

Upper Cretaceous bivalves from the Glauconie de Lonzée near Gembloux (SE Belgium)

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Abstract

The bivalve fauna from the "Glauconie de Lonzée", a highly fossiliferous glauconitic sand of probable Santonian age, is described for the first time. Twenty-nine species have been recognised: a cucullaeid, a glycymeridid, two limids, three inoceramids, eight ostreoids, four pectinids, a spondylid, a trigoniid and eight heterodonts.

Palaeoecologically the major part of this fauna is interpreted as typical for an argillaceous to sandy environment in an open marine shallow subtidal, inner shelf setting.

Palaeobiogeographically the assemblage is nearest to the Lower Campanian fauna from Aachen, to Turonian-Santonian central European faunas on the coasts of the Hercynian massifs in Saxony and Bohemia and to the Middle Santonian Subhercynian Cretaceous Basin in Sachsen-Anhalt. The faunal composition indicates strong connections with central and eastern Europe. It does not confirm a direct relation with the Paris basin as was previously suggested.

Key-words: Mollusca, Bivalvia, Upper Cretaceous, Taxonomy, Palaeobiogeography.

Résumé

Les bivalves de la "Glauconie de Lonzée", un sédiment riche en glauconie et très fossilifère d'âge probablement Santonien, sont décrits pour la première fois. Vingt-neuf espèces ont été reconnues: un cucullaeidé, un glycymerididé, deux limidés, trois espèces d'inocérames, huit espèces d'huîtres, quatre pectinidés, un spondylidé, un trigonidé et huit espèces d'hétérodontes.

La faune est interprétée comme représentant un milieu franchement marin mais littoral, peu profond, à fond argileux à sableux.

Paléobiogéographiquement cette faune est fort proche de la faune campanienne d'Aix-la-Chapelle et des faunes littorales d'âge Turonien à Santonien retrouvées autour des chaînes hercyniennes en Europe centrale, tel qu'en Saxe, en Bohême ou dans le bassin subhercynien de la Saxe-Anhalt.

La composition de la faune de Lonzée indique une grande similitude à celles connues vers l'est et ne confirme aucunement l'opinion prévalente que la "glauconie de Lonzée" est une extension du Bassin Parisien.

Mots-clefs: Mollusques, Bivalves, Crétacé supérieur, Taxinomie, Paléogéographie.

Introduction

The highly fossiliferous Late Cretaceous "Glauconie de Lonzée" from Lonzée, near Gembloux in SE Belgium (Text-fig. 1) was reviewed by MALCHUS *et al.* (in press) based on the collections of the Institut royal des Sciences

naturelles de Belgique in Brussels (IRSNB), and of a preliminary section drawn by Maxime Glibert in 1936 (see Text-fig. 2). MALCHUS *et al.* (in press) surveyed the sedimentology, fossil content, biostratigraphy, and palaeoecology, with emphasis upon the European palaeoecologic and biostratigraphic distribution of the eight oyster species. The results are summarised below. The present paper concentrates on the taxonomic description of the bivalve fauna and its stratigraphic, palaeoecologic and palaeobiogeographic distribution (except for Ostreoidae). A description of the belemnite fauna from Lonzée is given by CHRISTENSEN (this volume).

Material

The molluscs from the "Glauconie de Lonzée" described here and in the following paper (CHRISTENSEN, this volume) are retained in the collections of the IRSNB and were collected/acquired:

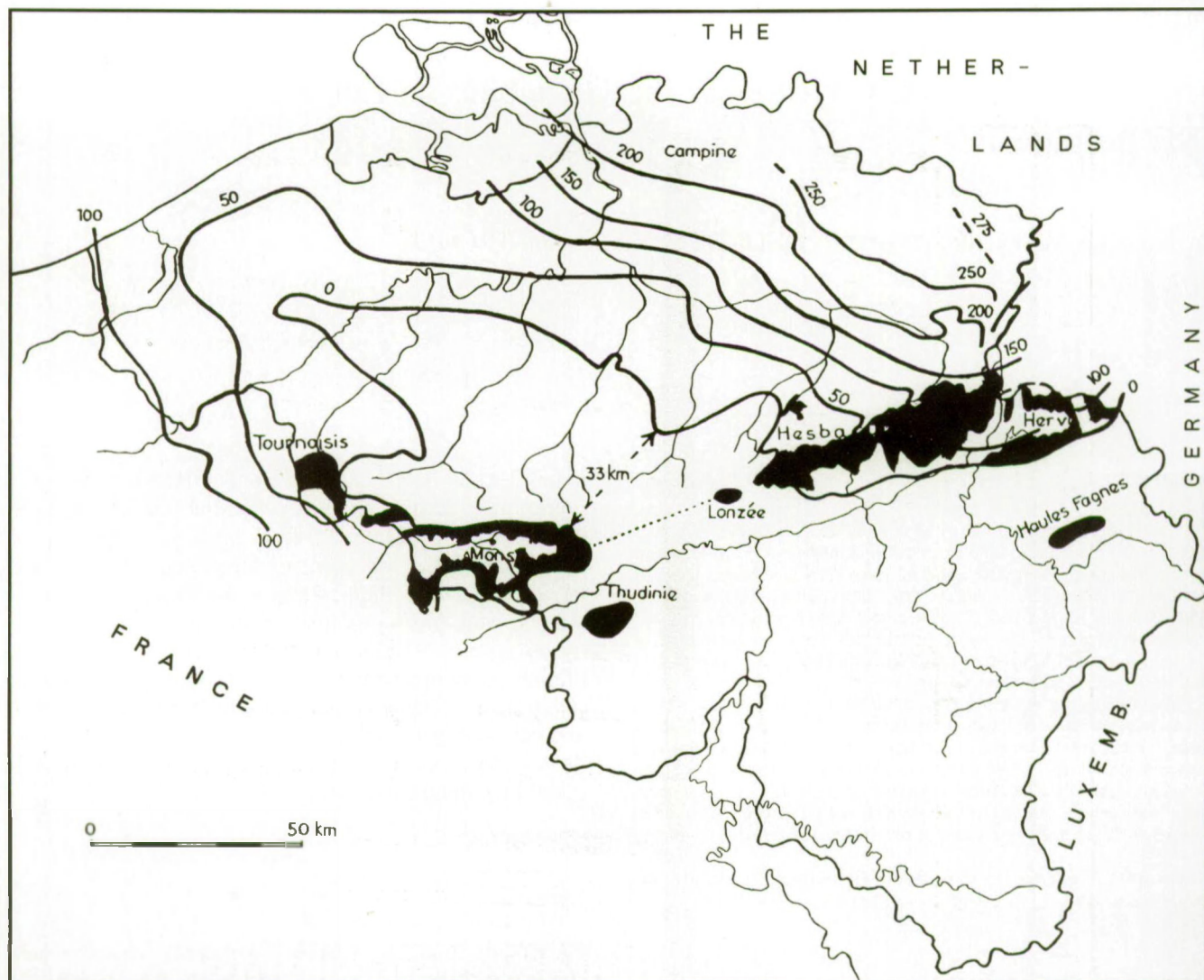
1, when the "glauconie de Lonzée" was still being exploited (before 1914): IG 4704 ("exploration Musée", 1881); IG 5793 (coll. Murlon, 1891); IG 6381 (? exploration Rutot-Wérihasse, 1896); IG 6840, 6841 (exploration Rutot-Wérihasse, 1902); IG 7065 (coll. Colbeau, 1906), IG 8254 (coll. Maillieux, 1911), IG 8261 (coll. De Jaer, 1911).

2, when the Musée royal d'Histoire naturelle (now: Institut royal des Sciences naturelles de Belgique) collected along a train/tram line: IG 8816, ("exploration Musée", 1920), IG 10511 ("exploration Musée", 1934) or dug a trench in the area, IG 11039 ("exploration Musée", 1936).

3, some collections were bought or donated to the Musée royal d'Histoire naturelle: IG 8816 (coll. Vander Bruggen, 1924); IG 9340 (coll. Malaise, 1930); IG 9694 (achat Piret, 1931).

Except for IG 11039, none of these specimens are accompanied by information as to the level from which they were collected, nor have locality data other than "Lonzée".

It is possible that not all the collections come from the same horizons and this might explain why e.g. *Inoceramus* cf. *koeneni* is only known from IG 5793 (coll. Murlon) and *I.* cf. *hercules* only known with certainty



Text-fig. 1 — Map indicating the geographical location of Lonzée (after MARLIÈRE, 1954).

from IG 4704 - as both collections were made prior to 1900, they could possibly come from older levels than those that were accessible later.

An attempt at dating those older collections by coccoliths has only shown the presence of a few long ranging taxa (pers. comm. E. Steurbaut, 1993).

Stratigraphy and faunas

The respective stratigraphic position of both sediment and faunas were correlated with a 'field notes' section drawn by Glibert (1936, MS, from bottom to top, see Text-fig. 2):

1 a, basal grey to green clay-silt, containing many moulds of bivalves and gastropods. It overlies the Silurian basement (on IRSNB labels: argile inférieure base);

1 b, above a grey-green glauconitic clay-silt with planar bedding; no macrofossils.

2, "argile plastique bleue", most abundant fossils are bivalves, belemnites, shark teeth, other vertebrates, fauna E of Glibert (on IRSNB labels: argile inférieure); thickness: 50 to 60 cm.

3, fine grey sand with large blocks of 'grés glauconifère', many bivalves, belemnites, microfauna a. o., fauna D of Glibert (on IRSNB labels: sable entre les argiles inférieure et supérieure); thickness: 145 cm.

4, "argile très glauconifère, vert bleu foncé compacte, plastique, avec dents et vertèbres de poissons", many bivalves, belemnites, shark teeth, fauna C of Glibert (on labels: argile supérieure inférieure); thickness: 20 cm.

Text-fig. 2 — Section of the "glauconie de Lonzée" drawn by Maxime Glibert in 1936, when the samples of IG 11039 were collected.

5, "lit irrégulier et discontinu de dalles, dures et compactes", fauna B of Glibert (on IRSNB labels: sable entre argile supérieure inférieure et argile supérieure - i.e. sand between clays); thickness: 15 cm.

6, "argile très sableuse, glauconifère, vert jaunâtre ou brunâtre avec très nombreux fragments de coquilles" yellow, very arenaceous, glauconitic "clays" with numerous silicified shelly fragments, fauna A of Glibert (on IRSNB labels: argile supérieure); thickness: 30 cm. The molluscan fauna of A and C are identical except for the lesser abundance of belemnites in A.

7, on top of the Cretaceous unconformably, "Bruxellian" (Lutetian, Eocene).

The belemnites of fauna A and E suggest a minimal time range from Early to Late Santonian for most of the section and a maximal range from the Middle Coniacian to the Early Campanian (including faunas A to E) (see CHRISTENSEN, this volume). The presence of *Inoceramus* cf. *hercules* (possibly in fauna D) and *I.* cf. *koeneni* (from an undefined level) would confirm the lowermost extension of the belemnite range, indicating a Coniacian age for the middle part of the section. It is assumed that the inoceramids originally belonged to older strata because sediment and fossils show signs of transportation and reworking.

The oysters, which are the most abundant bivalve group, are long ranging and are not biostratigraphically significant. Many of the species can be found in similar environments from Cenomanian to Maastrichtian strata throughout Europe from England to the Crimea.

In MALCHUS *et al.* (in press) a preliminary list of the bivalves of the "Glaucanie de Lonzée" was given. Further study of the material has made a few changes to this list necessary. The revised list is presented in Table 1.

Preservation

The preservation of the bivalve material at Lonzée varies depending on the horizon from which it was collected. All the horizons except the top horizon only contain fossils with calcitic shells; taxa with mainly aragonitic shells are occasionally preserved as moulds. In the top horizon the specimens are partly silicified. This explains why this "argile supérieure" has yielded so many heterodonts.

Mode of life and environment of the Lonzée bivalves

The following discussion is kept on a general level because,

- firstly, except for oysters which are the most abundant bivalves, there is not enough material available to present a statistical analysis,
- secondly, field observations cannot be made as the outcrops are no longer accessible,
- thirdly, part of the material was transported and re-

Table 1

Revised faunal list from the Glaucanie de Lonzée 1a, argile inférieure base; 2, argile inférieure (fauna E of Glibert); 3, sable entre les deux argiles (fauna D of Glibert); 4-6, argile supérieure (faunas A, B, C, of Glibert); A: topmost level of argile supérieure, with silicified fauna.

SPECIES	1a	2	3	4-6	6
<i>Cucullaea subglabra</i>				X	
<i>Glycymeris geinitzii</i>				X	
inoceramid fragments		X		X	
<i>Inoceramus (Heroceramus) cf. hercules</i>			X		
<i>I. (Volviceramus) cf. koeneni</i>			X		
<i>I. (Platyceramus) sp.</i>			X		
<i>Limatula</i> sp.				X	
<i>Plagiostoma hoperi</i>			X		
<i>Rastellum diluvianum</i>	X	X	X	X	
<i>Amphidonte (Ceratostreon) reticulata</i>	X	X	X	X	
<i>Amphidonte ?(Ceratostreon) sigmoidea</i>	X	X	X	X	
<i>Vultogryphaea laciniata</i>	X	X	X	X	
<i>Gryphaeostrea canaliculata</i>	X	X	X	X	
<i>Pycnodonte (Phygraea) vesicularis</i>	X	X	X	X	
<i>Pycnodonte ?(Phygraea) proteus</i>	X	X	X	X	
<i>Hyotissa semiplana</i>	X	X	X	X	
<i>Camptonectes virgatus</i>			X		
<i>Neitheia regularis</i>		X	X	X	
<i>Syncyclonema haeggi</i>				X	
<i>Syncyclonema nilsoni</i>		X	X		
<i>Spondylus fimbriatus</i>		X			
<i>Pterotrigonia vaeliensis</i>					X
<i>? "Lucina" subnumismalis</i>					X
<i>Vetericardiella ?benedeni</i>					X
<i>Eriphyla cf. lenticularis</i>					X
<i>Crassatella arcacea</i>					X
<i>Granocardium cf. productum</i>					X
<i>?Mesocallista subovalis</i>					X
<i>Cyprimeria discus</i>					X
<i>Caestocorbula ?angustata</i>					X
fauna of GLIBERT		E	D	C-A	A

worked, suggesting that there was a mixture of allochthonous and autochthonous shells.

We use the terminology of STANLEY (1970) to describe the different modes of life.

The arcoidean *Glycymeris* and the palaeoheterodont *Pterotrigonia* probably were shallow burrowers (see STANLEY, 1978 for trigoniids). The same is probably true for most of the heterodont species, i.e. those belonging to the genera *Vetericardiella*, *Granocardium*, *Crassatella* (which is fairly similar to *Astarte*), *Cyprimeria* (perhaps comparable to recent *Cyclinella*), and *Caestocorbula*. *Lucina* may have burrowed more deeply.

The limoidean *Limatula* and the pectinoidean *Camptonectes* are supposed to have been byssally attached, the former perhaps nestling. Some species of *Camptonectes* - not belonging to the material from Lonzée - show small elongate ridges on the inner side of the anterior ear of the RV which, according to WALLER (pers. comm. 1991), is typical of byssus bearing pectinoideans (ctenolium).

An epifaunal, reclining mode of life is suggested for: the arcoidean *Cucullaea*, the three inoceramid species (*Pterioidea*), the pectinoideans *Neitheia* and the large *Syncyclonema* species, for large specimens of the ostreoid *Rastellum* and for the two *Amphidonte* species. The

limoidean *Plagiostoma* may also belong here. A kind of jumping-swimming mode cannot be totally excluded for the thin shelled *Syncyclonema haeggi* and *S. nilsoni*.

Apart from the above mentioned exceptions each of the eight oyster species lived cemented to each other, to shells of *Spondylus*, *Neithea*, *Inoceramus*, or to bryozoans or small sponges. Many attachment surfaces could not be identified with certainty, but thin cylindrical forms belonged to branching bryozoa and perhaps also to octocorallia. The only other cemented bivalve is *Spondylus fimbriatus* which is mostly found on shells of oysters (a more detailed description is given in MALCHUS *et al.*, in press).

Following STANLEY (1970) all species found at Lonzée should be regarded as suspension feeders. Representatives of deposit feeders - recent species belong to the Nuculoidea and Tellinoidea - have not been specifically identified but were present: poorly preserved casts of nuculids and tellinids have been found in several levels.

Recent counterparts or species which are morphologically similar to the burrowing Lonzée bivalves are characteristically found in shallow subtidal environments with a muddy to coarse sandy bottom, sometimes with sediment trapped by sea-grass, and low to moderately agitated waters. The sediment samples from Lonzée comprise a similar spectrum of grain sizes.

The most fossiliferous layers of the "argile inférieure" and "argile supérieure" contain sands with considerable quantities of medium to coarse quartz and glauconite. The

existence of reclining species suggests that water energies were not very high or at least not turbulent. This environment was probably either more protected or somewhat deeper than the oyster-facies with sponges, bryozoans (? and gorgonaceans) which represents a higher energetic, subtidal environment, probably situated closer to a rocky shore with cliffs and boulders below sea level (MALCHUS, *et al.*, in press).

Palaeobiogeography

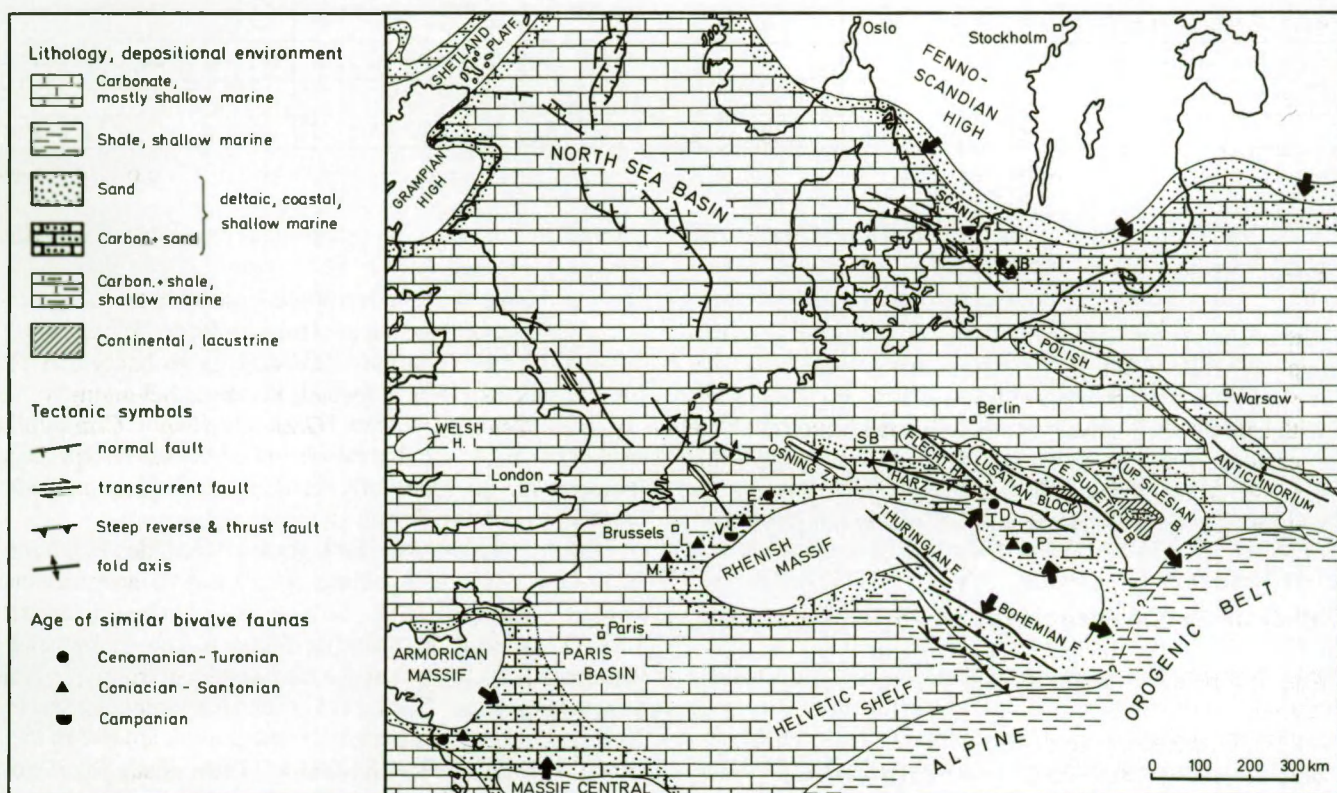
We attempt to compare the non-oyster fauna at Lonzée with other Upper Cretaceous faunas from Europe.

The details for oysters are given in MALCHUS *et al.* (in press).

Except for the inoceramids, most bivalve species from Lonzée are long-ranging, but sometimes ecologically restricted. Several of the Lonzée taxa are not known from white chalks but many are well known from Upper Cretaceous calcarenitic or sandy strata.

The strata at Lonzée are possibly mainly of Santonian age (see CHRISTENSEN, this volume).

MARLIERE (1954) considered the Cretaceous strata at Lonzée as a marginal facies of the Santonian "Craie de Trivières" from the Mons Basin. The "Craie de Trivières" - as many pure "white chalk" deposits - has yielded very few bivalve fossils, all of them from deeper shelf environments.



Text-fig. 3 — Palaeogeographical map for the Senonian-Danian of central Europe (after ZIEGLER, 1990). B - Bornholm; C - Commequiers; D - Dresden; E - Essen/Ruhr; J - Ifö; L - Lonzée; M - Mons; P - Prague; SB - Subhercynian Basin; V - Vaals.

Table 2

Qualitative comparison of the bivalve fauna from Lonzée with faunas from other areas, partially after personal research and partially after palaeontological literature: 1, Vendée, France: "Senonian" faunas; 2, Vaals-Aachen area, Lower Campanian; 3, Haltern, Westphalia, Germany: Lower Campanian faunas; 4, north western Harz and Braunschweig area, Harz, Germany: Coniacian-Santonian faunas; 5, eastern Harz and area near Quedlinburg in Sachsen-Anhalt, Salzberg Formation, Coniacian-Santonian; 6, Saxony, Germany: Turonian-Coniacian faunas; 7, "Bohemia", Czech Republic Turonian-Coniacian faunas; 8, Scania, Sweden: mainly Campanian; 9, Bornholm, Denmark: Coniacian-Santonian faunas; 10, Hochmoos Schichten, "Gosau", Austria: uppermost Santonian; 11, Maastricht Formation, near Maastricht, The Netherlands: Upper Maastrichtian; 12, Donbass (Campanian) and Crimea (Maastrichtian), The Ukraine.

SPECIES	LONZEE	1	2	3	4	5	6	7	8	9	10	11	12
<i>Cucullaea subglabra</i>	X		X	X	X	X	?	?	?	X	?	X	
<i>Glycymeris geinitzii</i>	X		X	X		X	?	?	?	?	?	X	
<i>Inoceramus (Heroceramus) hercules</i>	X									X			
<i>I. (Volviceramus) koeneni</i>	X					X	X			X			
<i>Limatula</i> sp.	X	X											
<i>Plagiostoma hoperi</i>	X		X	X	X	X	X	X	X	X		X	X
<i>Camptonectes virgatus</i>	X	X	X	X	X	X	X	X	X		X	X	X
<i>Neithea regularis</i>	X	X	X	X	X	X	X	X	X			X	X
<i>Syncyclonema haeggi</i>	X		X				X	X	X			X	
<i>Syncyclonema nilsoni</i>	X		?	?			?	?	X	?		X	
<i>Spondylus fimbriatus</i>	X	?	X		?		?	?	X			X	X
<i>Pterotrigonia vaelsiensis</i>	X	?	X	X		X	?	X		?		?	
" <i>Lucina</i> " <i>subnumismalis</i>	X		X		X		X	X	X	?			?
<i>Vetericardiella benedeni</i>	X		X										
<i>Eriphyla (Dozyia) lenticularis</i>	X		X		X	X	X	X	X			?	?
<i>Crassatella arcacea</i>	X		X		X	X	X	X	X		?	X	X
<i>Granocardium productum</i>	X		X	?	X	X	X	X	X		X	X	X
<i>Mesocallista subovalis</i>	X		X		X	X	X	?				X	
<i>Cyprimeria discus</i>	X		X				X	?	?		X	?	
<i>Caestocorbula angustata</i>	X										X		
number of species	20	5	16	8	10	11	16	15	13	8	7	14	8

The Mons Basin is a northerly extension of the Paris basin. But also there Santonian bivalve faunas seem limited. One of the better known of these faunas is found on the western margin of the basin - the Craie de Villedieu - to the north of Tours. It was studied by de GROSSOUVRE (1899) and more recently by JARVIS & GALE (1984). Between the Santonian Villedieu and Lonzée bivalve faunas there are almost no species in common; obviously the "chalks" at Villedieu and the sandy calcarenite at Lonzée represent two different environments.

FRENEIX & VIAUD (1985) described Santonian faunas from Vendée (Commequiers) found in shallow marine "Sables à Spongiaires" and "Marno-calcaires à Rudistes". These sediments partly represent a similar facies as at Lonzée. The generic composition of the Vendée faunas is comparable with those from Lonzée but few species are identical (Table 2, column 1): probably 5 species are common between the two regions, 4 of which are long ranging.

Outside the Paris Basin the fauna from Lonzée has been compared with:

1, the somewhat younger (Early Campanian) faunas

from the Vaalser Greensand near Aachen (Table 2, column 2); 16 species (i.e. 80 %) from Lonzée also occur near Aachen, but the inoceramids are different.

2, the Santonian faunas from Haltern, Westphalia, described by BEYENBURG (1937 and Table 2, column 3) contain 8 species (40 %) which also occur at Lonzée.

3, from the north western Harz region (Table 2, column 4) a large fauna was described by G. MÜLLER (1898), 10 species (50 %), including some short lived taxa from Lonzée, also occur there.

4, from the eastern Harz region from the Salzberg Formation near Quedlinburg, Sachsen-Anhalt (BRAUNS, 1875; G. MÜLLER, 1888, TRÖGER, unpublished data and Table 2, column 5) a similar fauna is known with 11 species (55 %) in common with Lonzée.

5, in Turonian - Coniacian strata in Saxony (ANDERT, 1934 and Table 2, column 6) 16 species (80 %) and in the Czech Republic (FRIC, 1877, 1883, 1889, 1893, 1897 and Table 2, column 7) 15 species (75 %) from Lonzée are also found.

6, in Campanian strata to the North, in Scania (Sweden) 13 species (65 %) occur also known from Lonzée

(HÄGG, 1930, 1935, 1947, 1954 and Table 2, column 8).

7, in Bornholm the Coniacian-Santonian (?) fauna contains only 8 of the species (40 %) found in Lonzée, including two of the short lived species - thought to be the same age but from a different environment (RAVN, 1921; TRÖGER & CHRISTENSEN, 1991 and Table 2, column 9).

8, the Tethyan Santonian "Gosau" fauna (Hochmoos Schichten) from Austria (ZITTEL, 1865-66; DHONDT, 1987 and Table 2, column 10) contains a similar fauna at generic level, but only 4 species which are certainly specifically identical.

9, in the Donbass (Campanian) and in the Crimea (Maastrichtian) 8 species known from Lonzée are also found but are long ranging taxa - of different age but from a similar environment (PASTERNAK *et al.*, 1968; KOCIUBYNSKI & SAVCZINSKAJA, 1974; SOBETSKI, 1977 and Table 2, column 12).

In MALCHUS *et al.* (in press) it has been shown that the distribution of the oyster taxa from Lonzée follows a very similar pattern.

Despite the limitations of such comparisons we would like to suggest that the bivalve faunas from Lonzée show strong affinities with those Late Cretaceous faunas of the European Temperate seas which are specific for shallow, littoral and fully marine environments, with a generally sandy sea bottom. The Lonzée faunas as far as we know them - bivalves and belemnites - suggest a direct marine connection with central and eastern Europe (compare CHRISTENSEN, this volume, fig. 1 and his concept "central European subprovince"). However, in belemnites and in bivalves mixed faunas containing elements from the central European and central Russian subprovinces have been found in Scania and Bornholm.

The faunistic data do not confirm the generally accepted idea that the "glauconie de Lonzée" was part of the Paris Basin. Whether these differences are purely generated by the environment or whether physical boundaries inhibited a westward distribution of the faunas remains open to speculation.

Taxonomy

The classification is mainly that used in the Bivalve volumes of the Treatise on Invertebrate Paleontology (MOORE, 1969 and STENZEL, 1971). In some cases, more recent publications offering approaches differing from the Treatise have been used. Thus, the supraspecific classification of pteriomorph bivalves generally follows WALLER (1978); species of the superfamily Ostreoidea are classified according to MALCHUS (1990); COOPER (1991) was consulted for the trigoniids.

Abbreviations:

C: convexity;

H: height;

L: length;

LV left valve;

PAMS: posterior adductor muscle scar (oysters);

R: rib number (*Limatula*, *Pterotrigonia*);

RV: right valve;

S: shell;

SLA: subligamental area (oysters);

UA: umbonal angle (pectinids).

BM (NH): British Museum (Natural History), London.

IG: "inventaire général" (collection n°), Institut royal des Sciences naturelles de Belgique, Brussels.

IRSNB MI: "Institut royal des Sciences naturelles de Belgique" Mesozoic Invertebrates, Brussels.

The definitions of C, H, L are in agreement with the Treatise (MOORE, 1969).

Measurements of C, H and L may refer to the right or left valve which will be indicated (RV, LV). Measurements of oysters normally refer to the left valve. In the case of oysters the terms 'small, medium and large' mean less than 50 mm, less than 100 mm and more than 100 mm in height respectively.

The term SLA was introduced by MALCHUS (1990) to describe a shelly solid fringe, adjacent to and anterior of the ligamental area in exogyne oysters.

Symbols used in the synonymy lists are:

* first valid use of the name.

. the author is certain that the reference applies to the species under discussion.

? doubt that the reference applies to the species under discussion.

pp pro parte

v vidi, vidimus

Phylum Mollusca

Class Bivalvia LINNÉ, 1758

Subclass Autobranchia GROBBEN, 1894

Superorder Prionodonta MACNEIL, 1937

Order Arcoidea STOLICZKA, 1871

Superfamily Arcoidea LAMARCK, 1809

Family CUCULLAEIDAE STEWART, 1930

Genus *Cucullaea* LAMARCK, 1801

Cucullaea subglabra (d'ORBIGNY, 1850)

Pl. 1, Fig. 1

- pp . 1837 *Arca glabra nobis* - GOLDFUSS, p. 148, pl. 124, fig. 1c.
- * 1850 *Arca subglabra*, d'Orb. - d'ORBIGNY, p. 244, n° 862.
- . 1889 *Cucullaea subglabra* d'Orb. - HOLZAPFEL, p. 206, pl. 22, figs. 3, 5.
- ? 1898 *Cucullaea subglabra* d'Orb. - G. MÜLLER, p. 51, pl. 7, figs. 7, 8.
- ? 1934 *Cucullaea subglabra* d'Orb. - ANDERT, p. 219, pl. 11, figs. 26 - 28.
- ? 1943 *Cucullaea subglabra* d'Orbigny - VAN DER WEIJDEN, p. 34, pl. 1, figs. 16, 17.
- 1956 *Cucullaea* (*Cucullaea*) *subglabra* d'Orbigny - VAN DE POEL, p. 7, pl. 1, fig. 1 (with synonymy).

MATERIAL: One incomplete, silicified valve from the "argile supérieure" IG 11039, IRSNB MI 10571.

DESCRIPTION: see VAN DE POEL (1956).

DISCUSSION: The hinge (Pl. 1, Fig. 1) leaves no doubt as to the identification of the specimen, which we compare with that figured in VAN DE POEL (1956). We refer to the same paper for the discussion of the synonymy of *Cucullaea subglabra*.

DISTRIBUTION: *Cucullaea subglabra* is only known from coarse sediments of Santonian-Campanian age, in NW Europe.

Superfamily Limopsoidea DALL, 1895
Family GLYCYMERIDAE NEWTON, 1922
Genus *Glycymeris* DA COSTA, 1778

Glycymeris geinitzii (d'ORBIGNY, 1850)

- . 1837 *Pectunculus sublaevis* Sow. - GOLDFUSS, p. 160, pl. 126, fig. 3. (non *sublaevis* J. de C. SOWERBY, 1824, p. 112).
- ? 1843 *Pectunculus sublaevis* Sow - GEINITZ, p. 14, pl. 2, figs. 19-21.
- * 1850 *Pectunculus Geinitzii*, d'Orb. - d'ORBIGNY, p. 196, n^o 132.
- . 1889 *Pectunculus Geinitzii* d'Orb. - HOLZAPFEL, p. 210, pl. 23, figs. 11, 12; pl. 24, figs. 1-10.
- ? 1934 *Pectunculus geinitzi* d'Orb. - ANDERT, p. 233, pl. 11, figs. 36 - 38, text-figs. 22, 23.
- ? 1943 *Pectunculus geinitzi* d'Orbigny - VAN DER WEIJDEN, p. 38, pl. 1, fig. 22; pl. 2, figs. 1, 2.
- 1956 *Glycymeris geinitzii* (d'Orbigny) - VAN DE POEL, p. 14 (with synonymy).

MATERIAL: Two incomplete, silicified valves from the "argile supérieure" IG 11039.

DESCRIPTION: see VAN DE POEL (1956).

DISCUSSION: GOLDFUSS (1837) considered specimens from Santonian - Campanian outcrops (Aachen and Quedlinburg) as belonging to an Aptian - Albian species described from England (see WOODS, 1899, p. 67). In 1850 d'ORBIGNY rightly thought that the GOLDFUSS Upper Cretaceous material was different from the Lower Cretaceous species and gave it a new name, *Pectunculus geinitzii*.

Many of the Cretaceous glycymeridids mentioned in palaeontological literature are based on steinkern material and specifically unidentifiable. Therefore we have restricted the synonymy list to references of which we were reasonably certain.

DISTRIBUTION: *Glycymeris geinitzii* has been recorded from Coniacian to Campanian of NW and central Europe.

Superorder Pteriomorphia BEURLIN, 1944
Order Pterioda NEWELL, 1965
Suborder Pteriina NEWELL, 1965
Superfamily Pterioidea GRAY, 1847
Family INOCERAMIDAE ZITTEL, 1881
Genus *Inoceramus* J. SOWERBY, 1814
Subgenus *Heroceramus* HEINZ, 1932

Inoceramus (Heroceramus) cf. hercules (HEINZ, 1932)

Compare:

- p. 1912 *Inoceramus Lamarcki* var. *Cuvieri* Sow. - WOODS, p. 323, text-figs. 82, 83.
- * 1932 *Heroceramus hercules* Heinz - HEINZ, p. 9.
- . 1984 *Inoceramus (Heroceramus) hercules* Heinz - TRÖGER, p. 47, pl. 1, fig. 4; pl. 2, figs. 1, 2.
- 1991 *Inoceramus (Heroceramus) cf. hercules* Heinz - TRÖGER & CHRISTENSEN, p. 30, pl. 1, fig. 17; pl. 3, fig. 4.

MATERIAL: Among the large inoceramid fragments from Lonzée some hinges have been preserved. From IG 4704 (exploration Musée 1881) a fairly complete hinge.

DESCRIPTION: This obviously large inoceramid species is represented by strong hinges.

Hinge with dentition (H of "teeth" = 12 mm); shell thickness on the valve 7 - 9 mm.

DISTRIBUTION: *Inoceramus (Heroceramus) hercules* has been reported from the Upper Turonian - basal Coniacian (Zones 18-21 of TRÖGER, 1989). At Lonzée the material is obviously transported.

Subgenus *Volviceramus* STOLICZKA, 1871.

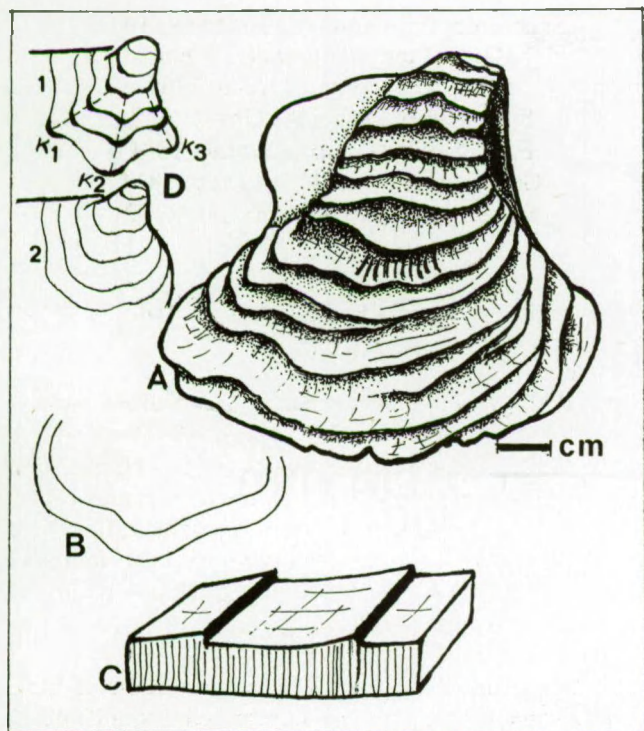
Inoceramus (Volviceramus) cf. koeneni G. MÜLLER, 1888

Pl. 1, Fig. 7, Text-figs. 4, 5.

Compare:

- * 1888 *Inoceramus (Volviceramus) Koeneni* n. sp. - G. MÜLLER, p. 412, pl. 17, fig. 1.
- . 1969 *Inoceramus koeneni* G. MÜLLER - TRÖGER, p. 69, text-figs. 1 - 8, pl. 1, figs. 1 - 6; pl. 2, figs. 1 - 5 (with synonymy).
- 1991 *Inoceramus (Volviceramus) koeneni* Müller - TRÖGER & CHRISTENSEN, p. 31, pl. 2, figs. 2, 3; pl. 3, fig. 7.

MATERIAL: One specimen, internal side of right valve and positive cast hereof; coll. Mourlon IG 5793, IRSNB MI 10577 from Lonzée. (The sediment of this specimen is somewhat different from the material of IG 11039; an attempt at dating it from its coccolith content by E.



Text-fig. 4 — A - *Inoceramus (Volviceramus) cf. koeneni* G. MÜLLER, from Lonzée. B - Shape of the undulations of *I. (Volviceramus) cf. koeneni* G. MÜLLER. C - Shell structure of *I. (Volviceramus) cf. koeneni* G. MÜLLER. D - 1: *I. (Cordiceramus) cordiformis* J. de C. SOWERBY (k1, k2, k3 corners); 2: *I. (Volviceramus) koeneni* G. MÜLLER.

Steurbaut was not conclusive: the sample contained only post-Cenomanian long-ranging taxa).

DIMENSIONS: Ratios Na/Ha, Vo/ Ha and the distances between the undulations are shown on Text-Fig. 4

DESCRIPTION: Right valve. Internal side of the valve with incomplete shell and positive cast of this valve. Small parts of the umbonal region, of the wing, and of the posterior and ventral margin are missing. Shape nearly trigonal, strongly involute, with concave anterior margin. Umbo bent towards the anterior margin. Growth axis opisthocline. Concentric undulations or rugae ("Anwachswellen" of R. HEINZ, 1928) with a rounded pentagonal course. Radial depression which follows the direction of the growth axis. On the exterior, small radial grooves can be seen between the undulations (see Text-Fig. 4, A).

DISCUSSION: For the Na/Ha and Vo/Ha ratios (Text-Fig. 5) the specimen from Lonzée is similar to *Inoceramus (Volviceramus) koeneni* (Pl. 1, Fig. 9). The figure of the holotype of *I. (V.) koeneni* shows a small radial depression which results in pentagonal-like shape of some undulations. Radial grooves on the interior cast have

also been mentioned in the original description of *I. (Volviceramus) koeneni*.

The pentagonal shape of the undulations of the specimen from Lonzée is also very similar to those of *I. (Cordiceramus) cordiformis* J. de C. SOWERBY, 1823 (Pl. 1, Fig. 10), but the corners k1, k2, k3, typical of the cordiceramid species, are lacking. An exact specific identification of the Lonzée specimen is impossible because the left valve and small parts of the umbo are not preserved. As far as can be ascertained from the available material the specimen from Lonzée is nearer to *I. (Volviceramus) koeneni* than to *I. (Cordiceramus) cordiformis*.

DISTRIBUTION: *Inoceramus (Volviceramus) koeneni* has its acme in the Middle Coniacian (Zones 22-23 of TRÖGER, 1989) (Coniacian).

Subgenus *Platyceramus* HEINZ, 1932

Inoceramus (Platyceramus) sp.

MATERIAL: Many fragments (IG 11039) of very large inoceramids, especially in the "sables entre les deux argiles". Part of the very fragmentary material has been reconstructed, suggesting an incomplete large inoceramid [H: (520) mm], which probably belongs to a platyceramid species.

DISCUSSION: Most of the inoceramid parts from Lonzée are too fragmentary to be identified specifically.

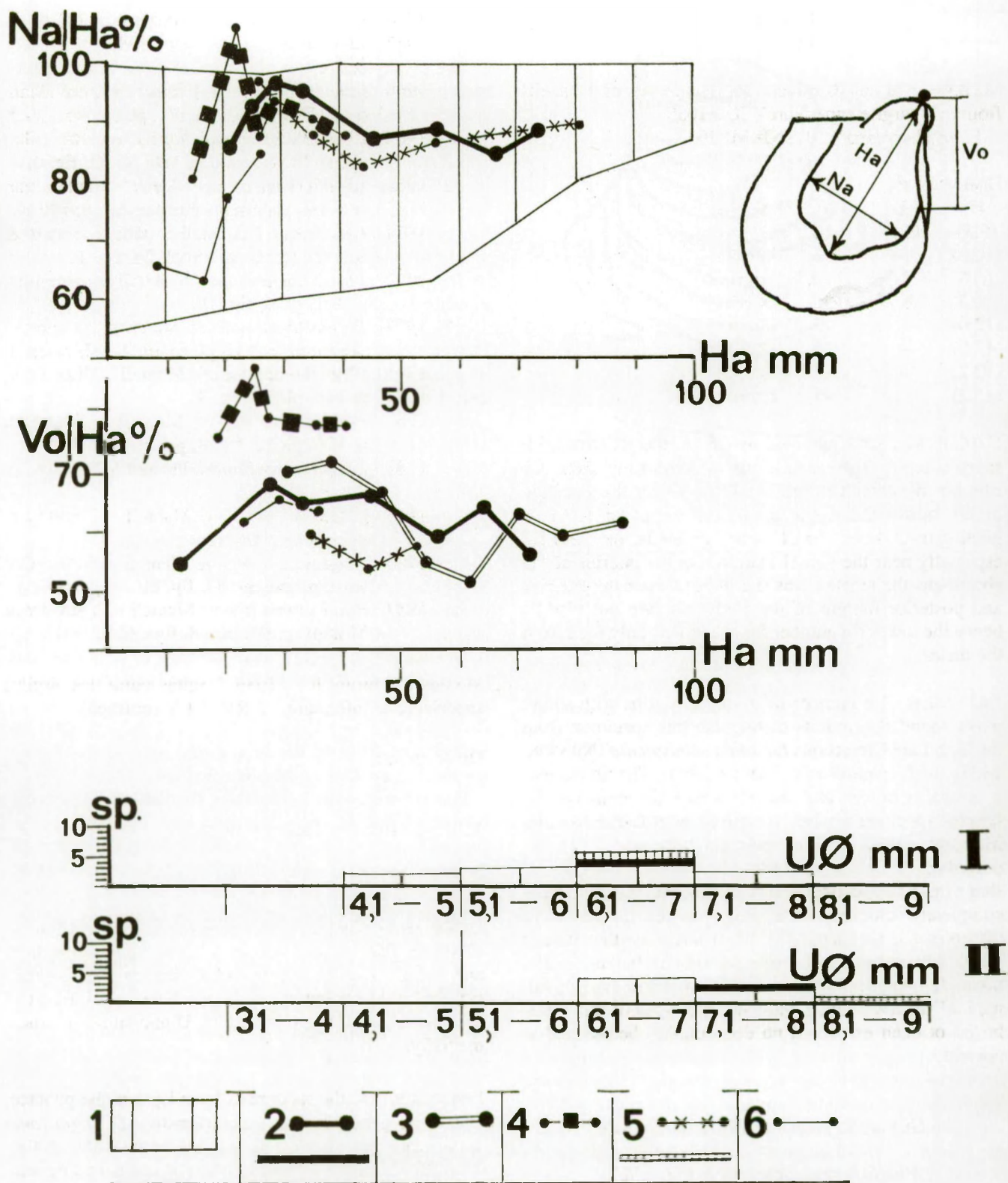
Furthermore, some of the thick shelled (shell thickness between 5 and 15 mm) fragments may belong to platyceramid species, but others could be from specimens of the large species *I. (Heroceramus) cf. hercules* (HEINZ, 1932).

Large platyceramids of Coniacian-Santonian age are known: examples:

— *Pl. platinus* (LOGAN, 1898) from the Niobrara (Santonian to lowermost Campanian, see also in SCOTT *et al.*, 1986, p. 18, fig. 12i) of the Western Interior of the USA); — *Pl. mantelli* de MERCEY, 1874 (*sensu* BARROIS, 1879) from the Coniacian - Santonian of Europe (*vide* SEITZ, 1961) and Japan (NODA & TOSHIMITSU, 1990).

The very incomplete reconstructed specimen from Lonzée shows a probable affinity with the equally reconstructed specimen figured by BARROIS (1879, pl. 4, fig. 1) from more or less coeval strata at Lézenne (near Lille, Nord, France). However, the Lonzée specimen lacks the hinge region and even an only tentative specific identification is not possible for it.

Order Limoida WALLER, 1978
Superfamily Limoidae RAFINESQUE, 1815
Family LIMIDAE RAFINESQUE, 1815
Genus *Limatula* WOOD, 1839



Text-fig. 5 — Ratios Na/Ha , Vo/Ha and average distances of the undulations (sp.= specimen) at 30-50 mm distance (I) and 50-70 mm distance (II) from the umbo in: 1 - population of 10 specimens of *Inoceramus (Volviceramus) koeneni* G. MÜLLER, from its type-locality; 2 - *I. (Volviceramus) cf. koeneni* G. MÜLLER, from Lonžée; 3. *I. (Volviceramus) koeneni* G. MÜLLER, holotype, Vo and Ha measured on the figure in G. MÜLLER, 1888, pl. 17, fig. 1. 4. *I. (Cordiceramus) cordiformis* J. de C. SOWERBY, specimen BM (NH) L 64247 (figured in WOODS, 1911, pl. 14, fig. 3); 5. *I. (Cordiceramus) cordiformis* J. de C. SOWERBY, holotype BM (NH) 43277; 6. *I. (Cordiceramus) cordiformis* J. de C. SOWERBY, Middle Santonian, Salzberg at Quedlinburg (Germany).

Limatula sp.

Pl. 1, Fig. 2.

MATERIAL: About 10 valves, mainly interiors of the shells from the "argile supérieure" IG 11039.

Figured specimen: IRSNB MI 10573.

DIMENSIONS:

H	L	R	Valve
(9.5)	(6.2)	18	exterior
(10.5)	—	13	interior
10.5	7.6	16	exterior
11.3	8.7	16	exterior
(12.0)	—	13	interior
(12.0)	—	14	interior
(12.2)	—	14	interior
(13.2)	—	11	interior

DESCRIPTION: Characterised by 15-18 unequal ribs with sharp summits all placed in the middle of the shell: the ribs on the areas are less developed than those in the middle of the rib field; areas smooth except for commarginal growth lines; small spines or knobs on the ribs, especially near the pallial margin. On the interior of the specimens the smaller ribs (i.e. those nearer the anterior and posterior margin of the shell) ribs are not visible; hence the lower rib number for specimens only seen from the inside.

DISCUSSION: Rib number relatively low; ribs with sharp, never rounded, summits distinguish this specimen from the high Late Cretaceous *Limatula semisulcata* (NILSSON, 1827) and *L. wintonensis* (WOODS, 1904). The rib number is probably lower and the rib shape different on the Lonzée specimens, when compared with *L. kunradensis* MARQUET, 1982. *L. oviformis* (J. MÜLLER, 1851), re-described by HOLZAPFEL (1889) seems to be narrower in shape than the specimens from Lonzée and furthermore is completely covered with riblets as in *L. decussata* (MÜNSTER in GOLDFUSS, 1835). It might be that further study will prove the Lonzée specimens belong to the taxon *L. orbigny* FRENEIX, 1985, from the Early "Senonian" of SW France, but since the types of this taxon have not been examined no decision can be reached at present.

Genus *Plagiostoma* J. SOWERBY, 1814

Plagiostoma hoperi MANTELL, 1822

Pl. 1, Fig. 3.

- * 1822 *Plagiostoma Hoperi* - MANTELL, p. 204, pl. 26, figs. 2, 3, 15.
- v. 1904 *Lima (Plagiostoma) Hoperi*, Mantell - WOODS, p. 17, pl. 4, figs. 7 - 12 (with synonymy).
- . 1932 *Lima (Plagiostoma) hoperi* Mantell - WOLANSKY, p. 20, pl. 3, fig. 2.

1934 *Lima hoperi* Mant. - ANDERT, p. 145.

1947 *Lima (Plagiostoma) hoperi* Mantell - HÄGG, p. 66.

- . 1968 *Lima (Plagiostoma) hoperi hoperi* (Mantell) - PASTERNAK, p. 179, pl. 37, figs. 3 - 5.
- v. 1968 *Lima (Plagiostoma) hoperi sowerbyi* (Geinitz) - PASTERNAK, p. 180, pl. 37, fig. 6.
- ? 1968 *Lima (Plagiostoma) hoperi* Mantell var. *bistriata* Lahusen - PASTERNAK, p. 180.
- . 1974 *Lima hoperi* Mantell - KOCIUBYNSKI & SAVCZINSKAJA, p. 95, pl. 28, fig. 11.
- v. 1977 *Plagiostoma hoperi* Mantell - SOBETSKI, p. 101, pl. 6, fig. 18.
- v? 1977 *Plagiostoma naidini* Sobetski, sp. nov. - SOBETSKI, p. 105, pl. 6, fig. 21; pl. 7, fig. 1.
- ? 1981 *Plagiostoma hoperi* Mantell - TZANKOV, p. 118, pl. 52, fig. 9.
- v. 1982 *Plagiostoma hoperi* Mantell - SOBETSKI, p. 124, pl. 12, fig. 8; pl. 32, figs. 1, 2.
- v. 1982 *Plagiostoma hoperi* Mantell - DHONDT, p. 89, pl. 4, fig. 1.
- v. 1985 *Plagiostoma hoperi* Mantell - DHONDT, p. 49.
- . 1986 *Plagiostoma hoperi* Mantell - ABDEL-GAWAD, p. 161, pl. 37, fig. 8.
- v. 1987 *Plagiostoma hoperi* Mantell - CLEEVELY & MORRIS, p. 93, pl. 18, figs. 6, 7.

MATERIAL: From IG 11039 "Sable entre les argiles supérieure et inférieure" 2 RV, 1 LV (crushed)

DIMENSIONS:

n°	H	L	Valve
11039-1	16.8	19.2	R
10573	(21.7)	22.3	R

DESCRIPTION: Small to average-sized, suborbicular to subovate *Plagiostoma*-species, valves wider than high and mainly smooth; slight radial ribs on the posterior side and light commarginal growth lines over the rest of the valves; small anterior auricle. Umbo situated almost medially.

DISCUSSION: On the specimens from Lonzée the punctae, which are generally very characteristic of *Plagiostoma hoperi*, are not visible. *Pl. cretaceum* (WOODS, 1904), from the Turonian - Maastrichtian of southern England, is very close to *Pl. hoperi* but is covered by many flat-topped ribs and generally has a narrower umbonal angle.

DISTRIBUTION: *Plagiostoma hoperi* has been recorded from Lower Turonian to Maastrichtian beds in Eurasia. It is more common in white chalks of northern and western Europe than in coarser deposits, but is also known from southern European chalks such as those from the Charente and from Crimea.

Order Ostreoida FÉRUSAC, 1822
 Suborder Ostreina FÉRUSAC, 1822
 Superfamily Ostreioidea RAFINESQUE, 1815
 Family PALAEOLOPHIDAE MALCHUS, 1990

Genus *Rastellum* FAUJAS-SAINT-FOND, ? 1799 (1802)

DIAGNOSIS: Sub-equivalve, sickle- to plate-shaped, convex posterior flank always steep, concave anterior flank steep only in sickle-shaped forms, completely ribbed, ribs medium to coarse, simple, dichotomising from keel, long spines in sickle-shaped forms sometimes developed (*Arctostrea* type), shell margin strongly plicate, at least anteriorly; PAMS postero-dorsal, large, comma-shaped; chomata pustules to short laths in some *Arctostrea* "forms", are accumulated postero-dorsally and ventrally, forming a single row at anterior and posterior margins and sometimes surrounding the entire inner margin; broader shaped specimens (*Rastellum* type) sometimes with long (up to 5 mm) lath chomata; microstructure of shell with many, mostly large, chambers, partly filled with chalky material ('mocret' sensu MALCHUS, 1990).

REMARKS: In contrast to MALCHUS (1990) the diagnosis given here includes pustule chomata as a characteristic for specimens of the *Arctostrea* type [specimens IG 5496, from the ? Cenomanian at Gussignies (Nord, France)].

Rastellum diluvianum (LINNAEUS, 1767)
 Pl. 2, Fig. 3, 5 - 8; Pl. 5, Fig. 4, 12 - 15.

- * 1767 *Ostrea diluviana* - LINNAEUS, p. 1148.
- . 1827 *Ostrea diluviana*, Linn. - NILSSON, p. 32, pl. 6, figs. 1a-c, 2.
- ? 1827 *Ostrea pusilla* NILSSON, p. 32, pl. 7, fig. 11a-c
- 1894 *Ostrea diluviana* L. - LUNDGREN, p. 36.
- . 1897 *Ostrea diluviana*, Linné - HENNIG, p. 16, pl. 2, figs. 1, 2 and 5.
- . 1898 *Ostrea diluviana* L. - G. MÜLLER, p. 12, pl. 2, figs. 1-3.
- v. 1912 *Ostrea diluviana*, L. - WOODS, p. 342, text-figs. 98-138 (with synonymy).
- 1930 *Ostrea diluviana* Linné - HÄGG, p. 45.
- 1938 *Ostrea diluviana* Linné - CARLSSON, p. 10.
- 1947 *Ostrea diluviana* Linné - HÄGG, p. 79.
- 1954 *Ostrea diluviana* Linné - HÄGG, p. 44.
- v. 1977 *Rastellum* (*Arctostrea*) *pectinatum* (Lamarck) - SOBETSKI, p. 136, pl. 9, fig. 2.
- v. 1977 *Rastellum* (*Arctostrea*) *deshayesi* (Fischer de Waldheim) - SOBETSKI, p. 136, pl. 9; fig. 3, pl. 10, fig. 2.
- . 1982 *Lopha diluviana* (Linné) - GRÜNDEL, p. 157, pl. 4, figs. 6-10.
- . 1982 *Rastellum* (*Arctostrea*) *carinatum* (La-

marck) - GRÜNDEL, p. 158, pl. 3, figs. 12-13, pl. 4, figs. 1-5.

- . 1982 *Rastellum* (*Arctostrea*) *pusillum* (Nilsson) - GRÜNDEL, p. 159, pl. 5, fig. 1.
- . 1985 *Rastellum* (*R.*) *gracilis* (Dujardin) - FRENEIX & VIAUD, p. 203, pl. 2, figs. 13-16.
- . 1985 *Rastellum* (*R.*) *frons* (Parkinson) - FRENEIX & VIAUD, p. 203, pl. 2, fig. 17.
- . 1986 *Rastellum* (*Rastellum*) *diluvianum* (Linné) - FRENEIX & VIAUD, p. 50, pl. 6, fig. 2a, b, 3.
- . 1986 *Rastellum* (*Rastellum*) *gracile* (Dujardin, 1837) - FRENEIX & VIAUD, p. 52, pl. 6, figs. 5 - 9.

MATERIAL: More than hundred large specimens, mostly worn, and hundreds of small specimens (mostly RV); IG 4704, 9340, 10511, 11039.

DESCRIPTION: Species large (H max. 124 mm), shell thick, up to 50 mm at posterior margin; shape broad, oval, weakly crescentic shaped, posterior flank weakly inclined, posterior flange often developed, attachment area often occupying entire posterior flank.

Ligamental area broad, straight to strongly opisthogyrate, posterior shell margin not always plicate, lath chomata may surround inner shell margin.

Tiny specimens attributed to this species do not exceed 20 mm in height; attachment area small; pattern of plicae as in large specimens, though more numerous with respect to size: 15-20 instead of 12-23; small lath chomata along entire inner shell margin.

Shell structure: larger specimens strongly chambered, small specimens with a shell thickness of 1 to 2 millimetres only with low angle cross foliation, no chambers (see Pl. 5, Figs. 13 & 14) and irregular complex cross foliation.

DISCUSSION: The interpretation of the Linnean species "*Ostrea diluviana*" has led to numerous, often conflicting views in palaeontological literature. The many morphotypes under which *Rastellum* taxa occur has resulted in a plethora of names for Cretaceous forms. It is outside the scope of this paper to discuss this problem in detail. A discussion of the probable variation of this group has been given in WOODS (1913). Generally we agree with the interpretation of WOODS, following which most *Rastellum* taxa from European Cretaceous strata belong to *R. diluvianum* (L., 1767). The specimens from Lonzée have a morphology [common in faunas from coarse sediments, see MALCHUS *et al.* (in press)] which closely resembles that of the Swedish specimens described by NILSSON (1827) and HENNIG (1897), and is probably also the same as that of the specimen described by LINNAEUS (1767). Hence, even though applying a narrow typological species concept, the name *R. diluvianum* is undoubtedly correct for the specimens from Lonzée.

It is suggested here that the small specimens - named *R. pusillum* (NILSSON, 1827) or *R. gracile* (DUJARDIN, 1837) (see synonymy) - are only young representatives of *R. diluvianum*. They occur very often in the same strata

and it seems strange that small, i.e. young, specimens of *R. diluvianum* had never been described previously.

Small shells may resemble small *Hyotissa semiplana* (J. de C. SOWERBY, 1825) but these pycnodonteine oysters have a circular muscle scar and larger and more crowded lath chomata. Additionally, their shell structure is vesicular (compare Pl. 6, Fig. 3).

Larger specimens of *Amphidonte* (*Ceratostreon*) *reticulata* (REUSS, 1846; see below) are sometimes very similar to large and worn shells of *Rastellum diluvianum*. However, in *A. (Ceratostreon) reticulata* the anterior ribs meet the shell margin at a more oblique angle and the ribs do not cause a very strong plication of the free margin; also the spiral coiling of the umbo is generally stronger than in *Rastellum diluvianum*.

DISTRIBUTION: *Rastellum diluvianum* is known from ? Valanginian to Maastrichtian, and is very widely distributed in Europe and North America.

Family GRYPHAEIDAE VIALOV, 1936

Subfamily EXOGRYINAE VIALOV, 1936

Tribe Nanogyriini MALCHUS, 1990

Genus *Amphidonte* FISCHER de WALDHEIM, 1829

Subgenus *Ceratostreon* BAYLE, 1878 (ex genere *Ceratostreon*, see MALCHUS, 1990)

***Amphidonte (Ceratostreon) reticulata* (REUSS, 1846).**

Pl. 3, Figs. 4, 6, 10.

- ? 1821 *Ostracites auricularis* - WAHLENBERG, p. 58 (fide HÄGG, 1954, syn. of '*Ostrea conica*').
- ? 1827 *Chama haliotoidea* Sow. - NILSSON, p. 28, pl. 8, figs. 3a-d.
- v. 1833 *Exogyra haliotoidea* Sow. - GOLDFUSS, p. 38, pl. 88, figs. 1a-d. (non *Chama haliotoidea* J. SOWERBY, 1813)
- ? 1833 *Exogyra auricularis* - GOLDFUSS, p. 39, pl. 88, figs. 2a, b (non fig. 2d = *Exogyra planospirites* GOLDFUSS, 1833 = ? *Vultogryphaea laciniata* (NILSSON, 1827)).
- * 1846 *Exogyra reticulata* - REUSS, p. 44, pl. 27, fig. 8.
- 1846 *Exogyra haliotoidea* Sowerby - REUSS, p. 44, pl. 27, figs. 5, 9, 10; pl. 31, figs. 8, ? 9, 10.
- ? 1846 *Exogyra squamula* - REUSS, p. 45, pl. 27, figs. 6, 7.
- pp ? 1889 *Exogyra auricularis* Wahlenb. - HOLZAPFEL, p. 255, pl. 29, fig. 11a, b (non fig. 10a, b ? = *Vultogryphaea laciniata auctorum*).
- ? 1889 *Exogyra* sp. - HOLZAPFEL, p. 255, pl. 29 fig. 8a, b, 9a, b.
- ? 1894 *Ostrea auricularis* Wahlenberg - LUNDGREN, p. 38.
- 1898 *Exogyra haliotoidea* Sow. - G. MÜLLER, p. 16, fig. 3.

- . 1911 *Exogyra haliotoidea* Sow. - FRIC, p. 47, fig. 211.
- . 1911 *Exogyra reticulata* Reuss - FRIC, p. 47, fig. 213.
- ? 1938 *Ostrea conica* Sowerby - CARLSSON, p. 13.
- ? 1947 *Ostrea conica* (Sowerby) - HÄGG, p. 78
- ? 1954 *Ostrea conica* (Sowerby) - HÄGG, p. 44.
- . 1965 *Exogyra reticulata* Reuss - ZARUBA, p. 151, pl. 1, figs. 1-5.
- . 1982 *Ceratostreon* (n. sg.?) *reticulata* (Reuss, 1846) - GRÜNDEL, p. 144, pl. 2, figs. 1-8; pl. 3, fig. 1.
- . 1982 *Ceratostreon* (n. sg.?) *haliotoidea* (Sowerby, 1813) - GRÜNDEL, p. 147, pl. 3, figs. 2-5; pl. 4, fig. 1.

MATERIAL: Hundreds of valves, many fragmentary; IG 11039.

DESCRIPTION: Size medium (H max. 71 mm); auricular, sometimes round; anterior flank of LV steep, angle often exceeding 90° (measured exteriorly between flank and attachment surface of shell), posterior flank often completely attached; radial ribs often present on anterior flank, then plicating the steep commissural shelf, no ribs on posterior; anterior flank with chomatal radial striae (relict chomata), often also visible on posterior flank; RV similar, anterior flank less high than on LV, consisting of narrow band of upright growth lamellae, with many regular short relict lath chomata; coiling of LV umbo amphidontinid with coiling axis nearly normal to commissural plane; attachment area of large specimens occupy all of posterior flank, growth lamellae of RV anteriorly with narrow band of reticulate pattern (often eroded in older specimens).

SLA (subligamental area) sickle-shaped, not large, contains elongated socket; lath chomata all around inner shell margin, anteriorly short, posteriorly elongated, often disintegrated into rows of shorter laths; PAMS large, oval, dorsal sinus weak or biconcave, long axis nearly parallel to posterior shell margin.

Small, young specimens (less than 30 mm in height) have much smaller attachment areas; their outline is round to oval (instead of ear shaped) and the characteristic biconcave shape of the PAMS is not yet developed.

NOMENCLATORIAL NOTE: WOODS (1913, p. 407) already pointed out that *Chama haliotoidea* J. SOWERBY, 1813 represents a morphotype of '*Exogyra*' *conica* (SOWERBY, 1813) with a large attachment area; ['*E.*' *conica* has as valid senior synonym *Rhynchostreon (Laevigyra) obliquatum* (PULTENEY, 1813) (see also COX, 1940). The assignment of the species to *Rh. (Laevigyra)* follows MALCHUS (in press). There is, however, disagreement about the correct genus or subgenus (see DHONDT, 1985; FRENEIX & VIAUD, 1986; MALCHUS, 1990). Detailed discussion of this matter is outside the scope of the present paper].

Because "*Chama haliotoidea*" SOWERBY, 1813 cannot

be applied to the taxon for which it has traditionally been used causes some problems when naming the numerous specimens from Lonzée. ? *Amphidonte* (*Ceratostreon*) *auricularis* WAHLENBERG, 1821, from Sweden, could be the next available name, but WAHLENBERG did not figure a specimen as far as we know (we were unable to see a copy of WAHLENBERG's paper). Among the later workers on Swedish bivalves, only NILSSON (1827) has figured a '*Chama halioidea*' and placed it into the synonymy of the WAHLENBERG species. NILSSON's figures appear very similar to the specimens from Lonzée, but they could equally represent *A. (C.) plicifera* (DUJARDIN, 1837) that occurs at Maastricht. Unfortunately, part of the collections of NILSSON (1827), HENNIG (1897) and HÄGG (1930, 1935, 1947, 1954) seem to be lost.

GOLDFUSS (1833) figured three specimens under the name '*Exogyra auricularis* WAHLENBERG'. Again those from Sweden (pl. 88, fig. 2a, b - GOLDFUSS Coll. 553 a, b, Museum Univ. Bonn, Germany) are identical with the Lonzée specimens and are stated to come from "Schonen" (= Scania). The third figured specimen (GOLDFUSS, pl. 88, fig. 2d) is stated to be from Maastricht, but cannot be found to-day in the GOLDFUSS Coll.). After comparing that figure with other specimens from Maastricht (from the IRSNB coll.) we came to the conclusion that on pl. 88, fig. 2d, GOLDFUSS figured a right valve of *Vultogryphaea laciniata* NILSSON, 1827.

It should be added that '*Exogyra planospirites*' of GOLDFUSS (pl. 88, fig. 3, GOLDFUSS Coll. 554) also belongs to *V. laciniata*. Similar specimens have also been figured in STENZEL (1971: fig. J96, 2a, b, 3) under the name '*Planospirites ostracina* LAMARCK, 1801' (see nomenclatorial note on *Vultogryphaea laciniata*, p. XXX).

Obviously it is not clear which species "*Ostracites auricularis*" WAHLENBERG represents and it seems sensible not to use the name "*auricularis*". Therefore we decided to use the next available species name "*Exogyra reticulata*" REUSS, 1846, which is fairly well illustrated and described by REUSS.

DISCUSSION: *Amphidonte* (*Ceratostreon*) *reticulata* shows all the characteristics of the subgenus including the plication of the steep anterior free margin (= commissural shelf). Growth tracks of the plicae are seen as more or less strong ribs on the flank (in LV). This feature is developed in most specimens and is also present in those from Saxony and Bohemia.

Such plicate forms have generally been attributed *A. (C.) 'halioidea'* (SOWERBY, 1813). But neither SOWERBY (1813, 1827) nor WOODS (1913) described or figured morphotypes with a plicate margin. We therefore think that the specimens under consideration here are specifically different. Our specimens differ even more from typical *Rhynchostreon* (*Laevigyra*) *obliquatum* (PULTENEY).

GRÜNDEL (1982) made morphometric measurements of *A. (C.) reticulata* and *A. (C.) 'halioidea'*. His measurements (p. 145; tab. 3.1) show that the average size of *A.*

(*C.*) *reticulata* is significantly smaller than that of *A. (C.) 'halioidea'* and from the text one can conclude that he separated these two 'species' according to their size and to the existence of a reticulate band which is normally much better developed in small specimens (i.e.: "*reticulata*"). In our view GRÜNDEL's statistical results are strongly biased and based on artificial separation. As shown above for *Rastellum diluvianum*, *A. (C.) reticulata* seems to be a small species whereas *A. (C.) 'halioidea'* from the same locality seems to lack small (young) representatives; but both taxa occur in the same environment.

Specimens from Lonzée show that the reticulate band is progressively eroded until it finally disappears in larger shells. Very probably this is also the case in GRÜNDEL's material. The fact that the collection from Saxony contains an overwhelming predominance of right valves suggests that the shells were transported (as is also the case at Lonzée). Thus, it seems probable that the two taxa represent simply different ontogenetic stages of the same species. GRÜNDEL's statement that left valves are not ribbed is incorrect as such ribbing is visible in his figures (pl. 3, figs. 5, 6 and pl. 4, fig. 1). It may be noted that what he described as 'Rippchen', 'feine radiale Kerbung' or 'fein senkrecht gekerbt' are respectively lath chomata or their growth traces (relict lath chomata).

Left valves of small individuals at Lonzée are difficult to separate from young *Vultogryphaea laciniata* specimens. But small right valves normally differ from *V. laciniata* by the presence of their reticulate band. Further, small right valves of *V. laciniata* normally do not show a plicate commissure.

DISTRIBUTION: *Amphidonte* (*Ceratostreon*) *reticulata* occurs in Late Cenomanian to Late Santonian, (? Campanian in Sweden); west and central Europe [Czech Republic, Germany (Saxony, Westphalia), Belgium].

Amphidonte ?(*Ceratostreon*) *sigmoidea* (REUSS, 1844)
Pl. 3, Fig. 7, 9.

- * 1844 *Exogyra sigmoidea* - REUSS, p. 180.
- . 1846 *Exogyra sigmoidea* Reuss - REUSS, p. 44, pl. 27, figs. 1-4.
- 1887 *Exogyra sigmoidea* Reuss - G. MÜLLER, p. 401.
- pp ? 1889 *Exogyra auricularis* Wahlenb. - HOLZAPFEL, p. 255, pl. 29, fig. 10 (non fig. 11).
- (1894) *Ostrea sigmoidea* Reuss - LUNDGREN, p. 7, 10, 15.
- . 1898 *Exogyra sigmoidea* Reuss - G. MÜLLER, p. 18, text-fig. 4.
- . 1911 *Exogyra sigmoidea* Reuss - FRIC, p. 46, text-fig. 209.
- . 1913 *Exogyra sigmoidea* Reuss - WOODS, p. 419, pl. 61, fig. 12.
- ? 1938 *Ostrea sigmoidea* Reuss - CARLSSON, p. 13.
- ? 1947 *Ostrea sigmoidea* (Reuss) - HÄGG, p. 83

- ? 1954 *Ostrea sigmoidea* (Reuss) - HÄGG, p. 45.
 . 1965 *Exogyra sigmoidea* Reuss - ZARUBA, p. 20, pl. 1, figs. 1-6, fig. 2 = neotype; pl. 2, figs. 1-5; pl. 3, figs. 1-7; pl. 4, figs. 1-4; pl. 5, figs. 1-5, pl. 6, figs. 1-17, pl. 7, figs. 1-5; pl. 8, figs. 1-5.
 . 1982 *Ceratostreon* (n. sg.?) *sigmoidea* Reuss - GRÜNDEL, p. 142, pl. 1, figs. 1-9.
 v non 1977 *Amphidonte sigmoideum* (Reuss, 1846) - SOBETSKI, p. 161, pl. 15, fig. 4 (unidentifiable single specimen).

MATERIAL: More than hundred RV, 6 LV; IG 4704, 6841, 9694, 10511, 11039.

DESCRIPTION: Size medium (H max. 60 mm), shell comma-shaped, shell margin postero-dorsally convex, becoming concave postero-ventrally, thus convergent with anterior shell margin and forming an elongated ventral tip. LV with steep anterior flank, posterior flank as attachment or reclining surface, sharp, prominent keel; relict lath chomata only on steep side; coiling of umbo amphidontinid.

RV corresponding. SLA more or less narrow and shallow socket, directly ventral of posterior bourrelet; lath chomata short, along anterior inner shell margin, posterior laths restricted to area of the SLA and few mm beyond in ventral direction, main posterior margin without chomata; PAMS postero-dorsal, large, nearly round to oval, dorsally flattened. Young specimens show the same characteristics.

DISCUSSION: ZARUBA (1965, pl. 1, fig. 1 a, b) designated a neotype and gave a detailed description of the right valves. The species differs from other amphidontinid species by its sigmoidal outline, caused by the tapering of the ventral margin. It lacks ribs or plications, lath chomata are reduced on the posterior margin and the adductor muscle scar is almost round. Right valves never show a reticulate band as they do in *Amphidonte* (*Ceratostreon*) *reticulata* (REUSS, 1846). Although the general appearance of *A. ? (C.) sigmoidea* is similar to *Amphidonte* species it is neither a typical *A. (Amphidonte)* nor an *A. (Ceratostreon)*. Therefore, GRÜNDEL (1982) may be right in suggesting the need for a new subgenus.

DISTRIBUTION: *Amphidonte ? (Ceratostreon) sigmoidea* is recorded from Late Cenomanian to Late Santonian (? latest Early Campanian); Czech Republic, Germany, Belgium, England, Sweden.

WOODS (1913) described and figured a single right valve of *Exogyra sigmoidea* said to be from the *Micra-ster coranguinum* Zone (Coniacian-Santonian) of England. LUNDGREN (1894) mentioned the species, only in faunal lists, from Ignaberga, Balsberg, Ifösjöen, (and Ugnsmunarna, *fide* HÄGG, 1947). HÄGG (1947) also added Ringelslätt, Karlshamn and Rosentorp. If these identifications are correct - it is difficult to decide from publications without figures nor descriptions - the species

could not have been very abundant in England or Sweden, but stratigraphically it would have reached into the latest Early Campanian (biostratigraphy data for Kristianstad area, Sweden, see CHRISTENSEN, 1975).

Tribe Exogyriini VIALOV, 1936
 Genus *Vultogryphaea* VIALOV, 1936

Vultogryphaea laciniata (NILSSON, 1827, sensu
 GOLDFUSS, 1833)
 Pl. 3, Figs. 8, 11, 12.

- ? 1801 *Planospirites ostracina* - LAMARCK, p. 400.
 ? 1820 *Ostracites crist. parasiticus* - SCHLOTHEIM, p. 244.
 ? 1827 *Chama laciniata* - NILSSON, p. 28, pl. 8, fig. 2b, ? non fig. 2a.
 ? 1827 *Chama cornu arietis* - NILSSON, p. 28, pl. 8, fig. 1a-d.
 v. 1833 *Exogyra laciniata* - GOLDFUSS, p. 35, pl. 86, fig. 12 a-d.
 1875 *Exogyra laciniata* (Nilss.) - BRAUNS, p. 394.
 1887 *Exogyra laciniata* Goldf. - G. MÜLLER, p. 402.
 1889 *Exogyra laciniata* Nilss. sp. - HOLZAPFEL, p. 254.
 ? 1889 *Ostrea (Exogyra) cornu arietis* Nilsson - GRIEPENKERL, p. 35-36, pl. 5, fig. 1a-c, pl. 6, fig. 1a-c.
 1894 *Ostrea laciniata* Nilss. - LUNDGREN, p. 39.
 ? 1894 *Ostrea cornu arietis* Nilss. - LUNDGREN, p. 38.
 . 1897 *Ostrea cornu arietis*, Nilsson emend. Griepengerl - HENNIG, p. 21, pl.
 . 1898 *Exogyra laciniata* Goldf. - G. MÜLLER, p. 17, pl. 3, fig. 1.
 1937 *Exogyra laciniata* Goldf. - BEYENBURG, p. 308.
 ? 1938 *Ostrea cornu arietis* Nilsson - CARLSSON, p. 13.
 ? 1947 *Ostrea cornuarietis* (Nilsson) - HÄGG, p. 79.
 ? 1954 *Ostrea cornu arietis* (Nilsson) - HÄGG, p. 44.
 v. 1977 *Exogyra (Costagyra) goldfussiana* Sobetski - SOBETSKI, p. 155, pl. 14, figs. 6-7.
 v. 1985 *Vultogryphaea ? laciniata* (Nilsson) - DHONDT, p. 60, pl. 2, figs. e, f.
 . 1986 *Costagyra laciniata* (Goldfuss) non Nilsson - FRENEIX & VIAUD, p. 43, pl. 4, figs. 6-12.

MATERIAL: Hundreds of well preserved LV, RV mostly broken ventrally; IG 4704, 6840, 9340, 11039.

DESCRIPTION: Size medium (H max. 89 mm), shape typically exogyrinid, round to oval. LV inflated, deeply cup-shaped; shell thin, smooth exterior shell with a few strong radial ribs which have a tendency to form hollow

spines; attachment area often large and irregular.

RV flat, forming a thin lid, growth lamellae anteriorly in an upright rather narrow band; posterior area is smooth and generally much larger, often with fine radial striae parallel to narrow band.

Coiling typically exogyrid, resulting in narrow ligamental area and narrow SLA (forming an overhang), with lath and pustulous chomata, laths may reach further down ventrally; PAMS large, round to dorsally flattened or with weak sinus, situated postero-dorsally; commissural shelf well developed. Young specimens (H approx. 30 mm) normally smooth externally, in rare cases with fine ribs at umbonal region, larger ribs do not occur before the shell reaches a height of 2 mm or more; chomata may surround inner shell margin completely; PAMS more round and nearer to the SLA than in larger specimens.

NOMENCLATORIAL NOTE: NILSSON's (1827) original figures and descriptions of '*Chama cornu arietis*' and '*Chama laciniata*' only vaguely define the taxa they should represent. Currently it is not possible to prove whether the specimens described by GOLDFUSS (1833) as *Exogyra laciniata* are really different from *Chama laciniata* NILSSON, as was stated by GRIEPENKERL (1889). HENNIG (1897) saw material from several places in Germany and Sweden, probably including the type localities of *Ch. laciniata* and *Ch. cornu-arietis*. He agreed with GRIEPENKERL that NILSSON's types of these two taxa belong to one species which he named *Ostrea* (*Exogyra*) *cornuarietis* NILSSON. HENNIG did not explicitly exclude *Exogyra laciniata* as understood by GOLDFUSS (1833) from his own species definition.

Until more information is available on the precise meaning of *Chama laciniata* NILSSON, 1827, we prefer to interpret the taxon as *Vultogryphaea laciniata* (NILSSON, 1827 *sensu* GOLDFUSS, 1833), since there can be little doubt as to the recognition of that taxon as it is well illustrated and described. The specimens from Lonžée show the same features. *V. laciniata* is also present in the Maastrichtian stratotypical area around Maastricht (The Netherlands). Comparable specimens from there had been described by LAMARCK (1801) under the name *Planospirites ostracina*. Whether this taxon is identical with *V. laciniata* and thus possibly the oldest available synonym will be subject of a future study on the stratotypical Maastrichtian oysters.

DISCUSSION: The relatively thin shell, with a smooth exterior, few but prominent ribs, few fine chomata and the often nearly round adductor scar are characteristic of the species. Young specimens (H smaller than 25 mm), however, may be very similar to young *A. (C.) reticulata*. Occasionally it is impossible to distinguish them from each other. Both can have few undulating ribs and the chomata may surround the entire inner shell margin.

SOBETSKI (1977) created a new name - *E. (Costagyra) goldfussiana* - to replace *Exogyra laciniata sensu* GOLDFUSS, which he considered to be different from *Chama laciniata* NILSSON. In doing so he relied: Firstly on the

assumption that GRIEPENKERL was right when he separated *Exogyra laciniata* GOLDFUSS from *Chama laciniata* NILSSON' (see nomenclatorial note), and secondly on BOBKOVA (1961) who placed *Chama cornuarietis* NILSSON in the synonymy of *Planospirites ostracina* LAMARCK.

The nomenclatorial note above attempts to demonstrate that we consider both of SOBETSKI's assumptions to be invalid. Furthermore, SOBETSKI (1977) described *E. (Costagyra) goldfussiana* in a way which is not very specific and includes the two taxa he tried to separate.

DISTRIBUTION: *Vultogryphaea laciniata* has been recorded from Late Cenomanian to Late Maastrichtian; west central France, central and northern Europe, SW Ukraine.

Subfamily GRYPHAEOSTREINAE STENZEL, 1971
(emend. FRENEIX, 1982, ex Gryphaeostreini)
Genus *Gryphaeostrea* CONRAD, 1865

Gryphaeostrea canaliculata (J. SOWERBY, 1813)
Pl. 5, Figs. 1 - 3, 5 - 11.

- * 1813 *Chama canaliculata* - J. SOWERBY, p. 68, pl. 26, fig. 1 (non *Ostrea canaliculata* J. SOWERBY, 1816, nec *Ostrea canaliculata* de SERRES, 1843 fide SHERBORN, 1902-1932).
- . 1827 *Ostrea lateralis* - NILSSON, p. 29, pl. 7, figs. 7-10.
- . 1846 *Exogyra lateralis* Nils. - REUSS, p. 42, pl. 27, figs. 38 - 47.
- 1847 *Exogyra lateralis* Reuss - J. MÜLLER, p. 40.
- 1888 *Exogyra canaliculata* Sowerby - G. MÜLLER, p. 401.
- 1889 *Exogyra lateralis* Nilss. - HOLZAPFEL, p. 256.
- . 1898 *Exogyra lateralis* Nilsson -G. MÜLLER, p. 15, pl. 3, fig. 2.
- . 1911 *Exogyra lateralis* Reuss - FRIC, p. 46, text-fig. 210.
- . 1913 *Ostrea canaliculata* (Sowerby, 1813) - WOODS, p. 375, pl. 56, figs. 2 - 16 (with synonymy).
- 1937 *Ostrea canaliculata* (Sow.) - BEYENBURG, p. 307.
- . 1938 *Ostrea canaliculata* Sowerby - CARLSSON, p. 12, pl. 3, fig. 5.
- 1954 *Ostrea canaliculata* (Sowerby) - HÄGG, p. 43.
- . 1982 *Gryphaeostrea canaliculata* (Sowerby, 1813) - GRÜNDEL, p. 156, pl. 3, figs. 4 - 11.
- v. 1985 *Gryphaeostrea canaliculata* (Sowerby, 1813) - DHONDT, p. 62, pl. 2, fig. b.
- . 1986 *Gryphaeostrea canaliculata* (Sowerby, 1813) - ABDEL-GAWAD, p. 164, pl. 38, figs. 1-3.

- . 1986 *Gryphaeostrea canaliculata* (J. Sowerby, 1813) - FRENEIX & VIAUD, p. 44, pl. 5, figs. 1a, b, 2a, b.
- v. 1987 *Gryphaeostrea canaliculata* (Sowerby, 1813) - DHONDT, p. 86, pl. 4, figs. 1, 2.

MATERIAL: IG 11039 several hundred LV, less RV; commissural shelf often broken.

DIMENSIONS: Only complete specimens are measured (all from IG 11039); values of C are measured at the antero-dorsal edge.

No.	H	L	C	L : H	C : H	S
11	22.63	18.33	8.27	0.81	0.37	LV
8	20.88	16.25	8.0	0.79	0.39	LV
15	14.79	11.29	—	0.76	—	RV

DESCRIPTION: Size small (H max. 29 mm); obliquely oval, higher than long; LV cup shaped; umbo very small, opisthogyrate; posterior flange more often developed than anterior, reaches further ventral; no radial sculpture, centrally smooth, flanks with imbricated growth lamellae; RV forms a thin lid, is faintly convex or concave, a single or a few central dorso-ventral riblets sometimes developed. Ligamental area triangular, opisthogyrate at the beginning, later straight, resilifer broader than bourrelets (convex in LV); subligamental gutter sometimes well developed; no chomata; commissure line visible all around inner shell margin.

PAMS postero-dorsal, round, rarely flattened dorsally; size and shape of RV reflected by commissure line in LV, beyond that relatively broad free commissural shelf.

DISCUSSION: It is very difficult to distinguish *Gryphaeostrea* species, whether from the Cretaceous or Early Tertiary. SOBETSKI (1977, for *G. canaliculata* and *G. lateralis*) and FRENEIX (1979, for *G. eversa*) tried to differentiate *Gryphaeostrea* taxa statistically. Their data indicated a general evolutionary trend from round to more elongate (in height) forms. Our measurements plot in between the dimensions for *G. lateralis* as understood by SOBETSKI and *G. eversa meridionalis* FRENEIX (1979). Thus we could propose a new species. There are several reasons for not doing so:

— SOBETSKI (1977, p. 163 etc.) measured only a few specimens (5 for "*G. canaliculata*" and also 5 for "*G. lateralis*"), although the text suggests that he had 300 to 400.

— It is not clear whether SOBETSKI (1977) and FRENEIX (1979) only measured complete specimens (the Lonzée material of the IRSNB comprises hundreds of specimens, but less than 50 are complete). It is also not clear how the convexity was defined or measured by these authors.

— The morphologic measurements of two populations of *G. eversa meridionalis* - from Morocco and Angola - differ significantly from each other. On the other hand, populations of the same subspecies should not vary much

in their size relations, especially if species are defined morphometrically.

— Finally, there are no data available showing the true variability of populations of any of the species, i.e. there is no basis for safe conclusions from statistical values.

We therefore consider the specimens from Lonzée as belonging to *G. canaliculata* (J. SOWERBY, 1813) in which we include *G. lateralis* (NILSSON, 1827).

DISTRIBUTION: *Gryphaeostrea canaliculata* has been recorded from Aptian to Maastrichtian strata and is widely distributed over Europe, northern Africa and central Asia.

Subfamily PYCNODONTEINAE STENZEL, 1959

Tribe Pycnodontini HARRY, 1985

Genus *Pycnodonte* FISCHER de WALDHEIM, 1835

Subgenus *Phygraea* VIALOV, 1936

Pycnodonte (Phygraea) vesicularis (LAMARCK, 1806)

Pl. 3, Figs. 1, 3, 5; Pl. 6, Figs. 1 - 12.

- * 1806 *Ostrea vesicularis* - LAMARCK, p. 160.
- . 1809 *Ostrea vesicularis* Lam. - LAMARCK, p. 375, figs. 3,5.
- v. 1833 *Ostrea vesicularis* Lam. - GOLDFUSS, p. 23, pl. 81, fig. 2.
- 1875 *Ostrea hippopodium* Nilsson, non Goldf. - BRAUNS, p. 394.
- 1888 *Gryphaea vesicularis* Lamk. - G. MÜLLER, p. 401.
- . 1889 *Gryphaea vesicularis* Lam. - HOLZAPFEL, p. 253, pl. 29, figs. 1, 2.
- . 1889 *Ostrea hippopodium* Nilss. - HOLZAPFEL, p. 252, pl. 29, figs. 3 - 7.
- 1894 *Ostrea vesicularis* Lamarck - LUNDGREN, p. 35.
- 1894 *Ostrea hippopodium* Nilss. - LUNDGREN, p. 36.
- . 1898 *Gryphaea vesicularis* Lamarck - G. MÜLLER, p. 14, pl. 3, figs. 10-15; pl. 4, figs. 1-2.
- . 1913 *Ostrea vesicularis* Lamarck - WOODS, p. 360, pl. 55, figs. 4-9, text-figs. 143-182 (with extensive synonymy).
- 1930 *Ostrea hippopodium* Nilsson - HÄGG, p. 46.
- 1934 *Ostrea hippopodium* Nilsson - HÄGG, p. 42.
- 1938 *Ostrea vesicularis* Lamarck - CARLSSON, p. 12.
- 1947 *Ostrea vesicularis* Lamarck - HÄGG, p. 83.
- 1954 *Ostrea hippopodium* Nilsson - HÄGG, p. 44.
- 1954 *Ostrea vesicularis* Lamarck - HÄGG, p. 45.
- . 1982 *Pycnodonte (Phygraea) vesicularis* (Lamarck) - GRÜNDEL, p. 152, pl. 1, figs. 1-4.
- v. 1985 *Pycnodonte (Phygraea) vesiculare* (Lamarck) - DHONDT, p. 54, figs. 3b, 4c, 4e, 4g (+ subsp.).
- . 1986 *Pycnodonte (Phygraea vesicularis* (Lamarck) - ABDEL-GAWAD, p. 162, pl. 38, fig. 5; pl. 39, figs. 5-7 (with synonymy)

- . 1986 *Pycnodonte (Phygraea) vesicularis vesicularis* (Lamarck) - FRENEIX & VIAUD, p. 33, pl. 2, figs. 11 - 14.
- ? 1986 *Pycnodonte (Phygraea) vesicularis* (Lamarck, forme *hippopodium* (Nilsson, 1827) - FRENEIX & VIAUD, p. 32, pl. 2, fig. 10.
- v. 1987 *Pycnodonte vesiculare vesiculare* (Lamarck) - DHONDT & JAGT, p. 84, pl. 3, fig. 6.
- . 1992 *Phygraea (Phygraea) vesicularis zululandensis* subsp. nov. - COOPER, p. 27, figs. 3 - 8.
- . 1992 *Phygraea (Phygraea) vesicularis pseudohippopodium* subsp. nov. - COOPER, p. 35, Fig. 9.
- v. 1993 *Pycnodonte (Phygraea) vesicularis* (Lamarck) - DHONDT, p. 242 (with synonymy).

MATERIAL: Several hundred well preserved shells; IG 11039.

DESCRIPTION: Size small (H max. 40 mm); shape round to obliquely oval. LV strongly convex, nearly globular; generally smooth exterior, occasionally few faint radial ribs (if attachment area small). RV flat, or forming a weakly convex lid, in later growth stages concave.

Ligamental area normally short, straight and triangular, dimensions of bourrelets and resilifer similar, bourrelets convex in LV; hinge line straight, short or elongated posteriorly, sometimes also anteriorly (elongation co-occurs with large flat or cylindrical attachment); PAMS postero-dorsal and mostly round; chomata vermiculate to lath, small but strong, restricted to small, often very deep gutters or sockets on both sides of hinge; to these correspond shell thickenings in RV; commissural shelf well developed.

DISCUSSION: The specimens from Lonžée differ from typical *Pycnodonte (Phygraea) vesicularis* in their much smaller size and the occasional development of faint ribs. They rarely exhibit the typical *Phygraea* shape, and their posterior flange is only incipiently developed or not at all.

Articulated shells are not present. Right valves which probably belong to the species have a shape corresponding to that of the left valves. They show small tooth-like protrusions on both sides of the hinge which fit into sockets of the lower valve. When they also possess a round, postero-dorsal adductor muscle scar and exterior vesicular shell layers the determination is certain.

Nevertheless, there are also many small valves in which one or several of these characters is lacking. Some of these definitely belong to *P. ?(Phygraea) proteus* (REUSS, 1846) (further discussion below). The specimens from Zululand for which COOPER (1992) erected two new subspecies are probably ecophenotypes; the morphometric variations indicated by him for one of the two new taxa are not compared to a similar sample of *Pycno-*

donte (Phygraea) vesicularis s.s. and therefore the taxonomic value of such variations is not demonstrated.

DISTRIBUTION: *Pycnodonte (Phygraea) vesicularis* has been recorded from (? Hauterivian, in Portugal) Aptian to Maastrichtian; cosmopolitan.

Pycnodonte ?(Phygraea) proteus (REUSS, 1846)

Pl. 3, Fig. 2; Pl. 4, Figs. 6 - 8.

- * 1846 *Ostrea Proteus* - REUSS, p. 41, pl. 27, figs. 12 - 27.
- . 1846 *Ostrea vesicularis* Lamk. - REUSS, p. 37, pl. 29, figs. 21, 22; pl. 30, fig. 1 - 8.
- . 1846 *Ostrea hippopodium* Nilsson - REUSS, p. 39, pl. 28, figs. 10 - 15; pl. 29, figs. 1 - 18; pl. 30, figs. 13 - 14.
- . 1846 *Ostrea operculata* - REUSS, p. 41, pl. 28, fig. 9; pl. 30, fig. 12.
- ? 1846 *Ostrea Naumanni* - REUSS, p. 41, pl. 27, figs. 48 - 53; pl. 28, fig. 1.
- ? 1846 *Ostrea minuta* Roemer - REUSS, p. 41, pl. 27, figs. 29 - 35.
- ? 1846 *Ostrea gibba* - REUSS, p. 42, pl. 27, fig. 28.
- . 1889 *Ostrea Proteus* Reuss - FRIC, p. 86, text-fig. 85.
- . 1911 *Ostrea hippopodium* Nils. - FRIC, p. 48, text-fig. 217.
- . 1911 *Ostrea operculata* Reuss - FRIC, p. 47, text-fig. 215.

MATERIAL: More than 50 large LV and RV, more than hundred small RV; IG 7065, 8816, 9694, 11039.

DESCRIPTION: Size medium (H max. 86 mm); shell thick in large specimens, shape more or less round to irregular, often higher than long; LV flat with free margins only slightly rising upwards when largely attached, otherwise cup shaped; posterior flange sometimes developed; exterior with rough growth welts; RV flat or slightly convex, shell thick in larger specimens.

Ligamental area mostly straight, bourrelets in LV flat, often remarkably broader than resilifer, boundaries of resilifer often subparallel; postero-dorsal PAMS large, round to dorsally flattened; chomata short laths, reaching further ventral than position of PAMS, occasionally somewhat longer chomata near hinge.

Vesicular shell layers are extremely rare and restricted to exterior of shell (from where they are easily eroded).

DISCUSSION: The morphology of *Pycnodonte* species is extremely variable, resulting in very different opinions about the taxonomic value of these 'morphotypes' (see e.g. WOODS, 1913; DHONDT, 1985; FRENEIX & VIAUD, 1986; MALCHUS, 1990). The identification is even more difficult when specimens are largely attached which is the case in the taxon under discussion.

The specimens identified here under the name *P. ?*

(*Phygraea*) *proteus* were described and figured by REUSS (1846) under several names: *O. hippopodium* NILSSON and *O. operculata* REUSS for large specimens, *O. proteus* REUSS (and others) for small, mainly right valves (also in Lonžée small left valves are completely missing). The figures in REUSS (1846) perfectly demonstrate the variability seen in the Lonžée material. The following questions remain:

a) whether the large specimens are specifically different from normal *Pycnodonte* (*Phygraea*) *vesicularis*;
b) whether the small specimens really belong to the same species as the large specimens. Right valves of large specimens are very similar to those of normal thick shelled *P. (Phygraea) vesicularis* s.l., but left valves have very fine and short lath chomata which sometimes surround the entire shell. This characteristic is more typical of Early Cretaceous *Texigryphaea* species (which do not occur in Europe) or of *Hyotissa* species. Chomata of *P. (Ph.) vesicularis* are more strongly vermiculate near the hinge; laths, if present, are longer and do not reach the ventral border.

The ligamental area in the Lonžée specimens is straight even in a cup shaped form, but in *P. (Ph.) vesicularis* it is spherically or opisthogyrately curved. Furthermore (in Lonžée) the bourrelets are flat and much broader than the resilifer which itself is narrow and almost triangular. Left valves of *P. (Ph.) vesicularis* have convex bourrelets and the resilifer is more triangular. Additionally, the vesicular shell structure which is well developed in *P. (Ph.) vesicularis* (also in small and thin shelled forms) is extremely rare in the Lonžée specimens. Generally species of the subgenus *P. (Phygraea)* differ in fewer characteristics than is the case between the two "species" from Lonžée. The possibility of ecological reasons cannot be totally excluded, and it might be that these taxonomic "differences" were simply induced by the environment.

The numerous small right valves can be split into three groups:

1. is characterized by a round muscle scar in a postero-dorsal position, externally well developed vesicular structure, a short straight hinge, with two pronounced lateral toothlike protrusions and a more or less oval shape. Such specimens could also belong to the small globular *P. (Phygraea) vesicularis* described above.

2. also shows vesicular shell layers but the specimens are very irregular in shape and normally lack the toothlike protrusions. Such shells probably represent young specimens of the *P. ? (Phygraea) proteus* REUSS.

3. similar to group 2 in size and shape but the muscle scar is not typically pycnodontine. Such shells might eventually belong to the liostreine genus *Acutostrea*, even though left valves of *Acutostrea* are not present in the collection and were also not described by REUSS from Bohemia.

Unfortunately, none of the small shells were found articulated so that any definite proof is lacking.

DISTRIBUTION: *Pycnodonte ? (Phygraea) proteus* has been

recorded from Late Cenomanian to Late Santonian; Bohemia, Belgium; but probably occurs throughout central Europe (under '*Ostrea*' *hippopodium* auctorum).

Genus *Hyotissa* STENZEL, 1971.

Hyotissa semiplana (J. de C. SOWERBY, 1825)

Pl. 4, Fig. 9.

- * 1825 *Ostrea semiplana* - J. de C. SOWERBY, p. 144, pl. 489, fig. 3.
- ? 1825 *Ostrea dorsata* - J. de C. SOWERBY, p. 144, pl. 489, fig. 2, non fig. 1.
- v. 1833 *Ostrea flabelliformis* Nilsson - GOLDFUSS, p. 12, pl. 76, fig. 1a-h.
- . 1833 *Ostrea sulcata* Blumenbach - GOLDFUSS, p. 13, pl. 76, fig. 2a, b.
- 1875 *Ostrea (Alectryonia) sulcata* Blumenbach (*Ostracites*), non Defrance - BRAUNS, p. 393.
- . 1877 *Ostrea semiplana* Sow. - FRIC, p. 141, text-fig. 138.
- 1888 *Ostrea sulcata* Blumenbach - G. MÜLLER, p. 400.
- 1889 *Ostrea semiplana* Sow. - HOLZAPFEL, p. 251.
- 1894 *Ostrea semiplana* Sowerby - LUNDGREN, p. 37.
- v. 1913 *Ostrea semiplana* J. de C. Sowerby - WOODS, p. 379, pl. 56, figs. 17-19; pl. 57, figs. 1-13; pl. 58, figs. 1-5; text-figs. 183-193 (with synonymy).
- v. 1918 *Ostrea semiplana* Sow. - RAVN, p. 30.
- 1930 *Ostrea semiplana* J. de C. Sowerby - HÄGG, p. 48.
- 1935 *Ostrea semiplana* J. de C. Sowerby - HÄGG, p. 43.
- 1937 *Ostrea (Alectryonia) semiplana* Sow. - BEYENBURG, p. 307.
- 1938 *Ostrea semiplana* Sowerby - CARLSSON, p. 11.
- 1947 *Ostrea semiplana* Sowerby - HÄGG, p. 82.
- 1954 *Ostrea semiplana* J. de C. Sowerby - HÄGG, p. 45.
- . 1982 *Hyotissa semiplana* (Sowerby) - GRÜNDEL, p. 153, pl. 1, figs. 5-9.
- v. 1985 *Hyotissa semiplana* (Sowerby) - DHONDT, p. 57, pl. 4, fig. f.
- . 1986 *Hyotissa semiplana* (Sowerby) - ABDEL-GAWAD, p. 163, pl. 37, fig. 10.
- . 1986 *Hyotissa semiplana* (Sowerby) - FRENEIX & VIAUD, p. 35, pl. 3, figs. 1-4.
- v. 1987 *Hyotissa semiplana* (J. de C. Sowerby) - DHONDT & JAGT, pl. 3, fig. 5.

MATERIAL: Hundreds of complete and broken shells; IG 4704, 6381, 6841, 8816, 9694, 11039.

DESCRIPTION: Size medium (H max. 53 mm); shape round, subequivalve to elongated dorso-ventrally; generally large attachment area; strongly plicate, plicae few (6) to many (20), fine at the beginning, irregular round crests, no hyote spines.

Ligamental area higher than long, triangular, more or less straight, bourrelets convex; crowded irregular lath to vermiculate type chomata, up to 4 mm long, on both dorsal margins, laths smaller in ventral direction, normally fading ventrally of PAMS. Young specimens show same characters as adults.

DISCUSSION: In general, *Hytissa semiplana* specimens can be easily identified. However, specimens with large attachment area, poorly developed free margin and lacking plicae, may be difficult to differentiate from *Pycnodonte* (*Phygraea*) spp. Small *H. semiplana* specimens can be confused with small *Rastellum* spp., but the latter do not have a round adductor muscle scar and lack vermiculate chomata.

DISTRIBUTION: *Hytissa semiplana* has been recorded from Turonian to Maastrichtian strata of Europe and is frequent in white chalks and shallow marine deposits.

Suborder Pectinina WALLER, 1978
Superfamily Pectinoidea RAFINESQUE, 1815
Family PECTINIDAE RAFINESQUE, 1815
Genus *Camptonectes* AGASSIZ in MEEK, 1864

Camptonectes virgatus (NILSSON, 1827)
Pl. 1, Fig. 5.

- v* 1827 *Pecten virgatus* n. - NILSSON, p. 22, pl. 9, fig. 15.
- v. 1972 *Camptonectes* (*Camptonectes*) *virgatus* (S. Nilsson) - DHONDT, p. 18, pl. 2, fig. 1 (with synonymy).
- v. 1977 *Camptonectes virgatus* (Nilsson) - SOBETSKI, p. 65, pl. 4, fig. 16.
- v. 1977 *Camptonectes perlucidus* Sobetski, sp. nov. - SOBETSKI, p. 66, pl. 4, fig. 17.
- . 1981 *Camptonectes* (*Camptonectes*) *virgatus* (Nilsson) - TZANKOV, p. 101, pl. 45, fig. 1.
- v. 1982 *Camptonectes virgatus* (Nilsson) - DHONDT, p. 81.
- v? 1982 *Camptonectes curvatus* (Geinitz) - SOBETSKI, p. 113, pl. 11, fig. 19.
- . 1984 *Camptonectes virgatus* (Nilsson) - DHONDT, p. 849.
- . 1985 *Camptonectes* (*Camptonectes*) *virgatus* (Nils.) - FRENEIX & VIAUD, p. 203, pl. 1, fig. 10.
- . 1986 *Camptonectes* (*Camptonectes*) *virgatus* (Nilsson) - ABDEL-GAWAD, p. 151, pl. 32, fig. 16.

- v. 1987 *Camptonectes virgatus* (Nilsson) - DHONDT, p. 67, pl. 3, fig. 3.

MATERIAL: From "sable entre argiles supérieure et inférieure", IG 11039, one LV.

DIMENSIONS: H (23) mm, L (19.8) mm.

DISCUSSION: The typical diverging exterior shell ornamentation is clearly visible on the specimen of *Camptonectes virgatus* from Loncée. The number of diverging ribs is high, resembling the specimens from Africa described by FRENEIX in DARTEVELLE & FRENEIX (1957) more than those from the Lower Campanian of Aachen, or from the Maastrichtian stratotype area.

DISTRIBUTION: *Camptonectes virgatus* has been recorded from Cenomanian to latest Maastrichtian, virtually world wide, but generally more common in coarser than in finer sediments.

Subfamily NEITHEINAE SOBETSKI, 1960
Genus *Neithea* DROUET, 1824

Neithea regularis (SCHLOTHEIM, 1813)
Pl. 1, Fig. 8; Pl. 2, Figs. 1, 4.

- * 1813 *Pectinites regularis* - SCHLOTHEIM, p. 112.
- . 1820 *Pectinites gryphaeatus* - SCHLOTHEIM, p. 224.
- v. 1847 *Janira quadricostata* - d'ORBIGNY, p. 644, pl. 447, figs. 1-7. (non *Pecten quadricostatus* J. SOWERBY, 1814, p. 121).
- v. 1850 *Janira Geinitzii* d'Orb. - d'ORBIGNY, p. 197.
- v. 1870 *Janira Faujasi* Pictet et Camp. - PICTET & CAMPICHE, p. 253.
- v. 1973 *Neithea* (*Neithea*) *regularis* (E.F. von Schlotheim) - DHONDT, p. 20, pl. 1, fig. 3; pl. 2, figs. 1 (with synonymy).
- . 1974 *Neithea quadricostata* (Sowerby) - KO-CIUBYNSKIJ & SAVCZINSKAJA, p. 88, pl. 25, figs. 15-17.
- . 1981 *Neithea* (*Neithea*) *quadricostata* (Sowerby) - TZANKOV, p. 107, pl. 47, figs. 3-6 (non *Pecten quadricostatus* J. SOWERBY, 1814).
- v. 1984 *Neithea regularis* (Schlotheim) - DHONDT, p. 852.
- v. 1985 *Neithea regularis* (Schlotheim) - DHONDT, p. 41, figs. 1 (d-f), (h-i).
- * non v. 1982 *Neithea regularis* (Schlotheim) - SOBETSKI, p. 115, pl. 11, fig. 20 [= *N. quinquecostata* (J. SOWERBY, 1814)].

MATERIAL: Very common in the "argile supérieure" at Lonzée (IG 11039), but generally collected in fragments.

Dimensions (mm):

	H	L	S
IRSNB MI 10578	(4.5)	5	LV (inside)
IRSNB MI 10582	(44.5)	50.6	LV
IRSNB MI 10579	48.5	47.6	RV

DESCRIPTION: *Neithea* species with six principal rounded ribs and three secondary ribs between each two principal ribs, bringing a total of 21 ribs. On the areas a few radial riblets; $H < L$ on left valves, $H > L$ on right valves; auricles subequal.

DISCUSSION: The ribs of the *Neithea regularis* specimens in Lonzée are narrower, and the interspaces wider, than on specimens from the stratotype Maastrichtian. Also the average specimen in Lonzée is somewhat less convex than those from the Maastricht area (Maastrichtian) or near Aachen (Hervian, i.e. Lower Campanian). These differences are possibly adaptations to different environments.

DISTRIBUTION: *Neithea regularis* has been recorded from latest Cenomanian to terminal Maastrichtian; it is frequent in coarse sediments, but very rare in chalks.

Family SYNCYCLONEMIDAE WALLER, 1978
Genus *Syncyclonema* MEEK, 1864

Syncyclonema haeggi DHONDT, 1971 (emended)
Pl. 1, Fig. 6.

- . 1827 *Pecten laevis* - NILSSON, p. 24, pl. 9, fig. 17 (non *laevis* PENNANT, 1777 nec DEFRANCE, 1825, fide SHERBORN).
- * 1971 *Syncyclonema haggi* nom. nov. - DHONDT, p. 48, pl. 2, figs. 1a-f (with synonymy).
- 1982 *Syncyclonema laeve* (Nilsson) - SOBETSKI, p. 101, pl. 6, fig. 25.
- . 1986 *Syncyclonema haeggi* Dhondt - ABDEL-GAWAD, p. 150, pl. 32, figs. 11-12.

MATERIAL: About twenty poorly preserved specimens from the "argile supérieure", two specimens from the "niveau supérieur" (IG 11039).

DIMENSIONS of a relatively complete specimen: H: 6.5 mm; L: 5.5 mm.

DESCRIPTION: Small subcircular *Syncyclonema* species with pronounced commarginal growth lines and slight, diverging radial striae; small auricles, almost subequal on the left valve, but unequal on the right valve.

DISCUSSION: As in the "Hervian" near Aachen-Vaals and

in the Upper Maastrichtian around Maastricht *S. haeggi* seems to have been fairly frequent at Lonzée. The species is virtually unknown from white chalks. The frequent occurrence of the very closely related *S. simplicia* (CONRAD, 1860) in the Lower Maastrichtian Coon Creek Formation of the Gulf and Atlantic Coastal Plains of North America shows the preference of *Syncyclonema* for coarse, shallow sands, during the Late Cretaceous.

DISTRIBUTION: *Syncyclonema haeggi* has been recorded from Turonian to Maastrichtian strata in Europe - in non-Tethyan regions.

Syncyclonema nilsoni (GOLDFUSS, 1835)

Pl. 1, Fig. 4.

- v. 1827 *Pecten orbicularis* - NILSSON, p. 23, pl. 10, fig. 12 (non *orbicularis* J. SOWERBY, 1817, p. 193).
- * 1835 *Pecten Nilsoni* m. - GOLDFUSS, p. 76, pl. 98, figs. 8a, b.
- v. 1971 *Syncyclonema nilsoni* (Goldfuss) - DHONDT, p. 54, pl. 4, figs. 1, 2 (with synonymy).
- ? 1981 *Syncyclonema nilsoni* (Goldfuss) - TZANKOV, p. 100, pl. 44, fig. 4
- ? 1982 *Syncyclonema nilssoni* (Goldfuss) - SOBETSKI, p. 102, pl. 6, fig. 26.
- v. 1985 *Syncyclonema nilsoni* (Goldfuss) - DHONDT, p. 37.
- . 1986 *Syncyclonema nilsoni* (Goldfuss) - ABDEL-GAWAD, p. 32, figs. 9 - 10.

MATERIAL: From "Sable entre les argiles", one left and one right valve; from dark green sand one left valve.

DIMENSIONS:

	UPD	W	S
IG 5793	(58)	(62)	LV
IG 11039	(28.2)	(31.8)	RV
"	(36.8)	(38.2)	LV

DESCRIPTION: Medium to large-sized *Syncyclonema*-species with strongly developed commarginal growth lines and a very wide apical angle; auricles strongly unequal on right valve, subequal on left valve.

DISCUSSION: the specimens from Lonzée though poorly preserved, clearly show the characteristics known from the extensive material at the Sint Pietersberg near Maastricht (DHONDT, 1971).

DISTRIBUTION: *Syncyclonema nilsoni* has been recorded from ? Cenomanian to terminal Maastrichtian outcrops in temperate European strata.

Family SPONDYLIDAE GRAY, 1826.
Genus *Spondylus* LINNÉ, 1758.

tributed in temperate European strata but mainly in chalk facies.

Spondylus fimbriatus GOLDFUSS, 1835.
Pl. 2, Fig. 2.

- v * 1835 *Spondylus fimbriatus* nobis - GOLDFUSS, p. 97, pl. 106, fig. 2.
- . 1847 *Spondylus Dutempleanus* d'Orbigny - d'ORBIGNY, p. 672, pl. 460, figs. 6-11.
- ? 1889 *Spondylus fimbriatus* Goldfuss - GRIE-PENKERL, p. 341.
- v . 1901 *Spondylus Dutempleanus*, d'Orbigny - WOODS, p. 125, pl. 22, figs. 11-14 (with synonymy).
- . 1968 *Spondylus fimbriatus* Goldfuss - PASTERNAK et al., p. 188, pl. 38, fig. 10.
- . 1968 *Spondylus dutempleanus* Orbigny - PASTERNAK et al., p. 189, pl. 58, figs. 12 - 14.
- . 1974 *Spondylus dutempleanus* Orbigny - KO-CIUBYNSKIJ & SAVCZINSKAJA, p. 94, pl. 28, figs. 4,5.
- . 1975 *Spondylus fimbriatus* Goldfuss - NESTLER, p. 56, text-fig. 73.
- . 1977 *Dianchora dutempleana* (Orbigny) - SOBETS-KI, p. 84, pl. 5, fig. 13.
- ? 1981 *Spondylus (Spondylus) dutempleanus* d'Orbigny - TZANKOV, p. 112, pl. 50, fig. 8.
- v . 1982 *Spondylus dutempleanus* d'Orbigny - DHONDT, p. 85, pl. 2, figs. 1 - 4; pl. 4, fig. 5.
- ? 1985 *Spondylus* affin. *dutempleanus* (d'Orb.) - FRENEIX & VIAUD, p. 203.
- . 1986 *Spondylus dutempleanus* d'Orbigny - ABDEL-GAWAD, p. 156, pl. 35, figs. 1-3 (with synonymy).
- . 1987 *Spondylus dutempleanus* d'Orbigny - CLEEVELY & MORRIS, p. 88, pl. 16, fig. 3.
- v . 1987 *Spondylus dutempleanus* d'Orbigny - DHONDT & JAGT, p. 82, fig. 3:7.
- v . 1990 *Spondylus fimbriatus* Goldfuss - DHONDT & DIENI, p. 169, pl. 1, fig. 1; pl. 3, figs. 1 - 6; text-figs. 2, 3, 8, 9 (with synonymy).

MATERIAL: Many fragments found with the *Neithea regularis* material - a few complete left valves are preserved in valves of *Vultogryphaea laciniata*: these oysters grew on a free spondylid valve. Only from "argile inférieure", IG 11039.

DIMENSIONS: A well preserved left valve: H: 39.5 mm; L: 38.5 mm.

DESCRIPTION: see DHONDT & DIENI, 1990.

DISCUSSION: The specimens from Lonzée provide no new information.

DISTRIBUTION: Cenomanian to Maastrichtian, widely dis-

Subclass Palaeoheterodonta NEWELL, 1965
Order Trigonioidea DALL, 1889
Superfamily Trigonioidea LAMARCK, 1819
Family TRIGONIIDAE LAMARCK, 1819
Genus *Pterotrignonia* VAN HOEPEN, 1929

Pterotrignonia vaelsiensis (J. BÖHM, 1884)
Pl. 4, Figs. 2, 4, 5.

- 1837 *Lyrodon aliforme* nobis - GOLDFUSS, p. 203, pl. 137, figs. 6 a - c. (non *Trigonia aliformis* PARKINSON, 1811, p. 176)
- 1865 *Trigonia scabra* Lam. - ZITTEL, p. 161, pl. 9, figs. 2a-c).
- v . 1865 *Trigonia limbata* d'Orb. - ZITTEL, p. 161, pl. 9, fig. 1).
- ? 1875 *Trigonia alata* Schlotheim (Donacites) - BRAUNS, p. 379.
- . 1883 *Trigonia limbata* d'Orb. - FRIC, p. 101, fig. 66.
- * 1884 *Trigonia Vaelsiensis* Joh. Böhm - J. BÖHM, p. 56.
- . 1884 *Trigonia Vaalsiensis* J. Böhm - HOLZAPFEL, p. 456, pl. 6, fig. 3.
- . 1885 *Trigonia Vaelsensis* (sic) Joh. Böhm - J. BÖHM, p. 99, pl. 2, fig. 1 (with synonymy).
- . 1889 *Trigonia Vaalsiensis* J. Böhm - HOLZAPFEL, p. 198, pl. 21, figs. 1-6.
- ? 1920 *Trigonia scabra* Lamarck, forme allongée - ROMAN MAZERAN, p. 85, pl. 8, figs. 3, 4, 6.
- . 1943 *Trigonia vaalsensis* J. Böhm - VAN DER WEIDEN, p. 41, pl. 2, figs. 8-11.
- ? 1981 *Trigonia scabra* Lamarck - TZANKOV, p. 133, pl. 66, figs. 6 - 10.
- ? 1987 *Pterotrignonia* ? spec. - DHONDT, p. 74.

MATERIAL: IG 11039: "argile supérieure": RV silicified and incomplete; about 10 incomplete silicified valves (L and R); IG 8594: incomplete well preserved RV (very dark green); IG 8254 Coll. Maillieux: incomplete LV; IG 9340 Coll. Malaise: incomplete well preserved LV.

DISCUSSION: The posteriorly rostrate *Pterotrignonia* specimens from Lonzée are characterised by a rib distribution which is identical to that of topotypical *Pt. vaelsiensis* specimens from the "Grünsand" in the Vaals - Aachen area. However, those latter specimens have tubercles which, though varying in size on an individual valve, are always strongly developed (see e.g. HOLZAPFEL, 1889, pl. 21, figs. 1-6). On specimens from Lonzée the narrow ribs bear sharp but small, closely set tubercles which are easier to feel than see. In both strata the specimens are silicified so the difference in the tubercles is not due to a differential preservation. It could be that

the specimens from Lonzée belong to a slightly different ecophenotype.

The shape of the shell and the ornamentation on the Lonzée specimens are also partly comparable to those of "*Trigonia*" *limbata* d'ORBIGNY, 1846 (p. 156, pl. 298, figs. 1-4) from the Coniacian - ? Maastrichtian of SSW France; the ornamentation is continuous and fine. It is generally understood that, *T. limbata* is characterised by "smooth" ribs. However, d'ORBIGNY (1846) mentions small tubercles ("à peine tuberculeuses du côté buccal") on some of the ribs. It is therefore not impossible that after the revision of the *Paléontologie Française* (in preparation, personal comm. S. FRENEIX), it will be confirmed that *T. limbata* bears small knobs on its narrow ribs. This might also prove "*T.*" *vaelsiensis* to be synonymous with *T. limbata*.

Whether *T. scabra* LAMARCK, 1819 and *T. limbata* are synonymous, as is stated by ROMAN & MAZERAN (1920), we cannot confirm with the material available to us. "*T.*" *vaelsiensis* has been assigned to *Pterotrigonia* VAN HOEPEN, 1929 because it agrees with the diagnosis given in COX (1969) and with most of the generic diagnosis in COOPER (1991). *Pt. thoracica* (MORTON, 1834) from the Coon Creek Tongue of the Ripley Formation (Lower Maastrichtian) at Coon Creek (Tennessee) has an overall similarity with *Pt. vaelsiensis* but is less convex and less opisthogyre, not so rostrate, has slightly fewer ribs (16 instead on 24 for a specimen of 65 mm long), and is covered with small spines rather than with more or less rounded tubercles.

The presence of an elongated posterior rostrum distinguishes *Pterotrigonia* from *Scabrotrigonia* DIETRICH, 1933, but the presence of costellae on the escutcheon which form chevrons with the flank ribs indicate *Scabrotrigonia*. "*T.*" *vaelsiensis* has an attenuated rostrum and the specific escutcheon ornamentation. Yet, no attempt has been made here towards a subgeneric assignment since according to COOPER (1991) several taxa need to be redefined.

DISTRIBUTION: *Pterotrigonia vaelsiensis* has been recorded from Late Santonian and Campanian strata in western and central Europe.

Subclass Heterodonta NEUMAYR, 1883
Order Veneroida H. ADAMS & A. ADAMS, 1856
Superfamily Lucinoidea FLEMING, 1928
Family LUCINIDAE FLEMING, 1928
Genus *Lucina* BRUGUIÈRE, 1797.

? "*Lucina*" *subnumismalis* d'ORBIGNY, 1850.

- ? 1846 *Venus laminosa* REUSS - REUSS, p. 21, pl. 41, figs. 6, 15 (non *laminosa* MONTAGU, 1808, nec PENNANT, 1812, p. 202, fide SHERBORN).
- . 1847 *Venus numismalis* MÜLLER - J. MÜLLER, p.

25, pl. 2, fig. 5 (non *Lucina numismalis* MATHERON, 1843)

- . 1850 *Lucina subnumismalis*, d'Orb. - d'ORBIGNY, p. 241.
- . 1851 *Lucina tenuis*, MÜLLER - J. MÜLLER, p. 66. [non 1850 *Lucina tenuis* (Koch, 1837) in d'ORBIGNY, p. 279 from the Bajocian of Germany (= *Venus tenuis* in KOCH & DUNKER, 1837).
- . 1885 *Lucina subnumismalis* d'Orbigny - J. BÖHM, p. 114.
- . 1889 *Lucina subnumismalis* d'Orb. - HOLZAPFEL, p. 187, pl. 19, fig. 1-3.
- ? 1893 *Venus laminosa*, REUSS - FRIC, p. 97, text-fig. 117.
- ? 1898 *Lucina subnumismalis* d'Orb. - G. MÜLLER, p. 59, text-fig. 17.
- . 1934 *Lucina laminosa* REUSS sp. - ANDERT, p. 253, pl. 12, figs. 6, 7.
- . 1943 *Lucina laminosa* (REUSS) - VAN DER WEIJDEN, p. 50, pl. 2, fig. 18.
- . 1986 *Lucina (Lucina) subnumismalis* d'Orbigny - ABDEL - GAWAD, p. 166, pl. 39, fig. 4.

MATERIAL: Three composite moulds; "argile supérieure", IG 11039.

DIMENSIONS (in mm):

H 18.5	W 20.2
19.8	20.5

DISCUSSION: Moulds characterised by a strong, concentric ornamentation forming more or less step-like commarginal "ribs" on which smaller concentric ridges are attached, are tentatively identified as ? "*Lucina*" *subnumismalis*. The Lonzée specimens lack hinges, but their ornamentation and contours are so similar to the material from Vaals figured by HOLZAPFEL that we think it very likely that these moulds represent the same species.

It is not impossible that the incomplete specimen figured by HOLZAPFEL as *Dosinia* sp. (pl. 12, figs. 3, 4, p. 173) also belongs here.

It is difficult to judge whether *Venus laminosa* REUSS, 1844 from the Czech Turonian is synonymous with the taxon from Vaals as suggested by various authors (e.g. ANDERT, 1934). REUSS (1846) figured the taxon insufficiently to allow a definite opinion.

DISTRIBUTION: "*Lucina*" *subnumismalis* has been recorded from the Turonian to Maastrichtian in western and central Europe.

Superfamily Carditoidea FLEMING, 1820
Family CARDITIDAE FLEMING, 1828
Genus *Vetericardiella* CHAVAN, 1969

Vetericardiella ? *benedeni* (J. MÜLLER, 1859)
Pl. 4, Fig. 3.

- * 1859 *Astarte Benedeni*, Müller - J. MÜLLER, p. 11, pl. 7, fig. 12.
- . 1889 *Venericardia Benedeni* Müll. sp. - HOLZAPFEL, p. 193, pl. 19, fig. 10.

MATERIAL: One silicified LV, H: 15 mm, W 15.5 mm; "argile supérieure", IG 11039

DESCRIPTION: The somewhat worn surface of a left valve from Lonzée, is covered with numerous narrow radial riblets which are crossed by fine commarginal growth lines, giving in places a cancellate aspect to the shell. The inner margin of the shell is strongly crenulate, except in the anterior hinge region.

DISCUSSION: *Vetericardiella benedeni* has been compared to the almost coeval *Cardita geinitzi* d'ORBIGNY, 1850 as described (from internal moulds and steinkern preservation) in ANDERT (1934, p. 240, pl. 11, fig. 43): the specimen from Lonzée does not have the strong commarginal ornamentation described by ANDERT in his "C." *geinitzi* specimens.

'*Cardita cancellata* WOODS, 1897 (see also CLEEVELY & MORRIS, 1987, p. 118, pl. 20, fig. 8) from the Chalk Rock (Turonian) of England has a cancellate ornamentation and a "carditid" hinge. It is similar to *Vetericardiella benedeni*, but not having seen a complete specimen of the English taxon it is difficult to decide whether it could fall in the synonymy of *V. benedeni*. In the same way *Venericardia santonensis* G. MÜLLER, 1898, from the Santonian of the Braunschweig area is very similar to *Vetericardiella benedeni*, but the former seems more rounded. However, it is only known from composite moulds and therefore difficult to judge precisely.

DISTRIBUTION: *Vetericardiella benedeni* has so far only been recorded from the Santonian of Lonzée and the Lower Campanian of the Vaals-Aachen area.

Superfamily Crassatelloidea FÉRUSAC, 1822

Family Astartidae d'ORBIGNY, 1844

Genus *Eriphyla* GABB, 1864

Eriphyla cf. lenticularis (GOLDFUSS, 1841)

- * 1841 *Lucina lenticularis* nobis - GOLDFUSS, p. 228, pl. 146, fig. 16.
- 1841 *Lucina lenticularis* Goldf. - J. MÜLLER, p. 23.
- 1883 *Eriphyla lenticularis* - FRIC, p. 101.
- 1885 *Dozyia lenticularis* Gfs. - J. BÖHM, p. 126.
- . 1889 *Eriphyla lenticularis* sp. - HOLZAPFEL, p. 195, pl. 14, figs. 5-7.
- 1894 *Eriphyla lenticularis* Goldf. - LUNDGREN, p. 48.
- ? 1898 *Eriphyla lenticularis* Goldf. sp. - G. MÜLLER, p. 56, pl. 8, fig. 3.

- . 1934 *Eriphyla lenticularis* Goldf. sp. - ANDERT, p. 244, pl. 12, figs. 1, 2 (with synonymy).
- . 1943 *Eriphyla lenticularis* (Goldfuss) - VAN DER WEIJDEN, p. 44, pl. 2, figs. 14, 15, 16.

MATERIAL: One composite mould, from "argile supérieure", IG 11039.

DIMENSIONS: H: 18.3 mm; W: 19.0

DISCUSSION: The mould from Lonzée does not have a hinge and therefore its identification remains purely tentative. Compared to the specimens described by HOLZAPFEL (1889) from Aachen-Vaals the Lonzée specimen is small (only about half the size).

DISTRIBUTION: *Eriphyla lenticularis* has been recorded from Cenomanian to Lower Campanian of central and western Europe.

Family CRASSATELLIDAE FÉRUSAC, 1822

Genus *Crassatella* LAMARCK, 1799

Crassatella arcacea ROEMER, 1841

- * 1841 *Crassatella arcacea* N. - F. A. ROEMER, p. 74, pl. 9, fig. 24.
- . 1889 *Crassatella arcacea* Roem. - HOLZAPFEL, p. 191, pl. 20, figs. 1-5, 7, 8.
- . 1889 *Crassatella arcacea* A. Römer - GRIEPENKERL, p. 59.
- . 1934 *Crassatella arcacea* A. Roem. - ANDERT, p. 246, pl. 11, figs. 46 - 48, text-figs. 25-29, (with synonymy).
- . 1943 *Crassatella arcacea* Roemer - VAN DER WEIJDEN, p. 46, pl. 3, figs. 3 - 7.
- 1947 *Crassatella arcacea* A. Römer - HÄGG, p. 85
- 1954 *Crassatella arcacea* Römer - HÄGG, p. 47.

MATERIAL: Two incomplete silicified umbonal parts of valves from the "argile supérieure", IG 11039.

DISCUSSION: The differences existing between *Crassatella arcacea* and *Cr. macrodonta* (J. de C. SOWERBY, 1832) as described by J. BOEHM (1885) are difficult to recognise. It is possible that both taxa simply represent different ontogenetic stages of one species. In ANDERT (1934) the wide variability of *Cr. arcacea* is briefly discussed.

Such a wide intraspecific variability due to different ontogenetic stages has been found in *Cr. vadosa* (MORTON, 1833) from the Campanian - Maastrichtian of the SE USA (De Cauwer, unpublished).

DISTRIBUTION: *Crassatella arcacea* has been recorded from the Cenomanian to Maastrichtian of Europe.

Superfamily Cardioidea LAMARCK, 1809
 Family CARDIIDAE LAMARCK, 1809
 Genus *Granocardium* GABB, 1869

Granocardium cf. productum (J. de C. SOWERBY, 1832)
 Pl. 4, Fig. 1.

Compare with:

- v* 1832 *Cardium productum* Sowerby - SOWERBY in SEDGWICK & MURCHISON, p. 417, pl. 39, fig. 15.
- 1889 *Cardium productum* Sowerby - GRIEPENKERL, p. 62.
- . 1889 *Granocardium productum* Sow. - HOLZAPFEL, p. 179, pl. 17, figs. 1-5.
- 1894 *Cardium productum* Sow. - LUNDGREN, p. 49.
- 1919 *Cardium (Trachycardium) productum* Sow. var. *subproducta* Th. et Peron et var. *Byzacenica* Perv. - GRECO, p. 2.
- . 1922 *Cardium productum* Sow. mut. *subtriangulare* nov. - COTTREAU, p. 153, pl. 5, figs. 13, 14.
- 1928 *Cardium productum* J. de C. Sowerby - LEES, p. 647.
- . 1937 *Cardium (Trachycardium) productum* Sow. - TREVISAN, p. 102.
- . 1943 *Granocardium productum* (Sowerby) - VAN DER WEIJDEN, p. 54, pl. 4, figs. 1, 2.
- 1949 *Cardium (Trachycardium) productum* Sow. - TAVANI, p. 8.
- 1961 *Cardium cf. productum* Sowerby - BOBKOVA, p. 137, pl. 13, fig. 3.
- 1961 *Cardium productum* Sowerby var. *dagana-kiiensis* Bobkova var. nov. - BOBKOVA, p. 139, pl. 13, fig. 4.
- . 1963 *Cardium productum* Sow. - GAMBASHIDZE, p. 136, pl. 2, fig. 5.
- ? 1986 *Granocardium (Criocardium) productum* (Sowerby) - ABDEL-GAWAD, p. 169, pl. 40, figs. 6 - 7.
- v. 1987 *Granocardium productum* (J. Sowerby) - DHONDT, p. 77, pl. 4, figs. 5, 6 (with further synonymy).

MATERIAL: Two silicified valves, one hinge region of a LV and one squashed somewhat decorticated LV, from the "argile supérieure", IG 11039.

DIMENSIONS: H = (42) mm.

DISCUSSION: Though poorly preserved, the specimens from Lonzée very probably belong to *Granocardium productum* because of their strong hinge; of the other shell characteristics only the ribbing is visible but the most external shell layer and the spines are missing.

The status of *G. noeggerathi* (J. MÜLLER, 1851) from

the Vaalser Grünsand is not clear - it might simply be a somewhat differently preserved *G. productum*, in which the outside layer is missing. If research on a large series of specimens from Vaals would reveal that *G. noeggerathi* was a separate taxon, then the specimens from Lonzée would have to be included in that species.

DISTRIBUTION: Widely distributed in the (? Cenomanian) Turonian - Campanian (? Maastrichtian) of Europe.

Superfamily Veneroidea RAFINESQUE, 1815
 Family VENERIDAE RAFINESQUE, 1815
 Genus *Mesocallista* COX, 1952

? *Mesocallista subovalis* (d'ORBIGNY, 1850)

- . 1841 *Venus ovalis* Sow. - GOLDFUSS, p. 247, pl. 151, fig. 5 (non J. de C. SOWERBY, p. 129, pl. 567, figs. 1, 2).
- 1841 *Venus fabacea* - F. A. ROEMER, p. 72, pl. 9, fig. 13.
- 1843 *Venus ovalis* Sow. - GEINITZ, p. 13.
- ? 1843 *Venus Faba* Sow. - GEINITZ, p. 13, pl. 2, figs. 7 - 9.
- 1847 *Venus ovalis* Sow. - J. MÜLLER, p. 24.
- * 1850 *Venus subovalis*, d'Orb. - d'ORBIGNY, p. 237, n° 534.
- . 1884 *Cytherea ovalis* Goldf. sp. - HOLZAPFEL, p. 464, pl. 7, figs. 2-4.
- 1885 *Cytherea fabacea* Ad. Römer sp. - J. BÖHM, 123.
- 1888 *Cytherea ovalis* Goldf. sp. - G. MÜLLER, p. 427.
- 1889 *Cytherea ovalis* Goldf. sp. - HOLZAPFEL, p. 169, pl. 13, figs. 11 - 15.
- ? 1889 *Venus ovalis* Sow. bei Reuss - FRIC, p. 80, fig. 69.
- . 1898 *Cytherea ovalis* Goldf. sp. - G. MÜLLER, p. 66, pl. 9, fig. 12.
- 1901 *Cytherea ovalis* Goldf. - STURM, p. 83.
- . 1934 *Cytherea ovalis* Goldf. sp. - ANDERT, p. 278, pl. 13, figs. 37 - 38; pl. 13, fig. 3; text-figs. 49, 50.
- . 1943 *Cytherea ovalis* (Goldfuss) - VAN DER WEIJDEN, p. 57, pl. 4, figs. 7 - 9.

MATERIAL: One incomplete somewhat worn left valve, two composite moulds with hinges, "argile supérieure", IG 11039.

DIMENSIONS:

H	W	Valve
—	19.5	LV
18.6	20.6	RV

DESCRIPTION: The valve is covered with fine commarginal ribbing: about 35 ribs per cm (starting from the

umbo); towards the pallial margin the distance between the ribs increases.

Depending on the preservation state of the shell the nature of the "ribs" changes. When the surface is not worn grooves delimit commarginal bands; when the surface is worn, narrow commarginal bands alternate with equally wide interspaces.

DISCUSSION: The erroneous interpretation of priority in nomenclature by HOLZAPFEL (1884), has resulted in a wrong usage, mainly in German literature for the taxon "*Venus ovalis*" GOLDFUSS (non SOWERBY). d'ORBIGNY (1850) corrected the name in *V. subovalis* but this was completely ignored by later authors. The generic attribution to *Cytherea* LAMARCK non FABRICIUS, used since HOLZAPFEL (1884), had to be revised. The available hinges on the Lonzée material are somewhat worn, but on specimens from Vaals they can be seen properly and by analogy we tentatively assign "*Cytherea ovalis*" auctorum (= *Venus subovalis* d'ORBIGNY, 1850) to *Mesocallista* COX, 1952.

The hinges of silicified specimens show the same teeth as complete specimens, but during silification part of the shell was dissolved and therefore the hinge looks less strongly developed than on complete specimens. Comparing *M. subovalis* specimens from Vaals with *M. andersoni* (NEWTON) specimens (BM L 86353 - 54) from the Campanian near Nauli, N. of Bonyere, western Ghana shows a close similarity, but the hinge in the African unsilicified specimen is heavier.

DISTRIBUTION: *Mesocallista subovalis* has been recorded from Turonian to Maastrichtian of western and central Europe.

Genus *Cyprimeria* CONRAD, 1864

Cyprimeria discus (MATHERON, 1843)

- * 1843 *Lucina discus* Math. - MATHERON, p. 144, pl. 13, fig. 12.
- ? 1845 *Arcopagia numismalis*, d'Orbigny - d'ORBIGNY, p. 415, pl. 379, figs. 1 -5.
- . 1851 *Lucina Geinitzii* Müller - J. MÜLLER, p. 66.
- v . 1865 *Circe discus* Math. sp. - ZITTEL, p. 128, pl. 3, figs. 7 a-f.
- 1885 *Dozyia Geinitzi* Jos. Müller - J. BÖHM, p. 130.
- . 1889 *Cyprimeria Geinitzii* Müll. sp. - HOLZAPFEL, p. 174, pl. 12, figs. 1-4.
- ? 1897 *Cyprimeria Geinitzii*, Müller sp. - FRIC, p. 53, fig. 58.
- v . 1987 *Cyprimeria ? discus* (Matheron) - DHONDT, p. 86 (with synonymy).

MATERIAL: One incomplete silicified right valve with a good hinge from "argile supérieure", IG 11039.

DIMENSIONS: H = (60) mm

DISCUSSION: This large venerid has been described and figured in detail by HOLZAPFEL (1889) who had complete silicified specimens at his disposal.

Specimens described as "*Cytherea subovalis*" auctorum from the Aachen-Vaals area appear to belong to *Cyprimeria discus*, but generally their steinkern preservation makes a precise identification impossible.

The North American species *Cyprimeria alta* (CONRAD, 1875) from the Maastrichtian of Coon Creek, Tennessee, as figured in WADE, 1926 (pl. 29, figs. 2-4, pl. 30, figs. 1, 8) and *Cy. major* GARDNER, 1916 from the Maastrichtian Monmouth Fm., at Brightseat, Maryland are very near *Cy. discus* (MATHERON, 1843).

To prove the relationship between these three taxa an ontogenetic series needs to be compared because the hinge changes with the size of the specimens.

DISTRIBUTION: *Cyprimeria discus* is recorded from ? Turonian (SE France), Santonian (Gosau, Austria; Lonzée) and Campanian (Vaals-Aachen area).

Order Myoida STOLICZKA, 1870

Superfamily Myoidea STOLICZKA, 1870

Family CORBULIDAE LAMARCK, 1818

Genus *Caestocorbula* VINCENT, 1910

Caestocorbula ? angustata (J. de C. SOWERBY, 1832)

- * 1832 *Corbula angustata* - J. de C. SOWERBY in SEDGWICK & MURCHISON, p. 417, pl. 38, fig. 4.
- v. 1865 *Corbula angustata* Sow. - ZITTEL, p. 112, pl. 1, fig. 8.
- v 1987 *Corbula ? angustata* J. Sowerby - DHONDT, p. 88, pl. 5, fig. 3 (with synonymy).

MATERIAL: One silicified left valve attached to an incomplete *Eriphyla* (?) valve (IG 11039 "argile supérieure") and one right and three left valves IG 8254 (Coll. Mailieux).

DESCRIPTION: A large more or less complete right valve: H: 5.5 mm; L: 7.5 mm.

Both valves are covered with coarse commarginal ribbing (12 to 15 ribs) per valve, which lie equi-distantly from the umbo to the pallial margin. The right valve has a rostrum.

DISCUSSION: Compared with topotypical specimens of *Caestocorbula substriatula* (d'ORBIGNY, 1850) from the Vaalser Grünsand (Lower Campanian), the specimens from Lonzée have more equally distributed coarse ribs. On *C. substriatula* the ribbing near the umbo is fine and it is only near the pallial margin that the ribs are coarse.

In *C. angustata* topotypes from the Gosau (Upper Santonian, Austria) the ribbing near the umbo is not as close together as in *C. substriatula*.

Corbula elegans SOWERBY, from the Blackdown Greensand (Albian, England) as figured in WOODS, 1908 (pl. 34, figs. 23 - 28) has a similar aspect as *Caestocorbula angustata* but the ribbing, though equidistant, is finer. *Corbula striatuloides* FORBES as described and illustrated from the Maastrichtian of Egypt in QUAAS (1902, p. 231, pl. 25, figs. 12 -15) has a rib pattern which is nearer that of *C. substriatula* d'ORBIGNY, 1850 than that of *C. angustata*, but as already QUAAS (ibid.) wrote the small Egyptian specimens are difficult to distinguish from *C. angustata*.

The coarse ribbing of the Lonzée material is also similar to that of the right valve of *Corbula crassiplica* GABB from Coon Creek as figured in WADE, 1926 (pl. 31, fig. 9) but the North American specimens do not belong to *Caestoborbula*.

DISTRIBUTION: *Caestocorbula angustata* has so far only

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been recorded from the Santonian of Austria and of Belgium.

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Explanation of Plates

PLATE 1

All specimens are from the Santonian of Lonzée, except where indicated otherwise.

- Fig. 1 — *Cucullaea subglabra* (d'ORBIGNY, 1850): left valve, X 2; IG 11039, "argile supérieure", IRSNB MI 10571.
- Fig. 2 — *Limatula* sp.: left valve, X 4, IG 11039, "argile supérieure", IRSNB MI 10572.
- Fig. 3 — *Plagiostoma hoperi* MANTELL, 1822: right valve, X 2, IG 11039, "sables entre les argiles inférieure et supérieure", IRSNB MI 10573.
- Fig. 4 — *Syncyclonema nilsoni* (GOLDFUSS, 1835): right valve, X 1.2, IG 11039, "sable entre les argiles inférieure et supérieure", IRSNB MI 10574.
- Fig. 5 — *Camptonectes virgatus* (NILSSON, 1827): left valve, X 2, IG 11039, "sable entre les argiles inférieure et supérieure", IRSNB MI 10575.
- Fig. 6 — *Syncyclonema haeggi* DHONDT, 1971: ? right valve, X 4.7, IG 11039, "argile supérieure", IRSNB MI 10576.
- Fig. 7 — *Inoceramus* (*Volviceramus*) cf. *koeneni* (G. MÜLLER, 1888): cast from inner shell, relief of a right valve, X 1, IG 5793, IRSNB MI 10577; ? Middle Coniacian of Lonzée.
- Fig. 8 — *Neithea regularis* (SCHLOTHEIM, 1813): incomplete left valve, interior view, X 5, IG 11039, IRSNB MI 10578.
- Fig. 9 — *Inoceramus* (*Volviceramus*) *koeneni* (G. MÜLLER, 1888): articulated shell, facing exterior of right valve, X 1, specimen from coll. K.-A. TRÖGER, Blankenburger Köpfe (Halberstadt, Germany), Middle Coniacian.
- Fig. 10 — *Inoceramus* (*Cordiceramus*) *cordiformis* (J. de C. SOWERBY, 1823): right valve, X 1, specimen from coll. K.-A. TRÖGER, Salzberg bei Quedlinburg (Germany), Middle Santonian.

PLATE 2

All specimens are from the Santonian of Lonzée

- Fig. 1 — *Neithea regularis* (SCHLOTHEIM, 1813): right valve, X 1, IG 11039, "argile supérieure", IRSNB MI 10579.
 Fig. 2 — *Spondylus fimbriatus* GOLDFUSS, 1835: facing interior of left valve, X 1, IG 8254, IRSNB MI 10580; shell is overgrown by left valve of a *Vultogryphaea laciniata* (NILSSON, 1827 sensu GOLDFUSS, 1833).
 Fig. 3 — *Rastellum diluvianum* (LINNAEUS, 1767): right valve exterior, X 2.5, IG 11039, "argile inférieure", IRSNB MI 10581.
 Fig. 4 — *Neithea regularis* (SCHLOTHEIM, 1813): left valve exterior, X 1, IG 11039, "argile supérieure", IRSNB MI 10582.
 Fig. 5 — *Rastellum diluvianum* (LINNAEUS, 1767): left valve, 5a = exterior, 5b = interior, X 3, IG 11039, "argile inférieure", IRSNB MI 10583.
 Fig. 6 — *Rastellum diluvianum* (LINNAEUS, 1767): left valve, X 1, IG 9340, IRSNB MI 10584.
 Fig. 7 — *Rastellum diluvianum* (LINNAEUS, 1767): right valve, X 3, IRSNB MI 10585.
 Fig. 8 — *Rastellum diluvianum* (LINNAEUS, 1767): two left valves, X 1, IG 8415, IRSNB MI 10586.

PLATE 3

All specimens are from the Santonian of Lonzée

- Fig. 1 — *Pycnodonte* (*Phygraea*) *vesicularis* (LAMARCK, 1806): left valve, 1a = exterior, 1b = interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10587.
 Fig. 2 — *Pycnodonte* ?(*Phygraea*) *proteus* (REUSS, 1846): right valve, 2a = interior, 2b = exterior, X 1, IG 11039, "argile inférieure", IRSNB MI 10588.
 Fig. 3 — *Pycnodonte* (*Phygraea*) *vesicularis* (LAMARCK, 1806): right valve exterior, X 1, IG 11039, "argile inférieure", IRSNB MI 10589.
 Fig. 4 — *Amphidonte* (*Ceratostreon*) *reticulata* (REUSS, 1846): right valve, 4a = exterior, 4b = interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10590.
 Fig. 5 — *Pycnodonte* (*Phygraea*) *vesicularis* (LAMARCK, 1806), right valve, 5a = exterior, 5b = interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10591.
 Fig. 6 — *Amphidonte* (*Ceratostreon*) *reticulata* (REUSS, 1846): right valve, 6a = exterior, 6b = interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10592.
 Fig. 7 — *Amphidonte* ?(*Ceratostreon*) *sigmoidea* (REUSS, 1844): left valve, 7a = exterior, 7b = interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10593.
 Fig. 8 — *Vultogryphaea laciniata* (NILSSON, 1827 sensu GOLDFUSS, 1833): left valve interior, X 1, IG 4704, IRSNB MI 10594.
 Fig. 9 — *Amphidonte* ?(*Ceratostreon*) *sigmoidea* (REUSS, 1844): right valve interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10595.
 Fig. 10 — *Amphidonte* (*Ceratostreon*) *reticulata* (REUSS, 1846): left valve interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10596.
 Fig. 11 — *Vultogryphaea laciniata* (NILSSON, 1827 sensu GOLDFUSS, 1833): left valve exterior, X 1, IG 9340, IRSNB MI 10597.
 Fig. 12 — *Vultogryphaea laciniata* (NILSSON, 1827 sensu GOLDFUSS, 1833): right valve exterior, X 1, IG 11039, "argile inférieure", IRSNB MI 10598.

PLATE 4

All specimens are from the Santonian of Lonzée.

- Fig. 1 — *Granocardium* cf. *productum* (J. de C. SOWERBY, 1832): anterior part of crushed left valve, IG 11039, "argile supérieure", IRSNB MI 10599.
 Fig. 2 — *Pterotrigonia vaeliensis* (J. BÖHM, 1885): broken right valve, 2a = hinge area, X 1, 2b = exterior, X 1.5, IG 8594, IRSNB MI 10600.
 Fig. 3 — *Vetericardiella benedeni* (J. MÜLLER, 1859): left valve exterior, X 2.5, IG 11039, "argile supérieure", IRSNB MI 10601.
 Fig. 4 — *Pterotrigonia vaeliensis* (J. BÖHM, 1885): right valve, X 1, IG 11039, "? argile supérieure", IRSNB MI 10602.
 Fig. 5 — *Pterotrigonia vaeliensis* (J. BÖHM, 1885): left valve, X 1, IG 9340, IRSNB MI 10603.
 Fig. 6 — *Pycnodonte* ?(*Phygraea*) *proteus* (REUSS, 1846): left valve interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10604.

- Fig. 7 — *Pycnodonte* ?(*Phygraea*) *proteus* (REUSS, 1846): left valve interior, X 1, IG 11039, "argile inférieure", IRSNB MI 10605.
 Fig. 8 — *Pycnodonte* ?(*Phygraea*) *proteus* (REUSS, 1846): two left valves, X 1, IG 11039, "argile inférieure", IRSNB MI 10606.
 Fig. 9 — *Hytissa semiplana* (J. de C. SOWERBY, 1825): left valve, 9a = exterior, 9b = interior, X 1, IG 11039, IRSNB MI 10607.

PLATE 5

All specimens are from the Santonian of Lonzée.

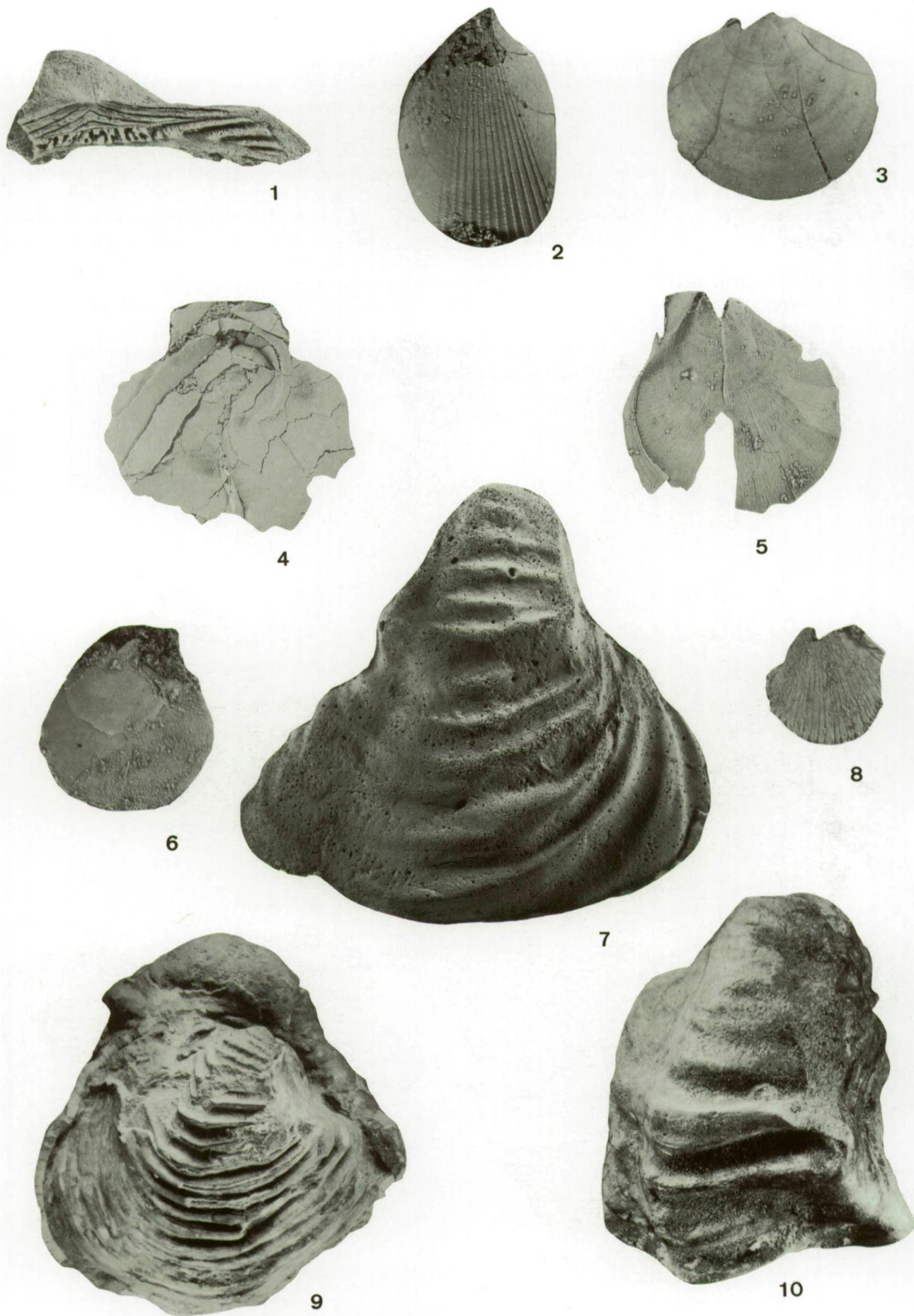
- Fig. 1 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): left valve, internal view, X 2.7 (SEM: C 128), IG 11039, "argile inférieure", IRSNB MI 10608: species of the subfamily Gryphaeostreinae lack chomata.
 Fig. 2 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): right valve, external view, X 2.5, IG 11039, "argile inférieure", IRSNB MI 10609.
 Fig. 3 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): left valve, external view, X 1.5, IG 11039, "argile inférieure", IRSNB MI 10610: shell shows large, smooth, leaf-like attachment surface typical of many of the Lonzée specimens.
 Fig. 4 — *Rastellum diluvianum* (LINNAEUS, 1767): right valve, small form, 4a = internal view, 4b = external view, X 3, IG 11039, "argile inférieure", IRSNB MI 10581: antero- and postero-dorsal small lath chomata visible.
 Fig. 5 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): right valve, external view, X 3 (SEM: NM 67), IG 11039, "argile inférieure", IRSNB MI 10611.
 Fig. 6 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): right valve, internal view, X 3.2 (SEM: NM 69), IG 11039, "argile inférieure", IRSNB MI 10612: round adductor muscle scar is typically situated in a postero-dorsal position.
 Fig. 7 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): same specimen as Fig. 5, external view, X 70 (SEM: NM 67): two prism layers of outer prismatic shell.
 Fig. 8 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): left valve, X 85, bar 1 mm (SEM: C 156,1), IG 11039, "argile inférieure", IRSNB MI 10613: cut dorso-ventrally, etched (2% formic acid) and polished, outer shell surface up, three shell layers are visible (from external to internal): complex irregular cross foliated, simply cross foliated and simply foliated.
 Fig. 9 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813), left valve, X 241, bar 100 µm (SEM: C 155), IG 11039, "argile inférieure", IRSNB MI 10614: broken ventral edge, outer shell surface up, etched (2% formic acid): simply cross foliated layer (compare Fig. 8).
 Fig. 10 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): same specimen as Fig. 8: close up of simply cross foliae, three stacks of foliae are visible, inclined in different directions, 2 light and 1 middle dark stack if compared to Fig. 8.
 Fig. 11 — *Gryphaeostrea canaliculata* (J. SOWERBY, 1813): left valve, X 810, bar 100 µm (SEM: C 156,2), IG 11039, "argile inférieure", IRSNB MI 10615: cut dorso-ventrally, etched (0.5% formic acid): inner surface of shell with very fine irregular complex cross foliation, visible part of single crystals measure about 2 to 5 µm, at least five different dip directions of stacks are visible.
 Fig. 12 — *Rastellum diluvianum* (LINNAEUS, 1767): left valve, X 2.5 (SEM: C 131), IG 11039, "argile inférieure", IRSNB MI 10583: internal view, short lath chomata on both sides of hinge.
 Fig. 13 — *Rastellum diluvianum* (LINNAEUS, 1767): right valve, X 160 (SEM: C 126), IG 11039, "argile inférieure", IRSNB MI 10616: inner surface in dorsal half of shell (untreated): irregular complex cross foliation.
 Fig. 14 — *Rastellum diluvianum* (LINNAEUS, 1767): left valve, X 442, bar 100 µm (SEM: C 137), IG 11039, "argile inférieure", IRSNB MI 10617: broken postero-dorsal edge near hinge, outer surface down, etched (2% formic acid): low angle cross foliation (in relation to surface of shell), intersected by irregular short pillars which are probably lath chomata which were altered during diagenesis.
 Fig. 15 — *Rastellum diluvianum* (LINNAEUS, 1767): left valve, X 360, bar 100 µm (SEM: C 134,1), IG 11039, "argile inférieure", IRSNB MI 10618: postero-dorsal edge, etched (2% formic acid): two 'bumps' of lath chomata, built up by weakly cross foliated sheets.

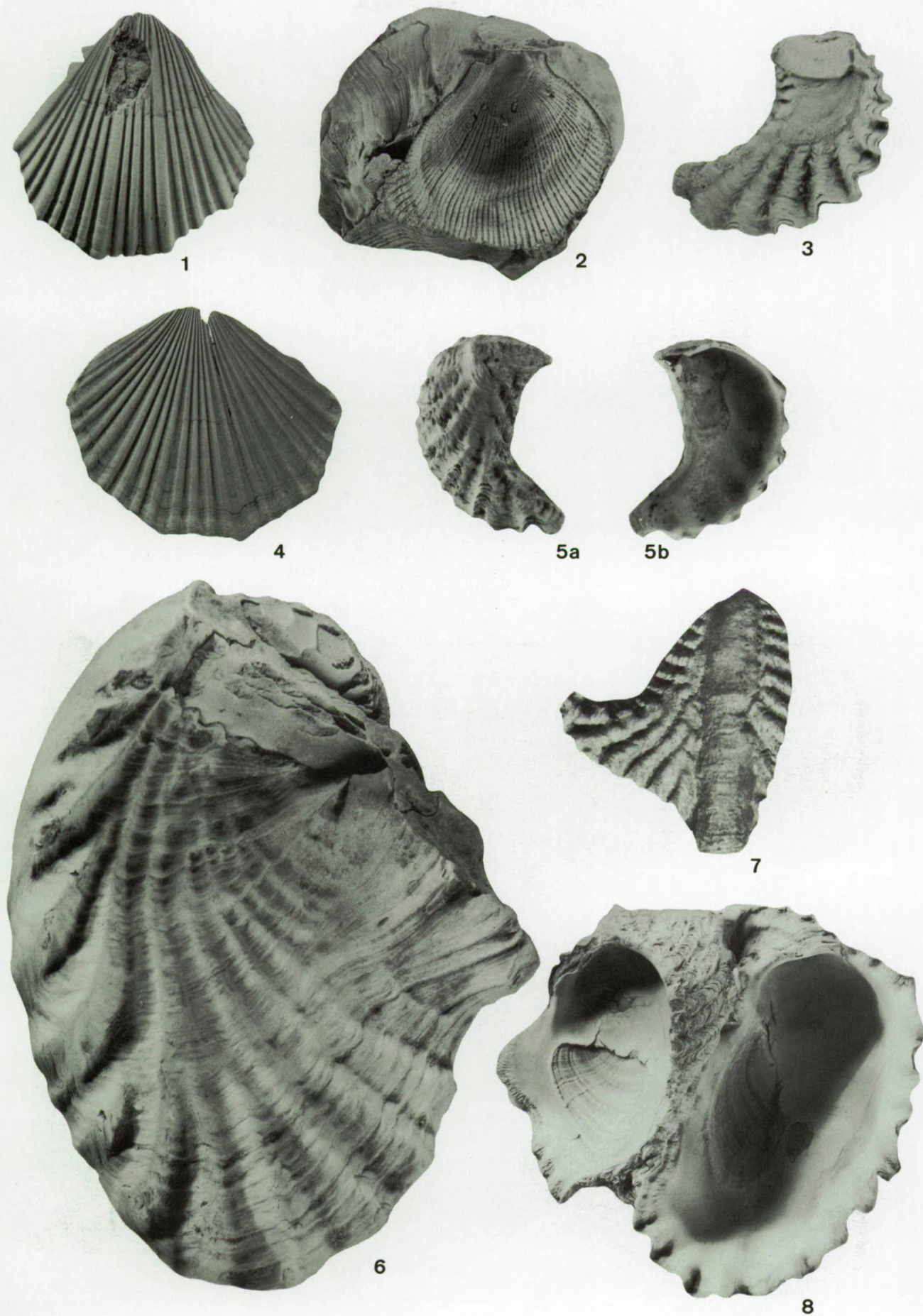
PLATE 6

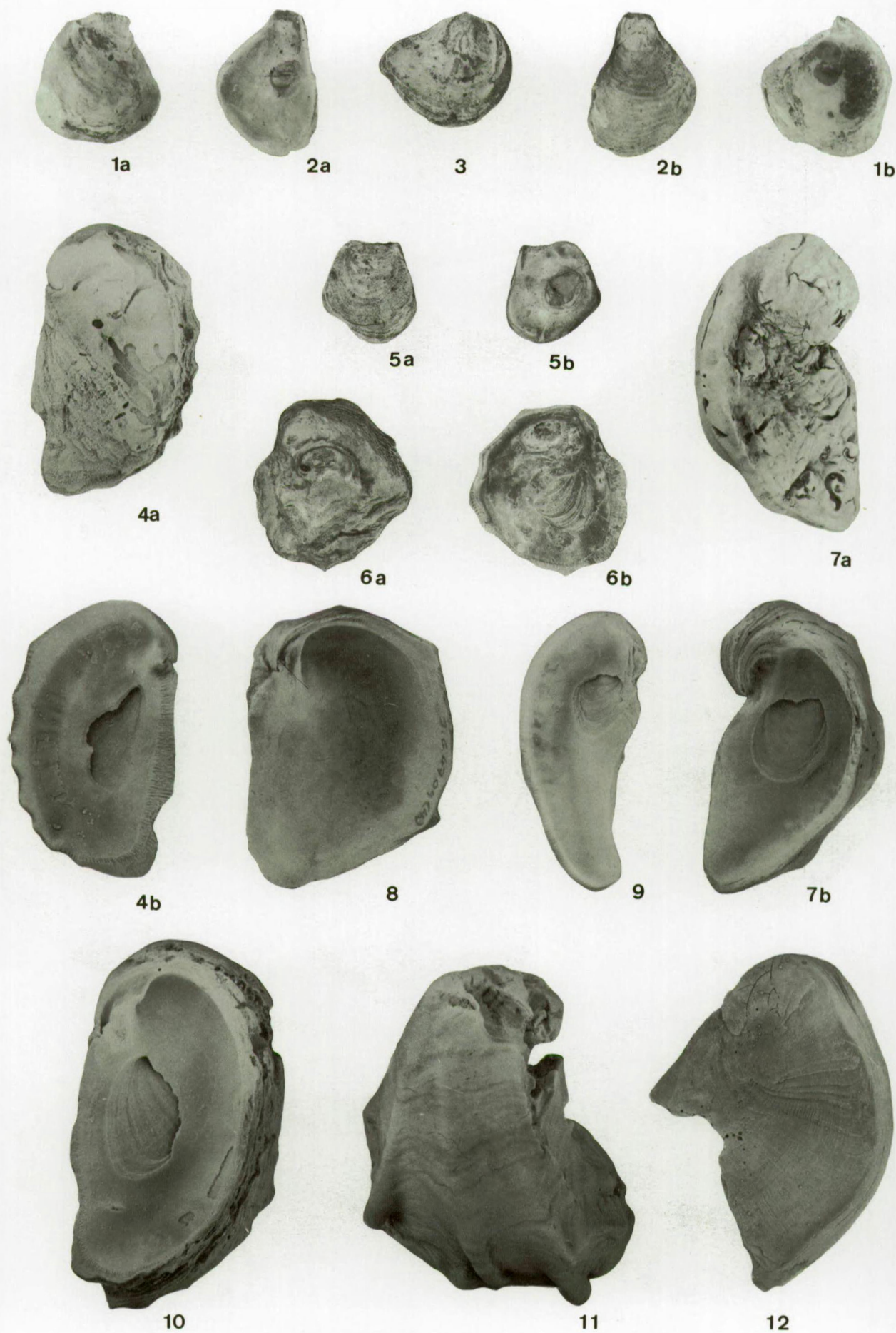
All specimens are from the Santonian of Lonzée.

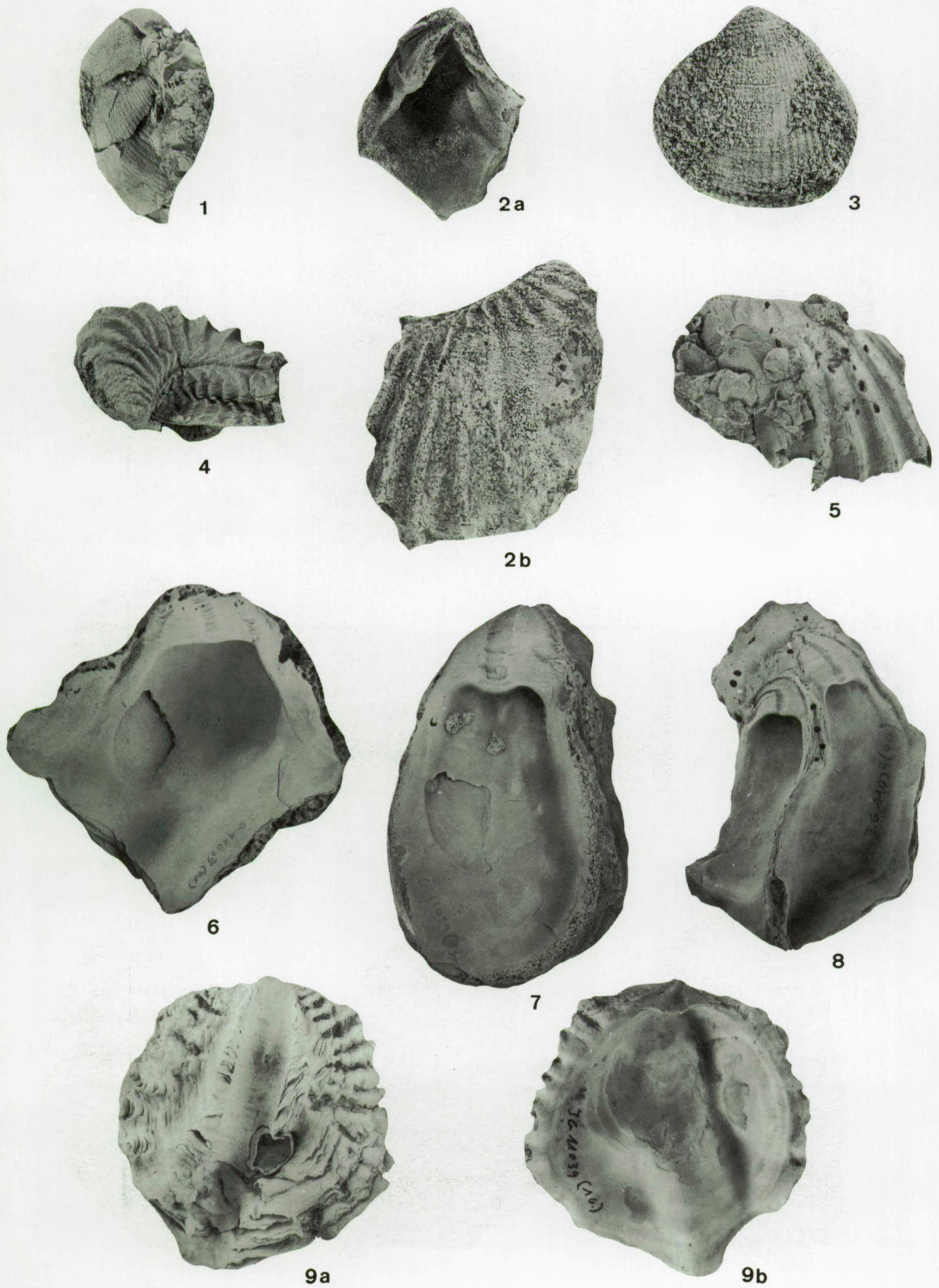
- Fig. 1 — *Pycnodonte* (*Phygraea*) *vesicularis* (LAMARCK, 1806): X 3 (SEM: C 158,2), right valve (exterior, beak is to the left), IG 11039, "argile inférieure", IRSNB MI 10619: the ventral exterior is covered with vesicular shell structure, some vesicles contain grains of green clay (probably glauconite).
 Fig. 2 — *Pycnodonte* (*Phygraea*) *vesicularis* (LAMARCK, 1806): close up of Fig. 1, X 6.3: the flanks of the straight and extended hinge show lath chomata, vesicles are visible in left centre.

- Fig. 3 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): X 115, bar 100 μ m, (SEM: C 121,2), left valve, IG 11039, "argile inférieure", IRSNB MI 10620: exterior of shell towards top, wavy simply foliate calcitic layers top a well developed layer of vesicular shell, in lower left follows a second vesicular layer.
- Fig. 4 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): close up of Fig. 3, X 925: upper left shows a primarily hollow vesicle filled with calcite during diagenesis. Unlike Figures 5 to 10, Fig. 4 presents the normal appearance of the vesicular part of the shell.
- Fig. 5 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): close up of Fig. 2, X 194, IRSNB MI 10619.
- Fig. 6 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): same specimen as Fig. 2, X 85, bar 1 mm: outer vesicular shell, the inner linings of the tubes are of unknown origin (? diagenetic, ? organisms).
- Fig. 7 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): close up of Fig. 6, X 1360: the inner lining of a single tube.
- Fig. 8 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): SEM, C159, X 274, IRSNB MI 10621: vesicular shell at the exterior and anterior shell margin, some vesicles are hollow, others are filled with strongly altered calcite.
- Fig. 9 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): close up of Fig. 8, X 549, bar 100 μ m.
- Fig. 10 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): same specimen as Fig. 8, X 274, bar 100 μ m: close up of vesicular layers from exteriorshell surface, strongly altered.
- Fig. 11 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): same specimen as Fig. 3, X 300, bar 100 μ m, IRSNB 10620: external broken surface, exterior of shell is up, herring bone cross foliation (see MALCHUS, 1990).
- Fig. 12 — *Pycnodonte (Phygraea) vesicularis* (LAMARCK, 1806): close up of Fig. 11, X 885, bar 100 μ m.











1



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3



4a



5



6



4b



7



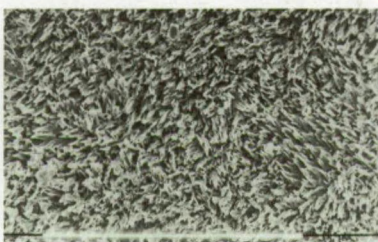
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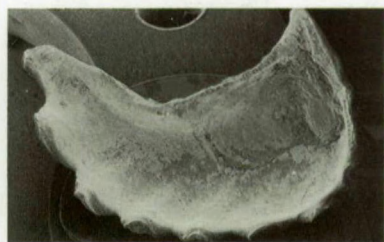
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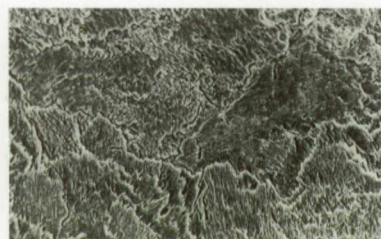
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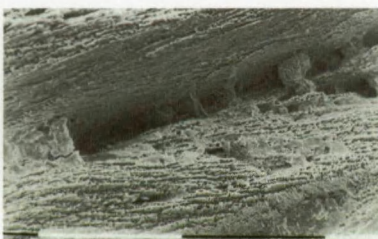
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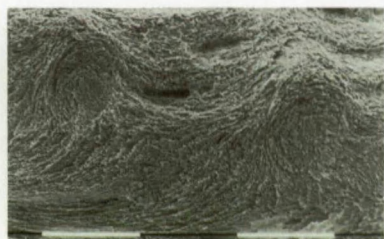
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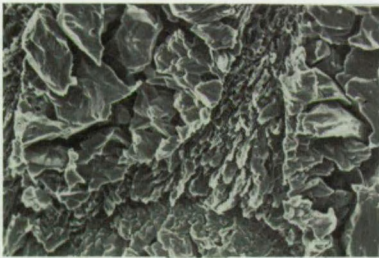
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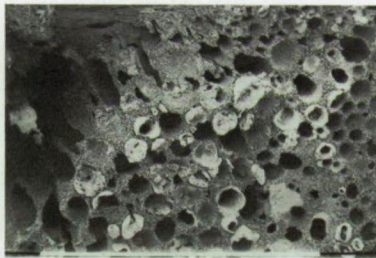
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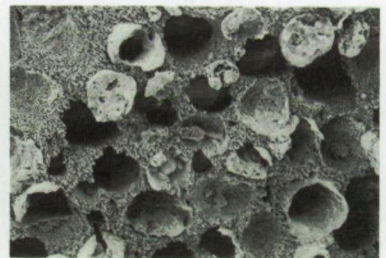
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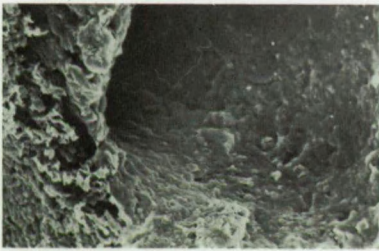
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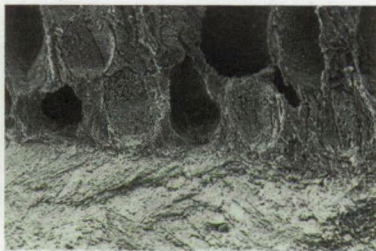
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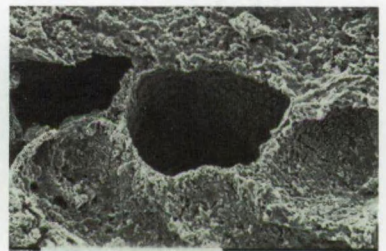
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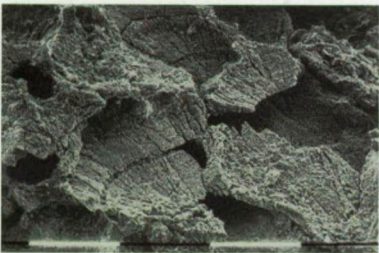
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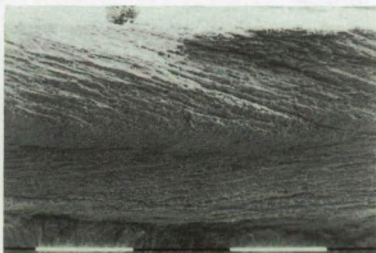
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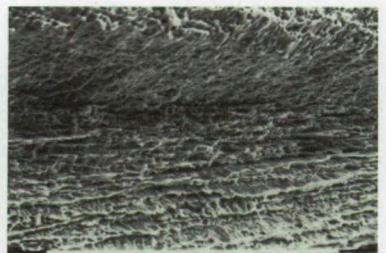
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