

## FUNCTIONAL MORPHOLOGY, ECOLOGY, AND EVOLUTION OF THE SCAPHITACEAE GILL, 1871 (CEPHALOPODA)

NEALE MONKS

Department of Palaeontology, Natural History Museum, Cromwell Road, South Kensington, London SW7 5BD  
e-mail: n.monks@nhm.ac.uk

### ABSTRACT

Scaphitids are heteromorph ammonites exhibiting morphological trends counter to those of the other main heteromorph ammonite groups. These trends include the shortening of the body chamber, lateral compression of the whorl, closure of the coil, and more regular, spiral coiling. Scaphitid-like morphologies may have appeared in other heteromorphs, but the Scaphitaceae are monophyletic. The most primitive scaphitids are known from the Albian, but an important radiation occurred in the Western Interior Seaway of North America from the Santonian to Maastrichtian, some of which spread to the Old World. The scaphitid morphology is consistent with improved swimming abilities, but scaphitids remained associated with the seafloor and are best considered to have been nektobenthos similar to modern nautiluses.

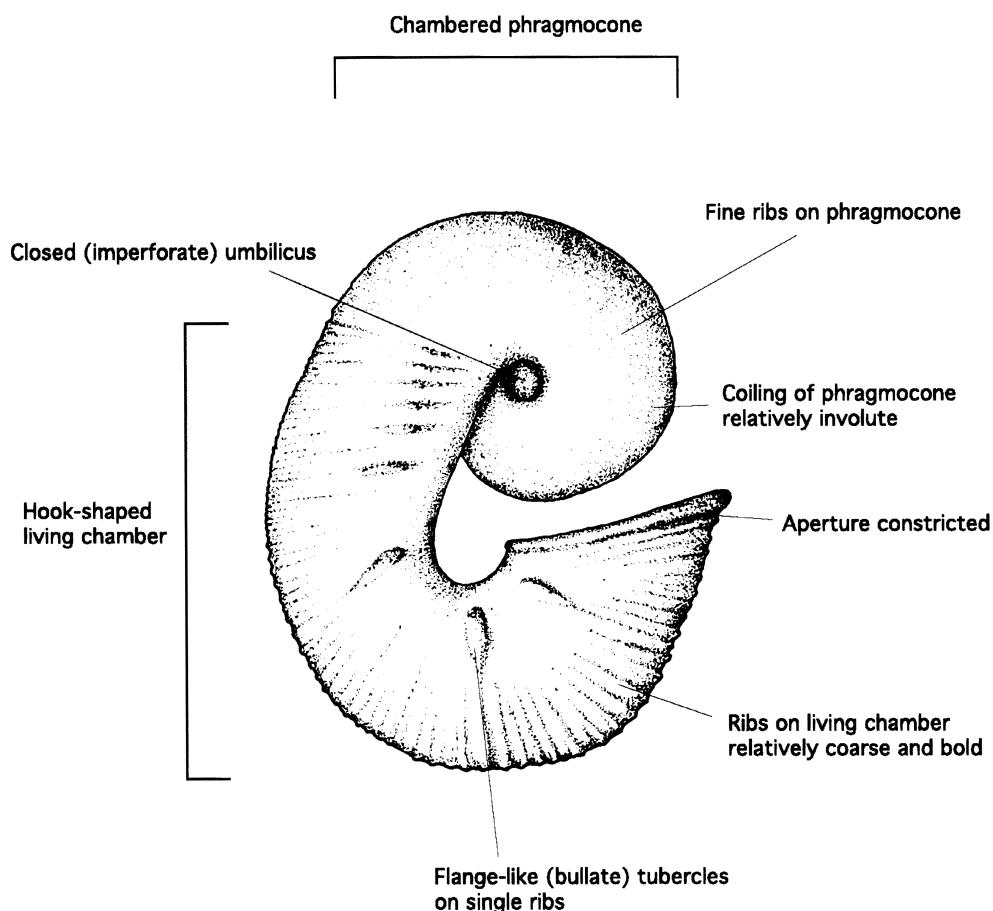
### INTRODUCTION

The Scaphitaceae were a diverse group of heteromorph ammonites which in many ways reversed the trends characteristic of heteromorph ammonites on the whole, such as the approximately regular spiral coiling of many species, and the lack of an open or helical initial coil. They do, however, retain some typically heteromorph features, most importantly the quadrilobate septum, at least during the early stages of ontogeny (Wiedmann, 1964). The Scaphitaceae is believed to be monophyletic, derived from the Hamitidae Gill, 1871, a probably paraphyletic group of primitive heteromorphs with simple septal walls, open, often crozier or paper-clip shaped shells and long narrow body chambers, but lacking any ornament more complex than simple annular ribs (Monks, 1999a). The group may also be ancestral to certain extant cephalopods, though this is controversial to say the least (Lewy, 1996). A typical scaphitid is illustrated in Fig. 1, *Scaphites hugardianus*, from the Late Albian (Lower Cretaceous).

Scaphitids were widespread during the Late Cretaceous, and in some areas have considerable importance in biostratigraphy, for example in the Chalk of Europe and the Western Interior Seaway deposits of North America. They were also persistent, ranging from the Late Albian to Late Maastrichtian, and are among the youngest of all ammonite fossils known (Kaplan *et al.* 1987; Landman & Waage, 1993; Emerson *et al.* 1994; Kennedy & Jagt, 1998). The systematics of the group has been subject to many studies, and they are generally considered to fall into two main groups, the Otoscaphitinae Wright, 1953 and the Scaphitinae Gill, 1871 both placed within a single family, the Scaphitidae Gill, 1871 (Wright *et al.* 1996). These subfamilies are taken to represent a divergence early in the evolution of the group, probably during the Late Albian (Wright, 1953). Cooper (1994) revised the systematics of the group using a cladogram and the morphological suites of characters which support it. In that study, the subfamilies Scaphitinae and Otoscaphitinae were elevated to family status but further divided into subfamilies corresponding to assumed evolutionary lineages. Cooper (1994) removed the most primitive species into a new family of their own, the Eoscapitidae Cooper, 1994. However, this family was not defined on the basis of any unique, shared derived characters but rather as the 'grade group' leading to the 'higher' scaphitids.

### Palaeobiology of scaphitids

Like ammonites in general, the palaeoecology of the scaphitids is less well studied than their distribution and systematics. Particularly well studied are the scaphitids of the North American Western Interior Seaway, which ran from the Gulf of Mexico up to Arctic Canada through the Late Cretaceous (Landman & Waage, 1993). Although this basin was open to the Atlantic (and to the North Pacific through



**Figure 1.** Reconstructed shell of a generalised saphitid, with the major morphological characteristics labelled.

Cenomanian to Campanian times) movement of animals in and out of the basin seems to have been limited, and it developed its own endemic ammonite fauna of which heteromorphs such as the saphitids were an important constituent (Kennedy & Cobban, 1976). The waters of the Seaway appeared to have been stratified, and at times bituminous shale was deposited indicating dysaerobic bottom waters (Gill & Cobban, 1966; Sageman *et al.* 1997). Differences or similarities in the isotopic compositions of the shells of benthic molluscs (like inoceramids and gastropods) and cephalopods allow some inferences of the ecology of different cephalopods to be made. Saphitids appear to have lived near the sea floor and have carbon and oxygen isotope values similar to those of the benthic molluscs (Whittaker *et al.* 1986). Furthermore, fossil saphitids frequently absent from the sediments

deposited during oxygen-poor bottom water conditions, or else occur in such numbers as to suggest a mass mortality (Batt, 1989; Landman & Waage, 1993). This contrasts with some heteromorphs like the straight-shelled baculitids, whose fossils are widely distributed in normal and oxygen-poor bottom water facies, and have carbon and oxygen isotope values consistent with having lived higher up the water column (Fatherree *et al.*, 1998). Such ammonites probably occupied a midwater, vertically-migrating niche similar to modern cranchid squids (Klinger, 1980).

However, heteromorph ammonites with open shells and hook-shaped body chambers such as the saphitids but also others such as the hamitids which are the presumed ancestors of the saphitids, are widely believed to have been more or less planktonic. This is mostly because

such shells would have produced a lot of drag, being covered in ribs and spines; and the long body chambers would make swimming inefficient, assuming propulsion was generated in a similar way to modern cephalopods. In addition, the hook shaped body chamber, if entirely filled with the soft body of the ammonite would hang beneath the phragmocone, as is the case with the living nautilus. In such an orientation, the aperture would point upwards, away from the sea floor, and it is difficult to visualise such an ammonite being benthic (Trueman, 1941; Klinger, 1980; Westermann, 1996). Hamitids are certainly widely distributed, with many species having near-global distributions despite being obviously poor swimmers, but are absent from sediments deposited during anoxic bottom water conditions (Batt, 1989, 1991). As noted above with the scaphitids, this would seem to indicate a benthic lifestyle.

This study attempts to tackle the twin problems of ecology and evolution, using a cladistic analysis to help define the likely phylogenetic trends, and then apply new theories about the functional morphology of ammonites to it to try and deduce the basic themes which characterise the radiation of the group.

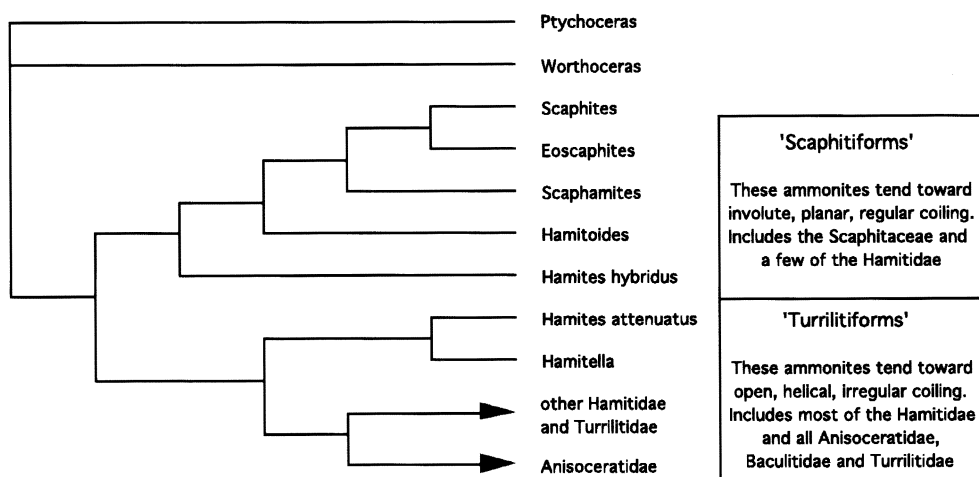
### PHYLOGENY

I have elsewhere described a cladistic analysis supporting the view of Wiedmann (1965) and Wiedmann & Marcinowski (1985) that the

Scaphitaceae are a monophyletic clade derived from a group of 'scaphitiform' hamitids which appeared late in the Early Albian (Monks, 1999). These scaphitiform hamitids show a tendency towards shorter body chambers, involute and more regular spiral coiling, characteristics exemplified by the Scaphitaceae (Fig. 2). *Eoscaphtes circularis* (J. de C. Sowerby in Fitton, 1836) is generally taken as the earliest genus of scaphitids, known from the Upper Albian; but while having close, involute coiling still retains an open umbilicus and more or less hamitid septal walls (Cooper, 1994). It is believed that there were two main radiations of scaphitids: the medium to large tuberculate and generally close-coiling Scaphitinae; and the more weakly ornamented, rather loosely coiling and diminutive, perhaps paedomorphic, Otoscaphitinae (Wright, 1953).

#### Analytical methods

To investigate the relationships between scaphitid genera, a phylogenetic analysis was accomplished using PAUP (Swofford, 1993). This program performs a cladistic analysis using parsimony. The analysis was based on a data matrix comprising 16 taxa and 21 characters. The characters are listed in Table 1. Terminology is essentially that of the recently revised Cretaceous ammonite volume of the *Treatise on invertebrate paleontology* (Wright *et al.* 1996) and the more detailed revisions of scaphitid morphology of Wiedmann (1965). They were based upon aspects of suture line, coiling mode, and shell morphology. A few characters were ordered; these are indicated in



**Figure 2.** Abbreviated phylogeny of the Albian heteromorphs as described by Monks (1999). The Scaphitaceae are a clade within the 'scaphitiform' heteromorphs, which show a tendency toward closed, regular spiral coiling.

**Table 1.** Characters used for the phylogenetic analysis*Suture line*

1. Trifid lateral lobe (0) or bifid (1).
2. Trifid umbilical lobe (0) or bifid (1).
- 3\*. Umbilical lobe narrower than adjacent saddles (0), similar in breadth (1) or broader (2). Ordering justified on assumption that in going from narrow to broad morphologies, or *vice versa*, an intermediate stage must be passed through.
4. Internal lobe comparable in size with umbilical lobe (0) or much smaller (1).
- 5\*. Suture quadrilobate throughout ontogeny (0), initially quadrilobate but with a single pseudolobe developing later on (1), initially quadrilobate but with two pseudolobes later (2), or initially quadrilobate but developing more than two adventitious pseudolobes (3). Ordered on basis of ontogenetic series: as scaphitids grow additional pseudolobes are added sequentially.

*Septal walls*

- 6\*. Early septal walls hamitid (0) or slightly scaphitid (1) or very scaphitid (2).
- 7\*. Late septal walls hamitid (0) or slightly scaphitid (1) or very scaphitid (2).

*Coiling*

8. Umbilicus perforate (0) or not (1).
- 9\*. Early whorl oval (0), approximately oval but slightly distorted (adpressed) where succeeding whorls are in contact (1), semilunate with succeeding whorls partially wrapped around one another (2). Ordered by comparison with ontogeny: scaphitids whorl section in all cases is initially oval, at least during the early post-hatching stages, with coiling becoming steadily more involute as the whorl develops.
- 10\*. Later whorls (hook shaped part of coil) approximately oval in section (0), adpressed (1), or semilunate (2). Ordering justified on assumption that in going from an oval to a semilunate whorl section, or *vice versa*, the intermediate stage must be passed through.
11. Straight sections of whorl free (0) or succeeding shafts laterally compressed into one another (1).
12. Septa persist from spiral into straight sections of shell (0) or confined to spiral section only (1).
13. Living chamber long and narrow (0), shallow hook (1), or "scaphitoid", i.e., short and broad (2).
14. Moderate overall size, from 1 to 10 cm in diameter (0) or very large, 30 cm upwards in diameter (1).

*Ornamentation*

- 15\*. Ribbing restricted to weak striations (0), bold unbranching ribs (1), or bold, periodically bifurcating and intercalated ribs (2). Ordered on the assumption that bold bifurcating ribs are a modification of bold simple ribs and not could only appear in those taxa whose ancestors had bold simple ribs.
16. Phragmocone and living chamber bear ribs (0) only phragmocone is ribbed (1).
17. Ribs uniformly well-developed throughout ontogeny (0), or become fine on living chamber (1).
- 18\*. No tubercles or spines (0), ribs pinched out into flange-like spines (1), or ribs bear discrete, circular spine bases or nodes (2). Ordered on assumption that the flange-like spine bases are the initial phases in the evolution of circular nodes, supported by the observation that in those scaphitids with circular nodes at maturity, earlier parts of the shell are ornament with the flange-like spines.
- 19\*. Single pair of spines attached to each rib (0), two pairs of spines attached to each rib (1), or numerous unpaired spines not obviously associated with ribs (2).
20. Aperture unconstricted (0) or constricted (1).
21. Aperture or microconchs plain (0) or ornamented with paired lappets (1).

by an asterisk. Where characters were ordered the justification for doing so is stated in Table 1. Otherwise, the majority of characters were unordered. The data matrix used is given in Table 2.

The PAUP search was performed by the branch and bound option. This guarantees finding the shortest tree. The ACCTRAN optimisation was selected, which prefers reversal to parallelisms. All characters had equal weighting. The number of outgroup taxa were chosen on the basis of Monks (1999). These

were *Ptychoceras* d'Orbigny, 1842 and three stem-group scaphitiforms.

## RESULTS

20 trees were found, of which the strict consensus is given in Fig. 3a; from these trees one was selected as being the best match with strati-

**Table 2.** Data matrix (a question-mark indicates an inapplicable character).

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<b>Taxon</b>																					
<i>Ptychoceras</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	?	0	?	0	0
<i>Hamites hybridus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	0	0
<i>Hamitoides</i>	?	?	?	?	?	?	?	0	0	0	0	0	0	0	1	0	0	0	?	0	0
<i>Scaphamites</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	1	0
<i>Eoscaphtes circularis</i>	1	1	1	0	0	0	1	0	0	2	0	1	1	0	2	0	0	0	?	1	0
<i>Eoscaphtes subcircularis</i>	1	1	1	0	0	0	1	0	0	2	0	1	1	0	2	0	0	1	0	1	0
<i>Scaphites hugardianus</i>	1	1	1	0	1	1	2	1	1	2	0	1	1	0	2	0	0	1	0	1	0
<i>Scaphites equalis</i>	1	1	1	0	1	1	2	1	1	2	0	1	1	0	2	0	0	1	0	1	0
<i>Clioscaphtes</i>	1	0	2	1	1	2	2	1	1	2	0	1	2	0	2	0	0	1	0	1	0
<i>Desmoscaphtes</i>	0	1	2	1	3	2	2	1	1	2	0	1	2	0	2	0	0	1	0	1	0
<i>Pteroscaphites</i>	1	1	0	0	1	2	2	1	1	2	0	1	1	0	2	0	1	1	0	1	1
<i>Hoploscaphtes</i>	1	1	2	1	3	2	2	1	1	2	0	1	2	0	2	0	1	2	0	1	0
<i>Jeletzkyites</i>	1	1	2	1	3	2	2	1	1	2	1	1	2	0	2	0	1	2	1	1	0
<i>Discoscaphites</i>	1	1	2	1	3	2	2	1	1	2	1	1	2	0	2	0	1	2	2	1	0
<i>Trachyscaphtes</i>	1	1	2	1	3	2	2	1	1	2	0	1	1	0	2	0	0	2	2	1	0
<i>Acanthoscaphites</i>	1	1	2	0	3	2	2	1	1	2	0	1	2	0	2	0	0	2	1	1	0
<i>Rhaeboceras</i>	1	1	2	1	2	2	2	1	1	2	1	1	2	1	2	0	0	2	1	1	0
<i>Worthoceras</i>	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	?	?	0	?	0	1
<i>Yezoites</i>	1	1	1	0	1	2	2	1	1	1	0	1	1	0	2	0	0	1	0	1	0
<i>Otoscaphtes</i>	1	1	1	0	1	2	2	1	1	1	0	1	1	0	2	1	0	1	0	1	1

graphy. This tree is given in Fig. 3b and is taken as the basis for the subsequent discussion of the phylogeny of the group. This tree has a length of 45, consistency index of 0.69, and a retention index of 0.89.

#### Statistical tests

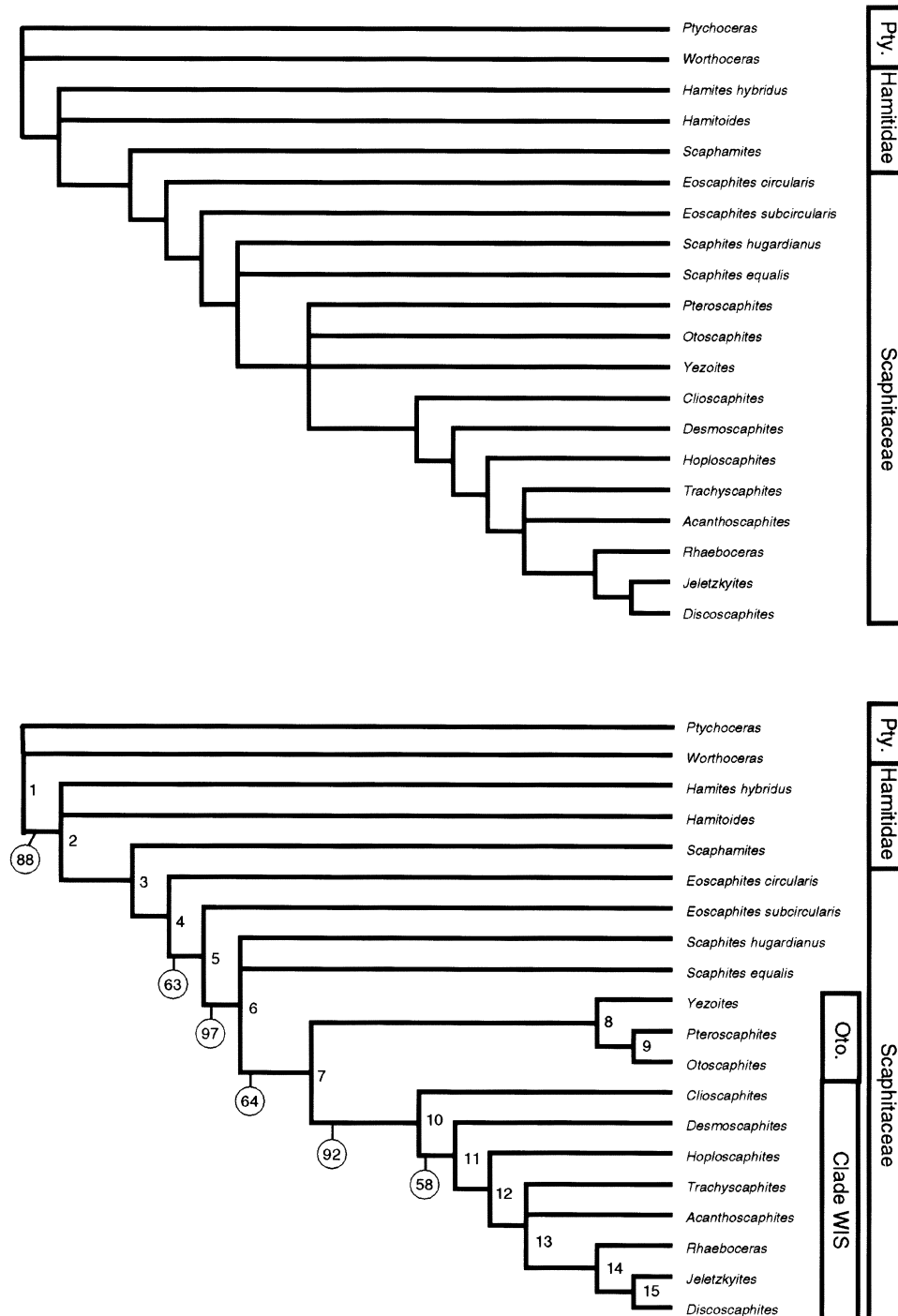
Bootstrap and branch-decay tests were also performed. Bootstrapping tests the robustness of tree topology (Felsenstein, 1985). Well supported branches will occur in a higher percentage of the 'bootstrap trees' than poorly supported ones. Branch decay (Bremer, 1988) tests the robustness of nodes by calculating the number of extra steps a tree needs to be lengthened by for a given node to collapse; the greater the number of steps, the more robust the node. The results of both of these tests are given in Fig. 3b.

#### Worthoceras and the 'scaphitiform' hamitids

The patterns of character distribution across the tree are fully described in Table 3 and form the basis of the following discussions. However, a number of important points need to be made here. The order of the stem scaphitiform hamitids leading to the Scaphitaceae given in the general analysis of Albian heteromorphs in Monks (1999a) is supported by this more inclusive

study; as is the exclusion of the genus *Worthoceras* Adkins, 1928 from the Scaphitaceae. As Wiedmann (1965) described, *Worthoceras* is convergent with the small scaphitids which are included in the Otoscaphtinae, but whereas those taxa have external ornamentation which degrades along the living chamber, *Worthoceras* has no ornament at all, excepting perhaps the lateral constrictions on the descending shafts of some species. Furthermore, the suture line retains the primitive trifid lateral and umbilical lobes of the heteromorphs, and lacks the pseudolobes characteristic of all the scaphitids except the most primitive genus, *Eoscaphtes*. *Worthoceras* is commonly included in the Otoscaphtinae (Cooper, 1994; Wright *et al.*, 1996), but that conclusion cannot be supported.

The transition from the scaphitiform hamitids (*Hamites hybridus* Casey, 1964, *Hamitoides* Spath 1925, and *Scaphamites* Wiedmann & Marciniowski, 1985) to the most primitive of the Scaphitaceae is marked by seven character state changes. Three of these relate to the septum: a bifid rather than a trifid umbilical lobe, together with slight broadening of the umbilical lobe and the loss of its narrow stem, and the overall subscaphitid shape of the septal wall. Four characters refer to shell shape: a semi-lunate whorl section; the absence of septae from the hook-shaped part of the whorl; a curved, hook shaped scaphitid living chamber free from the



**Figure 3.** Strict consensus of the 20 most parsimonious trees (3a) and the tree chosen on best fit with stratigraphy (3b). On the latter, percentage bootstrap support and branch decay values are plotted (in squares and circles, respectively).

coil; and finally a living chamber ornamented with often bifid annular ribs and bullate spines. Of these characters, the shape of the septal wall, the lack of chambers in the hook, and the bifurcations of the ribs are not reversed higher up the tree, and are therefore synapomorphies of the Scaphitaceae. The first two of these three characters were identified as such by Wied-

mann (1965), and all three are absent from *Worthoceras*.

#### *Systematics of the Scaphitaceae*

The Scaphitaceae are generally considered to comprise a single family divided into two sub-families, though Cooper (1994) has subdivided

**Table 3.** Tree description.

Description (apomorphy list) of the tree shown in Fig. 3b based upon the cladistic analysis described in the text. The character state changes pertaining to each node are listed, see appendix 1 for details of character states. Characters in **bold** type change in the listed way only once on the cladogram (i.e., have a consistency index of 1), and are therefore synapomorphies of that node. Abbreviations: L, lateral lobe; U, umbilical lobe; I, internal lobe; LC, final (mature) living chamber.

Node 1 to Node 2	1 (L lobe)	0 to 1
	10 (late whorl)	1 to 0
	<b>15 (scaphitid ribs)</b>	0 to 1
Node 2 to Node 3	<b>20 (aperture constricted)</b>	0 to 1
Node 3 to Node 4	2 (U lobe)	0 to 1
	3 (broad U lobe)	0 to 1
	<b>5 (late septal walls)</b>	0 to 1
	10 (late whorl)	0 to 2
	<b>12 (non-septate shafts)</b>	0 to 1
	13 (scaphitoid LC)	0 to 1
	<b>15 (scaphitid ribs)</b>	1 to 2
Node 4 to Node 5	<b>18 (tuberculation)</b>	0 to 1
Node 5 to Node 6	<b>6 (early septal walls)</b>	0 to 1
	<b>5 (late septal walls)</b>	1 to 2
	6 (pseudolobes)	0 to 1
	8 (umbilicus)	0 to 1
	<b>9 (early whorl)</b>	0 to 1
Node 6 to Node 7	<b>6 (early septal walls)</b>	1 to 2
Node 7 to Node 10	3 (broad U lobe)	1 to 2
	7 (diminutive I)	0 to 1
	13 (scaphitoid LC)	1 to 2
Node 10 to <i>Clioscaphtes</i>	2 (U lobe)	1 to 0
Node 10 to Node 11	5 (pseudolobes)	1 to 3
Node 11 to <i>Desmoscaphtes</i>	1 (L lobe)	1 to 0
Node 11 to Node 12	<b>18 (tuberculation)</b>	1 to 2
Node 12 to Hoploscaphtes	17 (ribs fine on LC)	0 to 1
Node 12 to Node 13	19 (spine density)	0 to 1
Node 13 to Node 14	<b>11 (lateral compression)</b>	0 to 1
Node 14 to Node 15	17 (ribs fine on LC)	0 to 1
Node 15 to <i>Discoscaphtes</i>	19 (spine density)	1 to 2
Node 14 to <i>Rhaeboceras</i>	5 (pseudolobes)	3 to 2
	<b>14 (gigantism)</b>	0 to 1
Node 13 to <i>Trachyscaphtes</i>	13 (scaphitoid LC)	2 to 1
	19 (spine density)	1 to 2
Node 13 to <i>Acanthoscaphtes</i>	7 (diminutive I)	1 to 0
Node 7 to Node 8	10 (late whorl)	2 to 1
Node 8 to Node 9	21 (apertural lappets)	0 to 1
Node 9 to <i>Pteroscaphtes</i>	3 (broad U lobe)	1 to 0
	10 (late whorl)	1 to 2
	17 (ribs fine on LC)	0 to 1
Node 9 to <i>Otoscaphtes</i>	<b>16 (no ribs on LC)</b>	0 to 1
Node 1 to <i>Worthoceras</i>	8 (umbilicus)	0 to 1
	21 (apertural lappets)	0 to 1

the superfamily more intensively. The basic topology of the tree indicates that the Scaphitinae are paraphyletic with respect to the Otoscapitinae (exclusive of *Worthoceras*). The Otoscapitinae include *Yezoites* Yabe, 1910, *Otoscapites* Wright, 1953, and *Pteroscaphites* Wright, 1953. This branch is described by a single character state change, having a late whorl section which is not semi-lunate but more triangular with a defined dorsal groove. However, this morphology is shared with *Ptychoceras* and *Worthoceras*, both of which have loosely adpressed coils, and cannot be taken as a unique feature of the Otoscapitinae.

The sister group of the Otoscapitinae includes *Clioscapites* Cobban, 1952, *Desmoscapites* Reeside, 1927, *Hoploscapites* Nowak, 1911, *Acanthoscaphites* Nowak, 1911, *Trachyscapites* Cobban & Scott, 1964; *Rhaeboceras* Meek, 1876; *Discoscaphites* Meek, 1871, and *Jeletzkyites* Riccardi, 1983. This clade includes the genera endemic to the Western Interior Seaway, so is hitherto referred to informally as Clade WIS. This clade is characterised by three state changes: further broadening of the umbilical lobe; an interior lobe smaller than the other primary lobes; and a shallow but broad living chamber. Some of these characters are reversed higher up the tree, and so cannot be used diagnostically for Clade WIS as a whole.

Cooper (1994) has described the most detailed phylogenetic analysis of the scaphitids to date, using a cladistic, but non-parsimonious, method. The topology of the tree described here contrasts with that study in a number of important respects. The genus *Eoscapites* was removed to its own family, outside of the higher scaphitids. However, on the basis of the cladistic analysis described here, the value of a formal grouping for the genus *Eoscapites*, even at generic, let alone family level, is questionable. The two species included in the analysis do not form a clade, and neither is defined on the basis of synapomorphies but rather the absence of characters shared by the progressively more crownward groups.

## DISCUSSION

The cladogram derived from this analysis can be redrawn with reference to stratigraphy following the technique described by Smith (1993) to produce a phylogeny of the group. Scaphitids appeared during the Albian, and most of the basal members of the clade, *Eoscapites* and *Scaphites* Parkinson, 1811, as well as their

immediate hamitid sister taxa, have Albian first appearances (the exception, *Scaphites equalis* J. Sowerby, 1813, is known from the Lower Cenomanian, but may be derived directly from *Scaphites hugardianus* d'Orbigny, 1842). *Yezoites* and *Otoscapites* appeared either in the Late Albian or the Early Cenomanian, while *Pteroscaphites* is not known before the Turonian. The topology of the Otoscapitinae and its relation to the basal scaphitids is therefore also congruent with stratigraphy. Clade WIS are the youngest scaphitids, and range from the Santonian (*Clioscapites*) to the Maastichtian (*Acanthoscaphites*), and once again seem to match stratigraphy well. Note that *Acanthoscaphites* lacks synapomorphies, and could be a direct development from *Trachyscapites*.

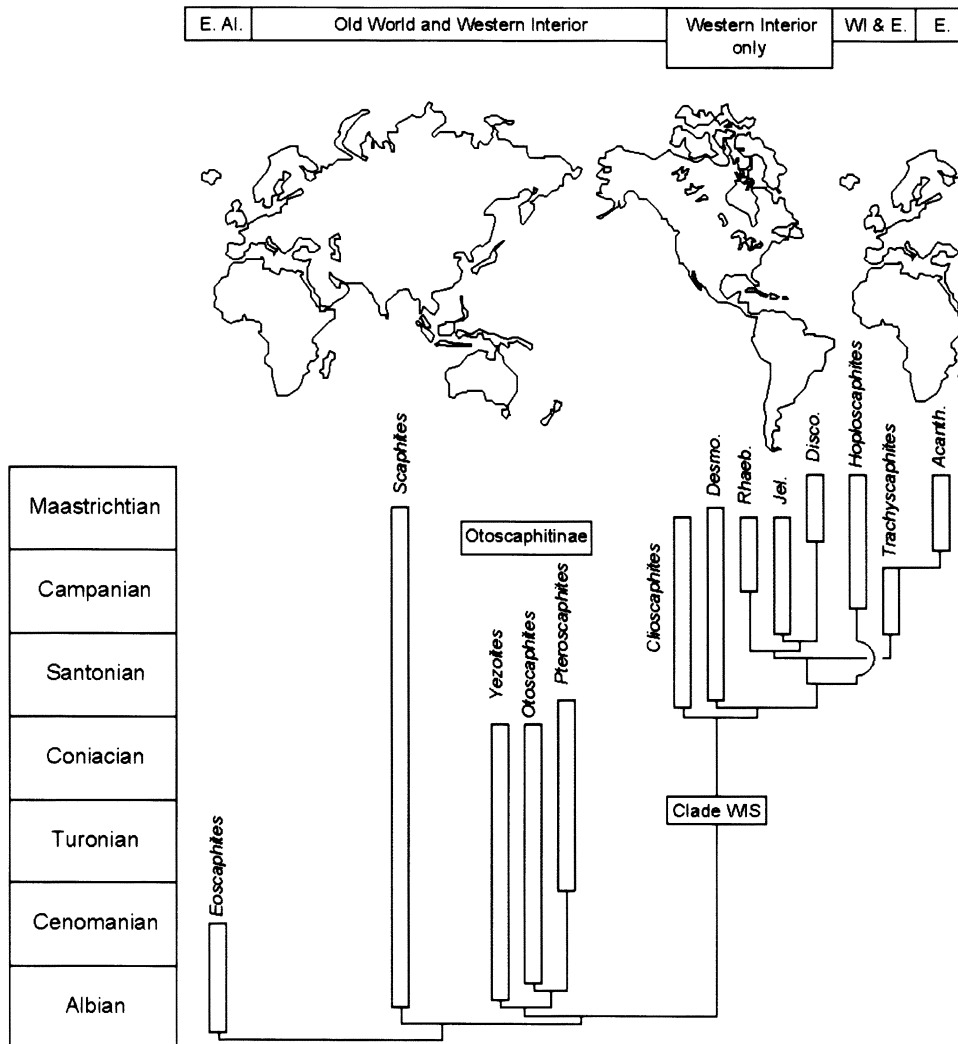
### *Comparisons with stratigraphy and palaeobiogeography*

Clade WIS is also interesting from a palaeobiogeographical perspective. As noted earlier, the Western Interior Seaway was home to a number of endemic genera of scaphitids. These were *Clioscapites*, *Desmoscapites*, *Discoscaphites* and *Jeletzkyites*. In addition, *Rhaeboceras* may also be endemic to the Western Interior, but there are questionable records from north-eastern Russia. *Hoploscapites* and *Trachyscapites* include species endemic to the Western Interior but also other species are found in Europe, South Africa and elsewhere. Alone of this clade, *Acanthoscaphites* is unknown from the Western Interior Seaway, but its geographic range overlaps with its likely ancestor, *Trachyscapites* in Europe (Fig. 4). This view of a separate radiation of scaphitids in the Western Interior Seaway was described in detail by Kennedy & Cobban (1976). They contrasted the tendency towards complex suture lines and tight coiling shown by Western Interior scaphitids with the absence of these trends among most scaphitids outside of this basin. The cladogram devised here is compatible with these observations.

### *Functional Morphology*

The functional morphology of scaphitids is problematic in part because the soft body parts are unknown. Only the shell is known for most species, with a few exceptional fossils having elements of the buccal mass preserved as well. Scaphitid shells have a mix of morphological features making close comparisons with either





**Figure 4.** Phylogeny, stratigraphy and biogeography of the Scaphitaceae compared. The cladogram described here matches stratigraphy well. Clade WS is ancestral to some scaphitids partially or completely found outside the Western Interior Seaway. Key: E = Europe; Al = Algeria; WI = Western Interior.

the extant nautilus or the other ammonites difficult. On the whole, they differ most noticeably from the hamitids in the loss of septae from the descending part of the hook and the overall shortening and broadening of the living chamber itself (characters 12 and 13). Short, stocky living chambers such as these are seen in modern nautilus. The closed umbilicus (character 8), the adpression of the early whorls (character 9), the involute coiling of the whorls (character 10), and the lateral compression in some species (character 11), are features also

seen in modern nautilus, as well as regularly coiled ammonites. However, unlike nautilus but like many other heteromorphs, scaphitids bore ribs and spines (characters 15, 16, 17, 18 and 19).

Muscle scars, radulas and aptychi (jaws) are known from a few scaphitids (Arkell, 1957; Landman & Waage, 1993; W. J. Kennedy, pers. comm.) and may provide some clues to their likely diet. From these it appears that the body was attached to the shell at two sites, dorsally close to the final septum by a pair of muscles,

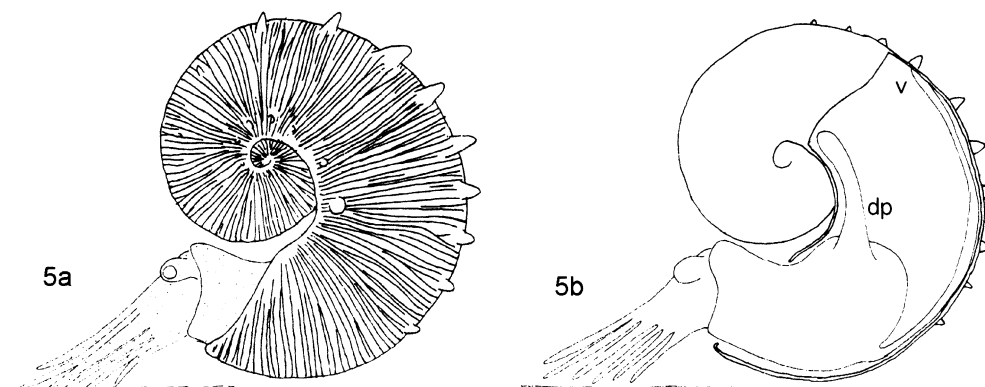
and ventrally by a single muscle, again close to the final septum. In *Rhaeboceras* at least, the radula teeth are robust but not at all elongate. The aptychi are very solid, weakly ornamented except for concentric growth rings, and more or less calcified. The lower aptychus is larger the upper one. The combination of the massive teeth and the solid aptychi would suggest scaphitids were able to process tough-shelled foods like smaller molluscs or crustaceans, rather than catching fishes or filter feeding on plankton.

The ornamentation of scaphitids contrasts with that of other heteromorphs in not being uniform along the conch. The phragmocone is usually finely ribbed and may bear small ventral or lateral spines, yielding to much coarser ribs and heavier spines on the descending shaft of the living chamber. There is another change on towards the aperture, with the ribs becoming finer again, and the spines either weakening or being lost altogether. The strongest spines are invariable on the ventral and ventrolateral surfaces of the descending shaft. Figure 5 is a reconstruction of a scaphitid (based upon *Jeletzkyites*, a Campanian member of the highly derived WIS clade). The orientation of the shell is inferred using the model I have discussed elsewhere (Monks & Young, 1998). This model supposes that ammonite bodies were gastropod-like and occupied only part of the living chamber, and when active were partially extended from the shell. Note that the spines are arrayed in such a way that they would provide a useful defence against predators from above, such as fishes, without dragging on the sea floor as the animal crawled about.

Compared with the "paper-clip" shaped heteromorphs, scaphitids do not have long

narrow body chambers and the ascending and descending limbs of the hook are rather brief. Long, straight body chambers probably prohibit nautilus-like swimming, but if the body was retracted quickly, the resulting jet would be sufficient for an escape reaction; perhaps functionally analogous to those scallops use to evade starfish (Monks, 2000). It seems probable that scaphitids were better swimmers, inasmuch as the mantle cavity was broad and shallow enough to take in and expel water sufficiently quickly and efficiently to provide continuous locomotion. Exactly how this might have worked is not clear, but paired dorsal and single ventral muscle scars can be observed in the living chambers of some species (Landman & Waage, 1993). If scaphitids were able to swim more consistently, and the ventilation of the living chamber provided useful amounts of propulsion, low-drag body forms would have been able to maximise the efficiency of this mode of locomotion.

Westermann (1996) postulated that scaphitids were midwater, with an epipelagic or vertically migrating lifestyle, and preferred moderate depths (in excess of 100 m). Juvenile and adult ecologies were essentially similar, and dispersion could have taken place throughout the lifetime of the ammonite and was not limited to the juvenile stage. In contrast, Marciniowski & Wiedmann (1985) compared the distribution of heteromorph and regular ammonites in the Albian of Poland, and noted that heteromorphs (including scaphitids) were confined to clay or marl facies, which they interpreted as having been deposited in relatively deep, quiet waters. They maintained that these heteromorphs were benthic, but noted their low



**Figure 5.** Reconstruction of a scaphitid in life (5a) and diagrammatically partially sectioned (5b). Paired dorsal (dp) and unpaired ventral (v) muscles are labelled, and the phragmocone is shaded.

tendency towards endemism compared with regular ammonites, specifically the observation that Boreal and Tethyan ammonite faunas have dissimilar regular ammonite species, but most heteromorph species are the same. This was explained by separating the benthic lifestyles of the adults from the planktonic nature of the juveniles, which would have been able to disperse freely. This hypothesis is consistent with the functional morphology trends revealed by the phylogenetic analysis performed here, specifically improvements in the streamlining of the shell and the orientation of the aperture towards the seafloor.

## ACKNOWLEDGEMENTS

The author gratefully acknowledges the assistance of A. B. Smith (NHM), M. R. Cooper (Durban) and W. J. Kennedy (Oxford) during the progress of this study, although the conclusions here reached are my own. The constructive comments of J. D. Taylor, P. D. Ward, and one anonymous reviewer on an earlier version of this paper are warmly appreciated. This work was partly funded by NERC grant GR3/11322.

## REFERENCES

- ADKINS, W. S. 1928. Handbook of Texas Cretaceous fossils. *University of Texas Bulletin* **2838**: 1-385.
- BATT, R. J. 1989. Ammonite shell morphotype distributions in the Western Interior Greenhorn Sea and some paleoecological implications. *Palaaios*, **4**: 32-42.
- BATT, R. J. 1991. Sutural amplitude of ammonite shells as a paleoenvironmental indicator. *Lethaia*, **24**: 219-225.
- BREISTROFFER, M. 1947. Sur les zones d'ammonites dans l'Albien de France et d'Angleterre. *Travaux Laboratoire de Géologie L'Université de Grenoble*, **26**: 17-104.
- CASEY, R. 1961. A Monograph of the Ammonoidea of the Lower Greensand, Part 2. *Monographs of the Palaeontographical Society* **493**: 45-118, pls. 11-25.
- CHAMBERLAIN, J. A. 1976. Flow patterns and drag coefficients of cephalopod shells. *Palaeontology*, **19**: 539-563.
- CHAMBERLAIN, J. A. 1980. Motor performance and jet propulsion in *Nautilus*: implications for cephalopod paleobiology and evolution. *Bulletin of the American Malacological Union*, **1980**: 123-127.
- COOPER, M. R. 1994. Towards a phylogenetic classification of the Cretaceous ammonites. 3. Scaphitaceae. *Neues Jahrbuch für Geologie und Paläontologie Abhandlung*, **193**: 165-193.
- EMMERSON, B. L., EMMERSON, J. H., AKERS, R. E. & AKERS, T. J. 1994. Texas Cretaceous Ammonites and Nautiloids. *Texas Paleontology Series*, **5**: 1-439. Paleontology Section, Houston Gem and Mineral Society, Houston.
- FATHERREE, J. W., HARRIES, P. J. & QUINN, T. M. 1998. Oxygen and carbon isotope "dissection" of *Baculites compressus* (Mollusca: Cephalopoda) from the Pierre Shale (Upper Campanian) of South Dakota: Implications for Paleoenvironmental reconstructions. *Palaaios*, **13**: 376-385.
- FITTON, W. H. 1836. 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.
- GILL, T. 1871. Arrangement of the Families of Molluscs. *Smithsonian Miscellaneous Collection*, **227**: 1-49.
- GILL, J. R. & COBBAN, W. A. 1966. The Red Bird section of the Upper Cretaceous Pierre Shale in Wyoming. *Geological Survey Professional Paper*, **393A**: 1-73.
- JACOBS, D. K. & LANDMAN, N. H. 1993. *Nautilus*—A poor model for function and behaviour of ammonoids? *Lethaia*, **26**: 101-188.
- KAPLAN, U., KENNEDY, W. J. & WRIGHT, C. W. 1987. Turonian and Coniacian Scaphitidae from England and North-Western Germany. *Geologische Jahrbuch*, **A103**: 5-39.
- KENNEDY, W. J. & COBBAN, W. A. 1976. Aspects of ammonite biology, biogeography, and biostratigraphy. *Special Papers in Palaeontology*, **17**: 1-94.
- KENNEDY, J. G. & JAGT, J. W. M. 1998. Additional Late Cretaceous ammonite records from the Maastrichtian type area. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Science de la Terre*, **68**: 155-174.
- KLINGER, H. C. 1980. Speculations on buoyancy control and ecology in some heteromorph ammonites. In: *The Ammonoidea. Systematics Association Special Volume 18* (M. R. House & J. R. Senior, eds), 337-355. Academic Press, London.
- LANDMAN, N. H. & WAAGE, K. M. 1993. Scaphitid ammonites of the Upper Cretaceous (Maastrichtian) Fox Hills formation in South Dakota and Wyoming. *Bulletin of the American Museum of Natural History*, **215**: 1-257.
- LEWY, Z. 1996. Octopods: nude ammonoids that survived the Cretaceous-Tertiary boundary mass extinction. *Geology*, **24**: 627-630.
- MARCINOWSKI, R. & WIEDMANN, J. 1985. The Albian ammonite fauna of Poland and its palaeogeographical significance. *Acta Geologica Polonica*, **35**: 119-219.
- MONKS, N. 1999. Cladistic analysis of Albian heteromorph ammonites. *Palaeontology*, **42** (5): in press.
- MONKS, N. 2000. Functional morphology of *Hamites* and *Stomohamites* and the origins of the Turrititidae. *Bolletino Malacologico*, in press.
- MONKS, N. & YOUNG, 1998. Body position and the functional morphology of Cretaceous heteromorph ammonites. *Palaeontologia Electronica*, **1** (www-odp.tamu.edu/paleo).
- ORBIGNY, A. 1842. *Paléontologie Française*. Paris.
- PARKINSON, J. 1811. *Organic Remains of a Former World, Volume 3*. London.
- SAGEMAN, B. B., KAUFMANN, E. G., HARRIES, P. J. & ELDER, W. P. 1997. Cenomanian-Turonian bio-

- events and ecostratigraphy in the Western Interior Basin: Contrasting scales of local, regional and global events. In: *Paleontological Events* (C. E. Brett & G. C. Baird, eds), 520-570. Columbia University Press, New York.
- SOWERBY, J. 1813. *Mineral Conchology*, vol. 3. London.
- SPATH, L. F. 1925. On Upper Albian Ammonoidea from Portuguese East Africa, with an appendix on Upper Cretaceous ammonites from Maputoland. *Annals of the Transvaal Museum* **11**: 179-200.
- SWOFFORD, D. L. 1993. *PAUP, Phylogenetic Analysis Using Parsimony*. Version 3.1. Apple Macintosh computer program.
- 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*, **46**: 339-383.
- WELLS, M. J. 1987. Ventilation and oxygen extraction by *Nautilus*. In: *Nautilus: the biology and paleobiology of a living fossil*. (W. B. Saunders & N. H. Landman, eds), p. 339-350. Plenum Press, New York.
- 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 U.K.*, **72**: 313-328.
- WESTERMANN, G. 1996. Ammonoid life and habitat. In: *Ammonoid paleobiology* (N. H. Landman, K. Tanabe, & R. A. Davis, eds), 608-707. Plenum Press, New York & London.
- WHITTAKER, S. G., KYSER, T. K. & CALDWELL, G. E. 1986. Paleoenvironmental geochemistry of the Claggett marine cyclothem in south-central Saskatchewan. *Canadian Journal of Earth Science*, **24**: 967-984.
- WIEDMANN, J. 1965. Origin, limits and systematic position of *Scaphites*. *Palaeontology*, **8**: 397-453.
- 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.
- WRIGHT, C. W. 1953. Notes on Cretaceous ammonites. I. Scaphitidae. *Annals and Magazine of Natural History (series 12)*, **6**: 473-476.
- WRIGHT, C. W., CALLOMON, J. H. AND HOWARTH, M. K. 1996. Cretaceous Ammonoidea. In: *Treatise on invertebrate paleontology. Part L. Mollusca 4 (Revised)* (R. L. Kaesler, ed.), L1-L362. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.
- YABE, H. 1910. Die Scaphiten aus der Oberkreide von Hokkaido. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und der Orients*, **23**: 159-174.