

Late Cretaceous Bivalves from the A 10 Exposures in Northern Aquitaine

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A. V. Dhondt. Late Cretaceous Bivalves from the A 10 Exposures in Northern Aquitaine. *Cretaceous Research* (1985) 6, 33–74. Fifty taxa of Late Cretaceous bivalves, collected between Saintes and Mirambeau during the construction of the A 10 motorway, have been identified. The pectinids, spondylids, limids and oysters are of better preservation and more diverse than the other groups. The faunas of Cenomanian age are from warm temperate to Tethyan seas. The assemblages collected from the Turonian–Coniacian strata are small and not diagnostic. Faunas of Santonian and Campanian age are diversified and the many *Plagiostoma* and *Pycnodonte* species indicate an upper shelf environment. These faunas have strong affinities with those from white chalks and other deposits from N.W. Europe. The fauna from the uppermost Campanian (equivalent to the top of the Aubeterre section, stratotype of the Campanian) indicates a much shallower environment and has many elements in common with the fauna from the Maastrichtian stratotype.

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KEY WORDS: Mollusca; Bivalvia; Taxonomy; Palaeobiogeography; Late Cretaceous; Cenomanian–Campanian; Aquitaine; Western France; N.W. Europe.

Parmi les Bivalves récoltés pendant la construction de l'autoroute A 10, entre Saintes et Mirambeau, 50 taxons ont pu être identifiés. Les Pectinidés, Spondylidés, Limidés et Ostrées sont mieux conservés et plus diversifiés que les autres groupes de Bivalves. Les faunes du Cénomaniens indiquent une provenance de mer tempérée plutôt chaude ou mésogéenne. Les assemblages récoltés dans les dépôts turoniens et coniaciens sont pauvres en espèces. Les faunes du Santonien et du Campanien sont très diversifiées et la présence de plusieurs espèces de *Plagiostoma* et de *Pycnodonte* indique un milieu "upper shelf". Ces faunes ont beaucoup d'éléments en commun avec celles de la Craie blanche et autres dépôts de l'Europe du NO. Au contraire, la faune du Campanien le plus supérieur (équivalent du sommet de la coupe d'Aubeterre, stratotype du Campanien) représente un milieu peu profond et a beaucoup d'éléments faunistiques communs avec la faune du stratotype du Maastrichtien.

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MOTS-CLÉS: Mollusques; Bivalves; Taxinomie Biostratigraphie; Paléobiogeographie; Crétacé supérieur; Cénomaniens; Campanien; Stratotype; Charente.

1. Introduction

The Cretaceous strata from the Charente (Northern Aquitaine, S.W. France) have been studied since the beginning of the 19th century. The exact stratigraphic age of the different outcrops in the Charente and in the nearby

Dordogne gave rise to numerous debates in French geology. Some of the opponents were d'Archiac, Coquand, Arnaud, Hébert, famous names in stratigraphy and palaeontology; their disputes make the reading of the *Bulletin de la Société Géologique de France* doubly interesting. The controversy has continued until fairly recently. The reasons for the disagreement are to be found in the originally, poorly-defined type-sections of the Coniacian, Santonian and Campanian stages, and in the difficulty of relating and integrating the uppermost Campanian from the Charente with the section in Limburg, at the Maastrichtian stratotype (near Maastricht, The Netherlands). Séronie-Vivien (1972) has written the only recent monograph on the Cretaceous stratotypes situated in Northern Aquitaine.

In the Charente outcrops (stratotypes and others) macrofossils of most groups are generally abundant and they have been known and studied since about 1830. Bivalves have been mentioned in many of the regional stratigraphic studies. However, "groups without stratigraphic importance", which include all Bivalves, except inoceramids and rudists, were only rarely studied. d'Orbigny (who was a native of S.W. France) in *Paléontologie Française* (volume on "Terrains Crétacés III. Lamellibranches", 1844–1847) described many species from the Charente deposits. Coquand (1859) also described many species, but the absence of illustrations makes the paper difficult to use. In 1869, the same author in *Monographie du Genre Ostrea* described and illustrated many oyster species of which some came from the Charente deposits. A monograph restricted to the Bivalves from the Cretaceous of the Charente, has never been written. Lists have been published; the latest one by Séronie-Vivien (1960). The absence of a study on Charente bivalves is regrettable: the faunas from that part of S.W. France are interesting, very diversified though often poorly preserved, different from the Paris Basic, in combining elements of the faunas from the temperate seas of N.W. Europe with those of the warmer Tethys. Some, probably endemic species, are also found in the Charente deposits, mainly in the Santonian.

2. Material and Methods

In 1979–1980, the construction of the Saintes–Mirambeau section of the A 10 motorway (l'Aquitaine: from Paris to Bordeaux), made temporary exposures accessible in the "Champagne charentaise", the region in which Coquand (1857) defined the stratotypes for the Coniacian, Santonian and Campanian stages. On those exposures, on behalf of the A 10 working group of the GFC (Groupe Français de Crétacé), under the supervision of Séronie-Vivien, careful collecting was undertaken to achieve a better biostratigraphic zonation in the "Senonian" stages (Groupe A 10, 1984, in this volume). Among the collected macrofossils, the bivalves form the most numerous group. The Inoceramidae have been studied by Sornay (this volume) and the rudists by Bilotte and Philip (this volume). I studied the bivalves which are known to be "without stratigraphic importance"; they were collected in most A 10 outcrops and were only lacking in exposures with numerous rudists. In all 1774 samples of these bivalves were collected, and numbered L1 to L1774. The abbreviations used in the taxonomic section of this paper are shown in the Appendix.

The identification was made by using the palaeontological literature, but whenever possible type-specimens were studied. The following type-collections were studied: Arkhanguelsky (1905) (MGRI, Moscow), Bobkova (1961) (VSEGEI, Leningrad), Coquand (1869, and others) (MAFI, Budapest), Eichwald (1865–1869) (LGU, Leningrad), Goldfuss (1833–1837) (University, Bonn), Hennig (1897) and Nilsson (1827) (University, Lund), d'Orbigny (1844–1847) and Péron (1888) (Muséum national-Paléontologie, Paris), Pasternak (1968) (National History Museum, Lwow), Rengarten (1964) (VSEGEI, Leningrad), Sobetzki (1977) (Palaeontological Institute USSR Academy of Sciences, Moscow), Sowerby (1812–1846, and others) (BM (NH), London), Woods (1899–1913) (BM (NH), London and Sedgwick Museum, Cambridge), Zittel (Naturhistorisches Museum, Vienna).

The purpose of the present paper is: (1) the systematic identification of the bivalves collected from the A 10 Cretaceous outcrops; (2) the indication of their stratigraphic distribution in the A 10 sections; (3) the comparison of these faunas with those previously described from northern Aquitaine, and with other Late Cretaceous faunas; (4) palaeoecological interpretations of the Northern Aquitaine Late Cretaceous faunas.

3. Systematic palaeontology

3.1. *Introduction*

After a preliminary identification, it became obvious that the faunas collected on the A 10 construction sites represented most of the bivalve families mentioned by d'Orbigny (1844–1847 and 1850). Unfortunately, because of the modern excavation methods used on the motorway construction, the collecting conditions were not ideal. For many families the bivalve material consists only of poorly preserved interior moulds. The first aim was the systematic identification of the material but because of poor preservation no taxonomic status could be assigned to about 25% of the samples. A further 25% could not be identified beyond the family level.

For the other samples specific identifications were made, but in many cases they remained tentative. As a result, for 12 taxa only the family/genus level has been indicated, whereas for 38 taxa the species/subspecies level has been reached. The uncertainties are almost always due to inadequate preservation. No attempt has been made at redescribing the identified species, but a few diagnostic remarks have been made when necessary. The types of many figured specimens were studied previously in various museums (see above) and the synonymies and interpretations have often been based on those. For those oyster species for which no recent species descriptions are available and for which confusion existed, a detailed synonymy list has been added. When the revision of the oyster species from the Coquand collection shall be completed, it is hoped that specific problems in Cretaceous oyster systematics will be, at least partly, solved. The classification used is largely that of Moore (1969, 1971).

3.2. *Systematic notes**Family Arcidae*(1) “*Arca*” species

Unidentifiable arcid moulds have been found at S7 (1419: Turonian). The specimens cannot be identified beyond a tentative generic level. d’Orbigny (1844–1847) described several species based largely on similar moulds from deposits of the same region. Further systematic conclusions cannot be reached without better material.

Family Cucullaeidae(2) “*Cucullaea*” species

Unidentifiable cucullaeid moulds have been found at the same locality as the previous “species”. In the same way their preservation is inadequate for identification beyond a tentative generic level. d’Orbigny (1844–1847) did not differentiate “*Arca*” and “*Cucullaea*”; hence, some of the *Arca* species described by him from the deposits around Sainte, would be considered today as belonging to *Cucullaea*.

Family Mytilidae(3) *Regoria dufrenoyi* (d’Archiac, 1837)

- . 1837 *Modiola Dufrenoyi* A. d’Archiac, p. 188, pl. 12, fig. 10a, b;
- . 1844 *Mytilus Dufrenoyi* d’Orbigny, 1844: A. d’Orbigny, pp. 284–285, pl. 343, figs 1–3;
- v. 1959 *Regoria dufrenoyi* d’Orbigny: S. Freneix, p. 196

Material A 10. One poorly preserved specimen from S3 (1078: Santonian).

Discussion

—The taxonomic affinities of *Regoria* are somewhat uncertain. As a mytilid it is unusual. *R. dufrenoyi* was originally described from Montendre (arr. Jonzac, Charente maritime) and is so far only known from the Santonian–Campanian of the Charente–Dordogne region.

Family Pinnidae(4) “*Pinna*” species

[Figure 1(a)]

Fragments of pinnid species have been found at S3 (1086: Santonian). Their preservation makes specific identification, always difficult with Cretaceous pinnids, impossible.

Family Bakevellidae(5) *Gervillia solenoides?* Defrance, 1820

1820 *Gervillie solénoïde* M. Defrance, pp. 502–503;

1959 *Gervillia solenoides* Defrance: S. Freneix, p. 200;

1969 *Gervillia (G.) solenoidea* L. R. Cox in R. C. Moore, p. N308, fig. C41, 4.

Material A 10. Found at S2 (1018: Santonian).

Discussion

—The preservation in this group is generally poor and Defrance's species has never been clearly defined. The specimen from the Charente probably belongs to this species group. The species was originally described from the "Calcaire à Baculites" in the Cotentin (probably of Maastrichtian age). It has later been recorded from many Late Cretaceous localities in Europe, but the often insufficient preservation makes it possible that some of those identifications are dubious.

Family Pectinidae(6) *Syncyclonema nilsoni* (Goldfuss, 1835)

. 1835 *Pecten Nilsoni* m. A. Goldfuss, p. 76, pl. 98, fig. 8a,b;

v. 1971 *Syncyclonema nilsoni* (Goldfuss, 1835): A. V. Dhondt, pp. 54–63, pl. IV (with detailed description and synonymy).

Material A 10. Found at P8 (705, probably Campanian).

Discussion

—The specimen found is incomplete, yet the auricles are present and this makes the identification almost certain. The species is widely distributed in temperate, warm-temperate and marginal Tethys deposits of Late Cretaceous age.

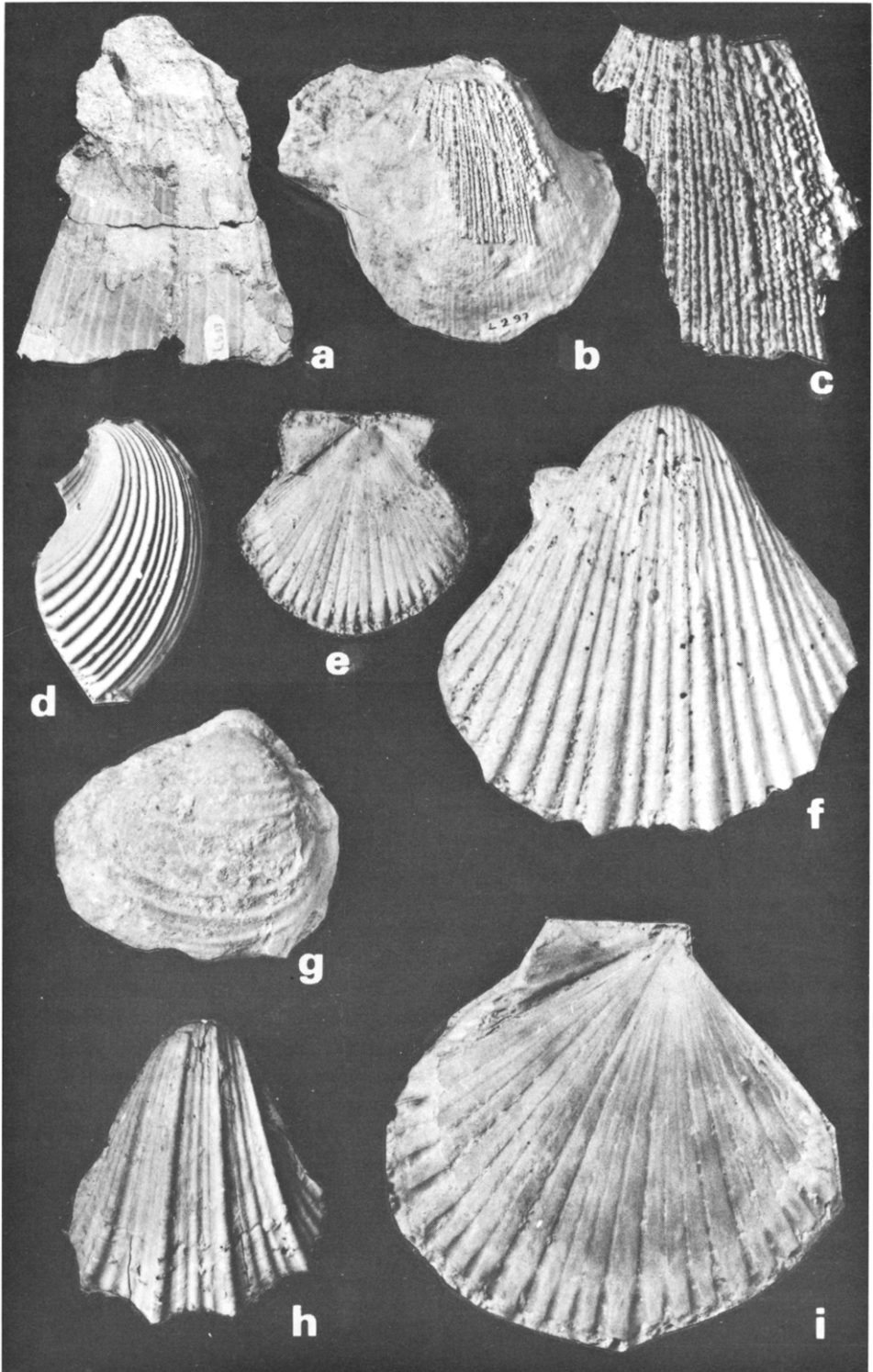
(7) *Lyropecten (Aequipecten?) ternatus* (Muenster in Goldfuss, 1833)

v. 1972 *Lyropecten (Aequipecten?) ternatus* (G. von Muenster in A. Goldfuss): A. V. Dhondt, pp. 42–56, pl. II, fig. 3(a,b), pl III, fig. 1a–d (with detailed description and synonymy).

Material A 10. Found in S8 (1482: Turonian), P6 (368–398: Coniacian), S4 (1143: Santonian), P8 (705: Campanian), J4 (514: Campanian). Preservation poor, but sufficient for identification.

Distribution

—Widely distributed in warm temperate Eurasian seas of Cenomanian to latest Maastrichtian age; rare in chalks, but common in calcarenitic and other coarse-grained deposits. d'Orbigny (1847) mentioned this species from the Charente as *Pecten dujardini* (pp. 615–616).



(8) *Chlamys* cf. *royana* (d'Orbigny, 1847)

v? 1847 *Pecten.royanus* A. d'Orbigny, p. 613, pl. 438, figs 7–12.

Material A 10. Found at P5 (Turonian), P8 (665, 722 low in the Campanian), J0 (uppermost Campanian).

Discussion

—The material is poorly preserved and a precise identification is impossible. The rib ornamentation is difficult to see and none of the specimens shows a complete shell. The rib number varies between 25 and 35. In 1973, I have considered (Dhondt, 1973a, p. 13) *Pecten royanus* as probably synonymous with *Chlamys faujasi* (Defrance). The material collected on the A 10 exposures is too incomplete to be compared with *Chlamys faujasi* or any other *Chlamys* species. The only certainty we derive from it, is the definite presence in the A 10 material of at least one *Chlamys* species.

(9) *Mimachlamys cretosa* (Defrance, 1822)

- . 1822 *Pecten cretosus* Defr.: M. Defrance in A. Brongniart, p. 251, 599, pl. 3, fig. 8;
- v. 1902 *Pecten (Chlamys) cretosus* Defrance: H. Woods, pp. 174–179, pl. 32, figs 4–6, pl. 33, figs 1–12;
- v. 1973 a *Mimachlamys cretosa* (M. Defrance in A. Brongniart, 1822): A. V. Dhondt, pp. 77–92, pl. 6, fig. 2, pl. 7, fig. 1 (with detailed synonymy and discussion);
- . 1983 *Mimachlamys cretosa* (Defrance, 1822): A. V. Dhondt, p. 851.

Material A 10. Found at S4 (1138: Santonian), S3 (1078: Santonian), J4 (500–501: Campanian), J2 (383: Campanian), J0 (uppermost Campanian). The specimens are relatively numerous especially in the J0 section. Preservation is adequate.

Discussion

—In 1973, I discussed the wide variability of *Mimachlamys cretosa* and mentioned the possible relation between the lithology of sediments and the ornamentation. Generally, the fine-ribbed—sometimes smooth-ribbed—variety, is found in fine-grained sediments such as White Chalk. Some of the specimens from J0 (a semi-coarse grained sediment) are ornamented with a pattern in which stronger and less pronounced ribs follow in the same way all over the shell. This pattern is found in the taxon *Pecten barbesillensis*

Figure 1. (a) *Pinna* species, A 10 material: L633 from S3 (Santonian), $\times \frac{1}{2}$; (b) *Spondylus santonenis* d'Orbigny, 1847, A 10 material: L293 from S3 (Santonian), $\times \frac{1}{2}$; (c) *Spondylus santonenis* d'Orbigny, 1847, same specimen as (b) detail of ornamentation, $\times 1$; (d) *Neithea regularis* (Schlotheim, 1813), side view of right valve showing areal and auricular riblets, A 10 material: L197 from S3 (Santonian), $\times 2$; (e) *Neithea regularis* (Schlotheim, 1813), inside of left valve, with ribs of almost equal development, A 10 material: L291, S3 (Santonian), $\times 2$; (f) *Neithea regularis* (Schlotheim, 1813), right valve, A 10 material L1556 from S3 (Santonian), $\times 2$; (g) "*Corbis*" *striaticostata*, d'Orbigny, 1844, A 10 material, L133 from S2 (Santonian), $\times \frac{2}{3}$; (h) *Neithea regularis* (Schlotheim, 1813), right valve, A 10 material: L1318 from J4 (Campanian), $\times 2$; (i) *Neithea regularis* (Schlotheim, 1813), inside of left valve, principal ribs more developed than intercalary, A 10 material, L1096 from J2 (Campanian), $\times 2$.

(d'Orbigny, 1847, p. 611, pl. 437, figs 5–8); *P. barbesillensis* is certainly a junior synonym of *Mimachlamys cretosa*.

Distribution

—Widely distributed from the Turonian to latest Maastrichtian, more frequent in fine-grained deposits.

(10) *Merklinia septemplicata* (Nilsson, 1827)

v. 1827 *Pecten septemplicatus* S. Nilsson, p. 20, pl. 10, fig. 8;

v. 1972 *Lyropecten? septemplicatus* (S. Nilsson, 1827): A. V. Dhondt, pp. 59–65, pl. 3, fig. 3 (with detailed synonymy and discussion);

v. 1983 *Merklinia septemplicata* (Nilsson, 1827): A. V. Dhondt, p. 85.

Material A 10. Found at J0 (288): two incomplete but identifiable specimens, from the uppermost Campanian.

Discussion

—Both specimens show the typical wide intercostal areas and ribs; the better preserved specimen also shows the fine riblets.

Distribution

—*M. septemplicata* has been found in northern Tethys areas from Santonian to late Maastrichtian (Austria, Bulgaria, N. Spain), and also in shallow coastal temperate seas of Campanian and Maastrichtian age (Belgium, the Netherlands, Germany (Harz), Sweden).

(11) *Neithea* cf. *quinquecostata* (Sowerby, 1814)

v. 1814 *Pecten quinquecostatee* J. Sowerby, pp. 122–123, pl. 56, figs 4–6;

v. 1973b *Neithea (Neithea) quinquecostata* (J. Sowerby, 1814): A. V. Dhondt, pp. 29–37, pl. 2, figs 2a–c (with detailed synonymy and description);

v. 1983 *Neithea quinquecostata* (Sowerby, 1814): A. V. Dhondt, p. 852.

Material A 10. Found at J3 (453: Campanian), J4 (493: Campanian).

Discussion

—Three incomplete specimens are considered as possibly belonging to *Neithea quinquecostata*. In two of their intercostal intervals only three intercostal ribs are present, whereas *N. quinquecostata* generally has four intercostal ribs in each intercostal interval. These specimens from the Charente could thus be considered as intermediate between *N. quinquecostata* and *N. regularis*, but this is not confirmed by the very numerous *N. regularis* specimens which never seem to have more than three intercostal ribs in the intercostal intervals.

Distribution

—*N. quinquecostata* has an unusually long existence (Albian to latest Maastrichtian) and has been found in most marine Cretaceous deposits.

(12) *Neithea regularis* (Schlotheim, 1813)

[Figure 1(d–f), (h–i)]

- 1813 *Pectinites regularis* E. F. von Schlotheim, p. 112;
 v. 1973b *Neithea (Neithea) regularis* (E. F. von Schlotheim, 1813): A. V. Dhondt, pp. 20–26, pl. 1, fig. 3, pl. 2, figs 1a–d; (with detailed description and synonymy);
 . 1983 *Neithea regularis* (Schlotheim, 1813): A. V. Dhondt, p. 852.

Material A 10. *Neithea regularis* is the most common pectinid in the A 10 sections and has been found in localities from the Coniacian to the Campanian: Coniacian: P6, S4 (1195), Santonian: S4 (1128), S4 (1143), S3 (1088), S3 (1078), S2 (1018), S2 (961), J6 (579), J6 (576), S1, Campanian: P8, J4 (513–515), J4 (500–501), J3 (453), J2 (383), J1, J0. In all about 140 specimens have been collected.

Discussion

—*N. regularis* is characterized by 21 ribs, six are more pronounced and in the intercostal intervals between those six there are three intercostal ribs of generally equal development. On the areas and on the auricles a few riblets are present in well preserved specimens. The difference between the six principal and the intercostal ribs can be more or less pronounced. On young (small) specimens the difference between principal and intercostal ribs is always more pronounced than on larger (older) specimens. d'Orbigny in 1847 described as *Janira quadricostata* (pp. 644–646, pl. 447, figs 1–7) specimens undoubtedly belonging to *N. regularis*, which came from the Charente.

Distribution

—*N. regularis* is widely distributed from the Turonian to latest Maastrichtian; it generally occurs in coarse-grained sediments and has been found from North America (frequently found in the Campanian of the Gulf and Atlantic Coastal Plains) to the Russian Platform in uppermost Cretaceous strata. It is mainly found in the more southern parts of the temperate seas.

(13) *Neithea sexangularis* (d'Orbigny, 1847)

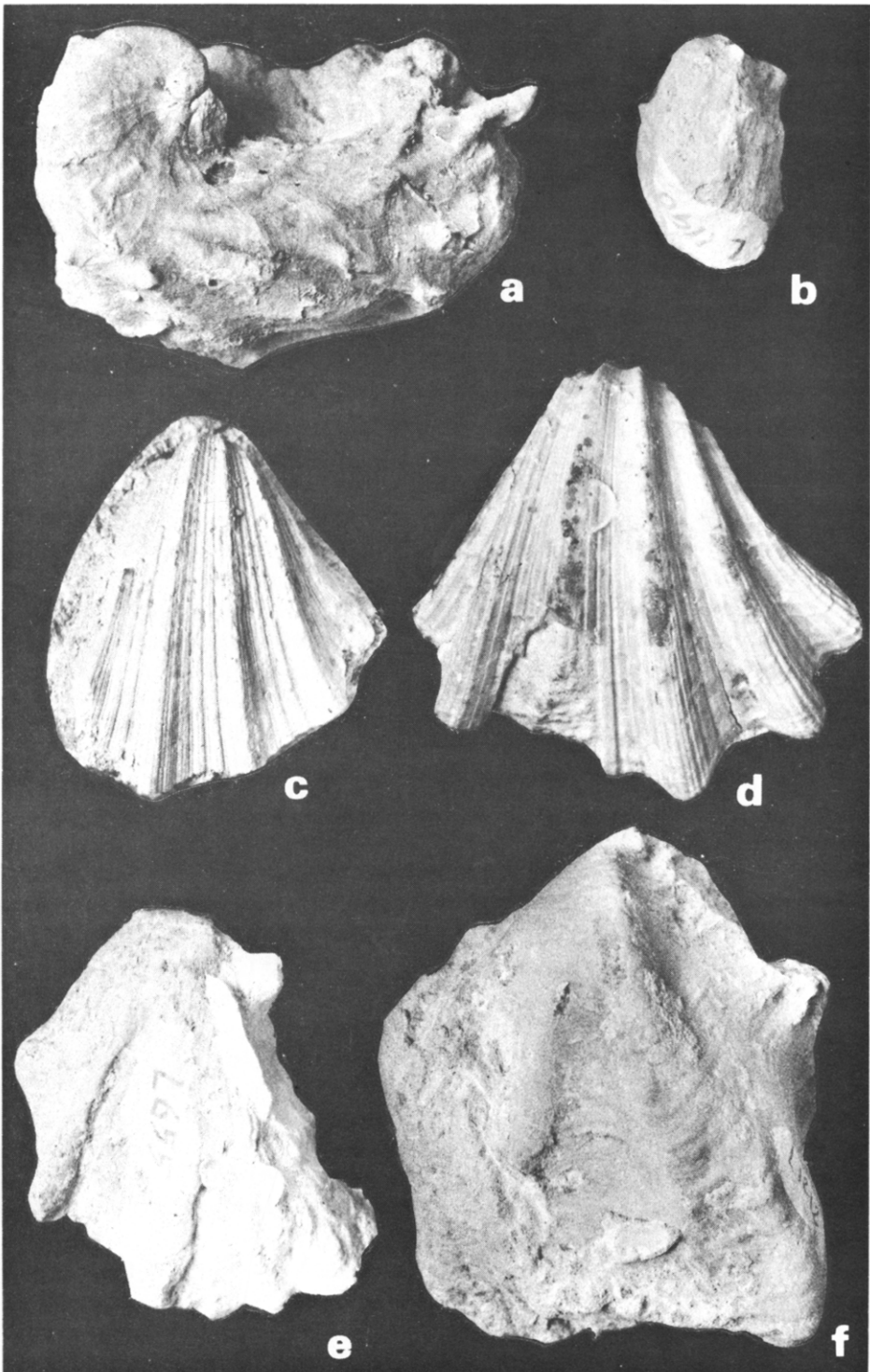
[Figure 2(d)]

- v. 1847 *Janira sexangularis* A. d'Orbigny, pp. 648–649, pl. 448, figs 5–8;
 v. 1973b *Neithea (Neithea) sexangularis* (A. d'Orbigny, 1847): A. V. Dhondt, pp. 53–55, pl. 3, fig. 3 (with detailed synonymy and description);
 v. 1983 *Neithea sexangularis* (d'Orbigny, 1847): A. V. Dhondt, p. 852.

Material A 10. Found only in the Campanian (J3, J4, P8).

Discussion

—The material of *Neithea sexangularis* and *N. striatocostata* collected on the A 10 exposures is relatively poorly preserved. Nevertheless it shows that,



contrary to my previous statements (Dhondt, 1973*a,b*, 1983), *N. sexangularis* cannot be accepted as a species: it is only an extreme variation of *N. striatocostata*. However, this extreme variation is not found in all strata in which *N. striatocostata* is known to occur, but is limited to the Campanian and geographically it seems restricted to warm temperate and northern Tethys seas. I have mentioned *N. sexangularis* as a separate taxon to draw attention to this change in variability.

(14) *Neithea striatocostata* (Goldfuss, 1833)

[Figure 2(c)]

v. 1833 *Pecten striato-costatus* A. Goldfuss, p. 55, pl. 93, figs 2a, b, g, f:

v. 1973*b* *Neithea* (*Neithea*) *striatocostata* (A. Goldfuss, 1833): A. V. Dhondt, pp. 48–53, pl. 3, figs 2a–d (with detailed synonymy and discussion);

v. 1983 *Neithea striatocostata* (Goldfuss, 1833): A. V. Dhondt, p. 853.

Material A 10. Found at S4, J6 (Santonian) and at P8, J4, J3, J2, J0 (Campanian).

Discussion

—*Neithea striatocostata* has been recognized as a very variable species in areas where it occurs frequently, such as the Late Maastrichtian deposits near Maastricht (Netherlands) (Dhondt, 1973). In the same article I described *N. sexangularis* from the Campanian of the Charente as a separate species which had evolved from *N. striatocostata* and had similar (but more strongly developed) characteristics: more strongly prominent principal ribs, more intercostal riblets, and a wider disc. The relatively numerous material from the sections of the A 10, despite its often poor preservation, shows that in the lower and middle Campanian exposures *N. striatocostata* has a wider and slightly different variability than it does in the underlying Santonian and in the overlying uppermost Campanian strata. *N. sexangularis* is an extreme of this wide variability series: the intercostal riblets are slightly thinner and more numerous, the principal ribs are somewhat more sharply angular, especially near the ventral margin. To draw attention to this change in variability I have kept *N. striatocostata* and *N. sexangularis* as separate taxa, but do not believe that they form separate biological entities. The change in variability in the Campanian may be due to a change in environmental conditions.

Family Spondylidae

(15) *Spondylus dutempleanus* d'Orbigny, 1847

Figure 2. (a) *Ceratostreon pliciferum* (Dujardin, 1837), left valve, A 10 material, L87 from S1 (Santonian), $\times \frac{3}{2}$; (b) *Gryphaeostrea canaliculata* (Sowerby, 1813), left valve, A 10 material, L1140 from J2 (Campanian), $\times 2$; (c) *Neithea striatocostata* (Goldfuss, 1833), right valve, A 10 material, L930 from J0 (uppermost Campanian), $\times \frac{3}{2}$; (d) *Neithea sexangularis* (d'Orbigny, 1847), right valve, A 10 material, L869 from P8 (Campanian), $\times 2$; (e) *Vultogryphaea laciniata* (Nilsson, 1827), left valve, A 10 material, L655 from S4 (Santonian), $\times 2$; (f) *Vultogryphaea laciniata* (Nilsson, 1827), left valve, A 10 material, L1212 from J3 (Campanian), $\times 2$.

- . 1847 *Spondylus Dutempleanus* A. d'Orbigny, p. 672, pl. 460, figs 6–11;
- v. 1901 *Spondylus Dutempleanus* d'Orbigny: H. Woods, pp. 125–127, pl. 22, figs 11–14, pl. 23, figs 1–5;
- v. 1982 *Spondylus dutempleanus* d'Orbigny: A. V. Dhondt, pp. 85–86, pl. 2, figs 1, 2, 3, 4, pl. 4, fig. 5.

Material A 10. Found at S4 (1143: Santonian), P8 and P8 (705) both Campanian, J4 (513–514: Campanian), J3 (Campanian).

Discussion and distribution

—*Spondylus dutempleanus* occurs frequently in the Late Cretaceous Chalks of the temperate seas of Eurasia. Occasionally, it has also been found in more coarse-grained deposits. On the A 10 exposures *Sp. dutempleanus* is infrequent, and was not mentioned by d'Orbigny as occurring in the Charente or in S.E. France. However, *Sp. royanus* from the uppermost Campanian of Royan (1847, p. 671, pl. 460, figs 1–5) and *Sp. hippuritarum* from the lower Senonian of S.E. France (1847, pp. 664–665, pl. 455) seem to be close to *Sp. dutempleanus*.

(16) *Spondylus* cf. *latus* (Sowerby, 1815)

- . 1815 *Dianchora lata* J. Sowerby, p. 184, pl. 80, fig. 2;
- . 1901 *Spondylus latus* (Sowerby, 1815): H. Woods, pp. 121–124, pl. 22, figs 1–10;
- . 1968 *Spondylus latus* (Sowerby, 1815): S. I. Pasternak, *et al.*, p. 187, pl. 38, figs 7–8;
- . 1974 *Spondylus latus* (Sowerby, 1815): O. V. Savchinskaja, p. 94, pl. 27, figs 11, 12.

Material A 10. Probable *Spondylus latus* specimens have been found at S3 and S4 (Santonian) and at J4 (Campanian).

Discussion

—The four specimens tentatively identified as *Sp. cf. latus* are poorly preserved (almost steinkern preservation). It is not impossible that *Sp. globulosus* described by d'Orbigny (1847, pp. 667–668, pl. 458) from Saintes and Cognac also belongs here. *Sp. latus* has been recorded from the Late Cenomanian to the Maastrichtian in temperate seas; generally in Chalks in Europe.

(17) *Spondylus santonensis* d'Orbigny, 1847

[Figure 1(b, c)]

- . 1847 *Spondylus santonensis* A. d'Orbigny, pp. 666–667, pl. 457, figs 1–4.

Material A 10. Found at S4 (1143) and at S3 (1087–1098), both Santonian; the specimens are largely steinkerns with patches of shell with the typical ornamentation.

Discussion

—*Spondylus santonensis* is a large, very spiny, free living spondylid which has been adequately described by d'Orbigny. The specimens from the A 10 have $W = 85$ mm, which makes them somewhat smaller than the dimensions given by d'Orbigny. The species seems to be restricted to the Santonian of the Charente. However, it could well be that *S. asper* described from the Santonian–Campanian of Westphalia by Goldfuss (1835, pp. 96–97, pl. 106, fig. 1) and not uncommon in Late Cretaceous temperate seas of Europe, is closely related to *Sp. santonensis*.

(18) *Spondylus* cf. *spinosus* (Sowerby, 1814)

- . 1814 *Plagiostoma spinosa* J. Sowerby, p. 177, pl. 78, figs 1–3;
- . 1837 *Spondylus Spinosus* (Sow.): A. d'Archiac, p. 186;
- . 1847 *Spondylus spinosus* (Sow.): H. Woods, pp. 127–134, pl. 23, figs 6–11, pl. 24, figs 1–7 (with detailed synonymy and description);
- . 1983 *Spondylus spinosus* (Sowerby, 1814): A. V. Dhondt, p. 854.

Material A 10. Found at S4 (1143: Santonian) and at J4 (500–501: Campanian), the specimens are relatively poorly preserved.

Discussion

—The specimens seem to have rather more, smaller spines and a higher ribnumber than the average *Spondylus spinosus*. Hence the doubt for the identification. The specimens here considered—especially that one found at S4—are difficult to classify. Their characteristics are almost intermediate between *Sp. spinosus* and *Sp. serratus* (Woods, 1901, pp. 124–125, pl. 21, figs 6–7).

Distribution

—Widely distributed in Turonian–Late Campanian strata, mainly in white chalks.

(19) *Spondylus truncatus* (Lamarck, 1819)

- . 1819 *Podopsis truncata* J. B. de Lamarck, p. 195, no. 1, pl. 188, figs 6, 7;
- . 1835 *Spondylus truncatus* A. Goldfuss, pp. 97–98, pl. 106, fig. 4a, b;
- . 1837 *Spondylus Truncatus* (Lam.): A. d'Archiac, p. 185;
- . 1837 *Spondylus truncatus* Deshayes: F. Dujardin, p. 228;
- . 1847 *Spondylus truncatus* Goldfuss: A. d'Orbigny, pp. 668–670, pl. 459, figs 1–6;
- ? 1977 *Dianchora truncata* (Lamarck, 1819): V. A. Sobetzki, pp. 85–86, pl. 6, figs 1–2.

Material A 10. Found at S4 (Santonian), P8 and J4 (Campanian).

Discussion

—The specimens from the Charente are very close to those which were described by d'Orbigny from Touraine.

Distribution.

—In Santonian to Campanian strata of the temperate Cretaceous seas of Europe.

Family Anomiidae(20) *Anomia species*

Probable anomiid specimens have been found at J0 (uppermost Campanian).

Family Limidae(21) *Lima dujardini* (Deshayes, 1832)

- . 1832 *Lima Dujardini* G. P. Deshayes, p. 353;
- v? 1835 *Lima squamifera* A. Goldfuss, p. 88, pl. 103, fig. 3a–b;
- . 1837 *Lima dujardini* Desh: F. Dujardin, p. 227, pl. 16, fig. 3a, b;
- v. 1847 *Lima Dujardini*, Desh: d'Orbigny, pp. 569–570, pl. 427, figs 1–4;
- 1959 *Lima (Lima) dujardini* (Deshayes): S. Freneix, pp. 218–219.

Material A 10. Found at S3 (1078: Santonian).

Discussion

—In the deposits of the Touraine (Coniacian–Santonian) *L. dujardini* occurs frequently. In the Charente it is rare: Arnaud (1877, p. 32) mentioned it from the Coniacian; in the BM (NH), London collections there is a specimen from the Coniacian of Cognac; on the sections of the A 10 one specimen has been collected in the Santonian. *Lima dujardini* is characterized by 35–42 straight, equal ribs with occasional irregularly disposed scales. *L. squamifera* described from the Late Maastrichtian of Maastricht by Goldfuss has similar characteristics but possibly more scales on the ribs.

L. dujardini as interpreted here, has an unusual distribution; Turonian (?) to latest Maastrichtian of the extended Paris Basin. It seems to prefer a coarse-grained sediment.

(22) *Ctenoides tecta* (Goldfuss, 1835)

[Figure 3(e)]

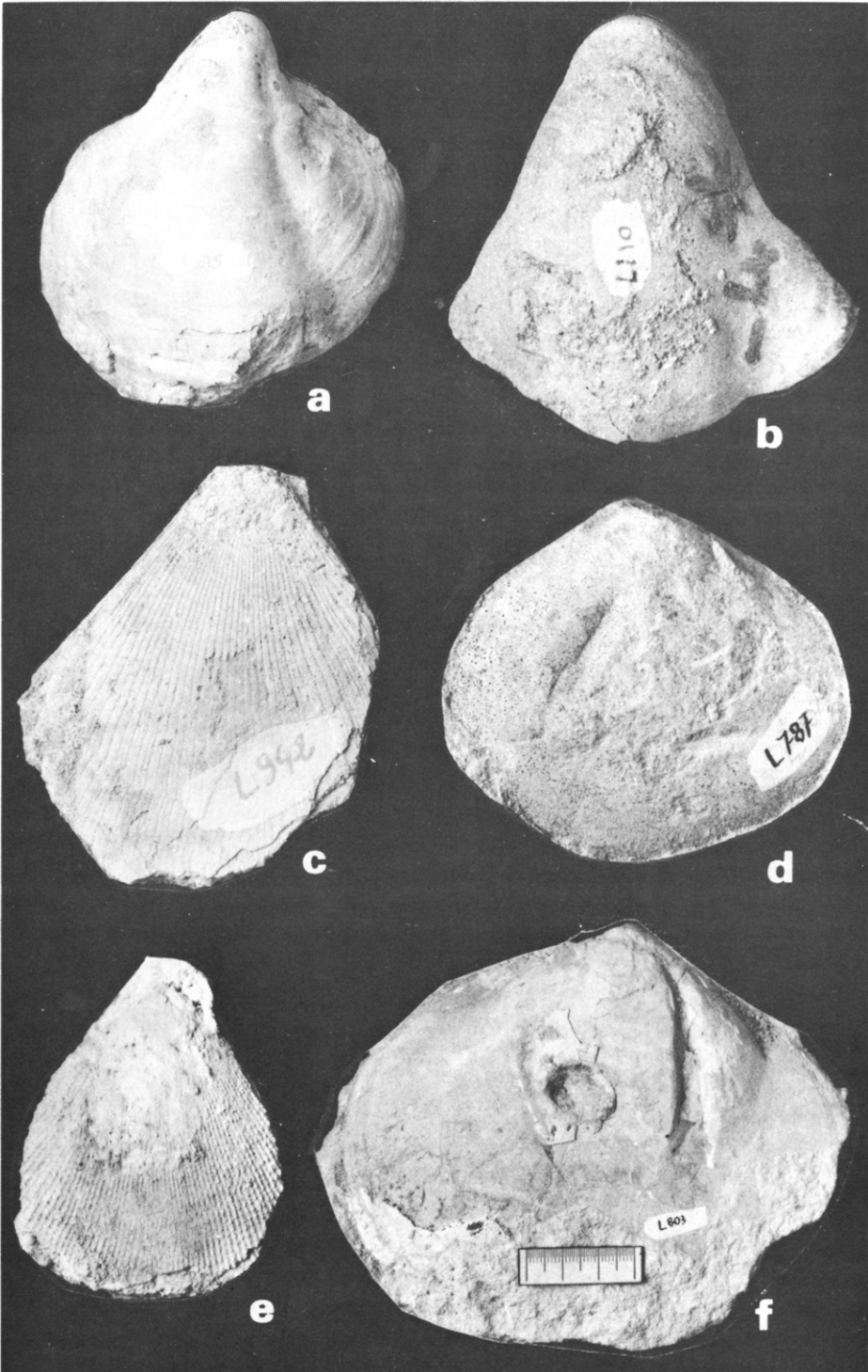
- v. 1835 *Lima tecta* A. Goldfuss, p. 91, pl. 104, figs 7a–c.

Material A 10. Found at S4, S2 and P9 (all Santonian).

Discussion

—Probably *Ctenoides tecta* which is a variable species, also includes the following taxa, which have sometimes been included in it previously or at

Figure 3. (a) *Rhynchostreon suborbiculatum* (Lamarck, 1801), left valve, A 10 material, L615 from S7 (Turonian), $\times \frac{2}{3}$; (b) *Pycnodonte vesiculare proboscideum* (d'Archiac, 1837), left valve, A 10 material, L110 from S2 (Santonian), $\times \frac{2}{3}$; (c) *Plagiostoma cretaceum* (Woods, 1904), A 10 material, L942 from J0 (uppermost Campanian), $\times \frac{2}{3}$; (d) *Plagiostoma santonense* (d'Orbigny, 1847), (note longitudinal mark), L787 from P8/9 (Santonian–Campanian boundary), $\times 1$; (e) *Ctenoides tecta* (Goldfuss, 1835), A 10 material, L166 from S2 (Santonian), $\times 2$; (f) *Plagiostoma santonense* (d'Orbigny, 1847), (note longitudinal mark and round (?) *Globidens*-tooth mark), L803 from P8/9 (Santonian–Campanian boundary), $\times \frac{1}{2}$.



least have been considered as closely related to it: *Lima divaricata* Dujardin, 1837 (p. 227, pl. 16, fig. 7 from the Senonian of Touraine), *Lima goupilii* Potiez and Michaud, 1844 (p. 96, pl. 52, fig. 6), *Lima frondosa* Dujardin, 1837 (p. 227, pl. 16, figs. 10a, b from the Lower Senonian of Touraine), *Lima rapa* d'Orbigny, 1847 (p. 546, pl. 419, figs 1–4 from the Cenomanian of Le Mans). *Lima difficilis* d'Orbigny, 1847 (p. 560, pl. 423, figs 10–11 from the Late Campanian of Royan, Charente) could also be included, but as the type specimen found at Royan, is missing, it is not possible to decide what exactly is the species. There are fairly strong discrepancies between the text and the figures in d'Orbigny. The species group of *Ctenoides tecta* is known from the Cenomanian to the latest Maastrichtian, it is very rare in chalks, but occurs frequently in coarse-grained sediments.

In the Charente deposits *Ct. tecta* appears to be rare.

(23) *Limaria species*

Material A 10. Found at S3 (Santonian).

Discussion

—A poorly preserved specimen of a *Limaria* is probably close to *Limaria marticensis* (Matheron, 1842) which occurs in northern Tethys Senonian deposits.

(24) *Limatula species*

Material A 10. Found at P8 (Campanian).

Discussion

—The steinkern preservation makes specific identification impossible.

(25) *Limea (Pseudolimea) granulata* (Nilsson, 1827)

- . 1827 *Plagiostoma granulatum* S. Nilsson, p. 26, pl. 9, figs 4a–b;
- v. 1847 *Lima granulata* Deshayes: A. d'Orbigny, pp. 570–571, pl. 427, figs 5–9;
- v. 1888 *Lima Meslei* A. Peron, pp. 147–149, pl. 1, figs 21–24;
- v. 1904 *Lima (Limea?) granulata* (Nilsson): H. Woods, pp. 54–57, pl. 7, figs 27–29;
- v. 1968 *Lima (Limea?) granulata* (Nilsson): S. I. Pasternak *et al.*, pp. 182–183, pl. 37, figs 10–12;
- . 1974 *Lima granulata* (Nilsson): O. V. Savchinskaja, p. 96, pl. 28, figs 12–14;
- v. 1982 *Pseudolimea granulata* (Nilsson, 1827): A. V. Dhondt, pp. 87–88, pl. 5, figs 7, 8.

Material A 10. Found at P6 (Coniacian), J6 (579: Santonian).

Discussion

—The tripartite ribstructure, characteristic for *Limea granulata*, makes it possible to identify specimens with only shell fragments preserved. How-

ever, complete steinkerns cannot be recognized specifically. The ribnumber varies widely and depends at least partially on the sediment-type. This interpretation differs from that given by Freneix (1959, pp. 227–228).

Distribution

—Widely distributed, but never occurring frequently, from the Turonian to the latest Maastrichtian in non-Tethyan Eurasian seas.

(26) *Limea (Pseudolimea) species*

Material A 10. Found at P3/4 (Turonian).

Discussion

—The steinkern preservation makes specific identification impossible.

(27) *Plagiostoma cretaceum* (Woods, 1904)

[Figure 3(c)]

- . 1904 *Lima (Plagiostoma) cretaceum* H. Woods, pp. 22–23, pl. 4, figs 13–14, pl. 5, figs 1–4;
- . 1959 *Lima (Plagiostoma) cretaceum* Woods: S. Freneix, p. 220;
- . 1974 *Lima cretacea* Woods, 1904: O. V. Savchinskaja, p. 95, pl. 28, figs 8–9.

Material A 10. Found at J2 (383) and J0, both localities Late Campanian.

Discussion

—*Plagiostoma cretaceum* is characterized by a narrow umbonal angle (90–100°) and by a rib-like ornamentation with intercostal punctate grooves, such as is also found on *Pl. hoperi*. *Pl. cretaceum* has not previously been mentioned from the Charente, but it could be that *Lima truncata* as recorded by H. Coquand (1859, p. 1005) from Aubeterre, belongs here. *Lima dissimilis* Coquand, 1859 (p. 1004) also from Aubeterre, has strong similarities with *Pl. cretaceum* (I saw the type specimen in MAFI in Budapest). Finally H. Arnaud mentions (1877, p. 32) *Lima ornata* from the Coniacian in the Charente: this could be either *Pl. cretaceum* or *Ctenoides tecta*.

Distribution

—*Pl. cretaceum* occurs from the Turonian to the Maastrichtian in the extended Paris Basin; it has also been found on the Russian platform. Because of the similarity with some specimens of *Pl. hoperi*, *Pl. cretaceum* has not always been described as a separate species.

(28) *Plagiostoma hoperi* Mantell, 1822

- . 1822 *Plagiostoma Hoperi* G. Mantell, pp. 204–205, pl. 26, figs 2, 3, 15;
- . 1847 *Lima Hoperi* Deshayes: A. d'Orbigny, pp. 564–565, pl. 424, figs 10–13;

- v. 1904 *Lima (Plagiostoma) Hoperi* Mantell: H. Woods, pp. 17–22, pl. 4, figs 7–12 (with detailed description);
 v. 1968 *Lima (Plagiostoma) hoperi hoperi* (Mantell, 1822): S. I. Pasternak *et al.*, pp. 179–181, pl. 37, figs 3–5;
 . 1974 *Lima hoperi* Mantell, 1822: O. V. Savchinskaja, p. 95, pl. 28, fig. 11.

Material A 10. Found at S8 (Turonian), S3 and S4 (Santonian), P8, J4 and J2 (Campanian).

Discussion

—The material of “smooth” *Plagiostoma*-species in the Charente is very abundant, but generally poorly preserved. The specimens of *Pl. hoperi* from the White Chalks of the Paris Basin and of Northern Europe are, on average, of better preservation. It is not impossible that some of the specimens which d’Orbigny considered as belonging to *Pl. marrotianum* from the Charente, are in fact *Pl. hoperi* specimens. Furthermore it is difficult to judge in how far the very numerous specimens of *Pl. santonense* (see below) belong to a different species, or are just *Pl. hoperi* specimens which have become unusually large.

Distribution

—Turonian to latest Maastrichtian in non-Tethyan European seas; generally relatively frequent in Chalks.

(29) *Plagiostoma marrotianum* (d’Orbigny, 1847)

- v. 1847 *Lima Marrotiana* A. d’Orbigny, pp. 561–562, pl. 424, figs 1–4;
 v. 1904 *Lima (Plagiostoma) Marrotiana* d’Orbigny: H. Woods, pp. 24–25, pl. 5, figs 6, 7;
 1959 *Lima (Plagiostoma) marrotiana* d’Orbigny: S. Freneix, p. 221;
 v? 1961 *Lima (Plagiostoma) marrotiana* d’Orbigny, 1847: N. N. Bobkova, pp. 112–114, pl. 4, figs 4–5;
 . 1974 *Lima marrotiana* d’Orbigny, 1847: O. V. Savchinskaja, pp. 94–95, pl. 28, figs 6, 7.

Material A 10. Found at P8 (Campanian).

Discussion

—*Plagiostoma marrotiana* is the only *Plagiostoma* species with ribs. The species probably evolved from *Pl. hoperi*. In the Charente the species is not very common, and occurs generally in the Campanian (and not in the Lower Senonian as stated by d’Orbigny). In Late Campanian strata in the White Chalks of England, the northern Paris Basin (Craie d’Obourg near Mons), and in the White Campanian Chalks of Westphalia the species occurs frequently. On the Russian platform it is found in strata of the same age. In Central Asia it is recorded from Turonian–Coniacian strata. The ribnumber in Central Asia is slightly higher than in the Campanian strata, so the two taxa might not be completely identical.

(30) *Plagiostoma maximum* (d'Archiac, 1837)

- . 1837 *Lima Maxima* A. d'Archiac, p. 187, pl. 13, fig. 13;
 v. 1847 *Lima maxima*, d'Archiac: A. d'Orbigny, pp. 567–568, pl. 426, figs.
 1–2;
 1859 *Lima (Plagiostoma) maxima* (d'Archiac): S. Freneix, p. 221.

Material A 10. Found at S3 (1085), S2, S1 and P9 in the Santonian, and J5, J2 and J1 in the Campanian.

Discussion

—*Plagiostoma maximum* is only known from specimens of steinkern preservation. Yet, the exceptionally large size ($W = 200$ mm) and the flattish valves (convexity is low) make the species easily recognizable. *Pl. maximum* is only known from the Late Campanian of the Charente and the Dordogne.

(31) *Plagiostoma santonense* (d'Orbigny, 1847)

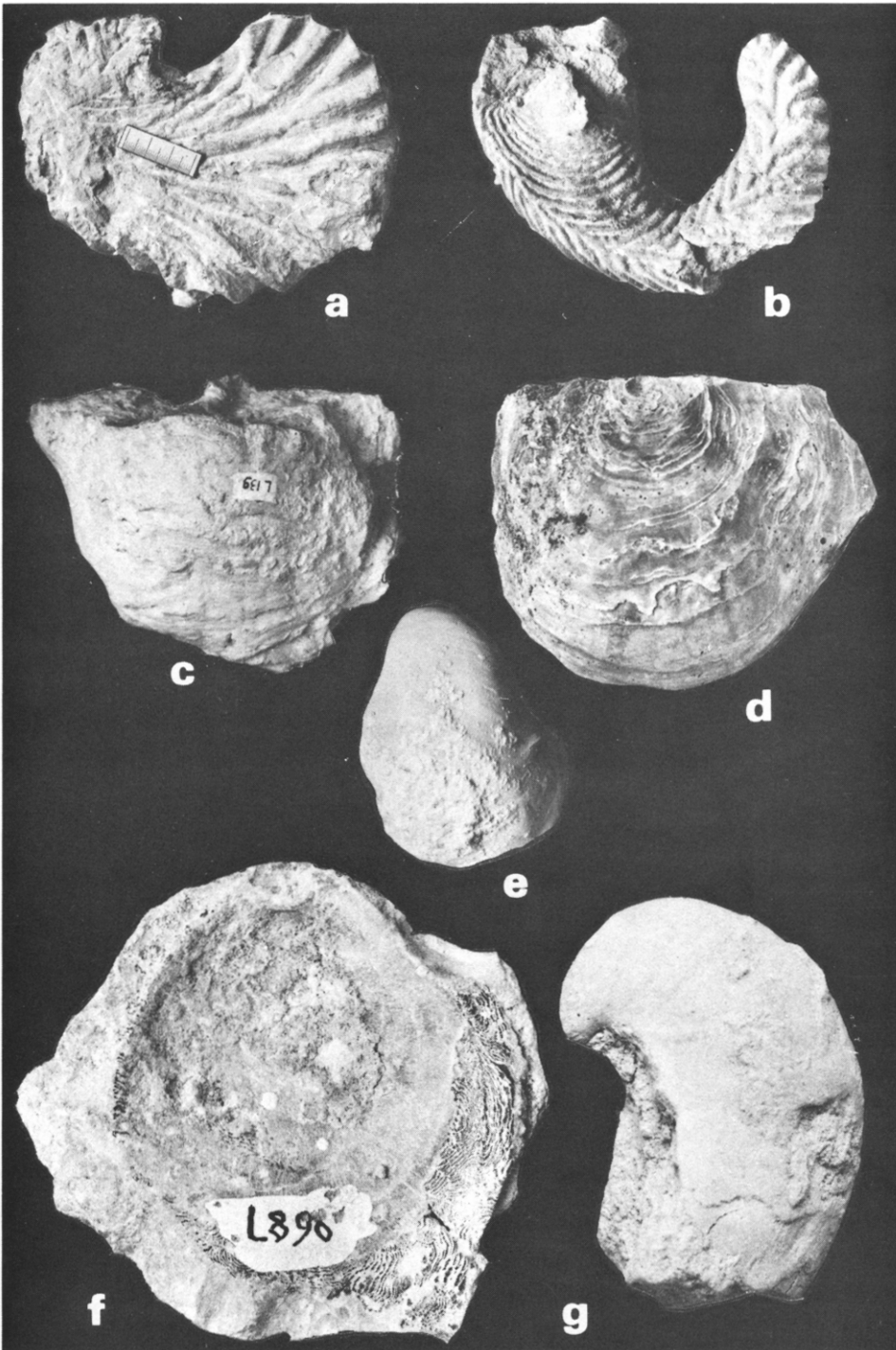
[Figure 3(d, f)]

- v. 1847 *Lima santonensis* d'Orbigny, 1845: A. d'Orbigny, pp. 565–566,
 pl. 425, figs 1, 2;
 1959 *Lima (Plagiostoma) santoniensis* d'Orbigny: S. Freneix, p. 221.

Material A 10. Found in great numbers in many Santonian and in some Campanian exposures: S4 (1128–1143), S3 (1085, 1088, 1078, 1049), S2 (1018), S2, S1, J6 (579–576) and P9 for the Santonian, and P8 and J4 (513–500) for the Campanian.

Discussion

—The material of *Pl. santonense* from the A 10 is very numerous but poorly preserved, and generally even the fairly complete specimens are preserved without shells. I stated above that *Pl. santonense* is probably, if not necessarily conspecific, certainly very closely related with *Pl. hoperi*. *Pl. santonense* seems to be generally larger, and to give an idea of this, I give the measurements of a series of specimens from the d'Orbigny collection in the Muséum national d'Histoire naturelle in Paris, from Saintes and probably of Santonian age: UPD (=height) varies from 52.7 to 138 mm, average 118.3 mm ($n = 16$); W (width) varies from 71.7 to 190 mm, average 135.3 mm ($n = 16$); convexity (both valves together) varies from 54.4 to 76.5 mm, average 66.7 mm ($n = 15$), (the smallest specimen measured for UPD and W is not complete enough to measure the convexity); umbonal angle varies from 95° to 116° , average 108.7° ($n = 15$). As far as can be seen all specimens are totally smooth and the rib-like ornamentation which can sometimes be found on *Pl. hoperi* does not exist. However, this seeming absence might be due to the preservation. In Woods (1904) *Pl. hoperi* is indicated as having a height of 26 to 52 mm (average 41 mm, $n = 12$), a width of 31 to 57 mm (average 45.5 mm, $n = 12$) and a umbonal angle of 115° to 117° . There is a difference in size between *Pl. hoperi* and *Pl. santonense* but, as far as can be ascertained, the other characteristics are the same.



It is interesting that many specimens of *Pl. santonense* from the A 10 material have marks. This can be seen on the figured specimens. Some are almost like folds and their origin is difficult to interpret. On the figured specimens these marks are visible on the left side on L787 (Figure 3d) and on the right side on L803 (Figure 3f). Dr R. G. Bromley (written communication) interpreted a similar mark as possibly of diagenetic origin. On L803 about in the middle of the shell under the umbo, there is a second mark: a round mark probably made by a largish tooth (diameter of the mark: about 15 mm). It does not completely resemble the Mosasaur marks figured and described by Kauffman and Kesling (1960) but is shallower and more conical.

Plagiostoma species are more frequent in chalks than in coarse, more shallow, deposits. With their thin smooth shells, they were probably easy preys for predators.

Distribution

—*Pl. santonense* is only known with certainty from the Charente–Dordogne deposits of Santonian–Campanian age.

Family Gryphaeidae

(32) *Pycnodonte* (*Pycnodonte*) *biauriculatum* (Lamarck, 1819)

- . 1819 *Ostrea biauriculata* J. B. de Lamarck, p. 219, no. 27;
- p.p.v. 1833 *Ostrea vesicularis* Brongn.: A. Goldfuss, p. 23, pl. 81, fig. 2p (non figs 2a–o);
- . 1847 *Ostrea biauriculata* Lamarck: A. d'Orbigny, pp. 710–721, pl. 476, figs 1–6;
- . 1869 *Ostrea biauriculata* Lamarck, 1819: H. Coquand, pp. 114–115, pl. 42, figs 1–7;
- . 1878 *Pycnodonte biauriculata* (Lamarck): E. Bayle, pl. 137, figs 1–4;
- . 1918 *Ostrea biauriculata*: J. Favre, pl. 27, figs 96a–e, figs 97 a–b, pl. 28, figs 97c–e, figs 98a–c;
- v? 1964 *Biauris biauriculata* Lamarck: V. P. Rengarten, pp. 27–28, pl. 3, figs 2, 3;
- . 1971 *Pycnodonte biauriculata* (Lamarck): S. Fabre-Taxy, p. 257, pl. 1, figs 1a–b;
- ? 1976 *Biauris biauriculata* (Lamarck): Z. N. Pojarkova, pp. 58–59, pl. 28, figs 4–7.

Material A 10. Found at P3 (Late Cenomanian).

Figure 4. (a) *Rastellum deshayesi* (Fischer de Waldheim, 1835), A 10 material, L672 from S4 (Santonian), $\times \frac{1}{3}$; (b) *Rastellum* species, A 10 material, L662 from S4 (Santonian), $\times \frac{1}{2}$; (c) *Pycnodonte vesiculare hippopodium* sensu Coquand, 1869, material A 10, L139 from S2 (Santonian), $\times \frac{1}{2}$; (d) *Pycnodonte biauriculatum* (Lamarck, 1819), from the Upper Cenomanian of Le Mans (Sarthe), coll. KBIN, $\times \frac{1}{2}$; (e) *Pycnodonte vesiculare nikitini* (Arkhanguelsky, 1905), material A 10, L161 from S2 (Santonian), $\times 2$; (f) *Hyotissa semiplana* (Sowerby, 1825), inside of valve, A 10 material L896 from P8 (Campanian), $\times \frac{3}{2}$; (g) *Pycnodonte vesiculare proboscideum* (d'Archiac, 1837), side view, A 10 material, L110 from S2 (Santonian), $\times \frac{3}{2}$.

Discussion

—*Pycnodonte (Pycnodonte) biauriculatum* is characterized by strongly un-equivalve but equilateral shells, showing no attachment area and having “floated” on the ooze on which they lived (Dhondt, 1984a).

Distribution

—*P. (P.) biauriculatum* has been found in great numbers in Late Cenomanian strata of western France from the Sarthe to Aquitaine, and has been found in lesser numbers in strata of the same age from Northern Spain to Central Asia.

Pycnodonte (Phygraea) vesiculare group in the Charente

Oysters are sessile animals and have an extremely variable shellshape mostly induced by the way of attachment and by the type of sediment on which they lived. The definition (sensu G. G. Simpson, 1961, p. 138: definition; “enclose within limits”) of a species or a subspecies becomes difficult under such conditions and measuring becomes pointless. When trying to interpret the material of *Pycnodonte (Phygraea)* known from the Late Cretaceous, it is preferable to take a pragmatic approach, because objective criteria seem non-existent. Hence, the subdivision used herein for *Pycnodonte (Phygraea) vesiculare* is typological.

The oldest *Pycnodonte (Phygraea)* species in *Pycnodonte (Phygraea) vesiculosum* (Sowerby, 1822) from the Aptian–Lower Cenomanian of Europe. In the deposits of the Albian temperate seas of Europe another pycnodonteid oyster is found which is, if not totally identical with, at least a direct ancestor of *Pycnodonte (Phygraea) vesiculare* (Lamarck, 1806). From deposits of temperate seas, all through the Cenomanian, small numbers of this species are recorded. From the Turonian onwards *P. (Ph.) vesiculare* became more common and especially in the chalk-like deposits it is a very frequently encountered species. At different localities in the Charente *P. (Ph.) vesiculare* is found in large numbers; morphologically the species is variable and the morphotypes are different from locality to locality. These morphological changes might have been induced by a changing environment. The morphological variations encountered on specimens of *P. (Ph.) vesiculare* from the Charente Late Cretaceous deposits are, for convenience’s sake, described hereafter as “subspecies”. With the study of material from more Late Cretaceous localities it might well be proven that the typologically distinct “taxa” belong, biologically, only to subinfraspecific categories and hence, could be systematically meaningless.

(33) *Pycnodonte (Phygraea) vesiculare* (Lamarck, 1806)

- . 1806 *Ostrea (vesicularis)* J. B. de Lamarck, pp. 160–161;
- . 1809 *Ostrea vesicularis* J. B. de Lamarck, p. 375, pl. 22 (27), fig. 3;
- v. 1827 *Ostrea vesicularis*: S. Nilsson, pp. 29–30, pl. 7, figs 3a–b;
- v. 1827 *Ostrea Hippopodium* *ibid.*, p. 30, pl. 7, figs 1a–b;
- v? 1827 *Ostrea clavata* *ibid.*, p. 30, pl. 7, figs 2a–b;
- v. 1833 *Ostrea vesicularis* Brongn.: A. Goldfuss, pp. 23–24, pl. 81, figs 2a–o;

- . 1847 *Ostrea vesicularis* Lamarck: A. d'Orbigny, pp. 742–746, pl. 487, figs 1, 2;
 p.p.v. 1869 *Ostrea vesicularis* Lamarck, 1806: H. Coquand, pp. 35–37, pl. 13, figs, 2, 3, 4, 7, 10;
 . 1878 *Pycnodonte vesicularis* Lamarck, sp.: E. Bayle, pl. 135, figs 1–7;
 p.p.v. 1913 *Ostrea vesicularis* Lamarck: H. Woods; pp. 360–374, pl. 55, figs 4–7, text figs 143–182 (with detailed discussion and synonymy);
 v. 1982 *Pycnodonte (Phygraea) vesiculare* (Lamarck, 1806): A. V. Dhondt, pp. 90–91; pl. 5, fig. 7;
 1983 *Pycnodonte vesiculare* (Lamarck, 1806): A. V. Dhondt, p. 859.

Material A 10. Found at S4, S3 and S2 (Santonian), at J4, J3, J2 and J1 (Campanian); poorly preserved specimens of Turonian age (at S7 and P5) and of Coniacian age (at P6) probably also belong here.

Discussion

—Typical *Pycnodonte (Phygraea) vesiculare vesiculare* specimens are frequently found in white chalks. Goldfuss (pl. 81, figs 2d, f, h), d'Orbigny (pl. 487, figs 1–2), Woods, (text fig. 182 on p. 373) have figured such specimens, which are about as wide as high, strongly convex on the left valve and flat or somewhat concave on the right valve. This typical shape is only achieved when the attachment area is small and when the sediment is very fine-grained. Young (small) specimens are not so orbicular but have a lateral extension on the posterior side.

The Charente specimens of *P. (Ph.) vesiculare* do not as a rule reach the size of the Northern European or Paris Basin specimens.

Distribution

—*P. (Ph.) vesiculare vesiculare* is widely distributed especially from the Santonian to Maastrichtian of Eurasia and the Gulf and Atlantic Coastal Plains of North America, in temperate seas and in Tethys. It occurs most frequently in white chalks.

(34) *Pycnodonte (Phygraea) vesiculare hippopodium* (sensu Coquand, 1869)
 [Figure 4(c)]

- ?1837 *Ostrea Vesicularis* V^{te}: A. d'Archiac, p. 183;
 p.p.v. 1869 *Ostrea hippopodium* H. Coquand, pp. 100–101, pl. 19, fig. 1, pl. 20, figs 2, 4, 5; (non pl. 18, figs 1, 4, 5, non pl. 20, figs 1, 3) (synonymy incorrect);
 non 1827 *Ostrea hippopodium* Nilsson = *Pycnodonte (Ph.) vesiculare vesiculare*
 non 1833 *Ostrea hippopodium* in Goldfuss = ? *Pycnodonte (Ph.) vesiculare vesiculare*.

Material A 10. Found at S4, S3, S3 (1085), S2 all of Santonian age, and at J2 (Campanian).

Discussion

—Large *Pycnodonte* (*Phygraea*) *vesiculare* specimens with extensive attachment area and relatively strong concentric plications occur in some near-Tethyan or Tethyan Late Cretaceous deposits. The convexity of the specimens depends on the size of the attachment area and sometimes it seems absurdly low.

Coquand has interpreted several taxa as belonging to one species which have virtually nothing in common except that they are pycnodontid species. Coquand did not check types and often unfortunately drew rash conclusions. I have seen the types of several of the references he has put in synonymy and cannot possibly agree. *Ostrea hippopodium* Nilsson (1827, p. 30, pl. 7, fig. 1 (not fig. 4 as mentioned by Coquand)) is a *P. (Ph.) vesiculare* specimen with a wide attachment area, but with the typical smooth shell of the species. This probably also applies to the specimens described by d'Orbigny. The types of Goldfuss are older, of Cenomanian age, and are so thin and flat that they make conclusions difficult. *Avicula lithuana* Eichwald is kept at the LGU in Leningrad—it is a large *Pycnodonte* (*Pycnodonte*) specimen which is close to *Pycnodonte* (*P.*) *mirabilis* (Rousseau) from the Maastrichtian of Crimea: these species are characterized by two slightly convex very wide and heavy valves without attachment scars in adult life. *Ostrea talmontiana* Archiac, 1837 (I have not been able to locate it in the paper by d'Archiac and I have not found any trace of the species otherwise. It may have been a manuscript species).

Distribution

—In the Charente *P. (Ph.) vesiculare hippopodium* sensu Coquand has been found in the Santonian and in the Campanian but it occurs most frequently in the Santonian (S2). Some specimens from near Sétif (Algeria) of Santonian age, kept in the Coquand collection in Budapest, could also belong here.

(35) *Pycnodonte* (*Phygraea*) *vesiculare nikitini* (Arkhanguelsky, 1905)

[Figure 4(e)]

- p.p.v. 1869 *Ostrea proboscidea* Archiac, 1837: H. Coquand, pp. 72–73, pl. 16, figs 6, 8, 9, 10 (non figs 1–5, 11, 12)
- v. 1905 *Ostrea Nikitini* A. D. Arkhanguelsky, pp. 7–8, pl. 4, figs 11–16;
- p.p.v. 1961 *Gryphaea vesiculosa* Sowerby subsp. *turkestanica* Bobkova, 1960: N. N. Bobkova, pp. 66–69, pl. 10, figs 1–6, 8, 10, 11, 12 (non figs 7, 9, 13–18);
- v. 1964 *Pycnodonta subvesiculosa* V. P. Rengarten; pp. 26–27, pl. 1, figs 12, 13, 14, pl. 2, fig. 1;
- . 1972 *Pycnodonte* (*Pycnodonte*) *vesicularis subvesiculosa* (Rengarten, 1964): S. Freneix, pp. 104–105, pl. 10, figs 4a, b, text figs 11, 12;
- . 1974 *Gryphaea nikitini* var A (Arkhangelskij, 1905): O. V. Savchinskaja, p. 103, pl. 35, figs 5–7;
- . 1983 *Pycnodonte vesiculare nikitini* (Arkhanguelsky, 1905): A. V. Dhondt, p. 859.

Material A 10. Found an S4 and S2 (1018) in the Santonian and in P8 (705) in the Campanian.

Discussion

—*Pycnodonte (Phygraea) vesiculare nikitini* is a small, oblique, almost comma-shaped pycnodonteid oyster which occurs often in large numbers in strata from which larger pycnodonteids seem to be absent. This “mass occurrence” is stratigraphically restricted to the Coniacian–Santonian, but in lesser numbers the species is also found in other Late Cretaceous strata.

Distribution

—*P. (Ph.) vesiculare nikitini* is found in Late Cretaceous strata at the northern margin of the Tethys but occasionally also occurs in more northern temperate seas deposits. Its range extends from Morocco to Central Asia.

(36) *Pycnodonte (Phygraea) vesiculare proboscideum* (d’Archiac, 1837)

[Figures 3(b) & 4(g)]

- v. 1832 *Gryphea elongata* Sowerby: J. Sowerby in Sedgwick and Murchison, p. 418, pl. 38, fig. 6 (non *Ostrea elongata*, Deshayes 1826);
- . 1837 *Ostrea Proboscidea* A. d’Archiac, p. 184, pl. 11, fig. 9;
- p.p. 1847 *Ostrea vesicularis* A. d’Orbigny, pp. 742–746, pl. 487, figs 6–9 (non figs 1–5, 10);
- p.p.v. 1869 *Ostrea proboscidea* Archiac, 1837: H. Coquand, pp. 72–73, pl. 16, figs 1, 2, pl. 18, fig. 1 (non pl. 15, figs 10, 16, figs 3–6, 8–12, pl. 18, fig. 3);
- ?1878 *Pycnodonta proboscidea* d’Archiac sp.: E. Bayle, pl. 136, figs 1, 2;
- v?1964 *Pycnodonta proboscidea* (d’Archiac) var. *elongata* (Sowerby): V. P. Rengarten, pp. 24–26, pl. 2, fig. 2, pl. 3, fig. 1.

Material A 10. Found at S2 and S2 (1018) Santonian.

Discussion

—*Pycnodonte (Phygraea) vesiculare proboscideum* has shells which are narrower and generally heavier than *P. (Ph.) vesiculare vesiculare*. These shells often have a very heavy, thick-shelled umbonal part and rarely show any sign of attachment.

Distribution

—*P. (Ph.) vesiculare proboscideum* is not known from Northern white chalks, but seems to be relatively frequent in border Tethys areas and in the Tethys, from Spain to Central Asia.

(37) *Hyotissa semiplana* (Sowerby, 1825)

[Figure 4(f)]

Stenzel (1971) has shown that *Hyotissa* is a pycnodonteid genus and can thus be recognized by its microstructure (cellules à craie). This characteristic had previously not been noticed. *Hyotissa semiplana* is a very variable species

whose shell adapted to the substratum and/or attachment area and this induced the shellshape. This has been recognized by many authors, and especially Woods has given an extensive synonymy list (1913, pp. 379–383). Unfortunately other oyster genera—such as *Lopha* (*Actinostreon*) Bayle, 1878, *Cameleolopha* Vyalov, 1936, *Nicaiolopha* Vyalov, 1936, *Acutostrea* Vyalov, 1936—can have shells which are homeomorph and occur isochronously with those of *Hyotissa semiplana*. Therefore to present a good synonymy list it would be necessary to check the microstructure of all the references. This falls outside the scope of the present paper.

Material A 10. Found only rarely: at S2 (1018: Santonian) and at P8 (708: Campanian).

Discussion

—*Hyotissa semiplana* has been mentioned by Coquand from Royan (1869, pl. 38, fig. 2) and the figure is plausible but not totally convincing. The folds which characterize *H. semiplana* are rounded especially on specimens with a small or without attachment area. The specimens from Algeria which Coquand figured as *H. semiplana* do not belong in this species: they are kept in the Coquand collection in Budapest.

Distribution

—*H. semiplana* occurs from the Coniacian to the latest Maastrichtian in the European temperate chalk seas. It is especially common in some Coniacian–Santonian strata (Craie de Maisières near Mons, Hainaut, Belgium and Bavnodde Grønsand on Bornholm, Denmark).

(38) *Exogyra auricularis* (Wahlenberg, 1821)

- 1821 *Ostracites auricularis* Wahlenberg, p. 58;
- ?1827 *Chama cornu arietis* S. Nilsson, p. 28, pl. 8, figs 1a–b;
- v?1833 *Exogyra auricularis* A. Goldfuss, p. 39, pl. 88, figs 2a, c;
- v. 1833 *Exogyra planospirites* A. Goldfuss, p. 39, pl. 88, fig. 3;
- . 1835 *Exogyra inflata* A. Goldfuss, p. 121, pl. 114, figs 8a, b;
- . 1851 *Exogyra pyrenaica* A. Leymerie, pp. 194–195, pl. 10, figs 4–6;
- . 1869 *Ostrea auricularis* Geinitz, 1849: H. Coquand, pp. 28–30, pl. 8, figs 1–12;
- . 1895 *Ostrea (Exogyra) auricularis* Goldfuss, 1833: F. Vogel, p. 11;
- . 1895 *Ostrea (Exogyra) subinflata* d'Orbigny: F. Vogel, pp. 11–12.

Material A 10. Found at P6 (Coniacian), and J3 (453), J1 (361) and J0 of Campanian age.

Discussion

—*Exogyra auricularis* is more or less smooth *Exogyra* species which can reach very large sizes. Its nomenclature is more than usually entangled because several authors have given names to the right valves, which cannot be identified specifically. The material from the A 10 deposits is not well preserved but probably belongs here. In how far *Exogyra decussata* Goldfuss, 1833 and *E. auricularis* are two different species remains to be studied.

E. decussata has sometimes an exogyrine ornamentation which is missing from *E. auricularis* but that may be a preservational difference. *E. auricularis* reaches larger sizes, but this may be also an interpretation (large specimens being automatically classified as *E. auricularis*).

Distribution

—From the Coniacian to the latest Maastrichtian in European temperate shallow sea deposits. It is particularly interesting that *E. auricularis* occurs at the uppermost Campanian strata (J0) and at the Maastrichtian stratotype and in Gensac (Haute Garonne) (type locality for *Exogyra pyrenaica* Leymerie).

(39) *Ceratostreon pliciferum* (Dujardin, 1837)

[Figure 2(a)]

- . 1822 *Gryphea auricularis* A. Brongniart, p. 321, 608, pl. VI, figs 9a, b;
- v. 1833 *Exogyra plicata* (Lamarck): A. Goldfuss, p. 37, pl. 87; fig. 5a (non figs 5b, c, d, e, f; probably *E. flabellata* Goldfuss);
- 1837 *Exogyra Auricularis* A. d'Archiac, p. 185;
- . 1837 *Gryphea plicifera* F. Dujardin, p. 229;
- . 1842 *Exogira spinosa* P. Matheron, p. 192, pl. 32, figs 6, 7;
- . 1847 *Ostrea Matheroniana* d'Orbigny, 1846: A. d'Orbigny, pp. 737–739, pl. 485, figs 1–7;
- v. 1866 *Ostrea Matheroniana* d'Orb, 1847: K. A. Zittel, pp. 121–123, pl. 19, figs 3a–e, 4a–b;
- v. 1869 *Ostrea plicifera* (Dujardin, 1837): H. Coquand, pp. 80–82, pl. 36, figs 6–18;
- . 1912 *Exogyra spinosa* Matheron: L. Pervinquier, pp. 191–192;
- . 1912 *Exogyra Matheroniana* d'Orbigny: L. Pervinquier, p. 193;
- v. 1961 *Ceratostreon spinosum* (Matheron, 1842): N. N. Bobkova, pp. 126–128, pl. 30, figs 2–6;
- v. 1961 *Ceratostreon spinosum* Matheron var. *malikensis* (Muzafarova, 1953): N. N. Bobkova, pp. 128–129, pl. 31, figs 1–6;
- v. 1961 *Ceratostreon flabellatum* N. N. Bobkova, pp. 125–126, pl. 31, figs 7–8;
- v. 1964 *Ceratostreon matheronianum* d'Orbigny: V. P. Rengarten, pp. 41–42, pl. 5, figs 6, 7;
- . 1968 *Exogyra plicifera* (Dujardin): S. Fabre-Taxy et E. Revest, p. 131, figs 1a–c;
- . 1968 *Exogyra plicifera* (Dujardin) var. *matheroni* d'Orbigny: S. Fabre-Taxy et E. Revest, pp. 131–133, figs 2a–c;
- . 1968 *Exogyra plicifera* (Dujardin) var. *auricularis* Brongniart: S. Fabre-Taxy et E. Revest, p. 133, figs 3a–c;
- . 1974 *Ceratostreon spinosum* (Matheron, 1842): O. V. Savchinskaja, p. 102, pl. 33, figs 5, 6, pl. 34, figs 1, 2;
- ?1974 *Ceratostreon spinosum* Matheron var. *malikensis* (Muzafarova, 1953): O. V. Savchinskaja, p. 102, pl. 33, figs 1–4.

Material A 10. From the Coniacian to the uppermost Campanian has been found in virtually all sections: Coniacian: at P6 and S4 (1195), Santonian: at S4 (1128, 1143), S3 (1049, 1078, 1085, 1088), S2 (1018), S2, J6 (579), S1, P9, Campanian: P8 (706), J4 (515, 513, 501, 500), J3 (543), J2 (382), J1 (361), J0.

Discussion

—S. Fabre-Taxy and E. Revest have discussed in detail how variable *Ceratostreon pliciferum* can be. The specimens from the Charente clearly show this variability, which can go from almost smooth shells to very spiny specimens. Some of the specimens show rather more folds than on the very spiny specimen shown in Figure 2(a), but have no spines. The same variability is found at the Sint Pietersberg near Maastricht (stratotypical Maastrichtian).

Distribution

—*C. pliciferum* occurs in Late Cretaceous strata (Turonian–uppermost Maastrichtian) from W. France to Central Asia, in shallow sediments in warm temperate and Tethyan deposits.

(40) *Vultogryphaea ? laciniata* (Nilsson, 1827)

[Figure 2(e), (f)]

- 1827 *Chama laciniata* S. Nilsson, p. 28, pl. 8, figs 2a, b;
- v. 1833 *Exogyra laciniata* A. Goldfuss, pp. 35–36, pl. 86, figs 12a–d;
- . 1847 *Ostrea laciniata* d'Orbigny, 1846: A. d'Orbigny, pp. 739–740, pl. 486, figs 1–3;
- v. 1869 *Ostrea laciniata* Orbigny, 1846: H. Coquand, p. 55, pl. 25, figs 1–6, pl. 41, fig. 5 (?);
- ?1871 *Exogyra laciniata* (Nilsson): F. Stoliczka, p. 460, pl. 38, figs 1–3;
- . 1888 *Exogyra laciniata* (Nilsson): E. Holzappel, pp. 254–255;
- p.p. 1889 *Ostrea (Exogyra) cornu arietis* Nilsson: O. Griepenkerl, pp. 35–36, pl. 5, figs 1a–c, pl. 6, figs 1a–c;
- . 1895 *Ostrea (Exogyra) laciniata* (Nilsson): F. Vogel, p. 11;
- ?1897 *Ostrea cornu arietis* Nilsson *emend.* Griepenkerl: A. Hennig, pp. 21–22;
- . 1942 *Ostrea (Gryphaea) voluminosa* W. J. M. van der Weyden, pp. 95–96; pl. 9, figs 1–5;
- ?1942 *Ostrea (Exogyra) cornu arietis* Nilsson var. *laciniata* Nilsson: W. J. M. van der Weyden, p. 91, pl. 9, figs 11–13;
- v. 1961 *Exogyra ostracina* (Lamarck, 1801): N. N. Bobkova, pp. 119–120, pl. 29, figs 1, 2;
- ?1974 *Exogyra ostracina* (Lamarck, 1801): O. V. Savchinskaja, pp. 101–102, pl. 34, figs 3–9.

Material A 10. Found at S2 and S4 (Santonian), J3 (453) and J2 (382) both Campanian.

Discussion

—The material of *Vultogryphaea ? laciniata* from the A 10 exposures is relatively rare. The species of this odd genus had already been described from the Charente sections by d'Orbigny, on specimens of better preservation than those from the A 10. However, contrary to my previous statements (Dhondt, 1984b), *V. laciniata* is also found in Santonian strata, at least in the Charente.

The Nilsson type material in Lund is lost. According to Hennig (1897) Nilsson's taxon is not conspecific with Goldfuss' *Exogyra laciniata*. The material of this *Exogyra* species in Sweden is generally very poorly preserved, though extremely frequent, at localities such as Ifö. With the type material of *E. cornu arietis* (Nilsson) also lost, the discussion as to the exact nature of these species becomes pointless. Therefore it might be easier so as to avoid confusion to consider *V. laciniata* sensu Goldfuss as the species designation, which is the way most authors have interpreted the species.

Vultogryphaea as a genus is known only in three species: *V. vultur* from the Carentonian (= Cenomanian) of Bonneuil-Matours, dép. Vienne (Coquand, 1869 type in the MAFI in Budapest), *V. digitata* (Sowerby, 1817) from the Upper Greensand (Cenomanian) of Dorset (England), and *V. ? laciniata*.

Distribution

—*V. ? laciniata* is known from shallow temperate seas deposits in Sweden (?), Germany (Köningslutter and Aachen), Belgium—the Netherlands (Limburg) and the Charente, mostly of Campanian age, except in the Charente. It is also found on the Russian platform, in Central Asia and in India in deposits of Campanian age.

(41) *Rhynchostreaon suborbiculatum* (Lamarck, 1801)

[Figure 3(a)]

- . 1801 *Gryphaea suborbiculata* J. B. de Lamarck, p. 398;
- 1813 *Gryphites Ratisbonensis* E. von Schlotheim, p. 105;
- . 1819 *Gryphaea columba* J. B. de Lamarck, p. 198;
- v. 1833 *Exogyra Columba* A. Goldfuss, pp. 34–35, pl. 86, figs 9c, d (non figs 9a, b, e);
- . 1847 *Ostrea columba*, Deshayes: A. d'Orbigny, pp. 721–724, pl. 477, figs 1–3;
- . 1869 *Ostrea Ratisbonensis* H. Coquand, 1859: H. Coquand, pp. 121–124, pl. 45, figs 8–12;
- . 1879 *Rhynchostreaon chaperi* E. Bayle, pl. 138, figs 1–5;
- p.p. 1939 *Exogyra columba* (Lam.): E. Dacqué, pp. 53–55, p. 128, pl. 13, figs 1, 2;
- v?1961 *Amphidonta columba* (Lamarck, 1819): N. N. Bobkova, pp. 130–133, pl. 32, figs 1–4 (non *A. columba* var. *chaperi* pp. 133–135, pl. 32, figs 5–8 ≡ *A. obliquatum* (Pulteney));
- v?1964 *Amphidonta columba* (Lamarck): V.P. Rengarten, pp. 49–51, pl. 7, figs 2, 3;
- v. 1964 *Amphidonta columba* Lamarck var. *chaperi* Bayle: V. P. Rengarten, pp. 51–53, pl. 7, figs 3–5, pl. 8, figs 1a, b;
- v. 1964 *Amphidonta columba* Lamarck var. *silicea* Lamarck: V. P. Rengarten, pp. 54–55, pl. 8, figs 2, 3;
- v?1964 *Amphidonta columba* Lamarck var. *plicatula* Lamarck: V. P. Rengarten, pp. 55–58, pl. 8, figs 4, 5;
- v. 1964 *Amphidonta columba* Lamarck, subsp. *monosulcata* V. P. Rengarten, pp. 58–59, pl. 8, fig. 6a, b;

- v. 1964 *Amphidonta columbaesimilis* V. P. Rengarten, pp. 59–60, pl. 9, figs 1, 2;
 v. 1964 *Amphidonta vediensis* V. P. Rengarten, pp. 60–62, pl. 9, figs 3a, b;
 . 1971 *Rhynchostreon suborbiculatum* (Lamarck, 1801): H. B. Stenzel, pp. N1122–1124, text fig. J97;
 1983 *Rhynchostreon suborbiculatum* (Lamarck, 1801): A. V. Dhondt, p. 859.
 (non 1913 *Exogyra columba* in H. Woods, pp. 413–417, text figs 243–249 = *Amphidonte obliquatum* (Pulteney)).

Material A 10. Found at S8 (1482), P2, S7 all of Turonian age, and at S4 (1143) of Santonian age.

Discussion

—*Rhynchostreon suborbiculatum* with its very narrow, highly incoiled umbo, wide, smooth, very convex left valve, rounded keel and with a radial sulcus on larger specimens, is one of the better known Cretaceous exogyrine oysters. The confusion which exists in its interpretation is due to Woods: in England *Rh. suborbiculatum* does not occur (it has been found in Northern Ireland) but Woods considered some very large smooth *Amphidonte obliquatum* (= *Exogyra conica*) as belonging to the species under discussion here.

Discussion

—*Rh. suborbiculatum* is widely distributed from W. Europe to Central Asia, possibly into India in strata from Late Cenomanian to Santonian age. It occurs often in large numbers in poorly diversified faunas.

(42) *Gryphaeostrea canaliculata* (Sowerby, 1813)

[Figure 2(b)]

This species has been discussed and described very completely by H. Woods (1913, pp. 375–379, pl. 56, figs 2–16) and no fundamental facts have been added since.

Material A 10. Found at S2 (933) and S2, Santonian exposures, and at J4 (513–515), J3 (455), J2 (363), Campanian exposures.

Distribution

—*Gryphaeostrea canaliculata* occurs in strata of Aptian to latest Maastrichtian age in most environments, but more frequently in shallow seas.

Family Ostaidae

(43) *Rastellum species*

[Figure 4(b)]

From the Middle Jurassic until the latest Maastrichtian *Rastellum* species are found. The specific definition and delimitation is very difficult to make and

most authors have had different approaches. None of the characteristics used (the number of plicae which form “teeth” at the commissure, the shell outline etc.): are constant within a population. In most cases the “wide” and “narrow” types are found together. The shape is probably partly induced by the sediment type, by the attachment area and possibly by other environmental conditions. Names abound, but until the ontogeny and variability of the “species” have been defined I prefer to avoid them. Hereunder all not clearly recognizable specimens from the A 10 deposits are mentioned.

Material A 10. Rastellum sp. fragments and more or less complete specimens have been found at: S8 (Turonian), S4 (1128), S4 (1143), S3 (1085, 1088), S3 (1078), S3 (1049), S2 (1018), S2 (933), J6 (579), P7, S1 (849), P9 all of Santonian age P8 (705) and J2 (363) both of Campanian age.

(44) *Rastellum deshayesi* (Fischer de Waldheim, 1835)

[Figure 4(a)]

- 1835 *Alectryonia Deshayesii* G. Fischer de Waldheim, p. 114;
- . 1847 *Ostrea Santonensis* d’Orbigny, 1846: A. d’Orbigny, pp. 736–737, pl. 484, figs 1–3;
- v. 1869 *Ostrea Deshayesi* H. Coquand, pp. 87–88, pl. 21, fig. 1, pl. 22, fig. 1, pl. 23, fig. 1–2, pl. 24, figs 1–3;
- v. 1977 *Rastellum (Arctostrea) deshayesi* (Fischer de Waldheim, 1835): V. A. Sobetski, pp. 136–137, pl. 9, fig. 3, pl. 10, fig. 2.

Material A 10. Found at S4 (1143) (Santonian).

Discussion

—The taxon *Rastellum deshayesi* is characterized by very heavy wide shells with relatively few plications. It is not possible to differentiate them in a systematically satisfying way from other *Rastellum* taxa.

Distribution

—*R. deshayesi*, as understood herein, has been found in the Santonian of Charente and in the Maastrichtian of Crimea.

Family Trigoniidae

(45) “*Trigonia*” sp.

Numerous “*Trigonia*” specimens have been found in the A 10 exposures. They are preserved as internal moulds and cannot be identified generically and specifically: S8, P2, P4, S7 (1419), S6 (1376) in the Turonian, S4 (1128), S3 (1078), S3 (1085–1088), S2 (1018), S2 (933), P9 in the Santonian, P8 (705), J4 (513–515) and J0 in the Campanian.

Family Fimbriidae

(46) “*Corbis*” *striaticostata* (d’Orbigny, 1844)

[Figure 1(g)]

. 1844 *Corbis striaticostata* A. d’Orbigny, pp. 114–115, pl. 281, figs 1, 2.

Material A 10. Restricted to the Santonian: S4 (1143), S4 (1128), S3 (1078), S2 (1018).

Discussion

—This species is of uncertain generic affinity because it is only known as interior moulds. It seems probable that it belongs to the Fimbriidae. The strong concentric ornamentation does occur in that family. The hinge is invisible.

Distribution

—d’Orbigny in 1850 indicated Royan and Mussidan (Dordogne), of Senonian age, as distribution. In the A 10 it is restricted to the Santonian but I have seen specimens belonging to *C. striaticostata* from the Late Campanian (Early Maastrichtian), deposits of the Cotentin.

Family Cardiidae

(47) “*Cardium*” sp.

Generically and specifically unidentifiable cardiid interior moulds have been found at S7 (1419: Turonian), S4 (1143) and S2 (1018) both of Santonian age.

(48) “*Cardium*” *productum* Sowerby, 1831

1844 *Cardium productum* Sowerby, 1831: A. d’Orbigny, pp. 31–34, pl. 247, figs 1–7.

Material A 10. One incomplete specimen with good ornamentation from J0 (uppermost Campanian).

Discussion. The limited material makes discussion pointless.

(49) *Protocardia* sp.

Moulds, generically identifiable, have been found at S3 (1078: Santonian), and P9 (Campanian).

Family Hiattellidae

(50) “*Panopea*” sp.

A mould of a possible *Panopea* sp. has been found at P8 (Campanian). d’Orbigny in *Paléontologie française* mentioned several “species” of *Panopea*—all poorly preserved moulds. The species concept of Cretaceous *Panopea* sp. is not yet sufficiently studied to allow further identification.

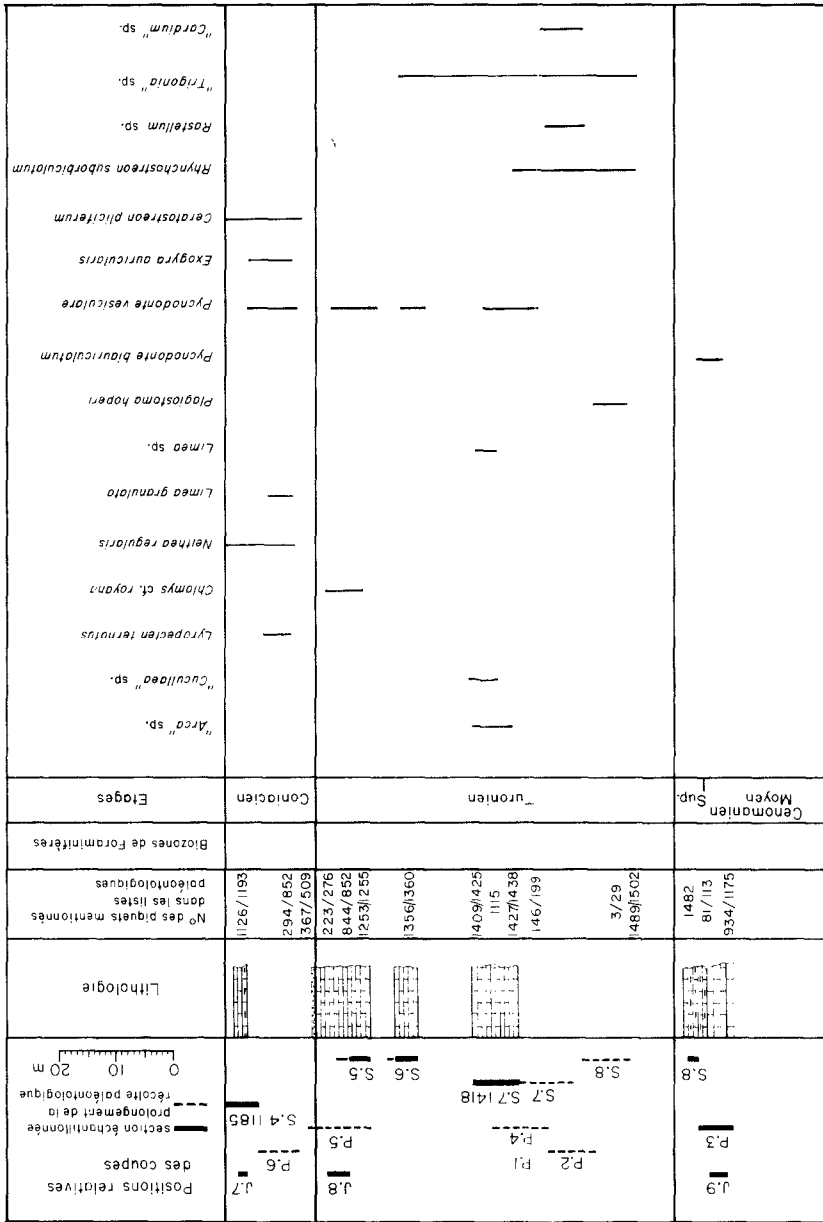


Figure 5. Stratigraphic distribution of bivalves from the A 10 motorway; Cenomanian to Coniacian.

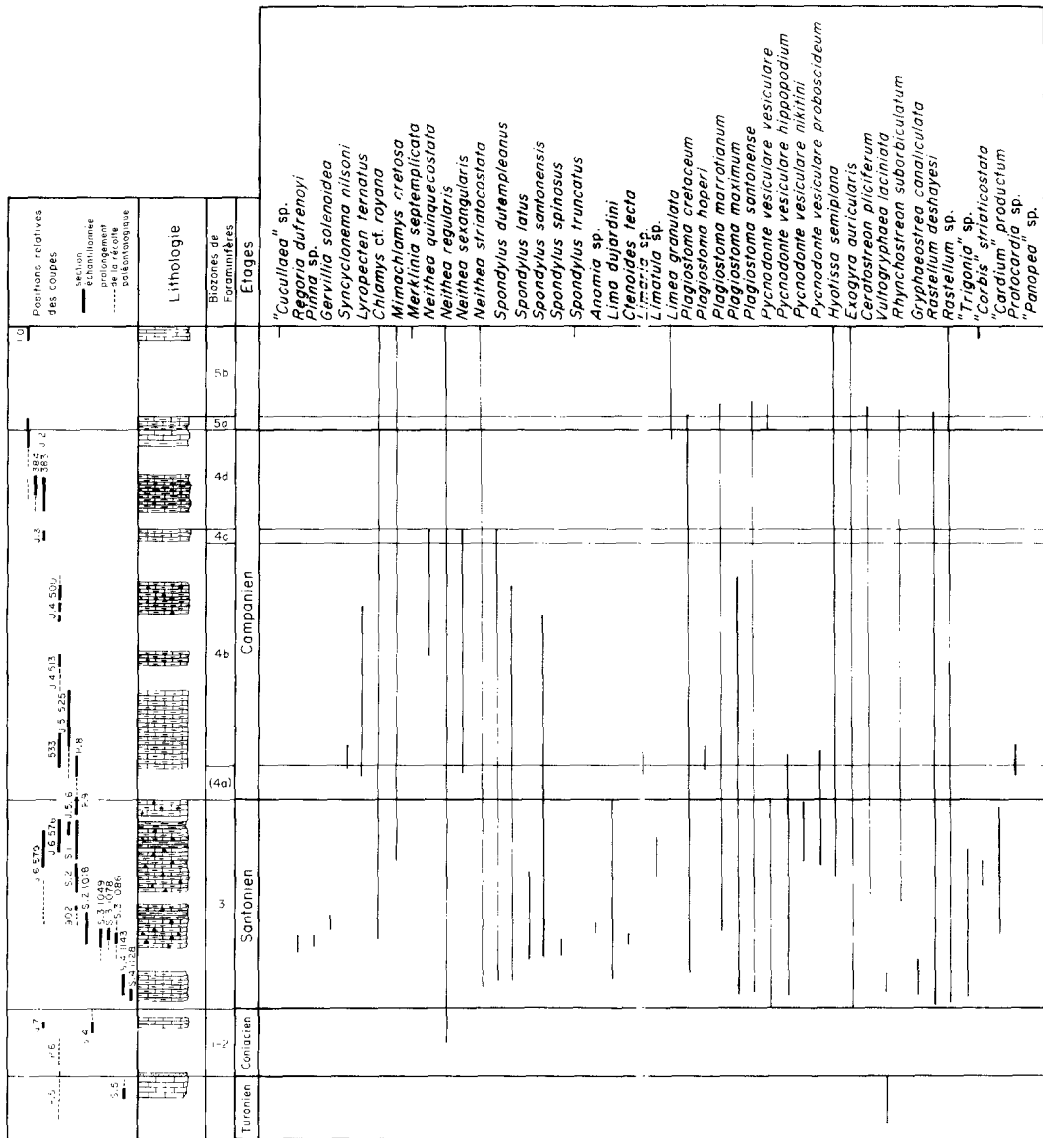


Figure 6. Stratigraphic distribution of bivalves from the A 10 motorway; Turonian to Campanian.

4. Biostratigraphic distribution

A detailed indication of the stratigraphic occurrence of the Bivalves from the A 10 outcrops can be found in Figures 5 & 6.

5. Faunal affinities

Among the bivalves collected and identified from the A 10 exposures, those with partially calcitic shells are, as usually in Cretaceous strata, the most numerous. Pectinids, spondylids, limids and oysters make up more than 75% of this fauna (39 species out of 50).

The Charente region—or Northern Aquitaine—is situated palaeobiogeographically between the Paris Basin and the Tethys. In the faunal comparisons I have considered five regions outside the Charente: (1) E. of the Charente, the Dordogne, with good Cretaceous deposits, especially important in the Campanian–Maastrichtian but even less studied than the Charente; (2) the “Tethys”: mainly data for Northern Spain are used herein, but where insufficiently known, data from other areas in Tethys have been added; (3) the Touraine, north of the Charente, has been often studied; the Craie de Villedieu of Coniacian–Santonian age contains a fine bivalve fauna which shows affinities with the more Northern white chalks faunas and with those of the Charente; (4) N.W. Europe: the chalks and the more coarse-grained deposits are taken into account: the faunas from the temperate cooler seas. The Senonian fauna from the stratotypical area is indicated separately in this column with an X; (5) “Maastricht”: the fauna from the stratotypical Maastrichtian, near Maastricht (The Netherlands): i.e. a fauna of Late Maastrichtian age. The age of the comparative columns is not always totally consistent with that of the fauna from the A 10 outcrops.

5.1. *Cenomanian*

In the “Colloque sur le Cénomanién” (1978) the Cenomanian of Northern Aquitaine is discussed in several papers (Moreau, 1978, Moreau, Neumann and Tronchetti, 1978) and more recently the ammonites have been restudied (Moreau, Francis and Kennedy, 1983). *Pycnodonte biauriculatum* is the major component of the Cenomanian bivalve fauna from the A 10 outcrops. It is restricted to Unit E of Moreau, Francis and Kennedy, and occurs from the Sarthe to Central Asia in warm temperate regions and in Tethys (Dhondt, 1984a).

5.2. *Turonian and Coniacian*

On the A 10 exposures only limited bivalve faunas were collected for those stages. The species are generally long-ranging and widely distributed.

5.3. *Santonian*

Twenty-nine species have been identified from the A 10 Santonian exposures (Table 1).

The affinity with the Tethys is relatively low, but with the Touraine and with N.W. Europe it is very high. Endemic to the Charente–Dordogne are

Table 1. Santonian faunas

| Species | A 10 | Dordogne | Tethys | Touraine | N.W. Europe |
|---|------|-----------------|-----------------|-----------------|-----------------------------|
| 1. <i>Regoria dufrenoyi</i> | + | + | O | O | O |
| 2. <i>Gervillia solenoides</i> | + | O | O | + | + |
| 3. <i>Lyropecten ternatus</i> | + | O | O | + | + |
| 4. <i>Mimachlamys cretosa</i> | + | + | O | + | + X |
| 5. <i>Neithea regularis</i> | + | + | O | + | + |
| 6. <i>Neithea striatocostata</i> | + | + | O | + | + |
| 7. <i>Spondylus dutempleanus</i> | + | O | O | + | + X |
| 8. <i>Spondylus latus</i> | + | O | O | ? | + |
| 9. <i>Spondylus santonensis</i> | + | O | O | O | ? |
| 10. <i>Spondylus spinosus</i> | + | O | + | + | + X |
| 11. <i>Spondylus truncatus</i> | + | O | O | + | + |
| 12. <i>Lima dujardini</i> | + | O | O | + | ? |
| 13. <i>Ctenoides tecta</i> | + | O | O | + | + |
| 14. <i>Limea granulata</i> | + | O | O | + | + X |
| 15. <i>Plagiostoma hoperi</i> | + | ? | O | + | + X |
| 16. <i>Plagiostoma maximum</i> | + | + | O | O | O |
| 17. <i>Plagiostoma santonense</i> | + | + | O | O | O |
| 18. <i>Pycnodonte vesiculare</i> s.s. | + | + | ? | + | + X |
| 19. <i>Pycn. vesic. hippopodium</i> | + | ? | + | O | O |
| 20. <i>Pycn. vesic. nikitini</i> | + | O | + | + | O |
| 21. <i>Pycn. vesic. proboscideum</i> | + | + | + | O | O |
| 22. <i>Hytissa semiplana</i> | + | + | O | + | + X |
| 23. <i>Ceratostreon pliciferum</i> | + | + | + | + | + |
| 24. <i>Vultogryphaea laciniata</i> | + | O | + | + | + |
| 25. <i>Rhynchostreon suborbiculatum</i> | + | O | + | + | + |
| 26. <i>Gryphaeostrea canaliculata</i> | + | + | + | + | + |
| 27. <i>Rastellum</i> sp. | + | + | + | + | + |
| 28. <i>Rastellum deshayesi</i> | + | O | + | O | O |
| 29. " <i>Corbis</i> " <i>striaticostata</i> | + | + | O | O | + |
| | 29 | 13-15 43-52% | 10-11 34-38% | 20-21 69-72% | 21-23 72-79% 7 24% |

3-4 species (10-14% of the fauna), three oyster taxa (10% of the fauna) are seemingly restricted to the Charente-Dordogne and the Tethys.

5.4. Campanian

Twenty-seven species have been identified from the A10 Campanian exposures (Table 2). The uppermost Campanian exposure J0 is considered separately below.

The overall picture is comparable to that of the Santonian, but there is a slightly higher affinity with the Tethys and a seemingly lower affinity with N.W. Europe. For the Touraine less data are available and this explains the difference in the results. 3-4 species (11-15% of the fauna) are endemic to the Charente-Dordogne, two taxa (7.4% of the fauna) are found in the Charente-Dordogne and in the Tethys.

5.5. Uppermost Campanian—locality J0

Eight species have been identified from J0 (Table 3).

The coarse-grained calcarenitic deposits of J0 (comparable to the top strata of the Aubeterre section, stratotype of the Campanian) contained not enough bivalves for conclusive data. The fauna shows a low diversity, but is

Table 2. Campanian faunas

| Species | A 10 | Dordogne | Tethys | Touraine | N.W. Europe | |
|---------------------------------------|------|-----------------|-----------------|-----------------|-----------------|----------|
| 1. <i>Regoria dufrenoyi</i> | + | + | O | O | O | |
| 2. <i>Syncyclonema nilsoni</i> | + | O | O | O | + | |
| 3. <i>Lyropecten ternatus</i> | + | O | O | O | + | |
| 4. <i>Chlamys cf. royana</i> | + | O | O | O | ? | |
| 5. <i>Mimachlamys cretosa</i> | + | O | O | ? | + X | |
| 6. <i>Neithea quinquecostata</i> | + | O | + | O | + | |
| 7. <i>Neithea regularis</i> | + | + | O | + | + | |
| 8. <i>Neithea sexangularis</i> | + | O | + | O | O | |
| 9. <i>Neithea striatocostata</i> | + | + | ? | + | + | |
| 10. <i>Spondylus dutempleanus</i> | + | O | O | + | + X | |
| 11. <i>Spondylus latus</i> | + | O | O | ? | + | |
| 12. <i>Spondylus ? spinosus</i> | + | O | + | + | + X | |
| 13. <i>Spondylus truncatus</i> | + | O | O | + | O | |
| 14. <i>Plagiostoma cretaceum</i> | + | O | O | ? | + X | |
| 15. <i>Plagiostoma hoperi</i> | + | ? | O | + | + X | |
| 16. <i>Plagiostoma marrotianum</i> | + | ? | O | O | + X | |
| 17. <i>Plagiostoma maximum</i> | + | + | O | O | O | |
| 18. <i>Plagiostoma santonense</i> | + | + | O | O | O | |
| 19. <i>Pycnodonte vesiculare</i> s.s. | + | + | + | + | + X | |
| 20. <i>Pycn. vesic. hippopodium</i> | + | O | + | O | O | |
| 21. <i>Pycn. vesic. nikitini</i> | + | O | + | + | O | |
| 22. <i>Hytissa semiplana</i> | + | + | O | + | + X | |
| 23. <i>Exogyra auricularis</i> | + | + | + | O | + | |
| 24. <i>Ceratostreon pliciferum</i> | + | + | + | + | + | |
| 25. <i>Vultogryphaea laciniata</i> | + | O | + | + | + | |
| 26. <i>Gryphaeostrea canaliculata</i> | + | + | + | + | + | |
| 27. <i>Rastellum</i> sp. | + | + | + | + | + | |
| | 27 | 11-13 41-48% | 11-12 41-44% | 13-16 48-59% | 19-20 70-74% | 8 30% |

Table 3. Uppermost Campanian faunas—J0

| Species | A 10 | Dordogne | Tethys | N.W. Europe | Maastricht | |
|-----------------------------------|------|--------------|--------------|--------------|--------------|---------------------|
| 1. <i>Chlamys cf. royana</i> | + | O | O | O | ? | |
| 2. <i>Mimachlamys cretosa</i> | + | O | O | + | + X | |
| 3. <i>Merklinia septemplicata</i> | + | O | + | + | + | |
| 4. <i>Neithea regularis</i> | + | + | O | + | + | |
| 5. <i>Neithea striatocostata</i> | + | + | + | + | + | |
| 6. <i>Exogyra auricularis</i> | + | + | + | + | + | |
| 7. <i>Ceratostreon pliciferum</i> | + | + | + | + | + | |
| 8. <i>Cardium productum</i> | + | ? | + | + | ? | |
| | 8 | 5 (62.5%) | 5 (62.5%) | 7 (87.5%) | 1 (12.5%) | 8(6-8) (75-100%) |

very different from the faunas of the underlying strata, and most species are also known from the stratotypical Maastrichtian. This similarity is probably partly due to the comparability of the sediments, hence, of the environment. Bivalves are facies fossils.

In 1984b I have compared the affinities of the Paris Basin Senonian faunas with those of S.W. France. The comparison of bivalve faunas from the Santonian, Campanian and uppermost Campanian from the A 10 outcrops

with those from other palaeogeographical regions confirms the conclusions reached in 1984. The better stratigraphic control on the A 10 exposures allows us to note differences between the Santonian, Campanian and uppermost Campanian. We can confirm the absence in S.W. France of: small species of *Lyropecten*, *Neithea sexcostata*, *Mimachlamys mantelliana*, small oysters of the genera *Acutostrea* and *Agerostrea*, which form a typical white chalk fauna, and are found in the stratotypical Senonian, in the E. Paris Basin.

6. Palaeoecological indications

6.1. Environment

The limids and gryphaeids show that Santonian and Campanian A 10 strata (at the localities S4 (1128) to J2) were deposited in a relatively deep environment. The presence of large *Plagiostoma* species and of several *Pycnodonte* (*Phygraea*) taxa indicates an upper shelf environment, definitely deeper than the tidal zone. This interpretation agrees with that of Douvillé (1910) who considered that in Royan (Campanian), the numerous pycnodonts lived in a depth probably greater than 100 m. And also in general this tallies with what Séronie-Vivien wrote (1972, pp. 155–168) for the depth variation in Santonian, Campanian and Maastrichtian (Maastrichtian sensu Séronie-Vivien, 1972 equals J0 in this paper).

6.2. Predation and other marks

Many of the *Plagiostoma santonense* specimens show long, narrow marks, from near the umbo straight towards the pallial margin, but not quite reaching it [Figure 3(d), (f)]. These marks are of uncertain origin and might even possibly be diagenetic (tentative opinion of R. G. Bromley, written communication, February 1984). On one of the *Pl. santonense* specimens [Figure 3(f)] a bite or crush mark is visible; it has a more or less conical shape, with a diameter of about 15 mm. Comparison with the *Ptychodus* marks (Kauffman, 1972) and the Mosasaur marks (Kauffman and Kesling, 1960) shows a marked difference. It could be that this mark was caused by a *Globidens*-like mosasaur.

7. Results

(1) The A 10 exposures in the Champagne charentaise (Northern Aquitaine) have yielded a diversified bivalve fauna of Cenomanian to latest Campanian age (50 taxa in all).

(2) The faunal coverage varies.

(a) The Cenomanian, Turonian and Coniacian stages are represented by limited faunas, more often than not specifically unidentifiable. The data assembled for those stages add little to the results of previous research.

(b) The Santonian and Campanian stages have yielded diversified faunas, of adequate preservation for the bivalves with calcitic shells (Pectinidae, Spondylidae, Limidae and Ostreacea). For those groups, a partial revision

of the monographs by d'Orbigny (1844–1847) and by Coquand (1869) is presented, applying more modern taxonomic concepts. For other bivalve groups, when possible, a tentative identification is given.

(3) Comparison of faunal affinities of the bivalves of Late Cretaceous age from Northern Aquitaine, shows a strong relation with N.W. European faunas of similar age. In the Santonian–Campanian a few species are endemic to Northern Aquitaine, and some occur only in Northern Aquitaine and in Tethys. Many species known from N.W. Europe in the Late–post Coniacian–Cretaceous white chalks did not reach Aquitaine. This does not apply to the species from the N.W. European Late Cretaceous coarse grained deposits.

(4) The faunas of Santonian age and most of those of Campanian age have been deposited in upper shelf environment. The uppermost Campanian was, on the contrary, deposited in a very shallow environment.

(5) Marks of unknown origin and probably crush or bite marks are found on *Plagiostoma santonense* specimens.

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Appendix—abbreviations

- A 10: autoroute A 10, l'Aquitaine, Paris–Bordeaux;
 GFC: Groupe français du Crétacé;
 WGCM: Working Group Coniacian–Maastrichtian of the Cretaceous Subcommittee on Stratigraphy;
 W: width of the specimens;
 UPD: umbo pallial diameter–height.

Collections

- BMNH: British Museum of Natural History, London;
 LGU: Leningrad State University, Leningrad, Geology and Paleontology Department;
 MAFI: Magyar Allami Földtani Intezet, Hungarian Geological Institute, Budapest;
 MGRI: Moscow Mining Institute, Moscow;
 VSEGEI: All Soviet Institute of Geological Research.

Signs in synonymy lists

- p.p.: *pro parte*;
 v: *vidi*;
 .: agreement with the identification quoted;
 ?: doubt on the identification quoted.