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TAPHONOMY OF AMMONITE ASSEMBLAGES FROM THE MIDDLE-UPPER OXFORDIAN (TRANSVERSARIUM? - BIFURCATUS ZONES) IN THE INTERNAL PREBETIC (BETIC CORDILLERA, SOUTHERN SPAIN): TAPHONIC POPULATIONS AND TAPHOFACIES TO SUPPORT ECOSTRATIGRAPHIC INTERPRETATIONS

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Key words: Ammonites, taphonomy, taphofacies, ecostratigraphy, sequence stratigraphy, Upper Jurassic, Prebetic, southern Spain.

Abstract. The taphonomic analysis conducted on ammonoid assemblages has proven useful for palaeobiological and palaeoenvironmental reconstructions in upper Middle-to-lower Upper Oxfordian epicontinental deposits of the Internal Prebetic (southern Spain). Taphonic populations close to type I indicate the proximity, even coincidence, of life areas for neritic ammonites (i.e. parautochthonous assemblages). The relationships among preservation mode, shell size, within-bed position, corrasion, fragmentation, and epibionts (encrustment included), with lumpy-oncolitic and condensed & bioclasts-rich lumpy-oncolitic limestones allows us to typify two taphofacies. Taphofacies I shows higher values of mean shell size, corrasion, epibionts and encrustments, as well as a high number of specimens in quasi-horizontal settlement. The opposite characteristics serve to identify Taphofacies II. Taphonomic features, taphofacies and lithofacies combine in coherence with progressing third-order transgressive-to-highstand system-tract conditions and the resulting ecostratigraphic trends, which are registered by fluctuations in ammonite assemblages.

Riassunto. L'analisi tafonomica condotta sulle associazioni ad ammonoidi si è dimostrata utile per le ricostruzioni paleobiologiche e paleoambientali nei depositi epicontinentali riferibili alla parte alta dell'Oxfordiano medio alla parte bassa dell'Oxfordiano superiore del Prebetico Interno (Spagna meridionale). Popolazioni tafoniche vicine al tipo I indicano la prossimità, perfino la coincidenza, delle aree di vita per gli ammoniti neritici (cioé associazioni parautoctone). Le relazioni tra modalità di conservazione, taglia della conchiglia, posizione nello strato, corrosione, frammentazione, ed epibionti (incluse le incrostazioni), con calcari grumoso-oncolitici e calcari grumoso-oncolitici ricchi di condensati e bioclasti, permettono di riconoscere due tipologie di tafofacies. La Tafofacies I mostra più alti valori di taglia media della conchiglia, corrosione, epibionti ed incrostazioni, come pure un elevato numero di esemplari in assetto quasi orizzontale. Le caratteristiche opposte servono ad identificare la Tafofacies II. I caratteri tafonomici, le tafofacies e le litofacies si combinano coerentemente con il procedere di condizioni da trasgressive di terzo ordine a quelle di sistema deposizionale da stazionamento alto, e con le risultanti tendenze ecostratigrafiche, che sono registrate dalle fluttuazioni nelle associazioni ad ammoniti.

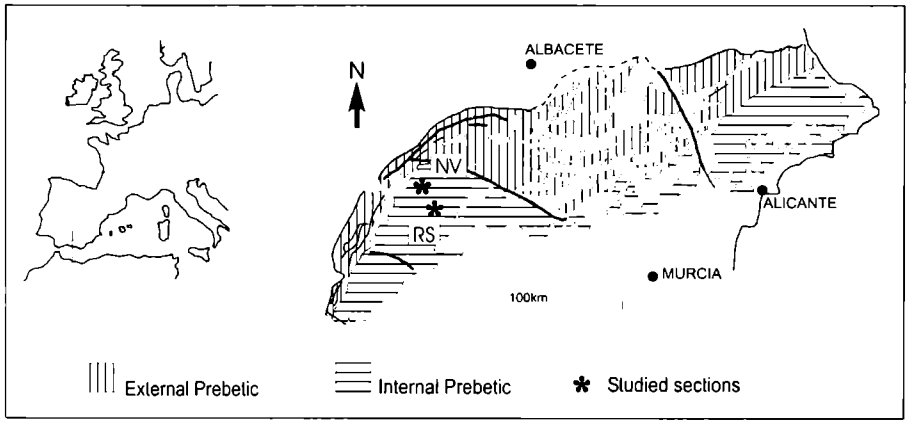

Fig. 1 - Location and geological sketch showing the placement of the sections studied. NV (Navalperal section), RS (Rio Segura section).

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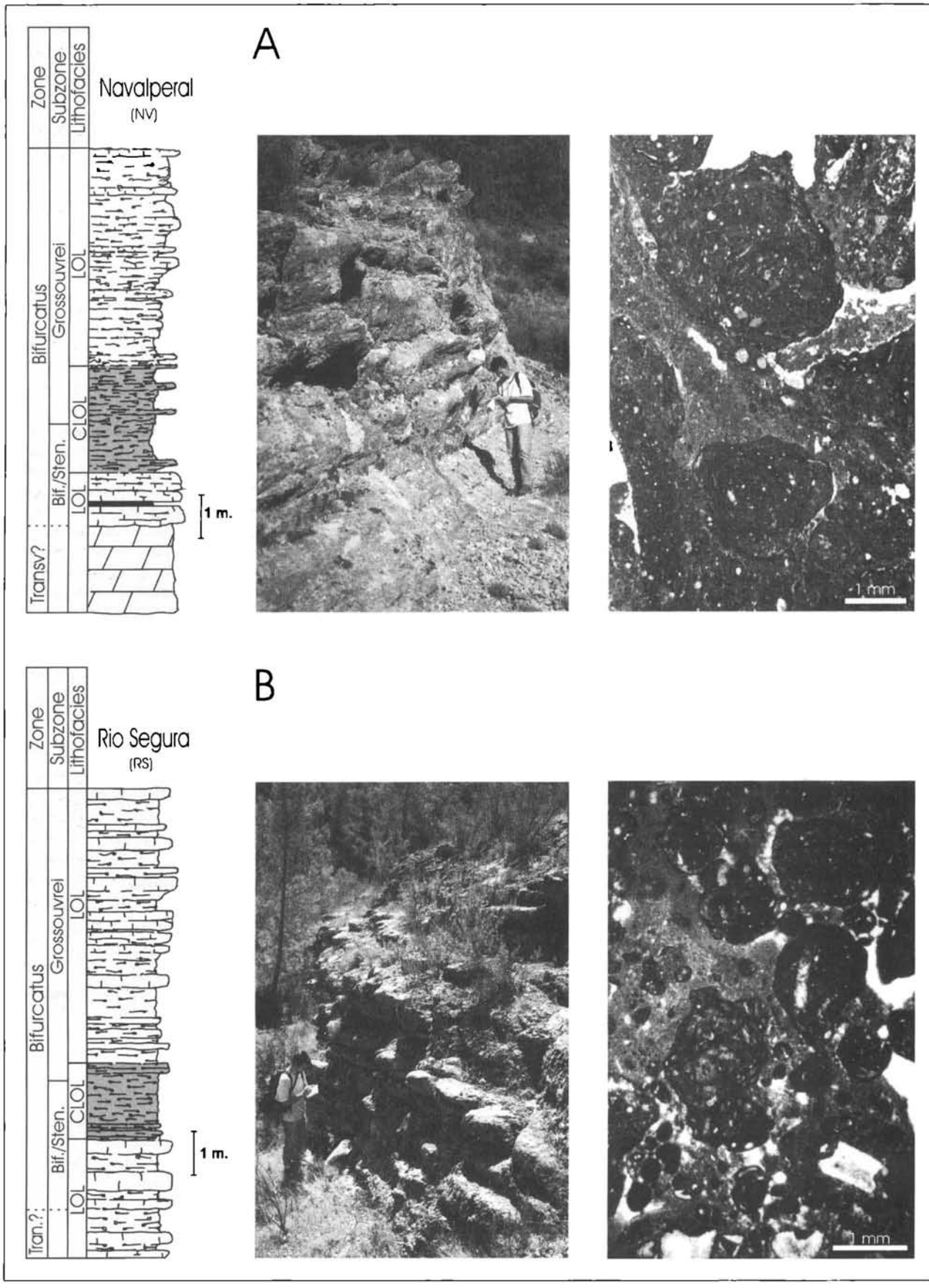


Fig. 2 - Stratigraphic columns, close views of outcrops, and microfacies. (A) Navalperal section. (B) Rio Segura section. Note that outcrops views only show lumpy-oncolitic limestones (LOL). Bif./Sten. (Bifurcatoides/Stenocycloides Subzone).

Introduction and geological setting

The Prebetic Zone (Betic Cordillera) shows epicontinental, shelf deposits accumulated on the south-Iberian palaeomargin during the Mesozoic (Fig. 1). The External and the Internal Prebetic (Jerez-Mir 1973) represent relatively proximal and distal areas, respectively, in this epicontinental environment located in southeastern Iberia. Oxfordian rocks indicate the first hemipelagic-pelagic sedimentation overlying the earlier Jurassic carbonate shelf (García-Hernández et al. 1981).

In order to identify and quantify taphonomic features in Oxfordian ammonites, and to establish their potential relationships with lithofacies, two sections were selected in the Internal Prebetic: the Navalperal and Rio Segura sections (Fig. 1). In these sections, mainly Bifurcatus Zone deposits were investigated; these are made up of lumpy-oncolitic limestone (LOL) and condensed & bioclasts-rich lumpy-oncolitic limestone (CLOL). In both of these sections, an uppermost part of the Transversarium Zone could be included at the bottom of the stratigraphic interval studied, but ammonite biostratigraphy does not provide a higher precision. Ammonite biostratigraphy allows the subdivision of the Bifurcatus Zone in the Prebetic Zone (Olóriz et al. 1999). In the studied sections, the lower Bifurcatoides/Stenocycloides Subzone has been recognized; this is mainly characterized by *Dichotomoceras bifurcatoides* Enay and *stenocycloides* (Ronchadzé), and the upper Grossouvrei Subzone containing *Dichotomoceras grossouvrei* (Siemiradzki), *bifurcatus* (Quenstedt) and *crassus* Enay, among other less known *Dichotomoceras*.

Navalperal section

This section is located in the Sierra de Segura (Jaén province) and crops out across the mountain road between Los Arroyos and the village of Segura de la Sierra. The section studied is 10.7 m thick (Fig. 2A), and mainly shows irregular bedding in nodular-like limestones. The lower 2 m are dolostones containing scarce and poorly preserved ammonites and brachiopods (Olóriz et al. 2002b). Above, the section is made up of 1 m thick LOL overlain by 2.2 m of fine-bedded horizons of CLOL rich in ammonites. The upper 7.3 m show the recurrence of LOL.

Rio Segura section

This section is located in the Sierra de Segura (Albacete province), at km 20 on the road between the villages of Yeste and Santiago de la Espada. The stratigraphic interval studied is 11 m thick (Fig. 2B), and bedding in nodular-like limestones is better expressed than in the Navalperal section. The lowermost 2.8 m are well-bedded limestone horizons (LOL). Overlying are 1.6 m composed of ammonite-rich condensed limestones with a more accentuated nodular appearance (CLOL). The upper 6.6 m shows the recurrence of limestones with decreasing nodular-like appearance (LOL).

Material and methods

In order to analyze the potential relationships between ammonite preservation and the type of embedding rocks, lithology, texture and fabrics have been carefully studied in the Navalperal and Rio Segura sections (Olóriz et al. 2002b), and semi-quantitative characterizations are in progress (Olóriz et al. 2002a, c). In these sections, a total of 1240 specimens and fragments of ammonites were collected through bed-by-bed sampling, in which the relative abundance of ammonites, benthic macroinvertebrates, and belemnites was established.

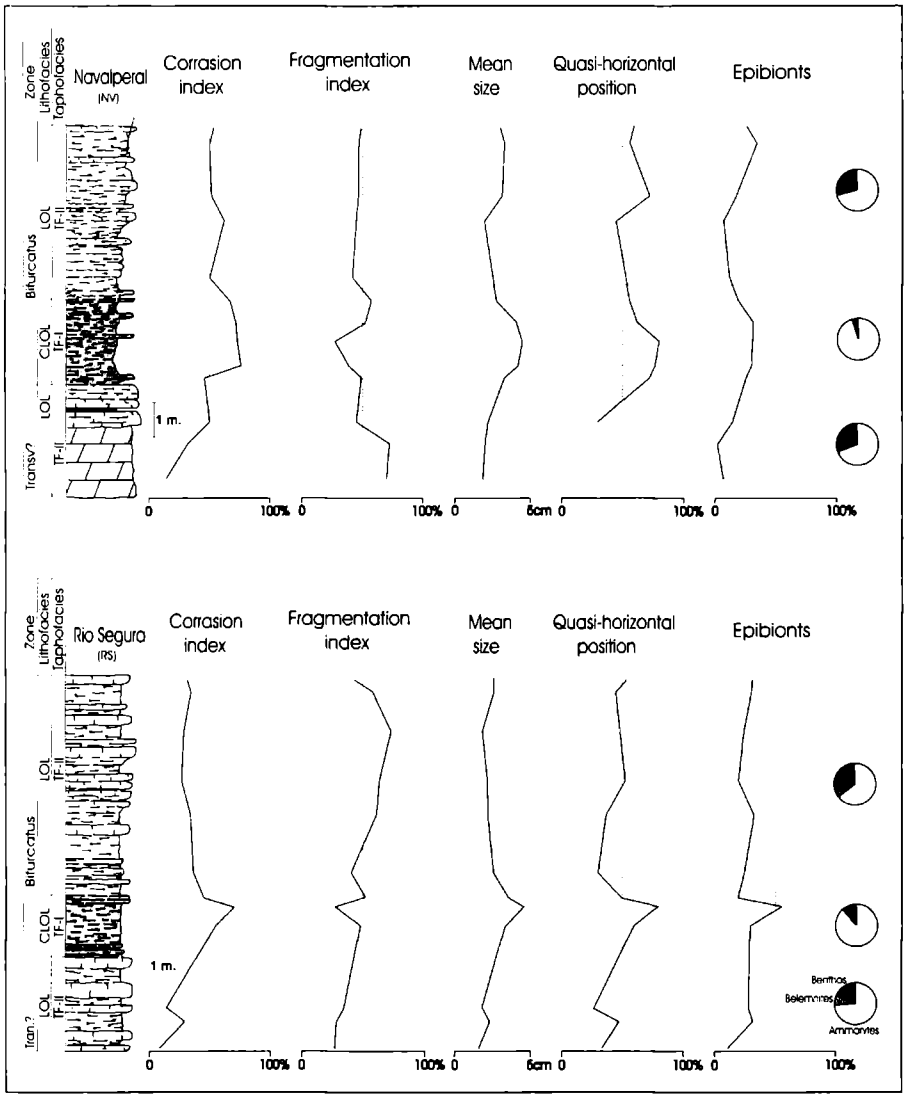


Fig. 3 - Stratigraphic columns showing lithology, taphofacies (TF-I and TF-II) and trends in taphonomic features and ammonite assemblages.

The following taphonomic features have been analyzed: a) preservation mode; b) shell size; c) within-bed position; d) corrasion (Brett & Baird 1986); e) fragmentation; f) epibionts and encrustment; and g) uncoupling and faceting.

The preservation mode refers to the relative occurrence of inner moulds with and/or without neomorphic shell, and to the type of sediments that filled up the ammonite carcasses. No quantification was applied to this taphonomic feature.

Shell size has been controlled to recognize its potential relationships with the variable completeness of ammonite remains (Fig. 3). Quantification of shell size allows the identification of size intervals, seeking to establish their potential relationships with lithofacies and, therefore, with stratigraphic intervals (Fig. 4).

Within-bed position was taken into account to consider the relative significance of quasi-horizontal (parallel to bedding or less than 10°), quasi-vertical (perpendicular to bedding or more than 80°), and oblique (with inclination between 10° and 80°) placement of ammonite remains (Fig. 3). Quantification of this trait expresses the number of ammonite remains in quasi-horizontal position against other, azimuthal positions.

Corrasion (Brett & Baird 1986) was considered as revealing the general degradation of the skeletal surface due to a variable combination of abrasion, bioerosion and dissolution (Pls. 1-2). This taphonomic feature was quantified (Fig. 3), according to the Corrasion index (Ci) proposed by Olóriz et al. (2002b). According to these authors, three grades of corrasion were established: low (LCD), medium (MCD) and high (HCD) for less than 10%, 10% to 60% and higher than 60% of worn material. Ci values were obtained from the equation below, where N is the total number of specimens, and n the number of specimens with HCD, MCD and LCD, respectively.

$$C_i = \frac{[(nHCDx100) + (nMCDx50) + (nLCDx1)]}{N}$$

Fragmentation was considered as the result of breaking but not disarticulation, the latter being interpreted as the separation of biologically articulated structures. To quantify fragmentation, the Fragmentation index (Fi) was applied to inform about the degree of fragmentation (Fig. 3) among a set of individuals (Olóriz et al. 2002b). According to these authors, low (LFD), medium (MFD) and high (HFD) degrees of fragmentation were identified: "LFD for fragmentation that does not affect significantly the shape and size of the specimens (ammonite remains are essentially complete; HFD for fragmentation that affects shape and size significantly (remains are little representative of original dimensions and shape; and MFD for fragmentation between the two degrees previously considered (HFD and LFD)". Fi values were obtained from the equation below, where N is the total number of specimens, and n the number of specimens with HFD, MFD and LFD, respectively.

$$F_i = \frac{[(nHFDx100) + (nMFDx50) + (nLFDx1)]}{N}$$

Epibionts and encrustment have been analyzed paying special attention to the potential difference between the upper and the lower side of the ammonites, in that concerning the type of organisms and density of colonization (Pl. 2). Qualitative quantification was based on naked eye and microscopic observations conducted on selected samples (Fig. 3, Pl. 2).

Uncoupling and faceting were also analyzed, the former pointing to disgregation of inner moulds following septal surfaces and lines of whorl overlapping (Olóriz et al. 2000). To confirm uncoupling as a taphonomic feature, but not an aftermost erosional one, the evidence for this trait was accepted from within-bed specimens only. The occurrence of facets and their relative position was analyzed.

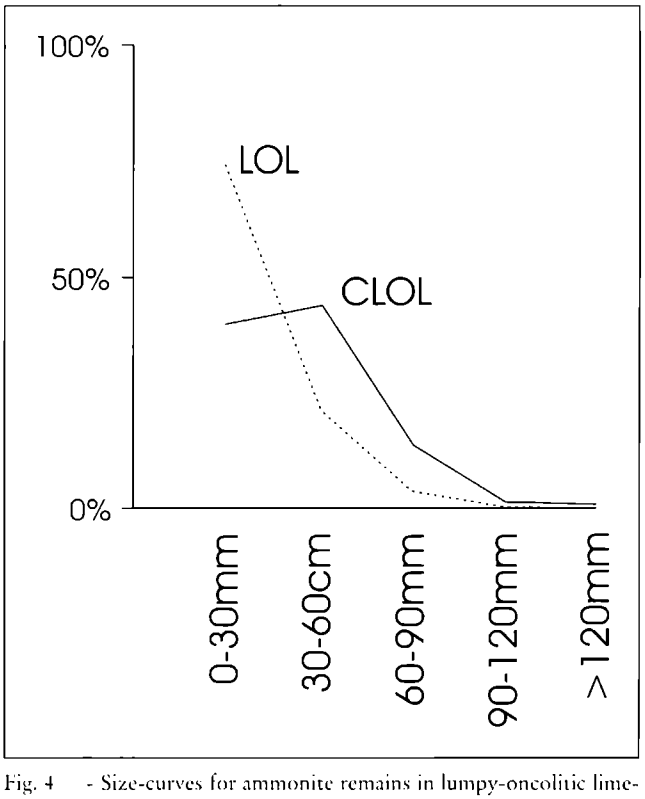


Fig. 4 - Size-curves for ammonite remains in lumpy-oncolitic limestone (LOL) and condensed & bioclast-rich lumpy-oncolitic limestone (CLOL).

Results

The nodular-like appearance of Bifurcatus Zone deposits in the Navalperal and Rio Segura sections is not related with nodules originated during early diagenesis as was the nodularity in typical ammonitico rosso and related facies (see Farinacci & Elmi 1981, for a wide-ranging review of this subject, and updated interpretations in Clari et al. 1984; Clari & Martire 1996; Martire 1996). In contrast, microfacies of wackestones and packstones rich in lumps, oncoids, intraclasts, aggregate grains, and peloids are typical (García-Hernández et al. 1981; Olóriz et al. 2002a, b, c; Fig. 2). Grain-supported fabrics are dominant. The moderate abundance in planktonic forams (Globuligerinidae) is characteristic, as is their peak in relative abundance in a lower part of the Bifurcatus Zone (mean value close to 45%). Lumpy-oncolitic limestone (LOL) can be considered the background facies, showing variability in nodular-like appearance, and recurrence in the Bifurcatus Zone. The proportion of ammonites per rock volume is usually low. Fine bedded, condensed and bioclasts-rich lumpy-oncolitic limestones (CLOL) are typical of a condensed interval showing a higher proportion of ammonites per rock volume. In these horizons, packestones dominate.

In the sections studied, ammonites are 75%, benthic macroinvertebrates 21%, and 4% belemnites. Major fluctuations in the composition of selected ammonite groups are shown in Fig. 3. Among ammonites, perisphinctids are 46%, phylloceratids 29% (*Sowerbyceras* 19%), haploceratids 17%, and lytoceratids 1%. The remaining specimens are indeterminate. Usually, the recog-

nition of suture lines is difficult, and aptychi are extremely rare. It is worth mentioning that the majority of the ammonites with identifiable suture lines are phragmocones, body chamber preservation being scarce and selectively more frequent in haploceratids (e.g. *Ochetoceras* (Pl. 1 D-E), *Trimarginites*, *Glochiceras* (Pl. 1 B-C)). Macroconchiate specimens are rare and represented by inner to middle whorls (e.g. *Passendorferia* (Pl.1I), *Subdiscosphinctes*, *Euaspidoceras* (Pl. 1A)), but incomplete phragmocones of great size ammonites exist (e.g. *Euaspidoceras*).

Ammonites show dominant preservation as inner moulds, with a variable presence of neomorphic, calcitic shell, especially in the flanks placed downwards, but exceptions occurs (Pl. 2). No significant difference has been identified between the composition of the shell infilling and that of the embedding sediment other than those related to infilling processes.

Average shell size from the two sections studied shows small values (Fig. 3), and minor variations between these sections (33 mm in Navalperal against 27 mm in Rio Segura section) are present. On the whole, shell size below 30 mm is 53% in the Navalperal section and 66% in Rio Segura section, and these values are obtained irrespective of the taxonomic group registered. However, a difference in the average shell size has been found between CLOL and LOL lithofacies (Fig. 4), the latter showing lower values (40 mm in CLOL vs. 25 mm in LOL). Fluctuation in average shell size was found throughout the studied stratigraphic interval in the Navalperal and the Rio Segura sections (Fig. 3).

Within-bed position largely depends on ammonite size, or on the size of ammonite remains. The greater the fossils the more frequent their quasi-horizontal position (registered in CLOL) (Fig. 3). Smaller ones offer a more variable orientation, which probably indicates a limited incidence of burrowing in mixing within the sediment-water inter-phase, together with a major probability for oblique settlement in smaller and/or more globose shells. Fluctuation in within-bed position was found throughout the studied stratigraphic interval in the Navalperal and the Rio Segura sections (Fig. 3).

Corrasion is well registered, but its intensity is variable as demonstrated by Ci values (Fig. 3). Higher values have been registered from CLOL and in specimens of greater size, which are more abundant in this lithofacies. Fluctuation in Ci values was found throughout the studied stratigraphic interval in the Navalperal and the Rio Segura sections (Fig. 3).

Fragmentation is high on the basis of the fact that a majority of ammonite remains showing suture lines are phragmocones. Concerning body chamber preservation, this is more common, even typical, in haploceratids (e.g. *Ochetoceras*, *Trimarginites*, *Glochiceras*), among which cases of preservation of lappets are known (e.g. *Glochiceras*) (Pl. 1B). However, adapertural (i.e. peristomal) structures are unknown from perisphinctids and other ammonites. On the whole, the thicker deposition and a relative higher fragmentation correlate in LOL. Fluctuation in Fi values was found throughout the studied stratigraphic interval in the Navalperal and the Rio Segura sections (Fig. 3).

Epibionts and encrustment were selectively registered in the upper and lower sides of ammonite remains, especially in evolute shells of greater size. The most significant difference was found in the composition of the colonizing biota. On the upper, exposed surfaces, epibionts are dominated by nubeculariids, *Tubiphytes*, and benthic microbial communities, the growth of the latter controlling the sedimentary covering of the umbilicus (Pl. 2C, D). On the lower, protected surfaces, serpulids, *Terebella*, and bryozoa are characteristic, but the latter are occasionally known from exposed surfaces (Pl. 2A-D). Ubiquitous colonizers (i.e., with no preference for a given surface) are siliceous encrusting forams and *Bullopora*. Fluctuation in the relative abundance of epibionts was found throughout the studied stratigraphic interval in the Navalperal and the Rio Segura sections (Fig. 3).

Uncoupling and faceting (anchor facets) are rather rare features, and mainly identified in perisphinctids from condensed intervals (CLOL). The precise identification of faceting is frequently limited by the combination of corrasion and encrustment.

Interpretation

Lithology, texture and bedding in CLOL compared to LOL, which show no difference in the dominant fabrics, support the interpretation of the former as condensed deposits. However, no taphonomic condensation (Gómez & Fernández-López 1994) has been proven in CLOL from ammonite biostratigraphy, except the possibility for a minor one related to maximum condensation close to the boundary between the Bifurcatoides/Stenocycloides Subzone and the Grossouvrei Subzone (microstratigraphic disorder resulting in a shared horizon for the last occurrence of *Dichotomoceras falculae* and the first one for *D. bifurcatus*?). In addition, the stratigraphic range of LOL reinforces its interpretation as representing background depositional conditions in the area.

At first, smaller average values of ammonite remains in LOL, and their higher significance, corresponds with the record in the Rio Segura section, which represents areas in the outer inner to middle shelf. The smaller shell size registered from LOL (Fig. 4), together with higher fragmentation, accords with a potentially higher incidence of transport for ammonite carcasses. Higher dominance of ammonites showing within–bed position parallel to bedding in CLOL should result, mainly, from lower energy conditions and less post-mortem transport during an early part of the Bifurcatus Chron, when the sedimentation rates were lower (Fig. 3). This interpretation accords with long lasting exposure of skeletals and inner moulds in CLOL, and

the registered increase of corrasion. The relatively lower fragmentation found in CLOL is also coherent with lower energy during lower sedimentation rates that characterized maximal condensation within an early part of the Bifurcatus Chron (Fig. 3). During that time, frequent colonization of skeletals and inner moulds by epibionts (encrustment included) supports the interpretation of frequent sedimentary pauses (hiatuses) with exposition of ammonite remains on the sea-floor, as well as the assumption of selectivity in colonizer epibionts (difference in relative photo-dependence). The rare occurrence of uncoupling and faceting agrees with the occurrence of episodes of higher energy affecting horizons relatively unconsolidated within the sediment-water inter-phase in the sea-bottom. The lower rate of sedimentation related to CLOL deposition would favor the incidence and record of episodic processes resulting in uncoupling and faceting. Heavy corrasion and encrustment make the latter occasionally identifiable only in axial sections under microscope.

Taken into account the composition and general taphonomic traits of the ammonite assemblages registered, it is possible to recognize taphonic populations close to the type 1 defined by Fernández-López (1995), which shows a high ratio of microconchiates to macroconchiates. However, the state of preservation with a usually moderate to high degree of encrustment impedes the precise recognition of suture lines and, therefore, that of juveniles. In addition, it is difficult to establish if fragmentation occurred mainly on the water column or on the seabed, but their combination can be assumed. No significant difference in the type of taphonic population has been recognized in the Bifurcatus Zone, other than a probably lower incidence of post-mortem transport in ammonite assemblages gathered from the condensed interval related to CLOL. A mixture of floated specimens and relatively autochthonous sunk ones (Pl. 1; differential sinking related, at least, to shell morphology and size; Chamberlain et al. 1981; Olóriz et al. 1996; for an extended, complementary treatment see Maeda & Seilacher 1996), is envisaged as a valid picture of the ammonite assemblages recovered, which are interpreted as parautochthonous.

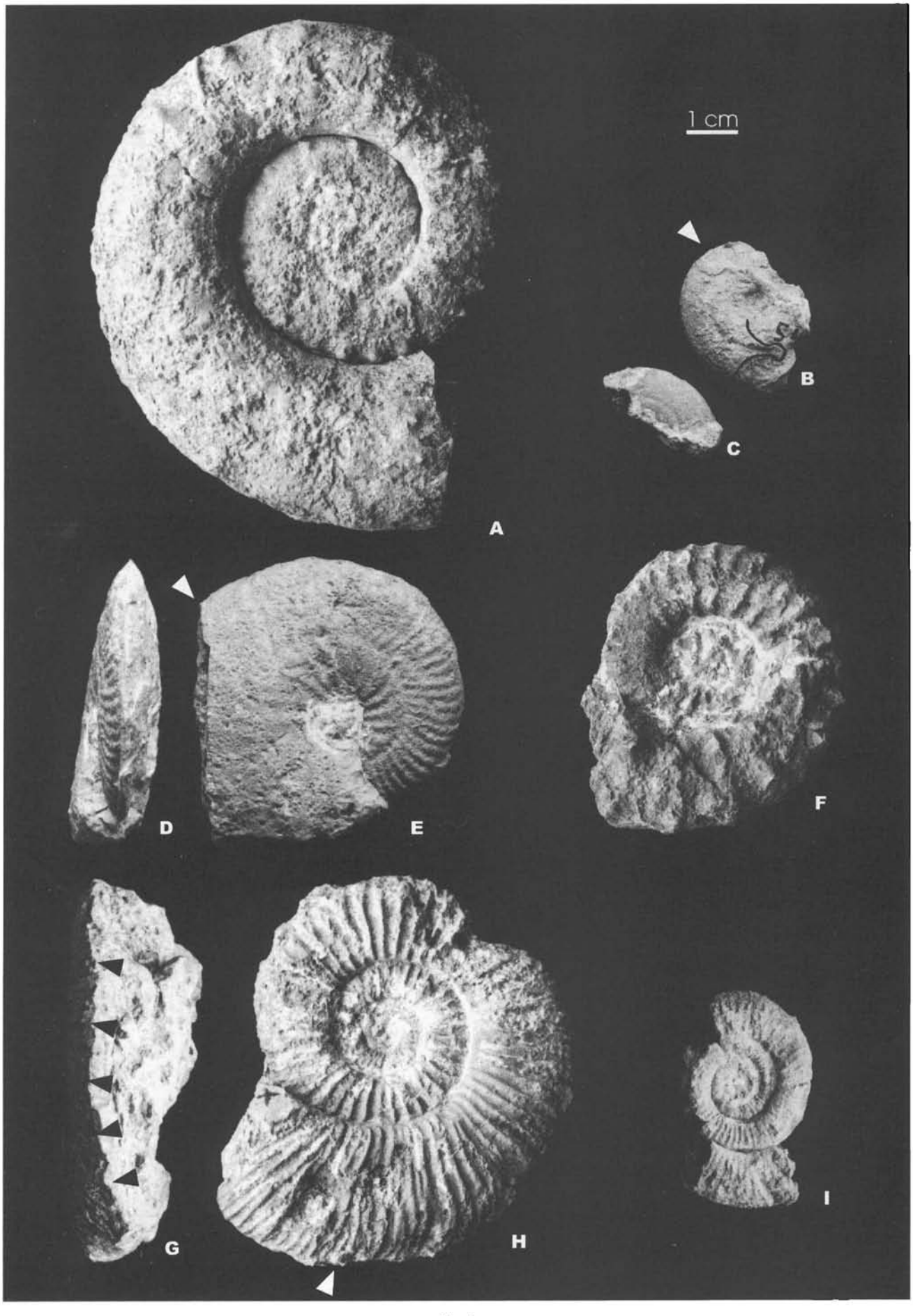
On the basis of the taphonomic and lithologic features, taphofacies I and II have been recognized and used to complement the interpretation of changes in depositional conditions (Figs. 3, 5). Taphofacies I, related to CLOL, shows the combination of higher values in quasi-horizontal position of ammonites remains, colonization by epibionts, average shell size and corrasion, the values of the latter two being specially higher than in taphofacies II (Figs. 3, 5). In contrast, lower fragmentation is typical of taphofacies I registered in CLOL. According to their respective stratigraphic ranges (Figs. 3, 5), taphofacies I is considered to be related to lower sedimentary rates and, therefore, it is restricted to the condensed interval composed of CLOL. On the other hand, taphofacies II is considered to represent background environmental conditions, which accords with the stratigraphic range of LOL (Fig. 3).

The increase in shell size, corrasion, encrustments and epibionts from the Transversarium? Zone to the lower part of the Bifurcatus Zone (Fig. 3) correlates with the turnover of taphofacies II by taphofacies I, and that of lithofacies LOL by CLOL. It is in accordance with an increased exposure time of ammonoid carcasses on the sea floor, which was favored by a decreased sedimentation rate.

The taphonomic trend described above is associated with the increase in ammonoids, against other macro-megainvertebrates, and agrees with deposition during developing transgressive-system-tract conditions (Olóriz et al. 2002a, b, c). The reversal of the taphonomic trend described was found in the upper part of the Bifurcatus Zone. The new trend correlates with the recurrence of taphofacies II and lithofacies LOL, and it is interpreted as resulting from a higher sedimentation rate, together with the concomitant diminishing of the exposure time of ammonoid carcasses in a higher energy environment. Throughout the upper part of the Bifurcatus Zone, the diminishing of ammonoid record accords with deposition during developing highstand-system-tract conditions (Olóriz et al. 2002a, b, c). On the basis of the above, the changes in the composition of ammonite assemblages depicted in fig. 3 are interpreted in terms of ecostratigraphic trends (Olóriz et al. 1995) that correspond to the enlargement and then restriction of ammonite ecospace on the Prebetic Shelf during the Bifurcatus Chron.

PLATE 1

Selected ammonites from the Bifurcatus Zone. Note body chamber preservation (white triangles) and peristomal structures (lappets stand out) in haploceratids against mainly phragmocone preservation (no marks) in evolute shells (euaspidoceratids, peltoceratids, perisphinctids). Irregular upper surface (probably due to the combination of faceting and corrasion (black triangles) is usual. (A) Right-side view of *Euaspidoceras* sp. showing the within-bed lower surface of incomplete phragmocone, NV-7-1; (B-C) Right- and left-side views of *Glochiceras* cf. *subclausum* (Oppel) showing a probably incompletely grown body chamber with the elongate arm of the lateral lappet and small spatulate end (the ventral lappet is well preserved: B), and fragmented body chamber with partial preservation of adorally concave ventro-lateral arch (C), both in the within-bed lower surfaces, NV-8-54, NV-8-55; (D-E) Ventral and right-side views of *Ochetoceras* (*Ochetoceras*) *canaliculatum* (v. Buch) showing body chamber preservation in within-bed lower surface, NV-14-31; (F) Left-side view of *Struebinia* sp. showing incomplete phragmocone in within-bed lower surface, NV-9-R; (G-H) Ventral and left-side views of large specimen of *Subdichotomoceras bifurcatus* (Quenstedt) showing irregular upper surface (right G) and better preserved within-bed lower surface with crowded ribbing in incomplete body chamber (H), NV-6-6; (I) Right-side view of nucleus of *Passendorferia* sp. resembling microconchiate adults ("*Enayites*") showing the within-bed lower surface; RS-6-6.



PL. 1

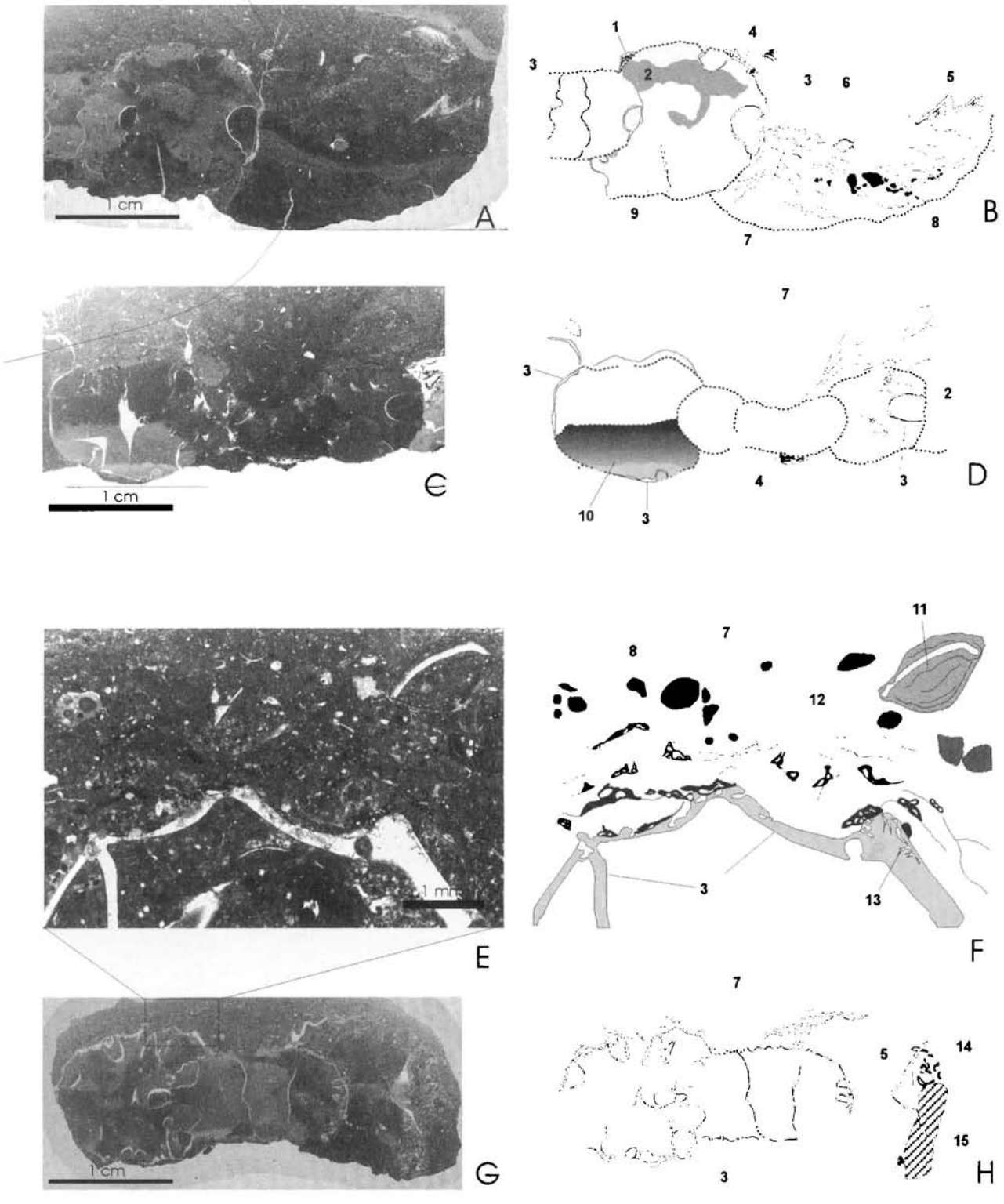


PLATE 2

Axial views in thin section, and complementary drawings, of microconchiate perisphinctids, mainly *Dichotomoceras*, showing better preserved lower side and irregularly corroded upper side according to within-bed position in CLOL. All specimens oriented according to their within-bed location. Dotted line for the periphery of inner moulds without shell preservation. (A-B) Inner mould with largely unpreserved epigenized outer shell in both the upper and lower sides, but preservation of septa in inner locations [3]. Note phragmocone showing probable burrowing favored by shell breaking before of the generalized dissolution of the outer shell [2] and displacement of shell debris [9], broken body chamber showing laminated and massive BMC growth [6-7] with trapped small lumps [8], and episodical exposure of hard surfaces evidenced by colonization of bryozoa [1] and serpulids [4] and edge contact with skeletals [5]; NV-8-20. (C-D) Inner mould with largely unpreserved epigenized outer shell in both the upper and lower sides, but inner and outer local preservation of shell material exists [3]. Note dome-like growth by laminated BMC controlling (restricting) the sedimentary covering of the umbilicus [7], local burrowing in phragmocone [2, see above], typical lower-side colonization by serpulids [4], and reversed geopetal infilling [10] indicating reworking of the inner mould (reelaboration, s. Fernández-López 1984); NV-6-38. (E-H) Inner mould showing preservation of epigenized outer shell in both the upper and lower sides, as well as in inner locations [3]. Note microboring [13], laminated BMC [7] with trapped nubeculariids [12], floated lumps [8] and oncoids [11] in the encasing matrix, probable truncation of the ammonite shell and juxtaposed dictyid sponge [15] and brachiopod [5] remains, and sections of small tubes of annelids [14]; NV-4-47.

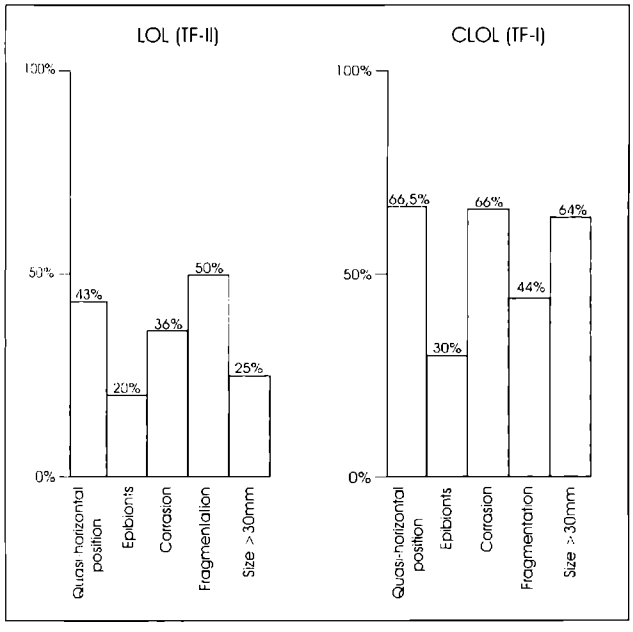


Fig. 5 - Averaged values of taphonomic features in lumpy-oncolitic limestone (LOL) and condensed & bioclasts-rich lumpy-oncolitic limestone (CLOL) used to identify taphofacies I and II (see text).

Conclusions

The taphonomic analysis conducted on ammonoid assemblages, gathered from lumpy-oncolitic limestones (LOL) and condensed & bioclasts-rich lumpy-oncolitic limestones (CLOL), serves to complement palaeobiological and palaeoenvironmental reconstructions in upper Middle-to-lower Upper Oxfordian epicontinental deposits of the Internal Prebetic (southern Spain).

The combination of quantification, as well as the semiquantitative-to-qualitative evaluation, of taphonomic features, and the analysis of their relationships with lithofacies, supports the characterization of taphonic populations and taphofacies. Taphonic populations close to type I indicate the proximity, even coincidence, of life areas for ammonites (i.e. rather parautochthonous assemblages). Two taphofacies have been distinguished: Taphofacies I shows higher values of mean shell size, corrasion, epibionts and encrustments, as well as a high number of specimens in quasi-horizontal settlement. The opposite characteristics serve to identify Taphofacies II.

Trends in taphonomic features are strongly related to changes in lithofacies and taphofacies, and can be interpreted in terms of systems tracts evolution during third-order tectono-eustatic cycles and their associated ecostratigraphic trends for ammonites.

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