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# SIGNIFICATIVE MEDITERRANEAN "ASPIDOCERAS" IN UPPER JURASSIC BIOSTRATIGRAPHY

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On the basis of paleogeographical, paleobiological and stratigraphical criteria is possible to obtain an evolutive scope of the mediterranean "Aspidoceras", and so, the taxa with higher bioestratigraphical significance. In this context the quantitative approach has been a profitable source of information.

Given this, in the present work the most significative chronological implications deduced from the application of a new systematic ordering are advanced.

According with the obtained data, a higher biostratigraphical yield in the upper Jurassic during the Kimmeridgian is recorded. Always at a level lower than that of the substage, the contributions of the different genera are the following:

- Aspidoceras: five species; four in the Kimmeridgian and one Kimmeridgian-Tithonian.

- Pseudowaagenia: three Kimmeridgian species.

- Orthaspidoceras: three Kimmeridgian species.

- Physodoceras: one Kimmeridgian species.

Two new genera appear as being good markers at the base of the Kimmeridgian and of the Tithonian.

Occasionally, the acmé of some species is considered as having biostratigraphical significance.

## INTRODUCTION:

Upper Jurassic ammonites of the Betic Cordilleras, in Southeastern Spain Peninsula, have been object of detailed studies since 1973. Among published works are of special interest those of ENAY & GEYSSANT (1975), OLORIZ (1976) and

OLORIZ y TAVERA (1981), where a first biostratigraphic scheme and comments on the Tithonian association, the first stratigraphic scheme of the Kimmeridgian and detailing on lower Tithonian, within the framework of a first approximation to detailed paleontological study, and a general view of subbetic upper Jurassic with commentaries about Subbetic basin, the developed facies and quantifications on faunal association, are respectively studied.

Qualitative interpretation on Tithonian "Aspidoceratidae" findings by ENAY & GEYSSANT (1975), recent paleontological studies by OLORIZ (1976) based on the guide-lines of BUCK (1958), and quantifications of upper Jurassic "Aspidoceras" by OLORIZ & TAVERA (1981) -determining the percent participation of this component in the association- are the basis for this work.

The object of this research is to obtain a reading of the fossil record through a new systematic proposition -CHECA (1984)- and thus reaching a double effect: the obtaining of a detailed biostratigraphy, that will even allow to know intervals of maximal frequency, and the deduction of evolutionary considerations that are only outlined here. The data here collected are based upon an earlier research by the authors, especially Checa, that from 1979 has deepened on monographic studies of mediterranean "Aspidoceras". A null hypothesis on the evolutionary behaviour of this group is presently in press -CHECA & OLORIZ (1984).

The main reason that leads to refer the fossil register to a new systematic approximation originates on the needs to unify criteria, so that to interpret the dynamics of that group of ammonites, that during $15.10^6$ years appears as standout component of the association within an ample differentiated paleobiogeographic distribution. On the other side, only a monographic study was allowed to reach a view without interferences, brought in by the treatments of different authors during more than a century.

METHODS:

Quantifications have decisive weight on the development of this research, thus implying directly the materials upon which work is done and its proccess of obtention, in other words, its sampling. Biostratigraphic scale turns out to be another main factor to which data will be later referred.

Material and sampling: Collections by OLORIZ (1976 and later) and CHECA (1979,

1984) have been studied, as soon as material coming from joint recollections of the authors, where special sampling technic has been carried out. As against other traditional practises, where differences in sampling deepness can be relatively frequent at different levels of a certain profil, preparations from top to bottom and successive outcrop surfaces with an approximate minimum of two square meters are prepared. These surfaces belong to rocky bodies of 10 to 15 cm. of maximal width. Consideration of maximal width implies that strata geologically differentiated have been subdivided with special attention to omission surface traces fused within other internal discontinuities or irregularities -this is specially interesting in the study of "condensed pelagic biomicrites" facies; cf. COMAS et al (1981) and MARTIN-ALGARRA et al (1983). This sampling technic not only allows for a better precission of biostratigraphical control, but it substantially improves the possibility of statistical approximation, diminishing the risk implied by punctual sampling. At the same time, simplifies the obtention of detailed sedimentological information, in any case complementary and often inevitable for a better interpretation of the fossil record.

In general, sampling has to be considered representative for it is the result of collections within profils distributed in a large geographic area, where upper Jurassic materials are geologically differentiated -areal distribution, paleotopographic location, deposit conditions, thickness... cf. OLORIZ (1976), COMAS et al (1981), CHECA et al (1983), MARTIN-ALGARRA et al (1983). A great number of samplings -950 specimens- originate from recollection carried out at the Kimmeridgian-Berriasian interval following sampling uniformity criteria. the rest has been obtained by intensifying sampling of those levels where "Aspidoceras" are more frequent and/or aboundant -Kimmeridgian to lowermost Tithonian. This has been unavailable face to a deep study of this ammonite group. As of now, terminal Oxfordian record should be considered comparatively defficient in number, even though may be evaluated as sufficiently representative given the low diversification of pre-Kimmeridgian "Aspidoceras". In summary, total collection size has been of 1.577 specimens: 1.275 Kimmeridgian; 340 Tithonian; 90 Oxfordian; 2 Berriasian.

Biostratigraphic intervals: The biostratigraphic scale of reference is that of OLORIZ (1976) and OLORIZ y TAVERA (1983), with a single modification incorporated by OLORIZ y TAVERA (1981) as far as a proposition of fruitful subdivision of Kimmeridgian, that includes the middle Kimmeridgian denomination for the interval of strata with O. uhlandi (OPPEL) -upper part of the Divisum zone- and those where the Kimmeridgian Hybonoticeras fauna develops -Beckeri

zone.

As far as Kimmeridgian, some of the known intervals show certain peculiarities that are associated to facies imposed by paleogeographic location and, more in detail, by paleotopography. The almost generalisation of Ammonitico Rosso facies where it is often difficult to differentiate strata or rock-bodies geologically individualized, does not simplify a feasible registry of great precision correlations, due to changes in thickness, coining, changes in detail in lithofacies, increase of nodulisation... Also, ammonite association characteristics imply a certain indefinition in some level when trying zonal or interzonal characterisation. This is particularly noticeable in the central sector of the Subbetic Zone for Platynota zone and middle Kimmeridgian -interval zone of Compsum and Cavouri zone. (OLORIZ, 1976, 1979; OLORIZ y TAVERA, 1981). Limitations of terminal Oxfordian are given mainly by factors associated to sedimentation. The situation is generally more favourable in Tithonian, even though difficulties are there for intrazonal subdivision, induced mainly by the conservative character of the fauna, specially Perisphictids.

As a result of the incidence of the indicated factors, it has not been possible to offer the same intrazonal yield for all recognized biozones. Intervals that have allowed for greater intrazonal biostratigraphical precision are the Strombecki an Divisum biozones, the interval zone of Compsum and the Beckeri, Hybonotum and Verruciferum biozones. Anyhow, information shown by the sampling carried out, as described, allows to foresee a high rate of precision within a short time. So far, it has been preferred to unify the expression of biostratigraphic intervals within its temporal extension, and therefore, not responding to the distribution of partial thickness. Further works have been carried to obtain a detailed thicknes correlation record.

**Quantifications:** Controling the number of individuals by stratum or level of reference, all registers by interval have been accounted for. Specimens that by its provenance do not allow for an accurate stratigraphical assignment, have been discharged. When material shows a register that affects a limit between zones or to a gap of time, unless it is not feasible to recognize its concrete location within the column, numerical expression has been obtained by dividing the "rough" data proportionally to percentages given by unequivocal stratigraphical register. This treatment accounts for fractionary counting that has been rounded up by excess or default -40.4 approximates 40. In no case indetermination was greater than the substage level.

Results thus obtained have been stratigraphically selected in agreement with the systematics proposed. This way, a general view of the behaviour of the fauna studied can be provided, along the time and within each interval, at family, genus and species level. In each case; the frequency is expressed in absolute frequency figures and rigurously reflected in the lateral extension of each species within the interval studied. To graphs that exclusively include information selected from a strictly systematic point of view, data discharged in other representations have been added, provided that systematic identification were not problematic.

RESULTS:

Figure 1 shows a hystogram of absolute frequencies referred to considered stratigraphic intervals -biozones. Occasionally, subdivisions have been observed at stratigraphical intervals that reflect the possibility to obtain a greater detail of information. It also implies that the hystogram reading should account for "comparative distortion" that implies redistribution of data of a standard interval -biozone- in others of second and ever third order -this is that the hystogram will show the "falls" induced by the greatest stratigraphical precision. Maximal frequency of Aspidoceratiforms is reached at the top of lower Kimmeridgian -Divisum- as shown in Figure 1. This implies a sevenfold greater register than that of the Bimammatum zone -upper Oxfordian- where the group originates.

A small increase of approximately 3% occurs at last Oxfordian strata. Already in the Kimmeridgian -Platynota zone- frequency increases a 67% with respect to the previous record, showing previously the tendency that will reach the maximum at the Divisum zone. During middle Kimmeridgian there is a marked fall of the fauna -31% less than the maximum of Divisum zone. This tendency will keep on till the extinction of the group at the Berriasian. Results are: upper Kimmeridgian ,Beckeri zone, 41%; lower Tithonian: Hybonotum zone 50%, Albertinum zone 75%, Verruciferum zone 86%, rest of lower Tithonian 97.5%. During upper Tithonian and Berriasian decrease is greater than 99% of the maximal frequency registered in Divisum.

Given this general view it may be interesting to analize its behaviour respect to the recognized taxa at the genus level. There are eight genera belonging to two subfamilies: Aspidoceratinae (Aspidoceras and Pseudohimalayites) and Physodoceratinae (Physodoceras, Benetticeras gen. nov., Orthaspidoceras, Simaspidoceras, Pseudowaagenia and Schaireria gen. nov.).

Aspidoceratinae (fig. 2)

Genus Aspidoceras: It shows the greatest stratigraphic distribution. The maximal frequency is registered at the Divisum (Uhlandi subzone)-Compsum interval, arriving to triple its presence as related to other pre-Tithonian levels. A fall of 60% is observed at the beginning of the Tithonian as compared to its representation at upper Kimmeridgian -Beckeri zone- even though that fall is of only a 80% of the lower third of the zone. During Verruciferum the drop is of more than 80% respect to final Kimmeridgian. Following registers show decreases greater than 97%.

Genus Pseudohimalayites: The scarce number of collected sample does not allow any significant comment. It represents 25% of Aspidoceratinae and 12% of total Aspidoceratiforms at the upper part of Verruciferum, which shows the scarcity of the group already in full decadence.

Physodoceratinae (fig.2)

During upper Oxfordian -Bimammatum zone- the two basic structures of this subfamily are registered -Physodoceras and Pseudowaagenia. Before middle Kimmeridgian the basic type was Physodoceras.

Physodoceras is 85% of Physodoceratinae at Bimammatum zone. At the Planula zone Physodoceras reaches 85% and a related type -Benetticeras- the 25%. The appearance of this last type reaches its maximal representation during Platynota zone -22%- and both genera account 99% of Physodoceratinae. There may be a correlation within this subfamily, between the disappearance of Benetticeras and the maximum of Physodoceras -97%- at the Strombecki zone. At the final strata of lower Kimmeridgian -Divisum zone- two new genera are registered -Orthaspidoceras and Simaspidoceras. Again, the dominating rôle falls on one of them, Orthaspidoceras, with a 79%, while Simaspidoceras accounts for 4%. Physodoceras, that was previously the dominating one, falls to 9%. It should be remarked that the other basic structural type of Physodoceratinae -Pseudowaagenia- recuperates levels near to those registered at its origin, 12%.

An unprecedent descent of the level of this subfamily -its representation falls in a 68%- is observed at the lower part of middle Kimmeridgian: Orthaspidoceras 15% -down 94%- Simaspidoceras 6% -down 50%- and Pseudowaagenia 69% -up 100%. The first registers of Schaireria are observed, 8%. Of the structural types, only Pseudowaagenia is represented at upper Kimmeridgian. In an interval where

the subfamily increases in a 30%, Pseudowaagenia does 86% and Schaireria 14%.

During lower Tithonian results show a maximum at Hybonotum zone with 99% for Schaireria and 1% Pseudowaagenia that is in its last and scarce register. Successive descent are produced at Albertinum and Verruciferum zones, that affects in each case an approximative 40% of the subfamily, now in clear descent. For the rest of the lower Tithonian, registers are absolutely residual.

*Results at the species level*

Control of quantifications at a specific level shows new and numerous fluctuations of fossil record. No comments have previously been made about intra zonal results for it was understood that information could be easily obtained from the graphs presented. Several comments will be made at the species level where specific representation are needed, regarding the most relevant species studied. Numerical expression of data is shown in figure 3 and its graphic representation in figures 4 and 5.

ANALYSIS OF RESULTS:

As it was observed by sampling of the four stages analized -Oxfordian to Berriasian- (figs. 1 and 3) register is progressively increasing just to the base of Divisum. Comparing the curve of the set of Aspidoceratiforms register with the eustatic curve of HALLAM (1978) a considerable parallelism can be deduced, being quite significant considering that Aspidoceratiforms should be among the most ubiquitous ammonites respect to facies. It is to remark that both curves adjust better at lower levels than middle Kimmeridgian. From there, a certain "dissonance" is observed that has a dual interpretation. At distal environments -mediterranean fauna in general terms- where environmental fluctuations were almost not felt, it should be expected a lesser adjustment; at proximal environments -submediterranean fauna- correlation could be greater, even though "local distortions" could be frequent and therefore ecological tolerance of this group should contribute to lessen environmental effects. Quantifying, it can be seen that maximal register of the top of lower Kimmeridgian implies a sevenfold increase of Oxfordian record; for a later similar equivalent interval on the descending branch of the fossil record of Aspidoceratiforms, decrease is only 50%, thanks to the "Tithonian renovation" -Schaireria, A. zeuschneri ZITTEL group. In relation with the so called "Tithonian renovation" is to be observed the fact that occurs in a moment when at least qualitatively -after the biostratigraphic correlation of the eustatic

curve of HALLAM (1978) in ENAY (1980)- sea level reached is comparable to that of the basis of the Kimmeridgian. Given that in both cases a repetition of basic structural types is registered, ecological factors could be implied -in this sense, it should be remained that maximal transgressive occurs with maximal frequency of this group and altogether with the greater diversification of basic structural types.

At the subfamily level, results are shown in figures 1 and 3. It should be emphasized the great difference at the diversification rate. In Aspidoceratinae, a single genus -Aspidoceras- balances out the spectrum of Physodoceratinae. This can be interpreted as an evidence of structural stability produced by the subjacent ecological tolerance of this genus. Even though this seem to be so at a first glance, it implies a paradox. Is it correct to speak of ecological tolerance in a stable environment? Two previous facts are evident: 1) an environment is considered stable when, besides global data such as Temperature, salinity... no other fluctuations of environmental parameters with innovation capacity are observed -plancton or other factors determining facies; paleotopography, even though differentiated, appears not to influentiate as far as this problem is concerned. 2) ecological sensibility should have two determining factors considering the extreme terms within a continuum of interrelationship; thus, in this case -an environment without apparent oscillations- the determinant will be endogenous or of biological character, tied to inherent limitations of a given organic functional mechanism.

Therefore, it may be interpreted, given the environmental conditions of distal environments, that the structural stability of the genus Aspidoceras should be linked to its physiological requirements and that the ecological tolerance mentioned reflects its low level of requirements of the environmental parameters as related to its biological answers. This interpretation implies a hypothesis such that final typic diversification is favoured in low stress environments. It is assumed, hereafter, for any further observation, the hypothesis that Aspidoceratinae and Physodoceratinae were two ammonite groups of similar non-induced change potential.

Looking again differential diversification of Aspidoceratinae and Physodoceratinae, the following observations will be carried out preferently at the species level, even though the systematic scheme of reference can be considered as homogeneous for it is the proposal of a single author -CHECA (1984). In any case , the main object will be the behaviour of the group at the subfamily level. As a consequence, two time intervals have been differentiated,

correlationable with the eustatic curve for that period of time, and two faunal associations with its genus-specific composition as related to subfamilies studied:

| | Mediterranean fauna | Subbmed. fauna | |
|---|---|---|---|
| Pre-middle Kimmeridgian | 2 Ph.,1 Btt.(1),3 O.(1) 1 S.: 7 (3) | 2 Ph.,2 O. 4 (0) | Physod. |
| | 4 A.(2) 4(2) | 2 A. 2 (0) | Asp. |
| Middle Kimmeridgian-lower Tithonian (Albertinum zone) | 3 Psw.(2),4 Sch., 1 O. 8(4) | 2 Psw.(1),3 Sch.(1) 1 O.(1): 6 (3) | Physod. |
| | 5 A.(4) 5 (4) | 4 A.(1) 4 (1) | Asp. |

Comparison between species of intervals I and II evidences that diversification of mediterranean Aspidoceratinae fluctuates about the 60% of that reached by Physodoceratinae, being slightly greater at interval II. Within submediterranean fauna level may be reduced to the 50%. In general, submediterranean association keeps a 62% level of mediterranean diversification. Nevertheless, a deviation is observed at interval II where submediterranean diversity goes from 54% to 69%. Considering fauna that is significantly related to paleogeographic area -numbers parenthezised in table 1- it will be seen how the 15% increase of diversification of interval II appears tightly related to the existence of real endemisms in submediterranean association. On the other side, it is of great interest the different rôle of the genus Aspidoceras within the two associations studied. this should be interpreted in agreement with the hypothesis mentioned about their greater physiological limitations, now restricted by environmental stress resulting from the progressive accentuation of the eustatic fall at the submediterranean province. In this line, the lesser diversification rate of submediterranean fauna permits a better évaluation of the capacity -or volume- of the stable mediterranean environment, that offered greater opportunities for diversification than submediterranean did, regardless that at this last one areal restrictions were noticeable.

At the genus level (fig. 2) mediterranean Aspidoceras do not offer stratigraphic yield. Its maximal frequency is linked to eustatic maximum and does not correspond to the time of greater specific diversification, that occurs at the base of interval II, and seems to correlate with the moment of greater geographic dispersion. As a consequence, the importance of geographic factor on diversification may be comprehended. Pseudohimalayites appears as an anecdotic

evolutionary branch, but of greater stratigraphic significance.

Differences of shell configuration in Physodoceratinae recommends to separate two lines: Physodoceras line -Physodoceras, Benetticeras, Orthaspidoceras, Simaspidoceras- and Pseudowaagenia line -Pseudowaagenia, Schaireria. The first one is restricted to interval I and, always at a low specific diversification level, there are several differences. On the contrary, it is observed a considerable frequency fluctuation related to eustatic maximum of the top of lower Kimmeridgian. At the genus level there is no stratigraphic signification of zonal order, except in the case of Benetticeras that seems to announce the following subgroup -Orthaspidoceras, Simaspidoceras- with greater diversification. When greater diversification is shown, the influence of geographical factor is evident and emphasized stratigraphical imbalance -sub-mediterranean and ethiopian fauna- reaching eventually almost zonal significance.

The second line -Pseudowaagenia, Schaireria- shows no relevant data at interval I. the oldest forms show a progressive change at species level. Both in mediterranean association -dietli- and in submediterranean one -hermanni- smaller deviations of that tendency have been detected. Greater alterations are responsible for Schaireria emergence, where morphological oscillations are considerable. This set of forms -Schaireria- gives rise to "Tithonian renovation", where structural models -that will be commented later- of interval I are repeated, even though should be caught in mind that this repetition keeps a significate equivalent within the subfamily configuration. Similarly to older forms, it is not possible to find zonal yield at genus level and geographic factor appears not to affect but the emergence of evolutionary marginal species -*Sch. episa* (OPPEL).

Given the object of this work. considerations at species level are restricted to those of stratigraphic interest. In this sense, should be beared in mind total distributions and acmés (figs. 3, 4 and 5). There are great differences as far as total distributions. As a set, there is a greater proportion of longevous species -minimum three zones- of Aspidoceratinae, while species with less than a two zones distribution are more aboundant in Physodoceratinae. Anyhow it should be brought out (fig. 6) that with the exception of O. uhlandi (OPPEL), all species of both subfamilies have older registers at mediterranean associations. This explains migrational movements of this ammonite group. Generally the greater stratigraphic precission seems to concentrate on the central part of both mediterranean subfamilies distribution. Pseudohimalayites,

as always, is an exception.

The acmés consideration is observed in figures 3, 4 and 5. First of all, it should be remarked how a maximal frequency interval never reaches the duration of two zones, being restricted ocassionally to only half a zone. Also, of great interest is acmés distribution. Maximal number of species at acmé phase occurs at Divisum zone -eustatic maximum. At that time, acmés of greater size are produced. With the exception of upper Kimmeridgian and the basis of Tithonian -three species- there are never more than one species at maximal frequency phase, implying a considerable alteration of subfamily configuration. Finally, acmé location appears to be tied up to environmental behaviour -acmés tend to approximate eustatic maximum, independently of the stratigraphical distribution of species. Thus, species originated before eustatic maximum and disappearing near that event will have their acmé at the end of its evolutionary course. Its corolary is also truth.

A comment is deserved by the interval of maximal frequency occurring at lower Tithonian -Hybonotum and Albertinum zones. This is what "Tithonian renovation" is. It is a remarquable diversification phase for not only two new species originate -Sch. avellana (ZITTEL), Sch. neoburgensis (OPPEL)- but that its emergence implies total dominance in the Aspidoceratiforms spectrum. Also of great interest is shell configuration of both species. They are globular forms, tuberculate or not, a repetition of some of the oldest Physodoceratinae -Physodoceras, Benetticeras- of lower Kimmeridgian. This configuration implies a clear deviation of characteristic design within the evolutionary line of Pseudowaagenia, where they belong. Finally, the stratigraphic position of the interval where this evolutive event appears is of interest. Considering the evolutionary history of Physodoceratinae in parallel with the eustatic curve of HALLAM (1978), certain relation may be deduced in a way such that globular types of Physodoceratinae appear at distances of eustatic maximum that imply similar levels. The "repetition" of the lower Tithonian signifies the revitalisation of a line where specializing reached a high grade and the generalisation of basic types, resulting almost exclusive at the subfamily spectrum, as previously registered at lower Tithonian

CONCLUSSIONS:

a) Intensive sampling and with the greatest stratigraphic detailing and strictness allow a quantitative approximation to evolutionary behaviour of Aspidoceratiforms.

b) As quantified, the evolutionary model excludes simultaneous generic codominance within one subfamily. For a certain structural type, acmês are out of phase within the time. At Aspidoceratiforms level, coincidence is interpreted as an expression of ecological differentiation.

c) Within the two differentiated evolutive lines of Physodoceratinae -Physodoceras and Pseudowaagenia- as far as different basic structural types, they evidence a different evolutive model within their respective acmês: diversification and specialization.

d) The wide stratigraphic distribution of mediterranean Aspidoceratiforms allows to compare the evolutive course of the group -defined as the absolute size of populations- with the eustatic curve proposed for that period of time. Also, the ubiquistic character of this fauna, gives significance to the sensible paralellism among both traces. In this sense, disagreements observed after lower Kimmeridgian are interpreted on ecological bases: scarce incidence of fluctuations at distal environments, and ecological tolerance and local paleogeographic factors at proximal environments. Another factor that punctually affects, no doubt, the design of the evolutionary course of this group is the specific diversification level. Any case, there seems to be a repercussion of the environmental volume on global size of populations.

e) Evolutionary stability of the basic structural type Aspidoceras -Aspidoceras genus- within an environment with no great fluctuations is interpreted as expression of physiological limitations. Tighly bounded to it should be considered differential diversification, in paleogeographical terms, between Aspidoceratinae and Physodoceratinae.

f) The greatest diversification in the mediterranean association positively values the stability and volume of the environment at the Aspidoceratiforms evolution. Geographical factor plays an important rôle in specific diversification at proximal environments in the associations -endemism.

g) At the genus level, stratigraphic yield is greater in groups with smaller morphological stability. In Physodoceratinae, Benetticeras, Orthaspidoceras and Simaspidoceras restrict their distribution in each case to a maximum of two zones. Within Aspidoceratinae the exception to null stratigraphical yield is Pseudohimalayites that breaks morphological stability of the subfamily.

h) At the species level, greater proportion of longevous species is found in Aspidoceratinae -binodum, sesquinodosum, longispinum, zeuschneri, rogoznicense-

while distribution of less than two zones is more aboundant in Physodoceratinae -ziegleri, garibaldii, uhlandi, bucki, dietli. Species that offer the greatest stratigraphic precission -one biozone or less- are: Aspidoceratinae: linaresi, steinmanni; Physodoceratinae: uhlandi, bucki, dietli.

i) At the species level, the maximal frequency interval -acmé- never reaches two zones and is occasionally restricted to half a zone. Species belonging to a very stable structural type may even show a second acmé.

j) An interesting relation among the stratigraphic position of acmé of each species and the absolute frequency curve, with a sensibly parallel tracing to that of the eustatic curve, is observed. Independently of stratigraphic distribution species, acmé tends to approximate the maximum of absolute frequency of the group and, at the same time, the eustatic maximum. Coincidence of eustatic maximum with the greater number of species at acmé phase is recognized.

k) From the non-coincidence of specific acmés within a subfamily, it is deduced the considerable alteration that implies the existence of species at maximal frequency phase with regard to the internal configuration of the subfamily. In the case of the "Tithonian renovation", this effect bypasses off subfamily limits and affects all Aspidoceratiforms.

l) "Tithonian renovation" turns out to be an evolutionary event where types already tried with success during lower Kimmeridgian -structural type Physodoceras- are repeated, and that implies a deviation from the specialization line previously dominant. Agreeing with this, the earliest manifestation of globular types -Physodoceras- and its repetition -Schaireria- are registered at "distances" from the peak of Divisum zone that imply comparable eustatic levels.

m) In the mediterranean association, the stratigraphic record of a given species is always oldest than in the submediterranean one -O. uhlandi (OPPEL), whose register is coetaneous in both environments, is an exception, even though the fact that this simultaneity could be an artifact delivering from its utilisation as an element of correlation, should not be discharged. This allows to interpret migratory directions towards proximal environments.

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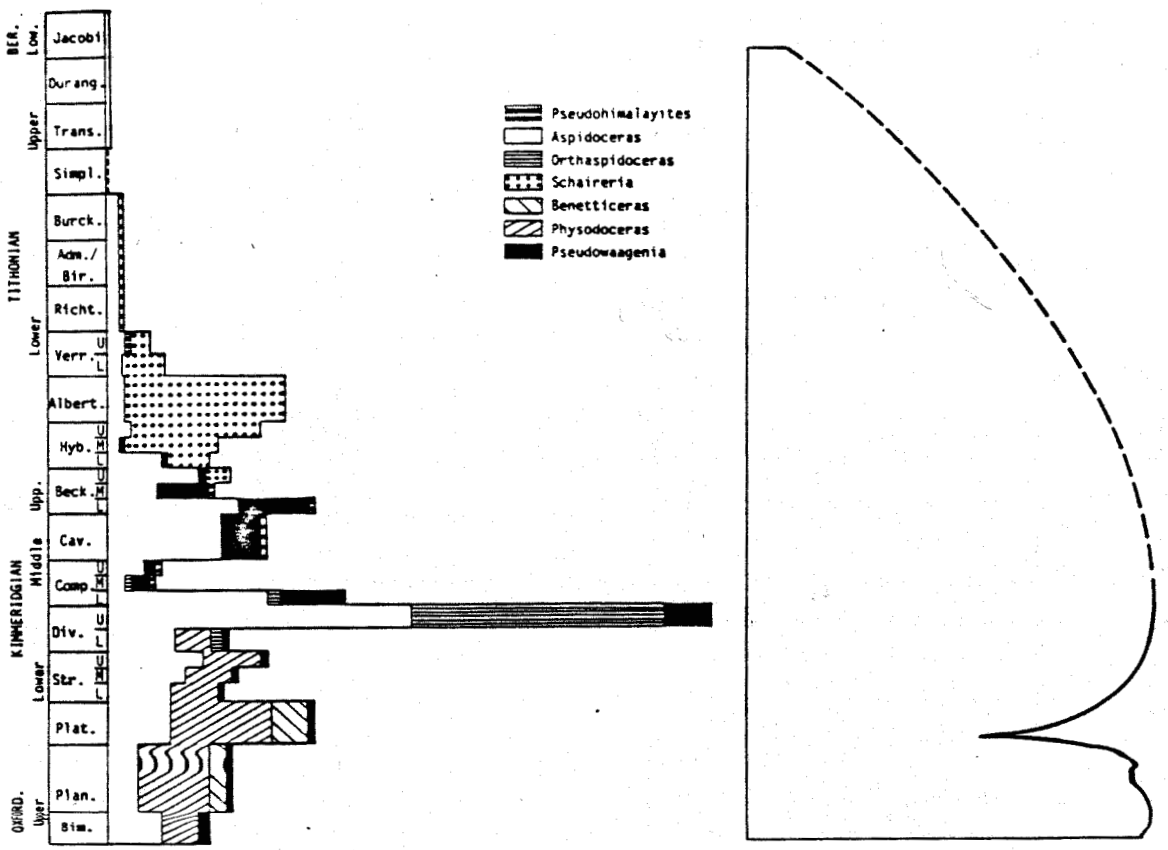


Figure 1: Hystogram of absolute frequencies at subfamily level. On the right, eustatic curve of Hallam(1978

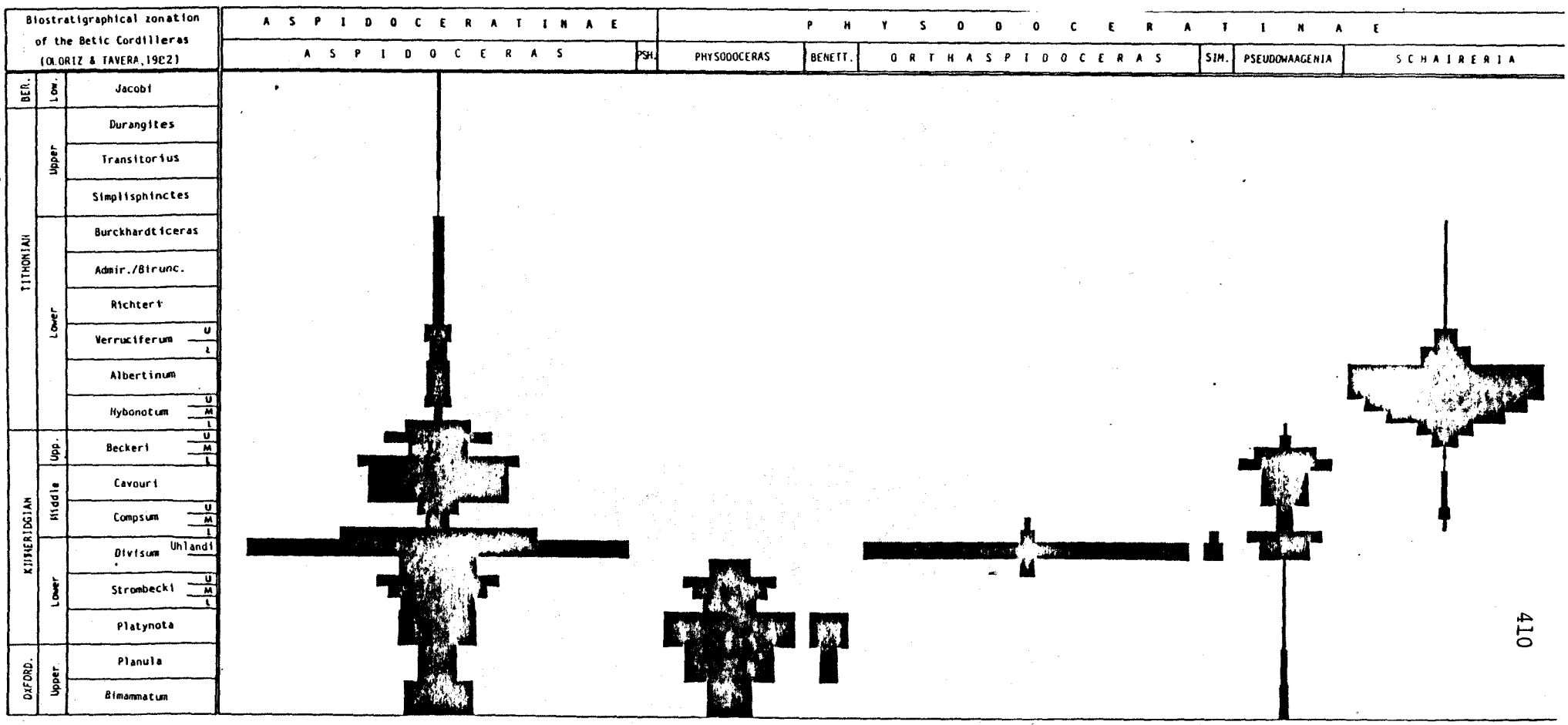


Figure 2: Quantitative record of Aspidoceratinae and Physodoceratinae at genus level.

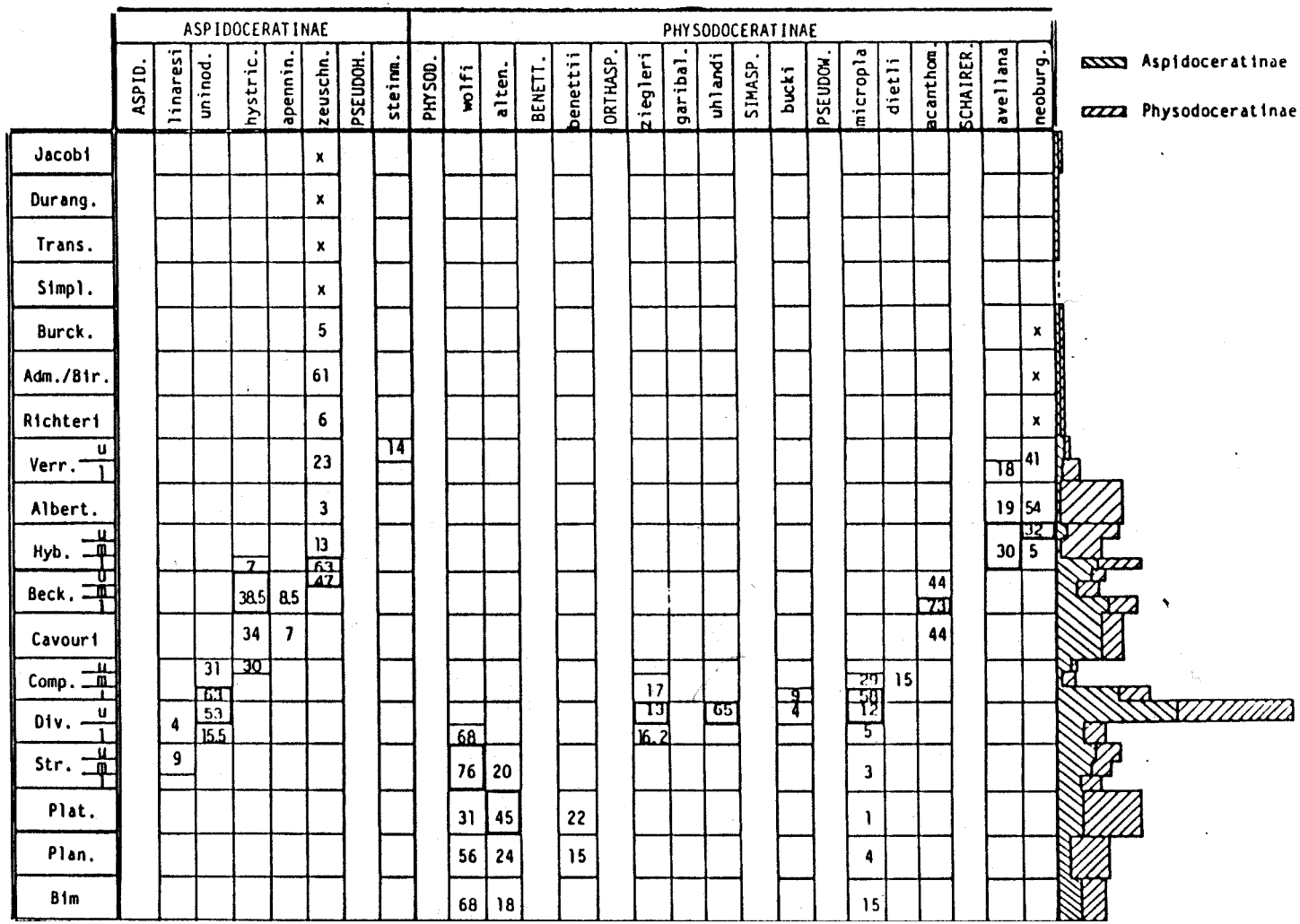


Figure 3: Control of maximal frequencies at speciel level in Aspidoceratinae and Physodoceratinae. Numbers refer to percentage within the subfamily. On the right, hystogram of absolute frequencies at subfamily level.

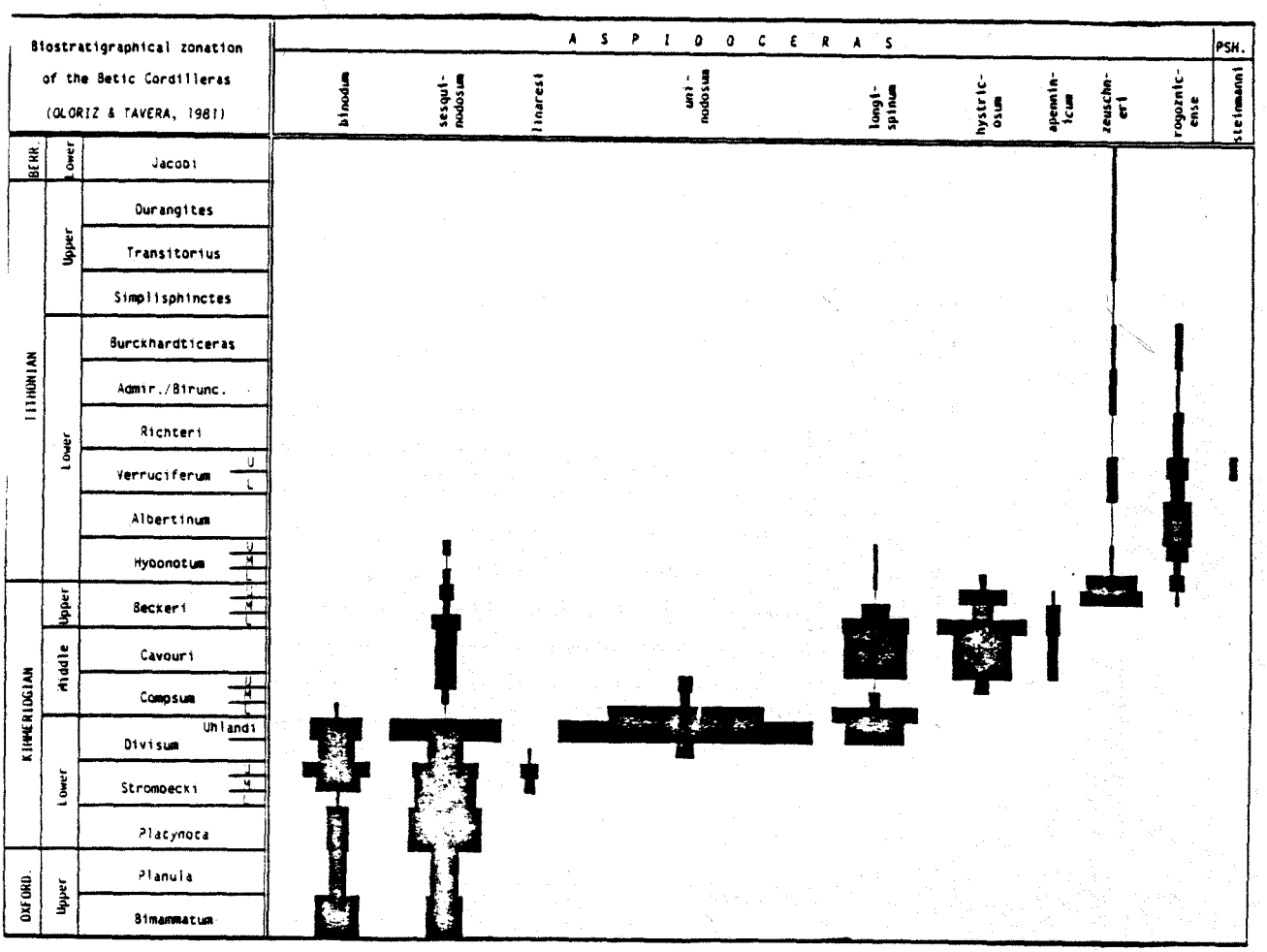


Figure 4: Quantitative record at species level in Aspidoceratinae.

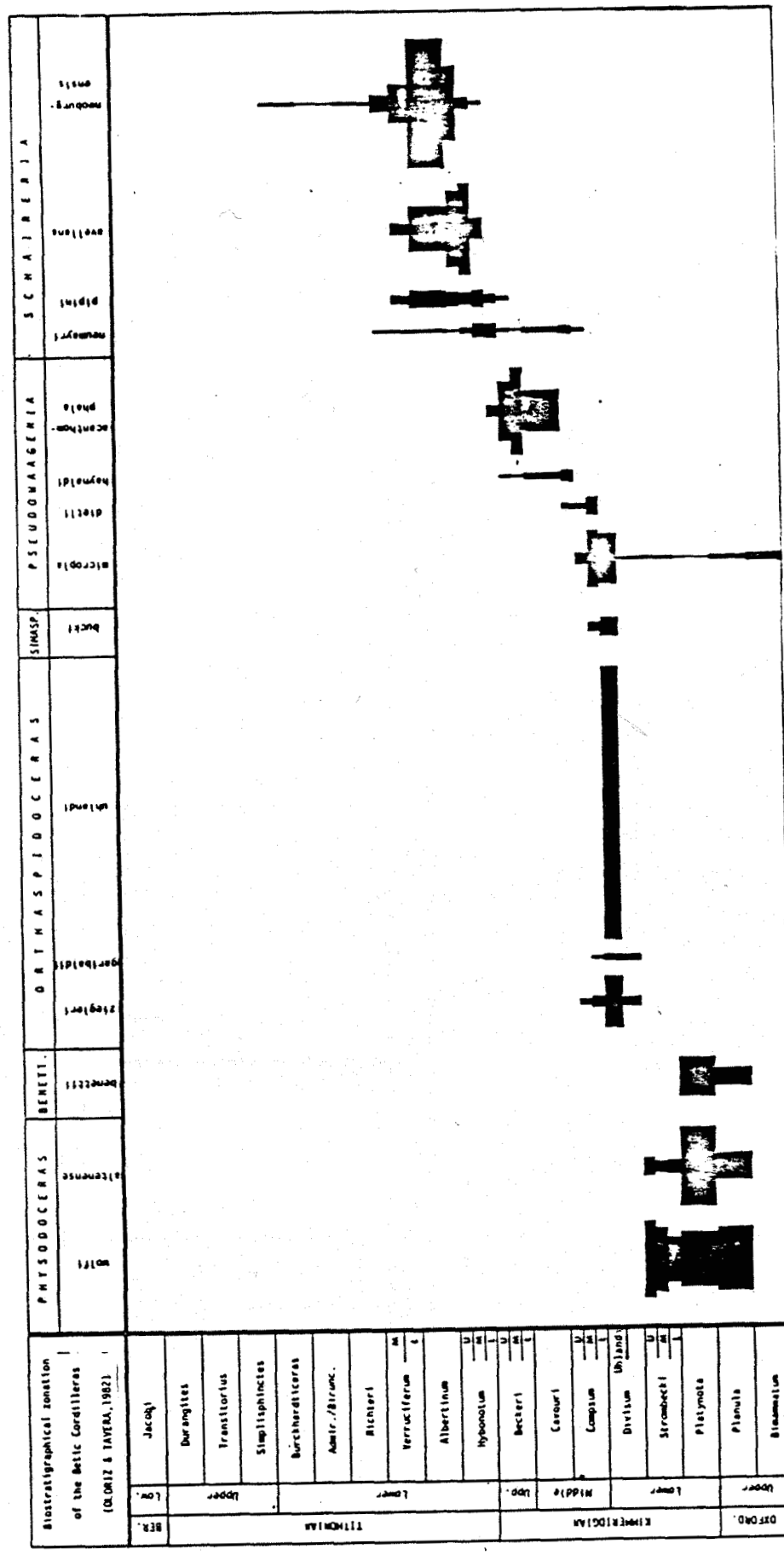


Figure 5: Quantitative record at species level in Physodoceratinae.

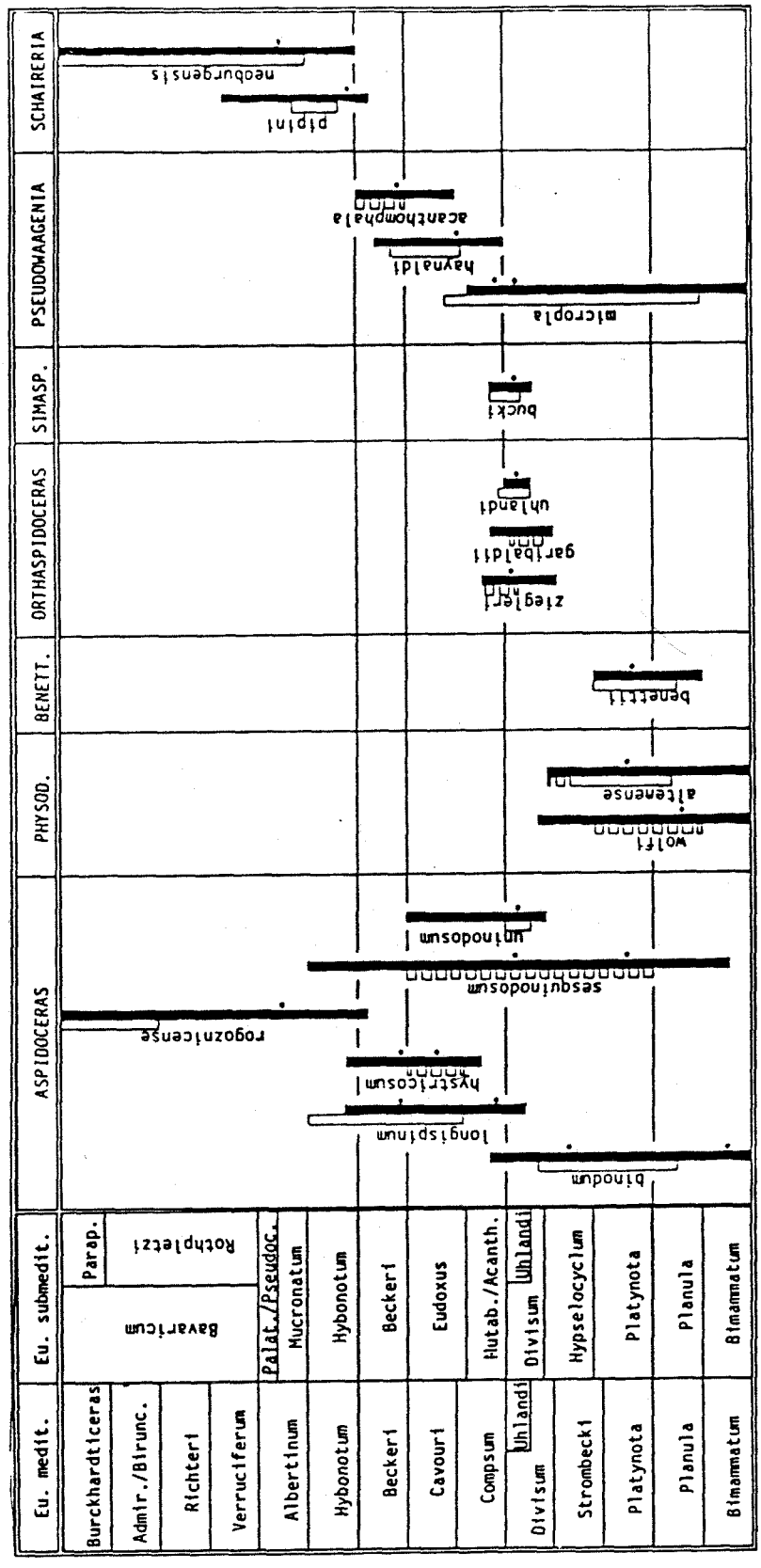


Figure 6: Biostratigraphical distribution of common mediterranean and submediterranean species of "Aspidoceras". Black: mediterranean range. White submediterranean range. Points indicate the position of maximal frequency phase/s.