ECOLOGY, STRATIGRAPHY AND PHYLOGENY OF THE HETEROMORPH AMMONOIDEA OF THE ALBIAN

NEALE MONKS

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SHORT ABSTRACT

The heteromorph ammonites (Mollusca: Cephalopoda: Ammonoidea: Ancyloceratida) of the Albian stage of the Cretaceous are reviewed from phylogenetic, morphological, and evolutionary perspectives. By use of cladistic analysis (using computer-based parsimony analysis) it is possible to hypothesise a likely evolutionary procession of ancestors and descendants, and to test the monophyletic nature of the families of Turrilitaceae, and to define the relationship of these families with each other and with the Ancyloceratecae from which they are presumed to have evolved.

Analysis of functional morphology indicates that heteromorph ammonites may have formed two distinct ecological groups: benthic or demersal forms which lived at a variety of depths on or close to the sea floor, and planktonic forms which were confined to deep water (greater than 100 to 200 metres) and were ecologically equivalent to modern *Spirula* and the cranchid squids. Both benthic and planktonic forms passed through a planktonic juvenile stage, which was may have been the important dispersive stage of the life cycle, resulting in the fossils of heteromorph ammonites being known from every continent.

Heterochronic processes are identified as important evolutionary mechanisms. The origin of the major planktonic groups of turrilitaceaen heteromorph ammonites can be characterised by progenesis, the precocious onset of maturity at a size and morphology comparable to the juveniles of the ancestors.

DETAILED SUMMARY

Heteromorph ammonites were an important and diverse element of the Albian (Lower Cretaceous) ammonoid fauna. They have been recorded from Europe, Asia Minor, Japan, northern and southern Africa, Madagascar, India, Australasia, Antarctica, western Canada, southern USA, Mexico, Venezuela, and Patagonia. These localities indicate that they were widely distributed throughout the Hoplitinid and Tethyan provinces. In the Gault Clay (Middle and Upper Albian) at Folkestone, heteromorph ammonites make up approximately one-quarter of the known species of ammonoid. They are absent from the Albian ammonite faunas of the Arctic (Gastroplitid) province.

Heteromorph ammonite phylogenetics have not been widely studied, and hitherto no computer based parsimony analyses have been performed. In this thesis a computer such an analysis is undertaken. Characters are derived from the gross morphology of the shell, the ornamentation of the shell, the ontogeny of the shell and rates of appearances of the ornamentation, and the shape and symmetry of the suture line. The resulting data matrix is searched using the Apple Macintosh computer program PAUP version 3.1.1 (Swofford, 1993) and the resulting trees examined using statistical tests such as Bremer decay indices and bootstrapping, and congruence with the stratigraphical record of the ammonites is also considered (Smith, 1993).

The heteromorph ammonites of the Lower Greensand, Gault Clay, Upper Greensand and Cambridge Greensand formations of southern England have not been comprehensively revised since the work of Spath (1923-1943) and Casey (1961). Also, while this thesis concentrates on the heteromorph ammonites of the Albian of southern England, global heteromorph ammonite faunas are also reviewed and compared. The phylogeny derived from the cladistic analysis is used to help revise the systematics at the family, genus and species level. The result is a full revision of the Albian Anisoceratidae, Baculitidae, Hamitidae, Ptychoceratidae, Scaphitidae, and Turrilitidae. The key changes are summarised below:

1. The Albian Anisoceratidae include the genera *Anisoceras*, *Protanisoceras*, *Rossalites*, *Idiohamites* and *Tuberolechites* (= *Lechites*(*Tuberolechites*)). With the exception of *Protanisoceras*, these are all monophyletic genera. *Protanisoceras* remains paraphyletic and something of a series of grade taxa of primitive Anisoceratidae. The entire family is monophyletic and derived from the Hamitdae, this is *contra* the proposal to amalgamate the families Anisoceratidae and Hamitidae proposed by Wiedmann & Marcinowski (1990).

2. During the Albian only two genera are recognised as members of a monophyletic family Baculitidae: these are *Lechites* and *Sciponoceras*. A new species of *Sciponoceras* is described here, *Sciponoceras skipperae*. The tuberculate baculiticone *Tuberolechites* is removed to the Anisoceratidae, the presence of paired nodes along the venter being a synapomorphy of that family. The inclusion of this subgenus as a tuberculate subgenus of *Lechites* as proposed by Cooper & Kennedy (1977) and Wright *et al* (1996) is not supported here.

3. The Hamitidae remains problematical. The family itself is paraphyletic, characterised only by the absence of the features diagnostic of the families of which it gives rise. Two monospecifc genera are recognised, *Metahamites* and *Scaphamites*. Other species previously included within *Metahamites* are shown to be members of the Anisoceratidae, specifically *Protanisoceras arrogans* (= *Metahamites elegans*) and *Protanisoceras dalpiazi*. The genera *Hamites*, *Lytohamites*, *Hemiptychoceras*, and *Hamitella* are grade groups of increasingly tightly coiled Hamitidae, some with helical juvenile whorls. Monophyly of none of these taxa can be convincingly proven. The genus *Stomohamites* is not supported at all by this analysis, even as a grade group, and its usage for certain Upper Albian Hamitidae is not endorsed.

4. The helical Albian heteromorphs comprise the monophyletic family Turrilitidae. This family is derived from the Hamitidae, the immediate sister group of Hamitidae being the genus *Hamitella*, which are characterised by relatively large helical juvenile coils. The tubercles of certain Turrilitidae are shown to be fairly unlike those of the Anisoceratidae and the hypothesised origin of these tuberculate Turrilitidae from that family (as stated by Matsumoto, 1967, Klinger & Kennedy, 1977) is not supported.

5. Although primarily Upper Cretaceous in range, the Scaphitidae appear in the Upper Albian. The genera *Scaphites* and *Eoscaphites* are recognised as forming a monophyletic family Scaphitidae derived from the Hamitidae. The genus *Worthoceras* is not included and referred to the Ptychoceratidae with which it shares morphological and sutural details, as proposed by Wiedmann (1965). The Scaphitidae are consequently not separate offshoots of the Lytoceratacеae, and the value of a superfamily Scaphitaceae to reflect an origin independent of the Turrilitaceae or Ancyloceratacеae as maintained by some authors (Wright, 1953, Besonov & Mikhailova, 1983) is questionable. However, the derivation of the Scaphitidae from the hamitid *Scaphamites* as proposed by Wiedmann & Marcinowski (1985) is not proven by this analysis.

6. The Ptychoceratidae are provisionally retained within the Ancyloceratacеae, including the genera *Ptychoceras* (=*Mastigoceras*), *Psilohamites*, and *Worthoceras*. *Worthoceras* has been previously included within the Scaphitidae (Henderson, 1973, Cooper, 1994a). The genus *Hamitoides* is also discussed and also retained within the Ancyloceratacеae, although familial rank is uncertain. It appears to be closely related to *Labeceras*, as proposed by Wiedmann & Dieni (1968), and this family is included within the paraphyletic Ancyloceratacеae (including the monophyletic Ptychoceratidae) which form the sister group to the monophyletic Turrilitaceae.

Heteromorph ammonites have been previously considered to have been planktonic to a greater or lesser degree (Nesis, 1986, Westermann, 1996), in this study the morphology of the shell is re-examined using mathematical and physical modelling techniques. The results indicate that ancylocones, aspinocones, and hamiticones could have been adapted to a benthonic habit. If the ammonite is restored as a small compact animal which does not fill the entire shell (see Monks & Young, 1998), and is then positioned near the aperture with the head and tentacles extended out of the shell, these shell morphologies will be oriented with the aperture toward the sea floor. Retraction of the body, using the paired head retractor muscles, shift the centre of mass and the orientation, pulling the aperture away from the sea floor. These morphologies are called "tilters" and could function in the way proposed by Kakabadza & Sharakadza (1993) but without the need to move water around the phragmocone to change the centre of mass. Baculiticones, ptychocones, and turriliticones are described as "non-tilters" since they do not change orientation if the body moves within the shell. They have a fixed orientation, with the long axis vertical, and show streamlining in that direction. This suggests that they were adapted to rapid or efficient vertical migration and could have been analogous in lifestyle to the modern vertically migrating coleoids such as *Spirula spirula* and the Cranchidae which live in moderately deep water by day (100 to 600m), rising to the surface to feed at night.

The ontogeny of the heteromorphs is conservative. The eggs of heteromorph ammonites are unknown, however the nepionic constriction is taken to indicate the size at hatching and indicates that most were about 1 mm in length when they hatched (Tanabe *et al*, 1980, Lebrun, 1996). This is consistent with modern oceanic cephalopods which produce large numbers of small eggs from which planktonic juveniles emerge (Mangold, 1987). The planktonic juveniles had smooth shells which were crioconic and coiled in one plane, this is the neanic stage. Helicosity appeared in the next stage of growth (if it appeared at all), described here as the *juvenile-A stage*. Coiling was still crioconic, but the shell also acquired the adult ornament, such as ribs or tubercles. The next stage is referred to as the *juvenile-B*

stage, at which point "heteromorph-coiling" becomes apparent, such as by the breaking of the regular spiral into either straight shafts, sharp bends, and hooks.

The relative duration of the juvenile-A and juvenile-B growth stages can be identified as evidence of heterochronic processes. The tilting morphotypes tend toward having juvenile-A and juvenile-B growth stages of approximately similar duration. In contrast, the non-tilting Turrilitidae can be derived from the hamitid genus *Hamitella* through progressive expansion of the helical juvenile-A stage and loss of the planar juvenile-B stage. Equally, the Baculitidae exhibit a dissimilarity between the proportions of the juvenile-A and juvenile-B growth stages. The juvenile-A growth stage is very reduced, and almost the entire shell is formed by a single straight shaft. The ontogeny of the Turrilitidae and the Baculitidae are discussed in reference to their modes of life, and it is concluded that both exhibit degrees of progenesis consistent with the view that these lineages remain planktonic as adults where the others become benthic or demersal.

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CHAPTER ONE: INTRODUCTION

Background And Development Of The Thesis

This thesis has its fundamental origins in discussions by a number of palaeontologists at the Natural History Museum on the state of ammonitology. Foremost among these were Andy Gale, Brian Rosen, and Noel Morris, whose attention had been drawn by the apparent reliance of modern ammonitologists on rather old and dated work for their concepts of ammonite palaeobiology. Brian had initially raised the problem of ammonite palaeoecology following a series of undergraduate classes he had been giving, finding that there had been very little review of the concepts within the subject in the last fifty years. Although the view that heteromorphs were decadent lineages characterising the overall decline of the ammonites which were heading toward inevitable extinction has now been refuted (see Wiedmann, 1969), our understanding of how these ammonites lived and evolved is still limited.

As a whole ammonitologists have been conservative, at least in part because the value of the group has been weighted more in favour of the stratigraphical utility of the fossils than on the ecology, morphology and evolution of ammonites as animals. What palaeobiology does exist is based on a limited number of paradigms, of which by far the most influential is the inferred similarity of ammonites with the 'living fossil' *Nautilus*. There are alternatives, of which one of the interesting is that ammonite shells need not have been external. A number of species of ammonite have been demonstrated to have at least partial enclosure of the shell in mantle during life (Doguzhaeva & Mutvei, 1989, 1993b). Parallels could be drawn between an endocochleate ammonite and the modern coleoid *Spirula spirula* which has an internal shell, and which lives in deep water feeding on plankton.

Cladistic methods have not been applied to ammonite taxonomy, which is consequently fragmentary and largely based on stratigraphical calibration of inferred morphological transitions (e.g., on certain Ancyloceratidae, Casey, 1960, on the Scaphitidae, Wiedmann, 1965, and on the Turrilitidae, Klinger & Kennedy, 1980). There are two obvious problems to these studies: the assumption that the fossil record is sufficiently complete to furnish all the critical data, and that the morphological transitions depend on *a priori* hypotheses of evolutionary progression that colour the nature and types of data studied.

To undertake a phylogenetic analysis two things are required: a sample of taxa sufficiently rich in characters to build up a data-matrix, and a certainty that the fossil species being studied belong to a monophyletic clade themselves, even if their exact relationships are

uncertain. Andy Gale's attention had been focused on the well preserved heteromorph ammonites of the stratigraphically detailed Albian section at Folkestone, Kent (FIGURE 1.0). The ammonites there are as diverse morphologically as any ammonite fauna anywhere in the world: of well over 200 species of ammonite recorded there, at least one-quarter are heteromorphs (Casey in Smart *et al*, 1966). Almost all of those heteromorphs belong to a single superfamily, the Turrilitaceae, and the section spans the history of the group from their first appearance of the earliest families, the Hamitidae and Anisoceratidae (Lower Albian, *Douvilleiceras mammillatum* Zone), through to the origin of three families which reach their zenith in subsequent stages (namely the Turrilitidae in the Middle Albian and Baculitidae in the Upper Albian). The Folkestone section also contains the earliest members of the Scaphitaceae (the genus *Eoscaphites*). The Scaphitaceae are partially recoiled heteromorphs of which are tremendously diverse and widespread in the Upper Cretaceous. While many of the fossils found at Folkestone can be found elsewhere, in most places they are part of poorly resolved or condensed series of beds (e.g., Escragnolles in south-eastern France, or the condensed Albian of the Tatra mountains in Poland). In contrast the Folkestone section is well understood and contains relatively few breaks in sedimentation (Owen, 1971a). All in all, the Albian can be thought of as a time of great diversification for the heteromorph ammonites, and the Folkestone Sands and Gault Clay at Folkestone perhaps the best place in the world to study it.

So, at heart the fundamental problem is this: Ammonitology has been slow to review established paradigms, with the result that a limited number of ideas have been infrequently challenged or discussed. And the collections in the Museum as well as easy access to new material from the Folkestone section provide the ideal material to make a detailed study of the evolution of the heteromorph ammonites. Thus, in, 1994 it was proposed that a biologist be given the opportunity to work with ammonites

Structure And Content Of The Thesis

Many theses are unwieldy aggregations of research and review articles, united by a common author and a title that bears a greater or lesser relationship with the actual content. My intention is that this thesis should not be one of those. I have attempted to write what amounts to a natural history of a diverse and successful, but hitherto poorly understood, group of cephalopods.

I have deliberately divided the main body of this thesis into three parts, although this is admittedly artificial and serves here only to make reading and reviewing easier. The first section is taxonomic, and concerned with using a modern technique (parsimony analysis) to

resolve the systematics of the group. Even this division glosses over the circular nature of phylogenetic studies. In practice while describing the morphology of individual species feeds directly into the character matrix on which the cladistics is based, the evolution of the data matrix and cladistic process itself causes changes in the way characters are considered and described. It is often said that this belies the subjective nature of cladistics as a science. My belief is that this circular action is a kind of 'fine tuning' of the definitions as views on the homology of characters changes rather than as fudging data to fit an hypothesis.

The second section is on the functional morphology, specifically on the relationship between shell geometry, orientation and position in the water column, and the mode of life of heteromorph ammonites. Parts of this work have been published in papers on the functional morphology of belemnites (Monks *et al*, 1995) and heteromorph ammonites (Monks & Young, 1998). My own view is that too much certainty has been applied to a relatively old model of ammonite anatomy (specifically, Trueman, 1941), and that there are equally plausible alternatives that better fit some of the available evidence.

The final section draws the first two threads together to produce a synthesis on the evolution of the Albian heteromorphs. Use of cladistics is new to ammonitology, and my own views on the functional morphology of the heteromorphs compared to other authors has (I submit) lead to new and important conclusions on the taxonomy and phylogeny of the group.

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I am genuinely grateful to the original supervisor of this project, Andrew Gale, for making it possible for me to work on such an interesting and challenging group of fossils. Although on paper his supervision of the project ended when he was appointed to the chair of geology at the University of Greenwich, his interest and support remained.

Noel Morris at the Natural History Museum and Howard Johnson at the Royal School of Mines ably provided additional discussion, supervision and direction, especially after Andy's departure from Imperial College. To both of them I am thankful.

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On matters taxonomic and phylogenetic I must especially thank Marcello Ruta (Natural History Museum) and W. J. Kennedy (University of Oxford Museum). Marcello helped explain how I might use cladistics, and was instrumental in the decision to use computer-based parsimony analysis as a key to understanding ammonite phylogeny. Jim Kennedy provided many references and commented on aspects of the taxonomy and stratigraphy of the heteromorph ammonites discussed here. However our conclusions may differ, I must acknowledge his contribution to my project. Thanks must also go to Mike Cooper (University of Durban, South Africa), J. David Hardwick (Imperial College), Gerd Westermann (McMaster University, Canada), and Janet Voight (Field Museum, Chicago) for their valuable discussions on the stratigraphy, ecology and evolution of the Cephalopoda.

I must also thank the Jackie Skipper for providing almost continuous moral support throughout my time at the museum, and wish her every success with her own project. The three years during which we shared an office were both educating and entertaining, and the PhD experience would have been very different without her.

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GLOSSARY OF TERMS

There are a large number of morphological, physical and ecological terms used in this thesis. To save explaining them at every instance, I have included this glossary. Based largely on the general ammonite reviews by Lehmann (1981) and Lebrun (1996). Asterisks (*) indicate new terms introduced in this thesis.

AMMONOIDEA: A subclass of the Cephalopoda, generally known as ammonoids. Sometimes divided into the mostly Palaeozoic "palaeoammonoids" and the largely Jurassic and Cretaceous "neoammonoids". The latter group includes the true ammonites, the order Ammonitida, and the heteromorph ammonites, the order Ancyloceratida.

ANCYLOCONIC: (FIGURE 1.1) Where coiling resembles the Aptian heteromorph *Ancyloceras*. Typically only part of the phragmocone is coiled in a planar or helical spiral. The later part of the phragmocone and the entire living chamber form a deep U-shaped hook with two subparallel shafts connected by a 180° bend. The ornamentation on the straight parts, and especially the living chamber, are often different to that of the phragmocone. Sometimes described as hamitid, along with hamiticones (q.v.) by certain authors (e.g., Spath, 1923-1943) the usage of Casey (1960) is adopted here.

ANNULAR RIB: A rib that goes around the entire circumference of the whorl. Annular ribs may or may not be weakened on the dorsal or ventral surface, but contrast with minor ribs which are limited to a small portion of the whorl (q.v.).

ASPINOCONIC: (FIGURE 1.2) Where coiling resembles the Aptian heteromorph *Aspinoceras*. Typically the entire phragmocone is a simple planar spiral with a regular rate of expansion. The living chamber is marked by a slight increase in expansion rate (and often a change in ornament) and the formation of a shallow hook. There are no straight shafts (c.f. ancyloconic coiling). Sometimes described as ancyloconic (e.g., Spath, 1923-1943) the usage of Casey (1960) is adopted here.

ASYMMETRY: (Of suture.) When viewed from the ventral or dorsal surface, the left and right hand sides of the suture line (q.v.) are usually similar. In some cases they are not, and one side may exhibit reduction, compression or simplification. Such a suture line is described as asymmetrical.

APICAL ANGLE: The angle formed by the sides of the shell of a helically coiled ammonite at the apex (the top of the spire).

BACULITICONIC: (FIGURE 1.3) Where coiling resembles the Upper Cretaceous heteromorph ammonite *Baculites*. The entire post-neanoconch shell forms a single straight shaft. Also referred to as orthoconic by some authors, although orthocone nautiloids lack the initial spiral.

BIFURCATION: Splitting of ribs into two, usually toward the venter. In cases where the splitting occurs at a tubercle, the rib may be described as being fibulate.

BULLA: A radially elongate structure on the internal mould of an ammonite indicative of a spine. The attached spine is rarely preserved. Bullate tubercles are typically tear-drop shaped. On turriliticone ammonites which bear them, the sharp end of the tubercle points toward the apex.

CENTRE OF BUOYANCY: Centre of mass of the fluid displaced by an object completely immersed in that fluid. By Archimedes' Rule, the volume of the displaced water is equal to the volume of the object. In effect, the pivot point of a free-floating object.

CENTRE OF MASS: Point through which the mass (weight) of an object can be considered to act. Also known as the centre of gravity.

COLEOIDEA: A subclass of the Cephalopoda, commonly referred to as the inkfish, and including the squid, cuttlefish, octopuses and vampire-squids. The dominant cephalopods of Cainozoic marine communities, they were also widespread in Mesozoic seas (such as the belemnites, order Belemnitida).

COLLAR: A thickened annular rib at the final aperture (peristome) of the shell usually associated with maturity (q.v.). Apertural collars may be singular or paired.

CONSTRICTION: A brief but distinct contraction of the diameter of the whorl. Constrictions may be periodic throughout ontogeny or associated with maturity only (q.v.).

CRIOCONIC: Where coiling resembles the Lower Cretaceous heteromorph *Crioceras*. The entire shell consist of an open planar spiral, with no change in rate of expansion at any stage (cf. aspinoconic).

EFFACEMENT: Reduction in the height (profile) of a rib.

FIBULATE: Also known as "button and loop". See bifurcation of ribs (q.v.).

HAMITICONIC: (FIGURE 1.4) Where coiling resembles the Albian and Cenomanian heteromorph *Hamites*. Only the initial part of the shell is a planar or helical spiral, the remainder of the shell consists of three subparallel straight shafts. The last shaft and the preceding bend are usually living chamber. The three shafts are not in contact (c.f. ptychoconic). There may be little or no difference in the ornamentation of the phragmocone and living chamber. Hamiticones and ancylocones are sometimes referred to as hamitid coiling (e.g. Spath, 1923-1943), the stricter sense of hamitid in Casey (1960) is considered here to be synonymous with hamiticone.

HETEROMORPH: Ammonites which have shells which depart from planar, regular spiral coiling. Heteromorph lineages are generally taken to be those which have reached this state secondarily, i.e., from regular coiled ancestors. This is reflected in the possession of a planar regular coiled phase in the earliest stages of ontogeny. Heteromorph ammonites appear periodically in unrelated lineages in the Triassic, Jurassic and Cretaceous (cf. Heteromorpha).

HETEROMORPHA: Term used in the sense of Casey (1960) in reference to the Ancyloceratacеae and Turrilitaceae of the Upper Jurassic and

Cretaceous. As a group characterised by uncoiled shells and a tendency in many lineages toward helicosity. In most taxa the suture line is quadrilobate. The origins of the group are uncertain.

HOMOMORPH: Planar, spiral coiled ammonite. This is the typical morphology of most ammonoids (cf. heteromorph).

***JUVENILE-A:** (FIGURE 1.6) A name coined here for the period of growth proceeding from the neanoconch and ending at the onset of juvenile-B growth (see below). Juvenile-A growth is characterised by regular spiral coiling, as with the neanoconch, but with the acquisition of adult-style ornament (e.g., tubercles). Possibly an arbitrary division, but the change in coiling may signify a change in ecology. In the adult, juvenile-A growth is represented by the early part of the phragmocone.

***JUVENILE-B:** (FIGURE 1.6) A name coined here for the period of growth proceeding from the end of juvenile-A growth (see above) and ending with the onset of mature growth. Juvenile-B growth is characterised by a departure from the regular spiral growth of juvenile-A. In the adult, juvenile-B is represented by the later part of the phragmocone.

LOBE: A part of the suture line (q.v.). Lobes represent the insertion of the posterior folds of the septa into the internal wall of the shell. They are very variable and have been used widely for taxonomy.

MAJOR RIB: An annular rib (q.v.). In contrast to minor ribs (or striae) which are incomplete.

MATURITY: (FIGURE 1.8) Maturity is marked by the approximation of the septa, which indicates a slowing down (or cessation) of somatic growth. Mature growth is taken here to comprise the final living chamber and any structure associated with it, such as collars.

MINOR RIB: An incomplete rib, usually covering only the ventral surface of the shell (c.f. major rib).

NEANOCONCH: The immediate post hatching phase of growth. The neanoconch lacks the ornament found on the juvenile and mature shell.

NODE: A structure on the internal mould of an ammonite indicative of a spine which is approximately circular at the base (c.f. bulla).

PEELING: A particular mode of predation in which a predator cuts away a narrow strip along the living chamber of a shell and can then draw out the soft tissues of the prey. Peeling predators are very common in modern seas, although most are benthic crustaceans such as crabs, mantis shrimps, and spiny lobsters.

RECTIRADIATE: A description of a rib which is arranged radially.

RURSIRADIATE: A description of a rib in which the ventral (peripheral) edge is oriented away from the aperture.

SADDLE: A part of the suture line (q.v.). Saddles represent the insertion of the anterior folds of the septa into the internal wall of the shell. They are not so variable as lobes and have less taxonomic value.

STABILITY: The ability of a structure or system to resist perturbation. Applies to ammonites and other free-floating or swimming animals relates to the ability of the animal to resist displacement.

SUTURE LINE: A suture line is a diagrammatic representation of the insertion of the folds of the septa into the internal wall of the shell. The line can be divided into lobes and saddles. Suture lines are very variable and have been widely used for taxonomic purposes.

TUBERCLE: Projections from the main body of the shell which give rise to spines.

TURRILITICONIC: (FIGURE 1.5) Where coiling resembles the Cenomanian heteromorph *Turrilites*. The entire post-neanoconch shell is coiled helically, the rate of translation usually being approximately constant.

UMBILICUS: The central whorls of an ammonite shell. In heteromorphs it is typically open, the whorls are not in contact and later whorls do not cover the preceding ones. In the Scaphitidae the umbilicus tends to be closed and later whorls overgrow the earlier ones.

CHAPTER TWO: CLADISTIC ANALYSIS

Summary

The Albian heteromorph ammonites can be divided into two groups, the monophyletic Turrilitaceae, and the paraphyletic Ancyloceratacеae. The Turrilitaceae may be further subdivided into at least four families, three of which (the Anisoceratidae, Baculitidae, and Scaphitidae) are here demonstrated to be monophyletic, and a fourth paraphyletic Hamitidae from which the other three are derived. The Ancyloceratacеae are poorly represented in the Albian, being more diverse in the Aptian, but at least one monophyletic family can be recognised, the Ptychoceratidae, which is the sister group to the Turrilitaceae.

Within the Turrilitaceae three distinct trends can be observed. One is toward the acquisition of tubercles, which characterises the Anisoceratidae and the Scaphitidae. A second trend is toward regular coiling and subsequent loss of the long body chambers and open whorls, this is seen in the Scaphitidae. A final trend is seen in the Anisoceratidae and the Hamitidae toward helicosity. Ammonites with tightly folded hamiticonic shells usually begin with a helical juvenile phase, helicosity persists through into adulthood among the Turrilitidae, together with asymmetry of the suture, closure of the umbilicus, and vertical shifting of the siphuncle.

Cladistic analysis provides an objective was of resolving ammonite taxonomy, although hitherto it has been deemed to have little value compared with stratigraphy. The conclusions derived from this analysis at least show a parsimonious pattern of character change, which satisfies modern thinking on taxonomic research. Equally, a well thought out phylogeny provides a good framework for deducing the evolution of ammonite form and function.

Introduction

Ammonites as cephalopods

Of the, 100,000 species of mollusc alive today, rather less than, 1,000 are cephalopods. The high level taxonomy of the cephalopods is currently in a state of flux, reflecting the gradual application of cladistic over traditional methods of systematic practise (Vecchione, 1994, Voight, 1997).

Traditionally, the extant cephalopods have been classified within two subclasses, the Nautiloidea and the Coeloidea. The Nautiloidea comprises a single order, Nautilida, with a single genus, *Nautilus*. The Coleoidea are far more diverse and includes four orders, the Sepioidea, the Teuthoidea, the Octopoda, and the Vampyromorpha. Voss (1977) has summarised this systematic approach (FIGURE 2.1). The relationship of the Ammonoidea with the other cephalopods has been debated, although historically they have been allied with the Nautiloidea on the basis of the external shell and the supposed shared characteristic of four gill lamellae (Miller & Furnish in Arkell *et al*, 1957).

More recently Berthold & Engeser (1987) proposed a revision of cephalopod taxonomy using cladistics (FIGURE 2.2). Their taxonomy reflects a belief that the Ammonoidea and Coleoidea are sister groups united into a taxon Angusteradulata on the similarity of the radula of these two groups compared with Nautiloids (Lehmann, 1967, Nixon, 1995). This change in taxonomy has caused a reassessment of the validity of *Nautilus* as a model for ammonite anatomy and lifestyle (Jacobs & Landman, 1994), and even the possibility of lineal descent of octopods from ammonites (Lewy, 1996). The problem remains that many of the ammonite taxa, especially the Palaeozoic and Triassic orders, are "grade groups" stating more about perceived evolutionary pathways than actual natural clades (Engeser, 1996).

There are two different views of heteromorph ammonite taxonomy that can be best described as being 'traditional' on the one hand and 'phylogenetic' on the other. The traditional school recognises at least three different superfamilies of heteromorph ammonites: the Ancyloceratáceae, Turrilitaceae, and Scaphitaceae (FIGURE 2.3). These groups evolved independently from the Lytoceratina (Wright, 1952) or from the Ammonitida (Casey, 1960) and are united under the 'Heteromorpha' on the basis of their uncoiled shells only.

Some authors have attempted to demonstrate intergradation of taxa by examining changes in a range of characters and not just coiling mode, and thereby create a phylogenetic basis to taxonomy (Wiedmann, 1965, 1969, Schindewolf, 1968). Wiedmann (1962) and Wiedmann &

Dieni (1968) undertook important reclassifications of the Albian heteromorphs using this approach. The suture line has been supposed to be an important source of taxonomic data, since it is complex but probably conservative within lineages, compared with external ornamentation, for example (Wiedmann, 1966). The resulting taxonomies differ from the traditional ones in a number of important ways, such as the positioning of *Worthoceras* with *Ptychoceras* and not *Scaphites*, and the unification of the Anisoceratidae and Hamitidae (FIGURE 2.4)

Examinations of suture lines have recently been used to suggest independent origins of the Ancyloceratoceae and Turrilitaceae, the former from the Ammonitida and the latter from the Lytoceratida (Doguzhaeva & Mikhailova, 1983), although this conclusion was rejected by Wiedmann & Kakabadza (1993) who demonstrated that the sutural morphology of the supposed ancyloceratacean *Ptychoceras* is variable and can be indistinguishable from that of a turrilitacean. As things stand now, the phylogenetic approach to ammonite taxonomy has not been fully tested. Wiedmann's studies lack a broad base of morphological characters and a wide ranging analysis of taxa, tending to concentrate on discrete lineages using supposedly diagnostic features. This makes it difficult to come to any general conclusions on the phylogeny of the group.

In general, the traditional heteromorph taxonomy is still the most widely used system, as summarised most recently in the revised *Treatise on Invertebrate Paleontology* (Wright *et al*, 1996). The *Treatise* is essentially concerned with pigeon-holing genera within a recognised framework, and accepts the polyphyletic nature of certain taxa.

The families of heteromorph ammonites are based around 'form genera' which epitomise the characteristics of the family as a whole. This is historical in origin and reflects the successive decomposition of certain very broad genera — i.e., *Baculites* Lamarck, 1799, *Turrilites* Lamarck, 1801, *Scaphites* Parkinson, 1811, and *Hamites* Parkinson, 1811 — from the early, 19th century into successively more exclusive genera within families such as the Baculitidae, Turrilitidae, Scaphitidae and Hamitidae. The evolution and breadth of these taxa are briefly summarised below.

Family Baculitidae Meek, 1876

There is probably only one genus representative of the Baculitidae in the Albian, the Upper Albian genus *Lechites* (Spath, 1923). Within that a distinctive subgenus *Tuberolechites* has been described, characterised by paired ventral tubercles (Cooper & Kennedy, 1977). The exact origins of the family remain cryptic but a monophyletic origin within the Hamitidae has

been presumed (FIGURE 2.5, Spath, 1941, Matsumoto, 1959, Matsumoto & Obata, 1963, Cooper & Kennedy, 1977). Indeed, the closeness of the Baculitidae and Hamitidae was underlined by the inclusion of the Hamitidae as a subfamily within the Baculitidae by Wiedmann, defining that group as having, 1 or 3 straight shafts (Wiedmann, 1962, 1968). Certainly the suture lines, ornamentation and apertural modifications of the early baculitids such as *Lechites* can be seen in many Hamitidae.

Family Turrilitidae Meek, 1876

In contrast with the Baculitidae, the Turrilitidae are fairly diverse throughout the Middle and Upper Albian. They are exemplified by the Cenomanian ammonite *Turrilites* which is helically coiled throughout post-neanic ontogeny. Within the Albian stage there are five generally recognised genera in total, *Proturrilitoides*, *Turrilitoides*, *Pseudhelicoceras*, *Mariella*, and *Ostlingoceras*(Wright *et al*, 1996), although Scholz (1979) considered *Proturrilitoides*, *Turrilitoides* and *Ostlingoceras* to be subgenera of *Turrilites* and removed *Pseudhelicoceras* to the Anisoceratidae as a subgenus of *Anisoceras*. *Mariella* and *Ostlingoceras* are restricted to the Upper Albian and range into the Lower Cenomanian. *Proturrilitoides* and *Turrilitoides* are so similar to juvenile Hamitidae that derivation of the former from the latter has been believed for a long time (Spath, 1937, Breistroffer, 1953). However, monophyly has not been presumed for the group. Spath (1937, 1939) and Matsumoto (1967) postulated a diphyletic origin for the Turrilitidae (FIGURE 2.6). The non-tuberculate Turrilitidae such as *Proturrilitoides* and *Turrilitoides* are derived from the Hamitidae, while the tuberculate Turrilitidae such as *Pseudhelicoceras* arise from the Anisoceratidae. Klinger & Kennedy (1978) discussed this possibility, but they did not propose dividing the family Turrilitidae into two monophyletic taxa, and believed that tuberculation may have evolved independently among the Turrilitidae.

Superfamily Scaphitaceae Meek, 1876

The Scaphitaceae were not originally viewed as turrilitaceaean derivatives because the suture lines commonly have more than four lobes. The origins and the affinities of the group remain problematical, opinion divided between an origin from the Lytoceratacеae independent of the Turrilitaceae (Wright, 1953, Besonov & Mikhailova, 1983), or derived from the Turrilitaceae, specifically the Hamitidae (Wiedmann, 1965, Wiedmann & Marcinowski, 1985).

Spath considered the Scaphitidae to be possibly polyphyletic derivatives of the Lytoceratacеae. Albian species such as *Eoscaphites circularis* was considered to

morphologically close to true *Lytoceras*, although superficial similarity with *Hamites* was noted. The genus *Worthoceras*, at that stage only known from North America, was cited as an independently evolving scaphitid, perhaps giving rise to American *Scaphites* where *Eoscaphites circularis* was ancestral to the Eurasian forms (Spath, 1937). In contrast, Wright (1952) believed the Scaphitaceae to be monophyletic, and rather than a separate lineage, *Worthoceras* represented an early offshoot of the Scaphitaceae, the subfamily Otoscaphitinae, characterised by small size and a quadrilobate suture. The remaining scaphitids were placed in the Scaphitinae (Wright, 1953). In a recent phylogenetic review of the Scaphitaceae, Cooper (1994a) recognised three families: the Otoscaphitidae, the Scaphitidae, and the Eoscaphitidae, containing the genus *Eoscaphites* only, from which the other two families are derived (FIGURE 2.7).

Wiedmann (1965) has demonstrated that even scaphitids with more than four lobes when mature are quadrilobate when young. The extra lobes develop from divisions within the umbilical saddle and were termed pseudolobes to distinguish them from the true lobes, which are present from the very start. Furthermore, Wiedmann could show a progressive increase in sutural complexity beginning with *Hamites*, through *Eoscaphites* and on through *Scaphites* and *Hoploscaphites*. This removed the direct link with the Lytoceratacеae which have similarly complex sutures, and instead derives the scaphitids from the Turrilitaceae through *Hamites*, rendering the suture line an example of convergence with *Lytoceras* rather than a shared, derived feature. Wiedmann & Marcinowski (1985) believe that *Scaphamites* is the link between the Hamitidae and the Scaphitaceae (FIGURE 2.8). The independent origin of *Worthoceras*, first postulated by Spath, was considered by Wiedmann to be correct, and that *Worthoceras* is a ptycoceratid offshoot (Wiedmann, 1965), although this has not been widely accepted (Henderson, 1973, Cooper, 1994a).

Families Anisoceratidae Hyatt, 1900 (In: Zittel, 1900) and Hamitidae Hyatt, 1900 (In: Zittel, 1900)

Separation of these families has been much debated, and so they are here considered together. While superficially quite distinct, problems arise when classifying species which seem to bridge the divide between the two families.

Initially, *Hamites* covered both tuberculate and non-tuberculate irregularly coiled ammonites, later Pictet (1854) devised the genus *Anisoceras* to include the tuberculate forms only. Both genera were included within the Hamitidae by Gill (1871). Hyatt later divided the family into the non-tuberculate Hamitidae and tuberculate Anisoceratidae (Hyatt, 1900 (In: Zittel, 1900)), this is still the most widely accepted taxonomy (Wright *et al*, 1996). This is based on a

presumed origination of tubercles in one Lower Albian stock, which gave rise through *Protanisoceras* to *Anisoceras*, *Idiohamites* and allied genera (Spath, 1923, 1925a). While the Anisoceratidae may well be characterised by the presence of tubercles, the Hamitidae remains an ill-defined group comprising those heteromorphs lacking features characteristic of the other taxa.

Wiedmann suspected that the separation of the tuberculate and non-tuberculate heteromorphs might be artificial, and that tuberculation may have evolved more than once, and included both sorts of heteromorphs within the family Hamitidae (Wiedmann, 1962, Wiedmann & Marcinowski, 1990). The likely flexibility of tuberculation as a character is underlined by the "incipient tuberculation" of *Hamites hybridus* and the "transitional forms" between *Hamites praegibbosus* and *Protanisoceras blancheti* recorded by Casey (1961). Other than the presence of tubercles, anisoceratids are very like hamitids in terms of ribbing, suture line morphology, and coiling mode. In addition, the small size of some species of *Hamites* and *Protanisoceras* results in the suture lines being relatively simple, so interpretation of the lobe morphology can be ambiguous (E. D. McKenzie, pers. comm.).

Hamitoides and *Ptychoceras*

The relationships of these genera to the other Albian heteromorphs is uncertain. *Hamitoides*, an incompletely known tuberculate ammonite, has superficially *Hamites*-like ornament, except that the annular ribs are often bifurcate. The bifurcations are slightly raised, and like *Scaphites*, may give rise to weak bullate tubercles. Spath considered it to be an aberrant member of the Anisoceratidae (Spath, 1939). Arkell *et al* (1957) considered the Labeceratidae, within which *Hamitoides* was provisionally placed, to be derived from the Lytoceratidae and allied with the Scaphitidae within the Scaphitaceae. On the other hand, Wiedmann & Dieni (1968) placed the Labeceratidae, including *Hamitoides*, within the Hamitidae. More recently the Labeceratidae have been demonstrated to be Ancyloceratacеae which resemble *Scaphites* (Förster, 1975, Henderson, 1990, Wright *et al*, 1996). *Hamitoides* is provisionally placed within this predominantly southern hemisphere family, but the fragmentary nature of its fossil record makes this assignment uncertain.

Equally perplexing is the dwarf heteromorph *Ptychoceras*. Wiedmann (1962) believed the separation of this genus into a family Ptychoceratidae within the Ancyloceratacеae to be artificial, considering the closeness of coiling mode with the unquestioned hamitid *Hemiptychoceras*. The suture line which had been believed to be more like that of typical Ancyloceratacеae in having trifid lateral and umbilical lobes was demonstrated to be an

unstable and probably undiagnostic character on which to base this assignment (Wiedmann & Kakabadza, 1993). Wright *et al* (1996) have maintained the position of the Ptychoceratidae within the Ancyloceratacеae.

Other than the families Ptychoceratidae and Labeceratidae, the Ancyloceratacеae appear to be absent from Albian ammonite faunas (Wright *et al*, 1996).

Ammonite phylogenetics and previous use of the cladistic methodology

The phylogenetic basis for taxonomy as propounded by Wiedmann (1962, 1965, 1969), Wiedmann & Dieni (1968) and Wiedmann & Marcinowski (1985) is attractive since it attempts to interpret the diversification of the group as a series of evolutionary events. However, these taxonomies suffer from the lack of an explicit methodology, tending to be a subjective analysis of characters such as the suture line in defence of an *a priori* hypothesis of heteromorph ammonite evolution. Ideally, a phylogeny should be built on as objective a series of data as possible, with the minimum number of assumptions made beforehand. Cladistics is a powerful method for constructing phylogenies, and parsimony analysis one of the simplest approaches.

Cladistic analysis makes two assumptions: that life itself originated once and subsequently diversified, and that the distribution of characters among organisms reflects a natural order which can be classified (Smith, 1994), and that the only taxonomic units that are meaningful, monophyletic ones, termed natural groups or *clades* (Hennig, 1966). Ammonites have been studied cladistically very rarely. Matsumoto (1967) and Klinger & Kennedy (1978) have constructed a fairly detailed phylogenies of the Nostoceratidae and Turrilitidae but did not substantiate their proposals with descriptions of the changes at the implied nodes. Landman (1989), Cooper (1991, 1992, 1994a, 1994b, 1997) and Engeser (1996) have used hand-crafted cladograms to elaborate on hypotheses of ammonoid evolution. Hand crafted cladograms are based on an intuitive or hypothetical belief in the natural order of a group of taxa, perhaps derived from stratigraphy or observable ecological trends. Usually the operator begins by trying to build all the possible trees and reserving those that match the original hypothesis. However, as a the number of taxa increases, it becomes less easy to appreciate all the possible trees. The solution to this is to use a computer, which is very good at doing these sorts of tasks very quickly. Computer-based parsimony analysis is one such method. It has never been used to construct cladograms for ammonite groups, perhaps because of the perceived lack of characters (T. Engeser, pers. comm.).

In this study parsimony analysis is used, specifically the Apple Macintosh program Phylogenetic Analysis Using Parsimony (PAUP version 3.1.1, Swofford, 1993). Parsimony analysis works on the premise that the tree (cladogram) with the fewest character state changes (steps) is the most likely to reflect the natural order (actual history) of the group *since it requires the least number of character origination events (homologies).* This means that the number of parallelisms (homoplasies) are minimised (Kluge, 1984).

The PAUP analysis works on a data matrix, which includes information on the morphological characters observed in the ammonites studied. This requires the characters to be coded, which makes the data available to the computer, and also builds into the data matrix assumptions on the nature of the characters. There is an extensive literature on the value of the two main coding methods, which will be briefly summarised here.

The simplest form of coding is Binary (or Absence/Presence) Coding. This has been advocated by Pleijel (1995) as being the least subjective method since it makes no prior assumptions of homology of the various characters and character states but treats every possible permutation of character presence and state as an individual character which is either absent or present. Binary coding would, for example, code bullate tubercles and clavate tubercles as individual, unique characters.

Pimental & Riggins (1987) and Meier (1994) reject Binary Coding in favour of Multistate Coding. Multistate Coding identifies discrete sets of states applicable to a specific character, and concludes that each state is homologous with every other state. The fundamental point is that while Binary Coding views every morphologically different feature as an independent character that is either there or not, Multistate Coding recognises more complex characters which may be absent or present in one of a range of morphologies. In terms of evolutionary theory, while a Multistate-based analysis would recognise a single origination event for a character followed by a radiation into *n* different states, a Binary-based analysis instead recognises *n* different, independent origination events. For this analysis I concur with Pimental & Riggins (1987) and Meier (1994) in the inappropriateness of binary coding for cladistic analysis, and have instead followed the pattern of Voight (1997), who produced a cladistic analysis of extant Octopoda. She used multistate characters, predominantly unordered, but including ordered characters where justifiable (see individual character descriptions, below). I find it difficult to justify coding for each different shape of tubercle as a separate character, or a bifid lobe as a separately evolved, distinct structure from a trifid one.

Ordering means that instead of the *n* different character states being considered to be able to interchange freely, it is assumed that the evolutionary progression happened along a certain

order, from state *a* to state *b* to state *c*...and so on. During the search this affects the length of the trees found. When character states are deemed unordered, then the length of the change from any one state to any other state is counted as, 1. In contrast, for an ordered character, the length is equal to the number of intermediate states it must pass through. The result is that during a parsimony analysis, trees which involve stepwise changes along a character state progression will be favoured (i.e., have fewer steps) than those which have character states changing through many different transitions (i.e., have more steps).

The construction of an evolutionary tree brings together the taxonomic organisation of the taxa from the cladistic analysis and the resolution of the stratigraphical record. Where a cladogram is exclusively about nesting taxa within a hierarchical structure through a formal character analysis, an evolutionary tree attempts to say something about the history of a group, especially in terms of ancestors and descendants (Smith, 1994).

For this study a specific procedure was procedure:

(1) **Identification and formalisation of the taxa to be analysed.** This study concentrates on the Albian heteromorph ammonites, of which the best collections have been made from the Gault Clay at Folkestone, England and Escragnolles, France, although ammonites from other localities were included. The full list of species studied is listed in Figure 2.4. The number of taxa studied is limited by the memory available to the computer and the ability of the computer program to analyse large data sets within a reasonable length of time.

(2) **Deciding on the coding method.** In this instance limited ordering was applied to a multistate character data matrix. The assumption being that a limited number of characters evolved along a set pathway, and that by allowing this *a priori* hypothesis to stand, polarisation of the cladogram in favour of the supposed ancestor - descendant lineage would be enhanced.

(3) **Derivation of the data matrix from the observable characters pertaining to each taxon.** One problem identified by colleagues (N. J. Morris, W. J. Kennedy) is to what extent the cladogram and the data matrix it is based on reflects the morphological variation within the various ammonite species studied. In this study it was decided that to avoid the question of whether a recorded character was representative of the taxon as a whole, *the data entered into the matrix would as far as possible be based on a comparison of holotype and lectotype material,* either through direct examination of the type material or by using published descriptive or figurative articles. Effectively this makes this an analysis of type specimen material rather than

species. Thus, by implication, the results are *valid for the species as defined by the type material.* The data were inputted via the Apple Macintosh computer program MacClade version 3.05 (Maddison & Maddison, 1992). This process required fully re-describing the species examined.

(4) **Searching of the data matrix using PAUP.** The search was performed under the ACCTRAN optimisation, which explains homoplasy in terms of reversals. The Heuristic algorithm was selected, using the random addition sequence and steepest descent options. Branch swapping was by the tree bisection-reconnection method. All trees were unrooted, and all characters unweighted. After the first run the characters are re-weighted by the Rescaled Consistency Index (RC) and the search performed again. At each stage, 10 replicates were run to maximise the chance of identifying all the shortest trees. After this search the trees are reserved for investigation.

(5) **Filtering the tees.** Where more than one tree is identified by PAUP it becomes necessary to filter the trees. Within PAUP it is possible to reserve more resolved trees over less resolved ones (i.e., excludes a tree with a polytomy where an alternative more resolved but compatible tree exists). This is based on an assumption that evolution has progressed by a series of dichotomies: i.e., one parent lineage has give rise to two daughter ones. A second approach is to select specific trees by identification of key topological features. Two features are looked for here: (a) the congruence of divergences on the cladogram with appearances of lineages or taxa within the stratigraphic record, and (b) the recognition of likely groups of taxa.

(a) **Stratigraphical congruence.** Congruence exists where elements of the topology of the tree are close to the pattern identifiable from the fossil record alone. In affect the assumption is that stratigraphy is a fair mirror of the phylogeny of an evolving lineage. Thus, of *n*-equally parsimonious trees, the ones which requires the fewest ghost lineages are more likely to be correct than ones with many ghost lineages.

(b) **Species clustering.** Some polytomies in the consensus tree will be brought about by individual taxa being located in different places on the basis of uncertainty (absence of data) or lack of resolution (insufficient diagnostic characters). If an assumption is made that where transitional forms can be observed in the fossil record between any given taxa, these taxa are more likely to be closely related to one another (i.e., form a clade) that to any other taxa. In practise this

allows the operator to select from *n* equally parsimonious trees those specific trees which contain the clade or clades believed *a priori* to exist on the basis of the these transitional forms.

(6) **Randomisation confidence testing.** This tests for the degree of order (covariation between characters) of the cladogram compared with a number of randomly generated trees derived from the same data set. Faith & Cranston (1990) suggest that if the cladogram is shorter than 95 percent of the random trees, then there is a 95 percent confidence level that the cladogram contains more hierarchical structure than would be expected by chance. However, such testing says nothing about the location of the regions of order within the cladogram. PAUP can generate random trees.

(7) **Bootstrap testing.** This is based on a method devised by Felsenstein (1985) in which sets of characters or taxa are randomly selected and resampled to build up a 'bootstrap' tree which can be compared with the original cladogram. A well-supported clade should occur in both the original cladogram and the bootstrap tree. PAUP includes a bootstrap testing option. Bootstrap values are considered to be highly conservative measures of the accuracy of tree structure (Smith, 1993), and Hillis & Bull (1993) found that bootstrap value of a give branch within a tree are consistently lower than the probability that the branch is correct.

(8) **Bremer support.** This is a test of the robustness of the clades within the cladogram by stepwise increases in the length of the trees retained. More robust clades will persist into longer trees, and the number of steps between the original cladogram (the shortest tree) and the point at which the clade collapses is the Bremer support value. This is based on an approach devised by Bremer (1988) and can be performed jointly with PAUP and Autodecay (Eriksson & Wikström, 1995).

Outgroup Taxon

My outgroup taxon is *Ancyloceras matheronianum* d'Orbigny, 1842, the type species of the genus *Ancyloceras*, the type genus of the family Ancyloceratidae, and a typical representative of the Ancyloceratacеae. This taxon provides a reference against which the character states of all the other taxa can be compared. In selecting an outgroup it is implicit that the selected taxon is considered to be "primitive" morphologically in comparison with the other taxa being studied. This statement can be argued either way: The Ancyloceratacеae *do* antedate the Turrilitaceae, and so must have evolved earlier. Also, the Turrilitaceae are believed to be a

separate, monophyletic group with respect to the Ancyloceratacеae. However, as discussed earlier the Turrilitaceae and the Ancyloceratacеae may have actually had quite separate origins among the regularly coiled Ammonoidea.

Ingroup Taxa

Sixty-eight taxa were included in the analysis, and cover most of the Albian heteromorph ammonite species known from Europe, the Near East, Africa, and Madagascar as well as many from North and South America, Australia, and Antarctica. The range of species chosen covers all the morphotypes and includes species from all the genera recorded with certainty from Albian rocks. Individual species have been included where the fossil record is sufficient to provide the suite of morphological characters needed. The morphological data is based on the type material, where possible from examination of the type specimens, otherwise from published descriptions. This ensures that the characters recorded for any given specimen is correct with respect to the species described, although other specimens attributed to that species may differ in some detail. The taxonomy below is based on that of Wright *et al* (1996). A detailed account of these species is provided in the next chapter, together with my own revision of this taxonomy.

Superfamily Ancyloceratacеae

Family Ptychoceratidae

Ptychoceras adpressum J. Sowerby, 1814 = *Mastigoceras adpressum* Boehm, 1925
Upper Albian of Europe, Mexico and Australia
Ptychoceras laeve (Pictet, 1847) = *Ptychoceras minimum* Rouchadzé, 1933
Upper Aptian and Lower Albian of Europe, Asia Minor and North Africa

Family Labeceratidae

Labeceras (Labeceras) plasticum Spath, 1925
Upper Albian of Southern Africa
Hamitoides rusticus Spath, 1939
Upper Albian of Europe

Superfamily Scaphitaceae

Family Scaphitidae

Scaphites hugardianus d'Orbigny, 1840 = *Scaphites meriani* Pictet & Campiche, 1861, *Scaphites simplex* Jukes-Brown, 1875

Upper Albian of Europe, Middle East, North Africa, and Madagascar

Eoscaphites circularis (J de C. Sowerby, 1836)

Upper Albian of Europe

Eoscaphites subcircularis (Spath, 1937)

Upper Albian of Europe, North Africa, and Madagascar

Worthoceras worthense (Adkins, 1920)

Upper Albian of North America and Japan.

Worthoceras pygmaeum Butjor, 1991

Upper Albian of Europe

Superfamily Turrilitaceae

Family Anisoceratidae, [1]

Anisoceras armatum (J. Sowerby, 1817)

Upper Albian of Europe, Middle East, Africa, India, Australia, and North America

Anisoceras arrogans (Giebel, 1852) = *Hamites elegans* d'Orbigny, 1842

Middle and Upper Albian of Europe

Anisoceras perarmatum Pictet & Campiche, 1861

Upper Albian of Europe, Madagascar and North America

Anisoceras saussureanus (Pictet, 1847)

Upper Albian of Europe, Africa, India, Australia, North and Central America

Protanisoceras (Protanisoceras) raulinianum (d'Orbigny, 1842) = *Toxoceras lardyi* Pictet & Renevier, 1854.

Lower Albian of Europe and North Africa

Protanisoceras (Protanisoceras) cantianum Spath, 1939

Lower Albian of Europe

Protanisoceras (Protanisoceras) coptense Casey, 1961

Lower Albian of Europe

Protanisoceras (Protanisoceras) blancheti (Pictet & Campiche, 1861)

Lower Albian of Europe

Protanisoceras (Protanisoceras) halleri (Pictet & Campiche, 1861)

Lower Albian of Europe and India

Protanisoceras (Protanisoceras) vaucherianum (Pictet, 1847)

Lower Albian of Europe

Protanisoceras (Protanisoceras) acteon (d'Orbigny, 1850)

Lower Albian of Europe

Protanisoceras (Heteroclinus) nodosum (J. Sowerby, 1818)

Lower Albian of Europe

Protanisoceras (Torquistylus) anglicum (Spath, 1939)

Lower Albian of Europe

Idiohamites tuberculatus (J. Sowerby, 1818)

Lower Albian of Europe and Australia

Idiohamites spiniger (J. Sowerby, 1818)

Upper Albian of Europe

Metahamites sablieri (d'Orbigny, 1842)

Middle Albian of Europe

Metahamites dalpiazi Wiedmann & Dieni, 1968

Upper Albian of Europe

Rossalites superbum (Collignon, 1949)

Lower Albian of Europe and Madagascar

Rossalites ricardii nov. sp. = *Rossalites imlayi* (Leanza, 1970) of Riccardi,, 1988.

Lower Albian of Europe and South America

Family Hamitidae [2]

Hamites attenuatus J. Sowerby, 1814

Middle Albian of Europe, India, Madagascar, and North and Central America

Hamites compressus J. Sowerby, 1814

Middle Albian of Europe, North Africa, and Madagascar

Hamites funatus Brogniart, 1822 = *Hamites ptychoceratoides* Spath, 1941

Upper Albian of Europe and Southern Africa

Hamites gardneri Spath, 1941

Middle and Upper Albian of Europe and Central America

Hamites hybridus Casey, 1961

Lower Albian of Europe

Hamites incurvatus Brown, 1837

Upper Albian of Europe

Hamites intermedius J. Sowerby, 1814 = *Hamites adkinsi* Scott, 1928

Upper Albian of Europe, North and Central America

Hamites maximus J. Sowerby, 1814

Middle and Upper Albian of Europe and Australia

Hamites nokonsis Adkins & Winton, 1920 = *Hamites subvirgulatus* Spath, 1941

Upper Albian of Europe, Middle East, North Africa, and North America

Hamites parkinsoni (Fleming, 1814) = *Hamites charpenteri* Spath, 1941, *Hamites duplicatus* Pictet & Campiche, 1861, *Hamites simplex* d'Orbigny, 1842, *Stomohamites renevieri* Breistroffer, 1947

Upper Albian of Europe, Middle East, Southern Africa, Madagascar, Australia and North America

Hamites praegibbosus Spath, 1941

Lower Albian of Europe, India and Madagascar

Hamites renzi Kennedy, 1996

Upper Albian of Europe

Hamites rotundus J. Sowerby, 1814

Middle Albian of Europe and Madagascar

Hamites tenuicostatus Spath, 1941

Middle Albian of Europe and Madagascar

Hamites tenuis J. Sowerby, 1814

Middle Albian of Europe and Madagascar

Hamites virgulatus Brogniart, 1822 = *Hamites venetizanus* Pictet, 1847

Upper Albian of Europe, Middle East, Southern Africa, Madagascar, North America, Antarctica and Australia

Hamitella annulatum (d'Orbigny, 1842) = *Hamites subrotundus* Spath, 1941, *Hamites helicoides* Wiedmann, 1962a, ? *Notostreptites exilis* Henderson, 1989

Middle and Upper Albian of Europe, Madagascar, and Australia

Hamites (Psilohamites) bouchardianus (d'Orbigny, 1842)

Upper Albian of Europe

Hamites (Lytohamites) similis Casey, 1961

Upper Albian of Europe, Southern Africa and Madagascar

Hamites (Lytohamites) sulcatostriatus Wiedmann & Dieni, 1968

Upper Albian of Europe

Hemiptychoceras gaultinum Spath, 1925

Upper Albian of Europe and Madagascar

Scaphamites passendorfferi Wiedmann & Marcinowski, 1985

Albian (exact horizon unknown) of Europe

Family Baculitidae [3]

Lechites (Lechites) gaudini (Pictet & Campiche, 1861)

Upper Albian of Europe, Southern Africa, Australia, Antarctica and Central America

Lechites (Lechites) moreti Breistroffer, 1936

Upper Albian of Europe

Lechites (Lechites) comanchensis (Adkins, 1920)
Upper Albian of North and Central America
Lechites (Tuberolechites) regifex Cooper & Kennedy, 1977
Upper Albian of Europe
Sciponoceras skipperae nov. sp.
Upper Albian of Europe

Family Turrilitidae

Proturrilitoides astierianus (d'Orbigny, 1842)
Middle Albian of Europe
Proturrilitoides senequierianus (d'Orbigny, 1842)
Middle Albian of Europe
Turrilitoides hugardianus (d'Orbigny, 1842)
Upper Albian of Europe
Turrilitoides densicostatus (Passendorfer, 1930)
Middle and Upper Albian of Europe
Turrilitoides intermedius (Pictet & Campiche, 1861)
Upper Albian of Europe
Pseudhelicoceras robertianum (d'Orbigny, 1842)
Middle and Upper Albian of Europe, Madagascar, and North America
Pseudhelicoceras gaultinum Spath, 1937
Upper Albian of Europe
Pseudhelicoceras pseudoelegans Spath, 1937
Upper Albian of Europe
Mariella bergeri (Brogniart, 1822) = *Turrilites worthensis* Adkins, 1920, *Turrilites circumataeniatus* Scott, 1926
Upper Albian of Europe, Middle East, North and Southern Africa, Madagascar and North America
Mariella cantabrigiensis (Jukes-Brown, 1877)
Upper Albian of Europe. North Africa, and Japan
Mariella gresslyi (Pictet & Campiche, 1861)
Upper Albian of Europe, North Africa and Madagascar
Mariella miliaris (Pictet & Campiche, 1861)
Upper Albian of Europe, North and Southern Africa, Madagascar, and North America
Mariella nobilis (Jukes-Brown, 1877)
Upper Albian of Europe and North America
Ostlingoceras puzosianum (d'Orbigny, 1842)

Upper Albian of Europe, Middle East and Madagascar

NOTES:

1. Of the taxa studied, *Heteroclinus* Casey, 1961 and *Torquistylus* Casey, 1961 have been variously regarded as full genera, subgenera, or simply synonyms of *Protanisoceras*. *Metahamites* is another problematic taxon which has been generally classified within the Anisoceratidae. However, the type species, *Metahamites sablieri* d'Orbigny, 1842, is non-tuberculate. Gebhard (1975) and Wiedmann & Boess (1984) have discussed this species at length and consider it to be a subgenus of *Hamites* and not a member of the Anisoceratidae at all.

2. *Hamites* has been repeatedly split into a different genera and subgenera. This is a reflection on the fact that *Hamites* is largely defined on the basis of not obviously being anything else rather than having any characteristic features of its own (such as tubercles or a micromorphic initial coil). *Stomohamites* is considered by many authors to be a straight synonym of *Hamites*. The type species is *Hamites virgulatus* Brogniart, 1822. *Stomohamites* has historically included most of the Upper Albian and later hamitids, frequently with apertural collars, and usually with approximately equally sized bifid lateral and umbilical lobes. *Stomohamites* has been variously used as a subgenus of *Hamites* or a separate genus in its own right (see Spath, 1941, Arkell *et al*, 1957). However, since not all supposed *Stomohamites* have apertural collars *and* similar size lobes, and the general trend was simply to lump all Upper Albian and later *Hamites* as *Stomohamites*, the name has largely been dropped (see Wright & Kennedy 1981, 1995, Wright *et al*, 1996). *Hamitella* is a rarely used generic name for predominantly helical hamitids. The type species is *Helicoceras annulatum* d'Orbigny, 1842. Breistroffer proposed the name in lieu of *Helicoceras* which is occupied by a gastropod (*Helicoceras* Koenig, 1825), although the identity of the type material was uncertain. Examination of the type material in the d'Orbigny Collection at the Natural History Museum in Paris seems to support the view that this species and *Hamites subrotundus* Spath 1941 are conspecific. *Lytohamites* is a genus of large, indistinctly ribbed hamitids with relatively florid suture lines. The type species is *Lytohamites similis* Casey, 1961. This species covers most of the specimens previously described as *Hamites multicostatus* Brown, 1837. However, the type specimen of that species is 'specifically indeterminate' and may in fact be simply a piece of *Anisoceras* (see Casey, 1961, Wright & Kennedy, 1995). *Plesiohamites* Breistroffer, 1947 is based on this same fragment, so is considered to be *nomen dubium*.

3. The baculitid *Lechites (Tuberolechites) regifex* Cooper & Kennedy, 1977 is only known from fragments. It is a straight shelled (baculiticonic) ammonite much like other *Lechites* but with paired ventral tubercles.

Characters Analysed

The comparative morphology of heteromorph ammonites is largely restricted to shell characteristics including coiling mode, ornamentation, apertural modifications, suture lines, and siphuncle morphology. No aptychi or radulae are known from Albian heteromorphs (although they are known from some Upper Cretaceous heteromorphs such as *Baculites*, see Arkell, 1957). Consequently, the selection of characters is based upon a pragmatic approach to what is observable in the fossil record. On the one hand, for a cladistic analysis to have any resolution, morphological distinctions need to be made, on the other it is important not to select characters or states of an ambiguous or subjective nature.

Essentially the characters can be divided into two suites based on the shell and the suture line. Shell characters reflect three aspects of the life of an ammonite: (i) the ontogeny (growth) of the animal, (ii) the sex of the ammonite, and (iii) the adaptive or functional morphology. The functional morphology of heteromorph ammonites is not well understood, and previous investigations have been limited in scope (see discussion in Monks & Young, 1998). Functional morphology has consequently not been coded for here.

Sexual dimorphism was probably quite common among ammonites, and apertural collars and constrictions may be useful indicators of this with heteromorphs (Wright & Kennedy, 1995), as may the differences in sizes of some species like *Hamites maximus* and *Anisoceras saussureanus* (pers. obs.). As Wright & Kennedy point out, while collars have been recorded from some Upper Albian *Hamites*, entire specimens of the Lower and Middle Albian *Hamites* have not been preserved and so the absence of records of collars in these species may be an artefact of an inadequate fossil record.

The ontogeny of the heteromorph ammonites is fairly well understood and the fossil record sufficiently detailed for almost the entire growth sequence (life cycle) to be followed. Thus ontogeny provides the richest source of characters for this analysis. At a gross level, coiling mode itself can be observed, but most characters vary through ontogeny, such as the tendency toward helicosity or the presence of tubercles. To code for this adequately, the ontogeny of the ammonite is here divided into four distinct stages:

(1) **Neanic.** A smooth shelled, probably planktonic stage. In all species the shell (neanoconch) consists of a planar regular coil, in most of the Turrilitaceae the coil is open. The coil is closed in the Ancyloceratacеae and most Scaphitaceae. The neanoconch reaches from a few millimetres to a centimetre or so in diameter before ornamentation appears, indicating the onset of the juvenile stages of growth.

(2) **Juvenile-A.** At this stage the ammonite has acquired ornamentation comparable to the adult, although there may be small differences (e.g., distribution of tubercles or density of ribs). Coiling mode is similar to that of the neanoconch.

(3) **Juvenile-B.** As juvenile-A, but with differences in coiling, usually heteromorphic in style. Some evidence of sexual dimorphism may be present, such as ultimate size, but collars, etc., absent.

(4) **Adult.** Maturity, shell growth may slow or stop, including the approximation of the septa. Sexual dimorphism, if present, is at this stage pronounced and complete.

For each stage of growth observations can be made on the whorl section, the presence and morphology of tubercles, and the presence and morphology of ribs. For each of these ontogenetic stages morphological characters can be different, so at each stage of ontogeny the characters were coded for independently.

The suture line is another highly variable feature, but with a less discernible relationship to ontogeny and functional morphology. However, in contrast to the gross morphology of the shell, the suture line can be well preserved on fragmentary material. The characters coded for here have been chosen as the least ambiguous characters possible, even at the risk of losing resolution: specifically, whether the lobes were bifid or trifid or the dorso-ventral saddle oblique or not. For example the relative sizes of individual lobes and sutures have not been considered, although this has been used previously, e.g., in defining *Stomohamites* (see Spath, 1941). This character is altogether too variable both within a species and through ontogeny as Cooper (1994a) has pointed out. Equally, the degree of symmetry of individual lobes and saddles (as distinct from the symmetry of the suture line *in toto*) has not been coded for. This character varies depending on the stage of ontogeny, especially if helical and planar fragments of the same specimen are compared, that the reliability of this character needs to be questioned. In short, only the basic features were coded for and a conservative series of states recognised, e.g., the lobe is *either* bifid *or* trifid. There is no 'asymmetrically bifid' or 'subtrifid' requiring subjective appraisals of the specimen. Such an approach makes it easy for another operator to code a specimen *in a way directly comparable with the method adopted here*, opening up the possibility for other workers to develop the data set and investigate the relationships of ammonites not described here.

The characters and character states are listed below. Where the character is deemed to be ordered it is stated and justified, otherwise all characters are unordered. The characters themselves are largely self explanatory, although reference to the preceding glossary of

morphological terms may be useful. The characters are based upon fully grown, individuals, so references to the phragmocone or living chamber, except where stated otherwise, imply the phragmocone at maturity and the final living chamber.

1. Siphuncle is ventral or lateral.

(0) Siphuncle lies along the mid-line of the shell along the ventral surface.
(1) Siphuncle is close to the mid-line but is displaced slightly adapically.
(2) Siphuncle displaced adapically and well away from the mid-line to the upper part of the exposed face.

ORDERED: The shifting of the siphuncle is only seen among helically coiled ammonite. It is probably fair to assume that this is an ordered, evolutionary series of events associated with the tightening the helical coil and assuming an orientation with apex of the shell upwards and the aperture downwards (see Klinger, 1980).

2. Shell coiling mode.

(0) Regular spiral.
(1) Aspinoconic
(2) Ancyloconic
(3) Hamiticonic
(4) Ptychoconic
(5) Baculiticonic

3. Micromorphic initial coil.

(0) Spiral coiling persistent from neanoconch into juvenile stage.
(1) Spiral coiling limited to neanoconch only.

4. Neanoconch is crioconic.

(0) The neanoconch is an involute, planar spiral with successive whorls in contact.
(1) The neanoconch is an open, planar spiral with the whorls not in contact.

5. Helicosity.

(0) No helicosity at any stage.
(1) Neanoconch planar, juvenile-A helical, juvenile-B and mature planar.

(2) Neanoconch planar, juvenile-A and juvenile-B helical, mature planar.
(3) Neanoconch planar, juvenile-A, juvenile-B, and mature helical.

ORDERED: Helicosity is relatively common among the juveniles heteromorphs, and is exhibited by progressively fewer taxa. My assumption is that this represents an evolutionary progression towards the more helical taxa from planar and weakly helical forms.

6. Helical part closed.

(0) Successive whorls of helix not in contact.
(1) Successive whorls of helix in contact but whorl section not affected.
(2) Successive whorls of helix strongly compressed and whorl section distorted.

ORDERED: Again associated with increasingly tight helical coiling. In all non-Turrilitidae heteromorphs the helical parts of the shell are not in contact.

7. Coiling imperforate.

(0) Initial part of planar spiral open (wide umbilicus).
(1) Initial part of planar spiral closed (narrow umbilicus).

8. Whorl section of juvenile-A.

(0) Circular.
(1) Laterally compressed.
(2) Dorso-ventrally compressed (= depressed) but whorls or shafts not in contact.
(3) Dorso-ventrally compressed, whorls or shafts in contact producing some distortion.
(4) Semi-lunate.
(5) Polygonal.

9. Whorl section of juvenile-B coil circular.

(0) Circular.
(1) Laterally compressed.
(2) Dorso-ventrally compressed (= depressed) but whorls or shafts not in contact.
(3) Dorso-ventrally compressed, whorls or shafts in contact producing some distortion.

(4) Semi-lunate.
(5) Polygonal.

10. Whorl section of mature coil circular.

(0) Circular.
(1) Laterally compressed.
(2) Dorso-ventrally compressed (= depressed) but whorls or shafts not in contact.
(3) Dorso-ventrally compressed, whorls or shafts in contact producing some distortion.
(4) Semi-lunate.
(5) Polygonal.

11. Apertural constriction.

(0) Absent.
(1) Present.

12. Periodic constrictions.

(0) Absent.
(1) Present.

13. Oblique constrictions.

(0) Absent.
(1) Present.

14. Paired collars.

(0) Absent.
(1) Present.

15. Single collar.

(0) Absent.
(1) Present.

16. Lappets.

(0) Absent.
(1) Present.

17. Major ribs.

(0) Absent.
(1) Present.

18. Major ribs dorsally effaced.

(0) Not effaced.
(1) Partially effaced.
(2) Effaced completely.

19. Minor ribs.

(0) Absent.
(1) Present.

20. Paired ventral tubercles.

(0) Absent.
(1) Present.

21. Paired ventrolateral tubercles.

(0) Absent.
(1) Present.

22. Ribs split on ventral surface or between ventral tubercles.

(0) Not split (= simple).
(1) Split (= fibulate, button-and-loop if associated with tubercles).

23. Ribs split ventrolateral surface or between ventrolateral tubercles.

(0) Not split (= simple).
(1) Split (= fibulate, button-and-loop if associated with tubercles).

24. Ventral tubercle distribution.

(0) None.
(1) Phragmocone only.
(2) Phragmocone and living chamber.
(3) Living chamber only.

25. Morphology of ventral tubercles.

(0) Bullate.
(1) Circular.
(2) Clavate.

26. Ventrolateral tubercle distribution.

(0) None.
(1) Phragmocone only.
(2) Phragmocone and living chamber.
(3) Living chamber only.

27. Morphology of ventrolateral tubercles.

(0) Bullate.
(1) Circular.
(2) Clavate.

28. Raised bifurcation.

(0) Absent.
(1) Present.

29. Ribs on phragmocone flattened ventrally.

(0) No.
(1) Yes.

30. Morphology of ribs on phragmocone.

(0) Straight.
(1) Sinuous.

31. Ribs on living chamber flattened ventrally.

(0) No.
(1) Yes.

32. Morphology of ribs on living chamber.

(0) Straight.
(1) Sinuous.

33. Secondary bulla.

(0) Absent.
(1) Present.

34. Suture asymmetrical.

(0) No.
(1) Early part of phragmocone only.
(2) All of phragmocone.

ORDERED: The asymmetry of the suture seen in the Hamitidae and the Turrilitidae can be observed to take place gradually through the series *Hamitella* to *Proturrilitoides* to *Turrilitoides*. It is probably an ordered, evolutionary series of events associated with the tightening the helical coil and assuming an orientation with the aperture downwards.

35. Pseudolobes.

(0) Absent.
(1) Present.

36. Internal lobes.

(0) Bifid.
(1) Trifid.

37. Lateral lobes.

(0) Bifid.
(1) Trifid.

38. Umbilical lobes.

(0) Bifid.
(1) Trifid.

39. Internal lobes.

(0) Bifid.
(1) Trifid.

40. Lateral Saddles.

(0) Bifid.
(1) Trifid.

41. Dorso-ventral saddle.

(0) Bifid.
(1) Oblique.

The data matrix for this analysis is presented in tabular form in APPENDIX 1 and in a NEXUS file format (readable by MacClade and PAUP) on the floppy disk.

Results

Tree statistics and topology

The PAUP analysis produced 2200 trees. The strict consensus and 50% majority rule consensus trees of this run are presented in FIGURES 2.9 and 2.10. These trees have a length of 173 steps.

The data set was re-weighted by the Rescaled Consistency Index using that option in PAUP and run again. This produced 158 trees. The strict consensus and 50% majority rule consensus trees of this second run are presented in FIGURES 2.11 and 2.12. Filtering within PAUP reduced the number of trees from 158 to 6. These six trees are presented in FIGURE 2.13. The following were identified as sources of variation within the six trees examined:

(1) The positioning of the taxa *Hamites tenuis*, *Hamites hybridus*, *Hamites praegibbosus* and *Scaphamites passendorferi*. These taxa form a sister group to *Metahamites sablieri*.

Resolution: Stratigraphically this group is difficult to resolve. *Hamites praegibbosus* and *Hamites hybridus* are both from the *Douvilleiceras mammillatum* Zone of the Lower Albian. *Hamites tenuis* and *Metahamites sablieri* both appear in the lower part of the Middle Albian. *Scaphamites* has an uncertain stratigraphical range, being recorded from condensed beds ranging from the *Douvilleiceras mammillatum* to *Stoliczkaia dispar* Zones of the Albian. Morphologically, *Scaphamites* can be distinguished from the other three species by the irregular helical coiling. On the other hand the suture line and overall ornamentation are very similar to *Hamites hybridus*. *Metahamites* and *Hamites tenuis* are hamiticonic, while *Scaphamites* and *Hamites praegibbosus* are broadly ancyloconic, and *Hamites hybridus* is aspinoconic. I would suggest making *Hamites hybridus* and *Scaphamites* sister taxa, since they share similar morphology and stratigraphical range may be compatible. The sister group to them would be *Hamites praegibbosus*, which is very similar to *Hamites hybridus* but is a more loosely coiled and with a trifid umbilical lobe. *Hamites tenuis*, the outgroup to these three species is yet more open in coiling (being hamiticonic) but is otherwise very similar.

(2) The positioning of the taxon *Hamites gardneri*, and the clade (*Hamites intermedius* + *Hamites intermedius*).

Resolution: This is impossible to resolve from the stratigraphy or the morphology since both clades have identical origins (upper Middle Albian, *Euhoplites meandrinus* Subzone). These three species are also very similar, and it could be argued that they form a range of morphotypes within one broadly recognisable species, *Hamites maximus*: tending toward reduction of ribbing (*Hamites intermedius*) or toward ancyloconic coiling (*Hamites gardneri*).

In conclusion, the 6 trees can probably be safely reduced to two on the basis of resolving the positions of *Hamites tenuis*, *Hamites hybridus*, *Hamites praegibbosus* and *Scaphamites passendorferi*. The positions of the *Hamites gardneri*, *Hamites intermedius* and *Hamites intermedius* cannot be resolved with any confidence. These trees are both figured here together with their topological statistics (FIGURE 2.14).

The Consistency Index and Retention Index values of both trees are the same: 0.39 and 0.75 respectively. The Consistency Index is a measurement of homoplasy, where lower values imply greater degrees of homoplasy within the data set (Goloboff, 1991). A value of 0.39 is relatively low and implies a high degree of homoplasy. The Retention Index is a reflection of the number of character state reversals (Smith 1993). The value of 0.75 is fairly high, suggesting that relatively few character state exist within the data set. The Rescaled Consistency Index is a compound of the two indices, and is a conservative estimate of the amount of order within the data set (Swofford 1993). Tree 1 has a slightly higher Rescaled Consistency Index than Tree 2, 0.30 compared to 0.29, although this difference is small and may be a rounding error. These values are relatively low.

Bootstrap values

The data matrix is searched using the bootstrap method described by Felsenstein (1985). The One hundred replicates were performed to maximise the reliability of the conclusions based on the search. The resulting bootstrap tree (FIGURE 2.15) gives support values for certain branches, the percentage values indicate the number of trees within which the clade concerned occurred, the more times the clade occurs, the better supported the clade, hence high values are best.

(1) The clade of *Psilohamites bouchardianus* + (*Ptychoceras adpressum* + (*Worthoceras worthense* + *Worthoceras pygmaeum*)) is weakly supported with a bootstrap value of 53%. However, the clade (*Ptychoceras adpressum* + (*Worthoceras worthense* + *Worthoceras pygmaeum*)) is very well-supported with a value of 98%. The clade of (*Worthoceras worthense* + *Worthoceras pygmaeum*) is has a moderately high bootstrap value of 68%, indicating that this clade occurred in about two-thirds of all the generated trees.

(2) The genus *Anisoceras* (i.e., *Anisoceras saussureanus*, *A. armatum*, and *A. perarmatum*) forms a robust clade with a bootstrap value of, 100%. The clade of *A. armatum* and *A. perarmatum* occurs in about two-thirds of all the generated trees, rating a bootstrap value of 68%.

(3) The clade *Protanisoceras raulinianus* and *P. cantianum* is recorded from rather less than two thirds of all the trees, rating a bootstrap value of 59%.

(4) The genus Idiohamites (i.e., *Idiohamites tuberculatum* and *I. spiniger*) is well-supported with a bootstrap value of 83%.

(5) The Scaphitidae (i.e., *Eoscaphites circularis* + (*Eoscaphites subcircularis* and *Scaphites hugardianus*) are moderately well-supported with a bootstrap value of 52%. However, the clade comprising *Eoscaphites subcircularis* and *Scaphites hugardianus* is very well-supported, occurring in 95% of the bootstrap trees.

(6) The Turrilitidae are fairly well-supported occurring in over two thirds of all the bootstrap trees, rating a bootstrap value of 68%. This family as tested includes *Proturrilitoides astierianus*, *Turrilitoides hugardianus*, *Mariella bergeri*, *Ostlingoceras puzosianum*, *Pseudhelicoceras robertianum*, *Ps. catenatum*, and *Ps. pseudoelegans*.

(7) A clade comprising *Proturrilitoides astierianus* and *Turrilitoides hugardianus* is well-supported, with a bootstrap value of 74%.

(8) A clade comprising *Mariella bergeri*, *Ostlingoceras puzosianum*, *Pseudhelicoceras robertianum*, *Ps. catenatum*, and *Ps. pseudoelegans* is well-supported with bootstrap value of 83%. Within this clade *Mariella bergeri*, *Ostlingoceras puzosianum*, *Pseudhelicoceras robertianum*, and *Ps. catenatum* form a nested clade with a bootstrap value of 86%, again a high score. Finally, a clade nested within that, comprising *Mariella bergeri* and *Ostlingoceras puzosianum* is well-supported with a bootstrap value of 88%.

Bremer support test

The Bremer support values are presented in FIGURE 2.16. The values recorded range from 0 to 18. The highest values occur at the following nodes, implying a high degree of robustness to these clades:

(1) **Bremer support value, 18.** The clade (*Scaphites hugardianus* + *Eoscaphites subcircularis*).

(2) **Bremer support value, 17.** The clade (*Mariella bergeri* + *Ostlingoceras puzosianum*).

(3) **Bremer support value, 16.** The clade (*Anisoceras armatum* + *Anisoceras perarmatum*).

All the remaining nodes have relatively low values, from 0 to 4.

Randomisation confidence test

The most parsimonious trees measure, 173 steps in length. One thousand randomly generated trees fall in the length ranges 414 to 474 steps. Thus the deduced cladogram is shorter than all the randomly generated trees, implying a high likelihood in the data set having phylogenetic signal.

Conclusions

From this analysis, the taxonomy of the Albian heteromorphs can be redrafted in the light of the likely phylogeny of the group. My trees broadly concur with the taxonomy of Wright *et al* (1996) in placing *Hamitoides* and *Ptychoceras* outside of the Turrilitaceae and within the Ancyloceratacеae. This cladistic analysis does not support the hypothesis that the Baculitidae and Ptychoceratidae are sister groups within the Turrilitaceae (Wiedmann & Dieni, 1968, Marcinowski & Wiedmann, 1990). The Turrilitaceae include the Anisoceratidae, Baculitidae, Hamitidae, and Turrilitidae. The Scaphitidae are also shown to be monophyletic once *Worthoceras* is removed to the Ptychoceratidae as proposed by Wiedmann (1965) and supported by this study. The need for a separate superfamily Scaphitaceae is questionable given the monophyletic origin of the scaphitids as studied here from the Hamitidae. However, since only a small proportion of the known scaphitids occur in the Albian, and these post-Albian species have not been examined, there is not the evidence to prove or disprove the monophyletic nature of the Scaphitaceae as a whole. So I provisionally retain the Scaphitaceae as a superfamily.

(1) **Validity of the Hamitidae uncertain.** Within this family are the origins of four other families: the Anisoceratidae, Baculitidae, Scaphitidae and Turrilitidae. The sister group of the Turrilitidae is a group of five hamitids with helical juvenile stages: *Hamitella annulatum*, *Hamites rotundus*, *Hamites gardneri*, *Hamites maximus*, and *Hamites intermedius*. These last four species should be transferred to the genus

Hamitella, making this a paraphyletic outgroup to the Turrilitidae. The sister group to the Turrilitidae + *Hamitella* clade is a clade comprising of *Hemiptychoceras gaultinum* and *Hamites parkinsoni*. I would propose that *Hamites parkinsoni* should be moved into *Hemiptychoceras*. *Hamites sulcatostriatus* and the Anisoceratidae form a polytomy with the clade of *Hemiptychoceras*, *Hamitella*, and the Turrilitidae. The next group down is *Lytohamites* a genus including two species, *Lytohamites similis* and *Lytohamites funatus*. The exact status of *Hamites sulcatostriatus* is uncertain, but I believe that it is closer to *Hemiptychoceras* than *Lytohamites* for more fully discussed in the entry for that species in the next chapter, but a key feature is that this species has constrictions along the body chamber, which are also a feature of *Hemiptychoceras*.

The remainder of the Hamitidae are very difficult to classify at this stage and require further work. There are twelve species, of which nine are generally recognised as *Hamites*:

Hamites attenuatus
Hamites compressus
Hamites hybridus
Hamites incurvatus
Hamites nokonsis
Hamites praegibbosus
Hamites renzi
Hamites tenuicostatus
Hamites tenuis

These species *do not* form a neat monophyletic clade which could be recognised as the true *Hamites*. They form an array of heteromorph ammonites with primitive turrilitaceaean features (such as simple annular ribs, planar coiling, and an open crioconic juvenile-A coil). They are here provisionally retained within *Hamites*.

Two hamitids studied here, *Scaphamites passendorferi* and *Metahamites sablieri*, represent monospecific genera. No other species of *Scaphamites* have been described thus far. The position of *Scaphamites* within the Hamitidae is supported (as in Wright *et al*, 1996), but marking this species out as the transition from the Hamitidae to the Scaphitaceae is not supported (as proposed by Wiedmann & Marcinowski, 1985). Metahamites is also recognised as a member of the Hamitidae, as proposed by Gebhard (1975) and Wiedmann & Boess (1984). The other alleged species of *Metahamites* which are tuberculate are here excluded from the Hamitidae on that

basis. These are '*Metahamites elegans*' = *Anisoceras arrogans* and *Metahamites dalpiazi*. Both are transferred to the Anisoceratidae on the basis of possession of symmetrically paired tubercles.

The problem of the position and validity of *Stomohamites* can be reviewed. *Hamites virgulatus*, the type species of *Stomohamites* does not form the basis of any obvious clades. It is a single species branching from a polytomy including the other systematically unresolved *Hamites*, and as such *Stomohamites* should probably be considered a straight synonym of *Hamites* at least until this genus can be more fully understood.

By and large the stratigraphy and phylogeny of the Hamitidae cannot really be assessed until the taxonomy of the group is more thoroughly investigated. However, in general it can be said that the more primitive species (*Hamites*, *Scaphamites*, *Metahamites*) either appear in or are confined to the Lower and Middle Albian, and the more derived *Lytohamites* and *Hemiptychoceras* are restricted to the Upper Albian (FIGURE 2.17). On the other hand, *Hamitella*, which is supposedly a more derived taxon than either *Lytohamites* or *Hemiptychoceras* ranges through the entire Middle and Upper Albian.

(2) **Anisoceratidae.** This genus includes the monophyletic genera *Anisoceras*, *Idiohamites*, *Tuberolechites*, and *Rossalites*. and the paraphyletic genus *Protanisoceras*. The union of this family with the Hamitidae (e.g., Wiedmann, 1962, Marcinowski & Wiedmann, 1990) is here rejected. There is a reasonable match with stratigraphy: the most derived genera are *Anisoceras*, *Idiohamites*, and *Tuberolechites* which are Upper Albian and Cenomanian in range, while the more primitive *Rossalites* and *Protanisoceras* are largely confined to the Lower and Middle Albian, as shown in the phylostratigraphy presented in FIGURE 2.17. The Anisoceratidae are determined to be offshoots of the Hamitidae, which have a comparable stratigraphical range, both groups being known from the Lower Albian (*Leymeriella tardefurcata* Zone).

Protanisoceras represents the primitive stock from which the more derived Anisoceratidae are derived. Although it is paraphyletic, it is recognised here because it forms a reasonable series of grade-groups between the outgroup (the Hamitidae) and the more derived genera (*Anisoceras*, *Idiohamites*, *Rossalites*, and *Tuberolechites*). However the subgenus *Protanisoceras* (*Heteroclinus*) is completely rejected since the two described species of *Protanisoceras* (*Heteroclinus*), *Protanisoceras (Heteroclinus) nodosum* and *Protanisoceras (Heteroclinus) halleri* do

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not form a monophyletic clade. On the other hand, the validity of *Protanisoceras* (*Torquistylus*) at generic or subgeneric rank is difficult to assess since it represents but one species. I only disregard it here because it forms part of a polytomy with *Protanisoceras acteon* and *Protanisoceras blancheti*.

Two species of *Protanisoceras* as recognised here have been previously included in other genera: *Anisoceras arrogans* (= '*Metahamites elegans*') and *Metahamites dalpiazi*. *Protanisoceras arrogans* is here the sister taxon of *Rossalites* and quite distinct from *Anisoceras* proper. It lacks the most characteristic synapomorphy of *Rossalites*, the fusion of ventral and ventrolateral tubercles on the living chamber, and so is left within the ancestral if unresolved *Protanisoceras* stock. Both this species and *Protanisoceras dalpiazi* had been included within the genus *Metahamites* (Wiedmann & Dieni, 1968, Wright *et al*, 1996). As I recognise that genus, a non-tuberculate hamitid, both of these species must be excluded since they have symmetrically paired tubercles. *Protanisoceras dalpiazi* is positioned in the cladogram as the sister taxon to all the other Anisoceratidae studied here. It may therefore be considered the most primitive member of the Anisoceratidae known.

Rossalites is an early offshoot and as mentioned above is easily recognised by the fusion of ventral and ventrolateral tubercles on the living chamber to form clavate ridges. This clade is strongly supported and recognition of *Rossalites* as discussed by Casey (1961) is agreed with here.

Anisoceras and *Idiohamites* are sister groups and appear at about the same time in the Upper Albian. Both taxa are monophyletic and supported by this analysis.

(3) **Scaphitidae.** The derivation of this group from the Hamitidae as proposed by Wiedmann (1965) is supported. Only three species of scaphite are recognised here, so the data are too limited to make any broad statements about this very large, mostly Upper Cretaceous, family. Two genera of scaphite are here included, *Eoscaphites* and *Scaphites*. *Worthoceras* is transferred to the Ptychoceratidae as originally proposed by Wiedmann (1965). Within the remaining Scaphitidae are three species. Because of the number of characters that support a clade comprising *Eoscaphites subcircularis* and *Scaphites hugardianus*, together with the strong bootstrap and Bremer support values, I propose returning *Eoscaphites subcircularis* to the genus *Scaphites* as originally placed by Spath (1937). Consequently, the single remaining species of *Eoscaphites*, *Eoscaphites circularis*, remains the sister taxon of the other scaphites. Although a monophyletic clade it barely reasonable to form a new family for this one species.

Thus a family, Eoscaphitidae, as proposed by Cooper (1994a) probably cannot be endorsed.

The match with stratigraphy is reasonable. The most primitive genus, the lower Upper Albian *Eoscaphites*, is the outgroup of the more derived upper Upper Albian to Upper Campanian genus *Scaphites* (FIGURE 2.17). The rooting of this family within the Hamitidae is also reasonable since that family is present in the Upper Albian.

Although few scaphites have been examined here, an important general statement can be made. The closed (imperforate) coiling of *Scaphites* and most other scaphites *is not* a primitive character even though it can be observed in many Ancyloceratacеae. In other words, the imperforate coiling of scaphites and of homomorph ammonites *are not homologous*. The ancestors of the Scaphitidae have open (perforate) juvenile-A coils, as does *Eoscaphites circularis*, the earliest known member of the Scaphitidae. Imperforate coiling among the Scaphitidae is a re-evolved or convergent feature, perhaps as a consequence of the general trend toward homomorphic coiling seen in this group. In addition, the tuberculation observed on some of the Scaphitidae evolved independently of that among the Anisoceratidae. Scaphitid tuberculation, at least as seen among the Albian forms, appears as raised areas where the ribs bifurcate over the ventral surface.

Given the derivation of the scaphites from the hamitids, the value in retaining a superfamily Scaphitaceae for the scaphites is questionable. This superfamily was devised in the belief that the origin of the scaphitiform heteromorph ammonites from the Lytoceratacеae was independent of the turrilitaceaen heteromorphs (Wright, 1953, Besonov & Mikhailova, 1983). If the scaphites are simply another group of turrilitaceaen heteromorphs derived from the Hamitidae (like the Anisoceratidae, Baculitidae, and Turrilitidae), then the need for a separate superfamily is negated.

(4) **Baculitidae.** This family contains *Lechites* and *Sciponoceras* but not *Lechites* (*Tuberolechites*), which is now identified as a probably orthoconic *Protanisoceras* derivative within the Anisoceratidae. The group as a whole is characterised by reduction of the juvenile-A coiling phase (micromorphy), the remainder of the shell being a single straight shaft. The sister taxon to the Baculitidae is *Hamites nokonsis*, which share similar ornamentation as well as apertural constrictions. The sister clade to the clade comprising both the Baculitidae and *Hamites nokonsis* is the clade of *Hamites sensu stricto*. Since *Hamites nokonsis* and the two baculitids have an Upper Albian range, this clade concurs well with stratigraphy (FIGURE 2.17). The origin of

the Baculitidae from the Hamitidae (see Spath, 1941) is therefore supported by this analysis.

(5) **Turrilitidae.** The monophyly of this group is supported. *Proturrilitoides*, *Turrilitoides*, *Pseudhelicoceras*, *Turrilites*, and *Ostlingoceras* form a clade derived from the Hamitidae via *Hamitella*. They are characterised by helical coiling throughout post-neanic ontogeny, asymmetry of the suture, and lateral displacement of the siphuncle. The polyphyletic origin of this group suggested by Klinger & Kennedy (1978) and Wright *et al* (1996) is consequently here rejected.

The phylogeny of the Turrilitidae matches stratigraphy very well (FIGURE 2.17). The most primitive genus *Proturrilitoides* ranges through the Middle Albian, the more derived *Pseudhelicoceras* and *Turrilitoides* from the upper Middle Albian to the lower Upper Albian, and the most derived *Mariella* and *Ostlingoceras* are confined to the upper Upper Albian.

The tuberculation of *Pseudhelicoceras*, *Ostlingoceras*, and *Mariella* and that of the Anisoceratidae are not homologous and do not imply a shared, derived feature (Klinger & Kennedy, 1978, Scholz, 1979). As stated above, tubercles appear as symmetrical pair on the ventral and ventrolateral surfaces of the Anisoceratidae. In contrast, the tubercles of those members of the Turrilitidae that bear them are *not* symmetrically paired, either morphologically or across the siphuncle, and develop serially along the rib, becoming more numerous with ontogeny as the rib becomes increasingly long and subdivided. Initially, each rib is divided into a small series of distinct bullate tubercles or ridges along the outer part of its length from which develop approximately circular spines. As ontogeny progresses, further division of the rib may give rise to additional tubercles on subsequent whorls. Generally, the first tubercle lies between the external lobe and the outer lateral lobe, and the remaining tubercles are distributed over the outer lateral and umbilical lobes. The tubercles of early whorls may be covered by succeeding whorls, but form distinct depressions in the overlying shell where the attached spine was overgrown.

(6) **Ptychoceratidae.** This is as a monophyletic family containing the three genera *Psilohamites*, *Ptychoceras*, and *Worthoceras*. *Worthoceras* (in being ancyloconic) probably deserves subfamilial distinction from the straight shelled ptychoceratids. I would therefore propose that two subfamilies should be recognised, the paraphyletic outgroup Ptychoceratinae, and the monophyletic ingroup Worthoceratinae. This broadly conforms with the inclusion of *Worthoceras* in the Ptychoceratidae suggested by Wiedmann (1965) but maintains the distinctiveness of *Worthoceras* as a *Scaphites*

homeomorph as well as its much later stratigraphical occurrence (Upper Albian to Lower Turonian) compared with *Ptychoceras* (Lower Aptian to Upper Albian). *Psilohamites bouchardianus* is included within the Ptychoceratinae. At one point Spath (1941, p. 655, 660) supposed that this species should be included within the genus *Mastigoceras* (now *Ptychoceras*) but later described it as a subgenus of *Hamites* and therefore a member of the Hamitidae (Spath, 1941). This analysis bears out that original view, although until the coiling is more fully known I retain the genus level distinction on the basis of the apparently orthoconic coiling of *Psilohamites* and the consistently ptychoconic coiling of *Ptychoceras*.

The stratigraphy does not match the phylogeny perfectly (FIGURE 2.17). While the most derived genus *Worthoceras* is also the geologically youngest (Upper Albian), the least derived genus *Psilohamites* is also Upper Albian. *Ptychoceras* itself extends at least into the Aptian, which may highlight a lack of resolution within this clade and a need for additional work.

(7) **Labeceratidae.** *Hamitoides* appears to be related to *Labeceras*, presumably within a family Labeceratidae (as proposed by Spath, 1925, 1939). The Labeceratidae are not members of the Turrilitaceae (as proposed by Arkell *et al*, 1957, Marcinowski & Wiedmann, 1990) but rather members of their outgroup, the paraphyletic Anycloceratacae (Wright *et al*, 1996).

Proposed Taxonomic Revision

A cladogram is an alternative to an hierarchical taxonomy, and not a supplement to it. Nevertheless, few ammonitologists are likely to use cladograms over taxonomies in the immediate future, and for this reason I have chosen to present the final review of the Albian heteromorphs in an orthodox, Linnaean hierarchical taxonomy. The topology of these trees and their affect on the systematics of the Albian heteromorphs are discussed in the next chapter, but a brief summary is given below. I believe the revision of the taxonomy of the Albian heteromorph ammonites that I present here is a first step toward a fully phylogenetic classification of the Albian heteromorph ammonites.

Superfamily Ancyloceratacea

Family Labeceratidae

Hamitoides rusticus Spath, 1939

Family Ptychoceratidae
Subfamily Ptychoceratinae

Psilohamites bouchardianus (d'Orbigny, 1842)
Ptychoceras adpressum J. Sowerby, 1814
Ptychoceras laeve (Pictet, 1847)

Subfamily Worthoceratinae

Worthoceras worthense (Adkins, 1920)
Worthoceras pygmaeum Butjor, 1991

Superfamily Turrilitaceae

Family Hamitidae

Hamites attenuatus J. Sowerby, 1814
Hamites compressus J. Sowerby, 1814
Hamites hybridus Casey, 1961
Hamites incurvatus Brown, 1837
Hamites nokonsis Adkins & Winton, 1920

Hamites praegibbosus Spath, 1941
Hamites renzi Kennedy, 1996
Hamites tenuicostatus Spath, 1941
Hamites tenuis J. Sowerby, 1814
Hamites virgulatus Brogniart, 1822
Scaphamites passendorfferi Wiedmann & Marcinowski, 1985
Lytohamites similis Casey, 1961
Lytohamites funatus Brogniart, 1822
Hemiptychoceras gaultinum Spath, 1925
Hemiptychoceras parkinsoni (Fleming, 1814)
Hemiptychoceras sulcatostriatus (Wiedmann & Dieni, 1968)
Hamitella annulatum (d'Orbigny, 1842)
Hamitella gardneri Spath, 1941
Hamitella intermedius J. Sowerby, 1814
Hamitella maximus J. Sowerby, 1814
Hamitella rotundus J. Sowerby, 1814
Metahamites sablieri (d'Orbigny, 1842)

Family Anisoceratidae

Anisoceras armatum (J. Sowerby, 1817)
Anisoceras perarmatum Pictet & Campiche, 1861
Anisoceras saussureanus (Pictet, 1847)
Rossalites superbum (Collignon, 1949)
Rossalites ricardii nov. sp.
Protanisoceras raulinianum (d'Orbigny, 1842)
Protanisoceras cantianum Spath, 1939
Protanisoceras coptense , 1961
Protanisoceras blancheti (Pictet & Campiche, 1861)
Protanisoceras halleri (Pictet & Campiche, 1861)
Protanisoceras vaucherianum (Pictet, 1847)
Protanisoceras nodosum (J. Sowerby, 1818)
Protanisoceras anglicum (Spath, 1939)
Protanisoceras acteon (d'Orbigny, 1850)
Protanisoceras arrogans (Giebel, 1852)
Protanisoceras dalpiazi (Wiedmann & Dieni, 1968)
Tuberolechites regifex Cooper & Kennedy, 1977
Idiohamites tuberculatus (J. Sowerby, 1818)
Idiohamites spiniger (J. Sowerby, 1818)

Family Baculitidae

Lechites (Lechites) gaudini (Pictet & Campiche, 1861)
Lechites (Lechites) moreti Breistroffer, 1936
Lechites (Lechites) comanchensis (Adkins, 1920)
Sciponoceras skipperae nov. sp.

Family Turrilitidae

Proturrilitoides astierianus (d'Orbigny, 1842)
Proturrilitoides senequierianus (d'Orbigny, 1842)
Turrilitoides hugardianus (Spath, 1923)
Turrilitoides densicostatus (Passendorfer, 1930)
Turrilitoides intermedius (Pictet & Campiche, 1861)
Pseudhelicoceras robertianum (d'Orbigny, 1842)
Pseudhelicoceras gaultinum Spath, 1937
Pseudhelicoceras pseudoelegans Spath, 1937
Mariella bergeri (Brogniart, 1822)
Mariella cantabrigiensis (Jukes-Brown, 1877)
Mariella gresslyi (Pictet & Campiche, 1861)
Mariella miliaris (Pictet & Campiche, 1861)
Mariella nobilis (Jukes-Brown, 1877)
Ostlinogoceras puzosianum (d'Orbigny, 1842)

Superfamily Scaphitaceae

Family Scaphitidae

Scaphites hugardianus d'Orbigny, 1840
Scaphites subcircularis (Spath, 1937)
Eoscaphites circularis (J de C. Sowerby, 1836)

CHAPTER THREE: SPECIES DESCRIPTIONS

Summary

The systematics of the Albian heteromorph ammonites are comprehensively revised with reference to the cladistic analysis presented in this thesis. This provides a more phylogenetic view of the nature of the families and genera of these ammonites. Full synonymies are given, together with location of the type material, as well as diagnoses, geographical, and stratigraphical occurrences.

Superfamily ANCYLOCERATACEAE Meek, 1876

This group has low diversity in the Albian, compared with its zenith in the Lower Aptian. Consequently, the phylogeny and systematics of the group cannot really be assessed from the few species studied here. However, a few observations can be made. Firstly, the validity of the suture line as a diagnostic character of this group must be questioned. All Anyclocerataceae have quadrilobate sutures. Although the lateral and umbilical lobes are usually trifid, they are bifid in some Ptychoceratidae. This has been noted by Wiedmann & Kakabadza (1992), although they resolved this by placing the Ptychoceratidae in the Turrilitaceae. This ignores the fact that many Hamitidae have trifid lobes, and this cladistic analysis indicates that the morphology of these lateral lobes are poor indicators of superfamilial rank. More characteristic seems to be the differences in early ontogeny. Ancyloceratacеae and Turrilitaceae. Most Turrilitaceae have open crioconic juvenile stages, at least early on. In contrast, the Anyclocerataceae generally have closed, moderately involute to evolute coils through most or all of the juvenile growth stages, opening up only for the latest part of the phragmocone and the hook-shaped living chamber. Even the Ptychoceratidae, which have reduced initial coils, follow this general pattern. Later straight shafts envelop preceding ones, so in this sense the coiling could be termed involute, albeit in a rather distorted way.

Family LABECERATIDAE Spath, 1925

I have not studied the Labeceratidae in any detail since they are a predominantly Austral group of ammonites with a low diversity in Europe and only one species is recorded from the Anglo-Paris basin. The relationship of that single species, *Hamitoides rusticus*, has been widely debated. The cladogram convincingly places this species outside of the Turrilitaceae but within the Ancyloceratacеae (*contra* Marcinowski & Wiedmann, 1990), but its position within the Labeceratidae must remain provisional until that family is more fully analysed.

Genus *HAMITOIDES* Spath, 1925

Large ancylocones with a planar, closed initial and juvenile coil, followed by a shallow, hook shaped living chamber. Whorl section circular, ornament hamitid-like, lacking tubercles, but with occasional bifurcating ribs. The suture line is quadrilobate with trifid lobes. Synonyms: none. Type species: *Hamitoides rusticus* (Spath, 1939).

HAMITOIDES RUSTICUS SPATH, 1939

1939 *Hamitoides rusticus* Spath, p. 602, pl. 64, fig 2, text-fig 217.

? 1939 *Hamitoides rusticus* Spath, Spath pl. 66, figs 3-5.

1982 *Hamitoides* cf. *studeri* (Pictet), Braga *et al* pl. 1, fig 6.

1990 *Hamitoides rusticus* Spath, Marcinowski & Wiedmann p. 46, pl. 3, fig, 12.

Type material Holotype by original designation of Spath (1939) BMNH C.850a, from the Upper Albian (probably *Diploceras cristatum* Subzone) of Folkestone, England.

Description Of uncertain form, since only fragments are known. Probably ancyloconic, no trace of helicosity recognised. Whorl section subcircular. Ornamentation consists of bold, simple, bi- and triplicate annular ribs, effaced dorsally. On the phragmocone the ribs are mostly simple (closely resembling fragments of *Hamitella maximus*), branching of the ribs becomes more pronounced over the hook and final shaft. The suture of this species is unknown, however other species in the genus possess a quadrilobate suture that is symmetrical across the siphuncle. The external, lateral, umbilical and internal lobes are trifid. The external saddle is trifid, the remainder are bifid.

Discussion The family Labeceratidae has been variously classified within the Ancyloceratacеae and as the Turrilitaceae, but it is currently placed within the Ancyloceratacеae by most taxonomists (Wright *et al*, 1996). The suture of *Hamitoides*, with predominantly trifid lobes, is typical of the Ancyloceratacеae, but the stratigraphical occurrence is much later than most of the Northern Hemisphere representatives of this superfamily. R. Casey (pers. comm.) believes that at least some fragments from Europe are pathological specimens of *Hamitella maximus*, and that any occurrences of this Southern Hemisphere family in Europe should be treated with caution.

Occurrence Upper Albian (*Diploceras cristatum* Subzone) of England. Polish specimens (from the Tatra mountains) are from condensed Albian beds (*Cleoniceras floridum* to *Mortoniceras altonense* Subzones).

Family PTYCHOCERATIDAE Meek, 1876

This family has been placed variously within the Turrilitaceae (Arkell *et al*, 1957), as a subfamily of the Baculitidae (Wiedmann & Dieni, 1968), and as a family in the Ancyloceratacеae (Wright *et al*, 1996). My cladistic analysis clearly shows that the Ptychoceratidae are the sister group of the clade comprising the Turrilitaceae (i.e., families Hamitidae, Anisoceratidae, Baculitidae, and Turrilitidae) and the Scaphitidae. Uniquely among the Ancyloceratacеae, these ammonite develop straight shells and have reduced initial spiral coils. They also lack annular ribbing. The Ptychoceratinae evolved appear during the Aptian and die out during the Upper Albian, the Worthoceratinae appear in the Upper Albian and range into the Turonian (FIGURE 2.17). Both subfamilies are widely distributed.

Subfamily PTYCHOCERATINAE nov. subfam.

With the inclusion of the genus *Worthoceras* within the Ptychoceratidae, a distinction is made here between the straight-shelled forms with simple apertures (the Ptychoceratinae) and the spiral coiled forms which have apertures ornamented with lappets (the Worthoceratinae).

Genus *PSILOHAMITES* Spath, 1941

Incompletely known, apparently straight shelled heteromorph ammonites. Initial coil unknown. Ornamentation absent. Suture quadrilobate, characterised by an oblique dorso-ventral saddle. Synonyms: none. Type species: *Psilohamites bouchardianus* (d'Orbigny, 1842).

PSILOHAMITES BOUCHARDIANUS D'ORBIGNY, 1842

1842 *Hamites bouchardianus* d'Orbigny p. 540, pl. 132, figs 11-13.

1941 *Psilohamites bouchardianus* (d'Orbigny), Spath p. 655, text-fig 240.

1947 *Psilohamites* sp. J. Sowerby, Breistroffer p. 48.

1957b *Hamites (Psilohamites) annulatum* (d'Orbigny), Wright in Arkell *et al* p. 216, text-fig 243 (2a, b).

1976 *Hamites (Psilohamites) bouchardianus* d'Orbigny, Kennedy & Hancock p. 9.

1977 *Psilohamites bouchardianus* d'Orbigny, Phillips p. 157-158.

Type material Holotype by monotypy the original of d'Orbigny (1842, pl. 32, figs 11-13). From the Upper Gault (Upper Albian, *Hysteroceras varicosum* Subzone) of Wissant, Pas de Calais, France.

Description Laterally compressed orthocone with no ornamentation. Initial coil unknown (perhaps a micromorphic planar coil?). No known apertural collars. Suture line poorly known. Juvenile sutures figured by d'Orbigny (1842) and Spath (1942): apparently quadrilobate and symmetrical across the siphuncle. The external and lateral lobes are of similar size and bifid, the umbilical lobe is also bifid but a shade smaller, and the internal lobe smaller still and bifid. No pseudolobes. The ventral saddle is indistinctly trifid. The remaining saddles are simple, fairly broad and bifid, the dorso-ventral saddle being slightly oblique and comparable in this respect with *Ptychoceras*.

Discussion As noted by Spath, the sutures are rather distantly spaced in the figured material (Spath, 1941, text-fig 240). This, together with the extreme simplicity of the suture itself and the small size of the fragments found, may suggest that the specimens previously figured belong to a juveniles. At one point, Spath (1941, p. 655, 660) believed that this material may be part of a *Ptychoceras* species, but the absence of a semi-lunate whorl section immediately distinguishes this species from any known Albian *Ptychoceras*, although the lack or ornament and the simple bifid lobes are very similar.

Occurrence Upper Gault (*Hysteroceras varicosum* Subzone) and possibly also from the Upper Greensand of Southern England and France.

Genus *PTYCHOCERAS* d'Orbigny, 1842

Small, tightly folded ptychocones. Neanoconch closed or nearly so. Whorl section distorted where adjacent shafts are in contact, the later shafts overgrowing and sometimes entirely covering the earlier shafts. Ornament weak or absent, although constrictions may develop periodically or at the aperture. Suture quadrilobate, characterised by an oblique dorso-ventral saddle. Synonyms: *Mastigoceras* Boehm, 1925, *Tricoloceras* Whitehouse, 1928. Type species: *Ptychoceras puzosianum* (d'Orbigny, 1842).

PTYCHOCERAS ADPRESSUM (PICTET, 1847)

Figures 3.1, 3.2

1814 *Hamites adpressus* J. Sowerby p. 140, pl. 61, fig 6.

1820 *Hamites adpressus* J. Sowerby, Defrance p. 248.

1824 *Hamites adpressus* J. Sowerby, Defrance p. 189.

1828 *Hamites adpressus* J. Sowerby, Fleming p. 250.

1837 *Hamites adpressus* J. Sowerby, Brown p. 3, pl. 2, fig 4.

1842 *Hamites adpressus* J. Sowerby, d'Orbigny p. 555.

1848 *Hamites adpressus* J. Sowerby, Quenstedt p. 294.

1850 *Ptychoceras adpressus* (J. Sowerby), d'Orbigny p. 125.

1852 *Ptychoceras adpressum* (J. Sowerby), Giebel p. 287.

1854 *Ptychoceras adpressum* (J. Sowerby), Morris p. 313.

1861 *Ptychoceras adpressum* (J. Sowerby), Pictet & Campiche p. 108.

1875a *Hamites adpressus* J. Sowerby, Neumayr p. 28.

1875b *Hamites adpressus* J. Sowerby, Neumayr p. 897.

1875 *Ptychoceras (Hamites) adpressum* (J. Sowerby), Topley p. 432.

1879 *Ptychoceras adpressus* (J. Sowerby), Price p. 76.

non 1897 *Ptychoceras adpressum* (J. Sowerby), Parona & Bonarelli p. 105.

1900 *Ptychoceras adpressus* (J. Sowerby), Jukes-Browne p. 459.

1904 *Ptychoceras closteroides* Etheridge p. 110, pl. 15, figs 6-9.

1923 *Diptychoceras mazapilense* Böse p. 137, pl. 10, figs 1-8.

1923 *Ptychoceras adpressum* (J. Sowerby), Spath p. 76.

1925 *Mastigoceras adpressum* (J. Sowerby) Boehm p. 202, pl. 10, figs 1-5.

1928 *Tricoloceras closteroides* (Etheridge), Whitehouse p. 279.

1932 *Ptychoceras* cf. *glaber* Whiteaves, Collignon p. 24, pl. 4, figs 20, 21.

1941 *Mastigoceras adpressum* (J. Sowerby) Spath p. 657, text-fig 241a-m.

1961 *Mastigoceras adpressum* (J. Sowerby) Schindewolf p. 105, text-fig 57.

1968 *Ptychoceras adpressum* (J. Sowerby), Wiedmann & Dieni p. 49, 50, pl. 4, fig, 14, text-figs, 17, 18.

1971 *Ptychoceras adpressum* (J. Sowerby), Hollis p. 592, text-fig 1.

1977 *Ptychoceras adpressum* (J. Sowerby), Phillips p. 158.

1990 *Ptychoceras adpressum* (J. Sowerby), Henderson p. 125, text-figs, 10a-f.

Type material Holotype by monotypy the original of J. Sowerby (1814, pl. 61 fig 6). From the Upper Gault (Upper Albian), locality unknown. This specimen is lost. Spath designated a neotype BMNH C.39930 (1941, p. 658) from the Upper Gault (Upper Albian, *Hysteroceras varicosum* Subzone) of Folkestone, England.

Description A small ptychocone. Whorl section of first shaft subcircular. The second and third shafts are approximately subcircular and partially enclose the preceding shafts. Annular

ribbing or tubercles are lacking, but the living chamber has periodic weak constrictions. Suture line quadrilobate and symmetrical across the siphuncle. The external and lateral lobes are of similar size and symmetrically bifid. The umbilical lobe is smaller but also bifid. The internal lobe is similar in size to the external and umbilical lobes but symmetrically trifid. No pseudolobes. The ventral saddle is trifid. The remaining saddles are simple, fairly deep and bifid.

Discussion *Mastigoceras* Bochm, 1925 is now considered to be a junior synonym of *Ptychoceras* d'Orbigny, 1842 (Wright *et al*, 1996). Originally *Mastigoceras* was established on the slight differences in the suture line (slightly distorted but still bifid) and the observation that all the known specimens of *Mastigoceras* had but two shafts, where *Ptychoceras* have three (Bochm, 1925). Further specimens later established that *Mastigoceras* does in fact have three shafts like *Ptychoceras* (Spath, 1941). Also, the suture lines of *Mastigoceras* may simply be distorted as a result of the tighter packing of the shafts (Wright *et al*, 1996).

Occurrence Middle and Upper Albian of England, France, Sardinia, Madagascar, Mexico and Australia. In England this species is recorded from the *Hysteroceras varicosum* Subzone only. Records from more southerly localities — including Madagascar and Australia — suggest the total range may be more, including the entire *Mortoniceras inflatum* Zone.

PTYCHOCERAS LAEVE MATHERON, 1842

Figures 3.3-3.5

	1842	*Ptychoceras laevis* Matheron p. 266, pl. 41, fig 3.
	1850	*Ptychoceras laevis* Matheron, d'Orbigny p. 115.
	1860	*Ptychoceras laeve* Matheron, Ooster p. 86, pl. 58, figs 9, 10.
	1862	*Ptychoceras laeve* Matheron, Coquand p. 285.
non	1869	*Ptychoceras laevis* Matheron, Gabb p. 144, pl. 25, fig 21.
	1897	*Ptychoceras adpressum* (J. Sowerby), Parona & Bonarelli p. 105.
	1907	*Ptychoceras laeve* Matheron, Pervinquière p. 90.
	1920	*Ptychoceras laeve* Matheron, Fallot p. 16.
	1933	*Ptychoceras minimum* Rouchadzé, p. 180, pl. 1, fig 8.
	1957	*Ptychoceras* sp., Almela & Revilla p. 9, figs 10, 11.
	1960	*Ptychoceras minimum* Rouchadzé, Druschitchic p. 265, pl. 11, fig 5.
	1962a	*Ptychoceras laeve laeve* Matheron, Wiedmann p. 90, pl. 7, fig. 1, text-figs 31, 32.

1987 *Ptychoceras laeve* Matheron, Immel p. 127.

1989 *Ptychoceras minumus* Rouchadzé, Doguzhaeva & Mutvei p. 94, pl. 3,4.

1989 *Ptychoceras laeve laeve* Matheron, Föllomi p. 120, pl. 3, fig. 17.

1992 *Ptychoceras minumus* Rouchadzé, Wiedmann & Kakabadza p. 396, text-fig 3.

Type material Holotype by monotypy the original of Matheron (1842, pl. 41 fig 3). From the Upper Aptian of Cassis and Gargas, South-Eastern France. The original appears to be lost.

Description A ptychoconic ammonite similar to *Ptychoceras adpressum* but the second and third shafts do not enclose the preceding shafts. No tubercles or ribs, but weak periodic constrictions may be present. Suture line quadrilobate and symmetrical across the siphuncle. The external and lateral lobes are of similar size and symmetrically bifid. The umbilical lobe is smaller, also bifid, but asymmetrically so. The internal lobe is similar in size to the external and umbilical lobes in size but symmetrically trifid. No pseudolobes. The ventral saddle is bifid or indistinctly trifid. The remaining saddles are simple, fairly deep and bifid.

Discussion This species has been confused with *Ptychoceras adpressum* from which it can distinguished by its greater size and a lesser degree of impression of the first shaft into the second. The ontogeny of this species, under the name *Ptychoceras minimum* Rouchadzé, 1933, has been fully described by Wiedmann & Kakabdzé (1992).

Occurrence From the Upper Aptian and Lower Albian of France, Austria, Switzerland, Mallorca, Spain, North-Eastern Africa, and Georgia. Also found in the condensed Middle Albian fauna of Escragnolles, France.

Subfamily WORTHOCERATINAE nov. subfam.

A group of small, aspinioconic ammonites similar to the Ptychoceratinae, exhibiting a lack of annular ribbing and periodic constrictions, but with apertures ornamented with lateral lappets.

Genus *WORTHOCERAS* Adkins, 1928

Small ancyloconic ammonites superficially similar to *Scaphites*. Neanoconch closed. Initial coil closed and largely covered by later whorls. Ornamentation weak or absent, although periodic apertural constrictions may be present, and the final aperture develops lappets in

some species. Suture quadrilobate, the dorso-ventral saddle being distinctly subsymmetrical and rather oblique. Type species: *Worthoceras worthense* (Adkins, 1920)

WORTHOCERAS WORTHENSE (ADKINS, 1920)

	1920	*Hamulina worthensis* Adkins p. 51, 71, pl. 2, figs 23-26, text-fig 3.
?	1923	*Macroscaphites?* sp., Böse p. 129, pl. 9, fig 23-28.
	1924	*Macroscaphites platydorsus* Scott p. 18, pl. 9, figs 6, text-figs 4, 6.
	1924	*Hamulina worthensis* Adkins, Scott p. 18.
	1928	*Hamulina worthensis* Adkins, Böse p. 146.
	1928	*Worthoceras platydorsum* (Scott), Adkins p. 219.
	1928	*Worthoceras worthense* (Adkins), Adkins p. 24, 219, pl. 20, figs 8, text-fig 3.
	1933	*Worthoceras worthense* (Adkins), Adkins p. 381.
	1937	*Worthoceras worthense* (Adkins), Spath p. 498.
	1942	*Worthoceras worthense* (Adkins), Spath p. 719.
	1942	*Worthoceras platydorsum* (Scott), Moreman p. 215.
non	1951	*Worthoceras worthense* (Adkins), Cobban p. 6.
	1953	*Worthoceras platydorsum* (Scott), Wright p. 474.
	1953	*Worthoceras worthense* (Adkins), Wright p. 474.
	1957b	*Worthoceras platydorsus* (Scott), Arkell *et al* p. 231, text-fig 255(3).
	1965	*Worthoceras platydorsum* (Scott), Clark p. 61, pl. 23, figs 4.
	1965	*Worthoceras worthense* (Adkins), Clark p. 61, pl. 23, figs 1-3, 5-10, text-fig 22a.
	1965	*Worthoceras platydorsum* (Scott), Wiedmann p. 439, pl. 59, figs 5, text-fig 10h.
	1965	*Worthoceras worthense* (Adkins), Wiedmann p. 439, pl. 59, figs 6, 7, text-fig 10a-c.
	1987	*Worthoceras platydorsum* (Scott), Matsumoto & Yokoi p. 43, 44.
	1987	*Worthoceras worthense* (Adkins), Matsumoto & Yokoi p. 44.
	1991	*Worthoceras platydorsum* (Scott), Bujtor, p 539.
	1991	*Worthoceras worthense* (Adkins), Bujtor, p 539.
	1994	*Worthoceras platydorsum* (Scott), Emerson *et al* p. 338.
	1994	*Worthoceras worthense* (Adkins), Emerson *et al* p. 338.
	1996	*Worthoceras platydorsum* (Scott), Wright & Kennedy p. 380.
	1996	*Worthoceras platydorsum* (Scott), Wright *et al* p. 258, text-fig 200a, b.

Type material Holotype by original designation BEG 20994 of Adkins (1920, pl. 2, fig 26). From the Pawpaw Formation (Upper Albian) , near Fort Worth, Texas, USA.

Description Ancylocone of small proportions (approximately, 10 mm in height) characterised by a lack of ornamentation and a simple suture line. The hook is a little deeper than the coil is

wide. Whorl section initially circular to slightly laterally compressed, becoming dorso-ventrally flattened and finally semilunate as the coil becomes progressively more involute. The whorl section of the descending shaft is dorso-ventrally compressed, flattened dorsally but not truly semilunate. The living chamber is similar. Ornament consists of occasional constrictions on the descending shaft, these can resemble oblique, bullate tubercles or nodes. Apertural collars unknown. Microconchs possess paired lateral lappets. Suture line quadrilobate and symmetrical across the siphuncle. Entire suture relatively simple. The external, lateral and internal lobes are of similar size, the umbilical a shade smaller. External lobe bifid. Lateral, umbilical and internal lobes approximately trifid. No pseudolobes. Ventral saddle indistinctly trifid. First lateral and umbilical saddles symmetrically bifid. The dorso-ventral saddle is subsymmetrically bifid.

Discussion The type of *Macroscaphites platydorsus* Scott, 1942 (= *Worthoceras platydorsum* (Scott, 1942)) is lost. This species appears to be very similar to *Worthoceras worthense* (Adkins), but somewhat smaller and the constrictions on the descending shaft are weak or absent, they are generally kept as a separate species within *Worthoceras* on the basis of differing stratigraphic occurrences even though only very limited material of *Worthoceras platydorsum* has been studied since (Clark, 1965). The suture lines are virtually identical, and position of the final septum for both species is very similar. The most apparent difference is the weakness or lack of constrictions in *Worthoceras worthense*. They are here suggested to be synonyms for a wider ranging, rather variable, ammonite.

Occurrence Principally recorded from the Upper Albian (*Mortoniceras inflatum* and *Stoliczkaia dispar* Zones) of Texas and Japan. Specimens described by Böse (1925) from the 'Vraconian' of Mexico appear to be *Worthoceras* of some sort, and may be conspecific with this species, although Wright & Kennedy (1996) believe a lower Upper Albian age to be more likely.

WORTHOCERAS PYGMAEUM BUJTOR, 1991

1991 *Worthoceras pygmaeum* Bujtor, p 537, text-fig 2.

1996 *Worthoceras pygmaeum* Bujtor, Kennedy in Gale *et al* p. 586, text-fig 30 (g, i, n).

Type material Holotype by original designation Hungarian Geological Institute K.13731 of Bujtor (1991, text-fig 2a, b). From a borehole into the Bóly Sandstone (Upper Albian) , made at Bóly, Hungary.

Description A very small ancylocone with an imperforate initial coil. The hook is approximately as deep as the coil is wide (resembling *Eoscaphites circularis* in this respect). Whorl section unknown (only compressed fossils are known). The later part of the coiled section overgrows the earlier parts to a modest degree but the umbilicus remains broad. There is no ribbing and tubercles are absent. Ornament consists of occasional constrictions on the descending shaft. Apertural collars absent. Microconchs possess paired lateral lappets. Suture line unknown.

Occurrence As holotype. Also the Upper Albian (*Stoliczkaia dispar* Zone) of France (Mont Risou).

Superfamily TURRILITACEAE Meek, 1876

This is the dominant group of Albian heteromorphs. Unlike the Ancyloceratacеae, the early part of shell is a crioconic spiral with the whorls widely spaced. Ornamentation is highly variable, but usually consists of annular ribs and tubercles. Suture line quadrilobate. Compared with the Anycloceratacеae there are more taxa with helical coiling, especially as juveniles.

Family HAMITIDAE Hyatt, 1900 (In: Zittel, 1900)

An ill-defined group of aspinoconic, ancylcoconic and hamiticonic ammonites. This group has no key synapomorphy and currently comprises those taxa not included in the recognised families Anisoceratidae, Baculitidae, Scaphitidae, or Turrilitidae. In a general way it can be viewed as the primitive stock from which these families are derived, and exhibits features common to them all, namely open coiling, simple annular ribs. Hamitids appear during the Lower Albian and persist on into the Cenomanian (FIGURE 2.17), and have been recorded from Europe, Africa, Asia, the Americas, Australia and Antarctica.

Genus *HAMITES* Parkinson, 1811

Non tuberculate aspinoconic, ancylcoconic or hamiticonic heteromorph ammonites, generally planar throughout (rarely with a weakly helical initial coil). Annular ribs simple and generally effaced dorsally, apertural collars present on microconchs of some species. Suture line quadrilobate. Synonyms: *Torneutoceras* Hyatt, 1900 (In: Zittel, 1900), *Stomohamites* Breistroffer, 1947. Type species: *Hamites attenuatus* (J. de C. Sowerby, 1814)

HAMITES ATTENUATUS J. SOWERBY, 1814

Figures 3.6-3.8

1814 *Hamites attenuatus* J. Sowerby p. 137, pl. 61, figs 4, 5.

1820 *Hamites attenuatus* J. Sowerby, Defrance p. 249.

1822 *Hamites attenuatus* J. Sowerby, Mantell p. 93, pl. 19, figs 29, 30 *non* pl. 23, figs 8, 13.

1825 *Hamites attenuatus* J. Sowerby, de Haan p. 153.

1828 *Baculita attenuata* (J. Sowerby), Fleming p. 250.

1837 *Hamites attenuatus* J. Sowerby, Brown p. 2, pl. 1, fig 5.

1837 *Hamites attenuatus* J. Sowerby, J. de C. Sowerby in Fitton p. 337, pl. 7, figs 3.

1838 *Hamites attenuatus* J. Sowerby, d'Archiac p. 306.

1838 *Hamites attenuatus* J. Sowerby, Michelin p. 102.

1842 *Hamites attenuatus* J. Sowerby, d'Orbigny p. 533 *pars*, non pl. 131, figs 9-13.

1847 *Hamites attenuatus* J. Sowerby, Graves p. 103.

1847 *Hamites attenuatus* J. Sowerby, Pictet in Pictet & Roux p. 132, pl. 388 *(pars?)*.

1848 *Hamites attenuatus* J. Sowerby, Quenstedt p. 288.

1851 *Hamites attenuatus* J. Sowerby, Cornuel p. 445.

1852 *Hamites attenuatus* J. Sowerby, Giebel p. 306.

1853 *Hamites attenuatus* J. Sowerby, Studer pp 83, 476.

1853 *Hamites attenuatus* J. Sowerby, Cotteau p. 16.

1854b *Hamites attenuatus* J. Sowerby, Pictet p. 708.

1854 *Hamites attenuatus* J. Sowerby, Morris p. 305.

1854 *Hamites attenuatus* J. Sowerby, Renevier p. 40.

1854 *Hamites attenuatus* J. Sowerby, Renevier p. 40.

1859 *Hamites attenuatus* J. Sowerby, Chenu p. 120.

? 1860 *Hamites attenuat*us J. Sowerby, Ooster p. 78.

1861 *Hamites attenuat*us J. Sowerby, Pictet & Campiche p. 78.

1861 *Hamites attenuat*us J. Sowerby, Pictet p. 17.

1868 *Hamites attenuatus* J. Sowerby, de Rance p. 168.

1871 *Hamites attenuatus* J. Sowerby, Phillips p. 441.

1874 *Hamites attenuatus* J. Sowerby, Price p. 363.

1875a *Hamites attenuatus* J. Sowerby, Neumayr p. 28.

1875b *Hamites attenuatus* J. Sowerby, Neumayr p. 897.

1875 *Hamites attenuatus* J. Sowerby, Topley p. 431.

1875 *Hamites attenuatus* J. Sowerby, Barrois p. 302.

? 1879 *Hamites attenuatus* J. Sowerby, Price p. 76.

1884 *Hamites attenuatus* J. Sowerby, Zittel p. 444.

1888 *Hamites attenuatus* J. Sowerby, Lapparet & Frietel pl. 14, fig 20.

non 1889 *Hamites attenuatus* J. Sowerby, Bristow p. 280.

? 1897 *Hamites* sp., Newton p. 77.

1898a *Hamites attenuatus* J. Sowerby, Crick p. 79, pl. 17, figs 6-9.

1900 *Hamites attenuatus* J. Sowerby, Jukes-Browne p. 459.

non 1900 *Torneutoceras (Hamites) attenuatus* (J. Sowerby), Hyatt in Zittel p. 586.

1907 *Hamites attenuatus* J. Sowerby, Kilian in Frech p. 62.

non 1907 *Hamites attenuatus* J. Sowerby, Steinmann p. 336, fig 581.

1910 *Hamites attenuatus* J. Sowerby, Pervinquière p. 18.

1912 *Hamites attenuatus* J. Sowerby, Ganz p. 61.

1918 *Hamites attenuatus* J. Sowerby, Tomitch p. 3.

? 1921 *Hamites attenuatus* J. Sowerby, Passendorfer p. 236.

1922 *Torneutoceras attenuatus* (J. Sowerby), Spath p. 148, 149.

non 1923 *Hamites attenuatus* J. Sowerby, Böse p. 132, pl. 9, figs 43-45.

1923 *Hamites attenuatus* J. Sowerby, Spath p. 75.

1923 *Hamites attenuatus* J. Sowerby, Spath p. 142.

1925a *Hamites attenuatus* J. Sowerby, Spath p. 189.

1925b *Hamites attenuatus* J. Sowerby, Spath p. 33.

non 1926 *Hamites attenuatus* Mantell, Diener p. 66.

? 1926a *Hamites attenuatus* J. Sowerby, Jayet p. 186, 189.

1926 *Hamites attenuatus* J. Sowerby, Whitehouse p. 225.

? 1927 *Hamites attenuatus* J. Sowerby, Ciry p. 564.

1930 *Hamites attenuatus* J. Sowerby, Spath p. 57.

? 1930 *Hamites attenuatus* J. Sowerby, Passendorfer p. 661.

1934 *Hamites attenuatus* Pictet, Heim & Seitz p. 203.

1934 *Hamites* cf. *attenuatus* Pictet, Destombes p. 6.

1938 *Hamites attenuatus* J. Sowerby, Roman p. 45.

1938 *Hamites attenuatus* J. Sowerby, Anderson p. 217.

1940 *Torneutoceras (Hamites) attenuatus* (J. Sowerby), Breistroffer p. 156.

1939 *Hamites attenuatus* J. Sowerby, Spath p. 605.

1941 *Hamites attenuatus* J. Sowerby, Spath p. 611 pl. 67, figs 14-18, pl. 68, fig, 1, text-fig 219.

1942 *Hamites attenuatus* J. Sowerby, Haas p. 173-174.

1942 *Hamites attenuatus* J. Sowerby, Spath p. 681.

1947 *Hamites attenuatus* J. Sowerby, Breistroffer p. 44.

1949 *Hamites attenuatus* J. Sowerby, Collignon p. 123.

1955 *Hamites attenuatus* J. Sowerby, Milbourne p. 238, 239.

non 1957 *Hamites* aff *attenuatus* J. Sowerby, Almela & de la Revilla p. 8, 36, pl. 9, fig 4.

1957b *Hamites attenuatus* J. Sowerby, Wright in Arkell *et al* p. 216, text-fig 243 (3a-c).

1958 *Hamites attenuatus* J. Sowerby, Owen p. 157.

1960 *Hamites attenuatus* J. Sowerby, Owen p. 373.

1966 *Hamites attenuatus* J. Sowerby, Casey (in Smart *et al*) p. 111.

1971a *Hamites attenuatus* J. Sowerby, Owen p. 34, 152.

1976 *Hamites attenuatus* J. Sowerby, Kennedy & Hancock p. 6, 7.

1977 *Hamites attenuatus* J. Sowerby, Phillips p. 79-80.

1979 *Hamites attenuatus* J. Sowerby, Collignon p. 5, pl. 1, fig 5.

1985 *Hamites (Hamites) attenuatus* J. Sowerby, Marcinowski & Wiedmann p. 209-211.

1989 *Hamites attenuatus* J. Sowerby, Föllmi p. 123, pl. 4, figs 4-6.

1990 *Hamites (Hamites) attenuatus* J. Sowerby, Marcinowski & Wiedmann p. 34, pl. 2 figs 9-11, text-fig 19.

? 1995 *Hamites* cf. *attenuatus* J. Sowerby, Seyed-Emami & Immel p. 382, text-fig 19.

Type material Lectotype by subsequent designation of Spath (1941), BMNH C.79895, the pyritic cast figured by J. Sowerby (1814, pl. 61, fig 4). The paralectotype, BMNH C.79896, (pl. 61, fig 5, 1814) is a mould in pale grey clay. Both are from the Lower Gault (Middle Albian) of Folkestone, England.

Description Planar or weakly helical initial coil, reaching a diameter of, 1.0 to 1.5 cms, followed by three straight shafts. The first two are more-or-less parallel, but the final shaft may curve or bend to some degree (but see discussion, below).The whorl section is slightly compressed laterally. The annular ribs are slightly sinuous, fine but blunt and moderately effaced dorsally. Rib index of 5 to 6. Ribbing is rectiradiate along the first shaft, becoming prorsiradiate along the second shaft, and then rectiradiate to slightly rursiradiate along the final shaft. Suture quadrilobate with symmetrically bifid lateral lobe, smaller trifid umbilical lobe and internal lobes. Quadrilobate, suture line symmetrical across the siphuncle. External and lateral lobes similar size, and larger than the similar sized umbilical and internal lobes. External and lateral lobes symmetrically bifid. Umbilical and internal lobes trifid. No pseudolobes. Ventral saddle indistinctly trifid, lateral and umbilical lobes fairly broad and symmetrically bifid. Dorsolateral saddle also bifid but somewhat smaller.

Discussion This species is not synonymous with *Hamites attenuatus* mutation *delta* Spath, 1941 which differs in a number of ways from typical *Hamites attenuatus*. The principal differences are in size and shape, *Hamites attenuatus* mutation *delta* being substantially larger and with a curved, laterally compressed living chamber. *Hamites attenuatus* sometimes has an irregular living chamber with a slight bend or kinks to it, but it is not comparable with the regular arc characteristic of *Hamites attenuatus* mutation *delta*. The suture lines are similar, with bifid external and lateral lobes and trifid umbilical and internal lobes, but *Hamites attenuatus* mutation *delta* has a larger, more deeply incised lateral lobe not seen in *Hamites attenuatus*. *Hamites attenuatus* mutation *delta* is a synonym of *Hamites tenuicostatus* Spath, 1941.

Occurrence From the lower Middle Albian (*Hoplites dentatus* and *Euhoplites loricatus* Zones) of Europe (England, France, Spain and Poland), India, Western Madagascar, Mexico and Western USA, possibly also Iran and Algeria.

HAMITES COMPRESSUS J. SOWERBY, 1814

Figure 3.91

1814 *Hamites compressus* J. Sowerby, p. 138, pl. 61, figs 7, 8.

1820 *Hamites compressus* J. Sowerby, Defrance, p. 249.

1825 *Hamites compressus* J. Sowerby, de Haan p. 154.

1828 *Baculita compressa* (J. Sowerby),Fleming p. 250.

non 1828 *Hamites compressus* J. Sowerby, Risso p. 102.

1837 *Hamites compressus* J. Sowerby, Brown p. 2, pl. 3, fig 7.

1840 *Hamites compressus* J. Sowerby, Roemer p. 92, pl. 8, fig 9.

non 1841 *Hamites compressus* J. Sowerby, Moxon pl. 8, fig 9.

1848 *Hamites compressus* J. Sowerby, Quenstedt *(pars)* p. 291, pl. 21, fig, 19.

1854 *Hamites compressus* J. Sowerby, Morris p. 305.

1861 *Hamites compressus* J. Sowerby, Pictet & Campiche p. 97.

? 1890 *Hamites compressus* J. Sowerby, Renevier p. 340.

1898a *Hamites compressus* J. Sowerby, Crick p. 61.

? 1916 *Hamites* cf. *compressus* J. Sowerby, Douvillé p. 96.

non 1928 *Hamites compressus* J. Sowerby, Neaverson p. 396, text-fig 57.

1932 *Hamites compressus* J. Sowerby, Collignon p. 24, pl. 4, figs 18, 19.

1939 *Hamites compressus* J. Sowerby, Spath p. 605.

1941 *Hamites compressus* J. Sowerby, Spath p. 617, pl. 68, figs 10, 11, 13, text-fig 222.

1941 *Hamites compressus* var. *gracilis* Spath p. 619, pl. 68, fig, 12.

non 1942 *Hamites compressus* J. Sowerby, Haas p. 175, pl. 43, figs 1a-e.

non 1942 *Hamites compressus* var. gracilis Spath, Haas p. 175, pl. 43, figs 2-4, text-fig 26a,b.

1947 *Hamites compressus* J. Sowerby, Breistroffer p. 45, 49.

1949 *Hamites compressus* J. Sowerby, Collignon p. 124.

1960 *Hamites* aff. *compressus* J. Sowerby, Owen p. 373.

1966 *Hamites compressus* J. Sowerby, Casey (in Smart *et al*) p. 111.

1966 *Hamites compressus gracilis* Spath, Casey (in Smart *et al*) p. 111.

1968 *Hamites (Hamites) compressus compressus* (J. Sowerby), Renz p. 64, pl. 11, fig 8 (a-c), text figs 23a.

non 1968 *Hamites (Hamites) compressus* J. Sowerby, Wiedmann & Dieni p. 57, text-figs 30, 31.

1971a *Hamites compressus* Spath, Owen p. 152.

1971a *Hamites compressus gracilis* Spath, Owen p. 152.

1976 *Hamites (Hamites) compressus* J. Sowerby, Marcinowski & Naidin p. 97, pl. 1, fig 2.

1977 *Hamites compressus* J. Sowerby, Phillips p. 80.

1979 *Hamites compressus* J. Sowerby, Collignon p. 5.

1989 *Hamites compressus* J. Sowerby, Föllmi p. 123, pl. 4, figs 12-13.

non 1995 *Hamites compressus* J. Sowerby, Seyed-Emami & Immel p. 383, text-fig 12, 13, 20.

Type material Lectotype by subsequent designation of Spath (1941) BMNH C.70387, the larger of the two specimens figured by J. Sowerby (pl. 61, figs 7). The smaller specimen BMNH C.79388 is the paralectotype (pl. 61, figs 8). Both are from the Lower Gault (Middle Albian) of Folkestone, England.

Description Planispiral aspinocone with distinctive extreme lateral compression and dense, sharp ribbing. Ribs approximately rectiradiate but varying, often toward being slightly prorsiradiate on the phragmocone. Rib index 5 to 10, effaced dorsally but very strong and sharp ventrally. Apertural collars unknown. No tubercles. Quadrilobate, suture line symmetrical across the siphuncle. External and lateral lobes of similar size, and slightly broader and deeper than umbilical and internal lobes. External lobe bifid, lateral lobe subsymmetrically so. Umbilical and internal lobes trifid. No pseudolobes. Saddles narrow and fairly florid. Ventral saddle trifid, lateral, umbilical, and dorsolateral saddles symmetrically bifid.

Discussion The most compressed and densely radiate forms (rib index 10 or more) were considered by Spath (1941) to be distinct variety, *Hamites compressus gracilis* (subgenotype BMNH C.89093). This subspecies is discussed in depth by Haas (1942).

Occurrence Lower Gault (Middle Albian, *Euhoplites loricatus* to *Euhoplites lautus* Zones) of Europe, Western Madagascar, and possibly also Angola.

HAMITES HYBRIDUS CASEY, 1961

Figure 3.10

1961 *Hamites hybridus* Casey, p. 97, pl. 22, figs 1, 2 (a-c), text-fig 33 (d-f).

Type material Holotype by original designation of Casey (1961, pl. 22, figs 1 & 2), GSM Zm.2195. Paratypes exist but not figured: GSM Zk 4876, Zk 4909. From the Folkestone Sands, Main Mammillatum Bed (Lower Albian) at Copt Point, Folkestone, England.

Description Seemingly an aspinocone a with subcircular to slightly dorso-ventrally compressed section. Annular ribs rectiradiate or very slightly rursiradiate. Rib index 4 or 5. Ribs attenuate dorsally, flattened very slightly ventrally, in some cases giving the impression of very weak tuberculation. Apertural collars unknown. Quadrilobate, suture line symmetrical

across the siphuncle. External and lateral lobes similar in size, umbilical and internal lobes smaller. External lobe symmetrically bifid. Lateral lobe asymmetrically bifid. Umbilical and internal lobes trifid. No pseudolobes. Saddles narrow and fairly florid. Ventral and lateral saddles symmetrically bifid. Umbilical saddle asymmetrically bifid. Dorsolateral saddle symmetrically bifid.

Occurrence As holotype.

HAMITES INCURVATUS BROWN, 1837

Figure 3.92

	1811	*Hamites* sp. Parkinson p. 10, pl. 1, fig 2.
	1837	*Hamites incurvatus* Brown p. 2, pl. 1, fig 2.
?	1848	*Hamites compressus* J. Sowerby, Quenstedt p. 291, pl. 21, fig, 18.
	1850	*Hamites intermedius* (*non* Sowerby), Mantell pl. 61, fig 2.
	1939	*Hamites incurvatus* Brown, Spath p. 605.
	1941	*Hamites incurvatus* Brown, Spath p. 619, pl. 68, figs 18, 19, text-fig 223.
?	1942	*Hamites compressus* J. Sowerby, Haas p. 175, pl. 43, figs 1a-e.
?	1942	*Hamites compressus* var. gracilis Spath, Haas p. 175, pl. 43, figs 2-4, text-fig 26a,b.
	1960	*Hamites* cf. *incurvatus* Brown, Owen p. 374.
	1966	*Hamites incurvatus* Brown, Casey (in Smart *et al*) p. 111.
	1968	*Hamites (Hamites) compressus* J. Sowerby, Wiedmann & Dieni p. 57, text-figs 30, 31.
	1977	*Hamites incurvatus* J. Sowerby, Phillips p. 81.
?	1979	*Hamites attenuatus* J. Sowerby, Collignon p. 5, pl. 1, fig 4.
	1985	*Hamites (Hamites) compressus* J. Sowerby, Marcinowski & Wiedmann p. 209.
	1990	*Hamites (Hamites) incurvatus* Brown, Marcinowski & Wiedmann p. 36.
non	1995	*Hamites incurvatus* J. Sowerby, Seyed-Emami & Immel p. 383, text-fig 21, 22.

Type material Holotype by monotypy BMNH C.79390 figured by Brown (1837, pl. 1, fig 4). From the Upper Gault (Upper Albian) of Folkestone, England.

Description Very similar to *Hamites compressus* J. Sowerby in being an highly compressed aspinocone with sharp, fine ribbing. Rib index approximately 7, effaced dorsally but very strong and sharp ventrally. Ribs generally fairly straight. Apertural collars unknown. No tubercle. Quadrilobate, suture line symmetrical across the siphuncle. External lobe bifid and similar in depth to the trifid umbilical lobe. Lateral lobe larger, deeply incised and subsymmetrically bifid. Umbilical lobe subsymmetrically bifid. Internal lobe symmetrically

trifid. No pseudolobes. Saddles narrow and fairly florid. Ventral saddle trifid, lateral, umbilical, and dorsolateral saddles symmetrically bifid.

Discussion The relationship between *Hamites compressus* and *Hamites incurvatus* probably reflects a gradual phenotypic change over time. Some authors do not recognise the division into two different species at all (e.g., Wiedmann & Dieni, 1968, Marcinowski & Wiedmann, 1985). *Hamites incurvatus* tends towards having slightly sparser ribs, and the ribs a little sharper in profile. Otherwise the two species are identical.

Occurrence Lower Upper Albian (*Diploceras cristatum* and *Hysteroceras orbignyi* Subzones) of England, perhaps also from the condensed Albian series of Wielka Rówien, Poland and possibly Angola.

HAMITES NOKONSIS ADKINS & WINTON, 1920

Figure 3.11

1920 *Hamites* sp. B Winton & Adkins, p. 23.

1920 *Hamites nokonsis* Adkins & Winton, p, 18, 39-40, pl. 6, figs 5-6.

1923 *Hamites nokonsis* Adkins & Winton, Adkins p 40.

1926 *Hamites nokonsis* Adkins & Winton, Scott, p 65.

1928 *Hamites nokonsis* Adkins & Winton, Adkins, p, 19, 208, pl. 12, fig 2.

1930 *Hamites nokonsis* Adkins & Winton, Adkins & Arick p 43.

1941 *Hamites (Stomohamites) duplicatus* (Pictet & Campiche), Spath pl. 72, fig, 15.

1941 *Hamites (Stomohamites) charpenteri* var. *lineata* Spath p. 64, pl. 72, fig, 19-22, text-fig 234i, j.

1941 *Hamites (Stomohamites) subvirgulatus* Spath, p. 645, text-fig 234a-c, g-h.

non 1941 *Hamites (Stomohamites) subvirgulatus* Spath, text-fig 234d, e.

1942 *Hamites compressus* J. Sowerby, Haas p. 175, pl. 43, figs 1a-e.

1942 *Hamites compressus* var. *gracilis* Spath, Haas p. 175, pl. 43, figs 2-4, text-fig 26a,b.

1942 *Hamites* cf. *nokonsis* Adkins & Winton, Haas, p, 183-184, pl. 43, fig 20a, b, text-fig 26k.

1961 *Hamites nokonsis* Adkins & Winton, Perkins, p 27.

1963 *Hamites (Stomohamites) subvirgulatus* (Spath), Collignon p. 36, text-fig 1091.

1963 *Stomohamites nokonsis* Adkins & Winton, Swensen, p 62-63, pl. 2, fig, 14.

1965 *Stomohamites nokonsis* Adkins & Winton, Clark, p 20-21, pl. 1, fig, 11, pl. 2, fig, 14, text-fig 3b.

1968 *Hamites (Stomohamites) subvirgulatus* Spath, Renz p. 66, pl. 11, figs 3, 4, text figs 23c, 24a.

1970 *Stomohamites subvirgulatus* (Spath), Kennedy p. 628.

1976 *Hamites (Stomohamites) subvirgulatus* Spath, Kennedy & Hancock p. 10.

1977 *Stomohamites subvirgulatus* Spath, Phillips p. 172.

1982 *Stomohamites* cf. *subvirgulatus* Spath, Gallois & Morton p. 357,362.

1994 *Hamites nokonsis* Adkins & Winton, Emerson *et al* p 288.

1995 *Hamites subvirgulatus* Spath, Wright & Kennedy p. 299, pl. 87, figs 3-5.

1995 *Hamites compressus* J. Sowerby, Seyed-Emami & Immel p. 383, text-fig 12, 13, 20.

1995 *Hamites incurvatus* J. Sowerby, Seyed-Emami & Immel p. 383, text-fig 21, 22.

1996 *Hamites subvirgulatus* Spath, Kennedy in Gale *et al* p. 567, fig 20 (d, e, j), fig 25 (g, h, j) fig 26 (j, k).

Type material Holotype by original designation of Adkins & Winton (1920, pl. 6, fig 6) BEG 20984 from the Duck Creek Limestone (Upper Albian, *Mortoniceras inflatum* Zone) at a site near Fort Worth, Texas.

Description Incompletely known aspinocone or shallow-hooked ancylocone. Initial coiling unknown. At least one, 180° bend and two subparallel straight shafts. Distinctive laterally compressed whorl section. Ribbing totally effaced dorsally but well developed ventrally. Rib index around 3 to 4 on the phragmocone, increasing nearer the aperture to 7 to 8. The ribs are variable in orientation and may be slightly sinuous. The apertures of microconchs are constricted, but paired ribs like those of *Hemiptychoceras parkinsoni* do not develop. Suture line is quadrilobate and symmetrical across the siphuncle. The external and lateral and umbilical lobes are of similar size, and the internal lobe is slightly smaller. External lobe symmetrically bifid. Lateral and umbilical lobes subsymmetrically bifid. The internal lobe symmetrically trifid. No pseudolobes. Ventral saddle small and trifid. Lateral, umbilical and dorso-ventral saddles rather broad and bifid.

Discussion The holotype of *Hamites nokonsis* is a poorly preserved fragment. Identification of this species with *Hamites subvirgulatus* is therefore tentative. They share a similar mode of coiling and have highly compressed whorl sections. In both the ribbing is sinuous and effaced on the dorsal surface. Stratigraphical range of the two species is identical.

Occurrence Upper Albian (Upper *Mortoniceras inflatum* and *Stoliczkaia dispar* Subzones) of Europe, Angola, Iran, and Texas.

HAMITES PRAEGIBBOSUS SPATH, 1941

Figures 3.12, 3.13

1939 *Hamites praegibbosus* Spath p. 605.

1941 *Hamites praegibbosus* Spath, Spath p. 627, pl. 70, figs 13-15, text-fig 227 (a-f).

1947 *Hamites praegibbosus* Spath, Breistroffer p. 24, 40.

1949 *Hamites praegibbosus* Spath, Collignon p. 124.

1951 *Hamites praegibbosus* Spath, Casey p. 97.

1961 *Hamites praegibbosus* Spath, Casey p. 94, pl. 22, figs 4 (a, b), 5 (a-c), text-fig 33 (a, b)

1961 *Hamites dixoni* Casey p. 97, pl. 22, figs 6 (a-c), text-fig 33c.

1960 *Hamites praegibbosus* Spath, Owen p. 369.

1977 *Hamites praegibbosus* Spath, Phillips p. 82.

1980 *Hamites praegibbosus* Spath, Krishna p. 49, 51-52, pl. 1, figs 1-5.

Type material Holotype by original designation of Spath (1941, text-fig 227a-c) BMNH C.47441 from the Casey Collection. From the Folkestone Sands, Main Mammillatum Bed (Lower Albian) of Copt Point, Folkestone, England.

Description Ancylocone with a subcircular to slightly dorso-ventrally compressed whorl section. Annular ribs effaced dorsally but sharp ventrally, slightly prorsiradiate on the phragmocone, becoming rectiradiate near the aperture. Rib index of 5 to 6. No known apertural collars. Tuberculation absent. Suture quadrilobate and symmetrical across the siphuncle. External and lateral lobes of similar size, umbilical and internal lobes rather smaller. External lobe symmetrically bifid. Lateral lobe subsymmetrically bifid. Umbilical lobe symmetrically trifid. Internal lobe symmetrically bifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical lobes rather broad, simple and subsymmetrically bifid. Dorsolateral saddle also bifid but somewhat smaller.

Discussion *Hamites dixoni* Casey is identical to this species in ornament, coiling mode and the characters of the suture line, the only differences lie in overall size, typical *Hamites dixoni* are generally larger than *Hamites praegibbosus*. It may be that *Hamites dixoni* is the microconch and *Hamites praegibbosus* the macroconch of a sexually dimorphic pair.

Occurrence Lower Albian (*Douvilleiceras mammillatum* Zone) of England, France, India and Western Madagascar.

HAMITES RENZI KENNEDY, 1996

Figure 3.14

1968 *Hamites (Plesiohamites) multicostatus* Brown, Renz pl. 11, fig 28 (a-c), text-fig 23q, 24d.

1968 *Hamites (Plesiohamites)* aff. *similis* Casey, Renz pl. 11, fig 29, 30, text-fig 23p, 24e.

1996 *Hamites renzi* Kennedy in Gale *et al*, p. 567, fig 20 (a, g, l), fig 25 (e).

Type material Holotype by original designation of Kennedy in Gale *et al* (1996, text-fig 20L), BMNH CA. 94119. From the Marnes Bleues, Upper Albian (*Stoliczkaia dispar* Subzone) of Mont Risou, Hautes-Alpes, France.

Description Aspinocone with laterally compressed whorl section. Fine annular ribs, weakened but not absent dorsally, more-or-less rectiradiate and slightly sinuous. Rib index 13-14 on phragmocone, decreasing to 8 nearer the aperture. Ribs moderately flattened in profile and the space between each rib is approximately equal to that of the width of the rib. No tubercles, apertural collars unknown. Suture line quadrilobate and symmetrical across the siphuncle. The external, lateral and umbilical lobes are of similar size, the internal lobe is smaller. The external lobe is symmetrically bifid, the lateral and umbilical lobes are subsymmetrically bifid. The umbilical lobe is trifid. There are no pseudolobes. The ventral saddle is trifid, the lateral, umbilical and dorso-ventral saddles are bifid.

Occurrence Upper Albian (*Stoliczkaia dispar* Subzone), geographical range as holotype, plus La Vraconne, Saint-Croix, Switzerland. A specimen in the Natural History Museum collection (BMNH C.4762) suggests the Cambridge Greensand (Upper Albian) of England as well.

HAMITES TENUICOSTATUS SPATH, 1941

Figure 3.9

1941 *Hamites attenuatus* mutation *delta* Spath p. 611, pl. 67, figs 3-7, 13, pl. 68, fig 5, text-fig 218 (i, j).

1941 *Hamites tenuicostatus* Spath p. 614 pl. 68, figs 2, 3, text-fig 220.

1947 *Hamites tenuicostatus* Spath, Breistroffer p. 44.

1949 *Hamites tenuicostatus* Spath, Collignon p. 123.

1958 *Hamites tenuicostatus* Spath, Owen p. 157.

1971a *Hamites tenuicostatus* Spath, Owen p. 17, 19, 40, 77, 152.

1977 *Hamites tenuicostatus* Spath, Phillips p. 83.

1979 *Hamites tenuicostatus* Spath, Collignon p. 4, pl. 1, fig 3.

1989 *Hamites tenuicostatus* Spath, Föllmi p. 123, pl. 4, figs 9.

Type material Holotype by original designation of Spath (1941, text-fig 220a) BMNH C.39761a. From the Lower Gault (Middle Albian) of Copt Point, Folkestone, England.

Description Ancylocone with lateral compression and a greater or lesser degree of ventral flattening. Ribs sharp and fine, dorsally effaced. The ribs are straight and slightly prorsiradiate to rectiradiate on the phragmocone but become sinuous and rursiradiate nearer the aperture. Rib index 12-15 on the phragmocone, down to around 8 nearer the aperture. No known apertural collars. Tuberculation absent. Suture quadrilobate and symmetrical across the siphuncle. External and lateral lobes bifid and of similar size, umbilical and internal lobes rather smaller and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical lobes narrow and bifid, dorsolateral saddle also bifid but somewhat smaller.

Discussion In the original description Spath acknowledges the close relationship between this species and *Hamites attenuatus*. Even so, fragments of this species can be distinguished from *Hamites attenuatus* on the basis of the greater whorl diameter, flattened ventral surface, and by the curved coiling. Some specimens lack ventral flattening but are otherwise identical to typical *Hamites tenuicostatus*. Such specimens were named by Spath *Hamites attenuatus* mutation *delta*, but are here considered to be merely varieties of *Hamites tenuicostatus*.

Occurrence Lower Gault (Middle Albian, *Anahoplites intermedius* to *Mojsisovicsia subdelaruei* Subzones) of England, France, and Western Madagascar.

HAMITES TENUIS J. SOWERBY, 1814

Figures 3.15, 3.16, 3.93, 3.94

1814 *Hamites tenuis* J. Sowerby p. 136, pl. 61, fig, 1.

1814 *Hamites gibbosus* J. Sowerby p. 140, pl. 62, fig 4.

1820 *Hamites gibbosus* J. Sowerby, Defrance p. 249.

1820 *Hamites tenuis* J. Sowerby, Defrance p. 249.

1825 *Hamites gibbosus* J. Sowerby, de Haan, p. 153.

1825 *Hamites tenuis* J. Sowerby, de Haan, p. 153.

1828 *Baculita gibbosa* (J. Sowerby), Fleming, p. 250.

1828 *Baculita tenuis* (J. Sowerby), Fleming, p. 250.

1829 *Hamites tenuis* J. Sowerby, Mantell, p. 211.

1832 *Hamites tenuis* J. Sowerby, Passy, p. 333.

1837 *Hamites gibbosus* J. Sowerby, Brown, p. 3, pl. 3, fig, 1.

1837 *Hamites gibbosus* J. Sowerby, Fitton, p. 367.

1837 *Hamites tenuis* J. Sowerby, Fitton, p. 113, 367.

1837 *Hamites tenuis* J. Sowerby, d'Archiac, p. 306.

1848 *Hamites tenuis* J. Sowerby, Quenstedt *(pars)* p. 295, pl. 21, fig, 17.

1898a *Hamites tenuis* J. Sowerby, Crick, p. 62.

1925 *Torneutoceras tenue* J. Sowerby, Spath, p. 189.

1940 *Hamites tenuis* J. Sowerby, Breistroffer, p. 156.

1928 *Hamites compressus* J. Sowerby, Neaverson p. 396, text-fig 57.

1939 *Hamites gibbosus* J. Sowerby, Spath p. 605.

1941 *Hamites gibbosus* J. Sowerby, Spath p. 625, pl. 70, figs 6-11, text-figs 226, 227 (g).

1939 *Hamites tenuis* J. Sowerby, Spath p. 605.

1941 *Hamites tenuis* J. Sowerby, Spath p. 628, pl. 68 fig, 14, 70, figs 2, 16, 17-15, pl. 71, fig 2, text-fig 228.

1947 *Hamites gibbosus* J. Sowerby, Breistroffer p. 45, 49.

1947 *Hamites tenuis* J. Sowerby, Breistroffer p. 45, 49.

1949 *Hamites tenuis* J. Sowerby, Collignon p. 124.

1955 *Hamites gibbosus* J. Sowerby, Milbourne p. 238.

1958 *Hamites gibbosus* J. Sowerby, Owen p. 157.

1960 *Hamites gibbosus* J. Sowerby, Owen p. 374.

1965 *Hamites tenuis* J. Sowerby, Wiedmann p. 444, text-fig 14.

1966 *Hamites tenuis* J. Sowerby, Casey (in Smart *et al*) p. 111, pl. 4, fig, 12.

1971a *Hamites gibbosus* J. Sowerby, Owen p. 152.

1971a *Hamites tenuis* J. Sowerby, Owen p. 152.

1971a *Hamites tenuis subarcuaria* Spath, Owen p. 152.

1977 *Hamites gibbosus* J. Sowerby, Phillips p. 80-81.

1977 *Hamites tenuis* J. Sowerby, Phillips p. 83-84.

1989 *Hamites tenuis* J. Sowerby, Föllmi p. 123, pl. 4, figs 12-13.

? 1995 *Hamites* cf. *gibbosus* J. Sowerby, Seyed-Emami & Immel p. 382, text-fig 14.

Type material Holotype by monotypy BMNH C.43989 figured by J. Sowerby (1814, pl. 61, fig, 1). From the Lower Gault (Middle Albian) of Copt Point, Folkestone, England.

Description Hamiticone with a planar spiral beginning and three subparallel straight shafts. The spiral and first shaft do not lie in the same plane as the final two shafts but rather meet at an angle of about 10°. Whorl section initially laterally compressed, becoming subcircular

through the first 180° bend and then dorso-ventrally compressed for the remainder of the shell. Annular ribbing initially rectiradiate to prorsiradiate along the coil and first shaft, very fine and dorsally effaced. After the first bend is characteristically rectiradiate, sharp and angular, giving a certain 'accordion-like' appearance making fragments of this species easy to identify. Suture quadrilobate and symmetrical across the siphuncle. External and lateral lobes bifid and of similar size, umbilical and internal lobes rather smaller and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical lobes narrow and bifid, dorsolateral saddle also bifid but somewhat smaller.

Discussion The early and late ontogenetic phases of this species were originally described by J. Sowerby (1814) as separate species: the rather finely ribbed spiral and first shaft as *Hamites tenuis* and the more coarsely ribbed and slightly dorso-ventrally compressed second and third shafts as *Hamites gibbosus*. More complete specimens clearly show that they belong together (FIGURE 3.14; reconstructed in FIGURE 3.16).

Occurrence Middle Albian and basal Upper Albian (upper *Anahoplites intermedius* to lower *Diploceras cristatum* Subzones) of England, France, and Western Madagascar, less certainly also the Upper Albian of Iran.

HAMITES VIRGULATUS BROGNIART, 1822

Figures 3.17, 3.18

	1822	*Hamites virgulatus* Brogniart in Cuvier & Brogniart, pl. 0, fig 6.
?	1842	*Hamites virgulatus* Brogniart, d'Orbigny p. 545, pl. 134, figs 1-4.
	1847	*Hamites virgulatus* Brogniart, Pictet & Roux p. 135, pl. 14, figs 8, 10.
non	1847	*Hamites virgulatus* Brogniart, Pictet & Roux pl. 14, figs 7, 9.
	1847	*Hamites venetzianus* Pictet in Pictet & Roux p. 134, pl. 14, fig 6.
	1850	*Hamites virgulatus* Brogniart, d'Orbigny p. 126.
	1852	*Hamites virgulatus* Brogniart, Giebel p. 311.
	1853	*Hamites virgulatus* Brogniart, Studer p. 476.
	1854	*Hamites virgulatus* Brogniart, Renevier p. 40.
non	1854b	*Hamites virgulatus* Brogniart, Pictet, pl. 56, fig 4.
	1860	*Hamites virgulatus* Brogniart, Ooster p. 79.
	1861	*Hamites virgulatus* Brogniart, Pictet & Campiche p. 85, pl. 54, figs 6, 7.
	1861	*Hamites virgulatus* Brogniart, Pictet p. 21.
	1861	*Hamites venetzianus* Pictet, Pictet & Campiche p. 98.
	1875a	*Hamites virgulatus* Brogniart, Neumayr p. 31.

1875b *Hamites virgulatus* Brogniart, Neumayr p. 899.

1875a *Hamites venetzianus* Pictet, Neumayr p. 30.

1875b *Hamites venetzianus* Pictet, Neumayr p. 899.

1879 *Hamites virgulatus* Brogniart, Price p. 76.

1881 *Hamites virgulatus* Brogniart, Penning & Jukes-Browne p. 151.

1887 *Hamites virgulatus* Brogniart, Meunier p. 62, pls., 1, fig 4.

1888 *Hamites virgulatus* Brogniart, Choffat p. 71.

1890 *Hamites virgulatus* Brogniart, Renevier p. 340.

1897 *Hamites virgulatus* Brogniart, Cowper Reed p. 116.

1900 *Hamites virgulatus* Brogniart, Jukes-Browne p. 459.

1905 *Hamites virgulatus* Brogniart, Choffat p. 39.

1907 *Hamites virgulatus* Brogniart, Pervinquière p. 84.

1907 *Hamites venetzianus* Pictet, Jacob p. 330.

1910 *Hamites virgulatus* Brogniart, Pervinquière p. 18.

1910 *Hamites venetzianus* Pictet, Pervinquière p. 18.

1912 *Hamites virgulatus* Brogniart, Ganz p. 12.

1921 *Torneutoceras virgulatum* (Brogniart), Spath p. 288.

1922 *Torneutoceras virgulatum* (Brogniart), Spath p. 148.

non 1923 *Hamites* cf. *venetzianus* Pictet, Böse p. 134, pl. 9, figs 50-53.

1925a *Torneutoceras virgulatum* (Brogniart), Spath p. 189.

, 1925 *Hamites virgulatus* d'Orbigny, Diener p. 70.

, 1925 *Hamites venetzianus* Pictet, Diener p. 70.

? 1926a *Hamites virgulatus* d'Orbigny, Jayet p. 186.

non 1927 *Hamites virgulatus* Brogniart, Ciry p. 564.

1930 *Hamites virgulatus* Brogniart, Passendorfer p. 660.

1930 *Hamites venetzianus* Pictet, Passendorfer p. 660.

1931 *Hamites virgulatus* Brogniart, Breistroffer p. 195.

1931 *Hamites venetzianus* Pictet, Breistroffer p. 195.

1932 *Torneutoceras virgulatum* (Brogniart), Spath p. 117.

1932 *Hamites virgulatus* Quenstedt, Barbu p. 15.

1933 *Hamites virgulatus* Brogniart, Breistroffer p. 234.

1934 *Hamites virgulatus* Pictet, Heim & Seitz p. 234.

? 1936 *Torneutoceras virgulatum* (Brogniart), Breistroffer p. 63.

1940 *Hamites (Stomohamites) virgulatus* (Pictet & Campiche), Breistroffer p. 84, 157.

1940 *Hamites (Stomohamites) venetzianus* (Pictet), Breistroffer p. 157.

1947 *Hamites virgulatus* Brogniart, Breistroffer p. 55.

1947 *Hamites brogniarti* Breistroffer p. 65, 77.

1948 *Stomohamites virgulatus* Brogniart, Collignon p. 124.

1957 *Hamites (Stomohamites) virgulatus* Brogniart, Almela & Revilla p. 35, pl. 9, fig, 1.

1957b *Stomohamites virgulatus* (Brogniart), Wright in Arkell *et al* p. 217.

1962 *Stomohamites venetzianus* (Pictet), Swensen p. 64, pl. 1, fig, 1-6, text fig 4, 5.

1962 *Stomohamites virgulatus* (Brogniart), Swensen p. 65, pl. 1, fig, 13, pl. 2, fig, 15, text fig 6.

1962 *Hamites (Stomohamites) virgulatus* (Brogniart), Wiedmann p.180, pl. 10, figs 3, text fig 40.

1962a *Hamites (Stomohamites)* cf. *virgulatus* (Brogniart), Wiedmann p. 97.

1965 *Stomohamites virgulatus* (Brogniart), Clark p. 21, pl. 1, fig, 13, pl. 2, fig, 15, text fig 5.

1965 *Stomohamites venetzianus* (Pictet), Clark p. 21, pl. 1, figs 1-6, text-fig 3c, 4.

1968 *Hamites (Stomohamites) venetzianus sulcatus* (Pictet), Renz p. 67, pl. 11, figs 27 (a-c), text figs 23n.

1968 *Hamites (Stomohamites) venetzianus venetzianus* (Pictet), p. 67, p. l, 11, figs 15 (a-c), 16 (a-c), text figs 23f, 24b.

1968 *Hamites (Stomohamites) virgulatus virgulatus* (Brogniart), Renz p. 65, pl. 11, figs 9 (a-c), 10 (a-c), 11 (a-c), text figs 23 (b-d).

1968 *Hamites (Stomohamites) virgulatus interruptus* Renz p. 66, pl. 11, figs 25 (a-c), 26 (a, b), text figs 23m, 24c.

1968 *Hamites (Hamites) virgulatus* Brogniart, Wiedmann & Dieni p. 53, pl. 5, figs 1, 2, 10, pl. 7, figs 1, 2, 10, pl. 16, fig, 1, text figs 21- 27.

? 1970 *Stomohamites venetzianus* (Pictet), Kennedy p. 628.

1975 *Hamites (Hamites) virgulatus* Brogniart, Förster p. 163, pl. 4, fig 4.

1976 *Hamites (Stomohamites) virgulatus* Brogniart, Kennedy & Hancock p. 10.

? 1976 *Hamites (Hamites)* aff. *attenuatus* J. Sowerby, Marcinowski & Naidin p. 98, pl. 1, fig 3.

1976 *Hamites (Stomohamites) virgulatus* Brogniart, Marcinowski & Naidin p. 98, pl. 1, figs 4, 5.

1977 *Stomohamites virgulatus* Brogniart, Phillips p. 172.

1979a *Hamites (Hamites) virgulatus* Brogniart, Scholz p. 18 *pars*.

1979b *Hamites (Hamites) virgulatus* Brogniart, Scholz p. 592, 605, pl. 1, figs 3, 4.

1980 *Hamites (Stomohamites) virgulatus* (Brogniart), Marcinowski p. 251.

1982 *Hamites (Hamites) virgulatus* Brogniart, Braga *et al* p. 706, text-figs 2-4.

1985 *Hamites (Hamites) virgulatus* Brogniart, Marcinowski & Wiedmann p. 209.

1987 *Stomohamites venetzianus* Pictet, Phillips p. 111.

1988 *Stomohamites* cf. *virgulatus* (Spath), Delanoy & Latil, p. 750.

1988 *Stomohamites virgulatus* (Brogniart), Delanoy & Latil, p. 752.

1989 *Hamites virgulatus* Brogniart, Föllmi p. 124, pl. 4, figs 24-26.

1989 *Hamites* cf. *virgulatus* Brogniart, Horvath pl. 2, fig, 1.

1990 *Hamites virgulatus* Brogniart, Henderson p. 130, pl. 13, figs a-e, i-q.

1990 *Hamites (Hamites) virgulatus* Brogniart, Marcinowski & Wiedmann p. 36, pl. 2, fig 2.

1992 *Hamites virgulatus* Brogniart, Kelly & Moncrieff p. 776, pl. 7e.

Type material Holotype by monotypy the original of Brogniart (in Cuvier & Brogniart pl. 0, fig 6, 1822). The specimen appears to be lost. From the Upper Albian of Montagne des Fiz, Savoy, France.

Description Aspinoconic to ancyloconic, broadly helical as a juvenile, although irregularly so. Whorl section subcircular or laterally compressed. Annular ribs straight and fine, effaced dorsally, rib index of 4 to 6. Ribs prorsiradiate along coiled section, tending toward being rectiradiate on straighter sections. Apertural collars unknown. Suture quadrilobate and symmetrical across the siphuncle. External and lateral and umbilical lobes of similar size, internal lobes rather smaller and simpler. External lobe symmetrically bifid, lateral and umbilical lobes subsymmetrically so. Internal lobe trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral, umbilical and dorsolateral lobes bifid, and rather broad and simple.

Discussion *Hamites virgulatus* is the genotype of the genus *Stomohamites* Breistroffer, 1940, distinguished by toxoceratiform coiling, dorsal effacement of the ribs, and a suture line with similar sized bifid lateral and umbilical lobes. Other species attributed to *Stomohamites* (*Hamites funatus*, *Hamites nokonsis*, *Hamites parkinsoni*) typically have apertural collars: these are *not* found on *Hamites virgulatus*, and these species do not form a clade with *Hamites virgulatus* that might be recognised as the genus *Stomohamites*. The suture line is not as consistent a character as Breistroffer believed (Wright & Kennedy, 1981) and *Stomohamites* is now generally considered to be a synonym of *Hamites* (Wiedmann & Dieni, 1968, Wright *et al*, 1996). *Hamites venetzianus* Pictet, 1847 has generally been recognised as a distinct species on the basis of slightly coarser ribbing, transitions between the two widely occur and they are probably no more than polymorphs of the one species (Scholz, 1979). I disagree with Scholz (1979) on the synonymisation of virtually all the Upper Albian hamitids: *Hamites virgulatus* can be clearly distinguished from the other species in lacking apertural collars. *Lytohamites funatus* and *Hamites parkinsoni* can also be distinguished consistently and should be recognised as separate species (see individual species entries for *Lytohamites funatus* and *Hemiptychoceras parkinsoni*).

Occurrence Upper Albian (at least from the *Callihoplites auitis* Subzone, perhaps earlier) into the Lower Cenomanian (*Calycoceras guerangeri* Zones), including the Upper Gault, Cambridge Greensand, and Lower Chalk formations. Widely distributed, including records from England and Europe, Crimea, Western Madagascar, Angola, Antarctica, Northern Australia, and North America.

Genus *SCAPHAMITES* Wiedmann & Marcinowski, 1965

Non tuberculate irregularly coiled ancylocone with helical initial phase and distorted final hook. Suture quadrilobate. Synonyms: none. A monospecific genus. Type species: *Scaphamites passendorferi* (Wiedmann & Marcinowski, 1985)

SCAPHAMITES PASSENDORFERI WIEDMANN & MARCINOWSKI, 1985

? 1930 *Heteroceras* sp. Passendorfer p. 670, pl. 4 fig 76, text-fig 27.

1985 *Scaphamites passendorferi* Wiedmann & Marcinowski, p. 453, text-figs 2, 3, 6.

1990 *Scaphamites passendorferi* Wiedmann & Marcinowski, Marcinowski & Wiedmann p. 47, pl. 5 (1-4).

1994 *Scaphamites* sp., Cooper p. 166.

1996 *Scaphamites passendorferi* Wiedmann & Marcinowski, Wright *et al* p. 241, text fig, 188 (2a, b).

Type material Neotype by original designation of Wiedmann & Marcinowski (1985) Podstawowej Institute of Geology, University of Warsaw WR.96. Five paratypes: IGPUW WR.90a, WR.91a, WR.92a, WR.93b, WR.95b. From the condensed Glauconitic Albian fauna (*Cleoniceras floridum* to *Mortoniceras altonense* Subzones) of Wiekla Rówien, Tatra Mountains of Poland, exact horizon unknown.

Description Ancylocone, rather similar to *Protanisoceras anglicum* (Spath, 1939) in mode of coiling, with a helical initial coil and an irregular hook. Whorl section dorso-ventrally compressed. Ribs twisted and weakened dorsally, slightly prorsiradiate to rursiradiate on the phragmocone, rectiradiate on the living chamber. Rib index 4 to 5. No known apertural collars, possible apertural constriction. Tuberculation absent. Suture quadrilobate, strongly asymmetrical across the siphuncle during the helical phase becoming symmetrical on the straight shafts. External and lateral lobes bifid and of similar size, umbilical and internal lobes rather smaller and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical saddles narrow and bifid, dorsolateral saddle also bifid but somewhat smaller.

Discussion Although considered by Wiedmann & Marcinowski (1985) to be a direct ancestor to the Scaphitaceae, Cooper (1994) believed it more likely to be an hamitid convergent in form with *Scaphites*, and more so with *Protanisoceras anglicum.*

Occurrence As holotype.

Genus *LYTOHAMITES* Casey, 1961

Non tuberculate hamiticonic heteromorph ammonites, planar throughout. Annular ribs simple and effaced dorsally. Ribbing becomes less dense near the final aperture, and apertural collars may be present on the microconchs. Suture line quadrilobate. Synonyms: none. Type species: *Lytohamites similis* (Casey, 1961)

LYTOHAMITES SIMILIS CASEY, 1961

Figures 3.19, 3.20

non	1822	*Hamites* sp. Mantell p. 123, pl. 23, fig 5.
	1837	*Hamites multicostatus* Brown p. 3, pl. 2, fig 9.
	1889	*Hamites multicostatus* Brown, Brown pl. 2, fig 9.
	1889a	*Hamites* sp., Crick p. 62.
	1921	*Hamites* nov. sp., Spath p. 257.
	1947	*Plesiohamites multicostatus* (Brown), Breistroffer p. 52, 62.
?	1957	*Hamites attenuatus* J. Sowerby, Almela & Revilla p. 35, pl. 8, fig 6.
?	1957	*Hamites rotundus* J. Sowerby, Almela & Revilla p. 36, pl. 9, fig 4.
?	1957	*Hamites* sp. nov., J. Sowerby, Almela & Revilla p. 36, pl. 9, fig 5.
	1957b	*Plesiohamites multicostatus* (Brown), Wright in Arkell *et al* p. 217, text-fig 243 (6a).
	1962	*Hamites (Plesiohamites) multicostatus* (Brown), Wiedmann p. 181, text-fig 41.
?	1963	*Hamites (Stomohamites)* cf. *multicostatus* (Brown), Collignon p. 25, text-fig 1077.
	1965	*Plesiohamites (Lytohamites) similis* Casey, Wiedmann p. 406, 444.
	1968	*Hamites (Plesiohamites) multicostatus* (Brown), Renz p. 64, pl. 11, fig 28 (a-c), text figs 23 (q, d)
	1968	*Hamites (Plesiohamites) similis* (Casey), Renz p. 64, pl. 11,figs 29 (a, b), 30 (a-c), text figs 23p. 24e.
	1976	*Lytohamites similis* Casey, Kennedy & Hancock p. 10.
	1976	*Hamites (Plesiohamites) similis* Casey, Marcinowski & Naidin p. 99, pl. 1, fig, 1.
	1977	*Lytohamites similis* Casey, Phillips p. 112.
	1979	*Hamites (Stomohamites) multicostatus* (Brown), Collignon p. 5.
pars	1979	*Anisoceras (Anisoceras) pseudoelegans* Pictet & Campiche, Scholz p. 28.
	1985	*Hamites (Plesiohamites) similis* Casey, Marcinowski & Wiedmann p. 205.
	1989	*Hamites similis* Casey, Föllmi p. 124, pl. 4, figs 27-29.
	1990	*Lytohamites similis* Casey, Henderson p. 132, text-figs, 13 (f-h), 14.
	1990	*Hamites (Plesiohamites) multicostatus* Brown, Marcinowski & Wiedmann p. 39, pl. 3, fig 5, pl. 25, fig 2.

non 1990 *Hamites (Plesiohamites)* aff. *multicostatus* Brown, Marcinowski & Wiedmann p. 40, pl. 15, fig 2.

1996 *Hamites (Lytohamites) similis* Casey, Wright et al p. 241, text-figs, 188 (4 a, b).

Type material Lectotype by subsequent designation of Casey (1961) BMNH C.4762a, previously figured by Spath (1941, pl. 71, fig, 16, text-fig 236f). From the Cambridge Greensand (Upper Albian) of Cambridge, England.

Description Hamiticone with a laterally compressed section and fairly sharp bends between the shafts. Fine subannular ribbing (completely absent dorsally), slightly rursiradiate, rib index of, 10 to 12 on earlier parts of shell, decreasing to about 8 near the aperture. Ribs moderately flattened in profile and the space between each rib is approximately equal to that of the width of the rib. Apertural collars not known, tuberculation absent. Quadrilobate suture line symmetrical across the siphuncle. External lobe similar in depth to umbilical lobe. Lateral lobe larger, deeply incised and subsymmetrically bifid. Umbilical lobe subsymmetrically bifid and a little smaller than the lateral lobe. Internal lobe smaller than umbilical lobe and symmetrically trifid. No pseudolobes. Saddles narrow and florid. Ventral saddle trifid, lateral, umbilical, and dorsolateral saddles subsymmetrically bifid.

Discussion Scholz (1979) believed that this species was derived from the *Anisoceras* through weakening of the tuberculation, making it a rather extreme form of *Anisoceras pseudoelegans* with which it shares deeply incised and florid bifid lateral lobes, very fine ribbing, and a subcircular to compressed whorl section. *Lytohamites similis* is not synonymous with *Hamites multicostatus* Brown (Figure 3.21, see also the discussion in Casey, 1961, p. 92) from the Lower Cenomanian of Sussex, England. The type of *Hamites multicostatus* is a compressed fragment generally considered to be 'generically and specifically indeterminate' (Kennedy, 1971). Since the genus *Plesiohamites* Breistroffer, 1946 is based on the type specimen of *Hamites multicostatus*, it is not available, despite use by some authors (see synonymy above).

Occurrence From the Upper Albian (*Stoliczkaia dispar* Zone) of England, France, Poland, Spain, Angola and Madagascar.

LYTOHAMITES FUNATUS BROGNIART, 1822

Figures 3.22-3.24

1822 *Hamites funatus* Brogniart p. 395, pl. 7(0), figs 7a, b.

1940 *Hamites funatus* Brogniart, Breistroffer p. 157.

1939 *Hamites funatus* Brogniart, Spath p. 605.

1941 *Hamites (Stomohamites) funatus* Brogniart, Spath p. 650, pl. 72, figs 1-2, 23, text-fig 237.

1947 *Stomohamites ptychoceratoides* (Spath), Breistroffer p. 60.

non 1968 *Hamites (Stomohamites)* cf. *funatus* Brogniart, Renz p. 69, pl. 11, figs 24a, 24b, text-fig 23(l).

1977 *Stomohamites funatus* Brogniart, Phillips p. 171.

1977 *Stomohamites ptychoceratoides* (Spath), Phillips p. 172.

? 1979 *Hamites (Stomohamites) funatus* Brogniart, Collignon p. 6, pl. 1, fig 6.

Type material Lectotype by subsequent designation of Spath (1941), the larger of the two specimens figured by Brogniart (pl. 7(0), figs 7a). From the Upper Albian of Montagne des Fiz, Savoy, France.

Description Hamiticone with lateral compression and characterised by very tight folding, markedly rursiradiate ribbing after each of the very tight, 180° bends, and the definite 'pinch' to these bends. Initial coiling helical, subsequent shafts planar. The ribs become more rectiradiate approaching the aperture where they seem to form rectiradiate to slightly rursiradiate irregular collars (at least on microconchs). No tubercles. Ribs are sharp and well defined, effaced dorsally, the rib index is 4. Along the living chamber the ribs tend toward a scale-like aspect, especially near the aperture of smaller individuals, the presumed microconchs. Sexual dimorphism marked, microconchs smaller at a whorl height of about 60-100 mm (about half the size of macroconchs) with coarse, scaly ribbing on the living chamber. Quadrilobate, suture line symmetrical across the siphuncle. Bifid external, lateral and umbilical lobes similar in size. Internal lobe slightly smaller and symmetrically trifid. No pseudolobes. Saddles narrow and fairly florid. Ventral saddle trifid, lateral, umbilical, and dorsolateral saddles symmetrically bifid.

Discussion At the bends the inner face appears to follow a different curve to the outer, so the midway point of the bend appears to be squeezed. The shafts widen very quickly after each bend. *Hamites* also have, 180° bends, but they are gentler and the ribbing is less rursiradiate or rectiradiate throughout. This tightness of the coiling is almost ptychoconic, but this species can be distinguished from true *Ptychoceras* by the absence of periodic constriction. Spath commented on the variation within the species but referred the smaller, somewhat coarse ribbed specimens to *Hamites ptychoceratoides*. This appears to be an unnecessary distinction, and *Hamites ptychoceratoides* is most likely the microconch of *Lytohamites funatus*. The macroconchs of *Lytohamites funatus* have very sharp angled ribs, which are only rarely scale-like.

Occurrence Upper Albian (*Stoliczkaia dispar*) of England and France.

Genus *HEMIPTYCHOCERAS* Spath, 1925

Non tuberculate hamiticonic heteromorph ammonites, with a helical initial coil or planar throughout. Density of ribs on the living chamber different to that on the phragmocone. Apertural collars may be present on the microconchs. Constrictions either periodic or restricted to final aperture. Suture line quadrilobate. Synonyms: none. Type species: *Hemiptychoceras gaultinum* (Pictet, 1847)

HEMIPTYCHOCERAS GAULTINUM (PICTET, 1847

Figure 3.25

	1847	*Ptychoceras gaultinum* Pictet in Pictet & Roux p. 139-140, pl. 15, fig 5, 6.
non	1865	*Ptychoceras gaultinum* Pictet, Stoliczka p, 195, pl. 90, fig, 10.
non	1907	*Ptychoceras gaultinum* Pictet, Boule, Lemoine, & Thévenin p. 56, pl. 13, fig, 1.
	1925a	*Hemiptychoceras gaultinum* (Pictet), Spath p.189.
	1938	*Ptychoceras gaultinum* (J. Sowerby), Roman p. 49.
	1957b	*Hemiptychoceras gaultinum* (Pictet), Arkell *et al* p. 216-217, text-fig 243 (5).
	1968	*Hemiptychoceras gaultinum* (Pictet), Wiedmann & Dieni p. 61, pl. 5 figs 6, 8, pl. 6, fig, 12, text-fig 34, 35.
?	1971	*Hemiptychoceras gaultinum* (Pictet), Macsotay p. 1708, pl. 3, fig, 1.
	1979	*Hemiptychoceras gaultinum gaultinum* (Pictet), Scholz p. 20.
	1982	*Hemiptychoceras gaultinum gaultinum* (Pictet), Braga *et al* pl. 1, fig 3, text figs 2-4.
	1987	*Hemiptychoceras gaultinum* (Pictet), Immel p. 127.
	1990	*Hemiptychoceras gaultinum* (Pictet), Marcinowski & Wiedmann p. 40, text-fig 22.
	1996	*Hemiptychoceras gaultinum* (Pictet), Kennedy in Gale *et al* p. 569-571, text-figs 21a-e, g-i, k, 22b, e-g, 23b.
	1996	*Hemiptychoceras gaultinum* (Pictet), Wright *et al*, 1996 p. 241, text-fig 188, 187.

Type material Holotype by monotypy the original of Pictet in Pictet & Roux (1847, pl. 15, figs 5, 6). From the Upper Gault (Upper Albian) of Saxonet, Savoy, France.

Description Hamiticone more closely folded than any *Hamites* but the shafts are not in contact and the whorl section is subcircular and not distorted. Initial coil unknown (although the tightness of the folding implies helical or micromorphic planar coiling). Annular ribs only

slightly effaced dorsally, rectiradiate throughout. Rib index 4 to 6 on phragmocone and rather less (3 to 4) on the living chamber. Both macro- and microconchs possess apertural constrictions and apertural collars consisting of a pair of expanded ribs. Suture line quadrilobate and symmetrical across the siphuncle. The external and lateral lobes are of similar size and symmetrically bifid. The umbilical lobe is smaller but also bifid. The internal lobe is similar in size to the external and umbilical lobes but symmetrically trifid. No pseudolobes. The ventral saddle is trifid. The remaining saddles are simple, fairly deep and bifid.

Discussion Sexual dimorphism limited to differences in size, the microconchs being about one third to one half the size of the macroconchs (see Kennedy in Gale *et al*, 1996). *Lytohamites funatus* Brogniart 1822 can look rather similar, but the ribbing tends to be sharper and somewhat oblique. The ribs on *Hemiptychoceras gaultinum* are straighter, rather broad and flattened in profile.

Occurrence Upper Albian and Lower Cenomanian of Southern Europe, Poland, Madagascar, and Venezuela. A specimen in the Manchester Museum (Dixon Collection), L. 6827 labelled as *Hamites compressus* from the Cambridge Greensand of Cambridge is the only specimen so far recorded from England.

HEMIPTYCHOCERAS PARKINSONI (FLEMING, 1814)

Figures 3.27-3.34

1811 *Hamites* sp., Parkinson p. 144, pl. 10, fig 5.

1828 *Baculita parkinsoni*, Fleming p. 250.

1837 *Hamites annulatus* (*non* Deshayes) Brown, p. 3, pl. 1, fig, 10.

1841 *Hamites compressus* J. Sowerby, Moxon pl. 8, fig 9.

1842 *Hamites simplex* d'Orbigny, p. 550, pl. 134, figs 12-14.

1847 *Hamites charpenteri* Pictet in Pictet & Roux p. 129, pl. 14, figs 1 (a-e).

1847 *Hamites virgulatus* Brogniart, Pictet in Pictet & Roux, pl. 14, figs 7, 9.

1848 *Hamites parkinsoni* Fleming, Bronn p. 568.

1850 *Hamites parkinsoni* (*non* J. Sowerby), pl. 61, fig 5.

1852 *Hamites parkinsoni* (Fleming), Giebel p. 306.

1854b *Hamites virgulatus* Brogniart, Pictet, pl. 56, fig 4.

1854 *Hamites parkinsoni* (Fleming), Morris p. 305.

1861 *Hamites duplicatus* Pictet & Campiche p. 98.

1861 *Hamites parkinsoni* (Fleming), Pictet & Campiche p. 98.

1866 *Hamites duplicatus* Pictet & Campiche, Pictet & Renevier p. 104.

1875a *Hamites duplicatus* Pictet & Campiche, Neumayr p. 29.

1875b *Hamites duplicatus* Pictet & Campiche, Neumayr p. 897.

1890 *Hamites duplicatus* Pictet & Campiche, Renevier p. 340.

1925a *Hamites duplicatus* Pictet & Campiche, Spath p. 189.

1930 *Hamites duplicatus* Pictet & Campiche, Breistroffer p. 195.

1940 *Hamites (Stomohamites) duplicatus* Pictet & Campiche, Breistroffer p. 157.

1940 *Hamites (Stomohamites) simplex* (d'Orbigny), Breistroffer p. 157.

1871 *Hamites parkinsoni* (Fleming), Phillips p. 441.

1939 *Hamites parkinsoni* (Fleming), Spath p. 605.

1940 *Hamites (Stomohamites) simplex* (d'Orbigny), Breistroffer p. 157.

1941 *Hamites (Stomohamites) duplicatus* (Pictet & Campiche), Spath p. 640-642, pl. 72. figs 12-14, 16, text-fig 232.

non 1941 *Hamites (Stomohamites) duplicatus* (Pictet & Campiche), Spath pl. 72, fig, 15.

1941 *Hamites (Stomohamites) charpenteri* (Pictet), Spath p. 642-645, pl. 72, fig, 17, 18, text-fig 234a-h.

non 1941 *Hamites (Stomohamites) charpenteri* var. *lineata* Spath p. 64, pl. 72, fig, 19-22, text-fig 234i, j.

1941 *Hamites (Stomohamites) ibex* Spath p. 647, pl. 71, fig, 14, text-fig 235.

1941 *Hamites (Stomohamites) parkinsoni* (Fleming), Spath p. 653, text-fig 239.

1947 *Stomohamites charpenteri* (Pictet), Breistroffer p. 52.

1947 *Stomohamites duplicatus* (Pictet & Campiche), Breistroffer p. 53.

1947 *Stomohamites lineatus* (Spath), Breistroffer p. 62, 65, 93.

1947 *Stomohamites parkinsoni* (Fleming), Breistroffer p. 53, 65.

1947 *Stomohamites renevieri*, Breistroffer p. 93.

1957b *Stomohamites duplicatus* (Pictet & Campiche), Wright in Arkell *et al* p. 217, text-fig 243 (4a,b), 244 (1a,b).

1949 *Stomohamites duplicatus* (Pictet & Campiche), Collignon p. 124.

1949 *Stomohamites charpenteri* (Pictet), Collignon p. 124.

1951 *Hamites (Stomohamites) simplex* (d'Orbigny), Wright & Wright p. 14.

1955 *Hamites simplex* d'Orbigny, Sornay (fasc., 18).

non 1959 *Hamites (Stomohamites) simplex* (d'Orbigny), Cielinski, p. 35, pl. 3, fig 7.

1963 *Hamites (Stomohamites) simplex* (d'Orbigny), Wright p. 597, pl. 87, fig, 1.

1964 *Stomohamites simplex* (d'Orbigny), Collignon p. 6, 9, pl. 318, fig, 1358, pl. 319, figs 1370-1372.

1964 *Idiohamites vohipalensis* Collignon, p. 8, pl. 319, figs 1366, 1367.

1966 *Hamites (Stomohamites) parkinsoni* (Fleming), Casey (in Smart *et al*) p. 111.

1968 *Hamites (Stomohamites) parkinsoni* (Fleming), Renz p. 68, pl. 11, figs 12 (a, b), 17 (a, c), text figs 23 (g, o).

1968 *Hamites (Stomohamites) duplicatus* (Pictet & Campiche), Renz p. 68, pl. 11, figs 19 (a, b), 20 (a, b), 21 (a-c), text-figs 23 (h-k).

1968 *Hamites (Stomohamites) lineatus* (Spath), Renz p. 68, pl. 11, figs 22 (a-c), 23 (a-c).

1968 *Hamites (Hamites) charpenteri* Pictet, Wiedmann & Dieni p. 56, pl. 5, figs 3, 9, text-figs 28, 29.

1970 *Stomohamites simplex* (d'Orbigny), Kennedy p. 631, 634, 638, 648, 651.

1971 *Stomohamites simplex* (d'Orbigny), Kennedy p. 6 *pars*, pl. 1 fig, 1.

1972 *Stomohamites* cf. *S. simplex* (d'Orbigny), Cobban & Scott p. 44,pl. 13, figs 5-10, pl. 17, figs 3, 4.

1975 *Hamites (Stomohamites) charpenteri* (Pictet), Förster p. 164, pl. 4, fig 5, text-fig 34, 35.

1975 *Stomohamites* cf. *S. simplex* (d'Orbigny), Hattin pl. 2 figs i, j.

1976 *Stomohamites simplex* (d'Orbigny), Juignet & Kennedy p. 51, pl. 1, figs 8-10.

1976 *Hamites (Stomohamites) parkinsoni* (Fleming), Kennedy & Hancock p. 9.

1976 *Hamites (Stomohamites) charpenteri* (Pictet), Kennedy & Hancock p. 10.

1976 *Hamites (Stomohamites) duplicatus* (Pictet & Campiche), Kennedy & Hancock p. 10.

1977 *Stomohamites* cf. *S. simplex* (d'Orbigny), Hattin fig 5.3.

1977 *Stomohamites* cf. *S. simplex* (d'Orbigny), Kauffman pl. 17, figs 8, 9.

1977 *Stomohamites charpenteri* (Pictet), Phillips p. 171.

1977 *Stomohamites duplicatus* (Pictet & Campiche), Phillips p. 171.

1977 *Stomohamites ibex* Spath, Phillips p. 171.

1977 *Stomohamites parkinsoni* (Fleming), Phillips p. 171.

1977 *Stomohamites simplex* (d'Orbigny), Phillips p. 172.

1978 *Hamites (Hamites)* cf. *S. simplex* (d'Orbigny), Kennedy & Hancock pl. 9, figs 5, 10-14.

1979 *Hamites (Stomohamites) charpenteri* (Pictet), Collignon p. 5.

1979 *Hamites (Stomohamites) simplex* (d'Orbigny), Kennedy, Chahida & Djafarian p. 9, pl. 1, fig 5.

? 1979 *Hamites (Hamites) simplex* (d'Orbigny), Immel p. 630, pl. 4, fig 3.

1980 *Hamites (Stomohamites) duplicatus* (Pictet & Campiche), Marcinowski p. 250, pl. 3, figs 1, 2.

1980 *Hamites (Stomohamites) simplex* (d'Orbigny), Marcinowski p. 251.

1983 *Hamites simplex* (d'Orbigny), Kennedy & Juignet p. 13, figs 15 (a-d), 17 (a-w), 26 (j), 37 (v, w).

1985 *Hamites (Hamites) charpenteri* (Pictet), Immel & Seyed-Emami, p. 109, pl. 7, fig 6.

1985 *Hamites (Hamites) duplicatus* (Pictet & Campiche), Immel & Seyed-Emami, p. 109, pl. 7, fig 7.

1985 *Hamites (Hamites) simplex* (d'Orbigny), Immel & Seyed-Emami, p. 109.

1986 *Hamites* cf. *simplex* (d'Orbigny), Kennedy, Amédro & Colleté, p. 210, fig 4g.

1987 *Hamites (Hamites)* cf. *simplex* (d'Orbigny), Immel p. 125.

1987 *Stomohamites charpenteri* (Pictet), Phillips p. 111.

1987 *Stomohamites duplicatus* (Pictet & Campiche), Phillips p. 111.

1987 *Stomohamites simplex* (d'Orbigny), Phillips p. 111.

1988 *Stomohamites* sp. aff. *duplicatus* (Pictet & Campiche), Delanoy & Latil, p. 752.

1989 *Hamites* cf. *simplex* (d'Orbigny), Cobban, Hook & Kennedy p. 56, figs 59, 92 (a-k).

1991 *Hamites (Stomohamites)* cf. *duplicatus*, Butjor, p 537.

1992 *Stomohamites simplex* (d'Orbigny), Thomel *(pars)* pl. 10, fig, 12, pl. 31, fig 4.

1996 *Hamites duplicatus* Pictet & Campiche, Kennedy in Gale *et al*, p 565, fig, 16 (l, n, p.), fig 20 (h, i, k).

Type material Holotype by monotypy is the original of Parkinson's figure (Parkinson, 1811, pl. 10, fig 5). This specimen is lost and a neotype was designated by Spath, BMNH C.88727, from the Upper Greensand (Upper Albian) of Devizes, Wiltshire (Spath, 1941).

Description Hamiticone with a helical juvenile whorl, followed by three, subparallel straight shafts and an approximately circular or laterally compressed whorl section. Ribbing moderately effaced dorsally, but sharp ventrally. On the helix the ribs are twisted and slightly prorsiradiate, but they straighten out and become rectiradiate over the shafts. Near the aperture the ribs become slightly prorsiradiate. Microconchs possess apertural collars, a pair of expanded final ribs separated by a clearly defined constriction. Rib density variable, but usually fairly fine and sharp, rib index around 4 to 7. Rib density increases near the aperture, to about 8. Suture line is quadrilobate and symmetrical across the siphuncle. The external and lateral and internal lobes are of similar size, and the umbilical lobe smaller. External lobe symmetrically bifid. Lateral and umbilical lobes subsymmetrically bifid. The internal lobe symmetrically trifid.

Discussion This species was previously included within *Hamites*. It differs from typical *Hamites* in the variation of rib density along the conch, something more commonly seen in *Hemiptychoceras* and also the development of apertural collars and constrictions. The position within the cladogram indicates this species is the sister taxon of *Hemiptychoceras gaultinum*. The final living chambers of both species display a change in ornament from the phragmocone to the living chamber, as well as paired annular collars and constrictions. A number of species are synonyms of *Hamites parkinsoni*: *Hamites charpenteri* Spath, 1941, *Hamites duplicatus* Pictet & Campiche, 1861, *Hamites simplex* d'Orbigny, 1842, and *Stomohamites renevieri* Breistroffer, 1947.

Occurrence Upper Gault, condensed Upper Albian faunas including the Cambridge Greensand, and the Lower Chalk (Upper Albian, *Stoliczkaia dispar* Zone to Lower Cenomanian, *Calycoceras guerangeri* Zone), widely distributed including records from

Southern England, North-Western and Central Europe, Iran, Western Madagascar, Northern Australia, and western North America.

HEMIPTYCHOCERAS SULCATOSTRIATUS (WIEDMANN, 1962)

1962 *Hamites (Plesiohamites) sulcatostriatus* Wiedmann p. 182, pl. 10, fig 5, pl. 13, figs 5, 6, text-fig 42, 43.

? 1962 *Hamites (Plesiohamites) sulcatostriatus* Wiedmann pl. 10, figs 4.

Type material Holotype by original designation of Wiedmann (1962, pl. 10, fig 5), Department of Geology and Palaeontology, Institute of Tübingen, Ce.1162/51. From the Upper Albian of Izudiaga, Navarre, Northern Spain.

Description Heteromorph of uncertain coiling mode, probably hamiticonic but only fragments (the holotype and syntype material) of this species are known. Whorl section more or less dorsoventrally compressed. Ornamentation consists of weak ribs when small, but otherwise quite smooth. There are periodic constrictions, but apertural modifications are unknown. No tubercles. Suture quadrilobate and symmetrical across the siphuncle. External lobe similar in depth to umbilical lobe. Lateral lobe larger, deeply incised and subsymmetrically bifid. Umbilical lobe subsymmetrically bifid. Internal lobe symmetrically trifid. External, lateral and internal lobes similar in size, umbilical lobe slightly smaller. No pseudolobes. Saddles narrow and fairly florid. Ventral saddle trifid, lateral, umbilical, and dorsolateral saddles subsymmetrically bifid.

Discussion *Plesiohamites*, in which Wiedmann placed this species, as *Hamites (Plesiohamites) sulcatostriatus*, 1962, is a *nomen dubium* used incorrectly for *Lytohamites*. The cladogram places this taxon within a three-fold polytomy with the Anisoceratidae on the one side and the clade (*Hemiptychoceras* + *Hamitella* + *Turrilitdae*) on the other. The sister group of this entire polytomous group is *Lytohamites*. Therefore, while affinity with *Lytohamites* cannot be denied, it cannot be proved either. More importantly, the periodic constrictions of this species are not a feature of *Lytohamites* (*Lytohamites funatus* notwithstanding) or hamitids in general. Apertural constrictions are common to some of the Anisoceratidae, all *Hemiptychoceras* and many Turrilitidae. This suggests that constrictions may be a derived feature, and may indicate a relationship rather closer to the Anisoceratidae, *Hemiptychoceras* or Turrilitidae. The Turrilitidae are too far removed on the cladogram to be relevant to the position of this species, besides the fact that the coiling is straight and not helical. Absence of tubercles excludes it from the Anisoceratidae. I classify it here with *Hemiptychoceras* provisionally, suggesting that the periodic constrictions may be

homologous with the apertural constrictions of *Hemiptychoceras gaultinum* and *Hemiptychoceras parkinsoni*. Possibly constrictions developed primitively all along the conch as seen in this species (and to some extent basal Anisoceratidae like *Rossalites*) and only subsequently — but independently — became restricted to the final aperture at maturity. We must await the discovery of more complete specimens to provide more characters for analysis before the position of this enigmatic and interesting species is fully resolved.

Occurrence As holotype.

Genus *HAMITELLA* Breistroffer, 1947

Non tuberculate aspinoconic, ancyloconic or hamiticonic ammonites, with a pronounced and tightly coiled helical initial phase becoming planar later. Annular ribbing simple, usually continuous on the helical sections but effaced dorsally on the planar parts. Apertural collars and constrictions absent. Suture line quadrilobate, strongly asymmetrical during the helical phase. Synonym: *Helicoceras* d'Orbigny, 1842 *non* Koenig, 1825. Type species: *Hamitella cantianum* (d'Orbigny, 1842)

HAMITELLA ANNULATUM (D'ORBIGNY, 1842)

Figures 3.35-3.37

non	1837	*Hamites annulatus* Brown p. 3, pl. 1, fig, 10.
	1842	*Helicoceras annulatum* d'Orbigny p. 611, pl. 148, figs 7-9.
	1850	*Helicoceras annulatum* d'Orbigny, d'Orbigny p. 127.
	1861	*Helicoceras annulatum* d'Orbigny, Pictet & Campiche p. 117.
	1865	*Helicoceras annulatum* d'Orbigny, Stoliczka (in Oldham) p. 183.
	1875b	*Turrilites annulatum* (d'Orbigny), Neumayr p. 900.
	1925a	*Helicoceras annulatum* d'Orbigny, Spath p. 190.
non	1932	*Hamites annulatus* Collignon p. 22, p. 14, fig 9.
	1938	*Helicoceras annulatum* d'Orbigny, Roman p. 447, pl. 45 fig 427, 427a.
	1939	*Helicoceras annulatum* d'Orbigny, Spath p. 604.
	1939	*Hamites subrotundus* Spath, p. 605.
?	1940	*Helicoceras* sp., Breistroffer p. 157.
	1941	*Hamites subrotundus* Spath, Spath p. 616, pl. 68, figs 6-9.
	1942	*Hamites subrotundus* Spath, Spath p. 681.
	1944	*Helicoceras annulatum* d'Orbigny, Shimer & Shrock p. 593.

	1947	*Helicoceras annulatum* d'Orbigny, Breistroffer p. 46, 95.
	1949	*Hamites subrotundus* Spath, Collignon p. 124.
non	1957	*Hamites* cf. *annulatum* d'Orbigny, Almela & de la Revilla p. 8, 36, pl. 9, fig 3.
	1957b	*Hamites (Hamitella) annulatum* (d'Orbigny), Wright in Arkell et *al* p. 216.
	1960	*Hamites subrotundus* Spath, Owen p. 152.
	1962a	*Hamites (Hamites) helicoides* Wiedmann, p. 96.
	1965	*Hamites subrotundus* Spath, Clark p. 20.
	1966	*Hamites subrotundus* Spath, Casey (in Smart *et al*) p. 111.
	1971a	*Hamites subrotundus* Spath, Owen p. 152.
	1976	*Hamites subrotundus* Spath, Kennedy & Hancock p. 7, 8.
	1977	*Hamites subrotundus* Spath, Phillips p. 83.
	1978	*Hamites subrotundus* Spath, Klinger & Kennedy p. 35, pl. 9, figs a-b.
	1980	*Hamites subrotundus* Spath, Krishna p. 49, 51-52, pl. 1, figs 1, 3.
	1985	*Hamites (Hamites) helicoides* Wiedmann, Wiedmann & Marcinowski p. 454.
	1987	*Hamites subrotundus* Spath, Phillips p. 41.
?	1989	*Notostreptites exilis* Henderson p. 136, text-figs, 15t-ff, 16a, 17b.

Type material The type material of this species is not known with certainty (W. J. Kennedy, pers. comm.), but the larger of the two specimens comprising d'Orbigny Collection 5843, appears to be the original of d'Orbigny (1842, pl. 148, fig 7). This specimen is from the condensed faunas (*Lyelliceras lyelli* to *Diploceras cristatum* Subzones) of Clar, near Escragnolles, France.

Description Ancylocone with open, helical initial coil and two subparallel shafts. Helicosity similar to that of some *Proturrilitoides*, though the coils are not in contact. The whorl section is circular, with oblique but sharp annular ribs, barely attenuate dorsally if at all. The ribs are prorsiradiate from within the helix, and rursiradiate from without, and noticeably twisted with respect to the siphuncle. The ribbing is approximately rectiradiate on the straight sections. There rib index is ranges from 4 to 7, with the less dense ribbing being characteristic of microconchs. The maximum diameter of the helix is about 4 cms for microconchs and 6 cms for macroconchs. No known apertural collars. Tuberculation absent. Suture quadrilobate, strongly asymmetrical across the siphuncle during the helical phase, which is protracted, becoming symmetrical on the straight shafts. External and lateral lobes bifid and of similar size, umbilical and internal lobes rather smaller and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical saddles narrow and bifid, dorsolateral saddle also bifid but somewhat smaller.

Discussion *Hamitella annulatum* can only be distinguished from *Hamitella rotundus* J. Sowerby, 1814 on the basis of the finer ribbing, although there is some variability, and

transition forms occur between the two. More generally known as *Hamites subrotundus* Spath, 1941. Comparisons between the type material of *Hamites subrotundus* and *Hamitella annulatum* indicate that they are conspecific. The small helical turrilitid *Notostreptites exilis* Henderson, 1989 may also be conspecific. The described fragments of that species appear to be juvenile stages of *Hamitella annulatum*. The asymmetrical suture, helical coiling and sparse, sinuous ribbing of the juvenile stage of *Notostreptites exilis* are identical similar to that of *Hamitella annulatum*. The slight displacement of the siphuncle which Henderson (1989) described, may also be observed in *Hamitella annulatum* juveniles where the preservation is adequate. W. J. Kennedy (pers. comm.) believes that this species may in fact be a juvenile specimen of *Prohelicoceras* sp., but unlike that genus the specimens in the d'Orbigny collection lacks any hint of tuberculation.

Occurrence Predominantly from the Lower Gault (Middle Albian) of England, France, and Western Madagascar. Also the condensed 'Vraconian' fauna (*Stoliczkaia dispar* Zone) of Salazac, France, and the Middle Albian condensed faunas (*Lyelliceras lyelli* to *Diploceras cristatum* Subzones) of Escragnolles, France. Possibly also from northern Australia.

HAMITELLA GARDNERI (SPATH, 1941)

Figures 3.38-3.40

1923 *Hamites intermedius* J. Sowerby, Böse p. 132, pl. 9, figs 46-49.

1939 *Hamites gardneri* Spath p. 605.

1941 *Hamites gardneri* Spath, Spath p. 624, pl. 70 fig 3-5.

1942 *Hamites gardneri* J. Sowerby, Spath p. 681.

1968 *Hamites (Stomohamites)* cf., *funatus* Brogniart, Renz p. 69, pl. 11, figs 24a, 24b, text-fig 23(l).

1977 *Hamites gardneri* Spath, Phillips p. 80.

1990 *Hamites (Hamites) maximus* J. Sowerby, Marcinowski & Wiedmann p. 34, pl. 3, fig, 1.

Type material Holotype by original designation of Spath (1941) BMNH C.37958. From the Upper Gault (Upper Albian) of Folkestone, England.

Description Aspinocone with early helical phase and planar living chamber. Whorl section circular. Ribs sinuous, fairly blunt, very like those of *Hamitella maximus*, slightly prorsiradiate and twisted on the helical part becoming straight and rectiradiate along the phragmocone. Rib index 4 to 5. No known apertural collars. Tuberculation absent. Suture quadrilobate, strongly asymmetrical across the siphuncle during the helical phase, which is

protracted, becoming symmetrical on the straight shafts. External and lateral lobes bifid and of similar size, umbilical and internal lobes rather smaller and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical saddles narrow and bifid, dorsolateral saddle also bifid but somewhat smaller.

Discussion Frequently misidentified with *Hamitella maximus* with which it clearly intergrades morphologically. Circular section and sinuous, blunt ribbing as well as the helical juvenile phase separate this species of *Hamites compressus* and *Hamites incurvatus*.

Occurrence Lower and Upper Gault (Middle and Upper Albian, *Euhoplites meandrinus* to *Hysteroceras orbignyi* Subzones) of England. Also from the condensed Albian faunas (*Cleoniceras floridum* to *Mortoniceras altonense* Subzones) of Wiekla Rówien, Southern Poland, and condensed *Stoliczkaia dispar* Zone faunas of Saint-Croix, Switzerland and Camacho, Mexico. Other records of *Hamitella maximus* may be *Hamitella gardneri*.

HAMITELLA INTERMEDIUS (J. SOWERBY, 1814)

Figure 3.41

	1814	*Hamites intermedius* J. Sowerby., p. 139, pl. 62, figs 3a, b, 4a, b.
non	1814	*Hamites intermedius* J. Sowerby, pl. 62, figs 2a, b).
	1822	*Hamites intermedius* J. Sowerby, Mantell p. 93, pl. 23, fig, 12.
	1825	*Hamites intermedius* J. Sowerby, de Haan p. 153.
	1828	*Baculita intermedia* (J. Sowerby), Fleming p. 250.
	1829	*Hamites intermedius* J. Sowerby, Mantell p. 24.
?	1833	*Hamites intermedius* J. Sowerby, Mantell p. 160, text-fig 3.
	1837	*Hamites intermedius* J. Sowerby, Brown p. 2, pl. 3, fig 2.
	1837	*Hamites intermedius* J. Sowerby, Fitton p. 113.
	1848	*Hamites intermedius* J. Sowerby, Quenstedt p. 290, pl. 21, figs 9 -12.
	1848	*Hamites intermedius* J. Sowerby, Bronn p. 567.
non	1850	*Hamites intermedius* J. Sowerby, Mantell pl. 61, figs 2, 5.
	1852	*Hamites intermedius* J. Sowerby, Giebel p. 307.
	1854	*Hamites intermedius* J. Sowerby, Morris p. 181.
	1875	*Hamites intermedius* J. Sowerby, Topley p. 432.
non	1879	*Hamites intermedius* J. Sowerby, Price p. 76.
	1887	*Hamites intermedius* J. Sowerby, Woodward p. 384.
non	1897	*Hamites intermedius* J. Sowerby, Cowper Reed p. 76.
	1898a	*Hamites intermedius* J. Sowerby, Crick p. 61.

	1900	*Hamites intermedius* J. Sowerby, Jukes-Browne p. 459.
	1923	*Hamites intermedius* J. Sowerby, Spath p. 75.
?	1923	*Hamites intermedius* J. Sowerby, Böse p. 132, pl. 9, figs 46-49.
	1928	*Hamites adkinsi* Scott p. 116, pl. 16 (10, 13).
	1925	*Hamites intermedius* J. Sowerby, Diener p. 67.
	1925	*Hamites intermedius* J. Sowerby, Dewey *et al* p. 8.
non	1926a	*Hamites intermedius* J. Sowerby, Jayet p. 186.
	1929	*Hamites intermedius* J. Sowerby, Gossling p. 252.
?	1930	*Hamites intermedius* J. Sowerby, Passendorfer p. 663.
	1931	*Hamites adkinsi* Scott, Adkins p. 208.
	1939	*Hamites intermedius* J. Sowerby, Spath p. 605.
	1941	*Hamites intermedius* J. Sowerby, Spath p. 632 pl. 70 fig, 19, 71, figs 3, 5, text-fig 229 (a-d, m).
	1941	*Hamites intermedius opalina* Spath p. 633 pl. 70, fig 20, text-fig 229 (e-g).
	1941	*Hamites intermedius distincta* Spath p. 633 pl. 71, figs 4-6, text-fig 229 (n -p).
	1942	*Hamites intermedius* J. Sowerby, Spath p. 681.
	1957	*Hamites* cf. *annulatum* d'Orbigny, Almela & de la Revilla p. 8, 36, pl. 9, fig 3.
	1962	*Hamites adkinsi* Scott, Swensen p. 61.
	1962	*Hamites intermedius* J. Sowerby, Swensen p. 60, pl. 1, figs 10, 14.
	1965	*Hamites adkinsi* Scott, Clark p. 19.
	1965	*Hamites intermedius* J. Sowerby, Clark p. 19, pl. 1, figs 10, 14, text-fig 3a.
	1966	*Hamites intermedius* Spath, Casey (in Smart *et al*) p. 111.
	1966	*Hamites intermedius opalina* Spath, Casey (in Smart *et al*) p. 111.
	1966	*Hamites intermedius distincta* Spath, Casey (in Smart *et al*) p. 111.
	1968	*Hamites (Stomohamites)* cf. *funatus* (Brogniart) p. 69, pl. 11, figs 24 (a, b), text figs 23 (l).
	1976	*Hamites intermedius* J. Sowerby, Kennedy & Hancock p. 9.
	1976	*Hamites intermedius opalina* Spath, Kennedy & Hancock p. 9.
	1976	*Hamites intermedius distincta* Spath, Kennedy & Hancock p. 9.
	1977	*Hamites intermedius* J. Sowerby, Phillips p. 81.
	1982	*Hamites intermedius* J. Sowerby, Gallois & Morton p. 357.
	1989	*Hamites intermedius* J. Sowerby, Föllmi p. 124, pl. 4, figs 17-23.
?	1989	*Hamites intermedius* J. Sowerby, Horvath pl. 6, fig 6.

Type material Lectotype by subsequent designation of Spath (1941) BMNH C.43994d, the original of one of the specimens figured by Sowerby (1814, pl. 62, fig 4b — third specimen, bottom row). Two of the specimens figured as *Hamitella intermedius* are in fact *Hamitella maximus* (pl. 62, fig 2 — the first two specimens from the left, top row).The remaining

specimens (pl. 62, figs 3a,b and 4a) are paralectotypes. From the Upper Gault (Upper Albian) of Folkestone, England.

Description Very similar to *Hamitella maximus*, differing primarily in having less dense, rather more sinuous, ribbing and a greater degree of dorsal effacement to the ribs. Hamiticone with early helical phase and three planar shafts including the living chamber. Whorl section circular. Ribs sinuous, fairly blunt, slightly prorsiradiate on the helix and on the first two shafts becoming straighter and more or less rursiradiate along the living chamber. Rib index 3 to 6, highest near the aperture. No known apertural collars. Tuberculation absent. Suture quadrilobate, strongly asymmetrical across the siphuncle during the helical phase becoming symmetrical on the straight shafts. External and lateral lobes bifid and of similar size, umbilical and internal lobes rather smaller and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical saddles narrow and bifid, dorsolateral saddle also bifid but somewhat smaller.

Discussion Like *Hamitella gardneri*, this species intergrades morphologically with *Hamitella maximus*. The taxonomic status of this species has been discussed by Swensen (1962) and Clark (1965), including the suppression of the variety *Hamites intermedius distincta* Spath and the synonymisation of *Hamites adkinsi* with the present species. The subspecies *Hamites intermedius opalina* Spath is a name applied to specimens from Bed IX at Folkestone, England, which have a characteristic metallic-pearly shine. As such, it has no taxonomic value.

Occurrence Upper Albian (*Mortoniceras inflatum* Zone) of England, France, Germany and western and south-western North America. Less certainly from the Upper Albian (*Stoliczkaia dispar* Zone) of Mexico.

HAMITELLA MAXIMUS (J. SOWERBY, 1814)

Figures 3.42-3.44

1814 *Hamites maximus* J. Sowerby p. 138, pl. 62, fig, 1.

1820 *Hamites maximus* J. Sowerby, Defrance p. 249.

1822 *Hamites maximus* J. Sowerby, Mantell p. 93.

1825 *Hamites maximus* J. Sowerby, de Haan p. 154.

1828 *Baculita maxima* (J. Sowerby), Fleming p. 250.

1837 *Hamites maximus* J. Sowerby, Brown p. 2, pl. 1, fig, 14.

1837 *Hamites rectus* J. Sowerby, Brown p. 3, pl. 1, fig, 11.

1837 *Hamites maximus* J. Sowerby, Fitton p. 113.

1841 *Hamites maximus* J. Sowerby, Moxon pl. 13, fig, 11.

1842 *Hamites maximus* J. Sowerby, Pictet in Pictet & Roux p. 129.

1848 *Hamites maximus* J. Sowerby, Quenstedt p. 289, pl. 21, figs 6 (a-c), 7 (a-c).

1848 *Hamites maximus* J. Sowerby, Bronn p. 508.

1852 *Hamites maximus* J. Sowerby, Giebel p. 306.

1854 *Hamites maximus* J. Sowerby, Morris p. 305.

1861 *Hamites maximus* J. Sowerby, Pictet & Campiche p. 96.

1874 *Hamites maximus* J. Sowerby, Price p. 363.

1875a *Hamites maximus* J. Sowerby, Neumayr p. 29.

1875b *Hamites maximus* J. Sowerby, Neumayr p. 898.

1875 *Hamites maximus* J. Sowerby, Topley p. 432.

1879 *Hamites maximus* J. Sowerby, Price p. 76.

1884 *Hamites maximus* J. Sowerby, Zittel p. 444.

non 1890 *Hamites maximus* J. Sowerby, Renevier p. 340.

non 1897 *Hamites maximus* J. Sowerby, Parona & Bonarelli p. 104, pl. 14, fig, 14.

1898b *Hamites maximus* J. Sowerby, Crick p. 79, pl. 17, figs 6-9.

1900 *Hamites maximus* J. Sowerby, Jukes-Browne p. 459.

non 1905 *Hamites maximus* J. Sowerby, Hitzel p. 878.

? 1912 *Hamites maximus* J. Sowerby, Ganz p. 48.

1923 *Hamites maximus* J. Sowerby, Spath p. 75.

1925 *Hamites maximus* J. Sowerby, Dewey *et al* p. 8.

? 1926 *Hamites* cf. *maximus* J. Sowerby, Whitehouse p. 226, pl. 39, fig 2.

1929 *Hamites maximus* J. Sowerby, Brown p. 6.

non 1931 *Hamites maximus* J. Sowerby, Breistroffer p. 212.

? 1934 *Hamites maximus* J. Sowerby, Heim & Seitz p. 205.

1938 *Hamites maximus* J. Sowerby, Destombes & Destombes p. 7.

1939 *Hamites maximus* J. Sowerby, Spath p. 605.

1941 *Hamites maximus* J. Sowerby, Spath p. 621 pl. 68, fig 20, pl. 69, figs 1-5, pl. 70, figs 1, text-fig 224 (a-e).

1941 *Hamites maximus rectus* (Brown), p. 623 pl. 68, figs 15-16, 20, pl. 69, figs 6-9, pl. 70, fig, 18, text-fig 224 (a-e).

1942 *Hamites maximus* J. Sowerby, Spath p. 681.

1947 *Hamites maximus* J. Sowerby, Breistroffer p. 49.

1949 *Hamites maximus* J. Sowerby, Collignon p. 124.

1954 *Hamites maximus* J. Sowerby, Owen p. 237.

1955 *Hamites maximus* J. Sowerby, Milbourne p. 237.

1960 *Hamites maximus* J. Sowerby, Owen p. 374.

1960 *Hamites maximus rectus* (Brown), Owen p. 374.

1960 *Hamites maximus* J. Sowerby, Owen p. 152.

1966 *Hamites maximus* J. Sowerby, Casey (in Smart *et al*) p. 111.

1968 *Hamites maximus* J. Sowerby, Jordan p. 50.

1971a *Hamites maximus* J. Sowerby, Owen p. 152.

1976 *Hamites maximus* J. Sowerby, Kennedy & Hancock p. 7-9.

1976 *Hamites maximus rectus* (Brown), Kennedy & Hancock p. 8, 9.

1977 *Hamites maximus* J. Sowerby, Phillips p. 81-82.

1977 *Hamites maximus rectus* (Brown), Phillips p. 82.

1982 *Hamites intermedius* J. Sowerby, Gallois & Morton p. 358.

1984 *Hamites maximus* J. Sowerby, Henderson pl. 49, fig 7.

1985 *Hamites (Hamites) maximus* J. Sowerby, Marcinowski & Wiedmann p. 209.

1987 *Hamites maximus* J. Sowerby, Phillips p. 41.

1989 *Hamites maximus* J. Sowerby, Föllmi p. 124, pl. 4, figs 14-16.

1990 *Hamites (Hamites) maximus* J. Sowerby, Marcinowski & Wiedmann p. 35, pl. 3, fig, 1.

1990 *Hamites (Hamites) rectus* (Brown), Marcinowski & Wiedmann p. 35, pl. 2, fig, 14, text-fig 20.

1995 *Hamites* cf. *maximus* J. Sowerby, Seyed-Emami & Immel p. 382, text-fig 15.

Type material Neotype by subsequent designation of Spath (1941) BMNH C.43993b, the original of one of the specimens figured by Sowerby (1814, pl. 62, fig, 1 — the curved fragment). The other specimen, BMNH C.43993a is the paralectotype (1814, pl. 62, fig, 1 — the straight fragment). From the Lower Gault (Middle Albian) of Folkestone, England.

Description Hamiticone with helical initial coil. Differs from the superficially very similar *Hamitella intermedius* in having denser ribbing, which is less sinuous (but still more so than *Hamitella annulatum* or *Hamitella rotundus*). Rib index 4 to 6. The ribs are fairly blunt in aspect, twisted on the helical section, becoming straight and more or less rectiradiate on the straight shafts. Whorl section circular. No known apertural collars. Tuberculation absent. Suture quadrilobate, strongly asymmetrical across the siphuncle during the helical phase becoming symmetrical on the straight shafts. External and lateral lobes bifid and of similar size, umbilical and internal lobes rather smaller and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical saddles narrow and bifid, dorsolateral saddle also bifid but somewhat smaller. The suture is considerably more florid than Spath's figure would suggest (Spath, 1941, text-fig 224e).

Discussion Muscle scars have been described near the final septum of this specimen (Crick, 1898). Probably the largest hamitid (although *Hamitella intermedius* and *Lytohamites similis* may be comparable). The helical section varies in diameter from 4 to 8 cms in diameter, and the whorl height of from 20 to 30 cms. This variation in size may represent sexual

dimorphism. The subspecies *Hamitella maximus rectus* (Brown) is based on one of the rather smaller, finer ribbed specimens, and Wiedmann & Marcinowski (1990) considered it to be a true species.

Occurrence Middle and Upper Albian. In the Gault of southern England from the *Euhoplites meandrinus* up to the *Diploceras cristatum* Subzone, from where it intergrades with *Hamitella intermedius*. Also from the condensed Middle and Upper Albian faunas of south-eastern France and the condensed Albian faunas of southern Poland. Possibly also from Germany and Eastern Australia.

HAMITELLA ROTUNDUS (J. SOWERBY, 1814)

Figures 3.45-3.48

	1814	*Hamites rotundus* J. Sowerby p. 136, pl. 61, figs 2, 3.
	1820	*Hamites rotundus* J. Sowerby, Defrance p. 249.
non	1822	*Hamites rotundus* J. Sowerby, Mantell pl. 7, figs 5 (a -c).
	1825	*Hamites rotundus* J. Sowerby, de Haan p. 154.
	1828	*Baculita rotunda* (J. Sowerby), Fleming p. 250.
	1837	*Hamites rotundus* J. Sowerby, Brown p. 2, pl. 2, fig 7.
	1837	*Hamites rotundus* J. Sowerby, J. de C. Sowerby in Fitton p. 337, pl. 7, figs 1-2.
	1841	*Hamites rotundus* J. Sowerby, Moxon pl. 13, fig, 12.
non	1842	*Hamites rotundus* J. Sowerby, d'Orbigny p. 536, pl. 132, figs 1-4.
?	1842	*Helicoceras gracilis* d'Orbigny p. 611, pl. 148, figs 10-15.
non	1847	*Hamites rotundus* J. Sowerby, Pictet in Pictet & Roux p. 129, pl. 14, figs 1 (a-e).
	1848	*Hamites rotundus* J. Sowerby, Bronn p. 568.
non	1848	*Hamites rotundus* J. Sowerby, Quenstedt p. 288.
	1852	*Hamites rotundus* J. Sowerby, Giebel p. 306.
	1854b	*Hamites rotundus* J. Sowerby, Pictet p. 708.
	1854	*Hamites rotundus* J. Sowerby, Morris p. 305.
non	1860	*Hamites rotundus* J. Sowerby, Mackie p. 84, fig 8.
	1861	*Hamites rotundus* J. Sowerby, Pictet & Campiche p. 120.
	1966	*Hamites rotundus* J. Sowerby, Casey (in Smart *et al*) p. 111.
?	1868	*Hamites rotundus* J. Sowerby, de Rance p. 170.
	1874	*Hamites rotundus* J. Sowerby, Price p. 363.
non	1875a	*Turrilites (Helicoceras) rotundus* J. Sowerby, Neumayr p. 33.
non	1875b	*Turrilites (Helicoceras) rotundus* J. Sowerby, Neumayr p. 901.
	1875	*Hamites rotundus* J. Sowerby, Topley p. 436.

non 1884 *Hamites rotundus* J. Sowerby, Zittel p. 444, text-fig 621.
1898a *Hamites rotundus* J. Sowerby, Crick p. 79, pl. 17, figs 6-9.
1898 *Hamites rotundus* J. Sowerby, Dollfus p. 9.
1900 *Hamites rotundatum* J. Sowerby, Jukes-Browne p. 459.
non 1900 *Torneutoceras rotundus* (J. Sowerby), Hyatt in Zittel p. 586, text-fig 1226.
1905 *Hamites rotundus* J. Sowerby, Hitzel p. 879.
1918 *Hamites rotundus* J. Sowerby, Tomitch p. 3.
? 1922 *Hamites rotundus* J. Sowerby, Heim & Seitz p. 205.
non 1922 *Hamites rotundus* J. Sowerby, Stieler p. 43.
1922 *Helicoceras rotundum* (J. Sowerby), Spath p. 150.
1925 *Helicoceras rotundum* (J. Sowerby), Spath p. 190.
1938 *Helicoceras rotundum* (J. Sowerby), Destombes p. 8.
1939 *Hamites rotundum* J. Sowerby, Spath p. 605.
1941 *Hamites rotundum* J. Sowerby, Spath p. 611 pl. 67, figs 14-18, pl. 68, fig, 1, text-fig 219.
1942 *Hamites rotundus* J. Sowerby, Spath p. 681.
1947 *Hamites rotundus* J. Sowerby, Breistroffer p. 44, 45.
1949 *Hamites rotundus* J. Sowerby, Collignon p. 123.
non 1957 *Hamites* aff *rotundus* J. Sowerby, Almela & de la Revilla p. 8, 36, pl. 9, fig 4.
1958 *Hamites rotundus* J. Sowerby, Owen p. 157.
1960 *Hamites rotundus* J. Sowerby, Owen p. 372, 373.
1966 *Hamites rotundus* J. Sowerby, Casey (in Smart *et al*) p. 111.
1971a *Hamites rotundus* J. Sowerby, Owen p. 152.
1976 *Hamites rotundus* J. Sowerby, Kennedy & Hancock p. 6, 7.
1977 *Hamites rotundus* J. Sowerby, Phillips p. 82-83.
1985 *Hamites (Hamites) rotundus* J. Sowerby, Marcinowski & Wiedmann p. 209.
1989 *Hamites rotundus* J. Sowerby, Föllmi p. 124, pl. 4, figs 27-29.
1990 *Hamites (Hamites) rotundus* J. Sowerby, Marcinowski & Wiedmann p. 36, pl. 2 fig, 13.

Type material Lectotype by subsequent designation of Spath (1941) BMNH C.43990a, the original of J. Sowerby (1814, pl. 61, fig 2 — the larger of the two figured specimens). Paralectotypes exist: BMNH C.43990b (1814, pl. 61, fig 2 — the smaller of the two figured specimens) and BMNH C.43990c (1814, pl. 61, fig 3). From the Lower Gault (Middle Albian) of Folkestone, England.

Description Ancylocone with open, helical initial coil and two subparallel shafts, very similar to *Hamitella annulatum*, differing primarily in the finer and more densely packed ribbing and a rather weaker degree of asymmetry to the suture line. The whorl section is circular, with

oblique but sharp annular ribs, barely attenuate dorsally if at all. The ribs are prorsiradiate from within the helix, and rursiradiate from without, and twisted with respect to the siphuncle. The ribbing becomes approximately rectiradiate on the straight sections. There rib index is ranges from 4 to 7, with the less dense ribbing being characteristic of microconchs. No known apertural collars. Tuberculation absent. Suture quadrilobate, strongly asymmetrical across the siphuncle during the helical phase, and becoming symmetrical on the straight shafts. External and lateral lobes bifid and of similar size, umbilical and internal lobes rather smaller and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid. First lateral and umbilical saddles narrow and bifid, dorsolateral saddle also bifid but somewhat smaller.

Discussion Separation of this species and *Hamitella annulatum* is based on fine detail of ornamentation only, the two species intergrade morphologically. The type material of *Helicoceras gracilis* d'Orbigny, 1842 is lost, but it seems to be very similar to *Hamitella rotundus*.

Occurrence Lower Gault (Middle Albian, *Hoplites spathi* to *Euhoplites nitidus* Subzones) of England, France, and Western Madagascar. Also from the Middle Albian condensed faunas (*Lyelliceras lyelli* to *Diploceras cristatum* Subzones) of Escragnolles, France, and the condensed Glauconitic Albian faunas (*Cheloniceras floridum* to *Mortoniceras altonense* Subzones) of Wiekla Rówien, Poland.

Genus *METAHAMITES* Spath, 1930

Non-tuberculate ancylocones, planar throughout. Annular ribs simple and effaced dorsally. Periodic constrictions along the phragmocone and living chamber. Apertural collars and constrictions unknown. Suture line quadrilobate. Synonyms: none. Type species: *Metahamites sablieri* (d'Orbigny, 1842)

METAHAMITES SABLIERI (D'ORBIGNY, 1842)

Figures 3.49, 3.50

non	1842	*Hamites sablieri* d'Orbigny p. 543, pl. 133, figs 6-10.
	1930	*Metahamites sablieri* (d'Orbigny), Spath p. 57.
	1957b	*Metahamites sablieri* (d'Orbigny), Wright in Arkell *et al* p. 220.
	1961	*Metahamites sablieri* (d'Orbigny), Casey p. 99.
	1968	*Hamites (Metahamites) sablieri* (d'Orbigny), Wiedmann & Dieni p. 58.

1979 *Hamites sablieri* (d'Orbigny), Scholz p. 17.

1979 *Hamites (Metahamites) sablieri*, Gebhard p. 53, pl. 2, figs 2-3, text-fig 29.

1984 *Hamites (Metahamites) sablieri* (d'Orbigny), Wiedmann & Boess p. 495, fig 4 (a-e, i).

1990 *Metahamites sablieri* (d'Orbigny), Marcinowski & Wiedmann p. 37.

1996 *Metahamites sablieri* (d'Orbigny), Wright *et al* p. 235.

Type material Lectotype by subsequent designation of Spath (1930), the original of d'Orbigny (1842, pl. 83, fig 6) Museum of Natural History, Paris, 5813a. Refigured by Wiedmann & Boess (1984, fig 4a-e). From the Lower Gault (Middle Albian), Quartier de Clar, Escragnolle, France.

Description Earliest stages unknown. Ancylocone with no trace of helicosity or twisting. The two shafts are straight and long and the bend between them is tight. Laterally compressed whorl section but with periodic constrictions. Fine annular ribbing on phragmocone straight and prorsiradiate. The final shaft, the living chamber, has the ribs becoming less prorsiradiate along its length and finally rectiradiate near the aperture. On the phragmocone and the living chamber the ribs are partially effaced on the dorsal surface, but only the living chamber has visible striae or secondary ribs on the dorsum. These striae are barely discernible on the flanks and absent ventrally. The rib density on the phragmocone is higher (approximately, 10) than on the living chamber (approximately 4). Apertural collars or constrictions unknown. No tubercules. Whorl height is approximately 60 mm. Suture line quadrilobate, florid and symmetrical across the siphuncle. External, lateral and umbilical lobes of similar size, internal lobe slightly smaller. External lobe symmetrically bifid. Lateral lobe asymmetrically bifid. Umbilical and internal lobes symmetrically trifid. Pseudolobes absent. The ventral saddle is trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly narrow.

Discussion This genus has previously been taken to include a number of tuberculate species along with a Metahamites sablieri, a non-tuberculate species. Consequently, the genus has been generally placed within the tuberculate Anisoceratidae (Wright *et al*, 1996). Cladistic analysis clearly shows that *Metahamites sablieri* is not included within a monophyletic Anisoceratidae, and is better referred to the Hamitidae. However, the tuberculate species are shown to be members of the Anisoceratidae. They cannot be considered to be part of a monophyletic genus *Metahamites*. These species are discussed below, provisionally as members of the genus *Protanisoceras*, *Protanisoceras arrogans* and *Protanisoceras dalpiazi*.

Occurrence Middle Albian (*Hoplites dentatus* Zone, especially the *Hoplites spathi* Subzone) of France, Sardinia, Poland. Possible *Metahamites sablieri* have been recorded from the Middle Albian (*Hoplites spathi* Subzone) at Maidstone, Kent.

Family ANISOCERATIDAE Hyatt, 1900 (In: Zittel, 1900)

A family of heteromorphs derived from the Hamitidae, and characterised by the acquisition of paired ventral and ventrolateral tubercles. Anisoceratids first appear during the Lower Albian and persist on into the Santonian (FIGURE 2.17). They have been recorded from Albian rocks around the world.

Genus *ANISOCERAS* Pictet, 1854

Ancylcoconic ammonites, with a helical initial coil becoming planar for the later part of the phragmocone and the living chamber. Annular ribs simple or fibulate, effaced dorsally. Striae (minor ribs) frequently develop on the dorsal surface running on to the lower parts of the flanks, situated between the annular ribs. Ventral and/or ventrolateral tubercles usually at point where ribs divide and are symmetrically paired across the siphuncle. Apertural collars present in some species. Suture line quadrilobate. Synonyms: none. Type species: *Anisoceras saussureanus* (Pictet, 1847)

ANISOCERAS SAUSSUREANUS (PICTET, 1847)

Figures 3.51, 3.54a

	1847	*Hamites saussureanus* Pictet in Pictet & Roux p. 118, pl. 13, figs 1-4.
	1850	*Ancyloceras saussureanus* (Pictet), d'Orbigny p. 125.
	1852	*Hamites saussureanus* Pictet, Giebel p. 298.
	1854b	*Anisoceras saussureanus* (Pictet), Pictet p. 705, pl. 61, figs 12, 12a.
	1859	*Anisoceras saussureanus* (Pictet), Chenu p. 93, fig 406.
	1860	*Anisoceras saussureanus* (Pictet), Ooster p. 97.
	1861	*Anisoceras saussureanus* (Pictet), Pictet p. 21 *pars?*
non	1861	*Hamites saussureanus* Pictet, Hauer p. 644, pl. 2, fig, 1.
	1866	*Anisoceras saussureanus* (Pictet), Stoliczka in Oldham p. 175, 176.
	1866	*Anisoceras saussureanus* (Pictet), Pictet & Renevier p. 103.
	1874	*Hamites armatus* J. Sowerby, Price p. 363.
	1875a	*Hamites saussureanus* Pictet, Neumayr p. 30.
	1875b	*Hamites saussureanus* Pictet, Neumayr p. 30.
	1875	*Anisoceras saussureanus* (Pictet), Jukes-Browne p. 288.
	1875	*Anisoceras (Hamites) saussureanus* (Pictet), Hébert & Toucas 74.

1879 *Anisoceras saussureanus* (Pictet & Campiche), Price p. 76.

1885 *Hamites saussureanus* (Pictet), Fallot p. 71.

non 1889 *Hamites saussurei* Pictet, Killian p. 289.

1897 *Anisoceras saussureanus* (Pictet), Cowper-Reed p. 116.

1907 *Hamites saussureanus* Pictet, Boule, Lemoine & Thévenin p. 35.

? 1918 *Anisoceras saussureanus* (Pictet), Tomitch p. 3, 5, 11.

1921 *Anisoceras saussureanus* (Pictet), Spath p. 289.

1922 *Anisoceras saussureanus* (Pictet), Spath p. 151.

1923 *Anisoceras saussureanus* (Pictet), Böse p. 144.

non 1925 *Anisoceras saussureanus* (Pictet), Diener p. 73.

1926 *Anisoceras saussureanus* (Pictet), Whitehouse p. 231.

1926a *Anisoceras saussureanus* (Pictet), Jayet p. 186.

1926b *Anisoceras saussureanus* (Pictet), Jayet p. 156.

1926c *Anisoceras saussureanus* (Pictet), Jayet p. 171.

? 1930 *Hamites* sp. (Pictet), Roche p. 393.

1932 *Hamites (Anisoceras) saussureanus* (Pictet), Collignon p. 20.

1932 *Anisoceras saussureanus* (Pictet), Spath in White p. 117.

1933 *Anisoceras saussureanus* (Pictet), Breistroffer p. 234.

1934 *Anisoceras saussureanus* (Pictet), Heim & Seitz pp, 199-217.

1936 *Anisoceras saussureanus* (Pictet), Collignon in Besairie p. 79, 197.

1938 *Anisoceras saussureanus* (Pictet), Roman p. 51, pl. 5, fig 48.

1939 *Anisoceras saussureanus* (Pictet), Spath p. 541, 551, pl. 61, figs 1, 2, pl. 62, fig, 1, pl. 64, fig 9, text-fig 193.

1957 *Anisoceras saussureanus* (Pictet), Wright in Arkell *et al*, p. 220, text fig 246 (5a-c).

1968 *Anisoceras saussureanus saussureanus* (Pictet), Renz p. 77, pl. 15, figs 2, 6, pl. 16, fig 8, text-fig 27e, 28b.

1968 *Anisoceras saussureanus trifasciatum* Renz p. 77, pl. 15, figs 5, text-fig 28h.

1968 *Anisoceras saussureanus* (Pictet), Wiedmann & Dieni p. 66, pl. 7, fig 7, text-fig 40.

1976 *Anisoceras saussureanus* (Pictet), Kennedy & Hancock p. 9, 10.

1977 *Anisoceras saussureanus* (Pictet), Phillips p. 16-17.

1994 *Anisoceras saussureanus* (Pictet), Emmerson *et al* p. 280.

1996 *Anisoceras saussureanus* (Pictet), Wright *et al* p. 237, text-fig 187 (3a-3c).

Type material Lectotype by subsequent designation of Whitehouse (1926), figured by Pictet in Pictet & Roux (1847, pl. 13, fig 2a). From the Upper Albian of Saxonet, Savoy, France.

Description Large ancylocone with a weakly helical juvenile coil (apical angle approximately 150°). Whorl section initially subcircular, becoming laterally compressed for the straight part of the phragmocone and all of the final living chamber. Ornamentation is

variable, but generally consists of annular ribs, moderately effaced dorsally, interspersed with minor ribs along the dorsal surface. On the straight part of the phragmocone the ventral tubercles are clavate and ventrolateral tubercles are circular. The ribs divide at the ventrolateral tubercles and pass through the ventral tubercles, becoming reunited at the opposite ventrolateral tubercle. This changes on the living chamber, where the ventral and ventrolateral tubercles become bullate, and he ribs do not divide. Non-tuberculate ribs are present on the phragmocone and the living chamber. The rib index is approximately 4 to 6, every second to fourth rib bearing tubercles. The suture line is florid with deeply incised lobes and saddles, quadrilobate, and symmetrical across the siphuncle. The external, lateral and umbilical lobes are of similar size and the internal lobe significantly smaller. The external lobe is bifid. The lateral and umbilical lobes are subsymmetrically bifid. The internal lobe is trifid. No pseudolobes. The ventral saddle is indistinctly trifid. The first lateral, umbilical and dorso-ventral saddles are subsymmetrically bifid.

Discussion One of the largest heteromorph ammonites of the Upper Albian, and can be easily distinguished from other *Anisoceras* by sheer size. The initial coil reaches a diameter of about, 10 cms, and the overall shell height is between 50 to 60 cms.

Occurrence Upper Albian. Cosmopolitan, having been recorded throughout Europe, North Africa, Angola, Western Madagascar, Southern India, Queensland, Australia, North and Central America.

ANISOCERAS ARMATUM (J. SOWERBY, 1817)

Figures 3.53, 3.54b

	1817	*Hamites armatus* J. Sowerby, p. 153, pl. 168.
?	1820	*Hamites armatus* J. Sowerby, Defrance p. 250.
non	1822	*Hamites armatus* J. Sowerby, Mantell p. 121, pl. 23, figs 3-4.
	1825	*Hamites armatus* J. Sowerby, de Haan p. 152.
	1828	*Baculita armata* (J. Sowerby), Fleming p. 250.
	1829	*Hamites armatus* J. Sowerby, Brogniart p. 403.
?	1832	*Hamites armatus* J. Sowerby, Passy p. 333.
?	1836	*Hamites armatus* J. Sowerby, Fitton p. 333.
	1837	*Hamites armatus* J. Sowerby, Buckland p. 65, pl. 64, figs 9, 10.
	1837	*Hamites armatus* J. Sowerby, Brown p. 2, pl. 2, fig 6.
	1837	*Hamites armatus* J. Sowerby, Roemer p. 94, pl. 15, fig 2.
	1842	*Hamites armatus* J. Sowerby, d'Orbigny p. 547, pl. 135.

	1842	*Hamites armatus* J. Sowerby, Matheron p. 266.
?	1844	*Hamites armatus* J. Sowerby, Raulin p. 173, 174.
	1847	*Hamites armatus* J. Sowerby, Pictet in Pictet & Roux p. 377.
	1847	*Hamites armatus* J. Sowerby, Quenstedt p. 292.
non	1849	*Hamites armatus* J. Sowerby, Geinitz p. 122.
non	1850	*Ancyloceras armatus* J. Sowerby, d'Orbigny p. 147.
?	1851	*Hamites armatus* J. Sowerby, Dixon pl. 29, fig, 13.
?	1851	*Hamites armatus* J. Sowerby, Lory p. 62.
?	1851	*Hamites armatus* J. Sowerby, d'Archiac p. 225, 372.
	1852	*Hamites armatus* J. Sowerby, Giebel p. 296.
	1854	*Hamites armatus* J. Sowerby, Morris p. 305.
	1854b	*Hamites armatus* J. Sowerby, Pictet p. 705.
	1856	*Hamites armatus* J. Sowerby, von Strombeck p. 491.
?	1858	*Hamites armatus* J. Sowerby, Mortillet p. 253.
	1861	*Anisoceras armatus* (J. Sowerby), Pictet & Campiche pl. 48, fig 3.
	1861	*Anisoceras pseudoelegans* Pictet & Campiche p. 69, pl. 50, figs 5, 8.
?	1861	*Anisoceras armatus* (J. Sowerby), Pictet p. 21.
?	1861	*Hamites (Anisoceras) armatus* (J. Sowerby), Hauer p. 644, pl. 1, figs 9, 10.
	1866	*Anisoceras armatum* (J. Sowerby), Stoliczka p. 172.
	1866	*Anisoceras armatus* (J. Sowerby), Pictet & Renevier p. 103.
non	1868	*Anisoceras armatus* (J. Sowerby), de Rance p. 168, 169.
?	1871	*Hamites armatus* J. Sowerby, Phillips p. 441.
?	1874	*Hamites armatus* J. Sowerby, Price p. 363.
	1875	*Anisoceras armatus* (J. Sowerby), Jukes-Browne p. 288.
	1875a	*Hamites armatus* (J. Sowerby), Neumayr p. 28.
	1875b	*Hamites armatus* (J. Sowerby), Neumayr p. 397.
	1875	*Hamites armatus* (J. Sowerby), Topley p. 431, 436.
?	1878	*Anisoceras armatum* J. Sowerby, Barrois p. 253.
	1879	*Anisoceras armatum* (J. Sowerby), Price p. 76.
	1884	*Hamites armatus* (J. Sowerby), Homersham in Judd p. 736.
	1889	*Hamites armatus* (J. Sowerby), Bristow p. 280.
?	1889	*Anisoceras armatum* J. Sowerby, Kilian p. 289.
	1890	*Anisoceras armatum* (J. Sowerby), Renevier p. 340.
	1895	*Anisoceras armatum* (J. Sowerby), Kossmat p. 149.
?	1897	*Hamites (Anisoceras) armatum* J. Sowerby, Simionescu p. 70.
	1897	*Hamites armatum* (J. Sowerby), Cowper Reed p. 116.
?	1899	*Anisoceras armatum* J. Sowerby, Popovici-Hatzeg p. 10.
	1900	*Anisoceras armatum* (J. Sowerby), Jukes-Browne p. 459.
non	1902	*Hamites armatus* (J. Sowerby), Anderson p. 89.

? 1905 *Anisoceras armatum* J. Sowerby, Choffat p. 41, pl. 1, fig 6.

1907 *Anisoceras armatum* (J. Sowerby), Jacob p. 333.

1907 *Hamites (Anisoceras?) armatum* J. Sowerby, Pervinquière p. 84, pl. 4, figs 3, 3.

1907 *Hamites (Anisoceras) armatum* J. Sowerby, Boule *et al* p. 55.

1939 *Anisoceras armatus* (J. Sowerby), Spath p. 543, pl. 59, fig 6, pl. 60, fig, 1, pl. 61, figs 9-11, pl. 62, fig 5, pl. 63, fig 5, text-fig 191.

1939 *Anisoceras pseudoelegans* Pictet & Campiche, Spath p. 556, pl. 59, fig 5, pl. 60, figs 2, 3, pl. 63, fig, 12, text-fig 196 (a-d).

1962 *Anisoceras armatum* (J. Sowerby), Wiedmann p. 186, text-figs 46, 47.

1965 *Anisoceras armatum* (J. Sowerby), Clark p. 25, pl. 5, fig 4, pl. 6, fig 6, text-fig 7a.

1968 *Anisoceras armatum* (J. Sowerby), Renz p. 75, pl. 15, figs 1, 3, text-fig 27d, 28a.

1971 *Anisoceras armatum* (J. Sowerby), Kennedy, p. 14, pl. 5, fig, 11.

1976 *Anisoceras armatum* (J. Sowerby), Kennedy & Hancock p. 10, 14.

1977 *Anisoceras armatum* (J. Sowerby), Phillips p. 16.

1979 *Anisoceras (Anisoceras) armatum* (J. Sowerby), Cooper & Kennedy, p. 200, text-figs, 13a, b, 14d, e, 16a, c, e, i, 17 -, 19.

1979 *Anisoceras (Anisoceras) armatum* (J. Sowerby), Scholz, p. 25, pl. 2, figs 1-10, pl. 3, figs 1-5, pl. 4, figs 1-3, text-figs 8a-c.

1977 *Anisoceras pseudoelegans* (Pictet & Campiche), Phillips p. 16.

1982 *Anisoceras (Anisoceras) armatum* (Pictet & Campiche), Braga *et al* pl. 1, fig 5, text figs 2-4.

1987 *Anisoceras armatum* (Pictet & Campiche), Immel p. 129.

1988 *Anisoceras* cf. *armatum* (J. Sowerby), Ali-Zade p. 344, pl. 18, fig 6a, b.

1989 *Anisoceras (Anisoceras) armatum* (Pictet & Campiche), Hovath pl. 1, fig 8, pl. 2, fig 2, pl. 3, fig 7.

? 1995 *Anisoceras* cf. *armatum* (J. Sowerby), Wright & Kennedy, p. 302, pl. 88, figs 3, 15, pl. 91, figs 8, 9, text-fig 130(1).

Type material Holotype by monotypy, University of Oxford Museum K675a, the specimen figured by J. Sowerby (pl. 168, 1817) from the Chalk Marl (Upper Albian) at Benson, Oxfordshire.

Description Ancylocone, similar to *Anisoceras saussureanus* in general morphology and coiling mode. Can be distinguished from that species by generally smaller size and differences in ornament. While the tuberculation on the phragmocone of both species is similar, the ribs are finer and more densely packed, with a rib index of 6 to 8. Also, tuberculation on the final living chamber is quite different: whereas the ventral and ventrolateral tubercles on *Anisoceras saussureanus* become bullate, they remain clavate on

Anisoceras saussureanus. The ventrolateral tubercles also become rather weak. The suture line is similar to *Anisoceras saussureanus*.

Discussion The immature suture has been described (Swensen, 1962, p. 67, text-fig 8), and resembles that of typical *Protanisoceras*. This may suggests that the relative complexity of the mature suture in *Anisoceras*, which is often taken to distinguish that genus from the otherwise similar *Protanisoceras*, may be a consequence of its much larger size.

Occurrence Upper Albian. Like *Anisoceras saussureanus*, very widely distributed, being recorded throughout Europe (including Southern England and the Isle of Wight, France, Hungary, Romania and Poland), Azerbaijan, North Africa, Angola and Western Madagascar, Southern India, Western North America (including Texas and Utah), and Queensland, Australia. This species may also range into the Cenomanian (Kennedy, 1971, Wright & Kennedy, 1995).

ANISOCERAS PERARMATUM PICTET & CAMPICHE, 1861

Figures 3.52, 3.54c

1861 *Anisoceras perarmatus* Pictet & Campiche, p. 65, pl. 48, fig, 1(2-4).

1861 *Anisoceras armatum* Pictet & Campiche, p. 62, pl. 48, fig 7, 8, pl. 49, figs 1-3, 5, 6, 7.

1866 *Anisoceras armatum* J. Sowerby, Stoliczka, p. 172, pl. 81, figs 8-10, pl. 82, fig, 1.

1866 *Anisoceras perarmatus* Pictet & Campiche, Pictet & Renevier, p. 13.

1890 *Anisoceras perarmatum* Pictet & Campiche, Renevier, p. 340.

1923 *Anisoceras perarmatum* Pictet & Campiche, Böse, p. 144.

1925 *Anisoceras armatum* Pictet, Spath p. 191.

1926 *Anisoceras picteti* Spath p. 432.

1928 *Anisoceras* cf. *perarmatum* Pictet & Campiche, Spath, p. 51.

1939 *Anisoceras perarmatum* Pictet & Campiche, Spath, p. 548, pl. 59, figs 1-3. pl. 61, fig 3-7, text-fig 192.

1947 *Anisoceras perarmatum* Pictet & Campiche, Breistroffer p. 62.

1955 *Anisoceras perarmatum* Pictet & Campiche, Reyment p. 12, pl. 1,fig, 1.

1963 *Anisoceras perarmatum* Pictet & Campiche, Collignon p. 50, text-figs, 1126, 1127.

1963 *Anisoceras perarmatum* Pictet & Campiche, Dieni & Massari p. 798.

1965 *Anisoceras perarmatum* Pictet & Campiche, Clark p. 25, pl. 6, figs 1, 3, 7.

1968 *Anisoceras perarmatum perarmatum* (Pictet & Campiche), Renz p. 74, pl. 13, fig 5, pl. 14, figs 1, 2, 3, 5, text-fig 27a, 28g.

1968 *Anisoceras perarmatum simplex* Renz p. 75, pl. 13, fig 7, pl. 14, fig 4, text-fig 27k.

1968 *Anisoceras vraconense* Renz p. 74, pl. 16, fig 2, text-fig 7b.

1976 *Anisoceras perarmatum* (Pictet & Campiche), Kennedy & Hancock p. 10.

1977 *Anisoceras perarmatum* (Pictet & Campiche), Phillips p. 16.

1977 *Anisoceras picteti* (Spath), Phillips p. 16.

Type material Lectotype by subsequent designation of Spath (1939) the original of Pictet & Campiche (1861, pl. 49, fig, 1) from the Upper Gault (Upper Albian) of Sainte Croix, Switzerland.

Description Ancylocone, similar to *Anisoceras armatum* in size, general morphology and coiling mode. Can be only be distinguished from *Anisoceras armatum* by differences in ornament. On the phragmocone the tuberculation is similar to *Anisoceras saussureanus* and *Anisoceras armatum*, but every rib bear tubercules, whereas there are two or three non-tuberculate ribs on both *Anisoceras saussureanus* and *Anisoceras armatum*. The ribs are rather more effaced on the dorsal surface than is the case with *Anisoceras armatum*. The living chamber is similar to *Anisoceras armatum*, although the ventrolateral tubercles are more strongly developed. The suture line is similar to *Anisoceras saussureanus*.

Occurrence Upper Albian. Widely distributed in Europe, also Western Madagascar and Texas.

Genus *ROSSALITES* Casey, 1961

Large tuberculate ancylcoconic ammonites. Initial coil unknown, remainder of shell planar. Annular ribs simple, effaced dorsally. Secondary (minor) ribs develop dorsally between the annular ribs. Ventral tubercles throughout, ventrolateral tubercles if present are separate on the phragmocone, but unite with the ventral tubercles along the living chamber. Tubercles symmetrically paired across the siphuncle. Non-tuberculate ribs interspersed between tuberculate ribs. Apertural collars unknown. Periodic constrictions may develop. Suture line quadrilobate. Synonyms: none. Type species: *Rossalites superbum* (Collignon, 1949)

ROSSALITES SUPERBUM (COLLIGNON, 1949)

Figure 3.55

1949 *Protanisoceras superbum* Collignon p. 53.

1961 *Rossalites superbum* (Collignon), Casey p. 115, pl. 38 (a-c).

1961 *Rossalites oweni* Casey p. 117, pl. 38 (d, e).

1963 *Rossalites gracilis* Collignon p. 32, pl. 254, fig, 1086.

1977 *Rossalites oweni* Casey, Phillips p. 161.

1996 *Rossalites superbum* (Collignon), Wright *et al* p. 235, text-fig 185 (6a-c).

1996 *Rossalites oweni* Casey, Wright *et al* p. 235, text-fig 185 (6d).

Type material Holotype by original designation of Collignon, 1949. From the Lemuroceras Beds, *Douvilleiceras mammillatum* Zone, of Ambarimaninga, Western Madagascar.

Description Ancylocone with subcircular to slightly compressed whorl section. Annular ribs on phragmocone prorsiradiate approaching final hook, fairly fine and weakened dorsally, rib index of 3. Every second to fourth ribs bears symmetrically paired ventrolateral and ventral nodes . The ventrolateral pair of nodes are slightly bullate, the ventral pair circular tending towards being clavate. Both pairs are quite distinct and separate on the phragmocone but become more elongate and merging on living chamber. Apertural constrictions or collars unknown. Suture line quadrilobate, florid and symmetrical across the siphuncle. External, lateral, and internal lobes of similar size. Umbilical lobe much smaller. External and lateral lobes symmetrically bifid. Umbilical lobes indistinct trifid. Internal lobe symmetrically trifid. Pseudolobes absent. The ventral saddle is trifid, the first lateral, umbilical and dorso-ventral saddles are bifid.

Occurrence As holotype. Also Lower Albian (*Douvilleiceras mammillatum* Zone) of England and perhaps France.

ROSSALITES RICCARDII NOV. SP.

Figures 3.56-3.58

non 1970 *Lechites inlayi* Leanza p. 211, pl. 10, figs 1, 2.

non 1977 *Lechites inlayi* Leanza, Cooper & Kennedy p. 653.

? 1986 cf. *Metahamites* sp. Bréhéret *et al* pl. 7, fig 7.

1988 *Rossalites inlayi* (Leanzá), Riccardi p. 57, pl. 12, fig 7-9.

Type material Holotype by monotypy here designated the original of Riccardi (pl. 12, figs 7-9, 1949), MLP 17369. From the Lower Albian (*Douvilleiceras mammillatum* Zone) of Santa Cruz, Argentina

Description Ancylocone with slightly compressed whorl section. Annular ribs on phragmocone prorsiradiate approaching final hook, fairly fine and weakened dorsally. Rib index on phragmocone approximately 6. Symmetrically paired ventrolateral and ventral nodes borne by every fourth to sixth rib. Both pairs of nodes are approximately circular in section. As with *Rossalites superbum* the ornamentation changes on the phragmocone: The ribs become less distinct on the hook and eventually merge into bullate, raised ribs. The rib index decreases to approximately 3. On the living chamber minor ribs are intercalated between the major ribs on the dorsal surface. Apertural constrictions or collars unknown. Suture line unknown.

Discussion This species is not conspecific with the holotype of *"Lechites" imlayi* figured by Leanza (1970) from the Upper Aptian of Patagonia with which it was originally identified by Riccardi (1988). It is similar to *Rossalites superbum*, but differs in finer, more densely packed annular ribbing and the presence of circular ventral and ventrolateral tubercles. Therefore I propose a new name, *Rossalites riccardii*, in honour of A. C. Riccardi. *"Lechites" imlayi* itself is a heteromorph of some sort according to Cooper & Kennedy (1977), but certainly not a true *Lechites* (which do not appear until the Upper Albian).

Occurrence As for the holotype. Also from the Lower Albian (*Leymeriella tardefurcata* Zone, *Leymeriella regularis* Subzone) of South Eastern France..

Genus *PROTANISOCERAS* Spath, 1923

Tuberculate aspinoconic or ancylcoconic ammonites. Initial coil planar or rarely helical, remainder of shell planar. Annular ribs simple, effaced dorsally. Secondary (minor) ribs absent. Ventral and ventrolateral tubercles separate on the phragmocone, and are symmetrically paired across the siphuncle. Density of tubercles unstable and distribution on living chamber and phragmocone often different. Apertural collars and constrictions unknown. Suture line quadrilobate, not so florid as *Anisoceras* but this may be reflection of the smaller size of *Protanisoceras* at maturity. Synonyms: *Heteroclinus* Casey, 1961, *Torquistylus* Casey, 1961. Type species: *Protanisoceras raulinianum* (d'Orbigny, 1842)

PROTANISOCERAS RAULINIANUM (D'ORBIGNY, 1842)

Figure 3.59

1842 *Hamites raulinianus* d'Orbigny p. 546, pl. 134, figs 5-8 only?

non 1847 *Hamites raulinianus* d'Orbigny, Quenstedt p. 192.

1847 *Hamites raulinianus* d'Orbigny, Pictet in Pictet & Roux p. 378, pl. 12, fig 4.

1850 *Hamites raulinianus* d'Orbigny, d'Orbigny p. 126.

1851 *Hamites raulinianus* d'Orbigny, Cornuel p. 126.

1852 *Hamites raulinianus* d'Orbigny, Giebel p. 300.

1853 *Hamites raulinianus* d'Orbigny, Cotteau p. 16.

1854 *Toxoceras lardyi* Pictet & Renevier p. 26, pl. 2, fig 3 (a-c).

1858 *Hamites raulinianus* d'Orbigny, Leymerie & Raulin p. 475.

non 1860 *Hamites raulinianus* d'Orbigny, Ooster p. 75.

1861 *Toxoceras lardyi* Pictet & Renevier, Pictet & Campiche p. 55.

1861 *Hamites raulinianus* d'Orbigny, Pictet & Campiche p. 79, pl. 3, figs 13-20.

1861 *Hamites raulinianus* d'Orbigny, Pictet p. 17.

1875a *Hamites raulinianus* d'Orbigny, Neumayr p. 899.

1878 *Hamites raulinianus* d'Orbigny, Barrois p. 271.

? 1885 *Hamites raulinianus* d'Orbigny, Fallot p. 114.

1905 *Hamites raulinianus* d'Orbigny, Hitzel p. 879.

1909 *Toxoceras lardyi* Pictet & Renevier, Sinzow p. 30.

1913 *Hamites raulinianus* d'Orbigny, Kilian p. 330.

1913 *Toxoceras lardyi* Pictet & Renevier, Kilian p. 356.

1915 *Toxoceras lardyi* Pictet & Renevier, Kilian & Reboul p. 74.

1918 *Hamites raulinianus* d'Orbigny, Tomitch pp 3, 7.

1923a *Protanisoceras raulinianum* (d'Orbigny), Spath p. 75.

1923b *Protanisoceras raulinianum* (d'Orbigny), Spath p. 32.

1926 *Hamites raulinianus* (d'Orbigny), Jayet p. 179.

1930 *Protanisoceras raulinianum* (d'Orbigny), Spath p. 58.

1933a *Protanisoceras raulinianum* (d'Orbigny), Breistroffer p. 194-195.

1936 *Protanisoceras raulinianum* (d'Orbigny), Casey p. 446.

1939 *Protanisoceras raulinianum* (d'Orbigny), Spath p. 565-568, text-fig 200 (a-c), *non* pl. 64, fig, 13.

1939 *Protanisoceras raulinianum* var. *communis* (d'Orbigny), Spath p. 566, pl. 64, fig, 13, text-fig 200 (g-h).

1939 *Protanisoceras cantianum* Spath p. 567, pl. 63, fig, 10, text-fig 201 (e-g).

1939 *Protanisoceras* aff. *alterno-tuberculatum* (Leymerie), Spath p. 568, pl. 63, fig, 13.

1942 *Protanisoceras raulinianum* (d'Orbigny), Spath p. 680.

? 1942 *Protanisoceras alterno-tuberculatum* (Leymerie), Spath p. 680.

1947 *Protanisoceras raulinianum* var. *communis* Spath, Breistroffer p. 26, 28, 40.

1947 *Protanisoceras* cf. *raulinianum* (d'Orbigny), Breistroffer p. 41.

1947 *Toxoceras lardyi* Pictet & Renevier, Breistroffer p. 28.

non 1947 *Protanisoceras raulinianum* (d'Orbigny), Wright & Wright p. 166.

1957b *Protanisoceras raulinianum* (d'Orbigny), Wright in Arkell *et al* p. 220, text-fig 246 (3a,b).

1951 *Protanisoceras raulinianum* (d'Orbigny), Casey p. 97.

1953 *Protanisoceras raulinianum* (d'Orbigny), Basse p. 610.

1954 *Protanisoceras raulinianum* var. *isis* (d'Orbigny), Moret & Malmoud p. 272.

1957b *Protanisoceras raulinianum* (d'Orbigny), Wright in Arkell *et al* p. 218-220, text-fig 246 (3a,b).

1961 *Protanisoceras (Protanisoceras) raulinianum* (d'Orbigny), Casey p. 100, pl. 23, fig 9, pl. 24 fig 6, pl. 25 fig 2, text-fig 34.

1961 *Protanisoceras (Protanisoceras) lardyi* (d'Orbigny), Casey p. 103, pl. 23, figs 5, 6, text-fig 35 (a-c).

1961 *Protanisoceras (Protanisoceras) ventrosum* Casey p. 103, pl. 23, figs 3, 4.

1976 *Protanisoceras (Protanisoceras) ventrosum* Casey, Kennedy & Hancock p. 5, 6.

1976 *Protanisoceras (Protanisoceras) raulinianum* (d'Orbigny), Kennedy & Hancock p. 5, 6.

1976 *Protanisoceras (Protanisoceras) lardyi* (d'Orbigny), Kennedy & Hancock p. 5, 6.

1977 *Protanisoceras lardyi* (d'Orbigny), Phillips p. 153.

1977 *Protanisoceras raulinianum* (d'Orbigny), Phillips p. 153.

1977 *Protanisoceras ventrosum* Casey, Phillips p. 153.

? 1995 *Anisoceras (Protanisoceras) raulinianum* (d'Orbigny), Seyed-Emami & Immel p. 383, text-fig 23.

1996 *Protanisoceras (Protanisoceras) raulinianum* (d'Orbigny), Wright *et al* p. 234, text-fig 184 (2a-c).

Type material Lectotype by subsequent designation of Spath (1939) Raulin Collection, School of Mines, Paris 762 *pars*, the originals of d'Orbigny (1842, pl. 134). From the condensed *Leymeriella regularis* to *Douvilleiceras mammillatum* bed of Machéroménil, Ardennes, France.

Description Ancyloconic, with a planar initial coil and two subparallel shafts. Whorl section subcircular, depressed during initial coiling, becoming less so along shafts. Straight annular ribs coarse and moderately attenuate dorsally and flattened ventrally, weakly prorsiradiate on initial coil becoming approximately rectiradiate along shafts and rursiradiate near aperture. Rib index approximately 2-4. Certain ribs bear paired circular ventral nodes and usually ventrolateral nodes. Every rib of the living chamber is tuberculate, earlier ribs, especially along the juvenile coil have irregularly distributed non-tuberculate ribs. The coiling phase may have two to three non-tuberculate ribs between tuberculate ones. The suture line is quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe much smaller. External lobe symmetrically bifid.

Lateral and umbilical lobes asymmetrically trifid. Internal lobes symmetrically trifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly broad and simple.

Discussion The reconstructed figure of d'Orbigny (1842) is in part incorrect: this species does not possess fibulate ribbing between the ventral nodes. *Protanisoceras lardyi* (Pictet & Renevier), *Protanisoceras raulinianum* variety *communis* (Spath), is distinguished on the basis of sharper ribbing and having three or more non-tuberculate ribs between tuberculate ones. Since *Protanisoceras raulinianum* have a similar proportion of tuberculate and non-tuberculate, rather fine, ribs during the coiling phase, and the holotype of *Protanisoceras lardyi* is also a juvenile coil, distinction between the two species is questionable. The suture line, coiling, and general appearance is otherwise very similar. *Protanisoceras ventrosum* Casey are also included within this species. The suture line is similar to typical *Protanisoceras raulinianum*. The major difference is that the ribs between the ventral nodes appear to be fibulate, but examination of the holotype suggest that this is an artefact of preservation: the ribs have been worn flat, and are quite different to the distinctly fibulate ribs of *Protanisoceras nodosum*.

Occurrence Lower Albian, *Douvilleiceras mammillatum* Zone (*Cleoniceras floridum* to *Protohoplites puzosianus* Subzones). Widely recorded from Europe (including France, Southern England, Switzerland, and Germany), also Egypt.

PROTANISOCERAS CANTIANUM SPATH, 1939

Figure 3.60

	1939	*Protanisoceras cantianum* Spath p. 567, pl. 63, fig, 10, text-fig 201 (a-d).
non	1939	*Protanisoceras cantianum* Spath p. 567, pl. 63, fig, 10, text-fig 201 (e-k).
	1942	*Protanisoceras cantianum* Spath, Spath p. 680.
	1947	*Protanisoceras cantianum* Spath, Breistroffer p. 40.
	1961	*Protanisoceras (Protanisoceras) cantianum* Spath, Casey p. 104, pl. 23, figs 1, 2, pl. 25, fig 3, text-fig 35 (q, r), 36a.
	1977	*Protanisoceras cantianum* Spath, Phillips p. 152.
	1989	*Protanisoceras cantianum* Spath, Föllmi p. 125, pl. 4, fig 30.

Type material Holotype by original designation of Spath (1939) BMNH C.48915. From the Main Mammillatum Bed (Lower Albian, *Douvilleiceras mammillatum* Zone) of Copt Point, Folkestone, England.

Description Ancyloconic with planar coiling initially and two subparallel shafts. Dorso-ventrally compressed except for the living chamber near the aperture which becomes more subcircular in section. Annular ribs coarse and straight, very weak dorsally and flattened ventrally, straight, prorsiradiate along shafts becoming rectiradiate along shafts and then rursiradiate near the aperture. Rib index 3 to 4 on septate parts of shell. All (or at least most) ribs bear paired circular ventral nodes, ventrolateral nodes weak or absent. Suture line similar to *Protanisoceras raulinianum*, being quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe much smaller. External lobe symmetrically bifid. Lateral and umbilical lobes asymmetrically trifid. Internal lobes symmetrically trifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly broad and simple.

Discussion Differs from *Protanisoceras raulinianum*. primarily in the weakness of the ventrolateral tuberculation and the irregular distribution of nodes.

Occurrence Lower Albian, *Douvilleiceras mammillatum* Zone of England, France and Austria.

PROTANISOCERAS COPTENSE , 1961

Figure 3.61

1961 *Protanisoceras (Protanisoceras) coptense* Casey p. 105, pl. 23, fig 7, text-fig 36b.

1977 *Protanisoceras coptense* , Phillips p. 152.

Type material Holotype by original designation of Casey (1961) BMNH C.71971. From the Main Mammillatum Bed (Lower Albian, *Douvilleiceras mammillatum* Zone) of Copt Point, Folkestone, England.

Description Shape and ornamentation of phragmocone similar to *Protanisoceras cantianum*, but with total absence of ventrolateral tuberculation, and the ventral nodes being found on only the second or third ribs. Living chamber unknown, probably similar to *Protanisoceras cantianum*. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe much smaller. External lobe symmetrically bifid. Lateral lobe subsymmetrically bifid. Umbilical lobe asymmetrically trifid. Internal lobe symmetrically trifid. Pseudolobes absent. The ventral saddle is indistinctly

trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly broad and simple.

Discussion Since this species is known only from a the holotype, the morphological range of this species cannot be compared with other *Protanisoceras*. Although the suture line is simple, the fragment appears to be of the coiled part of the phragmocone, and thus the simplicity of the suture may be consistent with an early stage of ontogeny. Whether the adult had a particularly simple suture line is unknown.

Occurrence As for the holotype.

PROTANISOCERAS BLANCHETI (PICTET & CAMPICHE, 1861)

Figures 3.62, 3.63

	1861	*Ancyloceras blancheti* Pictet & Campiche p. 33, pl. 47, figs 1-10.
	1875	*Hamites blancheti* (Pictet), Neumayr p. 897.
	1907	*Anisoceras blancheti* (Pictet & Campiche), Jacob pp 315, 326.
?	1910	*Ancyloceras blancheti* Pictet & Campiche, Sommermeir p. 377.
?	1912	*Ancyloceras blancheti* Pictet & Campiche, Ganz pp 61, 121.
	1939	*Protanisoceras blancheti* Pictet & Campiche, Spath pp 568, 572.
	1939	*Protanisoceras cantianum* Spath p. 567, pl. 63, fig, 10, text-fig 201 (h-k).
	1947	*Protanisoceras blancheti* Pictet & Campiche, Breistroffer p. 40.
	1961	*Protanisoceras (Protanisoceras) blancheti* (Pictet & Campiche), Casey p. 106, pl. 23, fig 8, pl. 24, figs 7-9, text-fig 35 (d, i), 36c.
	1977	*Protanisoceras blancheti* (Pictet & Campiche), Phillips p. 152.
	1987	*Protanisoceras blancheti* (Pictet & Campiche), Phillips p. 97.

Type material Lectotype by subsequent designation of Spath (1939), the original of Pictet & Campiche (1861, pl. 47, fig 2a-d). Refigured by Casey (text-fig 35d-f, 1961). From the Lower Albian of Sainte-Croix, Switzerland.

Description Ancylocone with planar coiled juvenile phase and two subparallel straight shafts. Whorl section subcircular, flattened ventrally, almost pentagonal in form. Annular ribs sharper and finer than *Protanisoceras raulinianum* and attenuate only slightly dorsally, flattened a little ventrally. Ribs straight on shafts, slightly prorsiradiate on coil tending to be approximately rectiradiate on straight sections and slightly sinuous over the bend between the shafts. Rib index 4 to 5. Most ribs on coiled sections bear paired circular nodes ventrally,

tuberculation becomes less regular on later stages and is weak or absent from the final living chamber. No ventrolateral nodes. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe much smaller. External lobe symmetrically bifid. Lateral lobe subsymmetrically bifid. Umbilical lobe symmetrically bifid. Internal lobe symmetrically bifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly broad and simple.

Occurrence Lower Albian, *Douvilleiceras mammillatum* Zone, *Cleoniceras floridum* Subzone, of England. Also from condensed Lower and Middle Albian series in Switzerland and France.

PROTANISOCERAS HALLERI (PICTET & CAMPICHE, 1861)

	1861	*Hamites halleri* Pictet & Campiche, p. 84, pl. 54, figs 1-5.
	1861	*Hamites halleri* Pictet & Campiche, Pictet p. 17.
	1875a	*Hamites halleri* Pictet & Campiche, Neumayr p. 29.
	1875b	*Hamites halleri* Pictet & Campiche, Neumayr p. 898.
	1907	*Hamites halleri* Pictet & Campiche, Jacob p. 315.
?	1918	*Hamites halleri* Pictet & Campiche, Tomitch p. 3, 5.
	1930	*Protanisoceras halleri* (Pictet and Campiche), Spath p. 58
	1939	*Protanisoceras halleri* (Pictet and Campiche), Spath p. 572-3, text-fig 204a-d.
non	1939	*Protanisoceras halleri* (Pictet and Campiche), Spath text-fig 204e-h.
?	1961	*Protanisoceras (Protanisoceras)* cf. *halleri* (Pictet and Campiche), Casey p. 111, pl. 24, fig, 10.

Type material Lectotype by subsequent designation of Spath (1939) the original of Pictet & Campiche (1861, pl. 54, fig, 1a-d). From the Middle Albian, Sainte-Croix, Switzerland.

Description Ancyloconc, imperfectly known, but similar to other *Protanisoceras*. Planar initial coil. Whorl section initially subcircular becoming somewhat laterally compressed. Annular ribs blunt and rather weak, moderately attenuate dorsally, flattened slightly ventrally. Ribs straight, slightly prorsiradiate on initial coil, becoming approximately rectiradiate on straight sections, if slightly sinuous over the bend between the shafts. Rib index 2 to 3. Every second rib on coiled sections bear pairs of circular nodes ventrally and ventrolaterally, the ventrolateral pair becoming rather weak or absent altogether from the straighter parts of the phragmocone and the living chamber. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical

lobe much smaller. External lobe symmetrically bifid. Lateral lobe subsymmetrically bifid. Umbilical lobe symmetrically trifid. Internal lobe symmetrically bifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly broad and simple.

Occurrence Lower Gault (Middle Albian, *Hoplites dentatus* Zone) of Southern England, France, Switzerland and India.

PROTANISOCERAS VAUCHERIANUM (PICTET, 1847)

1847 *Crioceras vaucherianus* Pictet (in Pictet & Roux) p. 367, pl. 12, fig, 1.

1861 *Ancyloceras vaucherianus* (Pictet), Pictet & Campiche p. 31, pl. 46, figs 1-4.

1961 *Protanisoceras (Protanisoceras) vaucherianum* (Pictet), Casey p. 107, pl. 25, fig 7, 8, text-fig 35 (m, n).

1977 *Protanisoceras vaucherianum* (Pictet), Phillips p. 152.

Type material Holotype by monotypy, the original of Pictet (1847, pl. 12, fig, 1). From the Lower Albian of Gorges, Bellegarde, Switzerland.

Description Ancylocone with paired ventral tubercles on every second or third rib on the phragmocone and living chamber. The ribs bearing the tubercles are somewhat raised compared to non-tuberculate ribs. Whorl section approximately circular. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe much smaller. External lobe symmetrically bifid. Lateral lobe subsymmetrically bifid. Umbilical lobe symmetrically trifid. Internal lobe symmetrically bifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly broad and simple.

Discussion. Can be distinguished from the similar *Protanisoceras blancheti* by the persistence of the ventral tubercles onto the living chamber.

Occurrence Lower Albian, *Douvilleiceras mammillatum* Zone of England and France.

PROTANISOCERAS NODOSUM (J. SOWERBY, 1818)

Figure 3.64

1818 *Hamites nodosus* J. Sowerby p. 30, pl. 216, fig 3.

non 1818 *Hamites nodosus* J. Sowerby, Fitton p. 113, 367.

1828 *Baculita nodosus* (J. Sowerby), Fleming p. 251.

1837 *Hamites spiniger* (*non* J. de C. Sowerby), J. de C. Sowerby in Fitton p. 337, pl. 7, fig 4.

1837 *Hamites aculeatus* Fitton p. 113.

1837 *Hamites nodosus* J. Sowerby, Brown p. 2, pl. 2, fig 5.

1842 *Hamites flexuosus* d'Orbigny p. 535, pl. 131, figs 14-16.

? 1847 *Hamites flexuosus* d'Orbigny, Pictet & Roux p. 126, pl. 12, figs 9, 10.

1848 *Hamites flexuosus* d'Orbigny, Bronn p. 567.

1842 *Hamites nodosus* J. Sowerby, d'Orbigny p. 528.

non 1842 *Hamites spiniger* Fitton, d'Orbigny p. 538.

1850 *Hamites flexuosus* d'Orbigny, d'Orbigny p. 126.

1852 *Hamites flexuosus* d'Orbigny, Giebel p. 304.

1852 *Hamites nodosus* J. Sowerby, Giebel p. 324.

1854 *Hamites flexuosus* d'Orbigny, Pictet p. 708.

1860 *Hamites flexuosus* d'Orbigny, Ooster p. 76.

1861 *Hamites nodosus* J. Sowerby, Pictet & Campiche p. 42.

1861 *Ancyloceras aculeatus* (Fitton), Pictet & Campiche p. 42.

1861 *Hamites flexuosus* d'Orbigny, Pictet & Campiche p. 93.

1861 *Ancyloceras spinigerum* (J. Sowerby), Pictet & Campiche p. 362.

1875a *Hamites aculeatus* Fitton, Neumayr p. 28.

1875a *Hamites flexuosus* d'Orbigny, Neumayr p. 29.

1875b *Hamites aculeatus* Fitton, Neumayr p. 897.

1875b *Hamites flexuosus* d'Orbigny, Neumayr p. 898.

non 1875 *Hamites (Turrilites) flexuosus*, Topley p. 432.

? 1875 *Hamites nodosus* J. Sowerby, Topley p. 432.

1878 *Hamites flexuosus* d'Orbigny, Barrois p. 271.

1878 *Hamites nodosus* d'Orbigny, Barrois p. 271.

1879 *Hamites flexuosus* d'Orbigny, Price p. 76.

1879 *Hamites nodosus* J. Sowerby, Price p. 76.

1879 *Ancyloceras spinigerum* (J. Sowerby), Price p. 76.

1888 *Ancyloceras spinigerum* (J. Sowerby), Prestwich p. 279, text-fig 145d.

1900 *Ancyloceras spinigerum* (J. Sowerby), Jukes-Browne p. 459.

1918 *Hamites flexuosus* d'Orbigny, Tomitch p. 3.

1923a *Protanisoceras? aculeatum* (J. Sowerby), Spath p. 75.

1925b *Protanisoceras? aculeatum* (J. Sowerby), Spath p. 33.

non 1926 *Hamites flexuosus* d'Orbigny, Jayet p. 186.

non 1926 *Appurdiceras nodosus* (J. Sowerby), Whitehouse p 230.

non 1930 *Hamites* cf. *flexuosus* d'Orbigny, Passendorfer p. 660

non 1933 *Metahamites flexuosus* (d'Orbigny), Breistroffer p. 234.

1936 *Protanisoceras* nov. sp.? Casey, p 447.

1939 *Protanisoceras nodosum* (d'Orbigny), Spath p. 573, pl. 54, figs 1-8, text-fig 205a-f.

1939 *Protanisoceras flexuosus* (d'Orbigny), Spath p. 577, text-fig 205 (g-p).

1961 *Protanisoceras (Heteroclinus) nodosus* (J. Sowerby), Casey, p. 98 (footnote).

1962a *Anisoceras (Protanisoceras) nodosum* (J. Sowerby), Wiedmann p. 109, pl. 7, fig 8, text-fig 34.

1977 *Heteroclinus nodosus* (J. Sowerby), Phillips p. 86.

1977 *Protanisoceras flexuosus* (d'Orbigny), Phillips p. 152-153.

1996 *Protanisoceras (Heteroclinus) nodosus* (J. Sowerby), Wright *et al* p. 234, text-fig 184 (3).

Type material Holotype by monotypy the original of Sowerby's figure (1818, pl. 216, fig 3) BMNH C.43997a. From the Lower Gault of Folkestone, England.

Description Ancylocone with a helical juvenile phase and two relatively short subparallel straight shafts, although the second shaft tends toward irregularity near the aperture. Like *Hamitella*, the helical coil overlies the rather closely packed straight shafts. Whorl section subcircular on helix tending to be slightly laterally compressed along the straight sections. Annular ribs fine, weakly attenuate dorsally but strong ventrally. Ribbing twisted and a little sinuous on helical phase and persisting thus onto the first shaft. On later parts of the first shaft and on the living chamber the ribs are prorsiradiate, becoming rectiradiate and then rursiradiate through bend and onto the living chamber, and finally rectiradiate again near aperture. Rib index of 6 to 8. No obvious constrictions at aperture. Every second to fourth rib bears a pair of circular ventral nodes, ribbing most dense on helix and thinning out over straight sections and onto the living chamber. Ventrolateral tuberculation absent. Between the ventral nodes the ribbing is flattened and slightly convex, almost fibulate in appearance. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe somewhat smaller. External lobe symmetrically bifid. Lateral lobe symmetrically bifid. Umbilical lobe symmetrically trifid. Internal lobe symmetrically trifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. The saddles are less broad than some other *Protanisoceras* but remain fairly simple.

Discussion *Protanisoceras flexuosum* d'Orbigny is based on a fragment of the juvenile coil allegedly from Wissant, France. The specimen on which the figure is supposedly is based, Museum of Natural History, Paris, R1034, is labelled as being from Boulogne, France, this

specimen is similar to juvenile *Protanisoceras nodosum* except that it is very slightly dorso-ventrally compressed. The specimen figured by d'Orbigny is laterally compressed, and probably conspecific with *Protanisoceras nodosum*. Therefore status of *Protanisoceras flexuosum* vis-à-vis *Protanisoceras nodosum* is therefore uncertain. The two are at least very closely related, most probably identical, and considered to be synonyms here.

Occurrence Widely recorded from the Lower Gault (Middle Albian *Lyelliceras lyelli* to *Anahoplites intermedius* Subzones) of England, France, and Germany.

PROTANISOCERAS ANGLICUM (SPATH, 1939)

Figures 3.65, 3.66

	1818	*Hamites nodosus* J. Sowerby p. 30, pl. 216, fig 3.
	1874	*Turrilites* sp. Price, p. 140.
	1936	*Helioceras* spp. Casey, p. 446.
	1939	*Prohelicoceras anglicum* Spath p. 562, pl. 63, fig, 14, text-fig 199 (a-g).
?	1940	*Prohelicoceras anglicum* Spath, Breistroffer p. 134.
	1961	*Protanisoceras (Torquistylus) anglicum* (Spath), Casey, p. 113, pl. 22, figs 7-12, text fig 37.
	1977	*Torquistylus anglicum* (Spath), Phillips p. 176.
	1979	*Prohelicoceras anglicum* Spath, Collignon p. 7, pl. 1, fig 7a, b, 8a, b.
	1996	*Protanisoceras (Torquistylus) anglicum* (Spath), Wright *et al* p. 234, text-fig 184 (1a-c).

Type material Holotype by original designation of Casey, BMNH C.48913 from the Main Mammillatum Bed (Lower Albian) of Folkestone, England.

Description Ancyloconic with a helical initial coil and an abbreviate hook distinctly twisted relative to the helix. Whorl section subcircular throughout, slightly flattened ventrally. Annular ribs fairly blunt and coarse, approximately rectiradiate but variable, rib index of 3 to 4. Ribbing attenuate dorsally and flattened ventrally between the nodes. Circular paired ventral nodes on every rib, but very weakly defined. No ventrolateral nodes. Nodes absent from the living chamber. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe smaller. External lobe symmetrically bifid. Lateral lobe symmetrically bifid. Umbilical lobe indistinctly bifid. Internal lobe symmetrically trifid. Pseudolobes absent. The ventral saddle is

indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. The saddles are rather broad and simple.

Occurrence Upper Greensand (Lower Albian). Predominantly from the condensed Regularis-Mammillatum Beds of Machéroménil, Ardennes, France and the condensed Mammillatum Beds of Southern England. Also from the Shenley Limestone (*Leymeriella regularis* Subzone) of Southern England. Possibly also from the Lower Gault (Middle Albian, *Hoplites dentatus* Zone) of Clar, Escragnolles, France.

PROTANISOCERAS ACTEON (D'ORBIGNY, 1850)

Figure 3.67

	1850	*Hamites acteon* d'Orbigny p. 126.
	1852	*Hamites acteon* d'Orbigny, Giebel p. 315.
	1907	*Hamites* nov. sp. cf. *virgulatus* Pictet, Jacob p. 315.
non	1940	*Hamites acteon* d'Orbigny, Breistroffer p. 134.
	1947	*Protanisoceras* cf. *raulinianum* (d'Orbigny), Wright & Wright p. 166.
	1948	*Protanisoceras blancheti* (Pictet & Campiche), Wright & Wright p. 85.
	1948	*Prohelicoceras anglicum* Spath, Wright & Wright p. 85.
	1953	*Protanisoceras blancheti* (Pictet & Campiche), Breistroffer & Villoutreys p. 70.
	1961	*Protanisoceras (Protanisoceras) acteon* (d'Orbigny), Casey p. 109, pl. 24, fig, 1-4, text-fig 35 (o, p.), 36d.
	1961	*Protanisoceras (Protanisoceras) hengesti*, Casey p. 110, pl. 25, fig 4-6.
	1977	*Protanisoceras acteon* (d'Orbigny), Phillips p. 152.
	1989	*Protanisoceras acteon* (d'Orbigny), Föllmi p. 126, pl. 5, fig, 1.

Type material Lectotype by subsequent designation of Casey (1961) from the Lower Greensand (Lower Albian) of Clar, near Escragnolle, South-East France. No specimens were figured by d'Orbigny, but one specimen from the d'Orbigny collection was figured in the full description given by Casey (1961, text-fig 35o,p, 36 d).

Description Ancylocone with a subcircular whorl section with distinct flattening between the ventral nodes. Ribs broad and fairly coarse, moderately attenuate dorsally and flattened ventrally, bearing paired circular ventral nodes. No ventrolateral nodes. Rib index 4 to 5. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe smaller. External lobe symmetrically bifid. Lateral lobe symmetrically bifid. Umbilical lobe indistinctly bifid. Internal lobe

symmetrically trifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. The saddles are rather broad and simple.

Occurrence Lower Albian (*Douvilleiceras mammillatum* Zone) of England, France and Austria.

PROTANISOCERAS ARROGANS (D'ORBIGNY, 1842)

Figure 3.68

non	1819	*Hamites elegans* Parkinson p. 543, pl. 133, figs 6-10.
	1842	*Hamites elegans* d'Orbigny p. 543, pl. 133, figs 1-5.
	1847	*Hamites elegans* d'Orbigny, Quendstedt p. 291, pl. 21, fig 8.
	1848	*Hamites elegans* d'Orbigny, Pictet p. 123, pl. 13, fig 8.
	1852	*Hamites arrogans* Giebelp. 305.
	1861	*Anisoceras pseudoelegans* Pictet & Campiche pl. 50, figs 6, 7.
?	1874	*Hamites elegans* d'Orbigny, Price p. 363.
	1926	*Anisoceras campichei* Spath p. 432.
	1939	*Metahamites? arrogans* (Giebel), Spath p. 559.
	1939	*Anisoceras campichei* Spath, Spath p. 559, text-fig 197.
non	1939	*Anisoceras campichei* Spath, Spath pl. 63, figs 6, 7.
	1940	*Hamites (Metahamites) elegans* (d'Orbigny), Breistroffer p. 155.
	1947	*Anisoceras campichei* Spath, Breistroffer p. 62.
	1968	*Anisoceras (Anisoceras) campichei* Spath, Renz p. 78, pl. 15, figs 7, 8, text-figs 27f, 28d.
	1968	*Anisoceras (Anisoceras) arrogans* (d'Orbigny), Wiedmann & Dieni p. 69, pl. 7, fig, 10, pl. 8, figs 5, 7, 11, text-figs 46-50.
	1989	*Anisoceras (Anisoceras) arrogans* (d'Orbigny), Föllmi p. 127, pl. 5, figs 6-8.
	1996	*Metahamites elegans* (d'Orbigny), Wright *et al* p. 235, text-fig 186 (1a-b).

Type material Lectotype by subsequent designation of Kennedy & Juignet (199x) a body chamber fragment from the Escragnolle material (Museum of Natural History, Paris d'Orbigny collection 5808). From the Lower Gault (Middle Albian), Quartier de Clar, Escragnolle, France.

Description Earliest stages unknown. Ancylocone with no trace of helicosity or twisting. The two shafts are straight and long and the bend between them is tight. Both shafts bear ventrally paired nodes and these may cover more than one rib. Laterally compressed whorl section but

with periodic constrictions. Fine annular ribbing on phragmocone straight and prorsiradiate. The final shaft, the living chamber, has the ribs becoming less prorsiradiate along its length and finally rectiradiate near the aperture. On the phragmocone and the living chamber the ribs are partially effaced on the dorsal surface, but only the living chamber has visible striae or secondary ribs on the dorsum. These striae are barely discernible on the flanks and absent ventrally. The rib density on the phragmocone is higher (approximately, 10) than on the living chamber (approximately 4). Tuberculation consists of circular based nodes, arranged symmetrically across the ventral surface, which may cover up to four ribs on the phragmocone. On the living chamber the nodes are present on every second or third rib. Apertural collars or constrictions unknown. Whorl height is approximately, 150 mm. Suture line quadrilobate, florid and symmetrical across the siphuncle. External, lateral and umbilical lobes of similar size, internal lobe slightly smaller. External, lateral and umbilical lobes bifid, internal lobe trifid. Pseudolobes absent. The ventral saddle is trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly narrow.

Discussion. This species is more widely known as *Metahamites elegans* (d'Orbigny, 1842) although the type species of *Metahamites* lacks tubercles. Wiedmann & Dieni (1968) removed this species to *Anisoceras*, leaving *Metahamites* within the non-tuberculate Hamitidae. My cladistic analysis does not support the inclusion of this species with *Anisoceras*, but placement within the Anisoceratidae more generally is supported. For that reason I provisionally include this species within the paraphyletic *Protanisoceras*. Spath (1939) discussed the synonymy of d'Orbigny's species *Hamites elegans* with *Hamites arrogans* Giebel, 1852.

Occurrence Middle and Upper Albian of England, France, Sardinia and Switzerland.

PROTANISOCERAS DALPIAZI (WIEDMANN & DIENI, 1968)

1968 *Hamites (Metahamites) dalpiazi*, Wiedmann & Dieni p. 60, pl. 6, fig 5, text-fig 32, 33.

1987 *Metahamites dalpiazi* Wiedmann & Dieni, Immel p. 126.

1990 *Hemiptychoceras dalpiazi* Marcinowski & Wiedmann p. 40.

Type material Holotype by original designation of Wiedmann & Dieni (1968) Museum of Natural History, Paris specimen 5813a from the condensed Middle and Upper Albian beds of Orosei, Sardinia. Exact stratigraphical horizon unknown.

Description Incompletely known, probably hamiticonic with a broadly subcircular whorl section flattened ventrally. Ribbing consists of heavier annular ribs with ventral tubercles (rib

index of about 2) interspersed with 0 to 2 finer, non-tuberculate ribs. Ribbing effaced slightly on the dorsum, ribs prorsiradiate. Tubercles circular in section. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External, lateral and internal lobes of similar size, umbilical lobe slightly smaller. Lateral lobe and umbilical lobes asymmetrically bifid. External and internal lobes symmetrical, external lobe bifid, internal trifid. Pseudolobes absent. The ventral saddle is trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. All saddles are fairly narrow.

Discussion Originally described as *Metahamites dalpiazi* Wiedmann & Dieni, 1968, Marcinowski & Wiedmann (1990) redefined *Hemiptychoceras* to include this species, characterising *Hemiptychoceras* as hamiticonic ammonites with a "profound change in the sculpture of the smaller shafts, final hook, and body chamber shaft." They also considered the suture line to be of value, especially the large trifid internal lobe. However, the possession of tubercles is quite unlike any known *Hemiptychoceras* and should exclude this species from the Hamitidae. Similarly, *Metahamites elegans*, the type species of *Metahamites*, lack tubercles, the planar initial coiling, irregularly distributed ventrally paired tubercles, and moderately deeply incised bifid lobes support referral to the genus *Protanisoceras*.

Occurrence As holotype. Also from the Upper Albian at Tennbodenbach, near Salzach, Germany.

Genus *TUBEROLECHITES* Cooper & Kennedy, 1977

Tuberculate baculiticonic ammonites. Unknown initial coil, remainder of shell straight. Annular ribs simple, effaced dorsally. Secondary (minor) ribs absent. Ventral tubercles symmetrically paired across the siphuncle. Apertural collars unknown. Suture line unknown. Synonyms: none. Type species: *Tuberolechites regifex* (Cooper & Kennedy, 1977)

TUBEROLECHITES REGIFEX COOPER & KENNEDY, 1977

Figure 3.69

1977 *Lechites (Tuberolechites) regifex* Cooper & Kennedy, p. 654, pl. 8, fig, 1-15.

1979 *Lechites gaudini nodosus* Scholz, p. 15, pl. 1, figs 11-16.

1996 *Lechites (Tuberolechites) regifex* Cooper & Kennedy, Wright et al p. 255, text-figs, 198 (4a, b).

Type material Holotype by original designation of Cooper & Kennedy (1977, pl. 8, figs 1-4) Sedgewick Museum, Cambridge B97675 and paratypes SM B7668, B97583, and B97675. From the Cambridge Greensand (Upper Albian, *Stoliczkaia dispar* Zone) of Cambridge, England.

Description Incompletely known — only straight fragments are known, so coiling is presumed to have been baculitid with initial micromorphic coil. Whorl section laterally compressed. Straight, prorsiradiate annular ribs, completely effaced dorsally. Rib index 2.5 - 5. Each rib bears a pair of cylindrical nodes, arranged symmetrically across the venter. Between the nodes the ribs are flattened slightly. No known apertural collars. Suture line unknown.

Discussion *Tuberolechites* can be confused *Idiohamites*, which occur at the same stratigraphical horizons. It can be distinguished from *Idiohamites* on the basis of differences in ornament: While *Idiohamites* generally have ventral and ventrolateral pairs of tubercles, *Tuberolechites* only have ventral tubercles. Secondly, on the straight sections of the phragmocone, the ribbing on *Idiohamites* is approximately rectiradiate, whereas that of *Tuberolechites* is strongly prorsiradiate. This species was originally included within the Baculitidae, as *Lechites* (*Tuberolechites*) *regifex* Cooper & Kennedy, 1977. However, all other baculitids lack tubercles, and the symmetrically paired ventral tubercles of *Tuberolechites* are very similar to those of the Anisoceratidae. Furthermore, the cladistic analysis performed here suggests that this species should be removed from the Baculitidae and into the Anisoceratidae, where it is a derived from the genus *Protanisoceras*, although the ontogeny and suture line have not yet been described, so this conclusion may need to be revised. *Tuberolechites* appears to have been straight-shelled member of the Anisoceratidae, perhaps convergent with the evolution of the Baculitidae from the Hamitidae.

Occurrence Upper Albian of southern England (Upper Gault and Cambridge Greensand) and Europe (Bakony Mountains, West Hungary, and Salazac, France).

Genus *IDIOHAMITES* Spath, 1925

Tuberculate ancyloconic ammonites, less closely folded than the otherwise similar *Anisoceras*, with the living chamber usually describing a shallow hook. Shell planar throughout ontogeny. Annular ribs simple and never fibulate (unlike *Anisoceras*). The ribs are effaced dorsally. Secondary (minor) ribs absent. Ventral and/or ventrolateral tubercles symmetrically paired across the siphuncle. Tubercles may be absent from living chamber.

Apertural collars unknown. Suture line quadrilobate. Synonyms: none. Type species: *Idiohamites tuberculatus* (J. de C. Sowerby, 1818).

IDIOHAMITES TUBERCULATUS (J. SOWERBY, 1818)

Figure 3.70

1818 *Hamites tuberculatus* J. Sowerby p. 30, pl. 216, fig 4, 5.
1828 *Baculita tuberculatus* (J. Sowerby), Fleming p. 251.
1842 *Hamites tuberculatus* J. Sowerby, d'Orbigny p. 528.
1848 *Hamites tuberculatus* J. Sowerby, Quenstedt p. 292.
1850 *Hamites tuberculatus* (J. Sowerby), d'Orbigny p. 125.
1861 *Hamites tuberculatus* (J. Sowerby),Pictet & Campiche p. 42.
non 1868 *Hamites tuberculatus* (J. Sowerby), de Rance p. 169.
non 1875 *Hamites tuberculatus* (J. Sowerby), de Rance p. 3436.
non 1879 *Ancyloceras tuberculatum* (J. Sowerby), Price p. 76.
non 1879 *Hamites tuberculatus* (J. Sowerby), Price p. 76.
non 1897 *Ancyloceras tuberculatum* (J. Sowerby), Cowper Reed p. 116.
1898a *Hamites tuberculatus* J. Sowerby, Crick p. 62.
1900 *Ancyloceras tuberculatum* (J. Sowerby), Jukes-Browne p. 459 *pars*.
1923 *Anisoceras tuberculatum* (J. Sowerby), Spath p. 76.
1925a *Idiohamites tuberculatus* (J. Sowerby), Spath p. 189.
1934 *Metahamites flexuosus* (d'Orbigny), Breistroffer p. 234.
1939 *Idiohamites tuberculatus* (J. Sowerby), Spath p. 582-584, pl. 64, fig, 12, pl. 65, figs 3,4,10, text-fig 206 (a-h).
1957b *Idiohamites tuberculatus* (J. Sowerby), Wright in Arkell *et al* p. 220.
1977 *Idiohamites tuberculatus* (J. Sowerby), Phillips p. 98.
1989 *Idiohamites tuberculatus* (J. Sowerby), Henderson p. 137, text-fig 18e-j.
1996 *Idiohamites tuberculatus* (J. Sowerby), Wright *et al* p. 237.

Type material Lectotype by subsequent designation of Spath (1939) BMNH C.43998c the original of J. Sowerby (1818 pl. 216, fig 5). The paralectotypes BMNH C.43998a and C43998b are also figured by Sowerby (1818 pl. 216, fig 4). From the Upper Gault of Folkestone, Kent.

Description A planar ancylocone with an initially spiral juvenile stage followed by two subparallel shafts. Whorl section laterally compressed throughout. Straight annular ribs, fairly sharp and fine, slightly effaced dorsally. Rib index of 4 to 6. On the initial spiral phase the

ribs are slightly rursiradiate to rectiradiate, becoming prorsiradiate on the straight part of the phragmocone and then rectiradiate on the living chamber. There are no known apertural collars or constrictions. About every third to fifth rib bears paired circular to bullate ventral nodes. The same ribs may or may not bear circular ventrolateral nodes. Tuberculation becomes weaker on the later parts of the phragmocone, and may be absent from the living chamber altogether. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External and lateral lobes of similar size and larger than the similarly sized umbilical and internal lobes. External lobe symmetrically bifid. Lateral and umbilical lobes subsymmetrically bifid. Internal lobe symmetrically bifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. The saddles are rather narrow and florid.

Discussion *Idiohamites spiniger* (see below) differs from *Idiohamites tuberculatus* in having stronger ventrolateral tuberculation and deeper and more clavate ventral nodes. The ribbing of *Idiohamites spiniger* is slightly more dense and a little finer. Even so, the two species are probably closely related, and Spath (1939) commented on the many specimens which are intermediate in morphology between the two species.

Occurrence From the Upper Gault (Upper Albian *Hysteroceras varicosum* to *Callihoplites auritis* Subzones) of England, France and Australia.

IDIOHAMITES SPINIGER (J. SOWERBY, 1818)

Figure 3.71, 3.72

	1818	*Hamites tuberculatus* J. Sowerby p. 30, pl. 216, fig 4, 5.
	1818	*Hamites spiniger* J. Sowerby p. 29, pl. 216, fig 2.
	1828	*Baculita spiniger* (J. Sowerby), Fleming p. 251.
	1841	*Hamites spiniger* J. Sowerby, Moxon pl. 13, fig, 13.
	1842	*Hamites spiniger* J. Sowerby, d'Orbigny p. 528.
	1848	*Hamites spiniger* J. Sowerby, Quenstedt p. 292, pl. 21, fig 20.
	1850	*Ancyloceras spiniger* (J. Sowerby), d'Orbigny p. 125.
	1852	*Ancyloceras spiniger* (J. Sowerby), Giebel p. 324.
	1861	*Ancyloceras spiniger* (J. Sowerby), Pictet & Campiche p. 42.
non	1874	*Ancyloceras spinigerum* (J. Sowerby), Price p. 362.
?	1874	*Toxoceras* sp., Price p. 363.
	1875a	*Hamites spiniger* J. Sowerby, Neumayr p. 30.
	1875b	*Hamites spiniger* J. Sowerby, Neumayr p. 899.

non 1875 *Ancyloceras spinigerum* (J. Sowerby), Topley p. 431, 436.

? 1878 *Ancyloceras spiniger* (J. Sowerby), Barrois p. 271.

non 1882 *Ancyloceras spinigerum* (J. Sowerby), Fischer p. 398, pl. 3, fig, 10.

non 1884 *Ancyloceras spinigerum* (J. Sowerby), Homersham in Judd p. 736.

1898a *Hamites spiniger* J. Sowerby, Crick p. 62.

1900 *Ancyloceras tuberculatum?* (J. Sowerby), Jukes-Browne p. 88.

1923 *Ancyloceras spinigerum* (J. Sowerby), Spath p. 76.

1925b *Ancyloceras spinigerum* (J. Sowerby), Spath p. 36.

? 1926 *Hamites flexuosus* d'Orbigny, Jayet p. 186.

1926 *Appurdiceras spinigerum* (J. Sowerby), Whitehouse p. 229 *pars?*

1939 *Idiohamites spiniger* (J. Sowerby), Spath p. 584-587, pl. 64, figs 10, 11, pl. 65, fig, 12, text-fig 206i, 207.

1939 *Idiohamites subspiniger*, Spath p. 586, text-fig 208.

1942 *Idiohamites spiniger* (J. Sowerby), Haas, p. 195, pl. 46, figs 4a-c, text-figs 31a, b.

1957b *Idiohamites spiniger* (J. Sowerby), Wright in Arkell *et al* p. 220, text-fig 246 (6a-d).

1977 *Idiohamites spiniger* (J. Sowerby), Phillips p. 98.

1979 *Idiohamites subspiniger* (Spath), Collignon p. 12, pl. 3, figs 2a, b.

1987 *Idiohamites spiniger* (J. Sowerby), Immel p. 130.

1989 *Idiohamites subspiniger* (Spath), Henderson p. 137, text-fig 18a-d, 19a.

1996 *Idiohamites spiniger* (J. Sowerby), Wright *et al* p. 237, text-fig 187 (2d).

Type material Lectotype by subsequent designation of Spath (1939) BMNH C.43996a, the larger of the three fragments figured by J. Sowerby (1818 pl. 216, fig 2). The remaining fragments, BMNH C.43996b and C.43996c are the paratypes and appear to be lost. From the Upper Gault of Folkestone, Kent.

Description A planar ancylocone with an initially spiral juvenile stage followed by two subparallel shafts. Whorl section laterally compressed throughout. Straight annular ribs, fairly sharp and fine, slightly effaced dorsally. Rib index of 6 to 6. On the initial spiral phase the ribs are slightly rursiradiate to rectiradiate, becoming prorsiradiate on the straight part of the phragmocone and then rectiradiate on the living chamber. There are no known apertural collars or constrictions. Approximately every fifth rib bears paired clavate ventral and circular ventrolateral nodes. Tuberculation fairly strong throughout, even on the living chamber. Suture line quadrilobate, moderately florid and symmetrical across the siphuncle. External and lateral lobes of similar size and larger than the similarly sized umbilical and internal lobes. External lobe symmetrically bifid. Lateral and umbilical lobes subsymmetrically bifid. Internal lobe symmetrically bifid. Pseudolobes absent. The ventral saddle is indistinctly trifid, the first lateral, umbilical and dorso-ventral saddles are bifid. The saddles are rather narrow and florid.

Occurrence From the Upper Gault (Upper Albian *Hysteroceras varicosum* to *Callihoplites auritis* Subzones) of England and France.

Family BACULITIDAE Meek, 1876

Heteromorph ammonites characterised by the reduction of the post-neanic juvenile-A coiling, the ammonitella and neanoconch leading straight into an orthoconic shaft. Aperture usually modified, with collars, constrictions or lappets. The Baculitidae appear during the Upper Albian (FIGURE 2.17) although at a low diversity, becoming a much more important and diverse group during the entire Upper Cretaceous. Albian baculitids have been recorded from Europe, Africa, the Americas, Australia and Antarctica.

Genus *LECHITES* Nowak, 1908

Non tuberculate baculiticonic ammonites. Planar throughout ontogeny, initially a small open spiral which straightens into a single shaft. Annular ribbing simple, often reduced and irregular. Apertural modifications distinctive: microconchs possess constrictions and collars like some *Hamites*, macroconchs develop a curved hood but lack constrictions. Suture quadrilobate. Synonyms: none. Type species: *Lechites gaudini* (Pictet & Campiche, 1861).

LECHITES GAUDINI PICTET & CAMPICHE, 1861

Figure 3.73

	1861	*Baculites gaudini* Pictet & Campiche, p. 112, pl. 45, figs 5-9.
non	1861	*Baculites gaudini* Pictet & Campiche, p. 112, pl. 55, figs 10, 11.
	1862	*Baculites gaudini* Pictet & Campiche, von Hauer p. 648, pl. 2, figs 5-10.
	1865	*Baculites gaudini* Pictet & Campiche, Stoliczka p. 119, pl. 91, figs 9-7.
	1866	*Baculites gaudini* Pictet & Campiche, Pictet & Renevier p. 119, pl. 91, figs 9-7.
	1879	*Baculites gaudini* Pictet & Campiche, Price p. 76.
	1890	*Baculites gaudini* Pictet & Campiche, Renevier p. 340.
	1895	*Baculites gaudini* Pictet & Campiche, Kossmat p. 154.
	1897	*Baculites gaudini* Pictet & Campiche, Simionescu p. 271.
	1899	*Baculites gaudini* Pictet & Campiche, Popovici-Hatzeg p. 11.
	1900	*Baculites gaudini* Pictet & Campiche, Jukes-Browne p. 459.
	1907	*Baculites gaudini* Pictet & Campiche, Boule, Lemoine & Thévenin p. 64, pl. 15, fig, 1.
	1908	*Baculites gaudini* Pictet & Campiche, Nowak p. 350.
	1910	*Baculites gaudini* Pictet & Campiche, Pervinquière p. 11.
	1912	*Baculites gaudini* Pictet & Campiche, Ganz p. 19.

1923 *Baculites* cf. *gaudini* Pictet & Campiche, Böse p. 157.

1923 *Lechites gaudini* (Pictet & Campiche), Spath p. 76.

1925 *Lechites gaudini* (Pictet & Campiche), Diener p. 60.

1926 *Lechites gaudini* (Pictet & Campiche), Whitehouse p. 225.

1929 *Baculites gaudini* Pictet & Campiche, Collignon p. 70, pl. 7, fig, 12.

1932 *Baculites gaudini* Pictet & Campiche, Barbu p. 16.

1933 *Lechites gaudini* (Pictet & Campiche), Breistroffer p. 195.

1933 *Baculites gaudini* Pictet & Campiche, Collignon p. 25, pl. 5, fig 8.

1935 *Lechites gaudini* (Pictet & Campiche), Shimzu p. 185.

1936 *Baculites gaudini* Pictet & Campiche, Venzo p. 118, pl. 10, fig 3.

1936 *Lechites gaudini* (Pictet & Campiche), Breistroffer p. 66.

1940 *Lechites gaudini* (Pictet & Campiche), Breistroffer p. 158.

1941 *Lechites gaudini* (Pictet & Campiche), Spath p. 662, pl. 72, figs 4-7, 9, 10, text-figs 242.

1941 *Lechites* aff. *moreti* Spath p. 665, pl. 72, fig 8, text-figs 243 (e-k).

1941 *Lechites communis* Spath p. 666, text-figs 244 (a-c).

1947 *Lechites gaudini* (Pictet & Campiche), Breistroffer p. 63.

1947 *Lechites gaudini* var. *raricostata*, Breistroffer p. 63.

1951 *Lechites gaudini* var. *raricostatus* Breistroffer, Wright & Wright p. 16.

1957b *Lechites gaudini* (Pictet & Campiche), Wright in Arkell *et al* p. 218, text-fig 245 (1a-c).

1963 *Lechites gaudini* (Pictet & Campiche), Collignon p. 25, text-fig 1075.

? 1963 *Lechites* cf. *gaudini* (Pictet & Campiche), Collignon p. 25, text-fig 1076.

1968 *Lechites gaudini* (Pictet & Campiche), Wiedmann & Dieni p. 64, pl. 6, figs 1-5, 7-9, text fig 36.

1968 *Lechites italicus*, Wiedmann & Dieni p. 64, pl. 6, fig, 10, text fig 37.

1968 *Lechites gaudini* (Pictet & Campiche), Renz p. 80, pl. 17, figs 1-4, text-fig 29e.

1968 *Lechites communis* Spath, Renz p. 81, pl. 17, figs 6, 13, text-fig 29 (c-d).

1968 *Lechites raricostatus* Renz p. 82, pl. 16, figs 11, pl. 17, fig 7, text-fig 29 (l).

1968 *Lechites campichei* Renz p. 82, pl. 17, figs 8-10, text-fig 29m.

1968 *Lechites vraconensis* Renz p. 82, pl. 17, figs 11, 12, 14, 15, text-fig 29 (b, g, h, k).

1971 *Lechites fasciata* Scholz, Renz p. 431, text-figs, 1-2.

1977 *Lechites gaudini* (Pictet & Campiche), Cooper & Kennedy p. 641-654, text-fig 1, 2, 4-8.

1977 *Lechites gaudini* (Pictet & Campiche), Phillips p. 105.

1977 *Lechites communis* Spath, Phillips p. 105.

1977 *Lechites gaudini gaudini* (Pictet & Campiche), Scholz p. 12, pl. 1, figs 1-9, text-figs 5 (a, b).

non 1977 *Lechites gaudini moreti* (Breistroffer), Scholz p. 14, pl. 1, figs 10, text-fig 5c.

1977 *Lechites gaudini nodosus* Scholz p. 15, pl. 1, figs 11-16.

1982 *Lechites gaudini* (Pictet & Campiche), Braga *et al* pl. 1, fig 4, text-figs 2-4.

1985 *Lechites gaudini* (Pictet & Campiche), Seyed-Emami p. 112 pl. 7, figs 11.

1987 *Lechites gaudini* (Pictet & Campiche), Immel p. 128

1987 *Lechites gaudini* (Pictet & Campiche), Phillips p. 54-55.

1988 *Lechites gaudini* (Pictet & Campiche), Delanoy & Latil, p. 752, pl. 1, fig 5.

1989 *Lechites* aff. *gaudini* (Pictet & Campiche), Föllmi p. 120, pl. 3, fig, 17.

1989 *Lechites communis* Spath, Horvath pl. 3, fig 8.

1989 *Lechites gaudini* (Pictet & Campiche), Horvath pl. 1, fig 6.

1990 *Lechites gaudini* (Pictet & Campiche), Henderson p. 129, text-fig 12 (a-m).

1992 *Lechites gaudini* (Pictet & Campiche), Kelly & Moncrieff text-fig 12.

1994 *Lechites gaudini* (Pictet & Campiche), Emerson *et al* p. 319.

1996 *Lechites gaudini* (Pictet & Campiche), Wright *et al* p. 255, text-figs, 198 (3a-e).

Type material Holotype by monotypy the original of Pictet & Campiche (1861, pl. 14, figs 5-9). The specimen is now lost. From the Upper Albian of Sainte-Croix, Switzerland.

Description Micromorphic planar initial coil followed by a single, straight shaft. Whorl section approximately circular or slightly laterally compressed. Ribbing moderately to very fine, straight and prorsiradiate on the straight section, rib index from 3 to 8. Tuberculation absent. Apertural modifications develop in both micro- and macroconchs: in the microconchs this takes the form of constrictions similar to those of *Hamites nokonsis*, in the macroconchs the aperture curves dorsally to form the so-called apertural hood. Quadrilobate suture line symmetrical across the siphuncle. The external, lateral, and umbilical lobes are similar in size and bifid, the internal lobe is smaller and trifid. There are no pseudolobes. The ventral saddle is indistinctly trifid. The first lateral, umbilical, and dorso-ventral saddles are rather narrow and bifid.

Discussion A variable, widespread species, Cooper & Kennedy (1977) synonymised *Lechites communis* Spath with *Lechites gaudini* on the basis of the many transitions which occur.

Occurrence Recorded from the Upper Albian of Europe, Angola, Madagascar, Australia, Antarctica and Mexico.

LECHITES MORETI BREISTROFFER, 1936

1861 *Baculites gaudini* Pictet & Campiche, p. 112, pl. 45, figs 10, 11.

1936 *Baculites moreti* Breistroffer, p. 66.

	1941	*Lechites moreti* Breistroffer, Spath p. 665, text-figs 243 (a-d).
non	1941	*Lechites* aff. *moreti* Spath p. 665, pl. 72, fig 8, text-figs 243 (e-k).
	1965	*Lechites moreti* Breistroffer, Clark, p. 23.
	1968	*Lechites moreti* Breistroffer, Wiedmann & Dieni p. 64, pl. 6, fig, 11.
	1977	*Lechites moreti* Breistroffer, Cooper & Kennedy, p. 651.
	1977	*Lechites moreti* Breistroffer, Phillips p. 105.
	1977	*Lechites gaudini moreti* (Breistroffer), Scholz p. 14, pl. 1, figs 10, text-fig 5c.
?	1989	*Lechites moreti* Breistroffer, Horvath pl. 3, fig 3, pl. 4, fig, 1.

Type material Holotype by monotypy the original of Pictet & Campiche (1861, pl. 14, fig, 10). From the Upper Albian of Sainte-Croix, Switzerland.

Description Similar to *Lechites gaudini* Pictet & Campiche but differing in ornamentation. The ribs are heavy and rather scale like, producing internal moulds with slight but characteristic periodic constrictions. Rib density fairly low (rib index of 1 to 2). The ribs are somewhat sinuous, being prorsiradiate along the dorsum, straightening across the flanks and over the venter. Quadrilobate suture line symmetrical across the siphuncle. The external, lateral, and umbilical lobes are similar in size and bifid, the internal lobe is smaller and trifid. There are no pseudolobes. The ventral saddle is indistinctly trifid. The first lateral, umbilical, and dorso-ventral saddles are bifid and perhaps a little broader and simpler than those of *Lechites gaudini*.

Occurrence Upper Albian (*Stoliczkaia dispar* Zone) faunas of England, France and Hungary.

LECHITES COMANCHENSIS (ADKINS, 1920)

	1919	*Baculites* sp. Winton & Adkins, p. 21, 69.
	1920	*Baculites comanchensis* Adkins, p. 51, 74, pl. 2, figs 20-22.
	1928	*Cyrtochilus (?) comanchensis* Adkins, Adkins p. 207, pl. 10, fig 9.
	1928	*Baculites comanchensis* Adkins, Böse p. 146.
	1941	*Cyrtochilus (?) comanchensis* (Adkins), Spath, p. 666.
	1965	*Lechites comanchensis* (Adkins), Clark, p. 23, pl. 3, figs 1, 2, 5-11, pl. 4, fig, 16, text-fig 6a.
	1977	*Lechites comanchensis* (Adkins), Cooper & Kennedy, p. 653.
	1994	*Lechites comanchensis* (Adkins), Emerson *et al* p. 319.

Type material Lectotype by subsequent designation of Clark (1965) the original of Adkins (1920, pl. 2, figs 20) BEG 20997. The remaining specimens figured are paralectotypes: BEG 20998 and BEG 20999. From the Pawpaw Shale (Upper Albian) of Fort Worth, Texas.

Description Very similar to *Lechites moreti* (with which it may be synonymous) but with a slightly higher rib density (rib index 2-3) and a less scale-like aspect to the ribbing.

Occurrence As holotype. Also from the Upper Albian (*Stoliczkaia dispar* Zone) of Utah and Northern Mexico.

Genus *SCIPONOCERAS* Hyatt, 1894

Baculitid ammonites similar to *Lechites* but lacking annular ribbing. Periodic constrictions along the ventral surface, otherwise the shell is quite smooth. Apertural collars different to Lechites, consisting of a series of exaggerated folds or constrictions similar to those on the body chamber plus a high collar and sometimes Suture quadrilobate. Synonyms: none. Type species: *Sciponoceras baculoides* (Mantell, 1822).

SCIPONOCERAS SKIPPERAE NOV. SP.

Figure 3.74

1941 *Lechites communis* Spath p. 667, text-fig 244(f-h).

1968 *Lechites* sp. indet Renz p. 83, pl. 17, figs 16, 17, text-fig 29f.

Type material BMNH C.93268 from the Upper Albian (*Stoliczkaia dispar* Zone, *Mortoniceras perinflatum* Subzone) of Melcombe Horsey, Dorset, England.

Description Straight shells lacking any annular ribbing but with very weak prorsiradiate periodic constrictions on the ventral surface, running over the lower park of the flanks. Whorl section laterally compressed. Suture line is preserved on only one of the available specimens, and at that poorly, but appears to comprise bifid lateral and umbilical lobes.

Discussion New species based on fragments (BMNH C.93268, C.93267) collected by H. G Owen and W. J. Kennedy from the Upper Greensand of Dorset. The distinctive constrictions of *Sciponoceras* distinguish this species from the more common Upper Albian baculitid *Lechites gaudini*. *Sciponoceras skipperae* is similar to *Sciponoceras baculoides* Mantell, 1822

which is found in the Lower Cenomanian, but shows a lesser degree of lateral compression and the constrictions are weaker. The suture line is seems to be less deeply incised, but this may be a reflection of the relatively small size of the fragments examined. Even so, the closeness of general form may indicate that this species is the immediate forerunner of *Sciponoceras baculoides*. Both fragments are of the living chambers and suggest an absolute length 600 mm. Named in honour of my colleague Jackie Skipper, at the Natural History Museum, London.

Occurrence As holotype and elsewhere in Dorset, England. Also from the Upper Albian of La Vraconne, Switzerland.

Family TURRILITIDAE Meek, 1876

Heteromorph ammonite derived from the Hamitidae and characterised by persistent post-neanic helical coiling, apical shifting of the siphuncle, acquisition of non-symmetrically paired tubercles, and an asymmetrical suture line. The Turrilitidae appear during the Middle Albian and persist through into the Cenomanian (FIGURE 2.17). Middle Albian species have been recorded mainly from Europe while Upper Albian representatives of this family are known from the Americas, Africa, Asia, and Australia.

Genus *PROTURRILITOIDES* Breistroffer, 1940

Loosely to moderately tightly coiled helical ammonites with low spire. Umbilicus closed. Where whorls are in contact profile concave, otherwise the whorl section is approximately oval or subcircular. Ribbing complete, sinuous and without tubercles or bullae. Aperture lacks collars or constrictions. Siphuncle not displaced towards apex. Suture quadrilobate and asymmetrical. Synonyms: none. Type species: *Proturrilitoides astierianus* (d'Orbigny, 1842).

PROTURRILITOIDES ASTIERIANUS (D'ORBIGNY, 1842)

Figure 3.55

1842 *Turrilites astierianus* d'Orbigny, p. 578, pl. 140, figs 8-11.
1930 *Heteroceras* cf. *senequierianum* (d'Orbigny), Passendorfer p. 696, text-fig 26.
1937 *Turrilitoides astierianus* d'Orbigny, Spath p. 525.
1947 *Proturrilitoides astierianus* (d'Orbigny), Breistroffer p. 46.
1953 *Proturrilitoides astierianus* (d'Orbigny), Breistroffer p. 1350.
1957b *Proturrilitoides astierianus* (d'Orbigny), Arkell *et al* p. L220, text-fig 248(1).
1978 *Proturrilitoides astierianus* (d'Orbigny), Klinger & Kennedy pl. 9, figs h, i.
1987 *Proturrilitoides astierianus* (d'Orbigny) Phillips p. 98.
1985 *Proturrilitoides astierianus* (d'Orbigny), Marcinowski p. 209.
1990 *Proturrilitoides astierianus* (d'Orbigny), Marcinowski & Wiedmann p. 49, pl. 4, fig 5.

Type material The original of d'Orbigny (1842, pl. 140, figs 8-11) from Astier, near Escragnolle, France. This specimen appears to be lost (W. J. Kennedy, pers. comm.).

Description Low spired turriliticone (apical angle approximately 80°) coiling dextrally or sinistrally. The umbilicus is closed although may become open for final living chamber. Whorl section compressed where successive coils are impressed but otherwise subcircular to oval. Ornament very similar to that of *Hamitella* being simple annular ribs and rather sinuous and oblique over the flanks. Rib index 6-8 (typically 36 ribs per whorl on the phragmocone). Toward the aperture the ribbing becomes rather stronger and the spaces between each rib more constricted, but otherwise paired collars like those of *Turrilitoides* unknown. Unlike *Turrilitoides* the siphuncle is not displaced. Suture line similar to *Turrilitoides*: quadrilobate and asymmetrical. The external and lateral lobes are of approximately similar size, the umbilical and internal lobes being rather smaller. The external, lateral and umbilical lobes are bifid, the internal lobe is trifid. The saddles are rather broad and bifid.

Discussion *Proturrilitoides* was proposed as a subgenus of *Turrilitoides* with which it is clearly related (Breistroffer, 1940). It differs most obviously from *Turrilitoides* in having an open coil and a generally more obtuse apical angle.

Occurrence Middle Albian (*Euhoplites loricatus* and *Euhoplites lautus* Zone) of France and Poland. The French material is confined to condensed sequences at Escragnolle, which may indicate a range extending into the *Hoplites dentatus* Zone.

PROTURRILITOIDES SENEQUIERIANUS (D'ORBIGNY, 1842)

Figure 3.76

	1842	*Turrilites senequierianus* d'Orbigny, p. 579, pl. 141, figs 1, 2.
non	1930	*Heteroceras* cf. *senequierianum* (d'Orbigny), Passendorfer p. 696, text-fig 26.
	1937	*Turrilitoides senequierianus* d'Orbigny, Spath p. 525.
	1947	*Proturrilitoides senequierianus* (d'Orbigny), Breistroffer p. 46.
	1989	*Turrilitoides (Proturrilitoides)* cf. *senequierianus* (d'Orbigny), Föllmi p. 119.
	1990	*Proturrilitoides senequierianus* (d'Orbigny), Marcinowski & Wiedmann p. 49.
	199x	*Proturrilitoides senequierianus* (d'Orbigny), Kennedy & Juignet p. 109, pl. 230.

Type material The original of d'Orbigny (1842, pl. 141, fig, 1, 2) from Aiglun, near Var, south eastern France. This specimen appears to be lost (W. J. Kennedy, pers. comm.).

Description Similar to *Proturrilitoides astieranus* but differing in having finer, more densely packed ribbing. The whorl section is more circular than in that species, and the apical angle

more acute, but otherwise the coiling mode is comparable. Suture line similar, quadrilobate and asymmetrical.

Occurrence A rare, Middle Albian (*Euhoplites loricatus* and *Euhoplites lautus* Zone) form so far recorded only from south-eastern France and Vorarlberg, Austria.

Genus *TURRILITOIDES* Spath, 1923

Moderately tightly coiled helical ammonites. Umbilicus closed, but whorls only just in contact and whorl section not distorted or flattened. Ribbing complete, sinuous and without tubercles or bullae. Aperture constricted and bordered by paired collars similar to those of *Hamites parkinsoni*. Siphuncle displaced towards apex. Suture quadrilobate and asymmetrical. Synonyms: none. Type species: *Turrilitoides hugardianus* (d'Orbigny, 1842).

TURRILITOIDES HUGARDIANUS (D'ORBIGNY, 1842)

Figure 3.77

	1842	*Turrilites hugardianus* d'Orbigny, p. 588, pl. 147, figs 9-11.
	1847	*Turrilites hugardianus* d'Orbigny, Pictet & Roux p. 155, pl. 15, fig, 12.
	1848	*Turrilites hugardianus* d'Orbigny, Bronn p. 1329.
	1850	*Turrilites hugardianus* d'Orbigny, d'Orbigny p. 127.
	1854	*Turrilites hugardianus* d'Orbigny, Pictet, p. 712.
	1860	*Turrilites hugardianus* d'Orbigny, Ooster p. 95.
	1861	*Turrilites hugardianus* d'Orbigny, Pictet & Campiche p. 128, pl. 62, figs 1-7.
	1866	*Turrilites hugardianus* d'Orbigny, Pictet & Renevier p. 105.
non	1874	*Turrilites hugardianus* d'Orbigny, Price p. 363.
non	1875	*Turrilites hugardianus* d'Orbigny, Topley p. 431.
	1875a	*Turrilites hugardianus* d'Orbigny, Neumayr p. 32.
	1875b	*Turrilites hugardianus* d'Orbigny, Neumayr p. 901.
	1890	*Turrilites hugardianus* d'Orbigny, Renevier p. 339.
	1897	*Turrilites hugardianus* d'Orbigny, Cowper Reed p. 116.
non	1900	*Turrilites hugardianus* d'Orbigny, Jukes-Brown p. 431.
non	1907	*Turrilites hugardianus* d'Orbigny, Jacob p. 327.
non	1923	*Turrilites hugardianus* d'Orbigny, Spath p. 75.
non	1925	*Turrilites hugardianus* d'Orbigny, Spath p. 34.
	1926	*Turrilitoides hugardianus* (d'Orbigny), Spath p. 339.

? 1931 *Turrilitoides* cf. *hugardianus* (d'Orbigny), Breistroffer p. 232.

1934 *Turrilites* cf. *hugardianus* (d'Orbigny), Heim & Seitz p. 209.

1936 *Turrilitoides hugardianus* (d'Orbigny), Breistroffer p. 67.

1937 *Turrilitoides hugardianus* (d'Orbigny), Spath p. 526, pl. 58, figs 13-19, text-fig 184.

1937 *Turrilitoides hugardianus* var. *crassicostatus* Spath p. 527, pl. 58, figs 12, 20.

1940 *Turrilitoides hugardianus* (d'Orbigny), Breistroffer p. 150.

1947 *Turrilitoides hugardianus* (d'Orbigny), Breistroffer p. 60.

1947 *Turrilitoides hugardianus* var. *crassicostatus* Spath, Breistroffer p. 60.

1967 *Turrilitoides hugardianus* (d'Orbigny), Matsumoto p. 336.

1968 *Turrilitoides hugardianus* (d'Orbigny), Wiedmann & Dieni p. 78, pl. 9, fig 3, text-figs 57, 58.

1968 *Turrilitoides hugardianus* (d'Orbigny), Renz p. 84, pl. 17, figs 18-21, text-figs 30a.

1968 *Turrilitoides hugardianus crassicostatus* (Spath), Renz p. 84.

1978 *Turrilitoides hugardianus* (d'Orbigny), Klinger & Kennedy pl. 9, fig K.

1979 *Turrilitoides (Turrilitoides) hugardianus* (d'Orbigny) Scholz p. 34, pl. 7, figs 1, 3, 5, 8, 9, 13, text-figs, 11a-d (only).

non 1979 *Turrilitoides (Turrilitoides) hugardianus* (d'Orbigny) Scholz pl. 7, figs 2, 4, 6, 7, 10-12, 14, 16.

1985 *Turrilitoides hugardianus* (d'Orbigny), Marcinowski & Wiedmann p. 209.

1988 *Turrilitoides hugardianus* (d'Orbigny), Delanoy & Latil p. 752.

1989 *Turrilitoides (Turrilitoides) hugardianus* (d'Orbigny), Föllmi p. 119, pl. 3, fig, 16.

1990 *Turrilitoides (Turrilitoides) hugardianus* (d'Orbigny), Marcinowski & Wiedmann p. 50, pl. 4, figs 9, 10.

1996 *Turrilitoides hugardianus* d'Orbigny, Wright *et al* p. 241, text-fig 189 (3).

1996 *Turrilitoides hugardianus* d'Orbigny, Kennedy in Gale *et al* p. 580, text-fig 16a-d.

Type material The smaller of the two specimens from the Upper Albian at Montagne des Fiz (South East France) figured by d'Orbigny (1842, pl. 147, figs 10, 11) by subsequent designation of Spath (1937).

Description High spired turriliticone (apical angle approximately 20°) coiling dextrally or sinistrally. The umbilicus is closed. Whorl section compressed where successive coils are impressed but otherwise subcircular to oval. Ornament very similar to that of *Hamites*, simple annular ribs but rather sinuous and oblique. Rib index 4-6 (typically 24 ribs per whorl on the phragmocone) although varying on the final living chamber. At the aperture paired collars separated by a single constriction may develop (microconchs?). The siphuncle is displaced and does not lie over the internal lobe, it is raised laterally toward the spire and lies between the lateral and umbilical lobes. Suture line strongly asymmetrical, the inner half of the suture line being simpler and more compressed than the outer half. Suture quadrilobate. The external

and lateral lobes are of approximately similar size, the umbilical and internal lobes being rather smaller. The external, lateral and umbilical lobes are bifid, the internal lobe is trifid. The saddles are rather broad and bifid.

Discussion *Turrilitoides* is similar to *Proturrilitoides* but is characterised by a the displacement of the siphuncle (toward the apex of the spire), the smaller apical angle, more close packing of the whorls, and a closed umbilicus. Both *Turrilitoides* and *Proturrilitoides* lack the bullate tubercles seen in the other Albian Turrilitidae such as *Mariella*, *Ostlingoceras*, and *Pseudhelicoceras*. On the other hand, their ornamentation bears comparisons with some of the Hamitidae. Scholz considered the two other species of *Turrilitoides* to be no more than subspecies of *Turrilitoides hugardianus* (Scholz, 1979). Marcinowski and Wiedmann prefer a separation to be maintained although they acknowledge that the only differences slight morphological variations and separation may be difficult (Marcinowski & Wiedmann, 1990).

Occurrence Upper Albian (*Mortoniceras inflatum* Zone), exact range unknown. Recorded from England (predominantly the Cambridge Greensand), Switzerland, Hungary, Poland, Sardinia, and France. Perhaps also Pakistan.

TURRILITOIDES DENSICOSTATUS (PASSENDORFER, 1930)

Figure 3.78

1874 *Turrilites hugardianus* d'Orbigny, Price p. 363.
1875 *Turrilites hugardianus* d'Orbigny, Topley p. 431.
1900 *Turrilites hugardianus* d'Orbigny, Jukes-Brown p. 431.
1907 *Turrilites hugardianus* d'Orbigny, Jacob p. 327.
1923 *Turrilites hugardianus* d'Orbigny, Spath p. 75.
1925 *Turrilites hugardianus* d'Orbigny, Spath p. 34.
1930 *Turrilitoides densicostatus* Passendorfer, pl. 4, fig 70.
1937 *Turrilitoides densicostatus* (Passendorfer), Spath p. 529, pl. 58, figs 5-7, text-fig 186.
1953 *Turrilitoides hugardianus* (d'Orbigny), Breistroffer p. 1350.
? 1963 *Turrilitoides densicostatus* (Passendorfer), Collignon p. 46, text-fig 1119.
1966 *Proturrilitoides densicostatum* (Passendorfer), Casey in Smart et al, p. 110.
1978 *Turrilitoides densicostatus* (Passendorfer), Klinger & Kennedy pl. 9, figs M, O.
1979 *Turrilitoides (Turrilitoides) densicostatus* (Passendorfer), Scholz p. 35.
1985 *Turrilitoides densicostatus* (Passendorfer), Marcinowski & Wiedmann p. 209.
1989 *Turrilites (Turrilitoides) hugardianus* d'Orbigny, Hovarth pl. 1, fig, 1, pl. 2, fig 6.

1990 *Turrilitoides (Turrilitoides) densicostatus* (Passendorfer), Marcinowski & Wiedmann p. 50, pl. 4, figs 11, 12.

Type material Holotype by monotypy the specimen from the Upper Albian of Wiekla Rówień, Tatra (Poland) figured by Passendorfer (1930, pl. 4, fig 70).

Description High spired turriliticone similar to *Turrilitoides hugardianus* but differing in the greater apical angle (approximately 25°) and the finer more closely packed ribbing (rib index 8). The whorl section is oval, compressed somewhat where the whorl impacts against the preceding part of the shell. Apertural collars and constriction well developed on microconchs. No tuberculation. Suture similar to that of *Turrilitoides hugardianus*.

Occurrence Middle and Upper Albian, *Euhoplites lautus* and *Mortoniceras inflatum* Zones of England and Poland. The specimen recorded from the Middle Albian of Madagascar (Collignon, 1963) is considered by Marcinowski & Wiedmann (1990) to be uncertain. It is very small and worn, and the ornamentation is unclear.

TURRILITOIDES INTERMEDIUS (PICTET & CAMPICHE, 1861)

1861 *Turrilites intermedius* Pictet & Campiche, p. 127, pl. 57, fig, 14.

1890 *Turrilites intermedius* Pictet & Campiche, Renevier p. 339.

1937 *Turrilitoides intermedius* (Pictet & Campiche), Spath pp. 527, 529, 530.

1947 *Turrilitoides intermedius* (Pictet & Campiche), Breistroffer p. 60.

1962a *Turrilitoides intermedius* (Pictet & Campiche), Wiedmann p. 189, pl. 13, fig 7.

1968 *Turrilitoides (Turrilitoides) intermedius* (Pictet & Campiche), Renz p. 84, pl. 17, figs 24-26, text-fig 30f.

1979 *Turrilitoides (Turrilitoides) intermedius* (Pictet & Campiche), Scholz pl. 7, figs 2, 4, 6, 7, 10-12, 14.

1985 *Turrilitoides intermedius* (Pictet & Campiche), Marcinowski & Wiedmann p. 209.

1990 *Turrilitoides (Turrilitoides) intermedius* (Pictet & Campiche), Marcinowski & Wiedmann p. 50, pl. 4, figs 6-8.

Type material Lectotype by subsequent designation of Renz (1968) the specimen from the Upper Albian of Sainte-Croix, Switzerland figured by Pictet & Campiche (1861, pl. 57, fig, 14).

Description High spired turriliticone similar to *Turrilitoides hugardianus* but with a much greater apical angle (approximately 45°) and the slightly finer and more closely packed

ribbing (rib index 6). There are typically about 30 ribs per whorl on the phragmocone. The ribs are less sinuous than in *Turrilitoides hugardianus* . Whorl section similar to *Turrilitoides hugardianus* . Apertural collars and constrictions unknown. No tuberculation. Suture similar to *Turrilitoides hugardianus* .

Occurrence Upper Albian (*Mortoniceras inflatum* Zones) of England, France, Switzerland, Hungary, Spain and Poland.

Genus *PSEUDHELICOCERAS* Spath, 1921

Loosely to moderately tightly coiled helical ammonites with low spire. Umbilicus open. Whorl section is approximately oval or subcircular. Ribbing complete although weakened on the inside of the spire. Tuberculation well developed and consists of series of bullate to circular ridges interspersed between the plain annular ribs. Siphuncle displaced towards apex. Suture quadrilobate and asymmetrical. Synonyms: *Spiroceras* Meek, 1876 non Quenstedt, 1858, *Subhelicoceras* Breistroffer, 1953, *Parahelicoceras* Breistroffer, 1953. Type species: *Pseudhelicoceras robertianum* (d'Orbigny, 1842).

PSEUDHELICOCERAS ROBERTIANUM (D'ORBIGNY, 1842)

Figure 3.79

1842 *Turrilites robertianus* d'Orbigny, p. 585, pl. 162, figs 1-4.
1847 *Turrilites robertianus* d'Orbigny, Pictet & Roux p. 143.
1848 *Turrilites robertianus* d'Orbigny, Bronn p. 1329.
1848 *Turrilites robertianus* d'Orbigny, Quenstedt p. 302, pl. 22, fig 5.
1850 *Turrilites robertianus* d'Orbigny, d'Orbigny p. 127.
1854 *Helicoceras robertianus* (d'Orbigny), Pictet, p. 713, pl. 56, fig, 10.
1859 *Turrilites robertianus* d'Orbigny, Chenu p. 96, text-fig 422.
1861 *Helicoceras robertianum* (d'Orbigny), Pictet & Campiche p. 121.
1866 *Helicoceras robertianum* d'Orbigny, Pictet & Renevier p. 105.
? 1874 *Turrilites* sp. Price p. 76.
1875a *Turrilites robertianus* d'Orbigny, Neumayr p. 33.
1875b *Turrilites robertianus* d'Orbigny, Neumayr p. 901.
1879 *Helicoceras robertianus* d'Orbigny, Price p. 76.
1881 *Turrilites robertianus* d'Orbigny, Wright pp. 201, 244, text-figs 95, 144.
1890 *Turrilites robertianus* d'Orbigny, Renevier p. 339.

non 1896 *Helicoceras robertianum* d'Orbigny, Parona & Bonarelli p. 106.

1907 *Turrilites robertianus* d'Orbigny, Jacob p. 330.

1907 *Ancyloceras?* sp. Etheridge, p. 16, pl. 9, figs 2, 3, pl. 10, figs 4, 5.

1918 *Turrilites robertianus* d'Orbigny, Tomitch p. 7.

1921 *Pseudhelicoceras robertianum* (d'Orbigny), Spath p. 112.

1926 *Turrilites robertianus* d'Orbigny, Jayet p. 186.

1932 *Turrilites (Helicoceras) roberti* d'Orbigny, Collignon p. 18, pl. 1, figs 21, 21a.

1933 *Pseudhelicoceras robertianum* (d'Orbigny), Breistroffer p. 234.

1934 *Turrilites robertianus* d'Orbigny, Heim & Seitz pp.199, 206.

1936 *Pseudhelicoceras robertianum* (d'Orbigny), Breistroffer p. 66.

1937 *Pseudhelicoceras robertianum* (d'Orbigny), Spath p. 532, pl. 63, figs 34-37, text-fig 187, 189b.

1937 *Pseudhelicoceras quadrituberculatum* Spath p. 531, text-fig 190d-f.

1940 *Pseudhelicoceras quadrituberculatum* Spath, Breistroffer p. 46.

1942 *Pseudhelicoceras quadrituberculatum* Spath, Haas p. 200, pl. 44, fig 7, pl. 45, fig 8, text-fig 33a.

1953 *Pseudhelicoceras robertianum* (d'Orbigny), Breistroffer p. 1350.

1957b *Pseudhelicoceras robertianum* (d'Orbigny), Arkell *et al* p. L222, text-fig 248(2).

1965 *Pseudhelicoceras robertianum* (d'Orbigny), Clark p. 38, pl. 8, figs 5, 6, pl. 9, fig 5, pl. 10, fig, 1.

1965 *Pseudhelicoceras robertianum* (d'Orbigny), Clark p. 38, pl. 8, fig 8, pl. 9, fig 4, pl. 10, fig 5.

1968 *Pseudhelicoceras robertianum* (d'Orbigny), Wiedmann & Dieni p. 75, pl. 8, fig, 12, text-fig 54.

1977 *Pseudhelicoceras robertianum* (d'Orbigny), Phillips p. 154.

1979 *Anisoceras (Pseudhelicoceras) robertianum* (d'Orbigny), Scholz p. 30, pl. 6, figs 5-11, text-fig 9.

? 1979 *Pseudhelicoceras* sp. Collignon p. 13, pl. 3, fig 3.

1985 *Pseudhelicoceras robertianum* (d'Orbigny), Marcinowski p. 209.

1989 *Pseudhelicoceras robertianum* (d'Orbigny), Föllmi p. 128, pl. 5, fig, 12.

1990 *Pseudhelicoceras gracile* Henderson p. 133, text-figs, 15a-l, 16b, 17a.

? 1990 *Pseudhelicoceras* cf. *robertianum* (d'Orbigny), Marcinowski & Wiedmann p. 48.

Type material Lectotype by subsequent designation of Spath (1937), the larger of the two specimens figured by d'Orbigny (1842, pl. 142, figs 1, 2). From the Middle Albian of Pert-du-Rhône, France.

Description A loosely coiled helical ammonite. Whorl section laterally compressed. Ornamentation consists of thickened annular ribs bearing four (rarely three) circular bullae,

the ribs being almost completely effaced on the inside of the spire. The second and third bullae are larger than the first and fourth. One or two simple ribs may be intercalated between the bullate ribs. Rib index 3-4, approximately 24 ribs per complete whorl. No apertural constrictions or collars are known. Suture line quadrilobate and asymmetrical. External, lateral and umbilical lobes bifid, internal lobe trifid.

Discussion Comparisons with Anisoceratidae have been made and some authors refer this genus to that family, either at generic rank (Föllmi, 1989) or as a subgenus of *Anisoceras* (Scholz, 1979). More conservatively, others propose that this species connects the tuberculate turrilitids with the Anisoceratidae (Wright *et al*, 1996). I agree with the observation of Klinger & Kennedy (1978) that the tuberculation seen in the Anisoceratidae and the Turrilitidae are not alike, and may imply convergence rather than common ancestry. The presence of three rather than the usual four tubercles in some specimens of *Pseudhelicoceras robertianum* is similar to the instability of the fifth row of tubercles seen in some *Mariella*. The tubercles seen in members of the Anisoceratidae develop in matching pairs on the ventral and ventrolateral surfaces. Each tubercle within each pair is identical at any given stage of growth. In contrast, the tubercles of *Pseudhelicoceras* and *Mariella* develop as longitudinal series, and there is no symmetry across the long axis. Tubercles appear as bullae, or ridges, to the ribs, which become increasingly developed as the shell grows. The last row often does not appear until late in ontogeny. This supports the idea of a different mode or regulation of development, and thus an absence of homology between anisoceratid and turrilitid tubercles.

Occurrence Widely recorded from the Middle and Upper Albian (*Euhoplites lautus* and *Mortoniceras inflatum* Zones) England, France, Sardinia, Austria, Angola, Madagascar, and Texas.

PSEUDHELICOCERAS GAULTINUM SPATH, 1937

Figure 3.80

1937 *Pseudhelicoceras gaultinum* Spath p. 538, pl. 63, figs 27-30.

1977 *Pseudhelicoceras gaultinum* Spath, Phillips p. 154.

Type material Holotype BMNH C.38225 by original designation of Spath. From the Gault Clay of Folkestone (Upper Albian, *Mortoniceras inflatum* Zone).

Description Moderately tightly coiled helical ammonite with four rows of tubercles, the first two being fairly rounded and well developed, and the last two more elongate and rather faint.

A weakening or break in the ribbing between the second and third tubercle running slightly below the widest point of the whorl is reminiscent of *Ostlingoceras*. Apical angle approximately 30° to 40°. Whorl section oval, compressed laterally. Ribbing much finer than *Pseudhelicoceras robertianum*. The ribs are sinuous, strong on the upper and lower surfaces but weakened between the second and third row of tubercles and effaced on the inside of the spire. Rib index 4-5, and about 30 ribs per complete whorl. The umbilicus is closed. Apertural collars and constrictions unknown. Siphuncle displaced laterally as with other *Pseudhelicoceras*. Suture incompletely known but apparently similar to *Pseudhelicoceras robertianum*.

Occurrence As holotype.

PSEUDHELICOCERAS PSEUDOELEGANS SPATH, 1937

Figure 3.81

	1854	*Turrilites elegans* d'Orbigny, Morris p. 313.
	1874	*Turrilites elegans* d'Orbigny, Price p. 363.
	1875	*Turrilites elegans* d'Orbigny, Topley p. 432.
?	1879	*Turrilites elegans* d'Orbigny, Price p. 78.
	1900	*Turrilites elegans* d'Orbigny, Jukes-Brown p. 460.
	1925	*Pseudhelicoceras* sp., Dewey p. 264.
	1937	*Pseudhelicoceras pseudoelegans* Spath p. 534, pl. 62, figs 29-35, pl. 63, figs 31-33, text-figs, 188a-c, 189a.
	1940	*Pseudhelicoceras pseudoelegans* Spath, Breistroffer p. 48.
?	1970	*Mariella patagonica* Leanza, p. 214, text-fig. 12.
	1977	*Pseudhelicoceras pseudoelegans* Spath, Phillips p. 154.
	1987	*Pseudhelicoceras pseudoelegans* Spath, Phillips p. 99.

Type material Holotype by original designation of Spath BMNH C.32894 from the Gault Clay (Upper Albian, *Diploceras cristatum* Subzone) of Folkestone.

Description A moderately tightly coiled helical ammonite. Apical angle approximately 40°. Ribs tuberculate, rather sharper and more sinuous than *Pseudhelicoceras gaultinum*. Rib index of abut 4, and approximately 24 ribs per complete whorl. Umbilicus open, the whorls are not in contact. Whorl section basically a laterally compressed oval but slightly polygonal on the tuberculate side. Three or four rows of elongate tubercles similar to those of *Mariella*, the first row is just above the siphuncle, which is displaced upwards and runs at about the

widest point of the whorl. When small only the first three rows are fully developed and the final row is just a simple ridge or bulla to the rib. Apertural modifications unknown. Suture line similar to that of *Pseudhelicoceras robertianum*.

Occurrence From the lower Upper Albian (*Mortoniceras inflatum* Zone, *Diploceras cristatum* Subzone) of England and France. Possibly also from the Upper Albian of Patagonia, Argentina.

Genus *MARIELLA* Nowak, 1916

Moderately to very tightly coiled helical ammonites. Whorls tightly packed and section flattened at point of contact. Umbilicus closed. Ribbing incomplete and divided into bullae. Siphuncle displaced adapically. Suture quadrilobate and highly asymmetrical. Synonyms: *Paraturrilites* Breistroffer, 1947, *Bergericeras* Wiedmann, 1962. Type species: *Mariella bergeri* (Brogniart, 1822).

MARIELLA BERGERI (BROGNIART, 1822)

Figure 3.82

1822 *Turrilites bergeri* Brogniart p. 395, pl. 7, figs 3a, b.
1837 *Turrilites bergeri* Brogniart, Buckland p. 65, pl. 44. fig, 14.
1842 *Turrilites bergeri* Brogniart, d'Orbigny p. 590, pl. 143, fig 5.
1848 *Turrilites bergeri* Brogniart, Bronn p. 1329.
1850 *Turrilites bergeri* Brogniart, d'Orbigny p. 127.
1854 *Turrilites bergeri* Brogniart, Pictet p. 712, pl. 56, fig 7.
1859 *Turrilites bergeri* Brogniart, Chenu p. 96, text-fig 420.
1860 *Turrilites bergeri* Brogniart, Ooster p. 94.
1861 *Turrilites bergeri* Brogniart, Pictet & Campiche p. 134, pl. 63, figs 1-4.
1875 *Turrilites bergeri* Brogniart, Pictet & Renevier p. 106.
1875 *Turrilites bergeri* Brogniart, Jukes-Browne p. 289.
1875 *Turrilites bergeri* Brogniart, Topley p. 431.
1875a *Turrilites bergeri* Brogniart, Neumayr p. 32.
1875b *Turrilites bergeri* Brogniart, Neumayr p. 901.
1878 *Turrilites bergeri* Brogniart, Barrois p. 302.
1879 *Turrilites bergeri* Brogniart, Price p. 78-79.
1890 *Turrilites bergeri* Brogniart, Renevier p. 339.

1897 *Turrilites bergeri* Brogniart, Cowper Reed p. 116.

1900 *Turrilites bergeri* Brogniart, Jukes-Browne p. 460.

1906 *Turrilites bergeri* Brogniart, Douvillé p. 210, pl. 14, figs 6, 7.

1907 *Turrilites bergeri* Brogniart, Boule *et al* p. 38.

1907 *Turrilites bergeri* Brogniart, Jacob p. 333.

1912 *Turrilites bergeri* Brogniart, Ganz p. 3.

1925 *Turrilites bergeri* Brogniart, Diener p. 80.

1926 *Turrilites bergeri* Brogniart, Jayet p. 156.

1926 *Turrilites bergeri* Brogniart, Scott p. 114, 144-145, pl. 2, fig 2.

? 1929 *Turrilites bergeri* Brogniart, Collignon p. 66, pl. 4, fig, 19.

1930 *Turrilites bergeri* Brogniart, Passendorfer p. 66, pl. 4, fig, 19.

1931 *Turrilites bergeri* Brogniart, Breistroffer p. 1203.

1936a *Turrilites bergeri* Brogniart, Breistroffer p. 63.

1936b *Turrilites bergeri* Brogniart, Breistroffer p. 66, pl. 4, fig, 19.

1937 *Mariella bergeri* (Brogniart), Spath p. 509, 510-514, pl. 62, fig 28, text-fig 178.

1937 *Mariella bergeri* var. *crassituberculata* Spath p. 513.

1940 *Mariella bergeri* var. *conduciensis*, Breistroffer p. 149.

1947 *Paraturrilites bergeri* var. *crassituberculata* (Spath), Breistroffer p. 62.

1953 *Paraturrilites bergeri* (d'Orbigny), Breistroffer p. 1351.

1958 *Turrilites bergeri* (Brogniart), Anderson p. 193, pl. 11, fig 2.

1957b *Mariella bergeri* (Brogniart), Wright in Arkell et *al* p. 222, text-fig 248 (4).

1962 *Paraturrilites (Bergericeras) bergeri* (Brogniart), Wiedmann p. 189.

1962 *Paraturrilites (Bergericeras) bergeri crassituberculata* (Spath), Wiedmann p. 190, pl. 11, fig, 1.

1963 *Paraturrilites (Bergericeras) bergeri* (Brogniart), Dieni & Massari p. 798.

1968 *Mariella (Mariella) bergeri bergeri* (Brogniart), Renz p. 85, pl. 17, fig 37, 41, pl. 18, fig 3,4, 8, text-fig 31f,k.

1968 *Mariella (Mariella) bergeri* cf. *conduciensis* Breistroffer, Renz p. 86, pl. 17, fig 37, 27, text-fig 32o.

1968 *Mariella (Mariella) crassituberculata crassituberculata* Spath, Renz p. 86, pl. 18, figs 5, 6, text-figs 31a, 32i.

1968 *Mariella (Mariella) crassituberculata extrema* Renz p. 87, pl. 18, fig 9.

? 1968 *Mariella (Mariella)* nov. sp. Renz p. 87, pl. 18, fig 7, text-fig 32(l).

1968 *Paraturrilites (Bergericeras) bergeri* (Brogniart), Wiedmann & Dieni p. 80, pl. 7, fig 9, pl. 9, figs 2, 5.

1977 *Mariella bergeri* (Brogniart), Phillips p. 116.

1978 *Mariella bergeri* (Brogniart), Klinger & Kennedy p. 28, pl. 1h, text-fig 6e.

? 1978 *Mariella* cf. *bergeri* (Brogniart), Klinger & Kennedy p. 28.

1982 *Turrilites (Bergericeras) bergeri* (Brogniart), Braga *et al* pl. 1, fig, 1, text-figs 2-4.

1982 *Mariella bergeri* (Brogniart), Seyed-Emami p. 419, pl. 2, figs 11, 12.

1985 *Mariella bergeri* (Brogniart), Seyed-Emami p. 111 pl. 2, figs 11, 12.

1987 *Turrilites (Bergericeras) bergeri* (Brogniart), Hovarth pl. 4, fig 4.

1988 *Mariella bergeri* (Brogniart), Ali-Zade p. 344, pl. 7, fig 2.

1988 *Mariella bergeri* (Brogniart), Delanoy & Latil, p. 752, pl. 1, fig 5.

1995 *Mariella (Mariella) bergeri* (Brogniart), Seyed-Emami & Immel p. 384, text-figs, 17, 18.

1996 *Mariella bergeri* (Brogniart), Wright *et al* p. 243, text-fig 190 (3).

Type material Holotype by monotypy the original of Brogniart (1822, pl. 7, fig 3). From the Upper Albian of Fiz, Savoy, France.

Description Turriliticone with closed coiling is closed, the whorls compressed sufficiently to produce angular, polygonal whorl section. As with other *Mariella*, coiling can be dextral or sinistral. During the neanoconch stage, the shell coils in one plane. Coiling quickly becomes more helical through the early juvenile-A stage to form the high spire characteristic of the genus. At maturity, the apical angle is approximately 30°. The subannular ribs are initially divided into four distinct bullate tubercles or ridges, becoming more circular with ontogeny. A fifth tubercle gradually differentiates from the fourth tubercle on the latest whorls. The first tubercle lies between the external and lateral lobes. The second and third tubercles are over the lateral lobe itself. The fourth and fifth tubercles are between the lateral and umbilical lobes. They are generally covered by succeeding whorls and form distinct depressions where the attached spine was overgrown by the later shell growth. The individual ribs are slightly oblique (about 20° to 30° to the vertical), approximately 20 or more to each whorl. Suture line is quadrilobate, clearly asymmetrical across the siphuncle. The external and lateral lobes are of approximately similar size, the umbilical lobe is somewhat smaller, and the internal lobe very smaller still. External lobe weakly asymmetrical and bifid, the outer leaf slightly larger but similar in shape to the inner leaf. Lateral and umbilical lobes are asymmetrically bifid, the umbilical lobe being slightly smaller than the lateral lobe. The internal lobe is symmetrically trifid. No pseudolobes. Ventral saddle trifid, first lateral, umbilical, and dorsolateral saddles asymmetrically bifid.

Discussion Confusion has existed over the validity of the name *Mariella* in respect to the use of the genus name *Mariaella* for a gastropod. Breistroffer proposed the name *Paraturrilites*, with the species *Mariella gresslyi* as type (Breistroffer, 1947). Subsequently, Wiedmann (1962) considered *Mariella bergeri* to be sufficiently distinct from *Paraturrilites gresslyi* as to warrant a separate subgenus, *Bergericeras*. Klinger & Kennedy (1978) declared that *Mariella* is a valid name and these alternatives should be abandoned, and I have not used them here.

Occurrence Cosmopolitan distribution throughout the latest Upper Albian (*Stoliczkaia dispar* Zone) including much of Europe, Azerbaijan, North Africa, Mozambique, Madagascar, Australia, California and Texas.

MARIELLA CANTABRIGIENSIS (JUKES-BROWNE, 1877)

Figure 3.83

1877 *Turrilites catabrigiensis* Jukes-Browne p. 493.

1897 *Turrilites wiesti* var. *cantabrigiensis* Cowper Reed p. 116.

1926 *Turrilites catabrigiensis* Jukes-Browne, Spath p. 429.

1937 *Mariella catabrigiensis* Jukes-Browne, Spath p. 518, pl. 57, fig 36, pl. 58, figs 1, 2, text-fig 181a,b, 182 d, e.

1940 *Mariella gresslyi* var. *cantabrigiensis* (Jukes-Browne), Breistroffer p. 150.

1947 *Paraturrilites gresslyi* var. *cantabrigiensis* (Jukes-Browne), Breistroffer p. 60.

? 1968 *Mariella* cf. *cantabrigiensis* (Jukes-Brown), Nakai & Matsumoto p. 7, pl. 1, fig 4.

1968 *Mariella (Mariella) catabrigiensis* (Jukes-Browne), Renz p. 88, pl. 17, fig 31, text-fig 31h, 32n.

1977 *Mariella cantabrigiensis* (Pictet & Campiche), Phillips p. 116.

Type material Lectotype by subsequent designation of Spath (1937, p. 518) Sedgewick Museum, Cambridge B.38502, one of the specimens collected by Jukes-Browne. (1861, pl. 57, fig, 11a-c). From the Cambridge Greensand (Upper Albian) near Cambridge, England.

Description Turriliticone with closed coiling is closed, coiling dextrally or sinistrally. The whorls are compressed sufficiently to produce angular, polygonal whorl section. Apical angle similar to or slightly greater than, that of *Mariella bergeri* (30° to 40°). Subannular ribs initially divided into three small bullate to circular tubercles, later whorls see the gradual appearance of a fourth bullate tubercle close to the third. It is covered by subsequent growth. There are approximately 20 ribs per whorl. The first and second tubercles are close together and lie between the external and lateral lobes. The third tubercle lies over the lateral lobe. The fourth tubercle, if present, is between the lateral and umbilical lobe. Each rib is slightly oblique (about 30° to the vertical). The tubercles have bullate sections at the base throughout. Suture line perhaps slightly more like that of *Turrilitoides hugardianus* than *Mariella bergeri* in that the external, lateral and umbilical lobes are of approximately similar size. The suture is quadrilobate and clearly asymmetrical across the siphuncle. The external, lateral and umbilical lobes are of approximately similar size and the internal lobe very much smaller.

External lobe very weakly asymmetrical and bifid, the outer leaf a little larger but similar in overall shape to the inner leaf. Lateral and umbilical lobes are asymmetrically bifid. The umbilical lobe is slightly smaller than the lateral lobe. The internal lobe is symmetrically trifid. No pseudolobes. Ventral saddle trifid, first lateral, umbilical, and dorsolateral saddles asymmetrically bifid.

Discussion. This species is very similar to *Mariella gresslyi*, and they probably intergrade, making separation of the two difficult (Breistroffer 1947, Nakai & Matsumoto 1968). The principal differences are the slightly greater apical angle of this species the rather smaller circular tubercles.

Occurrence Upper Albian (*Stoliczkaia dispar* Zone) of England, France, Switzerland, Tunisia and probably Japan.

MARIELLA GRESSLYI (PICTET & CAMPICHE, 1861)

1861 *Turrilites gresslyi* Pictet & Campiche p. 132, pl. 57, figs 11-13.

1875a *Turrilites gresslyi* Pictet & Campiche, Neumayr p. 32.

1875b *Turrilites gresslyi* Pictet & Campiche, Neumayr p. 901.

1890 *Turrilites gresslyi* Pictet & Campiche, Renevier p. 339.

1910 *Turrilites gresslyi* Pictet & Campiche, Pervinquère p. 54.

1923 *Turrilites gresslyi* Pictet & Campiche, Böse p. 147.

1925 *Turrilites gresslyi* Pictet & Campiche, Diener p. 83.

? 1929 *Turrilites gresslyi* Pictet & Campiche, Collignon p. 65, pl. 1, fig, 15.

1936a *Turrilites gresslyi* Pictet & Campiche, Breistroffer p. 65, pl. 1, fig, 15.

1937 *Mariella gresslyi* (Pictet & Campiche), Spath p. 516, pl. 58, figs 3, 4, text-fig 180.

1940 *Mariella gresslyi* (Pictet & Campiche), Breistroffer p. 149.

1947 *Paraturrilites gresslyi* (Pictet & Campiche), Breistroffer p. 60.

1949 *Paraturrilites gresslyi* (Pictet & Campiche), Collignon p. 47, pl. 258, fig, 1122.

1953 *Paraturrilites gresslyi* (Pictet & Campiche), Breistroffer p. 1350.

1968 *Mariella (Mariella) gresslyi bifurcata* Renz p. 89, pl. 17, fig 42, text-fig 31e, 32c.

1968 *Mariella (Mariella) gresslyi gresslyi* (Pictet & Campiche), Renz p. 89, pl. 17, fig 30, 32, 33, text-fig 31c, 32a, b.

1977 *Mariella gresslyi* (Pictet & Campiche), Phillips p. 116.

? 1978 *Mariella* cf. *gresslyi* (Pictet & Campiche), Klinger & Kennedy p. 26, pl. 7e

Type material Lectotype by subsequent designation of Spath (1937, p. 516) the original of Pictet & Campiche (1861, pl. 57, fig, 11a-c). From the Upper Albian of Sainte-Croix, Switzerland.

Description Turriliticone with closed coiling is closed, coiling may be dextral or sinistral. The whorls compressed sufficiently to produce angular, polygonal whorl section. Apical angle similar to that of *Mariella bergeri* (approximately 30°). Subannular ribs initially divided into three small and circular tubercles, the latest whorls may bear a fourth row of tubercles, approximately 20 ribs per whorl. The fourth tubercle, if present, is usually enveloped by succeeding shell growth. The distribution of tubercles is similar to that of *Mariella bergeri*. The suture is quadrilobate and clearly asymmetrical across the siphuncle. The external, lateral and umbilical lobes are of approximately similar size and the internal lobe very much smaller. External lobe very weakly asymmetrical and bifid, the outer leaf a little larger but similar in overall shape to the inner leaf. Lateral and umbilical lobes are asymmetrically bifid. The umbilical lobe is slightly smaller than the lateral lobe. The internal lobe is symmetrically trifid. No pseudolobes. Ventral saddle trifid, first lateral, umbilical, and dorsolateral saddles asymmetrically bifid.

Occurrence Upper Albian (*Stoliczkaia dispar* Zone) of England, France, Switzerland, Algeria, and Western Madagascar.

MARIELLA MILIARIS (PICTET & CAMPICHE, 1861)

Figure 3.84

1861 *Turrilites bergeri* var. *miliaris* Pictet & Campiche p. 136, pl. 58, fig 5.

1903 *Turrilites bergeri* var. *miliaris* Pictet & Campiche, Choffat p. 15.

1936a *Turrilites bergeri* var. *miliaris* Pictet & Campiche, Breistroffer p. 66.

1937 *Mariella miliaris* (Pictet & Campiche), Spath p. 514, pl. 57, figs 25, 26, text-fig 179.

1968 *Mariella (Mariella) miliaris* (Pictet & Campiche), Renz p. 88, pl. 18, fig, 10, text-fig 31m, 32h.

1977 *Mariella miliaris* (Pictet & Campiche), Phillips p. 116.

1978 *Mariella miliaris* (Pictet & Campiche), Klinger & Kennedy p. 29, pl. 3j, text-fig 8e.

Type material Holotype by monotypy the original of Pictet & Campiche (1861, pl. 58, fig 5). From the Upper Albian of Sainte-Croix, Switzerland.

Description Turriliticone with closed coiling is closed, dextrally or sinistrally coiled. The whorls are compressed sufficiently to produce angular, polygonal whorl section. Apical angle greater than that of *Mariella bergeri* (approximately 70°) producing a squatter, almost trochoform, coil. Subannular ribs initially divided into four small but distinct bullate tubercles or ridges, becoming more circular with ontogeny. Ribs are oblique as with *Mariella bergeri* but each rib is much finer, with up to 40 per complete whorl. Suture line is quadrilobate, clearly asymmetrical across the siphuncle. The external, and lateral are of approximately similar size. The umbilical lobe is somewhat smaller and the internal lobe very smaller still. External lobe weakly asymmetrical and bifid, the outer leaf slightly larger but similar in shape to the inner leaf. Lateral and umbilical lobes are asymmetrically bifid, the umbilical lobe being slightly smaller than the lateral lobe. The internal lobe is symmetrically trifid. No pseudolobes. Ventral saddle trifid, first lateral, umbilical, and dorsolateral saddles asymmetrically bifid.

Discussion The validity of this species has been questioned, in may be a variety of *Mariella bergeri* (Wiedmann & Dieni, 1968). It is distinguished only by more dense, but rather finer, tuberculation and a greater apical angle, but transitions between the two are known (Spath, 1936).

Occurrence Widespread, cosmopolitan distribution similar to that of *Mariella bergeri* throughout the Upper Albian (*Stoliczkaia dispar* Zone) including much of Europe, Madagascar, South Africa and California.

MARIELLA NOBILIS (JUKES-BROWNE, 1877)

Figure 3.85

1877 *Turrilites nobilis* Jukes-Browne p. 493, pl. 21, fig, 1.

1897 *Turrilites nobilis* Jukes-Browne, Cowper Reed p. 116.

1900 *Turrilites nobilis* Jukes-Browne, Jukes-Browne p.460.

1926 *Turrilites nobilis* Jukes-Browne, Spath p. 429.

1937 *Turrilites nobilis* Jukes-Browne, Spath p. 520, pl. 58, figs 10, 11, text-fig 182.

1947 *Paraturrilites nobilis* (Jukes-Browne), Breistroffer p. 60.

1947 *Paraturrilites nobilis* var. *cruciana* Breistroffer p. 60.

1947 *Paraturrilites nobilis* var. *brownei* Breistroffer p. 96.

1968 *Mariella (Mariella) nobilis brownei* (Breistroffer), Renz p. 90, pl. 17, fig 35, 36, 38, 39, text-fig 31i, 32e.

1968 *Mariella (Mariella) nobilis cruciana* (Breistroffer), Renz p. 90, pl. 17, fig 34, text-fig 31b, 32d.

1968 *Mariella (Mariella) nobilis nobilis* (Jukes-Browne), Renz p. 89, pl. 17, fig 28, 40, text-fig 31(l), 32k.

1977 *Mariella nobilis* (Jukes-Browne), Phillips p. 117.

Type material Holotype by monotypy the original of Pictet & Campiche (1861, pl. 58, fig 5). From the Upper Albian of Sainte-Croix, Switzerland.

Description Turriliticone with closed coiling is closed, the whorls compressed sufficiently to produce angular, polygonal whorl section. Apical angle similar to that of *Mariella bergeri* (approximately 30°). Subannular ribs initially divided into three, occasionally four, small but circular to clavate tubercles. Distribution of tubercles similar to that of *Mariella cantabrigiensis*. Approximately 20 ribs per whorl. The fourth tubercle, if present, is usually enveloped by succeeding shell growth. The suture is similar to that of *Mariella cantabrigiensis*.

Discussion Compared with the very similar *Mariella cantabrigiensis* this species is characterised by a more sinuous ribbing and rather weaker tuberculation. The earliest whorls lack any obvious tuberculation at all.

Occurrence Upper Albian (*Stoliczkaia dispar* Zone) of England, France and Switzerland. Also from Texas.

MARIELLA WORTHENSIS (ADKINS & WINTON, 1920)

1920 *Turrilites worthensis* Adkins & Winton, Adkins p. 78, pl. 3, figs 1, 6.

1920 *Turrilites* sp. Adkins p. 78, pl. 3, figs 2, 4.

1920 *Turrilites* sp. B. Adkins p. 45, pl. 7, figs 7, 8.

1920 *Turrilites* sp. Adkins & Winton pl. 7, figs 9-12.

1920 *Turrilites* sp. Winton & Adkins p. 69.

1920 *Turrilites worthensis* Adkins & Winton p. 28, 44-45, pl. 7, figs 10, 11, 13.

1925 *Turrilites worthensis* Adkins & Winton, Winton p. 59, pl. 6, fig 4.

1926 *Turrilites circumtaeniatus* Scott p. 79, 144-145, pl. 1, figs 10', 10'', 11.

1928 *Turrilites worthensis* Adkins & Winton, Adkins p. 24, 215, pl. 21, fig, 1.

1928 *Turrilites worthensis* Adkins & Winton, Böse p. 146-147.

? 1947 *Paraturrilites worthensis* (Brogniart), Breistroffer p. 66.

1961 *"Turrilites" worthensis* Adkins & Winton, Perkins p. 39.

1962 *Mariella (Mariella) worthensis* (Adkins & Winton), Clark p. 303-304, text-fig 2.

1965 *Mariella (Mariella) worthensis* (Adkins & Winton), Clark p. 41-42, pl. 11, fig 3, 6, pl. 12, figs 1-9, pl. 16, figs 4, 5, text-fig 16.

1994 *Mariella worthensis* (Adkins & Winton), Emerson *et al*, p. 297.

Type material Holotype by original designation the specimen figured by Adkins & Winton (1920, pl. 7, fig. 10) from the Pawpaw Clay formation at Sycamore Creek near Forth Worth, Texas.

Description A very small turriliticone with closed coiling. The whorl section in circular to somewhat angular (but less so than other *Mariella*). Coiling dextral or sinistral. Apical angle approximately 40°. Subannular ribs initially divided into three distinct bullate tubercles or ridges, becoming more circular with ontogeny. A fourth tubercle gradually appears on the later whorls. On all save the final living chamber the fourth tubercle is covered by succeeding whorls but distinct depressions persist where the spine was overgrown. The individual ribs are slightly oblique (about, 10° to the vertical), approximately, 15 to 20 ribs per whorl. Suture line similar to *Mariella bergeri*.

Discussion This form is closely related to *Mariella bergeri* which is virtually identical at a comparable size, and only differs when large. Differences between mature *Mariella bergeri* and *Mariella worthensis* are the slightly blunter apical angle and fewer tubercles. This ammonite almost certainly represents a dwarf form of *Mariella bergeri*, exhibiting progenetic growth, i.e., maturity in *Mariella worthensis* is reached at a size and morphology closely comparable with that of immature *Mariella bergeri*. It may be better to refer to this species as a subspecies of *Mariella bergeri*.

Occurrence Restricted to the Upper Albian of Texas and adjacent areas.

Genus *OSTLINGOCERAS* Hyatt, 1900

Highly compressed, high-spired helical ammonite with closed umbilicus and angular whorl section. Ribbing distinctive: very straight and sharply defined, with one or two rows of small bullae on the adapical surface divided by a weakening or break in the ribbing, forming a shallow groove. Siphuncle displaced adapically. Suture quadrilobate and highly asymmetrical. Synonyms: none. Type species: *Ostlingoceras puzosianum* (d'Orbigny, 1842).

OSTLINGOCERAS PUZOSIANUM (D'ORBIGNY, 1842)

Figure 3.86

1842 *Turrilites puzosianus* d'Orbigny p. 523, pl. 143, figs 1, 2.

1847 *Turrilites puzosianus* d'Orbigny, Pictet & Roux p. 151, pl. 15, figs 9a, b.

1848 *Turrilites puzosianus* d'Orbigny, Bronn p. 1329.

1850 *Turrilites puzosianus* d'Orbigny, d'Orbigny p. 127.

1854 *Turrilites puzosianus* d'Orbigny, Pictet p. 712.

1861 *Turrilites puzosianus* d'Orbigny, Pictet & Campiche p. 139, pl. 59, figs 3-6.

1866 *Turrilites puzosianus* d'Orbigny, Pictet & Renevier p. 106.

1875a *Turrilites puzosianus* d'Orbigny, Neumayr p. 33.

1875b *Turrilites puzosianus* d'Orbigny, Neumayr p. 901.

1878 *Turrilites puzosi* d'Orbigny, Bayle pl. 49, figs 1, 2.

1878 *Turrilites puzosianus* d'Orbigny, Barrois p. 302.

1890 *Turrilites puzosianus* d'Orbigny, Renevier p. 339.

1897 *Turrilites puzosianus* d'Orbigny, Cowper Reed p. 116.

1900 *Turrilites puzosianus* d'Orbigny, Jukes-Browne p. 460.

1907 *Turrilites puzosianus* d'Orbigny, Jacob p. 333.

1907 *Turrilites (Ostlingoceras) puzosianus* d'Orbigny, Pervinquière p. 100.

1912 *Turrilites puzosianus* d'Orbigny, Ganz p. 3.

? 1930 *Turrilites* cf. *puzosianus* d'Orbigny, Passendorfer p. 672.

1936 *Ostlingoceras puzosianum* (d'Orbigny), Breistroffer p. 63.

1937 *Ostlingoceras puzosianum* (d'Orbigny), Spath p. 533, pl. 58, figs 38-40, text-fig 183.

1937 *Ostlingoceras puzosianum* (d'Orbigny), Stolley p. 51.

1947 *Ostlingoceras puzosianum* (d'Orbigny), Breistroffer p. 62.

1953 *Ostlingoceras puzosianum* (d'Orbigny), Breistroffer p. 1350.

1957b *Ostlingoceras (Ostlingoceras) puzosianum* (d'Orbigny), Wright in Arkell et *al* p. 222, text-fig 248 (7).

1979 *Turrilites (Ostlingoceras) puzosianum* (d'Orbigny), Scholz p. 42, pl. 9, figs 4-13, text-fig 11k.

1963 *Ostlingoceras puzosianum* (d'Orbigny), Collignon pl. 257, fig, 1113.

1968 *Ostlingoceras (Ostlingoceras) puzosianum* (d'Orbigny), Renz p. 92, pl. 18, figs 12-15.

1968 *Ostlingoceras (Ostlingoceras) puzosiforme* Spath, Renz p. 93, pl. 18, fig, 18.

1968 *Ostlingoceras (Ostlingoceras) puzosianum* (d'Orbigny), Wiedmann & Dieni p. 79, pl. 9, fig, 1-4.

1977 *Ostlingoceras puzosianum* (d'Orbigny), Phillips p. 132.

1977 *Ostlingoceras puzosianum* (d'Orbigny), Seyed-Emami p. 128.

1982 *Ostlingoceras puzosianum* (d'Orbigny), Seyed-Emami p. 426, pl. 3, figs 12, 13, pl. 4, figs 1-3, 12, 13.

1988 *Ostlingoceras puzosianum* (d'Orbigny), Delanoy & Latil p. 752.

1989 *Turrilites (Ostlingoceras) puzosianum* d'Orbigny, Hovarth pl. 4, figs 2, 7.

? 1989 *Ostlingoceras* sp. indet. Owen p. 377, pl. 1, fig 9.

Type material Holotype by monotypy the original of d'Orbigny (1842, pl. 143, figs 1, 2). Specimen in the Puzos Collection at the School of Mines, Paris. From Reposoir, Savoy, south eastern France.

Description A high spired turriliticone immediately recognisable by the flattened whorl profile and sharp ribbing with distinctive adapical groove. The whorl section is polygonal and the flattened faces of adjacent whorls fit neatly together giving the entire spire a very closely packed, conical appearance. Laterally the whorl profile is also flattened in contrast to the convex, subcircular profile of *Mariella*. The ribs are incomplete, being absent on the inner surface of the whorl. Approximately 35 to 40 straight ribs per whorl, each rib bears one or two small bullate to circular tubercles divided by a weakening or break in the rib. Apertural collars and constrictions unknown. The suture line is comparable to *Mariella bergeri*, being quadrilobate but highly asymmetrical.

Discussion The relationship between this species and the rare Lower Cenomanian form *Ostlingoceras puzosiforme* Spath, 1937 is uncertain, the latter may be merely a variety. It is distinguished by having sinuous rather than straight ribbing, see discussion in Renz (1968). Scholz (1979) considered *Ostlingoceras* to be a subgenus of *Turrilites*. However, *Ostlingoceras* is much more flattened on the outer whorl surface than any *Turrilites* or *Mariella*, and their are only two tubercles which are much smaller than those of *Turrilites* and most *Mariella* (although perhaps comparable with *Mariella miliaris*). Most authors therefore consider *Ostlingoceras* to be quite distinct from either *Mariella* or *Turrilites*.

Occurrence From the Upper Albian and the Lower Cenomanian of north west Europe, including England, France, Sardinia, and Poland, also from Madagascar and Iran.

Superfamily SCAPHITACEAE Gill, 1871

The validity of this taxon cannot be fully justified on the basis of this cladogram. As originally conceived, the Scaphitaceae comprised a number of divergent lineages (including *Worthoceras* as well as *Scaphites* and *Eoscaphites*) with a monophyletic origin within the Lytoceratacеae (Wright, 1953). This is in contrast with the derivation of the Turrilitaceae from the Ancyloceratacеae. It has been proposed by Wiedmann (1965) and supported by this cladistic analysis that the true scaphites, the family Scaphitidae, can be derived from the Hamitidae within the Turrilitaceae, and that the dwarf scaphite *Worthoceras* is rather an offshoot of the Ptychoceratidae. It would appear then the Scaphitidae are a monophyletic family of recoiled heteromorph ammonites derived from the Hamitidae of equivalent standing to the Turrilitidae, Baculitidae, or Anisoceratidae.

Family SCAPHITIDAE Gill, 1871

Recoiled heteromorph ammonite characterised by closure of the umbilicus within a more or less involute spiral phragmocone. Ribbing also tends to bifidity, the divergence being raised somewhat and often producing bullate tubercles. The aperture of some species ornamented with a single constriction and collar. The Scaphitidae appear during the Upper Albian but become much more diverse through the Upper Cretaceous. They have been recorded from Albian deposits in Europe, North Africa, Madagascar, and the Middle East.

Genus *EOSCAPHITES* Breistroffer, 1947

Non tuberculate shallow hooked ancyloconic ammonites. Planar throughout ontogeny, initial coil closed (imperforate), not as globose or involute as *Scaphites*. Annular ribs occasionally divide over ventral surface. Apertural modifications unknown. Suture quadrilobate. Synonyms: none. Type species: *Eoscaphites circularis* (J. de C. Sowerby, 1836).

EOSCAPHITES CIRCULARIS (J. DE C. SOWERBY, 1836)

Figure 3.87

1836 *Ammonites circularis* J. de C. Sowerby p. 337, pl. 11, fig 20.

1837 *Ammonites circularis* J. de C. Sowerby, Brown pl. 20, fig, 10.

1848 *Ammonites circularis* J. de C. Sowerby, Bronn p. 37.

1854 *Ammonites circularis* J. de C. Sowerby, Morris p. 296.

1868 *Ammonites circularis* J. de C. Sowerby, de Rance p. 168.

1875 *Ammonites circularis* J. de C. Sowerby, Topley p. 431.

1933a *Scaphites circularis* (J. de C. Sowerby), Spath p. 427, text-figs 4 (d-j).

1934 *Scaphites circularis* (J. de C. Sowerby), Spath p. 496.

1934 *Scaphites circularis* (J. de C. Sowerby), Spath p. 496.

1937 *Scaphites circularis* (J. de C. Sowerby), Spath p. 499, pl. 62, figs 1-9, text-fig 174.

1942 *Scaphites circularis* (J. de C. Sowerby), Spath p. 680.

1957b *Eoscaphites circularis* (J. de C. Sowerby), Wright in Arkell et *al* p. 228, text-fig 255 (6a-c).

1965 *Eoscaphites circularis* (J. de C. Sowerby), Wiedmann p. 404, pl. 53, figs 1-3, text-figs, 1 (a-c).

1977 *Eoscaphites circularis* (J. de C. Sowerby), Phillips p. 59.

1985 *Eoscaphites circularis* (J. de C. Sowerby), Wiedmann & Marcinowski 456-461, text-figs 4 (a-d), 5 (a, b).

1996 *Eoscaphites circularis* (J. de C. Sowerby), Wright *et al* p. 260, text-figs 202 (1a-c).

Type material Holotype by monotypy the original of Fitton (1836, pl. 20, fig, 10), though this appears to be is lost. Spath has designated BMNH C.41555 as neotype (Spath, 1937). From the Upper Gault (Upper Albian) of Folkestone, Kent.

Description Ancylocone with a perforate, convolute initial coil and a shallow hook about equal in depth to the diameter of the coil. Whorl section circular initially, becoming increasingly dorso-ventrally compressed through the coil and shafts. The shell becomes flattened dorsally where descending shaft overgrows initial coil. Annular ribs straight and fine, rectiradiate to slightly prorsiradiate. Dorsally the ribs are weakened only very slightly. Rib index of 8 to 10 on initial coil, decreasing to about 6 on the descending shaft as well as becoming coarser. Ribs moderately flattened in profile. Space between ribs irregular, but is approximately equal to that of the width of the rib. Ribs occasionally branch ventrolaterally, raised slightly at the bifurcations to form incipient bullate nodes. Apertural collars unknown. Suture line quadrilobate and symmetrical across the siphuncle. External and lateral lobes similar in size and bifid. Umbilical lobe smaller and bifid. Internal lobe almost as large as external and lateral lobes, but simpler and trifid. Pseudolobes absent. Ventral saddle weakly trifid, first lateral, umbilical, and dorsolateral saddles bifid.

Discussion The ornament of *Eoscaphites circularis* resembles that of *Lytohamites similis*, as discussed by Wiedmann (1965). Early (coiled) stages of *Lytohamites similis* have not been described, though curved sections of comparable size show weaker ornamentation and a more

complex suture line than similar size fragments of *Eoscaphites circularis* (e.g., BMNH C.4525).

Occurrence Lower part of the Upper Albian (*Mortoniceras inflatum* Zone), of England, France.

Genus *SCAPHITES* Parkinson, 1811

Tuberculate shallow hooked ancyloconic ammonites. Planar throughout ontogeny, initial coil closed (imperforate) in most species, usually fairly globose and involute. Annular ribs divide over ventral surface, tubercles present where ribs bifurcate. Apertural modifications may be present in some species, consisting of a constriction followed by a single collar. Suture quadrilobate during initial stages of growth, pseudolobes develop with maturity and may produce five or more lobes in total (see Wiedmann, 1965). Synonyms: *Holcoscaphites* Nowak, 1916. Type species: *Scaphites hugardianus* d'Orbigny, 1840.

SCAPHITES HUGARDIANUS D'ORBIGNY, 1840

Figure 3.88

	1840	*Scaphites hugardianus* d'Orbigny p. 521.
	1847	*Scaphites hugardianus* d'Orbigny, Pictet in Pictet & Roux p. 370, pl. 12, figs 2a-d.
	1848	*Scaphites hugardianus* d'Orbigny, Bronn p. 1118.
non	1848	*Scaphites hugardianus* d'Orbigny, Pictet p. 370, pl. 12, figs 2a-d.
	1850	*Scaphites hugardianus* d'Orbigny, d'Orbigny p. 125.
	1854b	*Scaphites hugardianus* d'Orbigny, Pictet p. 702.
	1859	*Scaphites hugardianus* d'Orbigny, Chenu p. 91.
	1860	*Scaphites hugardianus* d'Orbigny, Ooster p. 3.
	1861	*Scaphites hugardianus* d'Orbigny, von Hauer p. 649, pl. 2, figs 11, 12.
	1861	*Scaphites meriani* Pictet & Campiche p. 16, pl. 44, figs 6a, b.
	1865	*Ammonites (Scaphites) equalis* (J. de C. Sowerby), Seeley p. 225 *pars*.
	1865	*Ammonites (Scaphites) meriani* Pictet & Campiche, Seeley p. 225.
	1866	*Scaphites meriani* Pictet & Campiche, Pictet & Renevier p. 102.
	1875	*Scaphites equalis* (J. de C. Sowerby), Topley p. 432.
	1875	*Scaphites hugardianus* d'Orbigny, Hébert & Munier-Chalmas p. 116, pl. 5, figs 7a, b.
	1875	*Scaphites hugardianus* d'Orbigny, Neumayr p. 42.
	1875	*Scaphites hugardianus* d'Orbigny, Neumayr p. 925.

1875 *Scaphites meriani* Jukes-Browne, p. 287, pl. 14, fig, 1.

1875 *Scaphites meriani* Pictet & Campiche, Neumayr p. 225.

1875 *Scaphites meriani* var. *simplex* Jukes-Browne, p. 287, pl. 14, fig 3.

1879 *Scaphites hugardianus* d'Orbigny, Price p. 76 *pars.*

1879 *Scaphites meriani* Pictet & Campiche, Price p. 78.

1879 *Scaphites simplex* Jukes-Browne, Price p. 78.

1890 *Scaphites hugardianus* d'Orbigny, Renevier p. 339 *pars.*

1890 *Scaphites meriani* Pictet & Campiche, Renevier p. 339.

1891 *Scaphites meriani* Pictet & Campiche, Woods p. 131.

1891 *Scaphites meriani* var. *simplex* Jukes-Browne, Woods p. 131.

1897 *Scaphites hugardianus* var. *meriani* Pictet & Campiche, Cowper Reed p. 116.

1897 *Scaphites hugardianus* d'Orbigny, Cowper Reed p. 116.

1897 *Scaphites meriani* var. *simplex* Jukes-Browne, Cowper Reed p. 116.

1900 *Scaphites hugardianus* d'Orbigny, Jukes-Browne p. 459 *pars.*

1900 *Scaphites meriani* Pictet & Campiche, Jukes-Browne p. 459.

1907 *Scaphites meriani* Pictet & Campiche, Jacob p. 333.

1910 *Scaphites hugardianus* d'Orbigny, Pervinquière p. 24, pl. 2, figs 1, 2, text-fig 8.

1916 *Holcoscaphites hugardianus* (d'Orbigny), Nowak p. 57, 62.

non 1923a *Scaphites hugardianus* (J. de C. Sowerby), Spath p. 76.

1925 *Scaphites hugardianus* d'Orbigny, Diener p. 119 *(pars).*

1925 *Scaphites hugardianus* d'Orbigny, Diener p. 199.

non 1925b *Scaphites hugardianus* (J. de C. Sowerby), Spath p. 36.

1926a *Scaphites hugardianus* d'Orbigny, Jayet p. 186.

1926b *Scaphites hugardianus* d'Orbigny, Jayet p. 156.

1926c *Scaphites hugardianus* d'Orbigny, Jayet p. 171.

? 1929 *Scaphites hugardianus* d'Orbigny, Collignon p. 29.

? 1929 *Holcoscaphites meriani* (Pictet & Campiche), Passendorfer p. 659.

? 1931 *Scaphites hugardianus* d'Orbigny, Breistroffer p. 1203.

1931 *Scaphites meriani* Pictet & Renevier, Breistroffer p. 1203 *(pars?).*

1931 *Scaphites* cf. *hugardianus* d'Orbigny, Breistroffer p. 232.

1936 *Scaphites hugardianus* d'Orbigny, Breistroffer p. 67.

1936 *Scaphites meriani* Pictet & Campiche, Breistroffer p. 67 *(pars?).*

1937 *Scaphites hugardianus* d'Orbigny, Spath p. 502, pl. 57, fig 24, text-figs, 175a, b,, 176a, b, g-i.

1937 *Scaphites simplex* Jukes-Browne, Spath p. 504, pl. 57, figs 13-23, text-figs, 176c-f,, 177a-e.

1942 *Scaphites hugardianus* d'Orbigny, Spath p. 680.

1942 *Scaphites simplex* Jukes-Browne, Spath p. 680.

1963 *Scaphites meriani* (Pictet & Campiche), Collignon p. 57, text-fig 1142.

1965 *Scaphites (Scaphites) hugardianus* d'Orbigny, Wiedmann p. 423, pl. 54, fig 5, pl. 57 figs 1, 2, 6, 7, text--figs 5d, e.

1965 *Scaphites meriani* (Pictet & Campiche), Wiedmann p. 426, pl. 54, fig 6, pl. 57, figs 3, 4, text-figs 5 (a-c).

1965 *Scaphites simplex* Jukes-Browne, Wiedmann p. 412, pl. 54, figs 1, 7, pl. 55, figs 4, 5, text-fig 3e.

1968 *Scaphites (Scaphites) hugardianus* d'Orbigny, Renz p. 93, pl. 18, figs 17.

1968 *Scaphites (Scaphites) meriani* (Pictet & Campiche), Wiedmann & Dieni p. 84, pl. 7, fig 4, pl. 8, fig 4, pl. 15, fig 8.

1968 *Scaphites (Scaphites) simplex* d'Orbigny, Renz p. 93.

1968 *Scaphites (Scaphites) hugardianus* d'Orbigny, Wiedmann & Dieni p. 83, pl. 7, fig 3.

1976 *Scaphites (Scaphites) simplex* (Jukes-Brown), Marcinowski & Naidin p. 99, pl. 1, fig 7.

? 1976 *Scaphites (Scaphites)* cf. *hugardianus* (d'Orbigny), Marcinowski & Naidin p. 100, pl. 1, fig 8.

? 1976 *Scaphites (Scaphites)* cf. *meriani* (Pictet & Campiche), Marcinowski & Naidin p. 100, pl. 1, figs 9, 10.

1977 *Scaphites hugardianus* d'Orbigny, Phillips p. 163.

1977 *Scaphites simplex* Jukes-Browne, Phillips p. 163.

1979 *Scaphites (Scaphites) hugardianus* d'Orbigny, Scholz p. 43, pl. 1, figs 20-25.

1979 *Scaphites (Scaphites) meriani* Pictet & Campiche, Scholz p. 44, pl. 1, figs 26, 27, 28.

1982 *Scaphites hugardianus* d'Orbigny, Braga *et al* p.7, 10, text-figs 2-4.

1982 *Scaphites simplex* Jukes-Browne, Braga *et al* p.7, 10.

1989 *Scaphites (Scaphites) hugardianus* d'Orbigny, Hovarth pl. 1, fig. 3.

1989 *Scaphites (Scaphites) meriani* Pictet & Campiche, Hovarth pl. 2, fig. 4.

1990 *Scaphites (Scaphites) hugardianus* d'Orbigny, Cooper

1990 *Scaphites hugardianus* d'Orbigny, Henderson p. 127, text-fig 10 (i-m).

1994a *Scaphites hugardianus* d'Orbigny, Cooper p. 168, text-fig 1 (e-g).

1996 *Scaphites (Scaphites) hugardianus* d'Orbigny, Kennedy in Gale *et al* p. 589, 590, text-fig 17 a-c, g.

? 1996 *Yezoites subevolutus* Böse, Gale *et al* p. 589, text-fig 30 (b, c, h, j, k).

Type material Spath designated the specimen figured by Hébert & Munier-Chalmas (1875, pl. 5, fig 7) as lectotype in the absence of preserved types in the d'Orbigny collection (Spath, 1937, p 503, Wiedmann, 1965 p 423-424). Although Hébert & Munier-Chalmas examined d'Orbigny's material, the figured specimen is not from the same locality: the d'Orbigny specimens were stated to be from the Upper Gault of Fiz, Savoy, France, while that of Hébert & Munier-Chalmas is from the Upper Gault of Salazac, Gare, France. Under International Commision on Zoological Nomenclature rules this renders Spath's designation invalid. The status of the type material remains uncertain.

Description A morphologically variable, small (Shell height 40-50 mm.) scaphitiform ammonite. Globose in form with an involute imperforate initial coil with a semi-lunate whorl section and a shallow, hooked living chamber. Ribs annular, fine and sinuous across the venter very much weakened dorsally and absent where whorls impact. Ribbing becomes bifurcate ventrally across the living chamber. Rib index variable, from, 10 to 26 (highest where ribs are bifurcate), though typically ribs become less densely packed near the aperture. Constricted aperture with a collar consisting of a single thickened rib. Tuberculation variable but sparse, confined to the latest part of the phragmocone and the living chamber, ventrolaterally paired nodes bullate to circular, covering one or two ribs arising where the ribs divide. Suture line essentially quadrilobate but with small pseudolobe developing late in ontogeny, symmetrical across the siphuncle. External, lateral and internal lobes similar in size, umbilical lobe and pseudolobe smaller. External lobe bifid. Lateral lobe subsymmetrically bifid. Umbilical lobe subsymmetrically trifid. Internal lobe trifid. A pseudolobe is present, it is symmetrically trifid, but not parallel with the true lobes. Ventral saddle indistinctly trifid. First lateral, umbilical, and dorsolateral saddles symmetrically bifid.

Discussion The synonymy of *Scaphites meriani* and *Scaphites simplex* with *Scaphites hugardianus* (e.g., Scholz, 1979, Cooper, 1990, Cooper, 1994a) has not been accepted by all authors (e.g., Kennedy in Gale *et al*, 1996). The specimens recorded as *Yezoites subevolutus* (Böse) in Gale *et al* (1996) differ from the type material of that species in being imperforate, having very weak bullate tuberculation, and possessing bifurcating ribs, additionally, *Yezoites* is otherwise only recorded from the Upper Cretaceous. It is more likely that these are simply small *Scaphites*.

Occurrence Widely recorded from the Upper Gault (Upper Albian) of Europe and elsewhere (England, France, Spain, Sardinia, Hungary, Switzerland, Crimea, Iran, Algeria, and Western Madagascar), also the Cambridge Greensand (Upper Albian) of England.

SCAPHITES SUBCIRCULARIS (SPATH, 1937)

Figure 3.89

1874 *Scaphites circularis* (J. de C. Sowerby), Price p. 363.

1879 *Scaphites circularis* (J. de C. Sowerby), Price p. 76.

1900 *Scaphites hugardianus* (d'Orbigny), Jukes-Browne p. 459 *pars.*

1923a *Scaphites hugardianus* (J. de C. Sowerby), Spath p. 76.

1925b *Scaphites hugardianus* (J. de C. Sowerby), Spath p. 36.

1933a *Scaphites circularis* (J. de C. Sowerby), Spath p. 427.

1937 *Scaphites subcircularis* Spath p. 501, pl. 62, figs 10-12, text-fig 175e.

1942 *Scaphites subcircularis* Spath, Spath p. 680.

1963 *Scaphites* cf. *subcircularis* (Spath), Collignon p. 57, text-figs, 1143, 1144.

1965 *Eoscaphites subcircularis* (Spath), Wiedmann p. 404, pl. 53, figs 4-6, pl. 54, figs 2, 3, 4, 8, 9, pl. 55, figs 1-3, text-figs, 1 (d-f), 2.

1977 *Eoscaphites subcircularis* (Spath), Phillips p. 59.

1985 *Eoscaphites subcircularis* (Spath), Wiedmann & Marcinowski p. 456-461, text-figs 4 (e-l), 5 (c, d).

1989 *Eoscaphites subcircularis* (Spath), Föllmi p. 120, pl. 3, fig, 18.

1996 *Eoscaphites subcircularis* (Spath), Wright *et al* p. 260, text-figs 202 (1d, e).

Type material Holotype BMNH C.38206 by original designation of Spath (1933, pl. 62, fig, 10, text-fig 175e). From the Upper Gault (Upper Albian) of Folkestone, England.

Description Scaphiticone with a tightly coiled (but perforate) initial coil partially enveloped by the descending shaft. Whorl section dorso-ventrally compressed initially, semi-lunate later. Annular ribs fine, sinuous and bifurcating across the venter of the phragmocone, becoming straighter, coarser and less branched on the living chamber. Near the aperture the ribs become branched once more, with slight bullate nodes where they divide on the ventrolateral surface. Rib index of about 8. Aperture slightly constricted, single inflated rib forms collar. Suture quadrilobate and symmetrical across the siphuncle. External and lateral lobe similar in size and bifid, the lateral lobe slightly subsymmetrical. Umbilical lobe subsymmetrically bifid and smaller. Internal lobe similar in size to external and lateral lobes but narrower and trifid. Pseudolobes absent. Ventral saddle indistinctly trifid, first lateral, umbilical, and dorsolateral saddles fairly broad and bifid.

Discussion This species is more like typical Scaphitidae than *Eoscaphites* in having bullate nodes, branching ribs with distinct sinuosity and an apertural constriction. On the other hand, the initial coil is still perforate and the suture lacks pseudolobes. The cladistic analysis indicates a closer affinity to *Scaphites hugardianus* than *Eoscaphites circularis*, although it has previously been included within *Eoscaphites*. Therefore I provisionally move this species to *Scaphites*, although this must be reviewed with reference to the other Scaphitidae in due course.

Occurrence Lower part of the Upper Albian (*Mortoniceras inflatum* Zone), of England, France, Austria, Algeria and Western Madagascar.

CHAPTER FOUR: FUNCTIONAL MORPHOLOGY

Summary

A number of methods are identified and discussed for estimating physical parameters such as centre of mass, centre of buoyancy and orientation of a range of heteromorph ammonite morphologies. These involve either mathematical modelling (using spreadsheet analysis software) or making scale models. These methods indicate that there heteromorph ammonite morphologies can be divided into two groups: tilters and non-tilters. Tilting ammonites could orient themselves by moving the body to the aperture, which would cause the shell to rotate such that the aperture would point toward the seafloor. In such a position, the ammonite would be well able to feed and crawl about. This class of ammonite includes aspinocones, ancylocones, and hamiticones, although these shell shapes produce drag, the geometry would allow this tilting action to occur more efficiently than a regular spiral. The non-tilting ammonites lack this ability to tilt and they are fixed in a single, head-downwards orientation. They also exhibit streamlining, and are more likely to have been vertically migrating, planktonic filter feeders or predators comparable to modern cranchid squids or *Spirula*.

Introduction

The functional morphology of ammonites has been widely debated and heteromorph ammonites are no exception. Modern cephalopods can be divided into the externally-shelled nautiloids and the internally-shelled coleoids. Inevitably, most comparisons have been made between the ammonites and the modern nautiloids, but recently the validity of this comparison has been questioned (Jacobs & Landman, 1993).

Functional Morphology of the Nautilus

Nautilus is the only ectocochleate cephalopod, and consequently more comparisons have been made between ammonites and *Nautilus* than with any other extant cephalopod (Jacobs & Landman, 1993). It lives on the distal edges of the continental shelves and around offshore islands of the tropical Indo-Pacific (Saunders & Ward, 1987, Ward, 1987). The shell is very well known, perhaps even having been described by Aristotle in the Fourth Century BC (Barnes, 1985). It is a simple logarithmic spiral, divided up by concave septa, except for the final living chamber which accounts for approximately one third of the final whorl (FIGURE 4.1, Owen, 1832). The chambers are emptied as the animal grows and provides near neutral buoyancy (Ward *et al*, 1977, Chamberlain, 1979).

Personal observations of captive *Nautilus* suggest that it spends much of the time on the bottom of aquaria and is not so active as cuttlefish or octopus, and this appears to be true for *Nautilus* in the wild (Carlson, 1987, O'Dor *et al*, 1993). Ventilation is achieved in two ways, when inactive by simple undulations of the anterior flaps of the mantle, which form a funnel (the hyponome) drawing water over the gills, and when more active by pulling the head into the shell and forcing an exchange of water within the mantle cavity (Johansen *et al*, 1978, Wells, 1987).

The *Nautilus* is an slow swimmer compared with squid or cuttlefish and cannot sustain maximum speed for long (Chamberlain, 1980a, Baldwin, 1987). Swimming is inefficient because the centre of mass, though which the locomotive force is exerted, is below the centre of buoyancy. This results in a rocking motion like a pendulum (Chamberlain, 1980a, 1991, 1993). The shell shape is also rather depressed and produces a lot of drag (Chamberlain, 1969, 1976, 1980b). However, *Nautilus* is able to direct the jet using the hyponome, which sticks out of a notch in the ventral part of the shell (the hyponomic sinus).

When threatened, the *Nautilus* does not swim away but relies on its shell for defence. It is able to withdraw the head and arms into the mantle cavity, and seals the aperture with the hood. It cannot respire with the hood down because it cannot ventilate (Wells & Wells, 1985, Wells et al, 1992). The blood of *Nautilus* constitutes a greater part of body mass than in any other cephalopod alive today, and it is thought that the blood is the main store of oxygen when the animal is closed up inside the shell (Redmond, 1978).

Ammonites and *Nautilus* compared

Ammonite shells are diverse, but typically have longer body chambers than nautiloids; as much as one whorl or more, compared with the one-third of a whorl of *Nautilus* (Ebel, 1990). The head retractor muscles are relatively small and there is no hyponomic sinus (Mutvei, 1964, 1975, Doguzhaeva & Mutvei, 1991). Finally, comparisons with *Nautilus* indicate that ammonite shells produced more drag, especially open coiled forms (Chamberlain, 1976). This has lead to the conclusion that most ammonites were worse swimmers than *Nautilus* (von Pia, 1923, Lehmann, 1975), and that only some of the most streamlined forms were even comparable (Bayer, 1982). Heteromorph ammonites may even have been incapable of swimming at all, open or strongly ornamented shells may have created too much drag for the jet to overcome (Ward & Westermann, 1977).

The relationship between shell shape and ecology of ammonites in general has been widely debated (Westermann, 1996). The aberrant form of many heteromorph ammonites has been cited variously as evidence for a being sessile (e.g., *Nipponites*, Morton, 1958), as benthonic crawlers (e.g., *Macroscaphites*, Ebel, 1985), as shoaling nektobenthonic opportunists (e.g., *Polyptychoceras*, Matsumoto & Nihongi), as planktonic drifters (e.g., *Diplomoceras*, Nesis, 1986), as vertical migrators (e.g., *Turrilites*, Ward, 1979), and as active swimmers of the upper waters (e.g., *Baculites*, Matsumoto, 1962).

Ammonites and coleoids compared — squid, cuttlefishes, and octopuses

If ammonites could not swim then perhaps parallels could be drawn with the planktonic mesopelagic squids like *Cranchia* and the unusual little cuttlefish *Spirula* rather than *Nautilus* (FIGURES 4.2 & 4.3). *Cranchia* is typical of a large number of planktonic or weakly swimming squids which retain ammonium ions in their tissues to provide buoyancy (the Cranchidae). In life the are oriented with the head downwards, snatching any small fish or shrimps. Cranchid squid often perform vertical migrations, rising into shallow water to feed at

night, and then sinking into the depths during the day (Clarke, 1962, 1965, Denton, 1973). *Spirula* is similar in habit and morphology, but instead of ammonium ions has an open coiled shell within its body superficially like that of a small ammonite (Bruun, 1943, 1955, Denton & Gilpin-Brown, 1971).

Another coleoid with which ammonites have been compared is the cuttlefish *Sepia*. *Sepia* has an internal shell (unlike *Nautilus*) but the shell nevertheless retains its buoyancy function (Denton & Gilpin Brown, 1961a, 1973). The shell is divided into many small chambers, each of which is bounded by a thin layer of siphuncular tissue (Denton & Gilpin Brown, 1961c). By adjusting the amount and distribution of gas within these chambers the orientation of the animal can be regulated, as well as its absolute density (Denton & Gilpin Brown, 1961b, 1971). Kakabadza & Sharakadza (1993) proposed that ammonites may have been able to regulate the cameral gases and fluids in a comparable way, and in doing so changed the orientation of the shell relative to the sea floor.

Sepia (like most coleoids) ventilates the mantle cavity by contraction of the circular muscles which make up the mantle (Packard & Trueman, 1974). The water is expelled through the siphon, which is a structure analogous to the hyponome of *Nautilus* in function, this action serves both to draw fresh water over the gills and remove waste, and also to provide the thrust needed for rapid swimming (Young, 1959, Packard, 1972, Chamberlain, 1993). Jacobs & Landman (1993) have suggested that ammonites also had circular muscles around the mantle cavity, and could ventilate in a similar way. *Sepia* also has muscular fins along the flanks, these serve are used for slower swimming (Trueman, 1983). Belemnites may have had similar fins (Monks *et al*, 1996) but there is no evidence that ammonites had them.

Finally, it is possible that some heteromorph ammonites may have been benthonic like octopuses. Diener (1912) proposed this first, and the idea has been recently revised by Ebel, who proposes that ammonites may have been negatively buoyant (Ebel, 1983, 1985) and that the body chamber was too long to allow jet propelled swimming after the *Nautilus* model (Ebel, 1992, 1993). Within the model proposed by Ebel, the coiling of the shell is not an adaptation to locomotion, but rather a reflection of the way the shell was folded up as a result of some regulatory process during growth. As Ebel (1992, p. 185) comments, "...it is possible that the shell [shape] was of less importance to the animal than to the taxonomist."

A new idea — the floating gastropod model

Okamoto (1987) suggested that in some heteromorphs the orientation of the shell may be reflected by the morphology of the annular ribs. Except for the planktonic juvenile-A stage

rib obliquity appears to indicate the aperture maintained a regular angle to the sea floor, suggestive of a benthonic lifestyle. Okamoto proposed that although the shell *was* neutrally buoyant, that neutral buoyancy was so the shell could be carried easily by the essentially benthonic animal, and not to raise the animal off the sea floor or to facilitate swimming or vertical migration.

Monks & Young (1998) elaborated this model, and demonstrated that by moving the body within the shell, even ammonites with hook or U-shaped body chambers need not necessarily be oriented with the aperture upwards, but could be oriented with the aperture forwards or toward the sea floor. This would allow the ammonite to crawl about using its arms. Monks & Young interpret the ammonite as occupying a relatively small part of the living chamber compared with *Nautilus*, as such it is able to move freely from the front to the back of the relatively long living chamber. The shell retains a defensive function, but does not need to be streamlined since the ammonite does not swim. Because the ammonite is effectively weightless, the arms need not be particularly muscular, just strong enough to push the animal gently in the direction it wished to travel. It would also be very light, movement over soft or silty substrates would be without the threat of sinking and the mantle cavity and gills could easily be kept clear of the sediment.

Possible Paradigms

From these comparisons, it is possible to formulate four basic cephalopod functional morphologies with which ammonites could be compared: neutrally buoyant *Nautilus*, the cuttlefish which is able to change density and orientation by regulating the fluid and gas within the shell, the octopus, which is negatively buoyant and crawls about on its arms, and finally a sort of floating gastropod-like model. These are summarised below. Animations (MOVIES 1 to 3) are used to demonstrate the relationship between the centre of mass, centre of buoyancy, and the orientation of the ammonite.

The *Nautilus* model. In this model the ammonite shell is taken to be strictly analogous with the shell of *Nautilus* in form and function. The animal fills the living chamber completely, and orientation and buoyancy are effectively static (MOVIE 1). This is the model formalised by Trueman (1941) and is the most widely used, e.g., in the *Treatise on Invertebrate Paleontology* (Arkell *et al*, 1957).

The cuttlefish model. This model is similar to that of the *Nautilus* model, except that the ammonite is capable of moving cameral fluids about within the shell in a manner similar to

that of the modern cuttlefish (MOVIE 2). This model was proposed by Kakabadza & Sharakadza (1993).

The gastropod model. This is the model devised by Ebel (1992) within which the ammonite fills the entire living chamber but the phragmocone itself is not large enough to make the shell neutrally buoyant. As a result, the ammonite cannot swim or float, and instead crawls about on the sea bed. Since the ammonite isn't floating, posture depends not on the shell but on the position at which the body is adopting as it crawls about (FIGURE 4.4).

The floating gastropod model. This model is a combination of the cuttlefish and gastropod models. The shell is neutrally buoyant, and the ammonite swims or crawls about on or near the seafloor. Such a lifestyle was suggested by Okamoto (1987) and I have developed a functional explanation of how this might work in Monks & Young (1998).

Deducing posture and density

A freely floating, completely immersed body (like an ammonite) reaches a stable equilibrium when the centre of mass is vertically below the centre of buoyancy. By locating the centre of buoyancy and the centre of mass, it is possible to infer the vertical axis of a resting ammonite at equilibrium. A swimming ammonite would be subject to additional forces (thrust, from the jet of water, and drag, as the ammonite is propelled through the surrounding sea water). These two forces are not considered here.

The *centre of buoyancy* is the centre of mass of the water displaced by the object, and is effectively the pivot point about which the shell rotates. Since the density of water is uniform, it is a function of the *shape* of the displaced water only. The *centre of mass* is the point through which the weight of the object acts: but since the ammonite is made up of a heterogeneous group of materials of differing density, the centre of mass is a function of the composition as well as of shape.

If a straight line is drawn passing through the centre of mass and the centre of buoyancy, since at equilibrium the centre of mass will lie vertically below the centre of buoyancy, the vertical axis of the shell can be deduced (FIGURE 4.5a). Also, since the centre of buoyancy is dependent on the shape and volume of the water displaced by the ammonite (which is more or less a fixed point) it can be taken to be a *pivot*. If the ammonite is rotated, a force will be developed which will cause the ammonite to rotate back to stable equilibrium. This force is the *restorative force*. Since the ammonite will rotate about the pivot (the centre of buoyancy), the restorative force is directly proportional to the angle between the angle made by the line

passing through the original vertical axis and a line passing through the centre of buoyancy and the centre of mass in the disturbed orientation (FIGURE 4.5b).

However, if the centre of mass moves within the shell, it will cause the ammonite to depart from the stable equilibrium and a restorative force will be developed (FIGURE 4.5c). In this case, since the centre of mass has moved, the ammonite will rotate about the pivot until it acquires a new orientation which positions the centre of mass vertically below the centre of buoyancy (FIGURE 4.5d).

Therefore, if the orientation of the ammonite is to be deduced, then the locations of the centres of mass and buoyancy need to be found. There are two ways of doing this:

(1) **Use a computer to model the ammonite mathematically.** This can be done by using a spreadsheet program such as Microsoft Excel or ClarisWorks. The ammonite is reconstructed as a volume of rotation, and this volume can be divided up into a series consisting of a series of cylindrical elements running along the line of rotation. Each cylinder is made up of concentric rings of different materials (e.g., tissue, water, cameral gases, aragonite or calcite). The volume, and therefore mass, of each of these rings can be calculated. From these data it is possible deduce the displacement and therefore the density of the ammonite. By taking moments for each of these cylinders it is possible to locate the centres of mass and buoyancy. I developed this method for investigating belemnite functional morphology (Monks *et al*, 1996). Although precise, delightfully simple and easy to manipulate, this approach is limited to shapes approximating to cones or cylinders (i.e., baculiticones and turriliticones).

(2) **Physically model the ammonite and investigate the behaviour of the shape empirically.** This is less precise but is useful for shapes that cannot be reduced to simple volumes of rotation. Monks & Young (1998) used this approach when devising the floating snail hypothesis of ammonite functional morphology.

Spreadsheet analysis of ammonite orientation

The great advantage of mathematical models is that the affect of changing one or more parameters can be easily investigated. For example, what happens if the thickness of the shell is increased? What is the maximum loading a certain sized phragmocone could carry? What is the affect of changing the density of the shell material or soft tissues? These sorts of questions can be answered by using this approach, and the optimality (or otherwise) of the shell design investigated. A key question is this: Is the phragmocone large enough to carry an entirely

filled body chamber? If not, then this could be cited as evidence against the *Nautilus* model and in favour of the floating gastropod model.

There are basically three stages. Firstly the centre of buoyancy is located. Then the centre of mass. Finally, the orientation and the density of the ammonite can be deduced. The shell will be oriented with the centre of mass vertically below the centre of buoyancy. Density can be found by calculating the mass of the ammonite and the mass of the water it displaces. The mass of the ammonite divided by the mass of the displaced water gives the density. By analogy with modern cephalopods, we would anticipate the density of the ammonite to be equal to that of sea water, such that the ammonite had neutral buoyancy.

This analysis was performed on approximations of the baculiticonic ammonite *Sciponoceras* and the closely coiled turriliticone *Ostlingoceras*. The values for phragmocone, shell, and tissue density are taken from Okamoto (1988) which are based on published values taken from living *Nautilus*, and the living chambers of both ammonites are considered to be entirely filled with soft tissues. From specimens of *Sciponoceras* in the collections of the BMNH the overall length of the shell is estimated to be 600 mm, of which the body chamber comprises the final 300 mm, with a whorl diameter of 33 mm. The whorl is assumed to be circular and the conch a perfect cone. The specimen of *Ostlingoceras* is taken 60 mm in height, with an apical angle of 23° , where the umbilicus comprise a conical empty space (apical angle = 6°) bounded by the conch. The living chamber accounts for the final whorl, or about 20 mm of the height of the helix.

Stage 1: Locating the centre of buoyancy

(1) A silhouette of the ammonite is drawn on graph paper. The length of the ammonite is becomes the x-axis, and the width the y-axis.

(2) The volume of rotation of this silhouette along the x-axis will generate a solid of the same shape as the original ammonite.

(3) The volume of rotation is divided into a series of cylinders along the x-axis. The volumes of each of these cylinders is calculated.

(4) The volume of each cylinder is multiplied by the density of sea water (approximately 1.025 mg per cubic millimetre).

(5) The sum of all masses of all the cylinders is the mass of the water displaced by the ammonite.

(6) The centre of buoyancy lies at the centre of mass of this displaced water. The distance of each cylinder (taken here from the origin of the x-axis) multiplied by its mass gives the moment of the entire solid. The sum of all these moments divided by the sum of the masses of each cylinder gives the distance of the centre of mass of the displaced water from the origin of the x-axis.

Stage 2: Locating the centre of mass

(1) Each of these rectangles can be subdivided into rectangles consisting of gas, soft tissues, and shell. Water within the mantle cavity is equal in density to the external medium and can be ignored since it is freely communicating with the outside sea water and so is not 'part' of the animal. These are arranged in a series from the x-axis outwards. The phragmocone will consist of gas first and then shell. The mantle cavity will consist of either soft tissues and then shell. Finally, the head and arms will be made of only soft tissues.

(2) Each of these materials has different densities. The density of these tissues is based on Okamoto (1987). Shell = 2.62 mg/mm^3, phragmocone = 0.1048 mg/mm^3, and tissues = 1.067 mg/mm^3. Note: the density of the phragmocone includes the (a density of 0.1 mg/mm^3, and the septa, which occupy 4% of the phragmocone and have a density equal to that of the shell (FIGURE 4.5).

(3) The mass of each volume of rotation is calculated by finding the volume of each region within the volume of rotation, calculating the mass of that region, and then summing the masses for all the regions within the volume of rotation.

(4) The centre of mass is located by dividing the sum of the moments of all of these volumes of rotation by the sum of the masses of the volumes of rotation with respect to an arbitrarily chosen point.

Stage 3: Estimating the orientation and density

(1) The centre of mass will be located vertically below the centre of buoyancy providing the object is freely floating and completely immersed.

(2 The density of the animal will be equal to the total mass of the animal divided by the volume of the water it displaces. This can be found from the spreadsheet by summing the masses of the volumes of rotation and then dividing that by the mass of the water displaced by these volumes of rotation.

(3) This value can be compared with the density of sea water to see whether the animal is negatively, neutrally, or positively buoyant. By changing variables in the spreadsheet (such as the shell thickness) the affect on density can be seen.

Calculation of errors

The procedures for deducing density, centres of mass, and centres of buoyancy are repeated using values ±5% of the values used for the density of the phragmocone, shell and tissues. This gives an indication of the variability in the deduced values from these calculations brought about by a relatively small change in the inputted parameters, and hence the overall reliability of the deduced data.

Results

Baculiticonic and turriliticonic ammonites are most amenable to study in this way since they are essentially orthocones, although formed in different ways, although functionally they are thought to have behaved in similar ways (Klinger, 1980). FIGURE 4.6 summarises the data derived from these spreadsheets: the mass of the ammonites, the displacement of water, the overall density of the ammonites of the two shells, and the relative positions of the centre of buoyancy and centre of mass. The full spreadsheets are presented on the floppy disk as Microsoft Excel version 4 files.

(1) *Sciponoceras* The density of this ammonite, 1.26 mg/mm^3, is 123% of that of seawater, therefore this ammonite would be negatively buoyant as reconstructed here and could not have floated. The centre of mass lies nearer the apex of the shell than the centre of buoyancy. Therefore the orientation of the of this ammonite would be with the aperture downwards.

(2) *Ostlingoceras* The density of this ammonite, 1.18 mg/mm^3, is 115% that of seawater. Like *Sciponoceras*, as reconstructed, this ammonite would not float. The centre of mass lies nearer the apex of the shell than the centre of

buoyancy. Therefore the orientation of the of this ammonite would also be with the aperture downwards.

In summary, it can be stated that as reconstructed here using values for the density of the shell, phragmocone, and soft tissues taken from *Nautilus*, neither *Sciponoceras* nor *Ostlingoceras* would have had sufficient buoyancy to be free-floating as they are generally thought to have done. How do these calculated densities change if the inputted values for the density of each material is changed?

The 5% errors to the densities of the phragmocone, shell material, and soft tissues as described in Okamoto (1987) were calculated, these are listed here in tables (FIGURES 4.7a, b), and graphically(FIGURES 4.8a, b). It appears than small changes in the values used for the density of the phragmocone, shell material, and soft tissues have only a minor affect on overall density. Changes in the density of the phragmocone have hardly any affect (less than 1%) in both cases. The affects of changing the other parameters are summarised below:

(1) *Sciponoceras* A 5% increase or decrease in the density of the shell material produces a 2% increase or decrease in overall density. A 5% increase or decrease in the density of the soft tissues produces a 3% increase or decrease in overall density.

(2) *Ostlingoceras* A 5% increase or decrease in the density of the shell material produces identical changes to those calculated for *Sciponoceras*.

The greatest variations occur where the density of the soft tissues are changed. For *Sciponoceras* the range is from 1.23 to 1.30 mg/mm^3, for *Ostlingoceras*, 1.15 to 1.21 mg/mm^3. While we can estimate the density of the shell using fossil shell material as a guide, and the density of seawater now is presumably similar to the density of seawater during the Cretaceous, the density of the soft tissues cannot be directly known. Ammonite tissues have not been preserved as fossils. The values used here, taken from Okamoto (1987), are based on comparisons with modern *Nautilus* and other living cephalopods. Changing the value of the density of soft tissues, as described above, produces changes in overall density. Nevertheless, the conservative estimates of shell and tissue density used results in ammonites substantially more dense than seawater (from 115 to 123% the density of seawater). It is reasonable to state that ammonites with an anatomy exactly like the ones modelled here could not have been neutrally buoyant, and that the excess density margin is so great that this probably not simply because of an inappropriate estimate of shell material or tissue density.

These preliminary results would seem to indicate that if ammonites were built in a *Nautilus*-like way, with the living chamber filled with relatively dense tissues, then they may not have been neutrally buoyant. Let us assume that ammonite ecology requires that ammonites, like many cephalopods in general, floated. Is it possible to "redesign" these ammonites so that they were neutrally buoyant? If the values of shell, soft tissue, and seawater density remain the same, there are two important ways the reconstruction of the ammonite could be changed. The first is to increase the size of the phragmocone, in affect providing more buoyancy. The shape and size of shell are known from the fossils, so this cannot be done. The second alternative is to reduce the payload, i.e., make the animal within the same sized shell *smaller*:

(1) *Sciponoceras* A 50% decrease in the amount of "payload" in the living chamber reduces the density to 0.86 mg/mm^3. Such an ammonite would easily float, since this value is below the density of seawater.

(2) *Ostlingoceras* A similar reduction in payload results in a similar decrease in overall density. As with *Sciponoceras*, such an ammonite could easily float.

There is no compelling fossil evidence to indicate the size or shape of the soft body parts within the living chamber of ammonites, but most comparisons have been with *Nautilus*, which fills the relatively short body chamber of its shell. The "floating gastropod" model proposed by Monks & Young (1998) supposed that the animal's body was relatively small and occupied only part of the living chamber. This is consistent with the results of the above analysis which suggest that the living chamber might not have been entirely filled with soft tissues. For the next part of the analysis, this hypothesis is applied to shell forms not amenable to spreadsheet analysis, to see what the affect of a partially filled living chamber would be on orientation.

Using Plasticene models

Modelling a cephalopod using volumes of rotation works well where the animal has a single rotational axis of symmetry. Ancylocones, aspinocones, hamiticones and ptychocones lack this property so cannot be described as a radially symmetrical solid. Instead, I have adopted the method used by Monks & Young (1998), who modelled the ammonite in Plasticene. Experiments allow inference of the approximate orientation of the ammonite, but the mass of the ammonite in life and the total density are more difficult to estimate.

In the *Nautilus* model and the cuttlefish model the water displaced is approximately equal to the volume of the phragmocone and the living chamber, since both are filled (the

phragmocone with gas and cameral fluids, the living chamber with the animal). In contrast, the floating gastropod model of Monks & Young (1998) reduces the size of the animal such that most of the living chamber is empty. In effect, the water is displaced largely by the phragmocone, and the displacement of the animal is a small enough proportion of the entire displacement of the ammonite to disregard.

This procedure can be divided into three stages:

Stage 1: Locating the centre of buoyancy

The centre of buoyancy is the centre of mass of the displaced water. Since this is a function of shape alone, this can be estimated by modelling the part of the ammonite which displaces water and identifying its centre of mass with a material of uniform density, such as Plasticene. The Plasticene models (FIGURE 4.9a) are suspended from a series arbitrary points by a light thread and allowed to come to rest. A vertical line was drawn from the point of suspension downwards for each different suspension point. Where the lines cross is the centre of mass of the Plasticene shape, and therefore the centre of buoyancy of the ammonite (FIGURE 4.9b).

Stage 2: Estimating the centre of mass

The centre of mass is more difficult to deduce since we know nothing about the density or mass distribution of the ammonite soft body parts, or how much fluid was within the shell. While I agree with Trueman's (1941) estimation that the body was the most massive part of the ammonite, I believe that the body need not have occupied the entire body chamber, as has been suggested by Monks & Young (1998). Therefore I estimate the soft tissues of the animal to have occupied only a portion of the entire body chamber. The spreadsheet analysis described above suggests that an ammonite occupying fifty percent of the living chamber would be a sufficiently small payload to be buoyed by the phragmocone, so let us assume that the ammonite animal occupied about one half of the volume of the living chamber. The positioning of the body would now affect the position of the centre of mass, since the body could potentially be near the front of the aperture (i.e., with the head sticking out of the aperture), or near the final septum (i.e., with the head and arms withdrawn and the animal retracted to the back of the shell). The rest of the living chamber would be filled with seawater, freely communicating with the outside seawater, except for the mantle lining the shell and the retractor muscles (FIGURE 4.10).

Stage 3: Deducing the orientation of the ammonite

As described previously, the ammonite would orient itself with the centre of mass vertically beneath the centre of buoyancy. Therefore any movement of the centre of mass (as predicted by the floating gastropod model, and likely if the animal filled only a fraction of the living chamber) results in a change in orientation because of the change in the position of the centre of mass relative to the pivot point (the centre of buoyancy).

Results

Using a combination of mathematical (spreadsheet) and physical modelling, six different shapes of heteromorph ammonites were examined:

(1) Aspinocone (e.g., *Hamitella gardneri* FIGURE 4.11a)
(2) Ancylocone (e.g., *Anisoceras armatum* FIGURE 4.11b)
(3) Hamiticone (e.g. *Hamitella maximus* FIGURE 4.11c)
(4) Baculiticone (e.g., *Lechites gaudini* FIGURE 4.11d)
(5) Low, open turriliticone (e.g., *Hamitella* sp. juvenile FIGURE 4.11e)
(7) High, closed turriliticone (e.g., *Ostlingoceras puzosianum* FIGURE 4.11f)
(6) Ptychocone (e.g., *Ptychoceras adpressum* FIGURE 4.11g)

The centres of mass and buoyancy are plotted on diagrams of these shells using the floating gastropod model proposed here. A new parameter arises from applying the floating gastropod model to ammonite orientation, the "rotational angle". This is the angle formed at the intersection of the line passing through the centre of buoyancy and the centre of mass with the head out of the shell, and the line passing through the centre of buoyancy and the centre of mass with the head and body pulled back. Since the first line is the vertical axis of the ammonite with head emergent, and the second line the vertical axis when the animal is withdrawn, the angle describes the rotation of the shell between these two conditions. The rotational angles of the seven ammonites examined here are summarised in FIGURE 4.12.

Low Rotational Angles: Baculiticones, Ptychocones, and Turriliticones

Baculiticones, ptychocones, and turriliticones have rotational angles close to zero. The centre of mass when the head is extended is more or less vertically beneath the centre of mass when

the head is withdrawn. Both these points will lie beneath the centre of buoyancy. Thus, whatever the position of the body, these ammonites were oriented with the aperture more or less downwards. In baculiticones, this is because they are simple cones, and the centres of mass and buoyancy are all located along the long axis of the shell. Although ptychocones are similar to hamiticones, they differ in being highly involute (where hamiticones are open): this results in a shape more like an orthocone, but formed from three straight shafts pressed into one another. Functionally, it behaves more like an orthocone than an hamiticone, since moving the mass in the living chamber tends to raise or lower the centre of mass along a straight line roughly vertically beneath the centre of buoyancy. So while the proximity of the centre of mass to the centre of buoyancy may change, the angle of the line connecting the two points remains approximately constant. Turriliticones are convergent with baculiticones in producing an effectively conical shell, but do so by helically coiling around a single long axis.

High Rotational Angles: Aspinocones, Ancylocones, and Hamiticones

The aspinocones, ancylocones, and hamiticones have rotational angles from 30° to 100°. The centre of mass when the head is extended is not located vertically beneath the centre of mass with the head withdrawn. Therefore when the body moves between the aperture and the back of the shell, it will cause the shell to rotate. These ammonites can orient the aperture forwards and downwards when the head and arms are positioned toward the front of the aperture. Hamiticones have the greatest rotational angles. In these morphologies the living chamber (and sometimes the later part of the phragmocone) is hooked shaped, rather than simply carrying on the spiral of the juvenile-A shell. In aspinocones only the living chamber departs from the juvenile spiral, and then only slightly. The centre of buoyancy is within the spiral part of the shell, and the centre of mass moves within the final hook (FIGURE 4.11a). Ancylocones and hamiticones depart from spiral coiling earlier, giving rise to a deeper hook shape formed by two or more parallel shafts. The centre of buoyancy is located on the straight part of the phragmocone (FIGURES 4.11b, 4.11c), and the centre of mass moves along the straight final living chamber which runs parallel to the straight part of the phragmocone. This results in a wider angle of rotation.

Tilters and Non-Tilters: A new morphological classification?

These shells can thus be classified into two groups: tilters and non-tilters, depending on whether the rotational angle is sufficiently large to allow the shell to rotate when the body moves between the aperture and the back of the shell. The tilting shells are typified by the

ancylocones and especially the hamiticones, which possess large angles of rotation. This could allow the shell aperture to be oriented toward the substrate irrespective of the U-shaped body chamber simply by moving the body toward the aperture. Aspinocones have a smaller, more limited ability to rotate. Non-tilters, which include the baculiticones, turriliticones, and ptychocones cannot change orientation in this way, since the vertical line through the centre of mass and buoyancy is fixed. The centre of mass may move closer to or further from the centre of buoyancy, but its angle to that point is constant. These shells would be oriented with the aperture downwards. The application of this distinction between tilting and non-tilting morphologies is considered in the next chapter, and compared with the distribution and inferred ecology of the heteromorph ammonites.

CHAPTER FIVE: HETEROMORPH AMMONITE ECOLOGY

Summary

The heteromorph ammonites are very widely distributed throughout the European (hoplitinid) and Tethyan provinces although they seem to have been absent from the Arctic (gastroplitid) province. This indicates that heteromorph ammonites had an effective mode of distribution, possibly by actively swimming or drifting as adults, or more likely through a planktonic juvenile stage. Some species of ammonite, such as *Lechites gaudini*, can be found on every continent.

Although heteromorph ammonites of both the tilting and non-tilting morphotypes are found together in relatively deep water sediments, non-tilting forms are apparently absent from shallow water sediments. This indicates that the benthonic tilting ammonites were less sensitive to water depth. A brief review of published observations of heteromorph ammonite distribution seems to agree with the hypothesis that the non-tilting forms were planktonic animals and the tilting forms were benthonic or demersal.

Albian palaeogeography

The Albian Stage lasted from approximately 113 to 97 million years ago. FIGURE 5.1a is a palaeocontinental reconstruction of the lower Upper Albian around 100 million years ago, based on Barron (1987). Key events during this time are the opening of the Atlantic Ocean, the drifting of the African and Indian plates toward Eurasia, and the persistence of the connection between the Antarctic and Australasian plates. Through that time there was an overall increase in sea level (Haq *et al* 1987, Haq 1991), and this is reflected in the widespread occurrence of marine sediments of Albian age which have been recorded from localities around on every continent (Owen 1971a, Barron *et al* 1981, Frakes *et al* 1987, Kelly & Moncrieff 1992):

Eurasia

There appear to have been three broad marine connections across mainland Europe (FIGURE 5.1b). A small channel ran from southern England through northern Spain down to the Balearics (Wiedmann 1962, 1962a). A second much larger channel also begins in southern England, but instead occupied a band through northern and south-eastern France, across Austria and Switzerland and into the Balkans. Finally, a third channel occupied a broad area encompassing the North Sea, Denmark, parts of northern and central Germany, and central Poland (Owen 1979). These last two channels united at the Balkans, and spread out over much of the Caucasus, western Russia and down past the Caspian and into Iran (Immel & Seyed-Emami 1985, Seyed-Emami & Immel 1995). A separate region of Albian marine sediments is recorded from northern Russia, part of a transgression which opened up a connection between this west Siberian basin and the Arctic Sea, the ammonites and inoceramid bivalves recorded here are comparable with those of northern Canada and the gastropilitinid province in general (Owen 1973, Jeletzky 1980, Vakhrameev 1987). Albian strata in China are mainly non-marine and so lack ammonites, but heteromorph ammonites such as *Mariella* have been recorded from Albian sediments in Japan (Matsumoto 1963, Chen Pei-Ji 1987).

India and Madagascar

Marine sediments of Albian age have been recorded from few places in the Indian subcontinent, primarily from the west and the east (Spath 1930, Krishna 1980). Madagascar was still joined to the Indian plate during the Albian. In Madagascar the Albian sediments are

restricted to the westernmost edge of the island (Collignon 1963). Overall, the Indian-Madagscan plate was dry land during the Albian (Barron *et al* 1981).

Africa

Like India and Madagascar, most of Africa was dry land during the Albian, and marine sediments are relatively scarce. Ammonites have been recovered from sediments of Albian age in Angola, Algeria, Egypt, Mozambique, South Africa, and Tunisia (Spath 1921, 1922, 1925a, Haas 1942, Collignon 1979, Förster 1975, Klinger & Kennedy 1978). Anoxic conditions existed in the proto-South Atlantic running between the South American and African plates (Reyment *et al* 1987).

Australasia and Antarctica

Australasia, New Zealand, and Antarctica were joined together during the Albian. For the most part they were both dry land. Marine sediments are present from certain localities, indicating that a major seaway existed across Australia, running from northern Queensland down through into north-western Victoria and northern and central South Australia (Frakes *et al* 1987. Ammonites and other marine invertebrates recovered from Alexander Island indicate that this island along the edges of the Antarctic continent were at least periodically submerged (Kelly & Moncrieff 1992).

South America

Marine rocks of Albian age are largely confined to the southern part of the South American continent, which was experiencing a major phase of tectonic uplift (Riccardi 1987, 1988). Nevertheless, ammonites have been recovered from Venezuela, Peru, and Argentina, largely comparable with the Tethyan ammonites found in Eurasia and Madagascar (Leanza 1970, Macsotay 1971, Owen 1971a).

Central and North America

The Central and North American Albian marine sediments appear to have been deposited in three, largely separate basins. To the north west, along the western Canadian coastline and into Alaska lay part of the circum-Pacific basin which also included Japan. Ammonites

collected from the Albian of Canada and of Japan are similar (Jeletzky 1977). A second basin, covering central and northern Canada and the northernmost parts of the USA, forms part of the Arctic basin which also includes the northernmost fringes of Europe and Siberia (Owen 1979, Jeletzky 1980). There were no connections between these two basins as far as is known (Barron *et al* 1981), although there may have been sporadic faunal exchanges between the Arctic and the European marine realms (Owen 1984). A third basin occupied the southern and south-western part of the USA and the northern part of Mexico, this was the Western Interior basin (Reeside 1927, Jeletzky 1968, Kauffman 1977). This area of marine sediments opened into the southern part of the proto-North Atlantic.

Albian heteromorph ammonite palaeobiogeography

Albian ammonite faunas can be divided into distinctive faunal provinces. These provinces represent assemblages of ammonites which were to a degree isolated from one another. The overall pattern is of three distinct ammonite assemblages: an Arctic province covering the central and eastern Canada and part of northern North America, a north-west European province dominated by hoplitinids, and broadly Tethyan provinces everywhere else. Compared with the homomorph ammonites (where there is a distinction between the hoplitinids on one hand and the brancoceratids and mortonicerids on the other), the heteromorphs appear to have been distributed freely throughout the European and Tethyan provinces. There were, however, some centres of species level endemism such as the Late Albian Western Interior sea of the United States.

As far as north-west Europe is concerned, ammonites from Lower Albian sediments are predominantly forms associated with the European province, such as *Leymeriella*, *Sonneratia*, and *Douvilleiceras*. Middle and Upper Albian faunas remain European in overall composition, including various hoplitinids, but there are also some Tethyan ammonites. These include *Lyelliceras* and *Brancoceras* in Middle Albian and *Mortoniceras* and *Hysteroceras* in Upper Albian sediments. An ammonite species from the Arctic province ammonite has been recorded from the early Upper Albian at Folkestone, a single specimen of *Pseudogastroplites cantianus* (Owen, 1984). Below is a summary of all the major ammonite provinces of the Albian:

European ammonite provinces

Arctic (gastroplitid) province

This fauna has been studied in most detail in northern and eastern Canada but stretches across Greenland and the entire northern part of Eurasia, including Siberia (Jeletzky 1968, 1980). A characteristic genus of ammonites from the Arctic faunal province is *Gastropilites*. As noted above, ammonites from the Arctic province seem to have made only one incursion into the European province during the early Upper Albian, evidenced by a single specimen of *Pseudogastroplites cantianus* having been recorded from the lower *Diploceras cristatum* Subzone of Folkestone, England (Owen 1984). No ancyloceratacean or turrilitacean heteromorph ammonites have been recorded from the Arctic province during the Albian (although *Scaphites* and *Baculites* do occur in the later stages of the Cretaceous).

European (hoplitinid) province

The European province is characterised by a large number of endemic hoplitinid ammonites including the genera *Hoplites*, *Euhoplites*, *Anahoplites* and *Dimorphoplites*. This faunal province includes the entire Anglo-Paris basin, as well as much of central and northern Europe (including northern France, Germany, and Poland) and the western part of the Russia and around the Caspian Sea (Owen 1979). The heteromorph ammonite faunas are diverse here. Hamitids and anisoceratids occur throughout the Albian and are widely recorded, while turrilitids and ptychoceratids tend to be rarer. Although in general the species recorded in the European province may also be found elsewhere, such as *Hamites* and *Mariella*, there are a few endemic monospecific genera, such as *Scaphamites passendorferi*, *Psilohamites bouchardianus* and *Tuberolechites regifex*. These may reflect some degree of isolation at certain times.

Tethyan (brancoceratid) province

South of the European province, running from Spain and southern France as far east as Iran and Pakistan comprises, and south to Madagascar and Angola, and the Tethyan faunal province (Owen 1971a). The most characteristic ammonites of the Tethyan province are Lyelliceratid and Mojsisovicsiid ammonites. Characteristic genera of the Tethyan province include *Lyelliceras*, *Oxytropidoceras*, *Mortoniceras* and *Brancoceras*. There are some genera of heteromorph ammonite which are common throughout the Albian in the Tethyan province but are abundant only occasionally in the European province. These include the Middle Albian turrilitids and ptychoceratids such as *Pseudhelicoceras*, *Proturrilitoides*, *Turrilitoides*, *Worthoceras*, and *Ptychoceras*. On the other hand, species of *Hamites*, *Anisoceras* and *Protanisoceras* are common to both provinces, while *Metahamites*, *Rossalites*, and

Hemiptychcoceras are more commonly recorded from Tethyan faunas and occur hardly at all in European ones.

Non-European Tethyan ammonite provinces

North Pacific Province

The Albian ammonite faunas of the western parts of Canada and of Japan contrast with those of northern and western Canada in resembling the Tethyan fauna. Homomorph ammonites such as *Cleoniceras* and *Mortoniceras* are present but hoplitinids are lacking. There are a number of heteromorph genera in common between the North Pacific and Tethyan provinces, such as *Ptychoceras* and *Pseudhelicoceras*, and even some species in common with the Western Interior province of the Americas, including *Worthoceras worthense* and *Mariella cantabrigiensis* (Jeletzky 1977). Consequently, despite the proximity of this province to the Arctic Gastropilitinid province, it is clearly more akin to the Tethyan.

Australasian and Antarctic provinces

The Australian and Antarctic ammonite faunas are very close to that of the Tethyan, but do include rather more anycloceratacean than turrilitacean heteromorph ammonites such as *Myloceras* and *Labeceras* than are found in the European province. Overall the ammonite faunas are similar to those of the Tethyan province. The Australian and New Zealand heteromorph fauna does include some turrilitacean ammonites in common with the European fauna of north-west Europe, such as *Hamitella annulatum* and *Hamites virgulatus*, while the Antarctic fauna includes the baculitid *Lechites gaudini* (Henderson 1973, 1990, Kelly & Moncrieff 1992).

Western Interior province

This ammonite fauna is best known from Texas and Utah but also covers parts of California and the northern part of Mexico. The ammonite fauna appears to be closely related to that of the Tethyan realm, sharing many genera such as *Mortoniceras* and *Schloenbachia* (Emerson *et al* 1994). There are many heteromorph genera in common between the Texan and the European and Tethyan provinces, such as *Hamites*, *Idiohamites*, *Worthoceras*, *Mariella*, and *Anisoceras*, and even a number of shared species, such as *Anisoceras armatum*, *Hamitella*

intermedius and *Hamites nokonsis*. However, there are some endemic species, such as *Lechites comanchensis* and *Mariella worthensis* (Clark 1965).

South American province

This covers a number of faunas recorded from Peru, Patagonia, Venezuela and elsewhere, with homomorph ammonite faunas that compare well with those of the Tethyan province. The ammonites recorded include *Lyelliceras* and *Brancoceras*. Relatively few heteromorphs have been recorded from this province, but they broadly resemble those of the Tethyan province, including species of *Rossalites*, *Hemiptychoceras*, and *Hamites* (Macsotay 1971, Owen 1971a, Riccardi 1988).

Albian marine environments

Sea-level

The Albian is marked by an overall progressive rise in sea-level. There are two major transgressive episodes which are important to this thesis. The first marks the boundary between the Aptian and the Albian, during the Early Cretaceous the connection between the North Sea and Atlantic was only gradually opening, and at times the Channel was relatively shallow. The second event is the start of the Late Cretaceous transgression which began in the Albian, successively giving rise to the deeper water Upper Greensand and Chalk (Zeigler 1982, Haq 1984, Rawson 1992).

During the Late Aptian and the Early Albian marine sands indicate shallow connections between the North Sea, the Atlantic and the deeper sea over southern France. By the Late Albian deeper water marine clay facies covered eastern and south-eastern England which represent a deep water channel stretching to the south and east, while the shallow sand facies are more restricted to western England (FIGURE 5.2a). Owen (1974, 1992) has described the evolution of the Anglo-Basin. Early Albian sediments indicate a continuation of the Lower Greensand facies from the Aptian, and consist of shallow water sands and clays with evidence for periodic storm erosion. On the basis of this evidence, a depth of less than 100m has been estimated for the Lower Greensand seas during the Early Albian (Owen, 1992). The ammonite fauna of the Lower Greensand is relatively restricted, lacking the Tethyan Phylloceratina and Lytoceratina, although there were repeated incursions of other Tethyan Ammonitina. About four-fifths of the recorded species are regularly coiled Ammonitina, and

the remaining fifth are ancyloceratacean heteromorphs. Closely related species can be found in the Tethyan province, indicating that the there were connections between the Anglo-Paris Basin and the southern European seas (Casey, 1960).

In the Anglo-Paris basin, the transition from shallow water sands and clays to deeper water clays indicate the boundary between the Lower and Middle Albian. (Casey 1955, Owen 1971a, Smart 1997), although the transition from Lower Greensand to Gault Clay facies took place at different times in different places, being dependent on the geomorphology of the location (Casey 1950, 1951, 1954, Owen 1958, 1960). In southern England, relatively few ammonites (heteromorphs or homomorphs) are found in the Gault Clays earlier than the Middle Albian, although deeper water clay facies similar to the Gault Clay existed earlier in southern France (such as the Vocontian Basin) and northern Spain, where heteromorph ammonites appeared earlier than they do in the Anglo-Paris basin (Wiedmann 1962, Bréhéret *et al* 1986).

The Late Albian was a period of relatively constant, rapid deposition indicating an increase in sea depth across southern and eastern England (FIGURE 5.2b). Uplift of the London Platform during the *Diploceras cristatum* subzone raised a section of seafloor sufficiently for a series of winnowing events to occur and give rise to phosphatic beds at intervals through the *Diploceras cristatum*, *Hysteroceras orbignyi*, and especially the *Hysteroceras varicosum* Subzones (Owen, 1971b, 1992). A period of erosion and subsequent reworking of *Stoliczkaia dispar* sediments during the Lower Cenomanian incorporated many Late Albian fossils in the Lower Cenomanian "Cambridge Greensand" of Cambridgeshire (Cooper & Kennedy 1977).

Price (1977) compared the relative abundance of benthonic and planktonic foraminifera (FIGURE 5.3) of the Anglo-Paris basin through the Middle and Upper Albian. From this it can be seen that while the trend is from a relatively small proportion of planktonic foraminifera to faunas almost exclusively composed of them, there are periods of low abundance of planktonic foraminifera during the base of the *Hoplites dentatus* Zone, at the top of the *Euhoplies loricatus* Zone, and during the middle *Mortoniceras inflatum* Zone. This could be read as implying that while a gradual increase in water depth occurred through the Albian, there were reversals. At Folkestone, for example, evidence of occasional breaks in sediment deposition, condensation, and reworking of older fossils into younger beds comes from series of phosphatic nodule beds, as noted above, the nearby tectonic activity may be responsible for some of these events (Owen 1971a).

Absolute depth of the Gault Clay at Folkestone is controversial. Estimates for the depth at Folkestone during the Middle Albian (*Hoplites spathi* Subzone) range from 30 metres to between 100 and 200 metres (Akpan, Farrow and Morris, 1982; Knight, 1994). Rosen (1977)

compared Upper Albian coral faunas at Folkestone and Haldon (East Devon), and concluded that the Haldon sediments represent a shallow bay (less than 50 metres). Heteromorph ammonites are absent from Haldon, but are common in sediments of the same age at Folkestone, which Rosen suggested were deposited in water of about 90 to 250 metres.

Temperature

Oxygen isotope analysis can be used to estimate palaeotemperatures, since the ratio of ^{18}O to ^{16}O incorporated into calcium carbonates and phosphates or calcium phosphate is temperature dependent. Studies performed by Douglas & Woodruff (1981, using calcium carbonate planktonic foraminifera tests and coccoliths), and Kolodny & Raab (1988, using calcium phosphatic fish bones, shark teeth) have indicated that the Cretaceous in general had a warm climate, building up to a peak during the Cenomanian and then declining toward the Maastrichtian. Consequently, the Albian can be interpreted as having been a period of steadily warming global temperature. Rosen (1977) has studied the Late Albian coral faunas at Folkestone, and suggested a water temperature of at least 17°C. Hudson & Anderson (1989) estimated a range of sea temperatures for north-west Europe during the latest Albian of 12-25°C (median = 18.5°C) using aragonitic macrofossils, and from 10-22°C (median = 16°C) using calcitic macrofossils, early Albian sea temperatures being 2-3°C lower. These temperatures are signicantly warmer than the present day North Sea or English Channel, and suggest a climate much more tropical in nature. The slight differences in the temperature ranges deduced from aragonitic and calcitic fossils reflect the different diagenetic pathways of aragonite and calcite.

Heteromorph ammonite ecology

If the abundance of planktonic foraminifera recorded by Price (1977) are taken to imply relative water depth, is there any pattern to the distribution of tilting and non-tilting heteromorph ammonites? FIGURE 5.4 plots a relative depth curve against a stratigraphical axis, and the occurrences of tilting and non-tilting genera are mapped against this. The Lower Albian is excluded since the overall diversity of heteromorph ammonites is low, and moreover the non-tilting forms are absent from England at this time. It can be seen that tilting heteromorph ammonites exist throughout the Middle and Upper Albian. In contrast, the non-tilting ammonites are more-or-less limited to deep water phases.

There are other pieces of evidence that support the idea that the division of morphologies into tilters and non-tilters reflects the division of heteromorph ammonite lifestyles into benthonic and planktonic.

(1) **Orientation of the shell.** Aspinocones, ancylocones, and hamiticones would be oriented with the aperture forwards and down when the animal was positioned near the aperture. This would be very convenient for gathering food as well as using its arms to crawl about like a modern octopus. The head down orientation of the baculiticones, turriliticones and ptychocones parallels a similar orientation seen in mesopelagic planktonic cephalopods such as *Spirula* and *Cranchia*. Their buoyancy devices — such as a gas filled shell or ammonium rich tissues — are located toward the posterior (Bruun, 1943, Denton, 1973). The arms and tentacles trail downwards to snare prey, which appear to be mostly pelagic crustaceans (Ballantine *et al*, 1981).

(2) **Orientation of the exhalent current.** The exhalent currents of baculiticones, turriliticones and ptychocones was supposed by Klinger (1980) to be more or less aligned with the long axis of the animal. This is broadly supported by this study. Although the exhalent siphons are not exactly aligned, the siphons of modern cephalopods are flexible and it is likely the siphons of ammonites were too, and so could be adjusted as required. This is the most efficient condition for swimming, if the animals were capable of doing so. In contrast, the exhalent currents of aspinocones, ancylocones, and hamiticones are not so aligned, and swimming would have been comparatively inefficient (FIGURE 5.5).

(3) **Streamlining of the shell.** Baculiticones, turriliticones and ptychocones are streamlined along the vertical axis of the shell, along which they would most likely have moved. The shell is also closed, reducing drag, so movement would have been efficient compared with the open, unstreamlined shells of the aspinocones, ancylocones, and hamiticones. Swimming would have been limited to vertical migrations, perhaps comparable with modern *Spirula* and midwater squid like *Cranchia*.

(4) **Annular ribbing.** Since ammonites could not seal the aperture with an operculum or hood, they must have relied on the mechanical strength of the shell to deter a predator. By analogy with gastropods and bivalves, the development of ribs, constrictions and spines could be seen as ways of enhancing the defensive potential of the shell (Vermeij, 1987). These ribs are fully developed in the tilting morphotypes. The non-tilting forms tend to have reduced ribbing (most Turrilitidae and Baculitidae) or have lost the ribs totally (some Ptychoceratidae). Annular ribs are

primarily useful for deterring peeling predators, which tend to be benthonic, and are usually seen on benthic animals like snails and clams (Vermeij, 1993). Spines are useful against predators that crush the entire shell or attempt to swallow the shell whole, and can be seen in benthic (e.g., sea-urchins and the cemented pecten *Spondylus*), nektonic (e.g., the porcupine fish *Diodon*), and planktonic animals (e.g., many larval fish and crustacea). Spines are found on non-tilting as well as tilting morphotypes.

(5) **Evidence of predation by benthic predators.** Evidence that at least some heteromorph ammonites were predated on by benthic crustaceans may come from a number of *Hamitella* specimens collected from Folkestone and in the Natural History Museum collections. (FIGURE 5.6 & 5.7). This form of damage is comparable to that classified by Hengsbach (1996) as *forma verticata* and one of the commonest pathologies, found on a wide variety of ammonites (Keupp, 1976). The ribs and shell have been peeled away in a narrow band, and subsequently repaired by the mantle causing the characteristic backward bending of the ribs and growth lines. These specimens can be compared to gastropod snail shells that have been peeled experimentally (FIGURE 5.8), and are different to those of other forms of predation or attack (Vermeij, 1993). Such attacks are performed by certain modern crustaceans which peel away the shell to expose the soft body of the snail. Since the specimens show repair as well, we can be sure that the ammonite was alive when the shell was attacked, and the damage is not a post-mortem effect. *Post-mortem* damage might be expected if the dead ammonite was eaten by some scavenger, or the shell was used by a hermit crab. During the Albian, there were benthic crustaceans that could have caused such damage, such as *Dianlax* which has been recorded from the Gault Clay and Cambridge Greensand (FIGURE 5.9, Wright & Collins, 1972).

(6) **Shell rotation.** Movement of the animal from the front of the living chamber to the back changes the orientation of tilting morphotypes. This raises the aperture, the weakest part of the shell, clear of the sea floor and perhaps make it more difficult for predators to handle.

(7) ***In situ* preservation as benthos.** There are examples where such ammonites seem to have been preserved as part of the benthos, e.g., a school of *Polyptychoceras* (an hamiticonic ammonite) preserved within the shell of the much larger homomorphic ammonites *Eupachydiscus* (Matsumoto & Nihongi, 1979). The *Polyptychoceras* are arranged in such a way as suggests rapid burial with none of the damage to these fragile shells associated with transport. As such, this implies the *Polyptychoceras*

swam into the empty *Eupachydiscus* shell, the authors suggests they were nesting in way comparable to modern octopuses in caves. Hamiticones are tilting ammonites.

(8) **Absence of tilters during bottom water anoxia events.** Batt (1989) and Westermann (1996) have commented on the general disappearance of *Scaphites* and *Hamites* from sediments during periods of bottom water anoxia. These ammonites occur in the preceding and succeeding normal marine conditions. In contrast the non-tilting Turrilitids and baculitids occur throughout, apparently unbothered by bottom water anoxia. Westermann even suggests that *Baculites* may have been able to tolerate anoxic conditions: this is unlikely, as all extant cephalopods are extremely aerobic organisms. Owen (pers. comm.) has observed that Albian heteromorph ammonites as well as benthic molluscs are absent from probably dysaerobic or anoxic sediments at Selbourne (Owen, 1963), where the hoplitinid ammonites, which were presumably upper water nekton, are well developed.

(9) **Facies association of tilting morphotypes.** Aspinocones, ancylocones, and hamiticones tend to be associated with clay or marl facies rather than sandy ones, which suggests that these ammonites were substrate dependent (or at least choosy), and tend to be scarce or absent from deep water and oceanic facies (Marcinowski & Wiedmann, 1990, Westermann, 1996).

(10) **Facies association of non-tilting morphotypes.** Baculiticones, turriliticones and ptychocones are more commonly associated with deep water, either the distal part of the shelf, the slope, or the open ocean. Helical forms are especially well known for their broad distribution and occurrence in a wide range of lithologies (Kennedy & Cobban, 1976), and a similar pattern is known for baculitids (Matsumoto & Obata, 1963).

(11) **Global distribution of tilting and non-tilting morphotypes.** Both morphotypes are characterised by a very wide distribution at species level (as described in the systematic part of this thesis). If aspinocones, ancylocones, and hamiticones were poor swimmers and most likely benthic crawlers, then their distributive phase must have been either as planktonic eggs or juveniles. While ammonites eggs are virtually unknown, the larval stages of both tilters and non-tilters seem to have been planktonic and occur in a wide variety of facies (Marcinowski, 1974, Kennedy & Cobban, 1976, Marcinowski, 1980). In this light, then the small ptychocones can be viewed as progenetic ammonites, and the baculiticones and turriliticones as neotenic ammonites. These forms extended the juvenile planktonic habit into maturity, either

by retaining small size (ptychocones) or slowing or arresting development (baculiticones and turriliticones).

(12) **Utility of helical coiling.** Helicosity is exhibited by many juvenile heteromorphs as well as adult Turrilitidae. The advantages of being helical are uncertain, but Rigby & Rickards (1989) and Rigby (1992) have suggested that rotation was common among vertically migrating planktonic graptolite colonies. Rotation allowed the colonies to sweep through more water than they would otherwise have done, since the colony would function as a kind of screw. Consequently they would have been able to gather more food. By analogy, helical heteromorph ammonites would have rotated while swimming up or down, and could have swept their tentacles through the water in a similar fashion.

(13) **Adaptations to deep water.** The complex sutures of helically coiled ammonites in general may indicate an ability to live in deep water (Batt, 1991). Most of the Turrilitidae have vertically displaced siphuncles (FIGURE 5.10, Klinger, 1980). This has been interpreted as an adaptation for decoupling the cameral fluids within each chamber from the siphuncle. In the modern cephalopods this appears to increase the efficiency of cameral emptying at depth, and may imply that these ammonite were capable of vertical migrations from deep water into shallow in a manner similar to *Nautilus* or *Spirula* (Ward, 1979). Baculiticones and ptychocones have siphuncles which run vertically (rather than spirally) down the shell, so vertical displacement of the siphuncle is not possible. Functionally, such a siphuncle is effectively decoupled anyway since only a small part of the it would be in contact with fluid (FIGURE 5.11).

CHAPTER SIX: HETEROMORPH AMMONITE EVOLUTION

Summary

Heteromorph ammonites are inferred to have passed through a five stage life cycle: egg, larva, juvenile-A, juvenile-B, and maturity. By comparing the phylogeny deduced from the cladistic analysis with the ontogeny and ecology of the individual species, it is possible to devise a likely evolutionary scenario accounting for the diversification of the heteromorph ammonites through the Albian. Heterochronic processes were clearly important, and both the Baculitidae and Turrilitidae can be viewed as paedomorphic derivatives of the Hamitidae. In both cases they retain characteristics of the juvenile morphologies of typical Hamitidae, and appear to have retained the juvenile habit within the plankton.

It is therefore proposed to place the Albian heteromorph ammonites into two ecological groups: meroplankton and holoplankton. Meroplanktonic forms include the Anisoceratidae, Hamitidae, and Scaphitidae, which passed through a planktonic juvenile stage but eventually settled on or near the sea floor when mature. In contrast, the holoplanktonic forms, the Baculitidae and Turrilitidae, were planktonic for their entire lives, and are derived (through paedomorphosis) from the planktonic stages of their ancestors. They most probably lived in moderately deep water and may have performed vertical migrations comparable to modern mesopelagic squid.

The Baculitidae were holoplanktonic derivatives of the Hamitidae. Their immediate ancestors had simplified their coiling mode from ancyloconic to aspinoconic. These hamitids probably retained the planktonic or slow swimming lifestyle of the crioconic juveniles of more typical hamitids. Baculiticones were also crioconic, but briefly, the remainder of the shell consisting of a single straight shaft.

The Ancyloceratidae are meroplanktonic derivatives of the Hamitidae, but are predominantly ancyloconic. They were largely benthonic in habit. Although spines appeared among the juveniles of the primitive species, the more derived species are tuberculate throughout.

Within the meroplanktonic Hamitidae there are three general body plans: aspinocones, ancylocones, and hamiticones. These modes of shell coiling allowed the animal to orient the aperture toward the sea floor so were well adapted to life on the sea floor. A helical juvenile

phase is commonly exhibited by hamiticones and allows the three straight shafts to be closely packed without interference from the early crioconic part of the shell. One species, *Hamites tenuis*, achieved the same result not by helical coiling but by the second and third shafts lying in plane slightly angled to that of the earlier part of the shell.

The Turrilitidae are holoplanktonic and maintain the juvenile mode of coiling of their hamitid ancestors throughout ontogeny. Tubercles also appear in this group, but independently of those in the Ancyloceratidae.

The Scaphitidae show convergence with homomorphic ammonites by reverting to regular and moderately involute spiral coiling together with closure of the umbilicus. Tubercles develop in this family as raised regions where ribs bifurcate.

Life cycles and life styles

The evidence summarised in Chapters Four and Five can be used to revise our understanding of heteromorph ammonite ecology. Most importantly, even if tilting heteromorphs inhabited the plankton as juveniles, as adults they lived on or near the sea floor, and at least three families of non-tilting heteromorph ammonites were adapted to life in the midwater plankton.

(1) **Egg stage.** Very little is known about ammonite egg biology. By analogy with *Nautilus*, the nepionic constriction is taken to indicate the point at which the ammonite hatched, so can be used to infer the approximate size of the egg itself (Tanabe *et al*, 1980, Lebrun, 1996). The Late Cretaceous heteromorph *Scaphites whitfieldi* for example reached a diameter of 0.7 mm at hatching (Landmann *et al*, 1996), and a specimen in the NHM of *Hamites tenuis* has an ammonitella measuring about 1 mm in diameter BMNH 39768, Spath, 1941). Ammonite hatchlings are comparable in size with the hatchlings of species which produce large numbers of planktonic eggs, primarily the oceanic squid such as *Dosidicus*. Species such as the cuttlefish *Sepia* and the coastal squid *Loligo*, or *Octopus*, which offers brood care, are much bigger at hatching (FIGURE 6.1, based partially on Mangold, 1987).

(2) **Neanoconch.** After hatching, the ammonite laid down a smooth, open spiral shell which is known as the neanoconch. This stage of the life cycle is the neanic growth stage, and appears to be common to ammonites in general (Kulicki, 1974, Shigeta, 1993, Bucher *et al* Ward, 1986, 1996). Some authors have suggested that this stage of the life cycle, which is absent from the life cycle of modern Nautilus, made ammonites particularly vulnerable to disturbance of the plankton, and may account for their demise at the end of the Cretaceous (Ward, 1986, 1992, Ward & Bandel, 1987).

(3) **Juvenile-A stage.** The end of the neanic growth stage is characterised by the appearance of adult ornamentation (e.g., ribs or spines). This is the first stage of juvenile growth, which I call the Juvenile-A growth stage, and is essentially "non-heteromorph". Coiling remains similar to that of the preceding stage, basically an open spiral, but helical in some taxa.

(4) **Juvenile-B stage.** This later stage of growth began with the departure from regular spiral coiling, i.e., the appearance of "heteromorph" shell coiling mode. The relative proportions of the spiral shell growth of the juvenile-A stage and the uncoiled growth of the juvenile-B stage define shell shape (FIGURE 6.2).

(5) **Maturity.** Indicators of maturity were the approximation of the septa and the development of the final living chamber, i.e., cessation of growth of the phragmocone. Associated with this were the development of sexual characters, such as lappets and collars. Ammonites in general appear to have had determinate growth, i.e., they reach a certain size and shape and then stop.

To summarise, mature turrilitaceaen ammonites produced large numbers of small eggs and probably offered little or no brood care. After hatching, the small juveniles drifted in the plankton. At maturity, some morphologies appear to have been adapted for a midwater, planktonic habit while others were more likely to have lived on or near the sea-floor.

These different shell morphologies can be described in terms of ontogeny. The relationship between ontogeny and phylogeny of ammonites has been discussed by various authors (Clark, 1962, Matsumoto, 1964, Korn, 1995). In this study , it is possible to use the cladistic analysis to indicate the likely morphological transitions.

Interpreting evolution from the cladogram

Connections between species have historically been deduced on the basis of similarity, two similar-looking species are likely to be closely related than to dissimilar species. Spath (1941) used this method to infer morphological transitions, and hence evolution of the Albian heteromorphs (FIGURE 6.3). The problem with this approach, or any non-phylogenetic approach, is that the *inferred directions and patterns are imagined first,* and then the taxa arranged to fit. An approach like this, based on an *a priori* hypothesis has many shortcomings, which have all been well discussed elsewhere (Smith, 1993). A taxonomic framework based on the minimum number of assumptions indicates the *directions* of the morphological transitions between taxa *before* the hypothesis of evolutionary or adaptational change is described. The cladogram deduced earlier gives us this information, by indicating which species are most closely related to each other, which taxonomic units are meaningful and which are not, and which species are primitive and which are derived.

I have reviewed the literature which exists on the diversification and origins of the five recognised families of Albian Turrilitaceae in Chapter Two. Monophyly of the Anisoceratidae, Baculitidae, Scaphitidae, and Turrilitidae has been established in Chapter Three. Also, all four of these groups have been demonstrated to be derived from the broad, paraphyletic group of heteromorphs generally referred to as the Hamitidae. The Hamitidae have been here interpreted as a group of ammonites with a planktonic juvenile stage and a

benthonic adult stage on the basis of the functional morphology of their shell shapes (aspinocones, ancylocones, and hamiticones). In contrast, the remaining two derived groups have unique coiling modes and a different way of life. They have been seen to be most likely planktonic and have non-tilting shell morphologies. With these inferred ecologies and life cycles, can the cladogram offer more detail on the exact progression of evolutionary change within each lineage, and tell us something about how and why these changes took place?

Origins and radiation of the Anisoceratidae

The Anisoceratidae are comparable with the Hamitidae in terms of coiling modes: ancylocones and hamiticones predominate. Ornamentation is similar, with simple annular ribs, although there is a tendency for ribs to bifurcate in some taxa (many *Anisoceras*, some *Protanisoceras*). The principal difference between the Hamitidae and the Anisoceratidae is the development on the latter of ventral and ventrolateral tubercles, these tubercles are different to those of other tuberculate heteromorphs as summarised below:

Anisoceratid tubercles: Tubercles approximately conical. Tubercle usually develops from a single rib. Symmetrically paired over the siphuncle. Always appear as pairs. Primitively ventral tubercles on the early part of phragmocone only, ventral and ventrolateral tubercles throughout ontogeny of most derived species only.

Scaphitid tubercles: Tubercles bullate, elongate and flange-like. Tubercles usually develop where the ribs bifurcate. Symmetrically paired over the siphuncle. Always appear as pairs. Primitively confined to the living chamber.

Turrilitid tubercles: Tubercles bullate. Tubercles develop from a single rib. Not symmetrically paired over the siphuncle. Two to five tubercles may be present. Even on earliest tuberculate turrilitids, tubercles weakest on early part of phragmocone becoming more numerous and well developed on the final living chamber.

The latest common ancestors of the Anisoceratidae, Scaphitidae and the Turrilitidae are the Hamitidae. They lack tubercles. Consequently, tubercles are *not* a primitive feature of the heteromorphs inherited from some ancestral tuberculate member of the Anycloceratacеae. They have instead arisen uniquely within the Anisoceratidae, Scaphitidae and the Turrilitidae. Morphologically they are also all quite distinct. The differences in morphology and the

separate origins of tubercles among the groups indicate by the cladistic analysis refutes the hypothesis that the tuberculate Turrilitidae are derived from the Anisoceratidae, since the tubercles in the two groups are not the same (see Klinger & Kennedy, 1978, Scholz, 1979, Wright *et al*, 1996).

The tuberculation exhibited by the various Anisoceratidae is not uniform. FIGURE 6.4 is a cladogram of the Anisoceratidae together with diagrammatic representations of the tuberculation on the phragmocone and living chambers. The more primitive species of this family tend to possess ventral tubercles largely confined to the phragmocone only, while the more derived species have ventrolateral tubercles as well and both pairs of tubercles extend onto the final living chamber. There are exceptions, *Rossalites* being most apparent. Species within this genus have well developed ventral and ventrolateral tubercles on the phragmocone, which fuse into thickened bullate nodes on the living chamber. Nevertheless, the general pattern stands and concurs well with the stratigraphy as has been discussed in Chapter 2.

The cladistic analysis suggests that the most primitive Anisoceratidae are the small (sub-30 cms whorl height) ammonites of the genus *Protanisoceras*. Even within this (admittedly paraphyletic) genus tuberculation is variable. This is summarised below, together with the stratigraphical occurrence. It should be noted that the cladogram contrasts with the stratigraphy somewhat, since the Lower Albian forms are not all considered primitive or the Middle and Upper Albian species as more derived.

Basal species (ventral tubercles on phragmocone only)

Protanisoceras dalpiazi (Middle & Upper Albian)
Protanisoceras anglicum (Lower Albian)
Protanisoceras acteon (Lower Albian)
Protanisoceras blancheti (Lower Albian)

Middle species (ventral tubercles on phragmocone and living chamber)

Protanisoceras coptense (Lower Albian)
Protanisoceras nodosus (Middle Albian)
Protanisoceras vaucherianum (Lower Albian)

Derived species (ventral and ventrolateral tubercles on phragmocone and living chamber)

Protanisoceras cantianum (Lower Albian)
Protanisoceras raulinianum (Lower Albian)
Protanisoceras halleri (Middle Albian)

This suggests that ventral tubercles appeared first on the juvenile stages of growth are primitive, and that retention of tubercles later into growth, and the acquisition of ventrolateral tubercles, are more advanced features. These tubercles may have been some sort of defence, as discussed earlier, perhaps having evolved initially as a defence for the planktonic juvenile stages. Juveniles of the modern teleost *Mola mola* or sunfish, and many larval crabs and mussels, bear spines immediately after hatching.

There are two derivative stocks from *Protanisoceras*: the Lower Albian *Rossalites* and the Upper Albian (and into the Cenomanian) *Idiohamites - Anisoceras* lineage. *Rossalites* is an ammonite at least fifty-percent larger than typical *Protanisoceras*, reaching a whorl height of 30 to 40 cms. Although *Idiohamites* is comparable in size with *Rossalites*, *Anisoceras* is much bigger, with a whorl height of 60 cms or more. All three genera bear ventral and ventrolateral tubercles, as well as modification to the final living chamber such one or more constrictions and apertural collars. In *Rossalites* the ventral and ventrolateral tubercles become fused into clavate or keyhole shaped ridges. In *Idiohamites* the ribs bearing ribs become less frequent than those which do not. *Anisoceras* shows the reverse of this, a decline in the number of non-tuberculate ribs, although the ribs, which are usually fairly coarse and fibulate on the phragmocone become straight and simple and rather fine. It is also the only one of these genera to known bear apertural collars. In all three general, but especially *Rossalites* and *Anisoceras*, the suture lines become more florid at maturity than those of *Protanisoceras*. Thus, this appears to be a size dependent feature, rather than a taxonomic character, so I would hesitate to use suture line floridity as a diagnostic character of either genus (cf. Wright *et al*, 1996).

Origins of the Baculitidae

Only a limited number of baculitids are known from the Albian: three morphologically intergrading *Lechites* species and one species of *Sciponoceras*. The nearest relatives to this clade are firstly *Hamites nokonsis*. This species has an open spiral shells, probably crioconic or aspinoconic, and coiling in one plane. Similar spiral coiling is ubiquitous to heteromorph ammonites during the juvenile-A stages, during which time the ammonites were probably transitional between life in the plankton and becoming more adapted to living on or near the sea floor (for which ancyloconic or hamiticonic shell shapes were best). Both *Lechites* and *Sciponoceras* pass through a brief, open spiral juvenile-A stage. This gives the impression of

the micromorphic coiling of the Baculitidae recapitulating phylogeny by echoing the juvenile-A coiling of the ancestral *Hamites*.

Although crioconic to aspinoconic in coiling mode, *Hamites nokonsis* is convincingly rooted within the predominantly ancyloconic or hamiticonic Hamitidae. If ancylocones and hamiticones of adult *Hamites* are the better adapted to life on the sea floor, then the coiling of *Hamites nokonsis* could be interpreted as a neotenic coiling mode, i.e., although the size of an adult *Hamites* it has a coiling mode more like that of a typical juvenile *Hamites*. Perhaps this form was better adapted to staying in the plankton. The baculiticonic coiling mode is derived from this, by reduction of the size of the open spiral part of the shell (micromorphy) and development of a single straight shaft which was perhaps better suited to a vertically migrating lifestyle (FIGURE 6.5a). While the single shaft could be homologous with the first of the three shafts, the spiral coiling of *Hamites nokonsis* suggests that the straight shafts characteristic of more basal hamitids had already been lost within this lineage. These is in contrast to the view of Wiedmann & Dieni (1968) that a natural group can be made of the baculitids and hamitids on the basis of the odd-number of straight shafts. Instead, the straight shells of the baculitids seems to have evolved (or re-evolved) independently.

Such an evolutionary history contrasts with that proposed by Matsumoto & Obata (1962), in which the primitive baculitids were viewed as benthonic (FIGURE 6.5b) and the later ones as planktonic or nektonic (FIGURE 6.5c). They suggested that the earlier baculitids (such as *Sciponoceras*) with circular whorl sections and apertural hoods, lived on the sea floor. The shell was raised off the sediment by its own buoyancy but the head and arms were oriented toward the sea floor and in this way the ammonite grubbed about for food. The later forms had laterally compressed whorl sections and ventral keels. These forms were interpreted as being more active swimmers in midwater. Matsumoto & Obata (1962) and Klinger (1980) suggested that some baculitids might have filled the apical chambers with water. This would counterbalance the head, and the shell would have adopted a horizontal attitude. Such water-filled chambers would have been comparable in function to the cameral deposits of orthocone nautiloids (Flower, 1955) or the guard of belemnites (Monks *et al*, 1996).

Origins of the Scaphitidae

Only a small number of scaphites are studied here, so only a limited discussion of this predominately post-Albian group of ammonites is possible. The Scaphitidae seem to have been derived from the Hamitidae but not via *Scaphamites* as proposed by Wiedmann & Marcinowski (1985). The most basal member of the family, *Eoscaphites circularis*, is an ancylocone, but much more tightly coiled than is a typical *Hamites*. Also, the whorl section is

more dorso-ventrally compressed. The more derived *Eoscaphites subcircularis* is similar, but with more compressed whorl section and a closed (imperforate) coil. Unlike *Eoscaphites circularis* which has simple annular ribs, those of *Eoscaphites subcircularis* bifurcate over the ventral surface. Where they divide they are slightly raised. The most derived species, and the only true Albian scaphite, is *Scaphites hugardianus*. This ammonite is similar to *Eoscaphites subcircularis* but the whorl section is yet more compressed, and the shell more depressed, becoming semi-lunate where the later whorls overgrow the younger. The shape is characteristic of scaphites in general, being rather round and globular. As with *Eoscaphites subcircularis* the ribs bifurcate, and where they do so small bullate or conical spines develop.

The trend among the Scaphitidae is towards increasingly depressed and compact ancyloconic shell forms with imperforate initial coils. The tubercles are different to those of the Anisoceratidae or the Turrilitidae, and develop from bifurcations of the annular ribs. This pattern is consistent with the derivation of *Scaphites* from *Eoscaphites*, and both from the Hamitidae, as proposed by Wiedmann (1965). The actual functional morphology of the Scaphitidae is less certain, although the ancyloconic coiling indicates a benthonic lifestyle. The recoiling of the shell and closing of the umbilicus could be indicative of improvements in swimming ability since these changes would have the affect of reducing the amount of drag produced by the shell. Possibly the Scaphitidae were more active nektobenthonic or demersal ammonites than the Hamitidae or Ancyloceratidae (FIGURE 6.6). Even so, the observations made by Batt (1989, 1991) indicate that scaphites were excluded from dysaerobic bottom waters, and probably lived near the sea floor, and were subject to the conditions there.

The Hamitidae and the origins of the Turrilitidae

The Turrilitidae are the sister group of the paraphyletic genus *Hamitella*, a group of hamitids characterised by protracted helical coiling and a general reduction in the length and number of the straight shafts. The evolution of the Turrilitdae can therefore be divided into three separate events: the appearance of helical coiling during the transition from *Hamites* to *Hamitella*, the disappearance of straight shafts and retention of helical coiling from *Hamitella* to the primitive non-tuberculate turrilitids, and finally the radiation of the Turrilitidae, especially the appearance of tuberculate forms like *Mariella*.

Of the Hamitidae of which juvenile shells are known, helical coiling is predominantly a feature of hamiticonic coiled species:

Helically coiled hamitids

Hamites attenuatus - hamiticone
Hamitella annulatum - hamiticone
Hamitella gardneri - ancylocone
Hamitella intermedius - hamiticone
Hamitella maximus - hamiticone
Hamitella rotundus - hamiticone
Hemiptychoceras parkinsoni - hamiticone
Scaphamites passendorferi - distorted ancylocone

Non-helically coiled hamitids

Hamites compressus - ancylocone
Hamites hybridus - aspinocone
Hamites incurvatus - ancylocone
Hamites nokonsis - ancylocone
Hamites praegibbosus - ancylocone
Hamites renzi - ancylocone
Hamites tenuicostatus - ancylocone
Hamites tenuis - hamiticone
Hamites virgulatus - aspinocone or ancylocone

Only one hamiticonic species was not helical at any stage, *Hamites tenuis*. In this species the three shafts do not lie in the same plane (FIGURE 6.7). The initial coil and the first shaft lies in one plane. The second and third shaft lie within a second plane about slightly angled (about 10°) to the first plane. If this change in plane did not occur, then the second shaft would eventually run into the juvenile-A coil and growth would have to stop, but since the second shaft is angled away from the initial coil growth can persist uninterrupted. Helical coiling of the juvenile-A shell provides exactly the same functionality but in a different way. By describing a helix for the first part of shell growth, the later shafts can all lie in the one plane without running into the juvenile-A coil (FIGURE 6.8). Helical coiling is therefore a mode of growth which allows tightly coiled hamiticonic shells to develop. ancylocones do not need an helical initial coil since the ascending part of the U-shaped body chamber terminates prior to it reaching the coil.

The cladogram indicates that the planar, and predominantly non-hamiticonic, hamitids occupy the more basal position (*Hamites*, *Scaphamites*, and as far as is known, *Metahamites*). *Lytohamites* is more derived, and *Hemiptychoceras* yet more so. *Hamitella* is the most derived helically coiling hamitid, and is the sister group of the Turrilitidae (FIGURE 6.9). No juvenile coils of *Lytohamites* have been found but they are hamiticonic and may have been

helical. Juveniles of only one species of *Hemiptychoceras* are known (*Hemiptychoceras parkinsoni*) but these are helical, all known species of *Hemiptychoceras* are hamiticonic. All juvenile *Hamitella* are helical. Furthermore, the sutures of *Hamitella* during the helical phase are asymmetrical and comparable with those of the Turrilitidae in this respect.

Within *Hamitella* there are five species (FIGURE 6.10). *Hamitella intermedius* and *Hamitella maximus* are two closely related and perhaps identical species that represent the least derived members of the genus. They are large hamiticones (whorl heights of over 30 cms, compared with the typical, 10 to 15 cms range of *Hamites*) with an helically coiled juvenile shells. *Hamitella gardneri* is a large aspinocone, which is more or less helical for most of its growth, although the living chamber is planar. The most derived species of *Hamitella*, *Hamitella rotundus* and *Hamitella annulatum*, are both rather small, compact ancylocones. While the helices are similar in size to the other *Hamitella* species, the U-shaped body chambers are very short compared with the first two shafts of *Hamitella maximus* or *Hamitella intermedius*, or with the hook of *Hamitella gardneri*. They may be progenetic *Hamitella* species (*sensu* McNamara, 1990), with the helical juvenile phase equivalent in size and form to the ancestral species, but with the later parts of the shell, i.e., the final hook shaped body chamber, being reduced.

These progenetic *Hamitella* species are the sister groups of the Turrilitidae. Compared with *Hamitella*, the Turrilitidae generally lack any hook shaped body chamber (although in some cases aberrant hooks may develop, W. J. Kennedy, pers. comm.). The most basal (and presumably most primitive) member of the Turrilitidae is *Proturrilitoides*. These ammonite is virtually identical to the juvenile phases of *Hamitella annulatum* or *Hamitella rotundus*, with a relatively low spired but fairly compact helical shell. The whorls are not in contact and are circular in section with annular ribs more or less continuous around the perimeter. This species can be easily derived from these later *Hamitella* by completely arresting the adult shell development. *Proturrilitoides* may therefore be a progenetic derivative of *Hamitella* (*sensu* McNamara, 1990). *Turrilitoides* is a more derived species and shows a tightening of the coil and a sharper apical angle.

The utility of the change from planar to helical adult coiling may therefore have complex historic reasons. Helicosity originally evolved to allow hamiticonic coiling. The 'giant' *Hamitella maximus*, for example, has a helical stage proportionally similar to the helix of *Hamites attenuatus*, but in absolute terms it must have taken a longer period of time to develop. Perhaps coincidentally the helix provided a good design for life in the plankton, for the reasons discussed above. The progenetic species of *Hamitella* have proportionally bigger helices compared with either *Hamites attenuatus* or *Hamitella maximus*. The hook-shaped living chamber, which I believe was an adaptation to life on the sea-floor, was a relatively

minor part of the shell. These species of Hamitella must have spent more of their lives in the plankton than either *Hamites attenuatus* or *Hamitella maximus*. Loss of the hook-shaped living chamber in the Turrilitidae indicates loss of the benthonic phase altogether, and adoption of a planktonic lifestyle throughout the life-cycle (FIGURE 6.11).

This evolutionary hypothesis fits the stratigraphy reasonable well. The planar coiling hamitids appeared in the Early Albian, and hamitids with brief helices such as *Hamites attenuatus* are known from the earliest Middle Albian. The progenetic *Hamitella* species with the reduced hook-shaped living chambers appear later in the early Middle Albian, and the first of the Turrilitidae, such as *Proturrilitoides*, are known from the middle part of the Middle Albian (FIGURE 2.17).

The origin of the Turrilitidae can therefore be explained by observing the development of helical coiling among the Hamitidae. The radiation of the Turrilitidae is marked by the acquisition of tubercles independently of their origin among the Anisoceratidae and Scaphitidae. The Anisoceratidae have been especially identified as possible ancestors of the Turrilitidae on the basis of tuberculation, as has been discussed earlier. Development of the tubercles has been generally described in Chapter Two, and for each species in Chapter Three, but the basic pattern in this: Initially, each rib is divided into a small series of distinct bullate tubercles or ridges along the outer part of its length from which develop spines. As ontogeny progresses, the rib may divide further to give rise to additional tubercles on subsequent whorls. Neither *Proturrilitoides* nor *Turrilitoides* possess spines. Ornamentation in these species is limited to hamitid-style annular ribbing.

Tuberculation is first seen in *Pseudhelicoceras*, a genus comprising three species of moderately tightly coiled ammonites with up to four tubercles on each rib. That there are four tubercles in this species has made comparisons with the Anisoceratidae attractive, and Scholz (1979a) considered *Pseudhelicoceras* a subgenus of *Anisoceras*. However, the tubercles do not develop as pairs symmetrically arranged across the siphuncle. The ontogeny of the tubercles in this genus is consistent enough to demonstrate a quite different pattern. At first only two or three tubercles are developed, lying over the lateral lobe and toward the umbilical lobe. The fourth tubercle only becomes evident at or near the final living chamber. In the most primitive species, *Pseudhelicoceras robertianum*, the tubercles are arranged on every second to fourth rib with non-tuberculate rib intercalated between them. The remaining species of *Pseudhelicoceras* and all *Mariella* and *Ostlingoceras* lack non-tuberculate ribs. The presence of non-tuberculate ribs may represent the primitive condition for tuberculate Turrilitidae.

In contrast to the development of the tubercles, the annular ribs become weaker and less complete through the Turrilitidae. This may reflect a change in the nature of the predators which these ammonites had to deal with. On the sea-floor, predators which peel shells may have been common, and were better dealt with annular ribs and collars. In the plankton such predators are rare, and more common were predators which swallow the shell whole, against which outward sticking spines are useful.

Mariella and *Ostlingoceras* are sister groups and represent the most derived Turrilitidae studied here. They are characterised by very compact, closed coiling and moderately to very acute apical angles. In *Mariella* species there are four or five bullate tubercles by the final living chamber, in *Ostlingoceras* there are only two tubercles. The tubercles in both genera tend to be fairly small compared with those of *Pseudhelicoceras robertianum* and circular and give rise to narrow spines.

Within *Mariella*, there are a number of observable differences, specifically variations in the apical angle, the coarseness of the ribbing, and the rate of development of the tubercles, which distinguished species.

Conclusion

The evolution of the turrilitacean heteromorph ammonites can be summarised as a series of diversification events, based upon the acquisition of novel morphological features on the one hand, and on changes in the rates of appearances of existing morphological features on the other. If these events can be compared with the inferred mode of life of the major groups of ammonites and their functional morphology, then the result is a hypothesis which links together ontogeny, phylogeny, and ecology.

As described here the seminal event is the radiation of the Hamitidae, which gave rise directly to the Anisoceratidae by acquisition of symmetrically paired tubercles, to the Baculitidae by reduction of the juvenile coil and development of a single, straight shaft, to the Scaphitidae through recoiling of the shell and truncation of the living chamber hook, and finally to the Turrilitidae by acquisition of a helical growth phase and truncation of the planar parts of the phragmocone and the living chamber. However, this study has been restricted to the Albian, and radiation of the Scaphitidae and the Baculitidae (and to a lesser extent the Turrilitidae) took place during the Cenomanian and later. Therefore an obvious extension of this work would be to use comparable phylogenetic techniques to investigate the further development of the heteromorph ammonites. Also, the origins of the post-Albian heteromorph ammonite groups Diplomoceratidae and Nostoceratidae cannot be commented on at all from this study.

Parallels in morphology between the Hamitidae and the Diplomoceratidae are especially strong (e.g., between *Hamites* and *Diplomoceras*).

CHAPTER SEVEN: CONCLUSIONS

Conclusions and disscussions

Heteromorph ammonites were the Cretaceous equivalent of the modern octopods. Like that group, they were primarily benthonic and displayed adaptations for life on or near the sea floor. The Anisoceratidae, Hamitidae, and Scaphitidae show a range of adaptations to a benthic life, such as being able to tilt the aperture toward the substrate, and the development of defense against benthic predators like crabs. Also like octopods, they gave rise to midwater and planktonic forms. In the case of the heteromorph ammonites, the planktonic midwater forms included the Baculitidae and the Turrilitidae, and probably the Ptychoceratidae. These forms have downward oriented apertures and streamlining along the vertical axis, consequently they would have been well suited to diurnal migrations similar to those of modern midwater cephalopods.

Does the division of the Albian heteromorph ammonite fauna into benthic and planktonic forms have any utility in understanding Cretaceous marine environments and ecosystems? Certainly the Albian heteromorphs were widely distributed and occur in almost all ammonite faunas known from the European and Tethyan provinces. The benthic forms — the tilting morphotypes — appear to have been present in the widest range of facies, ranging from relatively shallow to moderately deep water. In contrast, the planktonic non-tilting forms are more restricted and broadly associated with deep water, transgressive phases (FIGURE 7.1). We must be critical of such data, since the fact that shells are incorporated in sediments at a certain depth does not imply the ammonite lived in that particular location, since the shells may have come from elsewhere.

Post-mortem drift

Firstly, it is highly likely that ammonite shells drifted after death.. A good parallel may be *Spirula*, which has a small internal shell which becomes separated from the body after death and occasionally gets washed up on beaches. My own observations of these shells indicates a relatively diverse fauna of animals can encrust these shells (Taylor & Monks 1997), suggesting the shells may have drifted for weeks or months. Potentially, the substantially larger heteromorph ammonite shells could have drifted for even longer, and been transported far from the place the ammonite lived.

The resistance of heteromorph ammonite shells to damage would depend upon the coiling mode. The open hamiticones and the long, narrow baculiticones would be expected to be the most fragile, while the relatively compact and closed scaphiticones and turriliticones might be more durable. A cursory examination of the material in the Natural History Museum collections does suggest that while *Hamites* and *Lechites* are often found as fragments, there are many complete specimens as well. Also, although the helical turrilitids and scaphitids are relatively complete, they lack any encrustation of pseudoplanktonic organisms. While in life they may well have kept the shells clear of fouling organisms, clean shells are not consistent with having drifted in the plankton for long periods *post mortem*.

Together, these observations may suggest that these shells did not drift for long after death, if at all. The relatively complete hamiticones must have been interred soon after death. Even if scavengers like worms and crustaceans could have quickly eaten the soft parts out of the living chamber without damaging the shell, movement of the water could be expected to break up the shell. Equally, if the planktonic heteromorphs were like *Spirula*, then why do their shells lack a *post mortem* epifauna? The only conclusion can be that the shells sank rapidly after death. Thus a reasonable case can be argued for assuming that heteromorph ammonite shells are preserved in sediments close to where the animals themselves lived.

Defining the deep water habit

The second problem lies in the exact definition of deep water. There main factor that could affect the distribution of vertically migrating ammonites would be water depth.. Modern vertically migrating animals make up the DSL, or deep scattering layer, an assemblage of animals including latern fish, cranchid squid, euphausid crustaceans, and siphonophores. The name is a reference to their tendency to reflect sound, scattering the sonar waves used for navigation. During the day they remain in deep water, but at night, when the predators are unable to hunt they rise to feed on the plankton, and then sink back down again before daybreak. This cycle between the depths during the day and the surface at night is a *diurnal vertical migration* (Carson, 1956, Sumich, 1992).

Why do these animals make these diurnal vertical migrations? One hypothesis is that it provides a refuge from the predaors which live near the surface, such as sharks, tuna, loliginid and ommastrephid squids which generally hunt by sight. By sinking into deep water during the day they evade these predators. On the other hand, during the night these predators cannot hunt, so by rising into the surface water the DSL animals can feed more safely. So for vertical migration to be provide an effective refuge, the ammonites must be able to sink into depths adequate to escape from their predators. Depending on the turbidity of the water, visually

hunting predators occur in the top 100 to 200 metres of water, and typical DSL animals remain at about 100 to 600 metres during the day.

So by analogy, vertically migrating ammonites would be expected to have lived at depths in excess of 100 metres. Where these vertically migrating ammonites are lacking, such as in the Folkestone Sands and Gault Clays of the Lower and much of the Middle Albian in southern England, we can interpret these sediments as having been laid down at depths less than 100 metres.

Heteromorphs in an ecological context

I have made a case here for believing that heteromorph ammonites were more diverse than has been previously assumed. They *were not* all plankton feeders, drifting passively like siphophores or jellyfish do today. There were midwater forms, but they were well adapted for a diurnal, vertically migrating lifestyle, feeding on planktonic crustaceans and fishes at night and then retreating into deeper water during the day. Others were benthonic, crawling or swimming close to the sea floor, relying more on their shell for defence than escape. FIGURE 7.2 is a comparison between modern cephalopod faunas and the faunas of the Albian. The heteromorph ammonites may have filled-in niches which the more generalised homomorph ammonites did not, although there is great variation among homomorph ammonites and they may have been just as diverse in their habits.

MODERN FAUNA	ALBIAN FAUNA
Squid (e.g., *Loligo*)	Belemnites, homomorph ammonites
Cuttlefish (e.g., *Sepia*)	Homomorph ammonites (maybe *Scaphites*?)
Octopus (e.g., *Octopus*)	Tilters (*Hamites*, *Anisoceras*)
Spirula (e.g., *Spirula*)	Small non-tilters (*Ptychoceras*)
Cranchid squid (e.g., *Cranchia*)	Big non-tilters (*Lechites*, *Mariella*)
Pearly nautilus (e.g., *Nautilus*)	Homomorph ammonites and nautiloids

The sheer numbers of modern spirulas, cranchid squid and octopuses around today gives a fair indication of the productivity of such modes of life (Clark, 1965, Roper, *et al* 1984). If heteromorphs occupied comparable niches, then they may have been just as important to the marine ecosystem. If some were benthonically associated, perhaps they can be used to help interpret bottom water conditions. Far from being aberrant, heteromorphs were a key part of the ammonite faunas of the Albian, and are worthy of study in their own right, and not only in comparison with their better known cousins, the regularly coiled Ammonitina.

Further work

Two major problems were described in this thesis: the absence of a phylogenetic taxonomy, and the limitations of our understanding of heteromorph functional morphology. I have attempted to address both of these problems here. The taxonomy of these ammonites has been reviewed and revised using a computer-based parsimony approach, which is consistent with modern taxonomic practise. Functional morphology has been studied using relatively simple modelling techniques, but even so the results are interesting in showing that radically different ideas on the function of heteromorph ammonite shell geometry can be produced by re-assessing the assumptions on which the previous ideas were based. I have also tried to show how an understanding of the functional morphology can help us understand the cladograms which a parsimony-based cladistic approach produces, in essence devising an evolutionary story from the phylogeny.

However, the story is only as good as the data on which it is based, and there is good reason to believe that at least some of these approaches can be improved. Phylogenetic analysis is dependent on the quantity of the data and the methods used, and heteromorph ammonites could be considered to be rather poor in characters. Although the shell shape, coiling mode, and suture line are known from most species there are obvious gaps in other areas. The aptychi have not been described from Albian heteromorphs although they are known from baculitids and scaphitids from younger strata (Arkell, 1957). The record of muscle scars is scarcely any better, being known from *Hamitella maximus* only (Crick, 1898). Nothing is known about the gut contents, and like all ammonites, very little is known about the soft body anatomy of the heteromorphs.

Any of these sets of characters could contain information critical to understanding the phylogeny of the group, but until such time as specimens are found which yield this data, we must rely on the more limited shell-character data set. The existing data set could be analysed using other techniques. The computers used to analyses the data set used here are limited in power and speed to running only a heuristic search on data sets of this size. Such searches are *not guaranteed* to find the most parsimonious trees (Swofford, 1993). It is therefore possible that shorter trees were not found which would change the topology of the cladogram and could radically change the phylogeny of the group. Improvements in computing hardware make it possible that running the same data set on a faster machine could force a revision of the phylogenetic statements made here. More importantly, any of the characters I have used could be interpreted differently by another operator, most critically my statements of homology and ordered progression. Changing these assumptions would change the data

matrix, and consequently the results of the analysis. By making the data set available here in an explicit way, one of the strengths of the cladistic approach is highlighted: Any new operator can examine my data set and the character descriptions it is based upon, and then choose to revise and re-run the analysis.

Besides the taxonomy, the functional aspects of this thesis are open to a good deal of refinement. The modelling methods used here are crude, and better mathematical modelling could be used to estimate the density of the ammonites and the orientation of the shells. Although the baculiticones and turriliticones were analysed mathematically and are probably reasonably sound, the remaining morphologies were very largely based on guesswork, specifically in the estimation of the centre of mass (i.e., the size and mass of the soft body parts). Other modelling methods could be used to investigate the hydrostatics and hydrodynamics, such as the use of wind-tunnels as described in Monks *et al* (1996) in reference to belemnite morphology.

On balance while I believe that this thesis has opened up new channels of research, it has by no means exhausted them, and I hope very much that heteromorph ammonites will remain a focus of palaeobiological and systematic study.

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FIGURE 1.2: *Hamitella gardneri*, an ammonite with aspinoconic coiling.

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FIGURE 1.4: *Hamitella maximus*, an ammonite with hamiticonic coiling when mature.

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FIGURE 1.6: The *juvenile-A* stage persisted through the development of the post-neanic crioconic part of the phragmocone. Features which exist on this part of the shell are termed here to have been developed during the juvenile-A growth stage.

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FIGURE 1.8: The ammonite reached *maturity* when development of the phragmocone slowed down or ceased altogether. Mature characters are therefore those features apparent on the final living chamber. Modifications of the final living chamber, such as the development of apertural constrictions and collars, are apparent in some species.

FIGURE 2.1: The traditional taxonomy of the class Cephalopoda based on Voss (1977). The Nautiloidea and Ammonoidea are sometimes referred to as the Tetrabranchiata, on the assumption that ammonites had two pairs of gills, like modern *Nautilus*. All nautiloids and probably all ammonoids had external shells. The Coleoidea all have a single pair of gills, and are therefore named the Dibranchiata. Belemnites (order Belemnoidea) plus a number of other minor groups also belong to the Coleoidea. Coleoids have internal, often reduced, shells. They are the dominant cephalopods alive today.

FIGURE 2.2: Berthold & Engeser (1987) and Engeser (1996) have revised cephalopod taxonomy phylogenetically using both living and fossil groups. They have demonstrated that ammonoids and coleoids are more closely related to each other than either are to the nautiliods, despite the similarity of the external shells of nautiloids and ammonoids. This supports the union of the Ammonoidea and Coleoidea within the Angusteradulata as proposed by Lehmann (1967) and supported by Nixon (1995). Lewy (1996) has postulated that ammonoids may even be ancestral to certain octopuses by comparisons of the morphology of the shells of ammonites with the egg-cases of the pelagic octopus *Argonauta*.

FIGURE 2.3: A taxonomy of the heteromorph ammonites of the Albian discussed in this thesis, based on Spath (1923-1943), Breistroffer (1940, 1947), Casey (1961), Renz (1968), Cooper & Kennedy (1977), Cooper (1994a), and Wright *et al* (1996).

FIGURE 2.4: The proposed "phylogenetic" taxonomy of the heteromorph ammonites of the Albian devised and used by Wiedmann (1962) and Wiedmann & Dieni (1968), and most recently discussed by Marcinowski & Wiedmann (1990).

FIGURE 2.5: Origins of the Baculitidae as postulated by Spath (1941) and Matsumoto & Obata (1963).

FIGURE 2.6: The diphyletic origins of the Turrilitidae as described by Matsumoto (1967) and Klinger & Kennedy (1978). The tuberculate turrilitids (*Pseudhelicoceras*, *Mariella*, and *Ostlingoceras*) are seen to have a separate origin from the non-tuberculate turrilitids (*Proturrilitoides*, *Turrilitoides*).

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FIGURE 3.1 & 3.2: *Ptychoceras adpressum*. Dorsal and lateral views of the holotype, BMNH C.39330 from Bed X of the Gault Clay at Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.3: *Ptychoceras laeve*. BMNH C.3520. Lateral view of part of the second and third shafts. From the Middle Albian of Escragnolles, France. Exact stratigraphical horizon unrecorded.

FIGURE 3.4 & 3.5: *Ptychoceras laeve*. BMNH C.46837. Dorsal and lateral view of part of the second and third shafts. Also from the Middle Albian of Escragnolles, France.

FIGURE 3.6: *Hamites attenuatus*. Lateral view of BMNH C.8566 from the Gault Clay (Middle Albian) at Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.7: *Hamites attenuatus*. Criococonic juvenile whorl, BMNH C.8566 from the Gault Clay (Middle Albian) at Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.8: *Hamites attenuatus* transition to *Hamites tenuicostatus*. Lateral view of BMNH C.852 from the Gault Clay (Middle Albian) at Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.9: *Hamites tenuicostatus*. Lateral view. BMNH C.29874 from the Gault Clay (Middle Albian) at Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.10: *Hamites hybridus*. Lateral view of the holotype, Zm 2195 from the Main Mammillatum Beds at Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.11: *Hamites nokonsis*. Lateral view of BMNH C.39920 from the Upper Albian (*dispar* Zone) of Holworth House, Dorset. This specimen is the holotype of *Hamites subvirgulatus*, a species considered here to be junior synonym of *Hamites nokonsis*. Scale bar = 10 mm.

FIGURE 3.12: *Hamites praegibbosus*. Lateral view of BMNH C.47444 from the Main Mammillatum Beds at Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.13: *Hamites praegibbosus*. Lateral view of BMNH C.47442 from the Main Mammillatum Beds at Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.14: *Hamites renzi*. Lateral view of the holotype, BMNH C.94119 from the Marnes Bleues, Upper Albian (*dispar* Zone) of Mont Risou, Hautes-Alpes, France. Scale bar = 10 mm.

FIGURE 3.15a, 3.15b: *Hamites tenuis*. Lateral and ventral views of a specimen from the author's collection. From the Gault Clay (Lower Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.16: *Hamites tenuis*. Reconstruction of *Hamites tenuis*, here feeding on surface water plankton. The key diagnostic features of this species are labelled. The orientation of this ammonite is based upon Trueman (1941).

FIGURE 3.17: *Hamites virgulatus*. Lateral view of the BMNH C.77628 from the Cambridge Greensand (Upper Albian) of Cambridge. Scale bar = 10 mm.

FIGURE 3.18: *Hamites virgulatus*. Lateral view of the BMNH C.77635 from the Cambridge Greensand (Upper Albian) of Cambridge. Scale bar = 10 mm.

FIGURE 3.19: *Lytohamites similis*. Lateral view of the holotype specimen, BMNH C.4762a from the Cambridge Greensand (Upper Albian) of Cambridge. Scale bar = 10 mm.

FIGURE 3.20: *Lytohamites similis*. Part of the final shaft of a large specimen. BMNH C.4769a from the Cambridge Greensand (Upper Albian) of Cambridge. Scale bar = 10 mm.

FIGURE 3.21: "*Hamites multicostatus*". The holotype specimen, although the validity of the species name is questioned (see Kennedy, 1971). BMNH C.36572 from the Chalk Marl (Lower Cenomanian), Hamsey, Sussex. Scale bar = 10 mm.

FIGURE 3.22: *Lytohamites funatus*. Mature aperture of a microconch of BMNH C.39927 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Scale bar = 10 mm.

FIGURE 3.23: *Lytohamites funatus*. Lateral view of a macroconch, BMNH C.25176 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Note the appearance of the scale-like ribbing on the final living chamber. Scale bar = 10 mm.

FIGURE 3.24: *Lytohamites funatus*. Macroconchs, BMNH C.39923 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Scale bar = 10 mm.

FIGURE 3.25a, 3.25b: *Hemiptychoceras gaultinum*. Ventral and dorsal views of BMNH C.46855 from the Gault Clay (Upper Albian) at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.26: *Hemiptychoceras parkinsoni*. Lateral view of BMNH C.77637 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Scale bar = 10 mm.

FIGURE 3.27: *Hemiptychoceras parkinsoni*. Lower Cenomanian specimen BMNH C.72216 from Chinnor, near Dunstable, Bedfordshire. Scale bar = 10 mm.

FIGURE 3.28: *Hemiptychoceras parkinsoni*. Lower Cenomanian (*Turrilites costatus* assemblage, Cenomanian Basement Bed) specimen BMNH C.76361 from Buckland Newton, Dorset. This specimen shows the apertural constrictions and collars characteristic of the genus (toward the top of the photograph). Scale bar = 10 mm.

FIGURE 3.29: *Hemiptychoceras parkinsoni*. Lateral view of specimen BMNH C.76361 from the Upper Albian (*dispar* Zone) at Punfield Cove, Dorset. Scale bar = 10 mm.

FIGURE 3.30a, 3.30b: *Hemiptychoceras parkinsoni*. Neotype specimen BMNH C.76361 from the Upper Greensand Malmstone (Upper Albian, *dispar* Zone) from Devizes, Wiltshire. This is part of the weakly helical phragmocone, as evidenced by the twisted ribs. Scale bar = 10 mm.

FIGURE 3.31: *Hemiptychoceras parkinsoni*. Well preserved examples of the constriction and paired apertural collars typical of this species and the genus. BMNH C.76361 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge. Scale bar = 10 mm.

FIGURE 3.32: *Hemiptychoceras parkinsoni*. Lateral view of BMNH C.4761e from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Scale bar = 10 mm.

FIGURE 3.33 *Hemiptychoceras parkinsoni*. Lateral view of the mature living chamber of BMNH C.90889 from the Upper Albian, *dispar* Zone at Punfield Cove, Dorset. One of the apertural collars are visible toward the top of the fragment. Scale bar = 10 mm.

FIGURE 3.34a, 3.34b: *Hemiptychoceras parkinsoni*. BMNH C.77631 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Part of the tightly helically coiled phragmocone. Scale bar = 10 mm.

FIGURE 3.35: *Hamitella annulatum*. Helical phragmocone BMNH C.853 from the Lower Gault, (Middle Albian, from Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.36a, 3.36b: *Hamitella annulatum*. Lateral and ventral view of part of the phragmocone with the characteristically twisted ribs of this genus. BMNH C.39904 from the Lower Gault, (Middle Albian, from Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.37a, 3.37b: *Hamitella annulatum*. BMNH C.4568 from the condensed Gault Clay (Middle and Upper Albian) of Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.38: *Hamitella gardneri*. A specimen with a deeper, more ancyloconic hook than usual, and apparently transitional to *Hamitella maximus*. BMNH C.857 from the Upper Gault (Upper Albian), at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.39: *Hamitella gardneri*. BMNH C.73654 from the Upper Gault (Upper Albian), at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.40: *Hamitella gardneri*. Reconstruction in two possible modes of life: (a) as a planktonic drifter with upturned apertures, and (b) as a demersal or benthonic predator or scavenger with the aperture oriented downwards. The estimated positions of the centres of mass (black circles) and buoyancy (white circles) are labelled, and these are critical in determining orientation. See Chapters 4 and 5 for discussion on how these ammonite lifestyles were reconstructed.

FIGURE 3.41: *Hamitella intermedius*. Lateral view of BMNH C.852 from the Upper Gault (Upper Albian) at Copt Point, Folkestone, Kent. Note malformed (damaged?) rib just above crack on the right hand side of the specimen. Scale bar = 10 mm.

FIGURE 3.42a, 3.42b: *Hamitella maximus*. Lateral (3.42a) and ventral (3.42b) views of the helically coiled juvenile shell BMNH C.3012 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. This specimen belongs to the variety *rectus* of Spath (1941). This variety has finer ribbing than the type material of *Hamitella maximus*. Some authors consider it a separate species (e.g., Wiedmann & Marcinowski, 1990). Scale bar = 10 mm.

FIGURE 3.43: *Hamitella maximus*. Lateral view of BMNH C.852 from the Lower Gault (Middle Albian), at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.44: *Hamitella maximus*. Reconstruction of complete shell, with key diagnostic features labelled.

FIGURE 3.45: *Hamitella rotundus*. Helical coil of phragmocone and part of the first straight shaft. BMNH C.853 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.46a, 3.46b: *Hamitella rotundus*. Ventral and lateral views of a fragment of the helical part of the phragmocone. Uncatalogued specimen from the author's collection. From the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Note the malformed rib indicated by the arrow (Figure 3.46a). Scale bar = 10 mm.

FIGURE 3.47: *Hamitella rotundus*. Helical part of the phragmocone. BMNH C.849, from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.48: *Hamitella rotundus*. Almost complete specimen displaying the initial helix followed by the two straight shafts. Mature *Hamitella annulatum* are similar, but the two straight shafts are proportionally shorter. BMNH C.853, from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.49a, 3.49b: *Metahamites sablieri*. Ventral and lateral views of the later part of the phragmocone and the mature living chamber. BMNH C.54600 from the condensed Middle and Upper Albian Gault Clay at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.50: *Metahamites sablieri*. Lateral view. BMNH C.46904 from the condensed Middle and Upper Albian Gault Clay at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.51: *Anisoceras saussureanus*. A large specimen viewed laterally (3.51a) and ventrally (3.51b). BMNH C.3646 from the Upper Greensand (Upper Albian, *dispar* Zone) of the Isle of Wight, exact locality unknown. Scale bar = 100 mm.

FIGURE 3.52: *Anisoceras perarmatum*. Lateral (3.52a) and ventral (3.52b) views. BMNH C.36721 from the Upper Greensand (Upper Albian, *dispar* Zone), Hamsey, near Lewes, Sussex. Scale bar = 10 mm.

FIGURE 3.53: *Anisoceras armatum*. A reconstruction based on the holotype, University of Oxford Museum specimen K675a C.3646 from the Chalk Marl (Upper Albian, *dispar* Zone), Benson, Oxfordshire. Scale bar = 10 mm.

FIGURE 3.54: Diagrammatic representations of the sections of the shell of the three principal species of Albian *Anisoceras*, based upon the descriptions in the text. *Anisoceras saussureanus* (3.54a) develops bullate tubercles on the living chamber. *Anisoceras armatum* (3.54b) has clavate ventral tubercles and rather weak circular or clavate tubercles on the living chamber. *Anisoceras perarmatum* (3.54c) is similar to *Anisoceras armatum*, but lacks the intermediate, non-tuberculate ribs on the phragmocone and the ventrolateral tubercles on the living chamber are more strongly developed.

FIGURE 3.55: *Rossalites superbum*. Lateral (3.55a) and ventral (3.55b) views. BMNH C.71996 from the Lower Greensand (Folkestone Beds, Main Mammillatum Bed) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.56: *Rossalites riccardi*. Later part of phragmocone and final living chamber. Note the separate rows of ventral and ventrolateral tubercles fuse along the final living chamber into bullate ridges. This is characteristic of the genus. Uncatalogued specimens from the W. J. Kennedy collection, University of Oxford Museum. From the Lower Albian (*Leymeriella regularis* Zone), Col des Pré, Guittard, France. Scale bar = 10 mm.

FIGURE 3.57: *Rossalites riccardi*. Part of the phragmocone. Also from the W. J. Kennedy collection, University of Oxford Museum. From the Lower Albian (*Leymeriella regularis* Zone), Col des Pré, Guittard, France. Scale bar = 10 mm.

FIGURE 3.58: *Rossalites riccardi*. Spiral part of phragmocone. Uncatalogued specimens from the W. J. Kennedy collection, University of Oxford Museum. From the Lower Albian (*Leymeriella regularis* Zone), Col des Pré, Guittard, France. Scale bar = 10 mm.

FIGURE 3.59: *Protanisoceras raulinianum*. Viewed laterally (3.59a) and ventrolaterally (3.59b). BMNH C.30791 from the Lower Albian (Folkestone Beds, Main Mammillatum Bed) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.60: *Protanisoceras cantianum*. Viewed laterally (3.60a) and ventrally (3.60b). BMNH C.48915 from the Lower Albian (Folkestone Beds, Main Mammillatum Bed) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.61: *Protanisoceras coptense*. Lateral (3.61a) and ventral (3.61b) views of the holotype, BMNH C.71971 from the Folkestone Beds (Main Mammillatum Beds) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.62: *Protanisoceras blancheti*. Lateral (3.62a) and ventral (3.62b) views of BMNH C.84763 from the Folkestone Beds (Main Mammillatum Beds) at Copt Point, Folkestone, Kent. Note the weak ventral tubercles, a characteristic of this species. Scale bar = 10 mm.

FIGURE 3.63: *Protanisoceras blancheti*. Lateral (3.63a) and ventral (3.63b) views of BMNH C.84763 from the Lower Greensand - Gault Clay Junction Beds at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.64: *Protanisoceras nodosum*. Lateral view of a well preserved specimen, BMNH C.47539 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.65: *Protanisoceras anglicum*. Lateral (3.65a) and ventral (3.65b) views of the holotype, BMNH C.48913 from the Folkestone Beds (Main Mammillatum Beds) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.66: *Protanisoceras anglicum*. Lateral (3.66a) and ventral (3.66b) views BMNH C.48913 from the Woburn Sands Formation, Shenley Limestone (*tardefurcata* Zone, *regularis* Subzone) at Munday's Hill Pit, near Leighton Buzzard, Bedfordshire. Scale bar = 10 mm.

FIGURE 3.67: *Protanisoceras acteon*. Lateral (3.67a) and ventral (3.67b) views of BMNH C.71967 from the Folkestone Beds (Main Mammillatum Beds) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.68: *Protanisoceras arrogans*. Lateral (3.68a) and ventral (3.68b) views of BMNH C.46908 from the condensed Middle Albian beds of Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.69: *Tuberolechites regifex*. Lateral (3.69a) and ventral (3.69b) views of part of the living chamber of BMNH C.18325 from the Upper Gault (Upper Albian) at Glynde, Sussex. Note the malformed ribs. Scale bar = 10 mm.

FIGURE 3.70: *Idiohamites tuberculatus*. Lateral view of BMNH C.39943 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone)at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.71: *Idiohamites spiniger*. Lateral view of BMNH C.39821 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone)at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.72: *Idiohamites spiniger*. Lateral (3.72a) and ventral (3.72b) views of the early part of the phragmocone. Unlike *Anisoceras*, with which *Idiohamites* might otherwise be confused, the juvenile coil is planar like most *Protanisoceras*. BMNH C.39821 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone)at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.73: *Lechites gaudini*. Lateral view of BMNH C.77661 from the Upper Gault (Upper Albian, *inflatum* Zone) at Copt Point, Folkestone, Kent. This specimen is a macroconch, and exhibits the constriction and collar typical of the genus. Scale bar = 10 mm.

FIGURE 3.74: *Sciponoceras skipperae*. Lateral (3.74a) and ventral (3.74b) views of the holotype specimen, BMNH C.93268. This specimen consists mainly of part of the living chamber, although the final septum is preserved. From the Upper Albian, *dispar* Zone at Melcombe Horsey, Dorsetshire. Scale bar = 10 mm.

FIGURE 3.75: *Proturrilitoides astierianus*. BMNH C.46574b. From the condensed Middle and Upper Albian at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.76: *Proturrilitoides senequierianus*. BMNH C.46867. From the condensed Middle and Upper Albian at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.77: *Turrilitoides hugardianus*. BMNH C.3802. From the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridgeshire, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.78: *Turrilitoides densicostatus*. BMNH C.3802. From the Lower Gault (Middle Albian, *lautus* Zone, *nitidus* Subzone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.79: *Pseudhelicoceras robertianum*. Large piece of the final living chamber. BMNH C.3802. From the Upper Gault (Upper Albian, *inflatum* Zone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.80: *Pseudhelicoceras gaultinum*. BMNH C.38213. The break in the ribs between the second and third rows of tubercles are characteristic of this species. From the Upper Gault (Upper Albian, *inflatum* Zone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.81: *Pseudhelicoceras pseudoelegans*. BMNH C.38210. This specimen is shown from the ventral (3.81a) and lateral (3.81b) surfaces, in life, the shell would have been oriented on its side compared with planar coiled ammonites, with the lateral surface downwards. The bullate tubercles are labelled, from rows 1 to 5. From the Upper Gault (Upper Albian, *inflatum* Zone, *cristatum* Subzone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.82: *Mariella bergeri*. BMNH C.3802. The rows of tubercles are labelled from 1 to 4. In life the tubercles would have had long spines attached to them, the indentations made by the spines on early whorls can be seen on later whorls which overgrow the spines. From the Upper Greensand (Upper Albian, *dispar* Zone) at Warminster, Wiltshire. Scale bar = 10 mm.

FIGURE 3.83: *Mariella cantabrigiensis*. The relatively coarse ribbing and bullate tubercles are characteristic of this species. BMNH C.34739 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.84: *Mariella miliaris*. Compared with other *Mariella*, this species has fine ribs and slender, conical tubercles. BMNH C.93449 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.85: *Mariella nobilis*. BMNH C.38216 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.86: *Ostlingoceras puzosianum*. BMNH C.38199 from the Upper Albian, *dispar* Zone, at Man o' War Cove, Dorsetshire of. This specimen shows the reduced tuberculation and flattened sides characteristic of the genus. Scale bar = 10 mm.

FIGURE 3.87: *Eoscaphites circularis*. Neotype specimen, BMNH C.41555 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.88: *Scaphites subcircularis*. Holotype specimen, BMNH C.38206 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.89: *Scaphites hugardianus*. BMNH C.39662 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.90: *Scaphites hugardianus*. Restored shell with the key features labelled.

FIGURE 3.91: *Hamites compressus*. BMNH C.854 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.92: *Hamites incurvatus*. BMNH C.75247 from the Upper Gault (Upper Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.93: *Hamites tenuis*. BMNH C.852 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.94: *Hamites tenuis*. Uncatalogued specimen collected by A. S. Gale from the Speeton Clay (Middle Albian, *intermedius* Subzone), Speeton, Norfolk. Scale bar = 10 mm.

FIGURE 4.1: Hemisection through the shell of *Nautilus pompilius*, the common nautilus.

FIGURE 4.2: *Cranchia scabra*, based on specimens in the Spirit Collection of the Mollusca Section, BMNH. *Cranchia* is a mesopelagic squid, and is here oriented in its life position, with the head downwards.

FIGURE 4.3: *Spirula spirula*, based on specimens in the Spirit Collection of the Mollusca Section, BMNH. *Spirula* is a mesopelagic sepiid with a characteristic internal coiled shell, and is here oriented in its life position, with the head downwards. It is shown here in life (Figure 4.3a) and sectioned (Figure 4.3b).

FIGURE 4.4: An ammonite based on the hypothesis that ammonites were negatively buoyant animals which crawled about on the sea floor (Ebel, 1992, 1993). In this model, the shell does not provide buoyancy and so plays no part in the orientation of the animal relative to the sea floor, this is dependent on the centre of mass of the ammonite and the strength and adhesion of the arms.

FIGURE 4.5: An ammonite at stable equilibrium is positioned with the centre of mass vertically below the centre of buoyancy (Figure 4.5a). If the ammonite is rotated such that the centre of mass is moved through an angle ∂ (Figure 4.5b) a restorative force proportional to ∂ will be generated, tending to re-position the centre of mass vertically beneath the centre of buoyancy. Equally, if the centre of mass moves *within* the shell, another restorative force will be developed (Figure 4.5c), and the shell will tend to rotate and reposition the centre of mass vertically beneath the centre of buoyancy (Figure 4.5d).

FIGURE 4.6: Diagrammatic section through an heteromorph ammonite, with representative values for the density of shell, phragmocone, and soft tissues taken from Okamoto (1988). The density values are given in milligrams per cubic millimetre. Sea water has a density of approximately 1.025 mg/mm2.

FIGURE 4.7: Summary of the hydrostatic properties of *Sciponoceras* (Figure 4.7a) *Ostlingoceras* and (Figure 4.7b) based upon the analysis described in the text.

FIGURE 4.8: Variation in the density of the baculiticonic ammonite *Sciponoceras* (Figure 4.8a) and *Ostlingoceras* (Figure 4.8b) based upon ±5% variations in the density of phragmocone, shell material, and soft tissues.

FIGURE 4.9: Top, the plasticene models of equal volume and whorl expansion rate but differing in coiling mode (Figure 4.9a). From left to right: hamiticone, ancylocone, and aspinocone. Bottom, a schematic diagram of the testing rig used (Figure 4.9b).

FIGURE 4.10: Reconstruction of a the living chamber with the soft body parts restored (in section). The chamber is lined by mantle, and the main body of the animal attached anteriorally by a muscular collar and posteriorally by the paired retractor muscles (FIGURE 4.10a). The muscular collar does not completely seal off the aperture (FIGURE 4.10b),

allowing movement of water over the gills, as well as allowing water behind the animal to escape when the head is pulled back (FIGURE 4.10c).

FIGURE 4.11a: Reconstruction of an aspinoconic ammonite, *Hamitella gardneri*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

FIGURE 4.11b: Reconstruction of an ancyloconic ammonite, *Anisoceras armatum*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

FIGURE 4.11c: Reconstruction of an hamiticonic ammonite, *Hamitella maximus*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

FIGURE 4.11d: Reconstruction of a baculiticonic ammonite, *Lechites gaudini*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

FIGURE 4.11e: Reconstruction of a low spired turriliticonic ammonite, a juvenile *Hamitella* sp. with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

FIGURE 4.11f: Reconstruction of a high spired turriliticonic ammonite, *Ostlingoceras puzosianum*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

FIGURE 4.11g: Reconstruction of a ptychoconic ammonite, *Ptychoceras adpressum*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

FIGURE 4.12: Table of the seven ammonite morphologies described in the text (Chapter 4) together with the deduced rotational angles. Each shell morphology can be classified by whether it has "tilting" ability or not, which is dependent on the size of the rotational angle. As described in the text, tiltling morphologies have large rotational angles, and movement of the body between the aperture and the back of the shell would cause the ammonite to rotate, typically with the aperture toward the sea floor when the head and arms are extended. In contrast non-tilting forms have small or zero rotational angles, and movement of the body within the shell causes little or no change in orientation.

FIGURE 5.1a: Inferred position of the continents during the Lower Albian (105 to 100 million years ago) redrawn after Haq (1984).

FIGURE 5.1b: Coastlines of North West Europe during the same time period, based on Owen (1979) with the principal marine basins labelled. Names in brackets - e.g., **(Greenland)** - indicate present-day geographical locations.

FIGURE 5.2: Lower Albian (Figure 5.2a) and Upper Albian (Figure 5.2b) palaeogeographical reconstructions redrawn after Rawson (1992). Principal facies types are indicated.

FIGURE 5.3: Relative abundance of planktonic foraminifera as a percentage of total (planktonic + benthic) number of foramanifera. Based on Price (1977) the abundance are in terms of numbers of species recorded from each ammonite subzone.

FIGURE 5.4: Idealised section of the Gault Sea based on the estimates of water depth discussed in the text (Chapter 5). The ranges of the tilting morphotypes (aspinocones, ancylocones, and hamiticones) and the non-tilting morphotypes (baculiticones, ptychocones, and turriliticones) as inferred from their Occurence in the fossil record are plotted. The tilting forms are found in sediments suggesting a wider range of depths than the non-tilting forms, which were restricted to deeper water facies.

FIGURE 5.5: Lines of force generated by jet-propulsion compared in a tilting morphotype (Figure 5.5a, an aspinocone) and a non-tilting morphotype (Figure 5.5b, a baculiticone). The

line of force will act through the centre of mass. In the aspinocone, this line of force meets the vertical axis of the ammonite tangentially, consequently some of the force will produce a rotation of the shell around the pivot point (the centre of buoyancy). This rotation wastes energy and so swimming would be inefficient.. In contrast, with the baculiticone, the centre of mass, centre of buoyancy and the line of force are all lined up along the vertical axis and none of the energy is lost this way.

FIGURE 5.6: *Hamitella intermedius*. Uncatalogued specimen from Bed IX, Copt Point, Folkestone. Author's collection, BMNH. Oriented with apertural-end of shell toward bottom of the page. Shell damage and repair along the mid line of this specimen, note bisected ribs where the shell was peeled with only gradual reformation of later ribs. The original shell material is preserved in this specimen. Scale bar = 10 mm.

FIGURE 5.7: *Hamitella maximus*. BMNH C.73900, from Copt Point, Folkestone, exact stratigraphical horizon unrecorded. Oriented with the apertural-end of the shell towards the left hand side of the page. Shell damage in this specimen is slightly below the midline of the shell, and evidenced by deformation of the ribs. Original shell material of this specimen preserved. Scale bar = 10 mm.

FIGURE 5.8: *Ampullaria* sp. Example of an artificially "peeled" apple snail shell. The shell damage extends about 5 mm inwards from the aperture, roughly along the midline of the whorl. Subsequent repair has filled in part of the damage.

FIGURE 5.9: Restored claw of *Diaulax feliceps*. Based upon BMNH In.30098 from the Gault Clay at Folkestone. Robust chelipeds with smooth short chelae like these can be seen in modern crabs which peel shells open, such as *Calappa*. Crabs which crush shells, like *Cancer*, have chelae with molariform processes. Scale bar = 10 mm.

FIGURE 5.10: Diagrammatic section through a typical helically coiled ammonite of the family Turrilitidae. According to Klinger (1980) the helical coiling and displacement of the siphuncle observed in most Turrulitidae give rise to a situation whereby the siphuncle is 'de-coupled' from the cameral fluids. This supposedly increases the efficiency of cameral emptying.

FIGURE 5.11: Diagrammatic section through a typical baculiticonic ammonite of the family Baculitidae. A consequence of the coiling of baculiticones is that the siphuncle is effectively de-coupled for most of its length since it does not lie on the ventral surface of the shell, the usual position in most regularly coiled ammonites.

FIGURE 6.1: Comparisons of the sizes of various cephalopods at hatching. Based on Tanabe *et al* (1980), Mangold (1987), Lebrun (1996) and Landmann *et al* (1996). The *Nautilus* is demersal immediately after hatching, as is the common cuttlefish. The species of squid and octopus figured here represent extremes of the range of sizes known for these groups, and all appear to be planktonic for at least the early part of their life cycle. The two heteromorph ammonites are more comparable with the squid and octopus than with the *Nautilus*, and this suggests that they were planktonic after hatching. The scale bar is 50 mm.

FIGURE 6.2: Four ammonites for comparison of the coiling mode and relative sizes of the juvenile-A, juvenile-B, and mature growth phases: Figure 6.2a: *Hamitella gardneri*, Figure 6.2b: *Ancyloceras matheronianum*, Figure 6.2c: *Hamitella maximus*, Figure 6.2d: *Lechites gaudini*.

FIGURE 6.3: Interelationships between the Albian heteromorphs postulated by Spath (1923-1943).

FIGURE 6.4: Phylogeny of the Anisoceratidae based on the cladogram described in Chapter 2. The tuberculation on the phragmocone and the living chamber of each species is also figured diagrammatically, it clear that among the more primitive species tuberculation tends to be limited to the phragmocone, while tuberculation on the living chamber as well as the phragmocone is characteristic of the more derived species.

FIGURE 6.5: Evolution of the Baculitidae postulated here compared with the hypothesis suggested by Matsumoto & Obata (1964). In this thesis the baculitids are viewed as neotenic derivatives of the Hamitidae which were adapted to a planktonic lifestyle with the long axis vertical (Figure 6.5a). Matsumoto & Obata (1964) proposed that baculitids were originally benthonic (Figure 6.5b) and that the orthoconic shell shape was an adaptation for squid-like swimming with the long axis horizontal (Figure 6.5c).

FIGURE 6.6: *Scaphites hugardianus* reconstructed as a benthonic animal, with the aperture toward the sea floor.

FIGURE 6.7: *Hamites tenuis* is an hamiticonic hamitid with the planar coil and first shaft slightly angled with respect to the plane in which the second and third shaft lie, as illustrated by these ventral (Figure 6.7a) and lateral (Figure 6.7b) views of a restored shell.

FIGURE 6.8: *Hamitella maximus* is an hamiticonic hamitid which contrasts with *Hamites tenuis* by having all three shafts in a single plane, but with the juvenile coil being helical.

This is illustrated by these reconstructions of a juvenile (Figure 6.8a) and subadult (Figure 6.8b). The adults have three shafts, but for clarity a subadult with only two shafts is shown here.

FIGURE 6.9: Cladogram showing the relationships of the genera *Lytohamites*, *Hemiptychoceras*, *Hamitella*, *Proturrilitoides*, *Turrilitoides*, *Pseudhelicoceras*, *Mariella*, and *Ostlingoceras*.

FIGURE 6.10: Cladogram showing the relationships of the species *Hamitella annulatum*, *H. gardneri*, *H. intermedius*, *H. maximus*, and *H. rotundus*. with the Turrilitidae.

FIGURE 6.11: Ontogeny of *Hamitella maximus*. From this diagram, it is apparent that the more derived *Hamitella* (such as *Hamitella annulatum*) and the Turrilitidae may be derived by heterochronic processes. *Hamitella annulatum* has only two straight shafts and the helix is relatively larger, and is similar to the immature (but benthonic) *Hamitella maximus*. In contrast the Turrilitidae lack any straight shafts but instead have large and more persistent helices. They therefore resemble the planktonic juvenile H*amitella maximus*.

FIGURE 7.1: Relative numbers of tilting and non-tilting species of heteromorph ammonite through the Albian in Southeast England based upon Spath (1923-1943), Casey (1961, 1966), and Cooper & Kennedy (1977) but with reference to the species revisions presented in this thesis. The numbers of species of each functional morphotype recorded from each ammonite subzone.

FIGURE 7.2: Comparisons between modern and Albian marine cephalopods:

MODERN FAUNA	ALBIAN FAUNA
Squid (e.g., *Loligo*)	Belemnites, homomorph ammonites
Cuttlefish (e.g., *Sepia*)	Homomorph ammonites (maybe *Scaphites*?)
Octopus (e.g., *Octopus*)	Tilters (*Hamites*, *Anisoceras*)
Spirula (e.g., *Spirula*)	Small non-tilters (*Ptychoceras*)
Cranchid squid (e.g., *Cranchia*)	Big non-tilters (*Lechites*, *Mariella*)
Pearly nautilus (e.g., *Nautilus*)	Homomorph ammonites and nautiloids

APPENDIX ONE

Data matrix used in the cladistic analyses described in the text (Chapters 2 and 3). Question marks (?) indicate missing data.

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	3	3	3	3	3	3	3	3	3	4	4
TAXA:	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	8	9	0	1	2	3	4	5	6	7	8	9	0	1
ANCYLOCERATACEAE	0	2	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	3	3	3	4	0	0	1	0	1	0	0	0	0	1	1	1	0	0
LABECERAS	0	2	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0
PTYCHOCERAS	0	6	1	0	0	0	0	0	3	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
rusticus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	4	4	1	0	1	0	1	0	0	0	0	0	1	1	1	0	0
ANISOCERAS	0	2	0	1	1	0	0	0	2	1	1	0	0	1	0	0	1	1	1	1	1	0	1	2	2	2	2	1	1	1	1	1	0	0	0	0	0	0	1	0	0
armatum	0	2	0	1	1	0	0	0	2	1	1	0	0	1	0	0	1	1	1	1	1	0	1	2	3	2	2	1	1	1	1	1	0	0	0	0	0	0	1	0	0
perarmatum	0	2	0	1	1	0	0	0	2	1	1	0	0	1	0	0	1	1	1	1	1	0	1	2	3	2	2	1	1	1	1	1	0	0	0	0	0	0	1	0	0
arrogans	0	2	0	1	0	0	0	0	2	2	0	1	0	0	0	0	1	1	1	1	0	0	0	2	2	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
METAHAMITES	0	2	0	1	0	0	0	1	2	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0
dalpiazi	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	2	2	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
PROTANISOCERAS	0	2	0	1	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	2	2	2	2	0	1	1	1	1	0	0	0	0	1	1	1	0	0
cantianum	0	2	0	1	0	0	0	2	2	0	0	0	0	0	0	0	1	1	0	1	0	0	0	2	2	2	2	0	1	1	1	1	0	0	0	0	1	1	1	0	0
coptense	0	2	0	1	0	0	0	2	2	0	0	0	0	0	0	0	1	1	0	1	0	0	0	2	2	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0
blancheti	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	2	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
halleri	0	2	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	2	2	1	2	0	1	1	1	1	0	0	0	0	0	1	0	0	0
vaucherianum	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	2	2	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0
HETEROCLINUS	0	2	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	2	2	0	0	0	1	2	1	2	0	0	0	0	0	1	1	0	0
TORQUISTYLUS	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	2	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0
acteon	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	2	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0
IDIOHAMITES	0	2	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	2	2	2	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0
spiniger	0	2	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	2	3	2	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0
ROSSALITES	0	2	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	0	2	1	2	1	0	0	1	0	1	0	0	0	0	1	1	0	0
LECHITES	0	4	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
SCIPONOCERAS	0	4	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	1	0	0
TUBEROLECHITES	0	4	?	?	?	?	?	1	1	1	0	0	0	0	0	0	1	2	0	1	0	0	0	2	2	0	0	0	1	1	1	1	0	?	?	0	?	?	?	0	?
LYTOHAMITES	0	3	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
sulcatostriatus	0	3	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
renzi	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	1	0	0
HAMITES	0	3	0	1	1	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	0
compressus	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	0
funatus	0	3	0	1	0	0	0	1	1	1	1	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
hybridus	0	1	0	1	0	0	0	2	2	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0
incurvatus	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	0
nokonsis	0	2	0	1	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0
parkinsoni	0	3	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0
praegibbosus	0	2	0	1	0	0	0	0	2	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
virgulatus	0	2	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
tenuicostatus	0	3	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	1	1	0	0
tenuis	0	3	0	1	0	0	0	1	2	2	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	1	0	0
SCAPHAMITES	0	2	0	1	1	0	0	2	2	2	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	1	1	0	0
PSILOHAMITES	0	4	?	?	?	?	?	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HEMIPTYCHOCERAS	0	3	1	0	?	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0

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	3	3	3	3	3	3	3	3	3	4	4
TAXA:	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	8	9	0	1	2	3	4	5	6	7	8	9	0	1
HAMITELLA	0	2	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	1	0	0	0	1	1	0	0
gardneri	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0
intermedius	0	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	1	0	0	0	1	1	0	0
maximus	0	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	1	0	0	0	1	1	0	0
rotundus	0	2	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0
EOSCAPHITES	0	2	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0
subcircularis	0	2	0	1	0	0	0	2	4	4	1	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	1	0	0
SCAPHITES	0	2	0	1	0	0	1	2	4	4	1	0	0	0	1	0	1	1	0	0	1	0	1	0	0	4	1	1	0	1	0	2	0	0	1	0	0	0	1	0	0
pygmaeum	0	2	1	0	0	0	0	0	3	3	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?
worthense	0	2	1	0	0	0	0	0	3	3	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
PROTURRILITOIDES	1	0	0	1	3	1	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	1	1	0	0
TURRILITOIDES	2	0	0	1	3	2	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	2	0	0	0	1	1	0	0
MARIELLA	2	0	0	1	3	2	0	5	5	5	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	1	0	0
OSTLINGOCERAS	2	0	0	1	3	2	0	5	5	5	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	1	0	0
PSEUDHELICOCERAS	2	0	0	1	3	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	1	0	0
robertianum	2	0	0	1	3	1	0	5	5	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	1	0	0
catenatum	2	0	0	1	3	1	0	5	5	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	2	0	0	0	0	1	0	0

APPENDIX TWO

Distribution of the heteromorphs studied here from sediments of Albian age.

1 ANISOCERATIDAE

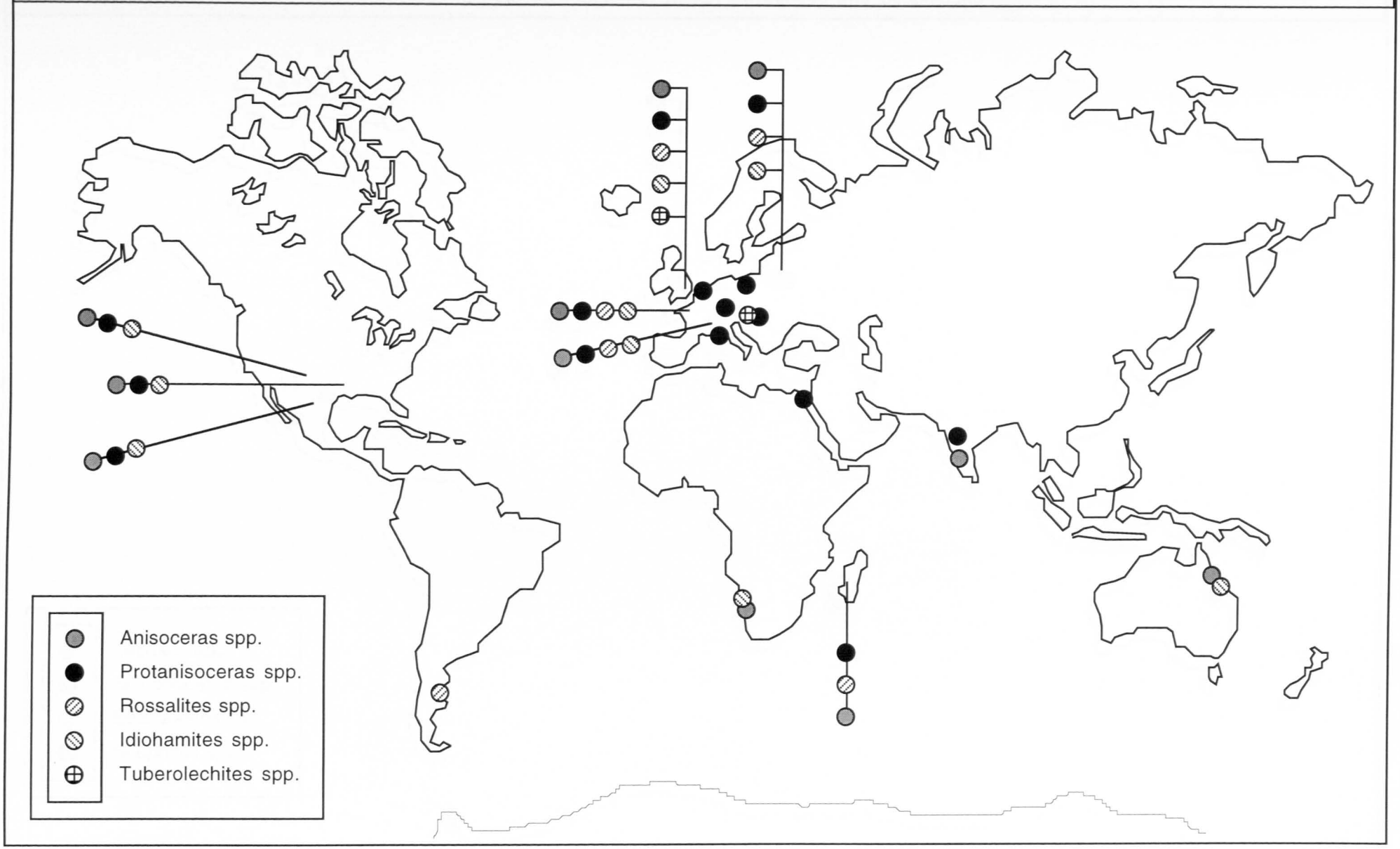
2 BACULITIDAE & SCAPHITIDAE

3 HAMITIDAE

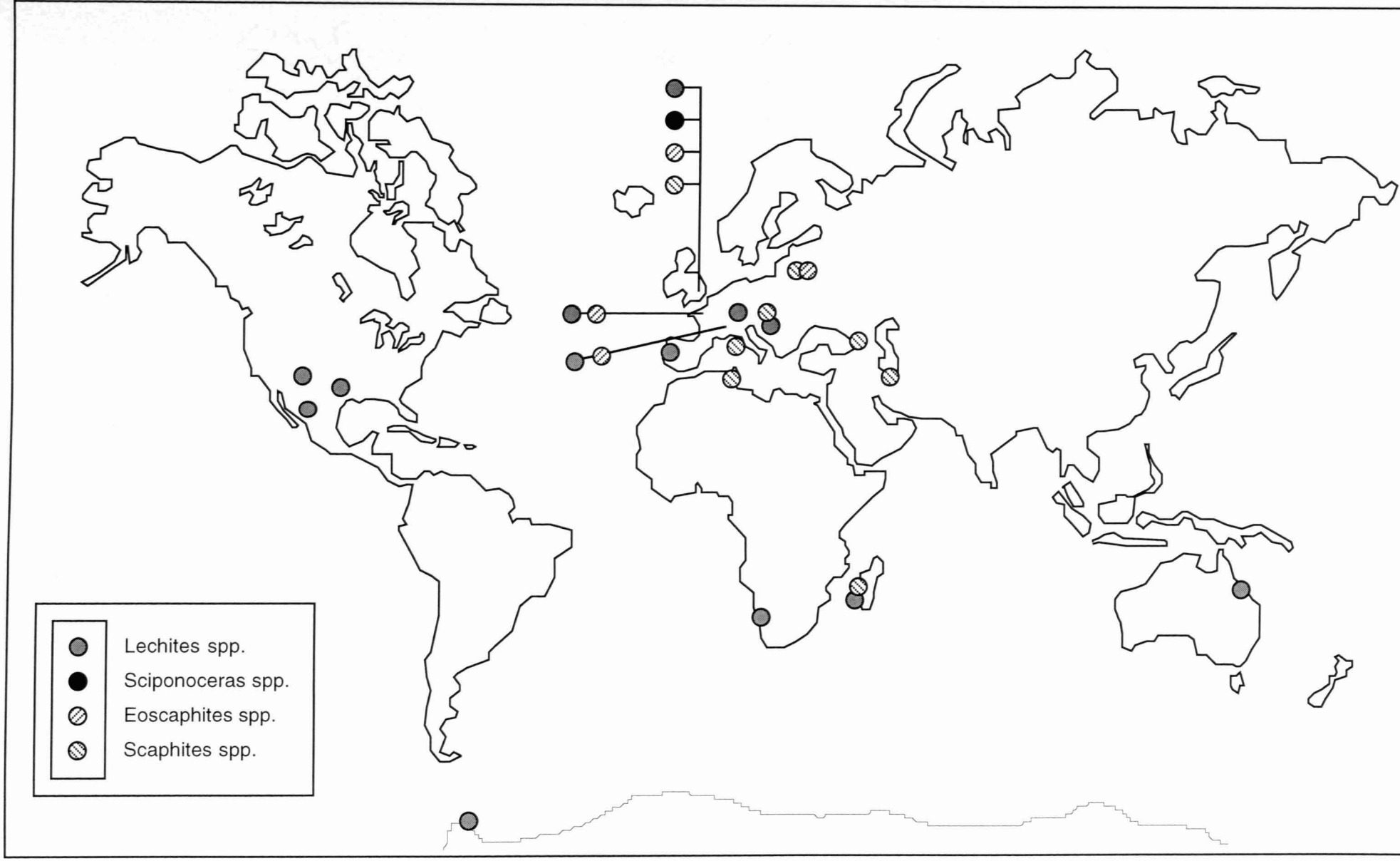
4 TURRILITIDAE

5 PTYCHOCERATIDAE & *HAMITOIDES*

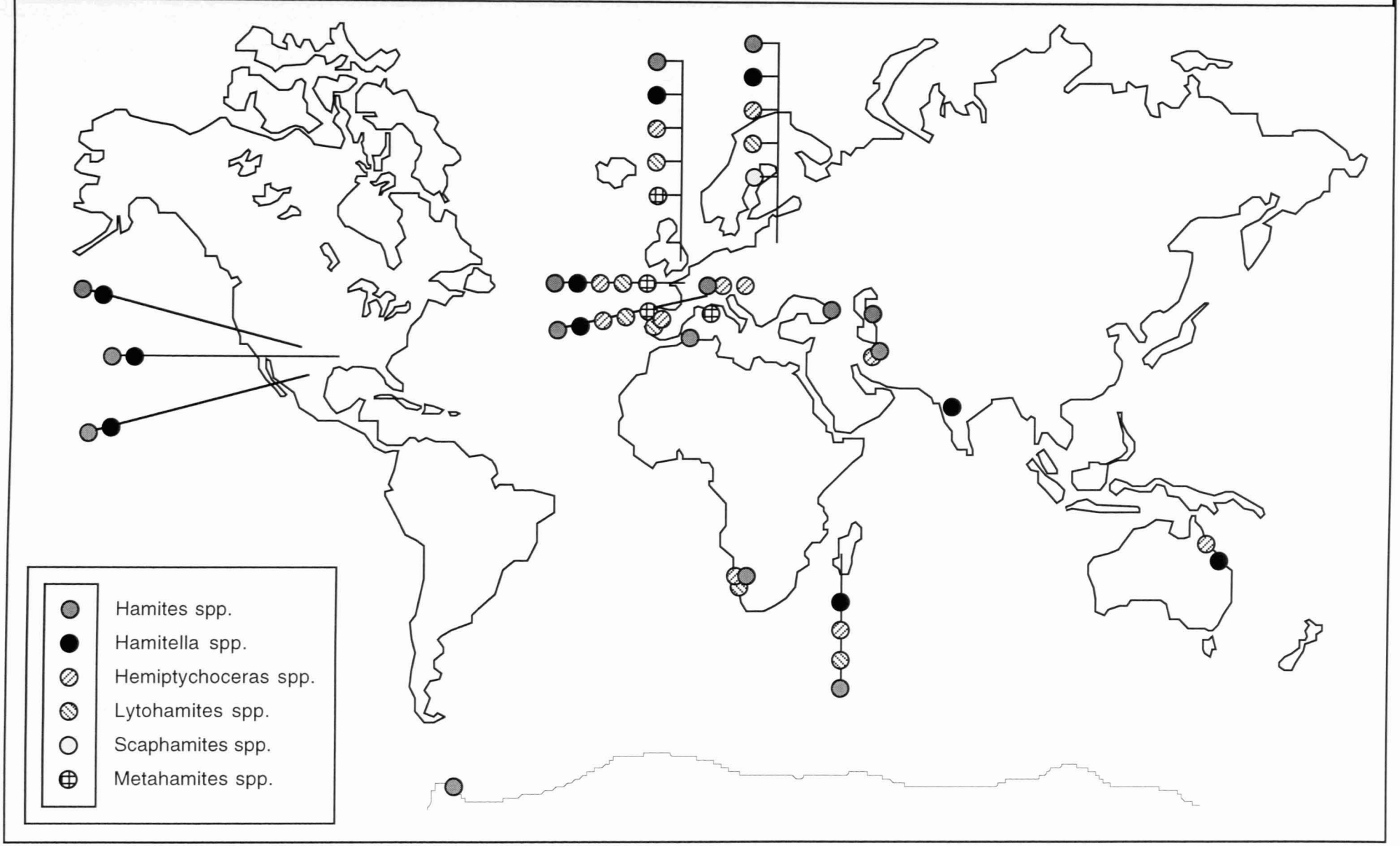
Appendix 2i: Distribution of Albian Anisoceratidae



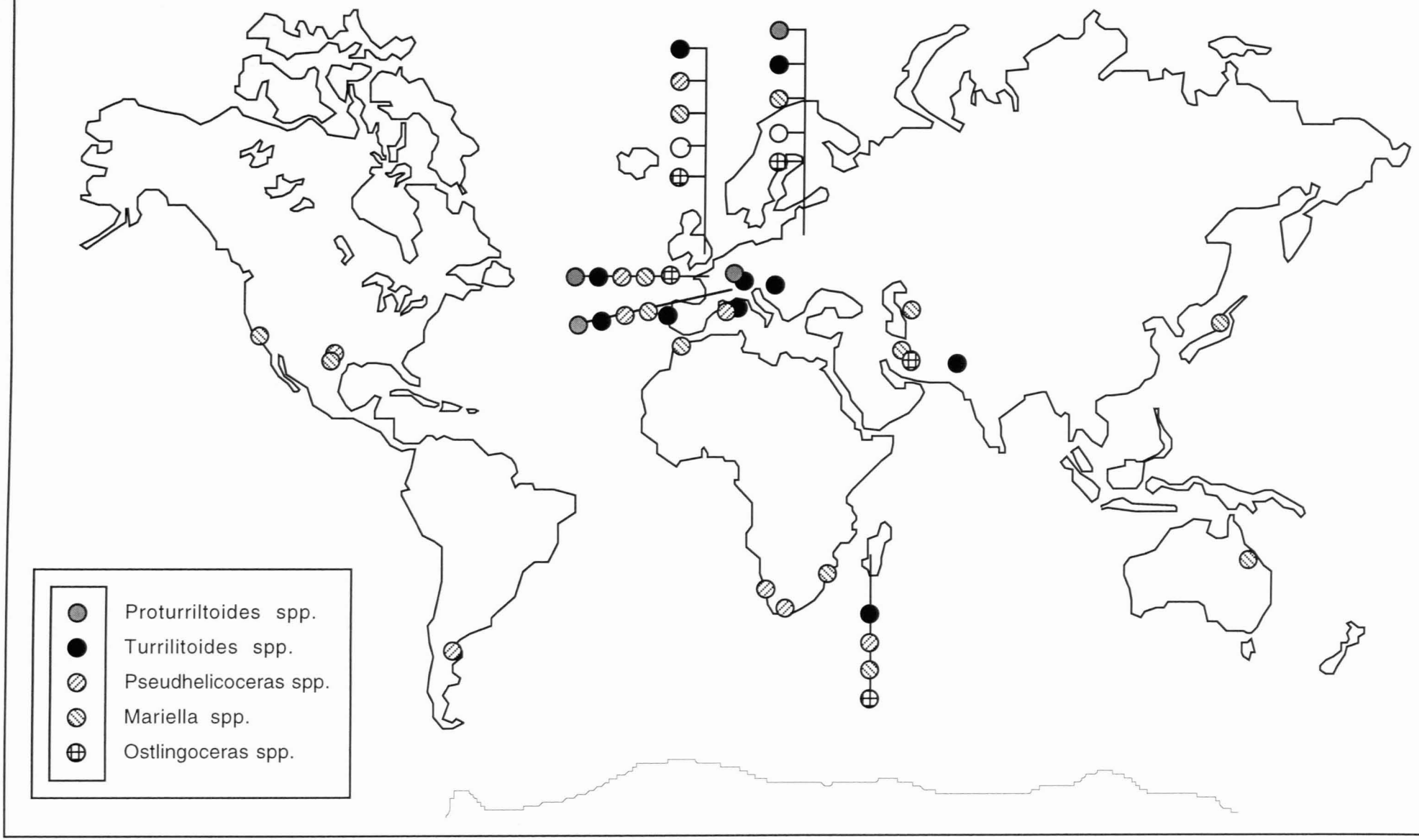
Appendix 2ii: Distribution of Albian Baculitidae and Scaphitidae



Appendix 3iii: Distribution of Albian Hamitidae



Appendix 3iv: Distribution of Albian Turrilitidae



Appendix 3v: Distribution of Albian Ptychoceratidae and Hamitoides



REFERENCES

Adkins W. S. 1920. The Weno and Pawpaw formations of the Texas Comanchean. **University of Texas Bulletin,** 1856: 1-172, 11 pls.

Adkins W. S. 1923. Geology and mineral resources of McLennan County. **University of Texas Bulletin,** 2340: 1-202, 4 pls.

Adkins W. S. 1928. Handbook of Texas Cretaceous Fossils. **University of Texas Bulletin,** 2838: 1-330, 37 pls.

Adkins W. S. & Arick M. B. 1930. Geology of Bell County, Texas. **University of Texas Bulletin,** 3016: 1-92.

Adkins W. S. & Winton W. M. 1920a. Paleontological Correlation of the Fredericksburg and Washita Formations in North Texas. **University of Texas Bulletin,** 1945: 1-128, 21 pls.

Akpan E. B., Farrow. G. E. & Morris. N. J. 1982. Limpet grazing on Cretaceous algal-bored ammonites. **Palaeontology,** 25: 361-367.

Alexander R. McN. 1990. **Animals.** Cambridge University Press, Cambridge, UK.

Ali-Zade A. A. 1988. **Cretaceous Fauna of Azerbaijan.** 344 pp. Academy of Azerbaijan SSR., Institute of Geology, Baku, Azerbaijan.

Almela A. & de la Revilla J 1957. Fósiles piritosus del Cretáceo de la Sierra de Ricote (Murcia). **Boletín del Instituto Geológico Y Minero de España,** 68: 45-83.

Anderson F. M. 1938. Lower Cretaceous Deposits in California and Oregon. **Geological Society of America Special Paper,** 16: 1-399.

Anderson F. M. 1958. Upper Cretaceous of the Pacific Coast. **Bulletin of the Geological Society of America,** 71: 1-378.

Anon. 1995. Gigantic fossils reveal new traits. **Geotimes,** August 1995: 7-8.

d'Archiac E. J. A. D. de St. S. 1839. Observations sur le Groupe moyen de la formation Crétacée. **Memoir de la Societe Geologique de France,** 1: 261-311.

Arkell, W. J., Furnish, W. M., Kummel, B., Miller, A.K., Moore, R. C., Schindewolf, O. H., Sylvester-Bradley, P. C., & Wright C. W. 1957a. Introduction to Ammonoidea, p. L1-L10. In Moore, R. C. (ed.), **Treatise on Invertebrate Paleontology, Part L, Mollusca 4. Geological Society of America & University of Kansas Press,** Lawrence, Boulder, Colorado & Lawrence, Kansas.

Arkell, W. J., Kummel, B., & Wright C. W. 1957b. Mesozoic Ammonoidea, p. L80-L490. In Moore, R. C. (ed.), **Treatise on Invertebrate Paleontology, Part L, Mollusca 4. Geological Society of America & University of Kansas Press,** Lawrence, Boulder, Colorado & Lawrence, Kansas.

Baldwin J. 1987. Energy metabolism of *Nautilus* swimming muscles, p. 325-330. In W. B. Saunders & N. H. Landman (eds.), ***Nautilus*: The Biology and Palaeobiology of A Living Fossil.** Plenum Press, New York, USA.

Ballantine J. A., Roberts J. C., & Morris R. J. Sterols of the cephalopod *Spirula spirula*. **Journal of the Marine Biological Association, UK,** 61: 843-850.

Bandel K. 1988 Operculum and buccal mass of ammonites, p. 653-678. In Wiedmann J. & Kullmann J. (eds.), **Cephalopoda—Present and Past. O. H. Schindewolf symposium (Second International Cephalopod Symposium) Tubingen 1985.** Schweizerbarts'che, Stuttgart, Germany.

Barbu I. Z. 1932. Catalogul Cephalopodelor fosile din Romania. Academia Romana. **Analele, Memoriile Sectiunii Stiintifico,** Series 3, Volume 8, Memoir 8: 1-35.

Barnes J. 1985. **The Complete Works of Aristotle.** Volume 1. pp. 1250. Princeton University Press, Princeton, New Jersey, USA.

Barrois C. 1878. Mémoire sur le Terrain Crétacé des Ardennes etudes régions voisines. **Annales de la Societe Geologique du Nord,** 5: 227-487.

Barron E. J., Harrison C. G.. A., Sloan J. L. & Hay W. W. 1981. Palcogepgraphy, 180 million years ago to the present. **Eclogae Geologicae Helvetiae,** 74: 433-470.

Barron E. J. 1987. Cretaceous plate tectonic reconstructions. **Palaeogeography, Palaeoclimatology, Palaeecology,** 59: 3-30.

Basse E. 1931. **Monographie Paléontologique du Crétacé de la Province de Maintiranon, Madagascar. Gouverment Géneral de Madagascar et Dépendencies Service des Mines,** p. 1-87, 13 pls.

Batt R. J. 1989. Ammonite shell morphotype distributions in the Western Interior Greenhorn Sea and some paleoecological implications. **Palaios,** 4: 32-42

Batt R. J. 1991. Sutural amplitude of ammonite shells as a paleoenvironmental indicator. **Lethaia,** 24: 219-225.

Bayer U. 1974. Die Runzelschicht — ein Leichbauelement der ammonitenschale. **Paläontologische Zeitschrift,** 48: 6-15.

Bayer U. 1982. Ammonite maneuverability — a new look at the function of shell geometry. **Neues Jahrbuch für Geologie und Palaontologie Abhandlung** 164: 154-157.

Behrens D. W. 1980. **Pacific coast nudibranchs: a guide to the opisthobranchs of Northeastern Pacific.** 112 pp. Sea Challengers, Los Osea, California, USA.

Benavides-Cáceras V. E. 1956. Cretaceous system in Northern Peru. **Bulletin of the American Museum of Natural History,** 108: 357-498.

Berthold T. & Engeser T. 1987. Phylogenetic analysis and systematization of the Cephalopoda. **Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, Neue Folge,** 29: 187-220.

Besonov N. V. & Mikhailova I. A. 1983. Evolution of the Jurassic-Cretaceous Ammonoidea. **Doklady Akademii Nauk SSSR** 269: 733-737.

Boehm, J. 1925. Fauna des oberen Alb bei Ootmarsum (Holland). **Zeitschrift der Deutschen Geologischen Gesellschaft,** 77: 198-205.

Boucher-Rodoni R. & Mangold K. 1994. Ammonia Production in Cephalopods, Physiological and Evolutionary Aspects, p. 53-60. In H. O. Pörtner, R. K. O'Dor & D. L. Macmillan (eds.), **Physiology of Cephalopod Molluscs—Lifestyle and Performance Adaptations.** Gordon & Breach Science Publishers S. A., Basel, Switzerland.

Bouchet, P. 1997. Inventorying the molluscan diversity of the world: what is our rate of progress? **Veliger,** 40: 1-11.

Boule M., Lemoine P., & Thévenin A. 1907. Paléontologie de Madagascar. 3. Céphalopodes crétaciques des Environs de Diego Suarez. **Annales de Paléontologie,** 1 (4): 173-192.

Böse E. 1923. Algunas Faunas Cretaceas de Zacatecas, Durango y Guerréo. **Boletin del Instituto Geologico de Mexico,** 25: 1-193.

Böse E. 1928. Cretaceous Ammonites from Texas and northern Mexico. **University of Texas Bulletin,** 2748: 143-312, 18 pls.

Boyle P. R. 1981. Molluscs and man. **Institute of Biology's studies in biology 134,** 1-66. Edward Arnold, London, UK.

Boyle P. R. 1987 Molluscan comparisons, p. 307-327. In P. R. Boyle (ed.), **Cephalopod Life Cycles, Part 2.** Academic Press, London, UK.

Boyle P. R. 1991. **The UFAW handbook on the care and management of cephalopods in the laboratory.** 63 pp. Universities Federation for Animal Welfare, Potters Bar, UK.

Boyle P. R., Grisley M. R., & Robertson G. 1986 Crustacea in the diet of *Eledone cirrhosa* Mollusca: Cephalopoda determined by serological methods. **Journal of the Marine Biological Association of the United Kingdom,** 66: 867-879.

Braga J. C., Company M., García-Hernández M., Linares A., Rivas P. & Sandoval J. 1982. El Albense Superior en el sector de Huescar (Province de Granada, Cordilleras Beticas). **Cuadermos Geologia Ibérica,** 8: 703-720.

Breistroffer M. 1931a. Sur l'étage Albien en Chantreuse (Isère et Savoie). **Compte Rendu de l'Academie des Sciences,** 93: 1202-1204.

Breistroffer M. 1933. Étude de l'étage Albien en Chartreuse (Isère et Savoie). **Travaux Laboratoire de Géologie L'Université de Grenoble,** 1933: 187-236.

Breistroffer M. 1934. Sur le gisement fossilifère albien d'Entrèves-en-Bauges (Savoie). **Association Francaise pour l'Avancement des Sciences de Chambery, Geólogie et Mineralogie,** 1933: 233-234.

Breistroffer M. 1936a. Les subdivisions du Vraconien dans le Sud-Est France. **Bulletin Societe Géologique de France,** [5] iv, 63-68.

Breistroffer M. 1936b. Sur quelques ammonites rares du Vraconien de France. **Compte Rendu Sommaire des seances de la Societe Géologique de France,** 2, 23-25.

Breistroffer M. 1940. Révision des ammonites des Vraconien de Salazac (Gard) et considerations générales sur ce sous-étage albien. **Travaux Laboratoire de Géologie L'Université de Grenoble,** 22: 1-101.

Breistroffer M. 1946. Sur l'âge exacts des grès verts de Cambridge (Angleterre). **Compte Rendu Sommaire des seances de la Societe Géologique de France,** 1946: 309-312.

Breistroffer M. 1947. Sur les zones d'ammonites de l'Albien de France et d'Angleterre. **Travaux Laboratoire de Géologie L'Université de Grenoble,** 26: 1-88.

Breistroffer M. 1953. L'évolution des Turrilitidés albiens et cenomaniens. **Comptes Rendus de Académie Sciences de France,** 237: 1349-1351.

Breistroffer M. & Villoutreys O. 1953. Les ammonites albiennes de Pielle (Alpes-Maratimes). **Travaux Laboratoire de Géologie L'Université de Grenoble,** 30: 69-74.

Bréhéret J. G., Caron M., & Delamette M 1986. Niveaux riches en matiere organique dans l'Albien Vocontien, quelqes caracteres du paleoenvironment, essai d'interpreation genetique. **Documents de la Bureau de Recherches Geologiques et Minieres,** 110: 141-191.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. **Evolution,** 42: 795-803.

Bristow H. W. 1889. **Geology of the Isle of Wight.** Memoir of the Geological Survey (England and Wales), second edition 349 pp. + 7 pls. Geological Survey UK, London, UK.

Brogniart A. 1822. In Cuvier G. L. C. F. D. & Brogniart A. (eds.), **Description géologiques des environs de Paris.** Paris, France.

Brogniart A. 1829. **Tableau des Terrains qui composent l'écorce du globe ou essai sur le structure de la partie connue de la Terre.** viii + 435 pp. Paris, France.

Bronn H. G. 1848. **Index Palaeontologicus, Nomenclator.** Volume 1, lxxxiv + 755 pp, volume 2 776-1382. Stuttgart.

Brown H. J. W. 1929. Notes on the Geology of the Vale of Holmesdale, between Maidstone and London. **Proceedings of the Croydon Natural History Society,** 10: 1-6.

Brown T. 1837. **Atlas of Fossil Conchology.** 273 pp + 97 pls. London, UK.

Brown T. 1889. **Atlas of Fossil Conchology.** Second edition, 230 pp + 97 pls. London, UK.

Bruun A. F. 1943. The biology of *Spirula spirula* (L.). Carlsberg Foundation's Oceanographic Expedition round the World 1928-1930. **Dana Report,** 24: 1-46.

Bruun A. F. 1955. New light on the biology of *Spirula*, a mesopelagic cephalopod, p. 61-72. **In Essays in the Natural Sciences in Honour of Captain Allan Hancock.** University of Southern California Press, Los Angeles.

Bucher H., Landman N. H., Klofak S. M., & Guex J. 1996. Mode and rate of growth in ammonoids, 407-461. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Buchsbaum R. 1968 **Animals Without Backbones.** Ninth UK edition. 2 volumes, 404 pp. Penguin Books, London, UK.

Buckland W. 1837. **Geology and Mineralogy, considered with reference to Natural Theology. Bridgewater Treatise 6.** 2 volumes. xvi + 599 pp, vii + 128 pp, 87 pls. William Pickering, London, UK.

Bujtor L. 1991. A new *Worthoceras* (Ammonoidea, Cretaceous) from Hungary, and remarks on the distribution of *Worthoceras* species. **Geological Magazine,** 128: 537-542.

Buvignier, A. 1852. **Statistique geologique, mineralogique, minerallurgique, et paleontologique du departement de la Meuse, &c.** li + 624 pp, atlas 52 pp. Paris, France.

Carlson B. A. 1987. Collection and maintenance of *Nautilus*, p. 563-578. In W. B. Saunders & N. H. Landman (eds.), ***Nautilus*: The Biology and Palaeobiology of A Living Fossil.** Plenum Press, New York, USA.

Carson R. 1956. **The Sea Around Us.** Penguin Books, London, UK. 224 pp.

Casey R. 1936. Recent Additions to the Ammonoid Faunas of Folkestone. **Geological Magazine,** 63: 444-448.

Casey R. 1950. The junction of the Gault and Lower Greensand in East Sussex and at Folkestone, Kent. **Proceedings of the Geologists' Association,** 61: 268-298.

Casey R. 1951. The Zonal Position of the Gault-Lower Greensand Junction Beds at Wrecclesham, Surrey. **Proceedings of the Geologists' Association,** 62: 95-99.

Casey R. 1954. Notes on the base of the Gault in Wiltshire. **Proceedings of the Geologists' Association,** 66: 231-234.

Casey, R. 1960. **A Monograph of the Ammonoidea of the Lower Greensand. Monographs of the Palaeontographical Society.** Volume 1, p. i-xxxiii, 1-44, pls. 1-10.

Casey, R. 1961. **A Monograph of the Ammonoidea of the Lower Greensand. Monographs of the Palaeontographical Society.** Volume 2, p. 45-118, pls. 11-25.

Chamberlain J. A. 1969. Technique for scale modelling cephalopod shells. **Palaeontology,** 12: 48-55.

Chamberlain J. A. 1976. Flow patterns and drag coefficients of cephalopod shells. **Paleontology,** 19: 539-563.

Chamberlain J. A. 1979. Cameral liquid in *Nautilus* and ammonites. **Paleobiology,** 5: 40-49.

Chamberlain J. A. 1980a. Motor performance and jet propulsion in *Nautilus*: implications for cephalopod palcobiology and evolution. **Bulletin of the American Malacological Union,** 123-127.

Chamberlain J. A. 1980b. The role of body extension in cephalopod locomotion. **Palaeontology,** 23: 445-461.

Chamberlain J. A. 1980c. Hydromechanical design of fossil cephalopods, p. 289-336. In House, M. R. & Senior, J. R. (eds.), **The Ammonoidea. Systematics Association Special Volume 18.** Academic Press, London. UK.

Chamberlain J. A. 1991. Cephalopod locomotor design and evolution. the constraints of jet propulsion, p. 57-98. **Biomechanics in Evolution, Society for Experimental Biology Seminar Series 36.** Cambridge University Press, Cambridge, UK.

Chamberlain J. A. 1993. Locomotion in ancient seas: constraint and opportunity in cephalopod adaptive design. **Geobios,** 15: 49-61.

Chamberlain J. A. & Westermann G 1976. Hydrodynamic properties of cephalopod shell ornament. **Paleobiology,** 6: 168-172.

Checa A. G. & Garcia-Ruiz J. M. 1996. Morphogenesis of the Septum in Ammonoids, 253-296. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Chen Pei-Ji 1987. Cretaceous paleogeography in China. **Palaeogeography, Palaeoclimatology, Palaeecology,** 59: 49-56.

Chenu J. G. **Manuel de Conchyologie et de Paléontologie conchyologique, Vol. 1.** vii + 508 pp.

Christensen W. K. 1976. Palacobiogeography of Late Cretaceous belemnites of Europe. **Palãontologische Zeitschrift,** 50: 113-129.

Cielinski S. 1959. The Albian and Cenomanian in the northern periphery of the Swiety Kryz Mountains. **Institute of Geology Prace,** 28: 1-95.

Ciry R. 1927. Revision de la Faune Albienne du Départment de la Côte d'Or. **Bulletin de la Societe d'Histoire Naturelle de Toulouse,** 62: 549-575.

Clark, D. L. 1962 Paedomorphosis, acceleration, and caenogenesis in the evolution of Texas Cretaceous ammonoids. **Evolution,** 16: 300-305.

Clark, D. L. 1965 Heteromorph ammonoids from the Albian and Cenomanian of Texas and adjacent areas. **Geological Society of America Memoir,** 95: 1-99.

Clarke, M. R. 1962 Respiratory and swimming movements in the cephalopod *Cranchia scabra*. **Nature,** 196: 351-352.

Clarke, M. R. 1966. A review of the systematics and ecology of oceanic squids. Advances in **Marine Biology,** 4: 93-300.

Cobban W. A. 1951. Scaphitoid cephalopods of the Colorado Group. **USGS Professional Paper,** 239: 1-42 + 21 pls.

Cobban W. A., Hook S. C. & Kennedy W. J. 1989. Upper Cretaceous rocks and ammonite faunas of south-western New Mexico. **Memoir of the New Mexico Bureau of Mines and Mineral Resources,** 45: 1-137.

Cobban W. A. & Scott G. R. 1972. Stratigraphy and ammonite fauna of the Graneros Shale and Greenhorn Limestone near Pueblo, New Mexico. **USGS Professional Paper,** 645: 1-108 + 41 pls.

Collignon M. 1932. Le ammonites pyriteuses de l'Albien superieur du Mont Raynaud a Madagascar. **Annales Geologique du Service des Mines,** 2: 5-36.

Collignon M. 1949. Recherches sur les faunes albiennes de Madagascar. 1. l'Albien d'Ambarimaninga. **Annales Geologique du Service des Mines,** 16: 1-128.

Collignon M. 1963. **Atlas des fossiles caracteristique de Madagascar: X Albien.** xv + 184 pp. Service Geologique, Tananarive, Madagascar.

Collignon M. 1964. **Atlas des fossiles caracteristique de Madagascar: XI Cenomanien.** xi + 152 pp. Service Geologique, Tananarive, Madagascar.

Collignon M. 1979. Ammonites du Cretacé Moyen-Superieur de l'Angola, p. 1-73, pls. 1-31. In Collignon M. (ed.), **Reconhecimento Cientifco de Angola.** Academia das Ciéncias de Lisboa, Lisbon, Portugal.

Cooper M. R. 1990. A revision of the Scaphitidae (Cretaceous Ammonoidea) from the Cambridge Greensand. **Neues Jahrbuch fur Geologie und Palaontologie Abhandlung** 178: 285-308.

Cooper M. R. 1991. Towards a phylogenetic classification of the Cretaceous ammonites. 1. Collingnoceratacae. **Neues Jahrbuch fur Geologie und Palaontologie Abhandlung** 182: 1-19.

Cooper M. R. 1992. Towards a phylogenetic classification of the Cretaceous ammonites. 2. Lyelliceratacae. **Neues Jahrbuch fur Geologie und Palaontologie Abhandlung** 185: 21-38.

Cooper M. R. 1994a. Towards a phylogenetic classification of the Cretaceous ammonites. 3. Scaphitaceae. **Neues Jahrbuch fur Geologie und Palaontologie Abhandlung** 193: 165-193.

Cooper M. R. 1994a. Towards a phylogenetic classification of the Cretaceous ammonites. 3. Phlycticrioceratacae. **Neues Jahrbuch fur Geologie und Palaontologie Abhandlung** 194: 361-378.

Cooper M. R. 1997. Towards a phylogenetic classification of the Cretaceous ammonites. 3. Euomphaloceratidae. **Neues Jahrbuch fur Geologie und Palaontologie Abhandlung** 203: 1-21.

Cooper M. R. & Kennedy W. J. 1977. A revision of the Baculitidae of the Cambridge Greensand. **Neues Jahrbuch fur Geologie und Palaontologie Monatshefte** 1977 (10): 641-658.

Cope, J. C. W. 1968. Epizoic oysters on Kimmeridgian ammonites. **Palaeontology,** 11: 19-20.

Coquand H. 1862. Géologie et paléontologie de la region sud de la Province de Constatine. **Memoir de la Societe d'Emulation de la Provence,** 2: 430-456.

Cornuel J. 1851. Catalogue des coquilles de Mollusques. Entomostracés et Foramanifères du terrain crétacé inféreur de la Haute-Marne avec diverses observations relatives à ce terrain. **Bulletin de la Societe Geologique de France (second series),** 9: 430-456.

Cotteau G. H. 1853. Études sur le Mollusques fossiles de départment de l'Yonne. **Bulletin de la Societe Sciences et l'Histoire Naturelles de l'Yonne,** 2: 430-456.

Cousteau J-Y, Bernard J F, & Diole P. 1973. **Octopus and squid: the soft intelligence.** 304 pp. Cassell, London, UK.

Crowther, P. R. 1990. Collection care and status material. In Briggs, D. E. G. & Crowther, P. R. (eds.), **Palaeobiology—A Synthesis.** Blackwell Scientific Publications, Oxford, UK.

Crick G. C. 1898a. **List of the Types and Figured Specimens of Fossil Cephalopoda in the British Museum (Natural History).** 103 pp. London, UK.

Crick G. C. 1898b. On the muscular attachment of the animal to its shell in some Fossil Cephalopoda (Ammonoidea). **Transactions of the Linnaean Society of London (Zoology),** 7: 71-113.

Dauphin Y 1979a. Contribution à l'étude de la formation des gisements de Céphalopodes. I. Les coquilles de Spirules (Dibranchiata) de Nouvelle Calédonie. **Cahiers Indo-Pacifique,** 1(2): 165-194.

Dauphin Y 1979b. Contribution à l'étude de la formation des gisements de Céphalopodes. II. Les coquilles de Spirules (Dibranchiata, Cephalopoda) de l'île Maurice (Océan Indien). **Cahiers Indo-Pacifique,** 1(3): 335-351.

Defrance M. J. L. **Dictionaire des Sciences naturelles, Conchyologie.** Volume 20: 1-572.

Delanoy G. & Latil J-L. 1988. Découverte d'un nouveau gisement Albien dans les environs de Drap (Alpes-Maratimes) et description d'une riche ammonitofaune d'age Albien terminal. **Geobios,** 21: 749-771.

Denton E. J. 1973. On buoyancy in the lives of modern and fossil cephalopods. **Proceedings of the Royal Society of London Series B,** 185: 273-299.

Denton E. J. & Gilpin-Brown J. B. 1961a. The buoyancy of the cuttlefish *Sepia*. **Journal of the Marine Biological Association of the United Kingdom,** 41: 319-342.

Denton E. J. & Gilpin-Brown J. B. 1961b. The effect of light on the buoyancy of the cuttlefish. **Journal of the Marine Biological Association of the United Kingdom,** 41: 343-350.

Denton E. J. & Gilpin-Brown J. B. 1961c. The distribution of gas and liquid within the cuttlebone. **Journal of the Marine Biological Association of the United Kingdom,** 41: 365-381.

Denton E. J. & Gilpin-Brown J. B. 1971. Further observations on the bouyancy of *Spirula*. **Journal of the Marine Biological Association of the United Kingdom,** 51: 363-373.

Denton E. J. & Gilpin-Brown J. B. 1973. Flotation mechanisms in modern and fossil cephalopods. **Advances in Marine Biology,** 11: 197-268.

Dewey H. The Geology of the Canterbury District. **Proceedings of the Geologists' Association,** 36: 257-290.

Destombes J. P. & Destombes P. 1938. Note sur le Gault de Wissant. **Annales de la Societe Geologique du Nord,** 62: 98-113.

Destombes P. & Destombes J. P. 1965. Distribution Zonale des Ammonites das l'Albien du Bassin de Paris. **Memoire du Bureau de Recherches Geologiques et Minieres,** 34: 255-270.

Diener C. 1912. Lebensweise und Verbreitung der Ammoniten. **Neues Jährbuch für Mineralogie und Geologie,** 2: 67-89.

Diener C. 1925. **Fossilium Catalogus. 1, Animalia. Pt 29, Ammonoidea neocretacea.** 244 pp. W. Junk, Berlin, Germany.

Dieni J. & Massari F. 1963. Le Crétacé inférieur d'Orosei (Sardaigne) et les analogies avec celui de sud-est de la France, p. 759-799. In Colloque sur le Cretace inferieur (Lyon, September 1963). **Bureau de Recherches Geologiques et Minieres Memoires 34.** xxi + 840 pp.

Dixon F. 1851. **The Geology of Sussex, or the Geology and fossils of the Tertiary and Cretaceous formations of Sussex** [edited, with preface by Sir Richard Owen]. xxiv + 469 pp, 65 pl. London, UK.

Doguzhaeva L. 1982. Rhythms of ammonoid shell secretion. **Lethaia,** 15: 385-394.

Doguzhaeva L. & Mikhailova I.1982. The genus *Luppovia* and the phylogeny of Cretaceous heteromorphic ammonoids. **Lethaia,** 15: 55-65.

Doguzhaeva L. & Mutvei H.1989. *Ptychoceras* — a heteromorphic lytoceratid with truncated shell and modified ultrastructure (Mollusca: Ammonoidea). **Palaeontographica A,** 208: 91-121.

Doguzhaeva L. & Mutvei H. 1991. Organization of the soft body in *Aconoceras* (Ammonitina), interpreted on the basis of shell morphology and muscle scars. **Palaeontographica A,** 218: 17-33.

Doguzhaeva L. & Mutvei H.1992. Radula of the Early Cretaceous ammonite *Aconoceras* (Mollusca: Cephalopoda). **Palaeontographica A,** 223: 167-177.

Doguzhaeva L. & Mutvei H. 1993a. Shell ultrastructure, muscle-scars and buccal apparatus in ammonoids. **Geobios,** 15: 111-119.

Doguzhaeva L. & Mutvei H. 1993b. Structural features in Cretaceous ammonoids indicative of semi-internal or internal shells, p. 99-114. In House, M. R. & Senior, J. R. (eds.), **The Ammonoidea. Systematics Association Special Volume 47.** Clarendon Press, Oxford, UK.

Doguzhaeva L. & Mutvei H. 1996. Attachment of the Body to the Shell in Ammonoids, 44-63. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Dollfus G. 1898. Discussion sur le Base de l'étage Cénomanien, Terrain Crétacique. **Feuille des Jeunes Naturilistes,** 328 (iii), 28: 1-13.

Dommergues J-L. 1994. The Jurassic ammonite *Coeloceras*: an atypical example of dimorphic progenesis elucidated by cladistics. **Lethaia,** 27: 143-152.

Donovon D. T. 1949. Observations on the Mesozoic Rocks of Geographical Society Ø, East Greenland. **Meddelelser om Grønland,** 149: 1-14.

Donovon D. T. 1953. The Jurassic and Cretaceous Stratigraphy and Palaeontology of Traill Ø, East Greenland. **Meddelelser om Grønland,** 111: 1-150.

Donovan S. K. 1989. Taphonomic significance of the encrustation of the dead shell of Recent *Spirula spirula* (Linné) (Cephalopoda: Coleoidea) by *Lepas anatifera* Linné (Cirrepedia: Thoracia). **Journal of Paleontology,** 63(5): 698-702.

Douvillé H. 1916. Terrains Secondaires Massif Moghara. **Memoir de la Academie Sciences de France,** 54: 1-184.

Douvillé R. 1906. **Esquisse géologique des Préalpes Subbétiques (partie central).** Dissertation, University of Paris.

Dubourdieu G. 1953. Ammonites nouvelles des Monts du Mellègue. **Bulletin du Service de la Carte Géologique de L'Algérie. 1-er Série Paléontologie,** 16: 1-76, + 4 pls.

Dzik Jerzy 1986 Uncalcified cephalopod jaws from the Middle Jurassic of Poland. **Neues Jahrbuch fur Geologie und Palaontologie Monatshefte,** 1: 405-417.

Ebel K. 1983. Berechnungen zur Schwebefähigkeit von Ammoniten (Calculations on the buoyancy of ammonites). **Neues Jahrbuch fur Geologie und Palaontologie Monatshefte,** 1983: 614-640.

Ebel K. 1985. Gehäusespirale und Septenform bei Ammoniten unter den Annahme vagil benthischer Lebensweise. **Paläontologische Zeitschrift,** 59: 109-123.

Ebel K. 1990. Swimming abilities of ammonites and limitations. **Paläontologische Zeitschrift,** 62: 25-37.

Ebel K. 1992. Mode of life and soft body shape of heteromorph ammonites. **Lethaia,** 25: 179-193.

Ebel K. 1993. Negative buoyancy of ammonoids–reply. **Lethaia,** 26: 260.

Emmerson B. L., Emmerson J. H., Akers R. E. and Akers T. J. 1994. **Texas Cretaceous Ammonites and Nautiloids. Texas Paleontology Series,** 5: 1-439. Paleontology Section, Houston Gem and Mineral Society, Houston, Texas.

Engeser T. 1996. The Position of the Ammonoidea within the Cephalopoda, p. 3-19. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Eriksson T. & Wikström N. 1995. **Autodecay. Version 3.** *Apple Macintosh computer program.*

Etheridge R. 1904. On the occurrence of the genus *Ptychoceras* (?) and other additional fossils in the Cretaceous beds of the Northern Territory of South Australia. **Records of the Australian Museum,** 5: 108-115.

Faith D. P. & Cranston P. S. (1990). Could a cladogram this short have arisen by chance alone?: On permutation tests for cladistic structure. **Cladistics,** 7: 1-28.

Fallot E. 1885. Étude géologique sur les Étages moyens et supérieur du Terrain Crétacé dans le Sud-Est de la France. **Annales de Sciences Geologique,** 3 (7): 289-299.

Fallot P. 1920. La Faunes de Marnes Aptiennes et Albiennes de la region d'Andraintz, Majorque. **Trabajos del Museo Nacional de Ciencias Naturales. Serie Geology,** 26: 1-68.

Favre, E. 1873. Sur la classification des ammonites. **Bulletin de la Societe geologique de France, 3. serie,** 1: 353-355.

Feduccia A. 1996. **The Origin and Evolution of Birds.** 420 pp. Yale University Press, New Haven, USA.

Felsenstein J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. **Evolution,** 39: 783-781.

Fitton W. H. 1835. Observations on some of the Strata between the Chalk and the Oxford Oolite in the South East of England. **Transactions of the Geological Society of London,** 2: 103-390.

Fleming J. 1828. **A History of British Animals.** 565 pp. London, UK.

Flower R. H. 1955. Cameral deposits in orthoconic nautiloids. **Geological Magazine,** 92: 89-103.

Föllomi K. B. 1989. Beschreibung neugefunder Ammonoidea aus der Vorarlberger Garschella-Formation (Aptian — Albian). **Jahrbuch der Geologischen Bundesanstalt,** 132: 7-104.

Förster R. 1975. Die geologosche Entwicklung von Süd-Mozambique seit der Unterkreide und die Ammoniten Fauna von Unterkreide und Cenoman. **Geologisches Jahrbuch,** 12: 3-324.

Frakes L. A., Burger D., Apthorpe M., Wiseman J., Dettmann M., Alley N., Flint R., Gravestock D., Ludbrrok N., Backhouse J., Skwaro S., Scheibnerova V., McMinn A., Moore P. S., Bolton B. R., Douglas J. G., Christ R., Wade M., Molnar R. E., McGowan B., Balme B. E., & Day R. A. 1987. Australian Cretaceous shorelines, stage by stage. **Palaeogeography, Palaeoclimatology, Palaeecology,** 59: 31-48.

Gabb W. B. 1864-1869. Geological Survey of California. **Palaeontology,** 1: 1-243, 2: 1-299.

Gale A. S., Kennedy W. J., Burnett J. A., Caron M. & Marshall J. D. 1997. The Late Albian to Early Cenomanian succession near Rosans (Drômes, S E France), an integrated study (ammonites, inoceramids, planktonic, nannofossils, oxygen and carbon isotopes). **Cretaceous Research,** 17: 515-606.

Gallois R. W. & Morter A. A. 1982. The stratigraphy of the Gault of East Anglia. **Proceedings of the Geologists' Association,** 93: 351-368.

Ganz E. 1912. Stratigraphie der mittleren Kreide (Gargasien und Albien) der oberen helvetischen Decken in der Nördlichen Schweizeralpen. **Neue Denkschriften der Schweizerischen Naturforschenden Gesellschaft,** 47: 1-148.

Geczy B. 1960 A Neoammoideak eletmodjarol . **Foldtani Kozlony Magyar Foldtani Tarsulat,** 90: 200-203.

Ghiretti, F. 1966 Respiration, p. 175-208. In K. M. Wilbur & C. M. Yonge (eds.), **Physiology of Mollusca, Part 2.** Academic Press, New York, USA.

Giebel C. G. 1852. **Die Fauna der Vorwelt Volume 3, Mollusken.** xvi + 856 pp. Leipzig, Germany.

Gienitz H. B. 1849. **Das Quadersandsteingebirge oder Kreideregebirge in Deutschland.** 293 pp, 12 pls. Freiburg, Germany.

Gill T. 1871. Arrangement of the Families of Mollusks. **Smithsonian Miscellaneous Collection,** 227: 1-???.

Goloboff P. A. 1991. Homoplasy and the choice among cladograms. **Cladistics,** 7: 15-232.

Gossling F. 1929. The Geology of the Country around Reigate. **Proceedings of the Geologists' Association,** 40: 197-259.

Gould S. J. 1977. **Ontogeny and Phylogeny.** Belknap Press, Cambridge, UK.

Graves L. **Essais sur le topographie geógnostique du départment. de l'Oise.** 804 pp. Beauvais, France.

de Haan G. 1825. **Monographiae Ammoniteorum et Goniatiteorum.** vii + 168. Lugdui Batavorum, Holland.

Grisley M. S. 1993 Separation and partial characterization of salivary enzymes expressed during prey handling in the octopus *Eledone cirrhosa*. **Comparative Biochemistry and Physiology,** 105B: 183-192.

Grisley M. S. & Boyle P. R. 1990 Chitinase, a new enzyme in octopus saliva. **Comparative Biochemistry and Physiology,** 95B: 311-316.

Haas O 1942. The Vernay collection of Cretaceous (Albian) Ammonites from Angola. **Bulletin of the American Museum of Natural History,** 81: 1-224.

Hancock J. M. & Kauffman E. G. 1979. The great transgressions of the Late Cretaceous. **Journal of the Geological Society of London,** 136: 175-186.

Hattin D. E. 1975. Stratigraphy and depositional environment of the Greenhorn Limestone (Upper Cretaceous) of Kansas. **Bulletin of the Kansas University Geological Survey,** 209: 1-128.

Hattin D. E. 1977. Upper Cretaceous stratigraphy, paleontology and paleoecology of Western Kansas with a section on the Pierre Shale by W. A. Cobban. **Mountain Geologist,** 14: 175-218.

von Hauer F. 1861. Uber die Petrefakten der Kreideformation des Bakonyer Waldes. **Sitzungs-Berischte kaiserlischen und koenigslischen der Akademie der Wissenschaften in Wien,** 44: 631-659.

Haq B. 1984. Paleoceanography: A synoptic overview of 200 million years of ocean history, 201-230. In Haq B. U & Milliman J. D. (eds.) **Marine Geology and Oceanography of the Arabian Sea and Central Pakistan.** Van Nostrand Reinhold, New York, USA.

Haq B. 1991. Sequence stratigraphy, sea-level change and significance for the deep sea. **International Association of Sedimentologists Special Publication,** 12: 3-39.

Haq B., Hardenbol, J. & Vail, P. R. 1987. Chronology and fluctuating sea levels since the Triassic. **Science,** 235: 1156-1166.

Hébert E. & Toucas A.1875. Matériaux pour servir à la description du terrain crétacé supérieur en France. Description du Bassin d'Uchaux. **Annales de Sciences Geologique,** 5: 1-132.

Heim A. & Seitz O. 1934. Die Mittlere Kreide in den alpen von Rheintal und Voralberg und das problem der Kondensation. **Denkschriften der Schweizerischen Naturforschenden Gesellschaft,** 69: 185-310.

Heller J. 1990. Longevity in Molluscs. **Malacologia,** 31: 259-295.

Henderson R. A. 1973. Clarence and Raukumara Series (Albian - ?Santonian) Ammonoidea from New Zealand. **Journal of the Royal Society of New Zealand,** 3: 71-123.

Henderson R. A. 1984. A muscle attachment proposal for septal function in Mesozoic ammonoids. **Palaeontology,** 27: 461-486.

Henderson R. A. 1990. Late Albian ammonites from the Northern Territory, Australia. **Alcheringa,** 14: 109-148.

Hengsbach R. 1996. Ammonoid Pathology, 581-605. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Hewitt R. A. 1985. Numerical aspects of sutural ontogeny in the Ammonitina and Lytoceratina. **Neues Jahrbuch für Geologie und Paläontologie Abhandlung,** 170: 273-290.

Hewitt R. A. 1996. Architecture and Strength of the Ammonoid Shell, 297-339. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Hewitt R. A, Westermann G. E. G., & Checa A 1993 Growth rates of ammonites estimated from aptychi, p. 203-208. In S. Elmi, C. Mangold & Y. Almeras (eds.), **3-eme Symposium international sur le Cephalopodes actuels et fossiles. Geobios Memoire Special 15.**

Hillis D. M. & Bull J. J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. **Heredity,** 83: 189-195.

Hitzel E. 1905. Sur les fossiles de l'Étage albien recueillis par M. A. Guébhard dans la region d'Escragnolles (Alpes-Maritimes). **Bulletin de la Societe Geologique de France, fourth series,** 2: 874-880.

Hollis E. 1971. Occurence of the ammonite *Ptychoceras gaultinum* (J. Sowerby) in the Upper Albian of Kent, England. **Palaeontology,** 14: 592-594.

House, M. R. 1993. Fluctuations in ammonoid evolution and possible environmental controls, p. 13-34. In House, M. R. & Senior, J. R. (eds.), **The Ammonoidea. Systematics Association Special Volume 47.** Clarendon Press, Oxford, UK.

Howarth M. K. 1992 **The ammonite family Hildoceratidae in the Lower Jurassic of Britain. Monograph of The Palaeontographical Society.** The Palaeontographical Society, London, UK.

Immel H. 1979. Cenoman-Ammoniten aus den Losensteiner Schichten der Bayerischen-Alpen, p. 607-644. In Wiedmann J. (ed.), **Aspekte der Kriede Europas: beitraege zum 1 Symposium Deutsche Kriede-Bindeglied zwischen Boreal und Tethyz-Muenster in Westfalen April 1978. International Union of Geological Sciences. Series A, Volume 6.**

Immel H. 1987. Die Kreideammoniten der Nördlichen Kalkalpen. **Zitteliana,** 15: 3-163.

Immel H. & Seyed-Emami K. 1985. Die Kreideammoniten des Glaukoniticalkes (O. Alb-O. Cenoman) des Kolak-Qazi-Gebirges südöstlich von Esfahan (Zentraliran). **Zitteliana,** 12: 87-137.

Ivanov A. N. & Pietresson de Saint-Aubin J. 1995. Sur le mode de vie planctonique des ammonites mesozoïques. **Association Geologique Auboise Bulletin Annuel,** 16: 41-48.

Jacobs D. K. & Landman N. H. 1993 *Nautilus*—A poor model for function and behaviour of ammonoids? **Lethaia,** 26: 101-188.

Jayet A. 1926a. Étude stratigraphique de la Perte-du-Rhône, près de Bellegarde (Ain). **Eclogae Geologicae Helvetiae,** 20: 159-222.

Jayet A. 1926b. Sur les mélanges de faunes de l'Albién du Genevois (Haute-Savoie). **Compte Rendu des seances de la Societe de Physique et d'Histoire Naturelle de Geneve,** 43: 155-158.

Jayet A. 1926c. L'Albien du Reposoir (Aravis, Haute-Savoie). **Compte Rendu des seances de la Societe de Physique et d'Histoire Naturelle de Geneve,** 43: 170-172.

Jeletzky J. A. 1968. Macrofossil Zones of the Marine Cretaceous of the Western Interior of Canada and their correlation with the Zones and Stages of Europe and the of Western Interior of the United States. **Canada Geological Survey Paper,** 64-11: 1-100.

Jeletzky J. A. 1977. Mid-Cretaceous (Aptian to Coniacian) history of the pacific Slope of Canada. **Mid-Cretaceous Events, Palaeontological Society of Japan Special Papers,** 21: 97-126.

Jeletzky J. A. 1980. New or formerly poorly known, biochronologically important gastroplitinid and coeniceratid (Ammonitida) taxa from the Middle Albian rocks of midwestern and Arctic Canada. **Canada Geological Survey Paper,** 79-22: 1-62.

Johansen K., Redmond J. R. & Bourne G. B. 1978 Respiratory exchange and transport of oxygen in *Nautilus pompilius*. **Journal of Experimental Zoology,** 205: 27-35.

Jones D. L. 1961. Muscle attachment impressions in a Cretaceous ammonite. **Journal of Paleontology,** 35: 502-504.

Jordan R. 1968. Zur Anatomie mesozoischer Ammoniten nach den Strukturalelementen der Gehäuse-Innenwand. **Beihefte zum Geologischen Jahrbuch,** 77: 1-64.

Juignet P. & Kennedy W. J. 1976. Faunes d'Ammonites et biostratigraphie comparée du Cénomanien du nord-ouest de la France (Normandie). **Bulletin Trimestriel de la Societe Geologique de Normandie et des Amis du Museum du Havre,** 63: 1-193.

Jukes- Brown A. J. 1900. **The Cretaceous rocks of Great Britain. Memoirs of the Geological survey of the United Kingdom. Volume 1: The Gault and Upper Greensand of England.** xiv + 499 pp, 5 pls.

Judd J. W. 1884. Nature and Relations of the Jurassic deposits which underlie London. **Quarterly Journal of the Geological Society of London,** 40: 724, 729-762.

Kakabadza M. V, & Sharakadza M. Z. 1993 On the mode of life of heteromorph ammonites heterocone, ancylocone, ptychocone), p. 209-215. In S. Elmi, C. Mangold & Y. Almeras (eds.), **3-eme Symposium international sur le Cephalopodes actuels et fossiles. Geobios Memoire Special 15.**

Kaplan U. & Schmid F. 1988. Die heteromorphen Ammoniten der Gattungen *Eubostrychoceras* und *Hyphantoceras* aus dem Turon NW-Deutschlands. **Geologie und Paläontologie in Westfalen,** 12: 47-87.

Kauffman. E. G. 1977. Illustrated guide to biostratigraphically important Cretaceous macrofossils, Western Interior Basin USA. **Mountain Geologist,** 14: 225-274.

Kelley S. R. A. & Moncrieff A. C. M. 1992. Marine molluscan constraints on the age of Cretaceous forests of Alexander Island, Antarctica. **Geological Magazine,** 129: 771-778.

Kennedy W. J. 1970. A Correlation of the Uppermost Albian and the Cenomanian of South-West England. **Proceedings of the Geologists' Association,** 81: 613-678.

Kennedy W. J. 1971. Cenomanian Ammonites from Southern England. **Special Papers in Palaeontology,** 8:1-133 pp, 64 pls.

Kennedy W. J. 1993. Ammonite faunas of the European Maastrichtian, diversity and extinction, p. 285-326. In House, M. R. & Senior, J. R. (eds.), **The Ammonoidea. Systematics Association Special Volume 47.** Clarendon Press, Oxford, UK.

Kennedy W. J., Amédro F. & Colleté C. 1986. Late Cenomanian and Turonian ammonites from the Ardennes, Aube and Yonne, eastern Paris Basin. **Neues Jahrbuch für Geologie und Paläontologie Abhandlung,** 172: 193-217.

Kennedy W. J., Chahida M. R. & Djafarian M. A. 1978. Cenomanian cephalopods from the Glauconitic Limestone south-east of Esfahan. **Acta Geologica Polonica,** 24: 3-50, pls. 1 -8.

Kennedy W. J. & Cobban W. A. 1976. Aspects of ammonite biology, biogeography and biostratigraphy. **Special Papers in Palaeontology,** 17:1-94 pp.

Kennedy W. J. & Hancock J. M. 1976. The Mid-Cretaceous of the United Kingdom. **Annales du Muséum d'Histoire Naturelle de Nice,** 4: 1-72.

Kennedy W. J., Hancock J. M. & Christensen W. K. 1980. Albian and Cenomanian ammonites from the island of Bornholm (Denmark). **Bulletin of the Geological Society of Denmark,** 29: 203-244.

Kennedy W. J. & Juignet P. 1983.A revision of the ammonite faunas of the type Cenomanian. 1. Introduction, Ancyloceratina. **Cretaceous Research,** 4: 3-83.

Keupp H 1976. Neue Beispiele für Regenerationsmechanisms bei verletzen und kranken Ammoniten. **Paläontologische Zeitschrift,** 51: 70-77.

Kilian W. 1907-1913. Unterkriede (Palaeocretacicum). In Frech F., **Lethaea Geognostic 2, Mesozoic, Volume 3, Kreide.**

Klassen G. J., Mooi R. D., & Locke A. 1991. Consistency indices and random data. **Systematic Zoology,** 40: 446-457.

Klinger, H. C. 1980. Speculations on Buoyancy Control and Ecology in some Heteromorph Ammonites, p. 337-355. In House, M. R. & Senior, J. R. (eds.), **The Ammonoidea. Systematics Association Special Volume 18.** Academic Press, London, UK.

Klinger, H. C. & Kennedy W. J. 1978. Turrilitidae (Cretaceous Ammonoidea) from South Africa, with a discussion of the evolution and limits of the family. **Journal of Molluscan Studies,** 44: 1-48.

Kluge A. G. 1984. The relevance of parsimony to phylogenetic inference. In Duncan, T. & Stuessey, T. F. (eds.), **Cladistics: Perspectives on the Reconstruction of Evolutionary History.** Columbia University Press, New York, USA.

Kluge A. G. & Farris J. S. 1969. Quantitative phyletics and the evolution of anurans. **Systematic Zoology,** 18: 1-32.

Knetchel M. M., Richards E. F. & Rathbun M. V. 1947. Mesozoic Fossils of the Peruvian Andes. **Johns Hopkins University Studies in Geology,** 15: 1-150, 50 pls.

Knight R. I. 1994. **Mid- and Early Late Albian benthic palaeoenvironments of the Anglo-Paris basin.** PhD Thesis (University of Oxford).

Knight R. I. 1997. Benthic palaeoecology of the Gault Clay Formation (mid and basal Upper Albian) of the western Anglo-Paris Basin. **Proceedings of the Geologists' Association,** 108: 81-103.

Kolodny Y. & Raab M. 1988. Oxygen isotopes in phosphatic fish remains from Israel: Paleothermometry of tropical Cretaceous and Tertiary shelf waters. **Palaeogography, Palaeoclimatology, Palaeoecology,** 64: 59-67.

Korn D. 1995. Paedomorphosis of ammonoids as a result of sea level fluctuations in the Late Devonian *Wocklumeria* Shale. **Lethaia,** 28: 155-165.

Kossmat F. 1895. Untersuchungen über die südindische Kreidformation. **Beitrage zur Paläontologie und Geologie Österreich-Ungarns und des Orients,** 9: 97-203.

Krishna J. 1980. Uncoiled ammonites of Middle Albian (Lower Cretaceous) age from Habur Series, Jaisalmer, Rajasthan. **Journal of the Palaeontological Society of India,** 23 & 24, 49-54.

Kulicki C. 1974. Remarks on the embryology and postembryonal development of ammonites. **Acta Palaeontologica Polonica,** 19: 201-224.

Kulicki C. 1979. The ammonite shell: Its structure, development and biological significance. **Palaeontologica Polonica,** 39: 97-142.

Kulicki C., Doguzheava L. A, & Kabanov G. K. 1988 *Nautilus* jaw like elements of a juvenile ammonite, p. 679-686. In Wiedmann J. & Kullmann J. (eds.), **Cephalopoda—Present and Past. O. H. Schindewolf symposium (Second International Cephalopod Symposium) Tubingen 1985.** Schweizerbarts'che, Stuttgart, Germany.

Landman N. H. 1989. Iterative progenisis in Upper Cretaceous ammonites. **Paleobiology,** 15: 95-117.

Landman N. H. & Cochran J. K. 1987. Growth and longevity of *Nautilus*, p. 401-420. In W. B. Saunders & N. H. Landman (eds.), ***Nautilus*: The Biology and Palaeobiology of A Living Fossil.** Plenum Press, New York, USA.

Landman N. H., Tanabe K., & Shigeta Y. 1996 Ammonoid embryonic development, p. 343-405. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Lane F. W. 1960. **Kingdom of the Octopus.** xx + 300 pp, 52 pls. Sheridan House, New York, USA.

de Lapparent A. A. & Fritel P. 1888. **Fossiles characteristiques des Terrains sédimentaires. Volume 2 Fossiles secondaires.** 20 pls. Paris, France.

Larcher C., Rat P. & Malampris M. 1965. Documents Paléontologiques et Stratigraphiques sur l'Albien de l'Aube. **Memoire du Bureau de Recherches Geologiques et Minieres,** 34: 237-253.

Leanza A. F. 1970. Ammonites nuevos o pocos concidos del Aptiano, Albiano y Cenomaniano de los Andes Australes con notas acerca de su posicion estratigrafica. **Revista de la Asociación Geológica Argentina,** 25: 197-261.

Lebrun P. 1996. Ammonites. **Minéraux et Fossiles, Hors-Série** 4: 1-96.

Lee P. G. 1994. Nutrition of cephalopods: Fueling the System, p. 35-52. In H. O. Pörtner, R. K. O'Dor & D. L. Macmillan (eds.), **Physiology of Cephalopod Molluscs—Lifestyle and Performance Adaptations.** Gordon & Breach Science Publishers S. A., Basel, Switzerland.

Lehmann U. 1967. Ammoniten mit Kieferapparat und Radula aus Lias-Geschieben. **Paläontologische Zeitschrift,** 41: 38-45.

Lehmann U. 1975. Über Nahrung und Ernährungsweise von Ammonites. **Paläontologische Zeitschrift,** 49: 187-195.

Lehmann U. 1981 **The Ammonites.** 246 pp. Cambridge University Press, Cambridge, UK.

Lehmann U 1985. Zur Anatomie der Ammoniten: Tintenbeutel, Kiemen, Augen. **Paläontologische Zeitschrift,** 59: 99-108.

Lehmann U. & Hillmer G. 1983. **Fossil Invertebrates.** xiv + 350 pp. Cambridge University Press, Cambridge, UK.

Lehmann U. & Weitschat W, 1973 Zur Anatomie und Okologie von Ammoniten: Funde von Kropf und Kiemen. **Palãontologische Zeitschrift,** 47: 69-76.

Lemoine P. 1911. **Géologie du Bassin de Paris.** 408 pp , 9 pls. Paris, France.

Leymerie A. & Raulin V. 1858. **Statistique géologique du départment de l'Yonne.** 864 pp, 4 pls. Paris, France.

Lewy Z. Octopods: Nude ammonoids that survived the Cretaceous-Tertiary boundary mass extinction. **Geology,** 24: 627-630.

Lory C. 1851. Sur la série des terrain crétacés du department de l'Isère. **Bulletin de la Societe Geologique de France (second series),** 9: 51-71.

Mackie S. J. 1860. Geology of Folkestone. **Geologist,** 3: p. 41-45, 81-90, 121-131, 201-207, 281-284, 321-327, 353-357, 393-396.

Macsotay O. 1971. Significado cronologico y palcoecologico de los amonites desenrollados dc la formacion Chupista del grupo Caracas. IV Congreso Geologico Venezolano 1969. **Boletin de Geologia, Special Publication,** 5: 1703-1714.

Madisson, W. P. & Madisson, D. R. 1992. **MacClade: Analysis of Phylogeny and Character Evolution, Version 3.05.** Sinauer Associates, Sunderland, Massachusetts, USA. *Apple Macintosh computer program.*

Malinowka L. 1989. **Geology of Poland, Part 2c, Mesozoic, Cretaceous.** 422 pp. Warsaw, Poland.

Mangold K. 1987 Reproduction, p. 157-200. In P. R. Boyle (ed.), **Cephalopod Life Cycles. Part 2.** Academic Press, London, UK.

Mantell G. A. 1822. **Fossils of the South Downs.** 320 pp, 43 pls. London, UK.

Mantell G. A. 1829. A scientific catalogue of the organic remains of Sussex. **Transactions of the Geological Society,** 2: 201-216.

Mantell G. A. 1833. **The Geology of South East England.** 415 pp, 7 pls. London, UK.

Mantell G. A. 1850. **Pictorial Atlas of Fossil Remains.** 72 pls. London, UK.

Marcinowski R. 1970. The Cretaceous transgressive deposits east of Czestochowa (Polish Jura Chain). **Acta Geologica Polonica,** 20: 413-449, pls. 1 -4.

Marcinowski R. 1974. The transgressive Cretaceous deposits (Upper Albian through Turonian) of the Polish Jura Chain. **Acta Geologica Polonica,** 24: 117-217, pls. 1 -30.

Marcinowski R. 1980. Cenomanian ammonites from the German Democratic Republic, Poland, and the Soviet Union. **Acta Geologica Polonica,** 30: 215-325, pls. 1 -18

Marcinowski R. & Naidin D. P. 1976. An Upper Albian ammonite fauna from Crimea. **Acta Geologica Polonica,** 26: 83-119, pls. 1 -9.

Marcinowski R. & Wiedmann J. 1985. The Albian ammonite fauna of Poland and its palcogeographical significance. **Acta Geologica Polonica,** 35: 200-219.

Marcinowski R. & Wiedmann J. 1990. The Albian ammonites of Poland. **Palaeontologica Polonica,** 50: 1-94 +24 pls.

Matheron P. P. E. 1842-43. **Catalogue methodique et descriptif des Corps organises fossiles du departement des Bouches-du-Rhone et lieux circonvoisins, precede d'un Memoire sur les terrains superieurs au Gres Bigarre du S.E. de la France.** 269 pp. 41 pls. Marseille, France. *Issued in four parts, of which the first (pp. 1-95, pls., i-xiii) appeared in 1842, the remainder, containing the whole of the paleontological text, in 1843.*

Matsumoto T. 1959. Upper Cretaceous Ammonites of California, part 1. **Memoirs of the Faculty of Science, Kyushu University, Series D, Geology,** 8(4): 1-171.

Matsumoto T. 1963. The Cretaceous p. 99-128. In F. Takai, T. Matsumoto, & R. Toriyama (eds.) **Geology of Japan.** University of Tokyo Press, Tokyo, Japan.

Matsumoto T. 1964. Ontogeny and evolution in some Cretaceous ammonites. **Fossils,** 8: 67-76.

Matsumoto T. 1965. Faunal changes in Cretaceous cephalopods. **Fossils,** 9: 24-29.

Matsumoto T. 1967. Evolution of the Nostoceratidae. **Memoirs of the Faculty of Science, Kyushu University, Series D, Geology,** 18(2): 331-347.

Matsumoto T. 1973. Late Cretaceous Ammonoidea, p. 421-429. In A. Hallam (ed.), **Atlas of Palaeobiogeography.** Elsevier, Amsterdam, Holland.

Matsumoto T. & Obata I. 1963. A monograph of the Baculitidae from Japan. **Memoirs of the Faculty of Science, Kyushu University, Series D, Geology,** 8(1): 1-116.

Matsumoto T. & Nihongi M. 1979. An interesting mode of Occurence of *Polyptychoceras* (Cretaceous Heteromorph Ammonoid). **Proceedings of the Japan Academy Series B,** 55: 115-119.

Matsumoto T. & Yokoi K. 1987. Tiny ammonite *Worthoceras* from Hokkaido (Studies of Cretaceous Ammonites from Hokkaido, Japan). **Transactions and Proceedings of the Palaeontological Society of Japan,** 146: 43-48.

McNamara K. J. 1990. Heterochrony. p. 111-119. In D. E. G. Briggs & P. R. Crowther (eds.) **Palaeobiology - A synthesis.** Blackwell, Oxford, UK.

Missouri Country. **Monograph, United States Geological and Geographical Survey of the Territories,** 9: 629 pp, 45 pls.

Meier R. 1994. On the inappropriateness of presence/absence recoding for non-additive multistate characters in computerized cladistic analyses. **Zoologischer Anzeiger,** 232: 201-212.

Meunier S. 1888. Contribution à la Géologie de l'Afrique occidentale. **Bulletin de la Societe Geologique de France,** 16: 61-63.

Michelin H. 1838. Note sur le argile dépendant du Gault, observée au Gaty, près Gérodot. **Memoir de la Societe Geologique de France,** 1: 97-103.

Milbourne R. A. 1955. The Gault at Greatness Lane, Sevenoaks, Kent. **Proceedings of the Geologists' Association,** 66: 235-242.

Monks N., Hardwick J. D., & Gale A. S. 1996. The function of the belemnite guard. **Paläontologische Zeitschrift,** 70: 425-431.

Monks N. & Young J. R. 1998. The functional morphology of Cretaceous heteromorph ammonites. **Palaeontologica Electronica,** 1.

Moret L. & Mahmoud I. G. E. 1954. Nouvelles observations stratigraphiques et paléontologiques sur l'Albien du Massif du Moghara. **Travaux Laboratoire de Géologie L'Université de Grenoble,** 31: 269-274.

Morris J. 1854. **A Catalogue of British Fossils.** 222 pp. London, UK.

Morton J. E. 1958 **Molluscs.** Hutchinson, London, UK.

Morton N. 1981 Aptychi: the myth of the ammonite operculum. **Lethaia,** 14: 57-61.

Moxon C. 1841. **Fossils of British Strata.** xiii + 34 pls. London, UK.

Mutvei H. 1964. Remarks on the anatomy of recent and fossil Cephalopoda. **Paläontologische Zeitschrift,** 49: 196-202.

Mutvei H. 1975. The mode of life of ammonoids. **Stockholm Contributions to Geology,** 11: 653-688.

Nakai I & Matumoto T. 1968. On some ammonites from the Cretaceous Fujikawa formation of Shikoku. **Journal of Science of the Hiroshima University, Series C,** 6(1): 1-15.

Neaverson E. 1928. **Stratigraphical Palaeontology.** xiv + 525 pp. London, UK.

Neumayr M. 1875a. Die Ammoniten der Kreide und die Sytematik der Ammoniten. **Zeitschrift der Deutschen Geologischen Gesellschaft,** 27: 854-942.

Neumayr M. 1875b. Über Kreide Ammonitiden. **Sitzungsberichte Akademie der Wissenschaften,** 71: 639-693.

Nixon M. 1987 Cephalopod diets, p. 201-219. In P. R. Boyle (ed.), **Cephalopod Life Cycles. Part 2.** Academic Press, London, UK.

Nixon M. 1988a The buccal mass of fossil and recent Cephalopoda, p. 103-112. In M. R. Clarke & E. R. Trueman (eds.), **The Mollusca. Volume 12, Paleontology and Neontology of Cephalopods.** Academic Press, London, UK.

Nixon M. 1988b. The feeding mechanisms and diets of cephalopods-living and fossil, p. 641-652. In Wiedmann J. & Kullmann J. (eds.), In Wiedmann J. & Kullmann J. (eds.), **Cephalopoda—Present and Past. O.H. Schindewolf symposium (Second International Cephalopod Symposium) Tubingen 1985.** Schweizerbarts'che, Stuttgart, Germany.

Nixon M. 1995. A nomenclature for the radula of the Cephalopoda (Mollusca)—living and fossil. **Journal of the Zoological Society of London,** 236: 73-81.

Nixon M. 1996. Morphology of the Jaws and Radula in Ammonoids, p. 815-824. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Nowak J. 1908. Üntersuchungen über die Cephalopoden der oberen Kreide in Polen. **Bulletin of the Academy of Science of Cracovie,** [B]: 327-353, pls. 40-45.

Nowak J. 1916. Uber die bifiden Loben der oberkretazischen Ammoniten und ihre Bedeutung fur die Systematik. **Bulletin of the Academy of Science of Cracovie,** [B]: 1-13.

O'Dor R. K., Forsythe J., Webber D. M., Wells J., & Wells M. J. 1993 Activity levels of *Nautilus* in the wild. **Nature,** 362: 626-628.

O'Dor R. K., Hoar J. A., Webber D. M., Carey F. G., Tanaka S., Martins H. R., & Porteiro F. M. 1994. Squid *(Loligo forbesi)* performance and metabolic rates in nature. **Marine and Freshwater Behaviour and Physiology,** 25: 163-17.

O'Dor R. K., Portner H. O. & Shadwick R. E. 1990 Squids as elite athletes: locomotory, respiratory, and circulatory integration, p. 481-503. In D. L. Gilbert, W. J. Adelman & J. M. Arnold (eds.), **Squid as Experimental Animals.** Plenum Press, New York, USA.

Okamoto T. 1988a. Analysis of heteromorph ammonoids by differential geometry. **Palaeontology,** 31: 35-52.

Okamoto T. 1988b. Developmental regulation and morphological saltation in the heteromorph ammonite *Nipponites*. **Paleobiology,** 14: 272-286.

Oldham T. 1865. **The Fossil Cephalopoda of the Cretaceous Rocks of Southern India.** Memoirs of the Geological Survey, Palaeontologica Indica. Calcutta, India.

d'Orbigny A. 1842. **Paléontologie Française.** 662 pp + 148 pls. Paris, France.

d'Orbigny A. 1850. **Prodrome de Paléontologie, Volume 2.** 428 pp. Paris, France.

Owen, R. 1832 **Memoir on the Pearly Nautilus *Nautilus pompilius* Linnaeus with illustrations of its external form and internal structure.** Richard Taylor, London, UK.

Owen R. 1844. A description of certain belemnites preserved with a great proportion of their soft parts in the Oxford Clay at Christian Malford, Wiltshire. **Philosophical Transactions of the Royal Society of London,** 1844: 65-85.

Owen H. G. 1954. The Gault at Greatness Lane, Sevenoaks. **Proceedings of the Geologists' Association,** 65: 235-242.

Owen H. G. 1958. Lower Gault Sections in the Northern Weald and the Zoning of the Lower Gault. **Proceedings of the Geologists' Association,** 69: 148-165.

Owen H. G. 1960. The Gault-Lower Greensand Junction and the Lower Gault of the Maidstone By-pass (East Section) Kent. **Proceedings of the Geologists' Association,** 71: 364-378.

Owen H. G. 1963. Some sections in the Gault of the Weald. **Proceedings of the Geologists' Association,** 74: 35-53.

Owen H. G. 1971a. Middle Albian Stratigraphy in the Anglo-Paris Basin. **Bulletin of the British Museum (Natural History) Supplement 8.** 164 pp + 3 pls. BMNH, London., UK.

Owen H. G. 1971b. The stratigraphy of the Gault in the Thames Estuary and its bearing on the Mesozoic tectonic history of the area. **Proceedings of the Geologists' Association,** 82: 187-207.

Owen H. G. 1973. Ammonite faunal provinces in the middle and upper Albian and their palaeogeographic significance. **The Boreal Lower Cretaceous, Geological Journal Special Edition 5,** 145-154.

Owen H. G. 1979. Ammonite zonal stratigraphy in the Albian of North Germany and its setting in the Hoplitinid fauanal province. p. 563-588. In Wiedmann J. (ed.), **Aspekte der Kriede Europas: beitraege zum 1 Symposium Deutsche Kriede-Bindeglied zwischen Boreal und Tethyz-Muenster in Westfalen April 1978. International Union of Geological Sciences. Series A, Volume 6.**

Owen H. G. 1984. Albian stage and substage boundaries. **Bulletin of the Geological Society of Denmark,** 33: 184-189.

Owen H. G. 1992. The Gault-Lower Greensand Junction Beds in the Northern Weald (England) and Wissant (France), and their depositional environment. **Proceedings of the Geologists' Association,** 103: 83-110.

Packard A. 1972. Cephalopods and fish: the limits of convergence. **Biological Reviews,** 47: 241-307.

Packard A. & Trueman E. R. 1974 Muscular activity of the mantle of *Sepia* and *Loligo* Cephalopoda during respiratory movements and jetting, and its physiological interpretation. **Journal of Experimental Biology,** 61: 411-419.

Parkinson J. 1811. **Organic Remains of a Former World, Volume 3.** Sherwood Neely & Jones, London, UK.

Parona C. F. & Bonarelli E. G. 1897. Fossili albiani d'Escragnolles, del Nizzardo e della Liguria occidentale. **Palaeontographica Italica,** 2: 53-112.

Passendorfer E. 1921. Sur le Cretace hauttatrique de la Tatra. **Bulletin de la Societe Geologique de Pologne,** 1: 217-250.

Passendorfer E. 1930. Étude stratigraphique et paléontologie du Cretacé de la Série hauttatrique dans les Tatras. **Travaux du Service Geologique de Pologne,** 2: 511-676.

Passy A. 1832. **Description géologique du départment de la Seine-Inférieur.** 371 pp. Rouen, France.

Perkins B. F. 1961. Biostratigraphic studies in the Comanche (Cretaceous) Series of Northern Mexico and Texas. **Geological Society of America Memoir,** 83: 1-138.

Pervinquere L. 1910. Sur quelques Ammonites du Crétacé Algérien. **Mémoir de la Societe Géologique de France, Paléontologie,** 17 (42): 1-86.

Phillips D. 1977. **Catalogue of the Type and Figured specimens of Mesozoic Ammonidea in the British Museum (Natural History).** 220 pp. British Museum (Natural History), London, UK.

Phillips D. 1987. **Additions to the Catalogues of the Type and Figured specimens of Mesozoic Ammonidea in the British Museum (Natural History).** 155 pp. British Museum (Natural History), London, UK.

von Pia J. 1923. Über die ethologische Bedeutung einiger Hauptzuge in der Stammesgeschlichte des Cephalopoden. **Annales der Naturhistorische Museum die Wien,** 36.

Pictet F. J. 1847. Descriptions des Mollusques fossiles qui se trouvent dans le Grès Verts des environs de Gèneve. 1. Céphalopodes. **Mémoir de la Société de Physique et d'Histoire Naturelle de Gèneve,** 11 (2): 257-412.

Pictet F. J. 1854a. Note sur le Succession des Mollusques céphalopodes pendant l'époque crétacée dans le region des Alpes Suisse et du Jura. **Archives de Sciences Bibl. Univ, Nouvelle Séries,** 10: 1-28.

Pictet F. J. 1854b. Cephalopodes, p. 583-716. In Pictet F. J. **Traité de Paléontologie.** Paris, France.

Pictet F. J. & Campiche G. 1861. Description des fossiles du Terrain Crétacés des environs de Ste. Croix **Matériaux pour la Paléontologie Suisse (2),** part 1: 29-380, pls. 1-43. Geneva, Switzerland.

Pictet F. J. & Renevier E. 1854. Description des fossiles du terrain aptien de la Perts-du-Rhone et des environs de Sainte-Croix. **Matériaux pour la Paléontologie Suisse (1),** part 1: 1-184, pls. 1-23. Geneva, Switzerland.

Pictet F. J. & Renevier E. 1866. Notices géologiques et paléontologiques sur les Alpes vaudoise et les régions environnants. **Bulletin de la Societe Vaudoise Sciences Naturelles,** 9: 117-138.

Pictet F. J. & Roux W. 1847. **Description des Mollusques fossiles qui trouvent dans les Grès Verts des environs de Genève.** 558 pp + 51 pls. Fick, Geneva.

Pimentel R. A. & Riggin R. 1987. The nature of cladistic data. **Cladistics,** 3: 201-209.

Pleijel F. 1995. On character coding for phylogeny reconstruction. **Cladistics,** 11: 309-315.

Price F. G. H. 1874. On the Gault of Folkestone. **Quarterly Journal of the Geological Society of London,** 30: 342-366.

Price F. G. H. 1879. **The Gault.** 81 pp. Taylor & Francis, London, UK.

Quenstedt F. A. 1845-49. **Petrefactenkunde Deuthschlands (i) Cephalopoden.** 6 volumes, 1: 1845, 2, 1846, 3, 1847, 4 & 5, 1848, and 6, 1849.

de Rance C. E 1868. On the Albian, or Gault, of Folkestone. **Geological Magazine,** 5: 163-171.

Raulin F. V. 1844. Note sur la position géognostique de la gaize ou pierre morte de l'Argonne. **Bulletin de la Societe Geologique de France, second series,** 1: 171-175.

Raup, D. M. 1966. Geometric analysis of shell coiling: general problems. **Journal of Paleontology,** 40: 1178-1190.

Raup, D. M. 1967. Geometric analysis of shell coiling: coiling in ammonoids. **Journal of Paleontology,** 41: 43-65.

Rawson P. F. 1992. Cretaceous. pp. 355-388. In P. McL. D. Duff & A. J. Smith (eds.) **Geology of England & Wales.** The Geological Society, London, UK.

Redmond J. R. 1978 Bohr effect of the pearly nautilus, *Nautilus macromphalus*. **Special Science and Technology,** 1: 45-50.

Reeside J. B. 1927. The cephalopods of the Eagle Sandstone and related formations in the Western Interior of the United States. **USGS Professional Paper,** 151: 1 -40 + 45 pls.

Reitner J. & Urlichs M. 1983. Echte Weichteilbelemniten aus dem Untertoarcium (Posidonienschiefer) Sudwestdeutschlands. **Neues Jahrbuch für Geologie und Paläontologie,** 165: 450-465.

Renevier E. 1890. Monographie des Hautes-alpes Vaudoises. **Materiaux pour la Carte Geologique de la Suisse,** 16: 1-563.

Renz O. 1968. Die Ammonoidea im Stratotyp des Vraconnien bei Sanite-Croix (Kanton Waadt). **Schweizerische Paläontologische Abhandlung / Mémoires suisses de Paléontologie,** 87: 1-99, pls. 1-18.

Reyment R. A. 1955. The Cretaceous ammonoidea of Southern Nigeria and the Southern Cameroons. **Bulletin of the Geological Survey of Nigeria,** 25: 1-112, 25 pls.

Reyment R. A. & Dingle R. V. 1987. Palaeogeography of Africa during the Cretaceous period. **Palaeogeography, Palaeoclimatology, Palaeecology,** 59: 93-116.

Riccardi A. C. 1987. Cretaceous paleogeography of Southern South America. **Palaeogeography, Palaeoclimatology, Palaeecology,** 59: 169-195.

Riccardi A. C. 1988. The Cretaceous System of Southern South America. **Geological Society of America Memoir,** 168: 1-161.

Rigby S. & Rickards R. B. 1989. New evidence for the life habit of graptoloids from physical modelling. **Paleobiology,** 15: 402-413.

Rigby S. 1992. Graptoloid feeding efficiency, rotation and astogeny. **Lethaia,** 25: 51-68.

Risso A. 1828. **Histoire naturelles des principales Productions de l'Europe Méridionale, volume 4.** xii + 439 pp. Paris, France.

Roche E. 1930. **Études géologiques dans le region méridionale du Maroc occidental.** 542 pp, 24 pls. Services des Mines et da la Carte géologiques. Macon, France.

Roemer F. A. 1840. **Die Versteinerung des Norddeutschen Kreidegebirges, part 1.** 48pp + 7 pls.

Roman F. 1938. **Les Ammonites Jurassiques et Crétacés.** 554 pp + 53 pls. Masson, Paris, France.

Roper C. F. E., Sweeney M. J., & Nauen C. E. 1984. **Cephalopods of the World. An annotated and illustrated catalogue of species of interest to fisheries.** FAO Species Catalogue Volume. 3. FAO Fisheries Synopsis 125, volume 3. United Nations Development Programme.

Saunders W. B. & Shapiro. E. A. 1986. Calculations and simulation of ammonoid hydrostatics. **Paleobiology,** 12: 64-79.

Saunders W. B. & Ward P. D. 1987 Ecology, distribution, and population characteristics of *Nautilus*, p. 137-162. In W. B. Saunders & N. H. Landman (eds.), ***Nautilus*: The Biology and Palaeobiology of A Living Fossil.** Plenum Press, New York, USA.

Schindewolf O. H. 1934. Uber Epoken auf Cephalopoden-Gehausen. **Palaontologische Zeitschrift,** 16: 15-31.

Schindewolf O. H. 1961. Studien zur Stammesgeschichte der Ammoniten. **Akademie der Wissenschaften und der Literatur zu Mainz. Abhandlung der Mathematische-naturwissenschaftlichen Klasse,** 1961: 1-136.

Schmidt H. 1930 Uber die Bewegungsweise der Schalen-cephalopoden. **Palaontologische Zeitschrift,** 12: 194-208.

Schoeller, H. 1942. Considérations sur les ammonites dites déroulés (l'origine de leus formes). **Bulletin Societe Géologique de France,** [5] vii, 233-250.

Scholz G. 1971. Uj Lechites faj a bakonyi felsöalbai rétegekböl. **Földtani Közlöny,** 101: 431-433.

Scholz G. 1979a. Die Ammoniten des Vracon (Oberalb *dispar*-zone) des Bakony-Gebirges (Westungarn) und eine revision des Wichtigsten Vracon-Arten der West-Mediterranen Faunenprovinz. **Palaeontographica A,** 165: 1-136, 30 pls.

Scholz G. 1979b Vracon-Ammoniten (Oberalb, dispar-Zone) aus dem Flammenmergel von Salzgitter, p. 589-606, 5 pls. In Wiedmann J. (ed.), **Aspekte der Kriede Europas: beitraege zum 1 Symposium Deutsche Kriede-Bindeglied zwischen Boreal und Tethyz-Muenster in Westfalen April 1978. International Union of Geological Sciences. Series A, Volume 6.**

Scott G. 1924. Some gerontic ammonites of the Duck Creek Formation. **Texas Christian University Quarterly,** 1: 1-31.

Scott G. 1928. Ammonites of the genus *Diploceras* and a new *Hamites* from the Texas Cretaceous. **Journal of Paleontology,** 2: 108-118.

Seilacher, A. 1960. Epizoans as a key to ammonoid ecology. **Journal of Paleontology,** 34: 189-193.

Seilacher A. & Wiesnauer E. 1978. Preservational history of the Belemnites. **Neues Jahrbuch für Geologie und Paläontologie,** 157: 145-149.

Seilacher A. & La Barbera M 1995. Ammonites as Cartesian Divers. **Palaios,** 10: 493-506.

Seyed-Emami 1982. Turrilitidae (Ammonoidea) aus dem Glaukonitkalk bei Esfahan (Zentraliran). **Neues Jahrbuch für Geologie und Paläontologie,** 163: 417-434.

Seyed-Emami & Immel H. 1995. Ammoniten aus dem Alb (Kreide) von Shir-Kuh (N'Yazd Zentraliran). **Paläontologische Zeitschrift,** 69: 377-399.

Shadwick R. E. 1994. Mechanical Organization of the Mantle and Circulatory System of Cephalopods, p. 69-86. In H. O. Pörtner, R. K. O'Dor & D. L. Macmillan (eds.), **Physiology of Cephalopod Molluscs—Lifestyle and Performance Adaptations.** Gordon & Breach Science Publishers S. A., Basel, Switzerland.

Shigeta Y. 1993 Post-hatching and early life history of Cretaceous ammonoidea. **Lethaia,** 26: 133-145.

Shimer H. W. & Shrock R. R. 1944. **Index fossils of North America.** ix + 837 pp. Wiley & Sons, New York, USA.

Shimzu S. 1935. The Upper Cretaceous Cephalopoda of Japan (1). **Journal of the Shanghai Science Institute,** 1: 159-226.

Simionescu J. 1897. Über eine Unter-Cenomanfauna aus den Karpathen Rumäniens. **Verhandlungen der Geologischen Reichsanstalt,** 1897: 267-273.

Smart J. G. O., Bisson G., & Worssam B. C. 1966. **Geology of the Country around Canterbury and Folkestone. Memoirs of the Geological Survey of Great Britain 289, 305 & 306 (combined).** 337 pp. HMSO, London, UK.

Smart P. J. 1997. The basal Gault and Gault-Woburn Sands junction beds in Chamberlain's Barn Quarry, leighton Buzzard, Bedfordshire, England. **Proceedings of the Geologists' Association,** 108: 287-292.

Sommermeir L. 1910. Die Fauna des Aptein und Albien im nördlichen Peru. **Neues Jarbüch für Mineralogie und Paläontologie,** 30: 313-382.

Sornay J. 1955. ***Hamites simplex.*** **Palaeontologia Universalis fasc. 18.** Museum National d'Histoire Naturelle, Paris, France.

Sowerby J. 1812-1822. **Mineral Conchology.** pls. 1-383. London, UK.

Sowerby J de C. 1823-1846. **Mineral Conchology.** pls. 384-648. London, UK.

Spaeth C. 1975. Zur Frage der Schwimmverhältisse bei Belemniten in Abhängigkeit von Primärgefüge der Hartteile. **Paläontologische Zeitschrift,** 49: 321-331.

Spath L. F. 1919 Notes on Ammonites, Parts 1 to 5. **Geological Magazine 6,** 27-35, 65-71, 115-122, 170-177, & 220-225 respectively.

Spath L. F. 1921. On Cretaceous Ammonoidea from Zululand. **Annals of the South African Museum**, 12: 217-321.

Spath L. F. 1922. On Cretaceous Ammonoidea from Angola. **Transactions of the Royal Society of Edinburgh**, 53: 91-160.

Spath L. F. 1923-1943. **A Monograph of the Ammonoidea of the Gault. Monographs of the Palaeontographical Society**, p. 1-787, pls. 1-72.

Spath L. F. 1923a. Excursions to Folkestone, with notes on the Zonation of the Gault. **Proceedings of the Geologists' Association**, 34: 70-76.

Spath L. F. 1923b. On the Ammonite horizons of the Gault and Contiguous Deposits. **Summary of progress of the Geological Survey of Great Britain and the Museum of Practical Geology**, 1922: 139-149, Appendix 2.

Spath L. F. 1925a. On Upper Albian Ammonoidea from Portuguese East Africa, with an appendix on Upper Cretaceous ammonites from Maputoland. **Annals of the Transvaal Museum**, 21: 179-200.

Spath L. F. 1925b. Notes on the Ammonites of the Lower Greensand and Gault, Folkestone and neighbourhood, p. 31-36. In Walton J. W. (ed.), **Folkestone and the country around**. HMSO, London, UK.

Spath L. F. 1925c. Sur quelques Ammonites de Gault, nommées par P. Reynès. **Annals de la Museé l'Histoire Naturelles**, 20: 1-15.

Spath L. F. 1926 On new ammonites from the English Chalk. **Geological Magazine**, 62: 77-83.

Spath L. F. 1928. The Albian Ammonoidea of Nigeria (Appendix to the Nigerian Coalfields). **Bulletin of the Geological Survery of Nigeria**, 12, pp 51-54.

Spath L. F. 1930 The fossil fauna of the Samana Range and some neighbouring areas, 5, The Lower Cretaceous Ammonoidea with notes on Albian Cephalopoda from Hazara. **Memoirs of the Geological Survey of India, Palaeontologica Indica (new series)**, 15: 50-66, pls. 8-9.

Spath, L. F. 1933a. The evolution of the Cephalopoda. **Biological Reviews**, 8: 418-462.

Spath, L. F. 1933b. **A Monograph of the Ammonoidea of the Gault, Part X. Monographs of the Palaeontographical Society.** pp 411-442, pls. 43-48.

Spath, L. F. 1934. **A Monograph of the Ammonoidea of the Gault, Part XI. Monographs of the Palaeontographical Society.** pp 443-496, pls. 49-56.

Spath, L. F. 1937. **A Monograph of the Ammonoidea of the Gault, Part XII. Monographs of the Palaeontographical Society.** pp 497-540, pls. 57-58.

Spath, L. F. 1939. **A Monograph of the Ammonoidea of the Gault, Part XIII. Monographs of the Palaeontographical Society.** pp 541-608, pls. 59-64.

Spath, L. F. 1941. **A Monograph of the Ammonoidea of the Gault, Part XIV. Monographs of the Palaeontographical Society.** pp 609-668, pls. 65-72.

Spath, L. F. 1942. **A Monograph of the Ammonoidea of the Gault, Part XV. Monographs of the Palaeontographical Society.** pp 669-720.

Spath L. F. 1946. Preliminary notes on the Cretaceous ammonite faunas of East Greenland **Meddelelser om Grønland,** 132: 1-12.

Stieler C. 1922. Über Gault- und Cenoman- Ammoniten aus dem Cenoman des Cap Blanc Nez, mit besonder Berücksichtigung der Gattung *Schloenbachia*, Neumayr. **Neues Jarbüch für Mineralogie und Paläontologie,** 42: 19-44.

Steinmann G. 1907. **Ein führung in die Palaeontologie (Cephalopoda).** xii + 542 pp. Leipzig, Germany.

Stolley E. 1937. Die Stratigraphie des nordeutchen oberen Gaults, *Minimus*-Tons und Flammenmergels im Vergleich mit dem englischen Lower und Upper Gault. **Neues Jährbuch für Mineralogie und Geologie,** 78: 1-65.

von Strombeck A. 1856. Über das Alter des Flammenmergels in nordwestlichen Deutschland. **Zeitschrift der Deutschen Geologischen Gesellschaft,** 6: 483-493.

Studer B. 1853. **Geologie der schweiz.** Volume 2 Nördliche Nebenzone der Alpen: Jura und Hügelland. vii + 447 pp.

Sumich J. L. 1992. **An introduction to the biology of marine life.** W. C. Brown, Dubeque, Indiana, USA. xii + 449 pp.

Swensen A. J. 1962. Anisoceratidae and Hamitidae (Ammonoidea) from the Cretaceous of Texas and Utah. Brigham Young University Geological Studies 9: 53-82.

Swofford, D. L. 1993. **PAUP, Phylogenetic Analysis Using Parsimony, Version 3.1.** *Apple Macintosh computer program.*

Tanabe K. & Fukuda Y. 1987 Mouth part histology and morphology, p. 313-322. In W. B. Saunders & N. H. Landman (eds.), *Nautilus*: **The Biology and Palaeobiology of A Living Fossil.** Plenum Press, New York, USA.

Tanabe K., Fukuda Y., & Obata L. 1980. Ontogenetic development and functional morphology in the early growth stages of three Cretaceous ammonites. **Bulletin of the National Science Museum, Tokyo, Series C Geology,** 6: 9-26.

Tanabe K., Obata I., & Futakami M. 1981. Early shell morphology in some Upper Cretaceous heteromorph ammonites. **Transactions and Proceedings of the Palaeontological Society of Japan, New Series,** 124: 215-234.

Taylor P. D. & Monks N. 1997. A new cheilostome bryozoan genus epiplanktonic on molluscs and algae. **Invertebrate Biology,** 116: 39-51, plus cover illustration.

Tazaki K. & Fyfe W. S. 1996. Biomineralization of Iron in Ammonites: Exceptional Preservation of Anatomical Structure in a Fossilized Ammonite. **Bulletin de l'Institute océanographique, Monaco Special Volume,** 14: 401-412.

Teall J. J. H. 1875. **The Potton and Wicken Phosphatic Deposits. Sedgwick Prize Essay for 1873.** Cambridge University Press, Cambridge, UK.

Thomel G. 1992. **Ammonites du Cénomanien et du Turoniien du Sud-Est France.** Volumes 1, 422 pp, volume 2, 383 pp. Nice, France.

Tomitch M. I. 1918. Contributions a la connaisance de l'étage Albien dans le Sud-est de la France. **Notes Provençales du Dr Guébhard,** 4: p. 1-12.

Topley W. 1875. **The Geology of the Weald. Memoir of the Geological Survey of the UK.** xiv + 503 pp, 8 pls. HMSO, London, UK.

Trueman A. E. 1941. The ammonite body-chamber, with special reference to the buoyancy and mode of life of the living ammonite. **Quarterly Journal of the Geological Society of London,** 384: 339-383.

Trueman E. R. 1983 Locomotion in molluscs, p. 155-198. In K. M. Wilbur & C. M. Yonge (eds.), **The Mollusca, Volume 4, Physiology Part 1.** Academic Press, New York, USA.

Vakhrameev V. A. Cretaceous paleogeography of the USSR **Palaeogeography, Palaeoclimatology, Palaeecology,** 59: 57-67.

Vecchione M. 1994. Systematics and the Lifestyle and Performance of Cephalopods, p. 179-192. In H. O. Pörtner, R. K. O'Dor & D. L. Macmillan (eds.), **Physiology of Cephalopod Molluscs—Lifestyle and Performance Adaptations.** Gordon & Breach Science Publishers S. A., Basel, Switzerland.

Venzo S. 1936. Cefalopodi del Cretacea medio-superiore dello Zululand. **Palaeontograhica Italica,** 36: 59-133.

Vermeij G. J. 1977. The Mesozoic marine revolutions: Evidence from snails, predators, and grazers. **Paleobiology,** 3: 245-258.

Vermeij. G. J. 1987. **Evolution and escalation.** Princeton University Press, New Jersey, USA. xv + 527 pp.

Vermeij G. J. 1993. **A Natural History of Shells.** Princeton University Press, New Jersey, USA. vii + 207 pp, 22 pls.

Voss G. L. 1977. Classification of Recent cephalopods. **Symposium of the Zoological Society of London,** 38: 575-579.

Waagen W. 1870. Ueber die Ansatzstelle der Haftmuskeln beim *Nautilus* und den Ammoniden. **Palaeontographica,** 17: 185-210.

Ward P. D. 1979. Functional morphology of Cretaceous helically-coiled ammonite shells. **Paleobiology,** 5: 415-422.

Ward P. D. 1983. *Nautilus macromphalus*, p. 11-28. In P. R. Boyle (ed.), **Cephalopod Life Cycles, Part 1.** Academic Press, London, UK.

Ward P. D. 1986. Cretaceous ammonite shell shapes. **Malacologia,** 27: 3-28.

Ward P. D. 1987. **The Natural history of *Nautilus*.** Allen & Unwin, London, UK. xiv + 267 pp.

Ward P. D. 1992. **On Methuselah's trail: living fossils and the great extinctions.** Freeman, New York, USA. xii + 212 pp.

Ward P. D. 1996. Ammonoid Extinction, p. 815-824. In: Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Ward P. D. & Bandel K. 1987 Life history strategies in fossil cephalopods, p. 327-350. In P. R. Boyle (ed.), **Cephalopod Life Cycles Part 2.** Academic Press, London, UK.

Ward P. D., Stone R., Westermann G. E. G. & Martin, A. 1977. Notes on animal weight, cameral fluids, swimming speed and colour polymorphism of the cephalopod *Nautilus macromphalus* in the Fiji Islands. **Paleobiology,** 3: 377-388.

Wells M. J. 1987 Ventilation and oxygen extraction by *Nautilus*, p. 339-350. In W. B. Saunders & N. H. Landman (eds.), ***Nautilus*: The Biology and Palaeobiology of A Living Fossil.** Plenum Press, New York, USA.

Wells M. J. 1994. Evolution of a Racing Snail, p. 1-12. In H. O. Pörtner, R. K. O'Dor & D. L. Macmillan (eds.), **Physiology of Cephalopod Molluscs-Lifestyle and Performance Adaptations.** Gordon & Breach Science Publishers S. A., Basel, Switzerland.

Wells M. J. & Smith P. J. S. 1985 The ventilation cycle in *Octopus*. **Journal of Experimental Biology,** 116: 375-383.

Wells M. J. & Wells J. 1985 Ventilation and oxygen uptake by *Nautilus*. **Journal of Experimental Biology,** 118: 297-312.

Wells M. J., Wells J., & O'Dor R. K. 1992 Life at low oxygen tensions: the behaviour of *Nautilus pompilius* and the biology of extinct forms. **Journal of the Marine Biological Association of the United Kingdom,** 72: 313-328.

Westermann G. E. G. 1971. Form, Structure and Function of Shell and Siphuncle in Coiled Mesozoic Ammonoids. **Life Sciences Contributions of the Royal Ontario Museum,** 78: 1-39.

Westermann G. E. G. 1975a. Model for origin, function and fabrication of fluted cephalopod septa. **Paläontologische Zeitschrift,** 49: 235-253.

Westermann G. E. G. 1975b. Remarks on Mutvei and Reyment's hypothesis regarding ammonoid phragmocones. **Palaeontology,** 18: 437-439.

Westermann G. E. G. 1982. The connecting rings of *Nautilus* and Mesozoic ammonoids: implications for ammonoid bathymetry. **Lethaia,** 15: 373-384.

Westermann G. E. G. 1990. New developments in ecology of Jurassic-Cretaceous ammonoids, p. 459-478. In: Pallini G., Cresta S., & Santantonio M. (eds.), **Fossili, Evolutione, Ambiente. Atti II Cenvenio Internationale Pergola 1987.** Comite Centenario R. Piccinini, Pergola, Italy.

Westermann G. E. G. 1993. On the alleged negative buoyancy of ammonoids. **Lethaia,** 26: 246.

Westermann G. E. G. 1996. Ammonoid life and habit, 607-707. In Landman N. H., Tanabe K., Davis R. A. (eds.), **Ammonoid Paleobiology, Topics in Geobiology Volume 13.** Plenum Press, New York, USA.

Westermann G. E. G. & Ward P. D. 1980. Septum morphology and bathymetry in cephalopods. **Paleobiology,** 6: 48-50.

Whitehouse F. W. 1926. The Cretaceous Ammonoidea of Eastern Australia. **Memoirs of the Queensland Museum,** 8: 195-242.

Whitehouse F. W. 1928. The correlation of the marine Cretaceous deposits of Australia. **Report of the 18th meeting, Australian Association for the Advancement of Science,** 1926: 275-280.

Wiedmann J. 1962. Ammoniten aus der Vascogotischen kreide (Nordspanien). 1. Phylloceratina, Lytoceratina. **Palaeontographica A,** 118: 119-237.

Wiedmann J. 1962a. Unterkreide-Ammoniten von Mallorca (1). **Akademie der Wissenschaften und der Literatur (Abhandlung der Mathematische-Naturwissenshaftlichen Klasse),** 1962 1: 1-148.

Wiedmann J. 1965. Origin, limits, and systematic position of *Scaphites*. **Palaeontology,** 8: 397-453.

Wiedmann J. 1966. Stammesgeschichte und system den posttriadischen ammonoideen, ein überblick. **Neues Jahrbuch für Geologie und Paläontologie Abhandlung,** 125: 49-79 & 127: 12-81.

Wiedmann J. 1969. The heteromorphs and ammonoid extinction. **Biological Reviews,** 44: 563-602.

Wiedmann J. & Boess J. 1984. Ammonitenfunde aus der Biskaya-Synkline (Nordspanien)-Kreidegliederung und Alter des Kreide-Vulkanismus. **Eclogae Geologica Helvetiae,** 77: 483-510.

Wiedmann J. & Dieni I. 1968. Die Kreide Sardiniens und ihre Cephalopoden. **Palaeontographica Italica,** 64: 1-171, pls. 1-18.

Wiedmann J. & Marcinowski R. 1985. *Scaphamites passendorferi* n. g. n. sp. (Ammonoidea, Cretaceous)-ancestor of Scaphitaceae Meek. **Neues Jahrbuch für Geologie und Paläontologie Monatshefte,** 8: 449-463.

Wiedmann J. & Kakabadza M. V. 1993. Suture investigations and the classification of Cretaceous heteromorph ammonites. **Geobios,** 15: 393-399.

Wignall P. B. & Hallam A. 1991. Biofacies, stratigraphic distribution and depositional models of British onshore Jurassic black shales, p. 291-309. In Tyson R. V. & Pearson T. H. (eds.), **Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication 58.**

Wilkinson M. 1992. Ordered versus unordered characters. **Cladistics,** 8: 375-385.

Winton W. M. & Adkins W. S. 1920. The geology of Tarrant County. **University of Texas Bulletin, 1931**: 1-122, 6 pls.

Woods H. 1891. **Catalogue of the Type Fossils in the Woodwardian Museum, Cambridge.** xii + 120 pp. Cambridge, UK.

Woodward H. B. 1887. **The Geology of England and Wales.** xv+ 670 pp. London, UK.

Wright. C. W. 1952. A classification of the Cretaceous ammonites. **Journal of Paleontology,** 26: 213-222.

Wright. C. W. 1953. Notes on Cretaceous ammonites. 1. Scaphitidae. **Annals and Magazine of Natural History Series 2,** 6: 473-476.

Wright. C. W. 1980. Cretaceous Ammonoidea. 157-154. In House, M. R. & Senior, J. R. (eds.), **The Ammonoidea. Systematics Association Special Volume 18.** Academic Press, London, UK.

Wright C. W., Callomon J. H., & Howarth M. K. 1996. Cretaceous Ammonoidea. L.1-L.362. In: Kaesler R. L. (ed.), **Treatise on Invertebrate Paleontology Part L. Mollusca 4 (Revised).** xviii + 362 pp. Geological Society of America & University of Kansas Press, Boulder, Colorado & Lawrence, Kansas.

Wright C. W. & Collins J. S. H. 1972. British Cretaceous Crabs. **Monographs of the Palaeontographical Society,** p. 1-114, pls. 1-22.

Wright C. W. & Kennedy W. J. 1981. The Ammonoidea of the Plenus Marls and the Lower Chalk. **Monographs of the Palaeontographical Society,** p. 1-148, pls. 1-32.

Wright C. W. & Kennedy W. J. 1984. The Ammonoidea of the Lower Chalk. Part 1. **Monographs of the Palaeontographical Society,** p. 1-126, pls. 1-40.

Wright C. W. & Kennedy W. J. 1995. The Ammonidea of the Lower Chalk. Part 4. **Monographs of the Palaeontographical Society,** p. 295-319, pls. 87-94.

Wright C. W. & Kennedy W. J. 1996. The Ammonidea of the Lower Chalk. Part 5. **Monographs of the Palaeontographical Society,** p. 320-403, pls. 95-124.

Wright C. W. & Wright E. V. 1951. A Survey of the fossil Cephalopoda of the Chalk. **Monographs of the Palaeontographical Society,** p. 1-40.

Wright T. 1878-1886. Monograph of the Lias Ammonites of the British Islands. **Monographs of the Palaeontographical Society,** p. 1-503.

Yonge C. M. & Thompson T. E. 1978. **Living Marine Molluscs.** Collins, London, UK. 288 pp.

Young J. Z. 1959. Squids, Cuttlefishes and Octopuses. **Proceedings of the Royal Institution of Great Britain,** 37: 394-411.

Zeigler P. 1982. **Geological Atlas of Western and Central Europe.** Shell International Petroleum Maatschappij B. V., Amsterdam, Netherlands. 130 pp.

Zittel K. A. 1884. **Handbuch der Palaeontologie.** Munich, Germany.

Zittel K. A. 1900. **Textbook of palaeontology.** Macmillan & Co., London, UK. *Translated by Eastman C. R.*

FIGURES

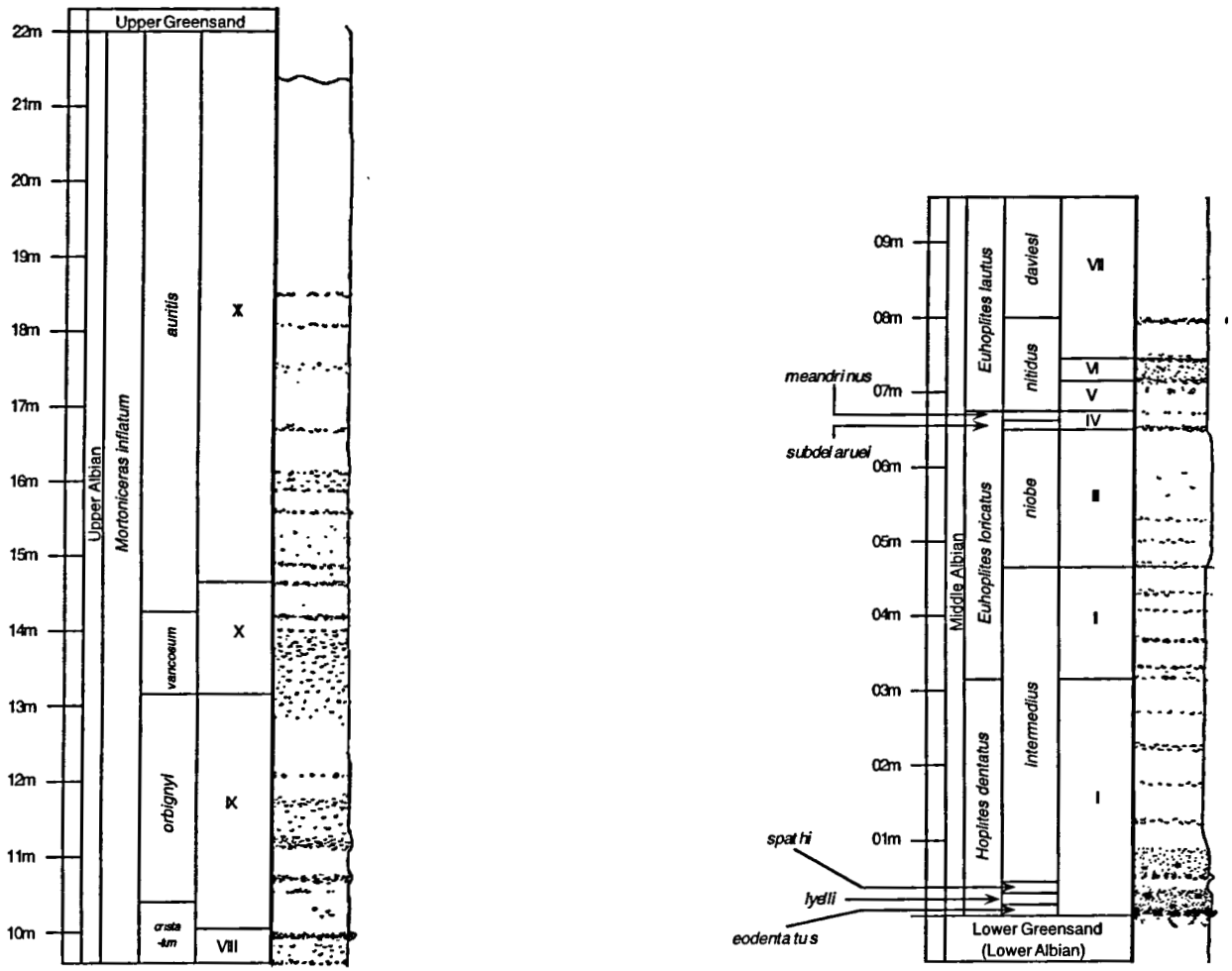


FIGURE 1.0 Stratigraphical logs of the Gault Clay section at Copt Point, Folkestone, Kent. Compiled with A S Gale.

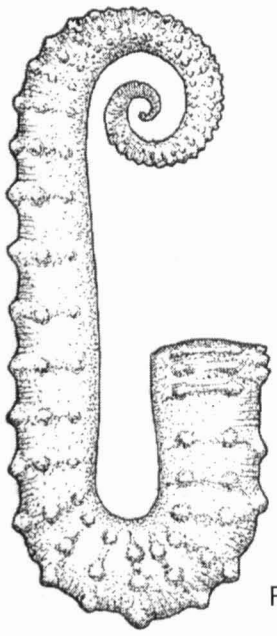


Figure 1.1

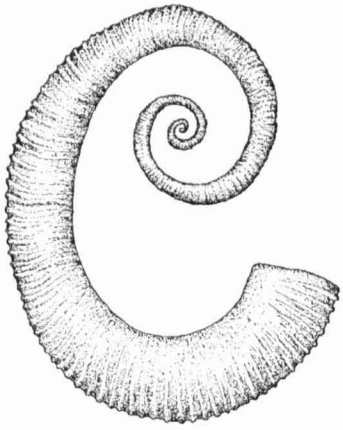


Figure 1.2

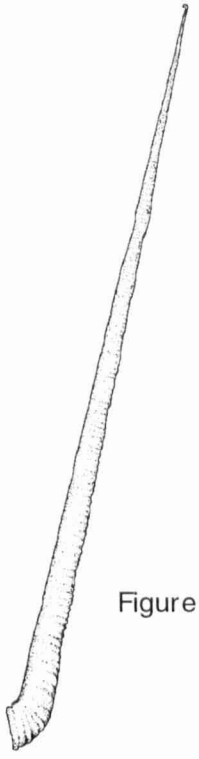
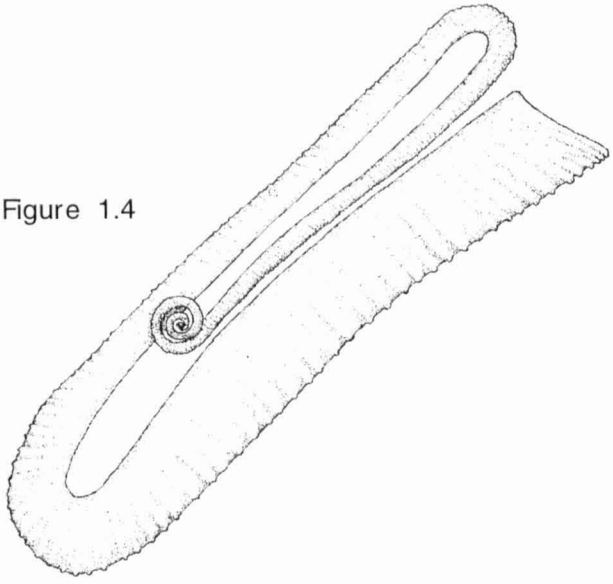


Figure 1.3

Figure 1.4



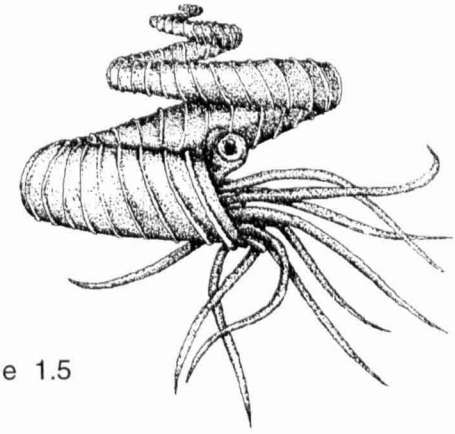


Figure 1.5

FIGURE 1.1: *Ancyloceras matheronianum*, an ammonite with ancycloconic coiling.

FIGURE 1.2: *Hamitella gardneri*, an ammonite with aspinoconic coiling.

FIGURE 1.3: *Lechites gaudini*, an ammonite with baculiticonic coiling.

FIGURE 1.4: *Hamitella maximus*, an ammonite with hamiticonic coiling when mature.

FIGURE 1.5: *Hamitella maximus*, an ammonite with turriliticonic (helical) coiling during the juvenile stage.

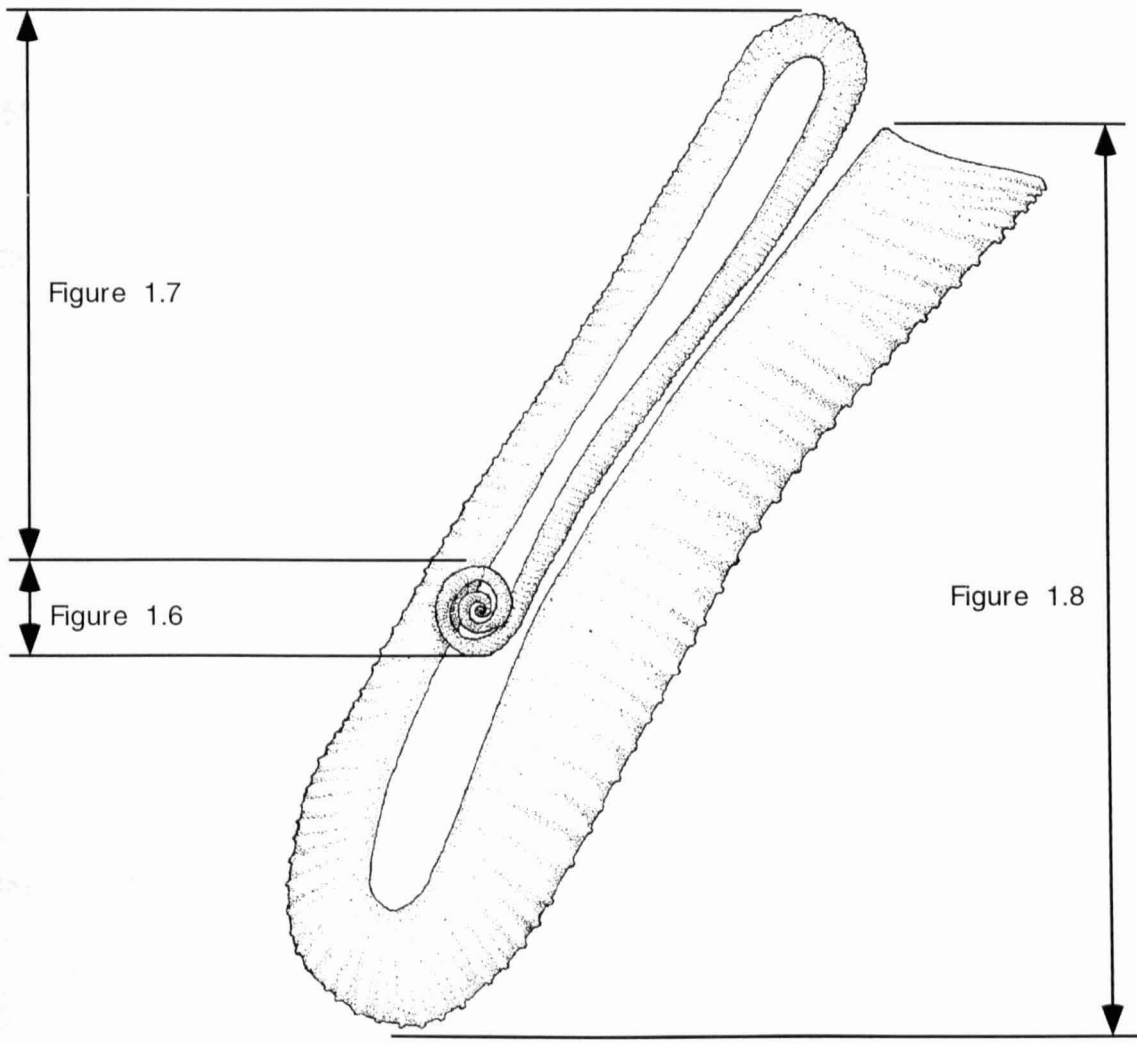


FIGURE 1.6: The *juvenile-A* stage persisted through the development of the post-neanic crioconic part of the phragmocone. Features which exist on this part of the shell are termed here to have been developed during the juvenile-A growth stage.

FIGURE 1.7: The *juvenile-B* stage immediately followed the juvenile-A stage. It is seperated from the juvenile-A stage by the appearance of a break in regular coiling. Features which appear on this part of the phragmocone are termed here to have been associated with the juvenile-B growth stage.

FIGURE 1.8: The ammonite reached *maturity* when development of the phragmocone slowed down or ceased altogether. Mature characters are therefore those features apparent on the final living chamber. Modifications of the final living chamber, such as the development of apertural constrictions and collars, are apparent in some species.

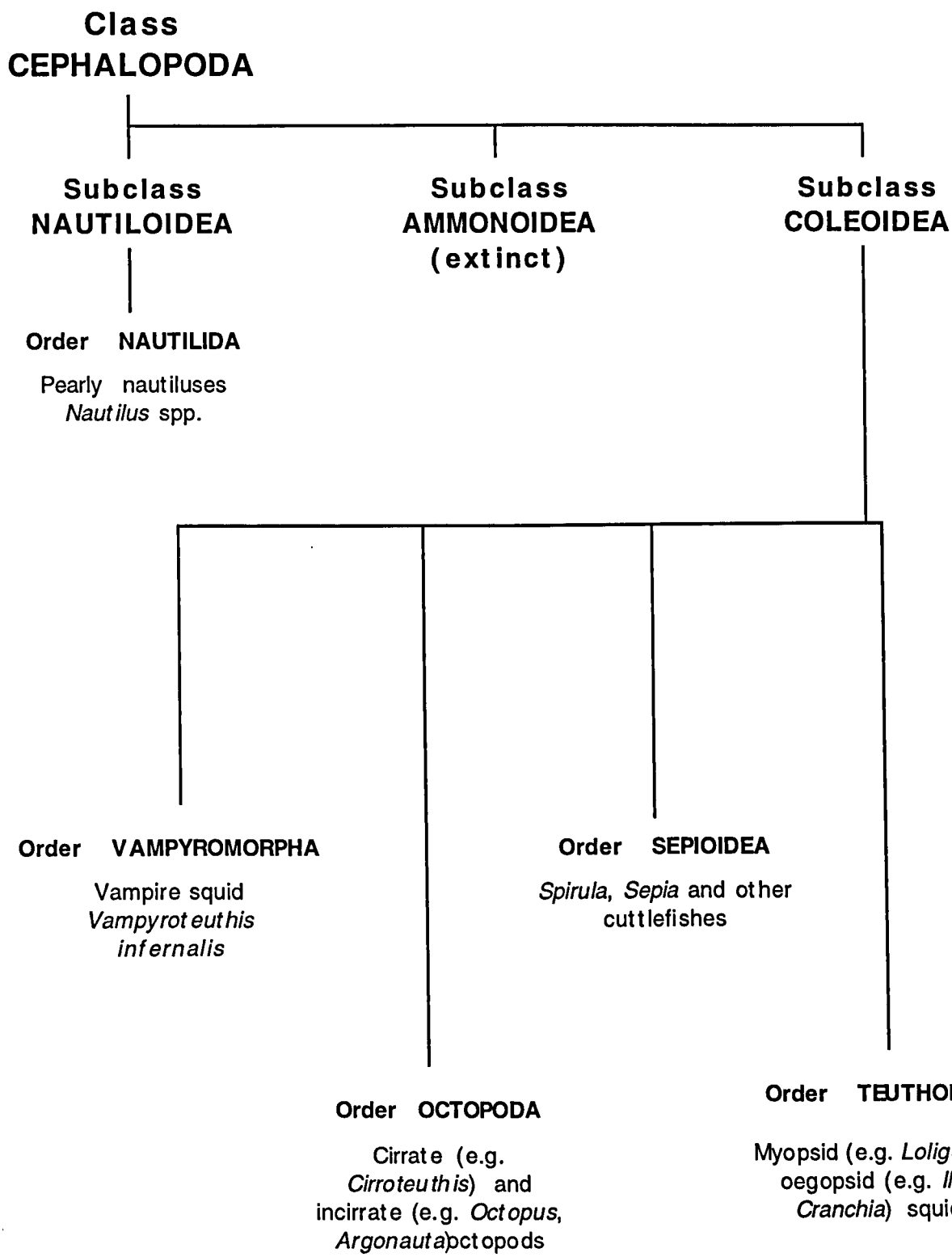


FIGURE 2.1: The traditional taxonomy of the class Cephalopoda based on Voss (1977). The Nautiloidea and Ammonoidea are sometimes referred to as the Tetrabranchiata, on the assumption that ammonites had two pairs of gills, like modern *Nautilus*. All nautiloids and probably all ammonoids had external shells. The Coleoidea all have a single pair of gills, and are therefore named the Dibranchiata. Belemnites (order Belemnoidea) plus a number of other minor groups also belong to the Coleoidea. Coleoids have internal, often reduced, shells. They are the dominant cephalopods alive today.

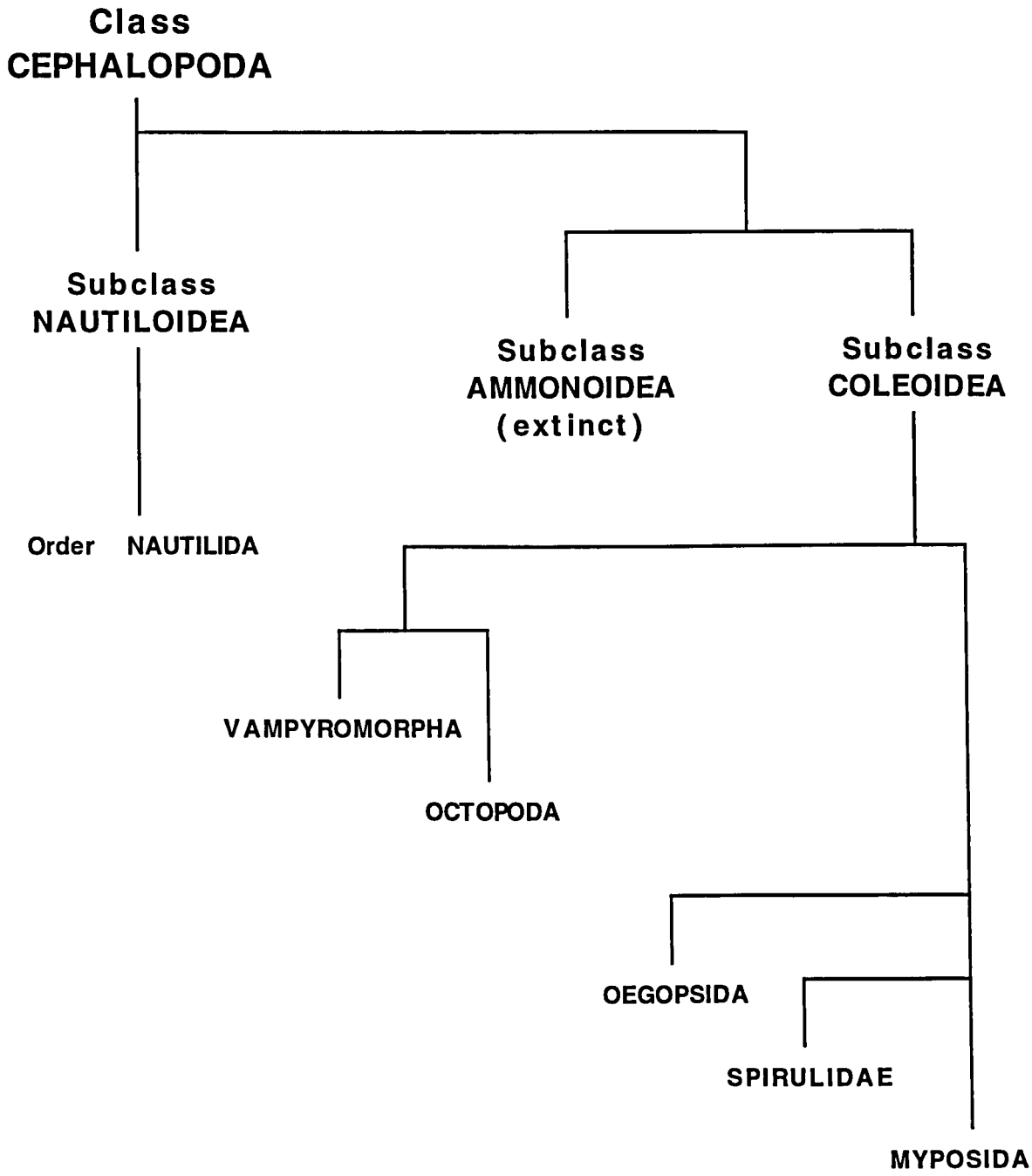


FIGURE 2.2: Berthold & Engeser (1987) and Engeser (1996) have revised cephalopod taxonomy phylogenetically using both living and fossil groups. They have demonstrated that ammonoids and coleoids are more closely related to each other than either are to the nautiliods, despite the similarity of the external shells of nautiloids and ammonoids. This supports the union of the Ammonoidea and Coeloidea within the Angusteradulata as proposed by Lehmann (1967) and supported by Nixon (1995). Lewy (1996) has postulated that ammonoids may even be ancestral to certain octopuses by comparisons of the morphology of the shells of ammonites with the egg-cases of the pelagic octopod *Argonauta*.

Superfamily Ancyloceratac eae Meek, 187 6

Family Ptychoceratidae Meek, 1876

Ptychoceras d'Orbigny, 1842

Family Labeceratidae Spath, 1925

Labeceras Spath, 1925
Hamitoides Spath, 1925

Superfamily Scaphitaceae Gill, 1871

Family Scaphitidae Gill, 1871

Subfamily Scaphitinae Gill, 1871

Scaphites Parkinson, 1811
Eoscaphites Breistroffer, 1947

Subfamily Otoscaphitinae Wright, 1953

Worthoceras Adkins, 1928

Superfamily Turrilitaceae Meek, 1876

Family Anisoceratidae Hyatt, 1900

Anisoceras Pictet, 1854
Protanisoceras Spath, 1923
Protanisoceras (Heteroclinus) Casey, 1961
Protanisoceras (Torquistylus) Casey, 1961
Rossalites Casey, 1961
Metahamites Spath, 1930

Family Hamitidae Hyatt, 1900

Hamites Parkinson, 1811
Hamites (Psilohamites) Spath, 1941
Hamites (Lytohamites) Casey, 1961
Hamites (Stomohamites) Breistroffer, 1940
Hemiptychoceras Spath, 1925
Scaphamites Wiedmann & Marcinowski, 1985

Family Baculitidae Meek, 1876

Lechites Nowak, 1908
Lechites (Tuberolechites) Cooper & Kennedy, 1977
Sciponoceras Hyatt, 1894

Family Turrilitidae Meek, 1876

Proturrilitoides Breistroffer, 1940
Turrilitoides Spath, 1923
Pseudhelicoceras Spath, 1921
Mariella Nowak, 1916
Ostlingoceras Hyatt, 1900

FIGURE 2.3: A Taxonomy of the heteromorph ammonites of the Albian discussed in this thesis, based on Spath (1923-1943), Breistroffer (1940, 1947), Casey (1961), Renz (1968), Cooper & Kennedy (1977), Cooper (1994a), and Wright *et al* (1996).

Superfamily Ancyloceratacea Meek, 1876

Family Labeceratidae Spath, 1925

Labeceras Spath, 1925
Hamitoides Spath, 1925

Superfamily Scaphitaceae Gill, 1871

Family Scaphitidae Gill, 1871

Scaphites Parkinson, 1811
Eoscaphites Breistroffer, 1947

Superfamily Turrilitaceae Meek, 1876

Family Anisoceratidae Hyatt, 1900

Anisoceras Pictet, 1854
Protanisoceras Spath, 1923
Protanisoceras (Heteroclinus) Casey, 1961
Protanisoceras (Torquistylus) Casey, 1961
Rossalites Casey, 1961
Metahamites Spath, 1930
Hamites Parkinson, 1811
Hamites (Psilohamites) Spath, 1941
Hamites (Lytohamites) Casey, 1961
Hamites (Stomohamites) Breistroffer, 1940
Hemiptychoceras Spath, 1925
Scaphamites Wiedmann & Marcinowski, 1985

Family Baculitidae Meek, 1876

Lechites Nowak, 1908
Lechites (Tuberolechites) Cooper & Kennedy, 1977
Sciponoceras Hyatt, 1894

Family Turrilitidae Meek, 1876

Proturrilitoides Breistroffer, 1940
Turrilitoides Spath, 1923
Pseudhelicoceras Spath, 1921
Mariella Nowak, 1916
Ostlingoceras Hyatt, 1900

Family Ptychoceratidae Meek, 1876

Ptychoceras d'Orbigny, 1842
Worthoceras Adkins, 1928

FIGURE 2.4: The proposed "phylogenetic" taxonomy of the heteromorph ammonites of the Albian devised and used by Wiedmann (1962) and Wiedmann & Dieni (1968), and most recently discussed by Marcinowski & Wiedmann (1990).

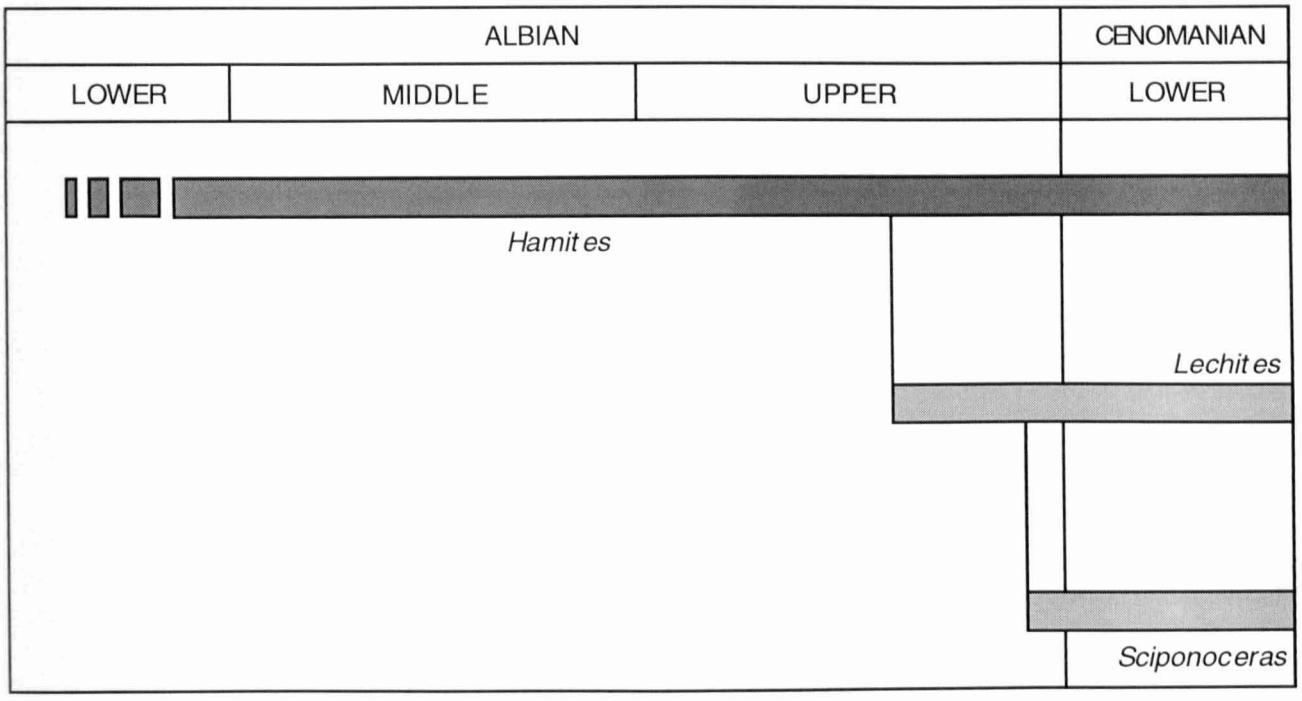


FIGURE 2.5

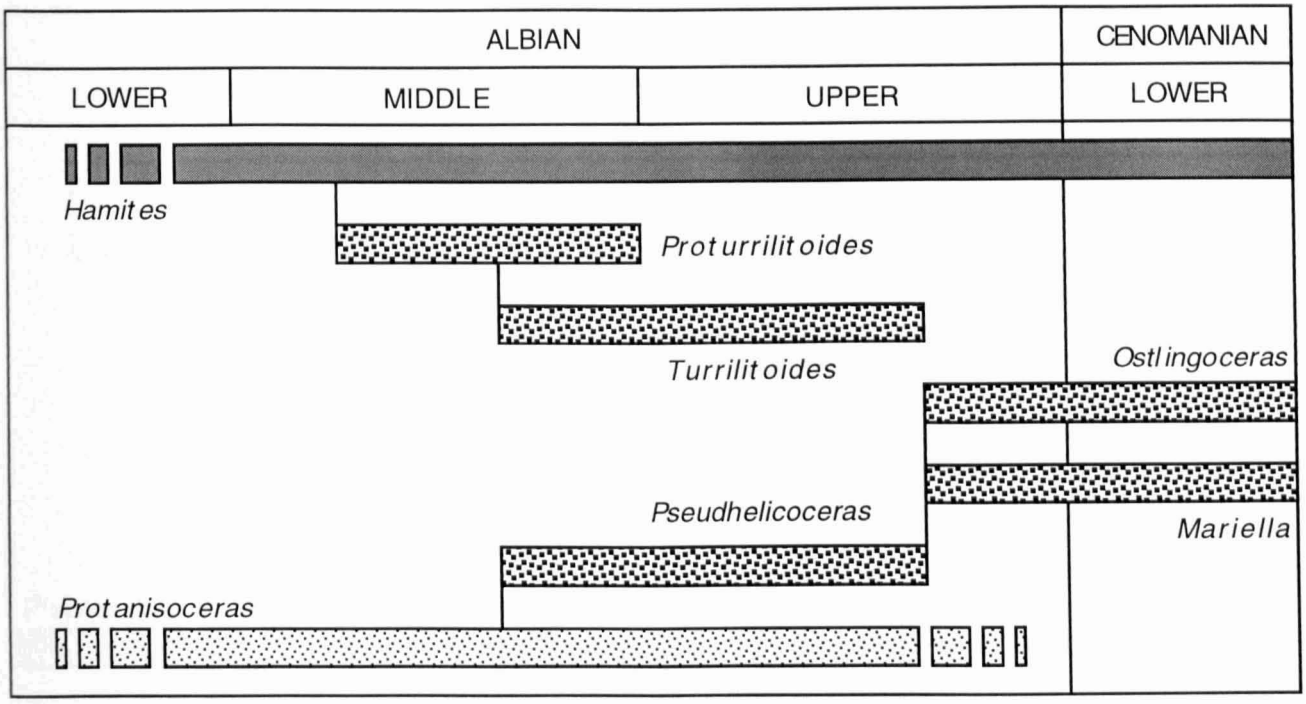


FIGURE 2.6

FIGURE 2.5: Origins of the Baculitidæ as postulated by Spath (1941) and Matsumoto & Obata (1963).

FIGURE 2.6: The diphyletic origins of the Turrilitidæ as described by Matsumoto (1967) and Klinger & Kennedy (1978). The tuberculate turrilitids (*Pseudhelicoceras*, *Mariella*, and *Ostlingoceras*) are seen to have a seperate origin from the non-tuberculate turrilitids (*Proturrilitoides*, *Turrilitoides*).

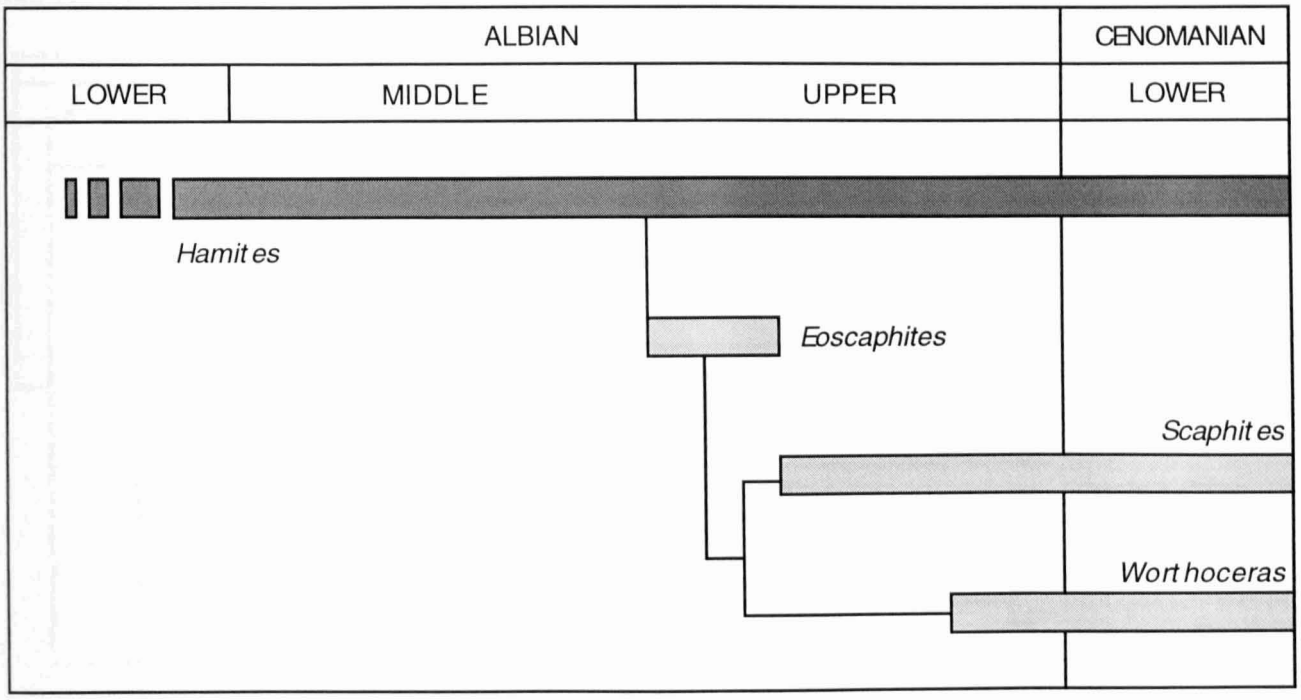


FIGURE 2.7

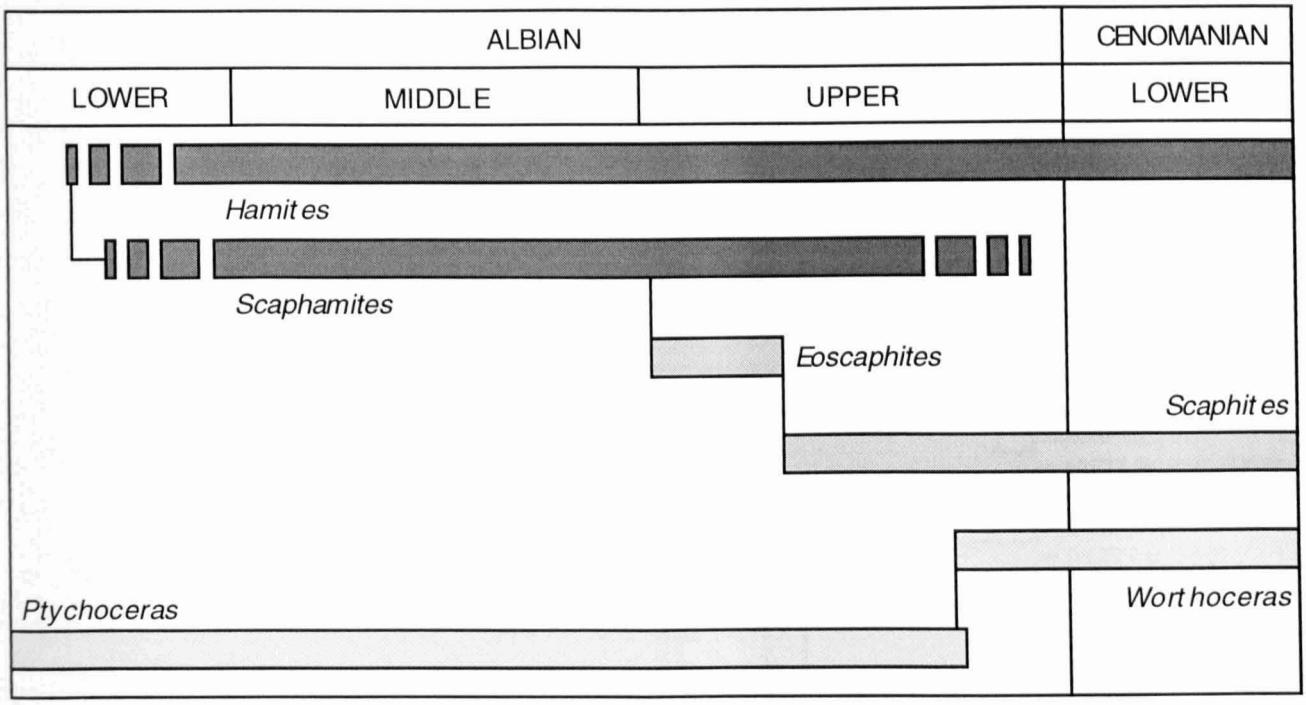


FIGURE 2.8

FIGURE 2.7: Phylogeny of the Scaphitaceæ, as described by Cooper (1994a). During the Albian, the Scaphitaceæ divide into the Otoscaphitinæ (including *Worthoceras*) and the Scaphitinaæ (including *Scaphites*).

FIGURE 2.8: Wiedmann (1965) and Wiedmann & Marcinowski (1985) exclude Worthoceras from the Scaphitaceæ, and trace the origins of the Scaphitaceæ to the hamitid genus *Scaphamites*.

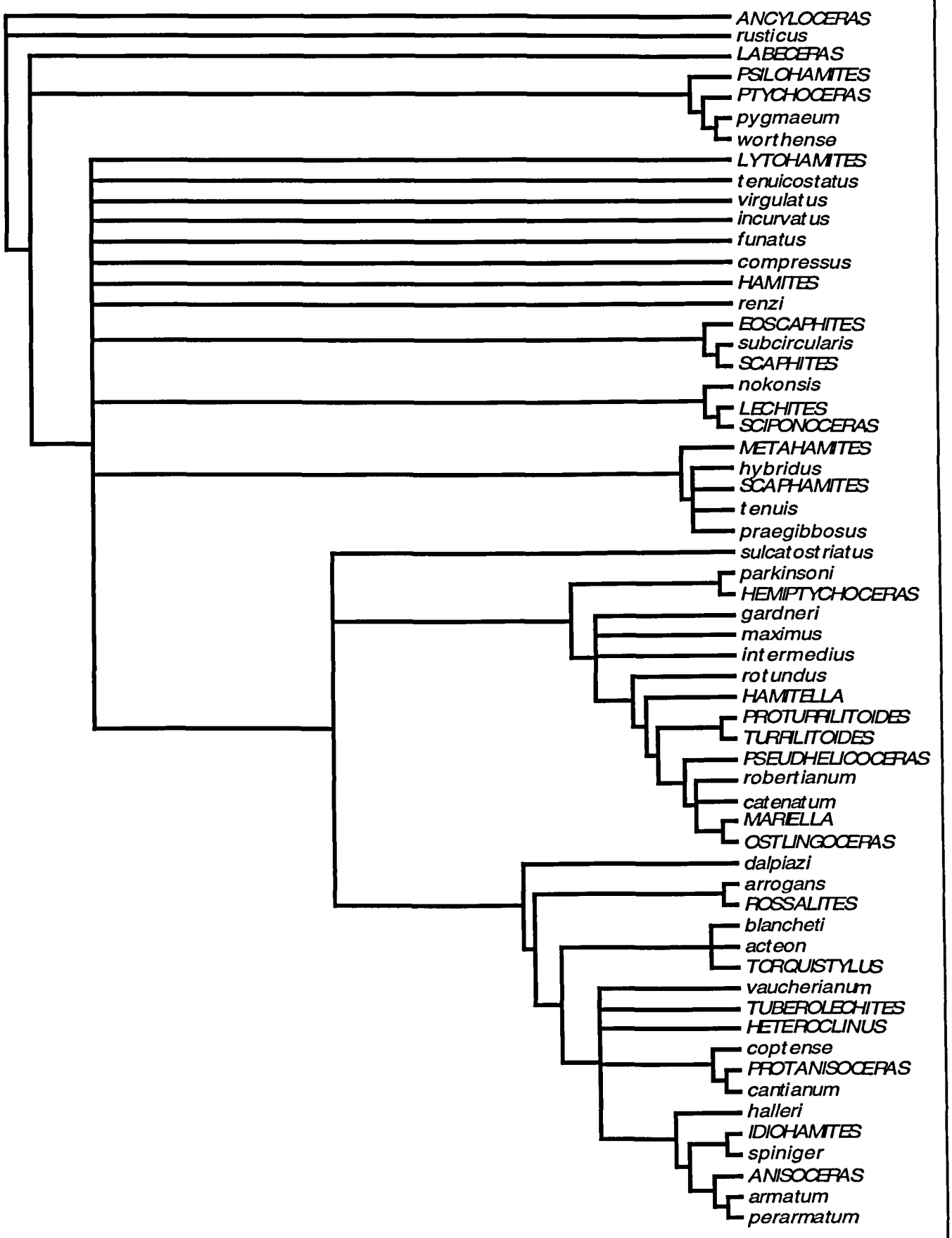


FIGURE 2.9: Strict consensus tree produced from 2,200 trees.

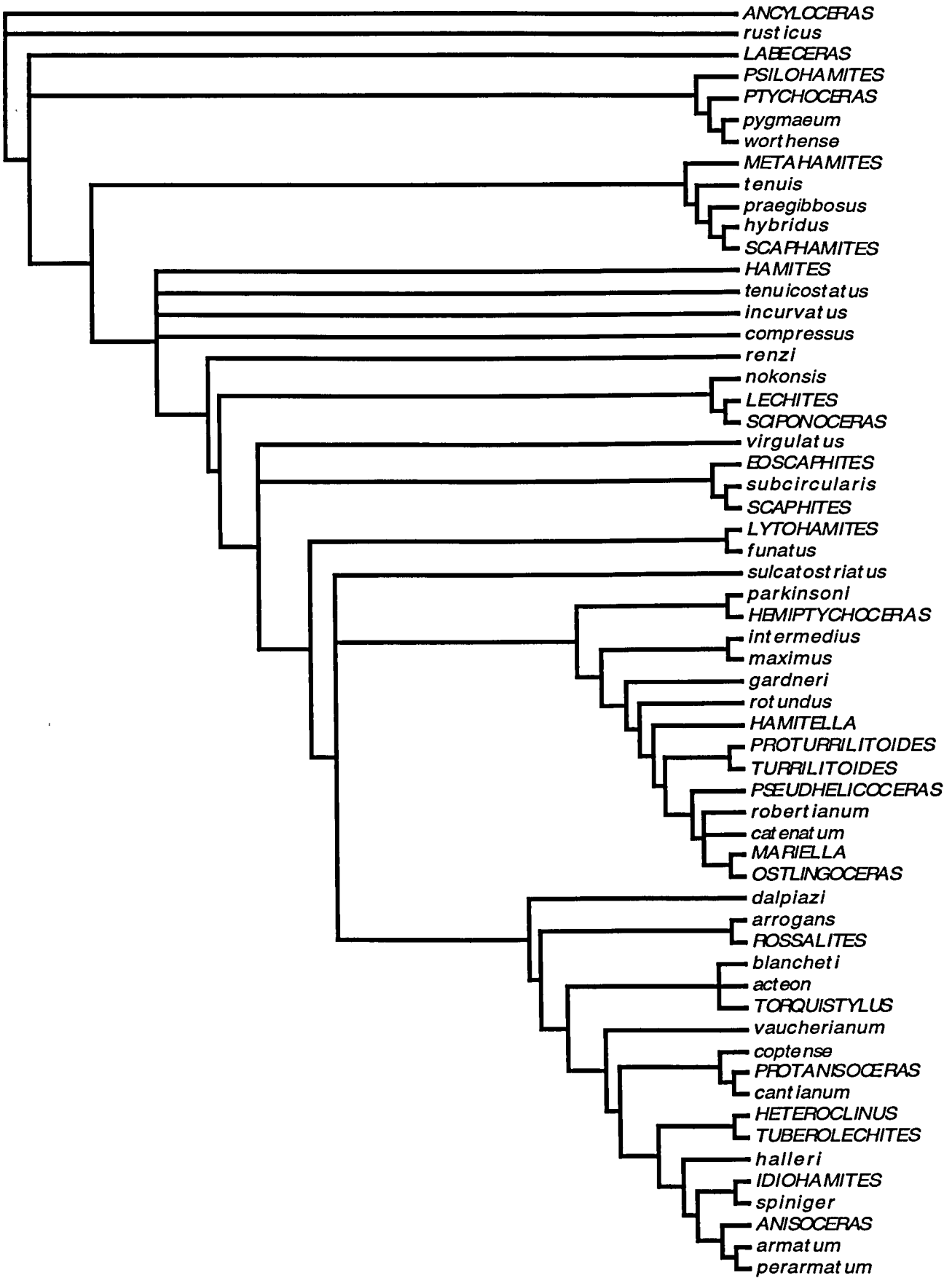


FIGURE 2.10: 50% majority rule consensus tree produced from 2,200 trees.

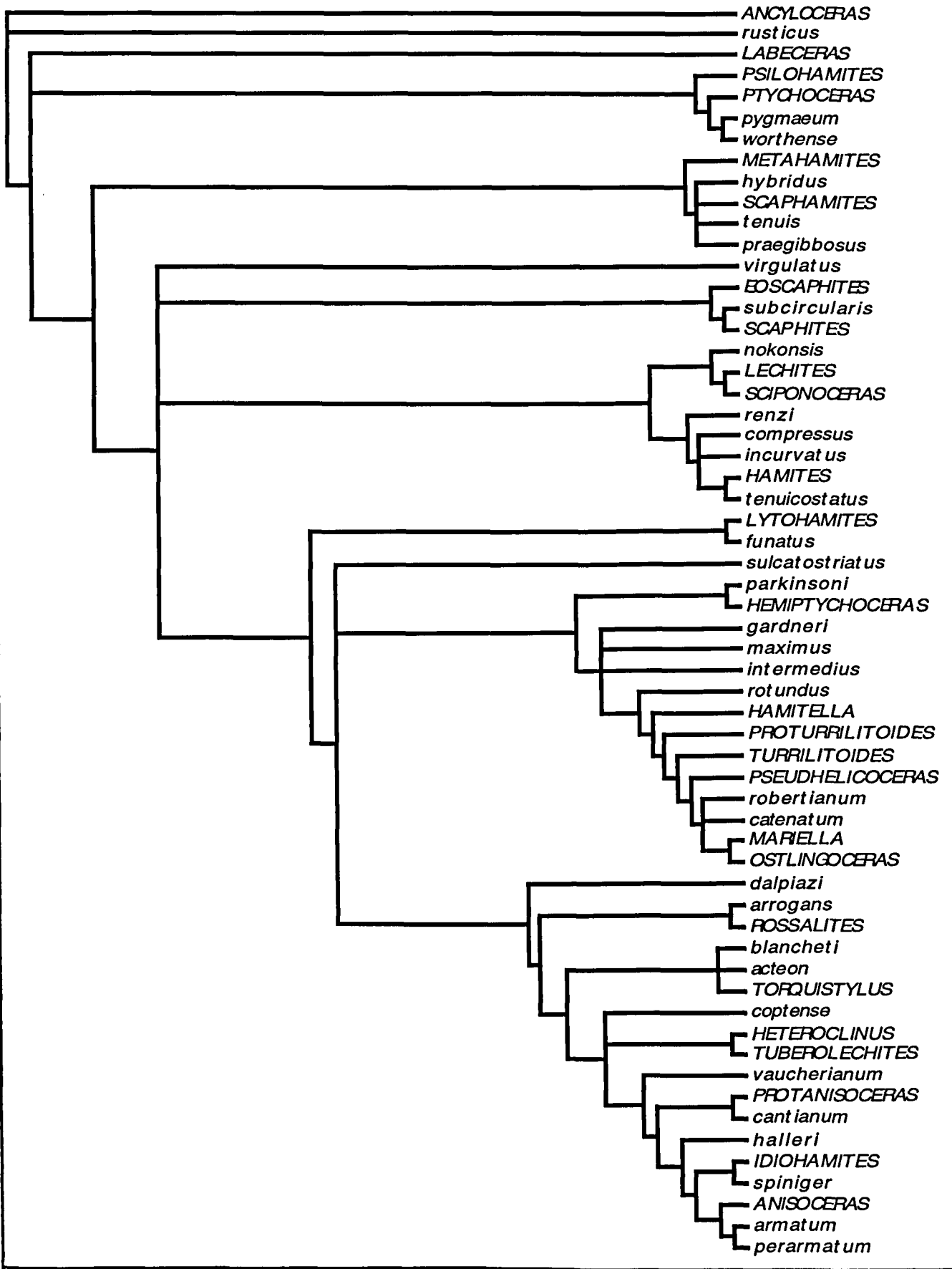


FIGURE 2.11: After reweigting, the strict consensus tree produced from 158 trees.

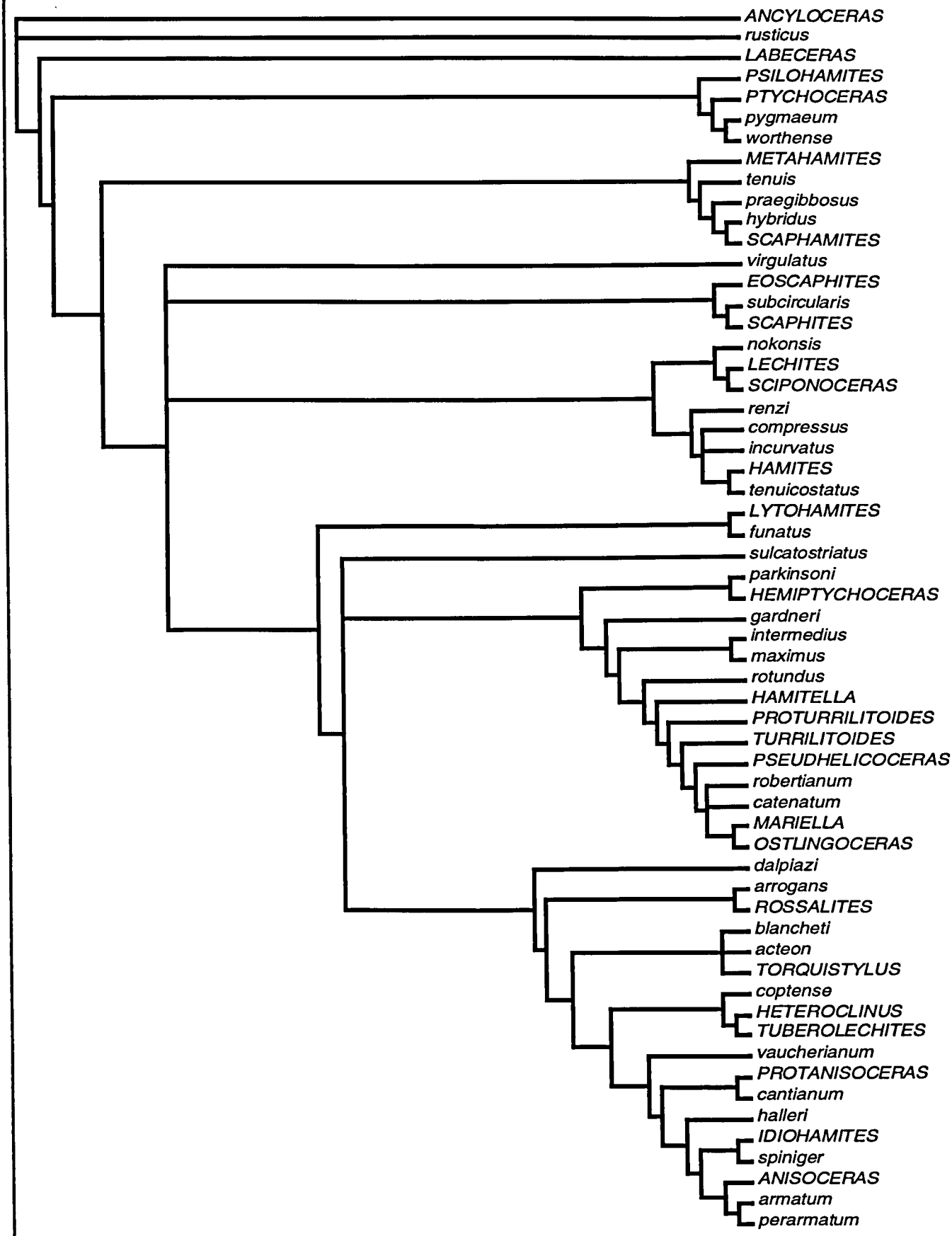


FIGURE 2.12: After reweigting, the 50% majority rule consensus tree produced from 158 trees.

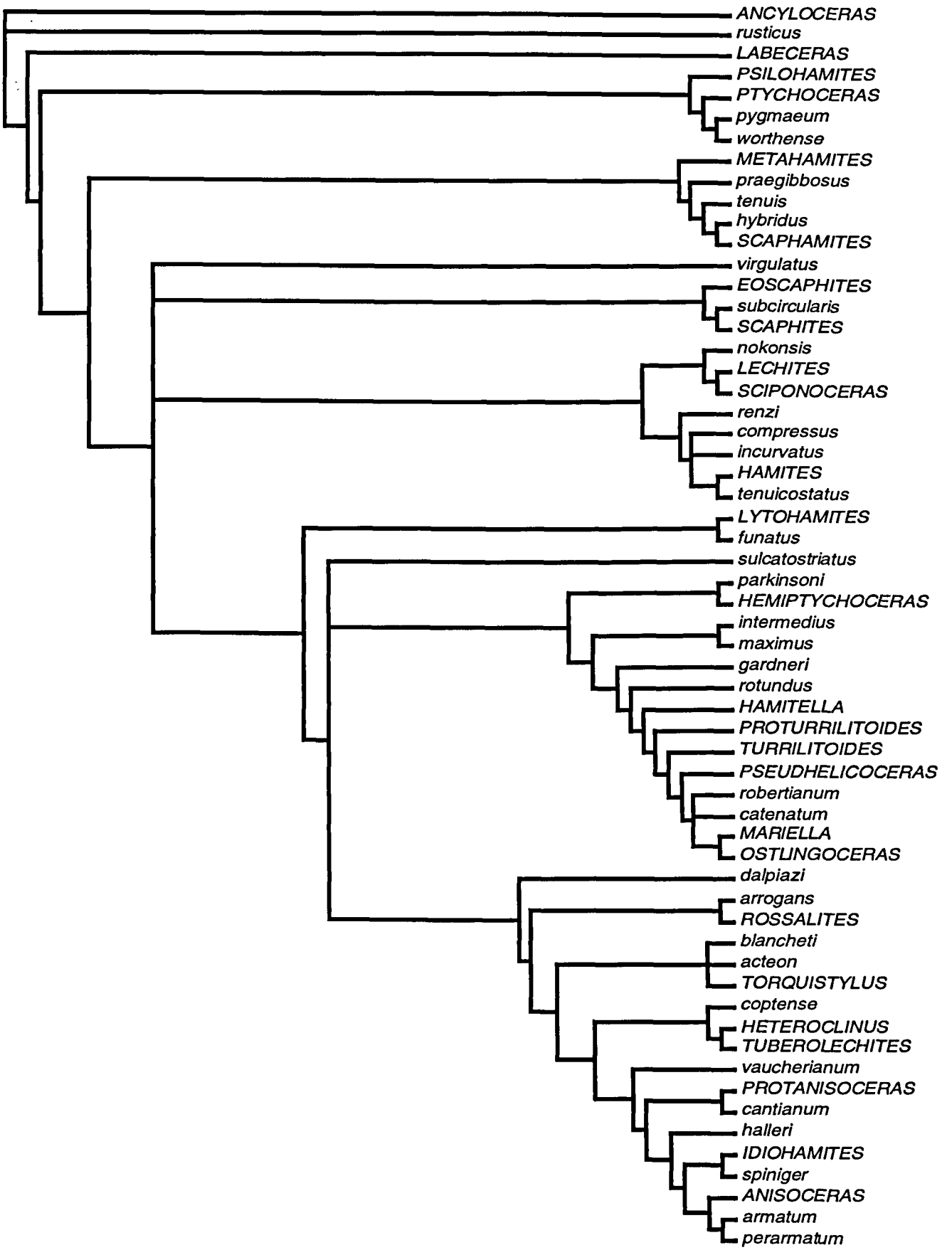


FIGURE 2.13a: One of the six reserved trees from the 158 reweighted trees.

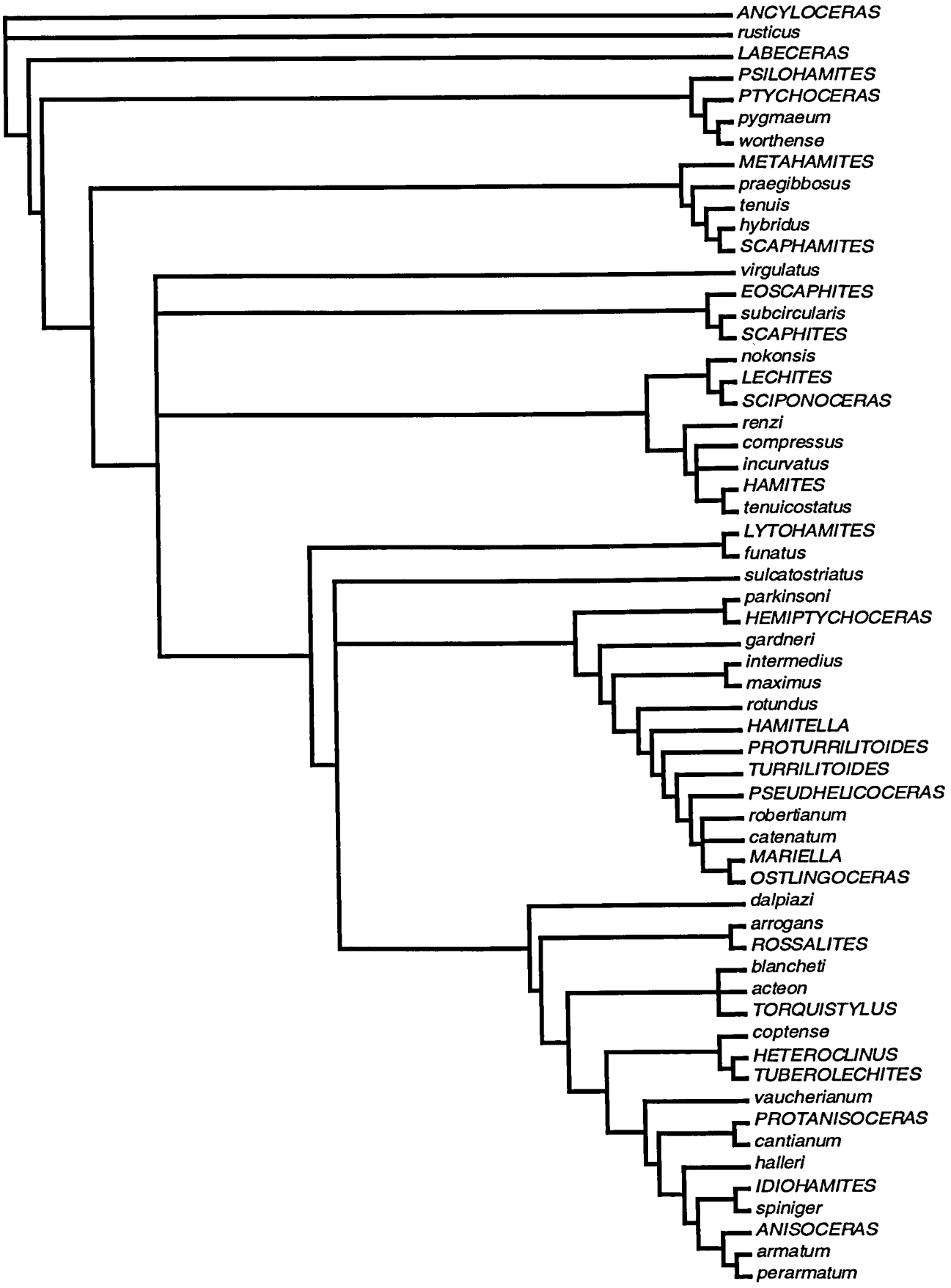


FIGURE 2.13b: One of the six reserved trees from the 158 reweighted trees.

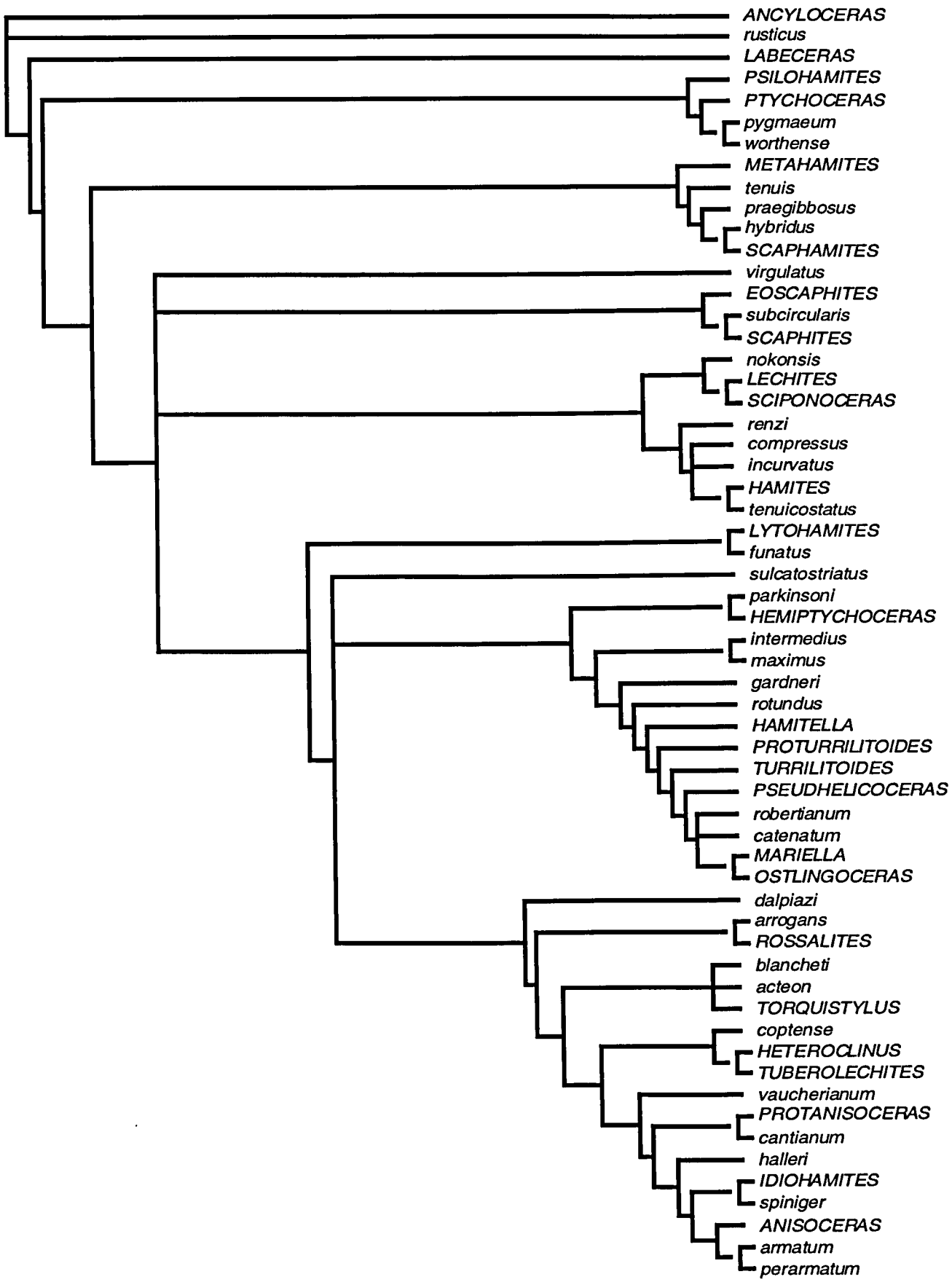


FIGURE 2.13c: One of the six reserved trees from the 158 reweighted trees.

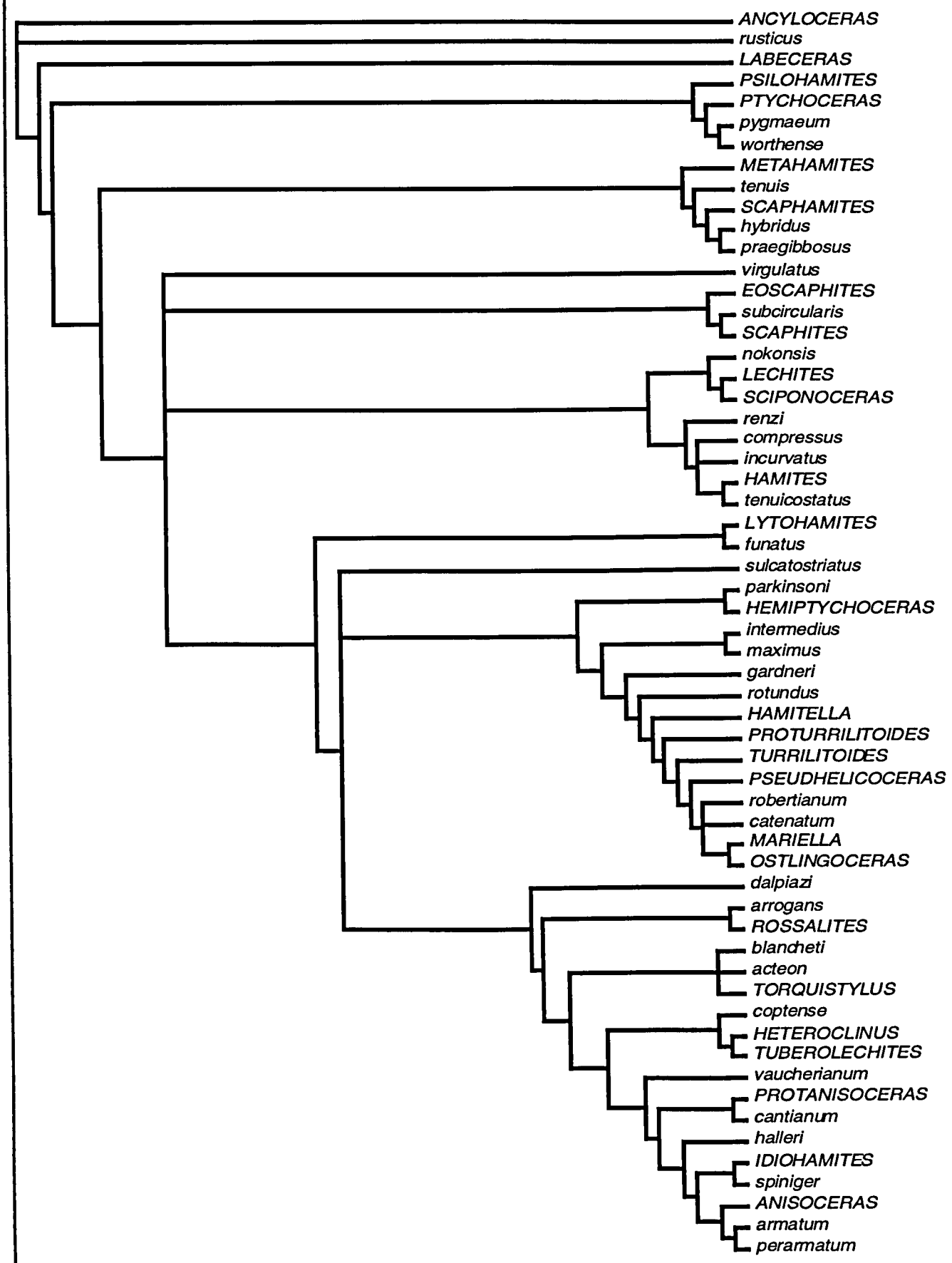


FIGURE 2.13d: One of the six reserved trees from the 158 reweighted trees.

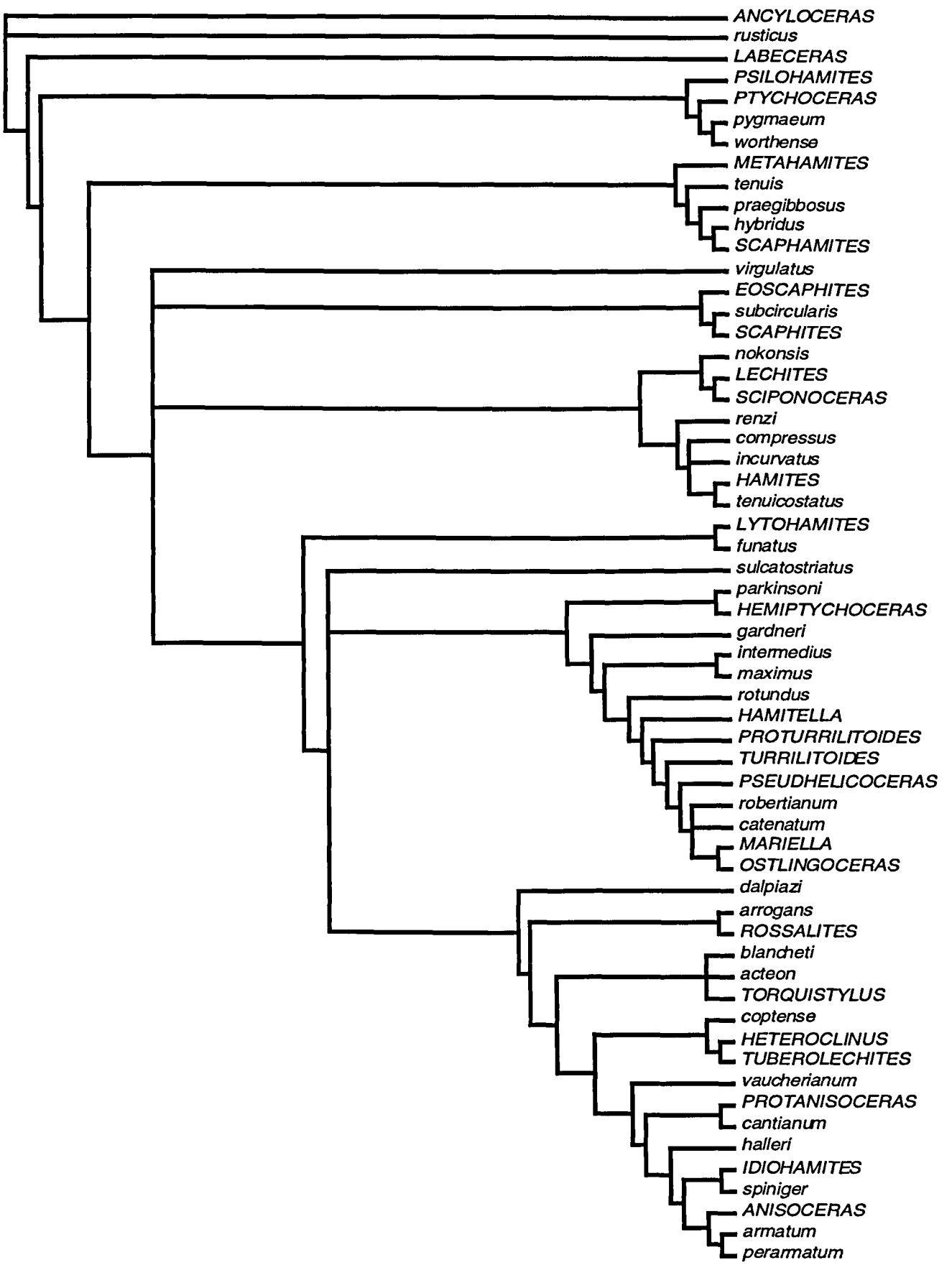


FIGURE 2.13e: One of the six reserved trees from the 158 reweighted trees.

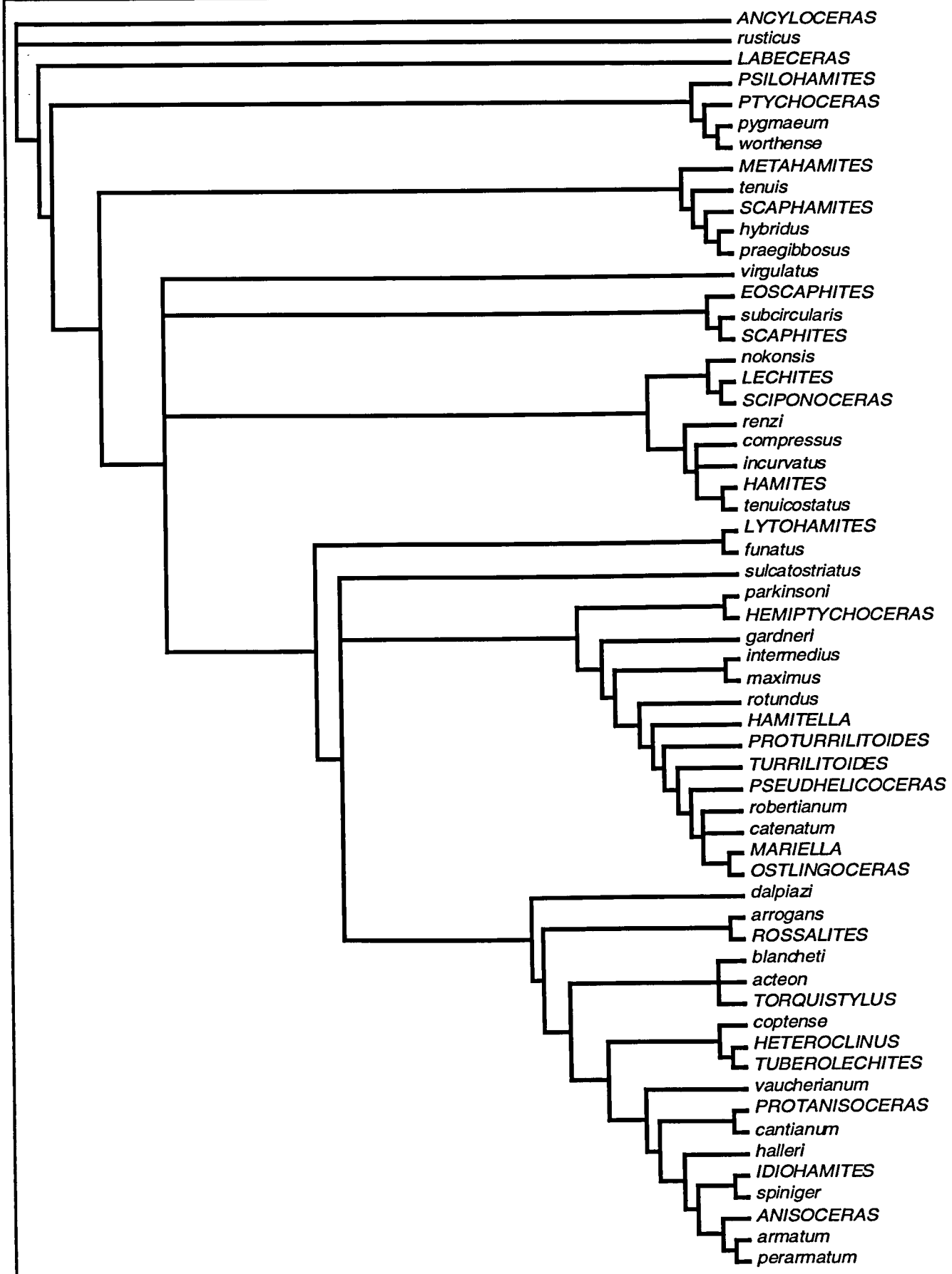


FIGURE 2.13f: One of the six reserved trees from the 158 reweighted trees.

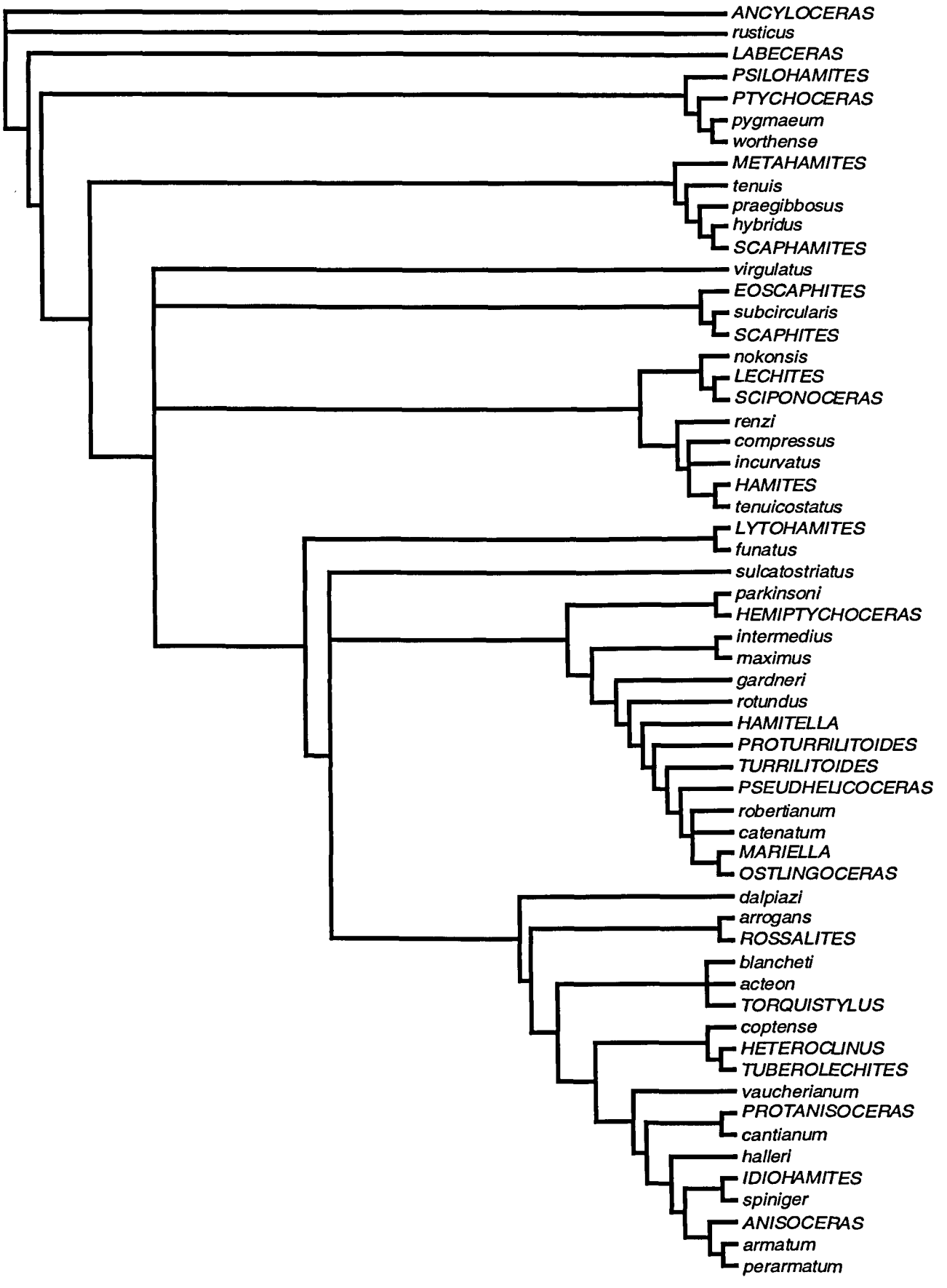


FIGURE 2.14a: One of the final two trees chosen.

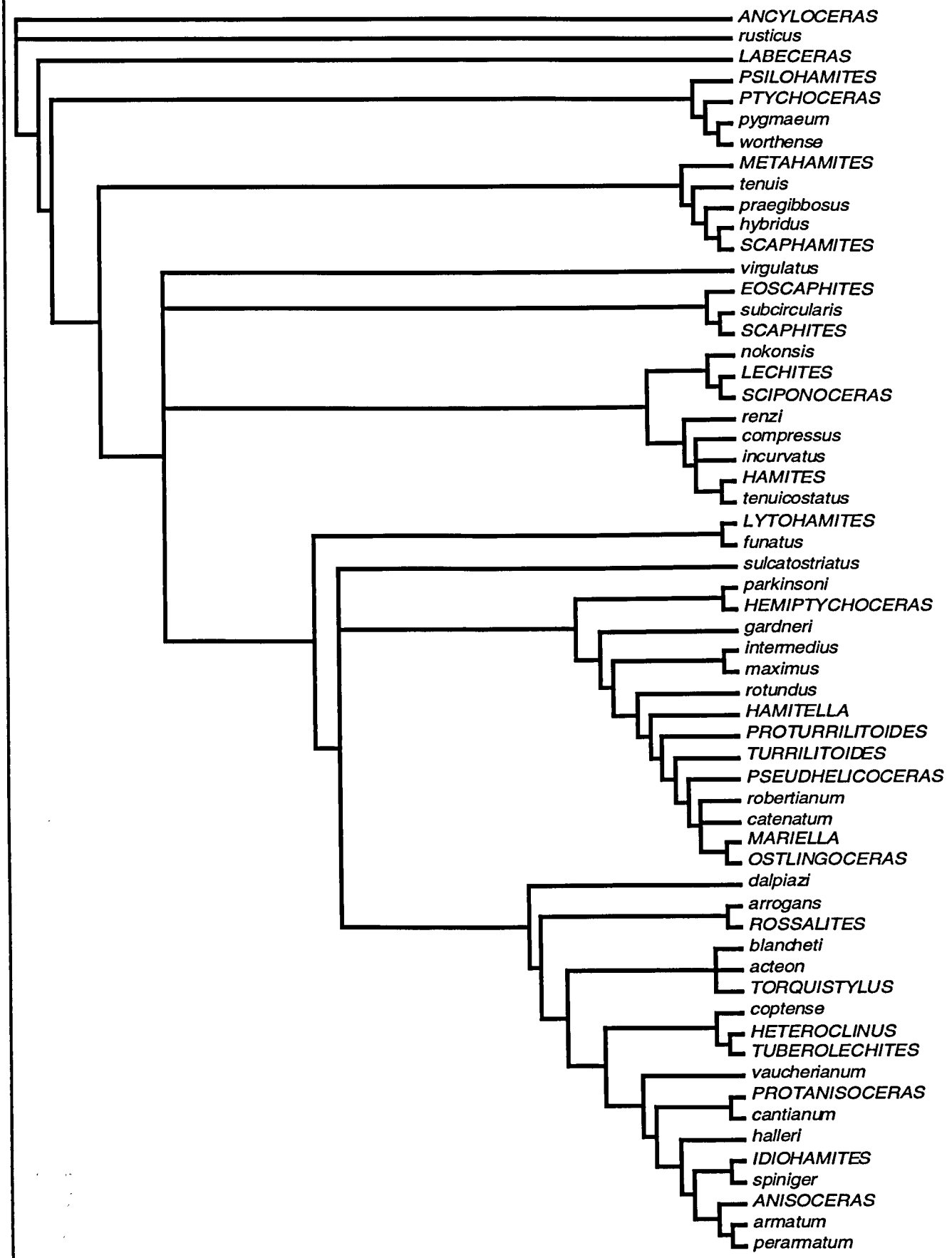


FIGURE 2.14b: One of the final two trees chosen.

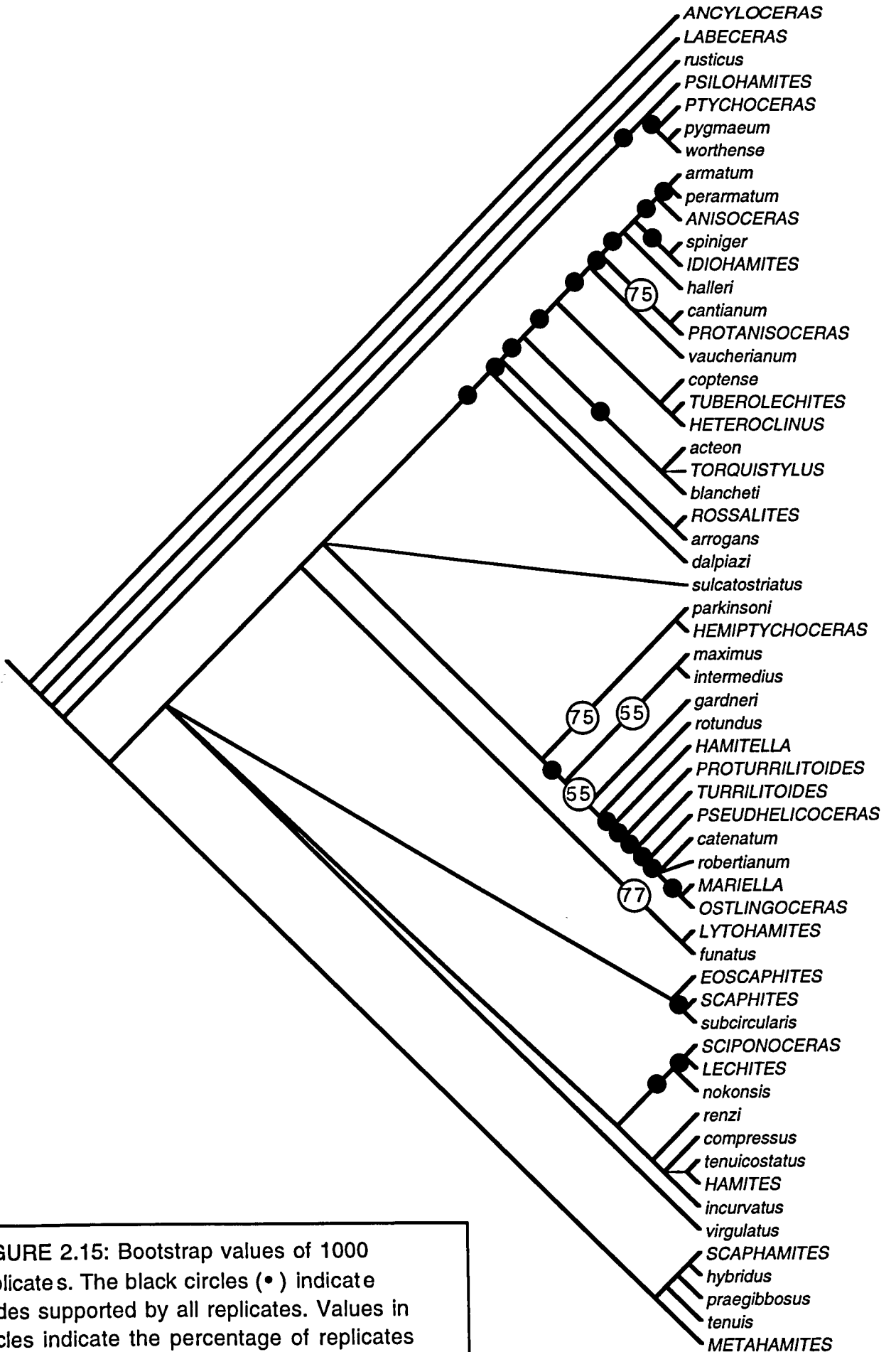


FIGURE 2.15: Bootstrap values of 1000 replicates. The black circles (•) indicate nodes supported by all replicates. Values in circles indicate the percentage of replicates containing that node.

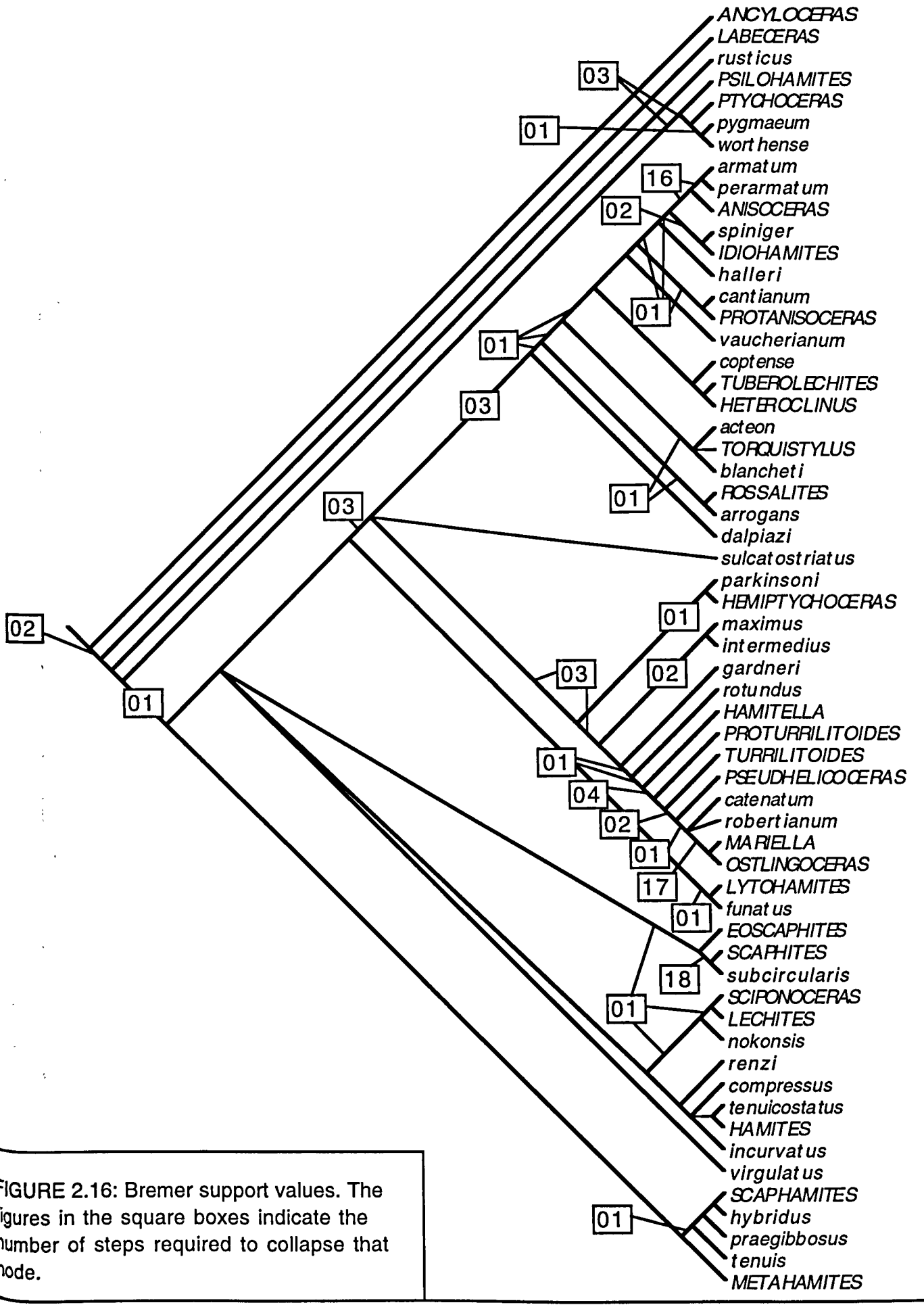


FIGURE 2.16: Bremer support values. The figures in the square boxes indicate the number of steps required to collapse that node.

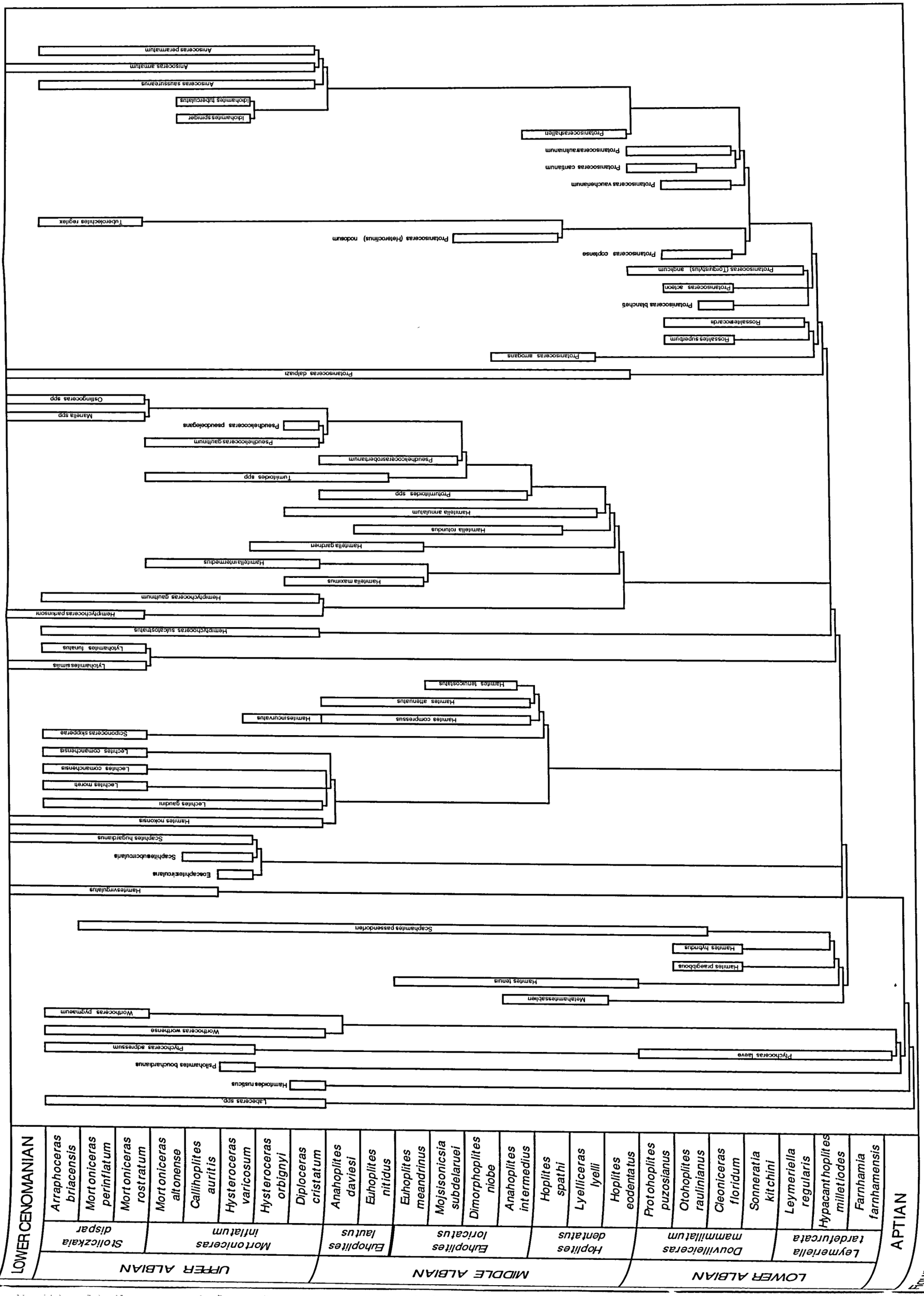


Figure 2.17: Phylostratigraphy of the Albian heteromorph ammonites

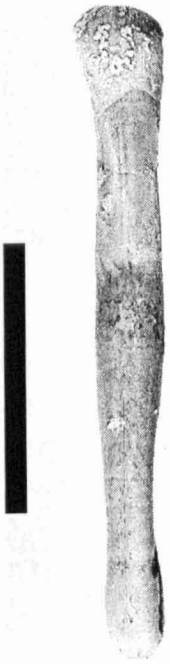


Figure 3.1

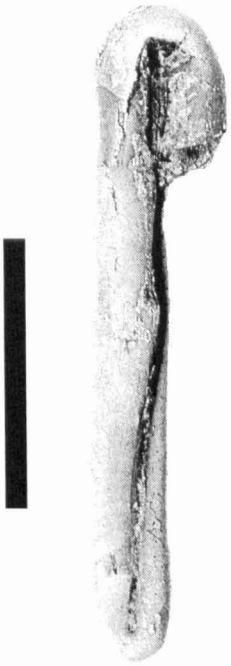


Figure 3.2



Figure 3.3

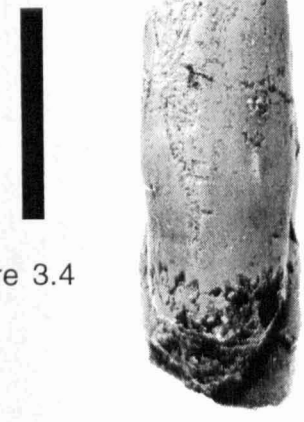


Figure 3.4

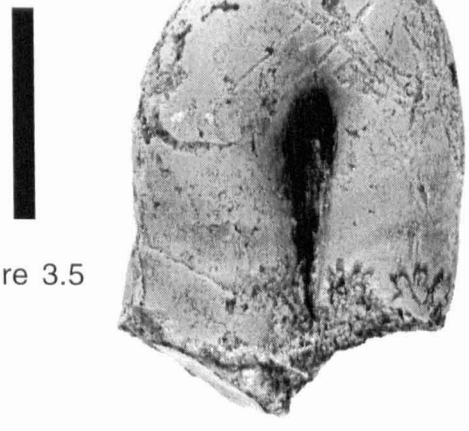


Figure 3.5

FIGURE 3.1 & 3.2: *Ptychoceras adpressum*. Dorsal and lateral views of the holotype, BMNH C.39330 from Bed X of the Gault Clay at Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.3: *Ptychoceras læve*. BMNH C.3520. Lateral view of part of the second and third shafts. From the Middle Albian of Escagnolles, France. Exact stratigraphical horizon unrecorded.

FIGURE 3.4 & 3.5: *Ptychoceras læve*. BMNH C.46837. Dorsal and lateral view of part of the second and third shafts. Also from the Middle Albian of Escagnolles, France.

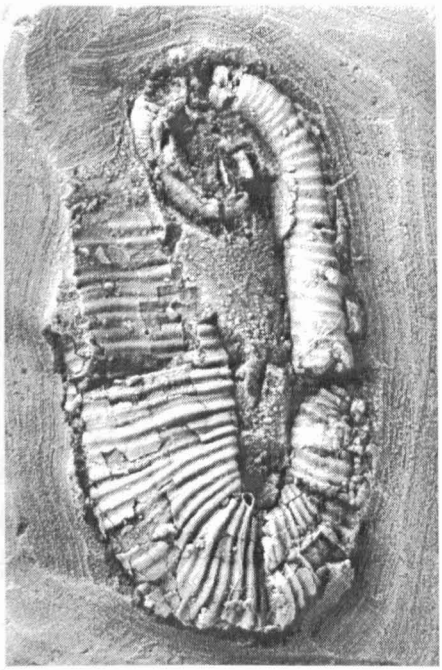


Figure 3.6

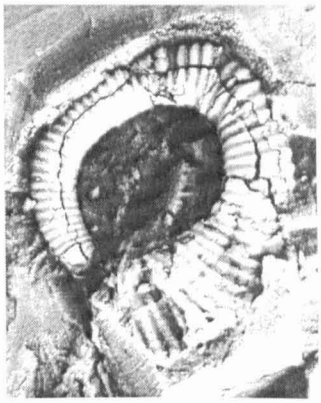


Figure 3.7

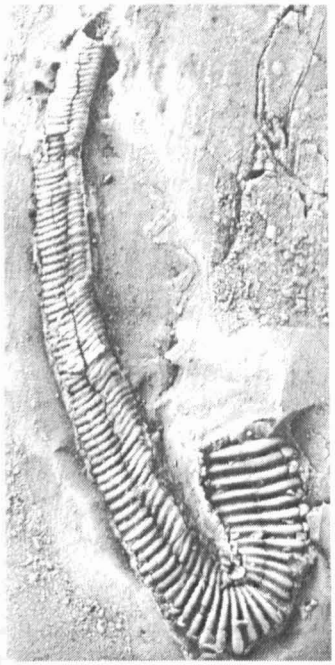


Figure 3.8

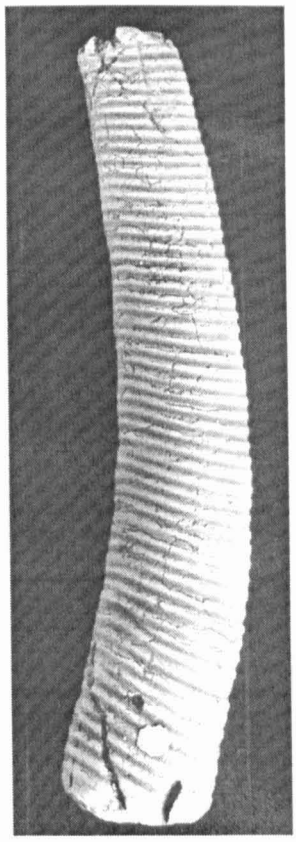


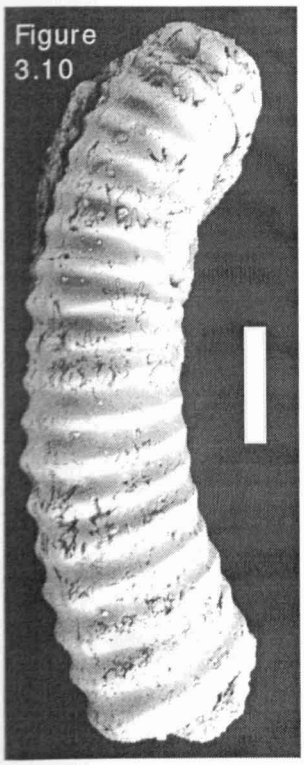
Figure 3.9

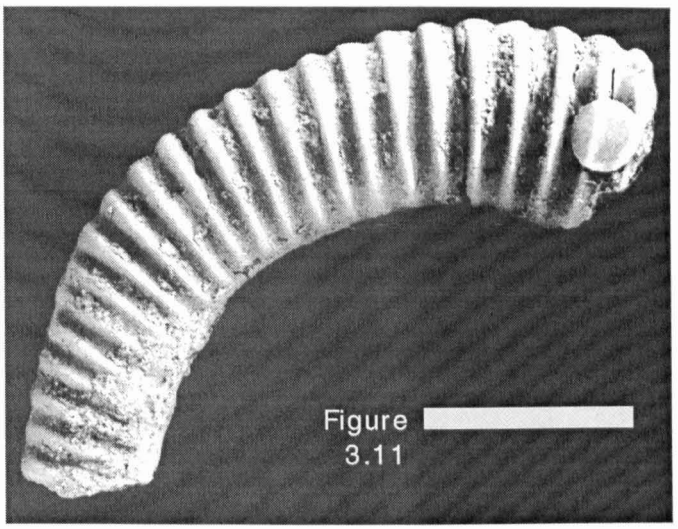
FIGURE 3.6: *Hamites attenuatus*. Lateral view of BMNH C.8566 from the Gault Clay (Middle Albian) at Copt Point, Folkestone. Scale bar = 10 mm.

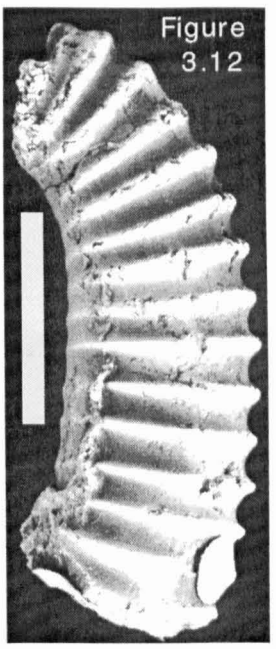
FIGURE 3.7: *Hamites attenuatus*. Criococonic juvenile whorl, BMNH C.8566 from the Gault Clay (Middle Albian) at Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.8: *Hamites attenuatus* transition to *Hamites tenuicostatus*. Lateral view of BMNH C.852 from the Gault Clay (Middle Albian) at Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.9: *Hamites tenuicostatus*. Lateral view. BMNH C.29874 from the Gault Clay (Middle Albian) at Copt Point, Folkestone. Scale bar = 10 mm.







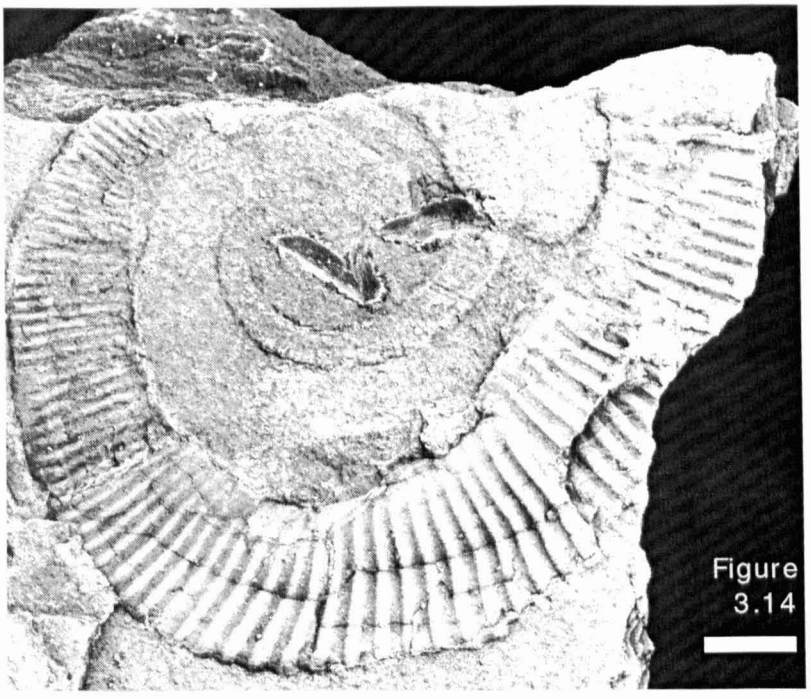


FIGURE 3.10: *Hamites hybridus*. Lateral view of the holotype, Zm 2195 from the Main Mammillatum Beds at Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.11: *Hamites nokonsis*. Lateral view of BMNH C.39920 from the Upper Albian (*dispar* Zone) of Holworth House, Dorset. This specimen is the holotype of *Hamites subvirgulatus*, a species considered here to be junior synonym of *Hamites nokonsis*. Scale bar = 10 mm.

FIGURE 3.12: *Hamites praegibbosus*. Lateral view of BMNH C.47444 from the Main Mammillatum Beds at Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.13: *Hamites praegibbosus*. Lateral view of BMNH C.47442 from the Main Mammillatum Beds at Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.14: *Hamites renzi*. Lateral view of the holotype, BMNH C.94119 from the Marnes Bleus, Upper Albian (*dispar* Zone) of Mont Risou, Hautes-Alpes, France. Scale bar = 10 mm.

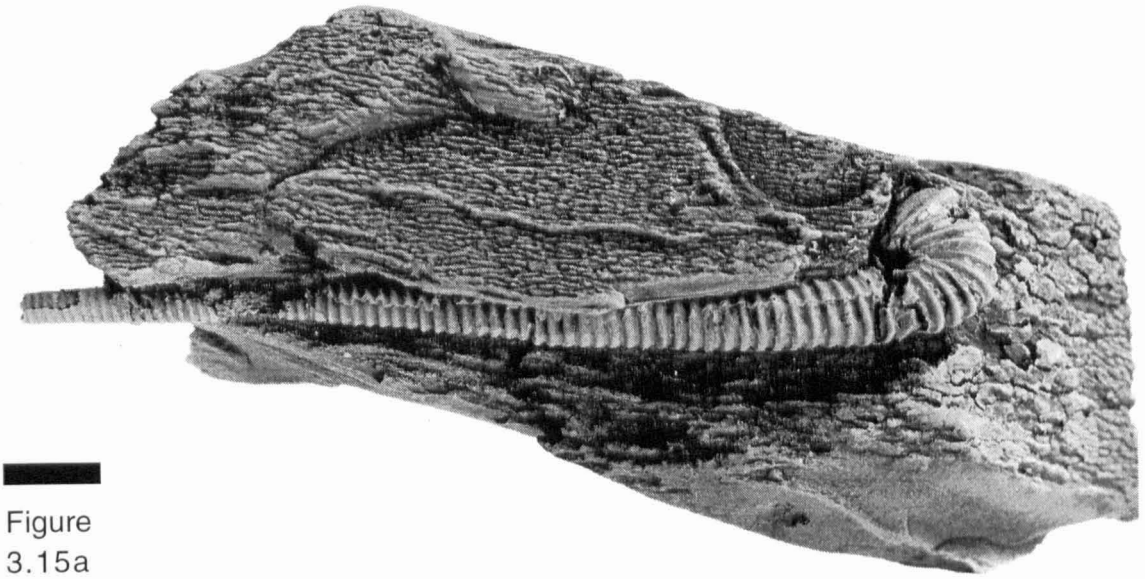


Figure
3.15a

Figure
3.15b

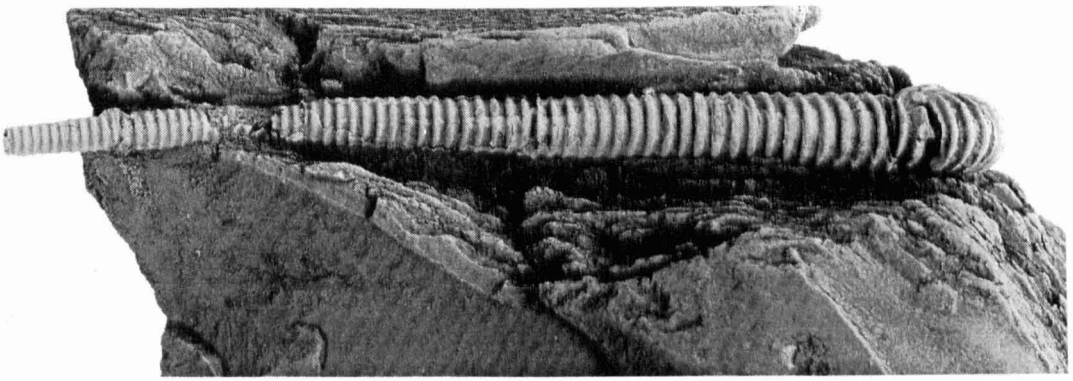


FIGURE 3.15a, 3.15b: *Hamites tenuis*. Lateral and ventral views of a specimen from the author's collection. From the Gault Clay (Lower Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

Figure 3.16

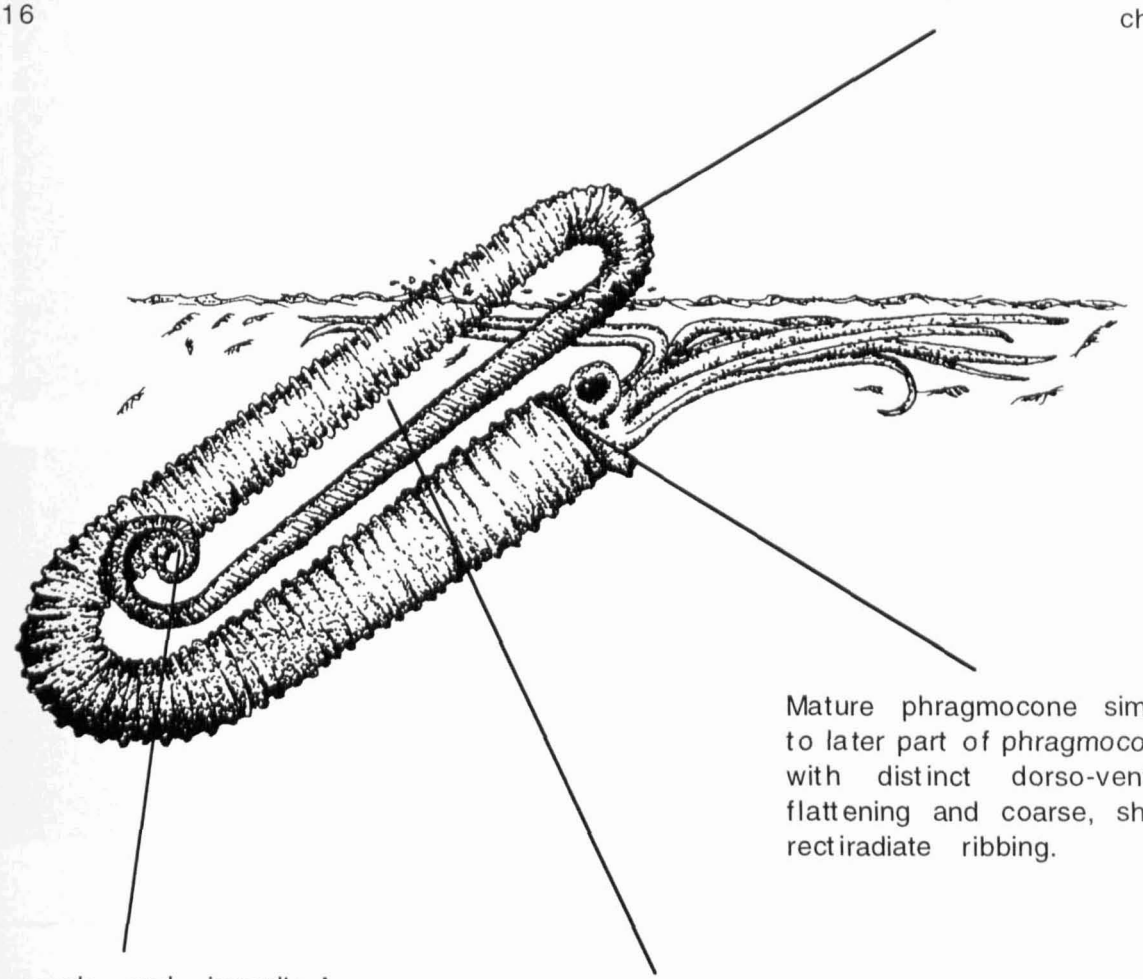
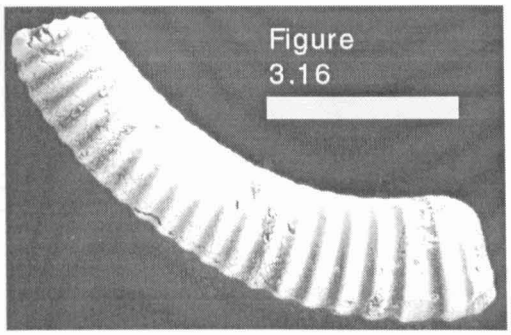
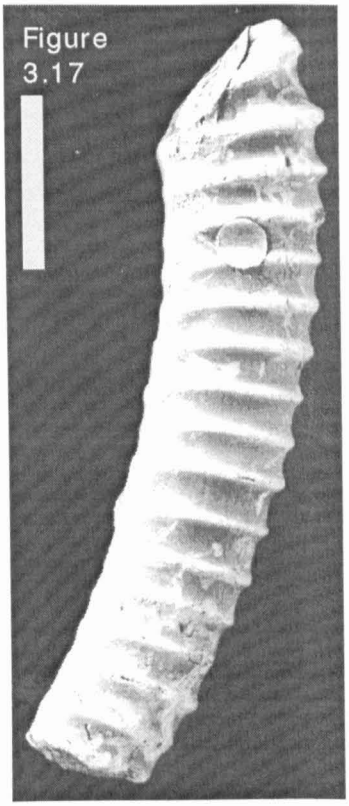
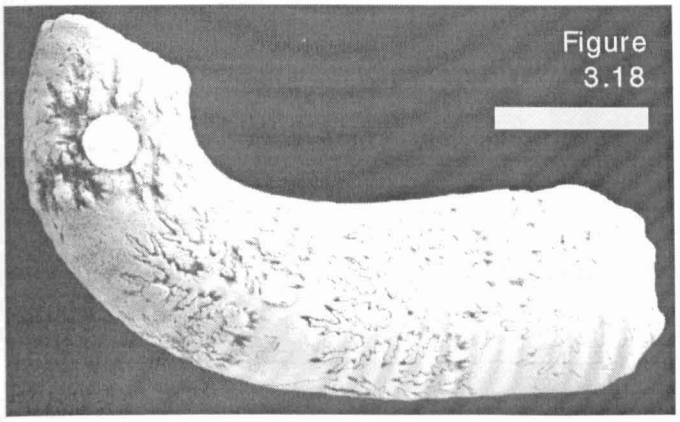


FIGURE 3.16: *Hamites tenuis*. Reconstruction of *Hamites tenuis*, here feeding on surface water plankton. The key diagnostic features of this species are labelled. The orientation of this ammonite is based upon Trueman (1941).







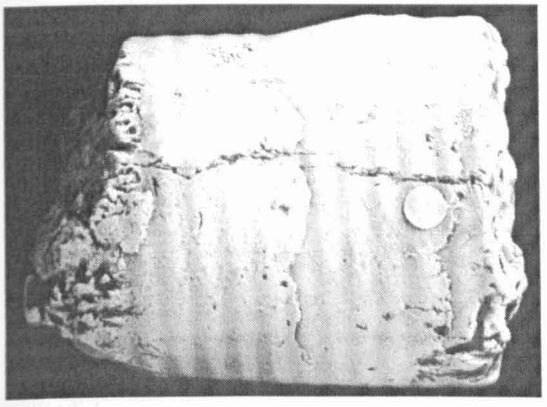


Figure
3.19

Figure
3.20

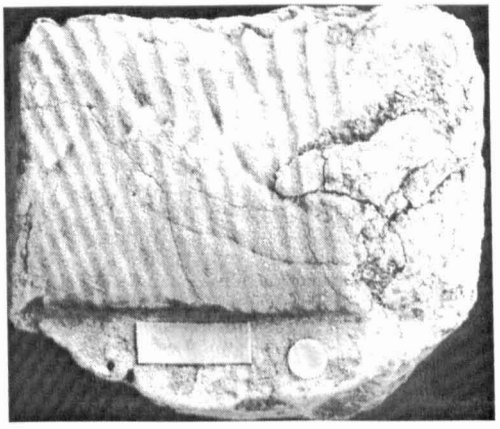


FIGURE 3.17: *Hamites virgulatus*. Lateral view of the BMNH C.77628 from the Cambridge Greensand (Upper Albian) of Cambridge. Scale bar = 10 mm.

FIGURE 3.18: *Hamites virgulatus*. Lateral view of the BMNH C.77635 from the Cambridge Greensand (Upper Albian) of Cambridge. Scale bar = 10 mm.

FIGURE 3.19: *Lytohamites similis*. Lateral view of the holotype specimen, BMNH C.4762a from the Cambridge Greensand (Upper Albian) of Cambridge. Scale bar = 10 mm.

FIGURE 3.20: *Lytohamites similis*. Part of the final shaft of a large specimen. BMNH C.4769a from the Cambridge Greensand (Upper Albian) of Cambridge. Scale bar = 10 mm.

FIGURE 3.21: "*Hamites multicostatus*". The holotype specimen, although the validity of the species name is questioned (see Kennedy, 1971). BMNH C.36572 from the Chalk Marl (Lower Cenomanian), Hamsey, Sussex. Scale bar = 10 mm.

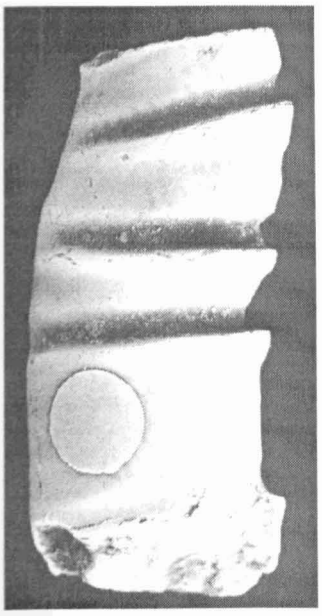


Figure 3.22

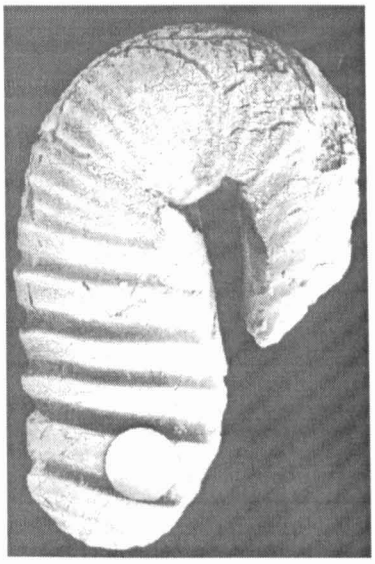


Figure 3.23

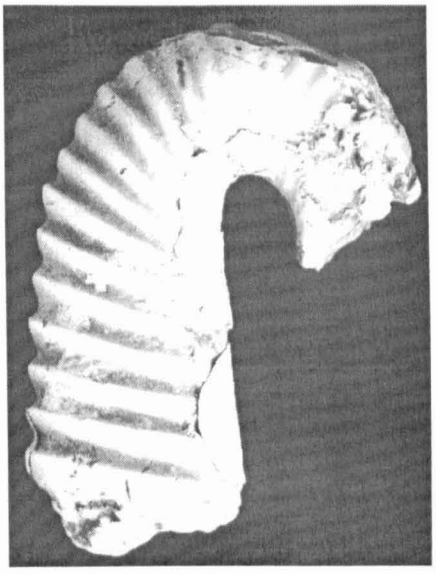


Figure 3.24

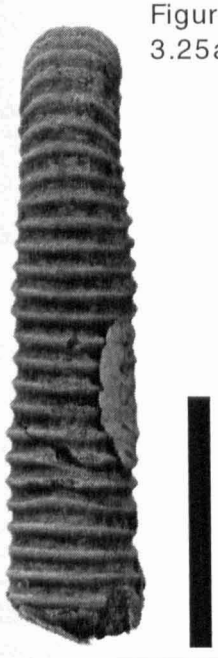


Figure 3.25a



Figure 3.25b

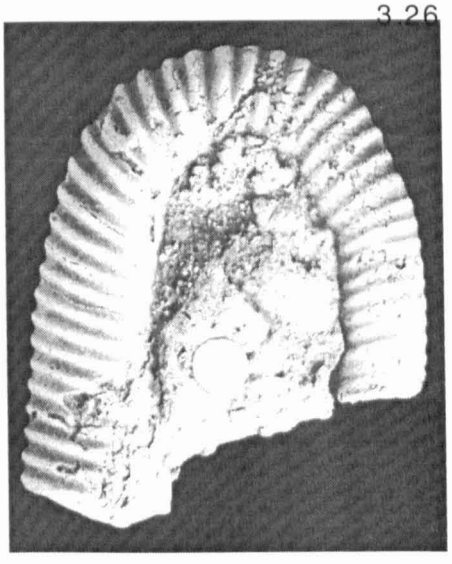


Figure 3.26

FIGURE 3.22: *Lytohamites funatus*. Mature aperture of a microconch of BMNH C.39927 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Scale bar = 10 mm.

FIGURE 3.23: *Lytohamites funatus*. Lateral view of a macroconch, BMNH C.25176 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Note the appearance of the scale-like ribbing on the final living chamber. Scale bar = 10 mm.

FIGURE 3.24: *Lytohamites funatus*. Macroconchs, BMNH C.39923 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Scale bar = 10 mm.

FIGURE 3.25a, 3.25b: *Hemiptychoceras gaultinum*. Ventral and dorsal views of BMNH C.46855 from the Gault Clay (Upper Albian) at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.26: *Hemiptychoceras parkinsoni*. Lateral view of BMNH C.77637 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Scale bar = 10 mm.

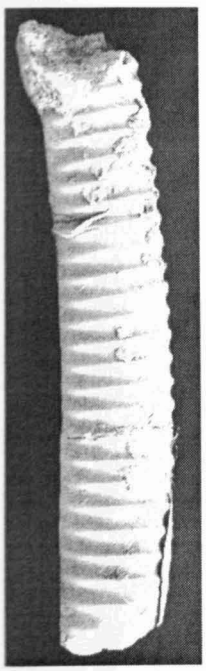


Figure 3.27

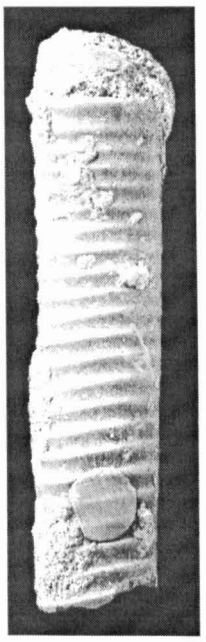
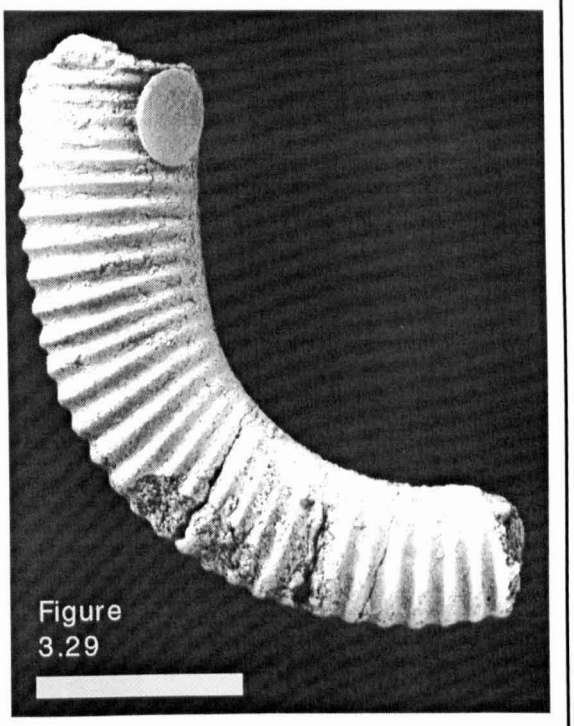
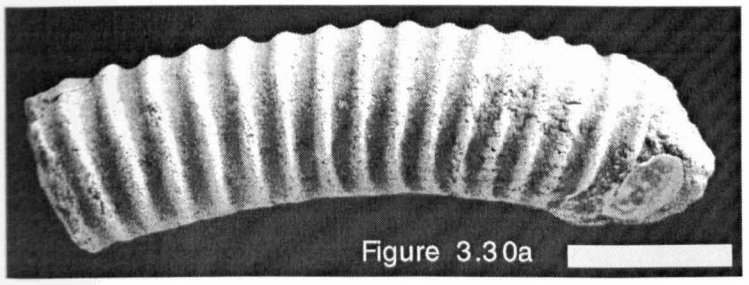
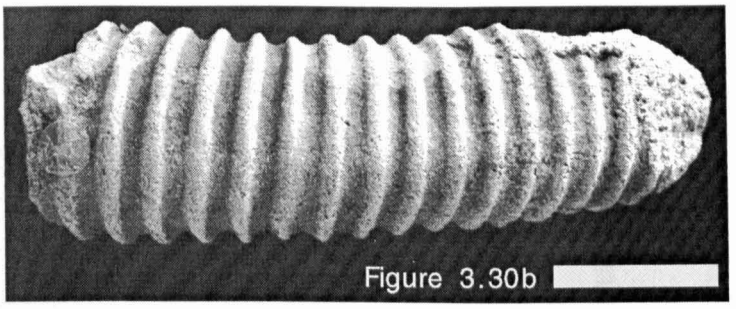


Figure 3.28







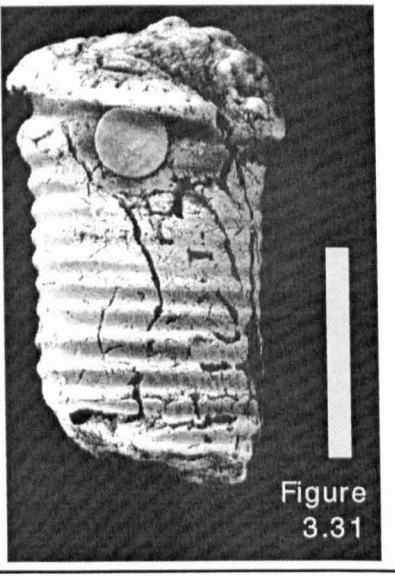


FIGURE 3.27: *Hemiptychoceras parkinsoni*. Lower Cenomaninan specimen BMNH C.72216 from Chinnor, near Dunstable, Bedfordshire. Scale bar = 10 mm.

FIGURE 3.28: *Hemiptychoceras parkinsoni*. Lower Cenomaninan (*Turrilites costatus* assemblage, Cenomanian Basement Bed) specimen BMNH C.76361 from Buckand Newton, Dorset. This specimen shows the apertural constrictions and collars characteristic of the genus (toward the top of the photograph). Scale bar = 10 mm.

FIGURE 3.29: *Hemiptychoceras parkinsoni*. Lateral view of specimen BMNH C.76361 from the Upper Albian (*dispar* Zone) at Punfield Cove, Dorset. Scale bar = 10 mm.

FIGURE 3.30a, 3.30b: *Hemiptychoceras parkinsoni*. Neotype specimen BMNH C.76361 from the Upper Greensand Malmstone (Upper Albian, *dispar* Zone) from Devizes, Wilshire. This is part of the weakly helical phragmocone, as evidenced by the twisted ribs. Scale bar = 10 mm.

FIGURE 3.31: *Hemiptychoceras parkinsoni*. Well preserved examples of the constriction and paired apertural collars typical of this species and the genus. BMNH C.76361 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge. Scale bar = 10 mm.

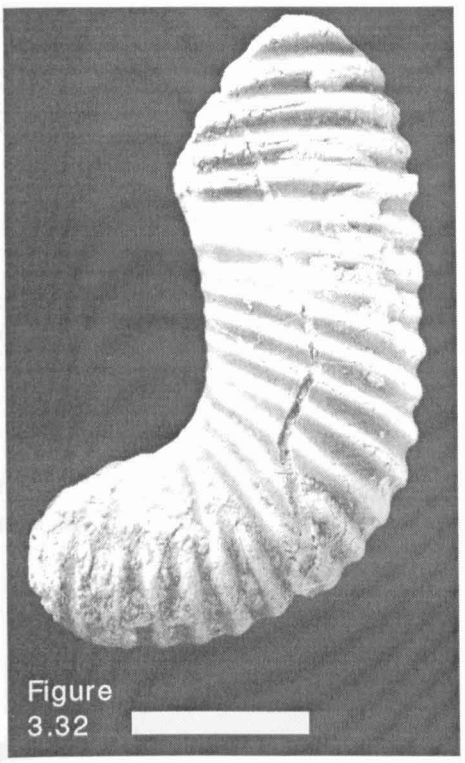


Figure 3.32

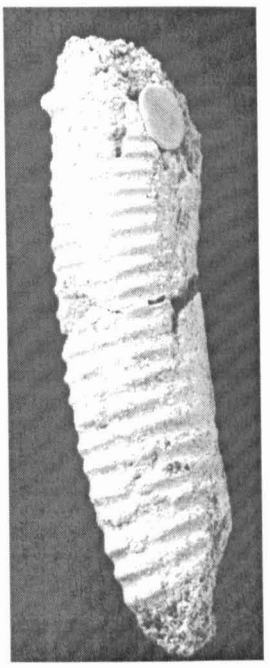


Figure 3.33



Figure 3.34a

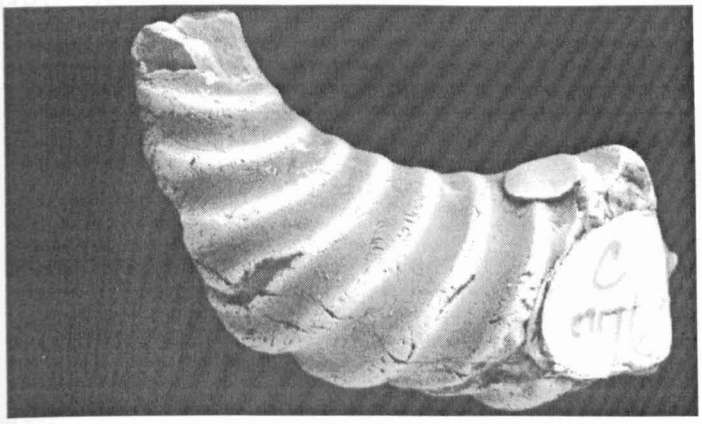


Figure 3.34b

FIGURE 3.32: *Hemiptychoceras parkinsoni*. Lateral view of BMNH C.47611e from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Scale bar = 10 mm.

FIGURE 3.33 *Hemiptychoceras parkinsoni*. Lateral view of the mature living chamber of BMNH C.90889 from the Upper Albian, *dispar* Zone at Punfield Cove, Dorset. One of the apertural collars are visible toward the top of the fragment. Scale bar = 10 mm.

FIGURE 3.34a, 3.34b: *Hemiptychoceras parkinsoni*. BMNH C.77631 from the Cambridge Greensand (Upper Albian, *dispar* Zone), Cambridge. Part of the tightly helically coiled phragmocone. Scale bar = 10 mm.

Figure 3.35

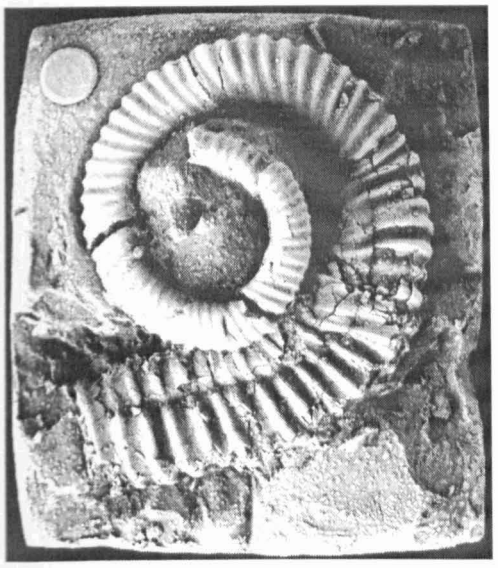


Figure 3.36a

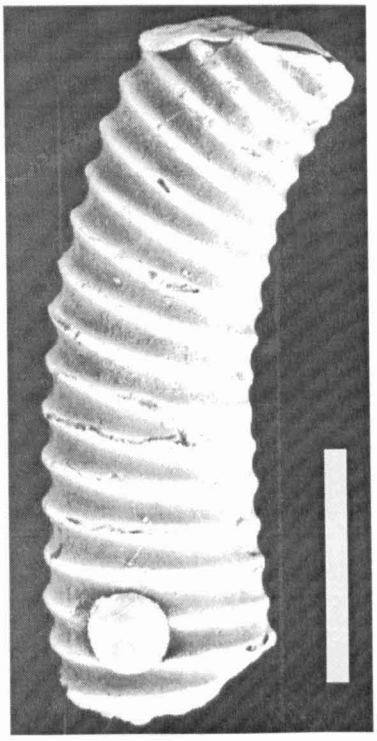


Figure 3.36b

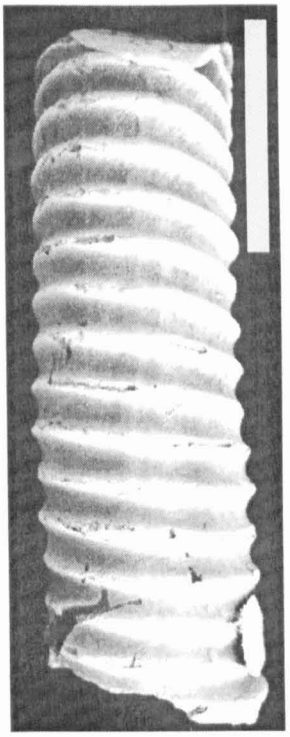
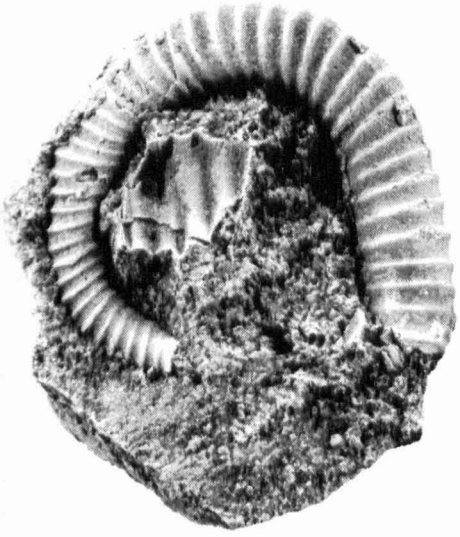


Figure 3.37a



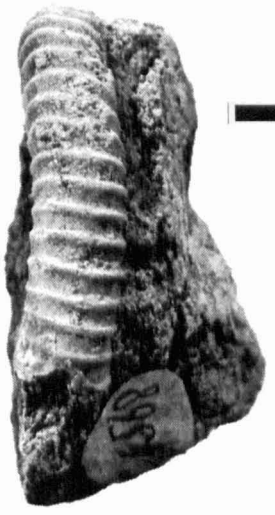


Figure 3.37b

FIGURE 3.35: *Hamitella annulatum*. Helical phragmocone BMNH C.853 from the Lower Gault, (Middle Albian, from Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.36a, 3.36b: *Hamitella annulatum*. Lateral and ventral view of part of the phragmocone with the characteristically twisted ribs of this genus. BMNH C.39904 from the Lower Gault, (Middle Albian, from Copt Point, Folkestone. Scale bar = 10 mm.

FIGURE 3.37a, 3.37b: *Hamitella annulatum*. BMNH C.4568 from the condensed Gault Clay (Middle and Upper Albian) of Escragnolles, South East France. Scale bar = 10 mm.

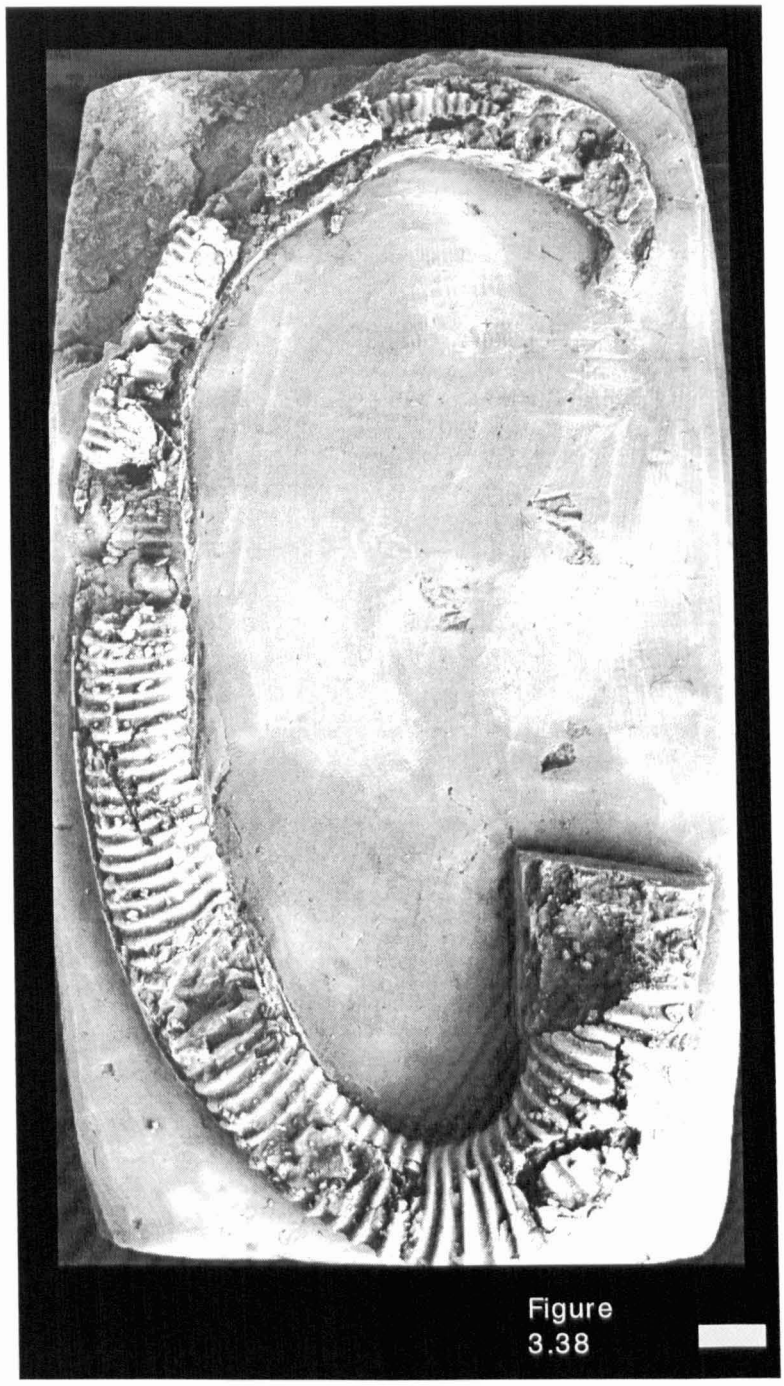


FIGURE 3.38: *Hamitella gardneri*. A specimen with a deeper, more ancycloconic hook than usual, and apparently transitional to *Hamitella maximus*. BMNH C.857 from the Upper Gault (Upper Albian), at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

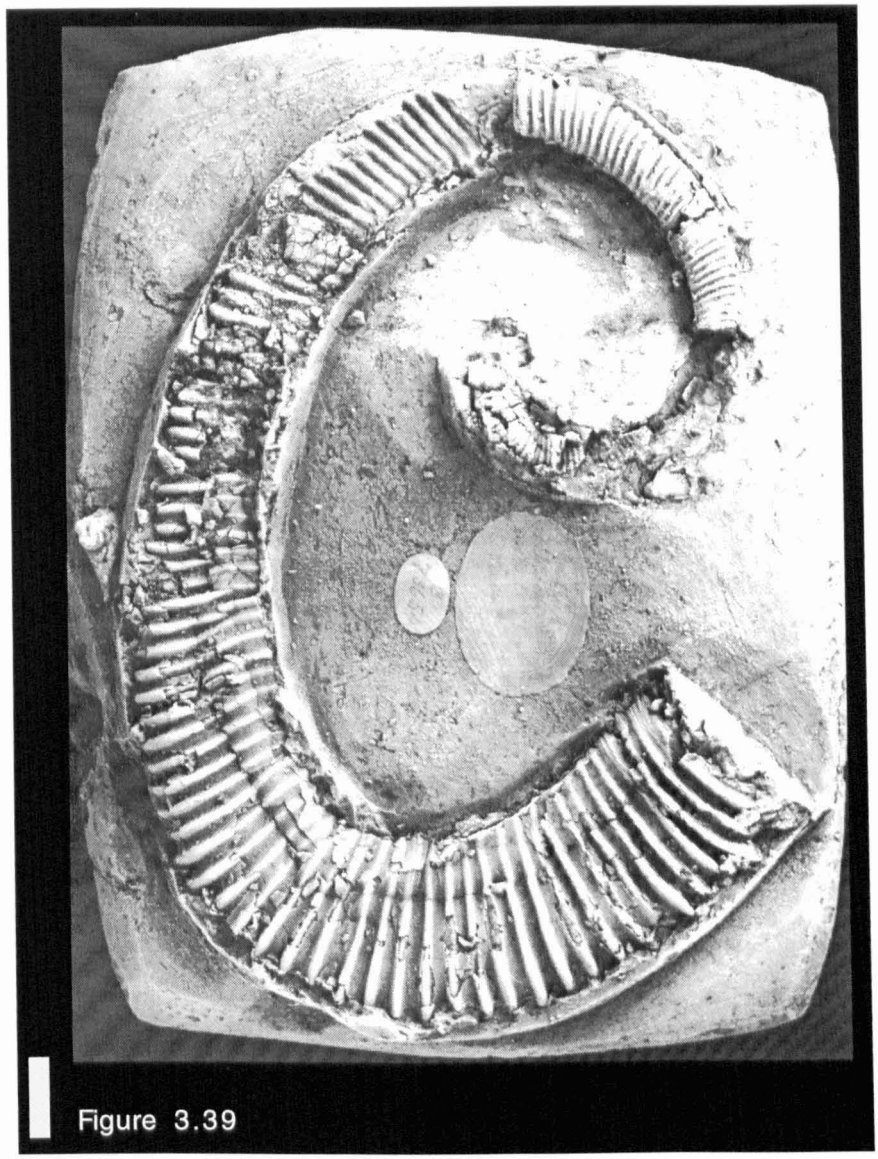


FIGURE 3.39: *Hamitella gardneri*. BMNH C.73654 from the Upper Gault (Upper Albian), at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

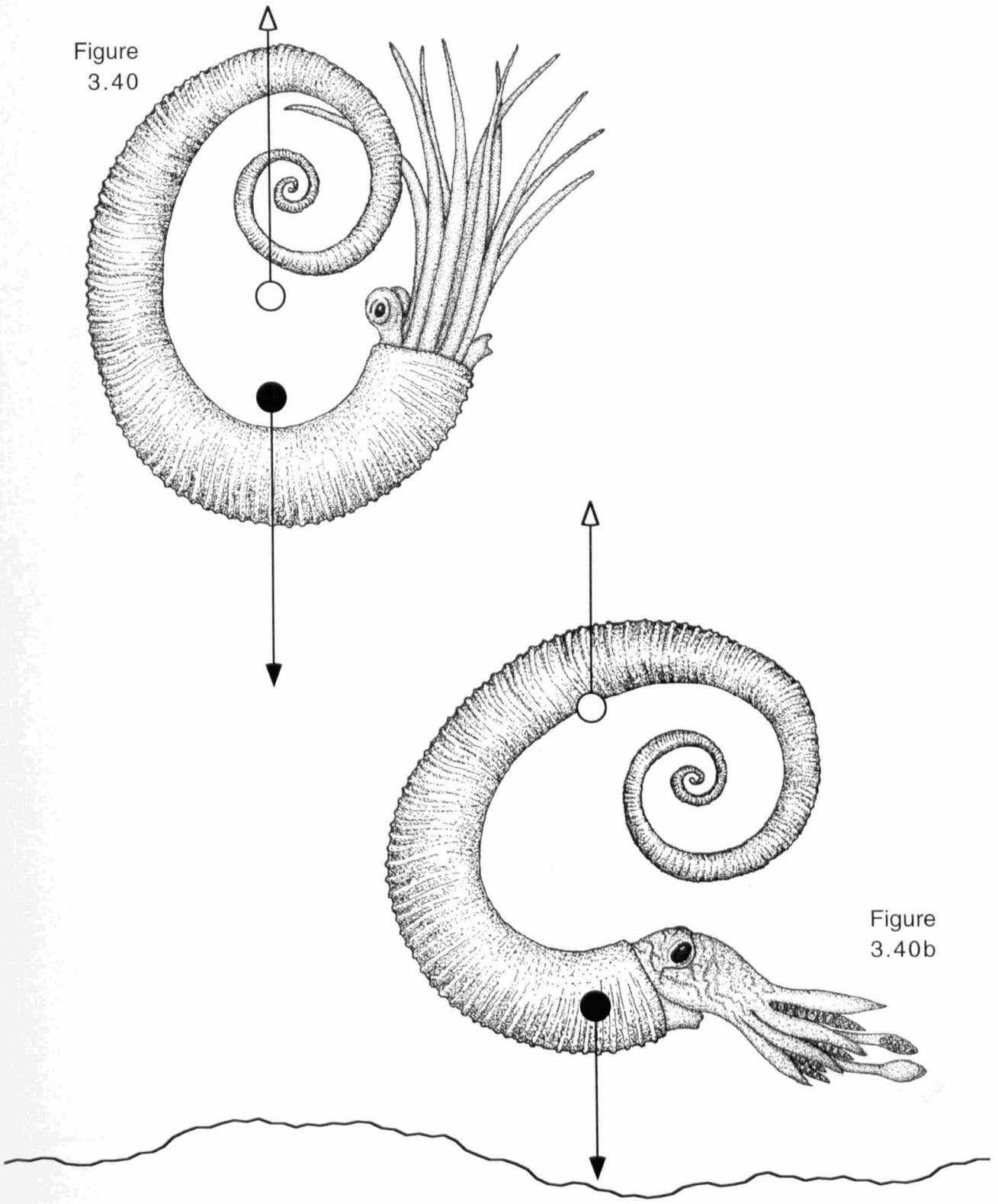
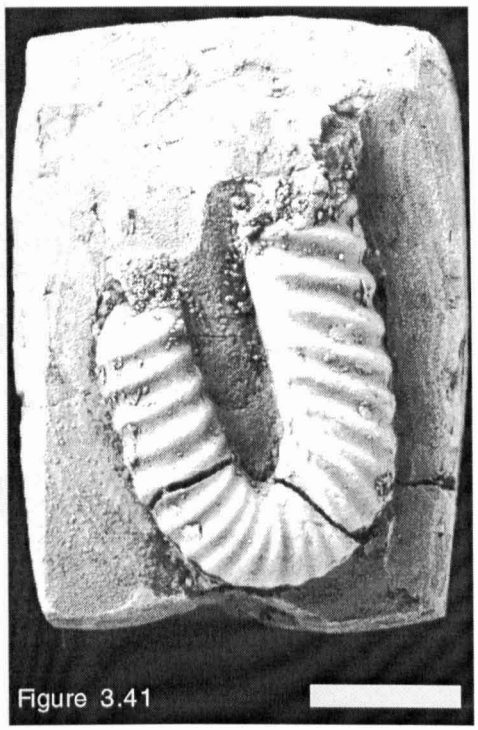


FIGURE 3.40: *Hamitella gardneri.* Reconstruction in two possible modes of life: (a) as a planktonic drifter with upturned apertures; and (b) as a demersal or benthonic predator or scavenger with the aperture oriented downwards. The estimated positions of the centres of mass (black circles) and buoyancy (white circles) are labelled, and these are critical in determining orientation. See Chapters 4 and 5 for discussion on how these ammonite lifestyles were reconstructed.



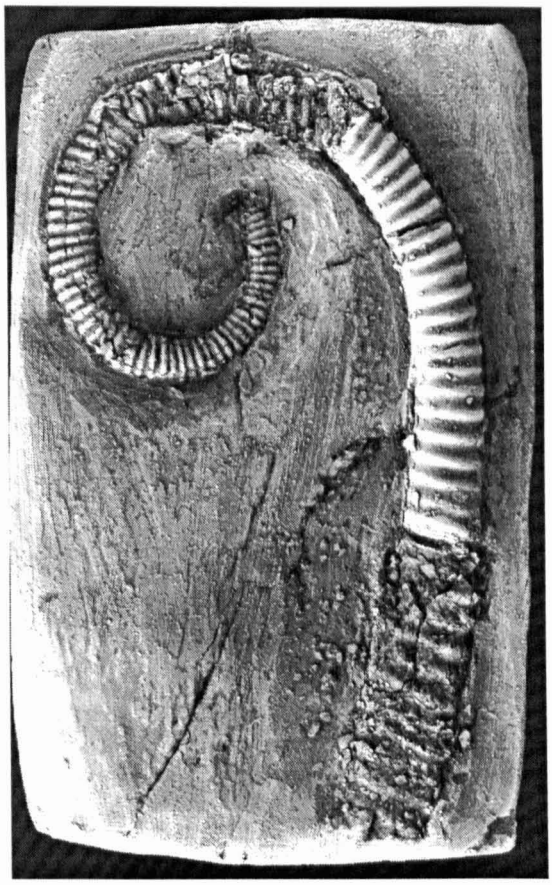


Figure 3.42a



Figure 3.42b

FIGURE 3.41: *Hamitella intermedius*. Lateral view of BMNH C.852 from the Upper Gault (Upper Albian) at Copt Point, Folkestone, Kent. Note malformed (damaged?) rib just above crack on the right hand side of the specimen. Scale bar = 10 mm.

FIGURE 3.42a, 3.42b: *Hamitella maximus*. Lateral (3.42a) and ventral (3.42b) views of the helically coiled juvenile shell BMNH C.3012 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. This specimen belongs to the variety *rectus* of Spath (1941). This variety has finer ribbing than the type material of *Hamitella maximus*. Some authors consider it a seperate species (e.g., Wiedmann & Marcinowski, 1990). Scale bar = 10 mm.

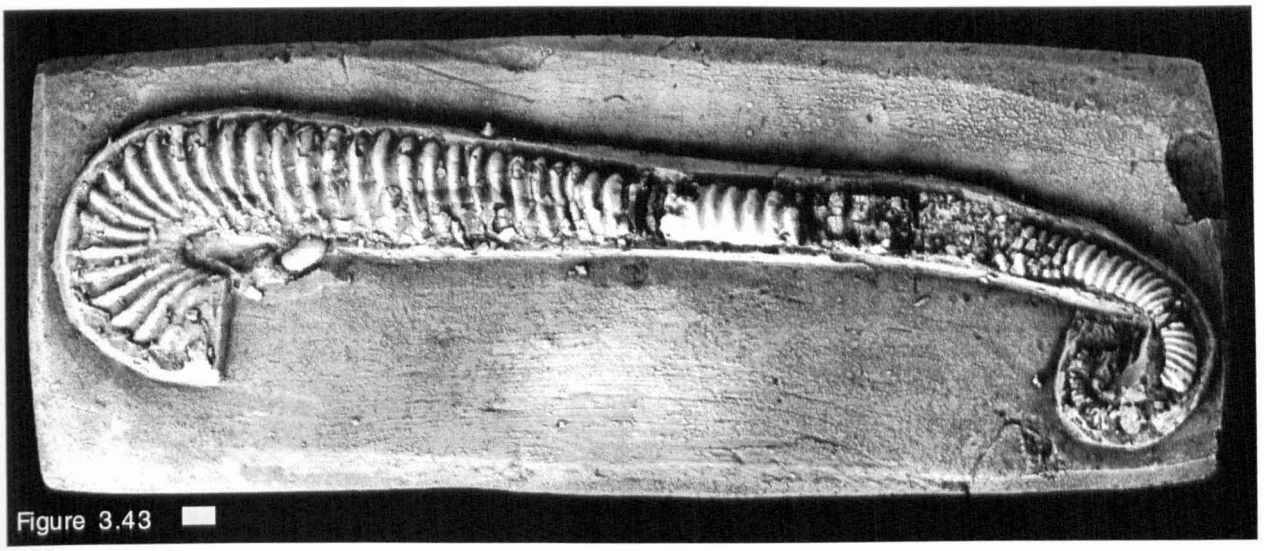


Figure 3.43

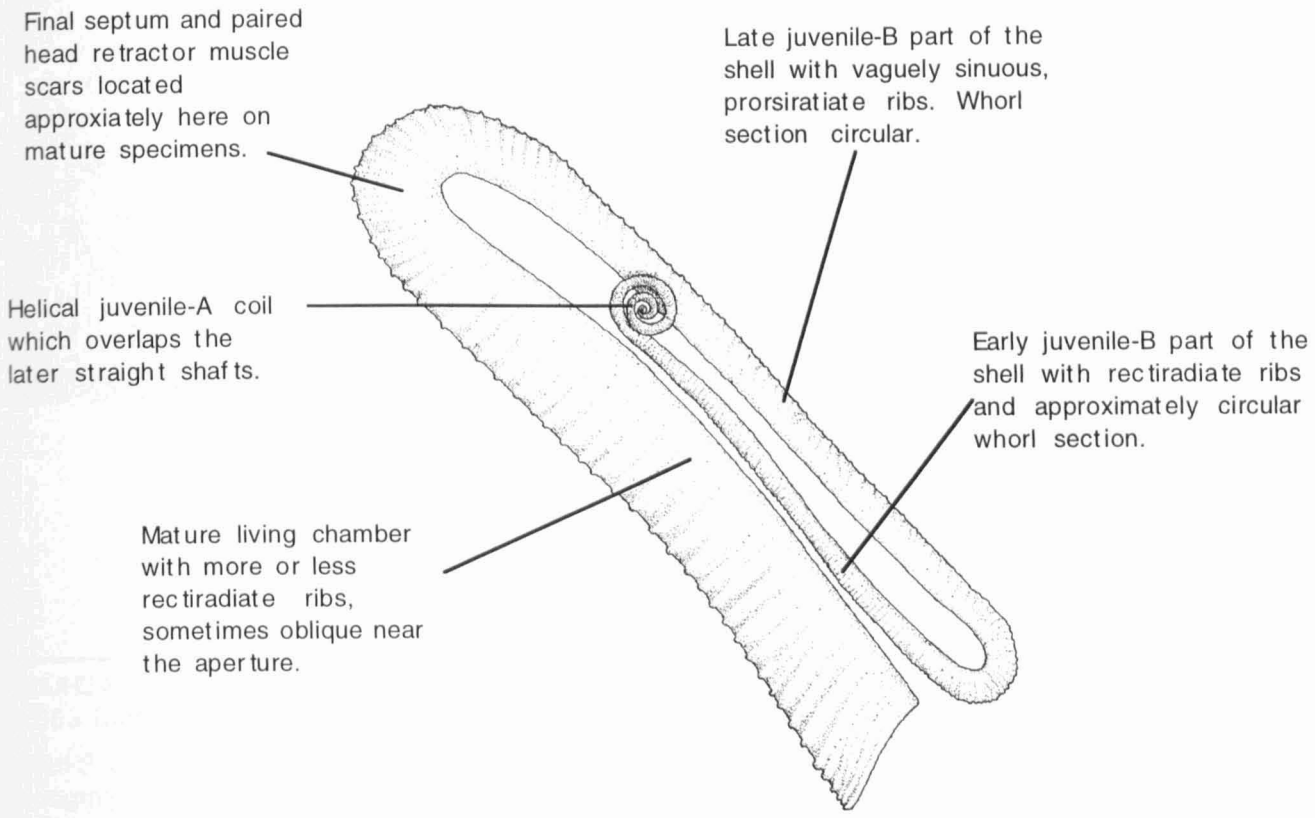


Figure 3.44

FIGURE 3.43: *Hamitella maximus*. Lateral view of BMNH C.852 from the Lower Gault (Middle Albian), at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.44: *Hamitella maximus*. Reconstruction of complete shell, with key diagnostic features labelled.

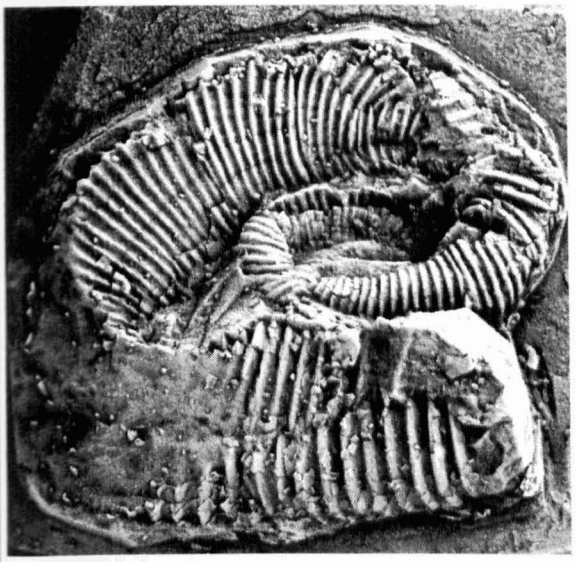
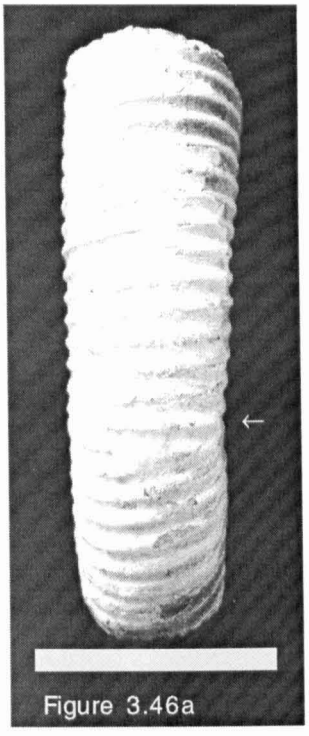


Figure 3.45



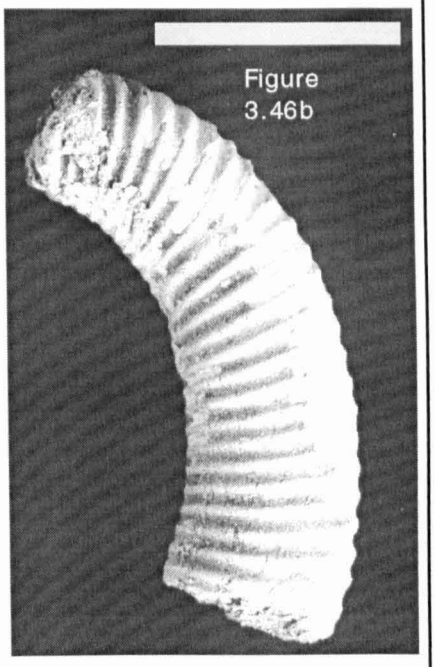


Figure 3.47



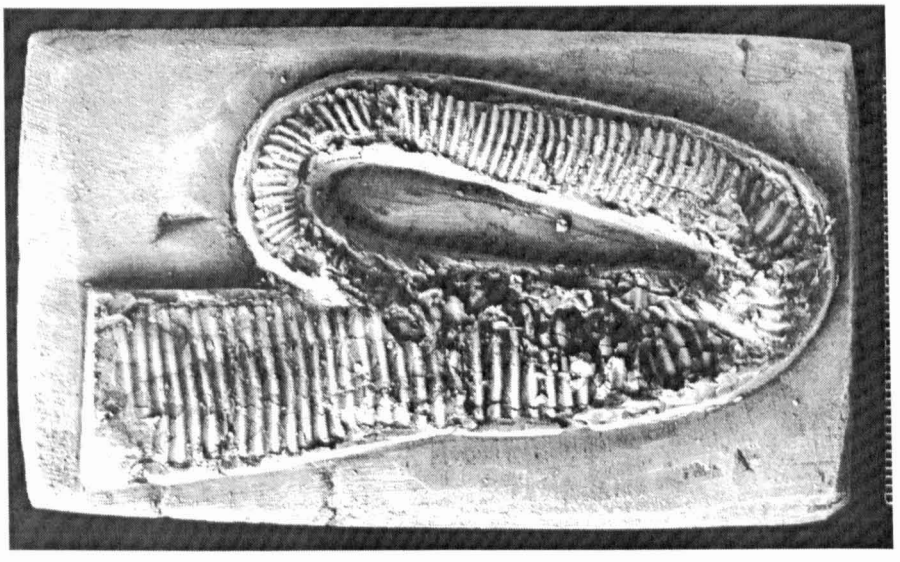


Figure 3.48

FIGURE 3.45: *Hamitella rotundus*. Helical coil of phragmocone and part of the first straight shaft. BMNH C.853 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.46a, 3.46b: *Hamitella rotundus*. Ventral and lateral views of a fragment of the helical part of the phragmocone. Uncatalogued specimen from the author's collection. From the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Note the malformed rib indicated by the arrow (Figure 3.46a). Scale bar = 10 mm.

FIGURE 3.47: *Hamitella rotundus*. Helical part of the phragmocone. BMNH C.849, from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.48: *Hamitella rotundus*. Almost complete specimen displaying the initial helix followed by the two straight shafts. Mature *Hamitella annulatum* are similar, but the two straight shafts are proportionally shorter. BMNH C.853, from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

Figure 3.49a

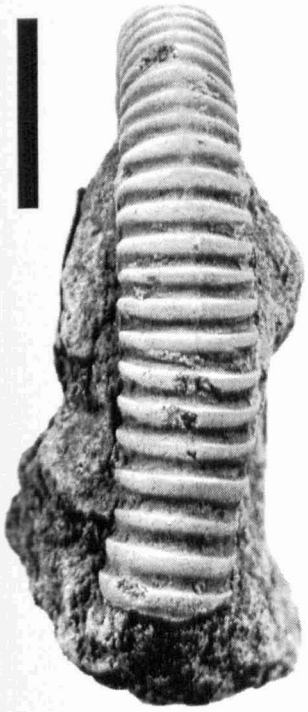


Figure 3.49b

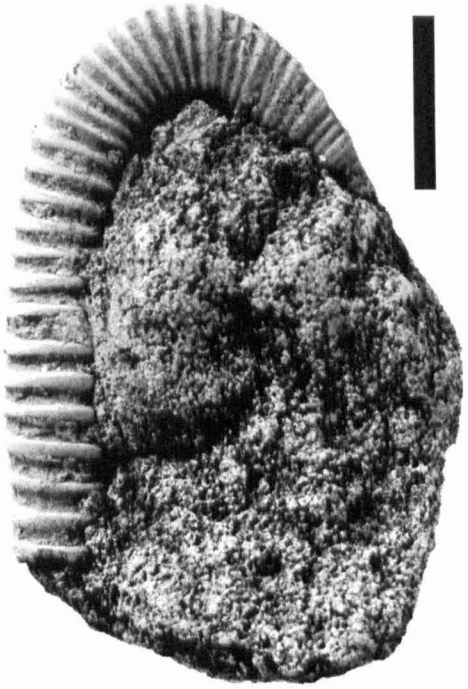




Figure 3.50

FIGURE 3.49a, 3.49b: *Metahamites sablieri.* Ventral and lateral views of the later part of the phragmocone and the mature living chamber. BMNH C.54600 from the condensed Middle and Upper Albian Gault Clay at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.50: *Metahamites sablieri.* Lateral view. BMNH C.46904 from the condensed Middle and Upper Albian Gault Clay at Escragnolles, South East France. Scale bar = 10 mm.

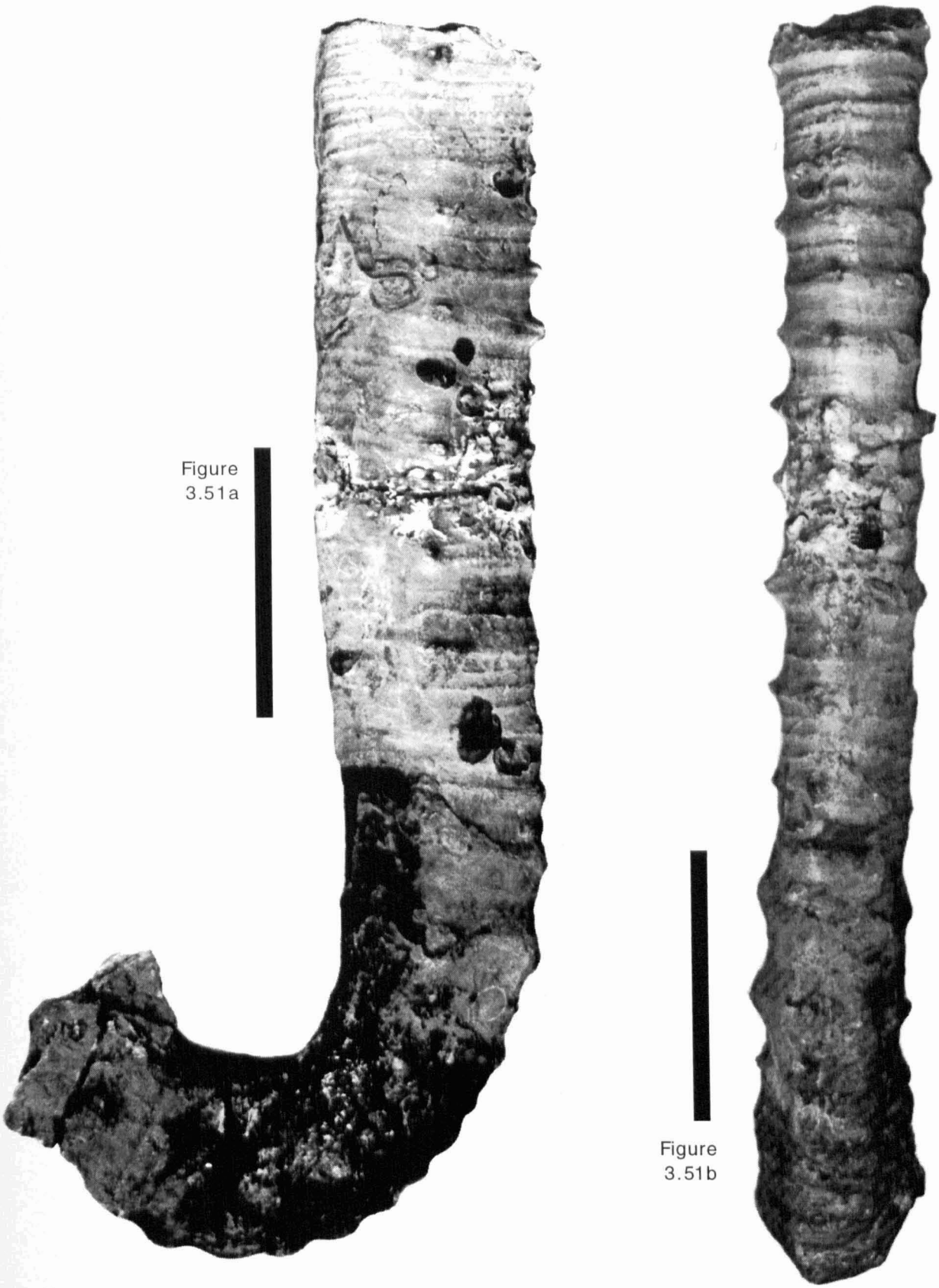


FIGURE 3.51: *Anisoceras saussureanus*. A large specimen viewed laterally (3.51a) and ventrally (3.51b). BMNH C.3646 from the Upper Greensand (Upper Albian, *dispar* Zone) of the Isle of Wight, exact locality unknown. Scale bar = 100 mm.



Figure
3.52a

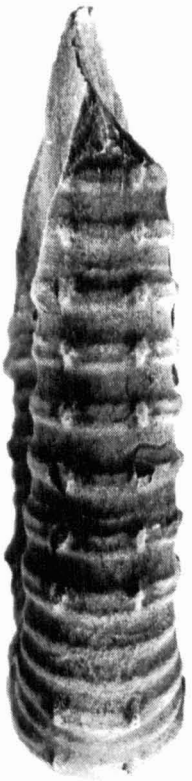


Figure
3.52b

FIGURE 3.52: *Anisoceras perarmatum*. Lateral (3.52a) and ventral (3.52b) views. BMNH C.36721 from the Upper Greensand (Upper Albian, *dispar* Zone), Hamsey, near Lewes, Sussex. Scale bar = 10 mm.

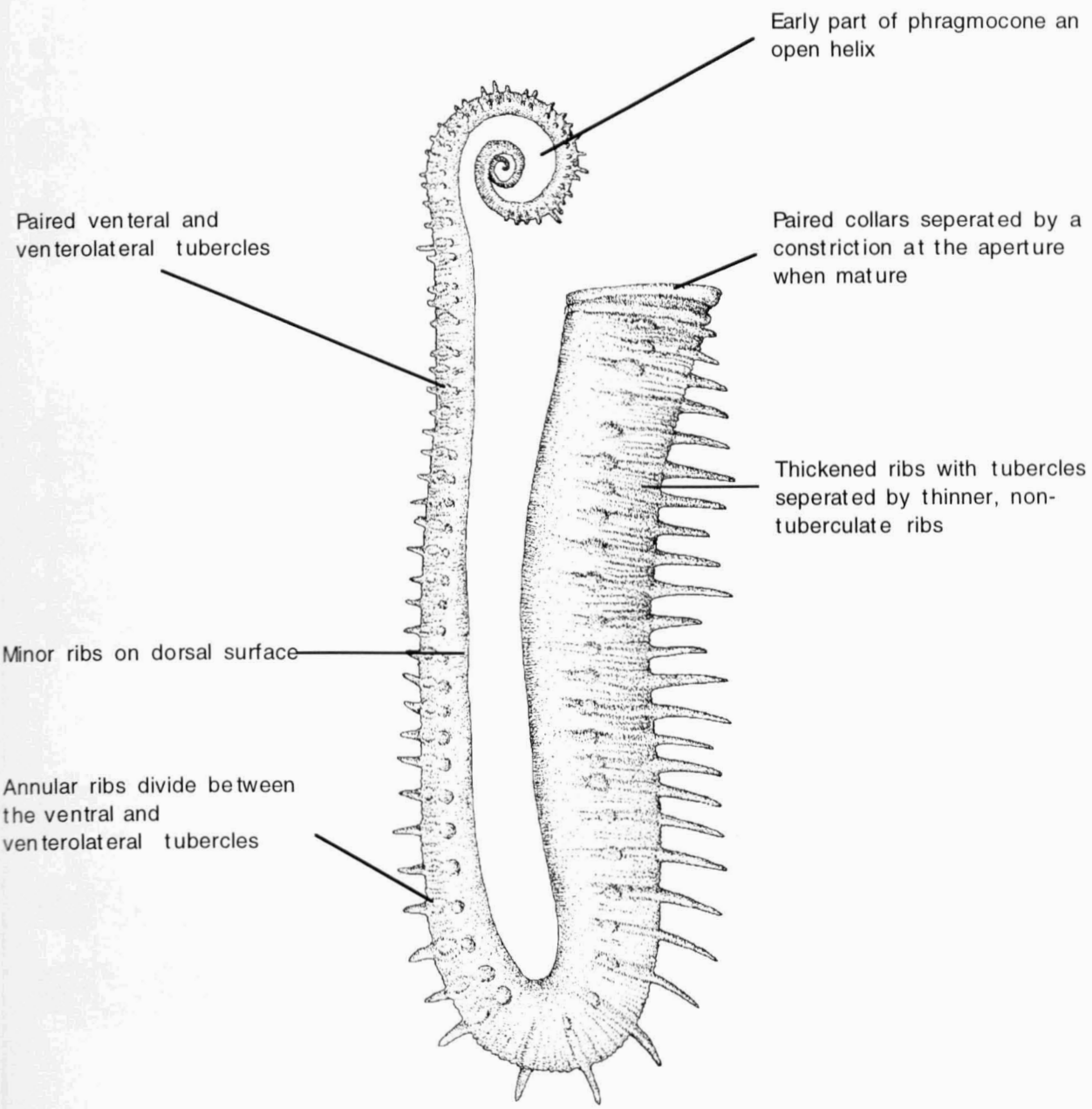
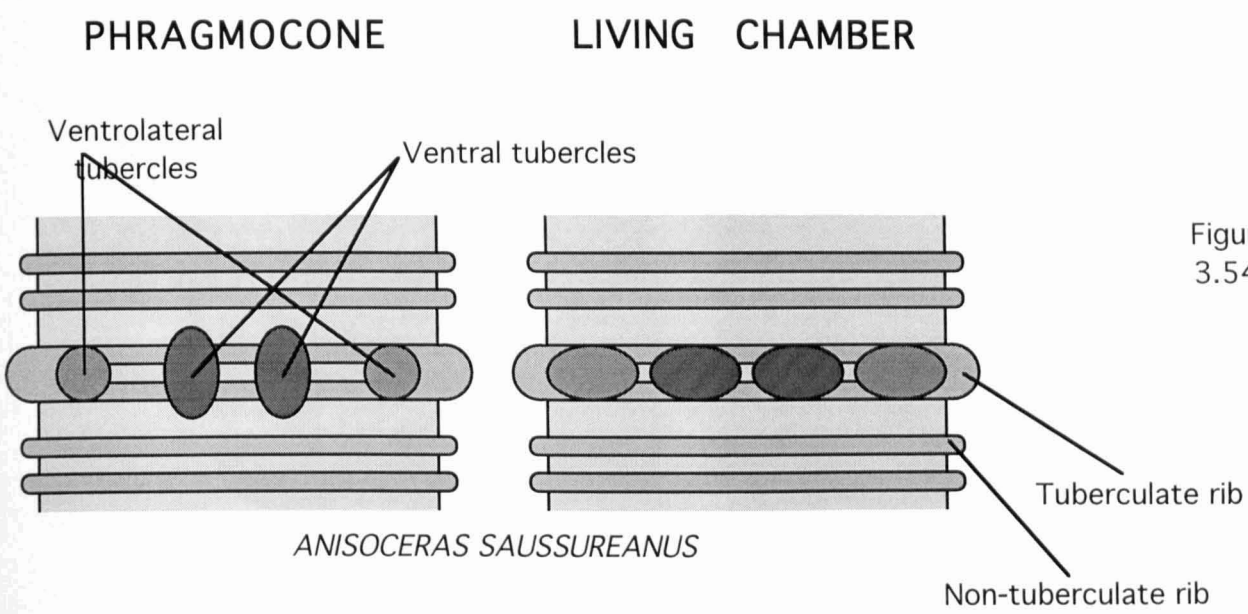


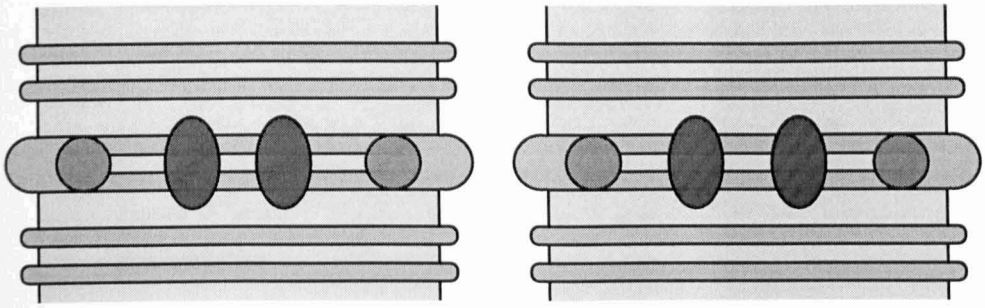
Figure 3.53

FIGURE 3.53: *Anisoceras armatum*. A reconstruction based on the holotype, University of Oxford Museum specimen K675a C.3646 from the Chalk Marl (Upper Albian, *dispar* Zone), Benson, Oxfordshire. Scale bar = 10 mm.



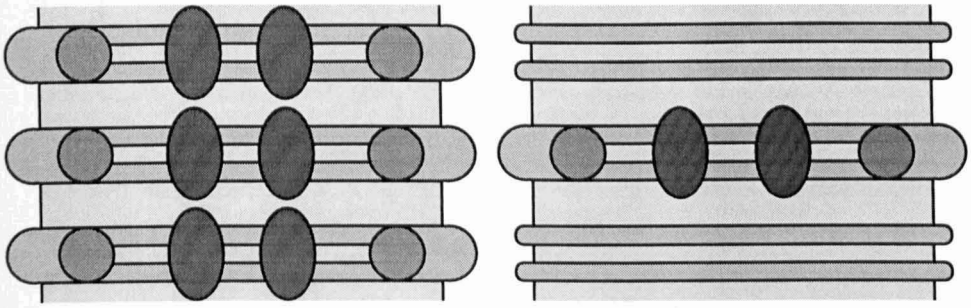
ANISOCERAS SAUSSUREANUS

Figure 3.54a



ANISOCERAS ARMATUM

Figure 3.54b



ANISOCERAS PERARMATUM

Figure 3.54c

FIGURE 3.54a - 3.54c: Diagrammatic representations of the sections of the shell of the three principal species of Albian *Anisoceras*, based upon the descriptions in the text. *Anisoceras saussureanus* (3.54a) develops bullate tubercles on the living chamber. *Anisoceras armatum* (3.54b) has clavate ventral tubercules and rather weak circular or clavate tubercles on the living chamber. *Anisoceras perarmatum* (3.54c) is similar to *Anisoceras armatum*, but lacks the intermediate, non-tuberculate ribs on the phragmocone and the venterolateral tubercles on the living chamber are more strongly developed.

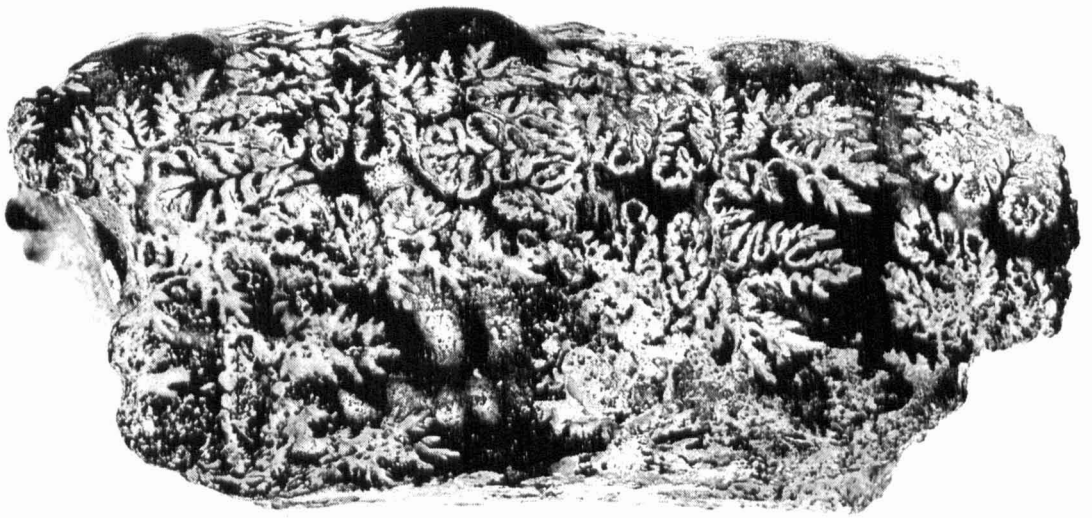


Figure
3.55a

Figure 3.55b

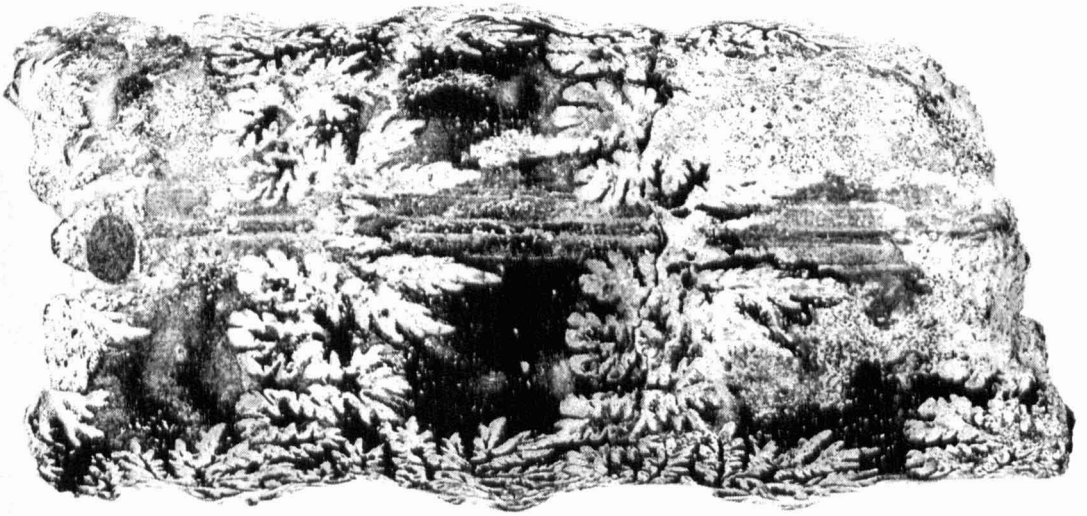


FIGURE 3.55: *Rossalites superbum*. Lateral (3.55a) and ventral (3.55b) views. BMNH C.71996 from the Lower Greensand (Folkestone Beds, Main Mammilatum Bed) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.



Figure 3.56

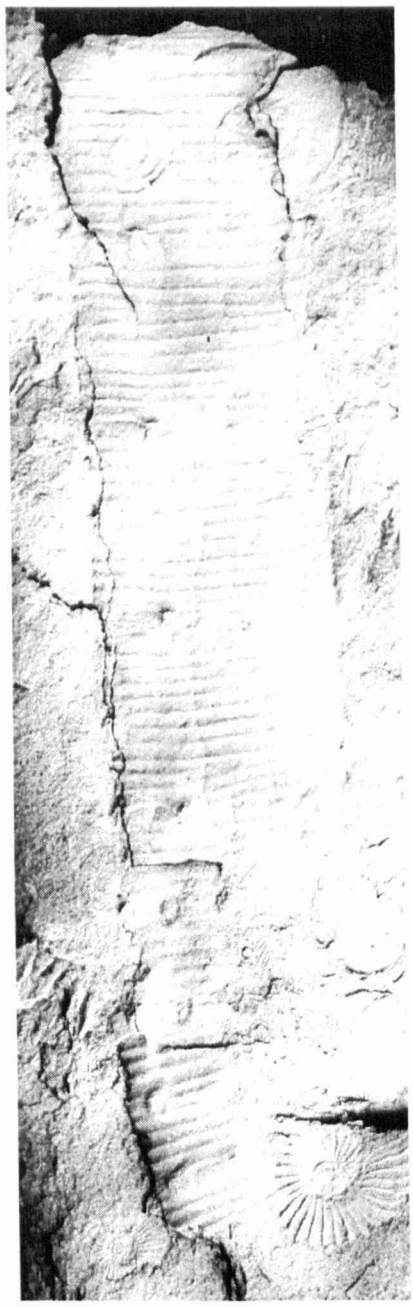


Figure 3.57

FIGURE 3.56: *Rossalites riccardi*. Later part of phragmocone and final living chamber. Note the separate rows of ventral and venterolateral tubercles fuse along the final living chamber into bullate ridges. This is characteristic of the genus. Uncatalogued specimens from the W. J. Kennedy collection, University of Oxford Museum. From the Lower Albian (*Leymeriella regularis* Zone), Col des Pré, Guittard, France. Scale bar = 10 mm.

FIGURE 3.57: *Rossalites riccardi*. Part of the phragmocone. Also from the W. J. Kennedy collection, University of Oxford Museum. From the Lower Albian (*Leymeriella regularis* Zone), Col des Pré, Guittard, France. Scale bar = 10 mm.

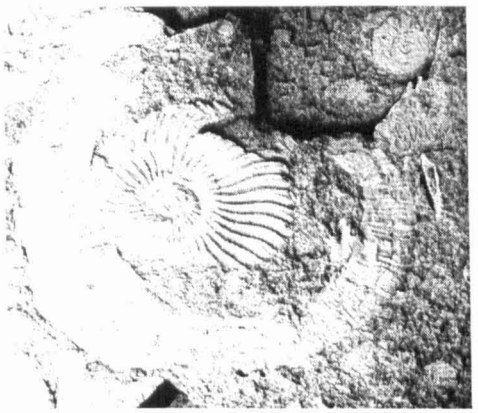


Figure 3.58

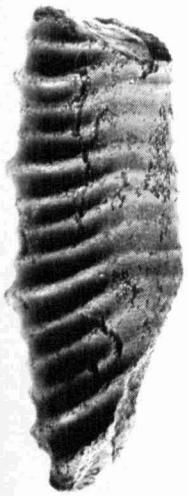


Figure 3.59a

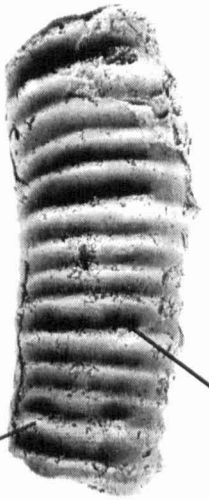


Figure 3.59b

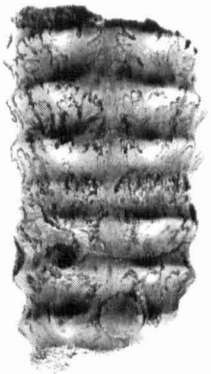


Figure 3.60a

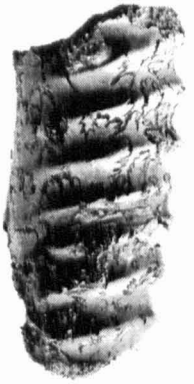


Figure 3.60b

FIGURE 3.58: *Rossalites riccardi*. Spiral part of phragmocone. Uncatalogued specimens from the W. J. Kennedy collection, University of Oxford Museum. From the Lower Albian (*Leymeriella regularis* Zone), Col des Pré, Guittard, France. Scale bar = 10 mm.

FIGURE 3.59: *Protanisoceras raulinianum*. Viewed laterally (3.59a) and ventrolaterally (3.59b). BMNH C.30791 from the Lower Albian (Folkestone Beds, Main Mammillatum Bed) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.60: *Protanisoceras cantianum*. Viewed laterally (3.60a) and ventrally (3.60b). BMNH C.48915 from the Lower Albian (Folkestone Beds, Main Mammillatum Bed) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

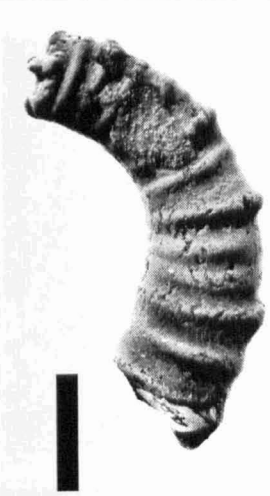


Figure 3.61a



Figure 3.61b



Figure 3.62a

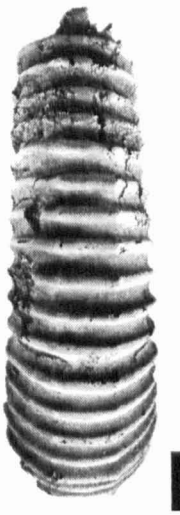


Figure 3.62b

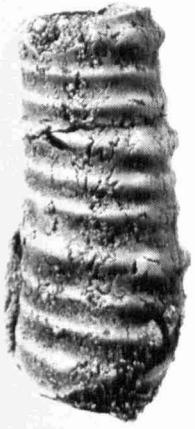


Figure 3.63a

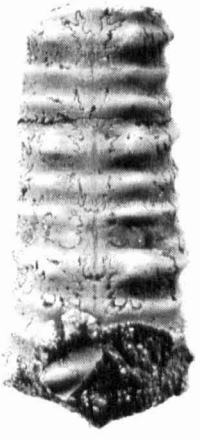


Figure 3.63b



Figure 3.64



Figure 3.65a



Figure 3.65b

FIGURE 3.61: *Protanisoceras coptense*. Lateral (3.61a) and ventral (3.61b) views of the holotype, BMNH C.71971 from the Folkestone Beds (Main Mammillatum Beds) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.62: *Protanisoceras blancheti*. Lateral (3.62a) and ventral (3.62b) views of BMNH C.84763 from the Folkestone Beds (Main Mammillatum Beds) at Copt Point, Folkestone, Kent. Note the weak ventral tubercles, a characteristic of this species. Scale bar = 10 mm.

FIGURE 3.63: *Protanisoceras blancheti*. Lateral (3.63a) and ventral (3.63b) views of BMNH C.84763 from the Lower Greensand - Gault Clay Junction Beds at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.64: *Protanisoceras nodosum*. Lateral view of a well preserved specimen, BMNH C.47539 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.65: *Protanisoceras anglicum*. Lateral (3.65a) and ventral (3.65b) views of the holotype, BMNH C.48913 from the Folkestone Beds (Main Mammillatum Beds) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

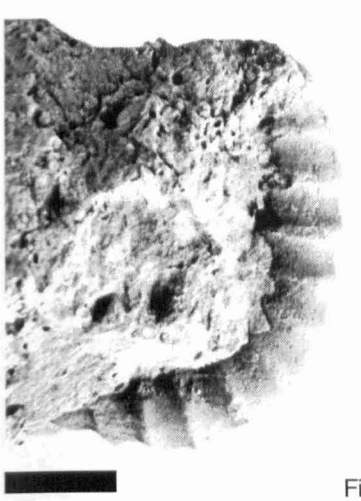


Figure 3.66a

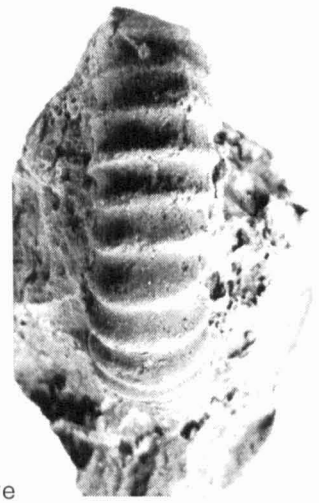


Figure 3.66b

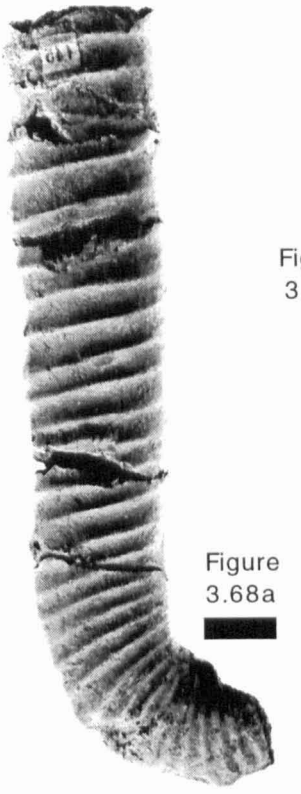


Figure 3.68a

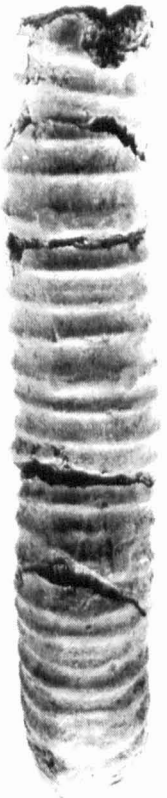


Figure 3.68b



Figure 3.67a

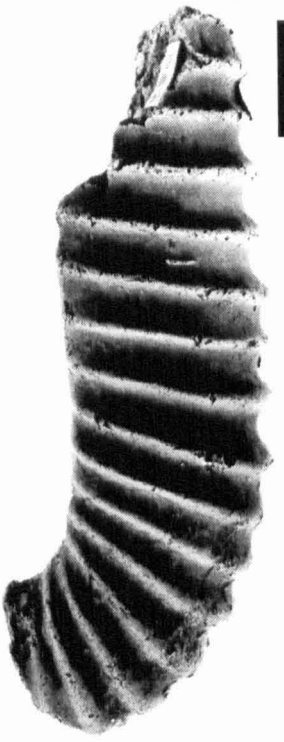


Figure 3.67b

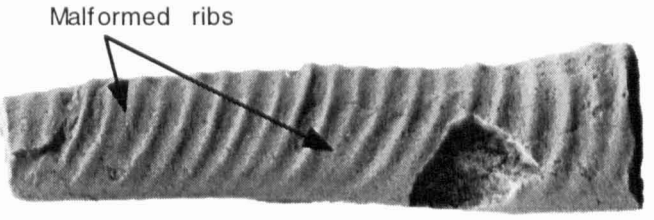


Figure 3.69a

Figure 3.69b



FIGURE 3.66: *Protanisoceras anglicum*. Lateral (3.66a) and ventral (3.66b) views BMNH C.48913 from the Woburn Sands Formation, Shenley Limestone (*tardefurcata* Zone, *regularis* Subzone) at Munday's Hill Pit, near Leighton Buzzard, Bedfordshire. Scale bar = 10 mm.

FIGURE 3.67: *Protanisoceras acteon*. Lateral (3.67a) and ventral (3.67b) views of BMNH C.71967 from the Folkestone Beds (Main Mammillatum Beds) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.68: *Protanisoceras arrogans*. Lateral (3.68a) and ventral (3.68b) views of BMNH C.46908 from the condesnsed Middle Albian beds of Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.69: *Tuberolechites regifex*. Lateral (3.69a) and ventral (3.69b) views of part of the living chamber of BMNH C.18325 from the Upper Gault (Upper Albian) at Glynde, Sussex. Note the malformed ribs. Scale bar = 10 mm.

Figure 3.70

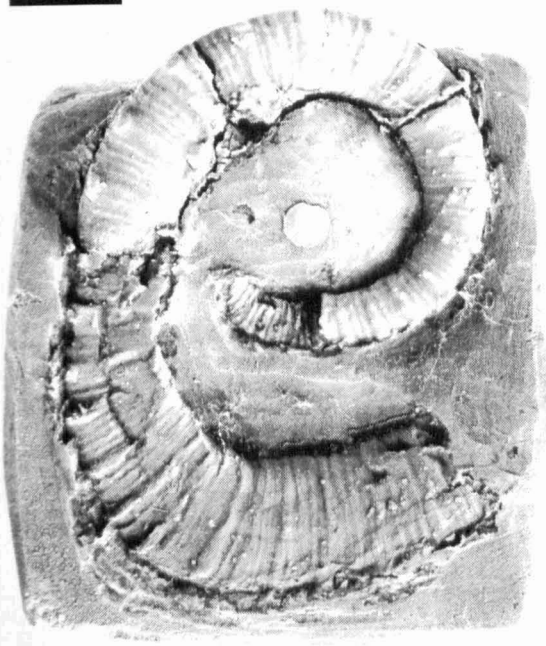
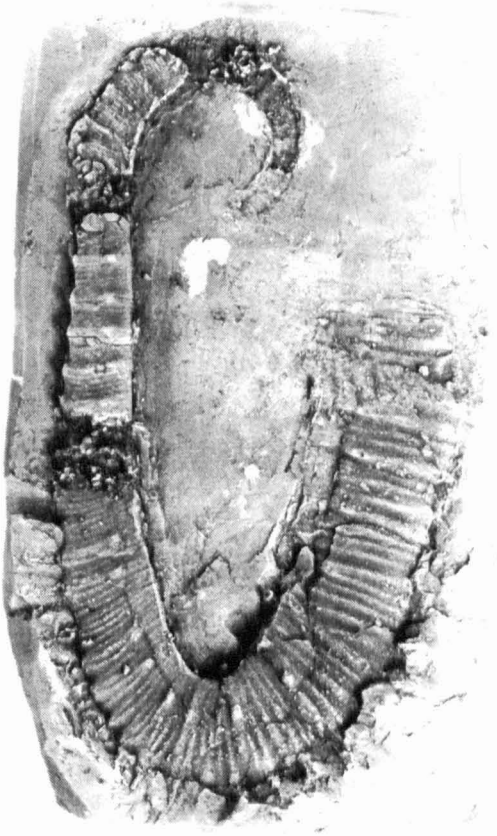


Figure 3.70



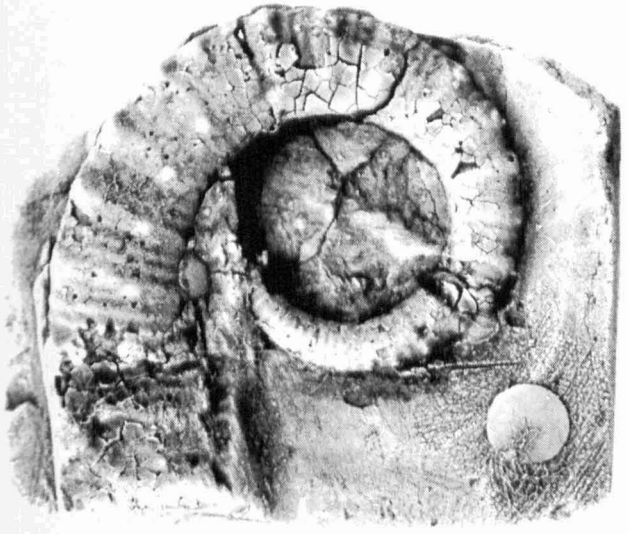


Figure 3.70a

Figure 3.70b

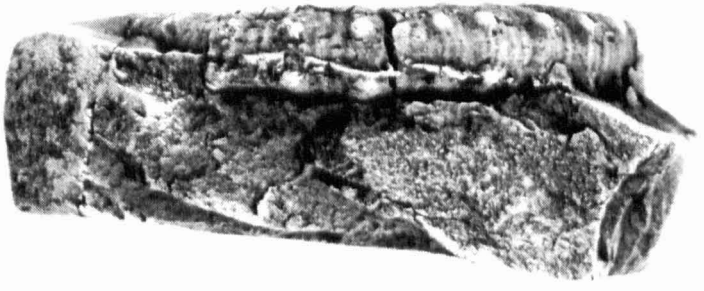


FIGURE 3.70: *Idiohamites tuberculatus*. Lateral view of BMNH C.39943 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone)at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.71: *Idiohamites spiniger*. Lateral view of BMNH C.39821 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone)at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.72: *Idiohamites spiniger*. Lateral (3.72a) and ventral (3.72b) views of the early part of the phragmocone. Unlike *Anisoceras*, with which *Idiohamites* might otherwise be confused, the juvenile coil is planar like most *Protanisoceras*. BMNH C.39821 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone)at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

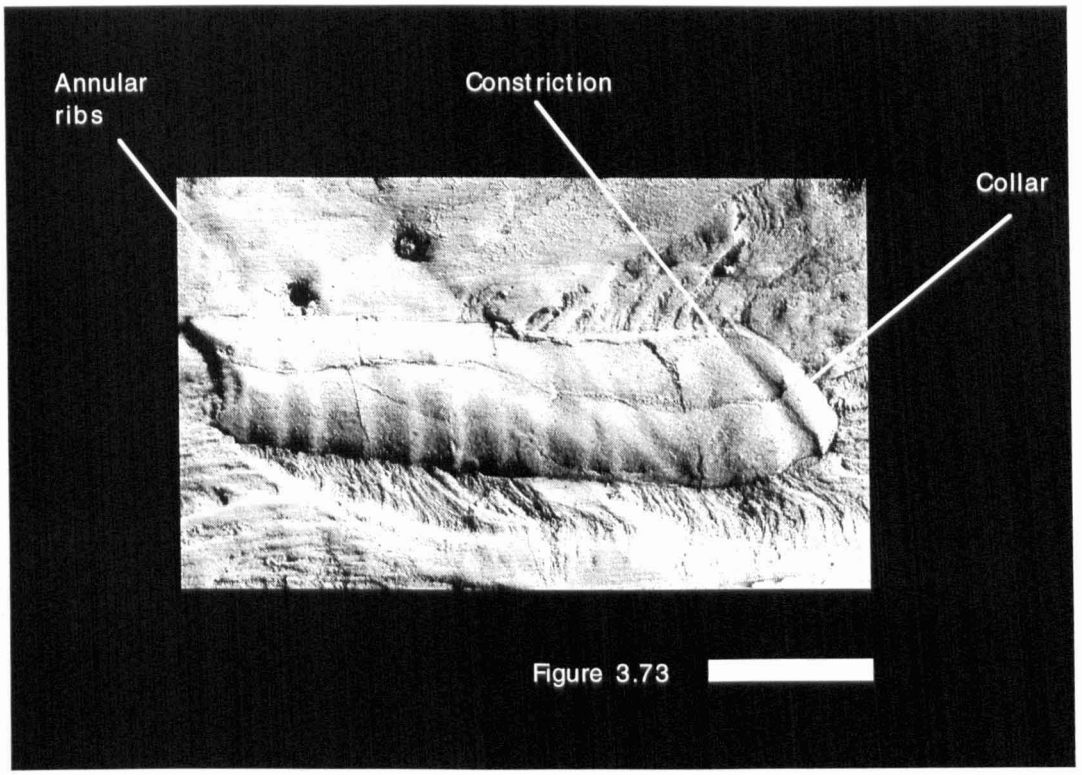




Figure 3.74a



Figure 3.74b

FIGURE 3.73: *Lechites gaudini*. Lateral view of BMNH C.77661 from the Upper Gault (Upper Albian, *inflatum* Zone) at Copt Point, Folkestone, Kent. This specimen is a macroconch, and exhibits the constriction and collar typical of the genus. Scale bar = 10 mm.

FIGURE 3.74: *Sciponoceras skipperi*. Lateral (3.74a) and ventral (3.74b) views of the holotype specimen, BMNH C.93268. This specimen consists mainly of part of the living chamber, although the final septum is preserved. From the Upper Albian, *dispar* Zone at Melcombe Horsey, Dorsetshire. Scale bar = 10 mm.

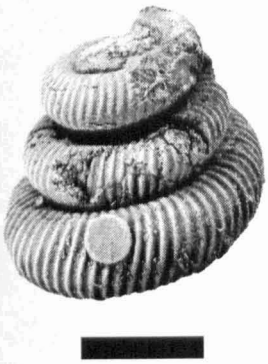


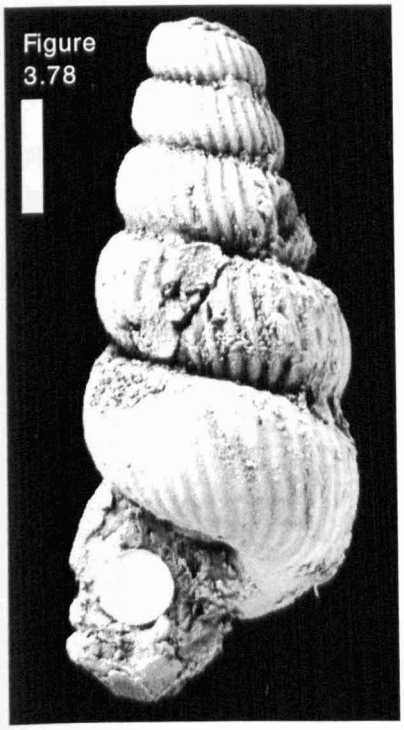
Figure 3.75



Figure 3.76



Figure 3.77



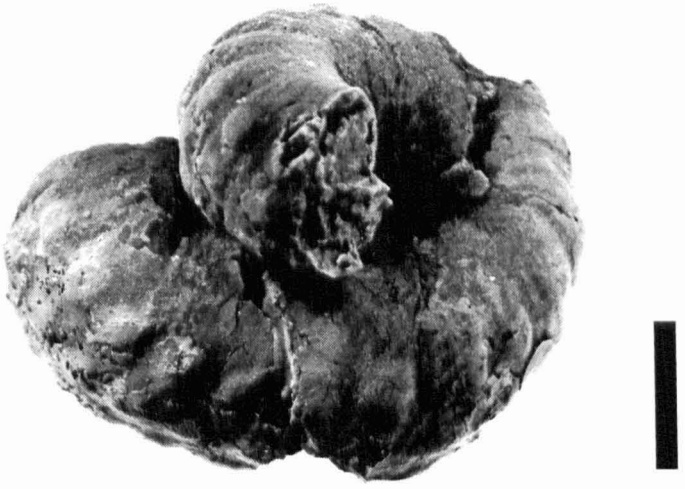


Figure 3.79

FIGURE 3.75: *Proturrilitoides astierianus*. BMNH C.46574b. From the condensed Middle and Upper Albian at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.76: *Proturrilitoides senequierianus*. BMNH C.46867. From the condensed Middle and Upper Albian at Escragnolles, South East France. Scale bar = 10 mm.

FIGURE 3.77: *Turrilitoides hugardianus*. BMNH C.3802. From the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridgeshire, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.78: *Turrilitoides densicostatus*. BMNH C.3802. From the Lower Gault (Middle Albian, *lautus* Zone, *nitidus* Subzone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.79: *Pseudhelicoceras robertianum*. Large piece of the final living chamber. BMNH C.3802. From the Upper Gault (Upper Albian, *inflatum* Zone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

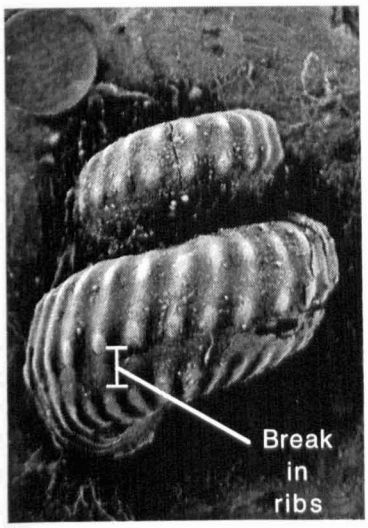


Figure 3.80

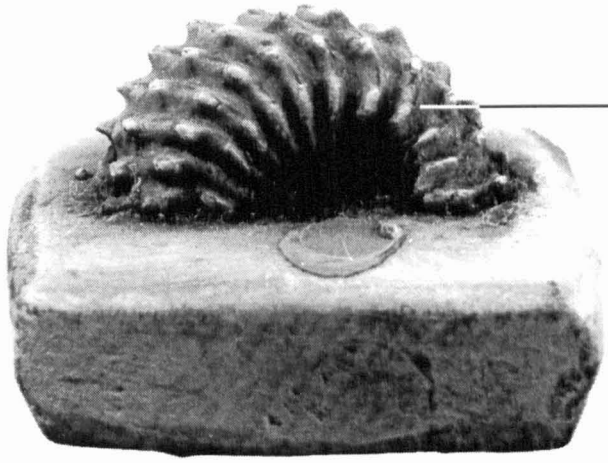
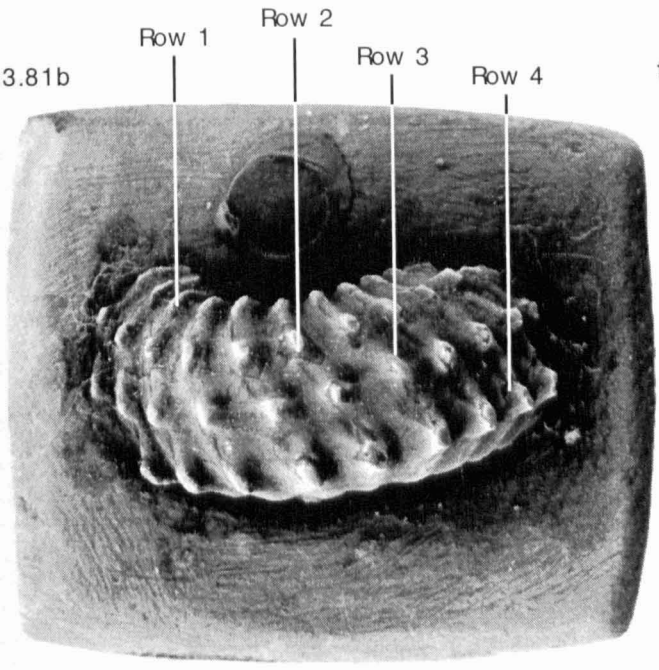


Figure 3.81a

Figure 3.82

Figure 3.81b



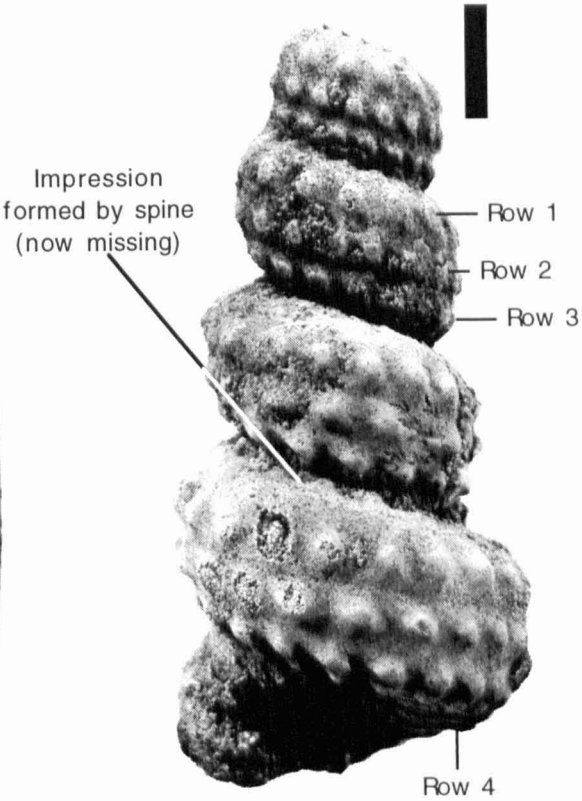


FIGURE 3.80: *Pseudhelicoceras gaultinum*. BMNH C.38213. The break in the ribs between the second and thrid rows of tubercles are characteristic of this species. From the Upper Gault (Upper Albian, *inflatum* Zone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.81: *Pseudhelicoceras pseudoelegans*. BMNH C.38210. This specimen is shown from the ventral (3.81a) and lateral (3.81b) surfaces; in life, the shell would have been oriented on its side compared with planar coiled ammonites, with the lateral surface downwards. The bullate tubercles are labelled, from rows 1 to 5. From the Upper Gault (Upper Albian, *inflatum* Zone, *cristatum* Subzone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.82: *Mariella bergeri*. BMNH C.3802. The rows of tubercles are labelled from 1 to 4. In life the tubercles would have had long spines attached to them; the indentations made by the spines on early whorls can be seen on later whorls which overgrow the spines. From the Upper Greensand (Upper Albian, *dispar* Zone) at Warminster, Wiltshire. Scale bar = 10 mm.

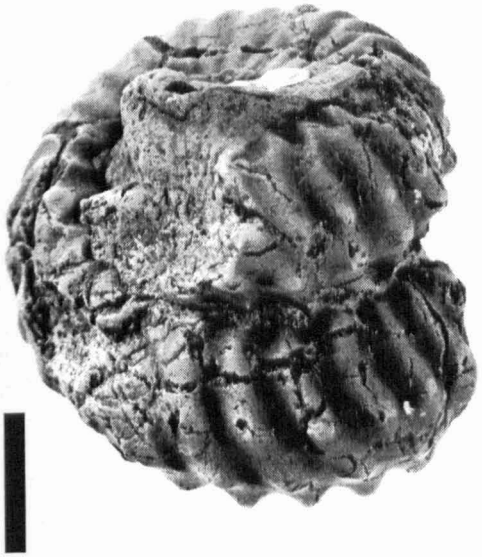


Figure 3.83



Figure 3.84



Figure 3.85

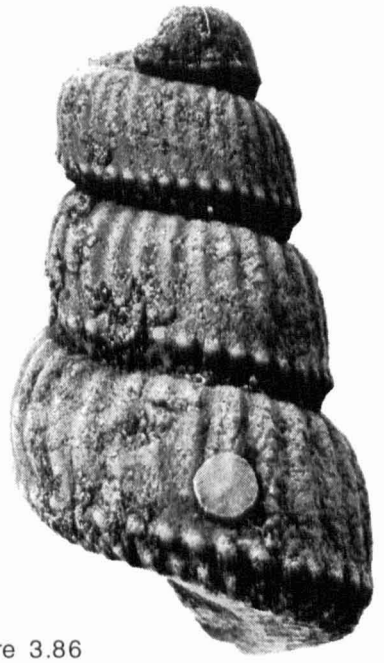


Figure 3.86

FIGURE 3.83: *Mariella cantabrigiensis*. The relatively coarse ribbing and bullate tubercles are characteristic of this species. BMNH C.34739 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.84: *Mariella miliaris*. Comapared with other *Mariella*, this species has fine ribs and slender, conical tubercles. BMNH C.93449 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.85: *Mariella nobilis*. BMNH C.38216 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.86: *Ostlingoceras puzosianum*. BMNH C.38199 from the Upper Albian, *dispar* Zone, at Man o' War Cove, Dorsetshire of. This specimen shows the reduced tuberculation and flattened sides characteristic of the genus. Scale bar = 10 mm.

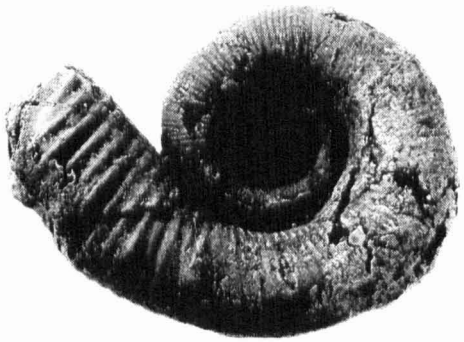


Figure 3.87

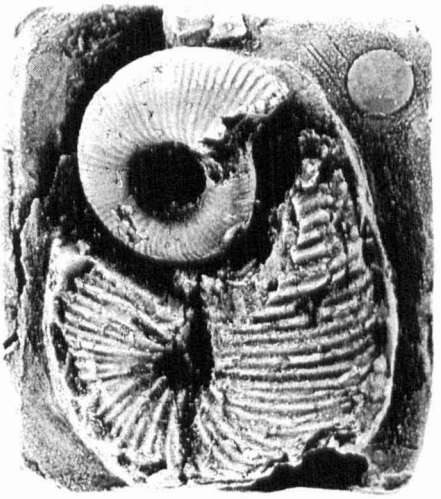


Figure 3.88

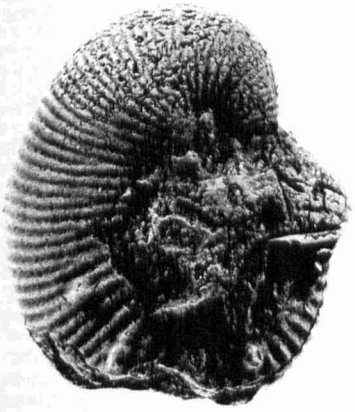


Figure 3.89

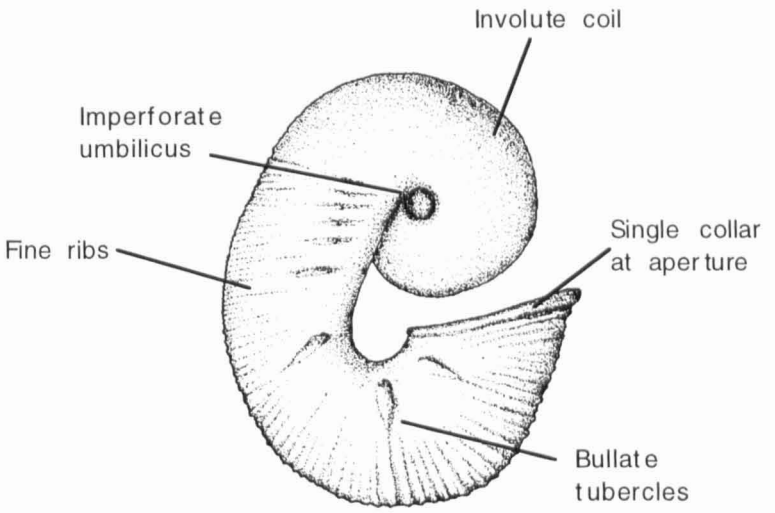


Figure 3.90

FIGURE 3.87: *Eoscaphites circularis*. Neotype specimen, BMNH C.41555 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.88: *Scaphites subcircularis*. Holotype specimen, BMNH C.38206 from the Upper Gault (Upper Albian, *inflatum* Zone, *varicosum* Subzone) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.89: *Scaphites hugardianus*. BMNH C.39662 from the Cambridge Greensand (Upper Albian, *dispar* Zone) of Cambridge, exact locality unrecorded. Scale bar = 10 mm.

FIGURE 3.90: *Scaphites hugardianus*. Restored shell with the key features labelled.

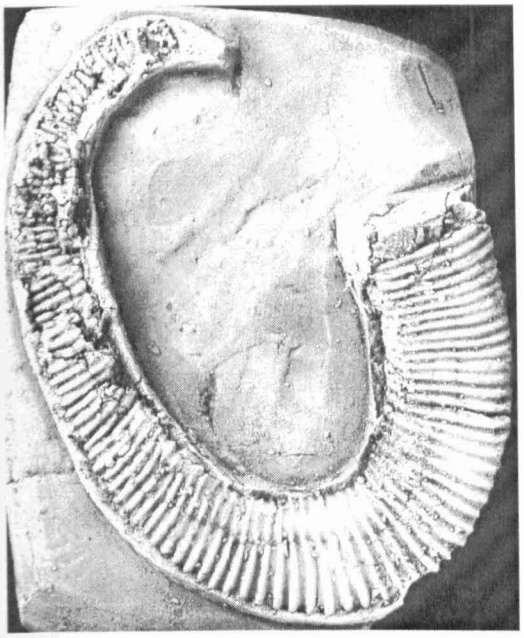


Figure 3.91

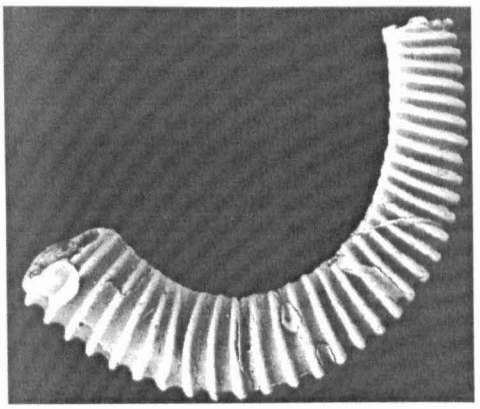


Figure 3.92

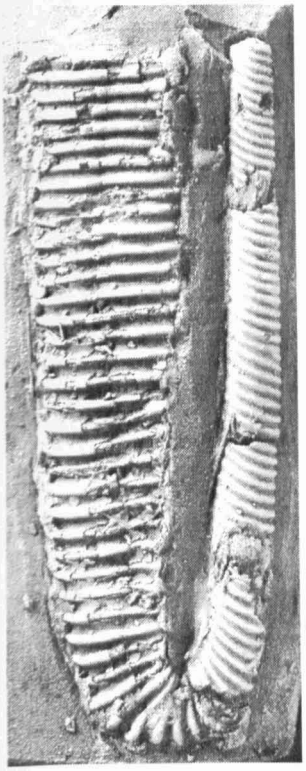


Figure 3.93

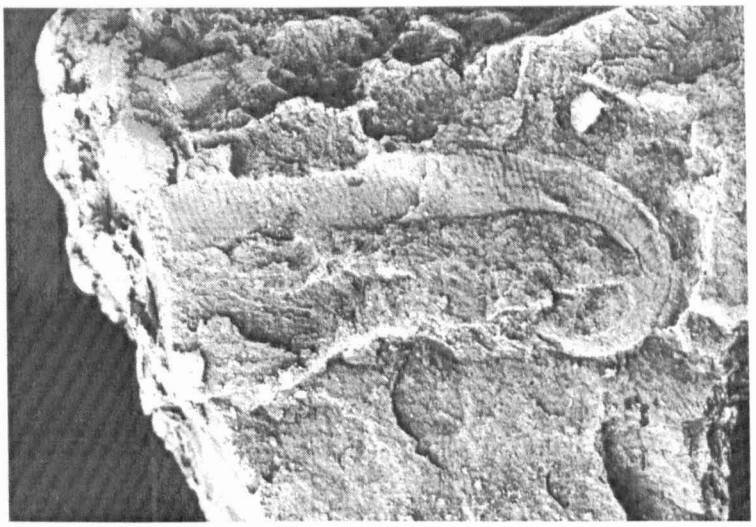


Figure 3.94

FIGURE 3.91: *Hamites compressus*. BMNH C.854 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.92: *Hamites incurvatus*. BMNH C.75247 from the Upper Gault (Upper Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.93: *Hamites tenuis*. BMNH C.852 from the Lower Gault (Middle Albian) at Copt Point, Folkestone, Kent. Scale bar = 10 mm.

FIGURE 3.94: *Hamites tenuis*. Uncatalogued specimen collected by A. S. Gale from the Speeton Clay (Middle Albian, *intermedius* Subzone), Speeton, Norfolk. Scale bar = 10 mm.

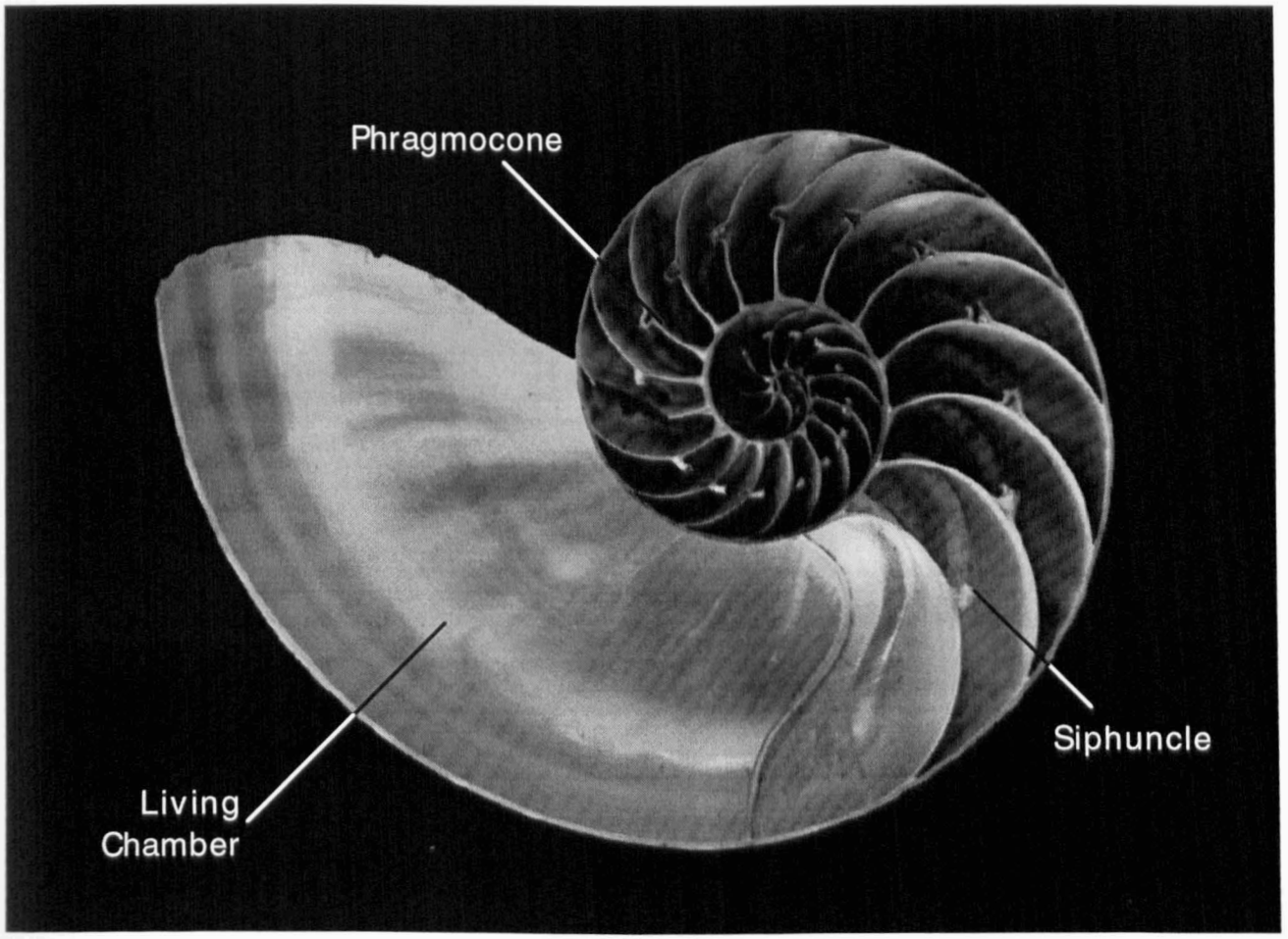


FIGURE 4.1: Hemisection through the shell of *Nautilus pompilius*, the common nautilus.

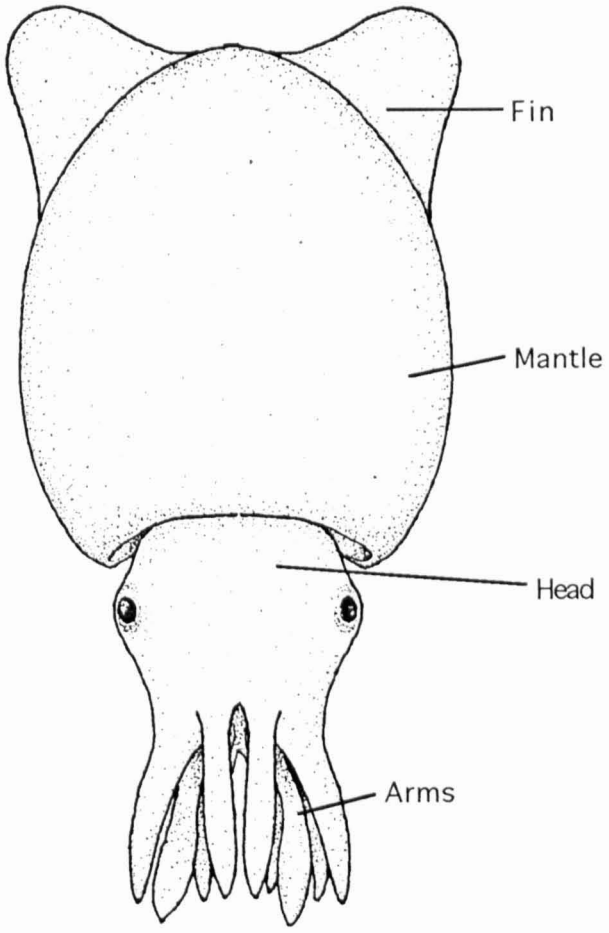


FIGURE 4.2

FIGURE 4.2: *Cranchia scabra*, based on specimens in the Spirit Collection of the Mollusca Section, BMNH. *Cranchia* is a mesopelagic squid, and is here oriented in its life position, with the head downwards.

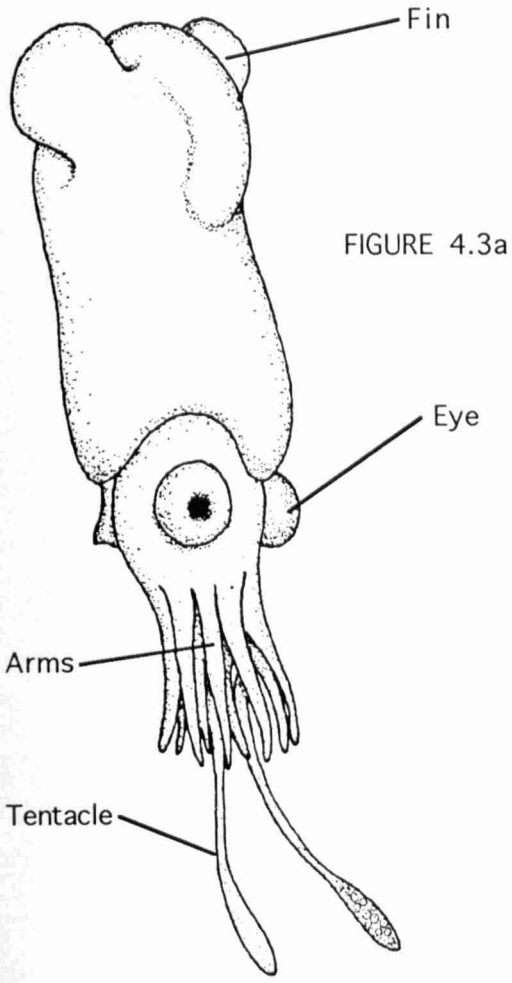


FIGURE 4.3a

FIGURE 4.3b

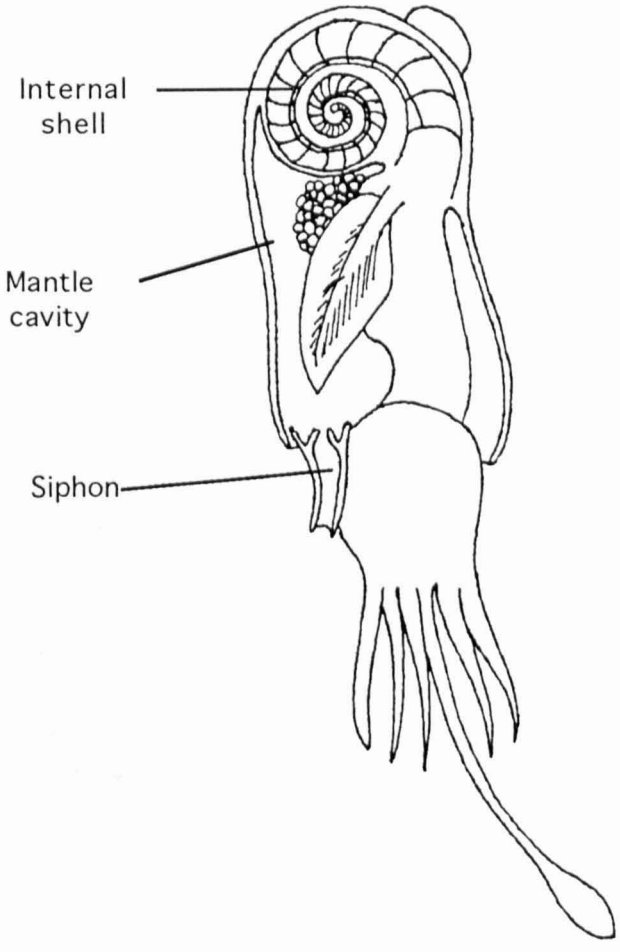


FIGURE 4.3: *Spirula spirula*, based on specimens in the Spirit Collection of the Mollusca Section, BMNH. *Spirula* is a mesopelagic sepiid with a characteristic internal coiled shell, and is here oriented in its life position, with the head downwards. It is shown here in life (Figure 4.3a) and sectioned (Figure 4.3b).

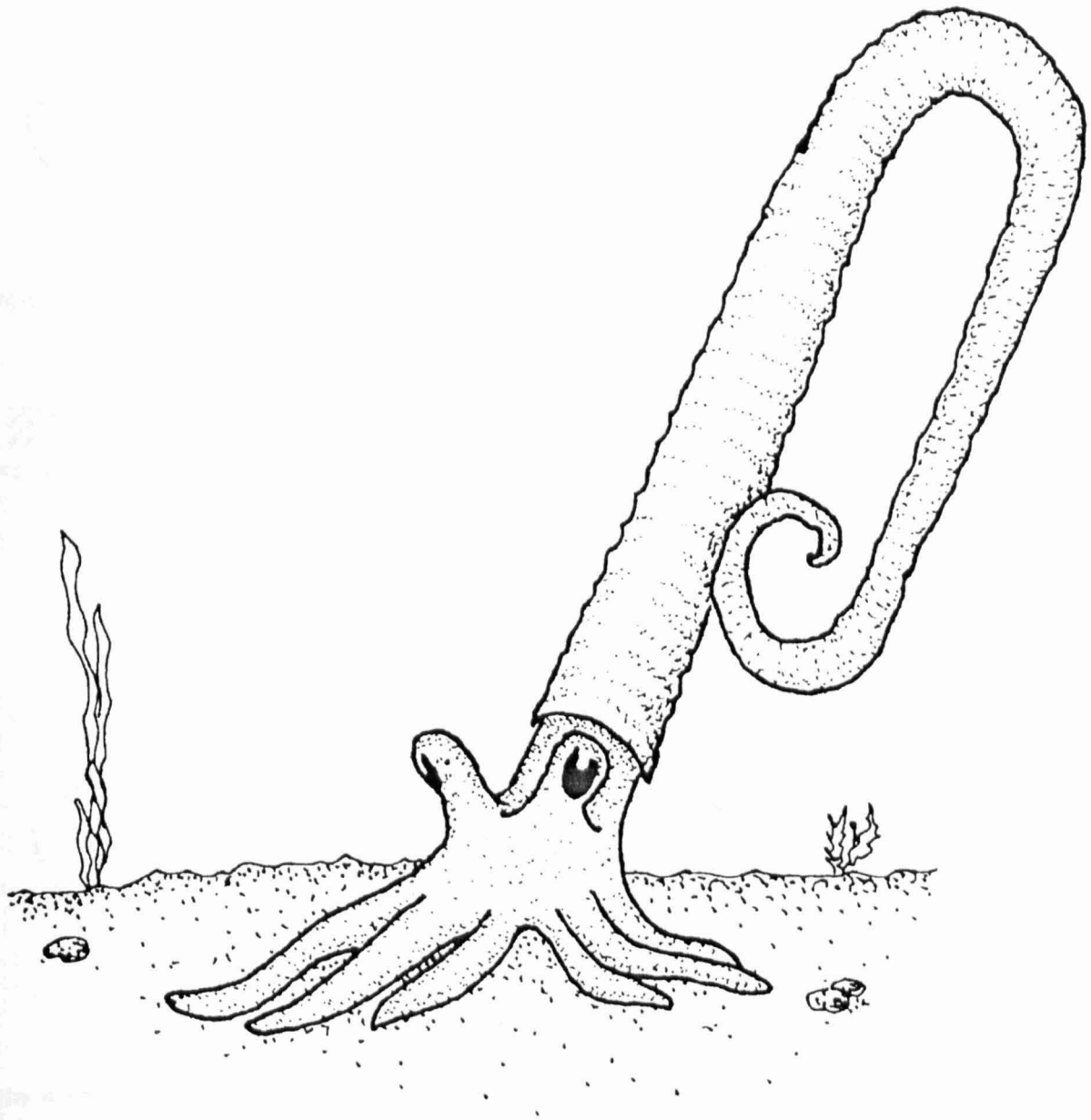


FIGURE 4.4: An ammonite based on the hypothesis that ammonites were negatively buoyant animals which crawled about on the sea floor (Ebel, 1992, 1993). In this model, the shell does not provide buoyancy and so plays no part in the orientation of the animal relative to the sea floor; this is dependent on the centre of mass of the ammonite and the strength and adhesion of the arms.

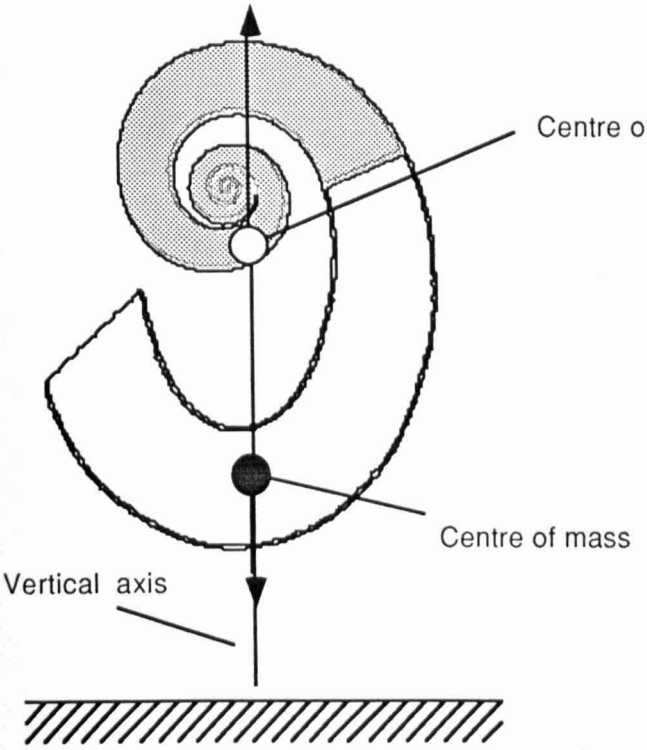


Figure 4.5a

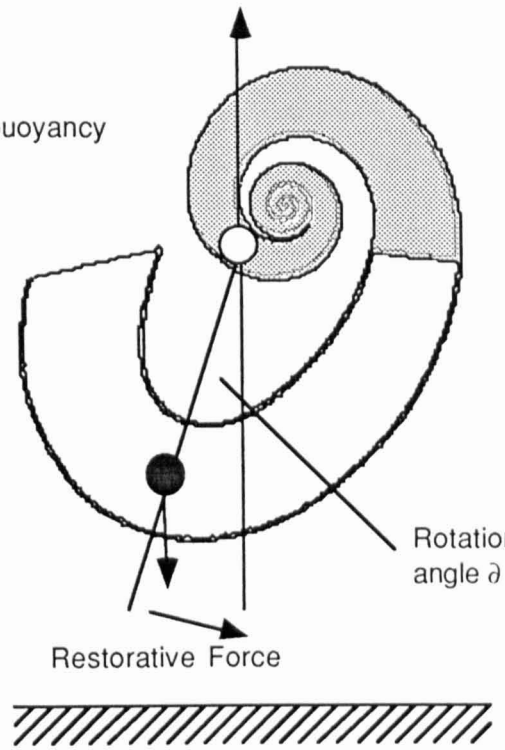


Figure 4.5b

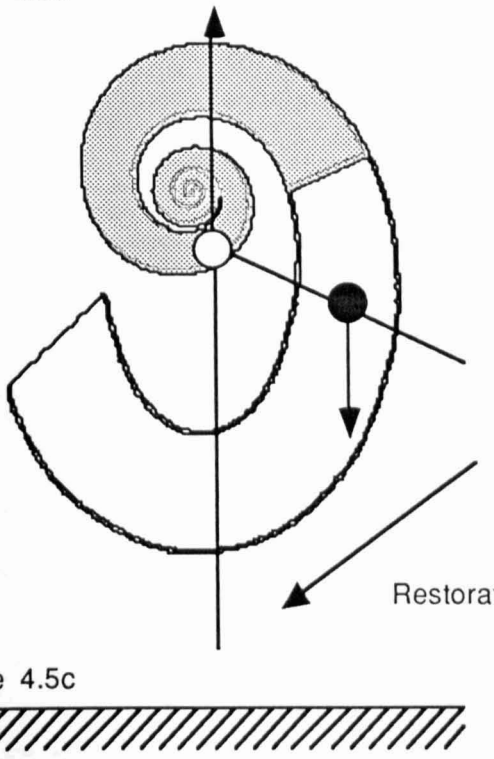


Figure 4.5c

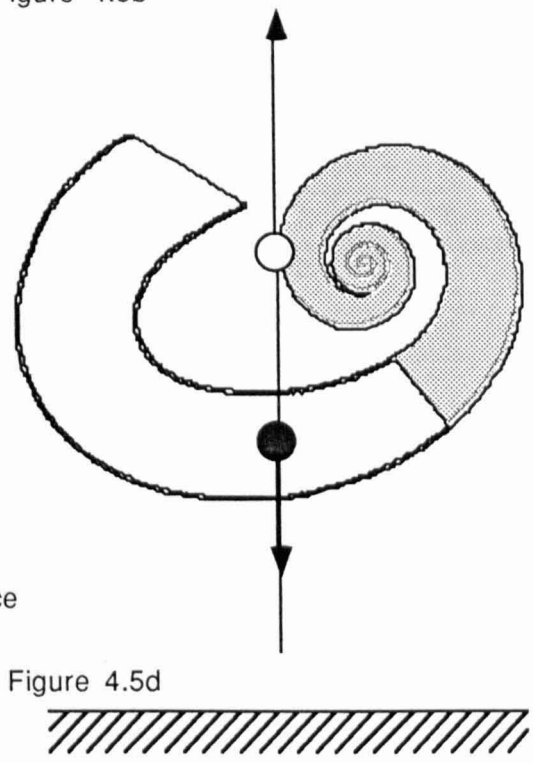


Figure 4.5d

FIGURE 4.5: An ammonite at stable equilibrium is positioned with the centre of mass vertically below thecentre of buoyancy (Figure 4.5a). If the ammonite is rotated such that the centre of mass is moved through anangle ∂ (Figure 4.5b) a restorative force proportional to ∂ will be generated, tending to re-position the centreof mass vertically beneath the centre of buoyancy. Equally, if the centre of mass moves *within* the shell,another restorative force will be developed (Figure 4.5c), and the shell will tend to rotate and reposition thecentre of mass vertically beneath the centre of buoyancy (Figure 4.5d).

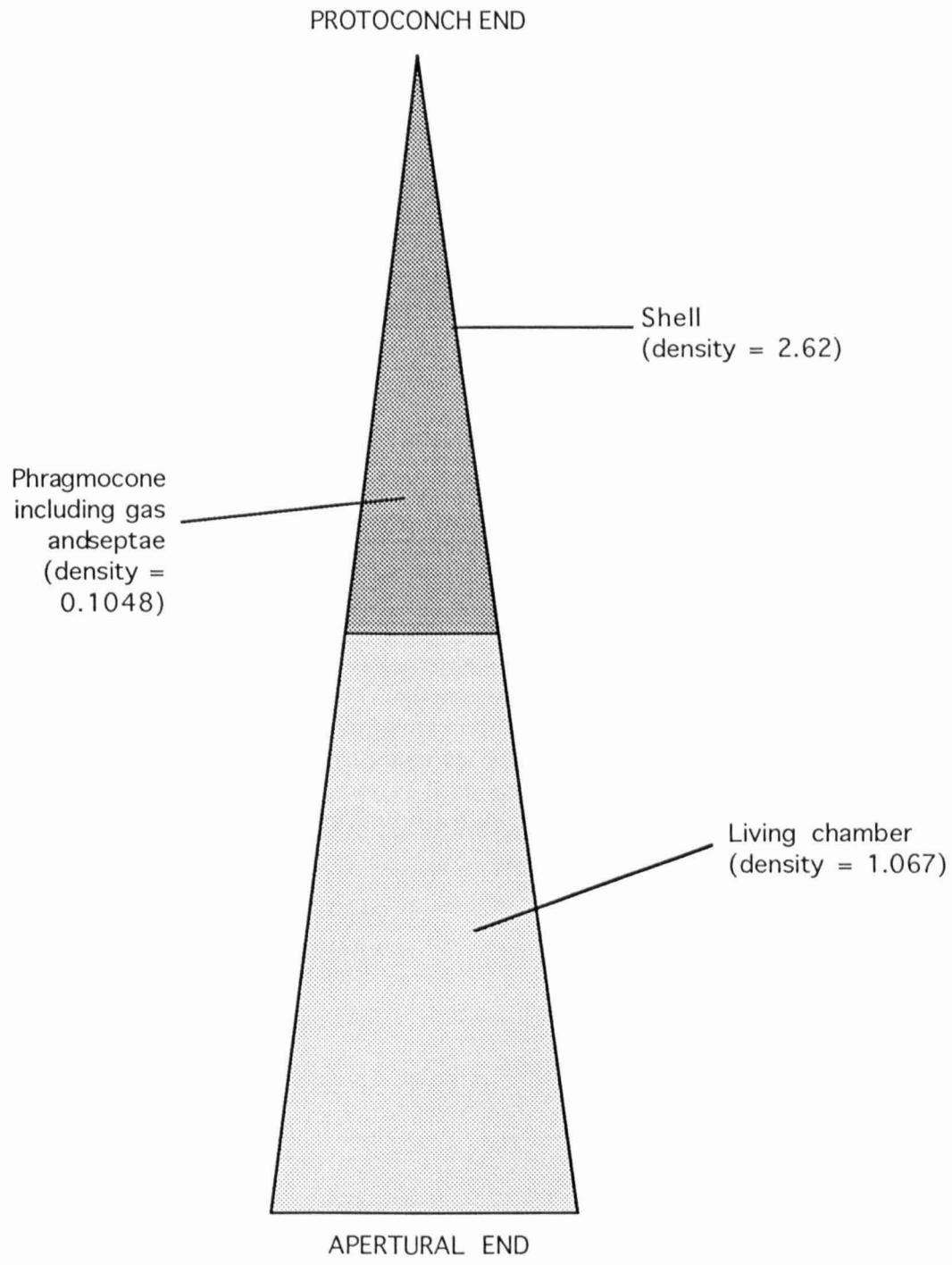


Figure 4.6

FIGURE 4.6: Diagrammatic section through an heteromorph ammonite, with representitive values for the density of shell, phragmocone, and soft tissues taken from Okamoto (1988). The density values are given in milligrammes per cubic millimeter. Sea water has a density of approximately 1.025 mg/mm^2.

Mass of ammonite (kilogrammes)	0.21331
Mass of water (kilogrammes)	0.18088
Volume of water (cubic metres)	0.00018
Density of ammonite (kilogrammes/cubic metres)	1.20875
Density of seawater (kilogrammes/cubic metres)	1.025
Centre of mass (metres from apex)	0.47236
Centre of buoyancy (metres from apex)	0.44997

FIGURE 4.7a

Mass of ammonite (kilogrammes)	0.01585
Mass of water (kilogrammes)	0.00959
Volume of water (cubic metres)	0.00001
Density of ammonite (kilogrammes/cubic metre)	1.69308
Density of seawater (kilogrammes/cubic metre)	1.025
Centre of mass (metres from apex)	0.04191
Centre of buoyancy (metres from apex)	0.04499

FIGURE 4.7b

FIGURE 4.7a: Summary of the hydrostatic properties of *Sciponoceras* based upon the analysis described in the text.

FIGURE 4.7b: Summary of the hydrostatic properties of *Ostlingoceras* based upon the analysis described in the text.

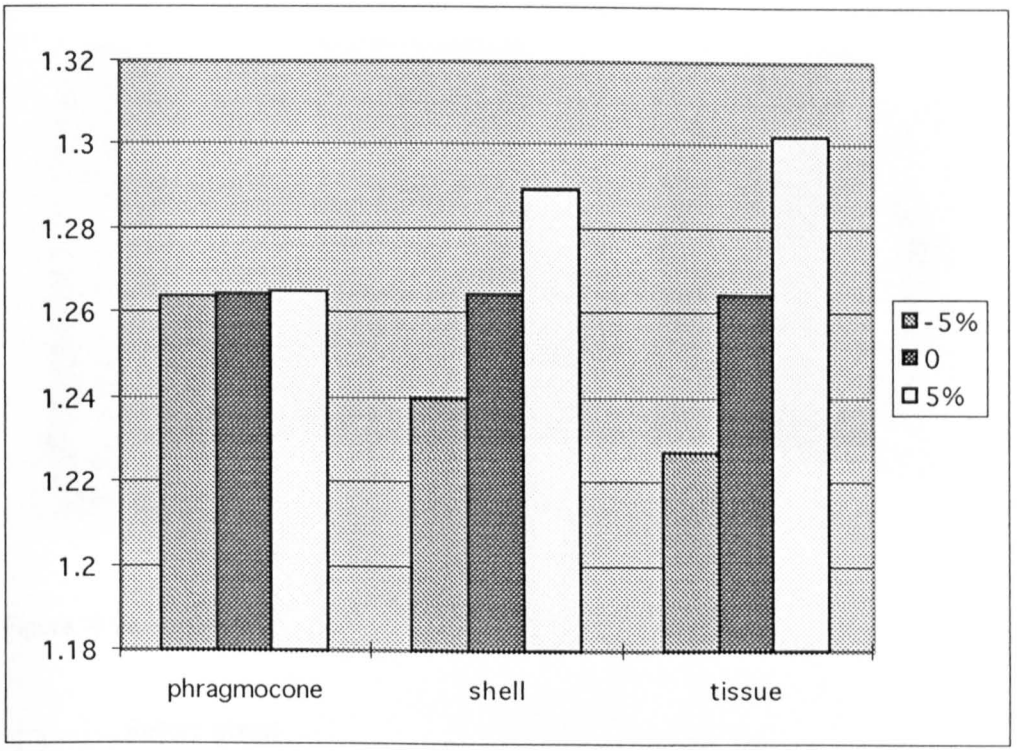


Figure 4.8a

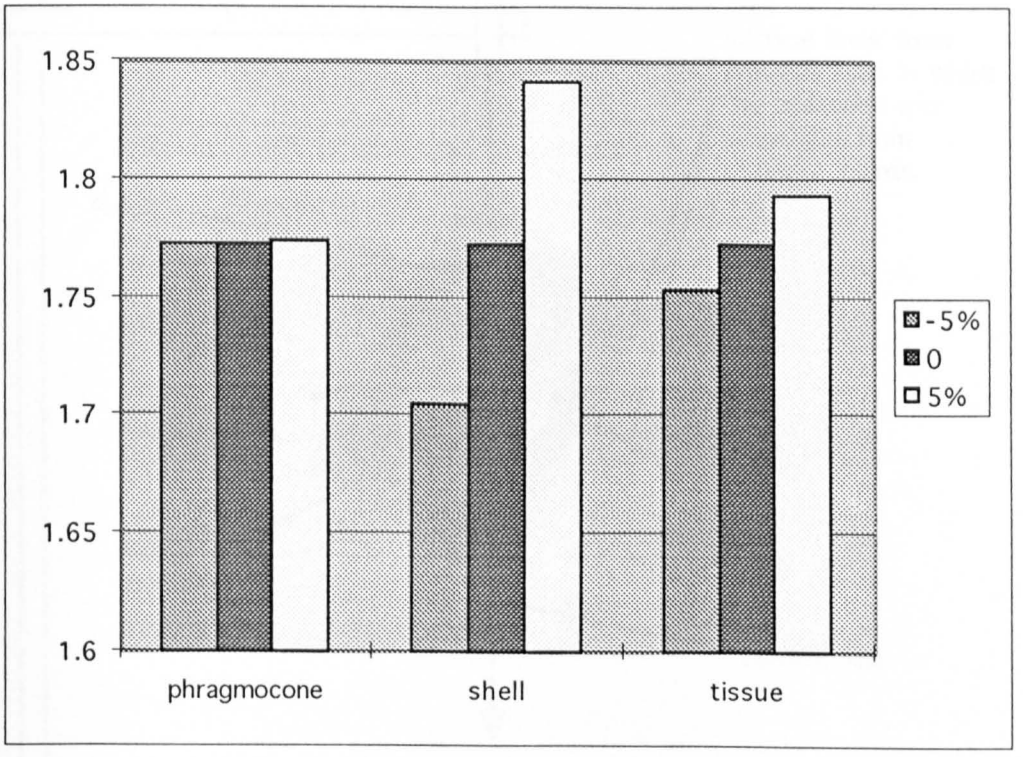


Figure 4.8b

FIGURE 4.8: Variation in the density of the baculiticonic ammonite *Sciponoceras* (Figure 4.8a) and *Ostlingoceras* (Figure 4.8b) based upon ±5% variations in the density of phragmocone, shell material, and soft tissues.

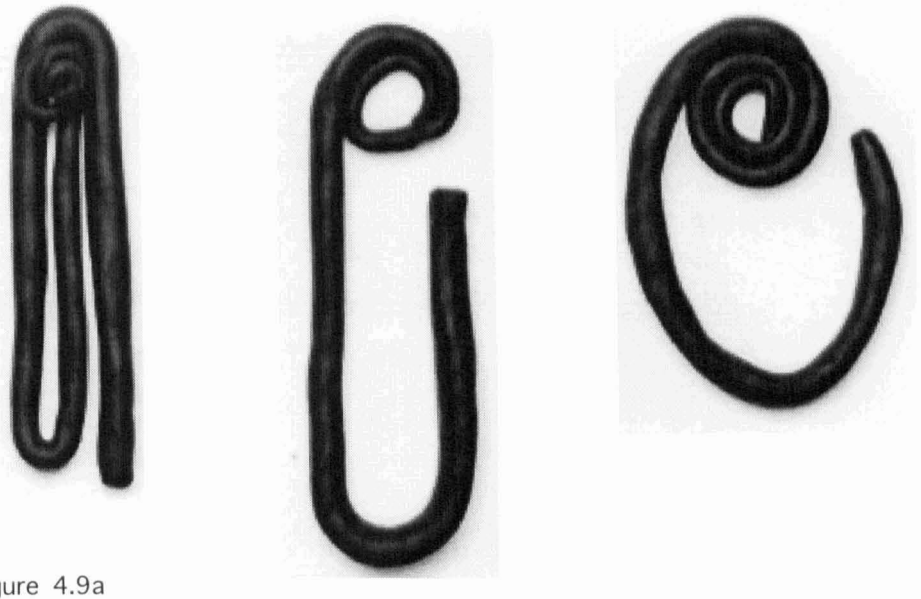


Figure 4.9a

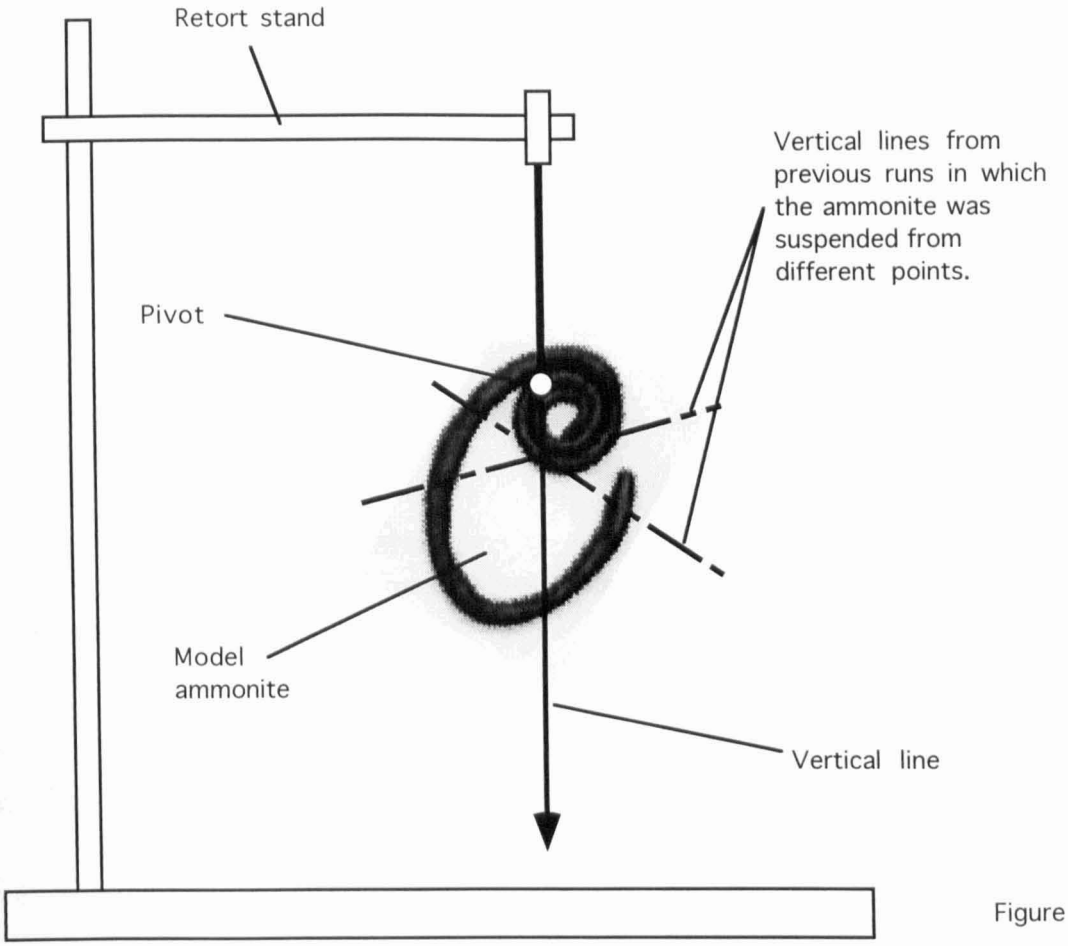


Figure 4.9b

FIGURE 4.9: Top. the Plasticene models of equal volume and whorl expansion rate but differing in coiling mode (Figure 4.9a). From left to right: hamiticone, ancylocone, and aspinocone. Bottom, a schematic diagram of the testing rig used (Figure 4.9b).

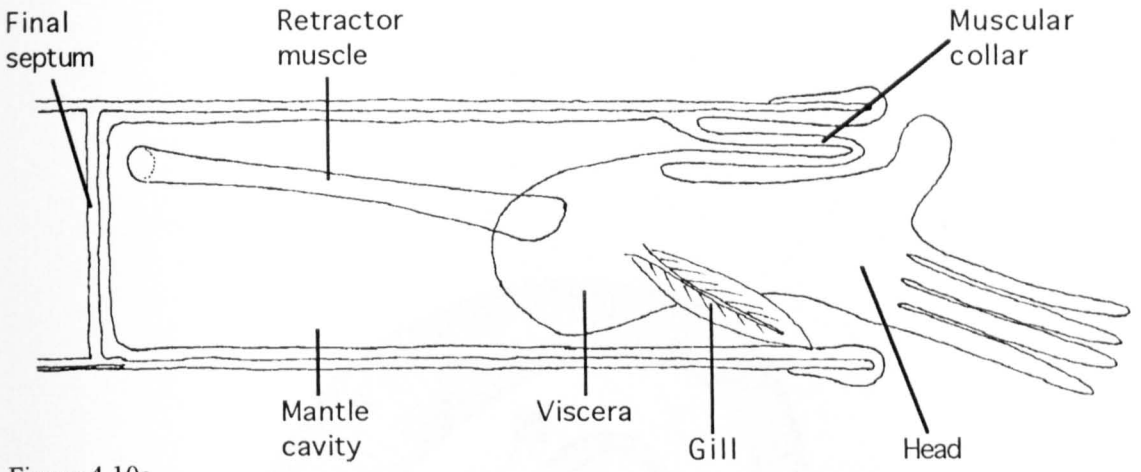


Figure 4.10a

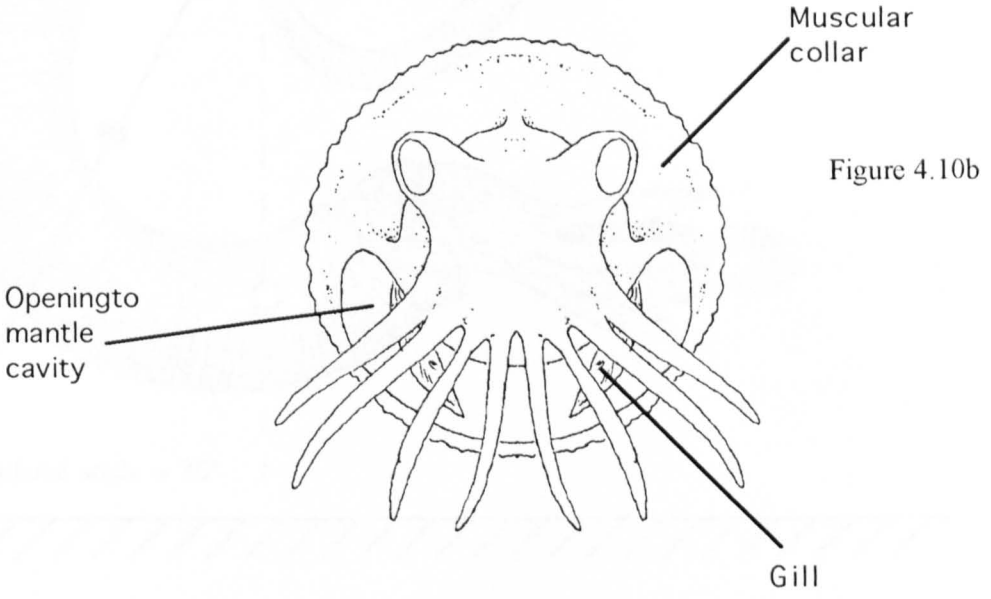


Figure 4.10b

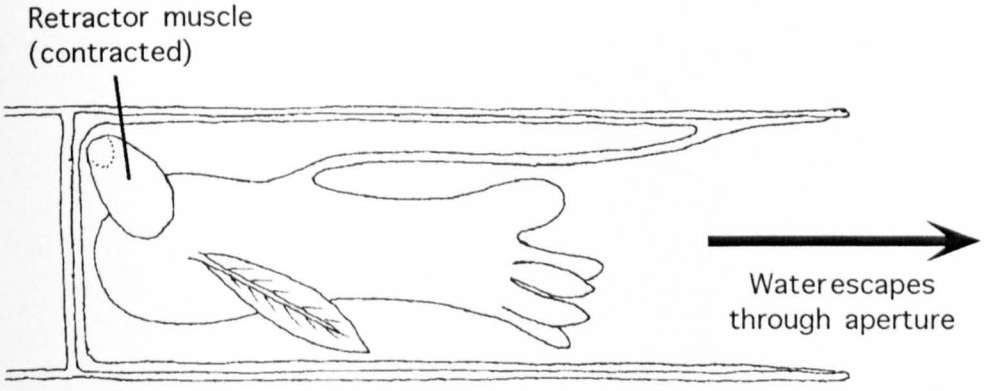


Figure 4.10c

FIGURE 4.10: Recomstruction of the living chamber with the soft body parts restored (in section). The chamber is lined by the mantle, and the main body of the animal is attached anteriorally by a muscular collar and posteriorally by the paired retractor muscles (Figure 4.10a). The muscular collar does not completely seal off the aperture (Figure 4.10b), allowing movement of water over the gills, as well as allowing water behind the animal to escape when the head is pulled back (Figure 4.10c).

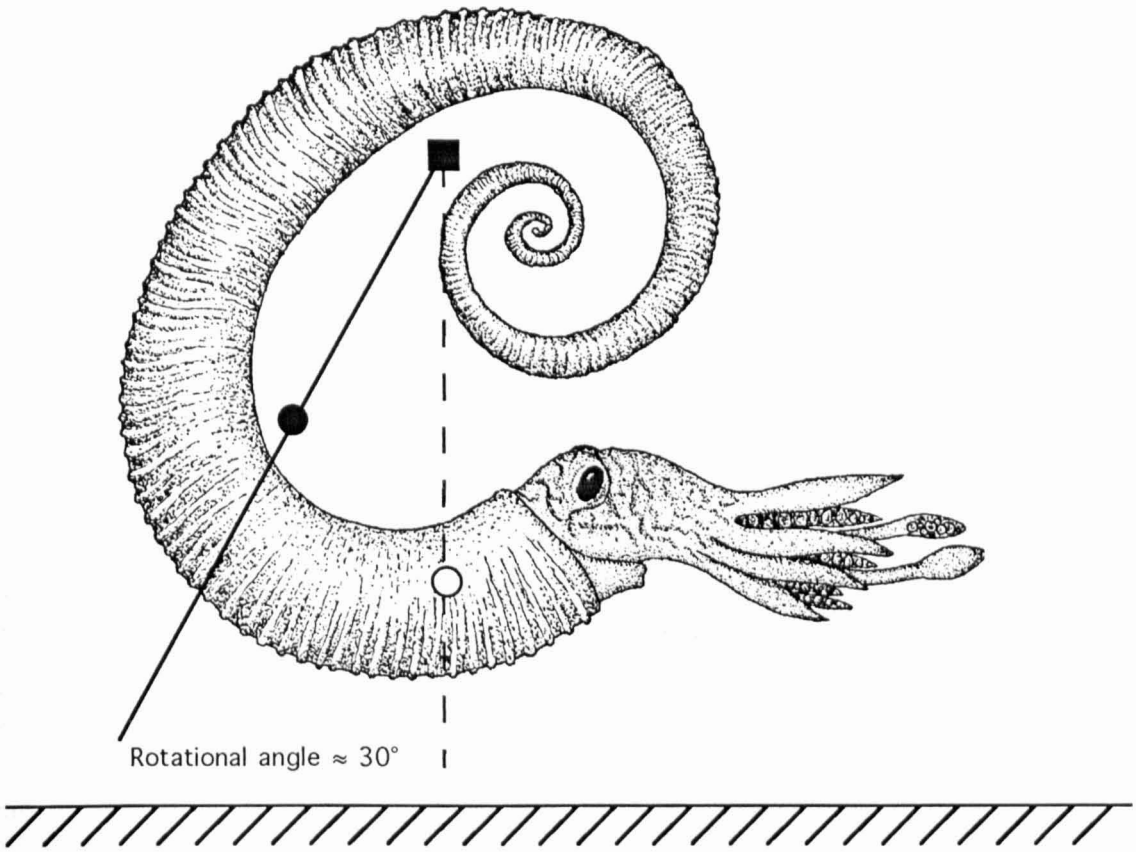


FIGURE 4.11a: Reconstruction of an aspinoconic ammonite, *Hamitella gardneri*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

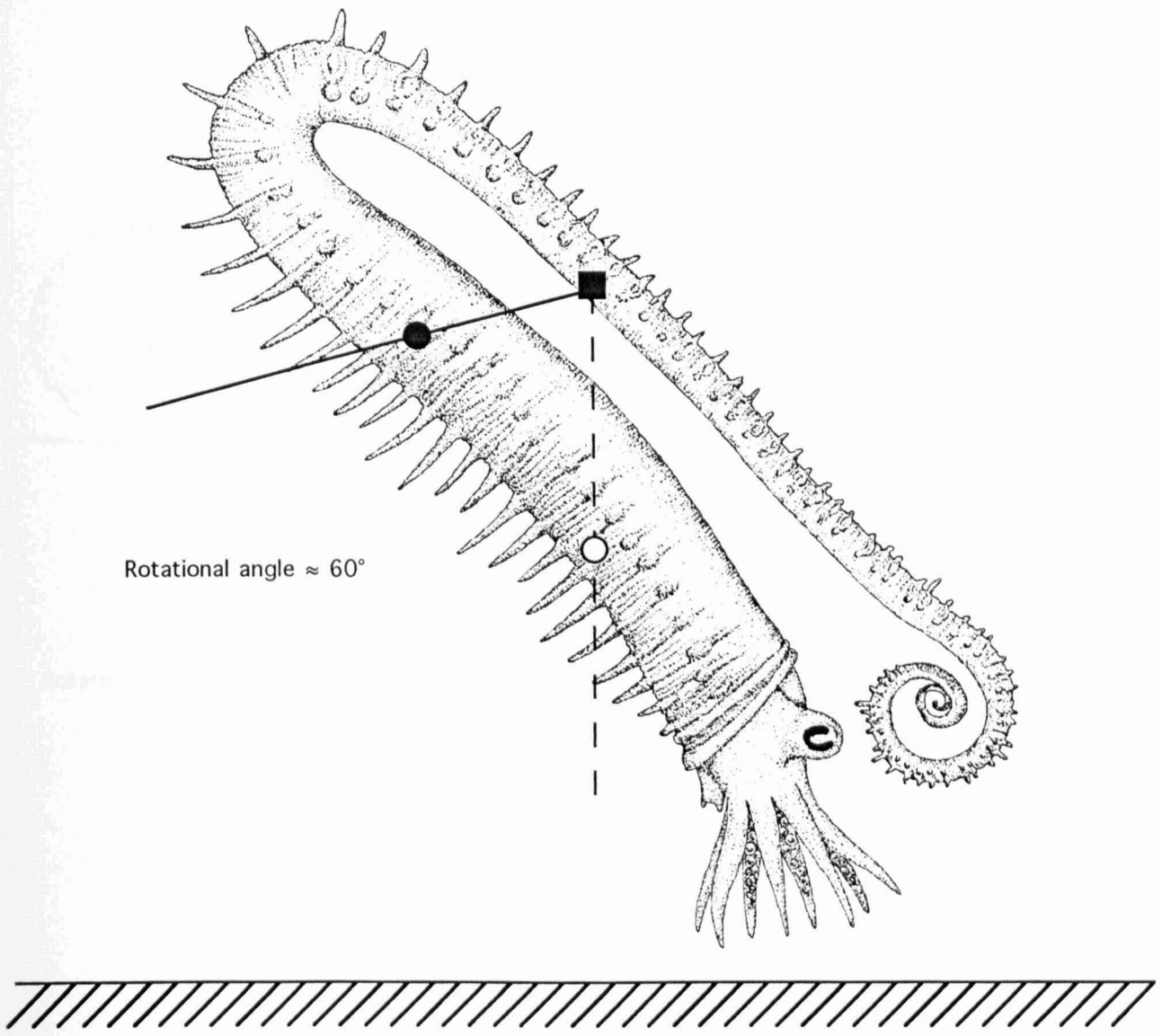


FIGURE 4.11b: Reconstruction of an ancycloconic ammonite *Anisoceras armatum* with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

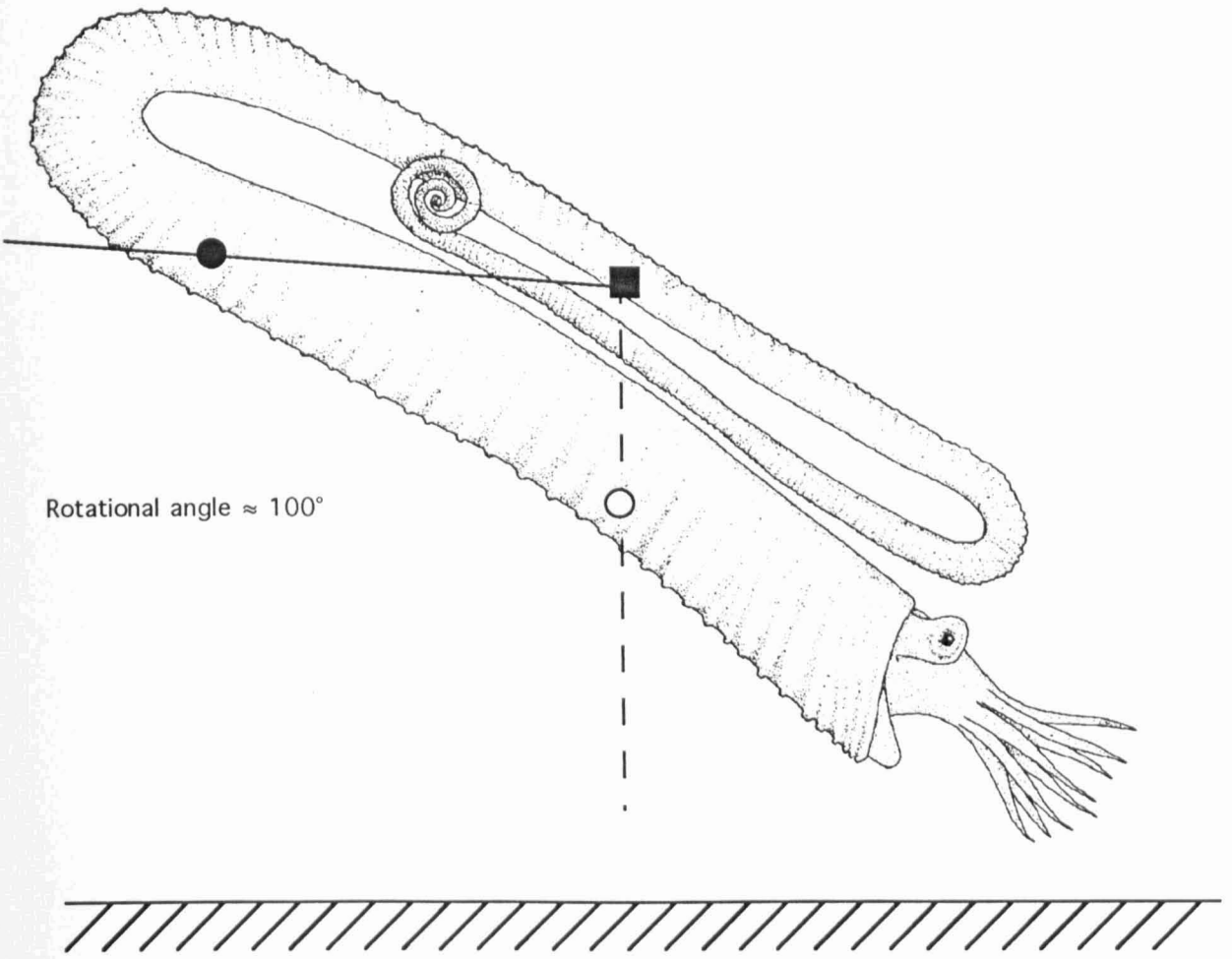


FIGURE 4.11c: Reconstruction of an hamiticonic ammonite, *Hamitella maximus*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

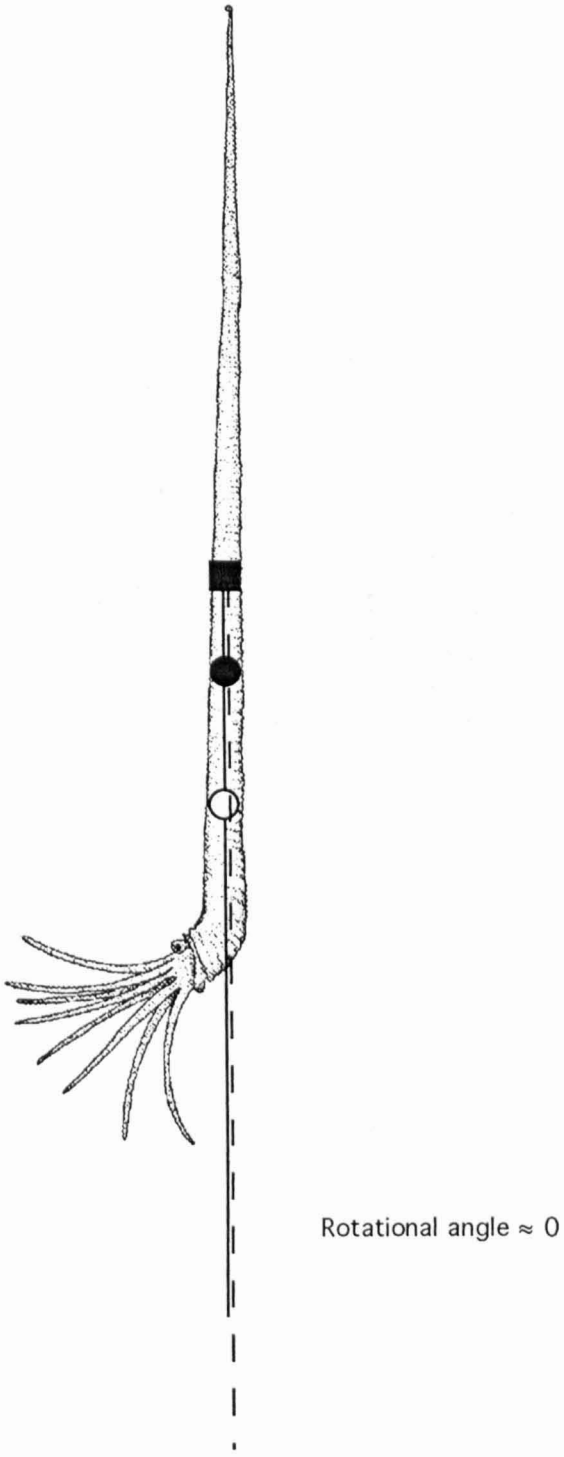


FIGURE 4.11d: Reconstruction of a baculiticonic ammonite, *Lechites gaudini*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

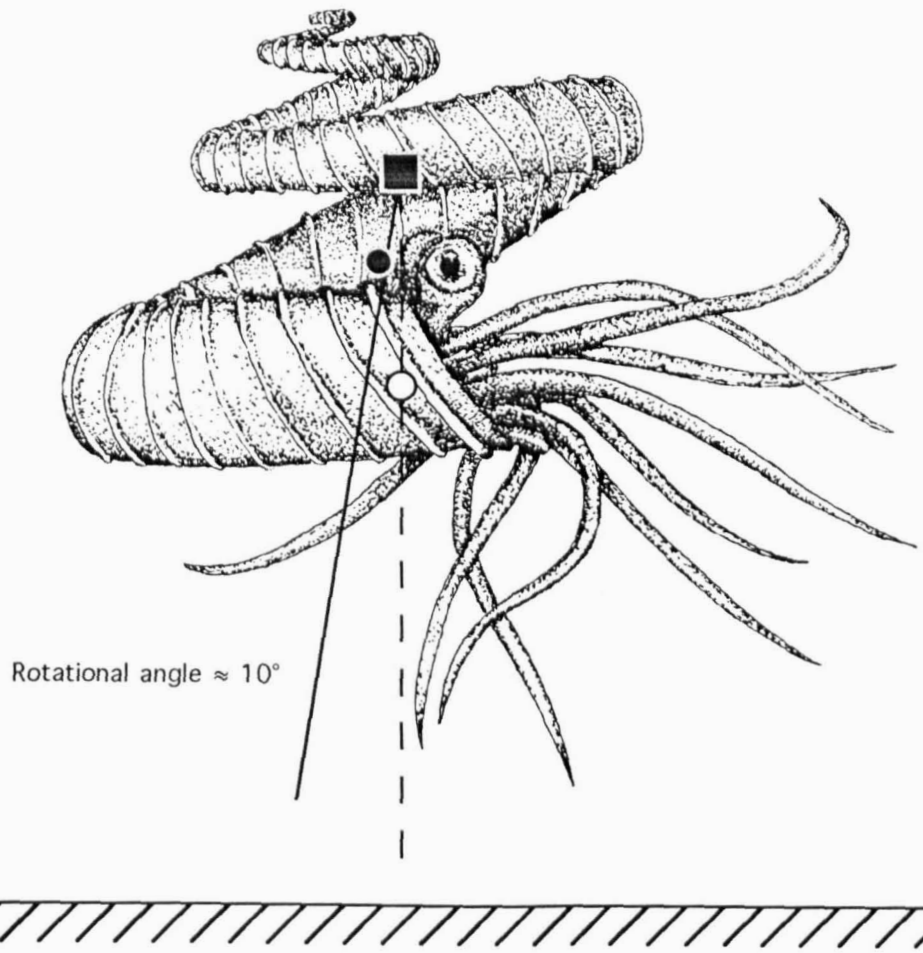


FIGURE 4.11e: Reconstruction of a low spired turriliticonic ammonite, a juvenile *Hamitella* sp. with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

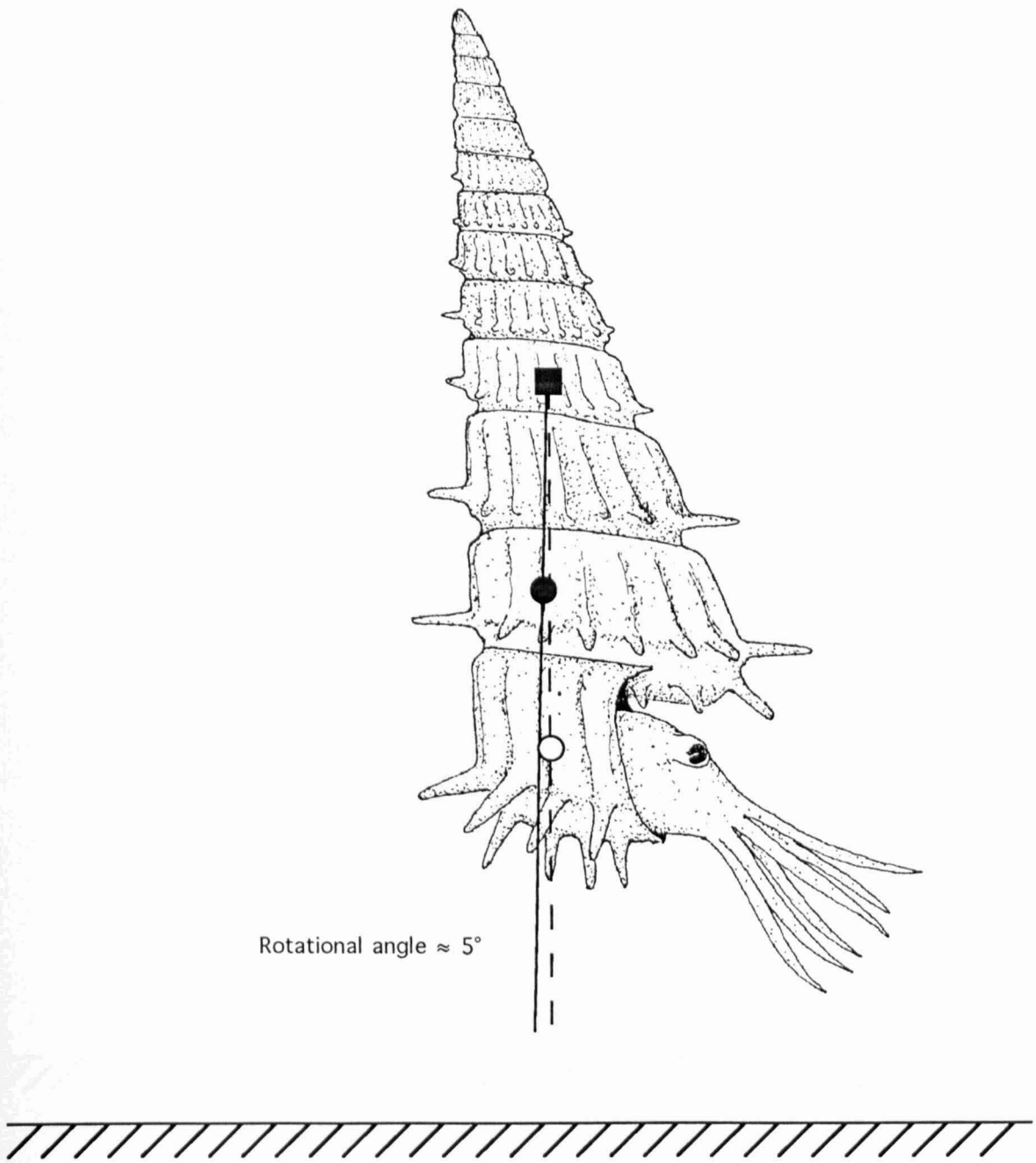


FIGURE 4.11f: Reconstruction of a high spired turriliticonic ammonite, *Ostlingoceras puzosianum*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

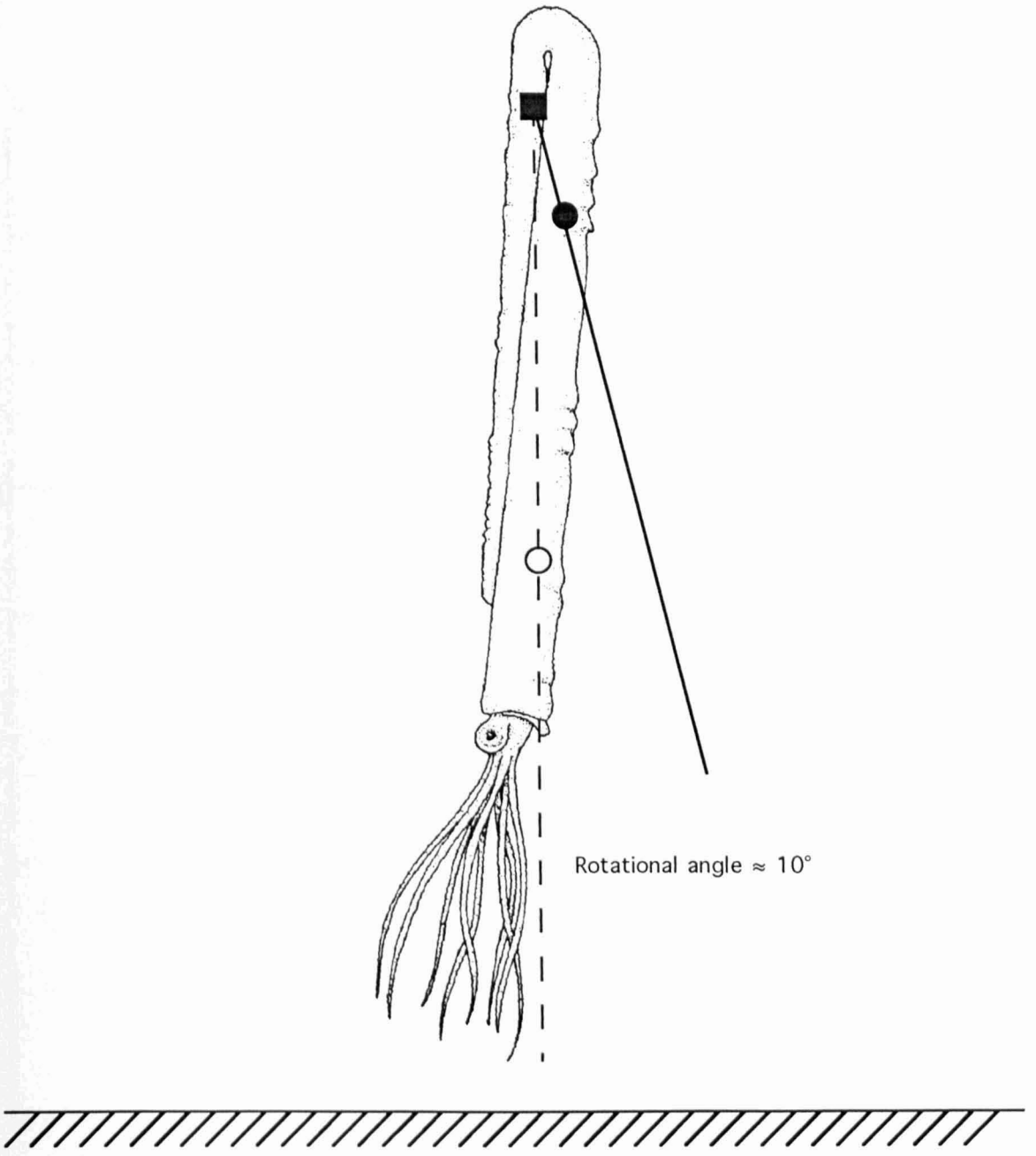
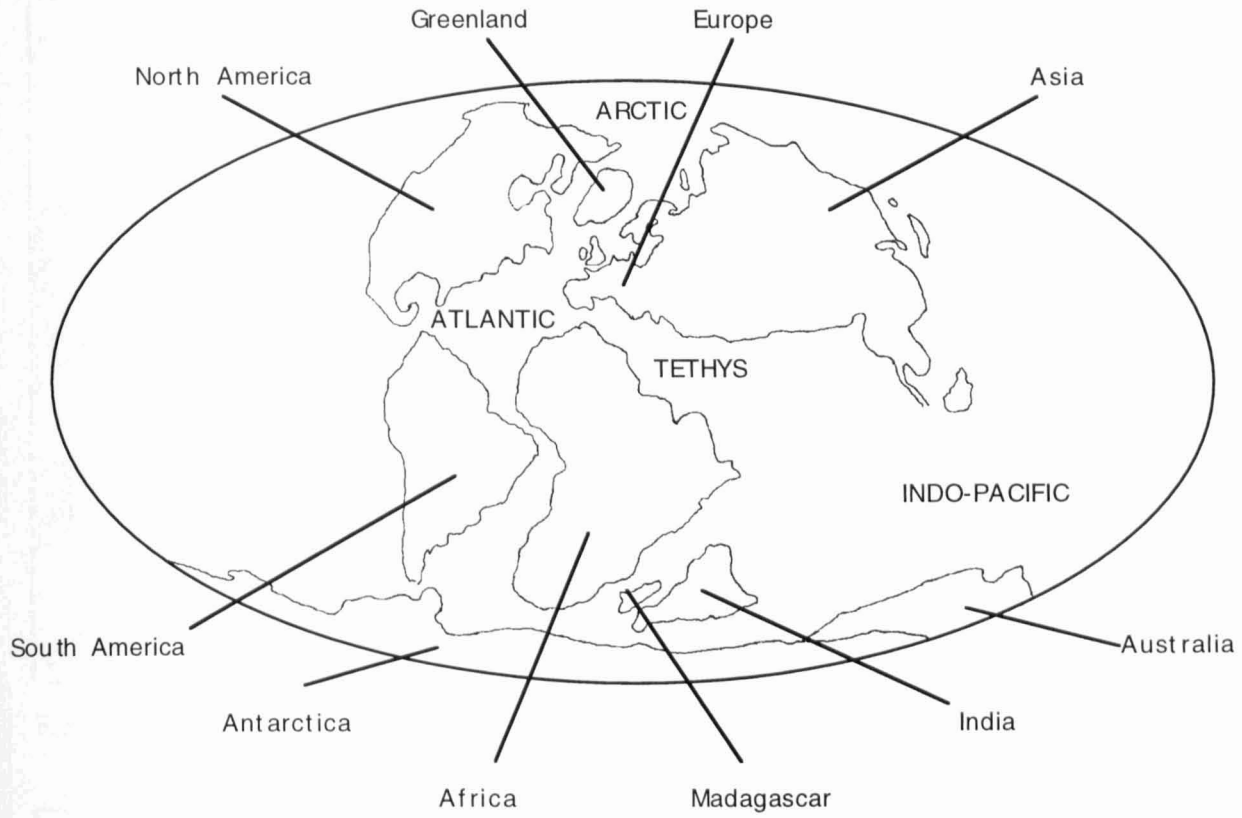


FIGURE 4.11g: Reconstruction of a ptychcoconic ammonite, *Ptychoceras adpressum*, with estimated centre of buoyancy (black square) and centres of mass with the head and arms extended (white circle) and withdrawn (black circle). A broken line indicates the vertical when the head and arms are extended, and a solid line when the head and arms are withdrawn. The angle at which these lines meet is the angle of rotation.

SHELL MORPHOLOGY	ROTATIONAL ANGLE	TILTING ABILITY
ASPINOCONE	30° (MODERATE)	YES
ANCYCLOCONE	60° (HIGH)	YES
HAMITICONE	100° (HIGH)	YES
BACULITICONE	0° (LOW)	NO
OPEN, LOW SPIRED TURRILITICONE	10° (LOW)	NO
CLOSED, HIGH SPIRED TURRILITICONE	5° (LOW)	NO
PTYCHOCONE	5° (LOW)	NO

Figure 4.11

FIGURE 4.12: Table of the seven ammonite mophologies described in the text (Chapter 4) together with the deduced rotational angles. Each shell morphology can be classified by whether it has "tilting" ability or not, which is dependent on the size of the rotational angle. As described in the text, tiltling morphologies have large rotational angles, and movement of the body between the aperture and the back of the shell would cause the ammonite to rotate, typically with the aperture toward the sea floor when the head and arms are extended. In contrast non-tilting forms have small or zero rotational angles, and movement of the body within the shell causes little or no change in orientation.



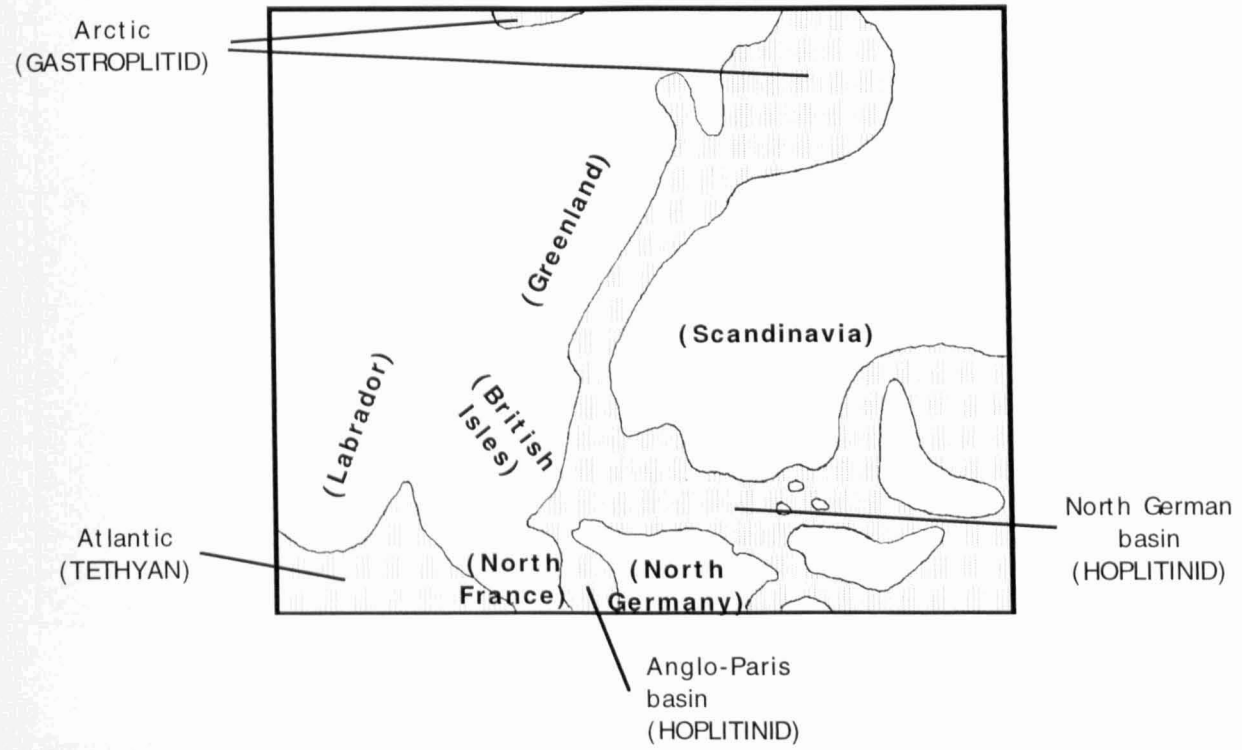


FIGURE 5.1a: Inferred position of the continents during the Lower Albian (105 to 100 million years ago) redrawn after Haq (1984).

FIGURE 5.1b: Coastlines of North West Europe during the same time period, based on Owen (1979) with the prinicpal marine basins labelled. Names in brackets - e.g., **(Greenland)** - indicate present-day geographical locations.

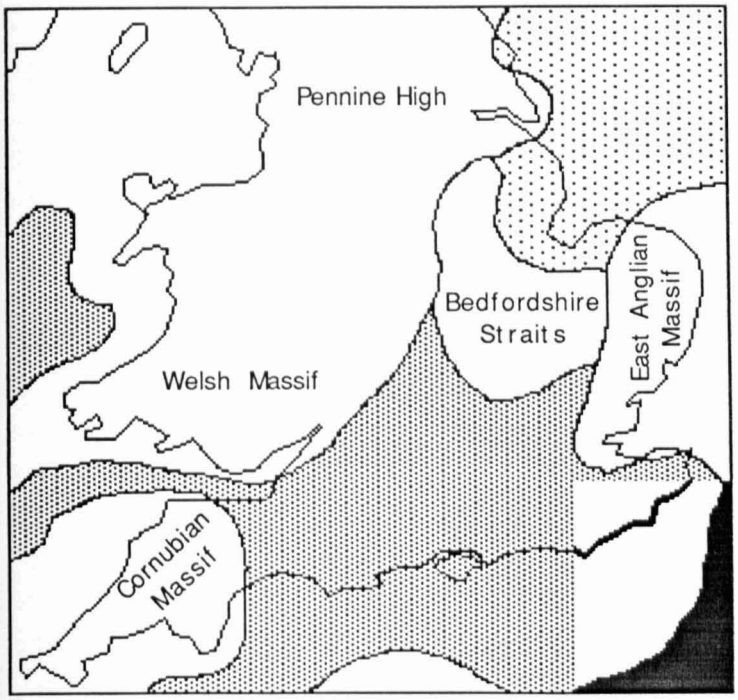


Figure 5.2a

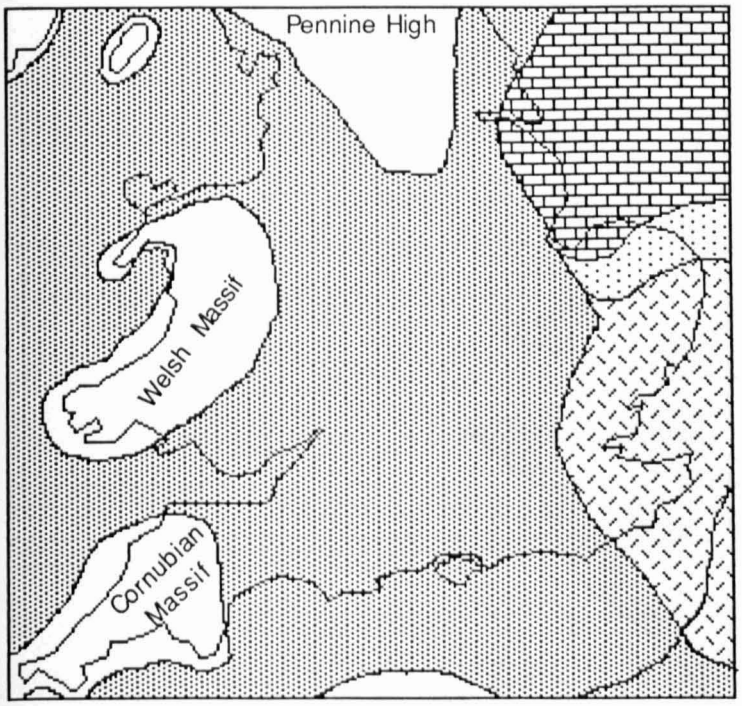


Figure 5.2b

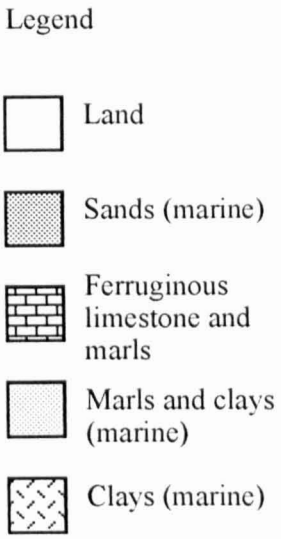


FIGURE 5.2: Lower Albian (Figure 5.2a) and Upper Albian (Figure 5.2b) palaeogeographical reconstructions redrawn after Rawson (1992). Principal facies types are indicated.

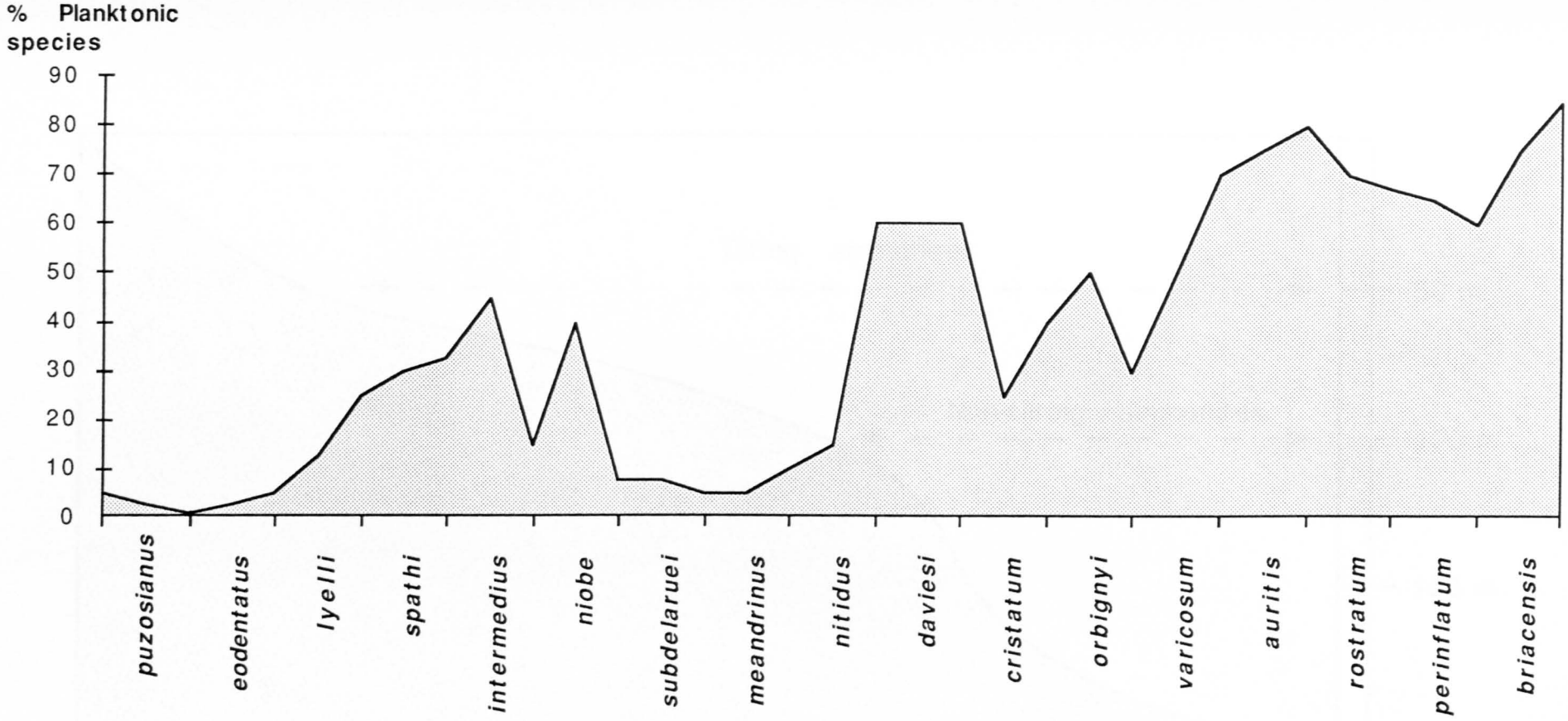


FIGURE 5.3: Relative abundances of planktonic foramaniferans as a percentage of total (planktonic + benthic) number of foramaniferans. Based on Price (1977) the abundances are in terms of numbers of species recorded from each ammonite subzone.

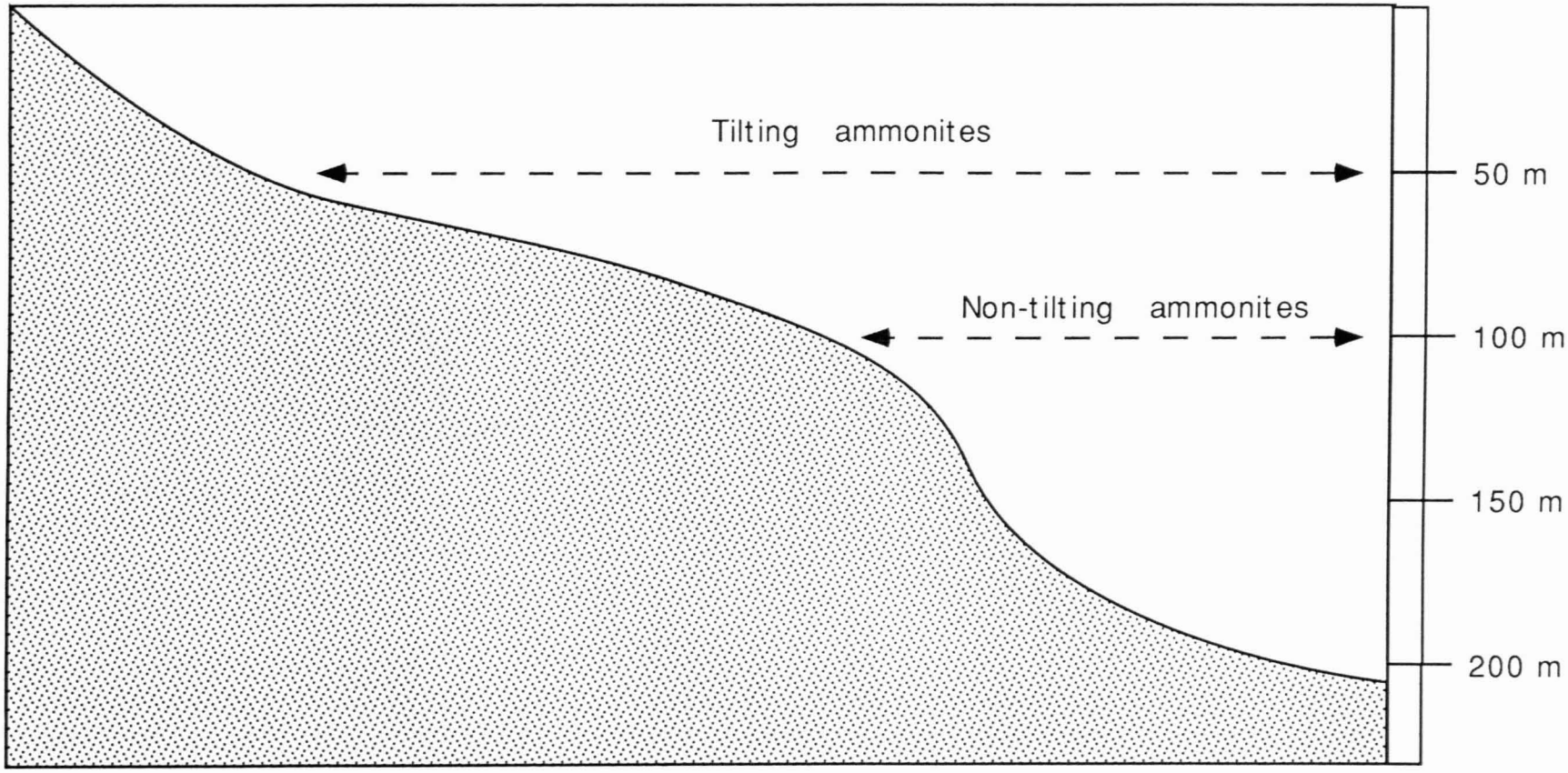


FIGURE 5.4: Idealised section of the Gault Sea based on the estimates of water depth discussed in the text (Chapter 5). The ranges of the tilting morphotypes (aspinocones, ancyclocones, and hamiticones) and the non-tlting morphotypes (baculiticones, ptychocones, and turriliticones) as inferred from their occurence in the fossil record are plotted. The tilting forms are found in sediments suggesting a wider range of deths than the non-tilting forms, which were restricted to deeper water facies.

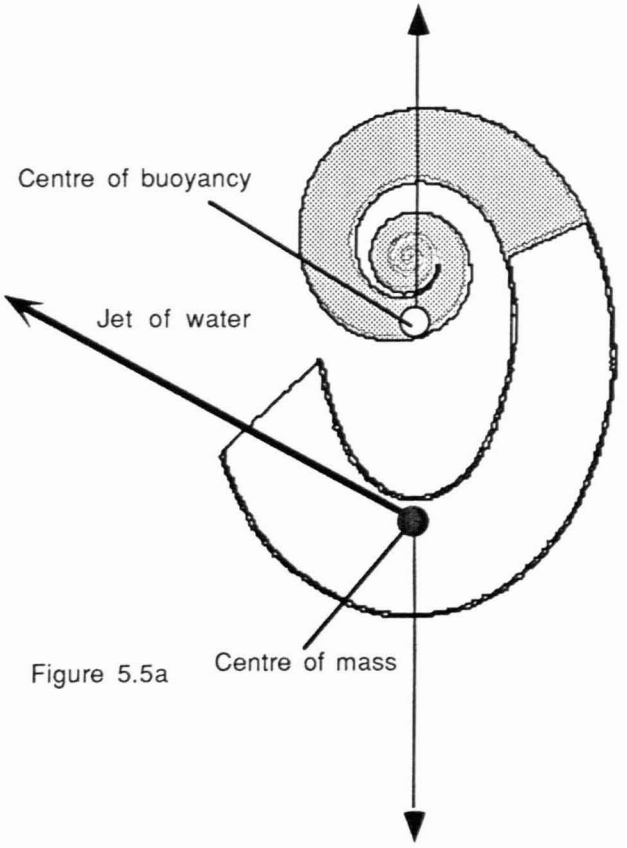


Figure 5.5a

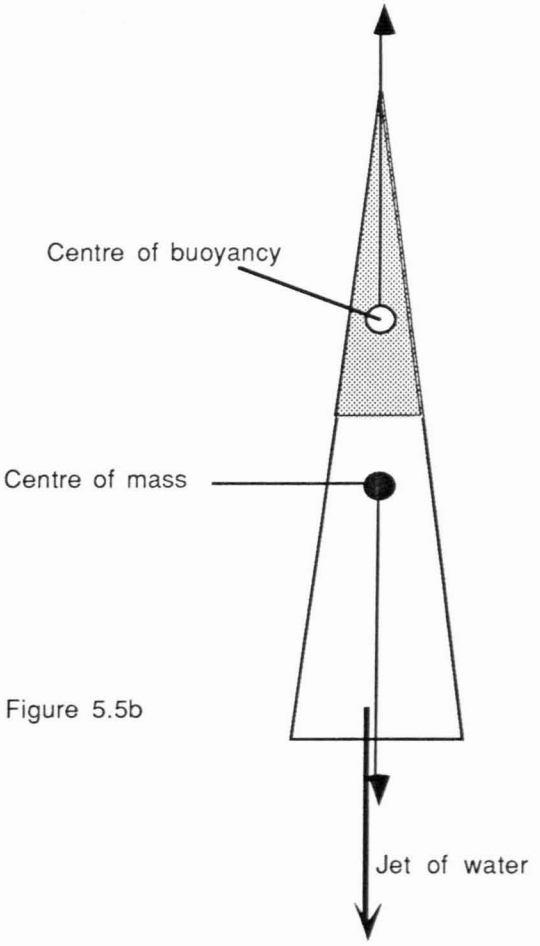


Figure 5.5b

FIGURE 5.5: Lines of force generated by jet-propulsion compared in a tilting morphotype (Figure 5.5a; an aspinocone) and a non-tilting morphotype (Figure 5.5b;a baculiticone). The line of force will act through the centre of mass. In the aspinocone, this line of force meets the vertical axis of the ammonite tangentially,consequently some of the force will produce a rotation of the shell around the pivot point (the centre of buoyancy). This rotation wastes energy and so swimmingwould be inefficient.. In contrast, with the baculiticone, the centre of mass, centre of buoyancy and the line of force are all lined up along the vertical axis and noneof the energy is lost this way.



Figure 5.6

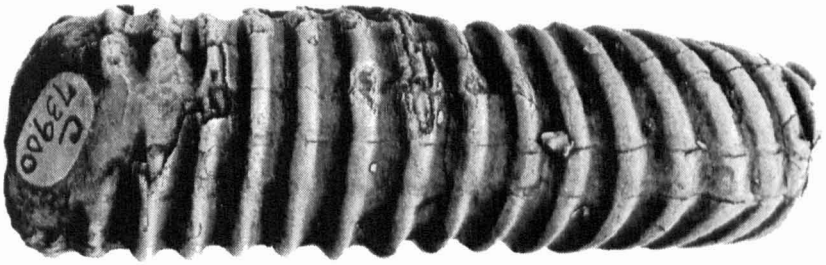


Figure 5..7

Figure 5.9

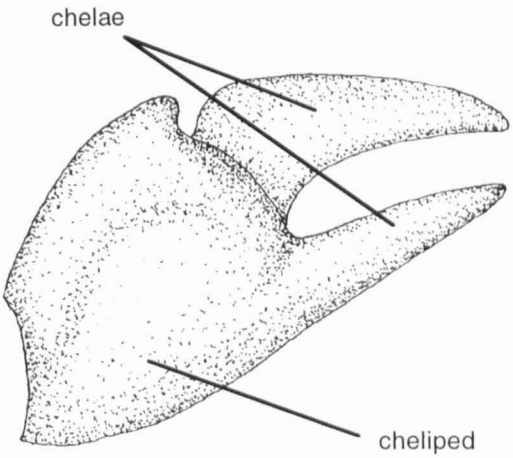


Figure 5.8

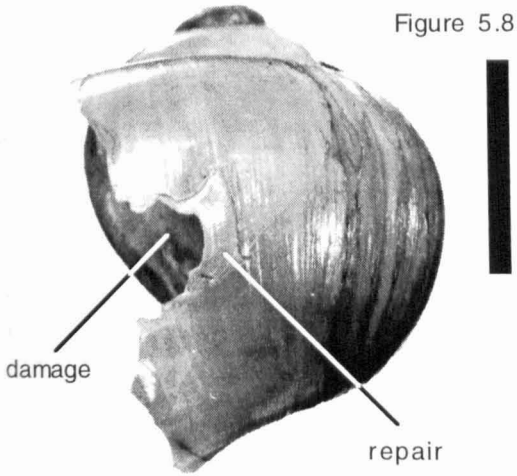


FIGURE 5.6: *Hamitella intermedius*. Uncatalogued specimen from Bed IX, Copt Point, Folkestone. Author's collection, BMNH. Oriented with apertural-end of shell toward bottom of the page. Shell damage and repair along the mid line of this specimen; note bisected ribs where the shell was peeled with only gradual reformation of later ribs. The original shell material is preserved in this specimen. Scale bar = 10 mm.

FIGURE 5.7: *Hamitella maximus*. BMNH C.73900, from Copt Point, Folkestone; exact stratigraphical horizon unrecorded. Oriented with the apertural-end of the shell towards the left hand side of the page. Shell damage in this specimen is slightly below the midline of the shell, and evidenced by deformation of the ribs. Original shell material of this specimen preserved. Scale bar = 10 mm.

FIGURE 5.8: *Ampullaria* sp. Example of an artificially "peeled" apple snail shell. The shell damage extends about 5 mm inwards from the aperture, roughly along the midline of the whorl. Subsequent repair has filled in part of the damage.

FIGURE 5.9: Restored claw of *Diaulax feliceps*. Based upon BMNH In.30098 from the Gault Clay at Folkestone. Robust chelipeds with smooth short chelae like these can be seen in modern crabs which peel shells open, such as *Calappa*. Crabs which crush shells, like *Cancer*, have chelae with molariform processes. Scale bar = 10 mm.

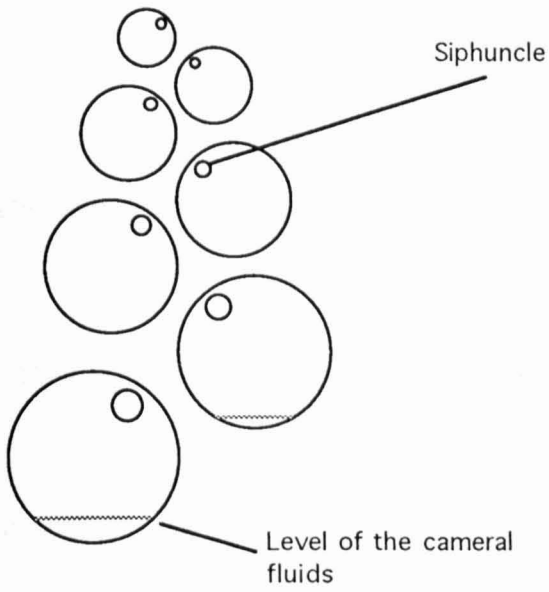


Figure 5.10

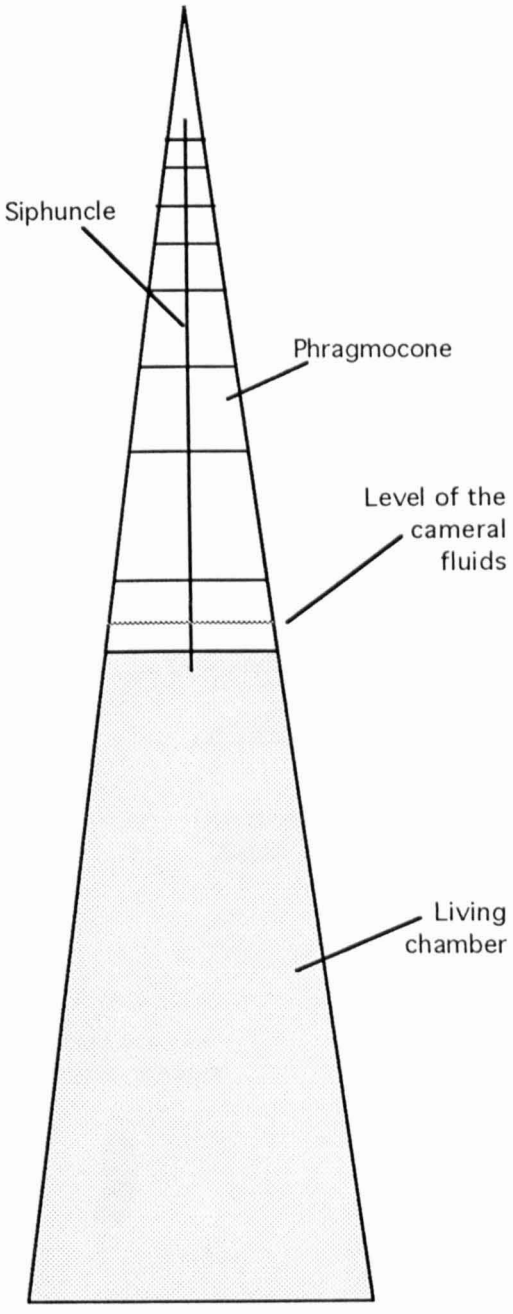


Figure 5.11

FIGURE 5.10: Diagrammatic section through a typical helically coiled ammonite of the family Turrilitidae. According to Klinger (1980) the helical coiling and displacement of the siphuncle observed in most Turrulitidæ give rise to a situation whereby the siphuncle is 'de-coupled' from the cameral fluids. This supposedly increases the efficiency of cameral emptying.

FIGURE 5.11: Diagrammatic section through a typical baculiticonic ammonite of the family Baculitidae. A consequence of the coiling of baculiticones is that the siphuncle is effectively de-coupled for most of its length since it does not lie on the ventral surface of the shell, the usual position in most regularly coiled ammonites.

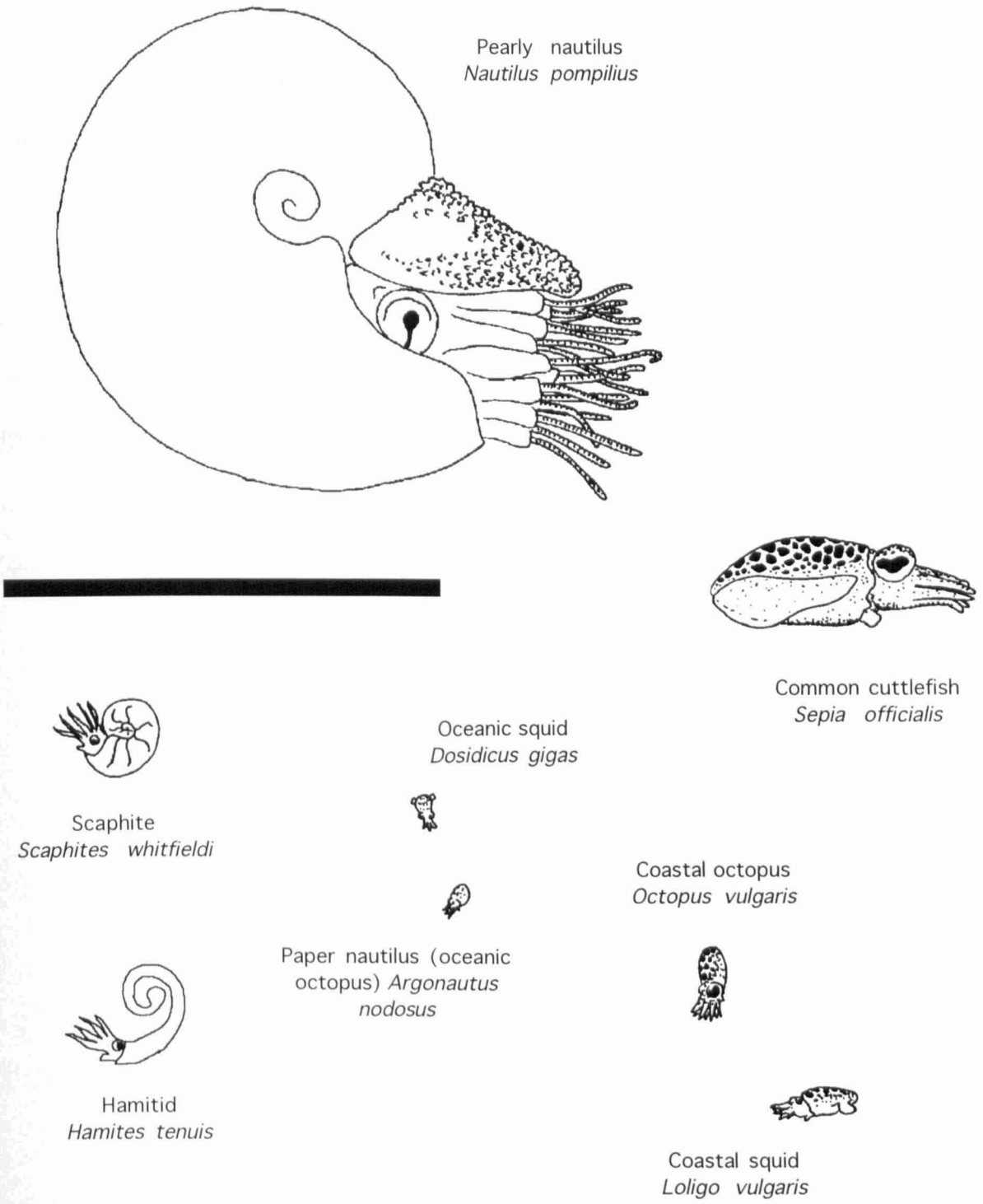


FIGURE 6.1: Comparisons of the sizes of various cephalopods at hatching. Based on Tanabe *et al* (1980), Mangold (1987), Lebrun (1996) and Landmann *et al* (1996). The *Nautilus* is demersal immediately after hatching, as is the common cuttlefish. The species of squid and octopus figured here represent extremes of the range of sizes known for these groups, and all appear to be planktonic for at least the early part of their life cycle. The two heteromorph ammonites are more comparable with the squid and octopus than with the *Nautilus*, and this suggests that they were planktonic after hatching. The scale bar is 50 mm.

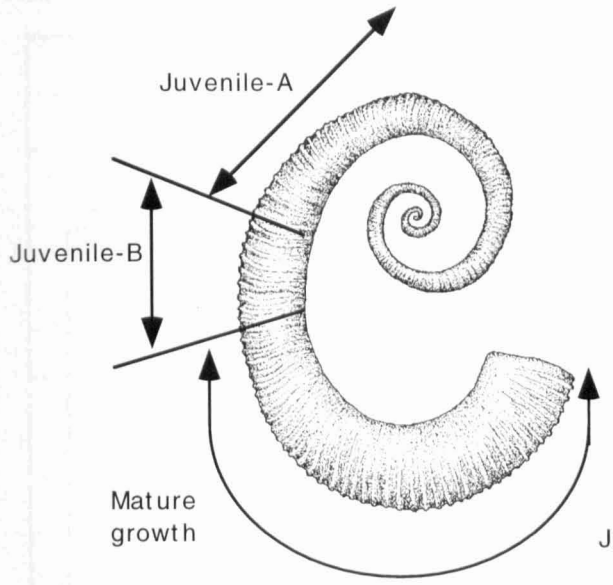


Figure 6.2a

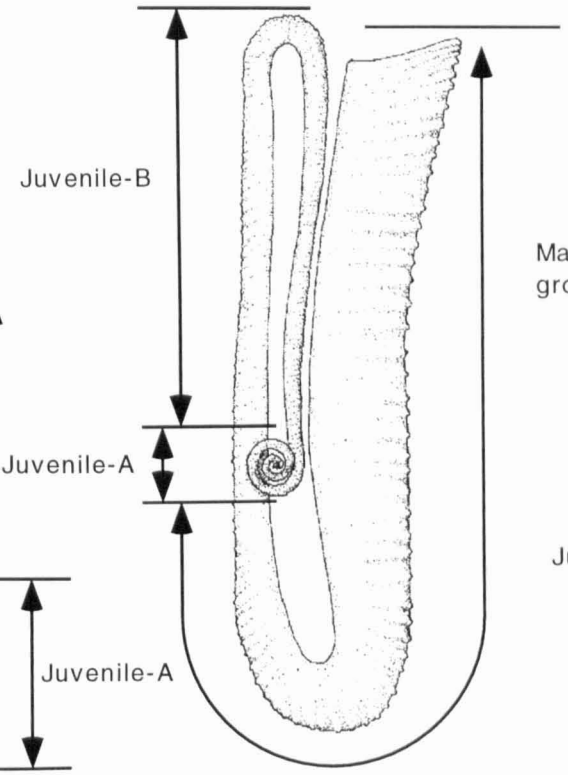


Figure 6.2c

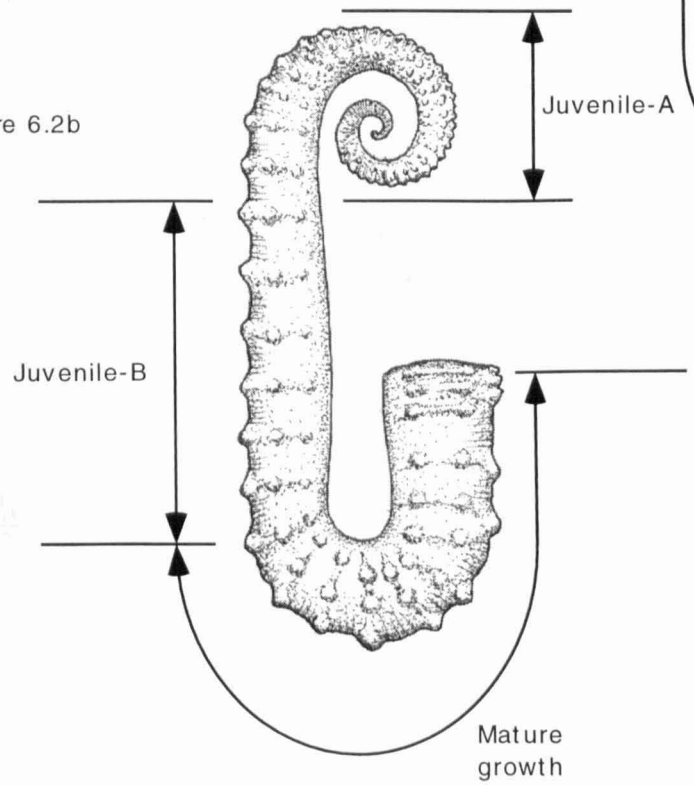


Figure 6.2b

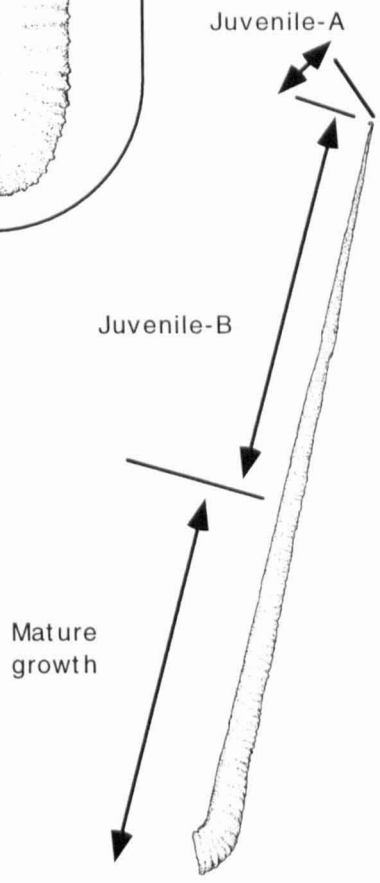


Figure 6.2d

FIGURE 6.2: Four ammonites for comparison of the coiling mode and relative sizes of the juvenile-A, juvenile-B, and mature growth phases:

FIGURE 6.2a: *Hamitella gardneri*
FIGURE 6.2b: *Ancycloceras matheronianum*
FIGURE 6.2c: *Hamitella maximus*
FIGURE 6.2d: *Lechites gaudini*

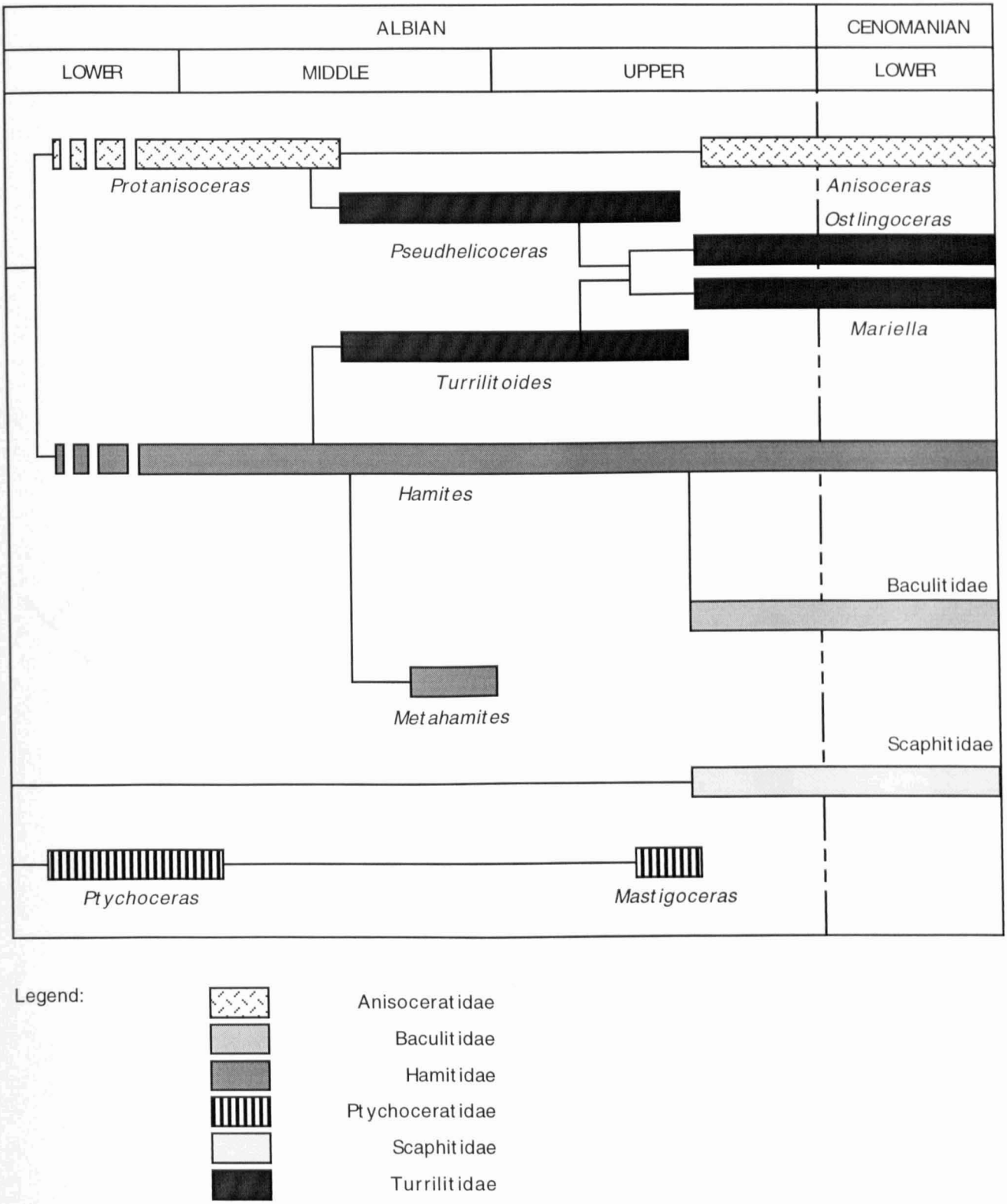


FIGURE 6.3: Interelationships between the Albian heteromorphs postulated by Spath (1923-1943).

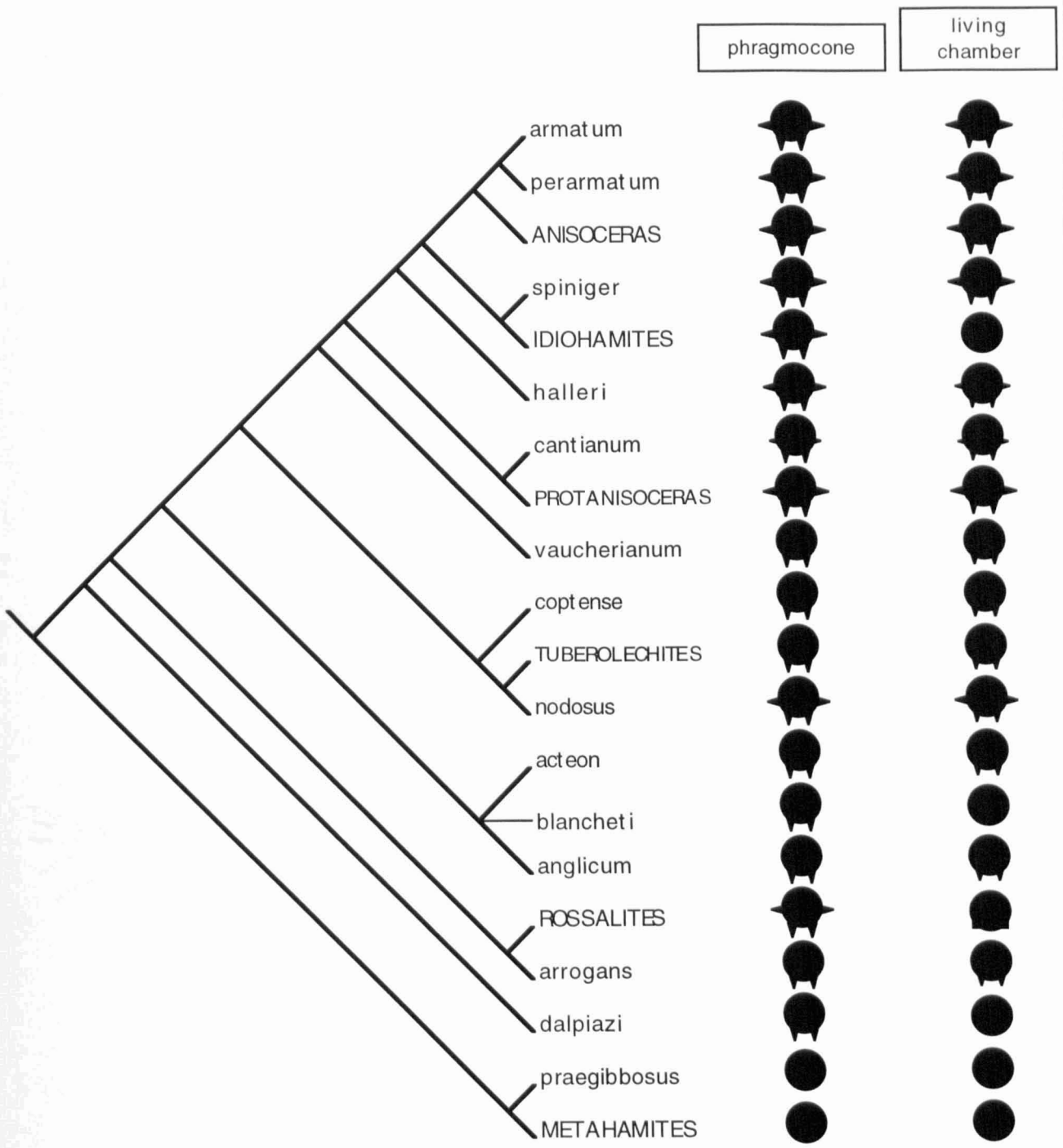


FIGURE 6.4: Phylogeny of the Anisoceratidæ based on the cladogram described in Chapter 2. The tuberculation on the phragmocone and the living chamber of each species is also figured diagrammatically; it it clear that among the more primitive species tuberculation tends to be limited to the phragmocone, while tuberculation on the living chamber as well as the phragmocone is characteristic of the more derived species.

Figure 6.5a

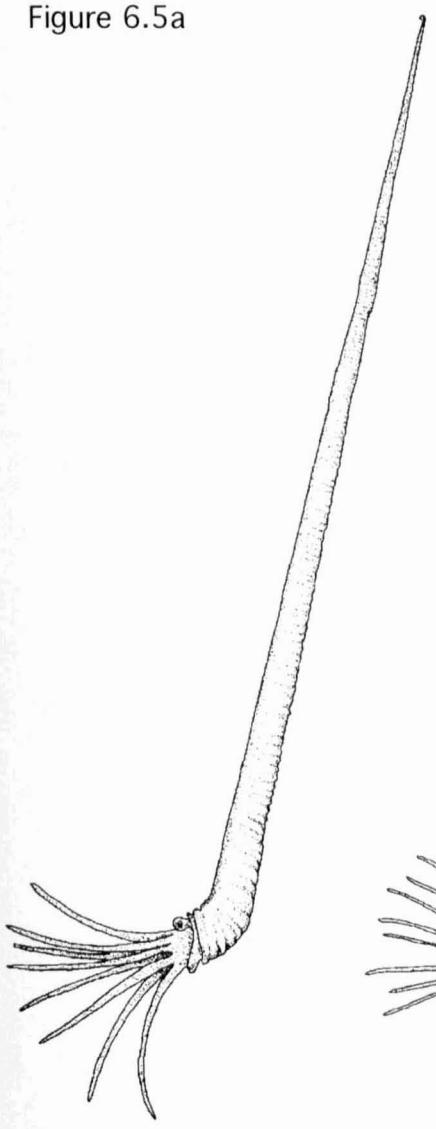


Figure 6.5b

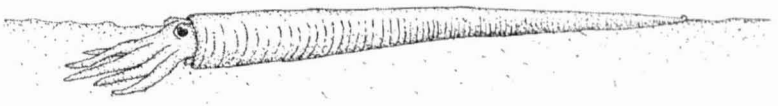


Figure 6.5c



FIGURE 6.5: Evolution of the Baculitidæ postulated here compared with the hypothesis suggested by by Matsumoto & Obata (1964). In this thesis the baculitids are viewed as neotenic derivatives of the Hamitidæ which were adapted to a planktonic lifestyle with the long axis vertical (Figure 6.5a). Matsumoto & Obata (1964) proposed that baculitids were originally benthonic (Figure 6.5b) and that the orthoconic shell shape was an adaptation for squid-like swimming with the long axis horizontal (Figure 6.5c).

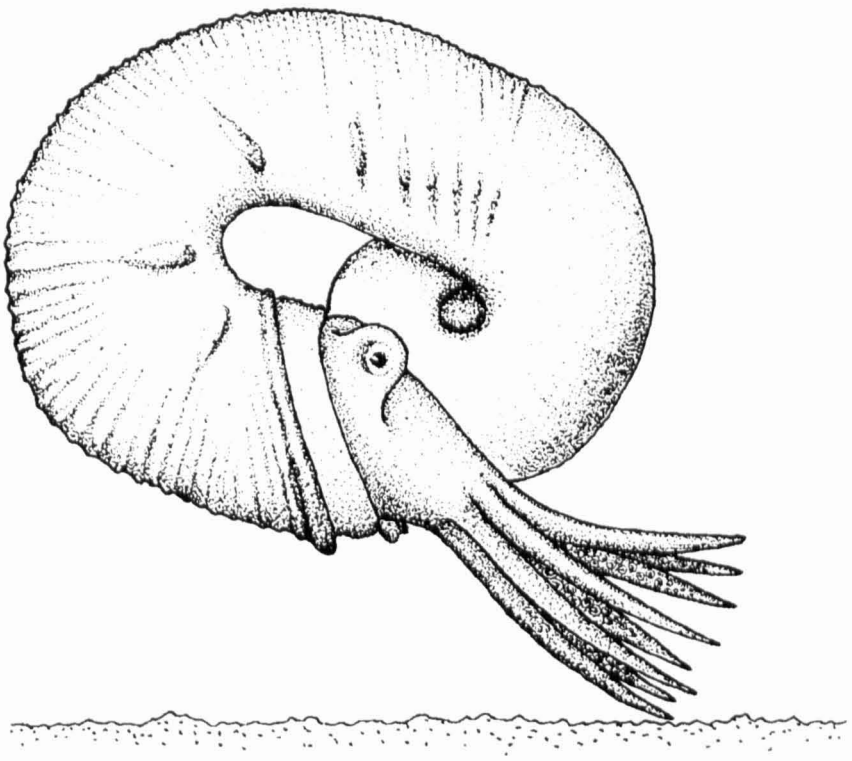


Figure 6.6

FIGURE 6.6: *Scaphites hugardianus* reconstructed as a benthonic animal, with the aperture toward the sea floor.

Figure 6.7a

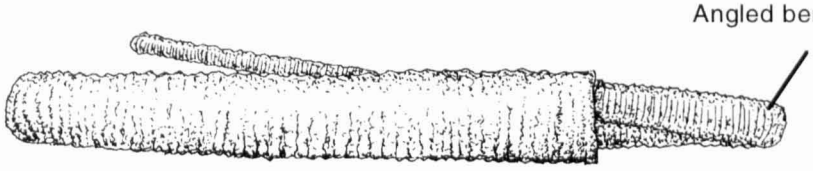


Figure 6.7b

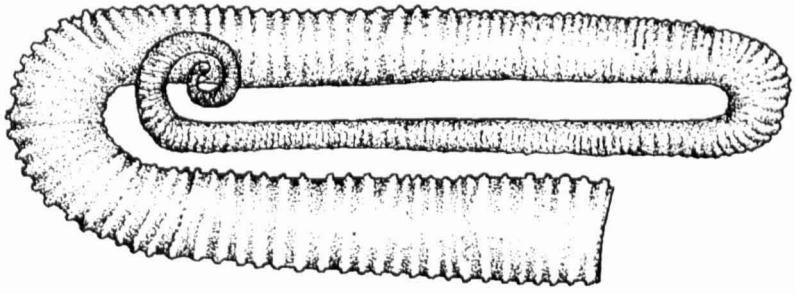


Figure 6.8a

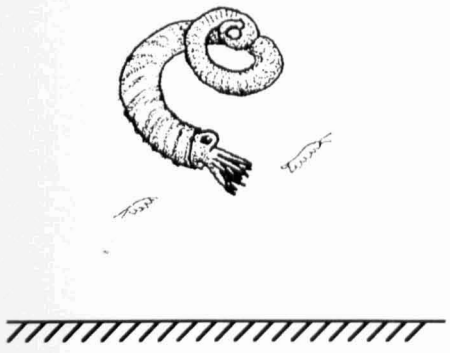


Figure 6.8b

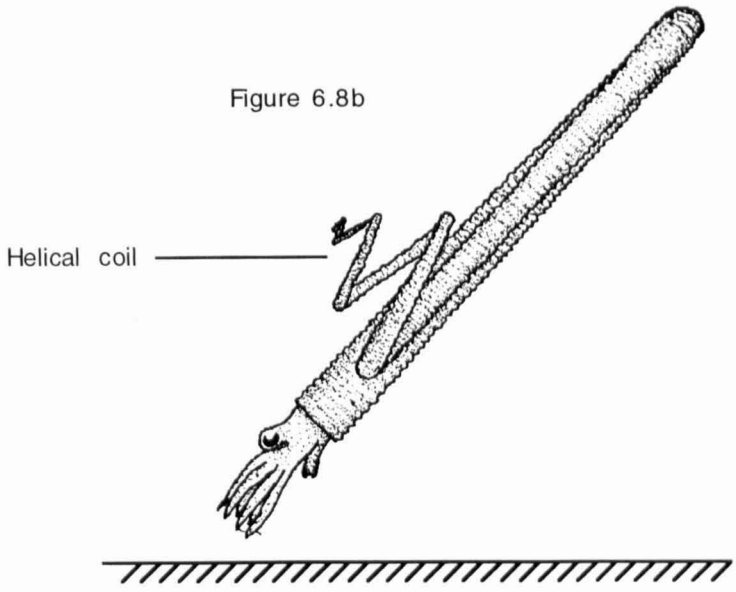
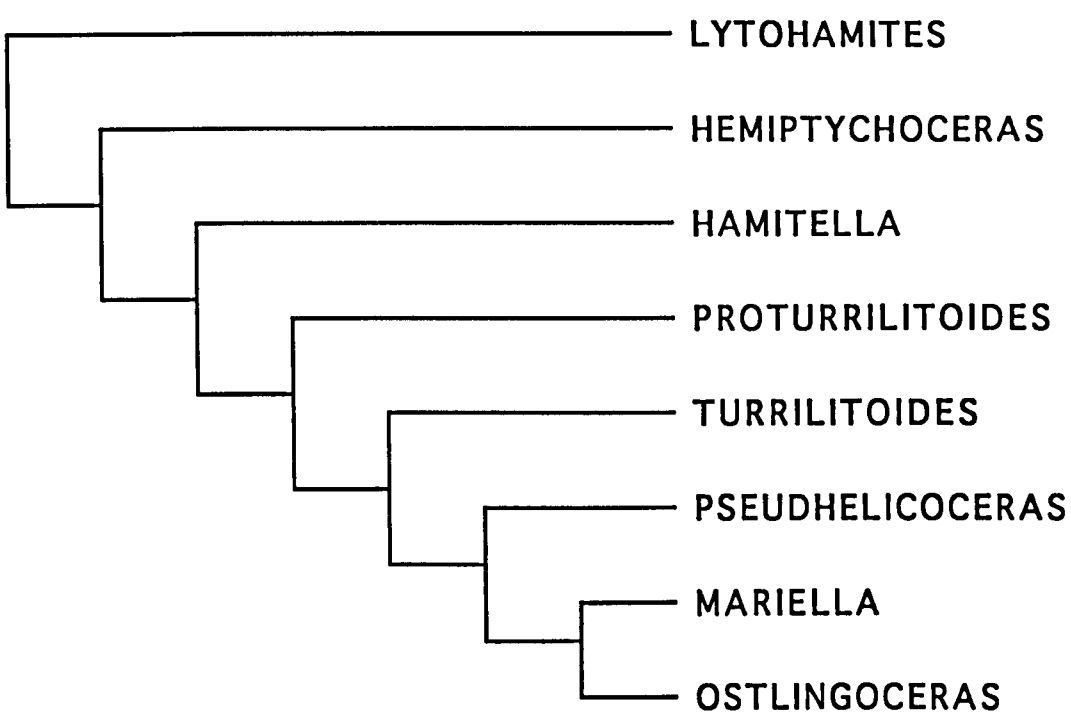


FIGURE 6.7: *Hamites tenuis* is a hamiticonic hamitid with the planar coil and first shaft slightly angled with respect to the plane in which the second and third shaft lie, as illustrated by these ventral (Figure 6.7a) and lateral (Figure 6.7b) views of a restored shell.

FIGURE 6.8: *Hamitella maximus* is a hamiticonic hamitid which contrasts with *Hamites tenuis* by having all three shafts in a single plane, but with the juvenile coil being helical. This is illustrated by these reconstructions of a juvenile (Figure 6.8a) and subadult (Figure 6.8b). The adults have three shafts, but for clarity a subadult with only two shafts is shown here.



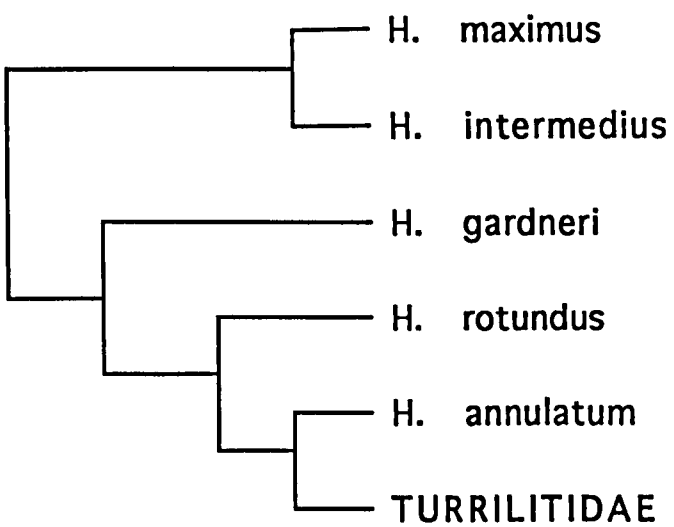


FIGURE 6.9: Cladogram showing the relationships of the genera *Lytohamites*, *Hemiptychoceras*, *Hamitella*, *Proturrilitoides*, *Turrilitoides*, *Pseudhelicoceras*, *Mariella*, and *Ostlingoceras*.

FIGURE 6.10: Cladogram showing the relationships of the species *Hamitella annulatum*, *H. gardneri*, *H. intermedius*, *H. maximus*, and *H. rotundus*. with the Turrilitidæ.

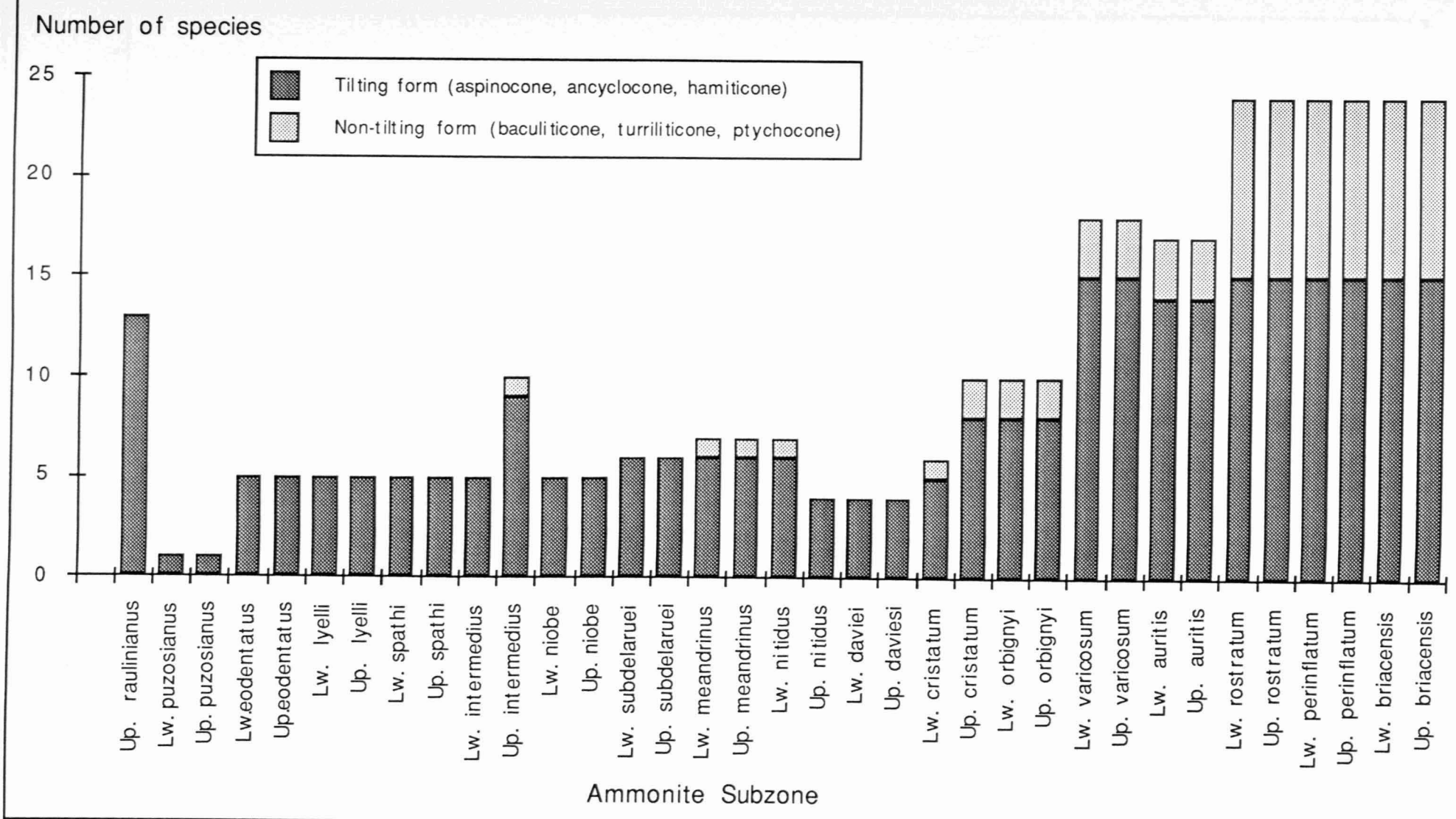


FIGURE 7.1: Relative numbers of tilting and non-tilting species of heteromorph ammonite through the Albian in South-East England based upon Spath (1923-1943), Casey (1961, 1966), and Cooper & Kennedy (1977) but with reference to the species revisions presented in this thesis. The numbers of species of each functional morphotype recorded from each ammonite subzone.

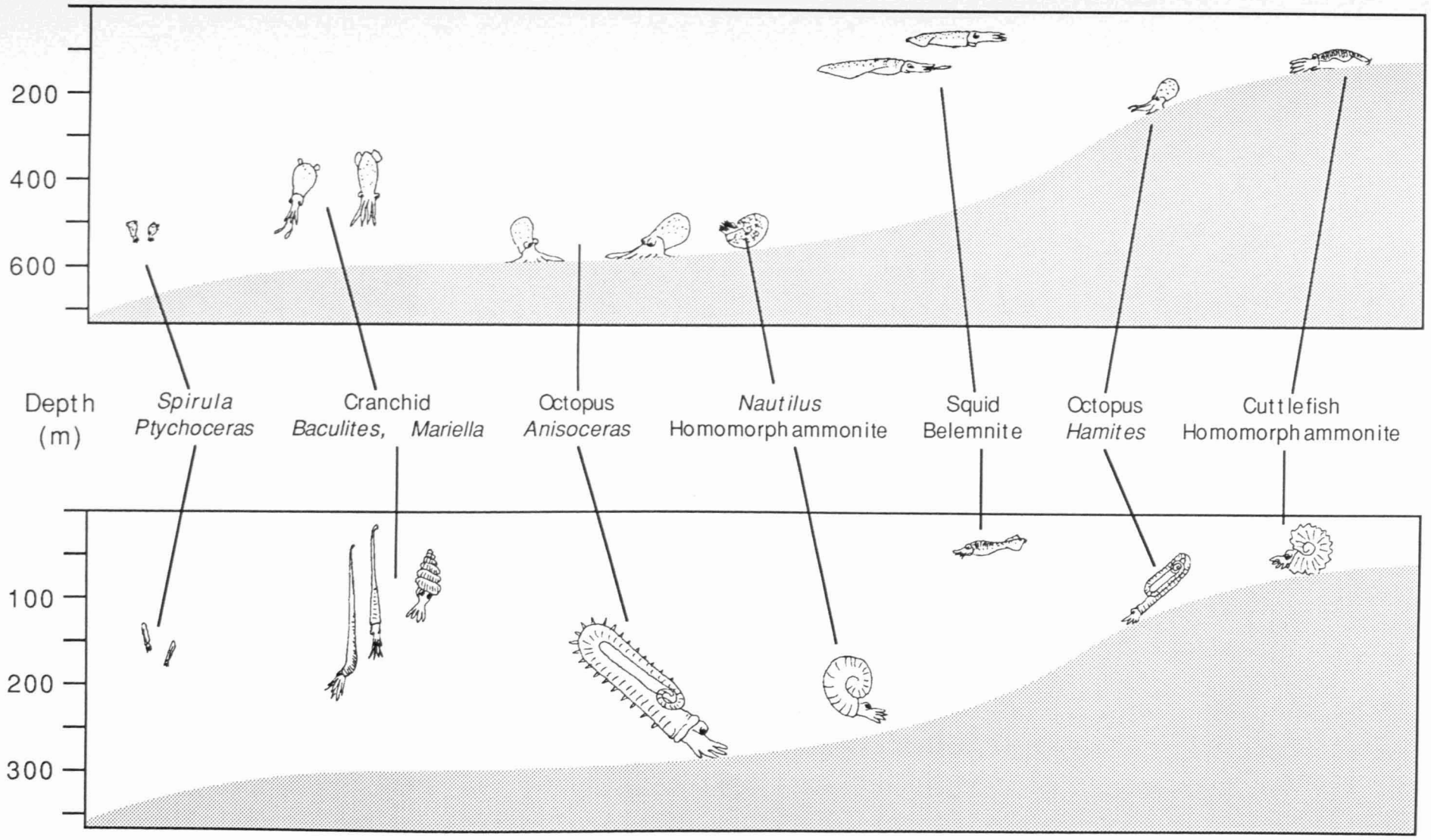


FIGURE 7.2: Comparison between modern and Albian cephalopods.

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A new cheilostome bryozoan genus pseudoplanktonic on molluscs and algae

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Abstract. The little-known bryozoan *Membranipora eburnea* HINCKS is redescribed and designated the type species of the new genus *Jellyella.* The twinned ancestrula of this malacostegan-grade cheilostome places it within the Membraniporidae, along with *Membranipora* and *Biflustra. Jellyella* is distinguished by the presence of intricately branched processes (spinules) projecting into the zooidal chambers, and a calcitic skeletal ultrastructure of transversely arranged, elongate spindles. The "Gulf weed bryozoan," *Membranipora tuberculata* (BOSC), is also assigned to the new genus as *Jellyella tuberculata.* Both species of *Jellyella* seem primarily to encrust floating substrates: based on available museum material, *J. eburnea* usually grows on drifting shells of dead individuals of the cephalopod *Spirula* but can also be found as an epizoan of the floating gastropod *Janthina* and on algae; *J. tuberculata* is normally an epiphyte of *Sargassum.* Collections of *Spirula* shells from beaches around the Indian, Pacific, and Atlantic Oceans are commonly encrusted by *J. eburnea* but very seldom by any other bryozoans. *Jellyella* is therefore interpreted as a rare example of a pseudoplanktonic genus among the typically benthic bryozoans.

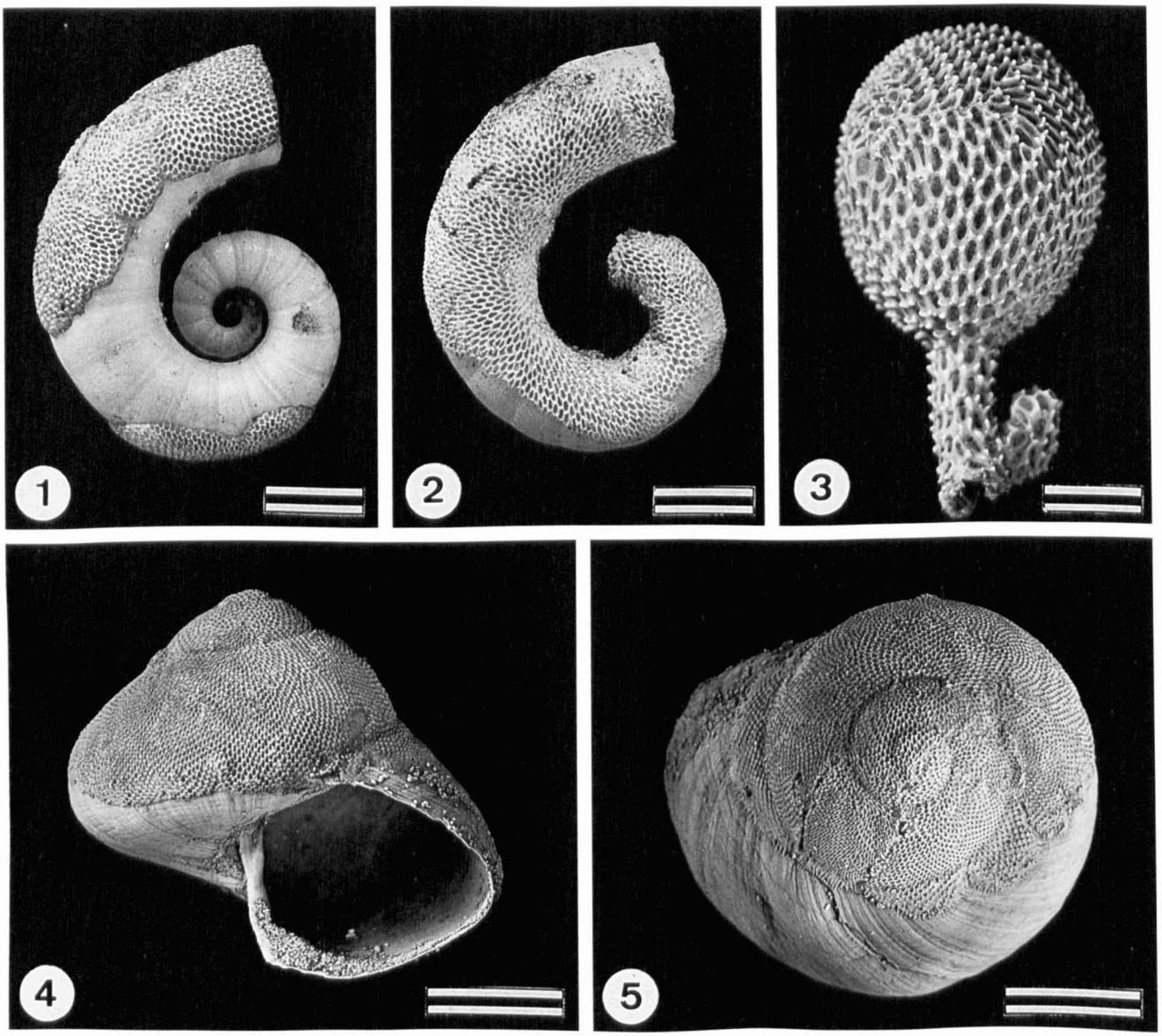
Additional key words: Membraniporidae, *Membranipora eburnea, M. tuberculata, Spirula, Janthina*

Bryozoans are typically benthic animals living as sessile components of sea-bed communities. However, they occasionally inhabit higher levels of the water column. Freshwater bryozoans often encrust floating substrates such as water lily leaves. A free-floating ctenostome bryozoan has recently been discovered in the Antarctic (Peck et al. 1995), and a pseudoplanktonic lifestyle is achieved by some marine species whose colonies become attached to floating or swimming substrates. For example, bryozoans may grow on floating algae, particularly *Sargassum,* and plastic artifacts (Winston 1982b; Stevens et al. 1996). Various species of bryozoans have been found living as epizoans of marine turtles (e.g., Frazier et al. 1992), seasnakes (e.g., Key et al. 1995), and the cephalopod *Nautilus* (e.g., Landman et al. 1987). Pseudoplanktonic bryozoans have also been recorded encrusting dead shells of another cephalopod, *Spirula* (Dauphin 1979a,b), but have never been thoroughly described.

The current study suggests that *Spirula* shells (Figs. 1, 2) provide a principal substrate for the cheilostome species originally described as *Membranipora eburnea* by Hincks (1891). The same bryozoan species is also here recorded for the first time encrusting shells of the planktonic gastropod *Janthina* (Figs. 4, 5), apparently while the snail was alive. Morphological similarities between *M. eburnea* and *M. tuberculata* (Bosc 1802), a species usually living as an epiphyte of floating *Sargassum* (Fig. 3), suggest that the species are congeneric with one another but not with the type species of *Membranipora, M. membranacea.* A new genus is therefore proposed for these two pseudoplanktonic bryozoans.

Shells of the cephalopod *Spirula spirula* LINNAEUS 1758 can be found in considerable numbers in beach drift in many parts of the world. *Spirula,* the only truly oceanic sepioid, has an open spiral shell, up to about 2 cm in diameter, with simple concave sutures. The shell is internal, occupying the hindmost end of the animal, whose normal orientation when living is with the head down and shell upwards (Bruun 1943), the shell providing neutral buoyancy (Denton & Gilpin-Brown 1973). *Spirula* is thought to be a vertically migrating predator. Juveniles commonly occur below 1000 m; adults may rise to depths of less than 100 m (Bruun 1943, 1955). Populations are concentrated around the Gulf of Mexico and Canary Islands in the North Atlantic; from the Cape of Good Hope along the East African coast in the Indian Ocean; and from

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Figs. 1, 2, 4, 5. *Jellyella eburnea* (Hincks). **Fig. 1.** Colonies encrusting a *Spirula* shell from Port Elizabeth, South Africa. NHM 1996.1.26.44. Scale bar, 5 mm. **Fig. 2.** Colonies encrusting a *Spirula* shell with broken umbilicus from Western Australia. NHM 1996.1.26.1. Scale bar, 5 mm. **Figs. 4, 5.** Large colonies encrusting the apical region of a *Janthina* shell from Port Elizabeth, South Africa. NHM 1996.1.26.43. Scale bars, 10 mm. **Fig. 3.** *Jellyella tuberculata* (Bosc). Colony encrusting a *Sargassum* bladder from the Atlantic. NHM 1996.1.26.60. Scale bar, 3 mm.

the south Indian coast, through the South-East Asian islands to the west coast of New Zealand in the Pacific (Clarke 1966). Bruun (1955) considered the distribution of *Spirula* to be limited by the 10° C thermocline at 400 m depth. After death, the shell becomes dissociated from the cadaver, and may float at the sea surface, sometimes accumulating a pseudoplanktonic biota (Dauphin 1979a,b; Donovan 1989).

The genus *Janthina* includes five species of pteneoglossid prosobranch gastropods (Laursen 1953). Janthinids are characterized by a holoplanktonic lifestyle, facilitated by the production and use of a bubble-raft, and are all thought to be predators, feeding on hydrozoan cnidarians such as *Velella* (Graham 1971). Epizoans of *Janthina* have been recorded by Laursen (1953) and Wilson & Wilson (1956). Laursen found a cluster of *Lepas* sp. attached to the apex of the gastropod shell, and egg ribbons of the opisthobranch *Glaucus atlanticus*. Wilson & Wilson also found *Lepas*, identified as *L. pectinata*, although these were growing

from a point on the columnella near the aperture, and colonies of the hydroid *Laomeda geniculata.*

The objectives of the current paper are: (1) to describe the skeletal morphology and revise the systematics of *Membranipora eburnea* HINCKS, placing it in the new genus *Jellyella* together with *Membranipora tuberculata* BOSC; (2) to recognize *Jellyella eburnea* as a widely distributed but largely overlooked fouling organism of floating *Spirula* and *Janthina* shells in the Indian and Pacific Oceans especially; and (3) to identify *Jellyella* as an ecologically unusual clade of bryozoans with a mode of life that appears to be predominantly pseudoplanktonic.

Methods

The impetus for this study came from a collection of bryozoan-encrusted shells of *Spirula* made in Western Australia during 1995 by A.S. Gale. Additional material was obtained by searching the bryozoan and cephalopod collections in the NHM (The Natural History Museum, London), FMNH (Field Museum of Natural History, Chicago; courtesy of J. Voight), and from Y. Dauphin (Université d'Orsay, Paris). All available specimens were dry.

For low resolution scanning electron microscopy of uncoated specimens (Figs. 6–15), we used an ISI ABT-55 microscope equipped with an environmental chamber and a back-scattered electron detector (see Taylor 1986; Taylor & Jones 1996). Specimens with membranes dried and damaged but partly intact were scanned *in situ* on their substrates. NaOCl-bleached specimens (treated with diluted sodium hypochlorite laundry bleach) were also scanned to give clearer images of the skeleton. Bleaching usually caused colonies to detach from their substrates allowing undersides to be examined (e.g., Fig. 13). For high resolution scanning electron microscopy of bleached, coated specimens (Figs. 16–19) for skeletal ultrastructure, we used an Hitachi S-800 field emission microscope.

Mineralogical compositions of skeletons were determined using an X-ray diffractometer.

Taxonomy

Family Membraniporidae BUSK 1852

Remarks. The Membraniporidae as here understood is a monophyletic family of malacostegine cheilostomes characterized by the apomorphy of a twinned ancestrula (and associated pattern of larval metamorphosis, see Stricker 1989). Hitherto two genera—*Membranipora* and *Biflustra*—have been assigned to the Membraniporidae, although some authors (e.g., Cook 1968) have placed *Biflustra* in synonymy with *Membranipora.* (*Nitscheina* CANU 1900 is an objective junior synonym of *Membranipora*; see Borg 1931). *Conopeum* is also sometimes included in the Membraniporidae but this genus lacks the diagnostic membraniporid apomorphy of a twinned ancestrula (Figs. 12, 13, 15) and is better placed in the paraphyletic Electridae STACH, pending a satisfactory subdivision of this family into monophyletic groupings.

The family Membraniporidae is normally attributed to Busk (1854). However, the name was first published as a valid indication by Busk (1852), the same year that d'Orbigny (1852: 217) apparently published the family Biflustridae, which is here placed in synonymy with Membraniporidae.

Jellyella new genus

Type species. *Membranipora eburnea* HINCKS 1891.

Other species. *Flustra tuberculata* BOSC 1802; *Membranipora* sp. of Winston (1982a).

Diagnosis. Membraniporidae with moderately to well-developed gymnocyst produced into tubercles and/or spines proximally and around the opesium; cryptocyst absent or forming a narrow, pustulose proximal shelf; lateral vertical walls occasionally with uncalcified bands; spinules typically numerous, elaborately branched; plectriform apparatus sometimes present; skeletal wall ultrastructure dominantly of elongate spindle-shaped crystallites arranged transversely to wall growth direction; skeleton calcitic; typically pseudoplanktonic.

Derivation of name. After Eliza C. Jelly in recognition of her important contributions to bryozoology during the last century (Jelly 1889).

Remarks. Species of *Jellyella* have more extensive gymnocysts than do most species of either *Biflustra* or *Membranipora,* and there are differences in the ultrastructure and sometimes mineralogy of the skeletal walls. These walls are spherulitic in *Membranipora,* laminar in *Biflustra,* but comprise elongate, transversely disposed spindles in *Jellyella.* Whereas *Membranipora* has an aragonitic skeleton (Bone & Wass 1990; confirmed herein), the skeletons of both *Biflustra* and *Jellyella* are calcitic. The type species of *Membranipora, M. membranacea* (Linnaeus 1758), is also distinguished by the presence of "tower cells," columnar kenozooids formed through modification of autozooids in late ontogeny (Cook & Chimonides 1980). *Biflustra* is more heavily calcified than *Jellyella* and has an extensive shelf-like proximal cryptocyst.

Soft part anatomy, with the exception of the dried operculum and frontal membrane, is unknown in the type species of *Jellyella.* However, in colonies of *J.*

tuberculata from Ghana, Cook (1985) observed that the zooids had 12 to 14 tentacles, each about 0.20 mm long, and which were protruded only as far as their bases. The larva in the type species is unknown but that of *J. tuberculata* is *Cyphonautes sargassi* LOHMANN 1904.

Jellyella eburnea (HINCKS 1891)

1891 *Membranipora eburnea* HINCKS, p. 289, pl. 7, fig. 5.
1898 *Membranipora tehuelcha* D'ORBIGNY var. *intertuberculata* WATERS, p. 676, pl. 48, figs. 1–2.
?1921 *Membranipora eburnea* HINCKS: Marcus, p. 7, fig. 4.
1979a *"Membranipora" eburnea* HINCKS: Dauphin, p. 175, pl. 2, figs. A, B, G, I, J; pl. 3, figs. e, f.
1979b *"Membranipora" eburnea* HINCKS: Dauphin, p. 343, fig. 4 h, i; fig. 5 a, c, f.
1996 *Membranipora eburnea* HINCKS: Stevens et al., pl. 1, fig. D.

Type specimens. Hincks' original description (1891) provides few clues useful in pinpointing the type material of this species. The figure is too stylized to be matched with a real specimen, and the only potentially useful information given is *"Loc.* ?Queensland (*Miss Jelly*)." The Hincks Collection at the NHM includes only one cavity slide (99.5.1.578) labeled *Membranipora eburnea* HINCKS, with no locality or collector data. This contains two dried pieces of algae, each encrusted by one colony. Zooidal morphology in the larger and better preserved colony (Fig. 8) corresponds fairly well with Hincks' description and figure of the species. The smaller colony is heavily abraded but is likely also to be of the same species. The species catalog for the Recent bryozoan collections states that specimen 99.5.1.578 "seems to be from Jelly." Therefore, the two colonies registered as 99.5.1.578 are interpreted as syntypes. The larger colony is herein chosen as the lectotype and the smaller the paralectotype of *J. eburnea.*

Other material (precise locality information is lacking for most specimens). NHM 1996.1.26.1 to 1996.1.26.9, Western Australia, A.S. Gale Collection, 1995; 1996.1.26.10, South Africa, Ponsonby Collection; 1996.1.26.11, Green Island, Great Barrier Reef, Queensland, Australia, M. Hill Collection, 1964; 1996.1.26.12, no locality, Bowerbank Collection; 1996.1.26.13, no locality, B.R. Lucas Collection; 1966.1.26.14 to 1966.1.26.16, Deuba, Fiji, G.S. & M.M. Robinson Collection, 1968-71; 1996.1.26.17, Mombasa Beach, Kenya; 1996.1.26.18, beach specimen, Kenyan coast, F. Pim Collection, 1986; 1996.1.26.19 to 1996.1.26.23, Kanumua (Ile des Pins), New Caledonia, Y. Dauphin Collection; 1996.1.26.24 to 1996.1.26.30, Phare Amédée, New Caledonia, Y. Dauphin Collection; 1996.1.26.31 to 1996.1.26.36, Noumea, New Caledonia, Y. Dauphin Collection; 1996.1.26. 37 to 1996.1.26. 39, Tuliar, Madagascar, Y. Dauphin Collection; 89.1.1.1, 1996.1.26.40 to 1996.1.26. 58, Port Elizabeth, South Africa. FMNH 83566a, Miami Beach, Florida.

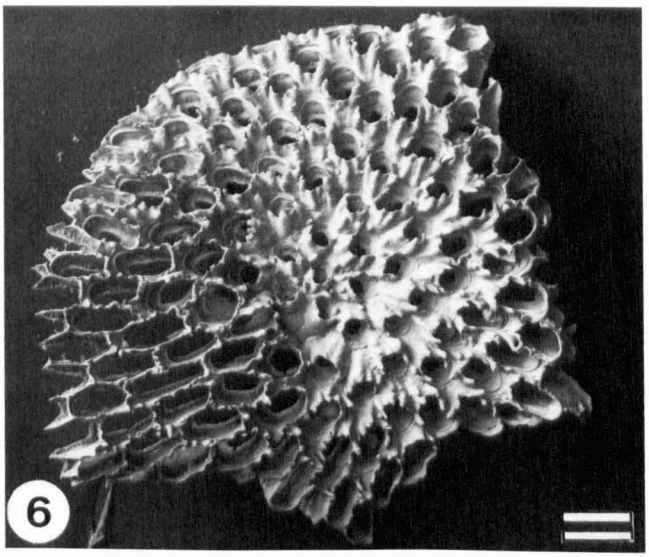
Description. Separate descriptions are provided for the type and other material because of contrasts in substrates, specimen condition, and observable morphological characters.

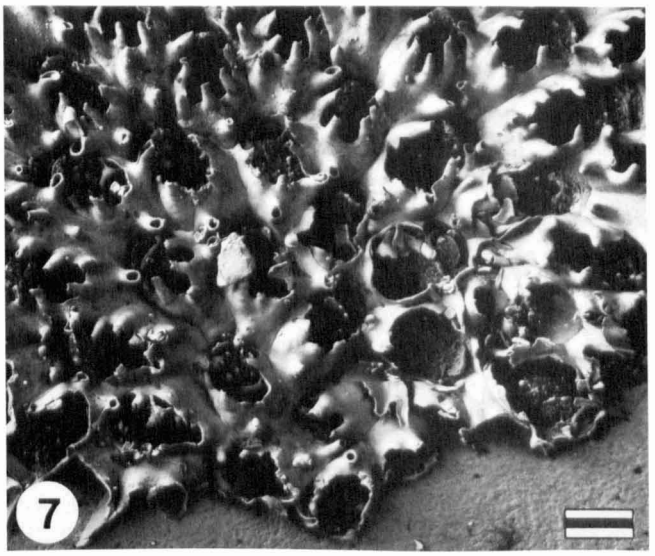
1. Lectotype and paralectotype: Colonies encrusting algal fronds, cracked and partly abraded. Lectotype colony 5.3 mm in maximum diameter, asymmetrical, without a circumferential growing edge, the two lateral edges of the colony not joining behind the colony origin. Paralectotype colony 2.3 mm in maximum diameter with a circumferential growing edge and a more or less central origin. Both lectotype and paralectotype are elongated at right angles to the initial growth direction of the colonies. Ancestrular area destroyed in lectotype, heavily worn in paralectotype but outline shape of twinned ancestrula still visible, the basal lengths of the two unequal-sized zooids being about 290 μm and 350 μm and their basal widths 150 μm and 180 μm.

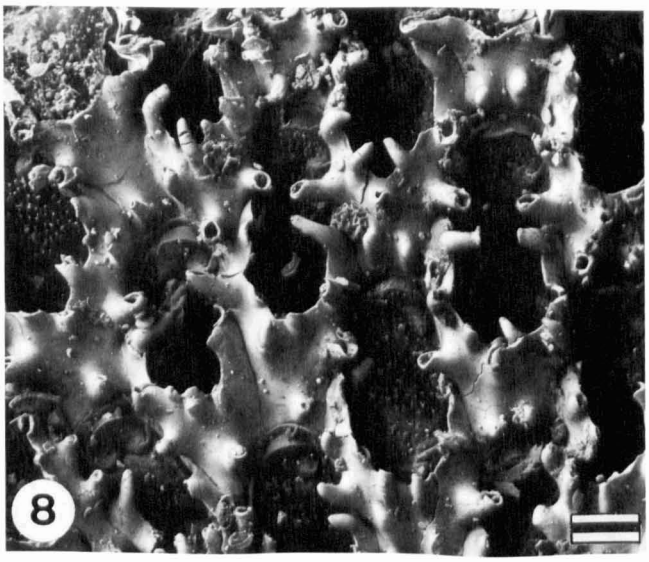
Autozooids elongate rhombic (Fig. 8), from 410 to 600 μm in length and 230 to 300 μm in greatest width, arranged approximately in quincunx. Proximal gymnocyst occupying one-third to one-half of the frontal length, tapering distally along lateral margins of opesium and lacking altogether in distal third of zooid;

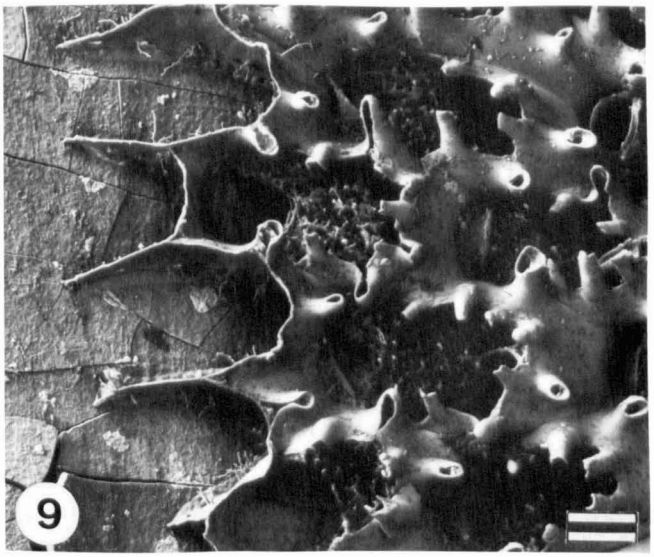
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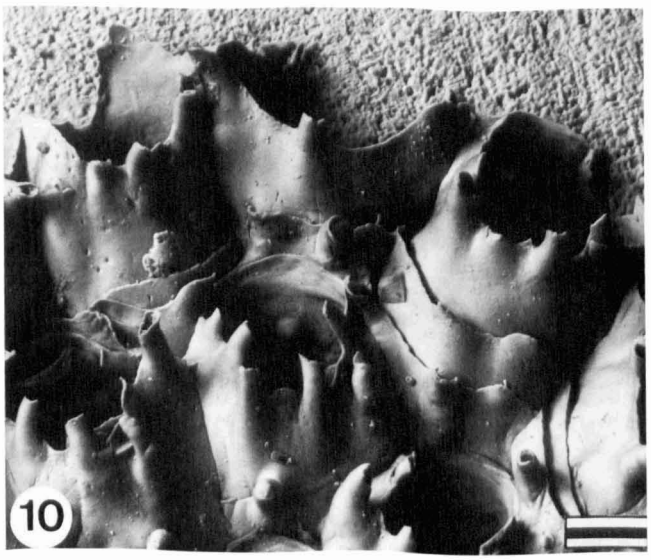
Figs. 6–11. *Jellyella eburnea* (HINCKS). Back-scattered SEMs of uncoated specimens. **Fig. 6.** Bleached colony detached from a *Spirula* shell; typically spinose zooids on the right and an unusual patch of lightly calcified zooids on the left. Western Australia. NHM 1996.1.26.7. Scale bar, 500 μm. **Fig. 7.** Early growth stages of a colony with a spiral growth pattern. Queensland. NHM 1996.1.26.11. Scale bar, 200 μm. **Fig. 8.** Group of unbleached zooids from the lectotype. ?Australia. NHM 99.5.1.578. Scale bar, 100 μm. **Fig. 9.** Growing edge of the colony in Fig. 7. Developing gymnocystal spines and spinules are visible in the new buds. Scale bar, 100 μm. **Fig. 10.** Growing edge of a different colony showing evidence of skeletal repair. Madagascar. NHM 1996.1.26.37. Scale bar, 100 μm. **Fig. 11.** Etchings on the surface of a *Janthina* shell from which a bryozoan colony has been removed by bleaching. Each shallow pit corresponds to the basal window of a bryozoan zooid. South Africa. NHM 1996.1.26.40, Scale bar, 200 μm.

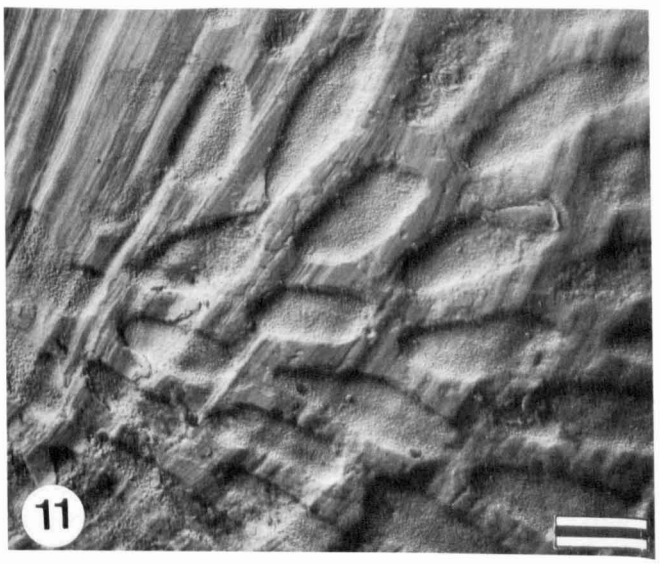

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calcification smooth; surface folded into rucks and spines that can be seen forming in zooids at growing edge. Spines variably developed, irregular, hollow, open-ended or closed, blunt, curved, up to 100 μm long; typically one or two short tubercle-like, distally curved spines near proximal end of gymnocyst; about 8–12 longer spines surrounding and overarching the opesium in zooids within zone of astogenetic repetition. Cryptocyst apparently lacking. Remnants of opercula visible at distal ends of some zooids, crescent-shaped, about 140 μm in maximum width, narrower along proximal hingeline. Surface of frontal membrane and operculum covered by widely spaced small pustules.

No ovicells, avicularia, or other heterozooids.

2. Other material: Colonies encrusting shells of *Spirula* or *Janthina,* up to 15 mm in maximum diameter, initially fan-shaped but developing a circumferential growing edge by about the 30-zooid stage following coalescence of lateral lobes of growing edge behind ancestrula (Fig. 6). Unequal growth of lateral lobes sometimes resulting in a spiral pattern of zooids around ancestrula (Fig. 7). Giant buds occasionally present, associated with prolonged zones of ontogenetic change. Ancestrular complex comprising two complete twinned zooids together with the proximal parts of one to three additional zooids budded between the twins (Fig. 12). Complex defined most clearly on colony underside (Fig. 13), subcircular, slightly elongated transversely, 380–440 μm long by 430–510 μm wide, bounded by a distinct furrow. Twinned ancestrular zooids, each longer than wide, ovoidal in frontal outline, joined proximolaterally for a little more than half of their length, long axes diverging at about 60°; basal wall almost entirely uncalcified; gymnocyst occupying at least two-thirds of frontal length, convex, proximally horizontal, distally sloping; proximal mural rim gently folded, usually without clear tubercles or spines except for a few colonies; opesium ovoidal, directed slightly distally; spinules absent.

Autozooids indistinctly rhombic in frontal outline, longer than wide, arranged approximately quincunxially. Basal walls invariably uncalcified apart from a marginal rim about 70 μm wide (rarely 300 μm) surrounding a basal window; substrate may be etched beneath basal window (Fig. 11); fissures representing cuticular insertions visible between adjacent zooid rows on colony undersides, lacking between zooids within a row. Gymnocyst well developed, proximal gymnocyst generally occupying about one-half to one-third of the frontal area except in skeletally immature zooids close to the growing edge, tapering distally and absent at distal end of zooids; smoothly calcified surface fluted or folded into rucks, tubercles, or spines variable in prominence and number (Fig. 9); spines short, hollow, sometimes open-ended (Fig. 8) but more often rounded and terminally closed, hook-like, those adjacent to the opesium bending over frontal membrane but not reaching the mid-line, occasionally with transverse furrows; one or sometimes more distally directed tubercles present in proximal part of gymnocyst, often originating along border with proximal neighboring zooid, very occasionally longer and spine-like. Cryptocyst lacking. Opesium ovoidal, longer than wide. Operculum crescent-shaped, about 130–150 μm wide, with a marginal sclerite. Vertical walls forming a narrow shelf at distal end of zooid, and often with minor buttresses in corners of zooids and at junctions with basal walls. Pore chambers lacking. Simple pores present in lateral vertical walls separating zooidal series, located close to basal walls, about 25 μm in diameter. Multiporous septulae developed in transverse vertical walls adjacent to basal walls; individual pores about 1 μm in diameter, centered within depressions separated by slight buttresses, sometimes two or more pores sharing the same depression. Spinules (Fig. 16) arising from lateral vertical walls and underside of gymnocyst in zooids close to growing edge but apparently broken-off or resorbed in more mature zooids; profusely and complexly branched, antler-like, very fine, about 5–10 μm in diameter at the base, tapering to less than 0.5 μm diameter at the tips; present from the first post-ancestrular generation onwards.

No ovicells or avicularia. Kenozooids present in areas of crowding, particularly where growing edges coalesce.

Skeletal walls largely comprising elongate spindle-shaped to fibrous crystallites, very small (~1 μm long by 0.2 μm wide) and seemingly disorganized in first-formed parts of walls (Fig. 17), becoming larger (up to 0.5 μm wide) and orientated transverse to wall growth direction in older walls (Fig. 18); fibers visible on undersides of basal walls meet in a chevron pattern where they converge on grooves formed by cuticular insertions between zooidal rows. Thin laminar layer (Fig. 19), apparently consisting of coalesced subhexagonal tablets, may overlie fibers and line zooidal chambers. Skeleton entirely of calcite.

Measurements. See Table 1.

Remarks. Subsequent to Hincks' original description of *J. eburnea* in 1891, this species name almost disappeared from the bryozoan literature apart from a brief citation by Waters (1898, p. 671) and a questionable record from Sumatra (Marcus 1921). In two papers on *Spirula,* however, Dauphin (1979a,b) figured colonies of *J. eburnea* from New Caledonia and Mauritius which had been correctly identified by E. Buge. Buge hinted at a possible generic re-assignment to

Table 1. Zooid dimensions measured in *Jellyella eburnea.* Each parameter was measured in 10 zooids from the epiphytic lectotype and one colony from Western Australia (Gale Collection) encrusting a *Spirula* shell.

		Mean ± SD (μm)	Range (μm)
zooid length	lectotype	510 ± 70	410–600
	W. Aust.	610 ± 30	570–630
zooid width	lectotype	270 ± 20	230–300
	W. Aust.	280 ± 30	230–320
opesium length	lectotype	330 ± 50	260–420
	W. Aust.	530 ± 20	480–570
opesium width	lectotype	180 ± 20	150–200
	W. Aust.	220 ± 20	200–260

Electra but the presence of a twinned ancestrula (Figs. 12, 13) precludes placing *J. eburnea* in this genus. Gordon & Parker (1991b, p. 119) suggested that *J. eburnea* may belong to their new genus *Mychoplectra* (type species *Lepralia pocula* HUTTON). However, *Mychoplectra* is characterized by the presence of a plectriform apparatus, a comb-like structure projecting down into the zooidal cavity from close to the proximal edge of the opesium (Gordon & Parker 1991a). A plectriform apparatus is clearly absent in *J. eburnea,* although it may exist in some specimens of *J. tuberculata.* Nevertheless, a fairly close relationship between *J. eburnea* and the type species of *Mychoplectra* may be possible to judge from similarities in zooidal morphology. Unfortunately, the ancestrula has not been described in *Mychoplectra.* Gordon & Parker (1991b) assigned their genus to the Electridae, implying a simple ancestrula, whereas *J. eburnea* has a twinned ancestrula and clearly belongs to the Membraniporidae. Carbonate mineralogy and skeletal ultrastructure are also unknown in *Mychoplectra.* More recently, Stevens et al. (1996) have recorded and figured one colony of *J. eburnea* encrusting a drift plastic bottle from a beach in northern New Zealand.

The formally named species showing greatest resemblance to *J. eburnea* is the widespread *"Membranipora" tuberculata* (BOSC), commonly found as an epiphyte of floating *Sargassum* (Fig. 3) and here re-assigned to *Jellyella.* Like that of *J. eburnea,* the proximal gymnocyst of *J. tuberculata* is generally well developed; typically, a pair of large tubercles (Fig. 14), which may coalesce, are developed on the proximal gymnocyst (Cook 1968, 1985; Marcus 1937; Osburn 1950; Mawatari 1974; Voigt 1993). These are reminiscent of the tubercles and gymnocystal spines of *J. eburnea.* Branched "spinous processes" (denticles or spinules) project into the zooidal chamber from the walls of the zooid (see Gordon & Parker 1991a; described as "cervicorn spines or rays" by Waters 1898, p. 675). However, *J. tuberculata* has a cryptocyst that forms a distinct shelf in most specimens (Cook 1968; Mawatari 1974) and may be pustulose (Fig. 14) or non-pustulose (compare Ristedt 1977, pl. 1, figs. 3 and 4). The comb-like spines (plectriform apparatus) present in some zooids of *J. tuberculata* (Gordon & Parker 1991a) have not yet been found in *J. eburnea.* The ancestrular complex of *J. tuberculata* (see Hastings 1930; Maturo 1957; Muñoz et al. 1991) is very similar to that of *J. eburnea* (compare Figs. 13 and 15).

The species described by Winston (1982a, p. 120) as *Membranipora* sp. is probably closely related to *J. eburnea.* This un-named species from the east coast of Florida was found only on wood and plastic objects in beach drift. The proximal gymnocyst is not as well developed as that in typical *J. eburnea,* and Winston mentions that, unlike those in *J. eburnea,* the ends of the gymnocystal spines may be bifid, but other aspects of skeletal morphology are strikingly similar.

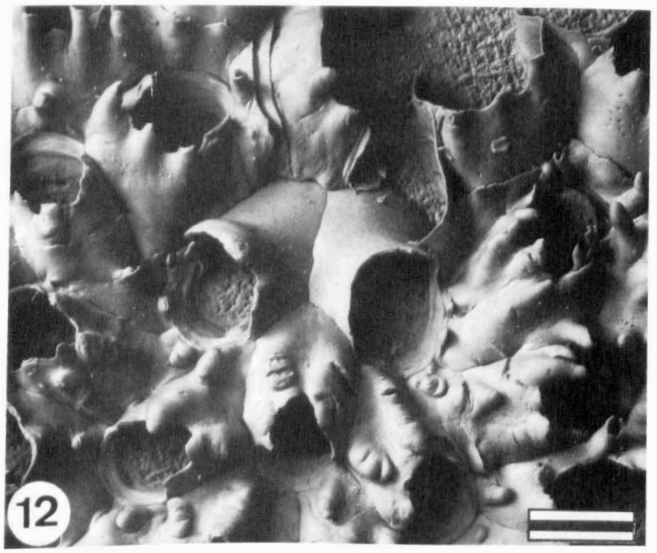
Variations in zooidal morphology occur among different populations of *J. eburnea.* In particular, the lectotype specimen has shorter zooids with proportionately longer gymnocysts than material from Western Australia, whereas colonies from Queensland and Madagascar have particularly well-developed gymnocystal spines, especially when compared to *Janthina*-encrusting colonies from South Africa. These variations, however, are typically less than astogenetic/microenvironmental variations which can be observed within single colonies (e.g., Fig. 6) and do not currently provide a useable basis for distinguishing more than one species.

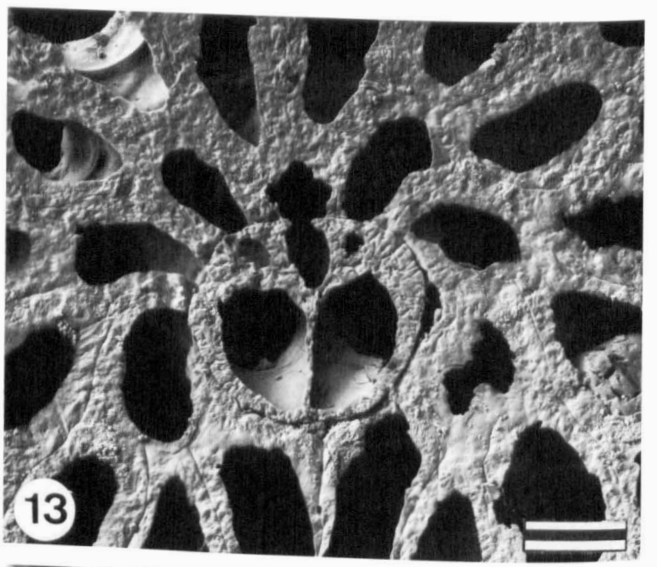
Discussion

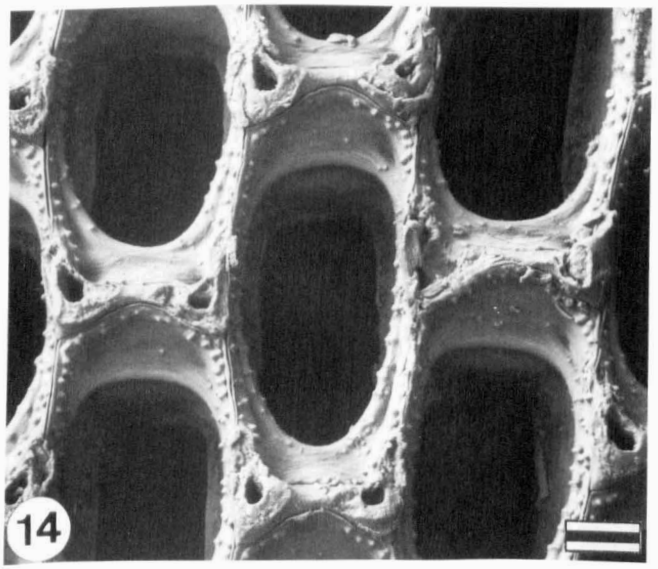
Morphology

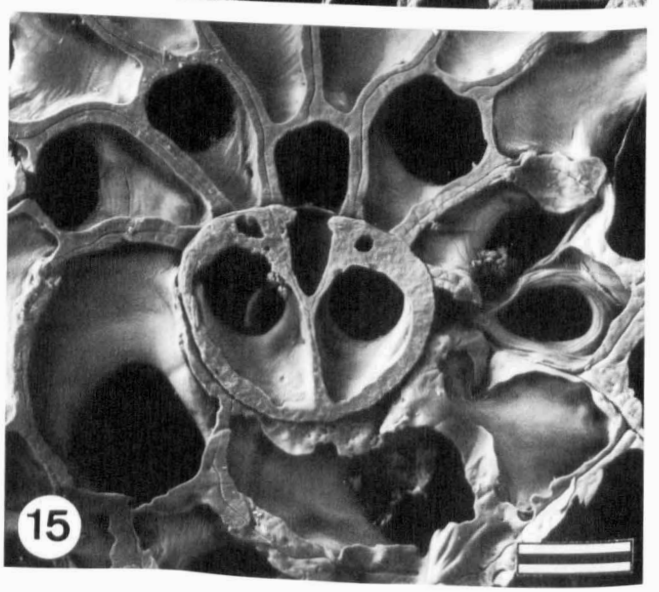
Jellyella is placed in the paraphyletic suborder Malacostegina. Malacostegans (i.e., cheilostomes with a cyphonautes larva) have a relatively low taxonomic diversity and lack the disparity in skeletal morphology found in ovicellate neocheilostomes: avicularia seldom occur in malacostegans, frontal walls are simple in structure, and a restricted range of colony-forms is developed (Taylor 1987). The recognition of the new genus *Jellyella* does not dilute this contrast appreciably. As is typical for malacostegans, the skeleton of *Jellyella* is comparatively uncomplicated, and polymorphic zooids are absent. However, the unusual spinules and gymnocystal spines, as well as the skeletal ultrastructure and mineralogy of the new genus, do deserve comment.

Spinules. Spectacular spinules (Fig. 16) project into the zooidal chamber from the lateral walls and the un-



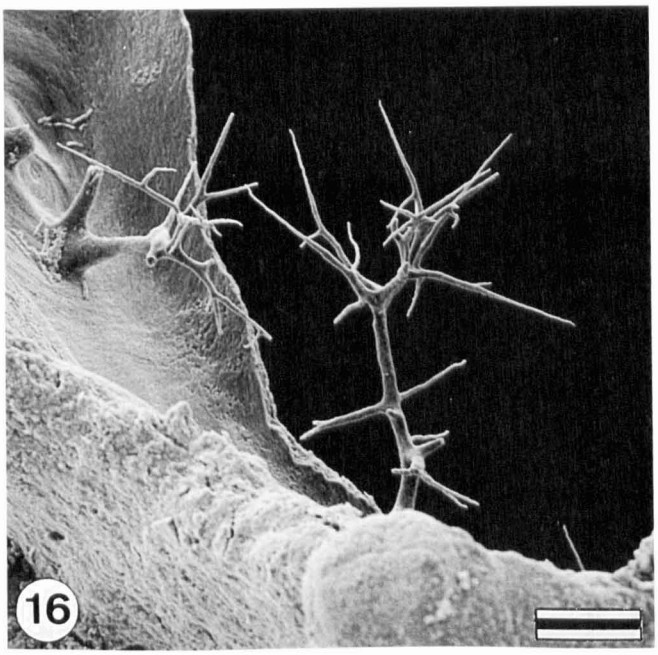


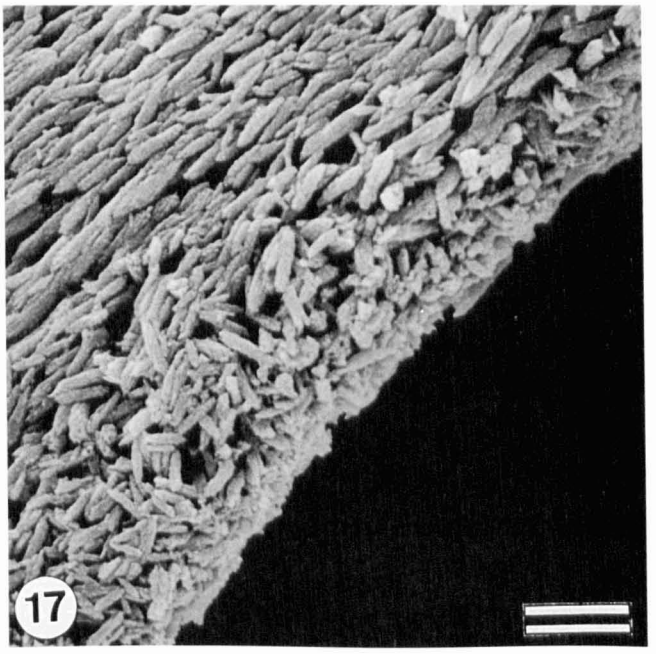


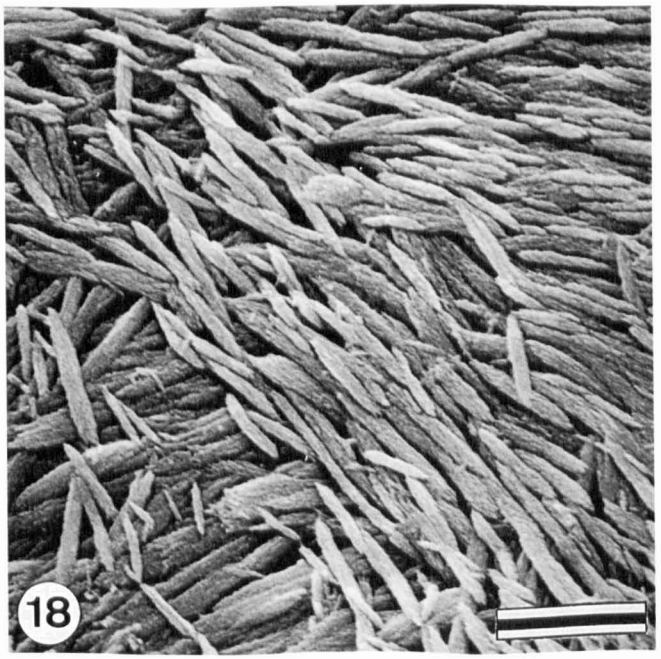


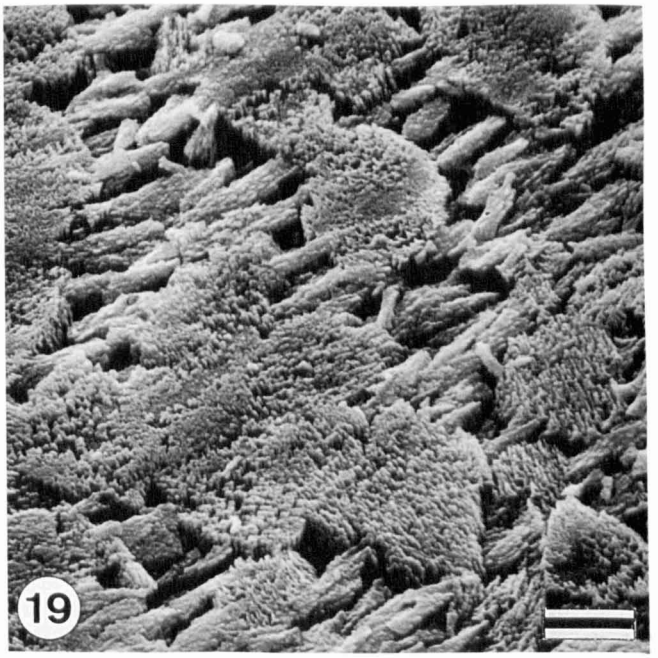
Figs. 12–15. Back-scattered SEMs of uncoated specimens. **Figs. 12, 13.** *Jellyella eburnea.* **Fig. 12.** Early growth stages showing twinned ancestrula (center). Distal is downwards. Madagascar. NHM 1996.1.26.37. Scale bar, 200 μm. **Fig. 13.** Ancestrular complex, clearly differentiated from the surrounding zooids, seen on underside of colony removed from its substrate by bleaching. Note windows in the basal walls of the zooids. Western Australia. NHM 1996.1.26.6. Scale bar, 200 μm. **Figs. 14, 15.** *J. tuberculata.* Atlantic. 1996.1.26.60. **Fig. 14.** Zooids with proximal tubercles which have been truncated by bleaching, showing the hollow interiors. Scale bar, 100 μm. **Fig. 15.** Underside of colony showing ancestrular complex. Scale bar, 200 μm.

derside of the gymnocyst in *J. eburnea.* These spinules are most clearly visible in new buds at the growing edges of colonies and do not generally persist in ontogenetically mature zooids where only their stumps are seen in chloroxed specimens. The disappearance of spinules during zooidal ontogeny may be due either to resorption or to breakage, the latter perhaps caused by the movement of the polypide. Similar structures were described by Voigt & Cook (1983) as "interior spinous processes" in the ascophoran cheilostome *Celleporina porosissima* HARMER 1957. Like the spinules of *J. eburnea,* those of *C. porosissima* are intricately branched and are most obvious in ontogenetically immature zooids. The functional significance of spinules in cheilostomes has been discussed by various authors (e.g., Harmer 1926; Ristedt 1977; Voigt & Cook 1983), most agreeing that they are likely to be defensive; however, similar mural spines in cyclostomes were regarded by Farmer (1979) as attachments for membranes and muscles.









Figs. 16–19. *Jellyella eburnea.* Secondary SEMs of coated specimens. Western Australia. **Fig. 16.** Branched spinules in a newly budded zooid. NHM 1996.1.26.8. Scale bar, 20 μm. **Figs. 17–19.** Skeletal ultrastructure. NHM 1996.1.26.9. **Fig. 17.** Distal growing edge of gymnocyst seen from the underside showing increase in crystallite size and transverse orientation of spindles with wall development. Scale bar, 2 μm. **Fig. 18.** Elongate spindles on the underside of the gymnocyst about 30 μm proximal to the growing edge of the wall. Many of the crystallites are partially dissociated from the wall, due to bleaching. Scale bar, 2 μm. **Fig. 19.** Basal wall of zooid seen from the interior showing thin zooecial lining of platey crystallites overlying main wall fabric of elongate spindles. Scale bar, 1 μm.

Gymnocystal spines. The crudely constructed gymnocystal spines (Figs. 7–10) of *J. eburnea* originate through folding of the proximal gymnocyst. Sometimes they develop into boss-like tubercles, but in other cases they form structures resembling gastropod varices. At their maximum development, these spines overarch much of the vulnerable frontal membrane of the zooid, suggesting an anti-predator role, as

with the spinules discussed above. If so, the variable development of gymnocystal spines among populations of *J. eburnea* could indicate differing levels of predation. The least spinose colonies encountered were epizoans of the living gastropod *Janthina* (see below), a host which may well have discouraged bryozoan predators. Conversely, some of the most spinose colonies show examples of skeletal repair of former growing edges (Fig. 10). Repair possibly followed damage inflicted by a predator which may attack growing edges of cheilostomes where the frontal membrane is thin (Ryland 1976, p. 423). Nothing is currently known about predators of *J. eburnea.* However, Cook (1985: p. 18, pl. 3A) found that a species of the nudibranch genus *Corambe* fed upon *J. tuberculata,* probably using a suctorial mechanism.

Skeletal ultrastructure and mineralogy. The skeletal walls of *J. eburnea* are composed predominantly of elongate spindle-like crystallites orientated transversely to the direction of wall growth (Fig. 17). Partly covering this fabric in some walls is a thin layer of platey crystallites (Fig. 19), seemingly only one crystallite thick and forming a zooecial lining. Ristedt (1977) described skeletal ultrastructures in various species of *Membranipora* sensu lato (including *Biflustra*) with which *J. eburnea* can be compared. He found three basic fabrics: (1) spherulitic with needles arranged perpendicularly to wall surfaces; (2) laminar with tablets flattened parallel to wall surfaces and with screw dislocations ("semi-nacre," see Weedon & Taylor 1995); and (3) a fabric of needles arranged more-or-less parallel to wall surfaces. Fabric 1 occurred in *Membranipora membranacea* (L.), the type species of *Membranipora,* as well as *M. tenuis* (Desor) and *M. arborescens* (Canu & Bassler). Fabric 2 characterized *"M." savartii,* the type species of *Biflustra,* and fabric 3 was found in *J. tuberculata.* Although Ristedt figured fabric 3 only in fractured walls, this fabric appears to be very similar if not identical to the fabric here found in *J. eburnea.* A correlation of skeletal ultrastructure with larger-scale characters of the skeleton in these two species corroborates the inference that they are closely related.

An analysis of bleached specimens using X-ray diffraction showed that *Jellyella eburnea, J. tuberculata,* and *Biflustra savartii* all have calcitic skeletons. However, *Membranipora membranacea* from the British Isles was found to have a skeleton of aragonite. Bone & Wass (1990: table 1) also found an aragonitic skeleton in Australian material of *M. membranacea.* The phylogenetic value of these mineralogical differences remains uncertain until more is known about mineralogical variations among cheilostome bryozoans. However, as calcite appears to be the primitive biomineral utilized by malacostegans, judging from the calcitic composition of early representatives of the "group," the aragonitic skeleton in *Membranipora* sensu stricto may be an autapomorphy of this genus.

Distribution and ecology

Evidence from the museum collections available suggests that *Jellyella eburnea* lives mainly as an encruster of the drifting shells of dead *Spirula* (Figs. 1, 2), although it is also found on algae and on shells of the snail *Janthina* (Figs. 4, 5). While this apparent preference for floating mollusc shells may have been exaggerated by the abundance of *Spirula* shells in museum collections, it is unlikely to be entirely a sampling artifact. Colonies of *J. eburnea* encrusting *Spirula* shells are known from Florida, South Africa, East Africa, Madagascar, Mauritius, Fiji, Australia, and New Caledonia. These data show that *J. eburnea* is very widely distributed on *Spirula* shells even though the data are largely derived from chance finds of beached shells collected for the sake of the molluscs rather than the bryozoans that encrusted them. A more complete picture of the geographical distribution of this potentially extremely abundant species would necessitate collections made specifically for bryozoans.

Dauphin found *J. eburnea* to be present on 36% of 300 *Spirula* shells from New Caledonia (Dauphin 1979a), and on 27% of 295 *Spirula* shells from Mauritius (Dauphin 1979b). It often shares this substrate with the stalked barnacles, *Lepas* spp. (see Dauphin 1979a; Donovan 1989) and with diatoms (Dauphin 1979a; pers. obs). However, with one exception, a single colony of a cheilostome (tentatively identified as *Electra tenella* Hincks) from Miami Beach, Florida (FMNH 83566), *J. eburnea* is the sole bryozoan found on the *Spirula* shells in the collections examined for this study or in those recorded in the literature. Colonies showed no obvious site pattern on these shells: they were found on both the umbilical and outer whorls, on the outer or inner sides of the whorls, and occasionally on the concave surfaces of septa.

The colonies of *J. eburnea* attached to *Janthina* shells all came from Port Elizabeth, South Africa, and were in a batch of specimens mixed with *Spirula* shells encrusted by *J. eburnea.* Unfortunately, it is not known whether the sample was from a single location, or whether it represented beach drift or was collected at sea. In each of the 10 encrusted *Janthina* shells the dominant bryozoan colony had its origin at the apex of the gastropod shell and extended down towards the aperture but did not extend onto the internal surfaces of the shell (Figs. 4, 5). This suggests encrustation of a living gastropod rather than a dead shell, an infer-

ence that is confirmed in one case by overgrowth and entrapment of bryozoan zooids by an advancing whorl of the gastropod shell (NHM 1996.1.26.41). Living individuals of *Janthina* hang downwards from a float consisting of mucus-coated air bubbles such that the shell apex is lowermost (Wilson & Wilson 1956, pl. 1, fig. 1). Therefore, the colonies developed preferentially on that part of the shell most distant from the float and the sea surface. This recruitment pattern (cf. Keough & Downes 1982) could result from early mortality of colonies in unfavorable locations, or larval settlement behavior. If the latter was the cause, then either negatively phototactic or positively geotactic crawling of the larvae on contact with the substrate could be involved. Positive geotaxis is thought to be more likely because, as Silén & Jansson (1972) have noted, the limited available evidence suggests that cyphonautes larvae, like those known in *J. tuberculata* and inferred for *J. eburnea,* are indifferent to light. Geotaxis occurs in some cheilostomes with coronate larvae (see Bishop 1988), but we have found no reported instances of a geopositive reaction (Ryland 1977; McKinney & McKinney 1993) of the sort inferred for colonies of *J. eburnea* encrusting *Janthina.* As noted above, there is no obvious pattern of distribution of colonies of *J. eburnea* on *Spirula* shells: the changing and variable orientation of drifting *Spirula* shells probably explains the lack of pattern even if the larvae settled consistently on the lowest part of the shell.

Two records of *J. eburnea* on brown algae are recorded: the type material of the species, which is thought to be from Australia, and some poorly preserved colonies, questionably of *J. eburnea,* from the Straits of Magellan (NHM 99.5.1.435). It is not known whether these algae were benthic or floating when encrusted. Artificial floating substrates may also be used by *J. eburnea*: Stevens et al. (1996) found one colony on a plastic bottle collected from a northern New Zealand beach.

The similarities in skeletal morphology discussed above imply that *J. tuberculata* is the closest relative of *J. eburnea.* These two species also show clear ecological and biogeographical parallels. Both are, or appear to be, predominantly pseudoplanktonic. *J. tuberculata* is best known as an epiphyte of the floating alga *Sargassum* (Fig. 3) and is sometimes called the "Gulf weed bryozoan" (Osburn 1950; Ryland 1974), although it may also be found in nearshore locations on various benthic algae (e.g., Winston & Eiseman 1980) and occasionally on other substrates including plastic, shells, stones, and pottery shards (Cook 1985; Stevens et al. 1996) and even sea snakes (Kropach & Soule 1973). Both species have very wide geographical distributions in tropical to warm temperate oceanic environments. *J. tuberculata* occurs in warm waters of the Atlantic, Indian, and Pacific Oceans, a pan-oceanic distribution paralleled by that of *J. eburnea.* As a genus, *Jellyella* can be characterized as species-poor but geographically widespread.

The larva of *J. eburnea* is either unknown or unrecognized but that of *J. tuberculata* is a long-lived cyphonautes called *Cyphonautes sargassi* LOHMANN. The absence of ovicells, the presence of a twinned ancestrula, and the general morphology of the skeleton (cf. Taylor 1987) are strong evidence that *J. eburnea* and "*Membranipora*" sp. of Winston (1982a) also possess cyphonautes larvae. Given the uncertainties in the systematics of membraniporids resulting from the paucity of taxonomic characters, it would be particularly useful to have more information about larval morphology in *Jellyella* for comparison with *Membranipora membranacea* and other malacostegans.

Most cheilostome species have coronate larvae that are brooded until their release, do not feed, and live only a short time (hours or days) in the plankton before settling. In contrast, cyphonautes larvae, characteristic of the paraphyletic malacostegans, are not brooded, have the potential to feed while in the plankton, and may live for a longer period (weeks or months) before settlement (although the cyphonautes larvae of some nearshore species are apparently shorter lived, see Dudley 1973). Possible adaptive values of such nonplanktotrophic and planktotrophic larval types, which can be found in numerous marine invertebrate groups, may be diverse (see Strathmann 1980, 1986). The long residency of cyphonautes larvae in the plankton could be of importance with respect to the pseudoplanktonic ecology of adult colonies of *Jellyella.* Long-lived larvae potentially have prolonged periods of competence during which they can settle, thus increasing the chances of the larva locating patchily distributed and ephemeral substrates. The drifting *Spirula* shells colonized by *J. eburnea* probably represent just such substrates.

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References

Bishop JDD 1988. Disarticulated bivalve shells as substrates for encrustation by the bryozoan *Cribrilina puncturata* in the Plio-Pleistocene Red Crag of eastern England. Palaeontology 31: 237–253.

Bone Y & Wass RE 1990. Sub-Recent bryozoan-serpulid buildups in the Coorong lagoon, South Australia. Aust. J. Earth Sci. 37: 207–214.

Borg F 1931. On some species of *Membranipora.* Ark. Zool. 22A(4): 1–35.

Bosc LAG 1802. Histoire naturelle des vers. In Histoire naturelle de Buffon, classée .... d'après le système de Linné. Buffon GLL de., ed., 270 pp. Déterville, Paris.

Bruun AF 1943. The biology of *Spirula spirula* (L.). Carlsberg Foundation's Oceanographic Expedition round the World 1928-1930. Dana Report 24: 1–46.

——— 1955. New light on the biology of *Spirula,* a mesopelagic cephalopod. In: Essays in the Natural Sciences in Honor of Captain Allan Hancock, pp. 61–72. Univ. of S. California Press, Los Angeles.

Busk G 1852. Catalogue of marine Polyzoa in the collection of the British Museum. Part I. Cheilostomata (part), pp. 1–54. British Museum, London.

——— 1854. Catalogue of marine Polyzoa in the collection of the British Museum. Part II. Cheilostomata (part), pp. 55–120. British Museum, London.

Canu F 1900. Revision des Bryozoaires du Crétacé figurés par d'Orbigny. Deuxième Partie.—Cheilostomata. Bull. Soc. Géol. Fr. (3) 28: 334–463.

Clarke MR 1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol. 4: 91–300.

Cook PL 1968. Polyzoa from West Africa. The Malacostega. Part 1. Bull. Br. Mus. Nat. Hist. (Zool.) 16(3): 115–160.

——— 1985. Bryozoa from Ghana. A preliminary survey. Annls. Mus. R. Afr. Cent., Sci. Zool. 238: 1–315.

Cook PL & Chimonides PJ 1980. Further observations on water current patterns in living Bryozoa. Cah. Biol. Mar. 21: 393–402.

Dauphin Y 1979a. Contribution à l'étude de la formation des gisements de Céphalopodes. I. Les coquilles de Spirules (Dibranchiata) de Nouvelle Calédonie. Cahiers Indo-Pacifique 1(2): 165–194.

——— 1979b. Contribution à l'étude de la formation des gisements de Céphalopodes. II. Les coquilles de Spirules (Dibranchiata, Cephalopoda) de l'île Maurice (Océan Indien). Cahiers Indo-Pacifique 1(3): 335–351.

Denton EJ & Gilpin-Brown JB 1973. Floatation mechanisms in modern and fossil cephalopods. Adv. Mar. Biol. 11: 197–268.

Donovan SK 1989. Taphonomic significance of the encrustation of the dead shell of Recent *Spirula spirula* (Linné) (Cephalopoda: Coleoidea) by *Lepas anatifera* Linné (Cirrepedia: Thoracia). J. Paleont. 63(5): 698–702.

Dudley JE 1973. Observations on the reproduction, early larval development, and colony astogeny of *Conopeum tenuissimum* (Canu). Chesapeake Sci. 14: 270–278.

Farmer JD 1979. Morphology and function of zooecial spines in cyclostome Bryozoa: implications for paleobiology. In: Advances in Bryozoology. Larwood GP & Abbott MB, eds, pp. 219–246. Academic Press, London.

Frazier JG, Winston JE, & Ruckdeschel CA 1992. Epizoan communities on marine turtles. III. Bryozoa. Bull Mar. Sci. 51(1): 1–8.

Gordon DP & Parker SA 1991a. The plectriform apparatus—an enigmatic structure in malacostegine Bryozoa. Bull. Soc. Sci. Nat. Ouest Fr. Mém. HS1: 133–145.

——— 1991b. A new genus of the bryozoan family Electridae, with a plectriform apparatus. Rec. S. Aust. Mus. 25(2): 113–120.

Graham A 1971. British Prosobranch and other Operculate Gastropod Molluscs. Linnean Society of London and Academic Press. 112 pp.

Harmer SF 1926. The Polyzoa of the Siboga Expedition. Part 2. Cheilostomata Anasca. Siboga-Expeditie 28b: 183–501.

——— 1957. The Polyzoa of the Siboga Expedition. Part 4. Cheilostomata Ascophora. Siboga-Expeditie 28d: 641–1147.

Hastings AB 1930. Cheilostomatous Polyzoa from the vicinity of the Panama Canal collected by Dr. C. Crossland on the cruise of the S. Y. "St. George." Proc. Zool. Soc. London 47 [for 1929]: 697–740.

Hincks T 1891. Contributions towards a general history of the marine Polyzoa. XV. South-African and other Polyzoa. Ann. Mag. Nat. Hist. (6) 7: 285–298.

Jelly EC 1889. A synoptic catalogue of the Recent marine Bryozoa including fossil synonyms. Dulau, London. 322 pp.

Keough MJ & Downes BJ 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54: 348–352.

Key MM Jr., Jeffries WB, & Voris HK 1995. Epizoic bryozoans, sea snakes and other nektonic substrates. Bull. Mar. Sci. 56(2): 462–474.

Kropach C & Soule JD 1973. An unusual association between an ectoproct and a sea snake. Herpetologica 29: 17–19.

Landman NH, Saunders WB, Winston JE, & Harries PJ 1987. Incidence and kinds of epizoans on the shells of live *Nautilus.* In: Nautilus. Saunders WB & Landman NH, eds., pp. 163–177. Plenum, New York.

Laursen D 1953. The genus *Ianthina.* Dana Report 38: 1–40.

Linnaeus C 1758. Systema Naturae. 10th edition Vol. 1, Lithophyta and Zoophyta, pp. 799–821. Stockholm.

Lohmann H 1904. Eier und sogenannte Cysten der Plankton-Expedition. Anhang: Cyphonautes. Ergebn. Plankton-Exped. Humboldt-Stiftung, 4N: 1–61.

McKinney FK & McKinney MJ 1993. Larval behaviour and choice of settlement site: correlation with environmental distribution pattern in an erect bryozoan. Facies 29: 119–132.

Marcus E 1921. Indo-Pacifische Bryozoen aus dem Riksmuseum in Stockholm. Ark. Zool. 14(7): 1–23.

——— 1937. Bryozoarios Marinhos Brasileiros I. Bol. Fac. Filos. Cienc. S. Paulo, Zool. 1: 1–244.

Maturo FJS 1957. A study of the Bryozoa of Beaufort, North Carolina, and vicinity. J. Elisha Mitchell Soc. 73(1): 11–68.

Mawatari S 1974. Studies on Japanese anascan Bryozoa. 3. Division Malacostega (1). Bull. Natl. Sci. Mus. Tokyo 17(1): 17–52.

Muñoz MR, Moyano HI, & Cancino JM 1991. El compleijo *Membranipora* (Bryozoa: Cheilostomata, Anasca) en Chile. Gayana Zool. 55(3): 203–211.

Orbigny A d' 1851–4. Paléontologie Française. Terrain Crétacé. Bryozoaires. Masson, Paris. 1192 pp.

Osburn RC 1950. Bryozoa of the Pacific Coast of America. Part 1, Cheilostomata-Anasca. Allan Hancock Pac. Exped. 14(1): 1–269.

Peck L, Hayward PJ, & Spencer-Jones ME 1995. A pelagic bryozoan from Antarctica. Mar. Biol. 123: 757–762.

Ristedt H 1977. Zur Ultrastruktur der Zooecien rezenter *Membranipora*-Arten. Biomin. Forsch. 9: 86–98.

Ryland JS 1974. Observations on some epibionts of gulfweed, *Sargassum natans* (L.) Meyen. J. Exp. Mar. Biol. Ecol. 14: 17–25.

——— 1976. Physiology and ecology of marine bryozoans. Adv. Mar. Biol. 14: 285–413.

——— 1977. Taxes and tropisms of bryozoans. In: Biology of Bryozoans. Woollacott RM & Zimmer RL, eds., pp. 411–436. Academic Press, New York.

Silén L & Jansson B-O 1972. Occurrence of *Electra crustulenta* (Bryozoa) in relation to light. Oikos 23: 59–62.

Stevens LM, Gregory MR, & Foster BA 1996. Fouling Bryozoa on pelagic and moored plastics from northern New Zealand. In: Bryozoans in Space and Time. Gordon DP, Smith AM, & Grant-Mackie JA, eds., pp. 321–340. NIWA, Wellington.

Strathmann RR 1980. Why does a larva swim so long? Paleobiology 6: 373–376.

——— 1986. What controls the type of larval development? Summary statement for the evolution session. Bull. Mar. Sci. 39: 616–622.

Stricker SA 1989. Settlement and metamorphosis of the marine bryozoan *Membranipora membranacea*. Bull. Mar. Sci. 45: 387–405.

Taylor PD 1986. Scanning electron microscopy of uncoated fossils. Palaeontology 29: 685–690.

——— 1987. Skeletal morphology of malacostegan grade cheilostome Bryozoa. In: Bryozoa: Present and Past. Ross JRP, ed., pp. 269–276. Western Washington University, Bellingham.

Taylor PD & Jones CG 1996. Use of the environmental chamber in uncoated SEM of Recent and fossil bryozoans. Microscopy and Analysis March 1996: 27–29.

Voigt E 1993. Über die wahrscheinliche Funktion der Frontalwand-Tuberkeln als Distanzhalter bei cheilostomen Bryozoen (fossil und rezent). Verh. naturwiss. Ver. Hamburg (NF) 33 [for 1992]: 131–154.

Voigt E & Cook PL 1983. Interior spinous processes in a cheilostome bryozoan: *Celleporina porosissima* Harmer, 1957. Verh. Naturwiss. Ver. Hamburg (NF) 26: 47–56.

Waters AW 1898. Observations on Membraniporidae. J. Linn. Soc. (Zool.) 26: 654–693.

Weedon MJ & Taylor PD 1995. Semi-nacreous ultrastructures in bryozoans: implications for comparative biomineralization of lophophorates and molluscs. Biol. Bull. 188: 281–292.

Wilson DP & Wilson MA 1956. A contribution to the biology of *Ianthina janthina* (L.). J. Mar. Biol. Assoc. U.K. 35: 291–305.

Winston JE 1982a. Marine bryozoans (Ectoprocta) of the Indian River area (Florida). Bull. Am. Mus. Nat. Hist. 173(2): 99–176.

——— 1982b. Drift plastic—an expanding niche for a marine invertebrate? Mar. Pollut. Res. 13: 348–351.

Winston JE & Eiseman NJ 1980. Bryozoan-algal associations in coastal and continental shelf waters of eastern Florida. Flor. Sci. 43(2): 65–74.

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The Function of the Belemnite Guard

Neale Monks, J. David Hardwick & Andrew S. Gale, London*

With 7 figures and 1 table

Kurzfassung: Anhand von *Cylindroteuthis puzosiana* (d'Orbigny) wurde ein Belemnitentier rekonstruiert, an dem Auftriebspunkt und Schwerpunkt bestimmt wurden. Die Gasfüllung des Phragmokons erwies sich als ausreichend für die Schwebfähigkeit des Tieres. Um die Bedeutung des Rostrums für die Schwebfähigkeit zu bestimmen, wurden physikalische Parameter eines Belemnitentieres ohne Rostrum berechnet. Ein Modell eines Belemnitentieres wurde im Windkanal getestet. Dabei zeigte es sich, daß Flossen am Rostrum zum Erzeugen von dynamischem Auftrieb gedient haben können.

Abstract: A reconstruction of the belemnite animal was performed on *Cylindroteuthis puzosiana* (d'Orbigny) to locate the centres of buoyancy and mass. The gas inclusion was found to be sufficient to provide neutral buoyancy. The reconstruction was modified to represent a belemnite without a guard, and its mechanics compared with the real belemnite. A model of a belemnite was tested in a wind tunnel, and showed that fins on the rostrum could have been used to generate dynamic lift.

Introduction

Belemnites are familiar fossils, but aspects of their palaeobiology are still unclear. Using exceptional fossils with soft body part preservation described by Reitner & Urlichs (1983), it is possible to observe the relative positions of the guard, phragmocone, jaws and arms and hooks. Belemnites lived in near-shore to mid-shelf environments (Christensen 1976; Wignall & Hallam 1991). A possible belemnite anatomy is given in Fig. 1. The aragonitic phragmocone is brevicone to orthocone, with simple concave sutures. Anterior to the phragmocone lies the pro-ostracum, a simple aragonitic plate similar to the gladius of squid. The guard, or rostrum, lies posterior to the phragmocone.

The phragmocone reduces the density of the animal and so increases buoyancy. Flower (1955), Chamberlain (1991) and others have discussed how the positions of the centres of mass and buoyancy affect shell hydrostatics. The centre of buoyancy is the point at which the lifting force of the flotation device can be considered to work, and can be located by finding the centre of mass of the displaced water. The shell is most stable with the centre of mass directly below the centre of buoyancy.

The guard, which is the part of the animal most often fossilised, is an external calcitic deposit (supposedly analogous to the internal cameral deposits of nautiloids), which acts as a counterbalance for the soft tissues anterior to the phragmocone (Seilacher & Wiesenauer 1978; Doyle 1985). Other functions for the guard have been considered. Zuyev & Makhlin (1965)

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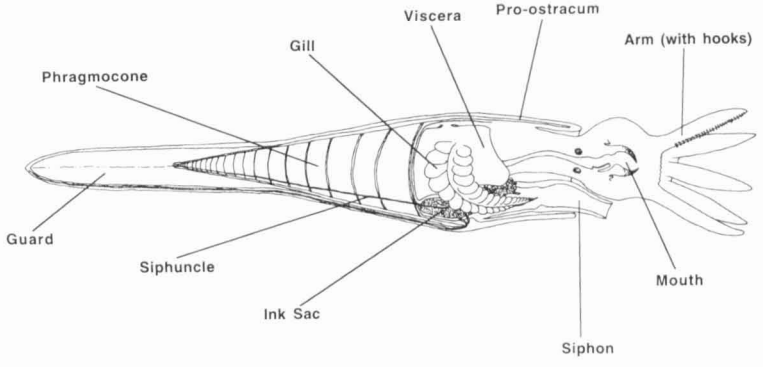


Fig. 1. Reconstruction of a longitudinal section through *Cylindroteuthis puzosiana*. It is noteworthy that the mantle cavity is relatively small, the gills, gonads and viscera needing to be packed into quite a small space compared with modern squid.

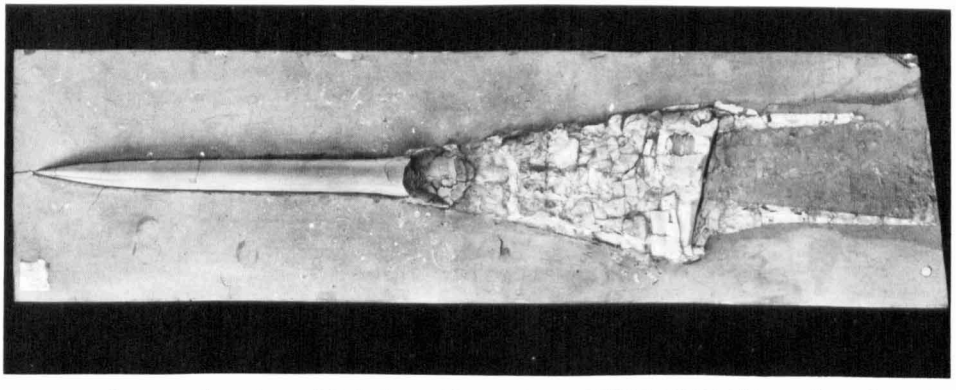


Fig. 2. A well preserved specimen of *Cylindroteuthis puzosiana* (BM(NH) 32572). This specimen shows the arrangement of the guard with the phragmocone (which has been compressed) and the pro-ostracum. Total length 450 mm.

suggested that the guard might have function as a wave cutter at the air-water interface, although with the exception of the short glides made by 'flying' squids, modern cephalopods all remain completely immersed. Spaeth (1975) believed that the guard was originally less massive, estimating up to 20% porosity. After death, additional cementation of the calcitic fibres occurred during an early stage of diagenesis. Stevens (1965) hypothesised that fins were attached to the guard, citing vascularization of the external surface of the guard and the so-called lateral grooves as evidence.

Soft body part preservation indicates that the guard can account for between one fifth and one third of the total length, including the arms (Owen 1844; Huxley 1864, 1877; Reitner & Urlichs 1983); so the guard represents a considerable investment of energy and materials. The question addressed by this study is this: what advantages did the guard provide that an orthocone shell with internal deposits could not? To this end, a well preserved specimen of *Cylindroteuthis puzosiana* (Fig. 2) was restored and its mass, centre of mass and centre of buoyancy calculated. The effect of the guard on density was investigated, as well as replacing the



Fig. 3. Reconstruction of *Cylindroteuthis puzosiana*. The fin has been shown with a simple flapping wave characteristic of slow moving squid in a gentle current. In stronger currents, the belemnite could hold the fins stiffly, generating lift, and soaring efficiently. At escape speeds, the fin could be held against the body to reduce drag.

guard with calcitic infilling and flooded chambers. The hypothesis that the guard could have functioned as a support for fins was tested by making a model and examining its behaviour in a wind tunnnel.

Experiments and results

Specimens of *Cylindroteuthis puzosiana* from the collections at the Natural History Museum, London, include many with alveolar, phragmocone, and pro-ostracum material well preserved. Specimen 32572 (Fig. 2, Callovian of Wiltshire, U.K.) is one of the most complete, and formed the basis of the restoration (Fig. 3). A perspex model (125 mm long) was constructed. Cardboard fins were attached using adhesive.

The volume of a reconstructed animal, its density and its centres of mass and buoyancy were calculated by diving the animal into simple cylindrical elements along its length. The guard was taken to be a solid piece of calcite of density 2.74 mg/mm^3. The phragmocone was assumed to be gas-filled and with a density of 0 mg/mm^3. Mantle, head and arms were estimated to be of density 1.075 mg/mm^3 based on *Loligo* muscle (ALEXANDER 1990). Mantle cavity was estimated to be three-quarters filled with seawater and one-quarter filled with tissue of density 1.050 mg/mm^3. The deduced physical parameters are given in Tab. 1.

Tab. 1. Summary of the physical parameters of the reconstructed belemnites. The reconstructed belemnite has a density below that of seawater so is buoyant. The guardless design ("Without Guard"), has centres of mass and buoyancy separated, so while it is buoyant it is also unstable. If the posterior chambers are flooded sufficient to make the two points coincident, and the mean density becomes greater than that of seawater ("Flooded Chambers") so the animal ceases to be buoyant. Infilling posterior chambers to do the same thing also increases the mean density, and the belemnite again loses buoyancy ("Cameral Deposits"). The mass of calcite used to create this result is the same as that of the guard in the normal belemnite: thus the guard produces stability without losing buoyancy.

	With Guard	Without Guard	Flooded Chambers	Cameral Deposits
Total Length (m):	0.50	0.35	0.35	0.35
Total Mass (kg):	1.02 $_{\text{guard = 0.1 kg}}$	0.93	1.05	1.03 $_{\text{deposits = 0.1 kg}}$
Centre of Mass (m, from tip of arms):	0.17	0.14	0.16	0.16
Centre of Buoyancy (m, from tip of arms):	0.17	0.16	0.16	0.16
Total Volume (dm^3):	1.02	0.99	0.99	0.99
Mean Density (mg/mm^3):	1.023	0.930	1.055	1.032

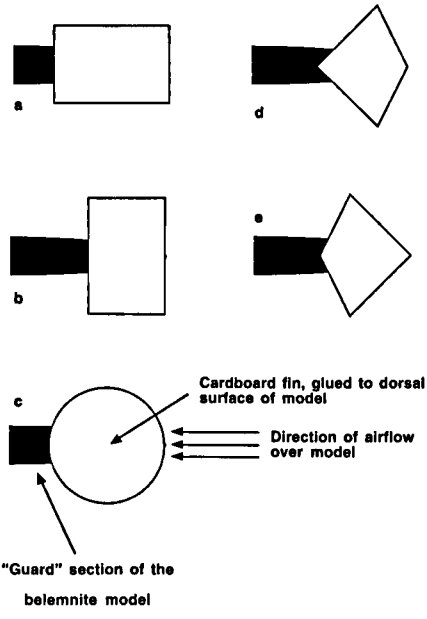


Fig. 4. Illustrations of the five designs of fin used. Each shape is of equal area, so that lift is dependent on the shape of the fin and not its size.

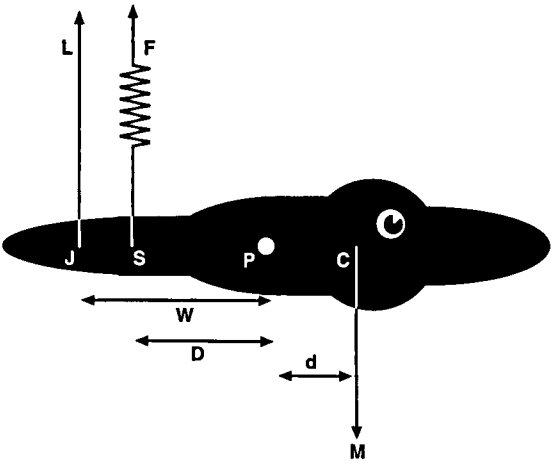


Fig. 5. Diagram illustrating the forces acting on the belemnite model (shown as a silhouette) in the wind tunnel. The mass of the model M acts through the centre of mass C. This is countered by the force of the spring, F acting through S. When the air is moving, a lifting force L is generated by the fins through J. The model is pivoted at a point P, from which moments are taken to deduce the magnitude of L. L is dependent on the speed of airflow and the shape of the fins.

Manipulating the data in a simple spreadsheet allows investigation of the effect of removing the guard, flooding posterior chambers of the phragmocone with seawater, and filling posterior chambers with calcite. These results are also given in Tab. 1. The masses of calcite used to produce the guard in a normal belemnite and internal deposits in a guardless form are also presented.

Five different fin designs were tried, each of equal surface area. The fin types are shown in Fig. 4: two rectangles, (a) and (b); a circle (c); and two kites, (d) obtuse angle leading; and (e) acute angle leading. The fins were attached to the dorsal surface of the guard, from the apex; and had the same curve as the guard from front to back but were otherwise not twisted.

Providing that the Reynolds' numbers are equal, the behaviour of a scaled-down model in a

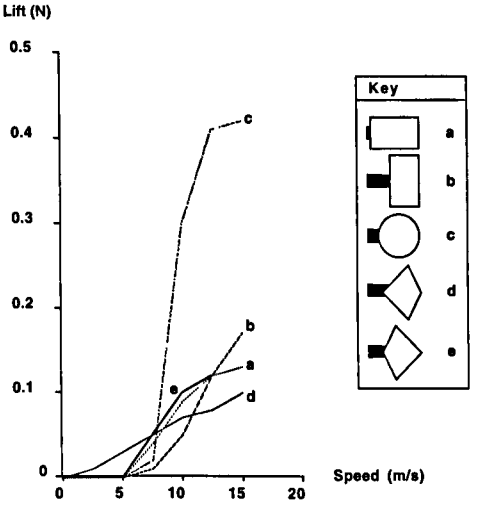


Fig. 6. Graph of lift against speed for the five fin shapes tested. The circular fin clearly outperforms the other designs at airspeeds greater than 8 m/s.

wind tunnel is identical to that of the full sized animal in seawater. Testing in air is advantageous largely because it is easier to work with at high speeds compared with water. Rapidly moving water in enclosed chambers tends to generate a great deal of turbulence, which interferes with the smooth flow of water over the model.

The model is pivoted at a point P and suspended by a spring of known elasticity and relaxed length at a point S (Fig. 5). The distance between the points P and S is the distance D. The mass of the animal M acts through a centre of mass C. C and P are separated by the distance d. Thus, a turning moment exists of magnitude Md. Opposing this turning moment is the moment of the spring at point S. This has a magnitude FD, where F is the force of the spring and is directly proportional to its extension.

When air moves, a lift force L is generated. This force acts at a point J (which for most wings is located at about one-fourth of the chord-distance from the leading edge) a distance W from the pivot. In both the model and the real belemnite, this is close to the tip of the guard. The lift force generates a moment LW which relieves some of the load on the spring, letting it extend. This extension is measured and the lift can be calculated. With increasing speed, lift increases and the spring extends. With each increase, a force was applied to the spring to push the model back to the horizontal so that the angle of attack was not a factor in how much lift was developed.

Tests were not carried out above 12.5 m/s (equivalent to a belemnite swimming at 0.23 m/s) for design (e): this particular fin design was the least stable at high speeds. In all other cases the belemnite model was taken up to 15 m/s (a real belemnite speed of 0.28 m/s). The results are summarised in Figure 6. These speeds are all relatively slow compared with modern squid. Cruising speed for squid (at least in captivity) appears to be between 0 and 1 m/s (O'Dor et al. 1990) and in the wild they can reach a maximum speed of at least 2.1 m/s (Alexander 1990).

Discussion

Mathematical modelling indicates that the guard is a better counterbalance than infilling with calcite or flooding posterior chambers. There is no need to invoke Spaeth's model of diagenetic cementation to 'explain away' the excess density of the guard: a belemnite with a calcitic guard is both stable and positively buoyant (see Tab. 1, "With Guard").

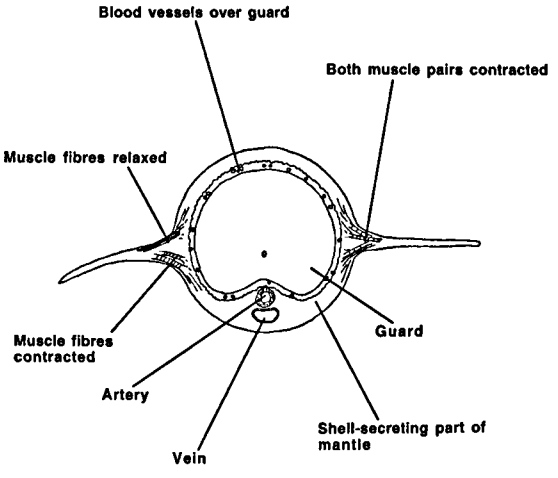


Fig. 7. Reconstruction of a transverse section through the guard of *Cylindroteuthis puzosiana*. The guard itself is sheathed in connective tissues and mantle. The fins are extensions of the mantle musculature (like modern squid), with paired muscles being used to maintain tone or generate waves.

Cuttlefish maintain stability in the desired orientation and water depth by emptying or flooding some of the chambers. The phragmocone must be sufficiently large to still provide adequate buoyancy. In the case of the belemnite, the phragmocone is not large enough. If enough of the shell is flooded to acquire the correct orientation, the overall density of the animal exceeds that of sea-water and the animal ceases to be neutrally buoyant (Tab. 1, "Flooded Chambers"). It is therefore unlikely that the phragmocone of the belemnite operated in a way analogous to the cuttlefish, with chambers being continually emptied and flooded to control orientation and buoyancy.

Instead, the belemnite would have behaved in a way more like that of *Spirula* (DENTON & GILPIN-BROWN 1971). Once a chamber was emptied, it remained so; and chambers were continually formed and emptied throughout the lifetime of the animal, keeping pace with growth. Like *Spirula*, the belemnite would have been neutrally or only slightly negatively buoyant. To migrate up or down the water column, the belemnite would have had to actively swim.

Infilling with calcite also reduces the buoyancy of the animal. Unlike an orthocone nautiloid, the phragmocone is not large enough to accept internal deposits and still provide sufficient lift to keep the animal neutrally buoyant (Tab. 1, "Cameral Deposits"). By putting the deposits on the outside, the belemnite gains stability without losing quite so much buoyancy. Although less buoyant than a guardless belemnite (Tab. 1, "Without Guard"); the centres of mass and buoyancy are coincident and so is more stable.

The guard provides a rigid structure from which such fins could generate lift and turning forces. Compared with a squid, a large proportion of the internal volume is taken up by phragmocone; implying a smaller amount left over for the mantle cavity, so the amount of water that could be expelled would have been less. This is a critical factor in cephalopod swimming efficiency (CHAMBERLAIN 1991). A belemnite has more dead weight and a smaller amount of water to jet with than a similar sized squid. Large fins would allow the animal to coast on ambient water currents in the manner suggested for some squid (O'DOR et al. 1994).

Lateral grooves can be seen in *C. puzosiana*, suggesting the fins may have been attached to the sides. In the model the fins were glued onto the dorsal surface for practical reasons. In life, the animal would have been able to alter the shape and angle of the fins. The model cannot reproduce this, since the fins are rigid. Overall, while the model gives an indication of how the fins might have behaved and what shape the fins might have been; the actual form and function of the fins, if they existed at all, could have been different.

A possible anatomy is this: The muscles are arranged in antagonistic pairs, distally forming the fin, and proximally spreading out into a circular structure and merging with mantle 'tunic' surrounding the guard (Fig. 7). The muscle pairs would raise or lower a part of the fin, and the whole series of muscles acting uniformly along the rostrum could either raise or lower the fin for manoeuvring. A swimming wave could be generated by the muscle pairs rhythmically raising or lowering part of the fin in a synchronised manner.

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References

ALEXANDER, R. McN. 1990. Animals. – 509 pp., Cambridge (Cambridge University Press).

CHAMBERLAIN, J. A. 1991. Cephalopod locomotor design and evolution. The constraints of jet propulsion. – Society for Experimental Biology Seminar Series 36 [Biomechanics in Evolution]: 57–98, Cambridge (Cambridge University Press).

CHRISTENSEN, W. K. 1976. Palaeobiogeography of Late Cretaceous belemnites of Europe. – Paläontologische Zeitschrift 50: 113–129, Stuttgart.

DENTON, E. J. & GILPIN-BROWN, J. B. 1971. Further observations on the buoyancy of *Spirula*. – Journal of the Marine Biological Association of the United Kingdom 51: 363–373, Cambridge.

DOYLE, P. 1985. Sexual dimorphism in the Belemnite *Yongibelus* from the Lower Jurassic of Yorkshire. – Palaeontology 28: 133–146, London.

FLOWER, R. H. 1955. Cameral deposits in orthoconic nautiloids. – Geological Magazine 92: 89–103, London.

HUXLEY, T. H. 1864. The Structure of Belemnitidae. – Memoir of the Geological Survey, U.K., Monograph 2: 1–22.

– 1877. A Manual of the Invertebrated Animals. – 698 pp., London (Churchill & Co).

O'DOR, R. K.; PORTNER, H. O. & SHADWICK, R. E. 1990. Squids as elite athletes. Locomotory, respiratory, and circulatory integration. – [In:] GILBERT, D. L.; ADELMAN, W. J. & ARNOLD, J. M. (eds.) Squid as Experimental Animals: 481–503, New York (Plenum Press).

O'DOR, R. K.; HOAR, J. A.; WEBBER, D. M.; CAREY, F. G.; TANAKA, S.; MARTINS, H. R. & PORTEIRO, F. M. 1994. Squid (*Loligo forbesi*) performance and metabolic rates in nature. – Marine and Freshwater Behaviour and Physiology 25: 163–177, Amsterdam.

OWEN, R. 1844. A description of certain belemnites preserved with a great proportion of their soft parts in the Oxford Clay at Christian Malford, Wiltshire. – Philosophical Transactions of the Royal Society of London 1844: 65–85, London.

REITNER, J. & URLICHS, M. 1983. Echte Weichteilbelemniten aus dem Untertoarcium (Posidonienschiefer) Südwestdeutschlands. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 165: 450–465, Stuttgart.

SEILACHER, A. & WIESENAUER, E. 1978. Preservational history of the Belemnites. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 157: 145–149, Stuttgart.

SPAETH, C. 1975. Zur Frage der Schwimmverhältnisse bei Belemniten in Abhängigkeit von Primärgefüge der Hartteile. – Paläontologische Zeitschrift 49: 321–331, Stuttgart.

STEVENS, G. R. 1965. The Jurassic and Cretaceous belemnites of New Zealand and a review of the Jurassic and Cretaceous belemnites of the Indo-Pacific region. – New Zealand Geological Survey Palaeontological Survey 36: 1–283, Wellington.

WIGNALL, P. B. & HALLAM, A. 1991. Biofacies, stratigraphic distribution and depositional models of British onshore Jurassic black shales. – [In:] TYSON, R. V. & PEARSON, T. H. (eds.) Modern and Ancient Continental Shelf Anoxia. – Geological Society Special Publications 58: 291–309, London.

ZUYEV, G. V. & MAKHLIN, V. Z. 1965. The functional significance of the guard of *Actinocamax*. – Palaeontologisk Zhurnal 1: 150–152, Washington, D.C.

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