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The rudist genus *Sellaea* Di Stefano, 1889 (Bivalvia, Hippuritida) in the Albian carbonate platforms of Cantabria (N Spain): biostratigraphical and paleobiogeographical implications

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ABSTRACT
During the Cretaceous, the gradual and extensive diversification of rudists led this group to colonise the carbonate platforms of tropical seas all over the world, structuring new ecosystems. The Albian genus *Sellaea* Di Stefano, 1889 has a worldwide distribution ranging from the Caribbean to Tibet, with maximum diversity centered in the Mediterranean province. This genus, recently studied in American faunas, is an important witness of the paleobiogeographical dynamics at work during this process of diversification, which generated significant endemism and helped characterise the paleobiogeographical provinces of the late Early Cretaceous. In order to add to our knowledge of this genus and the paleobiogeography of rudists, we report the existence of *Sellaea* in Cantabria, Spain. The middle and late Albian age is based on the presence of the ammonite *Anahoplites* Hyatt, 1900 and the rudists *Eoradiolites jumillensis* Masse, Fenerci-Masse, Vilas & Arias, 2007 and *Caprina choffati* Douvillé, 1898. Specimens have been identified as *Sellaea stryx* (Di Stefano, 1889), a species without pallial canals that belongs to the Mediterranean clade, a sister group to the American *Sellaea*. After describing in detail the localities where the specimens were found, we show the relevance of the presence of *Sellaea stryx* in the Cantabrian Albian faunas from a biostratigraphic point of view. We also discuss the impact of the presence of these faunas from a paleobiogeographical point of view.

KEY WORDS
Bivalvia,
Sellaea,
rudists,
ammonoids,
Spain,
Cretaceous,
Albian,
Basque-Cantabrian
basin,
paleobiogeography,
biostratigraphy.

RÉSUMÉ
Le genre de rudistes Sellaea *Di Stefano, 1889 (Bivalvia, Hippuritida) dans les plateformes carbonatées albiennes de Cantabrie (Nord de l'Espagne) : implications biostratigraphiques et paléobiogéographiques.*
Au Crétacé, la diversification progressive et importante des rudistes va amener ce groupe à coloniser les plateformes carbonatées des mers tropicales partout sur le globe, en structurant de nouveaux écosystèmes. Le genre albien *Sellaea* Di Stefano, 1889 est à répartition mondiale, présent des Caraïbes au Tibet avec un maximum de diversité centré sur la marge sud de la province méditerranéenne. Ce genre, récemment étudié pour ses faunes américaines, est un témoin important de la dynamique paléobiogéographique à l'œuvre durant ce processus de diversification ayant généré un endémisme important, et qui participe à la caractérisation des provinces paléobiogéographiques de la fin du Crétacé inférieur. Afin de compléter nos connaissances sur ce genre et sur la paléobiogéographie des rudistes, nous mentionnons l'existence de *Sellaea* en Cantabrie (Espagne) à l'Albien moyen et supérieur daté par la présence de l'ammonite *Anahoplites* Hyatt, 1900 et des rudistes *Eoradiolites jumillensis* Masse, Fenerci-Masse, Vilas & Arias, 2007 et *Caprina choffati* Douvillé, 1898. Les spécimens sont identifiés à l'espèce *Sellaea stryx* (Di Stefano, 1889), une espèce sans canaux palléaux appartenant au clade méditerranéen, groupe-frère des *Sellaea* américains. Après avoir décrit précisément les localités où ont été retrouvés les spécimens, nous montrons l'intérêt de la présence de *Sellaea stryx* dans les faunes cantabriques albiennes d'un point de vue biostratigraphique. Nous discutons également l'impact de la présence de ces faunes et des faunes associées du point de vue paléobiogéographique.

MOTS CLÉS
Bivalvia,
Sellaea,
rudistes,
ammonites,
Espagne,
Crétacé,
Albien,
Bassin basco-cantabrique,
paléobiogéographie,
biostratigraphie.

INTRODUCTION

Rudists are a diverse group of Late Jurassic to Cretaceous bivalves that gradually spread across the carbonate platforms of warm, shallow waters (Gili & Götz 2018; Skelton 2018). The study of Cretaceous rudist diversification requires a better understanding of its biogeographical modalities, with the invasion of tropical carbonate platforms throughout the world, which generated a notable endemism (Sha *et al.* 2020). The Albian genus *Sellaea* Di Stefano, 1889 is particularly interesting for its morphoanatomy, which makes it a potential sister group to the canaliculated rudists (Skelton & Masse 1998; Rineau *et al.* 2020). Also, its paleogeographical distribution links the Mediterranean and American provinces.

The genus *Sellaea* was first described from Italy, and has been subsequently recorded from Oman (Skelton & Masse 1998), Egypt (Steuber & Bachmann 2002), North America (Scott *et al.* 2016), and Tibet (Rao *et al.* 2015). It dates to the Albian, with one other occurrence from the Cenomanian of Western Europe (Orbigny 1842a; Rineau & Masse 2022). In the Middle East and the Mediterranean Tethyan domain, *Sellaea* was recorded from the southern margin. Its presence in Texas was first proposed by Coogan (1977), and subsequently formally described as new endemic species by Davis (1980). The presence of the genus *Sellaea* in North America was challenged by Skelton & Masse (1998), then fully recognized by Scott *et al.* (2016) and by Rineau & Masse (2022). A single species, *Sellaea minuta* Davis, 1980, is restricted to the Americas and is now considered as the sister group of all other *Sellaea*, a diverse group of at least 13 species gathered in a Mediterranean clade (Rineau & Masse 2022). The diagnostic characters of the genus include a conical right valve, a coiled left valve, and two accessory cavities in the left valve, one anterior and one posterior (Rineau & Masse 2022). The presence of canals flanking the anterior myophore of the right valve, formerly regarded as a generic character (Dechaseaux *et al.* 1969; Skelton & Masse 1998) was then considered by Rineau & Masse (2022) merely specific, as in *Pachytraga* Paquier, 1900. The inclusion of '*Caprotina*' *sensu* Di Stefano (1889) into *Sellaea* was based on the foregoing, coupled with cladistic analysis (Rineau *et al.* 2020; Rineau & Masse 2022).

The present paper deals with the discovery of *Sellaea* in the Basque-Cantabrian Basin (Northern Spain), and of its biogeographical and systematic significance. The genus is divided in two endemic clades, the first being composed of a single species, *Sellaea minuta* Davis, 1980, and restricted to the Americas, the second, being a diverse group of at least 13 species and known only from the Mediterranean province. Finally, we discuss potential biostratigraphic implications of this finding.

GEOLOGICAL SETTING

The Aptian-Albian sedimentary successions of the Basque-Cantabrian Basin are traditionally referred to as the Urgonian Complex, a rock package formed in various sedimentary environments ranging from fluviatile to nearshore, shallow-marine and marine deeper-water (García-Mondéjar 1979; Rat 1988). In the province of Cantabria, in the western Basque-Cantabrian Basin, differential subsidence was induced by syn-sedimentary tectonic activity and influenced the development of depositional highs with reduced sedimentation and lows with thick sequences (García-Mondéjar *et al.* 2004). Here, we highlight Albian sedimentary rocks in the Basque Cantabrian Basin that reveal previously unreported *Sellaea* rudist faunas in the Tethyan northern Mediterranean margin.

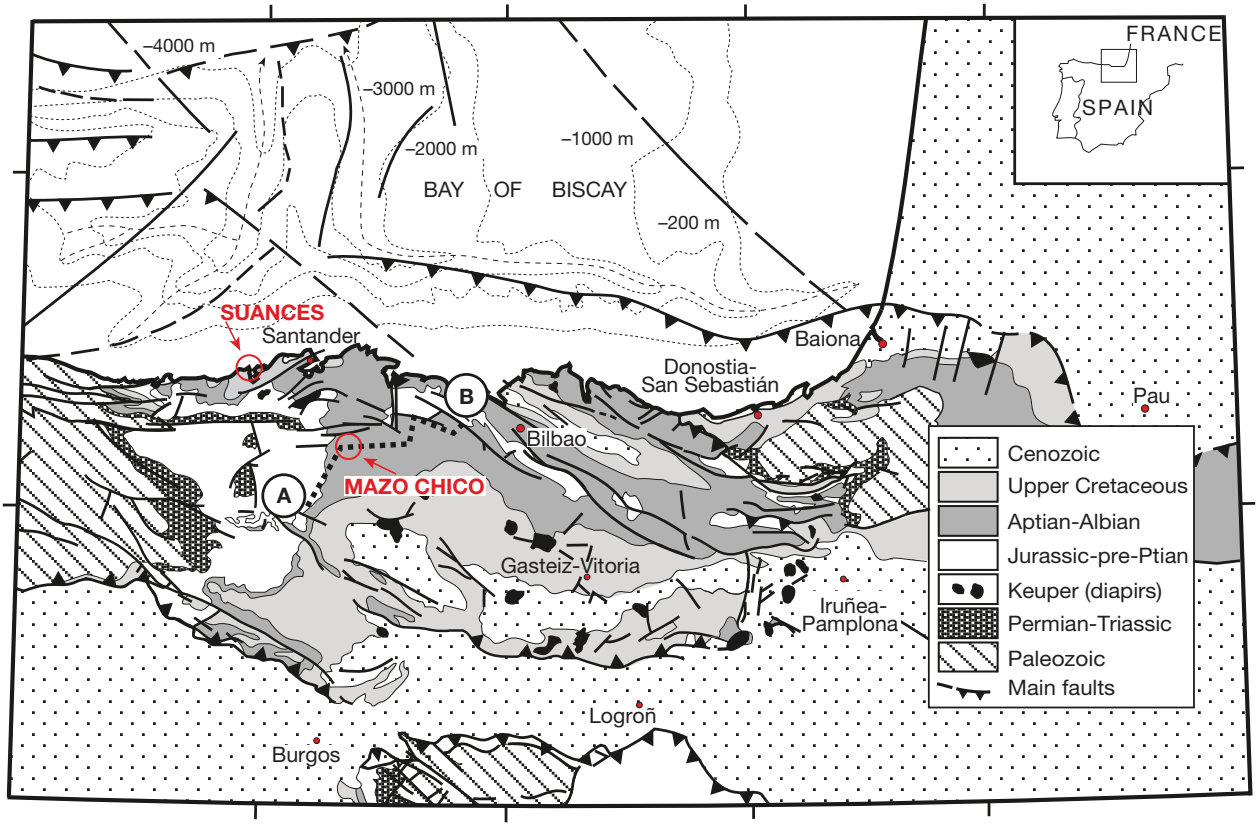

Fig. 1. — Geological map of the inverted Basque-Cantabrian basin (Western Pyrenees) with the localities bearing the rudist *Sellaea* sp. highlighted in red. Conceptualization and drawing: Mikel A. Lopez-Horgue.

Specimens of *Sellaea* were found at two localities in the Cantabria Province in northern Spain: the Soba valley (Mazo Chico) (Fig. 1), an area of relative high subsidence rate and thick deposits, and in Suances, with very reduced overall sedimentation rates and consequent thinner record (Fig. 1).

Soba valley (Mazo Chico)

The Soba municipality lies in SE Cantabria (Fig. 1). The *Sellaea* rudists are located north of La Gándara village on the Mazo Chico peak. This peak lies in the Hornijo Mountain chain and includes Cretaceous rocks of the Urgonian Complex (lower Aptian-middle Albian). The W-E trending Hornijo mountain (Fig. 2A) is composed primarily of shallow marine rudist limestones and reveals small basinward-trending limestone tongues, like San Pedro and Mazos. The Mazo Chico limestone peak at an altitude of 1.100 m at R: 454650 and H: 4786250 is part of the Mazos tongue (Fig. 2B). This limestone tongue progrades SE encompassing the Tejes, Mazo Chico and Mazo Grande peaks (Fig. 3). A frontal talus trends SE and additional talus margins trend toward the SW and NE (Fig. 4).

The Hornijo carbonate platform is made of shallow-water limestones of the Ramales Formation. The limestones interdigitate southwards with the basinal marly Soba Formation (García-Mondéjar 1985). The transition occurs through rapid facies changes from reef-mound limestones to talus breccias and further to basinal marly facies. The rectilinear platform margin and its vertically persistent character are related to synsedimentary block-faulting and differential subsidence. Offshore banks (Aja) and a prograding barrier tongue (Mazos) are highlighted in an E-W stratigraphic cross-section (Fig. 4). The Mazos tongue is composed of shallow-water limestones 0.3 km wide and 150 m thick and extends 3 km basinwards. The Mazos tongue cross-section reveals an internal stacking of reef-mounds (Fig. 4) and the origin of the prograding tongue is related to a sea-level lowering (García-Mondéjar 1985).

The Mazo Chico limestones lithosome nucleus is massive although at both western and eastern edges bedding is recognized (Figs 4; 5). This bedding dips away from the nuclear zone (Fig. 4). The Mazo Chico limestones are made up of scattered dominantly requieniid rudists floating in micritic matrix that pass laterally to clinoformal grainier limestones (Fig. 5) and farther downflank to marls, marly limestones and sandstones that formed in adjacent slightly deeper-water marine environments (García-Mondéjar 1979, 1985).

Towards the upper part of the Mazo Chico limestones, an outstanding unit is made up of a remarkable rudist assemblage composed of *Sellaea* (Fig. 5A).

The Mazo Chico limestone unit is divided into two subunits by a silicliclastic sandstone bed that locally pinches out in the Mazo Chico SE face (Fig. 5A, B). Locally both limestone subunits are welded and the lower subunit top displays sandstone paleokarstic infills in the topmost 2 metres. Fissure-filling siliclastic red mudstones (Neuweiler 1995) suggest a regressive episode with subaerial exposure.

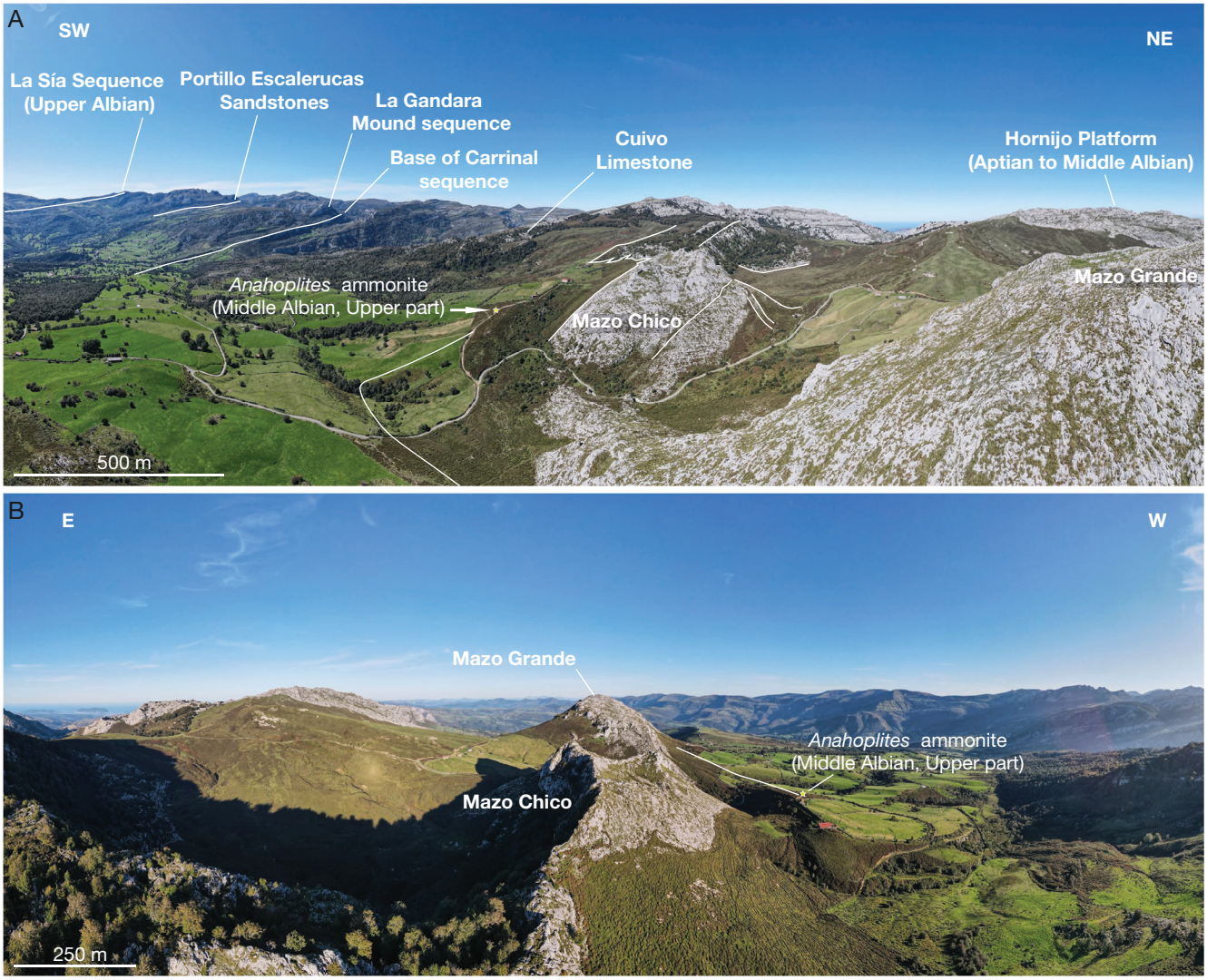

Fig. 2. — **A**, Aerial view of the Hornijo carbonate platform (Aptian-Middle Albian) to the la Sía sequence (Upper Albian) stratigraphic succession; the Mazo Chico is interstratified within the grass-covered basinal marls; the average dip is 20° southwestwards; **B**, aerial view of the Mazos tongue (limestone ridge), composed of the Mazo Chico and Mazo Grande outcrops. The ammonites new find (*Anahoplites* sp.) and its lateral stratigraphic bed line (dashed) are highlighted. Conceptualization: P. A. Fernandez-Mendiola/drawing: Juan Pedro Rodríguez-López.

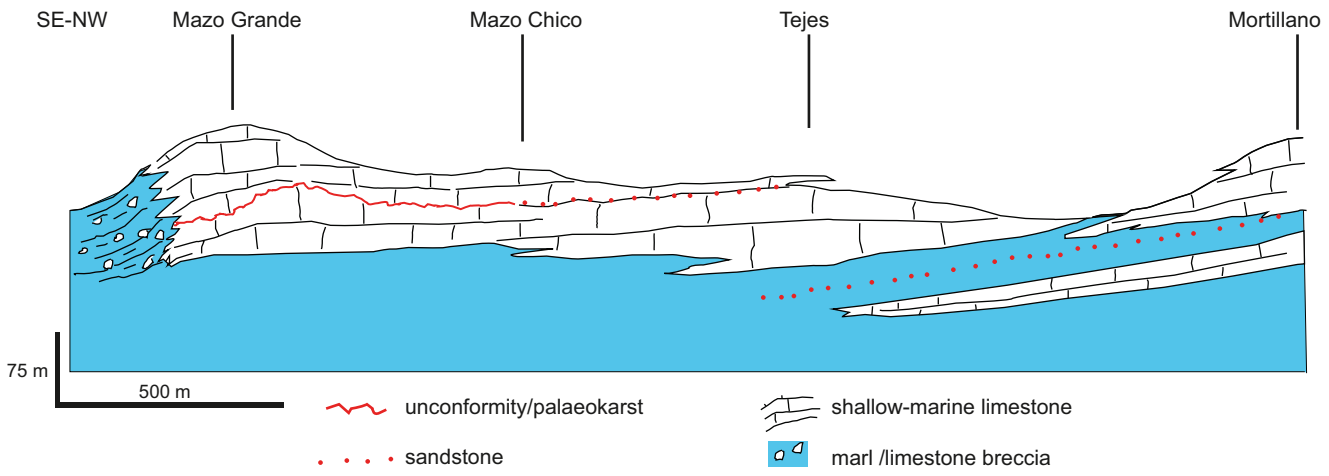

Fig. 3. — Longitudinal stratigraphic cross-section of the Mazos limestone tongue, prograding basinwards to the southeast. Conceptualization: P. A. Fernandez-Mendiola/drawing: Juan Pedro Rodríguez-López.

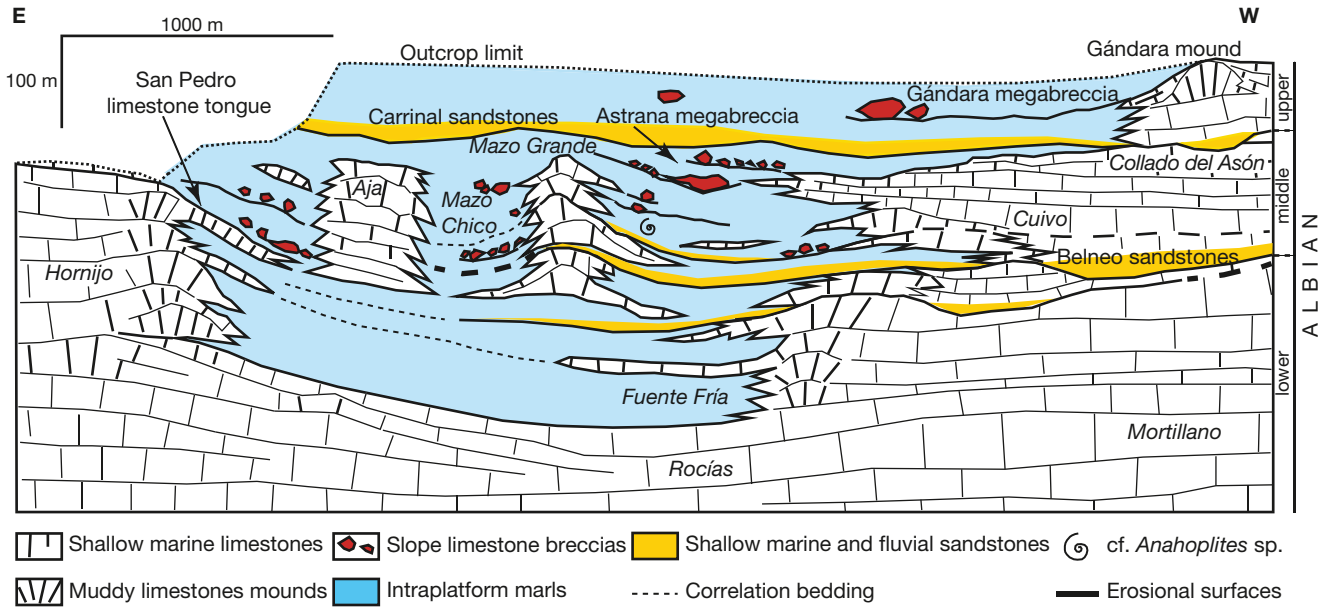

Fig. 4. — Stratigraphic framework of the Mazo Chico limestones in the the Sierra de Hornijo/valle de Soba area. In blue colour intraplatform basin trough, with carbonate mud mounds development inside it (Mazo Chico-Mazo Grande and Aja). Conceptualization: P. A. Fernandez-Mendiola/drawing: Mikel A. Lopez-Horgue.

The lower subunit reaches a maximum thickness of 70 metres and the upper subunit is 55 metres thick and recent erosion of its top prevents maximum thickness estimates.

The upper unit is dominated by beds of requieniid rudists (*Pseudotoucasia santanderensis* Douvillé, 1889) with a wackestone matrix, with local *Chondrodonta* Stanton, 1901 rudstones. Limestone beds with corals, requieniids, brachiopods and nerineid gastropods are locally observed. Near the top of Mazo Chico limestones, beds are subhorizontal (Fig. 5C). Within a succession of dominant scattered requieniid wackestones, an 8 m-thick outstanding limestone package contains a dense and rich *Sellaea* congregation together with *Horiopleura* Douvillé, 1889, *Eoradiolites jumillensis* Masse, Fenerci-Masse, Vilas & Arias, 2007, requieniids, caprotinids, and *Chondrodonta*. Patchy areas of micritic matrix with scarce rudists contrast with areas of dense aggregations of *Sellaea* and other metazoans. A 30 cm thick synsedimentary vein vertically crosscuts the micritic requieniid facies along a minimum horizontal distance of 3 m and deepens for at least 20 cm. The veins are filled with peloidal micrites devoid of rudists or metazoans. These veins are interpreted as synsedimentary fissures (neptunian dykes).

The Mazos tongue has been interpreted as a composite carbonate mound structure based on the depositional geometry, massive character and micritic composition (Pascal & Przybyla 1989; Neuweiler 1995). The Aja limestone lithosome represents an offshore bank that is laterally equivalent to the Mazos tongue (Fig. 4). In the lower part of the Mazos limestone, scleractinian corals, *Eoradiolites* Douvillé, 1909, *Polyconites* Roulland, 1830, *Arabicodium* Elliott, 1957, gastropods, the sponge, *Euzkadiella* Mercet, 1922, and lithistid demosponges, together with *in situ* peloidal facies revealing stromatolite/automicrite origin are common (Neuweiler 1995).

The mound flanks consist of grainstones and packstones and coral-rich limestones. A section of the southwestern Mazo Chico limestone clinoformal margin encountered coral fragments, gastropods, bryozoans, terebratulids, brachiopods, lithistid sponges, *Toucasia* Munier-Chalmas, 1873 like rudists, orbitolinas, *Ethelia* Weber-van Bosse, 1921, *Lithocodium* Elliott, 1956, *Arabicodium* Elliott, 1957 and *Euzkadiella* (Neuweiler 1995). The succeeding section is marly and silty with occasional talus/slope beds (breccias and megabreccias) which correlate with the topmost beds and the eroded Mazo Chico cap.

The mound flanks consist of marls and slope calcareous tongues of rudist and *Chondrodonta* rudstones, siltstones and sandstones with ferruginous concretions, micritic limestone, siltstones, brecciated slope tongues with limestone clasts containing *Eoradiolites jumillensis*, requieniids, and scleractinian corals, drapped by siltstones with pyritized ammonites (cf. *Anahoplites*; Appendix 1).

Suances area

Suances municipality lies on the coast of the Cantabria Province, northern Spain. *Sellaea* rudists are found in the nearby Punta del Dichoso headland section. This section lies about 50 km northwest of Soba and 20 km west of Santander (Fig. 1). The Punta del Dichoso sedimentary succession was previously described by Pascal (1985) and Najarro (2015). It is approximately 80 m thick, and it is composed of five Aptian-Albian lithostratigraphic units (Fig. 6): San Esteban Formation (lower Aptian), Rodezas Formation (lower-upper Aptian), Reocín Formation (late Aptian), Barcenaciones Formation (late Albian), and the Bielva Formation (late Albian-early Cenomanian). The sedimentary record at Punta del Dichoso (80 m) is significantly different than the coeval succession at Soba (3500 m;

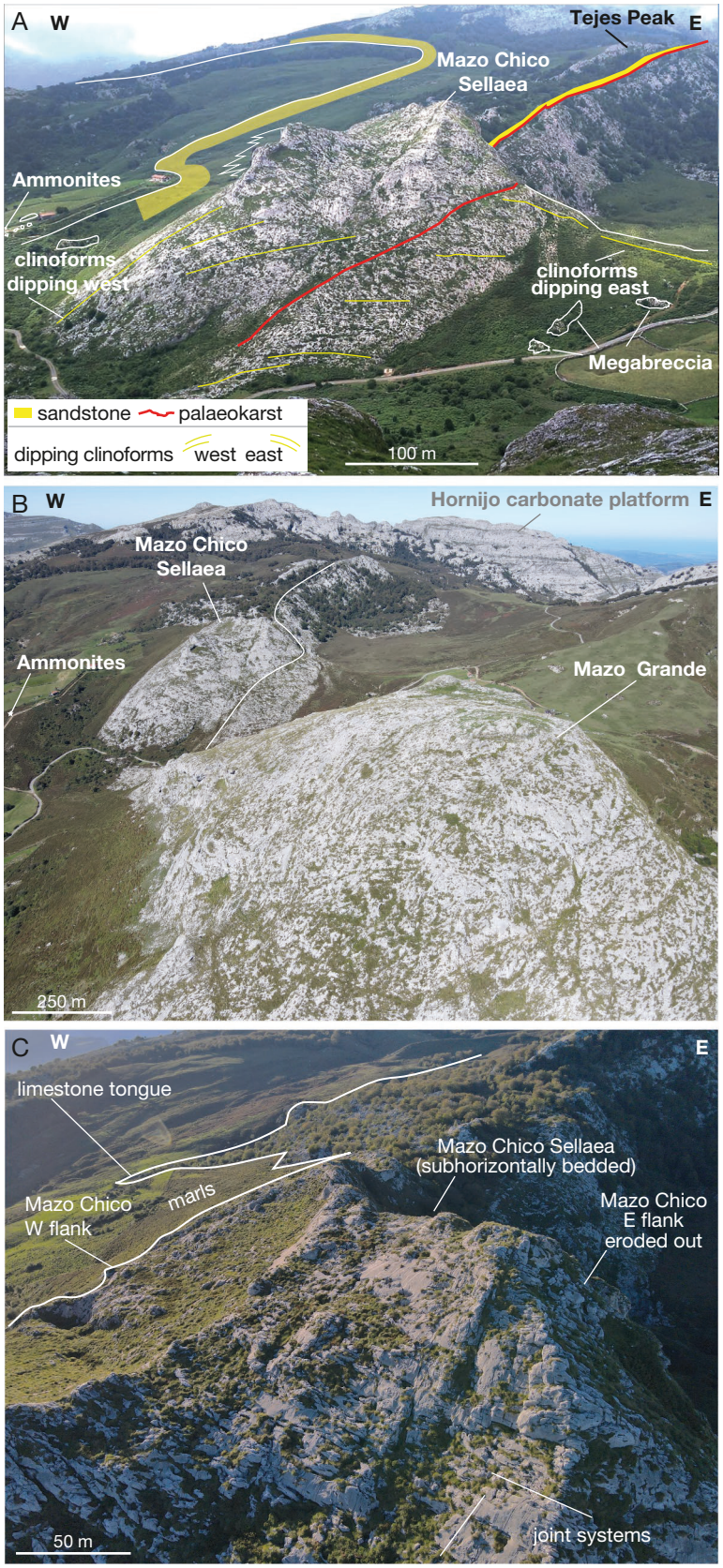

FIG. 5. — *Sellaea* sp. stratigraphic setting in the Mazos limestone tongue: **A**, two limestone units are recognized separated by an unconformity surface overlain by a sandstone; **B**, aerial view of the Hornijo carbonate platform in the back, and Mazo chico and Mazo Grande peaks forming the Mazos limestones unit and developing along perpendicularly to the platform margin. West of the Mazo Chico, the location of the *Anahoplites* ammonite is highlighted; **C**, Mazo Chico aerially viewed from the SE, with indication of the *Sellaea* outcrop in massive limestone with marked postdepositional joint systems. Western flanking beds and overlying marls are depicted. Conceptualization: P. A. Fernandez-Mendiola/drawing: Juan Pedro Rodríguez-López.

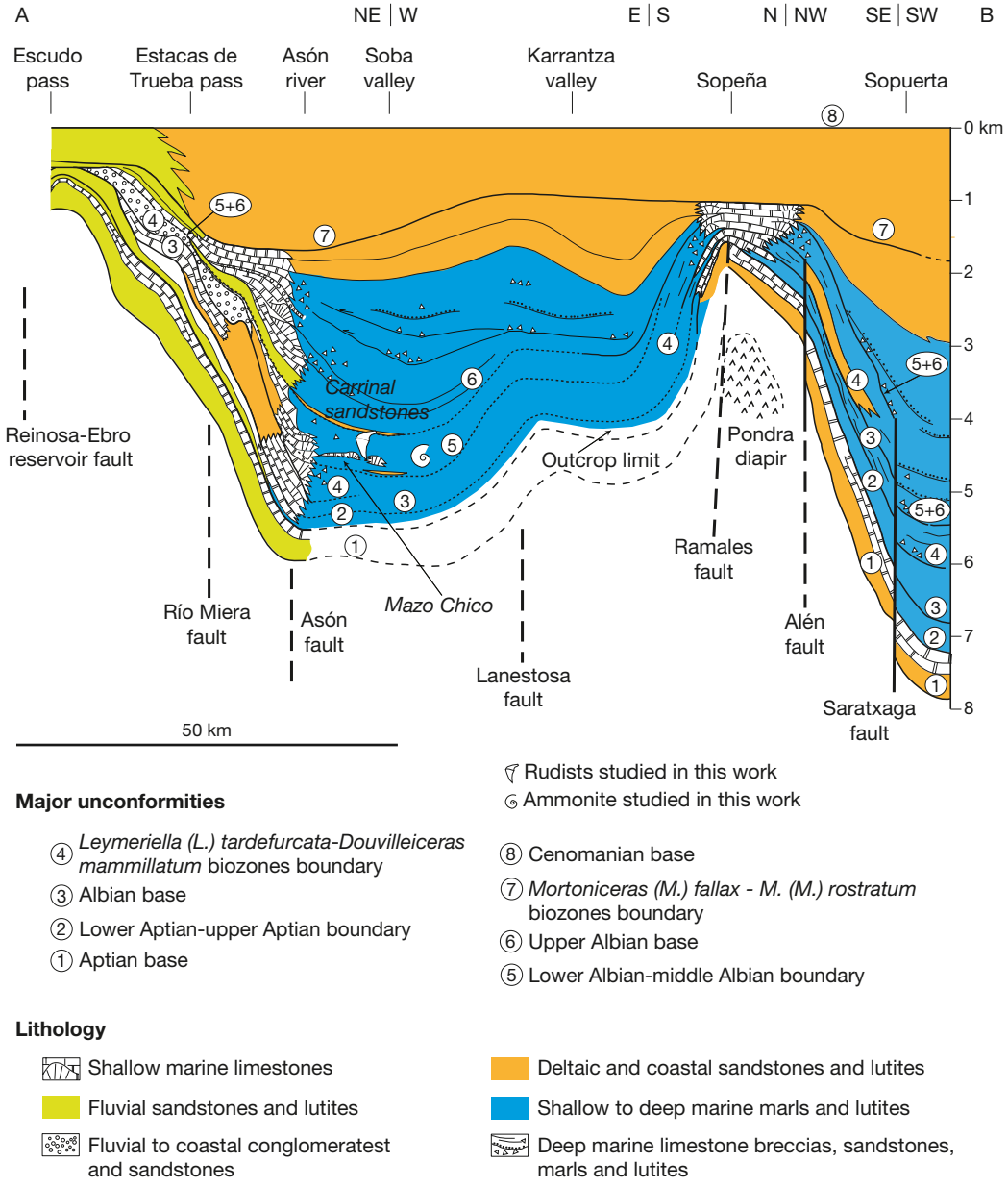

FIG. 6. — Stratigraphic cross section of the Aptian-Albian interval from the Escudo pass through Soba and Karrantza valleys to Sopuerta (near Bilbao) as to show the precise facies relatioships and major unconformities. Dating comes after biostratigraphical control based on ammonoids in deeper troughs and on orbitolinids in coeval shallow marine carbonate platforms (modified from García-Mondéjar *et al.* 2004). Mazo Chico limestones and coeval units including the *Anahoplites* ammonites are figured in the Soba trough. Upper Albian biozonation after López-Horgue & Owen (2004). For location of this A-B section see the Figure 1. Conceptualization: P. A. Fernandez-Mendiola/drawing: Mikel A. Lopez-Horgue.

García-Mondéjar 1979). This fact is explained by Punta del Dichoso occurring in an independent structural unit (Santander Coastal Block) that underwent much less subsidence than the structural domain to which the Soba area belongs (e.g., Barnolas & Pujalte 2004). On the other hand, the Punta del Dichoso sedimentary record was deposited on a local paleohigh (i.e., Punta del Dichoso Block; Pérez-Malo *et al.* 2017), thus resulting in a condensed section with stratigraphical gaps.

The rudists, *Sellaea* occur together with caprinids within the 13 m-thick Barcenaciones Formation (Fig. 7). The unit is heterogenous (mixed carbonate-siliciclastic) and is made up of calcarenitic beds containing variable amounts of clay and/or sand. Coarse-grained and cross-bedded grainstones are interspersed in the lower and middle parts of the unit. Up-section, different types of rudists (radiolitids, requieniids, caprinids, polyconitids) and corals become especially common. *Caprina choffati* Douvillé, 1898 rudists occur at several stratigraphic levels, especially in the uppermost 4-5 metres, where they appear together with *Sellaea* specimens (Fig. 7). The Barcenaciones was deposited in middle to outer platform environments (Najarro 2015). This mixed (carbonate-siliciclastic) platform

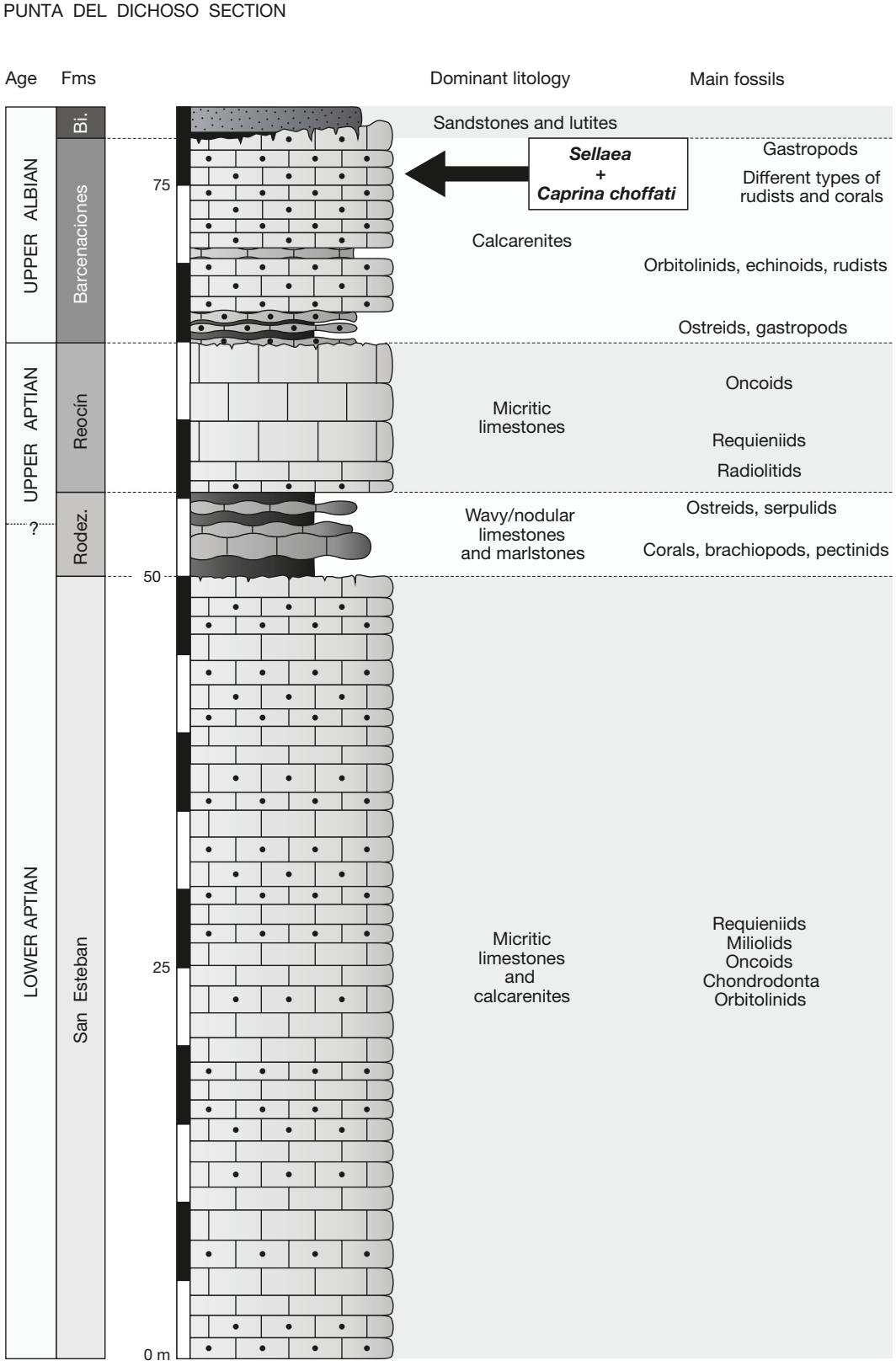

FIG. 7. — Synthetic stratigraphic log showing the five lithostratigraphic units outcropping in Punta del Dichoso headland: San Esteban Fm, Rodezas Fm, Reocín Fm, Barcenaciones Fm and Bielva Fm (*p.p.*). Dominant lithologies, main discontinuity surfaces and most frequent fossils are also displayed. Conceptualization and drawing: Joanaitz Pérez-Malo.

was subaerially exposed, and as a result, an irregular paleokarst surface with local paleorelief was developed. After that, sandstones and lutites of the Bielva Formation buried the Urgonian carbonate-platform succession of Punta del Dichoso section.

ABBREVIATIONS

aac	anterior accessory cavity;
am	anterior myophore;
at	anterior tooth;
ats	anterior tooth socket;
ct	central tooth;
cts	central tooth socket;
bc	body cavity;
lv	left valve;
pac	posterior accessory cavity;
pm	posterior myophore;
pt	posterior tooth;
pts	posterior tooth socket;
rv	right valve.

SYSTEMATIC PALEONTOLOGY

The suprageneric classification follows Carter *et al.* (2011) and Skelton (2013a, b). All terms and abbreviations used herein follow the homology redefinitions of Rineau *et al.* (2020).

Class BIVALVIA Linnaeus, 1758
Infraclass HETEROCONCHIA Gray, 1854
Order HIPPURITIDA Newell, 1965
Suborder HIPPURITIDINA Newell, 1965
Superfamily CAPRINOIDEA d'Orbigny, 1850
Family CAPRINULIDAE Yanin, 1990

Genus *Sellaea* Di Stefano, 1889

TYPE SPECIES. — *Caprotina zitteli* Di Stefano, 1889 (Di Stefano 1889: 28, 30, pl. 8, figs 1a, b, 2a, b, c, 3), by subsequent designation of Kutassy (1934).

DIAGNOSIS (from Rineau & Masse 2022). — Rudist with coiled left valve and uncoiled conical right valve. On the left valve, presence of a posterior cavity and an undivided anterior cavity. Posterior cavity filled with one or two septa in some species. The posterior myophore of the left valve is outwardly directed on a plate protruding into the posterior myophoral cavity on the right valve, facing the vertical posterior myophore of the right valve. On the right valve, canals can be present in a shell thickening located anteriorly from the anterior myophore.

Sellaea stryx (Di Stefano, 1889)
(Fig. 8A-F)

Caprotina stryx Di Stefano, 1889: XI, 23, 24, 40, pl. 7, fig. 1a-f. — Parona 1899: 381. — Parona *et al.* 1909: 186, pl. XXII, figs 2-3. — Kutassy 1934: 140, 141.

Caprotina cfr. *strix* – Parona 1897: 14.

Sellaea stryx – Rineau & Masse 2022: 2, 5, 9, 12, 13.

MATERIAL EXAMINED. — *Sellaea* is found in dense accumulation of both connected and isolated shells in Mazo Chico (Soba Valley) (Fig. 8G). Only outcrop photographs of natural sections have been studied due to the hardness of the limestone beds that prevent sampling specimens.

STUDY INTERVAL. — Mazo Chico limestones, Ramales Formation (upper middle Albian).

DESCRIPTION

Shell inequivalve; left valve conical and coiled (less than one whorl), right valve conical and straight, triangular in longitudinal section (Fig. 8A, B; mean height from umbo to commissure approximately 130 mm). Valves ovoid in transversal section (mean section 80 × 60 mm) with a ventral part straight to slightly depressed. Some right valves deformed in transversal section due to growing encrusted to other *Sellaea* individuals in bouquets (Fig. 8C). Outer calcitic shell layer very thin (mean thickness 0.5mm), generally not preserved. Inner aragonitic shell layer thick (mean thickness in ventral part 4 mm). Ligament invaginated in a reniform posterodorsal ligamentary cavity.

Left valve anatomy

Body cavity wide, triangular in transverse section due to ventral flexure. CTS slightly curved to the AT, deep, elongated and narrow, separated from the BC by a very thin blade (thickness < 0.5 mm). PAC well developed posteriorly to the PM (Fig. 8A), divided by a thick wall (mean thickness 4 mm) in two ovoid cavities (10 × 18 mm). A single row of six millimetric circular cavities extend the PAC ventrally on a single specimen (Fig. 8D). PM-LV vertical, inwardly directed, and rooted on a strong wall (mean thickness 5 mm), which separates CTS and PAC-LV, protruding on the RV. PT and AT centimetric, straight and conical. AAC-LV present anterodorsally (Fig. 8B). AM-LV vertical on a thick AM-LV/BC wall.

Right valve anatomy

Body cavity wide, triangular in transverse section due to ventral flexure. ATS and PTS circular, separated by a very large CT that can reach up to 40 mm in height. CT crescentic, surrounding the ATS and tilted towards the posterior side. PMC lying posteriorly, in which lies a vertical PM-RV facing the protruding myophore of the opposite valve. AM-RV rooted anteriorly from the BC on a horizontal shelf; shelf entirely devoid of canals (Fig. 8B).

DISCUSSION

The description of these shells can only match those of *Sellaea stryx* due to the AM-RV located on a horizontal shelf that lacks pallial canals (Fig. 8B). The absence of pallial canals is common to *Sellaea stryx* and *Sellaea sicula* (Di Stefano, 1889), formerly placed in *Caprotina* d'Orbigny, 1842 due to this absence and relocated in *Sellaea* after cladistic analysis (Rineau & Masse 2022). *Sellaea stryx* differs from *S. sicula* by its horizontal AM-RV, whereas it is vertical and protruding into the LV in *S. sicula* as in Caprinulidae Yanin, 1990. The row of pallial canals on the LV observed in a single shell (Fig. 8D) has never been observed in other *S. stryx* specimens. It is likely to be homologous to the PAC, which extends ven-

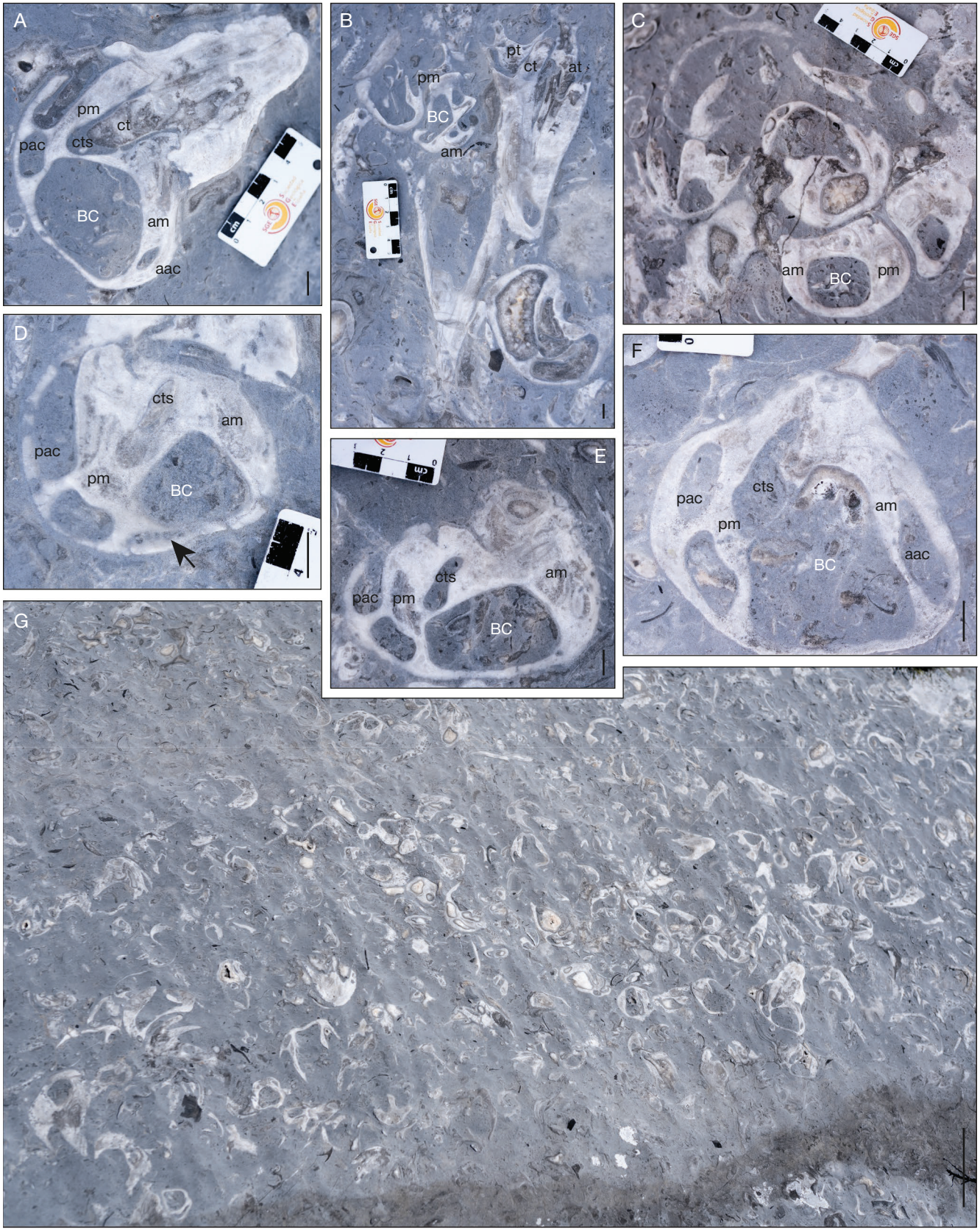

FIG. 8. — Field photographs showing *Sellaea* Di Stefano, 1889 shells discovered in the two areas described in this paper: **A**-**E**, detailed field photographs of *Sellaea stryx* from Mazo Chico showing characteristic anatomical features and ecology; **A**, *Sellaea stryx* LV with characteristic PAC and AAC-LV cavities; **B**, **C**, *Sellaea stryx* in life position showing the elevator habit in bouquets of individuals encrusting on each other in longitudinal (**B**) and transverse (**C**) views; **D**, *Sellaea stryx* LV showing an unusual row of small canals near the PAC; **E**, *Sellaea stryx* LV showing characteristic features of the genus; **F**, field photograph of *Sellae* sp. near *Caprina choffati* from Punta del Dichoso; **G**, field photograph of Mazo Chico limestone showing the *Sellaea* community with parautochthonous shells. Scale bars: A, B, C, D, E, F, 1 cm; G, 10 cm. Conceptualization and drawing: Valentin Rineau, Jean-Pierre Masse and P. A. Fernandez-Mendiola.

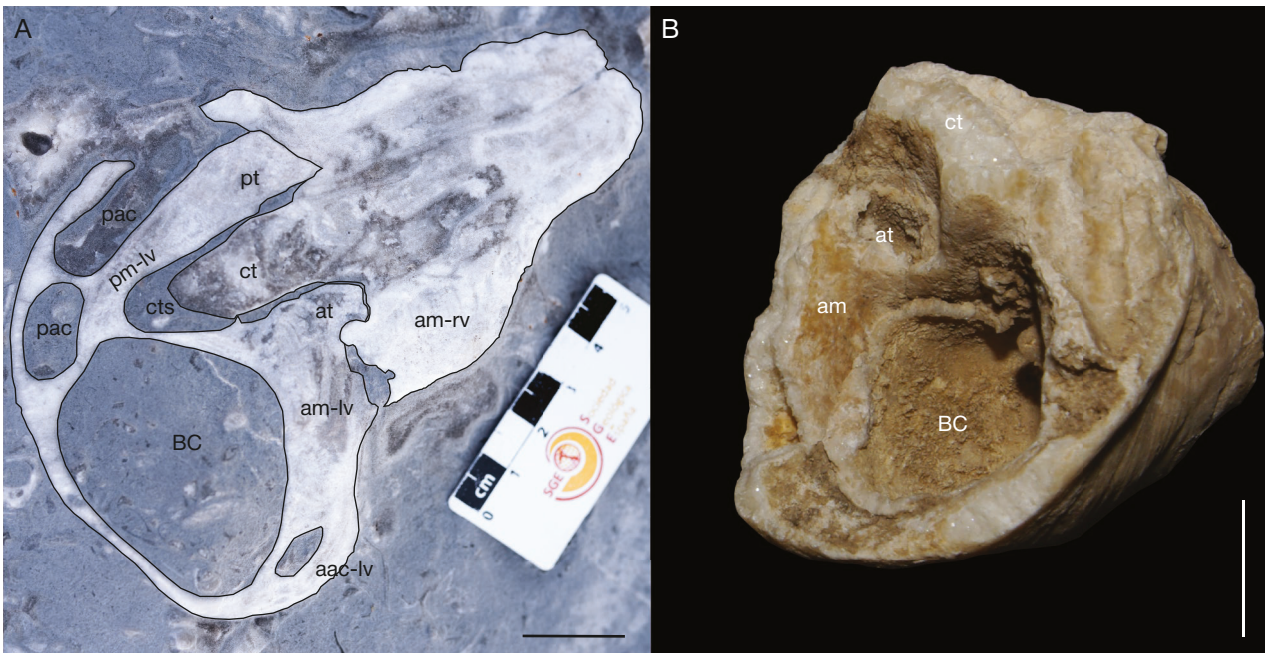

FIG. 9. — Comparison between a specimen of *Sellaea stryx* from Mazo Chico (Fig. 8A) with two valves in connexion (**A**) and a RV of an Apulian *Sellaea stryx* (Museo Geologico de Torino number 18369); the diagnostic characters of *S. stryx*, an AM-RV horizontal and devoid of canals, are all located on the RV. Scale bar: A, 2 cm; B, 1 cm. Conceptualization and drawing: Valentin Rineau and Jean-Pierre Masse.

trally and become partially canaliculated. It is however not sufficient to raise a new species at the present time, and we consider it here as part of the taxon's intraspecific variability.

Sellaea, formerly understood to be close to *Caprotina*, was placed in the Caprinulidae by Skelton (2013a) following Steuber & Bachmann (2002), who proposed the existence of a parallelism concerning the acquisition of pallial canals probably due to overall similarity, but without specifying synapomorphies. However, Rineau *et al.* (2020) tested the phylogenetic position of a *Sellaea* species for the first time within rudists at the family scale and found it to be a sister group to all canaliculated rudists, with Hippuritidae and Radiolitidae. The position of the genus *Sellaea* will require a more exhaustive cladistic study to precisely assess its position relative to other genera of Monopleuridae Munier-Chalmas, 1873, Caprinidae, and Caprinulidae in order to test the homology of accessory cavities and pallial canals. Furthermore, the monophyly of *Sellaea* has not yet been formally tested, particularly with regard to *Pachytraga*. On the other hand, Rineau & Masse (2022) have clearly demonstrated the existence of two clades within *Sellaea*, one restricted to Texas, and the other present in the Mediterranean province and Tibet. With the exception of *Sellaea quadripartita* (Orbigny, 1842), all *Sellaea* are considered to be of Albian age. *Sellaea quadripartita* was formerly described as a *Caprotina* species by d'Orbigny and reassigned to *Sellaea* by Rineau & Masse (2022). This species has all diagnostic features of *Sellaea*, with two accessory cavities in the LV and a row of canals in the RV. It is a Cenomanian species known from Western France, and it probably belongs to the Mediterranean *Sellaea* clade sensu Rineau & Masse (2022).

Sellaea sp.
(Fig. 8F)

MATERIAL EXAMINED. — Outcrop photographs of four natural sections in Suances municipality (Fig. 9F).

STUDY INTERVAL. — Punta del Dichoso, upper Albian of Barcenaciones Formation.

DESCRIPTION

Shell ovoid in transverse section, with ventral flexure on a salient ventral edge. Inner aragonitic layer thick. Ligamentary ridge visible. Presence of small and rounded to quadrangular AT, PT and associated sockets. Wide AAC-LV lying anterodorsally. Very small PMC. AAC-LV/BC and PMC/BC very thick, on which are rooted the myophores. PM-LV on a tongue-shaped myophoral blade along a wide and narrow PAC-LV.

DISCUSSION

These shells cannot be placed precisely in a species due to incompleteness of the sections. The only visible PAC-LV, while broken, seems undivided, suggesting that it is a different *Sellaea* species than *Sellaea stryx*.

DISCUSSION

PALEOECOLOGY OF *SELLAEA* MAZO CHICO PALEOCOMMUNITY

The *Sellaea* paleocommunity from Mazo Chico limestones is a parautochthonous accumulation of shells, mainly found disconnected, generally not broken, and orientated randomly. However, some bouquets of *Sellaea* are found in living posi-

tion. In the bouquets, the shells are deformed by growing close to each other (Fig. 8C). Encrusting is systematically through the RV, which is the classic configuration in the suborder Hippuritidina (Skelton 2013a, b). While encrusting affects all juveniles without exception in rudists, with a spyrogirally coiled encrusting RV, it concerns adult-sized specimens in several cases, as in *Caprotina*. In the *Sellaea* individuals from Mazo Chico, this ecological habit comes with a well-developed conical RV (Fig. 8B). *Sellaea* in this community grow in bouquets of adult attached elevators (Gili & Götz 2018) on the top of a carbonate mound, in marine shallow waters. They grow as the dominant species of a rich paleocommunity including *Horiopleura, Eoradiolites, Pseudotoucasia* Douvillé, 1911 and *Caprotina* associated with *Chondrodonta*, brachiopods, nerineid gastropods, and corals. The association of rudists did not create any relief and developed constratal lithosomes.

Biostratigraphy

Mazo Chico area

The postulated age of the Mazo Chico tongue is Clansayesian to early Albian (Neuweiler 1995; Pascal 1985) up to middle Albian (García-Mondéjar 1985). Pascal (1985), analyzed the Las Camas limestone Formation in the nearby Asón river section, which is laterally equivalent to the Mortillano and the Mazos limestone. The Las Camas displays *Orbitolina* (*Mesorbitolina*) *minuta* Douglass, 1960 in its lower part and *Simplorbitolina manasi* Ciry & Rat, 1953, *Hensonina lenticularis* Henson, 1948, and *Cuneolina* gr. *pavonia* d'Orbigny, 1846. According to Peybernès (1976) these two benthic foraminifers are index fossils of a non-basal Albian. Independently, we have found an ammonite specimen in marls laterally equivalent to the Mazos limestone, which provides a firm biostratigraphic marker horizon. The occurrence of the genus *Anahoplites* Hyatt, 1900 (Appendix 1) suggests a late middle Albian age (Cooper & Owen 2011) and helps refine the biostratigraphical framework of the Soba-Karrantza areas in the Basque Cantabrian Basin (Fig. 6). The presence of *Sellaea stryx* also supports an Albian p.p. age for the corresponding stratigraphic succession (Rineau & Masse 2022). The association of *Eoradiolites jumillensis*, a species recorded in the early and middle Albian of SE Spain (Masse *et al.* 2007), tends to corroborate this dating.

Suances area

The only potentially informative taxon in the Suances area is the rudist *Caprina choffati*, which was originally described from the *Polyconites*-levels of the early Albian *Mortoniceras inflatum* Zone of Portugal (Douvillé 1898). Pascal (1985) described *C. choffati* in the Basque Cantabrian Basin, as markers of the base of the "Vraconian stage" (*Mortoniceras dispar* Zone). Ultimately, *C. choffati* is an outstanding marker of the late Albian of the Pyrenees (Bilotte & Debroas 2014).

Paleobiogeography

The Albian genus *Sellaea* has been considered to be a southern Mediterranean, Arabo-African taxon that extended into the Caribbean and Southwestern Asia (Fig. 10). Its Tethyan and American species are two distinct clades (Rineau & Masse 2022). A single species, *Sellaea stryx*, in Cantabria, Spain and Apulia, Italy, extended to the northern margin of the Iberian block. This questions the conditions by which its migration was possible and why the other species of the genus were not associated with this migration. Paleogeographical, palinspastic, Aptian-Cenomanian reconstructions (e.g., Masse *et al.* 1993; Philip *et al.* 1993) show that the distance between Apulia and the Iberian block was in the range of 1000 km. This distance is assumed to be far less to account for a compositional disparity as a function of geographical distance (Miller *et al.* 2009). Biological exchanges of shallow water benthic organisms by planktonic larvae tend to ignore wide deep water, basinal barriers. The large paleobiogeographical distribution of *Sellaea*, from Texas to Tibet, with a diversity peak in Apulia (Rineau & Masse 2022), suggests that the genus had a significant larval dispersal potential, and is a good example of this trans-oceanic phenomenon. This ability may account for the trans-Mediterranean migration of the genus but the question of taxonomic selectivity of the phenomenon remains unsolved.

The presence of Albian shallow-water European ammonite biotas on the Mediterranean southern margin of the Iberian block suggests the influence of cooler-waters from the Anglo-Parisian basin and surroundings areas. It has been assumed that this northern fauna was restricted to the northern part of this region whereas the southern area was solely Mediterranean (Juignet *et al.* 1973; Yans *et al.* 2007).

Among the associated Albian rudist fauna *Eoradiolites jumillensis* was up to now documented only from the Prebetic domain (Masse *et al.* 2007). Its presence in Cantabria shows that it is also an Iberian taxon. *Caprina choffati*, already described from Portugal, Cantabria, and Southern Spain (Masse *et al.* 1992), becomes also Iberian, extending to the French Pyrénées (Bilotte *et al.* 2017). The complex, segmented palaeogeographical configuration of Albian rudist bearing shallow water carbonate areas from Iberia may be a clue for understanding the relative endemism of this province with episodic immigration of opportunistic taxa in a context of reduction in biodiversity associated with environmental deterioration (Masse *et al.* 1998).

It is worth noting that migrations of Arabo-African and Apulian organisms have been recorded in Iberia in the Hauterivian and Aptian-Albian, which may be related to a similar climatic regime and/or the influence of sea surface currents with a southward origin. Three shallow water benthic foraminifera have long been regarded as markers of the Mediterranean southern margin during the Hauterivian-Barremian and late Aptian-Albian intervals. First, *Campanelulla capuensis* De Castro, 1964 occurs in the Prebetic zone of the Hauterivian of the Albacete Province (Masse *et al.* 1993) and the Barremian of the Sierra de Cazorla and Segura (Schlagintweit *et al.* 2023). This species was an index of the "*Orbitolinopsis*" *capuensis* Province in the Mediterranean southern margin (Masse 1985; Bassoullet *et al.* 1985; Schlagintweit *et al.* 2023, among others). Second, *Paracoskinolina tunesiana* Peybernès, 1982, is a late Aptian Orbitolinidae in North Africa (Tunisia,

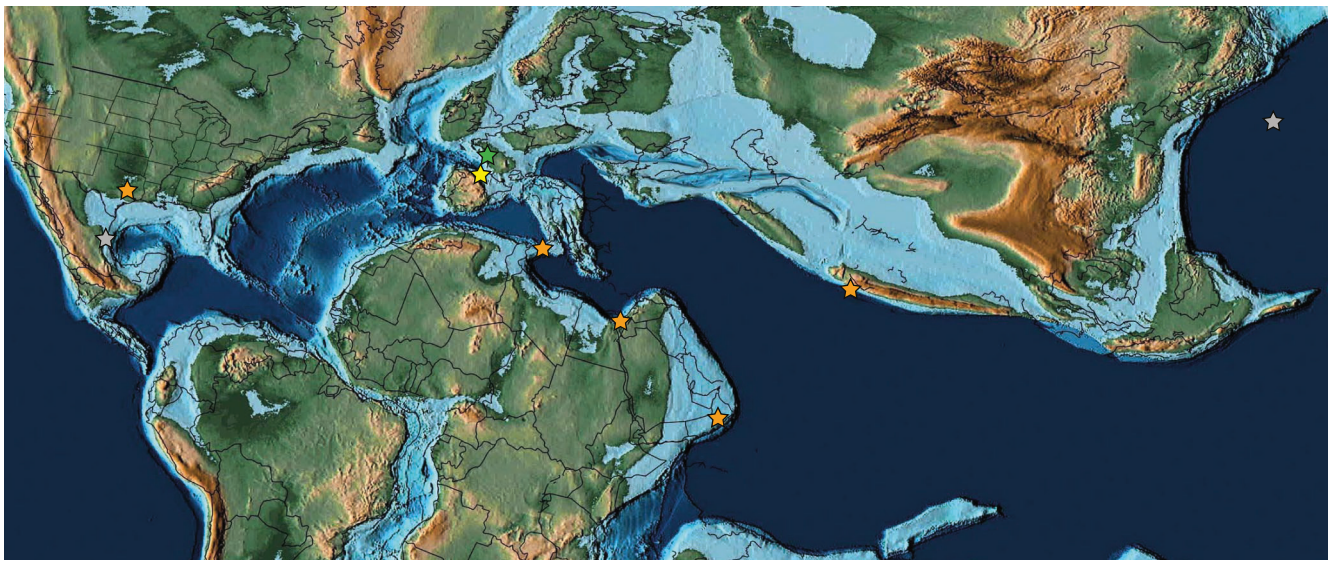

FIG. 10. — Albian map (reproduced from Scotese 2013) of *Sellaea* occurrences showing the paleogeographical extension of the genus. Colors: **yellow**, Cantabrian *Sellaea* described herein; **orange**, Albian *Sellaea*; **green**, Cenomanian *Sellaea*; **grey**, uncertain occurences of *Sellaea*. Conceptualization: Valentin Rineau. Courtesy of the author.

Algeria), in southern Turkey (Solak 2021), in Algarve (Peybernès *et al.* 1981), and in Cantabria (Schlagintweit *et al.* 2017). The generic position of this species was critically discussed (Cherchi & Schroeder 1982) and is currently re-assigned to *Carseyella* Schlagintweit, 2020. This geographical distribution demonstrates the migration of foraminifera from the Mediterranean southern margin into the Iberian block in the late Aptian-Albian. Third, *Neoiraqia convexa* Danilova, 1962 is a late Albian Foraminifera also from the Mediterranean southern margin (Moullade *et al.* 1979) and is present in the Iberian block (Bassoullet *et al.* 1985; Masse *et al.* 1992).

It is worth noting that the post-Aptian northward movement of the southern part of the European plate was assumed to have modified the geographical location of the "reef line", i.e. the boundary of rudist bearing carbonate platforms, which consistently was located at 30°N (Voigt *et al.* 1999). This movement did not affect the northern part of the Iberian block, which remained close to this critical latitude up to the Cenomanian when this line was actually crossed (Philip *et al.* 1993). Then the rudist-bearing biota, including *Sellaea*, extended into western France, where this specific taxon may represent an opportunistic outlier associated with a peak in taxonomic diversification.

CONCLUSIONS

In conclusion, we have reported for the first time the occurrence of the genus *Sellaea* from Cantabria in the Iberian province. Specimens could be identified to the species as representatives of the *Sellaea stryx* species due to the absence of pallial canals in the RV and a horizontal shelf supporting the AM-LV. At present, it is not possible to determine whether this paleocommunity is less rich than Apulia faunas in terms of *Sellaea* species diversity, or wether if the species were not recognized because the specimens could only be analyzed by field sections due to the hardness of rocks. The age of the paleocommunity is late and Upper Albian based on the presence of the ammonite *Anahoplites*, which is corroborated by the presence of the rudists *Eoradiolites jumillensis* and *Caprina choffati*. This dating is consistent with previous knowledge of the *Sellaea* genus, which is typical of the Albian except one Cenomanian species (*S. quadripartita*). Finally, we show that the distribution area of the southern Mediterranean/Arabo-African *Sellaea* species group is also part of the Iberian province.

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Appendix 1. — Ammonoid paleontology.

Order AMMONOIDEA Zittel, 1884
Suborder AMMONITINA Hyatt, 1889
Superfamily Hoplitoidea H. Douvillé, 1890
Family Placenticeratidae Hyatt, 1900
(*sensu* Cooper & Owen 2011)
Subfamily Anahoplitinae Breistroffer, 1947
(*sensu* Cooper & Owen 2011)

cf. *Anahoplites* sp.

Material. — A single specimen preserved as a pyritic uncrushed internal mould corresponding to a juvenile phragmocone. Despite pyrite is oxidized, suture line and overall shape are well preserved. Material deposited in the collections of the Museo de Ciencias Naturales de Álava (MCNA) with the repository number MCNA-17429.

Paleobiogeography. — The Anahoplitinae and Hoplitinae Douvillé, 1890 ammonites were restricted to the shallow epicontinental Albian seas of northern Europe during the (e.g., Owen *et al.* 2010) and characterized the European faunal province. The local occurrences of the European province anahoplitines in the study area suggests their incursion from colder areas and the opening of the seaway connections during the late middle Albian, in a basin typically Tethyan as indicated by its common ammonoid associations (e. g., Agirrezabala & López-Horgue 2017).

Occurrence. — Top middle Albian of Mazo Chico lutites. Valle de Soba, Cantabria, North Spain. *Anahoplites* occurs in the middle Albian and lower upper Albian of England and Transcaspia. In Russia, *Neanahoplites* occurs in the middle to upper Albian transitional *rossicus* Zone (= upper *Euhoplites lautus* Subzone and *Dipoloceras cristatum* Zone).

Description
Oxycone shape. Involute, with outer whorl covering more than a half of flank but coiling loss involution towards the last whorl preserved. Broad and slightly convex flanks are convergent towards venter. Whorl section is compressed, and umbilical wall steep. Umbilicus equals 16% of 18.0 mm diameter. Apparently smooth flanks. Narrow venter looks channeled due to loosing of the siphuncle, which is partially preserved only. Suture with shallowly bifid External lobe and narrower bifid lateral lobe.

Dimensions (in mm)

D	Wh	Ww	U
18.0	9.7	5.2	2.8
11.6	6.0	3.8	1.9

Discussion
The lack of preserved ornamentation such as tubercles or ribs may be due to weathering of juvenile delicate structures. However, the well-preserved suture line is indicative of only slight surficial dissolution. Accordingly, the specimen is suggested to be a non- or only slightly ornamented juvenile (Fig. S1).

The general shape of the specimen, being involute, with broad convergent flanks, high whorls (Wh/Ww = 1.86) and narrow venter are features shared by the genera *Anahoplites* and *Neanahoplites*, which are only distinguishable in the middle to adult stages. Namely, *Neanahoplites* was erected by Cooper & Owen (2011) for the uppermost middle Albian *Anahoplites* with coarser and sparser ribbing (see Spath 1925, 1926; Owen *et al.* 2010). The suture line of the studied specimen is simpler than that of *Anahoplites*, being like *Neanahoplites* suture by the shallow incisions of the external and lateral lobes (Cooper & Owen 2011: fig. 4).

The specimen occurs in lutites above lower Albian carbonates and below upper Albian siliciclastics and megabreccias (García-Mondéjar & Fernández-Mendiola 1989; López-Horgue 2000; López-Horgue *et al.* 2009).

Cooper & Owen (2011) included *Anahoplites* in the subfamily Anahoplitinae and *Neanahoplites* in Semenoviceratinae, both family Placenticeratidae. Anahoplitinae is a group that arose in the middle Albian and became extinct at the close of the Albian. *Neanahoplites* occurs in the topmost middle Albian *N. daviesi* (type species *Anahoplites daviesi* Spath, 1926) Subzone in Western Europe, and is derived from the longer ranging *Anahoplites* occurring from the base of the middle Albian to the lower upper Albian *H. choffati* Subzone (*sensu* Owen 2012; see also López-Horgue & Owen 2024). *Neanahoplites* forms the basal stock of Semenoviceratinae, a group of oxycones with simpler suture line than their ancestor *Anahoplites,* that gave rise to Placenticeratinae in the upper upper Albian (Cooper & Owen 2011).

The juvenile stage of the specimen prevents more precise assignation. However, its stratigraphical occurrence and the suture simplicity points to a late middle Albian age.

Appendix 2. — Figure S1: Juvenile ammonoid from the lutites of Mazo Chico, cf. *Anahoplites* sp., specimen MCNA 17429 (Museo de Ciencias Naturales de Álava): **A**, lateral view, SEM image; **B**, same view highlighting the best-preserved suture lines; **C**, lateral view of the specimen under natural light; **D**, ventral view under natural light; ventral groove is a preservational artifact whereas slightly elevated ventrolateral shoulders look original. Normal light photos: Mikel A. Lopez-Horgue/ SEM photos: P. A. Fernandez-Mendiola and Juan Pedro Rodríguez-López.