# 8 | Ammonoid Sutures in Ontogeny and Phylogeny

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Abstract: Because of their complexity ammonoid sutures offer the best method of recognizing homologies and, thus, phylogenetic relationships. The individual sutural elements (lobes and saddles) develop during ontogeny in various ways which permit large scale ammonoid classification. In some cases even the lower taxa can be classified by means of their sutures. Many examples show that suture phylogeny is related to suture ontogeny, for the genetic principle of additive typogenesis is mostly involved and the law of recapitulation therefore applies.

Sutural lobes have been described by symbols and complete suture lines by formulas. But complete unanimity of symbol terminology has not yet been achieved. Morphographic terminologies (i.e. that of Schmidt, 1921) have been abandoned, but there are still two contradictory morphogenetic terminologies in existence, i.e. Wedekind's original one (1913) and Ruzhentsev's (1949, 1957). Here Wedekind's terminology is favoured because of its priority and its easier and more general application to all Paleozoic and Mesozoic ammonites. This terminology is based on the five basic lobes E (external or ventral lobe), L(lateral lobe), I (internal or dorsal lobe), A (adventitious lobe) and U (umbilical lobe). Ruzhentsev's terminology is rejected mainly because he used Wedekind's prior symbols differently and applied different symbols for homologous elements. Also his system is completely inadequate for Mesozoic ammonites. The basic suture types and their implications for ammonoid classification are reviewed.

#### INTRODUCTION

During the last few decades considerable progress has been made in our knowledge of ammonoid evolution, largely by investigating

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sutures. Most ammonoid workers are therefore convinced of the importance of sutures for recognizing ammonoid phylogeny and as the main tool in ammonoid classification. The basis of every phylogenetic classification is the recognition of homologies. Without question sutures offer the best possibility of recognizing homologies because of their complexity. All other ammonoid characteristics, such as conch shape, sculpture, growth lines and dimorphism, are much less complicated, are therefore much more liable to homeomorphy and are thus of limited use in phylogenetic investigations. Moreover, sutures are linear and therefore easy to reproduce and compare.

To describe sutures we need a terminology which is easy to employ, morphogenetic in nature, applicable to both Paleozoic and Mesozoic ammonites and, moreover, is generally accepted. At present two modes of suture terminology are in use and need to be discussed. We are obliged to select one of these – if possible the simpler and more logical one – since terminology is the necessary basis for general understanding and uniform interpretation.

Although the course of sutural evolution in ammonoids is now well known, little can be said about the function of the marginal frilling of septa, i.e. the suture line. A variety of explanations is still under discussion: static requirements, buoyancy demands, muscle action, chamber fluid regulation and others. In any case, every septum is a replica of the adapical termination of the discontinuously growing ammonoid body at a particular growing stage. Thus it directly reproduces ontogenetic and, therefore, phylogenetic changes of one or several organs of the living animal.

There is a general trend of ontogenetic and phylogenetic evolution leading to a continuous increase of sutural frilling and lobe number. Only a few exceptions exist, which lead, by contrast, to suture reduction in ontogeny (Jurassic heteromorphs) and phylogeny (clymeniids, Cretaceous heteromorphs and pseudoceratitids). The great overall stability and phylogenetic irreversibility of sutural development strongly imply a complex system of pleiotropic genes and polygenic characters or evolution under strong selection pressure, or both. The suture must therefore contain a large amount of the genetic information of the organism, which again stresses the great importance of the suture in ammonoid phylogeny and classification.

The role of homologies (Remane, 1952) in ammonoid sutures has been extensively discussed by Schindewolf (1961-1968, 1969).

Their recognition can be tested in two ways: by stratigraphic succession and by ontogenetic development.

Usually the position and time of appearance of sutural elements remain unchanged during ontogeny and phylogeny. But in some cases changes occur which are of the following types (Schindewolf, 1969):

heterotopy, if the position of a lobe changes,

heteromorphy, if the lobe form changes, or

heterochrony, if the time of appearance during ontogeny changes. In the next section sutural terminology and the various modes of ontogenetic and phylogenetic lobe differentiation are discussed.

## SUTURE AND LOBE TERMINOLOGY

# 1. Prosuture, primary suture

It was Schindewolf (1927, 1929) who first stressed the obvious differences between the suture of the ammonoid protoconch (the so-called prosuture) and all subsequent sutures starting with the "primary suture" which is therefore the second one. The main difference is the absence of an external and an internal lobe in all prosutures; also there seems to be no direct homology between the elements of the pro- and the primary suture. These observations are supported by the study of shell structure which is indeed different in both, as was most recently demonstrated by Kulicki (1979). From these observations a three-stage ontogeny of ammonites has been deduced (Erben, 1962 et seq.) in which the proseptum would mark the transition from the embryonic to an intermediate larval stage. But this conclusion has not been generally accepted, and today a two-stage ontogeny is mostly favoured (Shimansky, 1954; Drushtchic, 1956; Birkelund and Hansen, 1974; Kulicki, 1974). In this the embryonic stage takes in the complete first whorl up to the nepionic swelling and then passes directly into post-embryonic development.

Like the following primary suture, the prosuture shows during phylogeny an increase in "lobe" elements from zero to three (Fig. 1). On the basis of the early work of Branco (1879) an *asellate*, *latisellate* and *angustisellate* type can be distinguished in ascending order. The first type is limited to the Devonian, the second comprises Devonian



Fig. 1. Types and phylogenetic evolution of prosutures (after Schindewolf, 1929).
(a) asellate type: Manticoceras, Frasnian. (b) asellate type: Tornoceras, Frasnian. (c) latisellate type: Merocanites, Lower Visean. (d) latisellate type: Paralobites, Carnian. (e) angustisellate type: Schlotheimia, Hettangian. (f) angustisellate type: Bifericeras, Sinemurian.

to Triassic ammonites and the third type starts from the Triassic. Despite the fact that Mikhailova (1978) again stressed the relationships between pro- and primary sutures, there seems to be no direct relationship between the type of prosuture and major systematic units.

The authors favour Schindewolf's views and would agree to name the lobes of the prosuture with the small letters l,  $u_1$  and  $u_2$  – in order of phylogenetic appearance – for easier distinction from the true lobes of remaining sutures (Schindewolf, 1929, fig. 8).

The primary suture is generally accepted as the basis for all the subsequent sutures. Based on the initial work of Noetling (1905, 1906) the first convincing system of lobe and suture terminology was established by Wedekind (1910, 1916) and refined by Schindewolf (1923, 1927, 1929, 1933, 1951, 1961–1968, 1969). This system is based on the morphogenesis of every lobe element and not on the accidental position of lobes in the adult. It is clear, simple and easy 

Fig. 2. Different types of sutural frilling (from Wiedmann, 1970b).

to apply and, moreover, older than the terminology of Ruzhentsev (1949b, 1957, 1960a, 1964), which will be briefly discussed later.

Every suture is divided into the apicad lobes and the orad saddles. By definition every new lobe has to originate from a saddle during ontogeny (Fig. 2(II)). By its final size, mode and position of its development a new lobe having a lobe symbol of its own, is easy to distinguish from a mere saddle incision (Fig. 2(I)). This distinction is generally easy to recognize, but in recent years an intermediate case has been described from the Cretaceous heteromorphic group of scaphitids where saddle incisions developed to lobe size and have been called pseudolobes (Wiedmann, 1965). On the other hand, in the Jurassic heteromorphs true lobes become reduced to the size of saddle incision during ontogeny (Schindewolf, 1963a).

Another mode of increase of suture elements during ontogeny is the subdivision of lobes (Fig. 2(IV)). In this case the original lobe symbol will be retained. If there is only a splitting into a dorsal and a ventral lobe portion, the indices d (dorsal) and v (ventral) may be added. In the case of a symmetric lobe splitting at the umbilical seam, Wedekind (1916) proposed the additional letter S (for sutural lobe, for example  $U_3 = S$ ).

Transitions are known where the new element ontogenetically starts at the saddle neck (Fig. 2(III)). In this case it is really difficult to decide whether the new element has to be regarded as a new lobe (coming from the saddle) or only as a lobe subdivision (normally starting from the lobe bottom). Both cases seem possible, and therefore a mixed symbol seems appropriate (Wiedmann, 1970b).



Fig. 3. Course and pattern of sutural evolution in ontogeny and phylogeny (after Schindewolf, 1969).

The first ammonoid primary suture is characterized by one lobe only. This is the external lobe (E) which is situated ventrally and found for the first time in Lobobactrites. The next step in evolution is the trilobate suture which becomes the basic primary suture of all Paleozoic ammonoids (Fig. 3); it has, in addition, an internal lobe (I) dorsally and the lateral lobe (L) on the flanks. These three lobes have been named protolobes by Schindewolf (1927). As shown in Fig. 3, further lobes (metalobes) can originate in two positions only: between E and L on the outer margin or between  $\hat{L}$  and I on the inner margin or umbilical seam. Both modes have been realized and correspond to the first major divergence in Paleozoic ammonoids. (i) The first mode starts with new lobes appearing on the outer margin during ontogeny; it is called A-type development and is restricted to the Paleozoic (Order Goniatitida). The additional new lobe is called the adventitious lobe (A) and every further lobe in the same position is numbered in accordance with its ontogenetic appearance  $(A_1, A_2, \ldots)$ . (ii) The new lobes between L and I are

called umbilical lobes (U) and numbered in the same way. This is the U-type development which is characteristic of the order Prolecanitida and all Mesozoic ammonites.

A number of homeomorphs developed by the appearance of U-lobes late in ontogeny in goniatitids, and by the appearance of A-lobes in prolecanitids and Mesozoic ammonites. In all these cases, careful investigation of the suture morphogeny is necessary.

The evolutionary mode of sutural development is that of additive typogenesis (Fig. 3): new elements are added at the end of ontogeny and then shifted back to earlier growth stages. As a result a new lobe sometimes enters the primary suture. Thus at the Permian-Triassic boundary the primary suture became quadrilobate by the appearance of the first umbilical lobe  $(U_1)$ . This type of primary suture is characteristic of most of the Triassic "meso"- ammonites; while the main groups of Jurassic and Cretaceous "neo"- ammonites achieve a quinquelobate primary suture with a lobe formula  $ELU_2U_1I$ . In the lytoceratid group of tetragonitids in the Upper Cretaceous still a third umbilical lobe  $(U_3)$  appeared in the primary suture. This "orthogenetic" trend is paralleled by the well known phylogenetic trend of increasing sutural frilling: most Paleozoic ammonoids have unfrilled sutures; in the ceratitic sutures of mesoammonites frilling starts in the lobes; this leads finally to the ammonitic bipolar frilling of the sutures of neoammonites, where frilling starts during ontogeny from lobes as well as from saddles.

Within this trend a variety of exceptions and reversions occur. In the previously described evolutionary trend of primary sutures one case of reversion is known from the Cretaceous. For in the large group of Cretaceous heteromorphs the reduction to a quadrilobate primary suture with the formula ELUI occurs again, and may be retained in most cases up to the adult. The only difference from the quadrilobate primary suture of Triassic ammonites is the presence of a median saddle in E, which is an advanced character of the ancestral quinquelobate primary suture of the Jurassic forerunners.

Wedekind's proposals include almost all terminological requisites needed in handling sutural evolution in ontogeny and phylogeny. It also clearly shows the major course of ammonoid evolution so that the broad outlines of a natural classification become obvious.

A few further subscript lobe symbols have been proposed in the meantime (Wiedmann, 1966b) and may be added here. They are



Fig. 4. Mesozoic internal lobes. A, lituid  $I(I_l)$  of phylloceratids. B, septal lobe  $(I_s)$  of lytoceratids. (From Wiedmann, 1972)

restricted to meso- and neoammonites and concern the stable forms of the lituid internal lobe  $(I_1)$  of phylloceratids and of the septal lobe  $(I_s)$  of lytoceratids (Fig. 4). Finally, in the Jurassic some stephanoceratids develop during their ontogeny one more umbilical lobe in an uncommon position, i.e. in the saddle between  $U_1$  and I. It looks much like a heterochronous  $U_1$  which naturally has to appear much earlier during ontogeny, i.e. in the primary suture. This heterochronous lobe has been labelled  $U_n$  by Schindewolf (1965).

A complete list of the terms used in this paper is as follows:

E external lobe (ventral lobe)

- L lateral lobe
- *I* internal lobe (dorsal lobe)
- I<sub>1</sub> lituid internal lobe
- I, septal lobe
- $A_1, A_2, \ldots$  adventitious lobes

 $U_1, U_2, \ldots$  umbilical lobes

- $U_n$  heterochronous umbilical lobe
- U = S sutural lobe

# 2. Remarks on Ruzhentsev's Suture Terminology

The general applicability of this terminology has been refuted or criticized by several authors (Schindewolf, 1963b, 1968; Popov, 1965; Kullmann and Wiedmann, 1970; Luppov, 1977). Their main objections are:

- (1) priority of Wedekind's terminology;
- (2) confusing changes in the use of Wedekind's symbols;
- (3) usage of different symbols for homologous lobes (Wedekind's L is called "O" if it is placed in an "omnilateral" position, but "U" if it is placed near the umbilicus, although in the latter case it is unrelated to Wedekind's real U); this leads to complete confusion and shows that Ruzhentsev's system is at least partly morphographic-descriptive;
- (4) very complicated suture formulas in many cases obscure the genetic relationships (see table 2 in Kullmann and Wiedmann, 1970).

The citations given in the paper by Kullmann and Wiedmann (1970, p. 21) show that Ruzhentsev's terminology obscures real relationships and leads to an artificial grouping of ammonites which is far removed from the natural system. This is easy to demonstrate by repeating only a few formulas:

# Ruzhentsev

Wedekind

Perisphinctes	$\cdot (V_1 V_1) U U^1 U_i^2 : U_i^2 I D$	$ELU_2U_3(U_4 = S)U_{1v}U_{1d}I$
Strenoceras	$(V_1V_1)UU^1U^2: U^3ID$	$ELU_2U_3U_4U_{1v}U_{1d}I$
Acanthohoplites	$(V_1V_1)UU^1U^2U^3:ID$	$ELU_{vv}U_{vd}$ : $U_dI$
Hypacanthoplites	$(V_1V_1)UU^1U_1^2:U_1^2ID$	$ELU_{vv}U_{vd}: U_dI$

In this example the close relationship between the Cretaceous "false hoplitids" Acanthohoplites and Hypacanthoplites, on the one hand, and that between the Jurassic Strenoceras and Perisphinctes on the other, are obscured in Ruzhentsev's terminology. Instead, this system would group Acanthohoplites with Strenoceras and Hypacanthoplites with Perisphinctes. Figure 5 shows how clearly suture ontogeny (Fig. 5(I)) parallels suture phylogeny (Fig. 5(II)) in the interesting group of "false hoplitids" which are in reality recoiled heteromorphs. It also shows that acanthohoplitid sutures are very different from perisphinctid ones (Fig. 16g).

To facilitate translation of Ruzhentsev's and also Popov's (1965) terminologies the following conversion table is reproduced:



Fig. 5. Congruency of suture ontogeny (I) and phylogeny (II) in Mid-Cretaceous acanthohoplitids (from Wiedmann, 1970b). I, Sutural ontogeny of Gargasiceras gargasense (d'Orb.) (e at whorl height of 4.5 mm). II, Adult suture lines of (a) Leptoceras (Hamulinites) munieri (Nickle's), Barremian; (b) Paraspiticeras schindewolfi Wiedmann, Barremian; (c) Cheloniceras cornuelianum (d'Orb.), lower Aptian; (d) Gargasiceras gargasense (d'Orb.), upper Aptian; (e) Hypacanthoplites clavatus (Fritel), uppermost Aptian.

Wedekind (1913)	Ruzhentsev (1949b)	Popov (1965)
E	V (ventral)	V
L	O (omnilateral)	L
	+ U (umbilical s. str.)	
Ι	D	D
$A_1, A_2, \ldots$	$L, L^1, \ldots$	N (neolateral)
Ui	I	· · ·
Un	$I^1$	K (Kehllobus
$U_2, U_3, \ldots$	$U^{1}, U^{2}, \ldots$	sensu
		H. Schmidt)

We repeat that any terminology is merely an aid in communicating an often extremely complicated set of observations. The system which is simplest, and above all most accurate in recognition and description of homologies, will always be preferable. The ambition to create new and more complicated terminologies should not be allowed to disturb what, after all, must be the goal of every terminology: international understanding. It would be sad if the continuing controversy over lobe terminologies should damage the reputation of lobe-ontogeny studies without bringing nearer what everyone wishes: a natural system of ammonoid classification.

# SUTURE EVOLUTION AND AMMONOID CLASSIFICATION

We give in the following pages a review of suture types, the pattern of suture evolution and the resulting ammonoid classification.

# 1. Palaeozoic Ammonoids

(a) Order Bactritida. The batritids exhibit the simplest sutural configuration among Ammonoidea; besides the typical "neck" lobe at the position of the siphuncle in all bactritids, only one group with well-developed lateral lobes (*Lobobactrites*) occurred.

(b) Order Anarcestida. The most primitive Lower Devonian genera (Anetoceras, Mimosphinctes) developed sutures with only two lobes, E and L. But the suture of the majority of Lower and Middle Devonian ammonoids is characterized by the elements ELI, which can be found in the adult sutures of most members of the super-families Agoniatitaceae and Anarcestaceae.

On the basis of a different interpretation of the lateral lobe, Ruzhentsev considered Agoniatitids and Anarcestids as separate suborders; in his terminology the Agoniatitids have an "omnilateral lobe" (O), and the Anarcestids an "umbilical lobe" (U). Because there is no genetic difference between both lobes, we regard them as homologous to L in Wedekind's terminology (for detailed discussion see Kullmann and Wiedmann, 1970, pp. 4, 7).

Advanced Middle Devonian forms already develop sutures with four elements, *ELUI* (Prolobitidae, *Clymenoceras*, Fig. 7e), or *EALI* (order Goniatitida, Tornoceratina). In a side branch of the Agoniatitidae, the ventral lobe appears to be split up into  $E_1E_2E_mE_2E_1$  (Augurites, Fig. 7b).

The suborder Gephuroceratina, mainly Frasnian in age, also belongs to the order Anarcestida. Its characteristic difference from the Anarcestina is the development of a median saddle and lobe in



Fig. 6. Ontogenetic development of suture in Marathonites (Almites) invariabilis Ruzhentsev, Lower Permian (lower Artinskian), USSR (southern Urals) (After Ruzhentsev, 1956, fig. 89a-f, i, 1). [Explanation: (a) prosuture; (b) primary suture; (c) 2nd suture; (d-g) intermediate stage sutures; (h) adult suture. The primary suture is trilobate; the second suture has an adventitious lobe that during ontogeny, like the umbilical lobe, divides into 3 lobes.]

the ventral lobe. The ancestral form of Pharcicerataceae (Manticoceras, Fig. 7c; Mesobeloceras, Fig. 7d) is Maenioceras (Fig. 7a), upper Givetian in age, with the sutural formula  $E_m E_1 L U_2 U_1 I$ ; true pharciceratids exhibit an increasing number of umbilical lobes: Pharciceras  $(E_1 E_m E_1) L U_2 U_4 : U_3 U_1 I$ , Neopharciceras up to  $U_{24}$ .

(c) Order Goniatitida. This order is characterized by the appearance of a first adventitious lobe (A) prior to formation of an umbilical lobe (U). This means that the lateral lobe remains in the umbilical area. The simplest formula is, therefore, *EALI* (*Tornoceras*, *Cheiloceras*). The following lobal ontogeny is valid for all later members of the order: primary suture *ELI*, then (usually second suture) *EALI*, and



Fig. 7. Adult sutures of Palaeozoic Anarcestida and Goniatitida. (a) Maenioceras terebratum (Sandberger), Middle Devonian (Givetian), Germany (from Bogoslovskiy et al., 1962, after Holzapfel, 1895). (b) Augurites mirandus Bogoslovskiy, Middle Devonian (Eifelian), USSR (from Bogoslovskiy, 1961). (c) Manticoceras sinuosum (Hall), Upper Devonian (Frasnian), USA (from Miller and Furnish, 1957, after Clarke, 1899). (d) Mesobeloceras thomasi Glenister, Upper Devonian (Frasnian), Australia (from Bogoslovskiy et al., 1962, after Glenister, 1958). (e) Clymenoceras insolitum Schindewolf, Upper Devonian (Famennian), Germany (from Bogoslovskiy et al., 1962, after Schindewolf, 1938). (f) Discoclymenia cucullata (von Buch), Upper Devonian (Famennian), Germany (from) Schindewolf, 1951). (g) Goniatites choctawensis Shumard, Mississippian, USA (from Miller and Furnish, 1957). (h) Eothinites kargalensis kargalensis Ruzhentsev, Lower Permian (Artinskian), USSR (from Ruzhentsev, 1956); (i) Pseudoschistoceras simile Teichert, Lower Permian, Australia (from Bogoslovskiy et al., 1962, after Teichert, 1944). (k) Delepinoceras bressoni cantabricus Kullmann, Upper Carboniferous (lower Namurian), Spain (from Kullmann, 1962).

later EALUI. Adult sutures of the formula EALUI occur most commonly within the suborder Tornoceratina (Middle Devonian – Upper Permian), i.e. the most primitive Goniatitida. An increase in the number of elements follows from an increase in the adventitious lobes, e.g. Discoclymenia:  $EA_3A_2A_1L$ : UI (Fig. 7f). The suborder Goniatitina differs from the suborder Tornoceratina principally in that the external lobe has a median saddle and lobe. Its sutural formula is  $(E_1E_mE_1)ALUI$ . The family Goniatitidae (Goniatites, Fig. 7g) has the basic suture from which sutures of other Goniatitina superfamilies differentiate. By and large the superfamilies Pericyclaceae, Dimorphocerataceae, Goniatitaceae, Neoglyphiocerataceae, Gastriocerataceae, Goniolobocerataceae and Paragastriocerataceae retain the formula  $(E_1E_mE_1)ALUI$ . Of the Early Carboniferous Goniatitina, only the family Dimorphoceratidae exhibit more or less irregular subdivisions of the ventral lobe (Asturoceras, Fig. 9c) and on occasion also of the adventitious lobe.

A number of groups of Late Carboniferous and Permian ammonoids show a tendency toward trifid division of some lobes. This is, for instance, typical of the superfamilies Shumarditaceae, Marathonitaceae, Cyclolobaceae and Popanocerataceae. Advanced forms of the Schistoceratidae subdivide only the  $U_2$  (into  $U_{2v}U_{2m}U_{2d}$ ), the Metalegoceratidae the lateral lobe L (into  $L_vL_mL_d$ ; Eothinites, Fig. 7h, the end form being Pseudoschistoceras, Fig. 7i).

Of the superfamily Goniatitaceae the Agathiceratidae similarly exhibits a tendency toward trifurcation (Agathiceras, Fig. 9a). The Delepinoceratidae display incipient trifurcation of  $E_1$  and A (Delepinoceras, Fig. 7k).

The superfamily Cyclolobaceae is characterized by trifurcation of all lobes except E. The same scheme of lobal development prevails in the superfamilies Shumarditaceae and Marathonitaceae (*Marathonites*, Fig. 6), but lobal multiplication results from repeated trifurcation of A and U only, while the lateral lobe remains single trifid. The superfamily Popanocerataceae is basically similar except for the insertion of further adventitious and umbilical lobes as in *Popanoceras* (Fig. 9b); in *P. sobolewskyanum* (teste Ruzhentsev, 1956), the sequence  $U_2$  and  $U_3$  cannot be verified with certainty.

The superfamily Adrianitaceae, in form and lobal arrangement very similar to the Agathiceratidae, increases its lobes by the formation of additional umbilical lobes. Characteristic of many Adrianitaceae is the breaking down of a lobe in the region of the umbilicus into numerous incisions, to which we can give no names. This is referred to as Suturallobus (S) by Wedekind. Examples are *Emilites* and *Crimites* (Fig. 9e).

In the superfamily Neodimorphocerataceae we find a totally



Fig. 8. Ontogenetic development of the suture in *Merocanites asiaticus* (Karpinskiy), Lower Carboniferous (lower Visean), USSR (from Karpinskiy, 1896, p. 187). The primary suture is trilobate; later on a 4th lobe is developed (umbilical lobe), which pushes the lateral lobe from its original umbilical position out onto the flanks. [(a) prosuture; (b) primary suture; (c-i) further stages of development; (k) adult suture.]

different lobal configuration. In the course of its phylogeny the ventral lobe was widening, and later representatives differ from typical Goniatitina in that the number of lobes of its suture increases through differentiation of the ventral lobe (*Neodimorphoceras*, Fig. 9d).

The superfamily Thalassocerataceae, finally, exhibited no additional lobal elements but developed an increasing serration and digitation of its lobes. (d) Order Prolecanitida. The oldest forms of the order Prolecanitida are similar to the Prionoceratidae (order Goniatitida, suborder Tornoceratina). The sutures of Eocanites and Protocanites possess the same number of elements as those of the contemporaneous Imitoceras and Gattendorfia, and the phylogenetic relationship between the Prionoceratidae and early Prolecanitidae is obvious. The origin of their five lobes is different, however: in Imitoceras EALUI and in Protocanites ELU<sub>2</sub>U<sub>1</sub>I. It was first observed by Karpinskiy in Merocanites asiaticus that during ontogeny no adventitious lobe was developed, and the lobal increase occurred through insertion of umbilical lobes. Later, Schindewolf confirmed this observation in Merocanites applanatus (Schindewolf, 1929, p. 41, fig. 20) and Protocanites (Schindewolf, 1959, fig. 2). But it is by no means certain that this mode of lobal increase occurs uniformly throughout the entire order. Schindewolf (1951, p. 22, fig. 15) reported the presence of an adventitious lobe in Neopronorites permicus - an interpretation which cannot be proved, since the trilobate primary suture is followed by a quinquelobate suture. This has been demonstrated also for the Permian species Artioceras rhipaeum (Ruzhentsev, 1949a, fig. 58) and for the late Carboniferous species Boesites gracilis (Hodgkinson in Nassichuk, 1975, fig. 14C). In all these cases the lateral lobe seems to remain in a lateral (or better, umbilical) position, and the second suture apparently shows both an adventitious as well as an umbilical lobe. This configuration, however, has been interpreted by Ruzhentsev (in Boesites primoris, 1960b, p. 182, fig. 56) as a series of umbilical lobes. Nevertheless, the possibility exists that the lobe taken to be L in advanced Prolecanitida is in fact the lobe A.

The basic family Prolecanitidae (*Prolecanites*, Fig. 9f) shows an increase in U from Protocanites  $(U_2)$  up to  $U_7$  in Acrocanites. In the Dataelitidae and Pronoritidae the number of umbilical lobes is increased even more (*Dataelites* up to  $U_9$  and *Neopronorites* up to  $U_{10}$ ) and, in addition, E is further developed.

The superfamily Medlicottiaceae (*Prouddenites*, Fig. 9g) retains the sutural development of the prolecanitaceae with modification of the external saddle in that parts of the lateral lobe lying near the external lobe become included in the external saddle. The incisions which result cannot be traced morphogenetically and commonly are not generically, or even specifically, typical. Furthermore, they may



Fig. 9. Adult sutures of Palaeozoic Goniatitida, Prolecanitida and Clymeniida. (a) Agathiceras uralicum Karpinskiy, Lower Permian (Artinskian), USSR (from Miller and Furnish, 1957). (b) Popanoceras sobolewskyanum (de Verneuil), Lower Permian (Artinskian), USSR (from Ruzhentsev, 1956). (c) Asturoceras subdivisum (Kullmann), Upper Carboniferous (lower Namurian), Spain (from Kullmann, 1962). (d) Neodimorphoceras texanum (Smith); Upper Pennsylvanian, USA (from Bogoslovskiy et al., 1962, after Miller and Downs, 1950). (e) Crimites subkrotowi Ruzhentsev, Lower Permian (Artinskian), USSR (from Ruzhentsev, 1956). (f) Prolecanites (Cantabricanites) postapplanatus Kullmann, Lower Carboniferous (upper Visean), Spain (from Kullmann, 1963). (g) Prouddenites primus Miller, Upper Pennsylvanian, USA (from Miller and Furnish, 1957). (h) Pseudosageceras multilobatum Noetling, Lower Triassic, USSR (from Bogoslovskiy et al., 1962, after Kiparisova, 1947). (i) Sphenoclymenia maxima (Münster), Upper Devonian (Famennian), Germany (from Schindewolf, 1957). (k) Cymaclymenia striata (Münster), Upper Devonian (Famennian), Germany (from Schindewolf, 1957).

be asymmetrical. Ruzhentsev's notation, therefore, would appear to be superfluous.

The superfamily Sagecerataceae is characterized by elaboration of the external lobe, as in *Pseudosageceras* (Fig. 9h).

The lobal development of some isolated groups systematically close to Praeglyphioceras, Karagandoceras and Prodromites remains unexplained. In these a median lobe develops in the external saddle  $(E_1E_mE_1)$ . The first two genera belong in the suborder Goniatitina, since the lobe lying laterally appears to be adventitious. The suture of *Prodromites*, on the other hand, has the formula  $E_mE_1LU_2U_3...$  and, therefore, probably belongs in the suborder Prolecanitina. It is possible that these are independent, restricted groups which existed for a short time and left no successors.

(e) Order Clymeniida. The order Clymeniida is restricted to the uppermost Devonian. The number of sutural elements is open to considerable fluctuation. The simplest (but not original) development of the suture line exhibits only two lobes: a lateral lobe on each whorl side, these being separated from each other by a ventral and dorsal saddle. However, the number of lobes can rise to 12, in Sphenoclymenia:  $EA_2A_1LU_1U_2I$  (Fig. 9i).

The lack of a ventral lobe in most members of the order Clymeniida and its secondary replacement by a ventral saddle represents a unique characteristic among Ammonoidea. As far as can be generalized, it seems that observations would indicate that clymeniids with a ventral saddle in adult stages initially developed an external lobe in the early juvenile stage. With flattening and fusion of the neighbouring L/Esaddles during ontogeny, the external suture line becomes transformed into a wide external saddle. One can deduce from this that possession of a ventral lobe should be looked upon as the original characteristic of clymeniids (suborder Gonioclymeniina).

Thus the greatest similarities with the Anarcestina are found in the suborder Gonioclymeniia. Lobal development proceeds from *ELI* via *ELUI* and *EALUI* to  $EA_2A_1LU_1U_2I$ . In some groups, just as in goniatites, the ventral lobe is divided by a median saddle. In this case a saddle rises from the base of the lobe, a part of the ventral lobe remaining lateral to this. At the apex of the median saddle a flat median lobe often originates, as is frequently encountered in goniatites. The dorsal lobe in clymeniids is usually retained throughout life; here there is evidently some relation to the siphuncle inside. In some members of the superfamily Parawocklumericeae, the dorsal lobe is either divided by a median saddle, or vanishes completely owing to the fusion of neighbouring saddles. It is among parawockumeriids that a lobal reduction occurs from  $(E_1E_1)L:(I_1I_1)$  to a fingle L. The suborder Platyclymeniina (Clymeniina) includes the typical clymeniids, where the ventral lobe is developed only in the earliest ontogenetic stages, and later replaced by a ventral saddle. The dorsal lobe persists throughout ontogeny. In general, the suture of Platyclymeniina is most simple: the basic suture is L:I, and advanced forms have either ALI or LUI. Cymaclymenia (AL:UI; Fig. 9k) is the most complicated genus of this suborder.

2. Mesozoic Ammonoids

Mesozoic ammonites are characterized by a progressive development of the suture which involves both the number of lobes in the primary suture and denticulation of the adult suture. Within both trends reversions appear. Including the very conservative configuration of the internal lobe (Fig. 4) as a further characteristic, the main groups of meso- and neoammonites may be characterized by their sutural features as follows:

Order Phylloceratida

Internal lobe lituid  $(I_1)$ , saddles ceratitic or phylloid

- 1. Suborder Phylloceratina Primary suture ELI (Permian) – ELUI (Triassic) –  $ELU_2U_1I$ (Jurassic-Cretaceous), saddles phylloid
- 2. Suborder Ceratitina Primary suture ELU<sub>1</sub>I, saddles mostly ceratitic, with unipolar frilling

Order Lytoceratida

Internal lobe not lituid, saddles denticulated, with bipolar frilling

- 1. Suborder Lytoceratina Primary suture  $ELU_2U_1I$  (Lytocerataceae) –  $ELU_2U_3U_1I$ (Tetragonitaceae), septal lobe  $I_s$
- 2. Suborder Ammonitina Primary suture  $ELU_2U_1I$ , internal lobe simple
- 3. Suborder Ancyloceratina Primary suture *ELUI*, internal lobe simple

Schindewolf's (1968) proposal to group Phylloceratina with Ceratitina and Lytoceratina with Ammonitina has much in favour, also in considering the prosutures development (Mikhailova, 1978). The recommendation of Schindewolf (1968) to assign subordinal

U4 = S U2 U3 U, 4 2 i h U4 = 3 252 U2 ξ 9 म्र U2 U3 U4 U1 1 U<sub>2</sub> U<sub>3</sub>U<sub>4</sub>U<sub>1</sub> 1 L U2U3 U1 1 L ſ t í L U2U3U1 I Ε 6 ชา LU2U1 1 £ a

rank to the pinacoceratids, arcestids and lobitids is not followed here because of the lack of detailed investigations on suture ontogeny in Triassic ammonites.

(a) Phylloceratida. Following Schindewolf (1961) the most important characteristic of true phylloceratids is the Suturallobenbildung in  $U_3$  or  $U_4$  (Fig. 10). In the meantime, Suturallobenbildung has been found in lytoceratids (Tetragonitaceae) as well as in some ammonitids (Desmocerataceae) and even goniatitids. The lituid form of the internal lobe appears to be more important because of its resemblance with the Triassic antecedents. There is only a very limited variation of this I in the Jurassic Tragophylloceras. Schindewolf's interpretations of the general evolution from a subdivided  $U_1$  to a "secondarily" undivided  $U_1$ , or of the importance of a one- or two-pointed internal lobe, does not seem to be correct, for many fluctuations in these characteristics can be observed (Fig. 11). Nevertheless, there are some differences in the suture evolution which permit a clear characterization of superfamilies.

The Otocerataceae, root stock of all Mesozoic ammonites, exhibit an augmentation of umbilical lobes up to five umbilical lobes (Xenodiscus, Fig. 12a; Ophiceras, Fig. 12b; Otoceras, Fig. 12c). There is no Suturallobenbildung, but the internal lobe is already lituid. Therefore, these forms represent first phylloceratids; the new suborder Paraceltitina Shevyrev, 1968, is not necessary. Judging from the little information available on Triassic sutural ontogenies the following groups can easily be assigned to Otocerataceae: Ussuritidae (Monophyllites, Fig. 12e) within the phylloceratids, Meekocerataceae with the bulk of previous "Noritaceae", Clydonitaceae (Trachyceras, Fig. 12f), Tropitaceae, Proptychitidae of Shevyrev's "Proptychitaceae" and, finally, Ceratitaceae (Fig. 12h) including "Hungaritaceae" (Longobardites, Fig. 13a).

The latter group is characterized by an even more pronounced proliferation of umbilical lobes (up to  $U_{11}$ ) which led to the separation of Ceratitina – Schindewolf suggested – from Phylloceratina.

Fig. 10. Suture ontogeny and Suturallobenbildung in U<sub>4</sub> of true phylloceratids: Sowerbyceras (Holcophylloceras) calypso (D'Orbigny), Valanginian, France (from Wiedmann, 1968). [(a) primary suture; (i) adult suture at whorl height of 3 mm.]



Fig. 11. Phylogeny of elements I and U<sub>1</sub>, within Jurassic-Cretaceous ammonites (after Wiedmann, 1966b). [Psiloc. = Psilocerataceae, Haploc. = Haplocerataceae, Hoplitac. = Hoplitaceae, Ancyloc. = Ancylocerataceae, Douvilleic. = Douvilleiceratidae, Astieric. = Astiericeratidae.]

The Triassic heteromorphs (lobe formula *ELUI*) belong to this group (*Choristoceras*, Fig. 12g).

A first lytoceratid mode of the splitting of the  $U_1$  resulting in a lobe formula  $ELU_{1\nu}U_{1d}I_1$  is found in Tirolitidae, Dinaritidae (Fig. 12i) and Hellenitidae of "Ceratitaceae" and in the Kashmiritidae and Sibiritidae of "Noritaceae", regarded as "Dinaritaceae" by Shevyrev (1968). The Palaeophyllitidae with Leiophyllites (Fig. 12d) have a somewhat intermediate position between the two mentioned suture types. The suture ontogeny of Leiophyllites (Wiedmann, 1970a) does not reveal clearly, whether the third umbilical lobe is an  $U_{1\nu}$  or an  $U_3$ . In any case, these sutures foreshadow the later suture pattern of lytoceratids (Fig. 14).

Turning back to the Suturallobenbildung of true phylloceratids (Fig. 15a) extending from the Carnian to the Maastrichtian, it has to be mentioned, that the suture type of Megaphyllitidae (Fig. 13c), lies very close to phylloceratids, having more than 20 incisions of  $U_3$ , symmetrically distributed on either side of the umbilical



Fig. 12. Phylloceratid adult sutures of the Upper Permian and Triassic.
(a) Xenodiscus sp., Upper Permian, Salt Range. (b) Ophiceras sakuntala Diener, Lower Triassic (lower Scythian), Himalayas. (c) Otoceras sp. cf. O. woodwardi Griesbach, Lower Triassic (lower Scythian), Himalayas. (d) Leiophyllites taramellii (Martelli), Middle Triassic (Anisian), Bosnia.
(e) Monophyllites sphaerophyllus (Hauer), Middle Triassic (Anisian), northern Alps. (f) Trachyceras sp. cf. busiris (Münster), Upper Triassic (lower Carnian), Tyrol. (g) Choristoceras marshi (Hauer), Upper Triassic (Rhaetian) northern Alps. (h) Ceratites nodosus (Bruguière), Middle Triassic, Germany. (i) Dinarites asiaticus Shevyrev, Lower Triassic (upper Scythian), USSR. (k) Procarnites kokeni (Arthaber), Lower Triassic (upper Scythian), USSR. (a-f, h from Schindewolf, 1968; g from Wiedmann, 1969; i, k from Shevyrev, 1968).

seam. This does not apply to *Procarnites* (Fig. 12k) which shows asymmetrical Suturallobenbildung and was placed in the Proptychitaceae by Shevyrev.

Also the Ptychitaceae (Sturia, Fig. 13a) have a symmetrical Suturalloben bildung within  $U_3$  and can also be placed close to the forms mentioned above. Separation is possible due to a stronger



Fig. 13. Adult sutures of Triassic Phylloceratida and Triassic-Cretaceous Lytoceratina. (a) Longobardites caucasicus (Shevyrev), Middle Triassic (upper Anisian), USSR. (b) Paralobites nautilinus (Münster), Upper Triassic (lower Carnian), Tyrol. (c) Megaphyllites prometheus Shevyrev, Middle Triassic (upper Anisian), USSR. (d) Arcestes bicarinatus (Münster), Upper Triassic (lower Carnian), Tyrol. (e) Sturia sansovinii (Mojsisovics), Middle Triassic (Anisian), USSR. (f) Trachyphyllites costatus Arthaber, Upper Triassic (Norian), Timor. (g) Derolytoceras tortum (Quenstedt), Lower Jurassic (upper Pliensbachian), Germany. (h) Gaudryceras tenuiliratum Yabe, Upper Cretaceous (Senonian), Hokkaido. (i) Tetragonites subbeticus Wiedmann, Lower Cretaceous (upper Aptian), Balearics. (a, c, e, from Shevyrev, 1968; b, d, h from Schindewolf, 1968; f, g from Wiedmann, 1970a; i from Wiedmann, 1962c).

frilling of saddles and internal lobe. The ptychitids have this feature in common with the restricted Arcestidae (Fig. 13d), in which, however, no Suturallobus seems to be present. Moreover, Schindewolf (1968) documented a quinquelobate primary suture, adventitious lobes and a heterochronous  $U_n$  between  $U_1$  and I (as in stephanoceratids); therefore arcestids stand markedly apart from most suture types of Triassic ammonites in general known to be very uniform.



Fig. 14. Suture ontogeny of true lytoceratids with I<sub>s</sub> and subdivided U<sub>1</sub>: Lytoceras juilleti (D'Orbigny), Valangian, France (from Wiedmann, 1968).
[(a) primary suture; (e) adult suture at whorl height of 2 mm, stippled, septal lobe.]

Similarly, the Lobitidae (*Paralobites*, Fig. 13b) with lobe-splitting in L,  $U_2$  and  $U_1$  seem to occupy a special position. Pinacoceratids are not yet sufficiently investigated. It is noteworthy that the different types of the sutural development of the Jurassic and Cretaceous ammonites were already present among Triassic ammonoids.



Fig. 15. Adult sutures of Jurassic-Cretaceous Phylloceratina and Ammonitina.
(a) Phylloceras onoense (Stanton), Lower Cretaceous (Aptian), USA.
(b) Psiloceras psilonotum (Quenstedt), Lower Cretaceous (lower Hettangian), Germany. (c) Eoderoceras armatum (Sowerby), Lower Jurassic (upper Sinemurian), England. (d) Phricodoceras taylori (J. de C. Sowerby), Lower Jurassic (lower Pliensbachian), Germany. (e) Pseudolioceras compactile (Simpson), Lower Jurassic (upper Toarcian), Germany. (f) Hammatoceras insigne (Zieten), Lower Jurassic (upper



Toarcian), France. (g) Paroecotraustes tenuistriatus (Grossouvre), Middle Jurassic (upper Bathonian), Germany. (h) Tmetoceras scissum (Benecke), Middle Jurassic (lower Bajocian), Italy. (i) Dorsetensia sp., Middle Jurassic (middle Bajocian), Germany. (k) Haploceras grasianum (D'Orbigny), Lower Cretaceous (lower Valanginian), France. (a from Wiedmann, 1962b; b from Wiedmann, 1970a; c, d from Schindewolf, 1962; e-i from Schindewolf, 1964; k from Wiedmann, 1966a.)



Fig. 16. Adult sutures of Jurassic-Cretaceous Ammonitina. (a) Otoites sp. cf. O. tumulosus (Westermann), Middle Jurassic (middle Bajocian), England. (b) Chondroceras tenue (Westermann), Middle Jurassic (middle Bajocian), Germany. (c) Bullatimorphites sp. cf. B. microstoma uhligi (Popovici-Hatzeg), Middle Jurassic (upper Bathonian), Germany. (d) Pachyceras lalandeanum (D'Orbigny), Upper Jurassic (lower Oxfordian), France. (e) Parkinsonia sp. cf. P. parkinsoni (Sowerby), Middle Jurassic (upper Bajocian), Germany. (f) Spiroceras bifurcati (Quenstedt), Middle Jurassic (upper Bajocian), Germany. (g) Grossouvria



sulcifera (Oppel), Upper Jurassic (Callovian), Germany. (h) Oosterella stevenini (Nicklės), Lower Cretaceous (upper Valanginian), Spain. (i) Eodesmoceras celestini (Pictet and Campiche), Lower Cretaceous (Valanginian), Switzerland. (k) Neosilesites balearensis (Fallot), Lower Cretaceous (upper Aptian), Balearics. (l) Lyelliceras lyelli (Leymerie in D'Orbigny), Lower Cretaceous (middle Albian), France. (a-e from Schindewolf, 1965; f from Schindwolf, 1961; g from Schindewolf, 1966; h, i from Wiedmann, 1966a; k, l from Widemann, 1966b.)

(b) Lytoceratida. In the light of the suture evolution the Lytoceratida appear to be very conservative. As already mentioned, the formation of a septal lobe  $(I_s)$  is the qualitatively new feature of this group and is found to occur as early as the Early Jurassic. The typical lytoceratid suture formula  $ELU_2U_{1v}U_{1d}I_s$  is formed by the combination of this feature with the subdivision of  $U_1$  (Figs 13f-i, 14). In gaudryceratids (Fig. 13h), an extended suspensive lobe in  $U_1$  first occurs, proceeding into a Suturallobenbildung in  $U_4$  in tetragonitids (Fig. 13i), which may indicate a certain convergence towards the phylloceratids.

The root stock of Ammonitina, the psiloceratids (Fig. 15b) combine characters of phylloceratids (sub-lituid I) and lytoceratids (subdivided  $U_1$ , no typical Suturallobenbildung, frilled saddles). We can imagine that psiloceratids originated at or near the point of divergence of the two main groups, phylloceratids and lytoceratids. The Upper Triassic *Phyllytoceras* was described (Wiedmann, 1970a) as a possible ancestor of Liassic psiloceratids. All younger Neoammonites can be easily linked to the psiloceratids (Schindewolf, 1961–1968). "Eoderocerataceae" have been included into Psilocerataceae due to an identical suture ontogeny and formula (*Eoderoceras*, Fig. 15c; *Phricodoceras*, Fig. 15d). Fusion of the subdivided  $U_1$  occurs in late forms of both groups.

Based on the supposition that a secondarily fused  $U_1$  may not split again, Schindewolf regarded the Hildocerataceae, the Hammatocerataceae and, finally, the Haplocerataceae to be diphyletic. We believe, however, that this feature (as well as Suturallobenbildung) is not as stable as Schindewolf thought and that reversions occured as mentioned above (Fig. 11).

While typical hildoceratids (*Pseudolioceras*, Fig. 15e) show a considerable proliferation of umbilical lobes (up to a dozen of U lobes) and an undivided  $U_1$ , true hammatoceratids (Fig. 15f) exhibit a subdivided  $U_1$  combined with an inferior number of (about four) umbilical lobes. Sutural reduction may, however, occur (*Tmetoceras*, Fig. 15h).

Haploceratid sutures (Fig. 15k) and oppeliid sutures (*Paroeco-traustes*, Fig. 15g), are closely similar in a further increase of umbilical lobe number; in true oppeliids the number can pass 13 lobes in combination with a subdivision of  $U_1$ ; in true haploceratids 10 umbilical lobes may occur in addition to an undivided  $U_1$ . The suture of Phlycticeratidae is found to be comparable with that of oppeliids,



Fig. 17. Suture ontogeny of stephanoceratids with  $U_n$  and subdivided  $U_1$ : Otoites sp. cf. O. tumulosus Westermann, Middle Jurassic (middle Bajocian), England (from Schindewolf, 1965). [(a) primary suture; (g) adult suture at whorl height of 2.5 mm; (i) at height of 5.8 mm.]

the sutures of Strigoceratidae and Cretaceous Mazapilinae and Aconeceratinae, however, are identical with that of haploceratids.

The Otoitidae (Figs 16a, 17), the first representatives of the Stephanocerataceae, also show a subdivided  $U_1$ , indicating (*teste* Schindewolf) their origin in the hammatoceratids. This subdivision

of  $U_1$  is abandoned in the simultaneously appearing Stephanoceratidae and all other members of this superfamily (Bullatimorphites, Fig. 16b). Nevertheless, most of these forms are united by the late appearance of a heterochronous  $U_n$  in the saddle  $U_1I$ . This exceptional type of lobe ontogeny is reproduced in Fig. 17. Lobe pictures of stephanoceratids published by Schindewolf (1965) suggest that this uncommon suture element may perhaps be a heterochronous  $U_{1d}$ . This would explain why an  $U_n$  was never found in the closely related Perisphinctaceae, with an almost universally present subdivided  $U_1$ . This would solve perhaps the problem of Parkinsoniidae (Fig. 15e), included by Schindewolf (1965) because of the  $U_n$  to the stephanoceratids, and would make the derivation of perisphinctids from stephanoceratids more likely than that from hammatoceratids (Schindewolf, 1966). In late stephanoceratids  $U_n$  again disappears (Bullatimorphites, Fig. 16c; Pachyceras, Fig. 16d).

Thus, in contrast to the very homogeneous Perisphinctaceae, the Stephanocerataceae show a notably large variation in configuration of sutures.

The Spiroceratidae (Fig. 16f) with their curious ontogenetic lobe reduction from a quinquelobate primary suture to a trilobate adult one  $(EU_2I)$  were generally placed in the descendence of parkinsoniids (Schindewolf, 1951; Dietl, 1978). Perisphinctaceae exhibit a reduced Suturallobenbildung in  $U_4$  (Grossouvria, Fig. 16g) in their majority;  $U_1$  is subdivided at first, but becomes fused in most of the Cretaceous members (Oosterella, Fig. 16h). In their suture formula  $ELU_2(U_3 = S)U_1I$  Holcodiscidae show closer affinity to perisphinctids than to desmoceratids.

Early Cretaceous democeratids (Eodesmoceratinae) probably have an undivided  $U_1$  and up to ten umbilical lobes (Fig. 16i). They can thus be related with the earlier haploceratids and with the later pulchelliids and acanthoceratids (*Lyelliceras*, Fig. 16l). In late Acanthocerataceae the formation of A-lobes in Sphenodiscidae is a slight derivation from this scheme. All younger desmoceratids (Desmoceratinae, Puzosiinae, Silesitidae, Kossmaticeratidae, Pachydiscidae) and, finally, most of the Hoplitaceae show a subdivided  $U_1$  and Suturallobenbildung in  $U_4$  (i.e. *Neosilesites*, Fig. 16k). This means that in this case no more than four U-lobes were built. Concerning their suture types Desmocerataceae and Hoplitaceae cannot be separated.



Fig. 18. Suture ontogeny of Cretaceous heteromorphs: Leptoceras studeri (Ooster), Berriasian, Switzerland (from Wiedmann, 1969). [(a) primary suture; (h) adult suture at whorl height of 3.5 mm.]

It may be open to question whether these desmoceratids and the complete bulk of Cretaceous ammonites have been descended from the haploceratids or from the perisphinctids (as Schindewolf, 1966 assumed); in any case, the Ammonitina of the Jurassic and Cretaceous constitute a monophyletic unit. Iterative evolution from the phylloceratid and/or lytoceratid root stock could not be confirmed. Transitions between lituid and frilled internal lobes do not occur (Wiedmann, 1962b).

A subject of special interest which illustrates the overriding importance of lobe ontogeny is that of the last group of Cretaceous



Fig. 19. Suture ontogeny of scaphitids: Scaphites hippocrepis (Dekay), Campanian, USA (from Reeside, 1927).

ammonites, the so-called Cretaceous heteromorphs and their derivatives. In contrast to their widespread interpretation as a polyphyletic collection of phylogenetic end forms, all these forms have been shown to be characterized by a quadrilobate primary suture. This suggests a monophyletic origin, although Mikhailova (1977, 1978) recently described some related forms with the original quinquelobate primary suture of neoammonoids, immediately followed by the reduced quadrilobate suture. This is the suborder Ancyloceratina.

The restricted true heteromorphs, the Ancylocerataceae (and Turrilitaceae) keep their original quadrilobate suture (*ELUI*) throughout life (Fig. 18).

Scaphitaceae also exhibits a quadrilobate primary suture. The U remains in the internal portion of the suture and becomes subdivided.



Fig. 20. Phylogeny of adult sutures and conch shape evolution in scaphitids (from Wiedmann, 1965).



Fig. 21. Phylogeny of adult sutures and conch shape evolution in douvilleiceratids (from Wiedmann, 1966b).

This means that the only persisting U of the heteromorphs might be homologous with the previous  $U_1$ . The previously presumed regenerated lobes in the saddle LU of scaphitids (Schindewolf, 1961, 1968), however, are homologous with the saddle incisions of the root form



Fig. 22. Strategies of suture evolution in Cretaceous heteromorphs. I. Standard evolution of Cretaceous heteromorphs (Ancylocerataceae). II. Suture development by lengthening of saddle LU, insertion of "pseudolobes" (p) and subdivision of  $U_1$  (Scaphitaceae). III. Suture development by subdivision of the lobes L and U (Douvilleicerataceae). IV. Suture development by subdivision of saddle  $U_2$ ?I = lobe regeneration (Deshayesitaceae). (From Wiedmann, 1970c)

Eoscaphites. They were called pseudolobes and labelled p, but the lobe formula of Scaphitaceae remains thus  $ELU_v U_d I$ . Scaphitid suture ontogeny and phylogeny are reproduced on Figs 19, 20.

Within the recoiled Douvilleicerataceae (comprising the Cheloniceratidae, Parahoplitidae, Acanthohoplitidae, Astiericeratidae, Trochleiceratidae), quadrilobate sutures occur with subdivided elements L and U and a final formula  $EL_vL_dU_v:U_dI$ . Figure 5 compares sutural ontogeny and phylogeny of a member of this stock, the evolution of which is reproduced on Fig. 21.

At least, the recoiled Deshayesitaceae show a genuine lobe regeneration, according to the formula  $ELUI \rightarrow ELU_2$ ? $U_3$ ?: $U_1$ ?I (Fig. 22).

Figure 22 gives an impression of the independence of the sutural evolution from shell morphology. This is really one of the basic observations: only suture characters present a system of homologous elements, while all other characters of ammonoid conch and sculpture are liable to convergency.

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