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# OXFORDIAN AND KIMMERIDGIAN "ASPIDOCERAS" IN THE MEDITERRANEAN. A METHODOLOGICAL APPROACH

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**RESUMEN**

En el presente trabajo se lleva a cabo un análisis contrastador de la Hipótesis Nula establecida como base metodológica para la investigación evolutiva de los "Aspidoceras" mediterráneos (Checa & Olóriz, 1985). Esta contrastación se lleva a cabo integrando nuevos datos y forma parte de un programa de investigación cuidadosamente planificado. Las diversas consideraciones paleogeográficas, sedimentológicas, estratigráficas y paleobiológicas han proporcionado nuevos modelos evolutivos que suponen una sustancial reorganización estructural de la Hipótesis Nula. En esta estructuración, las Configuraciones Evolutivas Básicas no son consideradas como meros grupos morfológicos, resultado de una lectura del registro fósil, sino que constituyen unidades evolutivas que pueden, por tanto, relacionarse entre sí.

**Palabras clave:** *ammonites, relaciones filogenéticas, evolución, Jurásico superior, Mediterráneo, Aspidoceratidae, Aspidoceras, Pseudowaagenia, Physodoceras, Orthaspidoceras, Benetticeras, Simaspidoceras, Schaireria.*

**ABSTRACT**

In this study we present a contrastive analysis of the Null Hypothesis, established as the methodological basis for the evolutive investigation of Mediterranean "Aspidoceras" (Checa & Olóriz, 1985). This contrast is carried out using new data, and is part of a research programme which has been carefully planned. Paleogeographic, sedimentological, stratigraphic and paleobiological considerations have provided new evolutive models which in turn lead to a structural reorganization of the Null Hypothesis. In this new structure, the Basic Evolutionary Conformations are no longer considered as mere morphological groupings, the result of a direct reading of the fossil record. In this way we propose morphological blocks, representing evolutive units which can be related to one another.

**Key words:** *ammonites, phylogenetic relations, evolution, upper Jurassic, Mediterranean, Aspidoceratidae, Aspidoceras, Pseudowaagenia, Physodoceras, Orthaspidoceras, Benetticeras, Simaspidoceras, Schaireria.*

## Introducción

In an earlier study (Checa & Olóriz, 1985) the authors presented the bases of a study project on European "Aspidoceras" considering it as having its origin related to the Subbetic Mediterranean association. In the organization of our research project two stages were established. In the first, data from studies by Olóriz (1976) and Checa (1981) were presented and discussed; this allowed us to propose the Null Hypothesis (Checa & Olóriz, 1985) which was to be contrasted with the data obtained from later observations. In this first stage the work was principally based on the stratigraphic examination of the Subbetic fossil record. Here, a series of Basic Evolutionary Conformations was established; these structures represented morphological groupings in which "species", were integrated either in their traditionally accepted sense or in the way they are used in the most recent works. The fundamental reason why this treatment was thought most appropriate was because we wanted to obtain an overall view of the morphological stability of these am-

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monites, on the basis morphological groupings which were of the most "cohesive" possible. In this way, the integration of "related species" was achieved, as was a certain degree of buffering of the distortion caused by the multiplicity of systematic criteria used by different authors. In addition, close stratigraphic examination allowed us to establish change paths which could express the dynamics of the group under study, although in a general manner. In this first stage of the project we did not discuss paleobiological questions which might cause systematic changes. Thus, we did not use concrete taxonomic references, except, naturally, those that were obligatory at a generic level in order to establish a clear basic order in the exposition of our hypothesis. We therefore used genera in their most usual sense and we further supplied a list of "classical species" included in the Basic Evolutionary Conformations.

The second phase of the study, following the original work plan, has been carried out taking into consideration general geological observations as well as those of paleogeographical, sedimentological and biostratigraphical nature. In this context, we have analysed the various associations, and we have evaluated the acquired characters and the fluctuations observed in those that were inherited. In this way we have given an interpretation of the significance of the morphological groupings we have recognized. These groupings undoubtedly represent morphospecies, but when subject to the above described treatment, they turn out to be justifiable approximations to the groups which were earlier biospecies of "Aspidoceras" in the Mediterranean Subbetic Basin. The most significant results in this second phase are presented in Checa & Olóriz (1985) and Checa (1985).

At the present moment the aim of this study is to show the results obtained from a contrast of the Null Hypothesis which served as the starting point for this research project. As a consequence we will provide an account of the present state of knowledge about Subbetic Oxfordian and Kimmeridgian "Aspidoceras".

## The structure of the Null Hypothesis

As we have outlined above and as has been presented in greater detail in Checa & Olóriz (1985), the structure of the Null Hypothesis is based upon ornamental configurations which are considered "sufficiently stable" (at least in principle) as to characterize Basic Evolutionary Conformations. Nonetheless, neither in the Basic Evolutionary Conformations nor in the interrelationships which really provide us with the design of the Null Hypothesis do we include evolutionary processes which must necessarily take place in order to induce the real process of the proposed structure. In this linear process we should expect to discover the possibility of recognizing a segregation which would imply different levels of influence of the evolutionary processes. As a result we could come close to an understanding of the organization of the structure, which would mean the knowledge of the evolutionary dynamics of the group under study. The Null Hypothesis which we have mentioned can thus be seen as an interpretation in which it is necessary to separate the strains of merely superficial effects from those which are intimately connected with the processes which determine the evolutive development. In order to achieve this we must contrast the Null Hypothesis with the data presently available and establish the differences which arise whe we contrast the latter with the starting point of our research project.

## New data

The most recent interpretation of "Aspidoceras" is to be found in the studies by Checa & Olóriz (1984) and Checa (1985). In the first of these studies paleobiogeographical considerations and stratigraphic examination occupy a central position. Starting from these considerations a monographical study of the aspidoceratiforms in Europe was carried out, and a new systematic ordering established, which takes into account the "evolutionary results" (cf. Gould, 1977) observed. In brief: in Oxfordian and Kimmeridgian forms recapitulatory phenomena (with or without terminal addition) are interpreted, such as, for example, evolutionary acceleration and hypermorphosis. Paedomorphosis (presumably neotenic) is also detected on occasions, and some cases of proportionate giantism were also observed. For the time being those examples where the obtaining of new characters cannot be determined by stratigraphic examination, have been interpreted as cases of clandestine evolution.

In Checa & Olóriz (1948) a quantitative analysis of the fossil record is carried out. This analysis is organized according to the systematic proposals made in Checa (1985), and the influence of the environment in the fluctuations of the group throughout the time assessed. The conclusions at the genus level are of special interest, as is the integration of the data at the subfamily level and the observations on the distribution of acmes at the species level. The parallelism observed between the eustatic curve (Hallam, 1978) and the profile of the fossil record in this group of ubiquitous ammonites, as well as considerations on distortions in relation to paleoecological factors are all subject to analysis. In this way the structural stability of the shells and their relation to continuity in time is clearly to be seen, as it is also the influence of paleobiogeographical-paleoecological factors on the stratigraphic distribution. Finally, the correlation of the environmental volume to the production, frequency and temporal extension of the acmes is also shown, as is the incidence of these factors in the configuration of the subfamilies.

## Contrast with the Null Hypothesis

A contrastive study of the Null Hypothesis, taken together with the new data available should be carried out on the basis of the Basic Evolutionary Conformations previously considered. To the extent to which the Basic Evolutionary Conformations contain groups of closely related species it will be possible to establish directly the different influence in the evolutive processes involved in the structure of this group of ammonites. We will therefore proceed to contrast the Null Hypothesis by genera, analysing the "real value" according to present day interpretations of the characters which define each Basic Evolutionary Conformation. Each of these structures (blocks in Checa & Olóriz, 1985) is potentially susceptible of a greater or lesser readjustment. As a consequence, the new configurations that are produced as a result will show us the evolutionary structure of the group at a generic level as a hierarchical organization of the evolutionary processes at work. Finally, we will compare and contrast the conclusions of a general nature (d to g in Checa & Olóriz, 1985) which affect this group of ammonites during the Oxfordian and Kimmeridgian in the Subbetic zone.

a) *Aspidoceras*

Taking into account the new information available on this genus we can say that the following characters are of little significance:

- the design of tubercle base (blocks A, C, D in Checa & Olóriz, 1985, fig. 1).
- the design of the whorl section (blocks B, D in Checa & Olóriz, 1985, fig. 1).
- the correspondence between umbilical and lateral tubercle rows (block C and the evolutionary base of block D in Checa & Olóriz, 1985 to be, fig. 1).

New characters which do seem to be of significance include:

- uncoiling in block D.
- the reappareance of external tubercles in the living chamber in the forms characteristic of block C.
- the restriction of external tubercles to inner whorls in the forms included in block C.

In the new structure given for the genus *Aspidoceras* (Fig. 1) we can observe considerable changes with reference to the stratigraphic distribution of the blocks. The Basic Evolutionary Conformations are now related according to those evolutionary facts which are most important for this genus. In this way it is possible to distinguish the following differences among change events which have proved to be essentially recapitulatory:

- the frequency with which evolutionary accelaration is found.
- the different influence on this process according to whether the A-B connection or the A-D-E connections, added terminally, accompany it.
- the comparative, secondary value of hypermorphosis, with or without terminal addition (B-C connection), and of proportionate giantism (block D).

In general, the contrast produces slight changes in the structure of the Null Hypothesis. This is probably due to the fact that, during the interval under study, the "functional plasticity" in this genus must have allowed changes to be produced without reaching a limit situation where deep restructuring would be the only alternative. In this case, therefore, we should not be surprised to find the appearance of little penetration of the paleobiological considerations in a morphological ordering which is based exclusively on a direct reading of the fossil record.

b) *Pseudowaagenia*

In this case, the new information obtained, has the effect of producing a deep restructuring of the Null Hypothesis. The appearance and disappearance of blocks and/or evolutionary bases of blocks, variations in the stratigraphic distribution and new connections are the facts which are most significant at first sight. Moreover, in one case (block C) the new interpretation implies the proposal of a new genus (which is phylogenetically related to the other): *Schaireria*.

Characters which are not very significant include:

- the correspondence between umbilical and lateral tubercles (block A).
- the presence of external tubercles in the outer whorls (block E and evolutive base of block D).

New characters which do acquire systematic importance are:

- the position of the external tubercles (block D).
- the considerable increase in size (new block).

In the new configuration of the Basic Evolutionary Conformations, both appearance (block F) and disappearance (block B and the evolutive base common to blocks C and D) are conditioned by the control of the evolutionary relations. Primitive block B turned out to be a polyphyletic grouping. The evolutionary fact which proved most important is paedomorphosis, which gives rise to the new genus *Schaireria* (block C). This genus develops its most typical species in the lower Tithonian its common ancestor is *Pseudowaagenia*. Factors of less importance in the new configuration are evolutionary acceleration (A, D, E) and proportionate giantism, which characterizes the new block F.

In general this contrast produces major changes, linked to evolutionary phenonema of great development potential (paedomorphosis) although it is not possible to interpret the original motivating process, due to the reduced number of observations available. We have also found minor changes in which, as in the case of the genus *Aspidoceras*, evolutionary acceleration and proportionate giantism are involved: the change does not produce a high level of morphological discontinuity either.

c) *Physodoceras* and *Orthaspidoceras*

This group undergoes important modifications after the contrastive analysis. The restructuring of the blocks is a profound one, and as a result new relations and new stratigraphic distributions are established. In one case one of the blocks which had been proposed previously (B) is now considered to represent a new taxon at the generic level (*Benetticeras*) after making the changes required according to the new information. Another of the original blocks (F) will now include representatives of a genus which had not been considered previously: *Simaspidoceras*.

Characters of no great importance are:

- the design of the tubercle base (block A).
- the increase in size shown in the evolutive base of blocks C and D.
- shell uncoiling in blocks C and E.
- the increase in the number of tubercles in block G.

New characters which do represent important systematic factors:

- the design and position of tubercles in block G.

According to the data we have outlined above, there appear four taxa at the generic level in the new configuration, instead of the two which we had proposed in the Null Hypothesis. One very important fact is the joining of the primitive blocks C and D and of their evolutionary bases, in one single block C/D. This new block has block A of the genus *Pseudowaagenia* as ancestor. In connection with this fact a series of distortions in the primitive structure takes place. The family relation between blocks A and C/D is reversed. Block C/D becomes the Basic Evolutionary Conformation and block B derives from it (in our previous proposal it was related to A). Block E becomes extremely significant, since it is now considered as the common ancestor for blocks F and G. Block G is subdivided as from the observations on the tubercles. We should emphasize the general nature of this reconsideration of the biostratigraphy in the new Basic Evolutionary Conformations.

As we have observed, this is the group of forms where the consideration of paleobiological data leads to the most drastic restructuring. This is due to the first-rank evolutionary processes which determine the connections between Basic Evolutionary Conformations. Indeed, neotenic paedomorphosis can be shown in 40% of the evolutive relations we have observed. We propose clandestine evolution for the origins of the blocks that are directly derived from basic C/D, and as the origin of block $G_1$ (in the cases mentioned this should not be interpreted as the product of inadequate or defective information). Finally, the appearance of block F provides an example of a change induced by a lower-rank factor, such as evolutive acceleration, which is encouraged by terminal addition and becomes as important as some of the cases of neoteny we have mentioned.

It is of special interest to note the presence of homeomorphism in this group of forms. *Benetti-*

*ceras* and *Orthaspidoceras* both derive from the same evolutionary line of *Physodoceras* with a stratigraphic difference of a little more than two biozones in the lower Kimmeridgian.

d) Our original statement that "no stock with primitive configuration continues beyond the lower Kimmeridgian" has been proved to be basically correct. Only one species, *Pseudowaagenia micropla* (OPPEL), penetrates the base of the middle Kimmeridgian (in the interval zone of Compsum). As a result, the middle Kimmeridgian may be considered as an interval where a renewal of Mediterranean aspidoceratiforms takes place. This group of ammonites is thus affected by the "faunal relay" which has been observed in the Mediterranean association during the middle Kimmeridgian (Olóriz, 1976; Olóriz & Tavera, 1981).

e) With regard to the "great diversification in the Strombecki and Divisum zones" it is necessary to make some qualifying remarks, following the quantification carried out by Checa & Olóriz (1984):

- the greatest diversification, together with the greatest development of the populations, occurs in the interval running from the Divisum zone up to the interval zone of Compsum; the data obtained on diversity in the Kimmeridgian show that this, above and below that maximun point, falls and is uniform.
- the most diversified genera are *Aspidoceras*, *Pseudowaagenia* and *Orthaspidoceras*. With the exception of *Orthaspidoceras*, which is limited to the top of the lower Kimmeridgian and the base of the middle Kimmeridgian, both others maintain their level of specific diversity almost constant from the Divisum zone till the end of the Kimmeridgian.

f) As regards the persistence of evolutionary lines in the middle and upper Kimmeridgian, we can state the following:

- after a very detailed stratigraphic examination we found that there are eight lines, and not six, as was proposed in the original Null Hypothesis.
- with the restructuring of the Basic Evolutionary Conformations we find that there are three (and not four) which originate in the Divisum zone (*Orthaspidoceras*: 1, *Simaspidoceras*: 1, *Aspidoceras*: 1); in the Strombecki zone there is one (*Aspidoceras*: 1) and not two; further, we have found two (*Pseudowaagenia*: 1, *Aspidoceras*: 1) which originate in the upper Oxfordian.

g) A first increase in size at the level of the Strombecki zone can now only be found, partially in *Aspidoceras*. In the group of forms belonging to *Physodoceras-Orthaspidoceras*, the increase in size occurs in the Divisum zone. In *Pseudowaagenia* it is found at the base of the middle Kimmeridgian.

Our estimates about the relation between the repetition of this phenomenon and the diversification of lines have been proved correct.

h) The observations on the persistence of the external row of tubercles should be limited to *Aspidoceras*. In *Pseudowaagenia* the fluctuations do not seem to be significant.

i) Our generalizing remarks on the developmental trends, which we applied to *Aspidoceras*, *Pseudowaagenia* and *Physodoceras*, could not be applied to this last genus. This new statement is based on the examination of the intraspecific evolutive relations detected.

j) The orientation and desing of tubercles in upper Kimmeridgian *Aspidoceras* have been shown to be a secondary character.

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## Appendix

Species to be included within each block according to the systematics proposed in Checa (1985).

block A: *A. binodum* (OPPEL)
block B: *A. sesquinodosum* FONTANNES
block C: *A. linaresi* CHECA and *A. uninodosum* TOULA
block D: *A. longispinum* (SOWERBY) and *A. hystricosum* (QUENSTEDT)
block E: *A. apenninicum* ZITTEL

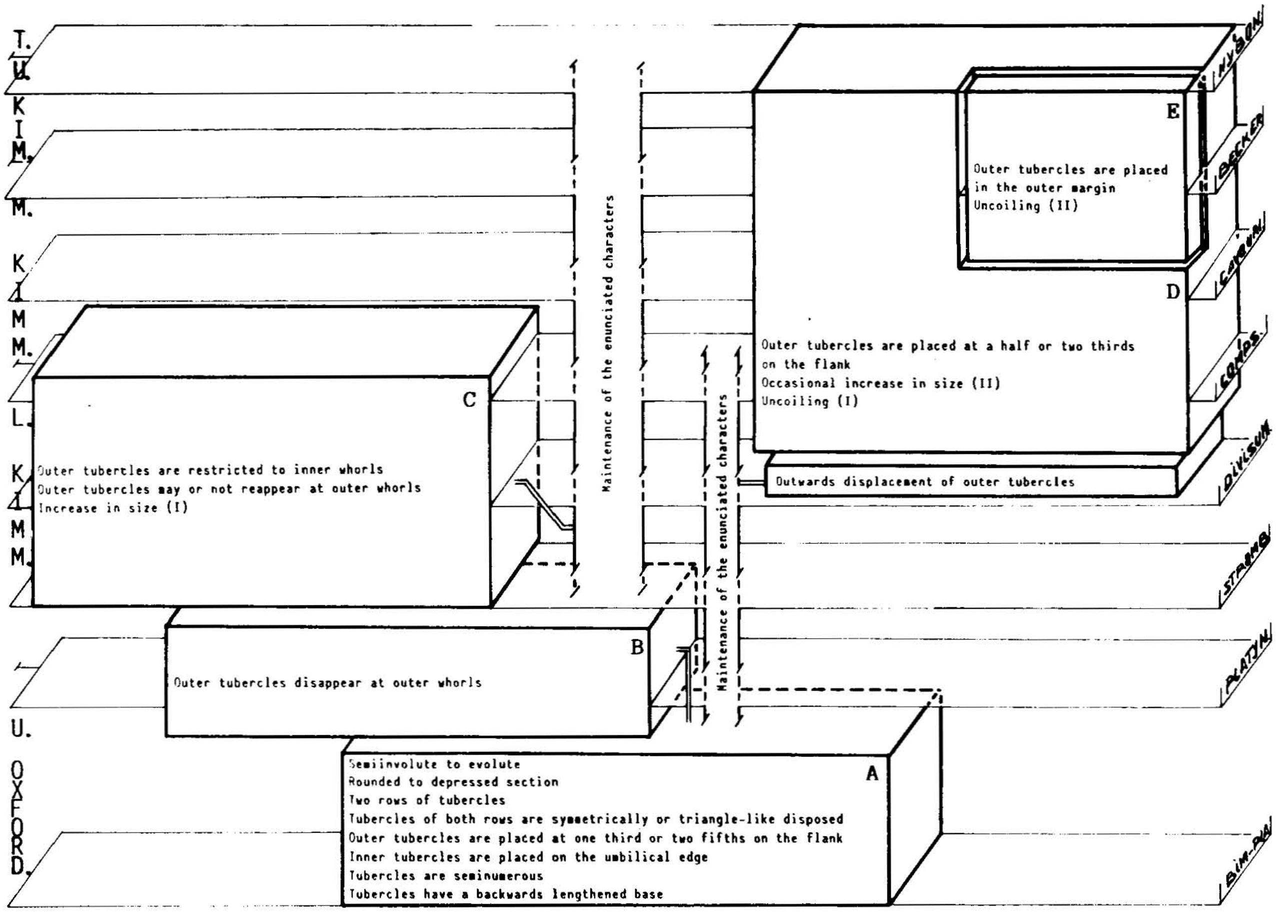


Fig. 1.—Evolutionary framework of the genus *Aspidoceras*.

block A: *Psw. micropla* (OPPEL)
block C: *Sch. neumayri* CHECA
block D: *Psw. haynaldi* (HERBICH)
block E: *Psw. acanthomphala* (ZITTEL)
block E: *Psw. dietli* CHECA

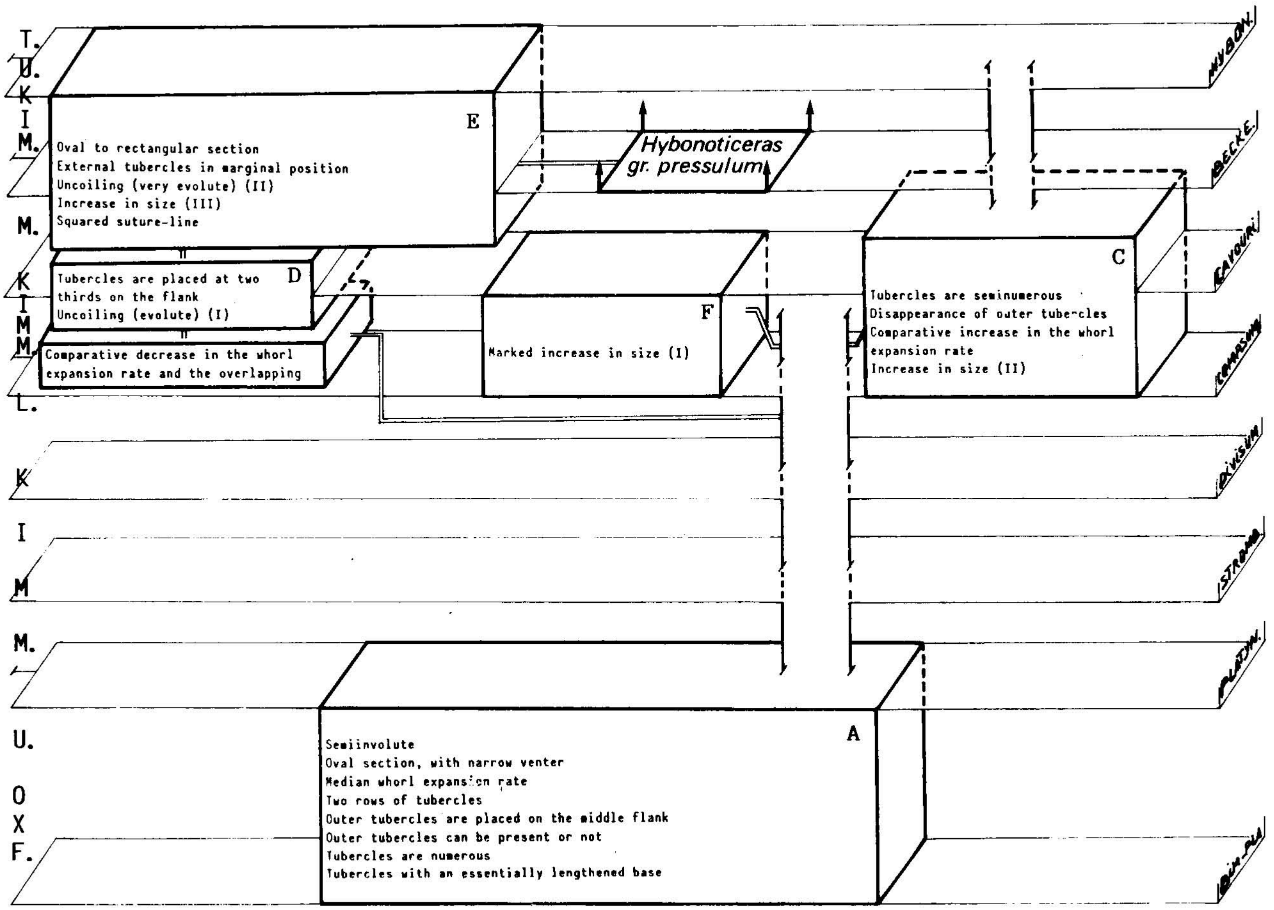


Fig. 2.—Evolutionary framework of the genera *Pseudowaagenia* and *Schaireria*.

block A: *Ph. altenense* (D'ORBIGNY)
block B: *Btt. benettii* CHECA
block C and D: *Ph. wolfi* NEUMAYR
block E: *O. ziegleri* CHECA
block F: *S. bucki* CHECA
block $G_1$: *O. garibaldii* (GEMMELLARO)
block $G_2$: *O. uhlandi* (OPPEL)

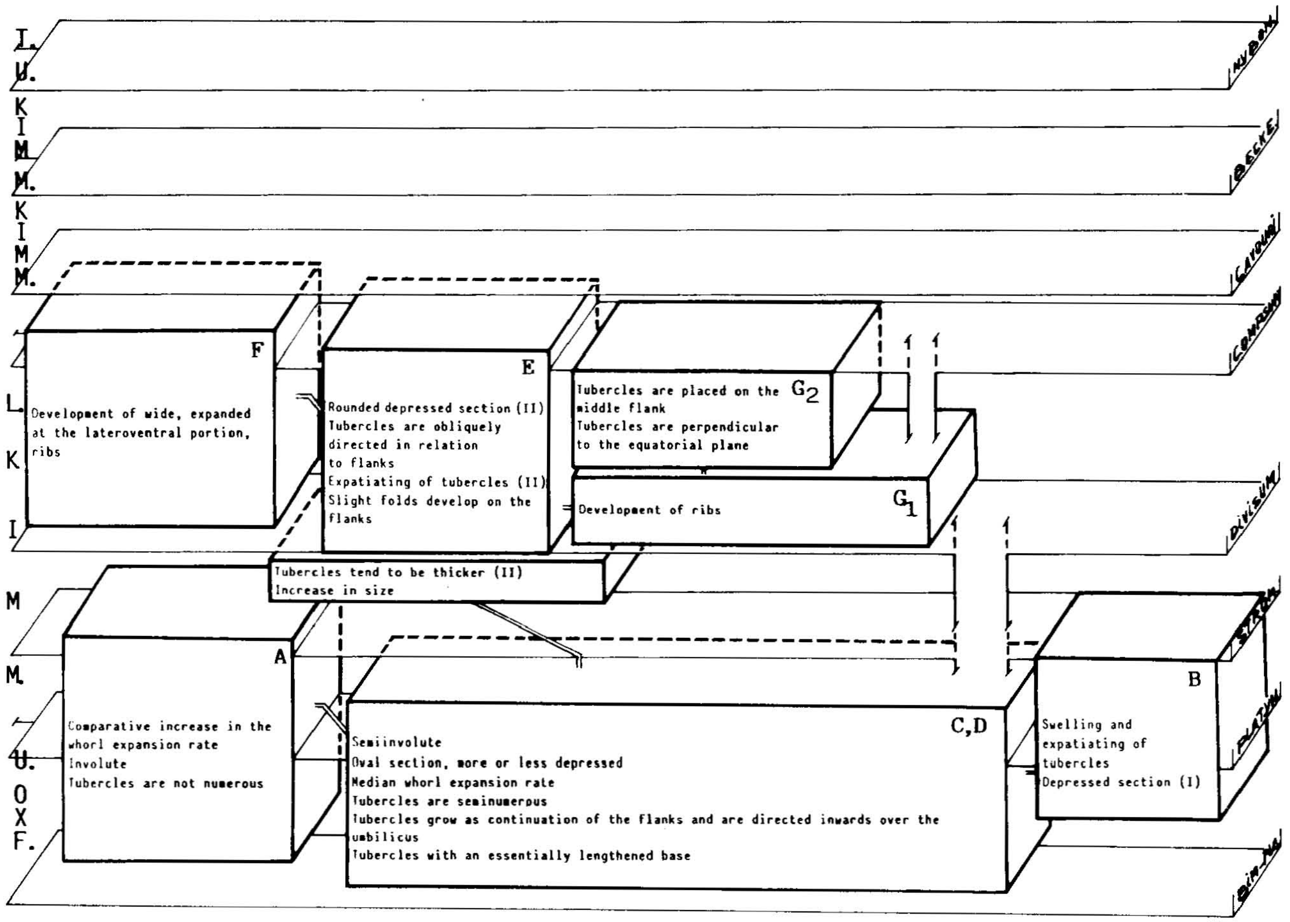


Fig. 3.—Evolutionary framework of the genera *Physodoceras*, *Benetticeras*, *Orthaspidoceras* and *Simaspidoceras*.