PHYLOGENETIC RELATIONS AMONG OXFORDIAN AND KIMMERIDGIAN ASPIDOCERATINAE « CLASSICAL SPECIES », DEDUCED FROM THE SUBBETIC RECORD (SOUTH SPAIN). A PROPOSAL

by

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SUMMARY

The present work aims to present a scheme, that must not be considered as definitive, which principal interest is the easening of an image on the relations between « classical species » of Aspidoceratinae in agreement with the information obtained in the Subbetic Zone (South Spain), altogether with the detailed stratigraphical reference of those species in this region. The last aspect reflects significant peculiarities showed by ammonites (Aspidoceratinae in this case) as are biostratigraphical differences related with their biogeographical distribution. The four european genera of Aspidoceratinae are analysed. *Physodoceras* and *Orthaspidoceras* appear narrowly related, being the basical morphologies of this last genus always obtained through the accentuation of single characters present in the corresponding species of *Physodoceras*. *Aspidoceras* has two main morphological tendencies, that giving rise to the *A. acanthicum* (OPPEL, 1863) group, that loses its upper row of tubercles through the ontogenetic development, and another more « conservative » tendency, producing in any case extreme morphologies. Within *Pseudowaagenia*, three of the four considered species, that show a chronological replacement, compose a very well morphologically recognized evolutive line.

RÉSUMÉ

Ce travail essaie de présenter un schéma, qui ne doit pas être considéré comme définitif et dont le principal intérêt réside dans le fait qu'il fournit une image sur les relations entre « espèces classiques » d'Aspidoceratinae, conformément à l'information obtenue dans la Zone Subbétique (Sud de l'Espagne), ainsi qu'à la référence stratigraphique détaillée de ces espèces dans cette région. Le dernier aspect reflète des particularités significatives montrées par les ammonites (Aspidoceratinae dans ce cas) comme le sont les différences biostratigraphiques en rapport avec leur distribution biogéographique. On analyse les quatre genres européens d'Aspidoceratinae. *Physodoceras* et *Orthaspidoceras* apparaissent en étroite relation, les morphologies de base de ce dernier genre s'obtenant toujours au moyen d'une accentuation de caractères simples présents dans les espèces correspondantes de *Physodoceras*. *Aspidoceras* présente deux tendances morphologiques principales ; celle qui donne lieu au groupe d'*Aspidoceras acanthicum* (OPPEL, 1963) qui perd le rang supérieur de tubercules à travers le développement ontogénétique, et une autre tendance plus « conservatrice » qui donne lieu, dans certains cas, à des morphologies extrêmes. Dans le genre *Pseudowaagenia*, trois des quatre espèces considérées, qui se relayent dans le temps, composent une ligne évolutive très bien reconnaissable morphologiquement.

KEY-WORDS : AMMONOIDEA, ASPIDOCERATINAE, *PHYSODOCERAS, ORTHASPIDOCERAS, ASPIDOCERAS, PSEUDOWAAGENIA*, PHYLOGENETIC RELATIONS, EVOLUTIVE TENDENCY, OXFORDIAN AND KIMMERIDGIAN BIOSTRATIGRAPHY, SUBBETIC ZONE.

MOTS-CLÉS : AMMONOIDEA, ASPIDOCERATINAE, *PHYSODOCERAS, ORTHASPIDOCERAS, PHYSODOCERAS, PSEUDOWAAGENIA*, RELATIONS PHYLOGÉNÉTIQUES, TENDANCE ÉVOLUTIVE, BIOSTRATIGRAPHIE OXFORDIENNE ET KIMMÉRIDGIENNE, ZONE SUBBÉTIQUE.

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CONTENTS

I. INTRODUCTION

The present work puts together conclusions from a previous unpublished work by A. Checa (1981), and also the way of the posterior research up today. The acomplished labour is centered on the systematic revision of the Aspidoceratinae of the Subbetic Zone, carried out by the author since 1980.

First of all, since this article will deal with evolutionary considerations on a group, whose systematic is under reorganization, there will be not so much of an emphasis denomination contemplated in detail, as it will be the recognition of certain morphological groups of wide spectrum that host a series of « classical species », among which might or might not be included new forms, to evaluate its significate in the evolutive history of the Aspidoceratinae. A general view of the most apparent modifications occurring in Aspidoceratinae can be obtained throughout the Upper Oxfordian and Kimmeridgian.

The interest of the study of the, presently considered, subfamily Aspidoceratinae ZITTEL, 1868 emend. SPATH, 1931 follows various aspects. On the first place, the essentially mediterranean and submediterranean character of this subfamily, and, therefore any review of this group must necessarily follow through a profound study of the Subfamily Aspidoceratinae in the Subbetic Zone, given the advantageous conditions of findings. This fact is notably reinforced given its incidence in the associations where they take part, reaching a 20-25% during the Kimmeridgian (Olóriz & Tavera, 1981), in other words they can be considered as a very important component of the Subbetic fauna at that period of time.

Other aspects such as the comparatively scarce complexity of the shell structuration and its ample stratigraphical distribution-there are recordings at the Berriasian-ratify the interest that in principle might have the application of the paleontological method in Aspidoceratinae. The study has been carried out on material belonging to the collections of the doctoral thesis of L. Sequeiros (1974) and F. Olóriz (1976) altogether with some of the author's sampling. The sample analysed was compounded by more than 1.000 specimens, the study has been as deep as possible on the morphological characteristics, as it has also been on the biostratigraphic aspects, in order to conclude a systematic treatment that will enable, definitely, a phylogenetic view of this group during the Oxfordian and Kimmeridgian.

A detailed description of the Aspidoceratinae and their temporal distribution has been provided by F. Olóriz (1976) and A. Checa (1981). The last one also presents a first approximation to the mathematical treatment of the data collected from the sample studied.

II — ANTECEDENTS

There is a large number of biostratigraphic studies of regional coverage where references are made to this group. Anyhow, the only monographic work on this subject belongs to W. Buck (1958) and it represents the first trial to a systematic ordering. This study has two main limitations, first it was carried out on Submediterranean fauna essentially, and now we can be conscious of the high significance that the strict

mediterranean forms have towards a global comprehension of this group. Second, the scarce diffusion of the work has contributed to the fact that the treatment of the Aspidoceratinae has not reached its previsible impact, that would also have open new ways. As far as the Subbetic fauna is concerned, the obligated reference is F. Olóriz (1976) that constitutes the most extensive review after W. Buck (1958) and the first approximation to a systematic treatment and biostratigraphic determination of the Aspidoceratinae species.

III — MORPHOLOGICAL CHARACTERISTICS

They are clearly different from other groups of their contemporary Perisphinctacea. The spiral is voluminous in general terms, although there are exceptions.

The living chamber rarely exceeds one-half a whorl and ends in a simple opening, its design along the umbilical wall reflects almost fully the tracing of the growth lines in this zone. The ornamentation is based on simple schemes of tubercles and, occasionaly, ribs. It is interesting, as the principal ornamental characteristic with systematic value, above all the number of rows of tubercles whose consideration reaches a first order rank, being a helpfull criterium, even for distinction at the generic level. There may be a single row as in *Physodoceras* and *Orthaspidoceras* or two as in *Aspidoceras, Pseudowagenia* and *Simaspidoceras.*

Also, looking at specific differentiation, it interestes the position of the row or rows on the flank and the persistence of them during the ontogeny.

The number of tubercles in each row might be a significant character at different levels.

A first order criterium for differentiation at the species level is the morphology of the tubercle, that remains uniform at this level and even at the generic one. Finally, the directionality of the tubercle is an important character at the genus level since they might follow a path toward the center of the umbilicus or might be oblique to it or even perpendicular to the flank.

A highly efficient differentiating criterium is the occasional presence of ribs.

The rest of the morphological characteristics, such as size, width of umbilicus, heigth and thickness of spiral, design of section, usually have an importance subordinated to the hierarchy imposed by ornamental criteria, although in some cases they may reach a significant rôle face to the detailed systematic ordering.

The suture line, as pointed out by W. Buck (1958), does not seem adequated for specific differentiation, being, however, useful to distinguish groups of species.

IV — DIFFERENTIAL DIAGNOSIS AT THE GENUS LEVEL

Genus **Aspidoceras** ZITTEL, 1868

Type species : *Ammonites rogoznicensis* ZEUSCHNER, 1846

Small to large size, in general voluminous, sections from amply oval to depressed. Always, at least in some stage, it develops two lines of tubercles of medium to large size. The relative position of the tubercles is varied on the flanks. In some species true ribs might appear, always associated to the second line of tubercles.

Genus **Pseudowaagenia** SPATH, 1931

Type species : *Ammonites haynaldi* HERBICH, 1868

Small size. Medium size shells are rare. Spiral of slow growth, oval and even rectangular. Tubercles are always, at least at some stage, developed in two lines of small size and quite irregular persistence. The relative position of tubercles on the flanks is variable. In some species folds of larger or smaller narrowness are developed and affect the ventral region. Occasionally is remarkable the density of periumbilical tubercles.

Genus **Physodoceras** HYATT, 1900

Type species ; *Ammonites circumspinosus* QUENSTEDT, 1858

Small to medium size. Voluminous spirals, of fast growth and generally of ovalated sections and of different extent. A single row of tubercles in a periumbilical position. The size and orientation of the tubercles varies within narrow limits. Folds of greater or lesser development appear occasionally, that sometimes affect the ventral region. In inner whorls, as in forms occurring in the Tithonian the absence of tubercles might be observed.

Genus **Orthaspidoceras** SPATH, 1925

Type species : *Ammonites orthocera* d'ORBIGNY, 1850

Medium to large size. Voluminous spirals with rounded or depressed sections and in some species ovalated. A single row of tubercles of large size and variable position between the umbilical edge and the middle of the flank. Tubercles might be perpendicular to the flank, usually they keep the density toward outer whorls although it might diminish slightly. There are ribs that originate in the tubercles or in the intertubercular spaces and cross the ventral region.

Genus **Simaspidoceras** SPATH, 1925

Type species : *Aspidoceras argobbae* DACQUE, 1905

Medium size (large in the original area : Ethiopian province). Voluminous spirals, rounded and of pentagonal contour that is more or less accused depending on the relief of the ornamentation. Two rows of tubercles, the external one latero-ventral and with radially elongated elements. Ribs or folds are developed in correspondence to tubercles.

V — PHYLOGENETIC CONSIDERATIONS

The scheme here presented should not be considered as definitive for works are still being carried out on the systematic ordering of this group. Nevertheless, its interest radicates on the easening of an image on the relation between « classical species » in agreement with the information obtained in the Subbetic Region. Probably, at the present time, the most significant aspect will be the detailed stratigraphical reference of those species, given that this must be considered into a context in which the geographical procedence and the implied peculiarities were valued. The exclusion of the strictly subbetic forms, together with any specific reinterpretation, is justified on the basis of the research under project at the present time. Therefore it will be of greater interest facing a classical treatment of this group. Some ribbed forms of *Aspidoceras*, already occuring in the upper Kimmeridgian, such as *Aspidoceras rafaeli* (OPPEL, 1863) and *Aspidoceras rogoznicensis* (ZEUSCHNER, 1846) are not referred to in this work, since they are too scarce to be representative at this level.

The only previous intent to establish a phylogeny of the subfamily at a specific level (Buck, 1958), will show significant differences with the model here proposed.

When faced with such scheme, the first problem rises for different reasons with respect to the origin of the Aspidoceratinae :

- Given the character of the Upper Oxfordian in the Subbetic Zone with reduced facies, probably somewath condensed and/or removed in the detail, it is not clearly known which is the first form to appear. Presently, intensive and detailed sampling is under way, in this interval, to obtain precise information.
- The interspecific relations of early forms are uncertain, in other words, their possible connections are not known.
- The absence of a systematic registry, with phylogenetic perspective, of the forms supposed to be related to Aspidoceratinae : the Euaspidoceratinae of the Upper Oxfordian (A. Miller, 1968, refers to Aspidoceratinae and Euaspidoceratinae as differentiated clades of Perisphinctacea).

Based on the available data, the first findings of Aspidoceratinae are located in the Bimammatum

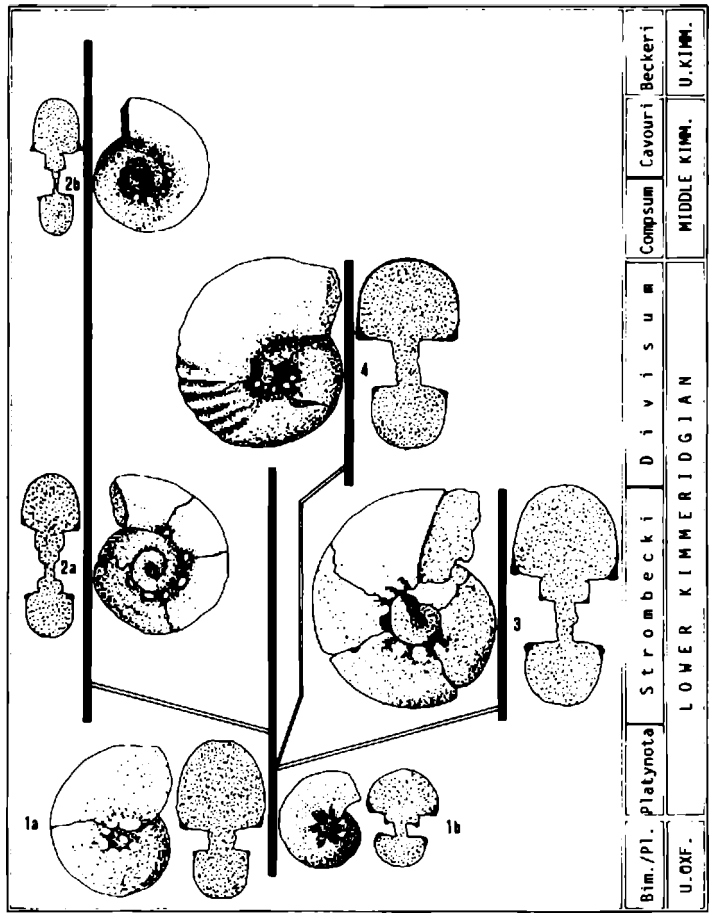

Fig. 1 — 1 a,b : **Group of *Ph. altenense* (d'ORBIGNY, 1847).**
2 a,b : **Group of *Ph. contemporaneum* (FAVRE, 1877).**
3 : **Group of *Ph. insulanum* (GEMMELLARO, 1874).**
4 : **Group of *Ph. insulanum* (GEMMELLARO, 1874) var. *serrana* (CANAVARI, 1903).**

Note : The illustrations of Aspidoceratinae in figures have been obtained from originals figured in F. Olóriz (1976) and A. Checa (1981), except for fig. 1/2b, fig. 2/4, fig. 2/3a, fig. 3/1, fig. 3/3b and fig. 3/4 that correspond to specimens not figured. All the exemplars were reduced to a quarter (1/4) of their original diameter.
In the figures, morphological successions within each group of species does not imply temporal segregation.
Extension of zones and subzones is conceived according to drawing convenience.

Les illustrations d'Aspidoceratinae dans les figures ont été obtenues à partir d'originaux figurés par F. Olóriz (1976) et A. Checa (1981), sauf les fig. 1/2b, fig. 2/4, fig. 2/3a, fig. 3/1, fig. 3/3b et fig. 3/4 qui correspondent à des spécimens non figurés. Tous les exemplaires ont été réduits à un quart (1/4) de leur diamètre original.
Dans les figures, les successions morphologiques, dans chacun des groupes d'espèces, n'impliquent pas de ségrégation temporelle.
L'extension des zones et sous-zones est soumise aux commodités du dessin.

Zone (Upper Oxfordian), where there are two well differentiated morphologies.

- *Aspidoceras binodum* (OPPEL, 1863). (bituberculated spiral, more or less rounded section and with an ample umbilicus, even though quite variable).

- *Physodoceras altenensis* (d'ORBIGNY, 1847) (unituberculated spirals, with reduced umbilicus and oval section).

The origin of both forms is uncertain. However, at this level there are forms of Euaspidoceratinae with rounded section and medium umbilicus, in which, the upper row of tubercles tends to displace itself toward the internal side of the flank. Likely *A. binodum* (OPPEL, 1863) is related to this type of forms, where also a change should be produced in the suture reaching a more complex pattern (see A. Miller, 1968). This hypothesis gathers the possibilities deduced from the observation of the morphology in adult stages. Anyway, it must not be left aside another possibilities as those that could be inferred from a possible reorganisation in the early ontogenetic stages.

Later, and evolving from these initial forms, two basic morphologies clearly independent are consolidated : *Aspidoceras* and *Physodoceras*, whose behaviour together with that of the other genera, is commented in the next section.

V.1 **Physodoceras and Orthaspidoceras** (fig. 1 and 2)

The first species to be considered as it has been already mentioned is *Physodoceras altenensis* (d'ORBIGNY, 1847), whose morphology is closely related to other near ones and coetaneous, therefore it will be possible to speak of the group of *Physodoceras altenense* (d'ORBIGNY, 1847) *-altenensis* (d'ORBIGNY, 1847), *circumspinosum* (OPPEL, 1847), *diastrophum* (FONTANNES, 1879). They are involute forms with a more or less depressed oval section and sometimes with trapezoid like features. There is only a row of periumbilical tubercles -semi numerous- with rounded base and directed toward into the umbilicus. The first modification appears in the Strombecki Zone.

Starting from the group of *Ph. altenense* (d'ORBIGNY, 1847) there is the group of *Ph. contemporaneum* (FAVRE, 1877). In this case an increase of the umbilicus and the number of tubercles is observed. The section in essentially oval.

At the same stratigraphic level and having morphological characters belonging to an evolutive line certainly different of that of the group of *Ph. altenense* (d'ORBIGNY, 1847), is found the group of *Ph. insulanum* (GEMMELLARO, 1874). In those forms there is a tendency to a fast growth of the spiral, and to a remarkably spacing and enlarging of the tubercles is produced ; also, incipient folds are developed on the flanks.

In the Divisum zone, and due to an accentuation of the characteristics given for the group of *Ph. insulanum* (GEMMELLARO, 1874), the radiation from which the *Orthaspidoceras* of the group of *Orthaspidoceras liparum* (OPPEL, 1863) is obtained *-liparum* (OPPEL, 1863), *schilleri* (OPPEL, 1863), *lallierianum* (d'ORBIGNY, 1848)- that comprehends the traditional spectrum of *Orthaspidoceras*. It consits of forms with oval or kidney-shaped section, and where there is a very patent increase in the size of tubercles. The tubercles have an oblique position to the flank, and show a progressive spacing along the ontogeny, that allows for very large intertubercular spaces. Size is also increased. The suture appears very simplified, specially as far as the accessory elements are concerned.

The group of *Ph. insulanum* (GEMMELLARO, 1874) var. *serrana* (CANAVARI, 1903), is also found in the Divisum zone showing characteristics belonging to *Physodoceras*, but at the same time an implantation of folds that originate at the periumbilical tubercles and are accentuated and well developed. These folds are one or two in number, and cross without interruption the venter. Its origin, given the morphological characteristics, could be found in the proximities of the group of *Ph. altenense* (d'ORBIGNY, 1847).

The last innovation, that includes ornamental characters without precedent in the subfamily, is constituted by the group of *Orthaspidoceras uhlandi* (OPPEL, 1863) *-uhlandi* (OPPEL, 1863), *subdogouense* (VENZO, 1942), *garibaldii* (GEMMELLARO, 1875). It is characterized by the appearance of true ribs that reach a regular distribution during the ontogeny. One or two ribs are developed from each tubercle and are not frequent intercalated ribs. Tubercles are displaced toward the middle of the flank or even further to the exterior, they have a radial orientation, connecting perpendiculary with the spiral. The easiest of hypothesis would seem to relate these forms to the group of *Ph. insulanum* (GEMMELLARO, 1874) var. *serrana* (CANAVARI, 1903), where the appearance of folds of regular distribution might be interpreted as the beginning of a tendency that would be totally culminated in the group of *O. uhlandi* (OPPEL, 1863).

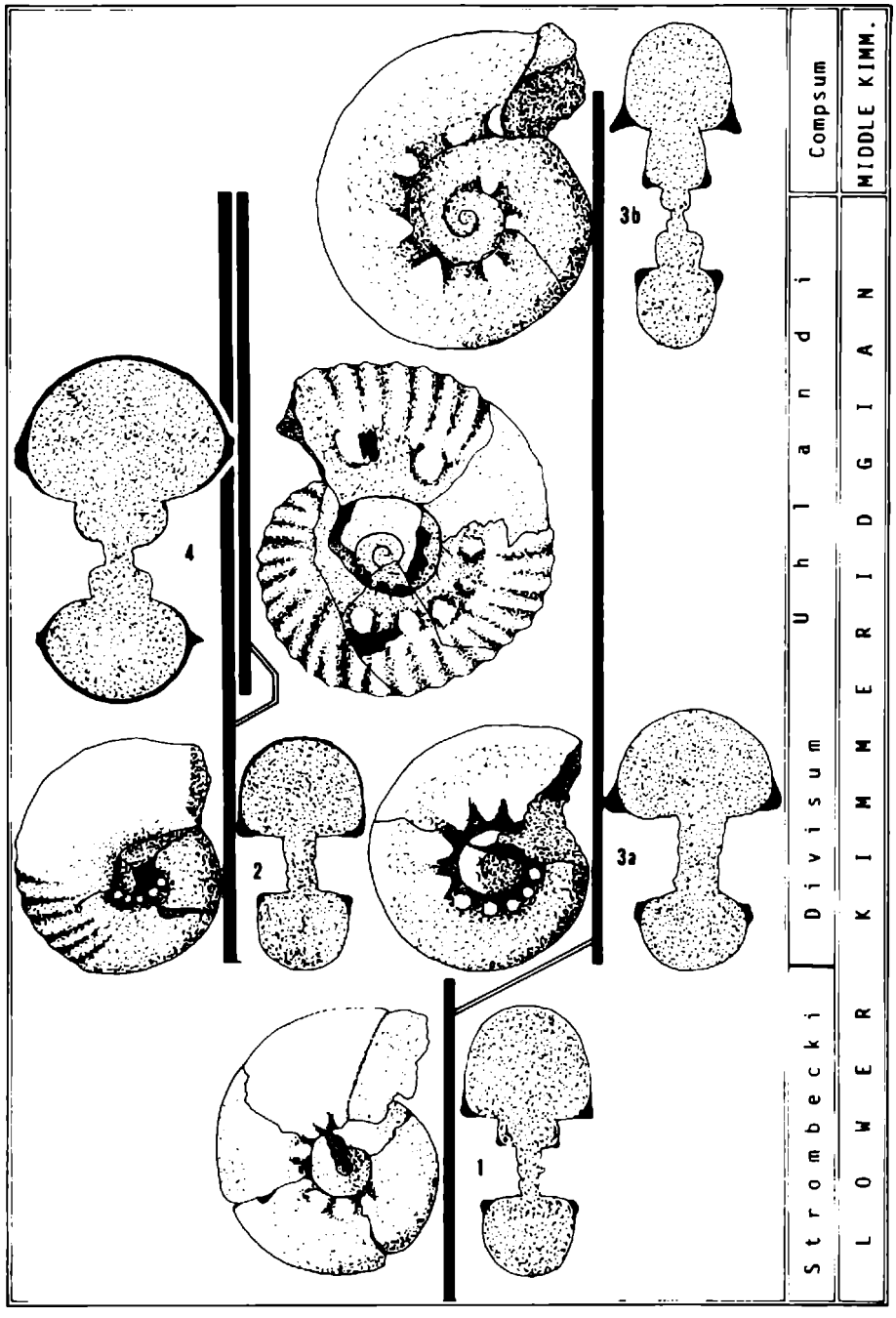

Fig. 2 — 1 : **Group of *Ph. insulanum*** (GEMMELLARO, 1874)

2 : **Group of *Ph. insulanum*** (GEMMELLARO, 1874) **var. *serrana*** (CANAVARI, 1903).

3 a,b : **Group of *O. liparum*** (OPPEL, 1863)

4 : **Group of *O. uhlandi*** (OPPEL, 1863)

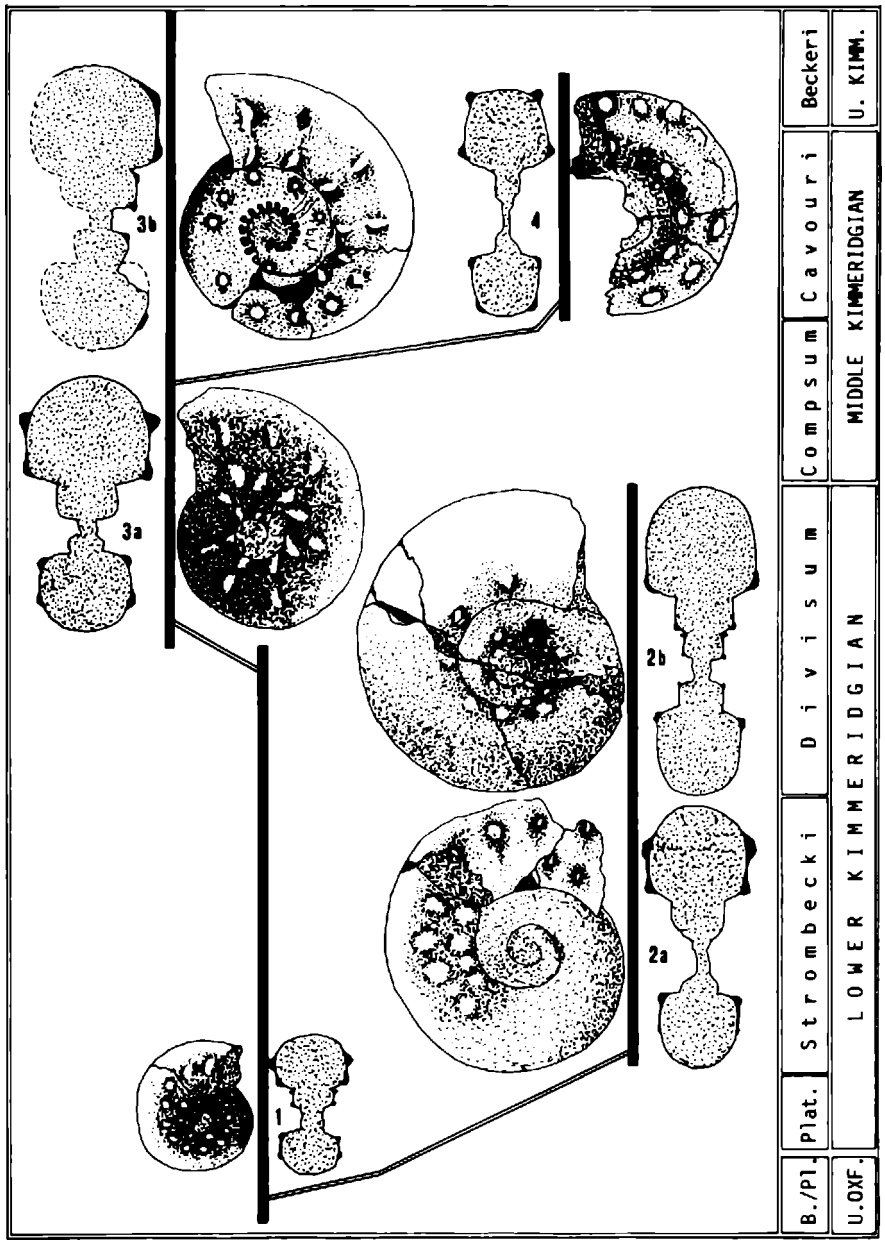

Fig. 3 — 1 : Group of *A. binodum* (OPPEL, 1863)
2 a,b : Group of *A. acanthicum* (OPPEL, 1863)
3 a.b : Group of *A. longispinum* (SOWERBY, 1825)
4 : Group of *A. apenninicum* ZITTEL, 1870.

V.2 **Aspidoceras** (fig. 3)

The initial forms are those of the group of *Aspidoceras binodum* (OPPEL, 1863) -*binodum* (OPPEL, 1863), *atavum* (OPPEL, 1863)- species of a great morphological plasticity, this, given its condition of evolutive basis results advantageous for this is considered the initial species of the genus. They are small in size, semiinvolute and have from rounded to kidney-shaped sections. The ornamental dispositive is composed of two rows of tubercles where elements are paired or present a triangular disposition -to each tubercle of the inner row there are two corresponding in the outer one. The outer row is located at one-third to two-fifths of the heigth of the flank and the elements of both rows are seminumerous.

From the Strombecki zone a set of forms with common morphological characters develops, and allows to put them together under the denomination of group of *A. acanthicum* (OPPEL, 1863). There, the outer row of tubercles is located at the middle of the flank or slightly above it, and is restricted to very internal whorls, that makes difficult to appreciate them in specimens poorly preserved. Elements of both rows are paired. At the living chamber, the outer row, whose location varies depending on the particular morphology that it might be treated of, reappears vigorously, in any case. Tubercles of the inner row show a radial or retroverse design and are present in a larger number than any of the others form previously commented. *Aspidoceras* of the group of *A. acanthicum* (OPPEL, 1863) might also reach greater sizes. This morphology may be considered without difficulty as derivating from the group of *A. binodum* (OPPEL, 1863), for they have the same configuration of internal whorls.

On the other hand, in the Divisum zone appear the first forms that could be attributed to the group of *A. longispinum* (SOWERBY, 1825) -*longispinum* (SOWERBY, 1825), *hoplisum* (OPPEL, 1863), *meridionale* GEMMELLARO, 1872, *caroli* SPATH, 1933- that seem to replace the group of *A. binodum* (OPPEL, 1863), with their shells persistently bituberculated, and develop throughout the rest of the Kimmeridgian. Probably its origin has to be found within the group of *A. binodum* (OPPEL, 1863) and the morphological relay is based on the lost of the kidney-shaped section, of the triangular disposition or tubercles and on the displacement of the outer row toward the ventral region, relocating itself even at two-thirds of the height of the flank. Lastly, it has to be pointed out a considerable and general increase of the size. The connection of this group with the one of *A. acanthicum* (OPPEL, 1863), should implicate the reappearance of some characters previously abandoned, and thus it would not seem to be the connexion to foresight.

Already in the Cavouri zone an interesting group appears, they are of interest not only for their morphological characters but also for being confined to the mediterranean Europe (*s. str.*). This is the group of *A. apenninicum* ZITTEL, 1870. The are forms from evolute to very evolute with a large number of tubercles and having the outer row displaced to a very marginal position -lateroventral- thus leaving a quadratic design to the section. The only trustworthy hypothesis would seem to be that of derivating the group of *A. apenninicum* ZITTEL, 1870 starting from the types of the group the *A. longispinum* (SOWERBY, 1825), where some of them show a shell structure very closely related.

V.3 **Pseudowaagenia** (fig. 4)

This genus starts at the terminal Oxfordian -Planula zone- with the group of *Ps. microplum* (OPPEL, 1863), a species relatively scarce in the mediterranean Europe (*s. str.*). They are semiinvolute forms, of oval sections and convex flanks, thus having a reduced ventral region. On the flank are located two rows of tubercles whose elements are paired in internal whorls, where they may appear even united by a softly shaped rib. Outer tubercles show an elongated design, sometimes radial, often retroverse and are located at one-half to two-thirds of the heigh, present or not at the external whorls. Tubercles of both lines are spiniforms, those of the internal row are directed toward the center of the umbilicus and are very numerous.

The group of *Ps. sesquinodosum* (FONTANNES, 1876) appears at the Divisum zone, and with respect to the group of *Ps. microplum* (OPPEL, 1863) presents a spiral with faster growth and greater size.

In this zone also appears the group of *Ps. haynaldi* (HERBICH, 1868), it is composed by clearly evolute forms, character that it directly related altogether with increase in the number of tubercles, the spiral also shows a smaller growth index. Related to the suture, both lobes and saddles show lateral margins that tend to be parallel and with accessory elements very little indented. Thus is obtained this morphology through an accentuation of certain characters in an inverted sense to the one considered for the group of *Ps. sesquinodosum* (FONTANNES, 1876). Again it seems that the morphology of the group of *Ps. micro*

plum (OPPEL, 1863) is the only one where an evolutive tendency could be established that might give place to the group of *Ps. haynaldi* (HERBICH, 1868).

At last the final forms of the genus appear at the Cavouri zone. They are a set of exclusively mediterranean forms, the group of *Ps. acanthomphalum* (ZITTEL, 1869) -*acanthomphalum* (ZITTEL, 1869), *carpathica* SPATH, 1931, *serbica* ANDELKOVICK, 1966. The main characteristic registered in the forms is an increase of the relative size of the umbilicus, thus obtaining very evolute forms. At the same time there is an increase in the number of periumbilical tubercles. The section is oval, and often rectangular in outer whorls, being trapezoidal and with tabular venter in inner whorls. Internal tubercles, when present, are placed in a marginal position. The suture shows saddles and lobes totally vertical and with parallel flanks, taking that way a quadratic appearence.

It is not difficult to recognize the group of *Ps. acanthomphalum* (ZITTEL, 1869) as the product obtained by the maximal accentuation of the morphologically dynamic characters implied in the line formed by the group of *Ps. microplum* (OPPEL, 1863) and *Ps. haynaldi* (HERBICH, 1868).

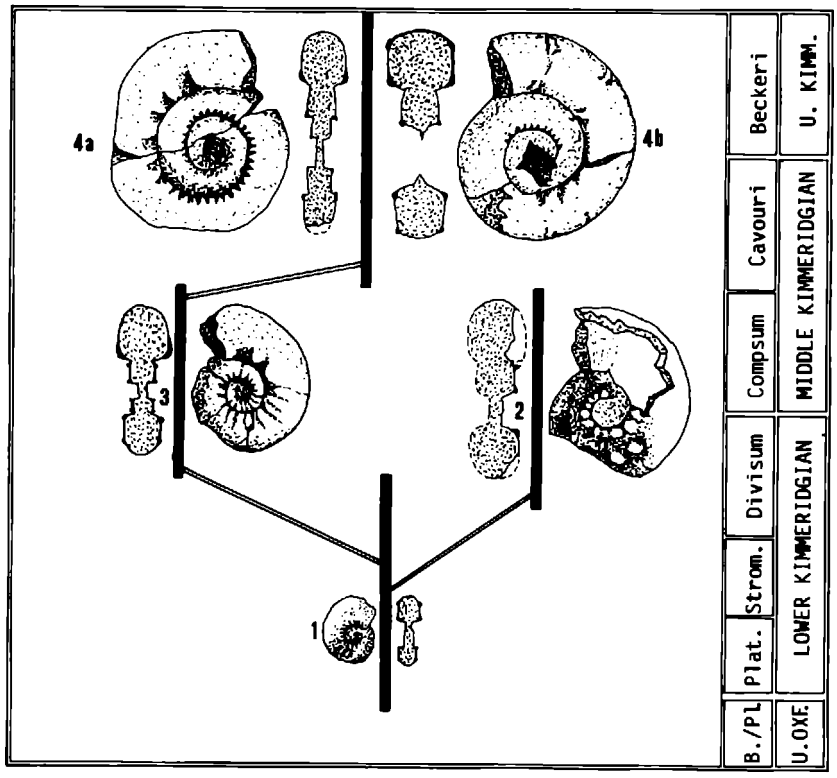

Fig. 4 — 1 : **Group of *Ps. microplum* (OPPEL, 1863)**
2 : **Group of *Ps. sesquinodosum* (FONTANNES, 1876)**
3 : **Group of *Ps. haynaldi* (HERBICH, 1868)**
4 a,b : **Group of *Ps. acanthomphalum* (ZITTEL, 1869).**

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