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Evolution in some early Jurassic ammonites: Asteroceratinae, Oxynoticeratidae and related forms

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ABSTRACT - The Asteroceratinae and Oxynoticeratidae, previously (Donovan 1987) regarded as a single evolutionary line, are now resolved into two separate lines of descent. Both of these probably originated in *Caenisites*.

One lineage (A), characterised by close, strong ribbing at least on the inner whorls, led from *Caenisites* to *Eparietites* and then *Oxynoticeras*. Probably then to *Carixiceras*. The trend in this lineage was towards more involute, compressed shells, smooth first on the outer whorls (*Eparietites*) and then throughout. Suture lines were simple in *Caenisites* and *Eparietites*, becoming more complex and closely spaced in the oxycones.

In the boreal sequences we find gaps between *Caenisites* and *Eparietites*, and between *Eparietites* and *Oxynoticeras*. This lineage flourished elsewhere and moved north for rather short periods.

The second lineage (B) began with *Asteroceras*, which flourished in the north in the absence of lineage A during the earlier part of the Obtusum Zone. *Aegasteroceras*, *Arctoasteroceras* and several endemic genera were developments from *Asteroceras* with loss of ventral ornament. *Epophioceras* is currently classed as an asteroceratine though it may have evolved independently from *Caenisites*. After the Obtusum Zone we lose sight of this lineage in the boreal province for some time, but similarity of inner whorls suggests that *Gleviceras* is descended from *Asteroceras* of the *stellare* group. Intermediate genera are not known.

A postulated third lineage (C) led to very evolute ammonites (*Epophioceras*) which are regarded as the ancestors of the Family Echioceratidae.

KEY WORDS: ammonites, Lower Jurassic, phylogeny.

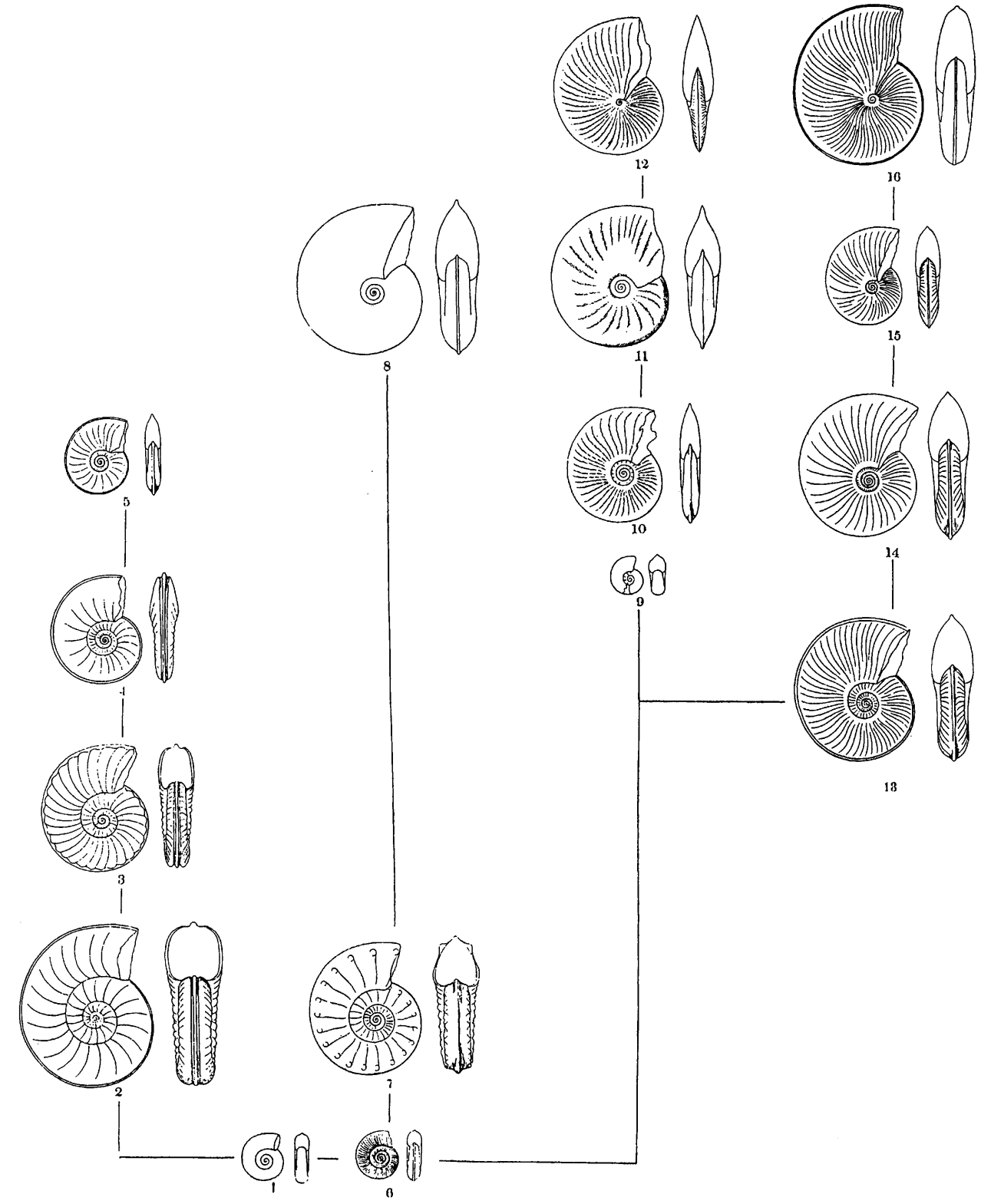
INTRODUCTION

The evolution of the Liassic ammonites formerly embraced in the family Arietitidae (now subdivided) has been studied in detail at least since the days of Alpheus Hyatt. Hyatt, working in America on collections of European ammonites which had been purchased by the Museum of Comparative Zoölogy at Harvard University, was disadvantaged by having only very generalised stratigraphical information. Nevertheless he established the evolution of oxycone shells from evolute serpenticones (1889, Summary Plate 13) and, further, believed that this evolutionary trend affected several independant lineages. Pia (1914) offered a generalised diagram of relationships which showed *Asteroceras* leading to *Gleviceras*, as does the present study, but then derived *Oxynoticeras* from *Gleviceras*, which is not in accordance with either stratigraphical or morphological facts. Hyatt was, I believe, more nearly right in keeping these two oxycones as separate developments. Hyatt's diagram is reproduced here for comparison (Fig. 1). A more general interpretation, of wider scope, was published by the present author (Donovan 1987), who now thinks that the phylogeny then offered, with a single line of evolution leading to the oxycones, was too simple.

This text and illustrations were prepared in the summer of 1990 and have not been revised to take account of work published since then.

Limitations of the present study

If the present study seems biased towards north-west Europe, this is because almost all the well-dated



SUMMARY PLATE XIII.

Fig. 1 - A reproduction of Hyatt (1889), Summary Plate 13. The numerals indicate the following taxa (modern names used): 1, *Cymbites laevigatus*; 2, *Asteroceras obtusum*; 3, *Caenisites turneri*; 4, *C. brooki*; 5, *Eparietites collenotii*; 6, *Euagassiceras striaries*; 7, *Agassiceras scipionianum*; 8, *Ag. "scipionis"*; 9, 10, *Oxynoticeras oxynotum*; 11, *O. simpsoni*; 12, *O. lymense*; 13, *Angulaticeras greenoughi*; 14, *Gleviceras guibalianum*; 15, *G. lotharingicum*; 16, *Radstockiceras oppeli*.

material, and the majority of the relevant fossils described in the literature, are from this area. Even so there are severe limitations. The famous coast sections in Dorset (England), some of the most intensively studied and collected in the world, have yielded (for example) only 5 horizons with *Asteroceras*. Assemblages of ammonites have not been studied or described, although extensive collections exist. Many of the species in question grow to large sizes (300 - 600 mm), but almost all the ammonites which have been described and figured, forming the basis of species and genera, are septate inner whorls of (sometimes much) larger individuals. An exception to the general failure to collect large specimens is provided by the late J. F. Jackson, whose collection from the beds in question is in the National Museum of Wales, Cardiff. It has not been published although the present author has examined it.

In the Tethyan realm, almost all published material, and virtually all the species named by classical authors, are of unrecorded stratigraphical horizon. This situation is now being remedied by French, Spanish and Italian workers, but not all the species of old authors have been rediscovered in their native horizons.

The origin of the lineages described here is to be found in the Arietitinae of the early Lower Sinemurian (Bucklandi and Semicostatum Zones), perhaps in genera such as *Vermiceras* (= *Am. latisulcatus* Quenstedt) rather than in the more specialised *Arnioceras* or *Coroniceras*.

The first part of this paper outlines hypothetical phylogenetic sequences in general terms. Part 2 comprises some notes on nomenclature and taxonomy, including some references to occurrences briefly mentioned in Part 1.

PART 1. PHYLOGENY

Lineage A (Fig. 2)

Caenisites turneri (J. de C. Sowerby) is typical of an evolute group of species, with little overlap of the whorls and umbilicus between 40% and 50% of the diameter. The ribs are sharp, straight on the whorl side, curving forwards through a quarter of a circle to run into the raised lateral margins of the ventral grooves. The keel is high, flanked by grooves which are broad and semicircular in cross section.

The more involute species typified by *C. brooki* (J. Sowerby) differ from the *turneri* group only in greater overlap of the whorls and a smaller umbilicus - about 35% of diameter. *C. brooki* is morphologically intermediate between the evolute species and *Eparietites*. However, it should be noted that it is not the latest species of *Caenisites*, and it occurs at only a single horizon in Dorset.

The suture line of *C. turneri* is simple and differs little from that of other early Arietitidae. The more involute *C. brooki* does not add any more elements to the suture but may broaden the 1st lateral saddle (Spath 1925, p. 266, fig. c), prefiguring the condition found in *Eparietites*.

The *Caenisites* evolutionary line disappears from Britain during the Obtusum and Stellare subzones, and when it reappears it has changed into *Eparietites*.

The inner whorls of *Eparietites* are very similar to the more involute forms of *Caenisites*, but the genus differs from *Caenisites* in three principal ways: the shell becomes more involute with relatively more compressed whorls; the ventral grooves have "degenerated" into smooth concave areas on either side of the sharp keel; and the ribs are lost on the outer whorls. Intermediate to some extent is *E. undaries* (Quenstedt) with umbilicus about 32%. Typical *Eparietites* have the umbilicus between 20% and 30% of the diameter.

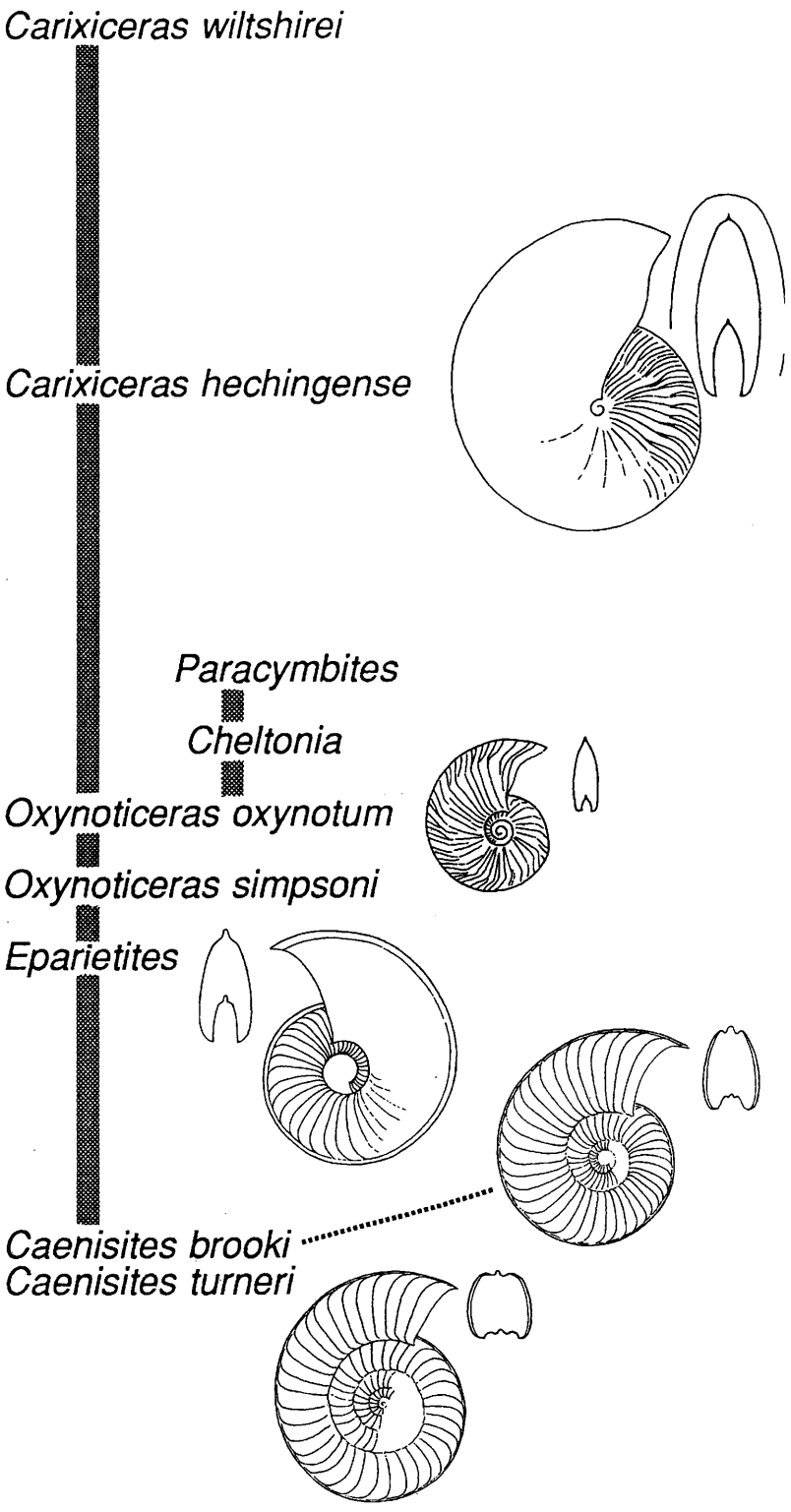
As already noted (Donovan, 1990, p. 255) *Eparietites* occurs in the Tethyan province, although forms such as Fucini's "*Asteroceras*" *varians* (1903, p. 142), with "uncoiling" body chamber at a relatively small size (50-90 mm) are distinct from the, usually much larger, boreal species. The genus also occurs in South America (Chile and Peru).

Oxynoticeras simpsoni [Bean](Simpson) is intermediate between *Eparietites* and *Oxynoticeras oxynotum* (Spath, 1925, pp. 108, 109). An intermediate form between *Eparietites* and *O. simpsoni*, , named *O. eboracense* by Spath (1925, p. 108; see also Wright, 1881, pl. 47, figs. 6, 7), retains the strongly ribbed innermost whorls of *Eparietites*. Suture lines of *O. simpsoni* (Spath, 1925, fig. on p. 110, b, c, e) are very similar to that of the holotype of *Eparietites denotatus* (Simpson) (Buckman 1912, Yorkshire Type Ammonites, pl. 67A) but differ in that the suture line "ascends" towards the umbilical suture (Spath, 1925, p. 110 called this an inverse suture line), a feature characteristic of *Oxynoticeras* (Fig. 5). *Oxynoticeras simpsoni* is best known from Britain, but Parona's *O. oxynotum* (1896, pl. 1, figs. 1a-c) from the Southern Alps appears in fact to be *O. simpsoni*, and possibly the lack of reports of the species from elswhere is due to non-recognition rather than non- occurrence.

The Denotatus, Simpsoni and Oxynotum subzones

Domerian
Figulinum
Capricornus
Maculatum
Luridum
Valdani
Masseanum
Jamesoni
Brevispina
Polymorphus
Taylori
Aplanatum
Macdonnelli
Raricostatum
Densinodulum
Oxynotum
Simpsoni
Denotatus
Stellare
Obtusum
Birchi
Brooki

Fig. 2 - Phylogeny of Lineage A. Column at left gives names of ammonite subzones.



are missing from the Dorset coast sections, but it is likely that elswhere in Britain, in thicker seqences, there is a nearly continuous evolutionary progression from *Eparietites* to *Oxynoticeras*.

Oxynoticeras oxynotum (Quenstedt) is a familiar fossil from southern England and southern Germany, but the species was based on the pyritic inner whorls of much larger ammonites. Outer whorls are generally not preserved, or at least not collected. *O. oxynotum*, like *O. simpsoni*, retains the concavities on either side of the keel, although these now merge into the whorl side without the sharp angles which are found in the ancestral *Eparietites*.

Lineage A reached the final evolutionary stage of oxycones with a small, or closed, umbilicus with *O. lymense* (Wright) from the Densinodulum Subzone of the Dorset coast. The end of this lineage is difficult to decipher, but *Oxynoticeras lymense* may have led to the form represented by *Ammonites oxynotus numismalis* Oppel (1853; see Quenstedt, 1885, pl. 37, figs. 1-7), shown by Schlatter (1980, p. 52) to come from the Polymorphus Subzone. Schlatter found this name to be preoccupied and re-named the species *Metoxynoticeras hechingense* (Schlatter, 1980, p. 52) after the type locality. It should probably be referred to Spath's genus *Carixiceras* (see below). The latter occurs in the Ibex Zone of Dorset. *Carixiceras* with characteristic suture line is reported from the Davoei Zone of the Bakony Mountains, Hungary (Géczy, 1976, p. 39).

The "dwarf" genus *Cheltonia*, with "uncoiling" body chamber at a very small size (about 25 mm), is an offshoot from *Oxynoticeras* as shown by its suture line which is identical with that of the inner whorls of *Oxynoticeras oxynotum* (Schindewolf, 1962, Figs. 91, 93, 94). It is possible that *Cheltonia* is the microconch of *Oxynoticeras* although in an unpublished English borehole it appears later than *Oxynoticeras* and persists later, into the Raricostatum Subzone. *Paracymbites*, another small form found in the Raricostatum Zone evolved from *Cheltonia* (Donovan, 1966), and has a similar suture line. *Hypoxynoticeras* (Spath, 1925, p. 111) from the Jamesoni Zone of northern Germany may be another of these small developments.

Lineage B (Figs. 3, 4)

The genus *Asteroceras* is cryptogenic in Britain, first appearing in the Dorset coast sections some 9 - 12 m above the highest *Caenisites*. Spath (1926, pp. 167, 168) thought that it was descended from *Caenisites* via forms like his species *C. obtusiformis* (1926, p. 167, pl. 11, fig. 4; only 22 mm in diameter), in the Turneri Zone, characters of *Asteroceras* appearing first on the inner whorls. The intervening stages are absent from the well-known sequences of north-west Europe.

Asteroceras is characterised by ribs which strike the margins of the ventral grooves at a distinct angle, in contrast to the condition in *Caenisites*. As noted by Spath (see above) this is seen only in the innermost whorls of *Caenisites*. The venter with broad rounded grooves is similar to that of *Caenisites*, but the grooves may become ill-defined on the outer whorls in species of the *obtusum* group. Another distinctive feature is the shell ornament, intersecting spiral lines and growth lines having small nodes at the intersections (Manley 1977). The suture line is relatively simple, with shallow incisions of the main elements. Suture lines are widely spaced. This is the "sparse" type of suture pattern of Donovan (1985).

The earliest British species of *Asteroceras* is *A. obtusum* (J. Sowerby), of which the type is wholly septate at about 145 mm diameter. Specimens in the Jackson collection from the Woodstones (Bed 83f of the Dorset coast), a nodule band in which the species is first found, show that it was 280 - 300 mm in diameter when complete with body chamber.

Asteroceras obtusum is succeeded in Dorset by *A. stellare* (J. Sowerby), the chief source of which in Dorset is nodules in bed 88f. The lectotype is only 75 mm in diameter, but specimens in the Jackson collection show that the species was septate to more than 300 mm and was probably 400 mm or more when complete. It is more involute and compressed compared with *A. obtusum* with a stronger keel and grooves.

Asteroceras stellare was so named because the innermost whorls show polygonal instead of spiral coiling, giving a "stellate" appearance. This is because, as noted by Spath (1926, p. 169) these whorls, of depressed section, bear about seven tubercles per whorl, and shell growth changes direction abruptly at each tubercle. The tubercles may bear auriculoids. After a diameter of about 15 mm this ornament changes rapidly to the strong ribbing which characterises the adult shell.

Asteroceras disappears from the north-west European sequences after the Stellare Subzone, being replaced by *Eparietites* of Lineage A. However, several evolutionary developments originated from the *Asteroceras* stock in the Obtusum Zone.

Lineage B, "main line" (Fig. 3)

Asteroceras of the *stellare* type gave rise, via unknown intermediates, to the oxycone genus

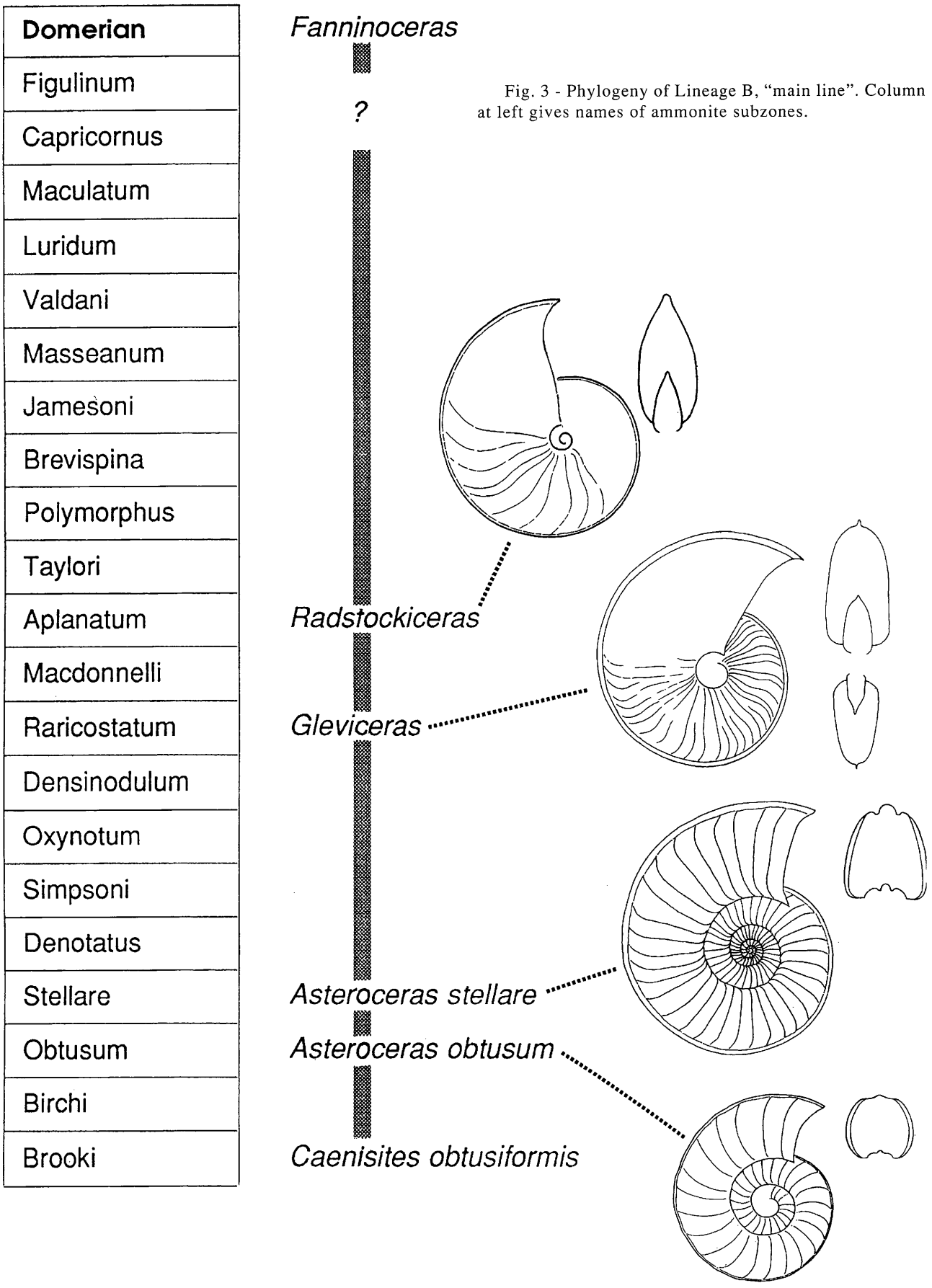


Fig. 3 - Phylogeny of Lineage B, "main line". Column at left gives names of ammonite subzones.

Gleviceras. The reason for proposing this connection is the close similarity of inner whorls between *A. stellare* and *Gleviceras*, the latter being carefully described by Buckman (1918) when he set up the genus. Buckman included in *Gleviceras* Oppel's (1862, p. 132) *Am. riparius*, based on a specimen only 9 mm in diameter. Schindewolf (1962, p. 490) proposed the genus *Riparioceras* for this form, but Oppel's species is founded on the innermost whorls of *Gleviceras*. The "*Riparioceras*" stage is rapidly followed, as in ancestral *A. stellare*, by normal ribbing. On later whorls this tends to become falcoid with intercalated secondaries.

The extreme development of the oxycone line of evolution in Lineage B was reached with *Radstockiceras*, with very small or closed umbilicus. This genus probably appeared late in the Raricostatum Zone (the type material is from the condensed facies of Radstock, England) and persisted for some time into the Pliensbachian. It persisted throughout the Lower Pliensbachian, as shown by reports from the Ibex Zone (Valdani/Luridum subzones) of the Causses (France) and the Northern Calcareous Alps (Meister, 1986, p. 30; Meister & Böhm 1993, p. 185)), and the Jamesoni/Ibex Zones and the mid-Davoei Zone in the Bakony Mountains, Hungary (Géczy, 1976, p. 39).

The long-ranging *Radstockiceras* or some related form may have given rise to *Fanninoceras*, a very similar oxycone which occurs in the late Carixian and throughout the Domerian substage. It appears to be restricted to North and South America.

Lineage B, Obtusum Zone radiation (Fig. 4)

In contrast to the long-lived oxycone lineage, there were a number of shorter-lived developments from *Asteroceras*, most of them seemingly confined to the Obtusum Zone.

Least altered from *Asteroceras* was *Arctoasteroceras* (Frebold, 1960), in which the ribs die out about two-thirds of the way across the whorl side, and the keel is obsolescent, leaving a rounded venter with faint traces of the grooves. First described from Arctic Canada, the genus was later reported from southern Alaska (Imlay, 1981, p. 33). The generic name, however, turns out to be misleading because the genus is also found in the Tethys, in the autochthon of the southern Alps (*Arct. actinotum* (Parona)), possibly in peninsular Italy (*Arct.*? *peregrinus* (Fucini), among the Liassic fossils from the mud volcanoes of Indonesia, and from north-eastern Papua New Guinea. Details of these occurrences are given below. *Arctoasteroceras* is reported from the Oxynotum and Raricostatum zones of North America. The tethyan occurrences are not well dated.

A more short-lived development than *Arctoasteroceras* was *Aegasteroceras*, in which the keel and grooves are also absent, and the ribs extend to the midventral line. Unpublished boreholes in southern England show that the genus occurs in the Denotatus Subzone, which accounts for its absence from the Dorset coast sections where this subzone is missing. *Asteroceras marstonense* (Spath, 1925, p. 267), where the grooves are lost on the outer whorl, is morphologically intermediate, but was based on an unstratified type of doubtful locality. Schlatter (1983, p. 252) notes another intermediate form figured by Hoffmann in 1938 (reference in Schlatter).

Aegasteroceras occurs in north-west Europe, in the southern Alps (*Aegasteroceras saltriense* Parona; see below) and the High Atlas, but does not seem to have been reported from other parts of the world.

Yet another evolutionary radiation from *Asteroceras* is represented by Tethyan forms which probably need a new generic name. They are characterised by a quadrate to compressed whorl section, with straight, sharp ribs which extend all the way across the whorl side with little or no curvature, in contrast to *Asteroceras* where the ribs are concave forwards. There appear to be several species, differing in whorl thickness and in size of umbilicus. An example is "*Asteroceras*" *reynesi* (Fucini). The genus is known from the alpine Fleckenmergel, from the autochthon of the southern Alps, peninsular Italy, Portugal, and possibly the Côte d'Or. Details are given below.

Parasteroceras (Dommergues, Fauré & Peybernès, 1986; see below) was described from Tunisia. In the fading of the ribs towards the venter, and the "degeneration" of ventral ornament, it shows some similarity to *Arctoasteroceras*. It is one of the few Sinemurian ammonites in which dimorphism has been illustrated.

Pompeckj long ago (1897) described an "*Asteroceras*" fauna from Portugal, with several new species. These species are distinct from the familiar northern European forms, and Spath (1925, pp. 267, 268) differentiated them as two new genera, *Pompeckioceras* and *Ptycharietites*. Dommergues & Mouterde (1987) have explained this local development as the result of endemic evolution in a small rift basin on the eastern margin of the future Atlantic Ocean.

Lineage C (Fig. 4)

The ancestry of the very evolute *Epophioceras* may lie in the very evolute *Caenisites pseudobonnardi*

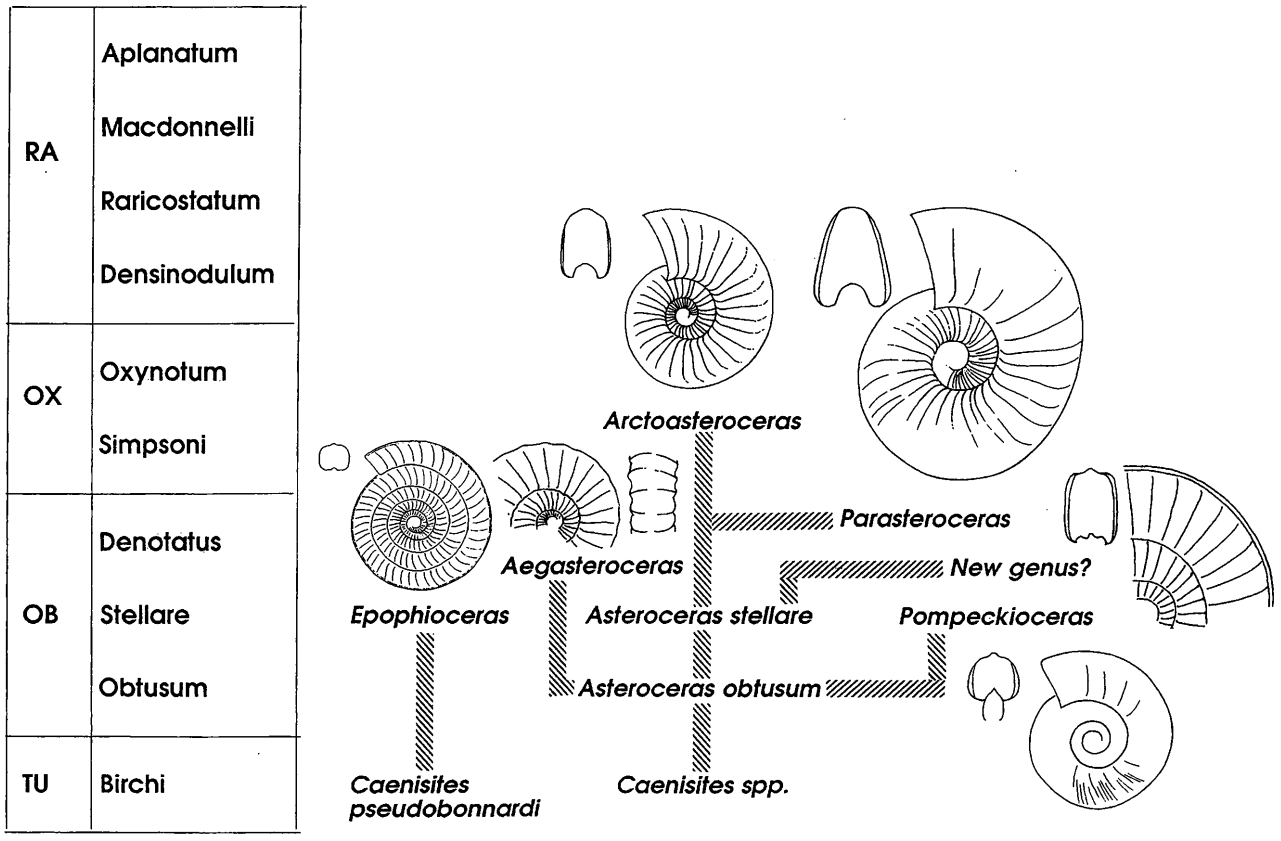


Fig. 4 - Phylogeny of Lineage B, branches mainly of Obtusum Zone age. Columns at left give abbreviated zonal names (Turneri, Obtusum, Oxynotum, Raricostatum) and names of subzones.

(Spath) (K. N. Page, pers. comm.) which is found in the Birchi Subzone in Dorset. Similar forms are absent from northern Europe during the succeeding Obtusum Subzone, *Epophioceras* being recorded from about the base of the Stellare Subzone in Dorset (Bed 87) and from the Stellare and Denotatus Subzones in unpublished southern English boreholes. In Switzerland (Kanton Schaffhausen) it is recorded above *Asteroceras stellare* (Schlatter, 1976).

Epophioceras is regarded (Getty 1973) as the ancestor of the Family Echioceratidae, which includes many very evolute species. This family provided the evolute, ribbed, often bisulcate serpenticones which, in the latest Sinemurian, replaced the often homeomorphous Arietitidae of shallow water assemblages of the Lower Sinemurian. It is not discussed in the present paper.

Evolutionary trends

In both main lineages (A and B) considered in this paper evolute platycones gave rise to oxycones (*Oxynoticeras*, *Gleviceras*). Neither lineage is present continuously in well-known sequences, so that the time taken for this evolutionary change is not well documented. The maximum time available is about 3 subzones in the *Caenisites- Oxynoticeras* case, and 5 subzones in the *Asteroceras-Gleviceras* lineage. There is no accurate way of translating these durations into years, since the length of subzones was doubtless variable. Westermann (1984, p. 27) allows just under half a million years per subzone in this part of the Jurassic, which would yield maximum figures of 1.5 m.y. in the first case and 2.5 in the second, but such estimates are only the roughest indications.

The oxycones both developed further into forms with smaller umbilicus (*Radstockiceras*, *Carixiceras*) which persisted through several zones with little obvious change. The idea of the oxycone shell form as a stable end product of evolution has been around at least since Hyatt (cf. Donovan 1973) and appears to be applicable at least to the present cases.

In contrast to the oxycone trend, the Obtusum Zone radiation from *Asteroceras* retained planulate, fairly evolute shells. All these branches have in common "degeneration" or loss of ventral ornament (keel, sulci), in *Aegasteroceras*, *Arctoasteroceras*, *Parasteroceras*, *Pompeckioceras*. The same trend is seen in the very evolute *Epophioceras*, which may be a separate phylogenetic line from *Caenisites*, as noted above. Some of these, at least (*Parasteroceras*, *Pompeckioceras*) were local endemic developments.

These genera with "degenerate" venters recall similar developments a zone or two earlier (*Agassiceras*, *Euagassiceras*) (Donovan 1987, p. 133).

The change from "sparse" to "dense" suture types (Donovan 1985), together with the fact that the earlier, serpenticone or platycone forms with "sparse" sutures are abundant in shallow water sediments, while the later oxycones with "dense" suture type are of sporadic occurrence and often relatively rare, suggests that the evolutionary change to oxycones was accompanied by a move to deeper water farther offshore. A change of mode of life is indicated. The oxycones could, perhaps, have become more active feeders taking larger prey. In our present limited knowledge of ammonite biology, such speculation is not very precise. Some more of it will be found in Donovan (1987, 1993).

In contrast to the oxycone lineages, the *Epophioceras* - Echioceratidae line consisted wholly of evolute shells with long body chambers and simple, often widely spaced, suture lines. While the oxycones had relatively short body chambers and probably a stable floating position, this was not the case with the evolute forms. This suggests that a stable floating position was not important for their mode of life. They are interpreted here as living in shallow water with perhaps a benthic or near-benthic mode of life.

PART 2. TAXONOMIC NOTES

Planulate genera

Aegasteroceras Spath 1925

Arietites (Asteroceras) saltriensis Parona (1896, p. 38) is a typical *Aegasteroceras*. Parona founded his species on more than 15 specimens of which two were figured. The larger of these, Parona's "best preserved example", his plate 8, figs. 2a, b; text-figure on p. 39) is here designated Lectotype of the species. It was preserved in the Stoppani Collection, Museo Civico di Storia naturale di Milano, but was destroyed during the 1939-45 war.

Arctoasteroceras Frebold 1960

Type species: *Arctoasteroceras jeleyzkyi* by original designation.

The type species was based on abundant material from Aklavik, NW Territories, Canada. The holotype (Geological Survey of Canada no. 14623) was figured by Frebold (1960, pl. 2, fig. 1a, b), is 62 mm in diameter and wholly septate. Most of the paratypes are likewise septate but a body chamber fragment (1960, pl. 3, fig. 1a, b) must have belonged to an individual approaching 150 mm in diameter.

The type material of *A. jeletzkyi* was associated with *Oxynoticeras oxynotum* of which a typical example was figured (Frebold, 1960, pl. 4, fig. 1; GSC no. 14631)[1]. If the two genera came from the same horizon, then the age of *Arctoasteroceras* in Canada is Oxynotum Zone. The genus is reported from southern Alaska in the Raricostatum Zone (Imlay, 1981, p. 16).

The innermost whorls of *Arctoasteroceras* are not well shown by the figured type material. The septate whorls have sharp, rather weak ribs, which die out about two-thirds of the way across the whorl side. The venter has a broad, ill-defined keel, hardly perceptible in some specimens, with no flanking grooves. The body chamber fragment has a broad arched venter with no keel. The suture line was not figured but stated to be fairly simple, only moderately incised, and often asymmetrical. From what can be seen in the half-tone figures it is more elaborate than that of *Asteroceras*.

The genus was stated by Frebold to be distinguished from *Aegasteroceras* by the weaker, more numerous ribs which do not continue on to the venter.

Occurrence of *Arctoasteroceras* outside northern North America: *Oxynoticeras actinotum* Parona (1896, p. 20) from Lombardy is now assigned to *Arctoasteroceras*. Parona studied five examples, of which two were figured, and the original of his plate 2, figures 1a-c (University of Pavia) is here designated Lectotype. It shows the typical ornament, including fine secondary ribs crossing the blunt keel. The suture lines are similar so far as can be judged. *Arctoasteroceras actinotum* has an umbilicus about 22% of the diameter compared with 30% in the type species.

Arietites (*Asteroceras*) *peregrinus* Fucini (1902, p. 6) hardly differs from the type species of *Arctoasteroceras*, except that the keel appears to be more sharply demarcated, a feature which could have been over-emphasised by the draughtsman. Possibly the same form was figured by Cecca et al. (1987, pl. 1, figs. 1a, b) as *Asteroceras* aff. *varians* Fucini. It is possible that these Italian forms with stronger ventral ornament are intermediate between *Asteroceras* and

[1]The associated "*Gleviceras* ?" (Frebold 1960 pl. 4, fig. 6a-c; GSC no. 14636) appears to be an *Oxynoticeras* also.

the typical *Arctoasteroceras*.

Asteroceras sparsicostatum Wanner & Jaworski (1931, p. 206, pl. 19, figs. 1a-e) from a mud volcano on Jamdena island, Indonesia, is a typical *Arctoasteroceras*.

Skwarko (1967, p. 70, pl. 10, fig. 4) described a *Tropidoceras*? sp. from the Balimbu greywacke formation of northeastern Papua New Guinea. This ammonite, illustrated in side view only, appears to be an *Arctoasteroceras*.

Parasteroceras Dommergues, Fauré & Peybernès 1986

Type species *Parasteroceras rakusi* Dommergues, Fauré & Peybernès by original designation. The species is dimorphic and the authors indicated a "holotype macroconque" and a "holotype microconque". As it is not possible for a species to have two holotypes, the "holotype macroconque" (Dommergues, Fauré & Peybernès, 1986 plate, 1, figs. 1a, b; no. OST P1) is here designated the Lectotype of the species.

The type species was found at Djebel Oust, Tunisia, in a glauconitic [condensed] bed together with a variety of forms, some new, which may suggest an Obtusum Zone age.

The innermost whorls are unknown. The inner whorls/microconch at a diameter of about 30-40 mm in side view rather closely resembles *Oxynoticeras* at the same size, but have a bluntly angular venter instead of the sharp venter of *Oxynoticeras*. The macroconch reached a large size with the last suture at a diameter of about 145 mm. It has strong, simple ribs and a rounded keel-less venter.

The genus could be regarded as intermediate between *Asteroceras* or *Eparietites* and *Oxynoticeras*,

New Tethyan genus. This genus is characterised by quadrate to compressed whorl section, bisulcate venter with strong keel, and straight, sharp, strong ribs. It differs from *Asteroceras* in that the ribs do not curve forwards towards the venter. An example of the form is *Asteroceras reynesi* Fucini (1903, p. 131) from the Monte Cetona. Fucini had three syntypes of which the one figured in his plate 19, figs. 8a-d, and text-fig. 77, said to be in the Museo di Pisa, is here designated as Lectotype of *A. reynesi*.

The form also appears to be represented by at least some of the ammonites figured by Parona from Saltrio as *Arietites obtusus* (1896, pl. 5), by Pompeckj's alleged example of the same species from Portugal (1897, text-figs. 1, 2; refigured by Mouterde & Rocha 1981, pl. 1, fig. 12), and by "*Asteroceras retusum* Reynès" of Schröder (1927, pl. 10, figs. 5a-c), from the Fleckenmergel of the eastern Alps. Guérin-Franiatte's *Asteroceras paucicostatum* (1966, p. 292), appears similar to Pompeckj's Portugese specimen, but the holotype (Guérin-Franiatte, 1966, pl. 169) comprises only one rather poorly preserved whorl so it is difficult to be certain.

Oxycones

Gleviceras Buckman 1918

Type species: *Gleviceras glevense* Buckman 1918 by original designation.

The type species was based on three figured specimens, the holotype (Buckman 1918, pl. 27, fig 2; pl. 28, fig. 1) and several paratypes. One figured paratype (1918, pl. 28, fig. 2) is in the collection of the British Geological Survey. The other figured paratype (pl. 27, fig. 3; pl. 29, figs. 3a-c; pl. 30, fig. 4) and the holotype are not known to exist in public collections. Another, unfigured paratype was described by Buckman on his page 291.

The stratigraphical horizons of the types are not well established. The holotype is from "the lower part" of Folly Lane brickyard, Cheltenham, Gloucestershire, England, stated by Buckman to be "above the *oxynotum* horizon (p. 288) and "*raricostatum* hemera" (p. 324). The larger figured paratype (pl. 28, fig. 2) was from an old collection, unstratified, and the other (pl. 27, fig. 3 etc.) from Folly Lane. Richardson (1904, p. 43) places the Folly Lane section in the Raricostatum Zone and the lower part in the *raricostatum* hemera, approximately equivalent to the Raricostatum Subzone.

All the types are wholly septate, the largest being the unfigured one which Buckman estimated to have been about 450 mm in diameter when complete with its body chamber.

Oxynoticeras Hyatt 1875

Type species *Ammonites oxynotus* Quenstedt 1843 by subsequent designation by Buckman (1909, Yorkshire Type Ammonites, p. *ii*) confirmed by ICZN Opinion 575, 1959.

The holotype was stated by Söll (1956, p. 390) to be the original of Quenstedt (1849, pl. 5, fig. 11) and to be lost. A representative series of topotypes was figured by Söll (1956). The type species is based on pyritic inner whorls (internal moulds), seldom more than about 60 mm in diameter, from the Lias of Swabia. These nuclei are the familiar strongly compressed oxycones (whorl thickness less than 20%

at diameter about 35 mm) with prorsiradiate secondary ribs and a sharp keel. An example figured later by Quenstedt (1884, pl. 22, fig. 31) is 100 mm in diameter, and would have been at least 130 mm when complete. However, the adult form of the species is not well known. It may have had a body chamber with rounded venter, and possibly uncoiling umbilicus, like many other oxycones.

The suture line of *Oxynoticeras* is distinguished by an umbilical culmination which appears early in ontogeny (Schindelwolf, 1962, fig. 91).

Paroxynoticeras Von Pia 1914

Type species *Ammonites salisburgensis* Von Hauer 1856, by subsequent designation by Spath (1924, p. 206).

The genus (wrongly spelt *Paraoxynoticeras* in the *Treatise*, p. L243) is founded on a species described from the *Ammonitico rosso* of Adnet, Austria. Topotypes figured by Pia are, unfortunately, of indifferent preservation, especially as regards the inner whorls. The latter may be compressed and *Oxynoticeras*-like. The umbilicus of the inner whorls is 15-20% of the diameter, as in *Oxynoticeras*, but the body chamber umbilicus opens out to about 30%. In one example measured by Pia the mature umbilicus reached 39% of the diameter. The body chamber has a rounded venter and bears a few coarse ribs. The stratigraphical range of the genus corresponds to the upper part of the Oxynotum Zone (Dommergues, Page & Meister 1994) and generic distinction from *Oxynoticeras* seems doubtful.

Slatterites Spath (1923) was founded on a small handful of specimens from Lincolnshire, England, of unknown stratigraphical horizon, figured by Wright (1882, pl. 50). Spath (1925, p. 110, explanation of figure) implied that they came from the Simpsoni Subzone. Specimens are complete with body chamber at quite a small size, about 65 mm. The body chamber is not unlike that of *Paroxynoticeras*, which raises the question of the identity of these two genera. The suture line (Spath, 1925, p. 266, fig. 6e) appears identical with that of *Oxynoticeras*. Yet another related "genus" is *Retenticeras* Buckman (1920; Type Ammonites), which Spath (1925, p. 108) compared with immature *Oxynoticeras simpsoni*. It is not very different from the inner whorls of *Slatterites*.

Oxycones with very small or closed umbilicus

There are 8 or 9 generic names available for this morphological group, of which the majority have in recent years been regarded as synonyms (e.g. Donovan, Callomon & Howarth, 1981, p. 137).

Radstockiceras Buckman 1918

This is the earliest available generic name for the group. Type species *R. complicatum* Buckman 1918 (p. 287, pl. 27, fig. 1, text-figs. 6, 12, 21). There was only one specimen, the holotype, wholly septate at a maximum size of 262 mm; Buckman estimated that it was about 380 mm when complete. The present location of the holotype is not known.

In the absence of the holotype it is not possible to say anything about its stratigraphical horizon. It was from the condensed Lias of Radstock Grove Quarry, Avon (see Donovan & Kellaway, 1984, p. 44). Buckman's guess of "beds yielding oxynotoids immediately below the so-called '*raricostatus* beds'" is certainly wrong. Its original horizon was probably Raricostatum or Jamesoni Zone.

Metoxynoticeras was proposed by Spath (1922, p. 515) in the words "*Metoxynoticeras* gen. nov. *oppeli* (Schloenbach)," with the footnote "genotype to be No. 2,141, identified with *Ammon. oppeli*, Schloenbach ... 1865, p. 161, pl. 26, figs. 4a-c.". *Am. oppeli* is the type species by monotypy, being the only species included without qualification. However the species was set up by Schloenbach in 1863 (p. 515) and the examples illustrated by him in 1865 had been acquired after the first description. The 1865 figures, and "No. 2,141" cited by Spath have therefore no status in relation to the original definition of the species. Schloenbach (1863) illustrated two specimens out of nine, one (his figs. 2a, b) in side and peripheral views, the other (fig. 2c) as a suture line only. The original of his plate 26, figures 2a, b is now designated lectotype. It was about 246 mm in diameter, and Schloenbach recorded that the largest specimen in his series was 524 mm, without body chamber.

The original record of *Metoxynoticeras* by Spath (1922) was from the Jamesoni Zone, probably the lower part, Polymorphus Subzone. Later he identified specimens recorded as *M.* cf. *flavum* (Simpson) and *M. lynx* (d'Orbigny) from about the same horizon on the Dorset coast (in Lang, 1928, p. 194).

Synonymy: It is difficult to find differences of generic significance between *Radstockiceras complicatum* and Schloenbach's 1863 and 1865 figures of his *Am. oppeli*. Suture lines are identical in proportions and in most of the detail. The shape of the ribs is the same, the shell form almost identical (*R. complicatum* has a slightly larger umbilicus).

Carixiceras Spath 1925

This genus was set up by Spath (1925, p. 112) for

Amaltheus wiltshirei Wright (1881, pl. 48, fig. 3). The figured specimen was referred to by Donovan (1954, p. 41) as the holotype, but in fact Wright (1882, p. 393) had two examples, and the one figured (BMNH no. C.2217) should probably be regarded as the Lectotype, designated by Donovan (1954), under Article 74(b).

Wright (1881, p. 394) said that the lectotype was "from the Green Ammonite Bed" near Charmouth Dorset, i.e. Davoei Zone, but Spath notes that an example in the BMNH (no. C.17869) was probably from the Belemnite Stone (Bed 121), i.e. Ibex Zone, Luridum Subzone. This example was probably aboput 400 mm in diameter when complete, with an "uncoiling" umbilical suture. The venter is fastigate, becoming rounded.

The shell form of *Am. wiltshirei* is indistinguishable from that of *Radstockiceras* and of *Am. oppeli* of Schloenbach (see above). However, the suture line is different: the external saddle is bifurcated, the 1st lateral saddle is long and narrow, and the remaining elements lie on a radial line instead of being "declined" as in *Radstockiceras*. For this reason *Carixiceras*, formerly placed in synonymy (Donovan, Callomon & Howarth, 1981, p. 137) is now upheld as separate from *Radstockiceras*.

The ammonite reported from the Davoei Zone of Hungary by Géczy (1976, p. 39) as *Radstockiceras wiltshirei* has the characteristic suture line of *Carixiceras* (op. cit. text-fig. 20, bottom figure).

Fanninoceras McLearn 1930

Type species by original designation: *Fanninoceras fannini* McLearn (1930, p. 4, pl. 1, fig. 3). These figures of the type species were outline drawings. The holotype was refigured photographically by McLearn (1932), who then provided a more detailed diagnosis and named several more species. The original finds were not associated with any other ammonites and were thought by McLearn to be Toarcian in age. Smith et al. (1988) have summarised information which shows that in fact *Fanninoceras* occurs in the uppermost Domerian.

In the *Treatise*, Arkell (1957), following McLearn's original idea, regarded *Fanninoceras* as a harpoceratid. Frebold (1967) regarded it as a member of Oxynoticeratidae close to *Radstockiceras*, and Donovan and Forsey (1973, p. 3) and Donovan, Callomon and Howarth (1981, p. 137) placed the genus as a synonym of *Radstockiceras*. Frebold (loc. cit.) and Imlay (1981, p. 36) have continued to regard it as a separate genus in Oxynoticeratidae.

In fact the suture line is different from that of *Radstockiceras* (fig. 5), and in view of this fact and its different age, it is now upheld.

Fanninoceras has been reported from South America (Argentina, Chile and Peru) by Hillebrandt (1981). It appears to be restricted to the Americas.

Abbreviations: BMNH = British Museum (Natural History), Department of Paleontology.

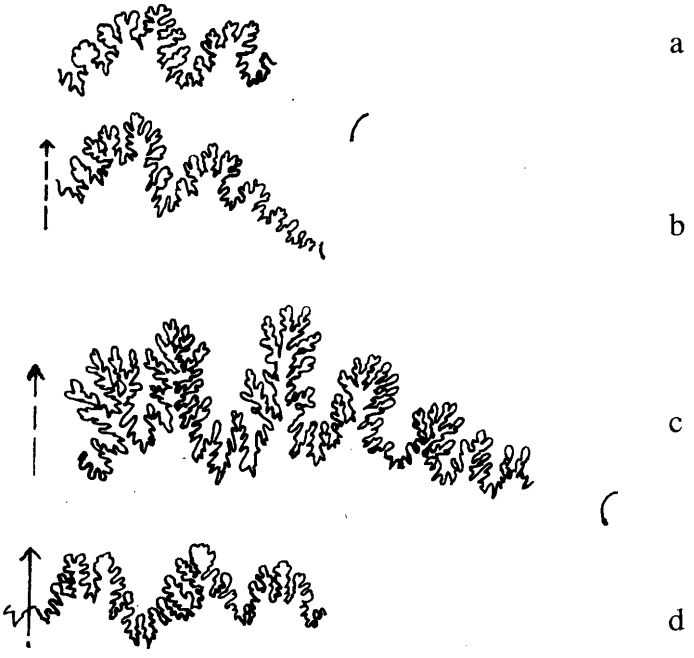


Fig. 5 - Suture lines of: a, b *Fanninoceras*; c, *Carixiceras*; d, *Oxynoticeras lymense*.

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REFERENCES

ARKELL, W. J. (1957) - [Jurassic ammonite genera in] MOORE, R. C. (Editor). Treatise on Invertebrate Paleontology, Part L.

BUCKMAN, S. S. (1909-1930) - Yorkshire Type Ammonites (**1**, **2**) continued as: Type Ammonites (**3-7**). London & Thame: Wheldon & Wesley, and the author.

BUCKMAN, S. S. (1918) - Jurassic chronology: I-Lias. *Quarterly Journal of the Geological Society of London* **73**, 257-327.

CECCA, F., DOMMERGUES, J.-L., MOUTERDE, R. & PALLINI, G. (1987) - Ammonites meditérranéennes du Lotharingien de Gorgo a Cerbara (M. Nerone, Apennin des Marches, Italie). *Cahiers de l'Institute Catholique de Lyon,* Sér. Sci., No. 1, 67-82, 3 pl.

DOMMERGUES, J-L., FAURÉ, P. & PEYBERNES, B. (1986) - Le Lotharingien inférieur du Djebel Oust (Tunisie); description d'ammonites nouvelles (Asteroceratinae, Arieticeratinae). *Compte Rendu de l'Academie des Sciences*, Paris **302**, 1111-1116.

DOMMERGUES, J.-L. & MOUTERDE, R. (1987) - The endemic trends of Liassic ammonite faunas as the result of the opening up of a narrow epicontinental basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* **58**, 129-137.

DOMMERGUES, J.-L., PAGE, K. N. & MEISTER, C. (1994) - A detailed correlation of Upper Sinemurian (Lower Jurassic) ammonite biohorizons between Burgundy (France) and Britain. *Newsletters on Stratigraphy* **30**, 61-73.

DONOVAN, D. T. (1954) - Synoptic supplement to T. Wright's 'Lias ammonites' (1878-86). London: *Palaeontographical Society*, 54 pp.

DONOVAN, D. T. (1966) - The Lower Liassic ammonites *Neomicroceras* gen. nov. and *Paracymbites*. *Palaeontology*, **9**, 312-318, pl. 53.

DONOVAN, D. T. (1973) - The influence of theoretical ideas on ammonite classification from Hyatt to Trueman. *University of Kansas Paleontological Contributions Paper* 62, 16 pp.

DONOVAN, D. T. (1985) - Ammonite shell form and transgression in the British Lower Jurassic. In: U. Bayer & A. Seilacher (editors), Sedimentary and evolutionary cycles. *Lecture notes in earth sciences* **1**, 48-57.

DONOVAN, D. T. (1987) - Evolution of the Arietitidae and their descendants. *Cahiers de l'Institute Catholique de Lyon*, Sér. Sci. No. 1, 123-138.

DONOVAN, D. T. (1993) - Ammonites in 1991. Pp. 1-11 in: The Ammonoidea: environment, ecology, and evolutionary change (ed. M. R. House). Systematics Association Special Volume **47**.

DONOVAN, D. T., CALLOMON, J. H. & HOWARTH, M. K. (1981) - Classification of the Jurassic Ammonitina. Pp. 101-155 in: *The Ammonoidea* (ed. M. R. House & J. R. Senior), Systematics Association Special Volume **18**, 101-155.

DONOVAN, D. T. & FORSEY, G. F. (1973) - Systematics of Lower Liassic Ammonitina. *University of Kansas Paleontological Contributions Paper* 64, 18 pp.

DONOVAN, D. T. & KELLAWAY, G. A. (1984) - Geology of the Bristol district: the Lower Jurassic rocks. *Memoir of the British Geological Survey*, vi + 69 pp.

FREBOLD, H. (1960) - The Jurassic faunas of the Canadian Arctic. Lower Jurassic and lowermost Middle Jurassic ammonites. *Geological Survey of Canada Bulletin* 59, 30 pp., 15 plates.

FREBOLD, H. (1964) - Illustrations of Canadian fossils. Jurassic of western and arctic Canada. *Geological Survey of Canada Paper* 63-4.

FREBOLD, H. (1967) - Position of the Lower Jurassic genus *Fanninoceras* McLearn and the age of the Maude Formation on Queen Charlotte Islands. *Canadian Journal of Earth Sciences* **4**, 1145-1149.

FUCINI, A. (1902) - Cefalopodi liassici del Monte di Cetona. Parte seconda. *Palaeontologia Italica* **8**, 131-217, pl. 12-26.

FUCINI, A. (1903) - Cefalopodi liassici del Monte di Cetona. Pal. Ital. Parte terza. *Palaeontologia Italica* **9**, 125-185, pl. 19-27.

GECZY, B. (1976) - Les Ammonitines du Carixien de la Montagne du Bakony. Budapest: *Akad. Kiadó*, 223 pp., 39 pls.

GETTY, T. A. (1973) - A revision of the generic classification of the Family Echioceratidae (Cephalopoda, Ammonoidea) (Lower Jurassic). *University of Kansas Paleontological Contributions*, Paper 63, 32 pp., 5 pls.

GUERIN-FRANIATTE, S. (1966) - Ammonites du Lias inférieur de France. Psiloceratacea: Arietitidae. Paris: C.N.R.S. 255 pp., 231 pls.

HILLEBRANDT, A. VON (1981) - Faunas de amonites del Liasico inferior y medio (Hettangiano hasta Pliensbachiano) de America del Sur (excluyendo Argentina). Com. Sudamer. Jur. Cret.: Cuncas sed. Jur. Cret. Amer. Sur, **2**, 499-538, 10 pls.

HYATT, A. (1889) - Genesis of the Arietidae. *Smithsonian Contributions to Knowledge* vol. 26, no. 673, xii + 238 pp.

IMLAY, R. W. (1981) - Early Jurassic ammonites from Alaska. *Geological Survey Professional Paper* 1148, 49 pp.

LANG, W. D. (1928) - The Belemnite Marls of Charmouth, a series in the Lias of the Dorset coast. *Quarterly Journal of the Geological Society of London* **84**, 179-257.

MC LEARN, F. H. (1930) - Notes on some Canadian Mesozoic faunas. *Transactions of the Royal Society of Canada* Series 3, Section 4, **24**, 1-7.

MC LEARN, F. H. (1932) - Contributions to the stratigraphy and palaeontology of Skidegate Inlet, Queen Charlotte Islands, British Columbia. *Transactions of the Royal Society of Canada* Series 3, Section 4, **26**, 51-84.

MANLEY, E. C. (1977) - Unusual pattern preservation in a Liassic ammonite from Dorset. *Palaeontology*, **20**, 913-916.

MEISTER, C. (1986) - Les ammonites du Carixien des Causses (France). *Mémoires suisses de Paléontologie* **109**, 209 pp., 23 pls.

MEISTER, C. & BÖHM, F. (1993) - Austroalpine Liassic ammonites from the Adnet Formation (Northern Calcareous Alps). *Jahrbuch der Geologischen Bundesanstalt*, **136**, 163-211.

MOUTERDE, R. & ROCHA, R. B. (1981) - Atlas des fossiles caractéristiques du lias portugais. I.-Lias inférieur. *Ciências da Terra* (UNL), Lisboa, No. 6, 49-76, 4 pl.

OPPEL, A. (1853) - Der mittlere Lias Schwabens. *Württ. Naturwiss. Jahreshefte*, 10 Jahrgang, 39-136, pls. 1-4.

OPPEL, A. (1862) - Ueber jurassische Cephalopoden. *Palaeontologische Mittheilungen* **3**, 127-162, pl. 40-50. Stuttgart: Ebner & Seubert.

PARONA, C. F. (1896) - Contribuzione alla conoscenza delle ammoniti liasiche di Lombardia. Parte I. Ammoniti del Lias inferiore del Saltrio. *Mémoires de la Société Paléontologique Suisse* **23**, 45 pp. Geneva.

PIA, J. VON 1914) - Untersuchungen über die Gattung Oxynoticeras und einige damit zusammenhängende allgemeine Fragen. *Abhandlungen der Kaiserlich-königlichen geologischen Reichsanstalt*, Wien, **23**, Heft 1. iv + 179 pp.

POMPECKJ, J. F. (1897) - Neue Ammoniten aus dem unteren Lias von Portugal. Zeitschrift der Deutschen geologischen Gesellschaft **49** (3. Heft), 636-661.

QUENSTEDT, F. A. (1849) - Petrefaktenkunde Deutschlands. Die Cephalopoden. Atlas. Tübingen: L. F. Fues.

QUENSTEDT, F. A. (1884) - Die Ammoniten des Schwäbischen Jura. I Band. Der Schwarze Jura (Lias). Parts 3-5, 97-240, pl. 13-30. Stuttgart: Schweizerbart.

QUENSTEDT, F. A. (1885) - Die Ammoniten des Schwäbischen Jura. I Band. Der Schwarze Jura (Lias). Parts 6-10, 241-440, pl. 31-54. Stuttgart: Schweizerbart.

RICHARDSON, L. (1904) - A handbook to the geology of Cheltenham and neighbourhood. *Cheltenham*: Norman Sawyer & Co. xii + 268 pp., 19 pl.

SCHINDEWOLF, O. H. (1962) - Studien zur Stammesgeschichte der Ammoniten. Lieferung 2. Akademie der Wissenschafter und der Literatur in Mainz, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse, Jahrgang 1962, Nr. 8, 111-257.

SCHLATTER, R. (1976) - Die Stufe des Lotharingium im unteren Lias des Klettgau (Kanton Schaffhausen, Schweiz). *Stuttgarter Beiträge zur Naturkunde* Ser. B, **21**, 20 pp.

SCHLATTER, R. (1980) - Biostratigraphie und Ammonitenfauna des Unter- Pliensbachium im Typusgebiet (Pliensbach, Holzmaden und Nürtingen; Württemberg, SW-Deutschland). *Stuttgarter Beiträge zur Naturkunde* Ser. B, **65**, 261 pp., 23 pls.

SCHLATTER, R. (1983) - Ein Fund von *Aegasteroceras* ex gr. *simile* Spath (Ammonoidea) aus dem Lotharingium des Wutachgebiets (Baden- Württemberg). *Jahresberichte und Mitteilungen des oberreheinischen geologischen Vereins* N.F. **65**, 243-256.

SCHLEGELMILCH, R. (1976) - Die Ammoniten des süddeutschen Lias. *Stuttgart*: Fischer. 212 pp., 52 pls.

SCHLOENBACH, U. (1863) - Ueber den Eisenstein des mittleren Lias im nordwestlichen Deutschland, mit Berücksichtigung der älteren und jüngeren Lias-Schichten. *Zeitschrift der Deutschen geologischen Gesellschaft* **15** (3. Heft), 465-566.

SCHLOENBACH, U. (1865) - Beiträge zur Paläontologie der Jura- und Kreide-Formationen im nordwestlichen Deustchland. *Palaeontographica* **13**, 4. Lieferung, 147-192.

SKWARKO, S. K. (1967) - Mesozoic Mollusca from Australia and New Guinea. 2. Mesozoic fossils from eastern New Guinea. *Bureau of Mineral Resources, Geology and Geophysics, Canberra, Bulletin* No. 75, 337-100.

SMITH, P. L., TIPPER, H. W., TAYLOR, D. G. & GUEX, J. (1988) - An ammonite zonation for the Lower Jurassic of Canada and the United States: the Pliensbachian. *Canadian Journal of Earth Sciences* **25**, 1503-1523.

SÖLL, H. (1956) - Stratigraphie und Ammonitenfauna des mittleren und oberen Lias-(greek beta) (Lotharingien) in Mittel-Württembergische Geologische Jahrbuch, **72**, 367-434, Hannover.

SPATH, L. F. (1922) - On the Liassic succesion of Pabay, Inner Hebrides. *Geological Magazine* **59**, 548-551.

SPATH, L. F. (1923) - The ammonites of the Shales-with-"Beef". *Quarterly Journl of the Geological Society of London* **79**, 66-88.

SPATH, L. F. (1924) - The ammonites of the Blue Lias. *Proceedings of the Geologists' Association*, London **35**, 186-211.

SPATH, L. F. (1925) - Notes on Yorkshire ammonites. *The Naturalist*, No. 819 (April, 1925), 107-112; No. 824 (September, 1925), 263-269.

SPATH, L. F. (1926) - In: The Black Ven Marls of Black Ven and Stonebarrow in the Lias of the Dorset coast, by W. D. Lang & others, Quarterly Journal of the Geological Society of London **82**, 165-179, pls. 9-11.

WANNER, J. & JAWORSKI, E. (1931) - Liasammoniten von Jamdena und Celebes. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, Beilage*-Bd. **66**, Abt. B, 199-209.

WESTERMANN, G. E. G. (1984) - Gauging the duration of stages: a new approach for the Jurassic. *Episodes* **7**, 26-28.

WRIGHT, T. (1881) - A monograph on the Lias ammonites of the British Islands. Part 4, pp. 265-328, pls. 22A, 22B, 41-48. London: *Palaeontographical Society*.

WRIGHT, T. (1882) - A monograph on the Lias ammonites of the British Islands. Part 5, pp. 329-400, pls. 49-69. London: *Palaeontographical Society*.

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