Iterative evolution of Middle Jurassic ammonite faunas

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The phenomenon of iterative evolution of homeomorphs in identical temporal sequences is exhibited by Aalenian and Bajocian ammonite faunas in the south German depositional basin. Within each evolutionary cycle, inflated, evolute, and ornamented shells with complex suture lines are successively replaced with discoidal, involute, smooth shells with simpler sutures. Three distinct and identical cycles of morphological change occur, and involve ammonites belonging to four different familial/subfamilial groups: the Leioceratinae, Graphoceratinae, Hammatoceratidae, and Sonniniidae. Geometric and statistical analyses of morphological change within each of these higher taxa reveal remarkable iteration in both the pattern and proportion of change with time. The iterative morphological cycles were not driven by orthogenesis or anagenetic transformation within lineages, as has been previously suggested. A clear correlation exists between the successive ammonite faunas and repeated cyclical changes in the physical marine environment of the depositional basin. ☐ *Ammonoidea, Aalenian, Bajocian, south Germany, iterative evolution.*

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Iterative evolution of morphologic types – the phenomenon of heterochronous homeomorphy – is well known to ammonite workers (Arkell 1957; Kennedy & Cobban 1977). Repeated convergence upon certain ammonite forms has received considerable attention from biostratigraphers and systematists, as widespread homeomorphy poses serious problems of miscorrelation in stratigraphy and polyphyly in systematics.

A less well studied phenomenon, however, is that of 'iterative repetition of identical evolutionary courses' [iterative Wiederholung stets gleicher Entwicklungsabläufe, Schindewolf (1940)], or 'evolutionary cycles' (Haas 1942) in which morphologic types are repeated in identical temporal sequences. The existence of such 'evolutionary cycles' in ammonite morphology was often used by earlier workers as a strong argument for the process of orthogenesis.

The phenomenon of iterative repetition of temporal morphological changes can clearly be seen in the Middle Jurassic ammonite faunas of the south German depositional basin. The examination of this interesting phenomenon in a detailed environmental context is the object of the present paper.

Evolution of the basin

In this section we give the palaeogeographical and sedimentological information necessary for the interpretation of temporal changes in the fauna. Asymmetric sedimentary cycles have been known for a long time to form a basic structure of parts of the Middle European Jurassic (Klüpfel 1917). It is usually assumed that these cycles reflect changes of water depth. However, the cycles discussed here are much smaller in magnitude than those given in the global Jurassic eustatic curve of Hallam (1978). At the present time it seems that they are local, rather than global, in nature – thus changes in the fauna reflect local faunal responses to environmental fluctuations with the depositional basin.

Palaeogeographic framework

The depositional basin under study is located in the southwestern corner of Germany (Fig. 1). The distribution of the main facies units, and a series of representative stratigraphic columns, is given in Fig. 1. The strata of the central and southern parts of the study area consist mainly of claystones with interbedded muddy carbonates. The latter are commonly rich in ammonites. In

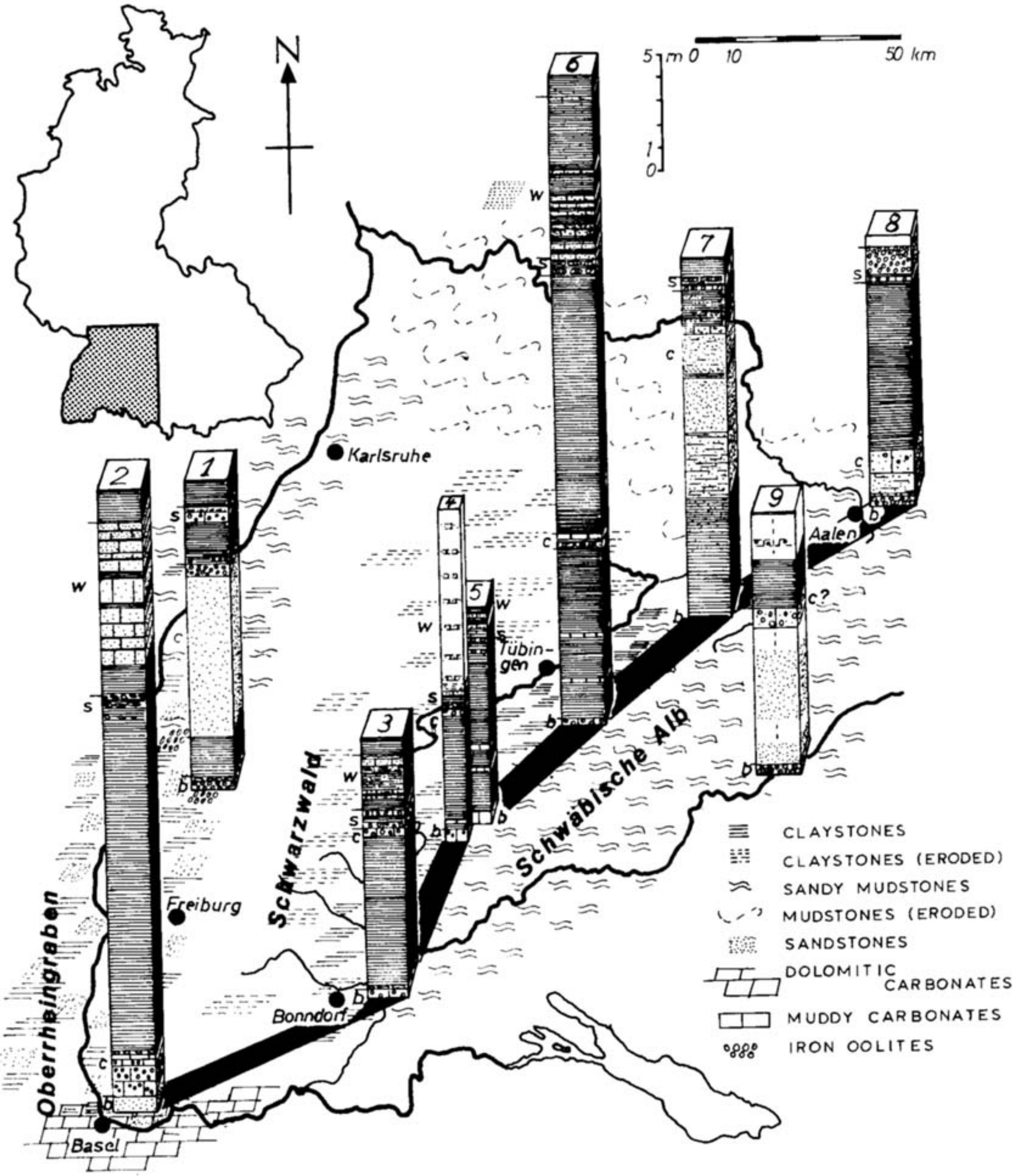


Fig. 1. Simplified geographic map of the study area in southern Germany. Generalized facies distributions within the upper Aalenian are indicated by the patterned regions. Finer details of lithofacies patterns in the region of the Aalenian–Bajocian boundary are illustrated in a series of stratigraphic profiles; see text for further discussion. The small letters adjacent to the profiles stand for local names of beds (except for 'b', *bradfordensis* subzone) which are a mixture of lithologic and biostratigraphic characterizations: c, *concava* bank or sandstone; s, *sowerbyi* bank; w, lower 'Wedelsandstein'. The heavy black line, from NE to SW along the Schwäbische Alb to the Oberrheingraben, outlines the line of the geologic cross section given in Fig. 2.

the eastern part of the study area – as is known both from outcrops and wells – sandstones dominate and they become increasingly abundant as one approaches the eastern margin of the basin. The coast line was approximately 200 km east of the study area and can be approximated by a line connecting Augsburg–München–Landshut–Straubing (Schröder 1962). The principal direction of currents within the basin was NW–SE, on the basis of cross-bedding and ripple marks (Rogowsky 1971; Werner 1959). To the north the basin was bounded by the Rheinische Schiefergebirge and the Ardennes. East of the Rheinische Schiefergebirge a sea-way connection to northern Germany was present, the so-called 'strait of Hessen'. A probable western boundary was the Vosges, which if not emergent at least formed a rise. There are also indications (largely the presence of stromatolites) for shallow water conditions in the southern Schwarzwald. From the analysis of sedimentary structures in the Oberrheingraben, Illies (1956) maintained that the Schwarzwald temporarily formed an island during the Middle Jurassic. There is little known about the boundary of the basin to the south below the northern front of the Alps. Classically it has been assumed that a landmass existed there (the 'Vindelizisches Land'). To the southwest it is likely that a connection to the Rhône Valley region existed. At the southwestern boundary a major facies change occurs, as south of the Schwarzwald the sediments are dominated by carbonates (Fig. 1).

Spatial and temporal pattern of facies

The overall pattern of facies distribution becomes more complicated when temporal relationships of strata are taken into account. The stratigraphic profiles given in Fig. 1 illustrate some of the spatial and temporal distributions of various lithologies. The time period represented spans from the *bradfordensis* subzone of the Aalenian to the *laeviscula* Zone (*stephani* subzone) of the Bajocian. The small letters adjacent to the profiles stand for local names of beds (except for 'b'; *bradfordensis* subzone), a mixed terminology based on lithologic and biostratigraphic characterizations: c; *concava* bank or sandstone, s; *sowerby* bank, w; lower 'Wedelsandstein'. These and additional local names are due to spatial and temporal replacements of facies units. Five main sediment types occur: sands, muddy sands and sandy muds, clays, oolites (iron oolites), and hardgrounds.

Correlation within the study area is complicated also by more than the complexities of spatial facies changes. Historically the basin was divided into three separate regions for stratigraphic and sedimentological studies. These regions were partly due to political boundaries which still existed in the area in the early 20th century. Occasionally these political boundaries corresponded with the three main facies areas of the basin: the sandstone facies in the northeast, the claystones in the southeast, and the area of the Oberrheingraben. These facies areas are enhanced by natural boundaries: the erosional gap formed by the Schwarzwald and its northern extension, and insufficient outcrops in the extreme clay facies near Tübingen (Fig. 1).

Weber (1967) was the first to notice the *overall* basinal pattern from his studies of the northeastern sandstone facies. Based on his bio- and lithostratigraphic study of the sandstone areas he found that the sandstones progressively extend to the south, into the deeper parts of the basin, from the *opalinum* Zone to the *concava* subzone (uppermost Aalenian). This offlapping feature of the sandstone horizons indicates a progressive shallowing of the basin during the study interval (Fig. 2). The regressive pattern continues into the lowermost Bajocian when sandstones in the northeastern area of the basin are replaced by a condensed pebble bed. A careful evaluation of the available stratigraphic data permits the recognition of the pattern of regression within the entire outcrop belt along the Schwäbische Alb (Fig. 2) and also to correlate this area with the westernmost outcrops in the Oberrheingraben (Bayer 1970). The profiles given in Fig. 2 were correlated by combining the two classical stratigraphical methods, those of biostratigraphy and lithostratigraphy, in a way such that the lithostratigraphic correlation was controlled by the biostratigraphic data.

The sand-bodies of the northeastern area and the condensed oolitic carbonates of the southwest merge towards the deeper areas of the basin into a series of muddy carbonates which are interbedded with clays. Within the larger sand-bodies a finer lithological subdivision is possible from the occurrence of iron oolites and hardgrounds which, under biostratigraphic control, can also be traced throughout the basin. The space–time pattern of facies reveals a series of sedimentological cycles which in the shallow wa-

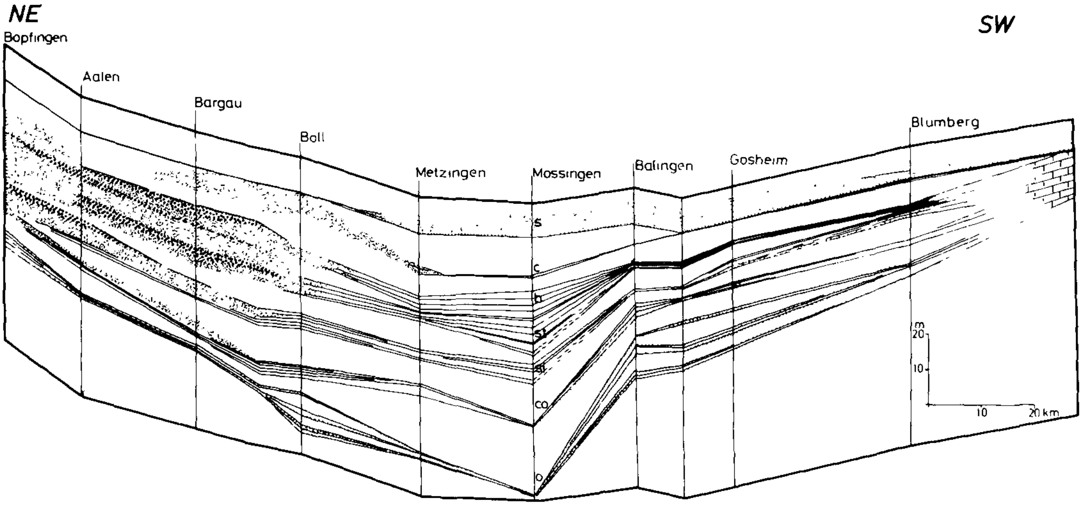


Fig. 2. Cross-section of upper Aalenian–lowermost Bajocian strata along the Schwäbische Alb (the eastern outcrop boundary of the study area, see Fig. 1). The stratigraphic and geographic distribution of major sand-bodies (stippled regions), muddy carbonate beds (black lines), and shale horizons (white regions) is given. See text for discussion.

ter areas show the repeated transition of clay–sandstone–oolite–hardground. In the deeper water areas the cycles are seen in a series of rhythms of clay–muddy carbonate in which the carbonate is mainly biogenetic. These fine cyclic structures are superimposed on the overall trend of regression within the basin.

The major sedimentary cycles

Sedimentary cycles which terminate in an erosional hardground, like those noticed above, have been observed in the Middle European Jurassic since the time of Klüpfel (1917) and have been attributed to sea level fluctuations by Aldinger (1965). In addition to these minor cycles and the overall regressive trend noted above, a larger cyclic pattern has been proposed by Urban (1966) and Bayer (1970) for the study interval. In the Oberrheingraben they found only three typical sequences of the clay–sand–oolite–erosion type which range in time as follows:

(1) from the *opalinum* Zone to the *bradfordensis (gigantea)* subzone

(2) from the *concava* subzone to the lower *discites* Zone

(3) from the *discites* Zone to the *ovalis (stephani)* subzone

The subzonal names in parentheses are assumed to correspond with the erosional phase. A correlation of the profile from the Oberrheingraben with the stratigraphic profiles of the northeastern and southwestern facies was given by Bayer (1970) and reveals that these major cycles are superimposed onto the small scale cyclic patterns previously discussed.

Throughout the entire basin the *staufensis* to *gigantea* subzone records a major state of regression. The erosional phase within the *gigantea* subzone can be traced as far as northwest of the Vosges, represented as the terminal event of iron oolite sedimentation in the Minette. It is also the reason why ammonites from the *gigantea* subzone and the lower *concava* subzone have not yet been described from southern Germany, as these strata are only preserved in a few places.

The secondmost major erosional event occurs in the *laeviscula* Zone (*stephani* subzone) at the top of the study interval. This last regression interval coincides with the maximum of the overall regression trend and led to the formation of widespread erosional hardgrounds especially in areas closest to the basin margin.

By summarizing all available data, the cyclic structure given in Fig. 3 is the most likely composite for the entire basin. The lower part of the profile – up to the *concava* subzone – is a standard profile for the northeastern Schwäbische

Alb. Because the lower Bajocian is strongly condensed in this area the upper part of the profile was added from the southwestern region. Nevertheless it is possible to separate the various subzones even in the condensed beds, as was shown by Parsons (1974) and Dietl & Haag (1980). The only Zone which is not yet known from the eastern Schwäbische Alb is the *discites* Zone.

The profile in Fig. 3 starts, like the study interval, at the highest part of the *opalinum* Zone and shows the progressive shallowing of the basin up to the *gigantea* subzone as well as the superimposed minor cycles. This regression led to the occurrence of new facies types – iron oolites and hardgrounds. During the regression the initial clay phase is reduced. A second regressive phase spans from the *concava* subzone to the lower *discites* Zone, beginning with muddy sandstones and terminating with iron-rich oolitic sands. A third regressive phase from the *discites* Zone to the *stephani* subzone repeats the pattern, but is terminated by a stronger erosional phase with oolitic limestones containing pebbles and reworked ammonite fragments. The overall pattern of regression is reflected by increasing condensation of the sediments.

Evolution of the ammonite fauna

Of particular interest in this section is the examination of evolutionary changes in the ammonite fauna which inhabited the basin during the span of time discussed in the previous section. Ammonites were here chosen for study as they are classically considered to have been, as nektic animals, among the least affected elements of the fauna during periods of physical change in the benthic marine environments.

The major ammonite taxa which inhabited the basin during the study interval are listed in Fig. 4. As only macroconchs were analyzed in the present study, microconch terminology is not included in Fig. 4. The southern German region was relatively species poor during the study interval, particularly in comparison with the ammonite fauna of the equivalent time period in southern England. The fauna of the Mediterranean region was also more diverse during this period, especially in members of the Hammatoceratidae. Fig. 4 lists all of the genera known in the study area, with the sole exception of *Lytoceras* (Lytocerataceae), which occurs in the lowest Aalenian *opalinum* Zone. We feel that Fig. 4 represents the best taxonomic compromise to date of the previous systematic studies of the fauna. Much of the fauna has been extensively

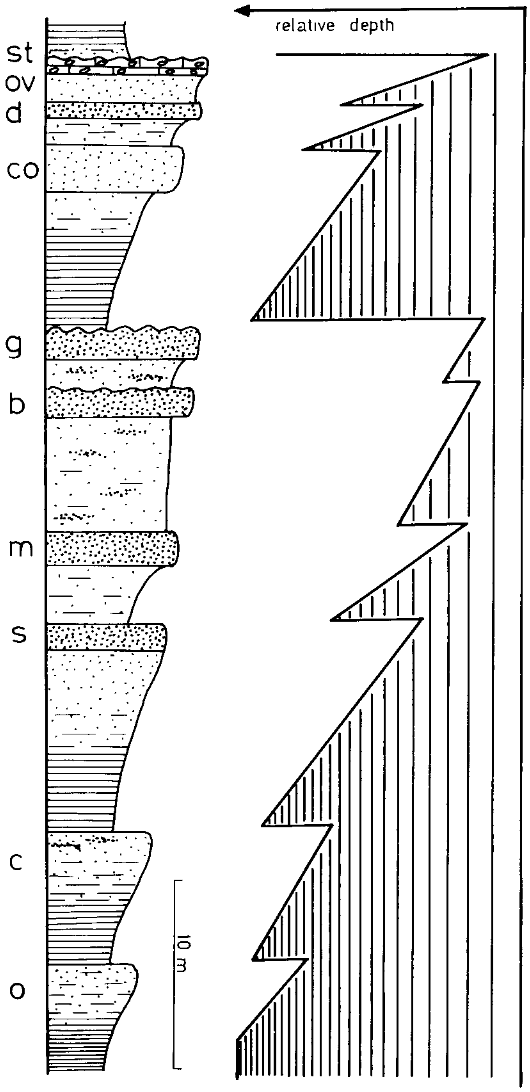


Fig. 3. Cyclic pattern of sedimentation during the study interval, modified and expanded from Bayer (1970). The generalized lithologic profile is here related to the relative water depth of the basin (constructed from the facies distributions of Fig. 2; see text for discussion). Additional facies types include iron oolites (dark stippled areas) and hardgrounds (wavy lines). Ammonite zonations are indicated by letters: o, *opalinum* Zone; c, *comptum* Zone; s, *sinon* Zone; m, *staufensis* subzone (*murchinsonae* sensu stricto); b, *bradfordensis* subzone; g, *gigantea* subzone; co, *comptum* s.s. subzone; d, *discites* Zone; ov, *ovalis* subzone; st, *stephani* subzone.

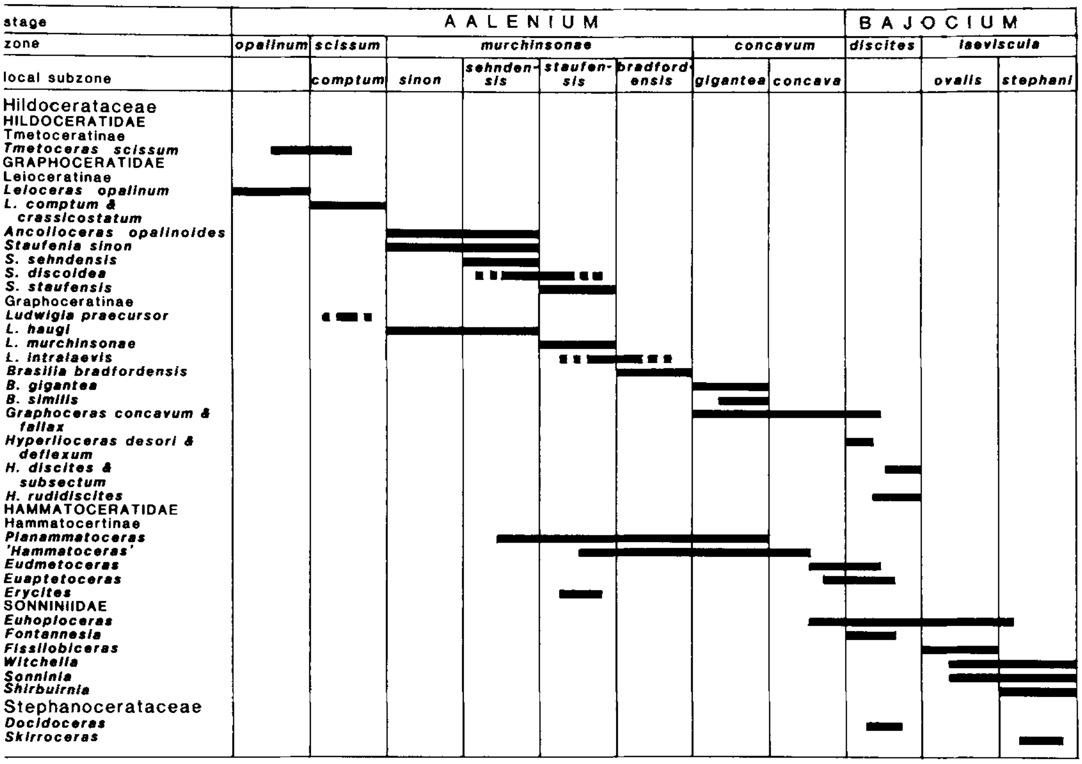


Fig. 4. The major ammonite taxa which inhabited the basin during the study interval, and their temporal distributions (macroconchs only). Stratigraphic ranges and taxonomy modified from the works of Dorn (1935), Oechsle (1958), Rieber (1963), Weber (1964), Spiegler (1966), Bayer (1968, 1969a, b), Contini (1969), and Dietl & Haag (1980).

oversplit at the species level – in many cases on the basis of stratigraphic horizon alone, rather than morphology.

Geometric analysis of ammonite morphology

Temporal patterns of change in the taxonomic composition of the ammonite fauna are outlined in Fig. 4. Of further interest, however, is the analysis of morphological change with time both within, and between, the various ammonite groups which inhabited the basin. In the analysis of morphological evolution it is useful to be able to consider the actual temporal patterns of change within a morphological continuum of theoretically possible shell forms. Using the logarithmic spiral model of shell form it is possible to construct such a geometric continuum of ammonite morphology, following the techniques of Raup & Michelson (1965) and Raup (1966, 1967).

In this study shell form will be characterized by the three geometric parameters W (the whorl expansion rate), D (the distance from the coiling axis to the generating curve), and S (the shape of the aperture). For a more detailed treatment and discussion of the geometric characterization of shell morphology and derivation of the parameters used herein the reader is referred to Raup (1966) and McGhee (1980). The three parameters can be calculated from traditional measures of ammonite form such as radial distance (r), whorl height (Wh), and whorl width (Wb) in the following fashion:

$$W = (r_\pi/r_0)^2;\ D = (r - Wh)/r;\ S = Wb/Wh$$

Other aspects of shell morphology, such as the extent and type of external sculpture and configuration of the suture lines, are more difficult to quantify in a continuum fashion and will be considered separately in a later section.

Measurements were taken from 507 speci-

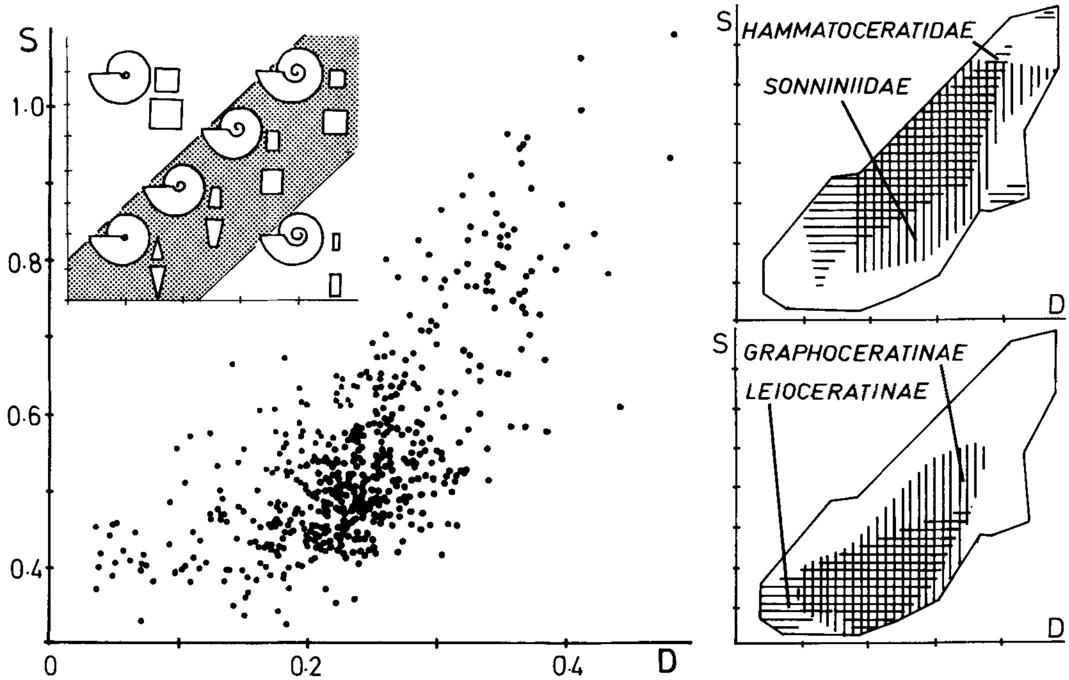


Fig. 5. Distribution of Aalenian–lower Bajocian ammonite shell geometries in the parameter space of *S* and *D*. The entire data set is given in the scatter diagram (N = 507); further subdivision by major taxonomic group is given in the two graphs on the right. For comparison, a simplified geometric continuum of shell forms (covering the data space) is given in the upper left hand corner.

mens, which were then used to calculate the parameters *W, D,* and *S*. In the present study, measurements were taken only from adult specimens or from specimens having a diameter greater than or equal to 5 cm. Thus ontogenetic changes in shell geometry have been here explicitly ignored, and only comparisons between adult shell morphologies will be discussed. In a subsequent work, however, the ontogenetic patterns of selected species members will be compared and discussed with relationship to the large scale morphologic patterns of the entire fauna described in the present study. For an interesting treatment of some developmental patterns seen within members of the Aalenian ammonite fauna which have been previously described in the literature the reader is referred to Rieber (1963).

Surprisingly, it was found that *W* varies very little among the various ammonite groups outlined in Fig. 4. For the entire data set values of *W* ranged from 1.5 to 3.0, with an average *W* value of 2.1. Morphologically, this means that the curvature of the shell is very similar among the various taxonomic groups, and that shell curvature did not change significantly during the span of the study interval. Further, it was found that variation in *W*, such that exists, is uncorrelated with either of the parameters *S* or *D*.

Variation in magnitude of *S* and *D* values is considerable, however, and is illustrated in Fig. 5 for the entire data set. For ease of visualization, a sketch of characteristic shell geometries at various parameter magnitudes is included in the upper left hand corner of Fig. 5. Although the ammonite groups do not differentiate themselves in terms of their respective whorl expansion rates, the major familial and subfamilial groups can be distinguished in terms of *S* and *D* (Fig. 5). As would be expected from the existence of the taxonomic divisions themselves, each familial/subfamilial group has its own characteristic distribution within the total morphological field, and the degree of overlap with other taxonomic groups can also be seen.

A clear temporal trend in the data can be seen in comparing the stratigraphic distributions of the familial/subfamilial groups in Fig. 4 and their morphological distributions in Fig. 5. The Leioceratinae have, on the average, lower values of *S* and *D* than the succeeding Graphoceratinae

Table 1. Regression statistics for the linear functions in S and D given in Figs. 6–8. See text for discussion.

Taxon	$S = mD + b$		$D = mS + b$		N	F
	m	b	m	b		
Graphoceratidae						
Leioceratinae	0.540	0.340	0.678	−0.108	184	104.9**
Phase Ia	1.045	0.249	0.402	0.036	113	80.3**
Phase Ib	0.300	0.390	1.140	−0.330	71	35.8**
Graphoceratinae	1.107	0.272	0.404	0.017	199	159.3**
Phase IIa	1.710	0.159	0.421	−0.002	113	286.0**
Phase IIb	0.462	0.382	0.612	−0.071	86	33.1**
Hammatoceratidae						
Hammatoceratinae (Phase IIc)	1.360	0.330	0.539	−0.120	31	79.7**
Sonniniidae (Phase III)	1.370	0.280	0.365	0.044	93	91.5**
All taxa	1.220	0.255	0.402	0.017	507	488.0**

** $P < 0.01$.

which, in turn, have lower S and D values than the still later Hammatoceratidae, and so on to the Sonniniidae. Thus during the span of the study interval there is an overall increase in the number of ammonites with wider whorl cross-sections, and with wider umbilici and more evolute shells.

In summary, the major familial/subfamilial groups can be recognized within a S–D morphospace. Further, an apparent gradual temporal trend from the lower S and D regions (narrow whorl cross-section, involute shells) of the morphospace to higher S and D regions (wider whorl cross-section, evolute shells) can be seen. This seemingly gradual trend is analyzed in greater detail in the following section.

Patterns of morphological evolution in the geometric space

Temporal patterns of morphological change *within* each of the four familial/subfamilial groups given in Fig. 5 are analyzed here, and will be discussed in relation to Figs. 6–8. Comparisons of morphological patterns of change *between* the taxonomic groups can be further facilitated by a series of regression analyses. Thus linear regression functions are also given in Figs. 6–8, and a list of relevant regression parameters is given in Table 1. As neither of the geometric parameters S and D can be clearly designated as dependent or independent of the other, two regression functions are given for each analysis (Table 1; Figs. 6–8).

A very similar pattern of overall morphological distribution, and temporal pattern of morphological change exists between the Leioceratinae and the Graphoceratinae. In both subfamilies there is a positive correlation between S and D (Table 1). Most significantly, however, is the fact that the observed trend in S and D reflects also a *temporal trend in morphological change within both subfamilies.* Within each subfamily the earlier species have shell geometries with higher magnitudes of S and D – and with time the magnitudes of each of these geometric parameters is successively reduced in the younger species.

In the Leioceratinae, the earlier species *Leioceras comptum* and *Leioceras crassicostatum* have shells with rounded to oval apertures (high S) and more evolute shell geometries (high D). With time, however, both S and D magnitudes are reduced in the species series from *Ancolioceras opalinoides* to *Staufenia sinon* to *Staufenia sehndensis* to *Staufenia staufensis*. The youngest species within the Leioceratinae, *Staufenia staufensis*, has a shell which is laterally compressed and triangular in whorl cross-section (low S magnitude). The shell is also involute, with a very

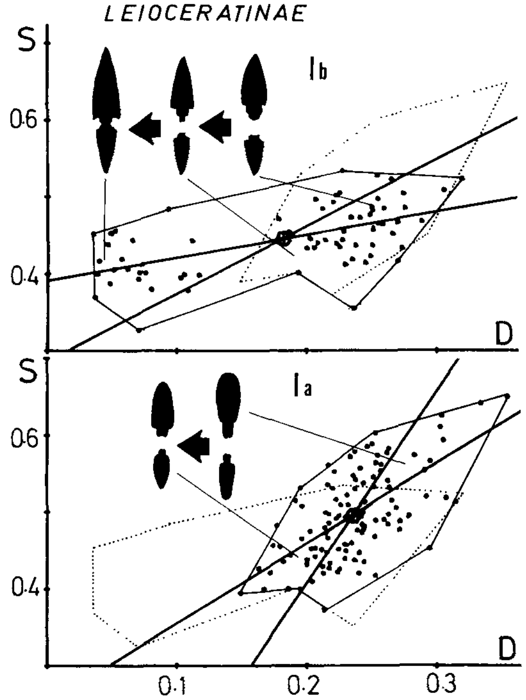


Fig. 6. Temporal patterns of morphological evolution within the Leioceratinae; phase Ia precedes (and partially overlaps) phase Ib in time. Ammonite cross-section identifications – For graph Ia, from right to left (older to younger species): *Leioceras comptum, Ancolioceras opalinoides.* For graph Ib, from right to left (older to younger species): *Staufenia sinon, Staufenia sehndensis, Staufenia staufensis.*

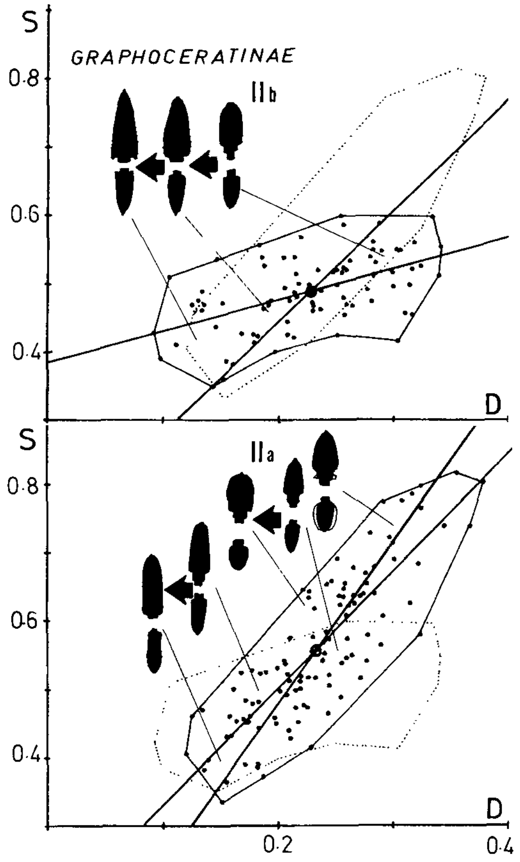


Fig. 7. Temporal patterns of morphological evolution within the Graphoceratinae; phase IIa precedes and overlaps phase IIb in time. Ammonite cross-section identifications – For graph IIa, from right to left (older to younger species): *Ludwigia haugi, Ludwigia obtusiformis, Ludwigia murchinsonae, Ludwigia intralaevis, Graphoceras concavum.* For graph IIb, from right to left: *Brasilia bradfordensis, Brasilia similis, Hyperlioceras discites.*

narrow umbilicus (low D magnitude). This trend in morphology with time is graphically illustrated by a series of cross-sections in Fig. 6.

The Graphoceratinae overlap in time the later species members of the Leioceratinae (Fig. 4). However, the same temporal morphological pattern is seen within this subfamily: *Ludwigia haugi, Ludwigia murchinsonae,* and other older species have evolute shells with inflated whorl cross-sections (cf. Fig. 4 and Fig. 7). Younger species, such as *Graphoceras concavum* and *Hyperlioceras discites,* have more involute shells and compressed whorl shapes. A series of ammonite cross-sections is again given in Fig. 7 for visual comparison.

Finer patterns of morphological change can also be discerned within the overall temporal trend from higher S and D magnitudes to lower. Each subfamily has a morphological distribution which can further be subdivided into two regions: a region of high regression slopes in S (designated as Ia for the Leioceratinae in Fig. 6 and IIa for the Graphoceratinae in Fig. 7), and a region of relatively lower regression slopes (designated as Ib for the Leioceratinae and IIb for the Graphoceratinae). In both groups the high slope region, or an earlier 'a-phase', occurs in the higher S and D region of the overall morphological region. The opposite is the case in both groups for the low slope region, or the later 'b-phase'. Thus, for both subfamilies, there is a greater rate of change in S (the shape of the aperture) in high D regions of the morphospace (the region of more evolute shell morphologies), and greater rate of change in D (the distance

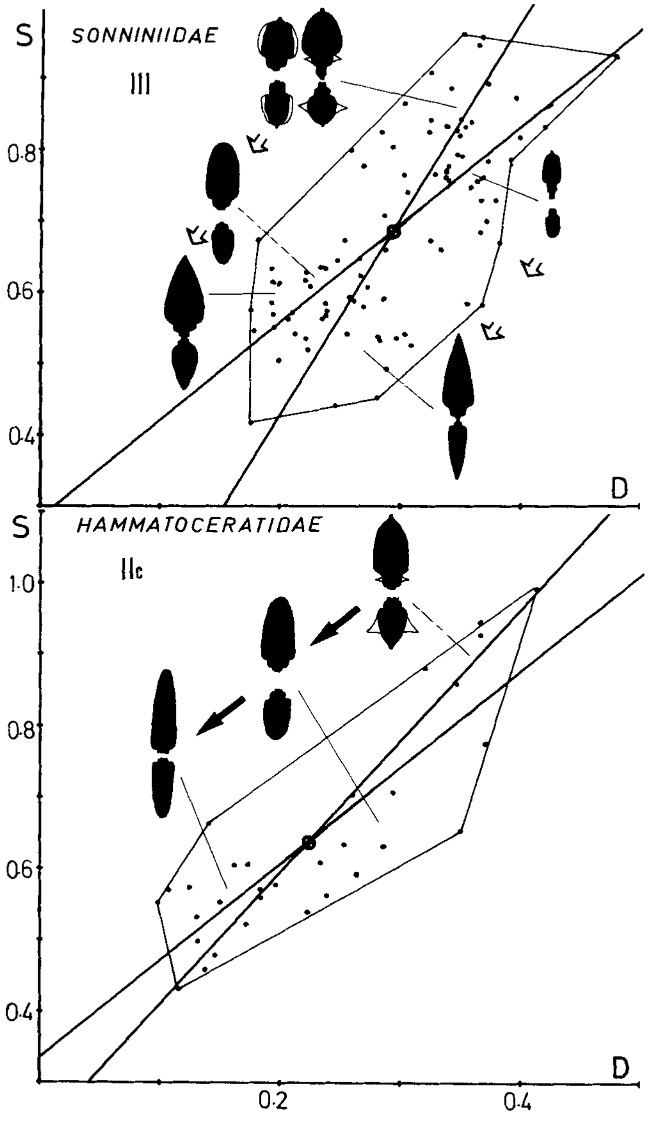


Fig. 8. Temporal patterns of morphological change within the Hammatoceratidae (graph IIc) and the Sonniniidae (graph III). Hammatoceratid cross-section identifications, from right to left (older to younger species): *Hammatoceras, Eudmetoceras, Euaptetoceras.* Sonniniid cross-sections, from right to left, lower row: *Fontannesia, Witchellia.* Upper row: *Euhoploceras, Fissilobiceras, Shirbuirnia.*

from the generating curve to the coiling axis) in the low S region of the morphospace (the region where shells have more compressed whorl cross-sections). This pattern exists for both groups even though the Graphoceratinae, which overlap and follow the Leioceratinae in time (Fig. 4), have average S and D values which are higher than those of the Leioceratinae (Fig. 5).

The similarity in pattern between the two subfamilies can also be seen in comparing the regression parameters given in Table 1. Although the two subfamilies occupy somewhat different regions of the morphospace, and thus have different average S and D values, the *slope* in S of the initial 'a-phase' and subsequent 'b-phase' is very similar for both groups (Ia = 1.045, IIa = 1.710; Ib = 0.300, IIb = 0.462).

The Hammatoceratidae appear in the study area somewhat later than the Graphoceratinae, though otherwise the family is largely contemporaneous with the Graphoceratinae. The Hammatoceratidae have, however, average S and D values which are higher than those of the Graphoceratinae (Fig. 5) – as was also the case between the Graphoceratinae and the older Leioceratinae. Within the Hammatoceratidae an identical morphological trend in *S* and *D* magnitudes between earlier and later species exists as for the overall trend among the Leioceratinae and Graphoceratinae (Fig. 8). However, insufficient data are present to recognize finer scale patterns or phases within the Hammatoceratidae. As the family is largely contemporaneous with the Graphoceratinae, it is here designated as a morphological 'phase IIc' for convenience in later discussions of the evolution of the entire ammonite fauna.

The last major familial group to appear in the basin during the study interval is the Sonniniidae (Fig. 4). The Sonniniidae also have yet higher *S* and *D* values than the Hammatoceratidae (cf. regression midpoints in Fig. 8), as has been previously seen between the Hammatoceratidae and Graphoceratinae, and the Graphoceratinae and Leioceratinae. Within the family, the temporal pattern of morphological change is also identical to those seen previously for other familial/subfamilial groups. The early sonniniids *Euhoploceras* and *Fontannesia* have evolute shells with inflated whorl cross-sections; later sonniniids such as *Shirbuirnia* and *Witchellia* have compressed, more involute shells with narrow umbilici (Fig. 8). In both the Sonniniidae and the Hammatoceratidae the rate of change of *S* relative to *D* is steep, and is more comparable to the 'a-phase' regression slopes for the Graphoceratinae and Leioceratinae (Table 1). As the Sonniniidae are the last major ammonite fauna to appear in the basin during the study interval, they are designated here for convenience as 'phase III' in Table 1. Condensation of the sediments does not allow a finer division at this time.

Summary of the quantified shell form parameters

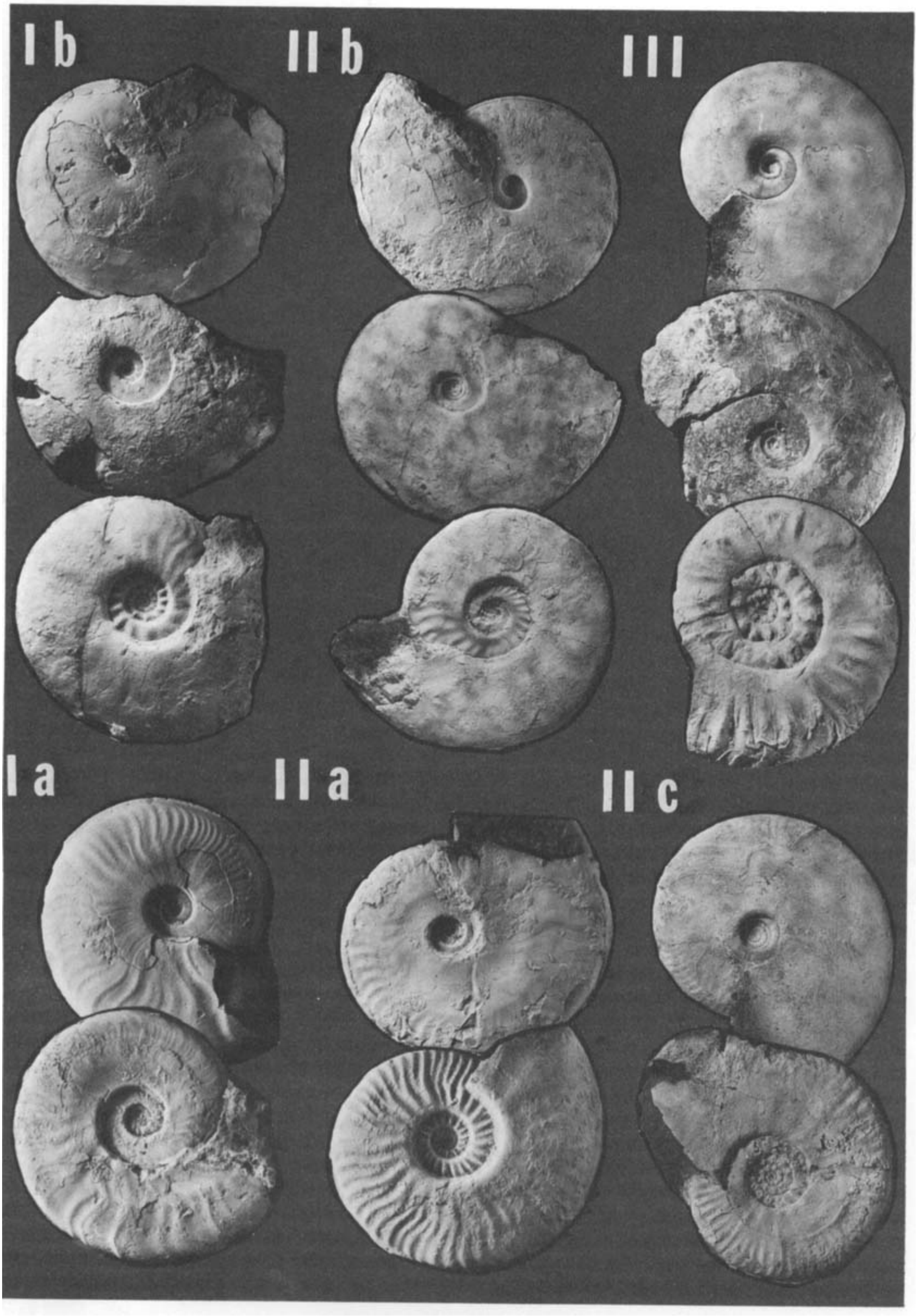
In summary, two distinctly different phenomenological levels of morphological evolution are observed in the ammonite faunas of the study area during the span of the Aalenian and lowermost Bajocian. At the level of the total fauna, there is a temporal trend within the geometric continuum towards higher *S* and *D* values – or the appearance through time of more shell morphologies of an evolute form with inflated whorl shapes (Fig. 4). However, while the appearance of each successively younger familial/subfamilial ammonite group appears to demonstrate a large scale evolutionary trend towards high *S* and *D* values over geologic time, *within* each familial/subfamilial group the direction of morphological change on a finer scale is exactly opposite. New forms repetitively appear with evolute, inflated shell forms, and then successively give way to compressed, involute shell forms (Figs. 6–8).

At the familial/subfamilial level, the trend towards lower *S* and *D* values over time – or the movement of characteristic shell forms from the upper right regions to lower left regions of each of the geometric plots given in Figs. 6–8 – occurs in a remarkably repetitive sequence. In three separate instances ammonites with evolute shells and rounded apertures appear within the study area: first within the Leioceratinae, then the Graphoceratinae and also the Hammatoceratidae, and lastly the Sonniniidae. In three separate occasions each group exhibits a remarkable convergence upon shell forms which are largely involute, with narrow umbilici, and with narrow apertures and highly compressed whorl shapes (cf. the cross-sections of *Staufenia staufensis, Hyperlioceras discites,* and *Witchellia* in Figs. 6, 7, and 8). Within these groups *the proportional changes in shell form* of the geometric parameters *S* and *D* are also very similar, as discussed previously in regard to the slope parameters (Table 1) of the regression functions given in Figs. 6–8.

In the present section the morphological evolution of the ammonite faunas has been considered within a geometric space utilizing quantified shell form parameters. Other, less easily quantified, aspects of shell form will be considered in the following section.

Other morphological patterns

It has been long recognized by ammonite workers that a correlation exists between degree of shell ornamentation and shell geometry. The correlation was particularly well described by Buckman (1892:313): 'Roughly speaking, inclusion of the whorls correlate with the amount of ornament – the most ornate species being the most evolute, and having almost circular whorls.' This relationship between shell form and ornamentation was named 'Buckman's Law of Covariation' by Westermann (1966), who clearly demonstrated the existence of such a correlation in the Bajocian sonniniids of Dorset, England. Similar patterns of geometry–ornament covariation have been reported for a number of other different and unrelated ammonoid stocks, as discussed by Westermann (1966:305–307). In addition, the


I b
II b
III
I a
II a
II c

same correlation was noted by Raup (1967:50–51) for all ammonoids in explicitly geometric terms. Spinose and tuberculated ammonoids were found to consistently have higher S and D values than forms which lack spines and tubercules (Raup 1967). The functional significance of such a geometry–ornament correlation remains unclear, however (see Westermann 1966:306–307; Raup 1967:51).

In the previous section it has been demonstrated that in three separate occurrences ammonites first appear in the study area with shells having higher S and D values, and that these parameters subsequently decrease in magnitude within each cycle. Given the observations of the workers discussed above, one could further predict that if 'Buckman's Law of Covariation' holds on a fine time scale, then *the degree of shell ornamentation should also decrease within each cycle.*

Such a prediction is in fact verified, and is illustrated in Fig. 9. Given in Fig. 9 are a series of photographs of ammonite shells from species present in each of the cycles or phases illustrated in Figs. 6–8. Each pair or triplet of shells is labelled in the same notation given in Figs. 6–8; in all cases the lower shells are from older species and upper shells from younger (cf. Fig. 9 and Fig. 4). Within each group the older shells are more strongly ornamented than the younger – and it can also be clearly seen that the older shells have wider umbilici (higher D values) than the shells which follow in time. In addition to becoming more involute with time, shells also become more compressed (lower S values; previously discussed in relation to Figs. 6–8). Thus the simultaneous decrease in degree of ornamentation with decreasing magnitudes of D and S is not clearly a function of either parameter alone.

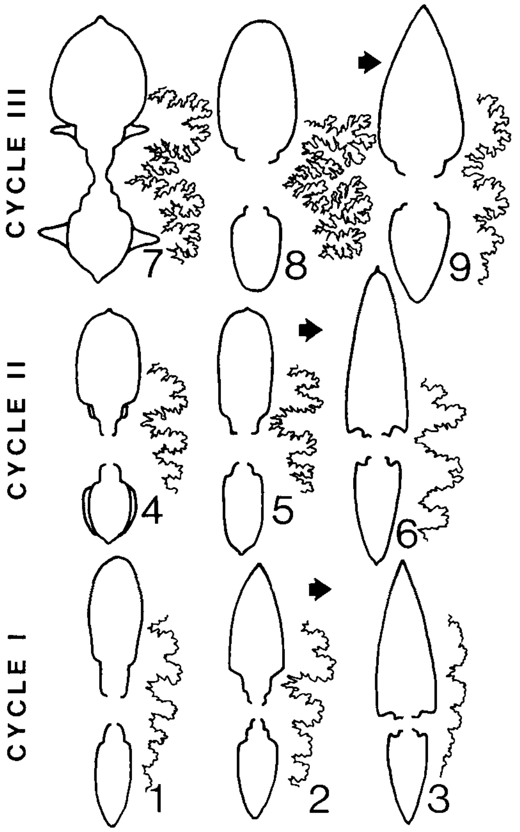


Fig. 10. Relationship between complexity of the suture, whorl cross-section, and width of the umbilicus. In each temporal cycle, the trend towards shells with narrow umbilici and compressed whorl shapes is accompanied by a reduction in the complexity of the suture line from left to right – older to younger species within each cycle. Ammonite identifications (from left to right in each cycle) – Cycle I: 1, *Leioceras comptum;* 2, *Staufenia sinon;* 3, *Staufenia staufensis.* Cycle II: 4, *Ludwigia haugi;* 5, *Brasilia bradfordensis;* 6, *Hyperlioceras discites.* Cycle III: 7, *Euhoploceras;* 8, *Fissilobiceras;* 9, *Shirbuirnia.*

A second important aspect of ammonite shell form which is not easily quantified is the pattern of the suture. However, here also a clear pattern of temporal change can be discerned: *within each cycle the complexity of the suture line decreases.* This phenomenon is illustrated in Fig. 10 with a series of representative species from each cycle. In each fauna the trace of the suture becomes less complex in the trend from globose evolute shells to compressed involute forms.

The cause of this temporal trend in sutural complexity is unclear, and we wish to note it here simply as an empirical observation. Also, the

Fig. 9. Covariation in the degree of external shell ornamentation and the width of the umbilicus. Within each cycle (Ia, Ib, etc.), shells with stronger ornamentation (ribs, tubercles, spines) are replaced in time by shells with either finer ornamentation or totally smooth exteriors. Likewise, shells with wide umbilici (high D) are replaced by forms with narrow umbilici (low D) with time. For each cycle older species are placed below younger ones in the Figure. Species identifications (from bottom to top) – Cycle Ia: *Leioceras comptum, Ancolioceras opalinoides.* Cycle Ib: *Staufenia sinon, Staufenia sehndensis, Staufenia staufensis.* Cycle IIa: *Ludwigia haugi, Graphoceras concavum.* Cycle IIb: *Brasilia bradfordensis, Brasilia similis, Hyperlioceras deflexum.* Cycle IIc: *Hammatoceras* sp., *Euaptetoceras* sp. Cycle III: *Euhoploceras* sp., *Fissilobiceras ovalis, Shirbuirnia stephani.* Figures not to scale.

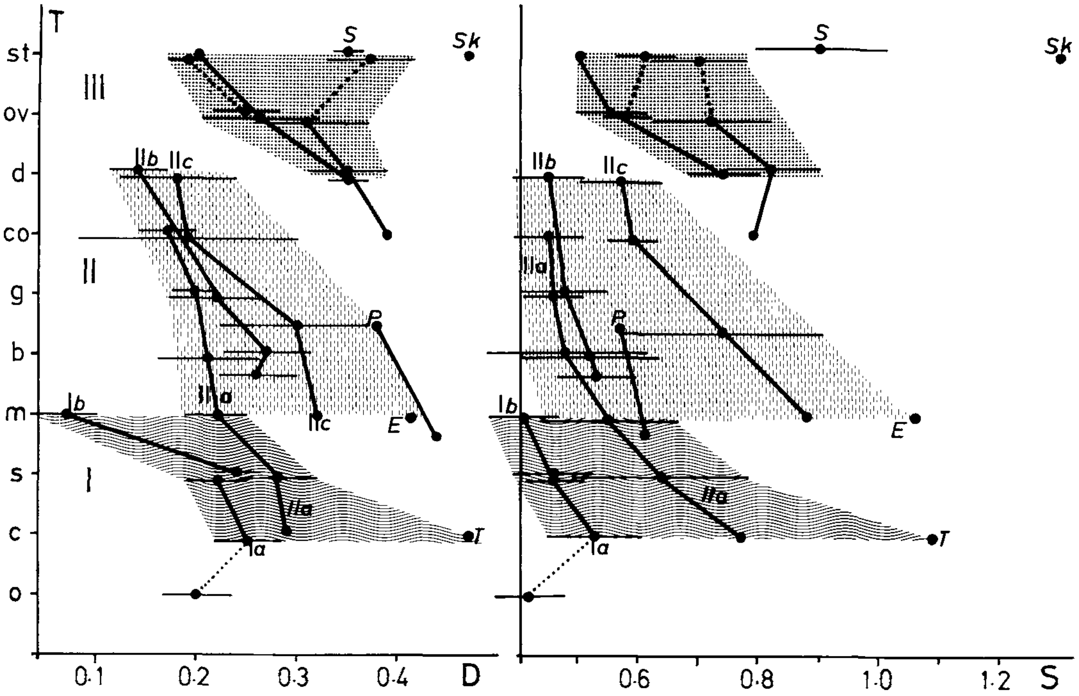


Fig. 11. Temporal trends in mean *D* and *S* values for south German ammonites during the duration of the study interval. Means (black dots) and standard deviations (horizontal lines) in *D* and *S* for the ammonite fauna of each zone or local subzone are here plotted. Each cycle is indicated by a different shading tone, and labelled following the format of Figs. 6, 7 & 8. Sporadic introductions of rare forms (usually at the initiation of a new cycle) are indicated by the capital letters: T, *Tmetoceras;* E, *Erycites;* P, *Planammatoceras;* S, *Sonninia;* Sk, *Skirroceras.* Abbreviations for zones and subzones as in Fig. 3.

relationship between shell form and sutural complexity observed in this study cannot be generalized to apply to other ammonite faunas. Arkell (1957:L119) has described a similar relationship: 'it is . . . the oxycones which most commonly display simplified, regressive, even pseudoceratitic types of suture . . .'. Bayer (1977a) has also previously noted that suture lines in many ammonites become simpler with a reduction in umbilical width and compression of the whorl cross-section. However, the exact reverse relationship – increased sutural complexity in discoidal involute shells relative to tumid evolute shells – has been described by Buckman (1892), Haas (1942), and Westermann (1966). In particular, Haas (1942) describes temporal *increases* in sutural complexity in his study of evolutionary cycles in Mesozoic ammonites, even though many of his other morphological observations are in agreement with those we have described in the present study.

Discussion and summary

A clear correlation exists between the three transgressive–regressive environmental cycles and the three successive ammonite faunas which occur in the south German depositional basin during the Aalenian and Bajocian. Several aspects of these environmental and faunal cycles are summarized in Fig. 11.

Three repetitions of the marine regressive clay–sand–oolite–hardground stratigraphic sequence occur in the study area. These span the time from the *opalinum* Zone to the *gigantea* subzone, the *concava* subzone to the lower *discites* Zone, and the *discites* Zone to the *stephani* subzone. Superimposed on these cycles is a larger overall pattern of regression within the basin, which is reflected in the increasing condensation of the sediments from cycle to cycle.

Three cycles of morphological change also can be seen in the south German ammonite fauna.

Furthermore, *the exact same pattern of morphological change iteratively occurs within each fauna.* Inflated, evolute, and ornamented shells with complex suture lines are replaced with discoidal, involute, smooth shells with simpler suture lines within each cycle. Superimposed on these cycles is an increase in mean D and S values from cycle to cycle (Fig. 11, see also Fig. 5) – thus each faunal cycle begins with more inflated and evolute shells than the former.

Interestingly, the new ammonite species which initiate each cycle are introduced into the basin during times of low water stand. Thus cycle I begins during a brief period of basin shallowing during the *comptum* Zone, cycle II fauna is introduced during the major shallowing interval of the *bradfordensis–gigantea* subzones, and the cycle III fauna invades during the period of low water stand during the *discites* Zone (Fig. 11).

The phenomenon of iterative evolution in ammonites is well known (Arkell 1957; Kennedy & Cobban 1977). However, most discussions of the phenomenon in the literature concern the problems which heterochronous homeomorphy pose for the biostratigrapher and taxonomist. Clearly, widespread homeomorphy in ammonites presents the danger of major errors in correlation to the stratigrapher and the problem of polyphyletic taxa to the systematist. Few studies have attempted to examine the phenomenon of 'evolutionary cycles' of homeomorphy (Haas 1942), however, though several workers have realized that many homeomorphic ammonites occur in definite temporal sequences and that *these morphological sequences are themselves iteratively repeated* in groups separated both in time and taxonomic affinity (Brinkmann 1929; Schindewolf 1940, 1950; Zoch 1940; Haas 1942).

The possible causal mechanisms behind such 'evolutionary cycles' are obviously of considerable interest, and most theories suggested by previous workers are strongly orthogenetic in nature. Zoch (1940) proposed a principle of 'repetition in the trends of the formative force' (Wiederholung der Gestaltungsmotive). Haas (1942:647) suggested transformation within a lineage: '... these evolutionary changes appear to proceed, quite gradually, along the same lines of definite anagenetic trends ...' Schindewolf (1950) used the occurrence of such 'iterative repetition of identical evolutionary courses' to argue forcefully for orthogenesis and against natural selection: 'There is therefore a progressive development of form which is not directly subject to selection and must be of some other method than that of adaptation directed by selection' (Schindewolf 1950:387; translation ours).

Possible relationships between morphological changes and environmental changes were not extensively examined, however, particularly on a fine temporal and geographic scale. Only Brinkmann (1929), in his monumental work on ammonite evolution, points out a relationship between changes in the ammonite fauna and major sedimentary cycles, though he later concludes: 'Whether the causes of these evolutionary changes, which frequently run in parallel in different lineages ... are determined by external or internal factors cannot be decided with certainty, though much speaks for the latter' (Brinkmann 1929:244; translation ours).

Conclusions

The phenomenon of 'iterative repetition of identical evolutionary courses' can clearly be seen in the ammonite faunas of south Germany during the Aalenian and Bajocian. We have argued in the present paper, however, that these iterative changes were also clearly in response to cyclical changes in the physical marine environment: similar environments were inhabited by ammonite faunas of similar morphology, and moreover, *similar directional changes in the physical environment are mirrored by similar morphological changes in the ammonite faunas.* We do not wish to extrapolate the environment–morphology correlation seen in the present study to areas outside the south German depositional basin [as, for example, was attempted by Scott (1940) for Texas ammonites – for a critique see Reyment (1955) and Arkell (1957)]; of more interest to us is the phenomenon of iterative change in the ammonite faunas within the basin.

In conclusion, iterative morphological changes in the ammonite faunas of the study area were in response to repeated cyclical changes in the marine environment. They were not driven by orthogenesis or anagenetic transformations within a lineage. Both endemic forms which clearly evolved *in situ* (within the Leioceratinae, genus *Staufenia*) and migrant forms from the Tethyan Realm (the hammatoceratids and sonniniids) were equally affected.

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