

Oysters (Bivalvia-Pteriomorpha) of the Upper Cretaceous rocks of Jordan. Palaeontology, Stratigraphy and Comparison with the Upper Cretaceous oysters of Northwest Europe.

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With 7 plates and 53 text-figures

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Zusammenfassung

Austern (Bivalvia-Pteriomorphia) stellen eine der vielfältigsten und besterhaltenen Fossilgruppen in den mesozoischen Sedimentgesteinen Jordaniens dar. Ihre größte Verbreitung erreichen sie in den oberkretazischen Ablagerungen. Obwohl sie in der Literatur häufig erwähnt werden, werden sie in keiner dieser Arbeiten als eigenständige Gruppe betrachtet. Im Rahmen dieser Dissertation werden die Paläontologie, stratigraphische Verbreitung, Paläoökologie, Biostratigraphie, Paläobiogeographie und die Gehäusemikrostruktur der jordanischen Austern als Tethys Vertreter diskutiert und mit gleichaltrigen borealen Vertretern aus NW-Europa verglichen.

Die Lithologie und Stratigraphie von zwei Profilen in Wadi Salihi (nördlich von Amman) und in Wadi Mujib (Zentral-Jordanien) dienen als Referenzprofile für die stratigraphische Einordnung der Austern Jordaniens.

Die in dieser Arbeit verwendete Austern-Systematik stützt sich auf die neuesten Ansätze zur Klassifikation dieser Organismen-Gruppe. Die wichtigsten morphologischen Merkmale der Austern werden kurz beschrieben und diskutiert. Die systematische Einordnung der Arten dieser Arbeit erfolgt nach Größe, Gestalt, internen Merkmalen, externen Merkmalen und der Mikrostruktur der Schale.

Aus den oberkretazischen Schichten Jordaniens werden insgesamt 17 Arten aus 10 Gattungen und 6 Untergattungen beschrieben. Darunter wird eine neue Art (*Oscillophra wala* n. sp.) aus dem Turon in Wadi Wala (Zentral Jordaniens) beschrieben. 4 weitere Arten (*Oscillophra figari* (FOURTAU), *Exogyra* (*Exogyra*) *italica* (SEGUENZA), *Laevigyra luynesi* (LARTET) und *Laevigyra dhondtae* (MALCHUS) werden zum ersten Mal aus Jordanien beschrieben. Zusätzlich werden noch zwei Arten (*Africogryphaea costellata* (DOUVILLÉ) und *Gryphaeligmus jabbokensis* (COX) aus dem Bathon (Mittel Jura) Zentral- und NW-Jordanien beschrieben. Zum Vergleich wurden außerdem 15 Arten aus 8 Gattungen und 4 Untergattungen aus der Oberkreide NW-Europas untersucht.

Die stratigraphische Verbreitung der in dieser Arbeit untersuchten Austern zeigt, daß die Austern in Jordanien ihre artreichste Zahl im Cenoman/Unterturon und im Campan erreichten. In NW-Europa haben die Austern ebenfalls ihre größte Zahl in Cenoman/Turon und im Campan/Maastricht. Diese hohe Diversität ist möglicherweise auf die Cenoman- und Campan-Transgressionen zurückzuführen, die den Austern neue Lebensräume eröffneten.

Die Austern bilden sowohl in Jordanien wie auch in NW-Europa kleinere bis größere Gemeinschaften, die meist von einer oder zwei Arten dominiert werden. Die artliche Zusammensetzung variiert jedoch von Lokalität zu Lokalität. Daher ist es schwierig erfolgreiche regionale biostratigraphische Zonierungen mit Hilfe von Austern zu erstellen. Jedoch können einige jordanische Austern wie z. B. *Oscillophra wala* n. sp., *O. figari* (FOURTAU), *Laevigyra luynesi* (LARTET), *L. dhondtae* MALCHUS, *Ambigostrea villei* (COQUAND) und *P. (Costeina)* sp. als Leitfossilien für bestimmte Zeitabschnitte (in Jordanien) angesehen werden. Die großen Austernbioherme in der Al Hisa Phosphorite Formation, die entlang des Phosphatgürtel Jordaniens verbreitet sind, können jedoch als separate lithologische Einheiten kartiert werden.

In den oberkretazischen sedimentären Einheiten Jordaniens lassen sich zwei Haupt-Austernfazies unterscheiden. Die erste besteht aus flachmarinen Plattform-Karbonaten (Kalke, mergelige Kalke, Mergel, Dolomite), die sich mit Siliziklastika verzahnen. Diese Fazies wurde in der transgressiven Ajlun-Gruppe (Cenoman/Turon) gebildet. Die Ablagerung erfolgte in flachem, ruhigen und warmen Wasser. Die zweite Fazies besteht aus Austernschillen und Grainstones sowie großen Austernbiohermen. Die Austernschille und Grainstones weisen großmaßstäbliche Kreuzschichtungen auf. Sie entstanden wahrscheinlich im Folge der Änderung der Schelf-Konfiguration von einer Karbonatplattform zu einer Karbonatrampe während der Transgression im Oberen Coniac. Die Fazies-Verteilung weist auf ein Hochenergie-Environment hin. Sie können mit ähnlichen Austernfazies in Negev (S. Israel) und auf der Sinai-Halbinsel (Ägypten) korreliert werden. Die oberkretazische Austern-Fazies NW-Europas unterscheiden sich von den jordanischen. Die meisten der untersuchten Arten des Cenomans und des Turons kommen in mergeligen, glaukonitischen grünen Sanden vor, während die meisten Austern des Senoniens in tieferen marinen Kreidekalken gefunden werden.

Kosmopolitische Arten wie *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK), *Pycnodonte* (*Phygraea*) *vesiculosum* (SOWERBY), *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS) und *Gryphaeostrea canaliculata* (SOWERBY) kommen sowohl in Jordanien wie auch in NW-Europa vor. Diese Arten sind nicht nur geographisch sondern auch zeitlich Durchläufer.

In Jordanien und in NW-Europa gehören die Austernfaunen hauptsächlich zur Familie Gryphaeidae, Unterfamilie Exogyreinae. In Jordanien dominieren jedoch Vertreter des Tribus Exogyriini (*Exogyra*, *Ilymatogyra*, *Laevigyra* und *Rhynchostreon*), während in NW-Europa, das Tribus Nanogyriini (*Amphidonte* mit den Untergattungen *A. (Amphidonte)*, *A. (Ceratostreon)*, *A. (Vultogryphaea)*) vorherrscht. Die Gattung *Vultogryphaea* wurde auf Grund der amphidonten rechten Klappe und der fischgräten-kreuz-foliaten Struktur mit Mokret-Linsen als Untergattung zur Gattung *Amphidonte* gestellt. Vertreter des Tribus Exogyriini haben unterteilte Endostraca mit unterschiedlichen Strukturen, die gebogen-foliate Struktur ist für die Gattungen *Rhynchostreon* und *Laevigyra* charakteristisch, während die Arten der Gattung *Amphidonte* Schalen mit fischgräten-kreuz-foliaten Struktur mit Mokret-Linsen bilden.

Abstract

Oysters (Bivalvia-Pteriomorphia) are one of the most diversified and best preserved fossil groups in the Mesozoic sediments (mainly Upper Cretaceous) of Jordan. They were often mentioned in the old literature, but none of the studies treated them as a separate group. In this work, the palaeontology, stratigraphic distribution, biostratigraphy, palaeoecology, palaeobiogeography as well as the shell microstructure of the Jordanian oysters (as representatives of the Tethyan realm) are discussed and compared with Upper Cretaceous oysters from Northwest Europe which represent the North Temperate realm.

The lithology and stratigraphy of two compiled columnar sections in Wadi Salihi, north of Amman and in Wadi Mujib, central Jordan, are discussed and used as reference sections for this study.

Oysters were reviewed according to the latest systematic classification concerning this group. The important morphological characters of oyster shells are briefly described and discussed. They are subdivided into: size, outline, internal characters, external characters and shell microstructure. This subdivision is made to provide a simple presentation of the systematic palaeontology of this work.

Seventeen species belonging to ten genera and six subgenera from the Upper Cretaceous sediments of Jordan are described. Among which, one new species (*Oscillophra wala* n. sp.) from the Turonian of Wadi Wala in Central Jordan is erected, and four species, *Oscillophra figari* (FOURTAU), *Exogyra* (*Exogyra*) *italica* (SEGUENZA), *Laevigyra luynesi* (LARTET) and *Laevigyra dhondtae* MALCHUS, are reported for the first time from Jordan. In addition, two species belonging to two Jurassic genera, *Africogryphaea costellata* (DOUVILLÉ) and *Gryphaeligmus jabbokensis* (COX) from the Bathonian (Middle Jurassic) sediments of central and northwestern Jordan, are reported.

From Northwest Europe, fifteen species belonging to eight genera and four subgenera are reported. Among which *Oscillophra dichotoma* (BAYLE) is reported for the first time.

The stratigraphic distribution of the studied oysters shows that the Upper Cretaceous oysters from Jordan are concentrated in the Cenomanian-Lower Turonian and in the Campanian stages; and those of Northwest Europe are concentrated in the Cenomanian-Turonian and in the Campanian-Maastrichtian stages. Such concentrations in the distribution are possibly related to major transgressions which occurred at the beginning of the Cenomanian and in the Campanian stages which enabled oysters among other fauna to open new suitable environmental niches.

Jordanian and Northwest European oysters are generally found in small to large accumulations, mostly dominated by one or two species which vary from one locality to another. Therefore it is difficult to establish successful regional biostratigraphic zonation based on oysters. However, oyster species such as *Oscillophra wala* n. sp., *O. figari* (FOURTAU), *Laevigyra luynesi* (LARTET), *L. dhondtae* MALCHUS, *Ambigostrea villei* (COQUAND) and *Pycnodonte* (*Costeina*) sp. characterise certain intervals within the Upper Cretaceous System of Jordan. Also the large oyster-bioherms of Al Hisa Phosphorite Formation (Campanian) which are distributed along the phosphate belt of Jordan can be mapped as separate units.

Two major oyster-facies patterns can be recognised within the Upper Cretaceous sedimentary sequences of Jordan. A shallow carbonate-platform facies pattern, where Cenomanian-Turonian platform-carbonate sediments (limestones, marly limestones, marls and dolomites) with minor tongues of siliclastics were deposited marking a series of pulses of transgression during the deposition of the Ajlun Group. Here oysters have generally lived in shallow, calm, warm-water. And an oyster-coquinal grainstone and oyster-bioherm facies pattern, where thick beds of large scale oyster-coquinal grainstone, large scale cross-stratified oyster-banks and large oyster-bioherms up to 30m thick were formed. It is possibly established as a result of a change in the configurations of the shelf from a platform to a ramp and of a concomitant rise in the sea level associated with the Late Cretaceous transgression. These facies patterns indicate a high energy environment of deposition concomitant to local unconformities, they are successfully correlated with similar oyster-facies from the Negev, southern Israel and Sinai, Egypt. Northwest European Upper Cretaceous oysters reflect different facies patterns. Most of the Cenomanian and Turonian studied species occur in glauconitic marly green sand facies, while most of the Senonian oysters are found in deeper marine white chalk facies.

Cosmopolitan species such as *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK), *Pycnodonte* (*Phygraea*) *vesiculosum* (SOWERBY), *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS) and *Gryphaeostrea canaliculata* (SOWERBY) are reported from Jordan as well as Northwest Europe.

Distribution of oysters in the different oyster-groups show that the Jordanian and the Northwest European ones are dominated by the family Gryphaeidae, subfamily Exo-

gyreinae. However, the Jordanian oysters are dominated by the tribe Exogyriini (*Exogyra*, *Ilymatogyra*, *Laevigyra* and *Rhynchostreon*), while the Northwest European ones are dominated by the tribe Nanogyriini (genus *Amphidonte*) with the subgenera *A. (Amphidonte)*, *A. (Cerastostreon)* and *A. (Vultogryphaea)*, the latter is attributed to this genus according to the amphidontid right valve and to the herringbone-cross-foliated structure with mocret lenses. Members of the tribe Exogyriini have divided endostraca with different structures, among which bent-foliated structure is characteristic of the genera *Rhynchostreon* and *Laevigyra*; while species of the genus *Amphidonte* build herringbone-cross-foliated structure with mocret lenses.

1. Introduction

1.1. Statement of the problem

Upper Cretaceous carbonate rocks cover more than 2/3 of the outcropping rock surface of the Hashemite Kingdom of Jordan. These carbonates are rich in both micro- and macro-invertebrate fossils. Efforts made by previous authors were concentrated mainly on studies concerning microfossils and few reports were published on macrofossils from the Kingdom. Oysters represent one of the most frequent and best preserved group of fossils throughout the Jordanian Upper Cretaceous strata. In the few published studies, oysters were partly or briefly discussed. In this study, a serious attempt is made to discuss the palaeontologic, taxonomic and stratigraphic values of the Jordanian oysters based on the Upper Cretaceous species, since they form the majority of oysters in Jordan. Some Jurassic oysters are also included in this study.

Also Upper Cretaceous oysters of the North Temperate Realm from North Europe are systematically reviewed and compared with the Tethyan oysters from Jordan.

Shell microstructure has recently gained an increasing importance in the classification and interpretation of many fossil taxa. It is becoming an integral part of bivalve systematics. A contribution to this character is made by investigating shell microstructures of the Jordanian as well as the North European oysters.

1.2. Material and methodology

For the purposes of this study, oyster samples were collected and documented throughout the outcropping Upper Cretaceous strata in Jordan. Samples were collected by the author in the time between April and August 1988. Most of the samples were collected along the eastern side of the Jordan Rift Valley from Irbid in the North to Ras-El-Naqab in the South. Jurassic oysters were collected from Bajocian-Bathonian strata of Wadi Zerqa River, Arda, Deir Alla, Old Jerash Bridge and King Talal Dam. Additional Upper Cretaceous oyster samples were kindly provided by Prof. K. BANDEL (Geol.-Palaeontol. Institute of the University of Hamburg), they were collected from different localities along the eastern flank of the Jordan Rift Valley. Two compiled columnar sections were measured in Wadi Salihi north of Amman and in Wadi Mujib in Central Jordan. The section in Wadi Salihi is modified after BANDEL & GEYS (1985), the nomenclature used in their work is shown in tab. (1).

Most of the North European material of this study was loaned from fossil collections of the Geological and Palaeontological Institute and Museum of the University of Hamburg. A selected oyster collection was loaned from the Ruhrlandmuseum in Essen. Oyster fossil collections in natural history museums in Münster and Essen in Germany, Paris in France and Brussels in Belgium were visited.

Specimens described in this study are housed in the collection of the Geological-Palaeontological Institute and Museum of the University of Hamburg (GPIMH).

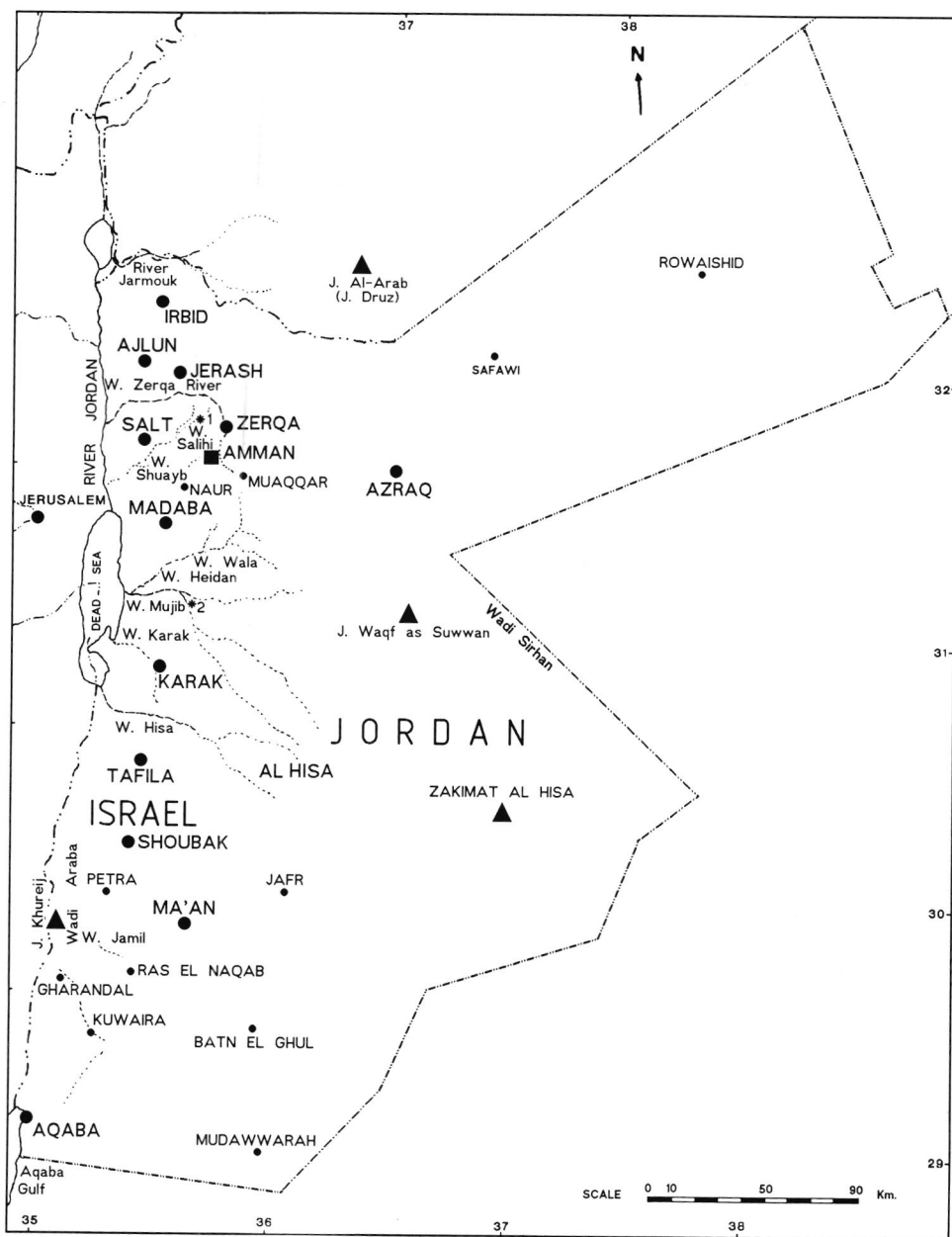


Fig. 1: Location map of Jordan showing the different localities mentioned in this study.

Samples of this study were cleaned by using hydrogen-peroxide (H_2O_2) method for the relatively soft samples and air-pressured sand technique for the hard samples. Over 100 thin-sections from oyster shells were made for the shell microstructure analysis of this study. These thin-sections were studied under the polarized microscope. Photos and drawings necessary for the photo-plates and for the different figures and maps of this study were also made.

2. General geological framework of Jordan

2.1. Geological setting

The Hashemite Kingdom of Jordan lies at the northwestern part of the Arabian Peninsula. It covers 89,544 km² between 29°30'–33°30' (Latitude) North and 35°–39° (Longitude) East. The Kingdom is bordered by Syria in the North, Iraq and Saudi Arabia in the East, Saudi Arabia and the Gulf of Aqaba in the South and the Dead Sea and Palestine in the West.

Sedimentation of the Mesozoic and early Cainozoic rocks was controlled by the configuration of the old Tethys Sea to the north and northwest of Jordan and the isostatic movement of the Arabian-Nubian Shield and its Palaeozoic rock cover in the south. Triassic and Jurassic sediments composed of alternating cycles of sandstones, carbonates, shales and some gypsum crop out in the central part of the Jordan Valley east of the Dead Sea and Wadi Zerqa River. These sediments reflect littoral, lagoonal and marine origin. They are restricted to the above mentioned localities and unconformably overlie Lower Palaeozoic sandstones, whereas further south the Palaeozoic strata are mainly overlain by Lower Cretaceous Kurnub Sandstones (see a. o.: COX, 1924, 1932; WETZEL & MORTON, 1959; PARKER, 1970; BASHA, 1981; BANDEL & KHOURY, 1981; AQRABAWI, 1987; SHINAQ, 1990).

Throughout the deposition of the Lower Cretaceous Kurnub Sandstone, the shore-lines lay off north Jordan with a NE-SW trend. Uplift of the hinterland of Jordan resulted in erosion and recycling of the Palaeozoic siliclastic sediments which were deposited on the pre-Kurnub peneplain as mature siliclastics in a fluvial braided stream environment (POWELL, 1989). The Lower Cretaceous sandstones are unconformably overlain throughout most of Jordan by a thick Cenomanian-Turonian sequence of predominantly carbonate rocks of the Ajlun Group which reflect a major transgressive sequence as the Tethys Sea advanced southward across the coastal plain, situated adjacent to the present-day Mediterranean coast (FLEXER et al. 1986). The Ajlun Group is unconformably overlain by another sequence of limestones, chalks, biogenic cherts and phosphorites with oyster bioherms (Belqa Group) of Coniacian-Eocene age. These sediments were deposited in inner- to midshelf environments during an extensive transgressive phase when the Tethys reached further south to Saudi Arabia (POWELL, 1989). Erosion and uplift occurred during a number of phases at Upper Eocene to Pleistocene removed much of the Belqa Group in east and Southeast Jordan and produced fluvial, lacustrine deposits of Oligocene to Miocene-Pliocene age near the margins of the Jordan Rift system, or Quaternary fluvial and lacustrine in East Jordan. Throughout the Quaternary detritus was transported into the Rift Valley, and the extensive Azraq-Wadi Sirhan and El-Jafr depression of East Jordan. These depressions were partly covered by fresh and brackish water lakes during pluvial periods of the Pleistocene, while fluvial conglomerates of the same period spread over extensive areas along the eastern slope of the mountain ridges bordering the eastern flank of the Wadi Araba-Jordan Rift (see a. o.: MASRI, 1963; BENDER, 1968, 1975; PARKER, 1970; BASHA, 1979; POWELL, 1989).

2.2. Lithostratigraphical nomenclature of the Upper Cretaceous rocks of Jordan:

Upper Cretaceous rocks crop out throughout most of Jordan overlying sediments of Lower Cretaceous Kurnub Sandstone Group. They are generally composed of limestones, marls, chalk, biogenic chert and phosphate of mainly marine origin. Age determinations of these rocks are based on the abundant micro and macrofossil contents. The different lithostratigraphical subdivisions

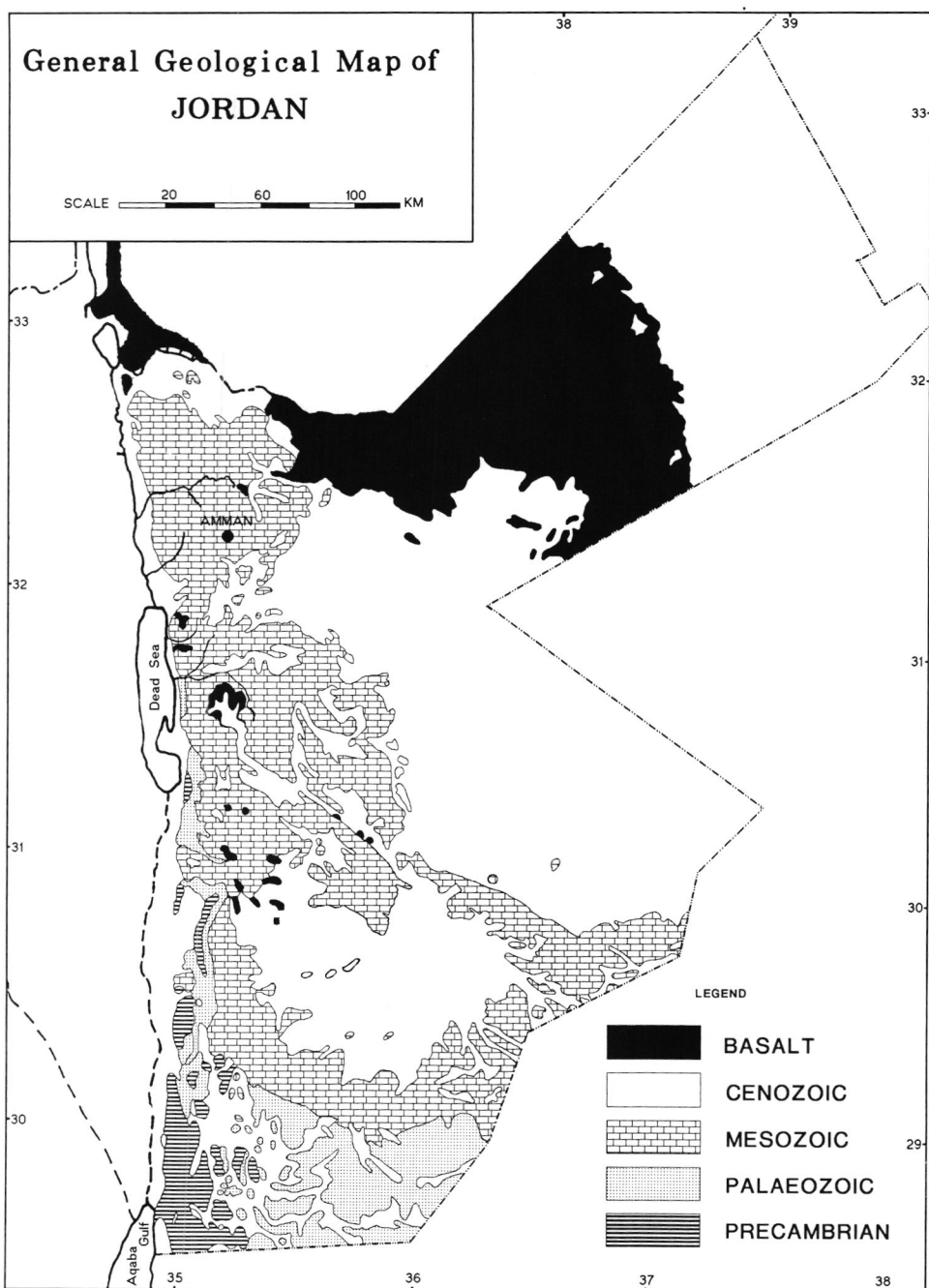


Fig. 2: Generalised geological map of Jordan (after BENDER, 1968).

are shown in (fig. 4), herein, the subdivisions of POWELL (1989) are currently considered. Ajlun Group (Cenomanian-Turonian) and the lower part of Belqa Group (Coniacian-Maastrichtian) form the base of this study because of their abundant oyster fossil contents. For the purpose of this study, two compiled columnar sections, as reference sections for the Upper Cretaceous rocks of Jordan,

were measured: the first in Wadi Salihi area (fig. 5) north of Amman (location fig. 1), and the second in Wadi Mujib (fig. 6) in Central Jordan (location fig. 1). Oyster samples were collected along the two sections and samples collected elsewhere were compared with these reference sections.

2.2.1. Ajlun group

Strata of this group directly overlie the Lower Cretaceous Kurnub Sandstone Group and crop out in North Jordan and along the margins of the Rift to Ras-El-Naqab area in the South (fig. 3). This group ranges in thickness from 600 m at Irbid in the North and decreases gradually in the southern and south-eastern directions (450 m in Wadi Mujib, 180 m in Ras-El-Naqab and zero in Batn-El-Ghul) (POWELL, 1989: 25, 27). According to POWELL (1989), the group is subdivided into six formations.

2.2.1.1. Naur Limestone Formation

This cliff-forming formation (?Albian-Lower Cenomanian) unconformably overlies the Kurnub Sandstone Group from northern to southern Jordan along the eastern margins of the Jordan Rift. It comprises a maximum thickness of 220 m and is subdivided into four members. The lower (Wadi Juhra Member) is mainly composed of sandy marls and dark grey shales with some shelly fauna and plant fossils mainly in the lower most part. It is followed by Member (B): a cliff-forming dolomite, dolomitic limestones and limestones with some chert nodules and abundant *Thalassinoides* burrows (filled with dolomite) which impart a distinctive nodular texture (ABED & SCHNEIDER, 1982). *Pycnodonte vesiculosus* (SOWERBY) (Wadi Salihi, North Jordan) and *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS) (Wadi Mujib, Central Jordan) associated with gastropod moulds which are very common especially in the middle part below the beds rich in the large foraminifera *Orbitulina concava* (LAMARCK). Member (C) consists of marls, dark grey shales and grey limestones with *Thalassinoides* burrows, gastropods, echinoids and bivalves with abundant *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS). Member (D) is composed of cliff-forming dolomites, dolomitic limestones with grey chert nodules. The upper part also contains *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS).

2.2.1.2. Fuheis Formation

This formation overlies the Naur Formation throughout most of North Jordan and has a maximum thickness of 80m. It is composed of fossiliferous marls and marly limestones with thin coquina oyster packstone beds – *Rhynchostreon mermeti* (COQUAND) in Wadi Salihi section (North Jordan) and *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS) in Wadi Mujib section (Central Jordan). *Laevigyra luynesi* (LARTET) and *Laevigyra dhondtae* MALCHUS are present. In addition to the oysters, moulds of bivalves, gastropods and echinoids are present. The formation is assigned to ?Middle to Upper Cenomanian age (see WETZEL & MORTON, 1959; BASHA, 1979; DILLEY, 1985; BARTOV et al., 1972; BANDEL & GEYS, 1985).

2.2.1.3. Hummar Formation

This formation crops out in North Jordan and thins rapidly south of Wadi Mujib-Central Jordan (60–85 m in Amman area and 10 m in Wadi Mujib). It cannot be recognised in central and southern Jordan due to lateral passage to soft marl-siltstone beds (POWELL, 1989). The formation is cliff-forming and consists of grey limestones, dolomitic limestones and dolomites with a relatively poor macrofossil content such as *Exogyra* (*Costagyra*) *olisiponensis* (SHARPE),

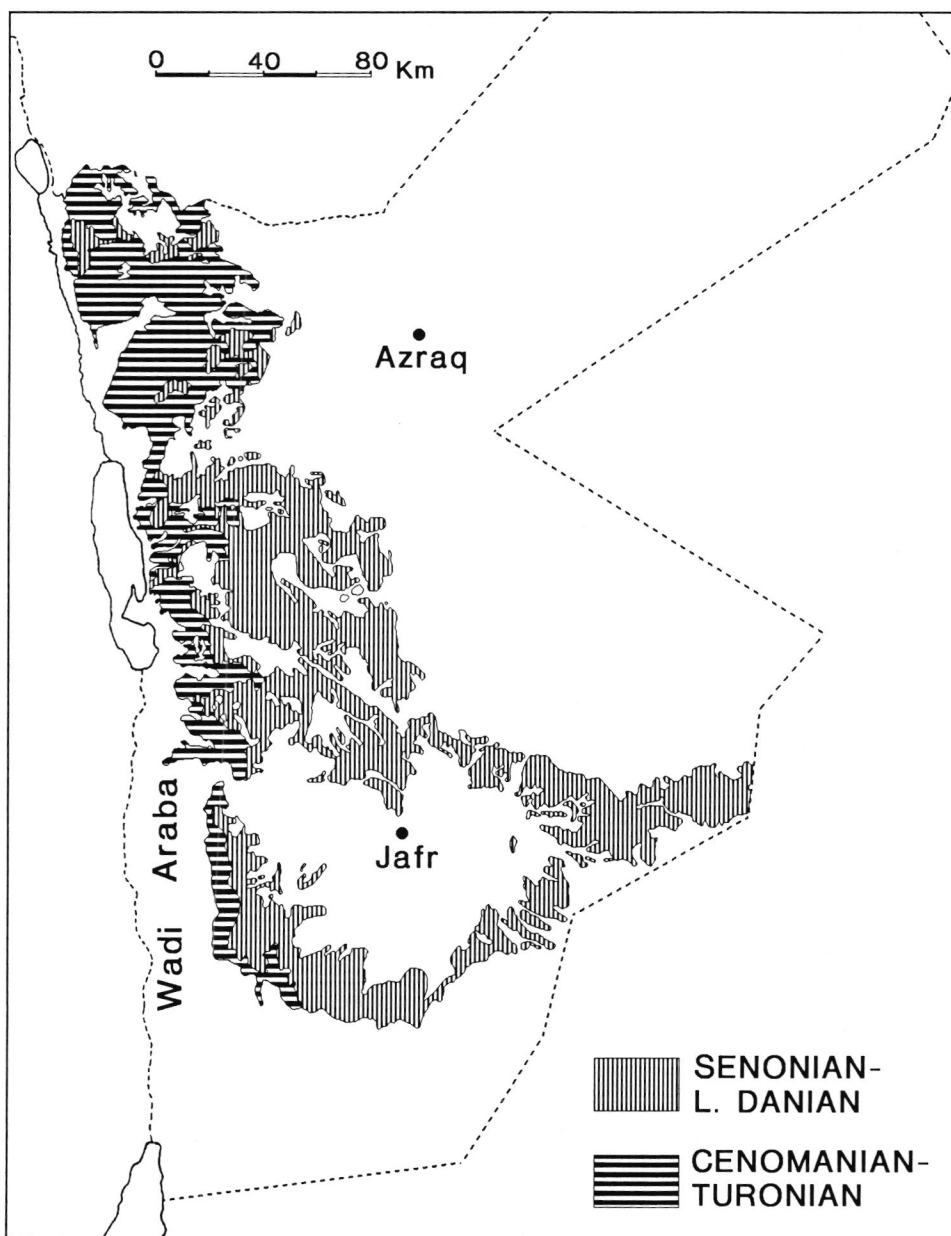


Fig. 3: Distribution of the outcropping Upper Cretaceous rocks in Jordan (data after BENDER, 1975). Cenomanian-Turonian represents the Ajlun Group, and Senonian-Danian represents the Upper Cretaceous part of Belqa Group.

Laevigyra luynei (LARTET) and *Plicatula auressensis* (COQUAND). It is assigned to Upper Cenomanian age (see POWELL, 1989: 48).

2.2.1.4. Shuayb Formation

This formation consists of about 50 m of thinly bedded limestone, marly limestone and marl. It has a soft-weathering appearance and it is fossiliferous in

most parts. This formation overlies the Hummar Formation in north-central and northern Jordan. In central and southern Jordan, where the Hummar Formation is absent, the base of Shuayb Formation is not traceable, it is included in the undifferentiated Fuheis/Hummar/Shuayb unit. The formation is assigned to Lower Turonian age according to its micro- (mainly foraminifera) and macrofossils. The marly parts are rich in oysters such as *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS), *Rhynchostreon mermeti* (COQUAND), *Ilymatogyra* (*Afrogyra*) *africana* (LAMARCK) and *Laevigyra luynesi* (LARTET) (only in the upper most parts) in addition to other bivalves and gastropods, echinoids and ammonites (see WETZEL & MORTON, 1959; DILLEY, 1985 (sensu POWELL, 1989); POWELL, 1989).

2.2.1.5. Fuheis/Hummar/Shuayb (undifferentiated)

The thickness of Fuheis, Hummar and Shuayb Formations decreases gradually southwards, the boundaries between the three formations are not traceable in central and southern Jordan. Therefore, they are treated as an undivided unit equivalent to the three formations of North Jordan. This unit consists predominantly of marls, mudstones, thin-bedded nodular limestone and gypsum. These rocks are subject to landslip and debris-flow which obscure the outcrop in most areas. They comprise about 150 m in Wadi Mujib-Central Jordan and about 50 m in Ras-El-Naqab area-South Jordan. The marly base of this unit is fossiliferous, it comprises diverse micro- and macrofauna mainly foraminifera, ostracoda, echinodermata, gastropoda and bivalvia of Upper Cenomanian-Lower Turonian age. Oysters present are: *Curvostrea rowvillei* (COQUAND), *Exogyra* (*Exogyra*) *italica* (SEGUEZZA), *Ilymatogyra* (*Afrogyra*) *africana* (LAMARCK), *Exogyra* (*Costagyra*) *olisiponensis* (SHARPE), *Laevigyra luynesi* (LARTET), *Laevigyra dhondt* MALCHUS, *Rhynchostreon mermeti* (COQUAND) and *Pycnodonte* (*Phygraea*) *vesiculosum* (SOWERBY).

2.2.1.6. Wadi As Sir Limestone Formation

Throughout most of Jordan, the Wadi As Sir Limestone Formation represents the topmost formation of Ajlun Group and is disconformably overlain by the white chalks of the Belqa Group. This formation is distributed along the Rift escarpment from north to south Jordan and is present to the east of Hamza-Azraq basin in Jabal Waqf As Suwwan and in Zakimat El Hasa. It wedges out southeastwards along the escarpment between Ras-El-Naqab and Batn-El-Ghul, where Turonian fluvial sandstones similar to the Lower Cretaceous Kur-nub facies were deposited (POWELL, 1989: 60). The formation consists of well-bedded massive limestones, dolomitic limestones and dolomites with some chert nodules and local beds of gypsum. It comprises a thickness of 140 m in Wadi Mujib, about 100 m in Amman area, about 120 m in Karak area and 65 m in Jabal Waqf As Suwwan. According to its Foraminifera and Ammonite contents, the formation is assigned to Turonian-Coniacian age (WETZEL & MORTON, 1959; BASHA, 1978). The base of the section in Wadi Wala is predominated by *Oscillophala wala* n. sp. whilst *Exogyra* (*Costagyra*) *olisiponensis* (SHARPE) is frequently present in the Salihi section north of Amman.

2.2.1.7. Khureij Limestone Formation

This formation is composed of 100–120 m thick soft-weathering alternations of marls, limestones, dolomitic limestones and dolomites. It overlies the Wadi As Sir Formation in Jabal Khureij (central to southern Wadi Araba) and is only locally developed due to non-deposition or pre-Belqa Group erosion or a combination of these effects, during the Coniacian. POWELL (1989: 72) suggested a Coniacian to Santonian age for the sequence in Jabal Khureij; his suggestion

SYSTEM		SERIES	STAGE	GROUP	FORMATION	MEMBER	
C R E T A C E O U S	TERT.		PALEOCENE	BELQA GROUP	MUAQQAR CHALK-MARL		
			MAASTRICHTIAN		AL-HISA PHOSPHORITE	Qatrana Phosphorite	
						Bahiya Coquina	
						Sultani Phosphorite	
			CAMPANIAN		AMMAN SILICIFIED LIMESTONE		
						Mutarammil Coquina	
			SANTONIAN	WADI UMM- GHUDRAN CHALK	Dhiban Chalk		
			CONIACIAN		Tafila		
					Mujib Chalk		
			TURONIAN	AJLUN GROUP	WADI AS-SIR LIMESTONE		
			CENOMANIAN		SHUAYB	Undifferentiated in Central and South Jordan	
					HUMMAR		
					FUHEIS		
					NAUR LIMESTONE		D
			C				
			B				
			Wadi Juhra				
		L.			KURNUB SANDSTONE		

Fig. 4: Nomenclature for the Upper Cretaceous rocks of Jordan (after POWELL, 1989).

is based on preliminary age determinations of ostracods and bivalves (no oysters).

2.2.2. Belqa group

The predominantly pelagic sediments of Belqa Group (chalks, marls, cherts and phosphates) disconformably overlie the Ajlun Group throughout most of Jordan (fig. 3). The group is assigned to Upper Cretaceous (Coniacian) to Tertiary (Upper Eocene) age. It comprises an outcropping thickness of about 600 m in Irbid area and 400–450 m in Ehd Dhira area in the north, 550–600 m in Shawbak area and more than 320 m in Gharandal in the south. The group is subdivided into six formations, four of which are within the Cretaceous period and two are within the Tertiary (see POWELL, 1989)

2.2.2.1. Wadi Umm Ghudran Formation

This formation is mainly composed of soft chalk with some limestone and chert beds or nodules. It overlies the Wadi As Sir Formation and can be traced from north Jordan to central Jordan along the eastern Rift margins, but south of Wadi Tafila the chalks are absent or very thin and the unit is not readily distinguished from the overlying Amman Silicified Limestone Formation. In the area south of Amman, between Madaba and Tafila, the formation is subdivided into three members: the Mujib Chalk, Tafila and Dhiban Chalk, the lithology of the lower and the upper members is similar, consisting of white to grey-white massive chalk with fish fragments, shark teeth, phosphate granules and small bivalve fragments. The middle, Tafila Member, is composed of chalks and chalky marls intercalated with thin lime-stone and chert beds and nodules. The formation ranges, in exposed thickness, between 87 m in Wadi Mujib, central Jordan and 32 m in Waqf As Suwwan, south-eastern Jordan. It is assigned to Upper Coniacian to Santonian age according to the presence of some ammonites, planktonic foraminifera, ostracoda and calcareous nanoplanktons. The small oyster *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK) forma *nikitini* (ARKHANGUELSKY) is found in the three members in many localities (see WETZEL & MORTON, 1959; BENDER, 1968; POWELL, 1989).

2.2.2.2. Amman Silicified Limestone Formation

This formation is composed of predominantly massive, dark-weathering cherts which exhibit a variety of textures ranging from homogenous to brecciated limestone (as beds or concretion), dolomitic chalky marls, oyster coquinal beds and minor amounts of phosphates (as granules or peloides). In Central Jordan, thin to thick oyster-coquinal beds are present. They consist of fragments or complete shells mainly composed of *Nicaiolopha nicaisei* (COQUAND). The cross-stratified beds indicate strong water currents that reworked and abraded the beds into dune-like banks. The thin beds without cross-bedding to the west and north suggest deeper water zones (POWELL, 1989: 95). The formation measures a maximum thickness of 100 m in Wadi Mujib, about 60 m in Amman-Zerqa area, about 50 m in Irbid area, 45 m in Ras-El-Naqab and only 13 m in Zakimat Al Hisa (POWELL, 1989:97). It is assigned to Campanian age according to its micro- and macrofaunal content. Oysters present are *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK) forma *typica*, *Nicaiolopha nicaisei* (COQUAND) and *Gryphaeostrea canaliculata* (SOWERBY).

2.2.2.3. Al Hisa Phosphorite Formation

This formation is as well heterogenous in lithology as the underlying Amman Silicified Limestone Formation. It consists of predominantly phosphate beds with chert, limestones (as beds or nodules), marls, chalky marls and oyster-coquinal beds or oyster-bioherms. The latter form a very distinctive feature in the phosphate belt in Central Jordan, where they are separately mapped as Si-waqa Coquina and Bahiya Coquina by the Jordanian Geological Mapping Divi-

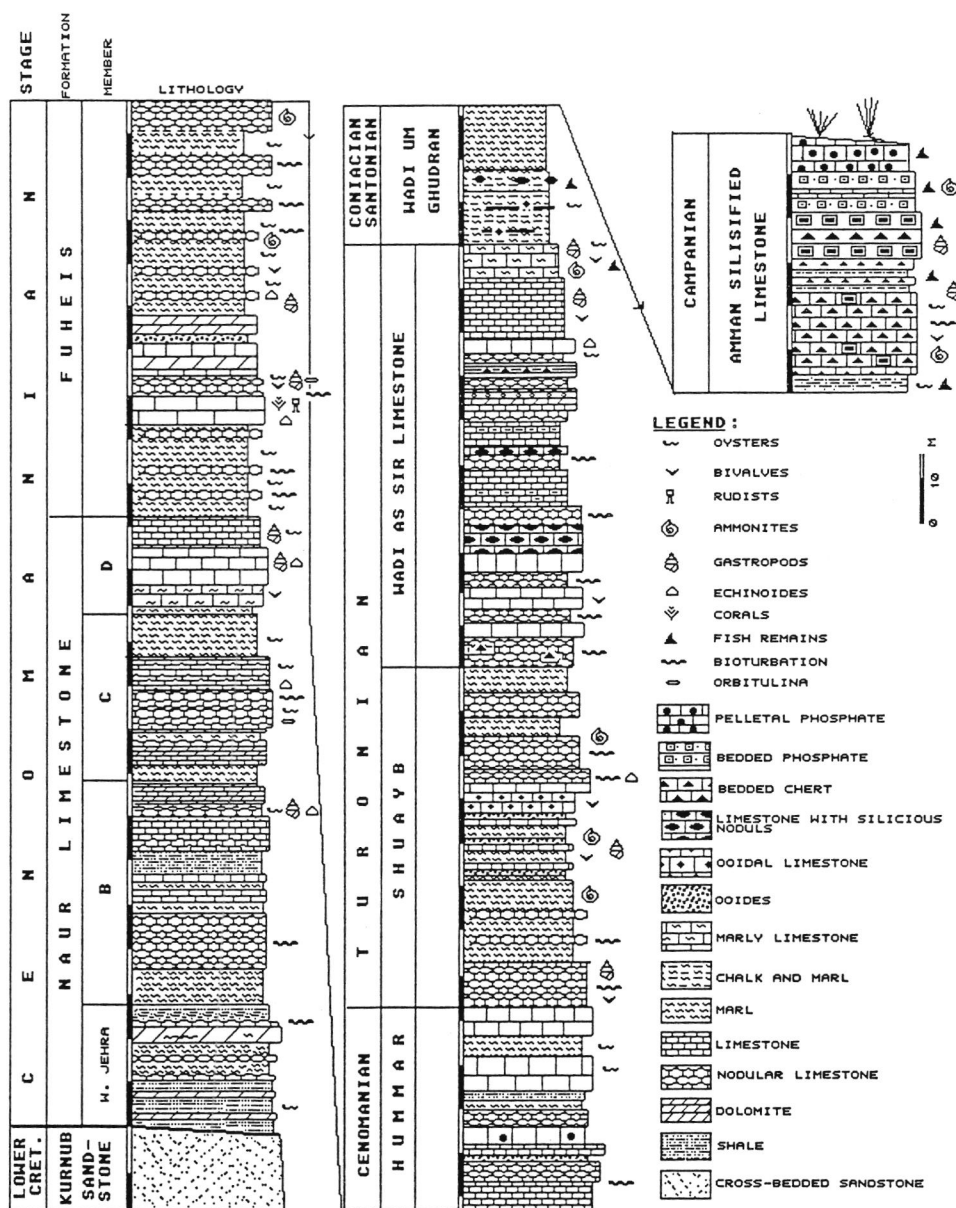


Fig. 5: Compiled columnar section of Wadi Salihi, north of Amman (modified after BANDO & GEYS, 1985).

sion-NRA (see EL-HIYARI, 1985; BARJOUS, 1986; KHALIL, 1986). These beds are composed of relatively fine oyster shell fragments or large complete oysters – *Ambigostrea villei* (COQUAND) and *Oscillophra figari* (FOURTAU) – and range from bioherm accumulations to parallel bedded strata (POWELL, 1989: 101–102). The formation is subdivided into four members: Siwaqa Coquina (up to 30 m thick), Sultani Phosphorite (15–20 m thick), Bahiya Coquina (up to 20 m thick) and Qatrana phosphorite (5–20 m thick). It is assigned to Campanian age according to age determinations done on ammonites, bivalves and microfossils. Oysters

present are: *Pycnodonte (Phygraea) vesiculare* (LAMARCK), *Nicaiolopha nicaisei* (COQUAND) and *Oscillopna figari* (FOURTAU).

2.2.2.4. Muwaqqar Chalk Marl Formation

This formation overlies the Al Hisa Phosphorite Formation along the Rift margin and spreads eastwards and forms the low-dipping terrains of the eastern Jordanian plateau. It is composed of soft, thick-bedded chalky marl, marl, and chalky limestone with harder beds and nodules of microcrystalline limestone and chert. It is assigned to Maastrichtian-Paleocene age and contains the Upper Cretaceous-Tertiary boundary in Jordan which is marked by foraminifera and ammonites (a. o. WETZEL & MORTON, 1959; BENDER, 1975; YASSINI, 1979). The formation varies in thickness from 330 m in Irbid area North Jordan to 20 m in Ras-El-Naqb South Jordan (POWELL, 1989: 110). Oysters were not found throughout the formation.

2.3 Biostratigraphy

Oysters in Jordan are mainly represented in small to large accumulations mostly consisting of one or two species which varies from one locality to another. For example: *Pycnodonte (Phygraea) vesiculosum* (SOWERBY) appears in Member (B) of Naur Limestone Formation in Wadi Salihi section, north of Amman, further south in Wadi Mujib, Central Jordan, it is replaced by *Amphidonte (Ceratostreon) flabellatum* (GOLDFUSS) in the same Member. Therefore, it is difficult to establish a successful biostratigraphic zonation. Furthermore, only a few studies were done on Upper Cretaceous biostratigraphy based on Jordanian macrofossils and non of which were based on bivalves. Thus, it was not possible to compare or include oysters in other biostratigraphic zones. However, the stratigraphic range of the Jordanian fauna shows that some species such as *Oscillopna wala* n. sp., *Oscillopna figari* (FOURTAU), *Laevigyra luynesi* (LARTET), *Laevigyra dhondtae* MALCHUS, *Ambigostrea villei* (COQUAND) and *Pycnodonte (Costeina)* sp. appear only in certain time intervals within the Upper Cretaceous of Jordan (see fig. 7). It is also possible to establish local mapable lithostratigraphic units based on large oyster bioherms such as Siwaqa Coquina and Bahiya Coquina (POWELL, 1989) which are restricted to localities within the phosphate belt of Jordan.

3. Comparison between Jordanian and Northwest European Upper Cretaceous oysters

3.1. Stratigraphic distribution of oysters in Jordan

Cox (1924, 1932) reported, among other bivalves and cephalopods, *Ostrea montiscaprilis* (KLIPSTEIN) from the Wadi Hisban area in the northwestern corner of the Dead Sea. The Triassic localities described by Cox were visited several times by the author and others and oysters could not be found. The only information known about this oyster is the description of Cox (1924), since material of this species is not available for this study for further microstructural and morphological analysis.

The first report on Jurassic oysters from Jordan was published by Cox (1925) on material collected by WYLLIE, CAMPBELL and LEES from the mouth of Zerqa River, north of Amman. He described *Ostrea jabbokensis* Cox (now known as *Gryphaeligmus jabbokensis* (COX)) and *Ostrea israelis* Cox which is not known from other reports. Later *Gryphaeligmus jabbokensis* (COX) and *Africogryphaea costellata* (DOUVILLÉ) were reported from the Bajocian-Bathonian strata of Jordan by many authors. They were placed in different genera in the

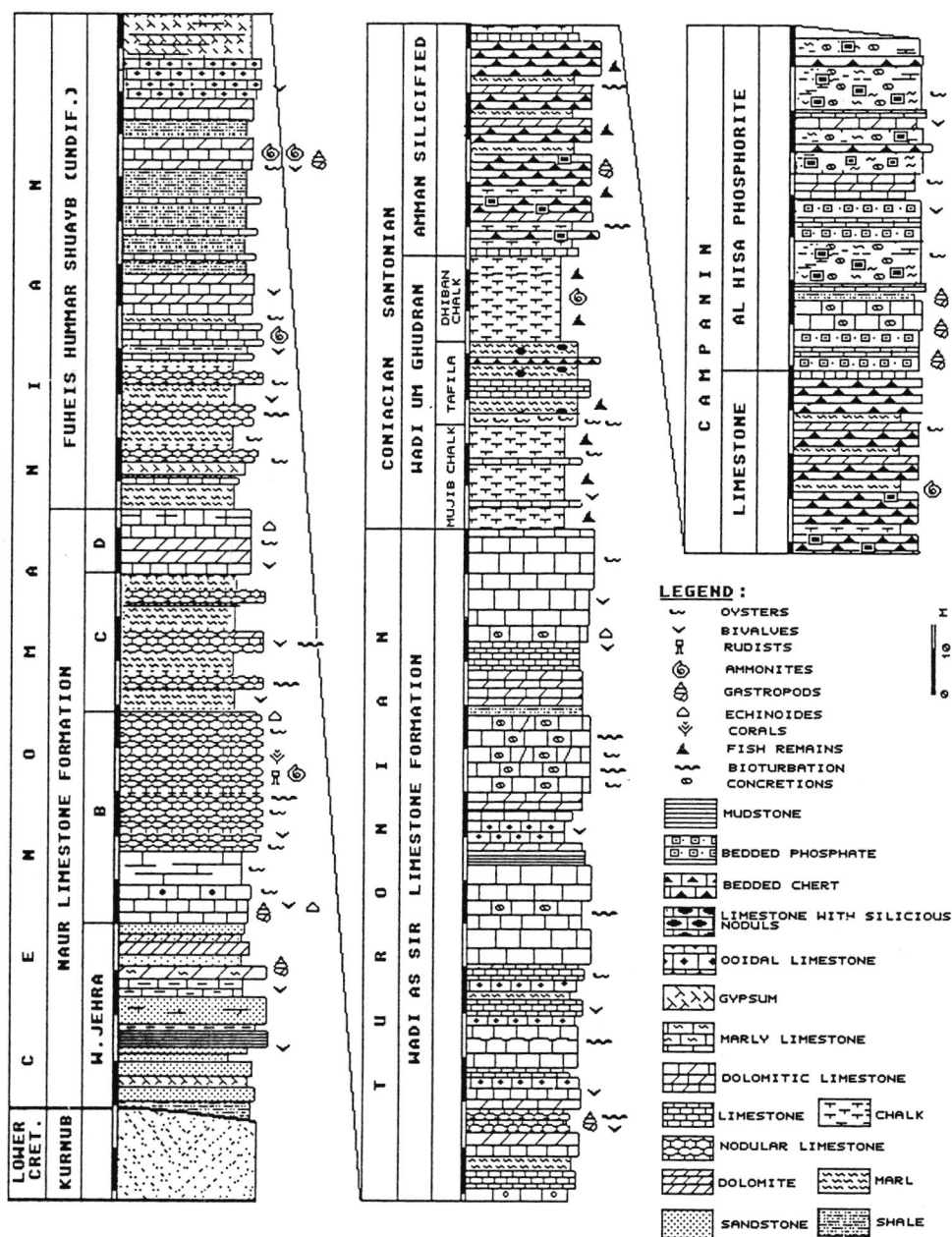


Fig. 6: Compiled columnar section of Wadi Mujib, Central Jordan.

families Malleidae and Ostreidae (see BLAKE, 1936; IONIDES & BLAKE, 1939; WETZEL & MORTON, 1959; and AQRABAWI, 1987). Material of this study was collected from the Wadi Zerqa River, Wadi Huni, Deir Alla, Old Jerash Bridge and Arda area, north and northwest of Amman. They were found associated with other bivalves, cephalopods and brachiopods of Bajocian-Bathonian age (see AQRABAWI, 1987: 58-68, 95, 100). *Gryphaeligmus jabbokensis* (Cox) is also known from Bajocian-Bathonian rocks of Sinai (HIRSCH, 1980; LEWY, 1982) and Central Ara-

bia (POWERS et al. 1966). *Africogryphaea costellata* (DOUVILLÉ) is known from Bathonian-Callovian rocks of Egypt and Tunisia (DOUVILLÉ, 1916; FRENEIX, 1965; HIRSCH, 1980; MALCHUS, 1990).

Oysters are not present throughout the Lower Cretaceous sequence in Jordan. Most probably, they did not exist in the changing depositional environments which produced the Kurnub Sandstone.

Upper Cretaceous carbonate rock sequences of Jordan are generally rich in fossils. Macrofossil groups such as echinoderms, cephalopods, gastropods and bivalves are present. Oysters are among the most frequent and best preserved shells within these sequences. *Pycnodonte* (*Phygraea*) *vesiculosum* (SOWERBY) appears first in the Member (B) of the Naur Limestone Formation in Wadi Salih section north of Amman. It is assigned to Lower Cenomanian age and represents the oldest oyster in this section. Further south, in Wadi Mujib section of central Jordan, it is replaced by *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS) in the same member.

The changing environment – from deeper marine in the north to shallower marine to the south and east – is possibly responsible for such replacement. According to MALCHUS (1990: 43), *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS) is the oldest known Cretaceous oyster in Egypt. It is assigned to Lower-Middle Albian to Upper Cenomanian age. In Jordan, it is known only from the Cenomanian.

Oysters are present throughout all Upper Cretaceous stages in Jordan, but they are better distributed in the Cenomanian-Lower Turonian and in the Campanian stages (fig. 7). Cenomanian to Lower Turonian oysters of Jordan are: *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS), *Ilymatogyra* (*Afrogyra*) *africana* (LAMARCK), *Pycnodonte* (*Phygraea*) *vesiculosum* (SOWERBY), *Exogyra* (*Costagyra*) *olisiponensis* (SHARPE), *Exogyra* (*Exogyra*) *italica* (SEGUENZA), *Rhynchostreon* *mermeti* (COQUAND), *Laevigyra* *luynesi* (LARTET), *Laevigyra* *dhondtae* MALCHUS and *Curvostrea* *rouvillei* (COQUAND). They are well distributed over the different formations of the Cenomanian-Lower Turonian stages. In the Middle and Upper Turonian only *Oscillopsa* *wala* n. sp. from the Wadi Wala in Central Jordan is reported. The Wadi Umm Ghudran Formation (Coniacian-Santonian) marks a disconformity surface between the Ajlun and Belqa Groups. Typical of this formation is *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK) forma *nikitini* (ARKHANGUELSKY). In the beginning of the Campanian, new sedimentation environments and ratios of deposition occurred and new faunal accumulations were created. Oysters such as *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK), *Gryphaeostrea* *canaliculata* (SOWERBY), *Nicaiolopha* *nicaisei* (COQUAND), *Ambigostrea* *villei* (COQUAND) and *Oscillopsa* *figari* (FOURTAU) are present in the Amman Silicified Limestone and Al Hisa Phosphorite Formations of Campanian age.

3.2. Stratigraphic distribution of Upper Cretaceous oysters in Northwest Europe

Oysters were a major component of the bivalve fauna throughout the Cretaceous System of northwestern Europe. They mostly lived in oyster-banks dominated, in most cases, by one species which varies from one locality to another (see also SURLYK, 1980: 36; DHONDT, 1984a: 53). The stratigraphic record of the Cretaceous oysters in northwestern Europe suggests that oysters were more represented in the Upper Cretaceous sediments.

The studied oysters from Europe can be subdivided, according to their stratigraphic distribution (fig. 8), into two groups:

C r e t a c e o u s										Series
Alb.	U p p e r									Stage
	Cenomanian			Turonian		Coniacian-Santonian		Campanian		Formation
	Naur	Limestone	Fuheis	Hummar	Shuayb	W. As Sir	Khureij	Wadi Umm	Amman	Al Hisa
	W. Jahra	B	C			Limestone	Limestone	Ghudran	Silicified	Phosphorite
										Oscillophra wala n. sp.
										Oscillophra figari
										A. (Ceratostreon) flabellatum
										E. (Exogyra) italica
										E. (Costagyr) olisiponensis
										Rhynchostreon mermeti
										I. (Afrogyra) africana
										Laevigyra luynesi
										Laevigyra dhondtae
										Gryphaeostrea canaliculata
										P. (Phygraea) vesiculosum
										P. (Phygraea) vesiculare
										P. (Costeina) sp.
										Nicaiolopha nicaisei
										Curvostrea rouvillei
										Curvostrea sp.
										Ambigostrea villei

Fig. 7: Stratigraphic distribution of the Upper Cretaceous oysters of Jordan.

The first group is more or less concentrated in the Cenomanian-Turonian stages. It includes: *Rastellum diluvianum* (LINNÉ), *Rastellum carinatum* (LAMARCK), *Amphidonte (Amphidonte) obliquatum* (PULTENEY), *Amphidonte (Amphidonte) sigmoideum* (REUSS), *Amphidonte (Ceratostreon) flabellatum* (GOLDFUSS), *Rhynchostreon suborbiculatum* (LAMARCK), and *Gryphaeostrea canaliculata* (SOWERBY).

SYSTEM	STAGE	<i>Rastellum diluvianum</i>	<i>Rastellum carinatum</i>	<i>Oscillopsa dichotoma</i>	<i>A. (Amphidonte) haliotoideum</i>	<i>A. (Amphidonte) signoides</i>	<i>A. (Amphidonte) obliquatum</i>	<i>A. (Cerastostreon) fiabellatum</i>	<i>A. (Cerastostreon) pliciferum</i>	<i>A. (Vultogryphaea) laciniatum</i>	<i>Rhynchostreon suborbiculatum</i>	<i>Gryphaeostrea canaliculata</i>	<i>P. (Phygraea) vesiculare</i>	<i>Hyotissa semiplana</i>	<i>Agerostrea unguolata</i>	<i>Agerostrea lunata</i>
C R E T A C E O U S	MAASTRICHTIAN															
	CAMPANIAN															
	SANTONIAN															
	CONIACIAN															
	TURONIAN															
	CENOMANIAN															
	ALBIAN															
	APTIAN															

Fig. 8: Stratigraphic distribution of the Upper Cretaceous oysters of Northwest Europe.

The second group is more or less concentrated in the Coniacian-Maastrichtian stages. It includes: *Oscillopsa dichotoma* (BAYLE), *Amphidonte (Cerastostreon) pliciferum* (DUJARDIN), *Amphidonte (Vultogryphaea) laciniata* (NILSSON), *Agerostrea unguolata* (SCHLOTHEIM), and *Agerostrea lunata* (NILSSON).

However, oysters such as *Amphidonte (Amphidonte) haliotoideum* (SOWERBY), *Pycnodonte (Phygraea) vesiculare* (LAMARCK), and *Hyotissa semiplana* (SOWERBY) have a relatively wider stratigraphic range. *Amphidonte (Amphidonte) haliotoideum* (SOWERBY) was originally described from Cenomanian rocks of England (SOWERBY, 1813), later reported from Cenomanian to Maastrichtian strata of northwestern Europe (NILSSON, 1827; GOLDFUSS, 1833; GRÜNDEL, 1982a). Specimens of this study represent the Campanian stage of southern Sweden. *Pycnodonte (Phygraea) vesiculare* (LAMARCK) is a well known cosmopolitan species with a wide geographic and stratigraphic range. European

specimens of this study were collected from the Senonian of North Germany. *Hyotissa semiplana* (SOWERBY) was first described from Campanian rocks of England (SOWERBY, 1813), later reported from Cenomanian-Turonian strata of Europe. Specimens of this study were collected from eastern Germany and Bohemia and represent, according to GRÜNDEL (1982b), Cenomanian-Turonian stages.

The stratigraphic distribution of the Northwest European oysters is comparable with that of Jordan and possibly with other Tethyan oysters from other localities in North Africa and South Europe (see DHONDT, 1981).

DHONDT (1981: 307) related the increase in number of species in the Cenomanian and in the Campanian to major transgression phases occurring at the beginning of these systems. She also related the decrease in number of species in the Turonian to Santonian to the relative short duration of these intervals and to sudden changes in facies.

3.3. Palaeobiogeography

The Cretaceous continents and oceans are subdivided according to the global distributions of the different Cretaceous bivalve fossils into three major palaeobiogeographic units (KAUFFMAN, 1973: 355) (fig. 9):

Tethyan Realm including the Mediterranean and Caribbean provinces; North Temperate Realm including the North European, North American and North Pacific provinces; and South Temperate Realm including the East African and Austral provinces.

According to this subdivision, the present Middle East was during the Cretaceous times a portion of the Mediterranean province which was covered by the Tethyan Sea; and the present Northwest Europe represented during the Cretaceous times the North European province of the North Temperate Realm which includes the main part of the "Boreal Realm" used by other authors.

KAUFFMAN (1973: 359), among other authors, considered most Cretaceous oysters as cosmopolitan (occur in more than one realm). However, a general look at the Upper Cretaceous oyster representatives in North European and Mediterranean provinces shows that some of these taxa may be endemic. The three major oyster families are represented in the Upper Cretaceous of both realms. Both realms are dominated by members of the subfamily Exogyreinae VIALOV of the family Gryphaeidae VIALOV. Members of the tribe Exogyreini VIALOV of the subfamily Exogyreinae VIALOV predominate oysters of Jordan (fig. 10) and other countries within the Mediterranean province such as Egypt (ABBASS, 1962; MALCHUS, 1990), Morocco (FRENEIX, 1972), South Italy (MORONI & RICCO, 1968) and Spain (DHONDT, 1984b).

On the other hand, the North European Upper Cretaceous oysters are dominated by members of the tribe Nanogyriini MALCHUS of the same subfamily (fig. 10) (see WOODS, 1913; DHONDT, 1985; FRENEIX & VIAUD, 1986). The only exogyrid species reported from the Upper Cretaceous of North Europe is *Rhynchostreon suborbiculatum* (LAMARCK), this species is not known from Jordan and the Middle East. Nanogyrids such as *Amphidonte* (*Amphidonte*) *haliotoideum* (SOWERBY), *Amphidonte* (*Amphidonte*) *sigmoideum* (REUSS) and *Amphidonte* (*Vultogryphaea*) *laciniata* (NILSSON) are not reported from the Mediterranean province, they are better known from the North European province of the North Temperate Realm. Exogyrids such as *Rhynchostreon mermeti* (COQUAND), *Ilymatogyra* (*Afroygyra*) *africana* (LAMARCK), *Laevigyra luynesi* (LARTET), *Laevigyra dhondtae* MALCHUS and *Exogyra* (*Exogyra*) *italica* (SEGUENZA) range in their distribution within the Tethyan Realm and are better known from the Mediterranean pro-

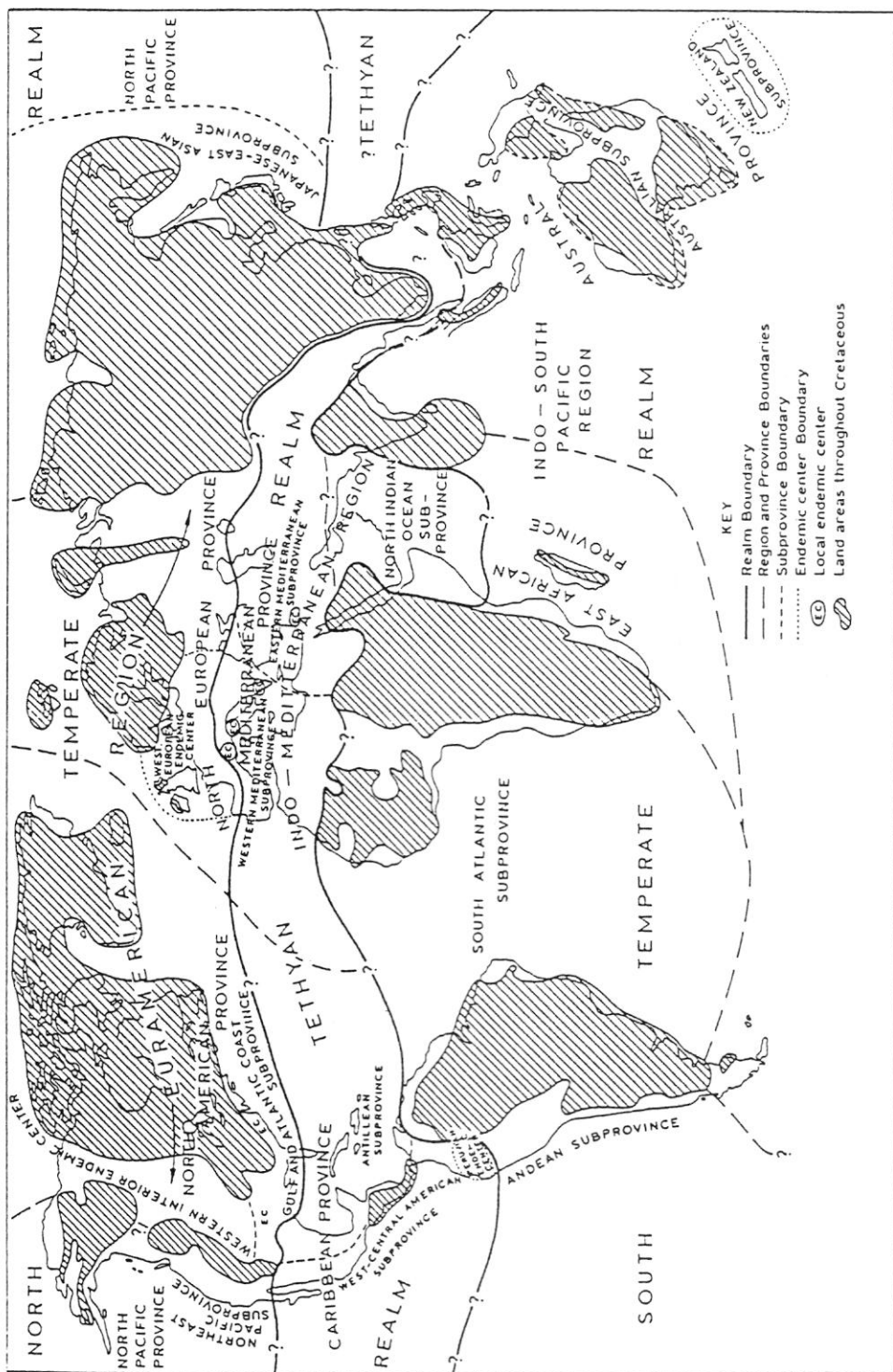


Fig. 9: Distribution of palaeobiogeographic units based on Upper Cretaceous bivalves. (after KAUFFMAN, 1973)

vince. Also Jordanian representatives of the tribe Liostreini MALCHUS and the tribe Ambigostreini MALCHUS such as *Nicaisolopha nicaisei* (COQUAND) and *Ambigostrea villei* (COQUAND) in addition to some members of the tribe Oscillophini MALCHUS such as *Oscillopoda figari* (FOURTAU) and *Oscillopoda wala* n. sp. are not reported from North Europe and most probably not anywhere within the North Temperate Realm. They are known from the Mediterranean province (see GRECO, 1918; FRENEIX, 1972; MALCHUS, 1990).

Hyotissa semiplana (SOWERBY) represents the oldest known member of the genus *Hyotissa* STENZEL. It is known from Coniacian to Upper Maastrichtian strata of North Europe (DHONDT, 1985) and ?Central Asia (BOBKOVA, 1961) and not reported anywhere within the present Mediterranean region. According to DHONDT (1985: 58) it is restricted to the North European province.

Cosmopolitan species such as *Pycnodonte (Phygraea) vesiculare* (LAMARCK) known from the Upper Cretaceous white chalks of North Europe is world widely distributed and known from similar sediments in the Tethyan and Temperate Realms (see also DHONDT, 1985: 55). Also *Pycnodonte (Phygraea) vesiculosum* (SOWERBY), *Amphidonte (Ceratostreon) flabellatum* (GOLDFUSS), *Gryphaeostrea canaliculata* (SOWERBY), *Agerostrea unguolata* (SCHLOTHEIM) and *Agerostrea lunata* (NILSSON) are known in world wide distribution in the Upper Cretaceous of the Tethyan and Temperate Realms. These species do not have a great value in the regional comparison of faunal accumulations.

According to MIDDLEMISS (1979:520), the main causes of the biogeographic changes appear to be related to the movement of the lithospheric plates, alterations in patterns of sedimentations and complex changes of the climate.

Although oysters are present throughout the Upper Cretaceous sediments of Jordan, they are stratigraphically concentrated and more diversified in the Cenomanian-Lower Turonian and in the Campanian rocks. Such concentrations in the stratigraphic distributions of oysters in the Cenomanian to Lower Turonian and in the Campanian to Maastrichtian sediments are known from other countries within the Mediterranean province such as Egypt (ABBASS, 1962; MALCHUS, 1990); Libya (ROSSI-RONCHETTI & ALBANESI, 1961); Morocco (FRENEIX, 1972), South Italy (MORONI & RICCO, 1968); Spain (DHONDT, 1984b). A decrease in the number of oyster species in the Turonian to Santonian is also noticed in North Europe (sources: WOODS, 1913; DHONDT, 1981, 1984b; FRENEIX & VIAUD, 1986). DHONDT (1981, 1992) studied the stratigraphic distribution and palaeobiogeography of some Cretaceous bivalve species with calcitic shells such as oysters, plicatulids, pectinids and limids. She suggested that the increase in the number of species during the Cenomanian was related to the sudden openings of new environmental niches followed the major transgression of the beginning of the Cenomanian. In the Turonian to Santonian times, the decrease in the number of species possibly resulted from fewer available niches due to facies changes. The increasing number in species in the Campanian and Maastrichtian can be possibly explained by the same reasons (see also KAUFFMAN, 1973).

3.4. Oyster-beds and related facies types in Jordan in comparison with Northwest Europe

Upper Cretaceous oysters of Jordan occur in small to large accumulations within the carbonate sequences of Ajlun and Belqa Groups which generally reflect shallow marine environment of deposition.

Two main facies patterns within the Jordanian Upper Cretaceous carbonate sequences can be recognized:

FAM.	TRIBE	JORDAN	NORTHWEST EUROPE
Palaeolophidae	Oscillophini	Oscillopha wala n. sp. Oscillopha figari	Oscillopha dichotoma Rastellum diluvianum Rastellum carinatum
Gryphaeidae	Nanogyryni	A. (Ceratostreon) flabellatum	A. (Ceratostreon) flabellatum A. (Ceratostreon) pliciferum A. (Amphidonte) obliquatum A. (Amphidonte) haliotoideum A. (Amphidonte) sigmoideum A. (Vultogryphaea) laciniata
	Exogyryni	E. (Exogyra) italica E. (Costagryra) olisiponensis Rhynchostreon mermeti I. (Afrogyra) africana Laevigyra luynei Laevigyra dhondtae	Rhynchostreon suborbiculatum
	Gryphaeostreini	Gryphaeostrea canaliculata	Gryphaeostrea canaliculata
	Pycnodontini	P. (Phygraea) vesiculosum P. (Phygraea) vesiculare P. (Costeina) sp.	P. (Phygraea) vesiculosum P. (Phygraea) vesiculare
	Hytissini		Hytissa semiplana
Ostreidae	Flemingostreini	Nicaisolopha nicaisei	
	Curvostreini	Curvostrea rouvillei Curvostrea sp.	Agerostrea unguata Agerostrea lunata
	Ambigostreini	Ambigostrea villei	

Fig. 10: Distribution of the studied oysters in the different oyster groups.

3.4.1. Shallow carbonate-platform facies combination

This combination of facies represents a shallow, warm-water carbonate platform (READ, 1985) which was established over a wide area during the Cenomanian and Turonian times. Within this platform, mainly carbonate sediments (limestones, marly limestones, dolomites and marls) with minor tongues

of siliclastics (sandstones, siltstones and mudstones) were deposited marking a series of pulses of transgression during the deposition of the Ajlun Group (POWELL, 1989).

Pycnodonte (Phygraea) vesiculosum (SOWERBY) in northern Jordan (Wadi Salihi) and *Amphidonte (Ceratostrongeon) flabellatum* (GOLDFUSS) in central Jordan (Wadi Mujib) mark the first appearance of oysters in the Ajlun Group. Both species occur at the base of the (B) member of Naur Formation in shelly wackestone beds, with local chert nodules, mostly originated in sub-tidal to inter-tidal conditions. They are mainly found associated with large gastropods and some bivalve moulds.

The relatively small oyster-bioherms or coquinal oyster-beds which are mostly composed of *Rhynchostreon mermeti* (COQUAND) or *Amphidonte (Ceratostrongeon) flabellatum* (GOLDFUSS) associated with gastropod moulds and some bivalves and echinoids (see WETZEL & MORTON, 1959; BANDEL & GEYS, 1985) in the middle and upper parts of the Fuheis Formation, indicate periodic colonisation of predominantly muddy substrates. The sub-tidal oyster-bioherms are alternated with inter-tidal algal laminated micrite during the deposition of this formation in Central Jordan like in Wadi Mujib area.

Oyster-rich dolomites and dolomitic limestones with *Exogyra (Costagyra) olisiponensis* (SHARPE) and/or *Amphidonte (Ceratostrongeon) flabellatum* (GOLDFUSS), sometimes associated with small rudists (*Biradiolites* sp.), are found in the middle and upper parts of the Hummar Formation. These beds indicate warm, shallow-water conditions following the deeper facies of Fuheis Formation.

Exogyra (Costagyra) olisiponensis (SHARPE) and *Rhynchostreon mermeti* (COQUAND) occur in shelly wackestone beds of Shuayb Formation. These beds suggest that a full oceanic circulation was briefly established over the inner-shelf, after the subsidence of the carbonate platform of Hummar Formation in northern Jordan (POWELL, 1989). In southern Jordan and parts of central Jordan where the Hummar Limestone Formation is absent, the thickness of the Fuheis, Hummar, Shuayb Formations is reduced and equivalent beds were formed in alternating marine to restricted-lagoon conditions (POWELL, 1989).

Oysters such as *Exogyra (Costagyra) olisiponensis* (SHARPE), *Ilymatogyra (Afrogyra) africana* (LAMARCK), *Exogyra (Exogyra) italica* (SEGUENZA) and *Curvostrea rouvillei* (COQUAND) are mainly accompanied with gastropod moulds, *Plicatula fourneli* (COQUAND) and *Plicatula reynesi* (COQUAND) and occur in alternating wackestone-packstone mostly originated in subtidal biostromes. In the Ras-El-Naqab area in South Jordan, oysters are associated with large gastropod moulds and occur in clayey carbonate beds alternated with bituminous marl horizons interbedded with some dolomites and gypsum indicating locally restricted-anoxic and evaporitic facies (see also POWELL, 1989: 59).

The Wadi As Sir limestones were deposited in a wide, shallow carbonate-platform extended to South Jordan during the Turonian times. Oysters such as *Exogyra (Costagyra) olisiponensis* (SHARPE) and *Laevigyra luynesi* (LARTET) accompanied with some bivalves such as *Protocardia* sp. and echinoids such as *Echinobrissus hierosolymitanus* BLANCKENHORN, *Echinobrissus luynesi* COQUAND and *Cardiaster moabiticus* COQUAND and occur in packstone beds mostly originated in a shallow, sub-tidal marine conditions with relatively quiet-water current; while *Oscillophra wala* n. sp. is found in coquinal horizons (for example in Wadi Wala in Central Jordan) indicating higher water currents.

3.4.2. Oyster-coquinal grainstone and oyster-bioherm facies:

The shallow marine platform carbonates of the upper part of Ajlun Group is disconformably overlain by the predominantly pelagic sediments of Belqa Group, most probably as a result of a change in the configurations of the shelf from a platform to a ramp (FLEXER et al., 1986), and of a concomitant rise in the sea level associated with the Late Coniacian transgression (POWELL, 1989).

Fish and bivalve fragments with scattered *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK) forma *nikitini* (ARKHANGUELSKY) occur in white chalks of Umm Ghudran Formation of Coniacian age which reflect a relatively shallow marine-environment with 30–50 m water depth (POWELL, 1989). Reworked oyster-banks, mainly consisting of *Pycnodonte* (*Costeina*) sp. in Amman area, are intercalated with horizons of cross-stratified, bioturbated sand suggesting periodic deposition within higher energy conditions.

Thick beds of large scale, cross-stratified oyster banks, mostly consisting of *Nicaisolopha nicaisei* (COQUAND) south of Wadi Mujib, or *Gryphaeostrea canaliculata* (SOWERBY) and/or *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK) forma *typica* in the Karak and Al Hisa areas, are frequently present within the Amman Silicified Limestone Formation of Campanian age. The beds are composed of fragments or complete shells and grainstone with large scale cross-bedding. The base and the top surfaces are mostly turbulated and has a gently undulated dune-form. Such beds suggest a strong, possibly storm-driven, waves or currents which reworked and abraded oyster beds into dune-like banks.

Large oyster-bioherms up to 30 m thick, consisting of *Ambigostrea villei* (COQUAND) and *Oscillopoda figari* (FOURTAU), occur as widely dispersed bodies within the phosphate belt of Jordan. They represent the Al Hisa Phosphorite Formation of Campanian age and maintain their greatest thickness in Al Hisa and Al Abiad phosphate mines in Central Jordan. The bioherms may form a core or mounded lithofacies composed of in-situ, slightly abraded, mostly whole, large oyster shells with maximum height of 25 cm, with grainstone matrix; or may form mega-scale cross-bedded lithofacies with grainstone or mixed chert-chalk-phosphate beds (see also POWELL, 1989: 102). The top surface of the bioherm may be either convex with onlapping thin-bedded chert-chalk-phosphate beds; or a planar surface with truncated oyster shell accumulations below, and flat-lying chert-chalk-phosphate beds above indicating erosive phase subsequent to the deposition of the grainstone complex. Oyster shell microstructure within the bioherms indicate late diagenetic processes such as silicification, formation of evaporites and the dissolution of evaporites as well as cementation and recrystallization of calcite. Oyster-bioherms of Jordan are developed in a high-energy, shallow marine environment, associated with local unconformities in the Campanian stage. Similar correlatable bioherms are known from the Senonian of the Negev in southern Israel and from Sinai in Egypt (REISS, 1962; BARTOV & STEINITZ, 1982). Also the Cenomanian-Turonian shallow carbonate platform facies patterns are correlatable with similar facies in Israel and Egypt (see REISS et al., 1985; MALCHUS, 1990).

Upper Cretaceous oysters of Northwest Europe reflect different facies patterns than those of Jordan. For example: Cenomanian and Turonian species such as *Rastellum carinatum* (LAMARCK), *Amphidonte* (*Amphidonte*) *obliquatum* (PULTENEY), *Amphidonte* (*Amphidonte*) *halioideum* (SOWERBY), *Amphidonte* (*Amphidonte*) *sigmoideum* (REUSS), *Rhynchostreon suborbiculatum* (LAMARCK) and *Oscillopoda dichotoma* (BAYLE) occur in glauconitic marly green sand facies comprising inter-tidal to sub-tidal conditions. While Senonian species such as *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK), *Rastellum diluvianum* (LINNÉ)

and *Agerostrea unguolata* (SCHLOTHEIM) are found in white chalk facies comprising deeper marine environment. The changes in configuration of the 'Boreal Sea' is responsible for producing such facies changes.

3.5. Biostratigraphy

In northwestern Europe, compared with Jordan, a great number of different fossil groups are used in Upper Cretaceous biostratigraphic zonations. Most of which are highly characteristic for local areas such as belemnites and echinoid zonation in Denmark (HANSEN, 1977; SCHULZ, 1979). Among bivalves, inoceramids were used in biostratigraphic zonations in Northwest Europe (SEITZ, 1970; TRÖGER, 1971; KAUFFMAN, 1977). Oysters were mentioned when present or used in local zones such as in Ifö Klack in South Sweden (SURLYK, 1980). Because of the lack in information and material for this study, it was not possible to compare the European oysters with the different biostratigraphic zonations.

3.6. Shell microstructure

Generally, all oysters build calcitic foliated endostraca. The endostracum layer occupies most of the shell and plays an important role in the recognition of oysters upon their shell microstructure. Oysters may build uniform endostraca with only one kind of arrangement of foliae throughout the layer such as in *Africogryphaea costellata* (DOUVILLÉ) (fig. 20: irregular-cross-foliated structure), or may build divided endostracum with more than one kind of arrangement of foliae which is the case in most oysters, for example: *Laevigyra dhondtae* MALCHUS (fig. 23: irregular-cross-foliated with bent-foliated structures).

Another important factor in oyster shell microstructure is formation of lenticular structures within the endostraca. The lenses may be originally empty or filled totally or partly with mocret. In fossil oysters, the empty and some of the mocret lenses are mostly filled with secondary material due to diagenetic processes. For example: *Oscillopha wala* n. sp. (fig. 11) and *Rastellum carinatum* (LAMARCK) (fig. 13).

The kind of microstructure and the amount and nature of the lenticular-structure are the major properties necessary for the identification and comparison of oyster groups.

3.6.1. Family Palaeolophidae MALCHUS

This family is generally characterised by strongly lenticular simply-foliated structure with large empty and/or mocret lenses.

Jordanian as well as Northwest European representatives of this family are restricted to the tribe *Oscillophini* MALCHUS. In Jordan, two species belonging to the genus *Oscillopha* MALCHUS were described: *Oscillopha wala* n. sp. (fig. 11) from the Turonian of Wadi Wala in Central Jordan and *Oscillopha figari* (FOURTAU) from the Campanian rocks of the phosphate belt of Jordan. The latter has more mocret lenses. *Oscillopha dichotoma* (BAYLE) from the Cenomanian Greensand of Germany shows also large empty lenses and some mocret lenses at the outer part of the endostracum.

The genus *Rastellum* FAUJAS-ST. FOND is also characterised by strongly lenticular, simply-foliated structure, but the lenses are concentrated within the umbonal region. This genus is not represented in Jordan, although it is reported from other Mediterranean countries such as Egypt (MALCHUS, 1990). It is represented in Northwest Europe by two species: *Rastellum diluvianum* (LINNÉ) (fig. 12) from the Cenomanian rocks of Sweden and Denmark and *Rastellum carina-*

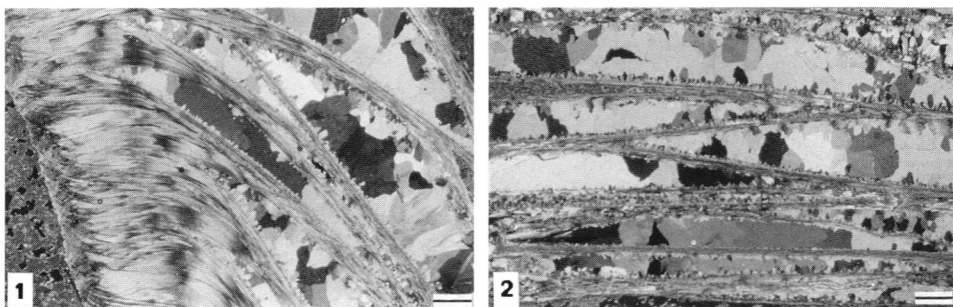


Fig. 11: *Oscillophra wala* n. sp., Wadi Wala, Central Jordan, strongly-lenticular-simply-foliated structure with large empty lenses, 1: at the umbonal region of the left valve, the lenses are filled with secondary crystals. Thin-section Nr. JOR-20, scale 0.5 mm, crossed nicholes; 2: right valve, thin-section Nr. JOR-21, scale 0.5 mm, crossed nicholes.

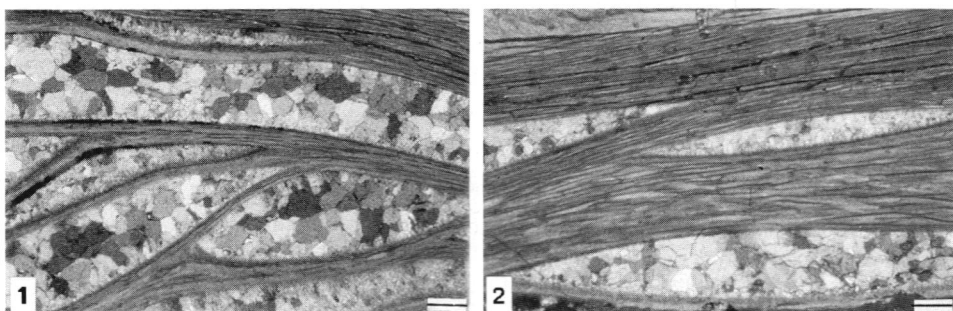


Fig. 12: *Rastellum diluvianum* (LINNÉ), Scania, southern Sweden, strongly-lenticular-simply-foliated structure with large empty lenses, 1: large lenses at the umbonal region filled with secondary calcite crystals, thin-section Nr. EUR-50, scale 0.5 mm, crossed nicholes; 2: simply-foliated structure is more clear at the central and ventral sides of the shell, thin-section Nr. EUR-50, scale 0.5 mm, crossed nicholes.

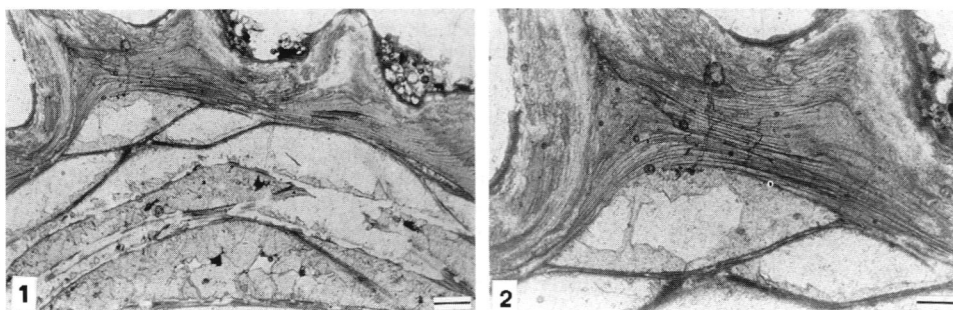


Fig. 13: *Rastellum carinatum* (LAMARCK), Green Sand, Essen-Germany, strongly-lenticular-simply-foliated structure with large empty lenses mainly concentrated at the umbonal region, the lenses are filled with secondary sparite, thin-section Nr. EUR-60, scale 1: 0.5 mm, 2: 0.25 mm, both are plane.

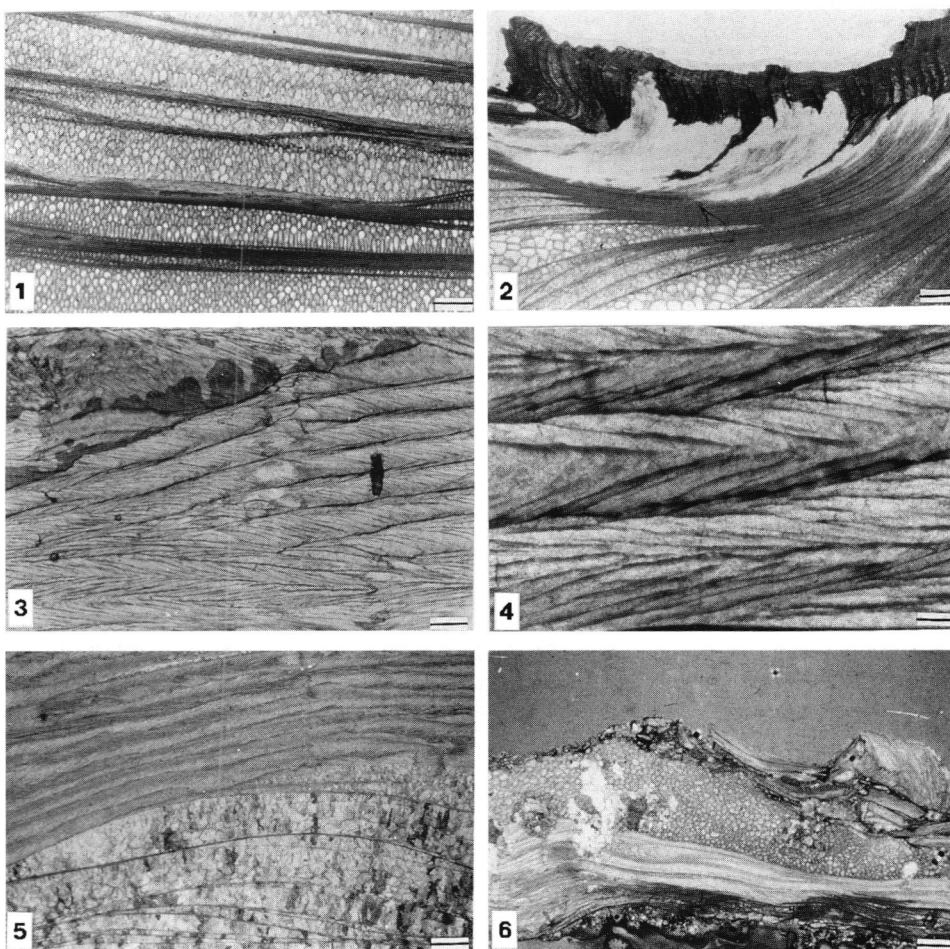


Fig. 14: Shell microstructure of the genus *Pycnodonte*. 1,2: *Pycnodonte (Phygraea) vesiculare* (LAMARCK), Lägerdorf, North Germany, 1: vesicular structure, plane, thin-section Nr. EUR-11, scale 0.5 mm 2: Ligostracum of the left valve, plane, thin-section Nr. EUR-10, scale 0.5 mm. 3-5: *Pycnodonte (Phygraea) vesiculosum* (SOWERBY), Wadi Salihi, north of Amman, 3, 4: herringbone-cross-foliated structure, crossed nicholes, thin-section Nr. JOR-42, scale, 3: 0.25 mm, 4: 0.1 mm, 5: herringbone-cross-foliated structure with vesicular shell structure, crossed nicholes, thin-section Nr. JOR-45, scale 0.5 mm. 6: *Pycnodonte (Costeina)* sp., Amman area, Jordan, herringbone-cross-foliated structure with vesicular shell structure, crossed nicholes, thin-section Nr. JOR-120, scale 0.5 mm.

tum (LAMARCK) (fig. 13) from the Cenomanian of the Greensand of Germany. The lenses in *Rastellum carinatum* are generally smaller than those of *Rastellum diluvianum* and are mostly filled with secondary crystals.

3.6.2. Family Gryphaeidae VIALOV

This family includes four different subfamilies with endostraca ranging from simple and uniform to divided and complex. Jordanian as well as North European oysters are predominated by the subfamily Exogyreinae VIALOV (fig. 10).

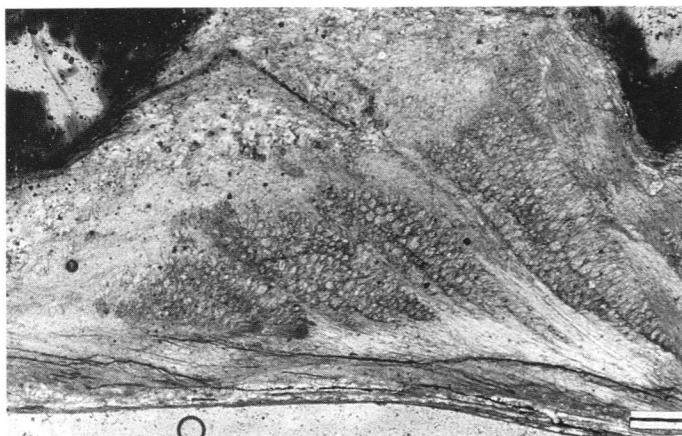


Fig. 15: *Hyotissa semiplana* (SOWERBY). Braunschweig, Germany. herringbone-cross-foliated structure with vesicular shell structure, crossed nicholes, thin-section Nr. EUR-30, scale 0.5 mm.

The subfamily Gryphaeinae VIALOV is only represented by the species *Afri-cogryphaea costellata* (fig. 20) (DOUVILLÉ) from the Middle Jurassic (Bathonian) of Jordan. Its microstructure is compact irregular-cross-foliated.

Members of the subfamily Pycnodontinae STENZEL are characterised by herringbone-cross-foliated structure with vesicular shell chambers. The tribe Pycnodontini STENZEL is represented in Jordan and in Northwest Europe by similar species: *Pycnodonte* (*Phygraea*) *vesiculosum* (SOWERBY) (fig. 14, 3–5) from the Cenomanian sediments of Jordan and England (not listed with the North European fauna because of the lack of material from England). *Pycnodonte* (*Phygraea*) *vesiculare* (LAMARCK) (fig. 14, 1–2) from the Coniacian-Santonian and Campanian rocks of Jordan and Coniacian to Maastrichtian of Northwest Europe. *Pycnodonte* (*Costeina*) sp. (fig. 14, 6) from the Coniacian-Santonian chalk of Jordan.

Although the recent members of the tribe Hyotissini HARRY are distributed world wide, the oldest known member of this tribe *Hyotissa semiplana* (SOWERBY) is restricted to Northwest Europe (STENZEL, 1971: N1108). It shows similar microstructure to the previous pycnodontids (fig. 15).

Shell microstructure of some members of the subfamily Gryphaeostreinae FRENEIX was studied by FRENEIX (1979 and 1982). She proved the presence of simply-foliated, simply-cross-foliated and irregular-cross-foliated structures with minor amounts of empty and mocret lenses. *Gryphaeostrea canaliculata* (SOWERBY) is reported from the Campanian rocks of Jordan and the Cenomanian to Campanian rocks of North Europe. Its shell microstructure is predominated by simply-foliated with the presence of simply-cross-foliated and irregular-cross-foliated structures.

Members of the extinct subfamily Exogyreinae VIALOV predominates both Jordanian and Northwest European Upper Cretaceous oysters. Both tribes of this subfamily (Nanogyridini, MALCHUS and Exogyridini VIALOV) have subdivided endostraca. According to MALCHUS (1990: 71), nanogyrids have generally less mocret and empty lenses than exogyrids, and can build herringbone-cross-foliated structure which is not known from exogyrids.

Nanogyrids dominate the Upper Cretaceous oysters of Northwest Europe with six amphidontids of a total of fifteen species. The genus *Amphidonte* Fi-

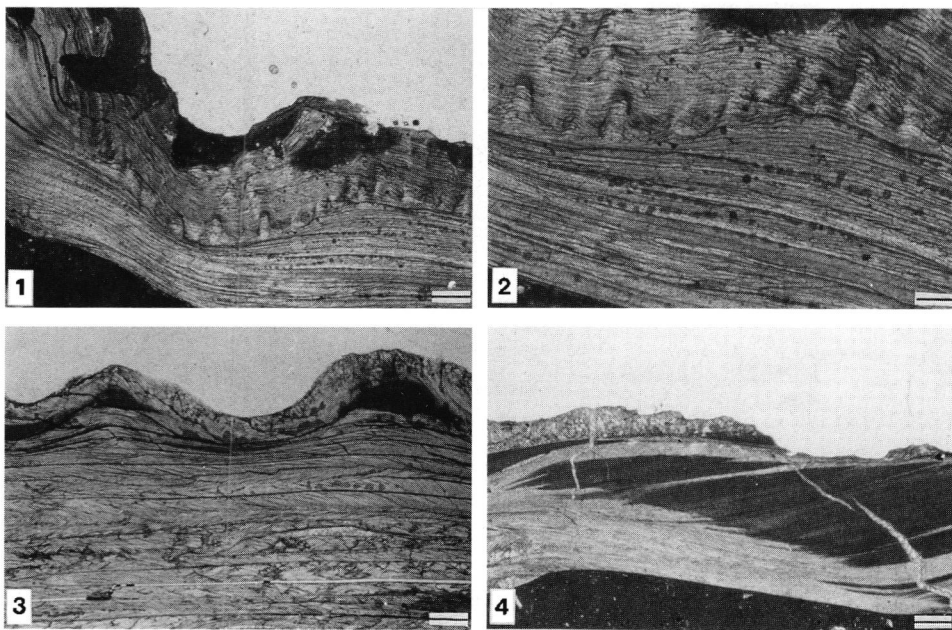


Fig. 16: *Amphidonte* (*Cerastostreon*) *flabellatum* (GOLDFUSS). 1,2: Wadi Salihi, north of Amman, chomata-influenced-cross-foliated structure, thin-section Nr. JOR-1000, both plane, scale 1: 0.5 mm, 2: 0.25 mm. 3: Wadi Mujib, central Jordan, herringbone-cross-foliated structure, crossed nicholes, thin-section Nr. JOR-1001, scale 0.5 mm. 4: Wadi heidan, central Jordan, mocret lenses near the adductor of the right valve, crossed nicholes, thin-section Nr. JOR-1002, scale 0.5 mm.

SCHER DE WALDHEIM is characterised by herringbone-foliated structure with mocret and/or empty lenses. The three subgenera attributed to this genus, *A. (Amphidonte)*, *A. (Cerastostreon)*, and *A. (Vultogryphaea)* have similar microstructure and are differentiated upon other morphological features (see descriptions). *Amphidonte (Amphidonte) obliquatum* (PULTENEY) from the Cenomanian of the Greensand of Germany shows simply-foliated structure predominating most of the endostracum. Herringbone-cross-foliated and minor mocret lenses are mostly present near the umbo. *Amphidonte (Amphidonte) haliotoideum* (SOWERBY) (fig. 17) from the Cenomanian rocks of Sweden shows simply-foliated structure with empty lenses within the umbonal region. *Amphidonte (Amphidonte) sigmoideum* (REUSS) (fig. 18) from the Cenomanian to Lower Turonian of Germany shows also simply-foliated structure with empty lenses within the umbonal region. The empty lenses are filled with secondary crystals.

A. (Vultogryphaea) is attributed to this genus according to its amphidontid outline and its herringbone-foliated structure. *Amphidonte (Vultogryphaea) laciniata* (NILSSON) (fig. 19) from the Greensand of Germany (Cenomanian) also shows a dominant simply-foliated structure. Herringbone-cross-foliated structure with long and narrow mocret lenses and minor empty lenses along the curvature of the left valve is present.

Amphidonte (Cerastostreon) flabellatum (GOLDFUSS) (fig 16) is a well known cosmopolitan species. In this study, it is reported from the Cenomanian-Lower Turonian rocks of Jordan and from the Albian (? Aptian) to Cenomanian rocks of

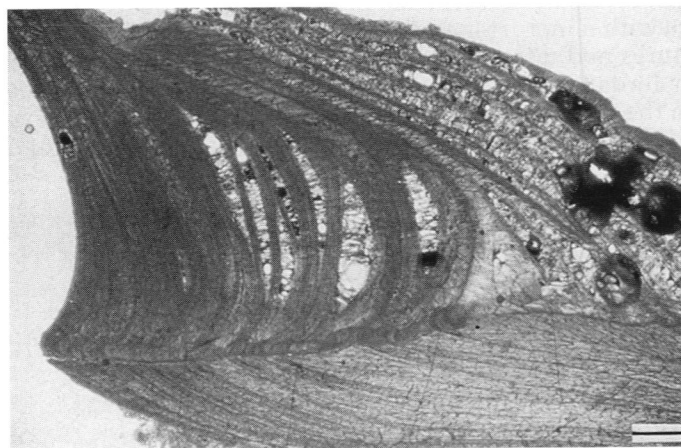


Fig. 17: *Amphidonte (Amphidonte) haliotoideum* (SOWERBY). Scania, southern Sweden, lenticular simply-foliated structure with herringbone-cross-foliated structure and empty lenses mainly near the umbo, plane, thin-section Nr. EUR-70, scale 0.5 mm.

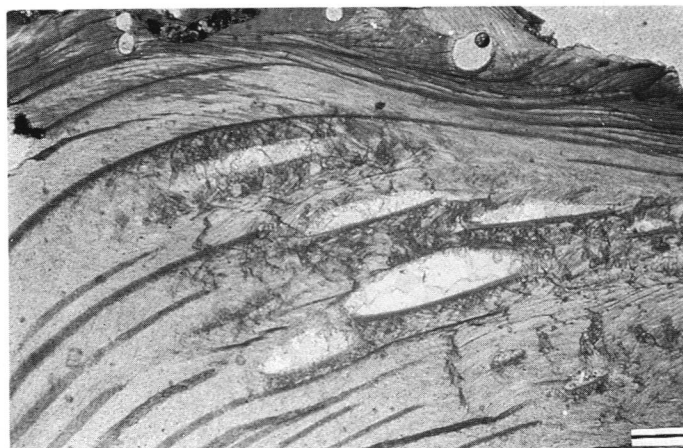


Fig. 18: *Amphidonte (Amphidonte) sigmoideum* (REUSS). Greensand, Essen, Germany. Lenticular simply-cross-foliated structure with empty lenses filled with secondary calcite, crossed nicholes, thin-section Nr. EUR-80, scale 0.5 mm.

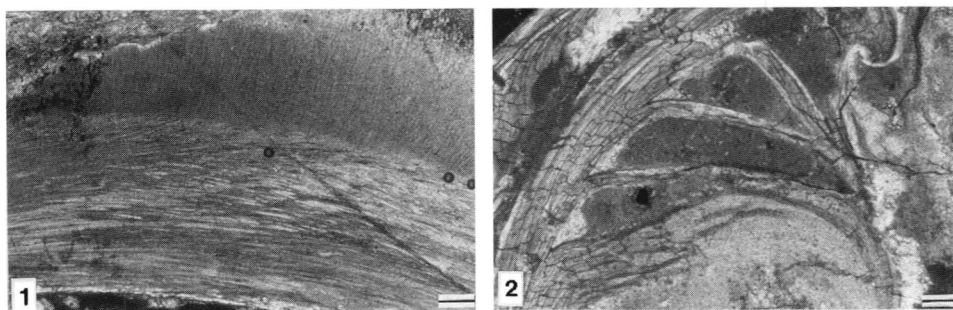


Fig. 19: *Amphidonte (Vultogryphaea) laciniata* (NILSSON). Greensand, Essen, Germany. 1: herringbone-cross-foliated structure with large mocket lenses, crossed nicholes, thin-section Nr. EUR-40, scale 0.25 mm. 2: mocket lenses near the umbo of the left valve, crossed nicholes, thin-section Nr. 42, scale 0.5 mm.

North Europe. It has an endostracum predominated by herringbone-cross-foliated structure with minor irregular cross-foliated, chomata-influenced-cross-foliated structures and minor mocret lenses. It is the only nanogyrid species reported from Jordan in this study. *Amphidonte* (*Ceratostreon*) *pliciferum* (DUJARDIN) from the Santonian to Upper Campanian of Germany has most probably similar endostracum as *A. (C.) flabellatum*. It was not possible to investigate

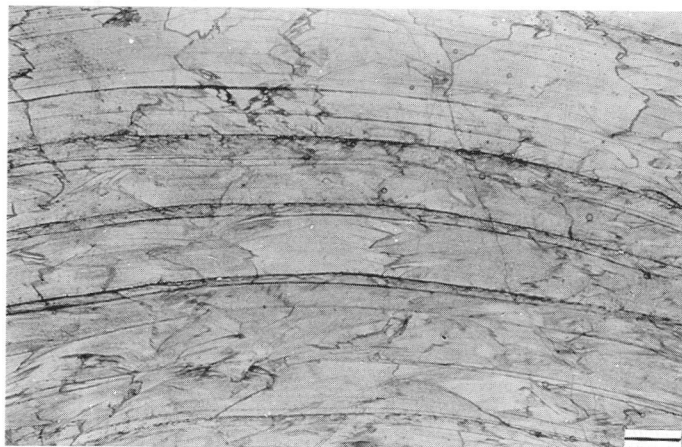


Fig. 20: *Africogryphaea costellata* (DOUVILLÉ). Wadi Zerqa River, north Jordan, compact irregular-cross-foliated structure, left valve, crossed nicholes, thin-section Nr. JOR-130, scale 0.5 mm.

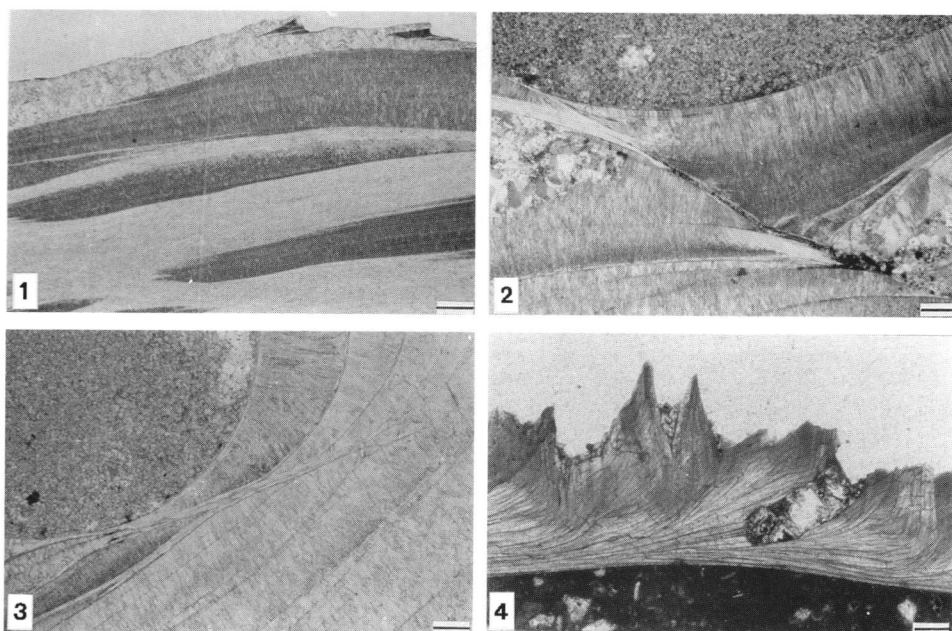


Fig. 21: *Exogyra* (*Costagyra*) *olisiponensis* (SHARPE). Ras-El-Naqab, South Jordan. 1: irregular-cross-foliated, simply-foliated structures and large, long mocret lenses, 2: traces of the myostracum of the adductor 3: traces of the myostracum of the Quenstedt muscle, 4: simply-foliated structure of the right valve. all plane, thin-section Nr. JOR-10, scale for all 0.5 mm.

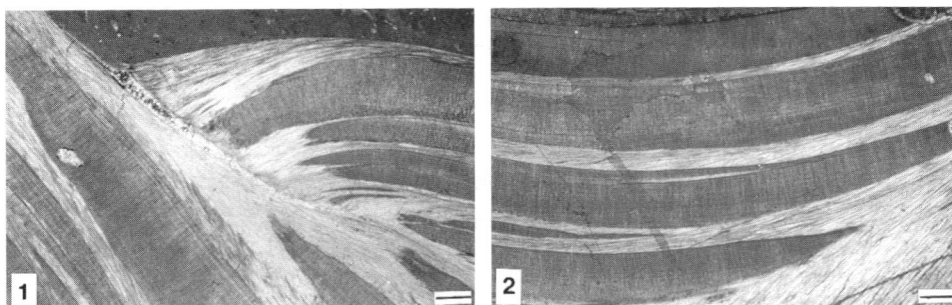


Fig. 22: *Exogyra (Exogyra) italica* (SIGUENZA). South Wadi Jamil, South Jordan. 1: Simply-foliated structure with large, long mocret lenses. 2: traces of the myostracum of the adductor of the left valve. Both plane, thin-section Nr. JOR-111, scale 0.5 mm.

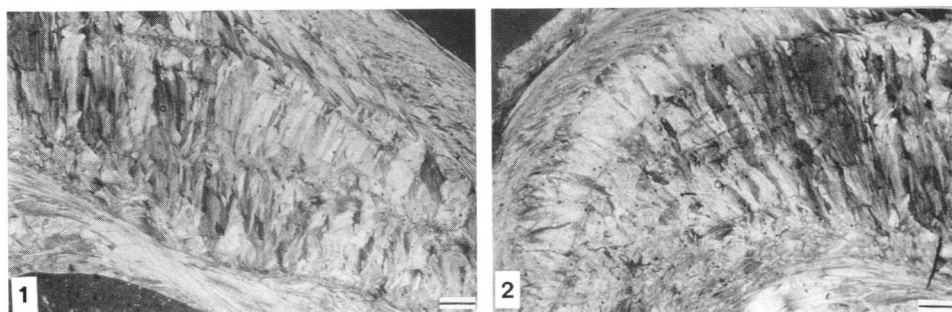


Fig. 23: *Laevigyra dhondtae* MALCHUS. Wadi Heidan, Central Jordan. Irregular-cross-foliated and bent-foliated structures, both under crossed nicholes, thinsections Nr. JOR-73, scale for both photos 0.5 mm.

the original microstructure because all shells available for this study are silicified and the original structure is damaged.

Six of a total of seventeen species of the Upper Cretaceous Jordanian oysters belong to the tribe Exogyrini VIALOV. Endostraca of the different genera of this tribe generally build lenticular structures with mocret and/or empty lenses. For example: the genus *Exogyra* SAY developed relatively large and long mocret and empty lenses, *Exogyra (Exogyra) italica* (SEGUENZA) (fig. 22) from the Ce-

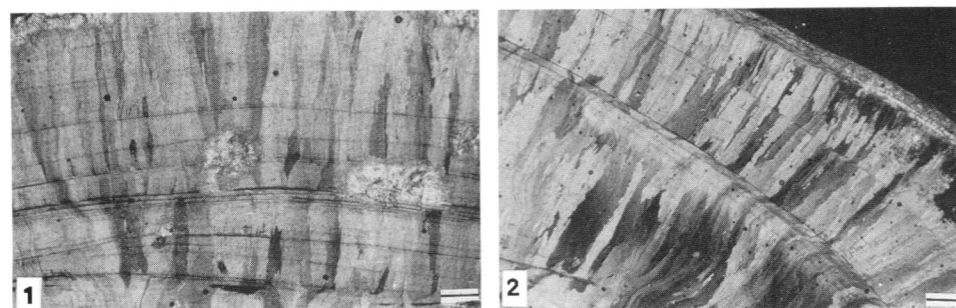


Fig. 24: *Rhynchostreon suborbiculatum* (LAMARCK). Greensand, Essen, Germany. Compact bent-foliated structure, crossed nicholes, thin-section Nr. EUR-20, scale 0.5 mm.

nomanian rocks of Jordan and *Exogyra* (*Costagyra*) *olisiponensis* (SHARPE) (fig. 21) from the Cenomanian rocks of Jordan have similar endostraca with relatively long and large mocret lenses. They are differentiated upon morphology of the shell (see descriptions).

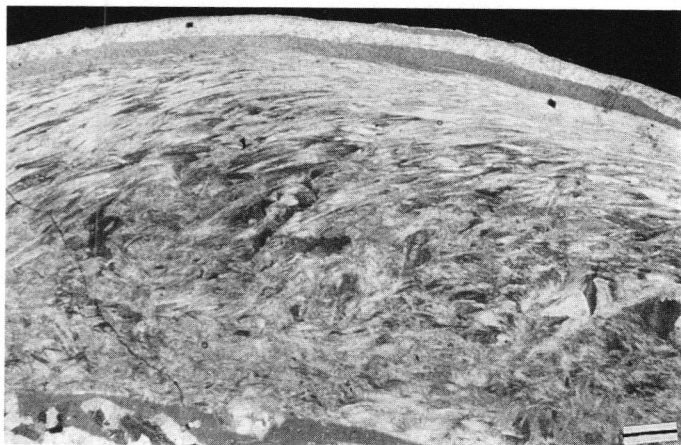


Fig. 25: *Rhynchostreon mermeti* (COQUAND) forma typica, Wadi Mujib, Central Jordan, divided endostracum with simply-foliated and irregular-cross-foliated structures, crossed nicholes, thin-section Nr. JOR-91, scale 0.5 mm.

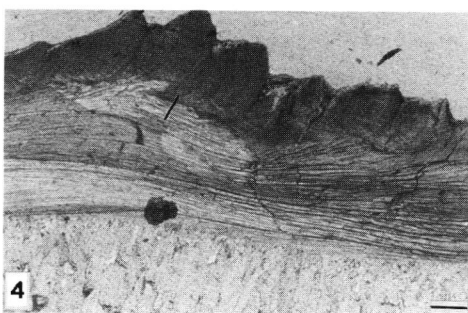
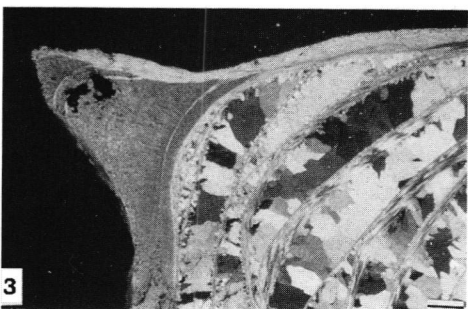
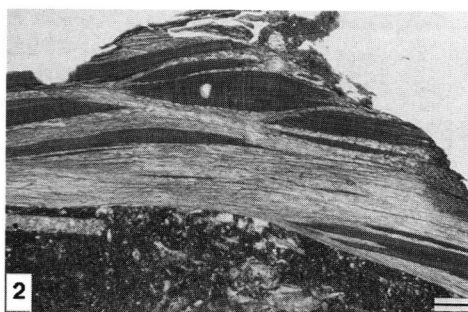
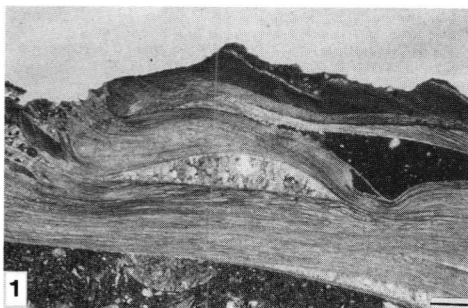


Fig. 26: *Ilymatogyra* (*Afrogyra*) *africana* (LAMARCK), 1, 2: Wadi Heidan, Central Jordan, forma typica, simply-foliated structure with mocret and empty lenses partly filled with secondary crystals, both under crossed nicholes, thin-section Nr. JOR-35, scale for both 0,5 mm. 3: simply-foliated structure of the right valve, plane, thin-section Nr. JOR-36, scale 0.5 mm. 4: Wadi Wala, Central Jordan, forma crassa, large empty lenses near the umbo filled with secondary calcite, crossed nicholes, thin-section Nr. JOR-34, scale 0.5 mm.

Ilymatogyra STENZEL can build, in contrast to other exogyrids, few to many, large or small empty and/or mocret lenses. *Ilymatogyra* (*Afrogyra*) *africana* (LAMARCK) (fig. 26) from the Cenomanian-Lower Turonian rocks of Jordan is a typical example.

Both *Rhynchostreon* BAYLE and *Laevigyra* MALCHUS can build bent-foliated structure. This kind of structure is not known from other investigated exogyrids in this study. *Rhynchostreon mermeti* (COQUAND) (fig. 25) from the Cenomanian to Lower Turonian rocks of Jordan is characterised by having a strongly divided endostracum with bent-foliated structure within the umbonal region, simply-foliated and irregular-cross-foliated structures with some mocret lenses. *Rhynchostreon suborbiculatum* (LAMARCK) (fig. 24) from the Cenomanian rocks of North Europe is characterised by having a compact bent-foliated endostracum. It is a well known cosmopolitan species and the only exogyrid described from Northwest Europe in this study.

Laevigyra luynesi (LARTET) from the Cenomanian rocks of Jordan shows endostracum with simply-foliated and simply-cross-foliated structures with minor mocret lenses. *Laevigyra dhondte* MALCHUS (fig. 23) from the Cenomanian of Jordan shows similar structures to that of *L. luynesi* but with portions of bent-foliated structure near the umbonal region.

3.6.3. Family Ostreidae RAFINESQUE

Members of this family have their endostraca mostly predominated by simply-foliated structure with or without lenticular structures. Few representatives of this family are reported from Jordan and North Europe. They are restricted to

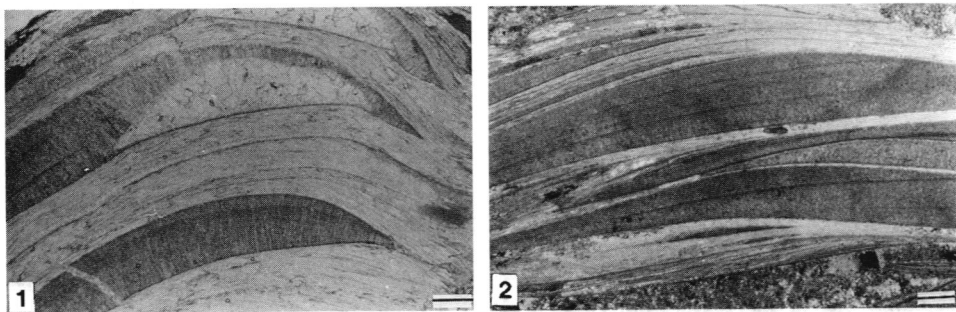


Fig. 27: *Nicaisolopha nicaisei* (COQUAND), Wadi Karak, Central Jordan. Simply-foliated structure with large empty and mocret lenses partly filled with secondary calcite, 1: plane, 2: crossed nicholes, thin-section Nr. JOR-82, scale for both 0.5 mm.

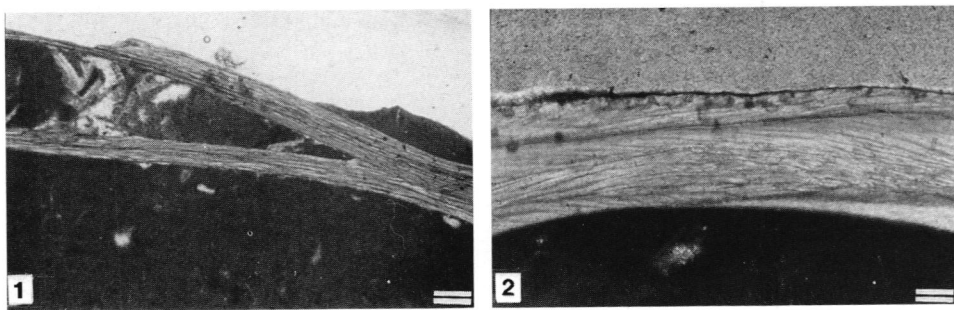


Fig. 28: *Curvostrea rouvillei* (COQUAND). Ras El Naqab, South Jordan. Simply-foliated structure with mocret lenses, both plane, thin-section Nr. JOR-160, scale 1: 0.5 mm, 2: 0.25 mm.

the subfamily Liostreinae MALCHUS which has, in comparison with other subfamilies of this family, fewer amount of lenses. The tribe Curvostreini MALCHUS of this subfamily has mostly compact simply-foliated structure. *Agerostrea unguolata* (SCHLOTHEIM) from the Maastrichtian of the Netherlands and *Agerostrea lunata* (NILSSON) from the Lower Maastrichtian of England have compact simply-foliated endostracum. Whereas *Curvostrea rouvillei* (COQUAND) (fig. 28) and *Curvostrea* sp. from the Cenomanian-Lower Turonian rocks of Jordan have simply-foliated structure with minor simply-cross-foliated and possible chomata-influenced-cross-foliated structures and minor amount of empty lenses.

The tribes Flemingostreini STENZEL and Ambigostreini MALCHUS are not represented in northwestern Europe. The Jordanian flemingostreids (genus *Nicaisolopha*) has, in contrast to the ambigostreids (genera *Ambigostrea* and *Gryphaeligmus*), more amount of mocret and/or empty lenses. *Nicaisolopha nicaisei* (COQUAND) (fig. 27) from the Campanian rocks of Jordan has simply-foliated structure with large empty and mocret lenses throughout both valves. While *Ambigostrea villei* (COQUAND) (fig. 29) from the Campanian rocks of Jordan is dominated by simply-foliated structure with minor empty or mocret lenses only within the umbonal region. And *Gryphaeligmus jabbokensis* (Cox) from the Bathonian rocks of Wadi Zerqa River area in North Jordan shows a compact simply-foliated endostracum possibly with minor chomata-influenced-cross-foliated structure.

Shell microstructures components of the Jordanian oysters are shown in (fig. 31), and those of the Northwest European ones are shown in (fig. 32).

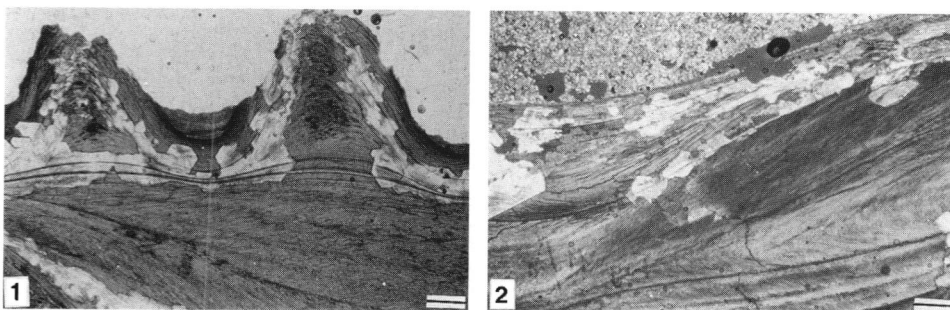


Fig. 29: *Ambigostrea villei* (COQUAND). Al Hisa Phosphate mine, Central Jordan. Simply-foliated structure with late diagenetic anhydrite crystals, both plane, thin-section Nr. JOR-103, scale 0.5 mm.

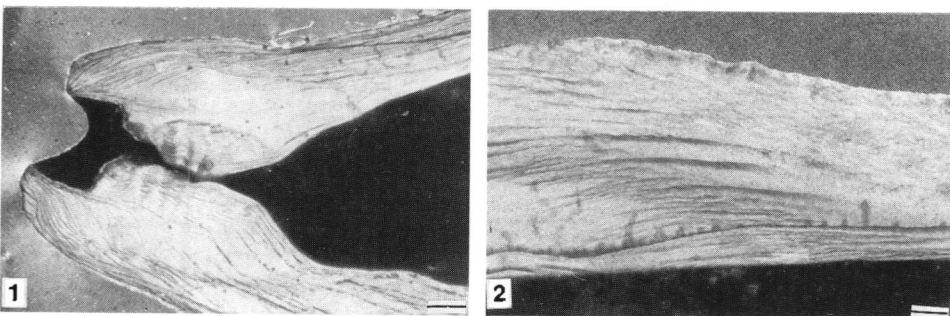


Fig. 30: *Gryphaeligmus jabbokensis* (Cox). Wadi Zerqa River, North Jordan. Compact simply-foliated structure with chomata-influenced structure, both plane, thin-section Nr. JOR-151, scale 1: 0.5 mm, 2: 0.25 mm.

FAUNA	Endostracum subdivisions							Lens Structures			
	SF	BF	SCF	ICF	ICCF	HCF	CICF	COMPACT	MOCRET	EMPTY	VESICULAR
<i>Oscillopha wala</i> n. sp.	D								R	D	
<i>Oscillopha figari</i> (FOURTAU)	D								D	R	
<i>A. (Ceratostreon) flabellatum</i> (GOLDFUSS)				P		D	P		P		
<i>E. (Exogyra) italica</i> (SEGUENZA)	P			P			R		D	R	
<i>E. (Costagyra) olisiponensis</i> (SHARPE)	P			P			R		D	R	
<i>Rhynchostreon mermeti</i> (COQUAND)	P	D ^u		P			R		R		
<i>I. (Afrogyra) africana</i> (LAMARCK)	P			P			R		P	R	
<i>Laevigyra luynei</i> (LARTET)	P		P				R		P		
<i>Laevigyra dhondtae</i> MALCHUS	P	P ^u		P			P		P		
<i>Gryphaeostrea canaliculata</i> (SOWERBY)	P		P	P					R	R	
<i>P. (Phygraea) vesiculosum</i> (SOWERBY)						D					D
<i>P. (Phygraea) vesiculare</i> (LAMARCK)						D					D
<i>P. (Costeina) sp.</i>						D					D
<i>Nicaisolopha nicaisei</i> (COQUAND)	D								P	D ^u	
<i>Curvostrea rouvillei</i> (COQUAND)	D			P			P		R		
<i>Curvostrea sp.</i>	D			P			P		R		
<i>Ambigostrea villei</i> (COQUAND)	D								R ^u	R ^u	
<i>Africogryphaea costellata</i> (DOUVILLE) JURASSIC				P	P			X			
<i>Gryphaeligmus jabbokensis</i> (COX) JURASSIC	D						P	X			

Fig. 31: Microstructure components of the Upper Cretaceous oysters of Jordan. SF: simply-foliated, BF: bent-foliated, SCF: simply-cross-foliated, ICF: irregular-cross-foliated, ICCF: irregular-complex-cross-foliated, HCF: herringbone-cross-foliated, CICF: chomata-influenced-cross-foliated, D: dominant, P: present, R: rare, u: near the umbo, X: compact.

FAUNA	Endostracum subdivisions							Lens Structures			
								COMPACT	MOCRET	EMPTY	VESICULAR
	SF	BF	SCF	ICF	ICCF	HCF	CICF				
<i>Oscillophra dichotoma</i> (BAYLE)	D								D	D	
<i>Rastellum diluvianum</i> (LINNE)	D								R	D	
<i>Rastellum carinatum</i> (LAMARCK)	D								R	D	
<i>A. (Amphidonte) haliotoideum</i> (SOWERBY)	P					P			R ^u	P ^u	
<i>A. (Amphidonte) sigmoideum</i> (REUSS)	P					R			R ^u	P ^u	
<i>A. (Amphidonte) obliquatum</i> (PULTENEY)	P						P		R ^u	P ^u	
<i>A. (Ceratostreon) flabellatum</i> (GOLDFUSS)				P		D	P		P	R	
<i>A. (Ceratostreon) pliciferum</i> (DUJARDIN)				P?		D?			P?	R?	
<i>A. (Vultogryphaea) laciniata</i> (NILSSON)	D					P			P ^u		
<i>Rhynchostreon suborbiculatum</i> (LAMARCK)		D		P	P			X			
<i>Gryphaeostrea canaliculata</i> (SOWERBY)	D		P	P							
<i>P. (Phygraea) vesiculare</i> (LAMARCK)						D					D
<i>Hytissa semiplana</i> (SOWERBY)						D					D
<i>Agerostrea unguolata</i> (SCHLOTHEIM)	D							X			
<i>Agerostrea lunata</i> (NILSSON)	D							X			

Fig. 32: Microstructure components of the Upper Cretaceous oysters of Northwest Europe. SF: simply-foliated, BF: bent-foliated, SCF: simply-cross-foliated, ICF: irregular-cross-foliated, ICCF: irregular-complex-cross-foliated, HCF: herringbone-cross-foliated, CICF: chomata-influenced-cross-foliated, D: dominant, P: present, R: rare, u: near the umbo, X: compact.

4. Palaeontology

4.1. Descriptive characters of oyster shells

4.1.1. General

Oysters are marine, sedentary, monomyarian, pteriomorph bivalve molluscs. Adult specimens lack an anterior adductor muscle and a muscular foot. Oysters differ from other monomyarian members of the order Pterioda by the fact that they are always attached by cementing the left valve to a firm substrate or to a solid object. Oysters live singly in small groups or are gregarious. Actual

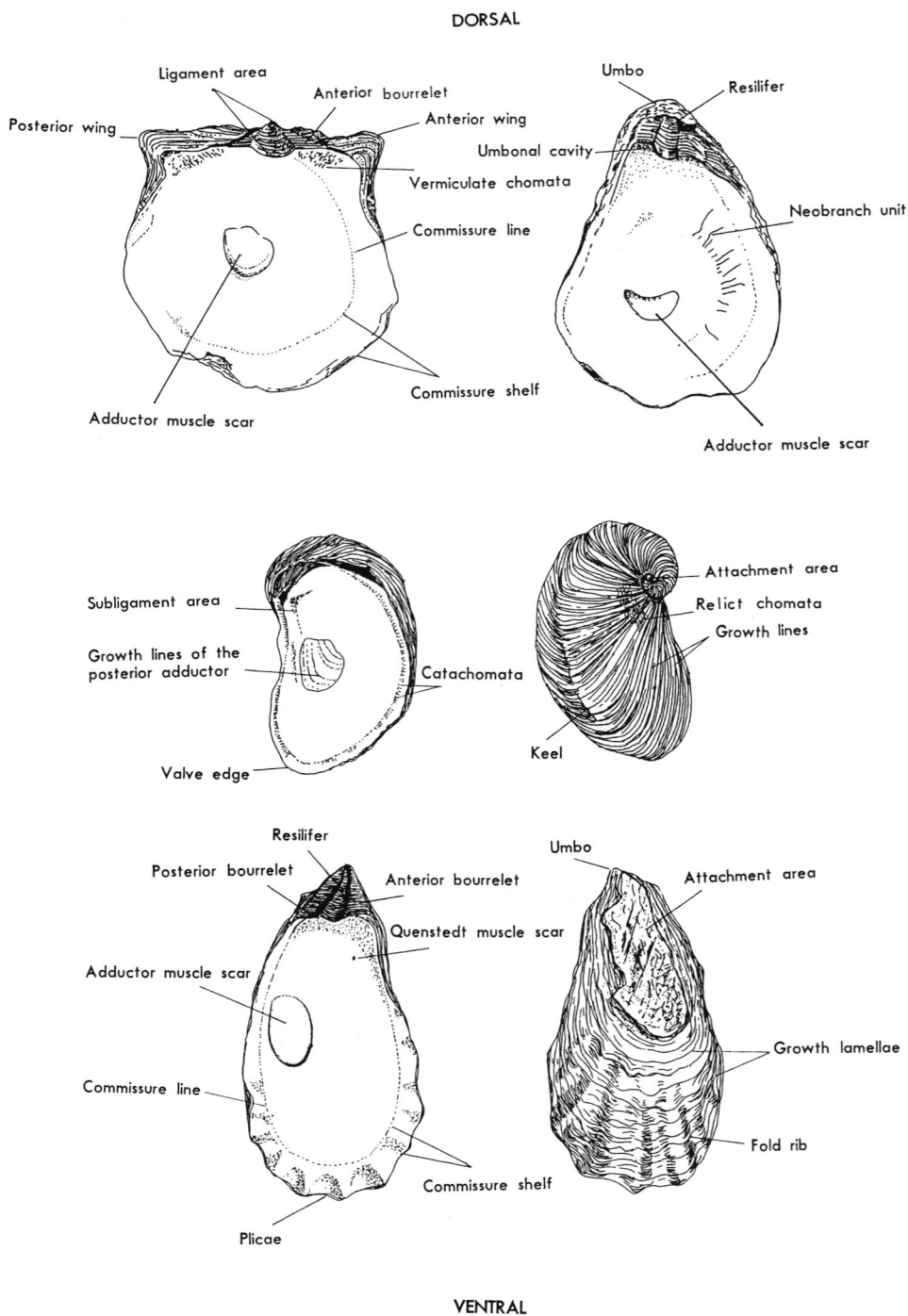


Fig. 33: Generalised morphological characters of oysters. (1: *Pycnodonte*, 2: *Nicaisolopha*, 3,4: *Amphidonte*, 5,6: *Ostrea*).

incrustations and reefs occur in on- and offshore environments of all continents except Antarctica. Some groups are found in various climatic zones from tropical to cool temperate seas, but they are most diversified in warm seas. At the adult stage, oysters feed by filtering the water for small food particles (plankton) with the aid of a mucus sheet and a complicated and highly efficient ciliary mechanism (see STENZEL 1971: N1000).

Environmental factors and genetic factors influence the shape of oyster shells (see STENZEL 1971: N1016-N1026). The extreme variability of the shape of oyster shells has always been a major problem in taxonomy and systematic classification of oysters, because they are primarily based on morphological characters of shells. Therefore, it is important to consider all possible morphological aspects, although only a few characters might be necessary for the identification of a taxon. On the other hand, living oysters are relatively well studied due to their economic value. The observations and assumptions made upon studies of the soft parts aid the determination of the degree of relationship between the living taxa as well as their possible relations to extinct taxa. For example: it is assumed that fossil members of the family Gryphaeidae (e.g. Pycnodonteinae) were oviparous or non-incubatory and had their intestine passing through the heart and that they had a promyal passage. This assumption is concluded from observations on living members of Pycnodonteinae (STENZEL, 1971; HOPKINS, 1979).

Recent Lophinae and Ostreinae are (as far as known) incubatory and have the intestine passing dorsally of the pericardium (HARRY, 1985), therefore it is assumed that the extinct genera belonging to these subfamilies had the same characters.

The oldest genuine oysters in the stratigraphic record are the genera: *Gryphaea* from the Carnian of Arctic province, *Palaeolopha* (better known as *Lopha* in the old literature) from the ?Anisian and Carnian of the Tethys realm, and *Liostrea* from the Norian of the North Pacific/Arctic province of the North Temperate realm. These genera continued into the Jurassic and reached their widest distribution during Cretaceous times. At the end of the Cretaceous period, many genera became extinct (see STENZEL 1971: N1056-N1059; HOPKINS 1979: 505; MALCHUS 1990: 184).

STENZEL (1971) divided oysters into two families (Ostreidae and Gryphaeidae) and suggested that they may have been evolved from different ancestors, possibly from two different genera of Carboniferous-Permian Pectinoidea (Pseudomonotidae) which are attached by the right valve. NEWELL & BOYD (1970, 1989) concluded the same origin for Gryphaeidae. WALLER (1978) concluded that, Ostreidae, Plicatulidae and Dimyidae are closely related and joined them (with superfamily rank) in the order Ostreoida-suborder Ostreinae. He based his conclusion upon comparative anatomy and palaeontology, and suggested that, oysters have a dimyarian, possibly non-pleurothetic, origin which cannot have evolved from the Pseudomonotidae which retained its foot and became pleurothetic. MALCHUS (1990) placed oysters in three families: Ostreidae, Gryphaeidae and Palaeolophidae, the latter is based upon the strongly lenticular simply-foliated microstructure of the earliest *lopha*-like oysters. MALCHUS (1990: 184) suggested a triphyletic origin possibly evolved from Triassic Terquemidae. CARTER (1990) studied the shell microstructure of bivalves and reviewed their systematic classification. His order Ostreoida has the same superfamily composition as WALLER's (1978) except for the superfamily Gryphaeoidae. CARTER (1990: 216, 230, 232) suggested that the Ostreidae, Plicatulidae and Dimyidae were evolved from a Late Palaeozoic, dimyarian, nacreous ancestral stock in the order Pterioidea, perhaps in the family Pterineidae. He also indicated that the family Gryphaeidae may be polyphyletic, with some taxa evolving from the fa-

mily Pseudomonotidae or from the ancestors of the Ostreidae, and others evolving from the Ostreidae.

According to HARRY (1985: 153), the recent members of the superfamily Ostreioidea are subdivided into two families and four subfamilies (Ostreidae: Crassostreinae, Ostreinae, Lophinae; Gryphaeidae: Pycnodontinae) with ten tribes, 24 genera and subgenera and 36 species.

In this chapter, the important morphological characters of oyster shells (fig. 33) are briefly discussed. They are subdivided into: size, outline, internal characters, external characters and microstructural properties of the shell. This subdivision has been made to simplify the systematic descriptions in this study.

4.1.2. Size

Oysters are inequivalve with their left valve larger than the right valve. Dimensions of the shell of oysters are in most cases related to the dimensions of the left valve. This is clearly seen in coiled oysters such as exogyrids and pycnodontids.

In this study, the terminology of the size of an oyster is based on the height of the left valve (fig. 34). Small (up to 5 cm), medium (5–12 cm), large (12–20 cm) and very large (more than 20 cm).

The largest recorded individual belongs to *Saccostrea cucullata* (v. BRONN, 1778) collected near Bombay (India) with a height of 76 cm and a length of 32 cm (STENZEL, 1971: N1027).

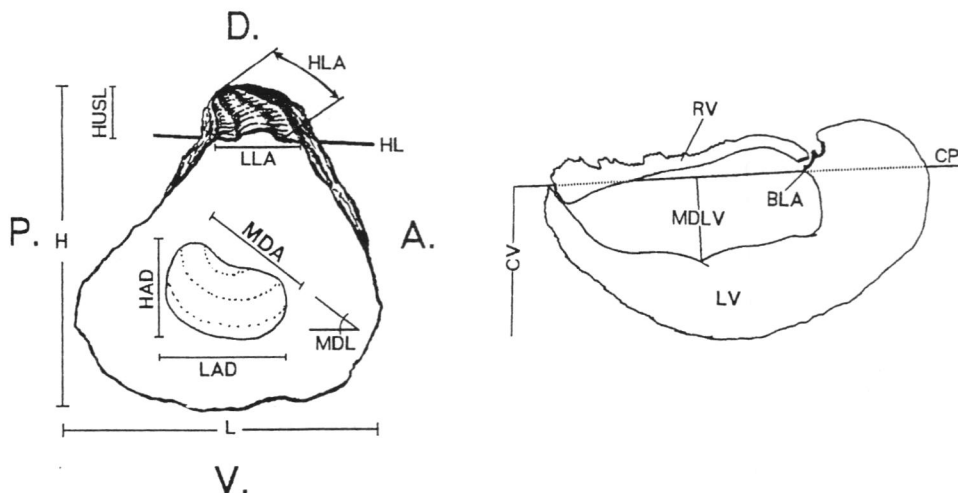


Fig. 34: Orientation and measurements of oyster shells. A.= Anterior side P.= Posterior side D.= Dorsal side V.= Ventral side H.= Height L.= Length HL= Hinge line HLA= Height of ligament area LLA= Length of ligament area HUSL= Height of umbo HAD = Height of the adductor muscle scar LAD= Length of the adductor muscle scar MDA= Maximum diameter of adductor muscle scar MDL= Angle between MDA and L CV= Convexity CP= Commissure plane BLA= Base of ligament area MDLV= Maximum depth of left valve.

4.1.3. Outline

The general outline of an oyster shell reflects the influence of environmental and genetic factors. These factors are closely connected with the sedentary life habit of oysters. Within the same species, different forms may develop as a consequence of, for example, the availability of space, and the nature and size of

attachment. When treated separately, these forms are sometimes interpreted as different or new species (see STENZEL, 1971: N1016-N1028; HOPKINS, 1979: 506-507).

Oysters studied herein are subdivided into two major groups according to their general outline:

4.1.3.1. Coiled group

The first group is characterised by coiled umbos and extremely inequivalve shells. It includes all members of the family Gryphaeidae (except for the Hyotissini) in addition to some members of the tribe Turkostreini of the family Ostreidae. This group shows two standard types (fig. 35):

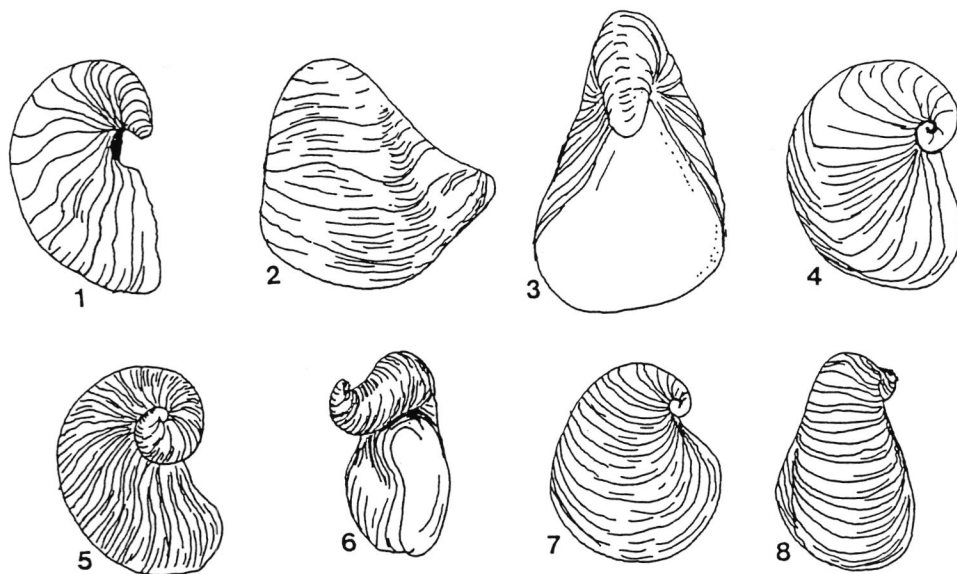


Fig. 35: Standard types of coiled outline group. 1-3: Orthogyrate coiled type 1, 2: *Pycnodonte*, 3: *Gryphaea*; 4-8: Helicoidally twisted type 4: *Amphidonte*, 5, 6, 8: *Ilymatogyra*, 7: *Rhynchostreon*.

4.1.3.1.1. Orthogyrate-coiled type:

Gryphaeinae and Pycnodonteinae except for the Hyotissini have convex cup-shaped, mostly smooth left valves and straight or slightly concave right valves. The axis of coiling of the umbo in this type runs parallel to the hinge axis producing a beak situated above the triangular ligament area which points towards the inner part of the shell (fig. 35: 1 and 3).

4.1.3.1.2. Helicoidally twisted type:

Members of this type such as the tribe Exogyrinae and some members of the tribe Turkostreini have convex, smooth or sculptured left valves and straight, slightly convex or slightly concave right valves (fig. 35: 4 and 8). The umbo is helicoidally twisted with variable axis of coiling. The degree of coiling (fig. 36) is variable as well and certain degrees are diagnostic of some genera (see *Ilymatogyra* and *Amphidonte*).

4.1.3.2. Noncoiled group

The second group has noncoiled umbos and subequivalve to almost equivalent shells. This group includes all members of the family Palaeolophidae and the

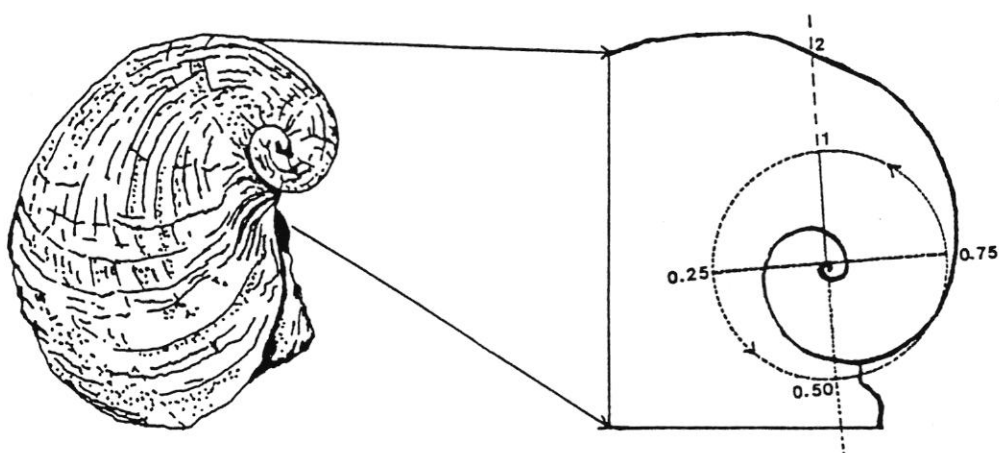


Fig. 36: The degree of coiling in the helicoidally twisted outline type (*Rhynchostreon*).

family Ostreidae (except for some members of the tribe Turkostreini) in addition to the tribe Hyotissini of the family Gryphaeidae. This group shows three major standard types (fig. 37):

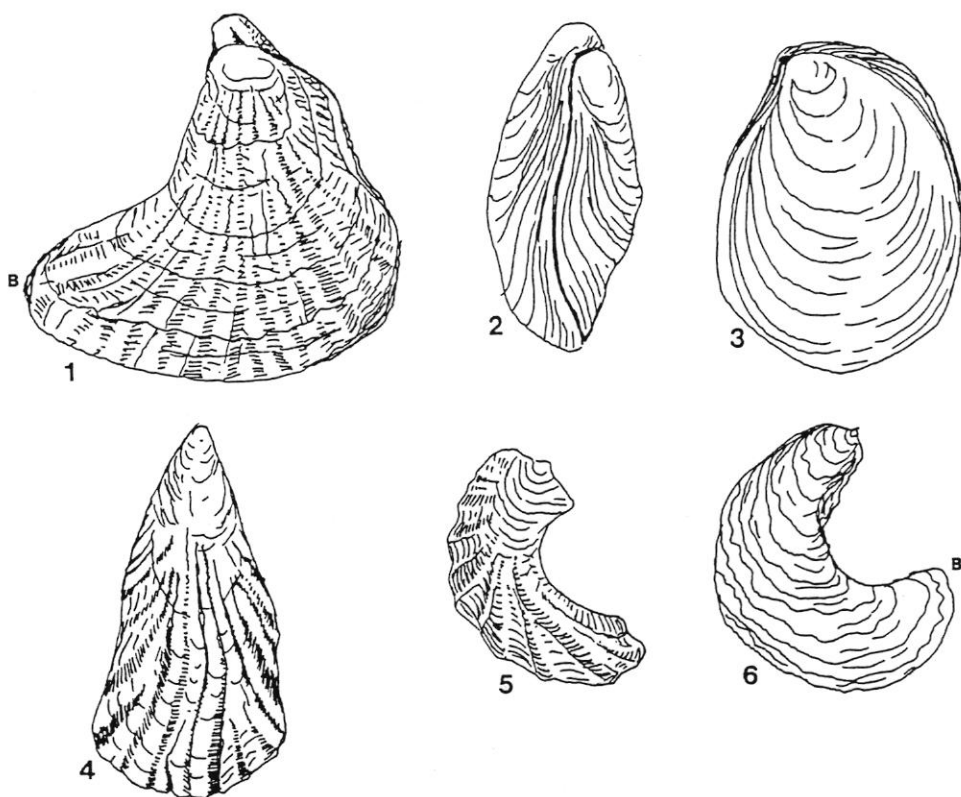


Fig. 37: Standard types of noncoiled group. (1, 4: Triangular type, *Ambigostrea*; 2, 3: Plate shaped type, *Gyrostrea*; 5, 6: Sickle-shaped type, *Agerostrea* B: Branchitellum.

4.1.3.2.1. Triangular type:

Members of this type such as *Ambigostrea* and *Cubitostrea* have both valves almost equal, slightly convex or nearly flat and sculptured or smooth. The umbo is high and triangular. The posterior margin is mostly extended and ends with a branchitellum (fig. 37: 1).

4.1.3.2.2. Plate-shaped type:

Members of this type such as the Ostreini, the Oscillophini and some members of the Flemingostreini have both valves subequivalve, they have almost flat, smooth or sculptured shells with plicated or non-plicated margins (fig. 37: 2 and 3). Most members of the plate-shaped type build circular or oval shells. It is represented in a large number of taxa, among which are the oldest known liostreid fossil oysters (see MALCHUS, 1990: 88).

4.1.3.2.3. Sickle-shaped type:

Representatives of this type such as *Rastellum* and *Agerostrea* are characterised by subequivalve, narrow, curved shells tapering postero-ventrally (crescentic) (fig. 37: 5 and 6). Both valves are generally plicated and in most cases have radial ribs. The branchitellum coincides with the postero-ventral tip of the shell. Wing-like extensions along the hinge axis are also common (see fig. 37: 5).

4.1.4. Internal Characters

4.1.4.1. Ligament area:

Adult oysters join the two valves with a horny elastic mass which acts like a spring to open the shell when the adductor muscle relaxes (ligament). Ligaments of recent oysters are amphidetic, alvincular and are composed of a middle fibrous, semi-translucent part (resilium) situated between two lamellar translucent parts (anterior and posterior lamellar ligaments) (see also STENZEL, 1971: N970).

The ligament area is the dorsal part along the hinge of the shell, where the growth tracks of ligament are seen. This area is composed of three vertical triangular parts: the resilifer (scar of the resilium) situated between the posterior and anterior bourrelets (scars of the posterior and anterior lamellar ligaments) (fig. 33).

MALCHUS (1990: 76–77) introduced five standard ligament area types as follows:

4.1.4.1.1. Ostreoid type:

Oysters of this type (Ostreinae, Lophinae, Palaeolophinae, Hyotissini and some members of Flemingostreinae and Crassostreinae) are characterised by a straight to slightly curved, triangular ligament area with a resilifer and both bourrelets are subequal (fig. 38a).

4.1.4.1.2. Gyrostreoid type:

Oysters of this type (*Gyrostrea* and some species of *Crassostrea*) have the top of the ligament area curved posteriorly running mostly within the commissure plane (fig. 38b).

4.1.4.1.3. Turkostreoid type:

In this type, many members of Turkostreini have the ligament area strongly posteriorly curved without strong reduction of the resilifer and bourrelets (fig. 38c).

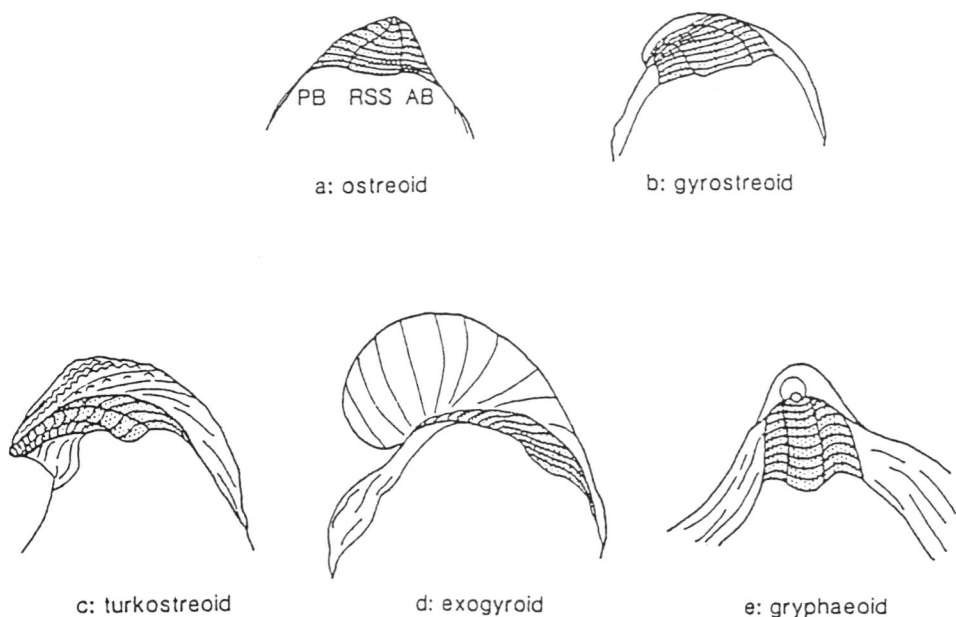


Fig. 38: Standard types of the ligament area of oysters. (PB: Posterior bourrelet, RSS: Resilifer, AB: Anterior bourrelet) (after MALCHUS, 1990).

4.1.4.1.4. Exogyroid type:

In this type, the bourrelets and the resilifer are strongly reduced because of the helicoidal twisting of the umbo (fig. 38d). This type is well represented in the subfamily Exogyrinae and occurs in some Turkosteoids.

4.1.4.1.5. Gryphaeoid type:

Members of this type (Gryphaeinae and Pycnodonteinae without the Hyotissini) have the ligament area high and triangular with the upper part curved towards the inner side of the shell forming a beak-like extension of the umbo (fig. 38e).

4.1.4.2. Subligamental area

The subligamental area is a term introduced by MALCHUS (1990) to describe a relatively small thickening of the left valve below the postero-dorsal side of the ligament area in the exogyroid ligament area type. It acts as an auxiliary abutment for the postero-dorsal part of the upper valve and supports the ligament which is weakened because of the strong helicoidal twisting of the umbo and the reduction of the ligament area. MALCHUS (1990: 79) introduced three standard types:

4.1.4.2.1. Ledge type:

The subligamental ledge forms an edge-shaped small area that starts at the postero-dorsal side with maximum thickness, becomes narrower in the anterior direction and vanishes at the centro-dorsal side (fig. 39c). This type characterises the genus *Exogyra*.

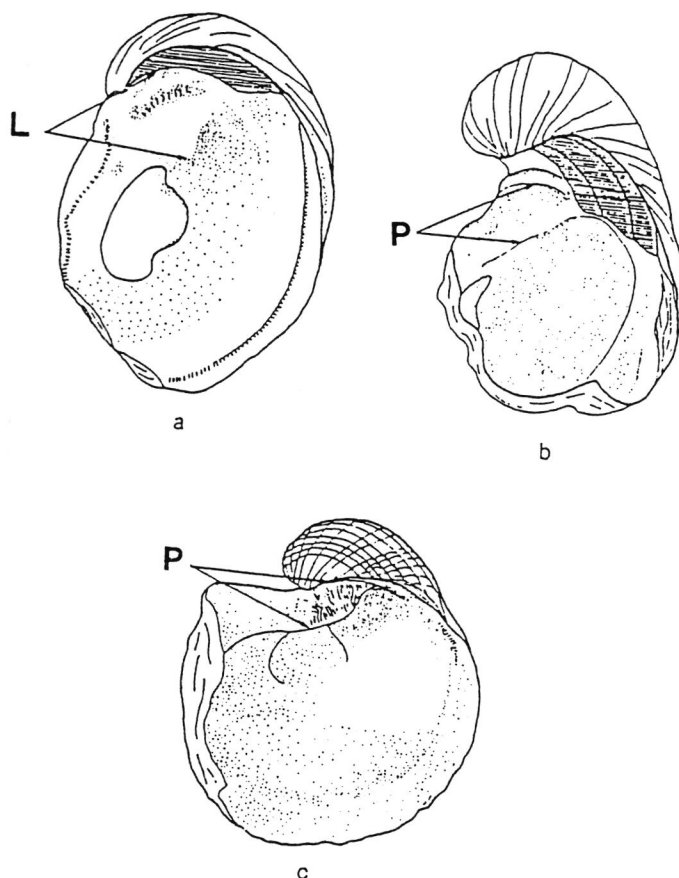


Fig. 39: Standard types of subligamental area. (a: *Amphidonte*, b: *Rhynchostreon*, c: *Exogyra*, P: Platform, L: ledge) (after MALCHUS, 1990).

4.1.4.2.2. Platform type (sensu Sockle-type of MALCHUS):

In this type, the subligamental area forms a slightly raised, small, solid platform above the adductor muscle scar at the postero-dorsal side. The maximum thickness is at the postero-dorsal side, then it becomes narrower in the anterior direction and vanishes at the antero-dorsal side (fig. 39a). This type is typical of the genus *Amphidonte*.

4.1.4.2.3. Transitional type:

In this type, the subligamental area is transitional form between the two previous types. It forms a combination of a blunt overhang and a thick platform (fig. 39b). This type is typical of many species of the subgenus *Ilymatogyra* (*Afrogyra*) and some species of the genus *Rhynchostreon*.

4.1.4.3. Umbonal cavity

Several oyster genera have an open cavity -umbonal cavity- beneath the ligament area of the left valve. It can be quite shallow or may reach the inner part of the umbo (fig. 33). This hollow chamber through the growth and extension of the ligament area, originates without filling the space below with shell material. Umbonal cavities are developed in recent non-incubatory genera such as *Crassostrea*, *Striostrea* and *Saccostrea*. They are best developed in *Crassostrea* and *Saccostrea* (see also STENZEL 1971:N994). Umbonal cavities are also known

from many fossil members of the subfamilies Gryphaeinae and Flemingostreinae and some members of the subfamilies Exogyreinae and Ostreinae. The size and shape of the umbonal cavity differ from one species to another, but within the same species, they tend to have similar dimensions. Until now, it is not proved whether there is any direct relationship between the formation of the umbonal cavities and any other morphological character of the shell or of the soft parts, therefore, it was not significantly useful in the general classification of oysters. However, it helps in the recognition of certain genera and species.

4.1.4.4. Quenstedt muscle scar

The Quenstedt muscle is a tiny, gill protractor muscle which is generally prominent in all oysters. It is attached to the antero-dorsal side of the shell below the umbo. The size of the scar of this muscle usually measures only a few millimetres, therefore, it is difficult to detect especially in fossil oysters (see also STENZEL 1971: N965). This character is typical of all oysters and was never used for differentiation and recognition of different oyster taxa.

4.1.4.5. Posterior adductor muscle scar

Post-larval oysters are monomyarian. The remaining posterior muscle is divided into a quick, translucent, dorsal part and a catch, opaque ventral part (see STENZEL, 1971: N962-N965). The two parts of the muscle are not separately

Adductor type Subfamily	Circular	Bleconcave	Comma-shaped	Crescentic\ Kidney-shaped
PALAEOLOPHINAE	 1	 2	 3  4  5  6	 7
GRYPHAEINAE				 8
PYCNODONTEINAE	 9  10			
GRYPHAEOSTREINAE				 11
FLEMINGOSTREINAE		 12	 13	 14  15
EXOXYREINAE		 16  17	 18  19  20	

Fig. 40: Adductor muscle scar types of some oysters of this study (table idea after MALCHUS, 1990) 1. *A. (Amphidonte) sigmoideum* (REUSS) 2. *A. (Amphidonte) haliotoidum* (SOWERBY) 3. *Rastellum carinatum* (LAMARCK) 4. *Rastellum diluvianum* (LINNÉ) 5. *Oscillopsa dichotoma* (BAYLE) 6. *Oscillopsa wala* n. sp. 7. *Oscillopsa figari* (FOURTAU) 8. *Africogryphaea costellata* (DOUVILLÉ) 9. *Hyotissa semiplana* (SOWERBY) 10. *Pycnodonte vesiculare* (LAMARCK, 1806) 11. *Gryphaeostrea canaliculata* (SOWERBY) 12. *Gryphaeligmus jabbokensis* (COX) 13. *Agerostrea unguata* (SCHLOTHEIM) 14. *Agerostrea lunata* (NILSSON) 15. *Ambigostrea viliei* (COQUAND) 16. *A. (Ceratostreon) pliciferum* (DUJARDIN) 17. *A. (Ceratostreon) flabellatum* (GOLDFUSS) 18. *Rhynchostreon mermeti* (COQUAND) 19. *I. (Afrogyra) africana* (LAMARCK) 20. *E. (Costagyra) olisiponensis* (SHARPE).

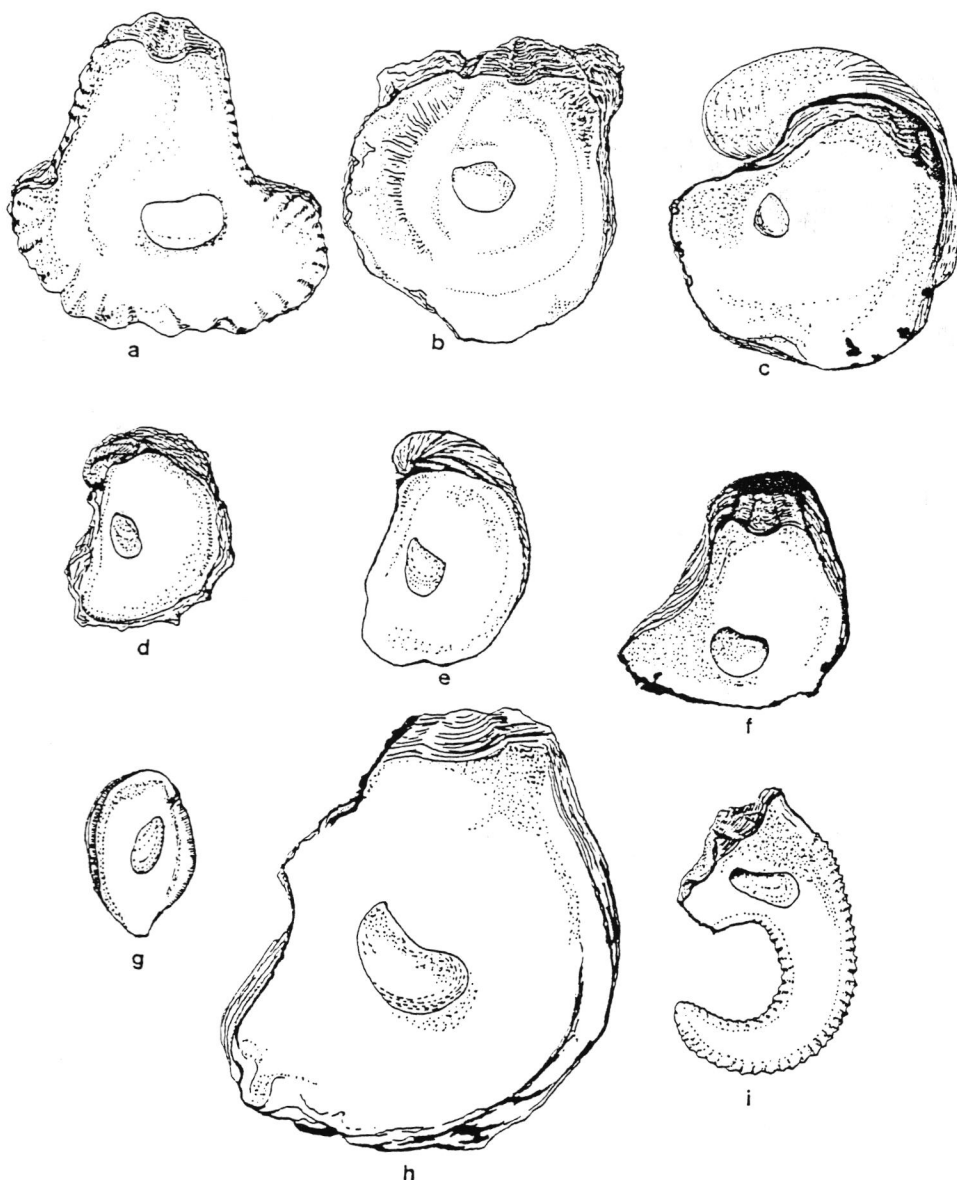


Fig. 41: Different kinds of adductor muscle scars of some oysters. (a: *Ambigostrea*; b: *Pycnodonte*; c: *Rhynchostreon*; d: *A. (Ceratostreon)*; e: *Ilymatogyra*; f: *Africogryphaea*; g: *A. (Amphidonte)*; h: *Oscillopha*; i: *Agerostrea*, origin of the figures: a, b, e: MALCHUS, 1990; c, d, f: own figures; g, i: DACQUE, 1922; h: GRECO, 1918).

shown in the imprint. Recent oysters have an aragonitic adductor muscle pad (CARTER, 1990: 230); in fossil oysters, the aragonitic pad and occasionally parts of its surroundings are dissolved without replacement, leaving cavities which might collapse as a result of rock pressure or be filled with secondary crystalline material or sedimentary matrix. The outline of the muscle imprint plays an important role in the general classification of oysters. It varies significantly at the family and for lower taxa level. The general outlook of the imprint can be affected within the same taxon by the shape of the individual, but it has almost al-

ways the same proportions referred to the valve shape. For example: individuals that tend to grow higher and narrower may have longer and narrower muscle imprints than other individuals within the same species which grow shorter and wider (see STENZEL, 1971: fig. J8). Different muscle imprint types of some taxa involved in this study are shown in figs. (40 and 41).

4.1.4.6. Chomata

Several oysters have small ridgelets or pits or tiny raised structures surrounding all or parts of the interior margins of the shell. These are collectively called chomata (singular choma). Chomata present on the left valve are called catachomata and those on the right valve are called anachomata. Relict chomata are those left behind as growth- tracks in older parts of the shell. They may be visible on the external side of the valve (see STENZEL, 1971: N993 and MALCHUS, 1990: 83). Protochomata is a term introduced by HARRY (1983) for chomata that run normal to the margins of the shell. Generally chomata have chalky cores which are less resistant to mechanical and chemical corrosion, therefore, they may become corroded or dissolved leaving visible grooves that sometimes can be seen from the outside. The presence of chomata may influence the microstructure of the foliated endostracum (see chomata-influenced-cross-foliated structure, section 4.6.3.3)

The function and origin of chomata is unknown until now. They have a great importance in the modern classification and recognition of the different oysters groups down to the genus level. HARRY (1985: 128) reported five types of chomata of living oysters, three of which (vermiculate, neopycnodontine and lath-chomata) represent the subfamily Pycnodontinae and two (lophine and ostreine chomata) represent some members of the family Ostreidae (HARRY, 1985: 133). Both lophine and ostreine chomata types may occur together in one individual such as in the genus *Dendostrea* and *Alectryonella* in which case the ostreine chomata are limited to the margin close to the hinge.

MALCHUS (1990: 83) has defined three standard chomata types from fossil oyster groups:

1. Vermiculate chomata: Worm-shaped tiny raised structures up to five millimetres long. They occur mostly very close to each other or interfinger. They are restricted to the vicinity of the hinge.

2. Straight chomata (Steg-Chomata *sensu* MALCHUS): Consist of narrow, straight, continuous ridgelets in right valves and corresponding grooves and measure one to five millimetre in length and 0.5–1.5 mm in width.

3. Pustulate chomata: One or more lines of pustules or lines of tubercles which range from one to few millimetres long. Chomata of this type are mostly concentrated near the dorsal side of the shell or may surround the outer shell margin.

Generally, members of the subfamily Palaeolophinae produce small straight chomata only in Upper Cretaceous times. Both Gryphaeinae and Gryphaeostreinae did not have chomata of any kind. Pycnodontinae (except for *Texigryphaea*) are characterised by vermiculate chomata. Members of the subfamily Exogyreinae had straight chomata in the Jurassic period, later some of them built vermiculate chomata. Flemingostreinae started without chomata until Middle Jurassic when some genera such as *Gryphaeligmus* built straight and pustulate chomata, later few of them built pustulate chomata. The oldest members of Lophinae may have first developed straight chomata, then built straight and pustulate chomata, while Crassostreinae and Ostreinae have straight chomata and rarely relict chomata (see MALCHUS, 1990: 83–88). The chomata types introduced by MALCHUS are applied in the systematic descriptions in this study.

4.1.4.7. Neobranch units

Neobranch units is a term introduced by HARRY (1985: 124) to indicate tube-like grooves or ridges (fig. 33) that cover parts of the shell interior of some oysters such as recent *Ostrea* species and extinct *Nicaisolopha*. This character may be useful in identifying some oyster taxa, but it is not known from many oysters to allow a comparative study.

4.1.5. External Characters

4.1.5.1. Pigmentation

The external surface of living oyster shells may display white, greyish or brown colouration, and some species may develop golden-brown colours as a result of the organic material of the exostracum (HARRY, 1985: 123). However,

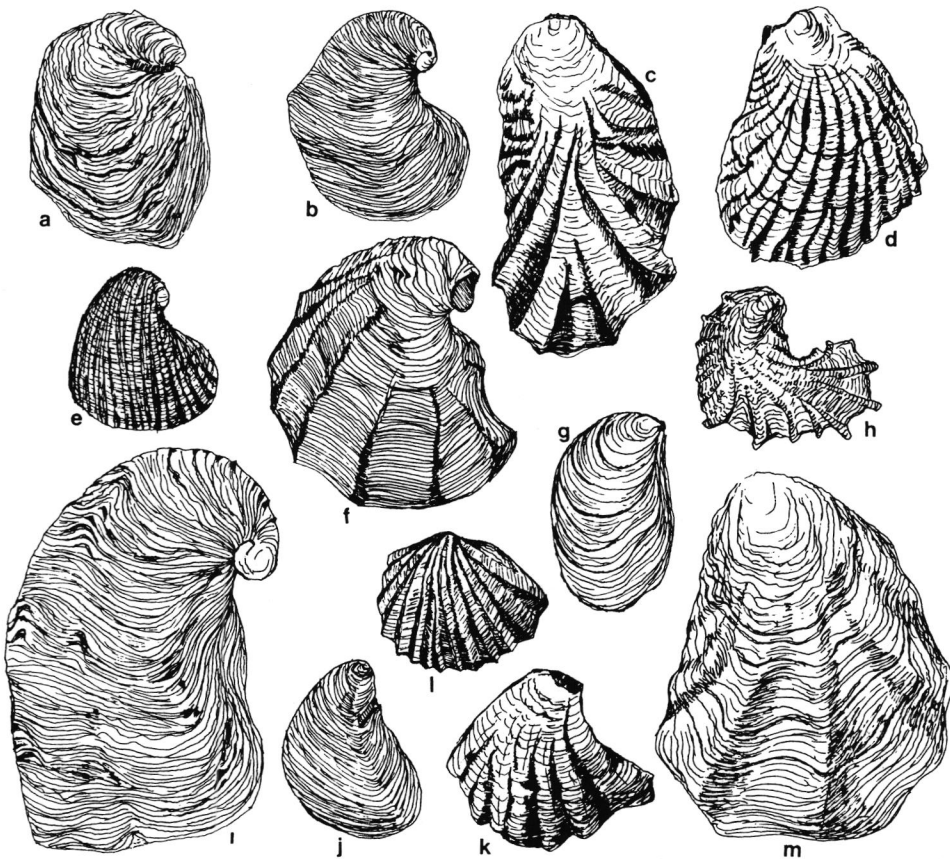


Fig. 42: Different sculptures of some of the studied oysters. a: *I. (Afrogyra) africana* (LAMARCK) forma crassa, growth-squamae. b: *Rhynchostreon mermeti* (COQUAND), smooth growth-lines. c: *Oscillopoda wala* n. sp., sharp irregular ribs. d: *Ambigostrea villei* (COQUAND), rounded radial ribs. e: *Rhynchostreon mermeti* (COQUAND), fine radial costae. f: *Exogyra olisiponensis* (SHARPE), radial ribs. g: *Curvostrea rouvillei* (COQUAND) smooth growth-lines. h: *A. (Ceratostreon) flabellatum* (GOLDFUSS), sharp hollow spines. i: *E. (Exogyra) italica* (SEGUENZA), nodes or tubercles. j: *Laeviggyra luynei* (LARTET), smooth surface with keel. k: *Africogryphaea costellata* (DOUVILLE), rounded irregular radial ribs. l: *Gryphaeligmus jabbokensis* (COX), sharply keeled regular radial ribs. m: *Nicaisolopha nicaisei* (COQUAND), wavy large folds.

some oyster shells show certain kinds of pigmentation patterns. For example: outer surfaces of *Ostreola*, *Planostrea*, *Undulostrea*, *Alectryonella* and *Parahyotissa* may be variously washed or striped with red, blue, purple or dark brown colours (HARRY, 1985). In some cases, HARRY (1985) used the internal shell colouration to differentiate between some species. For example: *Myrakeena* shows white to light green internal colour and *Undulostrea* shows greyish-white internal colour.

Fossil oysters normally do not show any pigmentation patterns, possibly as a result of diagenetic processes (LEWY, 1973: 65). However, some prominent exceptions such as species of the *Texigryphaea*, *Odontogryphaea*, *Ilymatogyra* and *Rhynchostreon* show patterns of pigmentations such as radial or concentric bands of dark brown or purple colours (STENZEL, 1971; POJARKOVA, 1973; LEWY, 1973, 1984). Own observations on different species of *Rhynchostreon* suggest that, the colour banding might be influenced by temperature. Specimens of *Rhynchostreon suborbiculatum* (LAMARCK) from Southern France and Northern Africa show stronger tendency of pigmentation than those collected from north-western Europe.

4.1.5.2. Beak and umbo

The terms beak and umbo were applied with different meanings by different authors, many authors treated them as synonymous. The beak is the area directly surrounding and including the larval shell and the term umbo is applied for the area of earliest growth surrounding the maximum curvature of the shell, it includes the beak in many cases such as in *Gryphaea* and *Pycnodonte*. Opisthogyrate is applied to umbos with beaks pointing posteriorly, prosogyrate umbos have their beaks pointing anteriorly, orthogyrate umbos are curved so that the beaks (viewed from the internal side of the shell) lie above the hinge area, and spirogyrate umbos are helicoidally twisted.

The importance of the coiling tendency of the umbo in the classification and the recognition of the different oyster groups is closely connected to the general outline of the shell, and the size and form of the ligament area. The same standard types of the ligament area can be applied to the umbo types. The twisting intensity of the spirogyrate umbos (fig. 36) is helpful in the differentiation of genera such as *Ilymatogyra* and *Rhynchostreon*.

4.1.5.3. Attachment area

Oysters become attached to a firm substratum at the end of their larval stages. Most species remain attached during their entire postlarval life, others may break away from the substrate and continue their life lying loose without attachment. All oysters (possibly except the ancestor) attach their shells by the left valve (fig. 33). The size of the attachment area of the different groups of oysters is variable when compared to each others. However, they have in many cases relatively constant relationships with the size, general outline of the shell and its ligament type. Recent oyster groups such as the tribes Ostreini, Crassostreini, which build reefs, and some members of the tribe Lophini attach single or in small groups with generally large attachment areas, while oysters that live in low water currents have smaller attachment areas.

Some oysters such as *Ilymatogyra arietina* (ROEMER) and some individuals of *Odontogryphaea thirsae* (GABB), *Rhynchostreon suborbiculatum* (LAMARCK) and *Exogyra laeviuscula* ROEMER do not show signs of attachment at the umbones. They may have managed to live virtually free throughout their entire life (STENZEL, 1971: N996, MALCHUS, 1990: 92).

4.1.6.1. Periostracum

The periostracum is an external thin film made of organic material acting as an outer cover for the shell. It is entirely composed of dark, non-mineralized organic material (mostly conchiolin) horny in appearance and flexible. It protects the underlying shell layers mainly against leaching by sea water, however, it is subject to bacterial decay. The thickness of the periostracum is variable, it ranges from few to several micrometers (CARRIKER et al. 1980: 145), it is fragile and easily broken when dried, therefore, it is difficult to find especially in fossil oysters. Among the living species *Hytissa* seems to have a poorly developed periostracum and *Striostrea* in comparison to others seems to have a strongly developed periostracum (see also STENZEL 1971: N977).

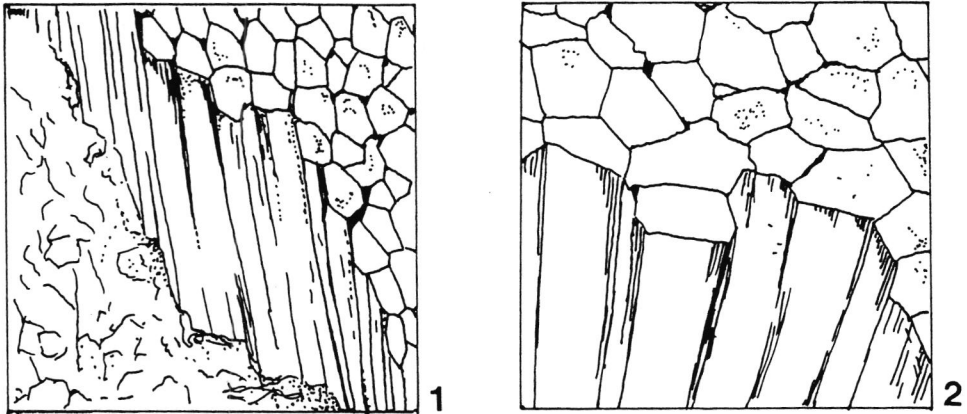


Fig. 44: Prisms of the exostracum seen under the scanning electron microscope. (Horizontal field of the figure in 1 = 120 μm and in 2 = 60 μm ; figures after CARRIKER et al., 1980, they represent the exostracum of *Crassostrea virginica* (GMELIN))

4.1.6.2. Exostracum

The calcitic prismatic outer layer (here exostracum) follows the periostracum film. This layer is generally composed of discrete, parallel, columnar, closely packed calcitic prisms with variable polygonal cross-sections (fig. 44). The prisms are delineated from each other by thin, non-mineralized, simple conchiolin walls. The long axis of the prisms does not exceed 84 μm (CARRIKER et al. 1980: 154). In recent oysters prisms of the left valve are generally shorter than those of the right valve, therefore, the layer is better detected in the right valve. In fossil oysters, it is mostly completely eroded or leaves only fractions overlying the calcitic endostracum.

The calcitic prismatic outer ostracum (exostracum) of the living oyster *Crassostrea virginica* (GMELIN) is fully described and discussed by CARRIKER et al. (1980: 145–155).

4.1.6.3. Endostracum

Under the thin layer of prisms of the exostracum lies the largest, massive, foliated layer of each valve of an oyster fig. (43). It consists of calcitic foliae or sheets delineated from each other by thin sheets of intercrystalline conchiolin. Each foil consists of numerous, very thin, calcitic laths or blades with an average thickness of 0.2 μm , the length of the laths is difficult to determine because of the indefinite orientation of the long axis of the laths relative to the fracture surface and because of the overlapping of the laths. However, the longest measured lath makes 9 μm (CARRIKER et al. 1980: 160). Within a single growth lamel-

la, the laths may take any possible orientation in regular or irregular forms. The arrangement of the foliae in this layer varies significantly from one group of oysters to another and plays an important role in the modern classification of oysters (see MALCHUS 1990: 63–76). The foliae of this layer may overlay each other in a compact form or may have various lenticular chambers or lenses. These lenses are variable in length and width and may be originally empty (figs. 11 and 13) or originally filled with chalky material (figs. 21 and 22) called "mocret" by MALCHUS (1990: 66) secreted by the oyster. Pycnodontids are characterised by having some shell layers resembling a sort of foam or spongy, honeycomb networks enclosing numerous small cavities or vesicles which may be originally empty or filled with mocret (vesicular lenses) (fig. 14 and fig. 15).

CARTER (1990: 350–362) subdivided the endostracum of the superfamily Ostreoidea into: regularly-foliated, crossed-foliated and complex-crossed-foliated. These subdivisions are similar to the subdivisions of MALCHUS (1990) consequently (simply-foliated, simply-cross-foliated and irregular-complex-cross-foliated). The following descriptions of the standard shell microstructures of the endostracum adopted in this study follow MALCHUS (1990):

4.1.6.3.1. Simply foliated structure

In this simple arrangement, the laths of a foil are oriented with their long axis parallel or subparallel to each other (fig. 45a). Growth planes of the foliae are parallel or in a very low angle to the exterior shell surface. This type structure is not restricted to any part of the endostracum. It may be combined with other foliated structures. The type is well represented in many members of the subfamily Flemingostreinae.

4.1.6.3.2. Bent foliated structure:

In this type, pseudoprismatic laths run parallel to each other forming stacks of foliae running subnormal to normal to the outer shell surface (fig. 24). This type may occupy large parts of the endostracum and is mostly combined with other structures. It is better represented near the umbo of some members of the subfamily Exogyreinae.

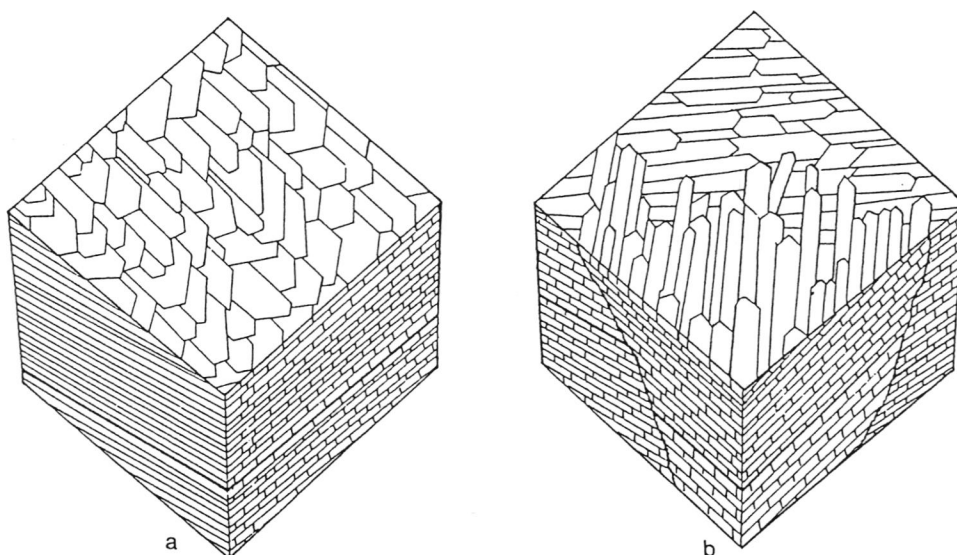


Fig. 45: Sketch showing a: Simply-foliated structure b: Simply-cross-foliated structure

4.1.6.3.3. Cross foliated structure

This type consists of laths forming stacks of foliae that overlap each others in regular or irregular forms in three dimensional orientations. In the simply-cross foliated-structure, the adjacent stacks of foliae dip in opposite directions perpendicular to the outer shell surface (fig. 45b). The irregular-cross-foliated structure (fig. 20) represents stacks of foliae in different orientations and inclinations but mostly stay perpendicular to the shell wall. A complicated network of stacks of foliae with all possible three-dimensional orientations is called irregular-complex-cross-foliated structure (fig. 23), this kind of structure is typical of some members of the subfamily Gryphaeinae.

In the herringbone-cross-foliated structure type (fig. 14 and fig. 16) several weakly inclined stacks of foliae form sublayers of a growth lamellae, with alternating dip directions, in overlying and underlying stacks. This type occupies parts of the endostracum of many amphidontids and pycnodontids. The shell structure of oysters rich in chomata may be distinctly disturbed. Thin sections show a wavy arrangement under polarized light where the crests of these "waves" appear dark as an effect of the presence of these chomata, this is called chomata-influenced-cross-foliated structure.

The above mentioned structure of the endostracum and their relationships to the amount of the mocret and/or empty lenses are important in the modern classification of oysters (see also MALCHUS 1990: 68-76).

4.1.6.4. Myostracum

The endostracum of each valve is crossed by two aragonitic film-thin layers; both begin near the umbo and mark the growth of the adductor and Quenstedt muscles (fig. 4.11 and fig. 3.15). These are called adductor and Quenstedt myostraca, they are secreted by oysters at areas of the inner part of the shell where the adductor and Quenstedt muscles are attached. Myostraca of the living oyster *Crassostrea virginica* are described and discussed by CARRIKER et al. (1980: 161-165). Fossil oysters may show only traces of these layers mostly filled with sediments or recrystalline calcite. This character does not have a significant value in the general modern classification of oysters.

4.1.6.5. Ligostracum

The ligostracum resembles the calcified part of the shell underlying the ligament (fig. 43 and fig. 14.2). It is composed of thin, distinct, mineralised, fibrous calcitic- aragonitic prisms. These prisms intersect the reflected foliae of the underlying layer at an angle of about 90 degrees (see CARTER, 1990: 347). The layer is easily broken and difficult to find in most fossil oysters. The ligostracum is found in all living oysters and probably in all fossil ones, however, it does not have a great value in the general classification of oysters. The ligostracum of the living oyster *Crassostrea virginica* is described and discussed by PALMER & CARRIKER (1979: 67-68).

4.2. Systematic description

This section consists of two parts: the first part contains the descriptions of the Jordanian oysters, and the second contains the descriptions of the North European ones. Descriptions on the species level are divided into five categories which include the most important morphological characters necessary for the descriptions. The categories are made to provide a simplified presentation of the different oysters described in this study. The systematic classification introduced by MALCHUS (1990) is used.

4.2.1. Description of the Jordanian oysters

Order **Pterioida** NEWELL, 1965

Suborder **Ostreina** FÉRUSAC, 1822

Superfamily *Ostreoidea* RAFINESQUE, 1815

Family *Palaeolophidae* MALCHUS, 1990

1990 *Palaeolophidae* MALCHUS, Rev. Kreide-Austern Ägypt., p.101.

Description: (According to MALCHUS, 1990) Both valves are plicated and/or ribbed, ribs are variable in size and number. Ligament area is higher than long. Chomata are not present in the Triassic and Jurassic representatives and few indistinct lath-chomata are present in some Cretaceous forms. Adductor muscle scar is rounded to comma-shaped and postero-dorsal. Shell microstructure in both valves is simply-foliated, few Triassic and Jurassic forms and many Cretaceous forms have hollow and mocket lenses.

Attributed subfamilies: *Palaeolophinae* MALCHUS, 1990.

Stratigraphic and geographic distribution: Triassic (?Anisian, Carnian)- Upper Cretaceous (Maastrichtian), world wide except in boreal region.

Differences: MALCHUS (1990: 101) defined a group of Mesozoic Lophinae-like oysters under the name *Palaeolophinae*. They differ from Lophinae by the strongly lenticular simply-foliated shell microstructure which is very often filled with mocket. Early representatives of this family have no chomata, only the Cretaceous ones have indistinct straight-chomata. MALCHUS (1990: 186) suggested that this group is possibly evolved from Triassic *Enantiostreon* (Terquemidae).

Remarks: (MALCHUS, 1990: 101) introduced both *Palaeolophidae* and *Palaeolophinae* with the same diagnosis. The subfamily can be omitted because it does not differentiate taxa within the family.

Tribe *Oscillophini* MALCHUS, 1990

1990 *Oscillophini*, MALCHUS, Rev. Kreide-Austern Ägypt., p. 102.

Type genus: *Oscillopha* MALCHUS, 1990.

Description: Shell medium in size, strongly plicate and/or ribbed, ribs are rather arcuate near the edges of the shell. Shell almost equivalve, elongate to crescent in outline. Chomata are rare and not well developed. The adductor muscle scar is comma-shaped and situated at the postero-dorsal to the median side. Shell microstructure of the Jurassic species is mostly with empty lenses and the Cretaceous species have more and larger mocket lenses.

Attributed genera: *Oscillopha* MALCHUS, 1990 and *Rastellum* FAUJAS-ST.-FOND, 1799.

Stratigraphic and geographic distribution: ?Triassic, Lower Jurassic (Lower Liassic) to Upper Cretaceous (Maastrichtian), almost world wide, except in boreal areas.

Differences: Members of the tribe *Oscillophini* are easily differentiated from other groups of oysters by their strongly lenticular simply-foliated shell structure. They differ from *Palaeolophini* MALCHUS (1990: 102) by the relatively increased number of empty lenses within the shell structure. In comparison with *Curvostreinae* MALCHUS, 1990 or *Pycnodontinae* STENZEL, 1959, this group has most probably no chomata. The *Hytissini* (plicated *Pycnodontids*) have no ribs and their shell structure is composed of chambers with vesicular structure.

Genus *Oscillopha* MALCHUS, 1990

1990 *Oscillopha* MALCHUS, Rev. Kreide-Austern Ägypt., pp.103.

Type species: *Ostrea dichotoma* BAYLE, 1849.

Description: Oscillophini with elongated outline and large mocret lenses of the shell microstructure.

Attributed species: *Oscillopha ?gregarea* (SOWERBY, 1813), *O. ?solitaria* (SOWERBY, 1813) of the Jurassic period, *O. dichotoma* (BAYLE, 1849), *O. figari* (FOURTAU, 1904) and *O. wala* n. sp. of the Upper Cretaceous period.

Stratigraphic and geographic distribution: Europe, North Africa, Middle East, and ?New Zealand (see WOODS, 1911).

Remarks: The different species belonging to this genus are discussed in full in SIEWERT (1972: 17) and MALCHUS (1990: 103).

Oscillopha wala n. sp.

Pl. 1, figs. 1a,b, 2a,b, 3a,b,c,d, 4, 5, 6, 7.

Holotype: Pl. 1, fig. 1a,b. Number GPIH-7WW100 (Geol.-Paläontol. Inst. & Museum, University of Hamburg), height 74mm, length 42mm.

Type locality: Wadi Wala, Central Jordan.

Type stratum: Upper Cretaceous (Turonian), Wadi As Sir Limestone Formation.

Derivatio nominis: The name of this species is derived from W. Wala in Central Jordan.

Material: More than 50, well to very well preserved, specimens collected from a coquina bed underlying massive beds in the centre of Wadi Wala, in Central Jordan.

Diagnosis: Medium in size. Thick shelled, elongated outline. Adductor drop-like or pearl-like. Radial ribs radiating from the centre towards the posterior and anterior ends. Shell microstructure strongly lenticular simply-foliated with relatively large mocret and empty lenses.

Differences: This species differs from other species of this genus by its larger size of the angular ribs. It is distinguished from *O. dichotoma* BAYLE by its narrower form and by the short sharp ribs that tend to curve toward both posterior and anterior ends. It differs from *Oscillopha figari* (FOURTAU) by its smaller size and the form of ribbing, also by the shell structure which contains smaller chalky lenses. *Oscillopha figari* (FOURTAU) is reported from the Maastrichtian of North Africa and has a larger adductor muscle scar and a deeper ligament area. Another minor difference is the shell periphery which is plicae-free.

Description: Size: Medium (maximum height 103mm)

Outline: Suboval, subequivalve, both valves mostly convex, length is greater than width.

Internal characters: Ligament area longer than high and relatively large in size. It starts strongly opisthogyrate, later it becomes semi-triangular. Resilifer at least double the length of the bourrelet. Umbonal cavities are not present. Adductor muscle scar is relatively large, deep, drop-like and postero-median.

External characters: Both valves are ornamented with radial ribs. These ribs are relatively large, bifurcating in most cases, sharply keeled, mostly tend to curve postero-ventrally. Shell periphery slightly to strongly plicated.

Shell microstructure: Strongly lenticular simply-foliated calcitic layers with large mocret and empty lenses.

Stratigraphic and geographic distribution: Turonian in Jordan.

Oscillopha figari (FOURTAU, 1904)

Pl. 2, fig. 1a,b

- 1904 *Ostrea* sp. FOURTAU, Faune crét. Egypte, p.309,311, pl. 5, fig. 1
1916 *Alectryonia figarii* (FOURTAU): GRECO, Fauna cret. Egitto, p.118, pl. 14, fig. 4, pl.15, figs. 1,2.
1990 *Oscillopha figari* (FOURTAU): MALCHUS, Rev. Kreide-Austern Ägypt., p. 104, pl. 2, fig. 1.

Holotype: FOURTAU (1904), pl. 5, fig. 1. (fide GRECO 1916: 118)

Type locality: Wadi Um Rockam, a branch of Wadi Abu Hammat at the northern side of South Galala, Egypt.

Type stratum: Upper Campanian (FOURTAU).

Material: Seven well to very well preserved specimens (three closed shells and four single valves) collected from a quarry at the western gate of the Hisa phosphate mine in Central Jordan.

Description: Size: Large to very large (up to 220 mm in height).

Outline: Generally oval to rounded with anterior side rather more straight, strongly biconvex to almost spherical. Left valve more convex than right valve.

Internal characters: Ligament area subtriangular, not very long and slightly pointed posteriorly. Adductor muscle imprint kidney-like with highest part running parallel to the height of the shell and situated postero-dorsally to postero-centrally. Shell periphery slightly plicated. Chomata not seen.

External characters: Shell thick. Both valves are sculptured with simple, mostly blunt radial ribs with equal intraspaces and crossed by heavy concentric growth lamellae. Attachment area variable, relatively small.

Shell microstructure: Strongly lenticular simply-foliated with mocrat and empty lenses.

Facies and associated fauna: The specimens of this study were collected from a large oyster-bioherm near Al Hisa phosphate mine that consists in addition to this species of *Ambigostrea villei* (COQUAND).

Stratigraphic and geographic distribution: The species is first reported from Campanian beds of Southern Galala in Egypt. ?Campanian to Maastrichtian (MALCHUS, 1990). In Jordan it is found in phosphate beds of Al Hisa Formation which comprises Campanian age.

Differences: This species builds large coquinal beds together with the similar *Ambigostrea villei* (COQUAND) in Central Jordan. However, *O. figari* has an inflated rounded outline and strongly lenticular simply-foliated microstructure, and *A. villei* a triangular outline and mostly compact simply-foliated microstructure. Both species are phylogenetically not related. *Oscillopha dichotoma* (BAYLE) compared to this species is smaller in size and has a plate-shaped outline and stronger dichotomous sculpture. The specimens of this species from Jordan are larger in size than the Egyptian ones. Otherwise they are identical.

Family *Gryphaeidae* VIALOV, 1936
Subfamily *Gryphaeinae* VIALOV, 1936

- 1936 *Gryphaeinae* VIALOV, Classific. huîtres, p. 19.
1990 *Gryphaeinae* VIALOV: MALCHUS, Rev. Kreide-Austern Ägypt., p. 107.

Type genus: *Gryphaea* LAMARCK, 1801

Description: (According to STENZEL, 1971) Small to large in size. Shell generally smooth or with growth lamellae or faint ribs. Outline round to oval. Left valve is slightly convex to straight, right valve is concave. Adductor muscle scar rounded, postero-dorsal. Shell structure mostly cross-foliated without empty lenses.

Attributed genera: *Gryphaea* LAMARCK, 1801, *Africogryphaea* FRENEIX, 1965.

Stratigraphic and geographic distribution: Triassic (Carnian?) – Jurassic (Oxfordian). In Triassic times it was restricted to the Arctic province, but later in the Liassic (early Jurassic) it had a world wide distribution (STENZEL, 1971).

Differences: The subfamily Gryphaeinae differs from other subfamilies belonging to this family by its rounded outline, postero-dorsal rounded adductor and by the mostly compact cross-foliated shell structure. Chomata generally not found.

Genus *Africogryphaea* FRENEIX, 1965

1965 *Gryphaea* (*Africogryphaea*) FRENEIX, Bivalv. Juras. Sahara Tunis. p.32

1990 *Africogryphaea* FRENEIX: MALCHUS, Rev. Kreide-Austern Ägypt., p.108.

Type Species: *Liogryphaea costellata* DOUVILLÉ, 1916.

Description: (According to FRENEIX, 1965) Shell medium to small in size, inequivalve, inequilateral with intermediate shell thickness. Outline tending to be higher than longer. Posterior area with ear-like extension due to the deep radial posterior sulcus. Left valve with somewhat irregular, strong and large radial ribs. Right valve flattened, slightly depressed, undulated and crowded with growth-lamellae. Muscle imprint medium in size, rounded to subovate in outline, convex ventrally, and drawn posteriorly. Ligament area ortho- to slightly opisthogyral, generally higher than long. Chomata not found. Shell structure compact and simply-foliated.

Attributed species: only *A. costellata* (DOUVILLÉ, 1916).

Stratigraphic and geographic distribution: Middle Jurassic, known from Bathonian rocks of North Africa, Southern Palestine, Jordan and Somalia.

Remarks: *Africogryphaea* is attributed to the Gryphaeids group due to the shell form, the adductor muscle scar and the ligament area. It is distinguished from other Gryphaeids by the shell structure and the unusual ribbed sculpture, (see MALCHUS, 1990: 109).

Africogryphaea costellata (DOUVILLÉ, 1916)

Pl. 1, fig. 8a,b.

- 1916 *Liogryphaea costellata* DOUVILLÉ, Les terrains Massif du Moghara, p. 58., pl VI, fig.10-12.
1921 *Lopha* (?) *philbyi* NEWTON, Juras. fauna Central Arabia, p.393, pl.XI, fig. 2,3.
1925 *Lopha philbyi* NEWTON: WEIR, Brach. Lam. Gastr. Somaliland, p.85, pl.12, fig. 12-14, 27
1935 *Gryphaea costellata* DOUVILLÉ: COX, Juras. Gastr. Lam. Somaliland, p.174, pl.17, fig.17
1936 *Gryphaea costellata* DOUVILLÉ: BLAKE, The Stratigr. of Palestine, p.70. 1939 *Gryphaea costellata* DOUVILLÉ: IONIDES & BLAKE, Report water ressource. Transjord., p72
1958 *Liogryphaea costellata* DOUVILLÉ: NAKKADY, Geology of Egypt, p.32.
1959 *Gryphaea costellata* DOUVILLÉ: JABOLI, Foss. Harar, p.37, pl. 5, figs.3-4.
1965 *Gryphaea* (*Africogryphaea*) *costellata* (DOUVILLÉ): FRENEIX, Bivalv. Juras. Sahara Tunis. p.81, pl.III, figs. 17-20.
1971 *Gryphaea* (*Africogryphaea*) *costellata* (DOUVILLÉ): STENZEL, Treatise, p.N1099, Fig. 147, 1.
1980 *Africogryphaea costellata* DOUVILLÉ: HIRSCH, Juras. Bival. Gastrop. N Sinai S. Isr., pl. 4, figs. 1-4
1987 *Gryphaea* (*Africogryphaea*) *costellata* (DOUVILLÉ): AQRABAWI, Biostrat. Jurassic Jordan, p.95, pl. V, Figs. 5-12.

Lectotype: DOUVILLÉ (1916) and FRENEIX (1965) did not designate a holotype or lectotype for this species. The specimen figured in DOUVILLÉ, 1916: pl. 6, fig. 10 a,b, is formally designated here as the lectotype of *Liogryphaea costellata* (Code, Art. 74).

Type locality: Gebel Moghara, Sinai, southern Egypt.

Type stratum: Bathonian.

Material: 21 well preserved specimens showing one or both valves collected along the Jordan Valley from Wadi Zerqa course, King Talal Dam, Arda and Deir Alla areas.

Description: See under the genus.

Dimensions: Maximum height 60 mm, maximum length 40 mm. and maximum width 25 mm.

Stratigraphic and geographic distribution: The species is known from Bathonian rocks of Egypt (DOUVILLÉ, 1916; NAKKADY, 1958), the Bathonian of Tunisia (FRENEIX, 1965), from the same age in Somalia Cox (1935) and in Palestine (BLAKE, 1936 and HIRSCH, 1980). In Jordan it has been reported from the Jordan Valley by BLAKE (1936); IONIDES & BLAKE (1939); and AQRABAWI (1987).

Subfamily *Exogyrinae* VIALOV, 1936

1936 *Exogyrinae* VIALOV, *Classific. huitres*, p. 20.

1990 *Exogyrinae* VIALOV: MALCHUS, *Rev. Kreide-Austern Ägypt.*, p.109.

Type genus: *Exogyra* SAY, 1820.

Description: (According to STENZEL, 1971) Attachment in the larval stages is with left antero-ventral shell periphery, in the postlarval stages becomes spiral and then in the adult stages strongly opisthogyral. Left valve generally convex, carinate and ornamented with concentric striae which is more or less lamellose and or with radial ribs which is generally fine and sometimes tuberculated or spinose. Right valve is generally flat and marked by concentric growth lines disposed in spirals of which the centre is at the peak of the posterior side of the shell. Sometimes it has radial ribs which are rarely tuberculated. The size of the attachment area is variable which effects the intensity of the twisting of the umbo. Ligament area is narrow and high, bourrelets are strongly reduced and umbonal cavity is clearly to weakly presented. Lath-chomata are almost always present (exception: *Aetostreon*), in the Cretaceous species vermiculate chomata and relict-chomata are observed. Adductor muscle imprint is rounded, slightly concave dorsally and rarely central. Shell structure in Jurassic species is compact-foliated to lenticular simply-foliated with mocret- and empty chambers, in the Cretaceous species the number of empty chambers increases to relatively very large (exception: *Rhynchostreon*).

Attributed tribes: Nanogyryni MALCHUS, 1990 and Exogyryni VIALOV, 1936.

Stratigraphic and geographic distribution: Middle Jurassic (Bajocian) to Upper Cretaceous (Maastrichtian), world wide.

Differences: Exogyrids are distinguished from other spiral oysters by the extreme opisthogyral twisting of the umbo which produces a narrower ligament area, and the reduction of bourrelets which produces a clear subligamental area. The reduction of the bourrelets can be a reversible process (MALCHUS, 1990). MALCHUS (1990: 109) related the exogyroid shell structure to the cross-foliated shell structure in *Gryphaea* and not to the compact-foliated shell structure in *Lioostrea* as it was previously suggested by SIEWERT (1972).

flat with a small fold crosses steeply to the posterior bourrelet and could be sub-parallel to it. Adductor muscle imprint postero-dorsal, simple or biconcave with length parallel to the length of the shell. Straight-chomata are clearly seen running parallel to the periphery of the shell also relict chomata could be present.

External characters: Umbo of the left valve is rather planispiral. Attachment area is clearly visible, mostly covering a relatively large area of the umbonal area. Sculpture consists of radial ribs which are variable in size and number; they start with many small ribs at the umbonal area then become larger, thicker and more concentrated at the anterior, antero-dorsal and dorsal areas, they mostly making an angle of 45 with the commissural plane. Ribs at the posterior side are finer and rather more discontinuous and could disappear, while at the anterior side they are clearly developed and occasionally bifurcate, they can also be spinose or tuberculated.

Shell microstructure: Left valve is lenticular foliated with mocret and empty lenses or irregular cross-foliated to herringbone-cross-foliated. Shell structure of the right valve is simply-foliated without mocret lenses.

Variability: MALCHUS (1990: 112) differentiated three forms of *Ceratostreon flabellatum* (GOLDFUSS) in Egypt: forma typica has a wide outline with moderately strong radial ribs and short spines, forma musa has a high, narrow, crescent-like outline with reduced number of radial ribs which are larger, more irregular and have larger spines, forma intermedia has an outline intermediate between both other forms with clear posterior sulcus, the form of the ribs is similar to that of forma typica but contains on both valves more short and discontinuous fine ribs at the posterior side. The specimens from Jordan show almost the same variations and the majority represent forma typica.

Stratigraphic and geographic distribution: Cretaceous (?Aptian - Cenomanian). Reported from Europe, Middle East and North Africa, Central and South Africa, North and Central America. In Jordan it has been reported by many authors such as BLANCKENHORN (1890, 1934); BLAKE (1936); WETZEL & MORTON (1959); BENDER (1968). It occurs in the different formations of Cenomanian-Lower Turonian age.

Facies and associated fauna: The specimens of this study are collected from many localities along the Wadi Araba and from North Jordan, mostly collected from limestones, marly limestones and marl occurring in oyster-banks or associated with other molluscs (mostly large casts of gastropods or rarely ammonites).

Differences: *Ceratostreon* has been described by many authors, and assigned to different ages within the Lower and Upper Cretaceous. According to MALCHUS (1990), *Ceratostreon flabellatum* (GOLDFUSS) is a chronostratigraphic species. He subdivided this species into three forms: typica, intermedia and minos (MALCHUS 1990: 112–113). *C. flabellatum* is differentiated from *C. pliciferum* (DUJARDIN) by its larger average size, wider outline and general shape and pattern of ribs. *C. flabellatum* is very similar to the American *C. texanum* (ROEMER) and *C. weatherfordense* (CRAGIN), they differ only in the stratigraphic distribution (Lower to Upper Albian). The Jordanian samples show less specimens with crescentic outline than the Egyptian samples, although they have the same outline and stratigraphic distribution.

Tribe *Exogyryni* VIALOV, 1936

1936 *Exogyrynae* VIALOV, Classific. Huitres, p.20

1990 *Exogyryni* VIALOV: MALCHUS, Rev. Kreide-Austern Ägypt. p.119.

Type genus: *Exogyra* SAY, 1820.

Description: Shell small to large in size and thick shelled in many cases. Outline generally convex and slightly arcuate with spirally curved umbo. Left valve very convex, carinate and mostly ornamented with concentric striae which are more or less lamellose and or with radial ribs with variable strength and patterns due to the different species, the ribs can be tuberculated or spinose. Right valve generally flat and marked by concentric growth-lines disposed in spirals of which the centre is at peak of the posterior side of the shell. Ligament area generally small and high, subligamental area forms an edge at the postero-dorsal side. Adductor muscle imprint orbicular or rounded to dorsally curved and mid-postero-dorsal in most cases. Attachment area small to very small in general. Chomata generally vermiculate especially at the subligamental area, straight-chomata and relict chomata are rare. Shell structure is mostly lenticular simply-foliated, partly with mocret and or empty lenses in many cases.

Attributed genera: *Exogyra* SAY, 1820, *Ilymatogyra* STENZEL, 1971, *Rhynchostreon* BAYLE, 1878, and *Laevigyra* MALCHUS, 1990.

Stratigraphic and geographic distribution: Cretaceous (?Aptian, Albian to Maastrichtian), world wide.

Differences: The strong spiral curvature of the umbo in Exogyrids is the major difference to the Nanogyrids and the other differences are mostly related to this fact (MALCHUS 1990: 119). Representatives of the genus *Amphidonte* do not have the same intensities of curvature of the umbo, and their umbo runs closer to the commissure plane. Their subligamental areas are socle-like while in Exogyrids it forms rather more a raised edge at the postero-dorsal side.

Genus *Exogyra* SAY, 1820

1820 *Exogyra* SAY, Observations zoophytes, shells, etc., p. 43

1990 *Exogyra* SAY: MALCHUS, Rev. Kreide-Austern Ägypt., p.133.

Type species: *Exogyra costata* SAY, 1820.

Description: (According to STENZEL, 1971) Shell generally medium to large in size, inequilateral and inequivalve. Outline rounded to oval with postero-dorsal side straight to slightly concave. Left valve very convex and clearly larger than the right valve which is mostly flat to slightly concave with concave postero-dorsal side. Umbo relatively thick and spirally curved. Keel not clear. Left valve is sculptured with growth-lamellae and /or radial ribs in different patterns. Right valve mainly ornamented with concentric growth-lamellae which run parallel to the shell peripheries and sometimes accompanied by faint short ribs. Ligament area small and high, the back bourrelet is reduced to a small edge and the front is not clear. Subligamental area is variable in size and makes a small platform under the ligament area with the largest part postero-dorsally situated and mostly covered with vermiculate chomata up to 7 mm long, straightchomata up to 3 or 4 mm long cover the antero-dorsal side while relict-chomata are only seen along the ligament area. Quenstedt muscle imprint very small, slightly elongated and situated at one mm. from the back end of the resilifer.

Attributed subgenera: *E. (Exogyra)* VIALOV, 1936 and *E. (Costagyra)* VIALOV, 1936.

Stratigraphic and geographic distribution: Cretaceous (?Albian, Cenomanian to Maastrichtian), world wide.

Remarks: This genus was subdivided by VIALOV (1936) into four subgenera, *E. (Exogyra)* (type species: *E. costata* SAY, 1820) and *E. (Costagyra)* (type species: *E. olisiponensis* SHARPE, 1850) are generally used. *E. (Nutogyra)* (type spe-

cies: *E.ourneti* (COQUAND, 1862)) and *E. (Fluctogyra)* (type species: *E. trigeri* (COQUAND, 1869)) are monospecific. MALCHUS (1990: 134) suggested that the last two subgenera are congeneric with *E. (Exogyra)* because of their internal and external morphology.

Subgenus *Exogyra* (*Exogyra*) VIALOV, 1936

1936 *Exogyra* section *Exogyra* s. str. VIALOV, Classific. Huîtres, p. 20.

1990 *E. (Exogyra)* VIALOV, MALCHUS, Rev. Kreide-Austern Ägypt., p. 138.

Type species: *Exogyra costata* SAY, 1820.

Description: General form and inner characters are as for genus. Left valve has mostly faint concentric growth lamellae, sometimes with soft, short discontinuous radial ribs with blunt keel and mostly regular intraspaces

Attributed species: *E. costata* SAY, 1820, *E. overwegi* v. BUCH, 1852, *E. cancellata* STEPHENSON, 1923, *E. ponderosa* ROEMER, 1852, *E. trigeri* (COQUAND, 1869), *E. upatoiensis* STEPHENSON, 1923, and *E. italica* SEGUENZA, 1883.

Stratigraphic and geographic distribution: Upper Cretaceous (Upper Cenomanian to Maastrichtian). N. Africa, Middle East, Europe, N. and S. America in shallow and warm seas.

Exogyra (Exogyra) italica (SEGUENZA, 1882)

Pl. 4, figs. 1a,b,c, 2.

1882 *Exogyra oxyntas* (COQUAND) var. *italica* SEGUENZA, Cret. Ital. Meridionale, p.178, pl. XVIII, Fig.1a.

1958 *Exogyra oxyntas* COQUAND: RUSSO, Lamellibranchi cenom.di Brancalione di Sicilia, pl. I, Fig. 3,4, pl. 2, Figs. 1-6,8, pl. 3, Fig. 1-5.

1968 *Exogyra ionica* MORONI & RICCO, Nuovi Stud. Fauna Cenom. Brancalione p.32, pl. IX, Fig. 1-4, pl. X, Fig. 1-6.

Holotype: SEGUENZA, 1882, pl. XVIII, fig. 1a.

Type locality: S. Giorgio near Brancalione, Calabria, S. Italy.

Type stratum: Cenomanian.

Material: 16 well to very well preserved specimens collected from south Wadi Jamil- SW Wadi Araba- S. Jordan from marly limestone and green shale of Cenomanian age.

Description: Size: Medium (maximum height of the Jordanian specimens 121mm).

Outline: Inequilateral, inequivalve, relatively narrow, elongated and sub-triangular in outline. Left valve convex to very convex and right valve oval in outline, straight to a little convex to concave ventrally.

Internal characters: Adductor muscle scar relatively large, suboval, slightly concave dorsally and situated postero-dorsally. Ligament area small and high. Subligamental area small and forms an edge-like area raised under the posterior side of the umbonal area. Straight-chomata covering the inner parts of the postero and antero-dorsal sides and relict chomata can be clearly seen on the dorsal edge of the right valve.

External characters: Left valve sculptured with a heavy cover of scaly growth lamellae and with short, discontinuous, radial tubercles or nods, only at the umbonal area some short, continuous arched radial ribs are observed. Right valve sculptured with ellipsoidal scaly growth lamellae, mostly with short tubercles starting dorso-ventrally and running parallel to the periphery of the shell leaving a small smooth area at the postero-dorsal edge. Edge-like keel of the left valve starts strongly with the early coiling and later runs parallel to the length of the shell running rather more flat at the central and ventral sides. Umbo relatively high, large, twisted helicoidally and raised above the commis-

sure line in a typical exogyrid form. Umbonal cavity present. Attachment area generally small.

Shell microstructure: Left valve is lenticular foliated with many large mocret and some empty lenses, right valve is mostly compact-foliated, few mocret lenses are possible.

Stratigraphic and geographic distribution: Upper Cretaceous (Cenomanian), Southern Italy, ?Algeria, ?Tunisia and ?Morocco. Herein, it is reported for the first time from Jordan.

Differences: *E. (Costagyra) olisiponensis* (SHARPE) is distinguished from this species by its smaller size, by the less elongated oval to rounded outline and by the twisting form of the umbo which is less helicoidal and runs within the commissure-plane.

Remarks: SEGUENZA (1882: 178) described this species as a variety of *E. oxyntas* which is synonymous with *E. overwegi* v. BUCH, 1852, and was described later by MORONI & RICCO (1968: 32) under the name *E. ionica*. Considering that "italica" is the older name and according to the Code (Art. 16) it has priority for the naming of the species under consideration.

Subgenus *Exogyra* (*Costagyra*) VIALOV, 1936

1936 Section *Costagyra* VIALOV, Classific. huitres, p.20.

1990 *E. (Costagyra)* VIALOV: MALCHUS, Rev. Kreide-Austern Ägypt. p.134.

Type species: *Exogyra olisiponensis* SHARPE, 1850.

Description: As for the genus, with nearly hemispherical outline and variable pattern of which radial ribbing covering the left valve mostly tuberculated or even spinose. Right valve has short, discontinuous radial ribs crossing the scaly growth-lamellae.

Attributed species: only *E. (C.) olisiponensis* SHARPE, 1850.

Stratigraphic and geographic distribution: Upper Cretaceous (Cenomanian to Lower Turonian). World wide, better known from the Tethys Realm.

Exogyra (Costagyra) olisiponensis SHARPE, 1850

Pl. 4, figs. 3, 4a,b, 5 a,b; Pl. 5, figs. 1a,b, 2

1850 *Exogyra olisiponensis* SHARPE, Second district Portugal, p.185, pl. 19, fig. 1,2.

1890 *Exogyra olisiponensis* SHARPE: BLANCKENHORN, Entwickl. Kreidesystem Syrien, p.74

1900 *Ostrea olisiponensis* SHARPE: BLANCKENHORN, N. zur Geol. u. Paläont. Ägypt, p.33

1929 *Exogyra olisiponensis* SHARPE: REESIDE, *E. olisiponensis* & *E. costata* Cret. West Interior, 268, pls.

1962 *Exogyra olisiponensis* SHARPE: SCHMID (in Bender 1968: Geol. Jordan.), p.74

1966 *Exogyra olisiponensis* SHARPE: BEYDOUN, E. Aden., p. 27.

1984 *Costagyra olisiponensis* SHARPE: DHONDT, Spanish Cret. Bivalves, p. 857.

1987 *Exogyra olisiponensis* SHARPE: BANDEL et al., Wadi Qena, p.440, pl. 2, fig. 3.

1989 *Exogyra (Costagyra) olisiponensis* SHARPE: KUSS & MALCHUS, Facies & Biostrat. NE Egypt., p.895.

1990 *Exogyra (Costagyra) olisiponensis* SHARPE: MALCHUS, Rev. Kreide-Austern Ägypt., p.134, pl. 10, figs. 1-6.

Holotype: SHARPE, 1850, pl. 19, fig. 1,2.

Type locality: Upper beds of hippurite limestone at Lisbon (Portugal).

Type stratum: Cenomanian.

Material: Over 40 well to very well preserved specimens, from S. Jordan (W. Tayieba and W. Jamil), Central Jordan (W. Heidan and W. Mujib) and N. Jordan (AJLUN and W. SALIH), collected from limestones and marly limestones of Cenomanian-Turonian age.

Description: Size: Medium (maximum height of the Jordanian specimens 85 mm).

Outline: Inequivalve and inequilateral, oval to rounded with the anterior side more straight than the posterior which is concave near the umbo and has a small sulcus in some cases. Left valve strongly convex.

Internal characters: Adductor muscle scar is relatively large and forms an oval outline with slightly concave dorsal side and situated postero-dorsally, subcentrally. Ligament area is small and high. Umbonal cavity is not prominent. Subligamental area is relatively large and forms a ridge-like surface situated posteriorly and covered with straight-chomata. Relict-chomata are concentrated on the rims of the right valve.

External characters: Umbo helicoidal, relatively small and runs very close to the commissure line. Attachment area variable. Sculpture on the left valve consists of a heavy cover of scaly growth lamellae crossed by 7 to 12 radial ribs, short to continuous with variable intraspaces, the ribs can be smooth tuberculated or even spinose. Keel on the left valve runs almost parallel to the length of the shell and hardly observed at the ventral side of the shell. Right valve subcircular, thick and mostly flat to slightly convex posteriorly and slightly concave anteriorly; sculpture on the right valve consists of strong scaly growth-lamellae running in oval lines and leaving in most cases a small smooth area under the umbo; these oval growth-lamellae can be crossed by short dichotomous radial ribs.

Shell microstructure: Left valve is lenticular-foliated with many mocret lenses and some empty lenses, right valve is mostly compact-foliated with the possibility of some mocret lenses.

Variability: The variability in the general form of the shell of *E. (Costagyra) olisiponensis* SHARPE is mostly effected by the variability of size of the attachment area (MALCHUS 1990: 136). This conclusion depended on the observations of the direct relationship between the general shape and the attachment area, where it is observed that almost all longer narrower specimens have small to absent attachment area, while the wider shorter forms maintain large to very large attachment areas, in the first case a free and complete process of coiling is possible. Similarly the keel in the first case is a little stronger which can also be related to the same concept. The variability of the sculpture together with the thickness of the shell are possibly affected by the water energy, where stronger thicker ribs with tubercles or spines indicate stronger water current.

Stratigraphic and geographic distribution: Upper Cretaceous (Middle Lower Cenomanian to Upper Cenomanian and Lower Turonian). It is reported from many localities spread over the Mediterranean province including Africa and Europe. Also known from USSR and South East Central Asia and South and North America. In Jordan it is reported by many authors such as BLANCKENHORN (1934); WETZEL & MORTON (1959); and BENDER (1968) representing mainly Cenomanian limestones and marly-limestones of Nodular and Echinoidal units and possibly the lower most part of Wadi Es Sir Formation of Cenomanian-Lower Turonian age.

Differences: *E. (C.) olisiponensis* maintains a great similarity to *E. (E.) italica*. But it can be differentiated by its larger size, longer form, stronger keel and by the more helicoidal twisting of the umbo. *A. (Ceratostreon) flabellatum* is distinguished from *E. (C.) olisiponensis* by the amphidontid shape and by the irregular-cross-foliated to herringbone-cross-foliated microstructure of the shell. Differentiations from other exogyroid oyster groups are fully discussed in; REE-SIDE (1929: 268-269); FRENEIX (1972:90-91); LEFRANC (1983:59-60); and MALCHUS (1989: 137- 138).

Genus *Ilymatogyra* Stenzel, 1971

1971 *Ilymatogyra* STENZEL, Treatise, p. N1119.

1990 *Ilymatogyra* STENZEL: MALCHUS, Rev. Kreide-Austern Ägypt., p. 119.

Type species: *Exogyra arietina* ROEMER, 1850.

Description: Shell small to medium in size. Outline narrow to wide elongated oval. Left valve strongly convex and right valve straight to slightly convex. Umbo mostly small and strongly helicoidal. Attachment area generally small to absent. Keel blunt and mostly clear. Posterior sulcus sometimes present. Sculpture on the left valve consists of concentric growth-lamellae, in some cases smooth and in others faint radial ribs are present. Right valve sculptured with rounded growth-lamellae which are concentrated more to the posterior side and leave a small smooth area under the umbo. Ligament area variable and depends on the intensity of the helicoidal twisting of the umbo. Umbonal cavity present. Subligamental area is generally small. Straight-chomata (up to 2 mm) cover the postero- and antero-dorsal sides. Adductor muscle imprint rounded to dorsally flat and postero-dorsal situated. Shell microstructure mostly lenticular simply-foliated with mocket and empty lenses.

Attributed subgenera: *Ilymatogyra* (*Ilymatogyra*) STENZEL, 1971 and *Ilymatogyra* (*Afrogyra*) MALCHUS, 1990.

Stratigraphic and geographic distribution: Upper Cretaceous (Lower to Upper Cenomanian), Middle East, North Africa, ?Madagascar, South Europe and USA (Western Interior and Gulf Coast).

Differences: *I. pellicoi* (VERNEUIL & COLLOMB, 1853) from the Aptian of Spain (DHONDT, 1984: 858) is very similar to *I. arietina* but differentiated by its stronger radial ribs on the left valve and by the concavo-convex right valve.

Subgenus *Ilymatogyra* (*Afrogyra*) MALCHUS, 1990

1990 *I. (Afrogyra)* MALCHUS, Rev. Kreide-Austern Ägypt., p. 120.

Type species: *Exogyra africana* LAMARCK, 1801.

Description: Shell small to medium in size. Outline elongated to oval. Umbo small. Attachment area variable. The intensity of the helicoidal twisting of the umbo is also variable from weak to very strong. Twisting axis is pointed to the commissure plane and not subparallel to the length of the shell. A blunt and mostly clearly developed keel appears antero-dorsally and shifts to the postero-ventral side. Sculpture on the left valve consists mostly of strong regularly spread concentric growth-lamellae, rarely crossed with faint radial ribs. Right valve flat to slightly convex or posteriorly concave and ornamented with fine, sharp, semi-ellipsoidal growth-lamellae starting postero-dorsally and tending to have more curvature at the anterior side. Ligament area depends on the intensity of helicoidal twisting and maintains a variable range of shape. Umbonal cavities sometimes present. Adductor muscle imprint medium in size with straight to slightly concave dorsal side and situated cenro-postero-dorsally. Shell microstructure of the left valve mostly lenticular foliated with mocket and empty lenses, right valve compact-foliated.

Attributed species: *I. (A.) cartledgei* (BÖSE, 1919), *I. (A.) africana* (LAMARCK, 1801), *I. (A.) laeviplexa* (KEMPER & WEBER, 1979), *I. ?(A.) drakei* (CRAGIN, 1893), *I. ?(A.) clarki* (SHATTUCK, 1903) and *I. ?(A.) pseudoafricana* (CHOFFAT, 1886).

Stratigraphic and geographic distribution: Upper Cretaceous (Lower to Upper Cenomanian), Mediterranean region, Madagascar, USA.

Differences: *I. (Afrogyra)* MALCHUS, 1990 differs from *I. (Ilymatogyra)* STENZEL, 1971, by its size, the absence of radial ribs 'except for *I. (A.) cartledgei*' and by the generally lower degree of coiling of the umbo. *I. (Afrogyra)* is also similar to the genus *Gyrostrea* which was assigned recently by MALCHUS (1990) to the subfamily Ostreinae according to its compact-foliated shell structure.

Ilymatogyra (Afrogyra) africana (LAMARCK, 1801)

Pl. 2, figs. 6a,b, 7a,b, 8, 9a,b, 10, 11; Pl. 3, figs. 1, 2a,b, 3

- 1801 *Gryphaea africana* LAMARCK, Syst. animaux s. vert., p.399, Encyclop. method. pl. CLXXXIX, figs. 5,6.
 1819 *Gryphaea secunda* LAMARCK, Hist. nat., p. 199, pl. 189, figs. 5,6.
 1852 *Exogyra densata* CONRAD, Office. Rep. Dead Sea, p.224, pl. 18, fig. 102, ?106.
 1862 *Ostrea auressensis* COQUAND, Paléont. Costantine, p.233, pl. XXII, figs. 12, 13.
 1910 *Gryphaea secunda* LAMARCK: PERVINQUIÈRE, Paleont. Univers., fichte 196.
 1934 *Exogyra africana* LAMARCK: BLANCKENHORN, Bivalv. der Kreideform. Syrien Palästina, p. 202.
 1937 *Exogyra africana* LAMARCK: DUBERTRET, Cont. Géol. Libano-Syrienne, p.16
 1959 *Exogyra africana* LAMARCK: WETZEL & MORTON, Contr. geol. Transjordan., p.140
 1962 *Exogyra africana* LAMARCK: SCHMID, in BENDER, Geol. Jordan, p.74, 76.
 1990 *Exogyra (Afrogyra) africana* LAMARCK (forma typica), MALCHUS, Rev. Kreide-Austern Ägypt., p.121, pl. 6, figs. 6-16, pl. 7, figs. 1-21, pl. 8, figs. 1-4.

Holotype: *Gryphaea africana* LAMARCK, 1801, Encyclop. pl. 189, figs. 5,6 = *Gryphaea secunda* LAMARCK, 1819, in PERVINQUIÈRE (1910), Palaeontol. Univers. fiche 196.

Type locality: Aurs (Algeria).

Type stratum: Cenomanian.

Material: More than 75 specimens variably preserved, most of them collected from Ras en Naqab, south east to Ma'an (South Jordan) and mostly representing forma crassa, and about 15 specimens collected from the middle of Wadi Heidan (Central Jordan) representing forma typica.

Description: Size: Small to medium (maximum height of the studied specimen 70 mm).

Outline: Oval or elongated-oval to semi-drop-like. Left valve is variable but commonly strongly convex. Right valve is flat to convex or slightly inflated.

Internal characters: Ligament area normally opisthogyrar or initially helicoidal then later grows in the dorso-ventral direction. Umbonal cavity is flat, subligamental area is small, sill-like, straight and without mould. Adductor muscle imprint is kidney-like or postero-dorsally peaked.

External characters: Umbo is variable, weakly twisted to helicoidally twisted and appears to be related to the size of the attachment area, where small attachments enables mostly the production of highly curved to helicoidal umbo curvature. Keel is blunt, later more rounded and mostly clearly developed. Sulcus is in many cases present. Left valve is ornamented with regular scaly or smooth growth-lamellae. Right valve is covered with finely spaced semi-ellipsoidal fine growth-lamellae which tends to run more rounded at the anterior side and leaves a small free patch at the postero-dorsal side.

Shell microstructure: Left valve is lenticular-foliated with more moeret and empty lenses at the ventral side, right valve is as well with moeret lenses.

Variability: MALCHUS (1990: 122) differentiated two forms of this species "forma typica and forma crassa". Forma crassa is generally larger in size, less convex, wider in outline, has a weaker keel and maintains more scaly growth-lamellae on the left valve which forms wave-like sculpture in most cases. It is possible that in both forms the umbo (especially in the older specimens) becomes thick and strongly helicoidally twisted (as in *Ilymatogyra s. str.*). That seems

more familiar in forma typica. This also affects the shape of the ligament area where the untwisted umbo enables the production of "ostreid" ligament area which seems rather more the case in forma crassa. The pattern of growth-lamellae on the right valve is also similar. They tend to become widely spaced and relatively thicker at the anterior and ventral sides more commonly in forma crassa. This reminds one of *Gyrostrea delettrei* (COQUAND) which has larger intraspaces and larger size of the lamellae than *I. africana*.

Stratigraphic and geographic distribution: Upper Cretaceous (Lower Middle Cenomanian to Upper Cenomanian), Southern Italy, North Africa, Niger, Middle East, South and Central America.

Differences: MALCHUS (1990: 123) stated that *I. (A.) africana* (LAMARCK) forma crassa MALCHUS has the same diagnosis of *E. delettrei* (COQUAND) sensu PERVINQUIÈRE (1912), GRECO (1918), which are differentiated from the original *Gyrostrea delettrei* (COQUAND, 1862: 224) by the relatively stronger twisting of the umbo and by the narrower intraspaces of the growth-lamellae on the right valve along with their different shell microstructure. MALCHUS concluded that *Gyrostrea delettrei* (COQUAND) does not exist in Egypt and suggested a transition between both species in Algeria and Tunisia with the possibility that *G. delettrei* might be a later ecomorph of *I. (A.) africana*.

The Jordanian *E. densata* CONRAD (1852: 224) is identical with forma typica of MALCHUS (1990), also *I. arietina* (ROEMER) var. *diceratina* PAULCKE and *E. africana* LAMARCK var. *peruana* STEINMANN described by PAULCKE (1903: 265) from Cenomanian rocks of Peru are synonymous with forma typica, while *E. reissi* PAULCKE described by the same author is identical with forma crassa of MALCHUS (1990). On the other hand forma typica is similar to *I. arietina* (ROEMER) but it does not reach the same intensity of helicoidal twisting and the twisting axis in typica makes a deep angle with the length of the shell which gives more elongated and less twisted form and affects the shape of the subligamental area. Some specimens of *Rhynchostreon mermeti* (COQUAND) are similar to forma typica but they can be differentiated by the fine radial ribbing on the left valve and by the different shell structure.

Genus *Laevigyra* MALCHUS, 1990

1990 *Laevigyra* MALCHUS, Rev. Kreide-Austern Ägypt, p.124.

Type species: *Ostrea luynesi* LARTET, 1872.

Description: Small to medium in size, thin-shelled with small umbo. Outline oval elongated, posterior side rather more straight to a little concave or a little convex. Attachment area variable. Left valve generally convex and smooth with clear keel at the early stages later becomes blunt or nearly flat. Right valve concavo-convex type, anterior side very narrow and covered with crescentic growth-lamellae, while other parts are smooth except for faint radial striae. Ligament area small and high. Subligamental area very small, weakly developed and forms an edge-like extension under the posterior side of the umbonal area and sometimes absent. Umbonal cavity present. Adductor muscle imprint oval, dorsally convex to slightly concave and situated postero-dorsally or centrally. Fine straight-chomata are present on the antero- and postero-dorsal sides. Microstructure of the shell is irregularly-cross-foliated, simply-cross-foliated to chomata-influenced-cross-foliated.

Attributed species: *L. luynesi* (LARTET, 1872), *L. dhondtae* MALCHUS, 1990, ?*L. bourgeoisi* (COQUAND, 1962), ?*L. langloisi* (COQUAND, 1869), ?*L. rhadamantus* (COQUAND, 1869), ?*L. inflata* (GOLDFUSS, 1833), = (?*L. subinflata* (D'ORBIGNY, 1847)), ?*L. winchelli* (WHITE, 1850).

Stratigraphic and geographic distribution: Cretaceous (?Albian, Cenomanian to ?Upper Maastrichtian), Middle East (Jordan and Palestine), North Africa (Egypt and Algeria), Europe (France and The Netherlands) and USA (Western Interior and the Gulf States).

Differences: In comparison with the other members of this group this genus is characterised by the smooth convex left valve and by the concavo-convex right valve as well as by having fewer straight-chomata. The general shape of the shell is similar to that in *Aetostreon* or *Amphidonte* but the first does not possess any chomata and builds empty lenses in the shell structure; furthermore it is restricted to the Lower Cretaceous. *Amphidonte* is comparatively thick-shelled, larger in size, the keel is always anteriorly situated and the left valve is flat to slightly convex.

Remarks: MALCHUS (1990: 124) suggested that *Laevigyra* could have developed from *Ilymatogyra*. He assigned 8 species to this genus, one of them is new, two were examined and the others were not studied and still require microstructural investigations.

Laevigyra luynesi (LARTET, 1872)

Pl. 3, figs. 13, 14 a,b, 15 a,b, 16

1872 *Ostrea luynesi* LARTET, Mer Morte, p.64, pl. X, figs. 17,18.

1900 *Exogyra luynesi* LARTET: BLANCKENHORN, Beitr. Geol. Syrien, p.75.

1990 *Laevigyra luynesi* MALCHUS: Rev. Kreide-Austern Ägypt., p. 125, pl. 8, figs. 10-14.

Holotype: LARTET, 1872: pl. X, Figs. 17,18.

Type locality: Wadi Heidan (Southern Madaba) in Central Jordan (designated herein).

Type stratum: Cenomanian.

Description: Size: Small (maximum height 38 mm).

Outline: Elongated oval, inequivalve and inequilateral. Umbo small and runs very close to the commissure plane, twisting intensity of maximum 1,75 degree. Left valve strongly convex with postero-dorsal side a little concave. Keel starts strong in the early stages, later becomes more blunt and runs parallel to the length of the shell. In the younger forms the keel can spread strongly until it reaches the ventral side. Right valve oval, slightly elongated, concavo-convex type.

Internal characters: Ligament area small and narrow. Subligamental area weakly developed. Umbonal cavity deep. Adductor muscle imprint rounded to oval, dorsally convex to slightly concave and situated postero-dorsally or centrally. Straight-chomata are present.

External characters: Attachment area variable in size but generally small. Left valve smooth except for faint concentric growth-lines. Posterior and central sides of the right valve are smooth, anterior and antero-dorsal sides are covered with concentric growth-lamellae, faint radial lines are observed on the posterior side of the right valve.

Shell microstructure: Mostly compact-foliated; ranges from simply-cross-foliated, simply-foliated to chomata-influenced-cross-foliated.

Stratigraphic and geographic distribution: Upper Cenomanian, Jordan and Palestine, Egypt and Madagascar.

Differences: Large specimens of *L. luynesi* (LARTET) look very similar to *R. mermeti* (COQUAND) forma typica and *I. (A.) africana* (LAMARCK) forma typica but *L. luynesi* is distinguished by its thin shell and its concavo-convex right valve. Furthermore, the ornamentation pattern of *mermeti* is not observed on any of the specimens of *luynesi*. *Aetostreon* in comparison has generally a stronger keel, larger specimens and no chomata.

Laevigyra dhondtae MALCHUS, 1990

Pl. 3, figs. 17, 18a,b.

- 1967 *Exogyra arietina* (STANTON): MISHNAEVSKÝ, Cenoman. oysters Israel, p.134, pl. F, figs. 5-6.
1979 *Exogyra cf. aficana* (LAMARCK): KEMPER & WEBER, Cenoman. El Salvador, pl. 2, fig. 2 a-c.
1990 *Laevigyra dhondtae* MALCHUS, Rev. Kreide-Austern Ägypt., p.126, pl. 8, figs. 5-9.

Holotype: MALCHUS (1990: pl. 8, fig. 5).

Type locality: Wadi Gunna, Southern Sinai (Egypt).

Type stratum: Upper Cenomanian, sandy marls.

Description: Size: Small (maximum height 27 mm)

Outline: Oval-elongated to drop-like with ventral and anterior sides convex and posterior side straight to slightly concave, occasionally with shallow sulcus. Left valve strongly convex mostly with blunt keel which runs within the length of the shell and can start fairly strongly near the umbo. Right valve of the concavo-convex type.

Internal characters: Ligament area small. Subligamental area also small, forming a tiny edge under the postero-dorsal side and is covered with straight-chomata. Adductor muscle imprint rounded to straight dorsally and situated postero-dorsally.

External characters: Shell relatively thick. Umbo generally small to very small and runs parallel to the commissure plane. Attachment area generally small. Anterior, antero-dorsal and antero-ventral sides covered with concentric growth-lamellae while the central and posterior sides are smooth.

Shell microstructure: Mostly compact-foliated, ranges from simply-foliated, simply- cross-foliated to chomata-influenced-cross-foliated.

Stratigraphic and geographic distribution: Upper Cenomanian, Egypt and Palestine. In Jordan it is reported by MALCHUS (1990: 126) from comparison material collected from Wadi Karak by Prof. J. KUSS (University of Bremen).

Differences: The species is differentiated from *L. luynesi* by its thicker shell, smoother keel, smaller umbo and by the relatively smaller smooth area on the right valve in addition to the smoother left valve. *L. dhondtae* is distinguished from *A. africana* by the concavo-convex right valve, (for more details see MALCHUS 1990: 126-127).

Genus *Rhynchostreon* BAYLE, 1878

1878 *Rhynchostreon* BAYLE, Fossiles princip. des terrains, pl. CXXXVIII.

1990 *Rhynchostreon* BAYLE: MALCHUS, Rev. Kreide-Austern Ägypt., 127.

Type species: *Exogyra suborbiculata* LAMARCK (= *Exogyra columba* LAMARCK, 1819 = *Rhynchostreon chaperi* BAYLE, 1878).

Description: Shell small to medium in size. Outline elongated oval or suboval to subcircular. Left valve strongly convex, smooth or covered with growth-lamellae crossed in many cases by different patterns of radial ribbing. Umbo relatively small, opisthogyral or almost orthogyral, helicoidally twisted and runs parallel to the commissure plane. Keel strong in early stages, disappears later. Right valve subcircular to oval, flat or slightly convex and generally covered with sharp concentric growth lines closely interspaced, leaving a small rounded smooth area at the centro-posterior side under the umbonal area. Ligament area very small and opens anteriorly. Subligamental area forms a tiny ridge-like area at the postero-dorsal side of the shell. Vermiculate chomata,

straight-chomata and relict-chomata are common and mostly reduced at the antero- and postero-dorsal sides. Adductor muscle imprint suboval to subcircular with a slight convexity at the anterior side, placed dorso- or centroposteriorly. Shell microstructure of left valve is simply-foliated, bent-foliated with some mocret and empty chambers.

Attributed species: *R. suborbiculatum* (LAMARCK, 1801), *R. mermeti* (COQUAND, 1862) *R. plicatulum* (LAMARCK, 1801), ?*R. columbella* (LAMARCK, 1806) and *R. laeviuscula* (ROEMER, 1852).

Stratigraphic and geographic distribution: Cretaceous (?Upper Albian, Lower Cenomanian to Santonian and ?Campanian), world wide.

Remarks: *Rhynchostreon* has a remarkable helicoidal twisting of the umbo which runs parallel to the commissure plane, also the shell microstructure distinguishes it from other exogyrid genera. The genera *Amphidonte*, *Laevigyra* and *Ilymatogyra* maintain a certain similarity to *Rhynchostreon* but they do not build bent-foliated chambers in the endostracum of the left valve. MALCHUS (1990: 127) suggested *Ilymatogyra* as a possible ancestor of *Rhynchostreon*. He stressed the similarity in morphology and shell microstructure between *R. plicatulum* and *R. mermeti* on one side and *I. arietina* on the other side.

Rhynchostreon mermeti (COQUAND, 1862)

Pl. 3, figs. 4a, b, 5a, b, 6, 7 a, b, 8a,b, 9, 10, 11, 12.

1862 *Ostrea mermeti* COQUAND, Paléontol. Constantine, p.234, pl. 23, figs. 3-5

1872 *Ostrea mermeti* COQUAND: LARTET, éssai Géol. Palestine, p.62, pl. 10, figs. 8-16 (var. communis, rugosa, carinata, major, minor and sulcata)

1900 *Exogyra mermeti* (COQUAND): BLANCKENHORN, Neues Geol. Paläontol. Ägypt., p.21

1990 *R. mermeti* (COQUAND): MALCHUS, Rev. Kreide-Austern Ägypt., p.128, pl. 8, figs. 15-17, pl. 9, figs. 1-21.

Holotype: COQUAND (1862: pl. 23, figs. 3-5).

Type locality: Col de Sfa, near Biskr'a in Algeria.

Type stratum: Carentonian (Upper Cenomanian)

Material: Over 160, well to very well preserved, specimens, collected from Wadi Salihi and Wadi Shueib (N Central Jordan), Wadi Wala and Wadi Mujib (Central Jordan) and several branches of Wadi Araba (South Jordan).

Description: Size: Medium (max. height of the Jordanian specimens forma typica 68 mm, forma minor 46 mm).

Outline: Elongated oval or oval to nearly subcircular. Left valve cup-like, convex to very convex. Keel generally blunt or absent or runs parallel to the elongation of the shell. Posterior side sometimes with sulcus or lobus. Right valve flat to slightly concave.

Internal characters: Ligament area variable in size and form and mostly small and narrow. Subligamental area small and forms a tiny ridge under the posterior side of the umbo. Adductor muscle imprint postero-central, almost circular with straight antero-ventral side. Vermiculate-chomata and straight-chomata are present.

External characters: Shell thick. Umbo relatively large, helicoidal with twisting intensity up to two and mostly close to the commissure line. Attachment area in most cases small to absent. Right valve covered with concentric ring-like growth squamae, mostly fine and leaving a small smooth area under the postero-central side. Ornamentation of the left valve consists of concentric growth squamae, variable in strength and sometimes crossed by fine to moderate radial ribs which generally start fine, later become thicker.

Shell microstructure: Mostly compact, simply-foliated, irregular-cross-foliated and bent-foliated with some mocret lenses.

Variability: The Jordanian *R. mermeti* shows two variants: *R. mermeti* forma typica, and forma minor. Forma typica differs from forma minor by its larger size, larger umbonal area and its higher intensity of twisting which reaches up to two degrees, also the right valve is in most cases a little concave or straight, rarely convex and shows always a small smooth area under the umbo. These two forms are also known from Egypt (MALCHUS, 1990: 129–130) and are identical to those of Jordan.

Differences: Small specimens of *R. suborbiculatum* are very similar and hard to differentiate from small or adults specimens of *R. mermeti* especially when they have the same ornamentation; however, adults of *R. suborbiculatum* grow larger than adults of *R. mermeti*, and have a relatively smaller umbo and finely smooth surface, their microstructure is almost throughout bent-foliated and their convexity is higher than *R. mermeti*. *R. suborbiculatum* is known as *E. columba* and does not occur in the Middle East. *A. obliquatum* (better known as *A. conica*) has in comparison to *R. mermeti* a typical amphidontid right valve and a different microstructure with herringbone-foliated structure.

Subfamily *Gryphaeostreinae* FRENEIX, 1982

1971 *Gryphaeostreini* STENZEL, Treatise, p. N 1125.

1982 *Gryphaeostreinae* FRENEIX, Disp. microstruc. Gryphaeost. et Gyrostrea p. 8.

1990 *Gryphaeostreinae* FRENEIX, MALCHUS, Rev. Kreide-Austern Ägypt., p. 142.

Type genus: *Gryphaeostrea* CONRAD, 1865.

Description: Post larval umbo and ligament area only in early adult stages spirally twisted, later become straight. Chomata not present. Microstructure of the left valve concentric cross-foliated, while in the right valve mocret lenses can be seen, umbonal cavity with empty chambers.

Stratigraphic and geographic distribution: Lower Cretaceous (Aptian)-Tertiary (Miocene). Europe, Asia, Africa, North and South America. In Miocene only recorded from Europe and North Africa.

Remarks: The shell structure investigations made by FRENEIX (1982) on different species of *Gryphaeostrea* lead to the introduction of *Gryphaeostreinae*. MALCHUS (1990) referred this subfamily to the family *Gryphaeidae* on microstructural criteria.

Genus *Gryphaeostrea* CONRAD, 1865

1971 *Gryphaeostrea* CONRAD: STENZEL, Treatise, p. N1125

1982 *Gryphaeostrea* CONRAD: FRENEIX, Disp. microstr. Gryphaeostrea et Gyrostrea, p. 8.

1990 *Gryphaeostrea* CONRAD: MALCHUS, Rev. Kreide-Austern Ägypt., p. 142.

Type species: *Ostrea eversa* MELLEVILLE, 1843.

Description: Small to medium in size. Outline elongated oval and thinly shelled. Attachment area normally large. Umbo spirally twisted and anteriorly curved, opisthogyr to almost straight. Left valve normally smooth, although radial ribs only on some young species are observed (see FRENEIX 1982). Right valve flat to slightly concave, oval or elongated oval to subtriangular and covered with regular sharp concentric growth lamellae. Ligament area deep, narrow, start as semispiral later almost straight. Shell microstructure compacted to lenticular simply-foliated with rare small mocret lenses. Endostracum partly cross-foliated but mostly compact.

Attributed species: *G. canaliculata* (SOWERBY, 1813) (= *G. lateralis* NILSSON, 1827), *G. trachyoptera* (WHITE, 1850), *G. eversa* (MELLEVILLE, 1843) and *G. miotauriensis* (SACCO, 1877).

Stratigraphic and geographic distribution: As for subfamily.

Remarks: STENZEL (1971) referred this species along with *Gyrostrea* to the tribe Gryphaeostriini which belongs to the subfamily Exogyreinae. But according to the shell microstructure analysis made by FRENEIX (1982) on both genera, this species is separated from *Gyrostrea* and assigned to the subfamily Gryphaeostreinae; recently *Gyrostrea* was reassigned to the Liostreinae (MALCHUS, 1990: 182).

Gryphaeostrea canaliculata (SOWERBY, 1813)

Pl. 5, fig. 4, 5 a,b.

- 1813 *Chama canaliculata* SOWERBY, J., Min. Conch. vol. I, p.68, pl. 26, fig. 1
1827 *Ostrea lateralis* NILSSON, Petrific. Suecana, p. 29, pl. 7, fig. 7-10
1848 *Ostrea canaliculata* SOWERBY: D'ORBIGNY, Pal. France. Terr. Crét., vol. III, p.709, pl. 471, figs. 4-8.
1869 *Ostrea canaliculata* SOWERBY: COQUAND, Monogr. Ostrea, p.128, pl. 45, figs. 13-14, pl. 47, figs. 7-10, pl. 52, fig. 13, pl. 60, figs. 13-15.
1869 *Ostrea lateralis* NILSSON: COQUAND, op. cit., p.96, pl. 18, fig. 12, pl. 30, figs. 10-14.
1871 *Exogyra canaliculata* SOWERBY: STOLICZKA, Cret. fauna S. India, vol. 3, p.463, pl. XLVIII, fig. 6-8.
1891 *Ostrea canaliculata* SOWERBY: PÉRON & THOMAS, Moll. foss. Tunis., p.163
1913 *Ostrea canaliculata* SOWERBY: WOODS, Cret. Lamellibr. Eng. p.375, pl. 56, figs. 2-16.
1971 *Gryphaeostrea vomer* STEPHENSON: STENZEL, Treatise, p. N1125, fig. J98: 2 a-e
1979 *Gryphaeostrea canaliculata* (SOWERBY) (= *G. lateralis* (NILSSON)): FRENEIX, Bivalve du Paléocène et l'Éocène Angola et Zaïre, p.67, pl. 2, fig.8a,b
1982 *Gryphaeostrea canaliculata* (SOWERBY): GRÜNDEL, Ostreen sächsischen Oberkreide, p. 156, pl. 3, figs. 4-11.
1985 *Gryphaeostrea canaliculata* (SOWERBY): DHONDT, Late Cret. Bivalves from A10, p. 62, fig.2b
1986 *Gryphaeostrea canaliculata* (SOWERBY): FRENEIX & VIAUD, Crét. supér. bassin Châlans, p.44, pl. 5, figs. 1a,b, 2a,b

Holotype: SOWERBY, J. (1813: pl. 26, fig. 1).

Type locality: Upper Green Sand of Shute near Warminster in England.

Type stratum: Cenomanian.

Material: 10 moderately preserved specimens and some badly preserved specimens all collected from a coquina bed at the top of the Phosphorite Limestone Formation from Wadi Hisa in Central Jordan.

Description: Size: Small (maximum height of the Jordanian specimens up to 50 mm).

Outline: Usually higher than long to oval elongated and very inequivalve. Left valve convex to a little inflated. Right valve operculiform or oval, considerably smaller than left valve.

Internal characters: Ligament area is small and incurved posteriorly. Chomata absent. Adductor muscle imprint is rounded and lies close to the postero-dorsal edge.

External characters: Attachment area is large and generally occupies the postero-dorsal portion of the left valve. Umbo is small and opisthogyal. Left valve sometimes carinated and generally smooth although faint concentric growth-lines can occur. Right valve is covered with concentric, thick, sharp growth-squamae with regular intraspaces.

Shell microstructure: Compact-cross-foliated with some moeret lenses only in the right valve.

Facies and associated fauna: The specimens of this study are collected from an oyster-bank in the phosphoritic limestone, the main bulk of this

bank is composed of *Ambigostrea villei* and *Oscillophofigari*, the rock sequence is partly crystalline with some gypsum or anhydrite crystals.

Stratigraphic and geographic distribution: Cretaceous (?Upper Aptian, Cenomanian to Maastrichtian), western Europe, Poland, USSR, India, Africa, and North America and Mexico.

Differences: *Chama canaliculata* SOWERBY is not identical with *Ostrea canaliculata* SOWERBY which is very similar to *Ostrea lunata* NILSSON, while *Ostrea lateralis* is synonymous with *Chama canaliculata* SOWERBY (WOODS, 1913). *G. canaliculata* (SOWERBY) (= *G. lateralis* (NILSSON)) are identical to *G. vomer* (STEPHENSON) from the Maastrichtian of Poland and North America (GRÜNDEL 1982: 157). FRENEIX (1979, 1982) and FRENEIX & VIAUD (1986) tried to define different species and subspecies of *Gryphaeostrea* upon size relationships and stratigraphic age. However, these taxa could all be related to one chronostratigraphic species namely *canaliculata*.

Subfamily Pycnodonteinae STENZEL, 1959

1959 *Pycnodonteinae* STENZEL, Cret. oysters S.W. North America, p.16

1990 *Pycnodonteinae* STENZEL: MALCHUS, Rev. Kreide-Austern Ägypt., p. 143.

Type genus: *Pycnodonte* FISCHER DE WALDHEIM, 1835.

Description: Small to large in size. Outline suboval to elongated oval or conical. Left valve cup-like and right valve flat to deeply concave. Umbo orthogyrate or opisthogyrate and rarely prosogyrate. Sculpture smooth, ribbed or plicate, right valve often with radial striae. Ligament area high or elongated triangular. Vermiculate-chomata, straight-chomata and/or pustule-chomata are present. Commissure shelf mostly wide. Adductor muscle imprint rounded to suboval and situated postero-dorsal to submedian. Shell microstructure is dominated with herringbone-cross-foliated with vesicular shell structure.

Attributed tribes: Pycnodontini STENZEL, 1959, Neopycnodontini HARRY, 1985 and Hyotissini HARRY, 1985.

Stratigraphic and geographic distribution: Lower Cretaceous (?Hauterivian, Barremian) to Recent. World wide.

Remarks: This subfamily is attributed to the family Gryphaeidae because of its similarity in general cup-like shape and rounded muscle imprint as well as because of its great similarity in shape and arrangement of the soft elements of the body (STENZEL, 1971: N1076, N1069; HARRY, 1985: 128). MALCHUS (1990: 143) investigated the shell microstructure of this subfamily and found great similarities with *Texigryphaea* which leads to the above conclusion.

Tribe Pycnodontini STENZEL, 1959

1990 *Pycnodontini* MALCHUS, Rev. Kreide-Austern Ägypt., p.143.

Type genus: *Pycnodonte* FISCHER DE WALDHEIM, 1835.

Description: As for subfamily, often thick-shelled. Attachment area large to absent. Not plicate and has no pustule-chomata.

Attributed genera: *Pycnodonte* FISCHER DE WALDHEIM, 1835 and *Texigryphaea* STENZEL, 1959.

Stratigraphic and geographic distribution: Lower Cretaceous (?Hauterivian, Barremian) to Tertiary (Miocene). World wide.

Differences: The members of the tribe Pycnodontini in comparison to those of Hyotissini are not plicate, and compared to those of the Neopycnodontini, the shell is thicker and has a shorter oval shape and no pustule-chomata.

Remarks: MALCHUS (1990: 143) derived the tribe Pycnodonteini (erroneously named by him Pycnodontini) from the subfamily Pycnodonteinae STENZEL, 1959 as a new tribe, according to the CODE (Art. 35 b, 37 a) the subordinate taxon with the same name and an other suffix have the same author and date (in this case STENZEL, 1959).

Genus *Pycnodonte* FISCHER DE WALDHEIM, 1835

1835 *Pycnodonte* FISCHER DE WALDHEIM, Quelques genres de coquilles Mus. Demidoff., p. 18.

1990 *Pycnodonte* FISCHER DE WALDHEIM: MALCHUS, Rev. Kreide-Austern Ägypt., p.144.

Type species: *Pycnodonte radiata* FISCHER DE WALDHEIM, 1835.

Description: As for tribe, umbo relatively small. Posterior sulcus mostly present. Left valve generally smooth although fine concentric growth squamae or radial ribs are possible. Ligamental area with flat bourelets and peak top, incurved toward the right shell. Umbonal cavities are not present.

Attributed subgenera: *Pycnodonte* (*Pycnodonte*) FISCHER DE WALDHEIM, 1835; *P.* (*Phygraea*) VIALOV, 1936; *P.* (*Costeina*) VIALOV, 1936; *P.* (*Eupycnodonte*) FRENEIX, 1979; *P.* (*Crenostrea*) MARWICK, 1931; and *P.* (*Pegma*) SQUIRES & DEMETRION, 1990.

Stratigraphic and geographic distribution: As for tribe.

Differences: *Pycnodonte* differs from *Texigryphaea* by its anatomic shell length and by its smoother cup-like shell shape (except for *P. radiata*). On the other hand *Texigryphaea* has a narrower and longer umbo, which is sometimes keeled and has one or more sulci. *Texigryphaea* has only relatively large straight-chomata and its ligament area is mostly pointed posteriorly. *Pycnodonte* is the older genus and is spread world wide, while *Texigryphaea* is only known from Albian to Cenomanian of southern West Texas and Mexico.

Subgenus *Pycnodonte* (*Phygraea*) VIALOV, 1936

1936 *Gryphaea* (*Gr.*) sec. *Phygraea* VIALOV, Classic. huitres, p.19

1990 *Pycnodonte* (*Phygraea*) VIALOV: MALCHUS, Rev. Kreide-Austern Ägypt. p.144

Type species: *Gryphaea pseudovesicularis* GÜMBEL, 1861.

Description: Shell small to large in size, relatively thin to thick-shelled. Outline very convex cup-like, rounded or oval, higher than long to subtriangular or even longer than high. Umbo mostly opisthogyrate and sometimes prosogyrate. Attachment area very large to absent. Keel not present. Posterior sulcus not very deep to almost flat. Left valve smooth or with fine growth-lamellae. Right valve normally covered with clear concentric growth squamae sometimes crossed by faint radial ribs or striae. Ligament area subtriangular, mostly longer than high. Bourrelets are almost equal in length to the resilifer. Straight-chomata, vermiculate-chomata and/or relict-chomata are possible.

Attributed species: *P.* (*Phygraea*) *vesiculosum* (SOWERBY, 1823); *P.* (*Phygraea*) *vesiculare* (LAMARCK, 1806); *P.* (*Phygraea*) *pseudovesiculare* (GÜMBEL, 1861); *P.* (*Phygraea*) *eburnea* (COQUAND, 1869); *P.* (*Phygraea*) *bocagei* (CHOFFAT, 1886); *P.* (*Phygraea*) *kansasense* BOTTJER et al, 1978.

Stratigraphic and geographic distribution: Lower Cretaceous (? Hauterivian, Barremian) to Tertiary (Miocene). World wide.

Differences: *P.* (*Phygraea*) differs from *P.* (*Pycnodonte*) by its general outline which shows almost always strong cup-like shell mostly with clear po-

sterior sulcus. *Phygraea* has normally no auricles and has larger umbo and umbonal area. It is also characterised by its smaller chomata and by its smoother surface on the left valve which has smaller interspaces between the growth-lines (for more informations and comparison see STENZEL, 1971: N1107; FRENEIX, 1979: 104; DHONDT, 1984: 859, 1985: 54; MALCHUS, 1990: 143-145).

Pycnodonte (Phygraea) vesiculosum (SOWERBY, 1823)

Pl. 5, figs. 15a, b, 16a, b.

- 1823 *Gryphaea vesiculosa* SOWERBY: Mineral Conch. Gr. Britain, p.93 pl. 369 (7 figs.)
 1869 *Ostrea vesiculosa* GUÉRANGER, COQUAND, Monogr. Ostrea, p.152, pl. 59, figs. 4,7
 1872 *Ostrea vesicularis* (LMK.) var. *judaica* LARTET, Essai Geol. Palestine, p.69, pl. 11, fig. 8-10.
 1913 *Ostrea vesiculosa* SOWERBY: WOODS, Cret. lamellibranch. Eng., p.374, pl.55, figs.10-14, pl. 56, fig. 1
 1934 *Gryphaea vesiculosa* (SOWERBY): BLANCKENHORN, Bivalv. Kreideform. Syrien-Palästina, p.200, pl. 9, figs. 42-43.
 1962 *Gryphaea vesiculosa* (SOWERBY): SCHMID; (In BENDER 1968: Geol. Jordan., p.74)
 1984 *Pycnodonte vesiculosum* (SOWERBY): DHONDT, Spanish Cret. Bivalves, p.859
 1986 *P. (Phygraea) vesiculosa* (SOWERBY): FRENEIX & VIAUD, Huitres crét. supér (Vendée), pl. 1, fig. 7
 1990 *P. (Phygraea) vesiculosum* (SOWERBY): MALCHUS, Rev. Kreide-Austern Ägypt., p. 145, pl. 2, figs. 2-7

Syntypes: SOWERBY, 1823, pl. 369

Type locality: Originally described from the Upper Greensand of Warminster (England).

Type stratum: Cenomanian.

Material: Over 70 specimens well to very well preserved, collected from the base of Wadi Salihi north of Amman.

Description Size: Small (the Jordanian specimens up to 45 mm height).

Outline: Subcircular or suboval to higher than long. Left valve convex to very convex, normally with clear posterior sulcus of variable strength. Right valve straight or concave, subovate to slightly elongated.

Internal Characters: Ligament area subtriangular, mostly longer than high. Bourrelets a little shorter or equal in length to the resilifer. Adductor muscle imprint rounded and postero-median. Straight-chomata are more often on postero-dorsal than on antero-dorsal side.

External characters: Umbo relatively small, subcircular, slightly opisthogyral to orthogyral. Attachment area generally very small to absent. Left valve almost smooth. Right valve covered with concentric growth lamellae of variable strength mostly with narrow interspaces and occasionally with small smooth mould.

Shell microstructure: Mostly herringbone-cross-foliated partly with vesicular shell structure.

Variability: *P. (Phygraea) vesiculosum* from Jordan shows two different variants, the first is longer and more convex with clear posterior sulcus, blunt keel and stronger growth squamae; the second is longer than high to almost circular with almost flat sulcus and no keel. Both variants are identical with forms from Egypt (MALCHUS, 1990, FRENEIX, 1972)

Facies and associated fauna: Specimens of this study were collected from limestones, marls and marly limestones representing Cenomanian age (Nodular Limestone). They were found together with *R. mermeti* forma typica, *Ceratostreon flabellatum*, *Micraster* sp. and large Foraminifera (*Orbitulina* sp.).

Stratigraphic and geographic distribution: Cretaceous (?Aptian, Albian to Cenomanian). Europe (England, France, Italy, and USSR); Africa (Egypt, Morocco and Tunisia); Asia (India, Palestine and Jordan). In Jordan it is reported from the Nodular limestone of Cenomanian age especially in the northern part of the kingdom where the deeper carbonate facies dominates.

Differences: The Jordanian specimens are identical with the Egyptian specimens figured by MALCHUS (1990) and with the Moroccan specimens figured by FRENEIX (1972). They show a relatively larger size. Also specimens from South Italy (MORONI & RICCO, 1968) show almost the same size and affinities. The large size of *P. vesiculare* as well as its stratigraphic position distinguishes it from *P. vesiculosum*. The comparison between *P. vesiculosum* and other taxa of the subgenus are fully discussed by FRENEIX (1972: 102-108); FRENEIX & VIAUD, (1986: 27-34); and MALCHUS, (1990: 146).

Pycnodonte (Phygraea) vesiculare (LAMARCK, 1806)

Pl. 5, fig. 3a,b,c.

- 1806 *Ostrea vesicularis* LAMARCK: Mem. foss. environs Paris, p. 160
- 1809 *Ostrea vesicularis* LAMARCK: op. cit. (vol. 5), p.375, pl. 22, figs. 3
- 1819 *Ostrea vesicularis* LAMARCK, Animaux sans vert., p.219
- 1913 *Ostrea vesicularis* LAMARCK: WOODS, Cret. lamellibr. Eng., p.360, pl.15, figs. 4-7, text-figs. 143-183.
- 1972 *P. (Pycnodonte) vesicularis* (LAMARCK): FRENEIX, Moll. Crét. Tarfaya, p.104, pl. 10, figs. 5-7, text. -figs. 11-12
- 1985 *P. vesiculare* (LAMARCK): DHONDT, Late Cret. Bivalves N. Aquitaine, p.54
- 1986 *P. (Phygraea) vesicularis vesicularis* (LAMARCK): FRENEIX & VIAUD, Huitre Crét. supér. (Vendée), p.33, pl. 2, figs. 11-14
- 1990 *P. vesiculare* (LAMARCK): MALCHUS, Rev. Kreide-Austern Ägypt., p.146, pl. 2, figs. 8-10, pl. 3, figs. 1-5.

Holotype: LAMARCK, 1809, pl. 7, fig. 3.

Type locality: Meudon, near Paris, France.

Type stratum: Upper Cretaceous (Campanian).

Description: Very similar to *P. (Phygraea) vesiculosum* LAMARCK with larger size and thicker shell. Attachment area very large or absent. Right valve is relatively more concave.

Material: 25 fairly to well preserved specimens collected from the southern part of Wadi Jamil, South Jordan, and near Irbid, North Jordan.

Facies and associated fauna: The specimens of this study collected from S. Jordan are found in sandy chalky marls or marly chalky beds with phosphatic pellets belonging to the upper parts of Phosphorite Limestone Formation and the lower parts of Chalk Limestone Formation of Campanian age. They are associated with *Baculites* ssp, *Nicaiolopha* and many other shell and fish teeth fragments. The specimens collected from N. Jordan are found in chalks from the Wadi Um Ghudran Formation of Coniacian-Santonian age associated with Ammonites and fish teeth and mollusc shell fragments.

Differences: MALCHUS (1990: 147-148) discussed 6 forms of *P. vesiculare* (LAMARCK) depending on shape and stratigraphic positions. Forma typica MALCHUS is elongated oval to rounded with convex left valve and clear sulcus and lobe, right valve flat to slightly concave. Forma hippopodium NILSSON represents a large form with large attachment area (only Santonian). Forma proboscideum D'ARCHIAC has elongated conical outline with very thick umbonal area and relatively small attachment area (only Santonian). Forma humilis MALCHUS is similar to hippopodium (see also COQUAND, 1869, pl. XIII, figs. 2-3) with posterior sulcus spreading to the umbo and has relatively wavy growth-lamellae. Forma

nikitini (ARCHANGUELSKY) is very small in size (1.5-2 cm high) and has a comma-like to elongated oval outline. And forma comunis MALCHUS which shows oval to subrounded outline with almost flat sulcus and no keel. The Jordanian specimens collected from North Jordan are identical to forma nikitini in size and stratigraphical position and the specimens collected from South Jordan are identical to forma communis which represents the same morphological and stratigraphical data (Campanian).

The comparison between *P. vesiculare* and other pycnodonts is fully discussed by MALCHUS (1990; 145-148).

Subgenus *Pycnodonte* (*Costeina*) VIALOV, 1965

1965 *P. (Costeina)* VIALOV, Some Paleogene oysters, p.5.

1990 *P. (Costeina)* VIALOV: MALCHUS, Rev. Kreide-Austern Ägypt., p.148.

Type species: *Ostrea costei* COQUAND, 1869.

Description: Pycnodontid with subcircular outline and relatively long dorsal side. Left valve convex and right valve concave. Vermiculate and straight-chomata are present. Sculpture consists of some rounded, discontinuous, partly dichotomous radial ribs.

Attributed species: *P. (C.) costei* (COQUAND, 1869); *P. (C.) arnaudi* (COQUAND, 1869); and *P. (C.) kugitangensis* (BORNEMAN, 1934).

Stratigraphic and geographic distribution: ?Upper Cenomanian, Lower Turonian to Santonian. France; USSR; North Africa and USA (Texas).

Differences: Members of this subspecies are distinguished from other pycnodontids by their radial ribs.

Pycnodonte (Costeina) sp.

Pl. 5, figs. 6, 7.

Material: 20 specimens, fairly to badly preserved, collected from Coniacian- Santonian chalks in eastern Amman area.

Description Size: Small (maximum height up to 50mm).

Outline: Circular to oval with posterior side long leaving the postero-dorsal side concave in form.

Internal characters: Ligament area small. Adductor muscle scar circular and shifted dorsally. Straight-chomata are often on the postero- and antero-dorsal sides.

External characters: Attachment area very small to absent. Sculpture consists of traces of few incontinuous radial ribs reaching the periphery of the left valve. Right valve is mostly smooth with traces of concentric growth lines.

Shell microstructure: Herringbone-cross-foliated with vesicular shell structure.

Stratigraphic and geographic distribution: Coniacian-Santonian of Amman area (Umm Ghudran Formation), not known from other localities in Jordan.

Remarks: Specimens of this study are fairly to badly preserved. The outer surface of the left valve is not clear, only traces of radial ribs are seen. According to the internal characters and the traces of the radial ribs, the specimens are placed within the subspecies *Costeina*.

Family *Ostreidae* RAFINESQUE, 1815
Subfamily *Liostreinae* MALCHUS, 1990

1991 *Liostreinae* MALCHUS, Rev. Kreide-Austern Ägypt, p. 150.

Type genus: *Liostrea* DOUVILLÉ, 1904.

Description: Small to large in size. Outline oval, rather more elongated. Left valve convex, right valve slightly convex to concave. Ligament area elongate triangular and straight or a little pointed. Adductor muscle imprint rounded or dorsally concave and situated postero-dorsally to postero-ventrally. Shell edges possibly plicated. Chomata (when present) ostreineid and rarely lophinid. Umbonal cavity present or absent. Sculpture is composed of strong growth-squama and/or different patterns of ribbing. Shell microstructure mostly compact-foliated, empty chambers are rarely seen and mcret lenses are first developed in the Upper Cretaceous times.

Attributed tribes: *Liostreini* MALCHUS, 1990; *Curvostreini* MALCHUS, 1990; *Ambigostreini* MALCHUS, 1990; *Flemingostreini* STENZEL, 1971.

Stratigraphic and geographic distribution: Upper Triassic (Norian) to Upper Cretaceous (Maastrichtian) and ?Tertiary. In Triassic times restricted to North Temperate realm, later world wide.

Differences: The different tribes and genera belonging to this subfamily are generally characterised by having a compact-foliated shell microstructure. MALCHUS (1990) investigated the development of the shell microstructure of the subfamily; he noticed that compact-simply-foliated structure dominates almost all forms belonging to this subfamily especially the old forms, later they tend to build empty lenses (mostly restricted to the umbonal area and outer ostracum) mainly in Late Cretaceous times where they possibly enter a new phase of strongly lenticular simply-foliated structure that is characteristic of the subfamilies: *Crassostreinae* and *Ostreinae*. MALCHUS (1990; 150) differentiated four tribes belonging to this subfamily according to different morphological criteria.

Tribe *Curvostreini* MALCHUS, 1990

1990 *Curvostreini* MALCHUS, Rev. Kreide-Austern Ägypt., p.151.

Type genus: *Curvostrea* VIALOV, 1936.

Description: Small to medium in size. Outline oval elongated to crescentic, inequivalve to almost equivalve and thinly shelled. Left valve slightly concave to convex and right valve slightly convex. Ligament area triangular, small and relatively narrow, straight or posteriorly pointed. Adductor muscle imprint ostreineid to lophinid and situated postero-ventrally. Relict chomata are mostly present. Shell surface generally smooth except for concentric growth-lines, although some forms could be ribbed or plicated.

Attributed genera: *Curvostrea* VIALOV, 1936; *Acutostrea* VIALOV, 1936; *Agerostrea* VIALOV, 1936; *Pseudoperna* LOGAN, 1899; and *Indostrea* CHIPLODKAR & BADVE, 1976.

Stratigraphic and geographic distribution: Cretaceous (Albian to Maastrichtian). Central Asia; India; Middle East; Africa; Europe; and America.

Differences: The tribes *Liostreini* and *Curvostreini* are morphologically similar, the only difference lies in the presence of chomata in the latter. In comparison to *Flemingostreini*, the *Curvostreini* are smaller in size, have a smaller ligament and a smoother shell surface. The same differences are considered in comparison to the *Ambigostreini* which also show a unique pattern of ribbing.

Genus *Curvostrea* VIALOV, 1936

1936 *Curvostrea* VIALOV, Class des huîtres, p.18

1990 *Curvostrea* VIALOV: MALCHUS, Rev. Kreide-Austern Ägypt., p.152.

Type species: *Ostrea Rouvillei* COQUAND, 1862.

Description: Curvostroid with left valve slightly convex and right convex to slightly concave. Shell surface almost smooth except for faint to moderate concentric growth-squama which forms a regular to irregular and sometimes wavy form.

Attributed species: *C. rouvillei* (COQUAND, 1862) = *C. rediviva* (COQUAND, 1869) = ?syn. *bourguinanti* (COQUAND, 1869); *C. heinzi* (PÉRON & THOMAS, 1891); *C. tevesthensis* (COQUAND, 1862) – ?syn. *tetragona* (BAYLE, 1878); ?syn. *thomasi* (PÉRON & THOMAS, 1891); ?syn. *brossardi* (COQUAND, 1869)– and ?*C. guathieri* (PÉRON & THOMAS, 1891); ?*C. papier* (PÉRON & THOMAS, 1891).

Stratigraphic and geographic distribution: Upper Cretaceous, ?world wide.

Curvostrea rouvillei (Coquand, 1862)

Pl. 5, figs. 8-12.

- 1862 *Ostrea Rouvillei* COQUAND, Paléontol. Costantine, p.232, pl. 22, figs. 9-11
1862 *Ostrea biskarensis* COQUAND, op. cit. p.231, pl. 21, figs.10-12
1869 *Ostrea Rouvillei* COQUAND, Monogr. Ostrea, p.89, pl. 21, figs. 3-6, pl. 24, figs. 7-11.
1869 *Ostrea rediviva* COQUAND, op. cit., p. 154, pl. 42, figs. 8-11, pl. 54, figs. 18-30
1869 *Ostrea biskarensis* COQUAND, op. cit. p.110, pl. 53, figs. 15-17
1961 *Liostrea rouvillei* COQUAND: ROSSI RONCHETTI & ALBANESI, Foss. Cenoman. Tripolitania, p.272, pl. 20, figs. 7-9.
1962 *Liostrea rouvillei* COQUAND: SCHMID (In Bender: Geol. Jordanien), p.74.
1972 *Liostrea rouvillei* COQUAND: FRENEIX, Moll. crét. Tarfaya, p.97, Text-fig. 10, A-D.
1986 *Curvostrea rouvillei* COQUAND: FRENEIX & VIAUD, Huîtres Crét. supér (Vendée), p.47 pl. 5, figs. 5a, b, 6, 7a, b, 8.
1990 *Curvostrea rouvillei* COQUAND: MALCHUS, Rev. Kreide-Austern Ägypt., p. 154, pl. 14, figs. 1-7, 16.

Holotype: COQUAND (1862), pl. 22, fig. 9-11 (one specimen).

Type locality: Not assigned by COQUAND, possibly Algeria.

Type stratum: Cenomanian.

Material: Over 30 double and single valved specimens of good to very good preservation collected from Ras El-Naqab, Southern Jordan.

Description: Size: Small (maximum height 34.5 mm).

Outline: Oval, mostly curved, plate-shaped and almost equivalve.

Internal characters: Ligament area narrow, high triangular, bourrelets not clear and small. Shell periphery with straight-chomata while relict-chomata are seen only on the antero-dorsal valve of the right valve. Adductor muscle imprint oval to almost rounded and postero-ventral.

External characters: Left valve thin, smooth except for faint wavy growth-lines. Umbo small, narrow, straight or pointed posteriorly. Right valve thin, less convex than right valve with a little shorter umbo.

Shell microstructure: Simply foliated with few mcret lenses.

Facies and associated fauna: The specimens are collected from yellow sandy marls intercalated with marly limestones and green clays. They are found together with *E. (Costagya) olisiponensis* SHARPE., *A. (Ceratostreon) flabellatum* (GOLDFUSS), *Micraster* ssp. and many moulds of gastropods.

Stratigraphic and geographic distribution: Upper Cretaceous (Cenomanian-Santonian). North and Central Africa, Middle East, USSR, and Europe. In Jordan it is found in strata belonging to the Echinoidal Limestone Member which is of Cenomanian age.

Differences: Both *O. rouvillei* (Santonian) and *O. rediviva* (Cenomanian) introduced by COQUAND (1862: 232) and (1869: 154) are identical. He differentiated them upon their stratigraphic position, *O. biskarensis* (COQUAND) and a part of *O. acutirostris* NILSSON. are also identical (PÉRON 1891: 137). *Curvostrea heinzi* (PÉRON & THOMAS) differs from this species by the lack of umbonal cavity, by the few large chomata on the edges of the left valve and by the compact-foliated microstructure of the shell. *C. tevesthensis* (COQUAND) (= *O. boucheroni* COQUAND) (fide MALCHUS 1990) from Coniacian/ Santonian of North Africa and ?Germany has a larger size and narrower longer outline (inner details are unknown). Different species old names and synonymies are fully discussed by MALCHUS (1990: 155-158).

Curvostrea sp.

Pl. 5, figs. 13, 14 a,b.

Material: Seven fairly to well preserved specimens of closed shells collected from Cenomanian limestones of Wadi Salihi north of Amman.

Description: Size: Small (maximum height less than 50mm).

Outline: Oval to subcircular. Left valve convex and right valve straight or slightly convex.

Internal characters: Obscure.

External characters: Attachment area relatively large. Umbo small and ostreoid in form. Ornamentation consists of relatively strong concentric growth lamellae covering both valves.

Shell microstructure: Simply-foliated with very few empty lenses mostly near the umbonal side.

Stratigraphic and geographic distribution: Cenomanian of Wadi Salihi north of Amman.

Remarks: Specimens of this species show only closed inflated shells and stronger ornamentation and thicker shells than that of the plate-shaped *Curvostrea rouvillei* (COQUAND).

Tribe *Flemingostreini* STENZEL, 1971

1971 *Flemingostreini* STENZEL, Treatise, p. N1150.

1990 *Flemingostreini* STENZEL, MALCHUS, Rev. Kreide-Austern Ägypt., p.163.

Type genus: *Flemingostrea* VREDENBURG, 1916.

Description: Shell thick, small to medium in size. Outline rounded to elongated oval, subequivalve and biconvex with left valve more convex. Umbo pointed or blunt. Attachment area variable (very small to absent in some genera). Ligament area elongated straight to opisthogyrate and rarely prosogyrate and later becomes straight. Furrows weak (absent in adult stage). Straight-chomata and relict chomata are present, relict chomata in the Cretaceous genera are posterior or postero-dorsal, later (phylogenetic) become more large and rotated and can be reduced. Adductor muscle imprint kidney-like to comma-like or straight posteriorly, rarely rounded, situated postero-dorsally to centrally. Sculpture consists generally of growth lamellae, mostly regular on the left val-

ve, radial ribs or wavy (terebratulid) folds are diagnostic to some genera. Shell microstructure is generally simply-foliated with some mocket lenses or empty chambers.

Attributed genera: *Flemingostrea* VREDENBURG, 1916; *Odontogryphaea* IHERING, 1903; *Kokanostrea* VIALOV, 1936; *Ostreonella* ROMANOVSKY, 1890; *Gyrostrea* MIRKAMALOV, 1963; *Cameleolopha* VIALOV, 1936; *Nicaisolopha* VIALOV, 1936.

Stratigraphic and geographic distribution: Cretaceous (? Aptian, Cenomanian) to Tertiary, world wide.

Remarks: STENZEL (1971) proposed the tribe Flemingostreini to involve (*Flemingostrea*, *Odontogryphaea*, *Kokanostrea* and *Ostreonella*), MALCHUS (1990: 164) added the other three according to morphological similarities, he found that *Gyrostrea* has concentric stage-like growth lamellae on the left valve similar to those of *Flemingostrea* as are the similarities in outline, ligament area, shape and position of the adductor muscle scar and microstructure of the shell. According to his conclusion *Nicaisolopha* and *Cameleolopha* are nothing but plicated Gyrostreids, therefore he included them in the group, (discussion and comparison by MALCHUS 1990: 164).

Genus *Nicaisolopha* VIALOV, 1936

1936 *Nicaisolopha* VIALOV, *Classific. des huitres*, p. 20

1990 *Nicaisolopha* VIALOV, MALCHUS, *Rev. Kreide-Austern Ägypt.*, p. 171.

Type species: *Ostrea nicaisei* COQUAND, 1862.

Description: Shell small to medium in size. Outline subcircular or oval to subtriangular, subequivalve to inequivalve and biconvex, left valve more convex to cup-like. Attachment area very variable. Umbo straight or pointed. commissure wavy or plicated. Ligament area elongated triangular, mostly pointed at the beginning, umbonal cavities are present in young specimens. catachomata and anachomata are clearly visible, relict chomata are present. Adductor muscle imprint kidney-like to comma-like and situated postero-ventrally to subcentrally. Sculpture consists of concentric growth lamellae partly step-like crossed by few undulating, simple, rarely dichotomous radial folds which diverse from the umbonal area. Microstructure of the shell simply-foliated with some empty and mocket lenses.

Attributed species: *Nicaisolopha nicaisei* (COQUAND, 1862); *N. tissoti* (PÉRON & THOMAS, 1891); *N. lyonsi* (NEWTON, 1898); *N. lugubris* (CONRAD, 1857); *N. lombardi* (FRENEIX, 1959); *N. pellaplicata* (SHUMARD, 1862).

Stratigraphic and geographic distribution: Upper Cretaceous (middle Turonian to Maastrichtian). North Africa and Central Africa (Camerun, Gabon, Congo, Angola); Middle East; North America (Western Interior, Gulf Coast, Mexico); South America (Peru).

Differences: This genus used to be attributed to the Lophinae (Tertiary-Recent), but according to its compact-foliated shell microstructure which was studied by KAUFFMAN (1965) and MALCHUS (1990) it is attributed to Liostreinae. The genus is characterised by large wavy, mostly simple folds or ribs on both valves, it differs from other plicated genera of Liostreinae by its few large wavy radial folds. Most of the inner details are comparable to those of *Gyrostrea*, and both genera could be phylogenetically related. *Cameleolopha* seems more similar and could be synonymous (MALCHUS, 1990: 172).

Description: Size: Medium to large (up to 200 mm height).

Outline: Triangular in general, in most cases elongated. Branchitellum mostly very clear. Biconvex with left valve a little more convex. A concave area on the anterior or posterior or on both sides is possible.

Internal characters: Ligament area triangular, elongated and tapering or blunt, straight or a little pointed. Umbonal cavities are seen clearly in the younger specimens, in the adult stages weak or absent. Adductor muscle scar relatively large, submedian to ventral. Chomata are not present.

External characters: Umbo generally subtriangular and blunt. Posterior furrow weak or not developed. Both valves are sculptured with many simple or sharp radial ribs, ribs can bifurcate and have more or less equal intraspaces, they are crossed by thick, stage-like growth-lamellae. Postero and antero-dorsal sides are mostly sculptured with fine ribs.

Shell microstructure: Simply foliated, mocket lenses are rare.

Stratigraphic and geographic distribution: Upper Cretaceous (Campanian- Maastrichtian) of North Africa, and Middle East. In Jordan it occurs in strata belonging to Al Hisa Phosphorite Formation of Campanian age, dominant near Al Hisa Mine in Central Jordan.

Facies and associated fauna: This species occurs together with *Oscilopha figari* (FOURTAU) in large oyster-banks between phosphates, phosphatic limestones /marly limestones, partly silicified with some secondary evaporites.

Differences: This species is differentiated by its triangular outline and by its many radial ribs on both valves. The Jordanian specimens show larger size and thicker shells than those of North Africa, but are otherwise identical. General relationships to other fossil oysters are listed by GRECO (1916: 113) and MALCHUS (1990: 181).

Genus *Gryphaeligmus* LEWY, 1982

1982 *Gryphaeligmus* LEWY, *Gryphaeligmus* new genus Middle East, p.812.

1990 *Gryphaeligmus* LEWY: MALCHUS, Rev. Kreide-Austern Ägypt., p.176.

Type species: *Ostrea jabbokensis* Cox, 1925.

Description: Shell thin, small in size, sub- to inequivalve. Outline crescentic to suboval with shorter anterior side, posterior wing-like carina and straight dorsal area. Left valve convex, right valve flat to slightly concave. Both valves bear strong sharp radial ribs starting under the umbonal area leaving the umbonal area smooth. Chomata straight or pustule-like. Shell microstructure compact-foliated.

Attributed species: *Gryphaeligmus jabbokensis* (Cox, 1925).

Stratigraphic and geographic distribution: Middle Jurassic (Middle and Upper Bathonian and ?Callovian). Middle East (Jordan, Palestine and Saudi Arabia); North Africa (Egypt).

Remarks: The type species of this genus was first described by Cox (1925: 171) as an *Ostrea*, but was later assigned by many authors to the genus *Eligmus* (Malleidae) due to the morphological similarities to *E. asiaticus* DOUVILLÉ, *E. rollandi* DOUVILLÉ and *E. integer* DOUVILLÉ which have a similar geographic and stratigraphic distribution. LEWY (1982: 812) described a new genus because of the different internal characters (ligament area and adductor muscle scar), but he related his genus to the family Malleidae until MALCHUS (1990: 176) transferred it to the tribe *Ambigostreinae* (Ostreidae) named upon compact-foliated microstructure, chomata and the radial ribbing on both valves.

Gryphaeligmus jabbokensis (Cox, 1925)

Pl. 7, figs. 6-9.

- 1925 *Ostrea jabbokensis* Cox, Bajoc.-Bathon. outcrop Jordan Valley, p.172, pl. 14, fig. 1a,b.
1936 *Eligmus rollandi* DOUV. var. *jabbokensis* (COX): BLAKE, Stratigr. Palestine, p. 70.
1939 *E. rollandi* DOUV. var. *jabbokensis* (COX): IONIDES & BLAKE, Water Res. Transjordan, p. 72.
1962 *Ostrea jabbokensis* COX: HOFFMANN (in BENDER: Geol. Jordanian), p.68.
1966 *E. rollandi* DOUV. var. *jabbokensis* (COX): POWERS et al., Geol. Saudi Arabia, p. D48, D52.
1979 *Gryphaea* sp., HIRSCH, Jur. biv. & Gastropod. N.Sinai, p.134, pl. 4, figs. 6-7.
1979 *Lopha* sp. HIRSCH, op. cit., p.134, pl. 4, figs. 8-9.
1982 *Gryphaeligmus jabbokensis* (COX): LEWY, *Gryphaeligmus* n. genus, Bathon. M. East, p.813, pl. 1.
1987 *Eligmus ardaensis* AQRABAWI, Biostratgr. Jur. Jordan, p.96, pl. 5, figs. 13-16
1987 *Eligmus jabbokensis* (COX): AQRABAWI, op. cit., p. 100, pl. 5, figs. 28-35.
1990 *Gryphaeligmus jabbokensis* (COX): MALCHUS, Rev. Kreide-Austern Ägypt., p. 176, pl. 20, figs. 9-15.

Holotype: Cox (1925: pl. 14, fig. 1)

Type locality: Wadi Zerqa River, northwestern Jordan.

Type stratum: Bathonian.

Material: 26 specimens well to very well preserved, 10 single and 16 double valves collected from Old Jerash Bridge area around the water of the lake of King Talal Dam at the Wadi Zerqa River.

Description: Size: Small (up to 40mm).

Internal characters: Ligament area subtriangular, pointed and small. Two kinds of chomata are present, straight-chomata on the ventral side, and pustul-chomata near the ligament and on the posterior side. Adductor muscle imprint rounded, postero-dorsal to central.

External characters: Attachment area normally very small. Branchitellum well developed. Ribs on both valves are sharp, can bifurcate before reaching the ventral side and are crossed by concentric growth lamellae. Umbonal cavity is not present.

Shell microstructure: Simply-foliated with rarely mocket or empty lenses.

Stratigraphic and geographic distribution: Jurassic (Middle to Upper Bathonian and ?Callovian). Egypt (Sinai): DOUVILLÉ (1916); MALCHUS (1990); Saudi Arabia: POWERS (1966); and Jordan: AQRABAWI (1987). In Jordan, it occurs in rocks belonging to the Arda Formation of Middle-Upper Bathonian age.

Facies and associated fauna: The specimens of this study are collected from fossiliferous yellow to grey sandy marls intercalated by thin beds of marly limestone; they occur together with *Eligmus asiaticus* DOUVILLÉ, *Africogryphaea costellata* (DOUVILLÉ) and many other bivalves, gastropods, corals and brachiopods.

Differences: This species has certain morphological similarities in general outline and in shape and form of ribs with *Eligmus asiaticus* DOUVILLÉ and *Eligmus integer* DOUVILLÉ from Bathonian rocks of North Africa (Egypt). The first is surely related to the genus *Eligmus* because of its inner aragonitic shell layer and the type of ligament, but for the latter, all examined specimens (1986 by the author) in the Egyptian Palaeontological Museum have not shown inner details and their outline lies in the category of *jabbokensis*. The question whether they could be synonymous to *jabbokensis* could be answered only by microstructure investigations. *G. jabbokensis* (Cox) is the oldest known oyster that has chomata which is of a certain importance in the phylogenetic evolution of oysters (see MALCHUS 1990: 79, 83).

4.2.2. Description of the Northwest European oysters

Family *Palaeolophidae* MALCHUS, 1990
Subfamily *Palaeolophinae* MALCHUS, 1990
Tribe *Oscillophini* MALCHUS, 1990
Genus *Oscillopha* MALCHUS, 1990
Oscillopha dichotoma (BAYLE, 1849)
(Text-fig. 46: a-c)

- 1833 *Ostrea armata* GOLDFUSS, Petref. Germ., p. 12, pl. 67, fig. 3
1849 *Ostrea dichotoma* BAYLE, RICHESSE min. Algérie, pt. I, p. 365, pl. 18, figs. 17, 18.
1962 *Loph dichotoma* BAYLE: ABBASS, Monogr. Egypt. Cret Pelecypods, p.81, pl. XI, fig. 2.
1990 *Oscillopha dichotoma* (BAYLE): MALCHUS, Rev. Kreide-Austern Ägypt., p.103, pl. 1, Figs. 5-9. Extended synonymy.

Holotype: BAYLE, 1849: pl. 18, figs. 17,18.

Type locality: Nza-bin-Messai, south of Batna in Algeria.

Type stratum: Santonian (sensu COQUAND) = ?Coniacian.

Material: Five very well preserved specimens from Dorsten area (Ziegelei Mertki), Central Germany. The specimens are loaned from the Ruhrlandmuseum in Essen with register numbers RE551.763.333 A 448/1,5, RE551.763.333 A 447/1-3.

Description: Size: Medium (maximum height of the examined specimens 111.5 mm).

Outline: Suboval, subequivalve, both valves mostly convex, longer than wide.

Internal characters: Ligamental area longer than high, triangular and relatively large in size. Resilifer at least double the length than the bourrelet. Umbonal cavity is not present. Adductor muscle scar is relatively large, postero-central, deep, kidney-like or oval, ventral and postero-ventral sides are a little raised. Straight-chomata are not well developed in most of the studied specimens.

External characters: Both valves are ornamented with radial ribs which are relatively large, bifurcating in most cases, sharply keeled, mostly tuberculated and tend to curve postero-ventrally. Shell periphery is plicated.

Shell microstructure: Strongly lenticular simply-foliated with large moeret and empty lenses.

Stratigraphic and geographic distribution: Upper Cretaceous (Santonian to Campanian), North Africa, Middle East, Iran, and Europe. The specimens from the Ruhrlandmuseum in Essen represent the Lower *lingua/quadrata* zone "Bottroper Marl", of Lower Campanian age.

Differences: This species is generally differentiated from other *Oscillophids* by its large dichotomous ribs. *Oscillopha figari* (FOURTAU, 1904) is reported from the Maastrichtian of North Africa and has in comparison to this species a larger size and a kidney-like adductor muscle scar; in addition, the ribs are rounded and mostly not dichotomous. Another minor difference is the plicated shell periphery in *Ostrea dichotoma* (BAYLE) while it is *O. figari* (FOURTAU) plicae-free. The Maastrichtian species *Ambigostrea villei* (COQUAND) from North Africa and the Middle East has similar ribs, but they are mostly not dichotomous, and generally can easily be differentiated from this species by its simple-foliated microstructure of the shell. *Oscillopha dichotoma* is very similar to the illustration of *Ostrea armata* GOLDFUSS (1833: pl. 76: 3) from the Greensand of Westfalia in Central Germany. The description of GOLDFUSS (1833: 12) matches the specimens described here, it is possibly the same species.

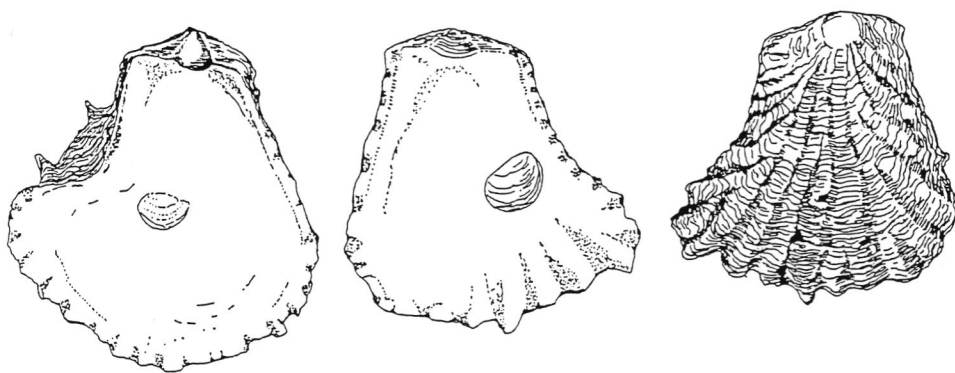


Fig. 46: *Oscillopsa dichotoma* (BAYLE), (specimens Nr.: RE551.763.333 A447/3 for a and A448/5 for b and c; Ruhrlandmuseum, Essen; Bottroper Marl, L. Campanian)

Genus *Rastellum* (FAUJAS-ST. FOND, 1799)

1799 *Gryphites* FAUJAS-ST. FOND, Hist. Natur. montagne St., p. 167.

1990 *Rastellum* F.-ST.-FOND: MALCHUS, Rev. Kreide-Austern Ägypt., p.105.

Type species: *Ostrea pectinata* LAMARCK, 1806 = *Ostrea frons* PARKINSON, 1811 = *Rastellum macropteryum* SOWERBY, 1824 = *Rastellum carinatum* (LAMARCK, 1806).

Description: (after STENZEL, 1971) Shell subequivalve and small to large in size (up to 240 mm). Outline crescentic, sickle-like or subtriangular. Posterior wing or ear is usually present and an anterior wing could also be present. Both valves are convex and usually taper towards the postero-ventral extremity, but occasionally expand at the end. Attachment area variable. Valves are sculptured with strong, angular ribs which extend from the median line to the margins and are slightly curved or straight. Margins of the two valves are strongly plicated, sharply pointed tooth-like projections are formed by the interspaces between the ribs on the valves. Umbo generally small, mostly opisthogyral and runs parallel to the commissure plane. Ligamental area starts small and curved in a long line, later becomes subtriangular. Umbonal cavities are present only in the young specimens. Straight-chomata are rare and found at the postero and antero-dorsal sides. Adductor muscle imprint relatively large and situated postero-dorsally. Microstructure of the shell is lenticular simply-foliated with small and large mooret- and empty lenses.

Attributed species: *R. diluvianum* (LINNÉ, 1767), *R. gracile* (DUJARDIN, 1837), *R. pectinatum* (LAMARCK, 1806) = *R. carinatum* (LAMARCK, 1806) and *R. pusillum* (NILSSON, 1829).

Stratigraphic and geographic distribution: Cretaceous (Albian to Maastrichtian), world wide.

Differences: *R. (Rastellum)* was first assigned to Middle Jurassic (Callo-vian) to Upper Cretaceous (Maastrichtian) by STENZEL (1971: N1165), but due to the restriction of the type species to the Cretaceous and considering the absence of the transitional forms of sickle and blade types in the Cretaceous times, the subgenus is confined to the Cretaceous -Albian to Maastrichtian- (MALCHUS, 1990: 106), this is also valid for *R. (Arctostrea)*. According to STENZEL (1971: N1166) *R. (Arctostrea)* is distinguished by the more crescentic long tapering outline, by the narrower shell which develops hyote spines. The distinction between both subgenera according to STENZEL (1971: N1166) is uncertain, according to WOODS (1913: 342-355) it is impossible to make such a distinction. The differen-

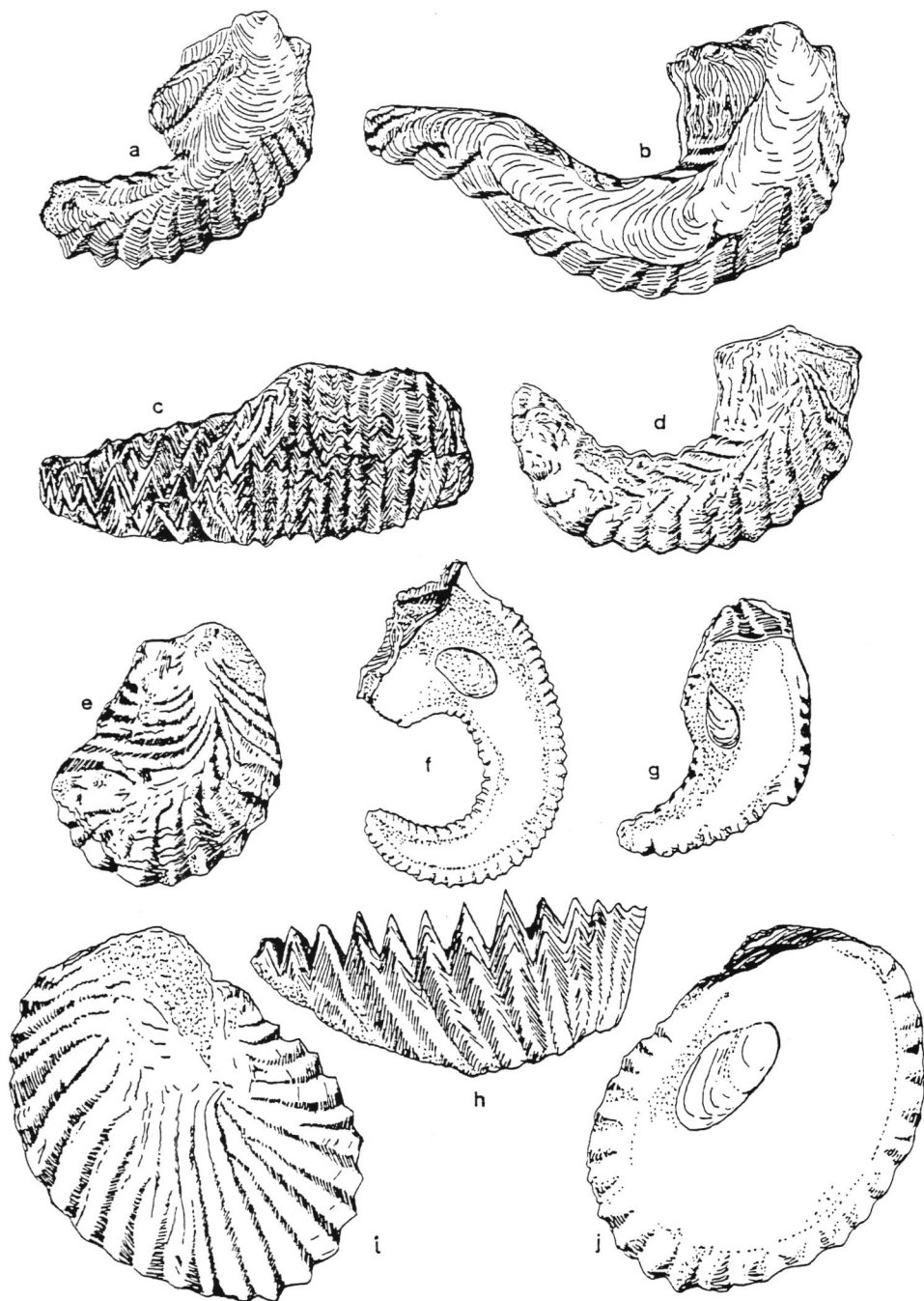


Fig. 47: a-d, f, g: *Rastellum carinatum* (LAMARCK); e, h-j: *Rastellum diluvianum* (LINNÉ).
figures: a-g: after WOODS (1913); h-j: after FAVRE (1918).

ces between *R. (Rastellum)* and *R. (Arctostrea)* can be accepted on the species level under the original genus *Rastellum*.

Remarks: Most of the species belonging to this genus and other genera such as *Nicaisolopha* or *Ambigostrea* are described in older literature under *Alectryonia* or *Lopha* but recent studies on the microstructural shell properties showed that they can easily be differentiated and grouped (see MALCHUS, 1990; CARTER, 1990).

Rastellum diluvianum (LINNÉ, 1767)

(Text-fig. 47: e,h,i,j)

1767 *Ostrea diluviana* LINNÉ, Sys. Nat. ed. 12, p.1148.

1819 *Ostrea diluviana* LINNÉ: LAMARCK, Anim. sans Vert., p.216. p.

1913 *Ostrea diluviana* LINNÉ: WOODS, Cret. Lamellibr., Eng., p.342, text-figs. 109, 115, 118, 119, 124, 125.

1968 *Arctostrea diluviana* (LINNÉ): CARTER, Func. stud. Cret. Oyster Arctostrea, p. 463, pl. 85, fig. 1.

1982 *Lopha diluviana* (LINNÉ): GRÜNDEL, Ostreen Sachsen, p.157, pl. 4, figs. 6-10.

1986 *R. (Rastellum) diluviana* LINNÉ: FRENEIX & VIAUD, Huître crét. supér. (Vendée), p.50, pl. 6, figs. 2 a, b, 3. Extended synonymy.

Holotype: LINNÉ, 1767 (figs. in HISINGER, 1837, pl. 14, fig. 5, (fide D'ORBIGNY, 1847 and COQUAND, 1869)).

Type locality: The Upper Chalk of Sweden (WOODS, 1913: 352).

Type stratum: Upper Cretaceous (?Campanian).

Material: 117 specimens; 11 very well preserved specimens from the collection of the Ruhrlandmuseum in Essen with the numbers RE551.763.31 A1624/1-8, A1629/1 and A1633/1-2; the other specimens are well to moderately preserved and belong to the collection of Prof. Dr. VOIGT in Hamburg collected from Schonen in Sweden (Ifi/1/1-30, Ifi/2/1-20, Ifi/3/1-50) and from the Harzregion in Germany (Groß-Bülten/1-6).

Description: Size: Medium to large (maximum height up to 150 mm).

Outline: Subequivalve, more or less oval or subrounded, biconvex and possesses a slight to moderate posterior curvature in the more elongated specimens. The thickest part of the shell is at the anterior and ventral sides. Posterior wing or ear is more or less clearly developed, more so in specimens with large attachment area. A small anterior wing can also be present. Margins of both valves are strongly plicated and form a tooth-like or zigzag projection with sharp ends.

Internal characters: Ligamental area triangular mostly with a slight posterior curvature. Umbonal cavity is not present. Subligamental area not developed. Adductor muscle imprint oval or kidney-like, relatively large and not very far from the hinge line. Straight-chomata are weakly developed, few and restricted to the antero-dorsal side.

External characters: Shell is generally thick with variable attachment area. Both valves are ornamented with strong, angular, mostly curved folds that start in most cases somewhere at the centre of the shell.

Shell Microstructure: Strongly lenticular simply-foliated with empty and mcret lenses.

Stratigraphic and geographic distribution: Upper Cretaceous (Cenomanian-Turonian- ?Campanian). Europe (L. Cenomanian of the Green Sand of Essen in Germany), Africa, Asia and North America.

Differences: D'ORBIGNY (1847), COQUAND (1869) and others have taken the specimens figured by HISINGER (1837) from the Campanian of Sweden as the type of LINNÉ and considered the ures of NILSSON (1827) as *O. frons* (which match here *R. carinatum*). WOODS (1913: 351-352) suggested that both *R. diluvi-*

anum and *R. carinatum* are varieties of the same species. In this study a large number of *R. diluvianum* were examined and compared to *R. carinatum*. Although, their general outline, the shape, form and intensity of folds as well as the posterior ear and shape and position of muscle scar cannot be neglected. But they are different, they may not warrant the designation of a subgenus, they may be accepted as differences of species (see also *R. carinatum*).

Rastellum carinatum (LAMARCK, 1806)
(Text-fig. 47: a-d, f, g)

- 1806 *Ostrea carinata* LAMARCK, Ann. du Museum, vol. 8, p.166.
1806 *Ostrea pectinata* LAMARCK, op. cit., p.165.
1811 *Ostrea frons* PARKINSON, Organic remains, vol. 3, p. 217, pl.15, fig. 4.
1819 *Ostrea carinata* LAMARCK, Anim. sans vert., vol. 6, p.216.
1910 *Ostrea carinata* LAMARCK: PERVINQUIÈRE, Palaeont. Universalis, 197.
1910 *Ostrea colubrina* LAMARCK: PERVINQUIÈRE, Palaeont. Universalis, 198.
1913 *Ostrea diluviana* LINNÉ: WOODS, Cret. Lamellibr., Eng., p.342, text-figs. 98-108, 110-114, 116,122, 123, 127-133, 135-138.
1982 *Rastellum (Arctostrea) carinatum* LAMARCK: GRÜNDEL, Ostreen Sachsen, p. 158, pl. 3, figs. 12-13, pl. 4, fig. 1-5.
1986 *Rastellum (Arctostrea) carinatum* LAMARCK: FRENEIX & VIAUD, Huître crét. supér. (VENDEE), p.49, pl. 6, figs. 1a,b. Extended synonymy.
1986 *Rastellum (Arctostrea) pectinatum* LAMARCK: FRENEIX & VIAUD, op. cit., p.51, pl. 6, figs. 4a,b.

Holotype: LAMARCK (T.6, part. 1, p.216, Nr. 9) figures in (PERVINQUIÈRE, 1910: fiche 197). Museum de Paris (Coll. LAMARCK).

Type locality: Le Mans, Sarthe, France.

Type stratum: Cenomanian.

Material: 11 very well preserved specimens loaned from the Ruhrlandmuseum in Essen with the numbers RE551.763.31 A1627/1-8, A1628/1-2, A489, in addition to more than 250 specimens from the collection of Prof. Dr. VOIGT, GPIM-Hamburg, collected from Lower Cenomanian rocks of Lamnay, Sarthe, France.

Description: Size: Medium (height up to 120mm).

Outline: Crescentic to sickle-like or comma-like with posterior ear or wing well developed and anterior ear weak, subequivalve, mostly strongly bi-convex. Median ridge or keel is variable but mostly strong and arch-like and sides of the shell are mostly steep.

Internal characters: Ligamental area curved or almost straight relatively small. Adductor muscle imprint kidney-like, with posterior side raised and always close to the posterior wing. Umbonal cavity usually not present.

External characters: Shell thick, Umbo normally blunt and relatively small, Attachment area variable. The margins of the valves are strongly carinated with sharp-pointed tips forming zigzag valve edges. commissure is strongly serrate. Sculpture is composed of many angular ribs that extend from the median ridge to the margin, the ribs can be bifurcated and may have sharp spines.

Shell microstructure: Strongly lenticular simply-foliated with mcret- and empty lenses.

Stratigraphic and geographic distribution: Upper Cretaceous (Cenomanian), world wide.

Differences: Oysters with plicated shell edges were described by many authors under the names *Lopha* BOLTEN, 1798 and *Alectryonia* FISCHER DE WALDHEIM, 1807. Both genera have been based on the same type species (*Ostrea cristagalli* LINNÉ, a recent species from the Indo-Pacific with very coarsely plicated commissure). *Arctostrea* was first introduced by PERVINQUIÈRE (1910) as a subgenus of *Alectryonia* with *Ostrea carinata* LAMARCK as type species distin-

guished by the branchiform shape, the sharply zigzagged commissure and the form and shape of the ribs. STENZEL (1971) placed the subgenus under the genus *Rastellum* with the same diagnosis but he was not sure of the distinction between *R. (Rastellum)* and *R. (Arctostrea)*. According to these facts and considering the diagnosis of PERVINQUIÈRE *Ostrea carinata* can be placed under the genus *Rastellum*. PERVINQUIÈRE (1910) gave reasons for treating *Ostrea colubrina* LAMARCK as a variety of the same species.

Family *Gryphaeidae* VIALOV, 1936

Subfamily *Exogyrinae* VIALOV, 1936

Tribe *Nanogyriini* MALCHUS, 1990

Genus *Amphidonte* FISCHER DE WALDHEIM, 1829

Subgenus *Amphidonte (Amphidonte)* FISCHER DE WALDHEIM, 1829

Type species: *Amphidonte humboldtii* FISCHER DE WALDHEIM, 1829.

Description: Shell medium in size, inequivalve with helicoidal right valve. Outline mostly ear-like or comma-like with relatively small umbo and mostly small attachment area. Keel weakly developed. Left valve a little convex to convex and right valve generally straight. Sculpture consists of concentric growth lamellae, sometimes interrupted by fine radial ribs. Lath-chomata and relict-chomata are present. Subligamental area relatively large, forms a raised sickle-like area along the postero-dorsal margin of the shell. Adductor muscle imprint subrounded to suboval with dorso-ventral side convex, situated postero-dorsal under the subligamental area. Shell microstructure as for genus.

Attributed species: *A. (A.) humboldtii* (FISCHER DE WALDHEIM, 1829), *A. (A.) obliquatum* (PULTENEY, 1813) = *A. (A.) conicum* (SOWERBY, 1813)), *A. (A.) haliotoides* (SOWERBY, 1813), *A. (A.) subhaliotoides* (NAGAO) *A. (A.) walkeri* (WHITE, 1850) = (*G. sinuata* var. *americana* MARCOU, 1858), *A. (A.) pyrenaicum* (LEYMERIE, 1851), *A. (A.) auricularis* (WAHLENBERG, 1821), ?*A. (A.) decussata* (GOLDFUSS, 1833), ?*A. (A.) arduennensis* (D'ORBIGNY, 1847), ?*A. (A.) blainvilli* (FISCHER DE WALDHEIM, 1829), *A. (A.) sigmoideum* (REUSS, 1844).

Stratigraphic and geographic distribution: Cretaceous (Upper Aptian to Maastrichtian), world wide.

Amphidonte (Amphidonte) obliquatum (PULTENEY, 1813)

(Text-fig. 48: a-f & text-fig. 50: a, d)

- 1813 *Chama obliquata* PULTENEY, Catalog. Birds etc. Dorsetshire, pl. 10, fig. 8. (May)
- 1813 *Chama conica* J. SOWERBY, Min. conch., vol. I, p. 69, pl. 26, fig. 3. (June)
- 1813 *Chama recurvata* J. SOWERBY, op. cit., p. 69, pl. 26, fig. 2.
- 1813 *Chama plicata* J. SOWERBY, op. cit., p. 70, pl. 26, fig. 4.
- 1913 *Exogyra conica* (SOWERBY): WOODS, Cret. Lamellibr., Eng., p. 407, Text-figs. 215-242.
- 1972 *Amphidonte conica* (SOWERBY): FRENEIX, Bassin Tarfaya, p. 85, pl. 5, figs. 1-2.
- 1972 *Amphidonte obliquatum* (PULTENEY): ZÁRUBA, Two invalid names U. Cret. Oysters, p. 107., pl. 2, figs. 1-3, 4a.
- 1986 *Amphidonte obliquatum* (PULTENEY): FRENEIX & VIAUD, Huîtres Crét. supér. (Vendée), p. 36, pl. 3, figs. 5-6 a,b, 7a-c. Extended synonymy.
- 1990 *Amphidonte obliquatum* (PULTENEY): MALCHUS, Rev. Kreide-Austern Ägypt, p. 114.

Holotype: PULTENEY, 1813, pl. 10, fig. 8,

Type locality: Melbury, Dorset, England.

Type stratum: Upper Cretaceous (Cenomanian).

Material: 16 well to very well preserved specimens borrowed from the Ruhrland-museum in Essen with the numbers RE551.763.31 A1497/1, A1652/1-2, A1653/1-3, A669/1-10. The specimens were collected from the "Essener Grünsand" in Mülheim/Heißen of early Cenomanian age.

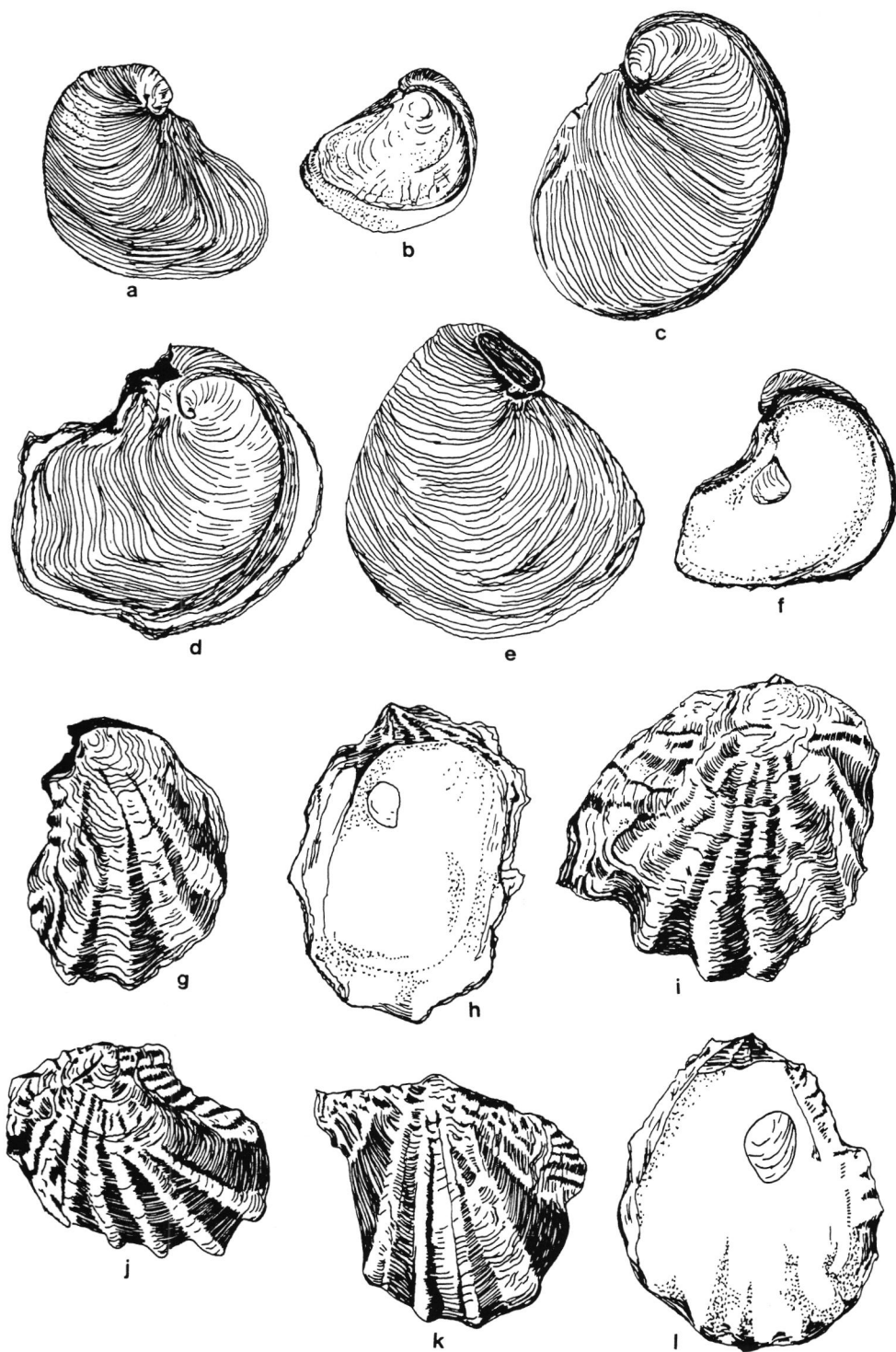


Fig. 48: a-f: *Amphidonte (Amphidonte) obliquatum* (PULTENEY); g-l: *Hyotissa semiplana* (SOWERBY). after WOODS (1913).

Description: Size: Medium (maximum height of the studied specimens 70 mm).

Outline: suboval to subtriangular, very inequivalve. Left valve convex to very convex and right valve concave or concavo-convex.

Internal characters: Ligamental area high and small, subligamental area produces a small raised area at the postero-dorsal corner. Lath-chomata surround the inner margins of the left valve and mostly the posterior side of the right valve. Adductor muscle imprint suboval with upper part straight or plicated, and situated at the postero-central side of the shell.

External characters: Shell relatively thin. Umbo small, typically amphidontid and lies parallel to the commissure line. Keel blunt and can be followed to the central part of the shell. Attachment area variable but generally small. Ornamentation of the left valve consists of concentric growth lamellae, rarely crossed by faint radial ribs mostly in the youth stages. Right valve has a strong pattern of concentric growth-lamellae at the anterior and antero-ventral sides; this covers the convex part of the valve and makes a small crescentic succession with sharply edged laminae, the other part of the valve is covered with faint growth-lamellae.

Shell microstructure: simply foliated, herringbone-cross-foliated structure with moeret and/ or empty lenses.

Stratigraphic and geographic distribution: Cretaceous (?Aptian, Albian, Cenomanian-Turonian), Europe, Middle East, Africa, and India.

Remarks: COX (1940: 125-126) has pointed out that *Chama obliquata* was named by PULTENEY (1813) a month before J. SOWERBY described the same species under the name *Chama conica*. Therefore the priority is given to PULTENEY's name, as the correct name and *conica* becomes a synonym (see also ZÁRUBA (1972: 107, DHONDT 1984: 856 and FRENEIX & VIAUD 1986: 36). WOODS (1913: 407-413 considered *A. haliotoideum* (SOWERBY) as a variety of this species but the type of convexity of the left valve of *A. obliquatum* was never described in *haliotoideum*. Furthermore, the ventral margin of *obliquatum* is rounded whilst it is pointed in *haliotoideum*. The differences between this species and *Rhynchostreon suborbiculatum* (LAMARCK) are fully discussed in ZÁRUBA (1972: 107). GRÜNDEL (1982: 155) has examined specimens of *A. obliquatum* from the Upper Cretaceous (Cenomanian to Upper Turonian) of Saxonia in Germany. He found out that only the young specimens could have faint radial ribs crossing the concentric growth-lamellae.

Many authors such as WETZEL & MORTON (1959) and BENDER (1968) have often mentioned the name "*Exogyra conica*" in their palaeontological lists and never mentioned "*columba*" or "*suborbiculatum*" or "*mermeti*" which gives the impression that they must have meant *Rhynchostreon mermeti* (COQUAND) which is distributed over a large area of Cenomanian outcrops in Jordan. It differs from *A. (A.) obliquatum* by having a larger umbo which is more helicoidally twisted, a thicker shell, exogyrid subligamental area, and by not having herringbone-microstructure.

Amphidonte (Amphidonte) haliotoideum (SOWERBY, 1813)

(Text-fig. 49: a-e, k & text-fig. 50: c, f, k)

1813 *Chama haliotoidea* SOWERBY, Mineral Conch., p.67, pl. 25, figs. 1-5.

1827 *Chama haliotoidea* SOWERBY: NILSSON, Petref. Suec. p.28, pl. 8, fig. 3.

1834 *Exogyra haliotoidea* SOWERBY: GOLDFUSS, Petref. Germ., p.38, pl. 88, fig. 1.

1834 *Exogyra auricula* GOLDFUSS, op. cit., p.39, pl. 88, fig. 2.

- 1834 *Exogyra planospirites* GOLDFUSS, op. cit., pl. 88, fig. 3.
 1846 *Exogyra haliotoidea* SOWERBY: REUSS, Vers. Böhm. Kreidform., p. 44, pl. 27, figs. 5, 9, 10, pl. 31, figs. 8, 9, 10.
 1847 *Ostrea haliotoidea* SOWERBY: D'ORBIGNY, Paléont. France, p. 724, pl. 478, figs. 1-5.
 1869 *Ostrea haliotoidea* D'ORBIGNY: COQUAND, Monogr. Ostrea., p. 144, pl. 50, figs. 8-10, pl. 52, figs. 14-17.
 1898 *Exogyra haliotoidea* SOWERBY: MÜLLER, Molluskfauna Untersönen., p. 16, fig. 3.
 1909 *Exogyra haliotoidea* SOWERBY: WANDERER, Tierverst. Kreid. Sachsen, p. 37, pl. 6, fig. 7.
 1910 *Exogyra haliotoidea* SOWERBY: FRAAS, Petref. Sammler, p. 147, pl. 35, fig. 5.
 1911 *Exogyra haliotoidea* SOWERBY: FRITSCH, Böhm. Kreideform., p. 47, fig. 211.

Holotype: SOWERBY (1813, Vol. I, p. 67, pl. XXV, fig. 1-5)

Type locality: Green Sand Formation in the parish of St. Mary Donhead, Wiltshire, England.

Type stratum: Upper Cretaceous (Cenomanian).

Material: 147 well to moderately preserved specimens belonging to the personal collection of Prof. Dr. VOIGT, Univ. of Hamburg, who collected them from different localities in Schonen in Southern Sweden, of Campanian age.

Description: Size: Small to medium in size (average height 70mm and maximum height 125 mm).

Outline: Oval to subrounded with right valve almost straight or a little concave and left valve convex. Posterior margin of both valves thin, anterior of the left valve is marked by a relatively deeply curved longitudinal groove running from under the ligamental area to the centro-ventral end of the shell, anterior of the right valve has a shallower parallel groove.

Internal characters: Ligamental area small and opisthogyrate. Subligamental area amphidontid and relatively small. Adductor muscle imprint large, centro-posterior, subtriangular or elongated oval with posterior side straight and runs subparallel to the posterior margin. Pustule-chomata covers the margins of the right valve and most parts of the left valve.

External characters: Umbo blunt and small. Attachment area generally very large. Ornamentation on both valves consists of concentric growth lines which becomes lamellose and thick at the anterior margin.

Shell microstructure: Simply-foliated with empty lenses concentrated near the ligamental area.

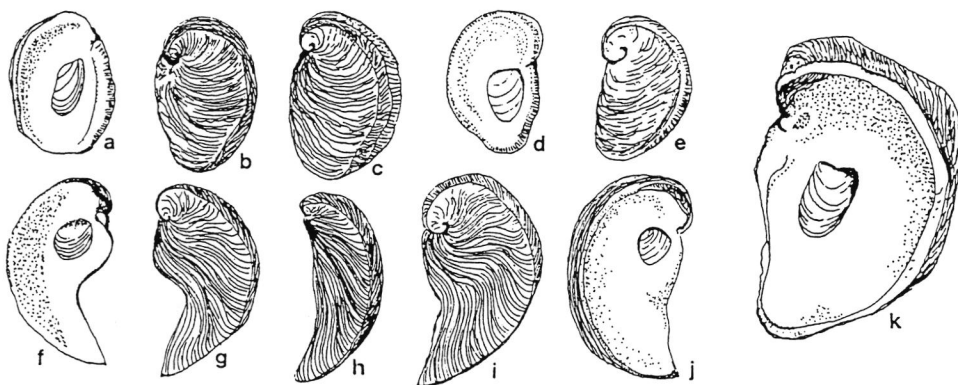


Fig. 49: a-e, k: *Amphidonte (Amphidonte) haliotoidea* (SOWERBY); f-j: *Amphidonte (Amphidonte) sigmoideum* (REUSS). a, b after FRAAS (1910); c-e, k after MÜLLER (1898); f-j after ZÁRUBA (1965).

Facies and accompanied fauna: The specimens of this study were collected from sandy kaolitic limestones or large encrusting oyster bioherms in association with a few *Spondylus labiatus* and the brachiopod *Crania stobaei* (see also SURLYK 1980:37).

Stratigraphic and geographic distribution: This species was first described from the Upper Green Sand Formation of England (Cenomanian) by J. SOWERBY (1813). Later reported from many localities in western Europe. GOLDFUSS (1833: 36-37) claimed that *Exogyra haliotoidea* exists only in the Essener Green Sand of Cenomanian age and considered NILSSON's "*Chama haliotoidea*" as *Exogyra auricularis* GOLDFUSS of Maastrichtian age of Central and Northwestern Europe, but the specimens of this study in addition to the figures and description of GOLDFUSS match those of SOWERBY which gives reasons to think that the distribution chart of this species involves Cenomanian to Maastrichtian of Central and Northwestern Europe.

Note: In this study it was not possible to get any specimens from Europe in addition to the specimens of Schonen.

Differences: This species differs from *Amphidonte obliquatum* by its less coiled umbo and by its flatter left valve which never forms a cup-like outline such as in *A. obliquatum*; also the adductor muscle imprint in this species is larger and longer. *Amphidonte sigmoideum* (REUSS) in comparison to this species has a crescentic outline with a more convex anterior side and a concavo-convex posterior side. Furthermore, the ventral side is sharply pointed, the adductor is more rounded and the growth-lines run in a steeper angle between anterior and posterior margins.

Amphidonte (Amphidonte) sigmoideum (REUSS, 1844)
(Text-fig. 49: f-j & text-fig. 50: d,e)

- 1844 *Exogyra sigmoidea* REUSS, Geognost. Skiz. Böhmen, v. II, p.180.
- 1846 *Exogyra sigmoidea* REUSS, Verstein. böhm. Kreideform., p.44, pl. 27, figs. 1-4.
- 1850 *Exogyra sigmoidea* REUSS: GEINITZ, Quadersandsteingeb. o. Kreidegeb., p. 204.
- 1866 *Ostrea (Exogyra)* cf. *sigmoidea* REUSS: ZITTEL, Bivalv. Gosauggeb., p.123, pl. 19, fig. 5.
- 1869 *Ostrea sigmoidea* REUSS: COQUAND, Monogr. Ostrea, p.93, pl. 34, figs. 5-7.
- 1872 *Ostrea (Exogyra) sigmoidea* REUSS: GEINITZ, Elbthalgeb. in Sachsen, p.186, pl. 41, figs. 14-27.
- 1898 *Exogyra sigmoidea* REUSS: MÜLLER, Moll. Untersenon Braunschweig, p. 19, fig. 4.
- 1909 *Exogyra sigmoidea* REUSS: WANDERER, Tierverst. Kreide Sachsen, p.37, pl. 6, fig. 8.
- 1911 *Exogyra sigmoidea* REUSS: FRITSCH, Böhm. Kreideform., p.46, fig. 209.
- 1913 *Exogyra sigmoidea* REUSS: WOODS, Cret. Lamellibr., Eng., p. 419, pl. 61, fig. 12.
- 1939 *Exogyra sigmoidea* REUSS: DACQUÉ, Regensburg. Kreide, p. 130, 206.
- 1964 *Exogyra sigmoidea* REUSS: ZÁRUBA, Ostreidae modern methods, p.18, pl. 1, figs. 1-3, 5, text-fig. 1.
- 1965 *Exogyra sigmoidea* REUSS: ZÁRUBA, Beitr. Kentn. Exogyra sigmoidea, p.11, pl. 1-8, text-figs. 1-10.
- 1982 *Ceratostreon sigmoidea* (REUSS): GRÜNDEL, Ostreen Sachsen, p.142, pl. 1, figs. 1-9, text-figs. 2.1, 3.1-3.5. Extended synonymy.

Neotype: ZÁRUBA (1965: pl. 1, fig. 2). National Museum in Prague/Czechoslovakia, register number O1475".

Type locality: The Valley of Libesice near Bilina, Bohemia, Czechoslovakia (fide ZÁRUBA op. cit.).

Type stratum: Upper Cretaceous, ?Middle Turonian (ZÁRUBA op. cit.: 20).

Material: 10 very well preserved specimens borrowed from the Ruhrlandmuseum in Essen (registration numbers RE551.763.31 A1656/2-11), and one specimen from the collection of Prof. Dr. VOIGT, Univ. of Hamburg. All specimens represent right valves and are collected from the Green Sand near Essen of Lower-Middle Cenomanian age.

Description: Size: Medium with maximum height of 88 mm.

Outline: Crescentic or sigmoidal with anterior side thick and convex, posterior side thin, sharp and concavo-convex and ventral side sharply pointed. Subequivalve shell.

Internal characters: Adductor imprint relatively large and almost rounded, situated postero-dorsally. A tooth-like prolongation at the postero-dorsal corner of the right valve is possible, which fits into a socket-like structure in the left valve, it is larger in older specimens. Other details as for *A. haliotoideum*.

External characters: Shell not very thick. Left valve similar to *A. haliotoideum*. Right valve with sharp keel that forms appointed wall-like continuity of the steeper, thicker anterior side, posterior side thin, sharp, convex dorsally and concave ventrally. Growth-lamellae of the right valve tend to form a kind of curvature that fits the concavo-convex periphery of the posterior side.

Shell microstructure: Simply-foliated with mcret and empty lenses.

Stratigraphic and geographic distribution: Upper Cretaceous (Cenomanian to Lower or ?Middle Turonian), Europe.

Remarks: The characteristic features of this species are mainly based on right valve morphology, the sigmoidal outline, the rounded muscle scar and the arrangement of the growth lines which follows the concavo-convex shape of the posterior side in addition to the sharp wall-like keel. These characters distinguish this species from *A. haliotoideum*, although left valves of both species could be similar.

Subgenus *Amphidonte* (*Ceratostreon*) BAYLE, 1878

Amphidonte (*Ceratostreon*) *flabellatum* (GOLDFUSS, 1833)

(Synonymy list and initial informations of the species are mentioned on page 63)

Remarks: *A. (C.) flabellatum* (GOLDFUSS) has a world-wide distribution. Generally European specimens compared to those of Jordan, are larger in size and less tuberculated or spinose. Although the holotype of this species comes from Cenomanian rocks of Boesefeld in Germany, the species is reported from ?Aptian, Albian to Cenomanian in Europe and North Africa (see DHONDT 1984: 856 and MALCHUS 1990:112). The importance of this chronostratigraphic species is fully discussed by MALCHUS (1990:112-113).

Amphidonte (*Ceratostreon*) *pliciferum* (DUJARDIN, 1837)

(Text-fig. 50: g-j, i, q, r)

- 1822 *Gryphaea auricularis* BRONGNIART, Sur quelques terrains de craie, p. 321, pl. 6, fig. 9. (non)
1869 *Ostrea plicifera* DUJARDIN: COQUAND, Monogr. Ostrea, p.80, pl.36, figs. 6-18.
1869 *Ostrea matheroniana* D'ORBIGNY: COQUAND, op. cit., p.62, pl.32, figs. 16,20.
1912 *Exogyra spinosa* MATHERON: PERVINQUIÈRE, Paléont Tunisie, p.191.
1974 *Exogyra plicifera* (DUJARDIN): KAEVER et al., Foss. Westfalens, p.152, pl.14, fig. 4.
1990 *A. (Ceratostreon) pliciferum* (DUJARDIN): MALCHUS, Rev. Kreide-Austern Ägypt. p.113, pl. 5, figs. 8-10. Extended synonymy.

Holotype: DUJARDIN (1837: Nr. 73.).

Type locality: Touraine (craie tufeau), France.

Type stratum: Senonian.

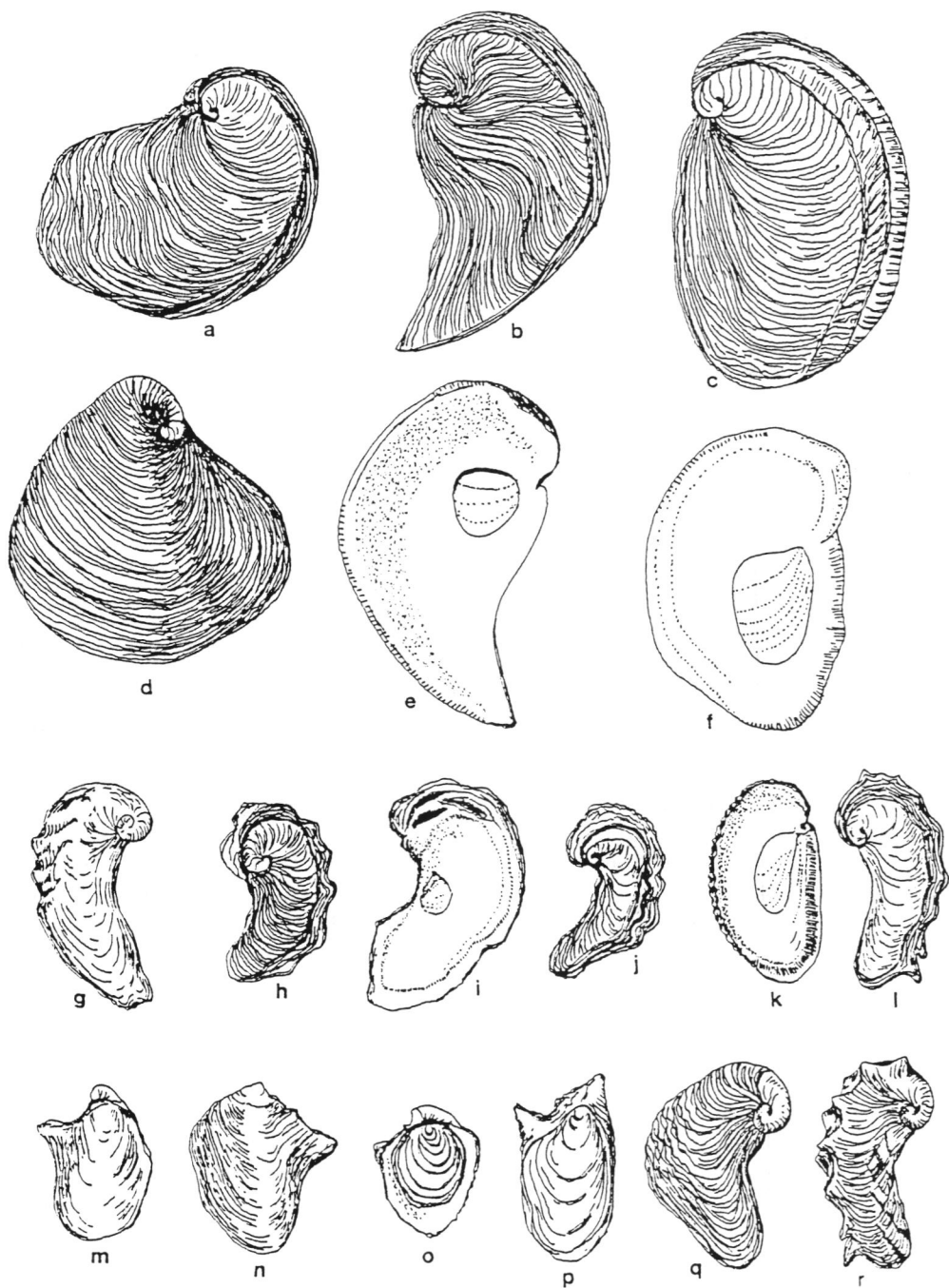


Fig. 50: a, d: *Amphidonte (Amphidonte) obliquatum* (PULTENEY); b, e: *Amphidonte (Amphidonte) sigmoideum* (REUSS); c, f, k: *Amphidonte (Amphidonte) haliotoideum* (SOWERBY); g-j, l, q, r: *Amphidonte (Ceratostreon) pliciferum* (DUJARDIN); m-p: *Gryphaeostrea canaliculata* (SOWERBY). a, d after WOODS (1913); b, e: after ZÁRUBA (1965); c, f: after MÜLLER (1898), k: after REUSS (1845); h, j, l: after FABRE-TAXY & REVEST (1968); g, i, q, r: after D'ORBIGNY (1847).

Material: 41 specimens from the personal collection of Prof. Dr. VOIGT (Geol.-Palaeontol. Institute, University of Hamburg) collected from the Coniacian of La Ribochère in France, in addition to 18 specimens of the same collection from an unknown location. The specimens of La Ribochère are well to very well preserved and the other specimens are fairly preserved.

Description: Size: Small with maximum height 45 mm.

Outline: Crescentic or ear-like to comma-like with helicoidally twisted umbo. Left valve convex and right valve convex or flat.

Internal characters: Ligamental area narrow, subligamental area variable in size, generally produces a small rim at the postero-dorsal side with a small mould. Adductor muscle imprint relatively large with dorsal and posterior sides almost flat with maximum height parallel to the elongation of the shell. Inner shell margins covered with straight-chomata.

External characters: Left valve sometimes with posterior sulcus. Keel of the left valve starts strong and later becomes weaker and vanishes near the ventral margin. It runs closer to the posterior side. Left valve covered with concentric growth-lamellae which are intersected mostly at the posterior side with radial ribs of variable strength, sometimes with hollow-spines or tubercles. Right valve sometimes with posterior sinus and also covered with concentric growth-lamellae, the keel is mostly sharper, and the posterior side is covered with relict-chomata.

Shell microstructure: Simply-foliated with few moeret lenses only in the outermost layers of the endostracum.

Stratigraphic and geographic distribution: Upper Cretaceous (?Turonian to Upper Maastrichtian). N. Africa, Europe. In Germany Santonian to Upper Campanian (KAEVER et al, 1974: 152).

Differences: *A. (C.) pliciferum* differs from *A. (C.) flabellatum* by its smaller size and narrower elongated form in addition to the different form of ornamentation having fewer radial ribs. FABRE-TAXY & REVEST (1968) suggested two varieties of this species "*matheroni* (D'ORBIGNY) and *auricularis* (BRONGNIART)", they differentiated them according to the degree of twisting of the umbo. The specimens of this study show a variability which goes beyond these two varieties. This is mostly revealed by some factors such as the space available for living and the attachment area. To consider such minor variations as individual taxa might lead to an unnecessary long list of names.

Subgenus *Amphidonte* (*Vultogryphaea*) VIALOV, 1936

Type species: *Ostrea vultur* COQUAND, 1869.

Description: Amphidonte with thin shell, highly convex left valve and almost flat right valve. Sculpture consists of concentric growth-lamellae crossed by a few, large, blunt irregular radial ribs with tubercles and/or hyote spines. Shell microstructure is simply-foliated with relatively large empty and/or moeret lenses.

Attributed species: *A. (Vultogryphaea) laciniatum* (NILSSON, 1827), *A. (Vultogryphaea) vultur* (COQUAND, 1869).

Stratigraphic and geographic distribution: Upper Cretaceous (Cenomanian-Campanian). Northwest Europe, USSR, Central Asia and India.

Differences: This subgenus differs from other members of the genus *Amphidonte* by its convexer left valve, as well as by its few, large, spinose or tuber-

culated radial ribs and by the microstructure which is characterised by the relatively large, long empty and mocret lenses. *A. (Amphidonte)* has smaller, shorter empty or mocret lenses which are mostly restricted to the dorsal side and the uppermost (outer) layers of the endostracum. *A. (Ceratostreon)* has a thicker shell than *A. (Vultogryphaea)*, it is more compact and rarely has mocret lenses in the layers of the base of the radial ribs.

Amphidonte (Vultogryphaea) laciniata (NILSSON, 1827)
(Text-fig. 51: p-u)

- 1827 *Chama laciniata* NILSSON, Petrif. suecana, p.28, pl. 8, fig. 2 a,b.
 1833 *Exogyra laciniata* GOLDFUSS, Petref. German., p.35, pl.86, fig. 12.
 1847 *Ostrea laciniata* D'ORBIGNY, Paléont. France, p.739, pl.486, figs. 1-3.
 1984 *Vultogryphaea laciniata* (NILSSON): DHONDT, Late Cret. Biv. A10, p.60, figs.2 e,f.
 1985 *Ceratostreon laciniatum* GOLDFUSS: FRENEIX & VIAUD, Sémon Vendée, pl. 2, fig. 4.
 1986 *Costagyra laciniata* GOLDFUSS: FRENEIX & VIAUD, Huître crét. supér. (Vendée), p.43, pl. 4, figs. 6-12. Extended synonymy.

Holotype: NILSSON, 1827, pl. 8, fig. 2 a,b.

Type locality: Sweden (?).

Type stratum: Campanian.

Material: 37 fairly to well preserved specimens from the collection BRANDES, University of Hamburg, all collected from Groß-Bülten in Germany.

Description: Size: Medium with maximum height 98 mm.

Outline: Ear-shaped or high oval to circular. Left valve convex and right valve straight or slightly concave.

Internal characters: Ligament area exogyrid type. Subligamental area platform type. Posterior adductor muscle scar is not seen in the examined specimens.

External characters: Umbo is helicoidally twisted. Attachment area is relatively large. Surface of the left valve is ornamented with concentric growth-lamellae crossed by few, irregular, relatively large radial ribs, sometimes with hollow spines which mostly occur at the end of the rib. Right valve is ornamented with concentric growth-lamellae.

Shell microstructure: Simply-cross-foliated to herringbone-cross-foliated with relatively large, long mocret or empty lenses mostly at the umbonal area.

Stratigraphic and geographic distribution: Upper Cretaceous (Campanian). Known from Sweden, Germany, Belgium and the Netherlands and France. It is also known from the Russian platform and India.

Differences: *A. (Vultogryphaea) vultur* (COQUAND) which was described from the Cenomanian of Bonneuil-Matours in France has in contrast to *A. (Vultogryphaea) laciniata* (NILSSON) a deeply concave right valve and narrower umbo and ligamental area. *A. (Vultogryphaea) digitata* (SOWERBY) from the Upper Greensand (Cenomanian) of Dorset-England (WOODS, 1913: 417-418, text-figs. 249-252) has in comparison to *A. (Vultogryphaea) laciniata* (NILSSON) strong folds with stronger spines, in addition, its outline tends to be more quadrangular than circular.

Remarks: The type material described by NILSSON (1827) in Lund (Sweden) are lost (DHONDT, 1985). Most authors have considered *A. (Vultogryphaea) laciniata* sensu GOLDFUSS as the species designation, however, NILSSON (1827) has the priority.

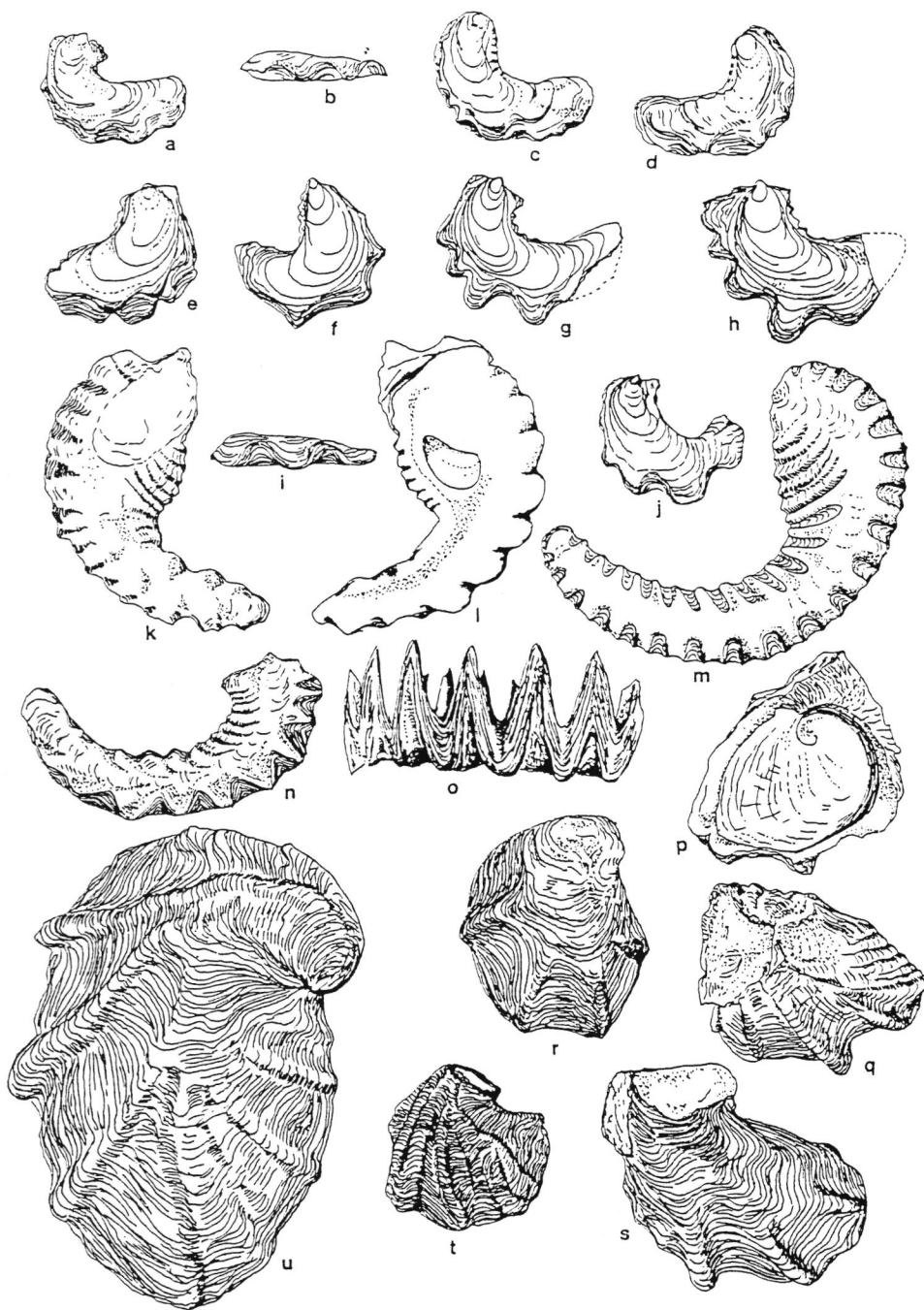


Fig. 51: a-j: *Agerostrea lunata* (NILSSON); k-o: *Agerostrea unguolata* (SCHLOTHEIM); p-u: *Amphidonte (Vultogryphaea) laciniata* (NILSSON). a-j: own figures; k, l: after MALCHUS (1990); m, n, p, q: after D'ORBIGNY (1847); o, r, s, t: after WOODS (1913); u: after GOLDFUSS (1833).

Tribe *Exogyriini* VIALOV, 1936
Genus *Rhynchostreon* BAYLE, 1878
Rhynchostreon suborbiculatum (LAMARCK, 1801)
(Text-fig. 52: j-q)

- 1801 *Gryphaea suborbiculata* LAMARCK, Systeme animaux, p.398, pl.23, figs. 3-4.
1972 *Rhynchostreon columbum columbum* (LAMARCK): FRENEIX, Moll. Tarafaya Maroc, p.88, pl. 5, figs. 3 a, b.
1972 *Rhynchostreon suborbiculatum* (LAMARCK): ZÁRUBA, Two invalid names of Cret Oysters, p.107, pl. 1, fig. 1, pl. 2, fig. 4, pl. 3, fig. 1.
1974 *Exogyra columba* (LAMARCK): KAEVER et al., Foss. Westfalens I, p.152, pl.14, fig. 2.
1986 *Rhynchostreon suborbiculatum* (LAMARCK): FRENEIX & VIAUD, Huitre crét. supér. (Vendée), p.37, pl. 3, figs. 8, 9, 12. Extended synonymy.
1990 *Rhynchostreon suborbiculatum* (LAMARCK): MALCHUS, Rev. Kreide-Austern Ägypt, p.132. Extended synonymy.

Lectotype: LAMARCK (1801: figs. in PERVINQUIÈRE (1910: fiche 190, fig. H1-3, fiche 190a, fig. H4.)) = (ZÁRUBA (1972: pl. i, figs. 1a-2c)).

Type locality: Le Mans (Sarthe, France).

Type stratum: Upper Cretaceous (Upper Cenomanian).

Material: Over 86 specimens fairly to well preserved three having the registration number RE551.776.331 A1456 in Ruhrlandmuseum in Essen and represent large adult specimens, 6 specimens having the registration number RE.551.763.31.A1648 and represent young specimens from near Essen-Westphalia, Germany.

The others are from the personal collection of Prof. Dr. VOIGT in the University of Hamburg collected from France and Czechoslovakia.

Description: Size: Medium (maximum height of the studied specimens 97 mm). Up to 116 mm according to FRENEIX & VIAUD (1986).

Outline: Subrounded to oval, higher than longer, large specimens mostly with faint posterior sulcus. Left valve very convex and right valve straight or slightly convex or slightly concave.

Internal characters: Ligamental area very narrow and relatively long, subligamental area very small and absent in the small specimens. Adductor muscle imprint rounded to oval and situated postero-centrally. The studied specimens do not show any traces of chomata although according to MALCHUS (1990:132) small specimens could have chomata.

External characters: Umbo relatively small and helicoidally twisted (up to 1.5 degree). Keel of the left valve starts strong and mostly vanishes before reaching the centre of the shell. Left valve of large specimens smooth except for faint concentric growth-lines, while small specimens show mostly faint ribs on the umbonal area which sometimes spread to cover the whole surface of the left valve. Pigmentation mostly present, especially on left valves of large specimens, and it consists of purple-brownish, wavy bands, radiating from the umbo of the left valve and scattered throughout the valve surface.

Shell microstructure: Compact bent-foliated without any moeret or empty lenses.

Stratigraphic and geographic distribution: Upper Cretaceous Upper Cenomanian-Santonian, ?Campanian, Europe, Central USSR, Morocco, ?Algeria and India.

Differences: This species is differentiated from *R. mermeti* by its larger size, smoother surface, by its smaller umbo, and by the degree of twisting of the umbo which reaches 2.5 degrees in *R. mermeti* and does not exceed 1.5 degrees in *R. suborbiculatum*. *Gryphaea plicatula* LAMARCK the type species of *R. plicatulum* in MALCHUS (1990:131), is figured in (PERVINQUIÈRE 1910, Palaeont. Univers. fiche 191) and is very similar to small specimens of *R. suborbiculatum*.

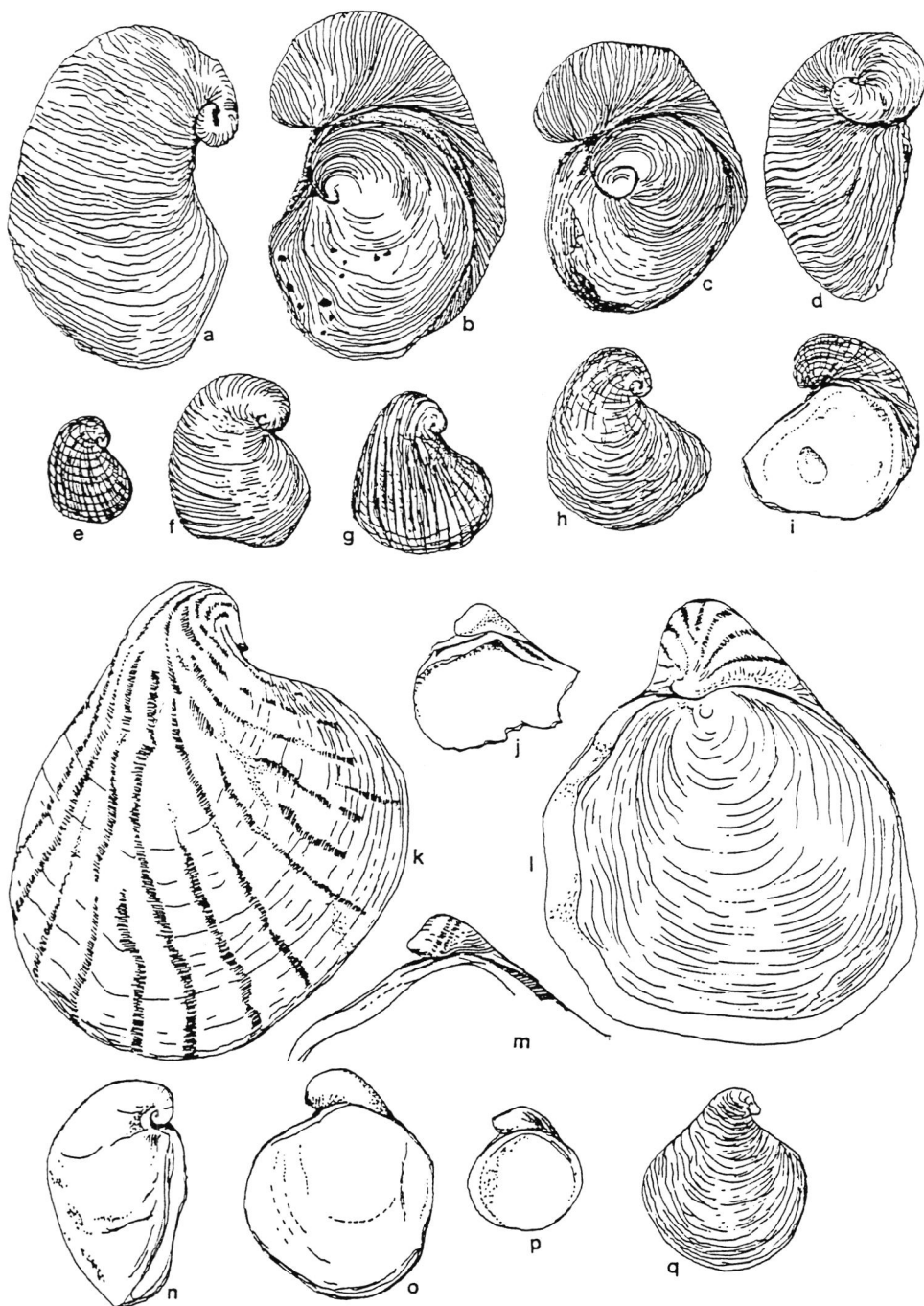


Fig. 52: a-i: *Rhynchostreon mermeti* (COQUAND) from the Cenomanian of Jordan; j-q: *Rhynchostreon suborbiculatum* (LAMARCK); a-i: own figures; k-l: after COQUAND (1869), Cenomanian of ?Algeria; j, m, p, q: after JOURDY (1924) Cenomanian of France; n, o: after RENZ (1955), Cenomanian of Greece.

Such specimens have faint ribs only on the umbonal area and might be synonymous with *R. suborbiculatum* (LAMARCK) or *R. mermeti* (COQUAND).

Subfamily *Gryphaeostreinae* FRENEIX, 1982
Genus *Gryphaeostrea* CONRAD, 1850
Gryphaeostrea canaliculata (SOWERBY, 1813)
(Text-fig. 50: m-q)

(Synonymy list and initial informations of the species are mentioned on page 76)

Material: 59 well to very well preserved specimens borrowed from the Ruhrland-museum in Essen with the registration numbers RE551.763.31 A1643/1-28 and RE551.763.32 A621/1-31, in addition to dozens of specimens from the personal collection of Prof. VOIGT and from the collection of the Palaeontological Museum in the University of Hamburg.

Remarks: *G. canaliculata* has a world-wide distribution. European specimens are morphologically identical to those from Jordan. They range from Aptian to latest Maastrichtian, while the Jordanian specimens are restricted to the Campanian-Maastrichtian ages only.

Subfamily *Pycnodonteinae* STENZEL, 1959
Tribe *Pycnodonteini* STENZEL, 1959
Genus *Pycnodonte* FISCHER DE WALDHEIM, 1835
Subgenus *Pycnodonte (Phygraea)* VIALOV, 1936
Pycnodonte (Phygraea) vesiculare (LAMARCK, 1806)
(Textfig. 53)

(Synonymy list and initial informations of the species are mentioned on page 80)

Material: Over 250 fairly to very well preserved specimens collected from many localities in Germany, Holland, Belgium, Denmark and Sweden, all belonging to the personal collection of Prof. Dr. VOIGT from the University of Hamburg.

Remarks: *Pycnodonte vesiculare* has an extremely wide geographical range, and is reported from S & N America, Africa, Asia and Europe. Morphologically, the species is variable from one locality to another. These variations might have been related to environmental changes. Specimens of this study from North Germany and Scandinavia have been found in white chalks of Maastrichtian age. They represent the largest and the most variable of the European specimens. The European specimens when compared to those from Jordan are larger in size and represent many variable forms. The different morphological forms of this species are discussed by DHONDT (1985: 54) and MALCHUS (1990: 147).

Tribe *Hyotissini* HARRY, 1985

1985 *Hyotissini* HARRY, Synop. Supraspecific Class. living Oysters, p.130
1990 *Hyotissini* HARRY: MALCHUS, Rev. Kreide-Austern Egypt., p.143.

Type genus: *Hyotissa* STENZEL, 1971.

Description: (After HARRY, 1985: 130) Pycnodontini with vermiculate chomata always present near the hinge. Right valve with thin prismatic layers, frequently eroded and has rarely tuck-grooves. Anterior of the valves have a moiré luster. Margins of left valves are regularly or irregularly plicated. Ornament consists of few to many regular to irregular folds in both valves.

Attributed genera: *Hyotissa* STENZEL, 1971 and *Parahyotissa* HARRY, 1985.

Stratigraphic and geographic distribution: Upper Cretaceous (Cenomanian) to Recent. World wide.

Differences: *Hyotissini* differs from *Pycnodontini* and *Neopycnodontini* by having plicated margins of both valves and by having an ornamented surface.

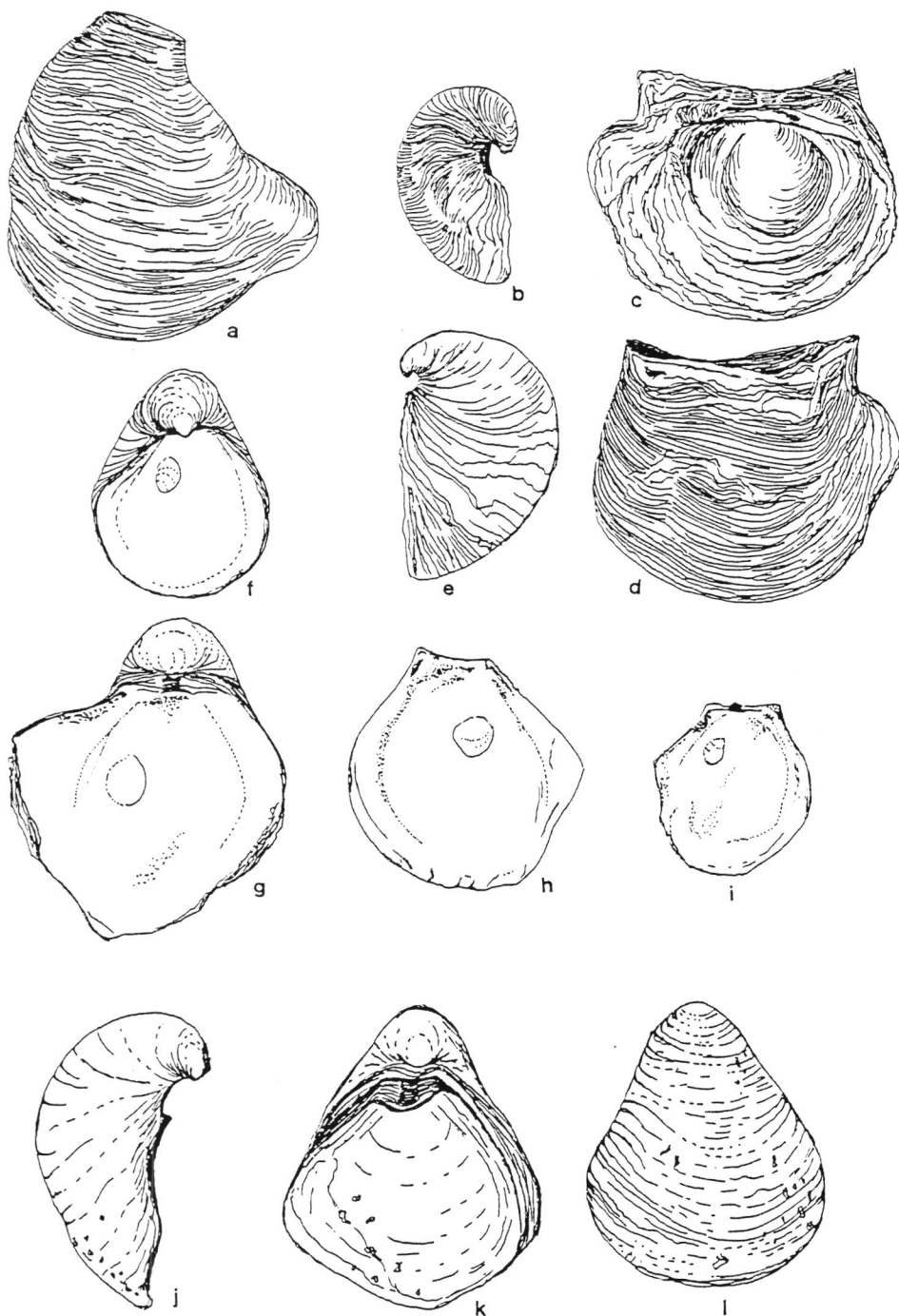


Fig. 53: *Pycnodonte (Phygraea) vesiculare* (LAMARCK); a-d: after WOODS (1913), Maastrichtian of England; g-i: after MALCHUS (1990), Upper Campanian to Lower Maastrichtian of Egypt; j-l: own figures, Campanian of Jordan.

Genus *Hyotissa* STENZEL, 1971

- 1971 *Hyotissa* STENZEL, Treatise, p. N1107.
 1981 *Hyotissa* STENZEL: TORIGOE, Oysters in Japan, p.320.
 1985 *Hyotissa* STENZEL: HARRY, Synop. Class. living Oysters, p.130.

Type species: *Mytilus hyotis* LINNÉ, 1758.

Description: Small to very large in size (reaches more than 250mm "fide HARRY: 130"). Outline usually oval to subcircular and dorso-ventrally elongated. Both valves are relatively thick and mostly plicated. Ligamental area triangular and relatively small. Adductor muscle imprint rounded and lies at the centro-posterior part of the shell. Lath-chomata and vesicular chomata are present at the dorsal side. Pigmentation on both valves is common. Shell microstructure vesicular. For more information about living *Hyotissa* see TORIGOE (1981:320) and HARRY (1985: 130-131).

Attributed species: *H. hyotis* (LINNÉ, 1758), *H. imbricata* (LAMARCK, 1801), *H. chemnitzii* (HANLEY), *H. inaequalis* (SOWERBY, 1813) and *H. semiplana* (SOWERBY, 1813).

Stratigraphic and geographic distribution: The oldest known member of this genus is *H. semiplana* (SOWERBY) from the Upper Cretaceous (Turonian to Maastrichtian), while the others belong to living species. World wide.

Differences: The species of this genus have been placed in *Lopha* by many authors, it was also included in *Dendostrea* or removed to *Pretostrea* by some others until STENZEL (1971) gathered them successfully in the genus *Hyotissa*. This genus differs from *Parahyotissa* HARRY, 1985 by its larger size and by the presence of lath-chomata in addition to the left promyal passage which is in contrast to *Parahyotissa* not always closed.

Hyotissa semiplana (SOWERBY, 1825) (Text-fig. 48: g-l)

- 1825 *Ostrea semiplana* J. de C. SOWERBY, Miner. Conch., vol.5, pl.489, fig. 3.
 1836 *Ostrea sulcata* BLUMENBACH: GOLDFUSS, Petref. Germ., p.12, pl.76, fig. 2 a,b.
 1846 *Ostrea flabelliformis* NILSSON: REUSS, Versteiner. Böhm. Kreideform., p. 39, pl.28, fig.16, pl.29, fig. 19.
 1846 *Ostrea sulcata* BLUMENBACH: REUSS, op. cit., p.39, pl. 28, figs. 2-4,8.
 1847 *Ostrea semiplana* (SOWERBY): D'ORBIGNY, Paléont. France, p.747, pl.488, fig. 4-5.
 1869 *Ostrea semiplana* (SOWERBY): COQUAND, Monogr. Ostrea., p.74, pl.28, figs. 1-15.
 1889 *Ostrea semiplana* (SOWERBY): HOLZAPFEL, Moll. Aachen. Kreide., p.251, pl.28, figs. 5-6, 10-14, 16, 18, 19.
 1898 *Ostrea semiplana* (SOWERBY): MÜLLER, Moll. Untersenen Braunschweig, p.8, pl. 1, figs.1-4, pl. 3, fig. 3.
 1910 *Ostrea semiplana* (SOWERBY): FRAAS, Petrefaktensammler, pl.34, fig. 11.
 1913 *Ostrea semiplana* (SOWERBY): WOODS, Cret. Lamellibr., Eng., p.379, pl.56, figs. 17-19, pl.57, pl. 58, figs. 1-5, textfigs. 183-193.
 1961 *Lopha semiplana* (SOWERBY): BOBKOVA, Ostreids Cret. Tadzhik, p.86, pl.16, fig. 4.
 1962 *Lopha semiplana* (SOWERBY): Brit. Mesozoic fossils, 1.59, fig. 4.
 1968 *Lopha semiplana* (SOWERBY): CARTER, Funct. St. Cret. Oyster Arctostrea, p. 482, pl.90, figs.1-2.
 1977 *Hyotissa semiplana* (SOWERBY): PUGACZEWSKA, U. Cret. Oysters Poland, p. 193, pl.14, figs. 1-3.
 1977 *Hyotissa lunata* (NILSSON): PUGACZEWSKA, op. cit., p.193, pl.15, figs.1-7.
 1977 *Hyotissa armata* (GOLDFUSS): PUGACZEWSKA, op. cit. p.194, pl.12, figs.4-5.
 1980 *Hyotissa semiplana* (SOWERBY): DHONDT, Repart.des Bivalves Crét. Moyen, p. 317.
 1982 *Hyotissa semiplana* (SOWERBY): GRÜNDEL, Ostreen Sachsen p.153, pl. 1, figs. 5-9.
 1985 *Hyotissa semiplana* (SOWERBY): DHONDT, Late Cret. Biv. A10, p.57, fig. 4f.
 1986 *Hyotissa semiplana* (SOWERBY): FRENEIX & VIAUD, Huitre crét. supér. (Vendée), p.35, pl. 3, figs. 1, 2a,b, 3, 4. Extended synonymy.

Type species: J. DE C. SOWERBY (1825: pl.489, fig. 3.).

Type locality: Norwich, Norfolk, England.

Type stratum: Zone of *Belemnitella mucronata* (fide Woods 1913: 387, B.M.N.H. 1961: 162) = Campanian.

Material: More than 850 fairly to very well preserved specimens borrowed from the personal collection of Prof. VOIGT from the University of Hamburg. The material is collected from many localities in Germany and Czechoslovakia from Santonian and Campanian ages.

Description: Size: Medium (maximum height of the studied specimens 70 mm).

Outline: Extremely variable depending on the room available for living, and the size and shape of the object to which the left valve is attached. Freely grown specimens with relatively small attachment areas, show mostly oval, rounded or square shape with height larger than length and with both valves slightly convex and with posterior side slightly shifted.

Internal characters: Ligamental area relatively small, pointed triangular and mostly curved posteriorly. Adductor muscle imprint is rounded and situated postero-dorsally, mostly elevated in large specimens. Dorsal side dominated by lath-chomata, other sides are chomata free. Commissure can be plicated or undulated or free depending on the intensity of radial ribs on the outer surface of the valves.

External characters: Attachment area very variable and affects directly the shape of the shell. Surface of both valves covered with concentric growth-lamellae which are crossed by few to many radial ribs or folds, their intensity and size are extremely variable.

Shell microstructure: Herringbone cross-foliated, with vesicular shell structure.

Stratigraphic and geographic distribution: Upper Cretaceous (Turonian-Maastrichtian). Europe.

Remarks: Oyster genera such as *Actinostreon* BAYLE, *Cameleolopha* VIALOV, *Nicaiolopha* VIALOV and *Acutostrea* VIALOV can build shells very similar to *Hyotissa semiplana*, the only difference is the pycnodontid microstructure of the shell in *Hyotissa*. DHONDT (1985: 58) has examined the collection of COQUAND in Budapest and discovered that the figured specimens from Algeria in COQUAND (1869 pl.38 fig.10-12) do not belong to *H. semiplana*.

Family *Ostreidae* RAFINESQUE, 1815
Subfamily *Liostreinae* MALCHUS, 1990
Tribe *Curvostreini* MALCHUS, 1990
Genus *Agerostrea* VIALOV, 1936

1936 *Agerostrea* VIALOV, *Classific. des Huîtres*, p. 20.

1990 *Agerostrea* VIALOV: MALCHUS, *Rev. Kreide-Austern Ägypt.*, p.160.

Type species: *Ostracites unguatus* SCHLOTHEIM, 1813.

Description: Medium in size (maximum height 120 mm). Outline generally crescentic, anterior side convex, posterior side concave and both sides touch the commissure almost vertically. Auricle on both sides is possible. Commissure mostly wavy plicated with pointed or rounded ends. Ornament consists mostly of concentric growth-squama, sometimes with a smooth area at the centre of the shell. Ligamental area triangular and relatively small. Adductor muscle imprint relatively small, comma-like or oval and situated close to the postero-dorsal side. Shell microstructure compact-foliated, small mocket lenses are rare.

Attributed species: *A. ungulata* (SCHLOTHEIM, 1813), *A. falcata* (MORTON, 1827), *A. mesenterica* (MORTON, 1827), *A. lunata* (NILSSON, 1827), *A. rouxi* (DOUVILLÉ, 1910) (= ?*A. bursauxi* (DOUVILLÉ, 1910)) and *A? sannionis* (WHITE, 1850).

Stratigraphic and geographic distribution: Upper Cretaceous (?Upper Turonian, Coniacian to Maastrichtian). Europe, North Africa, Madagascar, Asia, India, and North America.

Remarks: CARTER (1968) and STENZEL (1971) suggested that *Agerostrea* has developed from *Rastellum* (*Arctostrea*). However, *Agerostrea* build compact foliated structure and *Rastellum* is characterised by its strongly lenticular foliated structure. In addition to the microstructure, the thin shell and the wavy-plicated commissure with the smooth area at the middle of the shell are the reasons that MALCHUS (1990: 160) gave to attribute this species to *Curvostreini*. Detailed comparison to other genera are discussed in MALCHUS (op. cit.).

Agerostrea ungulata (SCHLOTHEIM, 1813)
(Text-fig. 51: k-o)

- 1813 *Ostracites ungulatus* SCHLOTHEIM, Beitr. Naturgesch., p.112.
1846 *Ostrea larva* LAMARCK: D'ORBIGNY, Paléont. France, p.740, pl.486, figs.4-8.
1971 *Agerostrea ungulata* (SCHLOTHEIM): STENZEL, Treatise, p.N1152, fig. J133, 1a-e.
1982 *Agerostrea cf. ungulata* (SCHLOTHEIM): DHONDT, Bivalvia Hemmoor, p.91
1990 *Agerostrea ungulata* (SCHLOTHEIM): MALCHUS, Rev. Kreide-Austern Ägypt., p.162, pl. 15, fig. 8. Extended synonymy.

Holotype: SCHLOTHEIM (1813), refigured in STENZEL (1971: N1160, fig. J133 1,a,b).

Type locality: St. Pitsersberg near Maastricht in The Netherlands.

Type stratum: Upper Cretaceous (Maastrichtian).

Material: Only six well preserved specimens from the personal collection of Prof. Dr. VOIGT, Hamburg, two of them collected from Kanne (Albert-Kanaal), Belgium, two from St. Pitsersberg near Maastricht and two from Geulhem (The Netherlands). All from the Maastricht Formation of Late Maastrichtian age.

Description: Size: Medium with maximum height up to 120 mm (fide STENZEL).

Outline: Narrow, long sickle-shaped, falcately curved, flanks tapering gently from umbo. Anterior flank convex and posterior concave, both are almost vertical to commissure plane.

Internal characters: Ligamental area small and posteriorly curved, no umbonal cavity. Adductor muscle pad medium in size, comma-like and situated closer to the postero-dorsal margin. Straight-chomata present on dorso-posterior and dorso-ventral sides.

External characters: Attachment area small to large. Sculpture consists of many folds with rounded or sharp ends covering both anterior and posterior sides leaving a smooth central area that runs parallel to the elongation of the shell. The folds have mostly rounded edges raised over the smooth area at the centre of the shell, at the posterior side, the folds near the adductor pad, are smaller in size and closer to each other.

Shell microstructure: Compact simply-foliated.

Stratigraphic and geographic distribution: Upper Cretaceous (Middle to Upper Maastrichtian), Europe, N. Africa, Madagascar, Southern India and Pakistan.

Differences: *A. ungulata* is generally distinguished from other *Agerostreids* by its larger size and the form of folds at the posterior and anterior sides with the smooth central area of the shell. In *A. lunata* the folds are fewer and re-

latively larger when compared with the size of the shell. MALCHUS (1990: 163) mentioned that small specimens of the Egyptian *A. rouxi* are very hard to differentiate from small specimens of *A. unguolata* especially when they are associated together as in Egypt. This is not the case with the specimens from The Netherlands, where *A. unguolata* represents Upper Maastrichtian and *A. lunata* represents Lower Maastrichtian age.

Agerostrea lunata (NILSSON, 1827)

(Text-fig. 51: a-j)

- 1827 *Ostrea lunata* NILSSON, Petrif. Suecana, p.31, pl. 6, fig. 3.
- 1833 *Ostrea lunata* NILSSON: GOLDFUSS, Petref. Germ., vol. II, p.11, pl.75, fig. 2.
- 1834 *Ostrea nasuta* MORTON, Synop. Org. remains U.S., p.51, pl. 4, fig. 6.
- 1837 *Ostrea lunata* NILSSON: HISINGER, Lethaea Suecica, p.49, pl.14, fig. 4.
- 1849 *Ostrea lunata* NILSSON: BROWN, Illustr. foss. conch. Gt. Britain & Irland, p. 147, pl.61, figs. 20, 21.
- 1854 *Ostrea larva* MORRIS, Cat. Brit. foss., ed. 2, p. 173.
- 1869 *Ostrea unguolata* COQUAND, Monogr. Ostrea, p.58, pl.31, figs.6-10, ?11,12, non 13-15 (= *Agerostrea unguolata* COQUAND).
- 1884 *Ostrea (Alectryonia) larva* WHITE, Ostreidae of N. America, p.296, pl.42, figs. 2-5, ?6, non 7-9.
- 1894 *Ostrea lunata* NILSSON: HENNIG, Geol. Fören. Stockholm Förhandl., p.515.
- 1895 *Ostrea lunata* NILSSON: VOGEL, Holländische Kreide, p.10.
- 1907 *Ostrea nasuta* WELLER, Cret. Pal. N. Jersey, p.447, pl.43, figs. 7-8.
- 1913 *Ostrea lunata* NILSSON: WOODS, Cret. Lamellibr., Eng., p.393, pl.60, figs. 16-19, pl.61, figs.1-6, extended synonymy.
- 1918 *Ostrea larva* LAMARCK: FAVRE, Catal. collection Lamarck, pl.20, figs. 71- 74.
- 1962 *Liostrea lunata* (NILSSON): Brit. Mesozoic fossils, p.162, pl.59, fig. 3.
- non 1977 *Hytissa lunata* (NILSSON): PUGACZEWSKA, U. Cret. Oysters Poland, p.193, pl.15 figs.1-7 = *Hytissa semiplana* (SOWERBY).
- non 1962 *Lopha lunata* (NILSSON): ABBASS, Monogr. Egypt. Cret. Pelecypopds, p.83, pl.11, figs. 10-12 q =(? *A. rouxi* (DOUVILLE)).

Holotype: NILSSON (1827: pl. 6, fig. 3)

Type locality: Åhus Sandstone, Sweden.

Type stratum: Lower Maastrichtian (fide WOODS 1913: 395).

Material: 24 well to very well preserved specimens from Ciply near Mons/Belgium and more than 80 fairly preserved specimens from Trimmingham-Norfolk in England, all from the personal collection of Prof. Dr. VOIGT from the University of Hamburg.

Comparison Material: 39 well to very well preserved specimens from Navesink Formation in USA, collected by Prof. VOIGT, described under *Alectryonia falcata* MORTON by SHIMER & SHROCK (1949: pl. 154, figs. 10-11) from Lower Maastrichtian age.

Description: Size: Small (maximum height of the studied specimens 41 mm).

Outline: Crescentic or sickle-shaped, elongated between the umbo and the posterior edge. Left valve convex and right valve slightly convex or almost straight. Umbo usually curved posteriorly. Wing-like or ear-like extension at both sides of the umbo are possible.

Internal characters: Ligamental area small and narrow, triangular, straight or slightly posteriorly curved. Adductor muscle imprint relatively small, oval and situated close to the postero-dorsal side. Few straight-chomata are noticed only on the antero-dorsal side of right valves of some specimens, left valves do not show the same.

External characters: Shell thin, subequivalve inequilateral. Attachment area generally small to absent. Central parts of both shells are smooth except for concentric lines or very fine short radial ribs. Anterior margin with 4-5 wavy folds that have rounded or pointed ends, posterior side with 6-7 folds of similar type but smaller in size.

Shell microstructure: Compact simply-foliated.

Stratigraphic and geographic distribution: Upper Cretaceous (Lower Maastrichtian). North-western Europe: GOLDFUSS (1833), BROWN (1849), HENNIG (1897); N. America: WHITE (1884), WELLER (1907).

Differences: *A. lunata* in comparison to *A. rouxi*, from Egypt, figured by MALCHUS (1990: pl.14, figs. 17-20, pl.15, figs.1-7) has fewer number of wavy folds and finer concentric growth-lines at the other parts of the shell, in addition to, the folds of *A. rouxi* can start near to the umbo which is never the case in *A. lunata*. The American material of *A. falcata* are more similar to *A. rouxi* from Egypt but they have a clear broad wing at the posterior side and sometimes at the anterior side. *A. mesentrica* (MORTON) described in SHIMER & SHROCK (1949: 395, pl.155, fig.16), from the Atlantic and Gulf Coastal Plain/USA, is smaller than *A. falcata* with non-plicated central area and fewer folds, has more number of folds than *A. lunata* and builds triangular folds contrasting with the rounded broad folds of *A. lunata*.

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Plate 1

Figs. 1-7: *Oscillopha wala* n. sp., Turonian of Wadi Wala- Central Jordan. 1a, b: Holotype, Nr. GPIH.7WW100 2a, b: GPIH.7WW101 3a, b, c, d.: GPIH.7WW4 4: GPIH.7WW5 5: GPIH.7WW7 6: GPIH.7WW9 7: GPIH.7WW8

Fig. 8a, b: *Africogryphaea costellata* (DOUVILLÉ), Bathonian of Wadi Zerqa River, northern Jordan. GPIH.WZR1.

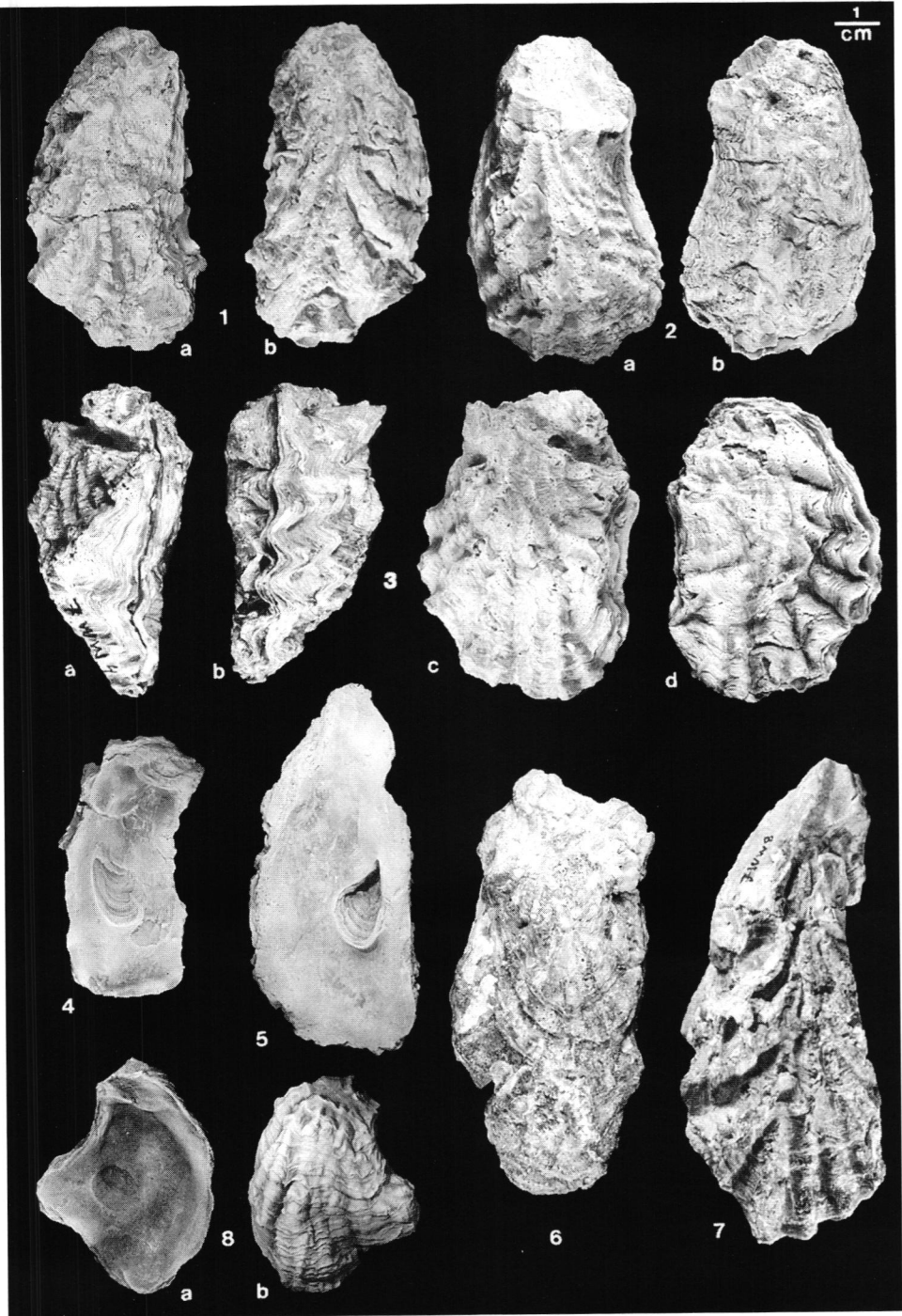


Plate 2

- Fig. 1a, b: *Oscillopsa figari* (FOURTAU), Campanian of Al-Hisa Phosphate Mine, Central Jordan. GPIH.HM1
- Figs. 2-5: *Amphidonte* (*Ceratostreon*) *flabellatum* (GOLDFUSS), Cenomanian. 2a, b: Wadi Zerqa Ma'in, central Western Jordan. GPIH.ZM1 3a, b: Wadi Zerqa Main. GPIH.ZM2 4a, b: Wadi Salihi, north of Amman. GPIH.WS1 5: South Wadi Jamil, a branch of Wadi Araba-southern Jordan. GPIH.SWJ1.
- Figs. 6-11: *Ilymatogyra* (*Afrogyra*) *africana* (LAMARCK), Cenomanian-Lower Turonian. 6a, b: Wadi Heidan, Central Jordan, forma crassa. GPIH.WH1 7a, b: Ras-El-Naqab, South Jordan, forma crassa. GPIH.RAS1 8: Wadi Heidan, forma crassa GPIH.WH2 9a, b: Wadi Heidan, forma typica, GPIH.M211 10: Wadi Heidan, right valve of forma crassa, GPIH.WH10 11: Wadi Heidan, forma typica, GPIH.M212

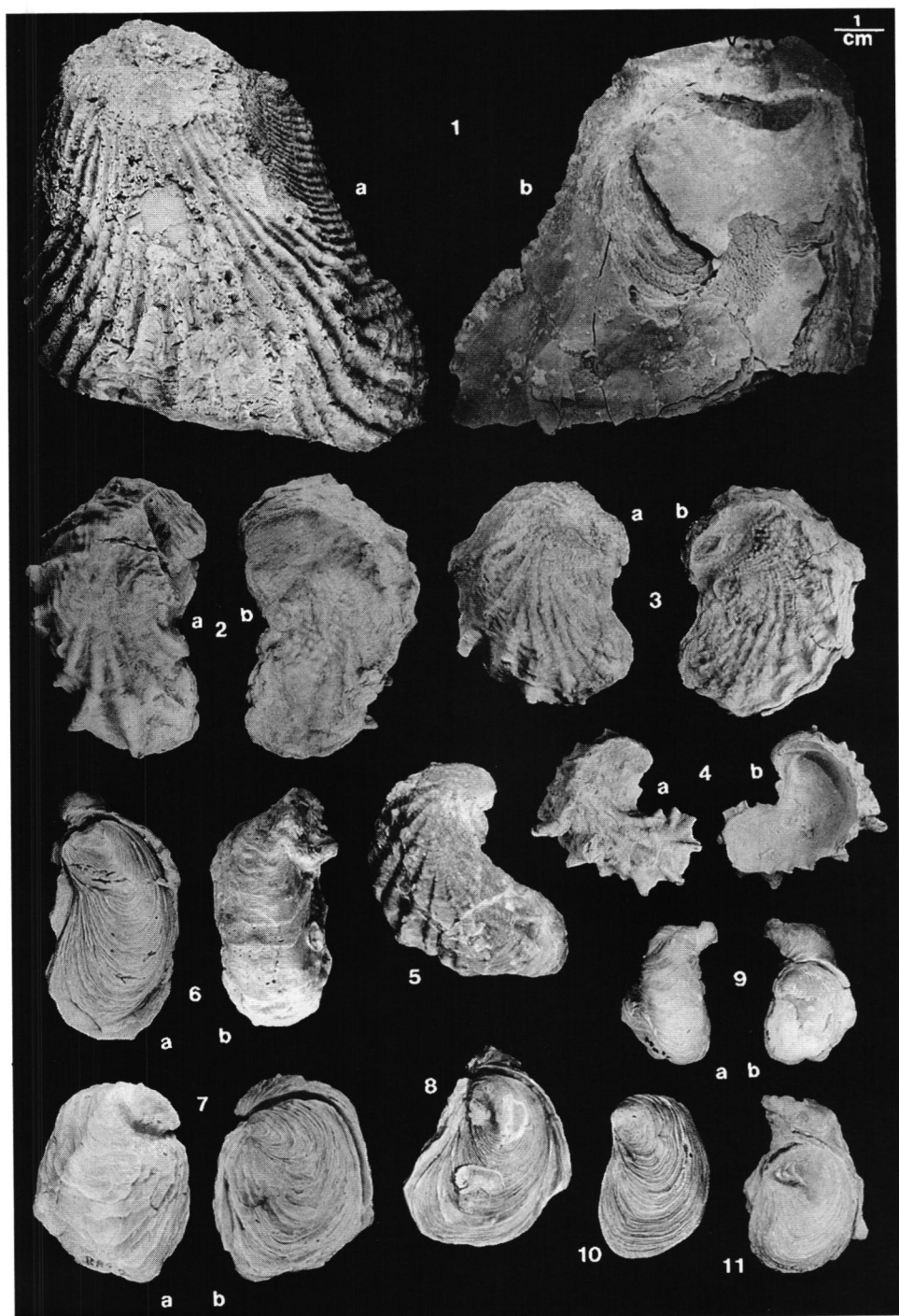


Plate 3

- Figs. 1-3: *Ilymatogyra (Afrogyra) africana* (LAMARCK), Cenomanian- Lower Turonian. 1: Ras-El-Naqab, South Jordan, forma crassa, GPIH.RAS3. 2a, b: Ras-El-Naqab, forma crassa, GPIH.RAS4. 3: Wadi Heidan, Central Jordan, forma typica, GPIH.WH11.
- Figs. 4-12: *Rhynchostreon mermeti* (COQUAND), Cenomanian. 4a, b: Wadi Wala, Central Jordan, GPIH.WW4. 5a, b: Wadi Mujib, Central Jordan, GPIH.MJ21. 6: Wadi Salihi, north of Amman, GPIH.M12. 7a, b: Wadi Wala, GPIH.WW5. 8a, b: Wadi Mujib, GPIH.MJ68. 9: Wadi Salihi, GPIH.WS10. 10: Wadi Salihi, GPIH.WS11. 11: Wadi Salihi, GPIH.WS12. 12: Wadi Salihi, GPIH.WS15.
- Figs. 13-16: *Laevigyra luynesi* (Lartet). Cenomanian. 13: Wadi Mujib, GPIH.MJ101. 14a, b: Wadi Mujib, GPIH.MJ102. 15a, b: Wadi Mujib, GPIH.MJ103. 16: Wadi Mujib, GPIH.MJ104.
- Figs. 17, 18: *Laevigyra dhondtae* MALCHUS, Cenomanian. 17: Wadi Heidan, GPIH.WH20. 18a, b: Wadi Heidan, GPIH.WH21.



Plate 4

Figs. 1, 2: *Exogyra (Exogyra) italica* (SEGUENZA), Cenomanian-Lower Turonian. 1a, b, c: South Wadi Jamil, South Jordan, GPIH.JJ3-6.1. 2: South Wadi Jamil, GPIH.JJ3-6.2.

Figs. 3-5: *Exogyra (Costagyra) olisiponensis* (SHARPE), Cenomanian-Lower Turonian. 3: Ras-El-Naqab, South Jordan, GPIH.RAS13. 4a, b: Wadi Jamil, South Jordan, GPIH.WJ10. 5: Ras-El-Naqab, GPIH.RAS14.



Plate 5

- Figs. 1,2: *Exogyra (Costagyra) olisiponensis* (SHARPE), Cenomanian-Lower Turonian. 1a, b: Wadi Mujib, Central Jordan, GPIH.Wj31. 2: Ras-El-Naqab, South Jordan, GPIH.RAS15.
- Fig. 3a,b,c: *Pycnodonte (Phygraea) vesiculare* (Lamarck), Campanian, south of Wadi Jamil, South Jordan, GPIH.JJB2.1.
- Figs. 4, 5: *Gryphaeostrea canaliculata* (SOWERBY), Campanian, Wadi Hasa area, Central Jordan, 4: GPIH.LHM1, 5a, b: GPIH.UHM1.
- Figs. 6, 7: *Pycnodonte (Costeina)* sp., Coniacian, Amman area, 6: GPIH.B11, 7: GPIH.B12.
- Figs. 8-12: *Curvostrea rouvillei* (COQUAND), Cenomanian-Lower Turonian, Ras-El-Naqab, South Jordan, 8: GPIH.RAS41, 9: GPIH.RAS42, 10: GPIH.RAS43, 11: GPIH.RAS44, 12: GPIH.RAS45.
- Figs. 13, 14: *Curvostrea* sp., Cenomanian - Lower Turonian, Wadi Salihi, north of Amman, 13: GPIH.WSB1, 14a, b: GPIH.WSB2.
- Figs. 15, 16: *Pycnodonte (Phygraea) vesiculosum* (SOWERBY), Cenomanian-Lower Turonian, Wadi Salihi, north of Amman, 15a, b: GPIH.S211, 16a, b: GPIH.S212.



Plate 6

- Figs. 1-5: *Nicaiolopha nicaisei* (COQUAND), Campanian, Central and southern Jordan. 1a, b, c: Wadi Hasa, Central Jordan, GPIH.BB21. 2: Wadi Hasa, GPIH.BB22 3: South Wadi Jamil, south Jordan, GPIH.HM10. 4: Wadi Hasa, GPIH.BB23. 5: South Wadi Jamil, GPIH.HM11.
- Fig. 6a, b: *Ambigostrea villei* (COQUAND), Campanian, Al-Hasa phosphate Mine, Central Jordan, GPIH.UHM50.

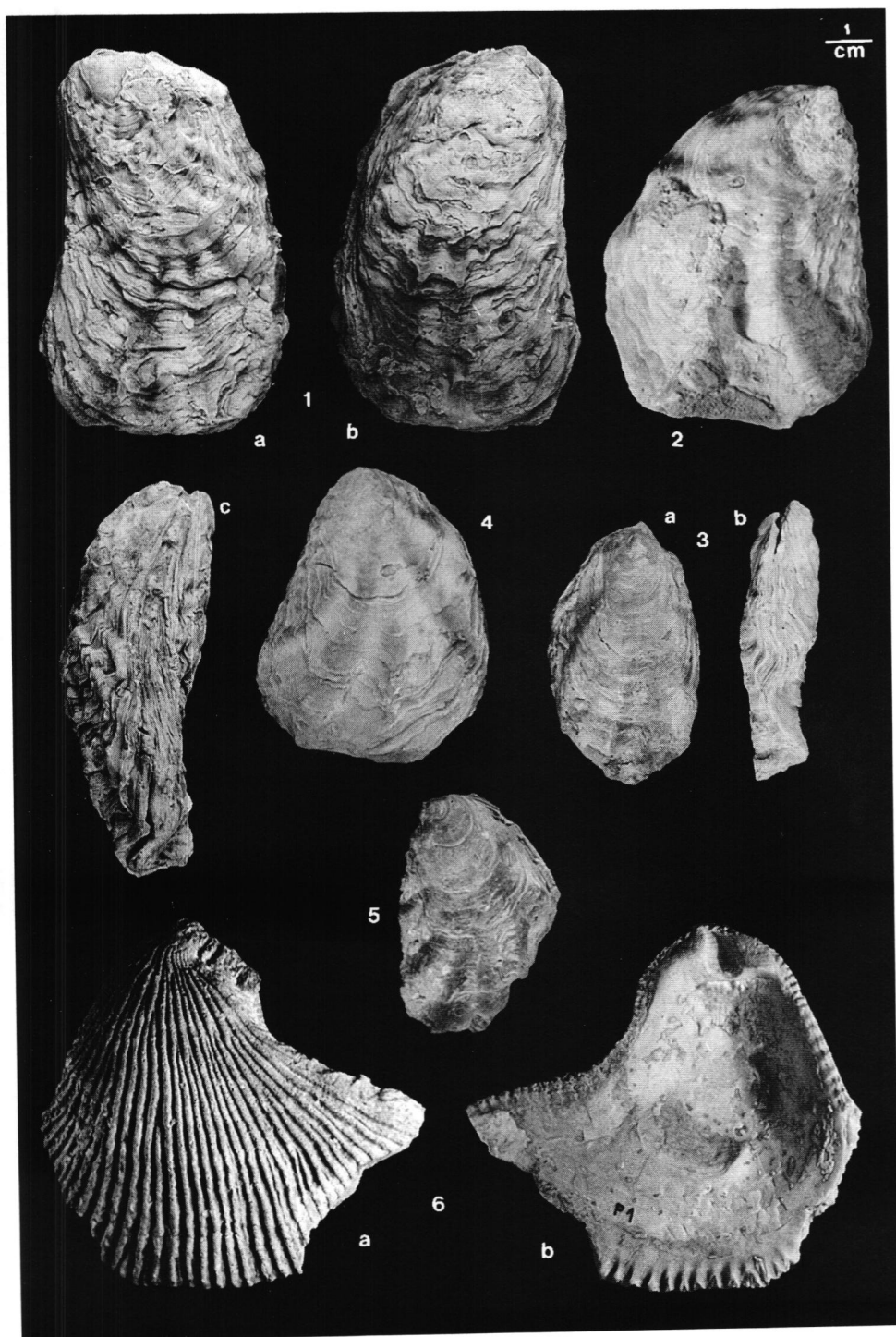


Plate 7

- Figs. 1-5: *Ambigostrea villei* (COQUAND), Al-Hasa phosphate Mine, Central Jordan, 1: GPIH.UHM51, 2: GPIH.UHM52, 3: GPIH.UHM53, 4a, b: GPIH.UHM54, 5: GPIH.UHM55.
- Figs. 6-9: *Gryphaeligmus jabbokensis* (COX), Bathonian. 6: Old Jerash Bridge, northern Jordan, GPIH.OJB1. 7: King Talal Dam, northwestern Jordan, GPIH.KTD1. 8: Old Jerash Bridge, GPIH.OJB2. 9: King Talal Dam, GPIH.KTD2.

