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The debated question of asymmetrical rhynchonellids (Brachiopoda, Rhynchonellida): examples from the Late Cretaceous of Western Europe

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Abstract – Many Cretaceous asymmetrical rhynchonellid brachiopods (Brachiopoda, Rhynchonellida) have long been considered as *Rhynchonella difformis* (Valenciennes *in* Lamarck, 1819). After a revision, Owen (1962) included the Cenomanian specimens from Europe in *Cyclothyris* M'Coy, 1844. Later, Manceñido *et al.* (2002) confirmed this decision and critically mentioned the name of another asymmetrical rhynchonellid genus from Spain, *Owenirhynchia* Calzada *in* Calzada and Pocovi, 1980. Specimens with an asymmetrical anterior margin (non particularly ecophenotypical), from the Late Coniacian and the Santonian of Les Corbières (Aude, France) and Basse-Provence (SE France) are here compared to specimens of the original Cenomanian species *C. difformis*. They are also compared to new material from the Northern Castilian Platform (Coniacian-Santonian, N Spain) and to *Rhynchonella globata* Arnaud, 1877 (Campanian, Les Charentes, Dordogne, SW France) and *Rh. vesicularis* Coquand, 1860 (Campanian, Charente, SW France). These observations document the great morphological diversity among all these species and lead us to erect a new species: *Cyclothyris grimargina* nov. sp. from the type material of Arnaud, and two new genera: *Contortithyris* nov. gen. including *Contortithyris thermae* nov. sp., *Beaussetithyris* nov. gen. including *Beaussetithyris asymmetrica* nov. sp. All of these brachiopods fundamentally present an asymmetrical state which origin is discussed.

Keywords: Brachiopoda / Rhynchonellida / asymmetry / Late Cretaceous / Western Europe / new genera and species

Résumé – La question débattue des rhynchonelles asymétriques (Brachiopoda, Rhynchonellida) : exemples dans le Crétacé supérieur d'Europe occidentale. De nombreuses rhynchonelles asymétriques du Crétacé (Brachiopoda, Rhynchonellida) ont longtemps été considérées comme des *Rhynchonella difformis* (Valenciennes *in* Lamarck, 1819). Après une révision, Owen (1962) a inclus les spécimens du Cénomanien d'Europe dans le genre *Cyclothyris* M'Coy, 1844. Plus tard, Manceñido *et al.* (2002) ont confirmé cette décision et mentionné de façon critique le nom d'un autre genre asymétrique de rhynchonelles provenant d'Espagne, *Owenirhynchia* Calzada *in* Calzada and Pocovi, 1980. Des spécimens avec une commissure antérieure asymétrique (pas particulièrement d'origine écophénotypique), du Coniacien supérieur et du Santonien des Corbières (Aude, France) ainsi que de Basse-Provence (sud-est France), sont comparés ici aux spécimens de l'espèce cénomanienne d'origine, *C. difformis*. Ils sont également comparés aux spécimens de la plateforme nord-castillane (Coniacian-Santonian, Espagne) et aux spécimens de *Rhynchonella globata* Arnaud, 1877 (Campanian, Charentes et Dordogne, sud-ouest de la France) ainsi qu'à ceux de *Rh. vesicularis* Coquand, 1860 (Campanian, Charente, sud-ouest France). Ces observations documentent la grande diversité morphologique de toutes ces espèces et conduisent à la description d'une nouvelle espèce : *Cyclothyris grimargina* nov. sp. provenant du matériel type d'Arnaud et de deux nouveaux genres : *Contortithyris* nov. gen. incluant *Contortithyris thermae* nov. sp. et *Beaussetithyris* incluant *Beaussetithyris asymmetrica* nov. sp. Toutes ces rhynchonelles présentent fondamentalement un état asymétrique dont l'origine est discutée.

Mots clés : Brachiopoda / Rhynchonellida / asymétrie / Crétacé supérieur / Europe de l'Ouest / nouveaux genres et espèces

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1 Introduction

Rhynchonelliform brachiopods (Brachiopoda, Rhynchonellida) generally present a bivalved shell with a bilateral symmetry. Variations or deviations from the plane of symmetry are common in rhynchonelliform brachiopods. Numerous authors (*e.g.*, Ager, 1965; Asgaard, 1968; Schumann, 1976, 1991; Asgaard and Bromley, 1991; Afanasjeva, 2014; Schrøeder *et al.*, 2017; Berrocal-Casero *et al.*, 2017) pointed that some variations are in relation to environmental conditions (crowded population, close attachment to a substrate preventing a normal shell growth). Thus, they correspond to an occasional modification of the normal symmetry in the shell, also named dissymmetry. Other variations are also related to particularly shifted/twisted anterior commissures, *i.e.*, shells with a bilobate anterior margin (right side-up/left side-down or the reverse), which seem rather of genetic origin (Fürsich and Palmer, 1984; Gaspard, 1991). This later case corresponds to the lack of normal symmetry in the shell, also named asymmetry. Among the brachiopods, asymmetry is merely observed in rhynchonellids and affects the whole population. Diverse examples have been observed in Jurassic and Cretaceous species (Asgaard, 1968; Fürsich and Palmer, 1984; Gaspard, 1991 and references herein), but the origins of the state of asymmetry remain an open question.

Several rhynchonellids with a right and left-handed asymmetry of the anterior margin are well represented during the Cretaceous (particularly the Middle–Late Cretaceous) till the Danian (Gaspard, 1991). For a long time, most of them have been identified as *Rhynchonella difformis* (Valenciennes *in* Lamarck, 1819). After a general revision of *Cyclothyris* M'Coy, 1844, some of these rhynchonellids have been assigned to *Cyclothyris difformis* by Owen (1962). This species was documented from numerous localities in the lower-middle Cenomanian of France (Normandy, Sarthe, Indre, Charente and Var), with close comparisons with the specimens of Belgium (Tourtia from Andregnies and Montignies-sur-Roc; Owen, 1962). Other specimens come from western England, particularly from Somerset, Dorset, south Devon (varieties in the sandy lower Cenomanian), southeast Devon (middle Cenomanian), Wiltshire (abundant specimens in the Upper Greensand), Isle of Wight, as well as from Northern Germany (Essen), Bohemian basin (Prague), and from the lower-middle Cenomanian of Bulgaria and from Poland (*e.g.*, Owen, 1962, 1988; Nekvasilova, 1973; Popiel-Barczyk, 1977; Gaspard, 1991; Motchurova-Dekova, 1994, 1995; Néraudeau *et al.*, 2013).

All the Cretaceous asymmetrical rhynchonellids should not be identified as *C. difformis*. Among the most common misinterpretations, specimens of *Cyclothyris compressa* (Valenciennes *in* Lamarck, 1819) are often misidentified by certain authors as *C. difformis,* (see discussion in Gaspard, 2014). Moreover, asymmetrical rhynchonellids from the Late Cretaceous (Coniacian–Campanian) were also identified as *C. difformis*. These examples were already discussed (Fürsich and Palmer, 1984; Gaspard, 1991, 2017; Motchurova-Dekova, 1994, 1995). Although *Rhynchonella globata* Arnaud, 1877 was considered as a possible variant of *Rh. difformis*, most of the ancient authors maintained the name, considering that this species pointed a remarkable event: its first occurrence coincides with the early Campanian. In other respects, the type series of *Rhynchonella globata* appears heterogeneous and needs also a revision.

The aim of the present work is to review and precise the complex situation of the Late Cretaceous (Senonian) asymmetrical rhynchonellids from Les Corbières (Aude, France), Basse-Provence (SE France), Les Charentes and Dordogne (SW France), and Castile (Spain), and to highlight the status of their asymmetry.

2 Material and methods

2.1 Material (Fig. 1)

Specimens of *Cyclothyris difformis* have been sampled in the lower Cenomanian layers (glauconitic chalk) in the cliffs of Bec de Caux (Normandy, France), and in the Cenomanian outcrops of Cadeuil in Charente-Maritime, France (Néraudeau coll., Université de Rennes 1: acronym IGR). Specimens from the northeastern Pyrenees come from the Coniacian–Santonian of Rennes-les-Bains and Sougraigne (Fig. 1.1) and were observed in the collections of the Muséum national d'Histoire naturelle (acronym: MNHN.F), Paris. Those from Basse-Provence (SE France: Le Beausset, La Cadière, Les Martigues; Fig. 1.2) have been sampled or observed in MNHN collections. Comparisons of Campanian specimens of *Rhynchonella globata* have been made with the material from the Aquitaine Motorway A10 in Charente (Gaspard, 1985), from Tercis (Landes, France: Gaspard and Odin, 2001), from Les Charentes and Dordogne (Arnaud coll., specimens of the type series in Sorbonne-Université: acronym SU.PAL.) (Fig. 1.3). For comparisons with the *Rh. globata* type series from the same region, Campanian *Rhynchonella vesicularis* Coquand, 1860 have been observed in Sorbonne-Université (Arnaud coll.) and MNHN collections. Moreover, the original type material has been also traced in the collection of Mining and Geological Survey of Hungary (acronym MBFSZ).

For other comparisons, Coniacian specimens of *Owenirhynchia* have been sampled in the Nidàguila Formation at the Villamartin section from the North Castilian platform (Fig. 1.4).

2.2 Methods

The specimens sampled are imaged and observed following the external morphology: global shape, details of the anterior margin, shape and number of costae, shape and size of the foramen and details of the deltidial plates. Some of them, selected from each studied area, have been included in an epoxy resin, oriented and then cut to observe the internal characters in sets of transverse serial sections that are drawn using a camera lucida with control of the shell thickness worn out between successive sections.

Two specimens were scanned using X-ray microtomography to complete the study. The radio-transparent substrate on which the specimens are positioned is adjusted to correspond to the axis of the X-ray nano-beam (AST-RX platform, UMS 2700, MNHN, Paris). The specimens were scanned according to the following parameters: (1) specimen MNHN.F.A59944 (Cenomanian, Normandy) – voxel size: 5.977 μm^3, tension: 80 kV, intensity: 120 μA, time exposure: 2000 ms, filtre: Cu

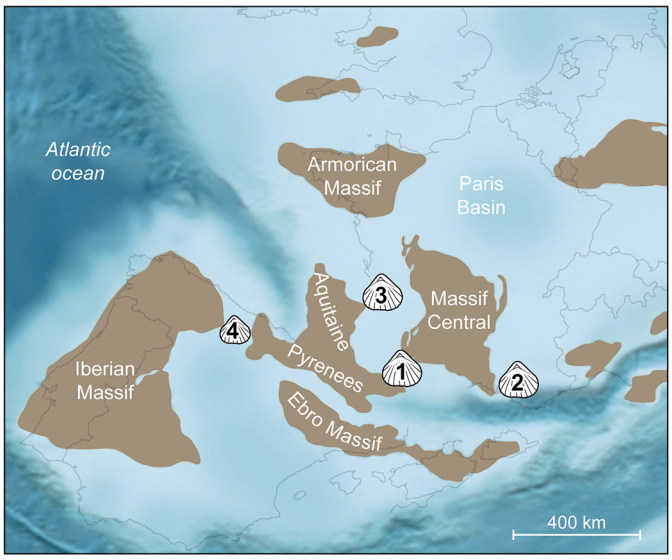

Fig. 1. Location of the Late Senonian asymmetric rhynchonellids observed: (1) Les Corbières (NE Pyrenees); (2) Basse-Provence (SE France); (3) Les Charentes and Dordogne (SW. France); (4) North Castilian Platform. All sites are located on a map extracted from the Paleogeography of Europe Series. Deep Time Maps (2011), Colorado Plateau Geosystems Inc. http://deeptimemaps.com/.

0.1 mm, 1800 images; (2) specimen MNHN.F.A26502 (Santonian, Basse-Provence) – voxel size: 9.517 μm^3, tension: 110 kV, intensity: 50 µA, time exposure: 2000 ms, filtre: Cu 0.1 mm) (for videos and successive virtual transverse sections, see online Appendices A–D).

Several other scanned specimens were too recrystallized to allow a 3D reconstruction, even a clear individualization of internal characters in virtual sections (see Gaspard, 2013).

In order to highlight details at the sites of the articulation (dental sockets, dental plates), hinge plates, crura, and dorsal septum, and to precise the orientation of the fibrous elements forming the low Mg-calcite secondary layer of the shell, some selected transverse sections were observed using a scanning electron microscope (JEOL SEM; MNHN, Sorbonne Université). These sections were observed after polishing, light acid attack (a few seconds with 12.5% rapid decalcifier RDC Laboratoire Moderne©) and gold coating (see online Appendix E).

3 Geological setting

3.1 Northeastern Pyrenees (Les Corbières) (Fig. 1.1)

The asymmetrical rhynchonellids from Les Corbières were first mentioned by d'Orbigny (1847–1851), d'Archiac (1854), Coquand (1860), Toucas (1880), Péron (1877), Fage (1934), Sénesse (1937) and Basse (1939). All these authors reported the presence of *Rhynchonella difformis* from the late Coniacian to the early Santonian.

In the present study, the asymmetrical rhynchonellids are mainly found in the Marnes à *Micraster* Formation at Rennes-les-Bains (Aude) and in the Marnes bleues de Sougraigne Formation at Sougraigne (Aude). The Marnes à *Micraster* Formation is middle Coniacian–middle Santonian in age and the Marnes de Sougraigne Formation is middle–late Santonian in age (Bilotte and Freytet, 1984). More precisely, the asymmetrical rhynchonellids of the Marnes à *Micraster* Formation are mainly found in the early Santonian *Nowakites carezi* ammonite biozone, and in the basal part of the early-middle Santonian *Texanites gallicus* ammonite biozone (Hancock, 1991; Kennedy *et al.*, 1995).

3.2 Basse-Provence (SE France) (Fig. 1.2)

The asymmetrical rhynchonellids from Basse-Provence were first mentioned by d'Orbigny (1847–1851), Toucas (1873, 1885), Vasseur (1894) and later by Babinot (1980), Tronchetti (1981), Babinot *et al.* (1984) and Grosheny (1986). After several discussions about the age of the outcrops, most of these authors reported the presence of *Rhynchonella difformis* in the Santonian of the region.

In the present study, the asymmetrical rhynchonellids have been found in La Cadière Formation at Le Moulin-de-la-Cadière (early Santonian, Grosheny, 1986) and in the Santonian at Le Beausset, Le Castellet and Les Martigues (Babinot *et al.*, 1984).

3.3 Les Charentes and Dordogne (SW France) (Fig. 1.3)

The asymmetrical rhynchonellids from Les Charentes were collected in the Cenomanian of Cadeuil (Charente Maritime). A well-preserved specimen of *Rhynchonella difformis* illustrated by Néraudeau *et al.* (2013: pl. 12d-e), shown here, is compared with the lower–middle Cenomanian specimens from the lectotype area (Normandy).

In other respects, specimens of *Rhynchonella globata* were either observed in collections or collected in the Campanian from Les Charentes and Dordogne. The type series listed by Arnaud (1877) appears heterogeneous and requires an in-depth study. Specimens of *Rhynchonella vesicularis* from the Campanian of Les Charentes (Aubeterre-sur-Dronne) and from Dordogne (Beaufort, Issac, Puyvigier, Sourzac) were also observed, including the type material.

3.4 North-Castilian Platform (Spain) (Fig. 1.4)

Asymmetrical rhynchonellid brachiopods have been found in the Upper Cretaceous of the North-Castilian Platform which geological setting is described in detail by Floquet (1978, 1991), Floquet *et al.* (1982) and Lamolda *et al.* (2002). The studied specimens were collected in the Nidáguila Formation at Villamartin section (Gaspard, 2010) and identified as *Owenirhynchia* Calzada *in* Calzada and Pocovi, 1980 by Lamolda *et al.* (2002), but as *Cyclothyris* aff. *globata* by Berrocal-Casero *et al.* (2017). More precisely, these asymmetrical rhynchonellids are late Coniacian in age (Floquet, 1991). Muñoz (1985, 1994) also recognized representatives of *Owenirhynchia*, later introduced by Manceñido *et al.* (2002) as a possible subgenus or a subjective synonym of *Cyclothyris*.

4 Systematic palaeontology

Brachiopoda Duméril, 1805
Rhynchonellida Kuhn, 1949
Hemithyridoidea Rzhonsnitskaia, 1956
Cyclothyrididae Makridin, 1955

Emended diagnosis after Manceñido *et al.* (2002). – Trilobate, sharply costate Hemithiridoidea, with anterior commissure uniplicate or sometimes asymmetrical; lamellose ornament frequently developed; squamma-glotta obsolescent. Middle Triassic–Late Cretaceous.

Cyclothyridinae Makridin, 1955
Emended diagnosis after Manceñido *et al.* (2002). – Fully costate Cyclothyrididae, rarely with posterior smooth area, beak massive, with large hypothyrid rimmed foramen (*i.e.*, deltidial plates produced into short tube around pedicle). Dorsal median septum usually very much reduced, septalium reduced or absent, crura canaliform (or at least distally concave modified raduliform). Characteristically strongly and densely costate. Middle Triassic–Late Cretaceous.

Cyclothyris M'Coy, 1844

Type species. – *Terebratula latissima* J. de C. Sowerby, 1829, by subsequent designation of Buckmann (1906).
Emended diagnosis after Manceñido *et al.* (2002). – Medium to large, wide, with uniplication low, arcuate, commonly asymmetrical; costellae numerous, fine posteriorly, beak erect, foramen large, auriculate, deltidial plates conjunct, well exposed. Dorsal septum short or absent; hinge plates distally concave; crura long, dorsally concave.

Cyclothyris difformis (Valenciennes in Lamarck, 1819)
Figures 2 and 3

Terebratula difformis Valenciennes *in* Lamarck, 1819: 255.
not *Rhynchonella difformis*. d'Orbigny 1847–1851: 41–43, pl. 498, figs. 6–9.
Cyclothyris difformis. Owen 1962: 51, pl. 1, figs. 1–7. [lectotype selection]. – Owen 1988: 84, pl.1, figs. 13–15, pl. 2, figs. 4–6, 10–15.
Type material – Lectotype selected by Clerc and Fabre (1918). It comes from the lower Cenomanian of Normandy coast (France) and is housed at the Muséum d'Histoire Naturelle, Geneva, in the Lamarck collection (for details see Owen, 1962).
Examined material from the Cenomanian – Five specimens MNHNF.A67478–A67480, A59944, A70585 (Gaspard coll.) from the cliffs of Cap de la Hève, Pays de Caux, Normandy (Figs. 2A–2N and 3; Appendices A–C); one specimen IGR23222 (Néraudeau coll). from the lower Cenomanian, of Cadeuil (Charente-Maritime) (Figs. 2O–2Q); specimens observed *in situ* from the middle Cenomanian of Île Madame (Charente-Maritime).
Description of external morphology (Fig. 2) – The medium-sized to large biconvex shell is wider than long, the ventral beak is sub-erect (slightly incurved) never approaching the dorsal umbo. Sometimes, the beak seems to be more inclined and longer on one side or the other. The foramen is round with a diameter of 1–2 mm bounded by the exposed deltidial plates, not conjunct at the juvenile stage (Figs. 2A and 2D), twice large at the anterior part and whose lateral expansions form a short tube in

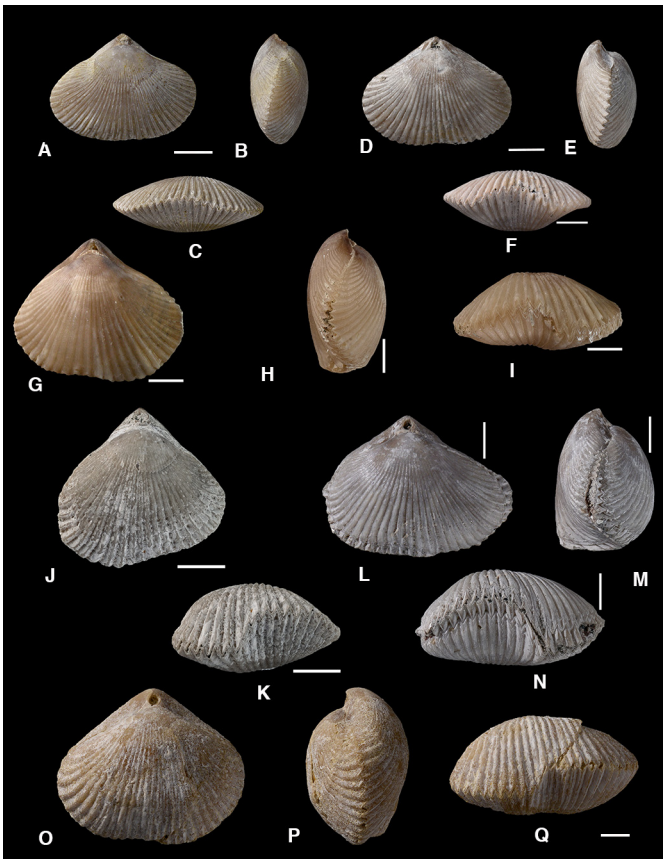

Fig. 2. *Cyclothyris difformis* (Valenciennes *in* Lamarck, 1819). A–N. Five specimens (Gaspard coll.) from the Cenomanian of Normandy (Cap de la Hève, France). A–C. Dorsal (A), lateral (B), and anterior (C) views of a juvenile specimen MNHN.F.A67478 with a faintly rectimarginate anterior margin. D–F. Monoplicate juvenile/preadult specimen MNHN.F.A67479. G–I. Adult specimen MNHN.F.A67480 showing right-asymmetrical anterior commissure. J, K. Small adult specimen MNHN.F.A70585 showing left-asymmetrical anterior commissure. L–N. Scanned specimen MNHN.F.A59944 (for video and virtual transverse and longitudinal sections see online Appendices A–C). O–Q. Specimen IGR23222 (Néraudeau coll.) from the Early Cenomanian of Cadeuil (Charente-Maritime, France). Photographs: P. Loubry. Scale bars = 5 mm.

adults (Figs. 2J, 2L, 2O). The shell is flat in juvenile stages (Figs. 2B and 2E). The lateral commissures are nearly straight with a deflection anteriorly in adults (Figs. 2B, 2E, 2H, 2M). The anterior commissure is rectimarginate in juvenile stages (Fig. 2C) then, progressively monoplicate (Fig. 2F) tending to become asymmetric in a more pronounced way in adults: right side-down/left side-up (Figs. 2I and 2N) or the reverse (Figs. 2K and 2Q). Numerous costae, small and round in juveniles then sharper and higher near the commissures (at least 30–45 in adults) ornament the shell, one to three of them take place along the shift between the side-up and the side-down of the anterior commissure.
Description of internal characters – The transverse serial sections of specimen MNHN.F. MNHN.F.A70934 (Fig. 3), and the virtual transverse and lateral views from the scanned specimen MNHN.F.A59944 (Appendices A–C) reveal: well-defined deltidial plates with the lateral expansions (Figs. 3a–3d),

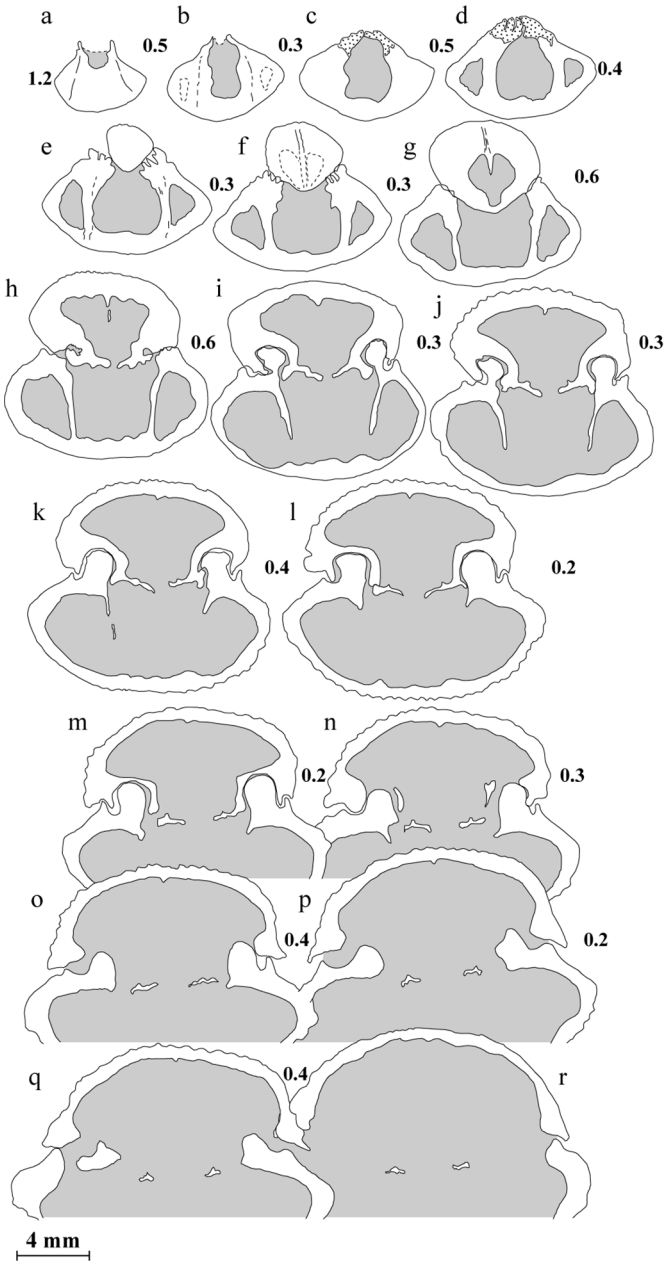

Fig. 3. Transverse serial sections in a shell of *Cyclothyris difformis* (MNHN.F.A70934, Cap de la Hève, Normandy, France) with a length of 25.0 mm. Internal characters from the posterior shell to the level of the crura. Each section is labelled with a letter and the worn thickness between two successive sections is indicated in millimetre (this mention is valid for all sets of transverse serial sections). Line drawings: D. Gaspard.

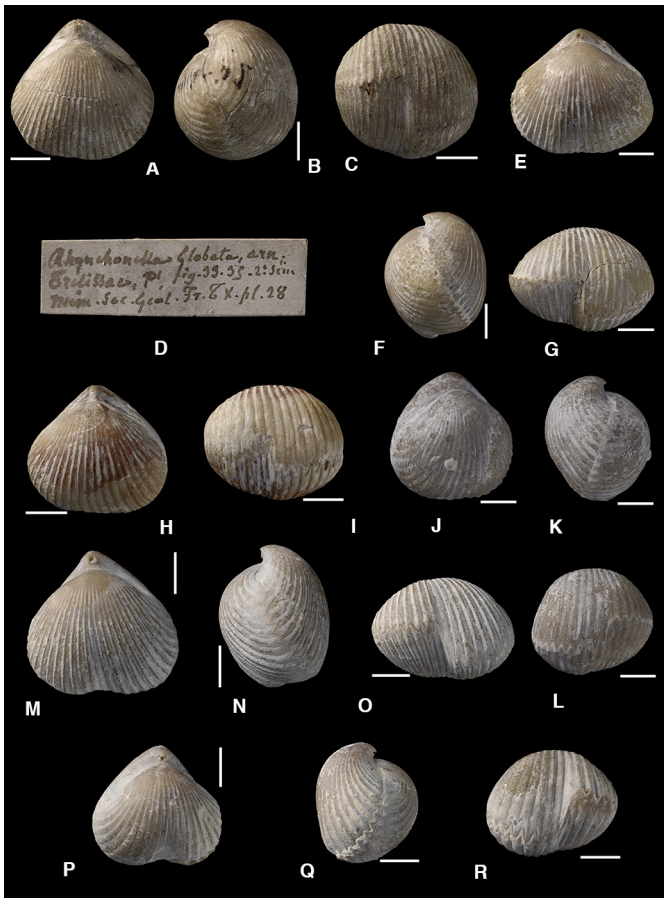

Fig. 4. *Cyclothyris globata* (Arnaud, 1877) from the Campanian of Les Charentes and Dordogne (France). A–C. Dorsal, lateral and ventral views of the lectotype SU.PAL.2018.0.55.29.1 from Trélissac. D. Original label of the lectotype. E–G. Paralectotype SU.PAL.2018.0.55.29.2 from Trélissac. H–I. Paralectotype SU.PAL.2018.0.55.29.3 from Trélissac. J–L. Specimen MNHN.F.A59949 (Gaspard coll.) from Eraville. M–O. Specimen SU.PAL.2018.0.55.138.1 (Arnaud coll.) from Viville, note also the dissymmetry of the shell. P–R. Specimen SU.PAL.2018.0.55.44.1 (Arnaud coll.) from Mainfonds. Photographs: P. Loubry except M–O: L. Cazes. Scale bars = 5 mm.

thick nearly parallel dental plates (Figs. 3d–3j), posterior sharp-pointed expensive dorsal septum (Figs. 3f–3j) then deceasing (Figs. 3k–3q), thick hinge teeth with small and brief lateral accessory teeth inserted in deep dental sockets and accessory counter parts (Figs. 3i–3n), slightly concave hinge plates, and raduliform to canaliform crura (Figs. 3m–3r).

Comments. – Cenomanian specimens referred to *Cyclothyris difformis* as reported by Néraudeau *et al.* (2013) present the same characteristics as those from Normandy. When well preserved, the material from the basal Cenomanian of Cadeuil is comparable in size and global shape with that from Normandy, the differences rest in the more rounded anterior part and a less deflection on one or the other side of the anterior margin (Fig. 2Q). We point out that assymmetrical specimen MNHN.F.A70585 (Figs. 2J and 2K) is also affected by a dissymmetry well visible in the dorsal and frontal views.

Cyclothyris globata (Arnaud, 1877)
Figures 4 and 5; Table 1

Rhynchonella globata Arnaud, 1877: 83, pl. 8, figs. 33–35.
not *Rhynchonella globata*. Arnaud, 1877: 83, pl. 8, figs. 36–38.
not *Rhynchonella difformis* var. *globata*. Fage 1934: 439, pl. 23, fig. Dg[1–5].
Cyclothyris aff. *globata*. Muñoz 1985: 43, pl. 1, fig. 2.

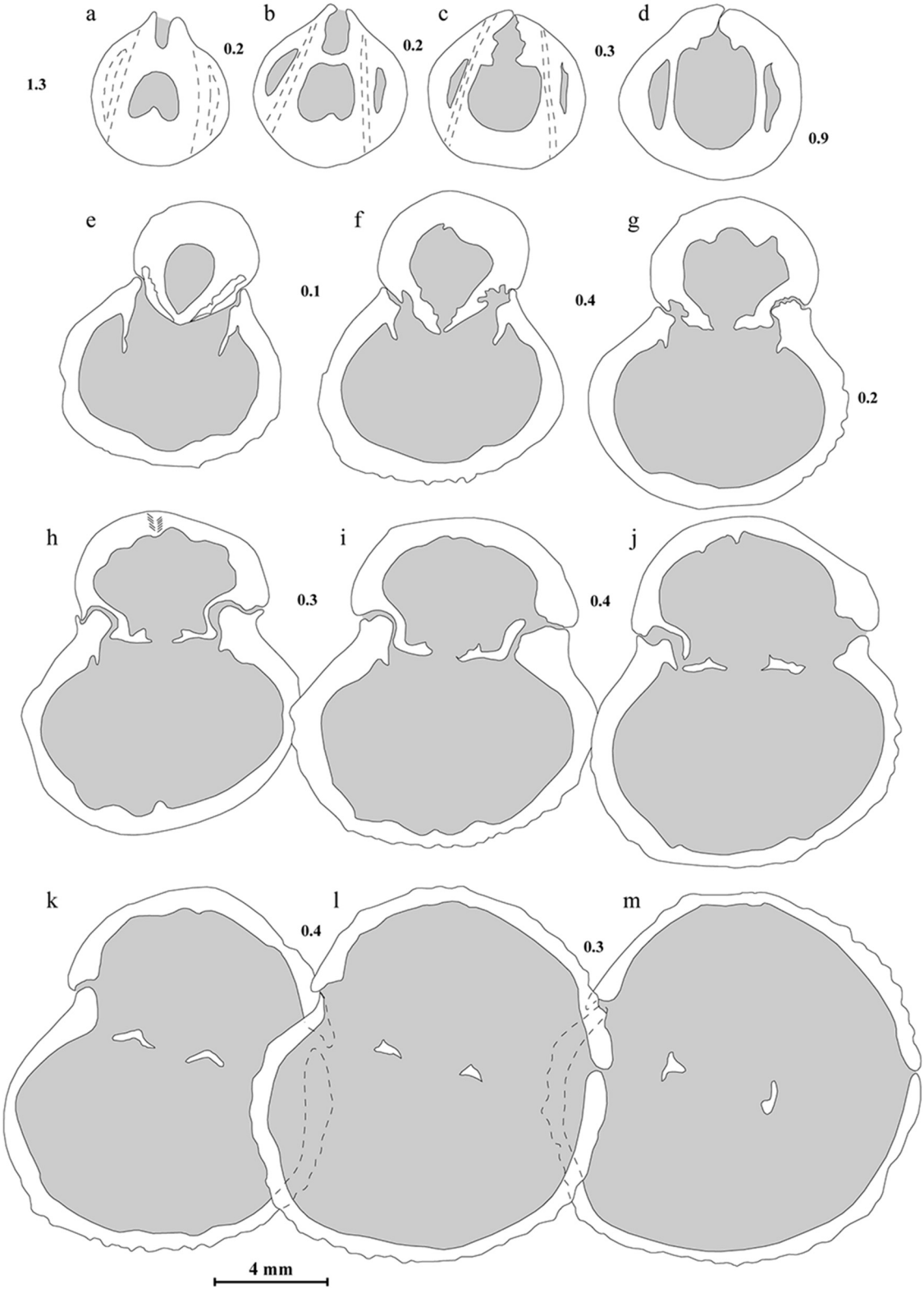

Fig. 5. Transverse serial sections in a shell of *Cyclothyris globata* (Arnaud, 1877) (MNHN.F.A70935) from the Campanian of Cavillac (Dordogne), with following measurements: 18.3 mm in length, 19.3 mm in width, 14.6 mm in thickness. Internal characters from the posterior shell till the level of the crura. Line drawings: D. Gaspard.

Table 1. List of the type material and additional specimens of *Cyclothyris globata* from the Campanian of Les Charentes and Dordogne. Stratigraphical levels P1–P3 of Arnaud (1877) correspond to biozones CI-CV of the Campanian sensu Platel (1977, 1982).

Collections	Statut	Localities	Stratigraphical levels	Numbers of specimens	Shifted commissure			Shifted commissure (%)	
					left down	right down		left down	right down
SU.PAL.2018.0.55.29.1	Lectotype	Trélissac (Dordogne)	P1	1		1	1	na	na
SU.PAL.2018.0.55.29.2-6	Paralectotypes	Trélissac (Dordogne)	P1	5	1	4	5	na	na
SU.PAL.2018.0.55.37.1-5		Belvès (Dordogne)	P1	5	2	3	5	na	na
SU.PAL.2018.0.55.12.10		La Grèze (Dordogne)		1		1	1	na	na
SU.PAL.2018.0.55.9.2-3		Perdigat (Dordogne)		2	2		2	na	na
SU.PAL.2018.0.55.9.6		Limeyrat (Dordogne)	P1	1	1		1	na	na
MNHN.F.A70646		Cavillac (Dordogne)		1	1		1	na	na
SU.PAL.2018.0.55.11.1-27		Dordogne	P2	27	14	13	27	52%	48%
SU.PAL.2018.0.55.10.1-39, SU.PAL.2018.0.55.17.1-54, SU.PAL.2018.0.55.13.1-14		Charente/Dordogne	P1	107	47	60	107	44%	56%
SU.PAL.2018.0.55.16.12-13		Tombe au Clerc	P1	2		2	2	na	na
SU.PAL.2018.0.55.137.1-2		Sarlat (Dordogne)	P1	2	1	1	2	na	na
MNHN.F.A69923 to A69931		Le Bugue (Dordogne)		9	4	5	9	na	na
SU.PAL.2018.0.55.41.1-3		Livernant (Charente)	P1	3	2	1	3	na	na
SU.PAL.2018.0.55.12.9		Livernant (Charente)	P2	1	1		1	na	na
SU.PAL.2018.0.55.39.1-2		Chadurie (Charente)		2	0	2	2	na	na
SU.PAL.2018.0.55.44.1-9		Mainfonds (Charente)		9	7	2	9	na	na
SU.PAL.2018.0.55.9.1		Montmoreau (Charente)	P1	1	1		1	na	na
SU.PAL.2018.0.55.9.4		Viré	P1	1		1	1	na	na
SU.PAL.2018.0.55.9.5		Ségeville (Charente)		1	1		1	na	na
SU.PAL.2018.0.55.14.1-61		Charente	P1	61	29	32	61	48%	52%
SU.PAL.2018.0.55.27.1-6, MNHN.F.A59949, A70913, A70814, A70896		Eraville (Charente)	P1	10	5	5	10	na	na
SUPAL.20180.55.110.1		Angoulême (Charente)		1		1	1	na	na
SU.PAL.2018.0.55.138.1-2		Viville (Charente)	P2	2	1	1	2	na	na
SU.PAL.2018.0.55.15.16		La Roquette (Charente Maritime)	P3	1		1	1	na	na
Total				256	120	136		47%	53%

Rhynchonella globata. Gaspard 1991: pl. 1, fig. 10 (non figs. 7–9).

Owenirhynchia globata. Muñoz 1994: 154, fig. 64.

not *Cyclothyris globata*. Motchurova-Dekova 1995: pl. 4, 5. Gaspard and Odin, 2001: pl. 1.1.

not *Cyclothyris aff. globata*. Berrocal-Casero *et al.*, 2017: 80, fig. 4.

Type material. – The original type material of Arnaud (1877) was composed of a non-assessable number of Campanian specimens from a large set of localities from Les Charentes and Dordogne (SU.PAL.2018.0.55.9.0 to SU.PAL.2018.0.55.44.0; see Tab. 1). Among them, the specimen SU.PAL.2018.0.55.29.1 (figured by Arnaud, 1877: pl. 8, figs. 33–35) is herein selected to be the lectotype (Figs. 4A–4D). Several paralectotypes have been identified and fit the original diagnosis of Arnaud (1877). They are listed in Table 1 and some of them are illustrated in Figures 4E–4R.

Type locality. – Trélissac, Dordogne, France.

Among the paralectotypes, some localities are hand-labelled by Arnaud (1877) and others are unfortunately groups of specimens without precise locality in Charente or Dordogne (see Tab. 1).

Type age. – Campanian (levels P1-P3 of Arnaud 1877 corresponding to benthic foraminiferal biozones CI-CV of Platel, 1977).

Additional examined material from the Campanian – see Table 1.

Description of external morphology (Fig. 4) – Medium sized (length: 11.4–20.6 mm; width: 13.9–23.4 mm; thickness: 10.3–17.7 mm), rounded shells with a curved ventral beak (Figs. 4B, 4F, 4K), ornamented by about 27–30 to 38 costae (number which is not always in correlation with the shell size). The ventral umbo is curved somewhat sharp-pointed and sometimes nearly reaching the dorsal umbo (Fig. 4Q), the limit of the joined deltidial plates bounding the small foramen (diameter around 1 mm in adults, even less in some cases) is visible. Sometimes the lateral expansions of these deltidial plates are best developed, although less than in *C. difformis*. The dorsal area on each side of the deltidial plates is smooth except a few fine growth-lines. The lateral commissure is more

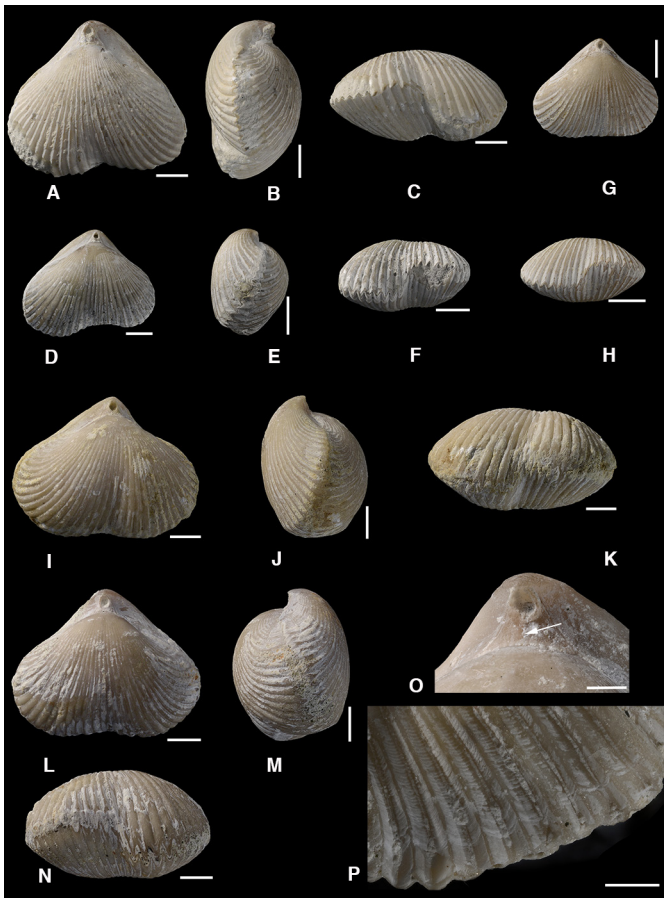

Fig. 6. *Cyclothyris grimargina* nov. sp. from the Campanian of Les Charentes and Dordogne, France (Arnaud coll.). A–C. Dorsal, lateral and anterior views of the holotype SU.PAL.2018.0.55.19.1 from Caillaud, Charente-Maritime. D–F. Specimen SU.PAL.2018.0.55.11.28 from Charente. G,H. Specimen SU.PAL.2018.0.55.11.29 from Charente. I–K. Specimen SU.PAL.2018.0.55.28.1 from Périgueux. L–O. Specimen SU.PAL.2018.0.55.28.3 from Périgueux with close-up view of the conjunct deltidial plates (O, see white arrow). P. Close-up view of costae and elementary growth marks on them revealed on specimen SU. PAL.2018.0.55.28.6 from Périgueux. Scale bars = 5 mm, except (O, P) = 2 mm. Photographs: P. Loubry.

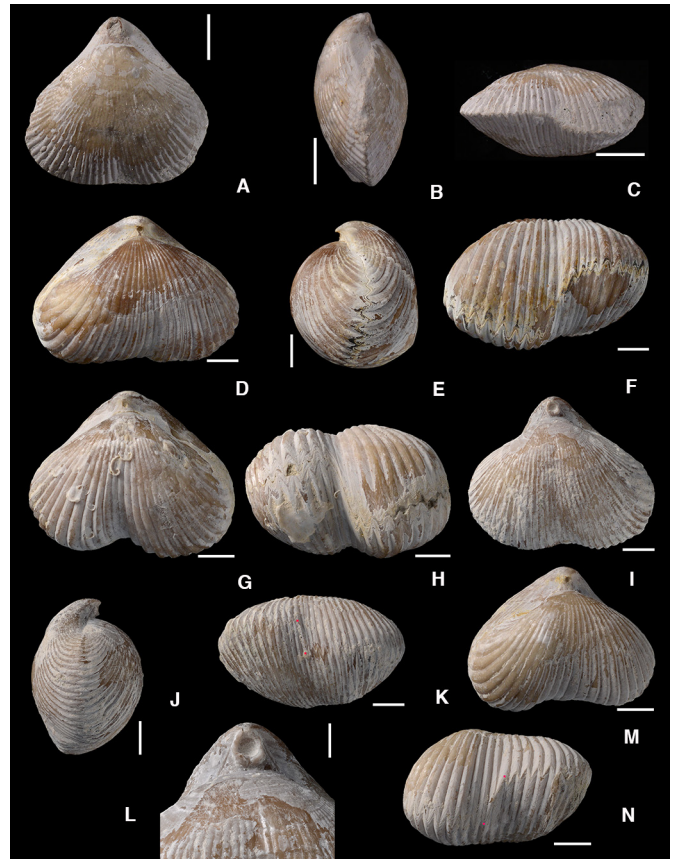

Fig. 7. *Cyclothyris grimargina* nov. sp. from the Campanian of Les Charentes and Dordogne. A–C. Subadult specimen MNHN.F.A70790 (Late Campanian from the road between Barbezieux and Barzan; Villier coll.). D–F. Specimen SU.PAL.2018.0.55.46.1 from Mensignac. G–H. specimen SU.PAL.2018.0.55.46.2 from Mensignac. I–L. Specimen SU.PAL.2018.0.55.34.2 from Caillaud/Talmont: the red dots precise the limits of the shifting; close-up view of the posterior shell with the wide rimmed foramen (L). M,N. Specimen SU. PAL.2018.0.55.36.2 from Saint-Hilaire (Charente). Scale bars = 5 mm, except (L) = 2 mm. Photographs: P. Loubry.

or less inclined ventrally (Figs. 4B, 4F, 4K, 4N, 4Q). The shifting of the lateral lobes of the anterior margin, left-up/right-down or the reverse, is most often revealed along about one costa (Figs. 4C, 4G, 4I, 4R).

Description of internal characters (Fig. 5) – Specimen MNHN.F.A70935: pedicle collar present, thick dental plates rapidly thinning down (Figs. 5a–5f), thick hinge teeth inserted in wide dental sockets (Figs. 5g–5j), slightly concave hinge plates (Figs. 5g–5j), raduliform to canaliform crura (Figs. 5k–5m).

Comments. – Muñoz (1994) proposed the new combination *Owenirhynchia globata* and was followed by several authors until Berrocal-Casero *et al.* (2017). The globose shape of all the type specimens and new specimens observed in this study is not compatible with the original diagnosis of *Owenirhynchia*. Indeed, these last authors precised that *Owenirhynchia* presents shells not globose, generally larger than longer, with subtriangular outline [literal translation of "*conchas no globulosas, generalmente más anchas que largas de contorno subtriangular*"]. We propose an assignment to *Cyclothyris* based on the shape deltidial plates whose lateral expansions form a tube.

Radulović and Motchurova-Dekova (2002) identified specimens of *Cyclothyris*? *globata* from the Santonian–Campanian of southeastern Europe (Pannonides, Carpatho-Balkanides, Dinarides). We note that until now this species is restricted to the Campanian and that some identifications proposed for the Santonian outcrops should be review.

Cyclothyris grimargina nov. sp.
Figures 6–8; Table 2

Rhynchonella difformis var. *globata*. Fage 1934: pl. 22, fig. Dg[1–5].
Rhynchonella globata. Gaspard 1991: pl. 1, figs. 7–9.
Etymology. – The specific epithet is a contraction of the Old Frankish *grima* (mask) and the Latin *margo* (commissure).

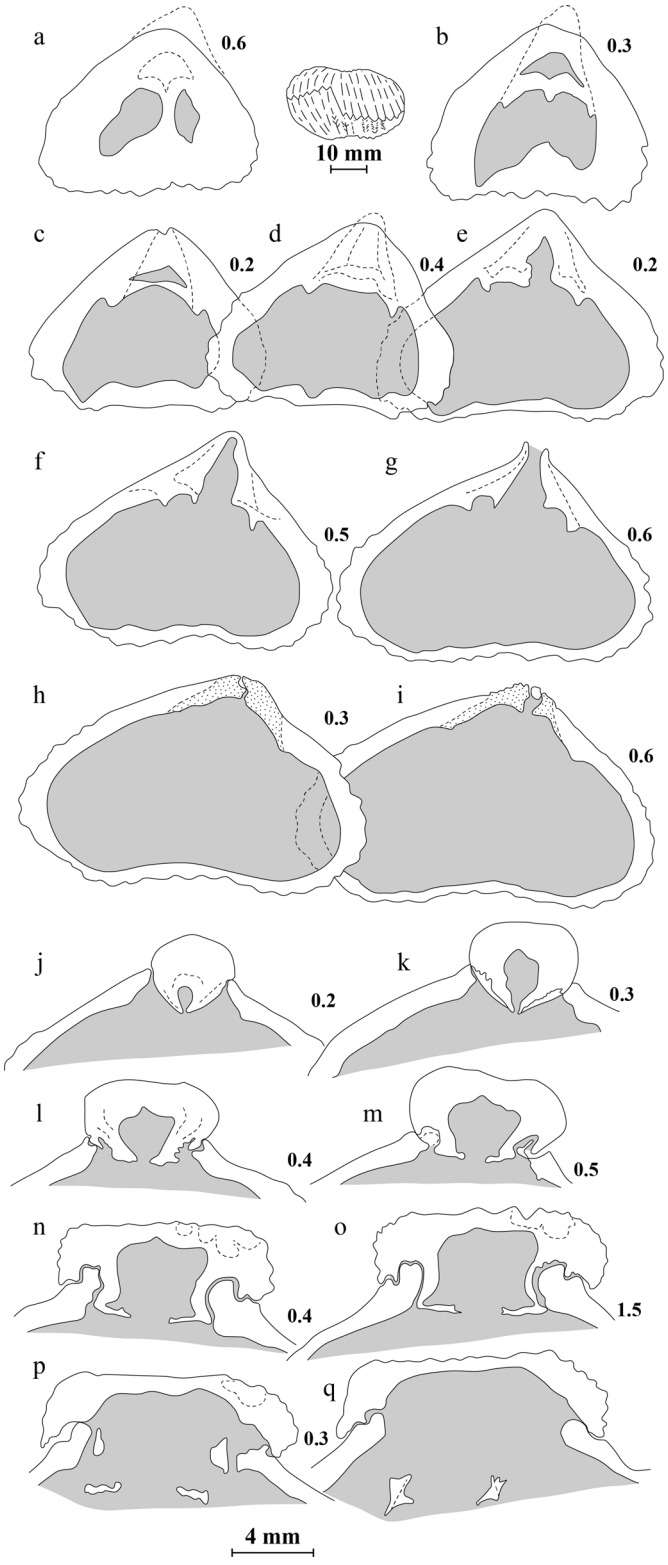

Fig. 8. Transverse serial sections in a shell of *Cyclothyris grimargina* nov. sp. (MNHN.F.A70936) from the Campanian of Gurat (Charente) (measurements: 21.3 mm in length, 31.3 mm in width, 18.6 mm in thickness). Line drawings: D. Gaspard.

Type material. – Holotype SU.PAL.2018.0.55.19.1. Several paratypes are listed in Table 2.

Type locality. – Caillaud, Charente-Maritime, France.

Type age. – Campanian.

Additional examined material from the Campanian. – See Table 2.

Diagnosis. – Biconvex globose and strongly costate shell with a wide-wing shape; conjunct deltidial plates whose lateral expansions form a tube; suberect to slightly curved ventral beak, asymmetric anterior margin with a more or less inclined shift line.

Description of external morphology (Figs. 6 and 7) – Wide sized subtriangular shells (length: 11.4–26.7 mm; width: 12.1–32.4 mm; thickness: 08.0–19.3 mm) with a medium curved to suberect pointed ventral beak (Figs. 6B, 6J, 6M, 7B, 7E), ornamented by about 27 to 38 coarse costae, exceptionally 50 (Figs. 6A, 7D, 7I, 7M) round and finer in the posterior shell, sharper and wider near the margins. The limit of the joined deltidial plates is visible (Figs. 6O and 7L); these later line the round foramen (around 1.5 mm in diameter). The lateral expansions of these deltidial plates are developed to form a short tube. The dorsal areas of the ventral beak are smooth except very fine growth lines. The shifting of the lateral lobes of the anterior margin left-up/right-down, or the reverse, is most often revealed along around two to four costae (Figs. 6C, 6F, 6K, 6N, 7F, 7H, 7K, 7N). Lateral margins more often inclined ventrally in the anterior shell part (Figs. 6E, 6J, 6M). Sometimes elementary growth lines are observed at the mid-anterior shell surface (Fig. 6P). Notice that subadult specimens reveal a proportional wider foramen (Fig. 7A), are flatter with straight lateral margins (Fig. 7B), a lateral and anterior end of valves forming a sharp angle and an anterior margin slightly asymmetrical with a weak shift (Fig. 7C).

Description of internal characters (Fig. 8) – Specimen MNHN.F.A70936: pedicle collar present, ephemeral dental plates, rapidly disappearing. Deltidial plates well-marked (Figs. 8g–8j), semi-rounded to sub-flattened dorsal posterior shell (Figs. 8j–8q), nearly constricted hinge teeth closely inserted in the dental sockets (Figs. 8l–8o), slightly concave hinge plates evolving to a subhorizontal position anteriorly (Figs. 8m–8o), thick raduliform to canaliform crura (Figs. 8p–8q).

Discussion. – This species is assigned to *Cyclothyris* based on the following characters: asymmetrical anterior commissure, deltidial plates forming short tube around foramen, beak suberect to slightly curved. It differs from *Cyclothyris difformis* by a stronger asymmetry with a well-developed lateral right/left shift at the level of anterior commissure forming two distended lobes sometimes unequal. It differs from *Cyclothyris globata* by the wing-shaped shells (very round globose shell in *C. globata*), the orientation of the shifting line (more inclined) of the anterior commissure and the stronger costae. It differs from *Cyclothyris vesicularis* by a straight thinner ventral beak, more and finer costellae and an asymmetric anterior margin rather slightly twisted than obliquely shifted in this last species. *Cyclothyris vesicularis* is in a whole relatively slender than *Cyclothyris grimargina* nov. sp.

Table 2. List of the type material and additional specimens of *Cyclothyris grimargina* nov. sp. from the Campanian of Les Charentes and Dordogne. Stratigraphical levels P1–P3 of Arnaud (1877) correspond to biozones CI-CV of the Campanian sensu Platel (1977, 1982).

Collections	Statut	Localities	Stratigraphical levels	Numbers of specimens	Shifted commissure		Shifted commissure (%)	
					left down	right down	left down	right down
SU.PAL.2018.0.55.19.1	Holotype	Caillaud (Charente Maritime)		1		1		
SU.PAL.2018.0.55.11.28-64, MNHN.F.A70796	Paratypes	Caillaud (Charente Maritime)		38	22	16	58%	42%
SU.PAL.2018.0.55.15.1-15, SU.PAL.2018.0.55.18.1-13		Mortagne-sur-Gironde/ Saint-Seurin d'Uzet (Charente Maritime)	P2-P3	28	10	18	36%	64%
SU.PAL.2018.0.55.26.1-4		Champagnac (Charente Maritime)		4	2	2		
SU.PAL.2018.0.55.35.1-3		Saint-Médard (Charente-Maritime)	P3	3	1	2		
SU.PAL.2018.0.55.16.1-11		Charente Maritime	P1	11	7	4		
SU.PAL.2018.0.55.12.1		Montmoreau (Charente)	P2	1		1		
SU.PAL.2018.0.55.12.2		Chalais (Charente)	P1-P2	1	1			
SU.PAL.2018.0.55.12.3		La Caillerie	P2	1	1			
SU.PAL.2018.0.55.21.1-8		Aubeterre-sur-Dronne (Charente)	P3	8	3	5		
SU.PAL.2018.0.55.36.1-6, SU.PAL.2018.0.55.40.1		Saint-Hilaire (Charente)	P2	7	5	2		
SU.PAL.2018.0.55.38.1		Grange de Viaud (Charente)	P2	1	1			
SU.PAL.2018.0.55.27.7-10		Eraville (Charente)	P1	4	1	3		
SU.PAL.2018.0.55.34.1-7		Espagnac (Charente)		7	3	4		
SU.PAL.2018.0.55.37.6-7		Belvès (Dordogne)		2		2		
SU.PAL.2018.0.55.45.1-2		Courlac (Charente)	P2	2		2		
SU.PAL.2018.0.55.41.4-5		Livernant (Charente)	P1	2	1	1		
SU.PAL.2018.0.55.9.7, MNHN.F.A70791, A70792		Birac (Charente)		3	2	1		
MNHN.F.A70790		Barbezieux to Blanzac (Charente)		1		1		
MNHN.F.A70793-A70795		Combiers (Charente)	CI-CII	3	1	2		
SU.PAL.2018.0.55.14.62 –103		Charente	P1	40	19	21	48%	53%
SU.PAL.2018.0.55.10.40-45, SU.PAL.2018.0.55.12.4-8, SU.PAL.2018.0.55.13.15-36, SU.PAL.2018.0.55.17.55-98		Charente/Dordogne	P1	77	38	39	49%	51%
SU.PAL.2018.0.55.9.8-9		Cavillac (Dordogne)	P1	2	1	1		
SU.PAL.2018.0.55.28. 1-13		Périgueux (Dordogne)		13	5	8		
SU.PAL.2018.0.55.42.1-2		Puy de Fourches (Dordogne)	P1	2	2			
SU.PAL.2018.0.55.46.1-2		Mensignac (Dordogne)	P1	2	1	1		
SU.PAL.2018.0.55.47.1-2		Ribérac-Coutures (Dordogne)		2	1	1		
Total				266	128	138	48%	52%

Cyclothyris vesicularis (Coquand, 1860)
Figures 9–11

Terebratula vesicularis Coquand, 1860: 122.
Rhynchonella vesicularis. Coquand, 1862: 332, 338, pl. 34, figs. 7–9.

Type material. – The original type material was composed of a few number of specimens from Aubeterre-sur-Dronne, Charente, France. Four syntypes have been traced in the palaeontological collections of the Mining and Geological Survey of Hungary at Budapest. Among them, specimen MBFSZ K 2019.10.4.1 is here selected to be the lectotype (Figs. 9A–9C). Two paralectotypes MBFSZ K 2019.10.4.3 and K 2019.10.4.4 (Figs. 9D–9F) are also considered. The last specimen MBFSZ K 2019.10.4.2 shows strong costae and thus probably does not belong to the species.

Type locality. – Aubeterre-sur-Dronne, Charente, France.

Type age. – Campanian

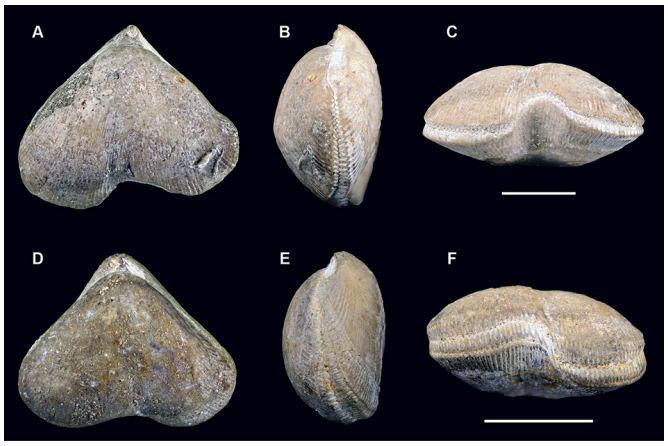

Fig. 9. Type material of *Cyclothyris vesicularis* (Coquand, 1860) from the Campanian of Aubeterre-sur-Dronne, Charente, France. A–C. Lectotype herein designated (MBFSZ K 2019.10.4.1, Coquand coll.). D–F. Paralectotype MBFSZ K 2019.10.4.4. Scale bars = 1 cm Photographs: Zoltán Lantos.

Examined material. – Three specimens MNHN.F.A70583, A70584, S08809 (Péron coll.) from Aubeterre-sur-Dronne (Charente). A set of well-preserved specimens (Arnaud coll.) from Aubeterre-sur-Dronne (SU.PAL.2018.0.55.21.1-8), Puyvigier, (SU.PAL.2018.0.55.22.1-3), Beaufort (SU.PAL.2018.0.55.23.1-3), Issac (SU.PAL.2018.0.55.24.1-4), Sourzac (SU.PAL.2018.0.55.25.1-7).

Description of external morphology (Figs. 9 and 10) – Large specimens globally triangular (length: 17.0–31.5 mm; width: 19.4–40.9 mm; thickness: 11.9–20.1 mm) (Figs. 10A, 10D, 10G, 10J), with a straight suberect to slightly incurved ventral beak (Figs. 10B, 10E, 10N), the maximum width in anterior position (Figs. 10A, 10D, 10J, 10M), a variable sized foramen (diameter: around 1 mm, sometimes more) lined by well-defined lateral expansions of the deltidial plates (Fig. 10I), and a typical twisted asymmetrical anterior margin (Figs. 10C, 10F, 10H, 10L). The shell is ornamented by 75 to 98 (even 100) costellae, fine posteriorly whose size increases near the margins revealing sometimes a gerontic aspect, even exaggerated in a mid-depressed anterior margin (Fig. 10O) and an unsual gathering of two or three fine costellae in a strong one (Figs. 10O–10P). The costellae present sometimes a digitation at mid-length (see Fig. 10J). In this species a longer lateral margin is observed where the down side lobe of the anterior commissure is concerned. Often the lateral and anterior margins are slightly depressed (Figs. 10C, 10F, 10L, 10O).

Description of the internal characters (Fig. 11) – Specimen MNHN.F.A70937 (length: 22.3 mm; width: 28.0 mm; thickness: 17.6 mm): strong dental plates (Figs. 11b–11i), developed deltidial plates (stippled) (Figs. 11f–11h), an ephemeral dorsal septum (Figs. 11j–11n), dental sockets deep and slightly crenulated posteriorly and wide anteriorly (Figs. 11j–11o), constricted then thick hinge-teeth (Figs. 11k–11o), hinge plates convex dorsally (Figs. 11k–11p), and crura distally raduliform (Figs. 11p–11r).

Contortithyris nov. gen.

Type species. – *Contortithyris thermae*, nov. sp., by monotypy.

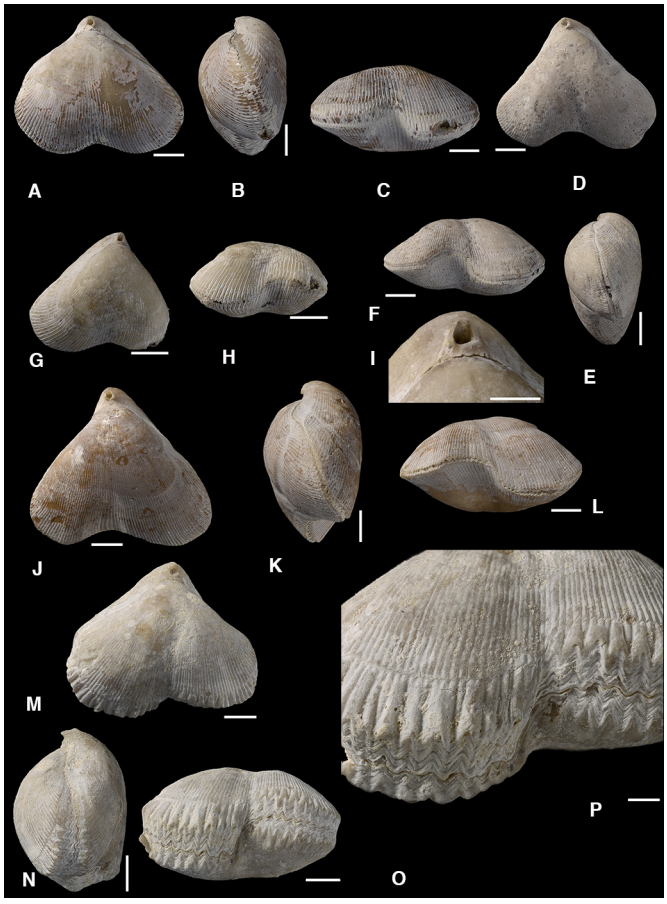

Fig. 10. *Cyclothyris vesicularis* (Coquand, 1860) from the Late Campanian of Aubeterre (Charente). A–C. Large specimen MNHN.F.A70583 (Péron coll.): dorsal view, profile revealing a depressed lateral commissure, and twisted anterior commissure. D–F. Specimen MNHN.F.A70584 (Péron coll.). G–I. Small adult specimen MNHN.F.S08809 (Péron coll.); close-up view of the ventral posterior shell with the foramen (I). J–L. Specimen SU.PAL.2018.0.55.22.1 (Arnaud coll.) from Puyvigier revealing some digitations of the costellae. M–P. Specimen SU.PAL.2018.0.55.22.2 of Puyvigier obviously with growing old signs (increasing thickness of the margins to the detriment of length and width), close-up view revealing that two/three costellae fused in one costa near the margins (P). Scale bars = 5 mm, except (I and P) = 2 mm. Photographs: P. Loubry.

Etymology. – From the Latin *contortus* (contorted) in allusion to the shifted shape of the anterior margin.

Diagnosis. – Medium to large sized shell, anterior margin commonly asymmetrical; costae posteriorly fine and slightly sharp on the margins, medium-sized foramen, suberect beak.

Discussion. – *Contortithyris* nov. gen. is assigned to the Cyclothyridinae based on the asymmetrical anterior commissure and the deltidial plates forming short tube around foramen. It differs from *Cyclothyris* by its more massive globose shape, curved umbo, more rounded commissure and slightly finer costae, from *Owenirhynchia* by a wider size and thicker to globose shell, less high height of the twisted anterior margin, and from *Beaussetithyris* nov. gen. by the biconvex profile. It differs from all the other genera of the Cyclothyridinae by the asymmetrical anterior commissure.

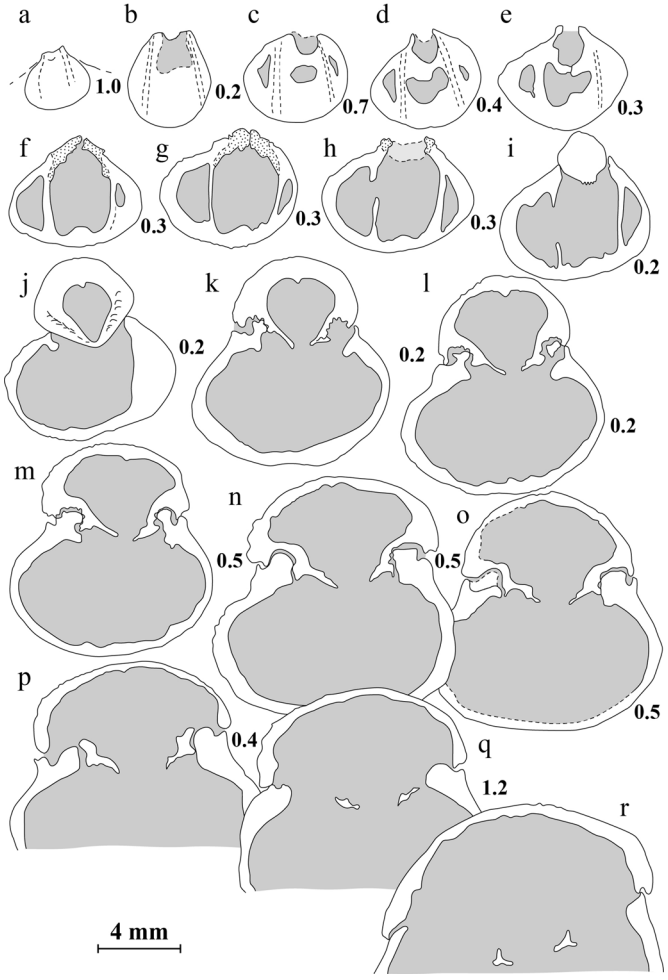

Fig. 11. Transverse serial sections in a shell MNHN.F.A70937 of *Cyclothyris vesicularis* (Coquand, 1860) from the Campanian (measurements: 22.3 mm in length, 28.0 mm in width and 17.6 mm in thickness). Internal characters from the posterior shell till the level of the crura. Line drawings: D. Gaspard.

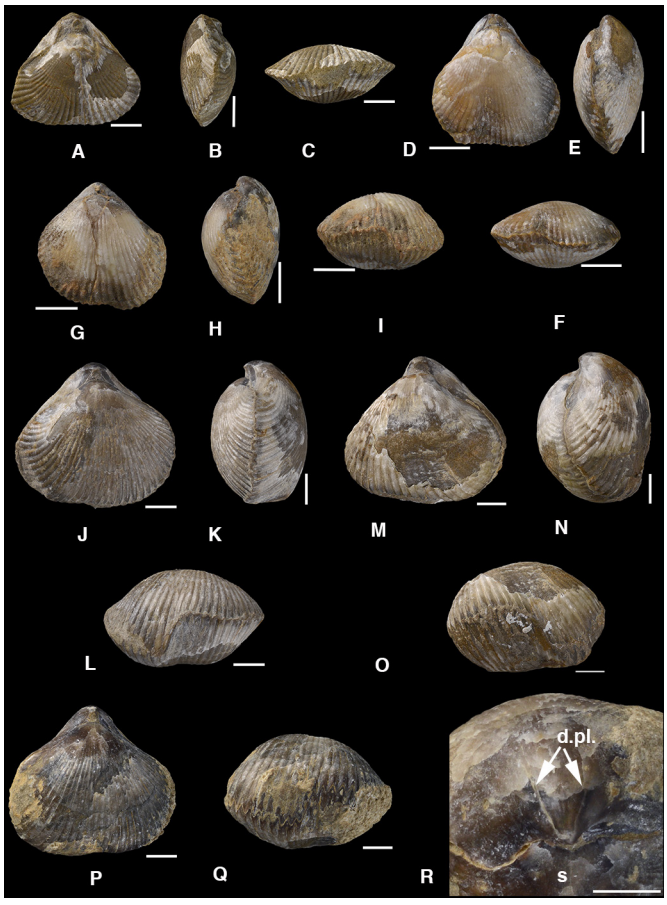

Fig. 12. Specimens of *Contortithyris thermae* nov. sp. from the Marnes à *Micraster* Formation, Early Santonian, Rennes-les-Bains (Aude, France). A–C. Juvenile specimen MNHN.F.A70586 with a rectimarginate anterior margin slightly distorted. D–F. Sub-adult specimen MNHN.F.A70587 with a beginning asymmetrical anterior margin. G–I. Young adult specimen MNHN.F.A70639 with an increasing asymmetry of the anterior margin. J–L. Adult specimen MNHN.F.A70640, with a pronounced left asymmetry (left side down) of the anterior margin. M–O. Adult specimen MNHN.F.A70641 with a pronounced right asymmetry (right side down) of the anterior margin. P–R. Adult specimen MNHN.F.A68144 with a worn posterior shell revealing traces of the dental plates (d. pl.) and dorsal septum (s) in a close-up view (R). Scale bars = 5 mm. Photographs: P. Loubry.

Contortithyris thermae nov. sp.
Figures 12–14

Etymology. – The specific epithet alludes to the Antique thermal baths of the type locality Rennes-les-Bains.

Type material. – Holotype MNHN.F.A59945. 32 paratypes from Rennes-les-Bains (MNHN.F. A68144–A68146, A70586, A70587, A70639–A70642, A70873-A70885, A70887–A70895, S09048), and three paratypes from Sougraigne (MNHN.F.A70643, A70644, A70597).

Type locality. – Rennes-les-Bains, Aude, Occitanie, France.

Type age. –Santonian (Marnes à *Micraster* Formation).

Diagnosis. – Medium to large size shell, biconvex, finely costate, posterior shell nearly smooth, medium round foramen, beak sharp, umbo suberect; anterior margin progressively to strongly asymmetrical with a pronounced high shift.

Description of external morphology (Figs. 12 and 13) – Globose shells hardly wider than long (length: 12.4–31.5 mm; width: 12.9–40.8 mm) with a curved short and massive ventral umbo (erect in juveniles) ending by a dorsally pointed beak accentuated by the lateral crests. The beak is not necessarily inclined on one side or the other (Figs. 12 and 13). The deltidial plates, 2.0–2.5 mm in height and 3–4 mm of basal width, are sometimes partly hidden, interrupted at their posterior part by the round/oval foramen of about 1.5–2.0 mm in diameter in adults. The foramen is lined by lateral expansions of the deltidial plates shaping an open tube. The dorso-lateral areas of the ventral beak are obviously smooth. The shells are ornamented by approximately 35–45 small acute angle costae (following the stage during ontogeny), not divided, of 1.0–1.5 mm at the basal part, thin, even blurred at the posterior part of valves. The lateral margins are globally straight. The anterior margin tends progressively and slightly to be asymmetrical from the juveniles (Figs. 12C and 12F) to

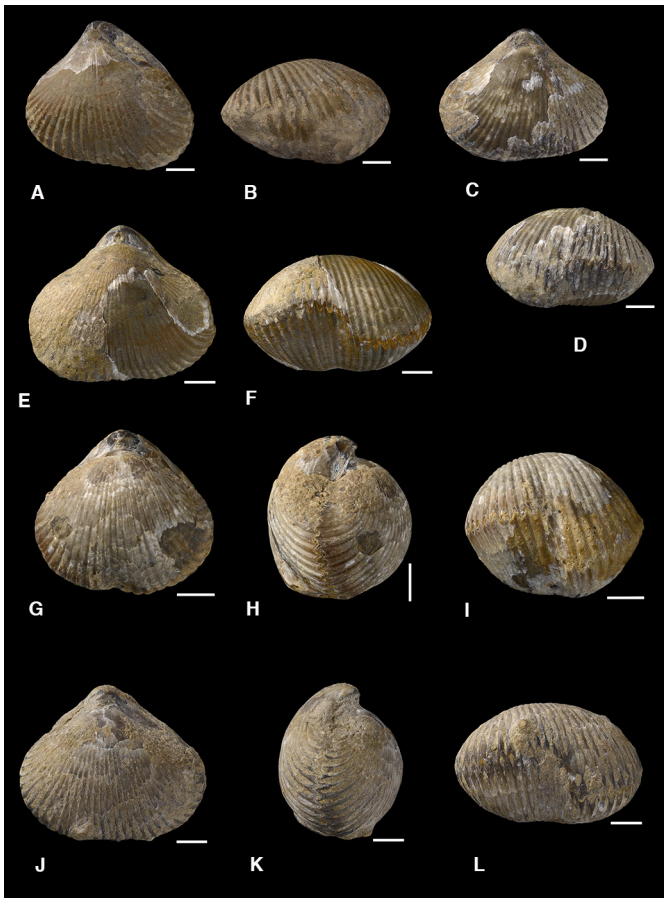

Fig. 13. *Contortithyris thermae* nov. sp. from the Marnes à *Micraster* Formation, Rennes-les-Bains, Aude, France (A–I) and from Sougraigne, Aude, France (J–L). A,B. Specimen MNHN.F.A68145. C,D. Specimen MNHN.F.A68146. E,F. Holotype MNHN.F.A59945 (specimen tentatively scanned using the AST-RX platform without positive result concerning the 3D modelling of the brachidium). G–I. Gibbous specimen MNHN.F.A70642. J–L. Specimen MNHN.F.A70643. Scale bars = 5 mm. Photographs: P. Loubry.

markedly asymmetric in the adults, shifted with one side pull-down and the other one turned-up (Figs. 12I, 12L, 12O, 12Q, 13B, 13F, 13I, 13L). The deflection between the two parts is important; it follows a slight inclined line never reaching a vertical position (Figs. 12L and 13I). The specimens less than 20 mm in length, are flatter than the fully mature ones, and consequently present a smaller deflection of the lateral margin (Figs. 12B and 12E). In adults, the deflection of the anterior margin concerns 1 to 2, even 3 costae (Figs. 12I, 12L, 12O, 13B, 13F, 13I, 13L). Worn shells allow observing traces of the dental plates at the posterior ventral beak and of the dorsal septum (Fig. 12R).

Description of internal characters (Fig. 14) – Transverse serial sections in specimens MNHN.F.A70938 and A70939 reveal: strong dental plates, slightly inclined, becoming parallel and thinner anteriorly. The incidence of the curvature of the ventral umbo with its sharp beak is marked, as well as the lateral expansions of the deltidial plates on each side of the foramen (Figs. 14Ac–14Ae, 14Bb–14Bc). In specimens between 21 to 33 mm in length, the dental plates are half to one-third of the umbo shell thickness at 1.5–2.0 mm from the posterior part of the ventral valve (Figs. 14Aa–14Af, 14Ba–14Be). The posterior dorsal valve reveals the beginning of the dental sockets (Figs. 14Af–14Ag, 14Be), deepening after (Figs. 14Ah–14Aj, 14Bf–14Bj), and a faint/moderate dorsal septum (Figs. 14Ai–14Am, 14Be–14Bm). The hinge plates are sub-horizontal. The hinge teeth are inserted faintly oblique in the crenulated dental sockets (Figs. 14Ah–14Aj, 14Bg–14Bj). These teeth are constricted by the outer socket ridge and by the accessory inner socket ridge (Figs. 14Ah–14Aj, 14Bh–14Bj). The crura are canaliform to subfalciform.

Microstructure. – Details of the crural bases and/or the relative shape of hinge teeth and dental sockets are presented in Appendix E.

Comments – The specimens from Sougraigne present the same proportions with those from Rennes-les-Bains, but some are wider than the standard and are thicker (Figs. 13J–13L). Some wider specimens from Sougraigne bear stronger costae (Fig. 13J). The peculiarity of all of these shells (both Rennes-les-Bains and Sougraigne) is the high shifted right/left asymmetry of the anterior margin.

Beaussetithyris nov. gen.

Type species – *Beaussetithyris asymmetrica* nov. sp., by monotypy.

Etymology – From the locality of the type species, Le Beausset, Var, Provence-Alpes-Côte d'Azur, SE France.

Diagnosis. – Large shell, erected to suberected beak, costellate shell, costae sharp on the margins; foramen round to lightly oval, auriculate deltidial plates; anterior margin asymmetrical.

Discussion. – *Beaussetithyris* nov. gen. is assigned to the Cyclothyridinae based on the asymmetrical anterior commissure and the deltidial plates forming short tube around foramen. It differs from *Cyclothyris* by its dorsibiconvex shell, often more massive, from *Owenirhynchia* by the size and the thickness of the shell, and from *Contortithyris* by slightly greater size, obvious wider foramen and stronger costae.

Beaussetithyris asymmetrica nov. sp.
Figures 15–17

Etymology. – The specific epithet alludes to the asymmetrical shape of the anterior commissure.

Type material – Holotype MNHN.F.A67492. Seven paratypes MNHN.F.A59946, A67493, A67481–A67485 from Le Beausset; one paratype MNHN.F.A26502 from La Cadière; five paratypes MNHN.F.A59948, MNHN.A70117, A70118, A70811, A70886 from Les Martigues. All are from Var department, SE France.

Type locality. – Le Beausset, Var, SE France.

Type age. – Early Santonian.

Additional material. – One specimen MNHN.F.S09235 (coll. Péron) from Le Castellet; two specimens MNHN.F.A70798, A70799 (d'Orbigny coll.) from La Cadière; two specimens MNHN.F.A61729, A70812 (d'Orbigny coll.) from Le Beausset; two specimens MNHN.F. A59947, A70645 from Les Martigues.

Diagnosis. – Medium to large shells, dorsibiconvex, conjunct deltidial plates, auriculate laterally, lateral margins slightly inclined ventrally, asymmetric anterior margin with a shift evenly high.

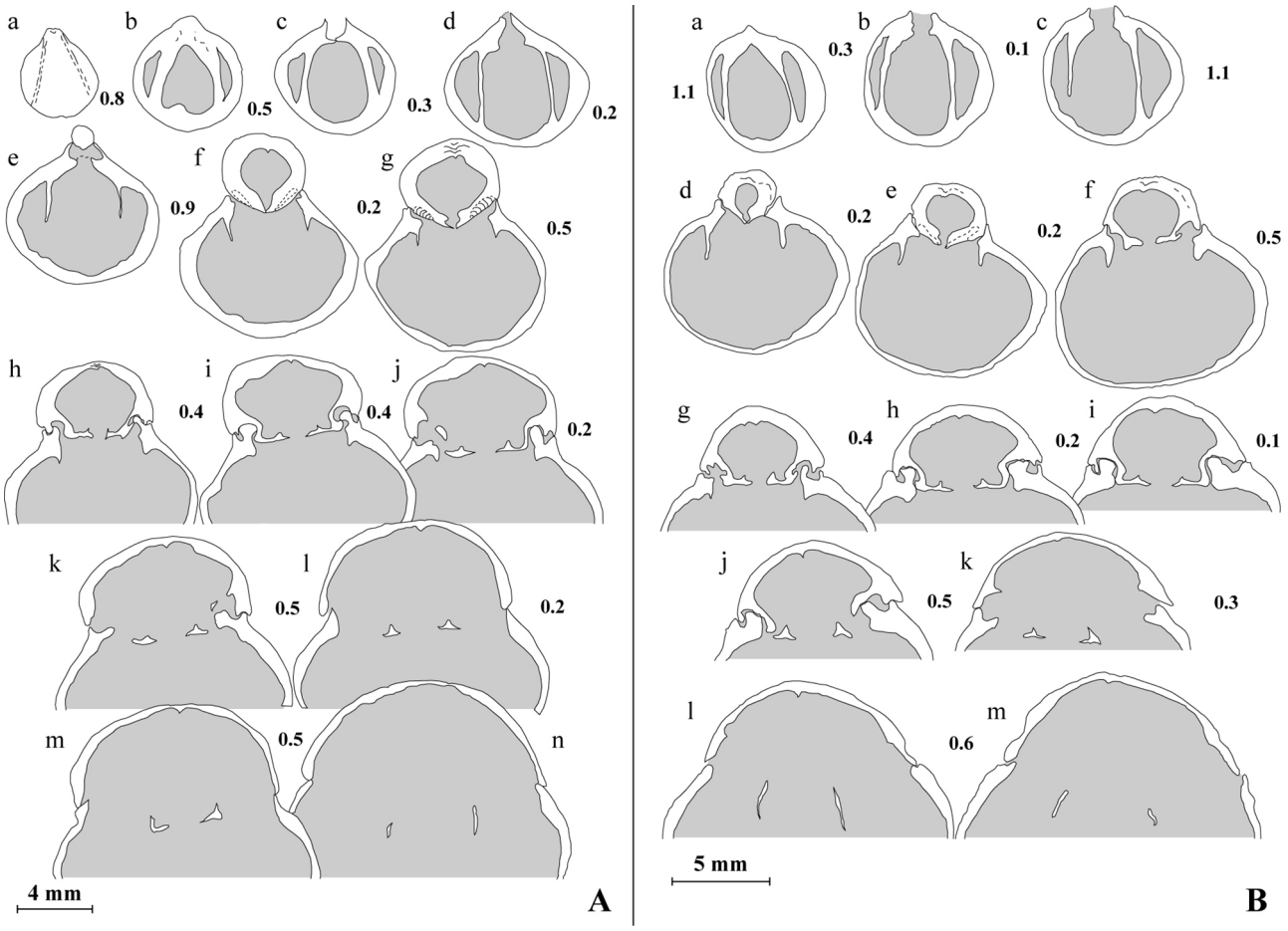

Fig. 14. Transverse serial sections in *Contortithyris thermae* nov. sp. from Rennes-les-Bains (A, MNHN.F.A70938) and Sougraigne (B, MNHN.F.A70939), from the posterior shell till the level of the crura, to locate the internal characters. Line drawings: D. Gaspard.

Description of external morphology. – (Figs. 15 and 16) Right and left asymmetric adult shells are mainly massive, dorsibiconvex, with a sub-erect ventral umbo, rarely ending by a pointed beak. The adult shells are 21.7 to 32.9 mm in length, 21.1 to 37.8 mm in width and 14.9 to 27 mm in thickness. The dorsal surfaces of the beak are smooth. The rounded foramen encroaches on the posterior part of the deltidial plates forming a short tube. The foramen is about 1.5 mm in diameter (even wider). The shells are ornamented by 29 to 36, even 39 costae. Few juvenile specimens and/or preadults (about 19.3 mm in length) show proofs of a beginning asymmetry with fine costae (1 mm at the margin). Some specimens reveal a displacement of the monoplication towards one side (Fig. 16G) rather than a displacement of the asymmetry as illustrated in Figure 16J.

Description of internal characters. – (Fig. 17) Transverse serial sections of the asymmetrical specimens from Le Beausset (Fig. 17A) and Les Martigues (Fig. 17C), and virtual transverse views from the scanned specimen MNHN.F. A26502 (La Cadière, Appendix D) reveal: globally parallel dental plates (17Ae–17Ah, 17Cb–17Cf), lateral expansions of the conjunct deltidial plates, an auriculate foramen, sometimes a more curved dorsal umbo (Figs. 17Ag–17Ai, 17Cf), a short dorsal septum becoming faintly higher anteriorly (Figs. 17Ak–17Au) compared to the more discreet one in les Martigues (Figs. 17Cf–17Cm), and hinge plates slightly undulating ventrally, then slightly oblique towards the ventral valve. The crura are raduliform (Figs. 17Ar–17At, 17Cl–17Co). A sub–asymmetrical shell from Le Beausset is illustrated for comparison (Fig. 17B).

Microstructural details. – Details of the crural bases and/or the relative shape of hinge teeth, dental sockets, and dorsal septum are presented in Appendix E.

Comments. – Some specimens herein identified as *Beaussetithyris asymmetrica* present subasymmetrical shells characterized by an uncommon shifted anterior margin with one side obviously longer than the other one (Figs. 16H–16J). These shells are more massive than the type material. They show a more erect umbo, and a wider foramen. They are biconvex to dorsibiconvex (length: 24.1–31.7 mm; width: 27.7–35.9; thickness: 19.4–21.7 mm). In adult specimens, the foramen is round (1.25–1.75 mm in diameter). They present longer dental plates (Figs. 17Bd–17Bq), an auriculate foramen (Figs. 17Bb–17Bg), an important dorsal umbo with an important dorsal median septum that has no equivalent in the shells previously described (Figs. 17Bh–17Bs), hidden and narrow posterior dental sockets (Figs. 17Bl–17Bm), thick

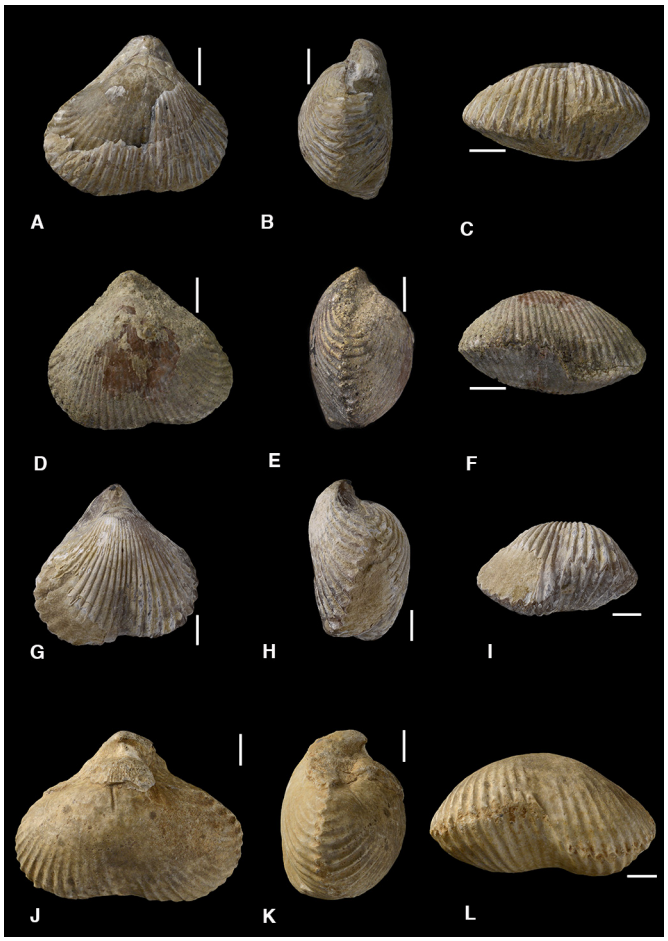

Fig. 15. *Beaussetithyris asymmetrica* nov. sp. from the Early Santonian of Basse-Provence, SE France. A–C. Holotype MNHN.F.A67492 (Péron coll.) from Le Beausset, Var. D–F. Paratype MNHN.F.A67493 (Péron coll.) from Le Beausset. G–I. Paratype MNHN.F.A.59946 (Péron coll.) from Le Beausset. J–L. Paratype MNHN.F.A26502 (d'Orbigny coll.) from La Cadière (see video online, Appendix D). Scale bars = 5 mm. Photographs: P. Loubry.

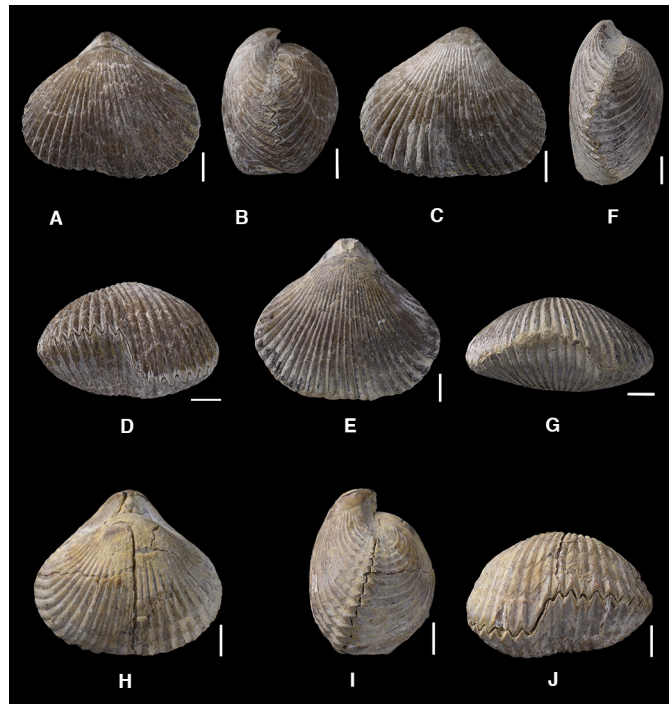

Fig. 16. *Beaussetithyris asymmetrica* nov. sp. from the Early Santonian of Les Martigues (Basse-Provence, SE France). A–D. Paratype MNHN.F.A59948, dorsal (A), lateral (B), ventral (C) views; note the step-like asymmetrical anterior commissure (D). E–G. Adult specimen MNHN.F.A59947 with a shape intermediate between monoplicate anterior margin and translatory motion of the anterior margin on one side (sub-asymmetrical shape). H–J. Adult specimen MNHN.F.A70645 with a strong shifted anterior margin but with a slight translatory motion of the anterior margin. Scale bars = 5 mm. Photographs: P. Loubry.

hinge teeth inserted more vertically in the dental sockets than in the previous (Figs. 17Bn–17Bq), small lateral accessory teeth and dental sockets (Figs. 17Bp–17Bs) and swollen hinge plates posteriorly then forming an open angle towards the dorsal floor, subcanaliform to raduliform crura (Figs. 17Bu–17By).

Comparisons between the two sets of sections (Figs. 17A–17C) reveal differences between the asymmetrical type specimens and the subasymmetrical ones. Only new additional specimens will allow to precise if the observed differences are linked to a great variability in *Beaussetithyris asymmetrica* or if it is necessary to distinguish two different taxa.

Owenirhynchia *Calzada* in Calzada and Pocovi, 1980

Type species. – *Owenirhynchia rubra* Calzada *in* Calzada and Pocovi, 1980

Owenirhynchia sp.

Figures 18 and 19

Examined material. – Specimens sampled from the Coniacian-Santonian (Nidáguila Formation) of the North Castilian Platform (Villamartin section), among them two MNHN.F. A70942, A70943 were used for transverse serial sections.

Description of external morphology (Fig. 18) – Medium sized subtriangular, equibiconvex multicostate shell, wider than long with a sub-erect ventral beak, deltidial plates shaping the typical short tube of the Cyclothyridinae around the subrounded foramen (diameter: often 1 mm, even more); slight asymmetry of the anterior margin (Figs. 18B and 18D).

Description of internal characters. (Fig. 19) – Sets of transverse serial sections of specimens from different levels reveal: joined wide deltidial plates which lateral expansions shape a tube around the foramen (Figs. 19Aa–19Ac, 19Ba, 19Bb), dental plates sub-parallel becoming slightly divergent (Figs. 19Aa–19Ae, 19Ba–19Be), supporting deeply inserted subquadrate hinge teeth, and consequently wide and deep dental sockets (Figs. 19Ad–19Ag, 19Bf–19Bh), hinge plates ventrally concave, crura canaliform to distally concave raduliform (Figs. 19Ag–19Ai, 19Bf–19Bh), reduced dorsal septum.

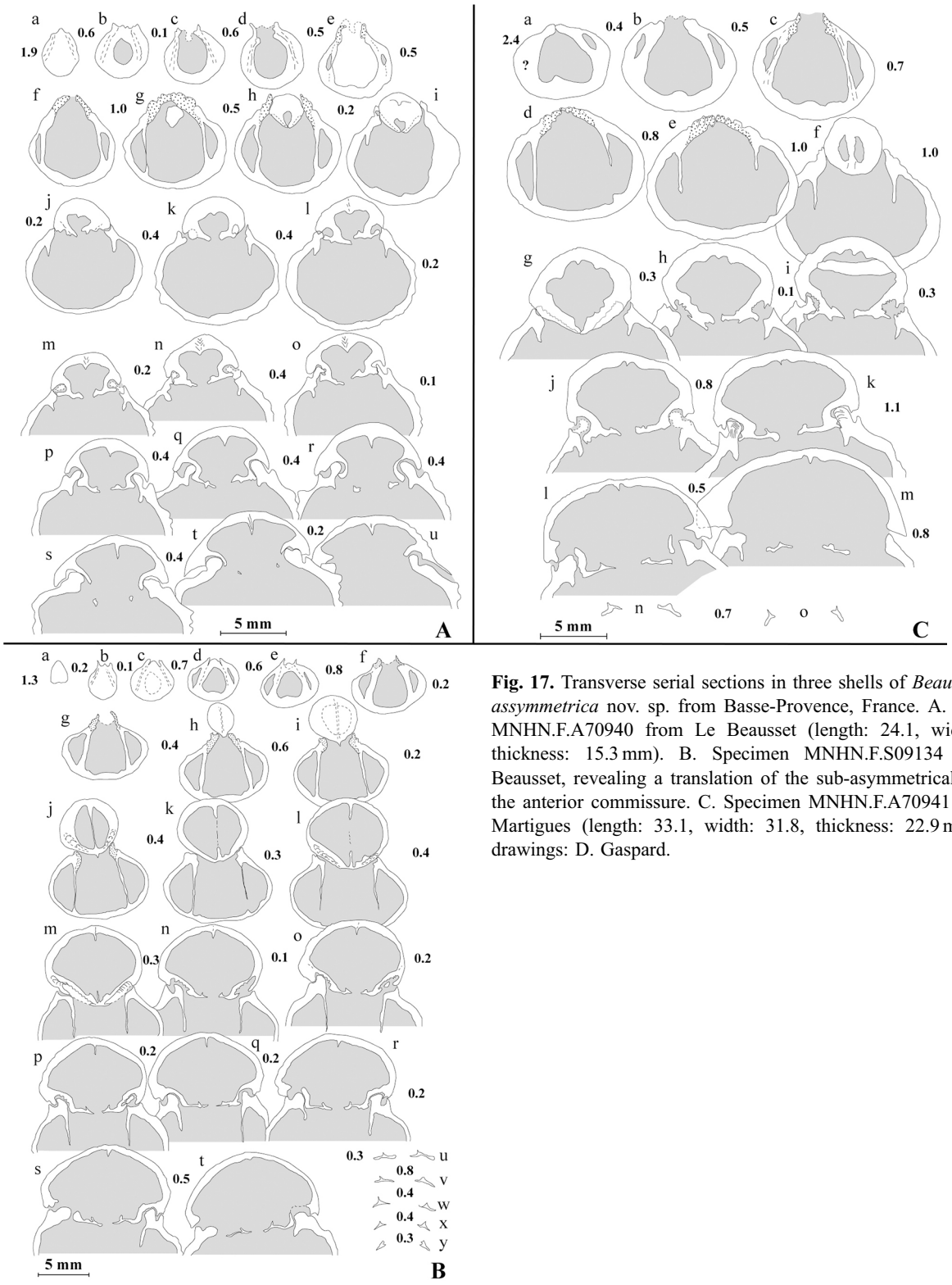

Fig. 17. Transverse serial sections in three shells of *Beaussetithyris assymmetrica* nov. sp. from Basse-Provence, France. A. Specimen MNHN.F.A70940 from Le Beausset (length: 24.1, width: 23.1, thickness: 15.3 mm). B. Specimen MNHN.F.S09134 from Le Beausset, revealing a translation of the sub-asymmetrical shape of the anterior commissure. C. Specimen MNHN.F.A70941 from Les Martigues (length: 33.1, width: 31.8, thickness: 22.9 mm). Line drawings: D. Gaspard.

Fig. 18. *Owenirhynchia* sp. from the Nidàguila Formation, Villamartin, Spain. A,B. Specimen MNHN.F.A70942. C,D. Specimen MNHN.F.A70943. Photographs: University Paris 11.

Comments. – The genus *Owenirhynchia* interpreted by Manceñido *et al.* (2002: 1334), as a possible subgenus of *Cyclothyris* or as a subjective synonym of this genus requires the observation of additional specimens for a deeper revision.

5 Discussion

Asymmetry is an important and widespread trait, having evolved numerous times in many invertebrate and vertebrate organisms and at many levels of organisation ranging from individual cells, through organs (*e.g.*, brain, heart) to entire body-shapes. Geneticists try to explain this reality highlighting that the asymmetrical structure of the proteins that composed the living species are responsible of the observed asymmetry (see Flamant, 2016). Stern (2002) explained that the asymmetries between the right- and left-hand sides of the bodies are initiated at an early stage of development. In their approach of asymmetry at the level of the biomineralization process, Addadi and Weiner (2001) exposed that "*understanding the formation of asymmetrical shapes during the growth of symmetrical structures is the first step towards understanding asymmetry in biology*". They reported that chiral shapes in biologically formed molecules lead to crystals involved in the formation of part of skeleton/exoskeleton of living organisms including vertebrates as well as invertebrates. Living organisms as well as fossils are concerned.

Among the invertebrates, brachiopods are concerned by asymmetry in their exoskeleton (shells). Among rhynchonelliform brachiopods, only rhynchonellids are affected by asymmetry. No modern example has been identified in the current state of our knowledge. Asymmetry is confined to rhynchonellids at certain times during evolution (Fürsich and Palmer, 1984). This observation goes against an ecophenotypical origin which logically should concern all groups of brachiopods at all times. Therefore, this rather suggests another origin, genetic, in some groups (*i.e.*, in some rhynchonellids) as illustrated here. Several outstanding examples were found during the Mesozoic (Jurassic–Late Cretaceous: Owen, 1962; Popiel-Barczyk, 1977; Fürsich and Palmer, 1984; Gaspard, 1985, 1991; Muñoz, 1985, 1994; Motchurova-Dekova, 1995 among others).

Since then and recently, several authors (Afanasjeva, 2014; Berrocal-Casero *et al.*, 2017; Schrøeder *et al.*, 2017) proposed new cases of brachiopods showing asymmetry or ecophenotypical asymmetry. Careful examination of these three publications lead us to identify a confusion between asymmetry and dissymmetry. Most of the discussed modifications in the symmetry of the brachiopod shells are linked to palaeoenvironmental conditions and thus are of ecophenotypical origins. They correspond to cases of dissymmetry (see precisions in the present introduction). For instance, Berrocal-Casero *et al.* (2017; see their Fig. 13) hypothesized that the "functional meaning asymmetry" of rhynchonellid brachiopods from Northern Spain may be interpreted to an adaptation to sinking in soft substrates taking place as a response to changes in palaeoenvironmental conditions, and thus proposed semi-buried specimens. We remark that their hypothesis of semi-buried specimens staying till the adult stage in a position on one side or the other is not relevant. Such a position would lead quickly to the infilling of the shell by the sediment and consequently to the inefficiency of the lophophore or the ability to feed. In conclusion, we note that Berrocal-Casero *et al.* (2017) presented true asymmetrical specimens and true dissymmetrical specimens but the origin of the modification of the shifted commissures are different for us: genetically based in the first case and linked to the palaeoenvironments in the second one. We remark that it is also possible to observed true asymmetrical specimens affected by dissymmetry (Figs. 2J, 2K, 4M–4O).

In the present study, we identify asymmetry in four rhynchonellid genera (*Cyclothyris*, *Contortithyris*, *Beaussetithyris*, *Owenirhynchia*) at level of the anterior commissure showing a left-up/right-down shift, or the reverse. The observation of the shifted anterior commissure with approximately 50% of right-asymmetrical specimens and 50% of left-asymmetrical ones in *Cyclothyris globata*, and *C. grimargina* (see Tabs. 1 and 2) militates in favour of a genetic origin rather than an ecophenotypical expression. We point out that in *Cyclothyris difformis*, *C. grimargina* and *Contortithyris thermae*, this asymmetrical expression is not visible at juvenile stage and does not hit the internal hard parts of the shell, *i.e.*, the crura.

Flamant (2016) explained that some genes (hidden or particularly associated) could be at the origin of asymmetry in different organisms. In our study, the origin of asymmetry is difficult to understand due to the lack of extant asymmetrical brachiopods. This prevents genetic observations and, as a matter of fact unable us to achieve a conclusion on the probability of a modification or the "freezing" of a morphogen. Following Fürsich and Palmer (1984), our feeling in the present cases is that the expression of asymmetry, genetically based, could emerge periodically in the course of evolution of brachiopods.

Supplementary Material

Appendix A. Video of the virtual transverse serial sections of specimen MNHN.F.A59944 of *Cyclothyris difformis*. (Patricia Wils, UMS 2700).
Appendix B. Video of the virtual longitudinal serial sections of the same specimen MNHN.F.A59944 of *Cyclothyris difformis*. (Patricia Wils, UMS 2700).
Appendix C. Virtual transverse serial sections of specimen MNHN.F.A59944 of *Cyclothyris difformis*. The numbered views correspond to a selection of virtual sections among the set of images.

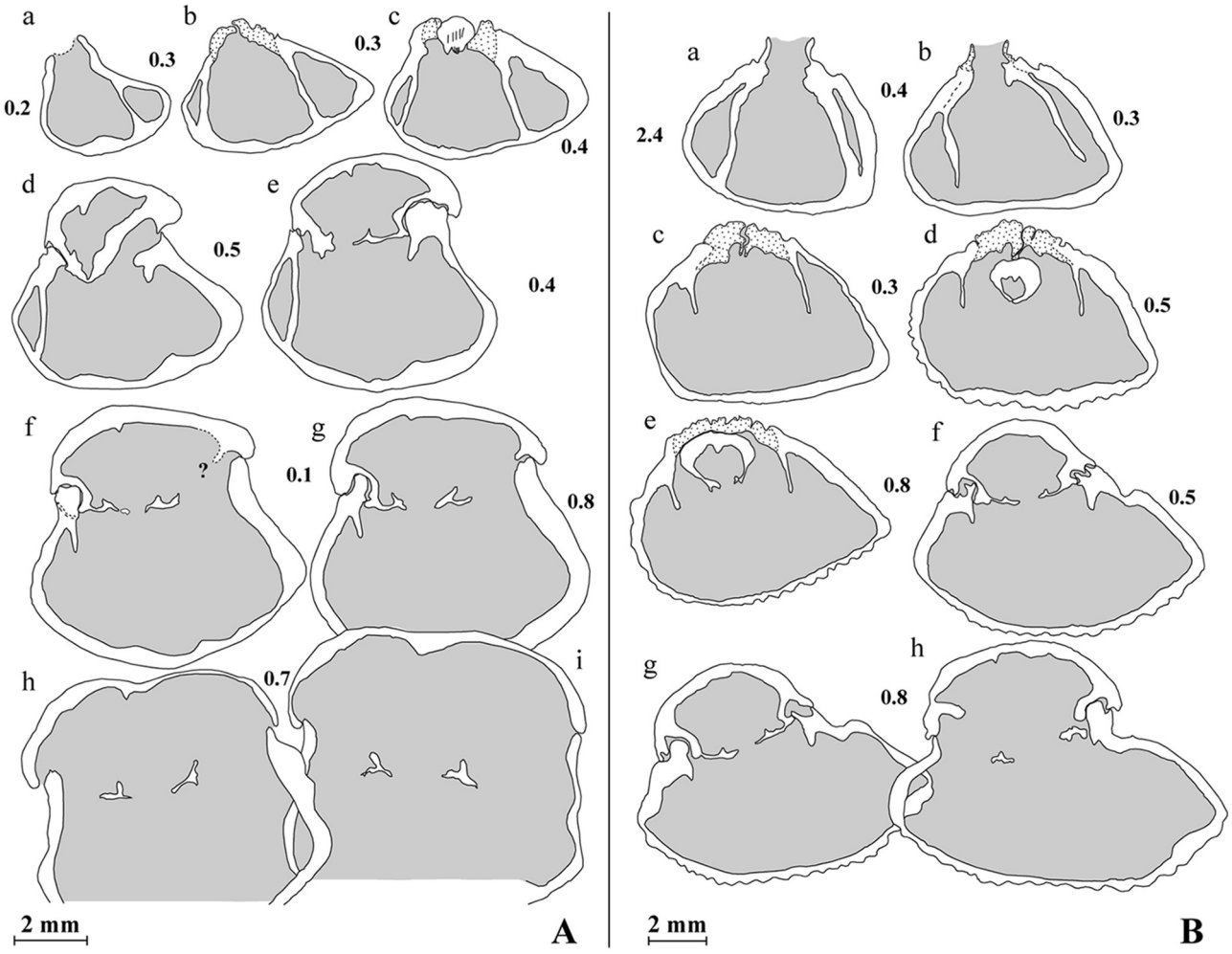

Fig. 19. Transverse serial sections from the posterior shell of specimens of *Owenirhynchia* sp. from two different layers: 127 (A, MNHN.F. A70942) and 128 (B, MNHN.F.A70943) of the Nidàguila Formation at Villamartin (Spain). Line drawings: D. Gaspard.

Appendix D. Video of the virtual transverse serial sections of paratype MNHN.F.A26502 of *Beaussetithyris asymmetrica* from La Cadière. (Patricia Wils, UMS 2700).

Appendix E. SEM views of selected transverse sections of Senonian asymmetrical rhynchonellid shells. A,B. *Beaussetithyris asymmetrica* nov. sp. from Les Martigues: details of the articulation in section (dental plates (d. pl.), hinge plates (h.pl.), teeth (t) and crus (cr) in (A), the arrowhead indicates the location of the close-up view of the crus (B). C,D. *Beaussetithyris asymmetrica* nov. sp. from Le Beausset: details of the articulation in a section, note the dental sockets (d.s), and close-up view in the right side (D) shown by the arrowhead. E–G. *Contortithyris thermae* nov. sp. from Sougraigne, details of the shell articulation in a section; close-up view of the septum (s) in a partly recrystallized shell (G).

The Supplementary Material is available at http://www.bsgf.fr/10.1051/bsgf/2019016/olm.

Taxa registration:

***Beaussetithyris*:** urn:lsid:zoobank.org:act:4E5DD696-F0A0-4B2F-834B-BA7DF0635E95
***Beaussetithyris asymmetrica*:** urn:lsid:zoobank.org:act:E057611E-0F7F-437F-925C-3F50B66D139E
***Contortithyris*:** urn:lsid:zoobank.org:act:AB1114CE-1DA0-4336-902E-40C1508EA90A
***Contortithyris thermae*:** urn:lsid:zoobank.org:act:814458A7-9B64-4F0E-ABE3-18E6B26C438C
***Cyclothyris grimargina*:** urn:lsid:zoobank.org:act:5E005E69-727F-4A67-8BB3-CDDBF3B3BD1A

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