

Brachiopods from the Albian–Cenomanian transition (Cretaceous) of the Eastern Prebetic (South-Iberian paleomargin)

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ARTICLE INFO

Article history:

Received 13 January 2023

Received in revised form

16 May 2023

Accepted in revised form 16 May 2023

Available online 31 May 2023

Keywords:

Cretaceous
Western Tethys
Cyclothyris
Sellithyris
Psilothyris
Biostratigraphy
Systematics

ABSTRACT

Brachiopod communities in the Albian–Cenomanian transition from the Eastern Betic Ranges were previously accredited and frequently considered as biochronostratigraphical tools to dating the hemipelagic successions of this timespan by correlation with other neighboring Tethyan basins. However, the knowledge of these mid-Cretaceous assemblages in this part of the South-Iberian paleomargin remained poorly understood so far. Brachiopod communities of this timespan are commonly dominated by homeomorphic terebratulides and asymmetrical multicostate rhynchonellides, these later recurrently attributed to *Cyclothyris difformis* due to the strong external similarity with their NW-European counterparts, and consequently, the Prebetic deposits were customarily assigned to the Cenomanian stage. In this work, the detailed analysis of the assemblages from the taxonomic and biostratigraphical standpoints allows for the identification of a new brachiopod fauna endemic to the Eastern Prebetic Domain, inhabiting platform environments with frequent terrigenous inputs in transition to the more offshore areas. This analysis has led to the formal description of two new species, *Cyclothyris bitrtrica* and *Sellithyris binalubensis*, together with *Cyclothyris ementitum*, recently erected as new species, plus *Psilothyris hispanica*, both endemic to the Prebetic area as well. The successive faunal replacement between two defined assemblages enclosing this fauna is a useful regional biomarker around the Albian–Cenomanian boundary. The bioevents typifying this turnover consist of a rhynchonellide taxa short-term replacement and the burst on diversity and abundance of smooth, nearly homomorphic terebratulides for the levels just underlying the base of the Cenomanian stage.

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1. Introduction

Brachiopod assemblages are widely recorded virtually in all Cretaceous stages from the Eastern Betic Ranges, especially in the Lower Cretaceous successions from the Prebetic and Subbetic domains (e.g. Jiménez de Cisneros, 1907, 1917; Calzada, 1975, 1985, 1988; Sulser and Calzada, 1991; Company et al., 1998; Iñesta, 1999; García-Ramos, 2005, 2009). They often coexist together with profuse ammonite faunas, thus facilitating calibration of the chronostratigraphical scales.

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Special mention should be made to the mid-Cretaceous brachiopod communities from this part of the South-Iberian paleomargin. The cartographical splitting and biochronostratigraphical dating of the hemipelagic successions from the Albian–Cenomanian transition are usually challenging topics mainly in the Prebetic domain due to the monotonous and homogeneous lithostratigraphy of the outcrops, generally made up of marly/marly carbonate facies (Leret et al., 1976) often with scarcity of micro and macrofauna. Thus, brachiopod assemblages frequently constitute the only biostratigraphic marker macrofauna for these Albian–Cenomanian monotonous successions.

The knowledge of mid-Cretaceous brachiopod communities in terms of abundance and diversity and their faunal succession is also globally crucial due to their occurrence prior to the Ce–Tu episode of biodiversity declining (= Bonarelli event), one of the most important ecological crisis worldwide in the Mesozoic,

implying extinction or significant turnovers of the entire marine biota (Harries and Kauffman, 1990; Kauffman and Hart, 1996; Harries and Little, 1999; Wang et al., 2003; Parente et al., 2008; Monnet, 2009; Elderbak et al., 2014; Reolid et al., 2015; Freymueller et al., 2019; Rodríguez-Tovar et al., 2020). The better understanding of the pre-existent brachiopods stock is essential to infer possible biotic responses of this group to the Ce–Tu event and can shed light on the diversity dynamics prior to this severe ecological disruption which seems to be subdued in magnitude for the brachiopod fauna (cf. Harries and Little, 1999; cf. Baeza-Carratalá and García Joral, 2020). Thus, the expanded sequences worked out in the Eastern Prebetic allow typifying the brachiopod faunal successions and their critical replacement events earlier in the late Albian–Cenomanian, analyzing the compositional structure of the assemblages.

In this context, brachiopod communities of this timespan are commonly dominated by homeomorphic terebratulides and asymmetrical multicostate rhynchonellides. The strongly differentiated morphology of this last group together with their conspicuous record in the South-Iberian paleomargin make these assemblages useful elements of correlation, being a potential tool as regional biostratigraphical markers around the Albian–Cenomanian boundary.

Cretaceous asymmetrical rhynchonellides from the External Betic Zones were attributed to *Cyclothyris difformis* (Valenciennes in Lamarck, 1819) due to the strong external similarity mainly with their British and French counterparts, and consequently, the Prebetic deposits where these morphotypes were recorded were customarily assigned to the Cenomanian. These Cenomanian occurrences of this taxon could be partially verified in several classical localities (Iñesta and Calzada, 1996; Gallemí et al., 1997; Mora-Morote, 2000), but a preliminary revision of this Prebetic asymmetrical stock (Berrocal-Casero, 2020; Berrocal-Casero et al., 2020b) suggested that the attribution to *C. difformis* was not cogent, and consequently these forms have been recently revised and assigned to the new species *Cyclothyris ementitum* (Berrocal-Casero et al., 2023).

In this work, new records of brachiopod assemblages from different Prebetic localities around the Albian–Cenomanian transition allow for the accurate determination and formal description in the light of the new taxonomic currents of the brachiopod assemblages, enabling to suggest diagnostic criteria and formally erecting new coexisting taxa, presumably endemic to the Prebetic basins. Additionally, the depositional environments of the entire assemblages are appraised, with special emphasis on the role of faunal turnovers as potential biostratigraphic markers, reviewing previous attributions of the asymmetrical rhynchonellides in the Prebetic Domain as well.

2. Geologic and geographic framework

Several localities in the Alicante province, SE Spain (Fig. 1), containing brachiopods from the Albian–Cenomanian transition have been revised either by new samplings or from the available faunal data from previous reliable selected literature.

The studied region is integrated in the Eastern Prebetic Domain (Vera et al., 2004) of the External Betic Zone, where the Mesozoic sedimentary rocks are part of the South-Iberian Paleomargin located in the Western Tethys Ocean. During the Cretaceous, the Eastern Prebetic was characterized by carbonate and mixed carbonate-siliciclastic shallow platform successions with environments ranging from tidal to outer platform, up to hemipelagic settings basinwards (Vilas et al., 2002; Vera et al., 2004).

Structural and paleogeographical subdivisions (Arias et al., 2004) allow for allocating all the studied localities (except for the Moraig Cave, Fig. 1A) in the Internal Prebetic from the Aspe–Jijona-Alicante Domain (Fig. 1B), where the Jurassic–Cretaceous sediments correspond to pelagic/hemipelagic marls and marly limestone sequences, mainly cropped out in anticline structures, being the synclines better represented by Paleogene–lower Miocene deposits (Martín-Chivelet et al., 2002). Prevailing orientations of these structures are concurrent with the regional SW–NE Betic alignment (Vera et al., 2004), except for rare areas with anomalous N–S orientation.

The Mesozoic syndepositional tectonics originated a complex horst/graben system leading to a variety of depositional settings, from carbonate shallow platforms to external platforms and pelagic environments (Martín-Chivelet et al., 2002; Vera et al., 2004). Only the westernmost locality (Moraig Cave) is incorporated in the Prebetic from the Onteniente–Denia Domain (Fig. 1B) with more complex tectonics and with frequent open marine, even pelagic, Cretaceous sedimentation.

3. Material and methods

A total number of 569 well-preserved brachiopods were analyzed. Most of them were newly collected bed-by-bed in the expanded and continuous deposits of the Sierra del Cid area. Additionally, the analysis was supplemented by asymmetrical rhynchonellide specimens sampled over the last decades in several Prebetic localities (outcrops 2, 4, and 6 in Fig. 1) and from the available faunal data from previous reliable selected literature (outcrops 3 and 5 in Fig. 1). The sampled specimens are deposited at the Earth and Environmental Sciences Department at the University of Alicante (DCTMA). The ammonoid chronostratigraphical zonal scheme is based on the standard biozonation proposed by Reboulet et al. (2018) for the Mediterranean province.

The descriptive terminology applied in this paper for external and internal features follows Manceñido et al. (2002, 2007) and Lee and Smirnova (2006). For the morphometric analysis, the main biometric parameters (L, W, T; i.e. respectively, length, width, and thickness) and indices were measured. Additional representative external biometric attributes were selected and measured when necessary to better assess possible intraspecific variability. In such a case, Bivariate Analysis considering the most representative variables was conducted together with Principal Components Analysis (PCA) as an exploratory method for variable reduction (Hammer and Harper, 2006). These analyses were carried out by means of the PAleontological Statistics (PAST) package (Hammer et al., 2001).

The internal structure was studied using the conventional method of preparing oriented transverse serial sections and taking acetate peels. The distance between serial sections was 0.1 mm. In the terebratulide taxa, given their intraspecific variability and their high homomorphism, it has been preferred to perform serial sections in the different morphotypes of each taxon. High resolution microphotographs of acetate peels were taken under an optical microscope. The obtained peels are deposited in DCTMA (Alicante) and DPUCM (Madrid) repositories. Whenever possible, specimens were coated with magnesium oxide prior to photographing.

Asymmetrical representatives of *Cyclothyris* M'Coy, 1844 were examined at different European historical collections by MBC (see revised repositories in Berrocal-Casero et al., 2017, Berrocal-Casero et al., 2020a, Berrocal-Casero et al., 2020b). Referring terebratulides, the neotype of *Sellithyris cenomanensis* Gaspard, 1982 (specimen MNHN.FA50555), as well as figured specimens of “*Terebratulata*

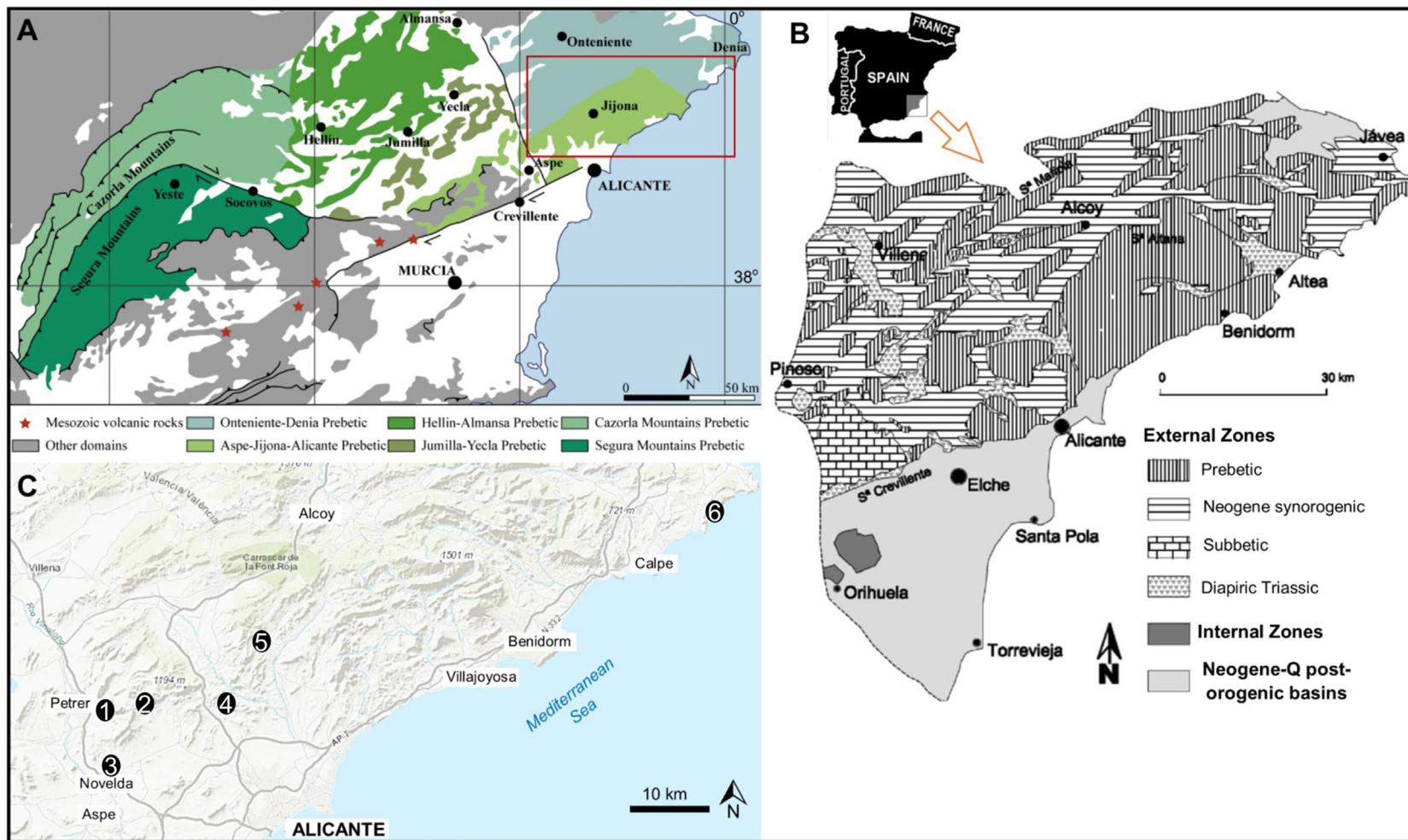


Fig. 1. A. Geological framework of the studied area among the different regional Prebetic domains (Eastern Betic Range). B. Geological sketch showing the studied area within the context of the Betic Cordillera in the Alicante Province (modified after Estévez et al., 2004). C. Geographical situation of the studied area including the revised localities from the Albian–Cenomanian transition with asymmetrical rhynchonellides and associated brachiopod fauna: 1. Sierra del Cid (expanded section of Fig. 2), 2. El Palomaret-Rincón Bello, 3. Casa Costera, 4. Sierra del Sabinar, 5. Xixona, 6. Moraig Cave.

biplicata" from the d'Orbigny collection were revised at the MNHN (París, France).

4. Depositional environment of the brachiopod-bearing beds around the Albian–Cenomanian transition from 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. Regionally, thin-bedded whitish marlstone/limestone deposits attributed to the Senonian overlay the Cenomanian succession, and a Turonian unit upwards is typified by marly limestone and greyish micritic limestone beds, occasionally with chert (Leret et al., 1976). Tracking the recurrent record of asymmetrical rhynchonellides by previous authors, a concise description of the depositional framework and lithostratigraphy of the Albian–Cenomanian transition is summarized for each locality where brachiopod assemblages are recorded around this timespan.

4.1. Casa Costera outcrop (Monforte del Cid)

The southernmost occurrences of asymmetrical *Cyclothyris* in the Alicante province are included into a diverse brachiopod assemblage previously reported near Novelda village (Fig. 1), attributed to the uppermost Albian deposits by Azéma (1977) and to the Cenomanian by Iñesta and Calzada (1996). They are recorded in marly deposits (about 45 m thick) with yellowish burrowed calcarenite and bioclastic limestone levels intercalated. Toward 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 appreciated in some sandy levels. This classical locality is almost missing nowadays due to the uncontrolled samplings and farming activities.

4.2. Sierra del Cid outcrops (Petrer)

Several outcrops are located in the Sierra del Cid, nearby Petrer village (Fig. 1). A detailed stratigraphical section is bed by bed studied in this area (Fig. 2) due to the continuity, the proper exposure, and the expanded character of the sediments (about 150 m thick) plus the record of copious brachiopod specimens, enabling analysis of their distribution and faunal successions and turnovers.

Brachiopod-bearing levels in the Sierra del Cid consist of a marly succession with alternating limestone–marly limestone beds. The basal part of the section is dominated by marly limestone levels with varied thickness, marly deposits are dominant in the middle-upper part, and a sporadic increase in carbonate content is observed toward the top of the section. The marly limestone deposits usually correspond to greyish wackstone thin-bedded levels, 15–30 cm thick. A mainly benthic biota is recorded in the entire section, constituting brachiopods the faunal core of the assemblage together with endobenthic echinoids (*Hemiaster* sp.). The analysis of microfossils in the marly beds was unproductive. Only some sandy marlstone levels revealed abundant orbitolinids. These orbitolinide-beds are represented by bioclastic wackstone where echinoids and brachiopods are also present together with glauconite and angular quartz lithoclasts. Scattered and very scarce ammonite individuals and fragments are occasionally recorded in some outcrops of this area.

Brachiopods are recorded in both marly and more carbonate levels, the latter showing wackstone microstructure and, apart from the brachiopods, serial benthic foraminifera and echinoids are

present together with quartz grains and glauconite. Occasionally, calcarenite levels with bioclasts, also with abundant brachiopods, are interspersed in the section, being more frequent near the top.

4.3. Palomaret-Rincón Bello outcrops (Petrer)

The outcrops around Palomaret–Rincón Bello (Fig. 1) are attributed to the early? Cenomanian (Leret et al., 1976; Iñesta and Calzada, 1996; Mora-Morote, 2000). Asymmetrical brachiopods recently attributed to *Cyclothyris ementitum* occur in a marly/sandy marlstone succession about 50 m thick. The record of brachiopods is more frequent in sandy levels in this locality, and they consist of ochre to greenish biocalcarene with fragments of brachiopods, echinoid, scarce bivalves, crinoid ossicles, and sponge spicules. The bed thickness is heterogeneous. Yellowish marly wackstone beds with scarce orbitolinids are also interspersed. The presence of calcarenite beds increases toward the top of the outcrops. These deposits typify a platform environment with frequent terrigenous inputs (Leret et al., 1976).

4.4. SE Xixona outcrop

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 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, *Cyclothyris difformis* (= *C. ementitum*) is recorded in the same mainly marly succession. The depositional environment is interpreted as representing a transition from the more offshore platform areas to the pelagic facies.

4.5. Sierra del Sabinar outcrop (Sant Vicent del Raspeig)

The upper Albian–lower Cenomanian strata in this area are well represented from bottom to top by a basal marly succession with carbonate and sandstone beds intercalated; a middle part with predominance of marly-sandy limestone levels which gradually decrease in thickness towards the top. In this middle part of the section, the formerly *Cyclothyris difformis* specially occurs. 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 infratidal facies linked to horsts were developed (Leret et al., 1976).

4.6. Moraig Cave outcrop (Benitatxell)

The intricate accessibility of this outcrop does not allow to specify accurately the lithostratigraphical framework of the specimens attributed to *C. ementitum* in this area, since they were sampled by professional divers in a submarine cave (Moraig Cave, Fig. 1). The surface lithostratigraphical units that crop out in the Sierra de Llorençà (where this site is located) correspond to the Sàcaras, 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) locating them in the undersea drowning 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 long from the cave opening), and the presence of a

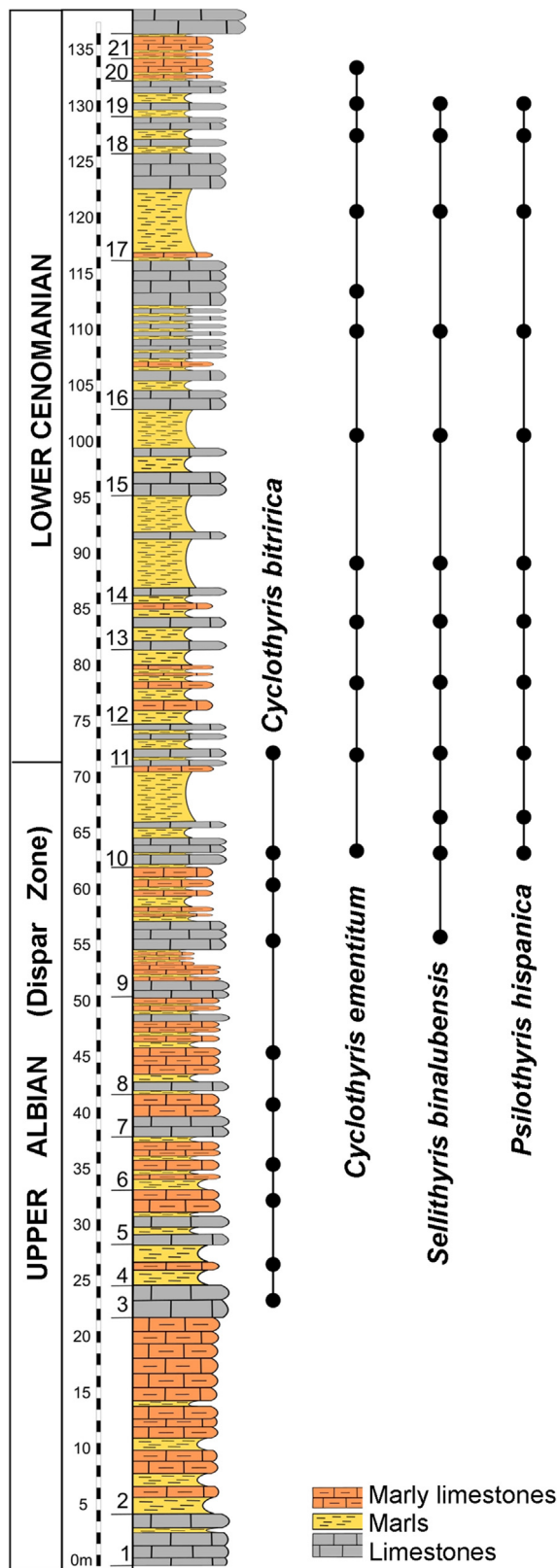


Fig. 2. Stratigraphic section of the Sierra del Cid (Eastern Prebetic; locality 1 in Fig. 1), showing the distribution of the recorded brachiopod fauna.

greyish marly matrix filling the samples, it is feasible suggesting that they derive from the uppermost lithostratigraphical terms (i.e. upper Albian–lowermost Cenomanian).

5. Systematic descriptions

Phylum Brachiopoda [Duméril, 1806](#)

Class Rhynchonellata [Williams, Carlson, Brunton, Holmer and Popov, 1996](#)

Order Rhynchonellida [Kuhn, 1949](#)

Subfamily Cyclothyridae [Makridin, 1955](#)

Genus *Cyclothyris* [M'Coy, 1844](#)

Type species. *Terebratula latissima* J. de C. Sowerby, 1825 in 1823–1825.

***Cyclothyris bitrtrica* sp. nov.**

[Figs. 3, 4](#)

? 1982 *Cyclothyris aturica* (Leymerie): [Pallí and Llompart](#), p. 233, pl. 2, figs. 6a–c.

2000 *Cyclothyris deluci* (Pictet): [Mora-Morote](#), p. 58; pl. 1; figs. 3a–d.

Etymology. From *Bitrir*, the ancient toponym of the Muslim settlement of Petrer, the vicinity where this species is currently profusely recorded.

Material and dimensions. 92 well-preserved specimens. Holotype: SC1001 ([Fig. 3A](#)) from Sierra del Cid, Alicante (Eastern Prebetic, Spain). Paratypes: SC0301 ([Fig. 3B](#)), SC0502 ([Fig. 3C](#)), SCS0511 ([Fig. 3D](#)), SC1023 ([Fig. 3E](#)), SC0402 ([Fig. 3F](#)), SC1002 ([Fig. 3G](#)), SC1013 ([Fig. 3H](#)), SC0604 ([Fig. 3I](#)), SC0501 ([Fig. 3J](#)), SC0503 ([Fig. 3K](#)), and SC1004 ([Fig. 3L](#)) from Sierra del Cid, Alicante (Eastern Prebetic, Spain).

Diagnosis. Medium-sized rhynchonellide, slightly dorsibiconvex. Lateral commissure ventrally inclined and anterior commissure uniplicate with a subtrapezoidal low fold. Shell ornamented with 38–42 rounded ribs. Beak erect, with small circular foramen. Crura canaliform, dorsally concave.

Description. External morphology. Small to medium-sized dorsibiconvex shells. Maximum width and thickness located at the midlength. The beak is small, suberect, with a small cyclothyrid foramen (deltidial plates protruded into a short tube around the pedicle foramen) (e.g. [Figs. 3.A4 and 3.C4](#)) and a small interarea. The lateral commissure is ventrally oriented. The anterior commissure is symmetrical, uniplicate, with a low subtrapezoidal fold. Each valve is ornamented with around 38–42 rounded ribs, being 12 of them situated in the median fold.

Internal morphology ([Fig. 4](#)). Incomplete pedicle collar ([Fig. 4B](#), section 0.1). The dental plates are thin, subparallel, delimiting relatively straight umbonal cavities ([Fig. 4B](#), sections 0.7–1.3). The teeth are poorly developed, subquadrangular ([Fig. 4B](#), section 1.6–1.9). Dorsal median septum is represented by a well-developed low ridge ([Fig. 4B](#), sections 1.4–1.9). Thin hinge plates, ventrally oriented initially ([Fig. 4B](#), section 1.6), then slightly dorsally concave ([Fig. 4B](#), section 1.7) becoming later subhorizontal ([Fig. 4A](#), section 1.9). Canaliform crura laterally divergent, being medially concave anteriorly ([Fig. 4A](#), sections 2.2–2.5) and medially to dorsally concave distally ([Figs. 4A](#), section 2.6) where the angle of the crura begins to diverge and changes to be reoriented dorsally ([Fig. 4A](#), section 2.6 and D).

Discussion. The genus *Cyclothyris* M'Coy (1844) is characterized by the presence of deltidial plates completely surrounding the foramen (cyclothyrid foramen). Regarding the internal characters, presence of canaliform crura with dorsal concavity is a diagnostic feature of the genus. The low dorsal septum and the subparallel dental plates are also typical and recurrent features of *Cyclothyris* ([Owen, 1962, 1988; Manceñido et al., 2002](#)).

The herein studied rhynchonellides are similar in general shape to *Cyclothyris compressa* ([Lamarck, 1819](#)) from the Cenomanian of

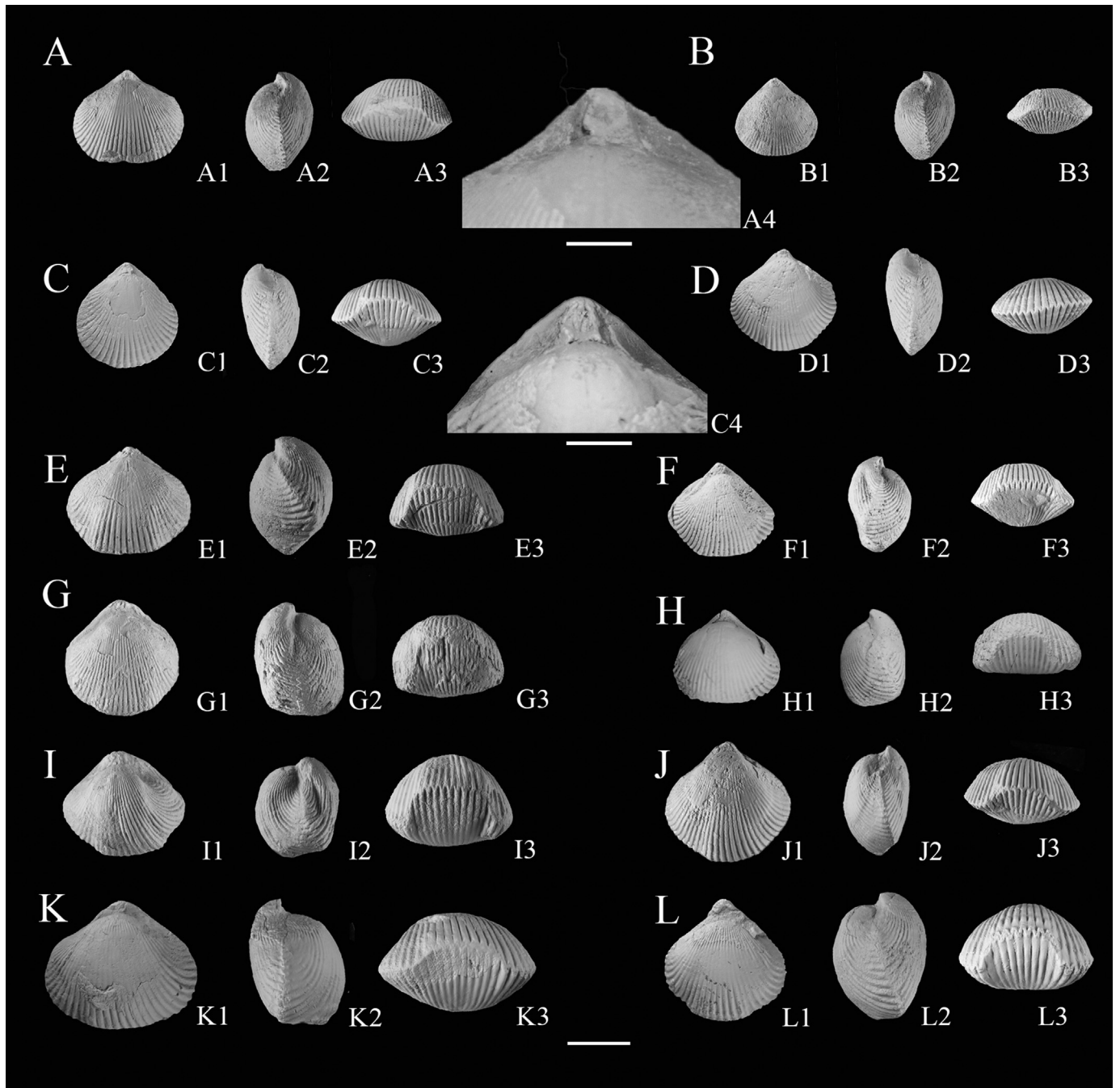


Fig. 3. *Cyclothyris bitirica* sp. nov. from the upper Albian deposits (Eastern Prebetic, Spain). (A) Holotype, specimen SC1001 from Sierra del Cid. (B–L) Paratypes, specimens SC0301 (B), SC0502 (C), SC0511 (D), SC1023 (E), SC0402 (F), SC1002 (G), SC1013 (H), SC0604 (I), SC0501 (J), SC0503 (K), SC1004 (L). Numbers indicate the views: dorsal (1), lateral (2), anterior (3), detail of the foramen (4). Specimens labeled according to the outcrop and level acronym (e.g. SC0301: specimen 1 collected in level 3 from the Sierra del Cid section – see Fig. 2). Scale bars: 1 cm, except for A4 and C4, in which the scale bar corresponds to 0.2 cm.

Sables du Perche (France), but *C. compressa* shows better developed interareas, sharper and less number of ribs on the fold (around 6) and certain tendency to the asymmetry in some specimens (d'Orbigny, 1819, p. 35, pl. 47, figs. 4, 6; specimen A25373).

On the other hand, the scarce records of *Cyclothyris bitirica* in the region were endorsed to *Rhynchonella* (or *Cyclothyris*) *deluci* Pictet, 1872 (p. 38–40, pl. 199, figs. 7–11), from the upper Aptian of Perle-du-Rhône (Switzerland). Some external features are similar in both species: small foramen, poorly defined interareas

and similar number of ribs. However, *C. deluci* shows a characteristic truncation on the anterior region allowing a more subtriangular shape. Calzada et al. (2013) alternatively synonymized some forms of *C. deluci* with *Cyclothyris aturica* (Leymerie, 1869). In this sense, the original type material of *C. aturica* was designated by Leymerie (1869, p. 315, pl. 3, fig. 5) from the East Pyrenean basins (upper Aptian–middle Albian). By checking the holotype of *C. aturica* (courtesy of Dr. Fauré) housed in the Leymerie collection (repository number MHNT.PAL.2017.0.10) at the Muséum de Toulouse (France), it is evident that *C. aturica* is

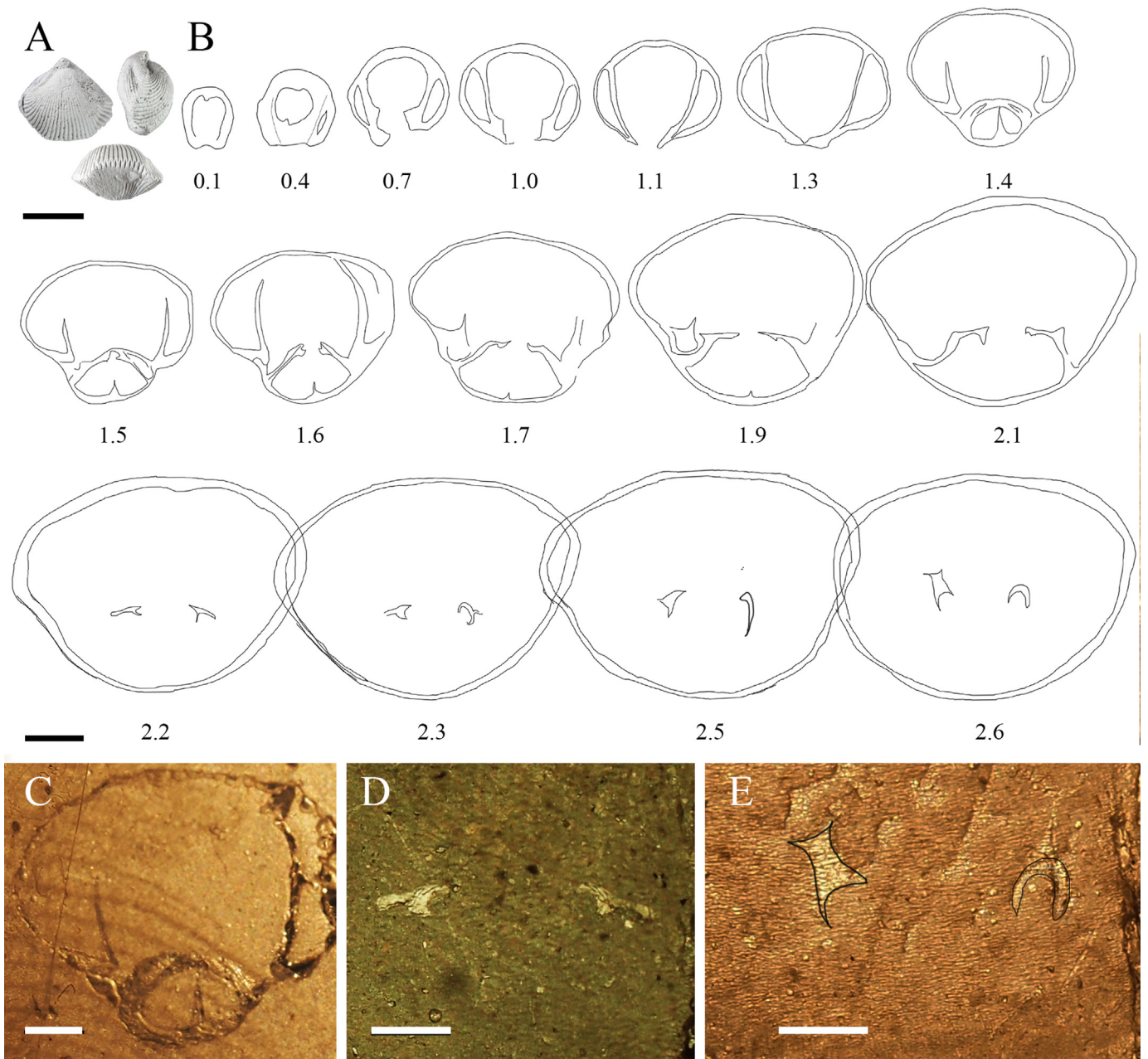


Fig. 4. Internal structure of *Cyclothyris bitrtrica* sp. nov. from the Albian–Cenomanian transition of Sierra del Cid (Eastern Prebetic, Spain). **A.** Specimen SC0402 in which serial sections were performed. Scale bar: 1 cm. **B.** Transverse serial sections through the same specimen (distance from the apex in mm). Scale bar: 1 cm. **C–E.** Microphotographs of acetate peels from the same specimen; Scale bars: 1 mm. (C) Section at 1.4 mm showing the dorsal median septum. (D) Section at 2.3 mm showing the crural bases. (E) Section at 2.6 mm revealing the dorsally concave crura.

typified by subtriangular symmetrical *Cyclothyris* but much large-sized (L: 22.5 mm, W: 24.0 mm, T: 15.5 mm) and with significantly lower number of ribs (22 ribs) if compared to *C. bitrtrica*. Different morphotypes of *C. aturica*, more consistent with the type material, were recorded in the Catalan Coastal Range (Montgrí Massif) by Pallí and Llompart (1981) together with *Sellithyris longella* (Leymerie) and “*Tamarella*” *oweni* (Peybernés and Calzada), therefore attributing the deposits of these outcrops to the middle–upper Albian. Recent studies in these lithostratigraphical units (Consorti et al., 2014) support this dating for the levels with *C. aturica*, due to the occurrence of *Involutina hungarica*, typical biomarker of the Albian.

Furthermore, *Cyclothyris deluci* figured by Calzada (1975, p. 25, pl. 5, text-fig. 8) from the Aptian of La Roqueta (Olivella, Barcelona) differs from *C. bitrtrica* in showing bigger foramen, more number of ribs (around 40, reaching up to 46) and a depression on the ventral valve. The same differences are applicable to the subspecies *Cyclothyris deluci clavelli* Calzada, 1975, considered as synonym of *C. aturica* by Calzada et al. (2013), being more subquadrangular and wider. Consequently, the record of *C. bitrtrica* encompasses all the previous occurrences of *C. deluci* accredited in the Albian of the Prebetic Domain, but definitively it must be unrelated to the original *C. deluci* (Leymerie) which seem to be restricted to the Pyrenees and pre-Pyrenean basins.

Cyclothyris bitrtrica is also similar to *Cyclothyris africana* Owen, 1980, from the upper Albian of Zululand (SE Africa) in the general outline, the short umbo, the small foramen, short interareas, and similar number of ribs (Owen, 1980, figs. 5, 6). However, *C. africana* shows acute posterior umbonal inflations and a broad fold on the brachial valve. Moreover, in *C. africana* the ribs are much more deeply incised towards the margins. Finally, *Cyclothyris polygona* d'Orbigny, 1847 (p. 31, pl. 496, figs. 1–4) from the Albian of Provence (France) shows a more convex dorsal valve and a characteristic narrower subpentagonal outline than *C. bitrtrica*.

Occurrence. The previous Prebetic attributions to *Cyclothyris deluci* (or *C. aturica*), now updated as *C. bitrtrica*, pointed to a pre-Cenomanian occurrence. Thus, Martínez del Olmo et al. (1978) recorded *Rhynchonella deluci* in the Prebetic of Castalla together with several Aptian–Albian macroinvertebrates such as “*Terebratulula tamarindus*” and “*Terebratulula moutoniana*” and a diverse microfossil assemblage attributed to the Albian, also substantiated by the occurrence of Albian ammonoid species of the genus *Hoplites*. It was also recorded in the Sierra del Cid region (Mora-Morote, 2000) in several sites different to the outcrop herein studied with unclear ascription to the Aptian–early Cenomanian.

In this work, *C. bitrtrica* is definitively attributed to the upper Albian, probably with its LOD in the Dispar Zone of the Eastern Prebetic (Southeastern Spain). The species has been recorded in the lower part of the Sierra del Cid section, in the Represa Formation (Van Veen, 1969).

Cyclothyris ementitum Berrocal-Casero, Baeza-Carratalá and García Joral, 2023
Figs. 5–7

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

Material and dimensions. 108 well-preserved specimens. Holotype SCT1003 (Fig. 5A) from Sierra del Cid, Alicante (Eastern Prebetic, Spain). Paratypes: SC1820 (Fig. 5B), SC1803 (Fig. 5C), SC2002 (Fig. 5D), SC1521 (Fig. 5E), SC2001 (Fig. 5F), SC2004 (Fig. 5G), SC1801 (Fig. 5H), SC2015 (Fig. 5I) from Sierra del Cid, Alicante, Spain. Specimens CM.1 (Fig. 6A), CM.2 (Fig. 6B) respectively showing a neomorphic Fe-oxide shell from the Moraig Cave. MU.21 and MU.221 (Fig. 6C–D) respectively from the Palomaret–Rincón Bello area. Specimens PR.Cd.1998.1 and SA.Cd.1 (Fig. 6E–F), respectively from Sierra del Sabinar outcrop.

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

Description. External morphology. Medium to big-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 at the anterior part of the shell. Maximum thickness located at the midlength. The beak is erect, prominent, with a hypothryid circular foramen (cyclothyrid foramen; i.e. deltidial plates protruded into a short tube around the pedicle foramen). 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. 7). Pedicle collar well-developed (Fig. 7B, section 0.8, Fig. 7C), with thick conjunct deltidial plates. Dental

plates are thin and subparallel, delimiting relatively narrow umbonal cavities (Fig. 7B, sections 1.6–2.3). Teeth massive, quadrate, crenulated and slightly recurved laterally, inserted in crenulated sockets (Fig. 7B, section 3.9, 7D). Lateral denticula and the 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 (Fig. 7B, section at 3.7 mm from the apex) becoming subhorizontal (Fig. 7B, section at 3.9 mm). The crura are long and canaliform in type, dorsally concave (Fig. 7B, section 5.7–6.2; Fig. 7E).

Discussion. As for *Cyclothyris bitrtrica*, this taxon properly accomplishes the diagnostic criteria of the genus *Cyclothyris* M'Coy, 1844 (i.e. deltidial plates completely surrounding the foramen, well-defined interareas, long canaliform crura with dorsal concavity, low dorsal septum and subparallel dental plates). This species has been recently erected as new and endemic for the Betic Ranges by Berrocal-Casero et al. (2023), where a comprehensive specific discussion and the range of intraspecific variability is established.

Occurrence. Albian–Cenomanian transition (FOD in the Perinflatum Subzone of the Dispar Zone; uppermost upper Albian–lower Cenomanian) of the Eastern Prebetic (Southeastern Spain). This species has been recorded in the section of Sierra del Cid in the Represa Formation (Van Veen, 1969).

Order Terebratulida Waagen, 1883

Superfamily Terebratuloidea Gray, 1840

Family Sellithyrididae Muir-Wood, 1965

Subfamily Sellithyridinae Muir-Wood, 1965

Genus *Sellithyris* Middlemiss, 1959

Type species. *Terebratulula sella* J. de C. Sowerby, 1823 in 1823–1825

Sellithyris binalubensis sp. nov.

Figs. 8–12

? 1982 *Sellithyris longella* (Leymerie): Pallí and Llompard, p. 232; pl. 2, figs. 3a–c.

1996 *Sellithyris* cf. *cenomaniensis*: Iñesta and Calzada, p. 21, pl. 1, figs. 3a–d.

1999 *Sellithyris* cf. *cenomaniensis* (Gaspard): Iñesta, p. 24, pl. 6, fig. 4.

2000 *Sellithyris cenomaniensis* (Gaspard): Mora-Morote, p. 58, pl. 2, figs. 2a–d.

Etymology. From the ancient Arabic toponymic [*binalūb*], that gives name to the region of Vinalopó nowadays, where the most prolific outcrops of this species are located.

Material. 145 well-preserved specimens. Holotype: SC1402 (Fig. 8A) from Sierra del Cid, Alicante (Eastern Prebetic, Spain). Paratypes: specimen SC1403 (Fig. 8B), SC1805 (Fig. 8C), SC1401 (Fig. 8D), SC1518 (Fig. 8E) and SC1516 (Fig. 8F), SC1301 (Fig. 8G), SC1303 (Fig. 8H) from Sierra del Cid, Alicante (Eastern Prebetic, Spain).

Diagnosis. Medium-sized terebratulide, ovate to subpentagonal in outline, equibiconvex to slightly ventribiconvex. Beak suberect. Foramen permesothryid. Anterior commissure sulciphate. Very fine “graphillate” ornamentation close to the anterior margin. Virgate hinge plates and poorly developed distal tips of the loop.

Description. External morphology. Medium-sized terebratulides, oval to subpentagonal in outline, longer than wide. Equi-to ventribiconvex. Maximum width located at the middle part of the shell-length or slightly posteriorly. Beak short, suberect. Foramen large, permesothryid. Beak ridges are short and blunt. Deltidial plates fused to the symphytium (Figs. 8G4, 8F4). Anterior commissure sulciphate, varying from strongly sulciphate specimens (Fig. 8C) to the slightly sulciphate ones (Fig. 8F). The shell shows radial ornamentation that is not

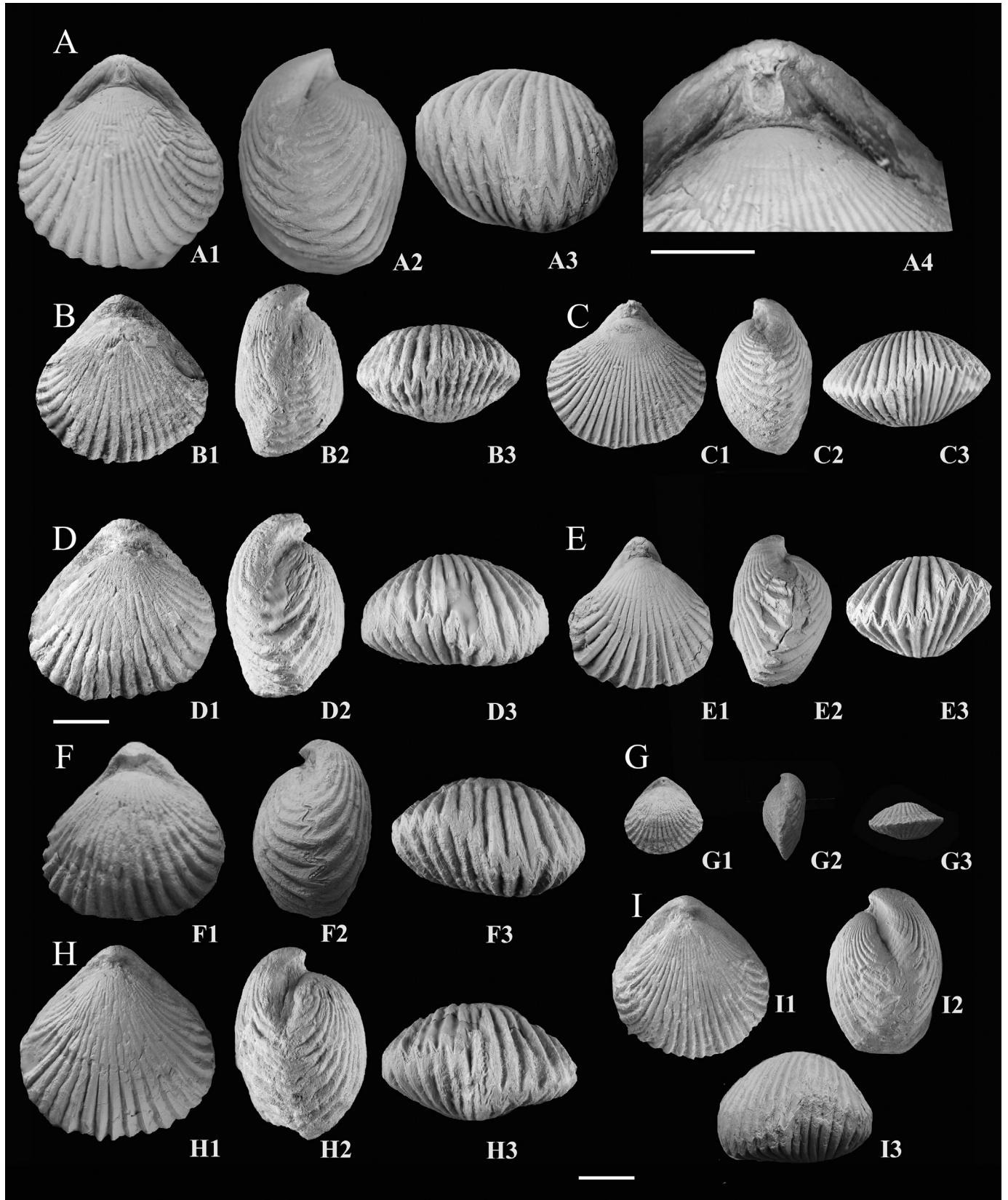


Fig. 5. *Cyclothyris ementitum* Berrocal-Casero et al., 2023, from the Albian–Cenomanian transition of the Sierra del Cid (Eastern Prebetic, Spain). **A.** Holotype, specimen SC1003 from Sierra del Cid. **B–I.** Paratypes, specimens SC1820 (B), SC1803 (C), SC2002 (D), SC1521 (E), SC2001 (F), SC2004 (G), SC1801 (H), SC2015 (I) from the same stratigraphic section and locality. Numbers indicate the views: dorsal (1), lateral (2) anterior (3), detail of the foramen (4). Specimens labeled according to the outcrop and level acronym (e.g. SC1820: specimen 20 collected in level 18 from the Sierra del Cid section – see Fig. 2). Scale bars: 1 cm, except for A4 (scale bar: 0.5 cm). (Specimens A, C and I re-illustrated from Berrocal-Casero et al., 2023).

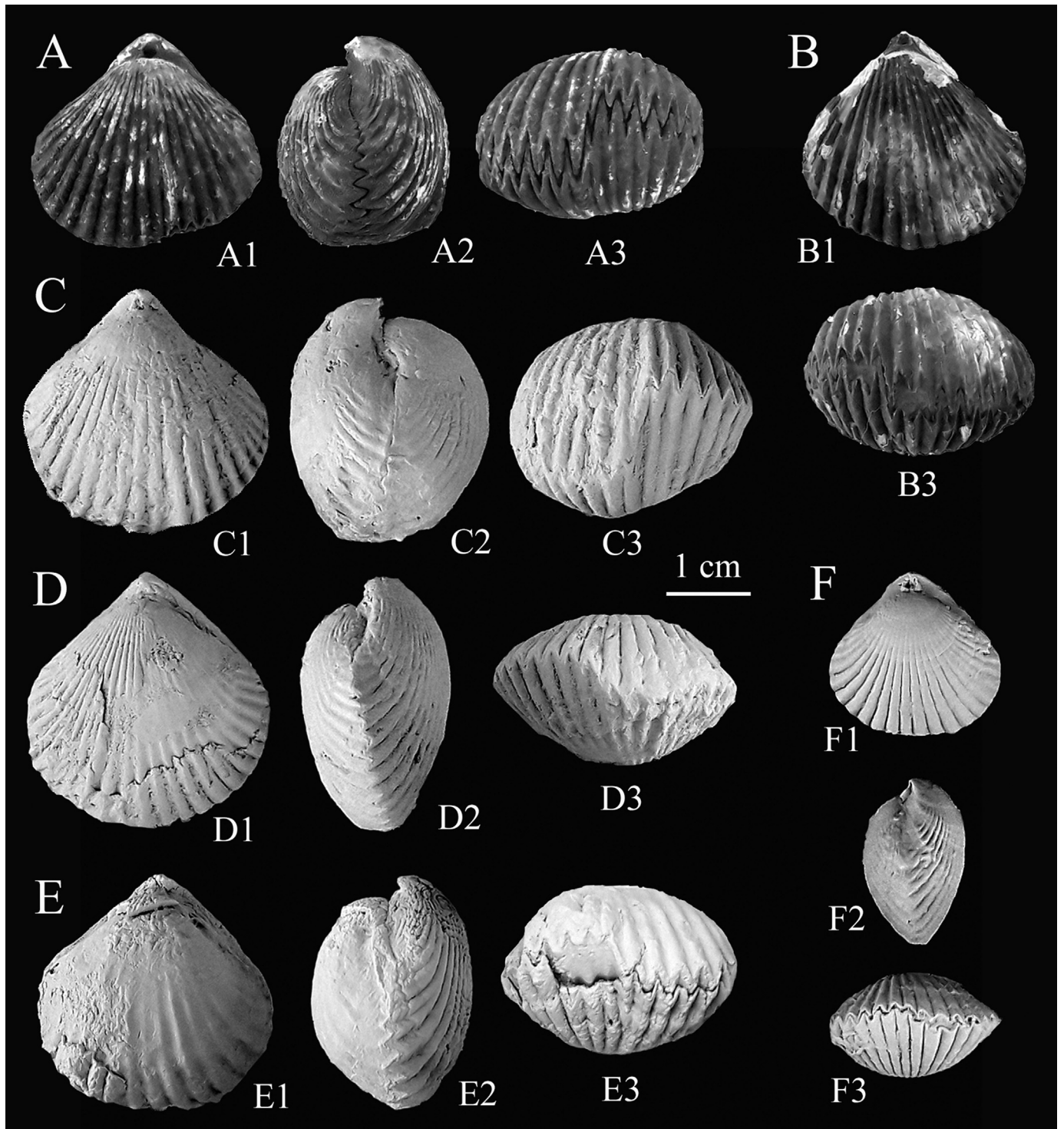


Fig. 6. *Cyclothyris ementitum* Berrocal-Casero et al., 2023. Revised specimens derived from several localities (included in Fig. 1), formerly attributed to *Cyclothyris difformis*. **A, B.** Specimens CM.1 and CM.2 respectively showing a neomorphic Fe-oxide shell from the Moraig Cave. **C, D.** Specimens MU.21 and MU.221 respectively from the Palomaret-Rincón Bello area. **E, F.** Specimens PR.Cd.1998.1 and SA.Cd.1, respectively from Sierra del Sabinar outcrop. Numbers respectively indicate the dorsal (1), lateral (2), and anterior (3) views. Scale bar: 1 cm. (Specimens A, C, D, E and F re-illustrated from Berrocal-Casero et al., 2023).

capillation, but rather takes the form of narrow and very shallow grooves in the shell surface (around 3–4 per mm) close to the commissure (“graphillate” *sensu* Middlemiss, 1978). This ornamentation is very weak and only distinguished towards the commissure (Fig. 8G).

Internal morphology (Figs. 9–11). Serial sections through three extreme morphotypes of variability (strongly sulcinate, Fig. 9; nearly rectimarginate, Fig. 10; and slightly sulcinate, Fig. 11) have been performed to better confirm their generic attribution. Pedicle collar present (Fig. 9, sections at 0.40 and 0.60, Fig. 9C). Cardinal

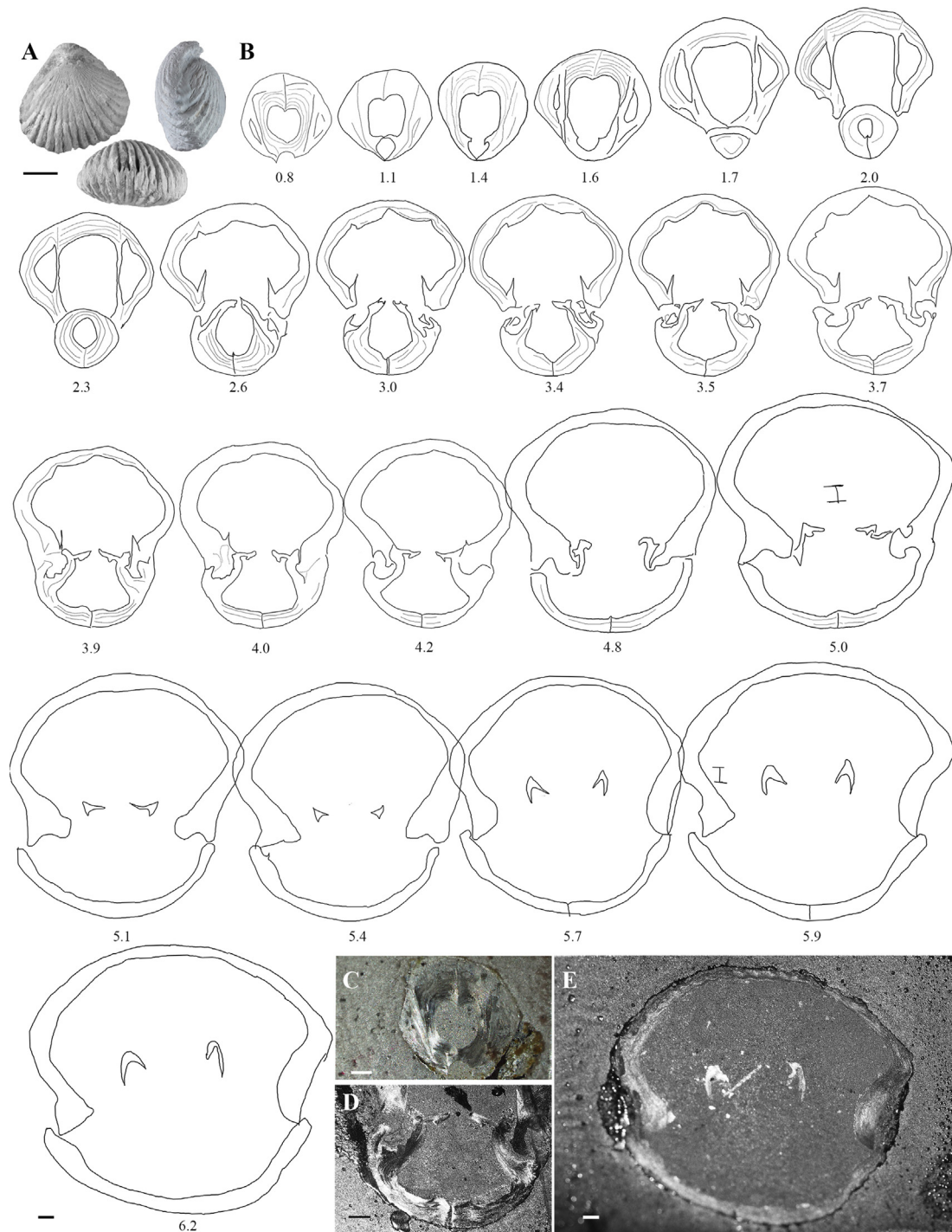


Fig. 7. Internal structure of *Cyclothyris ementitum* Berrocal-Casero et al., 2023, from the Albian–Cenomanian transition of Sierra del Cid (Eastern Prebetic, Spain). **A.** Specimen SC1522, collected in the level 15 from the Sierra del Cid section (see Fig. 2), in which serial sections were performed. Scale bar: 1 cm. **B.** Transverse serial sections through the same specimen (distance from the apex in mm). Scale bar: 1 mm. **C–E.** Microphotographs of acetate peels from the same specimen (scale bars: 1 mm). (C) Section at 0.8 mm revealing the pedicle collar. (D) Section at 2.5 mm showing the teeth interlocked in crenulated sockets. (E) Section at 6.2 mm showing the typical canaliform crura of the genus *Cyclothyris*.

process apparently bilobate and a weak striation is discernible in several sections (Fig. 9, sections at 3.60 and 4.10 and 9D, E). Hinge plates virgate, wide, concave, forming deep, U- to V-shaped troughs between socket ridges and crural bases (Fig. 9B, sections at 4.90 and 5.30; 9F–H); teeth and sockets feebly interlocked without crenulation, denticula present; loop wide, triangular; transverse band narrow and arcuate and short and poorly developed distal tips of the loop.

Discussion. Generic attribution of these forms into *Sellithyris* Middlemiss, 1959 is based on the diagnostic criteria of this genus: subpentagonal in outline, anterior commissure strongly sulcipliate, shell faintly capillate; beak short, erect, foramen large, permesothyrid; outer hinge plates wide, concave, forming deep, U-shaped troughs between socket ridges and crural bases; no inner hinge plates; and loop wide and triangular (Lee and Smirnova, 2006, p. 2062, fig. 1363, 1a–t).

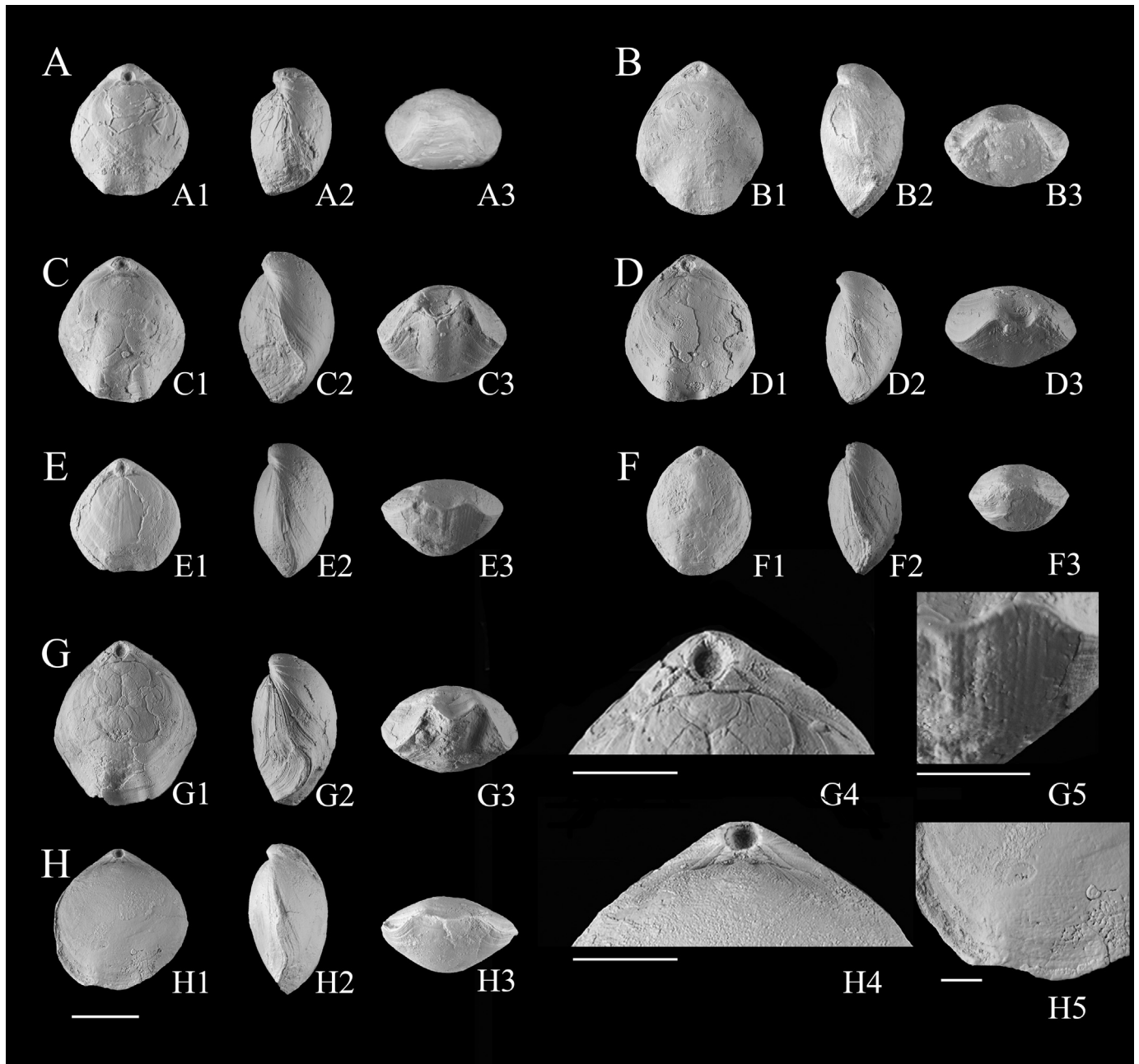


Fig. 8. *Sellithyris binalubensis* sp. nov. from the Albian–Cenomanian transition of Sierra del Cid (Eastern Prebetic, Spain). **A.** Holotype, specimen SC1402. **B–H.** Paratypes, specimen SC1403 (B), SC1805 (C), SC1401 (D), SC1518 (E), SC1516 (F), SC1301(G), SC1303 (H). Numbers indicate respectively the dorsal (1), lateral (2), anterior (3), detail of the foramen (4) views, and (5) detail of the “graphillate” ornamentation of the shell. Specimens labeled according to the outcrop and level acronym (e.g. SC1518: specimen 18 collected in level 15 from the Sierra del Cid section – see Fig. 2). Scale bars: 10 mm, except G4 and H4, in which the scale bars correspond to 5 mm.

The high external morphological variability of *Sellithyris binalubensis* has been explored through bivariate and multivariate analyses of several stocks sampled from the levels yielding more specimens (SC9–11, SC14, and SC18). A PCA based on 6 representative dimensional variables of the main morphological external features is performed for this species (Fig. 12A). The PC2 axis represents the morphological variation independent of the size, being the global width (W), the maximum height of the fold in the anterior commissure (Fh), and the distance from the apex to the maximum width of the shell (Wm), the most substantial criteria in the range of variability. In the upper part of the plots, the individuals with shorter W and longer Fh and Wm are widely

distributed, while the widest and those with the lower anterior fold are settled in the lower part of the graph (Fig. 12A).

In order to explain the possible ontogenetic variability, a bivariate analysis has been performed, plotting these biometric parameters against length (L), considered the variable that better reflects differences in size (Figs. 12B–D). In the L/W plot (Fig. 12B) both parameters are strongly correlated and show isometric growth with consistent little changes in shape. However, the correlation between L/Wm (Fig. 12C) reveals more range of variability in the larger specimens, from subrhombical to discoidal outlines. The greatest range of variability in *S. binalubensis* is revealed in the L/Fh relationship since the height of the fold can vary considerably in the

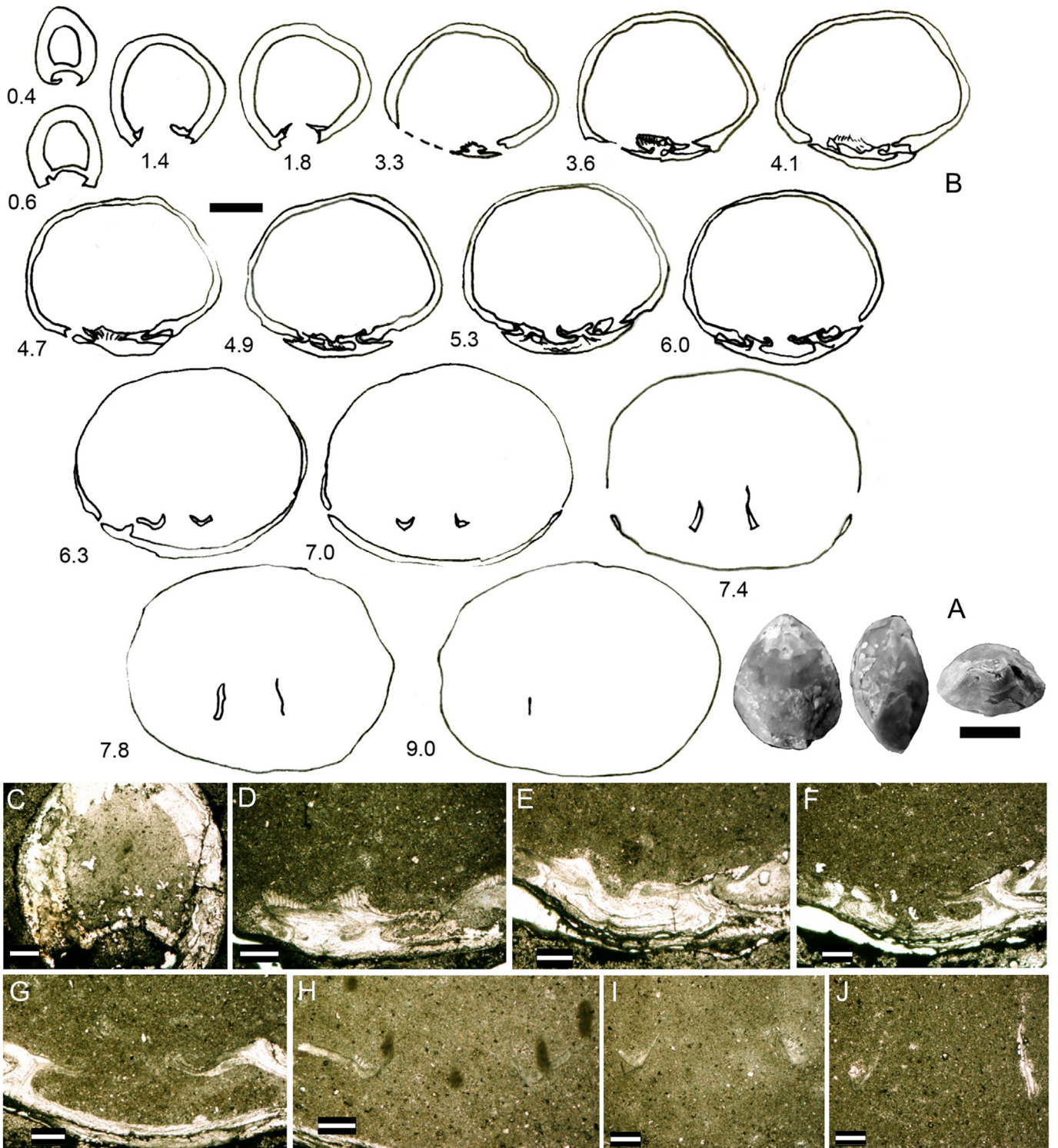


Fig. 9. Internal structure of *Sellithyris binalubensis* sp. nov. from the Albian–Cenomanian transition (Eastern Prebetic). **A.** Specimen SCe.T14.S1, collected in the level 14 from the Sierra del Cid section (see Fig. 2), in which serial sections were performed; scale bar: 1 cm. **B.** Transverse serial sections through the same specimen (distance from the apex in mm); scale bar: 2 mm. **C–J.** Microphotographs of acetate peels from the same specimen; scale bars: 0.5 mm. **(C)** Section at 0.6 mm showing the umbonal cavity with pedicle collar. **(D, E)** Sections at 3.6 and 4.6 mm respectively showing the progression of the cardinal process. **(F)** Section at 4.9 mm revealing the emerging apparently cuneate hinge plates and crural bases. **(G)** Section at 5.3 revealing the ventrally concave hinge plates anteriorly evolving to more virgate outlines. **(H–J)** Sections at 6.2, 6.9, and 7.4 mm respectively showing the crural processes development.

largest individuals. Therefore, the morphological variability in adult specimens of this species is expressed mainly between strongly plicate to weakly plicate anterior commissures, frequently linked to more subrhombical or more discoidal outlines, respectively.

This Prebetic stock of *Sellithyris* was considered as *Sellithyris* cf. *cenomanensis* by [Iñesta and Calzada \(1996, p. 21, pl. 1, fig. 3a–d\)](#) among others, in the nearby area of Novelda (Eastern Prebetic). *Sellithyris cenomanensis* from the Cenomanian of Sarthe, France, is

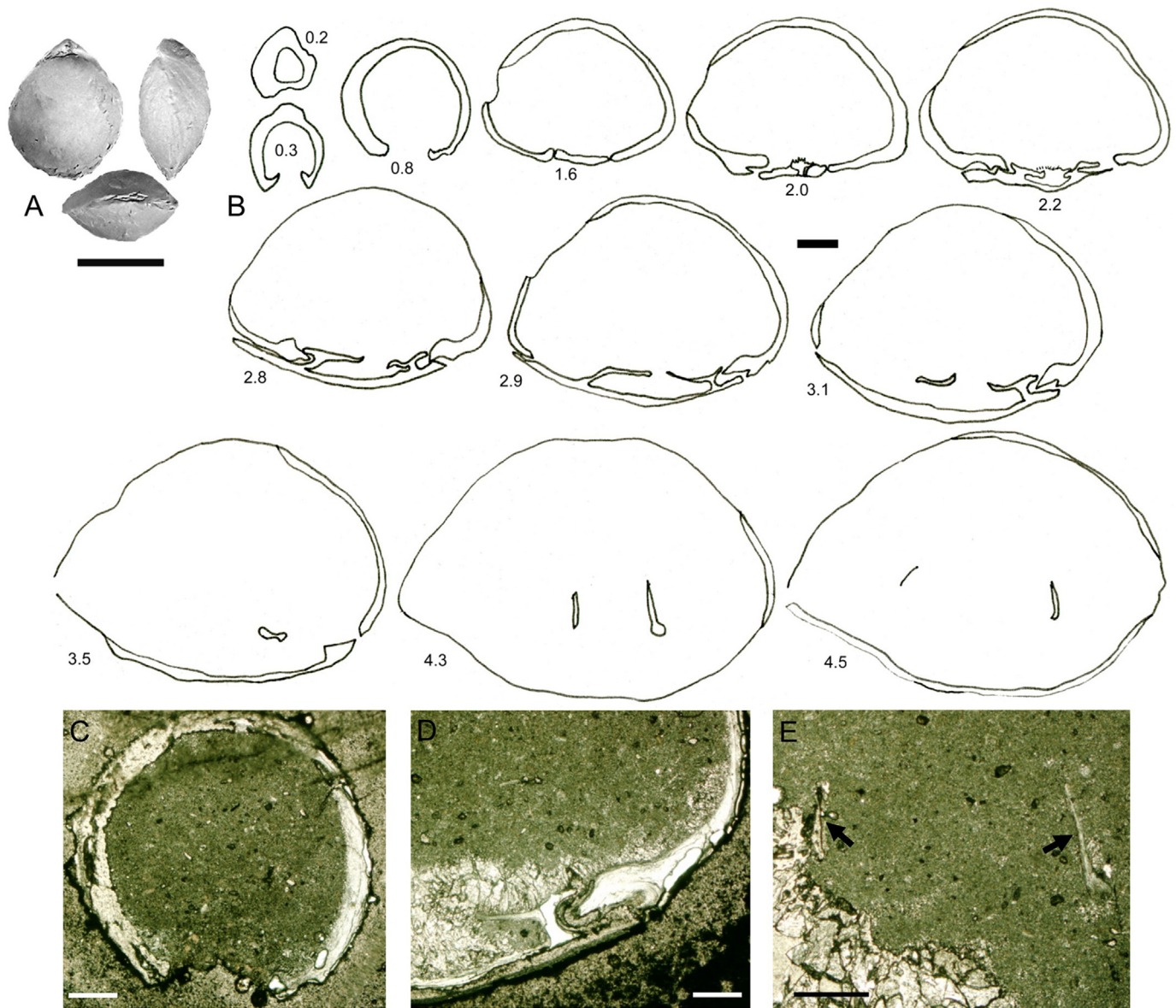


Fig. 10. Internal structure of *Sellithyris binalubensis* sp. nov. from the Albian–Cenomanian transition (Eastern Prebetic). **A.** Specimen THu.T15.1, collected in the level 15 from the Sierra del Cid section (see Fig. 2), in which in which serial sections were performed; scale bar: 1 cm. **B.** Transverse serial sections through the same specimen (distance from the apex in mm); scale bar: 1 mm. **C–E.** Microphotographs of acetate peels from the same specimen; scale bars: 0.5 mm. (C) Section at 0.8 mm showing the delthyrial cavity. (D) Section at 3.1 mm showing the hinge area with the hinge plate and the weakly interlocked dentition, despite the presence of denticula. (E) Section at 4.3 mm revealing the evolution of the crural processes and lamellae (black arrows) of the loop.

much more subpentagonal in shape and it shows a stronger sulcification than *S. binalubensis* nov. sp.. Moreover, in *S. cenomanensis*, the two folds of the sulcification are strongly marked on its dorsal valve (Gaspard, 1982, p. 205, pl. 1: 2a–c; revised neotype specimen <https://science.mnhn.fr/institution/mnhn/collection/f/item/j08117>).

Some of the specimens of “*Terebratula*” *biplicata* (Brocchi, 1814), from the Cenomanian of Sarthe, La Flèche, France, from d’Orbigny collection (e.g. 1847, p. 95; 1851, pl. 511, figs. 13–15; specimen MNHN.F.A25376) are very similar to *S. binalubensis*, but they show a less marked sulcification, and the internal features of these specimens remain unknown. The original specimen of “*Anomia*” *biplicata* from La Toscana (Italy) with unknown age figured by Brocchi (1814, p. 489, pl. 10, fig. 8) shows a more strongly marked

sulcification anteriorly displaced and elongated outwards the profile of the shell.

The specimens classified as *Sellithyris sella* (Sowerby, 1823) figured by Calzada (1975, p. 33, pl. 6, figs. 1–5, text–fig. 11) from Morella (Castellón, E–Spain) are similar to the herein studied terebratulide, but showing more subpentagonal outline and the lateral commissure is more ventrally displaced compared to *S. binalubensis*. On the other hand, *Sellithyris crusafonti* Calzada, 1975 (pl. 7, figs. 1, 2) from Morella and Tarragona (Eastern Spain), is also similar to the less sulcificated specimens of *S. binalubensis*. The same occurs with the less sulcificated *Sellithyris solei* Calzada 1975 (p. 35, pl. 7, fig. 3; pl. 9, fig. 3; text–figs. 12, 13) from Morella (E–Spain), but the biostratigraphical ranges of these congeneric counterparts (*S. sella*, *S. crusafonti*, and *S. solei*), Bedoulian (Aptian)

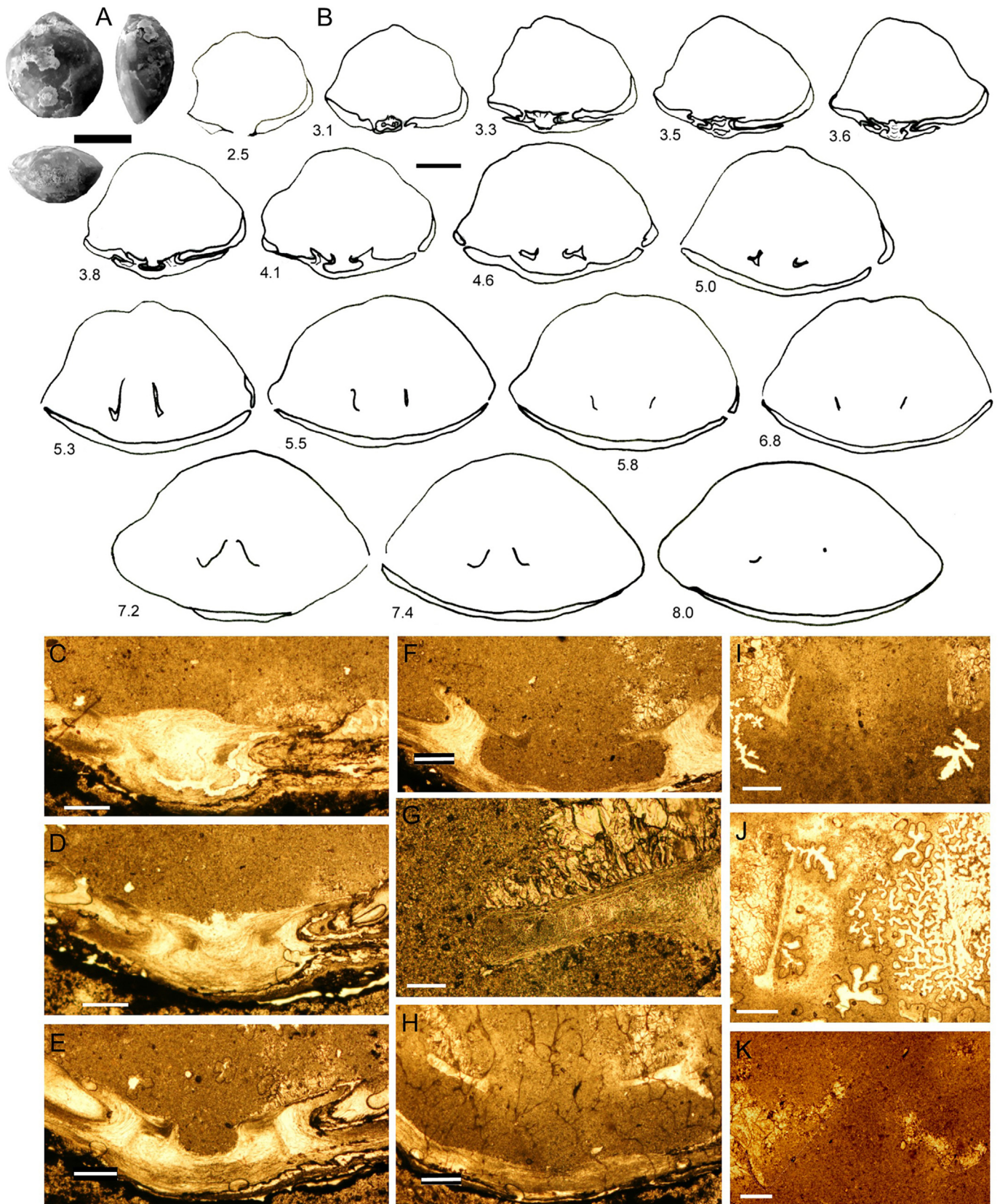


Fig. 11. Internal structure of *Sellithyris binalubensis* sp. nov. from the Albian–Cenomanian transition (Eastern Prebetic). **A.** Specimen PH.PT15.S1, collected in the level 15 from the Sierra del Cid section (see Fig. 2), in which serial in which serial sections were performed; scale bar: 1 cm. **B.** Transverse serial sections through the same specimen (distance from the apex in mm); scale bar: 2 mm. **C–K.** Microphotographs of acetate peels from the same specimen; scale bars: 0.5 mm, except for G (scale bar: 25 µm). **(C, D)** Sections at 3.5 and 3.6 mm respectively showing the evolution of the cardinal process. **(E)** Section at 3.8 mm showing the hinge plates/cardinal process relationship and the dentition mechanism with feebly interlocked teeth and sockets. **(F, G)** Section at 4.1 mm revealing the virgate and slightly cuneate hinge plates; G: detailed view of the hinge plate. **(H)** Section at 4.6 with the individualized hinge plates. **(I, J)** Sections at 5.1 and 5.3 mm respectively showing the evolution of the crural processes. **(K)** Section at 7.3 mm showing the traces of the transverse band.

in age, and *S. binalubensis* (Albian–Cenomanian transition) are clearly unconnected.

Occurrence. Albian–Cenomanian transition (FOD in the Perinflatum Subzone of the Dispar Zone; uppermost Albian) of the Eastern Prebetic (Southeastern Spain). The species has been recorded in the section of Sierra del Cid in the Represa Formation (Van Veen, 1969)

Superfamily Laqueoidea Thomson, 1927

Family Laqueidae Thomson, 1927

Subfamily Terebrataliopsinae Smirnova, 1990

Genus *Psilothyris* Cooper, 1955

Type species. *Terebratula tamarindus* J. de C. Sowerby, 1836

Psilothyris hispanica Iñesta and Calzada, 1996.

Figs. 13–16

1996 *Psilothyris hispanica* n. sp. Iñesta and Calzada: p. 22, pl. 2, fig. 2.
1999 *Psilothyris hispanica* Iñesta and Calzada, Iñesta: p. 34, pl. 10, fig. 4.

Material. 224 well-preserved specimens. Figured specimens from Sierra del Cid, Alicante (Eastern Prebetic). SCP1802 (Fig. 13A), SCP1811 (Fig. 13B), SCP1813 (Fig. 13C), SC1302 (Fig. 13D), SCP1333 (Fig. 13E), SCP1812 (Fig. 13F), SCPX27 (Fig. 13G), SCP1501 (Fig. 13H), SCP1901 (Fig. 13I), SCP1502 (Fig. 13J), SCP1304 (Fig. 13K), SCP1701 (Fig. 13L).

Emended Diagnosis. Small equibiconvex terebratellidines, subcircular to oval in outline, with smooth shell. Anterior commissure rectimarginate to slightly uniplicate or marginally sulcate, beak suberect to erect, foramen mesothyrid. Loop teliform. Presence of outer and inner hinge plates. Conjoined inner hinge plates. The well-developed dorsal median septum is fused to the inner hinge plates. Crural bases massive, triangular.

Description. External morphology. Small-sized terebratellidines, rounded, oval to subpentagonal in outline. The shell is ventribiconvex, with maximum convexity located at the midlength. The maximum width is attained at the middle of the shell or slightly shifted anteriorly, thus conditioning the eventual variability of its oval/pentagonal profile. Beak suberect to erect, with rounded beak ridges. Big mesothyrid foramen, rounded in outline (Fig. 13A4, C4, G4). Anterior commissure with high variability, from slightly plicated (e.g. Fig. 13B, G), rectimarginate (e.g. Fig. 13E), to slightly sulcated (e.g. Fig. 13I–L). The surface of the shell is totally smooth. Internal morphology (Figs. 14, 15). In this case, serial sections were performed through the two main morphotypes of external variability (ovoid, Fig. 14; and pseudopentagonal in outline, Fig. 15) to better confirm their generic attribution. Deltidial plates are thin and disjunct; short dental plates, subparallel to slightly divergent ventrally; wide and elliptical umbonal cavity; the cardinal process is not revealed. Strong teeth interlocked in wide and moderately deep sockets; weak denticula present; outer hinge plates broad and slightly inclined towards dorsal valve; posteriorly conjoined inner hinge plates, the well-developed dorsal median septum is moderately short ($\frac{1}{4}$ of the shell) and fused to the inner hinge plates, this system adopting the septalium function. Crural bases massive and triangular in shape, directed dorsally. Long crural processes. Teliform loop, with long and widely separate descending branches of the loop.

Discussion. The studied material accomplishes with the external diagnostic criteria for the genus *Psilothyris* (smooth, biconvex, ovate to subpentagonal, rectimarginate to uniplicate, umbo erect, mesothyrid foramen) as was erected by Cooper (1955, p. 10) and also

resumed by Mackinnon and Lee (2006, p. 2206, fig. 1462, 2a–d). Additionally, the internal morphology revealed on the sectioned specimens makes unquestionable their attribution to *Psilothyris*, since the main internal diagnostic features of this genus such as the presence of posteriorly conjoined inner hinge plates, the relatively short dorsal median septum and the shape of the septalium, have been substantiated. The presence of outer and inner hinge plates as well as triangular shape and position of crural bases here described were previously observed by Radulović and Radulović (2002) in *Psilothyris tamarindus* from the Aptian of eastern Serbia. These important features have been included in the emended diagnosis of the genus.

The specimens classified as *Psilothyris tamarindus* (J. de C. Sowerby, 1836) from the Aptian of eastern Serbia, described and figured by Radulović and Radulović (2002, p. 402, pl. 1, figs. 1–3; pl. 2, figs. 1–6; figs. 2–4) are similar to *P. hispanica* in the rounded to pentagonal outline of the shell and its internal morphology. However, besides their difference in age, *P. tamarindus* is bigger in size, it shows a more pronounced pentagonal outline and smaller foramen if compared to *P. hispanica*. *Psilothyris tamarindus* is equally moderately biconvex, while *P. hispanica* is ventribiconvex. Moreover, the anterior commissure of *P. tamarindus* is uniplicate, while *P. hispanica* shows more variability (from slightly plicated, rectimarginate, to slightly sulcated anteriorly).

The species *P. hispanica* shows a great external variability both in the outline and in the anterior commissure, early noticed even in the four specimens analyzed for the erection of the species (Iñesta and Calzada, 1996). The profuse record of this taxon in the Sierra del Cid allows for exploring its morphological variability through bivariate and multivariate analysis of two stocks corresponding to the levels yielding more specimens (SC-14 and SC-18 in Fig. 16). A PCA based on six dimensional variables considered as representative of the main morphological features is performed (Fig. 16A). The PC2 axis represents the morphological variation independent of the size, being the distance from the apex to the maximum width of the shell (W_m) and global width (W) the more relevant factors in the variability. In the upper half of the plots, the individuals with shorter W and longer W_m (maximum width closer to the anterior margin) are distributed, contrarily to those located in the lower morphospace (widest and with the maximum width closer to the apex), leading to an intraspecific variability ranging from elongate forms with subrhombical dorsal outline to more discoidal forms.

These differences can be explained in terms of allometry, as observed in Figs. 16B and 16C. In these graphs, W and W_m are plotted against length (L), considered the variable that better reflects differences in size. In the L/W plot, the point cloud is relatively restricted, corresponding satisfactorily with an exponential regression line, consistent with a single population. Thus, increasing in width is strongly allometric with length. However, the relationship L/W_m is not clearly dependent ($r^2 = 0.51$): the concurrence with an exponential distribution shows a tendency close to the isometry. Juvenile specimens are elongate and rhomboidal in outline, and adults show more variability, with elongate (SC-14.2 specimen in Fig. 16A) to more discoidal individuals (with greater relative width) but with both, maximum width closer to the apex (SC-14.5 specimen in Fig. 16A) or shifted towards the mid-length (SC-18.4 specimen in Fig. 16A). The variability is also extended to the anterior commissure, ranging from rectimarginate to moderately uniplicate forms, as also noticed in the type material by Iñesta and Calzada (1996), and a gently sulcation is detected in a few individuals.

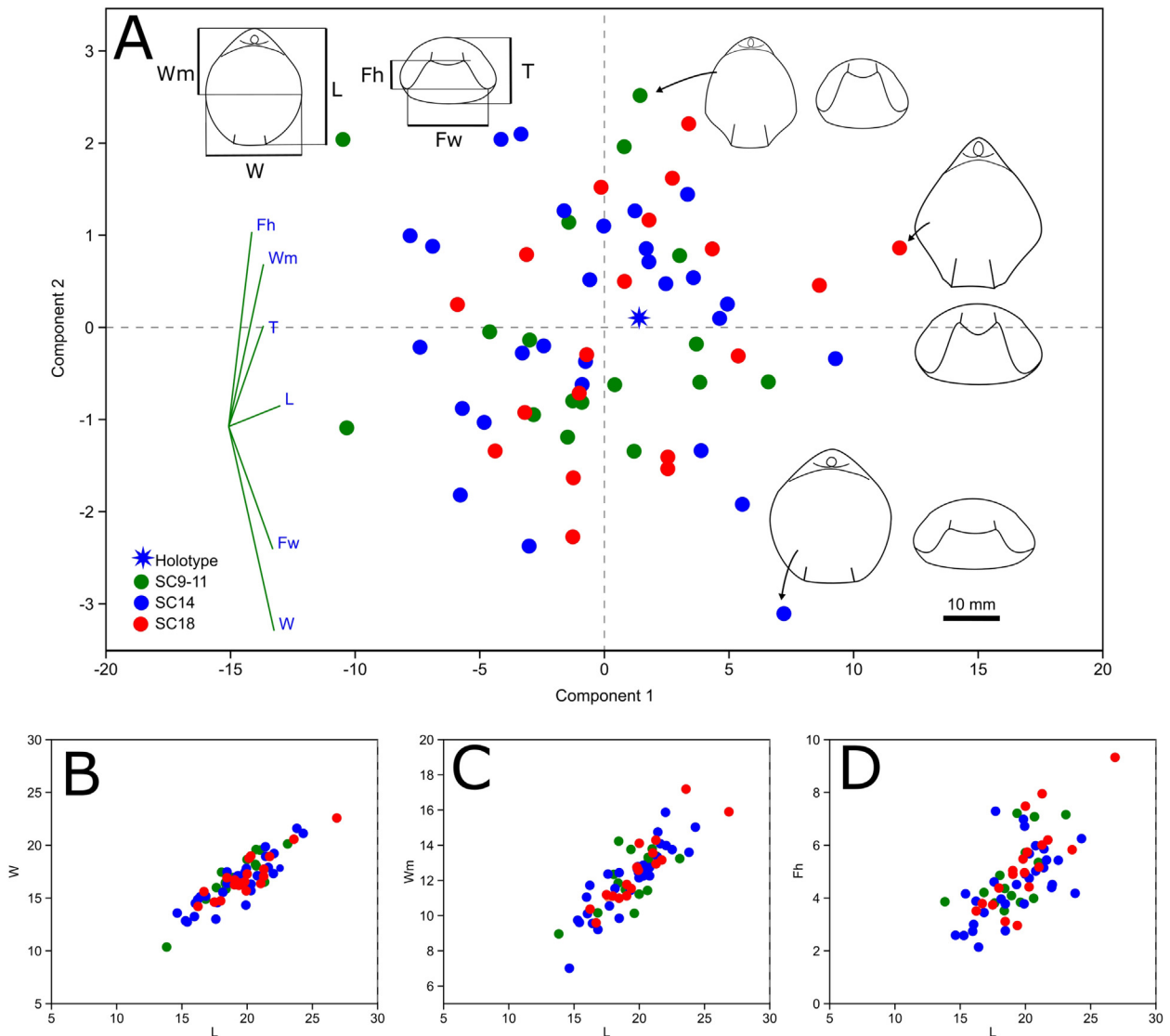


Fig. 12. Morphometrical scatter plots of the *Sellithyris binalubensis* studied specimens. **A.** Morphospaces defined by the two main axis of the Principal Component Analysis (PCA) taking into account six dimensional variables considered as representative: apart from the main biometric parameters: length, width, and thickness (L, W, T), the distance from the apex to the maximum width of the shell (Wm), the width of the dorsal median fold (Fw), and the maximum height of the fold in the anterior commissure (Fh) are considered. Dimensional vectors have been represented showing the main discriminating factors. **B, C, D.** Bivariate analysis plotting W, Wm, and Fh against length (L) for better understanding morphological variability in terms of allometry.

Occurrence. Albian–Cenomanian transition (FOD in the Perinflatum Subzone of the Dispar Zone; uppermost Albian) of the Eastern Prebetic (Southeastern Spain). The species has been recorded in the section of Sierra del Cid in the Represa Formation (Van Veen, 1969).

6. Brachiopods succession as potential biostratigraphical markers

6.1. Biostratigraphical approach of the Prebetic brachiopod-bearing deposits and update of the former *Cyclothyris difformis* records

The biochronostratigraphical data of the Cretaceous Prebetic asymmetrical rhynchonellides are controversial. Most of their previous occurrences were attributed to the Cenomanian bearing in mind the similarity of the specimens recorded with analogous forms attributed to *Cyclothyris difformis* in the classical European localities where this taxon occurs in the Cenomanian. Some other

evidences point to the Albian–Cenomanian transition as probable biostratigraphical range for the assemblages comprising these forms in the Prebetic. After the taxonomic differentiation undertaken in this work, these data in the Betic Range must be emphasized, considering previous records and localities.

The *Cyclothyris difformis*-bearing deposits (currently *C. ementium*) from the Sierra del Cid herein worked out were early attributed to the lower Cenomanian due to their regional stratigraphic position (Leret et al., 1976). Some eastwards Prebetic outcrops (Sabinar area) where these forms are recorded (Fig. 7D, E) were ascribed by the same authors (Leret et al., 1976) to the uppermost Albian in transition to the lower Cenomanian (Dispar Zone, Perinflatum Subzone). Similarly, *Rhynchonella defformis* (sic) was reported in close vicinity to this last outcrop by Leret et al. (1976) together with *Terebratula* sp. and an abundant echinoderm fauna (Sierra de los Tajos locality), thus correspondingly dated within the Dispar Zone, Perinflatum Subzone (uppermost Albian).

On the other hand, Azéma (1977) identified most of the deposits from the Sierra del Cid area, corresponding to the

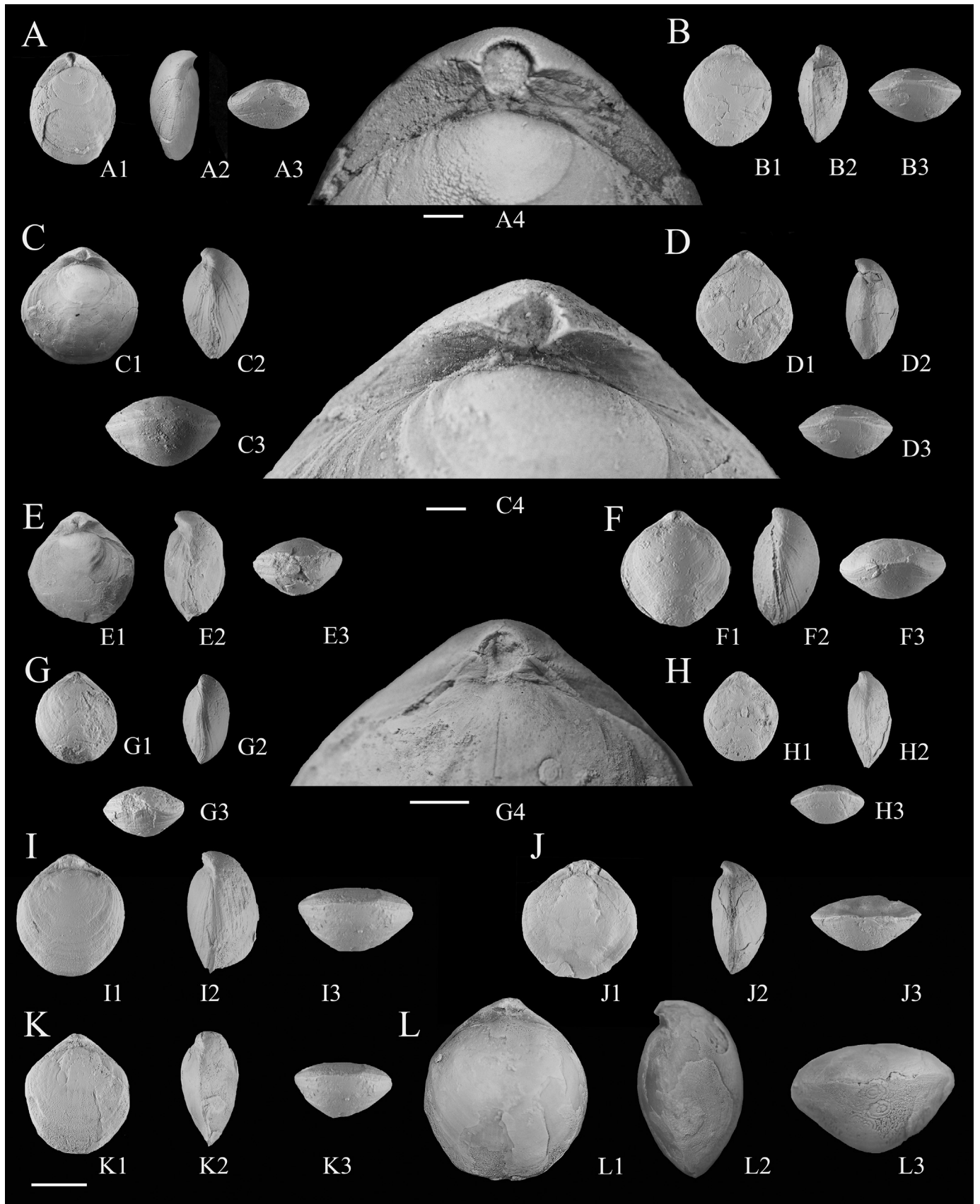


Fig. 13. *Psilothyris hispanica* Iñesta and Calzada, 1996, from the Albian–Cenomanian transition of Sierra del Cid (Eastern Prebetic, Spain). Specimens SC1802 (A), SC1811 (B), SC1813 (C), SC1302 (D), SC1333 (E), SC1812 (F), SCPX27 (G), SC1501 (H), SC1901 (I), SC1502 (J), SC1304 (K), SC1701 (L). Numbers respectively indicate the dorsal (1), lateral (2), anterior (3), and detail of the foramen (4) views. Specimens labeled according to the outcrop and level acronym (e.g. SC1813: specimen 13 collected in level 18 from the Sierra del Cid section – see Fig. 2). Scale bars: 1 cm, except A4 and C4 (scale bars: 1 mm).

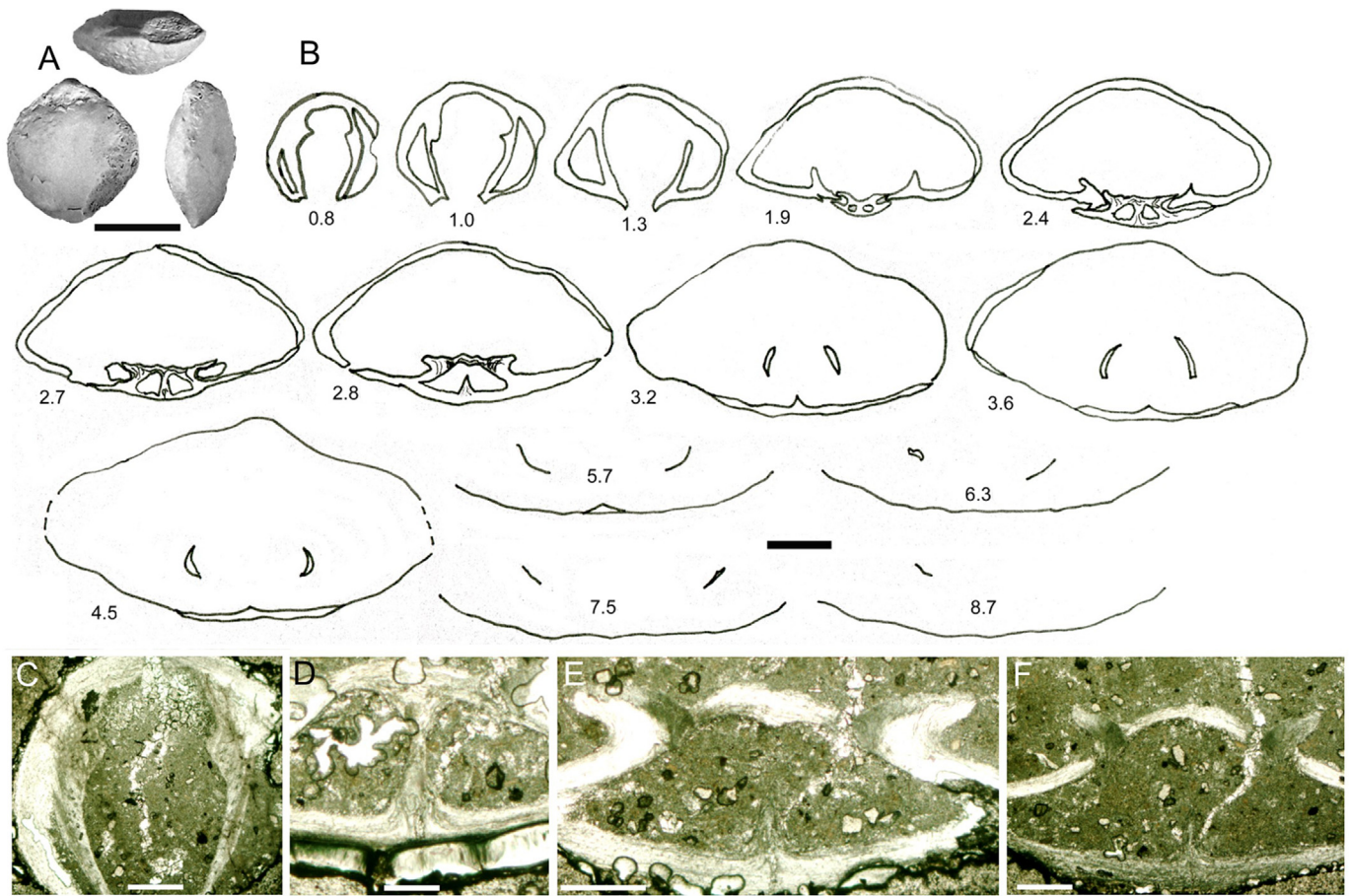


Fig. 14. Internal structure of *Psilothyris hispanica* [Iñesta and Calzada, 1996](#), from the Albian– Cenomanian transition (Eastern Prebetic). **A.** Specimen PH.T10.Sen.1, collected in the level 10 from the Sierra del Cid section (see [Fig. 2](#)), slightly sulcate morphotype in which serial sections were performed; scale bar: 1 cm. **B.** Transverse serial sections through the same specimen (distance from the apex in mm); scale bar: 2 mm. **C–F.** Microphotographs of acetate peels from the same specimen; scale bars: 0.5 mm. **(C)** Section at 0.8 mm showing pedicle cavity and dental plates. **(D)** Section at 2.5 mm showing the dorsal median septum-septalium system. **(E, F)** Sections at 2.7 and 2.8 mm showing the evolution of the conjoined hinge plates prior to the full development of crural bases.

lithostratigraphic unit which brachiopods in this work derived from, as marly sediments with *Terebratula* and *Rhynchonella*, assigning this unit to the uppermost Albian due to the finding of the ammonoid *Mortonicerias (Durnovarites) sp.*, biomarker of the Dispar Zone.

Similarly, the same problem occurs in several patchy outcrops around the central core of the Sierra del Cid containing brachiopods. One of the most prolific and reported localities in this area is the Casa Costera site in the southernmost part of this mountain, where the former *Cyclothyris difformis* is also recorded. This outcrop was studied by [Azéma \(1977\)](#) recording a diverse macro- and microfossil assemblage, among which, *Mariella cf. bergeri* and *Favusella washitensis* suggested its adscription to the uppermost Albian deposits. However, the same outcrop was attributed to the Cenomanian by [Iñesta and Calzada \(1996\)](#) on the basis of the record of *C. difformis* together with *Terebrirostra lyra*, *Orbirhynchia mantelliana*, *Sellithyris cf. cenomaniensis*, and *Dilophosina paraplicata*. Virtually the same brachiopod assemblage is reported from the Palomaret area northwards ([Iñesta and Calzada, 1996](#)) considering the same distribution range as well. The diversity and abundance of this brachiopod assemblage deserve discussing from a biostratigraphic perspective.

As mentioned above, *Cyclothyris difformis* is an index taxon of the early-middle Cenomanian from several Tethyan basins such as South-England (e.g. [Owen, 1988, 2002](#)), France and Belgium (e.g.

[Gaspard, 1997](#)), Bulgaria ([Motchurova-Dekova, 1997](#)), Poland ([Popiel-Barczyk, 1977](#)), Germany ([Owen, 1962](#)), among others. Further attributions extend the distribution range of this taxon, including the late Albian, as occurs in a lesser-ribbed stock from the upper Albian?–lower Cenomanian of Iran ([Binazadeh, 2017](#)) and *C. cf. difformis* from the upper Albian–lower Cenomanian from Poland ([Popiel-Barczyk, 1977](#)) typified by individuals with shorter beak and less developed median septum than the type material. Nevertheless, as updated in this work, and previously stated by [Berrocal-Casero et al. \(in press\)](#), the Prebetic stock of the former *C. difformis*, including the specimens reported by [Iñesta and Calzada \(1996\)](#), is rearranged into *C. ementitum*, disconnected from the typical true-*difformis* forms.

The same occurs with the attribution to *Sellithyris cf. cenomaniensis* by [Iñesta and Calzada \(1996\)](#). *S. cenomaniensis* is the final stock of the genus *Sellithyris* in the middle Cenomanian ([Gaspard, 1997](#)), even in the type-locality of this species ([Gaspard, 2013, 2014](#)). This species was formerly attributed to *Sellithyris biplicata* (e.g. [Gaspard, 1982; Gaspard and Mullon, 1983](#)) but always referred to specimens from the middle Cenomanian. On the other hand, *Orbirhynchia mantelliana* is an index species for the middle Cenomanian of England ([Pettitt, 1954; Owen, 1988, 2002](#)), even becoming a marker horizon: “*O. mantelliana*-band” ([Kennedy, 1969; Owen, 1988; Gaspard, 1997](#)). It is also recorded in the middle Cenomanian from Germany and N-France ([Gaspard, 1997](#)), and in the lower-middle

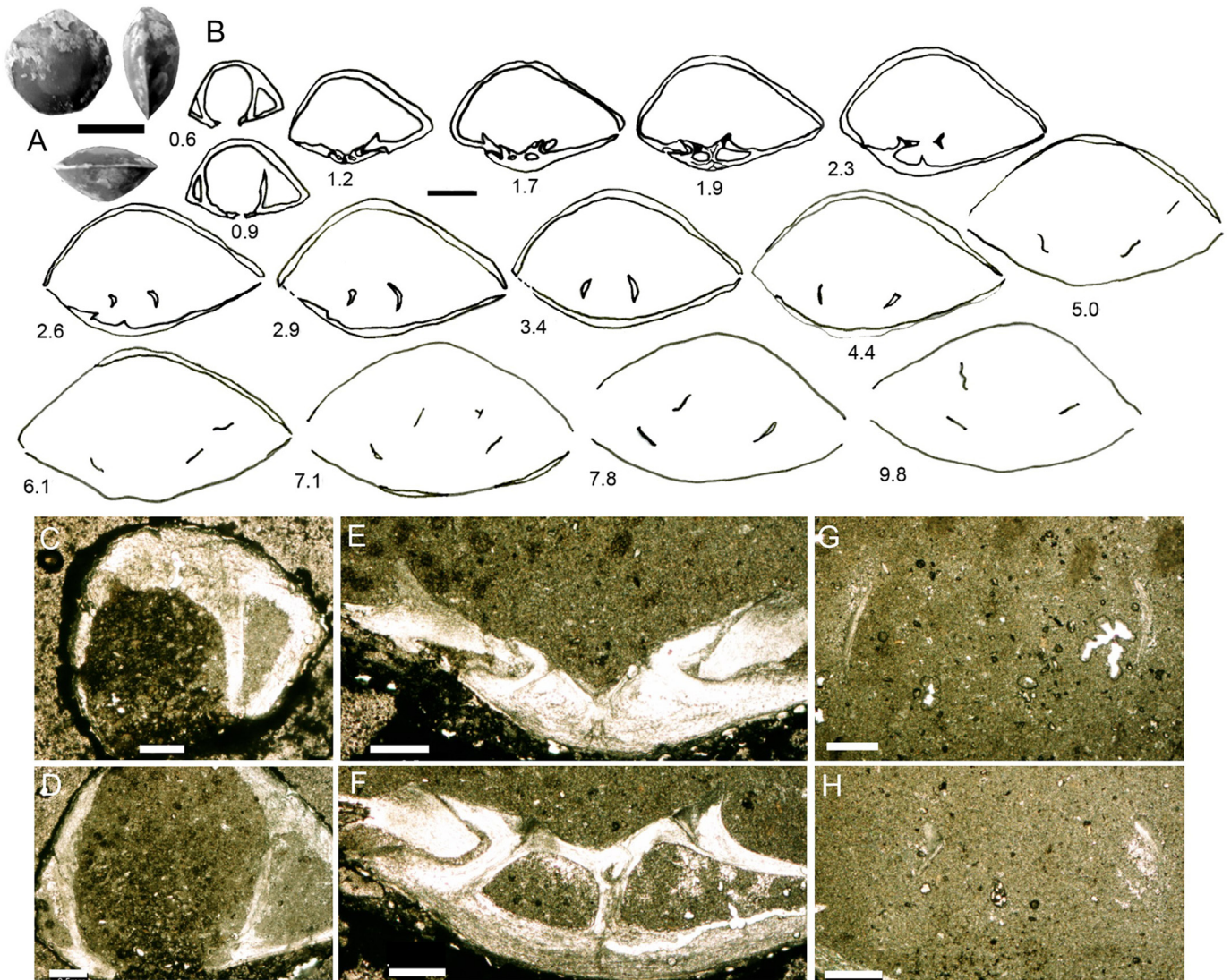


Fig. 15. Internal structure of *Psilothyris hispanica* [Inesta and Calzada, 1996](#), from the Albian– Cenomanian transition (Eastern Prebetic). **A.** Specimen PH.R.1, collected in the level 10 from the Sierra del Cid section (see [Fig. 2](#)), nearly rectimarginate morphotype in which serial sections were performed; scale bar: 1 cm. **B.** Transverse serial sections through the same specimen (distance from the apex in mm); scale bar: 2 mm. **C–H.** Microphotographs of acetate peels from the same specimen; Scale bars: 0.5 mm. **(C, D)** Sections at 0.4 and 0.8 mm respectively showing the umbonal region and evolution of the dental plates. **(E)** Section at 1.8 mm showing the onset of the teeth implementation and deep septalium. **(F)** Section at 2.0 mm revealing the median septum and septalium, hinge plates and the onset of crural bases. **(G, H)** Sections at 3.2 and 4.3 mm respectively showing the evolution of descending branches of the loop.

Cenomanian from Poland ([Popiel-Barczyk, 1977](#)). *Terebrirostra lyra* is recorded in the lower Cenomanian from Normandy and England ([Gaspard, 1997](#)) and *Dilophosina paraplicata* in the lower Cenomanian from Calvados ([Cooper, 1983](#)).

A similar brachiopod assemblage with the former *Cyclothyris difformis* as constituent is reported in the Cretaceous sediments environs the locality of Xixona ([Fig. 1](#)) by [Gallemí et al. \(1997\)](#). These authors identified the basal boundary of the Cenomanian stage included in an alternating yellowish marl/marly limestone unit, starting from a horizon with ammonites, bivalves, echinoids, brachiopods, and abundant microfauna, being the presence of the ammonite genus *Graysonites* distinctive for this attribution. Just overlying this horizon, [Gallemí et al. \(1997\)](#) reported the first occurrence of a diverse brachiopod assemblage consisting of *Cyclothyris difformis*, *Orbirhynchia* sp. nov., *Concinnithyris subundata*, *Moutonithyris dutempleana*, *Sellithyris* aff. *sella*, *Tropeothyris vectis*, *Kingena spinulosa*, and *Terebrirostra* cf. *lyra*. The succession

follows upwards with the record of *Orbirhynchia mantelliana* in the overlying horizon.

Referring to the brachiopod fauna of this assemblage, *Moutonithyris dutempleana* is reported worldwide in the Aptian–Cenomanian interval from Madagascar to the Caucasus and from Crimea to India ([Sulser and Friebe, 2002](#)), being the last representative of the genus *Moutonithyris* in the Albian–Cenomanian transition ([Gaspard, 1997](#)); *Kingena spinulosa* is reported, among others, from the upper Albian of England and France ([Owen, 1970](#); [Gaspard, 1997](#)) and the Cenomanian of Poland ([Popiel-Barczyk, 1972](#)); *Tropeothyris vectis* is recorded in the Cenomanian of the Isle of Wight ([Owen, 1988](#)) and *Concinnithyris subundata* is more representative of the middle Cenomanian successions ([Gaspard, 1997](#)).

The most northeastern Prebetic outcrop where asymmetrical *Cyclothyris* is sampled is the Moraig Cave ([Fig. 7A, B](#)). The brachiopod-bearing deposits of this locality were attributed to the

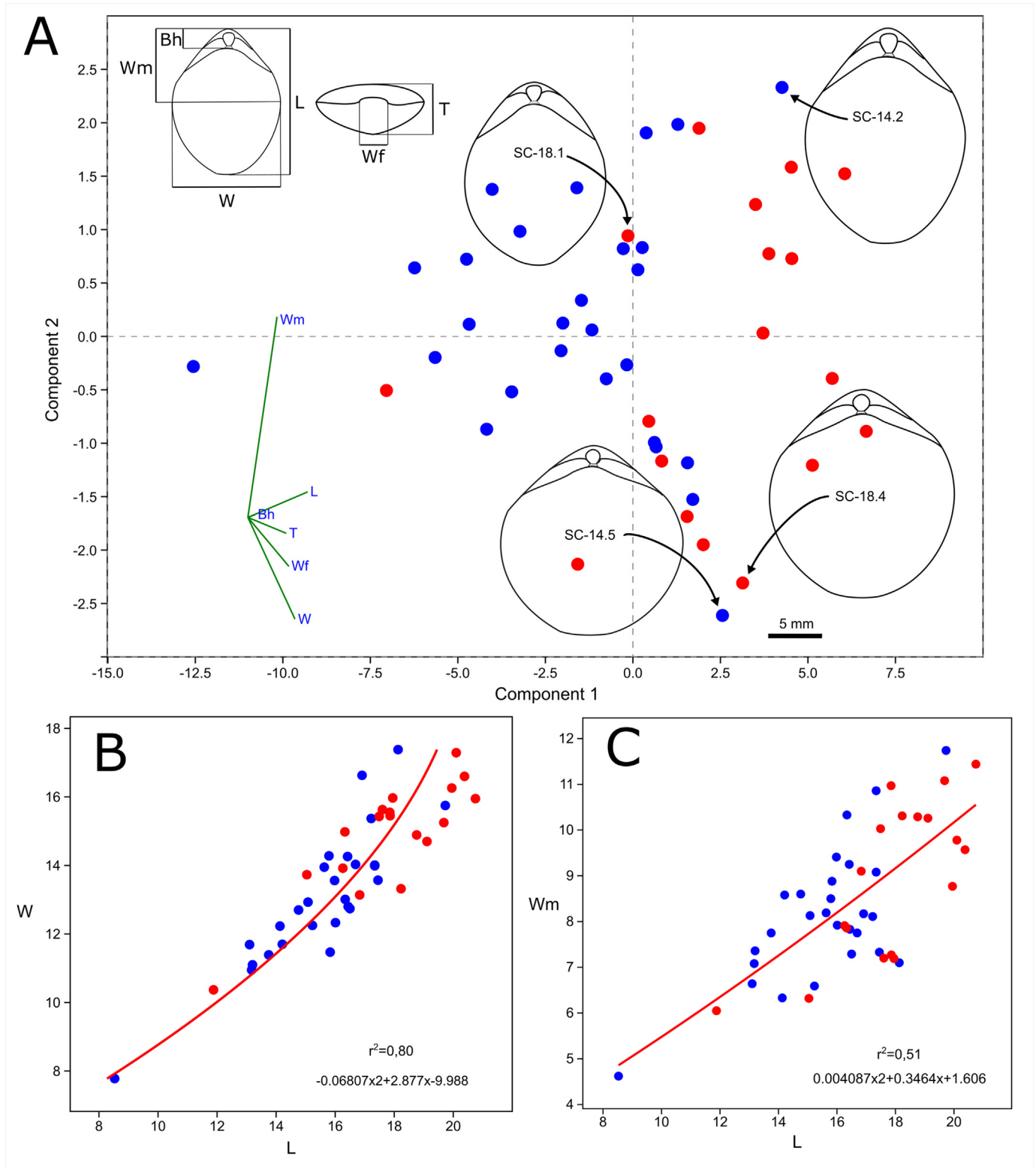


Fig. 16. Morphometrical scatter plots of the studied specimens of *Psilothyris hispanica* [Iñesta and Calzada, 1996](#) (blue and red dots correspond to the stocks of the SC-14 and SC-18 beds, respectively). **A.** Morphospaces defined by the two main axis of the Principal Component Analysis (PCA) taking into account six dimensional variables considered as representative: apart from the main biometric parameters: length, width, and thickness (L, W, T), the distance from the apex to the maximum width of the shell (Wm), the width of the dorsal median fold (Wf), and the length of the beak area (Bh) are considered. Dimensional vectors have been represented showing the main discriminating factors. **B, C.** Bivariate analysis plotting W and Wm against length (L) for better understanding morphological variability in terms of allometry.

Cenomanian by [Cabañas et al. \(1975\)](#). More recent and accurate biostratigraphical data ([Castro, 1998](#)) ascribed these deposits to the Albian–Cenomanian interval.

Additional eastwards Prebetic-type asymmetrical rhynchonellides from Ibiza ([Azéma et al., 1979](#)) were quoted adopting an open nomenclature (*Cyclothyris cf. difformis*) and were attributed to

the Albian. These specimens were recorded in marly facies without microfaunal markers similar to those herein studied in the Sierra del Cid outcrop.

On the other hand, the earliest record of rhynchonellides in the analyzed assemblages is represented by *Cyclothyris bitirica*, previously mainly attributed to *Cyclothyris deluci*. The biostratigraphic pre-Cenomanian occurrence of *C. bitirica* seems to be more unambiguous, as discussed above.

The calibration of the brachiopod assemblages with more accurate biostratigraphic markers has been possible due to the occasional finding of *Mortoniceras (Subschloenbachia) perinflatum* (Spath, 1922) around the level 11 of the studied section and in equivalent levels from a close outcrop about 200 m away from the main section studied, together with the brachiopods of the *Cyclothyris ementium* Assemblage herein later described. Its unquestionable ribbing pattern, prominent ventral keel and ornamentation become this ammonoid as useful index marker of the uppermost Albian (middle Subzone of the Stoliczkaia Dispar Zone) in several European basins as South-England, SE-France, Switzerland, Hungary, and even in the American basins (e.g. Kennedy et al., 2005; Reboulet et al., 2018).

Summarizing, most of the previous biostratigraphical data indicate the late Albian–earliest Cenomanian age for *C. ementium*, and in those stratigraphic logs where coexists with more accurate biomarkers, it is pointed toward the FAD of this taxon in the Dispar Zone, Perinflatum Subzone, marking the transition from the uppermost Albian to the basal Cenomanian successions. Only a few records of other taxa apparently coeval with *C. ementium* point to the mid-Cenomanian age, but their attributions are ambiguous. Thus, the adoption of an open nomenclature for *Sellithyris* cf. *cenomaniensis* by Iñesta and Calzada (1996) was a proper decision, since this taxon is now synonymized into the new species *Sellithyris binalubensis*, older than their middle Cenomanian counterparts. Similar situation occurs with the open quotation for *Sellithyris* aff. *sella* by Gallemí et al. (1997), since this taxon is widely accredited in the Hauterivian–Aptian from numerous Western Tethyan basins. Finally, in the Prebetic outcrops where bed-by-bed collections were carried out (Gallemí et al., 1997), the middle Cenomanian *Orbirhynchia mantelliana*-horizon is clearly recorded overlying the *Cyclothyris ementium*-bearing levels which mark the Albian–Cenomanian transition.

6.2. The Albian–Cenomanian rhynchonellides turnover in the easternmost Prebetic

The apparent homeomorphism existing in the smooth Cretaceous terebratulides predominant in the brachiopod assemblages prevent their choice as biostratigraphic markers of this timespan. Conversely, the rhynchonellides replacement between the multicostate symmetrical *Cyclothyris bitirica* and the asymmetrical *C. ementium* provides a useful biostratigraphic alternative due to their unambiguous diagnostic criteria. Thus, in the extended Sierra del Cid section, the arrangement of brachiopod assemblages is based on the rhynchonellides distribution as follows:

***Cyclothyris bitirica* Assemblage** (Fig. 2): It is virtually a monospecific assemblage consisting of *C. bitirica*. It is recorded in the lower to middle part of the Sierra del Cid section but the last records of this rhynchonellide can be found coexisting together with several taxa of the subsequent assemblage (levels 9–11 in Fig. 2). It is assigned to the Albian, with the LCO (Last Common Occurrence) previous to the Perinflatum Subzone of the Dispar Zone (upper Albian).

***Cyclothyris ementium* Assemblage** (Fig. 2): It is made up by *C. ementium* as the unmistakable index taxon, being the only rhynchonellide in the assemblage. A burst in abundance of nearly

homeomorphic terebratulides are coeval with this species: the sulcinate *Sellithyris binalubensis* with the dallinide *Psilothyris hispanica* (Iñesta and Calzada, 1996), both showing great intraspecific variability, the latter with specimens from elongate to sub-pentagonal outline, and from rectimarginate to uniplicate types (even stocks with slightly sulcate anterior commissure are recorded in the more marly levels: 10 and 15 in Fig. 2). This assemblage is recorded in the upper half of the section (from levels 9–10 upwards), probably related to the shift to more marly/sandy facies. The FAD of this assemblage is herein established around the Albian–Cenomanian boundary.

The replacement between these two assemblages evidences a well-defined faunal succession discernible in the Sierra del Cid section around the levels 9–10. The most remarkable bioevent is the rhynchonellide short-term replacement entailing the LAD of *Cyclothyris bitirica* and the FAD of *C. ementium* around the level 10. Additionally, in this faunal turnover, the sudden occurrence and subsequent progressive burst on diversity and abundance of smooth terebratulides is detected, with nearly homomorphic morphologies and strongly differentiated anterior commissure types (sulcinate, highly-uniplicate, sulcate, episulcate) dominating the assemblages. This compositional change suggests a facies-related control on the brachiopods distribution. In all the above-revised localities, *C. ementium* is recorded in a marly succession with marl-sandy limestone beds intercalated, typifying a platform environment with frequent terrigenous inputs in transition to the more offshore areas apparently with more marly content than the levels where *C. bitirica* is recorded. Comparable faunal replacements influenced by depositional sequences but with different environmental implications were previously reported in the Early Jurassic (Toarcian) and in the Early–Middle Jurassic transition brachiopod assemblages from the Iberian Range entailing premature turnovers and involving homeomorphic morphotypes (García-Joral et al., 1990; Baeza-Carratalá et al., 2016).

Owing to the biostratigraphical analysis carried out, it can be concluded that the FAD of the asymmetrical *Cyclothyris ementium* and the sudden burst of smooth terebratulides are useful index biomarkers for the levels just underlying the base of the Cenomanian stage in the Prebetic domain and its occurrence must be unrelated to that of the *C. difformis* (Valenciennes in Lamarck, 1819) in the remaining Tethyan basins. The biostratigraphic potential of the faunal replacement *C. bitirica* (with Albian affinity)–*C. ementium* (also coeval with the Cenomanian affinity fauna) is not only supported in the Sierra del Cid outcrops, but also in the most of the Prebetic localities (Leret et al., 1976; Azéma, 1977; Martínez del Olmo et al., 1978; Iñesta and Calzada, 1996; Gallemí et al., 1997; Mora-Morote, 2000).

7. Conclusions

The analysis of the brachiopod assemblages from the easternmost South-Iberian paleomargin in the Albian–Cenomanian transition has allowed the recognition of a new brachiopod fauna endemic to the Eastern Prebetic Domain, leading to the erection of two new species, *Cyclothyris bitirica* and *Sellithyris binalubensis*, recorded together with *Cyclothyris ementium*, also recently described as a new species, plus the terebratulid *Psilothyris hispanica*, likewise endemic to the Prebetic area hitherto, whose diagnosis has been herein emended due to its high intraspecific variability. This endemic character of the fauna can lead to new research lines on the palaeobiogeographic relationships between the Early and Late Cretaceous brachiopods biohermas.

After considering the facies and localities where the brachiopod fauna analyzed is recorded, depositional environments point to

platform habitats with frequent terrigenous inputs in transition to the more offshore areas.

The endorsement of all previous records of *Cyclothyris difformis* in the region to *C. ementitum* and the establishment of its diagnostic criteria and the accurate biostratigraphical range indicate that the younger Prebetic forms with obligate type of asymmetry (commissural asymmetry) must be unrelated to the proper Cenomanian records of *C. difformis* with facultative type of commissural asymmetry in the remaining Tethyan basins.

Brachiopod fauna of the studied region has been arranged into two assemblages with biochronostratigraphical significance: *Cyclothyris bitirrica* Assemblage and *C. ementitum* Assemblage. The first one is assigned to the late Albian, with the Last Common Occurrence prior to the Perinflatum Subzone of the Dispar Zone. On the other hand, the First Appearance Data of the *Cyclothyris ementitum*. Assemblage is established around the Albian–Cenomanian boundary. The successive faunal replacement between these two assemblages is a useful index biomarker, typified by a rhynchonellide short-term replacement entailing the LAD of *C. bitirrica* and the FAD of *C. ementitum*, and the sudden occurrence and subsequent burst on diversity/abundance of smooth, nearly homomorphic, and with strongly differentiated folding pattern terebratulides for the levels just underlying the base of the Cenomanian stage.

Acknowledgments

Authors would like to thank to Dr. Philippe Fauré from the Muséum of Toulouse (France), for his help with the specimens of the Leymerie Collection, providing us photographs and measurements of the holotypes of *Cyclothyris aturica* and *Cyclothyris regularis*. To Dr. Diego García-Ramos for his help providing ammonite data in assemblage together with *C. ementitum*. To Dr. Fernando Barroso-Barcenilla from the University of Alcalá, Spain, for review the specimens of the ammonites *Mortonicerias* (*Subschloenbachia*) *perinflatum*. The attention of the staff of the Department of Culture of the City Council of *Poble Nou de Benitatxell* (Alicante) providing several specimens from the Moraig Cave is highly appreciated. The preliminary fieldwork with the help of Christian Molina was very successful. The critical reviews and helpful comments of Editors, Prof. Barbara Radulović, from the Faculty of Mining and Geology, University of Belgrade, Serbia, and other anonymous reviewer have clearly improved the quality of the paper. This research has been partially financed by a Grant for young researchers to MB-C from the Spanish Society of Palaeontology 2021 (AJISEP-2021-XXXX1), and it is a contribution to the Research groups *Procesos Bióticos Mesozoicos* from the Complutense University of Madrid (UCM), Paleolbérica from the University of Alcalá (UAH), VIGROB-167 (University of Alicante), and to the IGCP-710 Western Tethys meets Eastern Tethys.

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