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Ethological-Trophic Groups of Bivalve Mollusks and Their Distribution in the Phanerozoic

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Abstract—Based on their adaptations to substrates, degree of mobility, and feeding modes, bivalve mollusks are subdivided into 30 ethological-trophic groups. This paper presents an account of their morphological characteristics, distribution in the Phanerozoic, and taxonomic changes through time.

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Key words: bivalve mollusks, ethological-trophic groups, Phanerozoic.

INTRODUCTION

The distribution and morphogenesis of bivalve mollusks, which still form a significant part of the marine benthos, have been influenced by numerous physical factors such as temperature, salinity, gas exchange regime, water dynamics, substrate type, depth, and availability of food, and also by biotic factors such as competition for food and habitat, predation, bioturbation, and symbiotic relationships.

Among the factors that affect the distribution of bivalve mollusks, the most important are feeding mode and lifestyle, i.e., the relationship to a substratum and the degree of mobility.

MAIN ETHOLOGICAL-TROPHIC GROUPS OF MOLLUSKS

The main trophic groups of benthic organisms include suspension feeders (sestonophages), selective and unselective detritivores (detritophages), predators, and herbivores (phytophages) (Turpaeva, 1948, 1953, 1957; Savilov, 1957, 1961; Scott, 1976; Walker and Bambach, 1974; Kuznetsov, 1976, 1980). Bivalve mollusks include members of all these groups except for unselective detritophages and phytophages. Passive predation is characteristic of a small group of genera belonging to the superorder Septibranchia. Forms of this group have gills transformed into a muscular wall, which grind small organisms coming through the inhalant siphon with special crests. Septibranch forms are known only since the Jurassic, but their absence in older deposits can be accounted for their small numbers and a rarity throughout their existence.

The most diverse among bivalves are suspension feeders; selective detritophages have a more limited taxonomic composition, whereas septibranch predators play an insignificant role. There is another group of bivalves feeding on metabolic products of symbiotic hemiautotrophic bacteria and microscopic algae. This feeding mode is typical for a number of unrelated taxa, as vesicomyids (*Vesicomya, Calyptogena*), solemyids (*Solemya, Acharax*), lucinids (*Epilucina, Lucinoma, Myrtea*), thyasirids (*Thyasira, Conchocele, Axinopsida, Axinulus*), and mytilids (*Bathymodiolus, Amygdalum*) in the hydrothermal areas of the seafloor, where mollusks are bacteriosymbiotrophes preserving the initial mode of seston-feeding (Kuznetsov et al., 1987; Squires, 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, occurring in completely different conditions (shallow-water habitats and reef constructions), have symbiotic microscopic photosynthesizing algae, zooxanthellae. This group includes rudists and, among the recent forms, tridacnids, some solemyids, cardiids, and others.

The majority of genera and families preserved their trophic preferences during the entire existence and belonged to one of the specified trophic groups. Only few taxa had a different feeding mode at some stage. Thus, the representatives of the family Tellinidae, feeding mostly on detritus, can sometimes change to suspension feeding (Kuznetsov, 1986); some brackish-water Cardiidae, in the absence of seston, roil the sediment with siphons and feed as detritivores (Romanova, 1963). Suspension feeders of different families (Lucinidae, Cardiidae, Mytilidae, etc.), as indicated above, include species that may feed on metabolic products of symbionts.

A number of ethological classifications based on the adaptations to different substrata and degree of mobility were proposed by both marine biologists (Thorson, 1957; Pérès, 1961) and paleontologists (Kudrin, 1957, 1966; Markovskii, 1966; Kauffman, 1969; Stanley, 1968; Kojumdgieva, 1976, 1977).

Two main substratal groups are recognized: infaunal (endobiontic) forms, living inside the sediment, and epifaunal (epibiontic) forms, living on the substrate (Thorson, 1957). The intermediate group is represented by semi-infaunal forms, which are partly immersed in a substratum with the posterior part of the shell protruding above the sediment surface.

A degree of mobility divides endobionts into superficially and deeply burrowing forms, boring forms, and forms living in cracks, cavities, etc. The epibiontic species can be rigidly (with cementation) or flexibly (with byssus) attached or be free-living (lying, crawling, floating).

The applicability of ecological and trophic-ethological classifications to fossil bivalves is based on the overall stability of alimentary adaptations in the majority of species, as well as in higher rank taxonomic groups, like superfamilies, families, and genera, with their forms belonging to either sestonophages or detritophages. Species with broad trophic preferences, capable of utilization of different nutritional sources, are relatively rare. One of the feeding modes usually dominates in these forms.

Ethological adaptations of species, genera, and sometimes whole families are believed to remain rather constant in time too (Thayer, 1974b, and others). For example, it is quite clear that the overwhelming majority of oysters were attached by cementation, mytilids were mainly byssally attached, nuculids crawled on the bottom and superficially burrowed, myids, solenids, and other burrowed deeply into the sediment, etc.

A change in life mode, as a rule, caused a change in morphology of an animal expressed in shell shape and morphology (Tevesz and Carter, 1979; Savazzi, 1981, 1984, 1989; Tevesz and McCall, 1985; Tashiro and Matsuda, 1988; Nevesskaja et al., 1986, 1987; Whittlesey, 1996; etc.). Taking this into account, it is possible to reconstruct not only the trophic, but also the ethological type of a certain fossil form, i.e., to get its comprehensive trophic-ethological characterization and classify it into one of the above mentioned groups.

The combination of trophic and ethological features has resulted in the recognition of a number of ethological-trophic groups (Stanley, 1968; Pojeta, 1971; Runnegar, 1974; MacKenzie, Pojeta, 1975; Nevesskaja, 1981; Thayer, 1983; Wake et al., 1986; Aberhan, 1994). With the addition of some morphological characters (presence or absence of byssus and siphons), it is possible to outline the following classification of ecological (ethological-trophic) groups (Fig. 1):

1. Suspension feeders (sestonophages)
    1.1. Infaunal (endobiontic)
        1.1.1. Superficially burrowing, without byssus and siphons
        1.1.2. Superficially burrowing, with byssus and without siphons
        1.1.3. Superficially burrowing, without byssus, with two siphons
        1.1.3a. The same, with byssus and siphons
        1.1.4. Superficially burrowing, without byssus, with one siphon
        1.1.4a. The same, with byssus and one siphon
        1.1.5. Relatively deeply burrowing, with long siphons
        1.1.6. Boring forms (with siphons)
        1.1.7. Burrowing and tube producing (with siphons)
        1.1.8. Burrowing, with excurrent siphon and anterior mucous tube
        1.1.8a. The same, with anterior mucous tube, without excurrent siphon
        1.1.9. Living in cracks, cavities, burrows (with byssus or without it; with siphons or without them)
    1.2. Epifaunal (epibiontic)
        1.2.1. Epibyssate, flexibly attached, without siphons
        1.2.1a. The same, attached to floating objects
        1.2.2. Epibyssate, flexibly attached, with one siphon
        1.2.3. The same, with two siphons
        1.2.4. Free-lying and/or crawling, without siphons
        1.2.4a. Free-living, capable of floating, without siphons, usually with byssus
        1.2.5. Free-lying, with one siphon, with or without byssus
        1.2.6. The same, with two siphons
        1.2.7. Cemented
        1.2.8. Epifaunal, having symbiotic relationships with photosynthesizing bacteria and/or algae
    1.3. Semi-infaunal
        1.3.1. Endobyssate, without siphons
        1.3.2. The same, with one siphon
        1.3.3. The same, with two siphons
        1.3.4. Semi-infaunal with siphons without byssus
2. Detritophages
    2.1. Superficially burrowing and crawling on the surface of sediment, without siphons, with labial palps
    2.2. Relatively deeply burrowing, with long siphons
    2.2/1.1.5. Infaunal detritophages with long siphons, which can also feed as sestonophages
3. Predators (infaunal, with siphons)

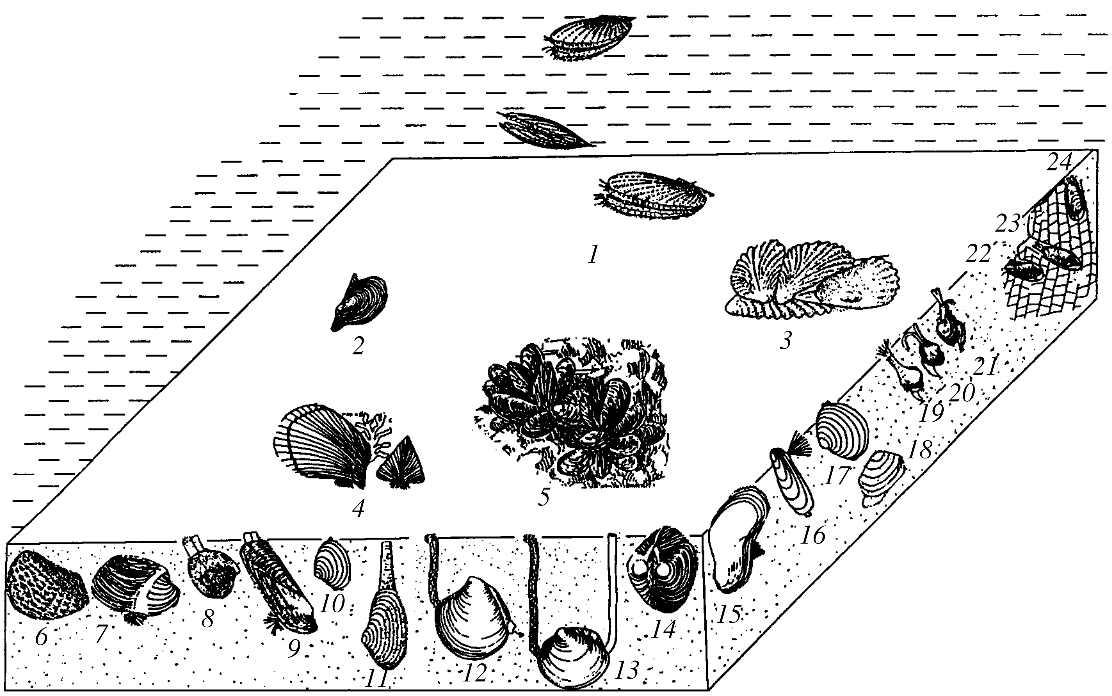

Fig. 1. Representatives of various ethological-trophic groups: (*1*) epifaunal, free-lying and/or crawling and capable to float suspension feeders without siphons (1.2.4/1.2.4a); (*2*) epifaunal, free-lying on a valve suspension feeders without siphons (1.2.4); (*3*) cemented suspension feeders (1.2.7); (*4*) epibyssate suspension feeders without siphons (1.2.1); (*5*) epibyssate suspension feeders with one siphon (1.2.2); (*6*) infaunal, superficially burrowing suspension feeders without byssus and siphons (1.1.1); (*7*) infaunal, superficially burrowing suspension feeders without siphons, with byssus (1.1.2); (*8*) infaunal, superficially burrowing suspension feeders with two siphons, without sinus (1.1.3); (*9*) the same, with byssus (1.1.3a); (*10*) infaunal, superficially burrowing suspension feeders with one siphon, without byssus (1.1.4); (*11*) infaunal, relatively deeply burrowing suspension feeders with long siphons (1.1.5); (*12*) infaunal suspension feeders with short excurrent siphon and anterior mucous tube (1.1.8a); (*13*) infaunal suspension feeders with long excurrent siphon and anterior mucous tube (1.1.8); (*14*) semi-infaunal suspension feeders without siphons and byssus (1.3.4); (*15*) semi-infaunal endobyssate suspension feeders without siphons (1.3.1); (*16*) the same, with one siphon (1.3.2); (*17*) semi-infaunal suspension feeders with siphons, without byssus (1.3.4); (*18*) infaunal detritivores, superficially burrowing or crawling on substratum, without siphons (2.1); (*19*) septibranch predators (III); (*20*) infaunal detritivores with long siphons with the ability of sestonophagy (2.2/1.1.5); (*21*) infaunal, relatively deeply burrowing detritivores with siphons (2.2); (*22*) suspension feeders living in shelters (1.1.9); (*23* and *24*) boring forms (1.1.6).

The life mode reflects the morphology of mollusks, including their shells, so that each ethological-trophic group had a certain morphological pattern.

MORPHOLOGICAL PATTERNS OF MAIN ETHOLOGICAL-TROPHIC GROUPS

Infaunal suspension feeders superficially burrowing, as a rule without siphons and without a sinus of the mantle scar, had an equivalvate, variably sculptured shell, frequently inequilateral, with a shorter anterior part. Beaks are usually prosogyrate. Paired muscular scars are almost equal. Forms with the internal ligament prevailed, but there were frequent forms with only the external ligament (usually opisthodetic), and sometimes both types co-occurred. The hinge is of the heterodont or schizodont type, rarely without teeth or of a different type. The sinus of the mantle scar is absent in most forms, rarely it is present as a shallow sinus. The gape is absent.

Infaunal relatively superficially burrowing suspension feeders without byssus, with one or two siphons. They had an equivalvate shell, smooth or decorated with a concentric or radial sculpture, less often with a complex sculpture, usually inequilateral with a shorter anterior part. The beak, as a rule, belonged to the prosogyrate type. Muscular scars are paired and nearly equal, the ligament is external and opisthodetic, less often, external and internal, or internal. The hinge is mainly of heterodont type. A mantle sinus is shallow or, rarely, deep. The gape occurs in few forms.

Infaunal relatively deeply burrowing suspension feeders with two siphons were characterized by an equivalvate or, less often, inequivalvate, mostly smooth, shell. More than half of genera had inequilateral shells with prevailing genera having a shorter anterior part; about one-third of forms had equilateral shells. Genera with prosogyrate beak prevailed. The paired muscular scars were typically of nearly equal size. The ligament is usually of the external type. Half of the genera had a heterodont hinge, and almost one-third of the genera had a desmodont hinge. The mantle sinus was developed in most genera, with nearly half of the genera having a deep sinus. About one-third of the forms had a gape.

Boring bivalves usually had equivalvate shells, with a complex sculpture, inequilateral with a shorter anterior part, and prosogyrate beak. They had paired muscular scars, with the anterior one being sometimes smaller and placed on the lateral side of the hinge area. The ligament is absent or present, of internal or external opisthodetic type. The hinge is frequently edentate. The mantle sinus is either not expressed or short, rarely deep. Some forms have an extensive gape protected by additional plates (Pholadidae).

Infaunal deeply burrowing suspension feeders with an anterior mucous tube replacing the incurrent siphon (Lucinidae) and a posterior siphon. They had equivalvate shells with a complex or concentric sculpture, usually equilateral, less often with a shorter anterior part, with a prosogyrate beak. Adductor muscle scars are usually paired, the anterior one is more elongated, finger-shaped. The ligament is external, opisthodetic, the hinge is of heterodont, rarely edentate, or dysodont type. The mantle line is entire and the gape is absent.

The epifaunal suspension feeders with byssus, lacking siphons and sometimes capable of a pseudo-planktonic life mode, being attached to floating objects. They mostly had equivalvate shells, with a radial or complex sculpture. Less often the shell was smooth or concentrically ridged, inequilateral with a shorter anterior part (50% of genera) or equilateral (30%) with prosogyrate or, less often, orthogyrate beak. Many of them had ears and a byssal notch (15–20%). There were either two more or less equal adductor muscle scars (65%); or a single scar (25%); or, less often, two scars of which the anterior was much smaller (about 10%). The ligament was usually internal (55%), frequently external opisthodetic (25%), or amphidetic (more than 10%). In half of the genera of this group, the hinge was of edentate type, and about 20% had a heterodont hinge. The mantle line is entire. A number of forms had a gape for the passage of byssus. Pseudo-planktonic forms had a thin-walled shell.

The epibyssate suspension feeders with a single siphon had equivalvate shells. They were mostly smooth or with radial sculpture, with terminal prosogyrate (53%) or anteriorly shifted (44%) beaks. The byssal notch and ears were absent. They had either two adductor muscle scars of which the anterior was much smaller (80%) or a single scar (15%). The ligament is of the external type, opisthodetic. The hinge is dysodont (more than 50%) or edentate (about 40%). The mantle line is entire. The gape is normally absent.

The epifaunal suspension feeders without byssus and siphons had a free-living life mode, lying on or moving along the substratum. They typically had equivalvate shells although with a considerable proportion (12%) of inequivalvate forms. Their shells had a smooth, ridged, or striated outer surface, and were inequilateral with a shorter anterior part, or equilateral with a typically prosogyrate or, less often, orthogyrate beak. Some shells had a byssal notch and ears. Adductor scars were usually paired, almost equal in size (75%). Not infrequently, however, only one scar was developed (25%). Typically, they had an internal ligament (65%) or, less often, an external opisthodetic one. The hinge is of the heterodont, edentate, or schizodont type. The mantle line is entire. The gape was normally absent.

Epifaunal free-living suspension feeders, sometimes attached by byssus, which could be absent in the adult forms. They had no siphons, could emerge above the substratum, and frequently had inequivalvate shells (about 50% of forms) with radial or complex sculpture. Shells are usually equilateral (75%), with a poorly protruding beak, with ears (more than 60%) and a byssal notch (about 50%). Only one adductor muscle scar is present. The ligament is typically of the internal type (more than 90%). The hinge is edentate (about 85%) or, less often, dysodont. The mantle line is entire. The gape (except for the byssal one) is usually absent.

Epifaunal freely living suspension feeders with siphons are known only in the Neogene and in the extant fauna. They have mainly equivalvate shells, smooth or variably sculptured, inequilateral with a shorter anterior part or equilateral with a prosogyrate (about 80%) or, less often, orthogyrate beak. No ears, byssal notch, or gape were present. The adductor muscle scars are of nearly equal size. The ligament is typically external, opisthodetic (about 60%) or, less often, internal (about 30%). Even more rarely the both types are present. The hinge is heterodont (about 90%), less often taxodont and dysodont. The mantle line is entire in 70% of forms. The siphons, if present, are short (30%).

Epifaunal forms fixed with cementation, without byssus, without siphons or with a complex siphonal system (rudists) had equivalvate or inequivalvate (about 50%) shells with a complex and radial sculpture, equilateral, more rarely with a shorter anterior part, with prosogyrate or opisthogyrate or, less often, with orthogyrate and spirogyrate beak, sometimes with ears and the byssal gape (10%). They had a single muscular scar (75%) or, more rarely, two almost equal scars (20%) or two unequal scars of which the anterior was smaller (about 5%). The ligament is internal (80%), internal and external (15%), or, rarely, of the external type only. The hinge is pachyodont (55%) or edentate (40%). The mantle line is entire; rudists had a complex system of pallial channels. Shells without a gape.

Semi-infaunal endobyssate suspension feeders without siphons. They had equivalvate, variously sculptured or, less often, smooth shells. Shells are inequilateral, with a shorter anterior part (60%) or equilateral (more than 30%), with a prosogyrate (about 70%) or orthogyrate (20%) beak, usually without ears and a byssal gape. There are typically two adductor muscle scars. They are nearly equal in size (more than 80%), less often with the anterior one smaller (10%), or with other proportions. The ligament is internal (more than 40%), external (about 40%), or both (15%). The hinge is heterodont (25%), edentate (about 20%) or, less often, of other types (taxodont, praeheterodont, pterinoid, actinodont). The mantle line is always entire. A shell gape is very rare.

Semi-infaunal endobyssate suspension feeders with siphons were represented by few genera in the Paleozoic and Mesozoic, and by two dozen genera in the Cenozoic and the recent fauna. They are characterized by equivalvate (80%) or inequivalvate, smooth or variably sculptured shells. Shells are inequilateral with a shorter anterior part (80%), less often equilateral, with prosogyrate (about 70%), orthogyrate (20%) or, rarely, opisthogyrate or spirogyrate beaks, without ears, byssal notch, or a gape. There are two muscular scars of nearly equal size. The ligament is external opisthodetic (more than 40%) or amphidetic (20%), or both internal and external (20%), less often only internal (15%). The hinge is usually of the heterodont type (about 45%), less often it is edentate (about 20%), schizodont or neotaxodont (15% each), and rarely of other types. The mantle line is entire (55%) or with a short sinus (45%).

The semi-infaunal suspension feeders without byssus and siphons had equivalvate, variably sculptured shell. It was inequilateral with a shorter anterior part or equilateral with prosogyrate and, less often, orthogyrate beaks. No ears, byssal notch, or gapes were present. They had paired, almost equal adductor muscle scars or, very rarely, a single muscular imprint. The ligament is typically of the internal type (about 70%), less often it is external, or both types are present. The hinge is schizodont (40%), or heterodont (more than 30%), less often edentate or has a different structure. The mantle line is entire.

Suspension feeders that lived in shelters and had equivalvate (about 70% of the genera), less often inequivalvate, smooth or variably sculptured, sometimes irregularly shaped shell. It was inequilateral with a shorter anterior part (70%) or equilateral, usually with a prosogyrate beak (about 90%), without ears and byssal notch, with two almost equal adductor muscle scars. The shell normally had an external ligament (more than 70%) of the opisthodetic and sometimes (about 20%) amphidetic types. Some forms had an internal ligament (about 20%) or both internal and external ones (about 10%). The hinge was of various types: heterodont, taxodont, edentate, and less often desmodont and dysodont. The mantle line is entire, a gape was present in 20% of the genera.

The infaunal, superficially burrowing detritivores without siphons had equivalvate, smooth or radially or concentrically sculptured shells. They had inequilateral or equilateral shells, with a shorter or longer anterior part, usually with opisthogyrate (about 70%), less often with orthogyrate and prosogyrate beaks, without ears or byssal notch. Two nearly equal adductor muscles were present. The ligament is of the internal or external type, less often of both. The hinge is ctenodont (more than 90%). The mantle line is entire. The gape is absent.

Infaunal detritivores with siphons had equivalvate, usually smooth or concentrically sculptured shells. They had inequilateral shells with a shorter anterior part or equilateral ones, without ears or byssal notch, with opisthogyrate (80%), less often prosogyrate or orthogyrate beaks. Muscular scars were almost equal in size, rarely with a larger anterior one. The ligament is internal and external (40%), only internal (30%), or only external (30%). The hinge is ctenodont (about 80%) or, less often, heterodont. The gape is usually absent.

Infaunal detritivores with siphons that could feed on seston by roiling the sediment (Tellinidae) were represented by 15–20 genera and only played an important role in communities from the Late Cretaceous. They had equivalvate (about 80%) or inequivalvate shells, smooth (25%), concentrically sculptured (55%) or with a complex ornamentation (20%). Shells were equilateral (about 50%) or inequilateral, with a shorter (85%) or longer (15%) anterior part, with opisthogyrate (60%) or orthogyrate (30%), less often prosogyrate beaks, without ears and byssal notch. Adductor muscle scars were of equal (about 75%) or unequal size with a larger or smaller anterior imprint (13% each). The ligament is external, opisthodetic. The hinge is heterodont. The mantle line with a sinus, which is typically deep (about 80%). The gape is not present.

Septibranch predators usually had equivalvate shells (80%) with a variable sculpture (typically with radial one), less often smooth. Shells were inequilateral with a shorter anterior part (55%) or equilateral, with prosogyrate (more than 85%) or orthogyrate beaks, without ears or byssal notch. Muscular scars are paired and equal in size. The ligament is internal (65%), internal and external (20%), less often external opisthodetic. The hinge is of desmodont (65%) or edentate (25%) or, less often, heterodont type. The mantle line with a sinus, usually shallow (about 55%), or entire (40%), and rarely with a deep sinus.

DISTRIBUTION OF ETHOLOGICAL-TROPHIC GROUPS IN TIME

To find out the distribution of ethological-trophic groups in time and changes in their taxonomic structure, all families and genera were characterized by the relation of their representatives to a substratum and a feeding mode, i.e., were referred to a certain group. It is worth noting that genera of the same families and even congeneric species can belong to more than one ethological-trophic group. For example, they might be epibyssate and/or endobyssate forms, lying on the bottom and/or being able to emerge above, etc. For these taxa all groups to which their representatives belonged are listed.

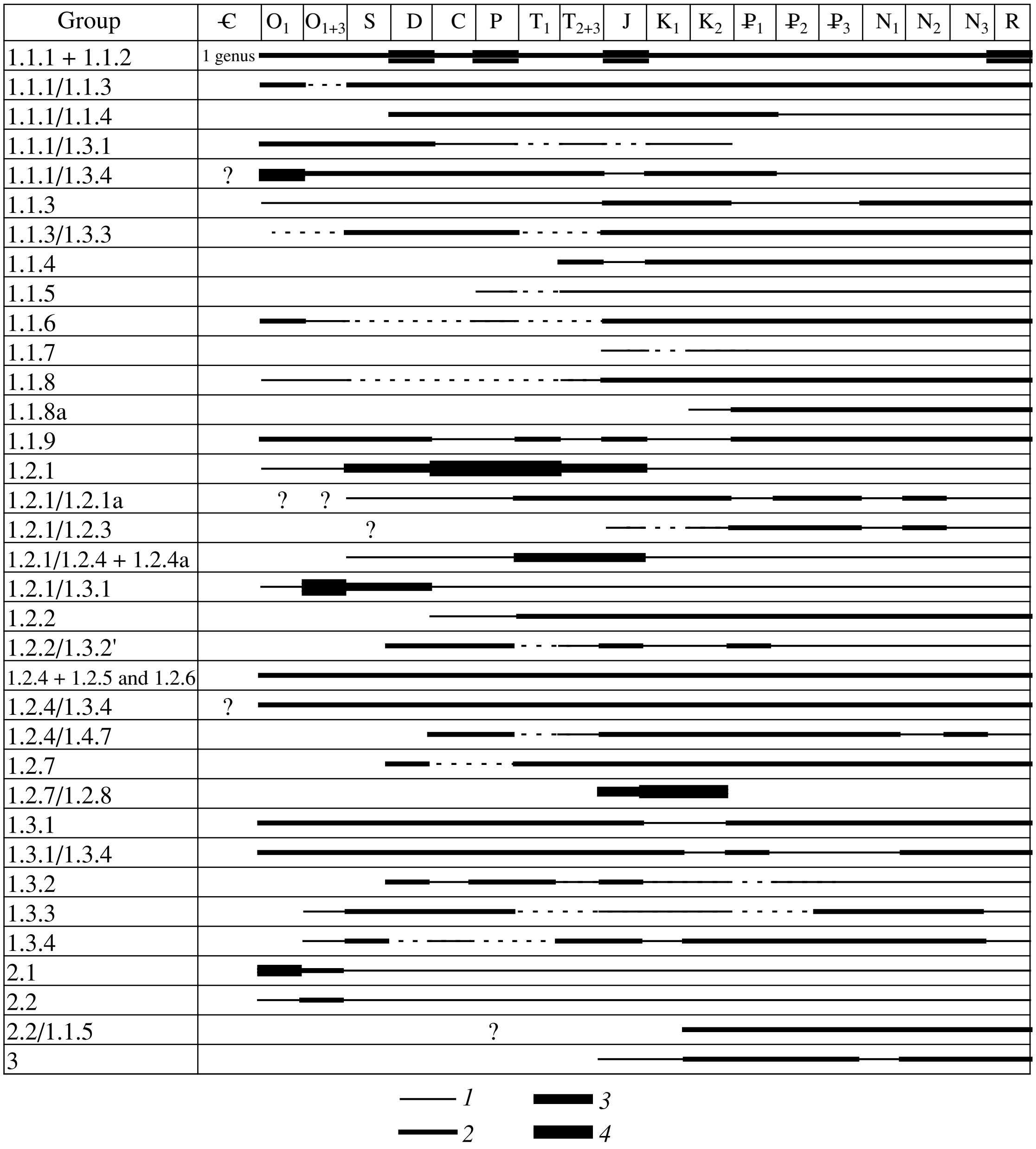

Fig. 2. Percentage of genera representing various ethological-trophic groups in different periods of the Phanerozoic: (*1*) less than 1; (*2*) 1–10; (*3*) 11–20; (*4*) more than 20.

Concerning the life mode of Cambrian bivalves, there are various points of view. Some authors (Pojeta and Runnegar, 1974; Pojeta, 1975; Krasilova, 1977) believe that members of *Fordilla* were superficially burrowing suspension feeders, whereas others (Tevesz and McCall, 1976) interpret them as epifaunal, free-living suspension feeders. Another relatively widespread genus, *Pojetaia*, is alternatively referred to epifaunal or infaunal detritivores (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, the ecological diversity increased considerably (Figs. 2, 3). In addition to the above-mentioned groups, which experienced a growth in genus-level diversity, a number of new groups appeared. They included infaunal superficially burrowing suspension feeders with siphons, epi- and/or endobyssate suspension feeders without siphons, rare boring forms and those living in shelters, as well as semi-infaunal suspension feeders that lie unattached on the substrate without byssus or siphon, and, probably, individual infaunal suspension feeders with mucous incurrent tubes (*Babinka*). Infaunal detritivores without

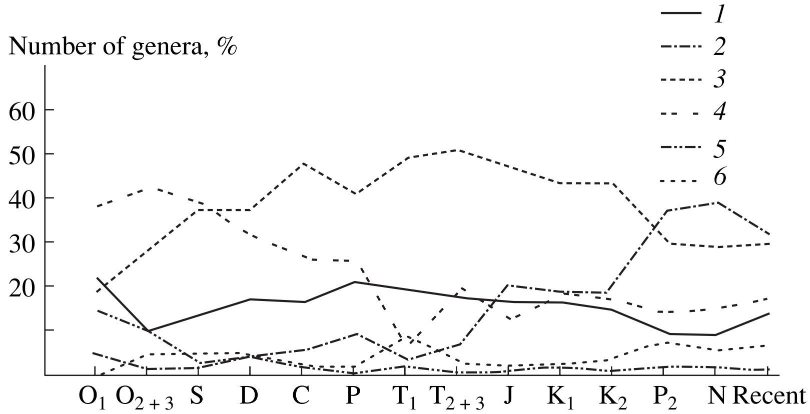

Fig. 3. Changes in the percentage of genera of bivalve mollusks in main ethological-trophic groups during the Phanerozoic: (*1*) infaunal suspension feeders, without siphons (the mantle line without a sinus) (1.1.1); (*2*) infaunal suspension feeders with siphons (the mantle line with a sinus) (1.1.3 and 1.1.5); (*3*) epifaunal suspension feeders (1.2); (*4*) semi-infaunal suspension feeders (1.3); (*5*) detritivores without siphons (with the entire mantle line) (2.1); (*6*) detritivores with siphons (the mantle line with a sinus) (2.2).

siphons (21% of genera) and epi- and/or endobyssate suspension feeders (19%) prevailed.

The same groups persisted in the Late Ordovician, accompanied only by the newly appeared infaunal detritophages with siphons, rare superficially burrowing sestonophages with siphons and byssus, and semi-infaunal suspension feeders with siphons. Epi- and/or endobyssate sestonophages (23%) and detritophages, which mostly included forms without siphons (16%), were predominant.

The Ordovician adaptive radiation was followed by a period of a relative stability (Stanley, 1968). The Silurian witnessed the appearance of suspension feeders attached by byssus to floating objects. The dominant groups of suspension feeders included epibyssate (12%), epi- and/or endobyssate (12% of genera), endobyssate semi-infaunal (10%) and semi-infaunal byssally attached or free-lying (10%), and also infaunal superficially burrowing (10%) forms.

The Devonian was the time of the appearance of first forms of suspension feeders attached by cementation and a group of epi- and/or endobyssate suspension feeders with a single siphon. The prevailing groups included byssus-attached epifaunal, epi- and semi-infaunal (15% each), and semi-infaunal (10%) forms, whereas infaunal superficially burrowing forms without siphons (13.5% of the genera) were also numerous. A considerable role was played by epifaunal suspension feeders without siphons, attached by byssus, and/or lying unattached on the seafloor (7.5%).

In the Carboniferous, there was the first appearance of rare floating suspension feeders. For the rest, the community retains the same structure with the most important role of epibyssate suspension feeders (about 30%) and, to a lesser extent, epifaunal byssus-attached free-lying forms without siphons (about 10%) and superficially burrowing suspension feeders without siphons (8.5%).

The Permian time witnessed the first arrival of rare, relatively deeply burrowing suspension feeders with long siphons. As in the Carboniferous, the dominant group included epibyssate suspension feeders without siphons (23%), and infaunal suspension feeders with (about 10%) and without (more than 10%) siphons. Epi- and/or semi-infaunal suspension feeders without siphons and without byssus, free-lying on the ground or partly submerged into the sediment (8.5%) were common.

In the Early Triassic, a less diverse taxonomic structure of bivalves led to a slightly lower diversity in the ethological-trophic groups (Fig. 2). This impression, however, may stem from an insufficient number of Lower Triassic sites. Epibyssate suspension feeders without siphons (22%) continued to prevail, epifaunal byssate and/or free-lying or floating (nektobenthos) forms were numerous (13%), while infaunal detritivores with siphons (11%) and superficially burrowing suspension feeders without siphons (8%) were common.

The Late Triassic time retains the ethological-trophic structure typical for the early Triassic only with a decreased role of infaunal detritivores. However, the ecological structure became more diverse basically due to the reappearance of previously known groups lacking in the early Triassic. Worth noting here are rare forms of doubtless infaunal suspension feeders with anteriorly directed incurrent mucous tubes and without excurrent siphon as well as infaunal superficially burrowing suspension feeders with a single siphon.

Jurassic bivalves, in addition to the earlier ethological-trophic groups, included suspension feeders with a reduced shell living in carbonate tubes, forms living in shelters with byssus and siphons, epibyssate forms with two siphons, forms with cementation, bivalves that developed symbiotic relationships with photosynthesizing algae and/or bacteria, and predators. All these forms were rare, and for the rest, the ecological structure was similar to that of the Late Triassic. The prevail-

Table 1. Changes in the composition of main families belonging to infaunal suspension feeders without a sinus of the mantle line (1.1.1) [In this and subsequent tables (+) stands for families containing forms, which played a significant role in a given ethological-trophic group; (r), families rarely represented in this group]

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
?Fordiliidae	r	r																
?Archaurellidae	r																	
Cycloconchidae		+	r	r														
Cardiolidae				+	r													
Grammysiidae		r	r	r	+	+	+	r	r									
Trigoniidae								r	+	+	+	+	r	r	r	r	r	r
Astartidae					r	r	r	r	r	+	+	+	+	+	r	r	r	+
Carditidae					r	?	?	?	r	r	r	+	+	+	+	+	+	+
Montacutidae														+		+	+	+

ing forms included epibyssate, epibyssate and/or free-lying, and free-lying suspension feeders that amounted to 13, 10, and 7%, respectively, as well as infaunal superficially burrowing suspension feeders with (11%) and without siphons (10%). The number of cemented forms increased.

In the Early Cretaceous, forms with cementation living in symbiosis with photosynthesizing bacteria and/or algae became widespread. They became especially numerous in the Late Cretaceous (14 and 18% of genera, respectively). Rare genera with the same alimentary adaptations (one genus in the Early Cretaceous, and two genera in the Late Cretaceous) are thought to be epibyssate and/or free-lying forms.

The Late Cretaceous is also the time of the first appearance of infaunal detritivores with long siphons, which could feed as sestonophages. In the Cretaceous, communities of infaunal superficially burrowing suspension feeders with or without siphons (11 and 8%, respectively) dominated. Infaunal and/or semi-infaunal suspension feeders without siphons, epibyssate and cemented (6.5% each) and epifaunal and/or semi-infaunal free-lying (6%) played a significant role.

During the Paleogene and Neogene and up to the present, the number of genera in the majority of groups (especially infaunal suspension feeders and detritivores) increased, but the number and proportion of groups remained unchanged. Infaunal suspension feeders with siphons prevailed, with 11% in the Paleocene, and 16–19.5% in the Eocene through to the Recent. Infaunal suspension feeders without siphons took second place (about 10%). A significant role was played by infaunal suspension feeders with incurrent mucous tubes and excurrent siphons (5–7.5%), infaunal deeply burrowing suspension feeders and detritivores with siphons (4.5–5 and 5–6%, respectively), and also boring forms (4–5%). The most widespread in groups of epifaunal bivalves were byssate (8.5% in the Paleocene, 6.5% in the Eocene, 4–5% in the Oligocene through the Recent), byssus-attached and/or free-lying and floating (4–6%) forms. A significant role was played by free-lying epifaunal and/or semi-infaunal suspension feeders (4.5–6.5%) (Fig. 2).

CHANGE IN TAXONOMIC STRUCTURE OF ETHOLOGICAL-TROPHIC GROUPS IN TIME

Morphological characteristics of ethological-trophic groups show that the majority of them were composed of distantly related taxa alternating in time. Only very few groups consist of genera of the same superfamily. Group 1.2.8 was represented by genera of the family Lucinidae; 1.1.4, by Astartidae; 1.2.4a, mainly by Pectinoidea; 2.1, by Ctenodontoidea and Nuculoidea; and 2.2/1.1.5, by Tellinidae.

Infaunal suspension feeders without a mantle sinus, i.e., probably lacking siphons, were represented by families Cycloconchidae (order Actinodontida) in the early Ordovician, by Cardiolidae (order Cyrtodontida) in the Silurian, and by Grammysiidae (order Pholadomyida) in the Devonian–Permian. In the Triassic, this group was dominated by Trigoniidae (order Actinodontida); in the Jurassic and Early Cretaceous, by Astartidae (order Astartida) and Trigoniidae; in the Late Cretaceous, by Trigoniidae and Carditidae (order Carditida); in the Paleocene, by Carditidae and Astartidae; in the Eocene, by the same families and Montacutidae (order Astartida); in the Oligocene, by Carditidae; and in the Neogene–Recent, by Carditidae, Montacutidae, and Astartidae (Table 1).

Infaunal superficially or moderately deeply burrowing suspension feeders with siphons were rare up to the Carboniferous. In the Late Paleozoic this group included Grammysiidae and Pholadomyidae (order Pholadomyida); in the Triassic they were absent from the dominant groups; in the Jurassic, the group included genera of the Arcticidae, Corbiculidae (order Venerida), and Pholadomyidae; in the Early Creta-

Table 2. Changes in the composition of main families belonging to infaunal suspension feeders with a shallow sinus of the mantle line (1.1.3)

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
Corbiculidae										+	+	+	r	r	r	r	r	r
Veneridae											+	+	+	+	+	+	+	+
Cardiidae									r	r	r	+	+	+	+	+	+	+
Mactridae												r	+	+	+	+	+	+

Table 3. Changes in the composition of main families belonging to infaunal suspension feeders with a deep sinus of the mantle line (1.1.5)

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 (2.2/1.1.5)											r	r	+	+	+	+	+	+
Mactridae												r	+	+	+	+	+	+

Table 4. Changes in the composition of main families belonging to the boring group (1.1.6)

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

ceous, genera of the Arcticidae, Corbiculidae, and Veneridae; in the Late Cretaceous, the family Cardiidae entered the group, and the Mactridae entered it in the Paleocene. This means that from the Early Cretaceous onwards all dominant genera of the group belonged to the order Venerida (Table 2).

Dominant infaunal deeply burrowing suspension feeders with a deep sinus of the mantle line were not diverse. Representatives of the group appeared only in the Carboniferous, and from the Late Paleozoic through the Jurassic it included only genera of the family Pholadomyidae. From the Late Cretaceous, genera of the family Tellinidae (order Venerida) took the dominant position. The Paleocene record has yielded only a few forms of Mactridae, and from the Eocene onwards, the group consists of genera of the families Mactridae and Tellinidae and rare genera of Pholadomyidae (Table 3).

Boring forms were rare up to the Late Cretaceous time. In the Ordovician, they included few genera of the family Modiomorphidae (order Actinodontida); in the Devonian to the Triassic, rare Mytilidae (order Cyrtodontida) and rare representatives of the family Pholadidae (order Venerida) appeared in the Jurassic. The latter became widespread from the Late Cretaceous followed by the appearance of a few genera of the family Veneridae (Table 4).

Infaunal deeply burrowing suspension feeders with a mucous tube replacing the anterior siphon and with or without a posterior siphon first appeared in the Early Ordovician, but they became common only in the Jurassic, being represented by the family Lucinidae (order Astartida) (Table 5).

Epibyssate suspension feeders without or with siphons do not occur as a pure group, that is the genera classified in this group typically contain endobyssate forms too (Table 6), and in some cases also epibyssate forms adapted to a pseudo-planktonic way of life, or free-lying forms without byssus and potentially floating. The group 1.2.1/1.3.1 is known since the Early Ordovician, but it gained the leading role in the second half of the Ordovician when it included genera of the families Modiomorphidae (order Actinodontida) and Ambonychiidae (order Cyrtodontidae). In the Silurian,

Table 5. Changes in the composition of main families belonging to infaunal suspension feeders with an anterior mucous tube (1.1.8 and 1.1.8a)

Family	€	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–R
?Babinkidae		+																
Lucinidae										r	r	+	+	+	+	+	+	+

Table 6. Changes in the composition of main families belonging to endobyssate suspension feeders without siphons (1.3.1) or with a single siphon (1.3.2)

Family	€	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–R
Cycloconchidae		+	r	r														
Modiomorphidae		r	+	+	r	r	r											
Ambonychiidae		r	+	r	+	r												
Cyrtodontidae		r	+	r	r													
Cardiolidae				+	r													
Pterineidae			r	+	+	r	r											
Bakevellidae							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	

this group comprised genera of the families Cardiolidae (order Cyrtodontida), Modiomorphidae, and Pterineidae (order Cyrtodontida); in the Devonian, Pterineidae and Ambonychiidae. In the Late Paleozoic and later, this group disappeared and was replaced by a more complex group (1.2.1/1.3.1/1.2.4). It included genera of Aviculopectinidae (order Cyrtodontida), the epifaunal byssate and byssus-free forms, with some forms leading a pseudo-planktonic way of life.

In the Mesozoic, epibyssate forms belonged to many complex groups, whereas the endobyssate forms reduced their distribution. The latter group in combination with epibyssate and free-lying forms were represented by genera of the family Bakevellidae (order Cyrtodontida). In the Paleocene, the endobyssate group had a vast distribution. From the Paleocene it included some genera and species of the family Carditidae (order Carditida); from the Oligocene, forms of the family Arcidae (order Cyrtodontida); and in the extant fauna, species of Galeommatidae.

Epi- and endobyssate suspension feeders with a single siphon belonged to the family Mytilidae (order Cyrtodontida), which occurs from the Triassic to the Recent.

In the Mesozoic and Cenozoic epibyssate suspension feeders without siphons belonged to many families along with forms adapted to a pseudo-planktonic life mode, as well as free-lying ones, and forms that can float above the bottom. In the Triassic, these were genera of the families Posidoniidae and Aviculopectinidae (1.2.1/1.2.1a/1.2.4) of the order Cyrtodontida, as well as Pectinidae and Limidae (1.2.1/1.2.4/1.2.4a) of the order Pectinida; in the Jurassic, these were Pectinidae, Limidae, Posidoniidae, and Inoceramidae (1.2.1/1.2.4) (order Cyrtodontida), and, since the Cretaceous, Limidae and Pectinidae (Tables 7, 8).

The group of epifaunal free-lying suspension feeders is also not clearly delimited and contains some genera with species that could have a different life mode, including a nektobenthic one (1.2.4a). In the Ordovician and Silurian, these were genera of the family Lunulacardiidae (1.2.1/1.2.4) (order Cyrtodontida); in the Carboniferous and Permian, Aviculopectinidae; and in the Triassic, Posidoniidae, Pectinidae, Aviculopectinidae, Bakevellidae, and Limidae. The Jurassic group included the same association without Aviculopectinidae, but with Inoceramidae; in the Early Cretaceous, these were Bakevellidae, Limidae, and Pectinidae; in the Late Cretaceous, the same families and Gryphaeidae (1.2.4/1.2.7) (order Cyrtodontida) and Inoceramidae; in the Paleocene, Carditidae (1.2.4/1.2.1/1.3.1/1.3.4/1.1.1) (order Carditida), Limidae, Pectinidae, Gryphaeidae,

Table 7. Changes in the composition of main families belonging to epibyssate suspension feeders without siphons (1.2.1)

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
Modiomorphidae		r	+	+														
Ambonychiidae		r	+	+	+	r												
Cardiolidae				+	r													
Pterineidae			r	+	+	r	r											
Lunulacardiidae			r	+	r	r												
Aviculopectinidae					r	+	+	+	+	r								
Bakevellidae							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 8. Changes in the composition of main families belonging to epifaunal suspension feeders with adaptations to be attached to floating subjects and to pseudo-planktonic life mode (1.2.1a)

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
Cardiolidae				+	+													
Praecardiidae				+	+	r												
Butovicellidae				r														
Posidoniidae						r	r	+	+	+	r							
Aviculopectinidae						+	+	+	+	r								
Pterinopectinidae						?r	?r											
Entoliidae								r	r									
Monotidae								r	r									

and Ostreidae (1.2.4/1.2.7) (order Cyrtodontida); in the Eocene, Carditidae, Limidae, Pectinidae, and Ostreidae; and from the Oligocene to the Recent, the same families added with Arcidae (1.2.4/1.2.3/1.2.6/1.3.3) (order Cyrtodontida) (Tables 9, 10).

The group of epifaunal cemented suspension feeders included genera with some species that could lie freely on one of the valves (1.2.7/1.2.4) or have a different life mode. In the Cambrian, Ordovician, and, probably, in the Silurian, this group was absent. In the Devonian, it included rare forms of Megalodontidae (1.2.1/1.2.4/1.2.7) (order Carditida) and Pterinopectinidae (order Cyrtodontida). In the Carboniferous and Permian, this group included Pseudomonotidae (order Cyrtodontida) and Anomiidae (order Pectinida); in the Triassic, Pseudomonotidae, Terquemidae (order Pectinida), rare Ostreidae (1.2.7/1.2.4) (order Cyrtodontida), Megalodontidae, and Anomiidae. In the Jurassic, the group included Terquemidae and rare genera of the families Ostreidae, Gryphaeidae (1.2.7/1.2.4), Anomiidae, Plicatulidae, Dimyidae, and Spondylidae (1.2.7/1.2.4) (order Pectinida).

In the Early Cretaceous, forms of Gryphaeidae and rudists Caprinidae and Radiolitidae dominated, whereas the genera of other families (Terquemidae, Anomiidae, Spondylidae, Ostreidae, Plicatulidae, Dimyidae) were not numerous. The same picture is observed in the Late Cretaceous with the addition of Ostreidae and Hippuritidae to the group of common families. Starting from the Paleocene, after the disappearance of rudists and Terquemidae, Ostreidae gained the most important role while the other above-listed families were represented by few genera (Table 12).

Similar to epifaunal groups, the groups of semi-infaunal suspension feeders, both endobyssate (1.3.1, 1.3.2) or byssus-free (1.3.4), with or without siphons, had a mixed composition as was already noted in the description of epifaunal suspension feeders. It is worth

Table 9. Changes in the composition of main families belonging to epifaunal free-lying suspension feeders without siphons (1.2.4)

Family	€	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–R
?Fordiliidae	r	r																
?Archaurellidae	r																	
Lunulacardiidae			r	+	r	r												
Aviculopectinidae					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 10. Changes in the composition of main families belonging to epibyssate suspension feeders without siphons and capable of swimming above the sediment (1.2.4a)

Family	€	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–R
?Aviculopectinidae						+	+											
Posidoniidae						r	r	+	+	+	r	r						
Pectinidae								r	+	+	+	+	+	+	+	+	+	+
Limidae						r	r	+	+	+	+	+	+	+	+	+	+	+
Entoliidae										r	r	r						

Table 11. Changes in the composition of main families belonging to semi-infaunal suspension feeders without siphons and byssus (1.3.4)

Family	€	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–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														+	+	+	+	+

noting that endobyssate and/or epibyssate forms were more widespread in the Early–Middle Paleozoic time. In the second half of the Ordovician these were representatives of families Modiomorphidae and Ambonychiidae; in the Silurian, Cardiolidae, Modiomorphidae, and Pterineidae; and in the Devonian, Pterineidae and Ambonychiidae. In the Mesozoic, this group included Bakevellidae, which also had free-lying forms (1.3.1/1.2.1/1.2.4), and Mytilidae. Carditidae became widespread starting from the Paleocene; and Arcidae,

Table 12. Changes in the composition of main families belonging to cemented suspension feeders (1.2.7)

Family	€	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–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 13. Changes in the composition of main families belonging to infaunal and epifaunal detritivores without siphons (2.1)

Family	€	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–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	+	+	+	+	+

in the Eocene. Some species of these families belonged to endobyssate or free-lying forms, superficially burrowing and/or resting on the ground (Arcidae).

Endobyssate and/or superficially burrowing forms with the posterior part projecting out of the substrate (1.3.1/1.3.4) were represented in the Ordovician by the family Cyrtodontidae. In the Silurian–Devonian, representatives of this family were rare; in the Devonian this group included some Carditidae with a broader ethological range (1.1.1/1.2.1/1.2.4/1.3.1/1.3.4). In the Carboniferous, the semi-infaunal byssate and byssus-free forms included rare genera of Astartidae, which also had some infaunal representatives (1.1.1, 1.1.4/1.3.2/1.3.4). In the Permian, the group was enriched with similarly ethologically diverse Inoceramidae (1.2.4/1.3.4/1.2.1/1.3.1) and rare Trigoniidae.

In the early Triassic, semi-infaunal forms were rare, and in the second half of the Triassic they were represented by Trigoniidae (which could also be infaunal), superficially burrowing forms (1.1.1/1.3.1/1.3.4) (order Actinodontida), Mytilidae (1.3.2/1.2.2), Bakevellidae (1.3.1/1.2.1/1.2.4), and more rare Astartidae, Inoceramidae, and Carditidae. In the Jurassic and Cretaceous, the most abundant groups were represented by Trigoniidae, Astartidae (1.1.1, 1.1.4/1.3.4/1.3.2), Mytilidae, Bakevellidae, and, starting from the Late Cretaceous, also by Carditidae and Pectinidae, with only some of their forms being endobiontic. Inoceramidae were less frequent. Carditidae, Mytilidae, Trigoniidae, Astartidae dominated in the Paleocene and Eocene; in the Eocene they were accompanied by Montacutidae (1.1.1/1.2.4/1.3.4), and Trigoniidae lost their leading role. In the Oligocene–Neogene, semi-infaunal bivalves were represented by some genera of the families Carditidae, Pectinidae, Mytilidae, Arcidae, and Montacutidae, and from the Pliocene, also by Condylocardiidae (1.1.2/1.2.1/1.3.1), which were scarcely known since the Eocene. In the modern fauna these very abundant families are accompanied by Astartidae and Galeommatidae (1.3.1/1.2.1/1.1.2) (Tables 6, 11).

Detritivores were considerably less diverse and thus experienced much less changes through time.

Cambrian superficially burrowing bivalves without siphons were represented by rare forms of uncertain classification conventionally placed in the family Praenuculidae. From the Early Ordovician to the Devonian, undoubted representatives of this family were widely known although not very diverse. From the beginning of the Ordovician they co-occur with few genera of the

Table 14. Changes in the composition of main families belonging to infaunal detritivores with siphons (1.2)

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 15. Changes in the composition of main families belonging 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													+	+	+	+	+	+

family Ctenodontidae that is known up to the Permian. In the Ordovician, this group also included rare Tironuculidae. Several genera of the family Nuculidae appeared in the second half of the Ordovician and remained rare up to the end of the Paleozoic. In the Mesozoic and Paleocene the genus-level composition of this family amounted to three genera; from the Eocene to the Recent, up to six genera (Table 13).

Infaunal siphonate detritivores were more diverse. In the Paleozoic and the beginning of the Mesozoic they were represented exclusively by protobranchs with the leading role of the families Malletiidae and Nuculanidae. The former group is known from the second half of the Ordovician. It was most diverse in the Ordovician–Silurian, the second half of the Triassic to Jurassic, and in the extant fauna, although in each period the family was represented by no more than ten genera. The first Nuculanidae are known from the Devonian, but they reached significant diversity only starting from the Late Cretaceous. Nevertheless, this group played a rather important role in Phanerozoic seas.

The group of siphonate detritivores included genera of the order Venerida (Autobranchia): forms of some families of the superfamilies Tellinoidea (Tellinidae, Psammobiidae) and Scrobicularioidea (Scrobiculariidae) (Table 14).

Septibranch predators are unknown up to the Jurassic time. They had a very restricted distribution and a uniform genus-level composition in the Phanerozoic. One genus of the family Cuspidariidae is known from the Jurassic–Early Cretaceous, three genera of the family Poromyidae have been recorded from the Late Cretaceous, and one genus of the family Verticordiidae is known from the Paleocene. The genus-level composition of Cuspidariidae and Verticordiidae showed a slight growth in diversity during the Cenozoic, but it did not exceed 5–9 genera (Table 15).

CONCLUSIONS

Bivalve mollusks, like other benthic organisms, were influenced by many factors of which the most important are their relationship with a substrate, degree of mobility, and feeding mode. Thirty ethological-trophic groups were recognized on the basis of the analysis of these characteristics. The defined groups comprise several main cohorts, like epifaunal, semi-infaunal, and infaunal suspension feeders and superficial and deeply burrowing detritivores. Passive predators (septibranchs) were less widespread.

Each ethological-trophic group consisted of forms with a similar morphology, thus allowing the ethology of fossil bivalve mollusks to be assessed.

Most groups have already been known since the early Paleozoic. Among the groups that appeared later are only deeply burrowing forms with well-developed siphons, forms dwelling in secreted carbonate tubes, epibyssate and endobyssate bivalves with a single siphon, epibyssate ones with two siphons, and cemented suspension feeders. But many groups were still represented by few genera.

In the early Paleozoic, the dominant group included semi-infaunal suspension feeders, while epifaunal sestonophages and forms with both epibyssate and endobyssate adaptations were numerous. Since the Devonian and up to the end of the Paleozoic, the role of epifaunal suspension feeders grew, and that of semi-infaunal forms decreased. Scarce infaunal suspension feeders and detritivores were dominated by genera without the mantle line sinus, i.e., without siphons.

In the Mesozoic, epifaunal suspension feeders dominated, semi-infaunal forms decreased notably in numbers, while the number of infaunal suspension feeders increased with the main role of siphonate genera. Detritivores had a more limited distribution and by that time included more forms with siphons.

Generally, during the Phanerozoic, the role of semi-infaunal suspension feeders decreased gradually, having reached their maximum in the Early Paleozoic. At the same time, the role of epifaunal suspension feeders increased from the early Ordovician up to the Mesozoic inclusive (with a maximum in the Triassic).

At the Mesozoic–Cenozoic boundary, the number of epifaunal forms dramatically dropped with a correlative sharp increase in the number of infaunal suspension feeders with siphons, although the number of infaunal genera without siphons has decreased too. The increased diversity and abundance of infaunal sestonophages was probably caused by the increasing activity of predators.

The role and diversity of detritivores during the entire Phanerozoic was clearly less than that of suspension feeders (Fig. 3).

The main trophic groups of bivalve mollusks, detritophages and sestonophages, differed in evolutionary potentials, with a faster evolution of suspension feeders. It accounts for a considerably larger fluctuations in phytoplankton content, the main nutrition resource of suspension feeders, compared to much more stable content of organic substances, including bacteria, in deposits. Special studies revealed much shorter time ranges of genera of suspension feeders (Levinton, 1974). For example, the analysis of selectivity in extinction of bivalves at the end of the Cretaceous has shown that the rate of extinction of sestonophages was about twice as high as that of detritophages (Jablonski and Raup, 1995). The trophic structure of communities of detritophages was considerably more conservative, and the number of ethological-trophic groups among them was disproportionally lower than in suspension feeders.

The taxonomic structure of individual ethological-trophic groups varied during the Phanerozoic. It means that they consisted of families with species that had identical ecological preferences, were not closely related, but had similar morphology, thus contributing to the appearance of homeomorphic taxa.

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