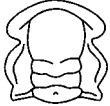


# Morphostructural constraints and phylogenetic overprint on sutural frilling in Late Jurassic ammonites

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The functional significance of frilled septa and complex sutures in ammonoids has generated ongoing debate. The 'classic' hypothesis envisages ammonoid shells and septa as designed for resisting ambient hydrostatic pressure, complex sutures being the evidence of strength in shells for colonization of deep habitats. Here we address the 'suture problem', focusing on the analysis and interpretation of variables in our database of Late Jurassic ammonites not included in previous studies, such as whorl height ( $W_h$ ), whorl shape ( $S$ ), shell coiling ( $WD$ ), taxonomic grouping and basic planispiral shell shape. The results indicate that sutural complexity, as measured by the fractal dimension ( $D_f$ ) value of the suture line, is positively correlated with  $W_h$ , and that the sutures of oceanic shells tend to provide, for a given  $W_h$  value, lower  $D_f$  estimates than do those of neritic shells. No general trend of increase in sutural complexity was noted for specimens recovered from swell areas belonging to oceanic fringes with respect to those that inhabited epicontinental shelves. In fact, Perisphinctoidea, the clade best represented in the database analysed, shows a higher  $D_f$  mean value in neritic species than in epioceanic ones. Significant differences in sutural complexity were detected for groups of ammonites classified according to shell shapes ( $WD$ ,  $S$ ). Oxycones and discocones, streamlined potential swimmers, show the highest  $D_f$  mean values, while spherocones and cardicones, which were presumably vertical vagrants, present the lowest ones. This indicates that sutural complexity was more related to shell geometry than to bathymetry. □ *Ammonoids, fractal analysis, Late Jurassic, shell shape, sutural complexity.*

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The functional significance of fluted septa and complex sutures in ammonoids has stirred debate during recent decades (for recent interpretations and controversy, see review and references in Saunders 1995; Seilacher & LaBarbera 1995; Jacobs 1996; Westermann 1996; Daniel *et al.* 1997; Olóriz *et al.* 1999; Lewy 2002). A persistent assumption has been that ammonoid shells are designed for resisting ambient hydrostatic pressure. According to this paradigm, first proposed by Buckland (1836), frilled septa have been interpreted as complementary structures of reinforcement against hydraulic stress during diving activity, and thus complex sutures have been considered as evidence of strength demands in shells of ammonites inhabiting deep habitats. Although Buckland's model did not claim explicitly that sutural complexity correlated with

bathymetry, the origin of the stress was assumed to be hydraulic, related to ambient pressure (mainly interpreted as hydrostatic pressure or loading by later authors) and thus proportional to water depth, as rightly assumed by Buckland (1836) and Pfaff (1911). Recent developments of this hypothesis (e.g. Hewitt & Westermann 1997) have emphasized the interdependence between critical compressive stress in the phragmocone and the curvature of the shell wall, thus supporting the interpretation of low-angle, anticlastic septal frilling as the way for the stiffening of compressed shells (i.e. the Second Buckland Law of Covariation of Westermann (1966)) through contraction that prevented major bending. Although the flatter the shell the weaker it was – an early assumption deduced from the fact that more complex suture lines

developed in flattened shells (Pfaff 1911) – the elastic support from septal fluting in the inner whorls postulated by Hewitt & Westermann (1997) was previously proposed by these authors as the complementary role of septa in preventing the spreading of perforations made by predators (Hewitt & Westermann 1990a), but see Kase *et al.* (1998; and comments below).

The marginal folds of the septa bend strongly forward and backward, approaching the inner wall of the ammonite at a low angle. Bayer (1977), as well as Westermann & Hewitt (1990a), stated the flexibility of low angle junctions of septal margins to the shell. The thickness of the septum decreases from the centre to the margin, reaching the minimum thickness at the folioles and lobules. The marginal fluting of the septa provides buttressing with a dendritic pattern (resembling columnar arches of Gothic churches; Lewy 2002) to increase the resistance of ammonite septal surface to adapical and adoral pressure (Kennedy & Cobban 1976, but see Bayer 1977). Although such construction and the marginal thinning of the septa were believed to act like a spring or shock absorber (Hewitt & Westermann 1997; Westermann 1999), Daniel *et al.* (1997), using finite element analysis, demonstrated that it actually reduces the resistance to external hydrostatic load. In addition, Saunders *et al.* (1999) suggested that more complexly sutured ammonites had shallower depth limits (see review in Lewy 2002). These interpretations are coherent with septal corrugation being involved in buoyancy control (Saunders 1995).

In any case, taking into account the preservation of suture lines in ammonite shells or inner moulds it is important to distinguish between habitat depth and depth of the sea floor where the shell of the dead animal settled (i.e. post-mortem transport in the water column, bottom sweeping and even reworking). Many authors (including the main supporters of Buckland's theory) now consider that most ammonites were epipelagic (up to 250 m water depth) in both oceanic–epioceanic and epeiric waters (Westermann 1990, 1996; Olóriz *et al.* 1993; Olóriz & Palmqvist 1995; Daniel *et al.* 1997; Olóriz *et al.* 1996, 1997, 1999; Westermann & Tsujita 1999; Olóriz 2000; Lewy 2002). This interpretation seems to be confirmed by assumptions on the ontogenetic decrease of siphuncle strength in Ammonitina (Westermann 1971), the clade that comprises the largest part of our database. Moreover, the limited but informative set of calculations of maximum habitat depth derived from shell wall and siphuncle strength data (Hewitt & Westermann 1990b; Hewitt 1996) indicates shallower habitats than assumed previously. In addition, post-mortem drifting of shells (documented in *Nautilus*;

from Reyment (1958) to Ward (1987)) is unfavourable in terms of shell preservation (known expatriation to shoreline environments), and even insignificant for ammonoid palaeobiogeography according to Chamberlain *et al.* (1981). Finally, the settlement of ammonite carcasses at water depths deeper than those preferred for living individuals may have occurred, but the preservation of inner moulds showing suture lines as well as siphuncle filling would preclude deposition below implosion depths. Thus, although correlations between habitat depth and deposition depth are not unequivocal, ammonite preservation can be used to exclude implosion depths (i.e. depths in excess of 400–700 m, or even lower, between 150 m and 400 m, for most ammonoids according to strength indices of connecting rings; e.g. Westermann 1982).

Other explanations of the 'suture problem' arise from the fields of functional/constructional morphology, physiology and developmental biology, including frilling of septa resulting from muscle or body attachment, mantle tie-points, inner gas-pressurization counteracting external water pressure, increase of overall weight for buoyancy control, viscous fingering in fluid interfaces or morphogen lateral inhibition during morphogenesis of septa, compression and decompression of a bladder by fleshy-membrane movability (i.e. the Cartesian divers model), complex septa facilitating respiration or transportation of cameral fluid, and marginal fluting forming septal recesses for storing cameral liquid to improve buoyancy adjustment (Newell 1949; Reyment 1958; Westermann 1958, 1971, 1975, 1996; Guex & Rakus 1971; Seilacher 1975, 1988; Kennedy & Cobban 1976; Bayer 1978a, b; Jacobs 1992, 1996; Hewitt 1985, 1996; Hewitt & Westermann 1986, 1987, 1997; García-Ruiz *et al.* 1990; García-Ruiz & Checa 1993; Seilacher & LaBarbera 1995; Saunders 1995; Saunders & Work 1996, 1997; Checa & García-Ruiz 1996; Daniel *et al.* 1997; Hammer 1999; Lewy 2002).

Higher-order fluting was limited to the septum margin, resulting in increased sutural complexity, and was accompanied by thinning of the septal margins; conversely, the centre of strong septa was progressively thickened to compensate for stress concentrations (Westermann 1975, 1996; Hewitt 1996), but see Daniel *et al.* (1997) and Lewy (2002). Hewitt & Westermann (1997) proposed that the fluted septa originated to buttress the wall of the inner septate whorls against an indirectly applied hydrostatic load (following Westermann 1958), and that sutural complexity resulting from septal folding acted like a spring or shock absorber and anti-predation device. The latter role, envisaged by Hewitt & Westermann (1997), could be difficult to assume in the case of mosasaur attacks, on the basis of the known behaviour of large, conically

toothed reptiles during predation (i.e. sudden-rude biting vertebrates; but see Tsujita & Westermann 2001, who envisaged an unusual, loose articulation in mosasaurs). The occurrence of ammonite jaws within stomach content in polycotyloid plesiosaurs (Sato & Tanabe 1998) proves predator–prey relationships between marine reptiles and ammonites. However, this evidence cannot be used as support for the interpretation of ‘bite-marks’ in well-preserved shells, according to experiments on shell breaking (Kase *et al.* 1998). In addition, the possibility of swallowing the whole shell and/or shell dissolution by stomach acid (Sato & Tanabe 1998) of living or death ammonites might be considered. Finally, Westermann (1999) has suggested that the central/marginal thickness ratio and sutural complexity tended to increase with habitat depth within higher taxa of Mesozoic ammonoids.

Results after using a large database ( $n > 500$ ) of Late Jurassic ammonites (Olóriz & Palmqvist 1995; Olóriz *et al.* 1997, 1999) indicate that sutural complexity, as measured by the fractal dimension values of the sutures, was similar in specimens inhabiting epicontinental shelves and epiocceanic plateaux. Hence, although mid-outer shelf and epiocceanic environments on seamounts (and even on assumed typically ‘deeper’ environments, e.g. depocentres for cherty and/or marly limestone rhythmites in the Subbetic Zone of the Betic Cordillera) cannot be conclusively distinguished bathymetrically, these results indicate that sutural complexity was not related primarily to bathymetry. Alternatively, there were no major differences in habitat depth for epicontinental and epiocceanic ammonites during the Late Jurassic. A similar picture can be assumed for the Early Jurassic ammonites according to data in Dommergues *et al.* (1996) indicating that shells with more complex sutures were not especially favoured during higher sea levels, nor were they affected by sea-level fluctuations. Thus, deeper habitats cannot be directly inferred for epiocceanic ammonites from complex sutures.

However, Westermann (1999) argued: (i) that we did not consider whorl diameter, a parameter that is positively correlated with sutural complexity (Olóriz & Palmqvist 1995); (ii) that most of our ammonoid families occur in both megafacies (i.e. neritic and epiocceanic environments), having been observed strong sutural simplification in epeiric (<100 m) versus oceanic (>200 m) relatives (depths approached through shell strength calculations); (iii) that distinct taxonomic groups (i.e. Orders/Suborders) were lumped together, regardless of strong phylogenetic effects; and (iv) that we did not use shell strength data for estimating bathymetry. Westermann’s comments are of interest and some clarifications apply.

## Basic palaeoecology, taxonomy and morphometric variables

Field data and numerical analysis must be taken into account for the right evaluation of any database of ammonite septal sutures. We shall comment on natural (ecological, geological) and technical aspects (morphometry) of the database with taxonomic control.

Late Jurassic ammonite distributions interpreted from field data of southern Spain, one of the few regions containing the fossil record of neritic and epiocceanic communities that inhabited the same continental margin, do not show significant differences between either community in terms of presence/absence of taxa at the family/subfamily level (Olóriz 1996). Olóriz (1996) stated that the evaluation at lower taxonomic levels cannot be conclusive because of the comparatively incomplete database for epicontinental deposits and identified differences affecting only relative abundances and diversities within families and subfamilies, as well as morphological specialization of phenotypes in genera and species. In addition, even some rare genera were reported from both epicontinental and epiocceanic deposits, but the ‘bizarre’ *Oxydiscites* and *Metastreblites* (Early Kimmeridgian) are known only from a few specimens collected in epicontinental (Prebetic) and epiocceanic (Subbetic) deposits, respectively. We therefore agree with point (ii) raised by Westermann (1999), given that most families and subfamilies in fact occur in both environments. Although they experienced differential adaptation, as deduced from changes in relative percentages, no significant variation in suture complexity was identified in ubiquitous genera such as the phylloceratid *Sowerbyceras*. Therefore, we have afforded a comparison of sutural complexity in neritic and epiocceanic ammonites distributed among superfamilies.

Westermann’s claim of lumping distinct Orders/Suborders in our approach [i.e. point (iii)] should not be surprising, since the interpretation of Phylloceratina and Lytoceratina as colonizers of deeper oceanic waters against neritic Ammonitina is a classic one assumed and accepted until recently by Westermann (e.g. 1990 and 1996). Olóriz (1985, 1990a, 1996) stated that Ammonitina were usual inhabitants in both neritic and epiocceanic waters, irrespective of depth, and discussed Upper Jurassic examples interpreting their palaeobiogeographic significance (Olóriz 1988, 1990b). Olóriz *et al.* (1996) envisaged preferred/usual depth ranges to be fairly shallow (50–250 m) for all Late Jurassic ammonites, in agreement with proposals made for most ammonites by Henderson (1984), Ward (1987), Hewitt (1993, 1996) and Westermann

(1996) on physiologic grounds (e.g. the controversy on decoupling and neutral buoyancy) and shell strength calculations. The recent evaluation by Gygi (1999) in the Upper Jurassic from northern Switzerland reinforces the estimated depth interval, especially for the lower range boundary assumed by Olóriz *et al.* (1996). A depth range within the upper part of the water column is especially true for ubiquitous Phylloceratina (e.g. *Sowerbyceras*) and all Ammonitina. The latter are the main component in both our database and macrofossil assemblages gathered from Upper Jurassic deposits, either epicontinental or epioceanic in southern Spain. Moreover, Ammonitina are the typically exclusive to near-exclusive ammonites in epicontinental macrofossil assemblages containing abundant inner- and mid-shelf bivalves elsewhere. In fact, specialized Phylloceratina and Lytoceratina (i.e. exclusively epioceanic) are generally secondary components in Upper Jurassic ammonite assemblages known from epioceanic deposits (ammonitico rosso and related facies) in southern Spain, especially the Lytoceratina. Thus, we assume ammonite ecology (prime factor) and the fossil record (ultimate factor, including deposition depth; see above) to determine data available for potential understanding of ammonite palaeobiology. In such a natural scenario (i.e. ecological and geological), we consider that our morphometric approaches were conducted on a reliable database compiled of Late Jurassic ammonites. On this basis, Westermann's point (iii) seems to disregard the known composition of Upper Jurassic ammonite assemblages, and so the relative distribution of their components in terms of precise depths will remain highly hypothetical. We predict an improvement through the future research of single-basin databases that should be interpreted in their sedimentological and stratigraphic context.

Westermann's points (i) and (iv) focus on technical matters concerning our morphometric data and conclusions. Here we show the results from a numerical approach conducted on variables related to those considered more relevant by Westermann (1999) for addressing the 'suture problem': (i) whorl height of phragmocones (estimated at the end-points of the suture measured), which is a parameter more closely related to sutural complexity than whorl diameter, according to partial correlation data (Olóriz & Palmqvist 1995; Pérez-Claros 1999); (ii) taxonomic grouping (at the superfamily level, since most specimens analysed belong to the Order Ammonitina); and (iii) basic planispiral shell shape, as defined by Westermann (1996), which was presumably related to lifestyle and habitat depth of ammonites. In our approach, the only exceptions for a precise evaluation of shell strength are direct measurements of thickness

of shell wall and septa, which were not available in our database, although two observations apply here: (i) the precise thickness measurement in epigenized shells is not unequivocal, nor is the specific gravity of the shell substance (Reyment & Eckstran 1957; Reyment 1958; Heptonstall 1970; Mutvei 1975), and (ii) stress-maximum values (which are equivalent for connecting rings and the whole shell in cephalopods; Ward 1987) do not provide information about the usual/preferred stress-field in a biological structure. The health safety factor (Ward 1987) between inhabiting and implosion depths in *Nautilus* is an appropriate example of this. In addition, growing evidence is emerging about structural differences between siphuncles in ammonites and nautilids (Drushchits *et al.* 1983; Doguzhaeva & Mutvei 1993; Schweigert & Dietl 1999; Tanabe *et al.* 1999), reinforcing their long-recognized and recently demonstrated difference in composition (Grandjean 1910; Mutvei 1967; Obata *et al.* 1980; Hewitt & Westermann 1983; Hasenmueller & Hattin 1985). This should prevent the use of the *Nautilus* siphuncle as a close reference for numerical statements on ammonites (see discussion on bathymetric calculations using siphuncle stress in Hewitt (1996)) and determine reasonable scepticism concerning reliability in transferring strength values to palaeodepth in metres. For extended comments, see Ward (1987). Moreover, although available stress calculations based on septal and siphuncle strength data would provide potential maximum depth limits, average habitat depths can be estimated from the variance of strength data (Hewitt & Westermann 1990b), which suggests that most ammonites lived between 50 and 250 m in the ocean realm as well as in neritic to epeiric seas (as proposed by Westermann 1996).

## Morphometric analysis

Fig. 1 shows the fractal dimension ( $D_f$ ) values of ammonite sutures in those specimens inhabiting normal neritic-to-epeiric seas ( $n = 239$ ) and epioceanic fringes ( $n = 41$ ) in relation to whorl height ( $W_h$ ,  $\log_{10}$ -transformed to avoid departures from normality) corresponding to the sutures analysed (see details on the methodology used for estimating  $D_f$  values in Lutz & Boyajian (1995), Olóriz & Palmqvist (1995) and Olóriz *et al.* (1997, 1999)).

A direct, statistically significant relationship between fractal dimension and whorl height is revealed by least-squares regression:

$$D_f = 1.245(\pm 0.024) + 0.146(\pm 0.018) \cdot \log(W_h) \quad (r = 0.432, F = 63.830, p < 0.0001, n = 280),$$

which clearly indicates that sutural complexity, as measured by the

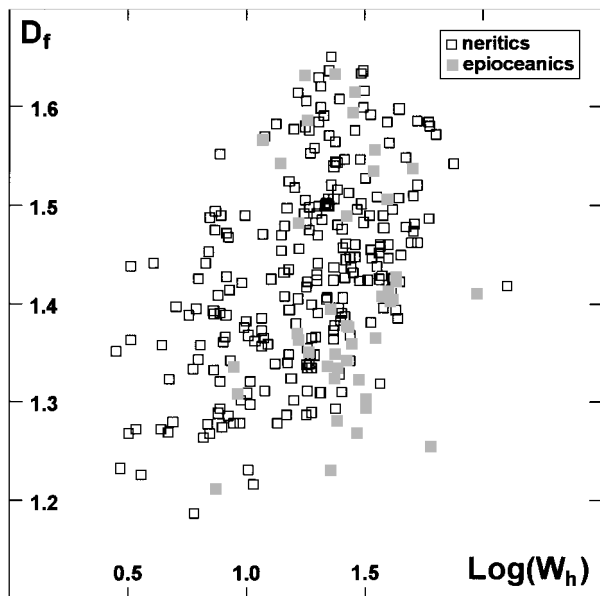


Fig. 1. Scatter-plot of fractal dimension values ( $D_f$ ) of sutures in Late Jurassic ammonites (database compiled by Olóriz et al. 1997, 1999) versus logarithms ( $\log_{10}$ ) of whorl height ( $W_h$ ), in mm.

adjusted  $D_f$  values, tends to be higher in those phragmocones with larger whorl height. The relatively high value obtained for the standard error of estimates for  $D_f$  (0.091, which represents a confidence interval of  $\pm 0.178$  for  $p < 0.05$ ) suggests, however, that phyletic 'noise' (i.e. somewhat like the genetic control claimed by Hammer (1999)) as well as other factors (e.g. intraspecific variability resulting from ecophenotype effects, covariation with other shell features, and constructional/developmental 'random' variation) should be responsible for extended vertical ranges of  $D_f$  values between particular  $\log(W_h)$  values.

The distribution on the scatter-plot of neritic and epioceanic ammonites (Fig. 1) reveals a substantial overlap in  $D_f$  values between both groups, but also shows that, for a given  $W_h$  value, the suture lines of

epioceanic shells tend to be, on average, simpler than those of epicontinental ones, as reflected in their comparatively lower  $D_f$  values. Leaving aside potential effects of differential preservation, this is suggested also by the somewhat higher mean  $D_f$  value obtained for neritic ammonites, which show, on average, lower whorl heights than epioceanic ones (Table 1). The difference between  $D_f$  mean values for both groups (1.432 and 1.412, respectively) is not statistically significant according to a  $t$ -test ( $t = 1.20$ ,  $p > 0.1$ ), but there is a significant difference between their  $W_h$  means (1.234 and 1.398, respectively;  $t = 4.13$ ,  $p < 0.0001$ ). Separate regression analyses for epicontinental and epioceanic phragmocones reveal a significant relationship between  $D_f$  and  $W_h$  in the former but not in the latter, which precludes statistical comparison of the regression coefficients:

$$D_f = 1.233(\pm 0.023) + 0.161(\pm 0.018) \cdot \log(W_h) \quad (r = 0.500, F = 78.901, p < 0.0001) \text{ for neritic ammonites } (n = 239),$$

$$D_f = 1.305(\pm 0.119) + 0.079(\pm 0.084) \cdot \log(W_h) \quad (r = 0.148, F = 0.875, p = 0.355) \text{ for epioceanic ammonites } (n = 41).$$

The equation for epicontinental shells predicts a  $D_f$  value of 1.458 for a  $W_h$  value of 1.398 (i.e. the mean for  $\log$ -whorl height in epioceanic phragmocones), which is significantly greater than the mean  $D_f$  value for epioceanic ammonites (1.412) according to a  $t$ -test ( $t = 2.92$ ,  $p < 0.01$ ).

The distribution of neritic and epioceanic ammonites among superfamilies is shown in Table 1. Inspection of  $D_f$  mean, minimum and maximum values reveals that there is no general trend-increase in sutural complexity for specimens gathered from swell areas in epioceanic fringes with respect to those inhabiting epicontinental shelves and inland seas. In fact, Perisphinctoidea, which is the clade best represented in the database, shows a higher mean fractal

Table 1. Statistics ( $n$ : number of cases;  $s.d.$ : standard deviation;  $min$ : minimum value;  $max$ : maximum value) of fractal dimension ( $D_f$ ) and whorl height ( $W_h$ , in mm,  $\log_{10}$ -transformed) in neritic and epioceanic ammonites from the database of Olóriz et al. (1997, 1999), distributed among superfamilies.

		Epicontinental platforms					Epioceanic fringes				
		$n$	Mean	s.d.	Min.	Max.	$n$	Mean	s.d.	Min.	Max.
All superfamilies	$D_f$	288	1.432	0.096	1.188	1.661	47	1.412	0.108	1.212	1.634
	$W_h$	249	1.242	0.304	0.447	2.101	45	1.398	0.218	0.871	1.975
Phylloceratoidea	$D_f$	10	1.493	0.063	1.423	1.615	3	1.504	0.081	1.411	1.557
	$W_h$	11	1.233	0.273	0.868	1.724	4	1.612	0.361	1.142	1.975
Lythoceratoidea	$D_f$	—	—	—	—	—	5	1.575	0.053	1.491	1.634
	$W_h$	—	—	—	—	—	6	1.289	0.137	1.074	1.455
Perisphinctoidea	$D_f$	197	1.436	0.093	1.188	1.661	32	1.363	0.080	1.212	1.615
	$W_h$	158	1.350	0.244	0.530	2.101	32	1.383	0.203	0.871	1.701
Haploceratoidea	$D_f$	81	1.420	0.105	1.227	1.652	7	1.479	0.091	1.351	1.634
	$W_h$	80	1.028	0.305	0.447	1.601	3	1.500	0.116	1.371	1.597

Table 2. Statistics ( $n$ : number of cases;  $D_f$  mean: mean;  $s.d.$ : standard deviation of mean;  $D_f$  min: minimum value;  $D_f$  max: maximum value) of fractal dimension ( $D_f$ ) values of ammonite sutures in the database of Olóriz *et al.* (1997, 1999), classified according to basic planispiral shell shapes (Westermann 1996). Mean values of  $WD$  (i.e. whorl expansion rate multiplied by distance to coiling axis),  $S$  (i.e. whorl shape index) and whorl height [ $\log_{10}(W_h)$ ] are also shown.

Planispiral shell types	N	$D_f$ mean	s.d.	$D_f$ min.	$D_f$ max.	$\log(W_h)$ mean	$WD$ mean	$S$ mean
Oxycones	14	1.507	0.070	1.374	1.635	1.326	0.354	0.443
Oxycones/discocones	12	1.517	0.123	1.310	1.652	1.266	0.249	0.527
Oxycones/platycones	8	1.444	0.056	1.330	1.502	1.351	0.464	0.526
Discocones	47	1.442	0.098	1.186	1.618	1.196	0.363	0.405
Discocones/platycones	87	1.409	0.096	1.188	1.634	1.349	0.603	0.869
Discocones/sphaerocones	9	1.392	0.065	1.300	1.482	1.244	0.678	1.067
Platycones	169	1.417	0.094	1.218	1.661	1.246	0.765	0.859
Platycones/serpenticones	59	1.429	0.080	1.232	1.592	1.266	0.925	0.955
Serpenticones	48	1.410	0.100	1.221	1.622	1.282	0.906	1.023
Planorbicoides	19	1.431	0.098	1.280	1.595	1.264	0.805	1.461
Cadicones	7	1.385	0.040	1.329	1.443	1.362	0.708	1.469
Sphaerocones	4	1.379	0.159	1.185	1.544	1.417	0.413	1.180
Elliptosphaerocones	5	1.310	0.061	1.229	1.390	0.737	0.357	1.240

dimension value in neritic species (1.436) than in epioceanic ones (1.363), this difference being statistically significant according to a  $t$ -test ( $t = 3.52$ ,  $p < 0.001$ ), with similar values of log-whorl height in both groups (1.350 and 1.383, respectively;  $t = 0.60$ ,  $p > 0.1$ ) (26.0 and 26.5 mm, respectively, for whorl height means calculated from non-log-transformed data). Haploceratoidea, the second group in abundance, presents a higher  $D_f$  mean value in epioceanic specimens than in epicontinental ones (1.479 and 1.420, respectively), in agreement with the prediction of Westermann (1999), although the difference is not significant ( $t = 1.28$ ,  $p > 0.1$ ). However, the mean  $W_h$  value is much higher in epioceanic haploceratids (1.500, 32.4 mm) than in neritic (1.028, 13.5 mm) individuals studied, this difference showing a high statistical significance ( $t = 4.67$ ,  $p < 0.001$ ), which helps to explain the slight difference found between their  $D_f$  mean values (i.e. for a given whorl height, neritic haploceratids will show higher  $D_f$  values than epioceanic ones). Finally, phylloceratid ammonites show similar  $D_f$  values in both groups ( $D_f$  means of 1.493 and 1.504 in neritics and epioceanics, respectively;  $t = 0.16$ ,  $p > 0.1$ ), although  $W_h$  values are also higher in the epioceanic species of this clade (1.233 and 1.612; 20.6 and 51.2 mm, respectively;  $t = 1.44$ ,  $p > 0.1$ ). These results indicate that sutural complexity, as measured by fractal analysis, was not related to bathymetry (i.e. that even if it were proved that epioceanic ammonites dwelled in deeper habitats, they did not show more complex sutures) or, more probably, that there were no major differences in habitat depth for epicontinental and epioceanic ammonites, as we interpreted previously (Olóriz & Palmqvist 1995; Olóriz *et al.* 1997, 1999) and was implicitly assumed by Westermann (1996) modifying his previous hypothesis (Westermann 1990), mainly

when concerned with major ecologic distributions of Ammonitina.

There are also noteworthy differences in the fractal dimension values of sutures for ammonites grouped according to basic planispiral shell shapes, as defined by Westermann (1990, 1996). Whorl section shape was approached morphometrically with the parameter  $S$  (Raup 1967) estimated as whorl width divided by whorl height,  $S < 1$  in compressed and oval whorls,  $S \sim 1$  in subcircular whorls and  $S > 1$  in depressed whorls. Shell coiling was estimated using the parameter  $WD$ , calculated multiplying whorl expansion rate ( $W$ ) by distance to coiling axis ( $D$ ).  $WD < 1$  in involute phragmocones and  $WD > 1$  in evolute ones (Raup 1967).

Despite substantial overlap in the range of  $D_f$  values among the groups analysed, inspection of data in Table 2 reveals significant differences in  $D_f$  means. Oxycones and compressed discocones show streamlined involute phragmocones ( $WD_{mean} = 0.354$  and 0.249, respectively) with compressed subtriangular or very high ovate whorl sections ( $S_{mean} = 0.443$  and 0.527, respectively). These morphologies present the highest  $D_f$  mean values ( $D_f > 1.5$  in both cases) and would correspond to potentially more active swimmers, with improved steering (i.e. manoeuvrability combined with directional stability) and relative speed during the pursuit of their prey or the escape from predators (in accordance with interpretations made by Bayer (1982) and Westermann (1996)), if active swimming for prey capture was a reality (as deduced from Reyment (1988)). These phragmocones show strong lateral compression (i.e. low thickness ratio,  $< 0.3$ , estimated as whorl width/shell diameter) and flattish flanks with little strength against buckling. In addition, the whorl section of these shells also has the greatest outer surface to inner volume ( $S:V$ ) ratio,

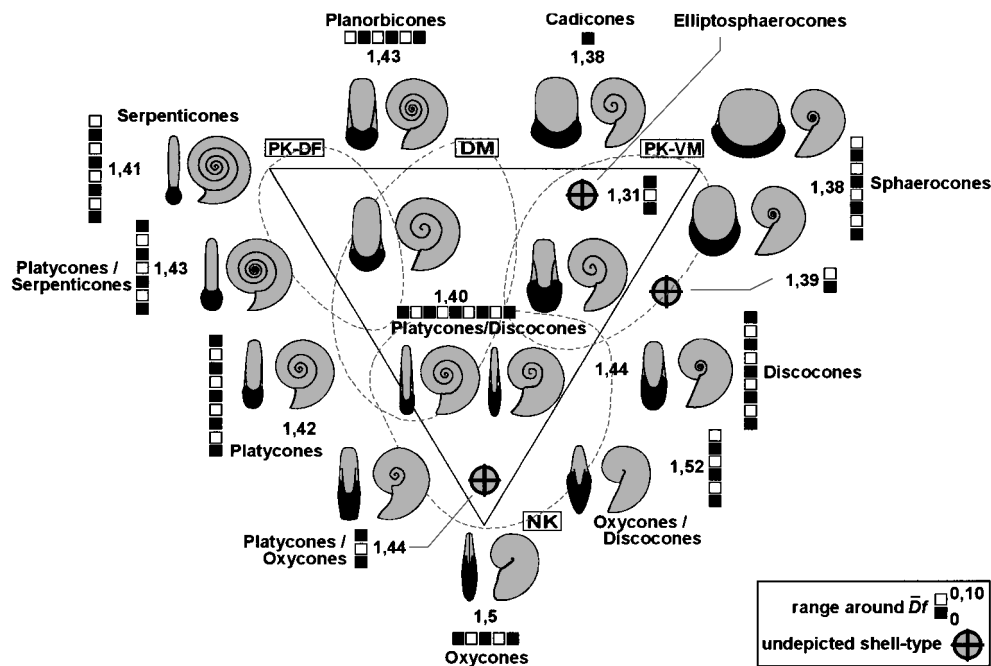


Fig. 2. Planispiral shell shapes analysed in Late Jurassic ammonites with indication of mean fractal dimension values ( $D_f$  mean) of septal sutures (approximate from data in Table 2) and their location in the triangle for principal whorl shapes and habitats (broken lines) according to Westermann (1996): PK-DF (planktic drifters), PK-VM (planktic vertical migrants); DM (demersals), NK (nekton). Note small ranges of  $D_f$  values around of  $D_f$  mean, related to particular shell shapes that were not represented across a wide taxonomic range in the database investigated, and the opposite for great ranges around of  $D_f$  mean that are interpreted to result from taxonomic noise.

which implies that the shell tube was weaker than one with a more circular (and thus lower  $S:V$  ratio) cross section (Olóriz & Palmqvist 1995; Olóriz et al. 1997, 1999). Their typically complex septal folding (and thus complex sutures) improved both strengthening for trimming, which also benefited from increased shell flexibility (as interpreted by Bayer (1977)), and complementarily buoyancy regulation, as in recent interpretations concerning transportation of cameral liquid (Saunders 1995; Saunders & Work 1996; Daniel et al. 1997). Therefore, complex septal folding, especially peripheral frilling, could have favoured physiologic requirements (e.g. respiration or cameral liquid transport) as well as hydrodynamics and manoeuvrability (see also Lewy 2002) rather than mainly shell reinforcement for resisting high stress in the shell wall (e.g. by hydrostatic pressure during fast swimming). This cautionary interpretation concurs with the claim for care before assuming oxycones and discocones as synonymous of well-adapted swimmers (Chamberlain 1990; Elmi 1993).

Discocones and platycones with compressed sections ( $S_{mean} = 0.405$  and  $0.859$ , respectively) and involute to intermediate coiling ( $WD_{mean} = 0.363$  and  $0.765$ , respectively) also present relatively high  $D_f$  mean values ( $\sim 1.44$  in both cases), in agreement with their high  $S:V$  ratio in comparatively less

streamlined shells with presumably less precisely controlled buoyancy and manoeuvrability.

Planorbicones (i.e. evolutes with subcircular to depressed whorls;  $WD_{mean} = 0.805$  and  $S_{mean} = 1.461$ ) and platycones (i.e. involute to moderately evolute shells, with subrectangular compressed whorls;  $WD_{mean} = 0.765$  and  $S_{mean} = 0.859$ ) may have been demersals with low to moderate swimming and variable steorage capabilities according to Westermann (1996), Olóriz et al. (1996) and Keupp (1999) relative to Late Jurassic perisphinctids. They show intermediate  $D_f$  mean values (1.431 and 1.417, respectively), as expected from their intermediate  $S:V$  ratios.

As usually recognized in planorbicones, serpenticones (i.e. very evolute to advolute shells, with subcircular to depressed whorls;  $WD_{mean} = 0.906$  and  $S_{mean} = 1.023$ ) and evolute platycones were longidomic, which made them poor or non-swimmers (Westermann 1996). In these ammonites, advantages envisaged by Jacobs & Landman (1993) for endowed propulsion could be largely counteracted by decreasing hydrodynamics through the combined effect of shell shape and sculpture, as shown in laboratory experiments by Chamberlain (1976, 1980), Chamberlain & Westermann (1976) and Elmi (1993), especially during foraging activities (Chamberlain & Wester-

mann 1976; Reyment 1988). In addition, the presence of a long body chamber would reduce the stability of the shell when using jet propulsion (Jacobs & Chamberlain 1996). These ammonites were presumably planktic (i.e. passive drifters; Westermann 1996) or alternatively vagrant benthics (Olóriz *et al.* 1996) more or less bottom related (Keupp 1999), the latter being rather the general aptitude interpreted for Late Jurassic ammonites in Switzerland (Gygi 1999).  $D_f$  mean values for serpenticones and evolute platycones are intermediate (1.410 and 1.429, respectively).

Finally, sphaerocones (i.e. subglobular shells with involute adult body chamber;  $WD_{mean} = 0.413$  and  $S_{mean} = 1.180$ ), cadicones (i.e. subglobular shells with open, angular umbilicus;  $WD_{mean} = 0.708$  and  $S_{mean} = 1.469$ ), elliptosphaerocones (i.e. adult body chamber showing decreased coiling;  $WD_{mean} = 0.357$  and  $S_{mean} = 1.240$ ) and intermediate morphologies between discocones and sphaerocones (Fig. 2) were highly involute to intermediate coiled with depressed to oval/subcircular sections, poorly streamlined, and could not have been active swimmers, especially while foraging. These ammonites are considered by Westermann (1996) to be demersal vertical migrants (although their depth range is unknown), an interpretation which embraces the modes of life proposed by Olóriz *et al.* (1996) for heavily and less sculptured cadicones–sphaerocones. Such morphologies present the lowest  $D_f$  mean values (1.379, 1.385, 1.310, and 1.392, respectively), as expected from their low S:V ratios. This suggests, again, that sutural complexity in ammonoids was not specifically related to habitat depth but rather to shell geometry, at least in Late Jurassic ammonites, as recently indicated by Olóriz & Palmqvist (1995) and Olóriz *et al.* (1997, 1999). Hence, accentuated septal folding, and thus sutural complexity, in our interpretation, would favour trimming in compressed, comparatively stiff, shells (potential hydrodynamics neither directly nor exclusively related to active swimming) among a plethora of combined functions controlling ammonite behaviour, those which are physiologically dependent being of prime importance (e.g. siphuncular pumping determining buoyancy).

## Conclusions

Within the debate on the interpretation of frilled septa and complex sutures in ammonoids, one of the functional hypotheses most widely accepted during past decades viewed complex septa as being designed for resisting wall stress caused by ambient hydrostatic pressure. It was thus interpreted as evidence of

demands on strength in flattish parts of the shell and/or in shells inhabiting deep habitats with increased hydrostatic load (Westermann 1958, 1971, 1975, 1996, 1999; Hewitt 1985, 1996; Hewitt & Westermann 1986, 1987, 1997). However, our results indicate that sutural complexity, as measured by the fractal dimension ( $D_f$ ) value, was remarkably similar in Late Jurassic ammonites inhabiting epicontinental shelves and epioceanic fringes. This suggests that the complexity of septal sutures was not mainly related to differences in potential habitat depth experienced in both these environments.

Sutural complexity is positively correlated with whorl height of phragmocones; however, although epioceanic ammonites in our sample tend to be, on average, slightly larger than neritic ones, they provide lower  $D_f$  estimates, which indicates that, other things being equal, ammonites from epioceanic fringes show less complex sutures than those which inhabited the epicontinental shelves. In addition, there is no general trend of differences in  $D_f$  values between neritic and epioceanic ammonites distributed among superfamilies, in accordance with the observed distribution showing no biogeographic separation at this level across the same continental palaeomargin. In fact, the palaeobiogeographic separation in southern Spain (the northwestern margin of Tethys) was limited and occurred rarely at the genus and presumably more frequently at the species and lower levels.

Significant wider ranges in  $D_f$  values have been detected between basic planispiral shells embracing platycones to discocones (see ranges around  $D_f$  mean values in Table 2 and Fig. 2). This suggests taxonomic imprinting due to taxonomic mixing in our sample within this large subgroup, derived from our focus on the analysis of principal shell shapes with no resolution for minor differences in traits determining the precise structure in these shell shapes. The highest sutural complexity is found in oxycones and compressed discocones, trimmed and potential nektic swimmers with requirements for precise control on buoyancy (as also happened in the case of planktic shells). Their relatively narrow range of  $D_f$  values probably indicates a comparatively high taxonomic homogeneity in the sample analysed. The lowest sutural complexity occurred in hydrodynamically poorer sphaerocones and cadicones, the former showing a broad range of  $D_f$  values even within a small sample size, which is probably due to differences among the analysed specimens in whorl height, stratigraphy and thus evolutionary time between microevolutionary lineages within the subfamily Physodoceratinae.

Interpretation of the distribution of  $D_f$  mean values in Fig. 2, based on the assumption of both the



behaviours proposed by Westermann (1996; glossary of terms in Landman *et al.* 1996), as well as mainly depth-related sutural complexity, enables us to clarify some significant facts and to advance the following hypotheses: (i) The highest  $D_f$  mean values were found for streamlined shell shapes, interpreted as belonging to nektonic organisms with limited swimming capability against weak currents (*NK* in Fig. 2). We suggest that trimming rather than habitat depth could explain strengthening through complex septal folding (note that no demersals seem to have been able to colonize bottoms at similar depths as to display such a high sutural complexity). In the Upper Jurassic of southern Spain these shell shapes were more frequent in neritic seas than in epiocenic deposits. (ii) The lowest  $D_f$  mean values corresponded to poorly streamlined shell shapes, interpreted as planktic vagrants, circadian vertical migrants (*PK-VM* in Fig. 2). We interpret that comparatively low septal folding in these spherical phragmocones, which were intrinsically strong against hydrostatic pressure, could indicate vertical movements within a narrow depth range within the upper part of the water column. These shell shapes were frequent in ammonites inhabiting Late Jurassic neritic and epiocenic seas during fairly short to moderately long intervals in southern Spain. (iii) Assumed demersals (i.e. bottom-dependent ammonites; *DM* in Fig. 2) and planktic drifters (i.e. buoyancy controlled vertical vagrants; *PK-DF* in Fig. 2) show no significant differences in  $D_f$  mean values. We interpret these Ammonitina to have inhabited water depths roughly similar to those experienced by planktic vertical vagrants (*PK-VM* in Fig. 2), since they were frequent in both neritic and epiocenic waters, a large proportion of them being nearly exclusive in horizons with abundant megabenthos, indicating inner- to mid-shelf deposits.

Our results indicate that sutural complexity was more related to shell geometry and hydrodynamic properties in Late Jurassic phragmocones than to habitat depth and wide bathymetric ranges, the latter long time assumed to be key factors controlling ammonite ecology. Thus, these results suggest that depth did not exert a major direct influence on the development of complex sutures, since no correlation is evident between epiocenic ecospace and depth according to the complexity of suture lines of the ammonites investigated, as well as according to current interpretations of depositional depths for lithofacies containing ammonites in the Betic Cordillera. Such interpretation agrees with proven high morphologic variability in rather narrow and shallow habitats (Callomon 1985; Dagys & Weitschat 1993a) as well as with changing relationships between septal folding (frilling included) and shell typology, accord-

ing to evolutionary timing within and between major ammonoid groups (Korn 1992; Dagys & Weitschat 1993).

Assuming that multifunction constrains biological design, the observed relationship between sutural complexity and the S:V ratio could provide shell-wall strengthening, and buoyancy control. It also could favour improved swimming behaviour in streamlined, compressed phragmocones. This interpretation concurs with the recent hypothesis that envisages septal complexity as driven by the need for improving buoyancy control to escape predation (Daniels *et al.* 1997). In addition, such a relationship operates within a range of depths shallower than usually envisaged, and with no major differences for Ammonitina and the majority of Phylloceratina in neritic and oceanic-epiocenic waters, Lytoceratina being a special case that is poorly represented in neritic waters during the Late Jurassic in Western Tethys. This interpretation is also in agreement with the modified Buckland's model for an increase in septal complexity in compressed versus rounded shells (Westermann 1966), as well as with hydrostatic pressure effects proposed by Heptonstall (1970), body movements during swimming (Jacobs & Landman 1993) and body anchorage (e.g. for improving aggressive predation; Lewy 2002).

Recent models based on the physiology of respiration and the transportation of cameral liquid, palaeobiogeographic data analysed at separate levels of the taxonomic hierarchy, and interpretations based on morphometry all provide growing evidence against the interpretation of combined swimming capability (in terms of active, rapid and continuous displacements) and depths greater than neritic ones as key points for understanding the behaviour of ammonites as adapted to low-speed swimming.

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