

## THE HETEROMORPHS AND AMMONOID EXTINCTION

By JOST WIEDMANN

*Geologisch-Paläontologisches Institut, Universität Tübingen*

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## I. INTRODUCTION

The image of heteromorph ammonoids is today linked in our minds with notions of aberrant shell form, degeneration, typolysis and phylogenetic extinction. In most palaeontological works dealing with evolutionary principles the so-called heteromorphs are seen as a welcome illustration of the more or less synchronous extinction of complete *Baupläne*, a phenomenon which cannot be observed in nature and is therefore explicable only with difficulty.

'There are furthermore aberrant forms which rapidly, one after another, show an ever stronger tendency to degenerate and produce biologically absurd structures which, if not directly lethal, have always been impartially understood as ridiculous for the basic concept of the ammonite form.' (Translated from Dacqué, 1935, p. 32.)

'Just as the great ceratitoid group of ammonoids produced retrogressive as well as stationary and progressive forms during the Trias, so from one, or several, of the families just mentioned there arose decadent lines of descent. . . Thus in *Baculites* the whole organization was affected by decadent influences, and it is therefore the most perfect impression of all-round retrogression among the ammonoids.' (Swinnerton, 1930, pp. 216 f.)

'It is of particular significance that the aberrant shell types with gastropod-type spirals and loosed whorls only appear in greater numbers in the crisis periods of ammonite development. . . The forms involved constitute short-lived peripheral lineages originating in evolutionary groups shortly before their extinction. It is therefore most likely by far that internal grounds are decisive for this extravagance of forms, which is, moreover, often found at the end of lineages undergoing extinction and commonly shows no sign of being adaptive. One may think of a senility of the stock or of a gradual decline of the strong determined form-control or of what one will; in any case no external factors are determinate. Against the interpretation of the peripheral lineages as results of adaptation is, in addition, their transience in

comparison with the longevity of their parent stocks.' (Translated from Schindewolf, 1936, pp. 74 f.)

'A survey of the development of the shelly cephalopods, above all the ammonoids, shows that in the last phase of their evolution, in the late Cretaceous, a hypertrophic transformation and dissolution of the shell type occurs (*Baculites*, *Scaphites*, *Crioceras*, etc.), and that the sculptural elements also to some extent show a hypertrophic dissolution (*Douvilleiceras*, *Inflatoceras*).' (Translated from Beurlen, 1937, p. 87.)

'Of extreme interest are the indications of degeneration of the cephalopods. Apart from the size excesses already mentioned they are manifest in a dissolution of the normal spiral coil, as well as in the imitation of ancient groups.' (Translated from Erben, 1950, p. 120.)

'In the course of the typolysis [of the ammonites], which appears above all at the end of the last phase of vitality, the obedience to form embodied in the type again becomes weak. Numerous indications of decline and degeneration are to be seen. Particularly characteristic are regressive processes which to some extent "throw to the wind" that which was created by progressive evolution.' (Translated from Müller, 1955, pp. 16 f.)

As is clear from these selected quotations, evolution has been credited with a certain endogenic rhythm comparable to the process of individual life. This view is most clearly expressed in O. H. Schindewolf's typrostrophy theory (1945, 1950a), for which the heteromorph ammonoids are, indeed, an essential support. Schindewolf's typrostrophic scheme with its early evolutionary typogenesis, typostasis, and late evolutionary typolysis is almost a faithful copy of the ammonoid phylogeny: the explosive burst of forms in the early Devonian, the continuous differentiation of forms in the late Palaeozoic and Triassic, a first extravagance of forms beneath the Triassic/Jurassic boundary, before which we suddenly find the first heteromorphs in immediate association with the extinction of all Triassic Ceratitina, and finally the ultimate morphological degeneration or typolysis before the conclusive extinction of the class on the Cretaceous/Tertiary boundary. Typolysis is accordingly completed automatically, the extinction it predicts being inevitable.

'The reason for the extinction of the morphologically so varied Triassic ammonites on the boundary to the Jurassic must be sought in the internal organization of the animal since external factors of the environment do not come into consideration. . . The extinction is preceded by *overspecialization* and *indications of senility* of the most different kinds. The so stable and strenuously maintained basic form of a shell coiled in a plane spiral degenerates. . . Moreover, after the younger ammonites have experienced a *phase of explosive development* and a long *period of gradually advancing specialization* they also arrive at a *phase of overspecialization and extravagance of forms*, quite analogous to the Triassic representatives. The nearer we approach the upper boundary of the Cretaceous and the final extinction of the ammonite stock, the more often do we encounter degenerate forms.' (Translated from Schindewolf, 1950a, pp. 168 ff.)

It is perhaps of historic interest that Haeckel postulated as early as 1866 an analogous tripartite pattern of phylogenetic development and described it with the terms *Epacme*, *Acme* and *Paracme*. It is then noticeable—at least in the German-speaking world—that the question of endogenic rhythms, phases or rules of evolution was especially actively discussed in the 1920s and 1930s (Wedekind, 1920; Abel, 1929; Hennig, 1929, 1932; Beurlen, 1930, 1937; Dacqué, 1935; Schindewolf, 1936, 1937). This might cause one to consider how far Spengler's *Morphologie der Weltgeschichte*, as the

*Untergang des Abendlandes* (1918–1922) is subtitled, might have also influenced thinking in the natural sciences.

Now that not only the German-language *Lehrbuch der Paläozoologie* (Müller, 1957, 1963), but also standard zoological works have taken over the typostrophic scheme (Osche, 1966) or modified it (Rensch, 1947), it seems necessary to summarize the recent views of the phylogenetic significance of the heteromorph ammonites; indeed, the more so now that the heteromorph forms of other invertebrate groups (e.g. lamellibranchs, gastropods, brachiopods, trilobites and crinoids) have proved on closer examination not to be degenerative but special, and often very successful, adaptive trends.

Thus, with the Triassic, Jurassic and Cretaceous heteromorphs as examples, the validity of the following questions, contained in the introductory quotations and implicit in the conception of typolysis, will be examined here:

(1) Do the heteromorphs really appear (*a*) iteratively and (*b*) explosively at the end of different evolutionary lineages?

(2) Is their development irreversible?

(3) Are we really dealing with short-lived, degenerative or overspecialized forms, in other words forms of negative selective value, which have lost the ability to adapt or change and are therefore condemned to extinction?

A positive answer to these premises would necessarily imply not only purely biologically endogenic guidance of evolution, but also a contradiction to the Darwinian selection theory which can give no explanation of the appearance of such selectively negative organisms. Reflexion on these problems inevitably leads to criticism of Dollo's 'law' of the irreversibility of evolution and to another new model for the cause of the phylogenetic extinction of the ammonoids—and numerous other groups—at the end of the Mesozoic.

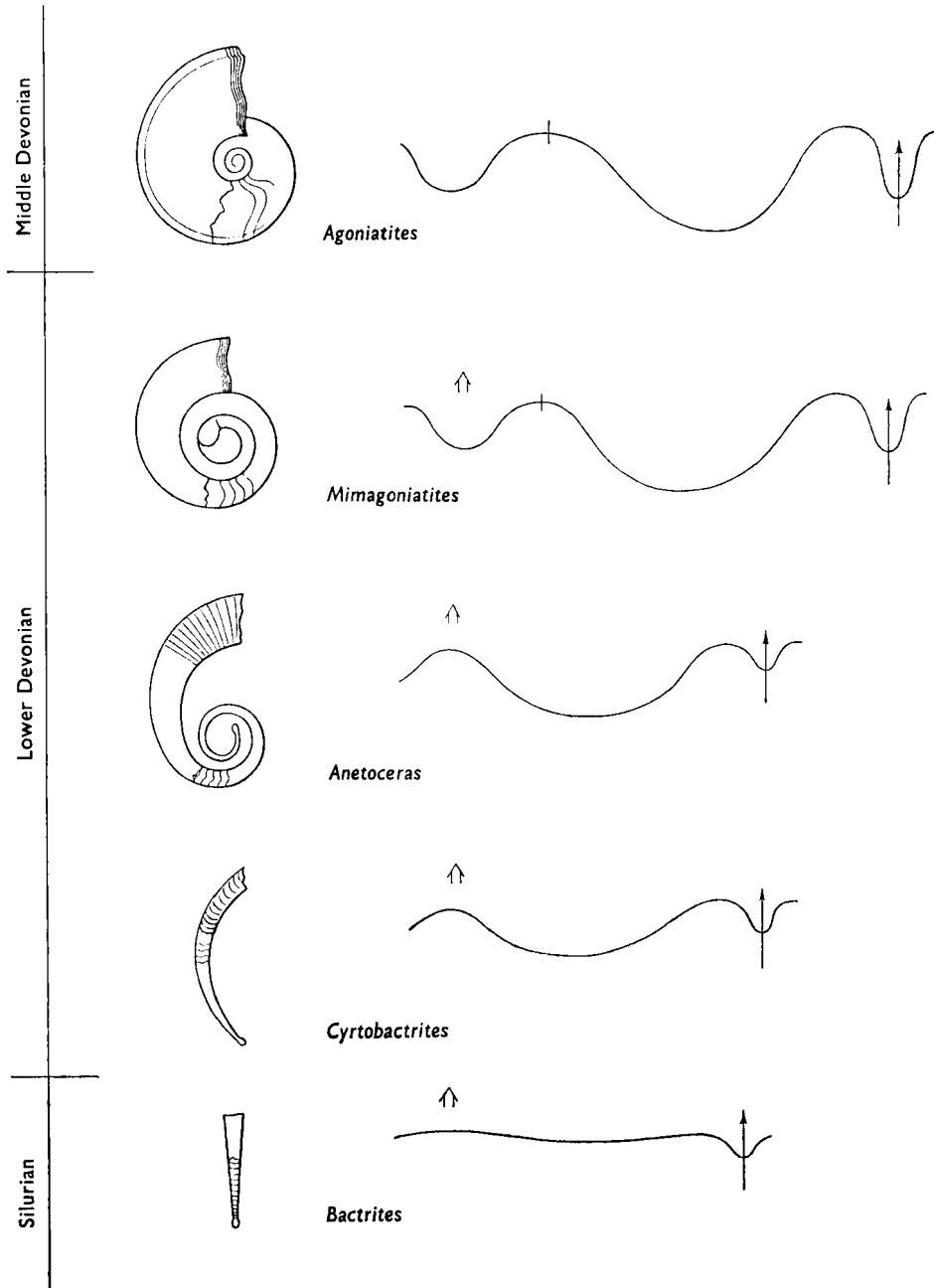
## II. DISCUSSION

The disconnected and iterative origin of heteromorph shells must apparently be admitted.

At this point it must be said that heteromorphs are here understood as only those aberrant forms in which a clear unrolling of either the whole or at least a part of the shell occurs. The weak scaphitoid unrolling of the living chamber which has been noted in many systematic groups (Wiedmann, 1965, fig. 13), can be disregarded in the present context.

Apart from the 'typogenesis' of the ammonoids in the early Devonian, which we must visualize as a continuous sequence originating from straight-shell forms (Text-fig. 1), heteromorph ammonite groups are known from the late Triassic, the middle Jurassic and especially from Cretaceous beds. In the ammonoid hand-books the Cretaceous heteromorphs especially are regarded as either the unrelated derivatives of different lineages (Spath, 1922; Roman, 1938; Luppov & Drushtchic, 1958) or the iterative descendants of a single stock, the lytoceratids (Basse, 1952; Arkell, 1957; Wright, 1957). Not only those in the Cretaceous but also the convergent forms in the Triassic and Jurassic seem to have appeared without warning; only from the early Cretaceous are transitional forms known: those described by Pictet (1863) between normally coiled

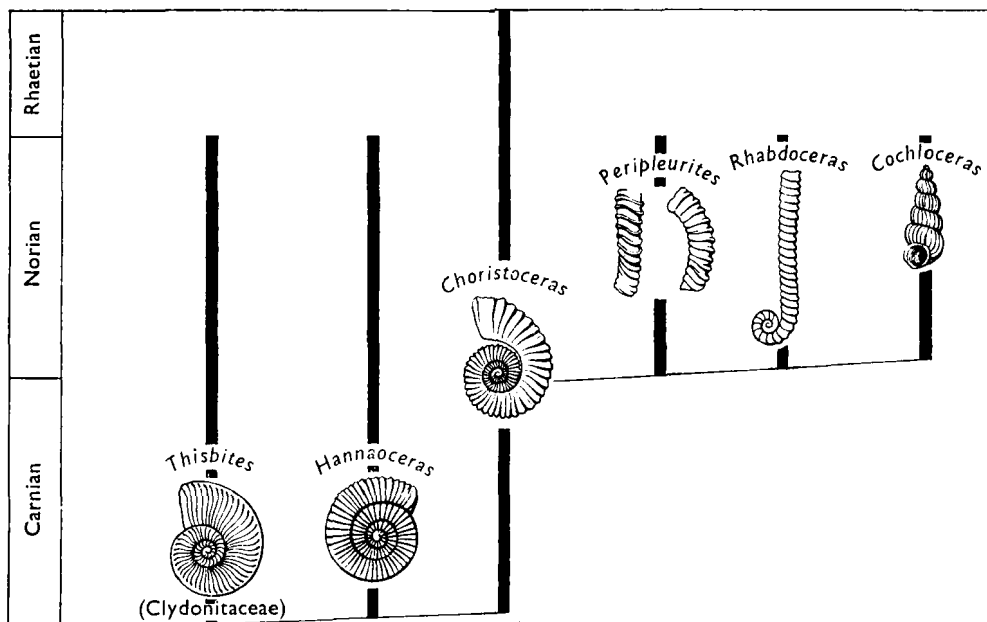
'neocomitids' and unrolled crioceratitids, which to the present day supply fuel for the opinion that at least in this group of heteromorphs one can see the process of unrolling at work (Sarasin & Schöndelmayer, 1902; Sarkar, 1955). More exact examination shows, however, that this picture must be considerably altered.



Text-fig. 1. The original coiling of ammonoids in the Devonian [from Wiedmann, 1966*b*].

## A. TRIASSIC HETEROMORPHS

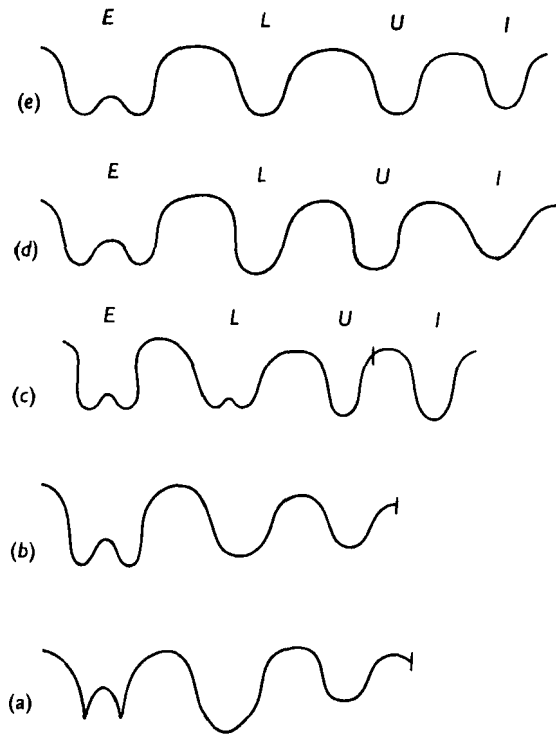
It is in dealing with the Triassic heteromorphs that it is most difficult to construct a causal connexion with the extinction of a large group, in this case the Ceratitina. The four existing late Triassic heteromorphous genera (*Choristoceras*, *Peripleurites*, *Rhabdoceras*, and *Cochloceras* incl. *Paracochloceras*) can be easily connected via *Choristoceras*, with its normally coiled involute to advolute phragmocone, to the wholly advolute genus *Hannaoceras* (incl. *Sympolycylus*) as starting form, and represent, therefore, a monophyletic unit (Text-fig. 2). The sutures (Text-fig. 3) support the supposition of a continuous development of the Triassic heteromorphs, as does the



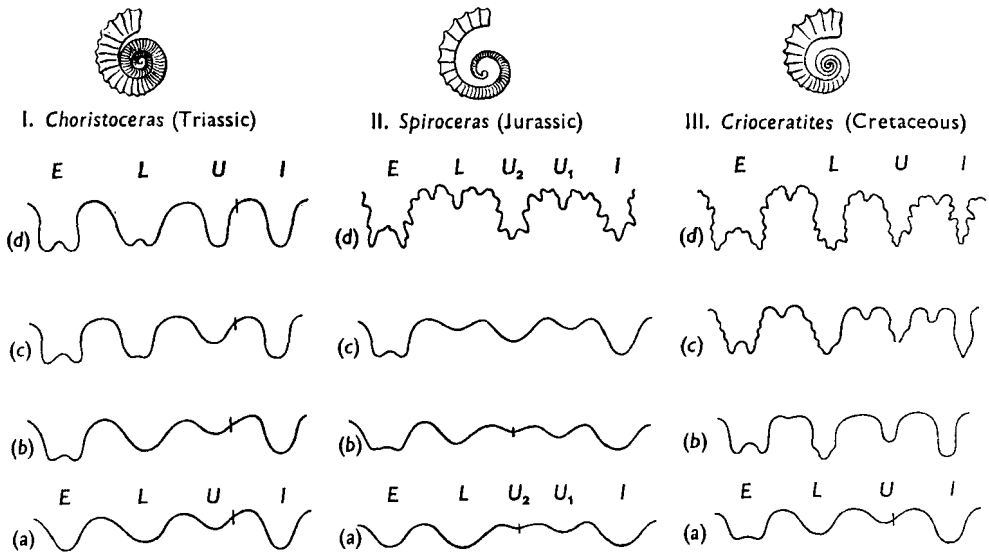
Text-fig. 2. Supposed evolution of Triassic heteromorphs from the clydonitid genus *Thisbites*.

derivation of the whole Choristoceratidae (incl. Cochloceratidae) from the Thisbitidae within the Clydonitaceae (Kummel, 1957, p. L 168). The ontogenetic development of the suture also serves as confirmation: *Choristoceras* (Text-fig. 4, I), for instance, possesses the quadrilobate primary suture (Text-fig. 4, Ia) characteristic of the main part of the Ceratitina, and which in the remainder of its ontogeny hardly changes from the preceding Thisbitidae.

This continuous and evidently monophyletic origin of the Triassic heteromorphs as well as their long stratigraphical range through the whole of the late Triassic suggests that we have to do with a purely adaptive change, perhaps to a more bottom-tied mode of life. There is certainly no reason to appeal to unselected, somehow internally impelled mutation, even though for the moment a convincing demonstration of their adaptation cannot be produced.



Text-fig. 3. Suture phylogeny of Triassic heteromorphs. Adult sutures of (a) the ancestral genus *Thisbites*, (b) *Hannaoceras*, (c) *Choristoceras*, (d) *Peripleurites*, (e) *Rhabdoceras*.



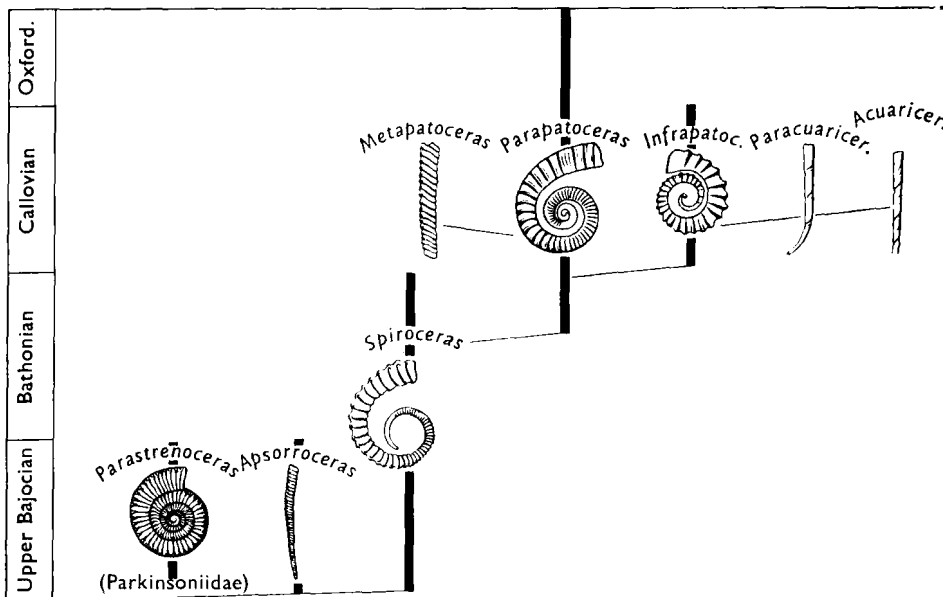
Text-fig. 4. Ontogenetic suture development of the heteromorphs. [II from Schindewolf, 1961; III from Wiedmann, 1963.]

The impetus for this supposed change in the mode of life could in this case have been provided by the world-wide regression of the sea which began in the late Triassic, reaching its climax in the Rhaetian, and affected wide areas especially of the shelf.

Since descendants of the Triassic heteromorphs are not known in Liassic beds it can be presumed that the abrupt transgression in the early Jurassic may have brought about the extinction of these narrowly adapted forms. To try to explain the simultaneous extinction of all the other Ceratitina groups with the same mechanism leads, however, to a number of difficulties. In any case it seems totally misplaced to see in the appearance and extinction of four monophyletically related heteromorph genera an indication for 'typolysis' in the almost contemporary demise of eight superfamilies (!) of the Ceratitina.

B. JURASSIC HETEROMORPHS

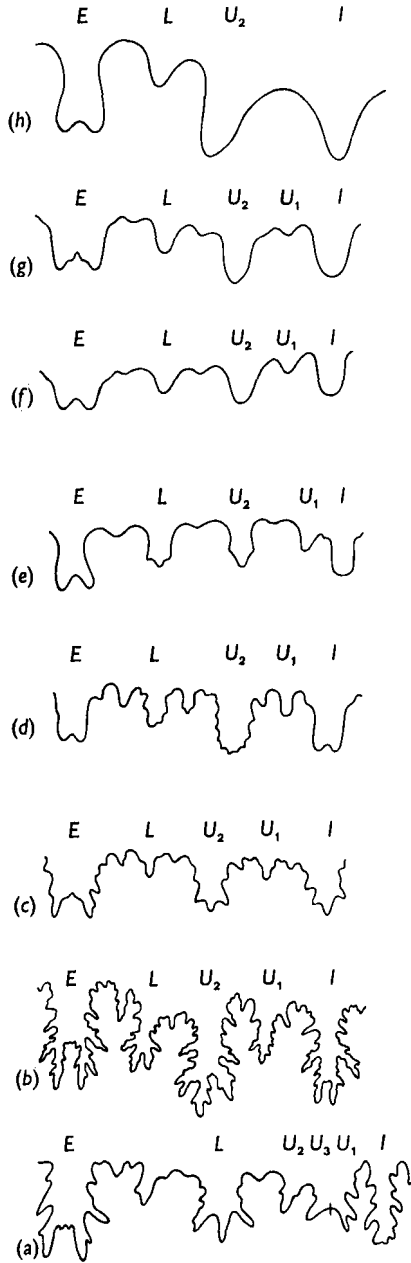
Exactly the same remarks are applicable to the heteromorphs of the Jurassic. Here seven genera (*Apsorroceras*, *Spiroceras*, *Parapatoceras*, *Infrapatoceras*, *Metapatoceras*; *Paracuariceras* and *Acuariceras*) are distributed between at most two families, and extend between the late Bajocian and the late Oxfordian. Whereas the author of the



Text-fig. 5. Supposed evolution of Jurassic heteromorphs from the parkinsoniid genus *Parastrenoceras*.

ammonoid Treatise, Arkell (1957), still believed in a link between this heteromorph group and the lycoceratids, the investigations made by Schindewolf (1953, 1961, 1963, 1965) and Westermann (1956) provided support for the original view that at least the Spiroceratidae join directly with the normally coiled parkinsoniid genus *Strenoceras*, which appears with the first spiroceratids. Only for the two genera *Paracuariceras* and *Acuariceras*, for which Schindewolf (1961) erected the family Acuariceratidae, may

in that author's opinion, have a separate origin in the lycoceratids. Recent investigations made by Ochoterena (1966), suggest that, even there however, there may be a genetic connexion with the spiroceratids and therefore a monophyletic origin for all the



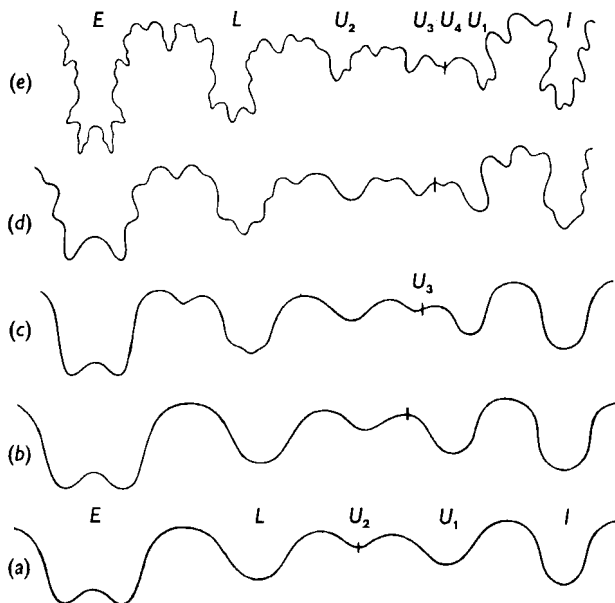
Text-fig. 6. Suture phylogeny of Jurassic heteromorphs. Adult sutures of (a) *Parastrenoceras*, (b) *Apsorroceras*, (c) *Spiroceras*, (d) *Parapatoceras*, (e) *Infrapatoceras*, (f) *Metapatoceras*, (g) *Paracuaticeras*, (h) *Acuariceras*.



Jurassic heteromorphs. The same author (1963) drew attention to the evolute forms around *Strenoceras lucretius* = *Parastrenoceras*, which is an even more easily acceptable ancestral form for the spiroceratids *sensu lato*.

If we accept this view, then the development of the Jurassic heteromorphs is characterized by two trends, depending on whether we look at the suture or the shell form:

(1) An advancing simplification of the suture from the ancestral *Apsorroceras* to the terminal *Acuariceras* (Text-fig. 6), affecting both the degree of slitting and the number of elements is noteworthy.



Text-fig. 7. Ontogenetic suture development of the parkinsoniid *Strenoceras subfurcatum oolithicum* (Quenst.). [From Schindewolf, 1965.]

(2) At the base of the spiroceratids, in the shape of *Apsorroceras*, are outstretched shells which appear to experience an advancing re-coiling via *Strenoceras*, *Infrapatoceras* and *Parapatoceras*, whilst in *Metapatoceras* and the acuariceratids a straight-shell form is preserved (Text-fig. 5).

It would, of course, be easier if we accepted *Spiroceras* itself as a transition form between the strenoceratids and the spiroceratids. However, from the degree of slitting of its suture it must be derived from *Apsorroceras*, even if according to our present knowledge it appears simultaneously with that genus—and with *Strenoceras* and *Parastrenoceras*! In any case the transition here must have been accomplished very rapidly, more rapidly than in the Triassic forms.

If one takes the ontogeny of the suture into consideration (Text-fig. 4, II) then clear differences can be seen in the adult sutures of *Strenoceras* (Text-fig. 7e) and *Spiroceras*, but on the other hand the quinquelobate primary sutures of both form groups are identical. Thus the Jurassic heteromorphs show themselves to be genuine representa-

tives of the Neoammonoidea, for which this configuration of the primary suture has up to the present been regarded as characteristic. The connexion of these forms with the preceding parkinsoniids appears for this reason to be fully justified. The advancing reduction of the spiroceratid suture, observable both in the ontogeny and phylogeny (Text-figs. 4, II; 6), may, on the other hand, be considered as a continuous adaptation of the septa to the new static requirements of the uncoiled shell (Westermann, 1956).

Thus in general one can say that the Jurassic heteromorphs also represent a monophyletic unit, and within the total framework of the Jurassic Ammonitina, Phylloceratina and Lytoceratina they are a very peripheral phenomenon. Certainly the evolution of the shell heteromorphy appears to have been completed more rapidly than by the convergent Triassic forms, but the contemporaneous reduction of the suture was completed quite continuously. Although the spiroceratids evidently disappeared without leaving descendants they nevertheless persisted successfully for a long period, and indeed, in *Parapatoceras*, they made an attempt at secondary re-coiling (Text-fig. 5).

Since clear breaks in the phylogeny of the ammonoids do not occur simultaneously with the development and extinction of the spiroceratids on the Oxfordian/Kimmeridgian boundary, the Jurassic heteromorphs, in contrast to those in the Triassic and Cretaceous, have rarely been used as indices for typolytic phenomena.

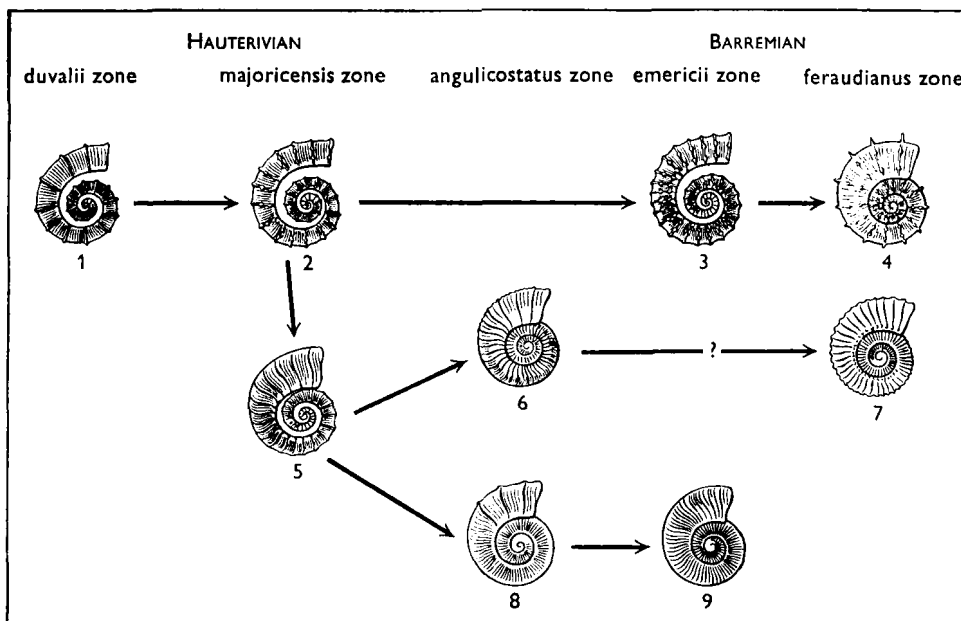
The successful and in part regressive development of the group outlined here also make such a connexion improbable. Therefore, in agreement with Ochoterena (1966), the author also sees the Jurassic heteromorphs as extremely specialized forms possibly adapted to a benthonic mode of life. The excellent preservation of the extremely fragile protoconch (e.g. in Ochoterena, 1966, pl. 2) may be an indication that the habitat of these organisms was not too far removed from the final place of sedimentation.

### C. CRETACEOUS HETEROMORPHS

With the Cretaceous heteromorphs we turn to the broadest group which, beginning in the Tithonian, had reached its full development in the early Cretaceous, then together with the normally coiled desmoceratids, true hoplitids, acanthoceratids, phylloceratids and lytoceratids persisted until the end of the Cretaceous, and indeed in an unreduced variety of forms. As indicated above, a partly iterative, partly polyphyletic origin for these Cretaceous heteromorphs is accepted in the modern ammonoid hand-books.

If we first consider and examine the single transition series between coiled and uncoiled forms up to now accepted, that is that described by Pictet (1863) between 'neocomitids' and crioceratitids, we find that careful stratigraphical control reveals that the 'descendant' crioceratitids (*C. duvalii*, *C. majoricensis* a.o.) are older and the 'ancestral neocomitids' (i.e. the genera *Pseudothurmannia* and perhaps *Hemihoplites*) are the younger forms. In other words the development must be read in the opposite direction to previous interpretations (cf. Wiedmann, 1962*b*, and Text-fig. 8 below). The re-coiling, as it is now, occurred in two parallel series and so continuously that it is scarcely possible to make a generic break between the uncoiled crioceratitids

and the pseudothurmanniids—which cannot be related to the neocomitids but are true re-coiled ‘heteromorphs’. Even in their sutures the two form-groups agree perfectly with one another, with regard both to the adult suture and the ontogeny of the lobes. The type of lobe development is, however, wholly different from the remaining Jurassic–Cretaceous Neoammonoidea (Wiedmann, 1963 ff.). Whilst the Neoammonoidea (Phylloceratina, Lytoceratina and Ammonitina) have without exception a quinquelobate primary suture, to which a greater or lesser number of lobes are added during ontogeny, the crioceratitids (Text-fig. 4, III)—as the main stock of the early

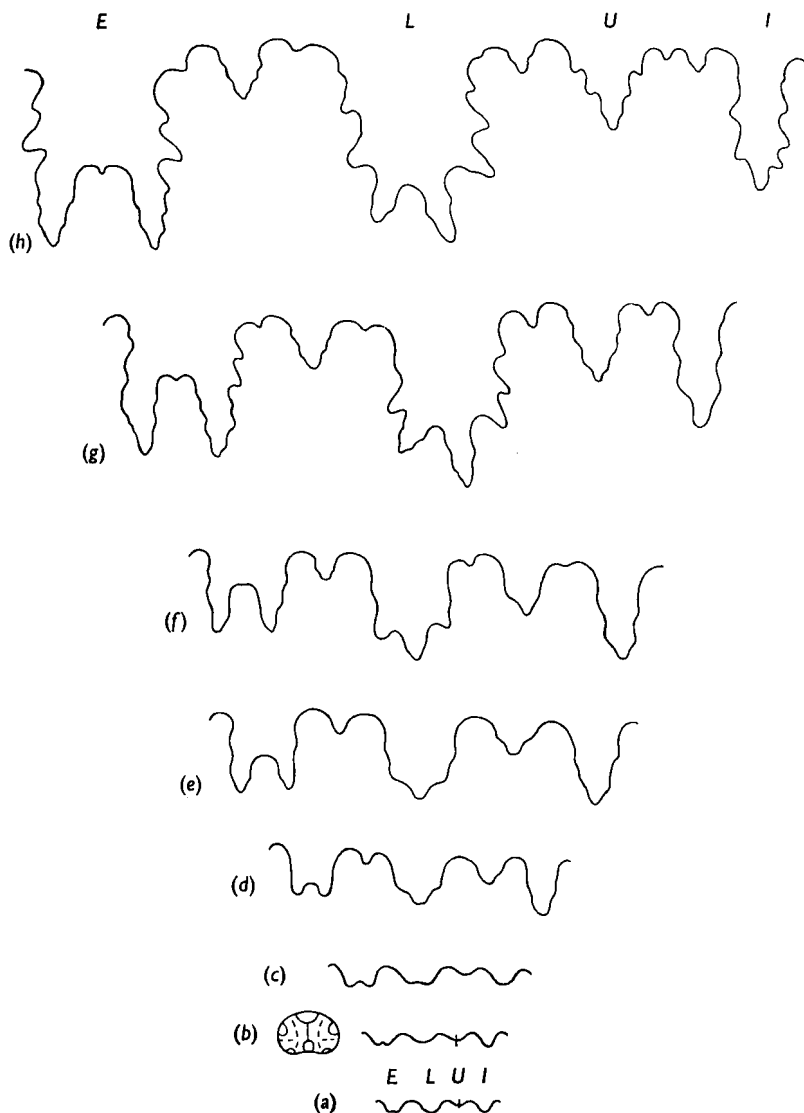


Text-fig. 8. The re-coiling trend in crioceratitids [after Wiedmann, 1962b]. (1) *Crioceratites* (*C.*) *duvalii* Lév., (2) *C. (C.) nolani* (Kil.), (3) *C. (C.) emericii* Lév. = ‘*Emericeras*’, (4) *C. (Sornayites) paronai* (Sark.), (5) *C. (C.) majoricensis* (Nol.), (6) *C. (Pseudothurmannia) angulicostatus* (D’Orb.), (7) *Hemihoplites feraudianus* (D’Orb.), (8) *C. (Pseudothurmannia) balearis* (Nol.) = ‘*Balearites*’, (9) *C. (Pseudothurmannia) ibizensis* Wiedm.

Cretaceous heteromorphs—possess a quadrilobate primary suture, which we otherwise only know in the Triassic heteromorphs. Comparable to the Triassic heteromorphs (Text-fig. 4, I) the crioceratitids and their derivatives retain the four protolobes *E*, *L*, *U* and *I* into maturity. The only clear differentiating feature appears during ontogeny: the bipolar slitting of the sutures which affects the lobes and saddles to an equal extent and is generally accepted as a characteristic for the Neoammonoidea. A further minute difference may be observable in the appearance of a median saddle in the external lobe, *E*, of the primary suture of the Cretaceous heteromorphs, which fails in the corresponding Triassic as well as in some Jurassic forms. In comparison with those in the Jurassic (Text-fig. 4, II) there are points of agreement (in the scarcity of elements in the adult suture) and clear differences (in the quadrilobate primary suture)

so that a genetic connexion between these two morphologically similar groups, separated moreover by the time interval of the Kimmeridgian, is scarcely to be contemplated. Moreover, the degree of slitting of the Cretaceous sutures is fundamentally greater than in the Jurassic end-forms (*Para-*, *Infra-*, *Metapatoceras*).

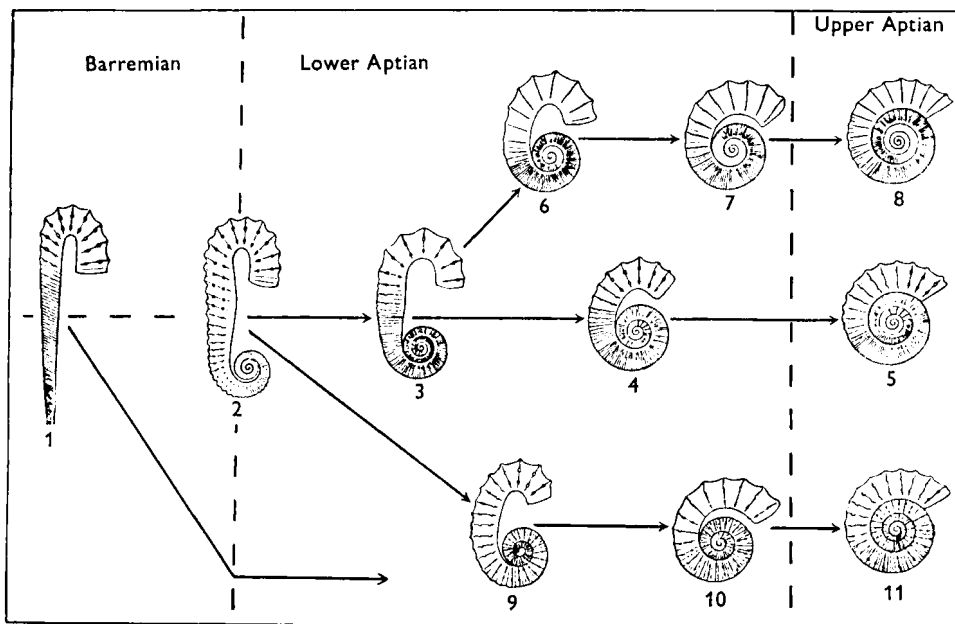
There is today common agreement that the origin of the early Cretaceous crioceratitids is to be found in representatives of the genera *Protancyloceras* and *Lepto-*



Text-fig. 9. Ontogenetic suture development of a Berriasian *Leptoceras*, *L. studeri* (Ooster) from Rufigraben-Justistal (Switzerland). Geol.-paläont. Inst. Tübingen coll. Ce 1372/2. circ 25/1. (a) First suture, (b) 10th suture and septal surface, (c) 13th suture, (d) 20th suture at whorl height 1.5 mm., (e), (f), (g) intermediate stages, (h) 45th suture at whorl height 3.5 mm.

ceras of the Tithonian and Berriasian (Pl. 1; Pl. 3, figs. 1, 2), which have an appropriate type of uncoiling and lobe development (Text-fig. 9). The question of the origin of the Cretaceous heteromorphs as a whole will be gone into after a discussion of the problem of polyphyletism.

A close phylogenetic connexion between the crioceratitids and the somewhat younger ancyloceratitids has never been seriously doubted except by Basse (1952). The sutures of both groups which I favour being united in a single family, are identical, and clear morphological transition forms are available (e.g. *Leptoceras*, *Aspinoceras*). It is remarkable, however, that Casey (1960, and Text-fig. 10 below) was able to distinguish a very similar re-coiling trend in the ancyloceratitids which runs synchronously with that of the crioceratitids and likewise in several parallel lineages. The genera *Australiceras*,



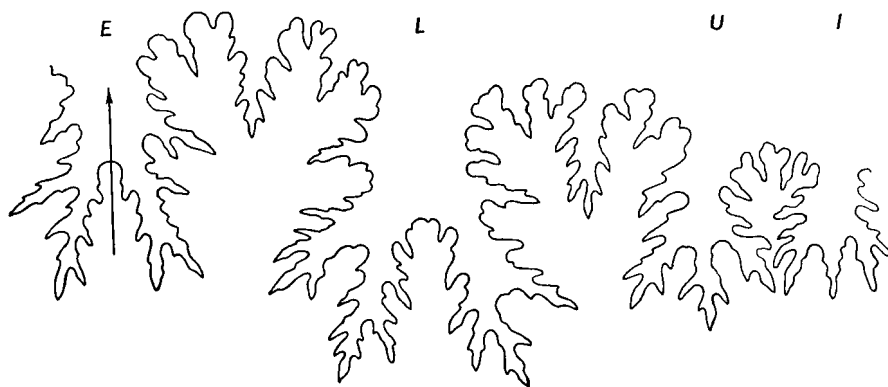
Text-fig. 10. The re-coiling trend in ancyloceratitids [from R. Casey, 1960]. (1) *Lithancyclus*, (2) *Ancyloceras*, (3) *Australiceras* (gr. *A. gigas*), (4) *Australiceras* (gr. *A. tuberculatum*), (5) *Australiceras* (gr. *A. jacki*), (6) *Tropaeum* (gr. *T. hillsi*), (7) *Tropaeum* (gr. *T. bowerbanki*), (8) *Tropaeum* (gr. *T. subarcticum*), (9) *Epancyloceras*, (10) *Ammonitoceras* (gr. *A. uctiae*), (11) *Ammonitoceras* (gr. *A. tovilense*).

*Tropaeum* and *Ammonitoceras* are re-coiled end-members of this development within the ancyloceratitids; *Parancyloceras*, *Menuthiocrioceras* and *Pedioceras* are further genera demonstrating this trend, which begins as early as the late Hauterivian.

Why the 'Turrilitaceae', subject though they are to a different mode of uncoiling, were regarded by Wright (1957) in the Treatise as of independent and iterative origin from the lycoceratitids of the early Cretaceous is not clear. The early Cretaceous ptychoceratitids as well as the predominantly late-Cretaceous proper turrilitids may be related without great difficulty to crioceratitid ancestors, with which they are

linked by a nearly identical quadrilobate septal suture (Text-fig. 11). It was therefore thought best (Wiedmann, 1962*b*) to abandon the Turrilitaceae as a superfamily and to place its families in the Ancylocerataceae, i.e. the entirety of the quadrilobate Cretaceous heteromorphs. It is also notable here that even among the extreme, uncoiled turrilitids the tendency to return to a normally coiled shell form is found in such genera as *Algerites*, *Neocrioceras*, *Axonoceras*, *Jouaniceras* or even *Anaklinoceras* (Text-fig. 16).

In contrast the scaphitids, with their involute phragmocone and hook-shaped uncoiled living chamber, have to the present appeared to occupy a special position within the Cretaceous heteromorphs. Nowak (1911), Reeside (1927) and Schindewolf

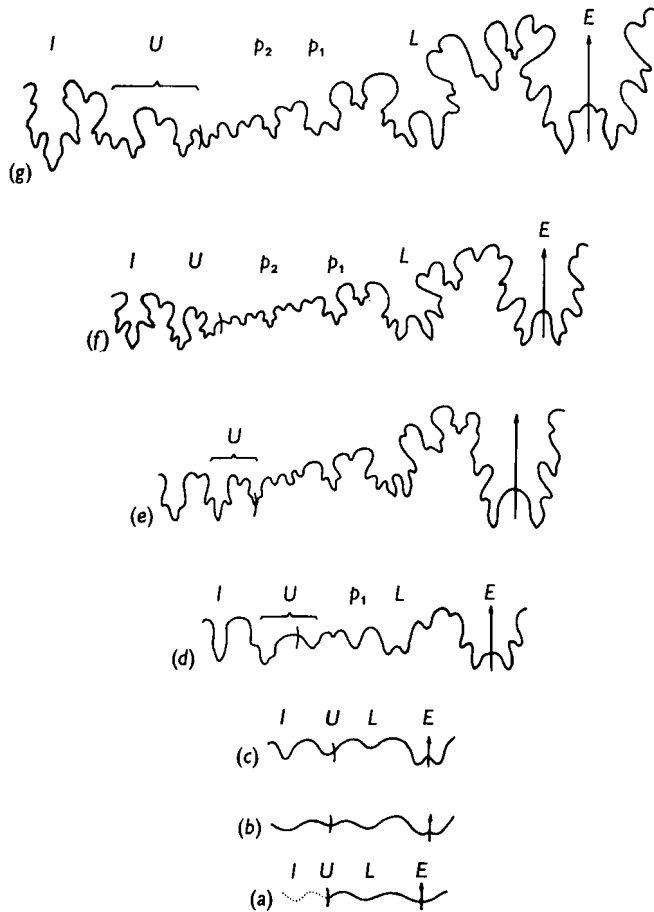


Text-fig. 11. Adult suture of the turrilitid *Pseudhelicoceras convolutum* (Quenst.) at whorl height 13 mm. [from Wiedmann & Dieni, 1968].

(1961) held the scaphitids for a totally heterogeneous, polyphyletic catch-all group. Opposed to this view, Luppov & Drushtchic (1958) suggested a monophyletic origin from representatives of the Ammonitina, and Spath (1933) from the Lytoceratina, whilst Wright (1957) supposed a diphyletic origin from the lytoceratids.

At the base of this wide divergence of opinion is on the one hand the appearance of bifid and trifid lobe forms, which in company with the shell sculpture were seen as evidence of polyphyletism (Nowak, 1911); and on the other hand the considerably more complicated suture line of the late Cretaceous forms, was regarded as an 'ammonitid' feature, in comparison with the less complicated suture of the ancestral forms in the Albian, which approaches the suture of the early Cretaceous heteromorphs (Schindewolf, 1961). After the continuous transition from bifid to trifid lateral lobes within the scaphitids was established (Cobban, 1952; Wiedmann, 1962*a*), the lobe development of the scaphitids was also elucidated. The most important result of these investigations (Wiedmann, 1965) is that the lobe development of the late Upper Cretaceous scaphitids is built on a quadrilobate primary suture and also in maturity has no more than four definitive lobe elements, despite the insertion of so-called pseudolobes (Text-fig. 12). This lobe ontogeny of the most advanced representatives runs parallel with the lobe phylogeny within scaphitid evolution from the Albian to the latest part of the Cretaceous (Text-fig. 13).

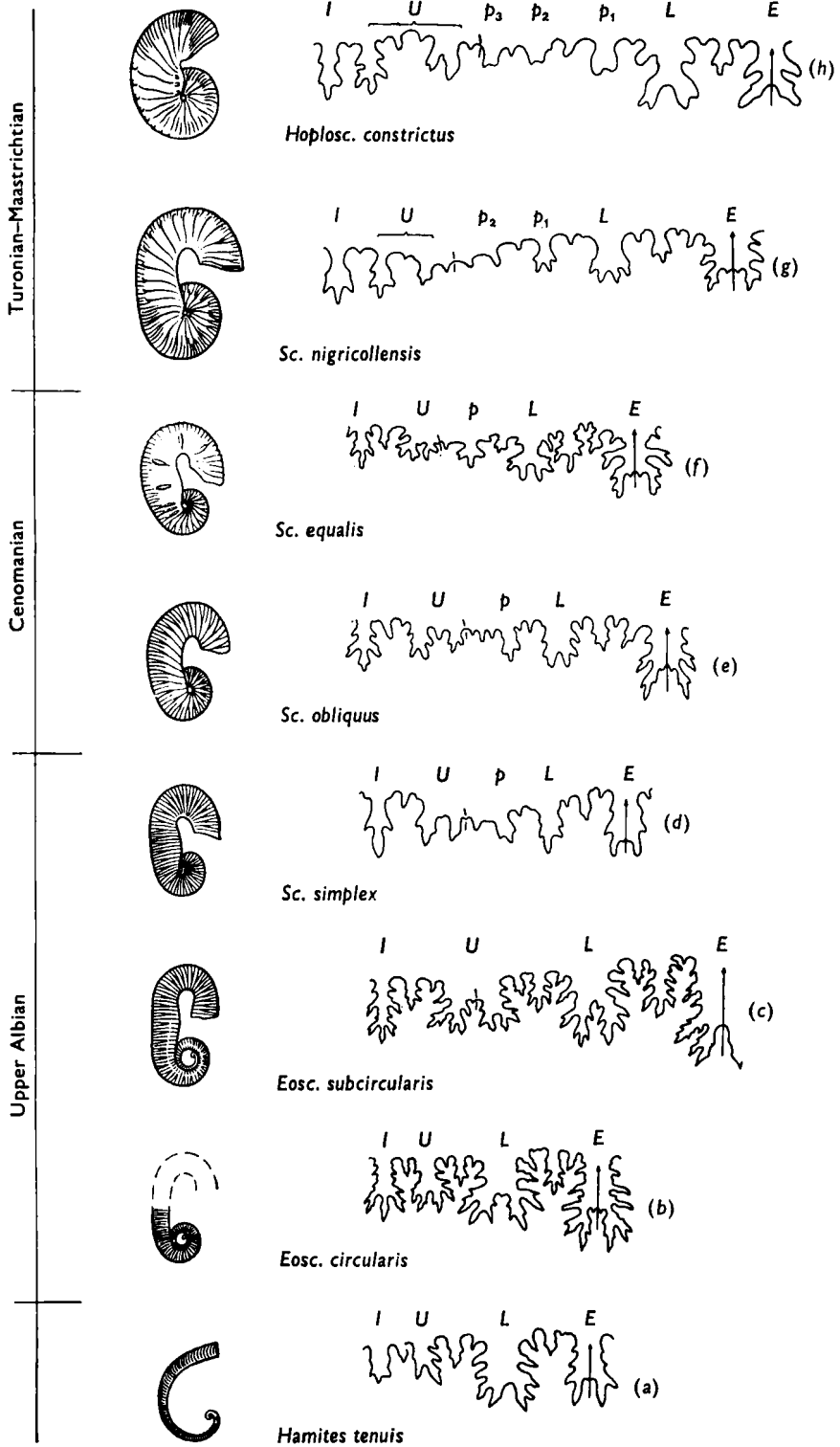
In the earliest member of this continuous series, the genus *Eoscaphtes*, the suture remains during the whole of the ontogeny that of a normal quadrilobate heteromorph (Text-fig. 13*b*). The resulting, but at first only vague, supposition that the origin of the entire scaphitids is to be found in the heteromorphs, finally received approval in the



Text-fig. 12. Ontogenetic suture development of a late Cretaceous scaphitid, *Scaphites* (*S.*) *hippocrepis* (Dekay) from the Campanian of Big Horn County (U.S.A.) [After Reeside, 1927; Wiedmann, 1965.]

demonstration of an open first spiral in *Eoscaphtes*, in which the development of its probable ancestor *Hamites* is clearly recapitulated (Text-fig. 13*a*). Thus the whole *Bauplan* of the scaphitids must be reinterpreted, in so far as these forms must now be understood as re-coiled heteromorphs (see especially *Rhaeboceras* and *Haresiceras*) and not as uncoiled lycoceratids and/or Ammonitina.

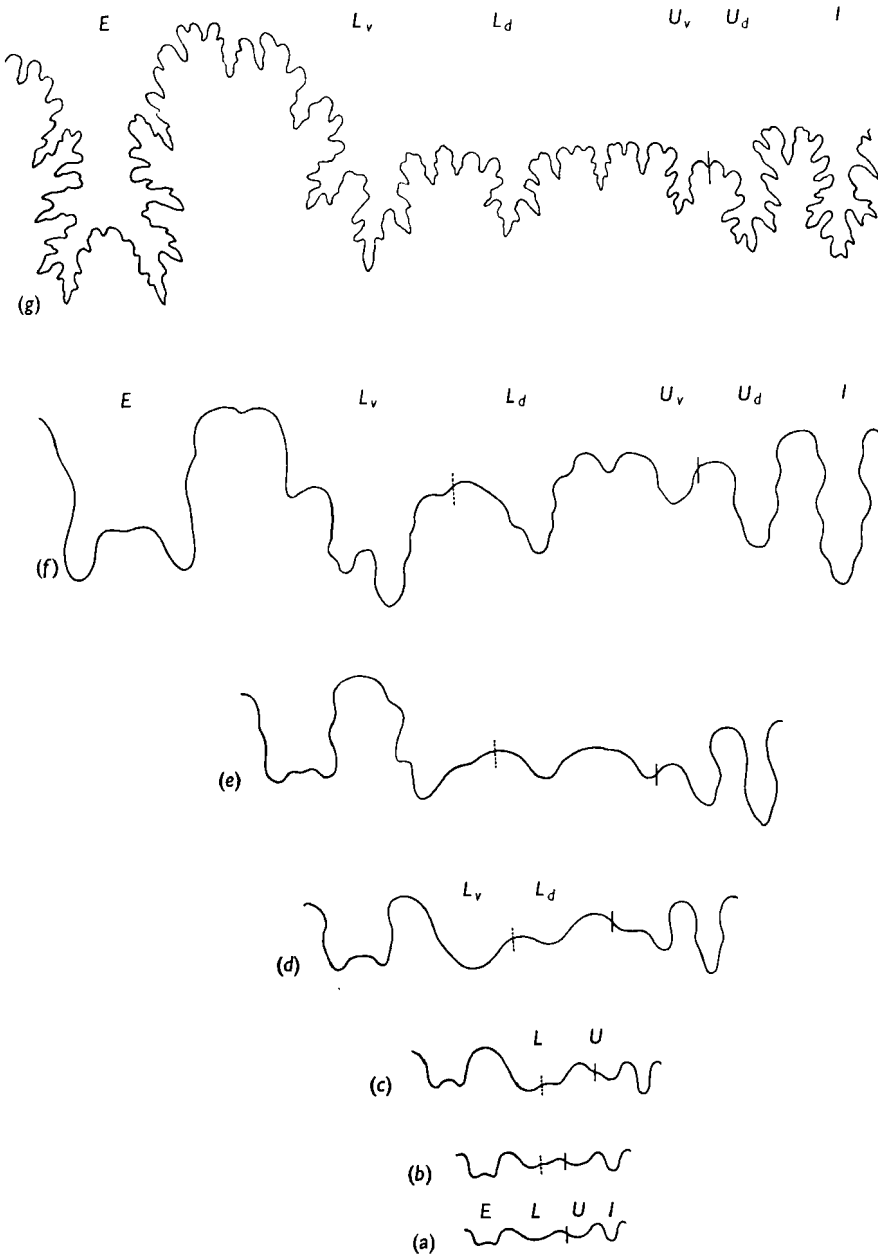
Still more surprising is the result brought by investigation of sutures and suture development of various representatives of the Cretaceous hoplitids. *Dowvilleiceras*, which can be regarded as typical of this strongly sculptured, moderately involute



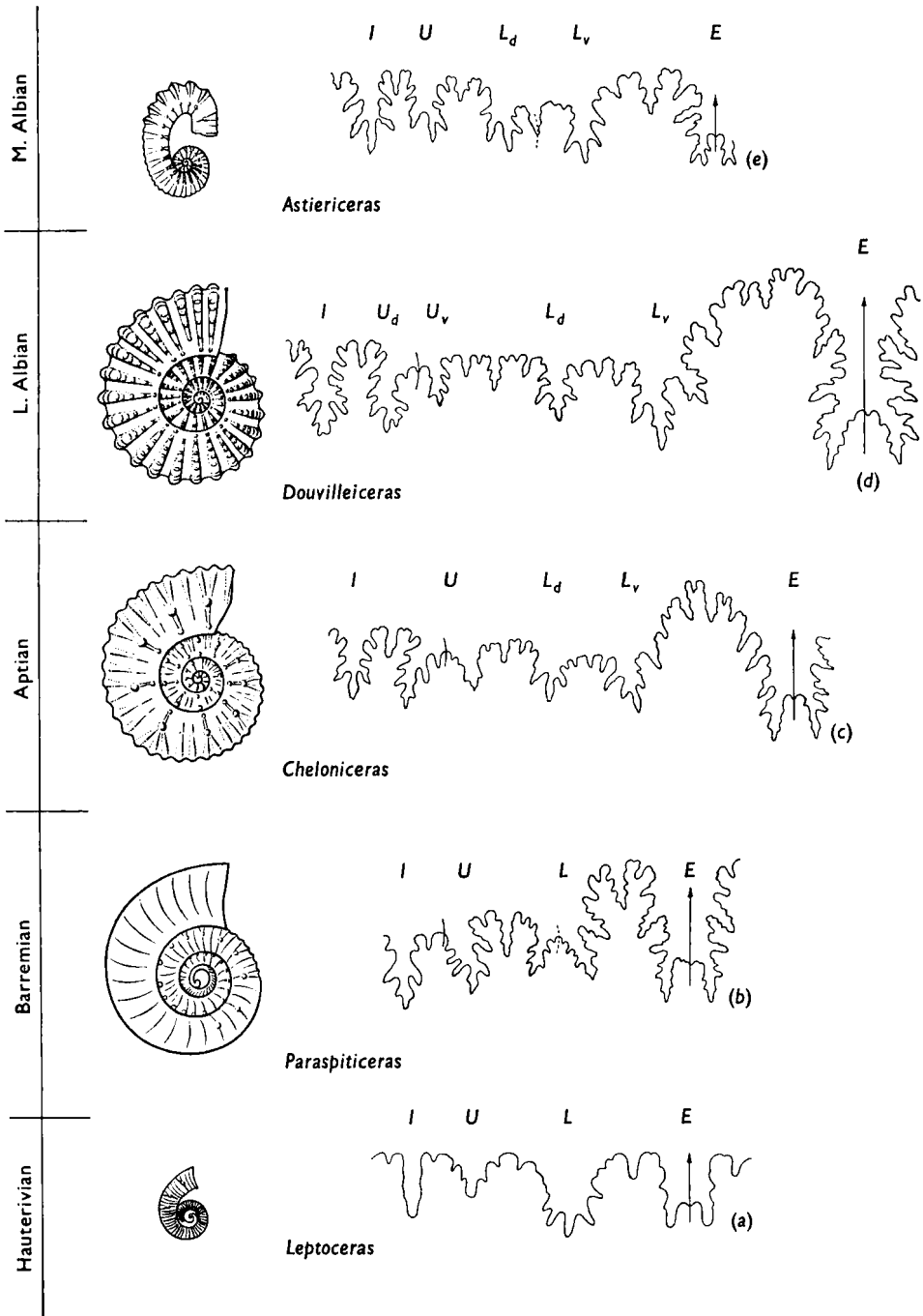
Text-fig. 13. Shell and suture phylogeny in scaphitids [From Wiedmann, 1965].



morphological group, and over the assignation of which to the hoplitids there has never been any doubt, has surprisingly a quadrilobate primary suture (Text-fig. 14a). In addition the apparently element-rich, strongly divided adult suture of this genus (Text-fig. 14g) can be traced easily to a quadrilobate configuration, just as has been



Text-fig. 14. Ontogenetic suture development of the 'false hoplitid' *Douvilleiceras mammillatum* (Schloth.). [From Wiedmann, 1966b.]



Text-fig. 15. Shell and suture phylogeny of douvilleiceratids. [From Wiedmann, 1966b.]

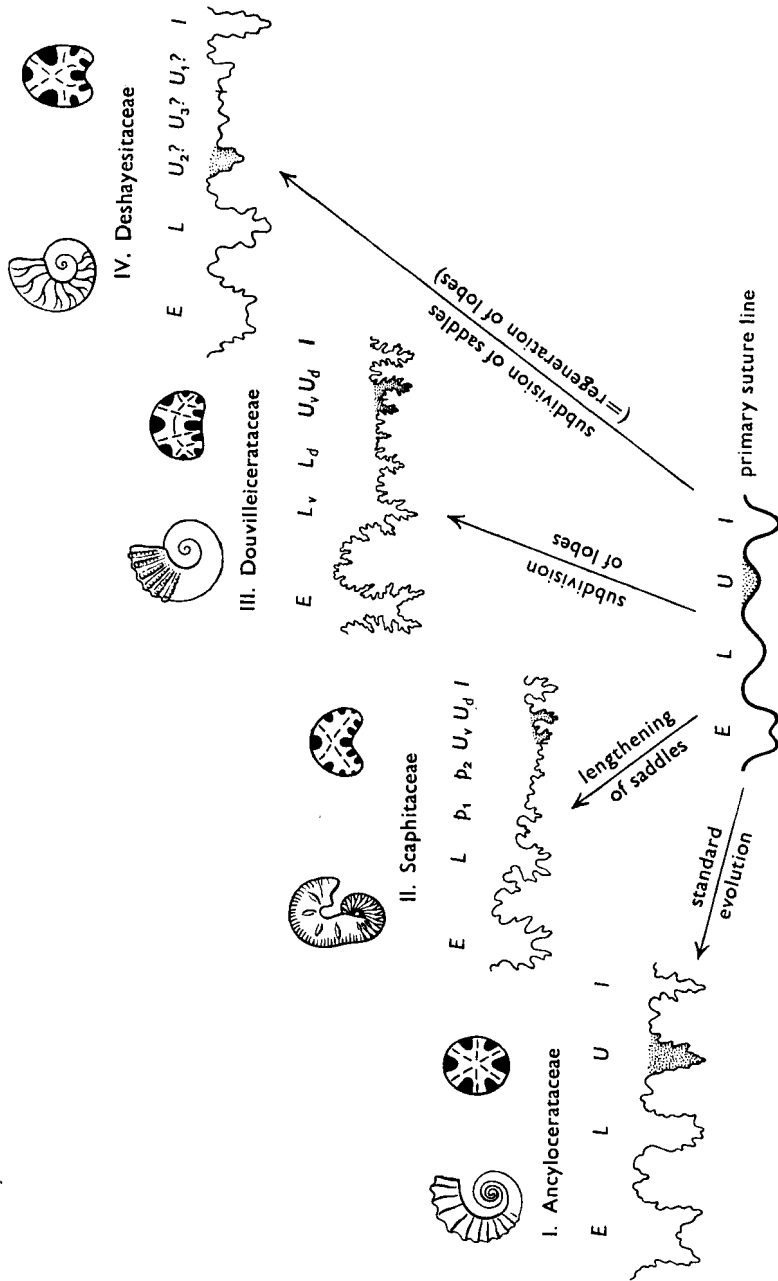
asserted for the scaphitids. Thus the lobe formula  $ELUI$  typical for the heteromorphs is also applicable to the douvilleiceratids. The only difference from the suture development of the scaphitids is the fact that in the latter the saddle between the lobes  $L$  and  $U$  experiences an extreme lengthening, whereas in the douvilleiceratids the lobes  $L$  and  $U$  become subdivided (Text-fig. 17).

Thus the douvilleiceratids may be treated as a test case of the systematic-classificatory and phylogenetic importance of the suture line and in particular the lobe development. If the suture is to be assigned any importance at all as a criterion of homology, then there must be further evidence in the suture phylogeny and perhaps in the early shell morphology of the douvilleiceratids which consolidates the tentative supposition drawn from the lobe development of *Douvilleiceras*, that we are dealing with derivatives of the heteromorphs.

The results of investigations in this direction (Wiedmann, 1966*b*) were that (1) in the inverted development series *Douvilleiceras*–*Cheloniceras*–*Paraspiticeras*, which is connected by all morphological transitions, the mentioned separation of the lobes  $L$  and  $U$  is reversed (Text-fig. 15). Comparable to the situation in the scaphitids, (2) *Paraspiticeras* at the very beginning of this lineage is a form with a genuine quadrilobate heteromorph suture not only in the primary suture but also as an adult, despite the fact that the *Paraspiticeras* shell has to the present in no way given a hint of being a heteromorph. However, the agreement with the situation in the scaphitids goes even further: (3) The search for transition forms between the perfectly normally coiled douvilleiceratids (cf. Wiedmann, 1966*b*, pl. 4, 5) and their supposed uncoiled antecedents led us—almost as expected—to the inner whorls of *Paraspiticeras* (Pl. 2, fig. 1), which comprises, like *Eoscaphtes*, an open spiral. As a consequence nothing now stands in the way of the derivation of the ‘hoplitid’ group of the douvilleiceratids from a heteromorph ancestor. The leptoceratids of the Barremian (Pl. 2, fig. 2) may be presumed to be these ancestral forms, which already display a weak tendency to re-coiling. The parallelism of the lobe ontogeny (Text-fig. 14) and phylogeny (Text-fig. 15), again clear in this group, can only be referred to in passing.

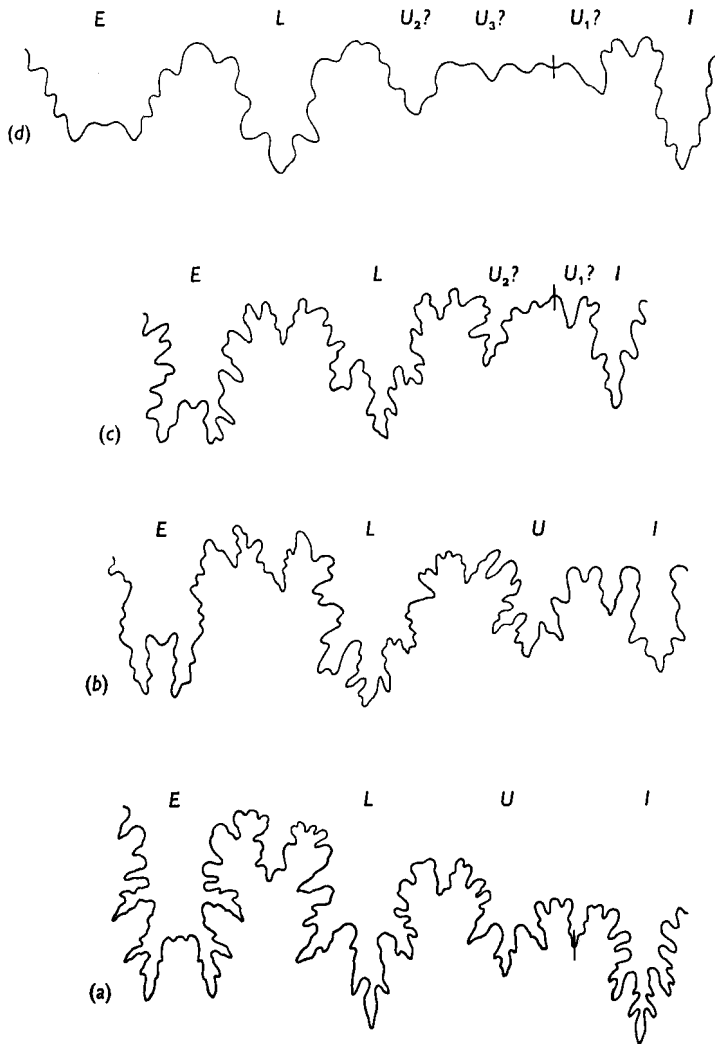
Finally, widening of the investigations resulted in recognition of the fact that not only the douvilleiceratids, in their proper sense, represented regenerated heteromorphs, but also that here again the trend to re-coiling occurs in several parallel lineages. The parahoplitids, acanthohoplitids and trochleiceratids belong to the same group of ‘false hoplitids’ and may be immediately linked with *Paraspiticeras* or *Cheloniceras*.

Moreover it became clear that the Deshayesitidae also with their quadrilobate primary suture represent ‘false hoplitids’, in which (in contrast to the groups previously dealt with) lobe regeneration accompanied the secondary re-coiling of the shell (Wiedmann, 1966*b*; Schindewolf, 1967). The clear differences in lobe development (Text-fig. 17, IV) from that of the douvilleiceratids allows one to suppose that the deshayesitids are to be traced to heteromorphic ancestors other than the former. There is thereby, however, still uncertainty whether the deshayesitids are end-members of an evolutionary series *Heteroceras*–*Colchidites*–*Turkmeniceras* (Tovbina, 1965) with helicoid initial coil or the series *Crioceratites*–*Hemihoplites* (Wiedmann, 1966*b*) with spiral coil.



Text-fig. 17. Modes of suture development in Cretaceous heteromorphs.

The sutures of *Hemihoplites* (Text-fig. 18a), *Colchidites* (Text-fig. 18b) and *Turkmeniceras* (Text-fig. 18c) are here added to that of *Deshayesites* (Text-fig. 18d) for comparison. In view of the extreme similarity of the sutures of the 'crioceratitid' *Hemihoplites* and the heteroceratid *Turkmeniceras* it would not be surprising if both genera were found to be identical. The initial coil of *Hemihoplites* is up to the present unknown, but from the



Text-fig. 18. Adult sutures of deshayesitids and their presumed ancestors. (a) *Hemihoplites* cf. *astarte* (Fall. & Term.); (b) *Colchidites* aff. *shaoriensis* Djanel.; (c) *Turkmeniceras turkmenicum* Tovb.; (d) *Deshayesites deshayesi* (D'Orb.) [(a) after Wiedmann, 1966b; (b) and (c) after Tovbina, 1965; (d) after Schindewolf, 1967].

specimen of the type species figured previously (Wiedmann, 1966b, pl. 6, fig. 3) an open initial coil can be presumed and thus it cannot be completely ruled out that it is helicoidal. In any case we have to deal with regenerated heteromorphs although likewise here the shell, sculpture, and suture type have a considerable resemblance to the

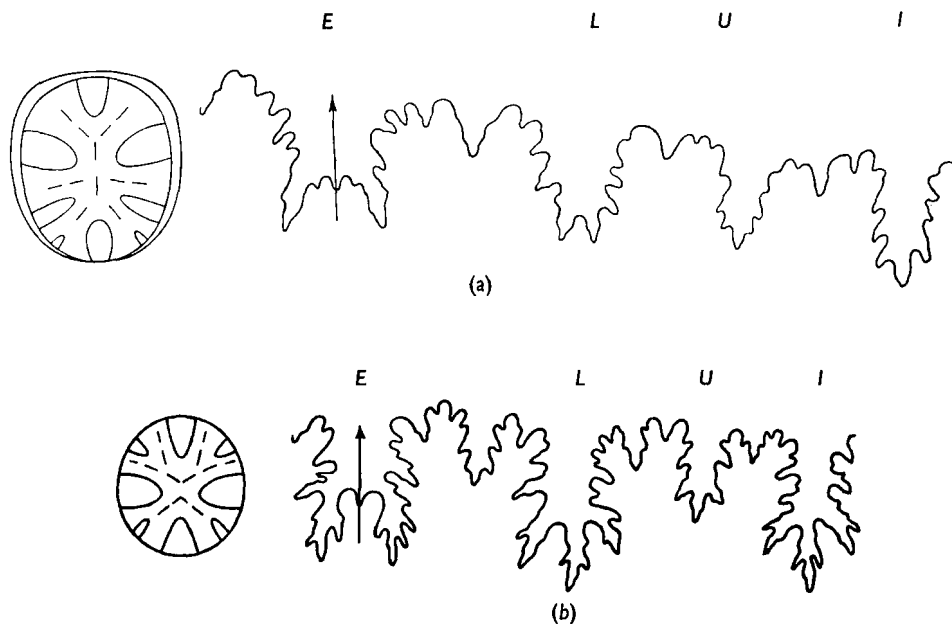
true hoplitids and as a result descent from heteromorphs has not to the present been suspected.

If we now review the entire evolution of the Cretaceous heteromorphs equipped with this new and in many respects surprising information, a pattern appears which is quite different from the text-book conception: although a number of groups, for instance the baculitids *sensu lato*, neglected in the above presentation, retained a heteromorph shell form until their extinction in the latest part of the Cretaceous, for the majority of the Cretaceous heteromorphs—namely the crioceratitids, ancyloceratids, anisoceratids, turrilitids, scaphitids, douvilleiceratids and deshayesitids—the tendency dominates for a return from an originally uncoiled to a secondarily, normally coiled shell form (Text-fig. 16). This was accomplished by the two last-named groups with such success that they can scarcely be distinguished from true hoplitids.

In this situation the most essential criterion of homology, at least within the Cretaceous heteromorphs and ammonoids, proves not to be aberrant shell form but instead the suture line inclusive of its ontogenetic development. The quadrilobate primary suture is the only distinguishing feature uniting the totality of Cretaceous heteromorphs and their re-coiled derivatives. As a rule, and in particular in the pure heteromorphic forms, the suture remains at the quadrilobate ancestral stage throughout the entire ontogeny. In contrast, in several groups the lobes react during ontogeny to the new static demands consequent on re-coiling by the lengthening of saddles, lobe splitting or lobe regeneration (Text-fig. 17). Continuous morphological transition forms and the uniform quadrilobate primary suture permit, moreover, the assertion that the whole complex of the Cretaceous heteromorphs comprising the present superfamilies Ancylocerataceae, Scaphitaceae, Douvilleicerataceae and Deshayesitaceae is monophyletically descended from a single common root.

Attention must now be directed with new vigour at this root of the heteromorphs in the Tithonian/Berriasian, where information about whence and in what way the heteromorphs arose may be available. Although early heteromorphs from all parts of the Tithonian have been mentioned in numerous publications (Zittel, 1870; Retowski, 1894; Ooster, 1860; Uhlig, 1903; Kellum, 1937; Mazenot, 1939; Imlay, 1942; Spath, 1950; Arnould-Saget, 1951; Thieuloy, 1966) total uncertainty prevails over the question of suture evolution and origin of these forms. This has its cause partly in the fact that in all areas where heteromorphs are found, namely in southern Europe, north Africa, central Asia and Central America, they appear quite unheralded and at the same time with a wide variety of shell forms. Although the earliest representatives, found in the earliest Tithonian, apparently possess without exception an ancyloceratid shell type (*Protancyloceras*), together with them in the early Tithonian appear both the crioceratid (*Leptoceras*?) and the baculitid types (*Bochianites*), whilst the helicoid uncoiled type (*Cochlocrioceras*), phylogenetically regarded as at first somewhat unsuccessful, emerged in the late Tithonian, and is thus probably a derived member. Plate 1 portrays a faunal cross-section of such a late Jurassic fauna in which representatives of the genera *Bochianites* and *Protancyloceras* are found in large numbers together with perisphinctids and haploceratids, both of which had been thought of as putative ancestral forms, as have been the at this time very insignificant lycoceratids.

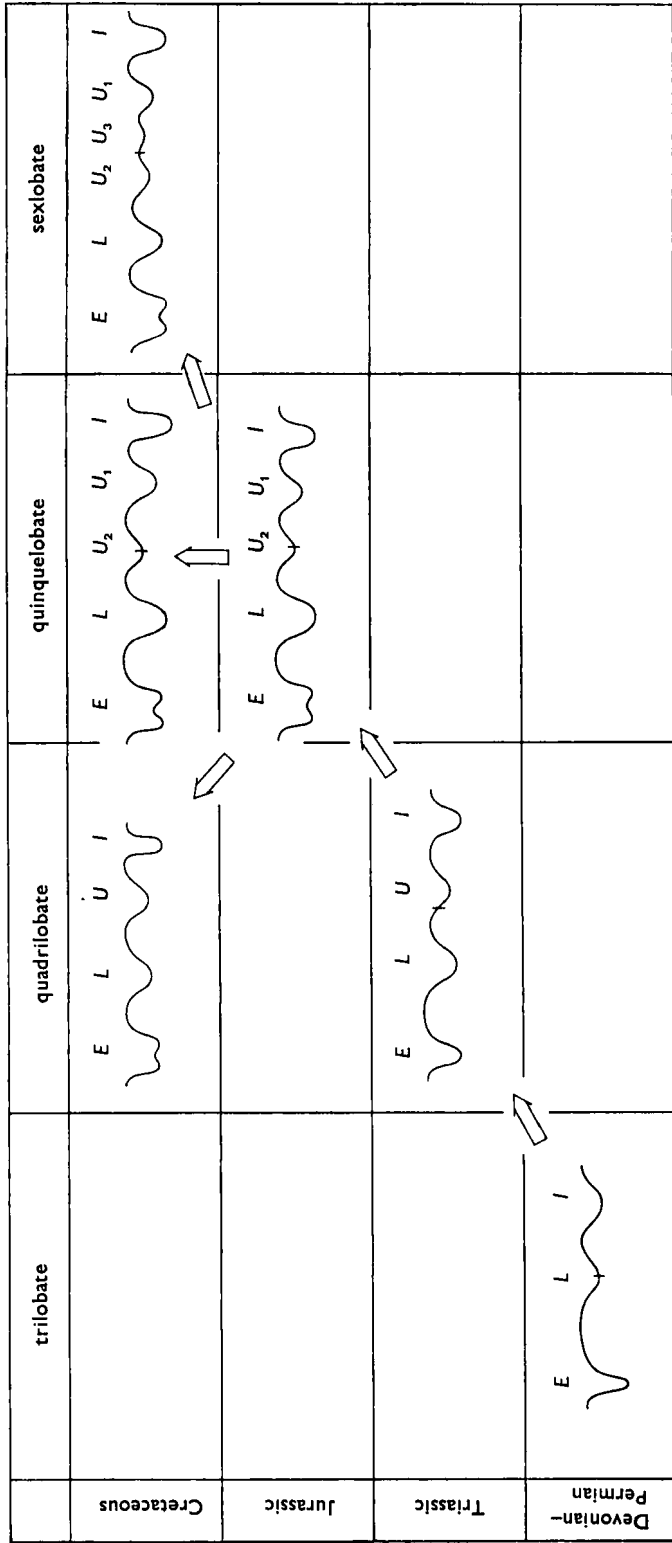
All these conjectures, a report of which would fill many pages, are up to the present wholly speculative, since we lack the slightest concrete evidence. One could perhaps in summary note that the sculpture of the early heteromorphs (at least the strongly sculptured protancyloceratids) are most reminiscent of the perisphinctids, whereas the element-poor suture and weak sculpture of bochianitids and leptoceratids speaks more for a relationship with the lytoceratids. The first lobe development available at present is of a *Leptoceras* from the Berriasian (Text-fig. 9) and with its quadrilobate primary suture and in its further development fits perfectly in the known pattern of the younger heteromorphs (Text-fig. 4, III). The adult suture of *Protancyloceras* and



Text-fig. 19. Adult sutures and septal surfaces of early heteromorphs of the Tunisian Berriasian. (a) *Protancyloceras punicum* Arn.-Sag. at whorl height 5.5 mm. Geol.-paläont. Inst. Tübingen coll. Ce 1372/10. (b) *Bochianites baculitoides* Arn.-Sag. at whorl height 6 mm. Geol.-paläont. Inst. Tübingen coll. Ce 1372/11. Both from Djebel Nara (Tunisia). [Leg. Dietl & Wiedmann.]

*Bochianites* (Text-fig. 19), of which the lobe development is not yet known, also fit perfectly in this general picture. I therefore suspect that these forms also possessed quadrilobate primary sutures, in which they differ clearly both from the perisphinctids and the lytoceratids, for which the quinquelobate primary suture of all Neoammonoidea is characteristic (Text-fig. 20).

Although further research is obviously needed, our present knowledge does make it very probable that the typical features of the Cretaceous heteromorphs—uncoiling of the shell and reduction of the primary suture—developed suddenly in the Tithonian.



Text-fig. 20. Progressive and regressive evolution of ammonoid primary sutures ('Primärsuturen').



## D. THE COURSE OF HETEROMORPH EVOLUTION

After discussion of the new facts let us now turn to the questions posed at the outset:

(1) The question (A) of the iterative origin of the Triassic as well as the Jurassic and Cretaceous heteromorphs can be answered negatively. All three form groups represent, so far as we know, genetically uniform, monophyletic units. The Cretaceous forms differ, however, markedly from the older heteromorph groups both in their mode of origin and later fate, so that a further differentiation is necessary. A distinction must, for instance, be made in regard to (B), the claimed explosive development which cannot be confirmed in the case of the Triassic and Jurassic forms. Here a continuous transition from normally coiled ceratitids or parkinsoniids is present and can be confirmed in the lobe development. The Triassic Choristoceratidae retain faithfully the lobe formula and development of the preceding forms, but in contrast the Jurassic Spiroceratidae preserve at least the primary suture of the preceding neo-ammonoids, whilst a reduction in the number of lobes and the degree of slitting follows only in the course of ontogeny and phylogeny. The situation within the Cretaceous heteromorphs is quite different. Here the heteromorphic shell form and lobe reduction appear suddenly in the late Jurassic; transitional links are not known, and in view of the reverted primary suture are also theoretically not to be expected. This suggests the hypothesis that the Triassic and Jurassic heteromorphs, with their restricted morphological variety, gradually developed as adaptive forms to a special (benthonic?) mode of life; whereas the sudden transformation of the Cretaceous heteromorphs may be interpreted as a kind of spontaneous reverse mutation which recapitulated early phylogenetic stages—the primary shell coiling in the Devonian and the ceratitid primary suture—with differing accuracy. The quite generally realized re-coiling of shells does not allow us to recognize the heteromorphs of Cretaceous age as specialists or overspecialized end-forms.

(2) The further 'success' of the heteromorphs also speaks for the above conclusions. Whilst the aberrant forms in the Triassic and Jurassic as adaptive forms very soon fell victim to slight environmental changes, e.g. those concomitant with the 'old cimmerian' movements and regressions, the spontaneous mutative origin of the Cretaceous heteromorphs may actually have made them selectively disadvantageous at first. The ability to return to normal coiling (and mode of life?) appears to have determined to a certain extent the success of these forms and to have made certain of their survival. Only in this way the general trend to normal coiling in all parts of the Cretaceous and in almost all heteromorphic groups can be explained.

(3) The basic assumption of the typolysis theory, which represents the heteromorphs as a selection-negative, inadaptable and doomed evolutionary cul-de-sac, is clearly refuted by the described reversions and the success of the Cretaceous heteromorphs, as Rensch (1947, p. 232), Simpson (1949, p. 203), Basse (1952, p. 674) and Osche (1966, p. 897) have already supposed.

## III. GENERAL REMARKS

Finally, a series of general conclusions can be drawn from the concrete results of the above investigations, and these should be at least briefly discussed.

## A. HOMOLOGIES AND SUTURES IN HETEROMORPHS AND AMMONOIDS

This first problem is of a phylogenetic-systematic kind and brings forward for discussion the criteria of homology used up to the present for the systematics of the ammonoids. The investigation of the heteromorphs has shown that the purely morphographic systematics of the younger ammonoids (Basse, 1952; Arkell, Kummel & Wright, 1957; Luppov & Drushtchic, 1958) has led finally to an artificial system. In the attempts at classification made up to the present, and in the ammonoid hand-books just mentioned, the form, the sculpture and at best the external suture of the adult shell have been favoured as criteria of homology. This must lead and has in fact led, for instance in the case of the 'false hoplitids', to considerable misinterpretation. The evolution of the scaphitids and the 'false hoplitids' has shown on the preceding pages the importance of morphogenetic methods of investigation, which take into account both the early development of the shell (*Eoscaphtes*, *Paraspiticerias*), as well as the early lobe development (*Douvilleicerias*, *Deshayesites*, *Scaphites*).

Despite all the modifications which the biogenetic *Grundgesetz* has undergone since its first formulation, we have still in the early ontogenetic development of the ammonoids numerous features which recapitulate early evolutionary stages and thereby, in addition to the characters of the adult shell, yield information about the real genealogical relationships. The morphogenesis of the shell and the suture can be used as the supreme criterion of homology in the construction of a Natural System of the ammonoids. This point must be emphasized since the significance of these features has recently still been neglected or denied (Arkell, Kummel & Wright, 1957; Donovan, 1959, 1964; Challinor, 1959).

It is often held against this opinion, verified above with numerous examples, that we know practically nothing of the functional importance of the ammonite septa. This is without doubt true, but I believe that pragmatism may be admitted here: The success of a method may decide its applicability even if we do not know exactly the significance of the individual components. But on the other hand exactly those facts presented here show that the differentiation of the suture can certainly not satisfactorily be explained as a function of the shell form as I myself once supposed when I tried (Wiedmann, 1963) to interpret the system in the Treatise.

It is true that at first sight the sutures of the Triassic, Jurassic and Cretaceous heteromorphs are similar, and so they are with respect to their small number of elements. In detail, however, clear differences can be recognized between the single heteromorph groups (Text-fig. 4). The same applies to the forms which revert to normal shell coiling, which modified their quadrilobate basic *Bauplan* in the most different directions without, however, essentially departing from it (Text-fig. 17).

If one takes into consideration the extraordinary large variety of shell form among the Cretaceous heteromorphs, of which Text-fig. 16 can only show a small part, then the

*absolute constancy of the quadrilobate suture* in all forms—the deshayesitids excepted—is extremely surprising. Moreover, it is exceedingly difficult to see a functional connexion between the quadrilobate suture of the Cretaceous heteromorphs and the shell form, since, as mentioned, the protoconch and first whorl in which the first septa are formed are normally coiled (Pl. 3, fig. 2).

It is regrettable that none of the prevailing interpretations of the septal function can give a satisfactory explanation for the general increase in the number of lobes and suture slitting in the course of ammonoid phylogeny, or for their reduction in the heteromorphs and pseudoceratitids.

Opposed to the hitherto most plausible theory, proposed by Pfaff (1911), that the ammonite septum satisfied the static requirements of the shell, is the observation that the Mesozoic shells with their complicated septa were certainly not subjected to greater static pressures than those in the Palaeozoic with their simple septa. Moreover, the present-day nautiloids live at greater depths than can be reckoned for many ammonoids; yet it is the nautiloids with the simplest imaginable septal type which have survived, whilst the neo-ammonoids with their (according to Pfaff) perfect response to static demands died out at the end of the Mesozoic. And, finally, it is the extremely fragile heteromorph shells, such as *Acuariceras*, which may have the simplest septal configuration within the Neoammonoidea. New examination of these points and the proposal of a septal terminology by Westermann (1956) have not contributed to clarification of the problem of statics.

The interpretation given by Schindewolf (1950a, p. 167) that the progressive folding of the septal margin can be explained as the 'increasing differentiation of the musculature of the septal skin, which is anchored in the furrows and notches of the septa' [translated] raises certain biological problems, and all the more so since Schindewolf holds at the same time to the idea of a 'pre-septal gas cavity' (Keferstein, 1866, Schmidt, 1925) between the septum and the 'septal skin' (Solger, 1901). But, even if today as a result of the basic investigations made by Denton & Gilpin-Brown (1966) on *Nautilus* we can rule out the presence of such a 'pre-septal gas cavity', the difficulty remains that the animal withdraws its 'septal skin musculature' from each abandoned septum, in order to attach it to each new septum for a short time. We should also expect signs of muscle attachment on the often exceedingly well preserved septa (cf. Schindewolf, 1968, pl. 5).

The supposition is correct that the abdominal mantle epithelium must be seen as a pattern for the septum it builds; why this mantle epithelium experienced an advancing differentiation of its margin is still not clear even after the investigations made by Denton & Gilpin-Brown.

Finally, another functional interpretation of septa is possible, on the basis of the observation of Denton & Gilpin-Brown that in *Nautilus* the epithelium of the inner septal surface forms a kind of drainage system after the dividing-off of a new chamber, to lead away the body fluid which hydrodynamically supported the septum during its formation as soon as possible to the siphuncle from the interior of the chamber. This process is said to be completed with the seventh last chamber in *Nautilus* and one can imagine that a still quicker disposal of this chamber fluid in the ammonites had a certain selection advantage. However, this model also encounters difficulty in so far as the folding of the marginal septum leads the fluid to the periphery of the chamber but not necessarily to the siphuncle which alone can fulfil the function of removal.

An interpretation given by Thompson (1942, p. 847) in which he suggested, as the cause of the differing complexity of folding of septa of the nautiloids and the ammonoids, that the former built an external and the latter an internal shell, is too divorced from the biological facts and needs no further discussion.

B. DEVELOPMENTAL PLASTICITY IN SPACE AND TIME  
IN HETEROMORPHS

A prominent characteristic of the evolution of the heteromorphs is the 'plasticity' peculiar to these forms which expresses itself in a very high variability and a rapid rate of evolution. Neither of these facts has yet been given sufficient weight. Although the extraordinarily high variability of the heteromorphs is clearly recognizable in every homogenous population (e.g. Pl. 1), basic statistical investigations are still not available. The result would without doubt considerably exceed the surprising findings of Reeside & Cobban (1960) on the gastropoditids or of Jones, Murphy & Packard (1965) on the variability in beudanticeratids. First, modest attempts have been made by Wiedmann (1962*b*) on the crioceratitids and anisoceratitids, and by Wiedmann & Dieni (1968) on the lechitids. But unfortunately in heteromorphs the bias towards a 'systematics of individuals' which classifies individuals and not species is still dominant (e.g. Sarkar, 1955).

It is of extreme interest that Kosswig (1963), when describing 'constructive' and 'regressive' evolutionary processes in recent vertebrate faunas, noted a similar high variability as characteristic of his 'regressive' groups. Moreover this high variability of Cretaceous heteromorphs may serve as an indication that the selection pressure here was nil or very small, but not the chief cause of the shell heteromorphy, as perhaps in the Triassic and Jurassic. The origin of the Cretaceous heteromorphs cannot be explained by selection only.

Heteromorphs also change extremely quickly with time. This rapid evolution and the multiplicity of changeable characters (coiling type, sculpture, suture) permit the recognition of the finest developmental steps and predestine the heteromorphs—in particular in the Cretaceous—to be zonal or subzonal fossils. In addition the wide regional distribution of the Cretaceous heteromorphs increases the stratigraphical importance of these forms. Unfortunately this fact has still not become generally accepted, even though it is in the late Cretaceous that we are still far from a generally valid system of standard divisions. Numerous attempts in this direction already exist (Cobban, 1952, 1962; Scott & Cobban, 1964; Casey, 1961; Wiedmann, 1962*b*); however, they have not yet found general acceptance, especially since endemic faunas have been employed in some cases. This endemism of certain heteromorphic groups can be seen as a further hint that some heteromorphs exhibit an extreme adaptation, perhaps to a mode of life closer to the sea floor.

C. PHYLOGENETIC 'LAWS' AND HETEROMORPHS

(1) *Haeckel's biogenetic rule*. It should have become clear from the special discussion that this most disputed of the phylogenetic 'laws' is a very essential basis for the morphogenetic investigation of the heteromorphs and the resulting new conclusions. In numerous and I hope convincing examples it has been possible to show that the early ontogeny accurately recapitulates the ancestral phylogeny, often in the finest detail. The biogenetic rule was therefore one of the essential means of clarifying often very obscure genealogical connexions. At the moment only at the base of the Cretaceous

heteromorphs does a character break remain to which morphogenetic investigations can contribute no explanation.

(2) *Cope's rule*. The view that phylogeny leads as a matter of course to increase in size which on 'orthogenetically' advancing in many cases exceeds the optimum of the conditions for life and consequently results in extinction (Schindewolf, 1950a, pp. 338 ff.) is not generally accepted today. There are without doubt numerous evolutionary series, from the Foraminifera to the vertebrates, in which increase in size produced an advantage in selection. However, there are just as many examples in which evolution went in exactly the opposite direction and resulted in dwarfs. An example is to be found among the ammonites, contrary to the opinions of Schindewolf (1950a), Erben (1950) or Müller (1955). The giant ammonites of the late Cretaceous (*Parapuzosia seppenradensis* from the Santonian/Campanian boundary), often used as a sign of the imminent total extinction of the ammonoids, neither stand at the end of ammonite evolution nor do they introduce the demise of the puzosiids, which together with the remaining ammonite families disappear only at the Maastrichtian/Danian boundary.

Collections made personally in the region of this boundary reveal rather that the at present youngest ammonites from the late Maastrichtian of Zumaya, Prov. Guipúzcoa, Spain (Pl. 3, figs. 3-10), are representatives of a pronounced dwarf fauna, the determination of which is very difficult as a result. This may serve as evidence that in the latest Maastrichtian optimal living conditions certainly did not exist for the ammonoids. It is interesting that Herm (1965, p. 320) also recognized a distinct dwarf fauna among the globotruncanids in the last metres of the Maastrichtian of the same section. The globotruncanids were likewise hit by mass extinction on the Cretaceous/Tertiary boundary.

For these reasons it is certainly not to be wondered at that the heteromorphs too do not obey Cope's rule of phylogenetic increase in size. It is true that the ancestral forms of the Cretaceous Ancyloceratina, the protancyloceratids, leptoceratids and bochianitids, must be reckoned with the smallest representatives of the whole suborder, but the size maximum lies clearly with certain ancyloceratids of the Barremian and Aptian and certainly not with the heteromorphs of the late Cretaceous, amongst which decidedly small forms such as *Axonoceras*, *Jouaniceras* and *Pteroscapites* are to be found. In the Jurassic heteromorphs indeed a phylogenetic decrease in size can be stated, in so far as the large-shelled genus *Spiroceras* stands at the beginning and the delicate *Acuariceras* at the end of this lineage.

(3) *Dollo's 'law'*. The most undisputed of the phylogenetic 'laws' has been up to the present the 'law of irreversibility', 'that an organism is unable to return, even partially, to a previous stage already realized in the ranks of its ancestors' (translated from Dollo, 1893). Palaeontologists especially have emphasized the absolute validity of this 'law' as a property of the historical character of organic evolution (Abel, 1929; Beurlen, 1930, 1937; Dacqué, 1935; Schindewolf, 1950a). On the other hand neontologists and in particular geneticists have always brought forward arguments against a too strict application of this rule (Plate, 1904, 1910; Oudemans, 1920; Fejérváry 1926; Weidenreich, 1931; Timoféeff-Ressovsky, 1937; Remane, 1952, 1967). After

Plate it was Remane (1952, pp. 286 ff.) who most clearly drew up the grounds for reflexion on the applicability and validity of a 'law' of irreversibility. His objections resulted as a consequence of (1) the reflexion that if evolution is essentially dependent upon mutations then the possibility of reverse mutations cannot be *a priori* ruled out (cf. Timoféeff-Ressovsky, 1937; Muller, 1939; Schwanz, 1959), and also (2) from the recognition of the pleiotropic character of most genes (Rensch, 1939).

Now the heteromorph ammonoids and their descendants can be cited as a credible example from the field of palaeontology of the occurrence of reverse mutations. That 'a re-coiling of forms which have become secondarily rod-like does not occur', since 'it involves degenerate end-members of disappearing lineages' (translated from Schindewolf, 1950a, p. 218), has not been confirmed. On the contrary, the heteromorphs are in fact not only secondarily re-coiled but tertiarily, if one takes into account the primary coiling early in their evolution in the Devonian, and they may even quaternarily uncoil (Text-fig. 15e). Moreover the reversion by no means affected only single characters, which might be taken as a restriction to its operation: in the deshaysitids, for example, not only is a hoplitid sculpture type acquired and the shell newly recoiled, but also simultaneously the reduction of the number of lobe elements is reversed. An almost perfect reversion is shown above all by the return of the Cretaceous heteromorphs to the quadrilobate primary suture of the Triassic meso-ammonoids. Only the presence of a median saddle in the external lobe *E* shows the heteromorphs to be an advanced form-group (Text-fig. 4, IIIa).

As a rule of evolution and with reference to the whole organism—of which only a modest fraction is available to the palaeontologist—Dollo's 'law' may continue to have unrestricted validity but in making it absolute a danger arises just as great as that involved in a too strict interpretation of the biogenetic rule.

#### D. FACTORS IN HETEROMORPH EVOLUTION

Triassic, Jurassic and Cretaceous heteromorphs cannot be dismissed as degenerate end-forms and neither can a common cause for their origin be accepted: as demonstrated above, those in the Triassic and Jurassic are connected by transitions with normally coiled ancestors, whereas those in the Cretaceous arose suddenly. The former have been interpreted above as extreme adaptations which were eradicated by small environmental changes on the Triassic/Jurassic boundary; the latter as aberrant forms without any selection advantage, a spontaneous reverse mutation having affected the shell form and primary suture suddenly and simultaneously. That just this group should have been by far the most phylogenetically successful remains surprising and can partly be explained by the partial return to a normal shell coil. Two points are thereby demonstrated:

(1) The experiments allowed to geneticists are denied to palaeontologists, who can, however, also make statements concerning mutability, genetic constitution and possibly even the linkage of genes by a systematic study of entire evolutionary series, the origin of lineages, and reverse mutations—especially if, as here, the latter show character and thus perhaps gene coupling. The gap between palaeontology and genetics can thus be considerably narrowed.

(2) In view of the results here presented the phylogeny of the heteromorphic ammonoids can now also be explained as an interplay between mutation and selection only. Endogenic factors of some kind (extravagance of form, degeneration, typolysis) must also be rejected in the origin and development of the heteromorph ammonites just as for the other heteromorph invertebrates.

I agree completely with Kosswig (1963) that evolution comprises both constructive and regressive processes, which many times go hand in hand and which are partly interdependent. Many of our recent stocks are regressive in comparison with their forerunners. And thus there is no reason to label these form-groups as 'inferior' or to relate their appearance to the problem of phyletic extinction.

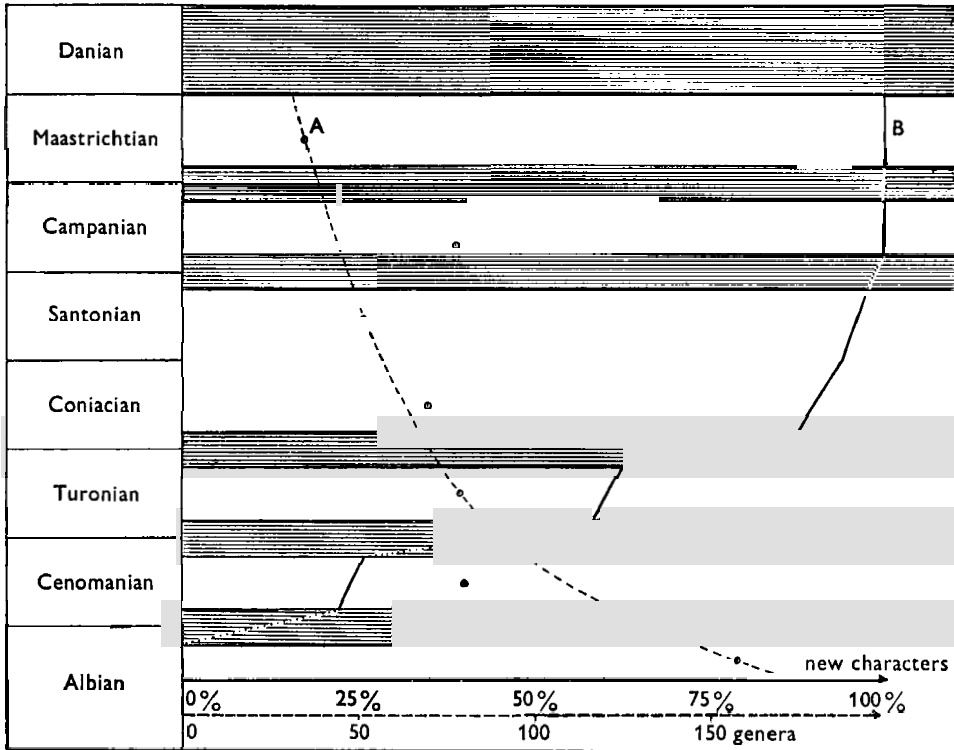
There is therefore just as little support from palaeontology for the acceptance of a *Paracme* in the sense of Haeckel or Schindewolf's 'typolysis' as neontologists have long recognized exists in their own field: there is 'no ground for the acceptance of an incalculable autonomy of development' (translated from Rensch, 1947, p. 240). A two-staged phylogeny, however, as proposed by Wedekind (1920) and supported by Schindewolf in 1936, Simpson (1944), Rensch (1947), Huxley (1958), appears to be a quite adequate explanation of the observed facts and is fully in accord with the theory of selection.

#### E. AMMONOID EXTINCTION

The way is now clear for a discussion of the actual factors which led to the extinction of the so-called heteromorphs and eventually the ammonoids as a whole. The arguments range from the biologic-ecological through diastrophic-geological to the catastrophic-cosmic, the latter in particular having been called on to explain the faunal break on the Cretaceous/Tertiary boundary. It is now scarcely possible to bring new arguments forward for discussion but it nevertheless seems necessary to examine the statistics soberly and to set aside some popular prejudices. To make biological competition responsible for the extinction of the ammonoids on the Cretaceous/Tertiary boundary (Simpson, Pittendrigh & Tiffany, 1957; Nicol, 1961; Newell, 1962) is from the outset scarcely promising. It is contradicted by the fact that very many totally different groups of organisms belonging to a wide variety of biotopes are more or less synchronously affected by this critical caesura. Neither is a suitable faunal competitor available to explain the total extinction of the Ceratitina on the Triassic/Jurassic boundary, apart from the ammonoids themselves which in the form of the Neo-ammonoidea replace the ceratitids at the base of the Jurassic with a massive and rapid radiation.

The influence of cosmic factors (cosmic rays, super-novae), brought into the discussion of the era boundaries and thus the Cretaceous/Tertiary break by Schindewolf (1950*b*, 1954) must, as a spontaneous event, be recognizable statistically. And indeed the investigations made by Herm (1965), for example, on the globotruncanids of the late Cretaceous speak for a unique catastrophic event just before the Maastrichtian/Danian boundary, where heteromorph and dwarfed forms in these pelagic foraminifers appear quite spontaneously. A quite different picture is shown, however, by the ammonoids. Although, as already mentioned, it is true that dwarf forms also appear

just before the Danian boundary, a quantitative statistical analysis of the genera (Text-fig. 21, A) shows that the extinction of the group can in no way be seen as connected with a unique catastrophic occurrence at the end of the Cretaceous. The reduction in the number of genera, and finally the demise of the ammonoids, begins at the base of the Upper Cretaceous and progresses continuously in a paraboloid curve to zero at the base of the Danian. If we reject the existence of inherent endogenic factors this regressive tendency, obvious from the Cenomanian on, can only be comprehended as symptomatic of a continuously effective, detrimental environmental influence.



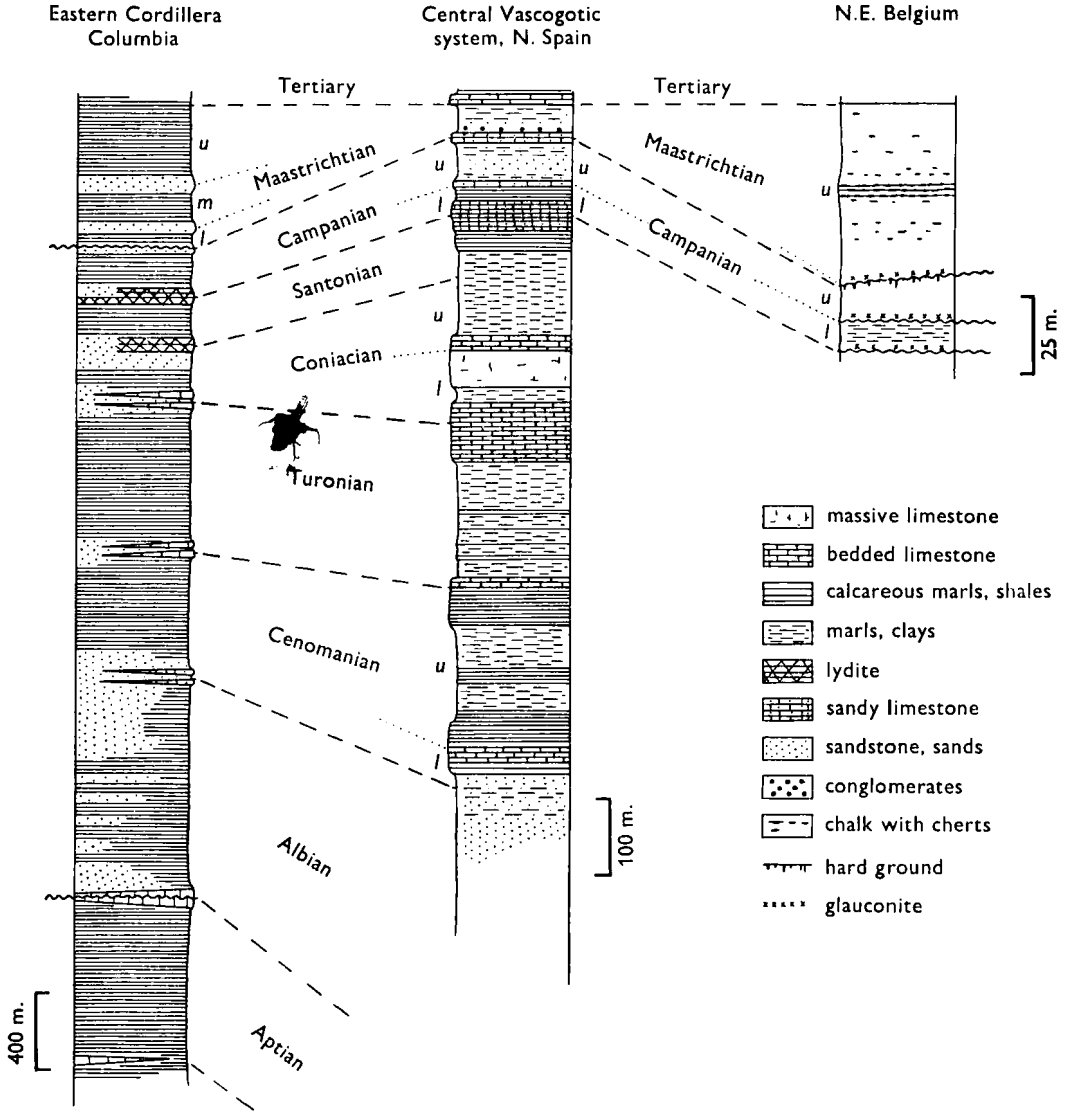
How this may have occurred is clarified by a second curve (Fig. 21, B), in which the trend described above is quantified in a different manner but placed on the same time scale. As a measure of evolution the character breaks recognizable at the base of each new ammonite family have been used instead of the number of genera. A similar broken paraboloid curve results and in it a clear progression can be seen in the Cenomanian and Turonian with an evolutionary deceleration and stagnation from the Coniacian which achieved its climax in the Campanian. In this stage and the following Maastrichtian qualitatively new characters of family rank cannot be observed. Thus the mutability and evolutionary capability of the ammonites began to diminish a con-



siderable time before their extinction: the crisis they suffered was not sudden but drawn out.

It is notable that the discontinuities in evolution or character breaks always coincide with stage boundaries at which the ammonoids appear to have been both positively (higher mutability) and negatively (higher mortality) affected. Within the stages evolution followed a continuous 'normal' course.

Careful biostratigraphic investigations in recent years have revealed that the



Text-fig. 22. The marine regressions at the Upper Cretaceous stage boundaries in Columbia [after Bürgl, 1964], Northern Spain [from Wiedmann, MS.] and Belgium [after F. Schmid, 1959]. Not to scale.

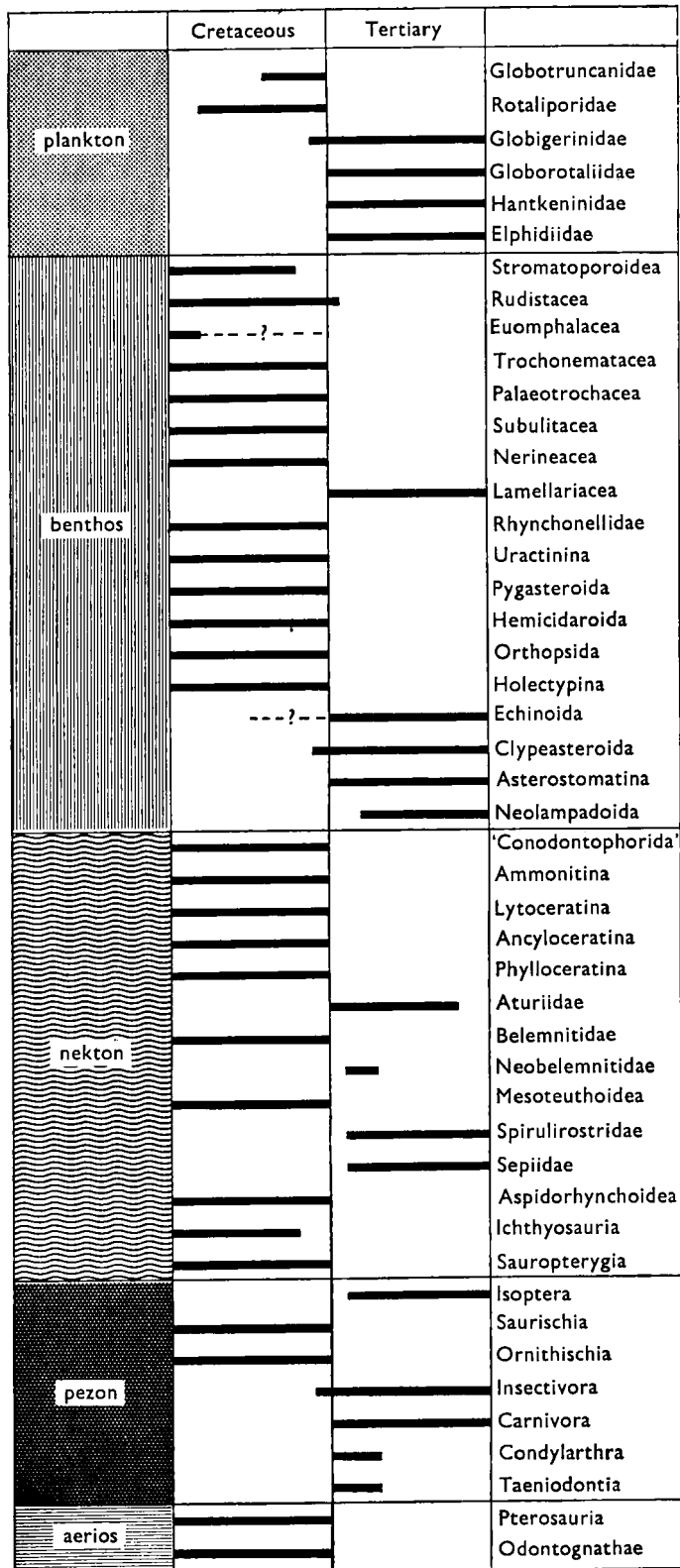
Cretaceous stage boundaries are marked on a broad regional scale (Schmid, 1959; Wiedmann, 1959; Bürgl, 1964) by breaks in the deposition of the cephalopod facies (sandy detritus and 'Grenzkalke' in Spain and Colombia, hard-grounds and omission horizons in wide areas of north-west Europe) (Text-fig. 22), which indicate 'rhythmic' regressions in just those shelf and epicontinental seas favoured by the ammonites. At these breaks which are quite typically for the Upper Cretaceous sedimentation the progress of evolution is upset over broad areas of the world, and only with the cephalopod favourable ingression of the succeeding stage is there a sudden resumption by a new, in part strongly modified, fauna. Without appealing to Cuvier's and D'Orbigny's catastrophism, a causal connexion between the alterations and breaks in sedimentation and those in organic evolution—especially those affecting whole biotopes—can scarcely be disputed. Only the exact nature of that relationship is in question.

It is quite plausible to suppose that the repeated retreating of the sea forced the ammonoids to evacuate their favoured environment on the shelves and continental margins and to migrate to deep ocean regions, from which we have no record. From the magnitude of the morphological break shown by the 'new' faunas (e.g. the mammitids on the base of the Turonian, the Coniacian tissotiids or the Santonian texanitids) on their appearance with the following ingression, one must conclude that either the break on the stage boundary represents a longer period of time than we have yet supposed, or that the necessity of adapting to a new environment brought with it a rise in the rate of evolution. With the return of the sea the ammonoids were once more able to colonize their favourite milieu, and with an unusually rich variety of forms. The scale of this, as I believe, environmentally determined radiation shows a tendency to weaken from break to break but still manifests itself within the individual stages, in so far as the greatest number and variety of species is found quite clearly at the base of each stage.

This justifies the supposition that the evolutionary potential of the late Cretaceous ammonites was so persistently weakened by the 'rhythmic' fluctuation of sea level (for which no acceptable mechanism has yet been proposed) that it needed only a small external impetus at the end of the Maastrichtian for the total extinction of this *Bauplan* previously so important in the Palaeozoic and Mesozoic. This impetus was provided by the almost world-wide regression of the Danian sea. The epirogenic events in the late Triassic followed a similar course and may have precipitated the faunal break on the Triassic/Jurassic boundary.

An objection to this theory which it is difficult to refute is that, on the Cretaceous/Tertiary or more exactly the Maastrichtian/Danian boundary, groups of organisms occupying almost all marine and continental biotopes die out almost simultaneously. Here also a statistical evaluation adds clarity to the picture of the extent to which the marine nektonic, planktonic and benthonic faunas, the land animals and insects (*Pezon*; Gr. τὸ πεζόν = footfolk), or the flying forms (*Aerios*; Gr. ἀέριος = flying) were affected by this sharp caesura (Text-fig. 23).

Such a scheme necessitates certain simplifications. Thus the benthonic foraminifera are here included with the planktonic; as an exception families are given in order to bring out the very elcar faunal break in the planktonic forms. All the gastropod groups are included under the



Text-fig. 23. The mass extinction at the Cretaceous/Tertiary boundary classified according to biotope.

heading 'benthos'. It must be mentioned that the lamellibranchs were more severely affected (Nicol, 1961) than is evident from the diagram. Also the semiaquatic habit of certain tetrapod groups is not adequately expressed.

Despite these shortcomings the scheme presented here shows clearly that the maximal extinction is to be found in the benthonic and nektonic inhabitants of the shelf and epicontinental seas: echinoderms, gastropods, di- and tetrabranchiate cephalopods. The dominance of benthos and the high proportion of sedentary forms (rudists, Stromatoporoidea, Rhynchonellidae, echinoids) underlines the supposed connexion between the 'rhythmic' regressions of the epicontinental sea and the at first continuous reduction and finally the extinction of numerous faunal elements in just this region. The simultaneously affected planktonic and continental faunas are markedly reduced and for their extinction rational arguments must certainly be available. Above all, however, the synchronous flourishing of new groups, which in part began in the Cretaceous (globigerinas, insectivores), also does not require an additional cosmic motivation but may be explained by the invasion of biotopes thinned by a high drop-out rate.

It is therefore possible to show, I believe, that there is just as little reason to appeal to immanent endogenic or cosmic factors to explain the extinction of the ammonites as for the faunal break on the Cretaceous/Tertiary boundary. As has been suggested already by Moore (1950, 1952) and Newell (1952, 1956) for the Permian/Triassic boundary, I believe with Ginsburg (1965) that also in the late Cretaceous the fluctuations of sea level provide sufficient ground for the gradual extinction of numerous Mesozoic groups of organisms. The observations presented by Ginsburg, that a variety of inhabitants of the Mesozoic shelves (terebratulids, echinoids, crinoids, and even fishes) have removed to the continental margin where they have survived with many original characters up to the present, is a strong support for these ideas.

#### IV. SUMMARY

The heteromorph ammonoids are quoted as a favourite example of degeneration and the decline of a *Bauplan* 'condemned' to extinction. With astonishing tenacity this view of the heteromorphs as 'phylogenetic end-forms' has embedded itself in the palaeontological literature and is still current. This is contradicted by the most recent investigations, directed especially at the Cretaceous heteromorphs, which necessitate correction of the typolysis concept as well as modification of the most uncontested of the phylogenetic 'laws', Dollo's 'law of irreversibility'. Contrary to the usual textbook hypothesis, the heteromorphs return in several evolutionary lineages to normal coiling of the shell and, in general, to a phylogenetically older type of suture line. At the same time these results encourage fresh reflexion on possible exogenous causes of phylogenetic extinction of the ammonoids. A clear causal connexion exists between this extinction and the far-reaching epirogenic changes in sea level in the late Cretaceous; cosmic explanations are unnecessary.

In conclusion it may be added that the precipitate formulation of phylogenetic 'laws' and 'principles' based on too little basic information has encumbered this branch of palaeontology with a stifling set of prejudices rather than providing it with

guide lines crystallized from long experience and observation. It is vitally necessary in the interests of palaeontology that interpretation and observation be separated far more than has been the case in the past.

My grateful thanks are above all due to Professor Dr O. H. Schindewolf, who gave much encouragement and many suggestions in particular with regard to the morphogenetic methods of investigation. I am indebted to him and to the Akademie der Wissenschaften und der Literatur zu Mainz for a travelling allowance for the investigation of the initial forms of the Cretaceous heteromorphs in the Tithonian and Berriasian of Tunisia. Dr H. A. Stalder, Bern, was kind enough to make available for preparation a number of leptoceratids from the Ooster collection. Mr W. Wetzel is responsible for the high quality of the photographs, and Mr F. Springer drew the majority of the diagrams. Last but not least I thank my colleague and friend Dr D. A. B. Pearson for critical reading and translation of the typescript.

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## EXPLANATION OF PLATES

## PLATE 1

Faunal spectrum of Berriasian ammonoids from Djebel Nara, Central Tunisia. Note the variability of smooth (*Bochianites*) and ribbed (*Protancyloceras*) heteromorphs. The contemporaneous normally coiled specimens belong to the perisphinctid genera *Berriasella*, *Neocosmoceras*, *Spiticerias* and *Neocomites* and to the haploceratid subgenus *Neolissoceras*. [Leg. Dietl & Wiedmann.]

## PLATE 2

Initial coils of true heteromorphs and 'false hoplitids'.

Fig. 1. The douvilleiceratid *Paraspiticerias schindewolfi* Wiedm. Holotype, Geol.-paläont. Inst. Tübingen coll. Ce 1310/47. Lower Barremian, La Querola/Sierra Mariola (Alicante, Spain). 15/1. [Leg. Wiedmann.] *a*: Lateral view; *b*: Ventral view.

Fig. 2. *Leptoceras pumilum* Uhlig (see Uhlig 1883, Pl. 29, fig. 6*a*). Paratypes, Staatl. Sammlg. f. Paläont. München AS III 98. Barremian, Straconka (Galician Beskides). Living chamber preserved. 4/1.

## PLATE 3

The Berriasian heteromorph *Leptoceras studeri* (Ooster).

Fig. 1. Specimen with initial part of living chamber. Geol.-paläont. Inst. Tübingen coll. Ce 1372/1 Berriasian, Thuner See (Switzerland). 6/1.

Fig. 2. Involute first whorl and protoconch. As can be seen, the straightening of the shell takes place with the formation of the so-called nepionic constriction—this means at the end of the larval stage. The shell is broken at the 11th septal surface. Geol. paläont. Inst. Tübingen coll. Ce 1372/2. Berriasian Rufigraben-Justistal (Switzerland). circ. 25/1.

The last known ammonites from the top Maastrichtian of Zumaya (Guipúzcoa, Spain).

Fig. 3. *Scaphites* (*Indoscaphites*) *pavana* (Forbes)?—Geol. -paläont. Inst. Tübingen coll. Ce 1372/3. 2/1

Fig. 4. *Brahmaites haugi* (Seunes)?—Geol.-paläont. Inst. Tübingen coll. Ce 1372/4. 2/1.

Fig. 5. *Pachydiscus* (*P.*) sp.ind.—Geol.-paläont. Inst. Tübingen coll. Ce 1372/5. 2/1.

Fig. 6. *Scaphites* (*Indoscaphites*) *pavana* (Forbes)?—Geol. -paläont. Inst. Tübingen coll. Ce 1372/6. 2/1

Fig. 7. *Pachydiscus* (*P.*) *llarenai* Wiedm.?—Staatl. Sammlg. f. Paläont. München 1956 I 554. 2/1.

Fig. 8. *Pachydiscus* (*P.*) sp.ind.—Geol.-paläont. Inst. Tübingen coll. Ce 1372/7. 1/1.

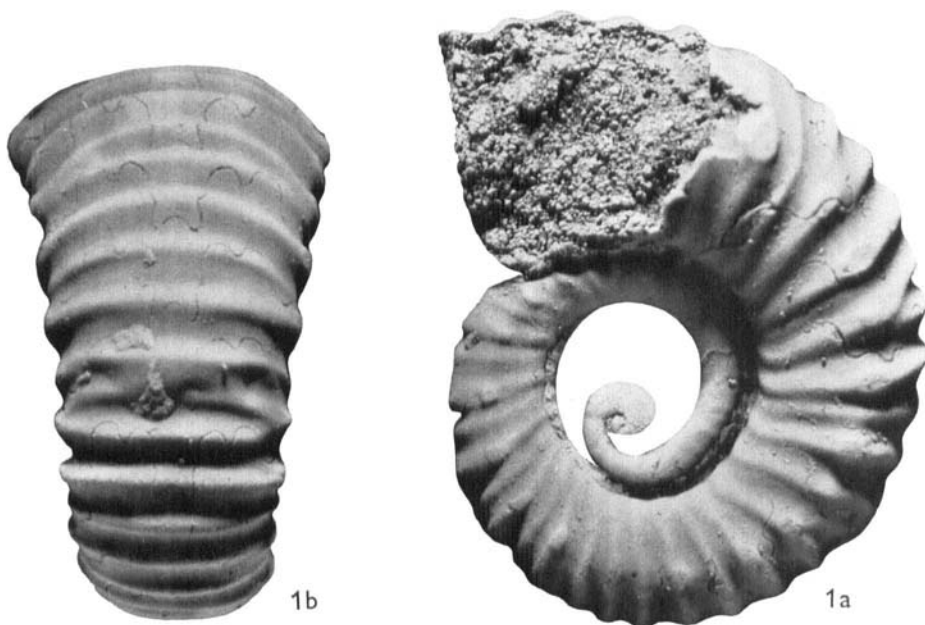
Fig. 9. *Diplomoceras* (*Glyptoxoceras*) *subcompressum* (Forbes)?—Geol.-paläont. Inst. Tübingen coll. C 1372/8. 1/1.

Fig. 10. *Pachydiscus* (*P.*) *llarenai* Wiedm.?—Geol.-paläont. Inst. Tübingen coll. Ce 1372/9. 1/1.

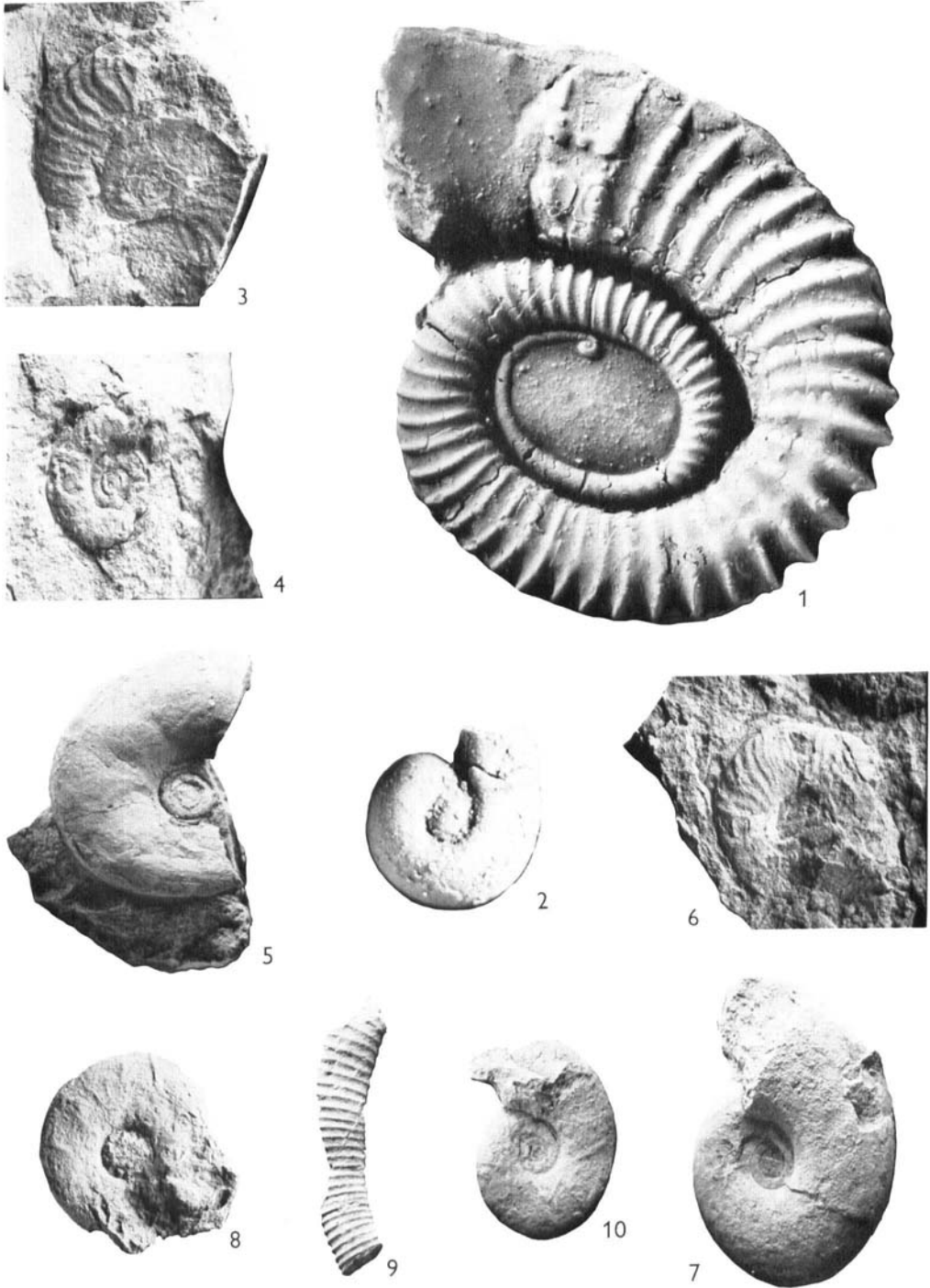
Figs 3, 4, 6, 8 leg. Wiedmann; Figs 5, 7, 9, 10 leg. Gómez de Llarena.







JOST WIEDMANN



JOST WIEDMANN