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SUTURAL SIMPLIFICATION IN PHYSODOCERATINAE (ASPIDOCERATIDAE, AMMONITINA)

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RESUMEN

El análisis estructural de la interrelación concha-septo en algunos ammonites del Jurásico superior lleva a concluir que las simplificaciones suturales aparecidas a lo largo de la filogenia fueron originadas por alteraciones ocurridas en la morfología externa de la concha. En el caso concreto de la subfamilia Physodoceratinae, la simplificación observada en la morfología de la sutura puede tener un doble origen. En primer lugar, un incremento en el tamaño de los tubérculos periumbilicales puede determinar una pérdida de profundidad de los elementos de la sutura, siempre acompañada de una disminución en las indentaciones (frilling) de sillas y lóbulos. En otros casos el acortamiento en profundidad está determinado por una disminución de la tasa de expansión de la espira, sin que se observe un acortamiento aparente de las ramificaciones secundarias.

Palabras clave: *ammonites, morfología construccional, sutura septal, Physodoceratinae, Physodoceras, Benetticeras, Orthapidoceras, Schaireira, Pseudowaagenia.*

ABSTRACT

The estructural analysis of the shell septum interrelationship in some Jurassic ammonites allows us to conclude that sutural simplifications occurred throughout the phylogeny, were originated by alterations in the external morphology of the shell. In the case of Physodoceratinae the simplification observed in the morphology of the septal suture may have a double origin. First, an increase in the size of periumbilical tubercles may determine a shallowing of sutural elements and a shortening of saddle and lobe frilling. In other cases, shallowing is determined by a decrease in the whorl expansion rate, an apparent shortening of secondary branching not being observed.

Key words: *ammonites, constructional morphology, septal suture, Physodoceratinae, Physodoceras, Benetticeras, Orthaspidoceras, Shaireria, Pseudowaagenia.*

Introducción

A fascinating aspect which has attracted great attention in ammonite paleontology is the study of the functionality of the suture and the interpretation of the different changes affecting it. A very commonly observed alteration is the loss of indentation and depth of sutural elements, that is to say, simplification.

At the present moment there are several points of view as to the real function of ammonite septa. Some views consider the septum as a structure which counteracts the hydrostatic pressure exerted on the phragmocone (Westermann, 1975). Other authors (Henderson, 1984; Ebel, 1985) claim a primary function of muscular attachment.

In the "pneu-model" (Seilacher, 1975; Bayer, 1978a, 1978b) septal morphology is considered as a result of pressure differences in the body-cameral gas interphase, so that sutural morphology seems to be connected with the pressure distribution along the whorl section and with locomotion activity (Bayer, 1978b, p. 153), thus depending only partly or indirectly on the depth of the organism's life.

In this paper we will focus on the analysis of some particular cases of Physodoceratinae, where a noticiable simplification and/or shallowing of

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sutural elements is appreciated. We are going to work on the phylogeny proposed by Checa (1985) and on the analysis of the structural interrelations present in Physodoceratinae (Checa, 1986a, 1986b). Also we should explain that our observations refer exclusively to the morphological simplification noted in individual sutural elements (always taking equivalent ontogenetic stages) considered apart from the sutural composition expressed as the number of umbilical lobes.

Simplification due to changes in the size of tuberculation

The cases reported are the following:

- *Benetticeras benettii* (Fig. 1B): the "normal" previous sutural morphology is that of *Physodoceras wolfi* and the main ornamental change consists of a considerable increase in the coarsening of the tuberculation. In both species the suture includes an incipient U_5 and the position of the periumbilical ornamental elements coincides with the saddle U_2/U_3.
- *Orthaspidoceras lallierianum* (Fig. 1D): this species, a homeomorph of the above described, is included in a phylogenetic line where, once more, the tendency consists of the increase in size of the periumbilical tubercles. The original non-simplified suture is, again, that of *Ph. wolfi*, though also containig an intermediate form, *O. ziegleri* (Fig. 1C), whose suture line already shows a certain loss of sutural complexity.
- *Schaireria pipini* (Fig. 2B): we may again consider this species as a homeomorph of the two ones above discussed, although it belongs to an evolutive line where the "normal" original suture, composed of six umbilical lobes, is that of *Sch. neumayri*. The remaining forms included in this evolutive line show, as does *Sch. pipini*, a suture with a high degree of simplification, although there is no appreciable shallowing of the elements.

Both *O. lallierianum* and *Btt. benettii* have *Ph. wolfi* as their common ancestor (Fig. 1). As has been stated elsewhere (Checa, 1986a) the size of the individual tubercles is correlated to that of the saddle U_2/U_3, upon which the ornamentation grows, due to the plastic nature of sutural changes in these forms. In *Ph. wolfi*, in coarsely tuberculate specimens, we already see extreme cases of stretching and subdivision of the saddle U_2/U_3 (Schindewolf anomaly). If we take into account the fact that from this species till *Btt. benettii* and *O. lallierianum* there exists an accentuation of the tendency leading to the increase in the coarseness of ornamentation, we may suppose that the sucessive lengthenings of the U_2/U_3 saddle will lead to the surpassing of a hypothetical limit of stability; as a consequence, a morphological reorganization would take place, possibly related to the fractal pattern of growth of ammonitic septal suture (Damiani, 1986). A considerable loss of indentation and depth of the sutural elements affected, that is to say, their simplification takes also about. Given again the fractal nature of the suture line, it must maintain a homogeneous composition in any case, so that the reorganization of the rest of the suture must be induced as a consequence of the partial remodelling noted in U_2/U_3.

The case of *Sch. pipini*, although differing from those mentioned above, may be explained by reference to a similar process. In this case an increase in tuberculation coarsening takes place once again, though it is not so spectacular as in *Orthaspidoceras* and *Benetticeras*. However, the suture-ornamentation relationship is now different, the tubercles being placed on the lobe U_3. As has been observed (Checa, 1986a) the lobes could be less capable of lengthening than the saddles. In *Sch. pipini* this fact is accentuated by the clearly internal position of U_3, so that a fairly weak lengthening would give rise to a complete sutural reorganization (Fig. 2). In this case we do not appreciate any significant change in depth of sutural elements.

Another interesing feature is the apparent shortening of secondary fluting (folioles), specially at the lateral portions of lobes and saddles. This loss of indentation has a special interest as regards present day hypotheses on septal functionality, and concretely in relation to that which contemplates sutural design as a mechanism of additional support of the outer shell against hidrostatic pressure. In fact, second order fluting certainly constitutes a remarkable portion of sutural length and their loss or reduction would considerably increase the unsupported shell area. Within the modifications above exposed it is possible to consider that the intensity of the expansion must be proportional to the magnitude of the resulting tubercular projection.

As along a single tubercle the distance perpendicularly projected to the flank decreases from centre to peryphery according to the longitudinal profil of the tubercle, it is to be supposed that the required expansion follows a similar value curve. Thus, the intensity of the expansion will vary depending on the point considered, so that the affected sutural portion will also display "zones" of different lengthening whose boundaries will, in

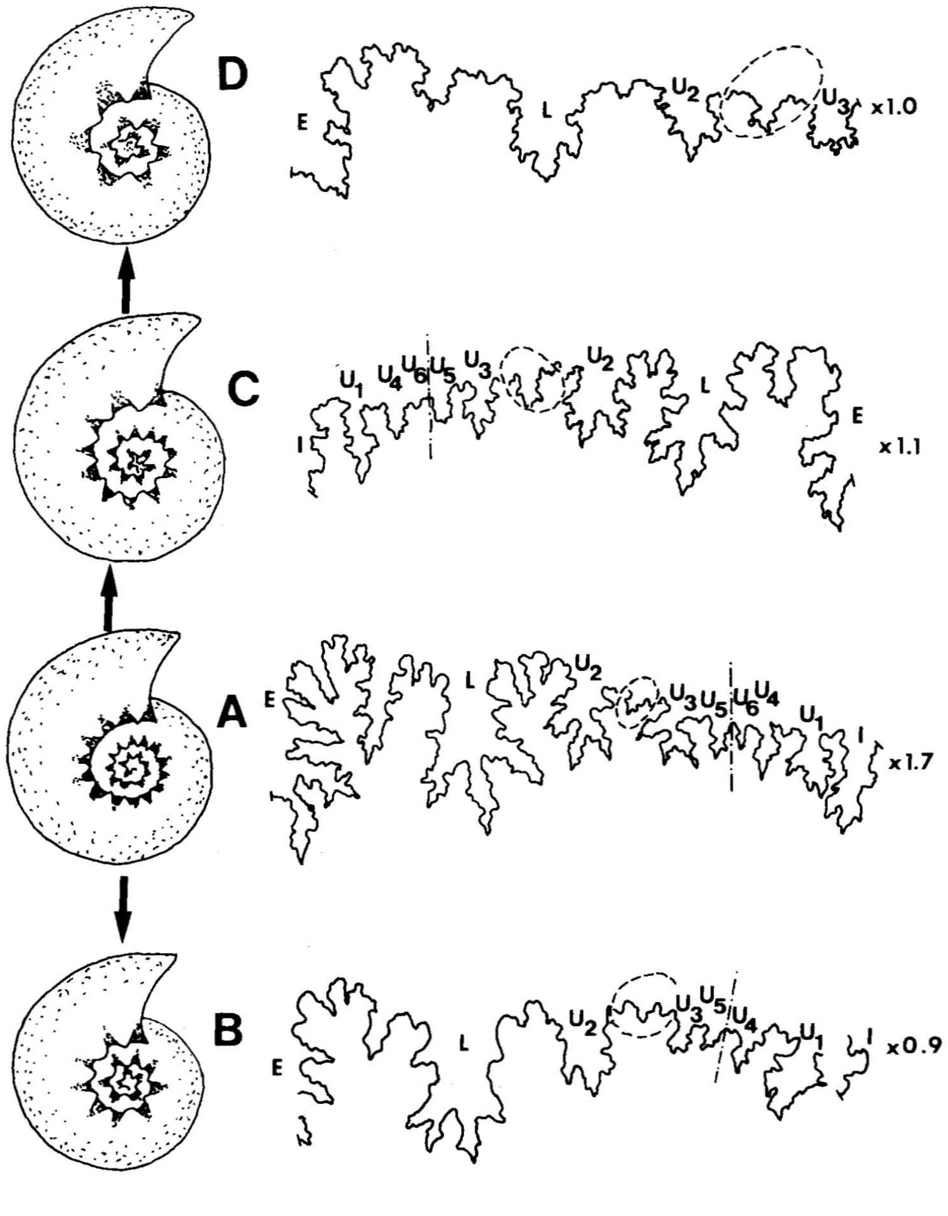

Fig. 1.—Schematic representation and suture of: A) *Physodoceras wolfi* (Ch.C_2.8); B) *Benetticeras benettii* (K.Q10.24.10); C) *Orthaspidoceras ziegleri* (F.G_{14}.6.5); D) *Orthaspidoceras lallierianum* (SS19). Arrows indicate phylogenetic connections.

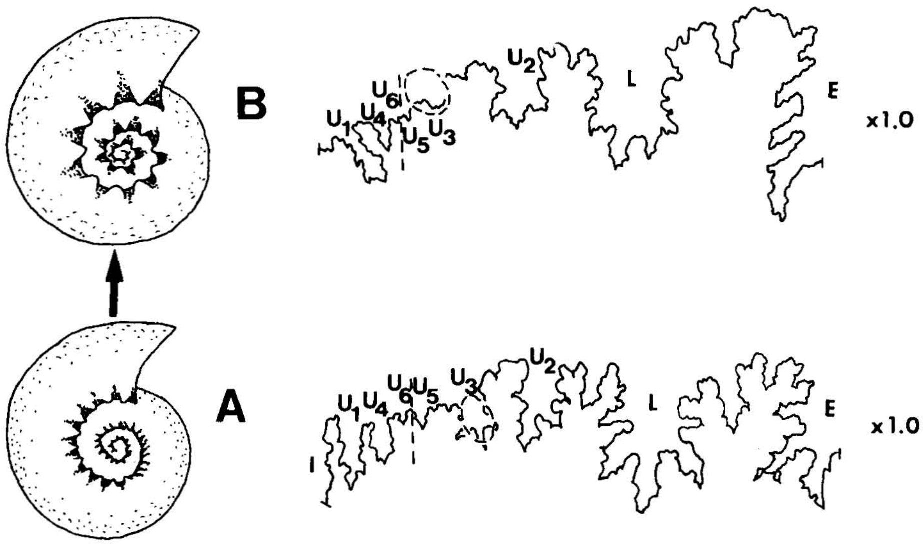

Fig. 2.—Schematic representation and suture of: A) *Schaireria neumayri* (F.G_{15}.14.1); B) *Schaireria pipini* (F.G_{11}.5.2).

principle, be continuous. On the other hand, given the plastic behaviour of the suture and the existence of "active centres" of expansion, there is no reason why intermediate spaces between two centres need to display a homogeneous compression along their entire width. In general terms, it may be supposed that shortening will be maximal at points closest to "pushing" zones and minimal at ones farthest from them. Bearing this in mind, it is possible to modify the scheme obtained for *O. lallierianum* and *Btt. benettii* by establishing strips of differential lengthening affecting saddles and differential compression along lobes. In *Sch. pipini*, inversely, elements affected by radial lengthening are lobes. In any case, total compression in lobes must be equivalent to lengthening undergone by saddles or viceversa, as circumpherential septal length remains constant.

In summary, lateral portions of saddles and lobes, profusely fluted, coincide in both cases with longitudinal strips of minimal radial lengthening and maximal radial shortening, so that the final result should be a marked reduction in size of branching present (Fig. 3).

Simplification due to changes in growth spiral parameters

This modality is well seen in the evolutive line of *Pseudowaagenia*. Here we can appreciate a marked reduction in the involution from *Psw. micropla* (lower Kimmeridgian) until *Psw. acanthomphala* (upper Kimmeridgian) which shows a noticeably simplified sutural desing (Fig. 4). *Psw. haynaldi* (lower-middle Kimmeridgian), whose suture suffers a slight loss of complication, may be considered as an intermediate species between the two. These morphological variations correspond to type 3 described in Checa (1986a) and first modality in Checa (1986b), consisting of a loss of shell wall at the umbilical seam followed by a subsequent reorganization of the section, whose result could be that of maintaining the periumbilical elements (tubercles) parallel to the equatorial plane; in this way, sections similar to ancestral ones are obtained, even though with a comparatively smaller surface (always considering equivalent ontogenetic stages). At this point, a first assumption can be made: the amplitude (width) of sutural elements is retained throughout the phylogenetic trajectory (unless there are superimposed ornamental variations of the type previously described).

On the other hand, width and depth of sutural elements depend on the widest distances to be spanned respectively (Seilacher, 1975). Moreover, it is possible to assert that, as soon as the amplitude of septal folds is imposed as a structural inheritance, their depth, among related forms, varies as a function of the distance to septum centre. Given that throughout the phylogenetic series, from *Psw. micropla* till *Psw. acanthomphala* section area decreases proportionately through the above mentioned process (considering a transformation by Cartesian coordinates), it is

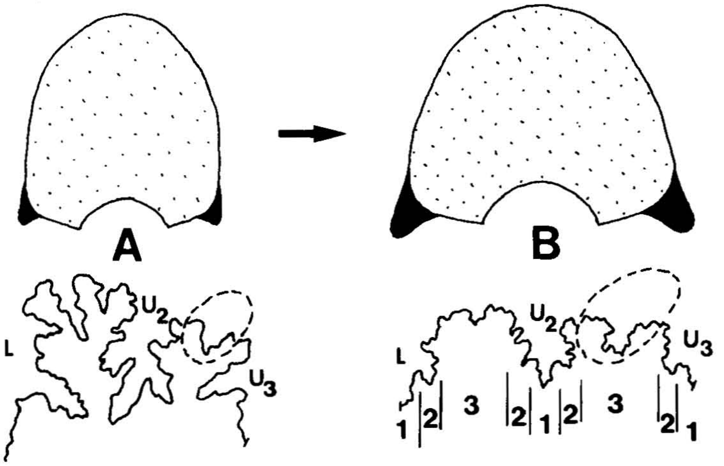

Fig. 3.—Shortening of sutural branching (folioles) as a consequence of tubercular coarsening from A) *Physodoceras wolfi* (Ch.C_2.8) to B) *Orthaspidoceras lallierianum* (SS19). 1: zone of minimal shortening; 2: zone of maximal shortening-minimal lengthening; 3: zone of maximal lengthening.

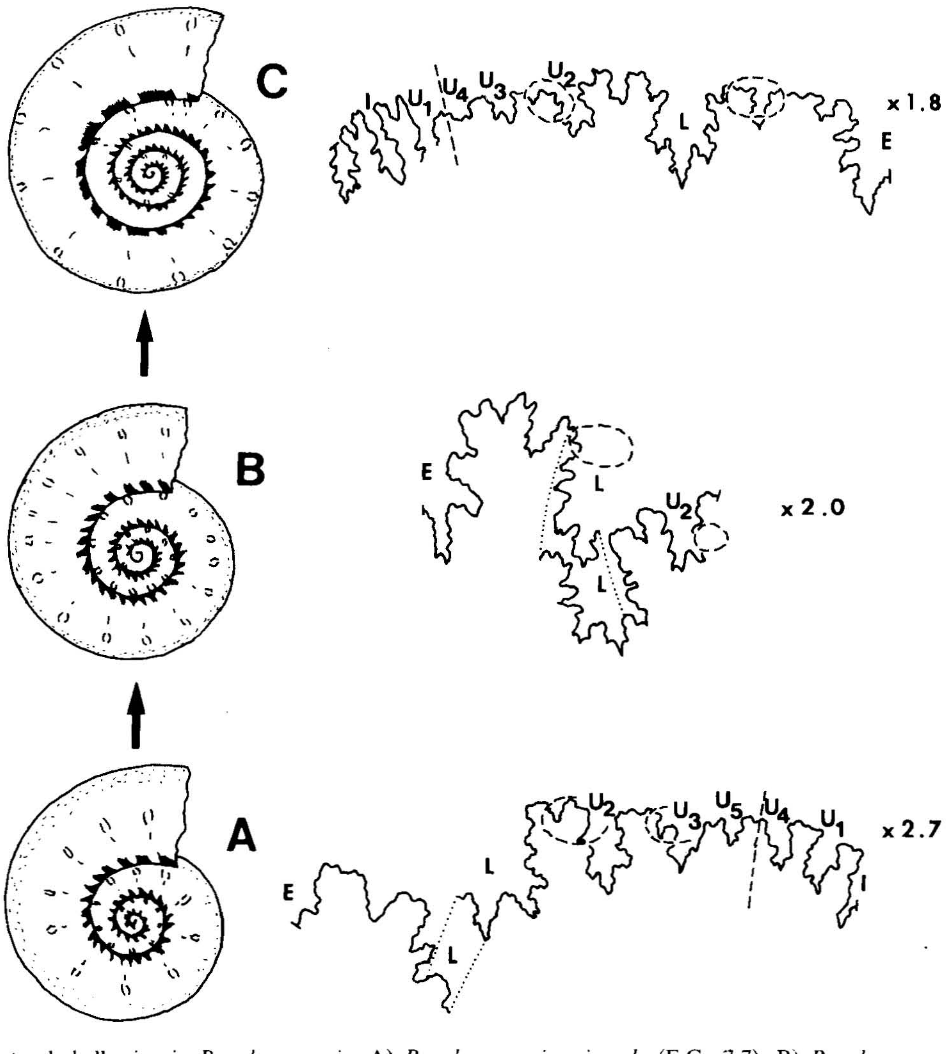

Fig. 4.—Sutural shallowing in *Pseudowaagenia*. A) *Pseudowaagenia micropla* (F.G_{14}.7.7); B) *Pseudowaagenia haynaldi* (Ch.G_{27}.6a.3); C) *Pseudowaagenia acanthomphala* (Ch.G_{27}.6c-d.1).

possible to infer that the distance from different points of the suture to septum centre diminishes consecutively. The resulting suture to septum centre diminishes consecutively. The resulting suture will therefore integrate elements whose respective proportional width remains unchanged and whose depth decreases, that is to say, they will display a higher shallowing rate.

As this kind of general transformation of the shell is frequently observed in ammonites, variations comparable to that determined in *Pseudowaagenia* have been detected in other upper Jurassic ammonites, which are at present under study.

In relation to the possibility of modifications in an inverted direction (case 1 in Checa, 1986a), the case of the genus *Physodoceras* (Physodoceratinae) may be adduced, where through a process with paedomorphic result the species *wolfi* gives rise to the more involute *altenense*, where it is possible to appreciate a slight increase in sutural depth (Fig. 6). Again, this transformation, apart from the shell wall increase (and appearance of a new umbilical lobe) at the umbilical seam, involves a reorganization of the section (see also Fig. 5). Outside the upper Jurassic, it is worth mentioning the Bathonian genus *Rugiferites*, evolute and with shallow suture as contrasted with its descendant *Bullatimorphites*, involute and with deeper suture (J. Sandoval, personal communication).

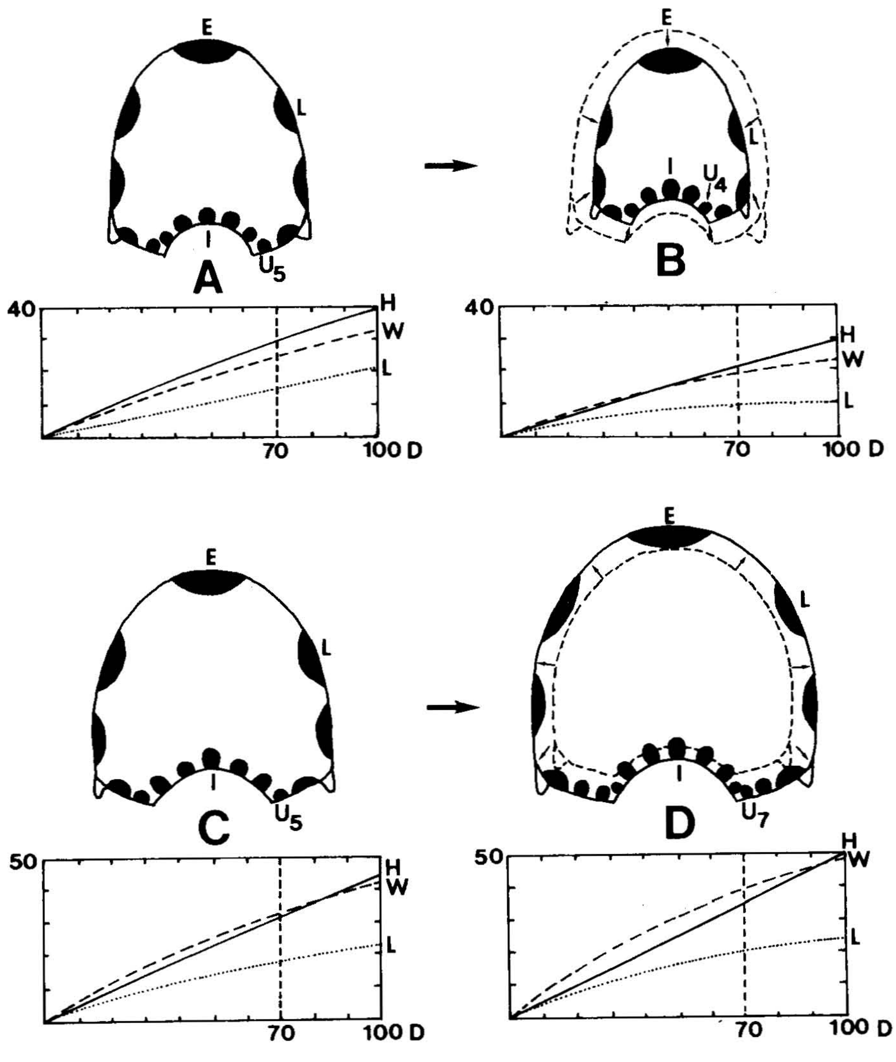

Fig. 5.—Changes in the absolute magnitude of the section and in the sutural distribution along the section of *Pseudowaagenia* and *Physodoceras*. Sections correspond to 70 mm. of D (diameter). A) *Pseudowaagenia micropla*; B) *Pseudowaagenia acanthomphala*; C) *Physodoceras wolfi*; D) *Physodoceras altenense*. H = whorl height (continuous line); W = whorl width (broken line); L = depth of lateral lobe (dotted line).

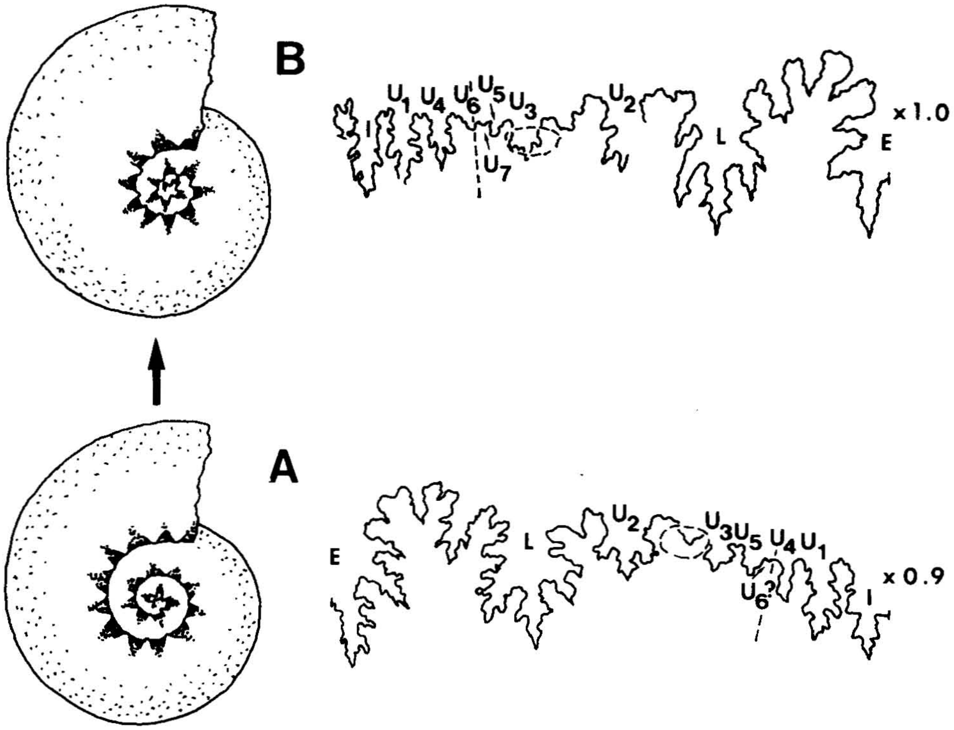

Fig. 6.—Sutural deepening in *Physodoceras*. A) *Physodoceras wolfi* (F.C_2.9.1); B) *Physodoceras altenense* (KM2.16.113).

Conclusions

Sutural modifications observed in Physodoceratinae correspond basically to two types of structural changes: (1) increase in the size of periumbilical tubercles and (2) changes in the whorl expansion rate. As far as ammonites are concerned, these modifications do not claim to be exclusive, although they may well occur frequently. In any case, observations in this respect must be based on a strict examination of the evolutionary dynanics and of the structural modifications introduced through it. We should point out that certain simplifications of the suture observed in other groups of Aspidoceratidae are due to the occurrence of morphological changes similar to those analyzed here, although the fact that we do not know the precise phylogenetic succession in these groups makes it difficult to comment on theses cases in more detail.

As has been stated, the sutural alterations studied are induced through variations of the external morphology of the shell, whose relation to the environmental variables is today under discussion. Anyway, as environment (mainly depth, as it has been considered up to now: Marchand, 1984; Tintant *et al.*, 1982) would affect the septum in an exclusively indirect manner (that is, through the external morphology), the variations which come about do not need to display an adaptative character in this sense. Rather they would be the result of transformations occurring in the outer shell (which could indeed develop towards a functional optimum). So then, the way in which the sutural alterations here described are produced should allow us to explain the fact sometimes observed that related species showing sutures with a different deepening rate do not display apparent biogeographic segregation, while, on the contrary, those with close sutural designs could appear linked to different paleohabitats.

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