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RESEARCH PAPER

Bivalve shell beds in the Triassic of the Sierra De Gádor (Alpujárride complex, Betic Cordillera, SE Spain)

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Abstract
The Peñón the Bernal section in the Sierra de Gádor comprises a succession of limestones, marly limestones and marls in the upper part of the Gádor unit, which belongs to the Alpujárride Complex in the Internal Zones of the Betic Cordillera. Several shell beds in this section and the locality of La Zarba in the same unit include relatively well-preserved macroinvertebrate assemblages. These beds reflect shell concentrations caused by storms and later colonised by epifaunal communities of cemented, epibyssate and endobyssate bivalves. Sedimentary features, fossil traces, and composition of bivalve assemblages indicate that the succession accumulated in a peritidal environment in a restricted carbonate platform with cyclic changes in water depth. The identified bivalve and ammonoid taxa suggest a Ladinian (Middle Triassic) age for the limestones, marly limestones and marls culminating the Gádor unit, so far considered as Upper Triassic in age. Like in other domains in the Betic Cordillera, the macroinvertebrate fauna has strong affinities with the Sephardic bioprovince.

Keywords Triassic invertebrates · Tempestites · Peritidal deposits · Ladinian · Gádor Unit

Resumen
La sección del Peñón de Bernal en Sierra de Gádor incluye una sucesión de calizas, calizas margosas y margas de la parte superior de la unidad de Gádor, que pertenece al Complejo Alpujárride de las Zonas Internas de la Cordillera Bética. Varias concentraciones de conchas en esta sección y en la localidad de La Zarba en la misma unidad incluyen asociaciones de fósiles de macroinvertebrados relativamente bien preservados. Estas concentraciones son el resultado de acumulaciones de conchas causadas por tormentas que luego son colonizadas por comunidades de bivalvos cementados, epibisados y endobisados. Las características sedimentarias, las trazas fósiles y la composición de las asociaciones de bivalvos indican que los depósitos estudiados se acumularon en medios peritidales, en una plataforma carbonatada restringida en la que se produjeron cambios cíclicos en el nivel del mar. Los taxones de bivalvos y ammonoideos identificados sugieren una edad Ladiniense (Triásico Medio) para las calizas, calizas margosas y margas de la parte superior de la Unidad de Gádor, hasta ahora consideradas como Triásico Superior. Como en otros dominios de la Cordillera Bética, la fauna de macroinvertebrados tiene una fuerte afinidad con la bioprovincia Sefardí.

Palabras clave Invertebrados triásicos · Tempestitas · Depósitos peritidales · Ladiniense · Unidad de Gádor

1 Introduction

Although the first paleontological report on the Triassic of the Sierra de Gádor (Almería, SE Spain) was published in the 19th century (Gonzalo y Tarín, 1882), studies on fossils from this mountain range are scarce and limited to fossil inventories and their potential chronostratigraphic significance. In the geological survey of the Sierra de Gádor, promoted by the economic interest of fluorite-Pb-Zn ore

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mining, Gonzalo y Tarín (1882) listed a series of fossil molluscs, namely "Miophoria *(M. Laevigata* and *M. Golfusi)*, Hinnites, Monotis, Avicula *(A. Bronni)*, Miacites and Rissoa", and assigned to the ore deposits a Triassic age, which had previously been uncertain. Years later, Mallada (1892) documented the presence of *Myophoria laevigata*, *M. goldfussi*, *Avicula bronni*, *Hinnites*, *Monotis* and *Myacites* based on the same fossil collection of Gonzalo y Tarín. Many decades later, in the memoirs of the geological maps covering the Sierra de Gádor in the 1980s, diverse lists of macroinvertebrates, conodonts, foraminifers, ostracods and ichnofossils were used to support the age attributed to the mapped units (Baena & Ewert, 1983; Baena & Voermans, 1983) with any precise indication of localities nor documentation of the listed fossils. The works of Martín-Rojas et al. (2009, 2012) provided more detailed inventories of macro and microfossils and their stratigraphic position in the carbonate succession, with a few illustrations of the reported taxa. The chronostratigraphic significance of fossil assemblages hypothesized by these authors was mainly based on benthic foraminifers, previously listed by Somma et al. (2009, 2010).

The scarcity of paleontological works has been probably due to a combination of the global paucity of Early and Middle Triassic fossils and the unfavorable diagenetic and metamorphic evolution of the Triassic carbonates of Sierra de Gádor, since part of them were affected by dolomitization, and all rocks underwent metamorphism that promoted recrystallization of clay and carbonates (Martín-Algarra, 2004; Bessière et al., 2022).

In this paper we document relatively well-preserved macroinvertebrate fossils occurring in several shell beds in a well exposed section some tens of meters thick. This is a very short interval in the thick sedimentary pile of the Alpujárride Complex in this mountain range, but the recorded taxa will contribute to the knowledge of Triassic faunas in the Betic Cordillera and add new information on the age of the carbonates in Sierra de Gádor. The sedimentary record of the Alpujárride Complex in its areas less affected by metamorphism, such as Sierra de Gádor, is key to understand the paleogeography of the Betic basin during the Triassic and, therefore, to establish possible relationships with Iberia and the current north of Morocco. This paleogeographic framework will help to understand the complex biogeography of marine faunas during the Ladinian in the western Tethys.

The objectives of this work are (a) to describe the lithology, lithofacies and sedimentary structures of the Peñón de Bernal section; (b) to document the macroinvertebrate fossils and taphonomic attributes of several shell beds in the section; (c) to interpret the paleoenvironmental setting of deposition of the section and formation of shell beds; (d) to discuss the chronostratigraphic meaning of the macroinvertebrate assemblages; and (e) to tentatively assess the paleobiogeographic relationships of the macroinvertebrate faunas in the Sierra de Gádor with other regions of the western Mediterranean.

2 Geological setting

The Peñón de Bernal section is located on the southern slope of the Sierra de Gádor in Almería, SE Spain (Fig. 1). This mountain is mainly made of Triassic rocks of the Alpujárride Complex in the Internal Zones of the Betic Cordillera (Voermans & Baena, 1983; Marín-Lechado et al., 2005; Janowski et al., 2017). The Internal Zones comprise three stacked major tectonic complexes: the Nevado-Filábride Complex, formed by Paleozoic or older metamorphic rocks (Gómez-Pugnaire et al., 2000, 2004; Jabaloy-Sánchez et al., 2018), the Alpujárride Complex encompassing Paleozoic to Mesozoic metasediments (Delgado et al., 1981), and the Maláguide Complex, with a Mesozoic to Cenozoic sedimentary cover overlying a Paleozoic basement (Lonergan, 1993; Martín-Martín, 1996). No rocks of the Nevado-Filábride Complex crop out in Sierra de Gádor and the attribution of a few small, dispersed outcrops to the Maláguide Complex in the area (Aldaya et al., 1983; Voermans & Baena, 1983) is questionable. Sierra de Gádor is a large, E–W to NEE–SWW trending antiform, which resulted from NNW–SSE compression due to convergence between the Eurasian and African plates since the late Miocene (Marín-Lechado et al., 2007).

The study materials belong to the Gádor tectonic unit (Gádor nappe, Jacquin, 1970), which according to Baena and Ewert (1983) is equivalent to the Lújar nappe (Aldaya, 1969). In the study area the Gádor Unit is overlain by the Felix Unit (Jacquin, 1970), composed of metamorphic siliciclastics followed by dolostones of undifferentiated Triassic age (Fig. 2a). The lithological succession of the Gádor Unit (Fig. 2b) consists of phyllites and quartzites at the base, which gradually change upward to calcphyllites and thick bedded to massive dolostones with limestone intervals. These lower carbonates pass upward to well-bedded limestones, locally intercalating marly limestones and thick dolostone packages. These materials are followed by limestones, marly limestones and minor marls and clays, which are internally divided by an unconformity surface. The Peñón de Bernal section and the La Zarba sampling site belong to the uppermost part of the succession (Fig. 2b).

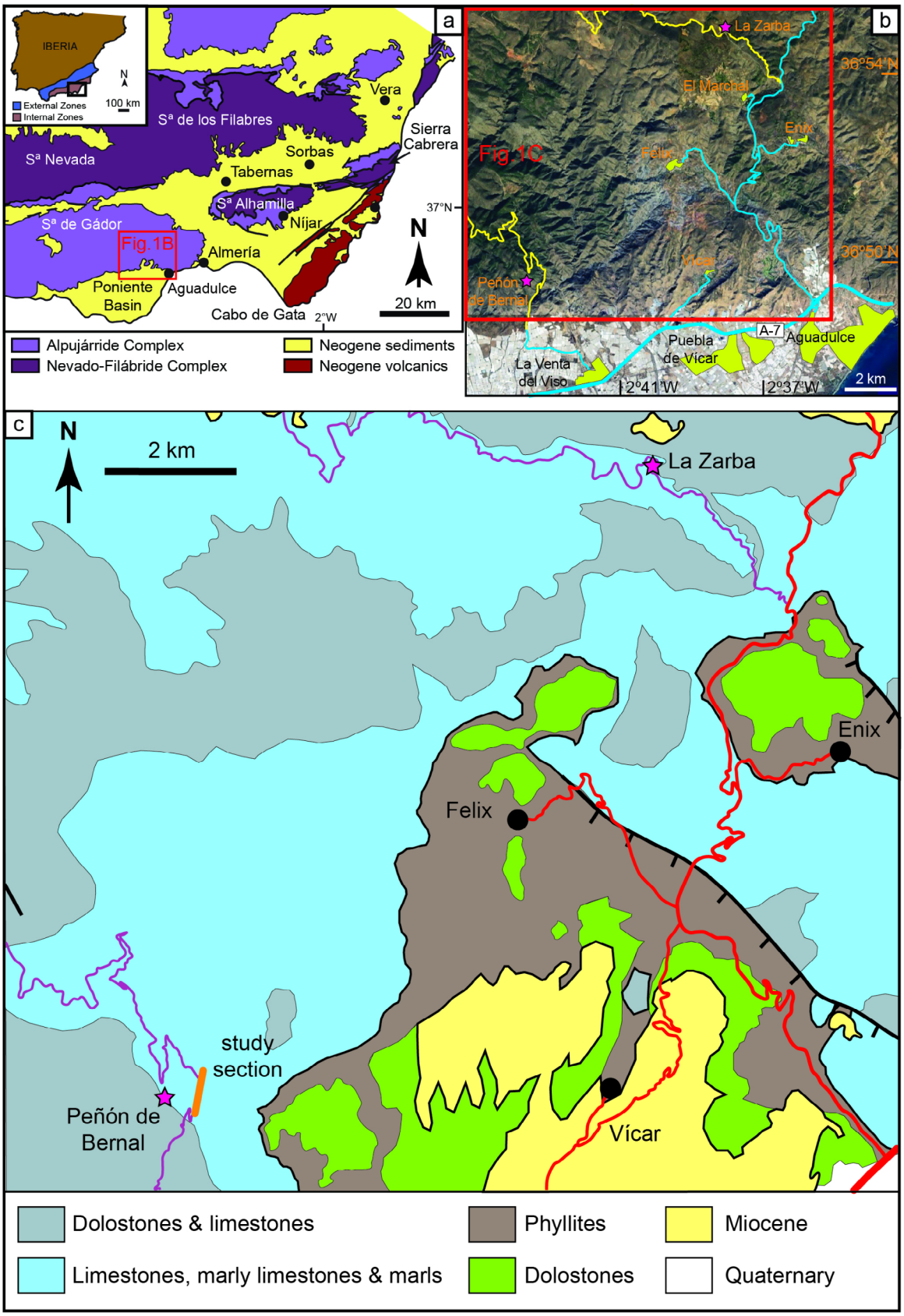

Fig. 1 **a** Schematic geological map of SE Spain (taken from Sola et al., 2022). **b** Access roads to study localities (Peñón de Bernal section and La Zarba). Paved roads in blue, unpaved roads in yellow. **c** Geological map with location of logged section and La Zarba sampling site

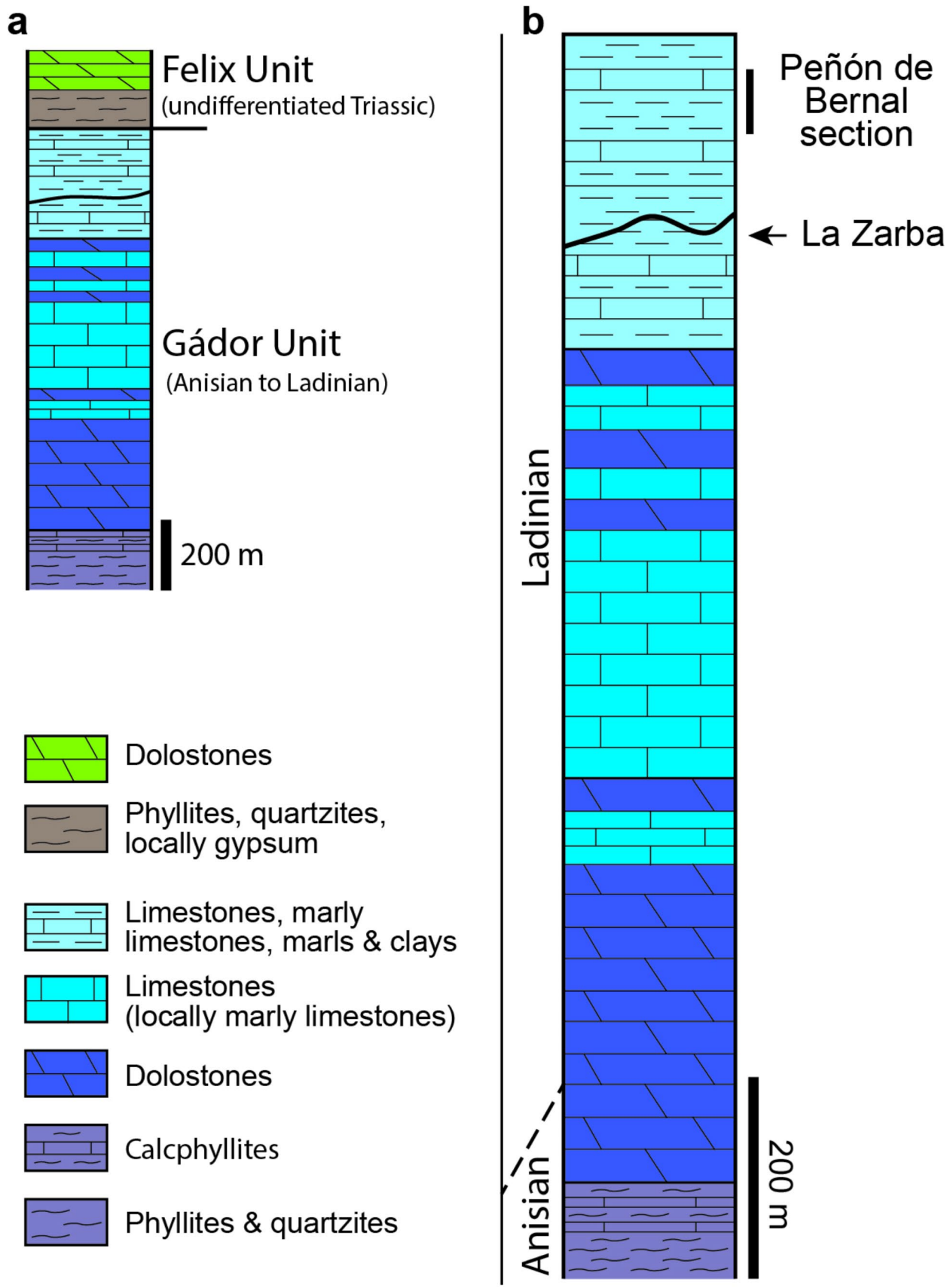
a
Felix Unit
(undifferentiated Triassic)
Gádor Unit
(Anisian to Ladinian)
200 m
Dolostones
Phyllites, quartzites, locally gypsum
Limestones, marly limestones, marls & clays
Limestones (locally marly limestones)
Dolostones
Calcphyllites
Phyllites & quartzites
b
Peñón de Bernal section
La Zarba
Ladinian
Anisian
200 m

Fig. 2 **a** Units of the Alpujárride Complex defined in the study area (Jacquin, 1970). **b** Schematic stratigraphic column of the Gádor unit and stratigraphic position of the study intervals. Due to widespread deformation, the thickness of the successive lithologies is roughly estimated. Position of the Anisian/Ladinian boundary after Martín-Rojas et al. (2012)

3 Methods

The Peñón de Bernal section was studied by detailed logging of lithology, lithofacies and sedimentary structures of the beds exposed along an unpaved track that goes up from the village La Venta del Viso to the top of the Sierra de Gádor (Fig. 1). Lithology and lithofacies were defined based on field observations supported by petrographic analysis of 14 thin Sect. (47 × 27 mm in size), which were stained with alizarin red-S to identify carbonate minerals. Lithofacies classification follows the Embry and Klovan (1971) modified version of the Dunham (1962) system. Although shell concentrations are common in the section (Fig. 3), the studied macroinvertebrate fossils were collected only in five shell beds, in which preservation at the top surface suggested a certain potential for identification. Additional observations and sampling of a shell bed were carried out in rocks with similar lithology and facies from a lower stratigraphic position in the La Zarba locality, 12 km northeast from the Peñón de Bernal section (Fig. 1).

The taphonomic attributes of the shell beds were assessed in the field and on large slabs collected to identify fossils in the lab at the Departamento de Botánica y Geología, Universitat de Valencia. A Leica MZ6 microscope with attached Leica camera 10,445,930 was used for fossil imaging. Processing of one sample of more than 2 kg per shell bed for conodont extraction was unsuccessful.

4 Results

4.1 Lithology and facies

The study section consists of 71 m of well-exposed limestone, marly limestone, marl, and clay (Fig. 4). The clay has a low degree of recrystallization due to the metamorphism undergone by the Alpujárride Complex. Marly limestone and marl beds show a certain degree of compaction and recrystallization. Limestone beds preserve the internal texture and their microfacies can be assessed and studied in detail.

There are five basic lithofacies, which repeatedly appear throughout the section in cycles of different order (Fig. 3):

- A *Bivalve rudstone lithofacies* generally consists of heterometric bioclasts and lithoclasts in a muddy matrix. Lithoclasts are subangular to subrounded and include black pebbles. Most bioclasts are disarticulated valves and fragments of bivalves (Fig. 5a). Gastropods and echinoderm fragments are also common. Calcified cyanobacteria (*Cayeuxia*), as well as cortoids (bioclasts with micrite margins) and bioclasts with thin ooid coatings occur in some beds. Beds are centimetres to decimetres in thickness, locally with slightly irregular bases.

- B *Packstone lithofacies* varies in grain size and is usually poorly sorted. Grains are generally subrounded. Bivalve, gastropod and echinoderm fragments and peloids are the main components. Small black intraclasts, the green alga *Acicularia* and benthic foraminifers also occur. Benthic foraminifers (Involutinidae) are the main components in some beds. "Revolver-like" remains of Charalean algae are observed in one sample. Beds are centimetres to decimetres in thickness, commonly with irregular bases (Fig. 5b). In some intervals, centimetre-scale packstone layers alternate with marly layers. Part of them have limited lateral extension and form discontinuous lenses that locally show poorly defined ripple cross lamination marked by different clay proportions. *Planolites* traces occur in a few beds.
- C *Bivalve wackstone lithofacies* consists of bioclasts, mainly bivalves dispersed in a muddy matrix. Beds are flat-parallel, centimetres to decimetres thick, generally showing lamination, millimetres to centimetres thick.
- D *Mudstone lithofacies* contains rare bioclasts, mainly bivalves, and varying proportions of clay (from limestone to marl lithology). Mudstone can be well stratified with beds centimetres in thickness and poorly defined internal parallel lamination. Laminae richer in clay separate the beds. Mudstone intervals can also show parallel lamination with laminae millimetres to centimetres in thickness (Fig. 6a). In some intervals of alternating mudstone and marl (clay), the lateral extension of limestone and marl laminae can be irregular, pinching out in centimetres to a few decimetres and forming discontinuous lenses (Fig. 6b). *Planolites* and *Thalassionoides*? traces are abundant in some beds. *Psilonichnus*-like (Y-shaped) traces (Fig. 7) can be observed in several mudstone beds with intercalated laminae of packstone at 44 m from the base.

- E *Marl lithofacies* intervals are laminated and include mudstone laminae with varying lateral continuity forming discontinuous lenses (Fig. 6b). In the upper third of the section, intimately alternating marl and mudstone layers are the dominant deposits.
- F *Clay lithofacies* mostly occur as fine seams alternating with other lithofacies. In a few cases clay beds are

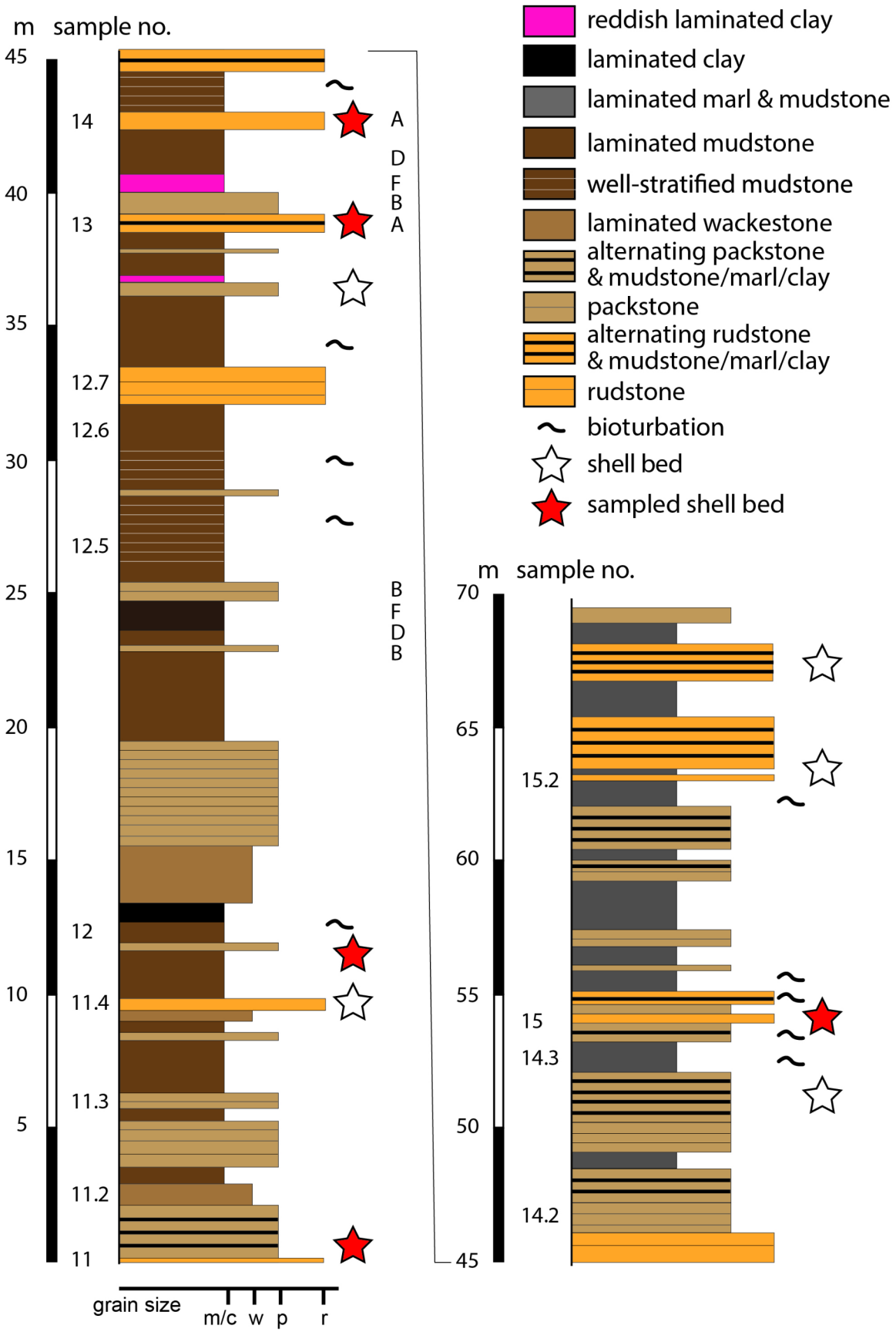
m
sample no.
45
40
35
30
25
20
15
10
5
14
13
12.7
12.6
12.5
12
11.4
11.3
11.2
11
A
D
F
B
A
B
F
D
B
grain size
m/c
w
p
r
reddish laminated clay
laminated clay
laminated marl & mudstone
laminated mudstone
well-stratified mudstone
laminated wackestone
alternating packstone & mudstone/marl/clay
packstone
alternating rudstone & mudstone/marl/clay
rudstone
bioturbation
shell bed
sampled shell bed
m
sample no.
70
65
60
55
50
45
15.2
15
14.3
14.2

Fig. 3 Detailed stratigraphic column of the Peñón de Bernal section. Capital letters mark two examples of metre-scale, asymmetric depositional cycles with a fining and shallowing lower part and a coarsening and deepening upper part. **A**: bivalve rudstone; **B**: packstone; **D**: mudstone; **F**: clay. Grain-size scale: m/c: mudstone, marl and clay; w: wackestone: p: packstone; r: rudstone

decimetres thick, two of which show reddish colours (Fig. 8).

4.2 Shell beds

All rudstone beds in the section are shell concentrations but the studied fossils were collected in five beds with relatively well-preserved mollusc fossils at the surface (Table 1). These shell beds have the following characteristics.

Shell bed 11 is an accumulation of molds of mostly unidentifiable bivalves, aligned and parallel to bedding (Fig. 9a). Most molds correspond to Pterioidea, namely *Gervillia* and *Bakevellia*. There are also some Myophoridae of varying sizes. This is a parautochthonous assemblage accumulated by water currents. Similar assemblages are frequent in intertidal to supratidal environments in Triassic deposits in the Iberian Ranges and the Prebetic Domain (López-Gómez et al., 1994).

Shell beds 12–15 consist of concentrations of imbricated and randomly oriented fragments of bivalves (Figs. 5a and 9b), locally with recrystallized shells (Fig. 9c), overlain by an autochthonous assemblage of cemented *Umbrostrea* and other epifaunal bivalves (Figs. 5a and 9b). The cemented form *Pseudoplacunopsis* occurs in shell bed 13. Only bivalves at the top surface of beds have a certain potential to be identified. A few gastropod molds and a single ammonoid internal mold were also recorded. In bed 14 several ophiuroids with diverse degrees of fragmentation occur.

5 Paleoenvironmental interpretation

Bivalve rudstone and packstone contain fossils and components of shallow-marine subtidal settings. The irregular base of in some rudstone beds and the taphonomic attributes of their fossil assemblages suggest that they are event beds, most probably accumulated by storms. In shell beds 12 to 15 the occurrence of imbricate and randomly oriented shell fragments with better preserved epifaunal bivalves at the top reflects an initial shell concentration caused by a storm (tempestite) (Fig. 9b, c). This hardened substrate was later colonised by an epifaunal community of opportunistic species, such as the cemented *Umbrostrea* and *Pseudoplacunopsis* among others (Aigner, 1985; Jiménez-Jiménez et al., 2003) (Fig. 9b). The relatively large size of the autochthonous bivalves suggests a prolonged time of dwelling on the surface before burial by finer-grained sediment.

Storms probably also drove the deposition of packstones with irregular, erosional bases (Fig. 5b) and thin packstone to rudstone beds that alternate with finer-grained deposits, as it occurs in modern tidal flats (Ginsburg & Hardie, 1975; Shinn, 1986). The common occurrence of black pebbles is related to peritidal settings (Strasser, 1984). Lenticular bedding locally with cross lamination, is typical of intertidal environments (Reineck & Wunderlich, 1968). Laminated wackestones and mudstones (Fig. 6a), as well as alternating mudstone and marls correspond to intertidal deposits in the Middle Triassic of the Catalan Coastal Ranges (Calvet et al., 1990) and in the Middle Triassic of the Eastern Iberian Ranges (Pérez-López et al., 2021). The lenticular bedding in mudstone facies (limestone and marl lenses, Fig. 6b) might be a primary structure but can also be the result of differential compaction and tectonic stretching (boudinage). *Psilonichnus*-like traces (Fig. 7) can be assigned to the Psilonichnus Ichnofacies characteristic of peritidal deposits (MacEachern et al., 2012). Beds rich in *Planolites* traces ("fucoides facies") have been interpreted as shallow subtidal (Pérez-López et al., 2021). Dense, low-diversity *Planolites* associations were considered indicative of restricted conditions in the Ladinian ramp carbonates of the Catalan Coastal Ranges (Mercedes-Martín & Buatois, 2021) and related to hypersaline environments in the Middle Triassic carbonates of the Tatra Mountains in the Western Carpathians (Jaglarz & Uchman, 2010). No obvious features indicative of subaerial exposure were observed, although the reddish colour in two clay intervals (Fig. 8) might reflect soil formation in supratidal environments. In summary, the carbonates and clays in the Peñón de Bernal section accumulated in peritidal settings in a restricted area of a carbonate shelf.

6 Cyclicity and trends

The deposits in the section show a clear, metre-scale cyclic pattern of repeated successions of the represented facies (Fig. 3). Cycles are generally asymmetric. In a complete lower half cycle, rudstone/packstone change successively upwards to laminated wackstone, laminated mudstone and marl/clay, or intimately alternating mudstone and clay, in a fining- and shallowing-upward succession. Most half cycles, however, only involve two or three facies. The upper half cycles show coarsening- and deepening upward successions with thicknesses usually different from those of the lower parts. In the logged section, 25 cycles were recorded, with cycle thickness ranging from 1 to 5.8 m (average 2.8 m, standard deviation 1.5 m, mode 1.8 m). Centimetre-scale alternations of facies reflect a higher-frequency cyclicity.

Fig. 4 Beds in the upper part of the Peñón de Bernal section. Limestones, marly limestones, marls and clays are well exposed on the road cut throughout the logged section. Notebook is 21 cm in size

Mixed marl/carbonate lithologies dominate the upper third of the section, which is generally richer in clay than the underlying deposits.

7 Paleontological remarks

Bivalvia Linnaeus, 1758.

Order Ostreida A. Férussac, 1822.

Superfamily Pterioidea Gray, 1847 (1820).

Family Bakevelliidae W. King, 1850 †.

***Bakevellia*cf.*costata*(Scholotheim, 1822).**

Figure 10a, b.

Shell of medium size and subequivalve, with a rhomboidal shape, slightly elongated in the anterior-posterior direction. Umbo small, pointed, significantly displaced towards the anterior margin. In the examined internal molds, the aliform expansions are not too patent, but the posterior ones can be observed. Fragments of the smooth shell were preserved, showing some growth lines. This species has been cited by Schmidt (1935) in the Ladinian of Esporlas and Espejeras sections, by Márquez-Aliaga (1983) in the Ladinian of Libros and Henarejos sections, and in the Fassanian of several localities in the Iberian Range (Escudero-Mozo et al., 2015). It has also been cited in the Ladinian of several Prebetic sections (Escudero-Mozo et al., 2016).

Superfamily Posidonioidea Neumayr, 1891.

Family Daonellidae Neumayr, 1891.

***Daonella*cf.*moussoni*(Merian, 1853).**

Figure 10c.

A specimen of *Daonella* cf. *moussoni* (Merian, 1853) has been recorded as an internal mold of the left valve. The specimen exhibits a somewhat circular and partially flattened shape. The umbo is near the hinge center. Radial ribs developed over the entire shell surface. Primary ribs are moderately broad, strong, straight, and separated by narrow furrows. The dorsal part of the shell is not visible. Additional specimens are required to confirm the identification

conclusively. *D. moussoni* is known to be very frequent in the lower Ladinian, Gredleri Zone of Monte San Giorgio, Switzerland (Schatz, 2001).

Superfamily Ostreoidea Rafinesque, 1815.

Family Ostreidae Rafinesque, 1815.

***Umbrostrea cristadifformis*(Schlotheim, 1820).**

Figure 10d-h.

Small-sized ostreiform shell, with suborbicular and irregular contour. Subequivalve (?) and subequilateral, with umbos in almost central position without protruding from the dorsal edge. The areas of attachment of the valve (right? or left?) to the substrate (xenomorphic areas) show variable convexity due to xenomorphism. The typical ornamentation consists of a system of coarse ribs in a radial arrangement, rounded on their outermost surface. The rib intersections with the growth lines have a very irregular scaly appearance. The course of ribs and the spacing between them do not remain constant and their number varies. The ribs bifurcate or trifurcate by successive subdivisions, more obvious in distal areas of the shell. *Umbrostrea* species belong to the Oyster-like Triassic cementing bivalve group. The left valve attaches to the substrate in the true oysters, but in *Umbrostrea*, due the structure of the shell, with an outer calcite foliar layer and an inner crossed-lamellar aragonite one, only the calcite layer is preserved. The muscle scar in the inner aragonite is not preserved and it is not possible to know which was the attached valve (Márquez-Aliaga et al., 2005). Formerly specimens of this species were attributed to *Enantiostreon difforme* (Goldfuss, 1833) and *Ostracites cristadifformis* Schlotheim, 1820. The affiliation of *Ostracites cristadifformis* to the genus *Enantiostreon* was proposed by Bittner (1912), who also included in the genus many Triassic bivalves formerly called oysters. More recently, Hautmann (2001) proposed the new genus *Umbrostrea* to encompass all Triassic oyster-like bivalves with an inner aragonitic layer. Based on this, *Ostracites cristadifformis* was formally included in the genus *Umbrostrea* (Márquez-Aliaga et al., 2005). It is a Middle Triassic species, frequent in the Germanic Muschelkalk and recorded in the early Ladinian of Israel (Lerman, 1960), and in the Ladinian of Monte Fogheras, Sardinia (Márquez-Aliaga et al., 2000; Stori et al., 2024). It is also common in the Muschelkalk facies (Ladinian) of the Iberian Peninsula (Catalan Coastal and Iberian ranges, and Prebetic Domain) (Márquez-Aliaga, 1985; Márquez-Aliaga & Martínez, 1996).

***Umbrostrea flabellum*(Schmidt, 1935).**

Figure 10i-l.

Medium-sized oval shell with several prominent ribs spaced one or two millimeters and directed to the ventral margin. The growth lines are not visible. This species has been included among other oyster-like bivalves and within the Ostreidae family. This species of Schmidt (1935) comes from the middle beds of the Longobardian of Hornos-Siles (Jaen). The author created the new species *Placunopsis flabellum* and in his discussion, he commented its similarity to *Ostrea spondyloides* (Schlotheim), a younger (Ladinian) frequent species in the upper Germanic Muschelkalk and in the late Ladinian of South France (Márquez-Aliaga et al., 2005). The Gádor specimens of levels 13 and 15 are like those recorded in the Prebetic Domain in Riopar (Albacete), in a section dated as early Ladinian (Fassanian) with ammonoids typical the Sephardic Province, including *Negebites zaki* Parnes, *Israelites ramonensis* Parnes, and *Protachyceras wahrmani* Parnes (Márquez-Aliaga et al., 1986, 2001).

Order Pectinida Gray, 1854.

Superfamily Plicatuloidea Gray, 1854.

Family Plicatulidae Gray, 1854.

***Pseudoplacunopsis teruelensis*(Wurm, 1911).**

Figure 11a, b.

Medium-sized inequivalve shell of irregular outline, with rounded to ovoid shape with maximum elongation in the umbo-paleal direction. The lower valve (right valve) is flat and shows smooth surfaces corresponding to attachment areas (xenomorphic areas). The upper or free valve is moderately convex to very convex. Shells subequilateral, with umbos almost central, irregular and not prominent. The cardinal area is very small and poorly defined. Anterior and posterior margins are subrectilinear. The ornamentation of the free valve consists of multiple very fine ribs, filamentous in appearance and irregularly arranged. The growth lines are thickened with irregularly spaced intervals, giving rise to circular, non-continuous “folds” that interrupt the radial ornamentation; the whole is reminiscent, in some specimens, of the overlapping layers characteristic of oysters but this is an Anomidae (formerly Terquemidae) species. Most specimens in level 13 have the shell preserved (Fig. 11a, b) because of the foliar external calcitic layer (Márquez-Aliaga & Márquez, 2000).

This species has been widely cited and is abundant in the Ladinian (mainly in the Fassanian) of the Iberian Ranges (Márquez-Aliaga, 1983; Escudero-Mozo et al., 2015) and recorded in the Prebetic Domain (Escudero-Mozo et al., 2016).

Order Limida Moore, 1952.

Superfamily Limoidea Rafinesque, 1815.

Family Limidae Rafinesque, 1815.

***Limea*cf.*vilasecai*(Schmidt, 1935).**

Figure 11c.

The record of *Limea* cf. *vilasecai* in level 13 is a right?, unequilateral? valve of small size and low convexity, with a subtrigonal-ovate outline. The anterior margin is not visible. The ventral margin is slightly curved. The posterior margin is rectilinear and the cardinal one very short, corresponding to one-third of the length of the anteroposterior diameter.


a
2 cm


b
50 cm

Fig. 5 **a** Top surface of a bivalve-rudstone bed (shell bed of sample no. 13). Randomly oriented, heterometric fragments of bivalves (upper part) in a micrite matrix form the bulk of the bed. Cemented *Umbrostrea* (arrows) grew on those storm deposits. **b** Packstone beds with irregular, slightly erosional bases

Umbo and auricles not visible. The ornamentation consists of radial ribs, prominent, narrow, with their length increasing from the umbo to the ventral edge and not all the same size. The ribs are separated by wider grooves. The specimen studied conforms to Schmidt's (1935) observations on specimens from the lower Muschelkalk of Camposines section (Tarragona). The scarce, badly preserved record does not permit a confident assignment. This species has been cited in Ladinian beds from the Catalan Coastal Ranges (Márquez-Aliaga, 1983), in the Moya section of the Iberian Ranges (Márquez-Aliaga et al., 1999), and the Prebetic Domain in Alicante province (López-Gómez et al., 1994).

Order Trigoniida.

Superfamily Trigonioidea Lamarck, **1819**.

Family Myophoriidae Bronn, **1849** †.

***Costatoria kiliani*(Schmidt**, 1935**)**.

Figure 11d.

The shell is small, oval-trigonal in shape, equivalve and unequilateral. The anterior-posterior diameter is slightly longer than the umbo-paleal diameter. The anterior margin is rounded and in continuous curvature with the ventral margin. The posterior margin is straight. The umbos are prominent, rounded, and in a slightly anterior position. The shell surface uniformly and moderately convex. The ornamentation consists of prominent, fine, equidistant, radially arranged ribs, separated by wider almost flat grooves. The growth lines are more pronounced in ventral areas. At their intersection with the ribs, they sometimes produce a nodular appearance, which is visible at high magnification. *C. kiliani* is closely related to *C. goldfussi* and *C. harpae*. A revision of Triassic *Costatoria* is necessary due to the taxonomic confusion surrounding this genus. *C. goldfussi* was cited by Márquez-Aliaga et al. (1986) in the Hornos-Siles section (Jaen). Recently, we obtained additional specimens from this section, and these materials have been reidentified as *Costatoria killani*. This revision also applies to *C.* aff. *harpae* from the Ladinian (Fassanian) of the Riopar section (Márquez-Aliaga et al., 2001). It is probable that the *Costatoria* initially reported in the Sierra de Gádor, identified as *C. goldfussi* by Gonzalo y Tarín (1882), is actually *C. kiliani*.

***Elegantinia betica*(**Hirsch, 1966**)**.

Figure 11e, f.

The valves show co-marginal ornamentation in the anterior zone and posterior radial grooves, characteristic of the genus. Most specimens are small with poor preservation as dark shells due to pyrite replacement. Notably, these specimens display characteristic features of the genus, such as co-marginal ornamentation in the anterior region and posterior radial grooves. It is a frequent infaunal record in Middle Triassic beds as an opportunistic species of intertidal environments. This species was established as *Myophoria betica* by Hirsch (1966) in the Sierra de Alhamilla (Almeria) in "intra Keuper" facies rocks in the Alpujárride Complex. In addition to other irrelevant citations, Simon and Kozur (1977) cite *Lyriomyophoria betica* (Hirsch) in the Orihuela Unit and in the Gádor Unit, which they date, with doubts, as Ladinian. *E. betica* occurs in the carbonate formation of the Cabo Tiñoso section (Murcia) with an association of bivalves attributable to the Ladinian (García-Tortosa, 2002). Martín-Rojas et al. (2012) report *E. betica* in the lower part of the meta-carbonate formation of the Gádor Unit in the Sierra de Gádor, in a shell concentration of bivalves and crinoids.

Gastropoda Cuvier, **1795**.

Superfamily Loxonematoidea Koken, **1889**.

Family Loxonematidae Koken, **1889**.

***Loxonema*sp.**

Figure 11g.

Determining species with internal gastropod molds is unreliable, as shown by recent specimens with preserved aragonitic shell. However, species citations based on internal molds are common in the literature on Triassic gastropods. On the other hand, in the Muschelkalk limestones of the Iberian Ranges there are many monospecific levels, with small specimens always preserved as internal molds. Several species of *Loxonema* that are characterised by a rapid growth with few whorls around a vertical axis have been recorded in the Germanic Muschelkalk. The gastropod specimen in level 12 is close to *Loxonema loxonematoides* (Giebel, 1848) and to *Loxonema* cf. *kokeni* (Picard, 1903) of 5 and 4 mm in size, respectively. Schmidt (1935) cited these species in the Ladinian of Espejeras (Alicante), although he commented the difficulty of their identification due to the absence of external ornamentation of shells.

Cephalopoda Cuvier, **1795**.

Order Ceratitida Hyatt, **1884**.

Superfamily Ceratitaceae Mojsisovics, **1879**.

Family Hungaritidae Waagen, **1895**.

***Negebites*? sp.**

Figure 11h.

In a sample from level 13 was identified an oxicone close to *Negebites* sp. (Antonio Goy personal communication, and Goy, 1995). This is of about 3 cm in diameter with suture lines of Hungaritidae type. *Negebites* has a ceratitic suture with numerous auxiliary elements, narrow and deep lobes and high, rounded saddles, visible in our specimen. It is characteristic of the Ladinian (lower part of the Fassanian) in the "Sephardic Province".

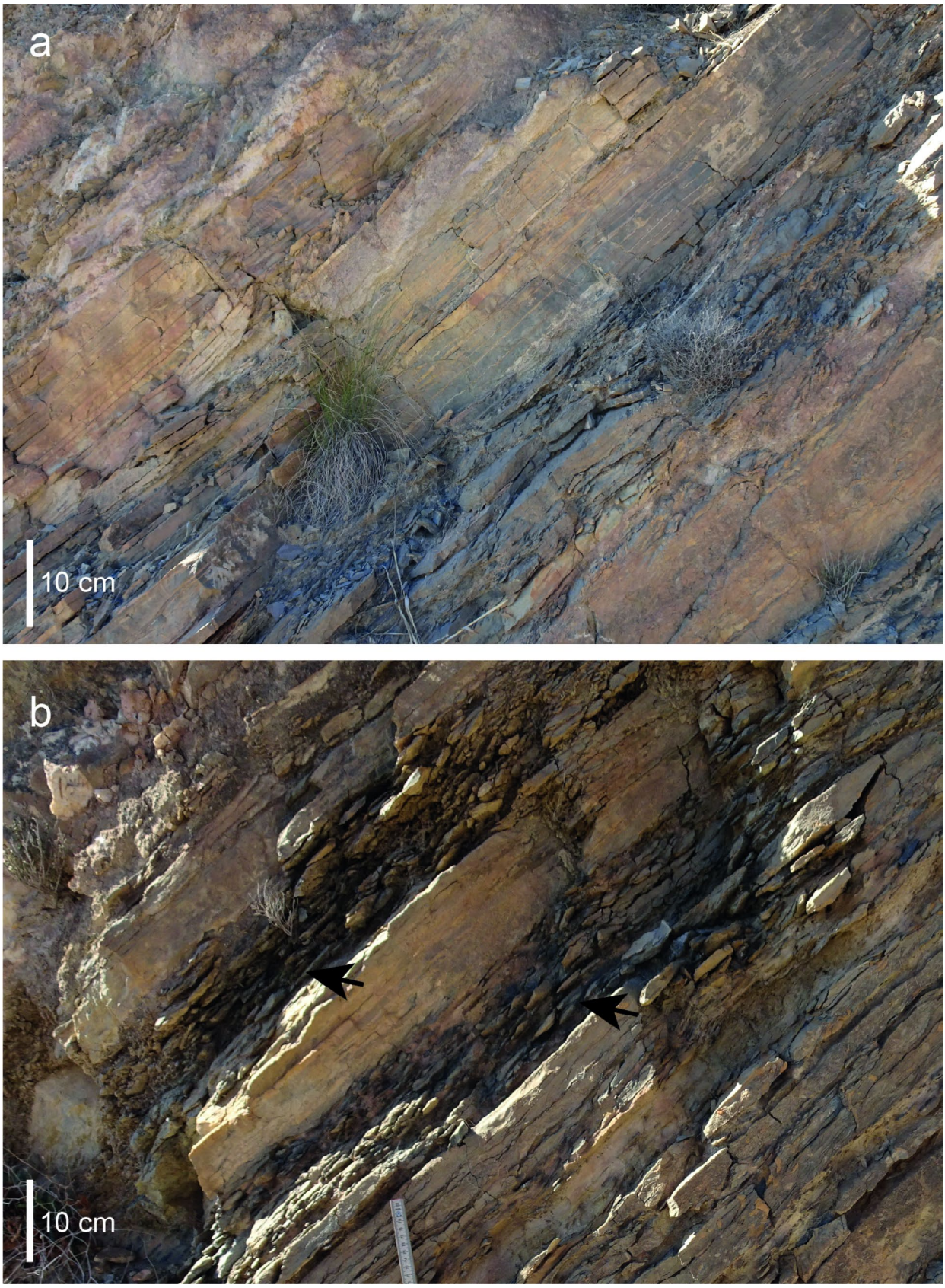

Fig. 6 **a** Mudstone beds showing parallel lamination with laminae millimetres to centimetres in thickness. **b** Beds of alternating mudstone and marl/clay (arrows) with irregular lateral extension of limestone and marl laminae, forming discontinuous lenses

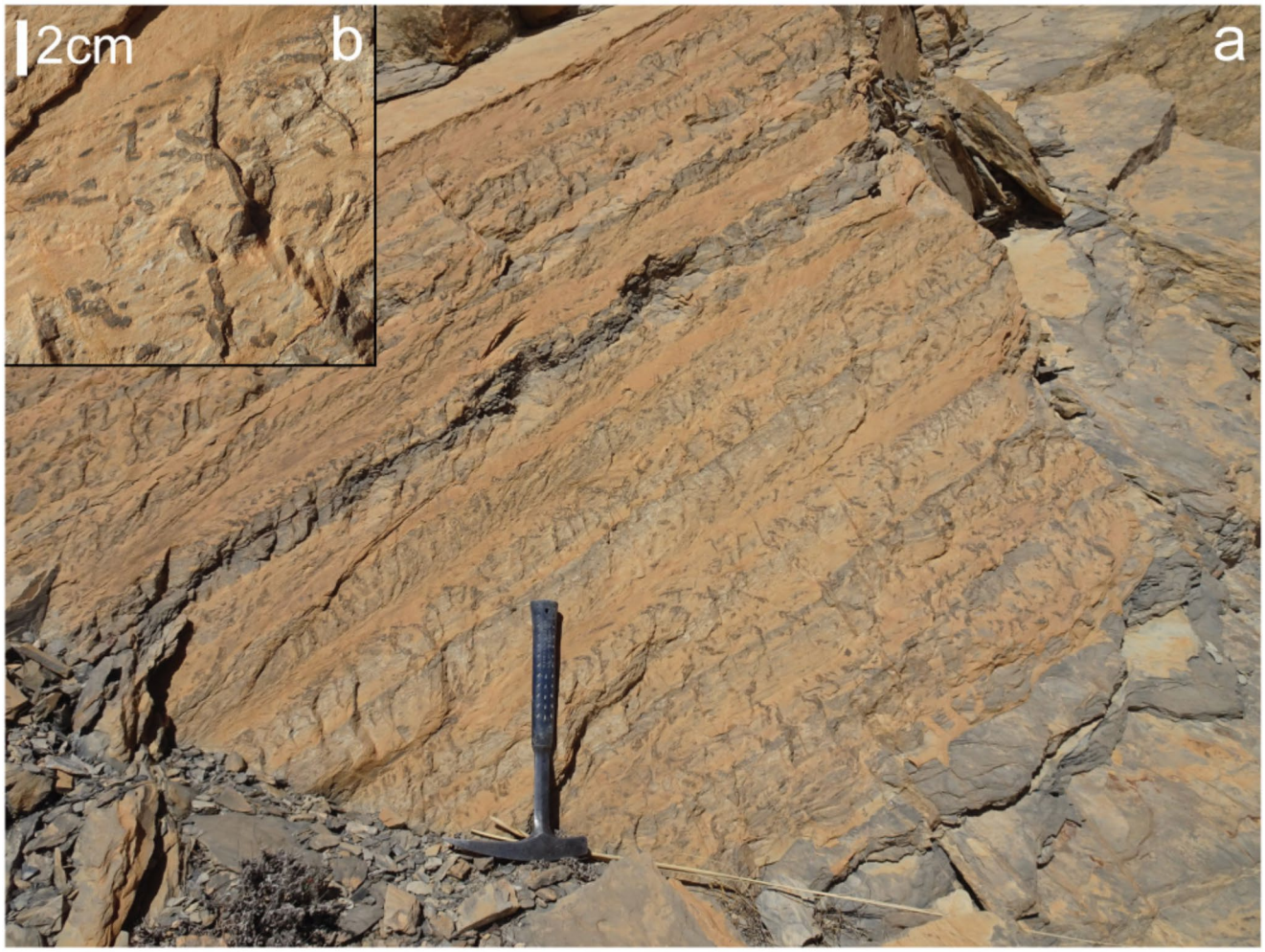

Fig. 7 **a***Psilonichnus*-like (Y-shaped) traces in mudstone beds with intercalated laminae of packstone. Hammer is 33 cm log. **b** Close-up of traces

Echinodermata Klein, **1778**.

Class Ophiuroidea Gray, **1840**.

Order Euryalida Lamarck, **1816**.

***Aspiduriella montserratensis*(**Calzada & Gutiérrez, 1988**)**.

Figure 11i, j.

According to Hans Hagdorn (personal communication), the specimens of Ophiuroidea from Sierra de Gádor are articulated and well-preserved examples of the Ladinian *Aspiduriella montserratensis*. This species was described as *Aspidura montserratensis* in the upper Muschelkalk of the Catalan Coastal Ranges, equivalent to the Ladinian (Virgili, 1958). Years later, Bolette (1998) showed that *Aspidura* Agassiz, 1835 (Ophiuroidea) was a younger homonym of *Aspidura* Wagler, 1830 (Serpentes) and substituted this name by *Aspiduriella*.

8 Discussion

8.1 Age of the section

Baena and Ewert (1983) reported the presence of bivalves "from the calcareous levels of the upper materials" in the Sierra de Gádor (names as in the original text): *Myssidioptera* cf. *tounmasii*, *Myophoria* cf. *goldfossi*, *Mytilus* cf. *compressiosculus*, *Omphaloptycha gregaria*, *Peronidella* cf. *sucaespitosa*, *Myssiodioptera* cf. *cainalfei*, *Myssiodioptera* cf. *klipsteiniana*, *Climacodichnus* cf. *corrugatus*, *Sestrostomella robusta*, which according to the authors indicate a Middle-Late Triassic age. The gastropod *Omphaloptycha gregaria* is a Naticidae very frequently found throughout the Muschelkalk, and the sponge *Sestrostomella robusta* was cited in Ladinan-Carnian rocks (Wengen and Cassian formations) of the Italian Dolomites (Tosti et al., 2014). *Mysidioptera* is a Limidae (Ros-Franch et al., 2014) with numerous species from the Italian Carnian. The validity of

Fig. 8 Metre-scale depositional cycle (marked with capital letters) at 40 m from the section base. This shallowing/deepening upward cycle is also indicated in Fig. 3. **A**: bivalve rudstone; **B**: packstone; **D**: laminated mudstone; **F**: red clay. The red clay probably records emersion and soil formation

Table 1 Abundance of invertebrate species recorded at the Peñón the Bernal section and the La Zarba locality with indication of life habits of species. Bivalve life habits adopted: Epifaunal attached (epibyssate), Epifaunal attached (cemented), semi-infaunal attached (endobyssate), Infaunal shallow-burrower. All bivalve species are suspension feeders. The mode of life of gastropods, cephalopods and echinoderms are also indicated

	Fossils	Shell beds/number specimens						MODE OF LIFE
		11	12	13	14	15	La Zarba	
BIVALVES	*Backevellia* cf. *costata*	4	2	1				endobyssate
	Gervillia sp.	2	3	3				endobyssate
	Daonella cf. *moussoni* (Merian, 1853)				1			epifaunal recliner/epibyssate
	Umbrostrea cristadifformis (Schlotheim, 1822)	1	3	8	21	18		cemented
	Umbrostrea flabellum (Schmidt, 1935)			7		6		cemented
	Pseudoplacunopsis teruelensis (Wurm, 1911)			7				cemented
	Limea cf. *vilasecai* (Schmidt, 1935)		5	2				epibyssate
	Costatoria kiliani (Schmidt, 1935)		2					shallow burrower
	Costatoria sp.		4					shallow burrower
	Elegantinia betica (Hirsch, 1066)				4		18	shallow burrower
	Neoschizodus sp.	3		2				shallow burrower
	Modiolus sp.	7		10				endobyssate
GASTROPODS	*Loxonema* sp.		1		1			epifaunal/infaunal
CEPHALOPODS	*Negebites?* sp.			1				nektobenthic
ECHINODERMS	*Aspidurella montserratensis* (Calzada & Gutierrez, 1988)				2			epibenthic

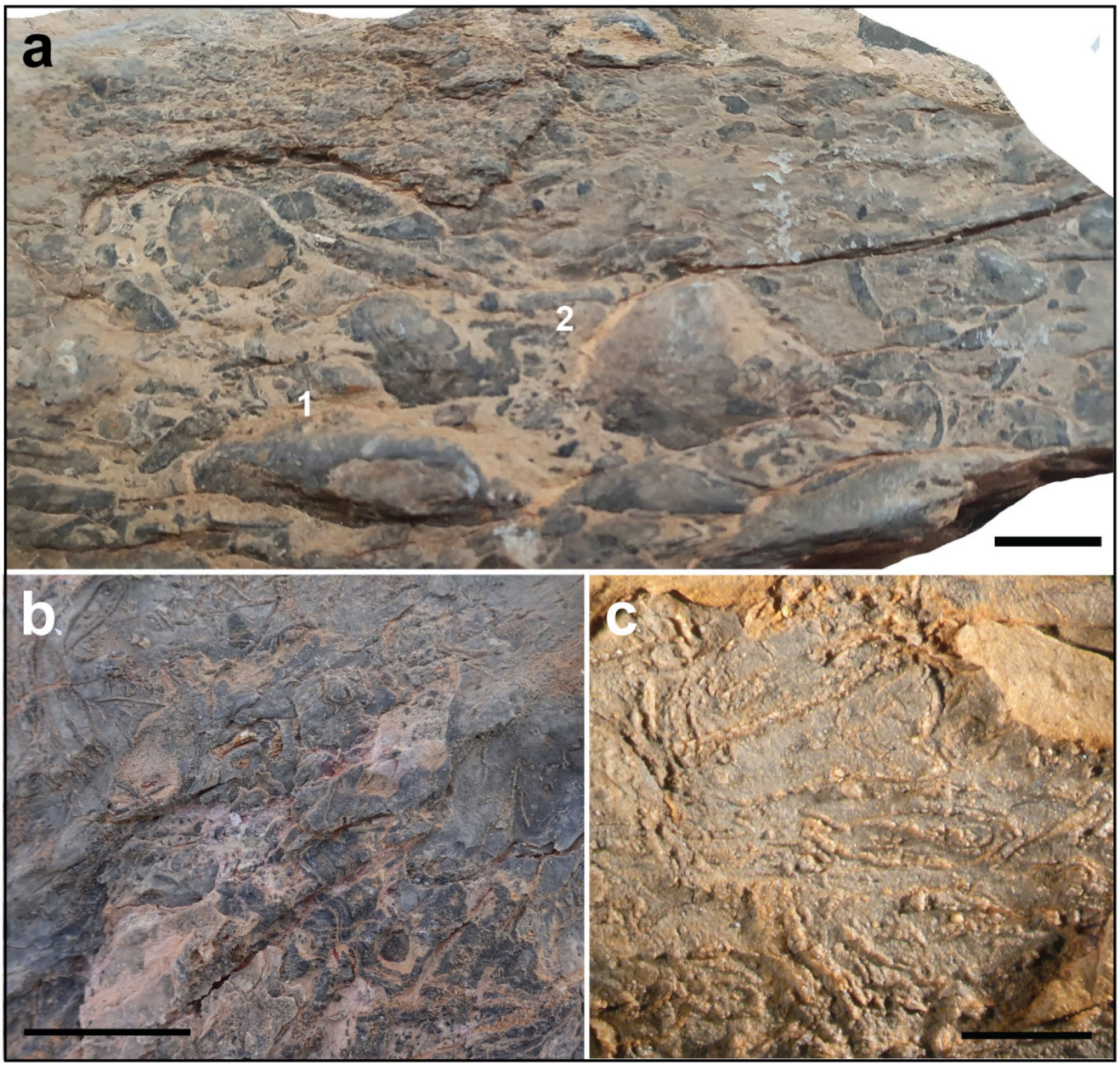

Fig. 9 **a** Upper surface of shell bed 11 showing several internal casts of mostly unidentifiable bivalves. *Gervillia* sp. (1), *Neoschizodus* sp. (2) can be identified. sample PB11 5, MGUV 40057B. **b** Randomly oriented bivalve fragments (upper left) overlain by a cemented *Umbrostrea* (lower right), sample PB 15. **c** Accumulation of randomly oriented unidentifiable bivalves, sample 135 J MGUV 40,062. Concentrations of randomly oriented shells were caused by storms. They created a hardened substrate colonised by epifaunal bivalves such as *Umbrostrea*

other genera mentioned requires revision. *Myophoria* possibly corresponds to *Costatoria kiliani*, as both exhibit significant similarities, and the latter is prevalent in the study area.

Somma et al. (2009) and Martín-Rojas et al. (2009) reported the presence of *Bakevellia* aff. *kiliani* Schmidt and *Lyriomyophoria betica* Hirsch within a lumachella containing crinoids. Additionally, they noted the occurrence of *Bactryllium* in the upper marly limestones of the Gádor Unit succession (Fig. 2). *Bactryllium* is an "incertae sedis" taxon previously cited in the Upper Triassic rocks of Italy, which was not observed in our materials.

Regarding foraminifera, Somma et al. (2009, 2010) and Martín-Rojas et al. (2012) reported in the lower limestones of the Gádor Unit (Fig. 2) an assemblage comprising *Lamelliconus* gr. *biconvexus-ventroplanus*, *Lamelliconus cordevolicus*, *Triadodiscus eomesozoicus*, *Lamelliconus procerus* and *Nodosaria ordinata*. Some of these species were also mentioned by Márquez and Pérez-López (2001)

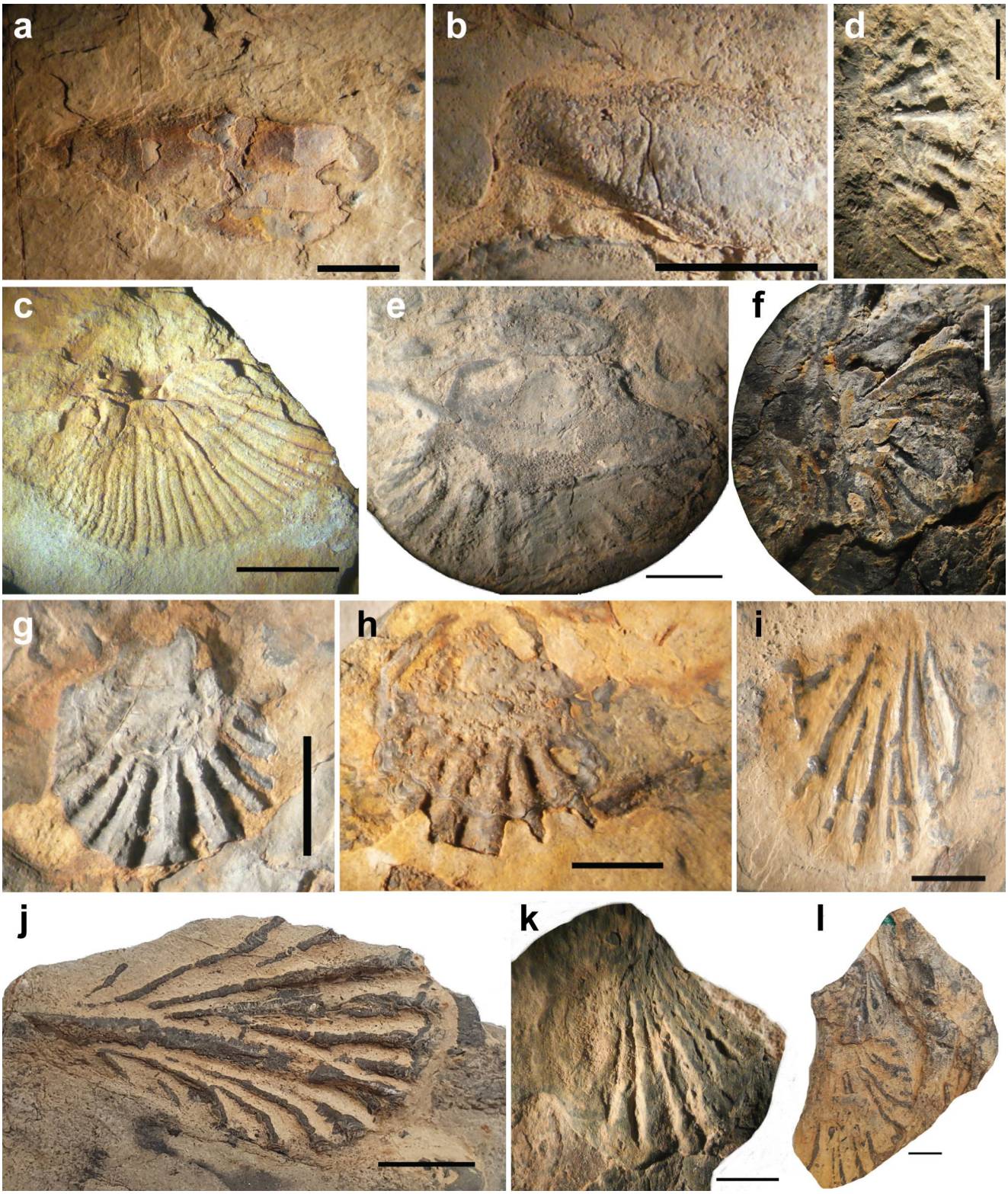

Fig. 10 **a**, **b***Bakevellia* cf. *costata* (Schlotheim, 1822), internal molds of left valves with no sculpture, 1333 MGUV 400,641 2. **c***Daonella* cf. *moussoni* (Merian, 1853), left valve internal mold with the typical radial ornamentation, PB 14, MGUV 40,055. **d**, **e**, **f**, **g**, **h***Umbrostrea cristadifformis* (Schlotheim, 1822), lower left? valve with xenomorphic area and irregular thick ribs, 1312 A 40,064 MGUV; 35I1 MGUV 40,062; 1312 MGUV 40,064; 1312 A MGUV 40,064 A; PB15 2, MGUV 40,066. **i**, **j**, **k**, **l***Umbrostrea flabellum* (Schmidt, 1935), upper valve with outer calcite shell layer preserved, showing the regular and medium sized ribs, PB 151, MGUV 40,066; 1312 MGUV 40,064; 136 A MGUV 40,063; 125 MGUV 40,060

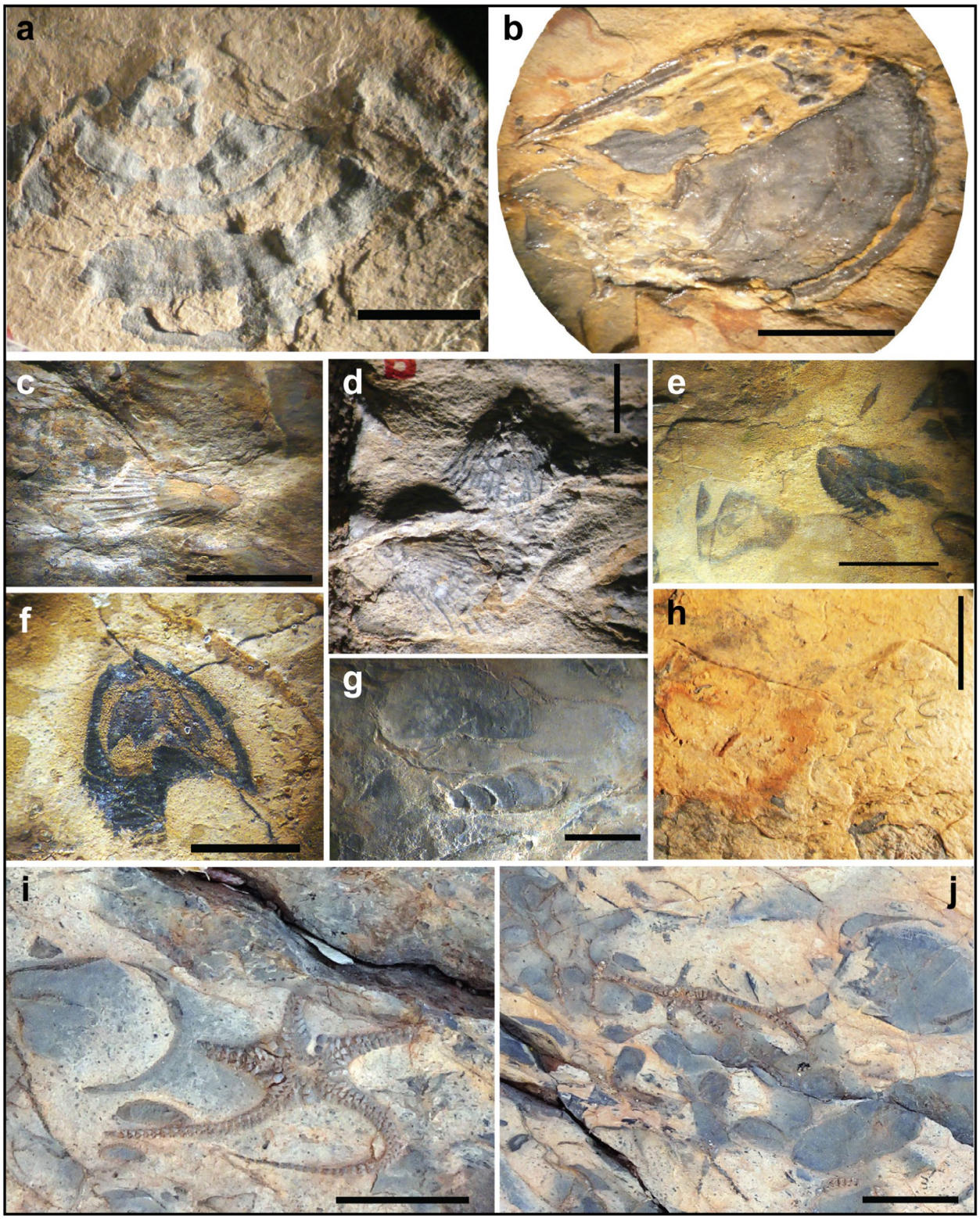

Fig. 11 **a**, **b***Pseudoplacunopsis teruelensis* (Wurm, 1911), free upper left valve with the outer calcite layer preserved, showing very fine ribs, 1311 A 40,064 MGUV; 135I MGUV 40,062. **c***Limea* cf. *vilasecai* (Schmidt, 1935), left valve with radial ribs, 121 A 40,053 A. **d***Costatoria kiliani* (Schmidt, 1935), two internal molds of triangular right valves, showing the fine radial ornamentation, 124B, 40,059 B. **e**, **f***Elegantinia betica* (Hirsch, 1966), left valves showing the commarginal ornamentation, La Zarba, MGUV 40,056. **g***Loxonema* sp., internal mold, 124 A, 40,059 A. **h***Negebites*? showing ceratitid suture lines, 135 K, MGUV 40,062. **i***Aspiduriella montserratensis* (Calzada & Gutierrez, 1988), ventral view, PB14 1. **j***Aspiduriella montserratensis* (Calzada & Gutierrez, 1988), dorsal view, PB14 2

as Longobardian-Carnian in the Subbetic Zone. Benjamini (1988) described a comparable assemblage in the Makhlesh Ramon series (Israel), with underlying levels ascribed to the uppermost Fassanian based on ammonoid fossils. Paleobiogeographically, these data suggest the migration of species from the Sephardic domain to southern Iberia during the early Ladinian (Fassanian). Those species later became common in Alpine basins during the late Ladinian (Longobardian) (Márquez, 2005).

Baena and Ewert (1983) reported the occurrence of the conodonts *Tardagondolella mungoensis mungoensis* and *Pseudofurnishius murcianus* in a single sample, which according to them dated the upper part of the thick dolostones as Ladinian-Carnian. However, the presence of *Pseudofurnishius murcianus* suggests the base of the Ladinian (Fassanian), while *Sephardiella mungoensis* marks the beginning of the Longobardian (late Ladinian) (Plasencia & Márquez-Aliaga, 2011; Plasencia et al., 2016).

All these findings led Martín-Rojas et al. (2012) to attribute a Ladinian age to the thick bedded to massive dolostones and the well-bedded limestones with thick dolostone packages (Fig. 2). These authors attributed the overlying limestones, marly limestones, marls and clays, i.e., the interval to which the Peñón the Bernal section belongs (Fig. 2), to the Carnian based on a single record of the "incertae sedis" *Bactryllium*.

However, the components of the macroinvertebrate assemblages recorded in the Peñón de Bernal section suggest that limestones, marly limestones, marls and clays in the upper part of the Gádor Unit are Ladinian in age. Although the poorly state of preservation prevents an unquestionable identification of the ammonoid as *Negebites*, representatives of this genus are characteristic of the Fassanian. Several other recorded species have been mostly found in the lower Ladinian. The numerous specimens of Myophoridae that can be attributed to *Elegantinia betica* (Hirsch) recorded at La Zarba (Fig. 11e, f) also point to a Ladinian age.

8.2 Paleobiogeographic affinity of the macroinvertebrate fauna

The Anisian–Ladinian interval marked a crucial phase in the evolution of the westernmost Tethys region, driven by significant tectonic shifts. During this period, major geodynamic events unfolded, including the subduction of the Palaeotethys to the north, the opening of the Neotethys to the south, and the northward drift of the Cimmeria microcontinent (Stampfli & Borel, 2002; Brühwiler et al., 2009). These tectonic movements played a key role in shaping sedimentary basins, expanding vast carbonate platforms, and establishing biogeographic migration routes.

The resulting tectonic activity also triggered rapid paleogeographic transformations, marked by the sequential closing and opening of seaways that connected distinct bioprovinces (Ziegler & Stampfli, 2001). These shifting seaways facilitated the westward spread of Tethys sea waters during the Anisian. Four major bioprovinces emerged during this time: the Germanic in the north, the Tethyan in the east, the Alpine in the east-northeast, and the Sephardic in the south (Hirsch, 1972, 1975, 1977).

Most bivalve taxa identified at the species level in the Sierra de Gádor have been reported in the Prebetic Domain in the External Zones of the Betic Cordillera. Bivalve and ammonoid assemblages in this domain are considered characteristic of the Sephardic bioprovince (Hirsch, 1977; Hirsch et al., 1987, 2014; Goy, 1995; Márquez-Aliaga & Martínez, 1996; Pérez-Valera, 2005; Pérez-López & Pérez-Valera, 2007; Escudero-Mozo et al., 2015). In particular, the occurrence of *Umbrostrea flabellum*, *Pseudoplacunopsis teruelensis*, *Limea* cf. *vilasecai*, *Costatoria kiliani* and *Elegantinia betica*, together with the Hungaritid ammonoid attributable with doubt to *Negebites* indicates a Sephardic affinity of the macroinvertebrate fauna in the Sierra de Gádor (Escudero-Mozo et al., 2015). *Elegantinia betica* has only been recorded in the Alpujárride Complex in the Betic Internal Zones, while the bivalve species *Umbrostrea flabellum* and *Costatoria kiliani*, which are abundant and characteristic in the External Zones of the Betic Cordillera have been reported from the Negev, Israel (Hirsch et al., 2014).

9 Conclusions

Although Triassic fossils are rare in the Alpujárride Complex due to unfavourable geological conditions (such as dolomitization and metamorphism), the collection of macroinvertebrate fossils in the Peñón de Bernal section and La Zarba site enhances the understanding of the Triassic marine record in the Betic Cordillera.

Sedimentary features, bioturbation, and composition of bivalve assemblages suggest that the Peñón de Bernal section formed in a shallow, peritidal marine setting in a restricted carbonate platform.

The fossil assemblages point to a Ladinian (possible Fassanian) Middle Triassic age of the limestones, marly limestones and marls in the upper part of the Gádor Unit, challenging previous assumptions that these deposits were Upper Triassic in age.

The fauna shows strong affinities with the Sephardic bioprovince, especially the Prebetic Domain, highlighting the role of the Tethyan seaways and tectonic shifts in species migration and faunal exchanges during the Ladinian period in the western Tethys region.

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Declarations

Conflict of interest We declare that they have no conflicts of interest between themselves and the research being submitted for publication in the journal.

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