THE A-MODE SUTURAL ONTOGENY IN PROLECANITID AMMONOIDS

by DIETER KORN, VOLKER EBBIGHAUSEN, JÜRGEN BOCKWINKEL *and* CHRISTIAN KLUG

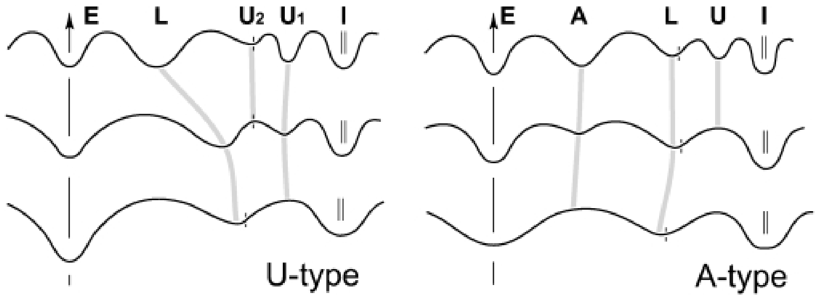
ABSTRACT. The generally accepted theory of a U-mode sutural ontogeny of prolecanitid ammonoids and their descendants is refuted. The basic suture formula of the order Prolecanitida is E A L U I (not E L U_2 U_1 I), resembling that of derived members of the suborder Tornoceratina (their phylogenetic ancestors), and of the suborder Goniatitina. During phylogeny of the prolecanitids, secondary umbilical lobes are introduced and lead to multilobate forms. In early ceratites, the original L lobe disappeared, and an increase in sutural elements took place by the introduction of supplementary U lobes. Consequently, sutural nomenclature of Permian ceratites and Mesozoic ammonoids has to be modified.

KEY WORDS: Carboniferous, Permian, Mesozoic, sutural ontogeny, ammonoids, Prolecanitida.

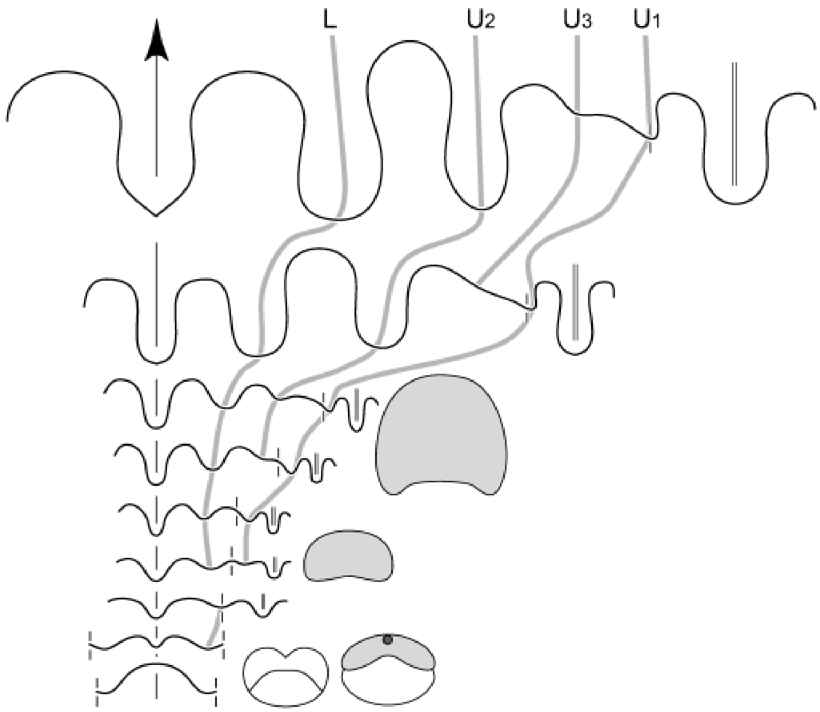
DISCRIMINATION of an A-mode (formation of an adventive lobe) and a U-mode [without adventive lobe, but with migration of the lateral (L) lobe towards the flank and formation of umbilical (U) lobes] sutural ontogeny in Palaeozoic ammonoids (Text-fig. 1) has been proposed as the most important criterion for subdividing the main Palaeozoic ammonoid groups (Schindewolf 1954; followed by Miller *et al.* 1957 and Ruzhencev 1960). The A-mode was regarded as a typical feature of the order Goniatitida, whereas the U-mode characterised the Devonian suborder Gephuroceratina as well as the Carboniferous and Permian suborder Prolecanitina. Both were formerly included in the order Agoniatitida, but this two-fold subdivision of Devonian and Carboniferous ammonoids is now regarded as outmoded. However, the principal subdivision into the orders Agoniatitida (or Anarcestida of other authors) with U-mode, and Goniatitida with A-mode sutural development was maintained by Russian palaeontologists into the late 1970s (e.g. Ruzhencev and Bogoslovskaya 1978). All Mesozoic ammonoids were, because of their interpreted origin from the prolecanitids, regarded as possessing a U-mode sutural ontogeny.

This classification, rooted in the investigations of Schindewolf (1929, 1951), was primarily based on the sutural ontogeny of the Early Mississippian prolecanitid genus *Michiganites* published by Karpinsky (1896) (Text-fig. 2). Its flank lobe has been interpreted as having an umbilical origin. This interpretation has been adopted by almost all subsequent authors (e.g. Ruzhencev 1960, although with another sutural terminology; see Kullmann and Wiedmann 1970, 1982) and has rarely been discussed. Doubts on the accuracy of the U-mode concept in prolecanitid ammonoids have been expressed in print only a few times (e.g. Kullmann and Wiedmann 1970). Spinosa *et al.* (1975) completely neglected the theory of U-mode development, regarding the prolecanitids as performing an A-mode ontogeny. However these researchers did not present unambiguous material to support their interpretation.

Vöhringer (1960) demonstrated that prolecanitid ammonoids derived from prionoceratid ancestors (order Goniatitida, suborder Tornoceratina) at the beginning of the Carboniferous, and constitute an independent evolutionary lineage. Consequently, the prolecanitid ammonoids have an origin fairly distant from the Devonian agoniatitids and must be separated from the order Agoniatitida. Both the prionoceratid ancestors (e.g. *Acutimitoceras*) and the earliest prolecanitids (e.g. *Eocanites*, *Becanites*) have the same number of sutural elements (Text-fig. 3), but the sutural formula has typically been specified as E A L U I in the prionoceratid and as E L U_2 U_1 I in prolecanitid ammonoids. These similarities allow doubt to be



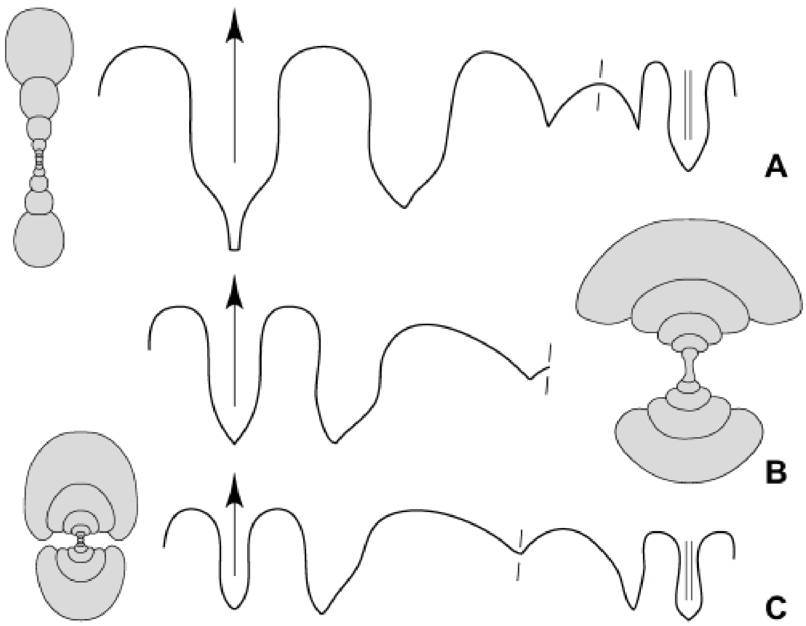
TEXT-FIG. 1. The U-mode (left) and A-mode (right) sutural development, as proposed by Schindewolf (1929, 1951, 1954) and Ruzhencev (1960). Redrawn after Ruzhencev (1960).



TEXT-FIG. 2. The ontogenetic development of the suture in *Michiganites asiaticus* (Karpinsky, 1896); whorl cross sections are arranged alongside the corresponding sutures. Redrawn after Karpinsky (1896).

cast on this commonly accepted classification. Hence the classical A-mode/U-mode theory is reconsidered and critically discussed in this paper. It will be shown that in well-preserved material of the early prolecanitid *Becanites*, collected from early Late Tournaisian rocks of the eastern Anti-Atlas of Morocco, these ammonoids display a sutural ontogeny which is characterised by an A-mode ontogeny, and that there remains no reason to maintain the theory of a U-mode sutural development in prolecanitid ammonoids.

All of the examined material is housed in the Museum für Naturkunde der Humboldt-Universität zu Berlin, catalogue numbers MB.C.3905, MB.C.3909, MB.C.3889–MB.C.3991, and MB.C.5339.

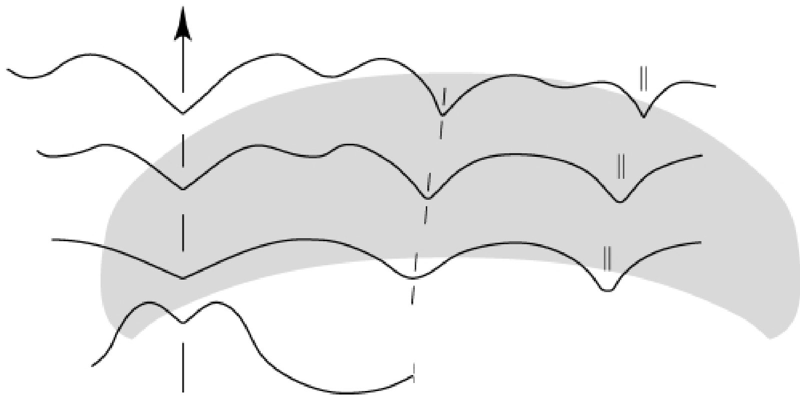


TEXT-FIG. 3. Suture lines and whorl cross sections in basal Carboniferous ammonoids. A, *Eocanites brevis* Vöhringer, 1960 and *Eocanites planus* (Schindewolf, 1926); cross section (×1·5) and suture line (at whorl height 7 mm; ×6); after Vöhringer (1960) and Korn (1994). B, *Gattendorfia costata* Vöhringer, 1960; cross section (×1·5) and suture line (at whorl height 13 mm; ×2·5); after Korn (1994). C, *Acutimitoceras subbilobatum* (Münster, 1832); cross section (×1·5) and suture line (at whorl height 15 mm; ×3); after Korn (1994).

THE CLASSICAL DISTINCTION OF AN A-MODE AND A U-MODE SUTURAL ONTOGENY

In his principal publication, Schindewolf (1929, p. 31) interpreted sectioned specimens of the genera *Tornoceras*, *Cheiloceras*, and *Reticuloceras* as showing an A-mode sutural ontogeny. All of these show a trilobate primary suture characterised by external (E), lateral (L), and internal (I) lobes. The four-lobed stage shows the introduction of a new lobe on the saddle between E and L. This adventive (A) lobe is formed between the tenth and the twenty-fifth suture line in Late Devonian genera; however, in *Reticuloceras* (early Pennsylvanian), it has already emerged in the second suture, seemingly due to heterochronic acceleration of sutural ontogeny. *Reticuloceras* thus recapitulates the sutural development of its Devonian ancestors. The fifth lobe, the umbilical (U) lobe, is then introduced, subdividing the saddle between L and I.

In contrast, Schindewolf interpreted sutural ontogenies of the Late Devonian genus *Manticoceras* and the Mississippian genera *Ammonellipsites* and *Merocanites* as being typical of the U-mode development. The primary suture likewise consists of three lobes (E, L, and I) with rounded saddles in between. The formation of additional lobes was defined by Schindewolf in contrast to the A-mode. The quadrilobate stage in *Manticoceras* shows a shallow lobe between the lateral and the internal lobe, which Schindewolf regarded as newly formed and consequently termed umbilical (U) lobe. The primary lateral lobe putatively migrates towards the flank. For *Ammonellipsites* and *Merocanites*, Schindewolf has shown a sutural development resembling that of *Manticoceras*. The difference between the two ontogenetic concepts concerns only the four-lobed stage and is solely based on the relative depth of the lobes between the external and the internal lobe (Text-fig. 1).



TEXT-FIG. 4. Early sutural ontogeny (prosuture and the three following sutures) of *Acutimitoceras* sp., specimen MB.C.5339 from Saalfeld, Thuringia, Germany (coll. Bartzsch and Weyer); ×45; the whorl cross section of the first stage is shaded; ×75.

SUTURAL DEVELOPMENT IN PRIONOCERATID AMMONOIDS

Early juvenile sutural ontogenies of prionoceratids were published by Schindewolf (1959, probably *Acutimitoceras* sp.) and House (1962, *Gattendorfia* (?) *louisianensis*). In *Acutimitoceras*, which can be regarded as ancestral to *Eocanites* (Vöhringer 1960; Korn 1994), the development from the trilobate primary suture towards the five-lobed sutural stage takes place on the second (four-lobed stage with the introduction of A) and third (introduction of U) sutures (Text-fig. 4). In this respect, *Acutimitoceras* is accelerated in comparison with the stratigraphically older *Torleyoceras* (Text-fig. 5B), and more closely resembles the Late Viséan *Lusitanoceras* (Text-fig. 5C), which, however, shows a longer three-lobed stage.

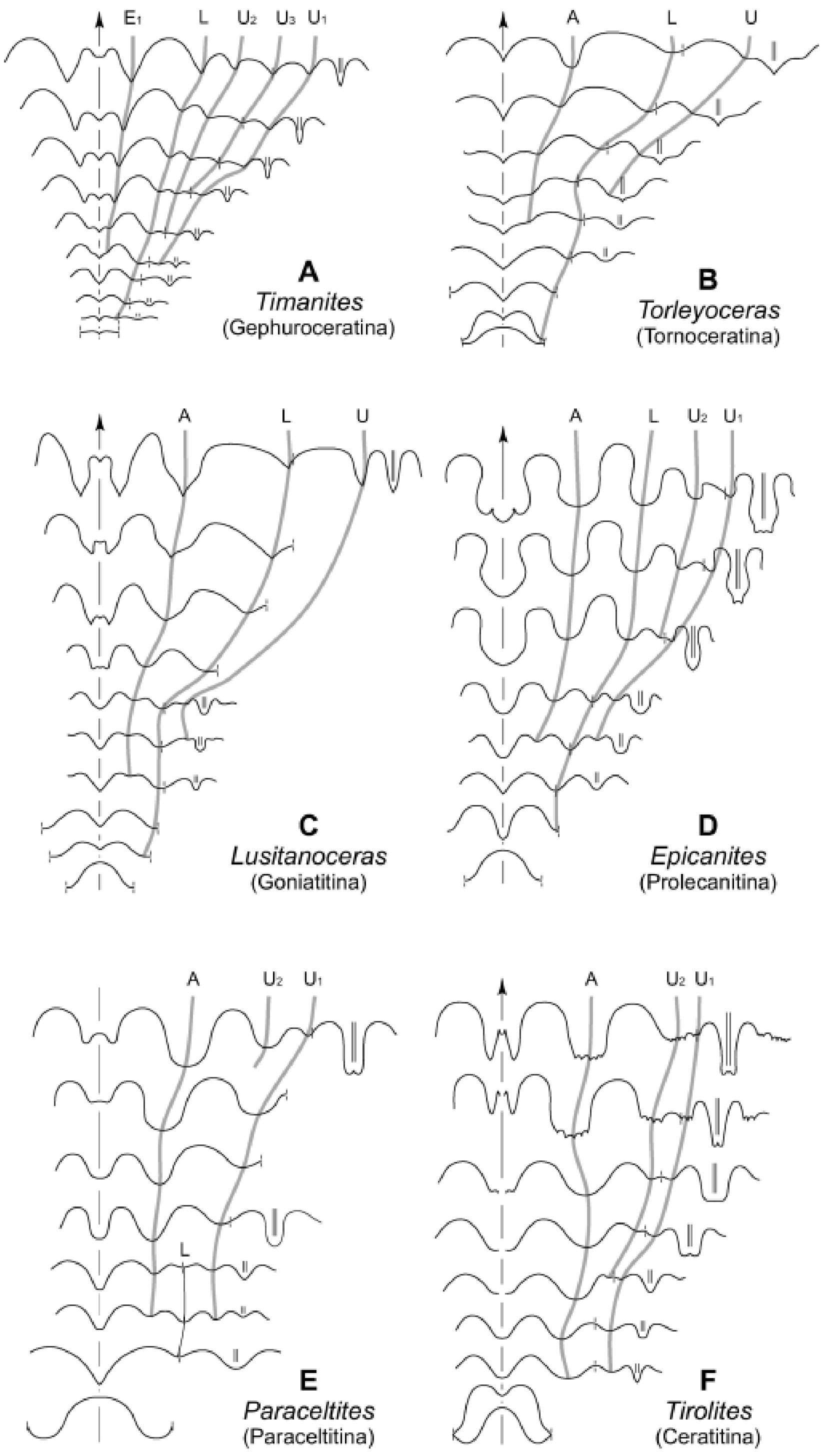
The similarity of position and shape of sutural elements in the earliest Carboniferous genera *Acutimitoceras*, *Gattendorfia*, and *Eocanites* (Text-fig. 3) suggests that all sutural elements are homologous. It follows that the sutures of *Eocanites* and all subsequent prolecanitids are, in principle, not constructed differently from *Acutimitoceras* and related prionoceratid genera such as *Gattendorfia*. Two tendencies in the development of the suture line can be observed in the proposed sequence *Acutimitoceras*–*Gattendorfia*/*Eocanites* (Text-fig. 3): (1) the lobes on flanks and venter (either A or E lobe) became modified from a V-shape to a lanceolate shape; (2) at the same time, the lateral lobe migrated towards the flank.

SUTURAL DEVELOPMENT IN PROLECANITID AMMONOIDS

Karpinsky's published figure of the sutural ontogeny in 'Prolecanites asiaticus'

In his frequently cited publication, Karpinsky (1896) published a detailed picture of the sutural ontogeny in his new species '*Prolecanites asiaticus*' (= *Michiganites asiaticus*). The figures (re-illustrated here in

TEXT-FIG. 5. Sutural ontogenies of different Devonian to Triassic ammonoids. A, *Timanites keyserlingi* Miller, 1938, Frasnian of the Timan; prosuture, first and second suture as well as development towards adult suture line; after Bogoslovsky (1969). B, *Torleyoceras balapanense* Bogoslovsky, 1971, early Famennian, Kazakhstan; prosuture, first and second suture line as well as development towards adult suture line; after Bogoslovsky (1971). C, *Lusitanoceras granosum* (Portlock, 1843), Late Viséan, Arkansas; prosuture, first suture, and development towards adult suture line; after Spinosa *et al.* (1975). D, *Epicanites loeblichi* Miller and Furnish, 1940, Late Viséan, Oklahoma; prosuture, first and second suture as well as development towards adult suture line; after Spinosa *et al.* (1975). E, *Paraceltites elegans* Girty, 1908, Roadian, Texas; prosuture, first to third suture as well as development towards adult suture line; after Spinosa *et al.* (1975). F, *Tirolites rossicus* Kiparisova, 1947, Scythian, South Russia; prosuture, first and second suture as well as development towards adult suture line; after Shevyrev (1968).


E1
L
U2
U3
U1
A
Timanites
(Gephuroceratina)
A
L
U
B
Torleyoceras
(Tornoceratina)
A
L
U
C
Lusitanoceras
(Goniatitina)
A
L
U2
U1
D
Epicanites
(Prolecanitina)
A
U2
U1
L
E
Paraceltites
(Paraceltitina)
A
U2
U1
F
Tirolites
(Ceratitina)

Text-fig. 2) are so accurate that there appeared to be little doubt regarding the correctness of the conclusion drawn from them.

The ontogenetic sutural development is characterised by a three-lobed primary suture and later stages in which additional lobes are introduced in the umbilical area. The adult sutural formula was interpreted by Ruzhencev (1949, p. 55) as V U U_1 U_2 I D (i.e. E L U_2 U_3 U_1 I in Wedekind's 1918 terminology). Since Karpinsky, no comparable detailed study on the sutural development of an early prolecanitid ammonoid has been published.

It is not easy, however, to interpret the figure provided by Karpinsky. The transformation from the three-lobed towards the four-lobed stage is ambiguous, allowing different possibilities of interpretation. Both Schindewolf (1929, 1951) and Ruzhencev (1949, 1960) interpreted the original lateral lobe as migrating towards the middle of the flanks, with a new umbilical lobe originating between the lateral and internal lobes. Further new lobes introduced near the umbilicus were then interpreted as umbilical lobes, thus giving the name for the U-mode sutural ontogenetic mode.

Schindewolf's figure of the sutural ontogeny in 'Merocanites applanatus'

Schindewolf's (1929, fig. 20) illustration of the sutural development in the late Tournaisian prolecanitid genus *Merocanites* was the second reason for the subsequent discrimination of a U-mode sutural ontogeny. However, this illustration suffers from the lack of exact documentation of the size in which the sutures were obtained from the specimen. Schindewolf only stated that the last shown suture was drawn from a specimen with a whorl height of 2·8 mm, i.e. a specimen of approximately 10 mm diameter.

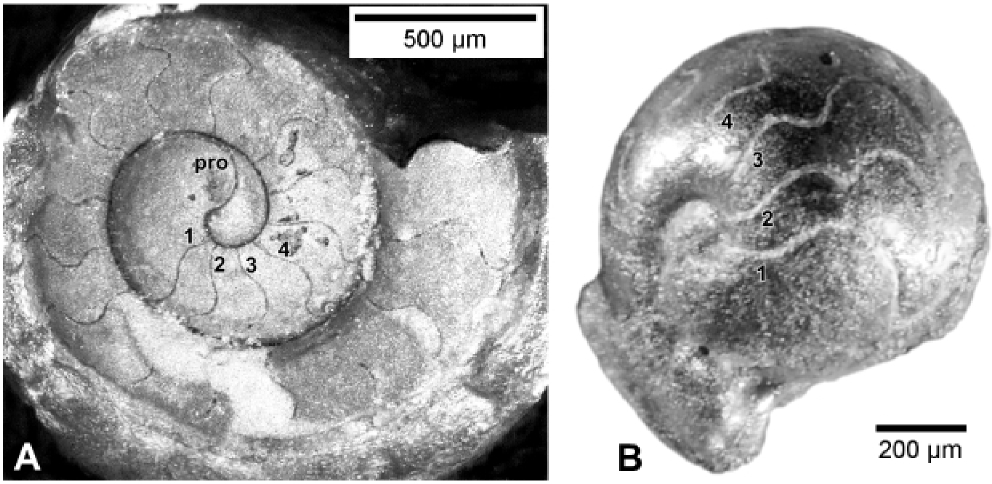
On his text-figure 20, the upper illustration probably shows the primary suture, consisting of the three primary lobes E, L, and I. The next, quadrilobate suture shows four lobes, which are termed E, L, U_I, and I. The U_I lobe is interpreted as a new element, originating from the former saddle between L and I. The third illustrated suture in the succession is then five-lobed, with another new lobe (U_{II}) that is supposed to originate by the subdivision of the saddle between L and U_I. Finally, the last sutural stage is six-lobed with another lobe (U_{III}) introduced between U_{II} and U_I.

Later, Schindewolf (1954, p. 134), when replying to doubts expressed by Schmidt (1952), admitted that the specimen on which he based his illustration of the sutural ontogeny was 'not particularly well preserved', and he incorporated Karpinsky's figure in his reillustration of the sutural ontogeny of *Merocanites*. Re-examination of the original material (long regarded as lost, but recently traced by Dieter Weyer, Berlin) could not confirm Schindewolf's (1929, fig. 20) interpretation. The specimen is in fact poorly preserved and does not allow an unambiguous interpretation.

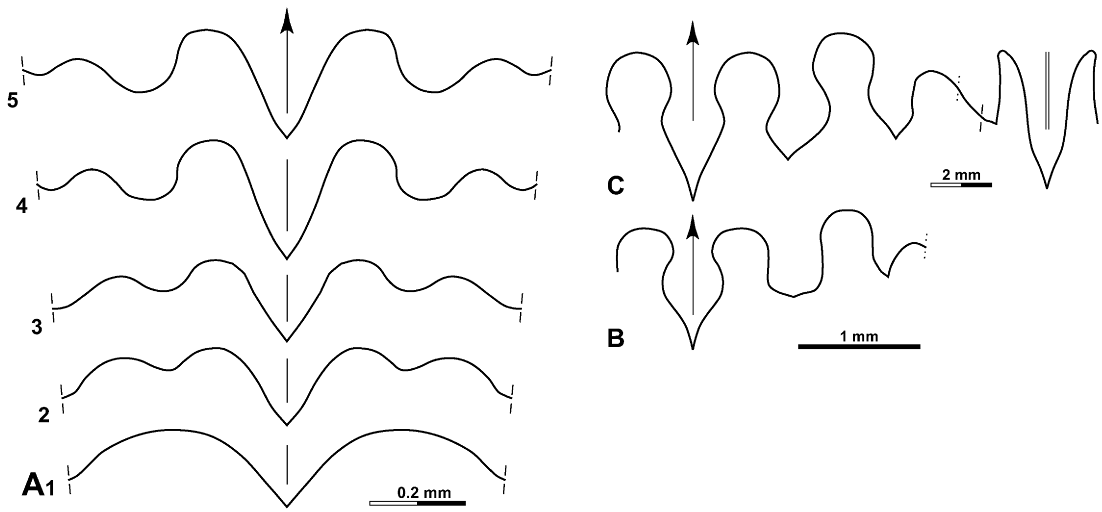
New early prolecanitid material from Morocco

A comparatively rich early Late Tournaisian ammonoid fauna was discovered by two of us (JB and VE; Korn *et al.* in press) near Taouz in the Anti-Atlas (Morocco). The material consists of more than 1250 specimens, of which approximately 180 belong to the new prolecanitid species *Becanites africanus* Korn *et al.*, 2003. All of the specimens are limonitic steinkerns and they often display the early ontogenetic development of the suture line (Text-fig. 6). Five specimens of *B. africanus* were intensively studied. The adult suture shows five lobes, as in the ancestral *Eocanites*, of which four have a lanceolate shape.

The dorsal portions of the sutures could not be prepared in the earliest whorls, but sutural ontogeny of the lateral and ventral portion can be seen in three specimens. The prosuture is simple with a very high, widely rounded external saddle. It is separated by a wide interspace (approximately one-third of a whorl) from the primary suture. This displays a shallow lobe near the umbilical seam and a big V-shaped external lobe (Text-fig. 7A), separated by a wide saddle that occupies the entire flank. The second suture shows a small midflank lobe in the wide midflank saddle. This lobe becomes continuously deeper within the subsequent suture lines and has, in the eighth suture, half the depth of the external lobe. On the first volution, the lobe near the umbilical seam migrates slowly to a dorsolateral position, whereas the midflank lobe remains stable in its position. This suggests that the second suture already shows the eight lobes of the adult conch. There is no migration of a lobe from the umbilicus to the midflank. Sutural ontogeny of



TEXT-FIG. 6. Micrographs of two specimens of *Becanites africanus* Korn *et al.*, 2003 from Ksar Bouhamed, Tafilalt, Morocco. A, specimen MB.C.3989 (coll. Klug); specimen with two whorls; note the long interspace between the prosuture and the primary suture; ×48. B, specimen MB.C.3990 (coll. Bockwinkel and Ebbighausen); specimen with one whorl; prosuture not visible; note the introduction of the adventive lobe in the second suture; ×60.



TEXT-FIG. 7. Sutural ontogeny of *Becanites africanus* Korn *et al.*, 2003 from Ksar Bouhamed, Tafilalt, Morocco. A, early sutural ontogeny of specimen MB.C.3991. 1, primary suture; 2, second; 3, third; 4, fifth; and 5, eighth suture; ×63. B, suture of paratype MB.C.3905 at diameter 4·8 mm, whorl width 1·8 mm, whorl height 1·55 mm; ×16. C, suture of paratype MB.C.3909 at whorl width 6·9 mm, whorl height 7·9 mm; ×4.

Becanites resembles that of *Acutimitoceras*, i.e. with an external (E), an adventive (A), and a lateral (L) lobe (compare Text-figs 4 and 7). The only difference is that the lateral lobe migrated a short distance to the inner flank.

The pre-adult and adult sutures are characteristic for the genus *Becanites* (Text-fig. 7B–C). The external lobe is extremely large and bulb-shaped; this is otherwise known only from stratigraphically younger and more derived descendent genera such as *Michiganites* Ruzhencev, 1962 and *Prolecanites* Mojsisovics,

1882. The adventive lobe and the lateral lobe, which are both located on the flank, are pouched and pointed at the bottom.

Hodgkinson's figure of the sutural ontogeny in Epicanites loeblichi

Hodgkinson's (1965) unpublished sutural ontogeny of *Epicanites loeblichi* Miller and Furnish, 1940 was later published by Spinosa *et al.* (1975). It displays three-lobed first and second sutures, and a five-lobed third suture. Later in ontogeny, a second U lobe is introduced on the ventral flank of the primary U lobe (Text-fig. 5D). The lateral lobe, which has a position on the umbilical seam in the first sutures, migrates towards the inner flank. Like the ancestral *Becanites*, *Epicanites* possesses a trilobate primary suture. Further sutural development is very similar with the exception of a supplementary umbilical lobe that is not developed in *Becanites*.

SUTURAL DEVELOPMENT IN CERATITID AMMONOIDS

The ancestry of the Permian ceratites is not clear, but it is generally assumed that they derived from prolecanitid ammonoids (Spinosa *et al.* 1975). However, according to the sutural ontogeny in the ancestral ceratid *Paraceltites elegans* Girty, 1908, it cannot be determined if an origin of ceratites from prolecanitid or goniatitid ammonoids is more likely.

Spinosa *et al.* (1975) demonstrated that in the ancestral ceratitid genus *Paraceltites* the sutural development shows a complete reduction of the lateral lobe (L lobe) during early ontogeny. The missing lobe is not replaced, but a new lobe formed near the umbilicus (Text-fig. 5E). Consequently, the suture formula changes from E L I (primary suture) to E A L U I (second and third suture) to E A U I (subsequent sutures), and finally E A U_1 U_2 I (mature suture).

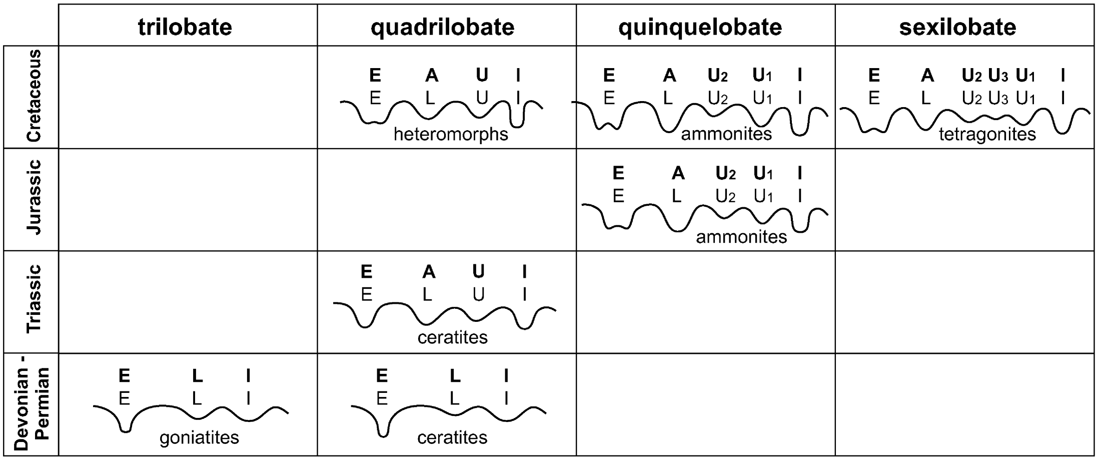
The Triassic ceratitid genus *Tirolites* does not perfectly recapitulate the sutural development seen in *Paraceltites*. The five-lobed stage of very juvenile *Paraceltites* is omitted (Text-fig. 5F); and the second, four-lobed suture may represent the four-lobed stage of *Paraceltites* after reduction of the lateral lobe. The sutural formula in *Tirolites* may thus be E A U I. *Tirolites* displays only an adult five-lobed suture (Shevyrev 1968) with the formula E A U_2 U_1 I, as in *Paraceltites*.

CONSEQUENCES FOR AMMONOID SUTURE TERMINOLOGY

Most authors have adopted the sutural classification introduced by Schindewolf (1929, 1951, 1954), and accepted a principal difference between an A-mode and a U-mode sutural development. His terminology thus stated that sutures of the order Goniatitida have to be described as E A L U I, while those of the orders Prolecanitida, Ceratitida, Phylloceratida, Lytoceratida, Ancyloceratida, and Ammonitida have to be termed E L U_2 U_1 I (Kullmann and Wiedmann 1970). Our findings demonstrate that this nomenclature can no longer be supported.

Consequences for ammonoid sutural terminology are as follows:

1. Agoniatitida. No consequence; according to Schindewolf (1929) and Bogoslovsky (1969), gephuroceratids definitely show a U-mode sutural ontogeny (Text-fig. 5A). However, it is a matter of interpretation whether the tripartite ventral lobe is termed E_1 E_m E_1, as usually accepted, or A E A, i.e. with the secondary lobes interpreted as adventive lobes.
2. Goniatitina. No consequences; the order is characterised by an A-mode sutural ontogeny.
3. Prolecanitida. The five principal sutural elements are E A L U I (and not E L U_2 U_1 I). Addition of further umbilical lobes is a common feature (only *Eocanites*, *Becanites*, and *Protocanites* have five lobes). In the superfamily Medlicottiaceae, the adventive lobe is subdivided.
4. Permian Ceratitida. Regardless of their origin, either from prolecanitids or goniatitids, the basic suture has the elements E A L U I. The loss of the lateral lobe and addition of a second umbilical lobe results in a sutural formula E A U_2 U_1 I.
5. Mesozoic Ammonoidea. The primary suture of Triassic Ceratitida is E A L I. According to heterochronic acceleration, the primary suture of Jurassic and Cretaceous ammonites has five lobes, E A U_2 U_1 I, rather than E L U_2 U_1 I as commonly accepted.



TEXT-FIG. 8. Primary sutures of ammonoids with their traditional and reinterpreted sutural formulae, lower and upper (bold) lines respectively.

Taking these data into account, the primary sutures of the ammonoids have to be termed as follows (Text-fig. 8): (1) trilobate (Palaeozoic orders Goniatitida, Prolecanitida, Ceratitida): E L I; (2) quadrilobate (Triassic Ceratitida and Cretaceous heteromorphs): E A U I; (3) quinquelobate (Jurassic and most Cretaceous ammonoids): E A U_2 U_1 I; (4) sexilobate (Cretaceous tetragonites): E A U_2 U_3 U_1 I.

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REFERENCES

BOGOSLOVSKY, B. I. 1969. Devonskie ammonoidei. I. Agoniatity. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **124**, 1–341.

—— 1971. Devonskie ammonoidei. II. Goniatity. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **127**, 1–228.

HODGKINSON, K. A. 1965. The Late Paleozoic ammonoid families Prolecanitidae and Daraelitidae. Unpublished PhD dissertation, University of Iowa, 232 pp.

HOUSE, M. R. 1962. Observations on the ammonoid succession of the North American Devonian. *Journal of Paleontology*, **36**, 247–284.

KARPINSKY, A. P. 1896. O nakhozhdenii v Asii *Prolecanites* i o razvitii ehtogo roda. *Izvestiya Imperatorskoy Akademii Nauk*, **4** (2), 179–194.

KORN, D. 1994. Oberdevonische und unterkarbonische Prionoceraten aus dem Rheinischen Schiefergebirge. *Geologie und Paläontologie in Westfalen*, **30**, 1–85.

—— BOCKWINKEL, J., EBBIGHAUSEN, V. and KLUG, C. 2003. An early Late Tournaisian (Early Carboniferous) ammonoid fauna from the Tafilalt of Morocco and its palaeobiogeographical implications. *Acta Palaeontologica Polonica*, **48**, 71–92.

KULLMANN, J. and WIEDMANN, J. 1970. Significance of sutures in phylogeny of Ammonoidea. *University of Kansas, Paleontological Contributions*, **47**, 1–32.

—— 1982. Bedeutung der Rekapitulationsentwicklung in der Paläontologie. *Verhandlungen des Naturwissenschaftlichen Vereins Hamburg, Neue Folge*, **25**, 71–92.

MILLER, A. K., FURNISH, W. M. and SCHINDEWOLF, O. H. 1957. Paleozoic Ammonoidea. L11–L79. *In* MOORE, R. C. (ed.).

Treatise on invertebrate paleontology, Part L, Mollusca 4, Cephalopoda, Ammonoidea. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 490 pp.

RUZHENCEV, V. E. 1949. Sistematika i evolyutsia semeystv Pronoritidae Frech i Medlicottiidae Karpinsky. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **19**, 1–206.

—— 1960. Printsipy sistematiki, sistema i filogeniya paleozoyskikh ammonoidey. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **133**, 1–331.

—— and BOGOSLOVSKAYA, M. F. 1978. Namyurskiy etap v evolyutsii ammonoidey. Pozdnenamyurskie ammonoidei. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **167**, 1–336.

SCHINDEWOLF, O. H. 1929. Vergleichende Studien zur Phylogenie, Morphologie und Terminologie der Ammoneen-Lobenlinie. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge*, **115**, 1–102.

—— 1951. Zur Morphogenie und Terminologie der Ammoneen-Lobenlinie. *Paläontologische Zeitschrift*, **25** (1/2), 11–34.

—— 1954. Über die Lobenlinie der Ammonoidea. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1954**, 123–140.

—— 1959. Adolescent cephalopods from the Exshaw formation of Alberta. *Journal of Paleontology*, **33**, 971–976.

SCHMIDT, H. 1952. *Prolobites* und die Lobenentwicklung bei Goniatiten. *Paläontologische Zeitschrift*, **26**, 205–217.

SHEVYREV, A. A. 1968. Triasovye ammonoidei yuga SSSR. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **119**, 1–272.

SPINOSA, C., FURNISH, W. M. and GLENISTER, B. F. 1975. The Xenodiscidae, Permian ceratoid ammonoids. *Journal of Paleontology*, **49**, 239–283.

VÖHRINGER, E. 1960. Die Goniatiten der unterkarbonischen *Gattendorfia*-Stufe im Hönnetal (Sauerland). *Fortschritte in der Geologie von Rheinland und Westfalen*, **3** (1), 107–196.

WEDEKIND, R. 1918. Die Genera der Palaeoammonoidea Goniatiten). Mit Ausschluß der Mimoceratidae, Glyphioceratidae und Prolecanitidae. *Paläontographica*, **62**, 85–184.

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