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A refugium for charophytes during the maximum post-Palaeozoic sea-level highstand in the Turonian of Tarragona (Catalonia, Spain)

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ABSTRACT

During the Cenomanian–Turonian interval, Europe was largely submerged under a shallow tropical sea within the Cretaceous Tethyan Archipelago, limiting non-marine lacustrine habitats to a few coastal lakes on the islands. This study reports an island refugium for charophytes in the Upper Cretaceous of Tarragona located at the palaeo-shores of the former Ebro Massif. The Upper Cretaceous of Tarragona comprises three carbonate formations that record a Cenomanian–Turonian transgressive-regressive sequence. This sequence is represented by a shallow marine platform to pelagic facies at the base, overlain by lacustrine and palustrine facies at the top. These non-marine deposits are newly attributed to the Turonian, based on the stratigraphic context and the presence of the species *Atopochara trivolvis* var. *multivolvis*. In addition to this dominant species, the charophyte assemblage contains a clavatoroidean species, represented by the thallus *Munieria grambastii* forma *sarda*, and is associated with freshwater gastropods. *A. trivolvis* var. *multivolvis* had a wide distribution in the Northern Hemisphere at a palaeolatitude of around 40ºN, occurring in the United States, Spain, France, and Armenia. The European localities suggest that the island charophyte flora in the Cretaceous Tethyan Archipelago was an impoverished version of the pre-highstand Early Cretaceous flora, which was dominated by clavatoraceans. This contrasts with coeval floras from the mainland (Chinese and Argentinian basins), where Turonian charophyte communities were diverse and already dominated by modern characean genera. The island lakes acted as refugia for the last clavatoracean-dominated charophyte communities before their complete replacement by modern characean communities during the latest Cretaceous.

KEYWORDS **Charophyta. Mid-Cretaceous. Catalan Coastal Chain. Biogeography. Biostratigraphy.**

INTRODUCTION

Charophytes from the dawn of the Late Cretaceous (Cenomanian–Turonian) are extremely rare in Europe. This is because by the beginning of the Late Cretaceous, the islands of the Cretaceous Tethyan Archipelago, including present-day Europe, were partly drowned by the most important sea-level rise since the Devonian (Haq *et al.*, 1987). As a result, only a few non-marine habitats were left for charophytes to grow in and to enter the fossil record.

The few charophyte records from the Cenomanian–Turonian Cretaceous Tethyan Archipelago, belong to two large islands, the Massif Central and Iberia. In the Massif Central island (France), Colin and Médus (1972) and Feist (1981) reported the richest charophyte flora known to date in Europe from this time span, while Feuillée and Grambast (1961) and Feist and Floquet (2022) found a similar assemblage for the same interval on the Iberian island (Spain). Additionally, Kyansep-Romashkina (1980) found a small charophyte flora in Armenia. Worldwide, three more records from the Cenomanian–Turonian are known, all of them corresponding to continental (mainland) lakes. In the United States, Peck (1957) reported a poorly diverse Cenomanian flora, while in the Turonian floras in Argentina (Musacchio, 2010; Uliana and Musacchio, 1978) and especially China (Li *et al.*, 2020), already contain richer assemblages formed from derived characean genera, which diversified in the latest Cretaceous and Cenozoic.

The Cenomanian–Turonian interval was one of the most significant in charophyte evolution, since it contains the youngest assemblages dominated by clavatoracean charophytes, before their almost complete substitution by characeans in the latest Cretaceous (Grambast, 1974). This worldwide turnover in charophyte floras has been compared in importance to the evolutionary changes occurring in seed plants during the Albian and Cenomanian with the rise of the angiosperms to dominance (Martín-Closas, 2003).

Herein, we report a new charophyte locality from this time interval in the Cretaceous Tethyan Archipelago. It corresponds to the city of Tarragona in Catalonia (Spain), which palaeogeographically belonged to the margin of the Ebro Massif Island (*e.g.* Dercourt *et al.*, 2000). The new locality gives valuable biostratigraphic information for the characterization of the non-marine Upper Cretaceous of Tarragona, providing additional information to compare the physiognomy of charophyte communities in European palaeo-islands with the coeval mainland charophyte communities known from China and Argentina.

GEOLOGICAL SETTING

The study area is located within the city of Tarragona (Catalonia, Spain) and forms part of the Catalan Coastal Chain (Fig. 1A). The reliefs observed in the city represent the southwestern end of the chain, linking to the northeast with the Bonastre High and the Montmell Massif (Fig. 1A) (Institut Geològic de Catalunya, 2010). These reliefs also mark the southeastern edge of the Neogene graben of El Camp de Tarragona. In the area of Tarragona, the materials that make up the pre-Quaternary basement can be subdivided into two main groups (Vilà *et al.*, 2016): the pre-Neogene materials that are Triassic to Paleogene in age, which were affected by the Alpine deformation, and the Neogene deposits, mainly Middle and Upper Miocene in age, which fill the graben of El Camp de Tarragona (Fig. 1B).

The Mesozoic rocks of this area were deposited in the so-called Garraf Basin, which was part of the Mesozoic Iberian Rift, defined in this area by normal faults, oriented northeast to southwest (Salas *et al.*, 2019). The alpine contraction resulted in the inversion of these faults and in the subsequent deformation of the Mesozoic succession. At present, the spatial distribution of the major structural units of the Catalan Coastal Chain is linked to the Neogene rift that affected the Catalan Continental margin during the opening of the western Mediterranean València trough (Cabrera *et al.*, 2004; Llopis Lladó, 1947).

From a structural viewpoint, the succession deformed by the Alpine orogeny in Tarragona consist of an overturned syncline, with a northeast to southwest direction, lying in the lower block of a thrust that verges to the northwest (Figs. 1B; 2) (Esteban, 1971, 1973). The upper block of this thrust is located along the Tarragona coast and in several Mesozoic outcrops located on the south-eastern margin of El Camp de Tarragona graben. The latter outcrops are interpreted either as *klippen* (Institut Cartogràfic i Geològic de Catalunya, 2013–2017), witnessing the Alpine compression (Figs. 1B; 3), or as olistoliths, resulting from major fault block rotation due to Neogene rifting (Esteban and Santanach, 1974). The Alpine structure of Tarragona is compartmentalised by normal faults associated with the Neogene extensional event and is overlain by Middle Miocene marine deposits (Figs. 1B; 2) (Institut Cartogràfic i Geològic de Catalunya, 2013–2017).

The Upper Cretaceous of Tarragona was deposited in the south-west of the Garraf Basin, within the Montmell Sub-Basin (Salas *et al.*, 2019), during the post-rift stage that affected the Iberian basins between the late Albian and the Paleogene (Salas *et al.*, 2001). These deposits record a transgressive-regressive sequence that is Cenomanian–Turonian in age (Figs. 3; 4; 5). It is characterised by a

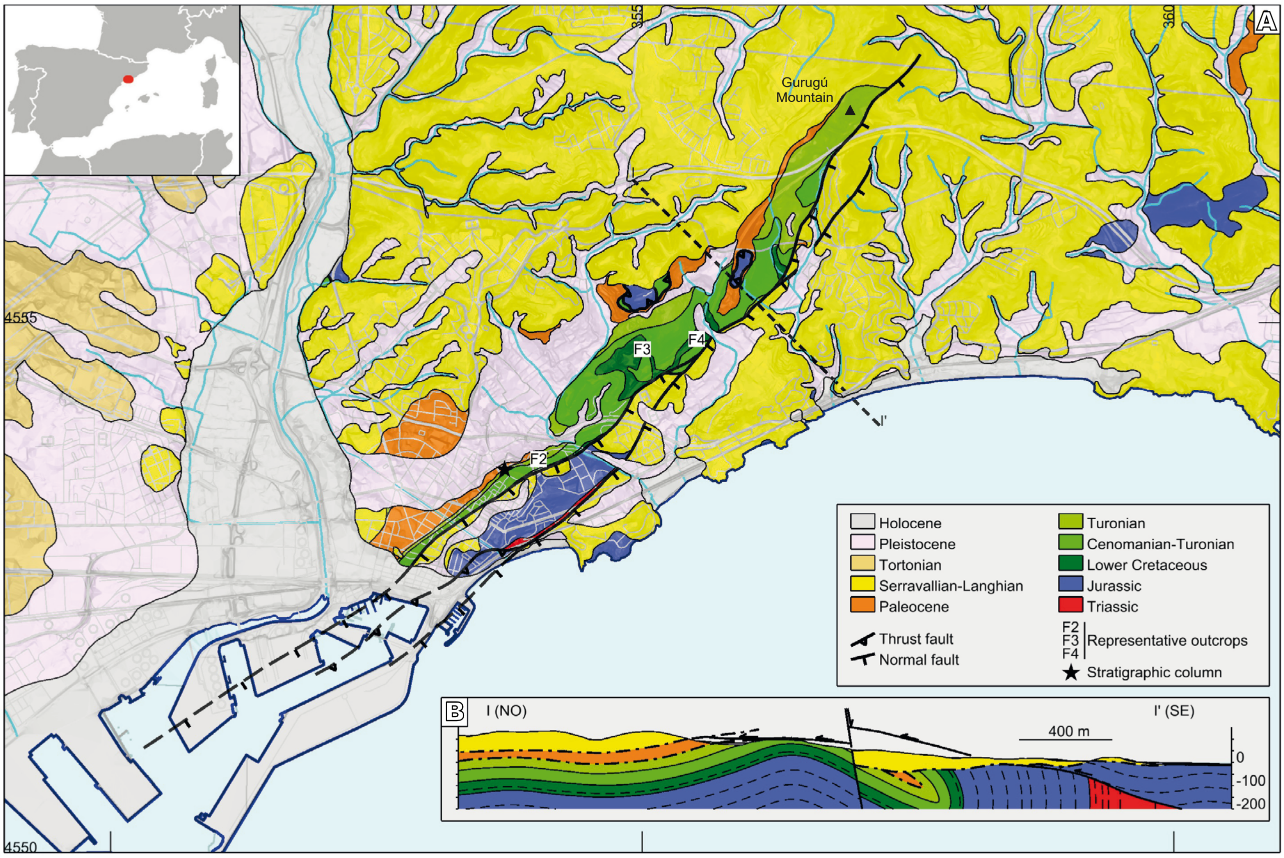

FIGURE 1. Geological setting of the study area based on the Institut Cartogràfic i Geològic de Catalunya (2013–2017) and Vilà *et al.* (2016). A) Geological map of Tarragona and its surroundings. B) Representative cross section I-I' of the study area. Representative outcrops F2, F3 and F4 refer to Figures 2; 3 and 4 respectively. The stratigraphic column is shown in Figure 5.

set of shallow-marine to pelagic carbonate deposits that progressively pass up towards non-marine carbonate deposits that are mainly of coastal lacustrine and palustrine environments. The rocks that make up this sequence crop out continuously along the entire folded structure that crosses the city of Tarragona before reaching the northeastern Gurugú Mountain (Fig. 1A). In the area of Tarragona, the Cenomanian–Turonian succession is stratigraphically framed between the Montmell Formation (Fig. 4) and/or the Utrillas Formation at the base, early Albian to early Cenomanian in age (Moreno-Bedmar *et al.*, 2017), and the Paleocene Mediona Formation (Anadón Monzón, 1978) at the top. In both cases the contact is marked by a regional unconformity (Fig. 3).

MATERIAL AND METHODS

The Upper Cretaceous of Tarragona has been previously the object of detailed stratigraphic studies by Esteban (1973), which are reviewed and updated here. In the area, several outcrops were found to contain significant records of non-marine Upper Cretaceous rocks (Figs. 1–4). From these outcrops, the section exposed along the schoolyard of the school Sant Pau in Tarragona was selected for a micropalaeontological study, since it contains the best exposure of the non-marine unit. The geographic coordinates of the base of this section are 41º 06' 14,71" N and 1º 15' 24,04" E.

Limestone samples SP1 to SP13 were collected from the Sant Pau schoolyard section (Fig. 5) and cut perpendicular to stratification to obtain thin sections that were c. 30μm thick. These thin sections were photographed with an optical microscope Zeiss Axiophot 40.

Marlstone samples SPM6 to SPM10 that were rich in charophytes were collected in the upper part of the Sant Pau schoolyard section (Fig. 5) and prepared following standard micropalaeontological procedures. Samples were disaggregated in water and hydrogen peroxide for several days before wet-washing using meshes with lumen sizes of 1mm, 0.5mm, and 0.2mm. The dried residues were manually screen-sorted under a binocular microscope at x20 magnification. Populations of up to several hundred utricles per sample were obtained. A selection of them

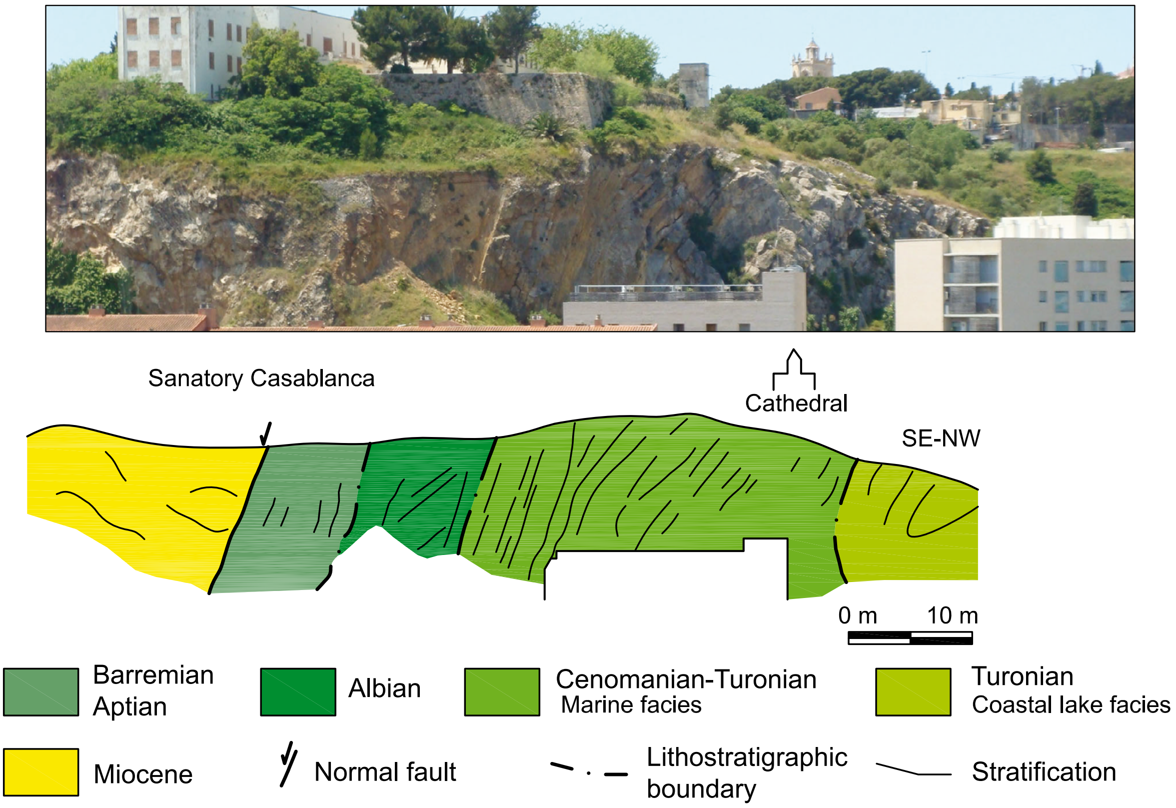

FIGURE 2. Photointerpretation of an abandoned quarry near Sanatori de Casablanca and below the Tarragona city walls, as viewed from Ermita de la Salut (F2 in Fig. 1). The outcrop shows the southern flank of the reversed syncline, with the Cretaceous units verticalised or inverted. To the left, Miocene deposits contact the Cretaceous deposits along a normal fault. Modified from Esteban (1973) and the Institut Cartogràfic i Geològic de Catalunya (2013–2017).

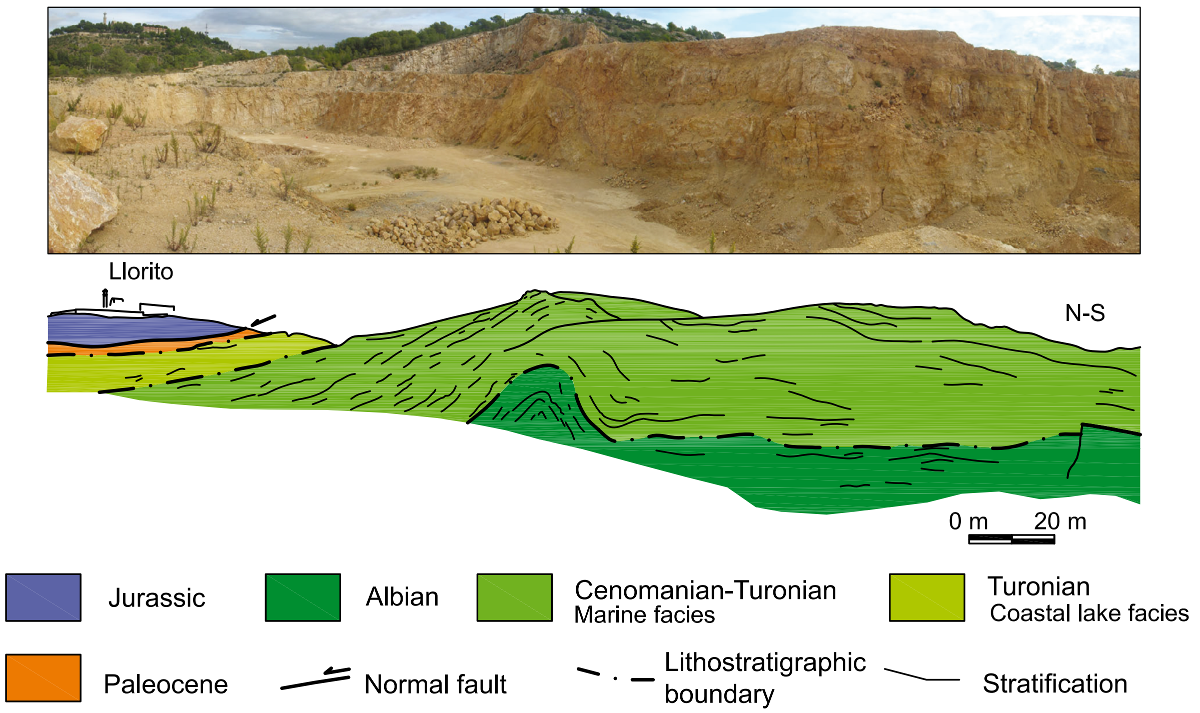

FIGURE 3. Photointerpretation of the outcrop of the La Budellera quarry (F3 in Fig. 1). The antiformal structure represents a folded Alpine structure towards the northwest of Tarragona. The core of the antiform contains the Albian and Cenomanian–Turonian units, while the *klippe* (Santuari de Loreto, also known as "Llorito"), formed mainly of Jurassic rocks can be observed at the top-left of the image. These rocks overthrust the Paleocene Mediona Formation. Modified from Institut Cartogràfic i Geològic de Catalunya (2013–2017).

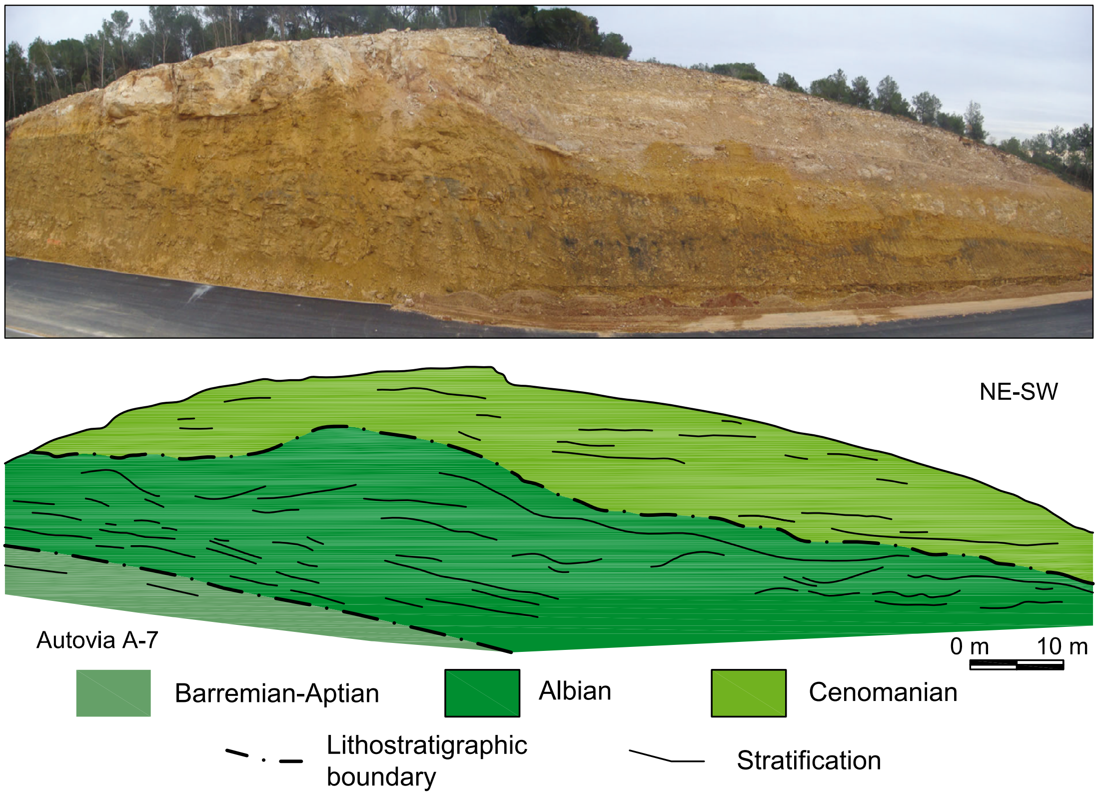

FIGURE 4. Photointerpretation of the outcrop along the trench of the motorway A-7, as viewed from the access road to "Llorito" (F4 in Fig. 1). Dolostones corresponding to the base of the Cenomanian–Turonian transgression onlap the stratigraphic unconformity capping Lower Cretaceous rocks. Modified from Institut Cartogràfic i Geològic de Catalunya (2013–2017).

were measured under a Zeiss Stemi 508 binocular microscope equipped with the Zeiss Zen 3.10 software and photographed in a Quanta-250 scanning electron microscope at the *Centres Científics i Tecnològics de la Universitat de Barcelona* (CCiTUB). The illustrated sieved charophyte samples are housed in the *Museu de Geologia del Seminari de Barcelona* under codes MGSB 89235 – MGSB 892342, while the remaining materials are housed in the charophyte collection of the Faculty of Earth Sciences of the University of Barcelona.

RESULTS

Stratigraphy and sedimentology of the Upper Cretaceous of Tarragona revisited

The lithostratigraphic framework of the Upper Cretaceous units in the study area was first provided by Esteban (1973) and formally defined by Robles (1982). The stratigraphic section studied here (Fig. 5) crops out along the Sant Pau schoolyard, in a cliff at the foot of the historical city walls of Tarragona. This section represents the inverted southern flank of the abovementioned syncline (Fig. 1B; 2). The synthetic log shows a stratigraphic series, about 75m thick, which comprises the following units from the base to the top:

Serra de Llaberia Tabular Dolostones and Praealveolina *Limestones Formation*

This consists of up to 30m of yellowish and greyish dolostones with intercalations of partially dolomitised beige limestone (Figs. 5; 6A), well-stratified in beds that are a few decimetres to a few metres thick. At the base of the unit, there are centimetre to decimetre-thick beds of ochre marly dolostones interbedded with centimetre-thick beds of ferruginous reddish lutite. In general, detrital components are more abundant at the base of the unit, where dolostones are clayey, with the carbonate content increasing at the top of the unit. From a petrographic viewpoint, the dolostones are classified as dolmicrite and, to a lesser extent, dolsparite. Moreover, in certain areas, they may have a marble appearance, which has been historically referred to in Tarragona as "Santa Tecla Stone". The limestone intercalations in this formation are mainly located towards the middle-upper part of the unit (Figs. 5; 6A). They are packstones and wackestones with bioclasts of bivalves, echinoderm plates, benthic foraminifera (miliolids, alveolinids, and nummoloculinids), and rare planktonic foraminifera (Fig. 6B). At the top of the unit, there are intervals of finely stratified limestone (with fenestral porosity, ostracods, and fragments of algae) that alternate with marly limestone. From a stratigraphic point of view, the base of the Dolostones and *Praealveolina* Limestones of

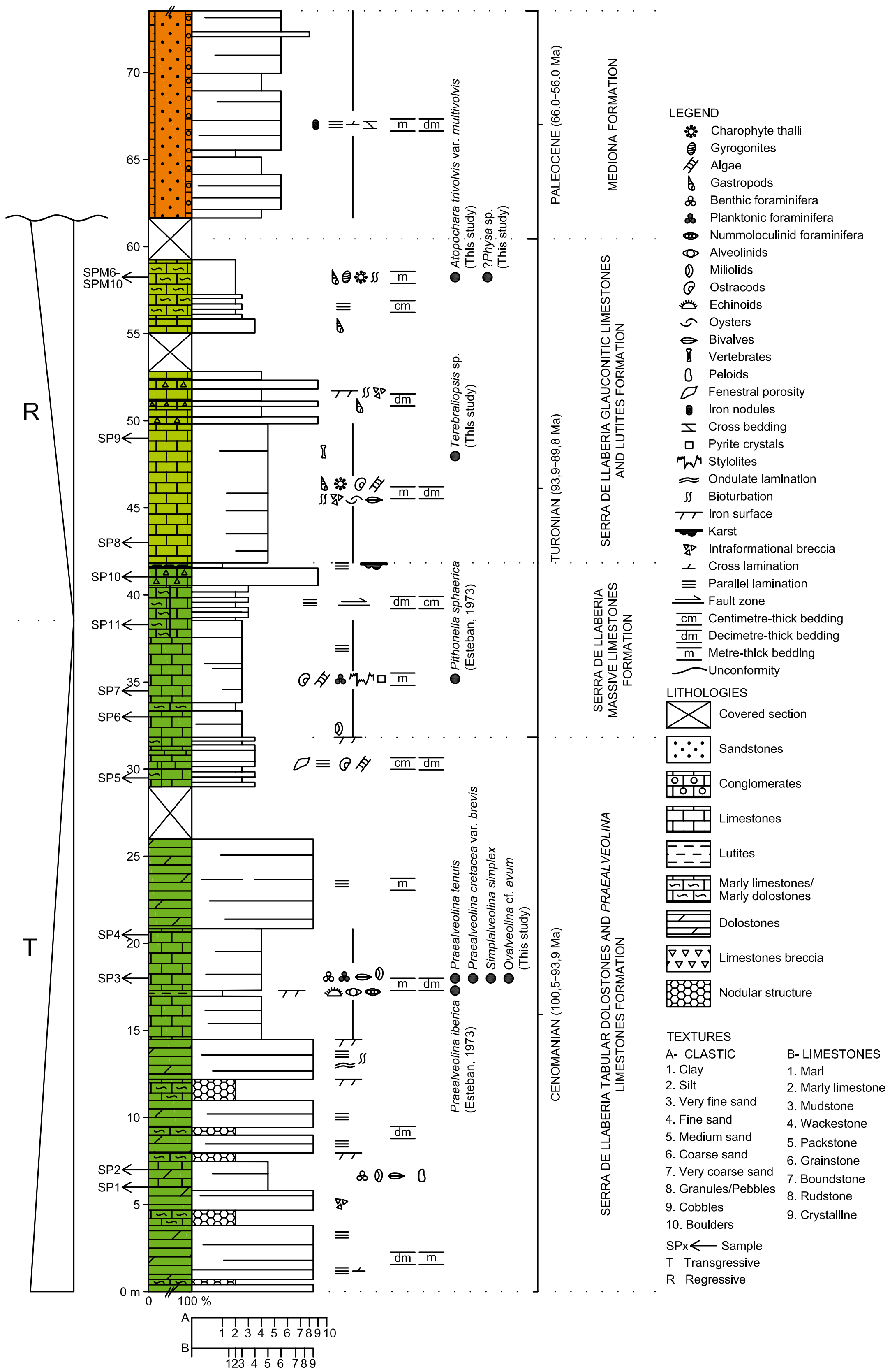

FIGURE 5. Stratigraphic section of the Cenomanian–Turonian units from the southern flank of the inverted syncline crossing the city of Tarragona logged along the outcrop of the Sant Pau schoolyard. T-R curve indicates the transgressive-regressive sequence. Colour codes as in Figure 1.

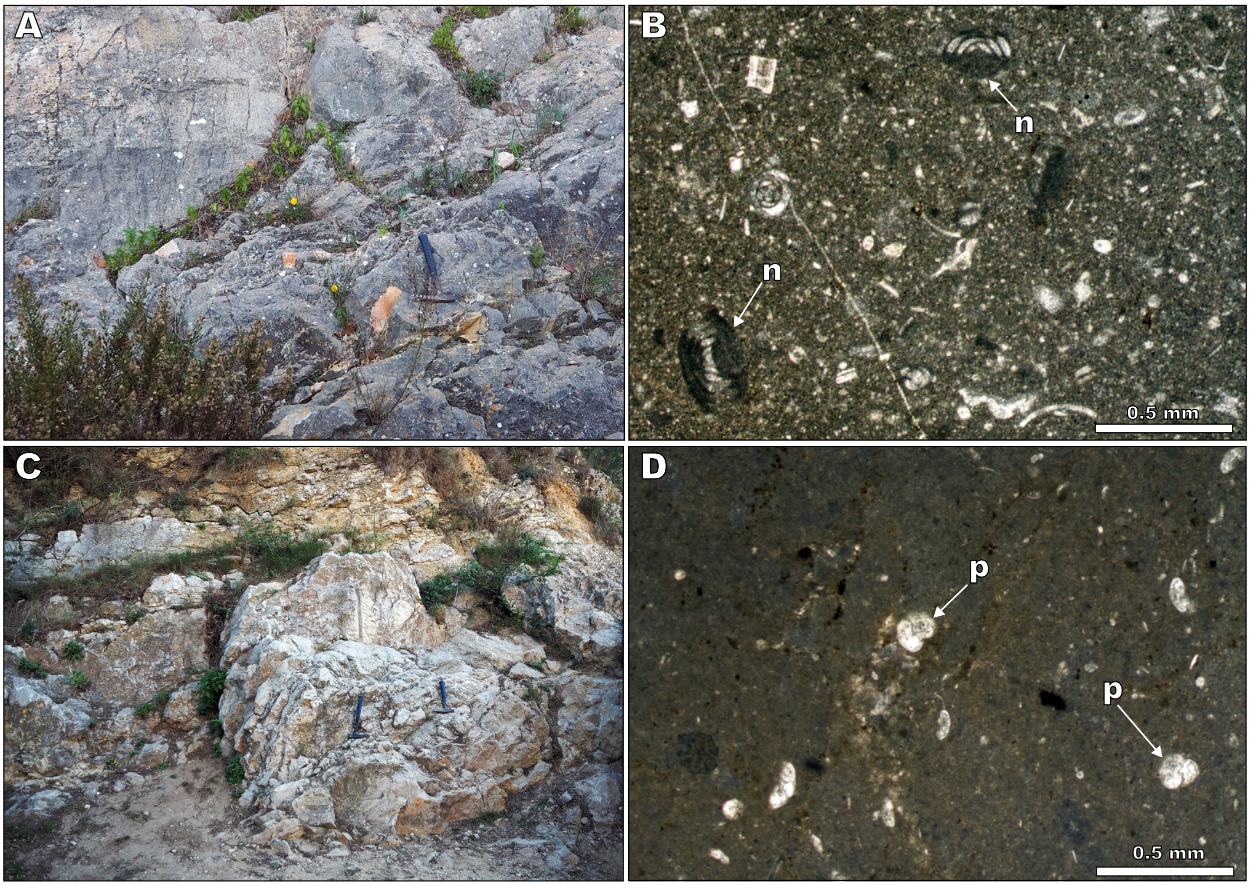

FIGURE 6. Outcrops and microphotographs of the Cenomanian–Turonian marine deposits in the study area. A) Outcrop view of the middle to upper part of the Serra de Llaberia Tabular Dolostones and *Praealveolina* Limestones Formation. Hammer (30cm long) for scale. B) Microfacies of the same unit showing nummoloculinids (n). C) Outcrop view of the Serra de Llaberia Massive Limestones Formation. D) Microphotograph of the same unit showing a mudstone-wackestone texture and planktonic foraminifera (p).

the Serra de Llaberia Formation is bounded via an angular unconformity by the underlying Montmell and/or Utrillas formations, marking the beginning of the Cenomanian–Turonian transgression (Fig. 4). This formation is interpreted as having been deposited in a shallow marine platform environment with tidal influence (Anadón *et al.*, 1979). In Tarragona, the presence of *Praealveolina cretacea* var. *brevis* REICHEL, *P. tenuis* REICHEL, *P. iberica* REICHEL, and *Simplalveolina simplex* (REICHEL) dates this formation to the Cenomanian (Esteban, 1973). Later, Robles (1982) refined the age of this unit to the middle to upper Cenomanian. However, the assemblage of larger foraminifera identified in the Sant Paul schoolyard section contained *Praealveolina cretacea* var. *brevis, P. tenuis, Simplalveolina simplex*, and *Ovalveolina* cf. *ovum* (D'ORBIGNY) that belongs to the upper Cenomanian cycle II of Calonge *et al.* (2002) (Fig. 7).

Serra de Llaberia Massive Limestones Formation

This unit consists of massive whitish-grey, limestones (Figs. 5; 6C) with mudstone-wackestone textures, and abundant stylolites. The main skeletal remains are ostracods, planktonic foraminifera, miliolids, and fragments of algae and bivalves (Fig. 6D). The upper part of the unit exhibits few metres of ochre-coloured, finely bedded limestones, with reddish stained becoming more pronounced at the top of the section. The limestones are overlain by a 1m-thick layer of calcareous breccias within a reddish lutite interval. The top of the unit exhibits karst features, characterized by large cavities, several decimetres in size, filled with reddish claystones and yellowish laminated siltstones. In the area of Tarragona, this lithostratigraphic unit is typically 18–20m thick. However, in the Sant Pau schoolyard stratigraphic section, it barely reaches 10m in thickness, likely due to displacement caused by a fault. It has been interpreted that this succession represents marine hemipelagic deposits formed during the late stage of the transgressive-regressive sequence (Fig. 5) and is associated with the global sea-level highstand that occurred between the late Cenomanian and the early Turonian (Haq, 2014). The lower and upper boundaries of the Serra de Llaberia Massive Limestones Formation were considered to be possible stratigraphic

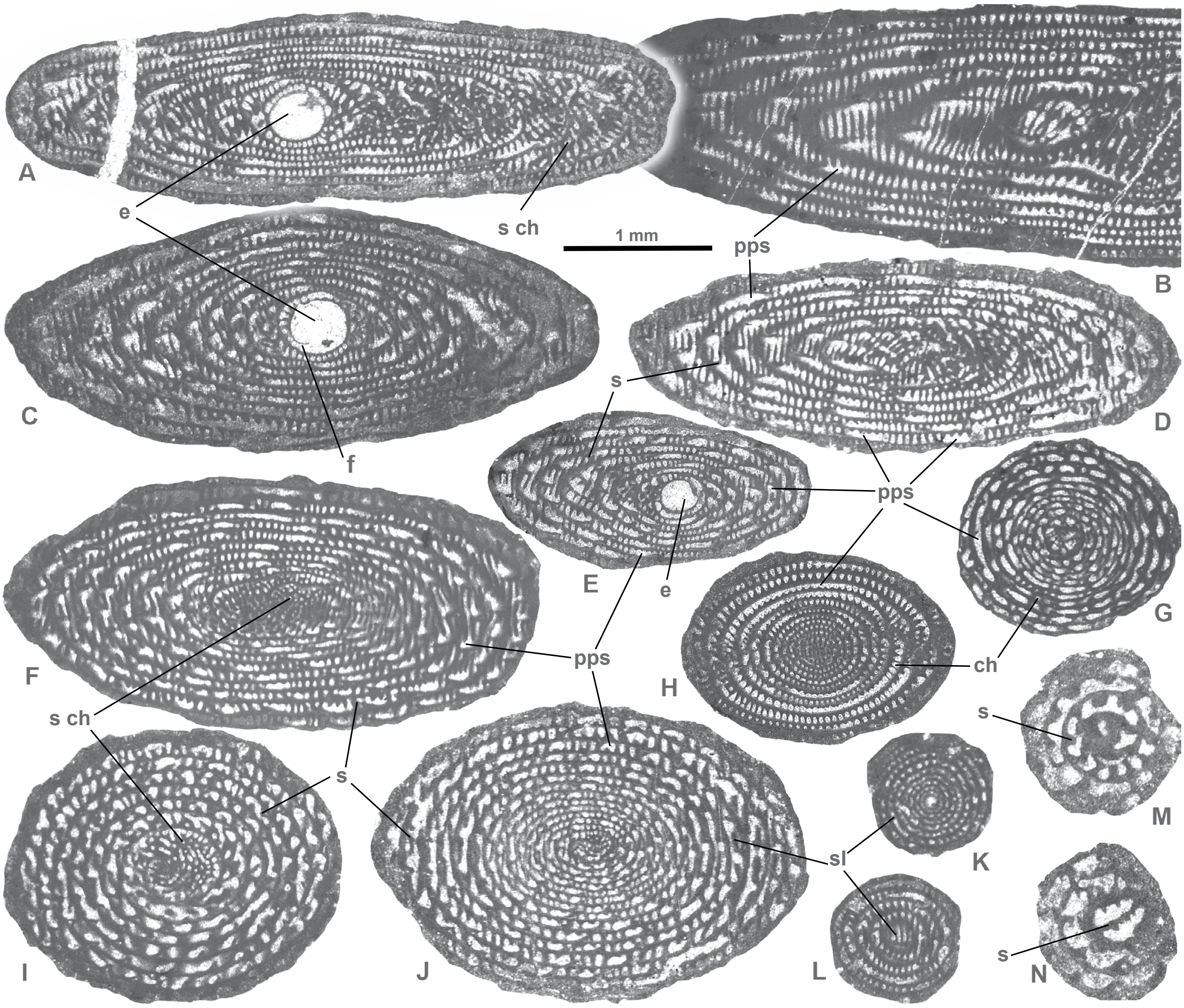

FIGURE 7. Larger benthic foraminifera from the Serra de Llaberia Tabular Dolostones and *Praealveolina* Limestones Formation (sample SP-3, Sant Pau schoolyard section). A-D, F, I-J) *Praealveolina tenuis* REICHEL (megalospheric forms: A, C, D?; microspheric forms: B, F?, I?-J). E, G-H) *Praealveolina cretacea* var. *brevis* REICHEL (megalospheric form: E; microspheric forms: G-H). K-L) *Simplalveolina simplex* (REICHEL) (megalospheric forms). M-N) *Ovalveolina* cf. *ovum* (D'ORBIGNY) (possible megalospheric forms). Abbreviations of structural elements: ch= chamberlet; e= embryo; f= flexostyle; pps= preseptal passage; s= septum; s ch= supplementary chamberlet; sl= septulum.

unconformities, based on the evidence of emersion and/or erosion, or caused by abrupt changes in palaeoenvironmental conditions that are recorded at the formation boundaries (Anadón *et al.*, 1979). However, in the study area we did not find evidence of such an unconformity between the Serra de Llaberia Tabular Dolostones and *Praealveolina* Limestone Formation and the Serra de Llaberia Massive Limestone Formation. Hence, both units were mapped together as a comprehensive Cenomanian–Turonian unit (Fig. 1). The breccias and cavities observed at the top of the Serra de Llaberia Massive Limestone Formation may be interpreted as a palaeokarst that is related to the Alpine orogeny or the Neogene rift. Esteban (1973) attributed this formation in Tarragona to the Turonian, based on the assemblage of *Pithonella sphaerica* (KAUFMANN in HEER) and *Whiteinella* cf. *paradubia* SIGAL (syn. *Hedbergella paradubia*). Furthermore, Robles (1982) constrained this age to the lower Turonian or even the Cenomanian in other parts of the Catalan Coastal Chain.

Serra de Llaberia Glauconitic Limestones and Lutites Formation

This unit is mainly composed of limestone beds that are up to 40m thick and intercalate with calcareous intraformational breccias, lutite, and marly limestones (Figs. 5; 8A-D). The latter are more developed towards the upper part of the unit and contain the charophytes studied herein. The limestones, locally known as Llisós Stone, are grey to dark grey in colour and occur in beds (Fig. 8A-B) that are metre to decimetre thick and are often exhibiting bioturbation at the top (Fig. 8D). The dominant texture of these limestones is packstone, although wackestone textures also occur. At the lower part of the formation, abundant fossils are present, including gastropods such as *Terebraliopsis* sp. (Figs. 5; 8C; 9A-C), fragments of bivalves, oysters, ostracods, miliolids, charophytes, and other algae. Additionally, remains of a crocodyliform reptile were identified in a building block of the same lithology found in the historical city wall of Tarragona (Fig. 9D-E). The upper part of this formation, studied in the Sant Pau schoolyard outcrop, consists of marly-limestones that are ochre to greyish in colour, show edaphic features (Figs. 5; 10A-B), and are rich in charophyte remains, *Physa?*, and other indeterminate gastropods, ostracods, and vertebrate remains. (Figs. 10C-D; 11). In the area of Tarragona, this lithostratigraphic unit is interpreted as deposited in a euryhaline coastal lake, during the regressive phase of the Cenomanian–Turonian transgressive-regressive sequence (Fig. 5). The fossil assemblage, including *Terebraliopsis* sp., suggests that brackish conditions prevailed at the base of the unit (*e.g.* Ősi *et al.*, 2021), shifting to predominantly freshwater conditions towards the top. In the Catalan Coastal Chain, the age of this formation has been a matter of debate. Colombo (1980) attributed it tentatively to the Campanian based on the charophyte flora, while Robles (1974) dated it to the Maastrichtian, based on the rudist fauna. The age of this unit will be reassessed in the present study.

Systematic palaeontology

Charophyte fructifications

Phylum: Charophyta MIGULA, 1897
Class: Charophyceae SMITH, 1938
Order: Charales LINDLEY, 1836
Family: Clavatoraceae PIA, 1927
Genus: *Atopochara* PECK, 1938
Atopochara trivolvis var. *multivolvis* (PECK, 1957) emend. MARTÍN-CLOSAS, 1996
Figs. 12A–E; 13

Material. Hundreds of utricles in all samples SPM-6 and SPM-8 to SPM-10.

Description. Utricle atopocharoid, about 1100μm across, globular, formed of three symmetrical units in its external structural layer. Each unit is formed of three branches starting from the basal pore of the utricle with three cells termed A, B, and C by Grambast (1974). The A cell is generally shorter than the B cell and bears two smaller cells, a1 and a3, with the former being regularly ellipsoidal and the latter changing in shape from ellipsoidal to sub-triangular (Figs. 12A-C; 13). In some cases, a1 can be subdivided into a1 and a1' (Fig. 13J). Cells B and C bear three cells each (termed b1, b2, and b3, and c1, c2, and c3 respectively), all being very elongated and reaching near the apical area (Figs. 12A-C; 13). Among these cells, only c1 is sometimes subdivided into c1 and c1' (Fig. 13J). The length of the cells c1 and b1 is similar to those of cells B and C respectively. All the cells of the utricle display clockwise torsion from the base to the apex in at an angle of about 45–60° with 4–5 turns being visible in the lateral view (Fig. 12A-C).

Remarks. *A. trivolvis* var. *multivolvis* from Tarragona shows similar utricle size, shape, and structure to those of other populations of the same variety described elsewhere. However, the subdivision of cells b1 and b1' was not observed in the utricles studied here.

Charophyte thalli
Genus: *Clavatoraxis* MARTÍN-CLOSAS ET DIÉGUEZ, 1998
Clavatoraxis sp.
Fig. 12F

Material. A few portions of poorly preserved thalli including several nodes in sample SPM-6.

Description. Portions of thalli show several swollen segments, probably belonging to whorls of spine-cell rosettes.

Remarks. These remains are affine to those observed in the phylloids of *Clavatoraxis robustus* by Martín-Closas and Diéguez (1998). However, the poor preservation of the remains from Tarragona rules out a more precise determination. The taxonomic affinity of these thalli to fructifications is still unclear. However, their regular association with atopocharoid utricles suggests that they may belong to the same plant, as indicated by Pérez-Cano *et al.* (2020).

Genus: *Munieria* (DEECKE, 1883) emend. GRANIER in GRANIER *et al.*, 2015
Munieria grambastii BYSTRICKÝ, 1976
Munieria grambastii forma *sarda* (CHERCHI *et al.*, 1981) nov. comb. PÉREZ-CANO *et al.*, 2022
Fig. 12G–I

Material. A dozen specimens in all samples SPM-6 and SPM-8 to SPM-10.

Description. Portions of corticated thalli include 2–3 nodes and their respective internodes, about 600–650μm across (Fig. 12G). Nodes formed by 10–11 barrel-shaped to sub-conical nodal cells, c. 200μm long and 100μm wide,

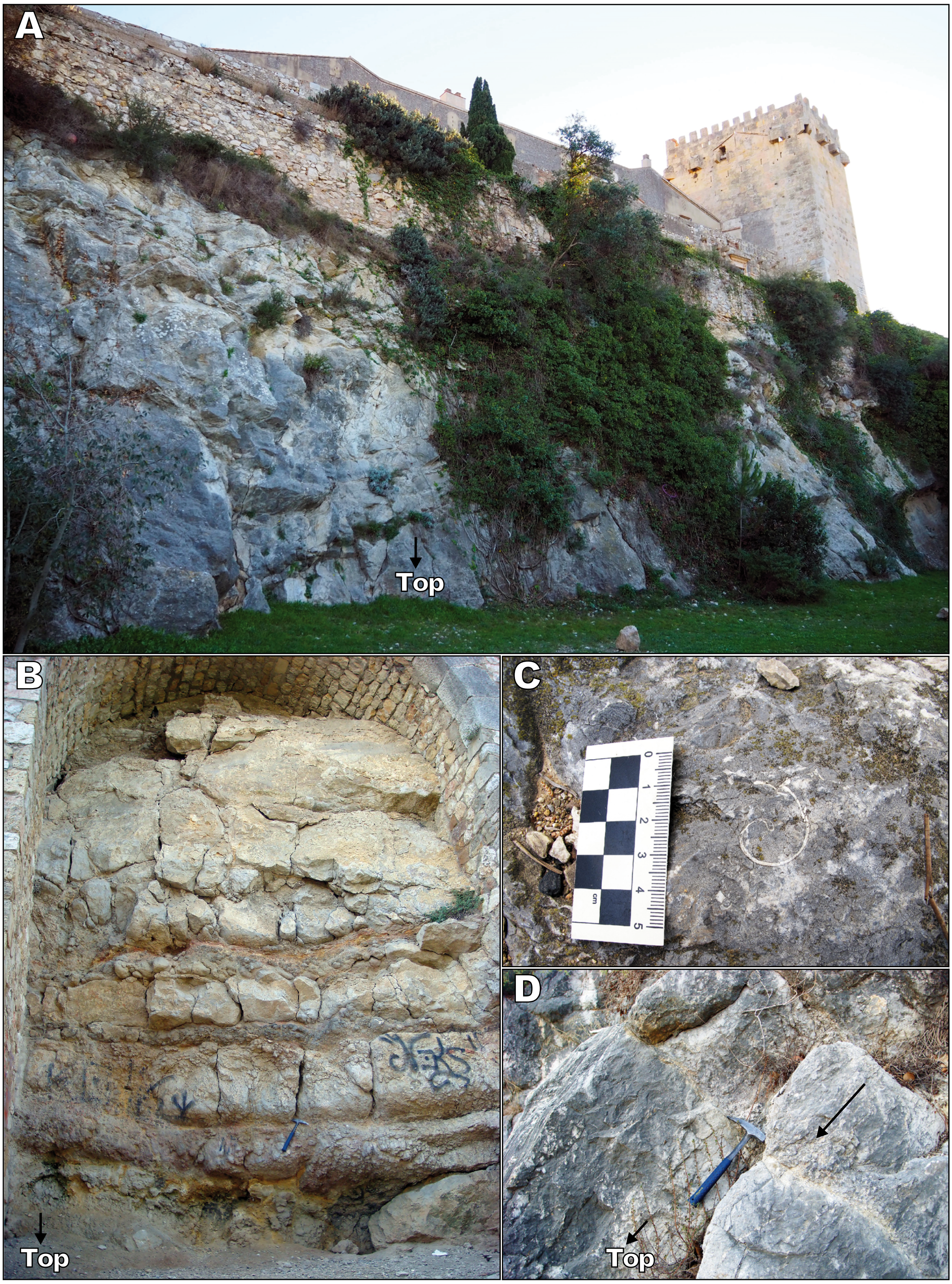

FIGURE 8. Outcrop views of the lower part of the Serra de Llaberia Glauconitic Limestones and Lutites Formation. A) Non-marine limestones of the lower and middle part of the formation in the Sant Pau schoolyard outcrop. Height of outcrop is c. 8m. B) Upper part of the formation showing intercalations of grey limestone and intraformational breccias with abundant ferruginous surfaces. Height of outcrop is 5m. C) Close-up view of a section of a freshwater gastropod. D) Close-up view showing abundant bioturbation (black arrow) at the top of the beds. Note that the bedding is inverted. Hammer (30cm long) for scale.

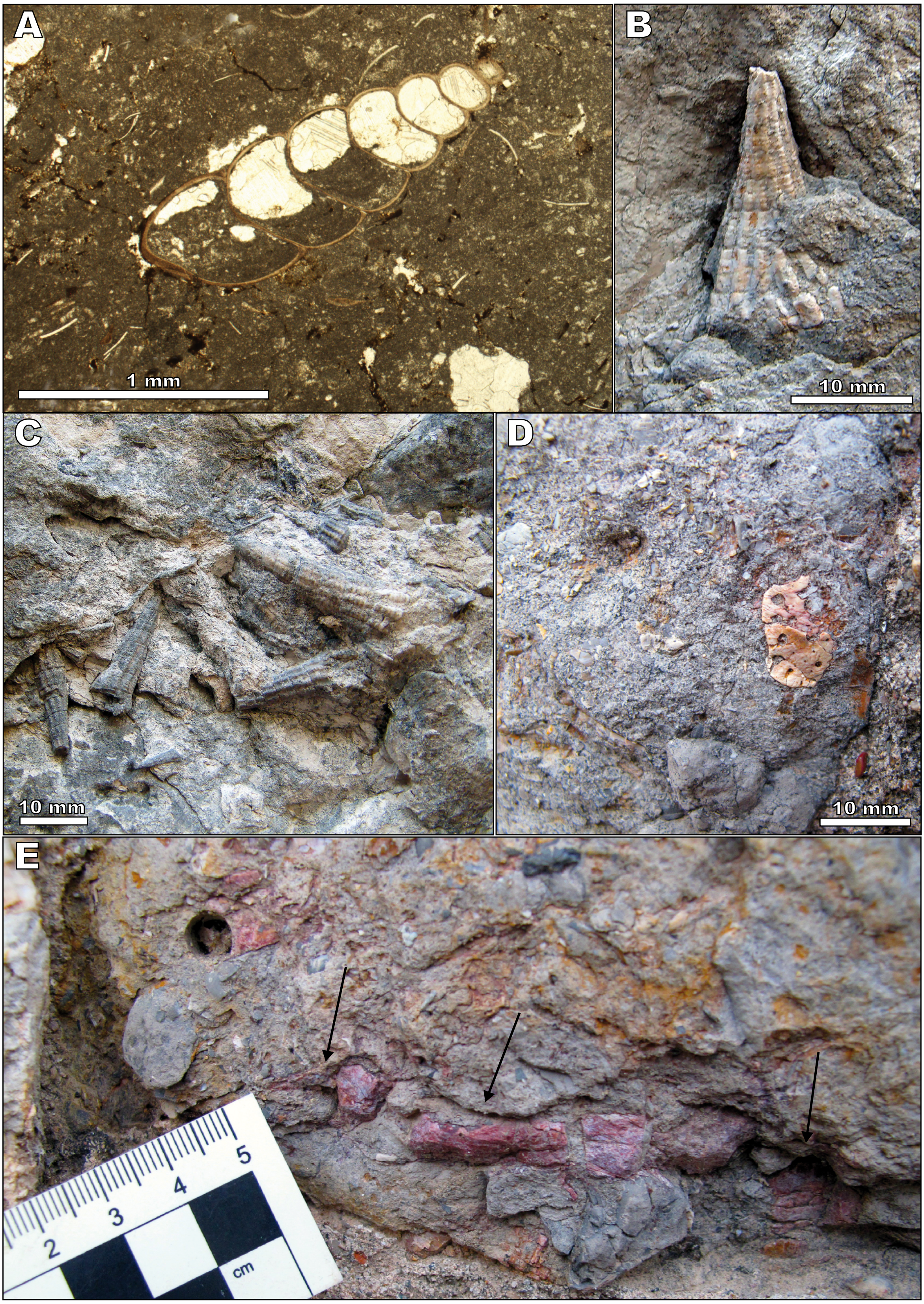

FIGURE 9. Palaeontological features of the lower part of the Serra de Llaberia Glauconitic Limestones and Lutites Formation. A) Microphotograph of a packstone-wackestone limestone showing a section of a gastropod shell and several ostracod carapaces. B-C) Shells of *Terebraliopsis* sp. D-E) Remains of a crocodylomorph reptile in a block of the city wall. D) Caudal osteoderm. E) Post-cranial bones (arrows).

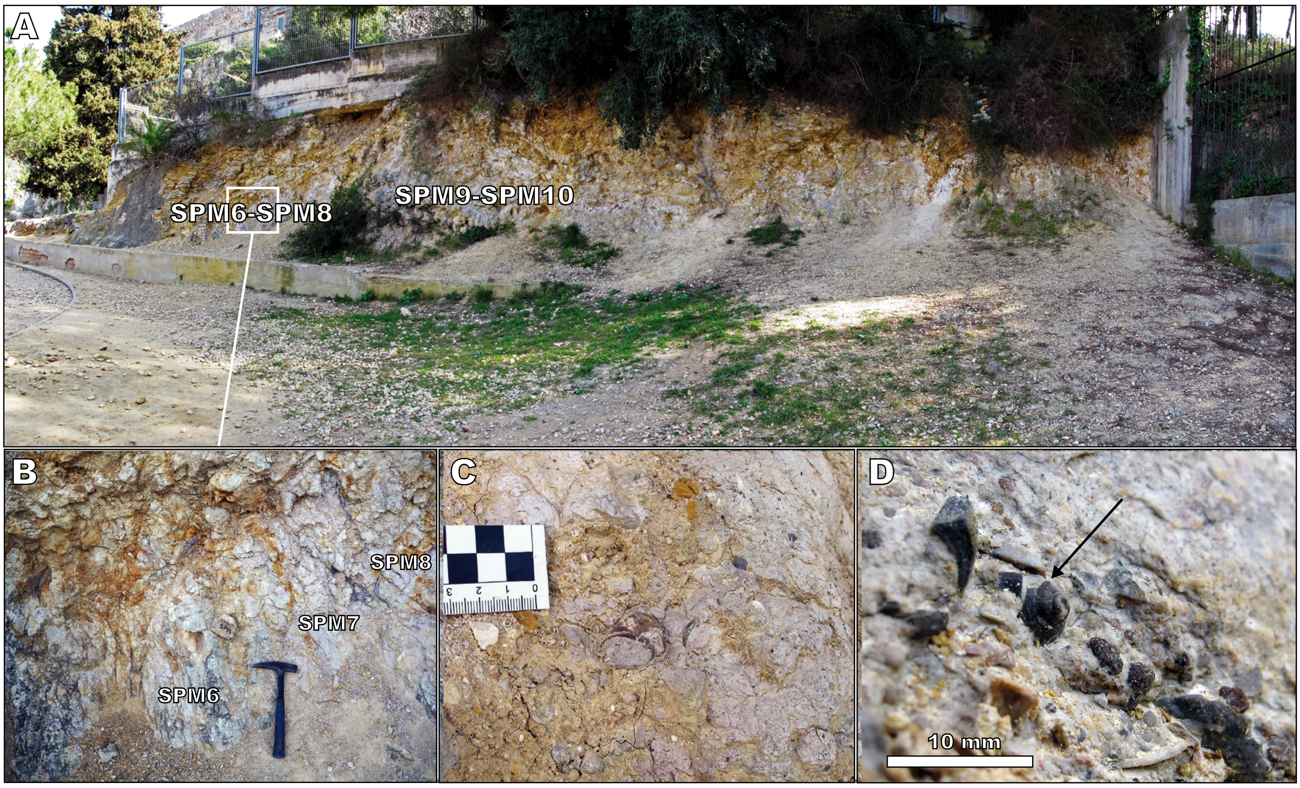

FIGURE 10. Outcrop views of the upper part of the Serra de Llaberia Glauconitic Limestones and Lutites Formation. A) General view of the marlstone unit in the Sant Pau schoolyard showing the location of the charophyte samples. Height of the outcrop equals 2m. B) Detail of the outcrop showing verticalised edaphic features. Hammer is 30cm long. C) Detail of the outcrop showing abundant remains of gastropods. D) Detail of a *Physa* sp.? shell (arrow) and indeterminate gastropods. Scale bar= 10mm.

arranged around the top of the internodal cell and opened to the outside by a small pore (Fig. 12H). Internodes formed by a large internodal cell, about 300μm across, coated by about 24 thin tubular cortical cells, about 100μm in diameter. Only the intercellular space between the internode and the cortical cells is calcified. The cortical cells emerge radially below and above nodal cells in groups of 5–6 (Fig. 12I). The cortical cells from adjacent nodes meet and interdigitate in the centre of the internode forming a zig-zag line (Fig. 12G).

Remarks. The biological affinity of the thallus *Munieria* for charophytes or dasycladaleans has been a matter of debate in the past (*e.g.* Feist *et al.*, 2003). Following the view of Pérez-Cano *et al.* (2020), we relate this parataxon to the thalli of charophytes, based on the interdigitation of the cortical cells at the centre of the internode. Pérez-Cano *et al.* (2020) also highlighted its affinity with the clavatoracean subfamily Clavatoroidae based on its particular calcification, which follows the same centripetal pattern as the gyrogonites of the same subfamily. However, this character could not be observed in thin sections of the material studied here since remains were recrystallised in sparry calcite, as usual in this genus. In the assemblage studied no fructifications belonging to the Clavatoroidae were found, but the occurrence of well-preserved thalli of *M. grambastii* forma *sarda* suggests that an unknown species from this subfamily coexisted with *Atopochara trivolvis* var. *multivolvis*.

DISCUSSION

Taphonomy and palaeoecology

Atopochara trivolvis var. *multivolvis* utricles are abundant and complete, but superficially corroded (Fig. 12A–E). This corrosion is attributed to the epi-diagenetic partial dissolution of the utricle surface. No evidence of fragmentation or erosion was observed. However, the lack of a corresponding abundance of utricles and thalli suggests that the assemblage may have undergone lateral transport from the charophyte meadow where they were originally produced. In contrast to the moderate preservation of *A. trivolvis* var. *multivolvis* utricles and *Clavatoraxis* sp. remains, the thalli *M. grambastii* were much better preserved, showing no signs of corrosion (Fig. 12G–I), suggesting that the recrystallisation of these thalli prevented epi-diagenetic corrosion.

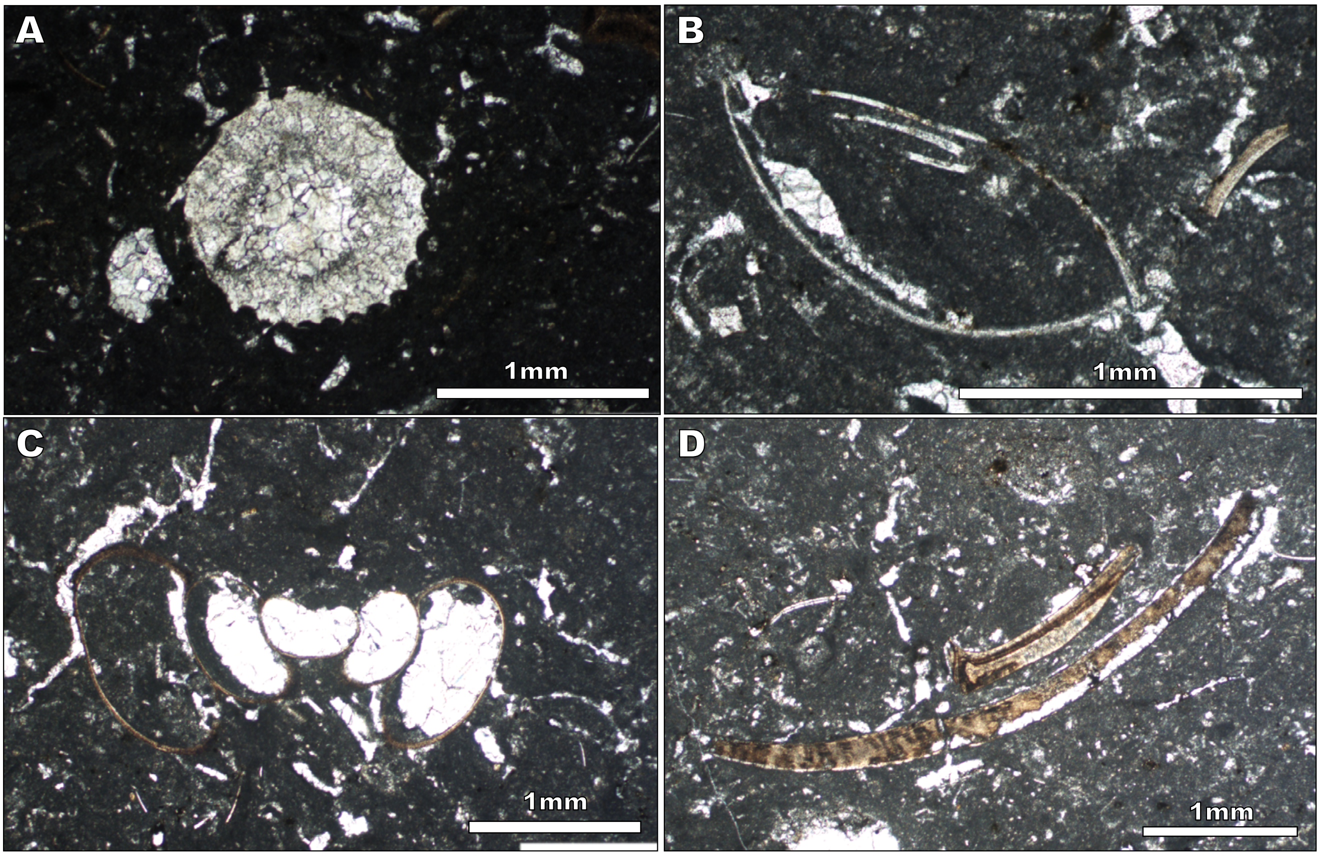

FIGURE 11. Photomicrographs of the non-marine limestones from the upper part of the Serra de Llaberia Glauconitic Limestones and Lutites Formation. A) *Atopochara* utricle showing a bottle-shaped uncalcified oospore and crenulation of the utricle cells. B) Ostracod carapace showing a smooth surface. C) Non-marine gastropod shell. D) Vertebrate remains.

Atopochara trivolvis is considered a eurytopic species that was capable of living in many different habitats ranging from freshwater lakes and ponds to brackish lagoons (Pérez-Cano *et al.*, 2022). However, the present assemblage is associated with freshwater molluscs with no evidence of marine influence, suggesting a freshwater environment.

Biostratigraphy

A. trivolvis var. *multivolvis* is considered middle Cenomanian–late Turonian in age, based on the correlation of the occurrence of this charophyte with marine biostratigraphic indicators (Riveline *et al.*, 1996). The first appearance datum of this charophyte was correlated with the occurrence of the larger foraminifera *Praealveolina iberica* and *Ovalveolina ovum* by FEUILLÉE ET GRAMBAST (1961) near Oña (Burgos province, north Spain) in the northern domain of the Castilian ramp. More recently, Feist and Floquet (2022) reviewed this occurrence and found *A. trivolvis* var. *multivolvis* in the Dosante Formation, just below a marine sequence containing *Praealveolina* gr. *cretacea* and *Orbitolina (Conicorbitolina)* cf. *conica* (D'ARCHIAC), indicating an age of middle Cenomanian.

The last appearance of *Atopochara trivolvis* var. *multivolvis* in the upper Turonian was correlated with the occurrence of rudists in Mazaugues (Var, France) by Feist (1981). The charophytes were found overlying the Mazaugues bauxite in marls deposited in a brackish environment. In this area, particularly in the west Caramy bauxite quarry section, the same brackish deposits contain *Hippurites (Hippuritella) vasseuri* DOUVILLÉ, which was abundant in the upper Turonian but may reach the basal Coniacian in other localities of southern France and Spain (Philip, 1970 and personal communication, December 2024). To date, *A. trivolvis* var. *multivolvis* has not been reported from strata younger than the upper Turonian.

In Tarragona, *A. trivolvis* var. *multivolvis* was found in non-marine deposits overlying the marine Serra de Llaberia Massive Limestones Formation, which contains an assemblage of calcareous dinocysts and planktonic foraminifera (*Pithonella sphaerica* and *Whiteinella cf. paradubia,* respectively) that has been attributed to the Turonian by Esteban (1973). In summary, this species in Tarragona is considered to

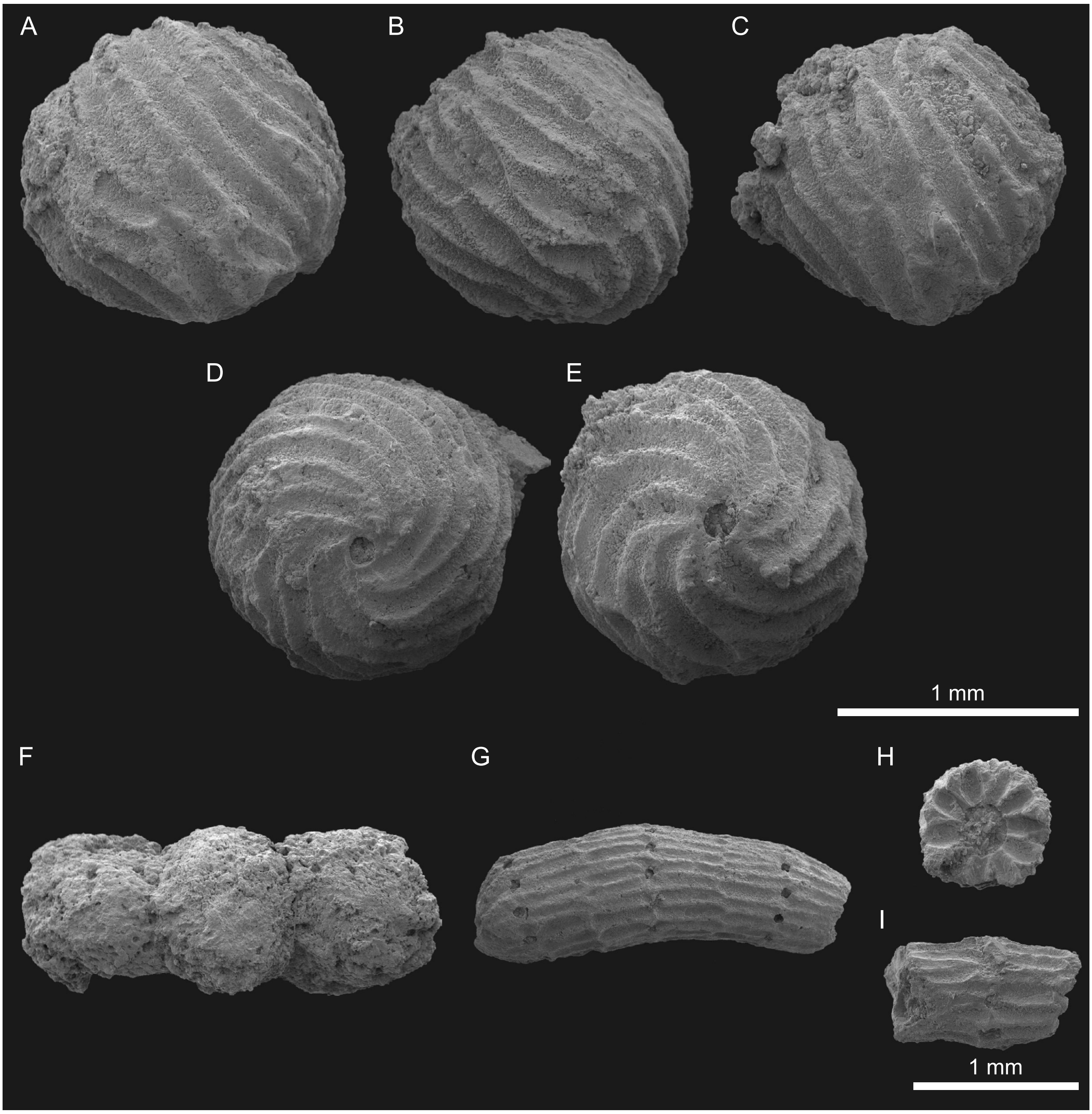

FIGURE 12. Charophyte assemblage from the Upper Cretaceous of Tarragona. A-C) *Atopochara trivolvis* var. *multivolvis*, lateral view of utricles MGSB-89235 to MGSB-89237 from samples SPM-8, SPM-14, and SPM-8 respectively. D) *Atopochara trivolvis* var. *multivolvis*, apical view of utricle MGSB-89238 from sample SPM-8. E) *Atopochara trivolvis* var. *multivolvis*, basal view of utricle MGSB-89239 from sample SPM-8. F) *Clavatoraxis* sp., lateral view of phylloid showing swollen whorls of spine-cell rosettes. Specimen MGSB-89240 from sample SPM-6. G) *Munieria grambastii* forma *sarda*, lateral view of thallus showing three nodes and two internodes. Specimen MGSB-89241 from sample SPM-11. H) *Munieria grambastii* forma *sarda*, transversal view of node. Specimen MGSB-89241 from sample SPM-6. I) *Munieria grambastii* forma *sarda* lateral view of the node, showing the departure of 5-6 cortical cells from a nodal cell. Specimen MGSB-89242 from sample SPM-6.

be Turonian in age. This casts some doubt on previous attributions of the Serra de Llaberia Glauconitic Limestones and Lutites Formation to the Campanian or Maastrichtian (Colombo, 1980; Robles, 1974, respectively). These chronostratigraphic attributions were based on provisional data that correspond to strata overlying the non-marine sequence in other localities near Tarragona, such as in the Serra de Llaberia, disconnected cartographically and difficult to correlate with the study area.

Palaeobiogeography

During the Cenomanian–Turonian interval, the biogeographic distribution of *A. trivolvis* var. *multivolvis* was extensive across the Northern Hemisphere (Table 1), spanning from the United States (Peck, 1957) to Western Europe (Colin and Médus, 1972; Feist, 1981; Feist and Floquet, 2022; Feuillée and Grambast, 1961), and Armenia (Kyansep-Romashkina, 1980) within a latitudinal belt near 40ºN (Fig. 14). This taxon did not extend further east, as Turonian charophyte assemblages from the Songliao Basin in China contained *Atopochara trivolvis* var. *restricta* (GRAMBAST-FESSARD), a less-derived morphotype of the *A. trivolvis* gradualistic lineage (Li *et al.*, 2020). In Europe, the latter variety was present during the Albian and gradually evolved into the more derived *A. trivolvis* var. *multivolvis* during the early and middle Cenomanian (Feist, 1981; Grambast, 1974).

In the Cretaceous Tethyan Archipelago, *A. trivolvis* var. *multivolvis* thrived either in freshwater (*e.g.* Tarragona, Catalonia) or brackish water (*e.g.* Mazaugues, France) coastal lakes, forming monospecific to paucispecific assemblages. In the latter case, it is usually associated with only one more species, that is either a clavatoracean or a characean (Table 1). Hence in the Cenomanian of Pantano de La Tranquera (Zaragoza, Spain) and in the Turonian of Mazaugues (Var, France) it was associated with one characean (*Lamprothamnium ovoideum* FEIST ET FLOQUET and *Mesochara fusiformis* FEIST, respectively), while in the Turonian of Tarragona it was associated with an undetermined representative species of the subfamily Clavatoroidae.

The paucispecific Turonian assemblages from the European palaeo-islands of the Tethyan Archipelago strongly contrast in biodiversity with the coeval assemblages from mainland lakes, as evidenced by the Chinese and Argentinian records. In the Turonian Songliao Basin (China), Li *et al.* (2020) reported assemblages comprising up to five species, *i.e. Atopochara trivolvis* var. *restricta* (GRAMBAST-FESSARD), *Nodosochara (Turbochara) heiolongjiangensis* (WANG, LU et ZHAO), *Lamprothamnium ellipticum* (WANG, LU et ZHAO), and *Lychnothamnus barbosai* (PETRI). Similarly, in the Turonian–Coniacian El Zampal (Neuquén Basin, Argentina), Uliana and Musacchio (1978) and Musacchio (2010) documented assemblages with up to five species, *i.e. Tolypella grambastii* MUSACCHIO, *Nitella* sp., and *Lychnothamnus barbosai*. The monospecific assemblage from the Cenomanian–Turonian of Utah reported by Peck (1957) is an exception to this pattern. However, this record may represent a record of a coastal setting rather than an inland lake (Fig. 14).

In summary, the available data suggest that Cenomanian and Turonian charophyte assemblages from the Tethyan Archipelago palaeo-islands dominated by *A. trivolvis* var. *multivolvis*, were an impoverished version of Lower Cretaceous assemblages, in which the dominant clavatoracean floral physiognomy was preserved. At the same time, assemblages dominated by derived characeans were already evolving in the mainland lakes of South America and especially in China. In these areas, early characeans have formed homogeneous populations since the Early Cretaceous (*e.g.* De Sosa Tomás *et al.*, 2022). The whole dataset suggests that during Cenomanian and Turonian the palaeo-islands of the Cretaceous Tethyan Archipelago acted as a refugia for the last communities with dominant clavatoraceans. While the Coniacian European charophyte flora is almost unknown (but see an exception in Ösi *et al.*, 2021), the last clavatoracean-dominated charophyte communities were completely substituted in the latest Cretaceous (Santonian to Maastrichtian) by communities constituted mainly of derived characeans, including the modern genera.

CONCLUSIONS

The Upper Cretaceous stratigraphic record studied in the Sant Pau schoolyard section of Tarragona has

TABLE 1. World occurrences of *Atopochara trivolvis* var. *multivolvis*

Species	Age	Accompanying species	Locality	State, Country	Reference
Atopochara multivolvis	Cenomanian– Turonian	none	Cannonville, Garfield County	Utah, United States	Peck (1957)
Atopochara multivolvis	Cenomanian	none	Oña, Burgos	Spain	Feuillée and Grambast (1961)
Atopochara multivolvis	Cenomanian	none	Simeyrols, Dordogne	France	Colin and Médus (1972)
Atopochara multivolvis	late Turonian	*Aclistochara gulistanica*	–	Armenia	Kyansep-Romashkina (1980)
Atopochara multivolvis	middle Cenomanian	*Atopochara restricta*	Laudun, Gard	France	Feist (1981)
Atopochara multivolvis	Turonian	*Mesochara fusiformis*	Mazaugues, Var	France	Feist (1981)
Atopochara multivolvis	middle Cenomanian	none	Oña, Burgos	Spain	Feist and Floquet (2022)
Atopochara multivolvis	middle Cenomanian	*Lamprothamiun ovoideum*	Pantano de La Tranquera, Zaragoza	Spain	Feist and Floquet (2022)
Atopochara trivolvis var. *multivolvis*	Turonian	Clavatoroidae (*Munieria grambastii*)	Tarragona (city)	Catalonia, Spain	This study

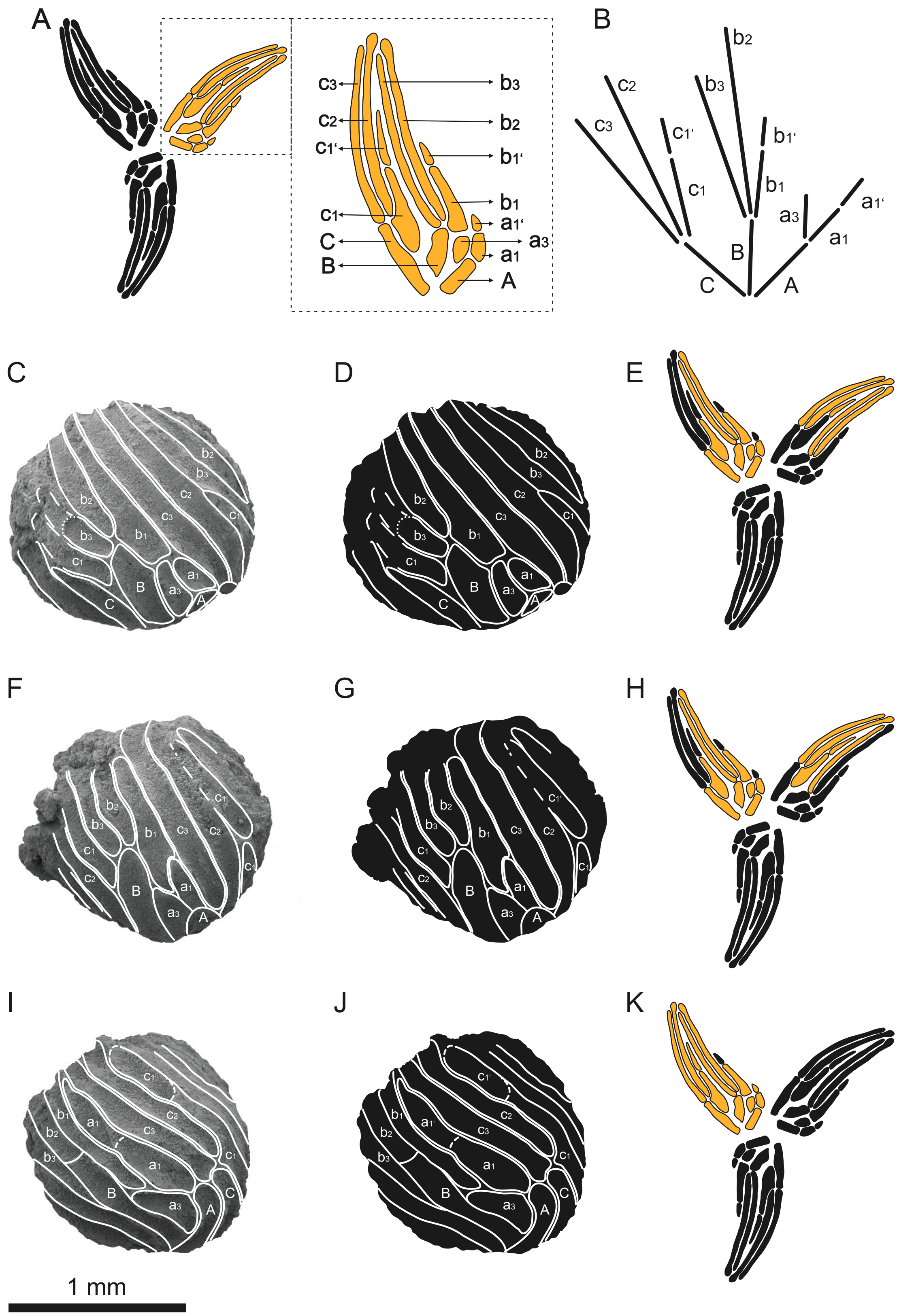

FIGURE 13. Interpretation of the utricle structure of *Atopochara trivolvis* var. *multivolvis* from Tarragona. A) Scheme of utricle structure (left), with indication of the utricle cell-nomenclature (right). B) Diagram of utricle cell structure and nomenclature. C-E) Utricle structure of utricle MGS-89235 and its interpretation. F-H) Structure of the utricle MGS-89237 and its interpretation. I-K) Structure of the utricle MGS-89236 and its interpretation. Diagrams A, B, E–K modified from Grambast-Fessard (1980) and Feist (1981).

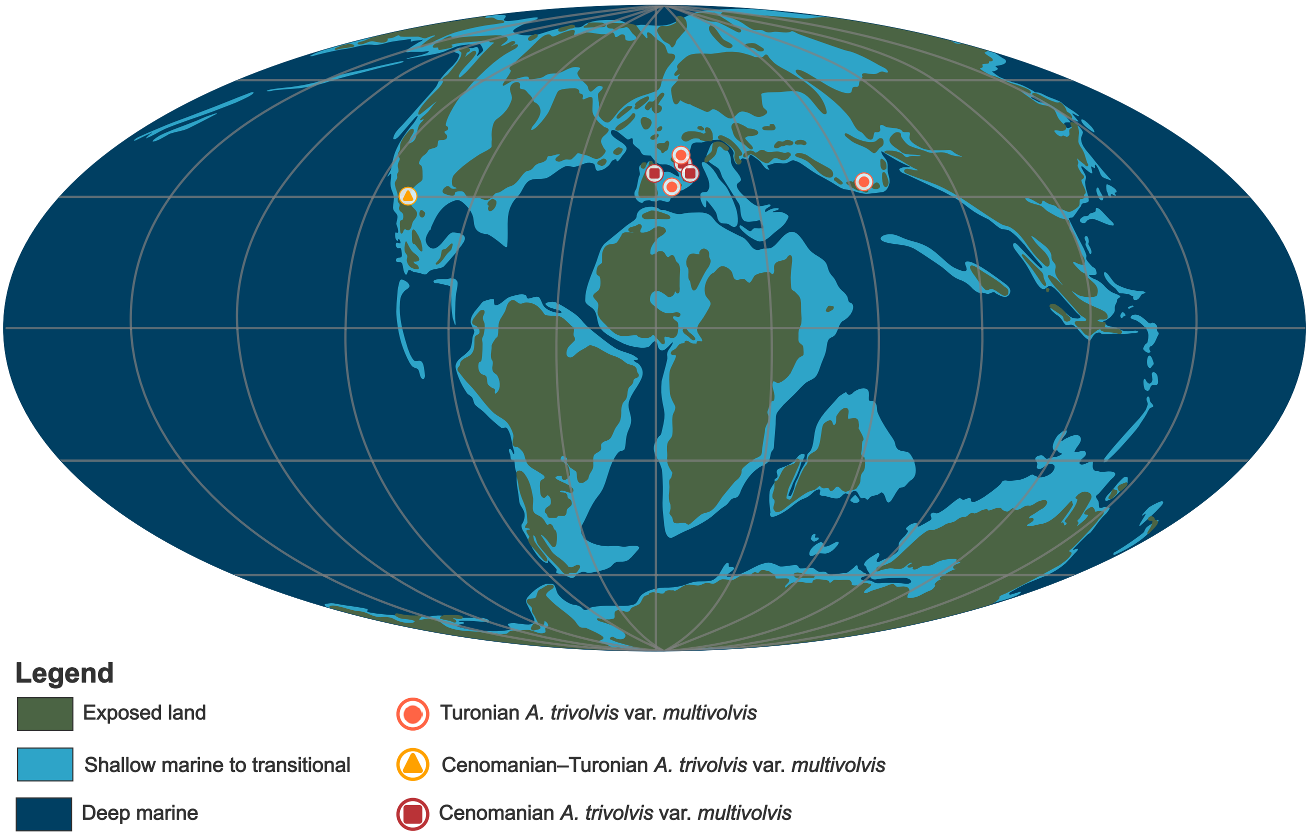

FIGURE 14. Worldwide biogeographic distribution of *Atopochara trivolvis* var. *multivolvis*. Palaeogeographic map modified from https://deeptimemaps.com/map-lists-thumbnails/global-paleogeography-and-tectonics-in-deep-time/.

been interpreted as a major transgressive-regressive sequence that is Cenomanian and Turonian in age. The transgressive deposits of this sequence encompass the upper Cenomanian Serra de Llaberia Tabular Dolostones and *Praealveolina* Limestones Formation and part of the Turonian Serra de Llaberia Massive Limestones Formation. The regressive part of the sequence is represented by the Turonian Serra de Llaberia Glauconitic Limestones and Lutites Formation. These formations have been revisited, and facies characterisation and biostratigraphic data have been updated.

The Serra de Llaberia Glauconitic Limestones and Lutites Formation yielded a poorly diverse charophyte flora dominated by *A. trivolvis* var *multivolvis*, and containing the clavatoroidean thallus *Munieria grambastii* forma *sarda* and freshwater molluscs (gastropods affine to *Physa* among others). This assemblage together with the stratigraphic and biostratigraphic data can be used to attribute this non-marine formation to the Turonian, ruling out more recent ages proposed by previous studies.

The new Turonian charophyte locality joins a small number of other coeval localities from Europe that are all characterised by monospecific to paucispecific assemblages dominated by *A. trivolvis* var. *multivolvis*. These species-poor assemblages thrived in freshwater to brackish coastal lakes on the islands of the Tethyan Archipelago during the global sea-level highstand of the Cenomanian–Turonian boundary.

This study highlights that the Tethyan Archipelago, which was home to a clavatoracean bioprovince throughout the Early Cretaceous, continued to function as a distinct biogeographic unit at least until the Turonian. Towards the end of its existence, the archipelago's island lakes served as refugia for archaic communities that were still dominated by clavatoraceans. By contrast, the mainland lakes in South America and China were already hosting more modern floras dominated by advanced characeans, including extant genera such as *Lamprothamnium*, *Lychnothamnus*, and *Nitellopsis*. These derived genera would colonise European lakes during the latest Cretaceous and especially the Paleogene.

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