

Chapter 6

Evolution of the Upper Cretaceous Oysters: Traditional Morphometrics Approach

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Idea and Aims

The faunal association, which is revealed by newly discovered, well preserved, and therefore highly diverse assemblages, enabled us to recognize some phylogenetic trends in the Upper Cretaceous oysters. In the present study, the oyster faunal collection from El-Sheik Fadl-Ras Gharib stretch, Eastern Desert, Egypt, identifies some of the processes by which distinct species may have transformed into another as a result of the change in the environmental conditions. The applied qualitative and quantitative techniques exhibited considerable stability in assigning the relationships among taxa.

Introduction

The origin of oysters is a much debated palaeontological issue. The knowledge of their total ranges and of evolutionary relationships still fragmentary; despite the Late Cretaceous oyster data have become available. The origin and taxonomic status of oysters (*Ostreidae* Rafinesque 1815) and oyster-like cementing bivalves, namely *Plicatulidae* and *Dimyidae*, have traditionally been controversial. Most hypotheses of relationship between the three families (and corresponding superfamilies) have relied on soft and hard part synapomorphies shared by recent taxa. Waller (1978) placed *Dimyoidea*, *Plicatuloidea*, and *Ostreoidea* in his suborder *Ostreina* (= *Ostreoida*). Alternatively, Yonge (1978, 1980) believed that the *Dimyidae* was not related to the *Ostreidae* or *Pectinidae*, but that they were likely ancestors of the *Plicatulidae*. Hautmann (2001) rejected Waller's hypothesis of relationships for the following three reasons:

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- (1) Ostreidae attach themselves to the substrate by their left valve, while Plicatulidae and Dimyidae are dextrally attached,
- (2) The inner shell layer of early oysters was probably nacreous, but crossed lamellar in Dimyidae and Plicatulidae, and
- (3) Secondary hinge teeth and secondary hinge ligament are absent in Ostreidae.

The opening of seaways by sea-floor spreading in the Atlantic led to a major global transgression in the Mid-Cretaceous. This is supposed to be the main reason for the generally observed, increasingly cosmopolitan character of bivalve faunas at the very end of the Early Cretaceous. Rising sea level eliminated geographical barriers, although it has been shown that sea-level rise probably also led to provincialism at that time. Taking into account the observations of earlier studies on oysters concerning constraints on the use of fossil data in palaeobiogeographical analyses, the invertebrate benthic fauna, occasionally oysters, are particularly useful because:

1. They seem to constitute a monophyletic group, and the taxa can be identified with high degree of precision; they are abundant in samples from facies favorable for their preservation;
2. They have a relatively complete fossil record and their environmental requirements are well known;
3. The stratigraphical framework of the sections containing sediments rich in oysters is well known, making it possible to construct a sequence of palaeobiogeographical charts for the Cretaceous;
4. The ages of the taxa and the available palaeogeographical reconstructions are closely linked.

Consequently, phylogeny is essential for reconstructing the taxonomic, environmental and biogeographical patterns of this group, and to understanding the causal processes responsible for them. Several authors dealt with the Upper Cretaceous oysters and their taxonomy, ecology and biogeography (i.e. Mancini 1978; Aqrabawi 1993; Malchus 1996; Seeling and Bengston 1999; Dhondt 1999, Dhondt and Jaillard 2005). Even though, the evolution of the Upper Cretaceous *Exogyrinae* oysters received little attention.

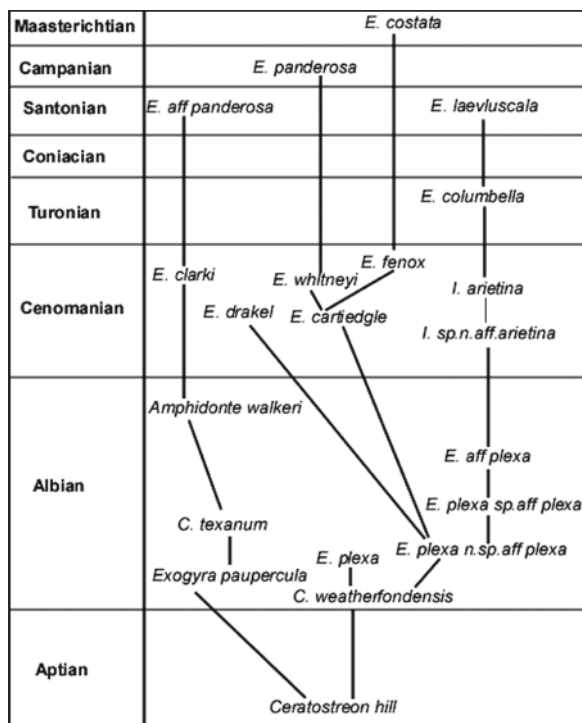
In the current study, we have two major goals:

1. To examine the morphological characters of the oyster group in order to evaluate the old phylogenetic schemes,
2. To assess the migration routes and other biogeographic relations between the different biotic provinces.

Previous Phylogenetic Schemes

The phylogeny of Upper Cretaceous oysters is firstly examined by Böse (1919). He thought that populations of *Exogyra plexa* and *Ilymatogyra arietina*, which are occurring at different stratigraphical levels, were sufficiently distinguishable; leading to the result of regarding some of them as new species (Fig. 6.1). Recently,

Fig. 6.1 Modified phylogeny tree of Texas exogyrid oysters proposed by Böse (1919), Genera are updated according to Moore (1969)



Malchus (1990) proposed a phylogeny, based on morphological and microstructure, showing that *E. plexa* lineage branches from the *Ceratostreon* lineage, and then giving rise to a major radiation of exogyrid oysters. Moreover Malchus noted that there are intermediate forms occurring between *E. plexa* and *I. arietina* from the strata of North America and North Africa (Fig. 6.2). Yurke and Charles (2006) made reference collections of populations of *E. plexa* and *I. arietina* from different stratigraphical levels similar to those examined by Böse (1919). They extended the genus *Ilymatogyra* to include *E. plexa* and *E. cartledgei* (Fig. 6.3), but they could not identify the ancestor of *Ceratostreon texanum* or *Exogyra plexa*.

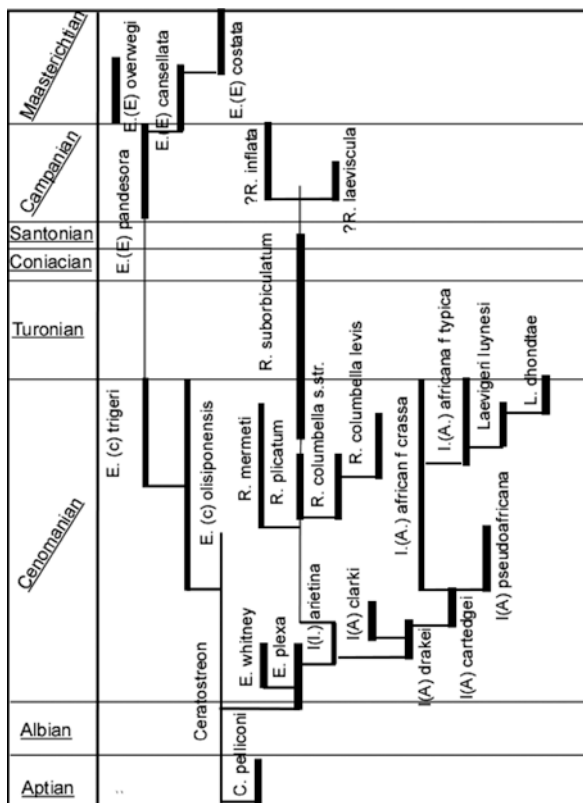
From the above mentioned studies, we conclude that:

- (1) There were misidentifications for most of the Exogyrinae oysters,
- (2) Some taxa exhibit dimorphism or even polymorphism,
- (3) The great abundances occur within the Cenomanian genera, while Turonian/Coniacian genera have the minimum diversity indexes.

Material and Methods

Six Stratigraphical sections are chosen from the study area according to their richness on macrofauna especially oysters. These sections extend from the SE to NW along the El-Sheik Fadl-Ras Gharib stretch, Eastern Desert, Egypt. They were

Fig. 6.2 A phylogeny of exogyrid oysters; proposed by Malchus (1990). The range of each oyster species is indicated by a *thick vertical black bar*



measured in the field as a bed by bed using handy lens, and their lithologies, sedimentary patterns and fossil occurrences were described (Fig. 6.4). Lithological and biostratigraphical data from these sections are herein presented. A total of 21 species were identified in the present study. The typical representatives of the whole assemblage are deposited at the Geological Museum of the Geology Department, Faculty of Science, Minia University, Egypt (ABO1: ABO21).

The study is based on a combination of fossil species identified from the field collections (Fig. 6.4), and from literatures. Fauna prepared, photographed, and a special emphasis is given to the morphological data for analytical methods concerning evolution.

Previous examinations of shell morphologies of taxa revealed unsuspected morphological differences, among *Exogyra*, *Ceratostreon*, *Rhynchostreon* and *Hymatogyra*; as all taxa have a wide range of shell pattern variation. Specimens were randomly selected from each location, and the shells photographed with a Sony DH9 digital camera (12 Mega pixel, 15X) or scanned with an HP 4870 Pro flatbed scanner. Only left valves were used in the analyses because of the inequivalve hinge morphology between left and right valves.

Fig. 6.3 Recent phylogeny of exogyrid oysters; proposed by Yurke and Charles (2006)

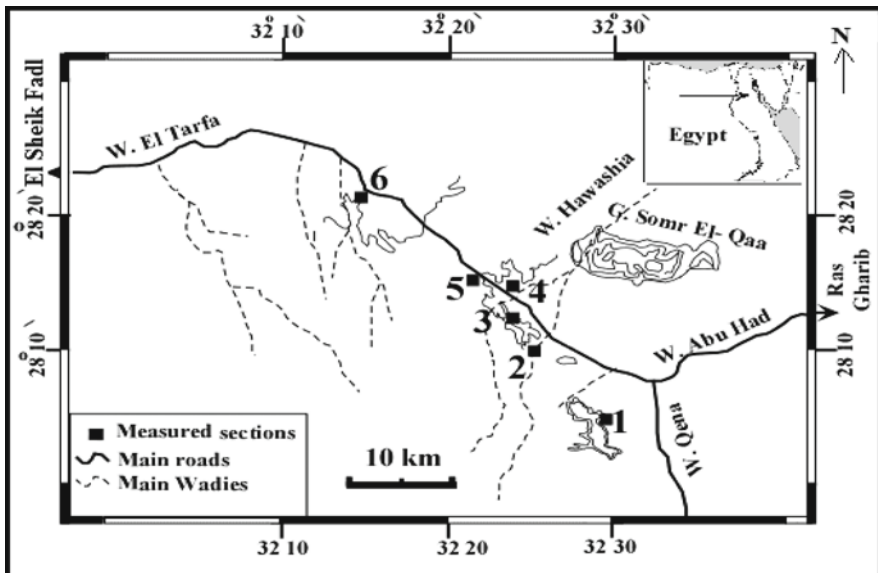
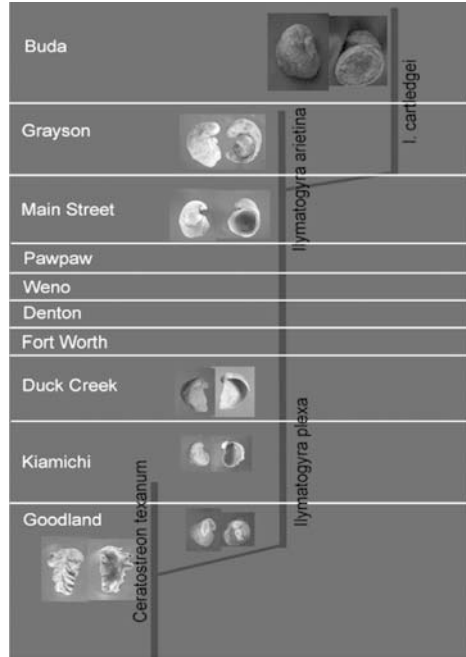
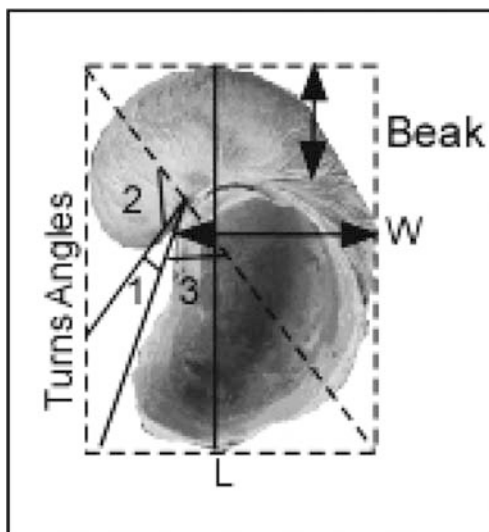


Fig. 6.4 Location map of the studied sections

Fig. 6.5 Internal view of left valve, showing measurements carried on the oyster shells



In order to explore the morphological affinities of Exogyrinae, we examined the distribution of qualitative morphological characters for 10 species from 4 genera of Exogyrinae oysters. Following preliminary analyses, the data comprise 9 qualitative characters (4 dimensions, 3 angles and 2 ratios) (Fig. 6.5). These variables are chosen in order to minimize the morphological proxies, for individual section a number of shell photographed, scanned then coordinates and angles were digitally captured from specimen images using the software TPSdig of Rohlf (1998). The obtained measures were analyzed using the PAST program, version 1.72, where we applied all the required quantitative techniques (for details see Oyvind et al. 2001).

Qualitative Observations

Important Criteria

The shortcomings of deriving phylogeny from the first and last appearances of taxa and the incompleteness of the fossil record have been widely discussed (Smith and Bengtson 1991). Recognition of attachment orientation is a very important criterion derived from the fact that oysters and other cementers (Prospodylidae, Plicatulidae, Dimyidae) usually have a slightly opisthogyrate umbo (Fig. 6.6), and the valve, as a whole, twists towards the posterior side, unless growth is hindered by irregularities of the substrate (Márquez-Aliaga et al. 2005). This character was maximally developed in Exogyrinae oysters and was not so evident in other cementers closely connected to pectinoids, such as Spondylidae. The stratigraphical occurrence also represents an important criterion, the vertical change in ecological parameters suggests the occurrence of related morphotypes, species and genera.

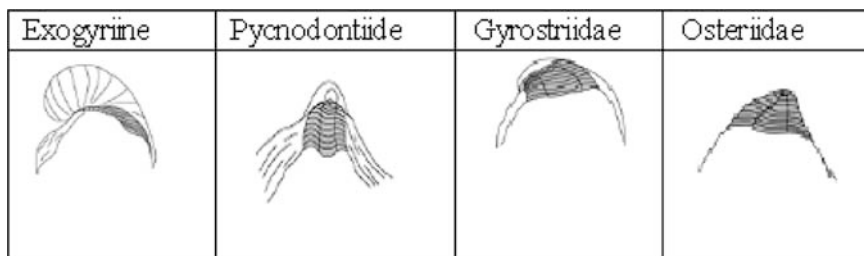


Fig. 6.6 Schematic key, based on umbonal area, for oysters differentiation

Distribution of specific taxa is influenced by environmental parameters. Some taxa have the ability to tolerate these parameters by giving rise to a morphotype with modification of some of its old morphological characters. It is important to note that the whole morphology of the morphotype is still governed by the close relation to the parent “original” type; these taxa can only be mentioned in evolutionary trends.

A final criterion, which can be used in combination with the above, is the valve convexity. In Pseudomonotidae, Prospondylidae, the majority of Ostreoidea, and many Plicatulidae and Dimyidae (as well as in other cementers) the right valve is less convex than the left one, Abdelhady (2007). In many oysters, both valves have similar convexities. Several hundreds of specimens have been examined from the late Albian to the early Turonian. These specimens were collected in the same states. Shell ornamentation patterns have been used as diagnostic characters for these species; the taxonomic status of which has not yet been revised following Moore (1969). Younger identified genera are also taken into account. By using the criterion of attachment orientation, stratigraphical occurrence, valve turns, valve convexity and beak size in addition to beak twisting, we herein suggest new evolutionary trends.

Body Size Evolution

Body size in Exogyrinae oysters has greatly increased (Fig. 6.8). This trend is evident both in raw data and when populations are binned into million-year intervals. The oldest population in the analysis is also the smallest; while later populations are nearly 50% larger in length. Most of the increase in size is over 8 million years. The temporal trend in body size mirrors the trajectory of bottom-water temperature, which heated most rapidly in the years of this interval (Fig. 6.7). Bottom-water temperature yields a highly positive relationship. Bottom-water temperatures that raised the body size in these oysters have increased. In agreement with the second prediction of the Cope–Bergmann hypothesis, an inverse correlation between temperature and body size is evident.

Intriguingly, over global heating, the average size of late Cenomanian *Exogyra* (*C.*) *olisiponensis*, *Gyrostrea delectrei* and *Ilymatogyra areitina* are the larger within Exogyrinae oysters. Dimensions indicate that the individuals of *I. (A.) Africana*

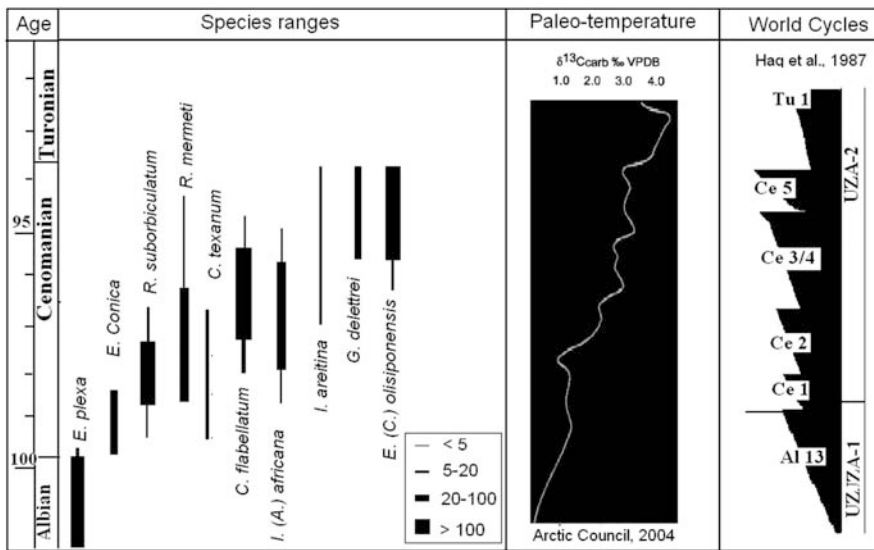


Fig. 6.7 Species ranges of Exogyrinae oysters versus age. The figure shows correlations with the paleo-temperatures of the Arctic Council (2004), and the world cycles of Haq et al. (1987)

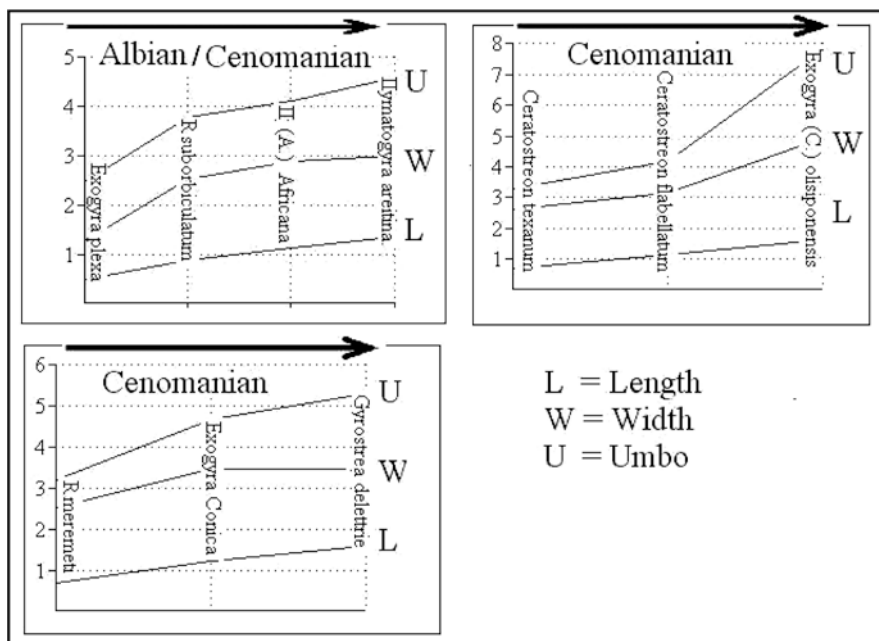


Fig. 6.8 The increase in body size of Exogyrinae oysters with time

exhibit intermediate size proportions when compared to the previously three largest species described. In general term, large body size reflects higher temperate latitudes with higher ocean productivity; herein is represented by the coarse carbonate beds with minor shales and mud intercalations of the Abu Qada Formation.

The Studied acme Zones

The acme zone takes its name from the taxon that has the greater abundance within its association. The late Albian/Cenomanian oysters of the studied sections led to divide the interval into the following acme Zones:

1. *Exogyra plexa*-*Exogyra ribose* Acme Zone (late Albian),
2. *Rhyncostreon suborbiculatum* Acme Zone (early Cenomanian),
3. *Ceratostreon flabellatum* Acme Zone (middle Cenomanian), and
4. *Exogyra (Costagyra) olisiponensis* Acme Zone (late Cenomanian).

Stage Boundaries

Albian/Cenomanian

The A/C boundary is defined herein at the LADs of *Exogyra plexa*, and is marked by the FADs of *E. plexa*. No marked depositional hiatuses or sharp changes are reported at this boundary, so it is believed that continuous sedimentation took place within the interval of latest Albian to Cenomanian, with sudden increase in species diversity and richness of Exogyrinae oysters.

Cenomanian/Turonian

The C/T boundary of the present study is determined by the LAD of *Exogyra (Costagyra) olisiponensis* and/or *Ilymatogyra areitina* (Fig. 6.7), where the oysters go vanish. The latest Cenomanian eustatic transgression thought to have been the most intense Phanerozoic flooding event. Maximum sea level during the C/T interval was probably 255 m higher (Haq et al. 1987), and shelf areas were twice as large as those of today. The levels of the atmospheric CO₂ were at least four times when compared with the present levels. The C/T boundary of the studied sections, therefore, represents a great mass extinction.

Morphometric Analyses

Dimorphism

Dimorphism has been reported to occur in some species of Exogyrinae; therefore we used the principal component analysis to examined two Exogyrinae species that are close to each other in their morphological characters:

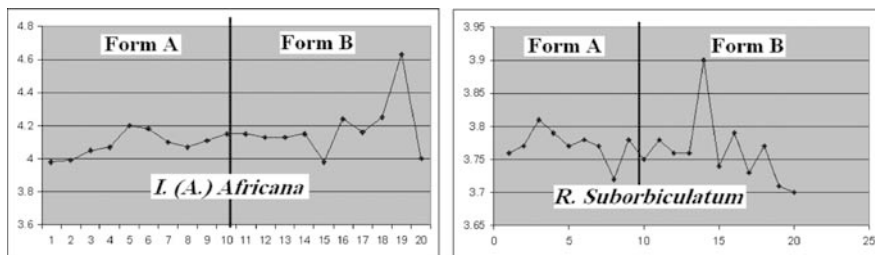


Fig. 6.9 Shell diameters of *I. (A.) Africana* and *R. suborbiculatum*

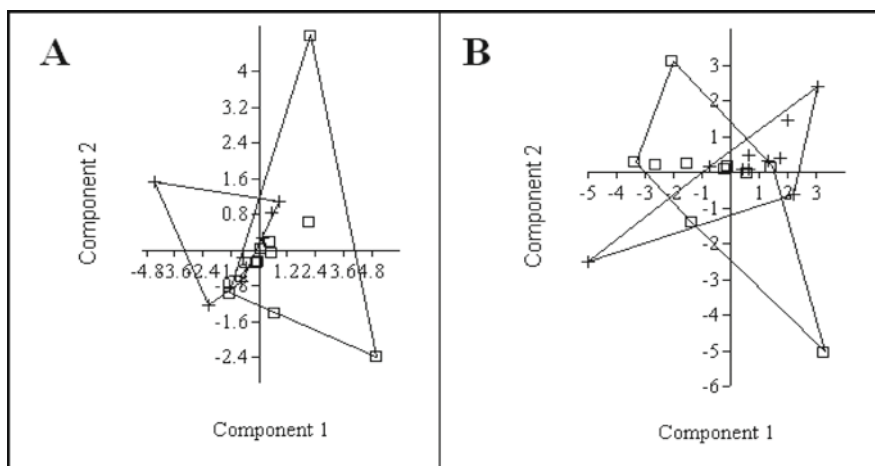


Fig. 6.10 Principle component scatter plot, based on correlation matrix with 95% confidence, for (a) *I. (A.) Africana*; percentage of variation in PC1 = 43.829, and (b) *R. suborbiculatum*, percentage of variation in PC1 = 57.82

1. *Hymatogyra (Afrogyra) Africana*, and
2. *Rhynchostreon suborbiculatum* (Fig. 6.9)

In Fig. 6.10, the PC scatter plot represents slight variation in morphologies of the two species, but without ability to isolate sub-specific characters. Figure 6.13a clearly shows the dimorphism of *I. (A.) Africana*; as it is believed by Malchus (1990), who subdivided *I. (A.) Africana* into two morphs, and suggested that such variation is related to the type of substratum.

For *R. suborbiculatum*, the two morphs are evident. These morphs may indicate two facts; the first is of Moore (1969), which indicates ontogenetic stage variation; while the other is dimorphism. We believe in the second evidence (dimorphism); as both forms have the same number of ribs, and the attachment area is equal, in addition to the overall shell characters of the genus *Rhynchostreon* Videt and Platel (2003).

Cluster Analysis

In the next step, we applied cluster analysis in order to evaluate the morphological similarities between Exogyrinae oysters. In cluster analysis we search for patterns in a data set by grouping the (multivariate) observations into clusters. The goal is to find an optimal grouping for which the observations or objects within each cluster are similar, but the clusters are dissimilar to each other. We hope to find the natural groupings in the data, groupings that make sense to the researcher. Cluster analysis has also been referred to as classification, pattern recognition (specifically, unsupervised learning), and numerical taxonomy. The techniques of cluster analysis have been extensively applied to data in many fields, such as medicine, psychiatry, sociology, criminology, anthropology, archaeology, geology, geography, remote sensing, market research, economics, and engineering. A common distance function is the Euclidean distance between two vectors, $\mathbf{x} = (x_1, x_2, \dots, x_p)$, and $\mathbf{y} = (y_1, y_2, \dots, y_p)$, which is defined as:

$$d(\mathbf{x}, \mathbf{y}) = \sqrt{(\mathbf{x} - \mathbf{y})'(\mathbf{x} - \mathbf{y})} = \sqrt{\sum_{j=1}^p (x_j - y_j)^2}$$

The combined tree provides better resolution of overall phylogeny (Fig. 6.11). At similarity equals 0.925 the major tree splits into four groups containing all genera and subgenera, these lineages have a distinct similarity distance and provide primary phylogenetic tree. The main problem is to estimate the time boundaries between species occurrences, which is absolutely undetermined by the cluster analysis, therefore we applied cladistic analysis in the next step.

Cladistic Analysis

We used cladistic analysis to assign time boundaries for the examined oyster members. Cladistic analysis is a semi-objective analysis of relationships between taxa from morphological or genetic evidence; the analysis searches the data matrix for the most parsimonious tree or trees. The results are presented in Fig. 6.12.

The first taxon, *Exogyra plexa*, is treated as outgroup, and is placed at the root of the tree. The topology of the tree indicates that substantial revision of the forms belonging to the genus *Ilymatogyra* is required. All the forms attributed to the genus do not lie on a single time unit or clade. *I. (A.) Africana* (morphotypes A and B) lies between different clades, indicating change in the environmental conditions with time. The genus *Rhynchostreon* represents forms (*suborbiculatum* morphotypes A and B) that are linked within a single clade or time unit (Fig. 6.12).

Matching with Stratigraphy

Since some characters are ordered with respect to the states exhibited by the earliest taxa, and *E. plexa*, the earliest species of Exogyrinae, is used as outgroup,

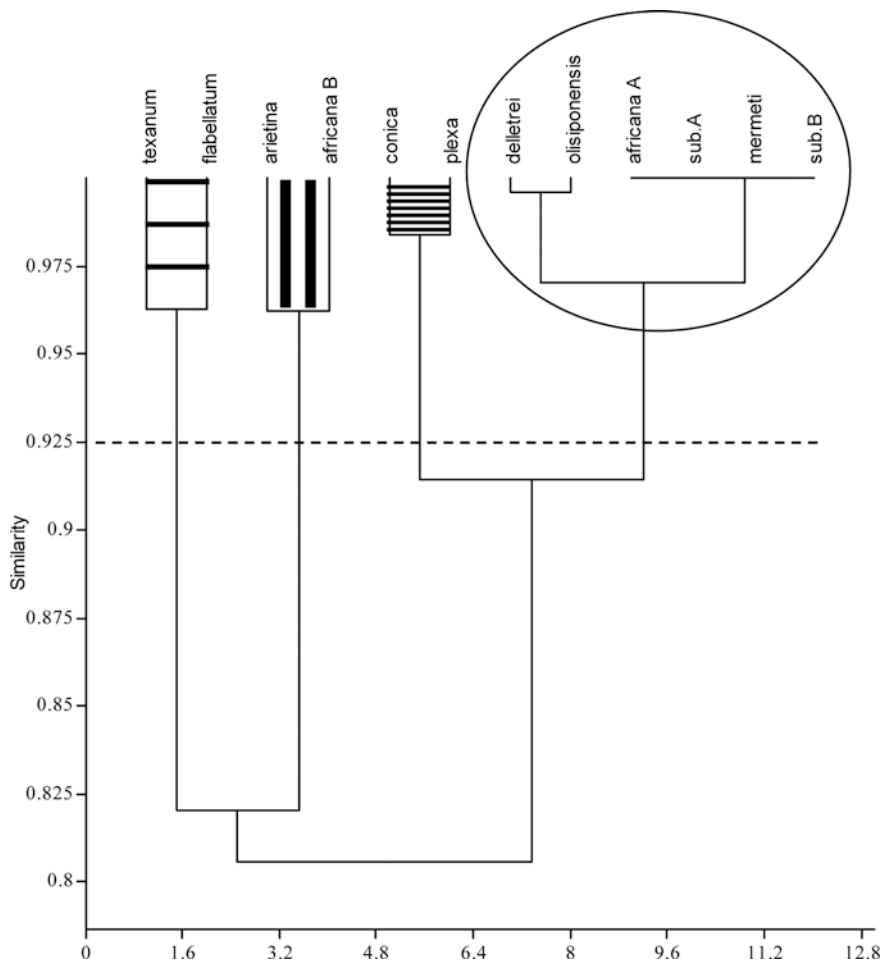


Fig. 6.11 Dendrogram obtained from Euclidean based clustering, after grouping the data matrix rows

it is therefore debatable whether there is quite good congruence between the cladogram and the stratigraphical occurrence of the fossils. The occurrence of *E. plexa* and *E. conica* at the base of the clade pattern agrees with their earlier stratigraphical occurrences at the late Albian/early Cenomanian interval. For the other cases, the cladogram has located *C. flabellatum* (late Cenomanian) at earlier stage than *C. texanum* (middle Albian). Furthermore, the cladogram placed *E. (C.) olisiponensis* and *Gyrostrea delletrei* (both of late Cenomanian age) at different levels.

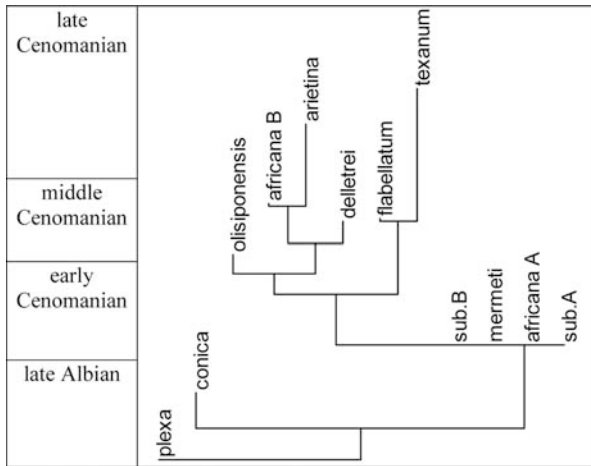


Fig. 6.12 Phylogram based on cladistic analysis

Correspondence Analysis

Since we could identify the morphological similarities of oyster members, subsequently we have to shade the light on the paleoecological factors that affected the species occurrences and richness, using correspondence analysis (CA).

Correspondence analysis is a graphical technique that represents the information in a two-way contingency table, which contains the counts (frequencies) of items for a cross-classification of two categorical variables. Using correspondence analysis, we can construct a plot that shows the interaction of the two categorical variables along with the relationship of the rows to each other, and of the columns to each other.

The algorithm of Davis (1986) is herein considered. The routine finds the eigenvalues and eigenvectors for a matrix containing the chi-squared distances between all data points. The eigenvalues, giving a measure of the similarity accounted for by the corresponding eigenvectors, are given for the first four most important eigenvectors (or fewer if there are less than four variables). The percentages of similarity accounted for by these components are also given. The main target of the Correspondence analysis is to reduce and interpret large multivariate ecological data sets with environmental or other gradients.

In correspondence analysis, we plot a point for each row and a point for each column of the contingency table. These points are, in effect, projections of the rows and columns of the contingency table onto a two-dimensional Euclidean space. The goal is to preserve as far as possible the relationship of the rows (or columns) to each other in a two-dimensional space. If two row points are close together, the profiles

of the two rows (across the columns) are similar. Likewise, two column points that are close together represent columns with similar profiles across the rows. If the two variables are denoted by x and y , then the assumption of independence can be expressed in terms of probabilities as:

$$P(x_i y_j) = P(x_i)P(y_j), i = 1, 2, \dots, a; j = 1, 2, \dots, b,$$

Where x_i and y_j correspond to the i th row and j th column of the contingency table, we can estimate:

$$p_{ij} = p_i \cdot p_j, i = 1, 2, \dots, a; j = 1, 2, \dots, b$$

Correspondence analysis and its plots suggest some important criteria on assessing morphological characters variation, with changes in the environmental conditions, within the different oyster species. From Table 6.1, it is evident that the first and second eigenvalues account for more than 96% of the trace. Consequently, Fig. 6.13 represents the scores of the 1st versus 2nd correspondences. The results are same as for cluster analysis, however environmental conditions can be predicted from correspondence analysis. The projection of the genus *Rhynchostreon* with its species and forms on a single point (Fig. 6.13) indicates the identity of the favorable conditions for all forms which occur on the same stratigraphical horizon (early Cenomanian), with equal response to the ecological factors, as the overall shell shape and size (L/W & L/B).

Figure 6.13 indicates that species of the genus *Ilymatogyra*, *I. arietina* and *I. (A.) Africana* morphotype B, are grouped according to the change in Theta1, the angle between the umbo and the tangent for the postero-ventral margin. Whereas, *I. (A.) Africana* morphotype A is located further away from the genus *Rhynchostreon*; suggesting the occurrence of an intermediate form between the two genera, with shell shape and ecological conditions related to the *Rhynchostreon*, and diagnostic features related to the genus *Ilymatogyra*. It is also observable, from the same figure, that Theta3, the angle between postero-ventral margin and the equator of the shell, assembles *C. texanum* and *C. flabellatum* within the same genus.

Table 6.1 Summary of correspondence analysis

Axis	Eigenvalue	% of total
1	0.0554519	58.52
2	0.0361253	38.124
3	0.00279102	2.9455
4	0.000358798	0.37865
5	E-052.68978	0.028386
6	E-062.62578	0.0027711
7	E-071.73952	0.00018358

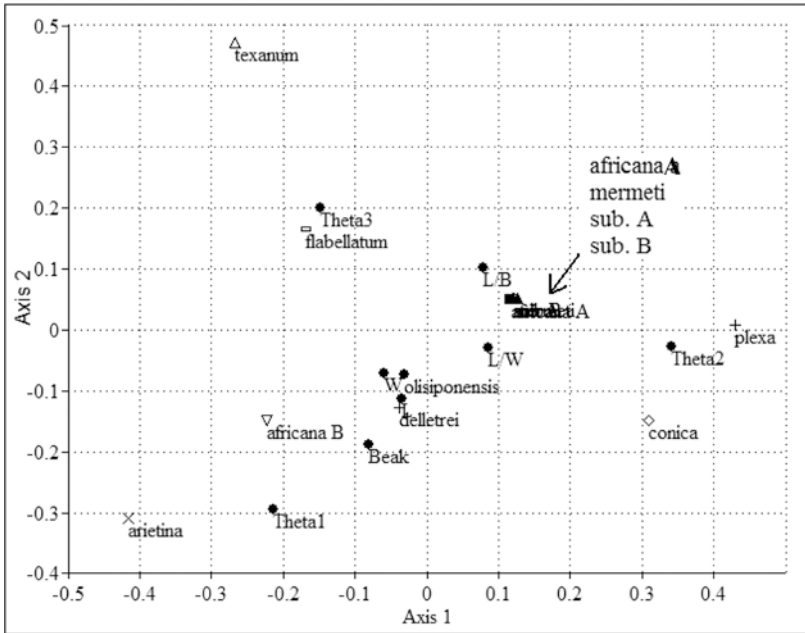


Fig. 6.13 Plot of points representing the 10 species on rows and the 8 variables on columns

E. plexa and *E. Conica* belong to each other by the angle Theta2, the angle between equator and the lower limit of the umbo. *E. (C.) olisiponensis* and *G. delletrei* are linked together because of the closeness of their shell diameters (L & W), while the other taxa are linked together based on the L/W & L/B ratios.

We can also conclude that Theta3 increases with the decrease of the valve periphery, which indicates a great convexity. This convex shape of the valve permits the epifauna to fix their bodies on the substratum more easily. In general, species with high convexity (*Exogyra*) are almost found on sandy substratum, while those with high Theta3 or large periphery accumulate with silt or mud substratum (*Ceratostreon*) (see Videt 2003).

The Proposed Phylogeny

Based on the collected material, and the literatures, we could propose the phylogeny shown in Fig. 6.14. Left valve illustrates some of the trends exhibited in the evolution of the *E. plexa* to *E. conica*. The most obvious trend is toward a larger beak with a greater number of turns, and a greater pitch. The overall size of the valve increases as well. Furthermore, the evolution of the *E. plexa* to *E. conica* is represented by the trend towards increasing the folds and the ribs. *E. plexa* possesses ribs near the tip of the beak. In addition, there is a trend towards reducing the attachment area. For

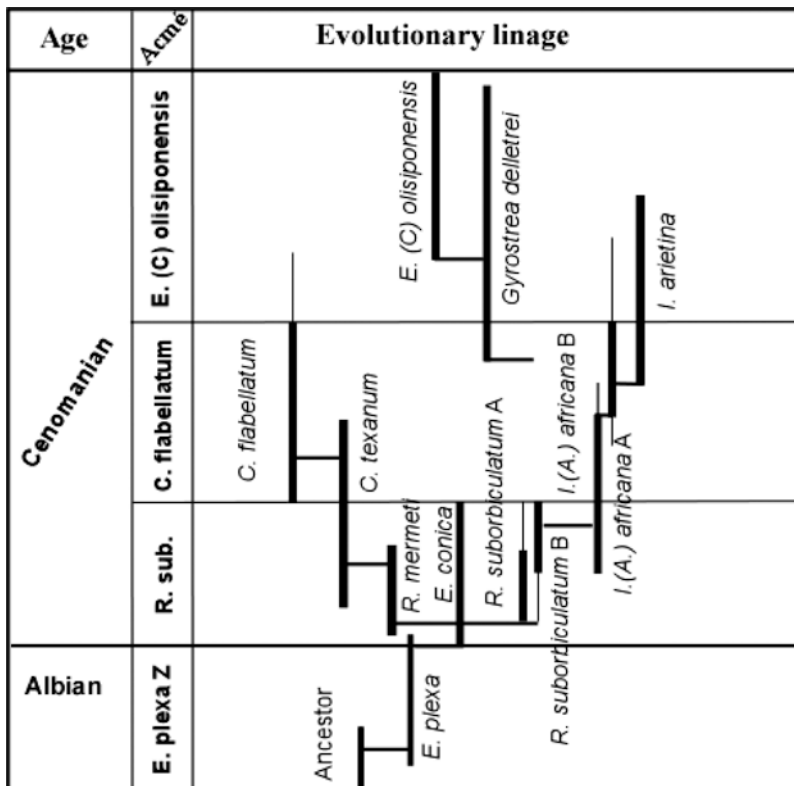


Fig. 6.14 Proposed phylogenetic tree in the Albian – Cenomanian Exogyrinae oysters

specimens of *E. plexa*, the attachment scar is often comparable to the valve in size. For *E. conica*, the attachment area is slightly absent.

We can observe the same evidence in the evolution from *I. arietina* to *I. (A.) Africana* (morphotypes A and B). There is a trend towards increasing the size with increasing the valve convexity, valve turns, and beak area. Another trend towards increasing the lower valve convexity and beak area can be shown in the evolution from *E. conica* to *R. suborbiculatum* morphotypes A and B, and *R. mermeti*. On the other hand, the ribs and valve turns decrease in the same path.

A good gradational transformation of *Ceratostreon texanum* to *C. flabellatum* is evident. This transformation is shown by increasing the size and surface ornament (ribs and nodes). The curvature of the beak is also increased with the decreasing of the valve turns. *C. flabellatum* is characterized by more conspicuous nodes than *C. texanum*, especially at the ventral margin. The beak turns also decrease through the same path.

Overall, the present study indicates that careful examination of microstructure and species from different stratigraphical horizons may reveal further details about systematics and phylogeny of the Upper Cretaceous oysters.

The Evolutionary Models

Modern theories of species evolution are determined by two famous models that reflect emphasis on different aspects of the evolutionary process. The first model is “Phyletic gradualism” that was originated with Darwin’s concept of organic evolution. The model holds that change in frequency of morphological characters occurs, gradually, in response to the selection pressure on the species populations. Abrupt change in morphology, in the fossil record, is viewed as something different from the speciation event (such as sampling, preservation failures or migration). If a complete record is preserved it would be expected to show continuous gradual morphological change from one species to the other.

The second model is called “punctuated equilibrium”; it characterizes species as real natural entities that are dominated, for most of their history, by morphological stability, and are characterized by abrupt origins and termination in space

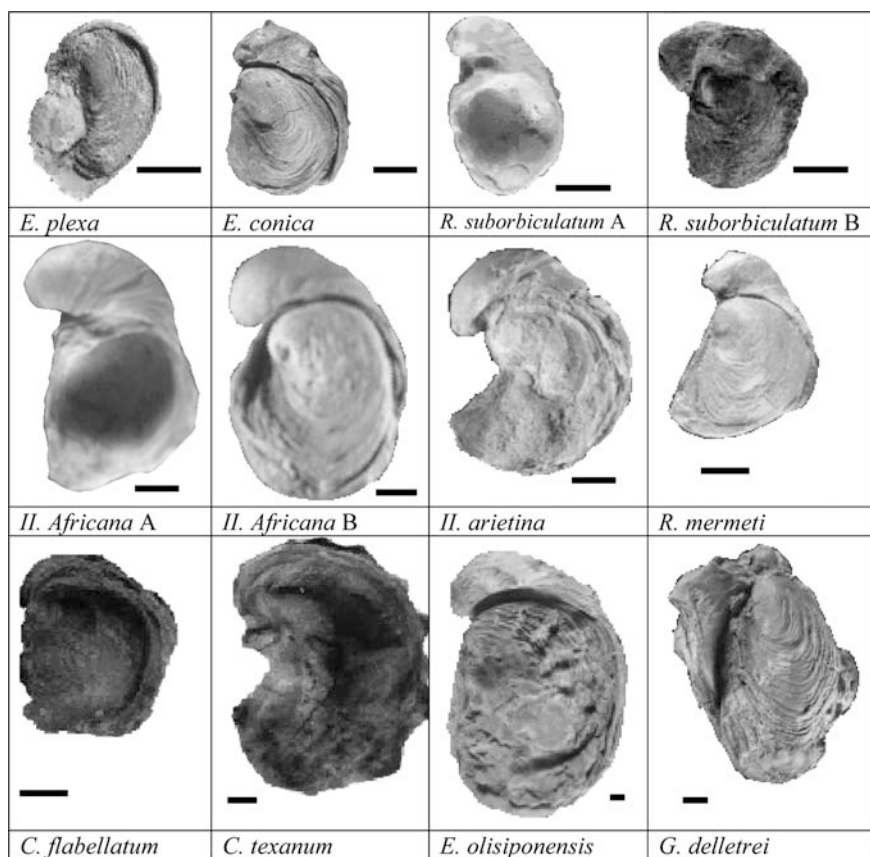


Fig. 6.15 Representatives of the examined oyster species

and time. Speciation is accomplished by the relatively rapid (perhaps 5,000–50,000 years as order of magnitude) development of reproductive isolation in some geographically isolated population of the parent species, followed by longer period of stasis in the daughter populations. Zonal boundaries for pyloric gradualism will be inherently imprecise, and errors will be introduced in attempted time correlation as a result of the difficulty for definition of species limits. On the other hand, punctuated equilibrium allows easily recognition of zonal boundaries precisely.

The investigated material (Fig. 6.15) suggests modification for the above mentioned models. It is believed that speciation goes flourished onward until reaching a maximum density, and then it is gradually vanished, due to the environmental

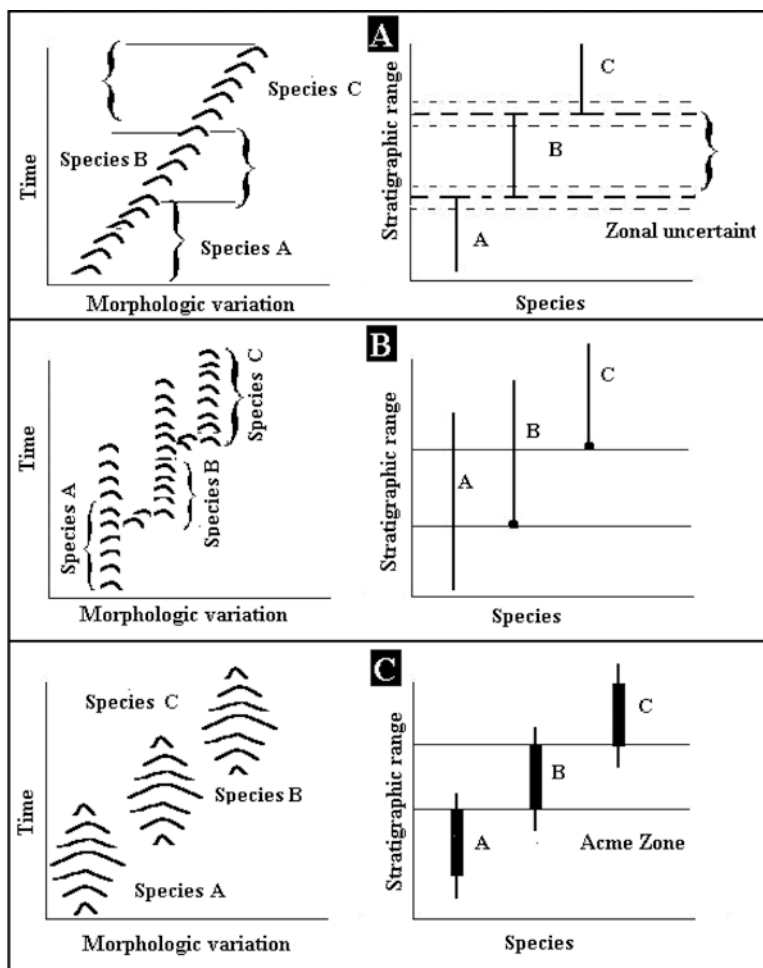


Fig. 6.16 Implication of species evolution models to the definition of biochronological zones. Phyletic gradualism (a), Punctuated equilibrium (b), Proposed model (c)

changes, with the appearance of gradational morphotypes of the same species. The stages of these morphotypes are almost of short duration. The morphotypes rise up to a new species that starts with low density, then its density increases onward, and repeats the cycle of the parent. Zonal boundaries according to this new model can easily be determined (Fig. 6.16).

In conclusion, we can ensure that the faunal associations, which are revealed by newly discovered, well preserved, and therefore, highly diverse assemblages, allowed the recognition of some phylogenetic trends of oysters. The vertical distribution of the identified taxa reveals six acme zones of the Upper Cretaceous age. The present study demonstrated that traditional morphometrics could provide a useful tool in the study of the oyster morpho-evolutionary changes.

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