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Ecological control of the Pelsonian colonisation event (Anisian, Triassic) leading to the first settlement of *Tetractinella*-beds (Brachiopoda) in the Iberian palaeomargins. Palaeobiogeographical and biostratigraphical significance

José Francisco Baeza-Carratalá [a], Alice Giannetti [a,*], Fernando Pérez-Valera [a], Juan Alberto Pérez-Valera [a], Alberto Pérez-López [b,c]

[a] *Departamento de Ciencias de la Tierra y del Medio Ambiente, Universidad de Alicante, Carr. Sant Vicent del Raspeig, s/n, 03690 Sant Vicent del Raspeig, Alicante, Spain*
[b] *Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avda. Fuentenueva, 18071 Granada, Spain*
[c] *Instituto Andaluz de Ciencias de la Tierra (CSIC-Universidad de Granada), Avda. de las Palmeras, 4, 18100 Armilla, Granada, Spain*

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ABSTRACT

Marine benthic biota recovery after the Permian/Triassic extinction is still a challenging topic in several fossil clades such as brachiopods. In fact, available data from the Early-Middle Triassic are scarce worldwide and their global record derives from limited localities throughout the Tethys Ocean. This work presents the first record of the Anisian *Tetractinella*-beds (Brachiopoda, Athyridida) in the peri-Iberian epicontinental platforms established in the westernmost Tethys margins. Their utility as a reliable biohorizon marker is emphasised as they provide an effective tool for age calibration and correlation in the middle Anisian (Pelsonian) successions, also supported by the co-occurring fossil assemblage. In the South-Iberian Palaeomargin, *Tetractinella*-beds occur in an intensively-burrowed shallow-marine succession. The rich ichnological content has been exhaustively evaluated in order to assess the ecological factors controlling the development of the brachiopod fauna. Three ichnoassemblages are documented dominated by *Oravaichnium, Balanoglossites* and *Thalassinoides*, respectively. The gathered faunal, ichnological, taphonomical, and sedimentological data reveal an alternation of sea-level changes influencing the composition of the Anisian marine communities. The first stage consists of near-shore restricted environments sporadically disturbed by short-term shallow-marine interludes, characterised by the presence of *Oravaichnium* and its associated fauna. Subsequently, the Pelsonian transgression event is recorded (MID-2), documented by a firm-ground surface pointed out by the development of a *Balanoglossites* surface, followed by the highstand, when shallow epicontinental environments developed in connection with open-marine areas. This phase involved the spreading of *Tetractinella* and deep-water bivalves. Finally, near-shore restricted conditions were re-established typified by *Oravaichnium* and the last occurrences of *Tetractinella,* with the disappearance of the open sea-water fauna. The maximum flooding reached after the Pelsonian transgression facilitated new palaeobiogeographical migration routes, allowing for an Alpine-Germanic dispersion of taxa throughout the North-South epicontinental Tethyan seaway as well as the earliest first faunal migration event from the Sephardic Bioprovince northwards to the South-Iberian palaeomargin.

1. Introduction

The phylum Brachiopoda is a key fossil group to unravel the macroevolutionary history of the marine benthic epifauna (Ager, 1956, 1983; Johnson, 1975; McNamara, 1982; Raup, 1986; Valentine and Jablonski, 2010; Carlson, 2016; Harper et al., 2017; Stigall, 2018) since it has been recurrently affected by all the classical great extinction and diversification events and numerous marine biotic crises throughout the

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* Corresponding author.
E-mail addresses: jf.baeza@ua.es (J.F. Baeza-Carratalá), alice.giannetti@ua.es (A. Giannetti), fperez@ua.es (F. Pérez-Valera), japerezv@ua.es (J.A. Pérez-Valera), aperezl@ugr.es (A. Pérez-López).

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Phanerozoic (Gould and Calloway, 1980; Chen et al., 2005; Curry and Brunton, 2007; García Joral et al., 2011; Carlson, 2016; Vörös et al., 2016, 2019; Harper et al., 2017; Baeza-Carratalá and García Joral, 2020). Their adaptive evolutionary strategies and resilience around such events, their wide-ranging record as well as their high abundance and diversity throughout the Phanerozoic make this group a valuable tool to shed light on the evolutionary success and diverse responses to environmental perturbations of marine benthic ecosystems over time.

After their Palaeozoic heyday and the severe diversity decline suffered because of the greatest mass extinction event at the P/T boundary (e.g. Gould and Calloway, 1980; Sepkoski Jr., 1996; Curry and Brunton, 2007; Carlson, 2007, 2016; Garbelli et al., 2017; Vörös et al., 2019), brachiopods thrived in the Early Triassic as one of the foremost constituents of marine ecosystems (Kummel, 1979; Sheng et al., 1984; cf. Kauffman and Erwin, 1995; Chen et al., 2005; Halamski et al., 2015). In this sense, the Anisian stage was crucial for the diversity dynamics and the evolutionary trajectories of several brachiopod clades. Their immediate recovery after the P/T extinction it is widely documented (Chen et al., 2005, among others), even in the earlier Triassic (Induan) seas, subsequently reaching the over-all diversity renewal and successive radiation of the "post-Palaeozoic type" fauna in the Anisian (Chen et al., 2005, 2010; Halamski et al., 2015; Friesenbichler et al., 2021; Guo et al., 2022, among many others).

Notwithstanding this diversity burst, the global Anisian brachiopod record is scarce worldwide (Guo et al., 2022): from China to Russia and from New Zealand to Romania, brachiopods derive from relatively limited fossiliferous localities in both Eastern and Western parts of the Palaeotethys Ocean. This poor record is also true for the peri-Iberian epicontinental platforms established in the westernmost Tethyan margins, where the Anisian brachiopods are only represented by isolated and sporadic occurrences of *Mentzelia* Quenstedt, 1871 (*M. mentzeli* Dunker, 1851; *M.* sp.), and *Koeveskallina koeveskalyensis* (Stur, 1865), mainly from Menorca and the Catalonian Coastal Range (Schmidt, 1935; Calzada and Gaetani, 1977; Escudero-Mozo et al., 2015).

This work describes the first report in the peri-Iberian platforms of the middle Anisian *Tetractinella*-beds. Their occurrence represents the earliest record so far of the post-Palaeozoic brachiopods from the Betic Ranges, together with the occasional cosmopolitan *Aulacothyris* and *Coenothyris* assemblages, which were recorded in the Internal Betic Zones (Simon, 1963). The co-occurrence of the *Tetractinella*-beds with a well-diversified fossil assemblage (nautiloids, bivalves and pollen), several isotopic signals (Pérez-Valera et al., 2023) and vertebrate remains of a marine reptile (Berrocal-Casero et al., 2023) supports the attribution of the studied deposits to the Anisian (Pérez-Valera et al., 2023).

The reconstruction of the environmental and depositional conditions that led to the establishment of *Tetractinella* accumulations in the Betic Ranges reinforces the hypothesis of a faunal migration reported in the westernmost Palaeotethys Ocean during the Pelsonian maximum flooding, which caused the connection of nearshore and shallow epicontinental environments with open-marine areas (Pérez-Valera et al., 2023 and references therein). This would have made easier the expansion of different groups out of their original habitat. In order to point out the ecological conditions around the *Tetractinella*-beds, an integrated analysis was performed, since the brachiopod-bearing beds are comprised in an intensively-burrowed shallow-marine interval. Therefore, the very rich ichnological content has been exhaustively analysed. The resulting ichnoassemblages were assessed and compared with previous analogous Triassic reports in the Western Tethys (Jaglarz and Uchman, 2010; Knaust and Costamagna, 2012; Giannetti et al., 2017; Knaust, 2021; Stachacz et al., 2022), appropriately enhancing the identification of frequently misinterpreted ambiguous ichnotaxa.

In absence of more accurate biostratigraphic markers, the Triassic brachiopod-beds are frequently used as alternative correlation biohorizons. In this work, the *Tetractinella*-beds are considered from their biostratigraphic and palaeobiogeographic perspectives, correlating the Iberian findings with nearby basins and emphasizing the Triassic brachiopod-beds as effective correlation tools in the Western Tethys.

In view of the scarcity of benthic macroinvertebrate assemblages in the Lower-Middle Triassic at the peri-Iberian platforms, the new data obtained from the compositional, ichnological, taphonomical, and sedimentological analyses of the External Betic Anisian succession are very significant, especially in the framework of the limited record of Anisian sedimentary sequences. The gathered data improve the understandig of the strategies of the Triassic fauna in nearshore environments, just in correspondence to the diversification of the benthic-biota after the Permian-Triassic extinction event.

2. Geological setting

In the Iberian Peninsula, Triassic rocks represent the first deposits linked to the rifting stage related to the break-up of Pangea (López-Gómez et al., 2019 and references therein). In this context, successive transgression-regression cycles are recorded in the margins of the Iberian plate through the westward expansion of the Neotethys (López-Gómez et al., 2002, 2019). As a result, Triassic rocks are characterised by the presence of the classical trilogy of the 'Germanic facies' that consists in the presence of Buntsandstein, Muschelkalk and Keuper facies (e. g., Virgili et al., 1977; Pérez-López, 1998; López-Gómez et al., 2002; Escudero-Mozo et al., 2015). These Triassic units were deposited in continental, fluvial (red beds) to evaporite coastal environments (Buntsandstein and Keuper facies, respectively) related with shallow marine epicontinental carbonates (Muschelkalk facies).

In detail, the arrangement of these facies allowed the subdivision of Triassic units of the Iberian Peninsula in different palaeogeographic domains, mainly according to the presence of one or two Muschelkalk carbonate units and their age (López-Gómez et al., 1998; Pérez-López and Pérez-Valera, 2007; Escudero-Mozo et al., 2015): i) Iberian Triassic (one carbonate unit of Ladinian age), ii) Mediterranean Triassic (two carbonate units of Anisian and Ladinian age, separated by an evaporite-detritic unit) and iii) Levantine-Balearic Triassic (one carbonate unit of Anisian-Ladinian age). Additionally, in the south of the Iberian Peninsula, Alpine marine facies can be found as part of the Internal Zones of the Betic Cordillera, showing mainly carbonate deposits (Delgado et al., 2004; Pérez-López and Pérez-Valera, 2007).

The studied area is located in the External Zones of the Betic Cordillera, which is geographically positioned in the southern region of the Iberian Peninsula (Fig. 1) and that constitutes the northern segment of the Betic-Rif Orogen. In this orogenic structure, the Betic and Rif cordilleras are linked by the Gibraltar Arc, which represents the western extremity of the Alpine, peri-Mediterranean fold belts, and consists of non-metamorphic rocks ranging from the Triassic to the Miocene. These rocks result from the folding and thrusting of sediments from the South-Iberian Palaeomargin, driven by the westward migration and collision of the Meso-Mediterranean (Alborán) Terrain during the Miocene period (Balanyá and García-Dueñas, 1987). These structures nowadays constitute the so called Internal Zones (Fig. 1). The External Betic Zones are further categorised into Prebetic and Subbetic according to their proximity or distality to the Iberian palaeomargin during the Mesozoic, particularly in the Jurassic and Cretaceous (Vera and Martín-Algarra, 2004). The more proximal Prebetic domain shows predominantly shallow, coastal-marine facies. In contrast, the Subbetic units, located in the most distal areas, exhibits a higher prevalence of hemipelagic facies.

This study has been carried out in the 'Las Atalayas' site, near the locality of Cehegín (Murcia province, Southeastern Spain; Fig. 1). In this area, Triassic units crop out extensively together with other Jurassic and Cretaceous material of the Subbetic Domain. The Triassic units are composed of several carbonate (Muschelkalk facies) and evaporite-detritic units (Keuper facies) that correspond to the distinctive units of the South-Iberian Triassic (Pérez-López and Pérez-Valera, 2007). Recently, Pérez-Valera et al. (2023) attributed the carbonates from 'Las Atalayas' to the Anisian stage and assigned them to the Lower

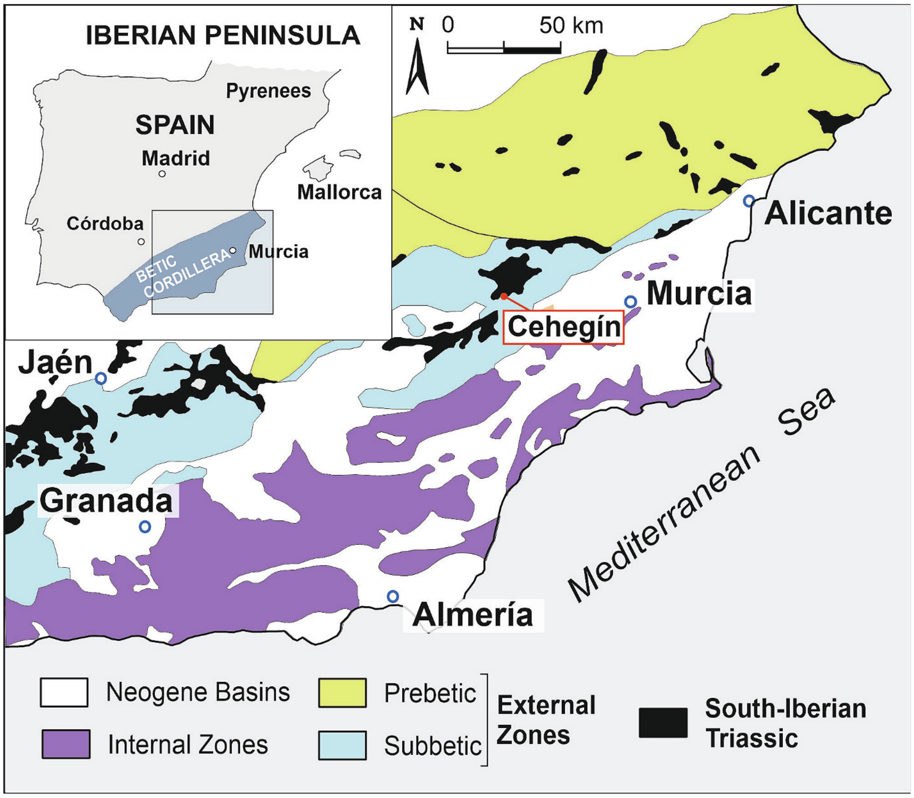

Fig. 1. Geological setting of the studied area in a general map of the eastern Betic Cordillera. Modified after Berrocal-Casero et al. (2023).

Muschelkalk (M1, Fig. 2A, B). This was the first record of these deposits in the External Zones of the Betic Cordillera. These carbonates, previously attributed to the Ladinian Cehegín Fm. (Pérez-Valera and Pérez-López, 2008), also present in the area (M3, Fig. 2A, B), reveal the existence of two carbonate units in this region, separated by a gypsum-rich, siliciclastic red beds unit (M2, Fig. 2A, B), which allows this sector of the Betic Cordillera to be included in the palaeogeographic domain of the Mediterranean Triassic (López-Gómez et al., 1998).

3. Material and methods

Amidst the great amount of Triassic outcrops prospected in the External Zones of the South-Iberian Palaeomargin over the last decades, Anisian brachiopods only have been collected and studied around the Las Atalayas site where new bed-by-bed sampling has been exhaustively carried out to achieve a high-resolution record. This resulted in a total number of 86 specimens making up a monospecific brachiopod community attributed to *Tetractinella trigonella* (Schlotheim, 1820). Taxonomic supra-generic assignments follow the published determinations, mainly by Kaesler (1997–2006) and Selden (2006). The sampled specimens and pavement slabs containing this taxon are deposited in the repository of the Earth and Environmental Sciences Department (DCTMA) at the University of Alicante (Spain), labelled under reference numbers CMB.1 to 80 and LAT.1 to 20. The main biometric parameters (in mm) and indices were measured for the taxonomical analysis when it was possible. A faunal comparative analysis was performed after review of the dataset from several European basins. In this sense, on the occasion of the 8th International Brachiopod Congress field trip (Milan, Italy; Tintori et al., 2018), authors were able to directly examine the samples of *T. trigonella* derived from the "*Banco a brachiopodi*" of the Calcare di Angolo from the Grigna Group, comparing these referential specimens with those recorded in the new Betic *Tetractinella*-beds. Statistical boxplots were performed in both populations to better evaluate differences in size and the intraspecific variability in the external outline.

The nautiloid specimens supplementing the biostratigraphical and palaeoenvironmental data of this work are also housed in the DCTMA repository (CH1-A1 to 4, CH1-C1 to 3, and CH2-A1 to 4). The ammonoid zonal scheme used is based on the standard zones proposed by Balini et al. (2010) modified by recent chronostratigraphic data from Pérez-Valera (2015) for the Betic Domain.

The Anisian global palaeogeographic map was computed with GPlates 2–2.0 in the framework of the Paleomap Project (Scotese, 2016). A more recent and detailed regional reconstruction of the westernmost Tethys Ocean, specially focused on the peri-Iberian margins and adjacent areas, is plotted on a palaeomap for the Anisian (Pelsonian) stage slightly modified after Pérez-Valera et al. (2023), elaborated in order to discuss palaeobiogeographical data. The interpretation of the global circulation of marine currents in the Anisian by Crasquin et al. (2010), Escudero-Mozo et al. (2015), Martindale et al. (2019), and Manzanares et al. (2020) were taken into account. Palaeobiogeographic categorisation of biochores follows the nomenclature proposed by Westermann (2000), subsequently adapted for the brachiopod fauna by several authors (e.g. Manceñido, 2002; Vörös et al., 2016).

In order to distinguish the different lithofacies, thirty-five rock samples were collected for thin section analysis. Alizarin Red S was used to distinguish dolomite. All specimens and polished slabs were coated with magnesium oxide prior to photographing when it was possible.

As for trace fossils, a bed-by-bed analysis was carried out measuring representative specimens of the different ichnotaxa and analysing tiering and filling, the latter both in hand samples and in thin section. Trace fossils morphology, presence/absence of scratches, type of filling and style of branching (where present) have been considered to classify trace fossils, together with all the criteria exposed by Knaust (2008, 2013, 2021) and Stachacz et al. (2022), which represent the most up-to-date and complete revisions of the ichnotaxa present in the studied outcrops.

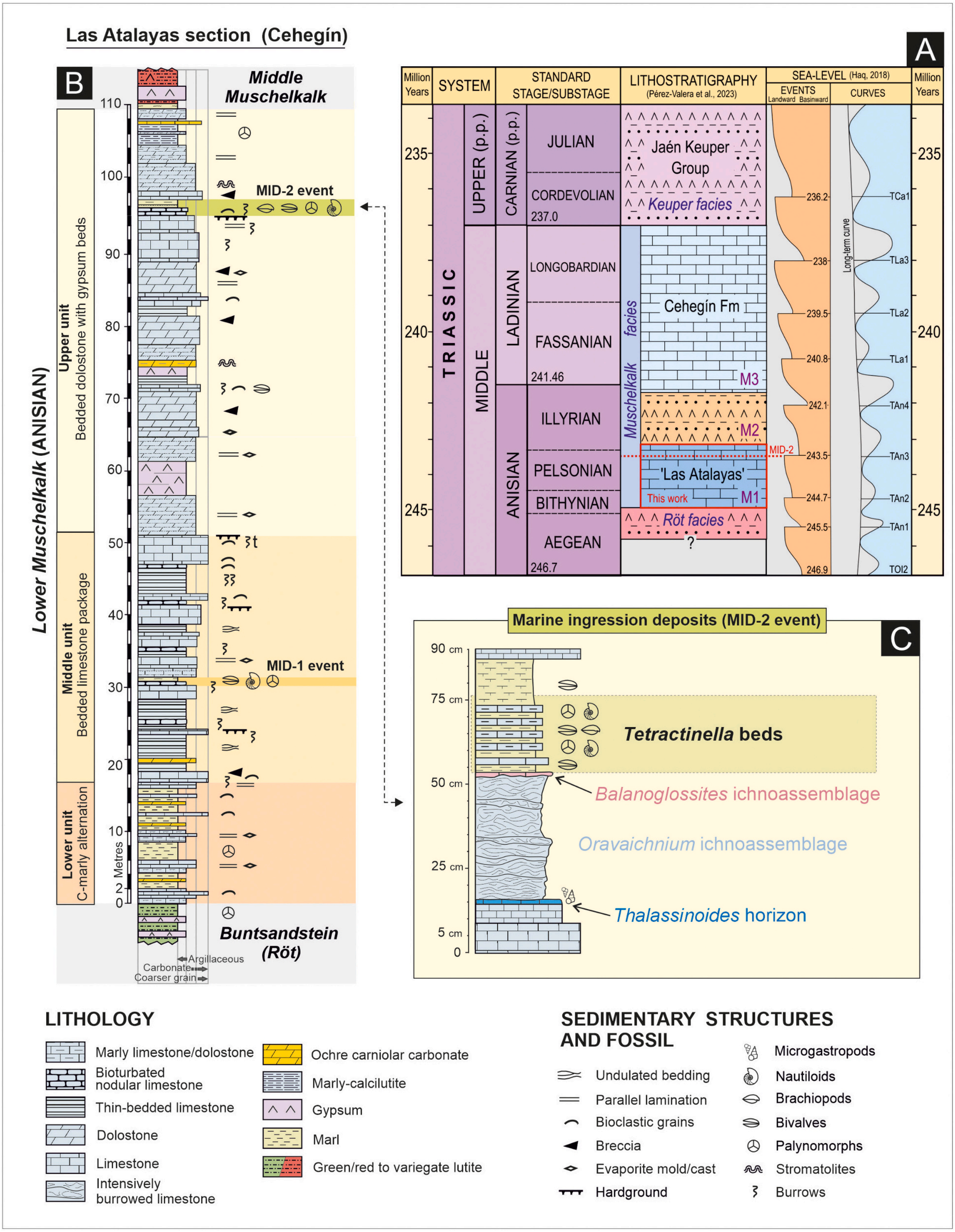

Fig. 2. A. Lithostratigraphy of the South-Iberian Triassic and their correlation with sea-level variations. Time scale after Ogg et al. (2020). M1, M2 and M3 correspond to the abbreviations of Lower, Middle and Upper Muschelkalk, respectively. B. Stratigraphic section of Las Atalayas, based on the work of Pérez-Valera et al. (2023), showing the distribution of the main ichnoassemblages and the *Tetractinella*-beds described in the present study. C. Detail of the Betic *Tetractinella*-beds, with nodular limestones and clayey interval, located in the upper member, related to a marine ingression event.

4. Lithostratigraphical characterisation of the Betic *Tetractinella*-beds interval

The stratigraphic sequence studied at Las Atalayas comprises a 110 m-thick succession subdivided in three lithological members (Fig. 2B), previously described in Pérez-Valera et al. (2023). The Lower Unit is composed of an alternation of green claystones and cm-thick carbonates with evaporite moulds that overlies the Röt facies (uppermost part of the

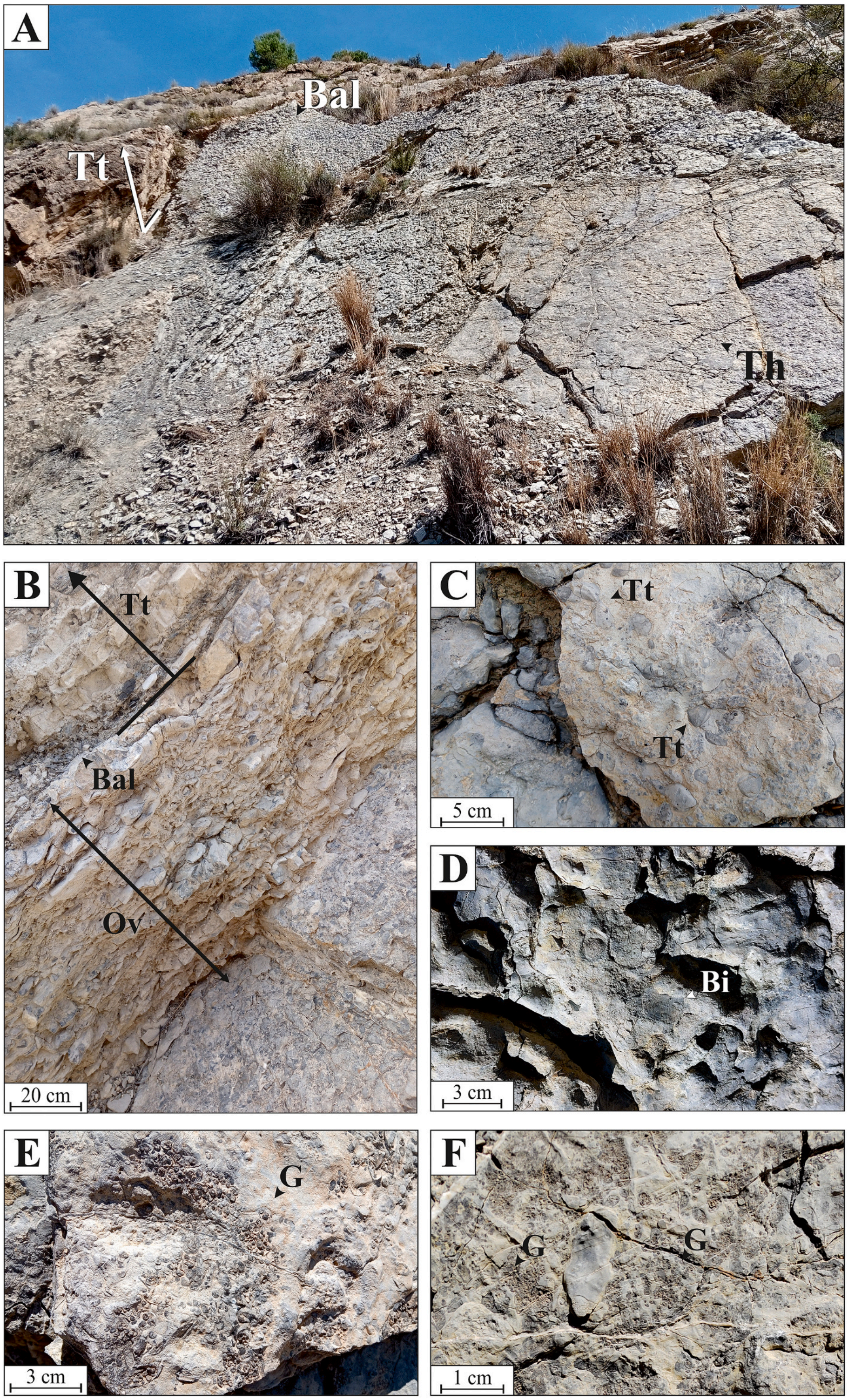

Fig. 3. A. Panoramic view of the Las Atalayas section. The position of the *Tetractinella*-beds is marked (Tt). The *Balanoglossites* (Bal) and the *Thalassinoides* (Th) surfaces are visible. Between them, the *Oravaichnium*-rich beds are developed. B. Middle part of the Las Atalayas section. *Tetractinella*-beds are marked (Tt), with the clayey interval positioned at the bottom of the bank. The *Balanoglossites* surface separates the *Oravaichnium*-rich interval from the *Tetractinella*-beds. C–D. Firmground with *Tetractinella trigonella* (C), bivalves belonging to the genera *Bakevellia*, *Unionites* and *Unicardium*, and very small gastropods. On the same surface, also open water thin-shelled, ribbed bivalves identificated as *Daonella* are present (D) E-F. Microgastropod accumulations in correspondence of the *Balanoglossites* (E), and of the *Thalassinoides* surface (F).

Buntsandstein, Fig. 2A). The Middle Unit basically consists of brown dolostone and dark limestone beds arranged in dm-thick well-bedded packages with a green marly intercalation interpreted by Pérez-Valera et al. (2023) as a marine ingression event (Fig. 2B, MID-1), and the Upper Unit comprises dm- to m-thick dolostone with dark limestone beds, and intervals of gypsum and occasional bioclastic beds (tempestites) interbedded (Fig. 2B). The top of the Las Atalayas section is characterised by grey-greenish claystone with dolostone beds, gradually transitioning to the Middle Muschelkalk evaporites and siliciclastic deposits (M2, Fig. 2A, B). *Tetractinella*-beds are found near the top of the section, in the upper part of the Upper Unit. Here, other thin marly beds are present (MID-2; Fig. 2 A,B,C), which are also interpreted as marine ingression deposits (Pérez-Valera et al., 2023).

A detailed analysis of the *Tetractinella*-beds has been carried out to characterise the fossil and ichnofossil content (Fig. 2C). Above a metric interval of massive, grey limestone (Figs. 3, 4), a significant surface with development of the ichnofossil *Thalassinoides* over a 'gastropods pavement' occurs (*Thalassinoides* horizon, Fig. 2C). Overlying this horizon, a 30 cm-thick interval of nodular, intense bioturbated grey limestone beds is developed, where the ichnogenera *Oravaichnium* and *Rhizocorallium* were identified together with some sparse bivalves (*Oravaichnium* assemblage, Fig. 2C). At the top of this interval, a surface with the trace fossil *Balanoglossites* appears (*Balanoglossites* ichnoassemblage, Fig. 2C). Here, the first specimens of *Tetractinella trigonella* are reported, with some bivalves and gastropods forming a shell pavement (Figs. 3, D; 4B). Over this surface, five cm-thick cycles of shaley marly carbonate are documented (Fig. 2C). Bioturbation is only present as isolated galleries, and relatively diverse faunal community consisting of brachiopods (*Tetractinella*), bivalves, and nautiloids is recorded in the marly carbonates, together with pollen and marine phytoplankton (acritarchs) in the shaley green claystone interval (Pérez-Valera et al., 2023). This cyclic interval shows an increase in marly content towards the top, capped by massive, grey carbonates locally presenting very thin bioclastic storm-layers (Fig. 4C–D).

5. Compositional analysis of the *Tetractinella*-beds

5.1. Brachiopod fauna. Morphological and taphonomical characterisation

The brachiopod-bearing levels come from two perfectly correlatable outcrops in very close proximity. The only brachiopod taxon represented in these outcrops is the athyridoid *Tetractinella trigonella* (Schlotheim, 1820). The assignment of all brachiopod specimens ($n = 86$) to the genus *Tetractinella* is unambiguous even for the small fragments, due to their distinctly representative shape. The external morphology is characterised by a pentagonal/trigonal outline with four prominent and restricted diagnostic plications bearing opposing pairs of costae on each valve and flat intercostal areas. A rectimarginate anterior commissure is present, being also straight the lateral one running in the middle of planareas. These diagnostic criteria distinguish *T. trigonella* from their closer (also Anisian) counterparts such as *T. hexagonalis* (Bittner, 1890), which shows blunt margins in the outline, maximum width more shifted posteriorly and the anterior commissure slightly uniplicate (Mantovani,

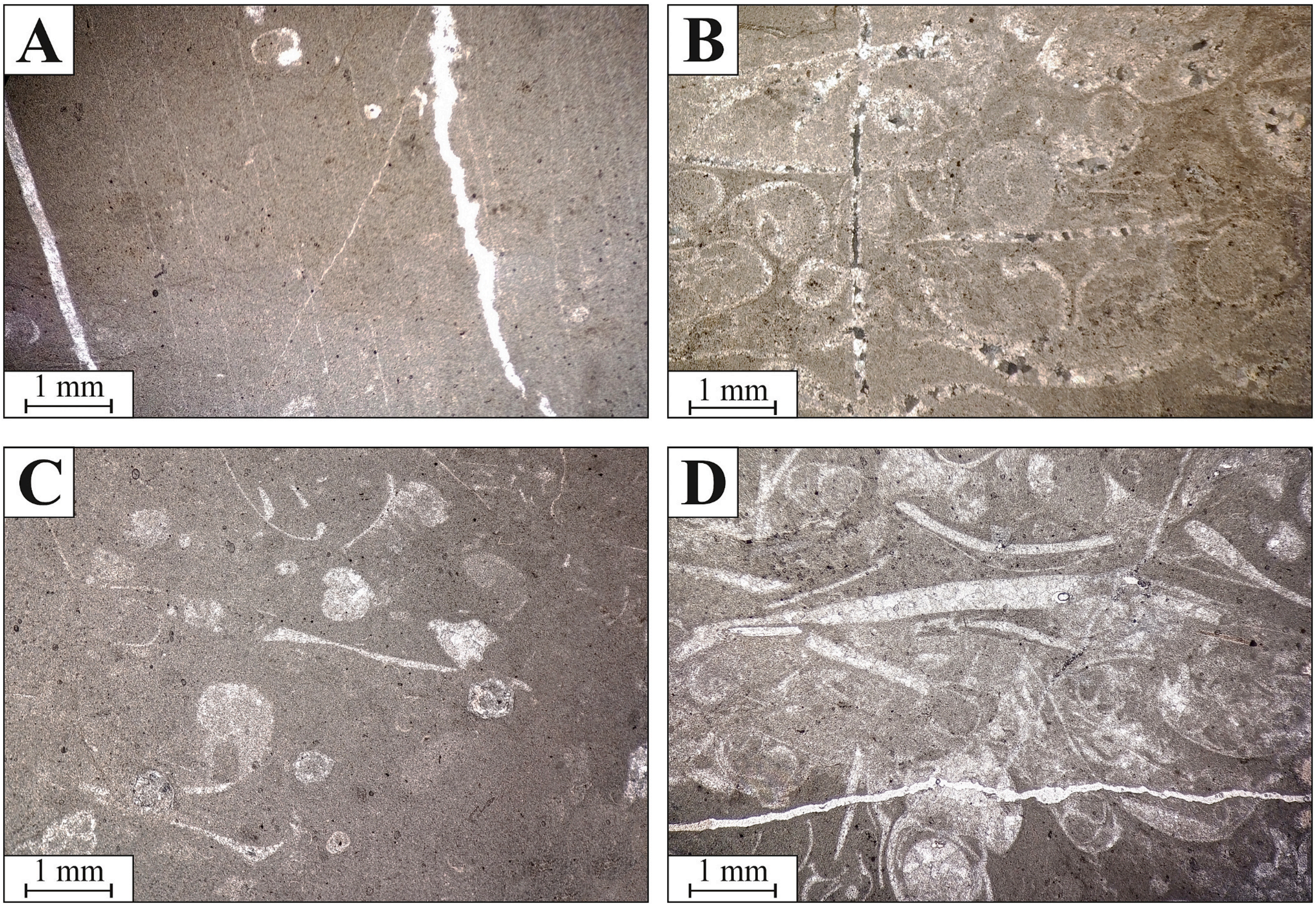

Fig. 4. A. Representative photomicrograph of the *Oravaichnium* ichnoassemblage, characterised by mudstone with sparse small gastropods and thin-shelled bivalves. B. Packed micrograstropods forming thin oligotypic layers in correspondence of the *Balanoglossites* ichnoassemblage. C–D. Thin bioclastic storm layer with pervasive shell recristallisation. Note the slightly erosive base of the level (D), the absence of preferred orientation and the high packing of the bioclasts.

2002). On the other hand, it has been unfeasible to obtain relevant data on the internal structure in the Betic specimens due to the scarcity of material and its poor conservation. An attempt of transverse serial sections has been performed in an isolated specimen and only the presence of impuctate shell, the absence of a long dorsal median septum, and possible vestiges of the spiralium were revealed, thus discarding any case of suprageneric homochronous homomorphism.

In the Betic outcrops, *T. trigonella* is recorded making up monospecific brachiopod assemblages, either as isolated individuals in marly clayey beds (Fig. 3B) or forming scattered patches in condensed pavements (Fig. 3C). Even though its mostly conservative shape, in some Western Tethyan basins, *T. trigonella* usually reveals a moderate range of variability. The Betic specimens show strong and incurved ventral beak and medium-sized pedicle foramen. They are typified by biconvex, triangular-pentagonal shells that tend to be equidimensional, with the maximum width slightly shifted towards the anterior ¼ of the shell. This feature makes them closer to those with more trigonal outline within the interval of the intraspecific variability usually showed by this taxon. However, the pentagonal archetypical stock, with wider than long shells, is also present among the Betic material (Fig. 5). Development of planareas is also a feature of relative variability. In the Betic samples, individuals show well-developed, shallow, and smooth planareas, but in most of the cases the planareas are better developed in the ventral valve, likely as results of the noticeable diagenetic flattening of the shells. This differs from some other representatives recorded by previous authors that show gently depressed planareas in the flanks limited by the lateral costae (e.g., Kaim, 1997, fig. 17; Mantovani, 2002, pl.1, fig. 12c; Pálfy, 2003, pl. Br-1, fig. 1b; Fig. 6 herein). The typical dense growth lines of *Tetractinella* are also visible in the Betic material but to a lesser extent.

In the Betic material, the posterior third of the shell is strong, with the maximum thickness and convexity shifted towards this posterior third and the beak and both the dorsal and ventral umbos recurved in most of the specimens. This conjunction of features influences the final shape of the samples after fossildiagenetic processes. The Anisian brachiopod fauna from Las Atalayas recurrently reveals taphonomic alterations showing disarticulation and shell-distortions. One of the most common is the flattening of the anterior half of the brachial valve. Another common alteration is the tectonic stretching preferentially in the left half of the shell, resulting an asymmetrical winged-shaped profile, also entailing the anterior elongation of the plicae (Fig. 5).

In the condensed pavements, *T. trigonella* is recorded as convex-up ventral valves, with the pedicle foramina towards the pavement. This apparently suggests shells preserved in life position (Fig. 7 A, B), but the high average of disarticulated or fragmented valves (≈ 98%) links this convex-up arrangement to the acquirement of better post-mortem stability in a relatively current-dominated scenario. On the contrary, disarticulation and fragmentation seem not to affect the individuals recorded in the marly clayey sediments (Fig. 5). Probably their preservation was favoured also by the strong cyrtomatodont dentition of *T. trigonella* that kept most of the specimens articulated (about 87%), despite undergoing intensive fossildiagenetic alterations such as in situ distortion or tectonic deformations.

5.2. *Ichnoassemblages and associated fauna in the Tetractinella-beds interval*

In order to better characterise the palaeoenvironment leading to the formation of the Betic *Tetractinella*-beds, analysis of both body and ichnofossils was carried out in the under- and overlying strata. Throughout the section, three ichnoassemblages have been defined, all characterised by high abundance but very low diversity.

5.2.1. *Oravaichnium ichnoassemblage*

This ichnoassemblage is characterised by the very great abundance of tubular, horizontally developed trace fossils occupying almost the whole bed surface (Fig. 8A, B, D). Burrows are about 1 cm in diameter and are elliptical to slightly subrectangular in cross-section, with the long axis parallel to bedding (Fig. 8B, D). This ichnoassemblage, resembling the so-called “vermicular limestone”, is common in very shallow-water Muschelkalk deposits in different areas of the Western Tethys (Jaglarz and Uchman, 2010; Knaust and Costamagna, 2012; Giannetti et al., 2017; Stachacz et al., 2022; Pérez-Valera et al., 2023), although the taxonomic position of its components is frequently quite complex to be determined due to the poor preservation of diagnostic features. The assignment followed herein is based on the most recent review of this ichnoassemblage by Stachacz et al. (2022), who attributed most of these trace fossils to the ichnogenus *Oravaichnium* Plička and Uhrová, 1990. In the studied outcrops, the predominant trace fossils show a bended, curved morphology and subrounded outline. According to the criteria resumed in Stachacz et al. (2022), they are herein ascribed to the ichnospecies *O. hrabei* Plička and Uhrová, 1990, while straighter and thinner burrows would represent the uppermost part of *O. carinatum* Stachacz et al., 2022. Well-defined square outlines are absent in most of these burrows possibly because of the poor preservation in very soft substrates, as pointed out by previous authors (Knaust, 2007; Stachacz et al., 2022). Chevron-like structures as those figured by Stachacz et al. (2022) were not observed in the studied section. The filling of the burrows has been studied in thin section and it is represented by a homogeneous, structureless micritic matrix identical to the host rock as described in Stachacz et al. (2022) for the filling of *Oravaichnium*. This type of filling differentiates these burrows from the ichnogenus *Planolites*, as they were previously classified (Pérez-Valera et al., 2023), which should present a filling different from the host rock (Pemberton and Frey, 1982).

In association, also very elongated forms of *Rhizocorallium commune* Schmid, 1876 are present with a marginal tube of about 1–1.5 cm in diameter (Fig. 8C, E). Scratches or pellets were not observed. The most abundant forms are represented by subhorizontal *R. commune* var. *irregulare* (Mayer, 1954b) about 5 cm wide and 30 cm long, characterised by its typical slightly winding shape (Fig. 8C, E). Also a partially preserved specimen of *R. commune uliarense* (Firtion, 1958) is present in the same ichnoassemblage.

The abundance of horizontal/subhorizontal trace fossils produced by mobile organisms and the predominance of deposit-feeding structures make possible to assign this ichnoassemblage to an impoverished *Cruziana* ichnofacies (MacEachern et al., 2007). This ichnofacies is typical for shallow water, permanently subtidal, soft-ground, fully marine environments usually above storm wave base (MacEachern et al., 2012a, 2012b).

5.2.2. *Thalassinoides horizons*

Thalassinoides suevicus Rieth, 1944 is present in a distinctive surface (Fig. 2) preserved as a positive epirelief (Fig. 9A, B, D). Mazes are extremely well developed, covering almost completely the top of the bed and forming a distinctive layer capping the underlying bed. Burrow diameter is about 2–3 cm and is quite homogeneous throughout the whole bed. Galleries are flattened, most probably as a consequence of the soft nature of the substrate, and show the distinctive Y-branching pattern. Most of the burrows are straight although few of them are gently bended. Vertical tunnels were not observed, this preventing the determination of the real colonisation horizon. Immediately above the *Thalassinoides* surfaces, the *Oravaichnium* beds are present again. The *Thalassinoides* horizon is developed in correspondence of a microgastropod layer. As for the previous ichnoassemblage, the *Thalassinoides* horizon can be considered as the expression of a very poorly diversified *Cruziana* ichnofacies developed in soft substrates.

5.2.3. *Balanoglossites ichnoassemblage*

This ichnoassemblage is present at about 96 m and it is recognizable on the whole bed surface (Fig. 9C). In top view, it is characterised by the typical funnel-shaped vertical tunnels partially filled by the overlying black clayey sediments (Figs. 9E–G). These burrows always occupy the

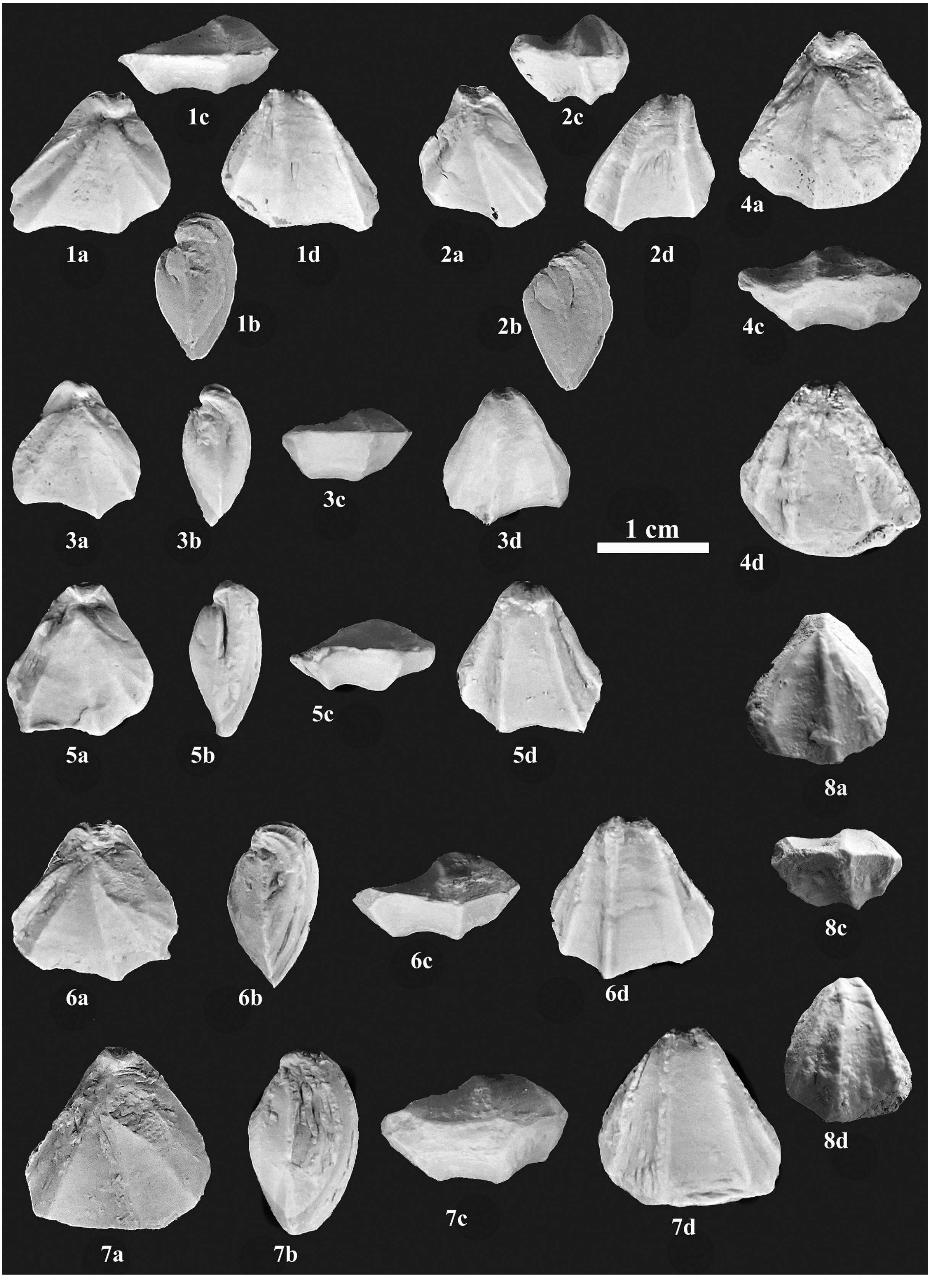

Fig. 5. Some representative specimens showing the intraspecific variability of *Tetractinella trigonella* (Schlotheim, 1820) derived from the Anisian (Pelsonian) Betic *Tetractinella*-beds (Murcia, SE-Spain). 1. Specimen LATB.2; 2. Specimen LATB.3; 3 Specimen LATB.6; 4. Specimen LATB.7; 5. Specimen CMB.1; 6. Specimen CMB.2; 7. Specimen CMB.6; 8. Specimen LATB.80. Notice the taphonomic alterations consisting on shell-distortion, flattening of the anterior half of the shell and lateral asymmetrical stretching of the specimens. Images are arranged in (a) dorsal, (b) lateral, (c) anterior, and (d) ventral views. All specimens were coated with magnesium oxide.

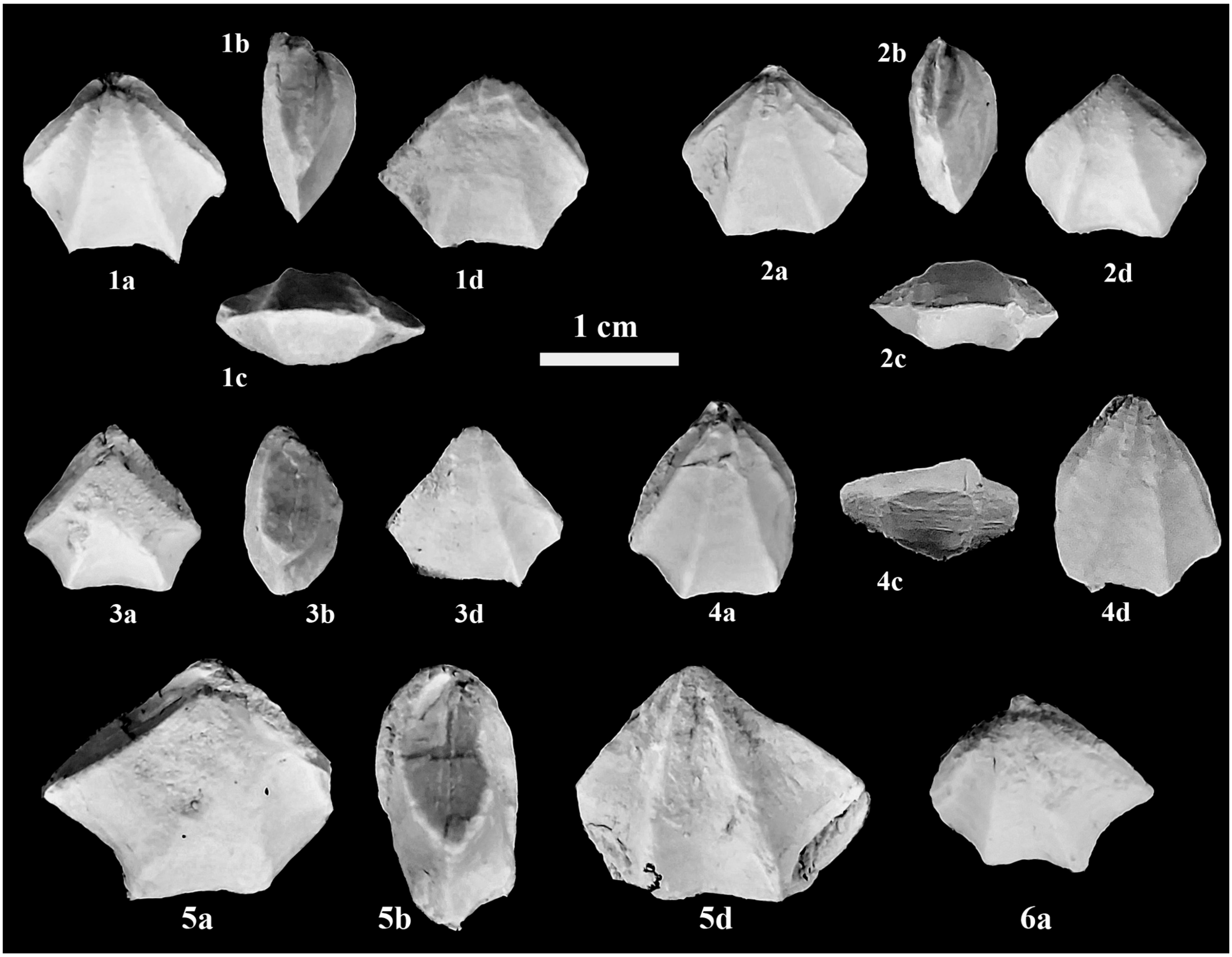

Fig. 6. Some representative specimens showing the intraspecific variability of *Tetractinella trigonella* (Schlotheim, 1820) derived from the Pelsonian Brachiopods-Bank (Grigna Mts., Italy). 1. Specimen GMTT.1; 2. Specimen GMTT.5; 3. Specimen GMTT.11; 4. Specimen GMTT.12; 5. Specimen GMTT.2; 6. Specimen GMTT.6. Images are arranged in (a) dorsal, (b) lateral, (c) anterior, and (d) ventral views. All specimens were coated with magnesium oxide.

shallowest tiers, being developed in the uppermost 3–4 cm of the bed. Locally, the very top bed surface is absent and the development of *Balanoglossites triadicus* (Mägdefrau, 1932) in the interior of the substrate is visible showing the non-uniform burrow diameter and the irregular network typical for this ichnogenus. The absence of the capping layer might be in part due to weathering, but locally it is surely due to erosion in the depositional environment, since the black clays directly overly the mid-tier *Balanoglossites* surface.

Balanoglossites is interpreted as the result of the burrower to bioeroder activity of feeding and dwelling worm-like animals, most probably polychaetids, and it is considered indicative for firm- to hardgrounds (Knaust, 2008, 2021; Knaust and Costamagna, 2012; Knaust and Dronov, 2013). This ichnogenus is quite common in the Muschelkalk deposits, although its abundance is possibly underestimated due to its difficult recognition in the outcrops (Knaust, 2021). *Balanoglossites* surfaces are a typical expression of the *Glossifungites* ichnofacies, a substrate-controlled ichnofacies related to firmgrounds with very slow sedimentation rate. Quite commonly, this ichnofacies is characterised by low diversity, although abundance can be very high, as occurs in the Las Atalayas section. The *Glossifungites* ichnofacies is the result of the colonisation of omission or erosion surfaces (MacEachern et al., 2007; MacEachern et al., 2012a, 2012b).

In terms of fossil content, in the very top surface of the *Balanoglossites* beds, representative taxa from both very shallow and deeper water habitats were recorded. Some bivalve species representing different life strategies are present, such as the infaunal shallow burrowers *Myophoria vulgaris* (Schlotheim, 1820) and *Neoschizodus laevigatus* (Goldfuss, 1837), infaunal deep burrowers such as *Pleuromya elongata* (Schlotheim, 1822) and *Unicardium schmidii* (Geinitz, 1842), but also epifaunal recliners (pelagic?) taxa assigned to the genus *Daonella* Mojsisovics, 1874 (Pérez-Valera et al., 2023), together with the brachiopod *Tetractinella trigonella*. This same horizon also contains abundant microgastropods and sporadic nautiloids attributed to *Germanonautilus saharonicus* (Parnes, 1986), indicating short intervals of opener marine conditions (Pérez-Valera et al., 2023).

6. Integrated analysis to appraise environmental conditions of the depositional scenario

The examined outcrops in the studied region, and specifically in the marine ingression deposits (MID-2), evidence a variety of sedimentary settings representing the temporal evolution of the palaeoenvironment as a response to sea-level changes. The correlation of MID-2 with other transgressive deposits in the Pelsonian of many European basins (e. g. Szulc, 2000; Götz and Feist-Burkhardt, 2012; Chatalov, 2013; Ajdanlijsky et al., 2020) suggests that sea-level oscillations respond to global

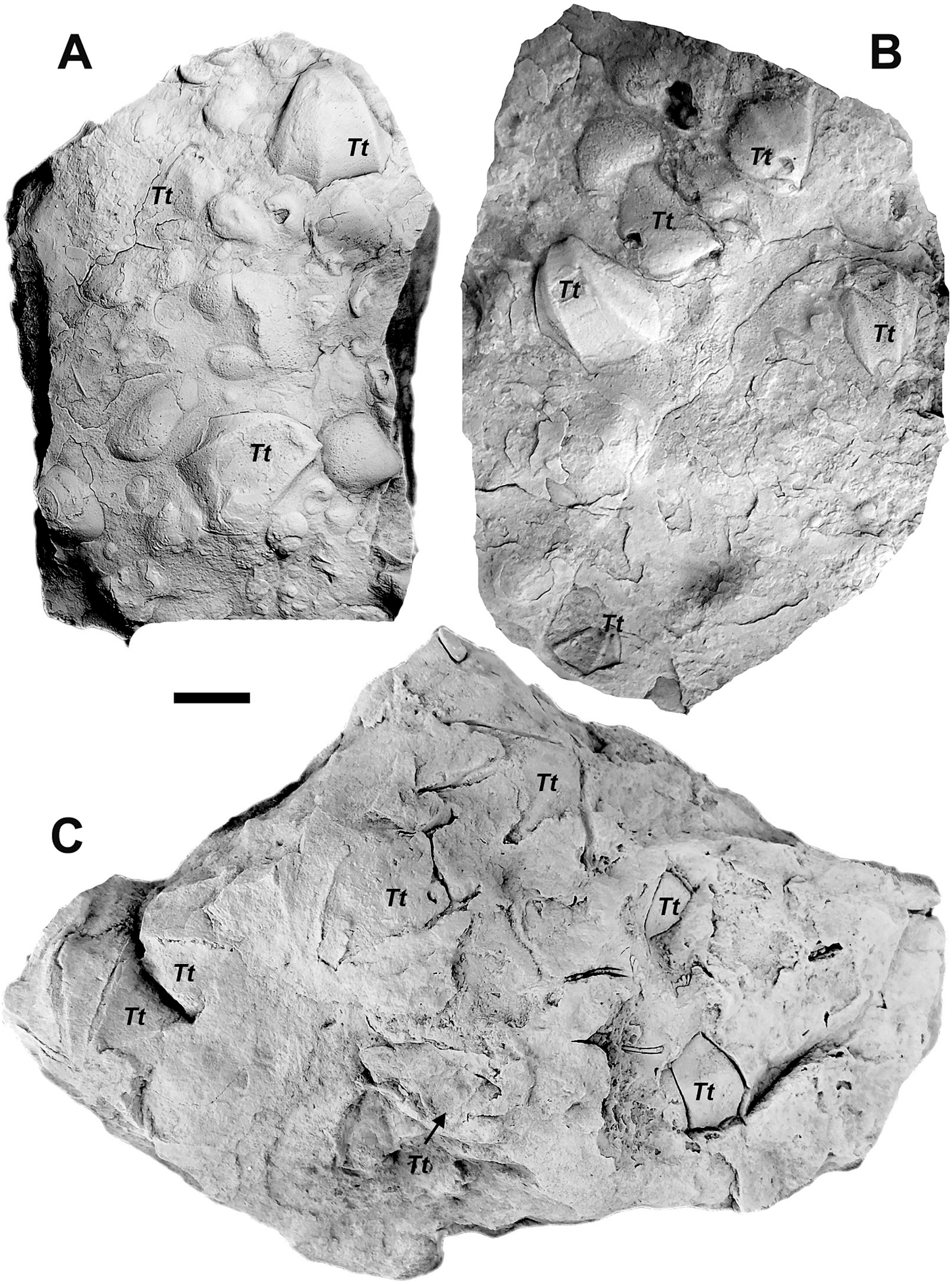

Fig. 7. A, B Slabs showing condensed pavements with scattered convex-up ventral valves of *Tetractinella trigonella* (*Tt*) from the *Tetractinella*-beds (Betic Ranges, SE-Spain). C. Slab showing the closely-packed distribution of *T. trigonella* specimens from the Brachiopods-Bank (Grigna Mts., Italy) for an outcropping comparison. Scale bar represents 1 cm.

changes more than to local influences or regional tectonic factors, and can be tentatively correlated with the TAn3 event detected by Haq (2018) (Fig. 2A).

6.1. Near-shore restricted lagoon sporadically disturbed by short-term shallow-marine episodes

The bottom part of the MID-2 section is characterised by the *Thalassinoides* horizon with microgastropods. Although *Thalassinoides* trace-makers vary throughout the Phanerozoic (Myrow, 1995), they are associated to decapod crustaceans at least since the Triassic (Myrow, 1995; Chrząstek, 2013), and became incredibly widespread in shallow water environments from the Jurassic onwards (Myrow, 1995). *Thalassinoides* is frequently related to shallow-marine oxygenated environments (Ekdale and Mason, 1988; Savrda, 1991, 2007; Pemberton et al., 2001, 2012; Boyer and Droser, 2011; Buatois and Mángano, 2011; Giannetti and Monaco, 2015) with rather good water circulation. In the Germanic Muschelkalk deposits, *Thalassinoides* mainly characterises middle and outer ramp settings, in more distal position with respect to the *Oravaichnium*-dominated ichnoassemblage (Chrząstek, 2013). The presence of *Thalassinoides* is described in other Muschelkalk outcrops (Szulc, 2000) and interpreted as a proxy for a better oxygenated

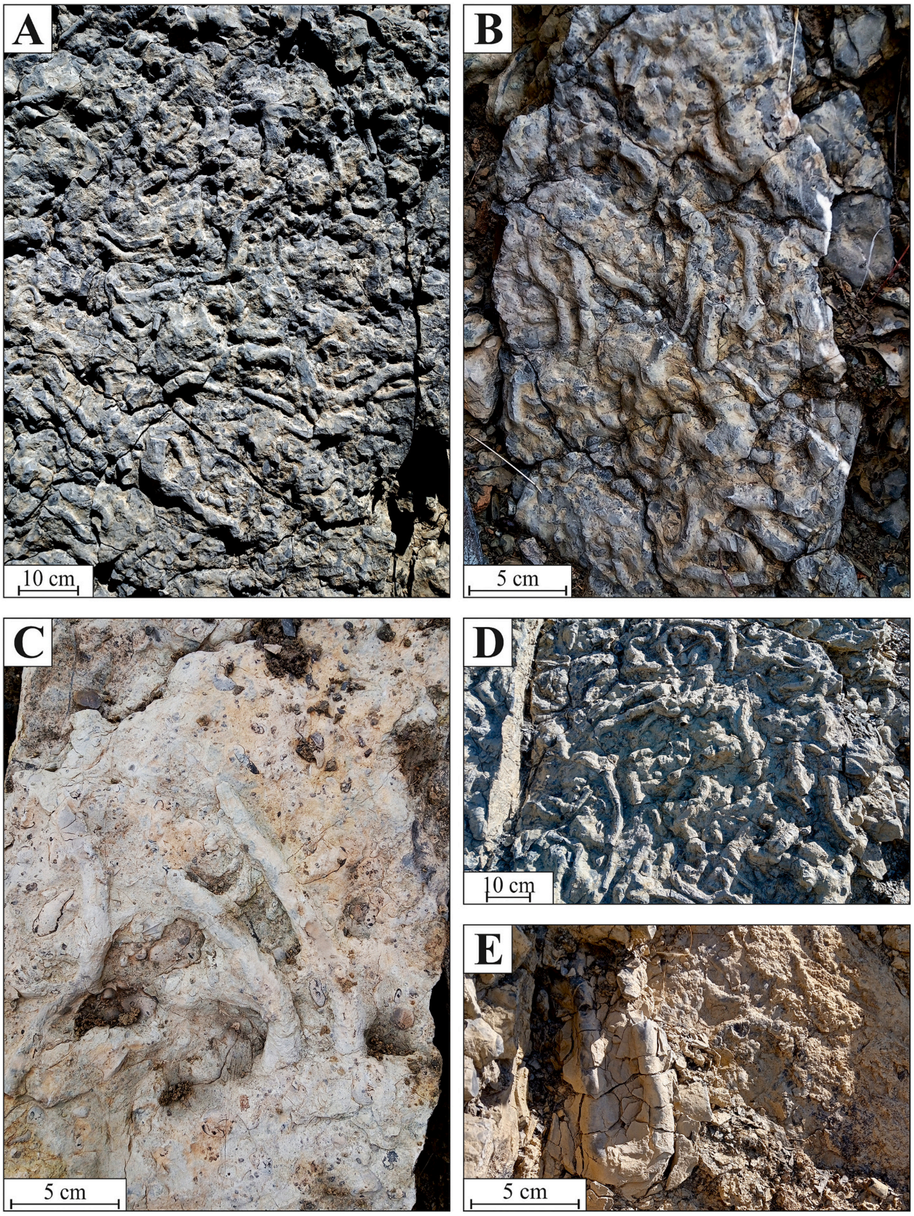

Fig. 8. *Oravaichnium* ichnoassemblage. A, B, D. Top surface of an intensely burrowed limestone (A) and detail of the *Oravaichnium* ichnoassemblage (B, D). *Oravaichnium* covers the whole bed surface. High intensity of burrowing produces tubes frequently cross-cutting each other. C, E. *Rhizocorallium commune* var. *irregulare*. In the studied area, *Rhizocorallium* has a very elongated, slightly sinuous appearance. Pellets are absent as well as scratches on the tube wall, which is completely smooth.

environment. Also in the Lower Jurassic platforms, *Thalassinoides* is found colonizing the distal part of lagoons or ramps, characterised by better circulation and oxygenation, substituted by bivalves towards the most proximal part of the platform system (Monaco and Giannetti, 2002; Giannetti and Monaco, 2004; Caracuel et al., 2005).

Regarding the microgastropods associated with the *Thalassinoides* surface (Fig. 3E, F), they were probably formed by parautochthonous processes according to Fraiser et al. (2005). These microgastropod-dominated shell-beds suggest subtidal deposition during continuous wave action or storm events. The presence of both small adults and numerous juvenile gastropods indicates opportunistic strategies and population adaptations to physically and chemically challenging habitats (Fraiser and Bottjer, 2004). These characteristics observed in the Lower Triassic microgastropod fauna indicate persistent environmental stress associated with factors contributing to the biotic crisis at the end of the Palaeozoic. The widespread occurrence of Lower Triassic microgastropod biofacies, together with biosedimentological features, provides palaeoecological evidence of prolonged and challenging conditions during the Early Triassic. The *Thalassinoides* horizon is overlayed by the *Oravaichnium* ichnoassemblage and its associated fauna (Fig. 2C). The absence of scratches and any type of ornamentation on the walls of the trace fossils is a clear evidence of an extremely soft bottom substrate (Knaust, 2013; Stachacz et al., 2022). Moreover, the extreme abundance of deposit feeders as the *Oravaichnium* and *Rhizocorallium* trace makers would indicate a high amount of organic matter in the very fine-grained sediments able to supply such an important infaunal population. These deposits record the development of a restricted very shallow water lagoon which bottoms were sporadically disturbed by storms, recorded by bioclastic packstones. The very high abundance but poor diversity of trace fossils and macroinvertebrates represents the characteristic of an oligotypic assemblage. Actually, this kind of facies has been described worldwide in various shallow-water Anisian–Ladinian deposits, and

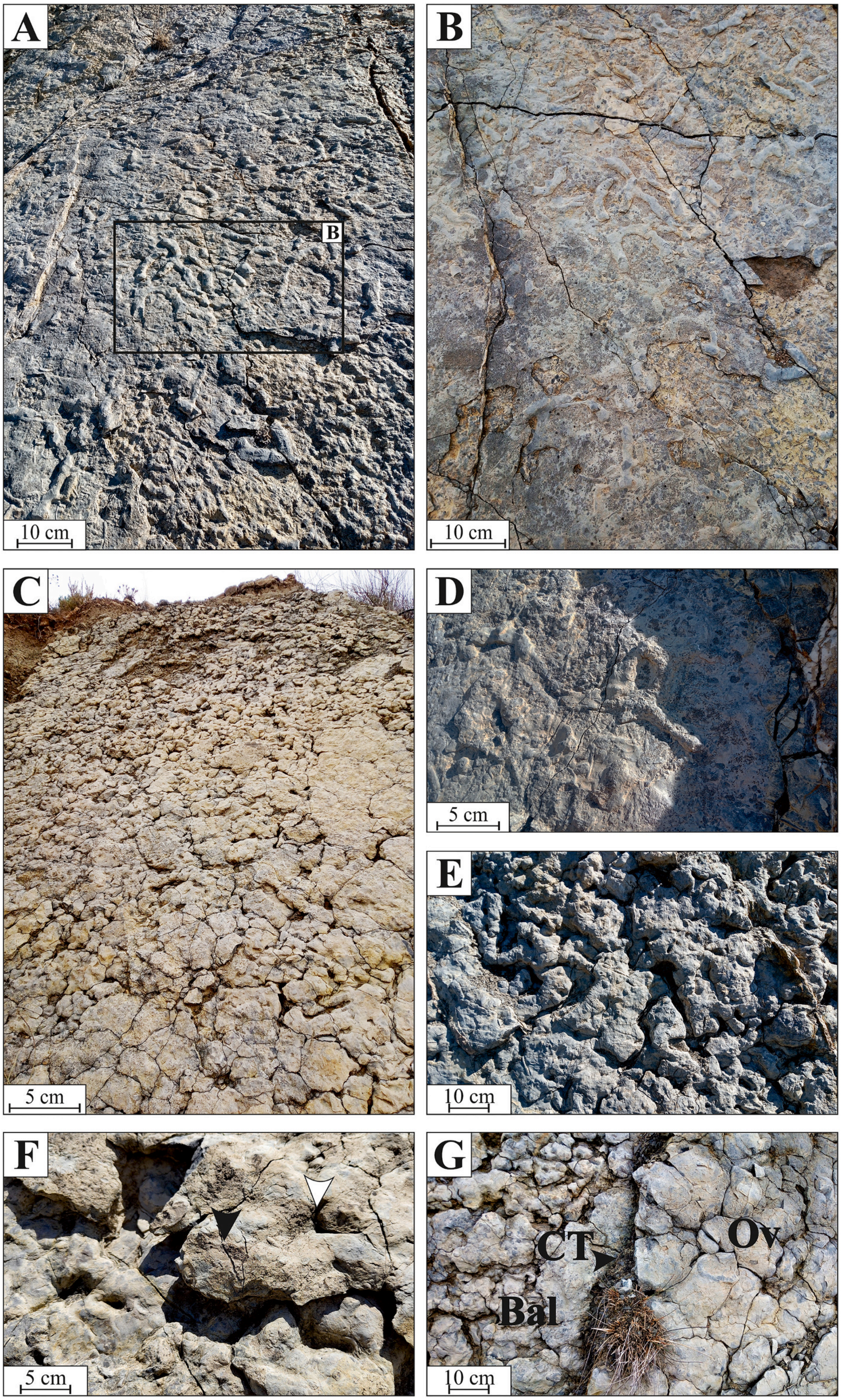

Fig. 9. *Thalassinoides* horizon and *Balanoglossites* ichnoassemblage. A, B, D. *Thalassinoides* horizon. A. Top view of the horizon completely burrowed by *Thalassinoides.* Note the extensive horizontal development of the burrows; B. Detailed view of A; D. Flattened appearance of the burrows in the *Thalassinoides* horizon probably due to the soft nature of the substrate. C. *Balanoglossites* ichnoassemblage, top view of the bed. Note the intensity of bioturbation and the lateral continuity of the surface. E, F. Detail of the *Balanoglossites* surface: the bioclastic layer (see black arrow in F) represents a condensed accumulation and develops just on the colonisation surface; the *Balanoglossites* entrance is visible (white arrow in F). G. Detail of the section with the *Balanoglossites* surface (Bal), the clayey interval with in situ *Tetractinella* (CT) and the re-establishment of the *Oravaichnium* ichnoassemblage (Ov).

locally it has been related to hypersaline stressed environments (e.g. Jaglarz and Uchman, 2010).

6.2. Settlement of *Tetractinella trigonella* and associated fauna

The development of these lagoon conditions is interrupted by an important change, marked by the appearance of the *Balanoglossites* surface (Fig. 2C). This trace fossil has been frequently recovered in restricted shallow-shelf, partly lagoonal environments (Knaust, 2021) and in many deposits just after important ecological crisis or extinctions events. It is considered therefore as produced by an organism capable to survive in stressed environments (Knaust, 2021) and it is related to firmgrounds, being an important constituent of the *Glossifungites* ichnofacies (MacEachern et al., 2012a, 2012b).

The development of this trace fossil marks discontinuities and it is therefore an evidence for flooding surfaces and sequence-stratigraphic boundaries (MacEachern et al., 2012a, 2012b; Knaust, 2021). This ichnoassemblage plays a key role in order to understand the palaeoenvironmental evolution just before the settlement of *Tetractinella*, since it marks the surface that records the MID-2 transgression up to the

Table 1
Brachiopod-beds commonly used as biostratigraphic markers and correlation biohorizons mainly in the Middle Triassic from different Western Tethyan basins. Occurrences of *Tetractinella trigonella* are emphasised in bold. Data of depositional scenario are given when available.

Biomarker horizon	Source	Locality/ basin	Age	Main index taxa	Depositional environment/ Formation
Brachiopoden-Kalk (*calcare a brachiopodi*)	Lepsius, 1878	Trento, Italy	Anisian	*Coenothyris vulgaris*	Top of Calcare di Angolo Fm. (*fide* Gaetani, 1969)
Banco a Brachiopodi	Gaetani, 1969	Trento, Italy	Anisian	*Coenothyris, Decurtella,* ***Tetractinella trigonella***	Top of Calcare di Angolo Fm.
Beds with *Tetractinella*	Lein and Siblík, 1978	Styria (Austria)	Cordevolian (Carnian)	*Tetractinella? dyactis, Caucasorhynchia*	Wetterstein Limestone Fm.
Terebratula-beds	Usnarska-Talerzak, 1988	Upper Silesia (Poland)	Anisian	*Coenothyris vulgaris,* ***Tetractinella trigonella***, among others	Storm-disturbed shallow-sea with shoals environment
Terebratula-beds	Popiel-Barczyk and Senkowiczowa, 1989	Holy Cross Mts. (Poland)	Anisian	*Coenothyris* spp.	Grey nodular limestones with terrigenous inputs
Brachiopod-bearing level (“Recoaro beds”)	Pálfy, 1991, 2003	Balaton Highland (Hungary)	Pelsonian (Anisian)	***Tetractinella trigonella,*** *Mentzelia mentzeli* (among many others)	Patch-reef foreslope
Recoaro Limestone	De Zanche et al., 1992	Pusteria Valley, Italy	Pelsonian (Anisian)	*Coenothyris vulgaris,* ***Tetractinella trigonella,*** *Decurtella decurtata*	Carbonate ramp with terrigenous inputs
Banco a Brachiopodi	Angiolini, 1993	Grigna Mts. Lombardy, Italy	Anisian	***Tetractinella trigonella***	Top of Calcare di Angolo Fm.
Brachiopod-beds/ *Coenothyris* beds	Török, 1993	Mecsek Mts. (Southern Hungary)	Anisian	*Coenothyris vulgaris,* ***Tetractinella trigonella*** (among others)	Homoclinal ramp with storm events
Terebratula-bed *Cycloides*-bank	Senkowiczowa and Popiel-Barczyk, 1996	Holy Cross Mts., Poland	Anisian	*Coenothyris vulgaris, Coenothyris cycloides*	Nodular limestones with quartz, sand, and glauconite inputs. Shaly marls intercalated
Brachiopod-bearing levels	Torti and Angiolini, 1997	Val Parina, Southern Alps, Italy	latest Anisian-early Ladinian?	***Tetractinella trigonella*** (among many others)	Edge of platform environments
Terebratula-beds	Kaim, 1997	Upper Silesia, Poland	Anisian	*Coenothyris,* ***Tetractinella trigonella***	Slope/basin
Hardground with *Tetractinella trigonella*	Kaim, 1997	Upper Silesia, Poland	Anisian	*Coenothyris,* ***Tetractinella trigonella***	Small patches in low-productivity environments
Brachiopod beds *Terebratula* beds	Benatov et al., 1999	Stara Planina, Bulgaria	Pelsonian (Anisian)-early Illyrian	*Coenothyris, Decurtella,* ***Tetractinella trigonella*** (among others)	Babino Fm., nodular clay-limestones and thin-bedded shelly or biodetritic limestones
Terebratula beds (*Terebratel-bänke*)	Szulc, 2000	Silesia, Poland	Anisian	*Coenothyris*	Transgressive episode
Spiriferina-bank *Tetractinella*-bank *Cycloides*-bank	Ockert and Rein, 2000	Thüringen, Germany	Anisian-Ladinian boundary	*Punctospirella fragilis,* ***Tetractinella trigonella,*** *Coenothyris cycloides,* respectively	*Trochitenkalk* Fm., *Meißner* Fm., and *Warburg* Fm.
Banco a brachiopodi	Mantovani, 2002	Grigna Mts., Southern Alps (Italy); Upper Silesia (Poland)	Pelsonian (Anisian)	***Tetractinella trigonella***	Calcare di Angolo Fm.
Spiriferinid beds	Sun et al., 2009	Guizhou, South China	Anisian	*Pseudospiriferina multicostata, Ps. pinguis, Punctospirella fragilis*	High energy, hard substrate, nutrient-rich environment
Brachiopod-beds	Brack and Kustatscher, 2013	Lombardy, Italy	Pelsonian (Anisian)	*Coenothyris vulgaris*	Upper part of Calcare di Angolo Fm.
Coenothyris bed	Feldman, 2005, 2017	Israel	late Anisian-early Ladinian	*Coenothyris*	Relatively shallow and calm setting in a transgressive scenario
Brachiopod-levels	Gaetani et al., 2018	Yemen	Anisian-Ladinian	*Nudirostralina mutabilis, Lepismatina, Koeveskallina, Spirigerellina* (among others)	Thin-bedded nodular limestone with alternating marls, representing a progressive deepening of the basin, resulting in a deep shelf environment
Brachiopods Bank	Tintori et al., 2018	Northern Grigna Mts., Italy	Anisian (Pelsonian)	***Tetractinella trigonella*** *Piarorhynchia*	Top of Calcare di Angolo Fm. Transgressive phase: rapid deepening of shallow restricted basin
Tetractinella-bank	Rein, 2019	Thüringen, Germany	late Anisian	***Tetractinella trigonella***	Transgressive phases in an inland sea
Spiriferina- bank	Rein, 2019	Thüringen, Germany	Anisian-Ladinian boundary	*Punctospirella fragilis*	Transgressive phases in an inland sea

maximum flooding highstand. The faunal communities recovered on the *Balanoglossites* surface contain taxa from both a lagoon and open marine environment, recorded just below and over the *Balanoglossites* level, respectively. This should indicate a condensed surface where, due to the very low sedimentation rate and the ongoing transgression, organisms from different habitats are found co-occurring together. In this sense, *Balanoglossites* indicates the establishment of a firm- to hardground here related to omission surfaces, as common for this trace fossil (Knaust, 2021). The subsequent establishment of relatively deep-water settings is proved by the thick dark clayey interval rich in pelagic markers as nautiloids, bivalves (*Daonella*), as well as the maximum abundance of marine phytoplankton (acritarchs) recorded in the entire Las Atalayas section (Pérez-Valera et al., 2023).

The condensed surface and the overlying clayey levels represents the habitat of *Tetractinella,* abundant in depositional settings deeper than the previous nearshore environments. For this reason, the origin of the *Tetractinella*-beds and most of the distinctive Anisian brachiopod-beds are linked to the well-established Pelsonian-Illirian transgressive episodes widely reported in the Western Tethys (Szulc, 2000; Götz et al., 2005; Götz and Török, 2008, 2018; Götz and Feist-Burkhardt, 2012; Chatalov, 2013, 2018; Ajdanlijsky et al., 2019, 2020; Pérez-Valera et al., 2023). These events triggered the deepening/drowning of the corresponding basins, resulting in the shift of the originally shallower to relatively deeper ecospaces, often in connection with the open sea and, in some cases, influenced by sporadic terrigenous inputs (Table 1).

The Betic *Tetractinella*-beds are found in relatively deeper sediments than the contiguous stratigraphic intervals, thus reinforcing the record of the MID-2 Pelsonian ingression event, also characterised by the presence of open-marine faunal constituents (e.g. nautiloids, bivalves, phytoplankton).

Noteworthy, the first occurrence of *Tetractinella* is revealed in condensed pavements with firm- to hard-substrata, occurring in small patches or as scattered convex-up fragmented shells (Fig. 7 A, B). This arrangement is only apparently similar to the Upper Silesia Pelsonian hardground assemblages described by Kaim (1997). Here, *T. trigonella* represents more than 70% in abundance of the fossil community and forms very closer clusters with joint valves, interpreted as adult specimens preserved in situ and in life position on a hard substratum. In the case of the Betic *Tetractinella* recorded in the hard pavements, specimens are less abundant and more loosely clustered, without sorting of individuals. The high average of fragmented convex-up ventral valves prevents to attribute the genesis of these pavements to in situ preservation and points to a reorientation conferring the valves better post-mortem stability as the result of the long-time exposure to biostratinomic processes.

Tetractinella is usually related to near-shore environments, as constituent of the epifauna attached by its short and strong functional pedicle to the available hard-substrata (cf. Kaim, 1997), thus tolerating the influence of relatively moderate to high hydrodynamic regimes as well as inhabitants of medium to high energy subtidal to reef-associated habitats (Iordan, 1993; Torti and Angiolini, 1997; Mantovani, 2002; Pálfy, 2003). Likewise, Kaim (1997) postulated that their functional pedicle allowed the immediate and strong attachment to hard substrata, collecting the nutrients from the detritus-sorting currents associated to the formation of the hardgrounds. These conditions together with its hydrodynamically optimised shell shape led to the ecological thrive of *Tetractinella.* In this sense, the development of hard substrata allowed the initial colonisation of *Tetractinella,* which populations developed successfully in this MID-2 transgression stage due to the nutrients availability and the increased biogenic productivity.

During the highstand, the bottoms were supplied by continuous deposition of fine-grained sediments (Pérez-Valera et al., 2023). This produced a quite water soft-ground with regular sediment input. These soft-bottoms led *Tetractinella* to acquire an adaptive free-lying mode of life by means transitional-type foramina (sensu Richardson, 1981) and the adaptation of the posterior parts of the shell, as documented in other athyridides (Álvarez, 2003). This strategy begins with the development of strong and functional pedicle enabling a short-term attachment and an easy rotation of the shell according to the direction of the currents. In subsequent ontogenetic stages, Álvarez (2003) reported in several Palaeozoic and Triassic species of athyridides a free lifestyle, which led to the development of a differential thickening in the umbonal regions. In this way, individuals can lay in stable position with the strong beaks resting in the soft-substrata (sensu Richardson, 1997). This may be the case of the Betic material: in the early ontogenetic stages, individuals could be attached to the hard substrata surface or to small fragments, but the scarcity of enough hard bottoms providing stability to the shell during adult stages and the evolution of the basin to fine-grained depositional settings led to the adaptation to free-lying on the soft substrata This can be inferred from the incurving of their umbonal areas, the shifting of their maximum convexity and thickness to the posterior third of the shell and of their strong beaks, observed in most of the articulated specimens recorded in the soft-bottoms represented by the marly clayey beds (Fig. 5).

This ecological adaptability is not unusual among athyridides, both for wide-expanded and wing-shaped morphotypes (Álvarez, 2003), or even for the last representatives of this clade (koninckinids) prior to their total extinction in the early Toarcian Extinction Event (Vörös, 2002; Baeza-Carratalá et al., 2015; Vörös et al., 2016). Koninckinids are the only athyridides reported so far in the Betic Ranges (Baeza-Carratalá et al., 2015, 2017). Vörös (2002) suggested for this concave-convex koninckinid fauna a comparable adaptation to muddy bottoms, consisting in the transformation of morphotypes with customary pedicle attachment to rocky bottoms (mainly inhabiting submarine horsts) to the more winged, posteriorly wide-expanded shapes. Similar adaptation would be inferred for those individuals with strongly convex pedicle valves, incurved beaks, and posteriorly thickened morphotypes, features developed for lying with the strong pedicle valve partially semi-buried in the soft substrata of the epicontinental seas.

As supported by previous authors (Table 1), the dispersal of *Tetractinella* throughout the Western Tethys is definitely linked to the achievement of comparable environmental conditions practically in all the basins. In the referential *Banco a Brachiopodi* from Lombardy (Fig. 7C), Tintori et al. (2018) recapitulated that the alternating carbonate-marly succession making up the Angolo Fm. was originated in a shallow restricted basin, but stratigraphically upwards the basin evolved towards an environmental diversification, allowing incursions of open-sea constituents such as microgastropods and foraminifera. In the topmost of the sections, the *Banco a Brachiopodi* with crinoids shows a connection with open sea in a transgressive phase, just as occurs in the marly clayey-carbonate Betic *Tetractinella*-beds, where thin-shelled bivalves, nautiloids and pectinides reinforce the presence of a higher water column.

On the other hand, the dispersal pattern led by *T. trigonella* in the Pelsonian, occupying vacant ecospaces during the maximum flooding of the MID-2 event, is distinctive of an opportunistic strategy (sensu Levinton, 1970; Harries et al., 1996) since it is often recorded as monospecific or oligospecific assemblages with abundant individuals (e.g. ≈600 in Balaton Highland, Pálfy, 2003; ≈1000 in the Italian pre-Alps, Mantovani, 2002, and see also Fig. 7C herein; oligotypic bursts in Upper Silesia, Kaim, 1997; monospecific bloom herein) and high morphological plasticity, conferring to this taxon great ability to tolerate different environmental conditions.

6.3. Reestablishment of the near-shore lagoon-associated conditions

A new sea-level change, in this phase corresponding to a regression, lead to the re-establishment of the lagoon conditions typified by the *Oravaichnium* ichnoassemblage in a nodular, intensely bioturbated carbonate sequence and to the final occurrences of *Tetractinella,* together with the disappearance of the open marine water faunal constituents (topmost levels in the Fig. 2 C).

7. Biostratigraphical significance of the Betic *Tetractinella*-beds

7.1. Triassic brachiopods in the peri-Iberian palaeomargins

The presence of *Tetractinella trigonella* in the middle Anisian represents the first report of this taxon in the peri-Iberian platforms and consequently the earliest record so far of Triassic brachiopods in the South-Iberian Palaeomargin. They co-occur with a relatively diverse fossil assemblage mainly represented by the nautiloid *Germanonautilus saharonicus* (Parnes, 1986), the bivalves *Unionites fassaensis* (Wissmann, 1841), *Pleuromya elongata* (Schlotheim, 1822) and *Neoschizodus laevigatus* (Goldfuss, 1837), and the palynomorphs *Stellapollenites thiergartii* (Mädler, Clement-Westerhof et al., 1974), *Tsugapollenites oriens* Klaus, 1964 and *Cristianisporites triangulates* Antonescu, 1969. This assemblage supports the unique attribution of these outcrops to the Anisian stratigraphical sequences in the External Betic Zones (see Pérez-Valera et al., 2023 for a detailed age discussion).

Additionally, these new Betic occurrences of *T. trigonella* contribute to the better knowledge of the sparse brachiopod record in the entire Triassic period, which is scarce not only in the Betic Domain, but also in all the westernmost Tethys margins.

Brachiopod occurrences in these Triassic epicontinental seas around the Iberian Massif were only previously reported in the Ladinian from the Iberian Range by Márquez-Aliaga et al. (1999, 2007), Escudero-Mozo et al. (2015) and Giannetti et al. (2017) through the monospecific and opportunistic bursts of the genus *Lingularia*, which taxonomic arrangement and adaptive strategies across the different phases of the Permian-Triassic extinction were recently reviewed (Posenato et al., 2014; Posenato, 2016, 2019). Likewise, four specimens unspecifically attributed to *Coenothyris* sp. (Márquez-Aliaga et al., 1994; Escudero-Mozo et al., 2015) and *C. vulgaris* (Schmidt, 1935), all of them mainly Ladinian in age, plus the sporadic Anisian *Mentzelia* (*M. mentzeli*, *M.* sp.), and *Koeveskallina koeveskalyensis,* from Menorca and the Catalonian Coastal Range (Schmidt, 1935; Calzada and Gaetani, 1977; Escudero-Mozo et al., 2015) were sparsely recorded. From the Betic Ranges, Anisian brachiopods mainly represented by *Coenothyris* and *Aulacothyris* were also reported as part of a benthic community in the Internal Betic Zones (Simon, 1963). Nevertheless, these outcrops are included in the palaeomargin of the Meso-Mediterranean Terrain and are located far south-eastern from the peri-Iberian platforms system.

In the South-Iberian palaeomargin, the record accomplishes the same paucity and patchy pattern. So far, the oldest Triassic brachiopod fauna was represented by the multicostate zeilleride *Misunithyris goyi* Baeza-Carratalá et al., 2018, sporadically reported in the latest Fassanian of the early Ladinian (ca. 231 Ma). The new finding of *Tetractinella* (Pelsonian; ca. 244 Ma, Ogg et al., 2020) reveals that the first occurrence and development of post-Palaeozoic brachiopods in these platforms system took place about 13 Ma earlier than thought hitherto.

Similarly, in the Late Triassic, the scarcity of brachiopods is also noticeable in the Betic Ranges, since only four taxa were recorded in the southern Internal Betic Zones (Unidad de las Nieves Domain). They correspond to the ambiguous record of *Crurirhynchia kiparisovae*? ascribed to the Norian by Chamón and Quinquer (1978) in a carbonate succession spanning the Carnian-Rhaetian interval (Dürr, 1967). The dating of such deposits by Dürr (1967) was based on coral taxa and a brachiopod assemblage consisting of *Rhynchonella* cf. *arpadica*, *Rh.* cf. *mentzeli*, and *Rh.* cf. *subrimosa*, nowadays systematically attributable to the genera *Vegirhynchia* (according to Dagys, 1974), *Mentzelia* (according to Bittner, 1890) and *Calcirhynchia* (according to Pearson, 1977) respectively.

Remarkably, the abovementioned singularity and scarcity of brachiopods in the Triassic fossil record transform their occurrences into valuable biostratigraphical and palaeobiogeographical correlation tools.

7.2. Triassic Brachiopod-beds as biostratigraphical tools. The Betic *Tetractinella*-beds in the context of the Western Tethys

Triassic marine successions commonly expose long-term barren intervals without accurate biostratigraphic micro- and macrofauna. In this context, the Anisian brachiopod record is globally scarce worldwide as well, i.e. brachiopods derive from relatively limited fossiliferous localities in both Eastern and Western parts of the Tethys Ocean (Guo et al., 2022). In the westernmost part of the Palaeotethys, occurrence of several brachiopod taxa or even biohorizons ("Brachiopod-beds") must be emphasised, since in most of the basins they often constitute the only biostratigraphic markers and correlation macrofauna for these unproductive Triassic successions. Among the different denominations (e.g. *Terebratula* beds*, Banco a brachiopodi,* Brachiopods bank*, Spiriferina* beds), the most common correlation guide-levels (Table 1) are the shell-beds containing abundant *Coenothyris* and *Tetractinella*, used as biomarkers in different Anisian timespans.

The important accumulations of *Tetractinella trigonella* (*Tetractinella*-beds herein) are considered as significant biohorizons of the Pelsonian substage (Anisian; Table 1). The *Tetractinella*-beds (so-called *Banco a brachiopodi* or Brachiopods-Bank sensu Gaetani, 1969; Ockert and Rein, 2000; Mantovani, 2002; Dynowski and Nebelsick, 2011) often include several other brachiopod species (Table 1), but the unambiguous systematic diagnostic criteria of this taxon and its conspicuous record make their occurrence a worthy element of correlation. Thus, this species can be considered as a distinctive Anisian biomarker from the Northern Alps (e.g. Bittner, 1890) and the Western Caucasus (Ruban, 2006). Remarkably, most of the occurrences are restricted to the Pelsonian substage, being long-established in the Pelsonian of the Mecsek Mts. (Török, 1993) and the Balaton Highland (Pálfy, 2003), Romania (Iordan, 1993; Grădinaru and Gaetani, 2019) and the Southern Italian Alps (e.g. Gaetani, 1969; Angiolini, 1993; Mantovani, 2002), extending Torti and Angiolini (1997) the range up to the early Ladinian in this area, the latest Pelsonian from Upper Silesia (Kaim, 1997), the Pelsonian-early Illyrian of Dolomites (Mantovani, 2002) and the middle-late Pelsonian from Stara Planina in Bulgaria (Benatov et al., 1999). Certain occurrences of *T. trigonella* attributed to the late Ladinian seem to have been misinterpreted. Thus, Siblík (1988) reported *T. trigonella* in the late Ladinian? from Iran, but posteriorly Siblík (1991) showed a fragmentary specimen practically from the same area (NE-Iran) probably Anisian in age, remarking the biostratigraphic uncertainty due to the strongly tectonised character of the stratigraphical successions (Siblík, 1991). This opinion was corroborated by Grădinaru and Gaetani (2019), who qualified such an occurrence with doubtful stratigraphic position. Similarly, the specimen depicted by Siblík in Slovakia (1972, pl. 61., fig. 6) was synonymised by Mantovani (2002) with the Ladinian *Trigonella dyactis*.

As can be deduced from Table 1, one of the richest and most regularly contrasted biohorizon of correlation is the Brachiopods-Bank (so-called *Banco a brachiopodi*) from the Southern Italian Alps, with exceptional outcrops in Grigna Mts. Together with the systematic study carried out in Hungary by Pálfy (2003), unquestionably the most complete population analysis of *T. trigonella* was performed throughout the outcrops from Lombardy (Table 1), emphasizing the comprehensive work of Mantovani (2002) who analysed about a thousand specimens from this area. Fortunately, on the occasion of the 8th International Brachiopod Congress field trip, authors of the present work were able to compare *T. trigonella* occurring in the so-called "*Banco a brachiopodi*" of the Calcare di Angolo from the Grigna Group (Figs. 6, 7C, 10) with the specimens now recorded in the Betic *Tetractinella*-beds (Figs. 5, 10).

As a consequence of this evaluation, it is possible to deduce that, among the profuse records of *T. trigonella* in the European basins, the Betic material reveals greater affinity with specimens from Northern Grigna and with those depicted by Mantovani (2002) and derived from the Anisian type-area (Tarnowitz). All of them display the plicae slightly exceeding the anterior commissure, thus extending the length of the

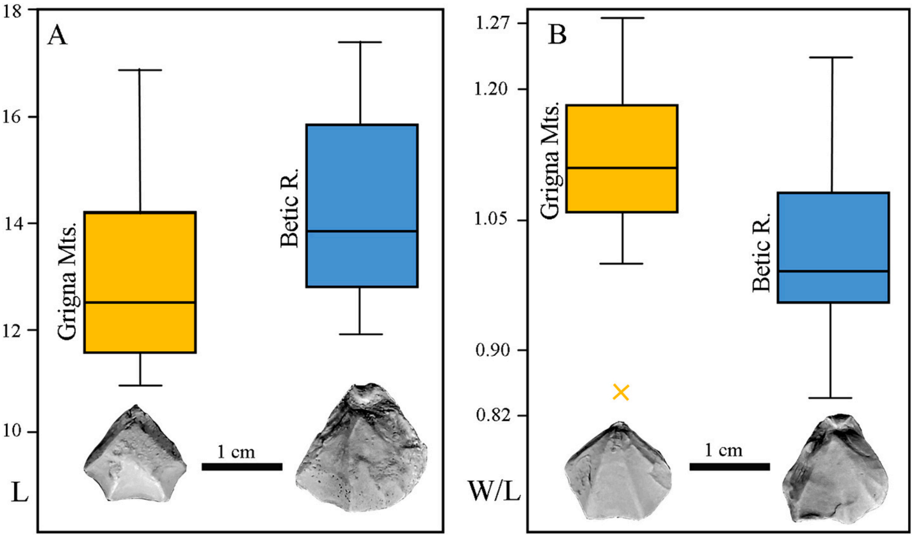

Fig. 10. Boxplots showing (A) difference in size (Length in mm) between the *Tetractinella trigonella* populations from the *Banco a Brachiopodi* in Grigna Mts. (Southern Italian Alps) and those from the *Tetractinella*-beds in the Betic Ranges and (B) Variability in the pentagonal/pseudotrigonal dorsal outlines between the same populations considering the W/L index.

anterior margin. In particular, the Betic material is typified to some extent by slightly larger specimens than the Lombardy ones (Fig. 10A) and tends to be equidimensional with trigonal outline if the W/L index of both brachiopod-beds constituents are compared (Fig. 10B). This trigonal outline was earlier depicted by Mantovani (Mantovani, 2002, pl. 2, fig. 2), and coincide with a higher gap distance between dorsal and ventral umbos, just like occurs in the Betic material. Stronger and more incurvate ventral beaks and shallower planareas are perceivable in the Betic material, but the aforementioned taphonomical alterations could possibly have modified these morphological traits.

Tintori et al. (2018), summarizing previous works on the Brachiopods-Bank at the top of the Angolo Limestone Fm. in the Northern Grigna, described this shell-bed as a prominent brachiopod *lumachella* dominated by *T. trigonella*. This forms a conspicuous horizon that can be traced over tens of km for most of Lombardy, in correspondence with a rapid deepening of a shallow depositional environment. As expected, both biostratigraphic and depositional setting of the Brachiopods-Bank are consistent with the Betic *Tetractinella*-beds, originated as a consequence of a transgressive maximum in the Anisian peri-Iberian platform system. Further resemblance with *Tetractinella*-bearing levels from the same palaeogeographic domain can be deduced comparing the isolated ventral valves scattered in the pavements from the Betic Range with the pre-Alpine material depicted by Torti and Angiolini (1997, see specially pl. 1, fig. 14), both stocks showing the maximum width slightly shifted to the anterior third and similar size and convexity.

On the other hand, the material from the Betic *Tetractinella*-beds (Figs. 5, 7 A-B) similarly falls within the wide intraspecific variability acknowledged by Pálfy (2003) for this taxon in the Balaton Highland. Pálfy (2003) included specimens with well-developed planareas, different angle between plicae, individuals from rectimarginate to gently plicate anterior margin, but specially embraces most of the samples with the greater width at anterior third as it occurs with the Betic *Tetractinella*-beds, and the greatest thickness at the mid-length.

7.3. Palaeobiogeographical contribution to the marine dispersal migratory routes

After the End-Permian extinction, bioprovincialism of Triassic brachiopods is not quite well-defined. In the Early Triassic, the relict Palaeozoic-type brachiopod fauna mixed with the new Mesozoic-type one, the development of endemic taxa and the different post-extinction recovery patterns in several basins (e.g. Chen et al., 2005, 2015; Grădinaru and Gaetani, 2019; Wu et al., 2023) generated a high multiprovinciality worldwide. Taking into account these factors, three bioprovinces were initially established in the Early Triassic (Induan-Olenekian) by Chen et al. (2005), i.e.: W-USA-Spitzbergen, South China, and the Palaeo-Tethyan margins as well as several sub-biochoremas (e.g., Japan, Alpine Europe, Himalaya). In the Western Tethys, previous authors focused the definition of more accurate domains and affinities in the Late Triassic (from Norian onwards), when brachiopods reached a maximum in diversity (Dagys, 1974, 1993; Ager and Sun, 1988; Manceñido, 2002) after concluding the several post-extinction and diversification phases. Thus, faunal affinities in the Late Triassic allowed to establish up to five high-rank biochoremas subdivided in several sub-realms, bioprovinces and other low-rank biogeographical regions (Dagys, 1974, 1993; Manceñido, 2002).

In this chronological framework, the Middle Triassic became a key timespan to elucidate the diversification and bioprovincialism between both the aforementioned situations, i.e. endemic multiprovinciality and well-defined biochores. During the Anisian-Ladinian interval, brachiopods fulfilled their global recovery after P/T extinction and the main diversification phase (Guo et al., 2022). One of the main diversification poles in the Anisian was placed in the Eastern Palaeotethys (“Qingyan Fauna”) with the development of more than 40 different species including cosmopolitan taxa such as *Mentzelia* or *Coenothyris*. Thus, Guo et al. (2020) considered South-China as the focal point of recovery, origin and diversification after the end-Permian extinction and, through a Jaccard similarity coefficient analysis, summarised the global Anisian brachiopod provinces into five biochoremas: Eastern Tethys, North-Siberia, Himalaya, New Zealand, and Western Tethys, the latter including the Alps, Hungary, and North-Caucasus grouped into a unique bioprovince with *Tetractinella* (among others) as index taxon. Subsequently, Guo et al. (2022) conducted a network analysis with faunal groups instead of biochores, deducing comparable biogeographic arrangement but with some remarkable peculiarities such as the grouping of the Western Tethys fauna with the Iranian/NW-Turkish one. Similar distinctions into subgroups were detected among the Eastern Tethys localities. Accordingly, the general common estimation points to the distinctly provincialism of the Anisian brachiopods, following the global multi-provincialism established in the Early Triassic (Guo et al., 2020, 2022).

In this sense, the Western Tethyan domain in the Anisian-Ladinian, which will give rise to the Southern Tethyan Sub-Realm in the Late

Triassic (cf. Dagys, 1993; Manceñido, 2002), involved several minor-rank biochoremas usually referred not only for establishing brachiopod affinities but also for cephalopods, conodonts, bivalves and other groups (Parnes et al., 1985; Hirsch, 1987; Pérez-López et al., 2003; Feldman, 2013, 2017; Pérez-Valera, 2015; Baeza-Carratalá et al., 2018; Pérez-Valera et al., 2023). Thus, the affinity of the faunal components from the SW-Tethyan basins can be discriminated, at least, into the Sephardic and Tethyan bioprovinces (the latter including minor-rank biochores, such as the Germanic or Alpine sub-bioprovinces; Fig. 11). The high degree of endemicity and low diversity is representative of the epicontinental Sephardic bioprovince (cf. Page, 1996). Conversely, in the Ladinian stage the Tethyan basins showed a more diverse and abundant brachiopod fauna, and even emerged new taxonomic groups (Dagys, 1993). This diversification phase could have started early in the Pelsonian, since the conditions of the Western Tethys platforms were propitious for a possible epifaunal radiation, especially on the Adrian promontory (South Alps in Italy, Balaton Highland, Dinarides, Balkans), where they reach species diversity and abundance practically comparable to those from the Eastern Tethys (Grădinaru and Gaetani, 2019).

In the peri-Iberian palaeomargins, the palaeobiogeographic affinities in the Middle Triassic remained uncertain due to the virtually absence of brachiopods, except for the isolated and sporadic record of the cosmopolitan and generalist *Lingularia, Coenothyris* or *Mentzelia*. In the Betic Ranges, a Sephardic affinity was suggested for the Ladinian brachiopod fauna by Baeza-Carratalá et al. (2018). All new species from Southern Israel arranged into the genera *Tubithyris, Coenothyris* and *Menathyris* by Feldman (2002, 2013, 2017) in the late Anisian-early Ladinian are endemic to the Sephardic Bioprovince. Nevertheless, since the multicostate zeilleriides are valuable palaeobiogeographic elements of correlation (Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá et al., 2014), a feasible faunal affinity can be established between the endemic Betic *Misunithyris* and the low-latitude Israeli *Menathyris* (endemic to the Sephardic province as well; Feldman, 2013), just as occurs with the Mediterranean multicostate zeilleriids in the Early Jurassic (Baeza-Carratalá and García Joral, 2012).

On the other hand, all the biogeographical index-taxa from the Tethyan-Germanic bioprovince are recorded northwards the South-Iberian Palaeomargin. It can be ascertained therefore that a twofold Sephardic/Tethyan-Germanic bioprovinciality was well-established during the Ladinian inferring a connection between the Sephardic and the South-Iberian shallow epicontinental platforms (Fig. 11). However, biogeographic boundaries remain ambiguous since towards the North of the Betic Range ubiquitous taxa with NW-European affinities are scarcely represented in the Levantine Sector of the Iberian Range, Menorca, and the Catalonian Coastal Range (for a revision see Baeza-Carratalá et al., 2018).

Notwithstanding the widespread bi- or multi-provincialism of brachiopods throughout the Triassic in the westernmost Tethys, this possibly got disrupted intermittently during the Anisian as can be deduced from the distribution of *T. trigonella* (Fig. 11). The maximum

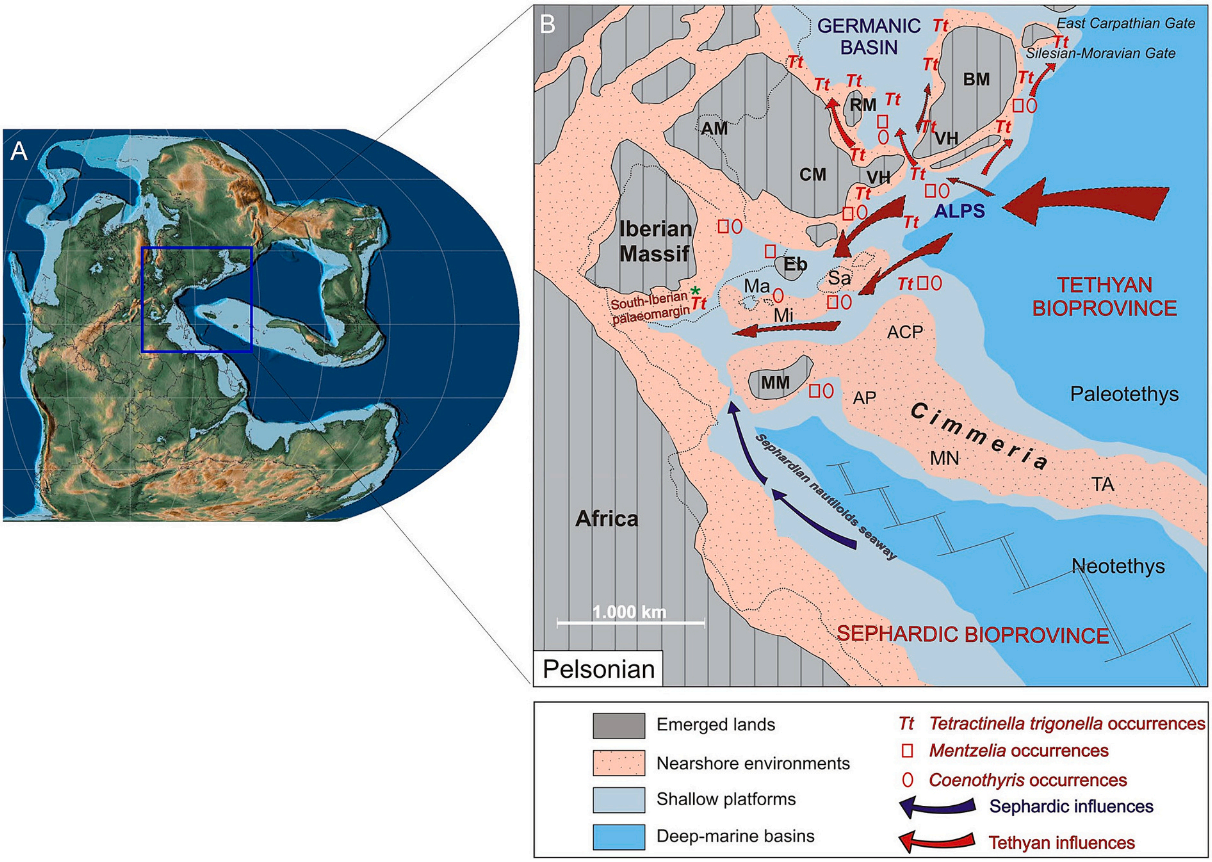

Fig. 11. A. Global palaeogeographic map for the Middle Triassic (Anisian), computed with GPlates 2–2.0 in the framework of the Paleomap Project (Scotese, 2016). B. Detailed palaeogeographic reconstruction for the Pelsonian (modified after Pérez-Valera et al., 2023) showing the distribution of *Tetractinella trigonella* in the westernmost region of the Tethys Ocean together with some pervasive taxa with Alpine/Germanic affinity such as *Mentzelia* and *Coenothyris*, occasionally recorded in the peri-Iberian palaeomargins as well. Colour of arrows and taxa symbolises the inferred palaeobiogeographical affinities. Global surface marine currents circulation is based on the interpretation by Crasquin et al. (2010), Escudero-Mozo et al. (2015), Martindale et al. (2019), and Manzanares et al. (2020). ACP: Apennine Carbonate Platform; AM: Armorican Massif; AP: Apulia; BM: Bohemian Massif; CM: Central Massif; Eb: Ebro Massif; Ma: Majorca; Mi: Minorca; MM: Meso-Mediterranean Massif; MN: Mani; RM: Rhenish Massif; Sa: Sardinia; TA: Taurus; VH: Vindelician High. Dotted lines show palaeogeographic position of the currently emerged land.

flooding event at the end of the Pelsonian transgression (MID-2 event) temporarily reduced the palaeogeographic barriers allowing for a better connection via the North-South epicontinental seaways. Thus, pervasive and opportunistic species such as *Tetractinella trigonella,* widely developed and settled in the Alpine, Germanic, and other North-European basins of the Tethyan bioprovince (Fig. 11), migrated, occupying vacant ecological niches and establishing their westernmost records in the South-Iberian Palaeomargin, although they never reach the further low-latitude regions of the Sephardic bioprovince. Other cosmopolitan brachiopods from the Germanic and Tethyan bioprovinces, such as *A. angustaeformis* and *Coenothyris* spp. recorded in the Internal Betic Zones (Simon, 1963) could have migrated to the South-East in the same Pelsonian MID-2 event. This NE-SW connection is strengthened by the record of other faunal elements typical of Tethyan sub-basins such as bivalves or foraminifera of the Alpine and Germanic basins (Pérez-Valera et al., 2023) co-occurring with *T. trigonella* in the outcrops herein analysed.

Consequently, one can expect that the unquestionable Sephardic faunal affinities started in the South-Iberian Palaeomargin from the Ladinian onwards. However, in the Pelsonian transgressive MID-2 event, some necto-planktonic elements, such as representatives of the nautiloid *Germanonautilus* and benthic bivalves such as *Gervillia*, both characteristic of the Sephardic province, are recorded around the Betic *Tetractinella*-beds. These occurrences might alternatively indicate that the first migration event of the Sephardic fauna northwards to the Betic palaeomargin took place in this Pelsonian maximum flooding by benefiting of the palaeogeographic barriers decline (Fig. 11). However, this migration episode did not trigger the radiation northwards of Sephardic brachiopods such as multicostate zeillerides, probably due to their short larval lecithotrophic stage and the unfavourable pattern of marine currents inferred for the Palaeotethys Ocean.

8. Conclusions

The bed-by-bed analysis of the only Anisian stratigraphical succession recorded in the South-Iberian Palaeomargin (External Betic Zones) allowed for a better characterisation of the environmental scenario leading to the settlement of the *Tetractinella*-beds, considered as a significant biohorizon of correlation of the Pelsonian substage (middle Anisian) recorded for the first time in the peri-Iberian platforms.

Reconstruction of palaeonvironments, leading to the *Tetractinella*-beds establishment in the Betic Ranges, emphasises the proposal of a migration episode virtually reported in the westernmost Tethys during the Pelsonian maximum-flooding, when nearshore and shallow epicontinental environments connected with open-marine areas. Thus, in the studied succession an inner, shallow-water platform is initially evidenced, very rich in soft-bottom dwellers, as recorded by the great abundance of the trace fossils of the *Oravaichnium* ichnoassemblage together with infaunal bivalves, probably responsible for the intense bioturbation.

In this quite homogeneous setting, a firmground has been pointed out represented by a *Balanoglossites* surface, where both shallow and slightly deeper benthic organisms are found. This surface represents a condensed level originated by the sea-level rise related to the Pelsonian transgression episode (MID-2 event). In this context, *Tetractinella* first appears, also prospering in the overlying beds, in correspondence to opener environments in connection with the deeper open-sea habitats.

The presence of *T. trigonella* in the peri-Iberian platforms reveals the migration southwards, from the Alpine and other North-European biochores, of opportunistic taxa that established their westernmost record in the Betic Ranges, never reaching further low-latitudes as the Sephardic Bioprovince. These migration routes show that the maximum Pelsonian flooding (MID-2 event) temporarily reduced the palaeogeographic barriers previously established, allowing for a dispersion of taxa throughout the North-South epicontinental Tethyan seaway. The occurrence of several faunal constituents of the Sephardic bioprovince together with *T. trigonella* also supports the first migration event of the Sephardic fauna northwards, appearing in the Betic palaeomargin in the studied MID-2 Pelsonian event.

CRediT authorship contribution statement

José Francisco Baeza-Carratalá: Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Alice Giannetti:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Fernando Pérez-Valera:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Juan Alberto Pérez-Valera:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Alberto Pérez-López:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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