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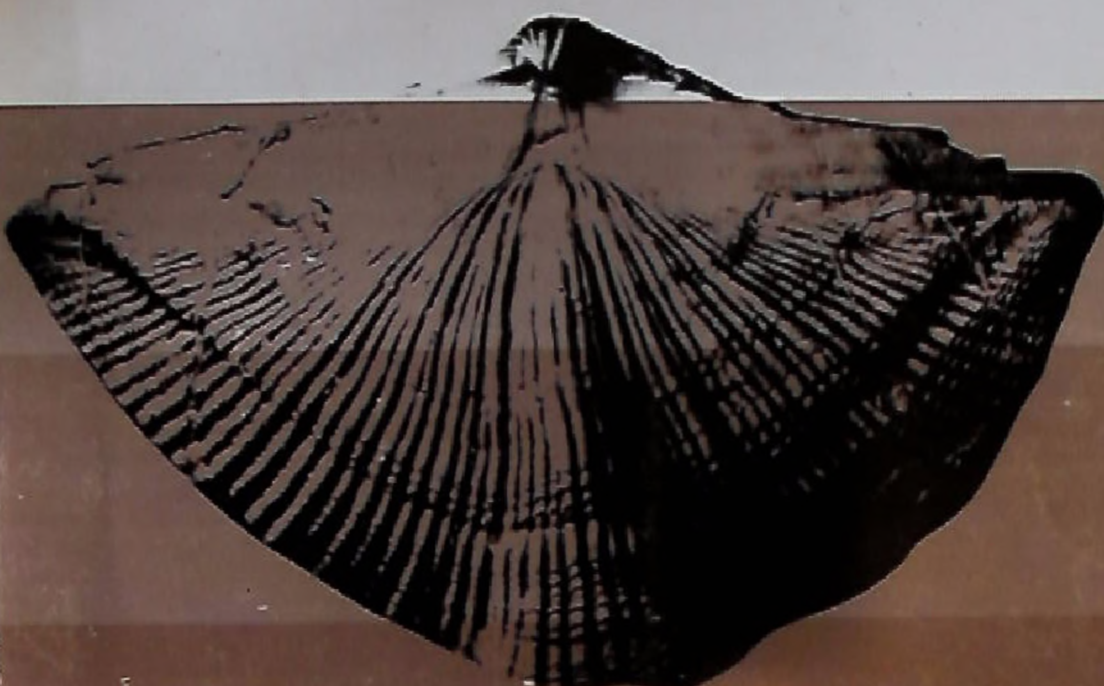

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MAJOR EVENTS IN THE HISTORY OF THE TRIASSIC AMMONOIDS

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Abstract: The history of the Early Mesozoic ammonoids began after the very profound Late Permian crisis and ended with their almost complete extinction at the end of the Triassic. Sixteen major events can be identified in the record of the Triassic ammonoids. These events were the appearances or disappearances of characteristic forms, some of which are commonly used for global correlations. These bioevents form a reliable basis for the stratigraphy of the Triassic.

История раннемезозойских аммоноидей началась после глубочайшего позднепермского кризиса и завершилась почти полным вымиранием их в конце триаса. В летописи триасовых аммоноидей можно различить 16 крупных событий. Они выражаются в появлении или исчезновении характерных форм, обычно используемых для глобальной корреляции. Эти биособытия образуют надежную основу для стратиграфии триаса.

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During the Triassic was a time of absolute predominance of the ceratites among the ammonoids. The ceratites appeared in the Early Permian, but until the end of the Paleozoic they occupied a quite modest position in the seas, living in the shadow of the more successfully thriving goniatites and prolecanites. Not until the Triassic did the ceratites begin their great flourishing, which was reflected in their enormous morphological diversity and extensive geographic distribution [2, 16, 17].

The most important events in the history of the ceratites were two profound crises — in the concluding phase of the Paleozoic, and at the end of the Triassic.

As a result of the first crisis, the ceratites very nearly shared the fate of most Paleozoic ammonoids, whose development was terminated at the end of the Permian. The goniatites, which

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had predominated in the Late Paleozoic, disappeared completely at this boundary, and the prolecanites, which only with difficulty survived the beginning of the Triassic, soon followed them into extinction. Among the ceratites, the Paraceltitinae disappeared and the Orthoceratinae, having just barely survived the Permotriassic boundary, became extinct. But in departing from the scene the Paraceltitinae managed to give rise to the phylogenetic line of the kashmiritids, from which all Triassic ammonoids developed.

The second great crisis, which occurred at the very end of the Triassic, led to the complete extinction of the ceratites. Among the Early Mesozoic ammonoids, only the phylloceratids survived to continue their development in the Jurassic, when they gave rise to the lythoceratids and the ammonitids.

The first great crisis took place against the background of a vast global regression, which at the very end of the Permian resulted in the almost complete disappearance of shelf seas from the Earth [5, 6, 15]. The second major crisis, separated from the first by an interval of 40 mln yr [11], in contrast developed under conditions of a definite transgression, which began at the end of the Triassic and continued in the Jurassic. A shallow epicontinental sea, evidently of considerably less than oceanic salinity, during the Rhaetian covered a large territory of northwestern Europe [7]. This transgression, by the way, was the principal reason why French and English geologists for a long time assigned the Rhaetian to the Jurassic system; but the fact that the Rhaetian fauna is far closer to the Triassic than to the Jurassic fauna was decisive in resolving the dispute over the stratigraphic position of the Rhaetian.

Between these two crises, a whole series of less prominent, but nevertheless considerable, bioevents can be discerned in the history of the Triassic ammonoids (table 1). These were manifested in the appearance or disappearance of characteristic forms that are usually employed for global correlations [14].

Event 1: The appearance, at the very beginning of the Triassic (the *woodwardi* phase), of the distinctive genus *Otoceras* and of ceratites with a fundamentally new mode of complicating their suture line during ontogenesis by the formation of umbilical lobes (genus *Metophiceras*). *Otoceras*, known in both Tethyan (Kashmir, Tibet) and Boreal (Siberia, Spitsbergen, Greenland, the Arctic islands of Canada, Alaska) seas, serves as a very convenient paleontological marker of the lower boundary of the Triassic, enabling it to be traced over a considerable territory [3, 18]. Attempts to change the position of this boundary in any way can only undermine its clarity and stability.

The desire to revise the lower boundary of the Triassic is generally due to the supposition that the ceratites of the *woodwardi* zone still have a Paleozoic character. This assertion, however, is valid only in relation to *Otoceras*, which caps the line of development of the Permian araxoceratids, being their direct descendant. It did not, however, lead to the species of the genus *Metophiceras*, which in the character of their morphogenesis are already true Triassic ceratites [3].

Event 2: Disappearance of the otoceratids and predominance of the ophiceratids in the *tibeticum* phase. In most parts of the world *Ophiceras* beds overlie those with *Otoceras*, but in some sections in Kashmir, *Ophiceras* is also found in the *woodwardi* zone [8, 9].

Event 3: The appearance of the first ceratites with a flat ventral side (family Meekoceratidae) and, perhaps, of the sageceratids at the beginning of the Middle Scythian

Table 1. Chronology of Triassic Bioevents

Series	Stage	Substage	Zone	Event
Late Triassic	Rhaetian		*Choristoceras marshi*	Event 16
			Rhabdoceras suessi	
	Norian	L	*Halorites macer*	Event 15
			Himavatites bogarti	
			Cyrtopleurites bicrenatus	Event 14
		E	*Juvavites magnus*	
			Malayites paulckei	
			Guembelites jandianus	
	Carnian	L	*Anatropites spinosus*	Event 13
			Tropites subbullatus	
			Tropites dilleri	Event 12
		E	*Austrotrachyceras austriacum*	
			Trachyceras aonoides	
Middle Triassic	Lodinian	L	*Frankites regoledanus*	Event 11
			Protrachyceras archelaus	Event 10
		E	*Eoprotrachyceras curionii*	Event 9
	Anisian	L	*Nevadites reitzi*	
			Aplococeras avisianum	
			Paraceratites trinodosus	Event 8
		M	*Balatonites balatonicus*	
			Aghdarbandites ismidicus	
			Nicomedites osmani	Event 7
		E	*Aegeiceras ugra*	Event 6
Early Triassic	Scythian	Late	*Dinarites carniolicus*	
			Tirolites cassianus	Event 5
		Middle	*Anasibirites pluriformis*	
			Meekoceras gracilitatis	Event 4
			Flemingites flemingianus	Event 4
			Prionolobus rotundatus	
			Gyronites frequens	Event 3
		Early	*Ophiceras tibeticum*	Event 2
			Otoceras woodwardi	Event 1

(*frequens* phase). This event is especially clear in sections in the Himalayans, the Solyanoy Kryazh and Primor'ye regions of the former USSR, and Ellesmere Island in Canada. Some investigators [10] believe that this event should be taken as representing the boundary between the Permian and the Triassic.

Event 4: A sharp increase in taxonomic diversity of the ceratites in the *flemingianus* and *gracilitatis* phases (the appearance of the prionitids, ussuriids, melagathiceratids, arctoceratids, inyoitids, lanceolitids, aspenitids, parananitids and hedenstroemiids). The ceratites of this geologic time interval have a very extensive geographic range; their zonal distribution still remains to be clarified. Certain difficulties are connected with the correlation of their deposits. In particular, the exact position of the boundary between the Indskian and the Olenikian stages in this scale remains unclear. Waterhouse's proposal [19] to raise the lower boundary of the Triassic to this level, therefore, seems inappropriate.

Event 5: The disappearance of the micoceratids, ussuriids, arctoceratids, hedenstroemiids, melagathiceratids and episageceratids and the appearance, at the beginning of the Late Scythian (*cassianus* phase), of the tyrolitids, dinaritids, dorikranitids, columbitids, khvalynitids, olenkitids and procarnitids. This was a marked event in the history of the Early Triassic ammonoids. All researchers acknowledge it as the beginning of a major new cycle in the evolution of the ceratites.

Event 6: The extinction of most Early Triassic ceratids (the ophiceratids, flemingitids, olenikitids, proptychitids, inyoitids, lanceolitids, procarnitids, aspenitids, tirolitids, dorikranitids, dinaritids, columbitids, sibiritids, kashmiritids, kazakhstanitids, and parananitids) and the appearance, at the beginning of the Anisian (*ugra* phase), of the aplococeratids, danubitids, longobarditids, gymnitids, aspenitids, paraponoceratids, styriids, isculitids, cladiscitids and megaphyllitids. Only two phylloceratid genera (*Leiophyllites* and *Ussurites*) remained common to the Late Scythian and the Anisian ages. the stratotype of the *ugra* zone is on the Greek island of Chios. Its chrono-equivalents are the *Lenotropites-Japonites* zone in China, the *taimyrensis* and *tardus* zones in Siberia, and the *caurus* zone in Canada and the USA.

Event 7: A flourishing of the beyrichitids, acrochordiceratids and balatonitids, beginning with the Middle Anisian (*osmani* phase). This boundary coincides with the base of the *Hollandites-Beyrichites* zone in China, the *decipiens* zone in Siberia, the *varium* zone in Canada, and the *hyatti* zone in the USA.

Event 8: An extremely flourishing development of the ceratitids (*Paraceratites*, *Semiornites*, *Kellnerites*) from the beginning of the Late Anisian (*trinodosus* phase). This time was marked by the appearance of the paraceratites with the three rows of lateral tubercles. The lower boundary of the *trinodosus* zone, whose stratotype is in the eastern Alps, corresponds to the base of the *rotelliforme* zone in Siberia and Nevada and also the base of the *deleeni* zone in Canada.

Event 9: The extinction of the proteusitids, japonitids and parapopanoceratids and the appearance, at the beginning of the Early Ladinian (*curionii* phase) of the trachyceratids with a ceratitic suture line (*Eoprotrachyceras*). The stratotype of the *curionii* zone is in the Dolomite Alps of Italy, where it occupies almost the whole sequence of the Buchenstein beds, except for the very lowermost part, which is assigned to the *reitzi* zone. Most European geologists lower the Anisian-Ladinian stadial boundary to the base of these beds. In the past few years, to be sure, some have begun to reject this view, which has deep historical roots, and are inclined to accept the *curionii* zone as the base of the Ladinian [4]. The lower boundary of this zone coincides with the base of the Siberian *oleshkoi* zone and the North American *subasperum* zone [1].

Event 10: The appearance of trachyceratids with an ammonitic suture line and a single row of tubercles on each side of their ventral groove (*Protrachyceras*), and also of the tanamitids, celtitids, carnitids, nathorstitids, lobitids, sphingitids and ioannitids at the beginning of the Late Ladinian (*archelaus* phase).

Event 11: The appearance of trachyceratids with two rows of tubercles on each side of the ventral groove (*Trachyceras*), and also of the lecanitids, badiotitids, nannitids, sandlingitids, sirenitids and discophyllitids at the very beginning of the Carnian age (*aonoides* phase).

Event 12: The appearance of the tropitids and tropiceltitids at the beginning of the Late Carnian (*dilleri* phase). These are distinctive ceratites with a ventral keel usually accompanied on both sides by grooves. The *dilleri* zone, whose stratotype is in California, can be clearly traced in British Columbia and Nepal. It is poorly represented in the Alpine-Mediterranean belt, and cannot be distinguished in Siberia or on the islands of the Canadian Arctic.

Event 13: The extinction of the sandlingitids and carnitids and the appearance of the cyrtopleurids and tibetitids at the beginning of the Norian age (*jandianus* phase). The *jandianus* zone is well represented in Nepal; its analogs are known in British Columbia and Nevada, where it corresponds to the *kerri* zone and the beds with *Guembelites* respectively.

Event 14: The appearance of the didymitids, noridiscitids and distichitids at the beginning of the Late Norian (*bicrenatus* phase). The *bicrenatus* zone has its stratotype section in the eastern Alps; its analogs can be identified in Nepal (the beds with *Metacarnites hendersoni*), on the island of Timor (beds with *Hauerites* and *Cyrtopleurites*), in China (*socius* zone), and in British Columbia (*rutherfordi* zone).

Event 15: The appearance of ceratites with a discrete shell (adjacent whorls not touching) (rhabdoceratids) at the beginning of the Rhaetian age (*suessi* phase). This even determines the lower boundary of the last stage of the Triassic system. The *suessi* zone can be traced in the Eastern Alps, the western Carpathians, Bulgaria, Hungary, Sicily, the Pamir Range, Timor and the Moluccas Islands, Chukotka, Canada, the USA, and Colombia.

Event 16: The gradual and complete extinction of the ceratites at the end of the Rhaetian age and of the Triassic period.

The above events in the history of the Triassic ammonoids contradict the Raup and Sepkoski hypothesis that there have been periodic extinctions at intervals of 26 mln yrs [12, 13]. In addition, these events compel one to think that these mass extinctions were due to various causes, which were most likely of terrestrial character. Finally, these bioevents constitute a reliable framework for the global stratigraphy of the Triassic.

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