

STRUCTURAL CHANGES IN THE PASSAGE EUASPIDOCERATIFORMS-ASPIDOCERATIFORMS (ASPIDOCERATIDAE, AMMONITINA)

A. Checa*

RESUMEN

El estudio integrador de las transformaciones morfológicas que explican el cambio entre Euaspidoceratiformes (Euaspidoceratinae) y Aspidoceratiformes (Aspidoceratinae y Physodoceratinae), permite concluir que la alteración primaria se basa en la desaparición de la costilla que conecta los tubérculos de las filas superior e inferior. A partir de aquí, las restantes modificaciones observadas entre los dos esquemas morfológicos pueden ser consideradas como una consecuencia directa de este cambio primario, sobre todo en lo que concierne a la independencia de las dos series ornamentales y a la obtención de esquemas más involutos. El modelo propuesto permite explicar igualmente las diferencias suturales observadas entre ambos grupos. Por último, se concluye que este proceso ha debido producirse a partir de los géneros *Euaspidoceras* y *Neaspidoceras* (Euaspidoceratinae), que dan lugar respectivamente a *Aspidoceras* (Aspidoceratinae) y *Pseudowaagenia* (Physodoceratinae).

Palabras clave: *Ammonites*, morfología construccional, Jurásico superior, *Aspidoceratidae*, *Euaspidoceras*, *Neaspidoceras*, *Aspidoceras*, *Pseudowaagenia*.

ABSTRACT

The structural change from Euaspidoceratiforms to Aspidoceratiforms involves as a primary change the loss of the ribbing connecting both series of tubercles. This alteration must have occurred simultaneously starting from the genera *Euaspidoceras* and *Neaspidoceras*, giving rise respectively to *Aspidoceras* and *Pseudowaagenia*. Remaining observed transformations between both morphological schemes may be considered as a direct consequence of this primary change, specially with regard to the independence of both ornamental series and the obtaining of more involute schemes.

Key words: *Ammonites*, constructional morphology, upper Jurassic, *Aspidoceratidae*, *Euaspidoceras*, *Neaspidoceras*, *Aspidoceras*, *Pseudowaagenia*.

Introduction

In a previous study (Checa, 1986) it was possible to define the structural interrelations within the whole of the family Physodoceratinae. The applied work methodology consisted in an integrated analysis of the different morphological changes observed throughout the phylogenetic succession with the aim of determining the foreseeable cause-effect relationships between them. The conclusions obtained were of various kinds: first, those characters with «constant» value were

established in each case, being those which control the effect of the «primary» variables upon the obtained final morphology and which constitute the main component of the evolutive dynamics. On the other hand, sutural variations observed allowed us to conclude that the suture must occupy prearranged positions along the whorl section, which are kept up during phylogenetic succession; moreover, given its plastic behaviour, it reflects those ornamental changes originated by the stretching or reduction in amplitude of the corresponding sutural element.

* Departamento de Paleontología y Departamento de Investigaciones Geológicas del C.S.I.C., Universidad de Granada, 18002 - Granada, Spain.

The aim of the present work will be the application of this methodology to the morphological transition (not implying any judgment about the gradualistic or punctualistic character of evolutive events)

between the last representatives of Euaspidoceratinae and the first components of Aspidoceratinae and Physodoceratinae. As was established by Checa (1985) these last two subfamilies appear indepen-

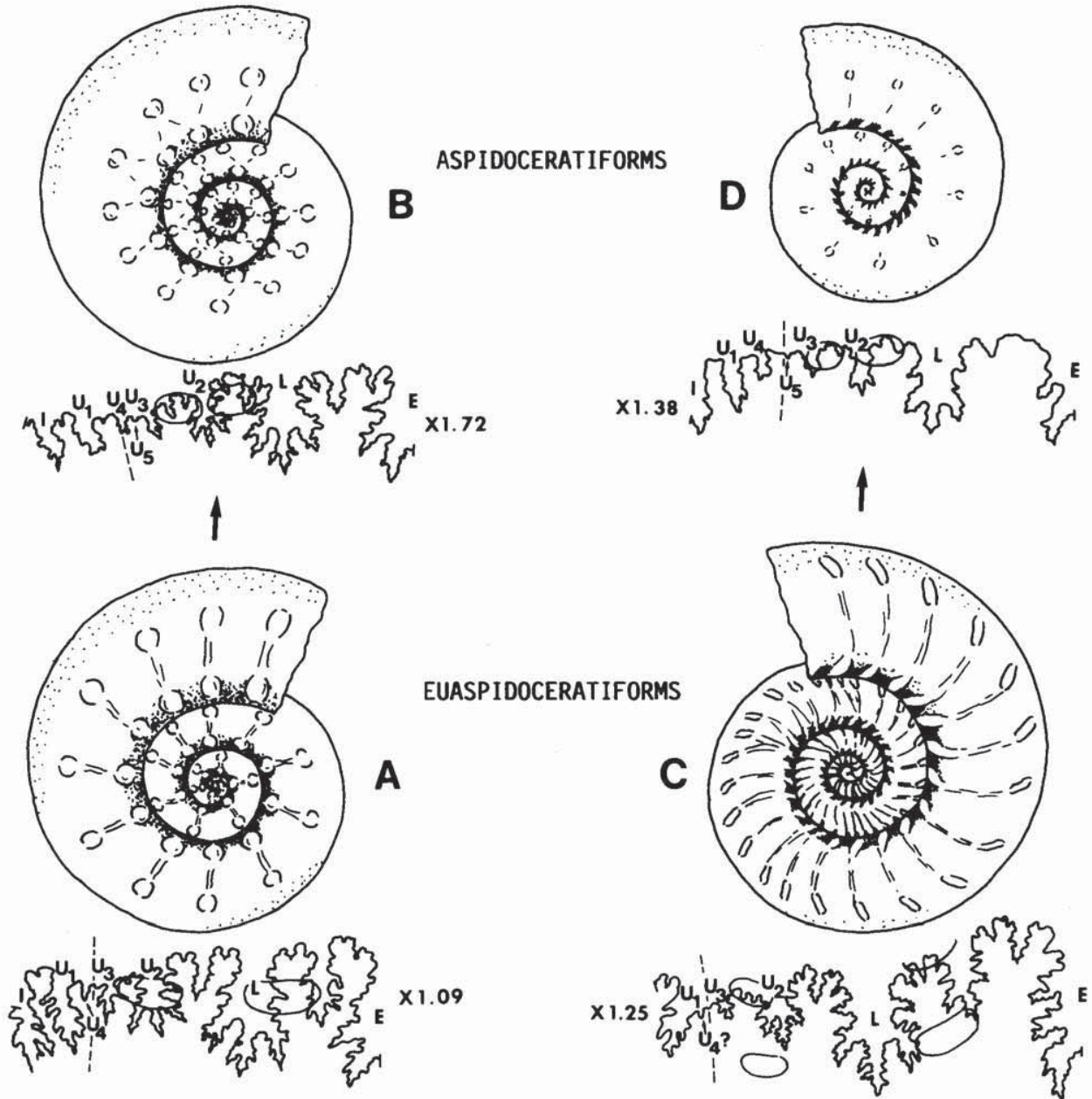


Fig. 1.—Phylogenetic relations between Euaspidoceratiforms and Aspidoceratiforms and observed structural changes. A) *Euaspidoceras* gr. *babeaunum* (D'Orbigny, 1847); sutura: TE.Q1.21.9. B) *Aspidoceras binodum* (Oppel, 1863); sutura: Ch.G_{25b}.4.4. C) *Neaspidoceras* gr. *clambus* (Oppel, 1863)-*schwabi* (Oppel, 1863)-*rotari* (Oppel, 1863); sutura: Ch.C₂.7. D) *Pseudowaagenia micropla* (Oppel, 1863); sutura: Ch.C₂.14.30. Arrows indicate phylogenetic directions.

Fig. 1.—Relaciones filogenéticas entre Euaspidoceratiformes y Aspidoceratiformes y cambios estructurales observados. A) *Euaspidoceras* gr. *babeaunum* (D'Orbigny, 1847); sutura: TE.Q1.21.9. B) *Aspidoceras binodum* (Oppel, 1863); sutura: Ch.G_{25b}.4.4. C) *Neaspidoceras* gr. *clambus* (Oppel, 1863)-*schwabi* (Oppel, 1863)-*rotari* (Oppel, 1863); sutura: Ch.C₂.7. D) *Pseudowaagenia micropla* (Oppel, 1863); sutura: Ch.C₂.14.30. Las flechas indican la dirección filogenética.

dently from the first one in the upper Oxfordian and, although the systematic assignment of the connection forms is known in an approximate way, those structural modifications conforming the evolutive change from one type to another are not easy to understand.

The interest of this study is evident since this is the way to understand rather than merely describe morphology. In the case of ammonites advantages are numerous for there is so far little known on the functional morphology of this group and perhaps this kind of study will allow an approach to these so difficultly accessible aspects. Another more concrete point of interest derives from the Euaspidoceratinae structuration itself, whose ornamental design includes ribs. The analysis of these elements has not previously been attempted and, even though it is not possible to generalize about a single constructional model for ammonite ribbing, perhaps conclusions here exposed could serve for application to researchers on other groups of ammonites.

The morphological and structural change

At first glance it is obvious that, even though the ornamental scheme in both groups is the development of more or less coarsened tubercles, in all genera of Euaspidoceratinae tubercles of the upper and lower row are invariably connected through a rib with more or less accentuated relief. This steadiness can be expressed by the fact that there always exists an equal number of inner and outer tubercles; thus, it is possible to infer that as soon these elements as the connecting rib form a single structural unit whose development will become a conditioning factor of the first order for the possible kinds and rates of morphological

variation within an Euaspidoceratoid structuration. As an immediate consequence, a constant within this ornamental structuration will be the proportional distance between both rows of tubercles; this is easily assumed taking into account that the most extreme Euaspidoceratoid morphologies (*Paraspidoceras*, *Epaspidoceras*) develop on the basis of an increase in size of outer tubercles and a similar reduction in that of the inner ones (which affects the dimensions of the growth spiral), but they never modify the size of the intermediate ribbing.

On the other hand, the development in Physodoceratinae of a tubercular element at a given point brings about a local expansion of the spiral taking that point as the centre of origin (Checa, 1986). In the case of a rib like that connecting both rows of tubercles in Euaspidoceratinae, it is difficult to recognize the kind of change undergone. Nevertheless, having in mind the phylogeny of the Euaspidoceratoid ornamentation, it may be supposed that these ornamental elements must develop starting from designs close to those found in the inner whorls of the genera *Peltoceras* and *Peltoceratoides*, composed of radial ribs branching at the marginal portion and crossing the ventral region; later local coarsening at the level of the umbilical edge and the division point conditions the development of both series of tubercles, at the same time as the intermediate ribbing space undergoes a lower level general coarsening.

From the phylogeny stated in Checa (1985) the subsequent analysis will refer to genera *Euaspidoceras* and *Neaspidoceras* (Euaspidoceratinae) and their respective descendants *Aspidoceras* (Aspidoceratinae) and *Pseudowaagenia* (Physodoceratinae). In these two last genera the relation between both series of elements is of occasional (and possibly chance) correspondence,

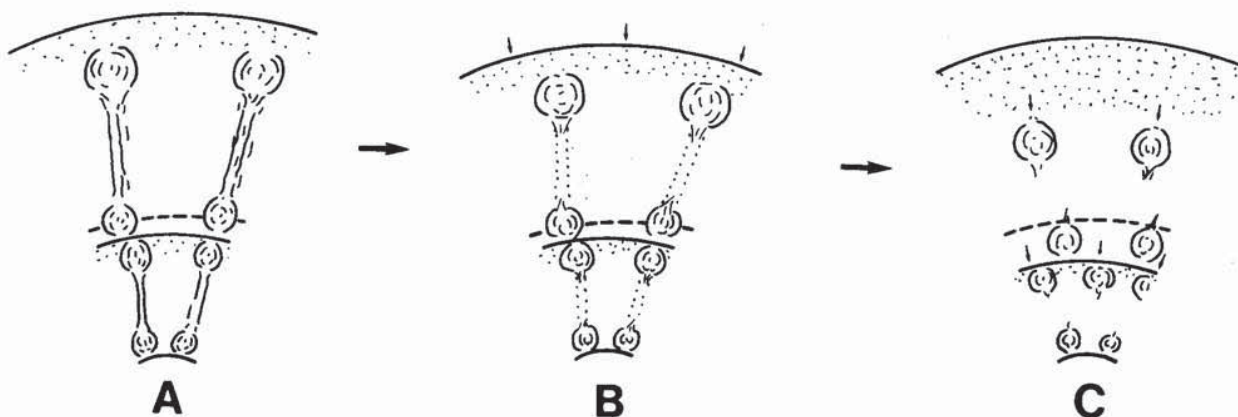


Fig. 2.—Schematic representation of the observed structural changes. A) Euaspidoceratiform stage. B) Hypothetical intermediate stage: loss of connecting ribbing. C) Aspidoceratiform stage: closing of both rows of tubercles and increase in the growth index.

Fig. 2.—Representación esquemática de los cambios estructurales observados. A) Estadio Euaspidoceratiforme. B) Estadio hipotético intermedio: pérdida de la costulación interconectante. C) Estadio Aspidoceratiforme: aproximación de las dos series de tubérculos y aumento del índice de crecimiento.

the existence of free elements occurring both in the inner and in the outer row. In this ornamental design the imposition represented by the connecting rib thus disappears. As a first consequence, resulting morphologies of both *Aspidoceras* and *Pseudowaagenia* have the possibility of modifying their growth spiral deeply in order to acquire more involute schemes. To accept this it must be pointed out that in the case of *Euaspidoceras* and *Neaspidoceras* the outer row sets the limit of interpenetration of successive whorls, as, through a principle of economy, it must not be comprised by later whorls. Moreover, the mobility interval of the outer row keeps very reduced given that the lower part of the ornamental whole is already placed on the umbilical edge and any other position below this level would be unfeasible as it should force the inner tubercles (perpendicular to flanks) to change their directionality (figure 2).

Thus, it is the disappearance of intertubercular ribbing which propitiates the existence of involute spirals within Aspidoceratidae given that, as an intermediate element with fixed length does not exist, the organism is able to regulate the spacing between both rows of tubercles. The alternative is always that of altering the position of the outer row on the flank, so that the

most involute designs in Aspidoceratinae correspond to those species —*A. binodum* (Opper, 1863), *A. rafaelli* (Opper, 1983)— where there exists a proportionately lesser radial distance between both ornamental rows, while forms like *A. apenninicum* (Zittel, 1870) and *A. caletanum* (Opper, 1863) show higher values for this parameter and, correlatively, a greater uncoiling rate. Within the Physodoceratinae spectrum, *Psw. micropla* (Opper, 1863) shows a strong involution and both rows of tubercles very close together, in opposition to the final form of this generic line, *Psw. acanthomphala* (Zittel, 1870), whose umbilicus turns out to be very wide, the external tubercles being late-ventrally placed.

Lastly, the lack of connection hinders the existence referred to above of reciprocal interchanges of volume between both rows of tubercles (always favouring the outer elements), as is observed in the case of *Paraspidoceras* and *Epaspidoceras*.

Modifications in the suture line

As was previously commented, local expansions of the spiral originate the stretching of that sutural ele-

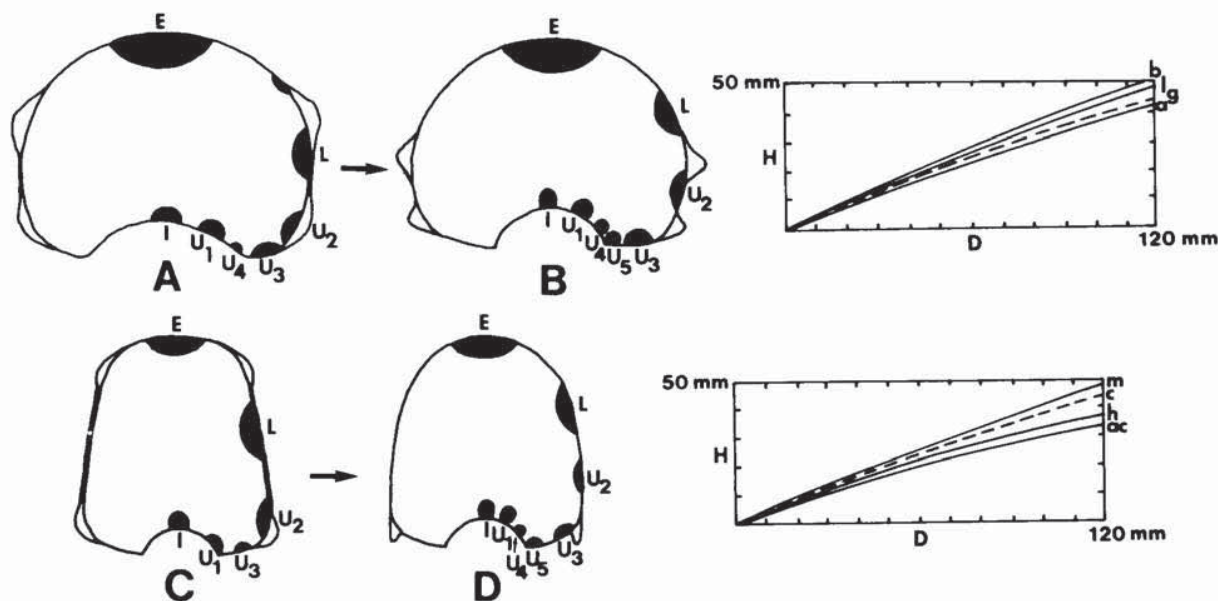


Fig. 3.—Distribución de la sutura a lo largo de la sección de la vuelta y posición de las curvas H/D (altura de la sección/diámetro) en *Euaspidoceratiformes* y *Aspidoceratiformes*. Las letras mayúsculas corresponden a las mismas formas que en la figura 1. b=*A. binodum* (Opper, 1863), 5U; l=*A. longispinum* (Sowerby, 1825), 5U; g=*Eu. gr. babeanum* (D'Orbigny, 1847), 4U; a=*A. apenninicum* Zittel, 1870, 5U; m=*Psw. micropla* (Opper, 1863), 5U; c=*N. gr. clambus* (Opper, 1863)-*schwabi* (Opper, 1863)-*rotari* (Opper, 1863), 3U; h=*Psw. haynaldi* (Herbich, 1878), 5U; ac=*Psw. acanthomphala* (Zittel, 1870), 4U. Note that curves corresponding to *Euaspidoceratiformes* (broken) are too high, to judge by the respective sutural compositions (see Checa, 1986).

Fig. 3.—Distribución de la sutura a lo largo de la sección de la vuelta y posición de las curvas H/D (altura de la sección/diámetro) en *Euaspidoceratiformes* y *Aspidoceratiformes*. Las letras mayúsculas corresponden a las mismas formas que en la figura 1. b=*A. binodum* (Opper, 1863), 5U; l=*A. longispinum* (Sowerby, 1825), 5U; g=*Eu. gr. babeanum* (D'Orbigny, 1847), 4U; a=*A. apenninicum* Zittel, 1870, 5U; m=*Psw. micropla* (Opper, 1863), 5U; c=*N. gr. clambus* (Opper, 1863)-*schwabi* (Opper, 1863)-*rotari* (Opper, 1863), 3U; h=*Psw. haynaldi* (Herbich, 1878), 5U; ac=*Psw. acanthomphala* (Zittel, 1870), 4U. Es de resaltar que las curvas correspondientes a *Euaspidoceratiformes* (discontinuas) están «sobrelevadas», a juzgar por las respectivas composiciones de las suturas (véase asimismo Checa, 1986).

ment upon which the expansion is produced. Having in mind the distribution of tubercles and ribs in the genera *Euaspidoceras* and *Neaspidoceras*, this stretching would affect, (although in an unequal manner) the interval comprised between the inner portion of the saddle E/L and the saddle U_2/U_3 , along the flank. Externally this lengthening would bring about a remarkable increase in whorl height, as it is produced following an axis parallel to ribbing and, therefore, to flanks. Given that, as stated by Miller (1968), the suture line in *Euaspidoceratinae* develops up to a third umbilical lobe (apart from some upper Oxfordian forms of *Euaspidoceras*, whose suture contains four umbilical lobes; observations of the author), the only way to determine this extra-stretching is to compare the correlation curves H (whorl height)/D (diameter) for identical sutural compositions in *Euaspidoceratinae* and *Aspidoceratiforms*, a comparative uprise for the curves corresponding to *Euaspidoceratinae* being foreseen. Even though there are not *Aspidoceratiforms* including exclusively three umbilical lobes in their suture (at least five in *Aspidoceratinae* and four in *Physodoceratinae*), the comparison (figure 3) turns always out to be advantageous to *Euaspidoceratinae* in the predicted sense.

After the loss of stretching, there appears in *Aspidoceratiforms* a «compression» of the sutural elements previously affected by ribbing and, at the same time, there exists a gain of sutural elements (up to a fifth umbilical lobe) conditioned by the accretion of shell wall at the umbilical seam, essential for the acquisition of the involute morphologies of *A. binodum* (Oppel, 1863) and *Psw. micropla* (Oppel, 1863) initial species of *Aspidoceratinae* and *Physodoceratinae* respectively (this process is carefully described in *Physodoceratinae* by Checa, 1986). This description allows us then to understand how apparently similar spiral morphologies (although the overlapping, obviously, varies) develop different sutural compositions.

The systematic characterization

Given that in *Euaspidoceratinae* a deep systematic revision has not been carried out, this study is restricted to what we may call morphological structurations and is, in principle, independent on the detailed systematic characterization. Anyway, this does not imply the ignorance of morphological types which take part, but rather appears conditioned by the ending of the integrating study (presently under way) of paleobiogeographical and paleobiological data. Nevertheless, given that the essential subject is the structural characterization and that this must be carried out a priori, the systematic incompleteness must not be an obstacle for an analysis like the one attempted.

In relation to *Aspidoceratinae*, the initial species *A. binodum* (Oppel, 1863) appears clearly related to *Euaspidoceras* gr. *babeatum* (D'Orbigny, 1847) sensu Dorn (1931) in Checa (1985), which possibly, from the data presently available, lacks any real connection with *Eu. babeatum* (D'Orbigny, 1847) s.s., so constituting a separate species. This form develops a suture composed of four umbilical lobes, a totally unusual fact in *Euaspidoceratinae* which indicates a certain approximation to the *Aspidoceroid* design (five umbilical lobes).

Pseudowaagenia—specifically *Psw. micropla* (Oppel, 1863)—clearly derives from *Neaspidoceras* gr. *clamibus* (Oppel, 1863)-*schwabi* (Oppel, 1863)-*rotari* (Oppel, 1863), perhaps with a morphological intermediate represented by *N. gr. radisense* (D'Orbigny, 1847)-*tietzei* (Neumayr, 1873), even though the criteria for specific segregation are not yet precise.

Conclusions

The present study emphasizes that the fact originating the appearance of *Aspidoceratiforms* from *Euaspidoceratiforms* lies in the loss of the connecting ribbing between both rows of tubercles. As a consequence, both ornamental lines become mutually independent and, more concretely, there exists the possibility to vary the position of the outer row on the flank; this allows the covering line to occupy lower levels and, subsequently, the obtaining of more involute spiral designs. At the same time, the analysis of sutural modifications gives us information about the manner of formation of ornamental elements. These approximations suggest that interconnecting ribs in *Euaspidoceratinae* may be considered as elongated structures with scarce relief whose origin involves an expansion of the whorl section agreeing with that morphology and similar to that described for the tuberculation of *Physodoceratinae* (Checa, 1986). This can be tested by the differences between whorl height and the number of umbilical lobes developed in the suture in one case and the other.

From this analysis it is possible to infer that most ornamental modifications in ammonites must have a more or less marked influence on growth spiral and on sutural morphology. Anyway, the only possible approach derives from a rigorous knowledge of the phylogeny of the group and from an integrating analysis (i. e. considering the organism as a «system», according to Thompson, 1961, and Bayer, 1978) of structural variations implied, in order to determine «primary» changes and those others derived from them. Within this study we must not forget the existence of parameters whose value remains constant and which control the character of the foreseeable types of modifications. In the present case the morphological break comes precisely determined by a change in the

sort of constants present within each phylogenetic line: two rows of tubercles perpendicular to the flank, joined by a rib with constant proportional length in *Euaspidoceras* and *Neaspidoceras*; two rows of tubercles perpendicular to the flank in *Aspidoceras*; inner tubercles parallel to the equatorial plane in *Pseudowaagenia*. As may be supposed, at first sight, the higher the structural imposition, the lesser the possible directions of change, which incides on the fact of the scarce change capability of the growth spiral in *Euaspidoceras* and *Neaspidoceras*.

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