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Cladistic analysis of the Middle Jurassic ammonite radiation

S. MOYNE & P. NEIGE*

Centre des Sciences de la Terre & UMR CNRS 5561 Biogéosciences, Université de Bourgogne, 6 bd Gabriel, F-21000 Dijon, France

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Abstract – Cladistic analysis of the Middle Jurassic ammonite radiation shows how the Aalenian-age ancestral stock, known variously as the Hammatocerataceae or Hammatoceratinae, gave rise to numerous new groups in Bajocian times. Cladistic analysis shows this ancestral stock is not a single lineage but two: the '*Erycites* group', which gave rise to the Stephanocerataceae, and the '*Hammatoceras* group', from which all other Bajocian groups derived.

Keywords: phylogeny, cladistics, ammonoids, Jurassic.

1. Introduction

Middle Jurassic ammonites underwent substantial faunal turnover at the very end of Aalenian times. This is invariably thought of as the radiation of a large clade whose earliest representatives appeared at the end of Early Jurassic times, during the Toarcian (e.g. Arkell, Kummel & Wright, 1957; Géczy, 1966; Donovan, Callomon & Howarth, 1981; Tintant & Mouterde, 1981; Page, 1996). This clade is variously attributed to different taxonomic levels: at the beginning of its history, during the Toarcian and Aalenian, it is named either Hammatocerataceae Schindewolf, 1964 (e.g. Rulleau, Elmi & Thévenard, 2001) or Hammatoceratinae Buckman, 1887 (e.g. Arkell, Kummel & Wright, 1957, or Donovan, Callomon & Howarth, 1981). To avoid any nomenclatural confusion we shall refer here to the hammatoceratins. This new fauna was initially rather limited in variety during the Toarcian; it then diversified during the Aalenian stage (see Neige, Elmi & Rulleau, 2001, for a morphological-based approach), and clearly radiated at the end of the Aalenian and at the Aalenian/Bajocian boundary. There, its representatives, which are assumed to be the direct descendants of the hammatoceratins, are classified into different taxa: Sonniniidae Buckman, 1892; Strigoceratidae Buckman, 1924; Haplocerataceae Zittel, 1884 (sometimes including the Strigoceratidae); and Stephanocerataceae Neumayr, 1875. The radiation occurred to the detriment of a root stock related to the Early Jurassic ammonite fauna generally named the Hildocerataceae Hyatt, 1867. The hammatoceratins and their direct descendants gave rise to all post-Aalenian Ammonitina (Donovan, Callomon & Howarth, 1981). These forms dominate at least the non-heteromorph component of (1) the Late Jurassic and (2) the Cretaceous ammonoid faunas (if Ancyloceratina are not include in the Ammonitina, but see Page, 1996, for an opposite view).

Transitions between Aalenian members of the hammatoceratins and their presumed descendants are very difficult to trace. There are various reasons for this: (1) relationships within the hammatoceratins root stock are still not clearly established; (2) members of the radiation display diverse morphologies featuring a complex mosaic of characters; and (3) the late Aalenian radiation occurred very rapidly with many new forms emerging in a brief span of time. The upshot is that although we are relatively familiar with the species and their stratigraphical positions, their groupings into genera and families are still controversial. Standard criteria on which to base phylogenetic relationships include shell morphology (tube geometry and ornamentation), suture line configuration, stratigraphical range and palaeogeographical distribution. Not all workers attribute the same significance to these criteria (although stratigraphical range is certainly the key criterion for most authors; see Rulleau, Elmi & Thévenard, 2001), and many conflicting phylogenetic reconstructions have been proposed, especially in the matter of the rooting of lineages (e.g. Donovan, Callomon & Howarth, 1981; Tintant & Mouterde, 1981; J. Sandoval, unpub. Ph.D. thesis, Univ. Granada, 1983; S. R. Fernandez Lopez, unpub. Ph.D. thesis, Univ. Complutense Madrid, 1985; Westermann, 1993). There are essentially two interpretations. The latest and most complete classification of the Jurassic Ammonitina (Donovan, Callomon & Howarth, 1981), followed in some recent works such as Wiedmann & Kullmann (1996), considers the hammatoceratins as a subfamily within the Phymatoceratidae Hyatt, 1867, which is itself included in the Hildocerataceae. For those authors, the hammatoceratins are a single lineage giving rise to all groups of post-Aalenian

* Author for correspondence: Pascal.Neige@u-bourgogne.fr

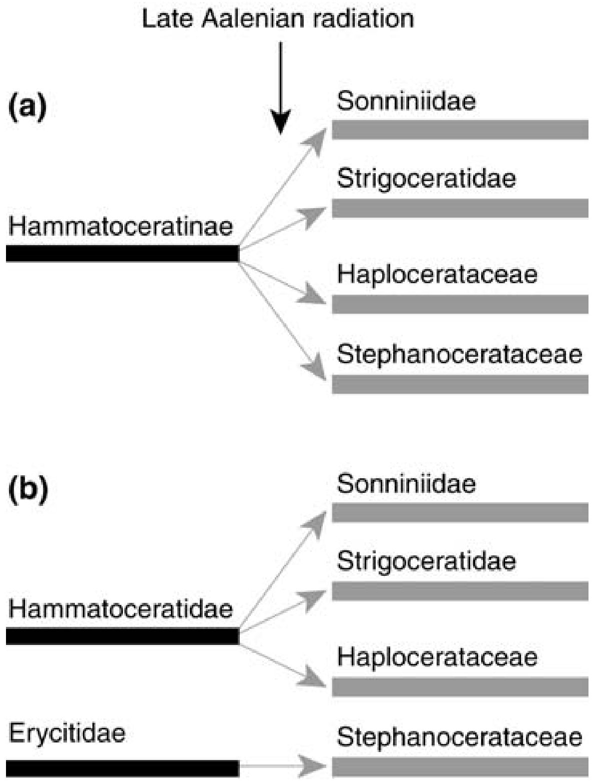

Figure 1. Phylogenetic relationships between the hammatoceratins (black bars) and their descendants (grey bars). (a) Single lineage hypothesis (e.g. Donovan, Callomon & Howarth, 1981): hammatoceratins are classified in a single group, named the Hammatoceratinae, and give rise to all Bajocian families. (b) Two-lineage hypothesis (e.g. Rulleau, Elmi & Thévenard, 2001): hammatoceratins are classified into two groups named the Hammatoceratidae and Erycitidae (both members of the Hammatocerataceae), and each of two families has descendants.

Ammonitina: Sonniniidae, Strigoceratidae, Haplocerataceae and Stephanocerataceae (Fig. 1a). Most authors agree with these relationships, albeit with some slight refinements; Sandoval (1986), for example, suggests the Haplocerataceae derived rather from the Graphoceratidae Buckman, 1905. The alternative interpretation has been proposed by several authors (e.g. Géczy, 1966; Westermann, 1993; Rulleau, Elmi & Thévenard, 2001) based on different taxonomic conceptions. The hammatoceratins are thought to be a superfamily, as suggested by Schindewolf (1964, 1965) and Tintant & Mouterde (1981), however, the main difference with the preceding classification is that the hammatoceratins may be divided into two separate lineages, following Westermann (1993). For Rulleau, Elmi & Thévenard (2001), these two lineages are the Hammatoceratidae Buckman, 1887 and the Erycitidae Spath, 1927, each of them with its own descendants: Sonniniidae, Strigoceratidae and Haplocerataceae for the former and Stephanocerataceae for the latter (Fig. 1b). It would be wrong to see the disagreement over these two phylogenetic hypotheses as evidence of a nomenclatural morass. Both interpretations lead to the conclusion that the hammatoceratins are not a clade (that is, not a monophyletic group), and the second hypothesis holds that the late Aalenian radiation proceeded from two different clades.

In contrast to the previous analyses of the hammatoceratins and their relatives, we propose here to establish a phylogenetic framework based solely on morphological characters (shell morphology, coiling and ornamentation) and character combinations interpreted in the context of a cladistic analysis. In this way we can establish hypotheses about phylogenetic relationships within a group, regardless of stratigraphical occurrences. Cladistic techniques have been applied to many fossil groups but ammonites remain largely understudied in this way. Only 11 studies of ammonite phylogeny have been published as part of a formal cladistic approach using parsimony (Landman, 1989; Landman, Dommergues & Marchand, 1991; Landman & Waage, 1993; Neige & Dommergues, 1995; Korn, 1997; Yacobucci, 1999; Monks, 1999, 2000, 2002; I. Rouget, unpub. Ph.D. thesis, Univ. Dijon; Rulleau, Bécaud & Neige, 2003), although some of them do not drastically contradict classical (that is, stratigraphical) interpretations of phylogeny. In the present study, we investigate the emergence of the hammatoceratins and their subsequent diversification (late Aalenian descendants) by focusing on several key genera. The study sample is drawn from an exhaustive analysis of bibliographical data supplemented by various specimens from our own field work.

2. Cladistic analysis

2.a. Ingroup taxa

Twelve genera belonging to the hammatoceratins and to their direct descendants were selected as key genera. This study should therefore be seen as a first step toward a complete reassessment of the Middle Jurassic ammonite phylogeny. Morphological characterization of these genera is based on an analysis of different species revealing the variability of the genus for the adult stage. Dimorphism is scarcely established for the ammonites under study. When suspected by some authors (as for *Riccardiceras*, *Docidoceras* and *Mollistephanus*), we have used macroconch shape in our analysis. Because the aim of the study is to establish phylogenetic relationships (1) within the hammatoceratins and (2) between hammatoceratins and their direct descendants (and not to establish relationships within each of the lineages emerging from the hammatoceratins), only the first genus to evolve in each presumed derived lineage of the hammatoceratins was selected: *Euhoploceras* Buckman, 1913 for Sonniniidae, *Praestrigites* Buckman, 1924 for Strigoceratidae, *Bradfordia* Buckman, 1910 for Haplocerataceae and *Riccardiceras* Westermann, 1995, *Docidoceras* Buckman, 1919 and *Mollistephanus* Buckman, 1922

Table 1. List of characters used for cladistic analysis; characters are not ordered

Number	Character	Character states
A	Coiling	(0) evolute; (1) intermediate; (2) involute
B	Relative whorl thickness (thickness/height)	(0) compressed; (1) intermediate; (2) depressed
C	Keel prominence	(0) none; (1) slight; (2) marked
D	Keel shape	(0) none; (1) rounded; (2) sharp
E	Demarcation of ventrolateral edge	(0) no; (1) yes
F	Flank shape	(0) flat; (1) arched
G	Demarcation of umbilical edge	(0) no; (1) yes
H	Orientation of umbilical edge	(0) receding; (1) perpendicular
I	Tubercles	(0) present; (1) absent
J	Primary ribs	(0) regular; (1) thickened
K	Ribs on umbilical edge	(0) non attenuated; (1) attenuated
L	Bifurcated ribs	(0) no; (1) yes
M	Rib shape	(0) radiate; (1) sinuous
N	Rib orientation	(0) projected; (1) radial
O	Ventral break in ribbing	(0) yes; (1) no
P	Hollow-floored keel	(0) yes; (1) no

for the Stephanocerataceae. For the hammatoceratins, the genera *Eudmetoceras* Buckman, 1920, *Csernyeiceras* Géczy, 1966 and *Abbasites* Buckman, 1921 were selected because they are the presumed ancestors of Bajocian groups. Note that for Rulleau, Elmi & Thévenard (2001), *Eudmetoceras* and *Csernyeiceras* belong to the Hammatoceratidae, whereas *Abbasites* belongs to the Erycitidae.

2.b. Outgroup taxa

Three genera were taken as outgroups. *Rarenodia* Venturi, 1975, which was considered by Donovan, Callomon & Howarth (1981) to be a synonym of *Phymatoceras* Hyatt, 1867, is now thought to be the first hammatoceratins genus (see Venturi, 1994; Rulleau, Elmi & Thévenard, 2001). *Hammatoceras* Hyatt, 1867 and *Erycites* Gemmellaro, 1886 represent the two lineages (respectively, Hammatoceratidae and Erycitidae) that are thought to occur within the Toarcian and Aalenian hammatoceratins root stock. The use of three outgroups will determine if ingroup taxa constitute a monophyletic group.

2.c. Characters

Various aspects of coiling and ornament are examined (Table 1). Most characters, qualitatively defined, have only two states (generally, present or absent) but some are multistate characters. These multistate characters are not ordered. No shape quantifications have been computed here, to avoid a mixture of qualitative and quantitative characters (thus needing a gap coding for some of them). Question marks indicate unknown character states. Autapomorphies have been removed from the matrix so that all characters are parsimony informative. Suture line characters are not used in this analysis because of their high variability between the different species of each genus. Moreover, using suture line characters for such different taxa would involve establishing clear homologies between the different sutural elements via an ontogenetic approach. The wide scope of the present study precludes this.

Table 2. Data matrix used for cladistic analysis

Characters	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
Taxa																
Rarenodia	0	0	1	2	0	1	0	0	0	0	0	0	0	1	0	?
Erycites	0	1	1	1	0	1	0	0	1	1	0	1	0	0	0	1
Abbasites	0	1	0	0	0	1	0	0	1	1	0	1	1	0	1	1
Riccardiceras	0	2	0	0	0	1	0	0	1	1	0	1	0	1	1	1
Docidoceras	1	2	0	0	0	1	0	0	1	1	0	1	0	1	1	1
Mollistephanus	0	1	0	0	0	1	0	0	0	1	0	1	0	1	1	1
Hammatoceras	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0
Euhoploceras	1	0	2	1	1	0	0	1	0	0	0	0	0	1	0	0
Eudmetoceras	1	0	2	2	1	0	1	1	0	1	0	1	0	1	0	0
Csernyeiceras	2	0	2	2	0	1	1	1	1	1	1	1	0	1	0	0
Praestrigites	2	0	2	1	0	0	1	1	1	0	1	1	1	1	0	0
Bradfordia	2	0	0	0	0	0	1	1	1	0	1	0	1	1	0	1

2.d. Method

PAUP 4 (Swofford, 1999) was used to construct the data matrix (Table 2) and perform the analysis. The heuristic option to find the most parsimonious trees was used here. However, because this procedure cannot guarantee that all of the most parsimonious trees will be found, the analysis was repeated many times. The process invariably yielded the same three most parsimonious trees (Fig. 2). Character state changes were established using the ACCTRAN (reversals preferred to convergences) option.

To synthesize the three most parsimonious trees, a strict consensus tree was computed (Fig. 3). Statistical tests were conducted to evaluate node robustness. The first of these was bootstrap resampling, which tests the robustness of the topology of the trees found (Felsenstein, 1985). Ten thousand replicates of randomly generated trees were compared. For each of them, characters were randomly sampled with replacement. The more often a branch occurs in bootstrap trees, the more robust it is. Bremer support was also performed (Bremer, 1988). This method consists of testing the number of extra steps needed to collapse a clade. The more steps needed to collapse a node, the more robust the node is.

3. Results

3.a. Tree description

The three most parsimonious trees are very similar and their general topologies are the same (Fig. 2).

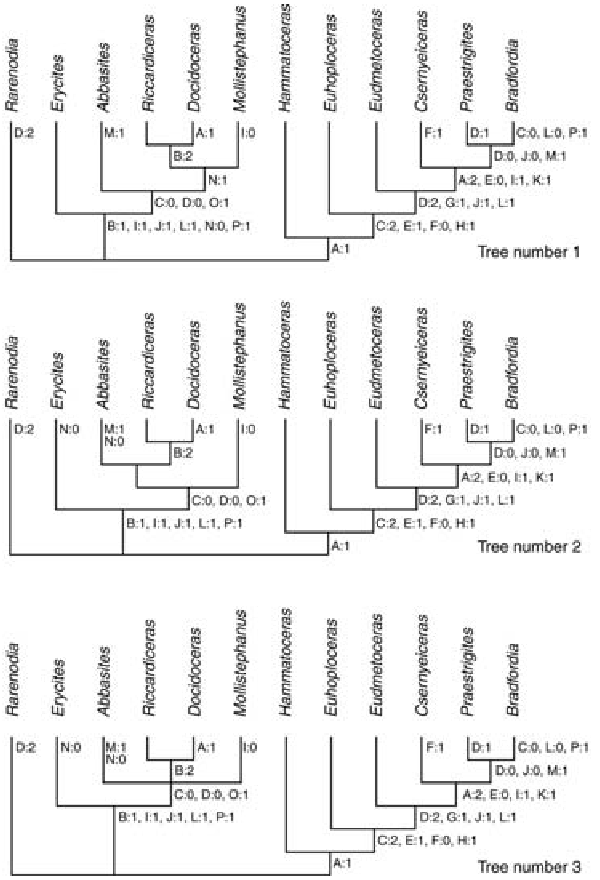

Figure 2. The three most parsimonious cladograms with character state changes labelled. These trees share the same overall topology except for the connection of *Abbasites*, *Riccardiceras*, *Docidoceras* and *Mollistephanus*.

They are 36 steps long. Consistency (ci), retention (ri) and rescale consistency (rc) indices have been calculated for individual characters and are identical for three most parsimonious trees (Table 3). They display an ensemble consistency index (CI) of 0.55 and an ensemble retention index (RI) of 0.69. Three sets (one monogenus and two monophyletic groups), rooting together as a basal polyphyletic topology are distinguished. The first is *Rarenodia* alone. The second is a set named here the '*Hammatoceras* group' clustering *Hammatoceras*, *Euhoploceras*, *Eudmetoceras*, *Csernyeiceras*, *Praestrigites* and *Bradfordia*. The topology within this set remains unchanged whichever most parsimonious tree is observed (Fig. 2). The third clade, named here the '*Erycites* group', is represented by *Erycites*, *Abbasites*, *Riccardiceras*, *Docidoceras* and *Mollistephanus*. Differences between the three most parsimonious trees occur within this last group: *Erycites* is always the rooting genus, but the topology between (1) *Abbasites*, (2) *Mollistephanus* and (3) *Riccardiceras* plus *Docidoceras* differs.

Although there is a very small number of most parsimonious trees and they are very similar, bootstrap

Table 3. Consistency, retention and rescale consistency indices (ci, ri, rc) for the characters used in this analysis; values are identical for the three most parsimonious cladograms

Character	ci	ri	rc
A	0.67	0.80	0.53
B	1.00	1.00	1.00
C	0.67	0.80	0.53
D	0.40	0.40	0.16
E	0.50	0.00	0.00
F	0.50	0.67	0.33
G	1.00	1.00	1.00
H	1.00	1.00	1.00
I	0.33	0.50	0.17
J	0.33	0.50	0.17
K	1.00	1.00	1.00
L	0.33	0.33	0.11
M	0.50	0.50	0.25
N	0.50	0.00	0.00
O	1.00	1.00	1.00
P	0.50	0.75	0.37

values and Bremer support values (Fig. 3) show that some nodes are not very robust. Only the '*Erycites* group' is well supported (bootstrap value 87 % and Bremer support 3). Other bootstrap values range from 54 % to 63 % and all other Bremer support values are 1.

3.b. Shell morphology

The distribution of characters on the cladograms, as exemplified by the ammonite drawings in Figure 3, shows that the different characters describing general shell morphology are more or less variable within each of the two monophyletic groups previously defined ('*Erycites* group' and '*Hammatoceras* group'), and between these two clades and *Rarenodia*. The latter has an evolute shell with slightly overlapping whorls. The whorl section of *Rarenodia* is very compressed and its coiling is platycone. The '*Erycites* group' displays a general morphology ranging from moderately evolute forms (*Erycites*) to very evolute ones (*Riccardiceras*). Shells of species in this group have a depressed whorl section. This is particularly marked for *Docidoceras*. The coiling of these ammonites may be platycone (*Mollistephanus*), serpenticone (*Riccardiceras*), or cadicone (*Docidoceras*). In the '*Hammatoceras* group', shell shape is highly variable, ranging from moderately evolute (*Euhoploceras*) to highly involute (*Bradfordia*). The whorl section of these genera is compressed and they display platycone (*Hammatoceras*) to oxycone (*Csernyeiceras*) coiling.

3.c. Ornamentation

Shell ornamentation is highly diversified among taxa in this study. Most of the ammonites studied have ribs, tubercles, keels and other ornaments. *Rarenodia* has tubercles on its latero-umbilical flanks. These tubercles are more or less connected with the primary ribs. The

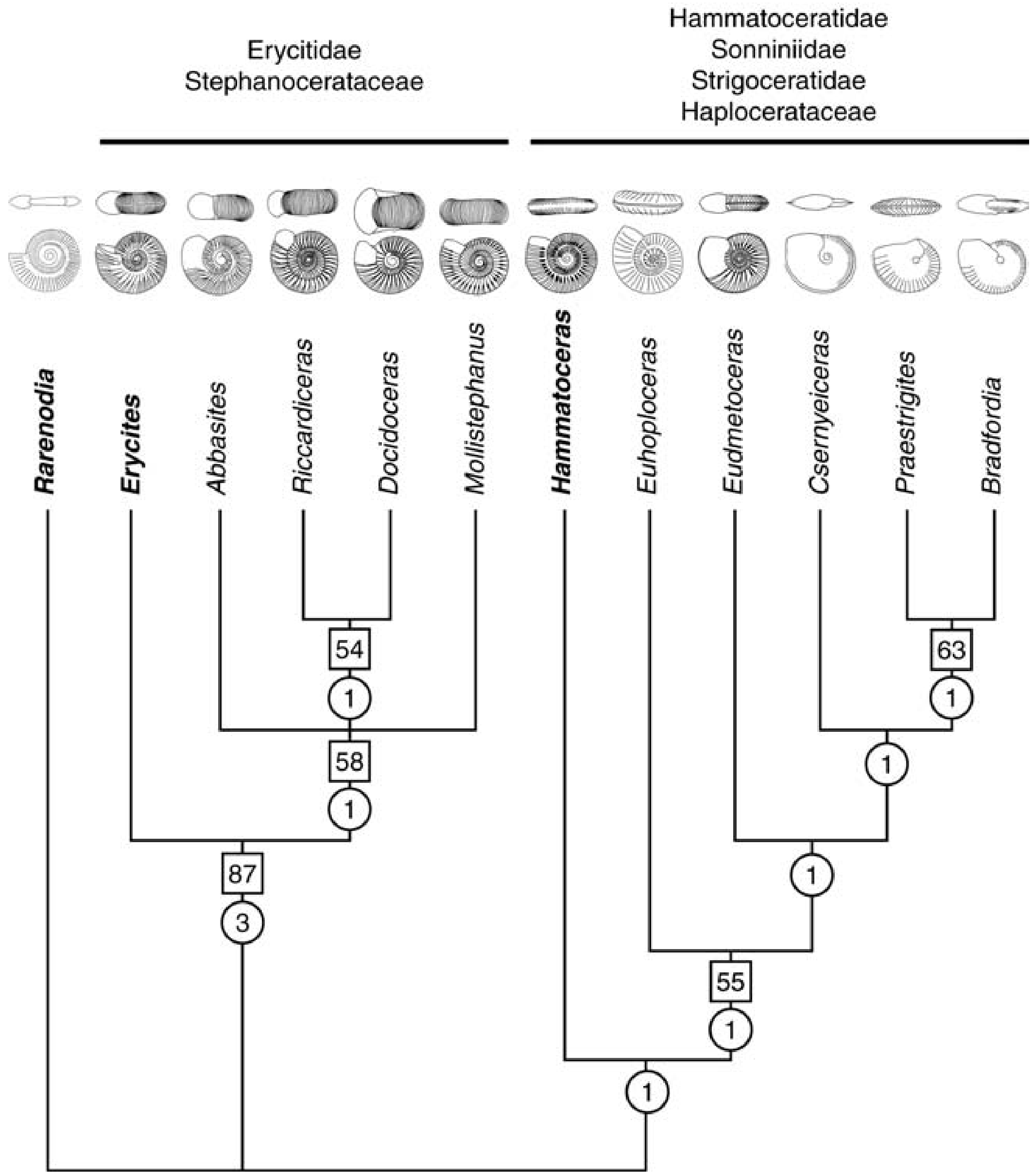

Figure 3. Strict consensus tree. Bootstrap (in squares) and Bremer support (in circles) values are shown. Values less than 50 % for bootstrap are not shown. Outgroups are in bold print.

ribs of *Rarenodia* are not divided but, when they are in contact with tubercles, many ribs may originate from the same tubercle. The ribs in this taxon are interrupted by a ventral smooth band. Generally, forms in the '*Erycites* group' share similar ornamentation except for a few characters. All taxa display dense, bifurcated ribbing. Ribs are continuous on the ventral side. *Erycites* is the only genus in this clade whose ventral ribbing is interrupted, it being associated with a ventral keel. Tubercles may occur where ribs bifurcate (*Mollistephanus*) or primary ribs may be thick (*Docidoceras* and *Riccardiceras*). Shell ornamentation of ammonites from the '*Hammatoceras*' group is subject to variation. *Eudmetoceras* and *Hammatoceras* have bifurcated ribs with thickened primary ribs. The ribs of other genera of this group are not bifurcate (*Euhoploceras*) and may be confined to the latero-ventral part of the shell (*Csernyeiceras*, *Praestrigites* and *Bradfordia*). Ornamentation may be very dense (*Eudmetoceras*) to sparse (*Euhoploceras*). The ribbing of all genera in this group is interrupted in the ventral area of the shell either by a smooth band or by a keel.

4. Implications for the Middle Jurassic ammonite radiation and its dynamics

The clades constructed here show that the ammonites in this study divide into two monophyletic groups plus *Rarenodia*. The main result of the present study is therefore that two different clades occur very early in hammatoceratins history.

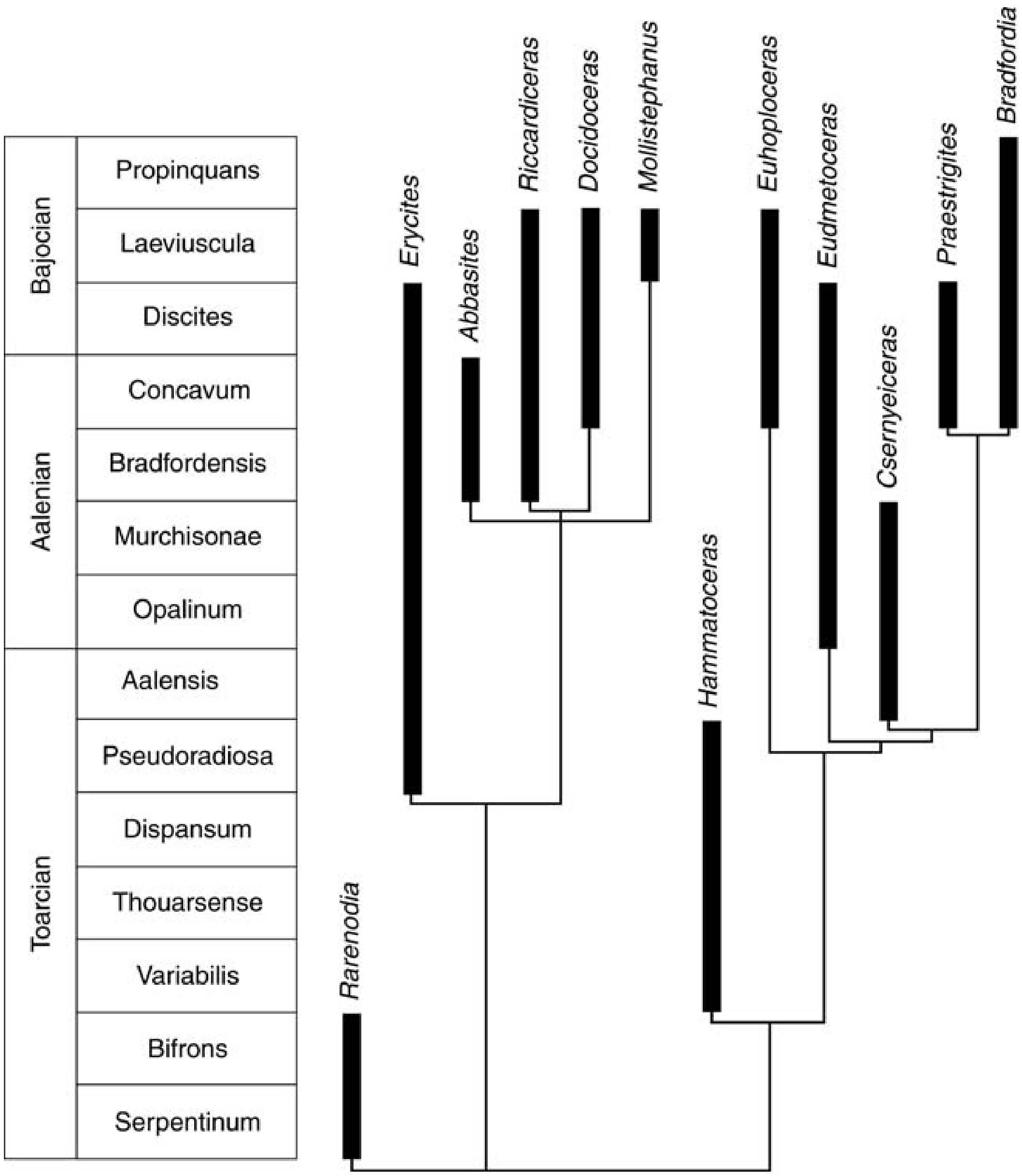

Figure 4. Phylostratigraphy of the Hammatocerataceae and initial members of Bajocian groups.

The first set ('*Erycites* group') is composed of *Erycites* and *Abbasites*, which are attributed to the Erycitidae *sensu* Rulleau, Elmi & Thévenard (2001), along with *Riccardiceras*, *Docidoceras* and *Mollistephanus*, which are invariably attributed to the Stephanocerataceae. Aalenian ancestors and Bajocian descendants are clearly separated: the Erycitidae are at the base of the clade while the Stephanocerataceae succeed them. This clustering indicates that the Stephanocerataceae branched from the Erycitidae as supposed by Elmi (1967), Westermann (1995), Sandoval, Linares & Henriques (2000) and Rulleau, Elmi & Thévenard (2001). For the latter authors, the origin of the Stephanocerataceae is even more complex and the two major groups of this superfamily have separate origins: *Abbasites* gives rise to the Otoitidae Mascke, 1907, which includes *Docidoceras* and *Riccardiceras*, while the Stephanoceratidae Neumayr, 1875, which includes *Mollistephanus*, derives from *Erycites*. This interpretation is not confirmed by our analysis.

In the second set ('*Hammatoceras* group'), *Hammatoceras*, *Eudmetoceras* and *Csernyeiceras* belong to the Hammatoceratidae *sensu* Rulleau, Elmi & Thévenard (2001) while *Euhoploceras*, *Praestrigites* and *Bradfordia* are representatives of all the Bajocian groups except for the Stephanocerataceae, respectively, the Sonniniidae, Strigoceratidae and Haplocerataceae. This confirms that the Sonniniidae (see Rulleau, Elmi & Thévenard, 2001), Strigoceratidae (see Géczy, 1966; Elmi, 1967; Westermann, 1969; S. R. Fernandez Lopez, unpub. Ph.D. thesis, Univ. Complutense Madrid, 1985; Sandoval, 1985; and Rulleau, Elmi & Thévenard,

2001) and Haplocerataceae (see Elmi, 1966; Tintant & Mouterde, 1981; and Westermann, 1993) originated in the Hammatoceratidae branch. Relationships between the Hammatoceratidae and their descendants are complex. Although *Hammatoceras* is at the base of the clade, other Hammatoceratidae members (*Eudmetoceras* and *Csernyeiceras*) are mixed in the cladogram among Bajocian genera. This complexity was also marked by the relatively low bootstrap values and Bremer support (see Fig. 3) and is a consequence of homoplasies affecting some characters, mainly those describing ventral section shape (characters D, E and F) and ribbing (characters J and L). This calls for further investigations using complementary characters.

In the cladogram, *Csernyeiceras* is the sister group of both *Praestrigites* and *Bradfordia*. This point of view was claimed for *Praestrigites* by Elmi (1967), Schweigert & Dietze (1998), Schweigert, Dietze & Balle (2000) and Rulleau, Elmi & Thévenard (2001), who consider *Csernyeiceras* as a possible ancestor for this genus. The origin of *Bradfordia* and thus of the Haplocerataceae is more difficult to establish and few authors have proposed phylogenetic relationships with the Hammatoceratidae. Some (Elmi, 1967; Tintant & Mouterde, 1981; Westermann, 1993) propose that *Bradfordia* derives from *Eudmetoceras* (or subgenus *Euaptetoceras* Buckman, 1922). This has not been confirmed by the cladistic approach. The position of the Strigoceratidae family within the Haplocerataceae superfamily is the subject of much debate: although many authors (Galácz, 1980; Donovan, Callomon & Howarth, 1981; S. R. Fernandez Lopez, unpub. Ph.D. thesis, Univ. Complutense Madrid, 1985) classify the Strigoceratidae with the Haplocerataceae, others (Tintant & Mouterde, 1981; Sandoval, 1985) link the Strigoceratidae with the Hammatocerataceae. In our analysis, we can see that the Strigoceratidae (*Praestrigites*) are closely related to the Haplocerataceae (*Bradfordia*), thus confirming the first interpretation.

A phylogenetic tree based on the consensus tree and adding stratigraphical occurrences of the studied taxa (Fig. 4) is proposed. This tree allows us to compare phylogenetic relationships with stratigraphy. The three outgroups are the older genera of the analysis. For the '*Erycites*' group, phylogenetic relationships are consistent with stratigraphy; *Riccardiceras*, *Docidoceras* and *Mollistephanus* are more recent than *Abbasites* and *Erycites*, which are their possible ancestors. On the other hand, for the '*Hammatoceras*' group, comparison of the relative positions of taxa on the tree with stratigraphy reveals conflicts (see the *Euhoploceras*–*Eudmetoceras*–*Csernyeiceras* stratigraphical versus topological successions). However, it has to be remembered that only key genera have been used here and not an exhaustive sample. A more detailed study needs to be conducted before any ghost lineages can be identified.

5. Conclusions

The cladistic analysis presented in this paper yields some interesting results for understanding (1) the phylogenetic relationships within the hammatoceratins and (2) their relationships with their supposed Bajocian descendants. As called for by Callomon for the hammatoceratins (pers. comm. in Westermann, 1993), an urgent revision is needed for this group since many phylogenetic hypotheses have been proposed by different authors. The principal result of the cladistic analysis presented here is that the ammonites under study form two groups, each including members of the hammatoceratins root group and their late Aalenian descendants. This confirms that the hammatoceratins group is in fact an association of two lineages ('*Hammatoceras* group' and '*Erycites* group') that diverged early on, during the Toarcian stage, in the history of the emerging clade as suggested by Rulleau, Elmi & Thévenard (2001). Late Aalenian and Bajocian genera are distributed between these two lineages, confirming that the Stephanocerataceae derived from the '*Erycites* group' and that the '*Hammatoceras* group' gave rise to all the other Bajocian groups. The consequence is that the late Aalenian ammonite radiation progressed from two separate clades rather than one.

Having established the phylogenetic relationships, it is possible to concentrate on the consequences of the taxonomic status of the different sub-families, families and super-families studied here. Because our sampling is not exhaustive, and taking into account the numerous homoplasies, the low bootstrap values and Bremer support (at least for the '*Hammatoceras* group'), we cannot propose a complete taxonomic reassessment at the present time. However, it is clear that the use of a hammatoceratins group, whatever its taxonomic status, clustering all Toarcian and Aalenian (before the late Aalenian radiation) members of the emerging clade, must be avoided in view of our results. If one wants to maintain a hammatoceratins clade, it has to include all their descendants, that is, all post-Aalenian Ammonitina. We recommend defining two clusters: one grouping *Erycites*, *Abbasites* and their relatives (Stephanocerataceae) and the other grouping *Hammatoceras*, *Eudmetoceras*, *Csernyeiceras* and their relatives (Sonniniidae, Strigoceratidae and Haplocerataceae). This changes ammonite taxonomy considerably but may be viewed as a first step toward establishing a useful taxonomy (as called for by Cracraft, 1981) for palaeogeographical, ecological or macroevolutionary studies.

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