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Status of Invertebrate Paleontology, 1953

V. *Mollusca: Cephalopoda*

BY BERNHARD KUMMEL

Museum of Comparative Zoology, Cambridge, Mass.

Few invertebrate classes possess (or are plagued with) the volume of literature and diversity of interpretation, or are so susceptible as media of philosophical speculation as the fossil cephalopods. A complete review of the literature and progress in the study of fossil cephalopods is beyond the scope of this paper. Therefore I will center attention on the geologic distribution of fossil cephalopods and current ideas on classification and evolution. The extent and degree of cooperation towards a uniformity of nomenclature — both morphological and taxonomic — that has prevailed in the past few years among the European and American authors responsible for the Cephalopoda for the Treatise has been truly inspiring. The results of this labor will place the study of these animals on a new threshold. It is a pleasure to acknowledge the data on Jurassic ammonoids furnished by W. J. Arkell; the data on Cretaceous ammonoids furnished by C. W. Wright; the data on Paleozoic ammonoids furnished by A. K. Miller; the data on the Dibranchiata furnished by L. Bairstow; and data on nautiloid genera by Curt Teichert. Of the three major groups of Cephalopoda, I will confine most of my remarks to the Ammonoidea. Recent tabulations indicate that there are approximately 3000 valid genera of fossil cephalopods with more than an additional thousand generic names which go into synonymy.

Within the Nautiloidea there are now recognized approximately 700 genera. Their evolutionary pattern is one of intense radiation in the Ordovician during the initial phases of their evolution, followed by a rapid and steady decline until the present day with our one remaining relic genus. The main pattern of distribution of nautiloid genera as illustrated on Figure 1 has been known for a long time. Morphologically the nautiloids are a highly diversified group but many of the orders that made their

appearance in the Ordovician became extinct by the Silurian and Devonian. During the latter half of the Paleozoic the evolutionary rate of the nautiloids was greatly diminished. A second surge occurred in the Upper Triassic which has a diversified nautiloid

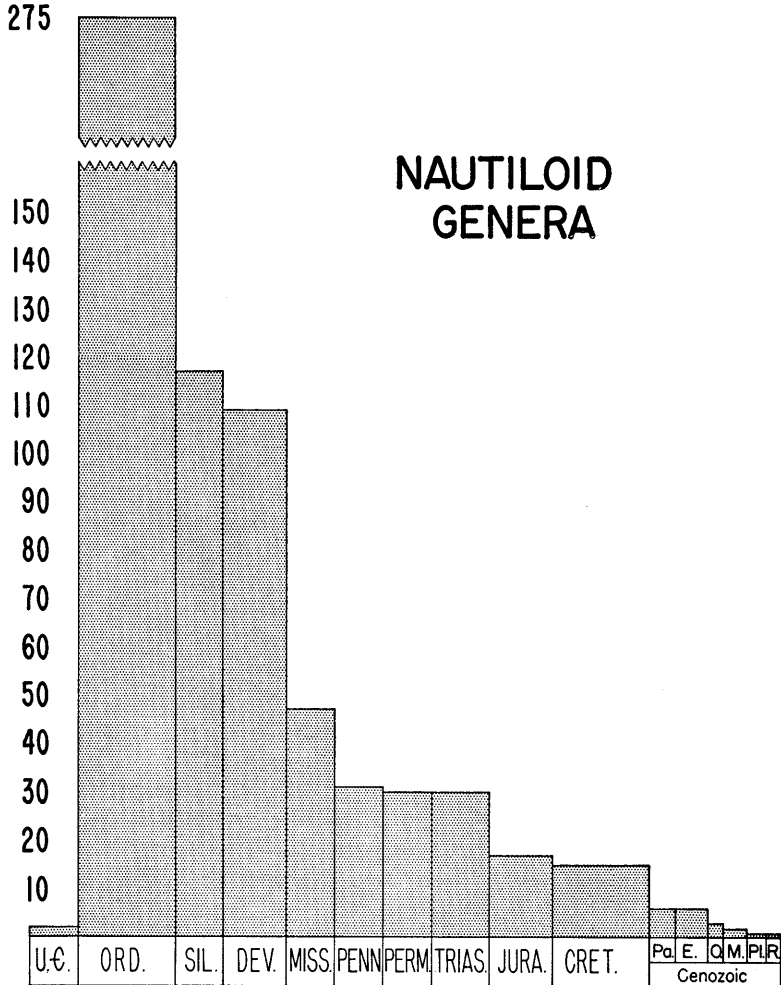


Fig. 1. Bar graph showing number of nautiloid genera in each geologic period. (Data from C. Teichert, personal communication.)

fauna, but nothing compared to that of the early Paleozoic. The evolutionary pattern of the nautiloids in the Triassic is merely a culmination of trends begun back in the Carboniferous. The Permian was not a period of crisis for the nautiloids as it was for the ammonoids, but in the late Triassic (Rhaetian) there was almost complete extinction of the nautiloids. No Rhaetian nautiloids are known, but a single specimen from the Carnian of New Zealand offers strong evidence that an offshoot of the Syringonautilidae survived into the Lias (Spath, 1927, p. 23; Kummel, 1953); from this family all post-Triassic nautiloids are derived. The Jurassic to Recent history of the nautiloids duplicates the general pattern shown by the Paleozoic forms; that is, there is an initial experimental phase of extensive radiation from which arose several more stable stocks, none of which, however, was long lived. In the Cenozoic only three new genera appear, of which only *Nautilus* survives.

Up until recently the classification of nautiloids has been completely dominated by the scheme proposed by Hyatt in the 1900 edition of the Zittel-Eastman Textbook of Paleontology. Today there is no doubt in anyone's mind that Hyatt's scheme is untenable. The rejection of Hyatt's classification is the rejection of a systematic arrangement based on a single character. The tentative scheme recently proposed by Flower and Kummel (1950) summarizing existing thinking can unquestionably be improved but it has had the very desirable effect of crystallizing attention on the more critical problems. There is wide agreement among nautiloid specialists that the number of orders proposed by Flower and Kummel should be reduced, but no agreement as yet as to how this should be done. Of the 13 orders recognized by these authors the Ellesmeroceratida, Endoceratida, Michelino-ceratida, Ascoceratida, Discosorida, and Oncoceratida are generally accepted as well defined groups and appear to need only minor revisions. The recognition of an Upper Triassic *Bisiphytes* (Family Nautilidae) which shows clear affinities to the Syringonautilidae changes the derivation of all post-Triassic nautiloids to the Triassic Syringonautilidae rather than the Paranautilidae as previously proposed (Kummel, 1953). This change necessitates the suppression of the Centroceratida and the joining of these families into the Nautilida. The Rutoceratida can most

probably also be included in the Nautilida but clear evidence of this relationship is not available (R. H. Flower, personal communication). Flower (1952) would derive the Rutoceratida from the Oncooceratida. The Liroceratidae, Ehippioceratidae, Paranautilidae, Clydonautilidae, and Gonionautilidae, all formerly placed in the Nautilida, may now need to be placed in a new order. At first it would seem that they would be logically included in the Barrandeoceratida; however, connecting forms from the Devonian have not been recognized as yet. The status of the Solenochilida, Tarphyceratida, Barrandeoceratida, and Bassleroceratida is a source of disagreement among specialists. The crux of the difficulties and confusion in nautiloid systematics and evolution lies in the great host of early Paleozoic families. Taxonomic stability of these forms will be approached as our knowledge and understanding of their complex morphology and modes of adaptation is increased. Agreement on the systematics of early Paleozoic nautiloids is near but is not quite yet a reality. Because of this no phylogenetic chart is presented.

It is significant to note that in the past few years very few new genera have been established in spite of the fact that several large new faunas have been described. It would be pleasant to think that possibly we are near the limit of the total number of genera in this order. This observation is encouraging in that maybe now more effort and thought can be concentrated on critical paleobiological problems.

Ever since William Smith's great discovery of the usefulness of fossils for correlation and geochronology, the ammonites have played a leading role as a stratigraphic tool. The pioneer work of d'Orbigny, Oppel, Quenstedt, Mojsisovics, Waagen, Neumayr and many others firmly established the ammonites as the leading actor in the drama of Mesozoic stratigraphy. Likewise the nature of the ammonoid shell and its manner of growth has lent itself beautifully to the pliable minds of evolutionary theorizers. Few people have had more influence on the study of fossil cephalopods than Alpheus Hyatt whose whole philosophy revolved around the recapitulation doctrine — a principle not accepted today by most cephalopod students. However, few text books of zoology or geology fail to illustrate some of Hyatt's cephalopods demonstrating recapitulation in action.

The recent taxonomic house cleaning of ammonoid genera enables the construction of the bar graph (Figure 2) on the geologic distribution of ammonoid genera. There is a total of approximately 1800 genera of ammonoids; of these 172 are from

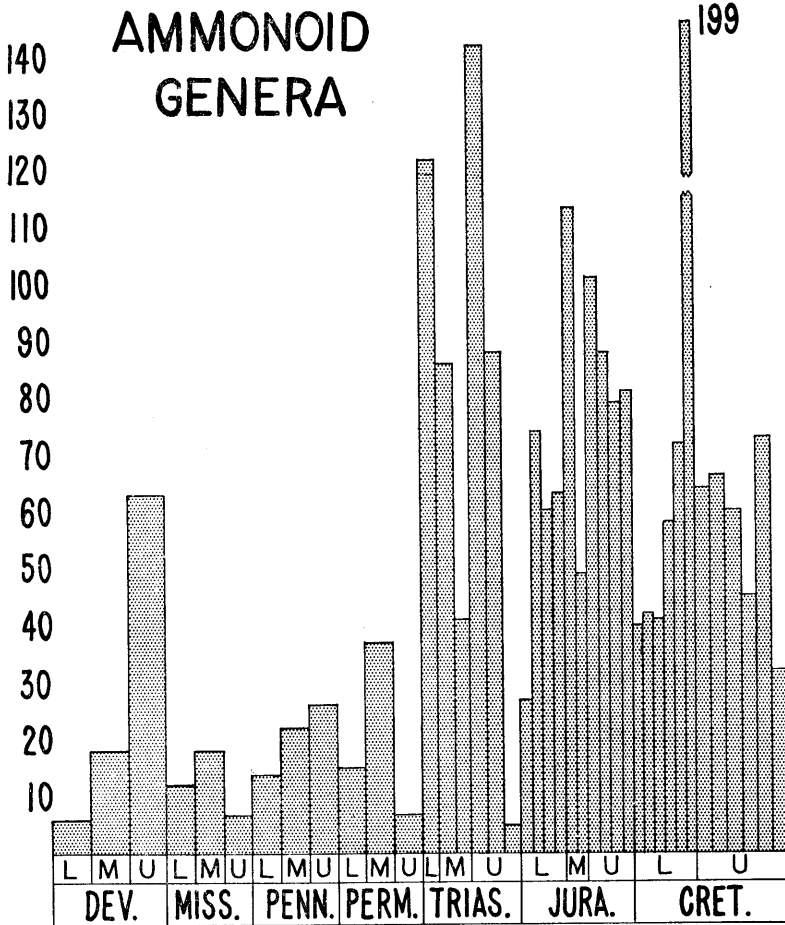


Fig. 2. Bar graph showing number of ammonoid genera in each geologic period. (Data on Paleozoic ammonoids from A. K. Miller, that on Jurassic ammonoids from W. J. Arkell, and that on Cretaceous ammonoids from C. W. Wright, personal communications.)

the Paleozoic, 370 from the Triassic, 735 from the Jurassic and 493 from the Cretaceous. There are an additional 1000 generic names that fall into synonymy. The largest number of these involve Jurassic ammonites.

The overall distribution of genera confirm commonly held views. In spite of specific instances of "monographic highs" and lack of record, it is the opinion of the Treatise ammonoid authors that the data reasonably reflect the history of this group of animals. In fact, C. W. Wright (personal communication), who compiled the list of Cretaceous ammonites, found his data most illuminating as a commentary on the validity of the Cretaceous stages. The most unusual aspects of the evolutionary history of the ammonoids are the three periods of crisis; during the first two such crises the group nearly became extinct and from but few surviving stocks even larger radiations developed until the final extinction of the group in the late Cretaceous. The two earlier periods of crisis are in the late Permian and in the late Triassic.

Several important aspects in the history of the study of ammonoids have greatly influenced our interpretation of ammonoid phylogeny and taxonomy. It is indeed remarkable that not until the 1860's did the splitting of the genus *Ammonites* really begin. The recognition of generic categories among the ammonoids developed rapidly after that date. Since this early period there have been proposed many taxonomic schemes for the Ammonoidea. Most of these, however, were based on a single character; the suture, sculpture, siphuncle, and length of body chamber have all been used in various manners with little success. Unit systems of classification invariably ended up by bringing together heterochronous homeomorphs.

Present interpretation of the relationships of Permian and Triassic ammonoids illustrates this point well. Figure 3 is a bar graph of total genera and new genera (dark stipple) of Permian and Triassic ammonoids. The average evolutionary tempo of Permian ammonoids is only slightly higher than that of the Carboniferous. The most striking feature is the presence of only seven genera in the Upper Permian. It should be kept in mind that the number of known fossiliferous Upper Permian deposits is indeed few. The ammonoid faunas of such classic areas as the

Salt Range, Djulfa, Timor, the Alps, Madagascar, and East Greenland are not abundant. The radiation of the ammonoids in the Lower Triassic is well demonstrated with its 128 genera. This radiation was not a sudden affair. Lowermost Triassic deposits, that is, those of Otoceratan age, are as scarce as marine Upper Permian strata. The smaller bar graph of Figure 3 shows the total genera and new genera for the six ages of the Lower Triassic. Only one genus carries on into the Triassic from the Upper Permian. It is not until the middle Seythian that a really large diversified fauna is encountered.

Figure 4 is a diagrammatic interpretation of the phylogenetic relationships of Permian and Triassic ammonoids. Of the two main groups of Paleozoic ammonoids, the goniatitids are represented by seven families in the Permian and the prolecanitids by five families. It has long been thought that many Middle and Upper Triassic ammonoids had their ancestry among these goniatitid families. However, the extensive researches of L. F. Spath over the past 30 years have demonstrated in a convincing manner the improbability of any of these goniatitid families being ancestral to any Triassic stocks. There are numerous cases of homeomorphy between many of these goniatitid genera and Middle and Upper Triassic genera. Permian ammonoids of the prolecanitid stock are included in two superfamilies. One of these — the Pronoritaceae — continues into the Triassic with a very modest development but did not give rise to any new stock. The ancestry of Triassic ammonoids is to be found in the Xenodisceaceae.

The most common and abundant lowermost Triassic ammonoids are the ophiceratids which show a wide range of variability in conch form. From this extremely variable ophiceratid stock arose directly or indirectly more than a dozen families of Lower Triassic ammonoids. This radiation is a continuation of that started at the base of the Triassic with the ophiceratids, and represents the height of the experimental phase in the eruptive comeback of the ammonoids after their near extinction in the late Permian. Most of the genera and families of this eruptive phase are short-lived but from a few of them arose the eight long-lived superfamilies that include most of the Middle and Upper Triassic ammonoids. Thus with the Anisian begins the stabilized phase in the evolutionary history of Triassic ammonoids.

The great decline and near extinction of the ammonoids in the Rhaetian has been known for a long time. From a peak of 140 genera in the Carnian there are left only a few species of 5 genera in the Rhaetian. There is a sharp decline in evolutionary development already in the Norian.

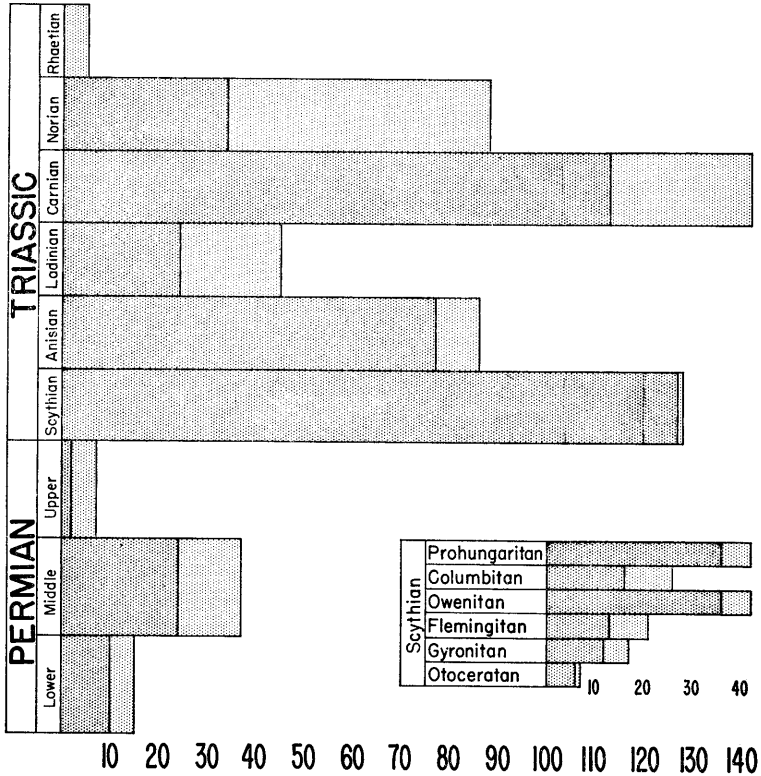


Fig. 3. Bar graph showing total number of ammonoid genera and new genera (dark stipple) in each stage of the Permian and Triassic.

A single stock carries through into the Lias to give rise to the great host of Jurassic and Cretaceous ammonoids. The evolutionary patterns of the ammonoids in these two periods is quite unlike that in the Paleozoic or Triassic. Two persisting, slowly evolving, root-stocks — the Lytoceratina and the Phylloceratina

— are the evolutionary reservoirs from which the great host of Jurassic and Cretaceous ammonoids are derived. The Lytoceratina and Phylloceratina are characteristic of the ancient Tethys; they are the leiostracous or smooth shelled forms. The trachyostreous or ornamented genera are most abundant in the epicon-

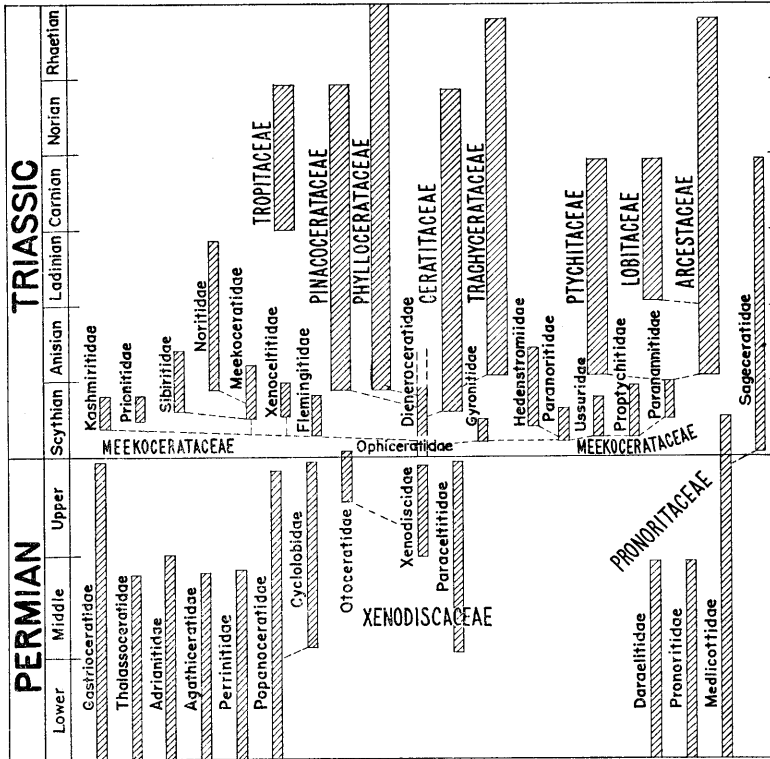


Fig. 4. Diagram showing inferred phylogeny and geologic distribution of Permian and Triassic ammonoids.

tinental seas adjoining the Tethys. Some 30 years ago Salfeld proposed his theory of Iterative Evolution in which he interpreted the innumerable throngs of the Ammonitina as arising through repeated radiations of offshoots from the conservative

stocks. Deciphering the countless threads connecting the Ammonitina and these conservative stocks is still evasive. More

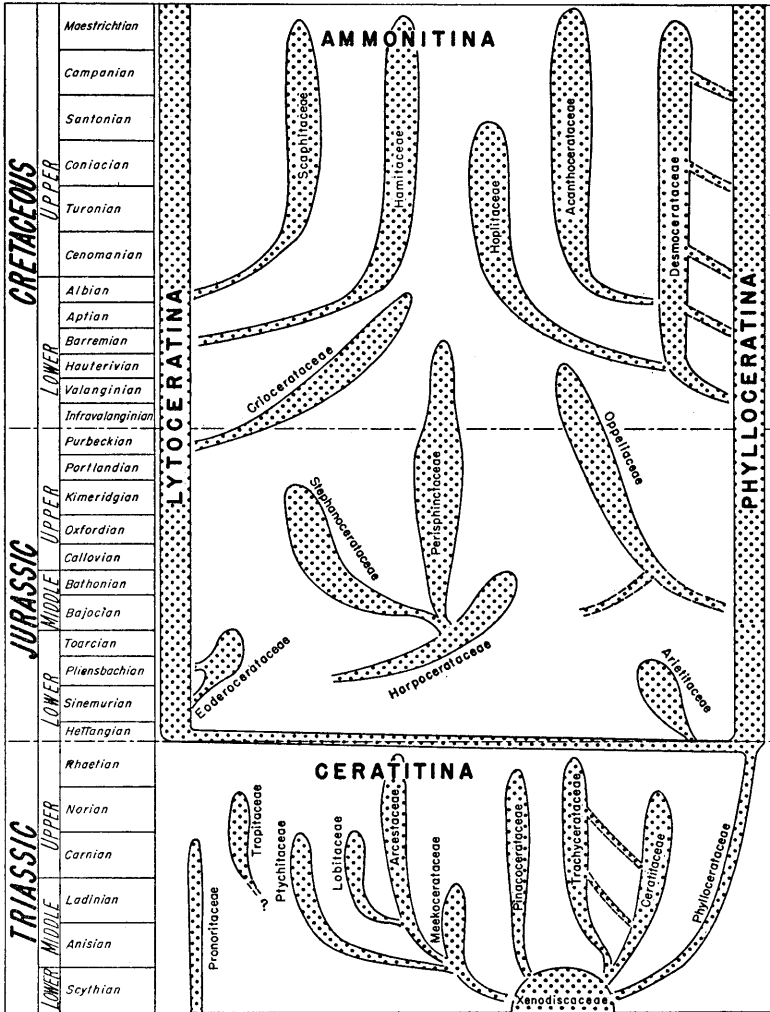


Fig. 5. Diagram showing inferred phylogeny and geologic distribution of Mesozoic ammonoids. (Adapted from Arkell 1950, Wright 1952, and Kummel 1952).

progress has been made with Cretaceous ammonites than with those of the Jurassic. When and if the various Jurassic and Cretaceous superfamilies can be more definitely tied to one or the other of the conservative root-stocks there will be need for modification of the suborder Ammonitina.

The Dibranchiata cephalopods have not received as wide attention as the nautiloids and ammonoids. Mr. Leslie Bairstow kindly furnished tentative and approximate data on the time

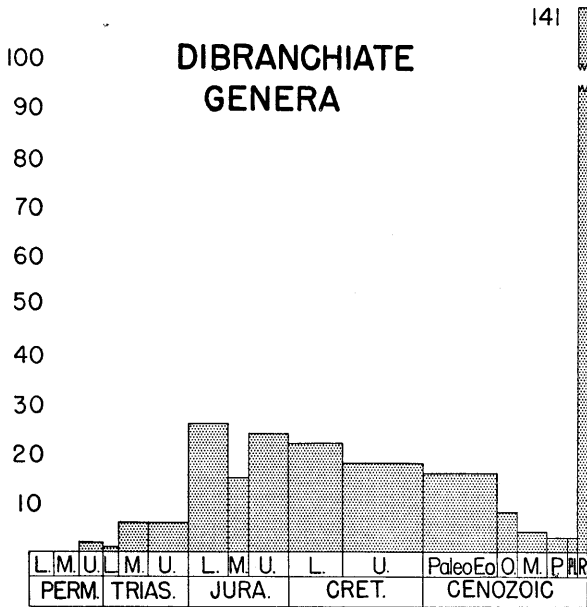


Fig. 6. Bar graph showing number of dibranch genera in each geologic period. (Data from L. Bairstow, personal communication.)

distribution of genera of Dibranchiata. The most striking feature of the bar diagram of Figure 6 is the great number of Recent genera; of the approximately 250 genera of Dibranchiata, 138 are known only from the Recent. The great diversity of Recent fauna, and the fact that many of the genera are very different from the nearest fossil forms known, imply the previous existence of many genera that are not actually known as fossils (L. Bairstow, personal communication). The incompleteness of the fossil

record of the dibranchs does not make them a suitable group for the study of evolutionary rates.

The present status of our knowledge of the fossil Cephalopoda presents an encouraging framework to direct and guide future research. The great success to which the cephalopods, especially ammonoids, have been used in stratigraphy has resulted in the major emphasis being placed on them as "tools" of stratigraphy. It is becoming more and more clear that a greater understanding of the animal and its ecology and adaptive range will add greatly to the value of the Cephalopoda as "tools" of stratigraphy and as "tools" for study of evolutionary processes.

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