

## DISTRIBUTION AND RECOGNITION OF PHASES IN APTIAN-TURONIAN (CRETACEOUS) BRACHIOPOD DEVELOPMENT IN NW EUROPE

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**Abstract:** Although represented during the Cretaceous (in three faunal provinces: Boreal, Jura, Tethyan), brachiopods have not commonly been considered as competitors of ammonites and foraminifers in the establishment of a standard zonation scheme. Occasionally brachiopods are well represented in thin layers where other faunal groups are absent or poorly represented. The paleontological evaluation (complementary morphological remarks with an illustration and distribution of most species) is given here for the Aptian-Turonian period, and the correlative value of the most important species is discussed. This analysis leads to a discussion-conclusion concerning: a) ecological considerations (for example, the fact that some genera are preferentially found in typical facies), b) designation of stratigraphic markers, c) location of the considered fauna elsewhere in the world and, d) a proposal for the recognition of phases in brachiopod development in the present stage of knowledge, with remarks concerning the distribution in correlation with transgressive-regressive movements.

**Key words:** NW Europe, Aptian, Albian, Cenomanian, Turonian, recognition of phases, distribution, brachiopods.

### Introduction

While well represented during the Cretaceous in the three faunal provinces (Boreal, Jura and Tethyan), brachiopods have not been considered as competitors of ammonites and foraminifers in the establishment of a standard zonation. Being mainly anchored benthic organisms, they are highly controlled environmentally and consequently their great variation may be responsible for their secondary zonal value. The lack of recognition of micromorphic species which is due to the small number of worldwide experts on the Cretaceous is also a disadvantage.

It is not easy to correlate brachiopod occurrences with ammonite zones, misleading, according to Middlemiss (1981), but this largely disregarded group has been collected in the past without the ammonite fauna and without other faunal markers. A better knowledge of successive faunas through time would help to reach a true appreciation of ranges of species.

Each population frequently reflects a dimorphism, a point particularly studied in the terebratulids (Sellithyridinae: Gaspard 1988). In addition, differences are observed between populations of *Phaseolina phaseolina* (Lamarck) from the Upper Cenomanian of Charentes, Sarthe, Vendée and Var (France), the province of Beira (Portugal) and the Bohemian Basin, a phenomenon known as polytypism. This phenomenon is also observed, among other species, e.g. between populations of *Sellithyris cenomanensis* (Gaspard) from Middle Cenomanian strata from Sarthe, Indre and Charentes. This variability in shape and size is related to local conditions. In the case of rhynchonellids, with their decorative characters, variability chiefly affects the ornamentation (mainly number of costae) in addition to this external morphology.

Brachiopods are, however, occasionally well represented in thin beds where major groups are absent. Thus they may

sometimes have local, regional or provincial correlative value. It does not appear necessary to redescribe entirely the species, but for a better understanding of the discussion, some complementary morphological remarks are presented and placed in their systematic context. The stratigraphical distribution of important genera and species through Aptian-Turonian strata is presented in Table 1. This will be referred to below in connection with the recognition of phases in the brachiopod development and a preliminary zonation.

### Paleontological evaluation: morphological remarks and distribution

This section does not correspond to new systematic data, but remarks on complementary morphological features are sometimes necessary, as well as precise data on the distribution of taxa, prior to any discussion concerning their stratigraphical value and recognition of phases of development.

Class Inarticulata Huxley 1869

**Remarks:** Inarticulates are not numerous in the Cretaceous, few examples are quoted.

Superfamily Linguloidea  
Family Lingulidae Menke 1828  
Genus *Lingula* Brugière 1797

**Remarks:** Apart from *Lingula subovalis* Davidson briefly recorded from the Upper Greensand near Warminster, (Davidson 1852, pl. 1, Figs. 29, 30) and from Wiltshire (Owen 1888, pl. 5), another species exists, *Lingula rauliniana* d'Orbigny 1847, which seems to be a synonym of *L.*

*truncata* Sowerby described also by Davidson (1852, pl. 1, Figs. 27, 28, 31). The shell of this species is thin, small, irregularly oval, flattened longitudinally, smooth with light growth lines more numerous towards the commissures on contrary of *L. subovalis* with regular shape and few concentric growth lines. It characterizes the Lower Greensand of Atherfield (Isle of Wight) and the environs de Grandpré (Ardenne).

Superfamily Cranoidea  
Family Craniidae Menke 1828

*Crania cenomanensis* d'Orbigny 1847  
Pl. II: Fig. 4

**Remarks:** The species has not been well studied in Europe. It is known from the Upper Greensand (Cenomanian) of le Mans (Sarthe). The description of the shell is based upon the material of de Vibraye coll. (M.N.H.N., Paris, no. B. 16440) because d'Orbigny coll., no. 6514, is non-existent now. From this material, the shell appears irregular, approximately oval transversally, the upper valve being somewhat conical. Muscle scars, brachidium and a narrow limbus are well represented on the internal surface of this valve (Pl. II: Fig. 4), while the Lower valve is unknown.

*Crania rhotomagensis* d'Orbigny 1847

Contrary to the preceding species, *C. rhotomagensis* has a longitudinally oval shell, with muscle fields closer to the commissures and a wide limbus. It is known from Rouen in d'Orbigny coll. (M.N.H.N., Paris no. 6515), but all specimens are broken. Both species may, in fact, be representatives of the genus *Ancistocrania*, according to the internal characters, but more material is needed to prove this.

Class Articulata Huxley 1869  
Family Rhynchonellidae Gray 1848  
Subfamily Cyclothyridinae Makridin 1955  
Genus *Cyclothyris* M'Coy 1844

*Rhynchonella latissima* J. de C. Sowerby 1829 is the type-species of the genus.

**Remarks:** The species described by Owen (1962) occurs in the Tropaeum subarcticum Subzone, Parahoplites nutfieldensis Zone of Berkshire, Cambridgeshire and Kent. Following Barbulescu et al. (1975) it is also known to occur in the Aptian of Baciliu, Rasova (Rumania) and probably in the Jura province.

*Cyclothyris depressa* (Sowerby 1825)

**Remarks:** D'Orbigny (1847) figured and described a common rhynchonellid species in synonymy with "*R.*" *depressa* Sowerby, widely represented in France (M.H.N.H. coll., no. 5148). But comparisons of pl. 491 (Figs. 1-7) with the holotype figured by Owen (1962, pl. 4, Fig. 11) do not compare favourably. The species is represented in P. nutfieldensis

Zone. "*R.*" *lata* specimens figured by d'Orbigny (M.N.H.N., no. 5149) seem to have more in common with "*R.*" *depressa* Sowerby.

*Cyclothyris antidichotoma* (Buvignier 1843)

**Remarks:** The species, revised by Owen (1962), is represented in the Upper Aptian (P. nutfieldensis Zone) in England, with *C. depressa* (Upware, Cambridge, Brickhill, Buckinghamshire), as well in the Aptian of Ahaus (Pictet, 1872, pl. 199, Figs. 13-15). Barbulescu et al. (1975) quoted the species from the Lower Aptian of Baciliu Rasova (Rumania). Though less common, the species is found in the Lower Albian of Grandpré, Novion (Ardenne) (d'Orbigny coll., no. 6014), Mont Saxonet, Goudinière, Savoie (France) and Bedfordshire (England). The characteristic feature of the shell of this species consists in grouping of fine costellae (38-40) into strong costae from mid-length or third-anterior towards the commissures.

*Cyclothyris scaldisensis* (d'Archiac 1846)

**Remarks:** The species is characterized by a shell broader than long, biconvex, with a large circular foramen and a massive slightly incurved umbo. The ornamentation is composed of numerous rounded costae. The species has been described from the Lower Cenomanian (Tourtia of Tournai, Belgium). It is recorded from the Lower Cenomanian of Normandy (France), England and in the Munster Basin at Essen, Germany. The material was observed in E.M. coll., Lyon.

*Cyclothyris difformis* (Valenciennes in Lamarck 1819)  
Pl. I: Fig. 15

**Remarks:** Apart from the type-series of Lamarck in Geneva, the species has been collected from the Greensand (Lower Cenomanian) near le Havre (Cap de la Hève). The specimens are in M.N.H.N. coll., le Havre (no. 1250), (Pl. I: Fig. 15a-b). Other specimens come from the Tourtia of Tournai (Lower Cenomanian, Belgium) and le Mans (Lower and Middle Cenomanian, E.M. coll., Lyon), and some have been collected from the Journeaux quarry (Valencay, Indre) in Middle Cenomanian. In addition to the previous localities, the species is recorded from England, in the Lower Cenomanian deposits of Essen, North Germany (Owen 1962) and probably in organo-detritic limestones near Prague (Predboj, Bohemia).

The species name of *Rh. difformis* was controversially employed. The species considered here has a variable shell shape, being transverse or subtriangular in outline, with a few marked growth lines. The width can attain 40 mm and the umbo is sometimes short or massive, and more or less erect. Two distinct deltidial extensions in juveniles (Pl. II: Fig. 15), evaluate to form a typical circle around the foramen in adults. The shell is ornamented by approximately 40 costae, fine near the umbo, becoming coarser near the margins. The anterior asymmetric margin is right or left-handed in adults.

The specimens from the Tourtia show certain resemblances with *C. scaldisensis*, but the anterior region is more gibbous, having an erect umbo and the anterior commissure asymmetrical.

It is necessary to separate all these Cenomanian specimens from the Upper Cretaceous ones from Charentes, Landes, Pyrenean region and S.E. of France, which also have an asymmetrical commissure.

*Cyclothyris compressa* (Lamarck 1819)

Pl. I: Fig. 11

**Remarks:** Agreeing with the first presentation of Owen (1962), I have observed this species in Lamarck coll. (pl. 19, specimen A-C, Coulaines near le Mans, kept under the no. 46183), M.N.H.N. coll., no. 6495 pr.p., Paris; E.M. coll., Lyon. The species has been sometimes misidentified, its representatives have a winged shell, somewhat flat and transverse, ornamented by 32 to 38 strong angular costae (7 in the fold) with a characteristic thickening of the commissures (Pl. I: Fig. 11b). The ventral, suberect, umbo is sharp dorsally. This species characterizes a formation in the Sarthe region named: "Les Sables du Perche", (upper part of Middle Cenomanian-lower part of Upper Cenomanian), Juignet (1974).

*Cyclothyris lamarckiana* (d'Orbigny 1847)

Pl. I: Fig. 17

**Remarks:** The species is also present in the Upper Cenomanian, C. naviculare Zone "Marnes à *Ostrea biauriculata*" of the Sarthe region, but is slightly transverse, with a suberect umbo. In comparison with *C. difformis* the ornamentation is composed of approximately 33-35 well defined costae from which, 6 are located in the fold (Pl. I: Fig. 17b) and the asymmetry is not common. The foramen is circular and the deltidial plates exposed (Pl. I: Fig. 17a). Representatives of the species have been observed in d'Orbigny coll., no. 6493, Pèron coll., Morgan coll. (no. B. 16046), de Vibraye coll., no. B16052 (M.N.H.N., Paris).

Genus *Burrirhynchia* Owen 1962

**Remarks:** This name was created by Owen (1962) to distinguish "*Rh.* *leightonensis* Walker (Bedfordshire, L. tardefurcata Zone) and "*Rh.* *cantabridgiensis* Davidson (Aptian, P. nutfieldensis Zone, Buckinghamshire), from *Cyclothyris*.

The genus is also represented by *B. gibbsiana* (J. de C. Sowerby 1826), redescribed by Owen (1956) (Lower Greensand of Folkestone) and *B. sigma* (Schloenbach 1867). As distinct from the first three species, *B. sigma* (Lower Cenomanian) is more commonly found in Europe (North Germany, Belgium, France, Poland, and also, Podolia). Popiel-Barczyk (1977) has illustrated the species by serial transverse sections of specimens from Poland (environs of Cracow, Czestochowa, Iwanovice, Annopol). In addition to the pentagonal outline, the shell is biconvex and the umbo suberect, but the striking feature is the M-shaped anterior commissure characterizing the species.

Subfamily Uncertain

Genus *Grasirhynchia* Owen 1968

*Grasirhynchia grasiana* (d'Orbigny 1847) is the type-species of the genus. The lectotype selected by Owen (1968) is

figured from the d'Orbigny collection, no. 6497 of the catalogue (M.N.H.N., Paris). The species is recorded from Warminster, Chute Farm, Isle of Wight (England), le Havre and Pas de Calais (France).

*Grasirhynchia martini* (Mantell 1822)

Pl. I: Fig. 16; Pl. II: Fig. 16

**Remarks:** This species has been described by Owen (1968). The shell is of small size, while *G. grasiana* is larger. Those collected in 1978 and 1995 in Grey chalk of Blanc Nez cliffs, between Escalles and Sangatte (Boulonnais) (upper part of the Lower Cenomanian and Middle Cenomanian), particularly in the bed above the 2nd *O. mantelliana* band, have the following dimensions (L: 6.0-8.4 mm; l: 5.8-7.4 mm; e: 3.7-5.7 mm). The deltidial extensions around the foramen, although not confined to the species, are well represented (Pl. II: Fig. 16).

Amédro (1993-1994, Fig. 3) indicated that the species is found at the top of bed 17 and in bed 18 "Formation du Cran" with *O. mantelliana* Sowerby and *Sciponoceras baculoides* (Mantell), in the same formation (set H') with *Micrabacia coronula* and other brachiopods including *Modestella geinitzi* (Schloenbach) and *Kingena concinna* Owen.

The species is also recorded from the Aube region (Montmorency-Beaufort quarry) in a chalky marl with the previous fauna (Amédro et al. 1994, Fig. 2).

Family Wellerellidae Likharev in Rzhonsnitskaya 1956

Subfamily Lacunosellinae Smirnova 1963

Genus *Orbirhynchia* Pettitt 1954

*Orbirhynchia mantelliana* (Sowerby 1826)

Pl. I: Figs. 12-13

**Remarks:** This species is a very important stratigraphic marker in the Cenomanian. Kennedy (1969) emphasized its position in different locations of England, highlighting the existence of an *O. mantelliana* band, stratigraphic marker, occurring at the upper limit of the T. costatus Subzone, A. rhotomagense Zone.

Kennedy (1969) quoted the species in Kent (coast): band 9 (mainly the top 30 cm) with *Sciponoceras baculoides* (Mantell), *A. rhotomagense* (Brongniart) and *Scaphites equalis* Sowerby, in band 10 (2.5 m) rich in specimens with *Acanthoceras*; in Kent (inland), in the vicinity of Blue Bell Hill Burham: band 4 (*T. costatus* fauna), in band 6 (*O. mantelliana* band with *Concinnithyris* sp., *Gemmarcula menardi* (Lamarck), *Grasirhynchia grasiana* (d'Orbigny) and *Kingena* sp.); in Sussex, near Eastbourne; in Isle of Wight (*O. mantelliana* band in Culver cliff and Compton Bay). The existence of this *O. mantelliana* band is summarized by Kennedy (1969, p. 531). Pettitt (1949-54) quoted and figured the species (p. 31, pl. 3, Figs. 10a-c) in Bedfordshire, Cambridgeshire, Kent, Surrey, Sussex with an A. rhotomagense Zone age.

The observations of Robaszynski et al. (1980) led to the recognition of the existence of *O. mantelliana* in some localities of Boulonnais, particularly at Escalles. Complementary observations allow Amédro (1993, 1994) to define the existence of three *O. mantelliana* levels: one in the "Formation du

Petit Blanc Nez”, set F, unit 10iv, containing also *Monticlarella brevisrostris*, another in the set G of the same formation, unit 15’ associated with *Rotalipora reicheli*, the later in set H’ of “Formation du Cran”, unit 18 (with *Modestella geinitzi* (Schloenbach), *Kingena concinna* (Owen) and *Grasirhynchia martini* (Mantell)) and mainly unit 19–19’ with *S. baculoides* (Mantell). The most important is the third level. Field-trips in 1978 and 1995 gave again the opportunity of collecting the species and accompanying fauna (Pl. I: Figs. 12–13). In addition, material from France has been observed in d’Orbigny coll. (M.N.H.N., Paris, no. 6911).

Comparisons have been made in Lower and Middle Cenomanian Chalks (Chalk Marl and Grey Chalk) between Blanc Nez cliffs and at Folkestone (Kent), across the Straits of Dover using Channel Tunnel boreholes correlations (Amédro 1994, Fig. 5, p. 78). In the same manner accurate lithological successions in the Paris Basin allow one to realize the great spatial continuity of several marker levels in Middle Cenomanian from Kent to Aube (Amédro et al. 1994).

Panow (1969, pl. CIX, Figs. 4a–c) quoted the species in Korskwie and probably Sudol. Schloenbach (1867) mentioned the species from the Mantelliceras mantelli and Acanthoceras rhotomagensis Zones, Northwestern Germany.

The *Orbirhynchia boussensis-wiesti-cuvieri* group  
Pl. I: Figs. 2–4

The genus *Orbirhynchia* has been studied by Pettitt (1949–50) in the context of the British chalk. Among other species the author described: *O. wiesti* (Quenstedt), Cenomanian; *O. multicostrata* sp. nov., Turonian (*Plenus* marl); *O. praedispana* sp. nov. (Turonian, basal I. labiatus Zone); *O. cuvieri* (d’Orbigny), basal I. labiatus Zone (for a long time considered as a stratigraphic marker); some other new species from I. labiatus Zone: *O. extensa*; *O. compta*; *O. orbignyi*; *O. heberti* (Terebratulina lata Zone); *O. reedensis* Etheridge (Hoplaster planus Zone). It seems that the species quoted after *O. cuvieri* have no or a few representants elsewhere in Europe! (e.g. *O. orbignyi* reported from Poland by Popiel-Barczyk 1977). In this context, only *O. wiesti* (Quenstedt), *O. cuvieri* (d’Orbigny) and *O. boussensis* Owen, a new species created by Owen (1988), will be discussed.

**Remarks:** Comparisons from figured specimens of *O. wiesti* and material from “Les Sables de Bousse” in the Sarthe Department (sampled or observed in collections), as well as the specimen of *O. boussensis* Owen shown here (Pl. I: Fig. 3) allow to observe that the figured specimen of *O. wiesti* (Owen 1988) is narrower than those from Bousse (Pl. I: Fig. 4, but only one specimen is shown!). *O. cuvieri* d’Orbigny which characterizes the basal part of I. labiatus Zone, is generally represented by specimens a little more globular, similar to individuals from Rouen, (E.M. coll., Lyon) with the anterior commissure a little less uniplicate or with an uniplication Lower than in specimens from Bousse. The figuration of Pettitt from Surrey (1949–54, pl. III, Fig. 12) and the lectotype chosen from d’Orbigny coll. (no. 6910a) do not show significant differences in the anterior commissure. In addition, Juignet et al. (1973) quoted numerous *O. wiesti* in the type-section at Bousse (near the ceme-

tery). Peake & Hancock (1970, p. 306) do not clarify this difficult situation, quoting *O. cuvieri* and *O. aff. wiesti* in the I. labiatus Zone of Norfolk. The number of costae does not always show a significant difference, leaving this situation as it stands unless we consider a lineage in the process of time with two main stages. However, it seems difficult to retain two markers (*O. boussensis* and *O. wiesti*) for the upper Upper Cenomanian. Also, one should keep in mind the possibility of polymorphism and polytypism.

In addition, Middlemiss (1991) quoted the presence of representants of the genus off Helgoland (North Sea).

Family Norellidae Ager 1959  
Subfamily Monticlarellinae Childs 1959  
Genus *Monticlarella* Wisniewska 1932

*Monticlarella brevisrostris* (Roemer 1840)

**Remarks:** The species is known from Germany. Else, a few specimens were sampled in 1995 from the first *O. mantelliana* band, in glauconitic marly facies of Petit Blanc Nez cliffs (Boulonnais) (L: 8.4–9.0 mm; I: 7.6–8.1 mm; e: 4.2–4.9 mm). These specimens have a somewhat triangular shell, with a ventral umbo slightly sharp and suberect and an oval foramen. Bifurcating costae are observed at mid-length. A widening is evident, close to the anterior limit of the shell. All these characters allow to recognize this small species.

According to observations of Amédro (1993, 1994), 13 marker levels have been recognized from Blanc Nez to Folkestone across the Straits of Dover. Amédro (1994, Fig. 4) postulated a vertical extension of the species from unit 3 to the top of unit 10 (with periods of abundance in units 8 and 10) of “Formation du Petit Blanc Nez”.

Else Middlemiss (1991) highlighted the presence of the genus in North Sea (sea-floor off Helgoland).

Superfamily Terebratuloidea  
Family Terebratulidae Gray 1840  
Subfamily Sellithyridinae Muir-Wood 1965

**Remarks:** In this subfamily the genus *Ovatathyris* Owen (1988) will not be discussed here without more precise data; as well as the genus *Boubeithyris* (Cox & Middlemiss 1978). *B. boubei* (d’Archiac) from the Tourtia of Tournai is the type-species, *B. diplopicata* being evoked below as *Praelongithyris fecampi* Gaspard.

Genus Sellithyris Middlemiss 1959

**Remarks:** The genus begins with *S. sella* (Sowerby) (type-species) in the early Cretaceous, species several times mentioned notably in North Africa (Benest et al., 1996), mainly in marly Hauterivian sediments and Lower Aptian in Spain, France, England (Gaspard 1988, p. 88–107; Middlemiss 1968), Hungary (Dêtre 1968), (Pl. II: Fig. 13). The genus ends with *S. cenomanensis* Gaspard, Middle Cenomanian (type-locality: la Butte du Mans, Sarthe), in “Jalais” level (Pl. I: Fig. 9). Both species are widely represented, although intermediate species such as *S. coxwellensis* (Middlemiss

1959), *S. longella* (Leymerie 1869), and *S. tornacensis* (d'Archiac 1846), (Pl. II: Fig. 1) are endemic: the first in the Upper Aptian of England (Faringdon Sponge Gravel, Berkshire and Wiltshire), the second in the Upper Albian of Spain and Pyrenean Greensand, the later in the Tourtia of Tournai, Belgium (Lower Cenomanian). All species have been previously described (d'Archiac 1848; Leymerie 1869; Peybernes & Calzada 1977; Gaspard 1988) or analyzed by multivariate analysis (Gaspard & Mullon 1983) and thus do not require complementary details in this context.

#### Genus *Loriolithyris* Middlemiss 1968

**Remarks:** For the period considered, the genus is represented by *L. russillensis* (Loriol) (type-species) ending in the beginning of the Aptian. This species, more characteristic of the Jura and the Tethyan province (Gaspard 1988), is found during the Aptian in southeast Morocco, eastern Spain (Mallada 1887), Alpes-Maritimes, Vercors and also Neuchâtel according to Middlemiss (1981).

#### Genus *Moutonithyris* 1976

Type-species: *M. moutoniana* (d'Orbigny 1847)  
Pl. II: Fig. 9

**Remarks:** The species is known from the Berriasian (mainly South of France) but its distribution until the Aptian of Germany, Westphalen (Schloenbach 1860) and probably Sardinia (Dieni et al. 1973) is interesting in this context. The genus becomes extinct with *M. dutempleana* (d'Orbigny), Upper Albian-basal Cenomanian (Gault-Upper Greensand), (Pl. II: Fig. 2). While ubiquitous, this species is well represented in the Boulonnais (France), as well in England (Gaspard 1976, 1985, 1988, p. 197–201) apart the Tethyan realm.

Representatives of both *M. moutoniana* and *dutempleana* are quoted from North Sea (Middlemiss 1991).

The species *M. obtusa* (Sowerby 1823) seems to be possibly confined to Cambridge Greensand.

#### Genus *Phaseolina* Gaspard 1985

**Remarks:** The genus presumably terminates the Sellithyridinae. At the moment, obviously, only one species is known: *P. phaseolina* (Lamarck).

*Phaseolina phaseolina* (Lamarck 1819)  
Pl. I: Fig. 5

The species, widely described in several populations (Gaspard 1983, 1985, 1988) is representative of the Upper Cenomanian (type-locality, Colline de la Goupillerie, Sarthe in "Sables *Catopygus obtusus*", Pl. I: Fig. 5), sometimes in company of *Orbirhynchia* group *boussensis-wiesti-cuvieri* (cf. "Sables de Bousse" lateral extension of the first formation), in other locations with *Ostrea biauriculata* (Maine & Loire) or *Calycoceras*, and in extreme position with *Gemmarcula carentonensis* (d'Orbigny) (Pl. I: Fig. 6) and *Arca* (Charente Maritime) (Gaspard 1985, 1988). It is also quoted in the Bohemian Basin (Nekvasilova 1973) and observed by

the present author from the Late Cenomanian in the collections of the Geological Institute of Freiberg University of Mining and Technology (Germany).

#### Genus *Praelongithyris* Middlemiss 1959

**Remarks:** The genus extends from the Aptian to the Cenomanian, with *P. praelongiforma* Middlemiss (1959) from the Upper Aptian (abundant at Upware, less present at Brickhill (?), and Faringdon) and *P. lankesteri* Walker (1868) (both possibly endemic in England), through the Lower Albian: *P. rogeri* (Gaspard 1974, Holotype selected from d'Orbigny collection, M.N.H.N., Paris, no. 6017A), in Leymeriella tardefurcata Zone (les Ardennes, France) (Pl. II: Fig. 6), (Gaspard 1988, p. 210–218), to the Lower Cenomanian (H. carci-tanensis–M. saxbii Zones) with *P. fecampi* Gaspard in Nièvre, Normandy, (Pl. II: Fig. 5), probably Tourtia of Tournai (I.R.S.N, Brussels, no. IG 10511/20, 21) and Southern England (Pl. II: Fig. 10; Gaspard 1985, 1988). This last species was described under the name of *Boubeithyris diploplata* by Owen (1988, p. 112, pl. 8).

#### Subfamily Rectithyridinae Muir-Wood 1965

##### Genus *Rhombothyris* Middlemiss 1959

**Remarks:** The species *Rhombothyris extensa* (Meyer 1864) is known from the Upper Aptian of Upware, Brickhill, Barge beds (*P. nutfieldensis* Zone, West Surrey) and glauconitic sands of Shanklin (Isle of Wight). *R. microtrema* (Walker 1868) was found in the two first localities, *R. meyeri* (Walker 1868) at Upware and *R. conica* Middlemiss (1959) at Brickhill. All these species seem to be confined in England.

##### Genus *Cyrtothyris* Middlemiss 1959

**Remarks:** As for the previous species, representatives are known in the Aptian of England (*C. uniplicata* (Walker 1870), *C. cantabridgiensis* (Walker 1870), *C. seeleyi* (Walker 1870), *C. dallasi* (Walker 1867), and also from Germany (Berklingen), Switzerland (Ste. Croix), *C. cyrta* (Walker 1868).

##### Genus *Rectithyris* Sahni 1929

**Remarks:** This genus may have been evolved from *Cyrtothyris* Middlemiss 1959 (Middlemiss 1984). It is represented by *R. viquesneli* (d'Archiac 1846), Upper Albian, *R. depressa* (Lamarck 1819), Lower Cenomanian (Tourtia of Tournai, Belgium) and has a restricted distribution (Pl. II: Fig. 3). This species was observed in the following collections (I.R.S.N., Brussels; M.N.H. N., Paris; E.M., Lyon.).

##### Genus *Tropeothyris* Smirnova 1972

**Remarks:** This genus not well represented, will not be discussed without more concrete data (cf. Owen 1988).

##### Genus *Concinnithyris* Sahni 1929

**Remarks:** Few papers concern the genus *Concinnithyris* previously placed in Gibbithyridinae. One of the last papers

(Middlemiss, 1991 p. 225) argued to place this genus in the subfamily Rectithyridinae; more investigations are needed to adopt definitively this position. The genus is not confirmed to be a transition from *Moutonithyris* (Middlemiss 1984, 1991), and is widely represented particularly in the Cenomanian and Turonian of Normandy, South England, Germany?, with *C. albensis* (Leymerie), *C. obesa* (Sowerby), *C. subundata* (Sowerby) and *C. protobesa* Sahni.

*Concinnithyris obesa* (Sowerby 1823)

Pl. I: Fig. 18

**Remarks:** This is an example for which the interpretation of the species is problematic because of the great variability of the global morphology of the shell. The propensity of Sahni (1929) to create many species around *C. obesa* does not facilitate discussions. The type-specimen probably does not reflect the median aspect of the species but the variants are so numerous that one can find medium-sized specimens, gibbous, but narrow with nearly parallel flanks or lateral commissures and sometimes a gentle beak angle (d'Orbigny 1847–51, pl. 513, Fig. 4).

These large or medium specimens, round gibbous or narrow, in collections, come from “La Craie de Rouen”, Côte Ste Catherine (Normandy), (d'Orbigny coll. no. 6912) which is now recognized as Middle Cenomanian (Juignet 1974). Some large specimens come from Neuville (Yonne, E.M. coll.) and St. Sauveur (Yonne; d'Orbigny coll., M.N.H.N., Paris). Owen (1988) also recognized this great variability.

To conclude, the object is to obtain a great number of specimens for multivariate analysis, from each locality, to determine (once and for all), the presence or not of one or a few other species.

*Concinnithyris protobesa* Sahni 1929

**Remarks:** This species has external morphological affinities with the narrow figured specimen from “La Craie de Rouen” in d'Orbigny, as well as with the specimen in Owen (1988, pl. 14) and with some specimens of *C. obesa* from the E.M. coll., Lyon. In other respects the specimen figured by Davidson (1852–54) has little to do with the type-species *C. protobesa* present in the Lower Turonian of England and Normandy, which has a shell characterized by a well curved beak and appressed to the dorsal umbo preventing the symphytium to be exposed. The foramen is large, circular or ovate and sometimes slightly labiate. The brachial valve is less convex than the pedicle one. The anterior margin is in intermediate expression between retimarginate and uniplicate.

*Concinnithyris subundata* (Sowerby 1813)

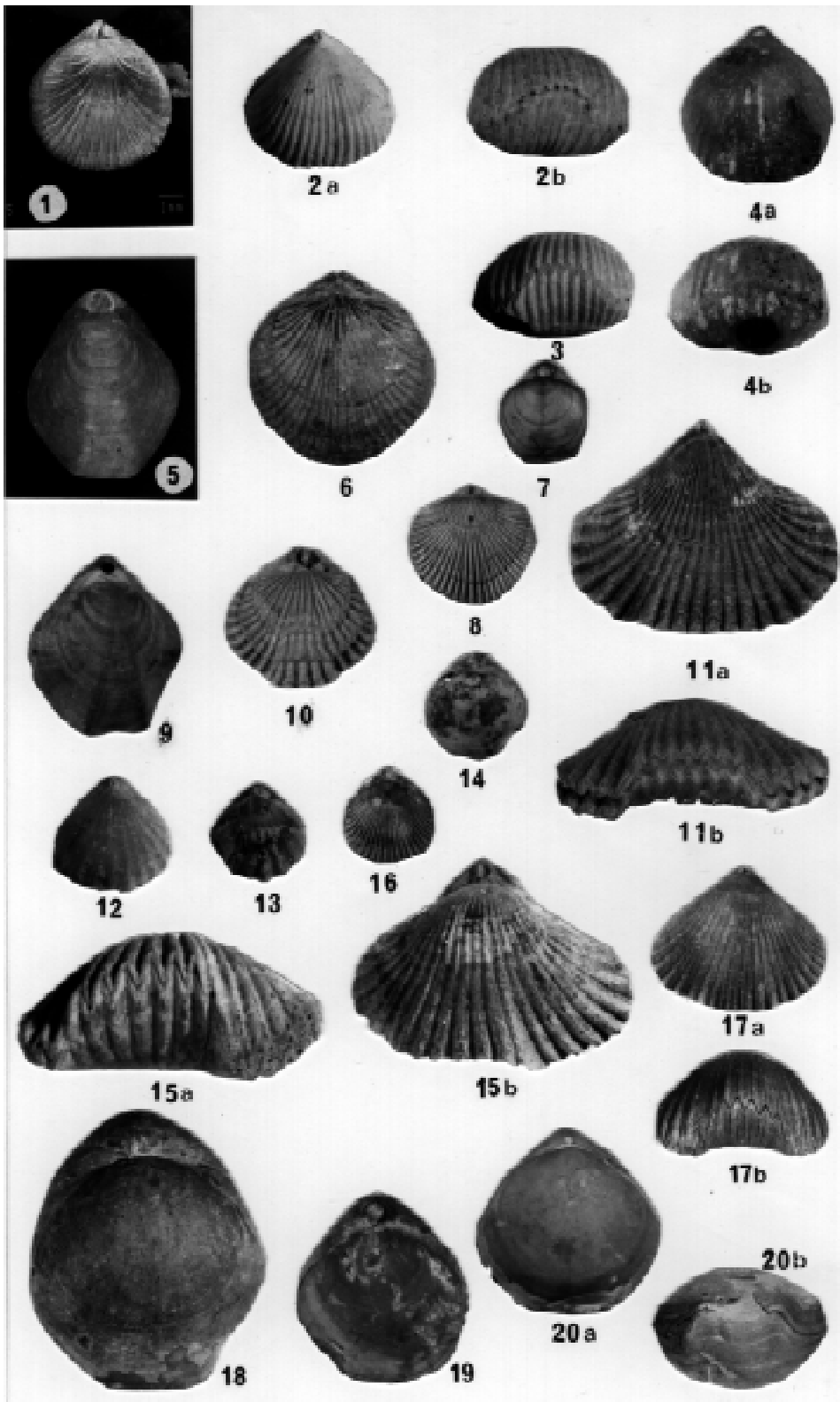
Pl. I: Fig. 19

**Remarks:** This species seems at first sight to be more easy to distinguish from *C. obesa*, because of the less biplicate and gibbous anterior commissural region while the shell shape is subpentagonal or subcircular. The species is represented in the Lower Chalk in England (Kennedy 1969; Peake & Hancock 1970) and France (particularly in Normandy and Boulonnais where juveniles specimens have been sampled).

Representatives of the genus have been quoted by Middlemiss (1991) in the North Sea and by Kennedy (1969) in the Middle Cenomanian, but often without determination in this last case. More often it is *C. albensis* (Leymerie) (Kennedy coll. in Br. Mus. Nat. Hist., no. B. 85783–4), or *C. subundata* (no. BF 48–49, BB 85781–2) from Kent, Sussex, Dorset (cf. A. rhotomagense Zone, *Orbirhynchia mantelliana* band). Kennedy (1969) highlighted the occurrence and particular abundance of *Concinnithyris* and sometimes *Gibbithyris* at the boundary of *T. acutus* with *A. jukesbrownei* assemblages.

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**Plate I: Fig. 1** — *Terebratulina lata* Etheridge (1881), Holotype, marker of the Middle Turonian (T. lata Zone), (British Geological Survey coll.) BSG GSM, no. 38693, ×4. **Fig. 2a–b** — One specimen of the genus *Orbirhynchia* from “Sables de Bousse”, Bousse, Sarthe (France), pers. coll., (a) dorsal view, (b) anterior view, ×1.2. **Fig. 3** — *O. boussensis* Owen (1988), from “Sables de Bousse”, Bousse, Sarthe (France), (anterior commissure), (British Museum): B.M. (N.H.) coll. no. BB 82131, ×1.2. **Fig. 4a–b** — *Orbirhynchia wiesti* (Quenstedt), Upper Cenomanian, Bed B, Little Beach Beer specimen figured by Owen (1988) (a) dorsal view, (b) anterior view. Coll. B.M.(N.H.) coll. no. BB 7126, ×1.2 (for comparison with Pl. I. 2,3). **Fig. 5** — *Phaseolina phaseolina* (Lamarck), “Sables à *Catopygus obtusus*”, Upper Cenomanian of Mezieres-sous-Ballon, Sarthe. Pers. coll., ×1.2. **Fig. 6** — *Gemmarcula carentonensis* (d'Orbigny), “Horizon A”, upper Cenomanian, Charente Maritime (France). (Collection of Ecole des Mines, location: Faculté des Sciences de Lyon), E.M. coll. FSL no. 20301, ×1.2. **Fig. 7** — *Kingena elegans* Owen (1970), Holotype, Turonian (*Holaster planus* Zone). B.M. (N.H.) coll. no. B55241, ×1.2. **Fig. 8** — *Dereta pectita* (Sowerby), from Upper Greensand (Cenomanian), near le Havre (France), E.M. coll., FSL no. 20302, ×1.2. **Fig. 9** — *Sellithyris cenomanensis* (Gaspard), from “Jalais” level (Middle Cenomanian), upper part of “Sables et Grès du Mans”, Sarthe (France). E.M. coll. FSL no. 20303, ×1.2. **Fig. 10** — *Gemmarcula menardi* (Lamarck), same level and location as Pl. I. 9. E.M. coll., FSL no. 20304, ×1.5. **Fig. 11a–b** — *Cyclothyris compressa* (Lamarck), characteristic of “Sables du Perche”, Sarthe, France. (a) dorsal view, (b) anterior view. E.M. coll., FSL no. 20305, ×1. **Fig. 12** — *Orbirhynchia mantelliana* (Sowerby), Lower Chalk, Middle Cenomanian (A. rhotomagense Zone, *T. costatus* assemblage, Eastbourne (Sussex), England). Kennedy coll., B.M. (N.H.), no. BF 50, ×1.2. **Fig. 13** — *O. mantelliana* (Sowerby), A. rhotomagense Zone, 2nd. *O. mantelliana* band, Boulonnais (between Escalles and Grand Blanc Nez). Pers. coll., ×1.4. **Fig. 14** — *Modestella geinitzi* (Schloenbach), above the 2nd *O. mantelliana* band (mid. Cenomanian), Blanc Nez Cliffs (Boulonnais). Pers. coll., ×1.5. **Fig. 15a–b** — *Cyclothyris difformis* (Lamarck), Lower Cenomanian, Normandy, (a) dorsal view, (b) anterior view. Mus. Havre coll., no.1250, ×1.2. **Fig. 16** — *Grasirhynchia martini* (Mantell), same level and location as Pl. I. 14. Pers. coll., ×1.75. **Fig. 17** — *Cyclothyris lamarckiana* (d'Orbigny), le Mans (Sarthe), “Marnes à *O. biauriculata*”. (a) dorsal view, (b) anterior view. E.M. coll., FSL no. 20307, ×1. **Fig. 18** — *Concinnithyris obesa* (Sowerby), from “La Craie de Rouen”, Côte Ste Catherine, Normandy. E.M. coll., FSL no. 20306, ×1. **Fig. 19** — *Concinnithyris subundata* (Sowerby), Lower Chalk, Middle Cenomanian (A. rhotomagense Zone, *O. mantelliana* band, Abbotscliff, Folkestone (Kent, England)). Kennedy coll. B.M. (N.H.), no. BB 85781, ×1. **Fig. 20a–b** — *Gibbithyris semiglobosa* (Sowerby), Turonian, Villevallier (Yonne, France: (a) dorsal view, ×1.2, (b) anterior view of another specimen, Pers. coll. ×1.



Subfamily Gibbithyridinae Muir-Wood 1965  
Genus *Gibbithyris* Sahní 1925

Two species are of interest for the periods concerned: *G. semiglobosa* (Sowerby) and *G. subrotunda* (Sowerby).

*Gibbithyris semiglobosa* (Sowerby 1813)  
Pl. I: Fig. 20a–b

**Remarks:** The species is quoted in Turonian by Sahní (1929), in British Chalks, in “La Craie de Meudon” (Paris Basin) by d’Orbigny (no. 7676 in his catalogue) and in the White Chalk from Fécamp (France). Specimens have been collected in the Turonian of Villevallier (Yonne, France) with a round shape biconvex, curved beak, minute circular foramen and a very gentle biplicate anterior commissure (Pl. I: Fig. 20b). Microstructure analysis of the shell reveal a prismatic tertiary layer.

*Gibbithyris subrotunda* (Sowerby 1813) seems to have the same vertical distribution as *G. semiglobosa*, and is better known from the Turonian. The species is characterized by a more appressed beak against the dorsal umbo and a greater breadth which involves a pronounced break with lateral commissures on contrary of *G. semiglobosa*.

Subfamily Capillithyridinae Cooper 1983  
Genus *Capillithyris* Katz 1974

**Remarks:** Erroneously identified as *Platythyris* (Popiel-Barczyk 1972; Middlemiss 1978; Bilinkevich & Popiel-Barczyk 1979). The genus is represented by several species, essentially from the Cenomanian: *C. capillata*, *C. squamosa*, *C. disparilis*. Representatives of the genus are quoted also from the North Sea.

*Capillithyris capillata* (d’Archiac 1846)  
Pl. II: Fig. 8

**Remarks:** Found in the Tourtia of Tournai (Belgium), basal Cenomanian, the species has a round shell, a large foramen and a slightly convex brachial valve. Strong growth lines are characteristic of the genus, and fine radiating lines give a regular wavy ornamentation at mid-length.

*Capillithyris squamosa* (Mantell 1822)  
Pl. II: Fig. 17

**Remarks:** Shells of medium size have been sampled in le Boulonnais in bed 17 (Middle Cenomanian) with particular growth-lines which give to this shell a regular step-like aspect. Fine radiating lines, better observed near the commissures, complete the ornamentation (Pl. II: Fig. 17).

*Capillithyris disparilis* (d’Orbigny 1847)  
Pl. II: Fig. 7

**Remarks:** This species sampled from Rouen presents an oval shell, elongated, gibbous in the half-posterior part, with

strong growth lines and a light ornamentation in zigzag towards the margins. The material was observed in d’Orbigny coll., no. 6503; de Vibraye coll., no. B 16056 and Péron coll., no. S 07523 (M.N.H.N., Paris).

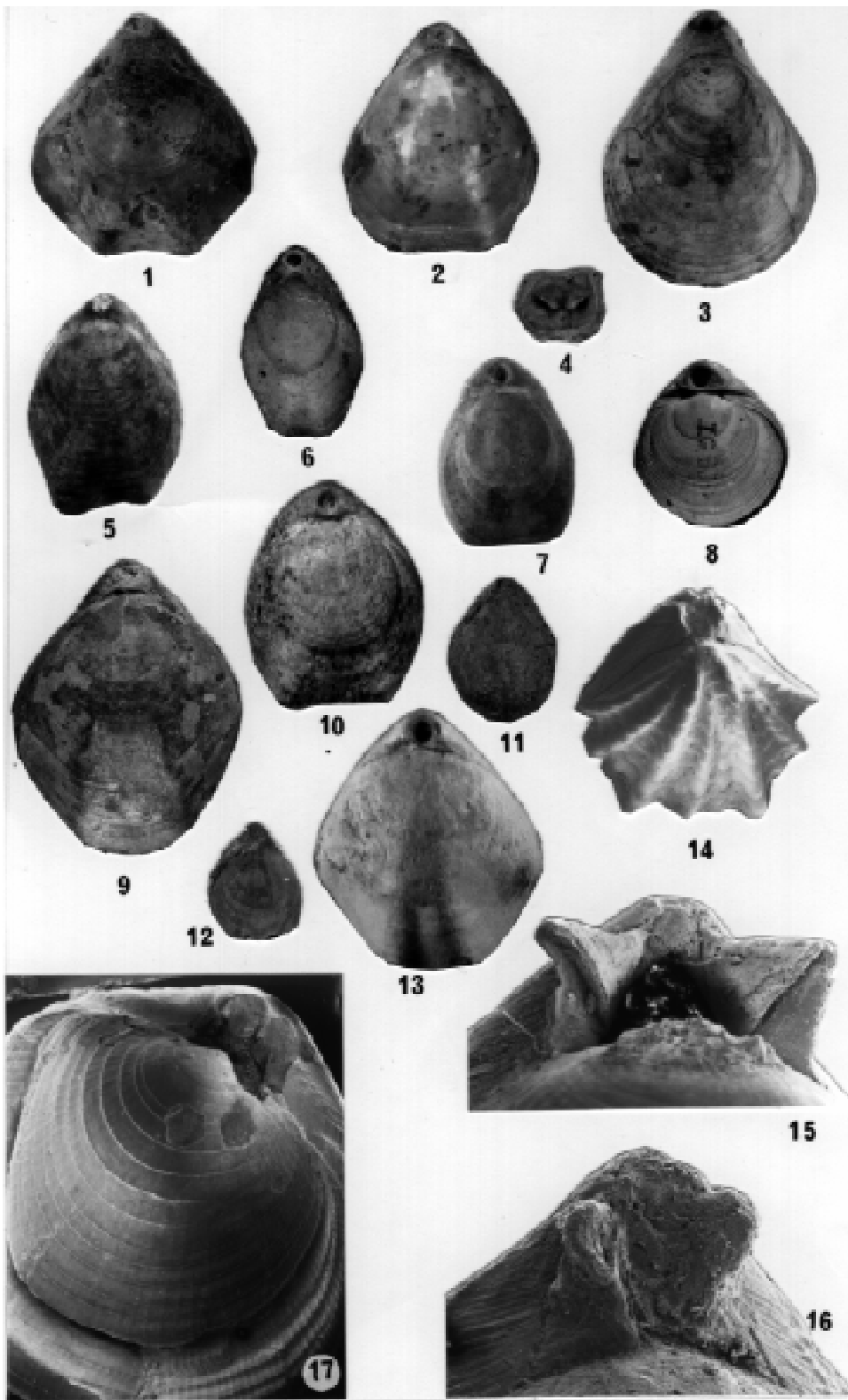
Superfamily Cancellothyridoidea  
Family Cancellothyrididae Thomson 1926  
Subfamily Cancellothyridinae Thompson 1926  
Genus *Terebratulina* d’Orbigny 1847

*Terebratulina martiniana* d’Orbigny 1847  
Pl. II: Fig. 12

**Remarks:** The species, observed in d’Orbigny coll., no. catalogue 6018 (M.N.H.N., Paris, general coll., no. B 14746) is defined as a little triangular shell, with a brachial valve less convex than the pedicle one, ornamented by fine costellae radiating from mid-length. The species is found in the Albian of Martigues (Gueule-d’Enfer, Bouches du Rhône, S. France) with *Gryphea* (Pl. II: Fig. 12) and near Villars de Lans (Isère, France). Dieni & Massari (1965) recorded the species with *Acanthoplites nolani* (Upper Aptian) from Orosei (Sardinia), while Dieni et al. (1973) recorded it from mid-Aptian to Upper Albian from France, England, Germany

**Plate II: Fig. 1** — *Sellithyris tornacensis* (d’Archiac), Tourtia de Tournai, Montignies-sur-roc (Belgium). E.M. coll., FSL no. 20308,  $\times 1$ . **Fig. 2** — *Moutonithyris dutempleana* (d’Orbigny), Barrington pit Cambridge, (Upper Greensand). Pers. coll.  $\times 1$ . **Fig. 3** — *Rectithyris depressa* (Lamarck), Tourtia of Tournai, Montignies-sur-roc, Belgium. E.M., coll., FSL no. 20309,  $\times 1$ . **Fig. 4** — *Crania cenomanensis* d’Orbigny, “Jalais” level, le Mans (Sarthe). de Vibraye coll. M.N.H. N., Paris, no. B.16440,  $\times 1.5$ . **Fig. 5** — *Praelongithyris fecampi* Gaspard, *H. carcitensis* and *M. saxbii* Zones, Val aux Clercs near Fécamp (type-locality, France). Mus. Rouen coll., no. 60473a,  $\times 1$ . **Fig. 6** — *Praelongithyris rogeri* Gaspard, *Leymeriella tardefurcata* Zone (Lower Albian, Grandpré, Ardennes, (France). E.M. coll., FSL no. 291 014,  $\times 1$ . **Fig. 7** — *Capillithyris disparilis* (d’Orbigny), Rouen (France). E.M. coll., FSL no. 20310,  $\times 1.3$ . **Fig. 8** — *Capillithyris capillata* (d’Archiac), Tourtia of Tournai, Montignies-sur-roc (Belgium), I.R.S.N. coll. (Institut Royal des Sciences Naturelles de Belgique),  $\times 1$ . **Fig. 9** — *Moutonithyris moutoniana* (d’Orbigny), Neocomian Chartreuse,  $\times 1$ . **Fig. 10** — *Praelongithyris fecampi* Gaspard, Upper Greensand, Warminster,  $\times 1.5$ . **Fig. 11** — *Terebratulina protostratula* Owen, Lower Cenomanian (glauconitic marl), from St. Catherine’s cliff above Rocken End (Isle of Wight). Evans’ Coll.,  $\times 1.5$ . **Fig. 12** — *Terebratulina martiniana* d’Orbigny, Albian, Martigues (Bouches du Rhône, France). d’Orbigny coll., M.N.H.N., Paris, no. catalogue 6018 (B. 14746).  $\times 1.5$ . **Fig. 13** — *Sellithyris sella* (Sowerby), Lower Aptian of I. of Wight. Pers. coll.,  $\times 1.5$ . **Fig. 14** — *Argyrotheca pectunculus* Quenstedt from the Upper Greensand near Neufchatel (Boulonnais). E.M. coll., FSL no. 20311,  $\times 8$ . **Fig. 15** — *Cyclothyris difformis* (Lamarck), posterior part of a juvenile shell from the Tourtia of Tournai (Belgium) showing the extensions of the deltidial plates around the foramen,  $\times 18$ . **Fig. 16** — *Grasirhynchia martini* (Mantell), posterior part of a shell from bed 17 in “Formation du Cran” (Boulonnais), showing the extension of the deltidial plates or auriculariations,  $\times 30$ . **Fig. 17** — *Capillithyris squamosa* (Mantell), upper part of bed 17 “Formation du Cran” (Boulonnais), exhibiting regular growth lines and a fine radiation more visible near the commissures,  $\times 5$ .





and Sardinia. Middlemiss (1991) recorded the species off Helgoland (North Sea).

*Terebratulina protostriatula* Owen 1988  
Pl. II: Fig. 11

**Remarks:** This species has been created to differentiate the Cenomanian forms from *T. striatula* (Mantell 1852), Upper Chalk. The species occurs in the Lower Cenomanian of England, Boulonnais and Normandy (France). Material of the British Geological Survey (BGS) has been observed, is composed of elongate shells ornamented with fine costae.

In addition to *T. martiniana* and *T. protostriatula*, two species of *Terebratulina*: *T. triangularis* Etheridge (1881), (Upper Greensand, Cambridge) and *T. nodulosa* Etheridge (1881), (Upper Albian to Lower Cenomanian and (?) Middle Cenomanian appear to be present in the material from Normandy (B. Ferré, Ph. D., University of Paris 6, Jussieu 1995).

*Terebratulina lata* Etheridge 1881  
Pl. I: Fig. 1

This species (ex variety of *T. gracilis*) has been created to prevent any confusion with the species *Terebratulina gracilis* Schlotheim previously described from the Senonian. *T. lata* is characterized by a somewhat plano-convex shell, round in outline, approximately 6 mm in length, with well observed deltidial plates and strong radiating nodulous costae dividing several times. This species, a stratigraphic marker in British Chalks (Middle Turonian), is considered in parallel with *Colignoniceras woolgari* (Wright & Wright) in international Ammonite Zones (Rawson et al. 1978). *T. lata* is observed particularly in North and Eastern part of France (d'Orbigny coll., no. 6914) and in England (Middle Chalk of Babraham road near Cambridge, at White Cliff near Seaton (Devon), Swanage Bay (Dorset), Buckinghamshire). The type-material is kept in the British Geological Survey, Nottingham, under the following registered numbers: no. BSG GSM 38693 (Holotype, Pl. I: Fig. 1), BSG GSM 29422–29433, BSG GSM 119253–119257.

Superfamily Zeillerioidea  
Family Zeilleriidae Allan 1940  
Subfamily Cheirothyridinae Baker  
Genus *Modestella* Owen in Casey 1961

*Modestella geinitzi* (Schloenbach 1866)  
Pl. I: Fig. 14

**Remarks:** After the revision by Owen (1988), I have sampled, in 1995, some new specimens of the species in Blanc Nez cliffs (Boulonnais). The shell is small, gibbous (L: 11–8.3; l: 10.5–7.4; e: 7.3–4.6 mm) approximately round pentagonal, with a large circular foramen. Some pronounced growth lines are situated in the third-anterior part of the shell. By its abundance the species is considered as one of the biomarkers in the Lower and Middle Cenomanian chalks across the Straits of Dover (Amédéo 1993, 1994) and localised in “For-

mation du Cran”: units 17 and 18, where it occurs with *Kingena concinna* (Owen), *Grasirhynchia martini* (Mantell) and, some *Orbirhynchia mantelliana* (Sowerby) at the top of unit 18.

Apart from North of France and England, the species is quoted from the Greensand of Essen, North Germany and the Cenomanian of the environs of Annopol (Poland).

Superfamily Megathyridoidea MacKinnon & Smirnova 1995  
Family Megathyrididae Dall 1870  
Genus *Argyrotheca* Dall 1900

**Remarks:** In addition to “*Argyrotheca*” *megatrema* (Sowerby 1836) described by Owen (1988) from Cambridge and from Warminster, another species, probably of Megathyridoidea, was observed in the E.M. coll., from the Upper Greensand of Boulonnais near Neufchâtel. This species considered as “*T*” *pectunculus* Quenstedt 1885 is very few ornamented (5–6 costae with few intercalations, Pl. II: Fig. 14), with less costae than in *A. megatrema*. No papillae are observed, but a lamellar aspect enhances the ornamentation. The few specimens in collections prevent us to practice transverse serial sections on the material, so no observations have been realized on the brachidium.

Superfamily Terebratelloidea  
Family Dallinidae Beecher 1893  
Subfamily Gemmarculinae Elliott 1947  
Genus *Gemmarcula* Elliott 1947

*Gemmarcula aurea* Elliott 1947

The type-species illustrated by Owen (1977, p. 211, pl. 1) is an endemic species from the Aptian (Lower Greensand) of Britain, confined to the Sponge Gravel of Faringdon. The species has some resemblance to *G. crassicosta* (Leymerie).

*Gemmarcula crassicosta* (Leymerie 1869)

**Remarks:** The plano-convex shell of this species from Vimport (France) is recognized in the type-level: Lower Clansayesian (Simplorbitolina manasi Zone) by Peybernes & Calzada (1975).

*Gemmarcula menardi* (Lamarck 1819)  
Pl. I: Fig. 10

**Remarks:** The type-series is in the Lamarck collection (M. H. N., Geneva) and is figured in the catalogue of Favre (1918, pl. 16, Fig. 93 (A-D)-99), collected from Coulaines near le Mans (Middle Cenomanian). Owen (1977, p. 215) selected the lectotype as specimen A.

In d'Orbigny collection (M.N.H.N., Paris, no. 6505), and in Deshayes coll. (E.M.), the species is well represented and following the aspect of the matrix probably comes from the “Jalais” level in the Sarthe region, France (Middle Cenomanian), (Pl. I: Fig. 10).

In his thesis, Juignet (1974) referred to the presence of *G. menardi* in “Sables et Grès de la Trugalle et Lamnay”

(Sarthe); at Savigné-l'Évêque with *Trigonia sulcataria* Lamarck under the hard-ground Longeville 2, with *O. columba* var *minor* Deshayes (upper part of hard-ground Longeville 1), at Parancé in Loyer quarry, at Lamnay in Louvre quarry, at Théligny in la Rouaudière quarry in "Sables et Grès de la Butte du Mans"; in the Lower part of "Sables du Perche" (Sarthe) in cavities of the "Jalais" level, *A. jukesbrowni* Zone. In any case, this species characterizes the upper part of the Middle Cenomanian.

In addition to the topotypes, *G. menardi* is found in the Middle Cenomanian of Valencay (Indre, Alcaydé 1966), in sandy glauconitic facies, at Langé in the same beds as *Sellithyris cenomanensis* Gaspard as in Sarthe, also with *Cyclothyris*, *Trigonia sulcataria* Lamarck, *T. crenulata* Lamarck, *Neithea quinquecostata* d'Orbigny, and *Catopygus columbarius* d'Archiac. Cephalopods collected in these beds are *Turrilites costatus* Lamarck, *Euomphaloceras sussexiense* Sharpe, *Acompsoceras rothomagense* Brongniart, all from the Middle Cenomanian, and showing similarities with the Sarthe region. Unfortunately, the species is not found in other localities elsewhere in France where *S. cenomanensis* Gaspard is present.

According to Kennedy (1969), *G. menardi* is found in England, in the Kent (coast): band 6 in the *A. rothomagense* Zone with *Concinnithyris albensis* (Leymerie). The species was also collected in the region of Burham (Kent) in the *Orbiryndia mantelliana* band (cf. tabl. IV.) as well as near Holborough Cement Works. The sections in Isle of Wight (Culver Cliff and Compton Bay) contain the species.

Specimens of *G. menardi* have been recorded from the North of Germany. Figs. 6a-c, pl. 1 of Popiel-Barczyk (1972) correspond to the species (Poland, Cracow region), but in other respects the citation of the species in Panow (1969) seems to be a misidentification.

*Gemmarcula carentonensis* (d'Orbigny 1847)

Pl. I: Fig. 6

**Remarks:** This species is characterized by a large shell, somewhat broader than long, an antiplicate anterior commissure, a median sulcus in the pedicle valve originating from the umbo and two faint folds, as well a suberect umbo with distinct beak ridges, a small circular submesothyrid foramen, and a distinct area. The ornamentation consists of numerous radiating costae (40) with bifurcations, some more marginal than others.

D'Orbigny assigned the species to the *Ammonites mantelli* (?) Zone at Port des Barques (Charentes, France) (d'Orbigny coll., M.N.H.N., no. 6506) and Eoux (Basses Alpes, France). Publications of Kennedy & Juignet (1973) and Juignet et al. (1973) define exactly the situation, localising "La Craie à *Terebratella carentonensis*": as Horizon A in parallel with the nodulous Chalk with *Sciponoceras gracile* Shumard, *Kanabicerus septemseriatum* (Cragin) and *Inoceramus* gr. *pictus* in Upper Normandy, as inferior part of Melbourn Rock with *S. gracile* in SE England and Faune remaniée with "Neocardioceras Pebble Bed" at the basal part of Middle Chalk in the Devon coast.

Subfamily Uncertain

Genus *Arenaciarcula* Elliott 1959

**Remarks:** Apart from *A. fittoni* (Meyer 1864) typical of the Upper Aptian of S England, another species is recorded from the Cenomanian of Europe it is: *Arenaciarcula beaumonti* (d'Archiac 1846).

Recognized in the Tourtia of Tournai, Belgium, by d'Archiac, the species has been revised by Popiel-Barczyk (1972) from Anopol (Poland), but was distinguished from *Oblongarcula* by Owen (1977). Geographically widespread, the species is recognized also in the Essen Greensand of North Germany, France (Middle Cenomanian of Indre for example), Denmark, and in the Cenomanian limestone of Devon and Russia.

Family Terebratellidae King 1850

Subfamily Trigonoseminae Elliott 1965

Genus *Dereta* Elliott 1959

*Dereta pectita* (Sowerby 1816)

Pl. I: Fig. 8

The shell of medium size is smaller than either *Gemmarcula carentonensis* or *G. menardi*, with which it might have been confused, and slightly biconvex. The beak is suberect with a circular foramen, larger than in *G. carentonensis*, but less than in *G. menardi*, and a straight hinge-line is observed. Numerous costae (around 40), thinner than in *G. menardi* and *G. carentonensis*, with bifurcation at mid-length of the shell, constitute the ornamentation. The sulcation and folds of the anterior commissure are light. The holotype comes from the Upper Greensand of Horningsham (Wiltshire). Apart from the type locality, the species is found near Warminster, quoted also from the *Mantelliceras mantelli* Zone (?) (Kennedy 1969) at Compton Bay (Isle of Wight) in glauconitic marl Dorset.

The specimens observed in the Kennedy collection (Br. Mus.), in d'Orbigny coll. (no. 6507) and in Deshayes coll. (E.M., Lyon) are smaller than the type, and come from le Havre and other localities in the glauconitic marl on Normandy coast (France).

Subfamily Uncertain

Genus *Terebrirostra* d'Orbigny 1847

*Terebrirostra arduennensis* d'Orbigny 1847

**Remarks:** The long pedicle umbo gives the shell an accentuated elongate aspect characterized by the aptitude of specimens of the genus to colonize soft substrates. The shell is covered by dichotomous costae. The species was described from the Lower Albian of Grandpré (Ardennes, France) by d'Orbigny (1847, pl. 519, Figs. 6-10) and by Barbulescu et al. (1975) from the Lower Aptian of Baciliu Rasova (Romania).

*Terebrirostra lyra* (Sowerby 1816)

**Remarks:** In common with the previous species, the shell is elongate, but the pedicle tube is comparatively longer in ju-

veniles. The species is characteristic of the Chloritic Chalk (Lower Cenomanian) of Cap de la Hève near le Havre (d'Orbigny coll., no. 6511 and E.M. coll.; Gaspard 1997) and is also found near Horningsham (England).

Family Kingenidae Elliott 1948, nom. transl.  
Subfamily Kingeninae Elliott 1948, emended Owen 1970  
Genus *Kingena* Davidson 1952

From this subfamily, 4 species are typical for the period: *K. spinulosa*, *K. arenosa*, *K. concinna* and *K. elegans*.

*Kingena spinulosa* (Davidson & Morris 1847)

**Remarks:** This species has been revised by Owen (1970, pl. 2). The topotypes come from the Upper Albian (Gault) of Norfolk and Cambridge. Two specimens were recorded from the Upper Albian of Orosei (Sardinia) by Dieni et al. (1973). Popiel-Barczyk (1972) recorded specimens from the Middle Cenomanian near Cracow and also the Lower Cenomanian (?) near Annopol on the Vistula. The author figured only one specimen with somewhat crushed hinge-line and anterior region, but this specimen can be compared to pl. 2, Fig. 6a and pl. 3, Fig. 8 of Owen (1970) with two sizes of pustules; although crushing prevent to appreciate the proportions of the shell.

*Kingena arenosa* (d'Archiac 1846)

**Remarks:** This species has been revised by Owen in 1970. The shell is biconvex, broad, pentagonal, the widest known among species of the genus with a homogeneous fine pustulation of uniform size, unlike *K. spinulosa*. The shell exhibits a great variability, it is generally broader in the posterior third, with a foramen marked by strong beak ridges. The species has been recorded from the Tourtia of Tournai (Tournai, Montignies-sur-roc, Guissignies (I.R.S.N. coll., no. IG 5694/1,2), Cherq, Belgium) known to be of Lower Cenomanian age. It also occurs with *Cyclothyris* sp., *Ovatathyris ovata* (Sowerby), *Dereta pectita* (Sowerby) and (?) *O. mantelliana* (Sowerby) in Wiltshire (Owen 1970, p. 56).

The species is noted in sandy facies of the Middle Cenomanian in Devonshire and along the Dorset coast as well as in Middle Cenomanian at Culver Cliff and Compton Bay (Isle of Wight). It is localized in the Lower Cenomanian and Middle Cenomanian limestones of Normandy; in the "Essen Tourtia" Lower Cenomanian of North Germany; in the environs of Nagorzanka on the Strypa River (Podolian fauna, Popiel-Barczyk 1972) and possibly Lower Cenomanian (?) near Annopol on the Vistula.

*Kingena concinna* Owen 1970

**Remarks:** The shell is broad to oval with a curved umbo, an anterior commissure generally rectimarginate, and a hinge line shorter than in *K. arenosa*. The species was collected from the Middle Cenomanian (A. rhotomagense Zone), in

the type locality between Folkestone and Dover (Kent). The paratypes come from Cambridge, Dover, Wiltshire, Lincolnshire, Yorkshire. The species is also found in the Boulonnais (France) in bed 17 of Blanc Nez cliffs with the network of punctae well exposed.

*Kingena elegans* Owen 1970  
Pl. I: Fig. 7

**Remarks:** Species characterized by a pentagonal-elongate shell, with a hinge-line broader than in *K. concinna*, as well as a larger foramen. The shell is marked by regular spaced growth lines, and a light sulcation affects the brachial valve. This species characterizes the Turonian (Holaster planus Zone) (Pl. I: Fig. 7), some specimens coming from the T. lata Zone (Norfolk).

Numerous specimens, collected by J. Phillip (Univ. Marseille), between la Bedoule and Cassis (Bouches du Rhône, France), on the slope (between platform and basin) have considerable affinities with the species, while being smaller than those from England.

#### Superfamily Thecidoidea

**Remarks:** Although the superfamily will not be discussed here, we can refer to the monograph of Pajaud (1970) demonstrating (p. 270, Fig. 117), the presence of *Thecidiopsis* Munier-Chalmas (1887), *Backhausina* Pajaud (1966), *Praelacazella* Smirnova (1969) and *Vermiculoidea* Elliott (1953) from the Albian to the Cenomanian.

### Conclusion-Discussion

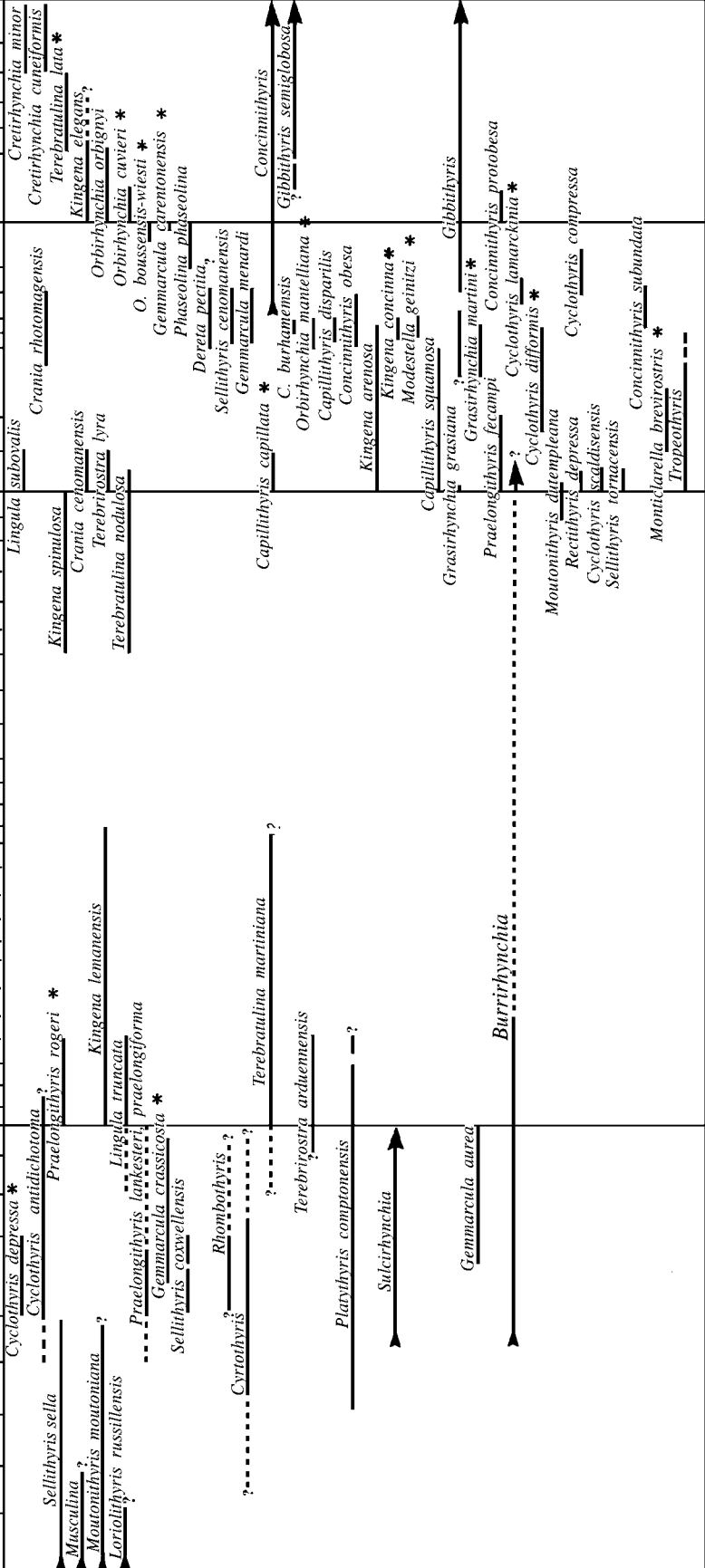
The stratigraphic distribution of the brachiopod species presented above is summarised in Table 1. While geographic distribution and ecological provinces emphasize the fact that some species are endemic and preferentially confined to special environments or facies (such as *Sellithyris tornacensis* (d'Archiac) Tourtia of Tournai and Montignies-sur-roc (Belgium), Essen Tourtia (Germany); *S. coxwellensis* Middlemiss, Sponge Gravel, (Faringdon, England)), others are cosmopolitan or ubiquitous.

#### (a) Facies and factors of variation

All brachiopod specialists have observed that some species always tend to be associated with particular sedimentary or biological facies. This is the case for *Cyclothyris*, as discussed by Ager (1965). Also *Cyclothyris* species with pronounced costae, are found in coarse sediments, or in conglomerates (*C. scaldisensis* (d'Archiac)). Other brachiopods associated with coarse sediments appear to be the costellate terebratellids such as *Gemmarcula menardi* (Lamarck) and *Arenaciarcula*, whereas the rhynchonellid *Grasirhynchia* is found in finer arenaceous sediments. Fine costellate terebratel-

**Table 1.** Occurrence of brachiopod species in NorthWestern Europe between the Aptian and the Turonian (this distribution does not reflect the totality of the faunas living during these periods). Ammonite biochronozones after J. Thierry et al. (1997). (\* = brachiopod markers).

TUONIAN		CENOMANIAN		ALBIAN				APTIAN		
93.5+0.2	U	NEPTUNI								
	M	WOOLGARI	DEVERIANUM							
			ORNATISSIMUM							
KALLESI										
L	NODOSOIDES	COLORADOENSE/DEVONENSE								
		COLORADOENSE								
98.9+0.6	U	JUDII GUERANGEI								
	M	GESLINIANUM								
		JUKEBROWNEI								
		RHOTOMAGENSE	ACUTUS COSTATUS							
	L	DIXONI								
		MANTELLI/CANTIANUM	SAXBII							
			CARCITANENSE							
	112.2+1.1	U	DISPAR	PERIINFLATUM						
				ROSTRATUM						
			INFLATUM	AURITUS						
VARISCUM										
ORBIGNYI										
CRISTATUM										
M		LAUTUS	DAVESI							
		LORICATUS	NITIDUS							
			MEANDRINUS							
SUBDELARUEI										
L		MAMMILATUM	CHALENSIS AURIFORMIS	EODENTATUS						
				BULLIENSIS						
	PUZOSIANUS									
TARDEFURCATA	RAULINIANUS									
	FLORIDUM									
	KITCHINI									
U	JACOBI	ANGLICUS								
		RUBRICOSUS								
		NOLANI								
L	NUTFIELDENSIS									
L	MARTINOIDES									
L	BOWERBANKI									
L	DESHAYESI									
L	FORBESI									
L	FISSICOSTATUM									



lids such as *Dereta pectita* (Sowerby) and rhynchonellids: *Grasirhynchia* and *Monticlarella* are more frequent in greensand, and chalk marls, while representants of the genus *Terebratulina* are often observed in marls.

*Moutonithyris moutoniana* (d'Orbigny), typical of the early Tethyan realm, occurs preferentially in clay sediments and later achieved its invasion northward (Germany, England (?)). The species is again found in clay and marly lithofacies. *Moutonithyris dutempleana* (d'Orbigny), evidently a descendant of *M. moutoniana* (d'Orbigny) is sometimes in the same context, sometimes in greensand or chalky sediments (Red Chalk). This fact excludes to find representatives of both *Cyclothyris* and *Moutonithyris* in the same facies.

Specific facies can occur in time, and thus *Sellithyris sella* (Sowerby), occurring in marly sediment during the Hauteriviian, is more often found in coarser sediments during the Early Aptian, this fact is in correlation to transgressive movements and migration routes. On the other hand *S. cenomanensis* Gaspard, a highly biplicate species (with variation of the anterior commissure) occurring during the Middle Cenomanian, is found in several lithofacies: in coarse sediments with *Cyclothyris* (Sarthe, Indre), in marly sediments (Charentes) or in chalky-marls (Var). *Phaseolina phaseolina* (Lamarck) from the Upper Cenomanian is found in different sediments in relation to the progression of the marine transgression westward (see discussion in Gaspard 1985, 1988). *Gibbithyris*, contrary to the previous species, occurs mainly in chalky facies.

The distribution presented above shows a great number of species occurring in the Aptian, albeit not considered in all the realms (the Jura fauna will be discussed in another paper), and the Cenomanian. These two periods correspond to large transgressive phases. Particularly in the Cenomanian, the brachiopods are considered to occur in littoral waters (Juignet 1974), probably more suitable for *Cyclothyris* with sharp costae, with particular environments: Tourtia of Tournai, Essen Tourtia for example. Brachiopod fauna living on softer sediments (e.g. marls) include genera like *Moutonithyris* (probably in deeper conditions), some *Sellithyris*, generally smooth-shelled terebratulids and *Terebratulina*.

The distribution of the different species and their migration routes already discussed (Middlemiss 1979; Gaspard 1988 mostly for Terebratulids) were dependent upon, and controlled by paleoenvironment: shallow-water and temperature, high-energy conditions (could be a barrier), argillaceous or muddy context (poor conditions). In this last context few genera survive, e.g. *Moutonithyris*. But morphological adaptations to this environment exist: e.g. *Terebrirostra* species, (Gaspard 1997). Many species disappear at the end of the Aptian and Cenomanian periods. Those which appear in the Upper Aptian seem to be confined mainly to unusual facies or are endemic (for example species from Faringdon Sponge Gravel). Numerous species appeared in the Lower Cenomanian such as new species of *Sellithyris*, *Rectithyris depressa*, *Capillithyris* (*disparilis* and *squamosa*) and species of *Orbirhynchia*, *Kingena*, *Gemmarcula*.

#### (b) Some stratigraphic markers

A preliminary approach in this work, after the presentation of the paleontological evaluation and distribution, indicates

that some species could be proposed as stratigraphic markers located according to the standard Ammonite zonation, or sometimes, the foraminiferal zone. They are denoted by (\*) in Table 1. These are: *Cyclothyris depressa* (P. nutfieldensis Zone), *Gemmarcula crassica* (Simplorbitolina manasi Zone, Upper Aptian), *Praelongithyris rogeri* (L. tardefurcata Zone), *Moutonithyris dutempleana* (Stoliczkaia dispar Zone, M. perinflatum Subzone and basal Hipoturrilites carcitanensis Subzone), *Capillithyris capillata* (H. carcitanensis Subzone), *Praelongithyris fecampi* (H. carcitanensis & Mantelliceras saxbii Subzones), *Monticlarella brevirostris* (upper-half of Mantelliceras cantianum and Lower part of M. dixoni Subzones), *Cyclothyris difformis* (part of M. dixoni Subzone and Middle Cenomanian), *C. lamarckiana* (Marnes à *O. biauriculata*, *Calycoceras naviculare*), *C. compressa* (*C. naviculare*, base of Upper Cenomanian), *Grasirhynchia martini* (upper part of Lower Cenomanian), *Modestella geinitzi* and *Kingena concinna* (lower part of Acanthoceras rhotomagense Zone), *Orbirhynchia mantelliana* from M. dixoni Zone to Turrilites acutus-T. costatus Subzones boundary in A. rhotomagense Zone), *Concinnithyris subundata* (*T. acutus* Subzone and part of A. jukesbrownei Zone), *C. obesa* (Middle Cenomanian), *Gemmarcula menardi* (A. jukesbrownei Zone), *Phaseolina phaseolina* (part of C. guerangei to upper part of Neocardioceras judii Zones), *Orbirhynchia bousensis-wiesti-cuvieri* group (N. judii Zone to basal I. labiatus Zone), *Concinnithyris protobesa* (Lower Turonian), *Terebratulina lata* (Collignon-iceras woolgari Zone=T. lata Zone of the English workers), *Kingena elegans* (H. planus Zone and (?) T. lata Zone). *Cretirhynchia* and *Gibbithyris* would certainly also supply some complementary Turonian markers.

#### (c) Presence of these faunas elsewhere in the world during the Aptian-Turonian periods

Before the discussion concerning a proposal for the recognition of phases in the brachiopod development during the Aptian-Turonian periods in NW Europe, it would be interesting to have a look at the presence, elsewhere, of some genera and species previously listed. The comparison is not easy because the Cretaceous is not well exposed worldwide, and even where it is exposed brachiopod specialists are not always on land to describe the faunas.

Some indications come from North America, Madagascar, China, Caucasus and the Crimea.

Representatives of *Moutonithyris*, a mainly subtethyan genus, are manifest also in North Africa, Madagascar (Collignon 1949, 1950), and the Caucasus, the Crimea and North America, particularly Central Mexico (Chiodi et al. 1988). Consideration of the brachiopod present in Canada and Mexico and North America is generally given by Sandy (1990a,b).

*Sellithyris* and *Praelongithyris* are also present in the Caucasus and the Crimea (Smirnova 1972) and in the Crimean region, Klikushkin (1973) referred to species of *Lingula* from Upper Cenomanian.

*Sellithyris*-*Praelongithyris* assemblages are known also in the limestones and marls of the Lower part of Langshan Formation, Northern Xizang (Sun 1987), but these are composed mainly of new species which need close comparison with European species. For example, Sun proposed a parallel between *Praelongithyris rogeri* Gaspard and *P. xiongmeinsis*

Sun or between *Sellithyris sella* (Sowerby) and *S. pentagonaris* Sun. Also an *Orbirhynchia-Parakingena* assemblage occurs in the limestones exposed near North Baingoin Lake, which are expected to be of Late Albian age by Sun.

Some Capillithyridinae are present in the South of URSS (Lobacheva 1986), most of the genera quoted in the study are also listed in Smirnova (1990). Some species are equivalent to those in Europe: *Moutonithyris moutoniana*, *Loriolithyris russillensis*, *Sellithyris sella*, *Praelongithyris praelongiforma*, *Rhombothyris extensa*, *Cyrtothyris cyrta*, *Rectithyris depressa*. If all these genera are represented, their species content differences and some representatives will need investigative work to be critically sure of its synonymy. Collaboration is needed to improve the genera and species stratigraphical distribution.

**(d) Recognition of phases in the brachiopod development**  
— A proposal

In addition to the appreciation of some markers, the above distribution summarised in Table 1 allows to approach the recognition of several phases in the brachiopod development for the period considered. These phases correlate with transgressions and regressions, their reality in time depends mainly upon the state of published data and is susceptible to be progressively improved with new supplies in stratigraphical distributions.

The proposal can be presented as follows:

“Phase A” could cover the Lower Aptian with many representative genera. The impact of the Northern transgression results in the differentiation of species approximately at the boundary of *Chelonicerias martinoides* and *Parahoplites nutfieldensis* Zones. The main genera recorded are: *Sellithyris*, *Musculina*, *Moutonithyris*, *Loriolithyris*.

“Phase B” beginning approximately with the *P. nutfieldensis* Zone includes representatives of *Cyclothyris*, *Praelongithyris*, *Platythyris*, *Gemmarcula (crassiscosta and aurea)*, *Rhombothyris*, *Sulcirhynchia*, *Burrirhynchia* and *Lingula truncata*.

“Phase C” corresponds to the extinction of species originating from the Aptian transgression. Some differentiations in fauna were apparently due to north-westward migration in the Paris Basin, or contrary to the Tethys.

“Phase D” beginning approximately at the limit of *Leymeriella tardefurcata* and *Douvilleicerias mamillatum* Zones is a quiet period without a great explosion of species during all the Middle Albian and mainly the Lower part of Upper Albian.

“Phase E” beginning approximately at the Albian-Cenomanian boundary presents a rich fauna in relation to the transgressive expansion, the top of which is highlighted by the upper limit of *Orbirhynchia mantelliana*.

“Phase F” during the Cenomanian, a second proliferation in the development of some species is characterized at the *T. costatus-T. acutus* Subzones boundary, by the differentiation of some *Concinnithyris* and *Gibbithyris* species which continue to evolve, by *Grasirhynchia*, *Cyclothyris* and *Modestella* for instance. This phase ends with *Phaseolina*, *Orbirhynchia boussensis-wiesti*, *Gemmarcula carentonensis*.

“Phase G” at the Cenomanian-Turonian boundary (*O. cuvieri*) concerns the expansion of *Concinnithyris*, *Gibbithyris*, *Cretirhynchia* in more chalky facies.

As a proposal these phases are not static and more precise data during material sampled worldwide in the future will be useful.

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