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A new asymmetric rhynchonellide from the Cretaceous of the Eastern Prebetic (Southeastern Spain)

Un nuevo rinconélido asimétrico del Cretácico del Prebético oriental (Sureste de España)

Mélani BERROCAL-CASERO, José Francisco BAEZA-CARRATALÁ & Fernando GARCÍA JORAL

Abstract: The external and internal features and the microstructure of the asymmetric rhynchonellides from the Albian–Cenomanian (Cretaceous) transition from the Alicante Province (Eastern Prebetic, Southeastern Spain) have been herein studied. Previous authors placed these rhynchonellides in *Cyclothyris difformis*, consequently attributing an unquestionable Cenomanian age (Upper Cretaceous) to the deposits in which they appear. The long dorsally concave crura and the leptinoid pattern microstructure of the shell confirm their attribution to the genus *Cyclothyris*. However, among other diagnostic criteria (*e.g.*, ribbing pattern, relative width), *C. difformis* shows facultative type of asymmetry; while the forms studied here show obligate asymmetry. Therefore, the new species *Cyclothyris ementitum* sp. nov. is formally described, being characterized by the biconvexity of its shell, its obligate type of asymmetry and an ornamentation of around 25 ribs on each valve. Thus, the study and revision of these rhynchonellides has contributed to updating the record and distribution of the asymmetric Cretaceous rhynchonellides of the genus *Cyclothyris.* This work opens a new line of research to better understand the biostratigraphical calibration of the Cretaceous sediments from the Eastern Prebetic, and a new insight into the possible origin of the obligate asymmetry present in *C. ementitum*.

Resumen: Se han estudiado las características externas, internas y la microestructura de los rinconélidos asimétricos de la transición Albiense–Cenomaniense (Cretácico) de la Provincia de Alicante (Prebético Oriental, Sureste de España). Autores anteriores clasificaron estos rinconélidos como *Cyclothyris difformis*, atribuyendo, por tanto, una edad Cenomaniense (Cretácico Superior) a los materiales en los que aparecen. Las cruras largas y dorsalmente cóncavas, así como el patrón leptinoide de la microestructura de la concha confirman su atribución al género *Cyclothyris*. Sin embargo, entre otras características (densidad de costulación o anchura relativa), *C. difformis* muestra un tipo de asimetría facultativa, mientras que las formas aquí estudiadas presentan un tipo de asimetría obligada. Por tanto, se ha descrito la nueva especie *Cyclotyris ementitum* sp. nov., caracterizada por la biconvexidad de su concha, su tipo de asimetría obligada y por presentar alrededor de 25 costillas en cada valva. Este estudio ha contribuido a actualizar el registro y distribución de los rinconélidos asimétricos del género *Cyclothyris*. Esta investigación abre nuevas posibilidades para realizar estudios bioestratigráficos con el fin de afinar la edad de los materiales cretácicos del Prebético Oriental, así como una nueva línea de investigación para descubrir el posible origen de la asimetría obligada presente en *C. ementitum*.

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INTRODUCTION

The rhynchonellide genus *Cyclothyris* M'Coy, 1844, is well represented in the Cretaceous of Europe (*e.g.*, Owen, 1988). Nevertheless, the correct taxonomical classification, and therefore the stratigraphical range and the geographical distribution, of asymmetrical Upper Cretaceous species of *Cyclothyris* was very confusing until a few years ago, when the asymmetric forms of this genus were updated. This was the result of an intensive revision of numerous specimens of *Cyclothyris* stored in historical collections from Europe and Northern Africa (*e.g.*, d'Orbigny and Coquand Collections, among others) and also the description of new species (Berrocal-Casero, 2020; Berrocal-Casero *et al.*, 2020a, 2020b). For this previous research, it was essential to distinguish between the terms proposed by Fürsich and Palmer (1984) as 'facultative' type of asymmetry of the anterior commissure, in which the individuals of the same species can develop both symmetric and asymmetric shells [*e.g.*, the Cenomanian *Cyclothyris difformis* (Valenciennes in Lamarck, 1819)], from an 'obligate' type of asymmetry, where all individuals of the same species display asymmetric shells [*e.g.*, the Santonian–Campanian *Cyclothyris globata* (Arnaud, 1877)]. Although the systematics, distribution and questions related with the evolution of the asymmetry of the Upper Cretaceous asymmetric *Cyclothyris* were recently studied and updated, the knowledge about the asymmetric forms from the Lower Cretaceous is currently less known.

Cretaceous asymmetrical rhynchonellides from the External Betic Zones (Southeastern Spain) have been traditionally attributed to *Cyclothyris difformis* due to the presence of commissural asymmetry (Iñesta & Calzada, 1996; Iñesta, 1999; Mora-Morote, 2000). A recent revision of the Prebetic asymmetrical stock suggested that the attribution of these forms to *C. difformis* is not cogent (Berrocal-Casero *et al*., 2020b). Actually, the nominal species *C. difformis* has been commonly misinterpreted over the last several decades, as stated by previous authors (*e.g.*, Owen, 1962, 1988; Gaspard, 1997; Motchurova-Dekova, 1995, 1997; Gaspard & Charbonnier, 2020; Berrocal-Casero *et al*., 2020a, 2020b).

In this paper, asymmetric rhynchonellides from the genus *Cyclothyris* from the Albian–Cenomanian transition of the Eastern Prebetic have been studied and compared with all known asymmetric species of *Cyclothyris* (specially with *C. difformis*), leading to the definition of the new species *Cyclothyris ementitum*.

GEOLOGICAL AND GEOGRAPHICAL SETTING

Several localities in the Alicante Province, SE Spain (Fig. 1), containing asymmetrical brachiopods from the Albian–Cenomanian transition have been revised either by new sampling or from an assessment of selected literature. These localities are integrated in the Eastern Prebetic Domain (Vera *et al*., 2004) of the External Betic Zone. During the Cretaceous, the Eastern Prebetic was characterized by carbonate and mixed carbonate-siliciclastic shallow-water platform successions with environments ranging from tidal to outer platform, up to hemipelagic settings basinwards (Vilas *et al*., 2002; Vera *et al*., 2004).

Based on structural and palaeogeographical subdivisions (Arias *et al*., 2004) all the studied localities (except for the Moraig Cave; Fig. 1A) are located within the Aspe-Jijona-Alicante Domain of the Internal Prebetic (Fig. 1B). In this domain, Jurassic–Cretaceous sediments correspond to pelagic/hemipelagic marls and marly limestone sequences, mainly cropping out in anticline structures, the synclines being better represented by Paleogene–Lower Miocene deposits (Martín-Chivelet *et al*., 2002). The prevailing orientation of these structures is concurrent with the regional SW-NE Betic alignment (Vera *et al*., 2004).

Depositional environment of the asymmetrical brachiopod-bearing sediments in the Eastern Prebetic

The hemipelagic deposits from the Albian–Cenomanian transition in the Eastern Prebetic are mainly represented by monotonous successions of marl and marly carbonate alternations (Leret *et al*., 1976). A concise description of the depositional framework and lithostratigraphy of the Albian–Cenomanian transition is summarized for each locality where asymmetrical rhynchonellides are recorded in this timespan:

Casa Costera outcrop (Monforte del Cid). The southernmost occurrences of asymmetrical *Cyclothyris* in the Alicante province are included in the diverse brachiopod assemblage previously reported near Novelda village (Fig. 1), attributed to the latest Albian by Azéma (1977) and to the Cenomanian by Iñesta and Calzada (1996). They are recorded in marly sediments (about 45 m thick) with yellowish burrowed calcarenite intercalated with bioclastic limestone horizons. Towards the top of this outcrop, limestone beds become more massive and thick-bedded. Together with brachiopods, scarce echinoids are recorded, and occasional orbitolinids can be found in some sandy levels. This classical locality has almost totally disappeared today due to the uncontrolled collecting of fossils and farming activities.

Sierra del Cid outcrops (Petrer). Several outcrops are located in the Sierra del Cid, nearby Petrer village (Fig. 1). A detailed bed by bed sampling and stratigraphical analysis has been carried out in this area due to the good exposure of the sediments and the prolific brachiopods, enabling analysis of their distribution and faunal successions. Brachiopod-bearing levels in the Sierra del Cid consist of a marly succession with alternating limestone-marly limestone beds. The basal part of these outcrops is dominated by marly limestone; marls dominate the middle-upper part; and a sporadic increase in carbonate content is observed towards the top of the outcrops. These facies were deposited in an external mixed platform environment (Vera *et al*., 2004).

Palomaret-Rincón Bello outcrops (Petrer). The outcrops around Palomaret-Rincón Bello (Fig. 1) are attributed to the early? Cenomanian (Leret *et al*., 1976; Iñesta & Calzada, 1996; Mora-Morote, 2000). Asymmetrical brachiopods occur in a marl/sandy marlstone succession about 50 m thick. The record of brachiopods in sandy levels is more frequent at this locality and the sediments consist of ochre to greenish biocalcarenite with fragments of brachiopods, echinoids, scarce bivalves, crinoid ossicles, and sponge spicules. These deposits typify a platform environment with frequent terrigenous input (Leret *et al*., 1976).

SE Xixona outcrop. The occurrence of asymmetrical *Cyclothyris* in this area could only be substantiated in previous reports by Gallemí *et al*. (1997). These authors established the Albian–Cenomanian boundary

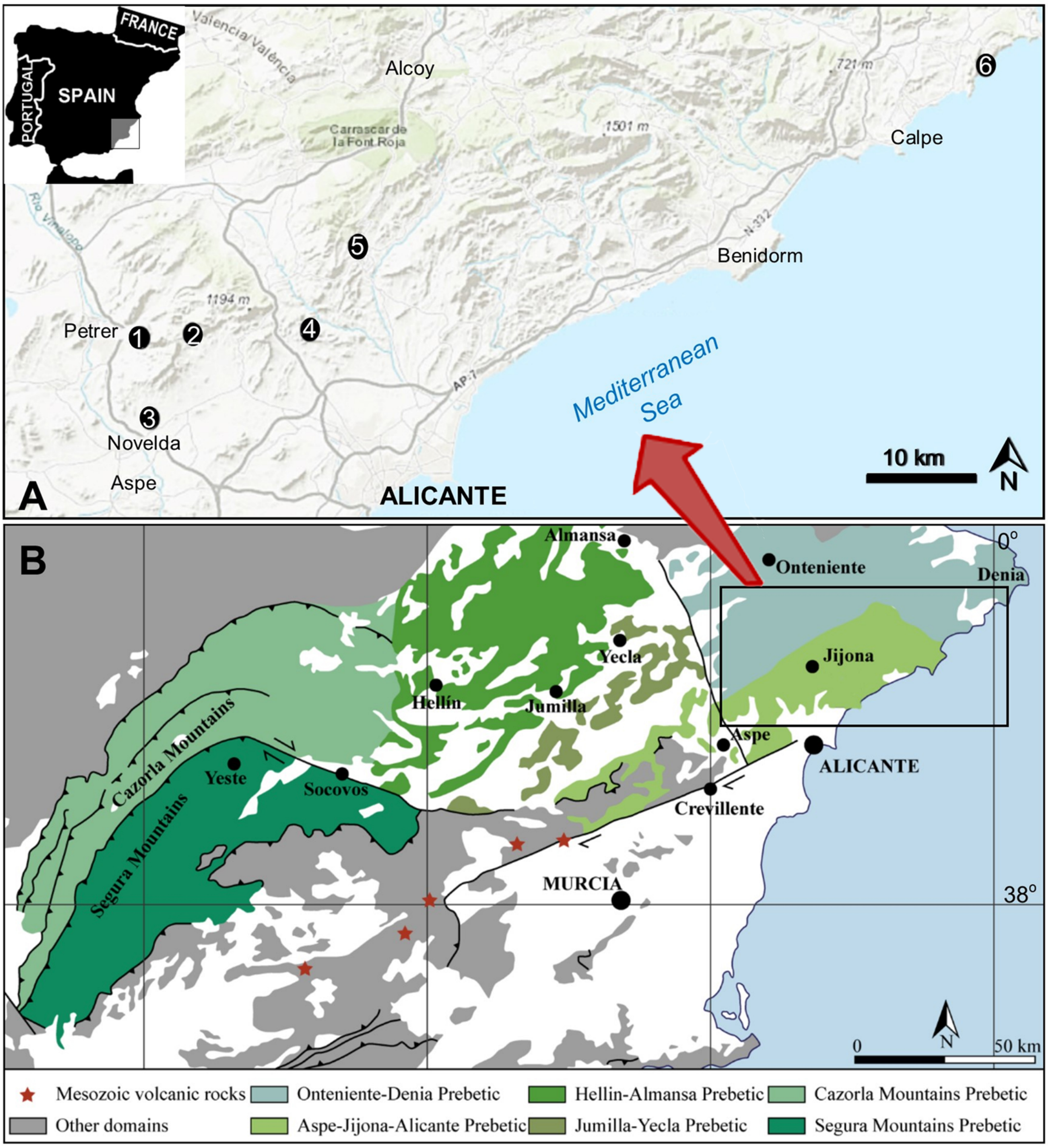

Figure 1. A, Geographical distribution of the localities where asymmetrical rhynchonellides were collected and revised: 1, Sierra del Cid, 2, El Palomaret-Rincón Bello, 3, Casa Costera, 4, Sierra del Sabinar, 5, Xixona, 6, Moraig Cave; **B,** geological framework of these localities among the different regional Prebetic domains (Eastern Betic Range).

included in an alternating yellowish marl/marly limestone unit with predominant calcareous marls. This unit starts with a basal bed with ammonites, bivalves, echinoids, brachiopods, and abundant microfauna, and, just overlying this horizon, asymmetric *Cyclothyris are* recorded in the same mainly marly succession. The depositional environment corresponds to transitional areas between external platforms and more pelagic environments.

Sierra del Sabinar outcrop (Sant Vicent del Raspeig). The Upper Albian–Lower Cenomanian facies in this area are represented by a basal marly succession with carbonate and sandstone beds intercalated; a middle part where asymmetrical *Cyclothyris* especially occurs, with predominant marl-sandy limestone levels. The uppermost sediments are represented by rhythmic intercalations of carbonate and marly levels with abundant echinoids and calcarenite beds with orbitolinids. The depositional environment is interpreted as subsiding external platform areas where shallower intratidal facies linked to horsts were developed (Leret *et al.*, 1976).

Moraig Cave outcrop (Benitatxell). Difficult access to this outcrop has not allowed the construction of a detailed lithostratigraphical framework for the occurrence of asymmetrical *Cyclothyris* from this area, as the specimens were sampled by professional divers in a submarine cave (picked up from the cave rocks) (Moraig Cave; Fig. 1). The surface lithostratigraphical units that crop out in the Sierra de Llorençà (where this site is located) correspond to the Sácaras, Jumilla, and Caliza de Jaén formations (Castro, 1998) spanning the lower Albian–Cenomanian interval. In this cave, these formations are displaced by a regional fault (Falla del Moraig) placing them in the submerged downfaulted block. Bearing in mind the regional vertical fault displacement (several hundred meters; Alfaro *et al*., 2004), the position where specimens were sampled (in a gallery 800 m from the cave entrance), and the presence of a greyish marly matrix filling the samples, it is possible that they are derived from the uppermost lithostratigraphical units (*i.e*., Late Albian–earliest Cenomanian in age) deposited in this area in open external platforms to hemipelagic environments.

MATERIAL AND METHODS

For the present research, numerous well-preserved specimens of *Cyclothyris ementitum* sp. nov. from different localities of Alicante (Eastern Prebetic, Southeastern Spain) housed at the Universidad de Alicante (**UA**) have been studied. Fieldwork to collect these specimens has been carried out mainly in the Represa Formation (Van Veen, 1969) in several outcrops such as Sierra del Cid, El Palomaret-Rincón Bello, Sierra del Sabinar, and the Moraig Cave (Fig. 1) from which the specimens herein have been collected.

Besides studying their external and internal features, these brachiopods have been compared with other Upper Cretaceous rhynchonellides. Asymmetrical representatives of *Cyclothyris* M'Coy, 1844, were examined from different European historical collections by MBC (see Berrocal-Casero *et al*., 2020a, 2020b). Specimens of *Cyclothyris* housed in the Owen Collection (1962–1988) and undescribed representatives of *Cyclothyris difformis* (Valenciennes in Lamarck, 1819) and *Cyclothyris globata* (Arnaud, 1877) were examined at the Natural History Museum (**NHM**, London, UK). Material from the d'Orbigny Collection (1847–1851) contains the types of *Cyclothyris*? *contorta* (d'Orbigny, 1847) and *Rhynchonella difformis* d'Orbigny, 1847, were reviewed at the Muséum National d'Histoire Naturelle (**MNHN,** Paris, France). Specimens of *Cyclothyris globata* (Arnaud, 1877) were examined in the Arnaud Collection at the Université Pierre et Marie Curie VI (**UPMC**, Paris, France) and in the Radulović/Motchurova-Dekova collection (Radulović & Motchurova-Dekova, 2002; Radoičić *et al*., 2010) at the Univerzitet u Beogradu, Rudarsko–Geološki Fakultet (**RGF,** Belgrade, Serbia). Additionally, *Rhynchonella claudicans* Coquand, 1879, *R. globata,* and *R. vesicularis* Coquand, 1860, were reviewed in the Coquand Collection (1860, 1862, 1879) at the Magyar Bányászati és Földtani Szolgálat (**MBFS,** Budapest, Hungary). In the Česká Geologická Služba (**CGS,** Prague, Czech Republic), the types of *Cyclothyris zahalkai* Nekvasilová, 1973 and specimens of *C*. aff. *difformis* in the Nekvasilová Collection (1973) were examined. The Natsionalen Prirodonauchen Muzey Sofia (**NPMS,** Sofia, Bulgaria) was visited to review specimens classified as *Rhynchonella compressa* Lamarck var. *difformis* d'Orbigny, 1847, from the Tzankov Collection and as *C. difformis* from the Cenomanian of Beloslav (Northeastern Bulgaria) revised by Motchurova-Dekova (1995) and included in the Jolkičev Collection (undetermined years; see Berrocal-Casero *et al*., 2020b, annex 1).

In this paper, some Cenomanian specimens of *Cyclothyris difformis* from England, housed at the Natural History Museum, belonging to the Owen Collection have been figured to make a better comparison with *C. ementitum*. Some of them comprise specimens previously figured by Owen from Le Havre, Normandy, France (the type area) (specimen NHM.BB.41433), and from the Lower Chalk of the White Hart Sandpit, Wilmington, Devon, England (specimen BB41433). Other specimens in this collection from the latter area have been figured here for the first time (reference numbers NHMBF79–NHMBF97).

The descriptive terminology applied in this paper for external and internal features follows Manceñido *et al*. (2002, 2007). Measures include: total length (**L**), total width (**W**), and total thickness (**T**) of the shell, and the height of the "step" of the frontal commissure (**SH**). The number of ribs (**R**) in each valve has also been counted. The coefficient (**C**) corresponds to the ratio R/W.

To study the internal features, serial transverse sections have been taken following the method proposed by Steward and Taylor (1965, p. 224–232), and acetate peels have been prepared. A Scanning Electron Microscope (**SEM**) examination of shell microstructure of some acetate peels has also been performed. The peels were coated with gold using a Cressington sputter coater 108 AUTO, and then examined with a SEM JEOL JSM-IT500 scanning electron microscope at the Centro de Asistencia a la Investigación of the Universidad de Alcalá (**UAH,** Madrid, Spain). The microstructure of the secondary layer of the shell has been used as an additional taxonomic criterion following Motchurova-Dekova (2001) and Manceñido and Motchurova-Dekova (2010). The thickness of the secondary layer and fibres have been measured close to the plane of symmetry. The long axis of the cross-section, parallel to the shell surface, is the width (**wf**) of the fibre. The short axis is the thickness (**tf**) of the fibre. The coefficient (**cf**) is the ratio wf/tf.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA Duméril, 1806
Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order RHYNCHONELLIDA Kuhn, 1949
Subfamily CYCLOTHYRINAE Makridin, 1955
Genus *Cyclothyris* M'Coy, 1844

Type-species. *Cyclothyris latissima* (Sowerby, 1829). Upper Aptian, United Kingdom.

Cyclothyris ementitum sp. nov.
Figures 2–3

1996 *Cyclothyris difformis* (Valenciennes in Lamarck, 1819); Iñesta & Calzada, p. 21, pl. 1, text-fig. 2.
1999 *Cyclothyris difformis* (Lamarck, 1819); Iñesta, p. 18, pl. 3, text-fig. 1.
2000 *Cyclothyris difformis* (Valenciennes in Lamarck, 1819); Mora-Morote, p. 47, pl. 1, text-fig. 2.

Etymology. From the Latin [*ementitum*]: "who utters false auspices", because of the prolific former attributions of this species to *Cyclothyris difformis* by previous authors, assigning a Cenomanian age to its occurrence.

Material and dimensions. (Figs. 2–3 and Tab. 1). 108 specimens from the Eastern Prebetic, Spain. Holotype specimen SC1003 from Sierra del Cid (Fig. 2A). Paratypes, specimens SC2001 (Fig. 2B) and SC215 (Fig. 2C) from Sierra del Cid. Specimens CM.1 (Fig. 2D) from the Moraig Cave, MU.21 (Fig. 2E), and MU.221 (Fig. 2F) from the Palomaret-Rincón Bello area, PR.Cd.1998.1 (Fig. 2G) and SA.Cd.1 (Fig. 2H) from Sierra del Sabinar outcrop. The types and serial sections are deposited in the collections of the Departamento de Ciencias de la Tierra y del Medio Ambiente, Universidad de Alicante (UA, Alicante, Spain).

Diagnosis. Medium to large-sized equibiconvex rhynchonellides. The anterior commissure is asymmetric, showing a "step" in the middle that displaces the two halves of the shell dorso-ventrally. Shell with about 25 ribs on each valve. The crura are long and of canaliform type, dorsally concave.

Description. *External morphology* (Fig. 2). Medium to large-sized (up to 30 mm in length) equibiconvex shells, with thickness about 3/4 of the length, oval to subtriangular in dorsal outline. Maximum width located in the anterior half of the shell. Maximum thickness located at midlength. The beak is erect, prominent, with a hypothyrid circular foramen (cyclothyrid foramen; *i.e.*, deltidial plates protrude into a short tube around the pedicle foramen) (Fig. 2, A4). Well-defined interarea. The lateral commissure is straight to sinuous. Shell twisted anteriorly, with asymmetrical anterior commissure showing a "step" between the two halves of the shell, that are displaced dorso-ventrally. The shell bears approximately 25 strong ribs on each valve, rounded to slightly sharp.

Internal morphology (Fig. 3). Pedicle collar well-developed (Fig. 3A, section 0.8; Fig. 3B) with thick conjunct deltidial plates. Dental plates are thin and subparallel, delimiting relatively narrow umbonal cavities (Fig. 3A, sections 1.6-2.3). Teeth massive, quadrate, crenulated and slightly recurved laterally, inserted in crenulated sockets (Fig. 3A, section 3.9, 3C). Lateral denticula and accessory sockets are well developed. The dorsal median septum is revealed as a very low ridge. The hinge plates are short, wide and slightly ventrally inclined (section at 3.7 mm from the apex) becoming subhorizontal (section at 3.9 mm). The crura are long and canaliform in type, dorsally concave (Fig. 3A, section 5.7-6.2; Fig. 3E).

Shell microstructure (Fig. 3F–3I). The secondary fibrous layer is 750 µm thick. Two main sublayers can be differentiated (Fig. 3F–3G). The thickness of the external sublayer is 302 µm thick, whereas the interior sublayer is 450 µm thick. The fibres show a rhomboidal to anvil form in cross section, being rhomboidal to anvil-like shape and more isometric towards the exterior part of the shell and mainly anvil like shaped and more anisometric towards the interior of the shell (Fig. 3G–3I). The fibres have been measured from the more isometric sublayer, being up to 40 µm wide (wf) and about 14 µm thick (tf) (cf = 2.85).

Discussion. *Cyclothyris* M'Coy, 1844 is characterized by the presence of deltidial plates completely surrounding the foramen (cyclothyrid foramen) and well-defined interarea. Regarding the internal structure, long canaliform crura with dorsal concavity are diagnostic criteria for the genus, as well as the typical low dorsal median septum and the subparallel dental plates (Owen, 1962, 1988; Manceñido *et al.*, 2002). The shell microstructure of *Cyclothyris ementitum* sp. nov. shows a leptinoid pattern of the secondary layer, linked to crura from the radulifer group (Radulović *et al.*, 2007, fig. 7; Manceñido & Motchurova-Dekova, 2010, fig. 13). Usually, several packages of fibres can be differentiated in *Cyclothyris* (Motchurova-Dekova, 2001, p. 323, fig. 2), being characterized by the presence of anisometric anvil-shaped

Table 1. *Cyclothyris ementitum* sp. nov., from the Albian–Cenomanian transition of several localities from the Alicante province (Eastern Prebetic, Spain). Holotype specimen SC1003 from Sierra del Cid. Paratypes, specimens SC2001 and SC215 from Sierra del Cid. Specimens CM.1 from the Moraig Cave, MU.21, and MU.221 from the Palomaret-Rincón Bello area, PR.Cd.1998.1 and SA.Cd.1 from Sierra del Sabinar outcrop.

Specimen	L (mm)	W (mm)	SH (mm)	R	C
SC1003	30.58	30.48	10.3	28	0.91
SC2001	30.91	30.9	6.5	28	0.90
SC215	20.69	20.62	5.8	28	1.35
CM.1	30.39	30.62	9.8	24	0.78
MU.21	20.59	20.61	3	27	1.31
MU.221	40.1	30.83	5.8	27	0.87
PR.Cd.1998.1	30.98	30.71	7.8	20	0.65
SA.Cd.1	20.59	20.61	3	27	1.31

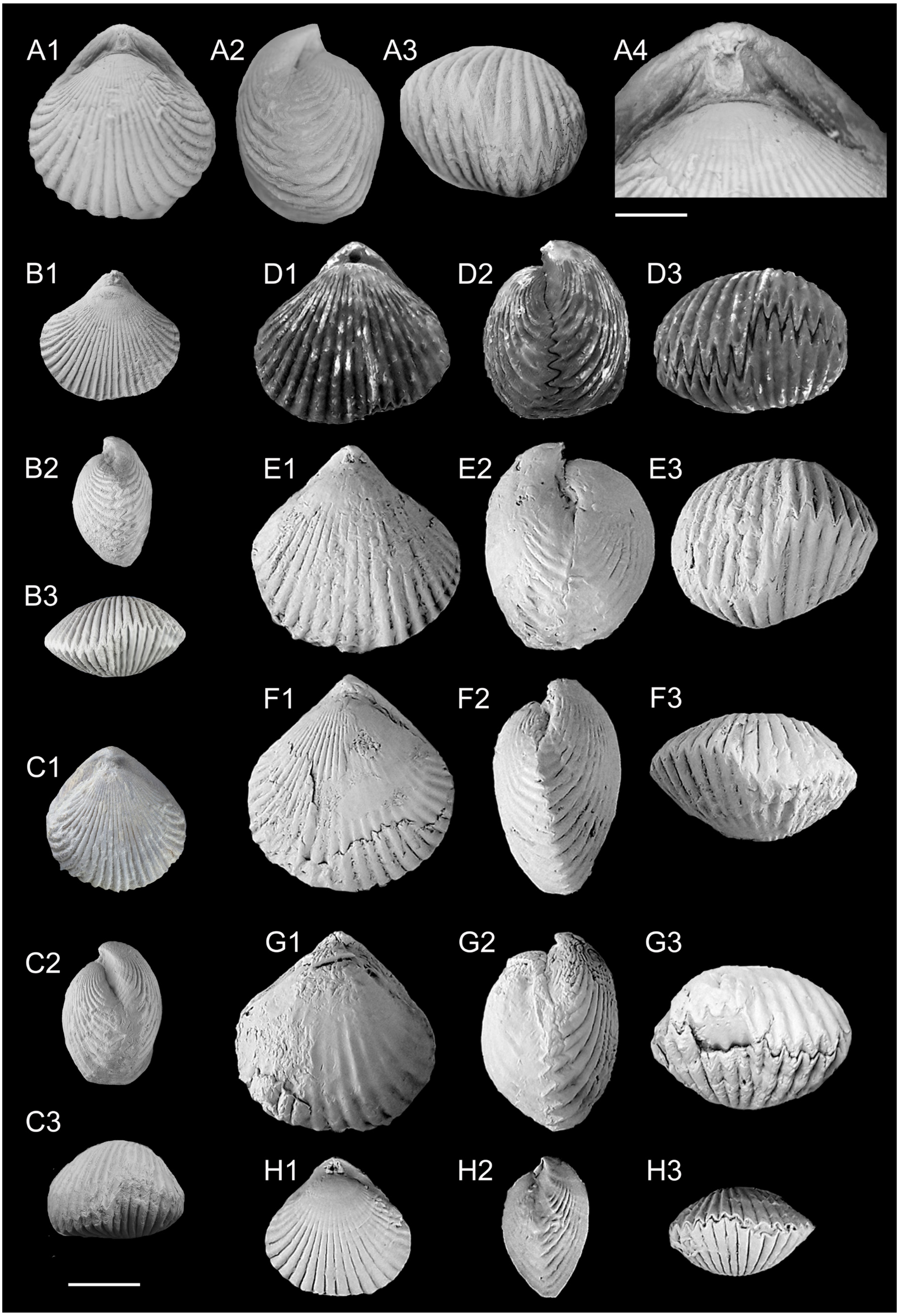

Figure 2. *Cyclothyris ementitum* sp. nov., from the Albian–Cenomanian transition of several localities from the Alicante province (Eastern Prebetic, Spain). **A,** Holotype specimen SC1003 from Sierra del Cid; **B,** paratypes, specimens SC2001; **C,** SC215 from Sierra del Cid; **D,** specimen CM.1 from the Moraig Cave; **E,** specimen MU.21; **F,** specimen MU.221 from the Palomaret-Rincón Bello area; **G,** PR.Cd.1998.1; **H,** SA.Cd.1 from Sierra del Sabinar outcrop. Numbers indicate the views: dorsal (1), lateral (2), anterior (3), detail of the foramen (4); scale bars = 1 cm, except for A4, for which the scale corresponds to 0.5 cm.

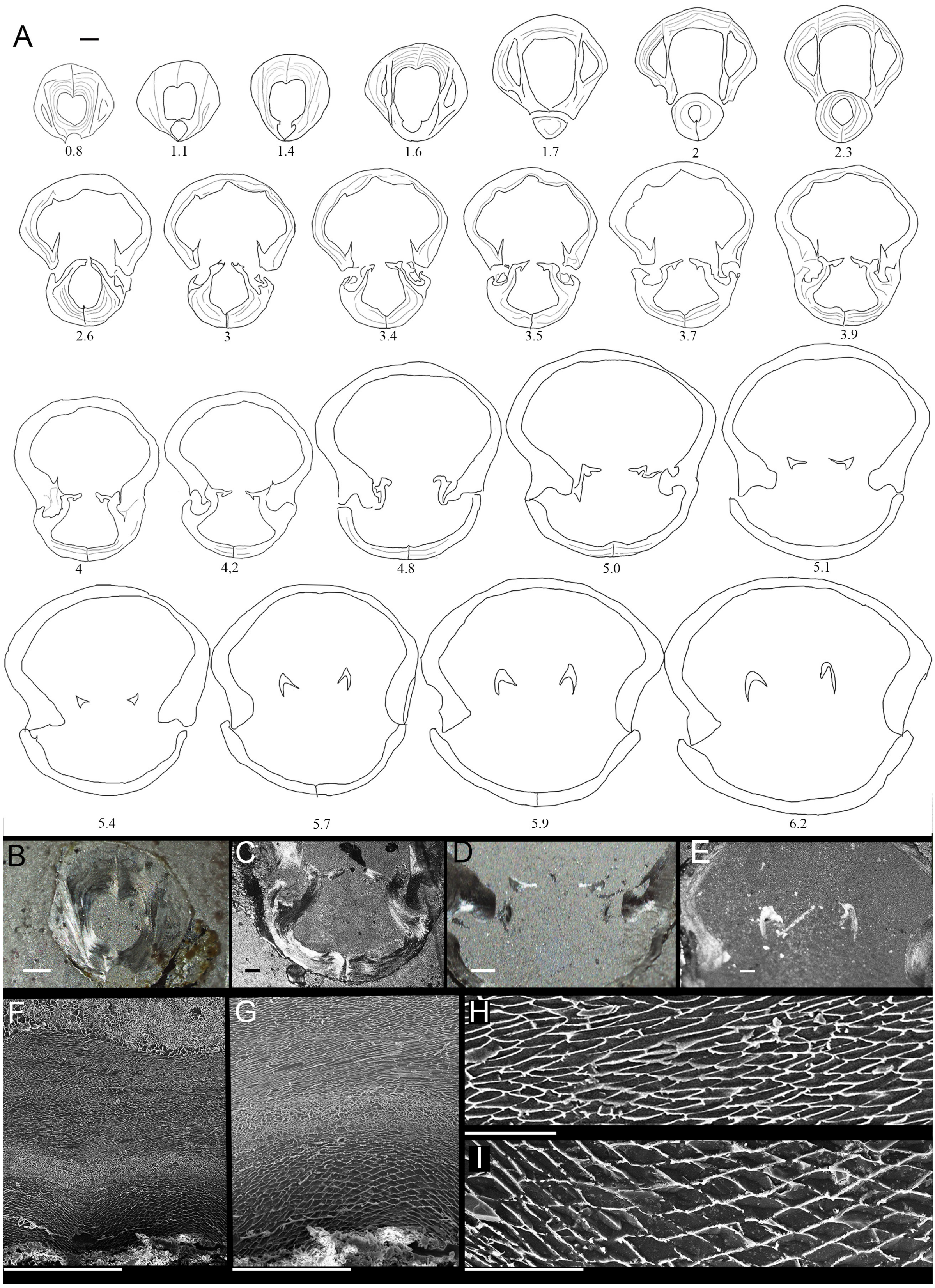

Figure 3. *Cyclothyris ementitum* sp. nov., from the Albian–Cenomanian transition of Sierra del Cid, Alicante (Eastern Prebetic, Spain). **A,** Serial sections of specimen SC1521; scale bar = 1 mm; **B,** acetate peel at 0.8 mm from the apex, in which the pedicle collar is observed; **C,** acetate peel at 3.5 mm from the apex, showing the teeth and crenulated sockets; **D,** acetate peel at 5 mm from the apex, showing the crural bases; **E,** acetate peel at 6.2 mm from the apex, showing the typical canaliform crura of *Cyclothyris*; scale bars for B–E = 1 mm; **F–I,** microstructure of the secondary layer of the shell; **F–G,** details of the secondary layer at two different magnifications, showing sublayers; **H,** detailed view of the more internal sublayer with anvil-like shaped fibres. **I,** detail of the more external sublayer with rhomboidal to anvil-like shaped fibres. Abbreviations: **sl,** secondary layer; scale bars = 500 µm for F, 100 µm for G, and 50 µm for H and I.

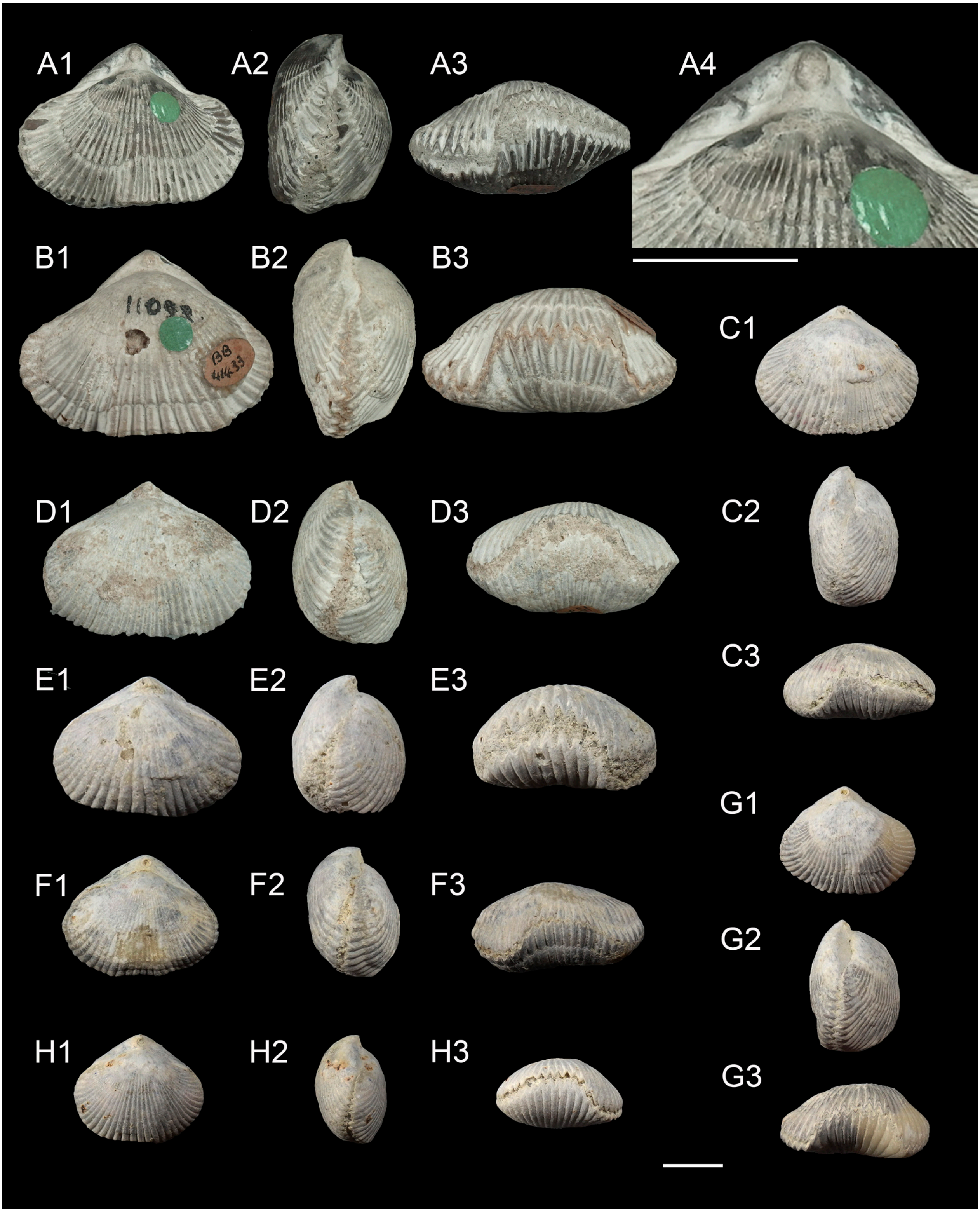

Figure 4. *Cyclothyris difformis* (Valenciennes in Lamarck, 1819) from the Cenomanian of France and United Kingdom. **A,** Specimen NHM.BB.41433, from Le Havre, Normandy, France; **B,** specimens NHM.BB41433; **C,** NHMBF96; **D,** NHM.BB15294; **E,** NHMBF97; **F,** NHMBF79; **G,** NHMBF80; **H,** NHMBF81 from Wilmington, Devon, United Kingdom. Views: (1) dorsal view; (2) lateral view; (3) anterior view; (4) detail of the foramen; scale bars = 1 cm.

(to rarely rhomboidal) fibres (Motchurova-Dekova, 2001, p. 327, tab. 1). Therefore, microstructural analysis performed in *C. ementitum* appropriately corresponds to the typical *Cyclothyris* shell microstructure.

Cyclothyris ementitum sp. nov. is similar to *Cyclothyris regularis* (Leymerie, 1869), from the Lower Cretaceous of Southeastern France, since both species show asymmetry on their anterior commissure, but the type of asymmetry in *C. regularis* is facultative (only some specimens from the same species show asymmetry), while *C. ementitum* shows obligate asymmetry (all specimens from the same species are asymmetrical). The holotype of *C. regularis* (Leymerie, 1869, p. 315, pl. 3, fig. 6a, 6b), labeled as specimen MHNT.PAL.2017.0.10 from Vimport, Pech de Foix, nord (Ph. Fauré, pers. commun., 2022) is wider, and shows a much greater number of ribs on each valve (45) if compared to *C. ementitum. Cyclothyris parvula* (Leymerie, 1869) can be included as a constituent of this asymmetrical stock and regarded as synonym of *C. regularis* (Ph. Fauré, pers. commun., 2022). Viera and Calzada (1991) figured asymmetric rhynchonellides classified as *C. regularis* from the Lower Albian of Aitzgorri Massif (Guipuzcoa, Northern Spain). Although is not clear if these specimens show facultative or obligate asymmetry, they show 50 ribs, differing considerably form *C. ementitum* in showing double number of ribs.

The new species *C. ementitum* has been customarily assigned to *Cyclothyris difformis* (Valenciennes in Lamarck, 1819) in the Prebetic Domain (Iñesta & Calzada, 1996; Iñesta, 1999; Mora-Morote, 2000). Nevertheless, a recent revision of the Upper Cretaceous asymmetric rhynchonellides questioned this (Berrocal-Casero *et al.*, 2020b). If compared to *C. difformis* (Fig. 4) from the Cenomanian of England and northwestern France, the Prebetic rhynchonellides are more biconvex, significantly less wide; the variability of their anterior commissure does not correspond to the asymmetry pattern of *C. difformis* (obligate asymmetry in *C. ementitum vs* facultative asymmetry in *C. difformis*) and their shell is ornamented with a considerably lower number of ribs (about 25 ribs in *C. ementitum* and 40 in *C. difformis*) (Figs. 2 and 4).

According to Iñesta and Calzada (1996), these asymmetrical forms from Alicante are very similar in number of ribs to the specimen NHMB–M.61466 (*Cyclothyris dimidiata* = *Cyclothyris difformis*) figured by Owen (1962; pl. 4, fig. 2a–2c) and classified as an extreme variant of *C. difformis* or a pathological form. In this sense, the validity of the species *C. dimidiata*, included in the synonymy of *C. difformis* by Owen (1962), was discussed by Iñesta and Calzada (1996), considering a possible attribution to it of the asymmetric specimens from Alicante. However, *C. dimidiata* is represented by just one specimen from the Cenomanian of Halldown, South-east Devon, a locality where *C. difformis* has been intensively collected and studied (Owen, 1988). A revision of the material of *C. difformis* housed at the NHM including hundreds of specimens of *C. difformis* from Devon (specimens labelled NHMBF79 to NHMBF97 and NHM.B.AQPAL2016110.1; see Berrocal-Casero *et al.*, 2020b, annex 1) led to conclude that *C. dimidiata* is an extreme variant among the high intraspecific variability of *C. difformis*. Additionally, there are no reports of brachiopods with obligate asymmetry in the Cretaceous of the United Kingdom, so in any case, *C. ementitum* cannot be related to any known British asymmetric species.

The specimens from the lower Cenomanian of Iran classified as *C. difformis* by Arab (2010) and Binazadeh (2017) show the shell surface ornamented with 20–25 costae on each valve. Since the number of ribs is an important feature of the species, its attribution to *C. difformis* is questionable (see Berrocal-Casero *et al.*, 2020b). This discrepancy has also been noted by Binazadeh (*op. cit.*). These asymmetric *Cyclothyris* from Iran are similar to *C. ementitum* in the number of ribs; however, the forms from Iran show facultative asymmetry (see Binazadeh, 2017, p. 341) and their shell is less globose.

Cyclothyris ementitum also differs from *Cyclothyris nekvasilovae* (Berrocal-Casero *et al.*, 2020b, fig. 2d–2f), from the Cenomanian of Prédboj, Czech Republic, from *Cyclothyris zahalkai* Nekvasilova, 1973, from the Turonian of the Czech Republic (Nekvasilová, 1973, figs. 17, 18, 20a–20b, 20d, 21e; pl. 5, figs. 1–2; pl. 7, figs. 3–4; pl. 11, figs. 1–4; pl. 5, fig. 1; Berrocal-Casero *et al.*, 2020b, fig. 2j–2o); and from *Cyclothyris claudicans* (Coquand, 1879), from the Santonian of La Cadiére, France (Coquand, 1879, p. 214; Berrocal-Casero *et al.*, 2020b, fig. 2v–2x), mainly because these three species show facultative asymmetry.

Concerning other Upper Cretaceous *Cyclothyris* with obligate type of asymmetry [*Cyclothyris cardiatelia* Berrocal-Casero, 2020, from the Coniacian of Northern Spain; *Cyclothyris globata* (Arnaud, 1877) from the basal Campanian of Southwestern France; and *Cyclothyris vesicularis* (Coquand, 1879), from the upper Campanian of France], all of them are different in age and show clear differences when compared to *C. ementitum.* In *Cyclothyris cardiatelia*, the anterior commissure shows a “step” dividing the shell into two unequally developed lobes, one larger than the other, and the beak is usually hooked towards the lobe of shorter length (Berrocal-Casero *et al.*, 2020a, figs. 9–10; 2020b, figs. 2s–2u). *Cyclothyris globata* is considerably smaller than *C. ementitum*, with a characteristic globose shell showing a more convex dorsal valve than the ventral one, and the lateral commissure has a well-developed squama–glotta (Arnaud, 1877, p. 83, pl. 8, figs. 33–38; Berrocal-Casero *et al.*, 2020b, fig. 2y–2d’). Finally, *Cyclothyris vesicularis* is much wider than *C. ementitum* and it shows two well-differentiated lobes, considerably staggered, with a characteristic ‘S’-shaped anterior commissure and ornamentation consisting of 50–70 very fine ribs (Coquand, 1860, p. 122; Berrocal-Casero *et al.*, 2020b, fig. 2e’–2j’).

Occurrence. Uppermost Albian–lowermost Cenomanian of the Eastern Prebetic (Southeastern Spain). Most of the specimens have been recorded in the Represa Formation (Van Veen, 1969) from the Sierra del Cid (Alicante), considered the type-locality for the new erected species.

LINKING THE *CYCLOTHYRIS DIFFORMIS* ATTRIBUTIONS TO THE BIOSTRATIGRAPHICAL APPROACH OF THE *C. EMENTITUM*-BEARING DEPOSITS

The genus *Cyclothyris* was erected by M'Coy (1844); subsequently Buckmann (1906) designated *Terebratula latissima* (Sowerby, 1829) as the type species of the genus. Several Cretaceous asymmetrical species have been placed into this genus, which is frequently reported from European basins, but with controversial taxonomic attributions. The correct taxonomic classification, and therefore the stratigraphical range and the geographical distribution of the asymmetrical species of *Cyclothyris* were widely discussed (*e.g.*, Muñoz, 1985, 1994; Gaspard, 1991; Motchurova-Dekova, 1995, 1997; Radulović & Motchurova-Dekova, 2002; Radoičić *et al*., 2010; Berrocal-Casero *et al*., 2017, 2020a, 2020b). Among them, *C. difformis* is probably the most prolific taxon. It was first defined by Valenciennes in Lamarck (1819) as *Terebratula difformis* from a picture selected from the "*Tableau Encyclopédique et Méthodique*" (Bonnaterre, 1789, p. 131, pl. 242, fig. 5), ascribed to the Cenomanian but with unspecified origin.

Since then, recurrent ambiguity in attributions to *R. difformis* proliferated. D'Orbigny (1851, pl. 498, figs. 6–9) arranged into this species the Santonian material from La Cadiére (SE-France) whereas Coquand (1879) considered these specimens synonymous with the Santonian *R. claudicans* from Argelia. Subsequently, *Rh. difformis* was reported in the Coniacian–Santonian from France (Péron, 1877; Toucas, 1886). Fage (1935) went even farther in considering most of the Late Cretaceous asymmetrical rhynchonellides as varieties of *R. difformis* (*R. difformis* var. *globata*; var. *rudis*; var. *vesicularis;* var. *lamarckiana*).

In this confusing taxonomic context, Owen (1962, 1988) studying the British *Cyclothyris*, re-established the original concept of the species, both from the systematic and biostratigraphic perspectives and excluded from *C. difformis* all the previously reported non-Cenomanian records, constraining its distribution range to the lower-middle Cenomanian and selected as lectotype of *C. difformis* the specimen deposited in the Lamarck Collection figured by Clerc and Favre (1918, pl. 15, fig. 84a–84d) from the lower Cenomanian of Le Havre (Normandy).

Since the erection of the lectotype, the Cenomanian condition of *C. difformis* was conventionally accepted. Thus, Nekvasilová (1973) reported *Cyclothyris* aff. *difformis* in the Cenomanian from Bohemia; Gaspard (1985) assigned some Cenomanian forms from Aquitaine to *C. difformis,* also suggesting the distinction of the Coniacian asymmetrical forms previously considered as *Rhynchonella difformis* from the true-*difformis* Cenomanian species (Gaspard, 1991); Motchurova-Dekova (1995) analyzed the genus *Cyclothyris* in the Late Cretaceous from Bulgaria, constricting *C. difformis* to the Cenomanian as well. Recently, Gaspard and Charbonnier (2020) adhered to the same standpoint in several records from Normandy and some other Western European localities.

In her PhD Thesis, one of the authors of this work (MBC) revised the stock of *Cyclothyris difformis* housed in the Natural History Museum (London, UK) as well as all taxa of Upper Cretaceous asymmetric *Cyclothyris* from Europe and Northern Africa housed at different European institutions (see "Materials and Methods" section in the present paper and Berrocal-Casero, 2020; Berrocal-Casero *et al*., 2020a; 2020b). This examination concluded that the Prebetic material differs from the British Cenomanian *C. difformis* in being more biconvex and a considerably narrower form, in the obligate type of asymmetry and in the lower number of ribs, therefore substantiating that a rhynchonellide asymmetrical stock separate from *C. difformis* occurs in the Prebetic area.

The deposits in which *C. ementitum* was found were formerly assigned to the Cenomanian because of the attribution of this asymmetric form to *C. difformis* (*e.g.*, Iñesta & Calzada, 1996), while regional data from several localities led some authors to place these deposits in the Albian–Cenomanian transition (see above). Thus, to date, it can be concluded that the Albian–Cenomanian transition is the chronostratigraphical range for *C. ementitum*. A review of more accurate biostratigraphical markers from these outcrops is necessary in order to update more precisely the stratigraphical range from which this form is recorded. With this intent ongoing research to study the faunal assemblages occurring with *C. ementitum* is in progress.

CYCLOTHYRIS EMENTITUM AND THE OBLIGATE TYPE OF ASYMMETRY

Reviewing the data about the asymmetry in the genus *Cyclothyris*, a hypothesis about the functional meaning of the asymmetry in the Coniacian (Upper Cretaceous) *Cyclothyris cardiatelia* Berrocal-Casero, 2020, from the Northern Castilian Platform has been proposed by Berrocal-Casero *et al*. (2017). This hypothesis was based on palaeoenvironmental and taphonomical observations suggesting that this species lay inclined in life position, partially buried, as a consequence of an important increase in fine detritic sediment inputs on the platform which made the substrate much softer. Taphonomical and palaeoenvironmental evidences support this hypothesis (see Berrocal-Casero *et al*. 2017, fig. 13; Berrocal-Casero *et al*., 2022).

Berrocal-Casero *et al*. (2020b) proposed another hypothesis concerning the origin of obligate asymmetry in Upper Cretaceous *Cyclothyris* from Europe. These authors suggested that the facultative asymmetry of some species with phenotypic plasticity (such as *Cyclothyris segurai*) could have been fixed by adaptation in succeeding species (such as *C. cardiatelia*) and then genetically assimilated to become obligate asymmetry. Thus, other subsequent species possibly related to *C. cardiatelia*, such as *C. globata* and *C. vesicularis,* which may occur in various different facies, would maintain the obligate asymmetry even in palaeoenvironmental conditions differing from those that induced the adaptive change (Berrocal-Casero *et al*., 2020b, fig. 6). This constitutes, for the moment, the single scenario in which a group with facultative commissural asymmetry could have evolved into taxa with obligate asymmetry.

At this point, the question is: can these hypotheses be applied to the asymmetric *C*. *ementitum* from the Eastern Prebetic? *C*. *ementitum* shows obligate type of asymmetry, being possibly the oldest known *Cyclothyris* showing this feature, but there is no information about possible precursors of this species adapted to a specific palaeoenvironment or circumstance that could induce the change leading to the asymmetry. Although the palaeoenvironment in the previously mentioned scenario and those that induced the asymmetry in *C*. *ementitum* precursors were different, the physiological response may have been common in both cases, related to the origin of the asymmetry. According to Berrocal-Casero and García Joral (2023), starting from the morphogenetic plasticity of the anterior commissure present in some lineages of rhynchonellides, different palaeoenviromental factors could lead the lophophore to works in an asymmetric way because the water currents enter in the shell preferentially by only one of the two sides. This could have occurred in response to limitations in vital space for living in closely packed clusters; to prevailing or unidirectional currents as usual in reefal or para-reefal environments; and/or to living on soft substrates. The common physiological response in these different scenarios seems to be the differential growth of the lophophore arms, which can lead to external asymmetry. The selection by adaptation of this asymmetry and its genetic assimilation would suppose the fixation of this trait giving rise to the obligate type of asymmetry, which could appear even when the palaeoenvironmental conditions are different to those that induced the adaptation (Berrocal-Casero *et al*., 2020b, Berrocal-Casero & García Joral, 2023, fig. 7). It will be necessary to study further cases with a continuous record of facultative and obligate asymmetric rhynchonellides in the same phyletic line to confirm this process. Currently, only one of these scenarios is documented (Berrocal-Casero *et al*., 2020b). Following on from this new research is focusing on the reconstruction of the phylogeny of Lower Cretaceous asymmetric *Cyclothyris* (Fig. 5).

CONCLUSIONS

The study of Albian–Cenomanian (Cretaceous) asymmetric rhynchonellides from several localities from the Alicante province (Southeastern Spain, Eastern Prebetic), formerly classified by previous authors as *Cyclothyris difformis*, has allowed to reassign them to the new species *Cyclothyris ementitum,* formally described in the present work. The diagnostic criteria of this new species are the biconvexity of the shell, its obligate type of asymmetry (commissural asymmetry), shell ornamented with about 25 strong ribs, and the presence of long and dorsally concave crura. *C. ementitum* is, so far, endemic to South-eastern Spain. This study allows

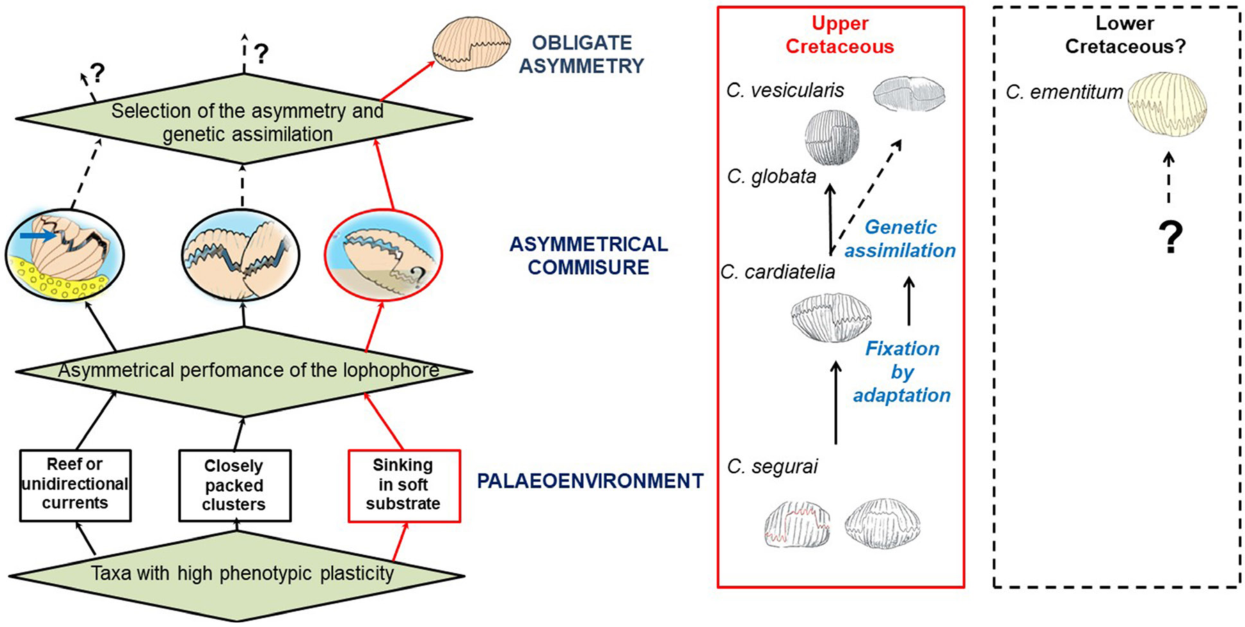

Figure 5. On the left, proposed scheme for the evolution of commissural asymmetry in rhynchonellides (modified from Berrocal-Casero & García Joral, 2023). On the right, in the red rectangle is shown the proposed evolution of commissural asymmetry in Upper Cretaceous (Coniacian–Campanian) *Cyclothyris* (modified from Berrocal-Casero *et al*., 2020b). *C*. *ementitum* (black discontinuous rectangle) possibly corresponds to the last stage of this evolution in the Lower Cretaceous, but earlier forms that would have played an equivalent role to *C. segurai* or *C. cardiatelia* are still unknown.

to update and refine the taxonomy and distribution of Cretaceous asymmetric *Cyclothyris* and remove some of the confusion surrounding these forms.

Previous misidentifications of *Cyclothyris ementitum* as *C. difformis* resulted in dating the outcrops in which the newly recognized species occurred as Cenomanian. In this regard, it is necessary to review the stratigraphy and faunal assemblages of the classical localities in which *C. difformis* has been recorded, to accurately elucidate the biostratigraphical range of this taxon and associated brachiopod assemblages. *C. emmentitum* is preliminarily attributed in this work to the Albian–Cenomanian transition.

This study has revealed that obligate asymmetry has occurred several times along the Cretaceous in the genus *Cyclothyris*. The new species here described could constitute one of the oldest *Cyclothyris* with this type of asymmetry recorded to date, also opening a new research line looking for its possible precursors and the possible scenarios who leaded to this asymmetry.

Supplementary material. New taxonomic name proposed in this paper has been registered in Zoobank, the online registration system for the ICZN: https://zoobank.org/References/B119EB42-C240-4C2D-B2C5-9EEB12624E14

Author contributions. MB-C carried out fieldwork, prepared and studied the material, both external and internal features (by preparing serial sections and acetate peels), as well as the microstructure (SEM), compared with material reviewed in her Thesis from other institutions from Europe, wrote the original draft and made Figs. 2–5. JFB–C realized previous fieldwork in the outcrops mentioned and directed the present and preliminary studies in the area, collecting some of the brachiopods. He carried out fieldwork in Sierra del Cid with MB–C and FGJ and contributed to the design and implementation of the research. He provided material from the University of Alicante from different localities and prepared material, preparing also some specimens in Fig. 2, wrote the geological and geographical context, and prepared Fig. 1, the biostratigraphical approach, provided bibliography and reviewed and improved the rest of the original draft. FGJ contributed to the design and implementation of the research, carried out fieldwork in Sierra del Cid, contributed to the preparation of specimens, contributed with his knowledge on asymmetric *Cyclothyris* and reviewed and supervised the manuscript.

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