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Scaphamites passendorferi n. g. n. sp. (Ammonoidea, Cretaceous) – ancestor of Scaphitaceae MEEK?

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With 7 figures in the text

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Abstract: From PASSENDORFER'S (1930) collection of the condensed Albian of the Tatra Mountains, southern Poland, a new hamitid – *Scaphamites passendorferi* n. g. n. sp. – is described. It has a helicoid phragmocone combined with a final scaphitid hook and is twisted throughout. Its significance as presumed ancestor of scaphitids is discussed; the inclusion of Scaphitaceae MEEK in Ancyloceratina WIEDMANN is therefore supported.

Key words: New taxon (*Scaphamites*), Lytoceratida (Hamatinae, Scaphitaceae), Albian, shell, phragmocone, classification; Polish Carpathians, Tatra Mountains.

Zusammenfassung: Aus den Aufsammlungen E. PASSENDORFER'S (1930) wird ein neuer Hamitide, *Scaphamites passendorferi* n.g. n. sp., aus dem kondensierten Alb der Tatra, S Polen, beschrieben. Die neue Gattung besitzt einen helicoid entrollten Phragmokon, kombiniert mit einem scaphitiden Wohnkammerhaken. Außerdem läßt das Gehäuse eine zunächst stärkere, später schwächere Torsion erkennen. Die besondere Bedeutung dieser Form liegt darin, daß sie als Übergangsform zwischen Hamiten und Scaphiten angesehen werden kann und damit Klarheit über die systematische Stellung der Scaphitaceae MEEK innerhalb der Ancyloceratina WIEDMANN verschafft.

1. Introduction

During the revision of PASSENDORFER'S ammonite collection, partly described in his outstanding monograph »Etude stratigraphique et paléontologique du Crétacé de la série hauttatrique dans les Tatras« (1930), a group of fragmentary ammonites was recognized which was difficult to relate to any known forms. The characteristics of this group are (1) an initial coil – identical with the

^{*} Nr. 179 siehe Anderson, Hemleben, Spindler & Lindsey; Marine Micropaleontology, in press.

phragmocone – forming a helicoid narrow spiral, (2) an open final hook of body chamber, (3) all fragments being more or less distinctly twisted, and (4) finally, a hamitid suture line.

With these characteristics the new forms can phylogenetically be placed between hamitids and turrilitids on one side, and scaphitids on the other. Since the origin of scaphitids is still obscure, and therefore controversial (ROMAN 1938, WRIGHT 1957, LUPPOV & DRUSHTCHIC 1958, SCHINDEWOLF 1961–1968, WIED-MANN 1965, MIKHAILOVA 1983), it is necessary to describe these forms separately (see also MARCINOWSKI & WIEDMANN in press) in order to elucidate this important question.

Abbreviations:				
D:	diameter	I:	internal lobe	
H:	whorl height	IGPUW:	Instytut Geologii Podstawowej,	
W:	whorl width		Uniwersytet Warszawski	
R/H:	ribs per whorl height	GPIT:	GeolPaläont. Institut Tübingen	
E:	external lobe	MGL:	Musée Géologique Lausanne	
L:	lateral lobe	MHNG:	Muséum d'Histoire Naturelle,	
U:	umbilical lobe		Genève	



Fig. 1. Location map and simplified stratigraphical section.

2. Regional and stratigraphic setting

Scaphamites passendorferi n. g. n. sp. makes up part of the condensed Albian fauna of Wielka Rowien, High-Tatric Series of the Tatra Mountains in southern Poland (Fig. 1). All the fragments to be included in the new genus were found in the glauconitic limestone (0,5 m thick), a layer rich in ammonites and representing a stratigraphic condensation ranging from the floridum Subzone of the Douvilleiceras mammillatum Zone up to the altonense Subzone of the Mortoniceras inflatum Zone. This condensation was the result of very slow sedimentation and redeposition of glauconite and phosphate bearing deposits. These processes took place on the High-Tatra swell, where after a short period of emersion, sedimentation on the Urgonian reefoid limestones began again in the upper Lower Albian and continued into the Turonian (MARCINOWSKI & WIEDMANN 1985).

3. Systematic description

Suborder Ancyloceratina WIEDMANN 1966 Superfamily Ancylocerataceae MEEK 1876 Family Baculitidae MEEK 1876 Subfamily Hamitinae HYATT 1900 Genus Scaphamites n. g.

Type species: Sc. passendorferi n. g. n. sp.

Diagnosis: Hamitid with rapidly increasing rounded whorls forming a narrow helicoidal phragmocone at first and with a scaphitid living chamber. The shell is twisted throughout. Ribs are mainly simple. Suture line with four lobes, umbilical lobe remains undivided.

Remarks: Characteristic of the new genus is a two- or possibly threefold ontogenetic development, of which only the middle and adult age is preserved. But from the geometry of the earliest known parts we can assume that the initial coil was open and formed a fragile, tiny whorl, comparable with the innermost whorl of *Eoscaphites*. This early "hamitid" stage is followed by an extremely rapid increase in whorl height and width, now forming a narrow helicoidal coil. This coil is distinctly twisted. In the adult, the living chamber forms a scaphitid final hook which again is twisted. This ontogenetic development as well as the stratigraphic occurrence support the idea that *Scaphamites* is the hamitid ancestor of Scaphitaceae.

Age: As the type species.



Fig. 2. Scaphamites passendorferi n. g. n. sp.

- A-C: Holotype, IGPUW WR. 96, phragmocone. A Ventral view, B Lateral view, C Frontal view. 2/1.
- D-F: Paratype, IGPUW WR (3). 93b (see also PASSENDORFER 1930, pl. 4, fig. 76), part of phragmocone. D Ventral view, E Lateral view, F Frontal view. 3/1.
- G-H: Paratype, IGPUW WR (2). 92a, bod hamber. G Ventral view, H Lateral view. 2/1.
- I-K: Paratype, IGPUW WR (2). 90a, bc hamber. I Ventral view, K Lateral view. 2/1.

Scaphamites passendorferi n. g. n. sp. Figs. 2 A-K, 3, 6

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

Holotype: Specimen IGPUW - WR. 96.

Paratypes: Specimens IGPUW - WR (2). 90a/91a/92a, WR (3). 93b/95b.

Derivatio nominis: In honour of Prof. Dr. EDWARD PASSENDORFER († 1984)

Diagnosis: Same as above. Whorl section broadly rounded with maximum thickness occurring on central flanks. About 30 single and straight ribs per whorl cross flanks and venter, but are diminished on dorsum. Suture line with 4 lobes and symmetrically divided main saddles. U relatively small and trifid, I larger and likewise trifid.

Description: The new species is known only from fragments, but the complete shape is easy to reconstruct (Fig. 6). At present only the innermost whorl is unknown. From the smallest fragment preserved and its geometry (Figs. 2 D-F) we can assume that the earliest whorl must have the same tiny and fragile shape we know from the initial *Eoscaphites* (Fig. 4 E). No dorsal concavity can be observed, but there is a feeble impression (Figs. 2E, F) at the upper umbilical seam marking the position of the necessarily tiny, rounded and somewhat twisted initial coil. This coil was most probably open.

Thereafter, the increase in whorl height and width is – again as in *Eoscaphi*tes – enormous (Figs. 2 A–F). The resulting helicoidal shape which coincides with the later phragmocone is finally followed by the scaphitid hook of the body chamber (Fig. 2 G–K). Twisting can be recognized throughout but is diminished with age. At the same time the whorl section changes from broadly rounded at first to circular, finally becoming broadly rounded again with a maximum thickness in the center of flanks. Only the venter is rounded, the dorsum being flattened. The sculpture remains the same throughout ontogeny. About 30 ribs occur per whorl and are single, sharp and distinctly narrower than the interspaces. They are less crowded in early ontogeny (5–6 R/H) and more crowded on the central hook (8–10 R/H). On the complete body chamber hook (Fig. 2 K), the final constriction at the mouth border can be observed and the beginning of biplicate ribbing.

Measurements:	D	H max.	W max.	R/H
Holotype IGPUW-WR. 96:	15 mm	7,4 mm	6,5 mm	8
Paratypes - WR(3). 93b:	14	6,3	6,3	6
•	12	5	6	5
- WR(2). 90a:	21	9	10	8
- WR(2). 92a:	19	8	9	8-10

It is interesting to note that the complete suture line is nearly symmetrical on both shell sides in spite of the fact that the whole septum is distorted (Figs. 2F, 3). The four lobes, E, L, U and I of Cretaceous heteromorphs can be recognized.



Fig. 3. Scaphamites passendorferi n. g. n. sp. Complete suture line of paratype IGPUW WR (3). 93b, at whorl height 5 mm.

Saddles EL and LU are symmetrically subdivided, the internal saddles and lobes are curved backward and therefore(?) asymmetric. I and U are trifid, U remains relatively small and undivided.

Comparison: PASSENDORFER (1930: 670) referred to the present fragments as *»Heteroceras*? sp.«, in which genus he classified the early turrilitids. And, indeed, there is some similarity of the early coil with that of *Proturrilitoides* BREIS-TROFFER. The twisted coiling, however, is typical of hamitids and anisoceratids as well. The same can be said about the suture line which still keeps its hamitid – anisoceratid character (cf. WIEDMANN 1962b, text-fig. 33b). But coiling is much narrower and the umbilicus of the phragmocone much smaller than is the case in true hamitids. Also, the extremely rapid increase in whorl diameter is unknown from any true hamitid. Scaphitid final hooks are not uncommon in hamitids (see *Hemiptychoceras, Metahamites*), but they are usually linked with pronounced sculptural change. *Hamitoides* is much larger and has biplicate ribs.

The nearest species within the hamitids may be *H*. (*Hamites*) helicoides WIEDMANN (pro »*Helicoceras*« annulatum D'ORBIGNY) which is, however, a true, open-coiled *Hamites*.

Very similar in its mode of coiling is, indeed, *Protanisoceras nodosum* (J. SO-⁴ WERBY) as figured in SPATH (1939, text-fig. 205e and pl. 64, fig. 2). But this is a true anisoceratid with periodic marginal tubercles. This is one more case of great similarity between hamitids and anisoceratids, actually separated in different families.

At the same time there are obvious similarities to the early turrilitid genus *Turrilitoides* SPATH as re-defined by WIEDMANN (1962a: 189). *Turrilitoides* s. l. is characterized by its open helicoidal spiral and the absence of any tuberculation on its single ribs. But neither twisted coiling nor scaphitid living chambers have been observed in *Turrilitoides*. Moreover, the genus first occurs with its subgenus *Proturrilitoides* BREISTROFFER in the Middle Albian.



Fig. 4. Eoscaphites BREISTROFFER.

A-D: Eoscaphites circularis (J. DE C. SOWERBY). A, B- Lateral and frontal view of phragmocone GPIT CE 1221/1, varicosum Subzone of Upper Albian, Folkestone (Kent, U. K.), 1/1. C, D- Lateral and frontal view of phragmocone MGL 12341/1, condensed Upper Albian, Perte du Rhône (Ain, F.), 1/1.

E-L: *Eoscaphites subcircularis* (SPATH). E- First whorl preserved of paratype MHNG Wi »SC«/3, frontal view. Upper Albian, Crioud? (Hte Savoie, F.) 6/1. F, G- Complete hypotype MHNG Wi »Sc«/2, lateral and ventral views, Lower Upper Albian, Mt. Saxonet (Hte Savoie, F.), 1/1. H-L: Complete hypotype MGL 12342, frontal, lateral and ventral views and frontal view of coiled portion (L), Lower Upper Albian, Perte du Rhône (Ain, F.). 1/1.

Finally, there is a great similarity to the early scaphitid Eoscaphites BREIS-TROFFER which was described in detail by WIEDMANN (1965). Some characteristic specimens of Eoscaphites circularis (I. DE C. SOWERBY) and E. subcircularis (SPATH) and their suture lines are reproduced (Figs. 4, 5) to permit a better comparison. As can be seen from Fig. 4, all Eoscaphites - E.(?) tenuicostatus (PERVIN-QUIERE) included - have a planispiral type of coiling, but they also start with a tiny and fragile whorl surrounding an open umbilicus (Figs. 4 A-E). The ventral concavity is a later development (Figs. 4 B, E) related to the rapidly increasing involution of the phragmocone which can be seen from Figs. 4 C, D, L. The increase of whorl height and width during one whorl is extreme (Fig. 4 E). Nearly the same development can be assumed for Scaphamites n. g. The final hook of E. circularis, the ancestral species, is not yet known; but from the most complete specimen, the neotype (SPATH 1937, pl. 57, fig. 1; WIEDMANN 1965, pl. 53, fig. 3), a similar shape as in Scaphamites passendorferi n. g. n. sp. without any lateral bulges, can be assumed. Also, the type of ribbing is very similar in both species. The only difference is that biplication of ribbing rapidly increases via E. circularis to E. subcircularis and is most probably also related to increasing involution.

Nearly the same can be said about the sutural evolution. Unfortunately, at the present time only advanced and late suture lines are known from *Scaphamites* n. g. and *Eoscaphites*. But from the minute early whorls (Fig. 4 E) only a quadrilobate primary suture is to be expected. At a whorl height of 1,7 mm this suture line is truly quadrilobate (Fig. 5 c). It remains quadrilobate throughout life in *Eoscaphites circularis* (Fig. 5 a, b) and, thus, is very similar to the suture line of *Scaphamites passendorferi* n. g. n. sp. (Fig. 3). In all these cases the lobe U is smaller than I and – more importantly – undivided. We can conclude that bi- or trifidity of U as well as the symmetry of saddle UI is related to the above mentioned retraction of the internal suture line. This retraction – and the resulting asymmetries – may or may not occur in hamitids and anisoceratids in one and the same species (cf. WIEDMANN & DIENI 1968, textfigs. 48–50).

The later subdivision of U in *Eoscaphites subcircularis* (Fig. 5 d) is the consequence of the formation of a distinct umbilical seam subdividing the umbilical lobe. The same occurs several times in Cretaceous heteromorphs (i. e. *Ptychoceras* in WIEDMANN 1962 b, text-figs. 31, 32) and cannot be related to a postulated lytoceratid ancestry (MIKHAILOVA 1983: 179).

The most important differences between *Scaphamites* n. g. and *Eoscaphites*, thus, remain the helicoidal phragmocone and the twisting which becomes less pronounced with age. But we have to consider that – as in most juvenile phyla – evolution was very rapid during the early »construction« of the scaphitid stock. *E. circularis* and *E. subcircularis*, both exhibiting distinct evolutionary steps in coiling and suture differentiation, evolved nearly at the same time, in the varicosum Zone of Early Upper Albian. *Scaphamites passendorferi* n. g. n. sp. may also d



- a, b: Eoscaphites circularis (J. DE C. SOWERBY). a- Specimen MGL 12341/1, Lower Upper Albian, Perte du Rhône, at whorl height 3,5 mm. b- Specimen GPIT Ce 1221/1, varicosum Subzone, Folkstone, at whorl height 5 mm.
- c, d: Eoscaphites subcircularis (SPATH). Specimen MHNG Wi »Sc«/3, Upper Albian, Crioud? c- at whorl height 1,7 mm (rounded whorl section, see also Fig. 4 E), d- at whorl height 3,5 mm.

have the same or a slightly older age. This means that we are really confronted with the juvenile, »explosive« phase of scaphitid evolution.

Occurrence: Scaphamites passendorferi n. g. n. sp. occurs in the condensed glauconitic Albian (floridum through altonense Subzones) of Wielka Rowien, High-Tatric Series, Tatra Mountains, Poland. The evolutionary position of this species (Fig. 7) suggests an uppermost Middle and/or lowermost Upper Albian age.

4. The origin of scaphitids

There is still much controversy about the origin and systematic position of scaphitids. While previous authors were convinced by the great variety of scaphitid sculptures and, consequently, regarded scaphitids as a group of polyphyletic origin (NOWAK 1911, REESIDE 1927, ROMAN 1938, SCHINDEWOLF 1961), most recently a monophyletic origin has been favoured. SPATH (1933, 1934) and WRIGHT (1953, 1957) related the later superfamily Scaphitaceae (WRIGHT & WRIGHT 1951) to the lytoceratids due to their loose coiling. PERVINQUIERE (1907) was the source of attribution of scaphitids to the suborder Ammonitina due to the existence of trifid lateral lobes (L) in both. He was followed by Ro-MAN (1938), LUPPOV & DRUSHTCHIC (1958), DRUSHTCHIC (1962), and others. But COBBAN (1952), in one of his magnificent papers, was able to demonstrate how easily bifid scaphitid lobes pass into trifid ones in one and the same evolutionary line. This was later confirmed for the Scaphites equalis-group by WIED-MANN (1962 a: 214), and moreover we have previously noted that U also easily changes its bifid or trifid shape in relation to changes in geometry of the internal suture line.

In his famous »Studien zur Stammesgeschichte der Ammoniten«, SCHINDE-WOLF initially (1961) misinterpreted the suture ontogeny of scaphitids and regarded Scaphitaceae – with the exception of the quadrilobate Eoscaphites – as offshoots of both lytoceratids and Ammonitina. The problem with most of these earlier interpretations was that they were mainly based on late Upper Cretaceous forms. This was one of the reasons to re-investigate the early scaphitid lineages in late Albian and early Cenomanian times (WIEDMANN 1965). The results were: early Eoscaphites have distinctly quadrilobate suture lines and open initial coils of hamitid shape. The later and more complicated suture lines are quadrilobate as well, but the lobe U rapidly becomes subdivided (U_v, U_d), and an increasing number of saddle incisions (»pseudolobes«) are developed in the saddle LU. The parallel development of ontogenetic and phylogenetic suture evolution was demonstrated (op. cit., text-figs. 14, 15), and the origin of the monophyletic group in late Middle Albian hamitids was postulated. Scaphitaceae were, therefore, included in Turrilitaceae. Later, with the discovery of »false hoplitids« and the establishment of the heteromorph suborder Ancyloceratina



Fig. 6. Reconstruction of Scaphamites passendorferi n. g. n. sp.

(WIEDMANN 1966), superfamily Scaphitaceae became re-established and defined by the development of »pseudolobes« (p1, p2, . . .), an opinion later shared by SCHINDEWOLF (1968).

MIKHAILOVA & TEREKHOVA (1982) and MIKHAILOVA (1983), however, returned to the view, that Scaphitaceae must be related to lytoceratids due to the subdivision of U and the positioning of the siphuncle. Moreover, these authors demonstrated that scaphitids start with a 5th lobe in the primary suture which becomes lost in very early ontogeny but reappears with age (MIKHAILOVA 1983: 179, fig. 62). But as far as can be documented, this general assumption again is based on only a few specimens, all of late Upper Cretaceous age. Therefore, these general assumptions are irrelevant to the problem of scaphitid origin. The sporadic re-appearance of a 5th primary lobe in Cretaceous heteromorphs (MIKHAI-LOVA 1983), has to be considered, but does not necessarily alter the concept of ancyloceratid classification (WIEDMANN 1966, 1969). The reappearing 5th lobe -»U'« in MIKHAILOVA's terminology (1983, fig. 62 l) – in late ontogeny of Scaphites puerculus is in reality the pseudolobe »p1« in the terminology of WIEDMANN (1965). This is easily be proven by comparing this »lobe« with the saddle incision in EL, which appears at precisely the same time. Subdivision of U is by no means an exclusively lytoceratid feature. It is known from many ammonitid superfamilies as well as from true heteromorphs. As mentioned above, WIEDMANN (1962 b, text-figs. 31, 32) was able to demonstrate that subdivision of U immediately follows the appearance of a dorsal concavity and an umbilical seam in the heteromorph species *Ptychoceras laeve* MATHERON. This observation was confirmed by MIKHAILOVA (1983, figs. 54, 55) in describing suture ontogenies of *Ptychoceras*. But it is again one of the difficulties with the Russian suture terminology that, in this case, the author preferred to establish a new lobe (*I'*). In true lytoceratids, however, even a third separate umbilical lobe ($*I_**$) is distinguished (MIKHAILOVA 1983, figs. 42, 43), and therefore no subdivision of the umbilical lobe is terminologically documented. In consequence, the only group with a terminologically observable subdivision of the umbilical lobe ($*I_**, *I_d*$) is the scaphitids (MIKHAILOVA 1983: fig. 62). And if we look for related suture lines, we are much surprised to find exactly the same suture ontogeny and formula' in the perisphinctid *Simbirskites* (MIKHAILOVA 1983: fig. 34).



Fig. 7. Phylogeny of early scaphitids.

Does Scaphamites passendorferi n. g. n. sp. really contribute to the solution of the problem of scaphitid origin?

First it must be stressed again that – as in the case of Douvilleicerataceae (WIEDMANN 1966) – the question of phylogenetic origin can only be solved by studying forms at the very base of the new stock and, of course, using all available systematic features. The opinion that *Eoscaphites circularis* can be regarded as the earliest scaphitid species is today generally accepted. The features which *E. circularis* has in common with *Scaphamites passendorferi* n. g. n. sp. are the following:

^{&#}x27;In Russian terminology this formula is V U U' I, Id D.

- suture line with four lobes (E L U I)
- umbilical lobe U is still undivided, smaller than I, but may be bifid or trifid
- shape of lobes and saddles
- a tiny, open-coiled initial part is recognized in the eoscaphitid and presumed to exist in the scaphamitid
- rapid increase of shell involution as well as of whorl height and width during mid-life
- the final scaphitid hook of the living chamber, without lateral bulges, not yet completely known from the eoscaphitid
- similar type of ribbing.

On the other hand, the differences between both species are:

- 1- the mode of coiling, which is in one plane in the eoscaphitid but helicoidal on the phragmocone and twisted throughout in the scaphamitid
- much stronger ribbing and the very beginning of biplications in the scaphamitid, and
- the less denticulated, more hamitid-like suture line of the latter.

Thus the degree of congruency is very high. On the basis of numerical taxonomy, *Scaphamites passendorferi* n. g. n. sp. might be included in *Eoscaphites*. But helicoid coiling and twisting are among the main characteristics of hamitids and anisoceratids, and therefore the new genus must be included in the Hamitinae (Fig. 7). But the high degree of congruency with *Eoscaphites*, and especially with *E. circularis*, elucidates the true relationships and, thus, the origin of the scaphitids in the Ancylocerataceae. Despite the continuity of transition, the separation of Scaphitaceae – on the basis of their specific suture and morphological features – can be maintained, and there is no need to separate them from the common suborder Ancyloceratina.

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