

CLADISTIC ANALYSIS OF ALBIAN HETEROMORPH AMMONITES

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ABSTRACT. A computer-based parsimony analysis of Albian heteromorph ammonites from the Tethyan and European faunal provinces is demonstrated. The results indicate that whilst Anisoceratidae, Baculitidae, Scaphitidae and Turrilitidae are monophyletic, Hamitidae is not. Previous studies of ammonite phylogenetics have used the coiling mode, ornamentation of the shell and the suture line as sources of characters. Comparison of the consistency and retention indices of these character suites indicates that whereas ornamentation is relatively consistent within clades, suture line morphology is highly homoplastic. The earliest known *Sciponoceras*, *S. skipperae* sp. nov., is described.

THE shortcomings of deriving phylogeny from the first and last appearances of taxa and the incompleteness of the fossil record have been widely discussed (Smith 1994). Although cladistic techniques have been applied to many fossil groups, ammonites have been considered hardly at all in this way. Landmann (1989) and Cooper (1994) used 'hand-crafted' cladograms to describe the evolution of a few Cretaceous ammonites, whilst Korn (1997) used a similar technique with goniatites. Neige and Dommergues (1995) compared a computer-based cladistic analysis with the patterns of evolution deduced from morphometrics and phenetics for the Jurassic harpoceratins and drew the important conclusion that whilst certain taxonomic units may be 'meaningful' from a morphological point of view, cladistic analysis indicated that these units have little if any phylogenetic value. The aim of the present paper is to investigate the phylogeny of one particular group of ammonites using a computer-based cladistic technique.

The heteromorph ammonites were diverse in form and habit, including morphologies which have been interpreted as being benthonic, nektonic and planktonic (Westermann 1996). In a few cases, the shell may have been internal, inside a cuttlefish-like animal (Doguzhaeva and Mutvei 1989, 1993). During the Albian, a group of ammonites, comprising the Scaphitaceae and Turrilitaceae, diversified and replaced the Ancylocerataceae which previously had been the dominant heteromorphs. These two groups remained important elements of Cretaceous ammonite assemblages right up to the Late Maastrichtian (Kennedy 1993). There seems little question that together the Scaphitaceae and Turrilitaceae form a clade; they share many characters in common (Wiedmann 1965; Wiedmann and Marcinowski 1985; Cooper 1994). On the other hand, they are also of diverse form, making them attractive subjects for a cladistic analysis. An analysis of the Albian species of this clade would provide a useful 'handle' on the radiation of the heteromorphs at a key stage in their evolution.

The most widely used classification of the Albian heteromorphs is that of Spath (1937, 1939, 1941) which has been broadly maintained in the *Treatise on invertebrate paleontology* (Arkell *et al.* 1957; Wright *et al.* 1996). Although Spath was working on the English Gault Clay, the heteromorphs present in that formation are known throughout the European and Tethyan faunal provinces. However, in the Boreal faunal province, heteromorph ammonites are unknown (Monks 1998). Scaphitaceae are identified on the basis of their tightly coiled morphology and complex suture lines, whereas Turrilitaceae have much more open coils and a suture line with fewer, and often simpler, lobes. Although Spath was unsure whether Scaphitaceae were descended from the Turrilitaceae, this view is broadly accepted now.

Following the divisions established by Spath (1937, 1939, 1941), most subsequent authors have considered Turrilitaceae to form a single group, characterized by a more or less open coiling mode and relatively simple sutures tending towards bifid rather than trifid lobes, which during the Albian divided into five families.

1. Anisoceratidae Hyatt, 1900. Helical or spiral phragmocones followed by hook-shaped living chambers. Ornamented with annular ribs and septate, usually conical, ventral and ventrolateral spines arranged in symmetrical pairs relative to the long axis of the shell.
2. Baculitidae Meek, 1876. Short initial coil opens to single long, straight shaft producing shell similar to that of orthocone nautiloids.
3. Hamitidae Hyatt, 1900. Like Anisoceratidae, but lacking spines. Ornamentation almost always of simple annular ribs only rarely branching. Helical coiling at some stage of ontogeny common. Spath (1939) also included in this family small, tightly folded 'paperclip-like' forms, smooth or with very weak ribs, such as *Ptychoceras* d'Orbigny. There are some species of *Stomohamites* Breistroffer and *Metaptychoceras* Spath which approach *Ptychoceras* in size and coiling, although retaining the typical annular ribbing of the family. More commonly, *Ptychoceras* and a few other very similar genera have been removed to their own family, Ptychoceratidae Gill, 1871 either within Turrilitaceae or Ancylocerataceae (Arkell *et al.* 1957; Wright *et al.* 1996). Wiedmann and Kakabadzé (1993), in a discussion of the sutural ontogeny of *Ptychoceras*, made a good case for retaining Ptychoceratidae as a distinct family within Turrilitaceae but, even so, the relationships between this family and Hamitidae remain obscure.
4. Labeceratidae. For a long time, the relationships of this family to the other Albian heteromorphs have been uncertain. One of the two genera, *Labecer* Spath, is restricted to the southern hemisphere (all the other families of the Turrilitaceae are more or less global in distribution). *Labecer* has a laterally compressed, loosely coiled whorl with sinuous ribs, broad rounded spines and a suture with trifid lobes; in all respects, it is very similar to the Aptian and earlier Ancylocerataceae (Wright *et al.* 1996). The second genus, *Hamitoides* Spath, has a similar mode of coiling and is known (albeit sporadically) from northern as well as southern hemisphere localities. In contrast with *Labecer*, *Hamitoides* lacks spines; it has an approximately circular whorl section, and the ribs are blunt, straight and branch regularly on the flanks, rather than sharp and sinuous with intercalated incomplete ribs. The suture line is, regrettably, unknown. Marcinowski and Wiedmann (1990) excluded *Hamitoides* from Labeceratidae, placing it within Hamitidae, pointing out the close similarities in ornament between *Hamitoides* and *Scaphamites* Wiedmann and Marcinowski.
5. Turrilitidae Meek, 1876. Helically coiled throughout, with or without spines. Spath (1937) was justifiably uncertain about the origins of this family, deriving some from the Hamitidae and some from the Anisoceratidae, a view broadly agreed with by Klinger and Kennedy (1978).

The postulated inter-relationships of these families are illustrated in Text-figure 1. Scaphitaceae appears to have diverged from the main stock of Turrilitaceae during the Late Albian. In the Albian, Scaphitaceae includes only *Eoscaphtes* Breistroffer, *Scaphites* Parkinson, *Worthoceras* Adkins and *Yezoites* Yabe, all of which are included in a single family, Scaphitidae. *Worthoceras* is really quite unlike all the other scaphitids. It lacks pseudolobes and an umbilical perforation, and ornamentation is completely absent except for weak, scale-like constrictions on the living chamber; Wiedmann (1965) believed it should be removed from Scaphitaceae.

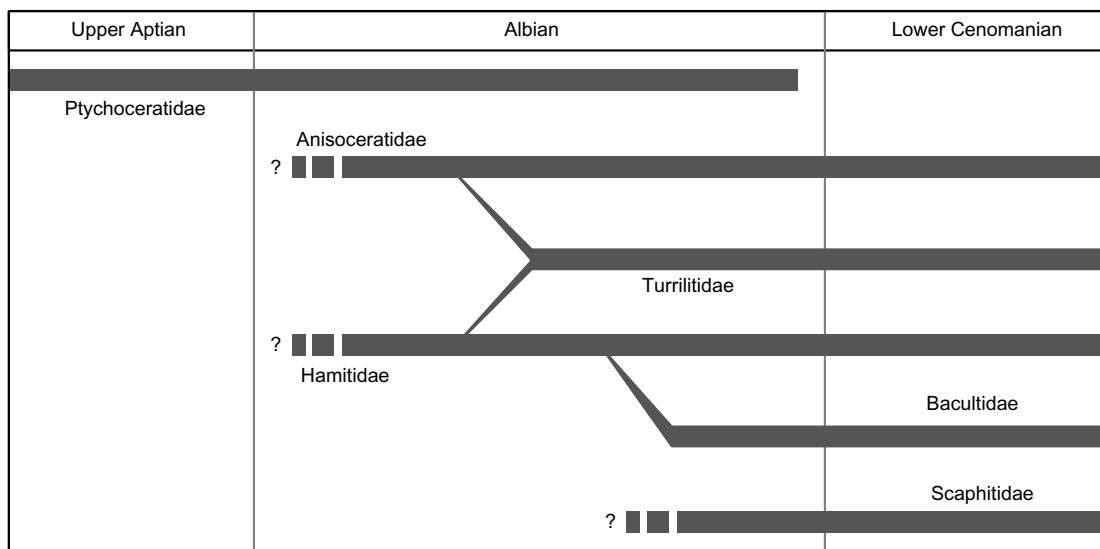
PHYLOGENETIC ANALYSIS

Assumptions

Phylogenetic studies of the ontogeny and sutural morphology have established that Turrilitaceae and Scaphitaceae together comprise a monophyletic group, with Turrilitaceae derived from Ancylocerataceae, and Scaphitaceae from Turrilitaceae (Wiedmann 1965, 1969; Wiedmann and Marcinowski 1985; Wiedmann and Kakabadzé 1993). The present study assumes that the Albian heteromorphs are part of this monophyletic group, characterized by the possession of a suture line with four primary lobes (see *Characters analysed*, below).

Outgroup taxa

The origins and the immediate ancestors of the Turrilitaceae are unknown. The oldest members belong to the Ptychoceratidae, which are known from the Barremian. Aptian Anisoceratidae and Hamitidae are



TEXT-FIG. 1. Phylogeny of the Albian heteromorphs as described by Spath (1941) and Arkell *et al.* (1957).

known only from fragments (Bréherét *et al.* 1986; Otilia Szives, pers. comm.), and have not been included in this analysis.

Ingroup taxa (Table 1)

The 25 ingroup taxa included in this analysis have been chosen to cover adequately the Albian Turrilitaceae. Labeceratidae were excluded, on the assumption that these are in fact members of Ancylocerataceae. Any computer-based cladistic analysis is limited by the number of taxa that the computer can process within a reasonable time. Therefore some selectivity is inevitable. In this analysis, this has been minimized by selecting, as far as possible, the type species of genera. Exceptions are where either the type is incompletely known, in which case a similar species was chosen, or where the type does not occur in the Albian. The species selected come from many different localities around the world; indeed, many species are common in both Tethyan (e.g. Australian, Madagascan) and European (e.g. English) ammonite assemblages.

Characters analysed

Choosing which characters are best for a phylogenetic analysis depends upon the level of analysis. Characters which provide good 'signal' at one taxonomic level may be homoplastic at another. Morphological characters, such as coiling and ornamentation, are widely used to describe species, but may be unreliable for deriving phylogenies. Neige and Dommergues (1995), in their study of the Lower Jurassic ammonites *Protogrammoceras* and *Fuciniceras*, have described in detail the different cladograms derived using ornament or shell shape. Schindewolf (1961) and Wiedmann (1969) have advocated the use of the suture line as a prime source of phylogenetic data.

In this analysis, both shell shape and suture line characters were used. As far as possible, gradational or continuous characters were avoided. Shell coiling mode, for example, varies considerably among species, especially among the hamitids (Spath 1941). By examining the consistency indices of the characters after the analysis, their value in reconstructing phylogenies can be estimated. The four major suites of characters used were siphuncle position, suture line morphology, coiling and ornamentation. These are listed in

TABLE 1. Ingroup taxa following the systematic arrangement of Wright *et al.* (1996).

Family	Species	Range	Type species?
Anisoceratidae	<i>Anisoceras saussureanum</i> (Pictet)	Upper Albian	Yes
Anisoceratidae	<i>Protanisoceras (Protanisoceras) raulinianum</i> (d'Orbigny)	Lower Albian	Yes
Anisoceratidae	<i>Protanisoceras (Heteroclinus) nodosum</i> (J. Sowerby)	Middle Albian	Yes
Anisoceratidae	<i>Protanisoceras (Torquistylus) anglicum</i> (Spath)	Lower Albian	Yes
Anisoceratidae	<i>Prohelicoceras moutonianum</i> (d'Orbigny)	Middle Albian	No
Anisoceratidae	<i>Metahamites sablieri</i> (d'Orbigny)	Middle Albian	Yes
Baculitidae	<i>Lechites gaudini</i> (Pictet and Campiche)	Upper Albian	Yes
Baculitidae	<i>Sciponoceras skipperae</i> sp. nov.	Upper Albian	Yes
Hamitidae	<i>Hamites attenuatus</i> J. Sowerby	Middle Albian	Yes
Hamitidae	<i>Hamites hybridus</i> Casey	Lower Albian	Yes
Hamitidae	<i>Stomohamites nokonsis</i> Adkins and Winton [= <i>Stomohamites subvirgulatus</i> Spath, <i>Hamites parkinsoni</i> Fleming, <i>H. charpentieri</i> Spath, <i>H. duplicatus</i> Pictet and Campiche, <i>Stomohamites ibex</i> Spath]	Upper Albian	No
Hamitidae	<i>Stomohamites virgulatus</i> Brongniart	Upper Albian	Yes
Hamitidae	<i>Hamitella annulata</i> (= <i>Hamites subrotundus</i> Spath)	Middle Albian	Yes
Hamitidae	<i>Lytohamites similis</i> Casey	Upper Albian	Yes
Hamitidae	<i>Scaphamites passendorferi</i> Wiedmann and Marciniowski	?Middle to Upper Albian	Yes
Scaphitidae	<i>Eoscaphtes circularis</i> (Spath)	Upper Albian	Yes
Scaphitidae	<i>Eoscaphtes subcircularis</i> (Spath)	Upper Albian	
Scaphitidae	<i>Scaphites hugardianus</i> (d'Orbigny)	Upper Albian	
Scaphitidae	<i>Worthoceras worthense</i> (Adkins)	Upper Albian	Yes
Turrilitidae	<i>Proturrilitoides astierianus</i> (d'Orbigny)	Middle to Upper Albian	Yes
Turrilitidae	<i>Turrilitoides hugardianus</i> (d'Orbigny)	Upper Albian	Yes
Turrilitidae	<i>Pseudhelicoceras robertianum</i> (d'Orbigny)	Middle to Upper Albian	Yes
Turrilitidae	<i>Paraturrilites gresslyi</i> (Pictet and Campiche)	Upper Albian	Yes
Labeceratidae?	<i>Hamitoides studerianus</i> (Pictet)	Middle to Upper Albian	No

Appendix 1. The siphuncle is the narrow, thread-like structure which connected the chambers of the phragmocone with each other and with the living chamber, and allowed the ammonite to empty the chambers as it grew. It is a conservative structure, and only a single character based on siphuncle position is included in this analysis. In most ammonites, it is located ventrally and runs parallel to the midline of the internal lobe. The siphuncle is laterally displaced in some helically coiled ammonites (Klinger 1980). In contrast, suture line morphology is very variable. The suture lines of all heteromorph ammonites have four lobes: the external lobe (usually denoted by the abbreviation E); the lateral lobe (L); the umbilical lobe (U) and the internal lobe (I). Many scaphitids have additional lobes between the umbilical and internal lobes, known as pseudolobes (Wiedmann 1965). Unlike the four main lobes, they are absent during the earliest stages of ontogeny. The principal lobes may be either trifold or bifid, usually denoted by a number following the abbreviated lobe name (e.g. L₃, a trifold lateral lobe, or E₂, a bifid external lobe). In addition, the lobes

may be symmetrical or not; one or other side of the lobe may be more strongly developed, resulting in a certain lopsidedness, referred to here as 'skew'. Description of this character has been confused, with ambiguous terms such as 'sub-bifid' or 'asymmetrically trifid' being commonplace; in this analysis, the direction of skew, if present, is stated explicitly and a skew towards E is treated as a separate character state from a skew towards I. In many cases, all the principal lobes are of similar size, but often the umbilical or internal lobes may be smaller than the other two. Coiling in heteromorphs varies considerably within species, but two parameters, perforation and helicosity, are consistent enough for use in the data matrix. The term perforation refers to whether the protoconch and successive whorls are free or closed. Helicosity is present in many heteromorphs. In some species, it is confined to the juvenile stages, in others it persists throughout ontogeny.

External shell ornamentation is diverse and provides a rich source of characters. Constrictions may be present at the final aperture, bordered by one or two thickened ribs. There may also be constrictions regularly spaced along the shell, or grouped along the final living chamber only. The aperture may be further ornamented with fluted collars (mature microconchs) or curved 'hoods' (mature macroconchs). The entire shell of most heteromorphs is ribbed. The ribs may be uniform, but often occasional ribs are inflated and more robust than the intermediate ribs. These are here called varices, by comparison with similar structures in gastropods. The annular ribs themselves may be entire or branched: either looped between nodes (fibulation) or bifurcating on the flanks (biplication). Where the rib bifurcates on the flanks, it may be raised into a bullate spine. These are here called 'ridge spines' in contrast with conical spines on the ventral surfaces of other heteromorphs. Conical spines may be in matched pairs on either side of the shell, either across the siphuncle or positioned over each lateral lobe; in other species, they are unpaired, being present on the left or right side of the shell only.

Most characters were treated as unordered, with the exception of number 13, helicosity, where ordering character states can be justified on ontogenetic grounds. Terminology is based upon Arkell *et al.* (1957). The data matrix based upon these characters is presented in Appendix 2.

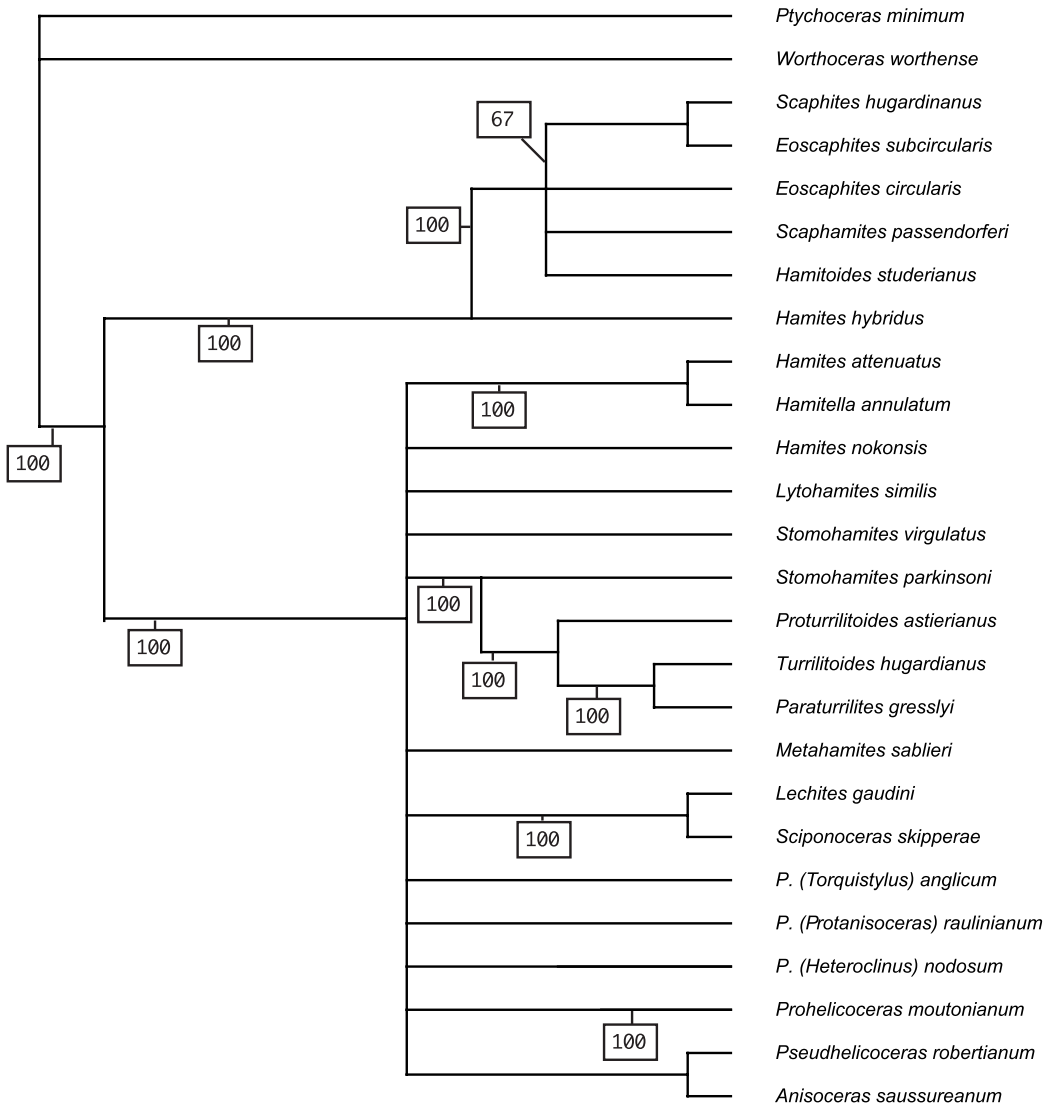
Analytical methods

The Apple Macintosh computer programs MacClade (Maddison and Maddison 1992) and PAUP (Swofford 1993) were used to build the data set and perform the analysis. The data set was searched in PAUP using the 'heuristic' search option to discover the most parsimonious trees. One hundred replicates using random stepwise addition of taxa with the steepest-descent option selected were run to maximize the likelihood of all the most parsimonious trees being found. Character state changes were optimized using the DELTRAN option which prefers convergences to reversals. This run resulted in 39 equally parsimonious trees being found. The semi-strict consensus of these trees is given in Text-figure 2. After this initial run, the characters were reweighted by rescaled consistency index and the data set run again, resulting in six trees. These trees were then filtered within PAUP, using the option to remove polytomous trees where compatible but more resolved trees exist. This reduced the total number of trees from six to two. One of these trees was preferred on the basis of stratigraphical congruence; it is given in Text-figure 3 and forms the basis for all subsequent discussion.

STATISTICAL TESTS

Bootstrap

Bootstrapping was performed using PAUP to test the robustness of the tree topology found in the analysis, as described by Felsenstein (1985). Bootstrap values are considered to be a highly conservative estimate of branch support (Smith 1994). One hundred replicates were performed. Well supported branches occur in the cladogram and the bootstrap trees, and the more bootstrap trees in which the branch occurs, the higher the support for that branch. The percentage of bootstrap trees in which a particular branch occurs is shown in Text-figure 4.



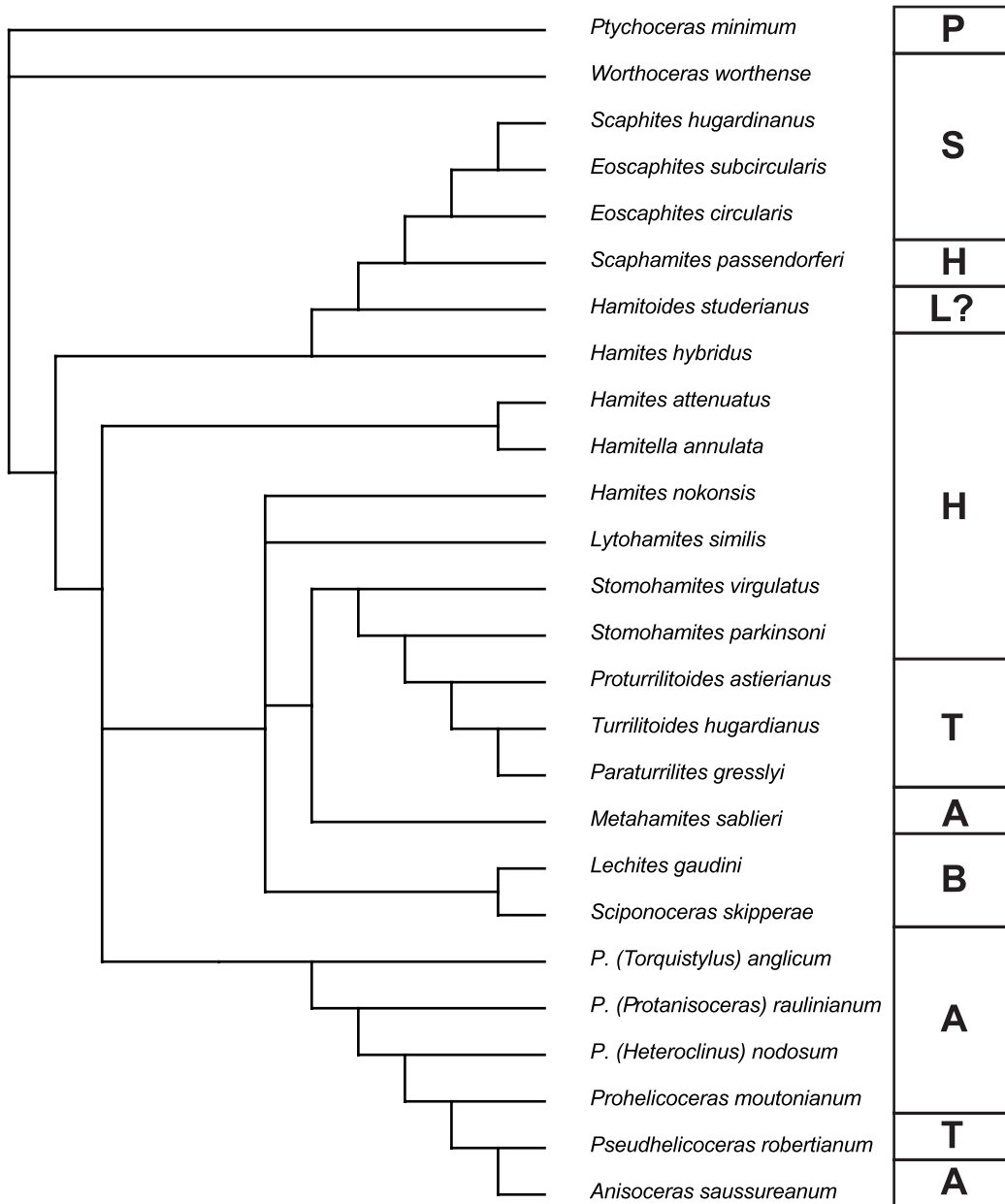
TEXT-FIG. 2. Semi-strict consensus tree. The numbers indicate the percentage of the 39 equally parsimonious trees in which the labelled branch occurs.

Bremer support

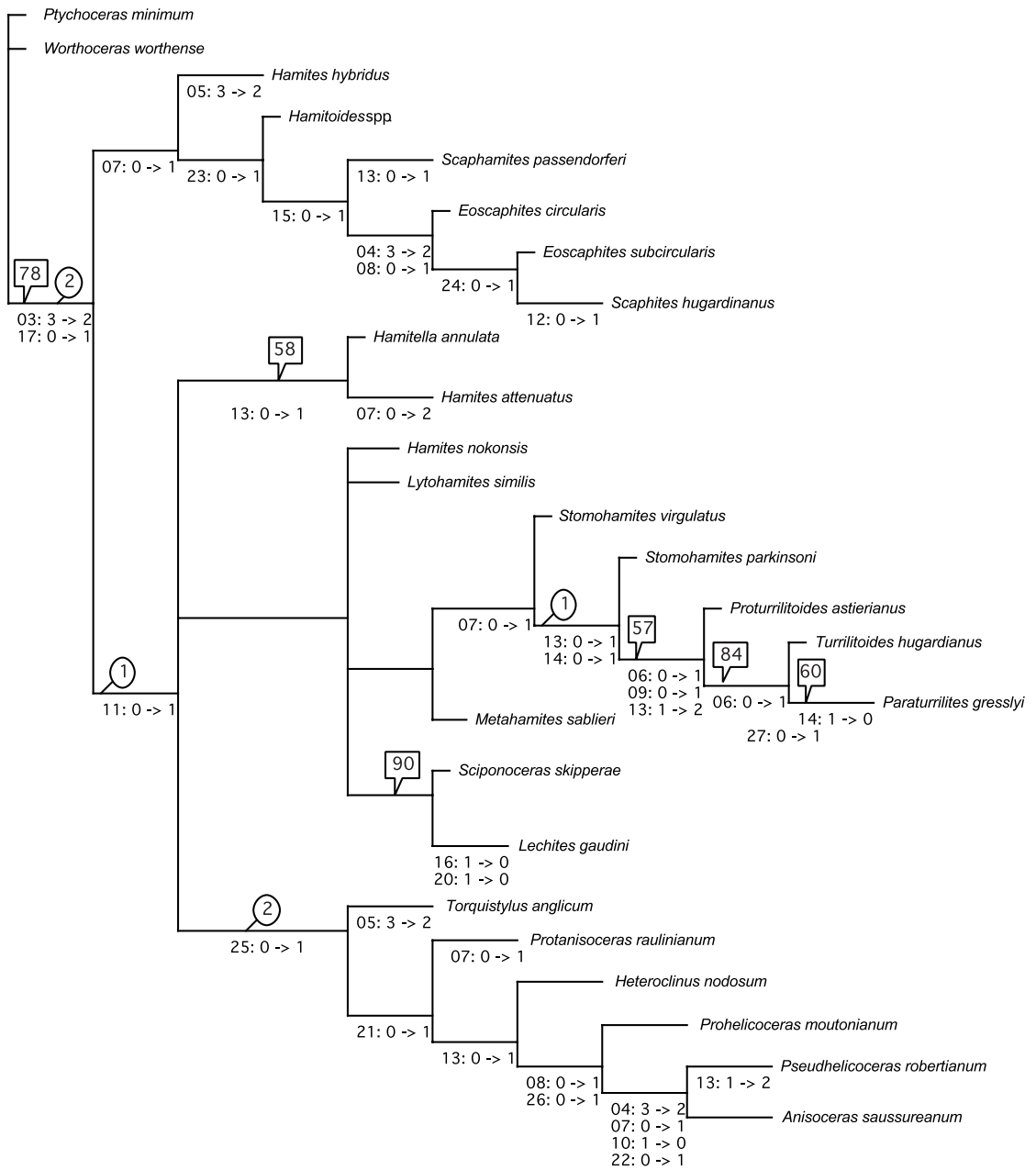
Bremer support was performed using PAUP and AutoDecay (Eriksson and Wikström 1995). This is a test of the number of extra steps needed to collapse a clade, as described by Bremer (1988). Higher numbers of steps imply a more robust clade. The results of this analysis are given in Text-figure 4.

TREE DESCRIPTION

Character state changes across the tree are presented in Text-figure 4. Those of the two character suites used in most ammonite taxonomies, the suture line and shell morphology, are discussed below.



TEXT-FIG. 3. Selected tree. Tree length = 46; Consistency Index = 0.63; Retention Index = 0.82. Conventional family attributions are listed in the right-hand column, based on the *Treatise* (Wright *et al.* 1996), where P = Ptychoceratidae; S = Scaphitidae; H = Hamitidae; L = Labeceratidae; T = Turrilitidae; A = Anisoceratidae; B = Baculitidae.



TEXT-FIG. 4. Cladogram of the Albian heteromorphs with character state changes labelled (see Appendix 2 for list of characters). Numbers in squares give the percentage of bootstrap trees in which the node indicated occurs, where this percentage exceeds 50 per cent. Numbers in ovals are Bremer support values.

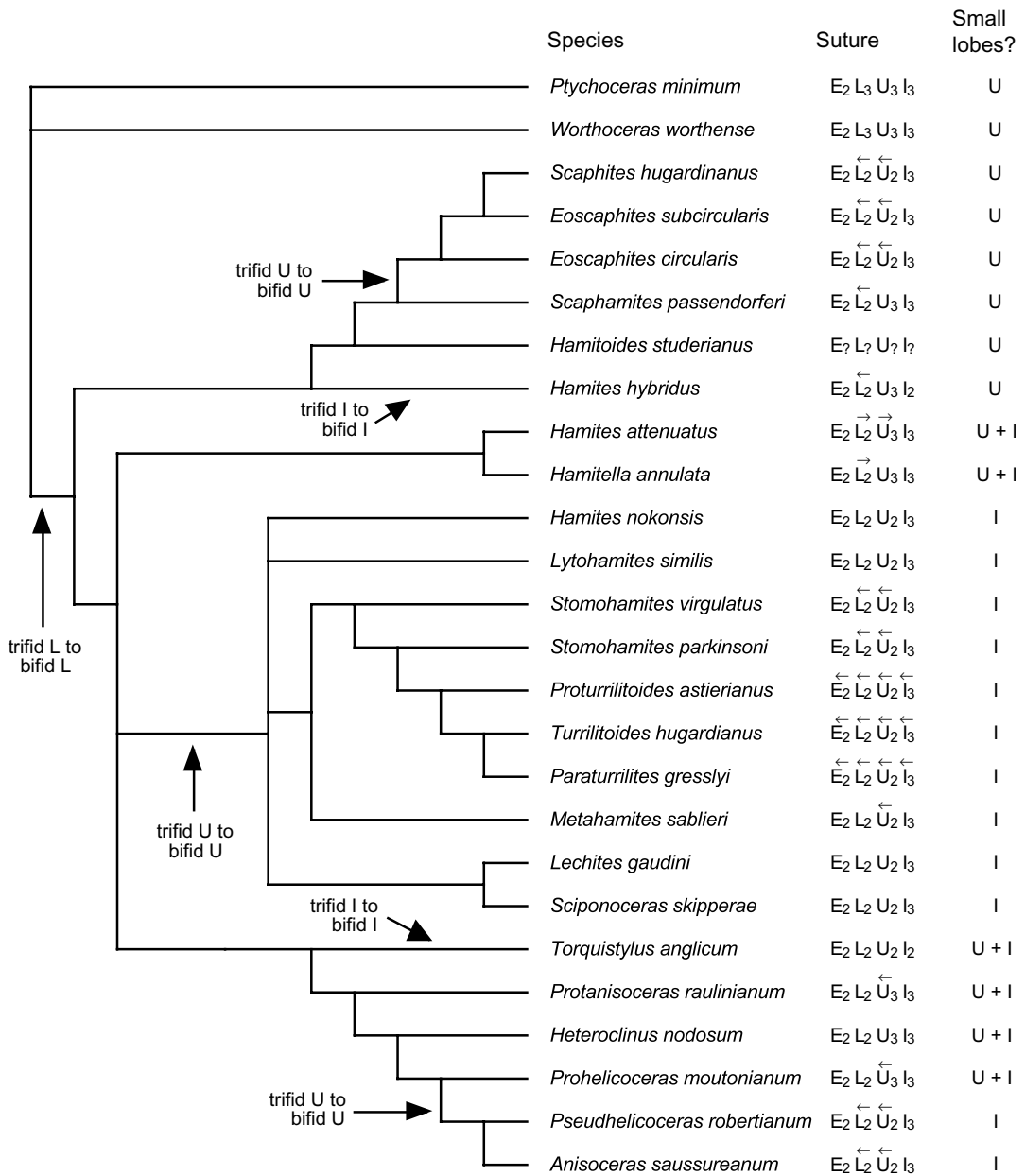
Suture line

The suture line character states are summarized in Text-figure 5. The sutures of the outgroup and the next most basal taxon, *Ptychoceras minimum* Rouchadzé and *Worthoceras worthense* (Adkins) respectively, are similar, with the morphology $E_2 L_3 U_3 I_3$, where each lobe is approximately symmetrical and U is rather smaller than the other lobes. The remainder of the cladogram is divided into two main sections, the ‘scaphitiform’ branch including Scaphitidae and some Hamitidae, and the ‘turrilitiform’ branch which, besides Turrilitidae, also includes Anisoceratidae, Baculitidae and many Hamitidae. A noteworthy observation is that in all cases, the lobes switch from being trifold to bifid and never from bifid to trifold. L is primitively trifold, as exhibited by *Ptychoceras* and *Worthoceras*, whilst in all higher taxa it is bifid. U is also trifold primitively, but becomes bifid in three separate lineages. This happens once in the more crownward part of the ‘scaphitiform’ lineage (*Eoscaphtes* + *Scaphites*), and twice in the ‘turrilitiform’ lineage, once within the Anisoceratidae (*Anisoceras* + *Pseudhelicoceras*) and again among the hamitids. I is also trifold primitively, and remains so for most of the higher species, although a bifid I develops twice, with *Hamites hybridus* Casey and *Torquistylus anglicum* Casey.

The most basal of the ‘scaphitiforms’ is the Lower Albian *H. hybridus* which, compared with many species of *Hamites* (as illustrated by Casey 1961), has a complex suture line of the form $E_2 L_3 U_3 I_2$. L is quite noticeably skewed, the side toward E being more strongly developed, and U is smaller in size compared with the other lobes. The incompletely known *Hamitoides studerianus* Pictet is the next taxon up. The suture line of *H. studerianus* is unknown. *Scaphamites passendorferi* Wiedmann and Marcinowski is the most derived hamitid in this clade, and would appear to be the sister taxon of Scaphitidae. It has a similar suture to *H. hybridus*, but L, although similarly skewed, is bifid rather than trifold. *Eoscaphtes circularis* (Spath) is the first of the scaphitids and, as noted by Wiedmann and Marcinowski (1985), its suture line is similar to that of *Scaphamites*, but with an asymmetrical bifid U rather than a symmetrical trifold one. *Eoscaphtes subcircularis* (Spath) and *Scaphites hugardianus* (d’Orbigny) are similar, but only the latter species has pseudolobes. Overall, the ‘scaphitiforms’ retain a number of presumably primitive sutural details also found in *Ptychoceras* and *Worthoceras*, i.e. bifid E, trifold I, and a small lobe U. The main morphological change in this lineage is the shift from symmetrically trifold lobes L and U to asymmetrically bifid ones which are skewed toward E.

Of the ‘turrilitiforms’, the clade including *Hamites attenuatus* J. Sowerby and *Hamitella annulata* (d’Orbigny) is the most primitive. These lower Middle Albian species have similar, moderately simple suture lines of the form $E_2 L_2 U_3 I_3$. The suture of *H. attenuatus* can be distinguished from that of *H. annulata* by the difference in the symmetry of lobes L and U, both of which are skewed toward I, whereas in *H. annulata*, only U is. The remaining ‘turrilitiforms’ divide into two branches which, in general, contrast with the preceding ones by having suture lines in which U is usually bifid. One branch is made up of the spinose ammonites and is equivalent to the family Anisoceratidae. The most basal member of this family is *Protanisoceras (Torquistylus) anglicum* Spath, which has a suture line $E_2 L_2 U_2 I_2$ with symmetrical lobes. As Casey (1961) noted, the suture line is very simple and the lobes only weakly incised with U and I somewhat smaller than E and L. The next species up is *Protanisoceras (Protanisoceras) raulinianum* d’Orbigny. Like *P. (T.) anglicum*, U and I are small although instead of being bifid, they are trifold. In addition, U is skewed, but in contrast with the asymmetry exhibited by *H. attenuatus* and *H. annulata*, the skew is toward E and not I. *Protanisoceras (Heteroclinus) nodosum* (J. Sowerby) is similar but U is not obviously skewed at all. *Prohelicoceras moutonianum* (d’Orbigny) has a similar suture line, but with an asymmetrically bifid U that is skewed toward E. The most crownward group of the Anisoceratidae clade includes *Anisoceras saussureanum* (Pictet) and *Pseudhelicoceras robertianum* (d’Orbigny) which have very similar suture lines of the form $E_2 L_2 U_2 I_3$. In both cases, the suture lines are quite florid, the lobes deeply incised and, unlike the preceding taxa on this branch, U is not smaller (although I is) and is similar in size and shape to L. Both L and U are asymmetrical, skewed toward E.

The second branch of the ‘turrilitiforms’ includes Turrilitidae as well as Baculitidae and a number of species usually included in Anisoceratidae and Hamitidae. Baculitidae, comprising *Lechites gaudini* (Pictet and Campiche) and *Sciponoceras skipperae* sp. nov., is located towards the base of this branch, as



TEXT-FIG. 5. Changes in suture line morphology across the cladogram based upon the characters described in Appendix 2. The suture morphology follows the notation used in the text. An arrow over a lobe indicates that it is skewed, and shows the direction of this skew, i.e. towards E or I. The right-hand column lists whether lobes U or I are less than 50 per cent. of the size of E and L.

are *Hamites nokonsis* Adkins and Winton and *Lytohamites similis* Casey. In all these species, the suture line has the form $E_2 L_2 U_2 I_3$. The lobes are symmetrical and, unlike the basal ‘turrilitiforms’ or *Protanisoceras*, only I is smaller in size compared with the other lobes. The next species up is *Metahamites sablieri* (d’Orbigny), followed by the two species of *Stomohamites* included here, the type *Stomohamites virgulatus* (Brongniart) and *S. parkinsoni* (Fleming). The suture line of *Metahamites sablieri*, $E_2 L_2 U_2 I_3$, is similar to that of the preceding members of this branch except that U is skewed slightly toward E. As noted by Spath (1941), the suture lines of *Stomohamites* species are quite distinctive, of the form $E_2 L_2 U_2 I_3$ but with both L and U being quite florid and of equal size, and somewhat skewed toward E. The most crownward species on this branch is a clade which is equivalent to the family Turrilitidae as defined by Scholz (1979) and which includes *Proturrilitoides astierianus* (d’Orbigny), *Turrilitoides hugardianus* (d’Orbigny), and *Paraturrilites gresslyi* (Pictet and Campiche). These species have similar suture lines ($E_2 L_2 U_2 I_3$) with asymmetrical lobes and a small lobe I. This contrasts with the helically coiled *P. moutonianum* and *Ps. robertianum*, in which E and I are asymmetrical.

Shell morphology

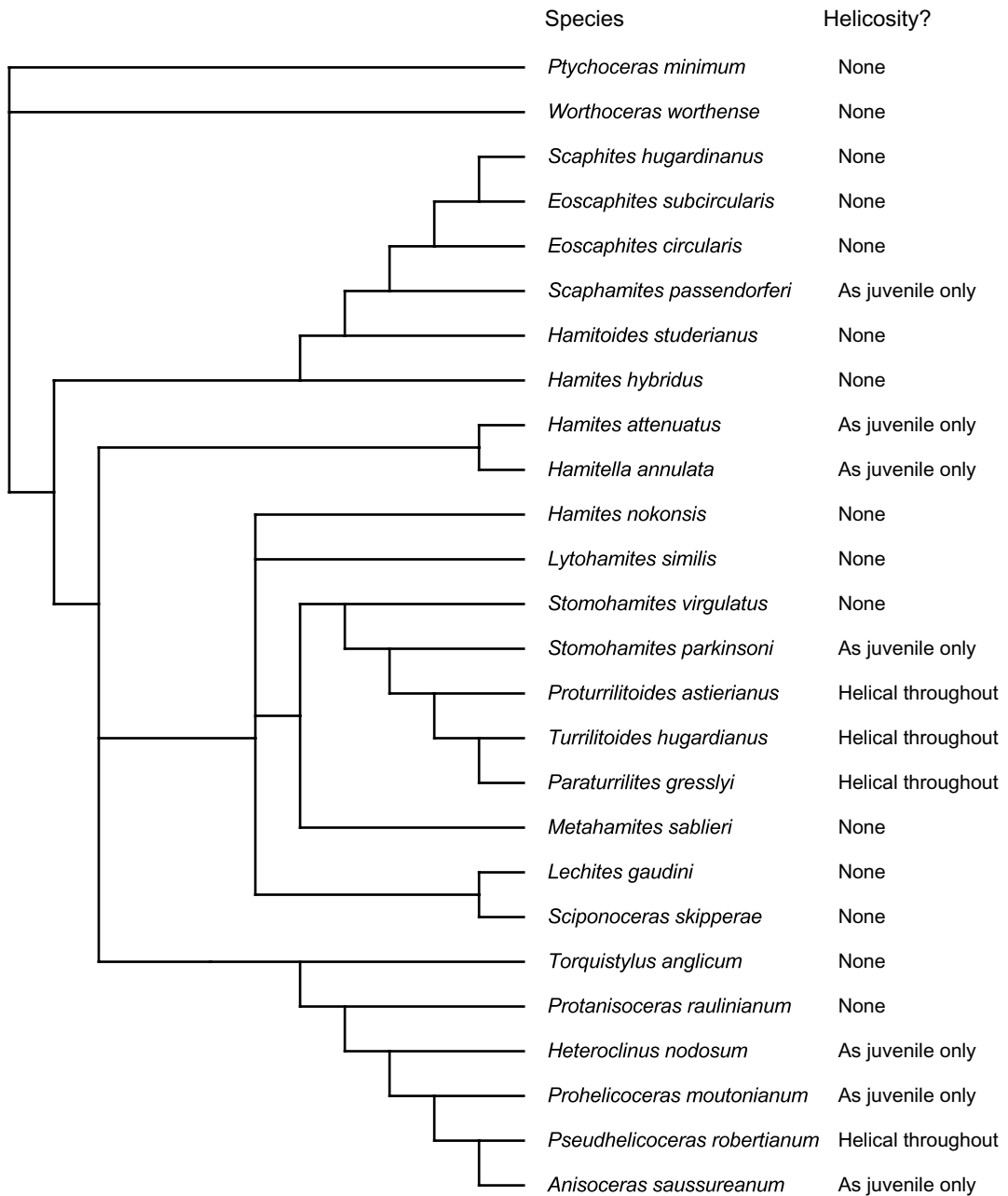
There are several important morphological attributes which seem to have taxonomic importance. Apertural modifications seem to be particularly useful in this respect. Baculitidae have unique apertural modifications which vary between macro- and microconchs. Macroconchs develop sharply curved hoods at maturity, whilst the microconchs have rather fluted, scoop-shaped collars. In contrast, the clade including *Scaphamites* and Scaphitidae have different apertural modifications which are, as far as is known, the same in both dimorphs. These consist of a sharp constriction just prior to the aperture, which then inflates into a thick band-like collar. A third kind of apertural modification is exhibited by the clade of (*S. parkinsoni* + Turrilitidae). Instead of a single collar, there are two bold ribs, and the constriction is located between them. This apertural modification has not been recorded in *P. gresslyi*, but is known from other species in the genus such as *P. circumtaeniatus* (Kossmat). The displacement of the siphuncle away from the ventral surface seems to be characteristic of the more crownward turrilitids, and the absence of this character, the lack of an apertural modification, and the fibulate ribbing do indeed seem to place *Pseudhelicoceras* outside of Turrilitidae, as discussed by Scholz (1979).

Most of the heteromorphs have simple annular ribs. Looped ribs and well-developed varices can be seen in the more crownward Anisoceratidae, whilst ribs which bifurcate along the flanks to form ridges are characteristic of the ‘scaphitiform’ lineage.

Shell coiling mode is, on the other hand, a feature to which less taxonomic weight can be applied. Helicosity arises four times in the phylogeny described by this cladogram: once with *Hamites attenuatus* and *Hamitella annulata*; again with *Scaphamites*; thirdly among the Anisoceratidae; and finally within the clade including *S. parkinsoni* and the Turrilitidae (Text-fig. 6). In all of these cases, either all or at least the basal members display helicosity during the early stages of growth only, the later parts of the shell being planar (typically, a hook shape). Only in two lineages do the later members coil helically throughout, i.e. *Pseudhelicoceras* from the Anisoceratidae, and the Turrilitidae from *Stomohamites*.

Morphological and sutural characters compared

Table 2 lists the suites of characters used with the calculated average consistency index (CI) and retention index (RI). Because only a single character based on the morphology of the siphuncle, and two on the mode of coiling were used, the significance of these indices with respect to siphuncle and coiling mode is difficult to assess and they are not discussed further. Morphological characters can be divided into those based on the aperture and those on shell ornamentation. These have high CI and RI values. In contrast, the suture line characters have much lower CI and RI values and are therefore more homoplastic. This implies that while ornamentation does not change very much within clades, suture lines do. Examination of the suture line alone is a much less safe basis for deriving a phylogeny than external shell morphology.



TEXT-FIG. 6. Appearance of helical coiling within the Albian heteromorphs. Helicosity is either absent (the shell coils in one plane throughout ontogeny), present during the juvenile stages but lost in later stages of shell growth, or persistent throughout.

TABLE 2. Mean consensus and retention indices (CI, RI) for the character suites used in this analysis.

Character suite	Character numbers	Mean CI	Mean RI
Siphuncle	1 (total = 1)	1.00	1.00
Suture line	2–11 (total = 10)	0.62	0.71
Coiling	12–13 (total = 2)	0.67	0.28
Aperture	14–19 (total = 6)	0.92	0.75
Ornament	20–27 (total = 7)	0.93	0.79

DISCUSSION

In the following section, three specific taxonomic problems outlined in the introduction are discussed with reference to the cladogram and the morphological changes described. These are the relationships between Anisoceratidae and Hamitidae, and how often spinosity evolved; whether Turrilitidae is monophyletic or diphyletic; and the origins of Scaphitaceae.

Monophyly of Anisoceratidae and Hamitidae

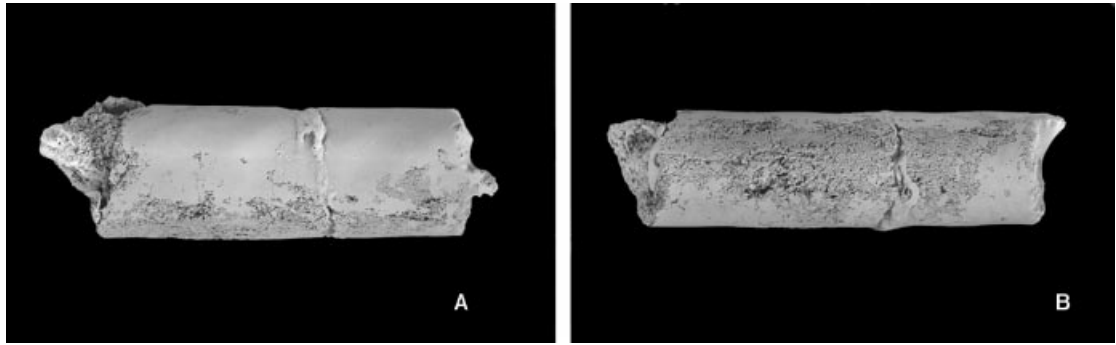
If *Metahamites* is excluded from Anisoceratidae, then that family is shown here to be a clade. *Metahamites* lacks the synapomorphy of Anisoceratidae, viz. conical spines in matching pairs on either side of the siphuncle. For this reason, Marcinowski and Wiedmann (1990) had included *Metahamites* as a subgenus of *Hamites*. However, whilst the type species lacks spines, other species assigned to *Metahamites* have them, and may well be anisoceratids; the retention of these species within *Metahamites* needs investigation.

Included in Anisoceratidae are the type species of *Anisoceras*, *Heteroclinus*, *Protanisoceras* and *Torquistylus*, plus a typical species of the genus *Prohelicoceras*, *P. moutonianum*. In addition, *Pseudhelicoceras robertianum*, the type species of the genus *Pseudhelicoceras*, is included, positioned in the cladogram as the sister taxon of *Anisoceras saussureanum*. Whilst *Pseudhelicoceras* has almost always been included in Turrilitidae (e.g. Marcinowski and Wiedmann 1990; Wright *et al.* 1996), this analysis indicates that Scholz (1979) was justified in considering it to be a member of Anisoceratidae. Consequently, the gap noted by Spath (1937) between the Early Albian *Protanisoceras* and the Late Albian and Cenomanian *Anisoceras* is seen to be linked by a series of intermediate forms, specifically *Prohelicoceras* and *Pseudhelicoceras*, which are both from the Middle and Upper Albian.

In contrast, Hamitidae lacks synapomorphies and is clearly not a clade but rather a taxonomic grade from which Anisoceratidae, Baculitidae, Scaphitidae and Turrilitidae arose. The type species of *Hamites*, *H. attenuatus*, forms a clade with the type species of *Hamitella*, *H. annulata*, near the base of the ‘turrilitiforms’, whilst *H. hybridus*, is at the base of the ‘scaphitiform’ lineage. Since *Hamitella* is part of a clade including the type species of *Hamites*, the view of Wright *et al.* (1996) that *Hamitella* is a junior synonym of *Hamites* may be justified. On the other hand, whilst *Stomohamites* has in recent years been considered to be a synonym of *Hamites* (Wright and Kennedy 1981, 1995), this analysis shows that it is not part of a monophyletic clade including the type of *Hamites*, and cannot be treated simply as a synonym. *Stomohamites* is paraphyletic with respect to Turrilitidae. *Lytohamites*, of which the type species is *L. similis*, is certainly excluded from Anisoceratidae, so the hypothesis put forward by Scholz (1979) that it represents an *Anisoceras* which has lost its tubercles is not supported.

Turrilitid origins and monophyly

If Scholz (1979) was correct in removing *Pseudhelicoceras* to the Anisoceratidae, then the remaining turrilitids form a clade derived from the hamitids. Previous workers have suggested that *Hamitella* may have been the immediate ancestor of the earliest turrilitids, such as *Proturrilitoides* (Breistroffer 1953; Klinger and Kennedy 1978). However, Spath (1941) did comment on the similarities between these early turrilitids and a helical variety of *Stomohamites parkinsoni* (then classified as a separate species,



TEXT-FIG. 7. *Sciponoceras skipperae* sp. nov.; BMNH C.93268, holotype; Upper Greensand (Late Albian, *dispar* Zone), Melcombe Horsey, Dorset; lateral (A) and ventral (B) views; $\times 1.5$.

Stomohamites ibex). This analysis shows that *Hamitella* differs from *Proturrilitoides* in the shape of the suture line and in lacking apertural modifications and is closer to *Hamites attenuatus*. Instead, it is *Stomohamites parkinsoni* which is shown to be the sister taxon of the Turrilitidae.

Scaphitid origins

This cladistic analysis supports the hypothesis advocated by Wiedmann and Marcinowski (1985) that Scaphitidae are derived from Hamitidae via a form similar to *Scaphamites*. In addition, the exclusion of *Worthoceras* from Scaphitidae and its closer affinities to *Ptychoceras*, as suggested by Wiedmann (1965), appears to be justified.

SYSTEMATIC PALAEOLOGY

Order TURRILITACEAE Gill, 1871
 Family BACULITIDAE Gill, 1871
 Genus SCIPONCERAS Hyatt, 1894

Diagnosis. Like *Lechites* but lacking, or with only very weak, annular ribs, and with constrictions along the body-chamber, not only at the final aperture.

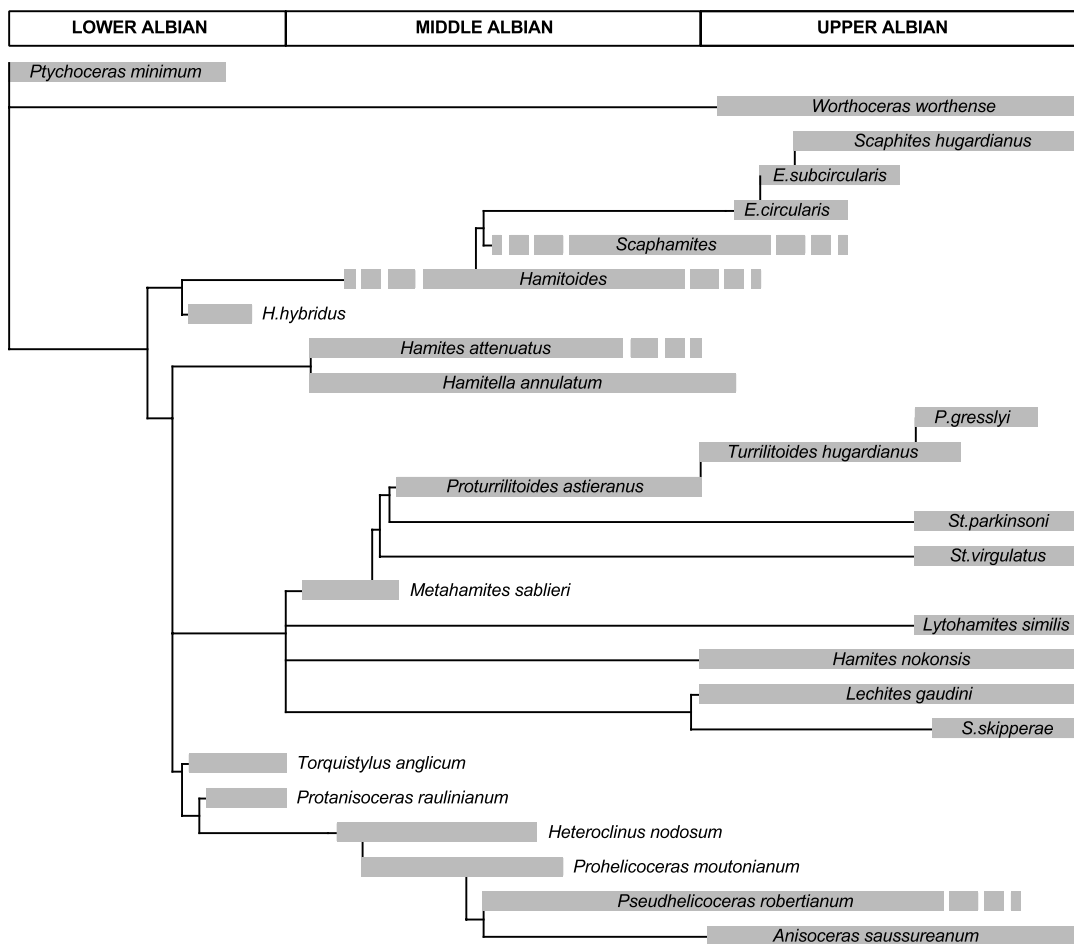
Sciponoceras skipperae sp. nov.

Text-figure 7

- 1941 *Lechites communis* Spath, p. 667, text-fig. 244f–h.
 1968 *Lechites* sp. indet. Renz, p. 83, pl. 17, text-fig. 29f.
 1990 *Sciponoceras* sp. Henderson, p. 130, text-fig. 12N–P.

Derivation of name. Named in honour of Dr Jackie Skipper, geologist at The Natural History Museum, London.

Holotype. C.93268, The Natural History Museum, Department of Palaeontology. From the phosphate pebble beds of the Upper Greensand of Dorsetshire Gap, Melcombe Horsey, Dorset, England. These beds contain indigenous early Early Cenomanian fossils, including ammonites. The phosphatic pebbles are Late Albian (*Mortonoceras perinflatum* and *M. briacensis* subzones) and earliest Cenomanian.



TEXT-FIG. 8. Phylogenetic tree of the Albian heteromorphs following the method described in Smith (1994).

Diagnosis. Baculiticonic ammonite. Completely lacking ribbing, but very weak prorsiradiate constrictions are present, strongest on the ventral surface and weakening on the flanks. The whorl section is slightly laterally compressed. Suture line similar to contemporaneous *Lechites*, of the form $E_2 L_2 U_2 I_3$. The lobes are symmetrical, but I is somewhat smaller.

Remarks. *Sciponoceras* has been widely reported from the Cenomanian and the Turonian; this is the first species known from the Albian. This species is represented by a number of specimens collected by H. G. Owen and W. J. Kennedy and deposited at The Natural History Museum, London, and in the W. J. Kennedy collection, at the University Museum, Oxford. Although *Sciponoceras skipperae* is similar to the Lower Cenomanian species *S. baculoides* Mantell, the lateral compression is weaker and the suture line much less deeply incised. These characteristics suggest that *S. skipperae* is an intermediate between Albian *Lechites* and Cenomanian *Sciponoceras*.

Distribution. As for holotype. Renz (1968) described very similar specimens from the Upper Albian of La Vraconne, Switzerland. Henderson (1990) also described specimens of *Sciponoceras* from the Upper Albian of Shoal Bay,

Northern Territory, Australia. Although the suture line is similar to that of *S. skipperae*, the constrictions are a little bolder and a hint of ribbing can be seen on the ventral surface.

CONCLUSIONS

A phylogenetic tree of the Albian heteromorphs based on this cladistic analysis is presented in Text-figure 8. This follows the method of Smith (1994) who mapped a cladogram against a stratigraphical axis, with 'ghost lineages' connecting synapomorphic sister taxa at the highest time horizon at which their implied latest common ancestor could have lived. Some taxa are not characterized by synapomorphies (i.e. are metataxa) and are interpreted here as potential ancestor 'grades', from which synapomorphic taxa may have evolved directly. The cladogram generally concurs with our knowledge of the stratigraphical occurrences of the Albian heteromorphs studied. Anisoceratidae and Scaphitidae, for example, proceed from basal Early Albian species to the more derived Late Albian ones in a stepwise manner. On the other hand, there are regions which imply extensive 'ghost lineages'. Most obviously fitting into this category are the Baculitidae, which are known only from the Upper Albian but for which the cladogram implies a separation from the hamitids no later than the early Mid Albian.

Such discrepancies between the cladogram and the stratigraphical record could have a number of explanations. The cladogram itself could be wrong. This could be caused by the data matrix not including an adequate range of species, gaps in the range of characters coded, or use of an inappropriate coding technique. Assuming that the cladogram is correct, it is likely that the fossil record is incomplete. The inadequacy of the fossil record has been widely discussed elsewhere and need not be commented on here. Ultimately, it remains for workers in the field of ammonite phylogenetics to determine characters, process data matrices built on these characters, and interpret the results before a truly phylogenetic classification of the heteromorphs can be devised.

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APPENDIX 1: CHARACTER LIST

Character suite	Number	Character
Siphuncle	1.	Siphuncle. Located ventrally (0) or displaced laterally (1).
	Suture line	2.
	3.	Lateral lobe shape. Trifid (3) or bifid (2).
	4.	Umbilical lobe shape. Trifid (3) or bifid (2).
	5.	Internal lobe shape. Trifid (3) or bifid (2).
	6.	External lobe skew. Symmetrical (0) or asymmetrical (1).
	7.	Lateral lobe skew. Symmetrical (0); skewed toward E (1); or toward I (2).
	8.	Umbilical lobe skew. Symmetrical (0); skewed toward E (1); or toward I (2).
	9.	Internal lobe skew. Symmetrical (0) or asymmetrical (1).
	10.	Umbilical lobe less than 50 per cent. size of E and L. No (0) or yes (1).
	11.	Internal lobe less than 50 per cent. size of E and L. No (0) or yes (1).
Coiling	12.	Imperforate initial coil. No (0) or yes (1).
	13.	Helicosity. Planar (0); helical initially, planar later (1); helical throughout (2).
Aperture	14.	Final aperture constricted, with a bold rib either side. No (0) or yes (1).
	15.	Final aperture constricted, followed by a single collar. No (0) or yes (1).
	16.	Periodic constrictions all along shell. No (0) or yes (1).
	17.	Constrictions along the final living chamber only. No (0) or yes (1).
	18.	Aperture with fluted collar (microconchs). No (0) or yes (1).
	19.	Aperture with curved hood (macroconchs). No (0) or yes (1).
Ornament	20.	Annular ribs. Absent (0) or present (1).
	21.	Varices. Absent (0) or present (1).
	22.	Fibulations. Absent (0) or present (1).
	23.	Biplications. Absent (0) or present (1).
	24.	Ridge spines on the flanks. Absent (0) or present (1).
	25.	Conical spines paired over siphuncle. Absent (0) or present (1).
	26.	Conical spines paired over lateral lobes. Absent (0) or present (1).
	27.	Conical spines, not paired. Absent (0) or present (1).

APPENDIX 2: DATA MATRIX

Characters:	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
Taxon:																											
<i>Ptychoceras minimum</i>	0	2	3	3	3	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Hamitella annulata</i>	0	2	2	3	3	0	0	2	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Hamites attenuatus</i>	0	2	2	3	3	0	2	2	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Hamites hybridus</i>	0	2	2	3	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Stomohamites nokonsis</i>	0	2	2	2	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Stomohamites parkinsoni</i>	0	2	2	2	3	0	1	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Stomohamites virgulatus</i>	0	2	2	2	3	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Lytohamites similis</i>	0	2	2	2	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Metahamites sablieri</i>	0	2	2	2	3	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Scaphamites passendorferi</i>	0	2	2	3	3	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0
<i>Hamitoides studerianus</i>	0	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0
<i>Lechites gaudini</i>	0	2	2	2	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
<i>Sciponoceras skipperae</i>	0	2	2	2	3	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
<i>Anisoceras saussureanum</i>	0	2	2	2	3	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0
<i>Prohelicoceras moutonianum</i>	0	2	2	3	3	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0
<i>Protanisoceras raulinianum</i>	0	2	2	3	3	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
<i>Heteroclinus nodosum</i>	0	2	2	3	3	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0
<i>Torquistylus anglicum</i>	0	2	2	2	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
<i>Pseudhelicoceras robertianum</i>	0	2	2	2	3	0	1	1	0	0	1	0	2	0	0	0	0	0	0	1	1	1	0	0	1	1	0
<i>Proturrilitoides astierianus</i>	0	2	2	2	3	1	1	1	1	0	1	0	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Turrilitoides hugardianus</i>	1	2	2	2	3	1	1	1	1	0	1	0	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Paraturrilites gresslyi</i>	1	2	2	2	3	1	1	1	1	0	1	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Eoscaphites circularis</i>	0	2	2	2	3	0	1	1	0	1	0	0	0	0	0	?	0	0	0	0	1	0	0	1	0	0	0
<i>Eoscaphites subcircularis</i>	0	2	2	2	3	0	1	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0
<i>Scaphites hugardianus</i>	0	2	2	2	3	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0
<i>Worthoceras worthense</i>	0	2	3	3	3	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0