Heteromorph Ammonoids of the Triassic: A Review

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Abstract—Tiny heteromorphs that suddenly appeared at the end of the Norian possessed semievolute, completely straight or slightly curved, twisted or turriconic shells, with coarse ornamentation and a simple four-lobed suture. They are represented by one superfamily, three families, six genera, and about thirty species. Apparently, they evolved from the Cycloceltitidae with a monomorph shell. The geographical range of the Triassic heteromorphs is wide. Their localities are known in the Tethyan Realm (from Sicily to Timor) and along the Pacific coast (from Chukotka to the Molucca Islands, from the Yukon Territory and British Columbia to Chile and Argentina). The ethology of heteromorphs remain mystery. They either crawled on the bottom or floated in the water. The extinction of heteromorphs, like that of all ceratitids, was apparently caused by a combination of unfavorable abiotic events at the very end of the Rhaetian, i.e., a sharp global drop in sea level and short-term global cooling resulting from intense volcanism leading to the pollution of the atmosphere by the products of the eruptions and a considerable decrease in the Earth's insolation.

Key words: Rhaetian, heteromorph ceratitids, classification, phylogeny, taphonomy, geography, ethology, extinction.

INTRODUCTION

It is well known that ammonoids first appeared in the Early Emsian. Their history began from gradual, though rapid, coiling of the straight bactritid shell into a planispiral shell, first with loose and later with contacting whorls (Fig. 1). This remarkable event is most fully recorded in the Hunsrück Shale of Germany (Schindewolf, 1935; Erben, 1964, 1966) and Zlichovian–Dalejan beds of the Czech Republic (Chlupáč and Turek, 1983). The resulting planispiral shell was evidently such a successful functional morphological construction that it survived until the extinction of the ammonoids at the end of the Maastrichtian, i.e., for almost 340 Myr (Gradstein *et al.*, 2004). The shell varied from completely flat (Triassic *Pinacoceras*) to spherical (Jurassic *Sphaeroceras*) and could be completely smooth or strongly ornamented. The monomorphic pattern of the whorl coiling always remained the major feature.

However, there were episodes in ammonoid evolution when shells with a different architecture quite unexpectedly appeared: with completely or partly uncoiled whorls, as in their Early Devonian ancestors, including screw-shaped, coiled with a hook-shaped curve, or twisted into the most peculiar shapes. The character of the coiling could change repeatedly during the life of the ammonite. For instance, the turriconic juvenile shell was gradually transformed at later ontogenetic stages into a flat spiral or into a construction of various hooks. These unusual shells came to be called heteromorphs, or collateral forms.

Kakabadze (1985, 1988) tried to classify this great variety. He suggested a morphological classification of heteromorph ammonoids. Kakabadze subdivided them into 31 groups based on coiling type, each of which was named after a characteristic taxon: protancylocone (from *Protancyloceras*), criocone (from *Crioconites*), ancylocone (from *Ancyloceras*), and so on (Fig. 2). According to the coiling type of the initial whorls, he united these morphological groups into four subtypes. The first subtype of Kakabadze included symmetrical shells which began uncoiling from the second whorl (Fig. 2, groups 1–10), the second included symmetrical shells that straighten from the second whorl (Fig. 2, groups 11–14), the third included symmetrical shells with contacting initial whorls (Fig. 2, groups 15–19), and the fourth included all asymmetrical shells (Fig. 2, groups 20–31). The development of a certain morphotype usually begins from the second whorl. In all cases, the ammonitella of heteromorphs had a normally coiled shell composed of a protoconch and initial whorl. According to Kakabadze (1985, p. 378), the proposed groups of heteromorphs represent ecologically similar morphotypes.

Heteromorphs have for a long time attracted the attention of scientists not only by their strange shape, which is "biologically absurd" according to Dacqué (1935, p. 32), but also by the suddenness of their appearance in the fossil record, which occurred three times: at the end of the Triassic, in the Late Bajocian–Middle Callovian, and the early Tithonian–Cretaceous. Their appearance is interpreted by some authors as an evidence of phylogenetic degeneration preceding extinc-
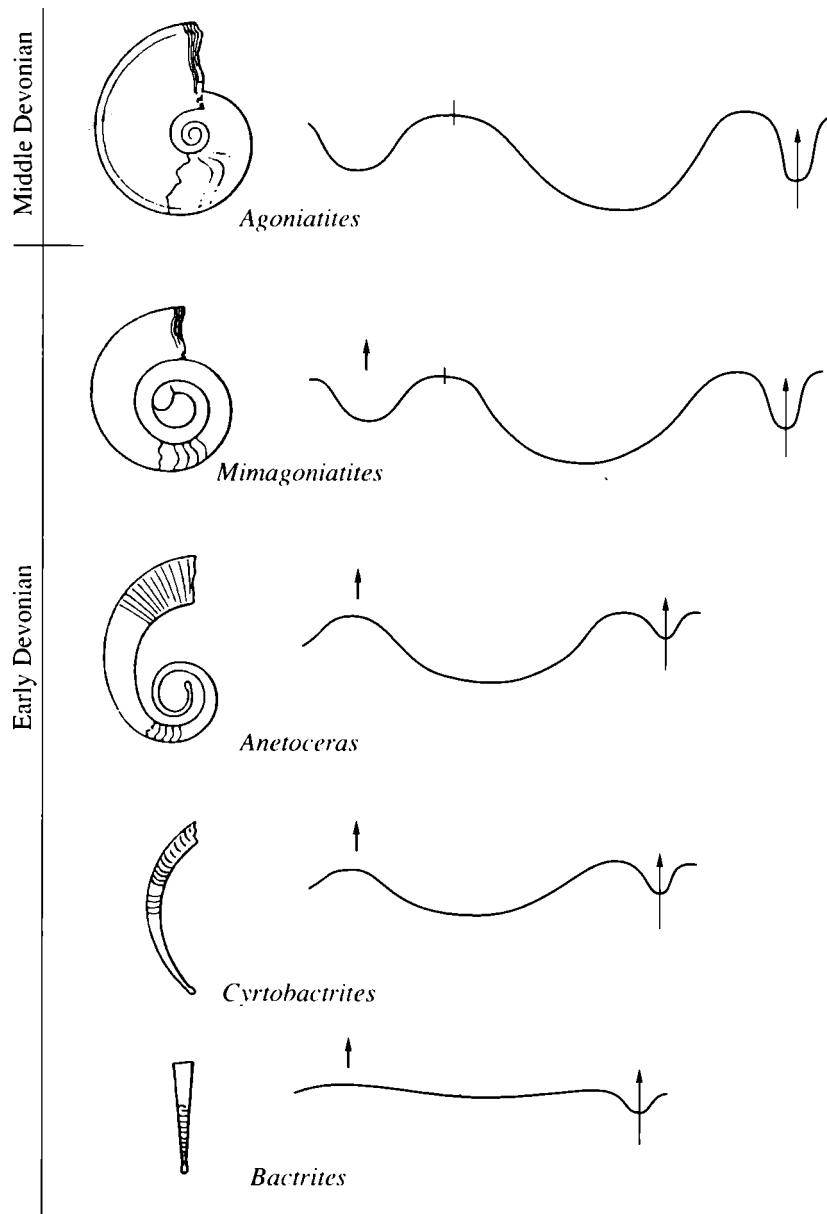
Fig. 1. Transition from the straight shells of bactritids to the spirally coiled shell of ammonites (Wiedmann, 1969).

tion (Swinnerton, 1930; Schindewolf, 1936, 1950; Müller, 1955), whereas others consider it to be an example of ecological specialization (Wiedmann, 1969, 1973a; Dietl, 1975, 1978; Dietl *et al.*, 1978; Kakabadze and Sharikadze, 1993; Cecca, 1997, etc.).

RESULTS AND DISCUSSION

Biochronology of the Terminal Triassic

After the Emsian, heteromorphs reappeared for the first time at the end of the Triassic at the Norian–Rhaetian boundary. Based on the Alpine sections of Austria, four ammonite zones are recognized in this stratigraphic interval: *Sagenites quinquepunctatus, S. reticulatus,*

Vandaites stuerzenbaumi (with the *"Choristoceras" haueri* and *V. stuerzenbaumi* subzones) and *Choristoceras marshi* (with the *Ch. ammonitiforme* and *Ch. marshi* subzones). Although the Rhaetian is an officially accepted stage, its geochronology is not formally established (Gradstein *et al.*, 2004). Hence, the stage affinity of the above zones is debatable. Some stratigraphers assigned all of them to the Rhaetian (Popow, 1961; Wiedmann, 1974; Wiedmann *et al.*, 1979), others draw the lower boundary of the Rhaetian at the base of the *reticulates* Zone (Tuchkov, 1962; Dagys and Dagys, 1990, 1994; Gradstein *et al.*, 1995), and some others raise it to the base of the *stuerzenbaumi* Zone (Krystyn, 1987, 1990; Kozur, 2003).
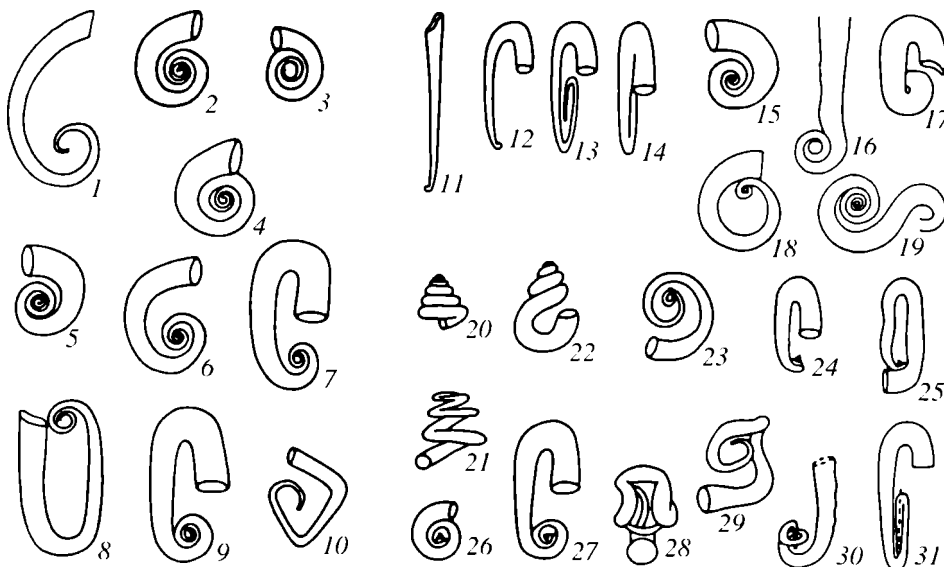
Fig. 2. Major morphotypes of heteromorph shells: (*1*) protancylocone, (*2*) criocone, (*3*) matheronicone, (*4*) pseudothurmannicone, (*5*) ammonitoceracone, (*6*) hoplocriocone, (*7*) ancylocone, (*8*) lytocriocone, (*9*) pseudocriocone, (*10*) trianglicone, (*11*) baculicone, (*12*) hamulicone, (*13*) hamiticone, (*14*) ptyhocone, (*15*) choristocone, (*16*) rhabdocone, (*17*) scaphicone, (*18*) leptocone, (*19*) pravitocone, (*20*) turricone, (*21*) emperocone, (*22*) nostocone, (*23*) scalaricone, (*24*) heterocone, (*25*) longiheterocone, (*26*) imericone, (*27*) colchicone, (*28*) nipponicone, (*29*) apertonipponicone, (*30*) muramotocone, and (*31*) rhyoptychocone (Kakabadze, 1988).

Until recently, I supported the first of these three opinions, believing that the appearance of heteromorphs in the *quinquepunctatus* Zone can be considered as an event that reliably marks the basal Rhaetian boundary at this particular level (Shevyrev, 1986, 1990). However, the overwhelming majority of modern stratigraphers are inclined to the second variant of the boundary. Apparently, Tozer (Orchard and Tozer, 1997) is also inclined to accept this level, although he did not recognize the Rhaetian at all and referred all the above zones to the Upper Norian (Tozer, 1980, 1984, 1994b).

Indeed, there are serious reasons to draw the Rhaetian boundary at the base of the *reticulatus* Zone. First of all, this level is marked by the almost complete disappearance of the bivalve genus *Monotis*, which previously had a global distribution, a decrease in the generic diversity of the monomorph ceratitids by more than one-third, the appearance of heteromorph cochloceratids, and the renewal of conodont assemblages (Orchard *et al.*, 2001). In addition, as shown by geochemical studies of the boundary beds of the Norian and Rhaetian near Williston Lake in northeast British Columbia (Sephton *et al.*, 2002), the above boundary coincided with sharp positive deviations in the isotopes of organic C and N. These distortions are interpreted as the result of stagnation and stratification of oceanic water, i.e., events that led to anoxia, accumulations of organic shales, and reduction of nitrates in the surface waters. Taking into account the large scale of the above biotic and geochemical events, I accept the lower boundary of the Rhaetian at the base of the *reticulatus* Zone. The upper boundary of the Rhaetian coincides with the base of the Jurassic and is traditionally drawn at the level of the first appearance of psiloceratids.

Morphology and Classification of Triassic Heteromorphs

The diversity of Triassic heteromorphs is relatively low, while each genus represents a distinct morphotype. In this respect, they are distinguished from Jurassic heteromorphs, in which shells of different types may be found within one species (planispiral, helicoidal, or straight) (Dietl, 1975, 1978). Another feature of heteromorph ceratitids is that they do not have shells with a hook-shaped body chamber, which are widespread among Cretaceous heteromorphs (Kaplan, 2002).

Some Triassic heteromorphs have a shell that is completely straight or slightly curved in the same plane as the ammonitella. They include the genus *Rhabdoceras* with two subgenera: *Rhabdoceras* (Figs. 3a–3c) and *Cyrtorhabdoceras* (Figs. 3d–3e). In other heteromorphs the phragmocone is formed by normally coiled whorls, and only the body chamber begins to become uncoiled. In some cases it uncoils in a screw-shaped manner (genus *Peripleurites*) (Figs. 3f–3i), while in others it uncoils in the same plane as the phragmocone (genus *Choristoceras*) (Figs. 3j–3l), while in some cases the volutions of the shell form a helicoidal spiral (genus *Vandaites*). Of the above genera, *Rhabdoceras* and *Peripleurites* represent the family Rhabdoceratidae, while *Choristoceras* and *Vandaites* represent the family Choristoceratidae. Finally, *Cochloceras* (Figs. 3m, 3n) and *Paraco-*
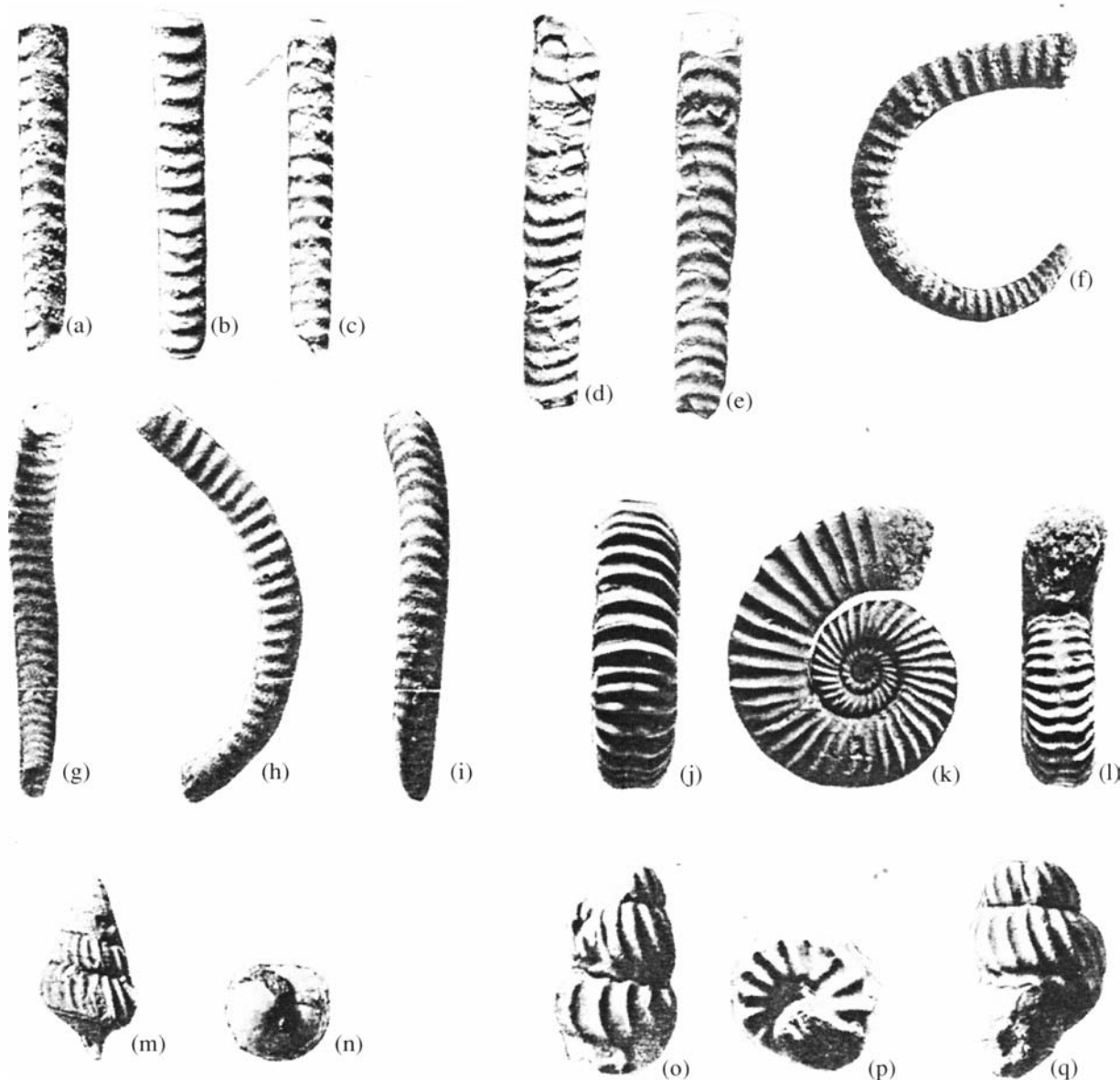
Fig. 3. Shells of Triassic heteromorphs: (a–c) *Rhabdoceras (Rhabdoceras) suessi* Mojsisovics, phragmocone, ×3: (a) dorsal view, (b) lateral view, and (c) ventral view; Austria; Rhaetian; (d, e) *Rhabdoceras (Cyrtorhabdoceras) curvatum* Mojsisovics, part of the body chamber, ×2: (d) lateral view, (e) dorsal view; the same age and locality; (f—i) *Peripleurites peruvianus* Wiedmann, (f) inner part of the phragmocone, lateral view, ×3; Peru, Suta; Rhaetian; (g–i) outer part phragmocone, ×1.5: (g) dorsal view, (h) lateral view, and ventral view; the same age and locality; (j–l) *Choristoceras marshi* Hauer, shell with a body chamber, ×3: (j) ventral view, (k) lateral view, (l) apertural view; Austria, Kendelbach Graben; Rhaetian, Kössen beds; (m, n) *Cochloceras obtusum* Mojsisovics, shell, ×2: (m) lateral view, (n) basal view; Austria, Wopfing; Rhaetian; (o–q) *Paracochloceras suessi* Mojsisovics, lectotype, ×2: (o) lateral view, (p) basal view, (q) apertural view; Austria, Stambach Graben; Rhaetian, Zlambach Marl (Wiedmann, 1973a).

chloceras (Figs. 3o–3q), which have turriconic shells, constitute the family Cochloceratidae.

All Triassic heteromorphs belong to the superfamily Choristocerataceae, which includes three families, six genera, and about 30 species. They all have small shells the diameter, length, and height of which usually do not exceed 30 mm, coarse ornamentation of transverse ribs,

and a very simple suture composed of four smooth lobes (Fig. 4).

The scheme of the classification of the Triassic heteromorphs can be represented as follows:

Order Ceratitida Hyatt, 1884

    Suborder Ceratitina Hyatt, 1884

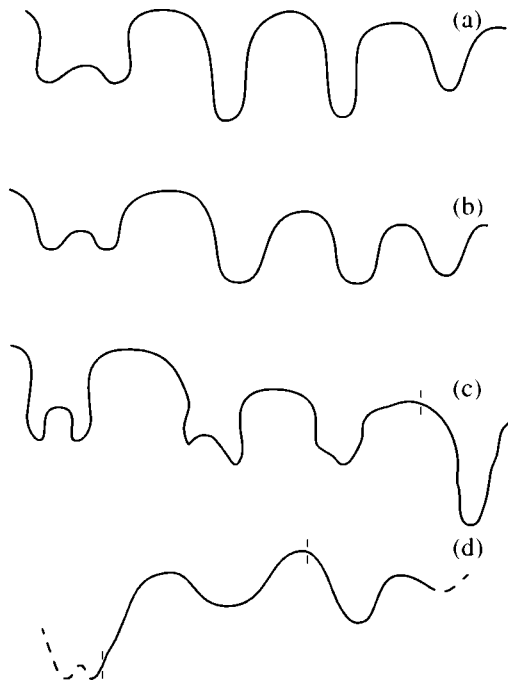   Superfamily Choristocerataceae Hyatt, 1890

Fig. 4. Sutures of Triassic heteromorphs: (a) *Rhabdoceras suessi* Hauer at WH = 7.5 mm; Austria, Hallstatt; Rhaetian; (b) *Peripleurites saximontanus* Mojsisovics at WH = 4 mm; the same age and locality; (c) *Choristoceras marshi* Hauer at WH = 6 mm; Austria, Kendelbach Graben; Rhaetian; (d) *Paracochloceras suessi* Mojsisovics at WH = 4.5 mm; Austria, Stambach Graben; Rhaetian, Zlambach Marl (Wiedmann, 1973a).

(nom. transl. Tozer, 1971 (ex Choristoceratidae Hyatt, 1890)

Family Rhabdoceratidae Tozer, 1979

Genus *Rhabdoceras* Hauer, 1860

Subgenus *Rhabdoceras* Hauer, 1860

Type species. *Rh. suessi* Hauer, 1860.

Subgenus *Cyrthorhabdoceras* Wiedmann, 1973

Type species. *Rhabdoceras suessi* var. *curvata* Mojsisovics, 1893 (= *Rh. curvatum* Mojsisovics, 1893).

Genus *Peripleurites* Mojsisovics, 1893

Type species. *P. (Choristoceras) romeri* Mojsisovics, 1883.

Family Choristoceratidae Hyatt, 1900

Genus *Choristoceras* Hauer, 1866

Type species. *Ch. marshi* Hauer, 1866.

Genus *Vandaites* Tozer, 1979

Type species. *Peripleurites (Choristoceras) stuerzenbaumi* Mojsisovics, 1893.

Family Cochloceratidae Hyatt, 1900

Genus *Cochloceras* Hauer, 1860

Type species. *C. fischeri* Hauer, 1860.

Genus Paracochloceras Mojsisovics, 1893

Type species. *Cochloceras canaliculatum* Hauer, 1860.

Roots and Phylogeny of Triassic Heteromorphs

The origin of Triassic heteromorphs is not quite clear. All modern workers consider them to be a monophyletic group, the ancestors of which should be looked for among small, normally coiled, coarsely ribbed ceratitids. Wiedmann (1969, p. 576) suggested that the genus *Hannaoceras*, which in many ways resembles *Choristoceras* could be such an ancestral taxon. Wiedmann's opinion was based on the erroneous inclusion of some Californian Carnian species into the genus *Choristoceras* and the incorrect assignment of the Late Norian Alpine species *"Polycyclus" leislingensis* Mojsisovics to the genus *Hannaoceras*. Soon after, Wiedmann discarded this hypothesis, justifiably restricting the stratigraphic range of *Hannaoceras* to the Carnian, and that of *Choristoceras* to the Upper Norian (Rhaetian), and suggested that the similarity of the above genera is a product of homeomorphy (Wiedmann, 1973a, p. 249). Later Wiedmann (Krystyn and Wiedmann, 1986) suggested that his new species *Pseudothetidites praemarshi* (family Clydonitidae) from the Hallstatt Limestone of the Upper Norian *macer* Zone of Timor was a direct ancestor of choristocerataceans. In its small shell and coarse transverse ribs terminating in two rows of ventral nodes, it indeed resembles species of the genus *Choristoceras*. However, the sutural outline of *P. praemarshi* does not support this close affinity. The suture of this species is more complex (five- rather than four-lobed), while the main lobes are serrated rather than smooth. Besides, a time gap remains between Wiedmann's species and the earliest species of the genus *Choristoceras*.

In all his phylogenetic reconstructions, Wiedmann considered *Choristoceras* to have been the ancestor of heteromorph ceratitids. This hypothesis is not supported by the fossil record. The earliest choristoceratacean was the genus *Rhabdoceras*, which should be regarded as the ancestor of all other Triassic heteromorphs (Shevyrev, 1986). It had a completely straight (subgenus *Rhabdoceras*) or slightly curved shell (subgenus *Cyrthorhabdoceras*), which only at the earliest ontogenetic stages is a compactly coiled planispiral of one and a half or two whorls (Janensch, 1906). Its surface possesses radial ring-like ribs. I believe that the ancestor of this genus belonged to the family Cycloceltitidae, species of which had small, evolute, coarsely ribbed shells with a four-lobed suture. The genus *Ophiorhabdoceras* from the basal horizons of the *cordilleranus* Zone (= *quinquepunctatus* Zone) of British Columbia has all these features (Tozer, 1994a). This genus can be regarded as an immediate predecessor of rhabdoceratids. The genus *Rhabdoceras* is related to the genus *Peripleurites* (Fig. 5), which is distinguished by the
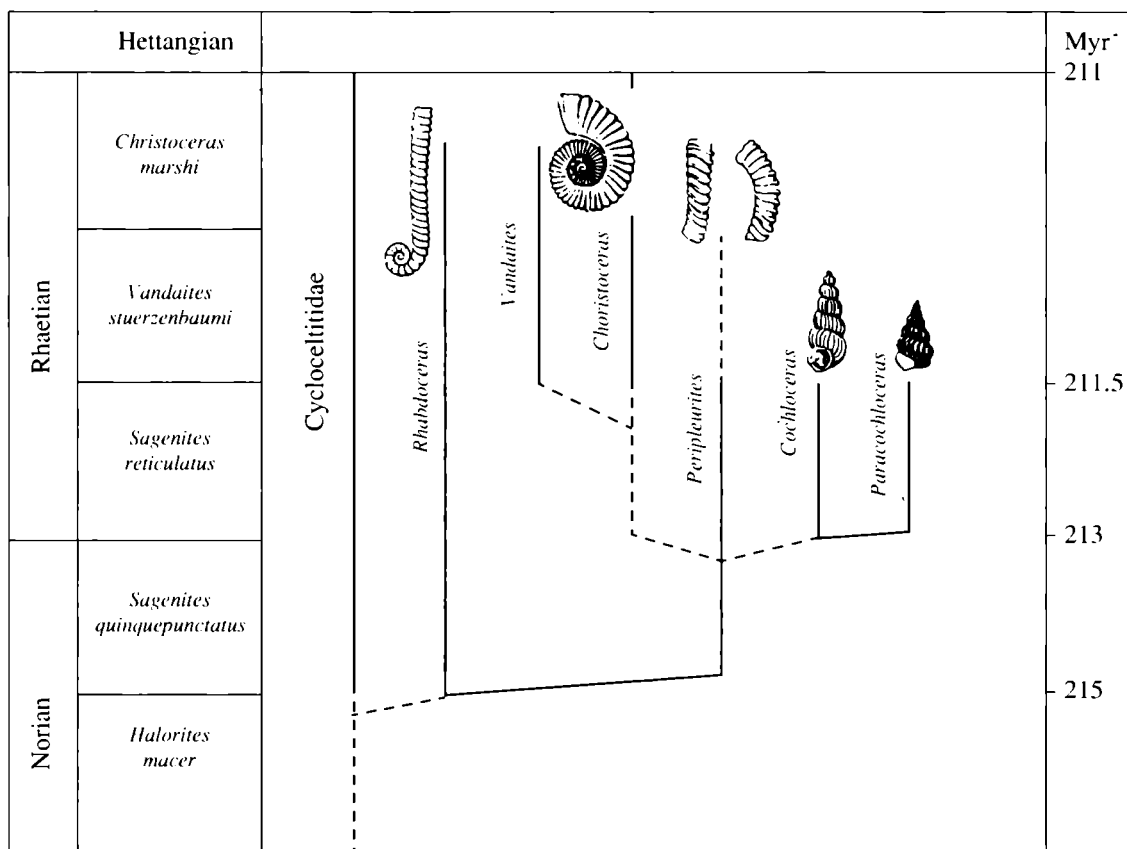
Fig. 5. Phylogenetic reconstruction of Triassic heteromorphs.

stronger curvature of the whorls of its shell (not curved in the same plane, but screw-like.) In the *reticilatus* Phase this trend could have led to the development of the tightly coiled turriconic shell of cochloceratids, which more closely resembles shells of gastropods rather than ammonoids. The genus *Choristoceras* appeared in the second half of the Rhaetian. In contrast to rhabdoceratids, it has a normally coiled planispiral shell that begins uncoiling only in the last whorl. In addition, the ribs in this genus are discontinued on the venter of the phragmocone to form nodes instead of crossing the venter as in rhabdoceratids. The origin of this genus is uncertain. It may be tentatively connected with *Rhabdoceras*. In its ornamentation *Choristoceras* is similar to *Vandaites*, which is distinguished by its helicoidal shell.

Geographical Distribution

The geographical distribution of Triassic heteromorphs is wide and interesting (Fig. 6). Their occurrences are known from several European countries, including the Austrian Alps, Italy, and Bavaria (Mojsisovics, 1893; Pompeckj, 1895; Zapfe, 1965, 1967a 1967b; Wiedmann, 1973a); Sicily (Gemmellaro, 1904); the Western Carpathians in Slovakia (Kollárová-

Andrusovová and Kochanová, 1973; Kochanová and Kollárová-Andrusovová, 1983); the Eastern Carpathians in Romania (Kutassy, 1928); the Balkan Mountains (Stara Planina) in Bulgaria (Zakharieva-Kovacheva, 1967); the Budai Mountains in Hungary (Kutassy, 1927, 1932, 1936); and the Dinaric Alps in Bosnia (Diener, 1917). In the 1960s, almost simultaneously, rhabdoceratids were discovered in the southeastern Pamirs (Kushlin, 1965) and western Chukotka (Afitskii, 1965, 1970). Triassic heteromorphs were also found in Timor (Welter, 1914; Tozer, 1980) and the Molucca Islands (Jaworski, 1915). In the New World, their localities are known from the Yukon Territory and British Columbia in Canada (Tozer, 1994a), from Nevada and California in the United States (Hyatt and Smith, 1905; Smith, 1927; Silberling and Tozer, 1968), from northwestern Mexico (González-León et al., 1996), from western Columbia (Trümpy, 1943; Kummel and Fuchs, 1953; Mojica and Llinás, 1984; Prinz-Grimm and Mojica, 1999), from the north of Peru (Jaworski, 1923; Kummel and Fuchs, 1953; Wiedmann, 1973a; Prinz, 1985; Hillebrandt, 1994), from Chile (Stipanicic, 1983; Gröschke and Hillebrandt, 1985; Hillebrandt, 1990), and from central Argentina (Riccardi and Iglesia Llanos, 1999; Riccardi et al., 2004).
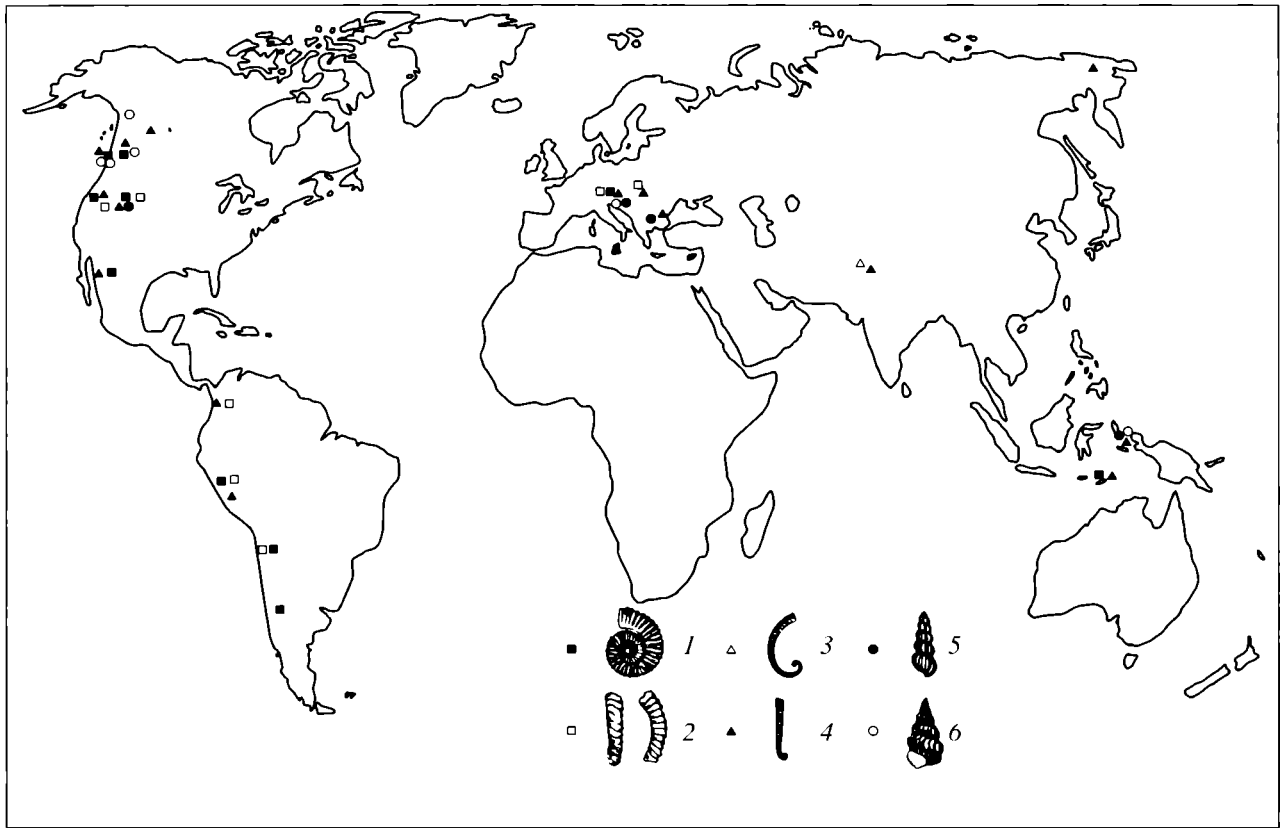
Fig. 6. Geographic range of Triassic heteromorphs. Explanations: (*1*) *Choristoceras*, (*2*) *Peripleurites*, (*3*) *Rhabdoceras (Cyr-torhabdoceras)*, (*4*) *Rhabdoceras (Rhabdoceras)*, (*5*) *Cochloceras*, and (*6*) *Paracochloceras*.

Interestingly, all localities of Triassic heteromorphs are restricted to the Tethyan Realm (from Sicily to the Molucca Islands) and to the coastline of the Pacific Ocean. The northernmost locality lies in Chukotka and, possibly, may have been brought to such high latitudes because of block movements toward the north occurring along the western Pacific coastline after the Triassic. In the western hemisphere, the localities of the Triassic heteromorphs occur along the Pacific coast of North and South Americas, from the Yukon Territory and British Columbia to central Argentina. In North America they occur in the Western Cordilleras and belong to about twenty terrains, which in the Triassic were islands and shoals of the Panthalassa and occurred at lower latitudes (Tozer, 1982, 1984). This is indicated by paleomagnetic data and the thermophilic nature of the accompanying fauna, lacking features of boreal affinity. At the end of the Jurassic, these terrains shifted northwards and joined the North American craton. The localities of Triassic heteromorphs in Chile were also formed in warm environments. This is indicated by the reefs in the synchronous beds (Prinz, 1991).

Taphonomy

Special taphonomic studies conducted in the Austrian Alps have shown that the localities of Triassic het-eromorphs are confined there to certain carbonate facies (Wiedmann, 1974, Fig. 1; Dietl *et al.*, 1978). *Rhabdoceras* shells often fill fractures in red Hallstatt limestones, which are thought to have been formed on seamounts, in marine basins with a continuous circulation supporting the oxidizing environment at the bottom. *Choristoceras* shells occur in the pelitic Kössen beds and Zlambach marls, which accumulated on either side of a barrier reef. Helicoidal shells of *Cochloceras* and *Paracochloceras* occur both in the Zlambach marls and in the fractures of the Hallstatt limestones.

Taphonomically, the section of the uppermost Triassic in the New York Canyon in west-central Nevada is very interesting. This is one of the rare outcrops displaying the Rhaetian–Hettangian transition. The Triassic is terminated there by the Gabbs Formation (a 128-m-thick series of mudstones and siltstones). It is subdivided into three members: lower (lime mudstones with thin siltstone interbeds), middle (bioclastic calcarenite packstones and calcareous siltstones), and upper (terrigenous sandy siltstones). Laws (1982) found four faunal associations in these beds. Two of these include heteromorphs. The association of *Cochloceras* found in the lower member is mainly composed of small *Cochloceras* (2 cm) and *Rhabdoceras* (4 cm). This association also includes bivalves: deposit-feeding *Nuculana* and

suspension-feeding *Myophoricardium*. Radiolarians, young shells of ammonites and bivalves, and ichthyosaur remains are abundant. The upper half of the middle member contains the *Nuculoma* Association dominated by bivalves; the protobranchians *Nuculoma* and Malletiidae and the suspension-feeding *Septocardia* comprise 80% of the association. It also includes a few cephalopod shells: *Choristoceras*, *Arcestes*, and *Pleuronautilus*.

In other regions of the world (Italian and Bavarian Alps, Sicily, Carpathians, Pamirs, Timor, Molucca Islands, Queen Charlotte Islands, etc.), the occurrences of heteromorphs are most often found in carbonate facies (sandy limestone and lenses and beds of limestone or marl). However, in Bulgaria, heteromorphs are found in clay shale; in Chukotka, in siltstone and sandstone; and in Chile, in clay shale and sandstone.

Possible Lifestyle

The lifestyle of ammonoids, including heteromorphs, is still a highly debatable subject.

Most paleontologists of the 19th century, including such respected experts as Quenstedt and Neumayr, considered ammonoids to be free-swimming mollusks. They attributed the global distribution of these extinct cephalopods to their active swimming.

Hyatt (1889), over 100 years ago, was the first to suggest a different view on the lifestyle of ammonoids. He noticed that shells of Mesozoic taxa lost the ventral (hyponomic) sinus, which was present in their Paleozoic ancestors and corresponded to the hyponomic cut in modern *Nautilus*. It was replaced by the ventral projection, or rostrum. From this, Hyatt concluded that Mesozoic ammonoids lost the hyponome and completely changed their lifestyle to become crawling, or even sessile. At the end of the 19th–beginning of the 20th century, this view on ammonoids as benthic animals became relatively widespread. Walther (1897) was the most dedicated supporter. Among Russian paleontologists, this view was supported by Borisyak (1905) and Zhirmunsky (1914). The supporters of this interpretation based their conclusions on the zoological studies of Willey (1895, 1897, 1902) and Dean (1901), according to whom the extant *Nautilus* was interpreted as an animal mostly crawling on the bottom.

Diener (1912) proposed a reasoned criticism of this interpretation and suggested that the extant *Nautilus* apparently had free-swimming ancestors and only recently changed to bottom dwelling. In addition, due to the considerable morphological diversity of ammonoids and the essential differences of their shells, he urged great caution when making comparisons with *Nautilus*, the same conclusion that Jacobs and Landman (1993) reached many years later. In the opinion of Diener, the whole shell structure in most ammonoids was designed for swimming. This is indicated by their light hydrostatic apparatus, a venter that is often subacute to facil-

itate passage through the water, hollow spines and nodes supporting floating and stability in the water, and the bilateral symmetry of their shells. Ammonoids, sometimes reaching the size of a carriage wheel, are easier to imagine swimming than crawling on the bottom. The benthic lifestyle is not supported by the frequent presence of long, thin lateral projections of the aperture (lappets) and the relative independence of these mollusks from facies. While assuming that most ammonoids were free-swimming animals, Diener also entertained the possibility that heteromorphs were crawlers.

Diener's paper was widely discussed among specialists. It was discussed in great detail by Rozanov (1914). He made several critical comments about Diener's conclusions. The most important was that all ammonoids should not be assumed to have the same lifestyle, because even the behavior of an individual animal may have changed at different times of its life.

Apart from the above scientists, ammonoid ecology was studied by other authors (Jaekel, 1902; Rothpletz, 1909; Scupin, 1912; Frech, 1915; Naef, 1921; Bubnoff, 1922; Dunbar, 1924; Schmidt, 1925; Berry, 1928; Currie, 1957; Ruzhencev, 1962). Almost all of them considered monomorph ammonoids to a greater or lesser extent as swimming mollusks, while heteromorphs were interpreted as either crawling on the bottom or floating freely in the water. While accepting the presence of the rostrum in Mesozoic taxa, most workers did not agree with Hyatt's hypothesis of the reduction of the hyponome. For instance, Schmidt (1930) suggested that the hyponome could be bipartite, located on both sides of the ventral projection.

In most cases, conclusions on the ethology of ammonoids were hypothetical and were not supported by actual data. Therefore, Trueman's (1941) study of the actual life position of ammonoids based on calculations attracted considerable attention. These studies showed that the volume of the body chamber is usually two to three times that of the gas chambers. The position of an ammonite at rest depended on the distance between the centers of gravity and buoyancy. In evolute shells with a long body chamber, both centers almost coincide, thus reducing stability. Apparently, the ammonite with such a shell could easily change its orientation, although at rest its aperture was orientated slightly upwards. In involute shells, like *Nautilus*, the center of gravity is considerably below the center of buoyancy, thus improving stability. At rest, the aperture of such ammonites apparently faced directly upwards. Heteromorphs with a semievolute shell or hook-shaped body chamber were apparently quite stable in the water, whereas their aperture faced slightly or directly upwards. The turriconic shell, perhaps, slightly deviated from the vertical orientation.

In the present day, there is increasing interest in the way of life of ammonoids. Modern paleontologists, like their predecessors, express a wide spectrum of opinions

on this subject. The wide range of views on the ethology of ammonoids is well illustrated by the following examples. Schniepp (1976) compared the maneuverability of the compressed smooth shell of Mesozoic ammonoids with a supermodern nuclear submarine, while Richter (1980) called these extinct animals "sleepy cannibals," which sluggishly crawled on the bottom, eating their own offspring. Birkelund (1981) believed that all ornamentation of ammonites was designed to economize on the material necessary for nektonic lifestyle. In the opinion of Lehmann (1976, 1990), ammonites, by contrast, lived on the sea bottom, moving slowly in search of food. They occupied the ecological niche of modern gastropods at depths of 50–200 m. In recent years this view has received the vigorous support of Ebel (1983, 1985, 1990, 1992, 1999), a professional engineer from Markdorf. Ebel carried out mathematical calculations on models and concluded that ammonite shells were too heavy for swimming. Their shell shape was controlled by the interaction between the forces of gravity and buoyancy, which were balanced by the muscle system. Normally coiled shells are formed when the weight is considerably greater than the buoyancy. If the weight is only slightly greater, shells with uncoiled whorls develop. Ebel seems to have been convinced that all ammonites, both monomorph and heteromorph, either crawled on the bottom with their shells positioned as in gastropods, or were semisessile, or even sessile. In his reconstructions, the soft body in heteromorphs with a hook-shaped body chamber was much larger than in Nautilus and more closely resembled the body of octopuses (Ebel, 1992).

Kröger (2001), paleontologist from the University of Hamburg, published a criticism of such interpretations. He reiterated that the appearance of the phragmocone should have freed these mollusks from the need to crawl and allowed their lifting from the bottom. In their evolution, this was as important as the appearance of wings in insects. According to Kröger, it is unclear how Ebel calculated the hydrostatics of ammonoids, and why he did not use other methods of determination of the shell volume used by his predecessors (Moseley, 1838; Trueman, 1941; Currie, 1957; Heptonstall, 1970; Saunders and Shapiro, 1986), who showed that the ammonoid shell was light enough to swim in the water. Kröger criticized Ebels's attempt to ascribe crawling or sedentary existence to orthoconic cephalopods. The main problem of these mollusks was not how to increase buoyancy, but how to decrease it, because without ballast their shell would have immediately surfaced (Crick, 1988; Westermann, 1998).

Ivanov (1979) argued that ammonites were planktonic animals, mostly ambush hunters. He connected the progressive complexity of their sutures with the improvement of the attachment of the soft body to the shell to prevent its ripping off while pulling towards prey. Based on the high diversity of ammonoid shells, Ward (1986), Barskov (1989), and Westermann (1996) suggested that ammonoids could have embraced all adaptive types existing in extant cephalopods, i.e., benthic, benthopelagic, nektobenthic, nektonic, and planktonic. At the same time Westermann emphasized that it is difficult or even impossible to distinguish between benthic and pelagic ammonoids and those swimming and drifting based solely on shell buoyancy.

However, at present many zoologists and paleontologists suggest that the way of life of monomorph ammonites was similar to that of extant Nautilus, i.e., most of the time they were hanging over the bottom looking for food (Ziegler, 1963, 1967; Mutvei and Reyment, 1973; Mutvei, 1975; Nesis, 1975; Zakharov, 1978; Müller, 1978; Zuev and Makhlin, 1979; Shevyrev, 1986). The form of their shells apparently was not designed to provide maximum speed, but to give better maneuverability, i.e., the ability to swiftly change swimming direction (Bayer, 1982). Apparently, ammonites, like Nautilus, made daily vertical migrations. In the opinion of some authors, they could descend deeper than 100 m (Mutvei, 1975), while others assumed that ammonitids did not live deeper than 100–200 m, while phylloceratids and lytoceratids, possessing a stronger siphuncle, could inhabit considerably deeper zones (Westermann, 1982, 1996).

Heteromorph ammonoids are usually interpreted as benthic or planktonic animals (Kushlin, 1965; Wiedmann, 1969, 1973a, 1973b; Dietl, 1978; Dietl et al., 1978; Ivanov, 1979; Kakabadze, 1981; Klinger, 1981). Dietl (1978) and Dietl et al. (1978) suggested that the Middle Jurassic heteromorphs were likely to have been active bottom dwellers. Their biotopes could have been dense thickets of algae. The hydrostatic apparatus of these mollusks made it possible to move easily in these algal thickets and quickly change position when necessary. The specific lifestyle of Middle Jurassic heteromorphs is indirectly suggested by their almost complete absence in localities containing planispiral ammonite shells. Perhaps they lived in cracks in the sea bottom, in calm water. Their high specialization precluded heteromorph ammonites from suitably responding to changes in the environment.

The same lifestyle was first suggested for Triassic heteromorphs by Wiedmann (1969, 1973a). However, soon he became doubtful (Dietl et al., 1978) because of mixed occurrences of heteromorphs and monomorphs (phylloceratids, arcestids, and megaphyllitids), apparently capable of active swimming in most Rhaetian localities.

Based on his studies of the occurrences in the New York Canyon in Nevada, Laws (1982) concluded that Triassic heteromorphs were epibenthic scavengers-micropredators (Fig. 7). This is indirectly supported by the absence of gastropods, whose ecological niche was presumably occupied by heteromoph ceratitids, in the same beds.

Klinger (1981) assumed that Cretaceous ammonites with a torticonic shell had a similar lifestyle. Those that had a shell with a small apical angle could make swift
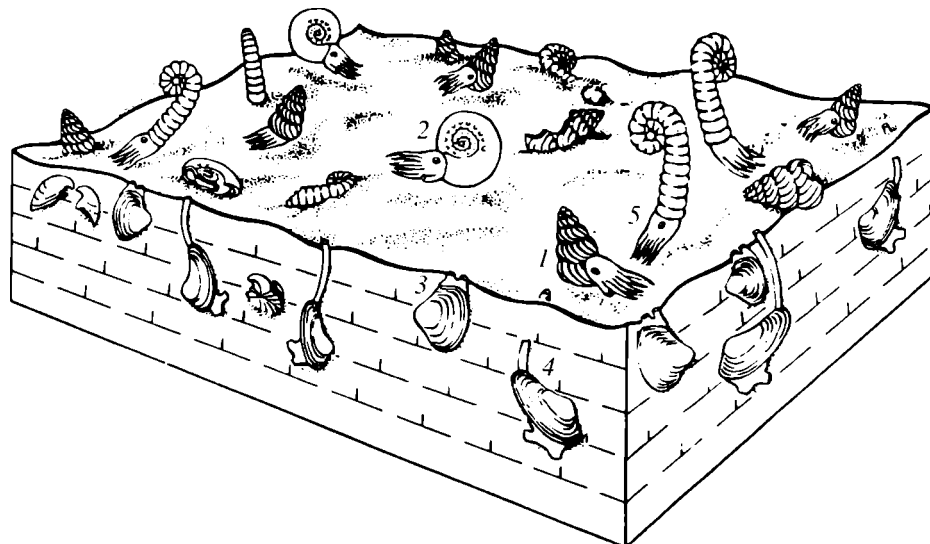
Fig. 7. Reconstruction of the community of the Rhaetian heteromorphs. Explanations: (*1*) *Cochloceras fischeri*, (*2*) *Eremites* sp., (*3*) *Myophoricardium* sp., (*4*) *Nuculana* sp., and (*5*) *Rhabdoceras suessi* (Laws, 1982).
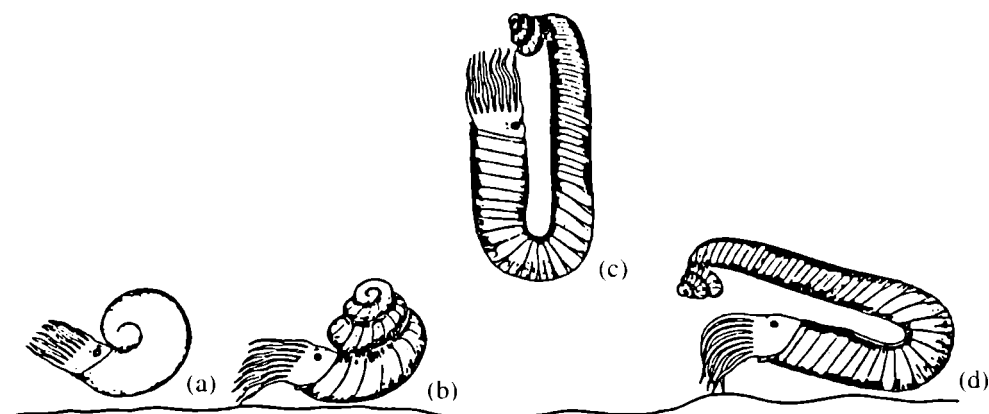

Fig. 8. Possible living position of ammonoids with a heteroconical shell: (a) at the stage of ammonitella, (b) at the helicoidal stage, (c, d) at the adult stage: (c) while swimming, and (d) while resting (Kakabadze and Sharikadze, 1993).

swipes, while torticones with a larger apical angle were simply browsing over the bottom.

Nesis (1986) had a different opinion. He emphasized that heteromorphs had a normally developed siphuncle and, hence, could regulate their buoyancy. Their center of gravity was much lower than the center of buoyancy, thus increasing their stability. With their uncoiled, coarsely ribbed shell with extremely poor streamlining they were certainly incapable of active lateral locomotion, i.e., were not nektonic animals. At the same time a normally functioning siphuncle excludes the possibility of their benthic dwelling. Nesis (1986, p. 9) believed that they were passive planktonic mollusks "capable of daily vertical migrations using an ionic mechanism of the buoyancy regulation, like cuttlefish and possibly *Spirula*." They fed on calcareous

nannoplankton and small foraminifers using mucous nets, which, as suggested by Nesis, could be present in the Cretaceous heteromorphs with a hook-shaped body chamber.

The view of Nesis is shared by Seilacher and Labarbera (1995), Westermann (1996), and Cecca (1997). They also suggest that heteromorphs were planktonic microphages making vertical migrations in the water in search of layers rich in food. A similar feeding pattern is suggested by the structure of the jaw apparatus of one of heteromorph ammonites from the Aptian of the Volga River Region (Doguzhaeva and Mikhailova, 2002). In the absence of a beak, such ammonites were unlikely to have been active carnivorous predators, while the large cavity between the jaws could have been used for filtration of water containing microplankton.

In the opinion of Kakabadze and Sharikadze (1993), those heteromorphs that changed their type of shell during ontogeny could have varied their life habits in different periods of their life (Fig. 8).

Moriya *et al.* (2003) approached the problems of the ammonoid ecology in a different way. They studied the oxygen isotopic content in the shells of planktonic and benthic organisms (foraminifers, bivalves, and gastropods) from the Campanian of Hokkaido. Based on these data, they determined the temperature of the surface and bottom waters of the Campanian basin, which were 26 and 18°C, respectively. The isotopic analysis of the shell of nine ammonite species from the same beds showed that the temperature of their carbonation did not exceed 19°C, i.e., was comparable with the temperature of the accompanying benthos. This suggested the conclusion that Campanian ammonoids, irrespective of their morphology and taxonomic affinity, were nektobenthic mollusks; i.e., lived near the bottom. In contrast to *Nautilus*, they were apparently incapable of considerable vertical migrations. However, this does not mean that all ammonoid were the same. Similar studies by Anderson *et al.* (1994) showed that the Late Jurassic stephanoceratoids were possibly planktonic and nektonic animals.

The lifestyle of ammonoids in general and heteromorphs in particular remains an intriguing and unsolved problem.

Possible Causes of Extinction

The extinction of Triassic heteromorphs is as mysterious as their lifestyle. Wiedmann (1973b, p. 314) suggested that the environments in which these ceratitids lived were profoundly affected by the Late Triassic marine regression. They became extinct because they could not survive the Early Jurassic transgression.

According to the most recent studies, the pattern of the extinction of heteromorphs was different and more complicated than was suggested by Wiedmann. Heteromorphs gradually disappeared from the fossil record. At the very beginning of the Rhaetian (*reticulatus* Phase), they included five genera; in the middle of the Rhaetian (*stuerzenbaumi* Phase), only three or four genera; at the beginning of Late Rhaetian (*marshi* Phase), three genera; and in the very end of the Rhaetian, only one genus, *Choristoceras*. Heteromorphs finally became extinct along with other ceratitids at the Triassic–Jurassic boundary. In this connection, the record of the genus *Choristoceras* from the Jurassic beds of the New York Canyon in Nevada (above the very basal beds in the Hettangian) (Guex, 1995; Guex *et al.*, 2004) is extremely surprising. Its sudden appearance at this level after the Rhaetian extinction is similar to the resurrection of the biblical Lazarus. Nowhere else have ceratitids been found in the Jurassic.

The extinction of heteromorphs during the short-term global regression and several other major geolog-ical events occurred at the end of the Rhaetian. Studies conducted in recent years on the Queen Charlotte Islands (Ward *et al.*, 2001, 2004), in Hungary (Pálfy *et al.*, 2001), in southwestern England and in eastern Greenland (Hesselbo *et al.*, 2002), and in the New York Canyon in Nevada (Guex *et al.*, 2003, 2004) revealed a sharp negative excursion of organic C isotopes in the Upper Rhaetian. This anomaly is considered to have resulted from a biological crisis that caused the destruction of the primary production in marine ecosystems (Guex *et al.*, 2004). The above events coincided with a general rise in volcanic activity in the magmatic province of the Central Atlantic where Pangea was breaking up (Cohen and Coe, 2002). The volcanism was accompanied by the eruption of sulfate aerosols and other pollutants (chlorine, heavy metals, acid rains) into the atmosphere, which significantly reduced the penetration of solar radiation and caused short-term climatic cooling.

Thus, the extinction of ammonoids at the end of the Rhaetian apparently was produced by a combination of several unfavorable conditions: a sharp global drop in sea level and simultaneous intensification of volcanism, which resulted in atmospheric pollution, exclusion of sunlight, and climatic cooling.

ACKNOWLEDGMENTS

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