

# ORIGIN, LIMITS, AND SYSTEMATIC POSITION OF *SCAPHITES*

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**ABSTRACT.** Up to the present interpretations concerning the origin and systematic position of the Cretaceous heteromorph *Scaphites* have been extremely divergent. On one hand, scaphitids have been regarded as a monophyletic group of either lytoceratid (e.g. Spath 1933, 1934; Wright 1953, 1957) or ammonitid origin (Luppov and Drushtchic 1958; Drushtchic 1962), on the other hand, as a more or less polyphyletic accumulation (Nowak 1911; Reeside 1927a; Schindewolf 1961). Wright and Wright (1951) established a superfamily Scaphitaceae, directly connected with the lytoceratid stock, while in the recent Russian literature they are placed in the Ammonitina. Reeside distributed the scaphitids among four different ammonitid lineages. All these possibilities of scaphitid classification are discussed here. A monophyletic but hamitid origin of the true scaphitids is asserted: 'Otoscapitinae' Wright are regarded as heterogeneous (*Otoscapites* is a true *Scaphites*, but *Worthoceras* should be placed in Ptychoceratinae), and Labeceratidae Spath are referred to the anisoceratids. The suture line of the restricted *Scaphites* was found to be quadrilobate throughout, as in all other heteromorphs. This makes the superfamily rank unnecessary, in the author's opinion, and places the remaining family Scaphitidae in the Aneylocerataceae, as recently defined by Wiedmann (1962b).

In the last half-century many opinions have been given about the systematic position and origin of the scaphitids. The divergent interpretations naturally depend on the different evaluations placed on features such as general morphology, sculpture, suture elements or suture development. They also depend on the stage of evolution, and we will obtain differing results through the study of primitive Upper Albian or highly specialized Maastrichtian material. It is a curious fact, but nearly all these opinions, Spath (1934) and Wright (1953) excepted, were founded on late uppermost Cretaceous species. This publication is based on early scaphitids of Upper Albian and Cenomanian age and traces a new outline of history and extent of these peculiar Cretaceous heteromorphs.

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I am also indebted to Dr. P. Rodda (Austin) for making Adkins's and Moreman's types of the Texan *Worthoceras* available to me, and to Professor Dr. W. P. Popenoe (Los Angeles) who kindly sent me some Californian *Otoscapites* from his collection for comparison. Further thanks are due to Mr. W. Wetzel (Tübingen) who made the photographs in a superior manner as always, and to Mr. Springer, the draughtsman of the Institute of Tübingen. Cordial thanks are also due to R. Pichler (Tübingen) who revised the English text, and especially to Mr. C. W. Wright (London) for critical reading of the typescript.

*Abbreviations.* The terminology of the suture-line used here is that of Wedekind and Schindewolf. It is not only the most simple, but also the most natural, now generally accepted in the Western [Palaeontology, Vol. 8, Part 3, 1965, pp. 397-453, pls. 53-60.]

hemisphere. In the scaphitids we find the most simplified suture-line, with only four true lobes: internal lobe (*I*), umbilical lobe (*U*), lateral lobe (*L*) and external one (*E*). In addition to these true lobe elements the term pseudo-lobe (*p*) will be introduced here for a group of saddle incisions, situated in *Scaphites* between the elements *L* and *U*, and increasing to normal lobe size. The saddles will be defined according to Schindewolf by the surrounding lobes, i.e. *L/E* for the so-called first lateral saddle, *L/U*, &c. The continuously proposed Russian terminology (Ruzhencev 1960) should definitely be rejected, because the lobe symbols of Wedekind are used in a completely different sense, which leads to general confusion. Moreover the Russian terminology is too complicated for application to Cretaceous ammonites (Wiedmann 1963).

The measurements are expressed with the following symbols:

- D* Greatest diameter of spiral portion and final hook,
- B* Maximum thickness of spiral portion and final hook,
- d* diameter of the spiral portion,
- h* maximum whorl height of the spiral portion,
- b* maximum whorl thickness of the spiral portion,
- u* umbilical diameter of the spiral portion.

The types described here are deposited in the following institutions: Institut für Geologie und Paläontologie, Tübingen (GPIT); Muséum d'Histoire Naturelle à Genève (MHNG); Musée Géologique de Lausanne (MGL); Bureau of Economic Geology, University of Texas, Austin (BEGA); Muséum National d'Histoire Naturelle à Paris (MHNP), and the British Museum of Natural History, London (BMNH).

#### PREVIOUS WORK AND CURRENT PROBLEMS

Subsequent to Parkinson who created the genus *Scaphites* in 1811, all Cretaceous heteromorphs with scaphitoid living chamber were included here. D'Orbigny (1842, p. 514) was the first to recognize that the Lower Cretaceous *yvanii* group should be separated, which was named *Macroscaphites* by Meek (1876). Furthermore Meek proposed a separate family Scaphitidae to include only the genus *Scaphites*. He did not, however, explain his concept of its relationship. One year before, Neumayr (1875) had published his reflections on the systematics of Cretaceous ammonites. He interpreted *Scaphites* as a true monophyletic group, and related them, because of the form of their inner whorls, suture-line, and aptychus, with the perisphinctid genus *Olcostephanus*. He was the first who stated that the scaphitids are distinguishable from all other heteromorphs through the presence of so-called 'auxiliary' (= umbilical) lobes. From this point on the family Scaphitidae was moved through nearly the complete ammonite system.

It was Zittel (1884) who placed *Scaphites* in the Stephanoceratidae, and *Macroscaphites*, according to its suture-line, correctly in the Lytoceratidae. The opinion that *Scaphites* might also represent a lytoceratid descendant was rigorously rejected by Grossouvre (1894) on the grounds that the strong ornamentation of the scaphitid shells is more significant than their bifid lateral lobes. Thus scaphitids were included in the Pulchelliidae or the Acanthoceratidae, and interpreted as direct derivatives of *Stoliczkaia dispar*.

Logan (1899) came to an unusual opinion; he placed *Scaphites* in the Stephanoceratidae as usual, but regarded the highly incised suture-line of *Scaphites* as a progressive and not degenerate feature. *Scaphites* was referred to the lytoceratids for the first time by Hyatt (1900), but there we also find the observation (op. cit., p. 572) that

the young stages of *Scaphites* 'possess the general aspect of *Pachydiscus*, and there are species transitional between them'. At the same time he proposed a number of new scaphitid genera, but without any diagnosing descriptions.

J. P. Smith (1901) seems to be the author of the polyphyletic theory. He thought of at least two different origins of scaphitids, one in the hoplitids, the other in lytoceratids. He was followed by W. D. Smith (1905) who studied the ontogenetic suture development of different scaphitid species. In *Sc. nodosus* and its allies the lateral lobe was found to be trifid at first, becoming bifid in the adult stage. The group of *Sc. perrini-inermis-condoni*, however, was said to have a bifid lateral lobe throughout, a wider umbilicus, and reduced ribbing. Thus the former were included in stephanoceratids, the latter in lytoceratids. Contrary to Logan he emphasized the reduction of the fourth main lobe (*U*) during the ontogeny, and therefore interpreted the scaphitid suture as degenerate. Pervinquière (1907) came to a similar result, believing that also in the scaphitid type species, *Sc. equalis*, the original shape of the lateral lobe is trifid, becoming bifid with age. Therefore and with regard to morphologic differences in the early ontogeny, the lytoceratid ancestry of true scaphitids as well as the attachment to *Stoliczkaia* was rejected. He returned to Neumayr's opinion, i.e. that of an olcostephanid (or holcodiscid) origin for the true *Scaphites*. Decisive for these interpretations was not only the originally tripartite *L*, but also the sculpture and general aspect of the primitive scaphitid whorls. He persisted in favouring a lytoceratid ancestry only for a restricted group of Upper Cretaceous forms like *Sc. cunliffei*, considering as significant a bifid *L* which keeps symmetry throughout, despite its different sculpture and general appearance.

Yabe's (1910) scaphitid classification using the internal saddle (*I/U*) should be mentioned. The species with entire saddles *I* and *U*, which form Yabe's new genus '*Yezoitites*', agree only in their small size. In reality they belong to three different scaphitid developments. It was Nowak (1911) who rectified this conception with the statement that the character of the internal suture should not be regarded exclusively, but only in combination with all other systematic features; shell form, sculpture, and, naturally, also external suture. He regarded the ontogenetic development in its complexity, as the main feature in ascertaining a natural relationship. Through this he proposed a treble origin of *Scaphites*: the Cenomanian *equalis* group was derived from *Olcostephanus*, the Campanian *tridens* group from *Acanthoceras*, and the Maastrichtian *constrictus* group was said to have a hoplitid origin. This conception is reflected in the new generic names which Nowak proposed: '*Holcoscaphtes*' (= *Scaphites* s. str.), *Acanthoscaphtes* and *Hoploscaphtes*. According to Nowak a scaphitid living chamber was produced repeatedly by parallel development.

It should be mentioned that J. P. Smith placed a subfamily Scaphitinae in Cosmocera-tidae in the 2nd edition of Eastman's Textbook.

In 1915 Frech tried to introduce a new grouping of scaphitids. This was based on the mode of ribbing and tuberculation, but it was of more stratigraphic than systematic significance, and therefore rejected by Nowak (1915).

As a curious fact we note the opinion of Rollier (1922), where the Upper Cretaceous *Scaphites* was related to Upper Jurassic oppeliids, the so-called *Proscaphites*. In his first paper dealing with scaphitid systematic, Spath (1922) retained Nowak's interpretation and related through sculptural evidence some of the Upper Senonian *Hoplo-* and *Acanthoscaphtes* to a hoplitid (*Hoplitoplacentoceras*), some others to a desmoceratid source

(*Menites*). This was probably the reason for Reeside (1927b) to propose a further generic name, *Desmoscaphites*, for a restricted group of Upper Senonian forms (*Sc. bassleri* and allies) which have the morphological appearance of *Desmoceras*. Furthermore Reeside gave the first correctly drawn development of the scaphitid suture from the Campanian *Sc. hippocrepis*. He recognized the quadrilobate first suture, consisting only of the elements *I*, *U*, *L*, and *E*. The adult suture-line was interpreted as having two or three 'auxiliaries' (= umbilical lobes). The lateral lobe was found to be bifid throughout.

In the same year Reeside published a summarizing paper (1927a) containing a review of all previous works and a catalogue of the known scaphitid species with their new generic attributes. He eliminated some of Nowak's genera, identifying *Hoploscaphites* with the American *Discoscaphites* Meek, and '*Holoscaphites*', '*Anascaphites*' Hyatt, '*Jahnites*' Hyatt, and '*Yezoites*' Yabe with the true *Scaphites*. In phylogenetic aspects he followed Nowak unreservedly and proposed the following arrangement for the four remaining genera:

- (1) *Scaphites* was placed into a subfamily of its own, which was referred to the Stepheoceratidae.
- (2) *Desmoscaphites* in the desmoceratid Silesitinae.
- (3) *Discoscaphites* in the Hoplitidae, and
- (4) *Acanthoscaphites* in the Acanthoceratidae.

This was the maximum ever attained in splitting the scaphitid heteromorphs.

In 1928 Adkins called attention to the Upper Albian scaphitoid group of '*Macroscaphites*' *platydorsus* Scott, for which he proposed the new genus *Worthoceras* of 'uncertain position'. It was said to differ from both *Scaphites* and *Macroscaphites* through its reduced suture-line in spite of its hooked body-chamber. Its sutural affinities with *Mastigohamites* and even with *Adkinsia* were considered and it was provisionally placed with the latter as an annex to the lytoceratid heteromorphs. *Scaphites* was still included in Stepheoceratidae.

In 1933 and finally in his monograph '*Ammonoidea of the Gault*' (1934, 1937) Spath brought new classifying aspects into the confusion of the scaphitid history. He drew attention to *Sc. circularis* (J. de C. Sowerby) of the British Upper Albian, an evidently lytoceratid member, which he considered to be the origin of all later *Scaphites*. Unfortunately this species remained poorly illustrated, as also the somewhat more advanced *Sc. subcircularis* Spath. The poor specimen illustrated by Spath of *Sc. circularis* makes it evident, that this species is a true heteromorph. It preserves a quadrilobate suture-line, bifid lateral lobe, fine lytoceratid striation of the shell, and a crioceratid uncoiling of its septate portion. Through the very insufficient figures of suture and inner whorls of *Sc. subcircularis* (Spath, op. cit., text-fig. 175e, pl. 57, figs. 10-12) we are unable to decide whether this species belongs to the same quadrilobate suture type or to that of the true Upper Albian *Scaphites*, like *Sc. hugardianus* or *Sc. simplex*. In these species the uncoiling of the chamber is distinct as also a highly differentiated umbilical suture and a sometimes 'trifid' lateral lobe. The only visible difference from *Sc. subcircularis* is the higher involution of the inner whorls.

Spath's attempt to connect a monophyletic scaphitid stock (*Worthoceras* included) with a true lytoceratid ancestor was not accepted by all succeeding authors.

Roman (1938) continued though to distribute *Scaphites* among three different ammonite families: Olcostephanidae (*Scaphites* and *Holcoscaphtes*), Palaeohoplitidae (*Hoploscaphtes*), and Acanthoceratidae (*Acanthoscaphites*). In full accord with Spath, Breistroffer (1947) proposed the separation of *Sc. circularis* and *subcircularis* into the new subgenus *Eoscaphtes*, which he regarded like Spath as the most primitive scaphitid member. In his magnificent paper Cobban (1952) treated the evolutionary lines of *Scaphites*, originating from the Colorado group (Turonian to Campanian) of the United States. He very clearly demonstrated (op. cit., text-fig. 3), that it is impossible to isolate the Upper Cretaceous forms with trifold *L* from their bifid forerunners. He made it evident that the connexion between these apparently different lobe types can be proven by all intermediaries. The different lineages of scaphitid development in the Colorado group were found to converge on a single initial-point, the Turonian *delicatulus* group, which is otherwise of evident morphologic relationship with the Cenomanian type *Scaphites*, *Sc. equalis*. This was the first detailed demonstration of the change in sutural characters which was entailed by the monophyletic interpretation of the scaphitid development as proposed by Spath. Cobban furthermore showed that the asymmetric development of *L* was accompanied by a progressive reduction of the uncoiled body chamber, which at the end overlapped the initial coil. At the same time the sculpture was found to decrease in its degree of differentiation (main and secondary ribs, tuberculation) and become denser and more uniform (op. cit., text-fig. 2).

In the same year C. W. Wright (1952) presented 'A Classification of the Cretaceous Ammonites' in relation to the forthcoming *Treatise on Invertebrate Palaeontology*. We find here a monophyletic superfamily Scaphitaceae (proposed one year earlier (1951) by Wright and Wright), derived from the lytoceratid main stock (op. cit., text-fig. 1). In a short note on Scaphitidae C. W. Wright (1953) explained his position in more detail. He agreed completely with Spath regarding *Eoscaphtes* as the 'probably earliest scaphitid' and the family Scaphitidae as a natural unity, with one exception; he believed that there is a parallel scaphitid stock with lappeted mouth-border and more evolute spiral portion, connecting *Worthoceras* with the Turonian *bladenensis* (= *Sc. auritus* auct.) group. For the latter he proposed the new generic name *Otoscaphtes* and grouped the two genera in a subfamily 'Otoscaphtinae' which were thought to originate, like the true *Scaphites*, in *Eoscaphtes*. In Wright (op. cit., p. 474) already we find the critical remark that 'were it not for the evidence that they are in series it might be thought that they were merely a group of separate lappeted offshoots of various Scaphitinae'. This question will be treated below in detail.

In 1952 the ammonite part of the 'Traité de Paléontologie' was published by the French ammonitologist Madame Basse. This first in the recent series of text-books needs no further discussion for our purpose, because the scaphitid classification was evidently taken from Wright (1952). Scaphitaceae were regarded as a monophyletic section of the Lytoceratina.

Second in the sequence of standard works about cephalopods, was the ammonite volume of the *Treatise of Invertebrate Palaeontology*. The excellent description of Cretaceous ammonites is due to C. W. Wright (1956) who standardized Spath's views of the scaphitid problem. The superfamily Scaphitaceae was included in Lytoceratina, containing Scaphitidae and (following Spath 1925, 1939) Labeceratidae, an exclusively Upper Albian group of hamitoid and scaphitoid uncoiled heteromorphs with trifold *L*.

Labeceratids are confined to the Southern hemisphere. The family Scaphitidae is said to be 'probably derived from some member of the Lytocerataceae'.

Two years later Luppov and Drushtchic (1958) published the Russian treatise on mesozoic ammonites, where Scaphitaceae are also regarded as a monophyletic unit, including both Scaphitidae and Labeceratidae. But here the superfamily is placed among the true Ammonitina, following the acanthoceratid family Vascoceratidae. Indeed we occasionally find in the Turonian *Vascoceras* (but also in some Senonian tissotiids) a tendency to scaphitoid uncoiling of the living-chamber. The trifid lateral in *Sc. equalis* and the labeceratids is responsible for the arrangement in the Ammonitina, as also the strong ornamentation of many scaphitid and labeceratid species.

In his doctorate thesis (Wiedmann 1960, published 1962*a*) the author was able to demonstrate that there is no good reason to assume an originally trifid lateral lobe in *Sc. equalis*. In the early ontogeny of this species the lateral shows a distinct bifid shape up to a diameter of 1.5 mm. Thereafter the lobe outline becomes more and more trifid through asymmetrical growth, but soon after it again acquires its original form. It is evident that Pervinquière recognized only the ultimate change. As in the case of the Senonian trifid scaphitids, the lytoceratid origin can be ascertained also for the Cenomanian type forms as Spath and Wright maintained. Neither the polyphyletic interpretation of scaphitids nor its derivation from acanthoceratids seems necessary. Reeside's suture development was reproduced (op. cit., text-fig. 1) and compared with that of other lytoceratids and phylloceratids. While the quadrilobate first suture-line was found to be in complete agreement with that of other heteromorphs (*Baculites*), the extreme degree of its sutural regeneration was noted. According to Reeside the acquisition of three additional umbilical lobes was supposed in the adult suture of *Scaphites*, while in all other heteromorphs the suture-line remains quadrilobate throughout (in the Lytocerataceae the first suture contains five elements, but a single additional lobe can occasionally be acquired). Thus the scaphitid suture development approaches to that of some phylloceratids. This convergence was interpreted as the result of the unusual increase of involution in *Scaphites*.

The last important contribution to the systematics of *Scaphites* was made by Schindewolf in the first part of his 'Studien zur Stammesgeschichte der Ammoniten' (1961). Here he describes the ontogenetic suture development of Phylloceratina, Lytoceratina, and the heteromorphs. Like Reeside he studied, in '*Acanthoscaphites*' *roemeri*, a highly developed Campanian member of the scaphitid stock, in which he also recognized (op. cit., text-fig. 58) up to three additional umbilical lobes in the adult suture. Different from the previous citations, however, is the existence of five elements in the first reproduced suture (as in all Lytocerataceae, Ammonitina, and Phylloceratina). The first suture reproduced by Schindewolf does not coincide with the true 'Primärsutur'.

Schindewolf regards this highly differentiated suture type as characteristic of all true *Scaphites* which he claims cannot be connected with the reduced quadrilobate sutures of *Eoscapites* or *Worthoceras*. He proposes to separate these, including Labeceratidae, from *Scaphites*, but the systematic position of the latter seems difficult to interpret. On the one hand, he does not hesitate to relate *Scaphites* and the other heteromorphs to the Lytoceratidae (p. 109, top); on the other, he states that the 'greater number of suture elements, shape and sculpture place *Scaphites* near those forms which are placed in the suborder Ammonitina' (translated from p. 109, bottom). The solution

to this interesting problem is announced for the summarizing part of his forthcoming 'Studien'.

Drushtchic (1962) gave a short review of the systematic position of the different superfamilies generally included in Lytoceratina. While Turrilitaceae and Tetragonitaceae are retained as true lytoceratids, he again proposes to remove Scaphitaceae (and also Ancylocerataceae) from the Lytoceratina to the true Ammonitina, because they were 'evidently separated from all lytoceratids by general shape, septal surface and trifold lateral lobe' (translated).

The present author discussed on another occasion (1962*b*) the systematics of the complete suborder Lytoceratina. Here Labeceratidae were separated from the Scaphitaceae, and included as a subfamily in the revised Anisoceratidae. The otoscapitids were elevated to family rank, and remained with the Scaphitidae in the superfamily Scaphitaceae.

To better illustrate the poorly known *Jauberticeras? majorcense*, I joined to the Balearic type material a supposed paratype (op. cit., pl. 10, fig. 5) from the Perte du Rhône (Ain, France). It agreed in general shape and dimensions completely with the Balearic types, with the exception of its greater size. In the meantime I became aware that I had been deceived by a striking shell homoeomorphy. The French form, in which the suture line was, as the only distinguishing feature, not perceptible, represents in reality the spiral portion of the poorly known Albian *Eoscapites subcircularis*. This error was the occasion for the present paper.

From this review the actual problem becomes evident. The extreme splitting of the scaphitids in up to four different ammonitid superfamilies needs no further discussion. It was rejected provisionally by Spath (1937) and Wright (1952) but mainly by Cobban, who gave a striking demonstration of the derivation of the trifold Upper Cretaceous lobe form from a bifid origin. Schindewolf's new 'polyphyletic' interpretation raises a different and more difficult problem: the incompatibility of the reduced quadrilobate suture of *Eoscapites* with the highly differentiated true scaphitid suture-line.

On the other hand, two monophyletic interpretations of the Scaphitaceae seem in principle to be possible, derivation via *Eoscapites* from the conservative main stock of Lytoceratina, or from some ammonitid ancestor, which is suggested by the trifold lobe shape, sculpture, and whorl involution.

The actually remaining questions are:

- (1) Is *Eoscapites* indeed a link between *Lytoceras* and *Scaphites*?
- (2) Is the regressive quadrilobate suture type of *Eoscapites* compatible with the progressive scaphitid suture line, containing four umbilical lobes?
- (3) Is a trifold lateral lobe (or 'second lateral') admissible for a member of Lytoceratina?
- (4) Is it possible to connect the closely coiled initial portion of *Scaphites* with the evolute *Lytoceras*?
- (5) What is the presumed ancestor of *Scaphites*?

We believe all these questions can be answered through the study of the early Upper Albian scaphitids, especially the poorly known *Eoscapites circularis* and *subcircularis*. In addition to these, the first true scaphitids will be treated, and thereafter the scaphitid relationship can be discussed.

## SYSTEMATIC DESCRIPTIONS

Family SCAPHITIDAE Meek 1876

Genus *Eoscaphtes* Breistroffer 1947*Type species. Amm.?* *circularis* J. de C. Sowerby 1836.

Following C. W. Wright (1957) and Wiedmann (1962a) *Eoscaphtes* will here be regarded as an independent genus including *Eoscaphtes circularis* (J. de C. Sowerby), *E. subcircularis* (Spath), *E.?* *tenuicostatus* (Pervinquier).

The latter can only be included with doubt, since the internal suture is still unknown. But in all other features it agrees with the preceding species that the proposed attachment to *Eoscaphtes* seems to be correct.

Breistroffer's (1947, p. 77) very brief diagnosis of *Eoscaphtes*: 'Sous-genre très primitif de *Scaphites*, caractérisé par ses cloisons lytocératiformes, ses tours internes plus ou moins évoluées et sa crosse macroscaphitoïde sans bouche individualisée', should be completed and modified in the following manner: Rounded whorls rapidly increasing in size. Whorls at first crioceratitoid, uncoiling, or in contact, but always with umbilical perforation. Final macroscaphitoid hook. Dorsal impression lacking on inner whorls, sometimes throughout. Fine and dense, sometimes bifurcating lytoceratid striation of the shell. No tubercles. Suture consists of the lobes *I*, *U*, *L*, and *E* only and remains quadrilobate throughout. *L* distinctly bifid, also *U*, but with the tendency to be largely divided by the incoming umbilical seam. Septal surface hamitoid. Constricted mouth-border seems to be present.

The genus seems to be restricted to the Upper Albian of England, Southern France, Madagascar, and the Cenomanian of Algeria.

*Eoscaphtes circularis* (J. de C. Sowerby)

Plate 53, figs. 1-3; text-figs 1a-c

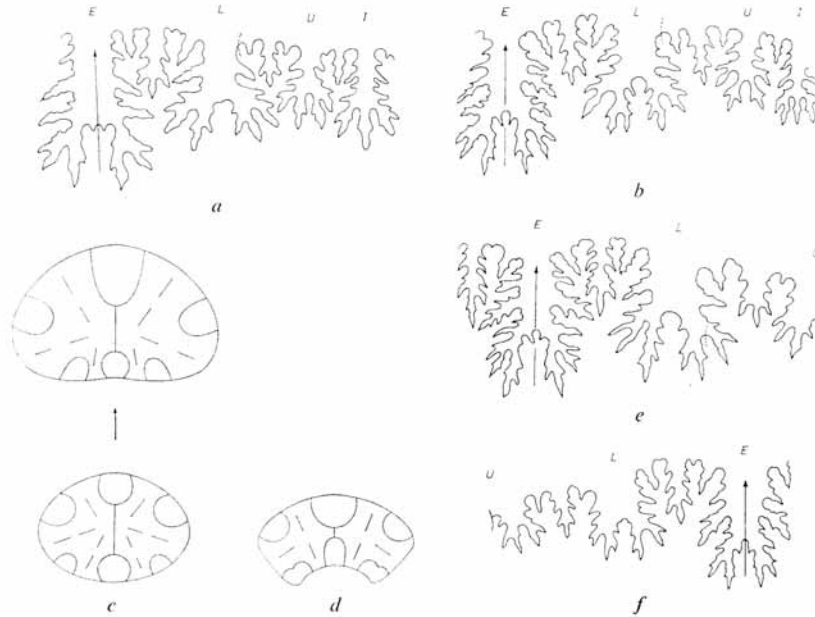
- 1836 *Amm.?* *circularis* J. de C. Sowerby in Fitton, p. 337, pl. 11, fig. 20.  
 1837 *Amm. circularis* Sowerby; Brown, pl. 20, fig. 10.  
 1933 *Scaphites circularis* (J. de C. Sowerby); Spath, p. 427, text-figs. 4d-j.  
 1937 *Scaphites circularis* (J. de C. Sowerby); Spath, p. 499, text-figs. 174a-i, pl. 57, figs. 1-9.  
 1947 *Sc. (Eoscaphtes) circularis* (J. de C. Sowerby); Breistroffer, p. 77.  
 1953 *Eoscaphtes circularis* (J. de C. Sowerby); C. W. Wright, p. 473.  
 1957 *Eoscaphtes circularis* (J. de C. Sowerby); C. W. Wright, p. L228, text-figs. 255, 6a-c.  
 1962 *Eoscaphtes circularis* (J. de C. Sowerby); Wiedmann, p. 212 (1962a).

*Type.* The neotype proposed by Spath (1937, pl. 57, fig. 1), from the Upper Albian (*varicosum* subzone) of Folkestone, preserved in the BMNH collection; here reproduced, Plate 53, fig. 3.

*Description.* Broadly rounded whorls without distinct dorsal impression at any stage, rapidly increasing in size. First whorls crioceratitoid uncoiled or in contact, but with umbilical perforation. Later whorls uncoiling anew; living-chamber is said to be scaphitid. Fine radiate ribbing of lateral sides and venter, consisting of single and bifurcating ribs, which are somewhat raised at the point of bifurcation on the middle side. Dorsum smooth. Suture with four elements of normal size; highly incised. *L* and *U* distinctly bifid, *I* trifid. Saddles symmetrically bipartite and normal-sized.



*Remarks.* Some of Spath's (1937) figurations of this interesting species are drawings. Therefore it was necessary to re-examine the type material deposited in the BMNH collection, where the drawings were found to be correct. However, I was unable to localize the specimen described by Spath (1937, text-fig. 174i) as 'transitional to *S. subcircularis*', the only one with a final hook. Neither in the collections of London nor



TEXT-FIG. 1. *Eoscaphtes*, suture and whorl sections. *a-c*: *E. circularis* (J. de C. Sowerby). *a*, Complete suture of the ammonitid coiled hypotype MGL 12341/1; Upper Albian, Perte du Rhône. *h* = 3.5 mm. *b*, Suture of the crioceratitid uncoiled specimen, GPIT Ce 1221/1; Upper Albian, Folkestone. *h* = 5 mm. *c*, Development of whorl section, and hamitid septal surface: the same,  $\times 4$ . *d-f*, *E. subcircularis* (Spath). *d*, whorl section and subscaaphitid septal surface, MGL 12342; Upper Albian, Perte du Rhône,  $\times 2$ . *e*, External suture-line, MGL 12340; same locality. *h* = 5 mm. *f*, External suture of the Madagascan hypotype (cf. Collignon 1963, fig. 1144); Upper Albian, Mt. Raynaud. *h* = 4 mm.

in the abundant French material which I studied, did I find any full-grown specimen attributable to *E. circularis*. Therefore the presence of a scaphitid living-chamber in this species remains doubtful for the moment. Whereas all specimens with ammonitoid or crioceratitoid coiling which I saw were septate throughout, in the case of the neotype the straightening of the outer whorl coincides with the beginning of the chamber. This makes it probable but not certain that the present species develops indeed a scaphitid final hook.

The first whorl is also generally not preserved, a result of its extreme fragility. There is no doubt though that it includes an open umbilical perforation. The whorl section is rounded at first, increasing rapidly in size (Pl. 53, fig. 1*b*), and becoming more depressed

in the adult stage. For this reason 'var. *depressa*' Spath becomes unnecessary, because it represents only the gerontic stage.

The coiling of the septate portion may be crioceratitoid (Pl. 53, fig. 2) or ammonitoid (Pl. 53, fig. 1). Here the whorls barely touch the preceding ones, and generally no dorsal impression can be observed. In the neotype for example, the dorsum of the initial part of the chamber remains completely flat. In this respect and with regard to the problem of scaphitid origin, the crioceratitoid portion here described (GPIT Ce 1121/1) seems significant. Plate 53, fig. 2*b* and text-fig. 1*c* makes it evident, that the dorsal impression gradually appears in late ontogeny, that *Eoscaphtes* though must be derived from completely uncoiled heteromorphs without dorsal impression, and that it leads to more involute ones. *Sc. subcircularis*, which I regard as the direct descendant of the present species, rapidly acquires an involute initial coil, but the dorsal impression is much more pronounced on the outer whorls. If *E. circularis* indeed represents the source of the true *Scaphites*, then the ammonitoid coiling of the septate portion is a secondary feature, and the final uncoiling a tertiary one. Then the origin of this peculiar group lies neither in normally coiled ammonitids or lycoceratids, but in uncoiled hamitids.

The type of suture and the septal surface are further arguments for this view. The latter offers a clear hamitid configuration (Pl. 53, fig. 2*b*; text-fig. 1*c*), and also the quadrilobate suture-line has a striking affinity to that of some Upper Albian hamitids, like *Plesiohamites* (= '*Lytohamites*' Casey) and *Stomohamites* Breistroffer, as figured in Spath (1941) or Wiedmann (1962*a*, text-figs. 42, 43). Especially the Upper Albian *Plesiohamites similis* (Casey) (= *Hamites multicostatus* Spath, non Brown) greatly resembles *Eoscaphtes* in mode of uncoiling, suture, and sculpture; it is difficult to distinguish them from fragmentary *E. circularis*. The constricted and collared mouth-border, a very characteristic scaphitid feature, and now recognized in *Eoscaphtes* (Pl. 54, fig. 4*b*), is furthermore a common feature of the adult *Stomohamites*.

Turning back from these speculations to *E. circularis*, we further note the fine and dense radiate striation which crosses the venter, and is interrupted on the dorsum. It consists of alternating simple and bifurcating ribs, the latter somewhat pronounced at the point of branching (Pl. 53, fig. 2*a*). This is applicable especially to the living-chamber

#### EXPLANATION OF PLATE 53

- Figs. 1–3. *Eoscaphtes circularis* (J. de C. Sowerby). 1, Ammonitid coiled hypotype, MGL 12341/1 (leg. Loriol); Upper Albian (?*varicosum* subzone), Perte du Rhône (Ain, France). *a*, Lateral, *b*, sagittal, *c*, frontal, *d*, ventral view. 2, Crioceratitid uncoiled hypotype, GPIT Ce 1221/1; Upper Albian (*varicosum* subzone), Folkestone (Kent, Great Britain). *a*, Lateral, *b*, dorsal view, showing the incoming dorsal impression, *c*, ventral view. 3, Neotype (*ex* Spath 1937, pl. 57, fig. 1), with straight portion of body-chamber, BMNH coll. (coll. Casey); Upper Albian (*varicosum* subzone), same locality. *a*, Lateral, *b*, frontal view;  $\times 1$ .
- Figs. 4–6. *E. subcircularis* (Spath). 4, Frontal view of septate hypotype, MHNG Wi 'Sc'/5 (leg. Pictet); Upper Albian (Hysteroceatan), Perte du Rhône (Ain, France). 5, Septate hypotype, MGL 12340 (leg. Loriol); Upper Albian (Hysteroceatan), same locality. *a*, Lateral, *b*, frontal view. 6, Septate hypotype, MHNG Wi 'Sc'/1 (leg. Pictet); Upper Albian (Hysteroceatan), Folkestone (Kent, Great Britain). *a*, Frontal, *b*, lateral view;  $\times 3$ .
- Fig. 7. *E. ?tenuicostatus* (Pervinquière). Holotype (*ex* Pervinquière 1910, pl. 2, fig. 18); Lower Cenomanian of Berrouaghia (Algeria). *a*, Ventral, *b*, lateral, *c*, frontal view.
- All  $\times 2$  unless otherwise indicated.

of the neotype. I believe that Spath's 'var. *rugosa*', which was based on this peculiarity, does not need separation.

The suture-line (text-figs. 1*a*, *b*) was found to be highly incised and consisting only of the elements *E*, *L*, *U*, and *I*. These, as well as the saddles, are of normal size, gradually decreasing from *E* to *U*. Only the trifold internal lobe exceeds *U* in depth. *U* and *L* are distinctly bifid, the latter occupies nearly the centre of the lateral sides. The saddles also are symmetrically bipartite, and subdivided by strong median incisions. Finally it should be mentioned that an absolute identity of suture-lines in the ammonitoid (text-fig. 1*a*) and the crioceratitoid specimens (text-fig. 1*b*) was observed. This proves that specific separation of these two types is unnecessary. The mode of coiling evidently possesses an extreme degree of plasticity, as it is common in phylogenetically primitive material—and again in *Hamites*.

The dimensions (in millimetres) of the specimens figured here are:

	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/1	~18	5.5 (0.31)	8.0 (0.45)	~9.0 (0.50)
MGL 12341/1	19	7.0 (0.37)	10.0 (0.53)	8.0 (0.42)
(penultimate whorl)		3.0 —	3.5 —	—

Both specimens foreshadow the next species, *E. subcircularis* through the loss of coiling and incoming of the dorsal impression.

*Distribution.* *E. circularis* is known from the base of the British Upper Albian, mainly the *varicosum* subzone (bed x) from Folkestone (Kent) and Glynde (Sussex). The species can also be recorded here from the condensed Upper Albian beds of the Perte du Rhône (Ain, France).

*Eoscapites subcircularis* (Spath)

Plate 53, figs. 4–6; Plate 54, figs. 2–4, 8, 9; Plate 55, figs. 1–3; text-figs. 1*d–f*, 2

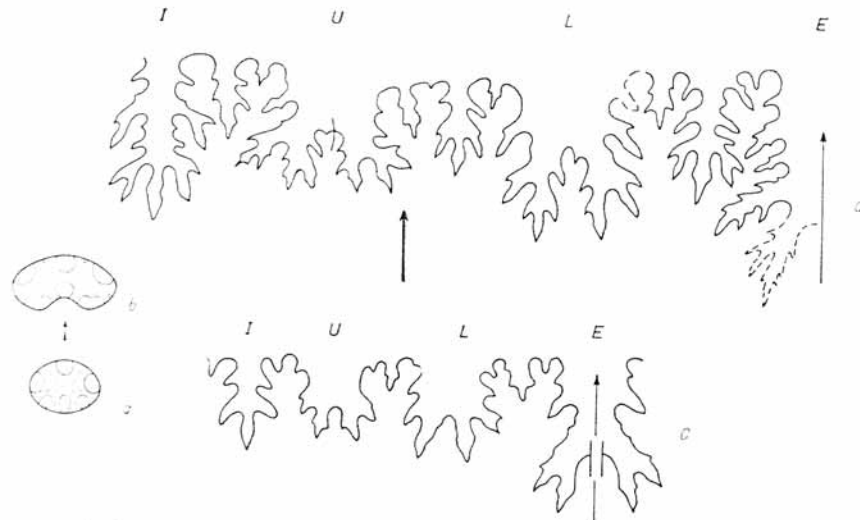
- 1937 *Scaphites subcircularis* Spath, p. 501, text-fig. 175*e*, pl. 57, figs. 10–12.
- 1937 *Scaphites simplex* Jukes-Browne; Spath pars, text-fig. 177*c* only.
- 1947 *Sc. (Eoscapites) subcircularis* Spath; Breistroffer, p. 77.
- 1962 *Jauberticeras ?majoreense* Wiedmann pars, pl. 10, fig. 5 only (1962*b*).
- 1963 *Scaphites* cf. *subcircularis* Spath; Collignon, p. 57, pl. 262, figs. 1143, 1144.

*Holotype.* BMNH specimen no. 38206, figured by Spath (1937, pl. 57, fig. 10) from the Upper Albian (*varicosum* subzone) of Folkestone; here reproduced Plate 54, fig. 8.

*Description.* First whorl slender, with almost circular section and umbilical perforation. Then rapidly increasing in size and involution, developing a distinct dorsal impression. Hooked body-chamber present. Sculpture like that of *E. circularis*, but stronger. Suture still quadrilobate and highly incised; with the beginning increase of saddles, saddle incisions, and umbilical lobe, which becomes divided by the incoming umbilical seam. Septal surface hamitid at first, later scaphitid.

*Remarks.* As in *E. circularis* all three specimens figured by Spath are defective, generally consisting only of the spiral portions, hence the original description and figuration of this species are inadequate (Pl. 54, fig. 8). For this reason I am glad to be able to validate this doubtful, but extremely interesting species through rich and well-preserved material from different French localities.

The main character of *E. subcircularis* is evidently its more involute septate whorls, and in consequence the existence of a distinct dorsal impression. But this impression does not persist throughout as Spath mentioned; I found an inner whorl of a somewhat surprising shape. In the centre of Plate 55, fig. 1*b* (arrow) there is a narrow, elevated ridge which marks the rapidly decreasing first whorl. This is so fragile, that I could not clean it from the adherent matrix, where the pronounced striation of the extremely inflated outer whorl is noticeable. To a diameter of 4.5 mm. corresponds a whorl



TEXT-FIG. 2. Suture development and septal surfaces of *E. subcircularis* (Spath), MHNG Wi · Sc'3; Upper Albian, Crioud (?). *a*, Whorl section and hamitid septal surface; *h* = 1.7 mm. *b*, Whorl section and subscaiphitid septal surface; *h* = 3.5 mm. *c*, Suture at *h* = 1.7 mm, *d* at *h* = 6 mm.

height and thickness of 1.5–2.0 mm. From all these features an open umbilical perforation can be expected. At the indicated whorl height the section is rounded throughout with distinctly convex and not impressed dorsal area; the septal surface shows the simplified hamitid configuration, and only the four, nearly equidistant, main lobes exist (text-fig. 2*a*, *c*). With the next whorl, which is visible in the background of Plate 55, fig. 1*b*, the whorl height and thickness become extremely amplified (300–400 per cent.). Now the dorsal impression gradually becomes visible, and the whorl section receives its typical depressed to coronate outline (Pl. 55, figs. 1*a*, *c*). The maximum whorl thickness is situated in the centre of the flanks, where a kind of lateral keel (like in *Jauberticeras*) is generally present.

At the same time the suture changes considerably (text-figs. 2*b*, *d*). It retains many aspects of the preceding species, for instance in the degree of incision, the distinctly bifid *L*, the trifid *I*, and the importance of the median saddle incisions. But the elements *U* and *L/U* now become more and more differentiated, evidently in relation to the in-

creasing involution. While *L* is now placed outside of the lateral keel, the umbilical lobe becomes divided through the umbilical seam and therefore more and more amplified. The saddle *L/U* also becomes lengthened and its median incision more pronounced. The suture-line continually loses its hamitid character, while the septal surface can already be designated as sub-scaphitid (text-fig. 2*b*).

The septate portion has an average diameter of 15 mm. Thereafter the body-chamber uncoils with a typical scaphitid hook, which is straight at first and then recurved (Pl. 54, figs. 2, 4). The mouth border, which does not overlap the spiral portion, seems to be constricted (Pl. 54, fig. 4*b*). The whorl section of the living-chamber is depressed with rounded sides and slightly impressed dorsum. The maximum thickness lies in the apical part of the chamber and near the final hook the whorl thickness decreases.

The sculpture is of the same type as in *E. circularis*, but the ribbing is more pronounced on the body-chamber, where it passes the dorsum with a distinct incurvation. The specimen from Folkestone here figured (Pl. 53, fig. 6) completely preserves the sculpture of the preceding species, while another specimen from Mt. Saxonet demonstrates an injured body-chamber and the mode and difficulty of its restoration (Pl. 54, fig. 9).

Intraspecific variation in the present species is also considerable, as in *E. circularis*. This can easily be shown through the dimensions (in millimetres) of the specimens studied:

	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
MGL 12342	33	15	16	7.2 (0.45)	12.6 (0.79)	4.5 (0.28)
MHNG Wi 'Sc'/1	—	—	10	4.5 (0.45)	6.8 (0.68)	3.0 (0.30)
MHNG Wi 'Sc'/2	24.5	11.5	14	6.0 (0.43)	9.0 (0.64)	4.7 (0.34)
MHNG Wi 'Sc'/3	—	—	17	7.0 (0.41)	13.5 (0.80)	4.5 (0.27)
			4.5	1.5 (0.33)	2.0 (0.44)	~2.0 (0.44)
MHNG Wi 'Sc'/4	—	—	14.5	6.3 (0.43)	9.4 (0.65)	4.0 (0.28)
MHNG Wi 'Sc'/5	—	—	16	6.0 (0.37)	10.5 (0.66)	5.4 (0.34)
MGL 12340	—	—	16.5	6.8 (0.41)	11.8 (0.72)	~6.0 (0.36)
Collignon's fig. 1143			12	5.0 (0.42)	9.0 (0.75)	3.5 (0.29)
Collignon's fig. 1144			11	4.5 (0.41)	7.1 (0.64)	3.2 (0.29)

Especially the whorl thickness of the spiral portion seems highly variable (0.64–0.80), not counting the dimensions of the slender first whorl. The same can be stated about the umbilical diameter (0.27–0.36). In order to receive an impression of this variability quite a number of specimens are figured here. Without any doubt the two specimens from Madagascar (Pl. 55, figs. 2, 3), labelled *E. cf. subcircularis* by Collignon (1963), also fall into the variability of the present species.

*E. subcircularis* connects directly *E. circularis* with the first true *Scaphites*, *Sc. simplex*. It agrees with *E. circularis* in the open initial coil with umbilical perforation, sculpture, and shape as well as suture of the first whorls. On the other hand, the distinctions are well pronounced in the incoming dorsal impression and the amplified suture elements *U* and *L/U*, caused by the more closely coiled initial portion. All these features foreshadow *Sc. simplex* with a completely closed initial spire, distinctly bipartite *U*, asymmetric *L*, and elongated saddle *L/U*. The open-whorled specimen from Entrèves-en-Bauges referred to *Sc. simplex* by Spath (1937, text-fig. 177*c*), evidently belongs to the present species. This demonstrates that these two species, as well as the genera *Eosca-phites* and *Scaphites*, are closely connected. If only the initial coil is present, *E. subcircularis* resembles the tetragonitid genus *Jauberticeras*, which is also laterally keeled.

Both also have a very similar sculpture. Only the suture-line gives us the decision that there is no real relationship.

The material which I located in the collections of Pictet and Campiche, was generally labelled '*Sc. meriani*' or '*Sc. hugardianus*'. However, these species are easily distinguishable from *E. subcircularis* through their pronounced ventrolateral tuberculation.

*Distribution.* Spath indicates that *E. subcircularis*, which was described from beds x and xi of Folkestone, Blue Bell Hill, Burham (Kent), and Glynde (Sussex), is of Upper Albian, *varicosum* to *auritus* subzone age. The French specimens here figured are from the condensed Upper Albian of the Perte du Rhône (Ain), Mt. Saxonet and Criou (?) (Haute-Savoie). (There are some specimens in the Pictet collection which are labelled 'Criou and Grand Bornand'. Dr. Lanterno kindly informed me, that these are two different localities in Haute-Savoie. Considering this fact, this material will be cited under the locality name 'Criou (?)'.) The '*simplex*' specimen which was incorrectly identified by Spath, has nearly the same provenance (Entrèves-en-Bauges). Approximately the same Hysteroцерatan age can be stated for the Madagascan material, originating from the famous Mt. Raynaud near Diégo-Suarez.

*Eoscaphtes* ? *tenuicostatus* (Pervinquierè)

Plate 53, fig. 7

1910 *Scaphites tenuicostatus* Pervinquierè, p. 28, text-fig. 12, pl. 2, figs. 17-19.  
1962 *Eoscaphtes tenuicostatus* (Pervinquierè); Wiedmann, p. 212 (1962a).

*Holotype.* The originally designated specimen (Pervinquierè 1910, pl. 2, figs. 17, 18) from the Cenomanian of Berrouaghia (Algeria); here reproduced Plate 53, fig. 7.

EXPLANATION OF PLATE 54

Figs. 1, 7. *Scaphites* (*Scaphites*) *simplex* Jukes-Browne. 1, One of the two syntypes of *Sc. 'hugardianus'* in coll. d'Orbigny (MHNP) 5805-1; Upper Albian (Hysteroцерatan), La Fiz (Haute Savoie, France). Lateral view. 7, Complete hypotype, GPIT Ce 1221/5; Vraconian, Cambridge Greensand. *a*, Lateral, *b*, frontal view.

Figs. 2-4, 8, 9. *Eoscaphtes subcircularis* (Spath). 2, Hypotype with complete body-chamber, MGL 12342 (coll. Campiche); Upper Albian (Hysteroцерatan), Perte du Rhône (Ain, France). *a*, Ventral, *b*, frontal, *c*, lateral view, *d*, frontal view of spiral portion. 3, Sagittal view of spiral portion, MHNG Wi 'Sc'/4 (leg. Pictet), in which the extreme increase of whorl thickness becomes visible. Same age and locality.  $\times 3$ . 4, Hypotype with preserved body-chamber, MHNG Wi 'Sc'/2, (leg. Favre); Upper Albian (Hysteroцерatan), Mt. Saxonet (Haute Savoie, France). *a*, Ventral, *b*, lateral view. 8, The crushed holotype (Spath 1937, pl. 57, fig. 10); Upper Albian (*varicosum* subzone), Folkestone (Kent, Great Britain). Lateral view. 9, Injured body-chamber, MHNG Wi 'Sc'/6 (leg. Favre); Upper Albian (Hysteroцерatan), Mt. Saxonet (Haute-Savoie, France). *a*, Lateral and *b*, ventral view of shaft, *c*, of hook.

Fig. 5. *Sc. (Sc.) hugardianus* d'Orbigny. The first figured specimen, which agrees with the original description (Hébert and Munier-Chalmas 1875, pl. 5, fig. 7); proposed lectotype (Spath 1937); Upper Albian (*substuderi* zone), Salazac (Gard, France). *a*, Lateral, *b*, ventral view.

Fig. 6. *Sc. (Sc.) meriani* Pictet and Campiche. Lectotype (cf. Pictet and Campiche 1861, pl. 44, fig. 1), MHNG P & C 'S-CR'/44, 1, (leg. Pictet); Vraconian, Sainte Croix (Vaud, Switzerland). *a*, Ventral, *b*, lateral view.

All figures natural size unless otherwise stated.

In the mode of uncoiling and in the involution of the initial coil *E. ? tenuicostatus* is very similar to the preceding species. It differs especially through its smaller size. From the holotype the following measurements (in millimetres) were taken:

<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
12	4.5	7.3	2.5 (0.34)	3.6 (0.49)	2.5 (0.34)

*E. ? tenuicostatus* differs from *E. subcircularis* in that the increase of whorl thickness is not so rapid and the sculpture is finer and more sinuate on the spiral portion, while it consists of straight single ribs on the hooked chamber. The sides are more rounded on the involute whorls and more flattened on the final hook. The suture-line (Pervinquière 1910, text-fig. 12) is much less incised than that of the preceding species but probably belongs to the same type. Since its internal portion is unknown, the attachment to *Eoscaphtes* remains somewhat doubtful.

From *E. ? tenuicostatus* it seems possible to derive a group of open-whorled Cenomanian species (*Sc. peroni*, *africanus* and *evolutus* Pervinquière), which are probably the direct fore-runners of the Turonian *auritus* group (= *Otoscaphtes* Wright). Up to the moment the species is known only from the Lower Cenomanian of Berrouaghia (Algeria).

#### Genus SCAPHITES Parkinson 1811

*Type species. Scaphites equalis* J. Sowerby 1813. The specimen figured originally by Parkinson (1811, pl. 10, fig. 10) was later described as *Sc. equalis* (J. Sowerby 1813) and subsequently designated as type species by Meek (1876).

The difficulty in summarizing the characteristics of the genus *Scaphites* become evident through the diagnosis given by C. W. Wright (1957, p. L228): 'Compressed to very inflated, more or less involute, early whorls invariably in contact, shaft short or moderately long, hook not curved over camerate whorls; aperture constricted and commonly collared, in some shells with long dorsal lappet; ribs normally branching or intercalated on coiled part, commonly single or joining at ventrolateral tubercles on shaft; umbilical and normally ventrolateral tubercles present on shaft or hook. Suture soon ceases to be regularly lytoceratid.'

It becomes evident that in *Scaphites* we have a high variation of different modes of coiling, sculpture, and even suture, lappeted or unlappeted mouth-borders joined inseparably. Even the acanthoceratoid, desmoceratoid, or sphaeroceratoid homoeomorphs of the Uppermost Senonian (*Acanthoscaphites*, *Desmoscaphites*, *Clioscaphtes*), preserved by C. W. Wright with a number of other Upper Senonian genera, are linked with the true *Scaphites* by intermediaries in a way which sometimes make generic separation doubtful. In particular the Wright's subfamily Otoscaphitinae, which I raised to family status (Wiedmann 1962b), now needs critical revision.

It might be noted that the splitting in scaphitids is nevertheless of reasonable extent. *Scaphites* is regarded as a long-living genus by Wright, persisting from the Upper Albian to the Campanian, and splitting off at this time into several divergent types. But in the Albian and Cenomanian scaphitid material here studied, a high degree of plasticity was also found. The main part of the diverging types here recognized (*meriani* stock, *similaris* stock) is inseparably connected with the *equalis* main stock, and needs no further separation. Subgeneric distinction seems necessary, however, for *Sc. thomasi* Pervinquière

(= *S. (Metascaphites)* Wiedmann) and the laterally keeled *S. stephanoceroideus* Yabe (= *S. (Hyposcaphites)* subgen. nov.). Contrary to Wright *Otoscaphites* will also be regarded here as a subgenus of *Scaphites*, in which *Pteroscaphites* Wright has already been (Wiedmann 1962a) included.

*Scaphites* favoured the Northern hemisphere including India and Northern Africa, but is recorded also from Madagascar and Australia.

For our problem, the development of the early scaphitids, only the Upper Albian and Cenomanian representatives of the genus and the cited subgenera are briefly treated here.

#### Subgenus SCAPHITES (SCAPHITES) Parkinson 1811

In pursuing the early scaphitid development I recognized three different lineages; the *equalis* main stock, the *meriani* stock, and the *similaris* stock.

#### THE *EQUALIS* MAIN STOCK

The species belonging to the main stock described here are, *Sc. (Sc.) simplex* Jukes-Browne, *Sc. (Sc.) obliquus* J. Sowerby, and *Sc. (Sc.) equalis* J. Sowerby. *Sc. (Sc.) simplex* connects these type forms with both the *meriani* and the *similaris* group. I regard as characteristic for the present stock the gradually increasing importance of untubercled primary ribs, the rounded to oval whorl section, and the absence of lateral bulges. This group appears with *Sc. simplex* in the higher Albian and can be traced into the Upper Campanian.

#### *Sc. (Scaphites) simplex* Jukes-Browne

Plate 54, figs. 1, 7; Plate 55, figs. 4, 5; text-figs. 3e,

- 1848 *Scaphites Hugardianus* d'Orbigny; Pictet, p. 370, pl. 12, fig. 2.  
 1861 *Scaphites Meriani* Pictet and Campiche pars, pl. 44, fig. 7 only.  
 1875 *Scaphites Meriani* var. *simplex* Jukes-Browne, p. 287, pl. 14, fig. 3.  
 ?1907 *Scaphites aequalis* Sowerby; Pervinquier, p. 118 pars, text-fig. 37, pl. 4, figs. 22, 23 only.  
 1937 *Scaphites simplex* Jukes-Browne; Spath, p. 504, text-figs. 176c-f, 177a, b, d, e (non c, sed *E. subcircularis*), pl. 57, figs. 13-22, ?23.  
 ?1962 *Scaphites (Sc.) simplex* Jukes-Browne; Wiedmann, p. 213, text-fig. 52, pl. 10, fig. 8.

*Holotype*. The fragmentary living chamber from the Cambridge Greensand, originally figured by Jukes-Browne (1875, pl. 14, fig. 3) and reproduced by Spath (1937, text-figs. 177a, b).

#### EXPLANATION OF PLATE 55

Figs. 1-3. *Eoscapites subcircularis* (Spath). 1, Spiral portion with first whorl preserved, MHNG Wi 'Sc'/3 (leg. Pictet); Upper Albian, Crioud? (Haute Savoie, France). *a*, Frontal, *c*, lateral view of outer whorl,  $\times 2$ . *b*, first whorl with hamitid septal surface; the adhering matrix shows the strong ribbing of the outer whorl, which is visible in the background,  $\times 6$ . 2, Madagascan hypotype (Collignon 1963, pl. 262, fig. 1143); Upper Albian (Zone à *Hysteroceeras binum*), Mt. Raynaud near Diégo-Suarez (Madagascar). *a*, Frontal, *b*, lateral view, spiral portion. 3, Madagascan hypotype (Collignon 1963, pl. 262, fig. 1144); same age and locality. *a*, Lateral, *b*, ventral view.

Figs. 4, 5. *Scaphites (Scaphites) simplex* Jukes-Browne. 4, Spiral portion, GPIT Ce 1221/4; Vraconian, Sainte Croix (Vaud, Switzerland). The sculpture of the inner whorl foreshadows that of the Cenomanian species. *a*, Frontal, *b*, ventral, *c*, lateral view. 5, Spiral portion of hypotype with nearly rectangular whorl section, GPIT Ce 1221/3; same locality. *a*, Frontal, *b*, lateral, *c*, ventral view.

Figures  $\times 3$  unless otherwise stated.

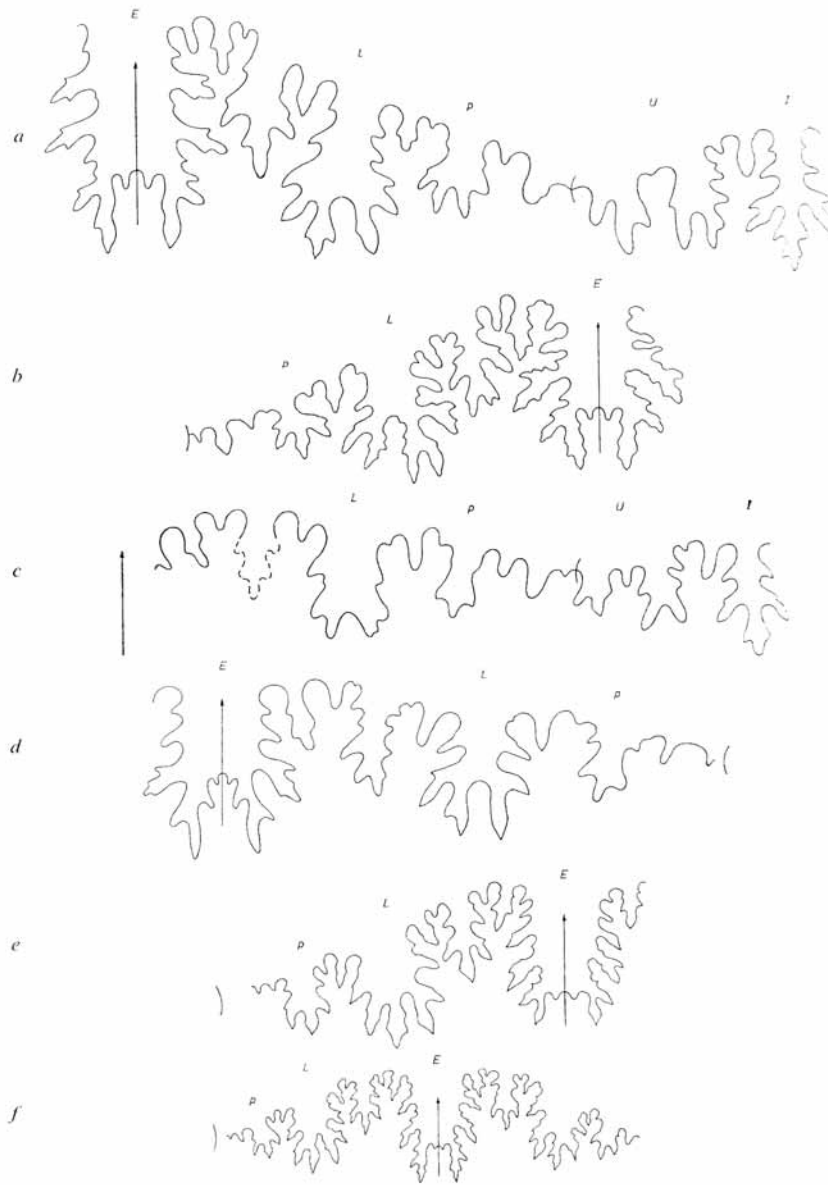


*Value and extent of the species.* Despite the deficient holotype, the species can be regarded a good one in the light of the additional description and figures given by Spath. The species, as interpreted by Spath, includes three different types, which differ only in the detail of sculpture. Besides the typical costate form there are specimens with an almost smooth cast ('var. *sublaevis*' Spath) and costate ones with umbilical tubercles on the shaft ('var. *nodata*' Spath). The latter links the *equalis* main stock with *Sc. hugardianus* of the *meriani* group. I agree with Spath and believe that *Sc. simplex* covers all these different sculpture types. Whether *Sc. hilli* Adkins and Winton belongs also to the present species, as I formerly believed (Wiedmann 1962a, p. 213), or not, will be discussed below. Here it is referred to the *similaris* stock, where a group of small-sized scaphitids and a further problem of early scaphitid development will be treated. The main distinguishing feature between these two stocks is their different size. Each species of the main stock can be matched with an extremely similar species of the smaller *similaris* stock. Isolated innermost whorls, like the Tunisian (Pervinquière 1907) or Spanish (Wiedmann 1962a) nuclei cited above, may be referred to the one as well as to the other.

*Description.* Globose spiral portion with semilunate whorl section, closely coiled umbilicus already at an early age. Final hook generally curved throughout, without long straight shaft; constricted mouth-border nearly touching initial spire. Sculpture of spiral part consists of fine and dense, generally bifurcated ribs, which are somewhat convex on the sides and cross the venter in a moderately concave sinus. The point of bifurcation seems to be tuberculate on the innermost whorl, sometimes also on the shaft. On the body-chamber the ribs become more radiate and pronounced and single ones are often intercalated. At the umbilical seam the suture-line is distinctly retracted, thus *L* becomes asymmetric; the median incision of the enlarged element *L/U* increases in size, and is therefore generally confused with the 'second lateral' of normally coiled ammonites. The bipartite *U* remains inside the umbilical seam, and cannot be recognized in the external suture of any true *Scaphites*.

*Remarks.* For the present, *Sc. simplex* is of importance as an intermediate link between *Eoscaphtes* and typical species of *Scaphites*. It combines the characters of both, and specimens were even confounded by Spath (1937, text-fig. 177c) with *E. subcircularis*. While preserving the sculpture-type and whorl-shape of the preceding, the ribs become more distinctly separated into primary and secondary ones, and the septate whorls are more closely coiled as in the Cenomanian species. The suture-line changes more noticeably, but also gradually. The umbilical lobe, originally divided through the umbilical seam in *E. subcircularis*, passes from its original position to the internal suture-line, where it remains bipartite in all subsequent scaphitids. At the same time *L/U* becomes more and more amplified by its adopted position on the umbilical seam; its median incision also increases distinctly in size. Because of its phylogenetic development, its distinctly trifid shape, and its position in the external suture-line, it is completely impossible to interpret this element as an equivalent of the so-called 'second lateral' or  $U_2$  of ammonites. Also the suture developments here represented (text-figs. 7-9, 15) make it evident, that this element which we propose to name pseudo-lobe (*p*) always remains outside the umbilical seam, where as a rule the true umbilical lobes originate.

Moreover the theory of an origin of the scaphitids in Ammonitina can easily be rejected



TEXT-FIG. 3. Suture of *Scaphites* (*Scaphites*). *a*, *Sc. (Sc.) equalis* J. Sowerby, complete suture of typical specimen, GPIT Ce 1221/12; Cenomanian, Chardstock. *h* = 6 mm. *b*, the same, external suture of inflated form, GPIT Ce 1221/13; Upper Cenomanian, Rouen. *h* = 9 mm. *c*, *Sc. (Sc.) obliquus* J. Sowerby, nearly complete suture of hypotype GPIT Ce 1221/9; Cenomanian, Rouen. *h* = 4.5 mm. *d*, *Sc. (Sc.) yonekurai* Yabe, hypotype GPIT Ce 1221/10; Upper Cenomanian, Rouen. *h* = 8 mm. *e*, *Sc. (Sc.) simplex* Jukes-Browne, GPIT Ce 1221/3; Vraconian, Ste Croix. *h* = 5 mm. *f*, the same, GPIT Ce 1221/4; same locality. *h* = 4 mm.

by the different suture-lines here figured (text-figs. 3e, f). In *Sc. simplex* the lateral lobe is distinctly bifid at first, but becomes more and more asymmetric through the retraction of the umbilical suture. I stated nearly the same development in *Sc. equalis*, where *L* recovers its originally bifid shape in the adult stage (Wiedmann 1962a, p. 214).

To give a clearer impression of the singular initial coil of the present species, I figure here (Pl. 55, figs. 4, 5), besides a typical Cambridge Greensand specimen, two well-preserved camerate portions from my collection. They make the identity of Pictet and Campiche's fig. 7 (especially the suture-line, fig. 7d) with the present species obvious. The same may be stated for the first complete suture-line of '*Sc. equalis*' in Pervinquière (1907, text-fig. 37) and reproduced by Nowak (1911, text-fig. 5), which has been regarded as typical for *Sc. equalis* up to the present. In reality it belongs to a completely closed initial coil, with semilunate section (Pervinquière 1907, pl. 4, figs. 22, 23), which belongs to *Sc. simplex* or *Sc. hilli*.

The measurements (in millimetres) of the specimens here figured are:

	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/3	—	—	11.5	7 (0.61)	10 (0.87)	—
GPIT Ce 1221/4	—	—	10	5.7 (0.57)	8.1 (0.81)	—
GPIT Ce 1221/5	26	16	15	8 (0.53)	13 (0.86)	—
GPIT Ce 1221/6	30	18	17	10 (0.59)	16 (0.94)	—
MHNP no. 5805 ( <i>Sc. 'hugardianus'</i> ex coll. d'Orbigny)	26.5	17	16	9.4 (0.59)	15 (0.94)	—

In comparison with the preceding species, there is little variation in height and thickness of the septate whorls, and also in absolute size. *Sc. simplex* foreshadows *Sc. hugardianus* of the *meriani* stock not only with its '*var. nodata*', but also with the tuberculation of the innermost whorls (Wiedmann 1962a, and here Pl. 55, fig. 4). One of the two poorly preserved syntypes of *Sc. hugardianus* d'Orbigny is reproduced here (Pl. 53, fig. 1), to demonstrate that it evidently belongs to the nodate variety of the present species. As can be seen in the table of measurements, it also agrees completely in its dimensions with the *simplex* specimens described here.

*Distribution.* In England *Sc. simplex* seems to be restricted to the lower part of the Upper Albian (*varicosum* to *aequatorialis* subzone age in Spath) from Folkestone, Maidstone (Kent), Glynde (Sussex), and the Cambridge Greensand. The species is also frequent in Southern France and Switzerland. It can be cited with certainty from the undivided Upper Albian from Entrèves-en-Bauges, Criou (?) and the Montagne La Fiz (Haute-Savoie), and the Vraconian of Ste Croix (Vaud). The citations from the Spanish Albian IV (Wiedmann 1962a) and the Tunisian Vraconian (Pervinquière 1907) remain doubtful. Nevertheless *Sc. simplex* is a long-living species which persists throughout the whole Upper Albian.

*Sc. (Scaphites) obliquus* J. Sowerby

Plate 56, figs. 5, 6; text-fig. 3c

- 1813 *Scaphites obliquus* J. Sowerby, p. 54, pl. 18, figs. 4-7.
- 1822 *Scaphites striatus* Mantell, p. 119, pl. 22, figs. 3, 4, 9, 11, 13-16.
- 1822 *Scaphites obliquus* Sowerby; Brongniart, p. 83, pl. 6, fig. 13.
- 1831 *Scaphites aequalis* Sowerby; Deshayes, p. 231, pl. 6, figs. 7, 8.
- 1832 *Scaphites obliquus* Sowerby; Passy, p. 333, pl. 14, figs. 5-7.
- 1842 *Scaphites aequalis* Sowerby; d'Orbigny pars, pl. 129, figs. 3-7 only.

- 1847/48 *Scaphites aequalis* Sowerby; Quenstedt, p. 274, pl. 20, fig. 14.  
 1850 *Scaphites obliquus* Sowerby; Dixon, p. 359, pl. 29, fig. 11.  
 1861 *Scaphites obliquus* Sowerby; Pictet and Campiche, p. 14.  
 non 1865 *Scaphites obliquus* Sowerby; Stoliczka, p. 168, pl. 81, figs. 1-3 (sed *Sc. (Sc.) yonekurai* Yabe).  
 non 1867 *Scaphites obliquus* Sowerby; Guéranger, p. 6, pl. 5, fig. 8 (sed *Sc. (Sc.) yonekurai* Yabe).  
 1872 *Scaphites aequalis* Sowerby; Schlüter, p. 72, pl. 23, figs. 1-4.  
 1872 *Scaphites aequalis* Sowerby; Fritsch pars, p. 41, pl. 13, fig. 5 only.  
 1876 *Scaphites aequalis* Sowerby; Simonović, Bačević, and Sorokin, pl. 6, fig. 6.  
 1951 *Scaphites obliquus* J. Sowerby; Wright and Wright, p. 13.  
 1959 *Scaphites aequalis* Sowerby; Cieśliński, p. 33, pl. 3, fig. 4.  
 ?1961 *Scaphites obliquus* Sowerby; Sučić-Protić, p. 124, pl. 6, figs. 2, 3.

*Holotype.* The specimen figured by J. Sowerby (1813, pl. 18, figs. 4-7) from the Cenomanian Hamsey Marl pit near Lewes (Sussex), here reproduced (Pl. 56, fig. 5), BMNH 4387a.

*Sc. (Sc.) obliquus* closely links *Sc. simplex* with the later *Sc. equalis*. It is often confused or wrongly identified with the latter because of the identical inner whorls and the fact that both species are generally found together. In reality it is not difficult to separate them, by means of the different coarseness of primary ribs on the living-chamber. Moreover *Sc. obliquus* is somewhat smaller in size and generally less inflated. But indeed there is little phylogenetical change between these two species, which nearly completely agree in suture (text-fig. 3a-c) and sculpture of the inner whorls.

On the other hand, there is also little progress from *Sc. simplex* to the present species. The sculpture type is the same in both, but the ribs are coarser in *Sc. obliquus*, and the point of bifurcation nearer the venter. The primary ribs are less numerous and more pronounced, both on the spiral portion and on the straight shaft. At the same time the initial coil is more evolute and compressed in section, but in this respect some variation can be observed. Variable is also the number of secondary ribs originating in each primary one. The same variation can be recognized in the figurations which Mantell gave of his *Sc. 'striatus'*. This species was regarded as identical with *Sc. obliquus* by subsequent authors, including Wright and Wright (1951, p. 13). In a recent paper, however, C. W. Wright (1963, p. 602) changed his opinion and retained *Sc. 'striatus'* by choosing

## EXPLANATION OF PLATE 56

- Figs. 1-4. *Scaphites (Scaphites) equalis* J. Sowerby. 1, Holotype. Sowerby Coll., BMNH no. 43986, figured by J. Sowerby (1813, pl. 18, figs. 1-3). Exact locality unknown: Cenomanian (?), almost certainly from the Dorset or Devon coast (Great Britain). a, Ventral, b, lateral view. 2, Representative hypotype with preserved mouth-border, GPIT Ce 1221/11. Cenomanian, Chardstock (Great Britain). a, Frontal, b, ventral, c, lateral view. 3, Compressed hypotype with finer costulation, GPIT Ce 1221/12; septate coil partly removed, to recognize the evolute, 'otoscapitid' inner whorls. Same locality. a, Frontal, b, ventral, c, lateral view. 4, Inflated specimen with stronger sculpture, GPIT Ce 1221/13. Upper Cenomanian, Rouen (France). a, Ventral, b, lateral view.  
 Figs. 5, 6. *Sc. (Sc.) obliquus* J. Sowerby. 5, Holotype, Sowerby Coll., BMNH no. 43987a, figured by J. Sowerby (1813, pl. 18, figs. 4-7). Varians Zone, Cenomanian, Hamsey Marl Pit near Lewes, Sussex. a, Frontal, b, lateral view. 6, Complete hypotype, GPIT Ce 1221/8. Upper Cenomanian, Rouen (France). a, Ventral, b, lateral, c, frontal view.  
 Fig. 7. *Sc. (Sc.) yonekurai* Yabe. Fragmentary hypotype, agreeing with *Sc. 'dailyi'* Wright; GPIT Ce 1221/10 (leg. Wiedmann). Upper Cenomanian, Rouen (France). Lateral view.  
 All figures natural size.

The photographs 1 and 5 were taken from casts made available through the kindness of Dr. M. K. Howarth.

as lectotype the figs. 9 and 11 of Mantell (1822, pl. 22). But unfortunately the proposed lectotype agrees completely with the diagnosis of *Sc. obliquus*, as given by J. Sowerby. There, two or three secondary ribs are indicated as typical for this species. If also forms with up to six secondaries belong to *Sc. obliquus* (Wright 1963, p. 602), I see no reason to renew *Sc. 'striatus'*. The proposed lectotype seems of interest in one aspect only; through its somewhat less pronounced primary ribs it is obviously intermediate to *Sc. simplex*.

It should be added that the number of secondaries is very constant (2 or 3) on the spiral portion; the indicated variability concerns the shaft, where the higher number (2-6) can only be observed. This can be predicted, however, by the intermediate position of *Sc. obliquus* between *Sc. simplex* and *Sc. equalis*.

The specimen from the Cenomanian of Rouen here figured (Pl. 56, fig. 6) can be regarded as typical. Its measurements (in millimetres) are:

<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
26	12.5	16	9 (0.56)	11 (0.69)	1.5 (0.09)

Including *Sc. 'striatus'* Mantell, the present species can be diagnosed as follows: Middle-sized scaphitid with moderately evolute spiral coil. The whorl section changes from broadly depressed to rounded on the innermost whorls, and to slightly laterally compressed on the shaft. Whorl thickness of spiral portion is variable. The shaft is straight at first, then slightly recurved, but without touching initial coil. Sculpture consists of strong main and subordinate secondary ribs. The point of bi- or tri-furcation is generally raised, but not tubercled, and situated outside of central flank. About twenty primaries on the last septate whorl; ribs generally bi- or trifurcating, curved slightly backward on lateral sides and venter. Common on the shaft are ten prorsiradiate main ribs, which are more or less pronounced, and give rise to generally three or four secondaries. On final hook sculpture of initial coil returns. The suture-line here figured (text-fig. 3c) is characterized by a distinctly bifid *L*, a well-developed *U*, the pronounced incision *p*, and an asymmetrically tripartite saddle *L/E*.

To *Sc. yonekurai* Yabe a number of similar forms will be referred, which differ from *Sc. obliquus* especially through their smaller size.

The age of *Sc. obliquus* from the British type localities was indicated by Wright and Wright as Lower Cenomanian, 'but perhaps also occurring earlier'. In France the species can be recorded also from the Upper Cenomanian, where the specimen from Rouen was collected. The German and Polish material again is of Lower Cenomanian age, while the Bohemian specimens may also be of Upper Cenomanian provenance. In Algeria and Tunisia the citation of the species (Pervinquière 1907, 1910) remains doubtful; the Serbian specimens figured by Sučić-Protić are in reality indeterminable, and the Indian forms will better be treated under *Sc. yonekurai* Yabe. Thus *Sc. obliquus* is a long-living species appearing probably in the uppermost Albian and overlapping here with *Sc. simplex*. It is frequent in the European Cenomanian, while all younger citations (for example Alth 1850) cannot be proven at the moment.

*Sc. (Scaphites) equalis* J. Sowerby

Plate 56, figs. 1-4; text-figs. 3a, b

1811 *Scaphites* Parkinson, pl. 10, fig. 10.

1813 *Scaphites equalis* J. Sowerby, p. 53, pl. 18, figs. 1-3.

- 1822 *Scaphites costatus* Mantell, p. 120, pl. 22, figs. 8, 12.  
 non 1831 *Scaphites aequalis* Sowerby; Deshayes, p. 231, pl. 6, figs. 7, 8 (sed *Sc. obliquus*).  
 1832 *Scaphites aequalis* Sowerby; Passy, p. 333, pl. 14, figs. 8, 9.  
 1842 *Scaphites aequalis* Sowerby; d'Orbigny pars, p. 518, pl. 129, figs. 1, 2 only.  
 1846 *Scaphites aequalis* Sowerby; Geinitz, p. 301, pl. 12, fig. 1.  
 non 1847/8 *Scaphites aequalis* Sowerby; Quenstedt, p. 274, pl. 20, fig. 14 (sed *Sc. obliquus*).  
 non 1850 *Scaphites aequalis* Sowerby; Alth in Haidinger, p. 206, pl. 10, fig. 31.  
 1850 *Scaphites aequalis* Sowerby; Dixon, p. 359, pl. 27, figs. 37, 38.  
 non 1865 *Scaphites aequalis* Sowerby; Stoliczka, p. 167, pl. 81, figs. 4–6 (sed *Sc. similis*).  
 non 1872 *Scaphites aequalis* Sowerby; Schlüter, p. 72, pl. 23, figs. 1–4 (sed *Sc. obliquus*).  
 1872 *Scaphites aequalis* Sowerby; Fritsch pars, p. 41, pl. 13, fig. 6 only.  
 non 1876 *Scaphites aequalis* Sowerby; Simonović, Bačević, and Sorokin, pl. 6, fig. 6 (sed. *Sc. obliquus*).  
 non 1888 *Scaphites aequalis* Sowerby; Herbich, p. 288, pl. 15, figs. 6, 7.  
 ?1907 *Scaphites aequalis* Sowerby; Pervinrière pars, pl. 4, figs. 24–26.  
 ?1907 *Scaphites aequalis* Sowerby; Boule, Lemoine and Thevenin, p. 51, pl. 13, fig. 6.  
 1911 *Hoploscaphites aequalis* Sowerby; Nowak, p. 566, text-fig. 5 only, pl. 10, fig. 11.  
 1927 *Scaphites aequalis* Sowerby; Reeside, p. 27, pl. 9, fig. 1, pl. 10, figs. 13–15 (1927a).  
 1928 *Scaphites aequalis* Sowerby; Adkins, pl. 24, figs. 4, 5.  
 non 1929 *Scaphites aequalis-obliquus* Sowerby; Collignon, p. 49, pl. 5, figs. 1–6 (sed *Sc. obliquus*).  
 1951 *Scaphites equalis* J. Sowerby; Wright and Wright, p. 13.  
 1959 *Scaphites aequalis* Sowerby; Moskvina pars, pl. 7, fig. 1 only.  
 non 1959 *Scaphites aequalis* Sowerby; Cieśliński, p. 33, pl. 3, fig. 4 (sed *Sc. obliquus*).  
 1962 *Scaphites* (*Sc.*) sp. juv. aff. *equalis* J. Sowerby; Wiedmann, p. 214, text-fig. 53, pl. 10, fig. 11.

*Holotype*. The incomplete specimen figured by Sowerby 1813, pl. 18, figs. 1–3 and here reproduced, Plate 56, fig. 1. BMNH 43986. Exact locality unknown. ? Cenomanian from Dorset or Devon coast.

In spite of the poorly preserved type and its evidently wrong drawing by Sowerby, this species can be recognized without any difficulty. If we recall that the evolutionary trend between *Sc. simplex* and *Sc. obliquus* consists of the tendency to get more evolved inner whorls and coarser sculpture especially on the shaft, the main features of *Sc. equalis* can be recorded theoretically.

*Diagnosis*. Middle-sized scaphitid, but generally larger than the preceding species. Spiral part relatively large with moderately open umbilicus. Final hook very inflated with its distinctly constricted mouth-border nearly touching initial coil. Sculpture of septate coil similar to the preceding form; primaries generally bifurcating on the middle of lateral sides; on the venter one intermediate rib generally intercalated. Number and course of ribs as in *Sc. obliquus*. Sculpture changes considerably on living chamber. Four to five distantly placed primary ribs persist only on the shaft, especially inflated on the outer margin. In the venter, the sculpture is completely different, consisting of two to six fine and dense secondary ribs rising from each primary one. Here also one or two intermediates are generally intercalated. The dorsum, however, remains completely smooth. Also in the well-defined *Sc. equalis* we find some variation in the coarseness of the sculpture and the shell inflation. In the more inflated forms the sculpture is generally coarser (Pl. 56, fig. 4), while the compressed specimens (Pl. 56, fig. 3) are more weakly ribbed. The intermediate specimen from Chardstock (Pl. 56, fig. 2) can be regarded as representative for this species.

In the case of the suture-line, there is little difference from that of *Sc. obliquus*. The umbilical suture of *Sc. equalis* is somewhat more retracted (text-figs. 1a, b), consequently

the saddle  $L/E$  seems to be very high and  $L$  somewhat more asymmetric (but never trifid). The incision  $p$  is also well developed and becomes occasionally (text-fig. 1a) bifid. Furthermore the element  $L/E$  is more asymmetrically bipartite than tripartite, and the suture as a whole is somewhat more incised.

The measurements (in millimetres) of the three specimens treated here are:

	$D$	$B$	$d$	$h$	$b$	$u$
GPIT Ce 1221/11	32	17.5	19	11 (0.58)	10 (0.53)	2.5 (0.13)
GPIT Ce 1221/12	29	14	17	9 (0.53)	9 (0.53)	4 (0.24)
GPIT Ce 1221/13	31	19	19	10 (0.53)	12 (0.63)	3.5 (0.18)

*Further remarks.* The specimen GPIT Ce 1221/12 (Pl. 56, fig. 3), evidently referable to the present species, is reproduced, to give an impression of the degree of uncoiling of the inner whorls. This fact is not unknown, since Nowak (1911, pl. 10, fig. 11) demonstrated the evolute, lytoceratid shape of the innermost whorls of *Sc. equalis*. But it needs recapitulation, because these inner whorls agree completely with those of true *Otoscaphtes* (Pl. 58, fig. 2), which were separated from the *equalis* stock and all true *Scaphites* by C. W. Wright.

The theory of an ammonitid origin of *Scaphites* was developed in part on the suture-line drawing given by Pervinquierè (1907, text-fig. 37) from a specimen collected in the Vraconian of Tunisia. This form shows a distinctly trifid  $L$ , which is said to become bifid with age, contrary to the expected derivation from *Lytoceras*. This was adopted without query, and therefore became the reason for many authors to connect *Scaphites* with the ammonitid stock (Pervinquierè 1907, Reeside 1927a, Nowak 1911, Drushtchic 1962). Unfortunately it was never proven on original *equalis* material, whether the development from the trifid to the bifid lobe form can be confirmed, or whether the attribution of Pervinquierè's specimen to *Sc. equalis* was correct. I think we have reason to doubt both.

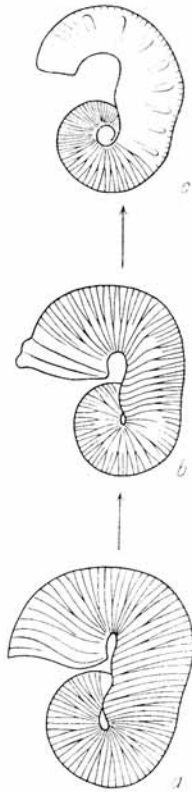
Above we noted the evolute lytoceratoid initial coil of *Sc. equalis*. The suture specimen in Pervinquierè (1907, pl. 4, figs. 22, 23) is, contrary to our knowledge of *Sc. equalis*, a nearly unsculptured and involute initial coil with a semi-lunate whorl section. The comparison with the different initial portions figured here, as well as the Vraconian age, and the distinctly asymmetric  $L$  verify that Pervinquierè's specimen belongs in reality to *Sc. simplex* (or *Sc. hilli*).

Now there naturally remains the question of an originally trifid  $L$  in true *Scaphites*. On the one hand, we demonstrated the intimate connexion between *Sc. simplex* and the eoscaphtid specimens with distinctly bifid  $L$ ; on the other, we were able to demonstrate the early suture development of one of the earliest representatives of the *equalis* group from the Spanish Vraconian (Wiedmann 1962a, p. 214, text-fig. 53).  $L$  was here found to be distinctly bifid at first, becoming more and more asymmetric up to the diameter which was studied by Pervinquierè. Thereafter the original symmetry rapidly returns; evidently this change was only observed by Pervinquierè. These are the somewhat defective reasons for attributing *Scaphites* to the Ammonitina.

*Distribution.* *Sc. equalis* like *Sc. obliquus* is a widespread Cenomanian species. It probably passes into the lower Turonian (Jefferies 1963). It can with certainty be cited from England, France, Bohemia, and Poland. The first but not absolutely proven representatives of the species were found in the Vraconian of Spain, Algeria, and Tunisia. All remaining citations from India and Madagascar probably do not belong to *Sc. equalis*.

THE *SIMILARIS* STOCK

In this group I join a number of species which differ from members of the main stock merely through their smaller size. I believe that as in the *equalis* stock, three species are sufficient to cover the complete small-sized Upper Albian and Cenomanian material. These species are: *Sc. (Sc.) hilli* Adkins and Winton, *Sc. (Sc.) yonekurai* Yabe, and *Sc. (Sc.) similaris* Stoliczka.



TEXT-FIG. 4. The development of the atrophic *similaris* stock. All  $\times 1.5$ . a, *Sc. (Sc.) hilli* Adkins and Winton (= *Sc. bassei* Collignon), b, *Sc. (Sc.) yonekurai* Yabe (*Sc. dailyi* C. W. Wright), c, *Sc. (Sc.) similaris* Stoliczka.

These forms are separated from the main stock and briefly treated here, because they make us aware of an interesting problem in scaphitid development. As evident from text-fig. 4, these species parallel the above described members of the main stock completely in ornamentation and general appearance (cf. text-fig. 13). They differ only in their smaller size and the presence of more or less pronounced bulges at the initial shaft, which covers the umbilicus. We believe that the lateral bulges depend on the reduced size, because in all scaphitids at hand, these peculiar bulges are restricted to small-sized specimens.

In his highly interesting paper about sexual dimorphism in ammonites, Makowski (1962, p. 31, text-pl. 4) also briefly treated *Scaphites*. For this purpose he had collected quite a number of *Hoploscaphites constrictus* from the same stratum and found that two forms of the same ornamentation, but separated by a distinct size gap, were present. This, and the abundance ratio 2:1 between the bigger (female) and smaller (male) specimens, were the basis for the establishment of sexual dimorphism in scaphitids, expressed here only through the different size.

Cobban (1952) drew attention to a similar phenomenon. Describing the scaphitids of the Western Interior United States, he was able to separate from the *Scaphites* main stock a lineage of dwarfed and mostly new species, which parallel the main development (Cobban, op. cit., text-fig. 1) and produce prominent lappets on the mouth-border (*Pteroscaphites* Wright). *Otoscaphites* evidently represents another micromorph development with lateral mouth lappets, which parallels the *Scaphites* main stock. The similarity of these lineages and Makowski's dimorphism is striking, especially if we agree with the Polish author, regarding the presence of mouth lappets as a common feature of the male sex in ammonites. But only the ptero- and otoscaphitids fulfil the suppositions for dimorphism:

to have the same stratigraphic and geographic distribution as the referable specimen of the normal lineage. The *similaris* forms diverge in both from the main stock: The large-sized stock seems to be restricted to the Northern boreal region of Europe, the *similaris*



group evidently favoured the Tethyan and Indo-Pacific areas. Moreover the latter generally have a longer stratigraphic range. Only in the Cenomanian of Northern France did I find both types together, where the separated areas may overlap. Thus the existence of the *similaris* group seems to have more ecologic and geographic reasons. *Sc. similaris* and its allies will be regarded as an atrophic parallel development to the main stock, which evidently favoured the boreal coldwater.

If this interpretation is correct, the generic separation of the present forms from the main stock is more reasonable than that of genus *Pteroscaphites* and family Otoscapitidae. Independent of these taxonomic problems is the question, whether the species of the *similaris* stock represent a true parallel development or single lateral offshoots of the equivalent species of the *equalis* group. For the moment this question cannot be decided.

*Sc. (Scaphites) hilli* Adkins and Winton

- 1907 *Scaphites obliquus* Sowerby: Pervinquierè, pl. 4, fig. 27.  
 ?1907 *Scaphites aequalis* Sowerby: Pervinquierè, pl. 4, figs. 22, 23 only, text-fig. 37.  
 1920 *Scaphites hilli* Adkins and Winton, p. 37, text-figs. 3, pl. 7, figs. 3-6.  
 1920 *Scaphites hilli* Adkins and Winton; Adkins, p. 79, text-figs. 6-8, pl. 2, figs. 1-12.  
 1928 *Scaphites hilli* Adkins and Winton; Adkins, p. 257, pl. 20, figs. 1-3, 7.  
 1929 *Scaphites Bassei* Collignon, p. 51, pl. 5, figs. 8, 9.  
 1931 *Scaphites Bassei* Collignon; Collignon, p. 46, pl. 5, fig. 6.  
 1955 *Scaphites bassei* Collignon; Sornay, p. 10, text-fig. 3, pl. 10, figs. 7, 11.  
 ?1962 *Scaphites (Sc.) simplex* Jukes-Browne; Wiedmann, p. 213, text-fig. 52, pl. 10, fig. 8 (1962a).

*Holotype.* The originally designated type specimen from the Pawpaw clay (Vraconian) of Fort Worth, Texas, in Adkins and Winton 1920, pl. 7, fig. 3.

The diagnosis given for *Sc. simplex* can be repeated here with the only difference, that *Sc. hilli* is smaller, develops a distinct living-chamber bulge which covers the umbilicus, and offers a somewhat more asymmetric *L*. The sculpture consists of the same fine ribs as in *Sc. simplex*, the spiral portion has the same closed umbilicus and initial tuberculation: it agrees in its more or less inflated whorl section, the strongly retracted umbilical suture and, consequently, the pronounced asymmetry of *L*. The congruence of *Sc. simplex* and *Sc. hilli* is so complete, that even the nodate variety (p. 413) can be recorded in *Sc. hilli* (Adkins 1928, pl. 20, fig. 3), and both species were combined on a previous occasion (Wiedmann 1962a). Indeed the initial coils of both species are indistinguishable, as the Tunisian and Spanish nuclei, cited in synonymy, make evident. If the body-chamber is present, then it is not difficult to separate them, because *Sc. hilli* does not attain a great diameter (D) of 15 mm. In *Sc. simplex*, however, we noted an average diameter of 30 mm.

There is no doubt that also *Sc. 'bassei'* Collignon, of the Mediterranean-Madagascan area, should be included here. Like the following species, also *Sc. hilli* survives its normal-sized equivalent: it is known from the uppermost Albian of Texas, Algeria, ? Tunisia and ? Spain, but the main distribution lies in the Cenomanian of Northern Africa and Madagascar.

*Sc. (Scaphites) yonekurai* Yabe

Plate 56, fig. 7; text-fig. 3d

- 1865 *Scaphites obliquus* Sowerby: Stoliczka, p. 168, pl. 81, figs. 1-3.  
 1867 *Scaphites obliquus* Sowerby: Guéranger, p. 6, pl. 5, fig. 8.

- ?1907 *Scaphites aequalis* Sowerby; Boule, Lemoine, and Thevenin, pl. 13, fig. 6.  
 1910 *Scaphites* (?) *Yonekurai* Yabe, p. 165, pl. 15, figs. 4-7.  
 1929 *Scaphites aequalis-obliquus* Sowerby; Collignon, p. 49, pl. 5, figs. 1-6.  
 1963 *Scaphites dailyi* C. W. Wright, p. 602, pl. 81, fig. 6.

*Lectotype.* The complete specimen figured by Yabe (1910, pl. 15, figs. 4, 6) from the *Scaphites* beds of the Opiraushibets region (Teshio, Hokkaido).

*Sc. yonekurai* as here interpreted covers a number of slightly different types which are, as we believe, inseparable. The diagnoses given by Yabe and C. W. Wright agree completely and can be summarized as follows: Like *Sc. obliquus* but smaller and with more globular, moderately involute initial whorls, and more or less pronounced bulge.

As in the case of *Sc. obliquus* we find all transitions between the preceding species and *Sc. similis*: on one side we have the finely ribbed Utatur specimen Stoliczka's (1865, pl. 81, fig. 3), on the other the coarser ribbed specimen from Diégo-Suarez as figured by Collignon (1929, pl. 5, fig. 1). Also variable is the bulge size which is less pronounced in the Japanese type, moderately in Indian material, and more evident in the Australian type of *Sc. 'dailyi'* or the here figured French hypotype (Pl. 56, fig. 7). But all these forms are connected through their inflated and moderately involute initial coil, where about twenty primary ribs per whorl are present, as in *Sc. obliquus*. They are likewise bi- or trifurcating, and slightly curved backward on lateral sides and venter. On the shaft the primaries are more pronounced and the secondaries sometimes more numerous, as always in the case of *Sc. obliquus*. Generally the primaries are equally spaced and projected on the shaft (text-fig. 4*b*), but in the forms with inflated bulges (Stoliczka 1865, pl. 81, fig. 2; Wright 1963, pl. 81, fig. 6; here Pl. 56, fig. 7), they seem to be bundled at the umbilical margin. The suture with a distinctly bifid *L* (text-fig. 3*d*) also agrees completely with that of *Sc. obliquus*.

In the present form the difference in size is less pronounced than in the preceding form. The French specimen figured here for comparison with *Sc. obliquus* and *Sc. 'dailyi'* has the following dimensions (in millimetres):

	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/10	22	11	14	7 (0.50)	9 (0.64)	2.5 (0.18)

A general distinguishing feature from *Sc. obliquus* is the much more opened umbilicus of *Sc. yonekurai*. Like *Sc. hilli*, the present species also favours the Southern hemisphere and outlasts the macromorph species. It is known from the Cenomanian of India, Madagascar, and the Bathurst Island (Northern Australia), from the Turonian/Coniacian of Hokkaido, and finally it was collected, together with *Sc. obliquus*, in the French type Cenomanian of the Sarthe. The Madagascan material links the present species with *Sc. similis*.

*Sc. (Scaphites) similis* Stoliczka

- 1865 *Scaphites aequalis* Sowerby; Stoliczka, p. 167, pl. 81, figs. 4-6.  
 1868 *Scaphites similis* Stoliczka, p. 36.

*Lectotype.* The specimen figured by Stoliczka (1865, pl. 81, fig. 5) from the Utatur group of Odium, Southern India.

This species is evidently a small-sized *Sc. equalis*, with which Stoliczka identified it at first. Besides the different size, the shell is somewhat less inflated as in the European

species. There is little difference, if not identity, with the somewhat younger *Sc. aequalis* mut. *turonensis* Roman and Mazeran (1913, pl. 4, figs. 10–14) of the Turonian from Uchaux (France) and Madagascar (?).

#### THE *MERIANI* STOCK

Through the possession of conical ventrolateral tubercles, a closed umbilicus, and an asymmetrically bifid *L*, the species here united: *Sc. (Sc.) hugardianus* d'Orbigny, *Sc. (Sc.) meriani* Pictet and Campiche, and *Sc. (Sc.) collignonii* sp. nov., are well distinguishable from the untuberculate groups treated above. But nevertheless they are so continuously connected with *Sc. simplex* that the generic separation from the main stock seems inadmissible. The three species mentioned above, are exclusively restricted to the Upper Albian.

#### *Sc. (Scaphites) hugardianus* d'Orbigny

Plate 54, fig. 5; Plate 57, figs. 1, 2, 6, 7; text-figs. 5*d, e*

- 1842 *Scaphites Hugardianus* d'Orbigny, p. 521, 525.  
 non 1848 *Scaphites Hugardianus* d'Orbigny; Pictet, p. 370, pl. 12, figs. 2*a–d* (sed *Sc. simplex*).  
 1850 *Scaphites Hugardianus* d'Orbigny; d'Orbigny, p. 125.  
 1861 *Scaphites Meriani* Pictet and Campiche pars, p. 16, pl. 44, figs. 5, 6 only.  
 1861 *Scaphites Hugardianus* d'Orbigny; v. Hauer, p. 649, pl. 2, figs. 11, 12.  
 1875 *Scaphites Hugardianus* d'Orbigny; Hébert and Munier-Chalmas, p. 116, pl. 5, fig. 7.  
 1875 *Scaphites Meriani* Pictet and Campiche; Jukes-Browne, p. 287, pl. 14, figs. 1, 2.  
 1910 *Scaphites Hugardianus* d'Orbigny; Pervinquier, p. 24, text-fig. 8, pl. 2, figs. 1, 2.  
 1911 *Scaphites Hugardianus* d'Orbigny; Nowak, p. 570, text-fig. 7.  
 ?1929 *Scaphites Hugardianus* d'Orbigny; Collignon, p. 53, pl. 5, fig. 12.  
 1937 *Scaphites Hugardianus* d'Orbigny; Spath, p. 502, text-figs. 175*a, b*, 176*a, b, g–i*; pl. 57, fig. 24.

The original description of *Sc. hugardianus* given by d'Orbigny (1842, p. 525) is inadequate: '... voisine du *Sc. aequalis*, en diffère par le manque des côtes, ces ornements étant remplacés par une pointe aigue. Elle se trouve dans le gault supérieur des Fis en Savoie.' Nevertheless this sentence allows us to recognize that the two syntypes which are preserved in d'Orbigny's collection do not correspond to the diagnosis.

Because d'Orbigny never figured a type specimen, it is not surprising that Pictet (1848), who figured the species for the first time, was unable to interpret it correctly. We agree completely with Spath in regarding these forms with three umbilical tubercles on the shaft as an extreme variety ('var. *nodata*') of *Sc. simplex*.

However, not only Spath but all subsequent authors followed the description given by Hébert and Munier-Chalmas (1875, p. 116), because these authors mentioned that they had examined d'Orbigny's type specimens. Here the species is interpreted as follows: 'Test orné de côtes fines, égales et équidistantes, partant deux par deux sur la spire et sur le commencement du tour projeté, de côtes en peu plus fortes venant de l'ombilic. La partie supérieure du tour projeté présente cinq ou six tubercules aigus et comprimés situés sur les flancs, plus près du dos que de la région ventrale; de chacun d'eux partent seulement deux ou trois côtes; les autres passent, simples ou bifurquées, entre ces tubercules, qui disparaissent quelquefois sur certains individus.'

The specimen figured by Hébert and Munier-Chalmas and here reproduced (Pl. 54,

fig. 5), unfortunately does not belong to d'Orbigny's types, but to the material from Salazac (Gard) described by these authors. Contrary to the rules of nomenclature it was proposed as lectotype by Spath. Naturally this proposal cannot be accepted, since the specimen did not come from the preserved type material nor from the type locality. Through the kindness of Dr. Sornay I received some of the original syntypes, but only two of the three specimens mentioned by Hébert and Munier-Chalmas are preserved. Unfortunately they are neither conspecific nor identical with *Sc. hugardianus* auct. Both are labelled 'La Fiz', but one of them is in greensand matrix and probably belongs to *E. subcircularis*; the other here reproduced (Pl. 57, fig. 1) is of phosphatic material and can evidently be identified with the nodate variety of *Sc. simplex*. In order to avoid any further confusion, we leave this problem open, hoping that the missing specimen will be found in the Sorbonne collections, not accessible at the moment. Here Hébert and Munier-Chalmas' types are deposited.

With these reservations some specimens are figured here from the Cambridge Greensand and Southern France which are referred to *Sc. hugardianus*. They exactly agree in their dimensions with the 'typical' specimen from Salazac, while d'Orbigny's tuberculate syntype also agrees in this respect with *Sc. simplex* (cf. p. 415).

	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/7	21	13	12.5	7 (0.56)	11 (0.88)	—
MHNG Wi 'Sc'/7	18	10	9.5	4.5 (0.47)	7 (0.74)	1.5 (0.16)
MHNG Wi 'Sc'/8	21	12	11	7 (0.64)	9.5 (0.86)	—
MHNG Wi 'Sc'/9	21	12.5	12	6.5 (0.54)	11 (0.92)	—

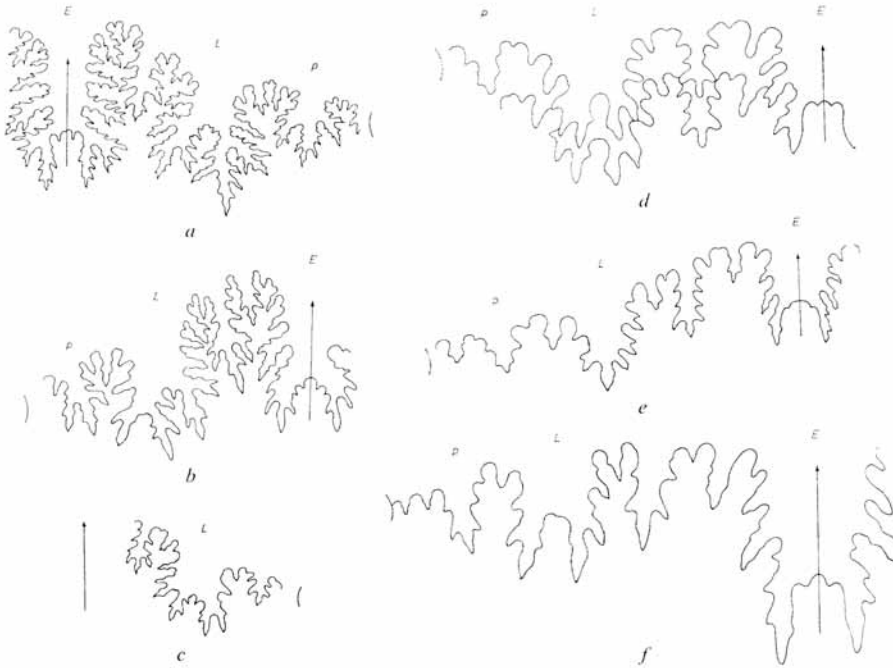
The material in my possession permits the following supplement to the diagnosis: *Sc. hugardianus* is a middle to small-sized species. The umbilicus of the phragmocone is generally completely closed (Pl. 57, fig. 6), but sometimes somewhat open (Pl. 57, fig. 7). Lateral bulges on the initial shaft may be present (Pl. 57, fig. 1) or not (Pl. 57, fig. 6a). This makes evident, that the presence of lateral bulges—introduced in the scaphitid classification by Collignon (1929), Sornay (1955), and C. W. Wright (1963)—is without great systematic significance, but a common feature of many small-sized specimens. The hooked body-chamber of *Sc. hugardianus* is of peculiar shape: broad, inflated, with distinctly constricted and collared mouth-border (Pl. 57, figs. 1, 7) nearly touching the initial coil.

In the suture-line are found some interesting variations. *L* generally has a subsymmetric bifid shape (text-fig. 5d), but in the Cambridge Greensand form figured here, which cannot be separated from the present species, the lateral lobe is nearly trifid (text-fig. 5e). This emphasizes the intimate relationship to *Sc. simplex*, with which *Sc. hugardianus* is linked through the forms just mentioned. As indicated above and visible in text-fig. 5, this asymmetrical outline of *L* depends especially on the general course of the umbilical suture-line. Where it passes straight over the sides and the umbilical seam (text-figs. 5d, f), *L* remains bifid; where the umbilical portion is retracted, however (text-figs. 5a-c, e), *L* becomes distinctly asymmetric. This is the real and simple reason for the attribution of an 'ammonitid origin' to *Scaphites*.

In comparison with the following *Sc. meriani*, the suture-line is less incised, the saddle *L/E* enlarged and nearly symmetrically divided by a pronounced median incision.

The feature which joins all forms described here or cited as synonymous, are the five

small but pronounced tubercles of the living-chamber. They are equally spaced, somewhat nearer to the venter. The generally single primary ribs trifurcate at the tubercles, while two single or bifurcating untuberculate ones are intercalated. The umbilical portion of these ribs is more or less (Pl. 57, figs. 2 to 7) pronounced. The initial coil preserves the fine, dense ribbing of the preceding *Sc. simplex*.



TEXT-FIG. 5. Suture-lines of the *Scaphites meriani* stock. *a-c*, *Sc. (Sc.) meriani* Pictet and Campiche. *a*, Lectotype, MHNG P & C 'S-CR'44, 1; Vraconian, Ste Croix. *h* = 6 mm. *b*, Madagascan hypotype (Collignon 1963, fig. 1141); Upper Albian, Mt. Raynaud. *h* = 5 mm. *c*, Hypotype GPIT Ce 1221/2; Upper Albian, Col de Teine. *h* = 4 mm. *d, e*, *Sc. (Sc.) hugardianus* d'Orbigny. *d*, Specimen with bifid *L*, MHNG Wi 'Sc'7; Upper Albian, Crioud (?). *h* = 4 mm. *e*, Specimen with retracted umbilical suture and asymmetric *L*, GPIT Ce 1221/7; Cambridge Greensand. Intermediate to *Sc. simplex*. *h* = 7 mm. *f*, *Sc. (Sc.) collignoni* sp. nov. Holotype (coll. Collignon); Upper Albian, Mt. Raynaud. *h* = 6 mm.

Without any doubt *Sc. hugardianus* is directly linked with the latter. But at the base of sculpture, shell size, and inflation, separation is always possible, even in the nodate forms of *Sc. simplex*. All these forms preserve the globular coil and size of the untuberculate type, and the always weak and less numerous tubercles of the chamber are arranged in the neighbourhood of the inner margin.

The specimen figured on Plate 57, fig. 7, resembles in its open initial coil and the smoothness of its initial body-chamber, the younger *Sc. pseudoaequalis* Yabe, which has

distinct and tuberculate primary ribs on the septate portion. We are unable to decide at the moment whether the specimen from Criou (?) perhaps belongs to a distinct species. The differences from the direct descendant *Sc. meriani* will be treated below.

*Distribution.* *Sc. hugardianus* is widespread in the French Upper Albian. It is known from the Montagne La Fiz, Mt. Saxonet and Criou (?) (Haute-Savoie), and Salazac (Gard). It seems to be present in the Vraconian of Ste Croix (Vaud, Switzerland), the Bakony Forest (Hungary), and Berrouaghia (Algeria). In England the species seems to be restricted to the Upper Albian *substuderi* subzone of the Cambridge Greensand. The species will soon be described from the Upper Albian of Orosei (Sardinia). Collignon's specimen from the Madagascan Cenomanian is too poorly preserved for any identification with *Sc. hugardianus*.

*Sc. (Scaphites) meriani* Pictet and Campiche

Plate 54, fig. 6; plate 57, figs. 3, 4; text-figs. 5a-c

- 1861 *Scaphites Meriani* Pictet and Campiche pars, p. 16, pl. 44, figs. 1-4, 8 only.  
 non 1875 *Scaphites Meriani* Pictet and Camp.; Jukes-Browne, p. 287, pl. 14, figs. 1, 2 (sed *Sc. hugardianus*).  
 non 1888 *Scaphites Meriani* Pictet and Camp.; Herbich, p. 28, pl. 13, figs. 5-10.  
 non 1929 *Scaphites* cf. *Meriani* Pictet and Camp.; Collignon, p. 54, pl. 5, fig. 15 (sed *Sc. sp. juv. indet.*).  
 1963 *Scaphites Meriani* Pictet and Camp. pars; Collignon, p. 56, pl. 262, fig. 1141 only.

*Lectotype.* The adult specimen figured by Pictet and Campiche (1861, pl. 44, fig. 1) from the Vraconian of Ste Croix, and here reproduced (Pl. 54, fig. 6). Preserved in the Pictet collection, MHNG P & C 'S-Cr'44, 1.

*Description.* Large species with completely involute, generally unsculptured initial coil. Different from the previously described scaphitids, first part of straight shaft always septate. Largely curved final hook. The specific feature is the sculpture of the body-chamber, consisting of looped main ribs amalgamating into nine or ten ventrolateral tubercles, and untuberculate intermediate ones. All ribs bi- or trifurcating at the height of the tubercles. On the spiral portion tubercles generally begin earlier than in the preceding species, but this is subject to variation. Very incised suture with asymmetric *L*. even in youth. Saddles moderately enlarged.

*Remarks.* *Sc. meriani* is not as common as generally believed. Its phylogenetic position is between *Sc. hugardianus*, with largely spaced tubercles on the chamber only, and *Sc. collignoni* sp. nov., with tuberculation on each second rib beginning at a very small diameter. The incoming of ribbing and tuberculation in the present species is evidently subject to variation. In the lectotype the septate coil remains nearly smooth with some very weak tubercles on the last half whorl (Pl. 54, fig. 6b). On the spiral portion here figured (Pl. 57, fig. 3), the ribs are more distinct as in the type (and the smooth initial coil figured by Pictet and Campiche as fig. 8), but no tuberculation can be observed up to a whorl height of 7.5 mm. In comparison with this, the nucleus figured by Collignon (1963, fig. 1141) and here regarded as synonymous (Pl. 57, fig. 4), is distinctly tuberculate at a whorl height of 2 mm. Despite this the sculpture has the same style (looped primary ribs, two intercalated untubercled ones, &c.) as the large lectotype. Also the

suture agrees so completely in all three forms (text-figs. 5a-c), that there is no possibility to separate them.

The second specimen which was referred to the present species by Collignon (1963, fig. 1142) differs in sculpture and suture-line so distinctly from *Sc. meriani*, that I propose to separate it as a new species.

*Distribution.* *Sc. meriani* occurs with certainty only in the Vraconian of Ste Croix (Vaud, Switzerland), and Col de Teine (Haute-Savoie). It is relatively abundant in the uppermost Albian of Orosei (Sardinia), and is also present in the Hysteroцерatan of Mt. Raynaud near Diégo-Suarez (Madagascar). The Cenomanian specimen figured by Collignon (1929) without suture drawing may belong, however, to *Sc. simplex* or *Sc. yonekurai*.

*Sc. (Scaphites) collignoni* sp. nov.

Plate 57, fig. 5; text-fig. 5f

*Holotype.* *Scaphites meriani* in Collignon 1963, pl. 262, fig. 1142, from the Upper Albian (Zone à *Hysteroцeras binum*) of Mt. Raynaud near Diégo-Suarez, Madagascar, and here reproduced Plate 57, fig. 5.

*Description.* Globular initial coil, belonging to the *meriani* stock. From a whorl height of 2 mm. every second primary rib provided with a small tubercle at the point of bifurcation; only one bifurcating and untubercled rib intercalated. Umbilicus completely closed and finally overlapped by a distinct lateral bulge. Body-chamber unknown. Suture moderately incised, and with distinctly bifid lateral lobe.

*Remarks.* *Sc. collignoni* sp. nov. can be regarded as the final member of the *meriani* stock. The lateral tuberculation in the present form starts at an early age and covers every second primary rib. Moreover the section of the initial coil is extremely globular (Pl. 57, fig. 5c), and the septal surface extremely incised by a great number of secondary elements. The number of tuberculate main ribs amounts to thirty per whorl (Pl. 57, fig. 5b). The suture-line (text-fig. 5f) is less incised than in *Sc. meriani*, even at a comparative diameter (text-fig. 5a). *L* has a distinctly bifid outline, and the element *L/E* is somewhat enlarged.

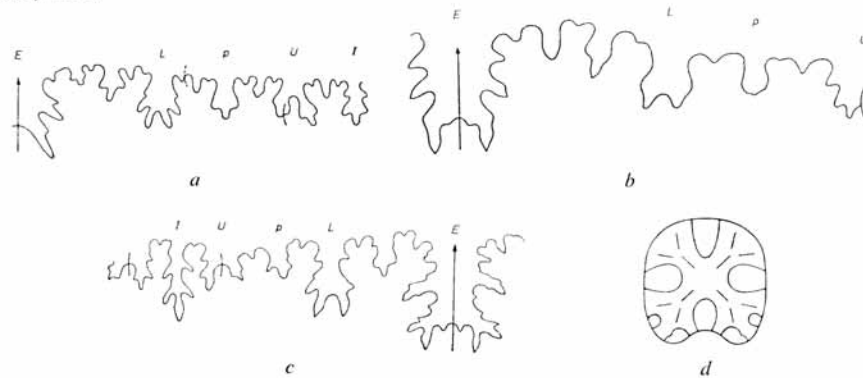
If we consider that in *Sc. meriani* only ten ribs per whorl are present which acquire ventrolateral tuberculation, and also that in this species sculpture and suture-line, even on the smallest known nucleus (Pl. 57, fig. 4, text-fig. 5b), completely agrees with that of the full-grown lectotype, then the separation of the present spiral portion becomes evident, despite the fact that the living-chamber is unknown. The inner whorl of the younger *Sc. pseudoaequalis*, as figured by Yabe (1910, pl. 15, fig. 2) approaches the present form, but there are no untuberculate ribs intercalated between the tuberculate ones. The species is known only from its holotype.

Subgenus SCAPHITES (METASCAPHITES) Wiedmann 1962

*Type species.* *Scaphites* (?) *thomasi* Pervinquière 1907.

Besides the three lineages treated above another early scaphitid stock developed in the Western Mediterranean area, which seems to be, however, of little phylogenetic interest. For the moment only two species can be included: *Sc. (Metascaphites) subthomasi*

Wiedmann and *Sc. (Metascaphites) thomasi* Pervinquière. Both are obviously different from the scaphitids hitherto described. They differ in their rectangular whorl-section (text-fig. 6*d*), and their strong and nearly straight main ribs which become tuberculated at the outer margin and cross the venter without bifurcation (Pl. 58, fig. 1). They differ also in the umbilical suture-line, where *U* remains on the umbilical seam. Thus they anticipate the general appearance of the Maastrichtian genus *Indoscaphites*. Therefore I proposed (1962*a*, p. 212) to separate these peculiar Upper Albian forms from the true *Scaphites*.



TEXT-FIG. 6. The different subgenera of *Scaphites*. *a*, Complete suture-line of *Sc. (Hyposcaphites) stephanoceroides* Yabe (ex Jimbo 1894, pl. 9, fig. 3*b*); Upper Turonian (?), Pombets, Hokkaido. *h* = 5 mm (?). *b*, External suture of *Sc. (Pteroscaphites) minutus* Moreman, holotype, BEGA 19814; Lower Turonian, Britton. *h* = 3.5 mm. *c*, Complete suture-line, and *d*, Septal surface of *Sc. (Metascaphites) subthomasi* Wiedmann (ex Wiedmann 1962*b*, text-figs. 57, 58); Upper Albian, Izurdiaga. *h* = 3.5 mm.

The origin of *Metascaphites* still remains doubtful, because there is nothing comparable in the Upper Albian. I believe that *Metascaphites* can be traced directly back to *Eoscaphites*, in spite of the much more simplified suture-line. As in the early *Eoscaphites* the umbilical lobe becomes subdivided through the umbilical seam, where it remains throughout. Moreover, the older *Metascaphites subthomasi* is much more evolute than the Vraconian type species with its completely closed spiral coil (Pl. 58, fig. 1). The lateral lobe is distinctly bifid, and thus we have little doubt that the present subgenus belongs to *Scaphites*, despite its acanthoceratoid sculpture.

If we compare the metascaphitid suture-line with that of *Otoscaaphites* (text-figs. 6*b*, 7) we find complete identity. Naturally it is difficult to make any decision about the systematic value of the definite position of *U*. The fixation of the latter on the umbilical seam can be regarded in scaphitids as a phylogenetically early feature; it is also present in the early ontogeny as well as probably depending on the degree of whorl evolution. If we use, therefore, the umbilical suture for systematic purposes, we risk combining not only early scaphitid representatives, but also micromorphs or evolute members of completely different scaphitid lineages. This becomes evident if we consider Yabe's genus '*Yezoites*' which was based nearly on the same feature: the presence of an undivided



saddle  $I/U$  naturally depends on the position of  $U$  on the umbilical seam. The three species joined in 'Yezoites' by Yabe in reality belong to three different scaphitid stocks.

These are the reasons why I do not directly connect with *Metascaphites* a group of scaphitids described from the Algerian Cenomanian by Pervinquière. These forms agree with the present in regard to suture-line and sub-rectangular whorl-section, but they differ in sculpture and whorl evolution. While in the present subgenus the tendency to close the umbilicus was observed, the spiral portion of the Cenomanian forms remain open whorled. Moreover, the untuberculate ribs are sigmoidal and bifurcating. These features are likewise representative for the Turonian *Otoscaphtes* to which the Cenomanian species are referred here. I believe that these forms also—like the similar *Metascaphites*—can be traced back to *Eoscaphtes*, and not to *Worthoceras*, as C. W. Wright believed. *Metascaphites* seems to be restricted to the Upper Albian of the Western Mediterranean region.

#### Subgenus SCAPHITES (OTOSCAPHITES) C. W. Wright 1953

*Type species. Amm. (?) bladenensis* Schlüter 1872.

Unfortunately *Amm. bladenensis* Schlüter (January 1872) is a very doubtful ammonitid species, known only through a small inner whorl with a diameter of 15 mm (Pl. 58, fig. 6). It differs through its single radial ridges considerably from the subsequently described but well-defined *Sc. auritus* Schlüter (March 1872). Here the ribs are distinctly sigmoidal, bi-, or triplicate; but Schlüter's syntypes (1872, pl. 23, figs. 5–9) vary considerably in the coarseness of their ribbing. Contrary to *Sc. bladenensis*, the later species can easily be referred to *Scaphites* in regard to its living-chamber and suture-line. The small size, the open-whorled spiral portion, and the presence of distinct lateral lappets at the mouth-border are further common features of the somewhat divergent syntypes.

Schlüter himself (1872, p. 77) intended to include *Amm. bladenensis* in the better-known *Sc. auritus*, but he was unable to localize *bladenensis*-like inner whorls in the full-grown *auritus* specimens. Thus *Amm. bladenensis* was abandoned by the majority of the subsequent authors. It was Diener at first (1925, p. 197), and C. W. Wright thereafter (1953), who preserved the anterior name according to the rules of nomenclature, and regarded *Sc. auritus* as synonymous with the poorly known *Sc. bladenensis*.

The material studied here permits the following decision. Schlüter's *auritus* syntypes belong to at least two different species. Only the third form (Schlüter's fig. 9) can be identified with *Amm. bladenensis*, which can be characterized through its pachydiscoïd lateral ridges in youth, and strong, sigmoidal ribs generally bifurcating at the centre of the sides in the adult stage. The specimen figured here (Pl. 58, fig. 2, text-fig. 7) belongs to this species, as also *Sc. 'auritus'* in Geinitz (1875, pl. 35, fig. 10). For the two remaining specimens in Schlüter the name *Sc. auritus* (lectotype the original of Schlüter 1872, pl. 23, figs. 5, 6) should, however, be preserved. The restricted *Sc. auritus* is then more closely and finely ribbed, the ribs trifurcate at small umbilical tubercles in the type, without tuberculation in the presumed paratype (Schlüter's figs. 7, 8). *Sc. 'auritus'* Fritsch (1872, p. 44, pl. 13, figs. 8, 9, 11, 14, 15) = *Sc. 'fritschi'* Grossouvre, agrees completely with this definition.

These identifications became curiously confirmed through Californian otoscaphtids,

for which I thank Professor Popenoe. The two specimens here reproduced (Pl. 58, figs. 3, 4) from the Cow Creek valley agree more with the original drawings of *Otoscaphtes bladenensis* than the European hypotypes mentioned above. These, and especially the specimen of Plate 58, fig. 2, offer more inflated and more involute inner whorls with less numerous lateral ridges. It may be regarded therefore as transitional to *Sc. (Otoscaphtes) cottae* (F. A. Roemer) with closed umbilicus. But the Californian hypotype (Pl. 58, fig. 4) agrees completely in whorl-section, degree of evolution and the elevated number of twenty lateral ridges per whorl with the juvenile holotype of *Otoscaphtes bladenensis*, while the adult specimen (Pl. 58, fig. 3) with the beginning of its chamber preserved, demonstrates the sculptural transition from lateral ridges to strong bifurcating ribs, as stated for the adult *Otoscaphtes bladenensis* (Schlüter 1872, pl. 23, fig. 9). Thus the latter can now be regarded as a valid and well-defined species.

For the question of the origin of otoscaphtids it is necessary to recall the fact that the sculpture of *Otoscaphtes bladenensis* corresponds with that of the inner whorls of the contemporaneous *Sc. geinitzii* d'Orbigny, which is regarded as a direct descendant of *Sc. equalis*. Thus we again face the problem of sexual dimorphism in scaphitids. Indeed it was Fritsch (1872, p. 44) who for the first time stated that the dwarfed 'auritus' forms may only be the males of the normal-sized *Sc. geinitzii*. This relationship between small and normal-sized scaphitids of the same stratigraphic level does not harmonize with the modern systematics. Wright (1953) pointed out that *Sc. bladenensis*, on which the new genus *Otoscaphtes* was based, belongs to an independent scaphitid lineage of small forms with constricted mouth-border, and can be connected with the Albian *Worthoceras*. The latter was said to be derived from *Eoscaphtes*, and thus 'Otoscaphtinae' were separated as a different subfamily from the scaphitid main stock. This separation was mainly based on four suppositions which should be discussed here.

1. *Scaphites minutus* Moreman, described from the Turonian of Texas, can be directly related to *Sc. bladenensis* of the European Upper Turonian.
2. *Scaphites minutus* can also be related to the Upper Albian *Worthoceras platydorsum* (Scott), with which it is linked by a number of worthoceratids in the Texan Albian, Cenomanian, and Lower Turonian.
3. The lineage *Worthoceras-Otoscaphtes* parallels the scaphitid main stock, from which

#### EXPLANATION OF PLATE 57

- Figs. 1, 2, 6, 7. *Scaphites (Scaphites) hugardianus* d'Orbigny. 1, Lateral view of typical hypotype, MHNG Wi 'Sc'8 (leg. Favre), with preserved mouth-border; Upper Albian (Vraconian?), Mt. Saxonet (Haute Savoie, France). 2, Hypotype GPIT CE 1221/7, with weak tuberculation, intermediate to *Sc. simplex*. Vraconian (*substuderi* zone), Cambridge Greensand. a, Ventral, b, lateral view. 6, Hypotype MHNG Wi 'Sc'9 (leg. Pictet), with closed umbilicus; Upper Albian, Crioud? (Haute Savoie, France). a, Lateral, b, ventral view. 7, Hypotype MHNG Wi 'Sc'7 (leg. Pictet), with open umbilicus, nearly smooth shaft and preserved mouth-border; same locality. Lateral view.
- Figs. 3, 4. *Sc. (Sc.) meriani* Pictet and Campiche. 3, Costate spiral portion, GPIT Ce 1221/2; Upper Albian, Col de Teine near Bonneville (Haute Savoie, France). a, Lateral, b, frontal view. 4, Tubercled spiral portion (cf. Collignon 1963, pl. 262, fig. 1141); Upper Albian (*Hysterocheras binum* zone), Mt. Raynaud near Diégo-Suarez (Madagascar). Lateral view;  $\times 3$ .
- Fig. 5. *Sc. (Sc.) collignoni* sp. nov. Holotype (cf. Collignon 1963, pl. 262, fig. 1142, sub *Sc. meriani*); same age and locality. a, Ventral, b, lateral, c, frontal view;  $\times 3$ .
- All  $\times 2$  unless otherwise stated.

it is principally distinguishable through the presence of lateral mouth lappets, and an open whorled spiral portion. This makes a subfamily of its own necessary.

4. The origin of these 'Otoscapitinae' was presumed to be some scaphitid member, probably *Eoscapites*. Therefore the subfamily 'Otoscapitinae' was included in Scaphitidae.

We are extremely glad to have received, just before completing this manuscript, some interesting *Worthoceras* and '*Otoscapites*' of the Texan Cretaceous, through the kindness of Dr. P. U. Rodda. Only for this reason is it possible to comment on the above-mentioned suppositions.

1. *Scaphites minutus* Moreman, here reproduced Pl. 58, fig. 5, text-fig. 6*b*, can neither be related to the European *Sc. bladenensis* nor included in Wright's genus *Otoscapites*. However, it is indistinguishable from the micromorph species *Sc. praecoquus* and *vetrinovus* Cobban of the Western Interior Carlile shale (Upper Turonian). Lateral lappets are also known from these forms, but Wright (1953, p. 474) indicates, that these are 'quite distinct from the type of lappets present' in *Otoscapites*. *Sc. minutus* makes it evident, however, that they are of the same type.
2. *Scaphites minutus* indeed agrees in its smaller size with the Turonian *Worthoceras gibbosum* Moreman, described from the same locality and here reproduced (Pl. 60, fig. 3, text-fig. 11*h*). But there is no further relationship between the two species, neither in sculpture, suture-line, nor in shape or septal surface of the spiral whorls.
3. We think that the arguments of lateral lappets, similar size and same occurrence are not important enough to retain the presumed relationship between *Worthoceras* and *Otoscapites*. This is indeed not surprising because:
4. *Worthoceras* absolutely differs in suture-line (text-fig. 11), sculpture and general appearance from all further scaphitids, and will be included here (p. 439) in Ptychoceratinae. *Otoscapites*, however, is a true *Scaphites* in all characteristic features. It is already represented in the Cenomanian and can thus be directly related to the fundamental genus *Eoscapites*.

In this way all problems concerning the subfamily 'Otoscapitinae' appear to be resolved. The results of a detailed study of *Worthoceras* may be anticipated here: As proven by its suture-line, lateral lobe, sculpture, and initial coil, *Worthoceras* is one of the common scaphitoid homoeomorphs, and should be completely separated from the family Scaphitidae. Therefore it is not treated here together with the early scaphitids, but with the convergent lineages (p. 439).

*Otoscapites*, however, cannot be separated from the *equalis* main stock. It agrees completely with true *Scaphites* in its suture-line (text-fig. 6*b*), septal surface (text-figs. 7*a*, *b*), and especially in its ontogenetic suture development (text-figs. 7, 8 to 15). The umbilical lobe becomes subdivided very early through the umbilical seam, where it remains throughout. *L* has a distinctly bipartite outline, and the median incision of *L/U* increases rapidly in size, and might be regarded as an independent element *p*. As pointed out above, its sculpture reflects that of the inner whorls of contemporaneous normalized species.

Thus we become confronted anew with the problem of parallel development in scaphitids. This question was largely treated above (p. 420), where the reason for the reduced

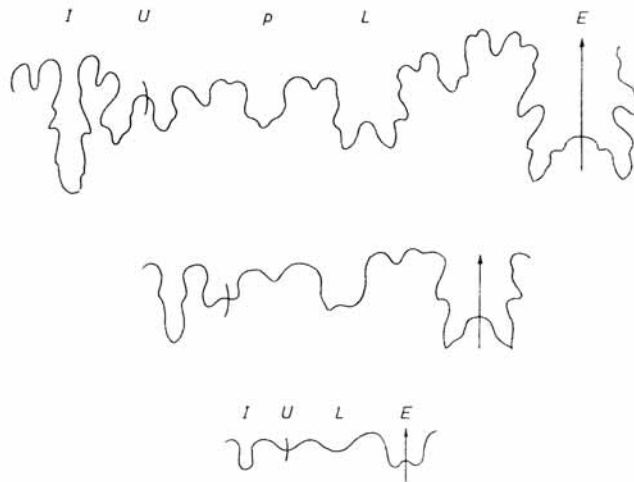
size of the *similaris* stock was found in geographic, probably ecologic factors. The European otoscapitids, however, are as well as the American pteroscaphitids of the same geographic and stratigraphic distribution as the normal-sized equivalents of the *equalis*



TEXT-FIG. 7. Suture development of *Sc. (Otoscapites) bladenensis* Schlüter, GPIT Ce 1221/14; Upper (?) Turonian, Postelberg. *a*, Septal surface at  $h = 2.5$  mm, *b*, at  $h = 5$  mm. *c-g*, Suture development, *g* at  $h = 5$  mm.

stock. These reasons, the small size and the presence of mouth lappets in both lineages seem to be important arguments for the interpretation as sexual dimorphs. But besides these speculations we have more motives for the inclusion of the 'Otoscapitinae' in the genus *Scaphites*. In Wright *Otoscapites* represents a peculiar scaphitoid lineage, restricted to the Turonian and Coniacian. In reality, otoscapitids are traceable—like *Scaphites*—through the complete Upper Cretaceous. We note the presence of some micromorph species (*Sc. peroni* and *africanus* Pervinquière) in the Cenomanian of

Northern Africa (Pervinquière 1907, 1910; Sornay 1955), which are identical with otoscapitid inner whorls. Especially in *Sc. peroni* is the congruence so striking, that the Algerian species may merely represent a variety of *Sc. bladenensis*. The lateral ridges on the inner whorls are the same (Pervinquière 1910, pl. 2, fig. 10), as also the sculpture of the ultimate septate whorl (ibid., fig. 12). Even if we ignore the possibility of sexual dimorphism, all these species and probably also *Sc. evolutus* Pervinquière, can be traced back to *Eoscapites*, which is represented through the small-sized *E.? tenuicostatus* in the Cenomanian of Algeria. We believe that this derivation of *Otoscapites* is



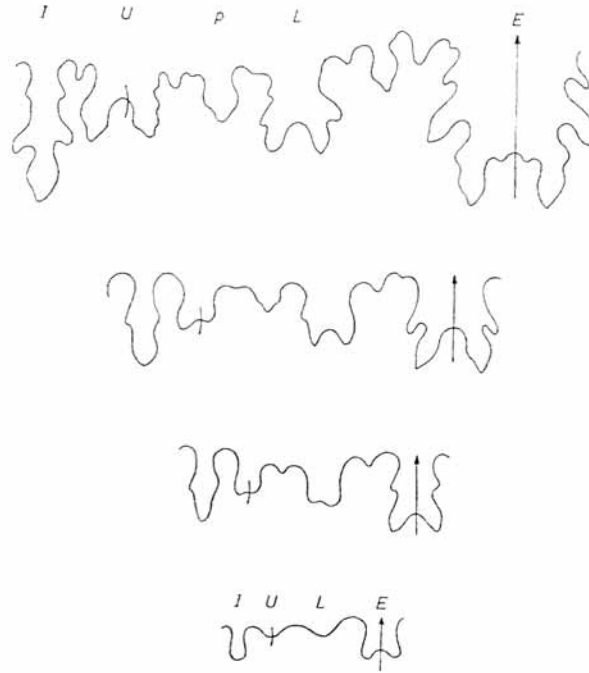
TEXT-FIG. 8. Suture development of *Sc. (Otoscapites) bladenensis* Schlüter, GPIT Ce 1221/16; Upper Turonian, Shasta County. Last suture at  $h = 3$  mm.

by all means more natural, than that from some *Worthoceras* in the Texan Turonian. Moreover, *Otoscapites* can now be recorded from the European Campanian. *Sc. pachydiscoides* Wiedmann, previously doubtfully referred to *Pteroscapites* (Wiedmann 1962a, p. 217), can now be included in *Otoscapites* as here redefined. This species was found to be a true *Scaphites*, and therefore not included into the separate subfamily 'Otoscapitinae' in spite of its *bladenensis*-like sculpture. The recent position of *Otoscapites* is in complete accordance also with these previous observations.

Naturally we are unable at the moment to decide whether the otoscapitids are sexual micromorphs or not. It is likewise impossible to find out whether they represent merely a number of lateral offshoots from the main stock, or a completely different micromorph lineage. Regarding these facts and the clear relations to the true *Scaphites* in suture and sculpture, we propose to consider *Otoscapites* as merely a subgenus of the latter.

With *Scaphites puerculus* Jimbo (= *Sc. inermis* Anderson) we provisionally include in the present subgenus a peculiar form from the Japanese and Californian Upper

Turonian. It seems necessary to confine this species (*puerculus*) to the specimens figured by Jimbo (1894, pl. 5, fig. 4) and Anderson (1902, pl. 3, figs. 74-77). Yabe's presumed hypotypes (1910, pl. 15, figs. 20-22), however, belong to a different species, *Sc. (Otoscaphtes) yabei* sp. nov. (holotype: *Yezoites puerculus* in Yabe 1910, pl. 15, fig. 20), characterized by distinct concave ribs, ventrolateral tubercles, a high number of fine



TEXT-FIG. 9. Suture development of *Sc. (Otoscaphtes?) puerculus* Jimbo, GPIT Ce 1221/18; Upper Turonian, Shasta County. Last suture at  $h = 2$  mm.

and dense secondary ribs on the venter, and a scaphitid living-chamber. In the true *Sc. puerculus* the ornamentation is very weak, nearly absent on the septate portion (Pl. 59, fig. 2). The sculpture of the living-chamber (Pl. 59, fig. 1) consists of weak primary ribs, which give rise to a high number of fine, sinuate secondary ones, at the centre of the lateral sides. The main characteristic of *Sc. puerculus* is the unusual living-chamber, which is only slightly uncoiled in the holotype. The adult form represented here for which I am also indebted to Professor Popenoe, can be regarded as an extreme variety with completely closed chamber of ammonitid coiling. Nevertheless, *Sc. puerculus* may belong to *Otoscaphtes sensu lato*, with which it agrees completely in suture-line and suture development (text-fig. 9).

*Sc. perrini* Anderson belongs to another group of small-sized scaphitids of the Pacific

area, which was referred to *Otoscaphtes* by Wright (1953, p. 476) and Matsumoto (1963). I will demonstrate that these forms, for which *Hyposcaphtes* nov. subgen. will be proposed, have nothing in common with *Otoscaphtes*, but are obviously related to *Pteroscaphites*.

The dimensions (in millimetres) of the otoscaphtid specimens reproduced here are:

	<i>Sc. (Otoscaphtes) bladenensis</i>					
	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/14	—	—	11.3	5 (0.44)	5 (0.44)	3.3 (0.29)
GPIT Ce 1221/16	—	—	7.5	3 (0.40)	3.2 (0.43)	3.2 (0.43)
	<i>Sc. (Otoscaphtes?) puerculus</i>					
GPIT Ce 1221/17	13.5	4.5	7.5	2.7 (0.36)	2.9 (0.39)	?
GPIT Ce 1221/18	—	—	7	2.8 (0.40)	2.8 (0.40)	2.5 (0.36)

Subgenus SCAPHITES (PTEROSCAPHTES) C. W. Wright 1953

*Type species. Scaphites auriculatus* Cobban.

The new genus *Pteroscaphites* was proposed by Wright for the group of micromorph species (*Sc. praecoquus*, *veterinovus*, *pisinnus*, *auriculatus* and *coloradoensis* Cobban) which parallel the true scaphitid stock in the Western Interior of the United States. The here reproduced holotype of Moreman's *Sc. minutus* (Pl. 58, fig. 5, text-fig. 6b) I regard as representative of this subgenus. It was regarded by Wright as a link between *Worthoceras* and *Otoscaphtes*, but it seems very near to the contemporaneous *Sc. veterinovus* and *Sc. auriculatus*, type species of *Pteroscaphites*.

The inner whorls are closely coiled, inflated to coronate, and generally provided with a weak lateral keel. This becomes lost with the beginning of the chamber. The latter coincides completely with the final hook which is distinctly separated from the coiled portion. Lateral and ventral lappets may be present on the mouth-border. The sculpture is similar to that of *Otoscaphtes*, consisting at first of lateral tubercles, and of an *equalis* like ribbing thereafter, which also approaches this lineage to the *equalis* main stock. The sculpture is generally reduced on the chamber (Pl. 58, fig. 5c). The suture (text-fig. 6b) is extremely similar to that of *Otoscaphtes*, likewise characterized by the fixation of *U* on the umbilical seam, and by a pronounced incision *p* in *L/U*. These elements and the lengthened saddle *L/U* make evident that there is no real relation to the worthoceratids, even to *W. gibbosum* (Pl. 60, fig. 3, text-fig. 11h). Shape and ornamentation of the spiral portion also differs considerably from that of *Worthoceras*, where the smoothness of the shells is an original feature, while it is a gerontic one in *Pteroscaphites*.

Despite the intimate relationship between *Ptero-* and *Otoscaphtes*, they are regarded here as different subgenera. In this way we receive a better idea of the surprising fact of parallel development in scaphitids, realized in completely the same manner in Europe and Northern America. This makes the interpretation as sexual dimorphism highly possible.

*Sc. (Pteroscaphites)* seems to be restricted to the Upper Turonian and Coniacian of Northern America. The specimen described recently by the present author as *Sc. (Pteroscaphites?) pachydiscoides* from the Spanish Campanian may be better referred to *Otoscaphtes*, as mentioned above.

## Subgenus SCAPHITES (HYOSCAPHITES) subgen. nov.

*Type species.* *Scaphites stephanoceroides* Yabe 1909.

*Description.* Small-sized *Scaphites* with coronate whorl section. Lateral sides tubercled and keeled throughout. Homoeomorphous with *Astiericeras*. *U* subdivided, but fixed on umbilical seam. The genus includes *Sc. (H.) stephanoceroides* Yabe and *Sc. (H.) perrini* Anderson.

*Remarks.* *Sc. stephanoceroides* Yabe and *Sc. perrini* Anderson were included in 'Yezoites' by Yabe, but in reality they can directly be connected to the early pteroscaphitid *Sc. praecoquus* Cobban. In the latter species all characters of *Hyoscaphites* are foreshadowed: the spiral portion and the final hook are distinctly laterally keeled, while only on the straight shaft is the rounded whorl-section of all other scaphitids preserved. Therefore *Sc. praecoquus* remains in *Pteroscaphites* for the moment, but a definite decision is impossible. Both subgenera agree completely in their early ontogeny. The shape of the spiral portion, its involution and coronate whorl-section are the same in *Ptero-*, as in *Hyoscaphites*. But while in the latter this coronate section persists also on the body-chamber where the ribbing becomes more pronounced, in *Pteroscaphites* the chamber has a rounded whorl-section and decreasing sculpture. Thus *Hyoscaphites* becomes completely homoeomorphous with the Albian *Astiericeras* Parona and Bonarelli belonging to the douvilleiceratids.

The attribution of *Sc. perrini* to *Otoscaphtes* is artificial, based on the presence of lateral mouth lappets, which are also present, however, in *Pteroscaphites* and *Hyoscaphites*. Because the proposed type species, *Sc. stephanoceroides* Yabe, never was described, a brief diagnosis will follow. *Hyoscaphites* seems to be restricted to the Upper Turonian and ? Coniacian of the Pacific border.

*Sc. (Hyoscaphites) stephanoceroides* Yabe

Plate 59, fig. 3; text-fig. 6a

1894 *Olcostephanus* sp., Jimbo, p. 33, pl. 9, fig. 3.

1909 *Scaphites stephanoceroides* Yabe, pp. 442, 443.

## EXPLANATION OF PLATE 58

- Fig. 1. *Scaphites (Metascaphites) thomasi* Pervinquieré. Holotype (ex Pervinquieré 1907, pl. 4, fig. 31); Vraconian, Djebel Mrhila (Tunisia). *a*, Lateral, *b*, ventral view;  $\times 2$ .
- Figs. 2-4, 6. *Sc. (Otoscaphtes) bladenensis* (Schlüter). 2, Hypotype GPIT Ce 1221/14, intermediate to *Sc. (O.) cottae* (F. A. Roemer); Upper (?) Turonian, Postelberg near Priesen (Bohemia). *a*, Ventral, *b*, frontal, *c*, lateral view of phragmocone;  $\times 3$ , *d*, frontal, *e*, lateral view of pachydiscoid inner whorl;  $\times 8$ . 3, Typical hypotype, GPIT Ce 1221/15 (leg. Popenoe and Matsumoto), with straight body-chamber fragment, showing the sculptural change; Upper Turonian (Romaniceratan). Little Cow Creek valley (loc. 1512), Shasta County (California, U.S.A.). *a*, Lateral, *b*, ventral view;  $\times 4$ . 4, Characteristic inner whorl, in complete agreement with the holotype; GPIT Ce 1221/16 (leg. Popenoe and Matsumoto); same age and locality. *a*, Lateral, *b*, ventral, *c*, sagittal view;  $\times 4$ . 6, The small holotype (ex Schlüter 1872, pl. 10, figs. 5, 6); Upper (?) Turonian, Rote Mühle near Bladen/Leobschütz (Silesia). *a*, Frontal, *b*, lateral view;  $\times 1$ .
- Fig. 5. *Sc. (Pteroscaphites) minutus* Moreman. Holotype (cf. Moreman 1942, pl. 34, figs. 9, 10), BEGA coll. no. 19814; Lower Turonian (Eagle Ford group), 2.7 miles S. Britton, E. Midlothian highway, Ellis County (Texas, U.S.A.) *a*, Ventral, *b*, frontal, *c*, lateral view;  $\times 3$ ; *d*, frontal, *e*, lateral view of phragmocone;  $\times 5$ .



1910 *Yezoites perrini* Anderson; Yabe, p. 172, text-fig. 3, pl. 15, figs. 28, 29.

1963 *Otoscaphtes perrini* (Anderson) (?); Matsumoto, p. 46, pl. 68, fig. 3.

*Holotype.* The specimen figured originally as '*Olcostephanus sp.*' in Jimbo 1894, pl. 9, fig. 3, and reproduced by Yabe (1910, pl. 15, fig. 29) and here Plate 59, fig. 3, text-fig. 6a. Probably lower part of Upper Yezo group (= Upper Turonian) from Pombets valley, Ishikari province, Hokkaido.

*Description.* Small *Scaphites* with coronate whorl-section throughout. Distinct lateral keel persisting and tuberculate. These lateral tubercles give rise to two or three strong ribs which pass radially venter. Mouth-border with elongated lateral lappets, covering a great part of involute initial spire.

*Remarks.* *Sc. stephanoceroides* was proposed for '*Olcostephanus sp.*' in Jimbo by Yabe (1909) in a footnote generally overlooked. One year later the name was abandoned by Yabe (1910, p. 172) himself, who included the Japanese material, in spite of obvious differences, in '*Yezoites perrini* Anderson. The Hokkaido specimens were referred to the same species also in the subsequent literature, but in the reproduction of Jimbo's plates by Matsumoto (1963, p. 46) with a query. This was indeed reasonable, and we propose to separate the Japanese forms, and to renew Yabe's species name. While in *Sc. perrini* the whorl section is much more rounded and the venter remains nearly smooth, in the Japanese forms the whorl section is more compressed, the lateral angle sharpened, and the venter passed by strong bi- or triplicate ribs (Pl. 59, fig. 3a). I figure for comparison a body-chamber fragment of *Astiericeras astierianum* (Pl. 59, fig. 4), which demonstrates the nearly complete homoeomorphy between these two species. By means of the suture-lines the species are well distinguishable (text-fig. 6a, 13).

Once more the striking sutural congruence of all scaphitid micromorphs is noticeable (text-figs. 6-9). The similarity of the suture-line of *Oto-*, *Meta-*, *Ptero-*, and especially of *Hyposcaphtes* consists in the position of *U* on the umbilical seam, which evidently can be regarded as a common feature of the dwarfed scaphitid lineages. They are extremely near one to the other as well as to *Scaphites*, and are included therefore as subgenera into the comprehensive genus *Scaphites*. *Sc. stephanoceroides* is known only from the Upper Turonian of Hokkaido, but it may pass also into the Coniacian (Yabe 1910).

#### THE SCAPHITID HOMOEOMORPHS AND THE SCAPHITID ORIGIN

Before the principles of scaphitid development and the new systematics of this group can be treated, the different homoeomorphs and the problem of scaphitid origin need to be discussed briefly.

*Macroscaphites.* That there is no real relationship between *Scaphites* and *Macroscaphites* of Barremian/Aptian age, as was believed by the early authors, has been known for a long time. It is interesting that *Macroscaphites* (text-fig. 13) in respect of suture-line and initial coil is indistinguishable from the true lytoceratid genus *Costidiscus*. Therefore it remained connected with the latter within Lytocerataceae, despite its uncoiled living-chamber. That this co-ordination is indeed reasonable becomes clear, if we compare the suture-line with that of lytoceratids and heteromorphs respectively. While in all lytoceratid heteromorphs the second umbilical lobe (*U*<sub>2</sub>) is reduced, it is generally retained

in the true *Lytoceras*. In *Costidiscus* and *Macroscaphites* two umbilical lobes are preserved, and, moreover, the suture remains highly incised. In *Scaphites*, however, the suture is quadrilobate throughout and simplified as in all other heteromorphs. This is the strongest argument against the occasionally presumed relationship between the two genera separated by an evident time gap. In regard to the scaphitid micromorphs it seems noticeable, that Uhlig (1883, p. 206) was also able to recognize a greater and smaller variety in the scaphitoid homoeomorph *Macroscaphites yvanii*. The smaller specimens with somewhat stouter final hook, were always found together with the greater-sized forms in the ratio 1:1. This fact was interpreted by Uhlig as sexual dimorphism.

*Other lytoceratids.* With exactly the same argumentation, the presence of more than one umbilical lobe, the general supposition of a scaphitid origin in any other true lytoceratid may be rejected (Spath 1934, Wright 1957), where not only in *Costidiscus* but also in *Gabbioceras* and *Jauberticeras* (text-fig. 13) convergent shell-types are developed. The resemblance between some of those species and the initial coil of *E. subcircularis* is striking. But in *Gabbioceras* two umbilical lobes are developed, in *Jauberticeras* even three, of which two are highly differentiated through their position on the umbilical seam, respectively the lateral keel. Thus we note in jauberticeratids a progressive tendency of suture development, and no suture reduction which is necessary for the derivation of *Scaphites*.

*Astiericeras.* '*Scaphites*' *astierianus* d'Orbigny of Middle Albian age has the greatest affinity to some early scaphitids, especially to *Sc. (H.) stephanocerooides*. This becomes evident through the living-chamber fragment from Quenstedt's collection, here reproduced (Pl. 59, fig. 4). This fragment is somewhat intermediate between the typical specimen with biplicate ribs (Parona and Bonarelli 1897, pl. 14, fig. 10), and the form with strong single ribs as represented by Quenstedt (1847/8, pl. 21, figs. 14a, b). Here the suture-line is also the decisive element. As visible in text-fig. 13, the complete suture-

## EXPLANATION OF PLATE 59

- Figs. 1, 2. *Scaphites (Otoscapites?) puerulus* Jimbo. 1, Hypotype GPIT Ce 1221/17 (leg. Popenoe and Matsumoto), with normal coiled body-chamber; Upper Turonian (Romaniceratan), Little Cow Creek valley (loc. 1512), Shasta County (California, U.S.A.). a, Lateral, b, ventral view;  $\times 3$ . 2, Septate hypotype, GPIT Ce 1221/18 (leg. Popenoe and Matsumoto); same age and locality. a, Lateral, b, ventral, c, frontal view;  $\times 5$ .
- Fig. 3. *Sc. (Hyposcapites) stephanocerooides* Yabe. Holotype (ex Jimbo 1894, pl. 8, fig. 3, sub *Olcostephanus* sp.); (Coll. Geol. Inst. Univ. Tokyo); Upper Turonian?, Pombets valley (Ishikari province, Hokkaido). a, Ventral, b, lateral view.  $\times 1$ .
- Fig. 4. *Astiericeras astierianum* (d'Orbigny). Quenstedt's suture specimen, GPIT Ce 3/21/14d; Lower Middle Albian, Escagnolles (Var, France). a, Ventral, b, lateral view;  $\times 1$ .
- Fig. 5. *Worthoceras platydorsum* (Scott). Holotype (ex Scott 1924, pl. 5, fig. 4; Adkins 1928) (Mus. Tex. Christ Univ.); Upper Albian, Upper Duck Creek, N. Denison, Grayson County (Texas, U.S.A.). Lateral view,  $\times 10$ .
- Figs. 6, 7. *Worthoceras worthense* (Adkins). 6, The fragmentary holotype, partly septate (cf. Adkins 1920, pl. 2, fig. 26, sub *Hamulina*), Bega 20994; Upper Albian (Pawpaw form.), Forth Worth, Tarrant County (Texas, U.S.A.). Lateral view,  $\times 5$ . 7, Hypotype BEGA 20995, shaft without dorsal impression and partly septate; same locality. a, Dorsal, b, ventral, c, lateral view;  $\times 4-5$ .
- Fig. 8. *Worthoceras vermiculum* (Shumard). Hypotype with nearly unlapped mouth-border, BEGA 35392; Lower Turonian (Eagle Ford group), Ellen Fork, Trinity River at St. Louis/Sta Fé-Railroad bridge, Dallas County (Texas, U.S.A.). Lateral view,  $\times 2$ .

line of *Astiericeras astierianum* (GPIT Ce 3/21/14d) contains two distinct umbilical lobes, while *L* becomes subdivided into two different 'lobes', as it is characteristic for all douvilleiceratids. Thus no comparison with the hyposcapitid suture is possible. *Astiericeras* indeed represents no more than a striking homoeomorph with some specialized scaphitids. It is regarded as a direct descendant of the ammonitid genus *Douvilleiceratid*.

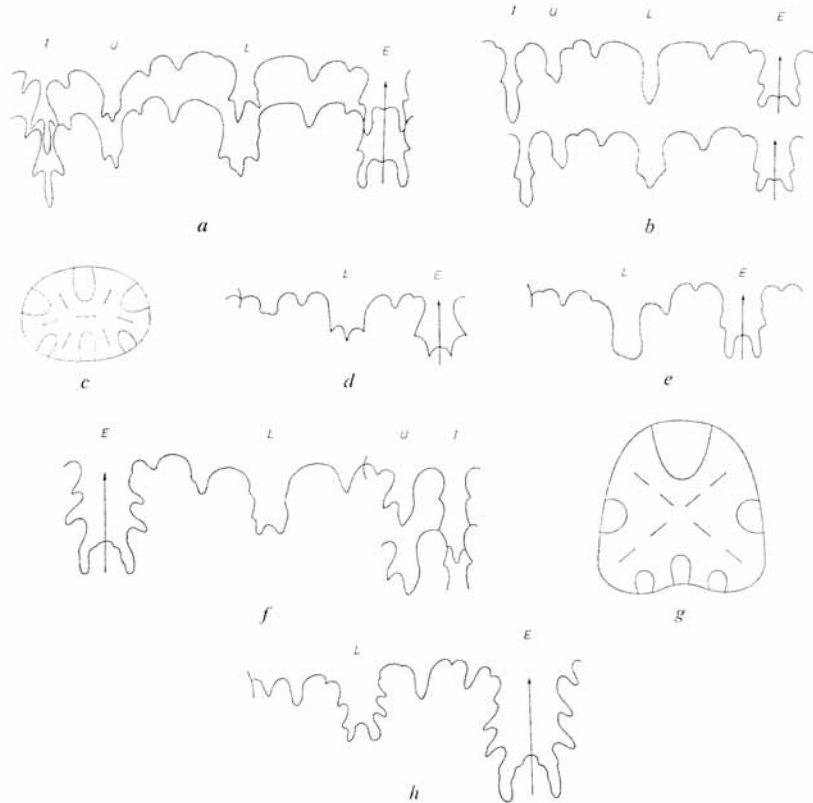
*Worthoceras*. Its systematic position and relationship to *Scaphites* is at the moment the most difficult problem, because *Worthoceras* was included in Scaphitidae and regarded as a direct ancestor of *Otoscapites* by Wright. It is evidently a New World form and has only occasionally been recognized in Europe, Northern Africa (?), and Madagascar. The different species which were separated in the Upper Albian, Cenomanian, and Turonian are merely distinguishable by their general appearance. They are of small size, nearly unsculptured, and with one exception provided with a completely open whorled initial coil. This is followed by a long straight shaft with flat, subparallel flanks and a distinctly impressed dorsum, which terminates in a final hook with occasionally lapped mouth-border.

The main distinguishing feature in *Worthoceras* is again the suture-line (text-figs. 10a, b, d-f, h), consisting of four narrow lobes, among them a distinctly trifold *L* and an undivided small *U*, despite the presence of a distinct dorsal impression. Also the septal surface (text-figs. 10c, g) preserves the simple, hamitid type. But there are more arguments against Wright's connexion of *Worthoceras* and *Eoscapites*.

The first representatives of the genus are *W. platydorsum* (Scott) (here Pl. 59, fig. 5) and *W. worthense* (Adkins), of which the holotype (Pl. 59, fig. 6, text-fig. 10a) and a further specimen are reproduced here (Pl. 59, fig. 7, text-figs. 10b, c). It may be mentioned that the last mentioned species was at first included by its author (Adkins 1920) in *Hamulina*. Later it was separated by the same author (Adkins 1928) in a new genus, *Worthoceras*, of 'uncertain position'. Both species are restricted to the Upper Albian of Texas, where *Eoscapites* is unknown up to the present. The distinct trifold outline of *L*, the undivided element *U*, the general character of the quadrilobate suture-line (text-fig. 10), and the originally flat and not impressed dorsum (Pl. 59, fig. 7a), make a heteromorph ancestor of *Worthoceras* evident. The ptychoceratids especially have nearly a world-wide distribution in the Albian, where they are represented by unsculptured dwarfed forms with trifold lateral lobes. Of further importance for this presumed attribution and the separation from *Eoscapites* is the fact that the phragmocone in early *Worthoceras* does not coincide with the spiral portion, as it does in *Eoscapites*. Generally almost all of the straight shaft is septate, as visible in the reproduced type material (Pl. 59, figs. 5-7). Moreover, no umbilical perforation is known from *Worthoceras*.

In Europe, the centre of the scaphitid development, only one worthoceratid species is known: *W. rochatianum* (d'Orbigny) of Cenomanian and Turonian age (Pl. 60, figs. 4-6). This species is barely distinguishable from the Albian *W. platydorsum* (Pl. 59, fig. 5). Even in regard to the sculpture, when it is preserved (Pl. 60, figs. 5b, 6a), it agrees with the forms of the Texan Albian. The suture-lines were found to be in accordance also; likewise in *W. rochatianum* (text-fig. 10d) they contain a distinctly trifold *L* and slightly enlarged saddles. The shaft is likewise septate (Pl. 60, fig. 4b). The only noticeable distinction is the dorsal impression (Pl. 60, fig. 4a), which is much more pronounced

than in the preceding species. It can perhaps be regarded as a reminiscence of the ptychoceratid ancestor, where the smaller shaft generally remains strongly impressed in the dorsum of the larger one.



TEXT-FIG. 10. *Worthoceras*. *a-c*, *W. worthense* (Adkins). *a*, The last suture-lines of the holotype, BEGA 20994; Upper Albian, Fort Worth. *h* = 3 mm. *b*, Last suture-lines, and *c*, Septal surface of hypotype, BEGA 20995; same locality. *h* = 2 mm. *d*, *W. rochatianum* (d'Orbigny), external suture of Madagascan hypotype (ex Collignon 1929, text-fig. 36); Cenomanian, Diégo-Suarez.  $\times 8$ . *e-g*, *W. vermiculum* (Shumard). *e*, Last suture of neotype (Moreman 1942), BEGA 19827; Lower Turonian, Britton. *h* = 3 mm. *f*, Last suture, and *g*, Septal surface of hypotypoid BEGA 35390; Lower Turonian, Dallas County. *h* = 3 mm. *h*, *W. gibbosum* Moreman, holotype, BEGA 19812; Lower Turonian, Britton; external suture at *h* = 4.5 mm.

Likewise the following species, the Lower Turonian *W. vermiculum* (Shumard) (here Pl. 59, fig. 8; Pl. 60, figs. 1, 2), is barely distinguishable from the forms described above. The spiral portion remains open whorled, the suture-line (text-figs. 10*e*, *f*) quadrilobate, the shell smooth and the final hook flat-sided and tender. In the septal

surface (text-fig. 10g) the simple configuration of the ptychoceratids is preserved. The differences concern the somewhat stouter final crozier, the shaft which is septate only in its lower part, the nearly bifid *L*, and especially the lateral mouth lappets perceptible only in this species.

The attribution of *W. gibbosum* Moreman of the Texan Lower Turonian to the present genus seems more difficult. The holotype, here reproduced (Plate 60, fig. 3, text-fig. 10h), has the general appearance of a true *Scaphites*, with a stout and inflated final hook which nearly touches the moderately involute spiral portion. The latter coincides with the septate whorls. Finally the suture, with its distinct bifid *L*, seems to belong to a true *Scaphites*. Therefore *W. gibbosum* was interpreted as a transitional form between *Worthoceras* and *Scaphites minutus* Moreman.

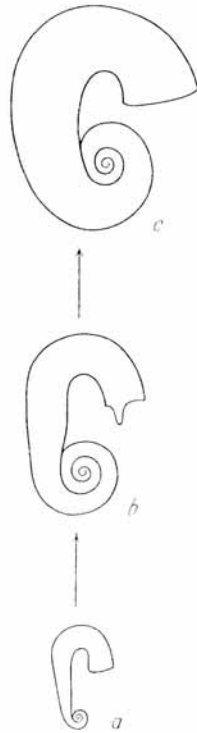
As indicated above, the latter species is a true *Scaphites* indeed, belonging to a group of dwarfed (and lappeted) forms which are separated from the *equalis* main stock as a distinct subgenus *Pteroscaphites*. After study of *W. gibbosum* we come to the following conclusion, that this species in all its characters belongs to *Worthoceras* and cannot be connected with *Sc. minutus* nor with any other known *Scaphites*. If we compare the suture-line (text-fig. 11h), the septal surface (Pl. 60, fig. 3a) and the ornamentation of the spiral coil (Pl. 60, fig. 3b) with that of its presumed descendant *Sc. minutus* (Pl. 58, figs. 5d, e; text-fig. 6b) or with the otoscapitid type species (Pl. 58, figs. 2-4; text-figs. 7, 8), then the fundamental differences become obvious. Unfortunately the internal suture-line is not exposed in the Texan forms, but it is possible to interpret it from the external portion and septal surface. As mentioned many times, all scaphitid micro-morphs are characterized through the position of the subdivided *U* on the umbilical seam and the importance of the median incision *p*. In *W. gibbosum* we find nothing comparable. Alone a small undivided *U* can be recognized, which remains in the internal suture, and the median incision of *L/U* does not increase in size. The initial coil of *Sc. minutus* is nearly closed and passes (as in all other *Ptero-* and *Otoscapitites*) through an inflated pachydiscoid stage. The initial whorls of *W. gibbosum* remain well exposed and completely smooth as in all other *Worthoceras* species. Finally no lateral lappets can be observed on the mouth-border, which, on the other hand, are well developed in *Ptero-* and *Otoscapitites*. It is therefore impossible to connect *Worthoceras* with any scaphitid member despite their striking homoeomorphy.

This is less surprising if we regard the phylogenetic position of *Worthoceras*. Its very slow evolutionary trend, which we intentionally demonstrated here in all details, makes it evident that the genus represents a phylogenetic end form. *Scaphites* is able to compete with the contemporaneous ammonites through genetic regeneration and the development of a high number of lateral offshoots, whereas *Worthoceras* is evidently unable to regenerate and thus does not pass the Turonian/Coniacian boundary. Regarding these reasons it might be better to place *Worthoceras* into Ptychoceratinae, as recently defined by me (Wiedmann 1962b).

The measurements (in millimetres) of some *Worthoceras* here represented are:

	<i>Worthoceras rochatianum</i>					
	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
MHNG Wi 'Sc'/10	20	4	6.8	2.8 (0.41)	2.5 (0.37)	2.6 (0.38)
MHNG Wi 'Sc'/11	—	—	7.0	3.0 (0.43)	2.5 (0.36)	3.0 (0.43)
MHNG Wi 'Sc'/12	—	—	7.0	3.0 (0.43)	2.7 (0.38)	2.8 (0.40)

<i>Worthoceras vermiculum</i>						
	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
BEGA 19827	14	4.4	7.0	3.0 (0.43)	3.0 (0.43)	2.8 (0.40)
BEGA 35390	15	4.0	6.5	2.8 (0.43)	2.7 (0.42)	2.7 (0.42)
BEGA 35392	17.5	5.1	9.5	3.8 (0.40)	?	3.2 (0.34)
<i>Worthoceras gibbosum</i>						
BEGA 19812	17.5	7.8	10	4.5 (0.45)	5.2 (0.52)	3.0 (0.30)



TEXT-FIG. 11. The trend of worthoceratid development.  $\times 2$ . *a*, *W. platydorsum* (Scott), *b*, *W. vermiculum* (Shumard), *c*, *W. gibbosum* Moreman.



TEXT-FIG. 12. The presumed development of the labeceratids.  $\times 0.25$ . *a*, *Labeceratid*, *b*, *Ellipsoceras*, *c*, *Myloceras*.

Finally we note the tendency to re-coil in *Worthoceras* (text-fig. 11), which seems to be a common trend in all Cretaceous heteromorphs (Cobban 1952, text-fig. 2; Casey 1960, text-fig. 5; Wiedmann 1962*b*, text-fig. 35; and here text-figs. 12 and 14).

*Labeceratidae*. The systematic position of the family Labeceratidae, included in Scaphitaceae by Spath, Wright and others, was discussed on a previous occasion (Wiedmann 1962b, p. 98). This restricted group of Upper Albian forms, known only from the Southern hemisphere, was characterized by the following features:

1. Sculpture, especially in the primitive representatives, is hamitid; but it becomes rapidly anisoceratid through the development of umbilical and marginal tubercles.
2. Mode of uncoiling is hamitid/crioceratid at first, the middle-aged whorls are sometimes in contact, followed by a straight septate shaft and a scaphitoid final hook with lappeted mouth-border. These are the unique similarities with *Scaphites*.
3. Suture-line consists of only four elements; *U* remains simple and undivided, and is trifold like *L*; the saddles are normal sized (text-fig. 13).

The lineage *Labeceras-Ellipsoceras-Myloceras* (text-fig. 12) represents, if correct, a further example for the general trend of many heteromorphs to re-acquire the original mode of coiling. This mode of uncoiling, the sculpture and especially the sutural characters are exactly the same as in some early *Anisoceras* like *Metahamites* or *Idiohamites*. *Hamitoides*, included in Labeceratidae by Spath and Wright, and perhaps the origin of the stock, is in all its characters a true *Anisoceras*. Therefore Labeceratidae were reduced to subfamily rank and included in Anisoceratidae by the author (1962b, p. 99). The reference of *Labeceras* to Hamitidae by Whitehouse (1926, p. 226) was found to be more correct than the attribution to the lytoceratid or scaphitid stock by Spath.

*Zuluscaphites*. This genus was established by van Hoepen (1955) on a single ammonitid spiral portion of Middle Albian (?) age. Its lateral lobe is trifold and no scaphitid living-chamber is known. It is impossible to regard a form with these negative characters as the source of the always later appearing *Scaphites*. I believe that *Zuluscaphites* merely represents a lyelliceratid inner whorl (Wiedmann 1962a, p. 209).

*Other ammonitids with uncoiled body-chamber*. True ammonitids with scaphitoid living-chamber are very common. They are represented in the Jurassic, with forms like the stephanoceratid genus *Kheraites* (text-fig. 13) or the oppeliid *Proscaphites*, as well as in the Cretaceous. Here especially in the acanthoceratids *Vascoceras*, *Fallotites* (text-fig. 13), *Pseudotissotia* and *Texasia*, the uncoiling of the body-chamber is a common feature. All these forms are evidently connected with the acanthoceratid stock, and cannot lead to *Scaphites* because of the presence of three or more umbilical lobes. The same difference can be stated for *Binneyites* which has recently been referred to Haplocerataceae by Wright in Casey (1961, p. 118). Already the external suture-line (text-fig. 13) is completely different from the scaphitid one.

No real relationship to *Scaphites* can be recognized in the above-mentioned lytoceratids, heteromorphs, and ammonitids of scaphitoid appearance. In the eoscapitid species the presence of an umbilical perforation and the absence of a dorsal impression was demonstrated. Therefore it seems that we can find the true scaphitid ancestor among the uncoiled heteromorphs. This presumption is supported through the fact, that in all early scaphitids the suture-line consists only of four elements. Not only in *Eoscapites* and early scaphitid ontogeny can the quadrilobate suture-line be stated, but it remains simplified throughout during the ontogeny of all scaphitids studied here. The presumed regeneration of three or four umbilical lobes in *Scaphites* cannot be accepted. *Scaphites*

is in its sutural characters a true heteromorph member. It should no longer be regarded as a degenerate offshoot of normal coiled ammonites; it is a hamitid heteromorph with the repeatedly noted trend to secondary re-coiling.

The similarity is striking if we compare the suture-line of *E. circularis* with that of contemporaneous hamitids, especially the Upper Albian *Plesiohamites* ('*Lytohamites*') *similis* (Casey). This form also agrees in sculpture and mode of uncoiling so completely, that the separation from *Eoscaphtes* seems to me to be more than arbitrary. If the biogenetic rule is of any phylogenetic significance, then the slender initial whorls of *Eoscaphtes* point to an also very slender hamitid species, of upper Middle Albian age, *Hamites tenuis*. This species is stratigraphically directly followed by the first *Eoscaphtes*, at the base of the English Upper Albian.

It might be added here, that the possibility of a hamitid source for *Scaphites* was briefly discussed but also abandoned by Spath (1942, p. 717), and therefore neglected thereafter.

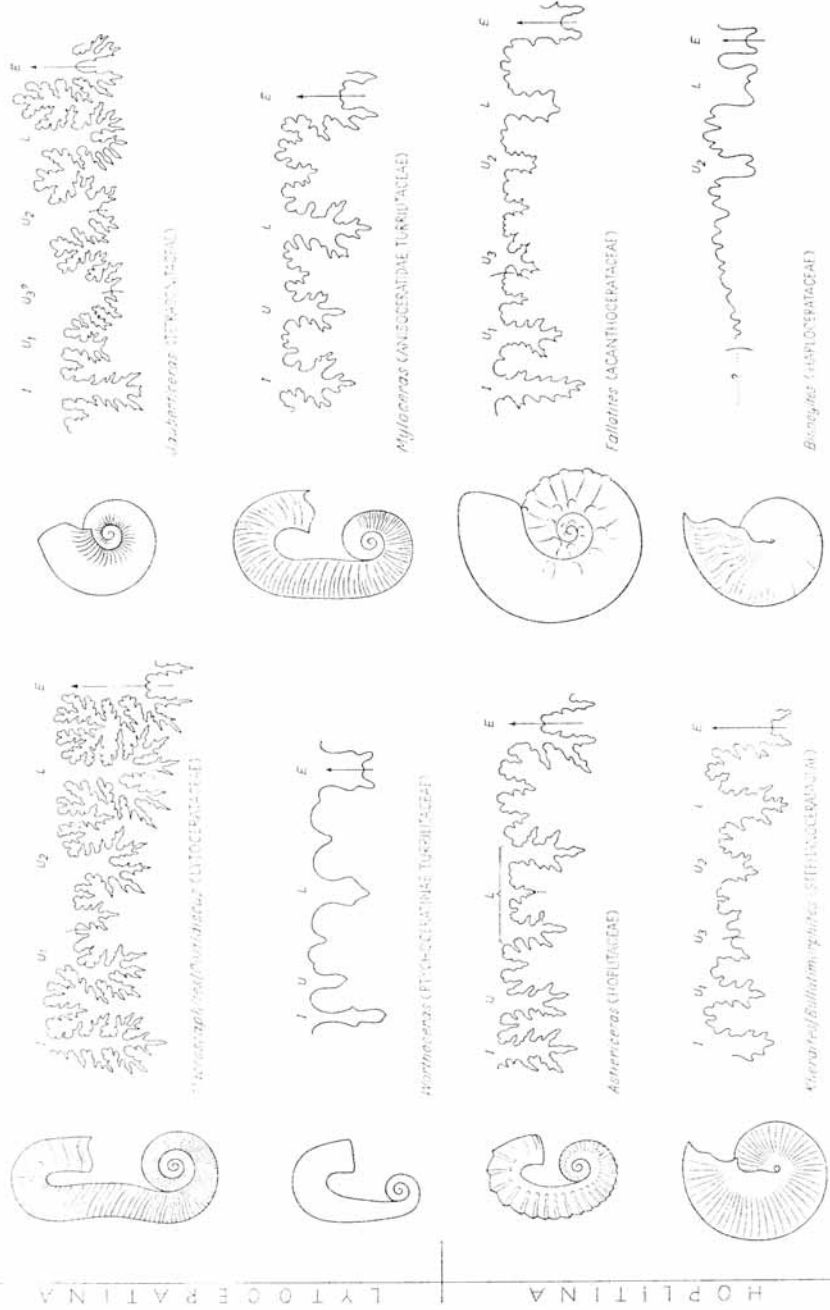
#### THE PRINCIPLES OF SCAPHITID DEVELOPMENT

Having pursued the early scaphitid development step by step from the base of the Upper Albian, we have reached not only an idea of the principles of scaphitid development, but also the solution to some of the problems of interest here. It has been possible to demonstrate that there is no difficulty in connecting the ostensibly different suture types of *Eoscaphtes* and *Scaphites*. Schindewolf doubted that the quadrilobate suture-line which exists throughout in *Eoscaphtes* could be compatible with that of true scaphitid species from the uppermost Senonian. In the early ontogeny five lobes were stated to occur in these forms, and seven in the adult stage (Schindewolf 1961, text-fig. 58). As text-fig. 14 shows, the first eoscaphtid species from the basal Upper Albian and the latest Maastrichtian scaphitids are connected by continuous transitions in the sutures. We therefore have to conclude that also in the late *Scaphites* not more than four lobes (*I*, *U*, *L*, and *E*) are present. The presumably regenerated umbilical lobes are in reality the secondary saddle incisions of *L/U*, and therefore named pseudolobes (*p*). This becomes underlined, when we consider the ontogenetic suture development (text-figs. 7-9, 15). Here the questionable elements always remain outside of the umbilical seam.

#### EXPLANATION OF PLATE 60

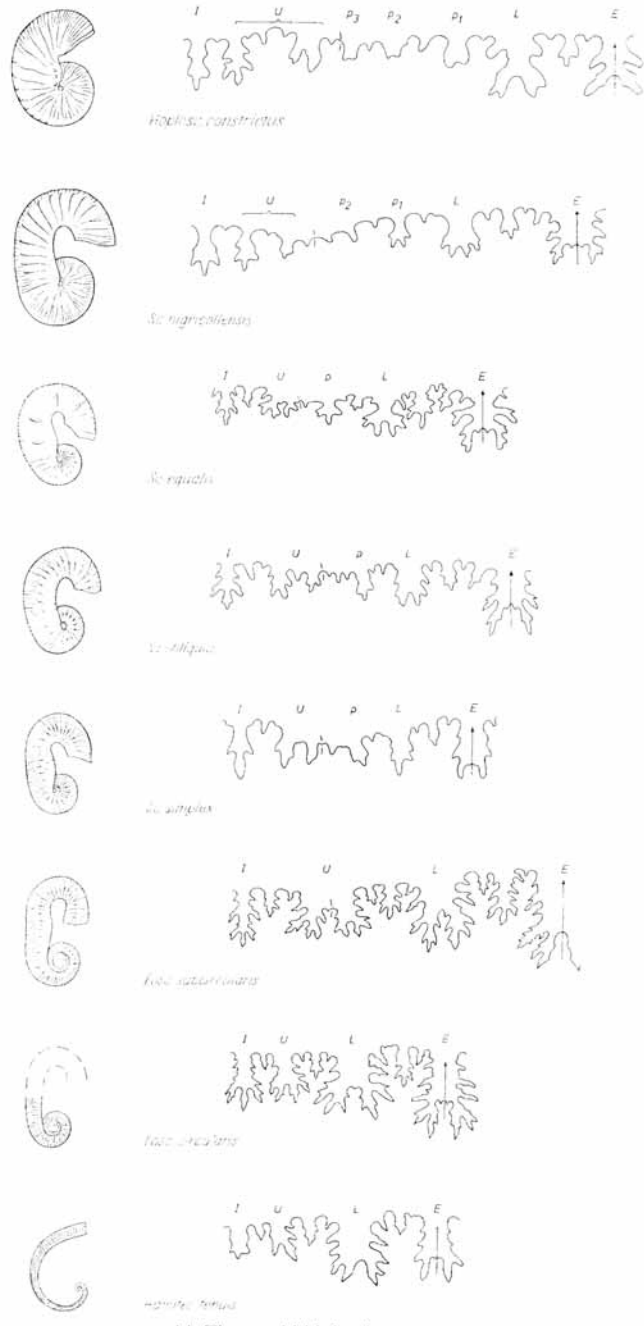
- Figs. 1, 2. *Worthoceras vermiculum* (Shumard). 1, Hypotype BEGA 35390; Lower Turonian (Eagle Ford group), Ellen Fork, Trinity River at St. Louis/Sta Fé-Railroad bridge, Dallas County (Texas, U.S.A.). The mouth-border seems unlappeted; the first half of the shaft is septate. *a*, Lateral, *b*, ventral view. 2, The neotype with preserved mouth-border; proposed by Moreman (1942, pl. 34, figs. 12, 13), BEGA 19827; Lower Turonian (Eagle Ford group), 2.7 miles S. Britton, E. Midlothian highway, Ellis County (Texas, U.S.A.). *a*, Frontal, *b*, ventral, *c*, lateral view.
- Fig. 3. *Worthoceras gibbosum* Moreman. Holotype BEGA 19812 (cf. Moreman 1942, pl. 34, figs. 7, 8); same age and locality. *a*, Frontal, *b*, lateral view of smooth phragmocone:  $\times 4$ ; *c*, ventral, *d*, lateral, *e*, frontal view:  $\times 2$ .
- Figs. 4-6. *Worthoceras rochatianum* (d'Orbigny). 4, Hypotype MHNG Wi 'Sc'/10, nearly complete, shaft is partly septate; Upper (?) Turonian, Uchaux (France). *a*, Frontal view with distinct dorsal impression, *b*, lateral view (leg. Rochat). 5, Hypotype with weak ribs, MHNG Wi 'Sc'/12 (leg. Rochat); same locality, *a*, Frontal, *b*, lateral view. 6, Hypotype MHNG Wi 'Sc'/11, with part of straight shaft; (leg. Rochat); same locality. *a*, Frontal, *b*, lateral view.
- All  $\times 3$  unless otherwise stated.





TEXT-FIG. 13. The scaphitoid homomorphs.

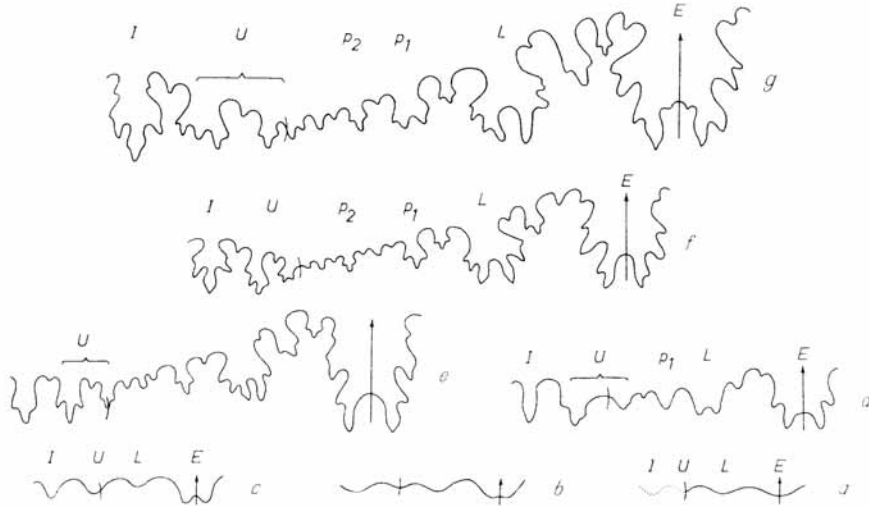
UPPER ALBINE TURONIAN-MAASTRICHTIAN



TEXT-FIG. 14. The scaphitid development.

where true umbilical lobes are generally produced. The suture development of the Campanian *Sc. hippocrepis* (Dekay) as given by Reeside (1927b), can now be shown precisely in the manner illustrated here (text-fig. 15).

Here the extreme lengthening of the external saddles, and the gradual increase of saddle incisions to lobe size, are the most obvious characters of the scaphitid suture development. Another important systematic feature is the element *U*, which becomes



TEXT-FIG. 15. The suture development of a late scaphitid species, *Sc. (Sc.) hippocrepis* (Dekay) (after Reeside 1927b, pl. 15); Campanian, Big Horn County.

divided by the umbilical seam at first (text-fig. 15d). Thereafter the two different branches become more and more separated, and pass to the internal suture-line (text-figs. 15e, f). *U* remained fixed on the umbilical seam only in the micromorphs, as in some primitive Albian forms. In the adult stage of the Upper Cretaceous forms (text-fig. 15g) a greater number of umbilical lobes are feigned. Naturally we come to wrong conclusions, if we pay exclusive attention to them. However, if we trace the suture development ontogenetically (text-fig. 15) and phylogenetically (text-fig. 14), we can easily recognize that the so-called umbilical lobes are merely the incisions ( $p_1, p_2 \dots$ ) of the lengthened saddle *L*. *U*. Also the species with a 'trifid' lateral lobe should not be regarded exclusively. We have seen that there are indeed forms (*Sc. simplex* and the members of the *meriani* group) in the immediate neighbourhood of the type species, in which a 'trifid' *L* becomes developed. If we consider, however, the phylogenetic and ontogenetic evolution of this element, then we prefer to use the term 'asymmetric'. This asymmetry evidently depends on the retraction of the umbilical suture-line of some Upper Albian species, especially *Sc. simplex*. In the subsequent species, *Sc. obliquus* and *equalis*, the suture-line is less retracted, and the original bifidity rapidly becomes re-established. In *Sc. equalis* the lobe development of its ancestors becomes recapitulated. Bifid at first, the

lateral lobe becomes asymmetrical in early ontogeny and regains the primary bifid outline thereafter. Only this ultimate change was observed by Pervinquier (1907) and since then regarded as evidence for an ammonitid origin of all scaphitids. Likewise in some Senonian species a 'trifid' *L* was cited, but Cobban (1952) demonstrated that also in these forms an originally bifid lobe gradually becomes asymmetrical. On the contrary, the trifidity of the so-called 'second lateral' or ' $U_2$ ' is the original outline of the misinterpreted median incision of the saddle *L/U*.

Corresponding to the suture development, the septal surface is always hamitid in early *Eoscaphtes* (text-fig. 1c). It rapidly receives its typical scaphitid shape (text-figs. 1d, 2b, 6d, 7a, b), characterized by its comparatively small lobes, elongated saddles and only one distinctly bipartite umbilical lobe on or near the umbilical seam.

Also in the sculpture development a gradual change between *Eoscaphtes* and the *Scaphites* type species can be observed. In *E. circularis* the sculpture remains simple and uniform (comparable with that of the contemporaneous *Hamites*). The branching of ribs, at first only occasionally observable, is a common feature in the first true *Scaphites*. Now the differentiation in primary and secondary ribs becomes more and more pronounced. While the primaries increase in strength, the point of bifurcation approaches the outer margin, and may be tuberculate or not.

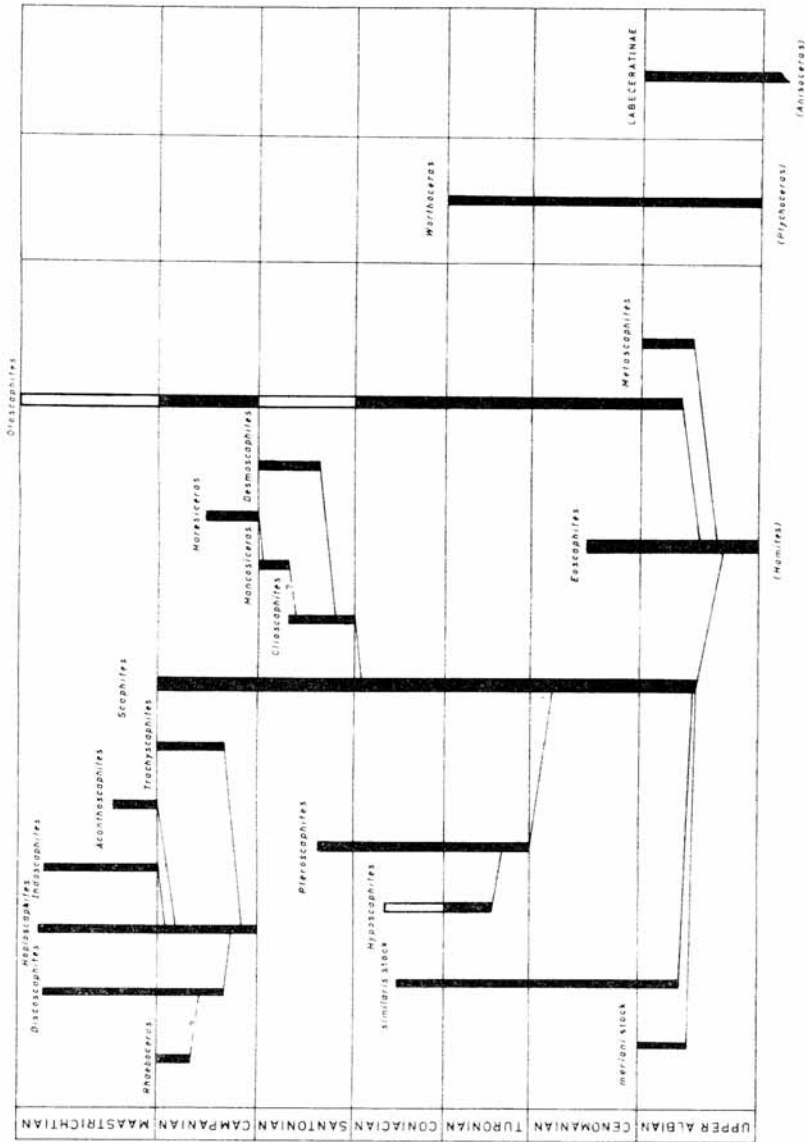
Likewise the degree of shell involution changes continually. In *Eoscaphtes* the first whorls are loosely coiled and no dorsal impression can be recognized. The first whorls are extremely slender and circular in section, but they rapidly increase in size (about 400 per cent. per whorl) and involution. This change can be followed step by step in the eoscaphtid species, and there is no doubt that *Eoscaphtes* had an uncoiled, hamitid ancestor. Already in the first true *Scaphites* (*Sc. simplex*) the maximum shell involution was reached. But an inversion of this tendency appears in the somewhat more open whorled Cenomanian species.

The final hook which is highly elongated in *Eoscaphtes* becomes more and more inflated and stouter in the true scaphitids. Finally, the mouth-border is merely separated from the initial coil. Here, one of the features of heteromorphous development becomes apparent, namely the tendency to abandon the loose coiling and to regain the normal ammonitid spire.

Through all these gradual transitions the generic separation between *Eoscaphtes* and *Scaphites* remains arbitrary. This separation, which we retain, may be based on the umbilical perforation of *Eoscaphtes*, its extreme increase of whorl size, the absence of a dorsal impression and the undifferentiated elements *U* and *L/U*.

In pursuing the development of early scaphitids, we recognized, contrary to the present knowledge, an extreme splitting off into different lineages, especially in the Upper Albian and Cenomanian (text-fig. 16). *Metascaphites* and *Otoscaphtes* can now be directly derived from an eoscaphtid origin, while the above separated *meriani* and *similaris* stocks originate from *Sc. simplex*, the first true *Scaphites*. All these forms merely need generic separation. *Sc. minutus* was erroneously regarded as a transitional form between *Worthoceras* and *Otoscaphtes* by Wright. While the former is now recognized as a homoeomorph development of ptychoceratid origin, *Otoscaphtes* is identified as a true scaphitid development, which parallels the *equalis* main stock, probably throughout the complete Upper Cretaceous.

Text-fig. 16 represents a convincing example for Schindewolf's typrostrophism. The



TEXT-FIG. 16. The scaphitid relationships.

three stages of divergent evolutionary rate, which Schindewolf recognized in many different fossil groups and regarded as an essential evolutionary principle, are well represented here. In the primary stage of explosive development (typogenesis) nearly all diverging types are produced during a relatively short period (Upper Albian Cenomanian). It is followed by a long and stable period (Turonian Santonian), where the types barely change (typostasis). Finally, in the Campanian and Maastrichtian, a new stage of explosive development can be observed, which is generally destructive in nature and announces the imminent extinction of the scaphitid stock (typolysis).

The problem of parallel development in scaphitids has repeatedly been emphasized. The members of the *similaris* stock, the ptero- and otoscapitids, are exclusively small-sized or dwarfed species, which almost exactly parallel the normal-sized members of the main stock. We have two solutions to this problem. The members of the *similaris* stock seem to represent atrophic equivalents of the normal-sized boreal scaphitids. They are restricted to the Southern areas and the Pacific border. The ptero- and otoscapitid micromorphs, however, are generally found together with the normal-sized specimens. In the literature of the last century this fact was often interpreted as sexual dimorphism, and the micromorphs were not separated from the large-sized species. In the modern scaphitid systematics, as created by Wright, the micromorphs were treated as a distinct genus (*Pteroscaphites*) or subfamilies (Otoscapitinae). I am unable to follow Wright in regarding the mouth lappets, which are common in these forms, as the basis for the proposed separation. It has been known for a long time, that lappeted and unlappeted forms are inseparably joined in many ammonitid stocks. Makowski (1963) made the fact, that smaller size and presence of (lateral) mouth lappets in ammonites characterize the male sex, highly possible. Naturally it is impossible to solve this problem absolutely. But all these arguments seem reason enough to re-integrate the micromorph series into the *equalis* main stock.

Thus we come to the conclusion that the systematics of 'Scaphitaceae' may be rigorously simplified. Excluding *Worthoceras* and the Labeceratids as convergent developments, the remaining true scaphitids may be restricted to one single family. If we regard the reduced number of four-lobe elements as a characteristic of all heteromorphs, these also may be grouped into one single superfamily, Ancylocerataceae, in which Scaphitidae, in the neighbourhood of the ancestral hamitids, can now easily be included.

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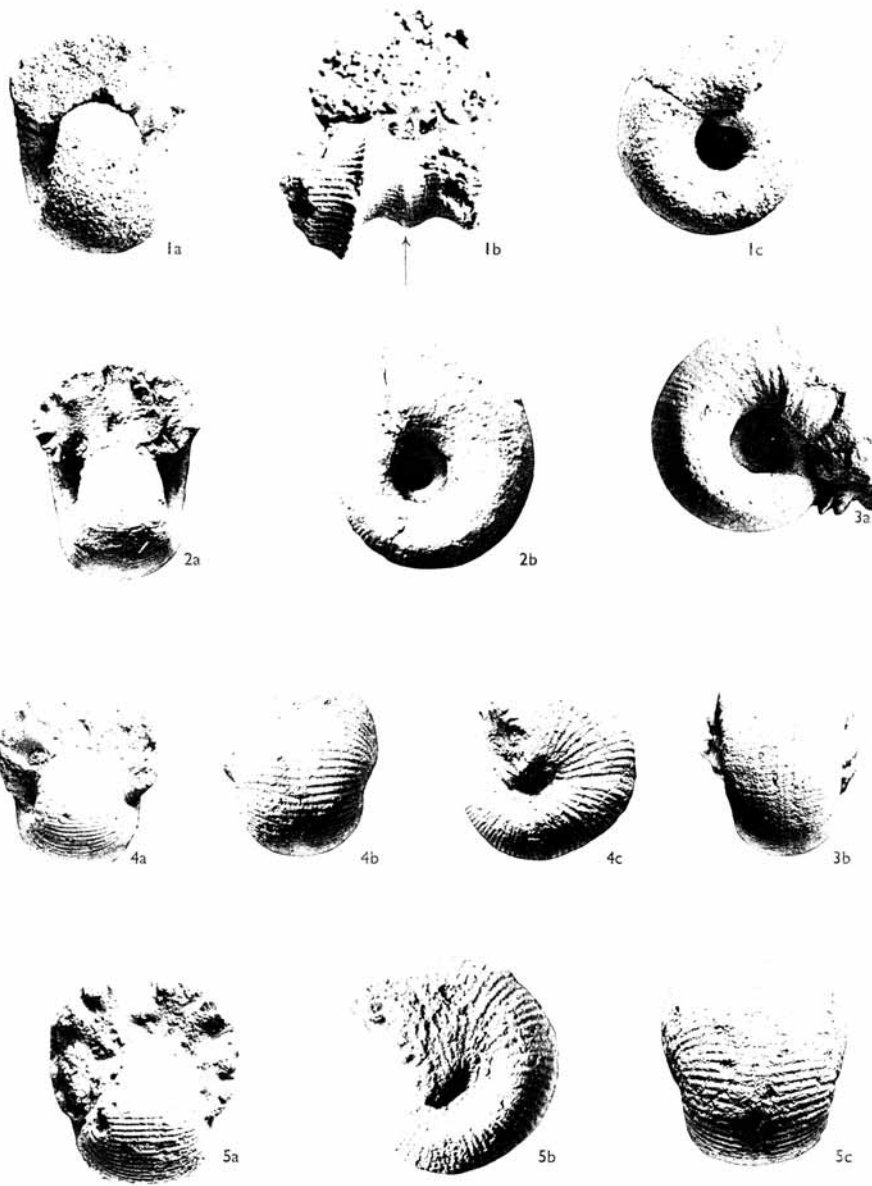
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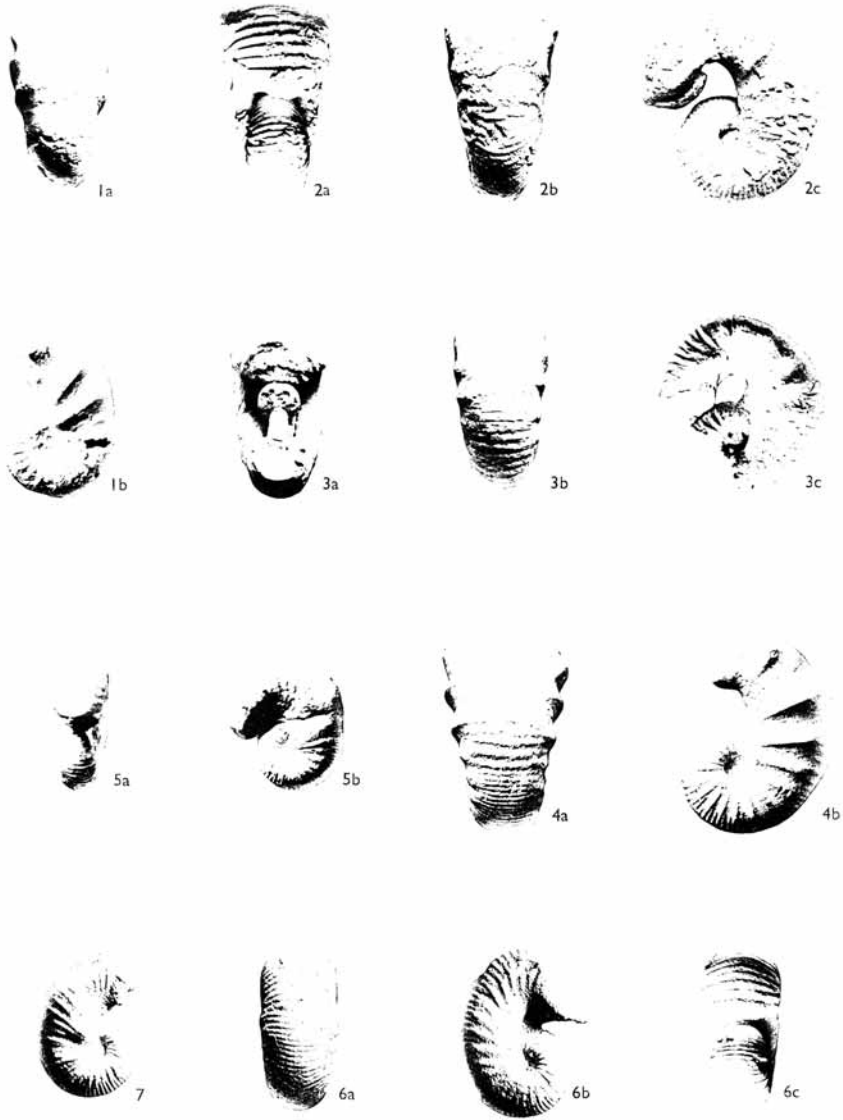
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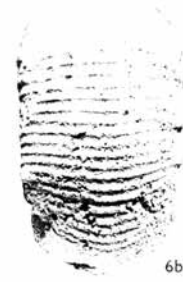
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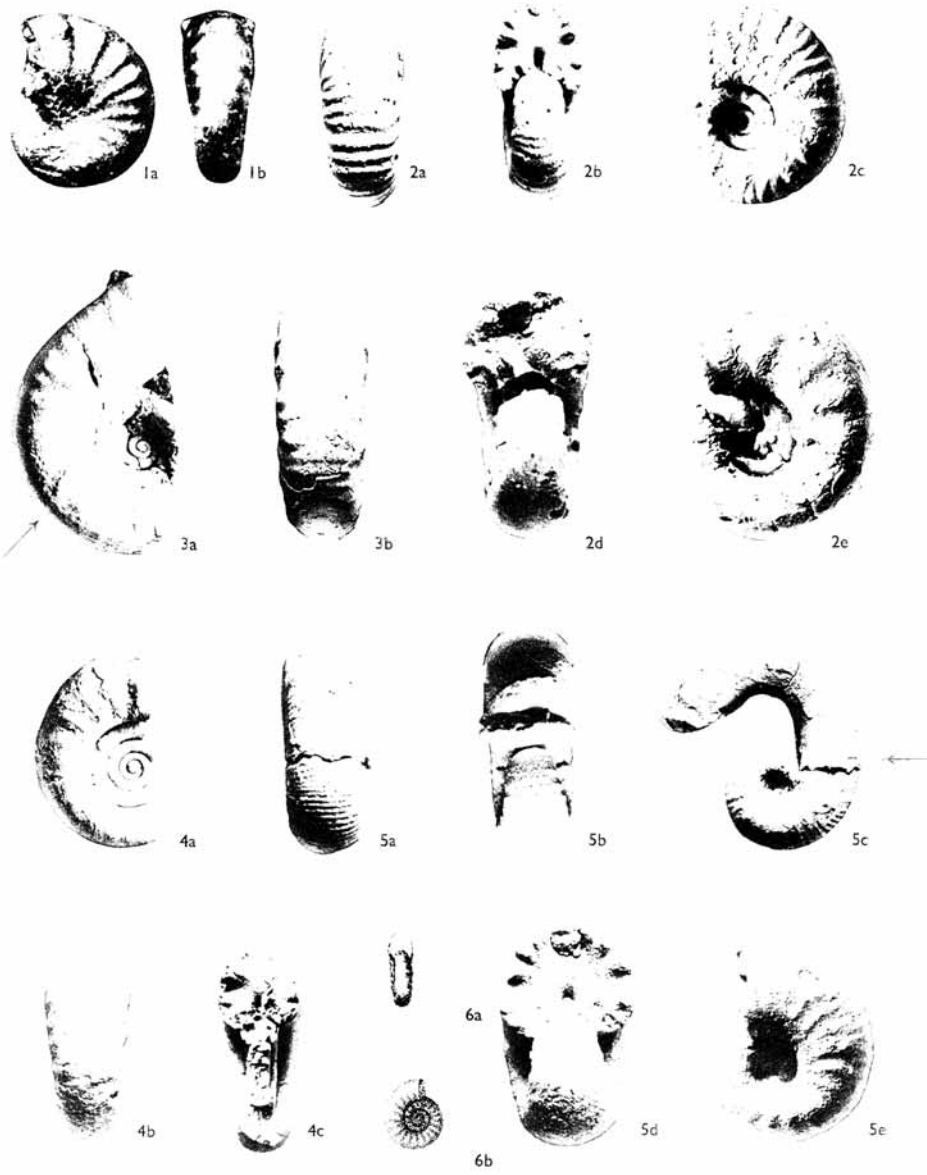


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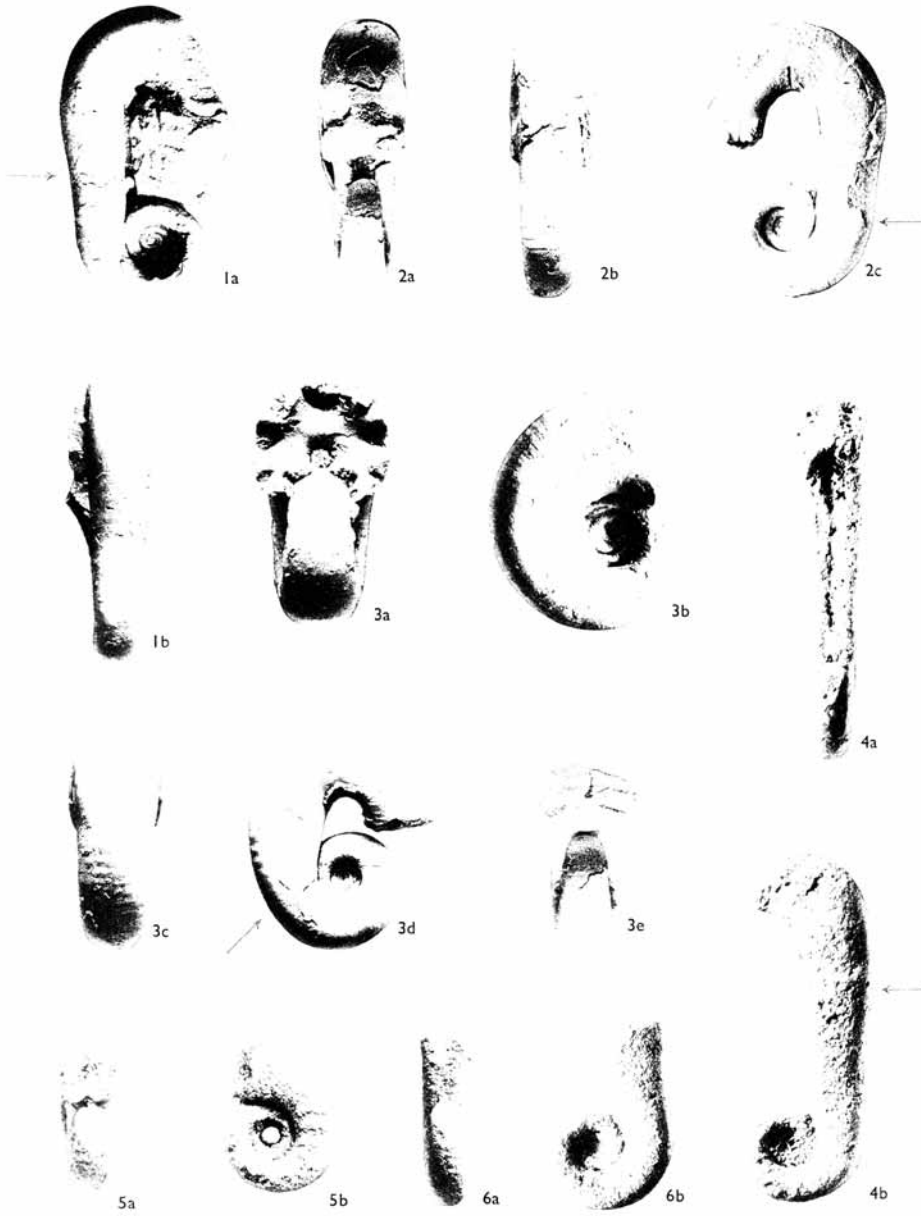


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