same, but with byssus and siphons;

I.1.4. Shallowly burrowing bivalves, lacking byssus, with one siphon;

I.1.4a. The same, but with byssus and one siphon;

I.1.5. Relatively deeply burrowing bivalves, with long siphons;

I.1.6. Boring bivalves (with siphons);

I.1.7. Burrowing bivalves forming a tubule (with siphons);

I.1.8. Burrowing bivalves with an exhalant siphon and anterior mucous tubule;

I.1.8a. The same, but with an anterior mucous tubule, lacking an exhalant siphon;

I.1.9. Bivalves inhabiting cracks, cavities, holes (with byssus or without it, with siphons or without them).

I.2. Epifaunal (Epibiontic):

I.2.1. Epibyssal, flexibly attached, lacking siphons;

I.2.1a. The same, but attached to floating objects;

I.2.2. Epibyssal, flexibly attached, with one siphon;

I.2.3. The same, but with two siphons;

I.2.4. Free-lying and/or crawling, lacking siphons;

I.2.4a. Free-lying, capable of swimming, lacking siphons, usually with byssus;

I.2.5. Free lying, with one siphon, with byssus, or lacking it;

I.2.6. The same, with two siphons;

I.2.7. Cemented;

I.2.8. Epifaunal, with symbiotic relationships with photosynthetic bacteria, and/or algae.

I.3. Semi-infaunal:

I.3.1. Endobyssal, lacking siphons;

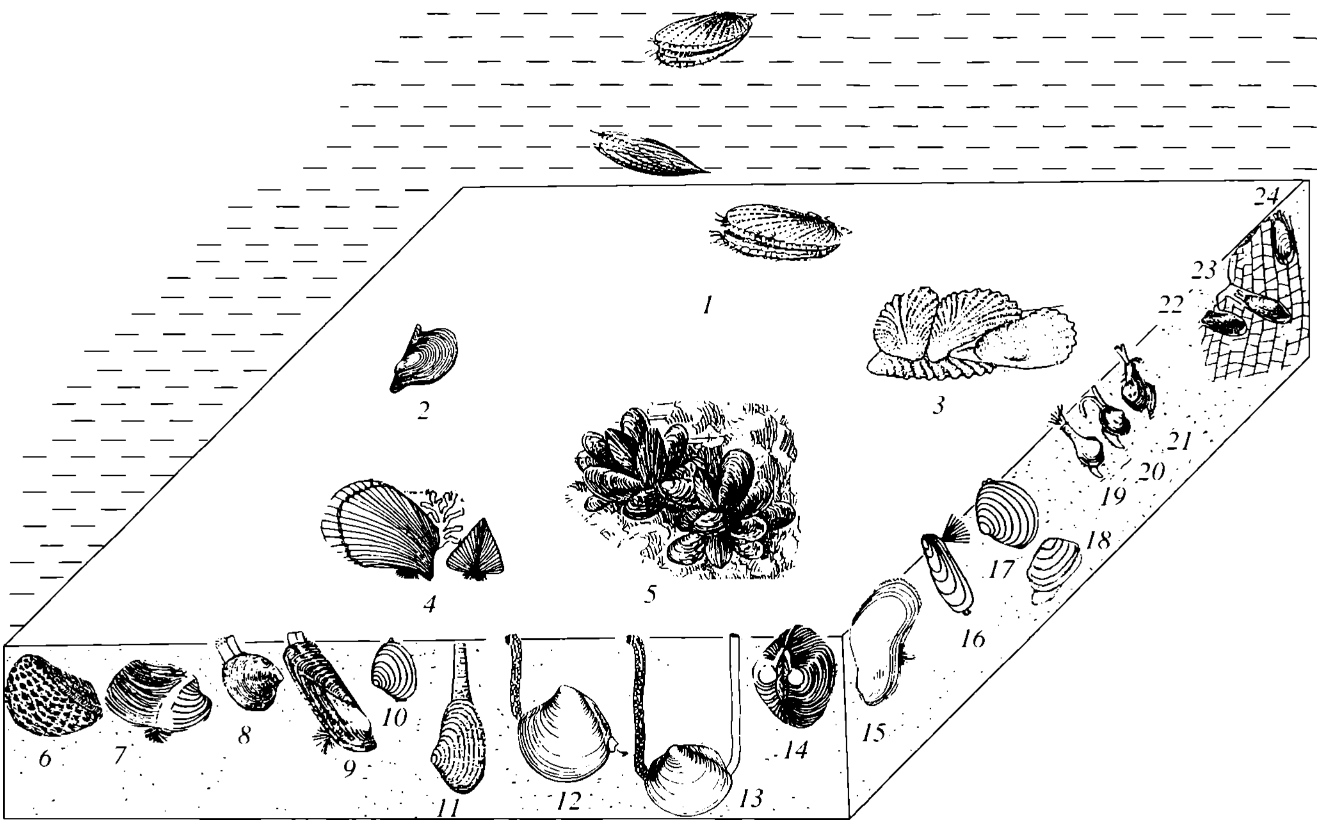


Fig. VI. 1. Members of different ethological-trophic groups: (*1*) epifaunal lying on the substrate and capable of swimming suspension-feeders lacking siphons (I.2.4/I.2.4a); (*2*) suspension-feeders lying on one valve and lacking siphons (I.2.4); (*3*) cemented suspension-feeders (I.2.7); (*4*) epibyssal suspension-feeders lacking siphons (I.2.1); (*5*) epibyssal suspension-feeders with one siphon (I.2.2); (*6*) infaunal suspension-feeders without byssus or siphons (I.1.1); (*7*) infaunal suspension-feeders lacking siphons, with byssus (I.1.2); (*8*) infaunal suspension-feeders without byssus, with siphons (I.1.3); (*9*) infaunal suspension-feeders with siphons and byssus (I.1.3a); (*10*) infaunal suspension-feeders lacking byssus, with one siphon (I.1.4); (*11*) infaunal suspension-feeders with long siphons, relatively deeply burrowing (I.1.5); (*12*) infaunal suspension-feeders with anterior inhalant mucous tubule and very short exhalant posterior siphon (I.1.8a); (*13*) infaunal suspension-feeders with anterior inhalant mucous tubule and long exhalant siphon (I.1.8); (*14*) semi-infaunal suspension-feeders lacking siphons and byssus (I.3.4); (*15*) semi-infaunal endobyssal suspension-feeders lacking siphons (I.3.1); (*16*) semi-infaunal endobyssal suspension-feeders with one siphon (I.3.2); (*17*) semi-infaunal suspension-feeders with siphons, but lacking byssus (I.3.4); (*18*) infaunal debris-feeders lacking siphons (II.1); (*19*) predators Septibranchia (III); (*20*) infaunal debris-feeders with long siphons, which could also feed like suspension-feeders (II.2/I.1.5); (*21*) infaunal debris-feeders with siphons (II.2); (*22*) suspension-feeders living in shelters (I.1.9); (*23*) and (*24*) boring suspension-feeders (I.1.6).

I.3.2. The same, but with one siphon;

I.3.3. The same, but with two siphons;

I.3.4. Semi-infaunal, with siphons, lacking byssus.

II. Debris-feeders

II.1. Shallowly burrowing bivalves and those able to move on the surface of the substrate, lacking siphons, with labial palps;

II.2. Relatively deeply burrowing bivalves, with long siphons;

II.2./I.1.5. Infaunal debris-feeders, with long siphons, which can feed like suspension-feeders.

III. Predators (infaunal, with siphons).

To decide whether or not the ethological-trophic classification can be applied to fossil bivalves, it should be taken into account that not only most species, but entire groups of a higher taxonomic rank (superfamilies, families, genera) often have a steady feeding type, i.e., belong to the same trophic type (suspension-feeders and debris-feeders). Rare flexible species can feed on different sources and in more than one way. Among bivalves, an example is provided by the family Tellinidae; its members were previously thought to be exclusively sorting debris-feeders, but were shown to also be suspension-feeders (Pohlo, 1969; Kuznetsov, 1976). Another example of a varying feeding strategy was noted in Caspian brackish-water cardiids (*Monodacna* and *Adacna*), which usually feed as suspension-feeders, but when the amount of the suspended matter is insufficient, they can whisk particles from the surface of the substrate with their siphons and feed like debris-feeders (Romanova, 1963). However, for all these trophically flexible species, one feeding strategy usually remains dominant.

Ethological features of species, genera, and sometimes entire families were apparently relatively stable in time (Thayer, 1974b, etc.). For instance, it can be assumed that the overwhelming majority of oysters were cemented; mytilids were mainly byssal; nuculids crawled on the substrate or burrowed shallowly; myids, solenoids, and some others burrowed deeply; etc.

A change in the mode of life usually caused a change in morphology. This was reflected in the shape and features of the shell (Tevesz and Carter, 1979; Savazzi, 1981, 1984b, 1989; Tevesz and McCall, 1985; Tashiro and Matsuda, 1988; Nevesskaja *et al.*, 1986, 1987; Whittlesey, 1996; etc.).

Hence, taking all this into account, it is possible to establish not only the trophic, but also the ethological type of an extinct bivalve, i.e., to obtain its complete trophological-ethological description and to assign it to one of the above groups.

To reveal the distribution of the ethological-trophic groups in time and the changes in their taxonomic composition, all families and genera were characterized by the relationships of their representatives to the substrate and feeding strategy, i.e., all were assigned to one group or another. It is noteworthy that genera belonging to the same family and even species belonging to the same genus could belong to two or more ethological-trophic groups. For instance, they could be epibyssal and/or endobyssal, could lie on the substrate and/or could float over the substrate, etc. For such taxa, all groups to which their representatives belonged are indicated (for the examples given above, I.2.1/I.3.1 and I.2.4/I.2.4a).

(b) Distribution of Ethological-Trophic Groups in Time

Views on the life style of Cambrian bivalves differ. Some researchers (Pojeta and Runnegar, 1974; Pojeta, 1975; Krasilova, 1977) consider *Fordilla* to be shallowly burrowing suspension-feeders, whereas others (Tevesz and McCall, 1976) consider them to be epifaunal, free lying suspension-feeders. Another, relatively widespread genus *Pojetaia* is also assigned sometimes to epifaunal, sometimes to infaunal(?) debris-feeders (Runnegar and Bentley, 1983). It is most likely that all early bivalves were epifaunal suspension-feeders (Tevesz and McCall, 1976; Vogel and Gutmann, 1980)).

In the Early Ordovician, ecological diversity significantly increased (Fig. VI. 2). Apart from the above groups, in which the number of genera increased, the communities included infaunal shallowly burrowing suspension-feeders with siphons (I.1.3), epi- and/or endobyssal suspension-feeders lacking siphons (I.2.1/I.3.1, I.2.1, I.3.1), rare boring bivalves (I.1.6) and those living in cavities (I.1.9), and also those free-lying on the surface (I.2.4), or semi-infaunal (I.3.4) suspension-feeders lacking byssus and siphons, and possibly occasional infaunal suspension-feeders with a mucous inhalant tubule (*Babinka*, I.1.8 or I.1.8a). The community was dominated by infaunal debris-feeders lacking siphons (21%) and by epi- and/or endobyssal suspension-feeders (19%).

The same groups were maintained in the Late Ordovician, supplemented by the newly appeared infaunal debris-feeders with siphons (II.2) and rare shallowly burrowing suspension-feeders with siphons and byssus (I.1.3a) and semi-infaunal suspension-feeders with siphons ((I.3.3). The community was dominated by the epi- and/or endobyssal suspension-feeders (23%), and debris-feeders, including mainly those lacking siphons (16%).

The Ordovician adaptive radiation was followed by a period of relative stability (Stanley, 1968). The Silurian was marked by the appearance of suspension-feeders attached by the byssus to floating objects (I.2.1a). The epibyssal (12%), epi- and/or endobyssal (12%), endobyssal semi-infaunal (10%), semi-infaunal attached by the byssus or free-lying (10%), and also infaunal shallowly burrowing suspension-feeders (10%) dominated.

The first cemented suspension-feeders (I.2.7 and I.2.4/I.2.7) and the group of epi- and/or endobyssal suspension-feeders with one siphon (I.2.2/I.3.2) appeared in the Devonian. The byssal epifaunal and epi- and semi-infaunal (I.2.1 and I.2.1/I.3.1) (15% each) and semi-infaunal taxa (I.3.1) (10%) were dominant. Infaunal shallowly burrowing suspension-feeders lacking siphons were also common (13.5%). A significant role was played by the epifaunal suspension-feeders lacking siphons, byssal and/or free lying on the substrate (I.2.1/I.2.4) (7.5%).

The first, rare, suspension-feeders capable of swimming (I.2.4a) are recorded in the Carboniferous, while the previously established groups were generally maintained. The most important group at this time was epibyssal suspension-feeders (ca. 30%) and, to a lesser extent, epifaunal, byssal, or free-lying suspension-feeders lacking siphons (ca. 10%) and shallowly burrowing suspension-feeders lacking siphons (8.5%).

The first, rare, deeply burrowing suspension-feeders with long siphons (I.1.5) are recorded from the Permian. As in the Carboniferous, the epibyssal suspension-feeders lacking siphons (23%) and infaunal suspension-feeders lacking siphons (over 10%) and those with siphons (ca. 10%) were dominant. The presence of epi- and/or endofaunal suspension-feeders lacking siphons and byssus, lying freely on the substrate, or partly sunk in it (I.2.4/I.3.4) (8.5%) was typical.

In the Early Triassic, the ethological-trophic composition was slightly impoverished (Fig. VI. 2) because of the impoverishment of the taxonomic composition (although this could result from an insufficient number of Lower Triassic localities). The epibyssal suspension-feeders lacking siphons (22%) continued to dominate. There were many (13%) epifaunal byssal and/or free-lying or swimming (nektobenthos, I.2.4a) taxa. Infaunal debris-feeders with siphons were frequent (11%), as well as shallowly burrowing suspension-feeders lacking siphons (8%).

In the Late Triassic, the proportions between the groups remained similar to that in the Early Triassic, although the role of infaunal debris-feeders decreased. However, the ecological composition became more diverse, mainly because of the presence of groups that

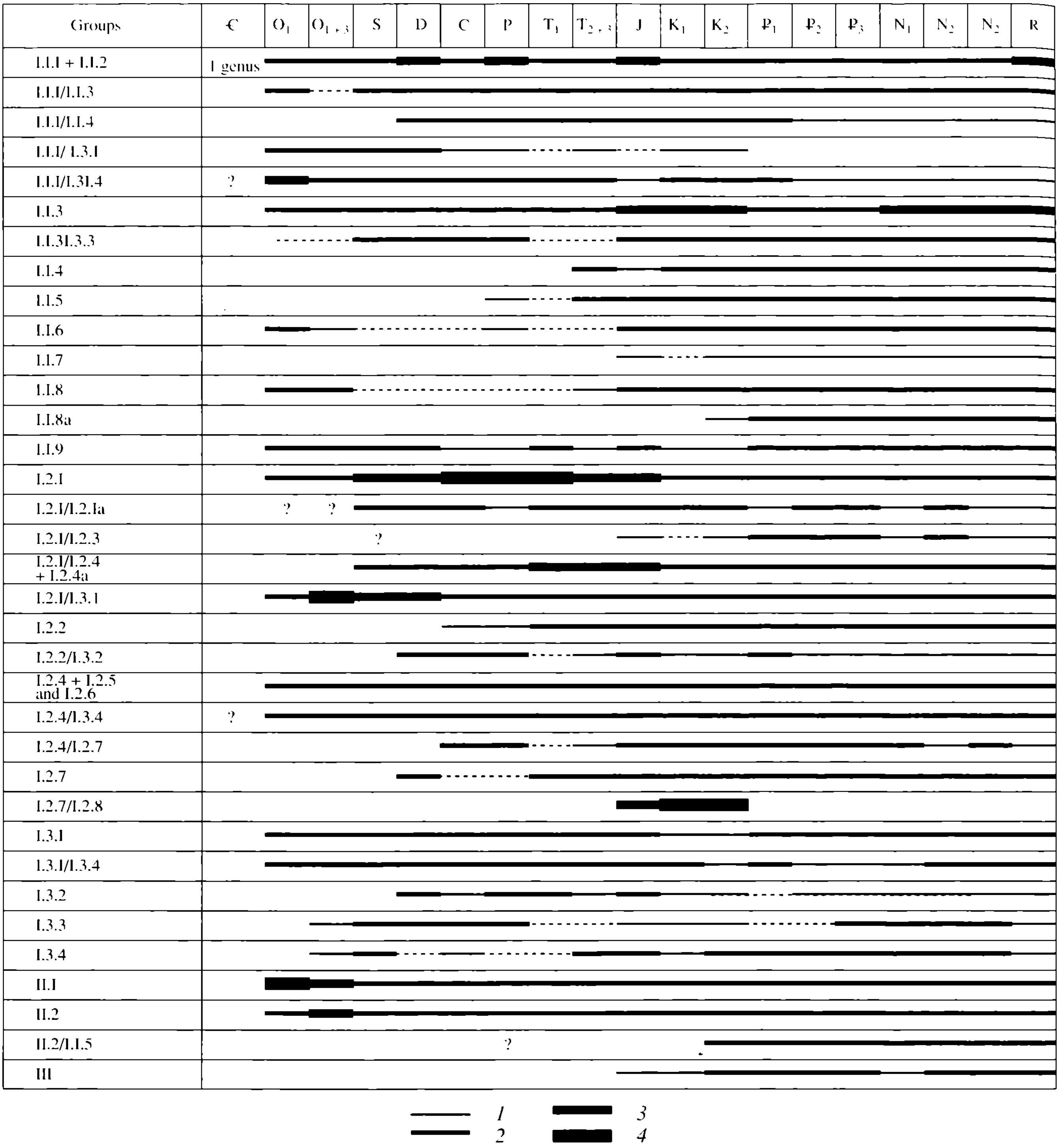


Fig. VI. 2. Proportion of genera belonging to different ethological-trophic groups in different periods of the Phanerozoic. For explanations of the groups, see the text: (*1*) less than 1%, (*2*) 1–10%, (*3*) 11–20%, and (*4*) over 20%.

are unknown from the Early Triassic, but recorded from the previous intervals. The presence of certain rare infaunal suspension-feeders with an anterior inhalant mucous tubule and exhalant siphon (I.1.8) and infaunal shallowly burrowing suspension-feeders with one siphon (I.1.4) is noteworthy.

Jurassic bivalves, apart from the genera belonging to previously known ethological-trophic groups, included suspension-feeders with a reduced shell and housed in calcareous tubules (I.1.7), living in shelters, with byssus and siphons (I.1.9), epibyssal with two siphons (I.2.3), cemented and having symbiotic relationships

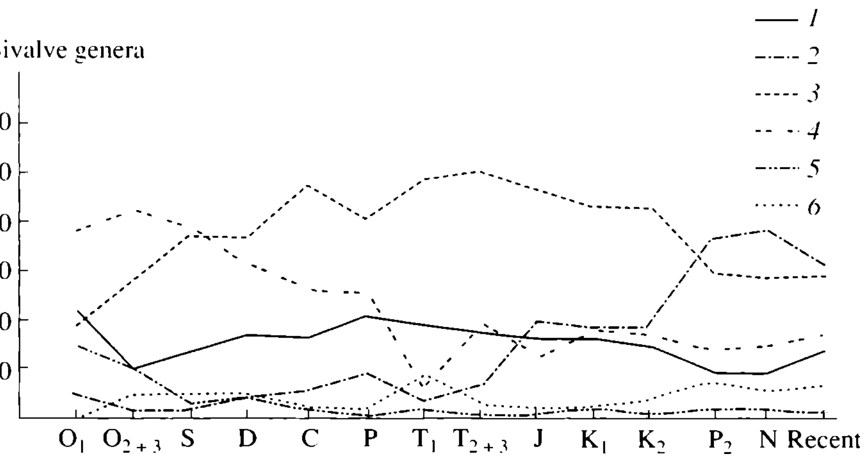


Fig. VI. 3. Changes of the percentage of bivalve genera within the major ethological-trophic groups in the Phanerozoic: (*1*) infaunal suspension-feeders, lacking siphons (without bissus of pallial sinus) (I.1.1); (*2*) infaunal suspension-feeders with siphons (with pallial sinus) (I.1.3+I.1.5); (*3*) epifaunal suspension-feeders (I.2); (*4*) semi-infaunal suspension-feeders (I.3); (*5*) debris-feeders with the entire pallial line (lacking siphons) (II.1); and (*6*) debris-feeders with pallial sinus (II.2).

with photosynthetic algae and/or bacteria (I.2.7/I.2.8), and predators (III). All these taxa were rare. In other respects, the ecological composition of bivalves was similar to that of the Late Triassic. The epibyssal (I.2.1), epibyssal and/or free-lying (I.2.1/I.2.4), and free-lying (I.2.4) suspension-feeders constituting 13, 10, and 7%, respectively; infaunal shallowly burrowing suspension-feeders with siphons (11%) and lacking those (10%) were dominant. The proportion of cemented bivalves increased.

Cemented taxa living in symbiosis with photosynthetic bacteria and/or algae (I.2.7/I.2.8) became widespread in the Early Cretaceous. These taxa became especially widespread in the Late Cretaceous (14 and 18%, respectively). Rare genera feeding in the same way but belonging to the epibyssal and/or free-lying groups (I.2.8/I.2.1/I.2.4) appeared at this time (one genus in the Early Cretaceous and two in the Late Cretaceous). The first infaunal suspension-feeders with an inhalant mucous tubule and lacking an exhalant siphon (I.1.8a) and infaunal debris-feeders with long siphons, which could feed like suspension-feeders (II.2 /I.1.5) are recorded from the Late Cretaceous. Cretaceous communities were dominated by infaunal shallowly burrowing suspension-feeders with or without siphons (I.1.3 and I.1.1) (11 and 8%, respectively). A significant role was played by the infaunal and/or semi-infaunal suspension-feeders lacking siphons (I.1.1/I.3.4), epibyssal and cemented (6.5% each), and epifaunal and/or semi-infaunal free-lying suspension-feeders (6%).

In the Paleogene and Neogene, up to the present day, the number of genera in most groups (especially infaunal suspension-feeders and debris-feeders) has increased, although the number and proportions of the groups have remained unchanged. The infaunal suspension-feeders with siphons (11% in the Paleocene, 16–19.5% from the Eocene to the present) were dominant. The infaunal suspension-feeders lacking siphons were in second place (ca. 10%). An important part was played by the infaunal suspension-feeders with a mucous inhalant tubule and exhalant siphon (5–7%), infaunal deeply burrowing suspension-feeders and debris-feeders with siphons (4.5–5 and 5–6%, respectively), and boring bivalves (4–5%). Of the epifaunal bivalve groups, the most widespread were byssal bivalves (8.5% in the Paleocene, 6.5% in the Eocene, 4–5% in the Oligocene and until the present), attached by a byssus and/or free-lying and capable of swimming (4–6%). An important role was played by free-lying epifaunal and/or semi-infaunal suspension-feeders (4.5–6.5%) (Fig. VI. 3).

Summarizing the above, it is noteworthy that, in the Early Ordovician, of the major groups of infaunal suspension-feeders (I.1), and debris-feeders (II), epifaunal (I.2) and semi-infaunal (I.3) suspension-feeders, the semi-infaunal suspension-feeders were dominant (38%). They were followed by the infaunal suspension-feeders (ca. 30%). Of those, genera lacking siphons prevailed (22%). Epifaunal suspension-feeders and infaunal debris-feeders lacking siphons constituted approximately 19 and 15%, respectively (Fig. VI. 3). In the Middle–Late Ordovician, the semi-infaunal suspension-feeders were dominant (42%). There were also many epifaunal genera (29%), and many of those were characterized by both the epibyssal and endobyssal life style (29.5% of the total number of genera, see Fig. VI. 3). The infaunal suspension-feeders and debris-feeders played a lesser role. Among both groups, the genera in which the sinus of the pallial line was absent (i.e., most likely without siphons) prevailed.

In the Silurian, the epifaunal and semi-infaunal suspension-feeders were equally important (37 and 39%, respectively). The percentage of the genera, representatives of which were both epi- and endobyssal, remained relatively high (12% of the total number of genera,

Fig. VI. 2). Other groups included a small number of genera.

Beginning from the Devonian and continuing to the end of the Paleozoic, the role of the epifaunal-suspension-feeders increased, whereas the role of the semi-infaunal taxa gradually decreased, although in the Devonian, the community still included many genera with epi- and/or endobyssal life style (15% of the total number of genera). Among the infaunal suspension-feeders, those lacking siphons continued to prevail. The proportion of debris-feeders was relatively low (4–9%), while the proportions of the taxa with siphons and those lacking them were approximately the same.

In the Mesozoic, the epifaunal suspension-feeders clearly dominated (43–50%), the proportion of semi-infaunal taxa considerably decreased (7–19%), whereas the proportion of infaunal suspension-feeders increased from 22% in the Early Triassic to 35% in the Jurassic and Cretaceous. Beginning from the Jurassic, taxa with siphons prevailed (up to 19–20% instead of 15–16%). The number of debris-feeders was less than that of suspension-feeders (ca. 5%). Among the latter, slightly more had siphons.

The first predators (genera of the Septibranchia) appeared in the Jurassic, although their proportion was not more than 1%.

In the Cenozoic and Recent, the infaunal suspension-feeders became dominant (45–47%). Of those, siphonate taxa sharply prevailed (31–38%). The epifaunal suspension-feeders (30%) were abundant, while the number of semi-infaunal taxa was half of this (ca. 15%). The infaunal debris-feeders were considerably less widespread (8–9%), and among those, most taxa had siphons. The proportion of predators did not exceed 2%.

Thus, the role of the semi-infaunal suspension-feeders gradually decreased after a peak in the Early Paleozoic. The role of the epifaunal taxa increased from the Early Ordovician to the Mesozoic inclusive (peak in the Triassic). At the Cretaceous–Tertiary boundary, the proportion of the epifaunal taxa sharply decreased, while the proportion of the infaunal suspension-feeders with siphons increased, and those lacking siphons decreased. The increase in the diversity and proportion of infaunal suspension-feeders was caused by increased predation on bivalves (see Section 1 of this chapter).

The role of debris-feeders was clearly less important than that of suspension-feeders throughout the Paleozoic (Fig. VI. 3).

It is noteworthy that the main trophic groups of bivalves, debris-feeders and suspension-feeders had different evolutionary potentials. The evolution of the suspension-feeders was more rapid. This was because the major source of food of suspension-feeders (phytoplankton) experienced considerably greater fluctuations than the content of the organic matter, including bacteria, in the sediment. A count of the length of existence of the genera of suspension-feeders showed that suspension-feeders were more short-lived (Levinton, 1974). For instance, the analysis of the selectivity of extinction of bivalves at the end of the Cretaceous showed that the rate of extinction of suspension-feeders was approximately twice as high as that of debris-feeders (Jablonski and Raup, 1995). The trophic structures of communities of debris-feeders was considerably more conservative, while the number of ethological-trophic groups among those were far less than among suspension-feeders.

CHAPTER VII. RELATIONSHIPS BETWEEN THE SHELL MORPHOLOGY OF BIVALVES AND THEIR MODE OF LIFE

Changes in shell morphology over time were discussed in detail in Chapter V. "MORPHOGENESIS," whereas this chapter addresses the problem of the relationship between the morphological characters and the bivalve's ecology.

(1) Morphological Characters of the Shell Indicative of the Mode of Life, Their Appearance and Evolution

There is a close connection between the ecological features of different bivalve groups and their shell morphology, which reflects the structure of the soft body. Problems of functional morphology and adaptive strategy of taxa were discussed by many authors, e.g., by Yonge (1953, 1967, 1973, 1978a, 1978b, 1982), Kauffman (1969), Stanley (1970, 1972, 1975, 1977b), Eager (1974), Waller (1978), Savazzi, 1981, 1983, 1984a, 1984b, 1985, 1987, 1989, 1990a, 1990b, 1996), Seilacher (1984), Tevesz and McCall (1985), Tashiro and Matsuda (1988), and others. The adaptive significance of several morphological characters, and their distribution in time, are discussed below (Fig. V. 22).

Shell shape. Shell shape was extremely diverse (ellipsoid, spherical, wedge-shaped, wing-shaped, rod-shaped, etc.). The earliest bivalves were ellipsoid or ovate. However, beginning from the Ordovician, wedge-shaped and wing-shaped shells appeared, while other shell types appeared gradually and reached the peak of their diversity in the Mesozoic.

The ellipsoid shell was characteristic of both infaunal shallowly burrowing bivalves, and semi-infaunal genera (lacking the byssus). The wedge-shaped shell usually belonged to epi- and/or endobyssal taxa, wing-shaped to epibyssal taxa, or those lying free on the substrate but capable of swimming. Deeply burrowing and boring bivalves usually had strongly elongated shells.

Degree of inequivalvity. The extent to which a shell is inequivalve indicates the position of the mollusk in relation to the substrate. Inequivalve shells are usually epifaunal, cemented (I.2.7), lying on one (more convex) valve or lying almost flat, but supported by the umbilical region (recliners, I.2.4). Rudists had an extremely inequivalve shell, with the lower valve considerably bigger than the operculum-shaped upper valve.

In the Cambrian and Early Ordovician, all bivalves were equivalve (Fig. V. 22). The earliest inequivalve bivalves appeared in the second half of the Ordovician, but their number was low. In the Silurian and Devonian (Pterineidae), and especially in the Carboniferous and Permian (Aviculopectinidae), their number increased. In the Mesozoic, the number of genera with an inequivalve shell was particularly high because of the wide distribution of the Gryphaeidae and Ostreidae, Pectinidae, and rudists, whereas in the Cenozoic and at present, their proportion decreased. Apart from the epifaunal taxa, some forms inhabiting shelters, infaunal deeply burrowing (I.1.5) and semi-infaunal suspension-feeders (I.3.1), infaunal debris-feeders capable of feeding like suspension-feeders (Tellinidae, II.2/I.1.5), and so-called infaunal predators (Septibranchia, III) were inequivalve. However, generally, equivalve bivalves dominated throughout the Phanerozoic.

Ornamentation. It is unclear whether or not the ornamentation is determined by any ecological conditions. In some cases, a certain type of ornamentation facilitated the burrowing of bivalves in the substrate and precluded their washout from the substrate in environments of high water turbulence (Stanley, 1981). Nevertheless, the majority of deeply burrowing bivalves (I.1.5 and II.2) had a smooth shell, while many epifaunal bivalves had well-developed ornamentation. Typically, the epifaunal free lying, sometimes, capable of swimming (I.2.4 and I.2.4a) and semi-infaunal endobyssal (I.3.1, I.3.2) suspension-feeders and septibranchial predators had radial ribbing. Boring bivalves (I.1.6), those with an anterior mucous tubule and posterior siphon (I.1.8), many cemented taxa and those living in shelters (I.1.9), and semi-infaunal suspension-feeders lacking a byssus (I.3.4) had a composite ornamentation. Other groups included genera and species with varying ornamentation, and no type was dominant.

Degree of inequilaterality. The development of the inequilateral shells was to some extent related to mode of life. For instance, taxa attached by a byssus (I.2.1, I.3.1, I.2.2, I.3.2) were often extremely inequilateral; in some cases, the anterior hinge line completely disappeared, so that the beak became terminal. Genera with such morphology first appeared in the second half of the Ordovician. However, nonattached burrowing bivalves were prominently inequilateral, whereas in some byssal taxa, the shell was almost equilateral. Originally (in the Cambrian and Ordovician), bivalves were either equilateral or weakly inequilateral. Then, the shells with a shorter anterior part of the valves became clearly dominant. These bivalves could be epi- or infaunal. A reverse proportion of the anterior and posterior parts of the shells is observed in many genera of infaunal debris-feeders lacking siphons (I.1.1 and I.1.2) (25%) and also in some genera assigned to other groups. Many infaunal suspension-feeders (I.1.1, I.1.2, I.1.3, I.1.4, I.1.5, I.1.8, I.1.8a), debris-feeders (II.1, II.2), and predators (III) and epifaunal and semi-infaunal suspension-feeders (I.2.1, I.2.4, I.2.4a, I.2.6, I.2.7, I.3.1, I.3.4) were equilateral.

Beak. The majority of suspension-feeders and predators had prosogyral beaks. Orthogyral beaks were typical of some infaunal and semi-infaunal suspension-feeders and debris-feeders, while opisthogyral beaks occurred in siphonate debris-feeders, which could also feed on seston (II.2/I.1.5) and deeply burrowing suspension-feeders (I.1.5). The spirogyral beak was characteristic of some cemented suspension-feeders.

Auricles and byssal notch. The presence of ear-shaped projections (auricles, wings) was typical of the epifaunal, and often, byssal bivalves (I.2.1, I.2.4), which appeared as early as the Early Ordovician. The byssal attachment is indicated by the presence of a byssal notch under the auricles, a character also known beginning with the Early Ordovician.

Muscular scars. The infaunal suspension-feeders (I.1.1, I.1.3, I.1.4) and debris-feeders (II.1, II.2) were usually isomyarian and only few deeply burrowing siphonate suspension-feeders (I.1.5) and debris-feeders capable of occasional feeding on debris (II.2/I.1.5), suspension-feeders with a mucous anterior tubule (I.1.8, I.1.8a), and boring bivalves (I.1.6) were anisomyarian. In boring bivalves, the anterior scar was smaller than the posterior, while in taxa with a mucous inhalant tubule (I.1.8, I.1.8a) and two long siphons (I.1.5), in contrast, the posterior scar was smaller than the anterior scar. In debris-feeders (II.2/I.1.5), both cases were present. The epifaunal and semi-infaunal suspension-feeders had both equal and unequal muscular scars, and could have one (posterior) muscular scar. The siphonate free-lying (I.2.6) and semi-infaunal (I.3.3) taxa were only isomyarian, while epi- and endobyssal (I.2.1, I.3.1) and epi- and semi-infaunal free-lying (I.2.4, I.3.4) suspension-feeders lacking siphons were mainly isomyarian. Epi- and endobyssal bivalves with one siphon (I.2.2 and I.3.2) were anisomyarian, with the anterior scar smaller than the posterior scar. One muscular scar was present in all suspension-feeders that were epifaunal, free-lying, and capable of swimming (I.2.4a), and in most cemented (I.2.7) and a considerable proportion of epifaunal byssal and free-lying suspension-feeders (I.2.1, I.2.2, I.2.4). Many boring bivalves had the adductor attached on the umbilical reflection.

Ligament. The majority of infaunal suspension-feeders with a mucous inhalant tubule and exhalant siphon (I.1.8) (97%) or those lacking siphons (I.1.8a) (57%); siphonate debris-feeders capable of feeding on seston (II.2/I.1.5) (100%); epi- and endobyssal suspension-feeders with one (I.2.2, I.3.2) or two (I.2.3, I.3.3) siphons and those living in shelters (I.2.9); many infaunal suspension-feeders with one or two siphons (I.1.3, I.1.5, I.1.4); epi- and endobyssal suspension-feeders lacking siphons (I.2.1, I.3.1); and infaunal debris-feeders (II.1, II.2) had the external ligament only. The presence of both the external and internal ligaments was characteristic of infaunal suspension-feeders with a mucous tubule and lacking the posterior siphon (I.1.8a), those with one siphon (I.1.4), and infaunal siphonate debris-feeders (II.2). Only the internal ligament was dominant in epifaunal and semi-infaunal suspension-feeders lacking byssus and siphons (I.2.4, I.2.

4a, I.3.4), cemented (I.2.7), epi- and endobyssal (I.2.1, I.3.1) and infaunal suspension-feeders lacking siphons (I.1.1) and with two siphons (I.1.5). Approximately half of the genera of deeply burrowing siphonate suspension-feeders (I.1.5) and debris-feeders lacking siphons (II.1) also had only the internal ligament. The ligament was absent in many boring bivalves.

Hinge. Changes in the hinge are discussed in detail in Chapter V. Here, it should be emphasized once again that, in the early evolution of bivalves in the Early Paleozoic, hinges were extremely diverse. The selection of hinges adapted to particular modes of lifes was gradual. For instance, the heterodont hinge typically occurring in a half or more genera of Cenozoic bivalves is present in the infaunal, mainly siphonate, bivalves (I.1.3, I.1.4) and was an adaptation to active burrowing in the soft substrate (Stanley, 1968). Deeply burrowing bivalves with long siphons (I.1.5, III) mainly had the desmodont hinge. The dysodont hinge was present in more than half of epibyssal suspension-feeders lacking siphons (I.2.1) and in many epi- and endobyssal genera with one siphon (I.2.2, I.3.2), and in epifaunal free-lying bivalves with siphons (I.2.5). Teeth were absent in the majority of boring bivalves (I.1.6) and many epifaunal free-lying suspension-feeders capable of swimming (I.2.4, I.2.4a), epi- and endobyssal suspension-feeders lacking siphons and with one siphon (I.2.1, I.2.2, I.1.3, I.3.2), and cemented suspension-feeders (I.2.7).

Representatives of a few genera with the pterinoid hinge were usually epibyssal. The schizodont hinge typically occurred in some infaunal shallowly burrowing suspension-feeders lacking siphons (I.1.1) and non-attached epifaunal bivalves lacking byssus and siphons (I.2.4). The pachyodont hinge was typical of many cemented bivalves (mainly rudists). The ctenodont (primary taxodont) hinge was present in almost all debris-feeders lacking siphons (II.1) and the majority of siphonate debris-feeders (II.2), whereas the neotaxodont (secondarily taxodont) hinge was present in most epibyssal bivalves with siphons (I.2.3) and many living in shelters (I.1.9), and also in representatives of other ethological-trophic groups. Other hinge types were rare and did not dominate any particular group.

Pallial line. The degree of the development of the sinus of the pallial line indicates the degree of the development of siphons. The sinus was absent in all or almost all shallowly burrowing infaunal bivalves (I.1.1), relatively deeply burrowing bivalves with a finger-shaped anterior muscular scar (I.1.8, I.1.8a), in almost all epifaunal bivalves, the majority of semi-infaunal suspension-feeders, and in shallowly burrowing debris-feeders (II.1). A shallow sinus was present in many burrowing taxa (I.1.3, I.1.5), boring bivalves (I.1.6), suspension-feeders living in shelters (I.1.9), predators (III), some epifaunal and semi-infaunal suspension-feeders (I.2. 3, I.2.6, I.3.3), and in the majority of deeply burrowing debris-feeders (II.2). A deep sinus was present in many deeply burrowing siphonate suspension-feeders (I.1.5) and also in the majority of debris-feeders capable of feeding on seston (II.2/I.1.5).

Summarizing all the above, it is noteworthy that none of the morphological characters is exclusive to any ethological-trophic group. A complex characterization of each group may prove to be more fruitful. Below, representatives of the most widespread groups are characterized in this way (see Chapter VIII).

(2) Homeomorphy in Bivalves

Homeomorphy (appearance of the same morphotypes in different phylogenetic lineages) was widely distributed among bivalves. The appearance of homeomorphs was determined mainly by similar environment and restrictions imposed by morphogenesis.

For instance, epifaunal bivalves inhabiting soft substrates developed wide wings, or the shell became more flattened (here called the ski strategy), or a mollusk partly sunk into the ground. In the latter case the lower valve either became strongly convex, or the shell increased in height (here called the iceberg strategy). In these cases, similar shapes appeared repeatedly and were present in unrelated taxa (Thayer, 1975; Chinzei *et al.*, 1982; Aberhan, 1994; Yancey and Stanley, 1999).

In oxygen deficient environments, bivalves had thin-walled shells and could either swim over the substrate to regions with a more favorable regime or were attached by byssus to floating algae to become pseudoplankton (Schubert and Bottjer, 1995; Kurushin, 1998; Amler and Winkler Prins, 1999).

Other examples of homeomorph genera and species are discussed in many publications (Davitashvili, 1970; Hudson and Palmer, 1976; Nevesskaja *et al.*, 1986, 1987; Crame, 1986; Aberhan, 1994; etc.).

CHAPTER VIII. MORPHOLOGICAL CHARACTERIZATION OF THE ETHOLOGICAL-TROPHIC GROUPS AND CHANGES IN THEIR TAXONOMIC COMPOSITION OVER TIME

(1) Morphological Characterization of Major Ethological-Trophic Groups

Infaunal, shallowly burrowing suspension-feeders, usually lacking siphons and pallial sinus (I.1.1) had an equivalve, variously ornamented shell, usually inequilateral, with a shorter anterior end. More rarely, shells in this group were equilateral, with a shorter posterior part. The beak was usually prosogyral; more rarely, orthogyral; and very rarely, opisthogyral. Paired muscular scars were almost equal. Shells with the internal ligament were dominant, but those with the external ligament only (usually opisthodetic) were frequent; however, occasionally, both external and internal ligaments were present. The hinge was heterodont or schizodont; occasionally the teeth were absent, or the hinge was of a different type. The majority of shells lacked a pallial sinus, or, rarely, a shallow sinus was present. The gape was absent.

Infaunal, relatively shallowly burrowing suspension-feeders lacking byssus and possessing two siphons (I.1.3) had an equivalve smooth shell or it was covered by concentric or radial ornamentation, or, more rarely, composite ornamentation. Shells in this group were usually inequilateral with a shorter anterior part, more rarely, equilateral. The beak was usually prosogyral. The muscular scars were paired and almost equal. The ligament was external, opisthodetic; more rarely, both external and internal, or only internal ligaments were present. The hinge was generally heterodont. The pallial sinus was shallow, more rarely, deep. A gape was only observed in a few taxa.

Infaunal, relatively deeply burrowing suspension-feeders with two siphons (I.1.5) had an equivalve, more rarely, inequivalve shell, which was usually smooth, but, more rarely, possessed radial, concentric, or composite ornamentation. More than half of all genera were inequilateral. Among these, genera with a shorter anterior part were dominant. A third of all genera were equilateral. Genera with the prosogyral beak were dominant. Relatively often beaks were opisthogyral. The paired muscular scars were usually almost equal, more rarely, the anterior scar was larger. The ligament was external, more rarely, external and internal, or only internal. The hinge in half of all genera was heterodont, and in one third of genera, desmodont. The pallial sinus was developed in the majority of genera, while a deep sinus was present in almost half of the genera. Approximately one-third of taxa had a gape.

Boring bivalves (I.1.6) usually had an equivalve and inequilateral shell with composite ornamentation, a shorter anterior end, and a prosogyral beak. Muscular scars are usually paired, but the anterior scar is smaller and is positioned on the upturned hinge margin. The ligament is absent, or there are internal or external opisthodetic ligaments. The hinge is usually toothless. The pallial sinus is undeveloped, or shallow, rarely deep. A large gape is often present, which is covered by the auxiliary plates.

Infaunal deeply burrowing suspension-feeders with the anterior mucous tubule replacing the inhalant siphon and the posterior siphon (I.1.8) had an equivalve shell with composite or concentric ornamentation, usually equilateral, more rarely, with a shorter anterior end, and with a prosogyral beak. Adductor scars are usually paired. The anterior scar is longer and finger-shaped. The ligament is external, namely, opisthodetic. The hinge is heterodont, rarely, toothless or dysodont. The pallial line is entire, and a gape is absent.

Epifaunal suspension-feeders, which had a byssus, lacked siphons (I.2.1), and were sometimes capable of a pseudoplanktonic mode of life (I.2.1a), usually had an equivalve shell with radial or composite ornamentation; more rarely, the shells were smooth or with concentric ribs. Shells in this group were inequilateral, with a shorter anterior part (50%), or equilateral (30%); they had the prosogyre or, more rarely, orthogyral beak. Many shells had auricles and a byssal notch (15–20%). There were two approximately equal adductor scars (65%), or one (25%); rarely (ca. 10%) the anterior scar was considerably smaller. The ligament was usually internal (55%); often, external opisthodetic (25%) and amphidetic (over 10%). In half of the genera in this group, the hinge lacked teeth, while approximately 20% had a heterodont hinge. The pallial line was entire. The byssal gape was present in some taxa. The pseudoplanktonic taxa had a thin-walled shell.

Epibyssal suspension-feeders with one siphon (I.2.2) were always equivalve. The shell was typically smooth, or with radial ribbing or striae, more rarely, with composite ornamentation, usually, with a terminal prosogyral beak (53%), or with a beak shifted toward the anterior margin (44%). The byssal notch and auricles were absent. The adductor scars were strongly unequal, with the anterior scar smaller (80%), or the anterior scar was absent (15%). The ligament was external opisthodetic. The hinge was dysodont (over 50%) or edentate (ca. 40%). The pallial line was entire. The gape is usually absent.

Epifaunal suspension-feeders; which lacked byssus and siphons, were free-lying or moving on the substrate (I.2.4) and usually equivalve. However, a considerable number were inequivalve (12%). The external surface was smooth, with radial ribbing, or composite ornamentation (with concentric ribbing or striate). The shell was inequilateral, with a shorter anterior part, or equilateral, usually with the prosogyral or, more rarely, orthogyral beak. Some shells had a byssal notch and auricles. The adductor scars were usually paired, almost equal (75%), although the shell often had only one scar (20%). The ligament was usually internal (65%), more rarely, external (opisthodetic). The hinge was heterodont, edentulous, or schizodont. The pallial line was entire. The gape was typically absent.

Epifaunal free-lying suspension-feeders that were sometimes attached by the byssus (in some cases, lost in adults), lacked siphons, and were capable of swimming over the substrate (I.2.4a) usually had an inequivalve shell (ca. 50%), with radial or composite ornamentation, usually equilateral (75%), with a weakly projecting beak, with auricles (over 60%), and a byssal notch (ca. 50%). The shell had a single adductor scar. The ligament was usually internal (over 90%), more rarely, internal and external. The hinge was edentate (ca. 85%) or, more rarely, dysodont. The pallial line was entire. The gape (except for the byssal gape) was usually absent.

Epifaunal free-living taxa with a siphon (I.2.6) are only known from the Neogene and the present. Their shells are mainly equivalve, smooth, or variously ornamented, inequilateral, with a shorter anterior part, or equilateral with the prosogyral (ca. 80%) or orthogyral beak. The auricles, byssal notch, and gape are absent. The adductor scars are almost equal. The ligament is more often external, opisthodetic (ca. 60%), more rarely, internal (ca. 30%), and even more rarely, both types of ligaments are present. The hinge is heterodont (ca. 90%), more rarely, taxodont or dysodont. The pallial line is entire in 70% and with a shallow siphon in 30%.

Epifaunal cemented taxa lacking byssus and siphons, or with a complex siphonal system (rudists)

(I.2.7) had an equivalve, or inequivalve (ca. 50%) shell with composite, or radial ornamentation, equilateral, more rarely, with a shorter anterior part, with the prosogyral and opisthogyral, more rarely, orthogyral and spirogyral beak, sometimes, with auricles and a byssal notch (10%). Usually, the shell had a single adductor scar (75%), more rarely, two scars almost equal in size (20%), or unequal, of which the anterior was smaller (ca. 5%). The ligament was internal (80%), or both internal and external (15%), more rarely, only external. The hinge was pachyodont (55%) or edentate (40%). The pallial line was entire, while in rudists, it had a complicated system of pallial canals. A gape was absent.

Semi-infaunal endobyssal suspension-feeders lacking siphons (I.3.1) had an equivalve; variously ornamented, more rarely, smooth; and inequilateral shell with a shorter anterior part (60%), or equilateral shell (over 30%), with the prosogyral (ca. 70%) or orthogyral (20%) beak usually lacking auricles, and a byssal gape. Shells in this group usually have two adductor scars, which are almost equal (over 80%). More rarely, the anterior scar is smaller (10%), or the ratio is different. The ligament was internal (over 40%), external (ca. 40%), or both internal and external (15%). The hinge was heterodont (25%), edentate (ca. 20%), or, more rarely, of other type (taxodont, preheterodont, pterinoid, and actinodont). The pallial line is always entire. The gape is rare.

Semi-infaunal endobyssal suspension-feeders with siphon (I.3.3), represented by a few genera in the Paleozoic and Mesozoic, and by around twenty genera at present, are characterized by equivalve (80%), or inequivalve shells, smooth, or variously ornamented, inequilateral, with a shorter anterior part (80%), more rarely, equilateral. Beaks are prosogyral (70%), orthogyral (20%), more rarely, opisthogyral, or spirogyral. Shells in this group lack auricles, a byssus, and a gape and have two almost equal adductor scars. The ligament is external, opisthodetic (over 40%), amphidetic (20%), or internal and external (20%), more rarely, internal (15%). The hinge is more often heterodont (ca. 45%), more rarely, lacking teeth (ca. 20%), schizodont, or neotaxodont (15% each), rarely, of other types. The pallial line is entire (55%) or with a shallow sinus (45%).

Semi-infaunal suspension-feeders lacking byssus and siphons (I.3.4) had an equivalve, variously ornamented, inequilateral shell, with a shorter anterior part, or equilateral shell, with the prosogyral, and, more rarely, orthogyral beak. The auricles, byssal notch, and gape were absent. The adductor scars were paired, almost equal; very rarely, the shell had only one adductor scar. The ligament was usually internal (ca. 70%), more rarely, external, or both were present. The hinge was schizodont (40%), heterodont (over 30%), more rarely, lacking teeth, or of different structure. The pallial line was entire.

Suspension-feeders living in shelters (I.1.9) had both equivalve (ca. 70%) and inequivalve shells, which were smooth or variously ornamented, inequilateral, with a shorter anterior part (70%), or equilateral. Usually, shells in this group had the prosogyral beak (90%), lacked auricles and byssal notch, and had two almost equal adductor scars. The ligament was more often external (over 70%), opisthodetic and, sometimes (ca. 20%), amphidetic, although some taxa had an internal ligament (ca. 20%), or both (ca. 10%). The hinge was of various types (heterodont, taxodont, edentate, more rarely, desmodont or dysodont). The pallial line was entire, the gape was developed in 20% of genera.

Shallowly burrowing infaunal debris-feeders lacking siphons (II.1) are all equivalve. The shell surface is smooth, or with radial or concentric ornamentation. Shells in this group are equilateral or inequilateral, with a shorter, or longer anterior part, usually with opisthogyral (ca. 70%), more rarely, with orthogyral, and prosogyral beaks, lacking auricles and a byssal notch. The adductor scars are almost equal. The ligament is internal, external, or, more rarely, both. The hinge is ctenodont (over 90%). The pallial line is entire. The gape is absent.

Infaunal debris-feeders with siphons (II.2) have equivalve, smooth, or concentrically ornamented shells, more rarely, with a radial or composite ornamentation. Shells in this group are inequilateral, with a shorter anterior part, or equilateral; lacking auricles and a byssal notch. The beaks are opisthogyral (80%), more rarely, prosogyral, or orthogyral. The adductor scars are almost equal; more rarely, the anterior scar is bigger. The ligament was internal and external (40%), or only internal (30%), or only external (30%). The hinge is ctenodont (ca. 80%), more rarely, heterodont. The gape was typically absent.

Infaunal debris-feeders with siphons that could also feed as suspension-feeders by agitating the sediment (II.2/I.1.5) are represented by 15–20 genera, and only became important in communities beginning from the Late Cretaceous. They have an equivalve (ca. 80%) or inequivalve shell, which is smooth (25%), concentrically ornamented (55%), or with composite ornamentation (20%); equilateral (ca. 50%), or inequilateral, with a shorter (85%) or longer (15%) anterior part. Beaks were opisthogyral (60%), or orthogyral (30%), more rarely, prosogyral. Auricles and a byssal notch are absent. The adductor scars were equal (ca. 75%), or unequal, with the anterior scar smaller or larger (13% each). The ligament was external, opisthodetic. The hinge is heterodont. The pallial line has a sinus, which is usually deep (ca. 80%). The gape is absent.

The predatory Septibranchia typically had equivalve (80%), variously ornamented (more often radially), more rarely, smooth shells. Shells in this group were inequilateral, with a shorter anterior part (55%), or equilateral, with the prosogyral (over 85%) or orthogyral beak; auricles and byssal notch were absent. Muscular scars were paired and equal. The ligament was internal (65%), internal and external (20%), or, more rarely, external opisthodetic. The hinge was desmodont (65%), edentate (25%), or, more rarely, heterodont. The pallial line had a sinus, usually shallow (ca. 55%), or was entire (40%), rarely, with a deep sinus.

The morphological characterization of the ethological-trophic groups indicates that the majority of those contained unrelated taxa. Only very few groups contained genera of a single superfamily (I.2.8 were represented by the genera of the family Lucinidae; I.1.4 were by the Astartidae; I.2.4a were by mostly the Pectinoidea; II.1 were by the Ctenodontoidea and *Nuculoidea*; and II.2/I.1.5 were by the Tellinidae).

(2) Changes in the Taxonomic Composition of the Ethological-Trophic Groups in Time

The ethological-trophic groups usually include different taxa, which replace each other in time (Tables VIII. 1–15).

Infaunal suspension-feeders lacking the pallial sinus, i.e., most likely lacking siphons (I.1.1) were represented in the Early Ordovician by the family Cycloconchidae (order Actinodontida), in the Silurian by the Cardiolidae (order Cyrtodontida), and in the Devonian to Permian by the Grammysiidae (order Pholadomyida). In the Triassic, this group was dominated by the Triginiidae (order Actinodontida); in the Jurassic and Early Cretaceous, by the Astartidae (order Astartida) and Trigonidae; in the Late Cretaceous, by the Trigoniidae, Astartidae, and Carditidae (order Carditida); in the Paleocene, by the Carditidae and Astartidae; in the Eocene, by the same families and Montacutidae (order Astartida); in the Oligocene, by the Carditidae; and in the Neogene and Recent, by the Carditidae, Montacutidae, and Astartidae (Table VIII. 1).

Infaunal suspension-feeders with siphons, shallowly and moderately deeply burrowing (I.1.3) were rare until the Carboniferous. In the Late Paleozoic, this group was represented by the Grammysiidae and Pholadomyidae (order Pholadomyida), whereas in the Triassic, they were not among the dominant taxa. In the Jurassic, this group included genera of the families Arcticidae, Corbulidae (order Venerida), and Pholadomyidae, while in the Late Cretaceous, the family Cardiidae was added; and from the Paleocene, the group was supplemented by the family Mactridae; i.e., from the Early Cretaceous, all dominant genera in this group belonged to the order Venerida (Table VIII. 2).

The composition of genera dominating the infaunal deeply burrowing suspension-feeders with a deep pallial sinus (I.1.5) was restricted. This group appeared only in the Carboniferous, while in the Late Paleozoic and Jurassic, it included only the genera of the family Pholadomyidae. From the Late Cretaceous, this group was dominated by genera of the family Tellinidae (order Venerida). In the Paleocene, the group additionally included only a few Mactridae, while from the Eocene to the Recent, the group contained genera of the families Mactridae, Tellinidae, and the rare Pholadomyidae (Table VIII. 3).

Boring bivalves (I.1.6) were rare until the Late Cretaceous. In the Ordovician, they possibly included a few genera of the family Modiomorphidae (order Actinodontida). In the Devonian–Triassic, they were represented by rare Mytilidae (order Cyrtodontida), whereas from the Jurassic, this group also included a few representatives of the family Pholadidae (order Venerida), which became widespread from the Late Cretaceous, when a few genera of the family Veneridae joined the group (Table VIII. 4).

Infaunal deeply burrowing suspension-feeders with a mucous tubule instead of the anterior siphon and with a posterior siphon (I.1.8), or without it (I.1.8a) first appeared in the Early Ordovician, but only became widespread from the Jurassic (family Lucinidae of the order Astartida) (Table VIII. 5).

The epibyssal suspension-feeders without siphons (I.2.1) and with siphons (I.2.2) belong to the genera that may have a different mode of life, i.e., usually contain endobyssal (I.3.1, I.3.2) species (Table VIII. 6) and, sometimes, epibyssal species that can lead a pseudoplanktonic mode of life (I.2.1a), or free-lying (I.2.4) species lacking byssus and capable of swimming (I.2.4a). Group I.2.1/I.3.1 is recorded beginning from the Early Ordovician, although it became dominant from the second half of the Ordovician, when it included genera of the families Modiomorphidae (order Actinodontida), Cyrtodontidae, and Ambonychiidae (order Cyrtodontidae). In the Silurian, this group included genera of the families Cardiolidae (order Cyrtodontida), Modiomorphidae, and Pterineidae (order Cyrtodontida), whereas in the Devonian, this group included genera of the Pterineidae and Ambonychiidae. In the Late Paleozoic and later, this group ceased to exist and was replaced by a group of a more complex composition (I.2.1/I.3.1/I.2.4), which included genera of the family Aviculopectinidae (order Cyrtodontida), represented by the epifaunal bivalves with or without byssus; some of these taxa could adopt a pseudoplanktonic mode of life.

In the Mesozoic, epibyssal taxa were part of many complex groups, while endobyssal bivalves were less common. In combination with epibyssal and free-lying bivalves, endobyssal forms were represented by genera of the family Bakevellidae (order Cyrtodontida). Beginning with the Paleocene, endobyssal taxa, which were widespread, included some genera and species of the family Carditidae (order Carditida), whereas from the Oligocene, they were represented by the family Arcidae (order Cyrtodontida), and in the Recent, by the Galeommatidae.

Epi- and endobyssal suspension-feeders with one siphon (I.2.2/I.3.2) were part of the family Mytilidae (order Cyrtodontida), ranging from the Triassic to the Recent.

Epibyssal suspension-feeders lacking siphons (I.2.1) in the Mesozoic and Cenozoic were part of many bivalve families, some of which were capable of a pseudoplanktonic mode of life, and were also free-lying and capable of swimming. In the Triassic, these were genera of the families Posidoniidae and Aviculopectinidae (I.2.1/I.2.1a/I.2.4) assigned to the order

Table VIII. 1. Change in composition of major families representatives of which belonged to infaunal suspension-feeders without a pallial sinus (?without siphons) (I.1.1) (in this and subsequent tables, (+) families representatives of which played a significant role in this groups, and (r) families rarely represented in this group)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q–R
? Fordiliidae	r	r																
? Archaurellidae	r																	
Cycloconchidae		+	r	r														
Cardiolidae				+	r													
Grammysiidae		r	r	r	+	+	+	r	r									
Trigoniidae								r	+	+	+	+	r	r	r	r	r	r
Astaridae					r	r	r	r	r	+	+	+	+	+	r	r	r	+
Carditidae					r	?	?	?	r	r	r	+	+	+	+	+	+	+
Montacutidae														+		+	+	+

Table VIII. 2. Change in composition of major families representatives of which belonged to infaunal suspension-feeders with a shallow sinus of the pallial line (I.1.3)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q–R
Lyrodesmatidae		r	r															
Grammysiidae		r	r	r	+	+	+	r	r									
Pholadomyidae						+	+	r	r	r	r	r	r	r	r	r	r	r
Arcticidae									r	+	+	+	r	r	r	r	r	r
Corbulidae										+	+	+	r	r	r	r	r	r
Veneidae											+	+	+	+	+	+	+	+
Cardiidae									r	r	r	+	+	+	+	+	+	+
Mactridae												r	+	+	+	+	+	+

Table VIII. 3. Change in composition of major families representatives of which belonged to infaunal suspension-feeders with a deep sinus of the pallial line (I.1.5)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q–R
Pholadomyidae						+	+	r	r	+	r	r	r	r	r	r	r	r
Tellinidae (II. 2/I.1.5)											r	r	+	+	+	+	+	+
Mactridae												r	+	+	+	+	+	+

Table VIII. 4. Change in composition of major families representatives of which belonged to boring bivalves (I.1.6)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q–R
Modiomorphidae		? r																
Mytilidae					r	r	r	r	r	r	r	r	r	r	r	r	r	r
Pholadidae										r	r	+	+	+	+	+	+	+
Veneridae												r	r	r	r	r	r	r

Table VIII. 5. Change in composition of major families representatives of which belonged to infaunal suspension-feeders with an anterior mucous tubule (I.1.8, I.1.8a)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q–R
? Babinkidae		+																
Lucinidae										r	r	+	+	+	+	+	+	+

Table VIII. 6. Change in composition of major families representatives of which belonged to endobyssal suspension-feeders lacking siphon (I.3.1) and with one siphons (I.3.2)

Family	Є	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q–R
Cycloconchidae		+	r	r														
Modiomorphidae		r	+	+	r	r	r											
Ambonychiidae		r	+	r	+	r												
Cyrtodontidae		r	+	r	r													
Cardiolidae				+	r													
Pterineidae			r	+	+	r	r											
Bakevelidae							r	r					r	r				
Mytilidae					r	r	r	r										
Carditidae					?r	?	?	?	r	r	r	r	r					
Astartidae					r	r	r	r	r									
Trigoniidae													r	r	r	r	r	r
Arcidae										r	r	r	r					
Condylocardiidae														r	r			
Galeommatidae														r	r	r	r	

Table VIII. 7. Change in composition of major families representatives of which belonged to epibyssal suspension-feeders lacking siphons (I.2.1)

Family	Є	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q–R
Modiomorphidae		r	+	+														
Ambonychiidae		r	+	+	+	r												
Cardiolidae				+	r													
Pterineidae			r	+	+	r	r											
Lunulocardiidae			r	+	r	r												
Aviculopectinidae					r	+	+	+	+	r								
Bakevelidae							r	+	+	+	+	+	r	r				
Posidoniidae						r	r	+	+	+	r	r						
Pectinidae								r	+	+	+	+	+	+	+	+	+	+
Mytilidae					r	r	r	r	+	+	+	+	+	+	+	+	+	+
Limidae						r	r	r	+	+	+	+	+	+	+	+	+	+
Inoceramidae							r	r	r	+	+	+						
Carditidae									r	r	r	+	+	+	+	+	+	+
Arcidae										r	r	r	r	r	+	+	+	+

Table VIII. 8. Change in composition of major families representatives of which belonged to epifaunal suspension-feeders capable of attaching to floating objects and of pseudoplanktonic mode of life (I.2.1a)

Family	Є	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	₽$_1$	₽$_2$	₽$_3$	N_1	N_2	Q–R
Cardiolidae				+	+													
Praecardiidae				+	+	r												
Butovicellidae				r														
Posidoniidae						r	r	+	+	+	r							
Aviculopectinidae						+	+	+	+	r								
Pterinopectinidae						?r	?r											
Entoliidae								r	r									
Monotidae								r	r									

Table VIII. 9. Change in composition of major families representatives of which belonged to epifaunal free-lying suspension-feeders lacking siphons (I.2.4)

Family	€	O$_1$	O$_{2-3}$	S	D	C	P	T$_1$	T$_{2-3}$	J	K$_1$	K$_2$	₽$_1$	₽$_2$	₽$_3$	N$_1$	N$_2$	Q–R
? Fordiliidae	r	r																
? Archaurellidae	r																	
Lunulacardiidae			r	+	r	r												
Aviculipectinidae					r	+	+	+	+	r								
Posidoniidae						r	r	+	+	+	r	r						
Pectinidae								r	+	+	+	+	+	+	+	+	+	+
Bakevellidae							r	?	+	+	+	+						
Limidae						r	r	+	+	+	+	+	+	+	+	+	+	+
Inoceramidae							r	r	r	+	+	+						
Gryphaeidae										r	+	+	r	r	r	r	r	r
Carditidae					r	?	?	?	r	r	r	+	+	+	+	+	+	+
Ostreidae									r	r	r	+	+	+	+	+	+	+
Arcidae										r	r	r	r	r	+	+	+	+

Table VIII. 10. Change in composition of major families representatives of which belonged to epibyssal suspension-feeders lacking siphons and capable of swimming over the bottom (I.2.4a)

Family	€	O$_1$	O$_{2-3}$	S	D	C	P	T$_1$	T$_{2-3}$	J	K$_1$	K$_2$	₽$_1$	₽$_2$	₽$_3$	N$_1$	N$_2$	Q–R
? Aviculipectinidae						+	+											
Posidoniidae						r	r	+	+	+	r	r						
Pectinidae								r	+	+	+	+	+	+	+	+	+	+
Limidae						r	r	+	+	+	+	+	+	+	+	+	+	+
Entoliidae										r	r	r						

Table VIII. 11. Change in composition of major families representatives of which belonged to semi-infaunal suspension-feeders lacking siphons and byssus (I.3.4)

Family	€	O$_1$	O$_{2-3}$	S	D	C	P	T$_1$	T$_{2-3}$	J	K$_1$	K$_2$	₽$_1$	₽$_2$	₽$_3$	N$_1$	N$_2$	Q–R
? Cycloconchidae		+	r	r														
? Fordiliidae	r																	
? Archaurellidae	r																	
Cyrtodontidae			+	r	r													
Carditidae					r	?	?	?	r	r	r	+	+	+	+	+	+	+
Astartidae							r	r	r	+	+	+	+	+	+	+	+	+
Inoceramidae							r	r	r	+	+	+						
Trigoniidae							?r	?r	+	+	+	+	r	r	r	r	r	r
Pectinidae								r	+	+	+	+	+	+	+	+	+	+
Montacutidae														+	+	+	+	+

Cyrtodontida, and the families Pectinidae and Limidae (I.2.1/I.2.4/I.2.4a) of the order Pectinida. In the Jurassic, they were genera of the families Pectinidae, Limidae, Posidoniidae, and Inoceramidae (I.2.1/I.2.4) (order Cyrtodontida); and beginning from the Cretaceous, the families Limidae and Pectinidae (Tables VIII. 7, VIII. 8).

The group of the epifaunal free-lying suspension-feeders (I.2.4) also includes genera, whose representatives could lead a different mode of life, in a particular, nektobenthic (I.2.4a). In the Ordovician and Silurian, these were genera of the family Lunulacardiidae (I.2.1/I.2.4) (order Cyrtodontida); in the Carboniferous and Permian, they were genera of the family Avicu-

Table VIII. 12. Change in composition of major families representatives of which belonged to cemented suspension-feeders (I.2.7)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	$₽_1$	$₽_2$	$₽_3$	N_1	N_2	Q–R
Megalodontidae					r	r	r	r	r									
Pterinopectinidae					r													
Pseudomonotidae						r	r	r	r									
Monotidae																		
Anomiidae						r	r	r	r	r	r	r	r	r	r	r	r	r
Ostreidae									r	r	r	+	+	+	+	+	+	+
Terquemidae									r	r	r	r						
Gryphaeidae										r	+	+	r	r	r	r	r	r
Plicatulidae										r	r	r	r	r	r	r	r	r
Dimyidae										r	r	r	r	r	r	r	r	r
Spondylidae										r	r	r	r	r	r	r	r	r
Caprinidae											+	+						
Radiolitidae											+	+						
Hippuritidae											r	+						

Table VIII. 13. Change in composition of major families representatives of which belonged to infaunal debris-feeders lacking siphons (II.1)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	$₽_1$	$₽_2$	$₽_3$	N_1	N_2	Q–R
Tironuculidae		r	r															
Praenuculidae	r	+	+	r	r													
Ctenodontidae		r	r	r	r	r	r											
Nuculidae			r	r	r	r	r	r	r	r	r	r	r	+	+	+	+	+

Table VIII. 14. Change in composition of major families representatives of which belonged to infaunal debris-feeders with siphons (II.2)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	$₽_1$	$₽_2$	$₽_3$	N_1	N_2	Q–R
Malletiidae			+	+	r	r	r	r	+	+	r	r	r	r	r	r	r	+
Nuculanidae					r	r	r	r	r	r	r	+	+	+	+	+	+	+
Tellinidae											r	+	+	+	+	+	+	+

Table VIII. 15. Change in composition of major families representatives of which belonged to predators (III)

Family	€	O_1	O_{2-3}	S	D	C	P	T_1	T_{2-3}	J	K_1	K_2	$₽_1$	$₽_2$	$₽_3$	N_1	N_2	Q–R
Cuspidariidae										+	+	+	+	+	+	+	+	+
Poromyidae													+	+	+	+	+	+
Verticordiidae													+	+	+	+	+	+

lopectinidae; and in the Triassic, they were genera of the families Posidoniidae, Pectinidae, Aviculopectinidae, Bakevellidae, and Limidae. In the Jurassic, these were the same families but without the Aviculopectinidae, and including the Inoceramidae. In the Early Cretaceous, these were the Bakevellidae, Limidae, and Pectinidae; and in the Late Cretaceous, the same families and the Gryphaeidae (I.2.4/I.2.7) (order Cyrtodontida), Carditidae, Ostreidae, and Inoceramidae. In the Paleocene, the group included the Carditidae (I.2.4/I.2.1/I.3.1/I.3.4/I.1.1) (order Carditida), Limidae, Pectinidae, Gryphaeidae, and Ostreidae (I.2.4/I.2.7) (order Cyrtodontida); in the Eocene, it included the Carditidae, Limidae, Pectinidae, and Ostreidae; from the

Oligocene until the present, the group included the same families, joined by the Arcidae (I.2.4/I.2.3/I.2.6/I.3.3) (order Cyrtodontida) (Tables VIII. 9, VIII. 10).

The epifaunal cemented suspension-feeders (I.2.7) also include genera some species of which could be free-lying on one valve (I.2.7/I.2.4), or have a different mode of life. In the Cambrian, Ordovician, and apparently Silurian, this group was absent. In the Devonian, it included a few Megalodontidae (I.2.1/I.2.4/I.2.7) (order Hippuritida) and Pterinopectinidae (order Cyrtodontida) with similar characteristics. In the Carboniferous and Permian, this group included a few Pseudomonotidae (order Cyrtodontida), Megalodontidae, and Anomiidae (order Pectinida). In the Triassic, this group contained the Pseudomonotidae and Terquemidae (order Pectinida), rare Ostreidae (I.2.7/I.2.4) (order Cyrtodontida), Megalodontidae, and Anomiidae. In the Jurassic, this group included the Terquemidae and rare genera from the families Ostreidae, Gryphaeidae (I.2.7/I.2.4), Anomiidae, Plicatulidae, Dimyidae, and Spondylidae (I.2.7/I.2.4) (order Pectinida).

In the Early Cretaceous, this group was dominated by the Gryphaeidae and the rudists Caprinidae and Radiolitidae, whereas genera of other families (Terquemidae, Anomiidae, Spondylidae, Ostreidae, Plicatulidae, and Dimyidae) were few. A similar pattern was observed in the Late Cretaceous, although the group of widespread families included the Ostreidae and Hippuritidae. Beginning from the Paleocene, the group was dominated by the Ostreidae, rudists, and the Terquemidae disappeared, whereas other families listed above were represented by a few genera (Table VIII. 12).

Semi-infaunal suspension-feeders (see Table VIII. 6) were endobyssal (I.3.1, I.3.2), or lacking a byssus (I.3.4), either with siphons, or without them. Their groups, like groups of epifaunal bivalves, were mixed, a fact that was previously noted in the case of epifaunal suspension-feeders. It is noteworthy that the endobyssal and/or epibyssal taxa were more widespread in the Early and Middle Paleozoic. In the second half of the Ordovician, these were representatives of the families Modiomorphidae and Ambonychiidae, while in the Silurian, these were represented by the Cardiolidae, Modiomorphidae, and Pterineidae; and in the Devonian, they were represented by the Pterineidae and Ambonychiidae. In the Mesozoic, this group included the Bakevellidae, which could also be free lying (I.3.1/I.2.1/I.2.4), and the Mytilidae. The Carditidae became widespread from the Paleocene, while the Arcidae became widespread from the Eocene; some of these taxa were endobyssal, whereas others were unattached, shallowly burrowing and/or lying on the substrate (Arcidae). The Ordovician Cyrtodontidae were endobyssal and/or shallowly burrowing with the posterior part projecting out of the substrate (I.3.1/I.3.4). In the Silurian and Devonian, representatives of this family were rare. In the Devonian, this group included some Carditidae, which had a wider ethological range (I.1.1/I.2.1/I.2.4/I.3.1/I.3.4). In the Carboniferous, the group of semi-infaunal bivalves, with or without a byssus, included rare genera of the Astartidae, some of which were infaunal (I.1.1, I.1.4/I.3.2/I.3.4). In the Permian, these taxa were joined by the Inoceramidae of various ethological groups (I.2.4/I.3.4/I.2.1/I.3.1) and by rare Trigoniidae.

In the Early Triassic, semi-infaunal taxa were rare, while in the second part of the Triassic, they included the Trigoniidae, which could also be infaunal shallow burrowers (I.1.1/I.3.1/I.3.4) (order Actinodontida), Mytilidae (I.3.2/I.2.2), Bakevellidae (I.3.1/I.2.1/I.2.4), and, less commonly, the Astartidae, Inoceramidae, and Carditidae. In the Jurassic and Cretaceous, the Trigoniidae, Astartidae (I.1.1, I.1.4/I.3.4/I.3.2), Mytilidae, and Bakevellidae were abundant; the Pectinidae, only few representatives of which were endobiontic, and the Carditidae became widespread beginning from the Late Cretaceous. The Inoceramidae were less common. In the Paleocene and Eocene, the Carditidae, Mytilidae, Trigoniidae, and Astartidae were dominant. In the Eocene, they were joined by the Montacutidae (I.1.1/I.2.2/I.3.4), whereas the Trigoniidae lost their dominance. In the Oligocene–Neogene, semi-infaunal bivalves were represented by certain genera of the families Carditidae, Pectinidae, Mytilidae, Arcidae, and Montacutidae; from the Pliocene, they were also represented by the Codylocardiidae (I.1.2/I.2.1/I.3.1), rare representatives of which were known beginning from the Eocene. At present, these large families are joined by the Astartidae and Galeommatidae (I.3.1/I.2.1/I.1.2) (Tables VIII. 6, VIII. 11).

The taxonomic composition of debris-feeders was considerably less diverse, and therefore changed less. Shallowly burrowing taxa lacking siphons (II.1) in the Cambrian were represented by rare taxa, poorly known taxonomically, assigned to the family Praenuculidae. Beginning from the Early Ordovician, certain representatives of this family were widespread, although they were not very diverse until the Devonian. From the beginning of the Ordovician, they were joined by a few genera of the family Ctenodontidae known until the Permian. In the Ordovician, this group also included rare Tironuculidae. Isolated genera of the family Nuculidae appeared in the second half of the Ordovician and remained rare until the end of the Paleozoic, while in the Mesozoic and Paleocene, this family contained three genera; and from the Eocene to the Recent, it contained up to six genera (Table VIII. 13).

Infaunal siphonate debris-feeders (II.2) were more diverse. In the Paleozoic and beginning of the Mesozoic, they were only represented by the Protobranchia, among which the families Malletiidae and Nuculanidae were dominant. The family Malletiidae is known from the second half of the Ordovician and was most diverse in the Ordovician and Silurian, the second half of the Triassic, Jurassic, and at present, although not more than 10 genera were present in each period. The first Nuculanidae are known from the Devonian, although they became more diverse only from the Late Cretaceous. Nevertheless, the role of this group was very noticeable in the Phanerozoic seas.

The siphonate debris-feeders include genera assigned to the order Venerida (Autobranchia), from families of the superfamilies Tellinoidea (Tellinidae and Psammobiidae) and Scrobicularioidea (Scrobilaculariidae) (Table VIII. 14).

Predatory Septobranchia (III) have not been recorded before the Jurassic. Their distribution in the Mesozoic and Cenozoic is very restricted, while their generic composition is not diverse. A single genus of the family Cuspidariidae is known from the Jurassic and Early Cretaceous, three genera of the family Poromyidae are recorded in the Late Cretaceous, and one genus of the family Verticordiidae occurs in the Paleocene. The generic composition of the Cuspidariidae and Vertricordiidae increased somewhat in the Cenozoic, although it did not exceed five to nine genera in total (Table VIII. 15).

CHAPTER IX. BIVALVE COMMUNITIES AND THEIR CHANGES IN THE PHANEROZOIC

(1) Taxonomic and Ethological-Trophic Composition of Bivalve Communities in Different Zones of Phanerozoic Seas

Cambrian

As mentioned above, bivalves were extremely rare and did not play any significant part in the benthic communities of the Cambrian seas. All genera known consisted of small, shallowly burrowing semi-infaunal or infaunal suspension-feeders lacking siphons and byssus (*Fordilla*), or shallowly burrowing and/or epifaunal probable debris-feeders lacking siphons (*Pojetaia*) (Pojeta and Runnegar, 1974; Pojeta, 1975; Runnegar and Bentley, 1983; Krasilova, 1987; Berg-Madsen, 1987; Dzik, 1994).

Ordovician

In the Early Ordovician, abundance and diversity of bivalves were still low, and they were not characteristic of benthic communities in any zone of the sea. Representatives of the most widespread families belonged to groups of suspension-feeders: endo- and/or epibyssal, lacking siphons (I.2.1/I.3.1, Modiomorphidae); endobyssal and/or semi-infaunal, lacking byssus (I.3.1/I.3.4, Cyrtodontidae); shallowly burrowing infaunal or semi-infaunal, lacking siphons, sometimes, with byssus (I.1.1/I.3.1/I.3.4, Cycloconchidae); epifaunal and semi-infaunal and/or shallowly burrowing, lacking siphons and byssus (I.1.1/I.2.4/I.3.4, Redoniidae); and infaunal, shallowly burrowing, possessing siphons (I.1.3, Lyrodesmatidae); and infaunal, shallowly burrowing debris-feeders lacking siphons (II.1, Praenuculidae and Tironuculidae).

In the Middle and Late Ordovician, the taxonomic and ecological composition of bivalves became more diverse. They were parts of benthic communities in all zones, and most commonly occurred in the coastal part and in the inner shelf. On the open shelf, they were not numerous, considerably fewer than brachiopods. Dominant families belonged to the epi- and/or endobyssal suspension-feeders lacking siphons (I.2.2/I.2.3, Modiomorphidae and Ambonichiidae), semi-infaunal suspension-feeders with or without byssus (I.3.1/I.3.4, Cyrtodontidae), the infaunal shallowly burrowing debris-feeders lacking siphons (II.1, Praenuculidae), and more deeply burrowing and siphons possessing debris-feeders (II.2, Malletiidae). Representatives of the families Pterineidae (I.2.1/I.2.4/I.3.1), Ctenodontidae (II.1), Orthonotidae (I.1.1/I.3.1/I.3.3), Cycloconchidae, Lyrodesmatidae, Lunulacardiidae (I.2.1/I.2.4), and Antipleuridae (I.1.1/I.2.4/I.3.4) were less diverse.

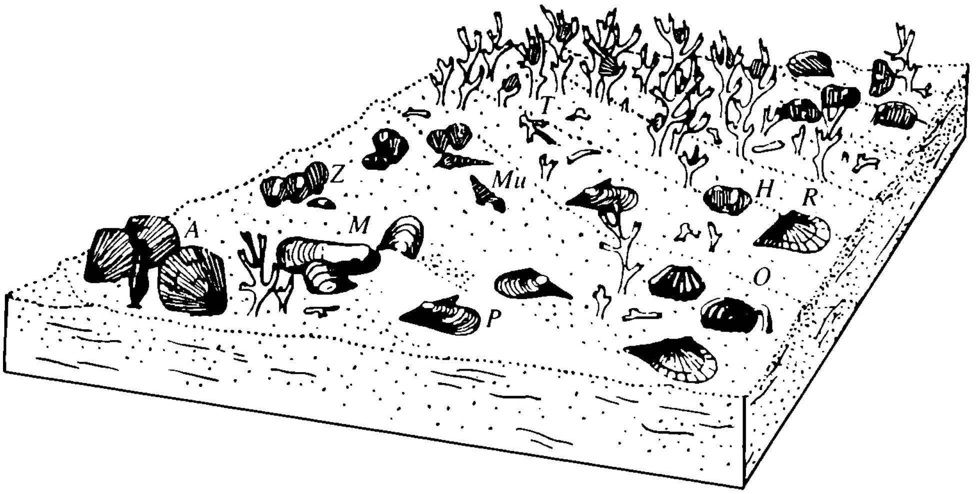


Fig. IX. 1. Reconstruction of the Late Ordovician coastal community of (*H, O, R, Z*) brachiopods; (*T*) bryozoans; (*A, M, P*) bivalves: (*A*) *Ambonychia*, (*M*) *Modiolopsis*, and (*P*) *Pterinea*; and (*Mu*) gastropods (Central Appalachians) (after Bretsky, 1969, text-fig. 7).

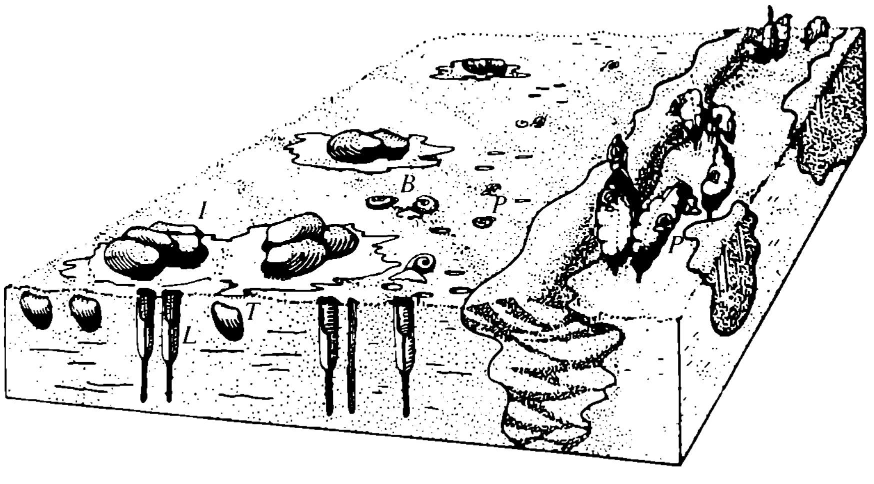


Fig. IX. 2. Reconstruction of the Late Ordovician community of the deltoidal zone, composed of (*L*) lingulid brachiopods; (*B*, *P*) gastropods; and (*I*, *T*) bivalves: (*I*) *Ischirodonta* and (*T*) *Tancrediopsis* (Central Appalachian Mountains) (after Bretsky, 1969, text-fig. 5).

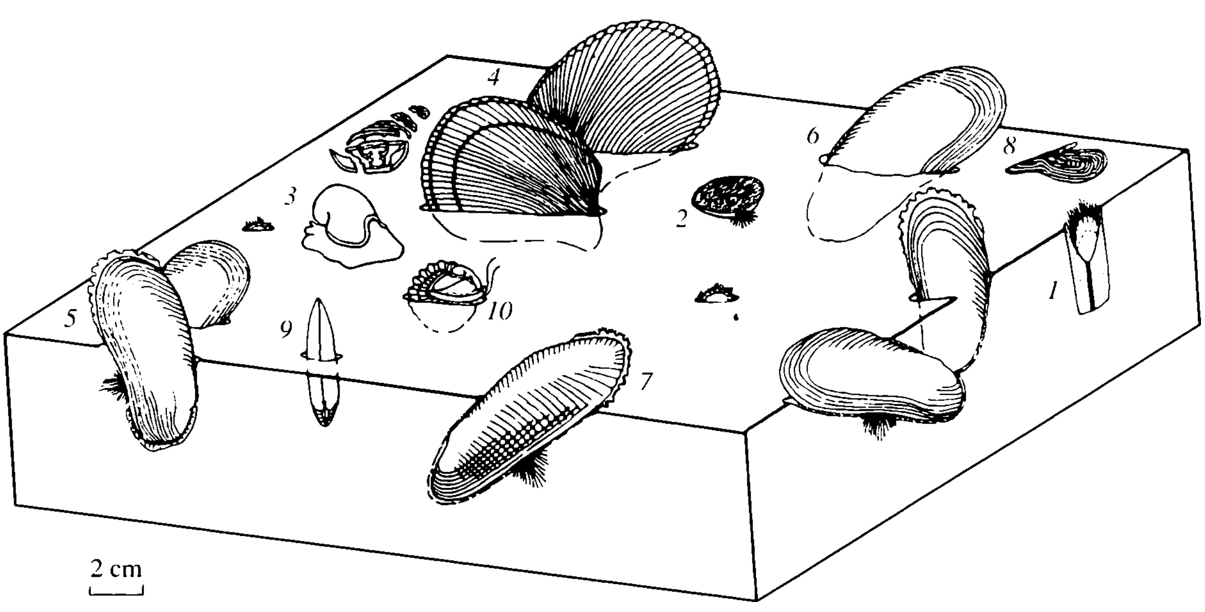


Fig. IX. 3. Reconstruction of the Late Ordovician community of muddy substrates of the shallow shelf: (*1*, *2*) inarticulate brachiopods; (*3*) monoplacophores; (*4–9*) bivalves: (*4*) *Ambonychia*, (*5*) *Corallidomus*, (*6*) *Modiolopsis*, (*7*) *Pholadomorpha*, (*8*) *Caritodens*, and (*9*) *Rhytimya*; and (*10*) trilobites (Indiana) (after Frey, 1987, text-fig. 4).

At that time, the most important role belonged to bivalves of the bottom communities of the marginal and coastal zones of the sea (Muller, 1988), where conditions were unfavorable for many other groups. Communities of these zones were dominated by debris-feeders shallowly burrowing and lacking siphons (*Ctenodonta*, *Praenucula*, *Palaeoconcha*, and *Tancrediopsis*). Infaunal debris-feeders with siphons (*Nuculites*, *Palaeoneilo*, and *Cardiolaria*) and epi- and/or endobyssal suspension-feeders (*Modiolopsis*, *Ambonychia*, *Pterinea*, *Colpomya*, *Vanuxemia*, *Byssodesma*, and *Ischirodonta*) were common. Shallowly burrowing infaunal suspension-feeders lacking siphons were rare (*Davidia* and *Glyptarca*, Figs. IX. 1, IX. 2).

Communities of the shallow shelf were dominated by epi- and/or endobyssal suspension-feeders lacking siphons (*Ambonychia*, *Modiolopsis*, *Orthodesma*, and the less abundant *Whiteavesia*, *Orthonella*, *Pholadomorpha*, *Goniophora*, *Modiolodon*, *Palaeopteria*, *Pseudocolpomia*, etc.); epifaunal free-lying on one valve (*Pterinea* and *Carditodens*), or byssal taxa (*Opistopteria* and *Psylonichia*); and semi-infaunal taxa with or without byssus (*Cyrtodontula*, *Cyrtodonta*, *Cuneamya*, *Ischirodonta*, *Cymatodonta*, and *Colpomya*). Infaunal, shallowly burrowing suspension-feeders without siphons, or with very short siphons (*Cycloconcha*, *Lyrodesma*, *Psiloconcha*, and *Rhytimya*) were considerably rarer. Muddy substrates were typically inhabited

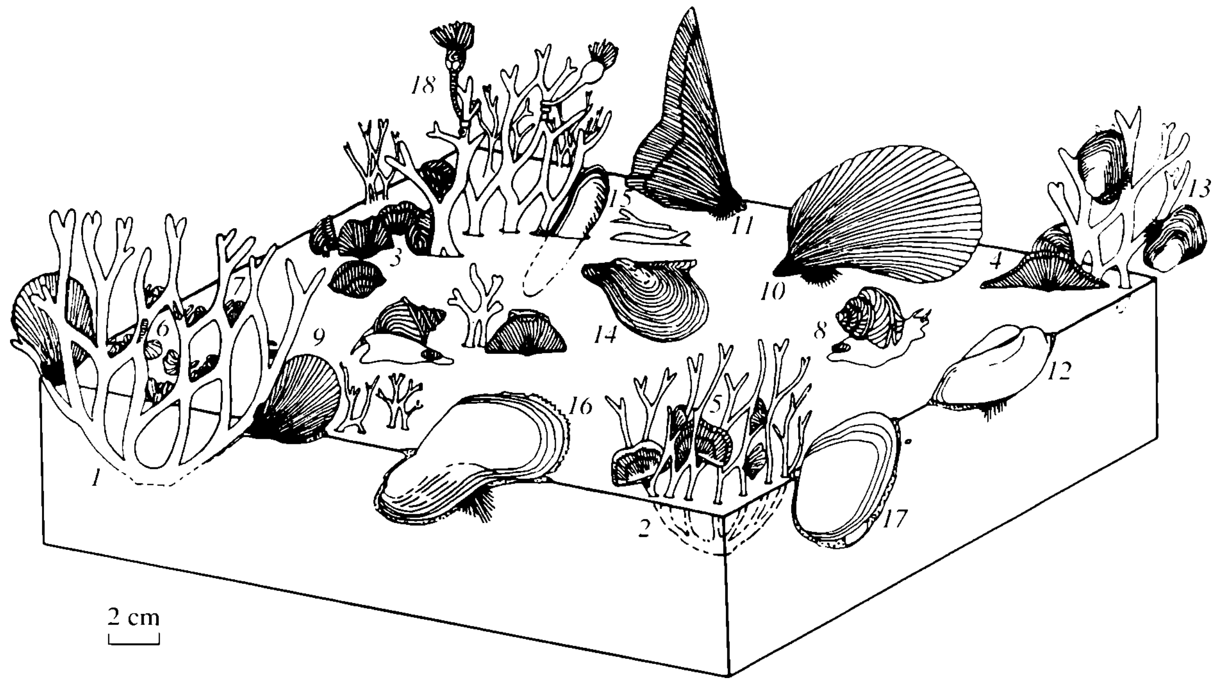


Fig. IX. 4. Reconstruction of the Late Ordovician bryozoan settlement and associated invertebrate assemblage of the shallow shelf: (*1, 2*) bryozoans; (*3–7*) brachiopods; (*8*) gastropods; (*9–17*) bivalves: (*9, 10*) *Ambonychia*, (*11*) *Opisthoptera*, (*12*) *Cyrtodonta*, (*13*) *Orthonella*, (*14*) *Caritodens*, (*15*) *Orthodesma*, (*16*) *Pseudocolpomya*, and (*17*) *Ischirodonta*; and (*18*) cystoids (Ohio) (after Frey, 1987b, text-fig. 7).

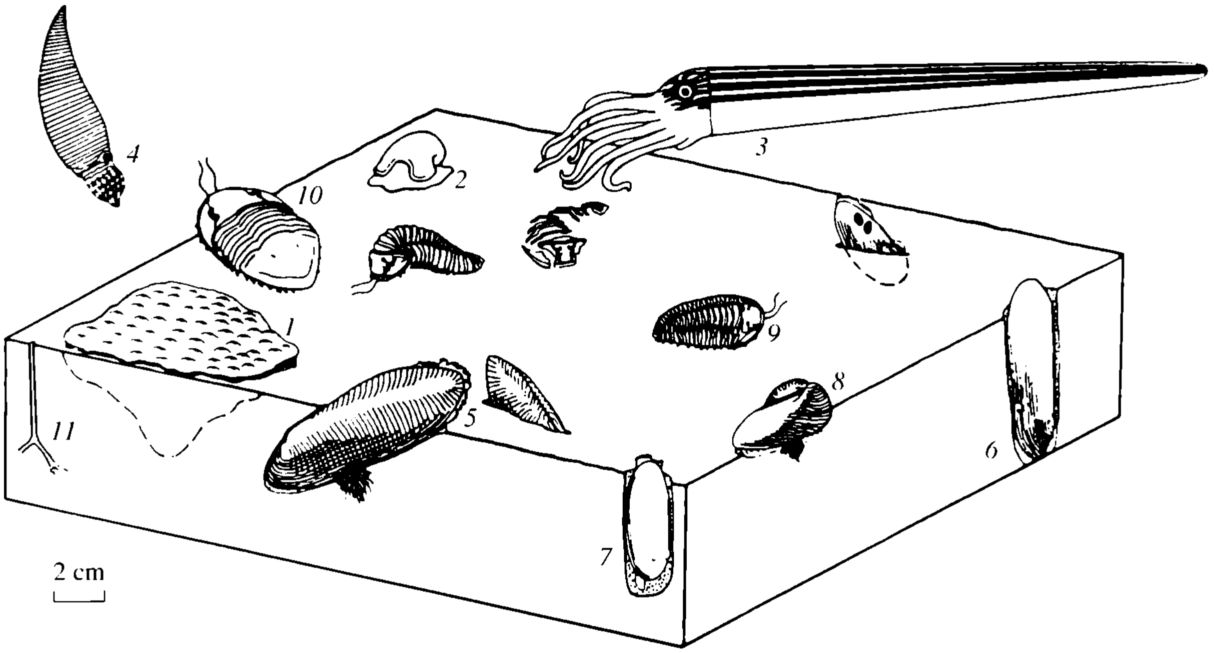


Fig. IX. 5. Reconstruction of the Late Ordovician community of the shallow shelf: (*1*) stromatoporoids; (*2*) ? monoplacophores; (*3, 4*) cephalopods; (*5–8*) bivalves: (*5*) *Pholadomorpha*, (*6*) *Cymatodonta*, (*7*) *Psiloconcha*, and (*8*) *Cuneamya*; (*9, 10*) trilobites; and (*11*) traces (Ohio) (after Frey, 1987a, text-fig. 5).

by infaunal debris-feeders lacking siphons (*Similidonta*, *Ctenodonta*, *Deceptrix*, *Praenucula*, and *Cleidophorus*) and with siphons (*Nuculites*, *Palaeoneilo*, and *Cardiolaria*), and, occasionally, by infaunal *Babinka*, which probably had an inhalant mucous tubule (Figs. IX. 3–IX. 5).

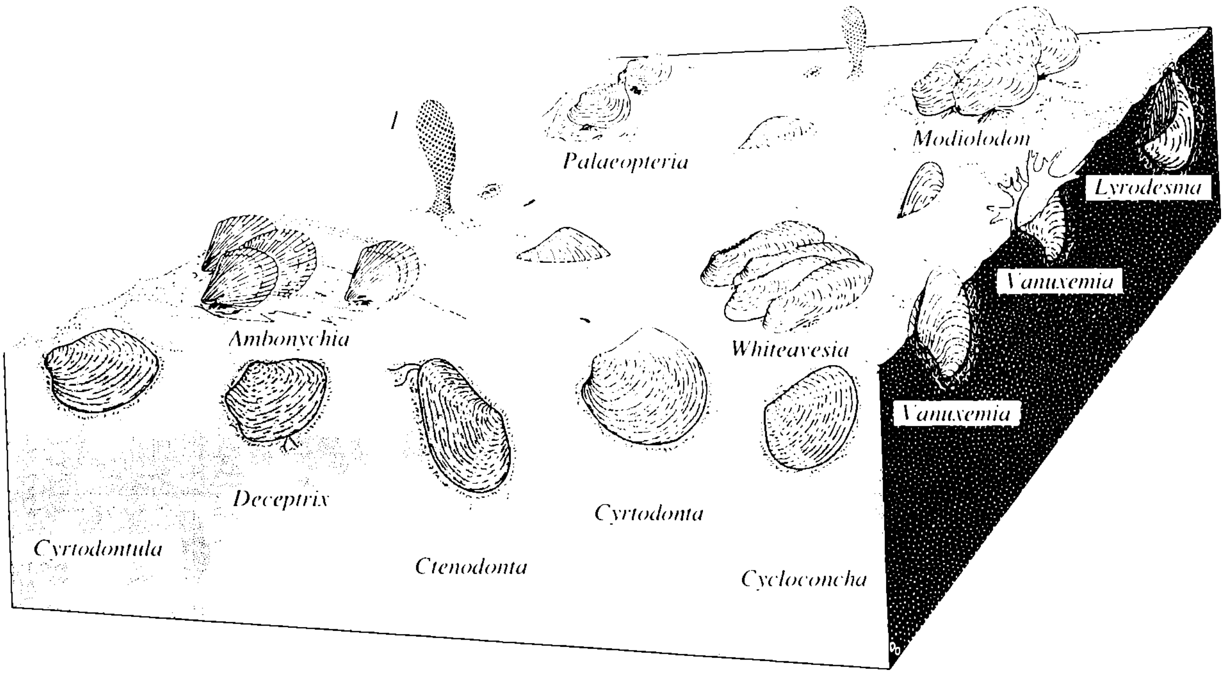


Fig. IX. 6. Reconstruction of the mode of life of Middle Ordovician bivalves: (*1*) hypothetical algae (after Pojeta, 1971, text-fig. 8).

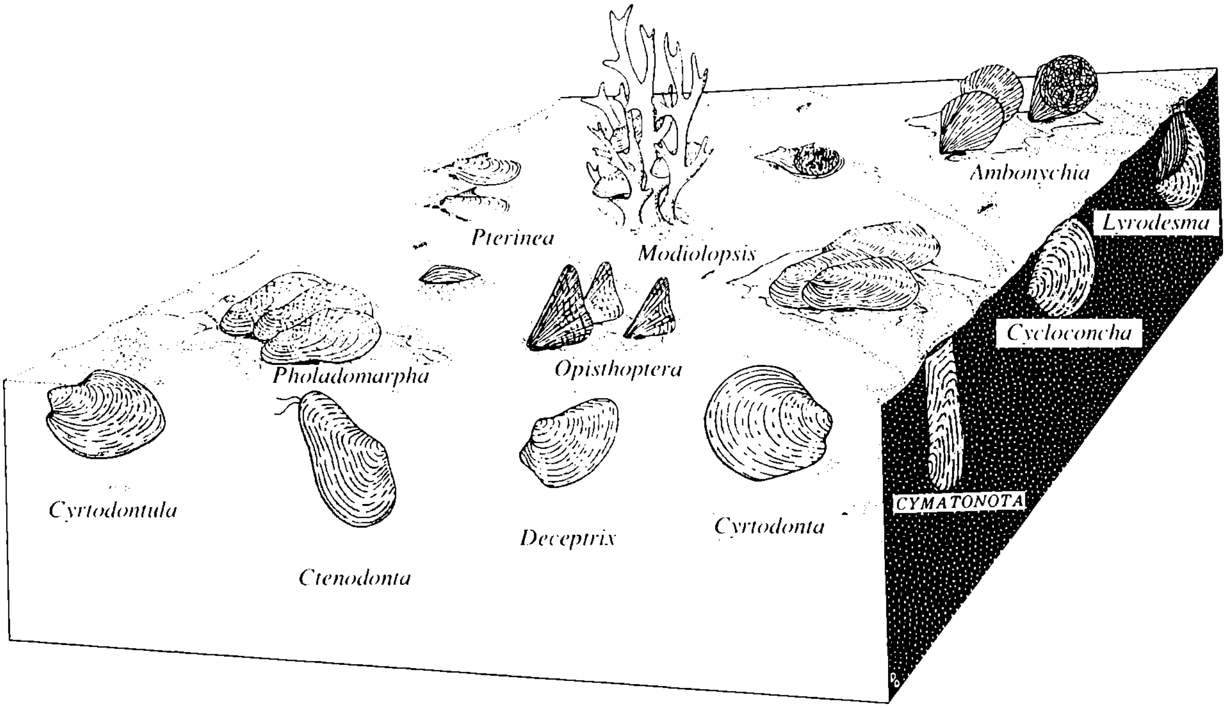


Fig. IX. 7. Reconstruction of the mode of life of Late Ordovician bivalves (after Pojeta, 1971, text-fig. 9).

In the zones of organic buildups, bivalves were scarce and not diverse. These areas were inhabited by *Cyrtodonta*, *Modiolopsis*, and *Ambonychia* attached by byssus to coral skeletons and their fragments. Endobyssal representatives of the same genera settled between the coral banks in association with the infaunal debris-

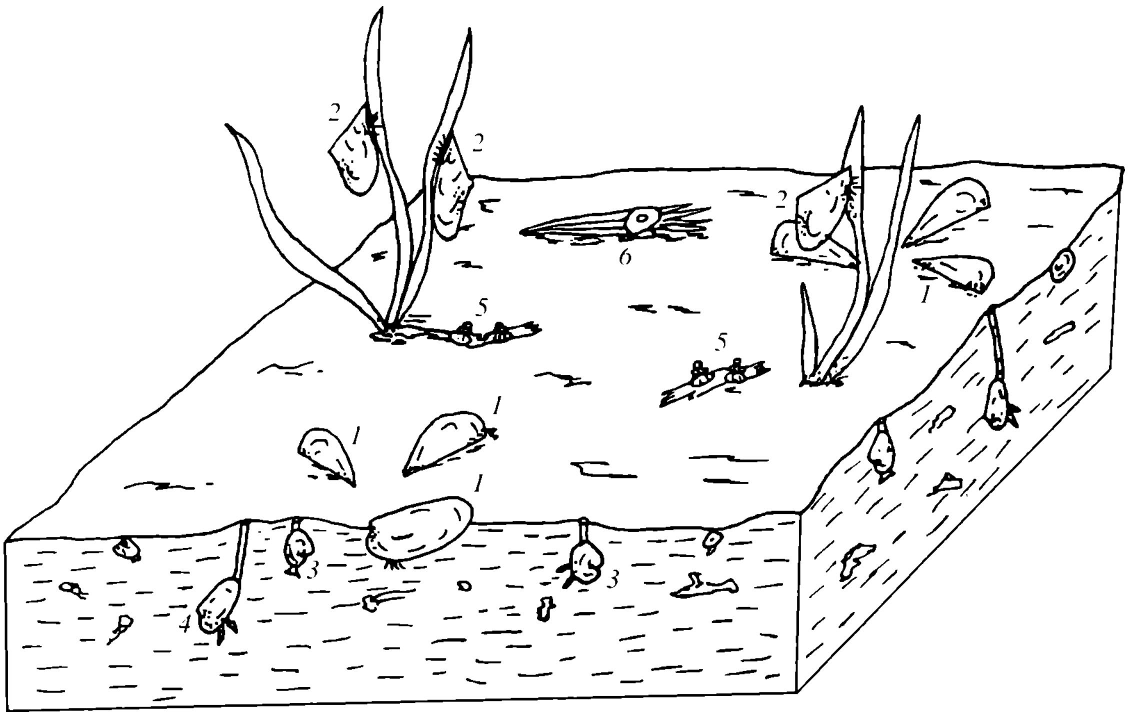


Fig. IX. 8. Reconstruction of the Early Silurian community of the tidal zone: (*1–4*) bivalves: (*1*) *Modiolopsis*, (*2*) *Pteronitella*, (*3*) *Nuculites*, and (*4*) *Palaeoneilo*; (*5*) gastropods; and (*6*) cephalopods (Nova Scotia, Canada) (after Walker and Bambach, 1974, text-fig. 2. 10).

feeders lacking siphons *Ctenodonta* (Bretsky, 1969; Daley, 1972; Morris, 1978; Frey, 1987a, 1987b).

In the zone of the deep shelf, bivalves were characteristic inhabitants mainly represented by the infaunal debris-feeders lacking siphons (*Ctenodonta, Cleidophorus, Praenucula*, and *Similidonta*) and siphonate and more deeply burrowing *Palaeoneilo* and *Nuculites*. Suspension-feeders were represented by epibyssal *Goniopora* and semi-infaunal endobyssal or lacking byssus *Colpomya* (Lehman and Pope, 1989).

The mode of life of the Middle and Late Ordovician bivalves has been reconstructed by Pojeta (1971) (Figs. IX. 6, IX. 7).

Silurian

In the Silurian, bivalves were abundant in the marginal and coastal zones, whereas on the shelves (shallow and deep) and in the area of organic buildups, they were common but less abundant than brachiopods and some other groups.

The dominant families were suspension-feeders. These included epi- and/or endobyssal taxa lacking siphons (I.2.1/I.3.1, Modiomorphidae and Ambonychiidae); epi- and/or endobyssal, less commonly shallowly burrowing, lacking siphons (I.2.1/I.3.1/I.1.1, Cardiolidae), epifaunal with byssus or free-lying taxa (I.2.1/I.2.4, Lunulacardiidae); infaunal, semi-infaunal, and epifaunal taxa lacking byssus (I.1.1/I.3.4/I.2.4, Antipleuridae); epifaunal with or without byssus and/or endobyssal (I.2.1/I.2.4/I.3.1, Pterineidae); semi-infaunal byssal, or nonattached burrowing bivalves (I.3.1/I.3.4, Cyrtodontidae); epibyssal and/or pseudoplanktonic (I.2.1/I.2.1a, Praecardiidae); and relatively deeply burrowing debris-feeders with siphons (II.2, Malletidae). Other ethological-trophic groups were less common.

In the marginal zone (lagoons, bays, and the tidal zone), the representatives of the most widespread taxa were endo- and/or epibyssal suspension-feeders lacking siphons (*Modiolopsis, Pterinea*, and *Leptodesma*); epibyssal suspension-feeders lacking siphons (*Pteronitella*); and infaunal siphonate debris-feeders (*Palaeoneilo* and *Nuculites*) (Fig. IX. 8). Shallowly burrowing debris-feeders lacking siphons (*Cardiolaria* and *Nuculoidea*) and infaunal suspension-feeders with short siphons (*Paracyclas*) were less common (Walker and Bambach, 1974).

In the coastal zone, the most characteristic taxa included the infaunal debris-feeders *Nuculites* and *Palaeoneilo* and epibyssal *Pteronitella*, while representatives of other genera were less common, although their ethological-trophic composition was quite diverse. Suspension-feeders included endo- and/or epibyssal taxa lacking siphons (*Modiolopsis, Cypricardinia, Ptychopteria*, and *Pterinea*); epibyssal bivalves lacking siphons (*Actinopteria, Mytilarca*, and *Cardiola*); endobyssal bivalves lacking siphons (*Goniophora* and the Grammysioidea); infaunal shallowly burrowing *Paracyclas*; infaunal *Illionia*, with a mucous tubule instead of an inhalant siphon; infaunal or semi-infaunal

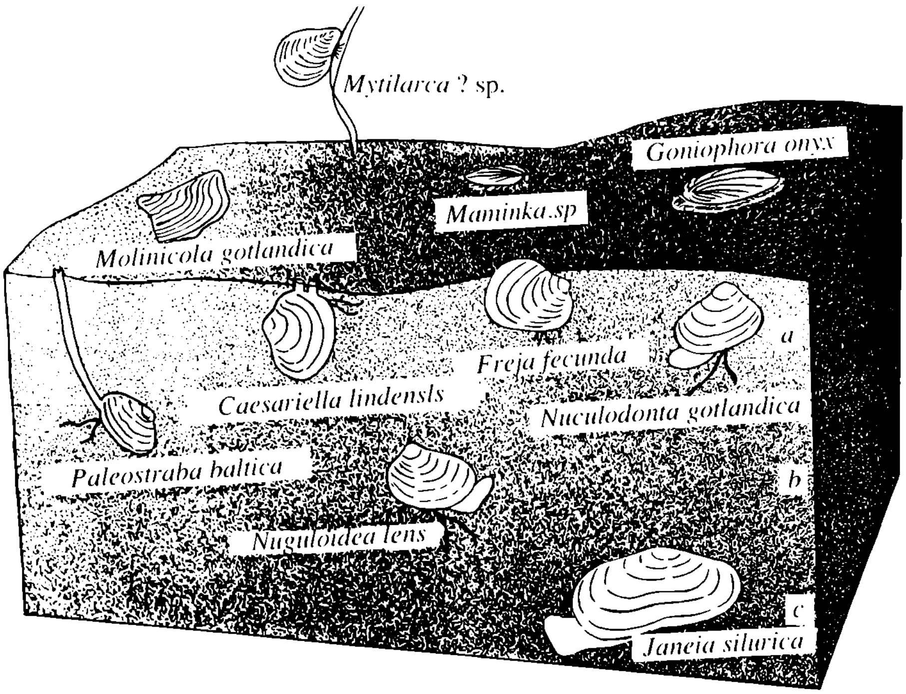


Fig. IX. 9. Reconstruction of the Early Silurian community of bivalves inhabiting the calcareous muddy substrates of the sublittoral zone: (*a, b, c*) three levels of feeding of debris-feeders inside the substrate (Gotland Island) (after Liljedahl, 1985, text-fig. 7).

Orthonota (without siphons, or with short siphons) and *Grammysia* (without siphons).

The generic composition of the communities of the shallow shelf was even more diverse, although the ethological-trophic composition was similar to the previous one. These communities were dominated by suspension-feeders, including endo- or epybyssal *Modiolopsis* and *Cypricardinia*, epibyssal *Actinopteria* and *Mytilarca*, and endobyssal Goniophore lacking siphons; infaunal debris-feeders with siphons (*Nuculites*) and without siphons (*Nuculoidea* and *Janeja*); infaunal suspension-feeders with short siphons (*Paracyclas*) or with an inhalant mucuous tubule and an exhalant siphon (*Illionia*); and infaunal and semi-infaunal taxa lacking siphons, or with short siphons (*Orthonota*). The endo- and/or epibyssal suspension-feeders *Ambonychia, Leptodesma, Pterinea*, and *Mamminka*; the epibyssal *Pteronitella, Amphicoelia, Praecardium, Megalomoidea*, and *Ptychopteria*; and the endobyssal *Grammyaioidea* and *Modiomorpha*; infaunal shallowly burrowing or semi-infaunal suspension-feeders lacking siphons (*Grammysia*) and infaunal debris-feeders (*Similidonta* and *Nuculodonta*) (lacking siphons), and *Caesariella* and *Paleostraba* (with siphons) were less common (Fig. IX. 9) (Ziegler *et al.*, 1968; Calef and Hancock, 1974; Lawson, 1975; Watkins, 1978a, 1978b, 1979, 1991, 1996; Watkins and Aithie, 1980; Cocks and McKerrow, 1984; Křiž, 1984; Liljedahl, 1985, 1991; Sinitsyna and Isakar, 1987, 1992).

The zone of organic buildups was inhabited by representatives of the same genera which lived on the shallow shelf. *Actinopteria, Modiolopsis, Megalonoidea* (often built banks), *Pterinea, Cypricardinia, Grammysioidea*, and *Mytilarca* were dominant. *Pteronitella, Grammysia, Goniophora, Ptychopteria, Palaeopecten, Illionia*, epibyssal *Plectomytilus* and *Amphicoelia*, and endobyssal *Newsonella* were less common (Sinitsyna and Isakar, 1987, 1992; Watkins, 1996).

The generic composition of bivalves in the zone of the deep shelf was almost identical to that characteristic of the shallow shelf. The community was like that in the shallower area dominated by endo- and/or epibyssal suspension-feeders (*Leptodesma, Modiolopsis, Goniophora, Actinopteria, Cypricardinia*, and *Cardiola*). Species with an apparently pseudoplanktonic lifestyle, which attached themselves using the byssus to floating algae and cephalopods, were typically present (*Butovicella, Duabina*, and *Slava*). Of the debris-feeders, *Nuculites* was common (Watkins, 1978a; Turek, 1983; Sinitsyna and Isakar, 1987, 1992).

Devonian

Bivalve families dominating in the Devonian seas belonged to suspension-feeders: epi- and/or endobyssal (I.2.1/I.3.1, Modiomorphidae and Ambonychiidae), epi- and/or endobyssal and/or epifaunal taxa lacking byssus (I.2.1/I.3.1/I.2.4, Pterineidae), epibyssal and/or

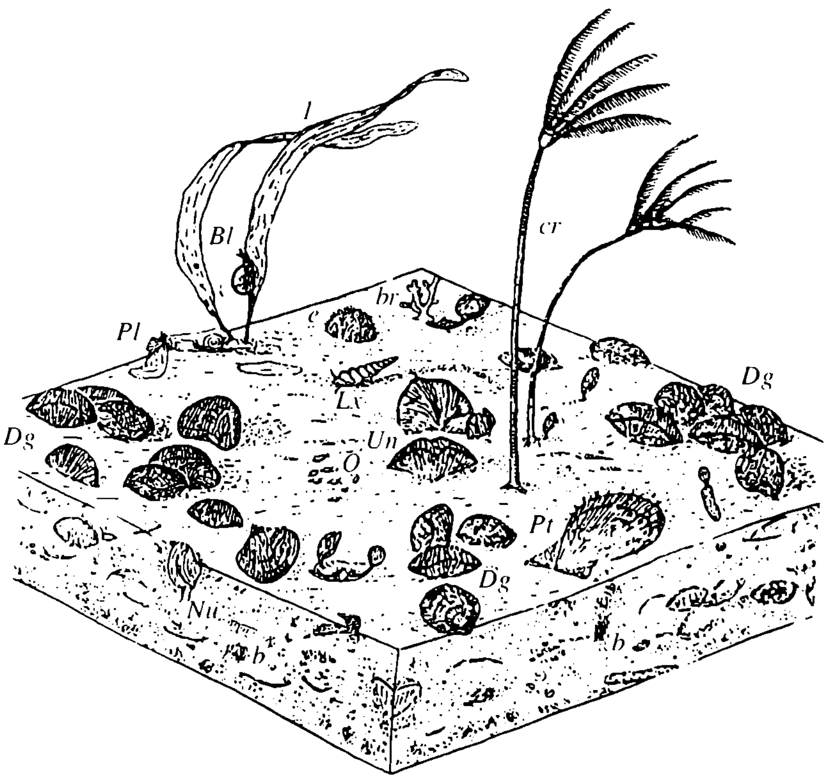


Fig. IX. 10. Reconstruction of the Late Devonian lagoonal community. Designations: (*b*) traces of burrowing; (*Bl, Lx, Pl*) gastropods; (*br*) bryozoans; (*cr*) crinoids; (*Dg, Un*) brachiopods; (*Nu, Pt*) bivalves; (*Nu*) *Nuculoidea* and (*Pt*) *Pterinopecten*; (*e*) echinoids; (*O*) ostracodes; and (*l*) hypothetical algae (Poland) (after Racki and Balinski, 1981, text-fig. 14).

epiplanktonic (I.2.1/I.2.1a, Praecardiidae), shallowly burrowing infaunal and/or semi-infaunal, with or without siphons, sometimes, with byssus (I.1.1/I.1.3/I.3.3/I.3.1, Grammysiidae) and infaunal debris-feeders with siphons (II.2, Malletidae).

Bivalves in the Devonian seas composed an important component of sea bottom communities in the marginal and coastal zones and the shallow shelves, whereas in the zone of organic buildups and in the deep shelf zones, they were characteristic, but not abundant.

The marginal zone (lagoons and tidal zones) was dominated by epi- and/or endobyssal suspension-feeders (*Leptodesma, Ptychopteria, Goniophora, Pterinopecten*, and other less common genera) and infaunal debris-feeders with siphons (*Palaeoneilo* and *Nuculites*) and lacking siphons (*Nuculoidea* and *Janeia*) (Fig. IX. 10). The shallowly burrowing suspension-feeders lacking siphons (*Schizodus*) and infaunal shallowly burrowing and/or semi-infaunal suspension-feeders with short siphons (*Edmondia*) were less common (McGhee, 1976; Racki and Balinski, 1981; Hecker, 1981).

The coastal zone was dominated by representatives of *Leptodesma* in association with *Pterinea, Modiomorpha, Ptychopteria, Ptychodesma, Goniophora*, and *Grammysioidea*, which belonged to the same ethological-trophic group of epi- and/or endobyssal suspension-feeders; and with the epibyssal *Lyriopecten, Actinopteria, Mytilarca*, and *Gosseletia*; epibyssal and/or free-lying on the surface of the substrate *Pseudoaviculopecten*; infaunal shallowly burrowing, or semi-infaunal and lacking siphons *Cypricardella, Eoschizodus, Nyassa*, and *Grammysia*; and infaunal and semi-infaunal *Sphenotus* and *Edmondia* possessing short siphons. Representatives of the genus *Paracyclas* occurring in this zone probably had an inhalant mucous tubule and an exhalant siphon. The infaunal debris-feeders *Palaeoneilo, Nuculites*, and *Nuculoidea* were typical (Bowen *et al.*, 1974; McGhee, 1976; Bailey, 1983) (Figs. IX. 11–IX. 14).

The generic composition of the communities inhabiting the shallow shelf was more diverse, although the ethological-trophic composition was similar to that of the marginal and coastal zones. Representatives of the endo- and/or epibyssal suspension-feeders (*Leptodesma, Modiomorpha, Leiopteria, Goniophora*, and *Ptychopteria*); endobyssal *Grammysia, Cypricardinia*; epibyssal *Actinopteria* and *Lyriopecten*; infaunal or semi-infaunal lacking siphons *Cypricardella* and *Eoschizodus*; the siphonate *Paracyclas, Edmondia, Palaeosolen*, and *Pholadella* were dominant. Infaunal

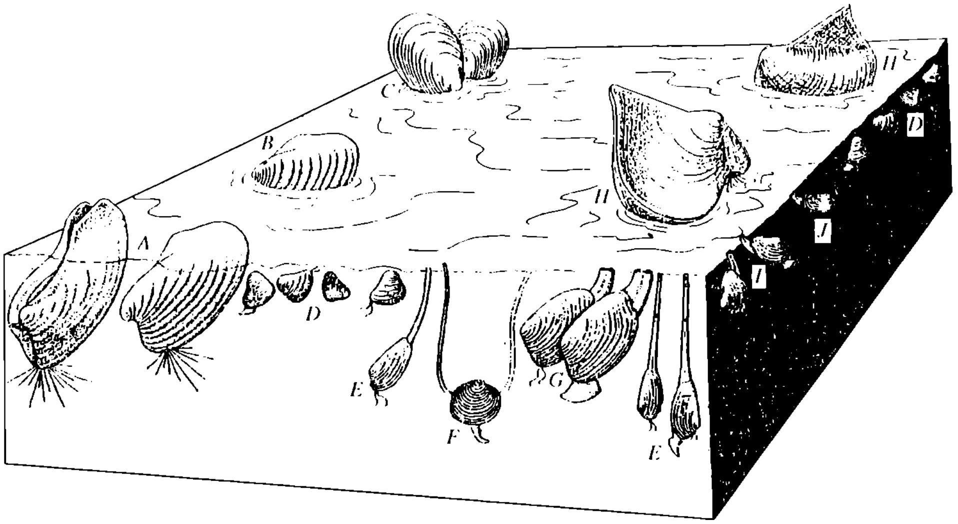


Fig. IX. 11. Reconstruction of the mode of life of the Middle Ordovician bivalves inhabiting muddy substrates of the coastal zone (New York State) (after Bailey, 1983, text-fig. 5): (*A*, *B*) *Grammysioidea*, (*C*) *Ptychodesma*, (*D*) *Nuculoidea*, (*E*, *J*) *Nuculites*, (*F*) *Paracyclas*, (*G*, *I*) *Palaeoneilo*, and (*H*) *Ptychopteria*.

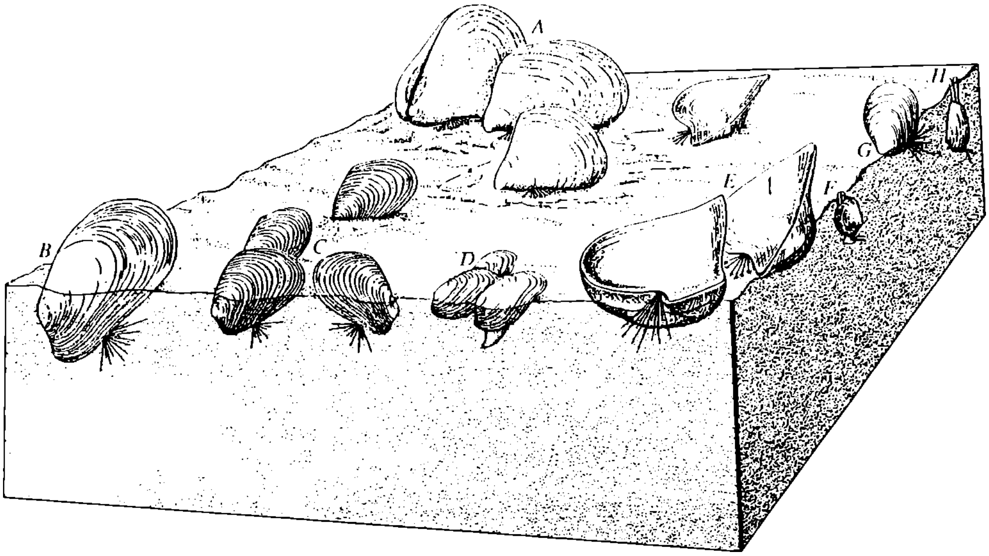


Fig. IX. 12. Reconstruction of the mode of life of the Middle Devonian bivalves inhabiting muddy-sandy substrates of the coastal zone (New York State) (after Bailey, 1983, text-fig. 6): (*A*) *Gosseletia*, (*B*, *C*) *Modiomorpha*, (*D*) *Nyassa*, (*E*) *Ptychopteria*, (*F*) *Palaeoneilo*, (*G*) *Ptychodesma*, and (*H*) *Nuculites*.

debris-feeders *Palaeoneilo*, *Nuculites*, and *Nuculoidea* were typical. Other suspension-feeders (epifaunal and semi-infaunal *Pterinea*, *Pseudoaviculopecten*, *Glyptodesma*, *Pterinopecten*, and *Mytilarca*; infaunal *Schizodus*, and some others) were less common (Bowen *et al.*, 1974; Thayer, 1974a; McGhee, 1976; Hecker, 1981; Brett *et al.*, 1983; Baird and Brett, 1983; Savarese *et al.*, 1986; Brett *et al.*, 1986; Grasso, 1986; Struve, 1989) (Figs. IX. 15–IX. 17).

In the zone of organic buildups, bivalves were common, but not diverse. They were represented by the epibyssal (*Mytilarca*, *Actinopteria*, and *Leptodesma*) and infaunal suspension-feeders living between the colonies of corals (*Schizodus* and *Paracyclas*) and debris-feeders (*Nuculoidea* and *Palaeoneilo*) (Williams, 1980; Li Zu-Han, 1986).

In the deep shelf, bivalves were also represented by a small number of genera. Suspension-feeders typically included endobyssal *Posidonia*, *Buchiola*, and *Pterochaenia* (possibly, epiplanktonic taxa attached to floating algae or nectobenthic organisms). The community also included infaunal debris-feeders (*Nuculites*, *Nucu-*

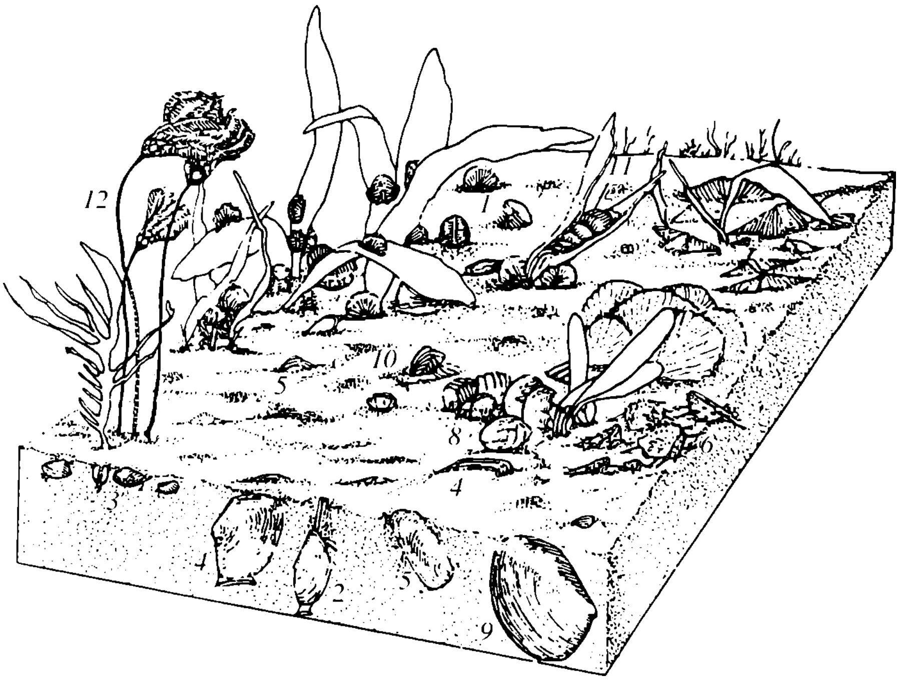


Fig. IX. 13. Reconstruction of the Late Devonian coastal community composed of (*1*, *11*) gastropods, (*6–8*, *10*) brachiopods, (*12*) pelmatozoans, and (*2–5*, *9*) bivalves: (*2*) *Palaeoneilo*, (*3*) *Nuculoidea*; (*4*) *Cypricardella*; (*5*) *Sphenotus*, and (*9*) *Eoschizodus* (Appalachian Mountains) (after Bowen *et al.*, 1974, text-fig. 11).

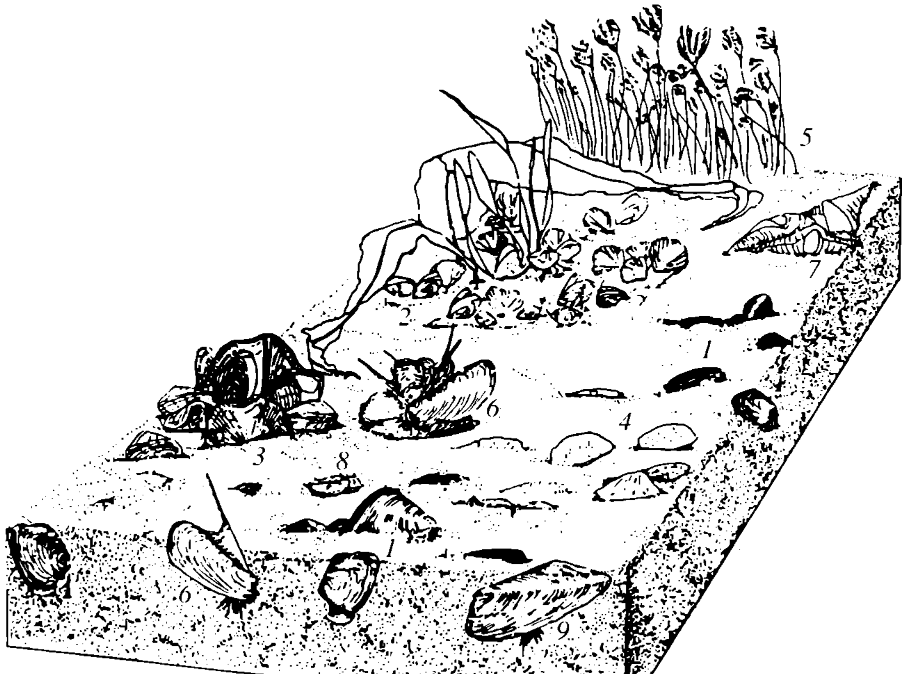


Fig. IX. 14. Reconstruction of the Late Devonian coastal community composed of brachiopods (*2–4*, *7*, *8*), pelmatozoans (*5*), and (*1*, *6*, *9*) bivalves: (*1*) *Cypricardella*, (*6*) *Leptodesma*, and (*9*) *Goniophora* (New York State) (after Bowen *et al.*, 1974, text-fig. 15).

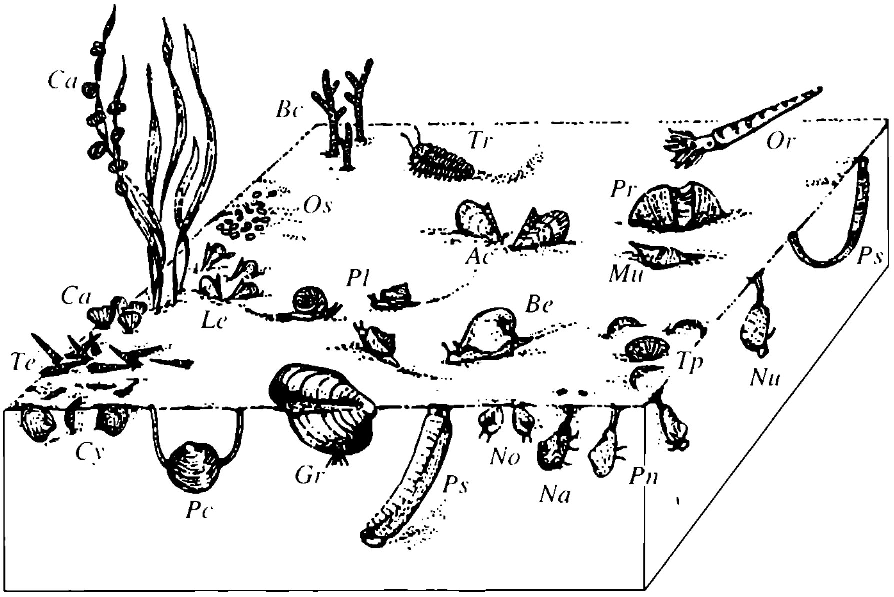


Fig. IX. 15. Reconstruction of the Late Devonian community of the shallow zone of the deltoidal platform, composed of (*Bc*) bryozoans, (*Ca, Mu, Pr, Tp*) brachiopods, (*Be, Pl*) gastropods, (*Or*) cephalopods, (*Te*) tentaculites, (*Tr*) trilobites, (*Os*) ostracodes, and bivalves: (*Ac*) *Actinopteria*, (*Cy*) *Cypricardella*, (*Gr*) *Grammysia*, (*Le*) *Leptodesma*, (*Na*) "*Nuculana*," (*Nu*) *Nuculoidea*, (*No*) *Nuculites*, (*Pc*) *Paracyclas*, (*Pn*) *Palaeoneilo*, and (*Ps*) *Palaeosolen* (New York State) (after Thayer, 1974a, text-fig. 18G).

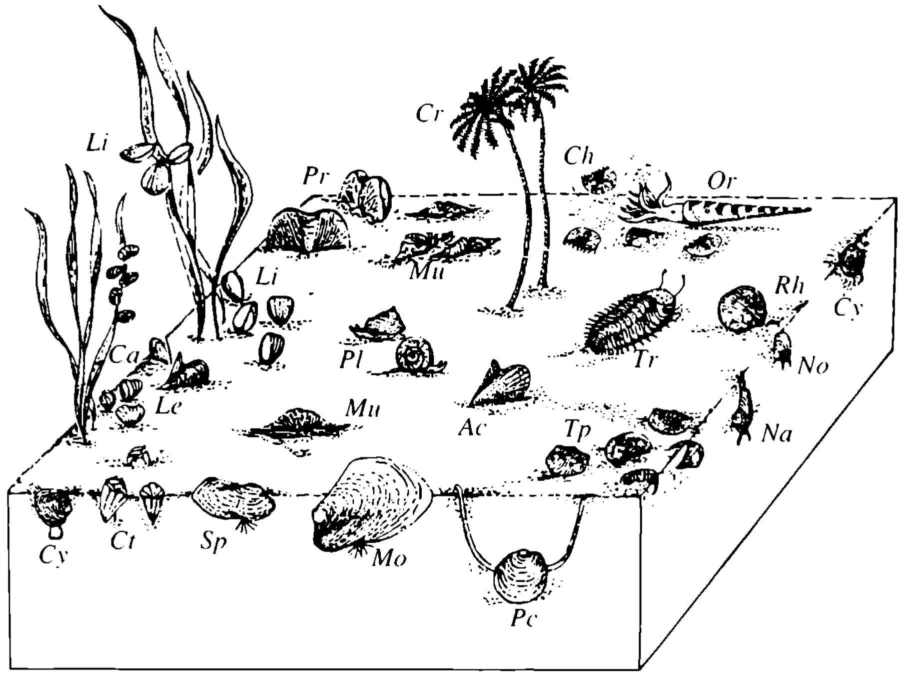


Fig. IX. 16. Reconstruction of the Late Devonian community of the sandy sublittoral zone composed of brachiopods (*Ch, Ct, Li, Mu, Rh*), (*Cr*) crinoids, and the bivalves (*Mo*) *Modiomorpha* and (*Sp*) *Sphenotus*. For other designations, see Fig. IX. 15 (Appalachian Mountains) (after Thayer, 1974a, text-fig. 18F).

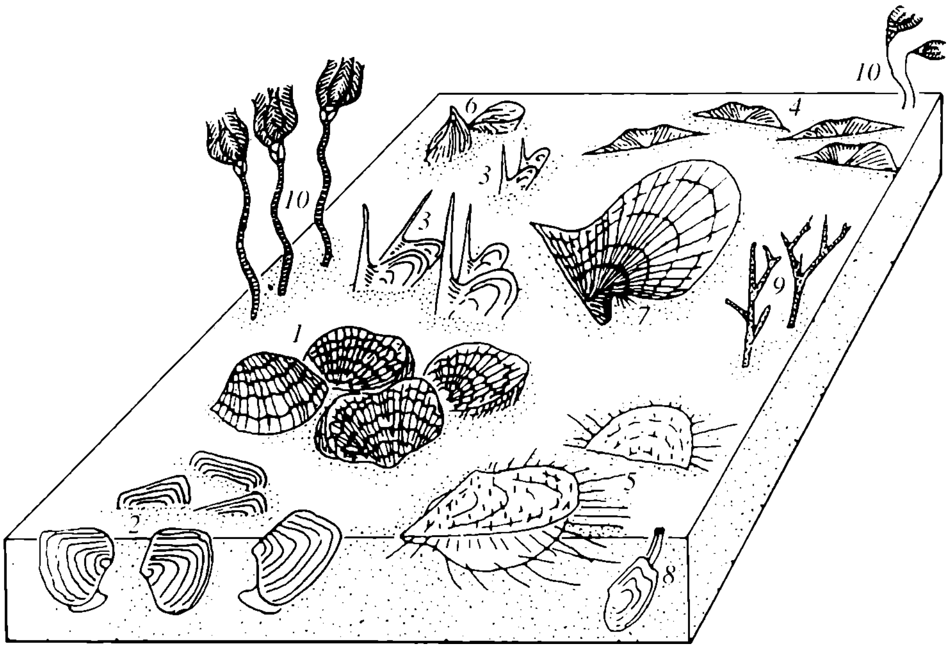


Fig. IX. 17. Reconstruction of the Late Devonian community of muddy substrates of the shallow shelf (prodelta and outer deltoidal platform), composed of (*1*, *4–6*) brachiopods, (*9*) bryozoans, (*10*) pelmatozoans, and (*2*, *3*, *7*, *8*) bivalves: (*2*) *Cypricardella*, (*3*) *Leptodesma*, (*7*) *Ptychopteria*, and (*8*) *Palaeoneilo* (Central Appalachian Mountains) (after McGhee, 1976, text-fig. 9).

loidea, *Palaeoneilo*), epi- and/or endobyssal (*Leptodesma*, *Cypricardinia*, and *Modiomorpha*), and infaunal suspension-feeders (*Sanguinolites* and *Paracyclas*) (Hickey and Younker, 1981; Brett *et al.*, 1983; Vogel *et al.*, 1987; Zhang, 1999).

It is noteworthy that, in the semi-closed basins, bivalves were more widespread in all zones, although brachiopods were still dominant, whereas in the temperate and boreal regions and in the Malvines-Kaffra Superrealm, bivalves were a dominant group along with brachiopods (McAlester and Doumani, 1966; Copper, 1977) (Figs. IX. 18–IX. 20).

Carboniferous

The most diverse families in the Carboniferous seas belonged to the epifaunal byssal, or free-lying suspension-feeders lacking siphons (I.2.1/I.2.4) (Aviculopectinidae and Myalinidae). Some representatives of the Aviculopectinidae could swim (I.2.4a). The Grammysiidae represented by infaunal or semi-infaunal suspension-feeders with or without short siphons, rarely endobyssal (I.1.1/I.1.3/I.3.3/I.3.1) and the Pholadomyidae, infaunal suspension-feeders with siphons (I.1.3/I.1.5) were also diverse. Debris-feeders were far less diverse.

Bivalves were typically present in all zones of the shelf, except shoals with organic buildups, where they also settled but were less abundant than other invertebrate groups. Nevertheless, even in places where bivalves were relatively diverse and numerous, brachiopods, bryozoans, foraminifers, and some other groups were dominant. Only in the most unfavorable environments of the marginal and coastal zones and in environments that were disaerobic or oversaturated with silica, some bivalves became dominant elements. Among these bivalves, pseudoplanktonic and swimming representatives were usually present.

In the marginal zone of the sea, suspension-feeders represented by the epibyssal *Aviculopecten* in association with other representatives of this ethological-trophic group (*Posidonia*, *Dunbarella*, and *Orthomyalina*) and epi- or endobyssal *Leptodesma*, endobyssal *Sanguinolites*, epibyssal or free-lying *Streblopteria* and *Streblochondria* were typically present. The infaunal shallowly burrowing taxa lacking siphons, or with short siphons (*Astartella*, *Schizodus*, and *Edmondia*) were less common. Infaunal debris-feeders lacking siphons (*Nuculopsis*), or with siphons (*Palaeoneilo*) were characteristic, but not abundant (Ivanova, 1958; Williams, 1960; Donahue and Rollins, 1974; Broadhead, 1976; Gibson and Gastaldo, 1987).

In the coastal zone, the taxonomic composition was more diverse. Along with the epibyssal taxa (*Aviculopecten*, *Parallelodon*, *Septomyalina*, *Myalina*, and *Dunbarella*), the endobyssal (*Cypricardinia* and *Pteronites*), byssal or free-lying epifaunal (*Streblochondria*), this zone was inhabited by diverse infaunal and semi-infaunal bivalves lacking siphons (*Schizodus* and *Pro-*

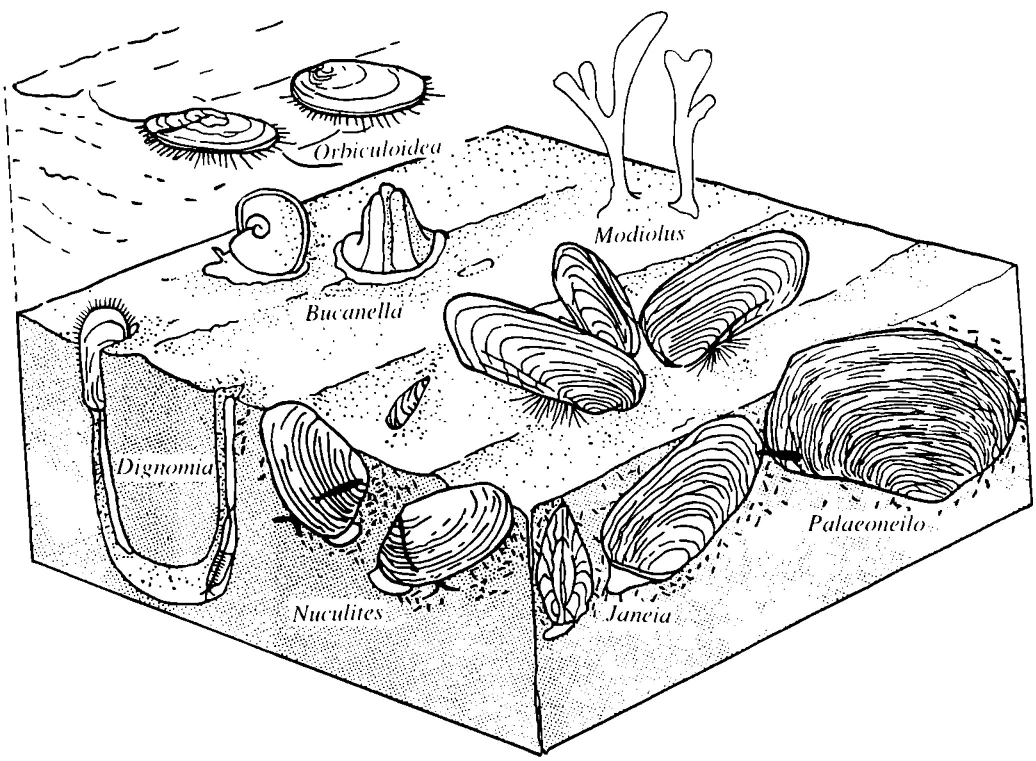


Fig. IX. 18. Reconstruction of the Early Devonian coastal community of the Parana basin in the Malvines-Kaffrarian Biogeographic Subrealm, composed of brachiopods (*Orbiculoidea* and *Dignomia*), the gastropod *Bucanella*, and bivalves: *Modiolus*, *Nuculites*, *Janeia*, and *Palaeoneilo* (Brazil) (after Copper, 1977, text-fig. 4).

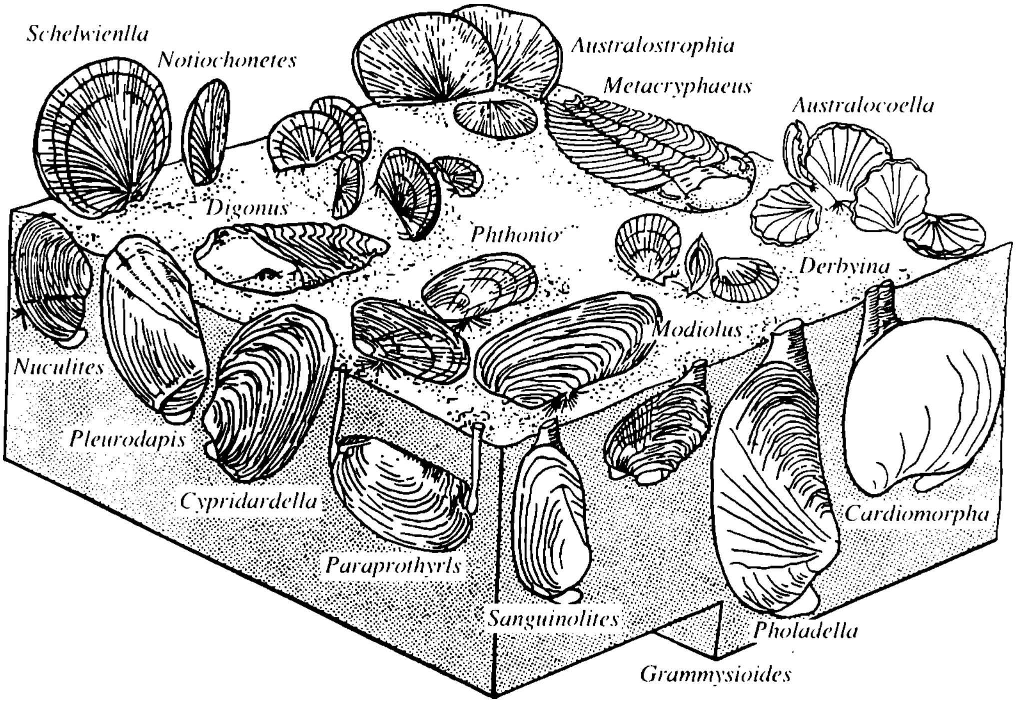


Fig. IX. 19. Reconstruction of the community of the sublittoral zone of the Early Devonian Parana basin, composed of the brachiopods *Australocoelia*, *Australostrophia*, *Derbyina*, *Notichonetes*, and *Schelwienella*; the trilobites *Digonus* and *Metacryphaeus*; and the bivalves *Cardiomorpha*, *Cypricardella*, *Grammysioidea*, *Modiolus*, *Paraprothyris*, *Pholadella*, *Pleurodapis*, *Phthonia*, and *Sanguinolites* (Brazil) (after Copper, 1977, text-fig. 5).

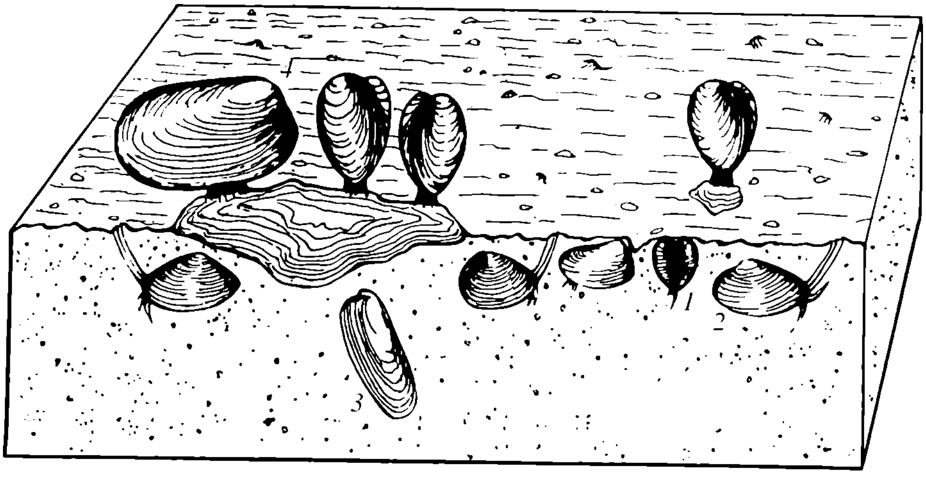


Fig. IX. 20. Reconstruction of the Early Devonian community of bivalves of sandy substrates of the shallow shelf of the Antarctic basin (after McAlester and Doumani, 1966, text-fig. 2): (*1*) *Nuculoidea*, (*2*) *Nuculites*, (*3*) *Ptothyris*, and (*4*) *Modiomorpha*.

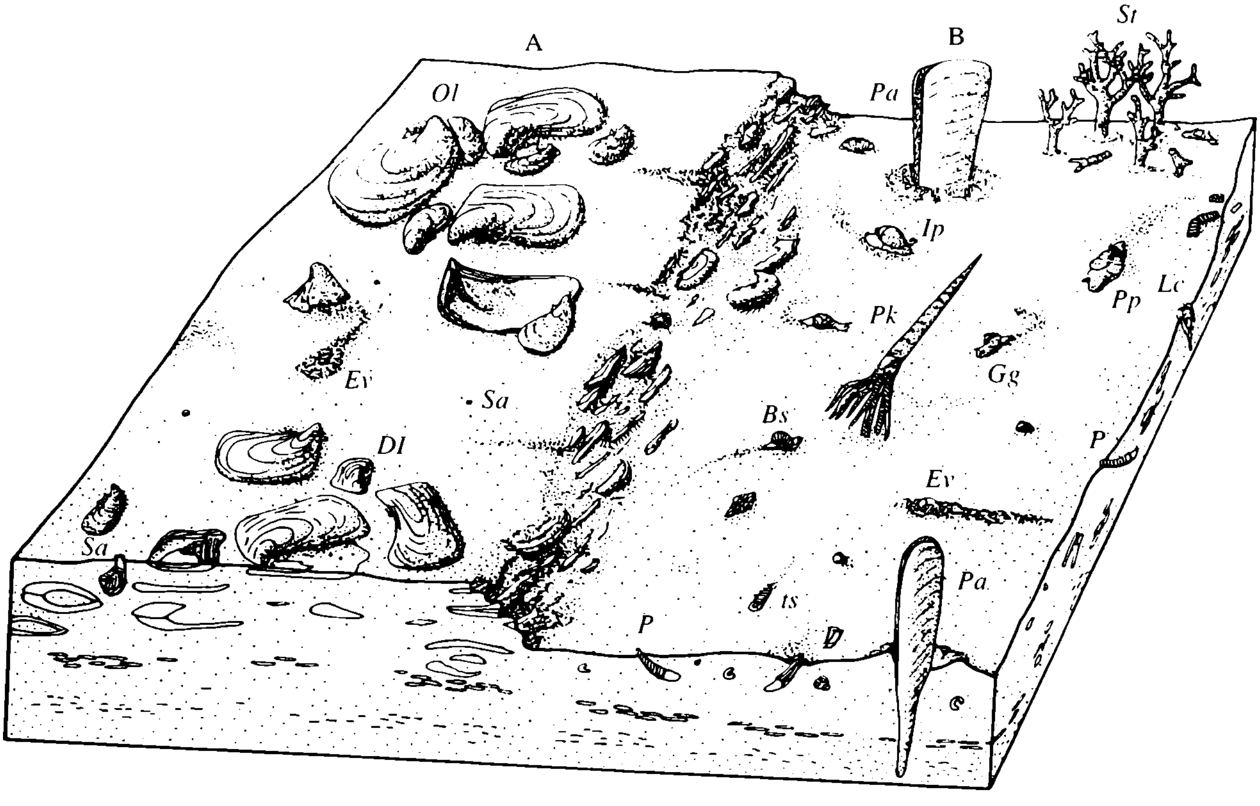


Fig. IX. 21. Reconstruction of the Late Carboniferous communities of the coastal shallow water zone, composed of (*Bs*, *Ev*, *Gg*, *Ip*, *Pp*) gastropods, (*Dl*, *P*) scaphopods, (*Lc*) brachiopods, (*St*) bryozoans, (*ts*) trilobites, (*Pk*) cephalopods, and bivalves: (*Ol*) *Orthomyalina*, (*Pa*) *Pteronites*, and (*Sa*) *Schizodus*. (A) community of muddy substrates stabilized by brachiopod valves; (B) community of clayey mud substrate (eastern North America) (after Rollins *et al.*, 1979, text-fig. 11).

thyris) or with short siphons (*Edmondia*, *Allorisma*, *Paracyclas*, *Astartella*, *Wilkingia*, and *Cardiomorpha*), infaunal debris-feeders without siphons (*Nuculopsis*, *Clinopistha*, and *Janeia*), and siphonate taxa (*Palaeoneilo*, *Paleyoldia*, and *Phestia*) (J. Williams, 1957; R. Johnson, 1962; Donahue and Rollins, 1974; Runne-

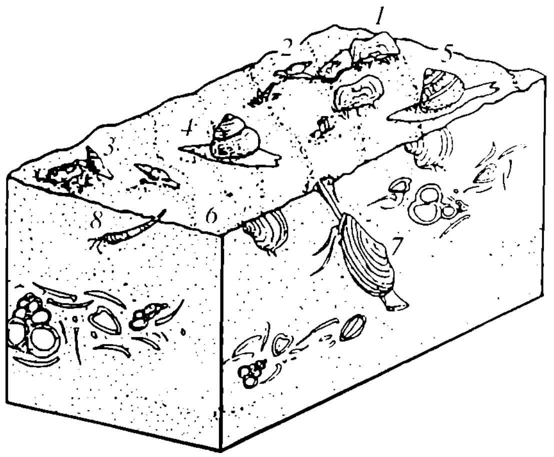


Fig. IX. 22. Reconstruction of the Late Carboniferous communities of muddy substrates of the shallow shelf, composed of (*1*) brachiopods, (*2–5*) gastropods, (*8*) scaphopods, and (*6, 7*) bivalves: (*6*) *Astartella* and (*7*) *Phestia* (North America) (after Rollins and Donahue, 1975, text-fig. 12).

gar and Campbell, 1976; Schram, 1979; Rollins *et al.*, 1979; Beus, 1984; Gibson and Gastaldo, 1987; Petzold *et al.*, 1988).

The taxonomic composition was most diverse in the shallow shelf. The community was dominated by representatives of the same ethological-trophic groups as in the coastal zones. Epibyssal suspension-feeders included *Aviculopecten, Acanthopecten, Sanguinolites, Leptodesma, Myalina, Pteronites, Orthomyalina, Bakevellia, Pinna, Pterinopecten, Limipecten*, and *Parallelodon*. The infaunal, shallowly burrowing suspension-feeders were represented by species of the genera *Edmondia, Prothyris, Promacrus, Pleurophorus, Allorisma, Wilkingia, Schizodus, Astartella, Pyramus, Oriocrassatella*, and *Pentagrammysia*. Infaunal debris-feeders lacking siphons (*Clinopistha, Nuculopsis*, and *Janeia*), and siphonate taxa (*Phestia, Paleyoldia*, and *Palaeoneilo*) were common (Figs. IX. 21, IX. 22).

The zone of shoals was mainly inhabited by byssal suspension-feeders (*Aviculopecten, Pterinopecten, Leiopecten, Parallelodon, Crenipecten, Myalina, Leptodesma, Pteronites, Modiolus, Dunbarella, Posidonia, Sanguinolites*, and *Caneyella*). Infaunal suspension-feeders were less common (*Edmondia* and some *Cardiomorpha*). The boring bivalves *Lithodomus* were typical, whereas infaunal debris-feeders were virtually absent (J. Williams, 1957; R. Johnson, 1962; Calver, 1968; Donahue and Rollins, 1974; Rollins and Donahue, 1975; Runnegar and Campbell, 1976; Ausich *et al.*, 1979; Rollins *et al.*, 1979; Sando, 1980; Huckey and Younker, 1981; Petzold *et al.*, 1988; Quiroz-Barroso and Perrilliat, 1998).

Carbonate mud mounds (so-called Waulsortian Reefs) were inhabited by epi- and endobyssal *Aviculopecten, Pterinopecten, Crenipecten, Leiopteria, Posidoniella, Parallelodon*, and boring bivalves *Lithodomus* (Parkinson, 1957; Cotter, 1965; Gutteridge, 1990).

In the deep shelf zone, the generic diversity of bivalves was much lower. Although genera inhabiting this zone were also typical for the shallow shelf, the composition of the dominant ethological-trophic groups was somewhat different. Infaunal debris-feeders (*Phestia, Nuculopsis, Quadratonucula, Palaeoneilo*, and *Clinopistha*) were dominant, while epibyssal suspension-feeders (*Aviculopecten, Dunbarella*, and *Posidonia*) were typical. Some representatives of the latter group could be pseudoplanktonic (*Posidonia*), whereas infaunal suspension-feeders (*Astartella, Allorizma*, and *Wilkingia*) were less common (Craig, 1954; Ivanova, 1958; Calver, 1968; Ausich *et al.*, 1979; Kammer *et al.*, 1986).

Permian

In the Permian, the families of suspension-feeders either attached by byssus or free-lying (I.2.1/I.2.4) (Aviculopectinidae and Myalinidae) were most diverse. Representatives of some genera of the Aviculopectinidae could swim above the bottom (I.2.4a). The community also included infaunal or semi-infaunal suspension-feeders lacking siphons or having a short siphon and, rarely, the endobyssal suspension-feeders (I.1.1/I.1.3/I.3.3/I.3.1) Grammysiidae and infaunal suspension-feeders with siphons, shallowly or relatively deeply burrowing (I.1.3/I.1.5, i.e., the ethological-trophic and taxonomic composition was the same as in the Carboniferous).

In the Permian seas of the Boreal and Notal realms, bivalves were abundant and widespread in all zones of the sea, while in the Tropical Realm, they occurred only in the marginal and coastal zones and in the zone of organic buildups, whereas in the shelf zone, they were typical, but not numerous. Bivalves were particularly widespread in semiclosed basins with salinity different from that of the sea.

The marginal zone and coastal lagoons of the seas of the Tropical and Boreal biogeographic realms were inhabited by representatives of various ethological-trophic groups (Fig. IX. 23). These were infaunal lacking siphons (*Schizodus*), infaunal or semi-infaunal with short siphons (*Wilkingia* and *Edmondia*), epibyssal (*Liebea* and *Myalina*), epibyssal and capable of swimming (*Aviculopecten*), epi- and/or endobyssal (*Pseudobakewellia* and *Pinna*), epifaunal cemented (*Pseudomontis*), and endobyssal (*Netschaewia, Pleurophorina*, and *Aviculopinna*) suspension-feeders; and debris-feeders lacking siphons (*Janeia* and nuculids) (Hattin, 1957; Suveizdis, 1967; West, 1976; Toomey *et al.*, 1988). Communities of the marginal zones of notal seas are insufficiently studied. These zones were also inhabited by epifaunal byssal taxa (*Atomodesma*) and infaunal taxa with siphons (*Vacunella*), which were suspension-feeders and debris-feeders with byssus

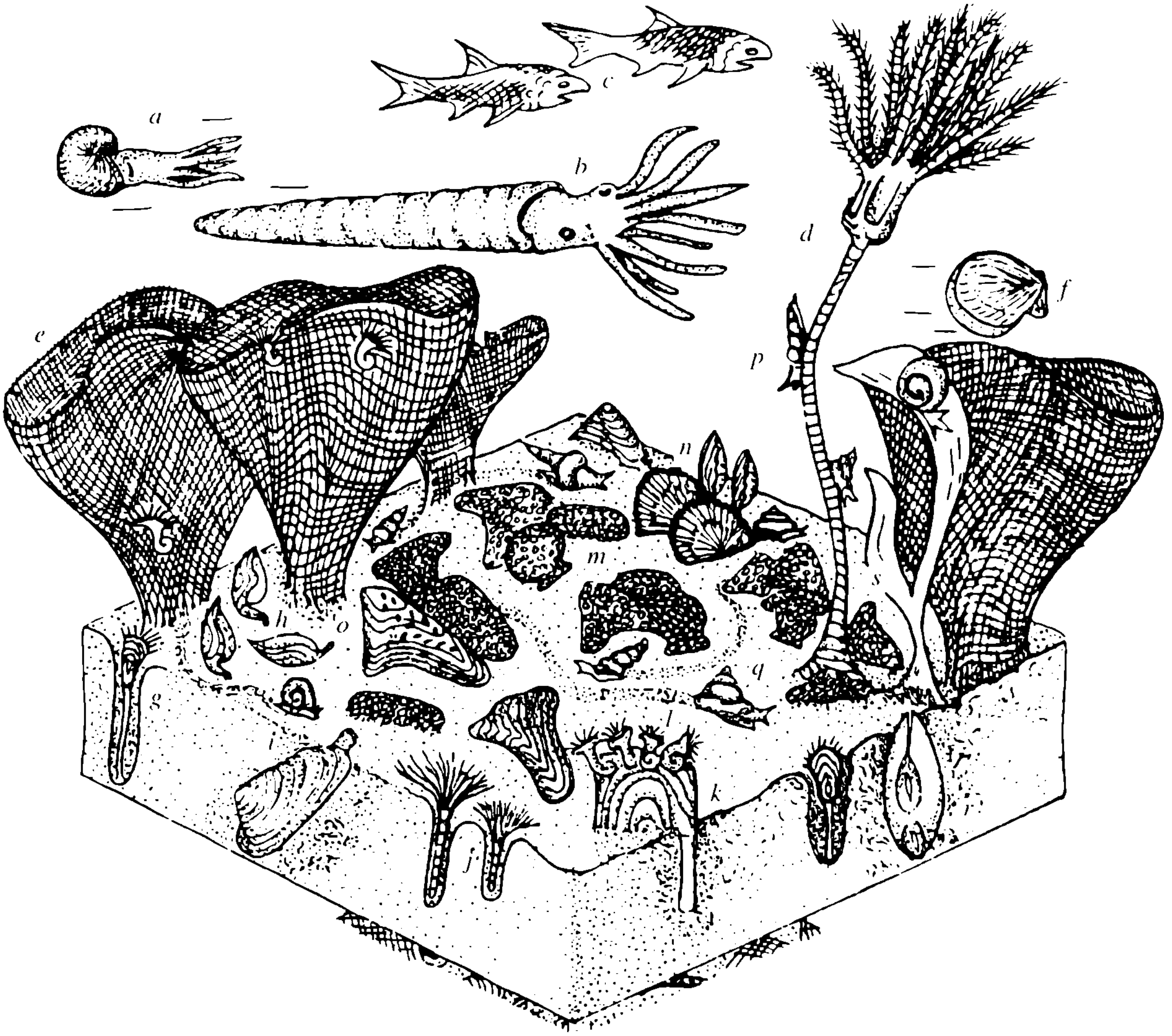


Fig. IX. 23. Reconstruction of the Early Permian community of coastal lagoons, composed of (*e*) bryozoans; (*g, h, n*) brachiopods; (*d*) crinoids; (*j, l*) worms; (*p, q*) gastropods; (*f, i, k, o, r*) bivalves: (*f*) *Aviculopecten*, (*i*) *Wilkingia*, (*k*) *Pinna*, (*o*) *Myalina*, (*r*) *Edmondia*; (*a, b*) nektobenthic cephalopods; and (*c*) fish. Thickets of algae were a characteristic feature (*m*) as well as the presence of aquatic plants (*s*) (Central North America) (Toomey *et al.*, 1988, text-fig. 10).

(*Glyptoleda* and *Paleoyoldia*) and without siphons (*Pseudonucula*) (Dickins, 1963, 1989).

In the coastal zone of the seas of the Boreal and Tropical realms, the systematic and ethologic-trophic composition was similar to that of the marginal zone. Suspension-feeders were represented by epibyssal (*Liebea*, *Bakevellia*, *Septimyalina*, and *Myalina*), epibyssal, capable of swimming over the bottom (*Aviculopecten*), endobyssal (*Aviculopinna*), epi- and endobyssal (*Cyrtodontarca*), epifaunal cemented (*Pseudomonotus*), infaunal and lacking siphons (*Stutchburia* and *Schizodus*), infaunal and/or semi-infaunal with short siphons (*Allorisma* and *Edmondia*), or lacking siphons (*Permophorus*), while debris-feeders were represented by taxa lacking siphons (*Palaeonucula*) or siphonate taxa (*Polidevcia*) (Hattin, 1957; McCrone, 1963; Stevens, 1966; Suveizdis, 1967; West, 1976). In the Notal Realm, this zone was inhabited by suspension-feeders including the epibyssal *Eurydesma*, epibyssal and capable of swimming *Aviculopecten*, free-lying *Deltopecten*, endobyssal *Merismopteria*, infaunal lacking siphons *Schizodus*, with short siphons or without them (*Pyramus* and *Myonia*), epi- or semi-infaunal lacking siphons, or with short siphons *Megadesmus*, and by debris-feeders including the siphonate *Phestia* (Dickins, 1989).

The shallow shelf was dominated by suspension-feeders, including epifaunal byssal; free-lying taxa and taxa capable of swimming, such as *Aviculopecten*; the epibyssal *Liebea*, *Bakevella*, *Palaeolima*, *Acantho-*

pecten, Euchondria, and *Myalina*; the epifaunal byssal and/or free-lying *Streblopteria*; the cemented *Pseudomonotis*; the epi- and/or endobyssal *Leptodesma*; epi- and/or endobyssal *Parallelodon* living in crevices in the rock; endobyssal or semi-infaunal, lacking byssus, or shallowly burrowing *Permophorus*; endobyssal *Pteronites*; the shallowly burrowing and lacking siphons *Schizodus* and *Stuchburia*; the infaunal or semi-infaunal siphonate *Edmondia* and *Wilkingia*; the infaunal *Myonia*, with or without siphons; and the infaunal, shallowly burrowing *Sanguinolites* and *Praeundulonomya*, possessing siphons. Among the bipolar genera, suspension-feeders also dominated. These included the epi- and/or endobyssal *Cigarella, Maitaia,* and *Atomodesma*; the epifaunal byssal, or free-lying *Aphanaia*; the epibyssal *Trabeculatia* and *Girtypecten*; infaunal taxa lacking siphons (*Oriocrassatella*); taxa with siphons (*Vacunella*); and taxa lacking siphons or with one siphon (*Astartella*). Communities of suspension-feeders in the boreal seas included the epibyssal *Intomodesma* and the endobyssal *Kolymia*. In the boreal and tropical seas, suspension-feeders included the epibyssal *Streblochondria* and *Promytilus*, whereas in the notal seas, they included the epibyssal *Eurydesma*, the infaunal *Astartila* lacking siphons and the siphonate *Pyramus*, and the endobyssal *Merismopteria* (Hattin, 1957; Mudge-Yochelson, 1962; Laporte, 1962; McCrone, 1963; Dickins, 1963, 1978, 1989; Suveizdis, 1967; Kerckmann, 1969; Ustritskii, 1970; Klets, 1988; Erwin, 1989; Astafieva, 1991b, 1993; Astafieva and Astafieva-Urbaitis, 1992). Debris-feeders were rare in all zones and were represented by siphonate genera (the cosmopolitan *Phestia*, the bipolar *Paleyoldia*, and the notal *Glyptoleda*).

The zone of organic buildups developed in the tropical seas was mainly inhabited by epifaunal suspension-feeders, including the byssal *Aviculopecten, Acanthopecten, Liebea, Bakevellia, Euchondria, Pteronites,* and *Myalina*; the byssal and/or free-lying *Streblopteria* and *Streblochondria*; the cemented *Pseudomonotis*; and epi- and/or endobyssal taxa that often inhabited cavities and crevices (*Parallelodon*). The infaunal genera *Schizodus* (without byssus), *Sanguinolites* and *Praeundulomya* (with byssus), and taxa that were apparently symbiotic with chemoautotrophic bacteria and algae (*Janeia*) (Kerckman, 1969; Hollingworth and Tucker, 1987) were less common.

Deepwater communities are unknown from the Permian. The deeper water zones of the upper sublittoral zone were inhabited by the epibyssal genus *Septimyalina*, the genus *Aviculopecten* capable of swimming, the endobyssal suspension-feeders *Pteronites*, and nuculoidean debris-feeders.

In semi-closed basins with abnormal salinity, the taxonomic composition of bivalves was impoverished, although they dominated over other benthic organisms. Debris-feeders were absent or rare. In environments of increased salinity, the coastal zone was inhabited by the epibyssal genus *Liebea*, the epi- and/or endobyssal genus *Pseudobakewellia*, and the infaunal genus *Schizodus* (lacking siphons). In addition to these genera, the shallow shelf was inhabited by representatives of the epibyssal *Parallelodon, Bakevellia, Aviculopecten,* and *Palaeolima*; by cemented, or bank-forming bivalves (*Pseudomonotis*); the epifaunal byssal or free-lying genus *Streblopteria*; the epi- and/or endobyssal *Pseudobakewellia*; the endobyssal genus *Netschaewia*; the infaunal genus *Schizodus*; and the infaunal and semi-infaunal *Permophorus* (also lacking siphons). A similar composition of bivalves was characteristic of bryozoan–cyanobacterial and bryozoan–algal buildups (*Pseudomonotis, Parallelodon, Bakevellia, Liebea, Streblopteria, Permophorus, Allorisma,* and *Schizodus*).

Zones with decreased salinity were inhabited by *Pseudomonotis, Pseudobakewellia, Netschaewia, Schizodus,* and *Liebea* (Forsh, 1951, 1980; Hecker, 1959; Slyusareva, 1959).

In the brackish Parana basin of the Caspian type, with the same ethological-trophic composition, each group was usually represented by endemic taxa (Runnegar and Newell, 1971; Runnegar, 1984). All these taxa were suspension-feeders, whereas debris-feeders were completely absent. The epibyssal taxa supposedly included *Coxeia*; the epibyssal and/or free-lying taxa included *Naiadites*, while the epifaunal free-lying taxa (lacking siphons) included *Ferrazia* and *Pinzonella*; free-lying or shallowly burrowing (lacking siphons) taxa included *Plesiocyprinella*; infaunal shallowly burrowing taxa with short siphons included *Casterella, Leinzia,* and *Pyramus*; and the deeply burrowing siphonate genera included *Roxoa*.

Triassic

Bivalve families dominating in the Triassic seas belonged to suspension-feeders, including epifaunal, byssal, free-lying, and/or capable of swimming and epiplanktonic taxa; endobyssal taxa (I.2.1/I.2.4/I.2.4a/I.3.1, Limidae; I.2.1/I.2.1a/I.2.4, Aviculopectinidae; and I.2.1/I.2.1a/I.2.4/I.3.1, Posidoniidae), infaunal taxa lacking siphons and/or semi-infaunal (I.1.1/I.3.1/I.3.4, Trigoniidae), and infaunal bivalves with siphons (I.1.3/I.3.5, Pholadomyidae) were less common.

Beginning with the Triassic, bivalves became a dominant group in all zones of the seas in all biogeographic regions. In the Early Triassic, the taxonomic composition of bivalves was quite restricted. The marginal and coastal zones were mainly inhabited by suspension-feeders, including epibyssal taxa lacking siphons (*Bakevellia, Myalina,* and *Leptochondria*), or, possibly, with one short siphon (*Promytilus*), and nonsiphonate bivalves attached by byssus and/or free-lying (*Streblopteria*). The infaunal suspension-feeders (*Myophoria*), infaunal and/or semi-infaunal suspension-feeders lacking siphons (*Permophorus*), and infaunal

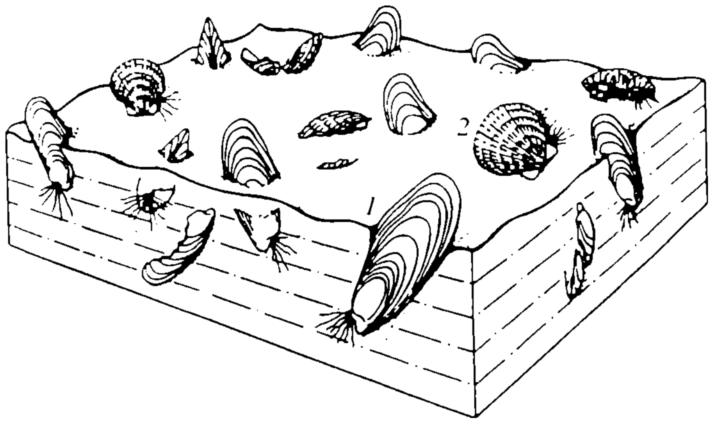


Fig. IX. 24. Reconstruction of the trophic core of the Late Triassic community of sandy-clayey substrates of the coastal zone (Canada) (after Laws, 1982, text-fig. 2): (*1*) *Curionia* and (*2*) Pectinidae.

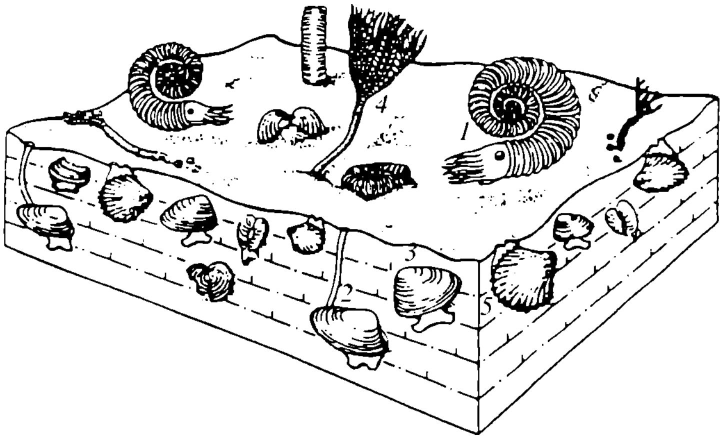


Fig. IX. 25. Reconstruction of the trophic core of the Late Triassic community of calcareous muddy substrate of the shallow water zone: (*1*) cephalopods; (*2, 3, 5*) bivalves: (*2*) Malletiidae, (*3*) *Nuculoma*, and (*5*) *Septocardia*; and (*4*) crinoids (Nevada) (after Laws, 1962, text-fig. 8).

debris-feeders with siphons (*Dacryomya*) were less common (Kummel, 1957; Kurushin, 1983, 1984, 1985, 1990a).

The same genera were present on the shallow shelf. In addition, this zone was inhabited by suspension-feeders, including epibyssal taxa (*Eumorphotis* and *Gervillia*) and/or free-lying *Otapria*, and bivalves capable of attaching by the byssus to floating objects (*Claraia*), epi- and endobyssal, and, sometimes, taxa capable of swimming above the sea bottom (*Plagiostoma* and *Aviculopecten*), cemented bivalves (*Pseudomonotis*), and a less common infaunal siphonate *Cardinia*. Debris-feeders were more diverse in these regions than in the coastal zones and included the siphonate *Malletia*, *Nuculana*, and *Taimyrodon* and nonsiphonate *Palaeonucula*.

The deep shelf was inhabited by infaunal debris-feeders with siphons (*Malletia* and *Taimyrodon*), epibyssal suspension-feeders *Bakevellia*, taxa occasionally capable of tearing byssus and swimming (*Streblopteria*), or capable of attaching to floating objects (*Claraia* and *Posidonia*). Infaunal siphonate bivalves (*Bureiomya*) were less common (Kummel, 1957; Kurushin, 1983, 1984, 1985, 1990a).

The Middle and Late Triassic seas in the marginal and coastal zones were dominated by suspension-feeders (Figs. IX. 24–IX. 26). These included epibyssal taxa lacking siphons (*Oxytoma*, *Bakevellia*, *Gervillia*, and *Myalina*); epifaunal byssal and/or free-lying bivalves (*Chlamys*, *Propeamussium*, and *Entolium*); recliners, i.e., free-lying with their beaks down (*Megalodon*); or lying on one valve (*Cassianella*); epibyssal, sometimes, pseudoplanktonic bivalves (*Monotis*); cemented bivalves (*Lopha*, *Newaagia*, *Enantiostreon*, and *Plicatula*); and/or free-lying bivalves (*Gryphaea*); epi- or endobyssal bivalves, possibly, with one short siphon (*Falcimytilus*); endobyssal Permophoridae (*Curionia* and others); infaunal bivalves lacking siphons (*Myo-*

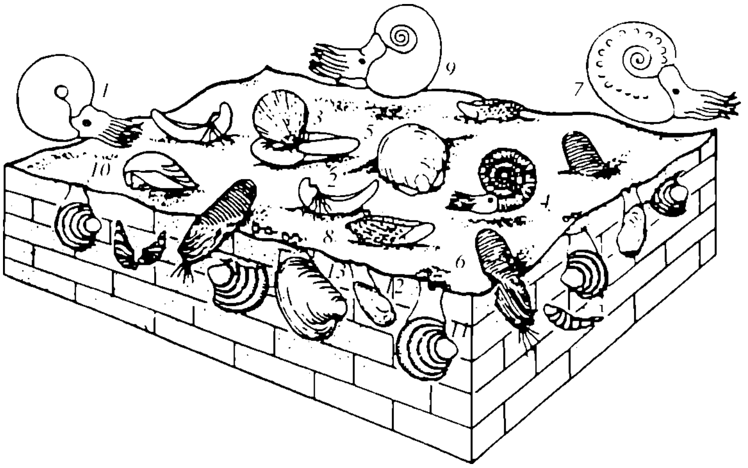


Fig. IX. 26. Reconstruction of the trophic core of the Late Triassic community of the coastal shallow water zone (Canada) (after Laws, 1982, text-fig. 7): (*1, 4, 7, 9*) cephalopods; (*2, 3, 5, 6, 8, 11–13*) bivalves: (*2*) *Cassianella*, (*3*) *Chlamys*, (*5*) Pectinidae, (*6*) Permophoridae, (*8*) *Plicatula*, (*11*) *Tutcheria*, and (*12, 13*) *Unionites*; and (*10*) brachiopods.

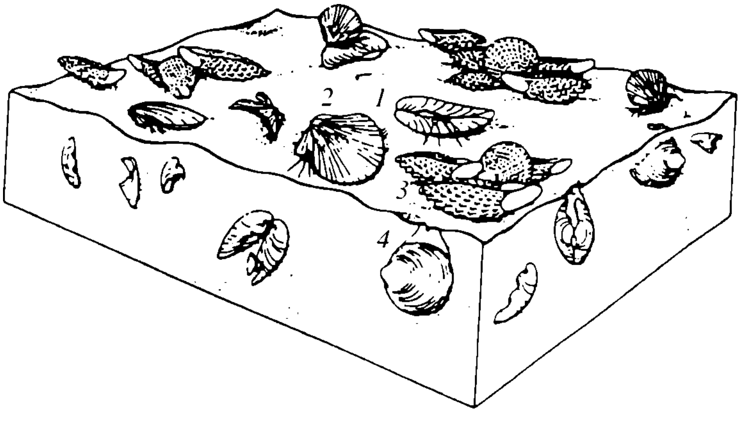


Fig. IX. 27. Reconstruction of the trophic core of the Late Triassic community of compact calcareous substrates of the shallow water zone (Nevada) (after Laws, 1982, text-fig. 6): (*1–4*) bivalves: (*1*) *Arcavicula*, (*2*) *Chlamys*, (*3*) *Plicatula*, and (*4*) *Schaufhaeutlia*.

phoria, *Tutcheria*, and ?Corbulidae); and those with one siphon (*Astarte*), or with two siphons (*Cardium*, *Unionites*, and *Septocardia*). Infaunal debris-feeders with siphons (*Nuculana*, Malletiidae) and without siphons (*Nuculoma*) were less common.

Bivalve communities of the shallow shelf were considerably more taxonomically diverse. Epibyssal suspension-feeders were represented by species of the genera *Bakevellia* (dominant), *Leptochondria*, *Eopecten*, *Posidonia*, *Myalina*, *Meleagrinella*, *Rhaetavicula*, *Monotis*, *Pteria*, *Camptonectes*, *Arcavicula*, *Oxytoma*, *Falcimytilus*, *Mytilus*, *Gervillia*, and *Mysidioptera*. The epifaunal byssal and/or free-lying bivalves included *Chlamys* (dominant), *Daonella*, *Halobia*, *Entolium*, *Hoernesia*, and *Lima*. The free-lying bivalves lacking byssus included *Megalodon*, *Ctenostreon*, *Cassianella*, and *Tosapecten*; the epibyssal or endobyssal taxa included *Parallelodon* and *Palaeocardita* (the latter could be without byssus and could lie free on the substrate, or slightly sink into it); and the endobyssal taxa included *Modiolus*. Cemented bivalves were very diverse (*Plicatula*, *Placunopsis*, *Atreta*, *Lopha*, and *Gryphaea*). There were many infaunal suspension-feeders, including those without siphons [*Myophoria* (dominant), *Pseudocorbula*, and *Tutcheria*] and with siphons [*Pholadomya*, *Panopea*, *Cardinia*, *Unionites*, *Pleuromya*, *Bureiamya*, and *Astarte* (with one siphon)]. Infaunal shallowly burrowing and/or semi-infaunal suspension-feeders with short siphons included *Protocardia*, *Septocardia*, and *Myophoricardium*, while those without siphons included *Neoschizodus*. Endobyssal suspension-feeders without siphons were represented by the genus *Modiolus*. Infaunal debris-feeders without siphons (*Janeia*, *Nuculana*, and *Palaeonucula*) and siphonate debris-feeders (*Dacryomya*, *Nuculana*, *Prosoleptus*, *Palaeoneilo*,

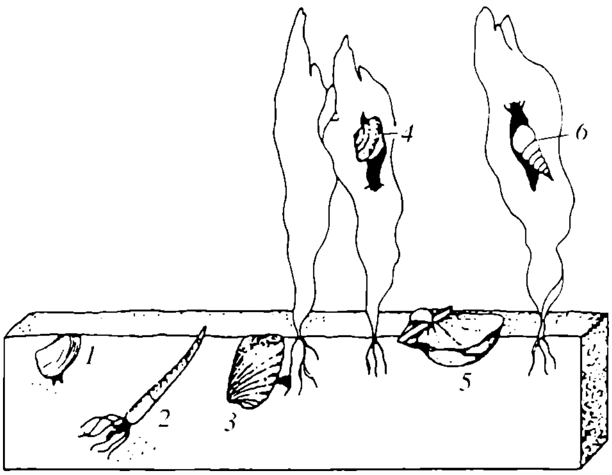


Fig. IX. 28. Reconstruction of the trophic core of the Late Triassic community of clayey-carbonate muddy substrates of the sublittoral zone (Alps) (after Fürsich and Wendt, 1977, text-fig. 12): (*1*, *3*, *5*) bivalves: (*1*) *Palaeonucula*, (*3*) *Palaeocardita*, (*5*) *Cassianella*; (*2*) scaphopods; and (*4*, *6*) gastropods.

Malletia, and *Taimyrodon*) were characteristic of this zone (Kummel, 1957; Fürsich and Wendt, 1977; Michalik and Jendreijaková, 1978; Laws, 1982; Michalik, 1982; Kurushin, 1984, 1990a, 1991, 1992; Dagis and Kurushin, 1985; Newton, 1986, 1987; Newton *et al.*, 1987; Kurushin and Kazakov, 1989; Aberhan, 1994) (Figs. IX. 27, IX. 28).

Diverse bivalves inhabited the zone of organic buildup, including reefs. Cemented taxa (*Lopha, Atreta, Pseudomonotis, Newaagia, Enantiostreon, Placunopsis, Plicatula, Terquemia, Dimyodon, Liostrea*, and *Gryphaea*), endobyssal taxa (*Modiolus*), epibyssal bivalves (*Monotis, Pteria, Rhaetavicula, Bakevelllia, Eopecten, Pleuronectites, Mytilus, Myalina, Mysidioptera, Antiquilima*, and *Gervillia*) (Fig. IX. 29), epi- and/or endobyssal taxa (*Parallelodon* and *Grammatodon*), and epifaunal byssal and/or free-lying bivalves (*Chlamys, Halobia, Dicerocardium, Propeamussium, Neomegalodon, Megalodon, Indopecten, Daonella, Hoernesia, Entolium, Plagiostoma, Lima*, and *Cassianella*) were numerous. Some of these bivalves could swim above the substrate (*Chlamys, Entolium*, and *Lima*). The infaunal suspension-feeders without siphons (*Myophoria*), with short siphons or lacking siphons (*Schaufhaeutlia* and *Astarte*), with well-developed siphons (*Homomya, Isocyprina*, and *Pleuromya*), and infaunal and/or semi-infaunal suspension-feeders without siphons (*Minetrigonia, Trigonodus*, and *Pachycardia*) were less common. Debris-feeders (*Nuculana*) were rare (Bosselini and Rossi, 1974; Fürsich and Wendt, 1977; Aigner *et. al.*, 1978; Hagdorn, 1982; Stanley, 1982; Dronov *et al.*, 1982; Flügel *et al.*, 1984; Dronov and Mel'nikova, 1986; Newton *et al.*, 1987; Pfeiffer, 1988; Gaetani and Gorza, 1989).

In the deep shelf, the taxonomic composition of bivalves was impoverished. Infaunal debris-feeders with siphons (*Malletia, Prosoleptus, Taimyrodon, Dacryomia*, and *Palaeoneilo*) and without siphons (*Palaeonucula* and *Sarepta*) were a dominant group (Fig. IX. 30). Epibyssal bivalves, which often became pseudoplanktonic (*Posidonia, Halobia, Daonella*, and *Monotis*) were typical. This zone was also inhabited by the epibyssal taxa *Bakevellia, Leptochodria, Meleagrinella*, and *Gervillia*; the epifaunal byssal or free-lying *Hoernesia* and *Streblopteria*; endobyssal *Modiolus*; and rare infaunal bivalves lacking siphons (*Pseudocorbula* and *Cardinia*) (Fürsich and Wendt, 1977; Kurushin, 1984, 1990a, 1992; Dagis and Kurushin, 1985; Kurushin and Kazakov, 1989; Aberhan, 1994).

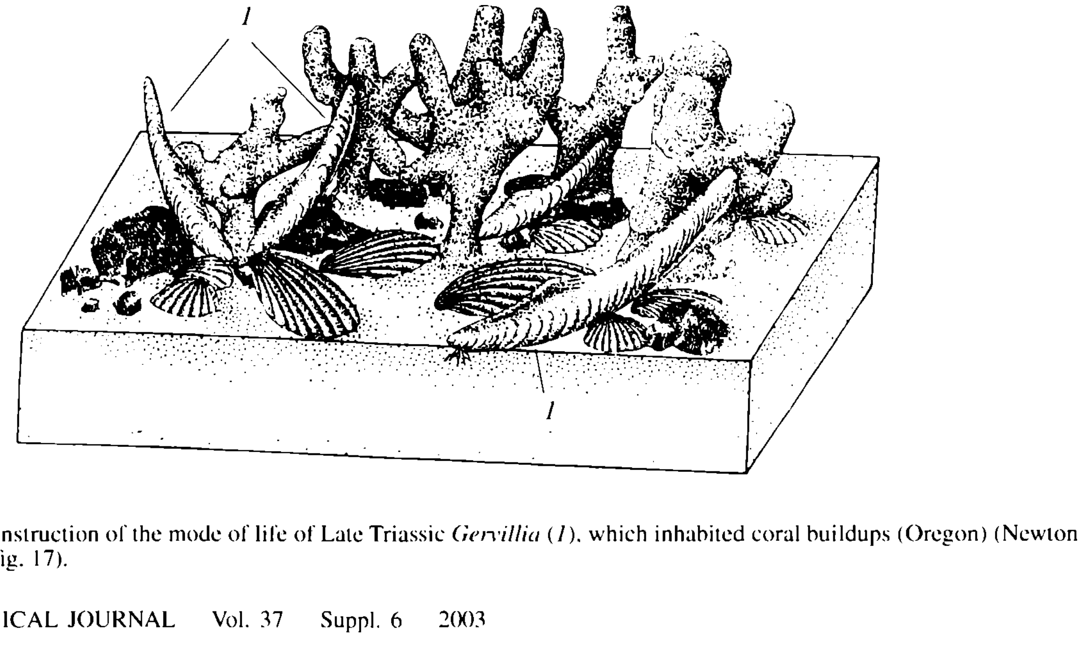


Fig. IX. 29. Reconstruction of the mode of life of Late Triassic *Gervillia* (*1*), which inhabited coral buildups (Oregon) (Newton *et al.*, 1987, text-fig. 17).

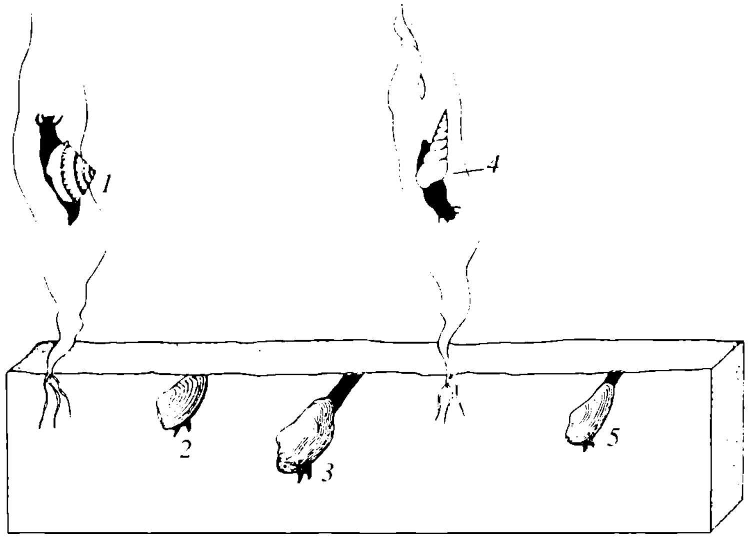


Fig. IX. 30. Reconstruction of the trophic core of the Late Triassic community of clayey substrates of the lower sublittoral (Alps) (after Fürsich and Wendt, 1977, text-fig. 11): (*2, 3, 5*) bivalves: (*2*) *Palaeonucula*, (*3*) *Prosoleptus*, and (*5*) *Palaeoneilo*; and (*1, 4*) gastropods.

Jurassic

Bivalves dominating in the Jurassic seas mainly belonged to suspension-feeders, including infaunal shallowly burrowing and/or epifaunal, taxa lacking siphons (Trigoniidae), or those with one siphon (Astartidae and Crassatellidae), or those with two short siphons (Arcticidae), epi- and/or endobyssal taxa (Mytilidae), epibyssal and/or free-lying taxa occasionally capable of swimming (Limidae, Posidonyidae, and Pectinidae), epifaunal cemented and/or free-lying taxa (Diceratidae), epi- and/or endobyssal or free-lying taxa (Bakevellidae and Inoceramidae), infaunal deeply burrowing bivalves with two siphons (Pholadomyidae), or with one exhalant siphon and an inhalant mucous tubule (Lucinidae). Bivalves dominated in the communities in all zones of seas in different biogeographic regions.

In the Arctic Subrealm and Boreal Biogeographic Realm, the taxonomic composition of communities was considerably less diverse than in other regions. The marginal zone of the Early Jurassic seas was inhabited by suspension-feeders, including shallowly burrowing siphonate taxa (*Tancredia, Cardinia, Astarte, Pronoella, Protocardia*, and *Hiatella*); more deeply burrowing and feeding through the mucous tubule taxa (lucinids); and epibyssal and/or free-lying (*Kolymonectes, Chlamys*, and *Buchia*) and cemented (oysters) taxa; and infaunal debris-feeders with siphons (*Malletia* and *Glyptoleda*).

In the coastal zone, the taxonomic and ethologic-trophic composition was more diverse. Suspension-feeders were represented by infaunal siphonate shallowly burrowing (*Tancredia, Astarte, Arctica, Pronoella*, and *Protocardia*) and deeply burrowing taxa (*Homomya, Pleuromya, Gresslya, Bureiomya*, and *Goniomya*), burrowing taxa lacking siphons (*Myophoria*), epibyssal taxa (*Meleagrinella, Eopecten, Radulonectites, Arctotis, Isognomon, Oxytoma, Arca*, and *Aguilleria*), epibyssal and/or free-lying (*Harpax, Mytiloceramus, Camptonectes, Boreionectes, Buchia, Entolium*, and *Plagiostoma*), endobyssal (*Pinna*), epi- and endobyssal (*Musculus*), cemented (*Ostrea*), and/or free-lying (*Liostrea*) taxa. Debris-feeders with siphons (*Dacryomya*) and without siphons (*Nuculoma*) were rare. *Tancredia, Homomya, Meleagrinella, Arctica*, and *Arototis* dominated (Figs. IX. 31a, IX. 32a).

The shallow shelf was also dominated by suspension-feeders, including infaunal, relatively deeply burrowing, taxa with siphons (*Homomya, Pleuromya, Goniomya, Bureiomya, Gresslya*, and *Thracia*); shallowly burrowing, or semi-infaunal, siphonate taxa (*Tancredia, Arctica, Pronoella, Astarte*, and *Protocardia*); epibyssal taxa (*Meleagrinella, Arctotis, Boreionectes, Isognomon*, and *Mytiloceramus*); epibyssal, or free-lying (*Entolium, Buchia, Camptonectes, Plagiostoma*, and *Oxytoma*), cemented (*Praeexogyra*), and epi- or endobyssal taxa (*Musculus*). Debris-feeders were scarce, and were represented by the genera *Nuculoma, Palaeonucula, Taimyrodon, Mesosaccella* (Figs. IX. 31b, IX. 32b^{I}, IX. 32b^{II}).

The deep shelf was dominated by infaunal siphonate bivalves (*Pleuromya, Homomya, Astarte, Tancredia, Pronoella*, and *Protocardia*), and by those possessing a mucous inhalant tubule and exhalant siphon (lucinids), epibyssal (*Boreionectes, Meleagrinella, Oxytoma*, and *Isognomon*), epifaunal byssal or free-lying (*Mytiloceramus*), and endobyssal taxa (*Modiolus*). There were many debris-feeders, especially those with siphons

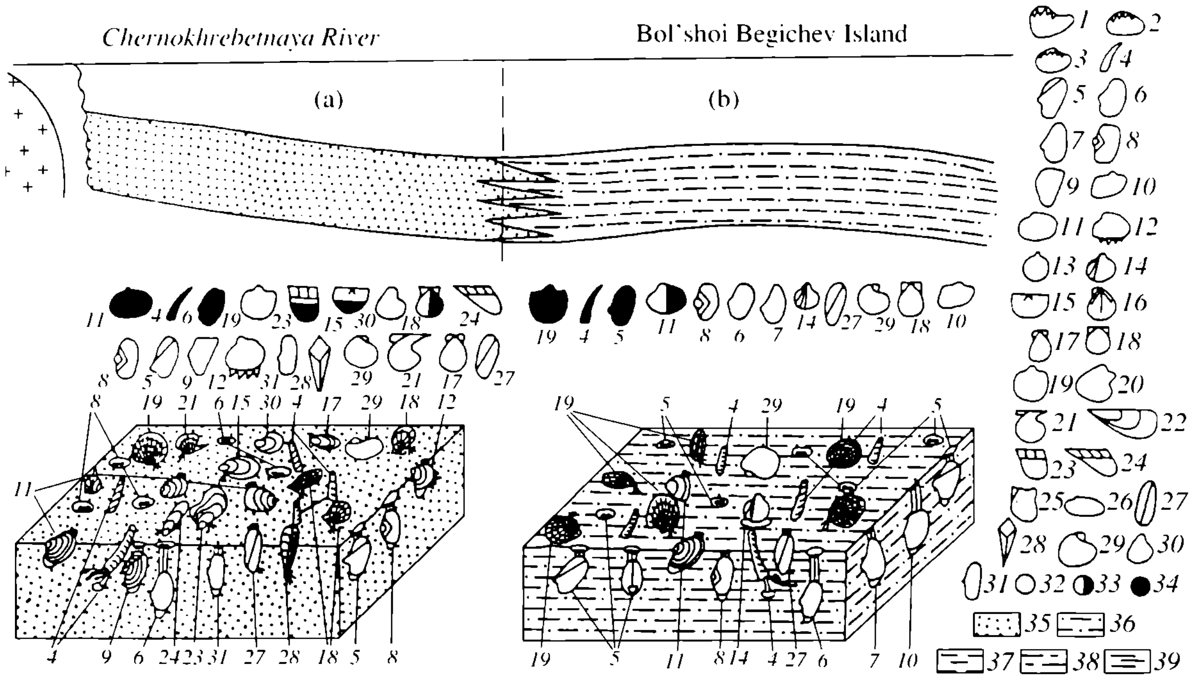


Fig. IX. 31. Distribution and composition of communities of the coastal zone and shallow water zone of the North Siberian Sea in the Callovian (after Zakharov and Shurygin, 1978, text-fig. 16d): (a) coastal zone and (b) shallow shelf: (*1*) *Dacryomya*, (*2*) *Malletia*, (*3*) *Nuculana*, (*4*) scaphopods, (*5*) *Homomya*, (*6*) *Pleuromya*, (*7*) *Gresslya*, (*8*) *Goniomya*, (*9*) *Tancredia*, (*10*) *Thracia*, (*11*) *Arctica*, (*12*) *Astarte*, (*13*) Lucinidae, (*14*) *Protocardia*, (*15*) *Boreionectes*, (*16*) *Parvamussium*, (*17*) *Entolium*, (*18*) *Camptonectes*, (*19*) *Meleagrinella*, (*20*) *Arctotis*, (*21*) *Oxytoma*, (*22*) *Mytiloceramus*, (*23*) *Isognomon*, (*24*) *Aguilerella*, (*25*) *Pseudomytiloides*, (*26*) *Modiolus*, (*27*) *Musculus*, (*28*) *Pinna*, (*29*) *Plagiostoma*, (*30*) *Liostrea*, and (*31*) "*Solecurtus*"; (*32*) rare, (*33*) frequent and abundant, (*34*) and extremely abundant; (*35*) sand, (*36*) muddy sand, (*37*) muddy substrates, (*38*) clayey mud, and (*39*) clay.

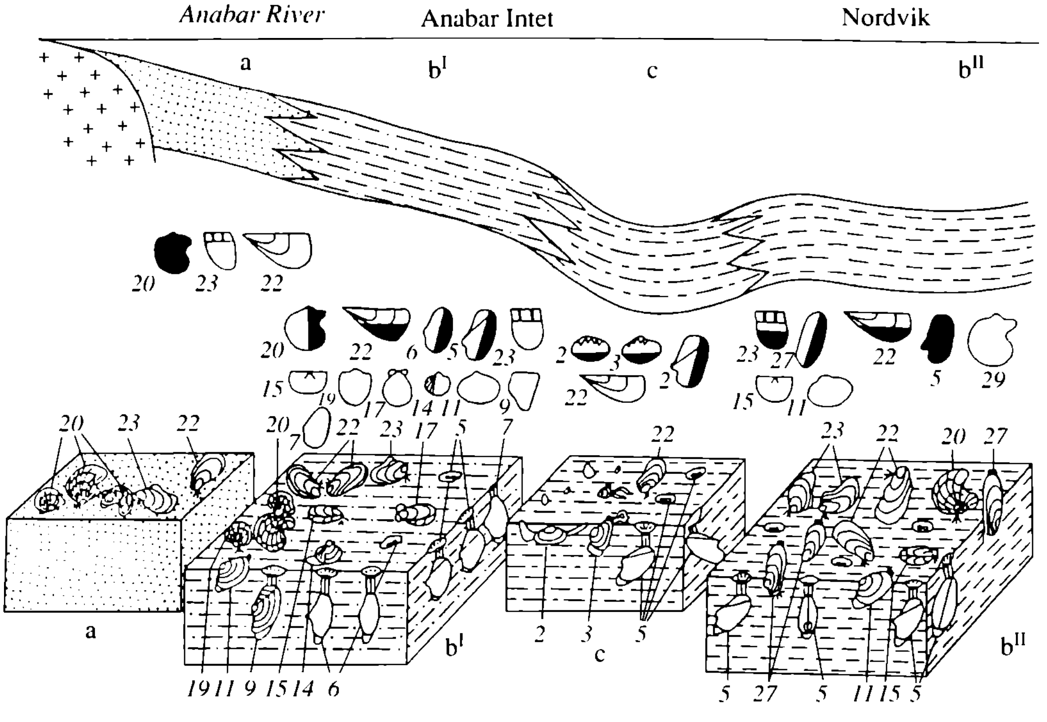


Fig. IX. 32. Distribution and composition of communities in (a) the coastal zone and (b^I), b^{II}) shallow and (c) deep shelf of the North Siberian Sea in the Bathonian (after Zakharov and Surygin, 1978, text-fig. 16c): For designations, see Fig. IX. 31.

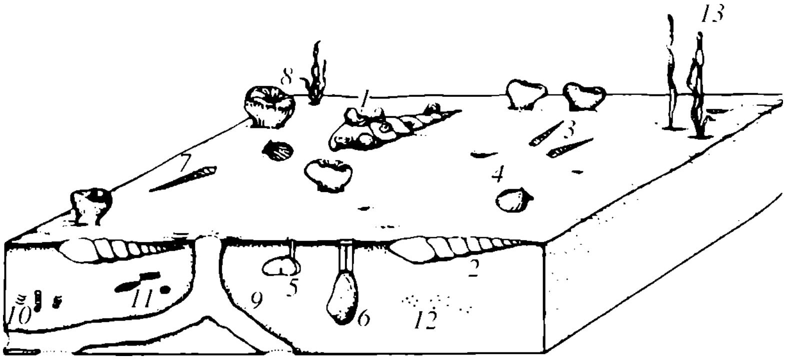


Fig. IX. 33. Reconstruction of the Late Jurassic lagoonal community of Anglo-Norman Sea (after Fürsich, 1977, text-fig. 22): (*1*) *Nanogyra*; (*2*, *3*, *7*) gastropods; (*4*) *Chlamys*; (*5*) sea urchin; (*6*) *Pleuromya*; (*8*) sponges; (*9*–*12*) traces; and (*13*) algae.

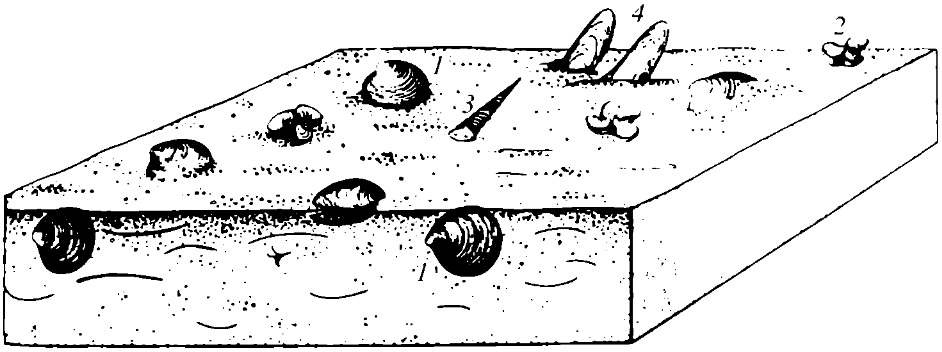


Fig. IX. 34. Reconstruction of the Late Jurassic community of the coastal zone of the Anglo-Norman Sea (after Fürsich, 1977, text-fig. 9): (*1*) *Neocrassina*, (*2*) *Nanogyra*, (*3*) gastropods, and (*4*) *Gervillella*.

(*Malletia*, *Nuculana*, *Dacryomya*, and *Taimyrodon*), while those without siphons occurred in lesser numbers (*Nuculoma* and *Palaeonucula*). The community contained epifaunal suspension-feeders capable of swimming above the substrate (*Aequipecten*, *Entolium*, etc.) (Fig. IX. 32c) (Zakharov and Mesezhnikov, 1974; Zakharov and Shurygin, 1978, 1979, 1985; Shurygin, 1979; Zakharov, 1981a, 1995; Yazikova, 1993, 1996a, 1996b, 1998).

In the Atlantic and Pacific subrealms of the Boreal Realm the taxonomic composition of bivalves was more diverse, while some ethological-trophic groups were dominated by representatives of other genera, different from those in the Arctic Subrealm. The marginal zone was dominated by infaunal shallowly burrowing suspension-feeders with siphons (*Anisocardia*, *Corbula*, *Tancredia*, *Isocyprina*, and *Astarte*). Infaunal deeply burrowing and siphonate suspension-feeders (*Pleuromya*) and shallowly burrowing suspension-feeders lacking siphons (*Neomiodon*, *Eomiodon*, and *Myrene*) were more poorly represented. Suspension-feeders, including the semi-infaunal endobyssal *Modiolus*; the epibyssal *Lima*, *Mytilus*, *Bakevellia*; epifaunal cemented *Placunopsis*, *Nanogyra*, *Ostrea*, *Lopha*; and free-lying, or epibyssal *Chlamys* played a large role in the communities. Communities included debris-feeders *Nucula* (Fig. IX. 33). Lagoons often contained oyster banks built by *Praeexogyra*.

In the coastal zone, the ethological-trophic composition was similar to that of the marginal zone, whereas the taxonomic composition was somewhat more diverse. It was dominated by suspension-feeders, including infaunal siphonate, relatively deeply burrowing taxa (*Pleuromya*, *Gresslya*, *Pholadomya*, and *Myopholas*); shallowly burrowing siphonate taxa (*Astarte*, *Cardinia*, *Anisocardia*, *Isocyprina*, *Corbulomima*, *Tancredia*, etc.); and those lacking siphons (*Neocrassina*), those with a mucous inhalant tubule (*Mesomiltha* and *Discomiltha*), endobyssal semi-infaunal taxa (*Pinna* and *Modiolus*); epibyssal taxa (*Oxytoma*, *Isognomon*, *Meleagrinella*, and *Gervillia*); epibyssal and/or free-lying (*Camptonectes*, *Plagiostoma*, *Entolium*, *Pseudolimea*, *Chlamys*, and *Limatula*), epi- and/or endobyssal taxa (*Gervillella*), cemented bivalves (*Nanogyra*, *Ostrea*, and *Plicatula*), cemented and/or free lying bivalves (*Gryphaea*) (Figs. IX. 34, IX. 35).

Bivalve communities of the shallow shelf were very diverse. This zone was dominated by suspension-feeders. The infaunal siphonate, relatively deeply burrowing taxa were mostly represented by the species of the

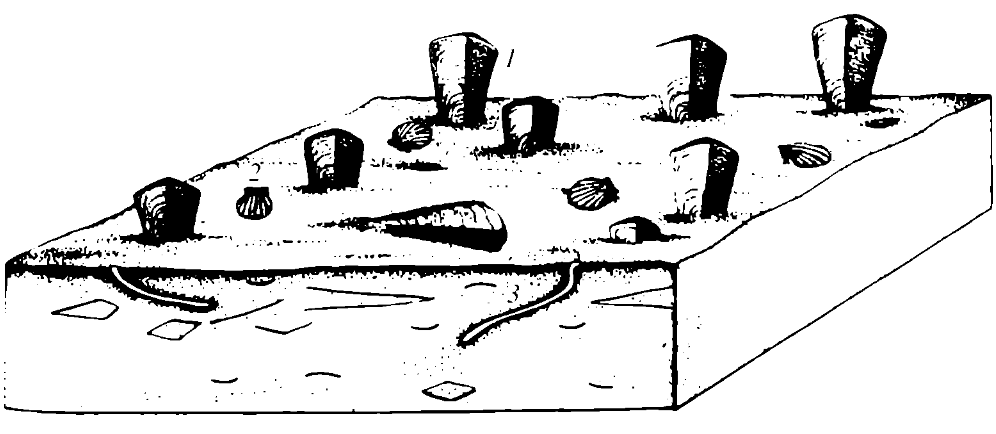


Fig. IX. 35. Reconstruction of the Late Jurassic community of the coastal zone of the Anglo-Norman Sea (after Fürsich, 1977, text-fig. 7): (*1*) *Pinna*, (*2*) *Chlamys*, and (*3*) traces.

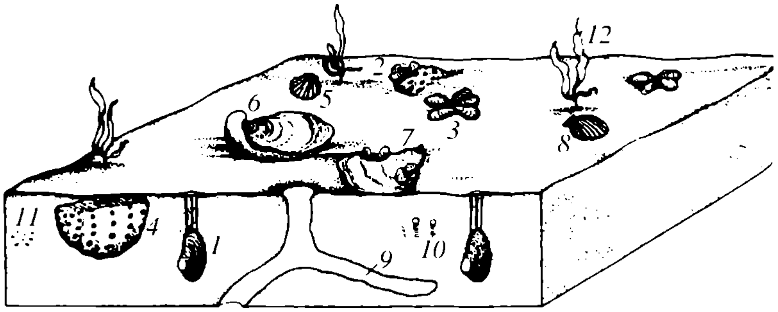


Fig. IX. 36. Reconstruction of the Late Jurassic community of the shallow water shelf of the Anglo-Norman Sea (after Fürsich, 1977, text-fig. 20): (*1*) *Pleuromya*, (*2*) juvenile *Gryphaea*, (*3*) "*Chlamys*," (*4*) *Myophorella*, (*5, 8*) *Chlamys*, (*6*) *Gryphaea*, (*7*) *Deltoideum*, (*9–11*) traces, and (*12*) algae.

genera *Pholadomya*, *Pleuromya*, *Goniomya*, *Thracia*, and *Gresslya*. Shallowly burrowing siphonate taxa were mostly represented by *Astarte*, *Anisocardia*, *Cardinia*, *Sowerbya*, *Corbula*, *Corbulomima*, *Isocyprina*, *Protocardia*, *Tancredia*, and *Corbicellopsis*. Infaunal bivalves lacking siphons were mostly represented by *Myophorella*, *Laevitrigonia*, *Trigonia*, *Vaugonia*, *Neocrassina*, *Nicaniella*, and *Trautscholdia*. Infaunal taxa with a mucous inhalant tubule included *Discomiltha*, *Mesomiltha*, and *Luciniola*. Semi-infaunal endobyssal taxa contained *Pinna* and *Modiolus*, while infaunal and/or semi-infaunal siphonate bivalves included *Protocardia* and *Arctica*. Epifaunal bivalves were very diverse, including epibyssal taxa (*Oxytoma*, *Pteroperna*, *Meleagrinella*, *Mytiloceramus*, *Lima*, *Bakevellia*, *Parallelodon*, *Gervillia*, *Arca*, *Mytilus*, and *Aguilerella*), epi- and/or endobyssal taxa (*Grammatodon*, *Isognomon*, *Musculus*, *Gervillella*, and *Cucullaea*), epibyssal and/or free-lying (*Chlamys*, *Pseudolimea*, *Entolium*, *Camptonectes*, *Buchia*, *Mytiloceramus*, and *Plagiostoma*), cemented taxa (*Liostrea*, *Atreta*, *Plicatula*, *Praeexogyra*, *Lopha*, *Nanogyra*, *Deltoideum*, *Ostrea*, *Exogyra*, *Placunopsis*, and *Anomia*), cemented and/or free-lying taxa (*Gryphaea* and *Ctenostreon*). The community contained many infaunal debris-feeders, including those with siphons (*Nuculana*, *Paleoneilo*, *Mesosaccella*, and *Ryderia*) and lacking siphons (*Palaeonucula* and *Nuculoma*) (Figs. IX. 36–IX. 43).

Shoals with organic buildups were typically inhabited by epifaunal suspension-feeders, including cemented taxa (*Praeexogyra*, *Lopha*, *Liostrea*, *Atreta*, *Spondylus*, *Nanogyra*, *Exogyra*, and *Plicatula*), epibyssal (*Isognomon*, *Barbatia*, and *Arca*), epi- and/or endobyssal *Trichites*, and boring bivalves *Lithophaga*. Muddy substrates between the coral colonies were inhabited by infaunal *Pholadomya*.

A similar taxonomic and ethological-trophic composition was characteristic of the communities inhabiting hardgrounds. These communities were dominated by cemented *Liostrea*, *Exogyra*, *Lopha*, *Plicatula*, *Atreta*, *Spondylus*, and *Nanogyra*; boring bivalves *Lithophaga*; and a few epibyssal and free-lying taxa (*Oxytoma*, *Chlamys*, *Plagiostoma*, and *Parallelodon*).

The deep shelf communities were not diverse. They were dominated by debris-feeders, including those with siphons (*Nuculana*, *Mesosaccella*, *Palaeoneilo*, and *Ryderia*) and without siphons (*Palaeonucula*). This

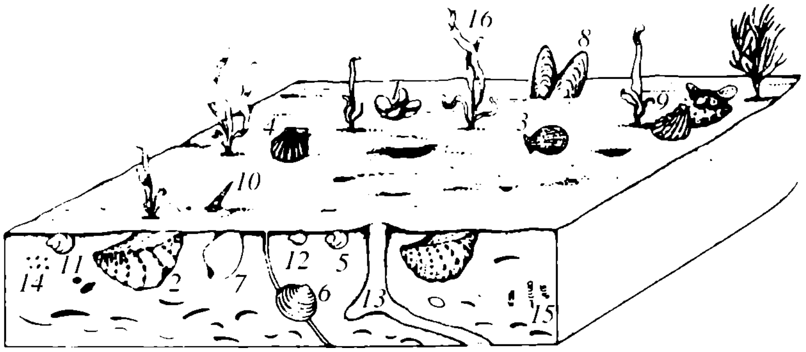


Fig. IX. 37. Reconstruction of the Late Jurassic community of the shallow water shelf of the Anglo-Norman Sea (after Fürsich, 1977, text-fig. 10): (*1*) *Nanogyra*, (*2*) *Myophorella*; (*3, 4*) *Chlamys*, (*5, 11, 12*) *Trautscholdia*, (*6*) *Discomiltha*, (*7*) *Cucullaea*, (*8*) *Gervillella*, (*9*) *Plicatula*, (*10*) gastropods, (*13–15*) tracks, and (*16*) algae.

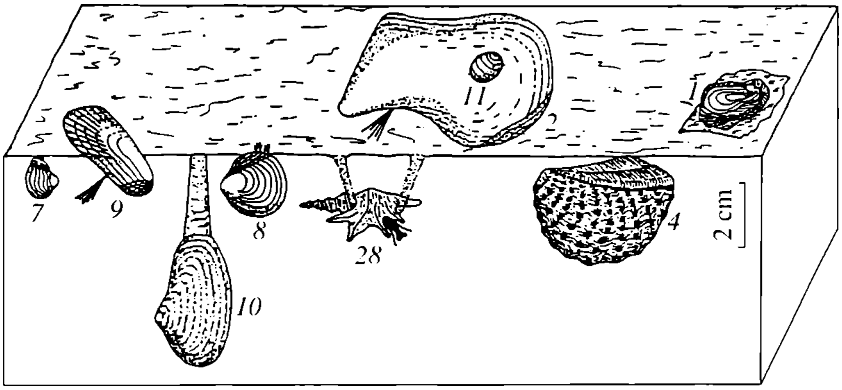


Fig. IX. 38. Reconstruction of the trophic core of the Late Jurassic community of the silty and fine sandy substrates of the shallow shelf (southern England) (after Oschmann, 1988, text-fig. 8): (*1*) *Nanogyra*, (*2*) *Isognomon*, (*3*) *Camptonectes*, (*4*) *Myophorella*, (*5*) *Liostrea*, (*6*) *Lucinidae*, (*7*) *Corbulomima*, (*8*) *Protocardia*, (*9*) *Musculus*, (*10*) *Pleuromya*, (*11*) *Anomia*, (*12*) *Entolium*, (*13*) *Thracia*, (*14*) *Pinna*, (*15*) *Ostrea*, (*16*) *Plagiostoma*, (*17*) *Jurassicorbula*, (*18*) *Laevitrigonia*, (*19*) *Plectomya*, (*20*) *Nicaniella*, (*21*) *Eocallista*, (*22*) *Corbicellopsis*, (*23*) *Mesosaccella*, (*24*) *Palaeonucula*, (*25*) serpulids, and (*26–28*) gastropods.

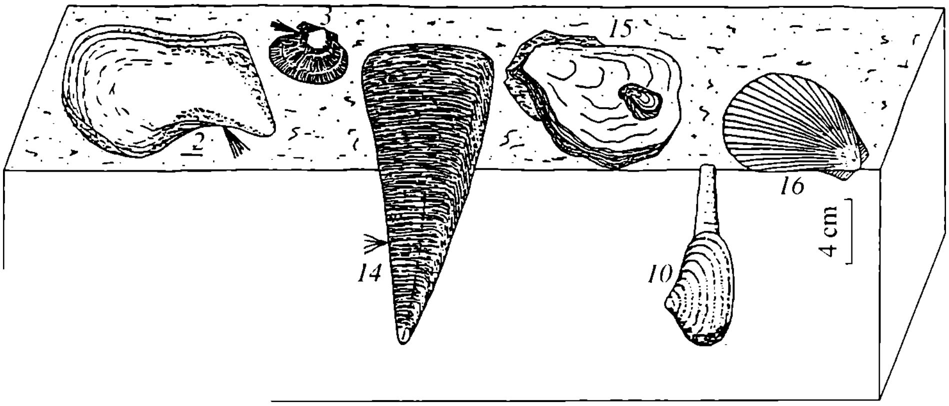


Fig. IX. 39. Reconstruction of the trophic core of the Late Jurassic community of the silty and fine sandy substrates of the shallow shelf (southern England) (after Oschmann, 1988, text-fig. 11). For designations, see Fig. IX. 38.

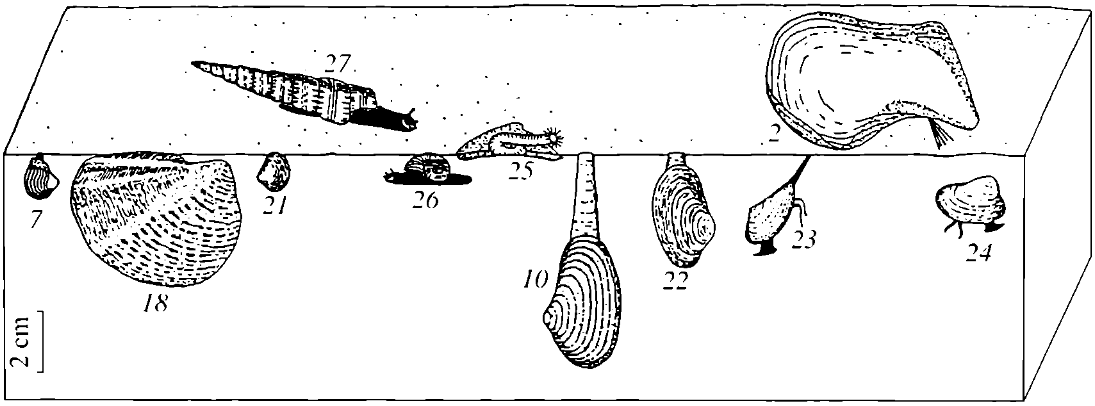


Fig. IX. 40. Reconstruction of the trophic core of the Late Jurassic community of the soft carbonate muddy substrates of the shallow shelf (southern England) (after Oschmann, 1988, text-fig. 16). For designations, see Fig. IX. 38.

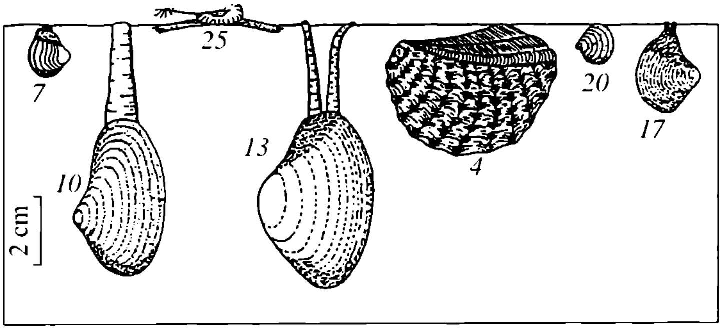


Fig. IX. 41. As in text-fig. IX. 40 (after Oschmann, 1988, text-fig. 12).

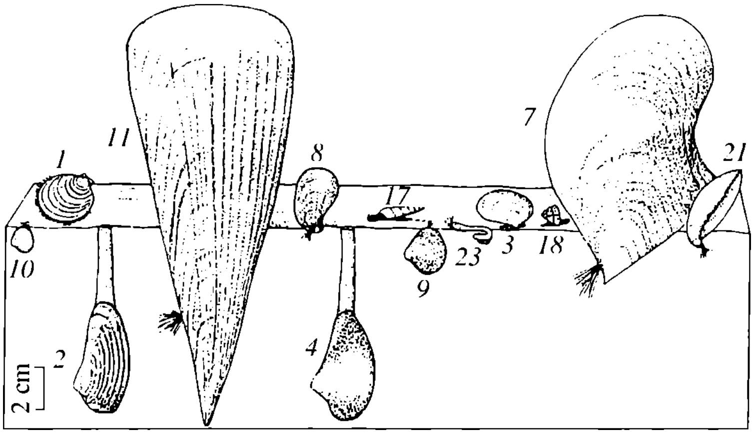


Fig. IX. 42. Reconstruction of the trophic core of the Late Jurassic community of sandy and sandy-clayey substrate of the shallow shelf (Greenland) (after Fürsich, 1984, text-fig. 26): (*1*) *Entolium*, (*2*) *Pleuromya*, (*3*) *Camptonectes*, (*4*) *Pholadomya*, (*5*) *Limatula*, (*6*) *Modiolus*, (*7*) *Isognomon*, (*8*) *Buchia*, (*9*) *Astarte*, (*10*) *Isocyprina*, (*11*) *Pinna*, (*12*) *Grammatodon*, (*13*) *Thracia*, (*14*) *Mesosaccella*, (*15*) *Protocardia*; (*16–19*) gastropods, (*20*) scaphopods, (*21*, *22*) brachiopods, and (*23*) *Cycloserpula*.

zone was also inhabited by epibyssal bivalves (*Bositra*), possibly attached to floating algae; the epibyssal, or free-lying, *Inoceramus*, *Entolium*, *Meleagrinella*, *Otapiria*, *Buchia*, and *Pseudomytiloides*; the epibyssal, or free lying, capable of swimming *Pseudamussium* and *Posidonotis*; bivalves feeding through a mucous tubule (*Luciniola*); infaunal, shallowly burrowing siphonate bivalves (*Protocardia*, *Corbulomima*, and

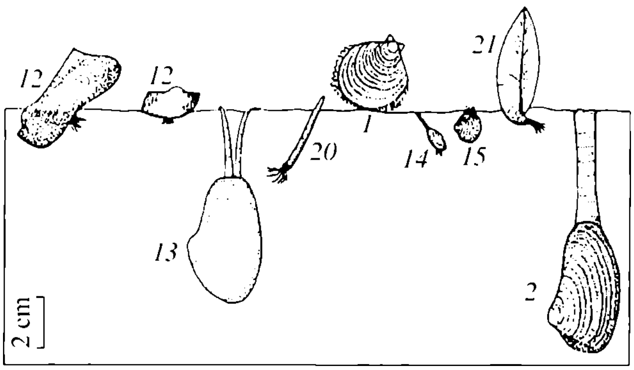


Fig. IX. 43. Reconstruction of the trophic core of the Late Jurassic community of the sandy and sandy-clayey substrates of the shallow shelf (after Fürsich, 1984, text-fig. 19). For designations, see Fig. IX. 42.

Isocyprina); and those without siphons (*Prorokia* and *Nicaniella*). In the disaerobic environment, muddy substrates of the Early Jurassic sea of northwestern North America contained a monospecific community of epifaunal byssal bivalves, which lost the byssus at the adult stage to become recliners, *Pseudomonotis* (Fig. IX. 44) (Arkell, 1935; Hudson, 1963, 1980; Farrow, 1966; Wobber, 1968; McKerrow *et al.*, 1969; Holder and Hollmann, 1969; Hallam, 1972, 1976; Duff, 1975; Fürsich and Palmer, 1975; Fürsich, 1976a, 1977, 1984; Palmer, 1979; Taylor, 1979; Palmer and Fürsich, 1981; Morter, 1984; Oschmann, 1988; Aberhan, 1994; Hudson *et al.*, 1995).

A similar composition of communities was characteristic of the seas of the inner states of the western United States (Imlay, 1957; Wright, 1973, 1974). In the Bajocian, coastal lagoons with somewhat increased salinity, and clayey and carbonate muddy grounds contained a community of epi- and/or semi-infaunal suspension-feeders lacking siphons (*Trigonia*), which also commonly contained shallowly burrowing bivalves with short siphons (*Pronoella*). Less commonly, the community contained the endobyssal *Modiolus*, epibyssal *Mytilus*, and shallowly burrowing siphonate *Corbula* and *Astarte*. Brackish-water Early Callovian lagoons with clayey and sandy-muddy substrates were dominated by epibyssal bivalves (*Meleagrinella*), whereas other epibyssal (*Camptonectes* and *Lima*), cemented (*Ostrea* and *Gryphaea*), and infaunal (*Myophorella, Tancredia, Isocyprina, Vaugonia*, and *Quenstedtia*) taxa played a secondary role, similar to that of debris-feeders of the family Nuculidae. In places *Gryphaea* formed accumulations (Fig. IX. 45).

Sandy movable grounds of the coastal shallow water zone were dominated by the infaunal, shallowly burrowing, siphonate *Tancredia*, whereas epifaunal *Ostrea, Meleagrinella*, and *Camptonectes* were less common (Fig. IX. 46). Occasionally, the community contained infaunal *Dosiniopsis, Panopea, Quenstedtia, Vaugonia*, and *Pleuromya*.

In the Middle Jurassic (Bajocian), the shallow water shelf was inhabited by the deeply burrowing bivalves with long siphons (*Pleuromya* and *Pholadomya*), and by the shallowly burrowing bivalves *Astarte, Pronoella*, and *Corbula*, the epifaunal cemented *Ostrea, Gryphaea*, and *Plicatula*, and the byssal *Camptonectes, Gervillia* and *Lima*. Oyster banks were occasionally present. In the Late Jurassic, this zone was also dominated by suspension-feeders, which formed various communities, including the epibyssal *Camptonectes, Lima*, and *Meleagrinella*; the epi- and/or endobyssal *Grammatodon*; the endobyssal *Modiolus*; the cemented *Gryphaea, Ostrea*, and *Alectryonia*; the infaunal shallowly burrowing and/or semi-infaunal *Trigonia, Myophorella, Corbula, Astarte, Pronoella*, and *Quensted-*

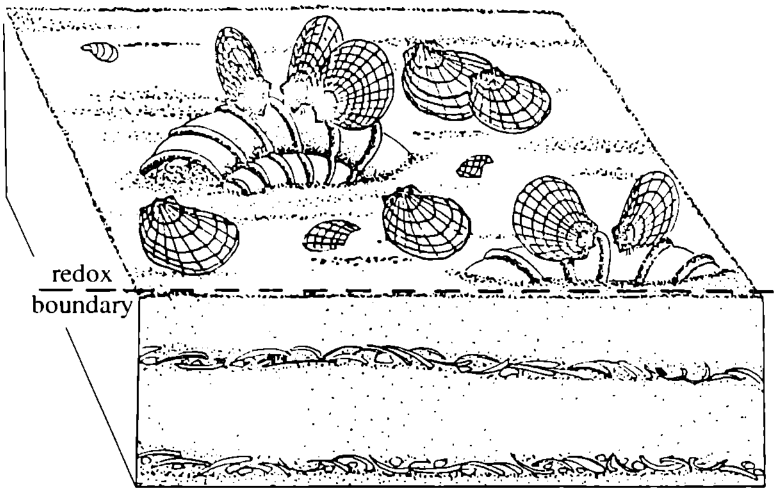


Fig. IX. 44. Reconstruction of the Early Jurassic monospecific community of *Posidonotis semiplicata* (muddy substrates), living in a anaerobic environment (Canadian Cordilleras) (after Aberhan and Pálfy, 1996, text-fig. 4).

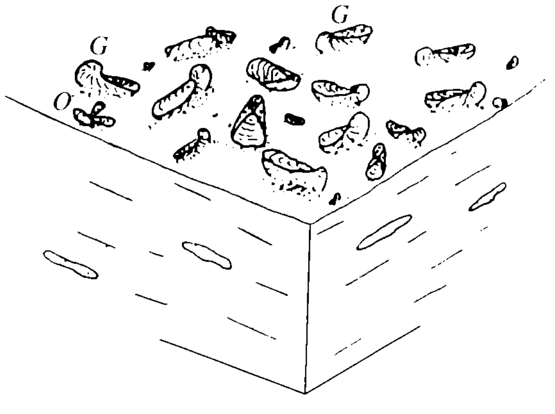


Fig. IX. 45. Reconstruction of the Late Jurassic lagoonal oyster community of the Midcontinental Sea (North America) (after Wright, 1974, text-fig. 4): (*G*) *Gryphaea* and (*O*) *Ostrea*.

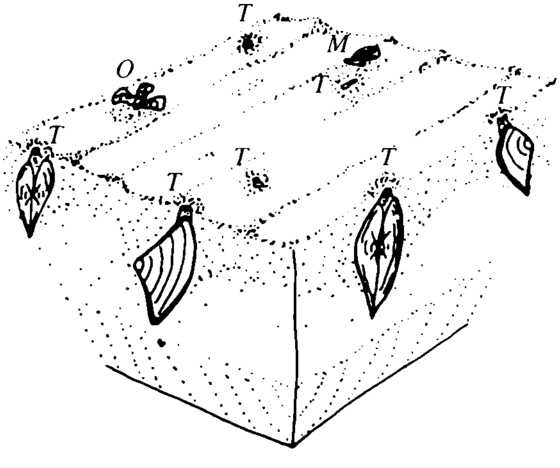


Fig. IX. 46. Reconstruction of the Late Jurassic community of the coastal shallow water zone of the Midcontinental Sea (North America) (after Wright, 1974, text-fig. 7): (*M*) *Meleagrinella*; (*O*) *Ostrea*; and (*T*) *Tancredia*.

tia; and the deeply burrowing *Pleuromya*, *Pholadomya*, and "*Myopholas*" with well developed siphons (representatives of the latter genus may have been capable of boring).

Seas of the Tethyan Biogeographic Realm, in their marginal zone, were dominated by suspension-feeders, both infaunal and epifaunal. The majority of infaunal taxa were shallowly burrowing and lacking siphons (*Nicaniella*, *Eomiodon*, and *Myrene*) or siphonate (*Jurassicorbula*, *Protocardia*, and *Corbulomima*). Among epifaunal taxa, cemented bivalves were most common (*Nanogyra*, *Praeexogyra*, *Placunopsis*, *Liostrea*, and *Anomia*) (Fig. IX. 47) (representatives of the former two genera formed banks). Byssal bivalves (*Isognomon*, *Arcomytilus*, *Lycettia*, and *Pteroperna*) were also very common. Endobyssal *Modiolus* was common. Infaunal deeply burrowing suspension-feeders (*Thracia*, *Pholadomya*, *Ceratomya*) and debris-feeders with siphons (*Mesosaccella*) and without siphons (*Palaeonucula*) were present (Fig. IX. 48).

Hypersaline lagoons contained epi- and/or endobyssal *Isognomon*, epibyssal *Trichites*, and cemented *Lopha*. Epibyssal *Camptonectes* and *Arcomytilus*, cemented *Nanogyra* and infaunal *?Discomiltha* were less common.

The coastal zone (sometimes, with decreased salinity) was dominated by cemented bivalves (*Nanogyra*, *Gryphaea*, *Atreta*, *Plicatula*, *Praeexogyra*, *Placunopsis*, and *Liostrea*), epibyssal bivalves (*Pteroperna*, *Chlamys*, *Arcomytilus*, and *Lycettia*), endo- and/or epibyssal *Isognomon*, endobyssal *Modiolus*, infaunal siphonate, deeply burrowing suspension-feeders (*Pleuromya*, *Pholadomya*) and shallowly burrowing taxa (*Corbulomima*, *Jurassicorbula*, *Isocyprina*, *Protocardia*, and *Thracia*), and suspension-feeders lacking siphons (*Cardinia*, *Nicaniella*, *Myophorella*). The siphonate *Mesosaccella* (Fig. IX. 49) was typical of infaunal debris-feeders.

The taxonomic and ethological-trophic composition of bivalvian communities of the shallow shelf was very diverse. Many genera (especially infaunal suspension-feeders) were represented by numerous individuals. These included infaunal siphonate, deeply burrowing taxa (*Ceratomya*, *Pleuromya*, *Pholadomya*, *Homomya*, *Laternula*, *Goniomya*, *Cardinia*, and *Arcomya*), shallowly burrowing taxa (*Corbulomima*, *Protocardia*, *Astarte*, *Tancredia*), taxa lacking siphons (*Trigonia*, *Nicaniella*, *Vaugonia*), bivalves feeding through a mucous tubule (lucinids), epibyssal bivalves (*Arcomyti-*

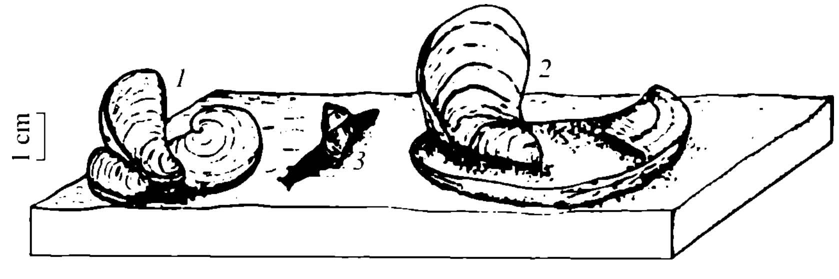


Fig. IX. 47. Reconstruction of the trophic core of the Late Jurassic oyster community of the brackish-water lagoons of the Lusitanian Basin (Portugal) (after Fürsich, 1981, text-fig. 9): (*1*) *Nanogyra*; (*2*) *Praeexogyra*; and (*3*) gastropods.

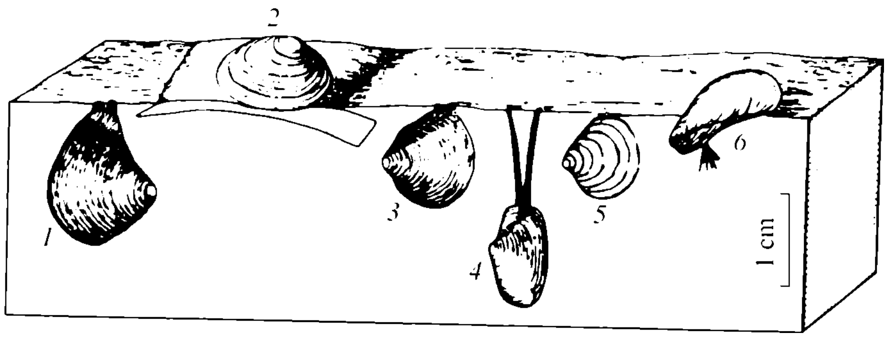


Fig. IX. 48. Reconstruction of the trophic core of the Late Jurassic community of soft substrates in the low-salinity lagoon of the Lusitanian Basin (Portugal) (after Fürsich, 1981, text-fig. 5): (*1*) *Jurassicorbula*; (*2*) *Placunopsis*; (*3*) *Protocardia*; (*4*) *Thracia*; (*5*) *Nicaniella*; and (*6*) *Modiolus*.

lus, Eopecten, Lima, Gervillia, Oxytoma, Pteroperna), epi- and/or endobyssal bivalves (*Gervillella, Trichites, Isognomon, Grammatodon*), epibyssal and/or free-lying bivalves (*Entolium, Mytiloceramus, Chlamys, Camptonectes, Aequipecten*), endobyssal bivalves (*Modiolus, Pinna, Inoperna*), cemented bivalves (*Ostrea, Lopha, Exogyra, Nanogyra, Liostrea, Praeexogyra, Diceras*), and/or free-lying taxa (*Gryphaea, Ctenostreon*). Of debris-feeder, *Palaeonucula*, Nucula, and *Dacryomya* were present (Figs. IX. 50, IX. 51).

The zone of organic buildups typically contained cemented (*Lopha, Liostrea, Ostrea, Spondylus, Plicatula, Diceras, Alectryonia*), epibyssal (*Chlamys, Trichites, Arcomytilus, Oxytoma, Gervillia, Parallelodon, Camptonectes*), and boring bivalves (*Lithophaga*). Soft substrates between bioherms were inhabited by *Pholadomya, Trigonia, Modiolus*, etc.

Hard substrates were inhabited by cemented (*Liostrea, Nanogyra, Exogyra, Diceras, Ostrea*, and *Plicatula*) and boring bivalves (*Lithophaga* and *Gastrochaena*) (Hallam, 1971; Baird and Fürsich, 1975; Fürsich, 1976b, 1981, 1993; Fürsich *et al.*, 1980; Bloos, 1982; Fürsich and Werner, 1986; Fürsich and Oschmann, 1986; Werner, 1986; Shvets-Teneta-Gurii, 1987; Machalski, 1989, 1998; Leinfelder, 1992).

Muddy substrates of the deep shelf were inhabited by epibyssal and/or free-lying suspension-feeders. Some of these bivalves could swim above the bottom (*Entolium, Plagiostoma, Aequipecten, Posidonia, Lima, Bositra, Aulacomyella*). Siphonate debris-feeders (*Nuculana*) and those lacking siphons (*Palaeonucula* and *Nuculoma*) were common. Infaunal suspension-feeders with siphons (*Pleuromya, Laternula, Myopholas, Goniomya*, and *Astarte*), the endobyssal *Inoperna* and the free-lying or cemented *Gryphaea* were less common. In the disaerobic environment, the benthos was impoverished and was composed of the epibyssal *Pseudomytiloides* and *Bositra* (Kauffmann, 1978a, 1978b; Schorr and Koch, 1985; Conti and Monari, 1992).

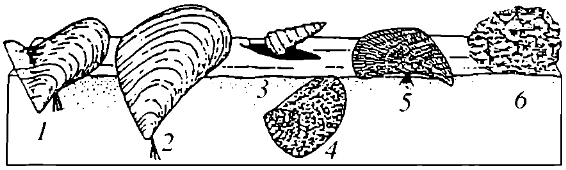


Fig. IX. 49. Reconstruction of the trophic core of the Late Jurassic community of the prodeltoidal zone with decreased salinity of the Lusitanian Basin (Portugal) (after Fürsich and Werner, 1986, text-fig. 8): (*1*) Bakevellidae; (*2*) *Isognomon*; (*3*) gastropods; (*4*) *Myophorella*; (*5*) *Arcomytilus*; and (*6*) corals.

Cretaceous

The dominant bivalve families in Cretaceous seas were epifaunal cemented and, less commonly, free-lying suspension-feeders, including symbionts with the microscopic algae *Zooxanthelle* (rudists Radiolitidae, Caprinidae, Hippuritidae, Requieniidae, Caprotinidae, and Monopleuridae); oysters Gryphaeidae and Ostreidae; infaunal, shallowly burrowing and semi-infaunal taxa lacking siphons (Trigoniidae, Unionidae) or/and with siphons (Veneridae, Astartidae, Arcticidae, Corbiculidae, Cardiidae); boring bivalves (Pholadidae), feeding through the mucous inhalant tubule (Lucinidae); epi- and/or endobyssal, less commonly, free-lying or swimming taxa (Bakevellidae, Mytilidae, Limidae, Pectinidae, Malleidae, and Carditidae); and infaunal debris-feeders with siphons (Tellinidae).

In the Early Cretaceous seas of the Arctic Subrealm of the Boreal Biogeographic Realm, the taxonomic composition of bivalvian communities was impoverished compared to those from other regions of this realm.

The marginal and coastal zones contained suspension-feeders, including infaunal, siphonate (*Homomya, Astarte, Tancredia, Pronoella, Protocardia, Hiatella*) and feeding through the mucous tubule (lucinids), epi- and/or endobyssal *Musculus*, epibyssal *Boreionectes* and *Arctotis*, epibyssal or free-lying on the umbilical part of the valve *Buchia*, cemented *Praeexogyra*, and debris-feeders (*Malletia* and *Nuculana*).

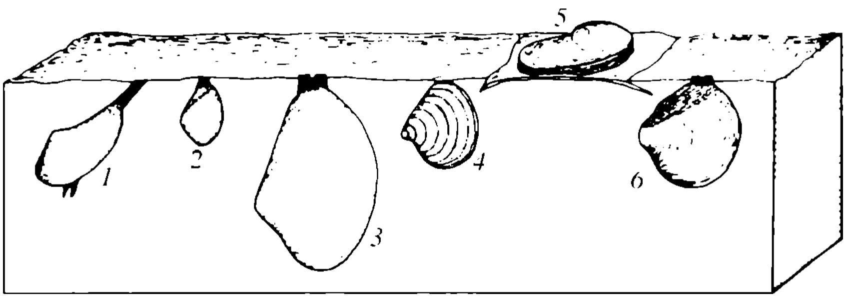


Fig. IX. 50. Reconstruction of the trophic core of the Late Jurassic community of the shallow shelf of the Lusitanian Basin (Portugal) (after Fürsich, 1981, text-fig. 3): (*1*) *Mesosaccella*; (2) *Corbulomima*; (*3*) *Isocyprina*; (*4*) *Nicaniella*; (5) *Nanogyra*; and (*6*) *Protocardia*.

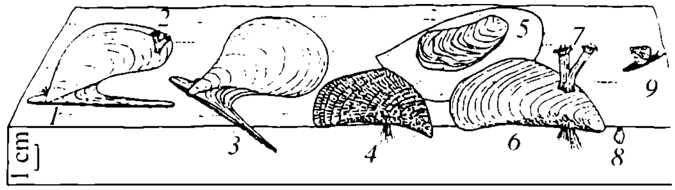


Fig. IX. 51. Reconstruction of the trophic core of the Late Jurassic community of the shallow shelf of the Lusitanian Basin (Portugal) (after Fürsich and Werner, 1986, text-fig. 5): (*1, 3*) *Pteroperna*; (2, 7) coral; (*4*) *Arcomytilus*; (5) *Praeexogyra*; (*6*) *Modiolus*; (*8*) *Corbulomima*; and (*9*) gastropods.

The open shallow water zone was dominated by *Buchia*, *Entolium*, and *Inoceramus*, which belonged to epibyssal or free-lying suspension-feeders; infaunal, siphonate shallowly burrowing *Astarte*, *Tancredia*, *Pronoella*, *Protocardia*, *Hiatella*, and *Arctica*; epibyssal *Boreionectes*, *Oxytoma*, and *Arctotis*; epibyssal *Pinna*, *Modiolus*, and *Musculus*. Deeply burrowing siphonate bivalves (*Pleuromya*, *Thracia*) and cemented *Anomia* were less common. Debris-feeders with siphons (*Dacryomya*, *Taimyrodon*, *Malletia*, and *Nuculana*) were relatively common.

The deep shelf was dominated by suspension-feeders, including epibyssal and/or free-lying (*Buchia*, *Oxytoma*, *Entolium*, *Limatula*, *Inoceramus*, etc.), siphonate shallowly burrowing (*Tancredia*, *Arctica*, *Astarte*) and deeply burrowing (*Pleuromya*), and endobyssal taxa (*Pinna*). Debris-feeders (*Dacryomya*, *Nuculana*, *Malletia*, *Taimyrodon*, and *Nucula*) were rare (Zakharov, 1966a, 1966b, 1981a, 1981b, 1983; Zakharov and Yudovnyi, 1974; Zakharov and Turbina, 1979; Sanin, 1979; Zakharov and Saks, 1983; Zakharov and Shurygin, 1984; Yazikova, 1999) (Figs. IX. 52, IX. 53).

In the Early Cretaceous seas of the Atlantic Subrealm of the Boreal Biogeographic Realm, the coastal zone was inhabited by cemented bivalves (*Arctostrea*, *Praeexogyra*, *Ostrea*, *Exogyra*, *Anomia*, and *Lopha*), epibyssal and/or free-lying bivalves (*Buchia*, *Entolium*, *Inoceramus*, *Limatula*, and *Syncyclonema*), epibyssal taxa (*Arctotis*, *Boreionectes*, and *Aguilleria*), epi- and/or endobyssal *Musculus*, infaunal siphonate taxa (*Venilicardia*, *Astarte*, *Arctica*, *Tancredia*, and *Homomya*), and bivalves feeding through a mucous tubule (lucinids).

On the shallow shelf, various suspension-feeders were abundant. These included epibyssal or free-lying bivalves (*Entolium*, *Camptonectes*, *Buchia*, and *Neithea*), epibyssal bivalves (*Oxytoma*, *Lima*, *Pteria*, and *Gervillia*), epi- and/or endobyssal bivalves (*Grammatodon*), cemented taxa (*Exogyra*, *Liostrea*, *Ostrea*, *Plicatula*, and *Lopha*), infaunal siphonate shallowly burrowing taxa (*Corbula*, *Protocardia*, *Astarte*, and *Thetironia*), and deeply burrowing taxa (*Homomya*, *Pholadomya*, and *Panopea*). Of debris-feeders *Nucula*, *Mesosaccella*, and *Nuculana* were most typical.

Hardgrounds were inhabited by cemented suspension-feeders (*Spondylus*, *Ostrea*, *Exogyra*, *Lopha*, *Arctica*, *Plicatula*, and *Pycnodonte*), and epibyssal suspension-feeders (*Aucellina*, *Inoceramus*, *Septifer*, *Pseudolimea*, *Barbatia*, and *Chlamys*).

The deepwater shelf was dominated by epibyssal or free-lying *Inoceramus*. *Aequipecten*, *Neithea*, *Chlamys*, and *Entolium* belonging to the same group and capable of occasional swimming above the bottom; *Spondylus* holding by spines on the soft muddy substrates; cemented bivalves (*Arctostrea*, *Plicatula*, and *Exogyra*); infaunal bivalves with siphons (*Thracia*, *Pholadomya*, and *Goniomya*); infaunal, feeding through the mucous tubule (Lucinidae); and debris-feeders (*Nucula* and *Nuculana*) were common.

In the Late Cretaceous, the marginal and coastal zones of the same subrealm were inhabited by suspension-feeders, including epibyssal or free-lying (*Inocer-*

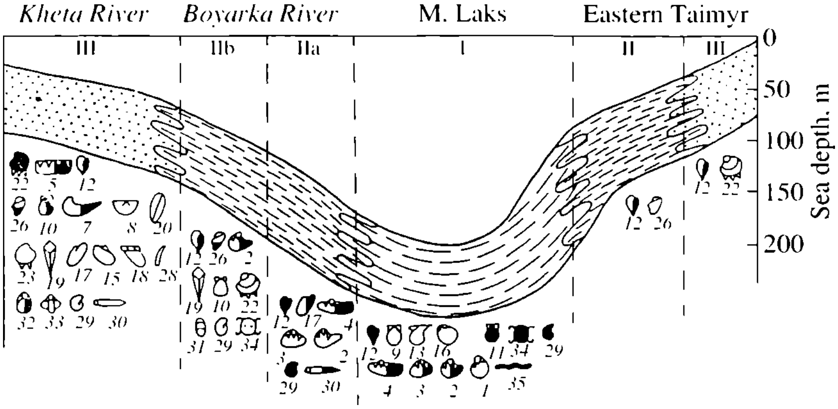


Fig. IX. 52. Distribution of invertebrate communities in the Early Berriasian Sea of the north of central Siberia (after Zakharov, 1981, text-fig. 114): (*I*) relatively deep and (*II*) moderately deep shelf (*IIa*) relatively distant from the shore and (*IIb*) near the shore; (*III*) coastal zone; and (*IV*) sandy mounds: (*1*) *Nuculoma–Praenucula*; (2) *Dacryomya*; (*3*) *Malletia*; (*4*) *Taimyrodon*; (*5*) *Grammatodon*; (*6*) *Cucullaea*; (*7*) *Praeexogyra*; (*8*) *Boreionectes*; (*9*) *Camptonectes*; (*10*) *Entolium*; (*11*) *Aequipecten*; (*12*) *Buchia*; (*13*) *Oxytoma*; (*14*) *Arctotis*; (*15*) *Limatula*; (*16*) *Limea*; (*17*) *Inoceramus*; (*18*) *Aequilerella*; (*19*) *Pinna*; (*20*) *Musculus*; (*21*) *Arctica*; (*22*) *Astarte*; (*23*) *Neocrassina*; (*24*) *Tancredia*; (*25*) *Lucina*; (*26*) *Homomya*; (*27*) gastropods; (*28*) scaphopods; (*29*) ammonoids; (*30*) belemnoids; (*31–33*) brachiopods; (*34*) crustaceans; and (*35–37*) traces. Completely blackened symbols mark large number of individuals, half-blackened symbols indicate frequent occurrence, and blank symbols indicate rare occurrence. Dots show sands, dense hatching indicates mud, and widely spaced hatching indicates clay.

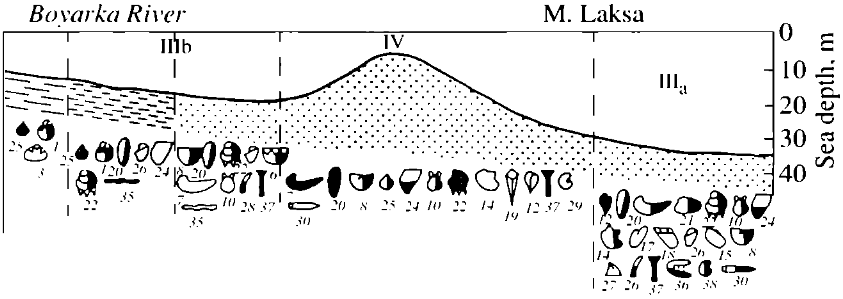


Fig. IX. 53. Distribution of invertebrate communities in the Early Hauterivian Sea in the northern part of central Siberia. For designations, see Fig. IX. 52 (after Zakharov, 1981, text-fig. 116).

amus, Chlamys, Camptonectes, Entolium, Neithea), cemented and/or free-lying (*Pycnodonte, Plicatula, Acutostrea, Lopha, Dianchora, Gryphaeostrea, Amphidonte, Exogyra*), epibyssal (*Lima, Pseudoptera, Oxytoma*), and endobyssal bivalves (*Pinna*). Infaunal suspension-feeders were uncommon (*Panopea, Protocardia, Astarte, Eriphyla, Venericardia*). Of debris-feeders, *Aenona, Nuculana*, and *Nucula* were present.

In the open shelf, the taxonomic composition was more diverse. The following suspension-feeders dominated: epibyssal and/or free-lying (*Inoceramus, Entolium, Camptonectes, Neithea, Chlamys, Syncyclonema*, and *Limatula*); epibyssal (*Lima, Plagiostoma, Oxytoma, Arca*, and *Pseudoptera*); cemented (*Dimyodon, Spondylus, Gryphaeostrea, Exogyra, Rastellum, Plicatula, Lopha, Dianchora, Anomia, Ceratostreon, Acutostrea, Liostrea*, and *Ostrea*) and/or free-lying (*Pycnodonte* and *Amphidonte*); epi- and/or semi-infaunal (*Trigonarca*); and infaunal siphonate, shallowly burrowing (*Arctica, Astarte, Venilicardia*, and *Cyprimeria*) and deeply burrowing bivalves (*Pholadomya, Aphrodina*, and *Panopea*). Infaunal debris-feeders with siphons (*Nuculana* and *Mesosaccella*) and lacking siphons (*Nucula*) were typical. Infaunal siphonate predators (*Cuspidaria* and *Liopistha*) were present.

Hardgrounds were inhabited by cemented (*Exogyra, Spondylus, Rastellum, Atreta*, etc.) and boring bivalves (*Gastrochaena*).

On the deep shelf, epifaunal bivalves (*Inoceramus, Pycnodonte, Acutostrea, Chlamys, Lima, Gryphaeostrea, Limatula, Neithea, Anomia, Gryphaea, Dianchora, Spondylus, Oxytoma, Pseudoptera, Arca, Entolium, Limea, Plagiostoma, Amphidonte*, and *Syncyclonema*) were typical. Some bivalves could swim above the bottom (*Oxytoma, Syncyclonema, Plagiostoma, Pseudoptera*, and *Chlamys*). Infaunal suspension-feeders (*Astarte, Pholadomya, Panopea*, and some others) were less common, whereas debris-feed-

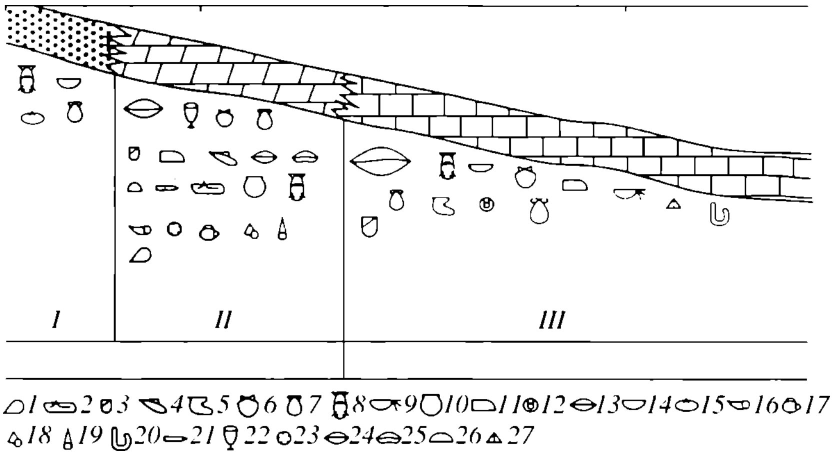


Fig. IX. 54. Distribution of benthos and nektobenthos in the southwestern part of the Russian Sea in the Santonian (after Sobetskii, 1978, text-fig. 73): (*I–II*) sublittoral zone: (*I*) sand, (*II*) carbonate-silty mud, (*III*) carbonate-clayey mud of the pseudoabissal zone. (*1*) *Nucula*, (*2*) *Arca*, (*3*) *Inoceramus*, (*4*) *Pseudoperna*, (*5*) *Oxytoma*, (*6*) *Entolium*, (*7*) *Chlamys*, (*8*) *Dianchora*, (*9*) *Plicatula*, (*10*) *Dimyodon*, (*11*) *Lima*, (*12*) *Anomia*, (*13*) *Acutostrea*, (*14*) *Pycnodonte*, (*15*) *Panopea*, (*16*) scaphopods, (*17–19*) gastropods, (*20*) worms, (*21*) belemnoids, (*22*) sponges, (*23*) corals, (*24, 25*) brachiopods, (*26*) sea urchins, and (*27*) cirripeds.

ers (*Nucula* and *Nuculana*) were common. Zones with disaerobic conditions were dominated by *Inoceramus* and *Pycnodonte*; *Neithea, Chlamys, Acutostrea, Syncyclonema*, and *Gryphaeostrea* were less common (Jeffries, 1962; Carter, 1972; Voigt, 1974; Michael, 1974; Kříž and Čech, 1974; Tröger, 1975; Hancock, 1975; Heinberg, 1979b; Taylor *et al.*, 1983; Nekvasilova and Zitt, 1988; Lommercheim, 1991).

A similar taxonomic composition was characteristic of the communities inhabiting the Late Cretaceous Russian Sea, which occupied the largest part of the East European Platform, and in the time of transgressions continued far to the north and east. In the north, it was connected to the epicontinental seas of the Arctic Realm; in the west, it reached the seas of Central Europe, which opened into the Atlantic; and in the southeast, it was connected to the Precaspian Basin, which opened to the seas of the Tethyan Realm (Sobetskii, 1966, 1977a, 1978; Savchinskaya, 1982; Sobetskii *et al.*, 1985).

The coastal zone was inhabited by cemented bivalves (*Dianchora, Lopha*, and *Acutostrea*); cemented and/or free-lying *Pycnodonte, Gryphaea*, and *Amphidonte*; bivalves attached by the byssus or free-lying (*Chlamys, Entolium*, and *Inoceramus*); byssal *Oxytoma*; infaunal suspension-feeders with siphons (*Panopea*); and, more rarely, by debris-feeders lacking siphons (*Nucula*).

The shallow shelf was also dominated by epifaunal suspension-feeders, including the cemented bivalves (*Gryphaeostrea, Liostrea, Diancora, Lopha, Acutostrea, Dimyodon, Anomia*) and/or free-lying (*Pycnodonte, Gryphaea, Amphidonte, Exogyra*, and *Spondylus*), attached by byssus or free-lying (*Inoceramus, Camptonectes*, and *Plicatula*), and bivalves capable of swimming (*Entolium, Lima, Limatula, Limea, Propeamussium, Chlamys, Plagiostoma*, and *Syncyclonema*), byssal (*Pseudoptera* and *Oxytoma*), epi- and/or endobyssal *Cucullaea* and *Pinna*, epibyssal *Arca*, epi- and/or semi-infaunal free-lying *Trigonarca* and *Pterotrigonia*. Infaunal suspension-feeders were less common. These included shallowly burrowing bivalves lacking siphons (*Trigonia* and *Linotrigonia*); those with short siphons (*Corbula, Arctica, Astarte, Protocardia*, and *Cyprimeria*); and deeply burrowing bivalves with long siphons (*Pholadomya, "Tellina,"* and *Panopea*). Infaunal debris-feeders with siphons (*Nuculana*) and without siphons (*Nucula*) were considerably less common.

Muddy substrates of the deep shelf were mainly inhabited by suspension-feeders, including epifaunal *Dianchora, Pycnodonte, Chlamys, Entolium, Inoceramus, Lima, Plicatula, Oxytoma, Anomia, Acutostrea, Neithea, Pseudolimea, Gryphaeostrea, Spondylus, Pinna, Gryphaea, Lopha, Amphidonte, Limatula, Pseudoptera, Limea, Syncyclonema*, and *Prohinnites*; epibyssal *Pinna*; and infaunal and/or semi-infaunal *Protocardia, Pholadomya*, and *Thracia*. The debris-feeders *Nucula* and *Nuculana* were less common (Figs. IX. 54, IX. 55).

Seas of the Pacific Subrealm of the Boreal Realm, in the coastal zone were inhabited by bank-building bivalves (*Crassostrea*); the epibyssal *Brachidontes*; the endobyssal *Pinna*; the infaunal shallowly burrowing and siphonate *Caestocorbula* and *Loxo*; the deeply burrowing siphonate *Leptosolen*; and bivalves lacking siphons, such as the shallowly burrowing or semi-infaunal *Aptotrigonia*.

The shallow shelf was inhabited by numerous *Inoceramus*, often building banks. The epibyssal *Mytilus*; the epibyssal or free-lying *Propeamussium*; epi- and/or semi-infaunal taxa (*Glycymeris, Pinna*, and *Modiolus*); the infaunal *Trigonia* (lacking siphons) and other trigoniids; the siphonate shallowly burrowing *Cymbophora*,

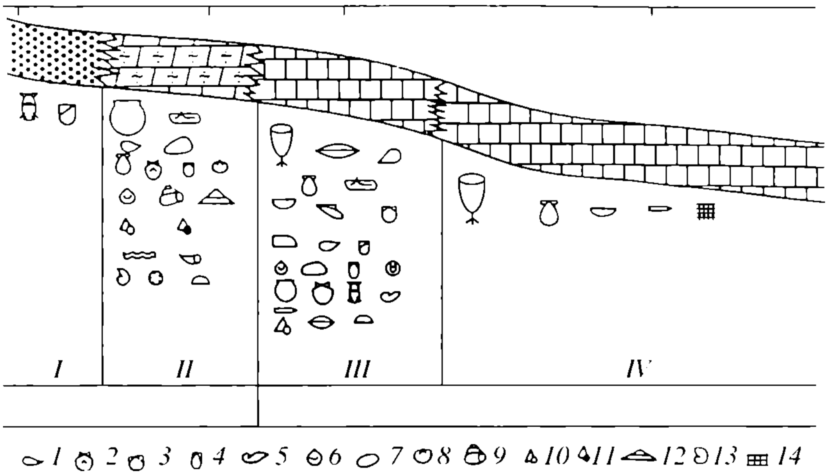


Fig. IX. 55. Distribution of benthos and nektobenthos in the southwestern part of the Russian Sea in the Late Campanian (after Sobetskii, 1978, text-fig. 89): (*IV*) fine-grained mud of the pseudoabyssal zone; (*1*) *Nuculana*, (*2*) *Propeamussium*, (*3*) *Limea*, (*4*) *Limatula*, (*5*) *Gryphaeostrea*, (*6*) *Astarte*, (*7*) *Tellina*, (*8*) *Venericardia*, (*9–12*) gastropods; (*13*) Ammonoidea, and (*14*) bryozoans. For other designations, see Fig. IX. 54.

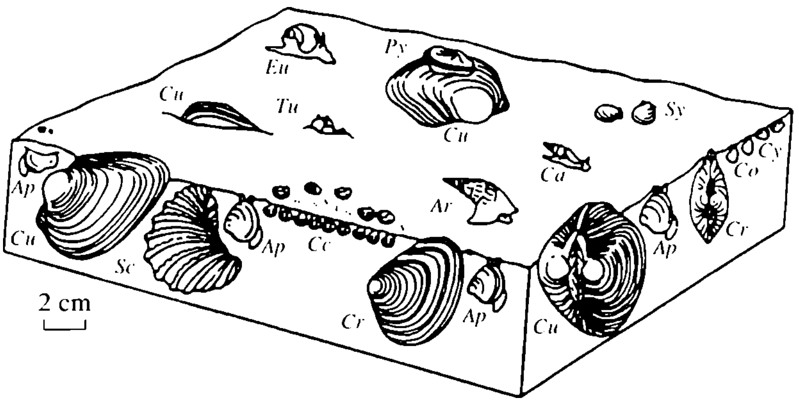


Fig. IX. 56. Reconstruction of the Late Campanian (Late Cretaceous) coastal community (Tennessee) (after Jablonski and Bottjer, 1983, text-fig. 10), composed of bivalves: (*Ap*) *Aphrodina*, (*Cc*) *Caestocorbula*, (*Co*) *Corbula*, (*Cr*) *Crassatella*, (*Cu*) *Cucullaea*, (*Cy*) *Cyclorisma*, (*Py*) *Pycnodonte*, (*Sc*) *Scabrotrigonia*, and (*Sy*) *Syncyclonema*; and (*Ar*, *Ca*, *Eu*, *Tu*) gastropods.

Protocardia and *Loxo*; the infaunal *Lucina* with a mucous tubule; infaunal debris-feeders with siphons ("*Tellina*" and *Jupiteria*) and lacking siphons (*Leionucula* and *Acila*) were typical. Cemented bivalves (*Ostrea*, *Anomia*, and *Crassostrea*), deeply burrowing suspension-feeders with siphons (*Periploma*, *Panopea*, and *Aphrodina*) were also present, although less commonly.

The deep shelf was inhabited by the epibyssal and/or free-lying *Inoceramus*; and/or capable of swimming taxa (*Propeamussium*); epi- and/or endobyssal, free-lying, or semi-infaunal taxa lacking siphons (*Grammatodon*); epi- and/or semi-infaunal bivalves (*Glycymeris*); infaunal suspension-feeders with an inhalant mucous tubule (*Lucina*); debris-feeders with siphons (*Jupiteria* and "*Portlandia*") and those lacking siphons (*Acila* and *Leionucula*); and by predatory bivalves (*Cuspidaria*) (Zhidkova *et al.*, 1974).

The Cretaceous Basin of the North American Midcontinent, in its marginal zone, was inhabited by suspension-feeders, including cemented taxa (*Crassostrea*, *Ostrea*, *Lopha*, *Flemingostrea*, *Anomia*, and *Exogyra*); epibyssal taxa (*Pteria*, *Gervillia*, *Lima*, and *Brachidontes*), endobyssal bivalves (*Modiolus*); epi- and/or endobyssal bivalves (*Cucullaea*); infaunal siphonate bivalves (*Protocardia*, *Cyprimeria*, *Veloritina*, *Ursirivus*, *Homomya*, and *Flaventia*) and those lacking siphons (*Scabrotrigonia*); and bivalves feeding through the mucous tubule (Lucinidae). In places, oysters built banks.

In the coastal zone, the ethological-trophic composition was similar to that of the marginal zone, while the taxonomic composition was more diverse (Figs. IX. 56–IX. 58). There were many cemented bivalves, occasionally forming banks (*Crassostrea*, *Ostrea*, *Exogyra*, *Lopha*, *Ilmatogyra*, *Textigryphaea*, *Ceratostreon*, *Pli-*

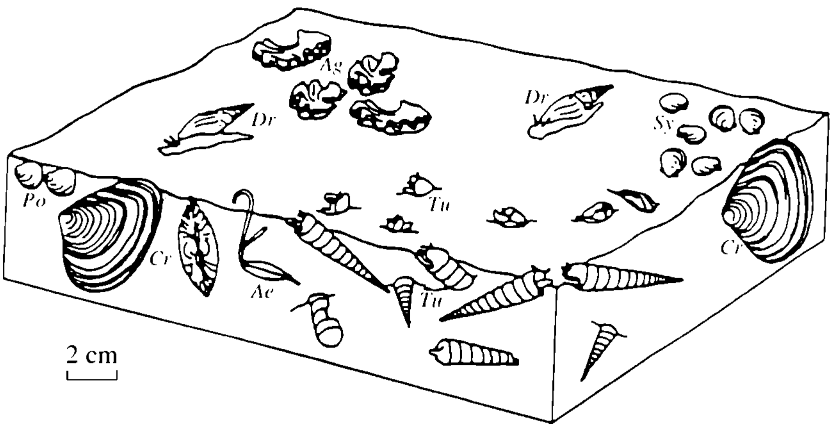


Fig. IX. 57. Reconstruction of the Early Maastrichtian (Late Cretaceous) coastal community (Mississippi) (after Jablonski and Bottjer, 1983, text-fig. 9), composed of bivalves: (*Ae*) *Aenona*, (*Ag*) *Agerostrea*, (*Cr*) *Crassatella*, (*Po*) *Postligata*, and (*Sy*) *Syncyclonema*; and (*Dr, Tu*) gastropods.

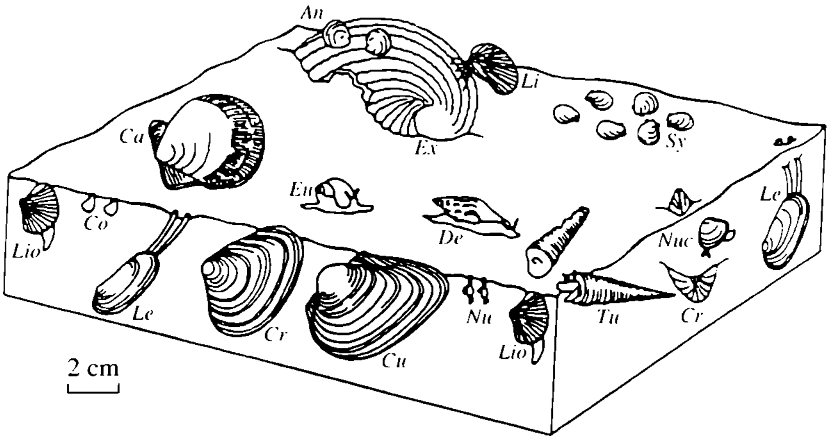


Fig. IX. 58. Reconstruction of the Middle Maastrichtian (Late Cretaceous) coastal community (Mississippi) (after Jablonski and Bottjer, 1983, text-fig. 11), composed of bivalves: (*An*) *Anomia*, (*Ca*) *Camptonectes*, (*Co*) *Corbula*, (*Cr*) *Crassatella*, (*Cu*) *Cucullaea*, (*Ex*) *Exogyra*, (*Le*) *Legumen*, (*Li*) *Lima*, (*Lio*) *Liopistha*, (*Nu*) *Nuculana*, (*Nuc*) *Nucula*, and (*Sy*) *Syncyclonema*; and (*De, Eu, Tu*) gastropods.

catula, *Pycnodonte*, *Anomia*, and *Agerostrea*). Epibyssal bivalves included *Oxytoma*, *Lima*, *Camptonectes*, *Breviarca*, and *Brachidontes*, while epibyssal and/or free-lying taxa included *Inoceramus*, *Syncyclonema*, and *Neithea*. Epifaunal or semi-infaunal bivalves lacking byssus included *Postligata*, while epi- and/or endobyssal bivalves included *Cucullaea* and *Parallelodon*. Infaunal suspension-feeders were represented by the siphonate *Cymbophora*, *Aphrodina*, *Caestocorbula*, *Caryocorbula*, *Cyclorisma*, *Crassatella*, *Corbula*, *Protocardia*, *Tancredia*, *Corbulamella*, and *Legumen* and the nonsiphonate *Scabrotrigonia*. Debris-feeders included *Nuculana*, *Malletia*, *Aenona*, *Tellinimera*, and *Nucula*; and predators included *Liopistha*.

The composition of bivalvian communities in the shallow shelf was very similar to the above (Fig. IX. 59). Among the suspension-feeders, there were many cemented bivalves (*Ostrea*, *Exogyra*, *Textigryphaea*, *Plicatula*, *Spondylus*, *Agerostrea*, *Anomia*, and *Pycnodonte*; the latter could lie unattached on the substrate), whereas the southern part of the basin contained banks formed by *Monopleura*, *Toucasia*, and *Chondrodonta*. Epibyssal bivalves included *Mytiloides*, *Phelopteria*, *Pseudoptera*, *Tenuipteria*, *Lima*, *Chlamys*, *Oxytoma*, and *Breviarca*; epibyssal and/or free-lying bivalves included *Inoceramus*, *Entolium*, *Syncyclonema*, *Neithea*, *Lima*, and *Camptonectes*. The majority of these bivalves could swim (*Lima*, *Chlamys*, *Entolium*, *Syncyclonema*, *Neithea*, and *Camptonectes*). Infaunal suspension-feeders included the siphonate shallowly burrowing *Corbulamella*, *Corbula*, *Caestocorbula*, *Cyprimeria*, *Dosiniopsis*, *Pleurocardium*, *Granocardium*, *Protocardia*, *Cymbophora*, *Tancredia*, *Crassatella*, *Astarte*, and the more deeply burrowing siphonate *Homomya* and nonsiphonate *Trigonia*, and taxa with a mucous inhalant tubule (Lucinidae). Debris-feeders

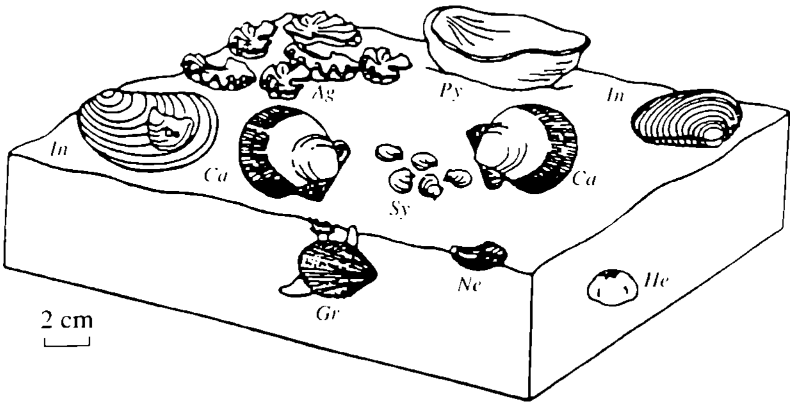


Fig. IX. 59. Reconstruction of the Early Maastrichtian community of carbonate muddy substrates of the open shelf (Arkansas) (after Jablonski and Bottjer, 1983, text-fig. 6): bivalves: (*Ag*) *Agerostrea*, (*Ca*) *Camptonectes*, (*Gr*) *Granocardium*, (*In*) *Inoceramus*, (*Ne*) *Neithea*, (*Os*) *Ostrea*, (*Py*) *Pycnodonte*, and (*Sy*) *Syncyclonema*; and (*He*) sea urchins.

(*Nuculana, Yoldia, Malletia*, and *Nucula*) and predators (*Liopistha*) were quite rare (Scott, 1970, 1975, 1977b, 1986b; Feldmann, 1972; Rhoads *et al.*, 1972; Kauffman, 1974, 1982a, 1982b, 1986; Reiskind, 1975; Jablonski and Bottjer, 1983; Fürsich and Kauffman, 1984; Hattin, 1986; Fürsich and Kirkland, 1986).

Coral reefs in the southern part of the sea contained free-lying rudists (*Coalcomana, Caprinuloidea, Petalodontia, Monopleura, Toucasia*, and *Eoradiolites*); cemented *Ostrea, Gryphaea, Chondrodonta, Pycnodonte*, and *Chama*; and free-lying and/or epibyssal *Pecten* (Robertson, 1972; Kauffman *et al.*, 1977; Scott, 1979, 1981).

Hardgrounds were inhabited by cemented bivalves (*Ostrea, Pycnodonte, Lopha*, and *Exogyra*) and epibyssal taxa (*Pteria, Lima*, and *Inoceramus*) (Scott, 1976; Bottjer, 1986).

The deep shelf was dominated by free-lying *Inoceramus* (especially in the disaerobic environment); cemented *Ostrea, Pycnodonte, Exogyra, Spondylus*, and *Anomia*; and/or free-lying *Mytiloides*; epibyssal *Phelopteria, Pseudoptera, Pteria*, and *Lima*; epibyssal and/or free-lying and sometimes swimming *Entolium, Neithea, Camptonectes*, and *Posidonotis*; infaunal siphonate *Cymbophora, Corbula*, and some others; and bivalves with a mucous tubule (Lucinidae, Thyasira). Of debris-feeders, *Nucula* was the most common taxon. *Nuculana, Malletia*, and *Yoldia* were present (Kauffman, 1967; Feldmann, 1972; Reiskind, 1975; Hattin and Cobban, 1977; Fürsich *et al.*, 1981; Bottjer, 1981; Jablonski and Bottjer, 1983; Sageman, 1989; Aberhan and Palfi, 1996; Sageman and Craig, 1997).

Bivalve communities in the seas of the Tethyan Biogeographic Realm contained many epifaunal cemented and/or free-lying rudists, dominating in all zones, except the deep shelf. Rudists were especially diverse in the Late Cretaceous communities.

The coastal zone of the Early Cretaceous seas contained biostromes of rudists, such as *Caprinuloidea, Eoradiolites*, and *Toucasia*, along with *Planocaprina* and *Requenia*, and bivalves building banks (*Texigryphaea* and *Chondrodonta*). All these taxa were cemented suspension-feeders, while rudists were also symbionts of algae (*Zooxanthelle*).

The open shallow shelf was dominated by epifaunal cemented bivalves (*Ceratostreon, Lopha, Spondylus, Amphidonte, Exogyra*, and rudists *Requienia, Monopleura, Toucasia, Radiolites*, and *Matheronia*). Epibyssal or free-lying bivalves (*Neithea, Chlamys, Lima, Entolium, Camptonectes, Propeamussium, Limaria*, and *Syncyclonema*) were common. The majority of these bivalves could swim above the bottom. Epibyssal taxa (*Oxytoma, Mytilus, Arcomytilus*, and *Arca*) and epi- and/or endobyssal bivalves (*Cucullaea* and *Grammatodon*) were also typical. Infaunal siphonate suspension-feeders (*Astarte, Protocardia, Ptychomya, Panopea*, and *Pholadomya*) and bivalves lacking siphons (*Iotrigonia*) and debris-feeders with (*Nuculana*) and without siphons (*Nucula*) were less common.

The zone of coral–algal buildups was dominated by rudists (*Toucasia, Petalodonta, Eoradiolites, Radiolites, Sauvagesia, Requienia, Monopleura*, and others) and also by *Chondrodonta*, which formed banks. The spaces between the buildups were inhabited by suspension-feeders (*Panopea, Plectomya*, and *Pterotrigonia*), while the buildups themselves were inhabited by boring bivalves (*Lithophaga* and *Lithodomus*).

The deep shelf had an impoverished composition of bivalves. The community in this area was dominated by free-lying *Inoceramus, Variamussium*, and others.

The Late Cretaceous seas contained an even more diverse community of rudists. Lagoons were inhabited by settlements of cemented *Biradiolites, Thyrostylon, Plagioptychus, Barretia, Durania, Distefanella*, and free-lying *Titanosarcolites* and *Antillocaprina*.

In the coastal zone, the rudist buildups contained other cemented bivalves (*Ostrea, Pycnodonte, Spondylus, Plicatula, Exogyra, Atreta, Gyrostrea*, and *Gry-*

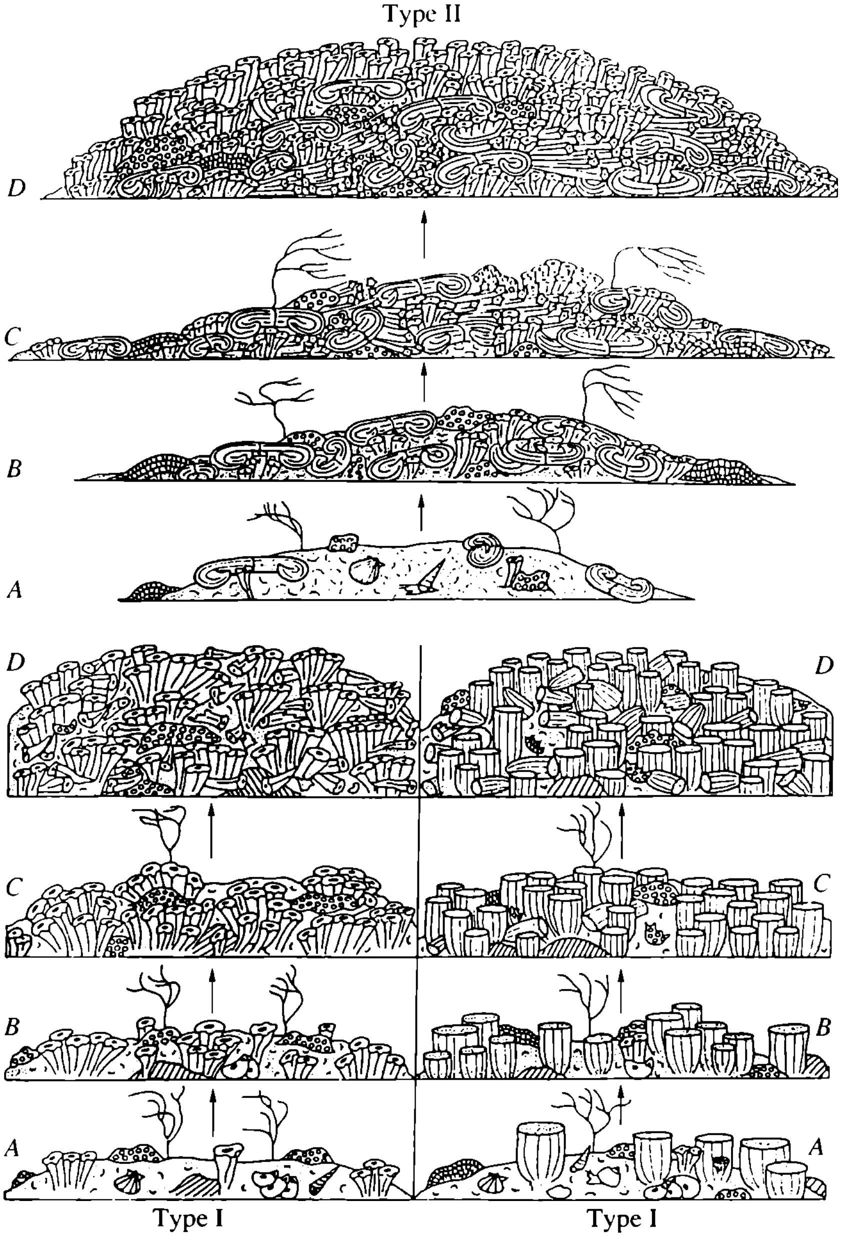


Fig. IX. 60. Scheme representing types I and II of the development of the organic buildup framework by rudists (after Kauffman and Sohl, 1974, text-fig. 26). Developmental type I either began from the settlement of small radiolitids, or hippurids (bottom left), or from large barrel-shaped taxa (bottom right); type II began from the settlement of large free-lying rudists. (*A*) association of loosely spaced individuals; (*B*) dense association, which formed aggregations; (*C*) stage of aggregations; and (*D*) stage of mature aggregations.

phaea; species of the latter two genera built banks), and also epibyssal (*Chlamys* and *Septifer*) and infaunal shallowly burrowing suspension-feeders lacking siphons (*Trigonia* and *Megatrigonia*).

The shallow shelf was commonly inhabited by the so-called meadows and banks formed by rudists. These meadows consisted of *Ichtyosarcolites, Orbignya*, and *Lapeirousia*, while the banks were built by *Biradiolites, Plagioptychus, Sauvagesia, Praeradiolites, Radiolites, Hippurites, Hippuritella, Vaccinites*, and also by oysters (*Liostrea, Gryphaea*, and *Gyrostrea*) in association with other cemented bivalves (*Exogyra, Rhynchostreon, Ostrea, Spondylus, Anomia, Lopha, Plicatula*, and *Ceratostreon*), free-lying *Neithea*, epibyssal and/or free-lying (*Inoceramus, Lima*, and *Chlamys*), endobyssal (*Modiolus* and *Glycymeris*), epibyssal suspension-feeders (*Septifer* and *Pteria*), infaunal shallowly burrowing suspension-feeders (*Korobkovitrigonia, Cyprimeria, Megatrigonia, Fimbria*, and *Corbula*), and deeply burrowing suspension-feeders (*Panopea* and

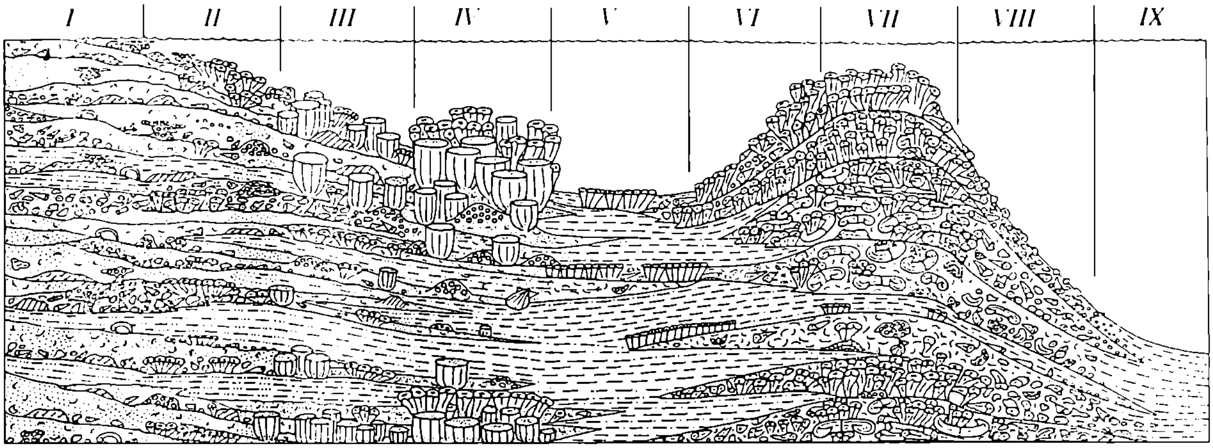


Fig. IX. 61. Model of distribution of rudists and their buildups in the shelf near the islands of the Caribbean (after Kauffman and Sohl, 1974, text-fig. 27): associations from (*I*) the tidal zone and shallow subtidal zone; (*II–IV*) the anterior slope of a lagoon: (*II*) inner, (*III*) middle, and (*IV*) outer zones; (*V*) the center of a lagoon; (*VI*) the slope of the rear barrier; (*VII*) rudist barrier; (*VIII*) shallow water zone of the anterior slope of the barrier; and (*IX*) the outer end of the anterior slope of the barrier, bordering the open shelf.

Pholadomya). Predators *Liopistha* were typical, while debris-feeders (*Tellina*, *Nuculana*, and *Arcopagia*) were rare.

In the zone of organic buildups, rudists were the main reef-building organisms (Figs. IX. 60, IX. 61). These included radiolotids (*Eoradiolites*, *Radiolites*, *Biradiolites*, *Sauvagesia*, *Sphaerulites*, and *Durania*), hippuritids (*Hippurites* and *Vaccinites*), caprinids (*Caprina*, *Caprinula*, *Caprinuloidea*, *Ichtyosarcolites*, *Mitrocaprina*, *Neocaprina*, and *Plagioptychus*), and requienids (*Requienia* and *Toucasia*). This habitat was also shared by the cemented *Chondrodonta*, *Exogyra*, and *Ostrea*.

Hardgrounds were inhabited by the cemented *Ostrea*, *Liostrea*, and *Exogyra*; the epibyssal *Gervillia*, *Mytiloides*, and *Inoceramus*; the cemented or free-lying *Pycnodonte*; and the boring *Lithophaga*.

The deep shelf was mainly inhabited by *Inoceramus* (free-lying, epibyssal, and capable of swimming). The presence of *Neithea*, *Syncyclonema*, and *Entolium* belonging to the same group; the epibyssal suspension-feeders *Avicellina*, *Propeamussium*, *Lima*, and *Camptonectes*; cemented suspension-feeders (*Plicatula*, *Liostrea*, *Dianochora*, and *Rhynchostreon*); and/or free lying suspension-feeders (*Pycnodonte*, *Acutostrea*, *Amphidonte*, and *Gryphaea*) were typical, while infaunal siphonate suspension-feeders (*Astarte* and *Pholadomya*) were scarce (Perkins, 1969; Benkö-Czabaly, 1970; Kennedy and Klinger, 1972; Philip, 1978a, 1978b; Kauffman, 1974; Kauffman and Sohl, 1974; Platel, 1974; Enos, 1974; Coates, 1977; Poyarkova, 1979, 1984; Turnšek and Buser, 1980; Chernov *et al.*, 1980; Masse and Philip, 1981; Bottjer, 1982; Pleničar, 1983, 1985; Dhondt, 1984; Scott, 1984a, 1984b, 1990; Höfling, 1985; Sartorio, 1986; Merkadier, 1986; Negra, 1987; Edson, 1988; Dzhalilov, 1988; Collins, 1988; Grosheny and Philip, 1989; Troumps, 1989; Michalik and Soták, 1990; Lescinsky *et al.*, 1991; Pleničar and Šribar, 1992; Caffau *et al.*, 1992; Johnson and Hayes, 1993; Fraser, 1996).

Only shallow water communities are known from the seas of the Notal Biogeographic Realm (Freneix, 1981; Krein, 1990). These communities typically contained suspension-feeders, including infaunal shallowly burrowing siphonate taxa ("*Bucardium*" and *Lahilla*), infaunal, taxa lacking siphons (*Pterotrigonia*) and/or semi-infaunal (*Cucullaea* and *Grammatodon*) taxa. Siphonate shallowly burrowing (*Venilicardia*, *Granocardium*, and *Nemocardium*) and deeply burrowing bivalves (*Platymyoidea*, *Aphrodina*, *Cyclorismina*, *Panopea*, *Pholadomya*, and *Goniomya*); nonsiphonate shallowly burrowing taxa (*Linotrigonia*) and/or those with short siphons (*Eriphila*); endobyssal bivalves (*Inoperna* and *Pinna*); epibyssal and/or free-lying species (*Limatula*, *Acesta*, *Entolium*, and *Camptonectes*); and infaunal debris-feeders (*Malletia*, *Leionucula*, and "*Neilo*") were present.

Paleogene

All families widely represented in the Paleogene belonged to suspension-feeders, including infaunal shallowly burrowing bivalves with siphons (Veneridae, Astartidae, and Cardiidae), infaunal taxa feeding through a mucous tubule (Lucinidae and Ungulinidae), epibyssal or free-lying, or semi-infaunal, or shallowly burrowing infaunal bivalves lacking siphons (Carditidae and Unionidae), boring bivalves (Pholadidae), epi- or endobyssal (Mytilidae), epibyssal or freely moving, and also swimming above the substrate (Pectinidae and Limidae), cemented, less commonly, free-lying taxa (Ostreidae), and some others. Among infaunal debris-feeders, relatively deeply burrowing bivalves with a siphon were dominant (Nuculanidae). The Tellinidae, which were mostly infaunal and siphonate suspension-feeders, but could feed as debris-feeders, were common.

The bivalvian communities in different zones of the sea were studied for the entire Paleogene, without subdivision into the Paleocene, Eocene, and Oligocene. Only Oligocene communities of the Paratethys are discussed separately.

Marginal seas of the east of the Atlantic Ocean (northwestern Europe), belonging to the boreal belt, in the marginal (estuaries, lagoons, and bays) and coastal zones of decreased salinity, were inhabited by epifaunal cemented (*Ostrea*) and byssal bivalves (*Mytilus*), infaunal suspension-feeders (*Polymesoda* and *Corbula*), and debris-feeders (*Nucula*) (Daley, 1972). The upper sublittoral was mainly inhabited by oysters, pectinids, *Cucullaea, Crassatellites, Pelecyora*, and other suspension-feeders (Daley, 1972; Thomsen, 1983).

Seas of the Eastern Atlantic and Western Mediterranean Realm of the Tethys (Spain, France, Italy, and North Africa), belonging to the tropical belt, contained bivalvian communities, which were more diverse than those in the boreal seas.

The marginal zone was inhabited by settlements of oysters (*Crassostrea, Cubitostrea*, and *Ostrea*), often building banks. Infaunal suspension-feeders with siphons (*Trachycardium, Nemocardium, Venus, Meretrix, Callista, Corbula*, and *Panopea*); epibyssal *Brachidontes*; epi- and/or semi-infaunal carditids; cemented *Anomia*; semi-infaunal *Glycymeris*; and suspension-feeders with a mucous tubule (*Lucina* and *Diplodonta*) were common.

The coastal zone also commonly contained the oysters *Ostrea* and *Pycnodonte, Ostrea* usually building banks. Other cemented bivalves (*Spondylus*) were also typical. Semi-infaunal *Glycymeris*, epibyssal *Barbatia* and *Chlamys*, epibyssal or free-lying *Lentipecten*, infaunal or semi-infaunal *Crassatella*, and infaunal siphonate *Venus* were common. Representatives of other ethological-trophic groups were rare.

The shallow shelf was inhabited by numerous and very diverse bivalves, mainly suspension-feeders, both epifaunal and infaunal. Epifaunal suspension-feeders included cemented oysters (*Ostrea* and others), *Spondylus, Chama*, and *Anomia*; epifaunal and/or free lying taxa (*Chlamys, Pecten*, and *Lentipecten*); epi- and/or endobyssal (*Musculus* and *Cucullaea*); endobyssal (*Limopsis, Modiolus*, and *Pinna*), epibyssal (*Arca, Barbatia, Pteria, Cardita*, and *Arcopsis*), and semi-infaunal bivalves lacking byssus (*Glycymeris*); infaunal siphonate shallowly burrowing bivalves (*Callista, Pelecyora, Pitar, Meretrix, Trachycardium*, and *Nemocardium*) and deeply burrowing taxa (*Solecurtus, Solen, Panopea, Pholadomya*, and *Thracia*); infaunal, semi-infaunal, or epifaunal bivalves lacking siphons (*Crassatella*) and those feeding through the inhalant mucous tubule (*Lucina*) (Piccoli and Massari, 1968; Plaziat, 1970; Gaemers, 1978; Savazzi, 1982; Piccoli and Savazzi, 1983).

Coral-reef buildups at depths of about 50 m were inhabited by cemented oysters and *Spondylus*, byssal pectinids, boring, and other bivalves (Gaemers, 1978; Martinius and Molenaar, 1991).

In platform and marginal seas of the Tethys, situated in the regions of present-day Eastern Europe and Western Asia, and also belonging to the tropical belt, lagoons were inhabited by euryhaline epifaunal (*Brachidontes* and *Anomia*) and infaunal (*Corbicula*) suspension-feeders.

The coastal zone was inhabited by epifaunal and semi-infaunal suspension-feeders (*Arca, Cucullaea*, and *Glycymeris*), the cemented suspension-feeder *Anomia*, infaunal suspension-feeders (*Corbula, Crassatella, Panopea, Taxivenus*, etc.), and debris-feeders (*Nucula, Nuculana*, and *Arcopagia*). In places, oysters (*Ostrea, Amphidonte, Gryphaea, Cubitostrea*, etc.) formed banks (Figs. IX. 62, IX. 63). Hardgrounds were inhabited by oysters and the boring bivalves *Lithophaga*.

Sandy and sandy-muddy substrates of the shallow shelf were inhabited by abundant and diverse bivalves. Among the suspension-feeders, cemented bivalves (*Ostrea, Anomia, Spondylus*, and *Chama*), byssal and/or free-lying bivalves (*Chlamys* and *Lima*), epi- and/or endobyssal (*Musculus* and *Cucullaea*), epibyssal (*Arca, Barbatia, Cardita*, and *Pteria*), endobyssal (*Modiolus, Pinna*, and *Limopsis*), infaunal siphonate, shallow burrowing (*Callista, Pelecyora*, and *Trachycardium*) and deeply burrowing (*Pholadomya, Cultellus, Thracia*, and *Panopea*), and infaunal bivalves with a mucous inhalant tubule (*Lucina* and *Linga*) were present. Debris-feeders were represented by the genera *Nucula, Nuculana*, and tellinids.

The deep shelf was mainly inhabited by suspension-feeders, including epifaunal bivalves capable of swimming (*Propeamussium, Palliolum, Lentipecten*, and *Limatula*); the epifaunal, free-lying *Pycnodonte*; semi-infaunal bivalves (*Limopsis* and *Bathyarca*); infaunal bivalves with an inhalant mucous tubule (*Thyasira, Megaxinus*, and *Goniomyrtea*); infaunal debris-feeders (*Nuculana, Nucula*); and predators, such as *Cardiomya* (Liverovskaya, 1953; Kulichenko, 1959, 1967; Hecker *et al.*, 1962; Tolstikova, 1964, 1967; Kuchuloriya, 1964; Alizade *et al.*, 1968, 1980; Merklin, 1969; Didkovskii *et al.*, 1971; Makarenko, 1971; Moroz and Savron', 1975; Kuznetsov *et al.*, 1979; Kecskeméthiné, 1990; Popov *et al.*, 1993).

In the Oligocene, the Paratethys (an epicontinental basin with a changeable salinity) developed on the northern margin of the Tethys (Popov *et al.*, 1993).

In times when normal salinity predominated, the open parts of the basin, lagoons, and brackish-water coastal zones were inhabited by euryhaline marine bivalves, mainly infaunal suspension-feeders, including *Sphenia, Lentidium, Ensis*, and *Pygocardia* (Early Oligocene); and *Cerastoderma, Pygocardia, Corbula*, and *Lentidium* (Late Oligocene).

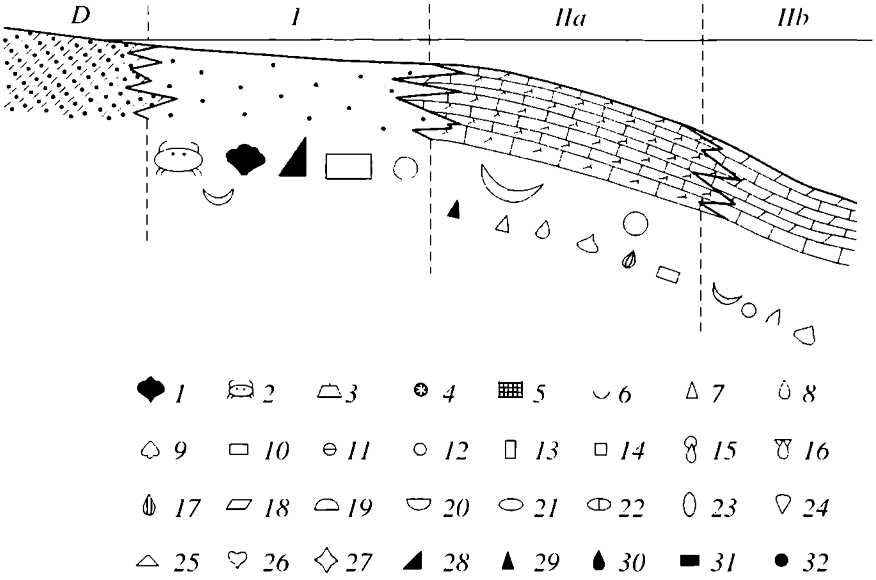


Fig. IX. 62. Scheme of the zonal distribution of sediments, fauna, and flora in Middle Suzak Time (Paleogene) in the Fergana Bay (after Hecker *et al.*, 1962, text-fig. 62): (*D*) deltoidal redbed rocks, (*I*) coastal zone (gravel, sand, terrigenous-carbonate sediments); (*II*) shallow shelf: (*IIa*) upper part (detrital, oolitic, foraminiferal carbonates, oyster banks, and coquinas), (*IIb*) lower part (fine-grained carbonate, dolomite-carbonate, and silty-carbonate muddy sediment); (*1*) calcareous algae; (*2*) burrowing crustaceans; (*3*) *Balanus*; (*4*) sea urchins; (*5*) bryozoans; (*6*) oysters; (*7, 28, 29*) gastropods; and (*8–27, 30–32*) bivalves: (*8*) "*Meretrix*," (*9*) *Cardita*, (*10*) *Panopea*, (*11*) lucinids, (*12*) *Glycymeris*, (*13*) *Perna*, (*14*) *Arctica*, (*15*) *Glossus*, (*16*) pectinids, (*17*) cardiids, (*18*) *Tellina*, (*19*) *Corbula*, (*20*) *Modiolus*, (*21*) *Nuculana*, (*22*) *Cucullaea*, (*23*) *Nucula*, (*24*) *Crassatella*, (*25*) *Arca*, (*26*) "*Modiolus*" *jeremejevi*, (*27*) *Cuneocorbula*, (*30*) "*Meretrix*" *tschangirtaschensis*, (*31*) *Unio*, and (*32*) *Diplodonta* aff. *renulata*. Blackened symbols indicate inhabitants of zones with decreased salinity; dotted symbols show euryhaline taxa, and blank symbols show polyhaline taxa.

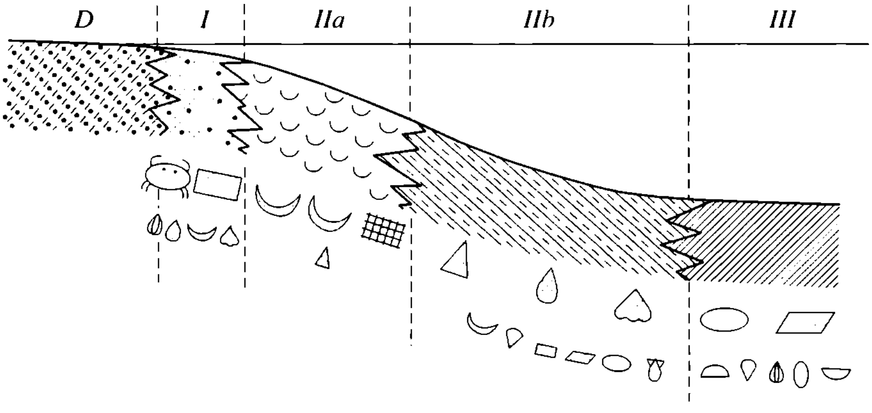


Fig. IX. 63. Scheme of the zonal distribution of sediments and fauna in Early Turkestan Tjme (Paleogene) in the Fergana Bay (after Hecker *et al.*, 1962, text-fig. 74): (*IIa*) upper part of the shallow shelf (oyster beds); (*IIb*) lower part of the shallow shelf (silty-clayey muddy substrates); and (*III*) relatively deep shelf (fine clayey and muddy substrates). For other designations, see Fig. IX. 62.

In environments of normal salinity, the coastal zones with coarse sand substrates were inhabited by suspension-feeders, including the cemented *Ostrea* and *Anomia*, the epifaunal free-lying *Pecten*, the semi-infaunal *Glycymeris*, the infaunal *Crassatella* lacking siphons, the shallowly burrowing siphonate *Corbula*, *Lentidium*, *Pelecyora*, *Venus*, *Callista*, *Parvicardium*, and *Nemocardium*, the deeply burrowing siphonate *Pholadomya*, *Ensis*, and *Panopea*, infaunal bivalves with an anterior inhalant mucous tubule (*Linga* and *Lucinoma*), and infaunal siphonate debris-feeders, such as *Nuculana* (Baldi, 1973; Popov *et al.*, 1993).

The taxonomic and trophic composition on the shallow shelf was similar. This zone was inhabited by suspension-feeders, including infaunal siphonate shallowly burrowing (*Callista*, *Nemocardium*, *Parvicardium*, *Glossus*, *Corbula*, *Pelecyora*, *Dosiniopsis*, *Astarte*, *Lentidium*, etc.) and deeply burrowing taxa

(*Cultellus, Ensis, Solecurtus, Pholadomya, Thracia,* and *Panopea*); epi- or semi-infaunal siphonate *Arctica*; epibyssal and/or free-lying taxa (*Chlamys, Palliolum,* and *Pecten*); the epibyssal *Pteria* and *Mytilus*; the semi-infaunal and nonsiphonate *Glycymeris* and *Atrina*; the infaunal, semi- or epifaunal, *Cardites* lacking siphons; infaunal bivalves feeding through a mucous tubule (*Pterolucina* and *Lucinoma*); infaunal debris-feeders with siphons (*Nuculana, Macoma,* and *Angulus*) and those lacking siphons (*Nucula*). The community also contained predators (*Cuspidaria*) and cemented (*Ostrea*) and free-lying suspension-feeders (*Pycnodonte*) (Kulichenko, 1959; Kazakhishvili, 1969; Merklin, 1969; Zosimovich, 1971; Didkovskii *et al.*, 1971; Baldi, 1973; Belen'kaya, 1974; Popov *et al.*, 1993).

The deep areas of the Oligocene Paratethys were, in periods of normal salinity, inhabited by debris-feeders, such as *Nucula, Nuculana, Malletia, Yoldia, Yoldiella, Macoma,* and *Abra*. Infaunal siphonate suspension-feeders were represented by the genera *Pholadomya, Laternula, Corbula,* and *Nemocardium*; suspension-feeders with a mucous tubule were represented by *Saxolucina, Gibbolucina, Thyasira, Lucinoma, Goniomyrtea,* and *Pterolucina*. Epifaunal bivalves capable of swimming (*Palliolum, Pseudoamussium, Propeamussium,* and *Lentipecten*) were common. Epi- and/or endobyssal bivalves lacking siphons or with short siphons (*Bathyarca*) and infaunal, epi- or semi-infaunal, taxa lacking siphons (*Cardites*) were typical, whereas free-lying or cemented suspension-feeders (*Spondylus* and *Pycnodonte*) and predators (*Cuspidaria*) were less common (Merklin, 1969; Baldi, 1973; Popov *et al.*, 1993).

In periods of decreased salinity, shelf communities of the entire basin were dominated by euryhaline marine bivalves, including infaunal suspension-feeders (*Sphenia, Lentidium, Cyrtodaria, Pelecyora, Callista, Panopea, Corbula,* etc.).

In periods of the lowest salinity, the semiclosed Eastern Paratethys was predominantly inhabited by species of brackish-water, endemic, and specific genera, including infaunal siphonate suspension-feeders (*Rzehakia, Urbnisia, Ergenica, Korobkoviella,* and *Merklinicardium*); epibyssal suspension-feeders (*Congeria*); and some euryhaline marine shallowly burrowing siphonate suspension-feeders, including *Cerastoderma, Corbula, Lentidium,* and *Janschinella* (Kazakhishvili, 1984; Popov *et al.*, 1985, 1993; Gontsharova, 1987; Popov *et al.*, 1989).

In the marginal seas of the Western Pacific (Russian Far East and Japan), belonging to the boreal belt, the coastal lagoons were inhabited by numerous cemented *Ostrea* in association with the epibyssal *Mytilus*, the semi-infaunal *Modiolus* and infaunal suspension-feeders (*Spisula, Solen,* and *Pitar*), and debris-feeders (*Nuculana*) (Zhidkova *et al.*, 1974).

The upper sublittoral was inhabited by infaunal shallowly burrowing suspension-feeders with siphons (*Spisula, Mactra, Pitar, Corbula, Nemocardium, Clinocardium,* and *Venericardia*), deeply burrowing suspension-feeders (*Solen, Cultellus, Mya,* and *Pholadomya*), infaunal debris-feeders with siphons (*Nuculana, Yoldia, Macoma,* and *Tellina* sensu lato) and without siphons (*Acila*). Epifaunal pectinids (*Chlamys* and *Pecten*), limids (*Lima* and *Limatula*), oysters (*Ostrea*), semi-infaunal bivalves (*Pinna*), and infaunal bivalves with an inhalant tubule (*Diplodonta*) were less abundant (Zhidkova *et al.*, 1974; Piccoli and Savazzi, 1983).

Deeper parts of the sea (middle and lower sublittoral) were dominated by suspension-feeders with a mucous tubule (*Thyasira*), infaunal siphonate taxa (*Nemocardium, Clinocardium, Mya,* and *Laternula*), and debris-feeders *Yoldia, Acila, Nuculana, Malletia, Tellina* sensu lato, and *Macoma*, whereas the deepest known communities typically contained free-moving and swimming *Delectopecten* (Zhidkova *et al.*, 1974; Savitskii, 1979a, 1979b).

The shelf of northern seas of the Pacific coast (Alaska) was mainly inhabited by infaunal shallowly burrowing suspension-feeders with siphons (*Pitar, Cyclocardia, Liocyma, Clinocardium, ?Serripes, Spisula,* and *Hiatella*) and deeply burrowing suspension-feeders (*Mya*). Epifaunal suspension-feeders (*Crenella*) and infaunal debris-feeders (*Acila* and *Macoma*) were less common (Allison and Marincovich, 1981).

In the southerner regions (Oregon) infaunal suspension-feeders were present, including shallowly burrowing (*Parvicardium, Nemocardium, Macrocallista, Pitar, Spisula,* and *Diplodonta*) and deeply burrowing taxa (*Panopea, Pandora, Thracia,* and *Solen*), as well as infaunal debris-feeders, including siphonate taxa (*Nuculana, Tellina, Macoma,* and *Semele*) and those lacking siphons (*Acila*) (Hickman, 1969).

In the seas of the Pacific coast of southern North America, the Mexican Gulf coast and the Caribbean coast (tropical belt), lagoons with decreased salinity were inhabited by oysters *Crassostrea*, which formed small banks (Westgate and Gee, 1990). The upper and middle sublittorals were inhabited by infaunal suspension-feeders with siphons (*Macrocallista, Cyclocardia,* and *Thracia*) and lacking siphons (*Solemya*) and with a mucous inhalant tubule (*Thyasira* and *Lucinoma*) (Fig. IX. 64), and infaunal debris-feeders (*Nuculana, Macoma,* and *Acila*) (Watkins, 1974; Hickman, 1984). Places overgrown by red algae forming rhodolithes were inhabited by cemented oysters and the boring bivalves *Lithophaga*, and the cavities between rhodolithes were inhabited by the endobyssal *Chlamys* and *Lima* (Manker and Carter, 1987).

The lower sublittoral was inhabited by a protobranchian community, including infaunal taxa, which were dominated by *Nucula, Acila, Yoldia,* and *Nuculana*, while *Malletia, Sarepta,* and septibranchial predators (*Cardiomya*) were less common. Predatory scaphopods (*Cadulus*) were typically present (Fig. IX. 65). The

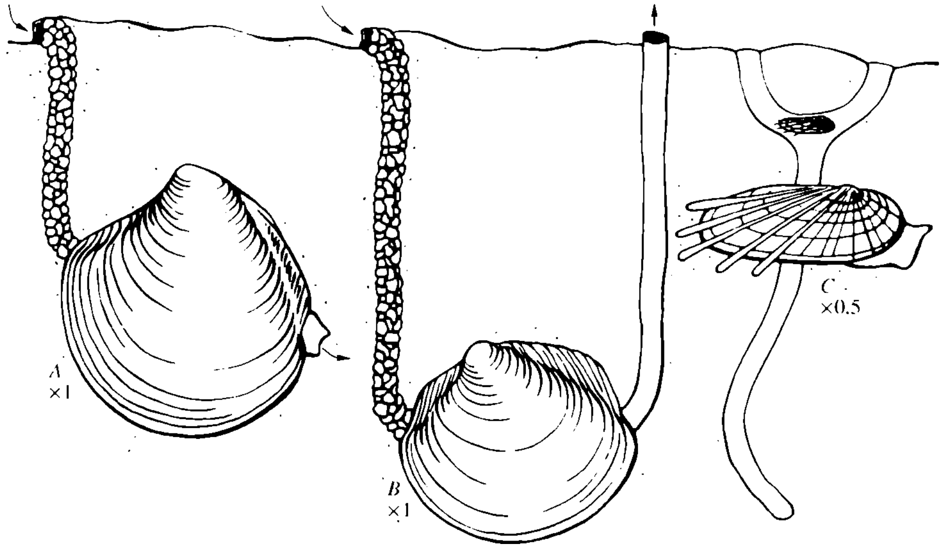


Fig. IX. 64. Reconstruction of the Paleogene community of bivalves of silty or diatom muddy substrates of the upper-middle sublittoral zone of the Pacific coast of North America (after Hickman, 1984, text-fig. 9): (*A*) *Thyasira*, (*B*) *Lucinoma*, and (*C*) *Solemya*.

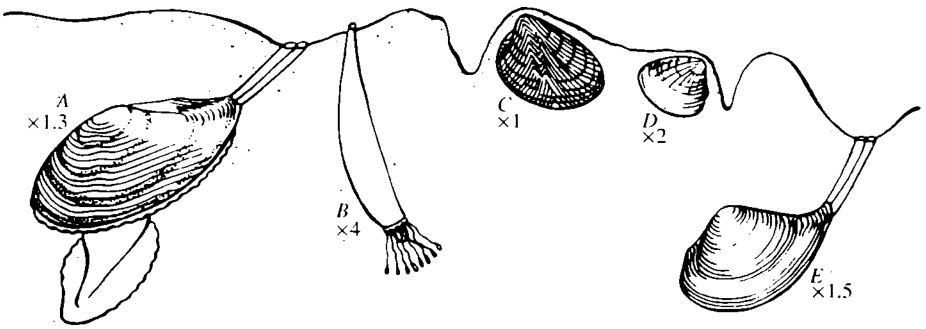


Fig. IX. 65. Reconstruction of the core of the Paleogene bivalvian community (Protobranchia) of silty and clayey muddy substrates of the deep shelf of the Pacific coast of North America (after Hickman, 1984, text-fig. 10): (*A*) *Yoldia*, (*C*) *Acila*, (*D*) *Nucula*, (*E*) *Nuculana*, and (*B*) scaphopods.

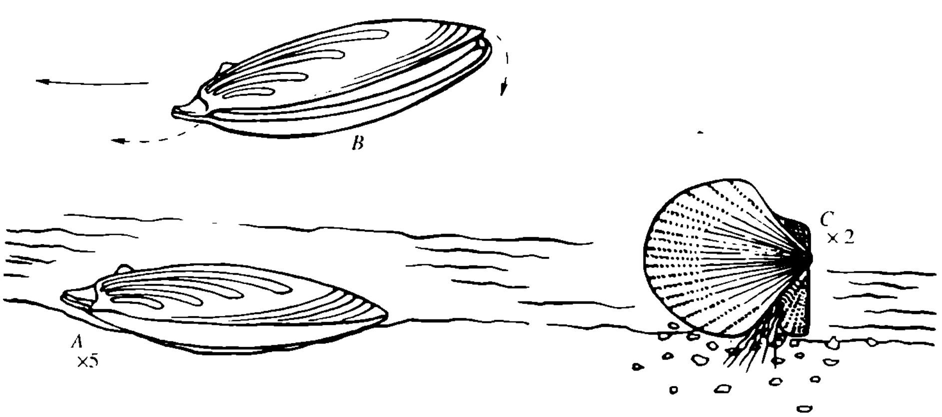


Fig. IX. 66. Reconstruction of the Paleogene community of pectinids of muddy substrates of the lower sublittoral zone of the Pacific coast of North America (after Hickman, 1984, text-fig. 8): (*A*) and (*B*) *Propeamussium*: (*A*) free-lying and (*B*) swimming, and (*C*) a thin-shelled byssal pectinid.

presence of pectinid communities, including the free-lying and swimming *Propeamussium* and *Delectopecten*, along with epibyssal taxa with a thin-walled shell, was typical (Fig. IX. 66). These taxa lived in association with infaunal suspension-feeders (*Thyasira*) and debris-feeders (*Yoldia*, Nuculanidae) (Watkins, 1974; Hickman, 1984).

It is noteworthy to mention an occurrence of bivalvian association in the Paleogene (Eocene) of the State of Washington, which was part of a community settled around a cold source in the sea bottom, living by chemosynthesis (symbiosis with chemoautotrophic sulfide-oxidizing bacteria). These taxa included species of the genera *Epilucina*, *Thyasira*, and *Vesicomya* (Squires and Gring, 1996).

Neogene

The Miocene and Pliocene seas were dominated by the same families of suspension-feeders, including infaunal shallowly burrowing bivalves with siphons (Veneridae, Cardiidae, and Mactridae); infaunal taxa feeding through a mucous tubule (Lucinidae and Ungulinidae); epi- or endobyssal taxa (Mytilidae); epibyssal and/or free-lying taxa sometimes capable of swimming (Pectinidae and Limidae); boring bivalves Pholadidae; epibyssal, and/or free lying, and/or semi-infaunal, and/or shallowly burrowing infaunal taxa lacking siphons (Carditidae, Condylocarditidae, and Erycinidae); and infaunal debris-feeders with siphons (Tellinidae and Nuculanidae).

The Atlantic coast of southern North America, the Mexican Gulf, and Caribbean Sea (Tropical Realm) were characterized by coral reefs inhabited by epibyssal bivalves (*Pteria*, *Chlamys*, *Arcopsis*, and *Carditomera*), and cemented taxa (*Anomia*, *Ostrea*, and *Plicatula*), whereas spaces between reefs with a soft substrate were inhabited by the semi-infaunal *Modiolus* and *Noetia*; infaunal siphonate bivalves (*Astarte*, *Eucrassatella*, *Crassinella*, *Panopea*, *Corbula*, *Dosinia*, *Chione*, *Mercenaria*, and *Ensis*); taxa lacking siphons (*Cyclocardia*); bivalves with a mucous inhalant tubule (*Lucina*, *Lucinoma*, *Parvilucina*, and *Diplodonta*); and infaunal debris-feeders (*Nuculana*, *Nucula*, *Semele*, *Asaphis*, *Cumingia*, *Tellina*, and *Abra*) (Fig. IX. 67, *II*, *III*).

The shallow shelf adjacent to the reef buildups was inhabited by suspension-feeders, including epifaunal taxa (*Pteria*, *Chlamys*, *Chesapecten*, *Placopecten*, and *Arcopsis*); epi- and/or endobyssal taxa (*Isognomon*); semi-infaunal taxa (*Glycymeris*, *Atrina*, and *Modiolus*); cemented (*Plicatula*) and living in shelters and/or semi-infaunal bivalves (*Anadara*, *Carditomera*, and *Hiatella*); infaunal siphonate shallowly burrowing (*Astarte*, *Eucrassatella*, *Crassatella*, *Crassinella*, *Mulinia*, *Rangia*, *Spisula*, *Ensis*, *Mercenaria*, *Chione*, *Callista*, *Dosinia*, *Corbula*, *Glossus*, etc.) and deeply burrowing taxa (*Panopea*); infaunal taxa lacking siphons (*Cyclocardia*); infaunal taxa with a mucous inhalant tubule (*Lucinoma*, *Lucina*, *Parvilucina*, and *Diplodonta*); and infaunal debris-feeders (*Gari*, *Asaphis*, *Macoma*, *Semile*, *Tellina*, *Cumingia*, *Abra*, *Nucula*, *Nuculana*, and *Yoldia*) (Fig. IX. 67, *I*, *IV*, *V*) (Bailey and Tedesco, 1986; Ketcher and Allmon, 1993).

In the Miocene, in the Mediterranean–East Atlantic Region situated between the boreal and tropical belts, the marginal and coastal zones were inhabited by the oysters *Crassostrea* and *Ostrea*, which built banks. This area was also inhabited by cemented *Anomia*; epibyssal *Mytilus* (also building banks), *Mytilaster*, *Brachidontes*, and *Arcopsis*; endobyssal *Modiolus*; infaunal siphonate debris-feeders *Sanguinolaria* and *Sphenia*; and infaunal bivalves feeding through a mucous tubule (*Loripes* and *Divaricella*). Boring bivalves *Lithodomus*, *Hiatella*, *Aspidopholas*, *Jouannetia*, *Lithophaga*, and *Gastrochaena* lived near the rocky coasts on pebbly substrate.

The shallow shelf was inhabited by suspension-feeders, including the cemented *Crassostrea*, *Neopycnodonte*, *Ostrea* (all these bivalves could build banks), *Anomia*, *Chama*, *Spondylus*, and *Hyotissa*; epifaunal, byssal and/or free-lying taxa (*Chlamys*, *Lentipecten*, *Pecten*, *Aequipecten*, *Amussium*, *Lima*, *Limaria*, etc.); epibyssal taxa (*Mytilus*, *Mytilaster*, *Barbatia*, and *Cardita*); endobyssal bivalves (*Modiolus* and *Pinna*); semi-infaunal *Glycymeris* and *Scalaricardita*; epi- and/or endobyssal *Isognomon*; infaunal shallowly burrowing siphonate bivalves (*Ervilia*, *Pelecyora*, *Callista*, *Venus*, *Clausinella*, *Venerupis*, *Timoclea*, *Dosinia*, *Acanthocardia*, *Parvicardium*, *Laevicardium*, *Cerastoderma*, *Glossus*, *Mactra*, *Lutraria*, and *Corbula*); deeply burrowing siphonate bivalves (*Panopea* and *Solen*); infaunal bivalves feeding through an inhalant mucous tubule (*Loripes*, *Linga*, *Divaricella*, *Lucinoma*, *Megaxinus*, and *Diplodonta*); infaunal, epi- or endobyssal, or free-lying nonsiphonate *Anadara*; infaunal shallowly burrowing, or epifaunal free-lying bivalves with siphons, or without those (*Lutetia*); and infaunal debris-feeders (*Nuculana*, *Nucula*, *Macoma*, *Abra*, *Moerella*, and *Peronaea*). Thickets of coralline algae contained epifaunal *Chlamys* and *Flabellipecten* and boring bivalves *Gastrochaena*, *Aspidopholas*, and *Lithophaga*.

Bivalves inhabiting the zone of organic buildups (reefs) composed of corals, red algae, bryozoans, and serpulids were mostly represented by suspension-feeders, including infaunal cemented bivalves (*Ostrea*, *Chama*, *Neopycnodonte*, *Spondylus*, and *Plicatula*); epibyssal bivalves (*Chlamys*, *Barbatia*, *Lima*, and *Musculus*); and boring bivalves (*Lithophaga*, *Jouannetia*, and *Gastrochaena*). Infaunal and semi-infaunal suspension-feeders and debris-feeders were rare.

The deep zones of shelf were inhabited by epibyssal or free-lying bivalves and those capable of swimming (*Lentipecten*, *Amussium*, *Chlamys*, *Palliolum*, *Propeamussium*, and *Limaria*); free-lying or cemented *Neopy-*

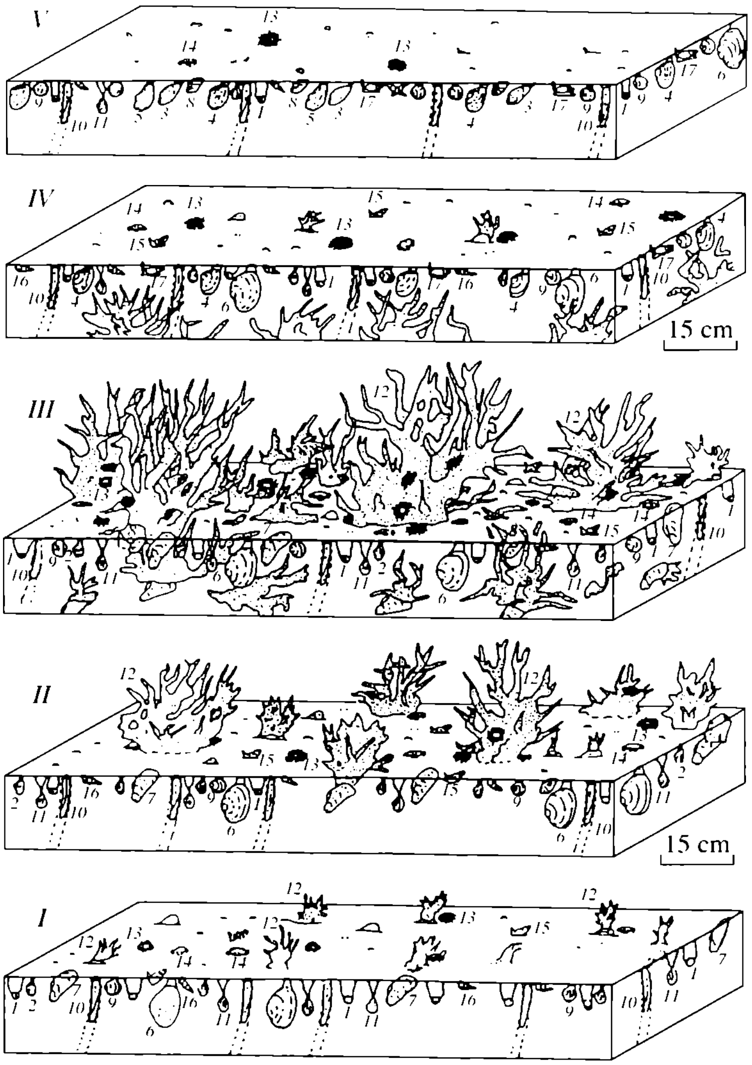


Fig. IX. 67. Change in the composition of Pliocene communities following the development of the coral settlement in the shallow water zone nearby the Atlantic coast of the southern North America (after Bailey and Tedesco, 1986, text-fig. 13): (*I*) initial stage of colonization by corals of bivalvian settlement, (*II*) early stage of the development of the coral aggregations, (*III*) stage of the maximum development of the coral aggregations, (*IV*) stage of the reduction of the coral settlements, and (*V*) stage of the maximum development of the bivalvian settlement: (*1–11*) bivalves: (*1*) *Parvilucina*, (*2*) *Caryocorbula*, (*3*) *Macrocallista*, (*4*) *Spisula*, (*5*) *Crassatella*, (*6*) *Mercenaria*, (*7*) *Modiolus*, (*8*) *Noetia*, (*9*) *Cyclocardia*, (*10*) *Ensis*, (*11*) *Cumingia*; (*12*) corals; (*13*) sea urchins; (*14*) decapods; and (*15–17*) gastropods.

cnodonte; infaunal siphonate bivalves (*Corbula*, *Venus*, and *Thracia*); infaunal bivalves with a mucous tubule (*Thyasira* and *Linga*); and infaunal debris-feeders (*Nuculana*, *Nucula*, and *Abra*) (Kazakova, 1952; Seneş, 1958; Baldi, 1959, 1961, 1986; Kudrin, 1966; Baluk and Radwanski, 1968, 1977, 1984; Bohn-Havas, 1973, 1984, 1985; Kojumdgieva, 1976a, 1976b; Hoffman, 1977, 1979; Hoffman *et al.*, 1978; Bosence and Pedley, 1982, 1992; Dabrio *et al.*, 1982; Demarcq *et al.*, 1983; Demarcq, 1984; Saint-Martin *et al.*, 1985; Freneix *et al.*, 1988; Braga and Martin, 1988; Agusti *et al.*, 1990; Demarcq and Demarcq, 1990; Braga *et al.*, 1990; Jimenez *et al.*, 1991).

In the Pliocene, the marginal zones of seas in this region were typically inhabited by infaunal suspension-feeders (*Cerastoderma*, *Corbula*, and *Tapes*) and debris-feeders with siphons (*Scrobicularia*, *Gastrana*, and *Angulus*), whereas in the coastal zone, suspension-feeders were represented by infaunal siphonate taxa (*Mactra*, *Spisula*, *Lutraria*, *Chamelea*, *Venus*, *Gouldia*, *Dosinia*, *Pitar*, *Acanthocardia*, *Laevicardium*, *Parvicardium*, *Corbula*, *Astarte*, and *Solen*) and bivalves with a mucous tubule (*Divaricella*, *Myrtea*, *Lucinoma*, and *Diplodonta*), epifaunal byssal and/or free-lying bivalves (*Chlamys*, *Pecten*, *Palliolum*, *Lima*, *Limaria*, and *Arca*), and semi-infaunal taxa (*Glycymeris*). Infaunal debris-feeders (*Gari, Abra, Moerella, Peronaea, Arcopagia*, and *Donax*) were diverse.

On the shallow shelf, communities consisted of suspension-feeders, including infaunal siphonate shallowly (*Astarte, Corbula, Acanthocardia, Laevicardium, Parvicardium, Pygocardia, Spisula, Mactra, Callista, Venus, Gouldia, Pitar*, and *Dosinia*) and deeply burrowing (*Solen*) bivalves; infaunal taxa with an inhalant mucous tubule (*Loripes* and *Myrtea*); semi-infaunal taxa lacking siphons and byssus (*Glycymeris*); epibyssal and/or free-lying bivalves (*Pecten, Chlamys, Palliolum, Lima, Limaria*, and *Arca*); and also infaunal debris-feeders with siphons (*Gastrana, Moerella, Abra, Gari*, and *Donax*) (Marasti, 1990, 1991; Benevenuti and Dominici, 1992).

In the semimarine seas of the Easter Paratethys, which were in the boreal belt in the second half of the Middle and Late Miocene and Pliocene, the marginal and coastal zones were dominated by infaunal shallowly burrowing siphonate suspension-feeders (*Cerastoderma, Obsoletiformes, Corbula, Ervilia, Mactra, Parvivenus*, and *Venerupis*); possessors of an inhalant mucous tubule (*Loripes*); and by the epibyssal *Musculus* and *Mytilaster.* In places, there were banks of oysters *Crassostrea* and *Ostrea*. In brackish water basins, the place of mytilids was occupied by dreissenids (*Congeria* and *Dreissena*), whereas infaunal suspension-feeders were represented by endemic genera of the family Cardiidae.

The shallow shelf of the semimarine seas was dominated by species of the same genera (*Cerastoderma, Obsoletiformes, Mactra, Ervilia, Venerupis, Parvivenus, Mytilaster, Loripes*, and *Crassostrea*), in association with the infaunal debris-feeders *Abra* and *Donax*. Communities of the brackish-water basins consisted of the infaunal and epifaunal Cardiidae (subfamily Limnocardiinae).

Buildups of lithotamnians, bryozoans, and serpulids in semimarine basins were inhabited by *Venerupis, Mytilaster*, and *Musculus*; and endemic cardiid genera (*Kubanocardium, Aviculocardium, Planacardium*, and *Obsoletiformes*).

The lower sublittoral was inhabited by infaunal suspension-feeders, including the infaunal siphonate euryhaline *Ervilia, Mactra, Venerupis*, and endemic genera (*Cryptomactra, Inaequicostates, Obsoletiformes*, and *Plicatiformes*); the epi- and/or endobyssal *Musculus*; and euryhaline debris-feeders, such as *Abra*. Brackish-water basins with this environment were inhabited only by suspension-feeders (byssal or free-lying Dreissenidae) (Merklin, 1950, 1969; Bagdasaryan, 1965, 1970, 1983; Hinkulov *et al.*, 1973; Kojumdgieva, 1976c, 1976d; Nevesskaja *et al.*, 1986, 2001; Gontsharova, 1989; Popov *et al.*, 1993a, 1993b; Paramonova, 1994).

In the Miocene, in the seas of the Far East, Japan, and the Pacific coast of northern North America, which was situated in the boreal belt, the marginal and coastal zones were inhabited by the bank-building oyster *Crassostrea*. *Ostrea* and other suspension-feeders, including the epibyssal *Crenomytilus, Chlamys*, and *Swiftopecten*; the endobyssal *Modiolus*; and the infaunal siphonate *Corbula, Mya, Mactra, Spisula*, and *Liocyma* were present in association with infaunal debris-feeders (*Macoma*) (Fig. IX. 68b). In the Pliocene, epibyssal and/or free-lying *Fortipecten* were abundant (Fig. IX. 68c).

On the shallow shelf in the Early Miocene, suspension-feeders were dominant and included epifaunal byssal or free-lying *Chlamys* and *Mizuhopecten*; epibyssal *Mytilus*; infaunal siphonate deeply burrowing (*Mya, Thracia*, and *Laternula*) and shallowly burrowing bivalves (*Clinocardium, Nemocardium, Spisula*, and *Pitar*); bivalves with a mucous inhalant tubule (*Thyasira*); endobyssal *Modiolus*; and infaunal debris-feeders with siphons (*Nuculana, Yoldia, Malletia, Macoma, Peronidia*, and *Tellina*) and those lacking siphons (*Acila*).

In the Middle and Late Miocene and Pliocene, the shallow shelf, apart from the genera mentioned as typical for the Early Miocene, was inhabited by suspension-feeders, including the infaunal *Cyclocardia* (lacking siphons), infaunal siphonate shallowly burrowing bivalves (*Liocyma, Dosinia, Mercenaria, Chione, Protothaca, Pseudoamianthis, Laevicardium, Serripes, Astarte*, and *Mactra*), deeply burrowing taxa (*Cryptomya, Panopea*, and *Siliqua*), taxa with an inhalant mucous tubule (*Lucinoma*), epibyssal taxa (*Arca, Swiftopecten*, and *Crenomytilus*), semi-infaunal *Glycymeris*, and epi- and/or endobyssal or shallowly burrowing or free-lying *Anadara*. Debris-feeders were represented by bivalves lacking siphons (*Nucula*) (Fig. IX. 68c).

On the deep shelf, bivalve communities of the Early Miocene included infaunal debris-feeders with siphons (*Nuculana, Yoldia, Megayoldia, Saccella, Malletia, Portlandia, Tellina*, and *Macoma*) and lacking siphons (*Solemya, Acila*, and *Nucula*) and suspension-feeders, including infaunal bivalves lacking siphons *Cyclocardia*, siphonate taxa (*Clinocardium, Laterunula, Panopea*, and *Mya*), bivalves with a mucous tubule (*Lucinoma* and *Thyasira*), epibyssal or free-lying and capable of swimming (*Delectopecten, Limatula*, and *Lima*) (Chinzei and Iwasaki, 1967; Zhidkova *et al.*, 1968, 1974; Gladenkov, 1969, 1972; Iwasaki, 1970; Salin, 1972; Chinzei, 1978, 1984; Ogasawara and Naito, 1983; Yoshida, 1987; Amano and Kanno, 1991; Suzuki *et al.*, 1992; Nobuhara, 1992; Honda, 1992; Taguchi, 1992; Marinkovith and Morija, 1992).

Neogene boreal seas of the Far East had characteristic changes of climate, causing alternations between cryophilic and thermophilic assemblages (Kafanov, 1979; Gladenkov, 1987; Gladenkov and Sinel'nikova, 1990, 1991).

In the seas of Japan, Korea and the Pacific coast of North America, which were in the Tropical-Subtropical Region, the composition of bivalves was somewhat different (Fig. IX. 68a). Areas near the shore, in the zone adjacent to the mangroves, contained banks built by *Crassostrea* and *Ostrea*. The coastal shallow-water

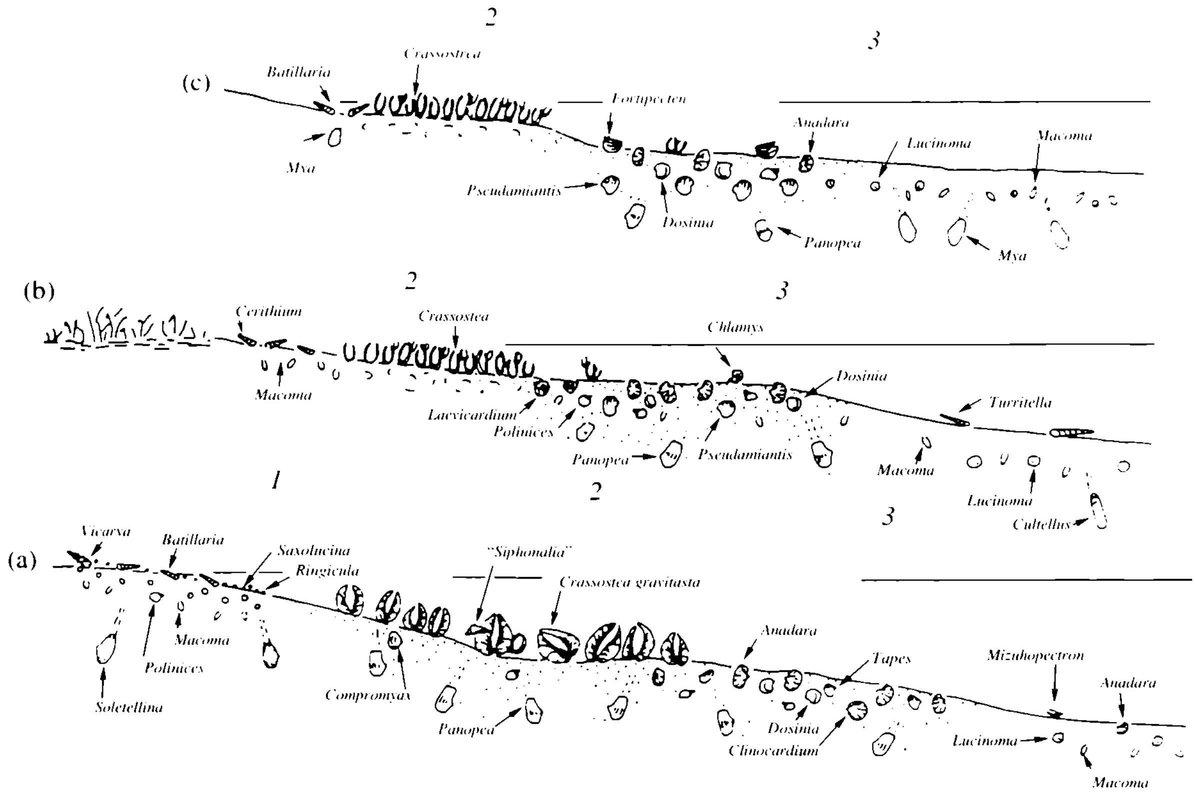


Fig. IX. 68. Distribution of mollusks in the basins: (a) Kadonozava (beginning of the Middle Miocene, Kadonozava Fauna); (b) Tanacura (Late Miocene, Shiobara Fauna); and (c) Sendai (Late Pliocene, Tatsunokusi Fauna); (*1*) tidal zone, (*2*) coastal zone, and (*3*) shallow shelf (after Chinzei, 1978, text-fig. 7).

zone and marginal zone were inhabited by cemented *Crassostrea* and *Chama*, epibyssal taxa (*Chlamys, Nanaochlamys, Striarca*, and *Mytilus*), the free-lying *Pecten*, the semi-infaunal *Glycymeris*, diverse infaunal suspension-feeders with siphons (*Dosinia, Protothaca, Trapezium, Solen, Vasticardium*, etc.) and with a mucous inhalant tubule (*Felaniella, Lucinoma, Saxolucina*, and *Megaxinus*), and bivalves lacking siphons (*Cyclocardia*). Infaunal debris-feeders with siphons (*Macoma, Tellina, Soletellina, Nuculana*, and *Yoldia*) and those lacking siphons (*Acila*) were less common.

In the Pliocene, the coastal zone was dominated by suspension-feeders, including the epifaunal *Pecten*, the semi-infaunal *Glycymeris*, the epi- and/or endobyssal and/or shallowly burrowing *Anadara*, and infaunal bivalves lacking siphons (*Cyclocardia*).

The shallow shelf in the Miocene was dominated by suspension-feeders, including cemented bivalves (*Ostrea, Crassostrea*, and *Chama*); epibyssal forms, and/or bivalves capable of swimming (*Chlamys, Nanaochlamys, Placopecten, Palliolum, Propeamussium, Mizuhopecten*, and *Lima*); the epibyssal or free-lying *Pecten*; the endobyssal *Limopsis*; the semi-infaunal *Glycymeris*; the epi- and/or endobyssal and/or shallowly burrowing *Anadara*; infaunal, shallowly burrowing bivalves with siphons (*Clinocardium, Nemocardium, Vasticardium, Dosinia, Pitar, Paphia, Venus, Clementia*, etc.) and those lacking siphons (*Cyclocardia*); deeply burrowing, siphonate taxa (*Panopea, Cultellus, Solen*, and *Thracia*); and bivalves with a mucous inhalant tubule (*Lucinoma* and *Felaniella*). The most common debris-feeders were *Macoma, Saccella*, and *Acila*. In the Pliocene, the shallow shelf was also typically inhabited by infaunal shallowly burrowing venerids (*Venus* and others) and cardiids (*Nemocardium* and others) and semi-infaunal bivalves lacking a byssus (*Glycymeris*).

The deepwater shelf in the Miocene and Pliocene was inhabited by infaunal debris-feeders with siphons (*Yoldia, Portlandia, Nuculana, Malletia*, and *Macoma*) and suspension-feeders, including the deeply burrowing *Cultellus* and *Periploma*, infaunal bivalves with a mucous inhalant tubule (*Lucinoma* and *Conchocele*), epifaunal byssal or free lying bivalves capable of swimming (*Delectopecten* and *Propeamussium*), the endobyssal *Limopsis*, and the epi- and/or endobyssal *Bathyarca* (Chinzei and Iwasaki, 1967; Iwasaki, 1970; Chinzei, 1978, 1984; Ogasawara and Naito, 1983; Colbath, 1985; Yoshida, 1987; Ueda, 1991; Amano and Kanno, 1991; Suzuki *et al.*, 1992; Lee, 1992; Nobuhara, 1992; Honda, 1992; Taguchi, 1992).

(2) Changes in the Ethological-Trophic Composition of Communities of Different Zones of the Sea in the Phanerozoic

The general trend of change in the ethological-trophic groups in the Phanerozoic seas discussed above was also reflected in changes in the ethological-trophic composition in different zones of the sea.

In the marginal zone (lagoons, gulfs, and deltas) in extreme environments with a changeable salinity, subject to increase or decrease, the communities were not diverse and had an impoverished composition.

In this zone, from the Early and Middle Paleozoic, up to and including the Devonian only epi- and/or endobyssal suspension-feeders (I.2.1/I.3.1) played an important role, while infaunal suspension-feeders lacking siphons (I.1.1) and with short siphons (I.1.3) and debris-feeders lacking siphons (II.1) and siphonate debris-feeders (II.2) (the latter only from the Early Silurian) were moderately common. Beginning with the Carboniferous, the epibyssal suspension-feeders (I.2.1) became dominant. They retained their importance later on. Other groups were represented by a small number of genera. In the Mesozoic, along with epibyssal taxa,

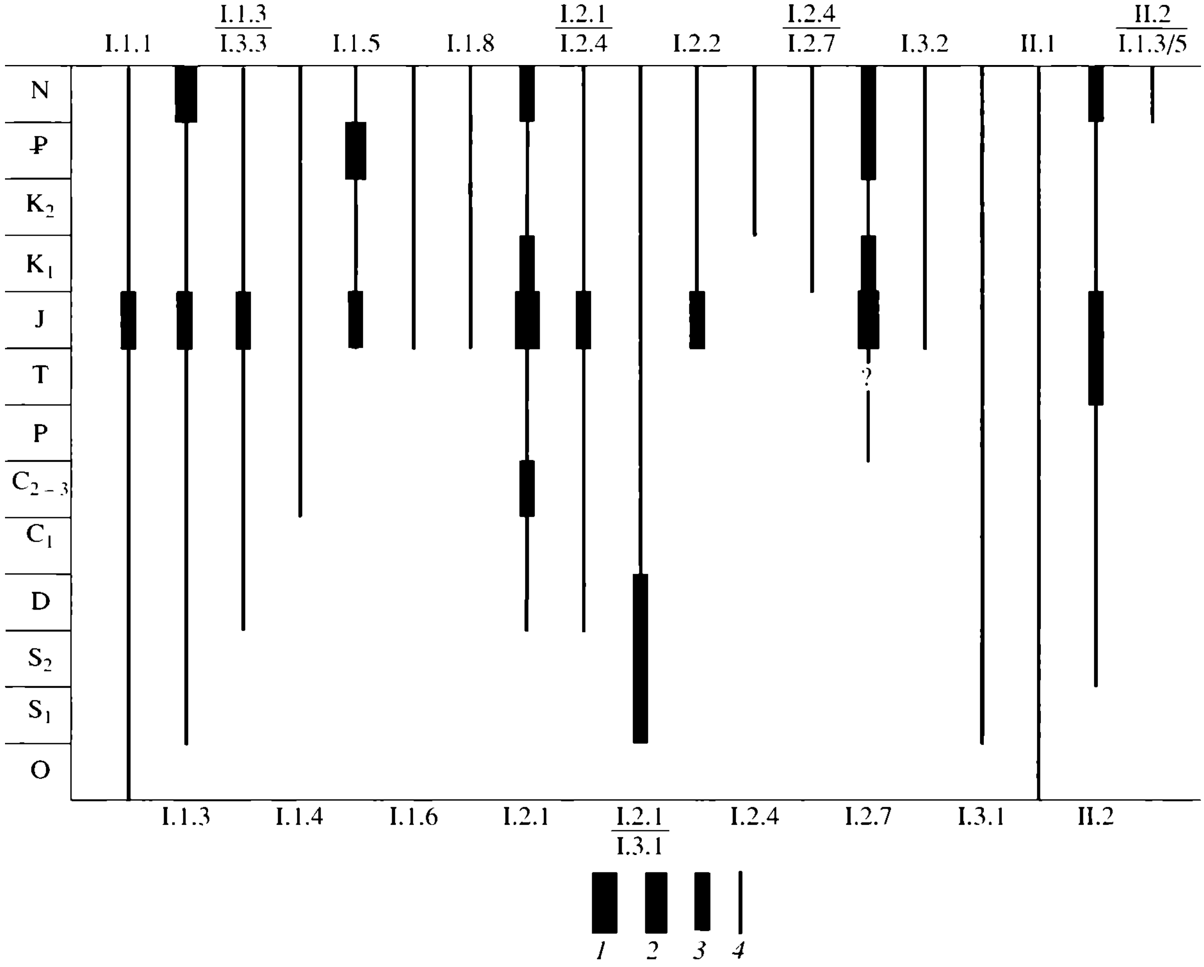


Fig. IX. 69. Ethological-trophic composition of bivalvian communities of the marginal zone of the sea in different periods of the Phanerozoic: ethological-trophic groups: (I.1.1) shallowly burrowing infaunal suspension-feeders lacking a pallial sinus (lacking siphons); (I.1.3) shallowly burrowing infaunal suspension-feeders with a pallial sinus (with siphons); (I.1.4) shallowly burrowing infaunal suspension-feeders with one siphon; (I.1.5) relatively deeply burrowing infaunal suspension-feeders with two long siphons; (I.1.6) boring bivalves; (I.1.8) relatively deeply burrowing suspension-feeders with an anterior mucous tubule and exhalant siphon; (I.1.8a) the same, but without exhalant siphon; (I.1.9) suspension-feeders, living in shelters; (I.2.1) epibyssal suspension-feeders lacking siphons; (I.2.2) the same, but with one siphon; (I.2.3) the same, but with two siphons; (I.2.4) epifaunal suspension-feeders lacking siphons and byssus, lying on the substrate; (I.2.4a) the same, but capable of swimming; (I.2.5) free-lying on the substrate with one siphon; (I.2.6) the same, with two siphons; (I.2.7) cemented; (I.3.1) semi-infaunal endobyssal suspension-feeders lacking siphons; (I.3.2) the same, with one siphon; (I.3.3) the same, with two siphons; (I.3.4) semi-infaunal suspension-feeders without byssus and siphons; (II.1) shallowly burrowing and crawling on the substrate debris-feeders lacking siphons; (II.2) relatively deeply burrowing debris-feeders with siphons; and (III) infaunal predators with siphons. In cases when genera belong to different groups, all these groups are indicated; (*1*) dominating in a particular period, (*2*) common, (*3*) moderately common, and (*4*) scarce.

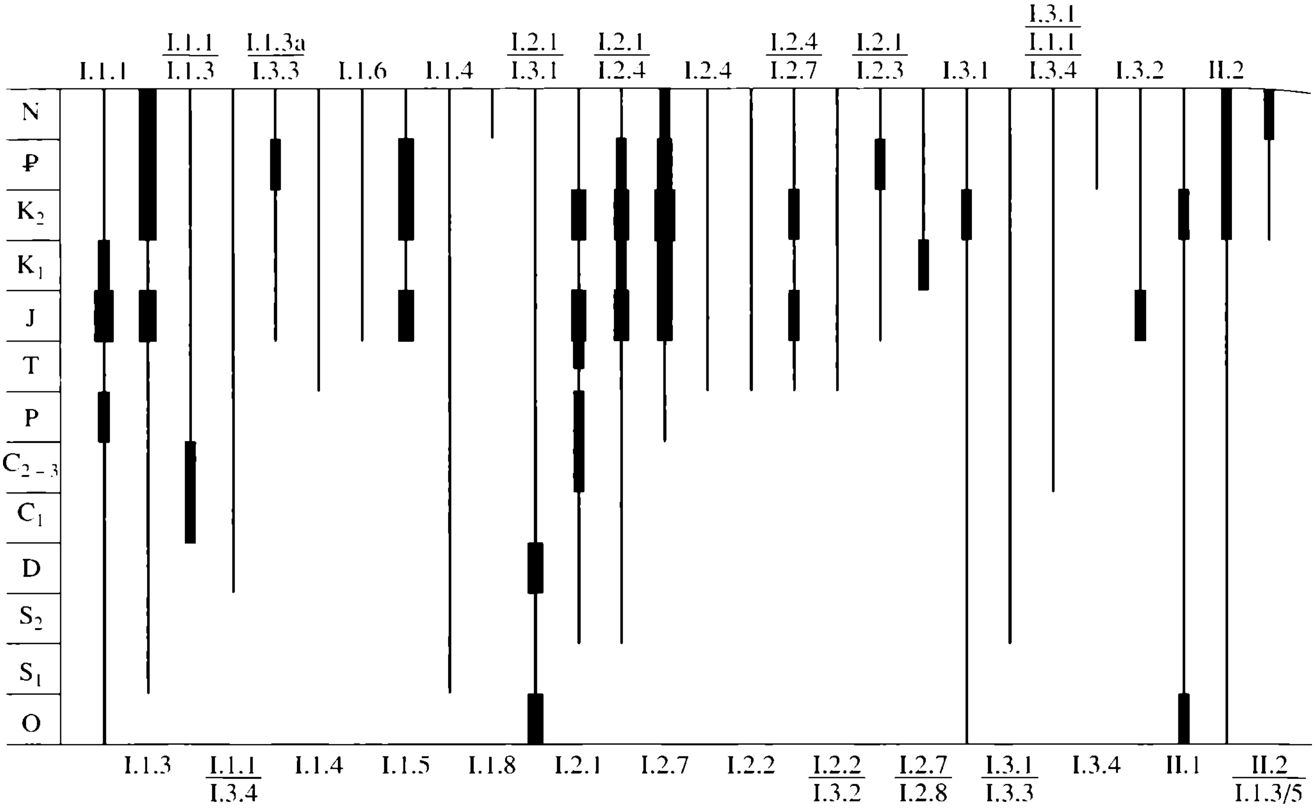


Fig. IX. 70. Ethological-trophic composition of bivalvian communities in the coastal zone of the sea in different periods of the Phanerozoic. For designations, see Fig. IX. 69.

the sessile (I.2.7) suspension-feeders became dominant. There were many infaunal siphonate (I.1.3) and nonsiphonate (I.1.1) suspension-feeders, epibyssal and/or free-lying bivalves lacking siphons (I.2.1/I.2.4), epibyssal suspension-feeders with one siphon (I.2.2), and infaunal siphonate debris-feeders (II.2). In the Paleogene and Neogene, the dominant role belonged to shallowly burrowing suspension-feeders with siphons (I.1.3); epifaunal cemented (I.2.7) and byssal (I.2.1) suspension-feeders; infaunal deeply burrowing siphonate suspension-feeders (I.1.5); and debris-feeders were typical (II.2) (Fig. IX. 69).

A similar pattern was characteristic of the coastal zone. In the Early and Middle Paleozoic, bivalve communities were dominated by epi- and/or endobyssal suspension-feeders (I.2.1/I.3.1) and debris-feeders lacking siphons (II.1). In the Late Paleozoic, the main role belonged to epibyssal (I.2.1) and infaunal suspension-feeders lacking siphons (I.1.1), and also to infaunal and/or semi-infaunal siphonate suspension-feeders (I.1.3/I.3.3).

In the Mesozoic, epibyssal suspension-feeders and infaunal suspension-feeders (I.1.3 and I.1.5) became very important, especially siphonate taxa. However, bivalves lacking siphons were also common (I.1.1). Cemented (I.2.7) and epibyssal and/or free-lying bivalves (I.2.1/I.2.4) were numerous, whereas sessile and/or free-lying (I.2.7/I.2.4) suspension-feeders and debris-feeders with or without siphons were common.

In the Paleogene and Neogene, the infaunal shallowly burrowing and epifaunal cemented suspension-feeders, and infaunal debris-feeders with siphons retained the leading role. In the Neogene, a major role was played by siphonate debris-feeders, which under certain conditions could feed like suspension-feeders (II.2/I.1.5). In the Neogene, epifaunal byssal and/or free-lying suspension-feeders were common (I.2.1/I.2.4).

Thus, the ethological-trophic composition of the marginal and coastal zones was similar throughout the Phanerozoic (infaunal suspension-feeders and debris-feeders and byssal epifaunal suspension-feeders), although certain changes occurred within these groups. Infaunal suspension-feeders lacking siphons (I.1.1) became less important than siphonate taxa (I.1.3) beginning with the Jurassic, while among debris-feeders, the siphonate taxa became more important; and epi- and endobyssal suspension-feeders (I.2.1/I.3.1), dominating in the Early and Middle Paleozoic, became less important and were replaced by epibyssal (I.2.1) taxa. In addition, many other groups first appeared in the Mesozoic (Fig. IX. 70).

Communities of the shallow shelf were most diverse. In the Early Paleozoic, epibyssal and/or endo-

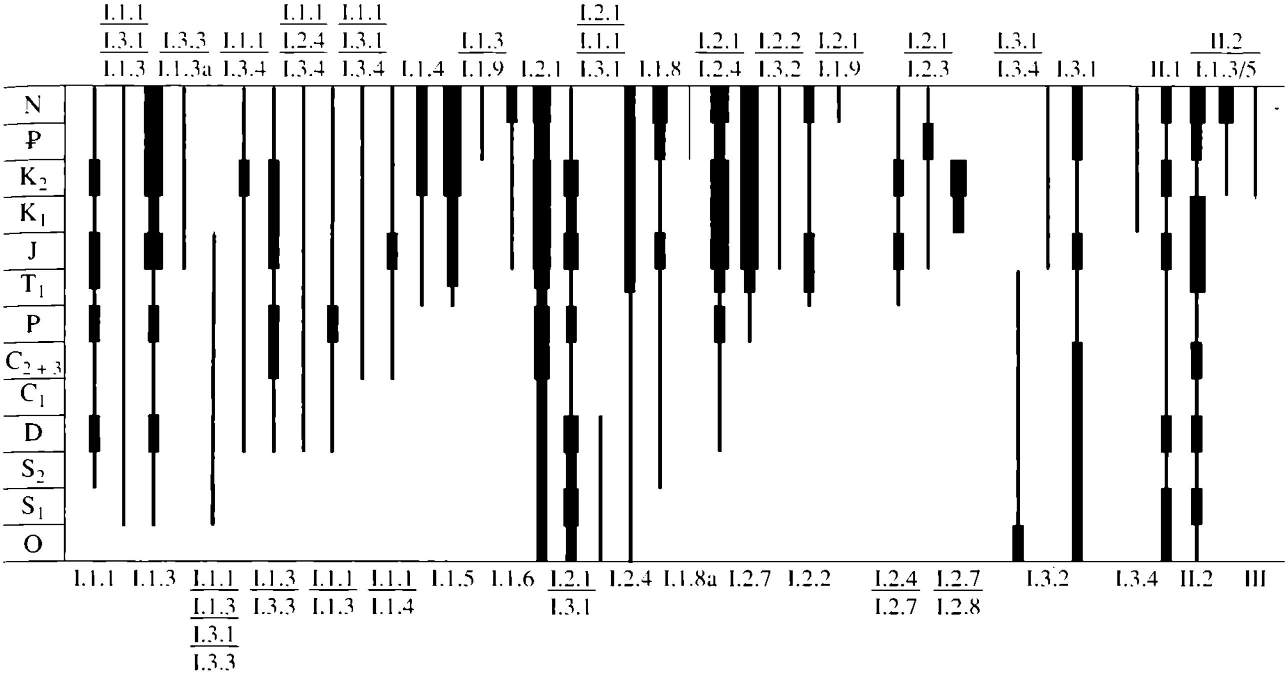


Fig. IX. 71. Ethological-trophic composition of bivalve communities in the shallow shelf in different periods of the Phanerozoic. For designations, see Fig. IX. 69.

byssal (I.2.1/I.3.1), exclusively epibyssal (I.2.1) and endobyssal (I.3.1) suspension-feeders, and debris-feeders lacking siphons (II.1) and with siphons (II.2) dominated. In the Devonian, they were joined by infaunal shallowly burrowing suspension-feeders with (I.1.3) and without (I.1.1) siphons. In the Late Paleozoic epibyssal (I.2.1) suspension-feeders became dominant, while the proportion of endobyssal bivalves (I.3.1) considerably decreased. Beginning with the Triassic, the numbers of infaunal siphonate deeply burrowing suspension-feeders considerably increased (I.1.3 and I.1.5), while epibyssal and epibyssal and/or free-lying (I.2.1/I.2.4) suspension-feeders and infaunal debris-feeders with siphons (II.2) were numerous; sessile suspension-feeders gradually became widespread (I.2.7). In the Jurassic and Cretaceous, epibyssal, epibyssal and/or free-lying, cemented, and infaunal shallowly burrowing suspension-feeders with siphons dominated. Among sessile bivalves (I.2.7), there were many symbionts with photosynthesizing algae (rudists). Debris-feeders, especially with siphons, and epi- and/or endobyssal suspension-feeders were also typical. In the Paleogene and Neogene, infaunal siphonate shallowly burrowing suspension-feeders (I.1.3) were distinctly dominant; deeply burrowing (I.1.5), cemented (I.2.7), epibyssal (I.2.1) and epibyssal and/or free-lying (I.2.1/I.2.4) suspension-feeders; and siphonate debris-feeders (II.2), including those capable of feeding as suspension-feeders (II.2/I.1.5) (in the Neogene) were numerous. There were many infaunal suspension-feeders feeding through a mucous tubule, which was formed by the foot (I.1.8). The role of major ethological-trophic groups of infaunal suspension-feeders and debris-feeders had also changed in this zone. This change was similar to that in the communities of the marginal and coastal zones. Beginning with the Late Paleozoic, epibyssal taxa became dominant over epi-endobyssal, whereas the diversity of the ethological-trophic composition sharply increased because of the appearance of deeply burrowing suspension-feeders (I.1.5), boring bivalves (I.1.6), suspension-feeders with an anterior mucous tubule (I.1.8), and cemented taxa (I.2.7) (Fig. IX. 71).

The majority of bivalves occurring in the zone of organic buildups in the Early Paleozoic were epibyssal and/or endobyssal (I.2.1/I.3.1), while exclusively epibyssal (I.2.1) or endobyssal (I.3.1) taxa were less common. In the Late Paleozoic (especially in the Permian), epibyssal suspension-feeders become dominant along with epi- and/or endobyssal suspension-feeders, whereas from the Middle Triassic, the ethological-trophic composition became more diverse. The above groups were joined by the epibyssal and/or free-lying (I.2.1/I.2.4) and cemented (I.2.7) suspension-feeders. In the Jurassic and Cretaceous, this composition remained the same, although sessile taxa included many symbionts with photosynthesizing algae (rudists). Representatives of other groups (various infaunal suspension-feeders and siphonate and nonsiphonate debris-feeders) were less common. In the Paleogene and Neogene, epibyssal and sessile suspension-feeders were dominant; boring bivalves (I.1.6), infaunal shal-

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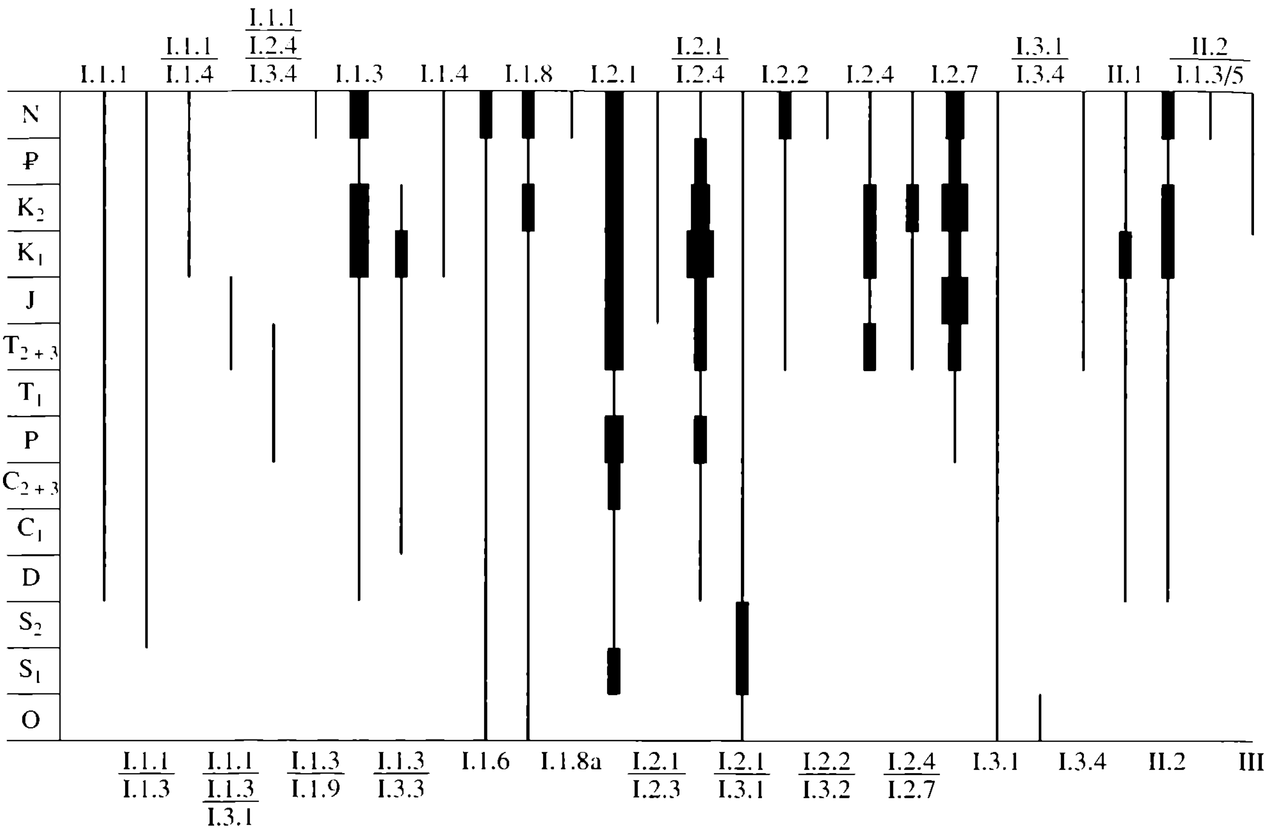

Fig. IX. 72. Ethological-trophic composition of bivalve communities in the zone of organic buildups in different periods of the Phanerozoic. For designations, see Fig. IX. 69.

lowly burrowing suspension-feeders with siphons, and siphonate debris-feeders were typical (Fig. IX. 72).

Hardground communities in the Paleozoic included epibyssal (I.2.1) and epibyssal and/or free-lying (I.2.1/I.2.4) suspension-feeders, whereas in the Mesozoic and Cenozoic, they included sessile (I.2.7) and epibyssal (I.2.1) suspension-feeders.

Paleozoic communities of the deep shelf, similar to other zones of the sea, were first dominated by epi- and/or endobyssal (I.2.1/I.3.1) and epibyssal (I.2.1) suspension-feeders, while later, they were replaced by exclusively epibyssal (I.2.1) taxa. The presence of debris-feeders was typical. In the Ordovician, they were without siphons (II.1) (*Ctenodonta, Cleidophorus, Praenucula*, and *Similidonta*) and siphonate (II.2) (*Palaeoneilo, Nuculites*); in the Devonian, those lacking siphons included *Nuculoidea*, whereas siphonate debris-feeders included *Palaeoneilo* and *Nuculites*; in the Carboniferous, they included taxa lacking siphons (*Nuculopsis* and *Clinopistha*) and the siphonate *Palaeoneilo* and *Phestia*. In the Mesozoic, the deepwater communities were mainly dominated by epibyssal and/or free-lying bivalves (I.2.1/I.2.4), sometimes capable of swimming over the bottom (I.2.4a, *Aequipecten, Entolium*, etc.), or pseudoplanktonic (I.2.1a, *Posidonia, Halobia, Daonella*, etc.). Infaunal, relatively deeply burrowing suspension-feeders with siphons (I.1.5, *Pholadomya, Goniomya, Thracia*, etc.) and bivalves with an anterior mucous tubule (I.1.8, Lucinidae) were numerous. Debris-feeders were represented in these communities by siphonate *Taimyrodon, Malletia, Palaeoneilo*, and *Dacryomya* and bivalves without siphons (*Palaeonucula* and *Sarepta*). In the Paleogene and Neogene, deepwater communities were dominated by infaunal debris-feeders with siphons (II.2, *Nuculana, Yoldia, Malletia*, etc.), infaunal suspension-feeders with siphons (I.1.5, *Pholadomya, Laternula*, etc.), those with an anterior mucous tubule (I.1.8, Lucinidae), and epifaunal bivalves capable of swimming (I.2.4a, *Chlamys, Paliolum, Lima*, etc.). Sessile (I.2.7) and free-lying (I.2.4) suspension-feeders, debris- feeders lacking siphons (II.1), and debris-feeders capable of suspension-feeding (II.2/I.1.5) were present (Fig. IX. 73).

At present, bivalves occur up to the greatest depths (over 10 thousand meters). These deepwater taxa include representatives of only a few families, i.e., Nuculanidae (*Yoldiella, Parayoldiella*, and *Spinula*), Malletiidae (*Malletia, Tindaria*, and *Bathyspinula*), Thyasiridae (*Axinulus*), and Vesicomyidae (*Vesicomya*). The Nuculanidae and Malletiidae are infaunal debris-feeders with siphons, the Thyasiridae are infau-

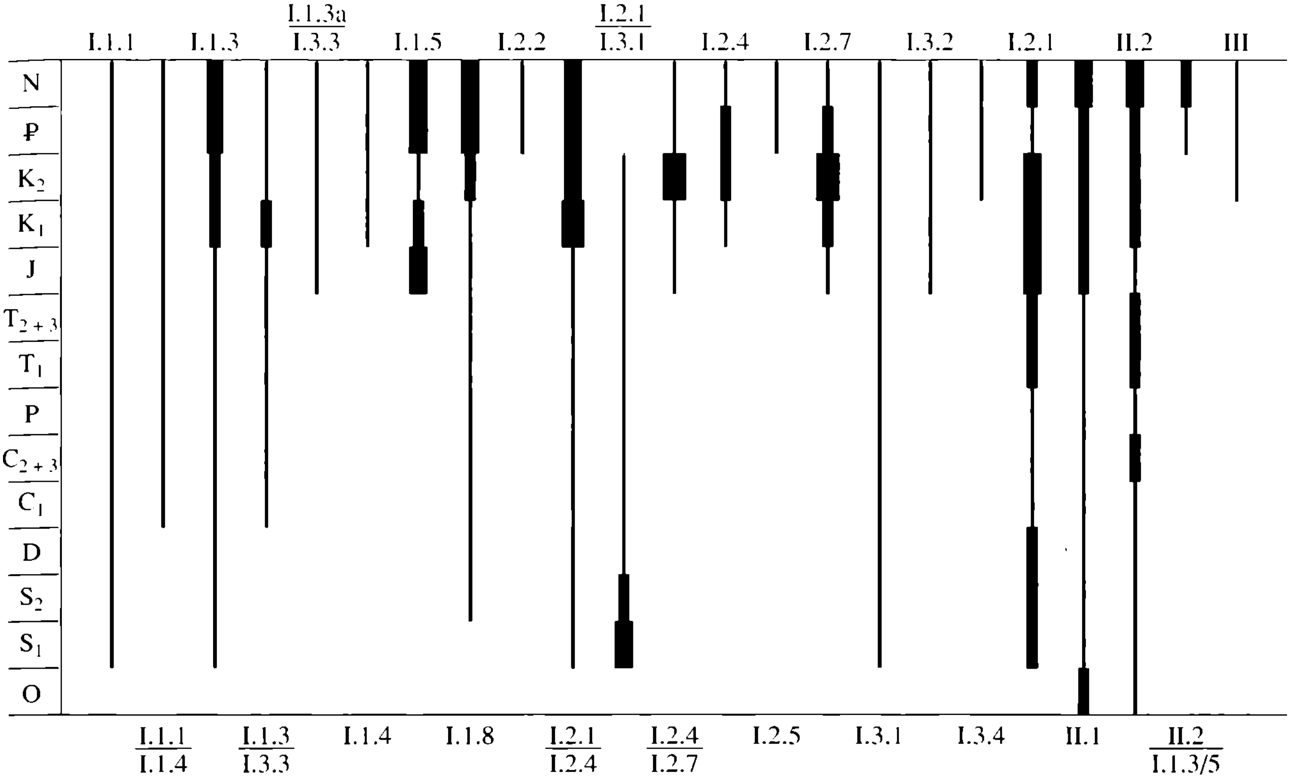

Fig. IX. 73. Ethological-trophic composition of bivalve communities in the deep shelf in different periods of the Phanerozoic. For designations, see Fig. IX. 69.

nal suspension-feeders with an inhalant mucous tubule, whereas the Vesicomyidae are infaunal suspension-feeders with two siphons (Belyaev, 1966, 1989; Vinogradova, 1977; Corselli, 1982).

All communities of the deepwater zone have a low diversity and a simple structure (Aberhan, 1994).

In the anaerobic environment, oxyphilic bivalves disappeared, and the leading role in the communities was occupied by opportunistic taxa. These environments were usually inhabited by infaunal debris-feeders and epibyssal suspension-feeders, which were attached to objects raised above the substrate (I.2.1), or were pseudoplanktonic (I.2.1a). In the anaerobic environment, debris-feeders disappeared completely. Devonian communities represented by the debris-feeders *Palaeoneilo*, *Nuculoidea*, and epibyssal suspension-feeders (*Buchiola*, *Pterochaenia*, etc.), which could attach to floating objects (Dick and Brett, 1986; Zhang, 1999) and Early Carboniferous communities dominated by *Euchondria* (I.2.1, ? I.2.1a) (Amler and Winkler Prins, 1999) are examples of such communities. In the Triassic, disaerobic environments were inhabited by the debris-feeders *Palaeoneilo* and epibyssal, apparently, pseudoplanktonic *Daonella*, *Posidonia*, and *Claraia* (Fürsich and Wendt, 1977).

In the Jurassic and Cretaceous seas, such habitats typically included debris-feeders (*Malletia* and *Glyptoleda*) and epibyssal bivalves attached to objects raised above the bottom and/or pseudoplanktonic (*Buchia*, *Posidonia*, *Aequipecten*, *Pseudomytiloides*, *Meleagrinella*, and *Pseudomonotis*) (Kauffman, 1978a, 1978b; 1982b; Morris, 1980; Savdra and Bottjer, 1987; Sageman, 1989; Aberhan and Palfy, 1996).

(3) Stability of the Composition and Structure of Communities and Consequences of Their Disruption

Against the background of the general picture of changes in the taxonomic and ethological-trophic composition in time, recurrent and ecologically similar communities with the same or similar structure [isocoenoses (Balogh, 1953; Baldi, 1959), parallel communities (Thorson, 1957, 1960), or isopaleocoenoses (Merklin, 1968, 1969)] develop in similar biotops. Isopaleocoenoses were composed of a certain set of living forms (ethological-trophic types), each represented by either related or unrelated taxa.

The oldest known isopaleocoenoses were composed of debris-feeders. In the Silurian, those inhabiting liquid muddy grounds were composed of nonsiphonate bivalves of the families Praenuculidae (*Praenucula* and *Cardiolaria*) and Ctenodontidae (*Praectenodonta* and *Tellinopsis*), while at present, they include nonsiphonate Nuculidae (*Nucula*) and Solemyidae (*Solemya*) and siphonate Tellinidae (*Macoma* and *Cumingia*). The compact muddy grounds in the Silurian were inhabited by representatives of the family Malletiidae (*Arisaigia* and *Nuculites*), whereas at present, they are inhabited by siphonate Nuculanidae (*Yoldia*) and Tellinidae (*Tellina* and *Macoma*) (Levinton and Bambach, 1975). Another described isopaleocoenosis included communities of endobyssal Pinnidae from the off-reef habitats of the Mississippian and Holocene seas, separated by an interval of 300 Ma. Along with pinnids, the community included epibenthic suspension-feeders, including free-lying brachiopods and epibyssal *Aviculopecten* in the Early Carboniferous, whereas in the Holocene, the community included cemented *Crassostrea* and epibyssal *Aequipecten*, capable of swimming above the bottom. The isopaleocoenosis occurred on fine-grained calcareous sands, which also had communities either of bryozoans (Carboniferous) or thickets of sea grass (Holocene), which were protection from currents (Radenbaugh and McKinney, 1998).

An isopaleocoenosis is known beginning from the Jurassic, which mainly contains cemented oysters and which has been, and is characteristic of lagoons, estuaries, and the coastal shallow water zone (Hecker *et al.*, 1962; Scott, 1974, 1986a; Wright, 1974; Feldman and Palubniak, 1975).

Isopaleocoenoses have been recorded from some Cenozoic seas (Merklin, 1968, 1969; Baldi, 1973; Hoffman, 1979; Nevesskaja, 1980; Chinzei, 1984; Nevesskaja *et al.*, 1986). For instance, carbonate mud of the deep shelf (depth 150-200 m or deeper) of the Paratethys from the beginning of the Oligocene to the Middle Miocene over 20 Ma, typically contained an isopaleocoenosis which included infaunal debris-feeders (*Nucula, Nuculana*, and *Abra*), infaunal suspension-feeders with an anterior inhalant mucous tubule (*Thyasira* and *Lucina*) and with two siphons (*Corbula, Hiatella, Thracia*, etc.), epifaunal byssal although capable of swimming suspension-feeders (*Lentipecten* and *Palliolum*), free-lying suspension-feeders (*Neopycnodonte*), and septibranchial predators (*Cuspidaria* and *Cardiomya*) (Merklin, 1969).

Communities inhabiting sandy substrates of the shallow zone of the Baden Sea (Middle Miocene) were dominated by infaunal siphonate suspension-feeders (genera *Venus* and *Chione*), and the Pleistocene community of the Black Sea (*Chione gallina*) can be assigned to one isopaleocoenosis. The period of existence of this paleocoenosis is estimated about 15–20 Ma (Nevesskaja *et al.*, 1986).

All these and other examples show that communities have a distinct tendency to maintain their composition and structure (community homeostasis), and to restore them in suitable environments.

The appearance of new taxa and communities composed of them were mainly caused by the disturbance of the stability of communities by changes in abiotic or biotic factors. This occurred at times of general crises of the marine biota (Permian–Triassic, Cretaceous–Tertiary, and other crises causing changes on a far lesser scale). Along with these global events, local changes were also prominent. For instance, a disturbance of the stability of the system of communities could have been produced by the closure of the intracontinental basins, when sharp changes in the hydrogeological regime led to the extinction of the majority of the marine fauna and dissolution of climax communities. In this situation, the evolutionary potential of bivalves could be revealed, but this was a dead-end type of evolution (Davitashvili, 1972; Iljina *et al.*, 1976).

At the first stages of the environmental change, only a small number of eurybiontic opportunistic species survived. Some of these species adapted to the environment and became widespread, occupying free niches (conservative eurybionts according to Merklin (1966), whereas others rapidly changed, experiencing explosive transformation and speciation (progressive eurybionts according to Merklin (1966), to give rise to new species and even genera. Opportunistic species and newly evolved species formed communities with different ecological relationships and occupied zones of the sea that were not typical of their ancestors. Such development was typical of bivalves in the Neogene basins of the Paratethys, which repeatedly changed (see Nevesskaja *et al.*, 1986, 2001).

For instance, in the semimarine Late Miocene basins (Sarmatian and Early Maeotian) inhabited by a very impoverished marine fauna, represented only by a few genera, the taxonomic composition of bivalvian communities was sharply different from that of the open sea communities of the same or similar age. These basins typically contained endemic communities, especially deepwater communities. Ecologically, the character of distribution of communities in the semimarine basins was similar to that of basins with normal salinity. Coastal zones were dominated by epibiontic attached suspension-feeders (I.2.1), deeper zones were mostly inhabited by endobiontic burrowing suspension-feeders (I.1.3), whereas zones of great depth with muddy substrates were inhabited by a community of deeply burrowing sorting debris-feeders (II.2) (community of *Abra*) (*A. reflexa* in the Sarmatian, *A. tellinoides* in the Maeotian, and *A. longicalis* in the modern Mediterranean). In the environment of the Middle Sarmatian basin, which was even more different from the normal marine environment, the community of debris-feeders was restricted. In the same environment, along with the above community, there was an endemic community consisting only of endobiontic suspension-feeders (I.1.3), i.e., species of the endemic genus *Cryptomactra* and some other genera characteristic of shallow zones of the open seas.

Basins that had been closed for a long time, usually brackish water, commonly contained a peculiar endemic and very diverse molluskan fauna (Nevesskaja *et al.*, 1986, 2001). The disappearance of many ecological types represented by marine taxa, including boring bivalves (I.1.6), epibiontic taxa freely living on the surface of the substrate (I.2.4), and others, led to the appearance of convergently similar taxa, ancestors of which did not have similar adaptations.

An example of such a community is the Karagan (Middle Miocene) pholadids, which, from boring in hard substrates (I.1.6), moved to live on the surface of the substrate (I.2.4), or in the uppermost layer of the substrate (I.1.3). Another example is brackish water cardiids, which became adapted in the Pliocene seas of the Paratethys to boring in muddy clayey substrates (I.1.6), whereas their ancestors were shallowly burrowing endobiontic suspension-feeders (I.1.3), and so on. This process was accompanied by morphological restrictions, which led to the appearance of homeomorphs, i.e., taxa similar morphologically, but evolving from very genetically distant species.

Sometimes, the entire malacofaunas were similar, e.g., the Permian molluskan fauna was of the Caspian type (Runnegar and Newell, 1971).

The trophic zonation in closed brackish water basins of the type of the modern Caspian Sea was also disrupted. These basins did not normally contain a zone of debris-feeders represented by bivalves. Such a pattern was observed in the Late Sarmatian and Late Meotian basins (only epibiontic suspension-feeders), and in many Pliocene and Quaternary basins of the south of the former Soviet Union (Nevesskaja, 1971; Nevesskaja *et al.*, 1986). These data supplement the data of Kuznetsov (1964, 1976), who noted that, in intracontinental seas with a salinity different from normal, the zone of nonselective swallowing debris-feeders is virtually absent. According to my data, the zone of collecting debris-feeders occupying its place in these basins had a considerably impoverished taxonomic composition, because it lacked bivalves usual for this zone in basins with normal salinity. This further increases the degree of eutrophication of closed and semi-closed basins.

Thus, these differences in trophic zonation and presence of taxonomically and ecologically endemic communities show that corresponding sediments were deposited in semi-closed, or closed basins, with salinity different from normal.

Thus, the study of ancient bivalve communities showed that, in the stable environment of the long-lived marine basins, benthic communities were highly stable. Communities with the same species composition could exist for a period of 100000 years, whereas parallel communities, or isopaleocoenoses, with a similar generic composition, are traced throughout several dozen, or even hundred million years.

In such stable marine benthic biocoenoses, the speciation and development of higher taxa was unlikely to be rapid, which is possibly the main reason for the slow evolution of bivalves and, possibly, of other benthic invertebrates.

The disruption of the stability of the marine environment in the semi-closed and closed epeiric seas caused the appearance of the endemic communities and the trophic zonation changed because of the complete disappearance of debris-feeding mollusks. A sharp change in biocoenoses and appearance of new communities, often replacing each other along with the changes in the hydrologic situation, created conditions necessary for rapid evolution and appearance of new endemic taxa of generic and even familial rank. However, these endemic taxa usually completed their existence quite soon, with the new changes in the hydrological regime of the basin.

Nevertheless, the development of fauna, and the bivalvian fauna in particular, may be a good illustration of the pattern of evolutionary change.

CONCLUSIONS

Bivalves appeared as early as the Early Cambrian, but at that time they were very rare. Beginning with the Early Ordovician onwards they became a typical component of the benthos. Bivalves reached the peak of their diversity and distribution in the Mesozoic, and retain the status of a widespread and diverse group to the present day.

The class includes three superorders and 14 orders, including over 260 families and approximately 2300 genera. The first representatives of the superorders Protobranchia and Autobranchia are known from the Early Cambrian, whereas the earliest genera assigned to the superorder Septibranchia are recorded from the Jurassic. The autobranchia were the most numerous and diverse. They include nine orders, over 230 families, and more than 2200 genera, whereas the Protobranchia include two orders, 20 families, and 140 genera; and the Septibranchia include three orders, each with a single family.

Of 14 bivalve orders, one is known from the Cambrian and Ordovician, six orders appeared in the Cambrian–Early Ordovician and continue to the present, whereas seven orders appeared in the second half of the Ordovician, Silurian, Carboniferous, second half of the Triassic, Jurassic, Late Cretaceous, and Paleocene, respectively; each continues to the present day.

Study of the changes in the taxonomic diversity of bivalves in the Phanerozoic revealed several major events, the first of which was the peak in the appearance of orders, superfamilies, and families in the Early Ordovician. This was responsible for the maximum diversification rate and maximum change in the taxonomic composition, whereas, for genera, these peaks were in the second half of the Ordovician. From the Silurian to the Permian, diversity remained rather stable, whereas in the Early Triassic, the maximum of all relative parameters was revealed for taxa below order level. These parameters include appearance, diversification, and extinction rates and the rate of the total changes in diversity. Later, up until the Late Cretaceous, the number of families and genera gradually increased. This was interrupted by a drop in the number of taxa ranking below order level at the end of the Cretaceous. From the beginning of the Paleogene to the present, diversity has considerably increased (with a slight decrease in the Oligocene). The events of the Ordovician adaptive radiation and crises at the Permian–Triassic and Cretaceous–Tertiary boundaries were similar to those in other marine groups, although these crises (seen only in taxa below order level) were less pronounced than in the majority of other groups.

Noteworthy, there was a relationship between the crises of biota indicated by the sharp decrease in diversity and appearance and extinction rates at the times of these crises.

Some researchers (McGee, 1990; Kalandadze and Rautian, 1993; Dmitriev, 2002) noted that a crisis of the biota could be caused not only by an increase in the extinction rate, but by a decrease in the rate of appearance of new taxa. This can, to some extent, be displayed by the indices of the extinct and newly appearing bivalve genera at the Permian–Triassic boundary, when the number of extinct genera was only slightly greater than the number of appearing genera. Therefore, this crisis of diversity cannot be explained by increased extinction.

The analysis of the changes of some taxonomically important morphological characters suggests that, at the beginning of the Early Paleozoic, the shell structure was more primitive and stable. Inequivalve, ornamented, and prominently inequilateral shells and shells with a complex hinge, pallial sinus, auricles, or a byssal notch were absent. However, beginning from the second half of the Ordovician, genera with an inequivalve shell, with concentric and/or radial ornamentation, a strongly inequilateral shell, a more complex hinge, and the pallial sinus appeared. The proportion of these genera, compared to the more primitive genera, increased over time. The most noticeable changes occurred in the hinge structure. In particular, the Early and Middle Paleozoic were dominated by toothless, ctenodont, preherodont, and actinodont genera, while the Late Paleozoic was dominated by genera lacking hinge teeth, and taxa with the heterodont hinge became noticeable. In the Mesozoic, the most widespread genera were those with the toothless or heterodont hinges. In the Cretaceous, they were joined by genera with the pachyodont hinge. In the Cenozoic, taxa with the heterodont hinge were dominant, while taxa with the toothless hinge were common. Generally, the diversity of the hinge structure increased, although taxa with other hinge types, apart from the heterodont and toothless hinges, were not widespread.

Bivalves, like many other benthic organisms, were largely dependent on many abiotic factors, including temperature, substrate, gas regime, food supply, etc.; and by biotic factors, including competition for food and habitats, predation, bioturbation, and symbiotic relationships.

In respect to substrate and degree of mobility, 30 ethological-trophic groups can be recognized. These groups belong to several larger divisions, including epifaunal, semi-infaunal, and infaunal suspension-feeders, and shallowly and deeply burrowing debris-feeders. Predatory bivalves (Septibranchia) were less common.

Each ethological-trophic group included taxa that had similar morphological characters, a fact that allows inferences to be drawn concerning the modes of life of extinct bivalves.

The majority of ethological-trophic groups are known as early as the Early Paleozoic. Deeply burrowing suspension-feeders, with well-developed siphons, which built and inhabited calcareous tubes; epibyssal and endobyssal bivalves with one siphon; epibyssal with two siphons; and cemented suspension-feeders were absent. However, many groups were represented by only a few genera.

The Early Paleozoic was dominated by semi-infaunal suspension-feeders, while epifaunal suspension-feeders and taxa capable of epibyssal and endobyssal modes of life were abundant. Beginning from the Devonian, and to the end of the Paleozoic, the role of epifaunal suspension-feeders increased, while the role of semi-infaunal taxa decreased. Among infaunal suspension-feeders and debris-feeders, which were not very diverse, genera lacking the pallial sinus, i.e., lacking siphons, were dominant.

In the Mesozoic, epifaunal suspension-feeders dominated, while the proportion of semi-infaunal taxa became considerably lower, and the proportion of infaunal suspension-feeders increased, and among these, siphonate genera became dominant. Debris-feeders were generally less common, but among those, taxa with siphons became more widespread.

At the Mesozoic–Cenozoic boundary, the content of infaunal suspension-feeders sharply decreased, while the role of infaunal suspension-feeders with siphons increased to the same extent. This was possibly caused by increased predation by gastropods, crustaceans, etc. The role of debris-feeders, as in earlier periods, was considerably smaller than that of suspension-feeders, and they were less diverse and more conservative.

The taxonomic composition of individual ethological-trophic groups changed throughout the Phanerozoic, i.e., they included families, representatives of which had similar ecology, but were not genetically related. This was reflected in the frequent appearance of homeomorphic taxa of different level.

Over most of the Phanerozoic, bivalves occurred in different zones of the sea, from the marginal zone to the lower part of the shelf zone (lower sublittoral); in the Cenozoic, they possibly, as now, occurred in the bathyal. In the Paleozoic, bivalves did not play a leading role in the bottom biocoenoses. In the Ordovician and Silurian, bivalves were in the core of communities only in the coastal–lagoon habitats, while in the Devonian, they also became characteristic of the shallow shelf, and only from the Late Paleozoic, did they become major, or characteristic elements of the faunas of all zones of the sea. In the Mesozoic and Cenozoic seas, as in the present, bivalves were the major component of the benthic fauna. This was helped by the fact that brachiopods, which occupied niches similar to those occupied by epifaunal bivalves, lost their importance.

Each sea zone had a certain set of ethological-trophic groups, which reflected the presence of trophic zonation in the basins.

The taxonomic composition and diversity of bivalvian communities, like those of other benthic organisms, were also dependent on the geographical position (climatic factor), i.e., differing degrees of temperature tolerance.

Early and Middle Paleozoic bivalves were apparently relatively eurythermal, and their communities in the Boreal and Notal realms were similar to those in the Tropical Realm. In the Permian, the differences between the Boreal and Notal communities from the Tropical ones were very distinct. The same is true for the Mesozoic.

In the Cenozoic, because of the paleogeographic changes, latitudinal zonation was supplemented by meridional zonation, each which led to the separation of several biogeographic provinces, with a specific taxonomic composition of bivalves.

Bivalves, having appeared in the Early Cambrian, gradually expanded their range to become, in the present, one of the dominant benthic groups occupying areas from the coast to the depths of the oceans. Their geological history provides an excellent opportunity to study evolutionary changes in particular taxonomic groups.

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