

08.09

THE SYSTEMATICS ASSOCIATION
SPECIAL VOLUME NO. 18



THE AMMONOIDEA

The evolution, classification, mode of life
and geological usefulness of a major
fossil group

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1981



Published for the

SYSTEMATICS ASSOCIATION

by

ACADEMIC PRESS

LONDON NEW YORK TORONTO SYDNEY SAN FRANCISCO

5 | Classification of the Jurassic Ammonitina

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Abstract: Early attempts to classify Jurassic ammonites were based almost wholly on morphology, and many unrelated forms with similar morphology were classed together. As detailed knowledge of stratigraphical distribution became available during the twentieth century, it became possible to construct a phylogeny as a basis for classification. Only then could these unrelated forms be separated. In the present classification major groups (superfamilies) reflect the major evolutionary radiations. Each of these is probably monophyletic. Earlier Jurassic superfamilies (Psilocerataceae, Eoderocerataceae and Hildocerataceae) have short durations (two or three stages). A major radiation in the Bajocian produced three new superfamilies, all derived from Hildocerataceae. Of these, the Stephanocerataceae died out in the Kimmeridgian but the Perisphinctaceae and Haplocerataceae were longer-lived and both survived into the Cretaceous. The idea of iterative evolution, the repeated "replenishment" of Ammonitina from Phylloceratina and/or Lytoceratina, though favoured by earlier workers is now rejected as a factor of any importance in Jurassic ammonite evolution.

Dimorphism has not been recognized as a regular feature in Psilocerataceae or Eoderocerataceae. It first appears, with consistent differences between

macroconchs and microconchs, in Hildocerataceae, and is important in the remaining three superfamilies.

The Middle Jurassic heteromorphs, the Spirocerataceae, are discussed but the Ancylocerataceae, which arise in the Tithonian but chiefly comprise Cretaceous forms, are not considered in detail.

INTRODUCTION

The stratigraphical usefulness of Jurassic ammonites became known early in the history of modern palaeontology. Taxonomic subdivision at first lagged behind stratigraphical employment. Oppel's 33 zones for the Jurassic were almost all named after species placed in the old comprehensive genus *Ammonites*. When generic subdivision came it was at first slow and moderate, but eventually, in the early twentieth century, it went too far, a situation for which British palaeontologists (Buckman, Spath, Trueman) must unfortunately bear much of the blame (Donovan, 1973). There was a good deal of mystique about some of these old boys. Arkell, who was just old enough to have known S. S. Buckman, told me (DTD) that Buckman used to offer his opinion on an ammonite with a measure of seriousness and pomposity. In contrast, the *Treatise* and its impending revision have forced us to try to define taxa more objectively and according to systematic criteria, and to produce a classification that is reasonably well balanced and in scale. It is the fate of all specialists, however eminent, to be challenged and eventually supplanted by their younger colleagues, and the present authors will doubtless not escape this fate. But if we are to offer a classification which we hope is better than the last one, the best that can be made on present evidence, let us at least try to do it on a logical basis and not just by gazing into a different crystal ball.

Jurassic ammonites are often cited as the ideal zonal fossils. The number of biostratigraphical events (mostly first appearances) within a given interval of geological time is probably greater than in other common fossil groups. Students tell us in their essays that one of the desirable attributes of a zonal fossil is that it should be easily recognizable. Most ammonites are not. The reason for this is not far to seek. Ammonite evolution affected a very limited range of characters. Homeomorphy is common, due to the re-appearance at different times of basically similar shell forms and ornament. When

complete, well-preserved specimens are available it is usually possible to specify differences; the whole ontogeny is not usually the same. But the biostratigrapher often has to work with poor material. With less than perfect specimens it may be impossible, for example, to distinguish *Coroniceras* from *Paltechioceras* which occurs four zones later. For this reason all the early taxonomic work, based on morphology without regard for stratigraphical position, was bound to produce an artificial classification, e.g. *Arietites* was used for all keeled bisulcate ammonites in the Lias, *Perisphinctes* for all evolute shells with uninterrupted ventral ribbing in the Upper Jurassic. It was not until attempts were made to set up a classification based on phylogeny that the numerous heterochronous homeomorphies were separated.

Hence, in addition to morphology we need stratigraphical criteria. There is an old joke that we tell against ourselves that we can identify an ammonite provided that we know what horizon it came from. It is, in fact, often much easier to identify a sequence of ammonites than a solitary one, since misidentification of homeomorphs can be more easily avoided.

How, then, do we set about constructing a phylogeny? At the most detailed level we look for morphological overlap between successive populations, such as those demonstrated by Howarth (1973) for *Dactylioceras* in the Toarcian and by Brinkmann (1929) for *Kosmoceras* in the Callovian. Usually we do not have this kind of evidence: in some cases it has not been collected or studied. Mostly it just is not there in the rocks. At best it provides short sections of lineages.

Recapitulation – the Biogenetic Law of Haeckel and Hyatt – has been rejected as a key to phylogeny (Donovan, 1973), because evolution may affect any part of the ontogeny of the shell.

Sutural pattern and ontogeny have fascinated many workers. In the Jurassic, in strong contrast to earlier systems, septal sutures are seldom useful even for defining major groups and are hardly ever employed at lower levels of classification.

We have to rely on morphological resemblance qualified by stratigraphical information. That is, we try to relate ammonites to forms which are stratigraphically near them. Large stratigraphical gaps between related genera are to be regarded with caution because in the past such linkages have often proved to be mistaken. It is

encouraging, however, to find that new information which has accumulated since the first edition of the *Treatise* (Arkell, 1957) often tends to fill in gaps rather than to upset current ideas on classification.

CLASSIFICATION INTO MAJOR TAXA

Three suborders are recognized in Jurassic Ammonitida: Phylloceratina, Lytoceratina and Ammonitina (Fig. 5). The first two will not be considered further in this paper. The origins of all three suborders are probably to be found in the Lower or Middle Trias and we are not here concerned with them. The diversification of all Jurassic ammonites from Phylloceratina in the latest Trias or earliest Jurassic, implied in the *Treatise* (Arkell, 1957, fig. 150) is now rejected. To this extent we agree with Wiedmann (1970), but Wiedmann's interpretation has been criticized by Tozer (1971). We do not pretend to be able to point out the detailed lines of descent by which the early Jurassic Lytocerataceae, Phyllocerataceae, Psilocerataceae and Eoderocerataceae originated from Triassic forms. The fossil record of ammonoids from latest Triassic and earliest Jurassic rocks is far too incomplete for this to be done, and a convincing interpretation must probably await the discovery of new faunas.

A major change in our view of ammonoid evolution in the Jurassic, as well as some simplification of phylogeny and classification, arises from our virtually complete abandonment of the theory of Iterative Evolution. Originating with Salfeld (1922), it was adopted by Spath (e.g. 1942) and by Arkell (1950). However, new discoveries and studies since the *Treatise* was compiled have not substantiated the idea of "replenishment" of groups by successive homeomorphic waves, especially from the conservative suborders Phylloceratina and Lytoceratina. These suborders now stand in even more isolation than before, clearly distinguished in morphology, and probably in habitat, from the contemporary Ammonitina.

In Jurassic ammonites the superfamily has long been used as the principal high level taxon (Arkell, 1950). The superfamilies employed here for the normally-coiled ammonites are the same as in the *Treatise* (Arkell, 1957). The heteromorphs have been reclassified as mentioned below. The probable relationships between the superfamilies are shown in Fig. 1 and discussed below where necessary.

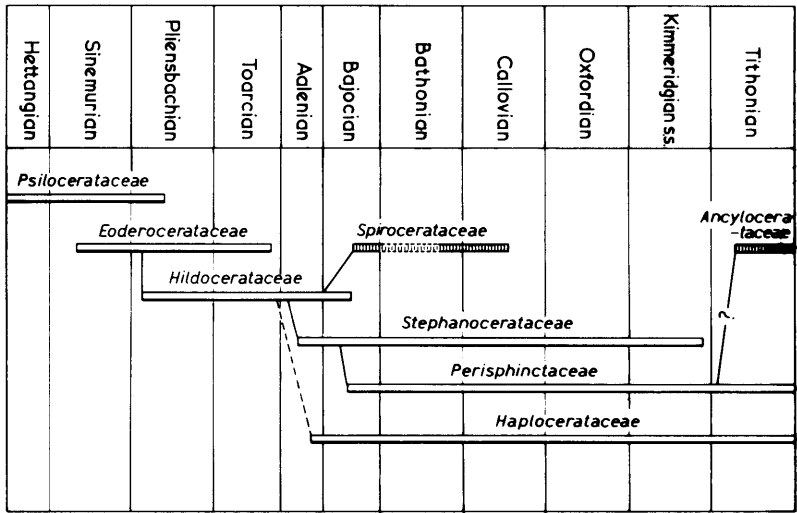


Fig. 1. Ranges and possible phylogenetic relationships of superfamilies of the suborder Ammonitina in the Jurassic System. Shaded bars indicate groups with heteromorph shell forms.

Although heteromorphs are not very conspicuous members of the well-known Jurassic faunas, we believe that uncoiled ammonites evolved from normal ones on at least two occasions. The origin of the Middle Jurassic Spirocerataceae is believed to lie in the Hildocerataceae, probably in Tmetoceratinae, although intermediate forms in the Lower Bajocian are not known. The origin of the latest Jurassic and early Cretaceous Ancylocerataceae is more problematical, but may lie in the latest Perisphinctidae. We see no reason to derive them from Lytoceratina.

The systematic text that follows presents a review of the classification of the Jurassic Ammonitina to be adopted in the projected revision of the ammonoid volume of the *Treatise*. In the space available the emphasis has to be largely on the higher taxa of the family-group, but it is at this level that the new discoveries since 1957 have created perhaps most interest. Formally, the extension of the *Rules* in 1960 and 1964 to include the taxa of the family-group makes it necessary to pay more attention to questions of priority in synonymy. Scientifically, however, the increasing confidence with

which phylogenetic relationships can be discerned makes the taxa of the family-group the natural vehicle for the expression of such relationships in classification. Attempts to do so involve questions of weight and balance that often conflict and the solutions must inevitably be highly subjective. Synonymies of published family names are given where possible, for the three major Middle and Upper Jurassic superfamilies, references to new family names proposed since the *Treatise* of 1957 being included in the bibliography. In the past, classification at levels above the genus-group has received only sporadic attention and most of the primary literature continues to ignore it. New family-taxa were therefore often published casually *en passant*. We believe the time has now come to consider these matters more seriously, and should be glad to hear of published names that have been overlooked.

The Ammonitina are discussed under the headings of superfamilies. These are summarized in Fig. 1. They are confined to the Jurassic with the exceptions of some of the Haplocerataceae and Perisphinctaceae that continue into the Cretaceous. In the latter, the dividing line between those discussed here and those considered by C. W. Wright in his Cretaceous contribution is largely arbitrary. Our treatment here of the Jurassic groups is variable, depending on their sizes, the amount of change since 1957 and the state of progress in the revision. The Psilocerataceae and Eoderocerataceae are largely the work of D. T. Donovan, revised from Donovan and Forsey (1973), with the exception of the Amaltheidae and Dactylioceratidae which were compiled by M. K. Howarth. Phyletic relationships are summarized in Fig. 2. The Hildocerataceae were compiled by M. K. Howarth, also down to generic level. The Haplocerataceae, Stephanocerataceae and Perisphinctaceae were compiled by J. H. Callomon. They are too large in scope to list at generic level, and so the discussion is limited to subfamilies and above. Phyletic relationships down to subfamily level are summarized in Figs 2 to 4. In Figs 3 and 4 the time scales are based on the numbers of standard ammonite subzones as units, and an effort has been made to indicate the ranges as known to this precision, especially as regards the important levels of first appearances. The Spirocerataceae, small but interesting out of all proportion to their size, was compiled by J. H. Callomon. Thanks to a thorough recent revision their classification should have now attained a degree of

permanence, and hence it is also reproduced here down to generic level. Ancylocerataceae are not dealt with in this contribution.

The classifications put forward here, and collated as the Appendix, are unlikely to be final. We hope that readers will regard them as a basis for discussion, and we would welcome comments and criticisms for consideration before the final draft of the revised *Treatise* is completed.

SYSTEMATIC CLASSIFICATION AND DISCUSSION

1. Superfamily *Psilocerataceae* (D.T.D.)

The Psiloceratidae have a smooth, rounded venter. The Schlotheimiidae developed characteristic ventral chevrons. All other families have a keel or an angular venter at some stage in ontogeny. The great majority of Psilocerataceae possess simple ribs only, but a few (some schlotheimiids; Pseudotropitinae; Oxynoticeratidae) develop secondary ribbing. There is a preponderance of evolute shells but some genera become more involute, and the Oxynoticeratidae are oxycones.

The Psiloceratidae, smooth or ribbed evolute shells, were a small and short-lived family. The Schlotheimiidae have sharp ribs on the inner whorls, with the well-known ventral chevrons which gave rise to the name *S. angulata*. On the outer whorls of all schlotheimiid genera ribbing becomes very weak.

Schlotheimiidae alone characterize the later Hettangian in NW Europe, but on the northern shores of the Tethys the earliest Arietitidae appear to have co-existed with them. At the base of the Sinemurian, the Arietitidae abruptly extended their geographical range into NW Europe, displacing Schlotheimiidae which are henceforth of sporadic occurrence.

The Arietitidae include a number of forms of standard basic shape: narrow-whorled evolute shells, with strong straight simple ribs, a ventral keel and grooves. They had long body chambers (≈ 1 whorl) and, following the reasoning of Trueman (1941), they did not have stable floating positions. The ribbing perhaps had a hydrodynamic function and it is even possible that the keel acted as a keel in the nautical sense, that is, as a structure whose function was to oppose

movement in a direction at right angles to the plane of symmetry of the shell.

The remarks about the Arietitidae apply equally to the Echioceratidae, which hardly differ from them except in age, and in a more restricted range of shell forms. They have nothing original to show.

The Oxynoticeratidae originate with rapid evolutionary development of the oxycone shell (via *Eparietites*) in the late Obtusum Zone. Ribbing is weak and can hardly have been of functional significance. These involute shells had shorter body chambers and therefore more stable floating positions. The familiar fossils of *Oxynoticeras* are of inner whorls with a very sharp venter, but many, if not all, these forms developed a rounded venter on the body chamber. The functional significance of this developmental change is not known. The family lasted, with little change in shell form, through five zones or even longer.

The suture-line of Psilocerataceae is simple (E, L, U_2, U_1, I of Schindewolf) and remarkably constant throughout the group. The only elaborations of sutural development concern the addition of extra subdivisions of U in a few of the more involute genera. In most genera the sutural elements themselves remain rather simple, with moderate indentation, but a few more involute genera (e.g. in Schlotheimiidae and Oxynoticeratidae) develop complex saddles, especially in large-sized individuals.

It is hard to say whether or not dimorphism existed in Psilocerataceae. Apertures are seldom preserved, and while some genera include both large and small species there is no particular reason to unite any of them as dimorphs.

The superfamily flourished during the Hettangian and Sinemurian stages. Only *Radstockiceras* and the Cymbitidae survived into the Upper Pliensbachian. In Europe north of the Alpine belt the bisulcate forms (Arietitidae, Echioceratidae) are characteristic of, and restricted to, the Sinemurian stage.

The Cymbitidae are attached to the Psilocerataceae largely as a matter of convenience. They are unlike all other early Liassic ammonites. They are small (1–2 cm) shells with sphaeroconic inner whorls and strongly contracted body chamber about one half of a whorl long. They range almost throughout the Sinemurian and Pliensbachian stages with hardly any change. According to

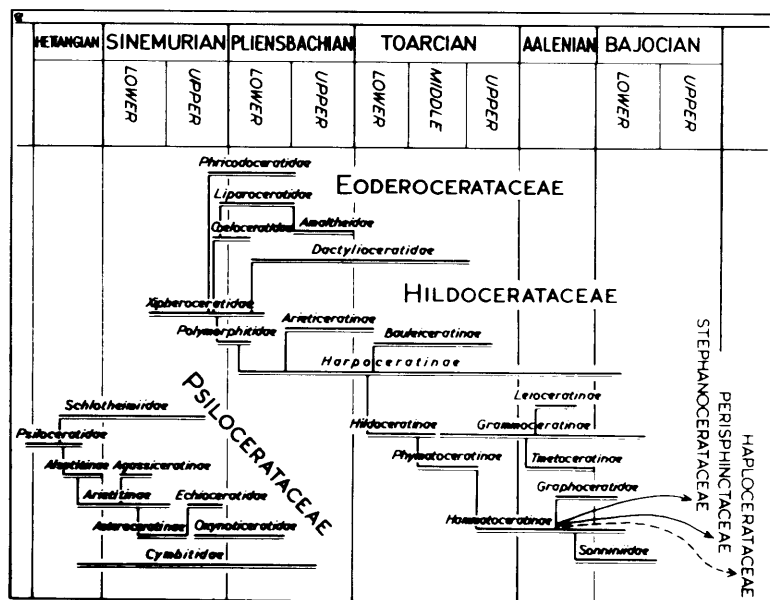


Fig. 2. Phylogenetic relationships between the family group taxa within the superfamilies Psilocerataceae, Eoderocerataceae and Hildocerataceae of the Lower and early Middle Jurassic.

Schindewolf (1962) their early sutural development is different from that of all contemporary Psilocerataceae and Eoderocerataceae, so perhaps they are really an isolated family of separate, unknown, origin.

2. Superfamily Eoderocerataceae (D.T.D., M.K.H.)

The phylogeny of this superfamily (Fig. 2) is more difficult to reconstruct than that of the Psilocerataceae, because the fossil record in the well-known north-west European sections is more sporadic. The earliest genus, *Microderoceras*, first appears in the Turner Zone of north-west Europe and probably at a corresponding horizon in the Tethyan area. It is of unknown origin although with some effort of the imagination it could be derived from late Hettangian/early Sinemurian lycoceratids such as *Analytoceras*. Schindewolf (1962) alternatively derived them from Psilocerataceae. The near-identity

of suture lines in the two superfamilies is striking, but otherwise the difference in morphology is considerable and no intermediate forms are known.

The most common shell form is an evolute serpenticone which is found from the earliest members (Xiphocerotinae) to the latest (Dactylioceratidae). Involute shells occur in Liparoceratidae and Amaltheidae. *Pseudoamaltheus* is an oxycone. The first two to four whorls are usually smooth. Simple radial ribs then develop in most genera. The ribs frequently bear tubercles or spines at their outer ends, and less frequently at their inner ends as well. Normally the number of outer and inner spines is the same, but in *Liparoceras* s.s. there are more outer spines than inner ones. In many genera striae or ribs pass over the venter. The venter is typically rounded but in some Polymorphitidae it is fastigate and Amaltheidae have a keel.

The majority of genera show little change of ornament with growth but there are notable exceptions such as *Androgynoceras*, *Epideroceras* and *Phricodoceras* in which strong modification of the outer whorls occurs. The adult size ranges from 20 mm or 30 mm to giants reaching 500 mm in such genera as *Apoderoceras*, *Epideroceras* and *Liparoceras*.

The serpenticones had long body chambers and would have had no stable floating position; in this they resemble the contemporary Psilocerataceae. One may conclude that stability was not at a premium during the Sinemurian, at least in the shallow epicontinental seas of north-west Europe. The function of the spines is open to speculation. They are unlikely to have been protective, because they are often small, and even the larger ones would not have deterred mollusc-eating fish and reptiles.

The suture line is very similar to that of Psilocerataceae except that in the interpretation of Schindewolf (1962) it lacks the minor umbilical element U_4 . Many genera have suture lines with highly subdivided arborescent saddles and a few have simplified suture lines.

Most Eoderoceratidae differ little from the common shell form in the superfamily as described above. The spines at the inner ends of the ribs, if present, are smaller than the outer ones. Dimorphism remains to be convincingly demonstrated.

Phricodoceratidae are characterized by large adult size and by marked change of shell form and ornament with growth, most

pronounced in *Phricodoceras* itself where inflated, strongly bispinose inner whorls become compressed and nearly smooth.

Coeloceratidae are characterized by coronate inner whorls in most of the included species. Most have outer tubercles only, but the bituberculate *Tetraspidoceras* is included as a possible ancestral member of the family, showing a strong resemblance to *Apoderocheras* except for the bituberculation.

The Polymorphitidae are a compact family, many of which possess ventral chevrons and/or a fastigate venter, which may become a true keel on the outer whorls of *Tropidoceras*. Typical shells are evolute, but more compressed than in most members of the superfamily. One genus, *Parinodiceras*, had an involute shell, slightly mimicking that of *Liparoceras* to which it was attached as a subgenus by Spath (1938). It is now regarded as a derivative of *Polymorphites*.

Liparoceratidae are an unsatisfactory family and the controversy concerning its origin and evolution is as far from being solved as in the days of Trueman (1919) and Spath (1938). It includes two extreme morphological types, inflated sphaerocones (*Liparoceras*) and evolute capricorns (*Aegoceras*). These are united in one family because of the appearance in the Ibex Zone of ammonites with capricorn inner whorls indistinguishable from contemporary species of *Aegoceras*, and outer whorls indistinguishable from *Liparoceras*, the "hybrids" or "variocostates" ("dimorphs" of Spath, 1938). After this the three types co-exist, and the variocostates and the capricorns show parallel evolutionary changes in ornament, such as the appearance of ventral chevrons. Thus the sphaerocones and capricorns appear to be intimately related, although the nature of the relationship is uncertain. It has been interpreted as sexual dimorphism (Callomon, 1963, 1969; and see Chapter 9).

The sphaerocones have two rows of tubercles, usually joined by ribs, with more tubercles in the outer row than the inner (imparinode). They have apertures with plain radial margins.

The capricorns bear strong simple ribs which pass over the venter. They have apertures with ventral rostra. At any given horizon, capricorns are smaller than sphaerocones.

The classification of the Amaltheidae adopted here is not different from that of the first edition of the *Treatise*. *Amaltheus* was derived from the Liparoceratid subgenus *Aegoceras* (*Oistoceras*) at the base of the Margaritatus Zone, and the family became extinct at the top of

the Spinatum Zone leaving no successors. The family is typically boreal in distribution and only rarely do examples go south as far as the middle of Tethys (e.g. Sicily). Dimorphism has not been described in *Amaltheidae*.

Dactylioceratidae is perhaps the most difficult family to classify in the Lower Jurassic. If accurate stratigraphical knowledge is not available, the family presents a large and continuous range of morphological variation that can only be divided arbitrarily (e.g. Buckman, 1926). More meaningful results are obtained when the stratigraphy, and especially single-bed assemblages are known, for it is then apparent that some features of the ornament are sufficiently consistent to be used as generic characters. It also reveals that single-bed assemblages have a very wide variation from compressed to highly depressed whorl shapes. The compressed and depressed forms are usually united by the "generic" character; e.g. in the Tenuicostatum Zone the compressed *Dactylioceras* (*Orthodactylites*) and the depressed "*Kedonoceras*" are united by the presence of single, annular ribs; in the Fibulatum Subzone compressed and depressed forms of the fibulate-ribbed genus *Peronoceras* occur together, and in the same beds compressed and depressed forms of *Zugodactylites* (and "*Omolonoceras*") are readily distinguished from *Peronoceras* by the presence of single sharp ventro-lateral tubercles on every rib. Complete gradations between the compressed and the depressed forms occur at many horizons, and generic separation is arbitrary. In most cases the depressed forms are clearly related to the compressed forms they accompany, and they do not form a separate evolving lineage of cadicones. Although fibulation (primary ribs looped in pairs to ventro-lateral tubercles) may be present in any tuberculate depressed form, regular fibulation in compressed forms first appears at the base of the Fibulatum subzone in *Peronoceras*, and the family is naturally divided at this point.

Dimorphism is another problem in Dactylioceratidae. In some areas (e.g. Britain) large collections from single horizons are not dimorphic. Dimorphism on size alone has been claimed for species of *Dactylioceras* in north-west Germany (Lehmann, 1968). Dimorphism has also been claimed for several species of *Zugodactylites*, *Porpoceras*, *Catacoeloceras* and *Collina* that are preserved as small pyritized specimens, including many apparently adult, in the Fibulatum and

Crassum subzones and the Variabilis zone in the Aveyron area, France (Guex, 1973).

The earliest Dactylioceratid, *Reynesocoeloceras*, occurs in the Ibex zone, and is derived from Jamesoni zone members of the family Coeloceratidae. There is no evidence in favour of derivation of the family from Lytoceratina, a view adopted by Arkell in the first edition of the *Treatise* (p. L252). The family became extinct at about the top of the Variabilis zone and left no descendants. They were the last of the Eoderocerataceae. *Sphaeroocoeloceras*, included in the family in the first edition of the *Treatise*, is not a Dactylioceratid; it is a Hammatoceratinid from the upper half of the Levesquei zone in Chile. *Subcollina*, also originally included in the Dactylioceratidae, is of Upper Bajocian age and is the macroconch of the Stephanoceratidae genus *Parastrenoceras*.

3. Superfamily Hildocerataceae

Typical Hildocerataceae are compressed and keeled and are ornamented with straight, sigmoidal or falcate ribs. Other shell forms evolved and include evolute planulates and involute oxycones. The keel is only rarely lost, and tuberculation occurs in some later derivatives. The suture lines are basically no different from those of Eoderocerataceae and Psilocerataceae. They become much subdivided in compressed involute genera, but simplified suture lines, even reverting to ceratitic-like forms, are found in the aberrant genera grouped together as Bouleiceratinae. The superfamily arose from the Eoderocerataceae family Polymorphitidae near the bottom of the Pliensbachian. Hildocerataceae were abundant up to their extinction at the top of the Lower Bajocian (Humphriesianum zone). All other Jurassic Ammonitina had their origins in this superfamily, probably in the subfamily Hammatoceratinae. The earliest examples of marked dimorphism occur here: microconchs have lateral lappets that originate in the falcooid or falcate bend in the ribbing, while the plain mouth-bordered macroconchs are so much larger that the ranges of variation in size of the two dimorphs do not overlap. Most dimorphic pairs can be satisfactorily linked together, and it is not considered necessary to have a separate nomenclature for dimorphs in this superfamily.

(a) Family Hildoceratidae

(i) Subfamily Harpoceratinae. The earliest members, *Protogrammoceras* and *Fuciniceras*, evolved from *Tropidoceras*, or a similar member of the Polymorphitidae, in the upper half of the Jamesoni Zone in eastern Europe (Hungary), and possibly in the central Mediterranean (Sicily) and north Africa. The Pliensbachian genera are notably Tethyan in distribution, and the subfamily only appeared in significant numbers in the Boreal areas of north-west Europe during the Toarcian. *Pseudolioceras* is the longest lived genus, surviving in the Arctic until the Laeviuscula Zone of the Lower Bajocian. *Tugurites* Kalacheva and Sey (1970) is a generic name that has been given to these late forms of *Pseudolioceras*. However, the type species, *Am. whiteavesi* White (1889), is an undoubted *Pseudolioceras* from the Aalenian* of the Alaska Peninsula, and *Tugurites* is therefore a synonym. The systematic position of the species *T. tugurensis* Kalacheva and Sey, which occurs in north-west Siberia, will remain in doubt until the question as to whether it has a floored (*Pseudolioceras*) or an unfloored (*Graphoceras*) keel is resolved. Apart from this, Concavum and Discites Zones *Pseudolioceras* and *Graphoceras* are homeomorphs. The first clear cases of dimorphism in Hildocerataceae occur in this subfamily: *Tiltoniceras* and some species of *Protogrammoceras* might be dimorphic, but from *Eleganticeras* onwards dimorphism is striking. The ratio of the averages of the diameters of the two dimorphs is about 4:1 or 5:1, and the size range of complete adults within each dimorph is at least 2:1. Adult mouth borders of the dimorphs are similar, any difference only reflecting the greater curvature of the ribs at the smaller size of the microconchs, and there are no lappets. So far as is known *Pseudolioceras* disappeared in the Lower Bajocian and left no successors. All the other subfamilies are derived from Harpoceratinae at various earlier times.

* In order to make the text and diagrams consistent in this paper, Aalenian is used as a stage name for the Opalinum to Concavum Zones inclusive. This used to be the Lower Bajocian. However, Lower Bajocian is used for the Discites to Humphriesianum Zones (originally the Middle Bajocian), and the use of Upper Bajocian for the Subfurcatum to Parkinsoni Zones is unchanged. It seems to one of the authors (MKH) that the use of Aalenian as a full stage is not justified in terms of history and comparability with the size of the other Jurassic stages. If used at all, Aalenian should be a substage, equivalent to the original sense of Lower Bajocian.

(ii) Subfamily Arieticeratinae. This subfamily consists of more evolute, mainly strongly ribbed forms, that evolved from *Fuciniceras* near the bottom of the Upper Pliensbachian. They are mainly Tethyan in distribution, where they far outnumber Amaltheidae, and only occasional representatives appear in Boreal regions. One of these is the youngest genus, *Arctomercaticeras*, which occurs in the Tenuicostatum Zone of north-east Siberia, and whose relationship with earlier genera is not known. Dimorphism has not yet been described.

(iii) Subfamily Hildoceratinae. These are quadrate-whorled forms that occur in the Falciferum and Bifrons Zones of the Toarcian. The earliest genus, *Hildaites*, probably arose from *Fuciniceras* or *Protogrammoceras* near the base of the Falciferum Zone, derivation from the Arieticeratinae being less likely. Later forms have highly angled falcate ribs, which leads to the development of the first real lappets in the microconchs of dimorphic species of *Hildoceras*. The latter genus or *Mercaticeras* is the origin of Phymatoceratidae and hence all later Jurassic Ammonitina.

(iv) Subfamily Grammocerotinae. Mainly evolute, straight-ribbed forms that evolved from Hildoceratinae at the base of the Variabilis Zone. More involute sinuous-ribbed forms appear at higher horizons. Dimorphism is marked in some genera, and microconchs can have large spatulate lappets. The subfamily became extinct at about the top of the Laeviuscula Zone.

(v) Subfamily Leioceratinae. *Leioceras* evolved from *Pleydellia* at the base of the Aalenian, and later genera are strongly ribbed or reduced suture line derivatives of *Leioceras*. The subfamily probably did not give rise to the Graphoceratidae in the Murchisonae Zone, and so it is removed from the latter family and placed in the Hildoceratidae as a subfamily. It became extinct in the Murchisonae Zone leaving no successors. Dimorphism is well marked.

(vi) Subfamily Bouleiceratinae. Collected together in this subfamily are six aberrant genera, which have a wide range of shape and ornament, all with simplified suture lines that are ceratitic in some. The usual view is that parent stocks are not identifiable, lineages are unknown, and they were probably derived from different genera. The view has been put forward, however, that they can all be

assembled into a single lineage, derived originally from the Arietoceratinid genus *Canavaria* ("Tauromeniceras") (Guex, 1974).

(vii) Subfamily Tmetoceratinae. Derived from Grammocerotinae in the top half of the Levesquei Zone, probably from *Catulloceras*. Species are dimorphic, and microconchs have short lateral lappets. *Tmetoceras* is now known to extend up to at least the Concavum Zone, and it might have given rise to the Upper Bajocian heteromorph family Spiroceratidae, though the Lower Bajocian stratigraphical gap has yet to be bridged.

(viii) A recurrent abnormality amongst some Hildoceratidae is the growth of some specimens without keels. In such individuals keels are absent from all whorls, large and small, and it is not easy to recognize them as abnormal because there are no asymmetrical features or monstrous deformations of the sort that are usually associated with abnormal growth (e.g. the keel displaced on to one side of the shell, which is a frequent abnormality in *Amaltheus*, *Pleuroceras* and *Hildoceras*). However, in all cases the individuals are otherwise identical with normal-keeled ammonites that occur in the same beds. The view taken here is that they are only due to abnormal shell growth and that the subfamily Monestieriinae Sapunov (1965) and the generic names given to them, are not necessary. The type genus, *Monestieria*, is based on an abnormal *Pseudogrammoceras* from the Upper Toarcian, Thouarsense Zone, of south-east France; so Monestieriinae is a synonym of Grammocerotinae. Several abnormal specimens of *Harpoceras* have also been referred to different species of *Monestieria*, e.g. *M. errata* (Simpson), an abnormal *Harpoceras exaratum* (Young and Bird) from Yorkshire, and another "species" is an abnormal specimen of *Phymatoceras*. *Praehaploceras* Monestier, 1931, and *Buckmanites* Guex, 1973 are based on keel-less specimens of *Pseudolioceras*, and *Phenakoceras* Maubeuge, 1949 is a *Dumortieria* without a keel. A keel-less *Tiltoniceras* is known but has not yet been described.

(b) Family Phymatoceratidae

The oldest genus, *Phymatoceras*, is descended from coarse-ribbed *Hildoceras* in the Bifrons Zone. The Phymatoceratinae gave rise to the Hammatoceratinae in the Thouarsense Zone, which then ranged up into the Lower Bajocian, giving rise to the Graphoceratidae and

the Sonniniidae in the Aalenian. The genus *Haplopleuroceras* is included here, transferred from the Sonniniidae. Finally *Erycites* gave rise to the Stephanocerataceae in the Murchisonae Zone. Dimorphism is well known in most Hammatoceratinae, and the microconchs have lateral lappets.

c) Family *Graphoceratidae*

This now stands as a family on its own, for the slightly older subfamily Leioceratinae is probably not directly related and is removed to the Hildoceratidae. Derivation of Graphoceratidae is uncertain: the earliest forms are coarsely ribbed species of *Ludwigia* that may have evolved from *Bredyia*, hence from the Phymatoceratidae, at the base of the Murchisonae Zone. Or the family may be derived from the Grammocerotinae as a parallel development to the Leioceratinae. Graphoceratidae are a very abundant component of the ammonite fauna (except for their apparent absence from western North America) up to the top of the Discites Zone, where they died out leaving no successors. Dimorphism is marked throughout. The whole group has unfloored keels, which allows *Graphoceras* to be distinguished from the otherwise homeomorphic *Pseudolioceras* that occurs in the Concavum and Discites Zones in some areas.

(d) Family *Sonniniidae*

Many unrelated genera were included in the Sonniniidae in the first edition of the *Treatise* (p. L267). The core of the family consists of the genus *Euhoploceras*, derived from the Hammatoceratinid genus *Eudmetoceras* in the Concavum Zone. All later Sonniniidae probably evolved from *Euhoploceras*: they are the tuberculate genera *Sonninia* and *Papilliceras*, the smooth involute genera *Fissilobiceras* and *Shirbuirnia* and the involute compressed genus *Dorsetensia*. Another group that may be a separate lineage consists of *Fontannesia* and *Witchellia*, and the closely related *Zurcheria* and *Guhsania*, for which the subfamily name Zurcheriinae is available. The origin of *Fontannesia* in *Euhoploceras* is possible but not certain. All these genera exhibit large morphological ranges, and often overlap, making delimitation difficult. For instance, it can be difficult to decide on the dividing line between *Euhoploceras* and *Sonninia*, and *Dorsetensia* has marked resemblance to some species of both *Witchellia* and *Sonninia*. The group of genera forms a united whole, and detailed relationships between them are far from clear.

The following genera are excluded from the Sonniniidae:

(1) *Poecilomorphus* (including *Micropoecilomorphus* for microconchs) may be a Haploceratid in the basal part of the Humphriesianum Zone. It evolved from *Toxamblyites* of the upper Sauzei Zone (Sturani, 1971).

(2) The Upper Bajocian, Garantiana Zone, *Diplesioceras*, and the Lower Bathonian *Vastites*, bear little resemblance to other Sonniniidae and are separated from them by a considerable stratigraphical gap. *Diplesioceras* is removed to the category incertae sedis, and *Vastites* is a strigoceratid.

(3) *Haplopleuroceras* and *Bajocia*. *Haplopleuroceras* is an ammonite without clear affinities. It bears little resemblance to any of the Sonniniidae, and it is unlikely to be a member of that family. A large *Haplopleuroceras* has many of the morphological features of a large *Tmetoceras*, except that the sulcate venter of the latter would have to evolve into the ventral keel of the former. Now that *Tmetoceras* is known up into the Concavum Zone, such an origin for the Concavum and Discites Zones *Haplopleuroceras* is possible. Perhaps the closest resemblances for *Haplopleuroceras*, however, are with the late Hammatoceratinid genus *Spinammatoceras* which is bituberculate and has a keeled venter. Unfortunately the type specimens of *Spinammatoceras* are all microconchs of somewhat uncertain age, and the corresponding macroconchs have not yet been identified. Dimorphism is not known in *Haplopleuroceras*. The Humphriesianum and Subfurcatum Zones genus *Bajocia* may be derived from *Haplopleuroceras*, and it appears to be related to *Collina* and *Parastrenoceras*, genera of the Stephanoceratidae. So *Bajocia* is included in the latter family, and *Haplopleuroceras* is placed in the Hammatoceratinae until more definite evidence is forthcoming as to its affinities.

4. Superfamily Haplocerataceae (J.H.C.)

Four major groups of this superfamily may be distinguished:

(a) The group *Strigoceras* - *Strungia* - *Phlycticeras* (Aalenian (Bradfordensis Z.) - Callovian). Characteristic features include strigation of the test (as in *Amaltheus*), a hollow floored keel and involute compressed coiling with often minute umbilici. The supposed microconchs are often aberrantly coiled, small and lappetted, and are taken to include *Cadomoceras* and the cryptic *Oecoptychius*.

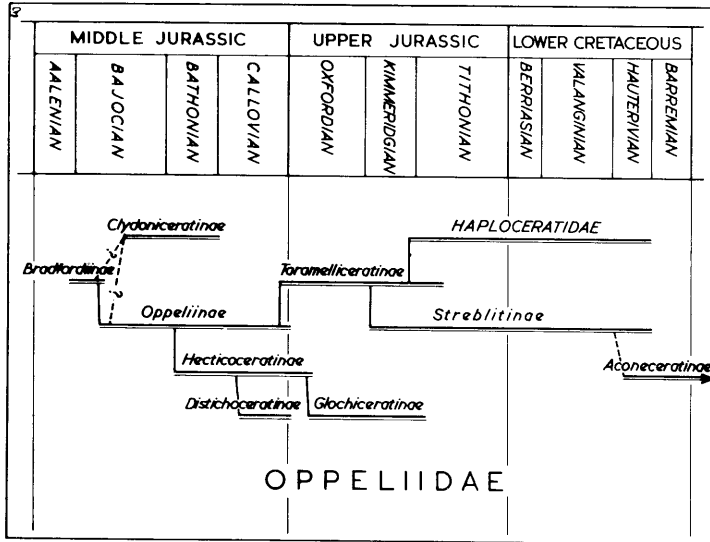


Fig. 3. Ranges and phylogenetic relationships of the subfamilies within the Family Opeeliidae, and range of the Family Haploceratidae within the Jurassic and early Cretaceous.

(b) The group *Bradfordia* – *Amblyoxyites* – *Praeoppelia* – *Oppelia* etc., with extensive subsequent developments and numerous phyletic divisions, including the group of *Taramelliceras* whose descendants survived into the Upper Cretaceous (Aalenian (Concavum Z.) – Coniacian). Dimorphism is strong to extreme, so that it is frequently difficult and sometimes impossible to suggest satisfactory pairings. As a result, previous classifications have in part placed what are probably merely dimorphs of single species into separate taxa up to family level. Microconchs include many small lapped forms, including *Oecotraustes* in the M. Jurassic and *Glochiceras sensu lato* in the U. Jurassic.

(c) The group *Lissoceras* – *Lissoceratoides* (L. Bajocian (Laeviuscula Z.) – M. Oxfordian). A former stratigraphical gap in its range in the Callovian has now been filled, and the morphology barely changes over the whole range of what may be taken to be a single genus. Microconchs (*Microlissoceras* Sturani, 1971) from their earliest appearance strongly resemble typical *Glochiceras*, with lappets.

(d) The group *Haploceras* (*elimatum* [M]/*carachttheis*, *leiosoma* [m] etc.) – *Neolissoceras*? (topmost Kimmeridgian (Beckeri Z., Setatum Sz.) – Neocomian, Hauterivian). This group can be satisfactorily derived from the Taramelliceratinae (*T. (Metahaploceras)* [M] and *Coryceras* [m]) in the Kimmeridgian (see however note (11) in Appendix). In the microconchs the lappets have shortened while in the macroconchs the adult peristome has flexuous lateral projections of almost the same proportions so that both dimorphs appear to be similarly, if only moderately, lappeted.

Groups (a)–(c) appear sharply and separately in the record around the Aalenian–Bajocian boundary, and while it is conceivable that *Lissoceras* of group (c) may have developed from *Bradfordia* of group (b), the first members of groups (b) (*Bradfordia liomphala*) and (a) (*Praestrigites praenuntius*) differ so strongly in almost every respect that no close connection can have remained at this level. Nor can any plausible ancestors be closely identified in the other well-known groups in the upper Toarcian or lower Aalenian. Yet the forms that evolved subsequently in all four groups cover ranges of morphology with so many similarities that a common and not far-distant origin seems certain, presumably in the Hammatoceratinae. For this reason it seems satisfactory to follow previous practice and to accord the groups family rank in parallel in a single superfamily Haplocerataceae.

The presumed phyletic relationships down to subfamily level are illustrated in Figs 2 and 6.

The superfamily is faunally provincial in being restricted largely to the Tethyan Realm in the Middle Jurassic to Neocomian, although there were minor but interesting excursions of single genera into the Boreal Province of the Boreal Realm both in the Middle and Upper Jurassic. These have however no consequences for classification at family group level.

5. Superfamily *Stephanocerataceae* (J.H.C.)

The classification of this superfamily has been difficult in the past because of the enormous range of morphologies its members encompass, ranging from the most evolute planulates to the most inflated sphaerocones and compressed oxycones. These create problems of homoeomorphism both within the superfamily and with

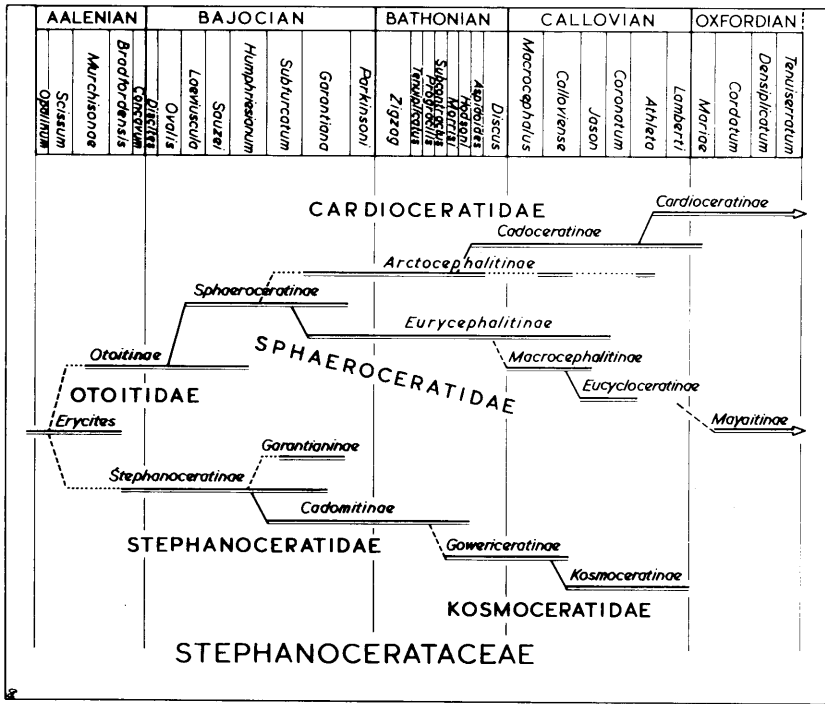


Fig. 4. Ranges and phylogenetic relationships of family group taxa within the superfamily Stephanocerataceae of the Middle Jurassic and early Upper Jurassic. The divisions on the right hand side of the zonal scale denote subzones, which have been drawn to a uniform thickness.

members of the other superfamily, the Perisphinctaceae, related to the Stephanocerataceae by descent. General morphological similarity is therefore often a poor indicator of phyletic relationships, and despite considerable effort no single character has been found to be much better. The considerable progress made in the last 20 years is the result largely of new collecting under the most careful stratigraphical control, in many parts of the world for the first time. The phylogenetic successions were put together piecemeal and the present state of knowledge is shown diagrammatically in Figs 4 and 6.

The principal new discovery in the superfamily has been the importance of faunal provincialism. In the Upper Bajocian three major realms became clearly differentiated for the first time: to the

Tethyan, of long previous history, were added the Boreal and Pacific. Although a certain differentiation into Tethyan and Boreal in a wide sense – perhaps more aptly called Sub-Boreal – had already occurred in some families, the almost total separation in the Middle Jurassic was something entirely new. Thus, as a consequence, although the time-scale in Fig. 4 is indicated in terms of a single scale of standard zones, that used in the best-known areas of Europe, the precise representation of the faunal successions in the different realms and provinces requires at least three separate scales in parallel. The areas of overlap between provinces, where they exist, are so narrow and still poorly known that precise correlations between the zonal scales are still not possible, and the starting levels of the Arctocephalitinae, Cadoceratinae, Eurycephalitinae and Gowericeratinae shown in Fig. 4 are therefore only approximate.

Some of the lineages are now known in impressive detail. Thus the record from the first of the Arctocephalitinae to the last of the Cardioceratinae is represented by nearly 100 successive faunas, and the 40 or so known faunas of the Kosmocerotidae include Brinkmann's classical descriptions of *Kosmoceras* from Peterborough. Such continuity allows one to make some evaluation of individual morphological characters for phylogenetic purposes. It seems that the mean adult size of a species in both its dimorphs tends to be a slowly changing character, as do the other manifestations of dimorphism. Major migrations from one faunal province to another could occur almost instantaneously, and were responsible for many of the previous discontinuities in the record. In the Stephanocerataceae these were common up to family group level and included, for example, the previously cryptogenic appearances of the Cardioceratidae, Macrocephalitinae and Kosmocerotidae in the Callovian of Europe.

Early sutural ontogeny, so exhaustively reviewed by Schindewolf (1961–1968), has turned out not to be a reliable guide to phylogeny in the Stephanocerataceae and Perisphinctaceae at levels below that of superfamily. The only character of systematic value consistently to have survived the stratigraphical tests appears to be the heterochronous development of an element U_n in the umbilical lobe of the Stephanocerataceae and not in the Perisphinctaceae (Schindewolf, 1965; Westermann, 1967). This supports, for instance, the removal of the sphaeroconic Tulitidae, homeomorphs (in the macroconchs only) of some Sphaeroceratidae, from the Stephanocerataceae into the

Perisphinctaceae, a conclusion already arrived at on independent grounds.

The broad outlines of the major phyletic branches shown in Fig. 4 leave out a number of minor but puzzling cryptogenic groups that were short lived and provincially highly restricted. They include *Arkelloceras* Frebold, 1958, *Parabigotites* Imlay, 1961 (northern Pacific), *Irianites* Westermann and Getty, 1970 (western Pacific), *Subcollina* Spath, 1925 [M]/*Parastenoceras* Ocheterena, 1963 [m] (eastern Pacific - Europe) and *Ermoceras* Douvillé, 1916 (northern Africa - Arabia). All are clearly related to Stephanoceratidae on general morphological grounds, but have evolved ventral smooth bands, grooves or tabulation with tubercles - features that are also found in the Garantianinae, the earliest Perisphinctidae and the later Kosmocerotidae. It is probably significant that these genera appeared abruptly at just those times in the Bajocian that Fig. 4 shows to have been times of much branching, diversification and faunal differentiation. The exact details of these are in many cases also still conjectural, as in, for example, the transition from Stephanoceratidae to Perisphinctidae. So these genera are probably to be regarded as yet further attempts in this direction that were but short-lived and then failed.

6. Superfamily Perisphinctaceae (J.H.C.)

Most of the general remarks made above in relation to the Stephanocerataceae apply equally well to the Perisphinctaceae and, if anything, even more so. The proverbial difficulties of classifying this group have been also greatly reduced by the discoveries of the last 20 years, which have joined stratigraphically and geographically many of the previously disconnected but often homoeomorphic groups of forms. A new classification can therefore attempt here to be primarily phylogenetic also. There stands revealed a family tree of almost innumerable trunks and branches, of all lengths and thicknesses and often still closely homeomorphic. This creates problems of balance, in trying to fit everything into the categories solely of families and subfamilies without the introduction of yet further subdivisions such as geographical races which could now in many cases be justified. A compromise adopted here is therefore to restore to full family group status a number of groups of genera clearly identified as having

evolved independently over a considerable time span, even if the differences in morphology would not have warranted such elevation alone – phyletic relationships where necessary take precedence over morphological similarities. Nevertheless, subfamilies may contain, besides the successive members of a major lineage, various minor elements such as offshoots of lesser duration or more localized occurrence, down to single genera of only sketchily-known affinities. The decision as to how important an evolving group has to be to become dignified with the rank of subfamily is therefore subjective and strongly dependent on the state of knowledge, something that varies greatly from group to group. For this reason the classification adopted is shown diagrammatically in Fig. 5 only down to family level.

As is well known, provincialism in the Perisphinctaceae reached a climax in the Upper Jurassic and Neocomian. A twofold division into a Boreal and Tethyan Realms would be an oversimplification of little value. It is possible to recognize numerous provinces defined by groups of a few genera or even by single genera – in fact almost all genera of Upper Jurassic Perisphinctaceae are to a greater or lesser degree restricted palaeogeographically. These provinces are of various kinds.

First, there is the latitudinal succession probably reflecting climatic belts, as first discussed by Neumayr and Uhlig. For example, at the top of the Jurassic one may distinguish a truly Boreal Province, including Greenland and Siberia, characterized by Dorsoplanitinae. Southwards follow two Sub-Boreal Provinces, the NW European with Pavloviinae and the Russian Platform with Virgatitinae. Further south comes the Submediterranean Province with mainly Lithacoceratinae and finally the Tethyan Province proper, with the classical Tithonian faunas of Simoceratidae, Spiticeratinae and Himalayitidae. These faunas and their distribution in the Tithonian have been reviewed in considerable detail by Enay (1972) and Enay and Geyssant (1975); similar gradations can be cited in the Oxfordian and Kimmeridgian. The association with climatic belts is reflected in the longitudinal and latitudinal extensions of the provinces and the closely parallel distribution of other climatic indicators, such as corals and bivalves and their diversities, and to some degree even lithofacies. It is then interesting but not surprising to see a similar sequence in reverse order going yet further southwards, with the (southern) Submediterranean faunas of

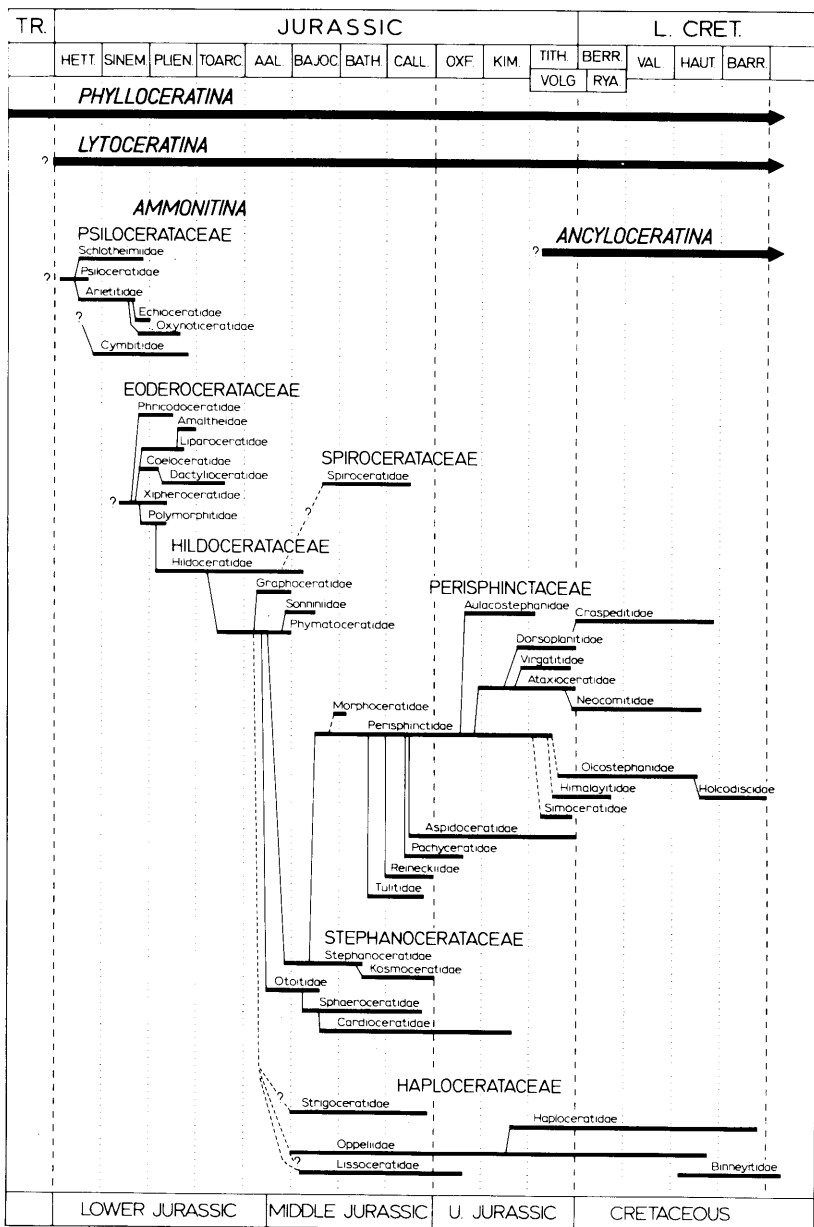


Fig. 5. Diagram showing the stratigraphical ranges and probable phylogeny of ammonite suborders, superfamilies and families during the Jurassic and earliest Cretaceous periods. (Note added in proof: Sphaeroceratidae range into the Oxfordian, and Oppeliidae into the higher Cretaceous. For Craspeditidae read Polyptychitidae.)

the Ethiopian Province followed by the Sub-Austral faunas of the Indo-Malgach Province, the analogue of the Sub-Boreal faunas of NW Europe: the astonishing similarity between the Middle-Upper Oxfordian faunas of Kenya, Madagascar and Cutch and those of Britain, Germany and France has long been famous. Since Sub-Austral distributions are also beginning to be recognized in the southern Andes, records of Boreal genera such as *Pavlovia* or *Dorsoplanites* should not therefore be dismissed out of hand as misidentifications. Some families and genera, such as *Perisphinctes* itself, are thus bipolar in their provincialism.

Secondly, there are some families and many genera restricted in their distribution more randomly and much more locally. Some are restricted to only one hemisphere, e.g. Mayaitinae (Sub-Austral) or Aulacostephanidae (Sub-Boreal), while others are confined to a very small area, e.g. *Virgatites* (Russian platform), *Ataxioceras* (European part of the north Submediterranean Province) or *Vinalesphinctes* (Caribbean). Almost every basin of deposition had its local speciality. Changes of province during evolution could be rapid and frequent.

To help unravel these complexities there are, besides stratigraphical continuity, a number of other morphological factors that can give valuable phylogenetic clues. Two may be mentioned here. Thus, as in the Stephanocerataceae, one of the main groups with numerous homoemorphs lost its lappets in the microconchs; and this identifies all the successors of the earliest *Pectinatites* through the Dorsoplanitinae into the last *Simbirskites* of the Polyptychitidae. It is an interesting general question whether any of the numerous lappeted descendants of the Hildoceratinae that later lost their lappets ever subsequently regained them. Lappets were abandoned also by the Pachyceratidae and the Aspidoceratinae; all the other groups shown in Fig. 5 retained theirs into the Cretaceous.

Another guide is provided by what may have been one of those rare events in ammonites, the appearance of a genuinely new morphological character corresponding to a true genetic innovation: the so-called virgatotome style of ribbing (see discussion by Geyer, 1961). It is seen *par excellence* in such genera as *Ataxioceras*, *Virgatites*, *Pseudovirgatites*, *Virgatosphinctes* and *Pectinatites* – in fact, most members of what used to be simply grouped together as the subfamilies Ataxioceratinae and Virgatosphinctinae. It occurred

first in the Upper Oxfordian, at the point at which the Perisphinctinae gave rise to the Ataxioceratidae. Subsequently it could disappear again (often in microconchs with strictly biplicate ribbing) but usually only briefly before sooner or later reappearing, very much like the expression of a single gene that oscillated between dominant and recessive. Its main use lies in tying to a common root the numerous fragmentary lineages in which it appears, not necessarily continuously, that could be pieced together by other means. Similarly, it serves to distinguish those lineages in which it seems never to occur at all and which therefore presumably lead back to the Perisphinctidae at an earlier point.

Finally, there are some groups that remain obstinately hard to place. Leading among these is the genus *Sutneria*. In a superfamily in which dimorphism can be clearly seen in almost every genus and even species, it has the distinction of being unmistakably a microconch, with lappets, whose evolution can be followed in abundance almost continuously from the Oxfordian into the Middle Tithonian and yet whose macroconch partners continue to defy identification.

7. Superfamily Spirocerataceae (J.H.C.)

The Middle Jurassic heteromorphs, although small in volume and range, constitute such a well-circumscribed and morphologically striking group that they are here separated at superfamily level, as in the *Treatise* of 1957. Their stratigraphy and systematics have been recently revised in an excellent monograph by Dietl (1978) which is unlikely to be improved, and so his classification is reproduced here unchanged at levels of subfamily and below.

The origin of the group continues, however, to be a matter of speculation and uncertainty. It is of special interest because it presents in acute form the more general problems of deducing phylogenetic relationships, involving as it does here probably the most fundamental of morphological characters in cephalopods, that of coiling as a whole. Various characters have come under consideration.

The early ontogeny of the septal suture of *Spiroceras* was studied by Schindewolf (1951; see further description and discussion in 1961, p. 92 (726)). He concluded that the first few sutures, including the quinquelobate primary suture, were exactly as found in many other Ammonitina and that this indicated the ultimate root of the

group to have lain in the Lytoceratina. Whether the derivation was direct, as implied by Arkell's placing in the *Treatise* of the Spirocerataceae in the suborder Lytoceratina, or indirect via some other normally coiled member of the Ammonitina, could, however, not be decided on the evidence of the early sutures alone. The ontogenetic development of the septa subsequently followed a specialized direction leading to adult sutures quite different from those of normally coiled Ammonitina, but Schindewolf agreed with Westermann (1956, p. 273) that this reflected merely the differing structural requirements of the uncoiled shell.

Sutural ontogeny having failed to give an answer, recourse had to be made in second place to other criteria. Schindewolf therefore reverted to the conventional method of selecting as ancestors of *Spiroceras* those forms of similar age bearing the strongest general morphological resemblance. Of the various candidates one could think of he selected the one already chosen by Buckman (1898, Table II) and Wetzel (1937, p. 84), namely *Strenoceras*. This merely deferred the problem elsewhere, however, for there is then the question of the origin of *Strenoceras*. This is not a trivial question, for this genus is almost as cryptogenic as *Spiroceras*. In Europe it appears as abruptly only one subzone earlier, at the base of the Subfurcatum Zone of the Upper Bajocian, a very short time for such a major evolutionary change to have taken place. The phyletic division could, of course, have occurred somewhat earlier, before either *Strenoceras* or *Spiroceras* appeared in the record, but such a hypothesis would in all logic then raise the question of which evolved from which. Perhaps with this possibility in mind Arkell in fact suggested that *Strenoceras* might have been merely a recoiled *Spiroceras* (1950, p. 359), but this was dismissed by Schindewolf as "of course impossible" (1961, p. 728) or "without doubt untenable" (1965, p. 24), on grounds of the structures both of the conch and of the suture – for reasons that were never given. *Spiroceras* being thus safely derived from *Strenoceras*, the latter was then attached (with *Garantiana*) to the Parkinsoniidae and hence the Stephanocerataceae, albeit with considerable reservations. An alternative suggestion, going back to Rollier (1911, p. 286) and Bentz (1925, p. 137), that *Strenoceras* and hence *Spiroceras* were derived from *Tmetoceras*, was also dismissed (1961, p. 223). The ontogeny of the early sutures was by no means against it, but the resemblance of the sculpture

was ascribed to convergent homoemorphism. The precise objections were not given, but they may well have been the large gap in the stratigraphical ranges as then known, between basal Aalenian and Upper Bajocian. In thus attaching *Spiroceras* via *Strenoceras* to the Parkinsoniidae, Schindewolf has been widely followed, notably by Wiedmann (e.g. 1969) and Dietl (1978). A minor variant was introduced by Ochoterena (1966) who saw an even closer connection between *Spiroceras* and what seemed to be a close relative of *Strenoceras*, namely *Parastrenoceras* Ochoterena, 1963.

The classification adopted here is also based on general morphological similarities but looks at these from a wider point of view. As discussed elsewhere in this paper, *Strenoceras* should not be regarded in isolation but considered as a member of a dimorphic lineage. This puts it as a microconch into the Garantianinae (q.v., above, and see Sturani, 1971, p. 159) of the Stephanoceratidae, which are here regarded as not closely related to the Parkinsoniinae of the Perisphinctaceae for reasons outlined on p. 146, note 2. This would in itself not rule out a connection between *Strenoceras* and *Spiroceras*, but the possible dimorphism of the latter should at least also be considered. Dietl correctly perceives the adult signs of maturity in shells of *Spiroceras*, stressing the form of the peristome where (rarely) preserved, slight variocostation of ribbing in some forms, and approximation of the last sutures. He attaches little importance, however, to another feature which seems to occur commonly if not invariably, namely a last brief change in coiling near the end of the adult body chamber, giving the gently curved shell a hook as in a walking stick. Combined with the presence of peristomal flares, this suggests that many of the small isocostate forms figured by him as juveniles are in fact adults; that the mild variocostation observed occurs always in larger forms; and that hence *Spiroceras* may be dimorphic according to the classical criteria: for example,

- Spiroceras orbigny* [M]: Dietl (1978) pl. 1, figs 1, 4, 5; pl. 2, figs 3, 5; pl. 3, figs 1, 2, etc.
[m]: pl. 4, figs 2, 3; pl. 5, figs 1-4, etc.
- Spiroceras sauzeanum* [M]: pl. 4, figs 2, 3; pl. 5, figs 1-4.
[m]: (*obliquocostatum*): pl. 3, fig. 6.
- Spiroceras annulatum* [M]: pl. 6, figs 1, 2.
[m]: pl. 6, fig. 3.

The dimorphic size ratio would be 2-3:1. The resemblance between *Spiroceras* ([m] + [M]) and *Strenoceras* [m]/*Garantiana* [M] ceases to be close.

Similar considerations apply to *Parastrenoceras*. Its macroconch has now also been plausibly identified (Torrens in Sturani, 1971, p.164): *Subcollina yeovilensis* Spath (1925) (= *Aegoceras densinodum* Wright (1880), pl. 38, figs 5, 6, non Quenstedt; Brit. Mus. (Nat. Hist.) no. C. 1932). This too bears little resemblance to *Spiroceras*. (New evidence suggests strongly, moreover, that neither was *Parastrenoceras* closely related to *Strenoceras*: see Sturani, 1971, p. 161.)

We are thus back to the search for alternative origins of *Spiroceras*, and the one put forward here lies in *Tmetoceras* as postulated by Rollier. The known range has been greatly extended in recent years. In England it has now been found repeatedly as high as the Concavum Zone at the top of the Aalenian (e.g. Senior *et al.*, 1970), and in Alaska it appears to range equally as high. Dimorphism is clearly discernible, beautifully illustrated in the late forms from Alaska by Westermann (1964). The size ratio is about 2-3:1. The microconchs have short but typical lappets, revealing descent presumably via *Catulloceras* as generally assumed, from the Hildoceratinae of the Lower Toarcian, the common root of all lappeted ammonites in the Middle and Upper Jurassic. The macroconchs are only slightly variocostate, just like those of *Spiroceras*; and both dimorphs are so evolute and loosely coiled that it would take only the gentlest of uncoiling to turn them into typical *Spiroceras*.

A possible objection remains in the stratigraphical gap between the top of the Aalenian and Upper Bajocian. In meeting this one can but discuss the probabilities. The act of postulating a bridge across a gap involves extrapolation into it from both ends. When trying to join groups that evolved rapidly one is therefore reluctant to tolerate any but small gaps. In the present case however both ancestors and descendants evolved very slowly. Thus *Tmetoceras* remained almost unchanged over its known range (U. Toarcian - Aalenian) of some ten subzones, as did *Spiroceras* over its range of about ten subzones (U. Bajocian - L. Bathonian: new records, H. S. Torrens, 1971). The gap between them is then also about ten subzones wide, but not impossibly so.

Another point of similarity between *Tmetoceras* and *Spiroceras*

lies in their distributions, which are both characteristically world-wide: circum-Pacific (Alaska to Argentine) and circum-Tethyan (East to North Africa, S. Europe). In contrast, the Garantianinae are confined to Europe and N. Africa. *Parastrenoceras* was even more restricted, to an area between Mexico, France and N. Italy.

Upwards, the gap between Spiroceratinae and Parapatoceratinae is also narrowing. If Dietl's brilliant suggestion is correct (1978, p. 55), *Epistrenoceras* also belongs to this group. This Bathonian genus has long been an embarrassment. No obvious ancestors came to mind in a part of the succession in which all the other Ammonitina can be claimed with some confidence to be rather well understood. Now that recoiling of heteromorphs has again become respectable, and in the Cretaceous even *de rigueur* (Wiedmann, 1969), *Epistrenoceras* finds a natural place in the Spiroceratidae. It is closely homoeomorphic with *Tmetoceras* and seems to be similarly dimorphic (*E. contrarium* (d'Orbigny) [including *E. haugi* (Douvillé, 1915, pl. 7, fig. 1)] [M] – *E. histricoides* (Rollier, 1911) [m]). Its sutural ontogeny is respectable, and it also has the same characteristic world-wide distribution.

Yet further upwards, there appear to be no reliable records of any other heteromorphs, or plausibly recoiled derivatives, between the Middle Callovian and *Protancyloceras* of the Lower Tithonian. This large gap, and some rather fundamental differences in the earliest septal sutures, seems to be the only objections to a direct link between the Spirocerataceae and Ancyloceratina. In many other respects the morphological similarities between these unusual forms are most striking. The question whether there was a direct connection, and hence whether the differences between quinquelobate and quadrilobate primary sutures have the overriding taxonomic importance claimed for them, can only be resolved by new evidence.

ACKNOWLEDGEMENTS

While the responsibility for the views expressed in the classification below remains that of the authors, it would only be just to acknowledge that they owe much to almost innumerable discussions with many colleagues over the years. We should like to mention in particular K. W. Barthel, R. Enay, T. A. Getty, C. Mangold, C. F. Parsons, the late C. Sturani, H. S. Torrens, G. E. G. Westermann, A. Zeiss and B. Zeigler. To them, and many others, we express our thanks.

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APPENDIX. CLASSIFICATION OF THE JURASSIC AMMONITINA

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Psilocerataceae Hyatt, 1867

Family Psiloceratidae Hyatt, 1867

Psiloceras Hyatt, 1867 [(= *Paraphylloceras* Salfeld, 1919; *Psilonotoceras* Quenstedt, 1883, obj.) *Planorbis* Z.], *Caloceras* Hyatt, 1870 [*Planorbis* and *Liasicus* Z.], *Psilophyllites* Spath, 1914 [(= *Hagenowiceras* Lange, 1921, obj; ? *Neophyllites* Lange, 1941) *Liasicus* Z.], *Laqueoceras* Lange, 1925 [*Liasicus* Z.].

Family Schlotheimiidae Spath, 1923

Schlotheimia Bayle, 1878 [(= *Anguliferites* Lange, 1951; *Scannoceras* Lange, 1924, obj.) *Angulata* Z.], *Angulaticeras* Quenstedt, 1883 [(= *Argoceras* Steinmann, 1925; *Boucaulticeras* Spath, 1924; *Pseudoschlotheimia* Spath, 1924) *Obtusum-Raricostatum* Z.], *Kammerkaroceras* Lange, 1941 [Hett.-? L. Sin], *Saxoceras* Lange, 1924 [*Liasicus* Z.], *Sulciferites* Spath, 1922 [(= *Charmasseiceras* Spath, 1924; *Encycloceras* Blind, 1963; *Hongkongites* Grabau, 1928) L. Sin.], *Waehneroceras* Hyatt, 1889 [(= *Curviceras* Blind, 1963; ? *Franziceras* Buckman, 1923; *Kammerkarites* Spath, 1924; *Macrogrammites* Buckman, 1928; *Megastomoceras* Lange, 1941; *Storthoceras* Lange, 1941; *Teneroceras* Lange, 1952, obj.) *Liasicus* Z.].

Family Arietitidae Hyatt, 1875

Subfamily Arietitinae Hyatt, 1875

Coroniceras Hyatt, 1867 [*Bucklandi* and *Semicostatum* Z.]
C. (*Coroniceras*) Hyatt, 1867 (= *Arnioceratoides* Spath, 1925, obj.; *Epammonites* Spath, 1922; *Pararnioceras* Spath, 1922; *Primarietites* Buckman, 1926). *C.* (*Arietites*) Waagen, 1869 (= *Arietoceras* Quenstedt, 1883, *nom. van.*; *Megarietites* Spath, 1922). *C.* (*Eucoroniceras*) Spath, 1922. *C.* (*Paracoroniceras*) Spath, 1922, *Arnioceras* Hyatt, 1867 [(= *Arniotites* Whiteaves, 1889; *Burkhardtceras* Lopez, 1967; *Eparnioceras* Spath, 1924; ? *Melanhippites* Crickmay, 1928) *Semicostatum-Obtusum* Z.], *Metarnioceras* Spath, 1925 [L. Sin.], *Tmaegoceras* Hyatt, 1889 [L. Sin.], *Vermiceras* Hyatt, 1889 [U. Hett.-*Bucklandi* Z.]
V. (*Vermiceras*) Hyatt, 1889 (= *Diplosellites* Buckman, 1925; *Discoceras* Hyatt, 1867, *non* Barrande, 1867; *Gyrophioceras* Spath, 1924; *Keynshamites* Buckman, 1926; *Metophioceras* Spath, 1924; *Protocymbites* Spath, 1923); *V.* (*Paracaloceras*) Spath, 1923 (= *Alpinoceras* Lange, 1941; ? *Centauroceras* Blind, 1963).

Subfamily Agassiceratinae Spath, 1924

Agassiceras Hyatt, 1875 [(= *Aetomoceras* Hyatt, 1900, obj.) *Semicostatum* Z.], *Euagassiceras* Spath, 1924 [(= *Paracoroniceras* Buckman, 1927) *Semicostatum* Z.].

Subfamily Alsatitinae Spath, 1924

Alsatites Haug, 1894 [(= *Gonioptychoceras* Lange, 1941; *Proarietites* Lange, 1922) *Liasicus* Z.], *Canavarites* Hyatt, 1900 [U. Hett./L. Sin.], *Pseudaetomoceras* Spath, 1923 [(= *Proarnioceras* Blind, 1963) U. Hett./L. Sin.].

Subfamily Asterooceratinae Spath, 1946

Asterooceras Hyatt, 1867 [Obtusum Z.], *Aegasteroceras* Spath, 1925 [(= *Arctoasteroceras* Frebold, 1960; *Ptycharietites* Spath, 1925) *Obtusum* Z.], *Caenisites* Buckman, 1925 [(= *Euasteroceras* Donovan, 1953) *Turneri* Z.], *Eparietites* Spath, 1924 [Obtusum Z.], *Epophioceras* Spath, 1924 [Obtusum Z.], *Pompeckioceras* Spath, 1925 [? *Obtusum* Z.].

Subfamily Pseudotropitinae Donovan, 1973

Pseudotropites Waehner, 1894 [L. Sin.].

Family Echioceratidae Buckman, 1913

Echiocheras Bayle, 1878 [(= *Echioceratoides* Trueman and Williams, 1925; *Ophioceras* Hyatt, 1867, *non* Barrande, 1865; *Pleurechiocheras* Trueman and Williams, 1925) *Raricostatum* Z.], *Gagaticeras* Buckman, 1913 [(= *Parechiocheras* Buckman, 1914) *Oxynotum* Z.], *Leptechioceras* Buckman, 1923 [(= *Psilechiocheras* Erben, 1956) *Oxynotum*-? *Raricostatum* Z.], *Paltechiocheras* Buckman, 1924 [*Raricostatum* Z.] *P. (Paltechiocheras)* Buckman, 1924 (= *Epechiocheras*, *Euechiocheras*, *Kamptechioceras*, *Metechioceras*, and *Plesechiocheras* Trueman and Williams, 1925; *Stenechiocheras* Buckman, 1927; *Vobstericeras* Trueman and Williams, 1925), *P. (Orthechiocheras)* Trueman and Williams, 1925 (= *Homechiocheras* Trueman and Williams in Buckman, 1925).

Family Oxynoticeratidae Hyatt, 1875

Oxynoticeras Hyatt, 1875 [(= *Hypoxynoticeras* Spath, 1925) *Oxynotum* Z.], *Cheltonia* Buckman, 1904 [*Oxynotum* Z.], *Gleviceras* Buckman, 1918 [(= *Glevumites* Buckman, 1924; *Guibaliceras* Buckman, 1918; *Riparioceras* Schindewolf, 1962; *Tutchericeras* Buckman, 1919; *Victoriceras* Buckman, 1918) U. Sin.], *Paracymbites* Trueman and Williams, 1927 [U. Sin.], *Paroxynoticeras* von Pia, 1914 [U. Sin.], *Radstockiceras* Buckman, 1918 [(= *Carixiceras* Spath, 1925; *Fanninoceras* McLearn, 1930; *Fastigiceras* Buckman, 1919; *Homoxynoticeras* Buckman, 1925; *Kleistoxynoticeras* Buckman, 1925; *Metoxynoticeras* Spath, 1922; *Phylloxynotites* Buckman, 1924; *Retenticeras* Buckman, 1920) U. Sin.-L. Pliensb.], *Slatterites* Spath, 1923 [U. Sin.].

Family Cymbitidae Buckman, 1919

Cymbites Neumayr, 1978 [(= *Metacymbites* Spath, 1923) Sin.-Pliensb.].

Superfamily Eoderocerataceae Spath, 1929*

Family Eoderoceratidae Spath, 1929

Xipheroceras Buckman, 1911 [Obtusum Z.], *Bifericeras* Buckman, 1913 [(= *Hemimicroceras* Spath, 1925; ? *Ophideroceras* Spath, 1925) Oxynotum Z.], *Cruciloboceras* Buckman, 1920 [Raricostatum Z.], *Eoderoceras* Spath, 1925 [(= *Deroceras* Hyatt, 1867, *non* Rafinesque, 1820) U. Sin.], *Metaderoceras* Spath, 1925 [L. Pliensb.], *Microderoceras* Hyatt, 1871 [Turneri Z.], *Neomicroceras* Donovan, 1966 [Raricostatum Z.], *Promicroceras* Spath, 1925 [Turneri & Obtusum Z.].

Family Coeloceratidae Haug, 1910

Coeloceras Hyatt, 1867 [Jamesoni Z.], *Apoderoceras* Buckman, 1921 [Jamesoni Z.], *Hyperderoceras* Spath, 1926 [L. Pliensb.], *Pimelites* Fucini, 1896 [L. Pliensb.], *Praesphaeroceras* Levi, 1896 [(= *Diaphorites* Fucini, 1896) L. Pliensb.], *Tetraspidoceras* Spath, 1926 [Raricostatum/Jamesoni Z.].

Family Phricodoceratidae Spath, 1938

Phricodoceras Hyatt, 1900 [(= *Hemiparinodiceras* Geczy, 1959) Pliensb.], *Epideroceras* Spath, 1923 [(= *Coeloderoceras* Spath, 1923: ? *Villania* Till, 1911) Raricostatum Z.], *Pseuduptonia* Bremer, 1965 [Raricostatum/Jamesoni Z.].

Family Polymorphitidae Haug, 1887

Polymorphites Haug, 1887 [Jamesoni Z.], *Acanthopleuroceras* Hyatt, 1900 [(= *Cycloceras* Hyatt, 1867, *non* McCoy, 1844) *Ibex* Z.], *Dayiceras* Spath, 1920 [Jamesoni Z.], *Parinodiceras* Trueman, 1918 [(= *Platynoticeras* Spath, 1938) Jamesoni Z.], *Gemmellaroceras* Hyatt, 1900 [(= *Leptonotoceras* Spath, 1925; *Tubellites* Buckman, 1924) Raricostatum & Jamesoni Z.], *Platypleuroceras* Hyatt, 1867 [Jamesoni Z.], *Tropidoceras* Hyatt, 1867 [*Ibex* Z.], *Uptonia* Buckman, 1897 [(? = *Jamesonites* Buckman, 1923; *Microceras* Hyatt, 1867, *non* Hall, 1845) Jamesoni Z.].

Family Liparoceratidae Hyatt, 1867

Liparoceras Hyatt, 1867 [Pliensb.] *L.* (*Liparoceras*) Hyatt, 1867; *L.* (*Becheiceras*) Trueman, 1918 (= *Anisoloboceras* Trueman, 1918; *Becheoceras* Dacqué, 1934, *nom. null.*); *L.* (*Vicininodiceras*) Trueman, 1918, *Aegoceras* Waagen, 1869 [*Ibex* and *Davoei* Z.] *A.* (*Aegoceras*) Waagen, 1869 (= *Amblyoceras* Hyatt, 1900); *A.* (*Beaniceras*) Buckman, 1913; *A.* (*Oistoceras*) Buckman, 1911, *Androgynoceras* Hyatt, 1867 [*Ibex* and *Davoei* Z.].

Family Amaltheidae Hyatt, 1867

Amaltheus De Montfort, 1808 [*A.* (*Amaltheus*) De Montfort, 1808, U. Pliensb., *Margaritatus*–*Spinatum* Z. (= *Proamaltheus*

* Nom. subst. because *Deroceras* Hyatt 1867 pre-occupied, but violates Art. 23(d)(i) of the *International Code*. Retained pending investigation.

Lange, 1932; *Nordamaltheus* Repin, 1968); *A. (Pseudoamaltheus)* Frebold, 1922, [U. Pliensb., *Margaritatus* Z., *Gibbosus* Sz.—*Spinatum* Z.], *Amauroceras* Buckman, 1913 [U. Pliensb., *Margaritatus* Z.—*Spinatum* Z.], *Pleuroceras* Hyatt, 1867 [U. Pliensb., *Spinatum* Z.].

Family Dactylioceratidae Hyatt, 1867

Reynesocoeloceras Géczy, 1976, [Pliensb., Davoei Z.—*Margaritatus* Z. (= *Indunoceras* Wiedenmayer, 1977, obj.; *Cetonoceras* Wiedenmayer, 1977)], *Prodactylioceras* Spath, 1923 [Pliensb., *Ibex* Z.—*Margaritatus* Z. (= *Paralytoceras* Frebold, 1922 (*non* Frech, 1902) obj.; *Praedactylioceras* Frentzen, 1937, obj.)], *Aveyroniceras* Pinna and Levi-Setti, 1971 [Pliensb., Davoei Z.—*Margaritatus* Z. (= *Bettoniceras* Wiedenmayer 1977)], *Reynoceras* Spath, 1936 [U. Pliensb.], *Dactylioceras* Hyatt, 1867 [? U. Pliensb., *Spinatum* Z.; L. Toarcian, *Tenuicostatum* Z.—*Bifrons* Z., *Commune* Sz. (= *Arcidactylites*, *Microdactylites*, *Anguidactylites*, *Leptodactylites*, *Peridactylites*, *Toxodactylites*, *Vermidactylites*, *Xeinodactylites* Buckman, 1926; *Athlodactylites*, *Curvidactylites*, *Koimodactylites*, *Nomodactylites*, *Parvidactylites*, *Simplidactylites* Buckman, 1927; *Rakusites* Guex, 1971; *Eodactylites* Schmidt-Effing, 1972)]; *D. (Dactylioceras)* [distribution as for genus]; *D. (Orthodactylites)* Buckman, 1926; L. Toarcian, *Tenuicostatum* Z.—*Falciferum* Z. (= *Kryptodactylites*, *Tenuidactylites* Buckman, 1926; *Kedonoceras* Dagens 1968)], *Nodiocoeloceras* Buckman, 1926 [L. Toarcian, *Exaratum* Sz.—*Commune* Sz. (= *Crassicoeloceras*, *Lobodactylites*, *Multicoeloceras*, *Spinicoeloceras* Buckman, 1926; *Mesodactylites* Pinna and Levi-Setti, 1971)], *Peronoceras* Hyatt, 1867 [L. Toarcian, *Fibulatum* Sz.], *Zugodactylites* Buckman, 1926 [L. Toarcian, *Fibulatum* Sz. (= *Omolonoceras* Dagens 1967; *Gabillytes* Guex, 1971)], *Porpoceras* Buckman, 1911 [L. Toarcian, *Fibulatum* Sz. (= *Telodactylites* Pinna and Levi-Setti, 1971; *Platystrophites* Levi-Setti and Pinna, 1971)], *Catacoeloceras* Buckman, 1923 [L. Toarcian, *Crassum* Sz.—*Variabilis* Z. (= *Transicoeloceras* Pinna, 1966)], *Collina* Bonarelli, 1893 [L. Toarcian, *Crassum* Sz.—*Variabilis* Z. (= *Mucrodactylites* Buckman, 1928; *Collinites* Atrops, 1972)].

Superfamily Hildocerataceae Hyatt, 1867

Family Hildoceratidae Hyatt, 1867

Subfamily Harpoceratinae Neumayr, 1875

Protogrammoceras Spath, 1913 [L. Pliensb., *Jamesoni* Z.—L. Toarcian, *Tenuicostatum* Z. (= *Wrightia* Gemmellaro, 1886 (*non* Agassiz, 1862); *Paltarpites* Buckman, 1922; *Argutarpites* Buckman, 1923; *Bassaniceras* Fucini, 1929, obj.; *Eoprotogrammoceras*, *Neoprotogrammoceras* Cantaluppi, 1970)], *Lioceratoides* Spath, 1919 [U. Pliensb., *Margaritatus* Z.—*Spinatum* Z. (= *Platyharpites* Buckman, 1927; *Praelioceras* Fucini, 1929; *Nagato-*

ceras Matsumoto, 1947; *Neolioceratoides* Cantaluppi, 1970)], *Fucinicer* Haas, 1913 [Pliensb., Jamesoni Z.—Spinatum Z. (= *Eofucinicer*, *Neofucinicer* Cantaluppi, 1970)], *Tiltonicer* Buckman, 1913 [L. Toarcian, Tenuicostatum Z. (= *Pacificer* Repin, 1970)], *Eleganticer* Buckman, 1913 [L. Toarcian, Exaratum Sz. (= *Elegantulicer* Buckman, 1913; *Leptarpites*, *Ochotocer* Repin, 1970)], *Harpocer* Waagen, 1869 [L. Toarcian, Exaratum Sz.—Crassum Sz. (*Harpoceratoide* Buckman, 1909; *Maconicer* Buckman, 1926; *Glyptarpites* Buckman, 1927; *Tardarpocer* Buckman, 1927; *Phaularpites* Buckman, 1928; *Falcifericer* Breistroffer, 1949, obj.; *Kolymocer* Dagis, 1970)], *Taffertia* Guex, 1973 [L. Toarcian, Falciferum Z.], *Ovaticer* Buckman, 1918 [L. Toarcian, Falciferum Sz.], *Whitbyicer* Buckman, 1913 [L. Toarcian, ? Exaratum Sz.], *Pseudoliocer* Buckman, 1889 [L. Toarcian, Bifrons Z.—L. Bajoc., Laeviuscula Z. (= *Praehaplocer* Monestier, 1931; *Pseudowalkericer* Maubeuge, 1949; *Osperleioicer* Krimholz, 1963; *Tugurites* Kalacheva and Sey, 1970; ? *Buckmanites* Guex, 1973)], *Pseudopolyplectus* Mattei, 1969 [Toarcian, Bifrons Z.—Levesquei Z., Dispansum Sz.], *Polyplectus* Buckman, 1890 [U. Toarcian (= *Micropolyplectus* Guex, 1973)], *Sphenarpites* Spath, 1936 [Toarcian].

Subfamily Arieticeratinae Howarth, 1955

Arieticer Seguenza, 1885 [U. Pliensb. (= *Seguenzicer* Levi, 1896, obj.; *Meneghinia* Fucini, 1931 (*non* Silvestri, 1889); *Naxensicer* Fucini, 1931 (*non* Checchia-Rispoli, 1917); *Trinacriocer* Fucini, 1931; *Proarieticer*, *Pseudoarieticer* Cantaluppi, 1970; *Geczya* Fantini Sestini, 1977)], *Leptaleocer* Buckman, 1918 [U. Pliensb.], *Canavaria* Gemmellaro, 1886 [U. Pliensb. (= *Tauromenicer* Mouterde, 1967 (= *Tauromenia* Fucini, 1931 (*non* Seguenza, 1885)); *Neoemaciaticer* Cantaluppi, 1970)], *Emaciaticer* Fucini, 1931 [U. Pliensb., Spinatum Z. (= *Seguentia* Fucini, 1931; *Ugdulenia* Cantaluppi, 1970)], *Fontanellicer* Fucini, 1931 [U. Pliensb.], *Arctomercaticer* Repin, 1968 [L. Toarcian, Tenuicostatum Z.]. (*Fieldingia* Cantaluppi, 1970 – indeterminate Arieticeratid nucleus).

Subfamily Hildoceratinae Hyatt, 1867

Hildaites Buckman, 1921 [L. Toarcian, Falciferum Z. (= *Murleyicer* Buckman, 1921; *Hildoceratoide* Buckman, 1921; *Harpohildocer* Repin, 1970)], *Hildocer* Hyatt, 1867 [L. Toarcian, Bifrons Z. (= *Gonihildocer* Seguenza, 1886; *Orthildaites* Buckman, 1923; *Urkutites* Géczy, 1967)], *Parahildaites* Blaison, 1967 [L. Toarcian, Bifrons Z.], *Mercaticer* Buckman, 1913 [L. Toarcian, Mercati (= Bifrons) Z.], *Renzicer* Arkell, 1951 [L. Toarcian].

Subfamily Grammoceratinae Buckman, 1905

Grammocer Hyatt, 1867 [U. Toarcian, Thouarsense Z. (=

Costigrammoceras Buckman, 1926)], *Pseudogrammoceras* Buckman, 1901 [U. Toarcian, Variabilis Z.—Thouarsense Z. (= *Monestieria* Cossmann, 1922)], *Padagrosites* Guex, 1973 [Toarcian, Thouarsense Z.], *Pseudolillia* Maubeuge, 1949 [U. Toarcian, Thouarsense Z.], *Shakraceras* Basse, 1957 [Toarcian], *Phlyseogrammoceras* Buckman, 1901 [U. Toarcian, Levesquei Z., Dispansum Sz. (= *Gruneria* Gabilly, 1974)], *Onychoceras* Wunstorff, 1905 [U. Toarcian, Levesquei Z., Dispansum Sz.], *Hudlestonia* Buckman, 1891 [U. Toarcian, Levesquei Z.], *Dumortieria* Haug, 1885 [U. Toarcian, Levesquei Sz.—Moorei Sz. (= *Phenakoceras* Maubeuge, 1949; *Phenakocerites* Maubeuge, 1950)], *Catulloceras* Gemmellaro, 1886 [U. Toarcian, Levesquei Sz.—Moorei Sz. (= *Dactylogrammites* Buckman, 1925)], *Pleydellia* Buckman, 1899 [U. Toarcian, Aalensis Sz.—Aalenian, Opalinum Z. (= *Cotteswoldia* Buckman, 1902; *Canavarina* Buckman, 1904; *Walkericeras* Buckman, 1913)], *Asthenoceras* Buckman, 1899 [Aalenian—L. Bojoc, Murchisonae Z.—Sauzei Z.].

Subfamily Leioceratinae Spath, 1936

Leioceras Hyatt, 1867 [Aalenian, Opalinum Z.—Murchisonze Z. (= *Ancolioceras* Buckman, 1899; *Cypholioceras* Buckman, 1899)], *Canavarella* Buckman, 1904 [Aalenian, Opalinum Z., Costosum Sz. (= *Geyerina* Buckman, 1913; *Costiceras* Contini, 1969)], *Cylicoceras* Buckman, 1899 [(sic, not *Cyclicoceras*, as in *Treatise* 1957, p. L262), Aalenian, Opalinum Z., Costosum Sz.], *Staufenia* Pompeckj, 1906 [Aalenian, Murchisonae Z.].

Subfamily Bouleiceratinae Arkell, 1950

Bouleiceras Thevenin, 1906 [L. Toarcian, Tenuicostatatum Z.—Falciferum Z. (= *Colcanapites* Collignon, 1958)], *Frechiella* Prinz, 1904 [L. Toarcian, Bifrons Z. (= *Achilleia* Renz, 1913)], *Leukadiella* Renz, 1913 [L. Toarcian, Bifrons Z.], *Paroniceras* Bonarelli, 1893 [U. Toarcian, Variabilis Z.—Thouarsense Z. (= *Jacobella* Jeannet, 1908)], *Oxyparoniceras* Guex, 1974 [U. Toarcian, Thouarsense Z.], *Kohaticeras* Fatmi and Hölder, 1975 [Toarcian].

Subfamily Tmetoceratinae Spath, 1936

Tmetoceras Buckman, 1892 [U. Toarcian, Levesquei Z.—Aalenian, Concavum Z. (= *Tmetoites* Westermann, 1964)].

Family Phymatoceratidae Hyatt, 1867

Subfamily Phymatoceratinae Hyatt, 1867

Phymatoceras Hyatt, 1867 [Toarcian, Bifrons Z.—Variabilis Z. (= *Pelecoceras* Hyatt, 1867; *Chartronia* Buckman, 1898; *Denckmannia* Buckman, 1898; *Picenia* Fossa-Mancini, 1919; *Loryella* Breistroffer, 1949 (pro. *Lillia* Bayle, 1878 (non Boie, 1844)); ? *Haugiella* Gabilly, 1974; *Rarenoidia* Venturi, 1975)], *Pseudomercaticeras* Merla, 1933 [U. Toarcian, Erbaense Z., Latum Sz. (= *Crassiceras* Merla, 1933)], *Brodieia* Buckman, 1898 [U. Toarcian, Variabilis Z. (Erbaense Z.) (= *Brodiceras*

Buckman, 1899, obj.; *Pseudobrodieia* Guex, 1972; *Merlaites* Gabilly, 1974)], *Haugia* Buckman, 1888 [U. Toarcian, Variabilis Z.], *Esericeras* Buckman, 1920 [U. Toarcian, Thouarsense Z., Striatulum Sz.], *Nejdia* Arkell, 1952 [U. Toarcian, ? Variabilis Z.].

Subfamily Hammatoceratinae Buckman, 1887

Hammatoceras Hyatt, 1867 [U. Toarcian, Thouarsense Z., Fallaciosum Sz.—Levesquei Z. (= *Ammatoceras* Hyatt, 1867, obj.; *Pachammatoceras* Buckman, 1921)], *Bredyia* Buckman, 1910 [Aalenian, Opalinum Z. (= *Pseudammatoceras* Elmi, 1963)], *Eudmetoceras* Buckman, 1920 [Aalenian—L. Bajocian, Murchisonae Z.—Discites Z. (= *Rodaniceras* Elmi, 1963)], *Planammatoceras* Buckman, 1922 [Aalenian, Murchisonae Z.], *Euaptetoceras* Buckman, 1922 [Aalenian—L. Bajocian, Murchisonae Z.—Discites Z. (= *Parammatoceras* Buckman, 1925; *Csernyeiceras* Géczy, 1966; *Pseudaptetoceras* Géczy, 1966)], *Puchenquia* Westermann and Riccardi, 1972 [L. Bajocian, Discites Z.], *Erycites* Gemmellaro, 1886 [U. Toarcian, Erbaense Z.—Aalenian, Murchisonae Z. (= *Abbasitoides* Géczy, 1966)], *Padagrosiceras* Maubeuge and Lambert, 1956 [Aalenian—L. Bajocian, Concavum Z.—Discites Z. (= *Erycitoides* Westermann, 1964; *Kialagvikies* Westermann, 1964)], *Spinammatoceras* Schindewolf, 1964 [Aalenian—L. Bajocian, Concavum Z.—Discites Z.], *Sphaerocoeloceras* Jaworski, 1926 [U. Toarcian, Levesquei Z.], *Haplopleuroceras* Buckman, 1892 [Aalenian—L. Bajocian, Concavum Z.—Discites Z.].

Family Graphoceratidae Buckman, 1905

Ludwigia Bayle, 1878 [Aalenian, Murchisonae Z. (= *Murchisonia* Engel, 1896 obj.; *Cosmogyrta* Buckman, 1898; *Welschia* Buckman, 1898; *Apedogyria*, *Crickia*, *Hyattia*, *Hyattina*, *Kiliana*, *Ludwigina*, *Manselia*, *Pseudographoceras*, *Rhaeboceras*, *Stophogyria* Buckman, 1899; *Lucya* Buckman, 1902)], *Costileioceras* Maubeuge, 1950 [Aalenian, Murchisonae Sz.], *Brasilina* Buckman, 1898 [Aalenian, Bradfordensis Sz. (= *Brasilina*, *Paquieria*, *Wiltshireia*, *Vacekia* Buckman, 1899; *Paineia* Buckman, 1904; *Planifastigites* Buckman, 1925)], *Graphoceras* Buckman, 1898 [Aalenian—L. Bajocian, Concavum Z.—Discites Z. (= *Ludwigella* Buckman, 1901; *Braunsina*, *Depaoceras*, *Platygraphoceras*, *Reynesia* Buckman, 1902; *Oedania*, *Stokeia* Buckman, 1904; *Hosoureites* Sato, 1958)], *Hyperlioceras* Buckman, 1889 [L. Bajocian, Discites Z. (= *Deltoidoceras*, *Dissoroceras*, *Toxolioceras* Buckman, 1904; *Deltotoceras* Buckman, 1904 (pro. *Deltoceras* Buckman, 1902 (non Hyatt, 1894))], *Reynesella* Buckman, 1902 [L. Bajocian, Discites Z.], *Darellia* Buckman, 1898 [L. Bajocian, Discites Z. (= *Braunsella* Buckman, 1904 (pro. *Braunsia* Buckman, 1902 (non Kreichbaumer, 1894)); *Darellina*, *Hugia*, *Lopadoceras* Buckman, 1904)].

Family Sonniniidae Buckman, 1892

Euhoploceras Buckman, 1913 [Aalenian—L. Bajocian, Concavum Z.—Laeviuscula Z., ? Sauzei Z. (= *Alaskina* Westermann, 1978 (pro. *Alaskoceras* Westermann, 1969 (non Miller and Furnish, 1945))), *Sonninia* Douvillé, 1879 [S. (*Sonninia*) Douvillé, 1879 (pro. *Waagenia* Bayle, 1879 (non Kreichbaumer, 1874))], L. Bajocian, Laeviuscula Z.—Sauzei Z. (= *Stiphromorphites*, *Sherbornites* Buckman, 1923), S. (*Papilliceras*) Buckman, 1920, L. Bajocian, Laeviuscula Z.—Sauzei Z. (= *Prepapillites* Buckman, 1927)], *Shirbuirnia* Buckman, 1910 [L. Bajocian, Sauzei Z.], *Fissiloboceras* Buckman, 1919 [L. Bajocian, Laeviuscula Z.], *Fontannesia* Buckman, 1902 [Aalenian—L. Bajocian, Concavum Z.—Laeviuscula Z. (= *Darellella* Buckman, 1904; *Nannoceras* Buckman, 1923; *Nannina* Buckman, 1927; *Latiwitchellia* Imlay, 1973)], *Witchellia* Buckman, 1889 [L. Bajoc., Laeviuscula Z.—Sauzei Z. (= *Zugophorites* Buckman, 1922; *Pelekodites* Buckman, 1923; *Sonninites* Buckman, 1923; *Hyalinites* Buckman, 1924; *Sonnites* Buckman, 1925; *Gelasinites* Buckman, 1925; *Rubrileites*, *Ankoleiites*, *Dundryites* Buckman, 1926; *Zugella* Buckman, 1927; *Macerites*, *Spatulites* Buckman, 1928)], *Guhsonia* McLearn, 1926 [L. Bajocian, Laeviuscula Z.], *Zurcheria* Douvillé, 1885 [L. Bajocian, Discites Z.—Laeviuscula Z.], *Dorsetensia* Buckman, 1892 [L. Bajocian, Sauzei Z.—Humphriesianum Z.].

Incertae Sedis

Asaphoceras Spath, 1924, Lower Jurassic, ? Sinemurian. *Diplesioceras* Buckman, 1920, U. Bajocian, Garantiana Z.

Superfamily Haplocerataceae Zittel, 1884

Family Strigoceratidae Buckman, 1924⁽¹⁾ [Aalen., Bradfordensis Z. — M. Callov.]

[⊃ Hebetoxytitidae Buckman, 1924⁽²⁾] [⊃ Phlycticeratidae Spath, 1925⁽³⁾] [⊃ Oecoptychitidae Westermann, 1956⁽³⁾].

Family Oppeliidae Douvillé, 1890

Subfamily Bradfordiinae nov.⁽⁴⁾ [Aalen., Concavum Z. — Bajoc., Sauzei Z.]

Subfamily Oppeliinae Douvillé, 1890 [Bajoc., Laeviuscula Z. — U. Callov.]

Subfamily Clydoniceratinae Buckman, 1924⁽⁵⁾ [U. Bajoc., Subfurcatum Z. — U. Bathon., Discus Z.]

[⊃ Thamboceratinae Arkel, 1952].

Subfamily Hectioceratinae Hyatt, 1900 [L. Bathon., Zigzag Z. — L. Oxford.]

Subfamily Distichoceratinae Hyatt, 1900 [Callov., Calloviense — Lamberti Z.]

[= Bonarelliinae Spath, 1925 (obj.)].

Subfamily Glochiceratinae Hyatt, 1900⁽⁶⁾ [M. Oxford. — L. Tithon.]

[= Ochetoceratinae Spath, 1928].

Subfamily Taramelliceratinae Spath, 1928 (1925) [U. Callov.,

Athleta Z. – L. Tithon.]

[= Neumayriceratinae Spath, 1925 (obj.)] [⊃ Mazapilitinae Spath, 1928⁽⁷⁾].

Subfamily Streblitinae Spath, 1925⁽⁸⁾ [L. Kimm., Hypselocyclum Z. – Hauteriv.]

Subfamily Aconeceratinae Spath, 1923⁽⁹⁾ [L. Hauteriv. – U. Alb.]

Subfamily Binneyitinae Reeside, 1927⁽¹⁰⁾ [Cenoman. – Coniac.]

Family Lissoceratidae Douvillé, 1885⁽¹¹⁾ [Bajoc., Laeviuscula Z. – M. Oxford., Transversarium Z.]

Family Haploceratidae Zittel, 1884 [Kimm., Beckeri Z. – Hauteriv.]

Notes on the Haplocerataceae

(1) The earliest known form is from the Bradfordensis Zone of the Aalenian, i.e. a little earlier than the first known *Bradfordia*, from which it differs in many respects. Hence a presumed independent derivative of some Hammatoceratid. Descendants are now known to occur, if rarely, up to the Upper Bathonian, and include *Amm. dorsocavatus* Quenstedt and the genera *Strungia* Arkell and *Vastites* Arkell.

(2) *Hebetoxyites hebes* is difficult to place. The holotype (only specimen not in doubt) from the Laeviuscula Zone resembles *Strigoceras* in general form and sculpture, but lacks strigations and, apparently, the hollow floored keel carrying the siphuncle in *Strigoceras*: *teste* Buckman himself, Westermann, 1969 and H. S. Torrens. Other specimens like it are *H. clypeus* Buckman (paratype only, 1924, pl. 496B), basal Sauzei Zone; *H. incongruens* Buckman (holotype, pl. 497), same horizon. Until the importance of a floored hollow keel can be further assessed, *Hebetoxyites* is here placed in the Strigoceratidae and not in the otherwise morphologically similar Oppeliidae.

(3) As *Phlycticeras* seems to be the direct and only descendent of *Strigoceras*, there is no need to retain Phlycticeratinae as a separate subfamily. The suggestion (C. Mangold) that *Oecoptychius* is the microconch of *Phlycticeras* would solve what has long been a baffling problem, in a way that seems satisfactory in all respects, morphological and stratigraphical, and certainly much more so than previous suggestions. After its sojourn in the Stephoceratidae, Reineckeidae, Morphoceratidae, Macrocephalitidae and Cadoceratidae, Schindewolf (1965, p. 185) brought it to rest in the Tutilitidae on the strength of its early sutural ontogeny. The earliest sutures of *Phlycticeras* and *Oecoptychius* illustrated by Schindewolf (1964, fig. 238 and 1965, fig. 270, respectively) show considerable differences, but it is not stated whether either are the primary sutures and fig. 238a suggests strongly that it is not. But the first incized sutures illustrated (238c and 270e) are almost identical.

(4) First appearance as *Bradfordia liomphala* Buckman (= *costata*, *inclusa* Buckman, 1910 and *etheridgii* Buckman, 1882?) in the Concavum Zone in Britain (new evidence), then extending up into *B. (Lokastelia)* of the Laeviuscula Zone or *B. (Amblyoxyites)* of the Sauzei Zone. There are plenty of forms intermediate to *Oppelia*, e.g. *Amblyoxyites amblys* (Laeviuscula Zone), "*Oppelia*" *praeradiata* Douvillé, *Praeoppelia oppeliiformis* Westermann, but so far none to bridge the gap to the first *Lissoceras semicostulosum* from the Laeviuscula Zone. Moreover, the microconchs of *Bradfordia* have not yet been identified. For these reasons *Bradfordia* is here placed in the Oppeliidae rather than the Lissoceratidae, but kept as a separate subfamily for the time being.

(5) The first member, *Thamboceras* Douvillé, 1916, is dated indirectly via *Ermoceras* in

Algeria to the Subfurcatum Zone of the Upper Bajocian, and an independent derivation directly from *Bradfordia* rather than via *Oppelia* cannot be ruled out.

(6) The genus *Glochiceras* has been used as a receptacle for what are probably merely the microconchs of almost all the Oxfordian and Kimmeridgian Haplocerataceae, having the common features of being small, almost smooth and lapped. Basing a family group name on such a genus therefore creates considerable difficulties, the resolution of which must depend on a subjective judgment of probable dimorphic affinities. The type species *G. nimbatum* (Oppel) occurs in the Lower Kimmeridgian and could be paired with either *Ochetoceras* (Ochetoceratinae Spath, 1928) or *Taramelliceras* (Taramelliceratinae Spath, 1925). What morphological evidence there is appears to favour slightly the former (Ziegler, *in litt.*), and Ochetoceratinae are therefore taken as synonymous with Glochiceratinae.

(7) *Mazapilites* resembles *Taramelliceras kiderleni* Berck. and Hölder from the White Jura so strongly that it can be safely incorporated into *Taramelliceras*. The only other genus included in Mazapilitinae by Arkell is under a stratigraphical cloud. *Submazapilites* Cantu, 1963 differs little from *Mazapilites*.

(8) Includes *Neochetoceras* which regains a lateral groove (*teste* Zeiss, 1968) and strongly resembles *Ochetoceras*.

(9) Descended from Streblitinae, presumably.

(10) Following Casey (1961).

(11) Some doubt must continue to attach to the position of the genus *Neolissoceras*. It is conventionally placed in the Haploceratidae, but its morphology and suture line resemble much more closely those of *Lissoceras* itself. The argument against direct derivation from this genus has always been the large stratigraphical gap, between M. Oxfordian and L. Tithonian, but a similar former gap between *Lissoceras* and *Lissoceratoides* has since also been filled. Should *Neolissoceras* and *Lissoceras* turn out to be directly related, the Lissoceratidae would range into the Hauterivian.

Superfamily Stephanocerataceae Neumayr, 1875

Family Stephanoceratidae Neumayr, 1875⁽¹⁾

[= Stepheoceratidae Buckman, 1898 (obj.).]

Subfamily Stephanoceratinae Neumayr, 1875 [Aalen., Concavum Z. — U. Bajoc.]

[⊃ Stematoceratinae Mascke, 1907] [⊃ Normannitinae Westermann, 1954].

Subfamily Cadomitinae Westermann, 1956 [L. Bajoc., Humphriesianum Z. — U. Bathon., Aspidoides Z.]

Subfamily Garantianinae Wetzels, 1937⁽²⁾ [U. Bajoc., Subfurcatum — Garantiana Z.]

Family Kosmocerotidae Haug, 1887⁽³⁾

Subfamily Gowericeratinae Buckman, 1926 [Boreal U. Bathon., Cranoccephaloides Z. — L. Callov., Calloviense Z.]

[= Keppleritinae Tintant, 1963].

Subfamily Kosmocerotinae Haug, 1887⁽⁴⁾ [L. Callov., Calloviense Z. — U. Callov., Lamberti Z.]

[⊃ Gulicmiceratinae Buckman, 1926].

- Family Otoitidae Mascke, 1907⁽⁵⁾ [Aalen., Murchisonae Z. – Bajoc., Humphriesianum Z. ?]
- Family Sphaeroceratidae Buckman, 1920⁽⁶⁾
- Subfamily Sphaeroceratinae Buckman, 1920 [Bajoc., Laeviuscula – Garantiana Z.]
- Subfamily Eurycephalitinae Thierry, 1976⁽⁷⁾ [U. Bajoc. – M. Callov. ?]
- Subfamily Macrocephalitinae Salfeld, 1921⁽⁸⁾ [L. – M. Callov., Macrocephalus – Jason Z., Medea Subz. in Europe]
- Subfamily Eucycloceratinae Spath, 1928⁽⁹⁾ [M. Callov.]
- Subfamily Mayaitinae Spath, 1928⁽¹⁰⁾ [L. Oxford. – L. Kimm. ?]
- Family Cardioceratidae Siemiradzki, 1891⁽¹¹⁾
- Subfamily Arctocephalitinae Meledina, 1968⁽¹²⁾ [Boreal Bathon. – U. Callov., Athleta Z.]
- Subfamily Cadoceratinae Hyatt, 1900⁽¹³⁾ [Boreal U. Bathon., Variabile Z. – L. Oxford., Mariae Z.]
- Subfamily Cardioceratinae Siemiradzki, 1891⁽¹⁴⁾ [U. Callov., Athleta Z. – Kimm., Autissiodorensis Z.]
- [⊃ Quenstedtoceratinae Meledina, 1977].

Notes on the Stephanocerataceae

(1) What appears to be at present the oldest known true *Stephanoceras* came from the Bradfordensis Zone, Gigantea Subzone of the top of the Aalenian (new evidence, Dorset). Its resemblance to *Erycites* of the group of *E. fallifax* from the Opalinum Zone is so close that direct descent can hardly be in doubt. The dividing line between the Hammatoceratinae and Stephanoceratidae is therefore arbitrary. The derivation of *Stephanoceras* from *Erycites* is, however, by branching rather than direct succession and replacement, for *Erycites* survived itself independently at least into the Bradfordensis Zone.

(2) On balance, *Garantiana* [M]/*Strenoceras* – *Pseudogarantiana* [m] resemble Stephanoceratidae (*Cadomites*/*Normannites*) more than early Perisphinctidae: coronate nuclei, short body chambers and the forms of the adult peristomes. See also the intermediate forms described by Pavia (1973). The ventral smooth band is here, as so commonly elsewhere, probably of little phylogenetic significance. In contrast, *Parkinsonia* is always evolute with long body chambers and resembles most strongly *Caumontisphinctes*, including even the ventrolateral tubercles. Hence *Garantiana* and *Parkinsonia* are not regarded here as simply linearly related. The origin of *Caumontisphinctes* is itself, of course, in some doubt; it probably arose from some slightly earlier Stephanoceratid, in line or in parallel with *Parabigotites* Imlay?

Could this subfamily also be used as a vehicle for *Ermoceras* Douvillé and *Arkelloceras* Frebald?

(3) What seem to be the earliest members appear sharply and abundantly in Greenland some six subzones below the base of the Callovian. They are still round-whorled and bear a striking resemblance in both dimorphs to typical *Cadomites* [M]/*Polyplectites* [m] of the Middle Bathonian. Derivation from Macrocephalitinae, as often previously postulated, is thus ruled out.

(4) The two subfamilies Gowericeratinae and Kosmocerotinae are retained on grounds only of convention and convenience and could probably be merged. The dividing line is usually

based on the presence of ventrolateral tubercles bordering a smooth tabulate venter in adult *Kosmoceras*, but a line based on this single proterogenetic character alone would create systematic difficulties arising from dimorphism: the microconchs have the Kosmoceratid form several zones earlier than the macroconchs, even at comparable diameters of the phragmacone.

(5) The group of *Abbasites* – *Docidoceras* – *Emileia*, the microconchs (*Trilobiticeras*, *Otoites*) with prominent lappets. The oldest-known firmly dated members are from the Murchisonae Zone (Dorset), low in the Aalenian. The genus *Docidoceras* (type *D. cylindroides* from the basal Bajocian, Discites Zone) has in the past been used to cover members of both Otoitidae (*D. cylindroides*) and Stephanoceratinae (“*D.*” *perfectum* Buckman, = *longalvum* (Vacek) ?), but at this level the two groups are already quite distinct. The latest members are probably to be found in the Pacific, e.g. *Zemistephanus?* persisting there into the Humphriesianum Zone.

(6) Gradual differentiation from the Otoitidae in the Laeviuscula Zone, via intermediates such as *Frogdenites* and *Labyrinthoceras*. The most significant changes are the loss of lappets in the macroconchs, the reduction of the dimorphic size ratio and the development of deep terminal constrictions, features revealingly retained in the descendants. Pandemic in Pacific and Tethyan Realms (including adjacent epicontinental provinces), but not found in the Boreal Province proper.

(7) An exclusively Pacific group including the forms for many years recorded from the Andes, peri-Pacific Mexico (Oaxaca) and Indonesia (in part) as *Macrocephalites*; from the Western Interior of the US and Canada, southern Alaska and the Bureya Basin of eastern Siberia as *Cranoccephalites*, *Arctoccephalites*, *Kheraicerases* or *Cadoceras* (in part, group of *muelleri/shoshonense* Imlay). The earliest member may be *Megasphaeroceras* Imlay from about the Subfurcatum Zone of the Upper Bajocian, the latest *Lilloetia* from the ?Middle Callovian. All are united by the tell-tale terminal constrictions not found in *Macrocephalites*, particularly in the macroconchs, and the variocostation of the microconchs characteristic of *Xenoccephalites*, also different from the microconchs of *Macrocephalites*. They span the Bathonian probably continuously (see, for example, Hillebrandt, 1970, for a summary of the faunas, including such undoubted Bathonian elements as *Epistrenoceras*); this stage was previously always regarded as missing in America because of misidentification of the Eurycephalitids as *Macrocephalites* and hence their assignment to the Callovian. Detailed successions remain to be worked out, and several faunal subprovinces will probably become evident, such as one for the extensive epicontinental shelf-sea deposits of Montana and Wyoming.

The Eurycephalitinae almost certainly did include the ancestors of the Macrocephalitinae, however, and the classification into subfamilies and families is therefore arbitrary. Eurycephalitinae as a subfamily of an enlarged family Macrocephalitidae might be equally acceptable (see however note 10).

(8) The sudden appearance more or less simultaneously throughout the Tethys and its borders, from the Pamirs via the Caucasus through Europe (but not to Cuba nor Caribbean Mexico) to N. and E. Africa, Gondwanan India and Sub-Austral Indonesia, marking the base of the Callovian, probably reflects merely a westwards migration from the Pacific Realm in which the ancestral Eurycephalitinae provide the link throughout the Bathonian to the Sphaeroceratinae. Resemblance to *Morrisiceras*, conventionally regarded as the ancestor, is homoeomorphic in the macroconchs only (see sub Tultitidae, Perisphinctaceae).

(9) Sub-Austral Indo-Malgach descendents of *Macrocephalites* into the Middle Callovian, questionably worth retaining as a separate subfamily.

(10) The position of this group has long been puzzling. It is confined to the southern borders of the Tethys and Pacific – Kenya, Madagascar, Cutch, the Himalayas, Sub-Austral Indonesia and now the southern Andes (Stipanovic *et al.*, 1975) – where it can be abundant. Sometimes it is accompanied by other elements but elsewhere it occurs alone and thus makes a characteristic Sub-Austral fauna. Where it occurs together with other groups allowing it to be dated independently, the age appears always to be Oxfordian, ranging from Cordatum to about Bimammatum Zones, but the total range including the beds in which it occurs alone may be rather greater. Even so, no *Mayaites* older than Cordatum Zone seems to be known.

Morphologically the group is notoriously homoeomorphic with the Macrocephalitinae, not only in some species but over the whole range of forms, and in both dimorphs: every Macrocephalitinid has an almost indistinguishable Mayaitinid double. The natural conclusion, to regard the Mayaitinae as descended directly from the Macrocephalitinae, was put in question only by the large stratigraphical gap, for the earliest *Mayaites* resemble most closely the earlier *Macrocephalites* of the Lower Callovian, not the latest Eucycloceratinae of the Middle Callovian: these, in turn, find their closest homoeomorphs among the later Mayaitinae of the Middle–Upper Oxfordian. An alternative, stratigraphically more acceptable connection was therefore preferred in the past, deriving the Mayaitinae from the Perisphinctacean Pachyceratidae. These are also morphologically similar, bridge the stratigraphical gap and are known to have migrated into the Sub-Austral Province in the Upper Callovian. A recent study of the ontogeny of the septal sutures (Thierry, 1975) seems to resolve the issue, however, The sutures of *Mayaites* follow those of *Macrocephalites* in every detail, including quite clearly the presence of umbilical element U_n characteristic of the Stephanocerataceae. They differ significantly from those of *Pachyceras* of the Upper Callovian, in which U_n is absent.

Systematically, therefore, the connection between Mayaitinae and Macrocephalitinae seems inescapable despite the stratigraphical gap. Such gaps are perhaps to be expected in the records of ammonite groups that evolved in the Pacific, an area in which so much Jurassic history has undoubtedly been permanently lost through subsequent tectonic events. The Mayaitinae are here given similar status to the Macrocephalitinae as a subfamily of Sphaeroceratidae, for the alternative, the separation of Macrocephalitidae as a full family, does not seem justified on grounds of either morphological or phyletic diversity.

(11) Continuous succession from the first member appearing abruptly throughout the circum-Arctic Boreal Province, *Cranocephalites borealis* Spath of the basal Boreal Bathonian (equivalent probably to a level in the Upper Bajocian), to the last *Amoeboceras* at the top of the Sub-Boreal Kimmeridgian. The first member bears such a strong resemblance, again in both dimorphs, to *Sphaeroceras* of the Humphriesianum Zone, particularly the North American form *S. (Defonticeras)*, that derivation from the Sphaeroceratinae seems assured.

(12) Strictly Boreal. Forms referred to *Cranocephalites* or *Arctocepalites* in S. Alaska, British Columbia, Alberta, Montana and Wyoming may be Eurycephalitinid homoeomorphs. The subfamily persisted into the Callovian after the Cadoceratinae split off in the upper Boreal Bathonian, as *Chamousettia*; last known member is *Ch. galdrynus* of the Athleta Zone.

(13) Includes all forms with the sharp umbilical edge to a crater-like umbilicus characteristic of adult *Cadoceras*, and hence *Longaeviceras* which persisted after *Quenstedtoceras* of the Cardioceratinae split off in the Athleta Zone. Latest known member is *L. staffinense* Sykes from the L. Oxfordian, Mariae Zone, Scarborough Subzone of Scotland.

(14) The earliest forms may be a fauna described as *Eboraciceras subordinarium* by Meledina (1977) from northern Siberia, probably still in the upper Athleta Zone, and intermediate

morphologically between ancestral *Longaeviceras* and the *Quenstedtoceras* proper that suddenly flooded southwards in Europe and Russia as far as trans-Caspian Mangyshlak in enormous numbers at the base of the Lamberti Zone – another example of differentiation by division at family group level associated with a major faunal migration.

The last members of the subfamily, *Nannocardioceras*, are remarkable for their minute size and dimorphism which has become so inconspicuous as so far to have evaded detection.

Superfamily Perisphinctaceae Steinmann, 1890

Family Perisphinctidae Steinmann, 1890

Subfamily Leptosphinctinae Arkell, 1950 [U. Bajoc., Subfurcatum Z., Banksi Subz. – Parkinsoni Z.]

[⊃ Bigotitinae Westermann, 1956].

Subfamily Parkinsoniinae Buckman, 1920⁽¹⁾ [U. Bajoc., Garantiana Z., Arcris Subz. – L. Bathon., Zigzag Z.]

[⊃ Pseudocosmoceratinae Sazonov, 1960⁽²⁾?]

Subfamily Zigzagiceratinae Schindewolf, 1925 [L. – M. Bathon.]

[⊃ Siemiradzkiinae Westermann, 1958⁽³⁾]

Subfamily Pseudoperisphinctinae Schindewolf, 1925⁽⁴⁾ [U. Bathon. – L. Oxford., Cordatum Z.]

[⊃ Grossouvriinae Spath, 1930].

Subfamily Proplanulitinae Buckman, 1921⁽⁵⁾ [L. – M. Callov.]

Subfamily Perisphinctinae Steinmann, 1890⁽⁶⁾ [U. Callov., Lamberti Z. – Kimm.]

Subfamily Epipeltoceratinae nov.⁽⁷⁾ [M. – U. Oxford.]

Subfamily Idoceratinae Spath, 1924⁽⁸⁾ [U. Oxford. – Kimm.]

Family Morphoceratidae Hyatt, 1900⁽⁹⁾ [U. Bajoc., Garantiana Z., Acris Subz. – L. Bathon., Zigzag. Z.]

[⊃ Berbericeratidae Westermann, 1956].

Family Tulitidae Buckman, 1921⁽¹⁰⁾ [M. Bathon. – U. Callov.]

[⊃ Morrisiceratidae Westermann, 1956⁽¹¹⁾].

Family Reineckeidae Hyatt, 1900⁽¹²⁾ [Callov.]

Family Pachyceratidae Buckman, 1918⁽¹³⁾ [M. Callov. – M. Oxford.]

[⊃ Erymnocheratidae Breistroffer, 1947].

Family Aspidoceratidae Zittel, 1895⁽¹⁴⁾

Subfamily Peltoceratinae Spath, 1924⁽¹⁵⁾ [U. Callov. – U. Oxford., Bifurcatus Z.]

Subfamily Aspidoceratinae Zittel, 1895⁽¹⁶⁾ [U. Callov. – U. Tithon.]

[⊃ Physodoceratinae Schindewolf, 1925] [⊃ Euaspidoceratinae Spath, 1931].

Subfamily Hybonoticeratinae nov.⁽¹⁷⁾ [U. Oxford – L. Tithon.]

Family Aulacostephanidae Spath, 1924⁽¹⁸⁾ [U. Oxford. – L. Tithon.]

[⊃ Pictoniidae Spath, 1924] [⊃ Raseniidae Schindewolf, 1925]

[⊃ Involuticeratidae Sazonov, 1960] [⊃ Ilovaiskioceratidae Sazonov, 1960].

Family Simoceratidae Spath, 1924⁽¹⁹⁾ [U. Tithon.]

Family Himalayitidae Spath, 1925⁽²⁰⁾ [M. Tithon. – Berrias.]

- Family Olcostephanidae Pavlow, 1892
 Subfamily Spiticeratinae Spath, 1924 [U. Tithon. – Berrias.]
 [⊃ Provalanginitinae Fatmi, 1972⁽²¹⁾ ?].
 Subfamily Olcostephaninae Pavlow, 1892 [Valang. – Hauteriv.]
 [⊃ Taraisitinae Cantu, 1966 ?].
- Family Ataxioceratidae Buckman, 1921⁽²²⁾
 Subfamily Ataxioceratinae Buckman, 1921 [Kimm.]
 Subfamily Lithacoceratinae Zeiss, 1968 [Tithon.]
 [⊃ Sublithacoceratinae Zeiss, 1968⁽²³⁾] [⊃ Franconitinae Zeiss, 1968⁽²³⁾] [⊃ Richterellinae Sapunov, 1977⁽²⁴⁾ ?] [⊃ Pseudosubplanitinae Nikolov and Sapunov, 1977 ?].
 Subfamily Virgatosphinctinae Spath, 1923⁽²⁵⁾ [M. – U. Tithon.]
 [⊃ Grayiceratinae Spath, 1925 ?].
- Family Neocomitidae Salfeld, 1921⁽²⁶⁾
 Subfamily Berriassellinae Spath, 1922 [U. Tithon. – Berrias.]
 [⊃ Paraboliceratinae Spath, 1928]
 Subfamily Neocomitinae Salfeld, 1921 [Berrias. – Hauteriv.]
 [⊃ Endemoceratinae Schindewolf, 1966] [⊃ Leopoldiinae Thieuloy, 1971].
- Family Oosterellidae Breistroffer, 1940 [U. Valang. – Hauteriv.]
- Family Virgatitidae Spath, 1923⁽²⁷⁾
 Subfamily Ilowaiskyinae Zeiss, 1968⁽²³⁾ [L. Volgian]
 Subfamily Pseudovirgatitinae Spath, 1924 [M. Volg./M. Tithon.]
 Subfamily Virgatitinae Spath, 1923 [M. Volg.]
- Family Dorsoplanitidae Arkell, 1950⁽²⁸⁾ (1925)
 [= Polytosphinctidae Schindewolf, 1925 (obj.)].
 Subfamily Pectinatitinae Zeiss, 1968⁽²³⁾ [L. – M. Volg.]
 Subfamily Pavloviinae Spath, 1931⁽²⁹⁾ [M. Volg. – Ryazan ?]
 Subfamily Dorsoplanitinae Arkell, 1950⁽³⁰⁾ (1925) [M. – U. Volg.]
- Family Polyptychitidae Spath, 1924⁽³¹⁾
 Subfamily Craspeditinae Spath, 1924 [U. Volg. – Ryazan.]
 Subfamily Garniericeratinae Spath, 1952 [Ryazan.]
 Subfamily Platylenticeratinae Casey, 1973⁽³²⁾ [L. – M. Valang.]
 Subfamily Tolloiinae Spath, 1952 [Ryazan. – M. Valang.]
 [⊃ Suritinae Sazanova, 1971]. [⊃ Menjaitinae Sazanova, 1971].
 Subfamily Polyptychitinae Spath, 1924⁽³³⁾ [M. – U. Valang.]
 Subfamily Simbirskitinae Spath, 1924⁽³³⁾ [Boreal Hauteriv.]
- Family Holcodiscidae Spath, 1924⁽³⁴⁾ [L. Hauteriv. – U. Barrem.]

Notes on the Perisphinctaceae

(1) The origin of *Parkinsonia* presents problems. Conventionally it has been derived from *Garantiana*, the connection being deduced from the common ventral furrow. This character appears to be phylogenetically so labile, however, in the sense that it can be shown to have arisen independently on almost innumerable occasions, that conversely it cannot be regarded as a strong phylogenetic guide. The differences between *Parkinsonia* and *Garantiana* consistently exceed the similarities in, for example, the length of the adult body chamber

(2) 9/10 whorl and 6/10 whorl respectively), the form of the dimorphism and the evolutesness of the coiling, especially on inner whorls. The early septal suture led Schindewolf (1965, p. 476) also to conclude that the two groups are not linearly related and to attach *Parkinsonia* to the Stephanocerataceae. The strength of this argument is, however, weakened by his inability to come to any firm conclusions at all about the origin of *Garantiana*. As the derivation of the Perisphinctaceae from the Stephanocerataceae only a relatively short time before is not in dispute, perhaps a clear-cut distinction is not to be expected. The Parkinsoniinae are therefore regarded here as Perisphinctids, perhaps derived from a common ancestor close to *Caumontisphinctes* (*Infraparkinsonia*). They are thus relatively short-lived, and do not deserve full family rank.

(2) Created for *Pseudocosmoceras* Mourashkin, 1930 and *Hemigarantia* Spath, 1928. Whatever the systematic position of the latter may be, it is certainly in no way related to the former. This leaves the nominate genus by itself. Its affinities and even its precise age are by no means clear: it seems to be a speciality of the Donets Basin. In view of this it seems of little value to retain it in a whole subfamily of its own.

(3) *Siemiradzka* Hyatt, 1900 = *Procerites* Siemiradzki, 1898 [m], shown by Sturani (1967) and Hahn (1969) to be closely related to *Zigzagiceras*; non *Pseudoperisphinctes* Schindewolf, 1923 here regarded as closer to *Choffatia* Siemiradzki, 1898, following Arkell (1959) and Hahn (1969). Hence Siemiradzkiinae are a synonym of Zigzagiceratinae rather than Pseudoperisphinctinae. Separation of these two subfamilies is not sharp and may well be arbitrary.

(4) *Nomen conservandum* under Art. 40 even if the genus *Pseudoperisphinctes* is regarded as junior subjective synonym of *Choffatia*.

(5) For the groups of *Proplanulites* (L. Callov., Sub-Boreal) and *Obtusicosites* (M. Callov., Sub-Austral) as previously, although they are probably not closely related.

(6) Smooth derivation from Grossouvriinae, which continue well into the L. Oxfordian; first member *Alligaticeras* in the Lamberti Zone of the U. Callovian. Precise choice of the last members not very clear, but *Perisphinctes*-like forms (*Orthosphinctes*) continue to at least the base of the Tithonian.

(7) A rather well-defined side branch in the Oxfordian, starting probably already with *Klematosphinctes* Buckman in the upper Mariae Zone, a typical grossouvirid microconch, and continuing through *Mirosphinctes* of the M. Oxfordian into *Epipeltoceras bimammatum*. The dimorphism in the higher members is however not clear: all the known forms from the Bimammatum Zone appear to be microconchs only.

(8) Branching off the main stem of the Sub-Boreal/Submediterranean Perisphinctinae in the basal Upper Oxfordian, Bifurcatus Zone, via *Passendorferia* Brochwicz-Lewinski, 1973 as intermediate, i.e. before the advent of virgatotome ribbing in the Ataxioceratidae, this group rose very much as a Tethyan entity via *Subnebrodites* (type species *S. planula*, olim *Idoceras* auctt.) and *Nebrodités* at least as far as *Mesosimoceras*, with tabulate smooth venter, just below the base of the Tithonian. The choice of nominate genus for the group is largely historically determined and, as so often in such cases, somewhat unfortunate; for the type species, *Idoceras balderum* (through subsequent designation by Spath, 1925, non Roman, 1938) from the Kimmeridgian, White Jura γ , is of uncertain affinities and at best atypical of the group as a whole.

(9) Cryptogenic appearance as fully-fledged *Dimorphinites* in the (top) Acris Subzone of the Garantiana Zone. Origin in Stephanoceratidae cannot be altogether ruled out.

(10) The Perisphinctid connections of this group are revealed by *i.a.* the form of the

dimorphism: the microconchs are small lappeted serpenticones (*Trolliceras* Torrens, 1971, olim *Krumbeckia* Arkell, 1951, non Diener, 1915). Forms like *Rugiferites* bridge the gap between *Tulites* and *Zigzagiceratinae*. Youngest member recorded by Hahn (1971, pl. 7, fig. 4) from the U. Callovian, *Athleta* Zone of S. Germany.

(11) Macroconchs of *Morrisiceras* resemble *Macrocephalites* on the one hand as much as *Tulites* on the other. Microconchs however are quite different: those of *Morrisiceras* are again small lappeted planulates (*Holzbergia* Torrens, 1971, olim *Berbericeras* Arkell, non Roman).

(12) The precise origins of this group are not clear. In the Tethys and its margins, *Reineckeia* appears everywhere fully formed in the Lower Callovian. In the Andes it is preceded by the genus *Neuqueniceras* whose outer whorls are exactly as in *Reineckeia* but whose inner whorls are non-tuberculate, constricted and *Perisphinctes*-like. If the ancestors of *Reineckeia*, the evolution of the Reineckeidae from the Perisphinctidae would have been in the opposite sense of the proterogenesis observed almost invariably elsewhere in the evolution of the Perisphinctaceae and Stephanocerataceae.

(13) The first members, *Erymnoceras* [M]/*Rollierites* [m] appear suddenly in the Sub-Boreal M. Callovian, derivable with no great difficulty from some Pseudoperisphinctid like *Subgrossowria*, and led through *Pachyceras* of the U. Callovian into *Tornquistes* [M]/*Protophites* [m] (?) of the L. — M. Oxfordian in the northern hemisphere. In the U. Callovian the group spread south and colonized also the Ethiopian and Sub-Austral Indo-Malgach Provinces; and the microconchs shed their lappets. The youngest forms include homoemorphs of *Bullatimorphites* (Tulitidae).

(14) The family continues to be used to cover two major long-ranging and only slowly changing phyletic branches, the Peltoceratinae and Aspidoceratinae, whose members share the characteristic feature of having one or two rows of strong tubercles at the edges of more or less quadrate flat-ventered whorl sections in the outer whorls of the macroconchs, a style of ribbing seen here again for the first time since its appearance in the Eoderoceratidae of the Lower Lias. Yet in many other respects these two groups differ profoundly. The Peltoceratinae always have extremely evolute inner whorls with dense, strong and largely simple ribbing, modifying dramatically in the highly variocostate macroconchs but staying almost unchanged in the microconchs, which bear long lappets. This morphology can be seen to evolve slowly and smoothly by the usual proterogenetic path from some Sub-Boreal Pseudoperisphinctinae in the Middle Callovian in the northern hemisphere. The group then spreads to become endemic in the whole of the Tethyan Realm and its borders in the Upper Callovian, and in the Pacific in the Lower Oxfordian. The Aspidoceratinae, in contrast, always have fairly involute inner whorls with only feeble ornamentation, in the earliest forms in the Upper Callovian most strongly resembling inner whorls of *Grossowria*, including parabolic nodes. Dimorphism is inconspicuous as the macroconchs modify little during growth, and lappets in the microconchs are so far unknown. The Aspidoceratinae have presumably been derived from the Peltoceratinae, but precisely how and when remains hidden. The branching may have occurred in association with the southerly migration in the *Athleta* Zone, for the Indo-Malgach faunas contain forms that may have been intermediate (*Metapeltoceras*). The Aspidoceratinae are also famous for their strongly calcified laevapytychi in the Kimmeridgian and Tithonian.

(15) Two branches in the early stages: one with the rursiradiate ribbing characteristic of *Peltoceras* but remaining essentially Perisphinctid in style — *Binatisphinctes* and *Pseudopeltoceras* of the Upper Callovian; and the other, starting with *Peltoceras* and going into *Gregoryceras*, the last member in the Upper Oxfordian, *Bifurcatus* Zone.

(16) Morphological evolution from evolute quadrate to involute round-whorled forms and

vice versa, with double or single rows of tubercles, external or internal, seems to have occurred repeatedly without any major phylogenetic branching; further subdivision of the subfamily therefore seems unnecessary.

The suggestion has been repeatedly made that the microconch of at least the later Aspidoceratinae may have been the elusive *Sutneria*, for the stratigraphical and geographical ranges of the two groups almost coincide. On the other hand, at least the Kimmeridgian forms of *Aspidoceras* seem already to have perfectly acceptable microconchs, resembling their macroconchs much more so than do *Sutneria*. A Lower Tithonian species identified as *Sutneria apora* by Ziegler (1974) has, moreover, an aptychus quite different from that of *Aspidoceras*, whereas the abundant aptychi in the Eudoxus Zone of England suggest that their structures were the same in both dimorphs.

(17) *Clambites* – *Pseudowaagenia* partim – *Hybonoticerias*. Microconchs of *Hybonoticerias* have small lappets.

(18) Aulacostephanidae and Pictoniidae were published simultaneously but the former have a much wider distribution in space and time than the latter. Four branches seems to be discernible, with a common root in *Perisphinctes* (*Liosphinctes*) of the Middle Oxfordian. The additional available family names could be used to label them if desired. The oldest is essentially Sub-Boreal and consists of the line *Decipia* – *Ringsteadia* – *Pictonia* – *Rasenia* s.s., terminating in the Cymodoce Zone of the Kimmeridgian. The first side branch divided in the Upper Oxfordian and colonized a European/Submediterranean subprovince (Germany, France): *Pachypictonia* (group of *albinea*, *indicatoria*) – *Eurasenia/Prorasenia* (group of *Eu. trimera*, and including *Prorasenia* (“*Ilovaiskioceras*”) *stephanoides*) – *Gravesia*? in the Lower Tithonian. A second branch split off from *Rasenia* in the lower Cymodoce Zone, giving rise to the fine-ribbed faunas of the Mutabilis Zone and occupying a sub-province intermediate between Sub-Boreal and Submediterranean: *Rasenioides* (group of *striolaris*) – *Aulacostephanites/Aulacostephanoides/Involuticerias*. A third branch continued from *Rasenia* in the upper Cymodoce Zone and colonized the Boreal Province: *Zonovia uralensis*) – *Xenostephanus*, the latter a form with fully developed aulacostephanid ribbing occurring at levels in the Mutabilis Zone well below the first appearance of true *Aulacostephanus* in the Sub-Boreal Province. This leaves the position of *Aulacostephanus* proper. It appears suddenly in many parts of Europe, to replace the fine-ribbed forms of the second branch with a very sharp faunal break, suggesting a rapid southerly migration by this genus as direct descendant of *Xenostephanus*.

This involved picture may be of little importance in the classification of the ammonites as a whole, but is instructive as an indication of how complex and rapidly changing may be the patterns of provincial evolution and migration revealed in favourable case in which really detailed information is available.

(19) A highly diverse group of Tethyan forms confined to the Tithonian. The exact origins are not certain, but there are two contenders. One of them is *Virgatosisoceras*, leading back to some late member of the Perisphinctinae. The other is the Idoceratinae, suggested by the close homoeomorphism between some of their late members (*Mesosimosoceras rachystrophum*) and *Simoceras* of the group of *S. volanense*.

(20) As commonly interpreted, including *Micracanthoceras* [M]/*Aulacosphinctes* [m], *Djurjuricerias*, *Corongoceras*, *Protacanthodiscus* [M]/*Durangites* [m], with perhaps extensions into the Neocomian, including *Neocosmoceras* and *Neohoploceras*. Resemblance to Berraisellinae is confined to the ventral furrow or smooth band, but this is probably coincidental. Plausible ancestors seems to be in some late members of the Perisphinctidae or Ataxioceratidae such as *Parapallasiceras praecox* (Schneid), in some of which interruption of the ribbing on the venter already occurs.

(21) For *Provalanginites* Fatmi, 1972, as sole genus, from Tithonian of Pakistan. Systematic position wholly problematical, and stratigraphical position not beyond doubt.

(22) The main grounds on which this family is separated from the Perisphinctidae are discussed in the general introduction. They are based on the appearance of a new morphological character, the virgatotome style of ribbing and its variants, polygyrate, fascipartite etc. The family remains one of the most difficult to classify in greater detail, for it is not easy to tell whether a rapid succession of rather similar forms, e.g. *Ataxioceras*, *Virgatataxioceras*, *Lithacoceras*, *Sublithacoceras*, *Franconites* etc. are to be regarded as linearly related or as successive homocomorphic off-shoots from the main evolving stock, whatever and wherever that may have been. After an initial burst of Ataxioceratinae, all the subsequent Submediterranean virgatitids are therefore placed in one further subfamily. There are reasons to believe that *Pseudovirgatites* is more closely related to another group, and the Pseudovirgatitinae are therefore no longer included here.

(23) Introduced as "tribes" within Pseudovirgatitinae, i.e. as infrasubfamilial taxa. These are coordinate with other taxa in the family group (Arts 35–36) and require type genera, which were not here explicitly designated. They are however automatically fixed by etymology (Art. 63), and hence the names are fully available.

(24) *Amm. richteri* Oppel has in the past been ascribed to several genera, including *Kossmatia* and *Berriasella*. The exact position of these small forms remains uncertain.

(25) Following Enay (1972), restricted to the southern Submediterranean and Sub-Austral Indo-Malgach Provinces. Origins may plausibly be sought in the group of *Katrolliceras* – *Torquatisphinctes* of the Lower Tithonian, itself probably not simply directly related to the similar but older forms (*Crussolliceras*) found in Europe. Ultimate origin in the Ataxioceratinae revealed by the reappearance of virgatotome ribbing in *Virgatosphinctes* [M]/*Aulacosphinctoides* [m] itself.

(26) Despite much recent work, the classification of the Berriasellids is by common consent at present in a state of chaos. This is due mostly to excessive taxonomic splitting arising from *i.a.* a failure to take proper account of the variability of ammonite species and the presence of dimorphism. Pending revision, the taxa of the family group are here still probably largely arbitrary collections of genera of variable merit. Whatever the final arrangement, there can be little call for a separation of Berriasellinae and Neocomitinae at full family level, and the classification shown here reflects the discovery that the Neocomitinae have priority.

(27) A second major branch of virgatitids derived from Ataxioceratinae, colonizing mainly the Sub-Boreal Russian Platform (Kutek and Zeiss, 1974; Zeiss, 1977). Characterized by furcation points of the secondary ribbing very low on the whorl-side, often even at the umbilical edge.

(28) The third major branch of virgatitids derived from Ataxioceratinae, the root of almost all subsequent Volgian/Portlandian – Neocomian faunas of the Boreal and Sub-Boreal Provinces. Lappets were lost in the microconchs at the base of the Volgian and replaced for a time in the Pectinatinae by ventral horns.

Dorsoplanitidae take precedence from 1925 in accordance with Art. 40(a), Rec. 40A of the *Rules*.

(29) Branched off from *Pectinatites* and remained in the Sub-Boreal Province, flourishing particularly in the restricted area of the Anglo-Portlandian Basin and including all the giants of the Portlandian beds. Should it include *Riasanites*, which closely resembles *Pavlovia* (*Pallasiceras*) in almost all respects except the ventral furrow?

⁽³¹⁾ Also branched off from the Pectinatitinae at the base of the Middle Volgian to flourish in the circum-Arctic Boreal Province in its most restricted sense. Probably the root of the Craspeditidae, the dividing line being largely arbitrary, via forms like *Laugeites* and *Cheraspedites*.

⁽³²⁾ Associated with the differentiation of many separate small faunal provinces in rapidly shifting basins of deposition on wide epicontinental shelves, there arose a profusion of forms of amazing morphological diversity, ranging from sphaeroconic *Polyptychites* to oxyconic *Platylenticeras*, not once but repeatedly. Generic classification remains somewhat confused, in part for the same reasons as in the Neocomitidae.

⁽³²⁾ Placed by him into Neocomitidae. Derivation from Garniericeratinae not impossible.

⁽³³⁾ Formerly in Olcostephanidae. Much new connecting material, and once again the form of the dimorphism, leaves the close relation to the Boreal Craspeditinae in little doubt.

⁽³⁴⁾ *Teste* Wiedmann on the basis of sutural ontogeny.

Superfamily Spirocerataceae Hyatt, 1900

Family Spiroceratidae Hyatt, 1900

Subfamily Spiroceratinae Hyatt, 1900

Spiroceras Quenstedt, 1857 [(= *Apsorroceras* Hyatt, 1900) U. Bajoc., Subfurcatum Z., Baculata Sz. – L. Bathon., Zigzag Z.].

Subfamily Parapatoceratinae Buckman, 1926

Parapatoceras Spath, 1924 [(= *Metapatoceras* Schindewolf, 1963, subj.; *Infrapatoceras* Ocheterena, 1966 subj.) U. Bathon. – M. Callov., Jason Z.], *Paracuariceras* Schindewolf, 1963 [L. Callov., Macrocephalus Z. – M. Callov., Jason Z.], *Acuariceras* Spath, 1933 [M. Callov., Jason Z.], ? *Epistrenoceras* Bentz, 1928 (Nov.) [(= *Pseudostrenoceras* Spath, 1928 (Dec.) U. Bathon.], ? *Sulcohamites* Wetzel, 1937 [?L. Bath.].

(*Non* Arcuceratidae Arkell, 1950, for *Arcuceras* Potonié, 1929, as sole genus, based on a single specimen subsequently identified as a crinoid (Donovan and Hölder, 1958).)

(*Non* *Ancyloceras mosellense* Terquem, 1857, cited from Upper Lias of France: not an ammonite;

nec *Helicoceras alpinum* Thalmann, 1923, cited from Aalenian of the Swiss Alps: probably a *Tmetoceras* (*sic*);

nec *Ancyloceras ischeri* Favre, 1876, cited from Upper Oxfordian of the Swiss Alps: tectonically deformed Perisphinctacean.

These include the sole records of the group outside the firmly established range from U. Bajocian to M. Callovian: details given by Dietl (1978).)