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Evolutionary trends in Oxfordian and Kimmeridgian Subbetic Aspidoceratinae (Southern Spain). A proposition of Null Hypotheses about the evolutionary course in a highly significant group of tethydian Upper Jurassic ammonites

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ABSTRACT — An extensive study of a large amount of « Aspidoceras » material from the subbetic Upper Jurassic has been carried out. Our principal aim has been to establish basic evolutionary conformations *based on the modifications of earlier characters and the incorporation of changes and innovations. This methodology has allowed us to propose several hypotheses suggesting possible relations among these* basic evolutionary conformations *and the establishing of evolutionary tendencies. The formulation of these hypotheses and their comparative evaluation permits us to present deductive models which represent the opinion of the authors with regard to the evolutionary framework of the group examined. These patterns give us the null hypotheses which will be tested in the next searching phases — species treatment either local and/or monographic. Moreover, they imply new relations among species if they are conceived in a traditional view. The conclusions reached are the first hypothesis on stratigraphically collected mediterranean « Aspidoceras ».*

RIASSUNTO — [Tendenze evolutive negli « Aspidoceras » dell'Oxfordiano e Kimmeridgiano subbetico (Spagna meridionale). Proposta di « null hypotheses » sui modelli evolutivi di un importante gruppo di ammoniti del Giurassico superiore] — *Lo scopo del presente lavoro è la formulazione di una « null hypothesis » sul comportamento evolutivo degli « Aspidoceras », documentata dalla testimonianza fossile. La ricerca è stata compiuta studiando una collezione di circa 1.000 individui campionati dagli Autori nella Zona Subbetica (Spagna meridionale). Tutto il materiale è stato sottoposto ad un preciso controllo stratigrafico, e si trova depositato presso il Dipartimento di Paleontologia dell'Università di Granada (Spagna).*

Dopo aver applicato tecniche statistiche ai caratteri misurabili, sono state riconosciute quelle che noi abbiamo battezzato « basic evolutionary conformations », *stabilite tra l'insieme dei caratteri ereditari. Per la loro rappresentazione grafica sono stati utilizzati « block-diagrams » tridimensionali, nei quali l'altezza corrisponde alla distribuzione stratigrafica accertata.*

Tra i diversi diagrammi inerenti le « basic evolutionary conformations » *si è cercato di trovare ipotesi di relazioni evolutive, selezionando quelle che evidenziavano le relazioni più dirette, cioè le ipotesi più economiche scientificamente. La decisione di tralasciare le interpretazioni o le ipotesi più complesse potrebbe sembrare il risultato di una certa preferenza per i modelli gradualistici, ma non è questo il caso, considerato che non è stata valutata la continuità dei processi evolutivi. In realtà la nostra pretesa è stata quella di considerare qualunque interpretazione evolutiva di questo gruppo in un contesto, iniziale, in accordo con la prevedibile stabilità dell'ambiente ecologico, e in concordanza con i limiti di tolleranza presupposti per questa fauna; tutto questo è stato considerato accettabile in questa fase della nostra ricerca. I diversi gruppi di* « basic evolutionary conformations », *relazionati tra loro, e distinti sistematicamente a livello generico, ci danno le « null hypotheses » da comprovare, studiandole monograficamente nei diversi settori paleogeografici, o meglio, in base ad un modello generale che ci permetta di integrare questi studi.*

La metodologia seguita ha fatto emergere tendenze a cambiamenti morfologici nel tempo, all'interno dell'insieme degli « Aspidoceras » mediterranei dell'Oxfordiano e Kimmeridgiano subbetico. I risultati debbono essere considerati come derivati da una lettura diretta della documentazione fossile, e le conclusioni derivanti possono così riassumersi: 1) *Necessità di creare nuove connessioni interspecifiche se si considera la sistematica tradizionale applicata in questo gruppo.* 2) *Durante il Kimmeridgiano e l'Oxfordiano superiore, ove ha origine, il genere* Aspidoceras *sviluppa una linea evolutiva in cui persiste la bituberculazione durante l'ontogenesi, in una seconda linea si manifesta la tendenza alla mancanza più o meno tardiva della serie di tubercoli esterni.*

3) Pseudowaagenia *sviluppa la sua morfologia più evoluta del Kimmeridgiano medio e superiore tra l'insieme di forme ad ampio ombelico e irregolarmente bituberculate, che originano gli* Hybonoticeras *del gruppo* pressulum *Neumayr.* 4) Physodoceras *e* Orthaspidoceras *giungono al loro massimo sviluppo durante il Kimmeridgiano inferiore. Le diversificazioni si producono a partire dall'incremento delle dimensioni e del numero dei tubercoli, ed anche per l'acquisizione di sezioni più arrotondate. Nella linea di ornamentazione più forte e nei giri voluminosi la diversificazione è elevata, però, la distribuzione stratigrafica è ridotta.* 5) *Nell'Oxfordiano terminale e Kimmeridgiano iniziale abbiamo trovato forme globose, la cui posizione sistematica rimane ancora incerta.* 6) *Generalmente nessuno stock di configurazione primitiva supera il Kimmeridgiano inferiore.* 7) *L'acme di diversificazione degli « Aspidoceras » si presenta nel Kimmeridgiano inferiore, nelle zone a Strombecki e Divisum.* 8) *Delle sei linee evolutive che superano il Kimmeridgiano inferiore, due si originano nella zona a Strombecki ed il resto nella zona a Divisum.* 9) *In tutte le linee l'incremento della grandezza si manifesta per la prima volta nella zona a Strombecki; questo fenomeno solo si ripete nelle linee evolutive molto diversificate.* 10) *Negli* Aspidoceras, Pseudowaagenia *e* Physodoceras, *la tendenza all'aumento dell'ombelico si manifesta in tutte le linee evolutive.* 11) *Nel Kimmeridgiano superiore il genere* Aspidoceras *sviluppa tubercoli periombelicali la cui configurazione è ad ampia base e orientazione radiale o retroversa.*

RESUMEN — El objetivo de este trabajo ha sido la argumentación de una « hipótesis nula » sobre el comportamiento evolutivo de los « Aspidoceras » mediterráneos basada en el registro Fósil. La investigación se ha realizado sobre una muestra de aproximadamente 1000 individuos, recolectados por los autores, en la Zona Subbética (España meridional). El conjunto del material ha sido obtenido bajo un estricto control estratigráfico, y se encuentra depositado en el Departamento de Paleontología de la Universidad de Granada (España). Tras la aplicación de tratamientos estadísticos a los caracteres mensurables se han reconocido las aquí denominadas Estructuraciones evolutivas básicas *segregadas de entre conjuntos de caracteres heredados en atención a las innovaciones detectadas.*

Para su representación gráfica se han utilizado bloques tridimensionales en los que la altura corresponde a la distribución estratigráfica comprobada. Entre los distintos bloques — Estructuraciones evolutivas básicas *— se han ensayado hipótesis de relación evolutiva, y entre ellas se han seleccionado aquellas que evidencian las conexiones más directas -es decir las hipótesis más económicas. La determinación de desechar las interpretaciones o hipótesis más forzadas podría parecer el producto de una cierta preferencia por los modelos gradualísticos, pero este no es caso necesariamente ya que no se ha valorado la continuidad de los procesos evolutivos; más bien la pretensión ha sido la de considerar cualquier interpretación evolutiva de este grupo en un contexto, en principio, acorde — y ésto lo hemos considerado aceptable en esta fase de la investigación — con la previsible estabilidad del medio del que formó parte ecológicamente, de acuerdo con los límites de tolerancia supuestos para esta fauna. Segregadas sistemáticamente a nivel genérico, los diferentes entramados de* Estructuraciones evolutivas básicas *constituyen las hipótesis nulas a contrastar por medio de estudios monográficos en los diferentes ámbitos paleogeográficos, o, a ser posible, a través de un modelo general que integrase tales estudios.*

La metodología seguida ha hecho emerger tendencias de cambio morfológico a lo largo del tiempo en el conjunto analizado de los « Aspidoceras » mediterráneos del Oxfordense superior y Kimmeridgense Subbéticos. Los resultados deben considerarse derivados de una lectura directa del registro fósil, y las conclusiones alcanzadas pueden resumirse como sigue: 1) *Necesidad de nuevas conexiones interespecíficas si se considera la sistemática tradicional aplicada en este grupo.* 2) *Durante el Kimmeridgense, y desde su origen en el Oxfordense superior, el género* Aspidoceras *desarrolla una línea evolutiva en la que persiste la bituberculación durante la ontogenia; en una segunda línea se manifiesta la tendencia a la supresión más o menos tardía de la serie de tubérculos externos.* 3) Pseudowaagenia *desarrolla sus morfologías más evolucionadas en el seno del conjunto de formas evolutas e irregularmente biturberculadas del Kimmeridgense medio y superior, que darán origen a los* Hybonoticeras *del grupo* pressulum *Neumayr.* 4) Physodoceras *y* Orthaspidoceras *alcanzán su máximo desarrollo durante el Kimmeridgense inferior. La distintas diversificaciones, se producen a partir del incremento de la talla y del número de tubérculos, así como a través de la adquisición de secciones más redondeadas. En la línea de ornamentación grosera y conchas más voluminosas la diversificación es alta, pero la distribución bioestratigráfica es reducida.* 5) *En el Oxfordense terminal y Kimmeridgense más antiguo se han detectado formas globulosas cuya posición sistemática queda por matizar.* 6) *En general, nigún stock de configuración primitiva sobrepasa el Kimmeridgense inferior.* 7) *La máxima diversificación de los « Aspidoceras » kimmeridgenses se produce en el Kimmeridgense inferior, zonas de Strombecki y Divisum.* 8) *De las seis líneas evolutivas que sobrepasan el Kimmeridgense inferior sólo dos se originan en la zona de Strombecki y el resto lo hace en la zona de Divisum.* 9) *En todas las líneas el incremento de talla se manifesta por vez primera en la zona de Strombecki; este fenómeno sólo se repite en líneas evolutivas muy diversificadas.* 10) *En* Aspidoceras, Pseudowaagenia *y* Physodoceras, *la tendencia al desenrrollamiento se manifiesta en todas las líneas evolutivas.* 11) *En el Kimmeridgense superior el género* Aspidoceras *desarrolla tubérculos periumbilicales cuya configuración incluye bases ámplias y orientaciones radiales o retroversas.*

INTRODUCTION

The present study takes as its starting point the works on Aspidoceratinae of the Subbetic Zone carried out by Oloriz (1976) and Checa (1981), and the results given are those of the first phase of a research programme which aims to present a monographic treatment of european Aspidoceratinae, with the specific objective of obtaining paleobiological evidence and providing an adequately argued and unified systematic treatment of the subject. This last aim, which we consider a « sine qua non » in such a paleontological approach as that outlined above, has led us to take as our prime objective here the precise determining of the evolutionary tendencies registered in the subbetic Kimmeridgian, established by means of an examinition of a series of what we may call « basic evolutionary conformations ». Based upon our analysis and on the chronological delimiting of the « basic evolutionary conformations » we will propose hypotheses as regards

possible evolutionary tendencies, and will conclude with the proposal of several schematic patterns which seem to us, at present, to be the most feasible.

The possibility to refute our hypotheses about evolutionary development is inferred from the anticipated study at the species level in all the encompassed geographical distributions of european Aspidoceratinae as well as from the consideration of speciation models in which the allopatry would be involved in some degree.

We will in no case mention specific concrete determinations — nevertheless, an elementary taxonomic guide-line for a better comprehension of the taxonomic spectrum of each « basic evolutionary conformation » in the Subbetic region is included. Moreover it is by no means difficult to recognize which of the « classic species », or species which have already appeared in literature, might fit in with each of the models that we have considered structurally basic in the evolutionary development of the Aspidoceratinae studied. So, necessarily over the species level, as it is traditionally interpreted in Aspidoceratinae, nonetheless, and as may be expected given that we are concerned with establishing a primary or basic order and a consistent level of reference, we are dealing with groups of « strongly related species » and consequently we will limit our remarks to the context of the traditionally accepted generic boundaries. If we would have adopted a more conventional procedure, that is to say, operating with specific references, we would simply have moved a step further within one of the many evolutionary frameworks which remain specially transitory, even though they may incorporate the most recent discoveries if we take into account the work to be carried out in the project above mentioned. Thus, once the sistematic treatment has been uniformly established we can proceed to identify which of the already established taxa, together with new ones, reach the level of paleobiospecies -«uniformly established» refers to the monographic treatment with the definite and permanent criteria taking into occount geographical, sedimentological and stratigraphical data; so will be possible to avoid the « noise » inherent to an information coming from different authors of different times and, logically, with differential hierarchical assessment of characters.

The use of the term « paleobiospecies » does not imply any value judgment, nor is there any suggestion or a comparison between this and other terms used to designate species in paleontology. Our choice of terminology was made to emphasize the paleobiological considerations which will be taken into account, without of course forgetting the implications inherent in the temporal features, which must never be overlooked in any paleontological analysis.

MATERIAL

We have worked on a sample of some 1.000 individuals collected in the Subbetic Zone with precise indications of location and stratigraphical level. This material is conserved in the collections of the Department of Paleontology at the University of Granada, Spain. For identification, each specimen is signed by letters and numbers which are the reference for collector, geographical location, stratigraphy and a first aproximation to the size of the sample from which is proveeding -i. e. $X.G_{23}.5.40$ is the fortieth in the bed number 5 of the profil number 23 of Sierra Gorda -the second letter always refers to the geographical location- and collected by Mr. « X » -collector's reference.

The amount of outcrops in which a bed by bed sampling has been realized is of more than 100, and their precise locations are referred in Oloriz (1976).

To this ammonite « Aspidoceras » collection, the usual measures for a paleontological study -i. e. for a given diameter (dm): umbilicus (U), height (H) and thickness (E) of the spire; also the end-diameter (Dm) and size of phragmocone; on the other hand, the ornamentation and the suture-line were analized. The compilation of data may be consulted in the tables, schemes and figures inserted in Olóriz (1976) and Checa (1981). In the last one, the mathematical treatment and delimitation of populations is graphically expressed by the reproduction of regression-lines. In the first one mentioned, the information about general stratigraphy, faunal spectrum in which each species is inserted, and so, is registered.

To conclude, our study has been focused on two different aspects:

1 - The differential diagnosis at the generic level.
2 - The typology and stratigraphic distribution of Aspidoceratinae.

A DIFFERENTIAL DIAGNOSIS ON A GENERIC LEVEL IN OXFORDIAN AND KIMMERIDGIAN « ASPIDOCERAS »

Genus ASPIDOCERAS Zittel (1868)

Type species — *Ammonites rogoznicensis* Zeuschner (1846).

Large or small in size (small size: less than 80mm; medium size: between 80 and 150mm; large size: more than 150 mm), with a generally spacious shell and sections ranging from oval-shaped to depressed. Two rows of medium or large size tubercles always

develop, at least, at one stage. The relative position of the tubercles on the flanks is variable.

Genus PSEUDOWAAGENIA Spath (1931)

Type species — *Ammonites haynaldi* Herbich (1968).

Small size; medium size shells are rare. Slow growth spirals, oval-shaped and some even rectangular. Two rows of small tubercles always develop, at least at one stage, though their degree of continuance varies widely. The relative position of the tubercles on the flanks is also variable. In some species more or less narrow folds develop which affect the ventral region. The density of the periumbilical tubercles can be considerable.

Genus PHYSODOCERAS Hyatt (1900)

Type species — *Ammonites circumspinosus* Quenstedt (1858).

Small to medium in size. Globose shells with rapid growth and sections generally oval-shaped and of variable width. There is one single row of tubercles in a periumbilical position. The size and orientation of the tubercles varies within strict limits. Sometimes more or less highly developed folds exist which may on occasions affect the ventral region. The absence of tuberculation can be clearly seen in the nuclei of some species.

Genus ORTHASPIDOCERAS Spath (1925)

Type species — *Ammonites orthocera* D'Orbigny (1850).

Medium to large in size. Globose shells with round or depressed sections, oval-shaped only in some species. Only one row of large size tubercles with a variable position between the umbilical edge and the middle of the flanks. The tubercles may be perpendicular to the flanks and their density is either maintained up to the outer whorls or diminished slightly. There exist ribs which cross the ventral region, originating in the tubercles or in the intertubercular spaces.

ASPIDOCERATINAE: TYPOLOGY AND STRATIGRAPHIC DISTRIBUTION

The observations which are the subject of this commentary refer to the proposed zonal intervals -seven- between the Upper Oxfordian and terminal Kimmeridgian proposed by one of the present authors (Olóriz, 1976; Olóriz & Tavera, 1981). In the Upper Oxfordian the Bimammatum and Planula zones are combined for convenience in the analysis of the Aspidoceratinae. We should point out that we have not commented on ribbed Aspidoceratinae of the Cavouri and Beckeri zones.

UPPER OXFORDIAN

Bimammatum zone - Planula zone — The Aspidoceratinae present a morphology that allows us to determine the following genera: *Aspidoceras, Pseudowaagenia* and *Physodoceras*. Only in the upper part of the interval — Planula zone — do we find some structures of the orthaspidoceras-type, though of small size. The origin of the first three genera mentioned has not been satisfactorily explained.

LOWER KIMMERIDGIAN

Platynota zone — In general we notice few changes. The only significant detail is the loss in some *Aspidoceras* of the second row of tubercles towards the outer whorls. *Orthaspidoceras* continue to be as scarce as in the previous discussed level, and they disappear without reaching the Strombecki zone.

Strombecki zone — There is a marked first differentiation phase which is shown in *Aspidoceras, Pseudowaagenia* and *Physodoceras*. In *Aspidoceras* we find, together with forms which have not evolved — characteristic which this genus has shown from its beginnings —, shells with a single row of tubercles in the outer whorls; further, these tubercles do not show a rounded base as do the more primitive forms and we can also observe a considerable increase in size.

In *Pseudowaagenia* we observe larger forms and the restriction of outer tubercles to inner whorls.

In *Physodoceras* larger sized shells with a certain increase in the number of tubercles are added. Among these new forms we can determine some specimens with a rapid growth of the spirals and a tendency to wider spacying and thickening of the tubercles, together with others whose most remarkable peculiarity is coiling and lengthening of the tubercle bases.

Divisum zone — In this interval we note a greater diversity. In *Aspidoceras* larger sized forms are developed, with two rows of tubercles throughout ontogeny, although the shape of the tubercle base is long and the outer row is somewhat displaced towards the ventral border of the flanks.

In *Pseudowaagenia* there is a great number of shells without the second row of tubercles in the living

chamber and uncoiling allows us to establish differentiations which will become more accentuated in later intervals.

In *Physodoceras* there is a general distribution of globose shells with a more or less definite development of slight folds on the flanks and in the ventral region.

In this zone we have the enlargement of *Orthaspidoceras* through evolute specimens with tubercles at an oblique angle to the flank; another group is formed of voluminous, large-sized shells where the most distinctive element seems to be the development of ribs that cross the ventral area.

MIDDLE KIMMERIDGIAN

Compsum zone — In this interval we can determine several interesting facts in the development of the Aspidoceratinae. In *Aspidoceras* the forms of primitive morphology seem to die out. Something similar occurs in *Pseudowaagenia* and *Physodoceras,* although in this later genus the most highly developed specimens continue. This apparent cycle of extinction and/or renewal also affects to *Orthaspidoceras.*

Cavouri zone — In *Aspidoceras* the bituberculated forms continue to predominate throughout ontogeny, and in them we can perceive new and different elements, such as, for example, the marginal placing of the second row of tubercles.

In *Pseudowaagenia* there only exists one typology, consisting of highly evolute shells with a great number of tubercles, flanks which are more or less flat, and parallel and irregular development of the marginal row of tubercles; these forms show a very peculiar suture-line — broad elements with few indentations — whose general shape is quadrate — square or rectangular; these may be considered the evolutionary base of *Hybonoticeras* of the *pressulum* Neumayr group.

The *Physodoceras* are now not common, and are only represented by their most highly evolute forms above referred.

UPPER KIMMERIDGIAN

Beckeri zone — We have found no changes here respect to the situation in the underlying beds appertaining to the immediately previous zones.

METHODOLOGY

This study has been carried out taking into account the extensive bibliography listed in the works of Olóriz (1976) and Checa (1981), and we have treated the information collected statistically. In some cases we have had to recourse to more classical types of collections such as those of Quenstedt, Fontannes and Oppel.

With the reliance coming from this precise material we have been able to establish an approach to the configurations and behaviour of « Aspidoceras » in the subbetic Upper Oxfordian and Kimmeridgian. Typology, stratigraphical and geographical considerations shall be the support of our observations and suggestions.

We have therefore experimented with the possibility of recognizing « basic evolutionary conformations » which on a generic level should provide us with a clearer understanding of the moment of evolution in each case, and the correlation with a determined and concrete stratigraphical level. These « basic evolutionary conformations » are based upon a consideration of the innovation which occur in the whole group of inherited characteristics. In order to represent these graphically we have made up a series of diagrams in which each of our « basic evolutionary conformations » is shown as a three-dimensional figure, drawn arbitrarily except for the time dimension. In order to make these diagrams quite clear, we have arranged that:

- the subdivisions of a block within the same time interval shows characters that must definitively have been established previously;
- the characteristics which are situated in the lower part of a block are those which are registered at this level for the first time;
- the vertical extension of the block indicates, unless there are indications, the duration of the characteristics mentioned;
- branching in opposite directions corresponds to more clearly marked differences. These will acquire most significance when they are placed on both sides of the central branch or body, and have most weight according to the age of their register: the older they are the more significant;
- those blocks which are not labelled A, B, ..., are considered as evolutionary platforms which are necessary for the development of one or more « basic evolutionary conformations ». The characters in these platforms tend to have a marked plasticity.

Finally, we postulate a series of hypotheses of relations between the various « basic evolutionary conformations » which, tested comparatively, are selected, giving as a result the hypotheses, ordered by genera, which most clearly reflect our opinions considered at the present moment.

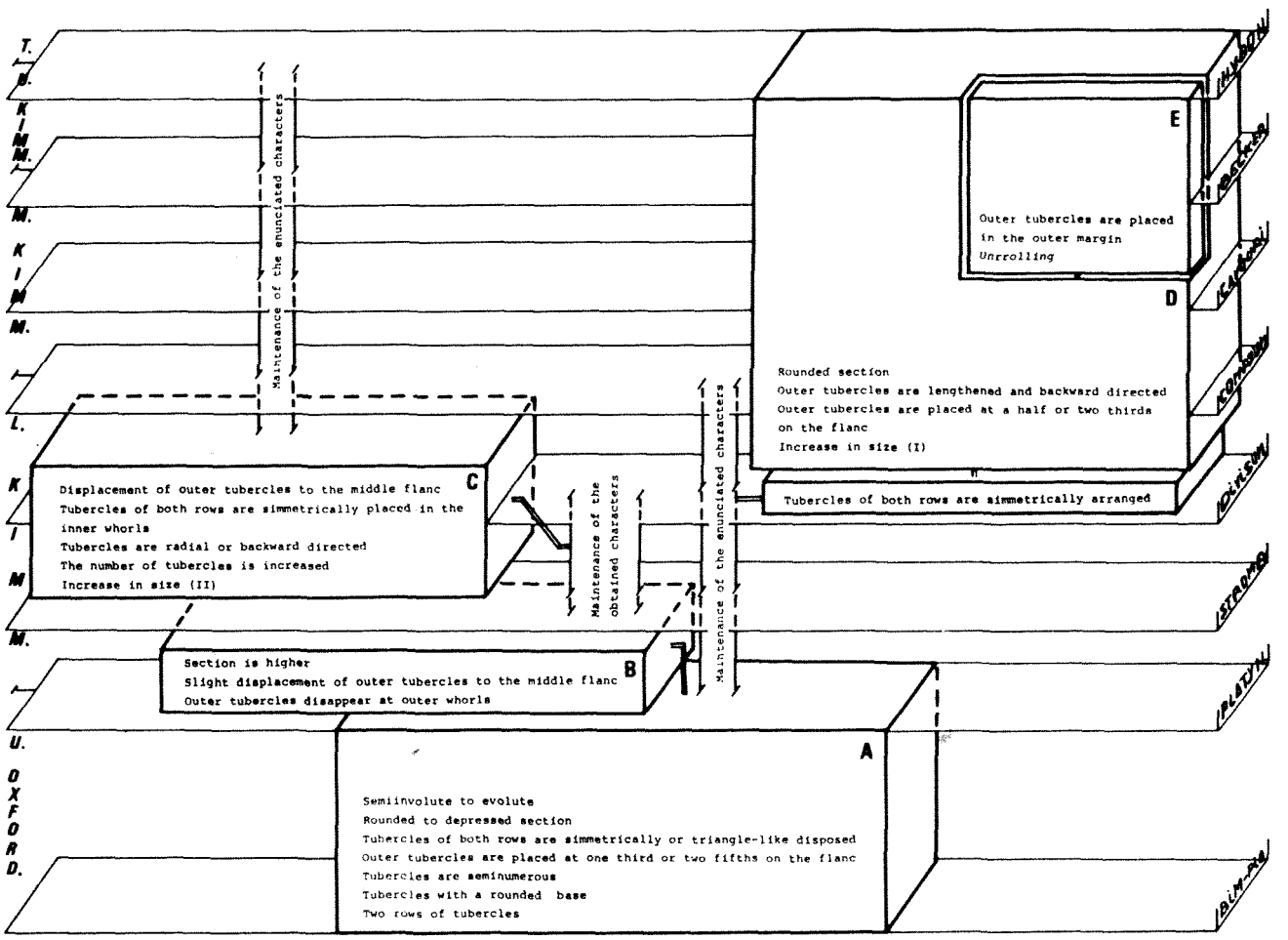
This methodology allows us to establish the principal events of the changes registered in Aspidocera-

tinae fauna, since these changes are constructed on the basis of high-level innovations — normally several characteristics are involved — in relation to the systematic hierarchical bases of the group. On the other hand, what could be called repetitive achievements are recognized. In the last resort, the results which we present here will have to be submitted to a rigorous test when we have at our disposal the results of the research project above referred. The observations which follow in this paper are, consequently, the results of the first phase of this project.

RESULTS

Basic Evolutionary Conformations: Hypotheses on possible relations

Having presented our preliminary observations on typology and stratigraphic distribution, we are now going to undertake a more detailed study, in which we will indicate, genus by genus, the most significant features — the «basic evolutionary conformations» — to be found, our aim being to propose various connection hypotheses.



Text-fig. 1 - Framework of the hypothetical relations between the different « basic evolutionary conformations » in *Aspidoceras*.
A = *A. binodum* Oppel group.
B = *A.* sp. 1 (*A.* sp. cf. *acanthicum* Oppel in Olóriz, 1976; *A.* sp. 1 Checa, 1981). *A.* sp. 2 (*A. acanthicum acanthicum* Oppel in Olóriz, 1976 *pars*; *A.* sp. 2 Checa, 1981).
C = *A. acanthicum* Oppel group.
D = *A. longispinum* Sowerby - *A. hoplisum* Oppel - *A. meridionale* Gemmellaro - *A. caroli* Spath groups.
E = *A. apenninicum* Zittel group (exclusively mediterranean forms).

Aspidoceras — We find the initial morphology of this genus is the Upper Oxfordian-Bimammatum zone. These are semiinvolute forms which become evolute towards the outer whorls. The section is rounded or typically reniform -kidney shaped. They are usually small in size. The ornamental design is composed of two rows of tubercles whose elements are paired off or in a « triangular arrangement » -each tubercle of the inner row is paired with two from the outer. The outer row is always found below the covering line, at a third or two fifths of the way up the flank. Similarly both rows show semi-numerous tubercles -8 to 13 outer tubercles and 8 to 17 inner tubercles. Finally, the essentially rounded shape of the tubercles is specially interesting. This initial morphology -A- is found up to the upper part of the Divisum zone.

In the Platynota zone and presumably on this basis we find innovations reflected in some changes which continue into the Divisium zone -B:

The sections are usually higher (rounded). The outer row of tubercles moves towards the middle of the flank. The tubercles continue to occupy the same positions that we observed previously in the inner whorls, but towards the end of the phragmocone the outer row of tubercles disappears, and in the inner row, which persists, the elements tend to space themselves out more.

In addition to the forms we have already mentioned, we find in the Strombecki zone a group of *Aspidoceras* -C- whose differential characteristics are as follows:

Outer tubercles situated half way up the flank. The outer row of tubercles is restricted to the inner whorls and its elements pair off with those of the inner row. The outer row sometimes reappears in the living chamber and we can even find instances of both rows disappearing at the beginning of the living chamber. The shape of the tubercle on the flank is radial or retroverse. The number of tubercles is greater than those of previous forms. The specimens are generally large in size (up to 175 mm). This morphological type continues up to the end of the Kimmeridgian, though from the Cavouri zone onwards it is significantly less common.

There are two alternative connection hypotheses which relate this group to those previously found. In the first case (C-A) we might consider a direct derivation from the most primitive forms. This would mean a sharp modification of the shell (rounded-reniform to ovoid), a restriction of the outer row to inner whorls, changes in the base of the periumbilical tubercles and increase in their number, and finally a considerable increase in size. All this would have occurred in the Strombecki zone.

The other alternative would be to suggest a derivation from the forms that developed as a result of the change in the two original types of the Platynota zone (C-B connection). In this case, and developing from forms in which the second row of tubercles does not reach the outer whorls, a pairing off the elements of both rows in the inner whorls would take place at the same time that the design of the tubercle base was modified; it is probable that in connection with the increase in size there would occur a similar increase in the number of tubercles.

Another group of forms -D- is to be found for the first time in the Divisum zone. This is a group whose essential differential characteristic is the development of two rows of tubercles symmetrically arranged throughout ontogeny. In this group:

The sections are generally rounded or somewhat depressed; reniform sections hardly exist. We find a noticeable increase in the size of the specimens (up to 150 mm). This morphology continues up to the Beckeri zone.

The appearance of this group allows us to propose at least three hypotheses (D-A, D-B, D-C), which can be reduced to two: D-A or D-B/C.

In the first case (D-A) the derivation from the primitive stock would be supported by the loss of a reniform section, of the « triangular arrangement » of the tubercles, and by the slight displacement towards the ventral region of the outer row and by the loss of strictly rounded base elements. The increase in size would not be a characteristic peculiar to this relation.

The second hypothesis (connection D-B/C) would mean basically the recuperation of characteristics which had previously disappeared in both groups (C and B), as well as the development of two rows of tubercles throughout ontogeny, the change in spiral shape and the return to smaller sizes.

The last differentiation -E- which we have found occurs in the upper part of the Middle Kimmeridgian — Cavouri zone — and consists in the enlargement of the umbilicus — these are forms which are evolute or highly evolute in outer whorls and with a great number of tubercles — and in the displacement of the outer row to a marginal position, so that the section has a quadrate shape.

According to the data at present available, there does not appear to exist any valid hypothesis except that of D-E if we wish to relate this group -E- to the bituberculated forms which develop during the Middle Kimmeridgian age -D.

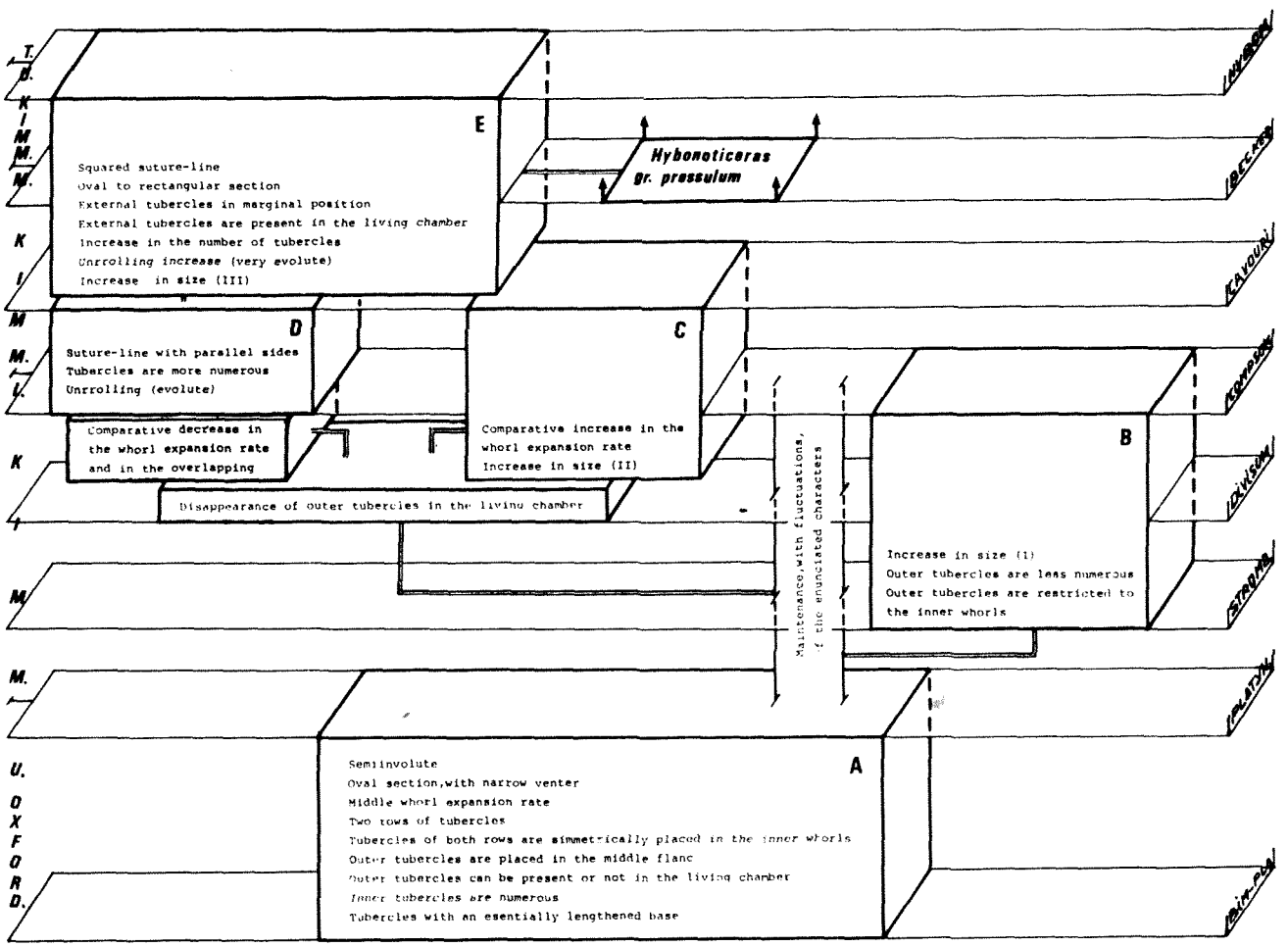
Pseudowaagenia — The *Pseudowaagenia* genus begins in the Bimammatum zone with a very characteristic morphology, since these forms have the following features:

They are semiinvolute with the U/D value increasing towards the outer whorls. The section is oval-shaped, with convex flanks and a small ventral region. The external tubercles show a long design, are at times radial, and often retroverse; they are situated half or two-thirds up the flank. The spirals are of medium growth. There are two rows of tubercles whose elements are paired off in inner whorls, and sometimes a slight rib can be seen between paired elements. The outer row of tubercles is situated half way up the flank and is of irregular shape; it may or may not be present in the living chamber. The tubercles of the inner row are very numerous (19-22) and have a prolonged base. Forms with these characteristics -A- continue throughout the Lower Kimmeridgian.

In the Strombecki zone we can distinguish another typology -B- with its own characteristic features within the genus:

The outer row is strongly limited to very internal whorls. It may even disappear on occasions, though this disappearance may be due to deficient conservation. In close relation to the characteristic just mentioned, we can observe a striking reduction in the number of tubercles in the outer row. There is an increase in size. This group of characteristics disappears in the transition from Lower to Middle Kimmeridgian.

Given that this is the first morphological group to be separated, there is no alternative to the assumption of a derivation from the stock of primitive forms. The whole process of differentiation must be presumed to have developed in the Platynota zone since these forms



Text-fig. 2 - Framework of the hypothetical relations between the different « basic evolutionary conformations » in *Pseudowaagenia.*
A = *Ps. microplum* Oppel group and related undescribed subbetic forms.
B = *Ps.* sp. 1 (*A. (Ps.) haynaldi haynaldi* Herbich in Olóriz, 1976 *pars*; *Ps.* sp. 1 in Checa, 1981).
C = *Ps. sesquinodosum* Fontannes grup.
D = *Ps. haynaldi* Herbich group.
E = *Ps. acanthomphalum* Zittel - *Ps. carpathica* Spath - *Ps. serbica* Andelkovick groups (exclusively mediterranean forms).

are already found in the base of the Strombecki zone; and we cannot altogether rule out their existence in the previous zone.

The following differentiation has been registered in the Divisum zone. These are forms which in any case do not present outer tubercles in the living chamber. Two typologies can be distinguished on this basis: one based on a rapid growth of the spiral and an increase in size -C-, a tendency which continues throughout the lower part of the Middle Kimmeridgian, and another more successful evolutionary line, which has as its prime characteristic a progressive enlargement of the umbilicus in the forms of which it is composed.

This second line reaches the last beds of the Upper Kimmeridgian and throughout its development it is possible to distinguish two clearly differentiated stocks which we will now analyze. In the first of these -D- we already have evolute shells:

Spirals with slow growth and less covering. There is a slight increase in the number of tubercles. The sutures show special characteristics, since both the lobes and the saddles have flanks which tend to be parallel and have accessory elements that are very little indented. The size is no greater than 75mm.

From the Cavouri zone onwards, and after the disappearance of the forms which we have just discussed, we note evidence of the second stock mentioned -E. In this case the shells are as follows:

The samples show an increase in size. The sutures have flanks which are now completely vertical and parallel, so that the lobes and saddles are quadrate. The saddles are very wide and have very shallow lobes. The lobes are narrow and shallow. The umbilical enlargement is clearly reached - these are evolute in outer whorls. The sections are ovalshaped and sometimes rectangular in outer whorls, and generally trapezoid with a tabular ventral region in the inner whorls. This characteristic is important in connection with the group of forms which they produce later (*Hybonoticeras*, at least in part). The external tubercles are lateroventral and sometimes are even to be found in the living chamber. There is a clear increase in the number of tubercles (they are very numerous); here we reach the highest values which have been observed for this characteristic in Aspidoceratinae (up to 26 tubercles).

We will now consider the various hypotheses which can be suggested based on the basic structural states we have presented. Without commenting further on the B-A relationship we will proceed to analyze the possibilities of the groups which are differentiated from the Divisum zone onwards. In the first place there are two possibilities:

— a) All these forms (C,D,E) are derived from the primitive stock -A.

— b) These forms are connected with the differentiated forms in the Strombecki zone -B.

In the first case (relation with A), every change would demand as a 'sine qua non' that the external tubercles be limited to the phragmocone. Later modifications would allow us to separate the two lines mentioned (C and D, E). The fact that both lines reach the disappearance of the external tubercles in different ways as we have mentioned, is something which cannot be proved at the moment, given the present state of research in the subject.

On the other hand, a derivation proceeding from B would mean the reimplanting of a character which had already disappeared — such as the development of outer tubercles throughout the phragmocone — from forms in which the same tubercles had been previously limited to the inner whorls. In the same way, in some cases -D-, there would also have to occur a regression to smaller sizes.

As far as the differentiation between C-D and E is concerned, this appears immediately due to the growth of the spiral and the umbilical enlargement of the shell. The alternative hypothesis would mean that D and E were derived from C; a third possibility would be that C originated from D.

The first hypothesis at least allows us to clarify the evolutionary tendencies. In the second case (D and E from C) we would have to assume an abrupt separation, with a complete renewal of characters, in which it would be difficult to explain the contemporaneity of the registers. We would have the same problem with the third hypothesis proposed.

Finally, there appear in the Cavouri zone forms related to E and belonging to another subfamily: Hybonoticeratinae, in which a more or less superficial groowe is developed in a tabular ventral region (*Hybonoticeras* of the *Hybonoticeras pressulum* Neumayr group).

Physodoceras. Orthaspidoceras — We feel that we are justified in treating these together, since we consider that there is a close interrelation between them, as we have observed.

The first forms — Bimammatum zone — belong to the *Physodoceras* genus and show the following characteristics:

Involute shells with an oval-shaped section (more or less depressed) sometimes with a trapezoid aspect. The spiral shows a low growth index and one single row of periumbilical tubercles develops on it; these tubercles are not numerous and follow the line of the flank, directed towards the center of the umbilicus.

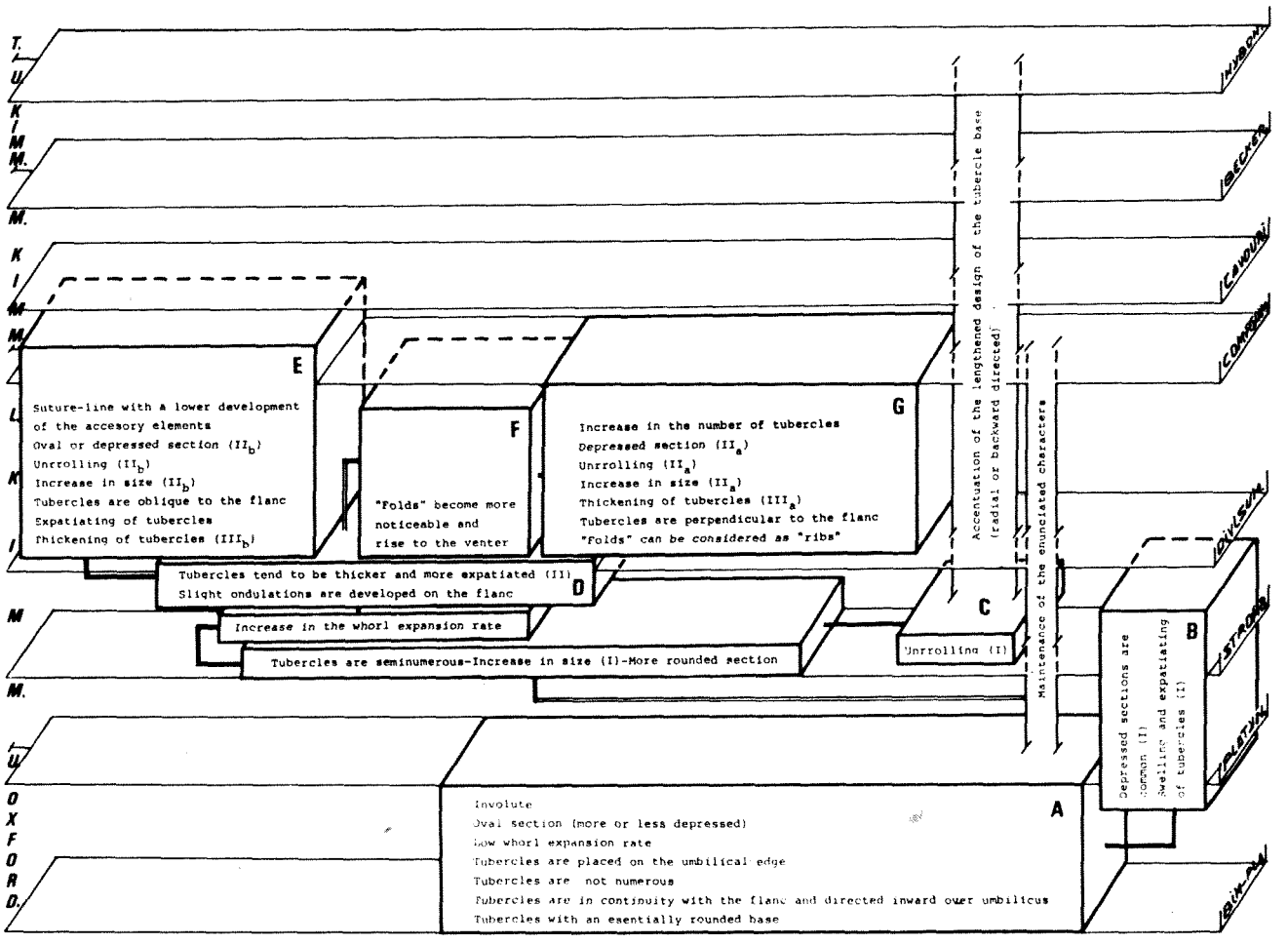
These elements have an essentially rounded base. This group of forms -A- can be found throughout the Lower Kimmeridgian.

Our preliminary differentiation -B- can be detected in the Planula zone and continues until the middle part of the Strombecki zone. This is a group of forms which are not common, and have peculiar characteristics:

There is a predominance of reniforms sections. We find a spacing out and thickening of the tubercles and therefore a reduction in their number. Sometimes the intertubercular spaces appear slightly depressed. This later characteristic leads us to consider the existence within this group of forms some of which belong both to the *Physodoceras* genus and to the *Orthaspidoceras*, so the typology of this latter group could be achieved by an accentuation of the characters referred to. These primitive *Orthaspidoceras* do not reach the upper limit of the Platynota zone.

As far as the possible origin of this group of forms is concerned, the only viable hypothesis is that of their derivation from the primitive stock during Upper Oxfordian.

The following innovations are present in the base of Strombecki zone and from here on all the forms show semi-numerous tubercles, a considerable increase



Text-fig. 3 - Framework of the hypothetical relations between the different « basic evolutionary conformations » in *Physodoceras* and *Orthaspidoceras*.

A = *Ph. altenense* D'Orbigny - *Ph. circumspinosum* Oppel groups (also, endemic forma as *Ph. diastrophum* Fontannes are included).

B = *O.* sp. 2 (*O. schilleri* Oppel in Olóriz, 1976 *pars*; *O.* sp. 2 Checa, 1981).

C = *Ph. contemporaneum* Favre group.

D = *Ph. insulanum* Gemmellaro - *Ph. montisprimi* Canavari groups.

E = O. *liparum* Oppel - *O. schilleri* Oppel - *O. lallierianum* D'Orbigny groups (classic morphological spectrum of *Orthaspidoceras*).

F = *Ph. serranum* Canavari emend. (*Ph. insulanum* Gemmellaro in Olóriz, 1976 *pars*; *Ph. serranum* Canavari emend. Checa 1981) (exclusively mediterranean forms).

G = *O. uhlandi* Oppel - *O. subdogouense* Venzo - *O. garibaldii* Gemmellaro groups.