Chapter 19

Crises in Ammonoid Evolution

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1. Paleozoic Ammonoids

During the Devonian, Carboniferous, and Permian periods, several severe changes occurred in the configuration of the tectonic plates, resulting in major changes in the areas of oceans and epicontinental seaways. The relatively rapid rate at which ammonoids evolved allows detailed information on changes in the environmental conditions and geological events that influenced the habitats of these animals (House, 1985a,b, 1989; Kullmann, 1983, 1985).

Periods of mass extinction have been discussed intensively, first by Schindewolf (1954) and Newell (1967) and then in detailed ammonoid studies by House (1983, 1989). Fluctuations of sea level in connection with anoxic oceanic overturns are regarded as major factors causing drastic changes in

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Table I. Number of Ammonoid Species (Bactritida Omitted) in the Paleozoic[a]

	Rad. Age	Myr	Spec.	Spec/Myr
Lower (part) and Middle Devon.	395–368	27	317	11.7
Frasnian	368–363.3	5	155	31.0
Famennian	363.3–354	10	660	66.0
Lower Carboniferous	354–319	35	959	27.4
Upper Carboniferous	319–295	24	512	21.3
Lower Permian	295–272	23	359	15.0
Upper Permian	272–250	22	442	20.0
Devonian (part)	395–354	41	1115	27.2
Carboniferous	354–295	59	1464	24.8
Permian	295–250	45	788	17,5
	395–250	~145	~3700	~25

[a]Rad. Age, estimated radiometric age, based on data derived from a number of sources (Claoué-Long *et al.*, 1992; Harland *et al.*, 1990; Jones, 1988; Menning, 1992; Roberts *et al.*, 1991); Myr, estimated duration in millions of years; Spec., approximate number of species based on data from the data base GONIAT, Tübingen (Korn and Kullmann, 1993); Spec/Myr, number of species per million years.

ammonoid diversity (House, 1989; Becker, 1993a,b). Global geotectonic influences, i.e., intervals of tectonic unrest in various parts of the world, are also thought to be reflected by changes in diversity (Kullmann, 1985; Korn and Kullmann, 1988). However, the fact that major diversity fluctuations seem to have occurred more frequently and more intensely during the Devonian than during the Carboniferous and the Permian, which were characterized by widespread geotectonic activities (Becker and Kullmann, Chapter 17, this volume), is in direct contrast to the idea that plate tectonic movements were the major source of perturbations in the ammonoid record (Kullmann, 1994). In addition, a number of as yet unidentified environmental, tectonic, and genetic factors (Ziegler and Lane, 1987) may also have contributed to changes in ammonoid diversity.

The overall diversity of Paleozoic ammonoids is reflected by the number of recognized species during the major time units of the Devonian, Carboniferous, and Permian (Table I). In this chapter, the number of Paleozoic taxa (species and genera) is based on data from the GONIAT data base, Tübingen, version 2.40 (Kullmann *et al.*, 1993; Korn and Kullmann, 1993; Korn *et al.*, 1994). Because this data base is not yet completed, these numbers represent approximations of the real numbers of taxa; taxa based on insufficient material or inadequate descriptions are omitted. Representatives of the Bactritida are extremely rare and insufficiently known and are, therefore, not included in this study.

1.1. Devonian

Ammonoids appeared suddenly in the upper Lower Devonian (lower Emsian, lower Zlichovian) with several lineages. The most important group was the Mimosphinctidae, loosely coiled ammonoids with a perforate umbilicus and a suture consisting of two or three lobes. Several species exhibited rather complicated ornament. The Auguritidae, known from only two localities in Central Europe and the Northern Urals, are the only forms with complicated sutures on the ventral side.

The earliest ammonoids (see Chapter 17, this volume, Fig. 2), about 50 species belonging to 13 or 14 genera, seem to have been widespread in the Northern Hemisphere. They are known from nearly 50 localities: Czech Republic, France, Germany, Russia (Northern Urals, Siberia), Spain, China, Middle Asia, and North America (United States, Canada).

During the uppermost part of the Zlichovian, the number of species seems to have decreased. It is not known, however, if there was a drastic decline of species immediately at the top of the Zlichovian. House (1985a, 1989) suggested that a special extinction event ("Daleje event") occurred at that time, which was related to a widespread facies change to black mudstones.

Ammonoid diversity was low at the base of the upper Emsian (Dalejan) but began to increase again in the middle part of the upper Emsian in the *serotinus* conodont zone. The early Zlichovian Mimagoniatitidae gave rise to two important groups, the Anarcestidae and Agoniatitidae, both of which proliferated in late Early Devonian and Middle Devonian. During Dalejan time, about 30 species were present and are recorded from more than 50 localities in Europe, North Africa, Central Asia, China, and North America.

In Eifelian and early Givetian times, the number of species increased to 120–130, and more than 30 genera can be counted in this time interval of about 10 to 15 million years. Slight changes in the composition of ammonoid faunas (extinction of *Pinacites*, appearance of *Tornoceras*) at the end of the Eifelian and beginning of the Givetian have led to the inference that a minor extinction event called the "Kacák event" occurred at this time (House, 1985a).

A total changeover in ammonoid succession was marked by the extinction of the index genus *Maenioceras* and the families Anarcestidae, Agoniatitidae, and Pinacitidae in the middle Givetian (middle *varcus* conodont zone); this is assumed to be connected with the Taghanic event. Except for *Tornoceras* and *Protornoceras*, no other genus is recorded as crossing this boundary; 12 genera with more than 30 species became extinct.

Following this drastic extinction event, the new stock of ammonoids included ones with complex sutures. Conch form as well as shell surface features varied considerably. Almost 20 new genera with 75 species are recorded at the start of the late Givetian and Frasnian intervals. The guide genus for the upper Givetian is *Pharciceras* (with about 20 species); this genus is restricted to the upper Givetian (*Pharciceras* Stufe); 11 genera with more than 120 species became extinct at the end Givetian at what is called the "Frasnes event" (House, 1985a).

Only five genera survived; about 20 genera and 70 species originated at the beginning of Frasnian time (*Manticoceras* Stufe; House, 1985a). One hundred thirty species (in 22 genera) are recorded from this interval. Among Frasnian goniatites, several genera with multilobate sutures were present, e.g., the Beloceratidae; variation in sculpture was minor.

At the top of the *Manticoceras* Stufe, the "Kellwasser event" apparently diminished the goniatite faunas; more than 40 species became extinct, and only four genera survived into the uppermost Frasnian *Crickites* zone (I delta). However, 70 species were still present.

The lower Famennian *Cheiloceras* Stufe is characterized by Tornoceratina with convex growth lines; the number of genera increased again to about 35, with 150 species. In general, the diversity in conch shape and sutural differentiation was relatively low. At the end of this time interval most genera and species disappeared. Because of an apparently short gap in one of the most complete sections (Enkeberg, Sauerland, Germany), an extinction event called the "Enkeberg event" has been postulated (House, 1985a).

The *Prolobites* Stufe that followed is marked by the appearance of the Clymeniida, which show migration of the siphuncle to a dorsal position during early ontogeny. The number of genera and species increased again to 45 genera (20 clymeniids, 25 tornoceratids) with about 180 species; these were the most diverse ammonoid faunas that existed in the Devonian.

The *Platyclymenia* Stufe is characterized by clymeniids that exhibit a conspicuous ornamentation and sculpture; index fossils include representatives of *Platyclymenia*. The diversity of the clymeniids stagnated; the tornoceratids decreased considerably (20 genera of clymeniids and 14 genera of tornoceratids, about 100 species in total). During this time span, black shales were deposited in at least parts of the Rheinische Schiefergebirge, known as the "annulata event." It is not known if this event had any global influence on the overall evolution of the ammonoids.

The last stage of Famennian ammonoid evolution (*Clymenia* and *Wocklumeria* Stufen) witnessed a tremendous diversification in conch form and sutural configuration in the clymeniids as well as in the tornoceratids but less in the prionoceratids. Clymeniid diversity increased to over 40 genera (10 genera of Goniatitida; a total of 275 species) and reached a second maximum in the uppermost Famennian *Wocklumeria* Stufe (Korn and Kullmann, 1988). The peak of this development was reached shortly before the final decline and extinction of the Clymeniida. In the last zone with diverse clymeniid faunas, the "upper *paradoxa* zone," the number of genera dropped to about 20 clymeniid and six goniatitid genera, and no more than about 100 species were present. The last representative of the Clymeniida occurred just below the Devonian–Carboniferous boundary; only a few (perhaps two) goniatitid lineages crossed that boundary. House (1985a) regarded this crisis as influenced partly by euxinic black shale facies of the Hangenberg Schiefer ("Hangenberg event").

1.2. Carboniferous (Mississippian, Pennsylvanian)

After the drastic decline at the end of the Devonian, goniatites proliferated again in the early Tournaisian (see Chapter 17, this volume, Figs. 5 and 6). In the lower Tournaisian, 80 species (12 genera) were present, and during the Lower Carboniferous (Mississippian), the diversity of ammonoids increased almost continuously. This is especially true for the Viséan; in early Viséan time, 140 species (more than 30 genera) can be recognized. At the end of the late Viséan a maximum of more than 500 species (almost 100 genera) was reached. It must be taken into account, however, that these intervals are of extremely long duration; the early Viséan is considered to span 9 million, and the late Viséan and early Namurian, 12 million years.

The absolute peak in the diversity of Paleozoic ammonoids was reached in the uppermost portion of the upper Viséan (middle and upper Chesterian). Several new features appeared, such as a change in the mode of coiling of the inner whorls (triangular coiling of the inner whorls), an increase in the size of the umbilicus of the inner whorls, and an increase in sutural elements and mode of sutural development. Most taxa of species and generic rank lasted only a short time (Kullmann, 1985).

Almost at the top of the Lower Carboniferous, most of the new goniatite species and genera of the *Eumorphoceras* Stufe (E) disappeared again; of 85 species (32 genera) in the uppermost zone (E_{2c4}) of the Lower Carboniferous, only four species seem to have survived the Lower–Upper Carboniferous boundary ("E_2 crisis"). Nine genera occurred in beds below and above this boundary.

At the beginning of the Upper Carboniferous, no goniatites are known from the New World, Africa, and Antarctica. The few lineages that survived the E_2 crisis produced a new stock of goniatites; in the *Homoceras* Stufe 30 species (11 genera) were new.

Beginning with the Bashkirian (Kinderscoutian, Halian, *Reticuloceras* Stufe), the ammonoids are again known from many places in the northern hemisphere. The radiation of different stocks which had begun in the *Homoceras* Stufe continued during the following interval. In the Kinderscoutian (early Halian) about 140 species (almost 40 genera) were present, but this number decreased considerably in the Marsdenian (middle Halian) to 50 species (about 25 genera). Seventy-five ammonoid species (more than 30 genera) were present in the late Halian interval, the Yeadonian (G_1). Half of them originated in this interval. More than 50 species became extinct at the end of the Yeadonian (Halian–Bloydian boundary).

The next step in ammonoid evolution was at the beginning of Westphalian time (late Bashkirian, Bloydian). The number of ammonoid species reached

100 (about 40 genera); most of the Reticuloceratidae, with many short-ranging index species, disappeared and were replaced by the Gastrioceratidae and Pseudoparalegoceratidae. The trend of diversifying sutural elements continued slowly. The most remarkable change was the onset of provincialism among goniatites. The Orulganitidae were restricted exclusively to Siberia; the separation of this area seemed to persist until the Early Permian (Sakmarian).

Starting with the Moscovian (Atokan and Desmoinesian), a period of low diversity began. In the Moscovian, which is thought to have spanned 9 million years, about 85 species (40 genera) were present; a relatively high number of long-ranging genera (e.g., *Agathiceras*, *Glaphyrites*, *Syngastrioceras*, *Somoholites*, *Boesites*, and *Stenopronorites*) predominated. But, in addition, ammonoids with complicated sutures (*Aktubites* of the Shumarditidae, *Wellerites* and *Winslowoceras* of the Welleritidae, and *Marathonites* of the Marathonitidae) appeared for the first time in the Goniatitida. The Prolecanitida persisted nearly unchanged from the late Early Carboniferous. In the Kasimovian (late Desmoinesian) diversity continued to decline (30 species, about 20 genera), but the appearance of the Adrianitidae (*Emilites*) and Thalassoceratidae (*Prothalassoceras*) added two new groups of multilobate ammonoids. At the same time, the first Medlicottiidae (*Prouddenites*) appeared, exhibiting broad complicated ventral prongs of the lateral lobe. In the Gzhelian, this group proliferated greatly.

1.3. Permian

The trend to complication of the suture and the addition of sutural elements became widespread at the beginning of the Permian, not only in the Goniatitida but also in the Prolecanitida. In addition, two major groups, which were derived from mid-Carboniferous neoicoceratаceans, persisted with long-ranging genera throughout the entire Permian: the Metalegoceratidae and the Paragastrioceratidae. The latter group maintained the basic suture of the Goniatitina $(E_1E_mE_1)ALUI$ [Russian: $(V_1V_1)L{:}UI$]* until the beginning of the Triassic. The changeover at the Carboniferous–Permian boundary is remarkable (see Chapter 17, this volume, Figs. 5–7); in the Gzhelian, about 115 species (almost 40 genera) were present, whereas in the Asselian, 75 species (37 genera) were present. Only 12 Gzhelian genera survived. In the Early Permian, however, the diversity of Goniatitida and Prolecanitida increased continuously until the middle of the Permian (Glenister and Furnish, 1981).

In the Roadian, the uppermost stage of the Lower Permian, a distinct changeover began, apparently connected with the appearance of the Ceratitida. In this interval, the numbers of genera in the Goniatitida, Ceratitida, and

*For suture terminology, see Chapter 17, this volume, Section 4.1.

Prolecanitida were about 30, 1, and 4, respectively (a total of more than 50 species). The peak diversity was reached in the following interval, the lower part of the Upper Permian Wordian stage; more than 150 species were present, and the numbers of goniatitid, ceratitid, and prolecanitid genera were about 50, 2, and 8, respectively. In the Capitanian (a total of almost 60 species), the number of goniatitid genera dropped to 10, the number of ceratitid genera increased to six, and only the number of prolecanitid genera remained constant. In the Dzhulfian stage (more than 110 species), the Ceratitida became predominant. More than 110 species were present belonging to ten goniatitid, 30 ceratitid, and two prolecanitid genera. The uppermost part of the Upper Permian (Dorashamian, Changxingian) yielded 26 ceratitid genera; of the Goniatitida, only one genus, *Pseudogastrioceras*, persisted until the Lower Triassic Griesbachian (Teichert, 1990). No prolecanitid genus was recorded, but some must have existed; *Episageceras*, the last member of the Medlicottidae, occurred in the Lower Triassic Griesbachian.

The main crisis at the end of the Permian affected the Goniatitida and Prolecanitida. Apparently only one genus of each order survived the Permian–Triassic boundary, but both became extinct in the Early Triassic. The Ceratitida, however, gave rise to the otoceratids at the beginning of the Triassic.

2. Mesozoic Ammonoids

The state of taxonomy of Mesozoic ammonoids is based on a number of diverse studies, which makes it difficult to arrive at any fixed conclusion. Statistical evaluation of radiations and extinctions as has been done for the Paleozoic is, for the time being, possible only for the Triassic. The synthetic paper of Tozer (1981) especially allows calculations on the generic and stage levels. Nothing comparable is available for the Jurassic and Cretaceous, at least since the publication of the ammonoid *Treatise* (Arkell *et al.*, 1957). This disadvantage is, however, of minor importance because no spectacular crises can be detected within the Jurassic and Cretaceous Periods nor at their mutual boundary. This is, indeed, different in the Triassic Period.

2.1. Triassic

A considerable amount of time was involved in recovering from the Permo–Triassic boundary crisis (Fig. 1). Late in the Nammalian, the first maximum diversity for the Lower Triassic was achieved, resulting in a total of 51 ceratitid genera and two genera of phylloceratids. A second maximum can be recognized at the top of the Spathian with a total of 61 ceratitid and four phylloceratid genera. But during the crisis that immediately followed, 48 ceratitid and three phylloceratid genera became extinct. This is the most severe event during the Triassic. Nine families did not cross the Lower to Middle Triassic boundary, i.e., the Xenodiscidae and the Xenodiscaceae as a

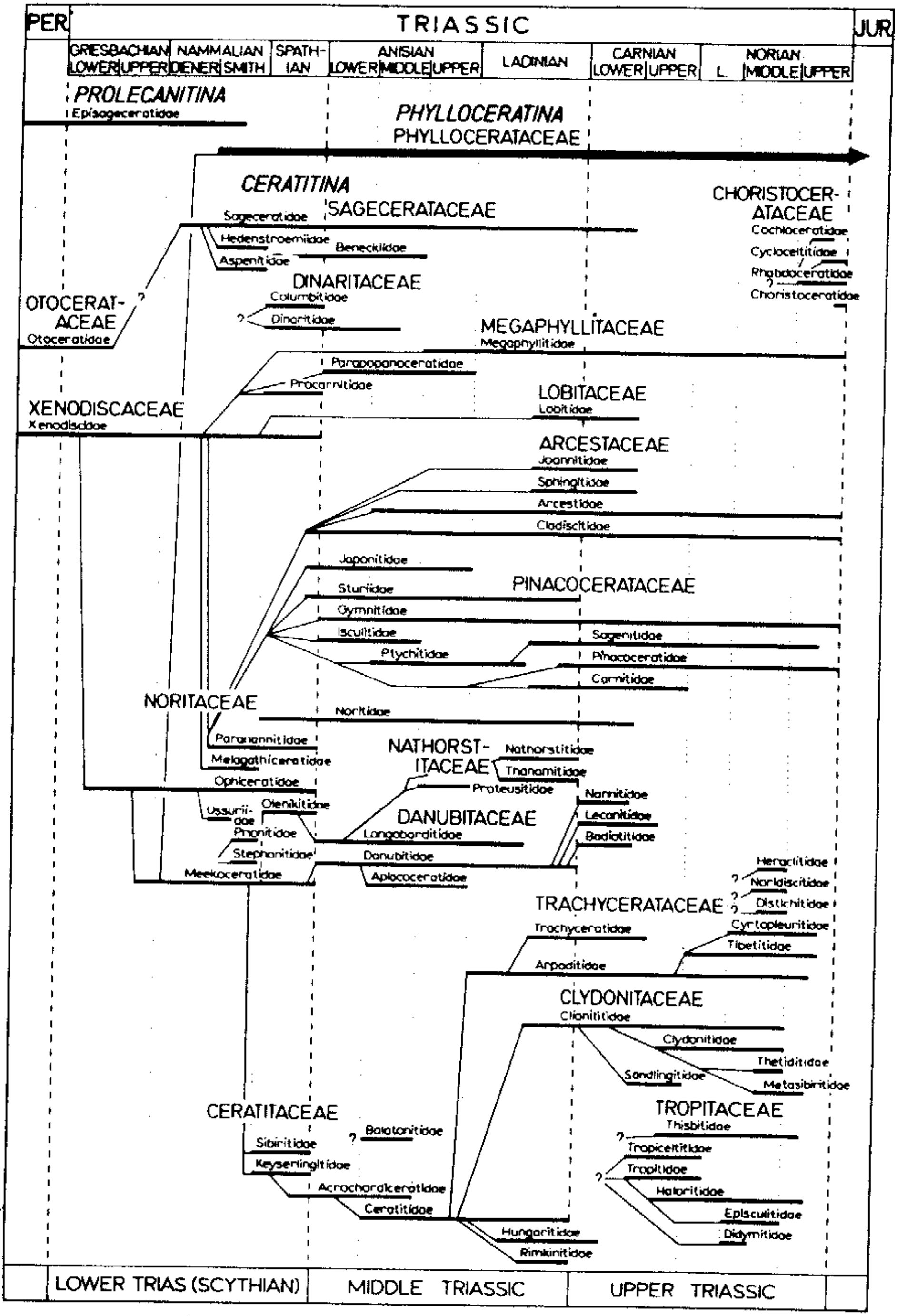

FIGURE 1. Evolution of Triassic ammonoid families (after Tozer, 1981).

whole: the Paranannitidae, Ophiceratidae, Olenikitidae, and Meekoceratidae of the Noritaceae; the Sibiritidae and Keyserlingitidae of the Ceratitaceae; the Columbitidae of the Dinaritaceae; and the Procarnitidae of the Megaphyllitaceae.

It is worth mentioning that there is a pronounced extinction peak at the Lower–Middle Triassic boundary as far as families are concerned according to the computation of Sepkoski (1986, Fig. 2). There is also a pronounced minimum at the same time when genera are counted (Sepkoski, 1986, Fig. 3).

Triassic ammonoids underwent their second severe crisis at the Anisian–Ladinian boundary. At this time, 40 of 61 ceratitid genera and two of four phylloceratid genera disappeared. This event involved four families, i.e., the Aplococeratidae of the Danubitaceae, the Proteusitidae of the Nathorstitaceae, the Parapopanoceratidae of the Megaphyllitaceae, and, finally, the Japonitidae of the Pinacocerataceae. No major crisis has been detected at this boundary according to Raup and Sepkoski (1984) and Sepkoski (1986).

Not as severe as the two previous crises is the Ladinian–Carnian extinction that followed. During late Ladinian time, ceratites and phylloceratids flourished again with a total of, respectively, 48 and three genera. The subsequent extinction at the boundary is characterized less by the disappearance of genera (ten) than by extinction at the family level. The Danubitidae of the Danubitaceae disappeared as well as the Ceratitidae and Rimkinitidae, together with most of the Ceratitaceae, the Nathorstitidae, and Thanamitidae, with all of the Nathorstaceae, and, finally, the Sturiidae of the Pinacocerataceae.

Another minor extinction event can be detected in the Carnian near or at the Jul–Tuval boundary. During the Jul, 39 ceratitid and five phylloceratid genera were present, of which eight and five, respectively, did not cross the boundary. Again, the number of families that became extinct was considerable. The Badiotitidae of the Danubitaceae nearly disappeared; the Noritidae of the Noritaceae, the Lobitidae of the Lobitaceae, and the Joannitidae and Sphingitidae of the Arcestaceae became extinct. Of the two extinctions of marine fossil genera detected by Sepkoski (1986) for the Triassic, the older one seems to correlate with this intra-Carnian crisis.

After some recovery, the diversity of ceratites increased for the last time to a total of 50 genera during the late Alaun. During Sevat and Rhaetian times, the final decline of the Ceratitina was continuous or at least stepwise. At the Alaun–Sevat boundary, e.g., 14 of these genera became extinct; on the family level, this "event" was again much more pronounced. Many families did not cross this boundary: the Heraclitidae; the Noridiscitidae and Distichitidae of the Trachycerataceae; the Clionitidae, Clydonitidae, and Thetiditidae of the Clydonitaceae; and the Episculitidae of the Tropitaceae. It is this crisis that may correlate with the "upper Norian extinction" recorded by Sepkoski (1986).

Only 19 genera of the Ceratitina and Phylloceratina persisted into the Rhaet, during which time they gradually disappeared. These included six genera of the Choristocerataceae, four genera of the Arcestidae and Cladisci-

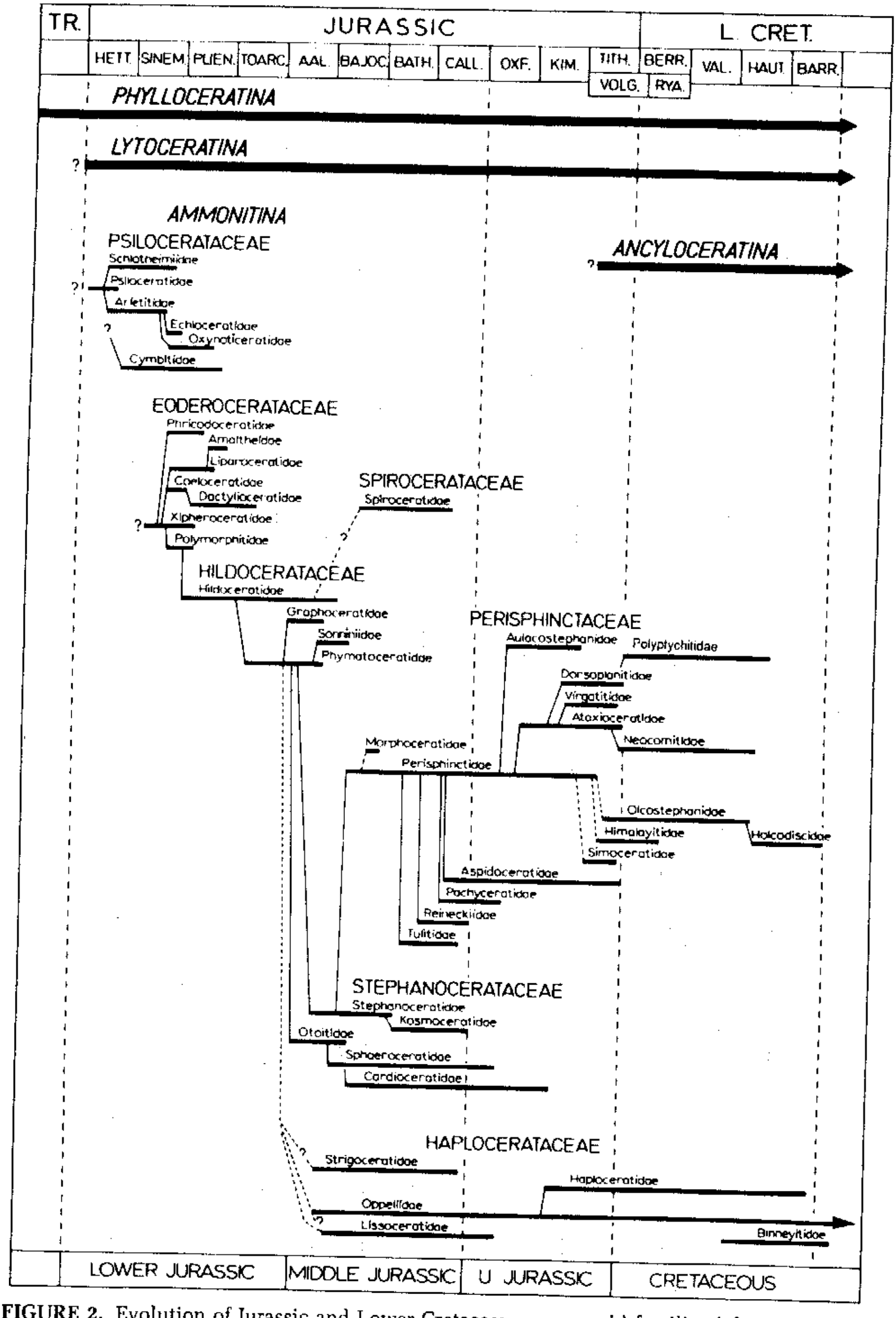

FIGURE 2. Evolution of Jurassic and Lower Cretaceous ammonoid families (after Donovan *et al.*, 1981).

tidae (Arcestaceae), one genus of the Megaphyllitidae and, thus, the Megaphyllitidaceae, and three genera of the Triassic phylloceratids, i.e., the Ussuritidae and Dicophyllitidae.

The picture given of the turnover of ammonoids at the Triassic–Jurassic boundary (Wiedmann, 1970, 1973a) is still fully valid. At present, no ammonoid genus or species is known that was common to both the Triassic and the Jurassic, although one must have existed. But despite the total disappearance of the highly flourishing Triassic Ceratitina, no sudden extinction can be recognized at this boundary.

2.2. Jurassic

Judging from a modern classification of the Jurassic ammonites, e.g., Donovan *et al.* (1981), it is very difficult to recognize any evolutionary crisis comparable to those previously discussed (Fig. 2). Significant extinctions have been described by Donovan (1988) within and at the end of the Sinemurian, when the Echioceratidae disappeared and the psiloceratids were replaced by the eoderoceratids. But the total rate of extinction was not spectacular.

A post-Pliensbachian extinction can only be inferred from other molluscs and various marine invertebrates (Hallam, 1986, 1987; Sepkoski 1986). The disappearance of the Amaltheidae should not be overemphasized, even though it coincides with the 26-million-year cyclicity described by Raup and Sepkoski (1984). In addition, the "lower Bajocian extinction" of Sepkoski (1986) is not well documented in ammonoids; instead, a stepwise extinction can be observed, first of the Hildoceratidae, then of the Sonniniidae, and, finally, during the mid-Bajocian, of the Otoitidae. A mid-Jurassic extinction peak at the generic level, as shown by House (1985b), may therefore be an artifact resulting from the relatively broad time slice considered.

No "upper Tithonian extinction" (Sepkoski, 1986) can be observed in ammonoids. Instead, two minor extinctions occurred near the Jurassic–Cretaceous boundary. At or near the boundary, five perisphinctid families disappeared, i.e., the Ataxioceratidae, Dorsoplanitidae, Virgatitidae, Aspidoceratidae, and Simoceratidae. The Perisphinctaceae persisted as a whole, however, well into the Cretaceous, as did the Haploceratаceae. The previously published picture of this boundary (Wiedmann, 1968, 1975) needs no major change.

2.3. Cretaceous

A second minor extinction event near the Jurassic–Cretaceous boundary coincided with the Berriasian–Valanginian boundary (Fig. 3). At this time, the perisphinctids Himalayitidae, Berriasellinae, Spiticeratinae, and Craspeditinae disappeared.

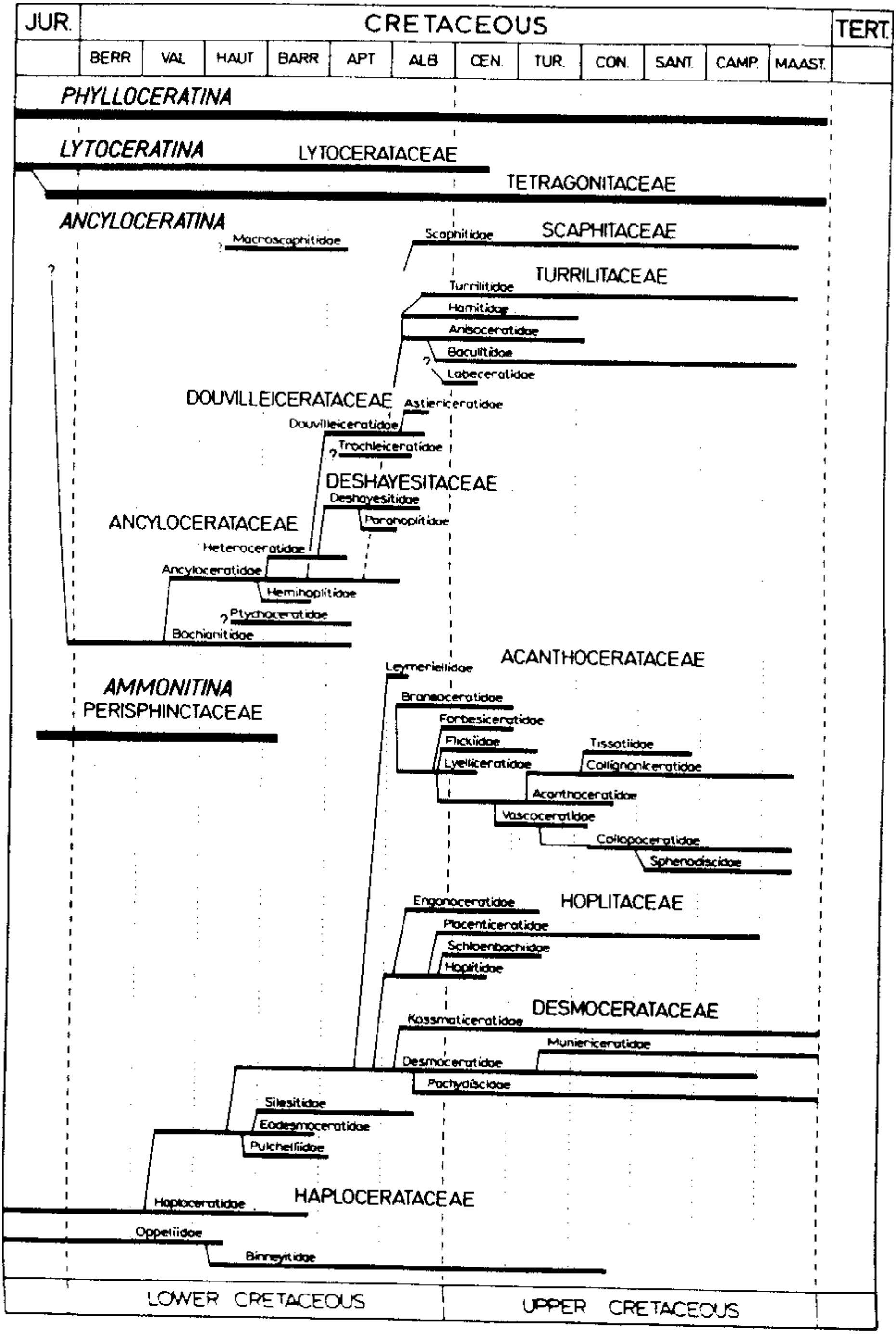

FIGURE 3. Evolution of Cretaceous ammonoid families (after Wright, 1981).

During the whole Cretaceous, however, no spectacular time of ammonoid extinction can be detected at the family level. The change in diversity during the Cretaceous perfectly mirrored changes in global sea level. Both increased continuously through the Lower Cretaceous towards the Cenomanian sea-level maximum and decreased thereafter except for a short-term sea-level rise during the lower Campanian.

It is interesting to compare our data for Cretaceous extinctions with those of Sepkoski (1986, Fig. 3). His early Aptian and late Cenomanian events, which fit perfectly into a 26-million-year cyclicity, do not involve ammonoids. The reason is that Sepkoski's "synthetic" way of calculating marine invertebrate diversity lumps together totally different events, such as the global regression during the early Aptian, which coincides with the drowning of Tethyan carbonate platforms (Schlager, 1981; Föllmi *et al.*, 1994), the global black-shale event at the close of the Cenomanian (Arthur *et al.*, 1990), and the really sudden marine surface plankton extinction event caused by a cosmic impact at the Cretaceous–Tertiary boundary (Alvarez *et al.*, 1980). Not only are the causes of all these extinctions totally different, but so are the fossil groups affected. Uncritical statistical analyses do not separate out the affected biotopes, which is an essential requirement for understanding any extinction event (see Wiedmann, 1969, Fig. 23); the resulting cyclicity is thus a mere artifact.

What can be said today about the ultimate ammonoid extinction at the close of the Cretaceous? Much effort has been spent during the last decade to explain how and why ammonoids disappeared. From our knowledge of the continuous boundary sections in the Bay of Biscay and in southwest France (Wiedmann, 1969, 1986, 1988a,b; Ward and Wiedmann, 1983; Ward, 1988; Hancock and Kennedy, 1993; Hancock *et al.*, 1993), we can summarize that it was very similar to the Triassic–Jurassic boundary, a long period of decline with a maximum number of extinctions long before the end of the Cretaceous. Of about 100 ammonoid genera that lived during the sea-level highstand in the lower Campanian, fewer than 50 persisted into the middle Maastrichtian. At the two most complete boundary sections, Zumaya and Hendaye (Wiedmann, 1986, 1988a,b; Ward, 1988), just eight genera are recorded 15 m (≈150,000 years) below the boundary and the well-documented iridium layer, i.e., *Neophylloceras*, *Gaudryceras*, *Saghalinites*, *Pseudophyllites*, *Vertebrites*, *Anapachydiscus*, *Pachydiscus*, and *Diplomoceras* with a total of ten species. In the last 0.5 m below the boundary at Zumaya, *Neophylloceras ramosum*, and at Hendaye, *Gaudryceras* sp., *Pachydiscus gollevillensis*, and *P.* sp., have been collected by the author (Fig. 4).

The ultimate extinction of ammonoids was, therefore, a continuous and long-lasting decline that can be traced over several million years and was comparable to the major extinctions at other Mesozoic system boundaries. This extinction was unrelated to the K–T boundary event itself, which affected the oceanic surface plankton and was of either cosmic or volcanic origin. It is worth mentioning that evolutionary rates in ammonoids decreased during the

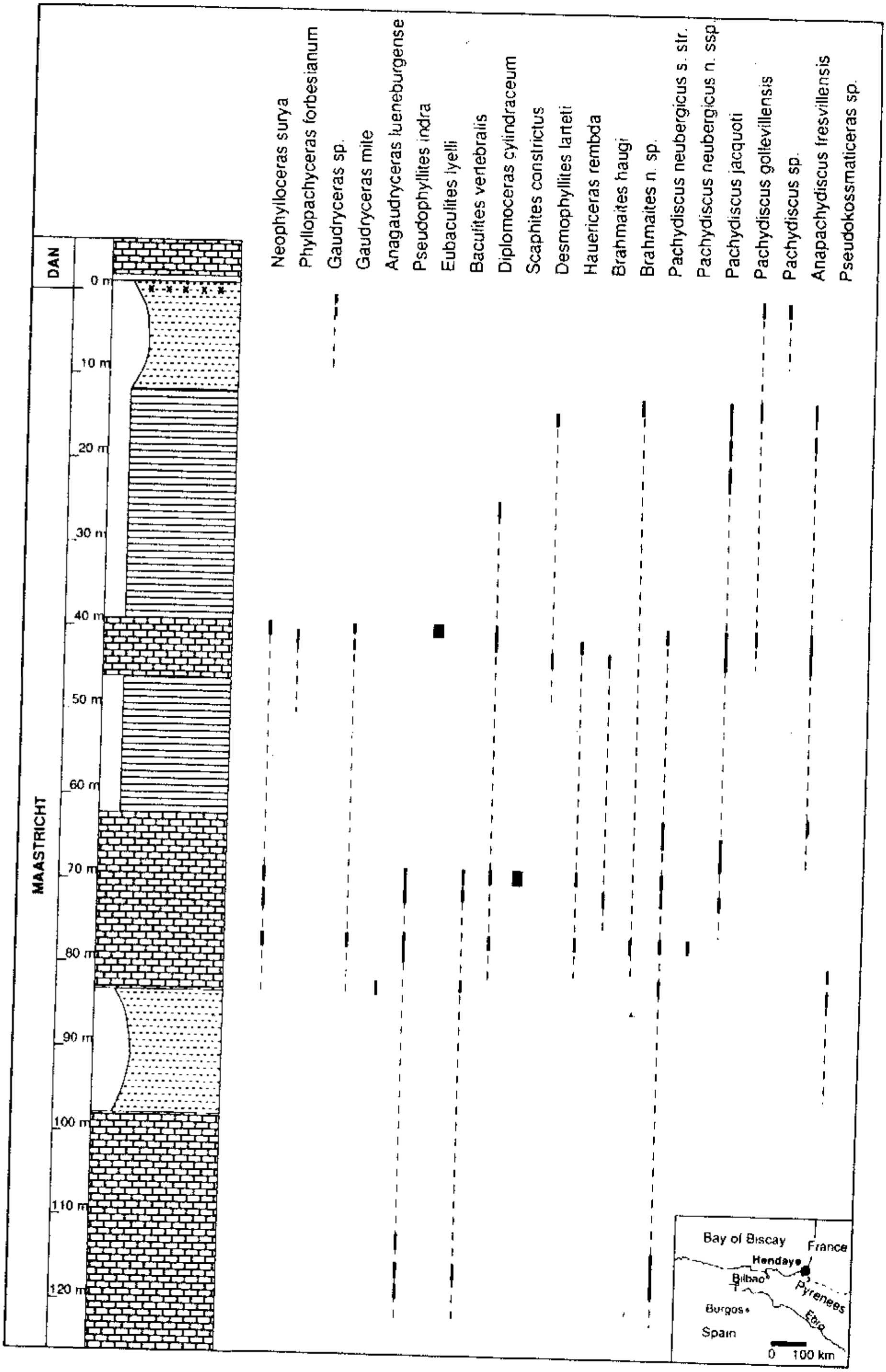

FIGURE 4. Ranges and decline of late Maastrichtian ammonoids in the Hendaye section, southwestern France.

Late Cretaceous (Wiedmann, 1969); for example, the Maastrichtian species had a much longer time range than the Turonian ones. It is also noteworthy that deep-water phylloceratids and lytoceratids were predominant among the last ammonoids. Two other important mollusc groups occupying the same habitat during the Cretaceous, i.e., belemnites and inoceramids, followed the same extinction pattern, the latter disappearing even somewhat earlier than the ammonoids (Wiedmann, 1988a,b).

2.4. Do Mesozoic Extinctions Have a Common Cause?

On the basis of the detailed knowledge we now have of all the Mesozoic system boundaries, which coincide with and are even based on major ammonoid extinctions, we can conclude that the pattern of ammonoid extinction was perfectly comparable, if not identical, at all these boundaries. In all these cases, the decline was continuous, and no sudden extinctions occurred. In most cases, the new forms that replaced the old ones developed long before the boundary, i.e., the Xenodiscaceae and Otocerataceae in the Permian (Spinosa *et al.*, 1975; Ruzhentsev, 1959), the Phyllocerataceae and, eventually, the Pinacocerataceae in the Triassic (Wiedmann, 1970, 1973a; Tozer, 1971, 1981), and the Ancyloceratina and Haplocerataceae in the Late Jurassic (Wiedmann, 1973b; Ziegler, 1974). Were the sexlobate Cretaceous Tetragonitaceae the prospective stock for Tertiary ammonoids, or were ammonoids genetically "exhausted" at the end of the Cretaceous? Both speculations have some support, but the final conclusion remains difficult. The evolutionary rate of ammonoids continuously decreased during the Late Cretaceous. However, the heteromorphic shapes of the Ancyloceratina do not indicate any genetic "exhaustion" ("Typolyse," Schindewolf, 1945), a theory that was completely refuted by Wiedmann (1969).

The Mesozoic deep-water stocks, i.e., the phylloceratids and lytoceratids, were not only well represented among the last few ammonoids, they generally exhibited the best survival rates; phylloceratids were the only form that unquestionably crossed the Triassic–Jurassic boundary. This may indicate that water depth was a factor in ammonite extinction. The pattern of major extinctions also suggests that explanations should be based on processes that operated over long time periods.

Few direct relations can be observed between plate tectonics and the diversity of ammonoids during the Mesozoic (Wiedmann, 1988b) except for (1) the breakup of Pangaea at the Paleozoic–Mesozoic boundary, (2) changing patterns of endemic versus cosmopolitan distributions, and (3) the presumed dependence of larger sea-level changes on pulses of ocean floor spreading.

To relate the course of ammonoid diversity to major sea-level changes, i.e., extinctions with regressions and radiations with transgressions, is by no means a new idea. It was put forward as a general explanation by Moore (1950) and Newell (1952) and has been discussed in the context of Mesozoic am-

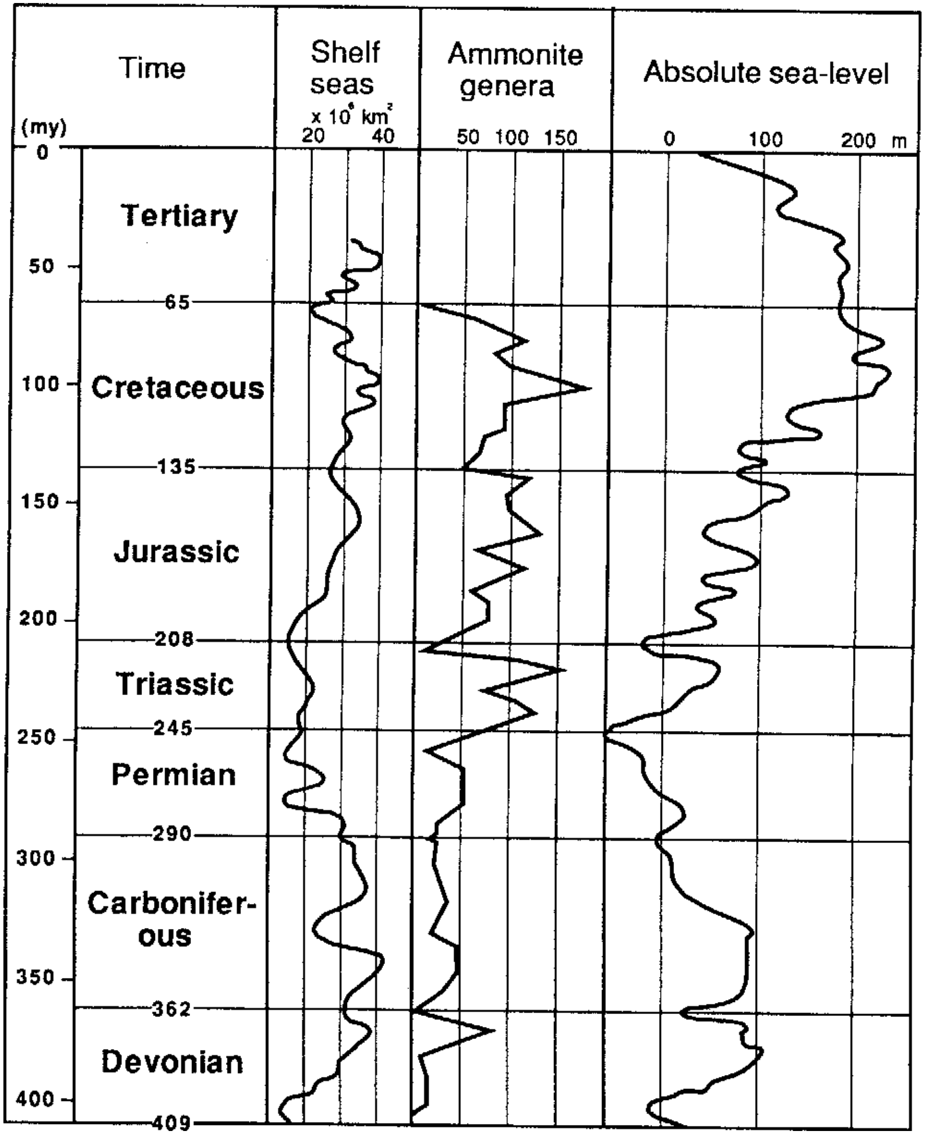

FIGURE 5. Comparison of ammonoid diversity through time (after House, 1985b) with sea-level fluctuations of shelf seas (after Sliter, 1976; Yanshin, 1973) and long-term eustatic sea-level changes (after Haq *et al.*, 1987; House, 1989).

monoids by Wiedmann (1969, 1973a, 1988c) and Hallam (1986, 1987) and in the context of Paleozoic ammonoids by House (1985a,b, 1989). The comparison of the pattern of ammonoid diversity through time with global sea-level changes or with first-order cycles in sequence stratigraphy (Fig. 5) shows such a striking similarity that the obvious conclusion is that they were related.

There is no need to involve a major cosmic impact to explain the final decline of ammonoids.

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