## Art. X.—*A Critical Phase in the History of Ammonites;* by C. Diener.

The extinction of ammonites, those masters of the Mesozoic seas, near the close of the Cretaceous period is a fact well known to all students of palæontology. The number of their families and genera is diminishing gradually during the Senonian epoch. Five species only reach into the stage of the Mæstrichtian. Not one passes the fatal border of the Danian.

It is, however, less known, that the existence of ammonites was threatened by a similar crisis at a considerably earlier period of the Mesozoic era. They passed through a very critical phase at the boundary of the Rhætic and Liassic stages. All but one phylum of Triassic ammonites became extinct at the close of the Rhætic epoch. By the survival of this single phylum, which in the Lower Lias gave rise to the development of a new and rich fauna, the ammonites were saved from complete extermination.

E. v. Mojsisovics was the first to notice this remarkable crisis in the history of Triassic ammonites. For fuller details the reader is referred to J. F. Pompeckj, "Ammoniten des Rhæt" (Neues Jahrb. f. Mineral., etc., 1895/II, pp. 1-46) and to some of my own memoirs.

The Upper Triassic deposits of Tethys are divided generally into three subdivisions, the Carnic, Noric and Rhætic stages. E. v. Mojsisovics divided both the Carnic and Noric stages into three substages, thus imparting to the Rhætic stage a taxonomic value inferior to that of the two preceding ones. Many genera belonging to all the known families of Upper Triassic ammonites reach the acme of their development in the Carnic stage. Although a considerable number of older genera are found for the last time at this level, the ammonite fauna of the Noric stage is a continuation and evolution of the Carnic fauna in every branch of life. The last life phase of the Noric stage seems to be the first which is distinguished from the preceding by the apparent extinction of numerous wide-spread and important genera and by the absence of any new elements either of foreign origin or derived from endemic forms. Nevertheless it is doubtful whether a single family of lower Noric ammonites becomes really extinct.

This decay is completed in the Noric epoch. From this stage eleven forms of ammonites only have been enumerated by Pompeckj, all of them of decidedly Triassic affinities. Five belong to the Noric genus *Choristoceras* and its subgenus *Peripleurites,* a phylogerontic descendant of the Ceratitidæ, whose last whorl became gradually uncoiled. *Arcestes,* the true leading genus of the Hallstatt limestone, is still represented by two species. To these are added one species of *Monophyllites* (*Mojsvarites*), of *Megaphyllites,* and a specifically undeterminable representative of *Cladiscites,* all genera of considerable vertical range. A single newcomer is indicated by *Hesperites,* a genus still imperfectly known, which is probably allied to the family of Trachyceratidæ.

It is noteworthy that not a single ancestral representative of Liassic ammonites is recognized in this assemblage. The discovery of one other genus is to be expected beds of Rhætic age. This is *Phylloceras* or, more exactly, with certainty, although it has as yet not been found in *Rhacophyllites,* if this subgeneric designation is extended to all widely umbilicated species of *Phylloceras. Rhacophyllites debilis* Hau. and *R. neojurensis* Quenst. are among the most common leading fossils of the upper Noric substage. In the Lower Lias, *Phylloceras, Rhacophyllites* and *Euphyllites* are remarkable for their richness and variety. The apparent intermittence of *Phylloceras* in the Rhætic is therefore purely accidental. It is in reality the only genus surviving the general extermination of Triassic ammonites.

The importance of the gradual decline of Triassic ammonites during the Rhætic epoch is evident from a comparison with the number of genera in the Carnic and Noric faunæ. Those faunæ do not contain less than 146 genera and subgenera of ammonites, which were reduced to six in the Rhætic stage. Hyatt was certainly right in speaking of a "culmination of ammonites in the Upper Trias after a period of uninterrupted progressive evolution from the early Devonian." Both the Carnic and Noric ammonites were highly varied, including forms with long and short body-chambers, with few and simple clydonitic sutures (*Lobites*) and with a very large number of the most complicated sutural elements (*Pinacoceras*); smooth, globose shells with serial lobes (*Arcestes*) and

extremely flattened shapes (*Pompeckjites*); shells exhausting almost every possible combination of sculpture from the most graceful ornamentation (*Acanthinites*) to stout ribs (*Heraclites*) and profusely tuberculated costations (*Trachyceras*).

The close of the Rhætic epoch is marked by the final disappearance of all Triassic types, excepting *Phylloceras*. Primitive and highly specialized forms were equally subjected to this general extermination.

In the eastern Alps the beds of the lowest Lias follow above those containing a Rhætic fauna without any unconformity. There is no trace of a hiatus nor of any diastrophic movement between the two groups. Nevertheless the ammonite fauna of the lowest zone of the Mediterranean Lias is entirely different from that of the Upper Trias. The first impression of this Liassic fauna is the sudden introduction of a large number of types which are only a little less manifold and diversified than those of the Upper Noric, but do not exhibit any phylogenetic affinities with them. We are indebted to F. Waehner for their careful and detailed examination.

There is little doubt that the extinction of the different phyla of Triassic ammonites prepared the way for the evolution of a new and vigorous stock, which originated from the genus *Phylloceras,* the only one which connects the faunæ of the Triassic and Liassic periods. *Phylloceras* is the ancestor of the two leading families of the lowest Lias, the Arietitidæ and Lytoceratidæ. Waehner and Pompeckj have demonstrated their intimate relationship with *Psiloceras,* the most primitive element of the Arietitidæ. Together with *Psiloceras,* more specialized types of the Arietitidæ: *Ægoceras, Schlotheimia, Arietites,* make their appearance in the deepest zone of the Lias. But they are comparatively rare, *Psiloceras* remaining the predominant genus in this and the following life-phase. All these genera are linked together most closely with the ancestral *Psiloceras.*

Of equal moment is the sudden appearance of the Lytoceratidæ in the Lower Lias, where they are represented by the genera *Lytoceras, Ectocentrites* and *Pleuracanthites.* Forms transitional between *Pleuracanthites* and *Psiloceras* have been described by Waehner. Thus *Phyl-*

*loceras* was destined to give rise to all Lower Triassic ammonites by the intervention of *Psiloceras*.[1]

Thus an aspect quite different from that of the Upper Trias is given to the ammonite fauna of the Lower Lias. Not one of the numerous and diversified genera of world-wide distribution, belonging to the families of Arcestidæ, Cladiscitidæ, Pinacoceratidæ, Haloritidæ, Tropitidæ, Didymitidæ, Ceratitidæ, Tirolitidæ, and Trachyceratidæ is represented in the latter. Their place has been taken by Arietitidæ and Lytoceratidæ. *Phylloceras,* which never played an important part in the fauna of the Upper Trias, was the only survival and was destined to become the ancestor of all Liassic ammonites.

In direct opposition to these facts, Steinmann denied the extermination of Triassic ammonites at the close of the Rhætic epoch. His reconstruction of a phyletic tree, in which *Macrocephalites* is branching off from *Juvavites, Sphæroceras* from *Halorites, Harpoceras* from *Discotropites, Desmoceras* from *Arcestes, Pachydiscus* from *Cladiscites,* need not be discussed here. It means toying with possibilities, the reality of which can never be proved.[2] One of his critical arguments, however, deserves consideration. He believes the palæontological record not to be sufficiently perfect to prove a real decline of the Triassic ammonites during the Rhætic epoch. It is true that cephalopod-bearing strata of Rhætic age have scarcely been discovered up to now outside the north-eastern Alps. But here they are as rich in ammonites as

[1] In connecting *Psiloceras* with *Phylloceras* (*Rhacophyllites*) I am following J. F. Pompeckj's view, which has been set forth by this author in his memoirs, "Note sur les *Oxynoticeras* du Sinémurien du Portugal, etc." (Comm. serv. géol. Portugal, VI, 1906-1907, p. 332) and "Zur Rassenpersistenz der Ammoniten" (3. Jahresber. d. niedersächs. Geol. Ver. Hannover, 1910, p. 82). E. v. Mojsisovics prefers to consider a specialised type of *Monophyllites* (*Mojsvarites planorboides* Winkler) as the ancestor of *Psiloceras.* Winkler's description and illustration, on which this suggestion has been based, are not absolutely reliable, and the type-specimen itself has, unfortunately, been lost.

It makes, however, little difference, whether the one or the other view is adopted, *Mojsvarites* itself being closely related to the Phylloceratidæ. According to Pompeckj, one genus only, *Phylloceras,* persists throughout the Triassic and Jurassic periods. In following E. v. Mojsisovics we have to record, simultaneously with the decline of *Monophyllites,* the first appearance of a new and transitional form, connecting this genus with *Psiloceras,* the undoubted ancestor of all Arietitidæ.

[2] Its only advocate is O. Wilckens (Naturwiss. Wochenschrift, N. F., X., No. 45, Jena, 1914, p. 20).

many beds of the Ladinic or Noric stages. Our knowledge of Rhætic ammonites is certainly not more limited than that of Permian ammonites after the discovery of the Artinsk and Sosio fauna. There is, consequently, as much evidence of a decline of the group during the Rhætic, as there is of a decline of the trilobites during the Carboniferous and Permian.

Such are the facts. They show us a great dying-out of ammonites towards the close of the Triassic and a rebirth, as it were, of a new fauna in the early Liassic, giving rise to the great wealth of Jurassic ammonite evolution. In entering into a discussion of the probable causes of this remarkable event in the life history of ammonites, we have to face the grave problem of the repeated extinction of large and flourishing groups of organisms. That this extinction has been partial only, affecting all but one stock of Triassic ammonites, marks the special case of our problem.

If we reflect on the multitude, the variety, and the complexity of the facts to be explained, and the scantiness of our information regarding them, we shall be ready to acknowledge that a full and satisfactory solution of so profound a problem is hardly to be hoped for, and that the most we can do in the present state of our knowledge is to hazard a more or less plausible conjecture.

In discussing the possible causes of the decay and final extermination of Upper Triassic ammonites, it will be best to follow the lines which have been traced by H. F. Osborn in his memoir on the causes of extinction of Mammalia (Amer. Naturalist, XL, 1906, p. 769).

*Changes of Geographical Conditions.*—The Triassic was on the whole a geocratic (land) period. A transgression of marine Rhætic beds is confined to the coasts of western Europe. It is counterbalanced by a regression of the sea in southern China, Japan, North and South America, where the Rhætic stage is represented by deposits of terrestrial and lacustrine origin only. There is but a small change in the distribution of land and sea during the Lower Lias, which in some regions of the ancient geosynclines is marked by a transgression of a rather limited range. The extinction of Triassic ammonites consequently does not admit of an explanation by changes of geographical conditions.

*Changes of Climate.*—The importance of this factor has

been advocated very strongly by C. Schuchert,[3] who insists on a general lowering of the temperature during the Liassic period, chiefly on the strength of the arguments of Handlirsch. I am happy to agree with this learned author in the opinion that the facts which prove the influence of climatic changes are many and weighty, but I think that the extinction of Triassic ammonites at the close of the Rhætic does not admit of this explanation.

It can hardly be too often repeated that the decay of ammonites, near the close of both the Triassic and Cretaceous periods, was gradual, that in the first instance it clearly began in the Upper Noric and continued throughout the Rhætic. Now, we are well informed about the climatic conditions of Upper Noric time, due to the discovery of rich faunæ of reef-building corals in this substage. Such faunæ are known to us from the Austrian Alps, from Timor, Nevada, Oregon and Alaska. J. Perrin Smith demonstrated the identity of nearly all his Alaskan species with types from the Upper Noric Zlambach beds of the Salzkammergut. The presence of this fauna under the 60th degree of north latitude is contradictory to the suggestion of a lowering of temperature in the Upper Noric seas. It may be equally well to call attention to the wide distribution of several species of ammonites and bivalves (*Pseudomonotis ochotica*) throughout the Pacific Ocean and into the arctic region (New Siberia), which is in favor of a comparatively equable but not of a low temperature.

Nor does the flora of the Rhætic stage exhibit any traces of increasing cold. It is of a remarkable uniformity in North America, England, Sweden, Germany, eastern Greenland, Spitzbergen, Persia, India, Japan, China, New South Wales, New Zealand, South Africa, Argentina, Chile and Honduras, and seems to prove a climate more uniform and milder in the polar regions than that of the present day.

If a period of cooling set in at the close of the Rhætic epoch—and I do not dissent from Professor Schuchert's opinion in this respect—it came too late to influence the extermination of Triassic ammonites, for this had been heralded long before by their gradual decay.

[3] Ch. Schuchert, Climates of geologic time, Carnegie Inst. Washington, Publ. No. 192, p. 284.

*Lack of Internal Adaptation and Inadaptability.*—*Arcestes* is one of the most persistent ammonite genera, ranging from the Anisic into the Rhætic stage, without undergoing any modifications of its characters. Thus its inadaptability can scarcely have been the primary cause of its extinction.

In the family of Ceratitidæ Hyatt signalized the first symptoms of general regression by the appearance of uncoiled and turriliticonic genera in the Noric stage. The development of uncoiled shells, which reaches its climax in the lower and middle Cretaceous, is considered as a sign of degeneration by many palæontologists. To this view I cannot assent. The best instance of this mode of development is *Lytoceras*. It is one of the most conservative types from the Lias up to the Neocomian, when suddenly a large number of uncoiled, straight, hook-shaped and even turriliticonic genera branch off from the old stem. All this stock flourishes for a considerable time. This does not mean degeneration, but adaptation to new and different forms of marine life, from a benthonic swimming to a chiefly creeping or even sessile mode of living. Still less can *Lytoceras* be stigmatized as degenerating, if we take into consideration the fact that it survives all its uncoiled offspring and persists into the Senonian stage. I consequently find in the development of uncoiled shapes in the family Ceratitidæ, which begins with *Choristoceras* in the upper Carnic and reaches its climax in the lower Noric substage, a sign of increased adaptability to new modes of life, not of degeneration.

*Peculiarities of Constitution.*—It is only touching the fringe of a great subject, if I venture to call attention to Brocchi's hypothesis, that the gradual and successive disappearance of species might be regulated by a constant law, that their death, like that of individuals, might depend on certain peculiarities of constitution. In our special case, as in many others, the extermination of a large and flourishing group of animals can be explained satisfactorily neither by external nor by such internal causes as are accessible to examination. In such cases Brocchi's hypothesis, although dealing with powers and influences of a still hitherto obscure nature, may yet serve its purpose as a first attempt to approach the solution of a hitherto unexplained problem.

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