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Cretaceous oysters from North Africa : origin and distribution

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Key words. – North Africa, Tethys, Cretaceous, Oysters, Distribution, Migration.

Abstract. – An overview of the diversified North African Cretaceous oyster faunas, which have a faunal distribution from Peru to Central Asia, is given. The faunal associations known as the "African facies" oysters originated in the uppermost Albian (Vraconian). These faunas present three main developmental stages : uppermost Albian to Upper Cenomanian, Coniacian-Santonian, Campanian-Maastrichtian. The first two stages are characterised by a probable west to east faunal migration. The Campanian-Maastrichtian interval shows a more complex pattern : it probably combines a east – west migration with an influence from the northern Tethys margin and/or from the Temperate Realm.

Huîtres crétacées d'Afrique du Nord : origine et distribution

Mots clés. – Afrique du Nord, Téthys, Crétacé, Huîtres, Distribution, Migration.

Résumé. – Les faunes très diversifiées d'huîtres du Crétacé d'Afrique du Nord sont discutées. Des faunes très semblables étaient distribuées du Pérou jusqu'en Asie centrale. L'association faunique, connue comme « in facies africana » débute à l'Albien supérieur (Vraconien).
Trois étapes peuvent être distinguées dans le développement de ces faunes : une première étape eut lieu de l'Albien supérieur au Cénomanien supérieur, une seconde du Coniacien au Santonien, et la troisième du Campanien au Maastrichtien terminal. Les deux premières ont été très probablement caractérisées par une migration de faunes de l'ouest vers l'est. pour l'intervalle Campanien-Maastrichtien la situation était plus complexe : elle a combiné une migration est-ouest, avec une influence de la marge nord de la Téthys et/ou du domaine tempéré.

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Introduction

Les huîtres sont un élément typique des dépôts téthysiens peu profonds du Pérou, d'Afrique du Nord, de la Calabre et de la Sicile, d'Asie mineure et centrale. Elles ont été étudiées depuis Lamarck [1801] et ont fait l'objet de nombreuses études dont les principales sont Coquand [1862, 1869], Lartet [1872], Thomas et Péron [1890-1891], Krumbeck [1906-1907], Pervinquière [1912], Fourtau [1917], Rossi Ronchetti [1953, 1962], Bobkova [1961] et Moroni et Ricco [1968]. Bien que fréquemment étudiées, peu de données précises stratigraphiques, statistiques et de microstructure existent pour ces faunes.

Matériel et méthodes

L'étude présentée rassemble les données de plusieurs études terminées ou en cours. Boumaza étudie les faunes algériennes, Dhondt les faunes du Tinrhert (Sahara algérien), de l'Equateur et du Pérou, la collection Coquand et a étudié les types de Bobkova, Malchus a étudié les faunes de l'Egypte et du SE des USA.

Evolution des faunes

Les étapes évolutives des huîtres téthysiennes d'Afrique du Nord sont les suivantes :
1) jusqu'à l'Aptien-Albien inférieur il n'y avait pas de faciès à huîtres. Dans l'intervalle Valanginien-Hauterivien-Barrémien deux faunes peuvent être distinguées : une faune « boréale » aussi bien dans l'hémisphère nord que sud, et une faune « téthysienne » qui s'étend d'Amérique latine, vers le Texas, autour de la Téthys *s.s.*, vers l'Afrique orientale et jusqu'au Japon;
2) à partir de l'Albien les huîtres connaissent un grand développement dans tous les groupes, aussi bien les huîtres pycnodontéines, exogyrines qu'ostréides.
Typiques pour cette période sont : *Oscillopha syphax*, *Ceratostreon flabellatum*, *Ilymatogyra (Afrogyra) africana*, *Rhynchostreon mermeti*, *Rh. suborbiculatum*, *Costagyra olisiponensis*, *Pycnodonte vesiculosa*, *Curvostrea rouvillei*, *? Gyrostrea delettrei*;
3) à partir du Turonien une nouvelle faune fait son apparition en Afrique du Nord; elle contient moins d'huîtres exogyrines, plus d'huîtres pycnodontéines et ostréines. Quelques exemples : *Oscillopha dichotoma*, *Nicaisolopha nicaisei*, *Pycnodonte costei*, *Py. vesicularis*, *Curvostrea heinzi*;
4) pendant l'intervalle Campanien supérieur-Maastrichtien la dernière faune du Crétacé nord-africain est caractérisée par *Exogyra overwegi*, *Amphidonte pyrenaicum*, *Acutostrea incurva*, *Agerostrea rouxi*, *Ag. ungulata* (uniquement dans le Maas-

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trichtien) et *Ambigostrea villei*. L'absence quasi entière d'huîtres pycnodontéines indique un milieu très peu profond, probablement en relation avec la régression maastrichtienne.

Origine des huîtres crétacées étudiées d'Afrique du Nord

Des listes fauniques avec une nomenclature revue d'après les travaux de Malchus [1990, 1996] sont présentées pour certaines régions d'Afrique du Nord et d'Asie :
- Maroc : Freneix [1972] (Tarfaya – Albien à Coniacien – tabl. I).
- Algérie : Valanginien à Maastrichtien (tabl. II).
- Tunisie : Pervinquière [1912] (Néocomien à Maastrichtien – tabl. III).
- Tinrhert (Sahara algérien) : matériel récolté par G. Busson – Cénomanien supérieur et Turonien (tabl. IV).
- Tripolitaine : Rossi-Ronchetti et Albanesi [1961] (Cénomanien).
- Cyrénaïque : Rossi-Ronchetti [1953] (Campanien supérieur-Maastrichtien).
- Sicile et Calabre : Russo [1958], Moroni et Ricco [1968] (Cénomanien – « facies africana »).
- Egypte : Malchus [1990] (Cénomanien à Maastrichtien – tabl. V).
- Jordanie : Aqrabawi [1993] (Cénomanien à Maastrichtien – tabl. VI).
- Asie centrale : Bobkova [1961] (Cénomano-turonien – tabl. VII).

Conclusions

Les huîtres des dépôts téthysiens crétacés d'Afrique du Nord sont relativement homogènes et diversifiées. De l'Albien au Santonien leur distribution a été influencée par des courants ouest-est. Des événements tectoniques à la transition santono-campanienne pourraient être à l'origine d'un changement vers un courant est-ouest; une influence venant de la bordure nord de la Tethys ou même du domaine tempéré n'est pas totalement à exclure pour l'intervalle campano-maastrichtien.

INTRODUCTION

Oysters are a very typical feature in shallow Cretaceous Tethyan outcrops. From Peru over Morocco to Egypt, and further into Central Asia they occur in great numbers.

Already in the 18 th century such oysters attracted the attention of scientific travellers. Thus, from specimens probably collected by his colleague Desfontaines, Lamarck [1801] described *Gryphaea africana* [today : *Ilymatogyra (Afrogyra) africana*], later shown to be probably from the Aurès mountains in Algeria, and of Cenomanian age [Pervinquière, 1912, p. 185].

Later authors described oysters from these "faciès à Ostracées" in North Africa, southern Italy (Sicily and Calabria – and known as "facies africana") and in the Near East.

Among such studies, the most famous is almost certainly Coquand's "Monographie du genre Ostrea – Terrain Crétacé" [1869] which is still today the basis for any work on Cretaceous oysters. Later authors described faunas from Tunisia [Thomas and Péron, 1890-1891; Pervinquière, 1912], from Cirenaica and Tripolitania [Krumbeck, 1906-1907; Maxia, 1940; Naldini, 1949; Parona, 1923; Rossi Ronchetti, 1953, 1962; Rossi Ronchetti and Albanesi, 1961], from Egypt [Fourtau, 1904, 1917], from Palestine [Lartet, 1872], Tadjikistan in Central Asia [Bobkova, 1961, Mirkhamalov, 1964, 1966], from Sicily and Calabria [Moroni and Ricco, 1968; Russo, 1958; Trevisan, 1937], to name but a few.

Data on these almost ubiquitous oysters in the mid-Cretaceous Tethys are numerous. Missing, however, are often precise stratigraphic data on their occurrence. For so long have they been assumed to be well known that when detailed work was done for oil geology, authors only very rarely bothered to include oysters in their outcrop descriptions.

As a result until quite recently "well-known" taxa existed, which very often had an uncertain stratigraphic age and had not been studied according to their microstructure or even simply taking into account the variability of the individual taxa. Freneix [1972] was the first author to give detailed statistical data for bivalve taxa from Tarfaya, Morocco (Albian-Cenomanian). Microstructure has been used recently; Malchus [1990] made a detailed study of Cretaceous Egyptian oysters developing the microstructure method and indicating for the first time precise biostratigraphic data for the taxa. His results simplify the somewhat confused oyster taxonomy. Aqrabawi [1993] made a similar study on Jordanian material. For other regions in Tethys, similar studies are not available.

MATERIAL AND METHODS

The result of several studies are presented herein, which were partially based on museum material and partially on personal fieldwork.

Boumaza studies material from Algeria, mainly from the Aurès mountains. Dhondt currently studies the faunas from the Tinrhert (Algerian Sahara, collected by G. Busson), from Ecuador and northern Peru (collected by E. Jaillard), revises the Coquand collection, and has studied the types of Bobkova [1961 – Oysters of Central Asia] at VSEGEI, St. Petersburg, Russia. Malchus has worked extensively on oyster taxonomy (Mesozoic and Cainozoic), on Egyptian Cretaceous oyster faunas, on Cretaceous and Cainozoic faunas from the SE USA and from northern Europe. On all the faunas studied by him, Malchus has also described the microstructure and on some the larval shells [Malchus, 1995].

These personally collected data were complemented with some from the literature – especially for Libya and Tunisia (though from this last country both Dhondt and Malchus studied specimens in museums). Malchus and Dhondt were closely associated with Aqrabawi when he prepared the study on Jordanian material – published in Aqrabawi [1993].

The stratigraphical and palaeobiogeographical data thus obtained give a qualitative overview of the faunas from the

Tethys – ranging from western South America to Central Asia, with special attention for the North African strata. The data are not complete and for Libya for instance not all the strata are documented. Nevertheless, it is considered that a faunal evolution can be understood from these data, and this is explained below.

FAUNAL EVOLUTION

Within North African Tethyan oysters the following faunal evolution steps can be seen.

Until the Aptian – Lower Albian no specific oyster facies existed.

Two faunas can be distinguished almost world wide in the Valanginian-Hauterivian-Barremian interval : a "boreal" fauna, found both in the northern and southern hemisphere, and a "tethyan" fauna which can be recognised from western South America, across the Caribbean, in Texas and around the Tethys proper (north and south of today's Mediterranean), down into E. Africa ("Tendaguru"), and further east all the way to Japan [Dhondt, 1992; Dhondt and Dieni, 1988] (fig. 1).

The main oyster taxa typical for these non-boreal faunas are : *Aetostreon latissimum* (LAMARCK, 1801), *Ceratostreon boussingaulti* (d'ORBIGNY, 1842), *Cer. tuberculiferum* (KOCH & DUNKER, 1837), *Gryphaeostrea canaliculata* (J. SOWERBY, 1813), *Rastellum rectangulare* (ROEMER, 1839). Some ostreids probably from very littoral or even brackish deposits are known especially from Aptian localities – an example is *"Ostrea" leymeriei* (LEYMERIE, 1842).

From the Albian onwards oysters develop strongly, in all groups – pycnodonteine, exogyrine and ostreid oysters *s.s.* This is undoubtedly connected with the wide transgressions forming shallow seas which were propitious for the evolution of oysters.

In North Africa this is seen for instance in Tarfaya (Morocco) [see Freneix, 1972] with the development of *Oscillolopha syphax* (COQUAND, 1862), *Ceratostreon flabellatum* (GOLDFUSS, 1833), *Pycnodonte vesiculosa* (J. SOWERBY, 1823).

In the Cenomanian also in Tarfaya [Freneix, 1972], and in Algeria (Batna, Tebessa, Tenoukla etc.) [Coquand, 1862, 1869], in Tunisia [Pervinquière, 1912], in Portugal and Spain, in S. Italy (Sicily [Russo, 1958; Trevisan, 1937], Calabria [Moroni and Ricco, 1968]), in Libya [Naldini, 1949; Rossi Ronchetti and Albanesi, 1961], in Egypt [Malchus, 1990], in Jordan [Aqrabawi, 1993], in Central Asia (especially Upper Cenomanian) [Bobkova, 1961] : *Ilymatogyra (Afrogyra) africana* (LAMARCK, 1801) (pl. I, figs. 1, 2), *Rhynchostreon mermeti* (COQUAND, 1862) (pl. I, fig. 4), *Rh. suborbiculatum* (LAMARCK, 1801), *Costagyra olisiponensis* (SHARPE, 1850) (pl. I, figs. 6, 7), *Curvostrea rouvillei* (COQUAND, 1862), ? *Gyrostrea delettrei* (COQUAND, 1862). Many of these taxa, or closely related ones, are also found in Cenomanian Tethyan strata of North and South America (fig. 2).

From the Turonian onwards a new fauna developed in North Africa, containing relatively fewer exogyrine oysters, more pycnodonteine taxa, and definitely more ostreine taxa which generally continues until the Campanian. A few examples are *Oscillolopha dichotoma* (BAYLE, 1849) (pl. I, figs. 3, 5), *Nicaisolopha nicaisei* (COQUAND, 1862) (pl. I, fig. 9], *Pycnodonte costei* (COQUAND, 1869) (from the Coniacian onwards); *Py. vesicularis* (LAMARCK, 1806) (in North Africa from the Santonian); *Curvostrea heinzi* (THOMAS & PÉRON, 1891); *Cu. tevesthensis* (COQUAND, 1862) (fig. 3).

From the uppermost **Campanian-Maastrichtian** the last Cretaceous North African fauna is recorded containing *Exogyra overwegi* VON BUCH, 1852; *Amphidonte pyrenaicum* (LEYMERIE, 1851); *Acutostrea incurva* (NILSSON, 1827); *Agerostrea rouxi* (DOUVILLÉ, 1910); *Ag. ungulata* (SCHLOTHEIM, 1813) and *Ambigostrea villei* (COQUAND, 1862) (pl. I, fig. 8). The almost complete absence of pycnodonteine oysters indicates a very shallow environment, probably related to the Maastrichtian regression (fig. 3).

ORIGIN OF THE NORTH AFRICAN CRETACEOUS OYSTERS

The Cretaceous oyster faunas from Morocco to Egypt are comparable, especially those from the Cenomanian interval. For the Coniacian – Maastrichtian interval extensive data are available from Algeria to Egypt.

In the Lower Cretaceous, the Tethys extended from western South America over North Africa virtually to Japan (fig. 1). This is visible in the bivalve faunas [Dhondt and

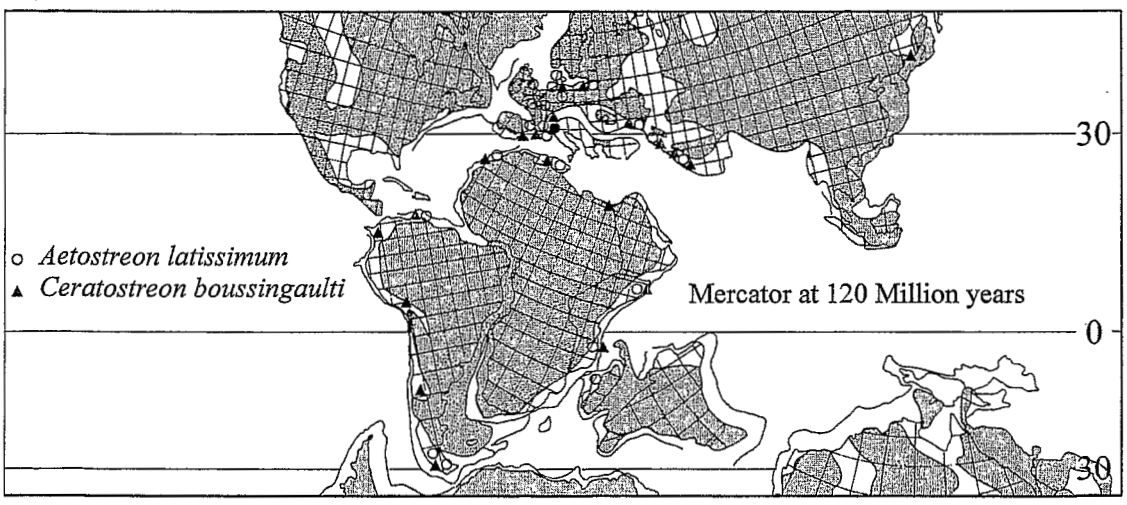

FIG. 1. – Distribution of Aptian non-boreal faunas. Palaeogeographic map after Barron *et al.* [1981].

FIG. 1. – *Répartition des faunes aptiennes non-boréales. Carte paléogéographique d'après Barron* et al. *[1981].*

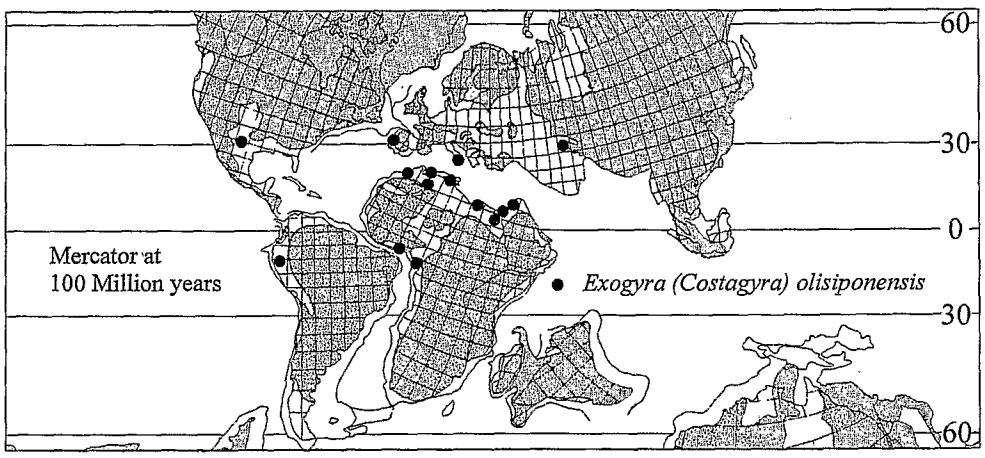

FIG. 2. – Distribution of *Costagyra olisiponensis* (SHARPE, 1850), Cenomanian – ? Turonian. Palaeogeographic map after Barron *et al.* [1981].
FIG. 2. – *Répartition de* Costagyra olisiponensis (SHARPE, 1850), *Cénomanien – ? Turonien. Carte paléogéographique d'après Barron* et al. *[1981].*

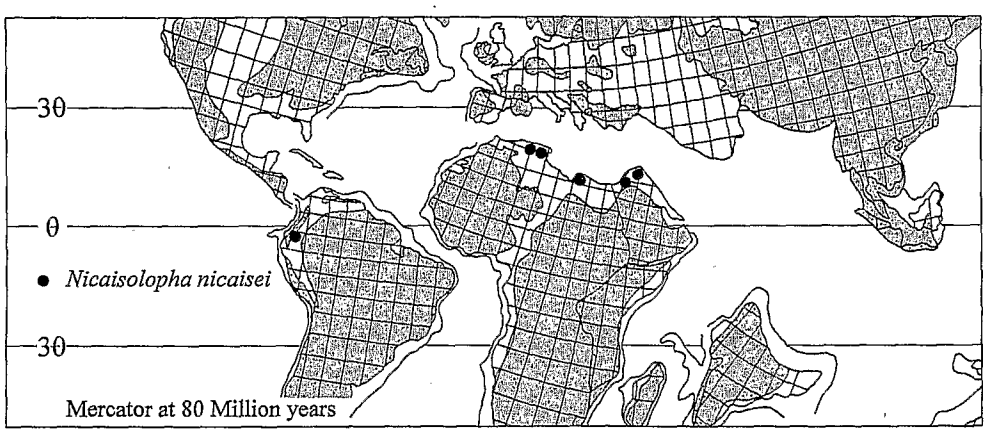

FIG. 3. – Distribution of *Nicaisolopha nicaisei* (COQUAND, 1862), Coniacian-Maastrichtian. Palaeogeographic map after Barron *et al.* [1981].
FIG. 3. – *Répartition de* Nicaisolopha nicaisei (COQUAND, 1862), *Coniacien-Maastrichtien. Carte paléogéographique d'après Barron* et al. *[1981].*

Dieni, 1988; Dhondt, 1992] especially during the Aptian. From the Albian onwards, it is obvious that the same faunal province continues into the Near East and largely also into Central Asia (though this region contains some endemic elements).

Work on N. Peru and Ecuador [Dhondt and Jaillard, 1997] illustrated that many North African taxa also occur in northern South America : in the Upper Albian : *Oscillolopha syphax, Ceratostreon boussingaulti*, in the Cenomanian : *Oscillolopha syphax, Ilymatogyra africana, Rhynchostreon mermeti, Costagyra olisiponensis*, in the Coniacian-Santonian : *Nicaisolopha nicaisei, Gyrostrea* aff. *roachensis* [Fourtau, 1917], in the Campanian-Maastrichtian : *Ambigostrea villei.*

We present faunal lists, with an updated nomenclature [following Malchus, 1990, 1996] from some of the North African and Asian Tethyan areas. In these lists no subgenera are used to avoid names becoming unnecessarily long.

Morocco (table I)

Freneix [1972] gave a detailed taxonomical description of bivalve faunas found at Tarfaya. These faunas are Albian to Coniacian, but most of the faunas are Albian-Cenomanian. Albian subdivisions used are : Alb SI : Albien supé-

PLATE I – PLANCHE I

Oysters from the Algerian Cretaceous – Quelques huîtres du Crétacé algérien.
FIG. 1a, 1b : *Ilymatogyra africana* (LAMARCK, 1801). Cenomanian from Batna; *Cénomanien de Batna*; × 1.25.
FIG. 2a, 2b : *Ilymatogyra africana* (LAMARCK, 1801). Cenomanian from Batna; *Cénomanien de Batna*; × 1.25.
FIG. 3 : *Oscillolopha dichotoma* (BAYLE, 1849). Santonian from Bordj Medjes Fouk ni Hodna; *Santonien de Bordj Medjes Fouk ni Hodna*; × 0.8.
FIG. 4 : *Rhynchostreon mermeti* (COQUAND, 1862). Cenomanian from Bechar; *Cénomanien de Bechar*; × 2.
FIG. 5 : *Oscillolopha dichotoma* (BAYLE, 1849). Campanian from Bordj Bou Arreridj; *Campanien de Bordj Bou Arreridj*; × 0.75.
FIG. 6 : *Costagyra olisiponensis* (SHARPE, 1850). Cenomanian from Bechar; *Cénomanien de Bechar*; × 1.2.
FIG. 7 : *Costagyra olisiponensis* (SHARPE, 1850). Cenomanian from Djebel Azeb, Batna; *Cénomanien de Djebel Azeb, Batna*; × 1.
FIG. 8 : *Ambigostrea villei* (COQUAND, 1862). Campanian from the Hodna Mountains; *Campanien des Monts Hodna*; × 0.66.
FIG. 9 : *Nicaisolopha nicaisei* (COQUAND, 1862). Campanian from El Kantara; *Campanien de El Kantara*; × 1.66.
FIG. 10 : *Nicaisolopha nicaisei* (COQUAND, 1862). Campanian from El Kantara; *Campanien de El Kantara*; × 1.5.
All specimens are from the collections of the "Institut des Sciences de la Terre", Université Houari-Boumédienne, Bab Ezzouar, Alger, Algeria.

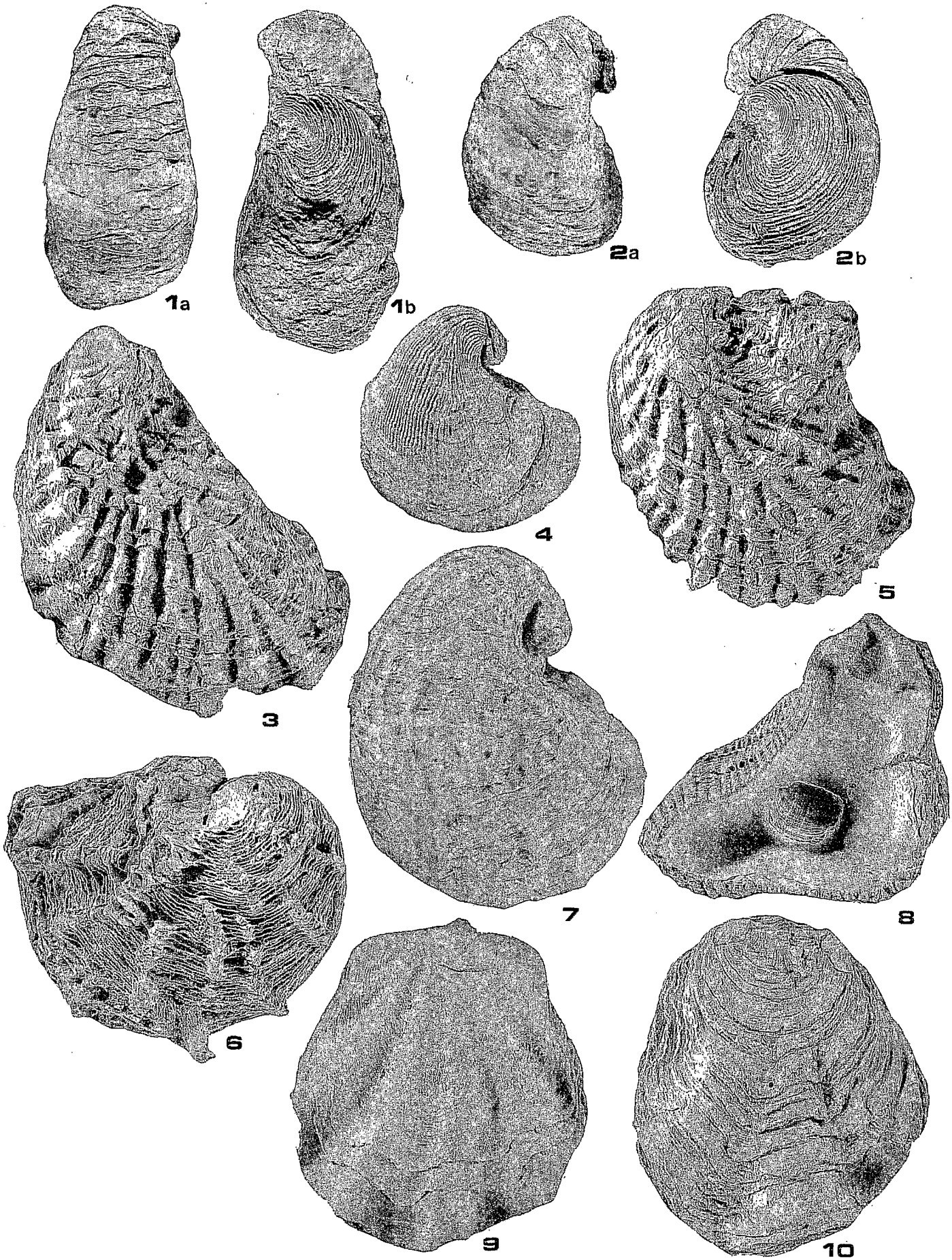
1a
1b
2a
2b
3
4
5
6
7
8
9
10

TABLE I. – Stratigraphical distribution of Cretaceous oysters at Tarfaya (Morocco).
TABL. I. – *Distribution stratigraphique des huîtres du Crétacé à Tarfaya (Maroc).*

	AlbSI	AlbSII	Cen	CenM	Tu	Co	Sa	Ca
Oscillolopha syphax	+	+	+	+				
Ceratostreon flabellatum		+	+					
? Laevigyra obliquata	+	+	+	+				
Rhynchostreon suborbiculatum					+			
Rh. mermeti				+				
Costagyra olisiponensis		+		+	?			
Pycnodonte vesiculosa	+		+					
Py. subvesiculosa						+		
Py. vesicularis								+
Py. flicki								+
Curvostrea rouvillei					+			
Gyrostrea delettrei				+				

rieur (zone à *Dipoloceras cristatum*) niveau inférieur à *Dipoloceras bouchardi*; Alb SII : Albien supérieur (zone à *Dipoloceras cristatum*) niveau supérieur à *Mortoniceras inflatum*.

Algeria (table II)

Coquand [1862] gave the first fairly complete description of the Algerian macrofossil Cretaceous faunas. His material mainly came from the "Province de Constantine". Coquand [1869] added some taxa to the Algerian fauna, and further details can be found in the papers of Thomas and Péron [1890-1891] and of Pervinquière [1912] where they compare Algerian taxa with those from Tunisia. A revision of the Algerian material is presently being undertaken by Boumaza, and Dhondt has studied the Coquand collection, housed at the "Institutum geologicum hungaricum (MAFI)", Budapest, Hungary. Data of Laffitte [1939] have been incorporated.

Tunisia (table III)

Pervinquière [1912] gave a detailed account of the macrofauna of parts of Tunisia. The faunas he studied vary in age from unspecified "Neocomian" to Maastrichtian.

Recent collections by Robaszynski and his group have confirmed the Upper Cretaceous data found in Pervinquière.

Sahara (table IV)

From the Algerian Sahara (Tinrhert), based on material collected by Busson, and under study by Dhondt and Busson.

Specimens from the Cenomanian (mainly Upper Cenomanian) – Turonian (mainly Lower Turonian) interval. CS1 to CS4 are local lithostratigraphical subdivisions used by Busson – all four belong to the Upper Cenomanian. TU inf : Lower Turonian.

Tripolitania

Based on Rossi Ronchetti and Albanesi [1961] who studied material collected by Desio in western Libya. Age : Cenomanian, undivided.
Rastellum sp.
Ceratostreon flabellatum
Ilymatogyra africana
Laevigyra obliquata

TABLE II. – Stratigraphical distribution of Cretaceous oysters in Algeria.
TABL. II. – *Distribution stratigraphique des huîtres du Crétacé en Algérie.*

	Va.	Ha.	Ba.	Apt	Alb	Ce.	Tu.	Co.	Sa.	Ca.	Ma.
Oscillolopha syphax					+	+					
Osc. dichotoma								+	+	+	
Rastellum "rectangulare"		+		+							
Rastellum sp.					+				+	+	
Aetostreon latissimum	+	+		+	?						
Amphidonte pyrenaicum										+	+
Ceratostreon boussingaulti				+	+						
Cer. flabellatum						+					
Cer. pliciferum										+	?
Ilymatogyra africana						+					
Laevigyra obliquata						+					
Rhynchostreon mermeti					+	+					
Costagyra olisiponensis						+					
Exogyra overwegi										+	+
Pycnodonte vesicularis								+	+	+	
Py. costei								+	?	+	
Curvostrea rouvillei						+					
Cu. heinzi								+	+		
Cu. tevesthensis								?	+	+	
Gyrostrea delettrei						+					
Gy. vatonnei								+			
Nicaisolopha tissoti								+	+	+	
Ni. nicaisei										+	+
Ambigostrea villei										+	+
Amb. tripolitana										+	+
"Ostrea" leymeriei				?							

TABLE III. – Stratigraphical distribution of Cretaceous oysters in Tunisia.
TABL. III. – *Distribution stratigraphique des huîtres du Crétacé en Tunisie.*

	"Neoc"	Apt.	Alb.	Ce.	Tu.	Co.	Sa.	Ca.	Ma.
Oscillolopha syphax				+					
Osc. dichotoma						+	+	+	+
Rastellum "rectangulare"	+								
Aetostreon latissimum	+	+							
Ceratostreon boussingaulti			+						
Cer. flabellatum				+					
Cer. pliciferum						+	+	+	+
Ilymatogyra africana				+					
Laevigyra obliquata				+					
Rhynchostreon suborbiculatum				+					
Costagyra olisiponensis				+					
Exogyra overwegi									+
Pycnodonte vesiculosa				+					
Py. vesicularis						+	+	+	+
Py. flicki							+	+	+
Py. costei						+			
Curvostrea rouvillei				+					
Cu. tevesthensis								+	+
Agerostrea rouxi									+
? Gyrostrea delettrei				+					
Nicaisolopha nicaisei					?		?	+	+
Ambigostrea villei								+	+

TABLE IV. – Stratigraphical distribution of middle Cretaceous oysters in the Algerian Sahara.

TABL. IV. – *Distribution stratigraphique des huîtres du Crétacé moyen du Sahara algérien.*

	CS1	CS2	CS3	CS4	TU inf.
Oscillolopha syphax	+	+			
Amphidonte sp.	+				
Ceratostreon flabellatum	+	+			
? Laevigyra luynesi	+	+	+	+	
Rhynchostreon suborbiculatum			+	+	
Costagyra olisiponensis	+	+	+	+	
Pycnodonte vesicularis		+	+	+	+
Gyrostrea delettrei					+
Curvostrea rollandi					+
Cu. rouvillei					+

? Rhynchostreon suborbiculatum minor
Rh. suborbiculatum s.s.
Costagyra olisiponensis
Curvostrea rouvillei
? Gyrostrea delettrei

Cirenaica

Data from east Libya, based on material collected by Desio, and studied by Rossi Ronchetti [1953]. Age : uppermost Campanian – Maastrichtian, undivided.
Oscillolopha dichotoma
Ceratostreon pliciferum
Exogyra overwegi
Amphidonte pyrenaicum
Gryphaeostrea canaliculata
Pycnodonte vesicularis
Agerostrea ungulata
Gyrostrea verneuili
Gy. cellae
Gyrostrea sp.
Nicaisolopha nicaisei
? Ambigostrea bretoni
? Amb. tripolitana
Amb. villei

Sicily and Calabria (S. Italy)

Trevisan [1937], Russo [1958] and Moroni and Ricco [1968] described Cenomanian faunas "in facies africana" from localities in Sicily and Calabria. Their taxonomic interpretations used concepts which today are not so frequently used. Hence, the number of taxa recognised in this paper is much smaller than that previously indicated by these authors. These faunas "in facies africana" are very close to those from Tunisia of the same age.
Oscillolopha syphax
Ceratostreon flabellatum
Ilymatogyra africana
? Laevigyra obliquata
Rhynchostreon mermeti
Costagyra olisiponensis
Pycnodonte vesiculosa
Gyrostrea delettrei

Egypt (table V)

The region considered is mainly the Sinai – Galala – Wadi Qena, as studied by Malchus [1990].

The stratigraphic data in Malchus are very precise, but could not be shown on our table; for the Cenomanian we have distinguished lower Upper and upper Upper Cenomanian, but for the other stages we have not made such differences. Age : varies from Albian to Maastrichtian.

TABLE V. – Stratigraphical distribution of the Albian-Maastrichtian oysters in Egypt.

TABL. V. – *Distribution stratigraphique des huîtres de l'interval Albien-Maastrichtien en Egypte.*

	Alb.	lUCen.	uUCen.	Tur.	Co.	Sa.	Ca.	Ma.
Oscillolopha dichotoma					+	+	+	?
Osc. figari							+	+
Rastellum sp.			+					+
Amphidonte pyrenaicum								+
Ceratostreon flabellatum	+	+	+					
Cer. pliciferum					?		?	
Ilymatogyra africana		+	+					
Laevigyra luynesi			+					
Laev. dhondtae			+					
Rhynchostreon mermeti		+	+					
Costagyra olisiponensis			+					
Exogyra overwegi								+
Pycnodonte vesiculosa			+					
Py. vesicularis							+	+
Py. costei					+			
Curvostrea isidis			+					
Cu. rouvillei			+					
Cu. heinzi					+	?		
Acutostrea aff. *incurva*								+
Agerostrea rouxi								+
Ag. ungulata								+
Gyrostrea antwani					+			
Gy. anubis					+			
Gy. vatonnei roachensis					+	?		
Nicaisolopha lyonsi					+			
Nic. tissoti					+	?		
Nic. nicaisei							+	+
Ambigostrea pseudovillei			+					
Amb. dominici			+					
Amb. bretoni							+	
Amb. villei							+	+
Amb. tripolitana								+

Jordan (table VI)

The Jordanian fauna was studied by Aqrabawi [1993] and the basic stratigraphic unit used by this author is the stage. Age : varies from Cenomanian to Maastrichtian.

Central Asia (table VII)

The Upper Cretaceous bivalve faunas from "Central Asia" (Tadjikistan, Uzbekistan) were most recently described by Bobkova [1961] and by Poyarkova [1976]. These faunas are extensive, but partially endemic. In interpreting them, the major problem is that the stratigraphical units used in these publications are not equivalent to those used further west, and we do not know precisely by which ammonites for instance the Upper Cenomanian or Upper Turonian are defi-

TABLE VI. – Stratigraphical distribution of Jordanian Upper Cretaceous oysters.

TABL. VI. – *Distribution stratigraphique des huîtres du Crétacé supérieur de Jordanie.*

	Cen.	Tu.	Co.	Sa.	Ca.	Ma.
Oscillolopha figari					+	
Osc. wala		+				
Ceratostreon flabellatum	+					
Ilymatogyra africana	+					
Laevigyra luynesi	+					
Laev. dhondtae	+					
Rhynchostreon mermeti	+					
Costagyra olisiponensis	+	+				
Exogyra italica	+					
Gryphaeostrea canaliculata						+
Pycnodonte vesiculosa	+					
Py. vesicularis					+	
Py. flicki				+	+	+
Pycnodonte (Costeina) sp.			+	+		
Curvostrea rouvillei	+					
Nicaisolopha nicaisei					+	
Ambigostrea villei						+

TABLE VII. – Stratigraphical distribution of some Cenomanian-Maastrichtian oysters from « Central Asia ».

TABL. VII. – *Distribution stratigraphique de quelques huîtres de l'interval Cénomanien–Maastrichtien de l'« Asie centrale ».*

	L.Cen.	U.Cen.	Tu.	Co.	Sa.	Ca.	Ma.
Oscillolopha sp.		+	+				
? Rastellum zeilleri					+	+	
Amphidonte pyrenaicum						+	+
Ceratostreon pliciferum			+		+	+	+
Ilymatogyra sp.		+					
Rhynchostreon plicatulum		+	+				
Rh. suborbiculatum		+	+				
Costagyra olisiponensis		+	+				
Pycnodonte vesicularis			+		+	+	+
Py. cf. *mutabilis*							+
Py. turkestanica			+				
? Py. costei			+	+			
Hyotissa sp.						+	
Curvostrea rouvillei		+	?				
Cu. gauthieri			+	+			
Ostreonella prima						+	
Agerostrea aff. *lunata*							+
Ag. cf. *ungulata*							+
Gyrostrea turkestanensis			+	?			
Gy. vatonnei			+				
Gy. antwani				+			
? Gy. delettrei			+				

ned. Also the oyster taxonomy is not easy to interpret because microstructure is not used and the authors often had no access to topotypical material of the western taxa which they use. We could only assess the value of part of the taxa, despite the fact that we studied the figured material of Bobkova [1961]. The taxon called *Gyrostrea turkestanensis* (BORNEMANN) as mentioned in Bobkova [1949] and [1961] should be ascribed to Bobkova (*Exogyra turkestanensis*) since the Bornemann "authorship" is based on a manuscript name. It is not synonymous with *Ostrea turkestanensis* ROMANOWSKY, 1878, since the original Bobkova name was *Exogyra turkestanensis*.

It has to be remembered that Palaeolophidae (genera *Oscillolopha* and *Rastellum*), Exogyrinae (genera *Amphidonte s.s.* and *Amphidonte (Ceratostreon*), *Ilymatogyra*, *Laevigyra*, *Exogyra* and *Exogyra (Costagyra)* and probably all Ostreidae (genera *Curvostrea*, *Acutostrea*, *Agerostrea*, *Gyrostrea*, *Nicaisolopha*, *Ambigostrea*) lived in very shallow seas (even brackish for some ostreine taxa), whereas the Pycnodonteinae (genus *Pycnodonte)* could have lived also in deeper seas and further away from the coasts.

Despite the limitations of the data available to us, it is obvious from comparing the oyster faunas that :

(a) in the Albian-Cenomanian interval, in a more or less homogeneous fauna, taxa from this fauna appear a little earlier in the South American, Moroccan and Algerian outcrops than they do further east : those areas contain :

– *Oscillolopha syphax* in the upper Upper Albian (sometimes = Vraconian) whereas in Tunisia - S. Italy this seems not to be the case. Further east *O. syphax* is not known, unless it were that the *O. dichotoma* specimens mentioned in Bobkova [1961] from Upper Cenomanian and Upper Turonian strata, and reinterpreted herein as *Oscillolopha* sp., would prove to belong to *O. syphax*

– *Ilymatogyra africana* is probably Lower Cenomanian in Peru, middle Cenomanian in Morocco , and further east Upper Cenomanian [see also Malchus, 1996]

– *Rhynchostreon mermeti* is Cenomanian (probably Lower Cenomanian in Peru), middle Cenomanian in Morocco, but Vraconian (Albian) in Algeria, lower Upper Cenomanian in Egypt

– *Rhynchostreon suborbiculatum* is possibly Turonian in Morocco, Cenomanian in Tunisia, upper Upper Cenomanian in the Algerian Sahara, Upper Cenomanian and Turonian in Central Asia; in northern Europe it often reaches the Turonian, and in northern Ireland even the Coniacian

– *Costagyra olisiponensis* is probably Lower Cenomanian in Peru, Albian and Cenomanian in Morocco, Cenomanian in Algeria, in the Algerian Sahara, in Tunisia, in Libya, Upper Cenomanian in Egypt, Cenomanian-Turonian in Jordan, Upper Cenomanian-Turonian in Central Asia.

A W-E migration seems likely, if not proven beyond doubt;

(b) Turonian Tethyan oysters are relatively scarce except in the Algerian Sahara : probably many seas were too deep for oysters during the Turonian. In Central Asia the continuation of the Cenomanian fauna is still seen in the Turonian;

(c) the Coniacian-Santonian interval brings a new fauna, which is characterised in the North African Tethys by *Oscillolopha dichotoma* [Bayle, 1849], by several *Pycnodonte* taxa, by the appearance of the genus *Nicaisolopha*, by a new series of taxa for the genera *Curvostrea* and *Gyrostrea* (especially in Egypt f.i. with the taxa *G. antwani* [Malchus, 1990], *G. anubis* [Malchus, 1990] and the *G. vatonnei* [Tho-

mas and Péron, 1891] group) and by the almost total absence of exogyrine oysters.

The genus *Nicaisolopha* occurs frequently in the Coniacian-Santonian Peruvian outcrops. The specimens have been assigned to *N. nicaisei* – they are identical in most characters with the Campanian topotypical specimens from Algeria, the only difference being that the Peruvian specimens are on average much larger than those from north Africa [Dhondt studied material from Peru collected by Jaillard, and material from Benavides, 1956]. In Algeria, possibly also in Tunisia and in Egypt, *Nicaisolopha* appears in the Coniacian-Santonian with *N. tissoti* (THOMAS and PÉRON, 1891) and *N. lyonsi* (BULLEN-NEWTON, 1898);

(d) the Campanian-Maastrichtian interval in North Africa contains forms which continue from the previous interval such as *Oscillolopha dichotoma* and *Pycnodonte vesicularis* and *P. costei*, new forms such as the exogyrine *Amphidonte pyrenaicum* and *Exogyra overwegi* (already Upper Campanian in Algeria, only Maastrichtian in Egypt), the ostreine *Nicaisolopha nicaisei* and *Ambigostrea villei* and *A. tripolitana* [Krumbeck, 1906] (Campanian and Maastrichtian in Algeria, Libya and Egypt). *Ambigostrea* taxa have been described by Malchus [1990] already in the Cenomanian of Egypt, but have not been recorded elsewhere of that age. Therefore it could be that the origin of the genus is in the eastern Tethys. This could find confirmation in the presence of *A. villei* in the Maastrichtian of Peru [see Dhondt and Jaillard, 1997]. It is the only oyster taxon certainly occurring in North Africa and in South America in the Maastrichtian, and could be interpreted as having migrated east to west, unlike oyster taxa from older strata.

The Maastrichtian of Tunisia, Libya, Egypt and Central Asia contains the genus *Agerostrea*. This genus is very common in Maastrichtian strata of the warm temperate strata both in North America and Europe, and its presence in North Africa could indicate the influence of temperate faunas in the Maastrichtian also seen at the same time for pectinids [Dhondt, 1992]. Malchus [1996] considers that *Agerostrea* originated in SE North America and migrated eastwards in the Tethys; the pattern maybe somewhat more complex because the presence of *A. lunata* [NILSSON, 1827] and of *A. ungulata* in the Maastrichtian of northern Kazakhstan [Dhondt *et al.*, 1996] might suggest another migration route through the temperate White Chalk Sea.

According to Guiraud and Bellion [1995] and Guiraud and Bosworth [1998] a late Santonian – early Maastrichtian (83-85 Ma) compressional episode took place along the northern African-Arabian plate margin. The resulting sea level changes might explain the faunal changes between the Coniacian-Santonian and the Campanian-Maastrichtian intervals.

CONCLUSIONS

The oyster faunas from the Cretaceous Tethys deposits in North Africa are relatively homogeneous and highly diversified.

Their distribution has probably been influenced by west-east currents in the Albian-Cenomanian, and in the Coniacian-Santonian. Tectonic events at the Santonian-Campanian transition might be the origin of the probable change in currents in the Campanian-Maastrichtian interval in which a partial east-west migration is assumed, but some faunal elements came probably from either the northern Tethys margin or even from the temperate realm.

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