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Some observations on bactritid cephalopods

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Abstract. The classification of the Class Cephalopoda and the systematic position of the Order Bactritida within it are reviewed. The Middle Ordovician genus Eobactrites was probably the first representative of the Bactritida. There is a definite record in the Silurian of the Czech Republic and a possible occurrence in Northern England. The mode of life of these cephalopods is briefly considered.

Key words: Cephalopoda, Bactritida, Silurian, Czech Republic, Northern England

Systematic position

The bactritids, though only a very small group within the vast array of the Class Cephalopoda, have assumed importance as the generally accepted origin of the ammonoids. Systematically they have been treated in various ways.

To take a reasonable starting point: In the Russian Osnovy, Volume V (Ruzhentsev 1962), the Subclass Ectocochlia was divided into five Superorders: The Nautiloidea, Endoceratoidea, Actinoceratoidea, Bactritoidea, and Ammonoidea. Shimanskii here dealt with the Bactritoidea. In the American Treatise on Invertebrate Paleontology, Part K, Mollusca 3, the first four of these Superorders were elevated to Subclasses of the Class Cephalopoda (Teichert and Moore 1964). In this volume Erben (1964) provided the section on the Bactritoidea. A footnote by R. C. Moore, the Director and Editor of the whole series of volumes of the Treatise, explained that Erben would have preferred to employ a Suborder Bactritina placed in the Order Ammonoidea, but was urged to do otherwise by Curt Teichert, who maintained that these cephalopods should be ranked at least level with the several nautiloid orders and considered to belong in an intermediate position between the Orthocerida and the ammonoids. Eventually the decision was made to employ a subclass. A most important element in future consideration was the widespread acceptance of Erben's (1966) establishment in the Lower Devonian of the Rheinische Schiefergebirge (Rhenish Slate Mts.) of a morphological series from *Bactrites* to coiled ammonoids. This series involves changes in the degree of coiling, changes in whorl section, and an increasing complexity of the suture. The ellipsoidal protoconch, ventral position of the siphuncle, ventral sutural lobe, and relatively long body chamber are characteristics of the whole series. Erben (1966) argued that this accelerated evolution of ammonoids in the Upper Siegenian took place in small geographically restricted populations.

In the same year as Part K of the Treatise appeared, Donovan (1964) took the opportunity in Biological Reviews to survey classification of the Cephalopoda on the basis of phylogeny. In his seven "Megataxa", the Coleoidea figured separately as one of these. The Ammonoidea were associated with the nautiloid Orders Barrandoceratida and Tarphyceratida, considered as derived through them.

There have continued to be divergent views on the taxonomic position of the bactritids. Teichert (1967) had already noted that "conspicuous lack of consensus regarding the taxonomic position of this group suggests that it may have multiple and complex relationships to other cephalopod groups". His own view of classification was to follow that of the Treatise. Thus the Bactritoidea fell in place as one of seven subclasses along with four for the nautiloids, one for the ammonoids, and one for the coleoids. House (1981) regarded the bactritids as a suborder of the ammonoid Order Anarcestida, the most primitive of the ammonoids. He very reasonably took the degree of coiling to be of low taxonomic value.

My own view of cephalopod classification remains largely but not completely that held in 1987. Though I have worked with many of these fossils since then, I maintain two subclasses as did Shimanskii (1962) and Jeletzky (1966). The name Endocochlea makes a logical pair with the Ectocochlea, but now there is no doubt of the widespread acceptance of the alternative name Coleoidea. The subclass includes all living cephalopods except for Nautilus. Its members, though very varied, are characterised by the presence of a guard and/or a reduced body chamber.

The name Ectocochlea is of course redundant to those who have several taxa of cephalopods level with the Coleoidea. I continue to find that the division of the nautiloid cephalopods into several subclasses – the Nautiloidea, Endoceratoidea, and Actinoceratoidea – in the Treatise, is artificial and unsatisfactory (see Flower 1976, Holland 1979, 1987). Its acceptance demands the elevation of the ammonoids to subclass status. The ammonoids are, of course, so common, so useful in biostratigraphy, and so much discussed that there is a tendency to disregard their relative uniformity compared with the diversity of the nautiloids. The relative complexity of the ammonoid suture is perhaps the one feature that we tend to fall back upon in justifying their separation. But even here we find

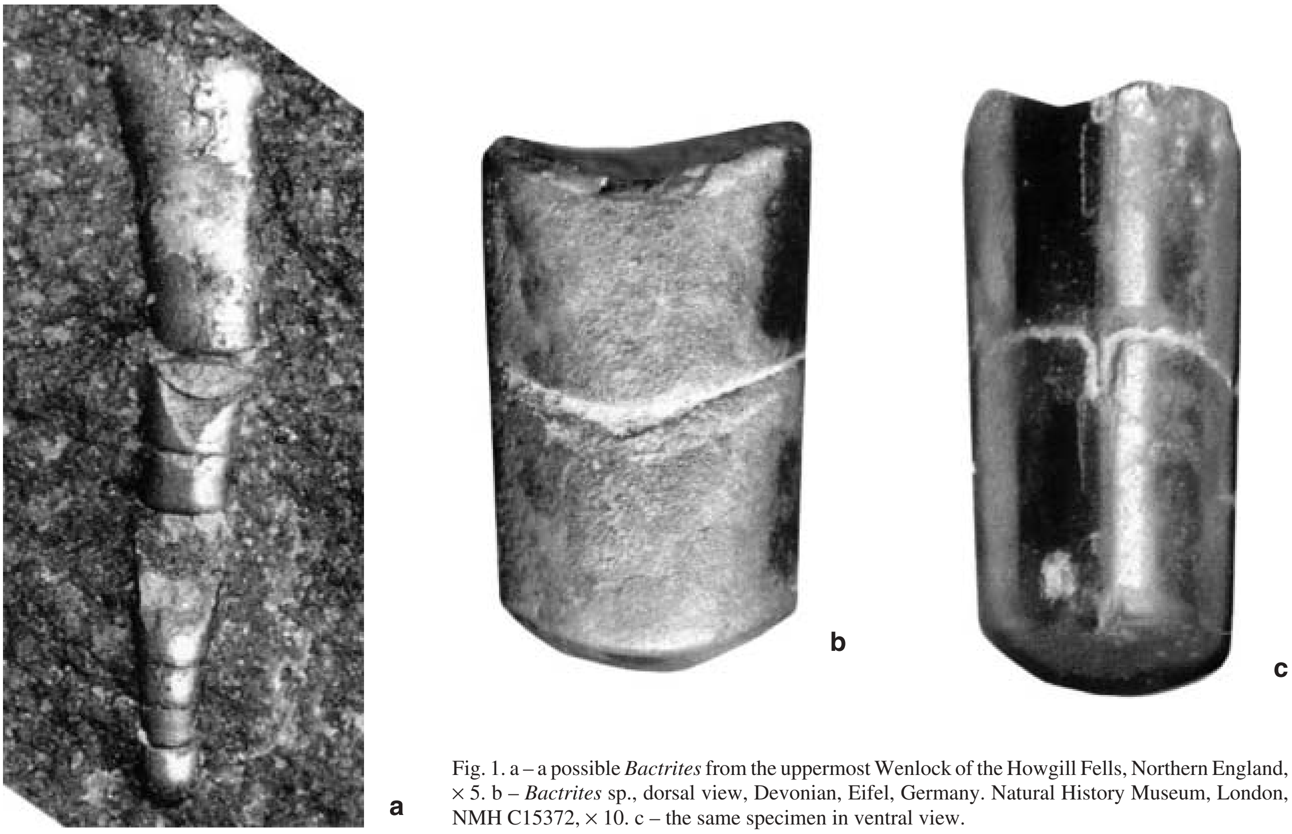

Fig. 1. a – a possible *Bactrites* from the uppermost Wenlock of the Howgill Fells, Northern England, × 5. b – *Bactrites* sp., dorsal view, Devonian, Eifel, Germany. Natural History Museum, London, NMH C15372, × 10. c – the same specimen in ventral view.

some Triassic and Tertiary nautiloids in which relatively complex sutures are present.

I find it best simply to employ orders as the next taxonomic category below the two subclasses (the Coleoidea and Ectocochlea). They are well used, well known taxa, within which our numerous families and genera can be placed. We shall all continue to use the informal terms nautiloid and ammonoid because they are rooted in the history of this part of palaeontology and, not least, because different groups of palaeontologists tend to concentrate upon them.

So where does all this leave the bactritids. The orthoconic nautiloids (be they Orthocerida or Ellesmeroceratida) are their obvious ancestors. Some of the former have the appropriate ellipsoidal protoconch. The assembly of that set of characters mentioned above, which the ammonoids share with the bactritids has suggested their gradational closeness. Hengsbach (1974) argued on cladistic grounds that the bactritids with their ventral (external) siphuncle and ventral sutural lobe must belong with the ammonoids. The importance of the bactritids in giving rise to the vastly important ammonoids does not alter the fact that their morphology grades along with other members of the Anarcestida, the first order of Paleozoic ammonoids. I previously followed House (1981) in regarding the Bactritina as a suborder of the Anarcestida.

However, this small intriguing group continues to yield debate and surprise. Doguzhaeva's meticulous work on ultrastructure culminated in her paper of 2002 on well preserved Late Carboniferous and Early Permian material from the South Urals. This has revealed previously unknown character of protoconchs and apical portions of phragmocones which suggest that the bactritids have an early ontogeny different from that of the ammonoids. They lack a primary varix, have different layering of the shell wall near the primary constriction, and some of them show a "primordial dome" on the protoconch. Some are said to show cameral deposits, though these could of course have evolved in the bactritids by Late Paleozoic times. Nevertheless, there remain significant differences. My suggestion now is that an Order Bactritida be employed, of equal status to the various nautiloid and ammonoid orders and lying between them in characteristics.

Full understanding of the nature of detailed evolution from nautiloids to ammonoids through the bactritids will be very difficult to achieve. We need more specimens of the Early Paleozoic bactritids, we need ultrastructural data on the Devonian forms.

The earliest bactritids

It is obvious that the bactritids must have arisen from an orthoconic nautiloid. Kolebaba (1973) demonstrated the variability in nautiloid protoconchs in a collection of Wenlock material from Prague. Some of them show characteristically appropriate ellipsoidal form with a constricted aperture.

Erben (1964), in his comprehensive account of the whole groups of bactritids, suggested a possible origin in the Ordovician, but with representation only in the form of an offshoot from the main evolutionary line leading to the genus *Eobactrites.* Originally described and illustrated by

Barrande (1867) from the Ordovician of Bohemia, *Bactrites sandbergeri* was given the new generic name *Eobactrites* by Schindewolf (1932). Sweet (1958) recorded it also from an equivalent level in the Middle Ordovician of Norway. One of his illustrations was used by Balashov (1962) in Osnovy. However, there it is placed in the family Baltoceratidae of the nautiloid Order Ellesmeroceratida. Flower (1964) also placed it in this family, suggesting that the stratigraphical gap between this form and the common Devonian species implied homeomorphy. Dzik (1984) also disputed the bactritid affinities of this genus. It is true that *Eobactrites* appears to have a slightly deeper and more tubular ventral sutural lobe and perhaps a somewhat more robust form. However, I am disinclined to follow Balashov, Flower, and Dzik in placing this genus in the Baltoceratidae. This slender shell with its narrow siphuncle is more probably the first known bactritid.

Erben in Teichert and Moore (1964) and other authors have put the origin of the Bactritida in the Silurian, based upon the record of a single specimen of *Bactrites* from Morocco (Termier and Termier 1950). The specimen was ill preserved and its illustration is unconvincing diagnostically as a bactritid; it is best disregarded.

Partly filling the stratigraphical gap more rigorously, Ristedt (1981) described small early ontogenetic phragmocones of a new bactritid species from the Upper Silurian (nilssoni Biozone, Gorstian Stage, Ludlow Series) of Bohemia. The ellipsoidal protoconch, relativelly long camerae, marginal siphuncle, and small v-shaped ventral sutural lobe are all clear.

Recently Professor R. B. Rickards of the University of Cambridge kindly gave me a small block of dark grey siltstone from the uppermost Wenlock graptolite shale facies (ludensis Biozone) of the Howgill Fells in northern England. It contained a small slender orthocone preserved in pyrite and having relatively long camerae and an ellipsoidal protoconch (Fig. 1a). In the Lower Devonian (Hunsrückschiefer) of Germany, the specimen would undoubtedly have been identified as *Bactrites* (compare Fig. 1b). After photography I attempted to release the mould from its matrix but, unfortunately, below the original convex surface there was only a powder of pyrite. It seems possible that this was indeed a *Bactrites* which had settled in the quiet waters of the basin floor with its slightly heavier ventral side downwards. It is important that small slender pyritized Silurian orthocones of this kind should be collected in the hope that a ventral sutural lobe may be found.

Mode of life

The ways in which orthoconic cephalopods combined the buoyancy attained through successively emptied camerae and the advantage of more or less horizontal orientation in the water have long been understood. Flower (1957), in particular, gave a vivid account of these weighting method. The early bactritids do not seem to have had the advantage of cameral or siphonal deposits and would therefore float with the shell above the soft body, the apex pointing upwards. Wedstermann (1998, fig. 20.9) illustrated this situation for orthocones without deposits.

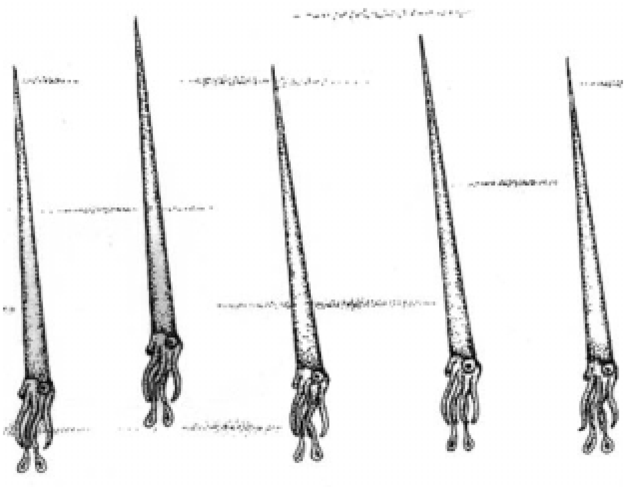

Fig. 2. Reconstruction of *Bactrites* in life.

The critical shift to a marginal siphuncle would exploit the advantage of providing sufficient ventral weighting to tip the shell slightly from the vertical. Thus the head and tentacles could now point slightly forward instead of directly downwards. This change could then lead on the gradual curving and eventual coiling of the ammonoids.

But what was the evolutionary advantage of light slender orthocones? The bactritids cannot be seen as benthic forms. In the environment represented by the Hunsrückschiefer of Hercynian Devonian facies they are to be seen rather as part of the plankton. In discussion of concentrations of Paleozoic nautiloid cephalopods, Holland et al. (1994) referred to schooling behaviour. Thorson (1971) had defined a school as an aggregation of fish in which the spacing and operation of the individuals is uniform. The members are kept together by vision. He quoted E. S. Iverson as writing that a member of a school has a better chance of living longer when chance of encounter by a predator and its limited capacity to eat are both considered. Perhaps groups of the near vertically oriented slender bactritid shells, with their relatively small soft bodies, found evolutionary advantage in this way (Fig. 2). After death they would readily be dispersed and destroyed.

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References

Balashov Z. G. (1962): Order Ellesmeroceratida. In: Ruzhentsev V. E. (ed.) Osnovy paleontologii. Vol. 5, Mollusca-Cephalopoda 1. AN USSR, Moscow, pp. 73–77 (in Russian).

Barrande J. (1865–1877): Système Silurien du Centre de la Bohême. Premiere Partie: Recherches paleontolgiques, vol. 2, Class des Mollusques, Ordre des Cephalopodes, 2.

Doguzhaeva L. (2002): Adolescent Bactritoid, Orthoceroid, Ammonoid and Coleoid shells from the Upper Carboniferous and Lower Permian of the South Urals. Abh. Geol. Bundesanstalt 57, 9–55, Wien.

Donovan D. T. (1964): Cephalopod phylogeny. Biol. Rev. 39, 259–287.

Dzik J. (1984): Phylogeny of the Nautiloidea. Palaeontol. Polonica 45, 1–219.

Erben H. K. (1966): Über der Ursprung der Ammonoidea. Biol. Rev. 41, 641–658.

Flower R. H. (1957): Nautiloids of the Paleozoic. In: Ladd H. S. (ed.) Treatise on marine ecology and paleontology, vol. 2, Paleoecology. Mem. Geol. Soc. Amer. 67, 2, 829–852.

Flower R. H. (1964): The nautiloid Order Ellesmeroceratide (Nautiloidea). New Mexico Inst. of Mining and Technol. State Bureau of Mines and Miner. Res., Mem. 12, 1–234.

Flower R. H. (1976): Ordovician cephalopod faunas and their role in correlation. In: Bassett M. G. (ed.) The Ordovician System: Proc. Palaeont. Assoc., Symp., Birmingham, September 1974. Univ. of Wales Press and Nat. Mus. of Wales, Cardiff, pp. 523–552.

Hengsbach R. (1974): Zur systematischen Stellung der Bactritina (Ammon., Cephalop.). Acta Biotheoretica 23, 35–41.

Holland C. H. (1979): Early Cephalopoda. In: House M. R. (ed.) The Origin of Major Invertebrate Groups. Academic Press, London, pp. 367–378.

Holland C. H. (1987): The nautiloid cephalopods: a strange success. J. Geol. Soc. London 144, 1–15.

Holland C. H., Gnoli M., Histon K. (1994): Concentrations of Palaeozoic nautiloid cephalopods. Bull. Soc. Paleont. Ital. 33, 83–99.

House M. R. (1981): On the origin, classification and evolution of the early Ammonoidea. In: House M. R., Senior J. R. (eds) The Ammonoidea. System. Assoc. Spec. 18, 3–36. Academic Press, London.

Jeletzky J. A. (1966): Comparative morphology, phylogeny, and classification of fossil Coleoidea. Mollusca. Univ. Kansas Paleont. Inst., Article 7, 1–162.

Kolebaba I. (1973): Embryonal stages of Wenlockian cephalopods from central Bohemia. Čas. Nár. Mus. 142, 1, 28–40.

Ristedt H. (1981): Bactriten aus dem Obersilur Bohmens. Mitt. Geol. Pal. Inst. Univ. Hamburg 51, 23–26.

Ruzhentsev V. E. (ed.) (1962): Osnovy paleontologii. Vol. 5, Mollusca -Cephalopoda 1. AN USSR, Moscow.

Schindewolf O. H. (1932): Zur Stammgeschichte der Ammoneen. Paleont. Zeitschr. 14, 164–181.

Shimanskii V. N. (1962): Subclass Ectocochlia. In: Ruzhentsev V. E. (ed.) Osnovy paleontologii, Vol. 5, Mollusca–Cephalopoda. AN USSR, Moscow, pp. 18–32 (in Russian).

Sweet W. C. (1958): The Middle Ordovician of the Oslo Region, Norway. Nautiloid cephalopods. Norsk. geol. Tidsskrift 38, 1–178.

Teichert C. (1967): Major features of cephalopod evolution. Essays in Paleont. and Stratigr. Univ. Kansas, Dpt. of Geol., Spec. Publ 2, 162–210.

Teichert C., Moore R. C. (1964): Introduction. In: Moore R. C. (ed.) Treatise on Invertebrate Paleontology, Vol. 5, part K, Mollusca 3, K2–K4.

Termier H., Termier G. (1950): Mollusques. Paléont. Marocaine, II. Invertebres de l'Ere Primaire. Fasc. 3. Service Géol. Protectorat de la Rep. Francais Marocaine. Notes et Mémoirs 78, 1–246.

Thorson G. (1971): Life in the sea. World Univ. Library. Weidenfield and Nicholson, London.

Wedstermann G. E. G. (1998): Life habits of Nautiloids. In: Functional morphology of the invertebrate skeleton. John Wiley and Sons, pp. 263–298.

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