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RESEARCH PAPER

Anisian bivalves from Serra (Valencia, Iberian Ranges): taxonomy, environments and biogeographic implications

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Abstract

An exceptional assemblage of Middle Triassic (Anisian) bivalves from the lower part of the Muschelkalk of Serra municipality (Sierra Calderona, Valencia, Spain), in the easternmost sector of the Iberian Ranges, is systematically studied and integrated to its stratigraphic, sedimentological and biogeographical framework. The assemblage contains cosmopolitan and diverse fauna including *Hoernesia socialis* (Schlotheim), *Myophoria vulgaris* (Schlotheim), *Pleuromya elongata* (Schlotheim), *Unionites fassaensis* (Wissmann), and *Neoschizodus laevigatus* (Goldfuss). Additionally, the ichnofauna of the site is described and studied for the first time, including the ichnogenera *Planolites*, *Oravaichnium*, *Taenidium* and *Thalassinoides*. Sedimentary facies record a variety of environments including coastal shabkha, carbonate tidal flats, subtidal agitated areas and shallow mid-ramp settings, that define the installation of a carbonate ramp in the area in response to the first broad marine Triassic transgression. The bivalve fossils were found in facies corresponding to well-oxygenated shallow-marine (mid ramp) environments, characterized by low energy conditions excepting moderate wave action during storms. These environments probably represent for this area the conditions of maximum marine flooding during the first extensive transgressive episode that occurred during the Middle Triassic in Iberia.

Keywords Bivalvia · Ichnofauna · Middle Triassic · Muschelkalk · Carbonate Ramp · Iberia

Resumen

Se estudia la sistemática de la asociación excepcional de bivalvos del Triásico Medio (Anisiense) que aparece en la parte inferior del Muschelkalk del municipio de Serra (Sierra Calderona, Valencia, España), en el sector más oriental de la Cordillera Ibérica, y se integra en su marco estratigráfico, sedimentológico y biogeográfico. La asociación refleja una fauna cosmopolita y diversa, incluyendo *Hoernesia socialis* (Schlotheim), *Myophoria vulgaris* (Schlotheim), *Pleuromya elongata* (Schlotheim), *Unionites fassaensis* (Wissmann) y *Neoschizodus laevigatus* (Goldfuss). Además, se describe y estudia por primera vez la icnofauna del yacimiento, incluyendo los icnogéneros *Planolites*, *Oravaichnium*, *Taenidium* y *Thalassinoides*. Las facies sedimentarias reflejan ambientes diversos: shabkha costera, llanura mareal carbonática, zona submareal agitada y rampa media, que definen la instalación de una rampa carbonatada en la zona en respuesta a la primera transgresión marina

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generalizada del Triásico. Los fósiles de bivalvos se encontraron en facies correspondientes a ambientes marinos someros de rampa media, de fondos bien oxigenados y caracterizados por condiciones de baja energía, exceptuando la acción moderada del oleaje durante tormentas. Estos ambientes probablemente reflejan localmente las condiciones de máxima inundación marina durante el primer episodio transgresivo ocurrido en el Triásico Medio en Iberia.

Palabras clave Bivalvia · icnofauna · Triásico Medio · Muschelkalk · rampa carbonática · Iberia

1 Introduction

During the lower interval of the Middle Triassic marine carbonates (Muschelkalk facies) in Sierra Calderona (Valencia Province, Spain), fossil-bearing sections provide bivalve assemblages of exceptional abundance and diversity (Márquez-Aliaga, 1985; Quintero & Revilla, 1958). In this paper, these bivalves are systematically described, and the assemblage is framed in its stratigraphic, sedimentological, ichnological, and biogeographical context. The association is stratigraphically located at the lower levels of the Muschelkalk facies succession. That interval records the first marine transgression in Iberia within the framework of the Alpine cycle, and its study allows for significant progress in the knowledge of the paleogeographic, tectonic and biogeographic patterns that defined the sedimentary basins during the Middle Triassic.

Sierra Calderona represents the SE end of the Iberian Ranges, a broad NW–SE mountain belt generated during Cenozoic times linked to Alpine contraction and related inversion of the former Iberian intracontinental basin (Fig. 1A, B). Rocks outcropping in Sierra Calderona consist of about 1000 m of Permian and Triassic sedimentary record. The general stratigraphy of Sierra Calderona was described by López-Gómez and Arche (1992) and Garay (2000, 2005a, 2005b), and recently reviewed by Ortí et al. (2020) and Hernaiz-Huerta (2024). The publication of these latest studies, and others carried out in neighboring areas, such as the Alt Palància (Ortí & Guimerà, 2015), has highlighted some of the up to now unresolved stratigraphic problems in the Middle Triassic of this area. These latest studies consider that the lateral extension of the so-called "Levantine-Balearic Triassic" (López-Gómez et al., 1998), which encompasses the entire Middle Triassic sedimentary record in Muschelkalk facies in a single unit, shows a reduction of several kilometers in its geographical extension. In cases where this situation occurs, the Muschelkalk facies is recorded by two carbonate units and another marly-evaporitic unit intercalated between them, an arrangement known as the "Mediterranean Triassic" (Virgili et al., 1977). This new arrangement proposed for the western part of this area, however, still presents many difficulties to be resolved in this study area, since not all the marly-evaporite units can be interpreted as the intermediate unit of the "Mediterranean Triassic", as these lithologies are easy to confuse with other similar ones from the Upper Triassic (Keuper facies), and even with other similar ones that represent the lateral sedimentary evolution of the carbonate units. A second aspect that also complicates the stratigraphic interpretation of these units by some authors, is the erroneous maintenance of the idea that the two carbonate units of these facies above mentioned have Anisian and Ladinian ages respectively, an aspect that changed with the new age proposed for the boundary between both stages (Brack et al., 2005). Therefore, it is necessary to obtain more precise ages for these units and detailed descriptions of them in order to solve these problems. The present work focus on a detailed description of these facies and their paleontological content in the Serra section to contribute to a future resolution of the aforementioned problems.

The fossil bearing beds are located 3.5 km north of the village of Serra (Valencia), in the vicinity of Puerto de l'Oronet. Several sections have been studied along the CV-310 road from Burjassot to Torres Torres, and the CV-3341 road from l'Oronet to Puerto del Garbí, in order to reconstruct sedimentary paleoenvironments and their evolution (Fig. 1C).

The fauna studied in this paper represents a post-extinction recovery marine assemblage following the end-Permian extinction event in the eastern Iberian Peninsula. European Muschelkalk (mostly Germanic Basin) contains the richest trace-fossil assemblage of any Triassic succession worldwide (Stachacz et al., 2022) but it is not the case of the Iberian Peninsula. The ichnofauna recovered for this study is among the first occurrences in the region after the end-Permian crisis where ichnofossils have been documented (see also, e.g., Baeza-Carratalá et al., 2024 in the Anisian of Betic Cordillera or Mercedes-Martín & Buatois, 2021 in the Ladinian of Catalan Coastal Ranges).

2 Previous paleontological work in Serra section

The first authors to document Triassic bivalves from the Serra Muschelkalk were Quintero and Revilla (1958), who referred to the data provided by Dupuy De Lôme during the preparation of the “Geological Map of Spain, 1:50,000, Sheet No. 668 of Sagunto” (Valencia) published in 1959. De Lôme (1959, p. 35) noted the presence of a well-preserved

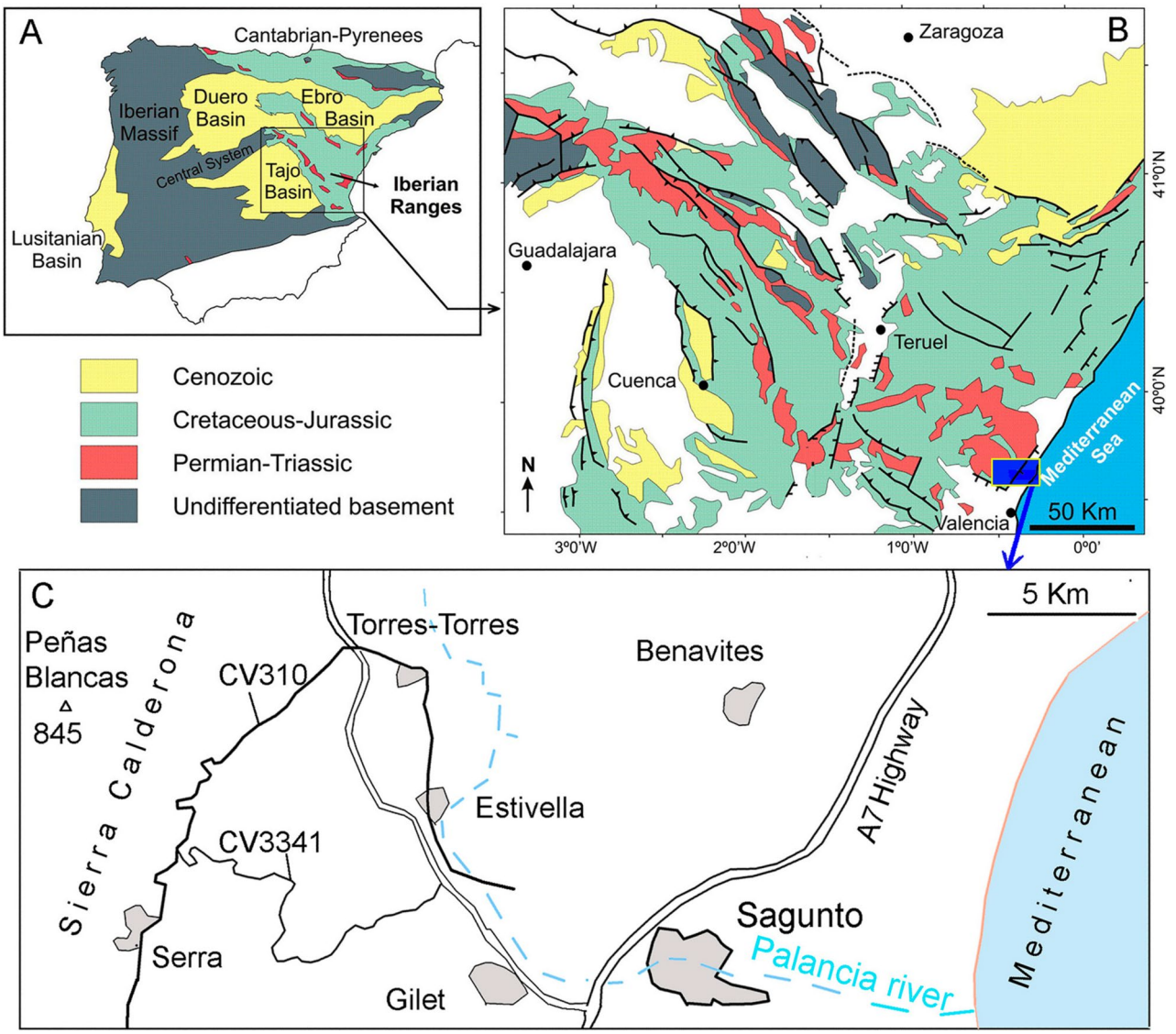


Fig. 1 Location of the study area

fossiliferous section along the road from Serra to Torres Torres at kilometer 28. Several bivalve species were reported, including *Avicula bronni* Aberti, *Mytilus eduliformis* Schlotheim, *Nucula subcuneata* D'Orbigny, *Nucula goldfussi* Alberti, *Myophoria vulgaris* (Schlotheim), *Myophoria sublaevis?* Schmidt, *Myophoria laevigata* Alberti, and *Anodontophora aff. fassaensis?* Wissmann. Subsequently, Fonollá et al. (1974) cited the same bivalve assemblage in the "Geological Map of Spain, Magna Series, Sheet 668, 29–26".

A comprehensive systematic review of the fossil record from the Serra section was conducted by Márquez-Aliaga (1976), who carried out paleontological studies on the Middle Triassic of the southern Iberian Range. In the studied section, "Corte de Serra - Torres Torres", located at kilometer 28 of the road between these localities, several bivalve species were recorded, including *Myophoria vulgaris* (Schlotheim), *M.* gr. *laevigata* Zieten, *Modiola* sp., and *Gervillia* sp. Subsequent fieldwork has expanded the paleontological record, yielding new fossils from equivalent stratigraphic levels. Ongoing research includes a taxonomic and taphonomic analysis of the fossil assemblage within a detailed stratigraphic framework.

The bivalves from Serra correspond to the fossil assemblages of the lower dolomitic section of the Middle Triassic in the southern sector of the Iberian Range (Márquez-Aliaga, 1985). The Serra section preserves the most representative lower Muschelkalk fossil record, which led to its designation as the "F-S" (= Serra Fauna by its Spanish abbreviation), or Serra bivalve association, because it was not found in any

other section of the cited range (Márquez-Aliaga & Martínez, 1996). Later, López-Gómez et al. (1998) proposed that the epicontinental deposits of the Muschelkalk of Serra belong to the Levantine-Balearic Domain, characterized by a single carbonate level. Although the Serra cut is recently being considered to fall outside this domain (e.g., Hernaiz-Huerta, 2024; Ortí et al., 2020), however, Márquez-Aliaga et al. (2001) described a possible correlation between the Serra deposits and those of the lower part of the Castellón and Menorca series, which belong to the Levantine-Balearic Domain.

The first study detailing the sedimentary, stratigraphic, and biostratigraphic characteristics of the Middle Triassic carbonate sediments (Muschelkalk facies) in the locality of Serra was conducted by Márquez-Aliaga et al. (2008). The authors identified a diverse Anisian fossil assemblage, including abundant bivalves such as *Hoernesia socialis* Schlotheim, *Myophoria vulgaris* (Schlotheim), *Pleuromya elongata* (Schlotheim), *Pleuromya* cf. *fassaensis* (Wissmann), and *Neoschizodus laevigatus* (Goldfuss). Additionally, rare and small gastropods (*Ampullina* sp. and *Loxonema* sp.), foraminifera (*Abriolina* cf. *mediterranea* Luperto), brachiopods (*Mentzelia?* sp.), and nautiloids (*Germanonautilus*) were described by the same authors.

3 Stratigraphy, facies, and paleoenvironments (Serra section)

The lower part of the Muschelkalk facies of the Serra stratigraphic section considered in this study is 35 m thick and easily distinguished from the underlying and overlying materials (Fig. 2). It rests on a heterolithic unit composed of finely stratified and alternating shales, evaporites, fine sandstones, and dolomitic carbonates, which corresponds to the Marines Formation defined by López-Gómez and Arche (1992), and that has been assimilated to the "Röt facies" in several stratigraphic studies. In turn, the succession is limited at the top by a sharp and slightly erosive surface, which marks the beginning of a 50 m thick, cliff-forming dolomitic unit, that consists of well-stratified dolomites in decimeter thick beds. This overlaying unit was named as "Pla de les Llomes member" by Garay (2005a).

The main stratigraphic features, sedimentary facies and fossil content of the studied succession, as well as the reconstructed paleoenvironments can be summarized, from base to top, as follows (Fig. 2):

3.1 Unit-I (11.2 m)

This unit is equivalent to "interval 2.2" by Márquez-Aliaga (1985) and to "Alcalá member" by Garay (2005b). Its base is defined by a gradual transition from the underlying heterolithic Marines Formation, lithologically marked by the onset of a sedimentation neatly dominated by carbonates.

Two main intervals can be recognized. The lower half part of Unit-I consists of finely stratified dolostones (centimeter-thick beds), which often show subhorizontal stromatolitic lamination or ripple lamination, as well as flat pebbles, gypsum pseudomorphs, desiccation cracks and rare tepee structures. The upper half is poorly stratified, often showing a chaotic aspect (Fig. 3a). Here, the dolomitic beds alternate with dolomitic marls and intraformational dolomitic breccias.

Interestingly, this unit yields small burrows attributable to *Taenidium*, an ichnogenus commonly found in continental to marginal coastal environments, characterized by episodic flooding and subaerial exposure (see systematic description below).

Deposits of Unit-I correspond to shabkha-type coastal systems, possibly characterized by a mosaic of subenvironments and ecological conditions rapidly changing in space and time. Carbonates and evaporites coexist with fine silicilastics, indicating influx of clastic material from land. Dolomitic breccias are interpreted as the result of post-sedimentary dissolution of evaporite deposits.

3.2 Unit-II (14.8 m)

This unit is equivalent to "interval 2.3" of Márquez-Aliaga (1985) and also to "Banyet Member" of Garay (2005a).

This unit is defined by well-stratified dolostones in decimeter-thick beds, which provide topographic prominence. Facies are dominated by calcarenitic dolostones, which frequently show cross-bedding with decimeter-scale sets (Fig. 3b, c). To a lesser extent, some centimeter- to decimeter-thick levels of semi-nodular muddy dolostones appear interbedded with the calcarenitic bodies. These show evidence of bioturbation (burrows) and faunal remains, primarily bivalves, including *Hoernesia socialis* (Schlotheim) and *Myophoria vulgaris* (Schlotheim) (fossiliferous level N1). Also found in a very subordinate manner are thin (millimeter-thick) levels of stromatolite nature, usually covering ripple beds or small bedforms. However, no evidence of subaerial exposure has been observed.

The base of Unit-II is a sharp contact with the underlying Unit-I, and it represents a transgressive surface over the shabkha deposits of the previous interval. The top of the unit is also sharp. However, this latter is defined by a quite irregular surface, that is enriched in iron oxides and that features abundant borings, which were made in a sedimentary surface that was at least partially lithified. Interestingly, this hardened surface develops on a 30 cm thick carbonate level that contains abundant unfragmented shells, mainly disarticulated bivalves and gastropods.

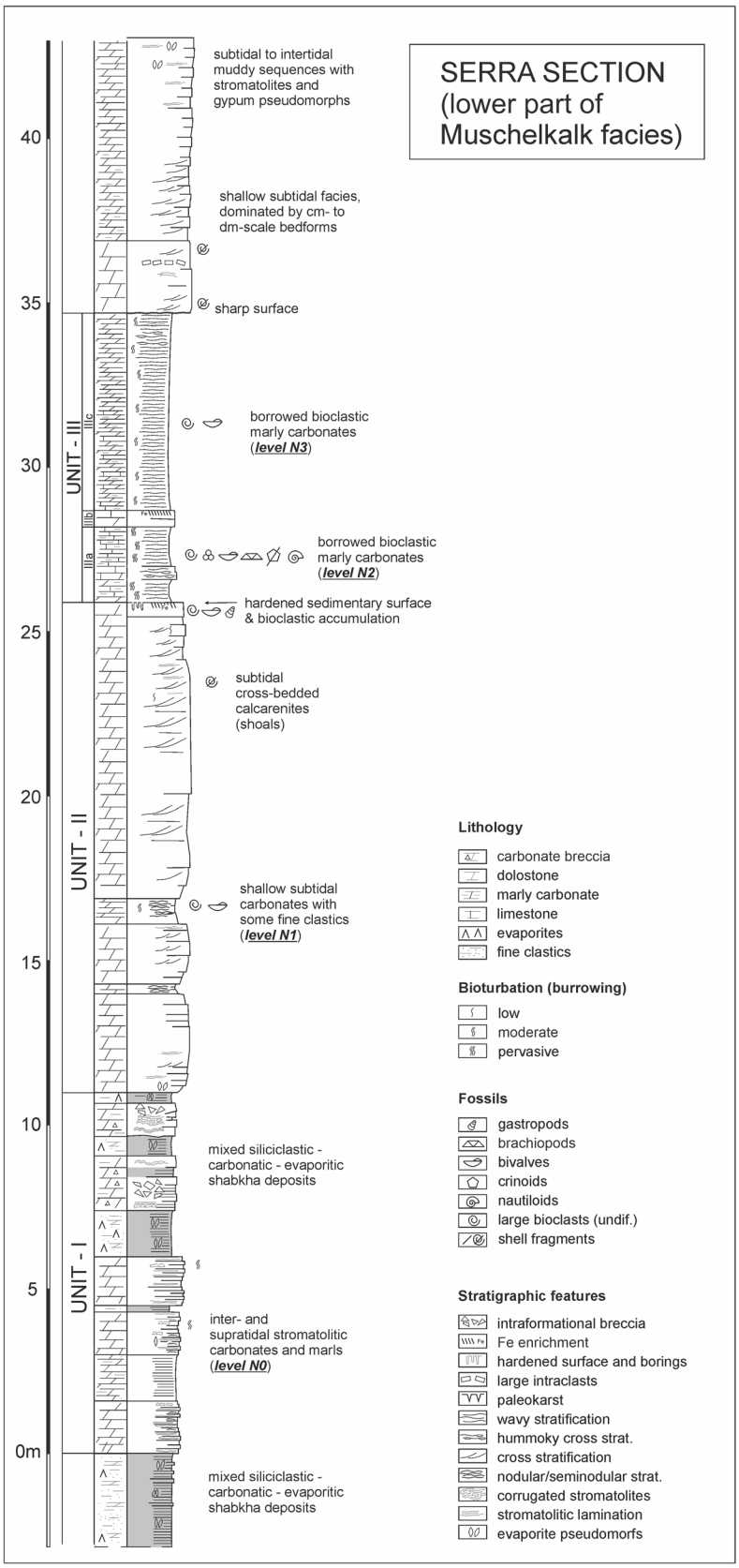


Fig. 2 Stratigraphic section for the lower Muschelkalk facies near Serra (Valencia). Fossiliferous levels N0, N1, N2 and N3 considered in this paper are indicated

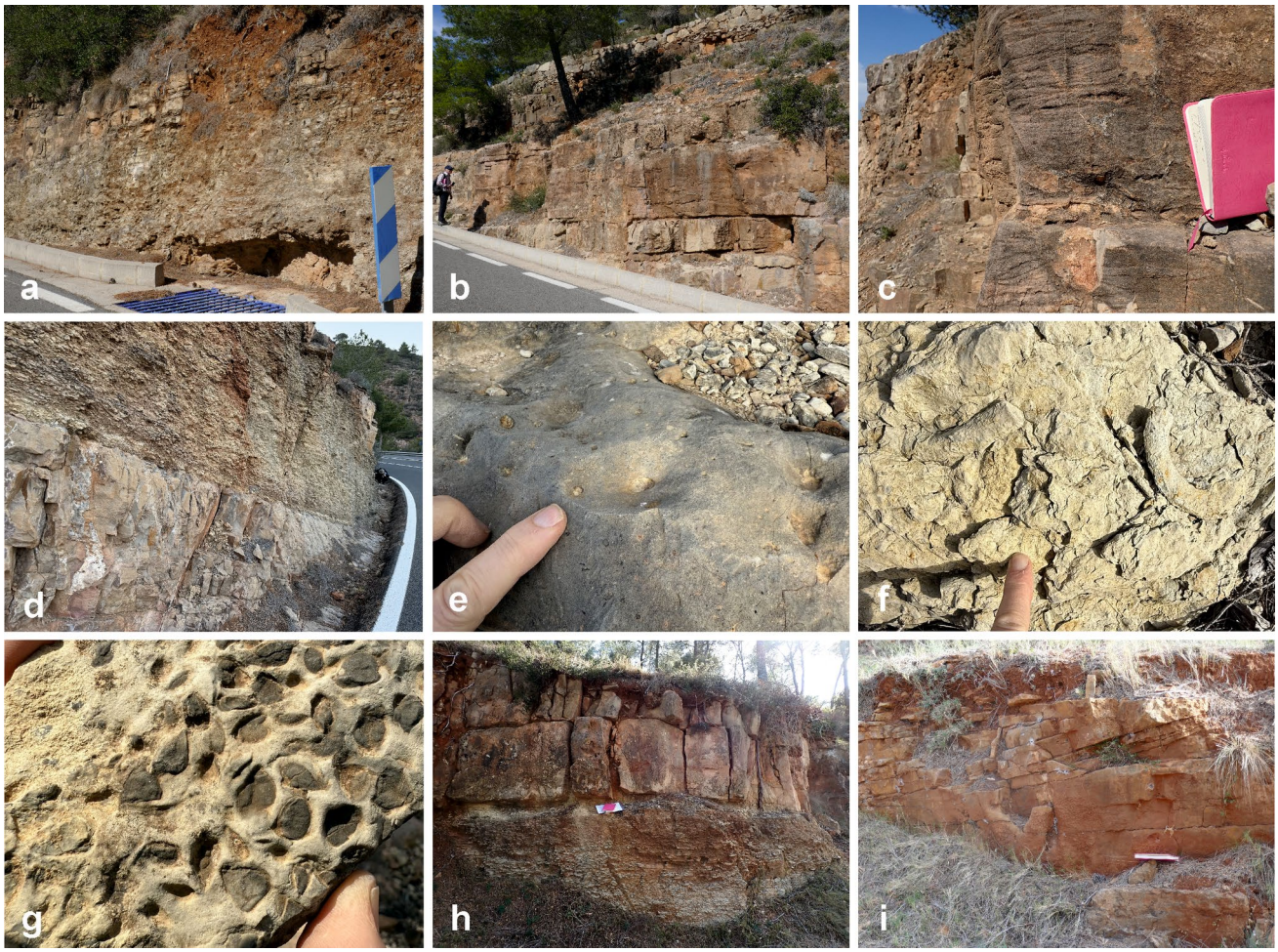


Fig. 3 Field photographs of stratigraphic units and facies in Serra section. **a** Contact between Unit-I and II, defined by a rapid increase in carbonate beds. **b** General view of Unit-II, dominated by dolomitic calcarenites. **c** Detail of Unit-II, showing cross bedded coarse grained dolostones. **d** Sharp contact separating Unit-II and Unit-III. **e** Detail of this contact, defined by a hardened sedimentary surface with abundant borings, developed at the top of a bioclastic bed, with gastropods and unfragmented valves of bivalves. **f** Borrowed facies of Unit-III. **g** Bivalve shell bed in Unit-III. **h** Sharp contact on Unit-III with the underlaying unit, whose lower beds consist of calcarenitic grainstones. **i**. Cross-bedded dolostones at the top of the section

This unit defines an initial transgressive pulse that involved the establishment of shallow marine conditions, dominated by high energy conditions. The depositional environment was shallow subtidal, in which the action of currents and waves determined the formation of medium-sized calcarenitic bedforms. The facies exhibit neither evident sequentially nor internal stacking patterns, suggesting a poorly structured subtidal system, an environment that fits well with an inner ramp setting dominated by high-energy conditions.

3.3 Unit-III (8.8 m)

It corresponds to "interval 2.4" of Márquez-Aliaga (1985) and to "Sagunt member" of Garay (2005a). The unit rests on the hardened surface at the top of Unit-II, and this sharp boundary defines an abrupt change in sedimentary facies (Fig. 3 d, e). The top of the unit is a neat surface that shows moderate erosion and marks a further sharp change in facies, as explained below.

This unit is formed by light beige, low competent dolomitic limestones and dolostones, with an original muddy texture being dominant. They show nodular or semi-nodular bedding, and their most characteristic feature is bioturbation (burrows) which is pervasive in some intervals (Fig. 3 f), mainly in the lower meters. In particular, horizontal *Thalassinoides*-type and *Planolites* burrow casts, can be found (see systematic description below). Much less bioturbated intervals can be also observed, these being characterized by thin laminated beds often showing wavy stratification, rippled beds and hummocky cross stratification. The unit yields abundant bivalve shells (Fig. 3 g) and, to a lesser extent,

other fauna remains including gastropods, nautiloids, and brachiopods. Occasionally, shell paved surfaces are found.

It should be noted that in the middle part of the interval, there is a 40 cm thick massive and compact bed of bioclastic dolostone, which displays ferruginization at its top. This bed (labelled as IIIb in Fig. 2), has conspicuous lateral continuity and allows to separate a lower subunit IIIa and an upper subunit IIIc, also within Unit-III. It should be noted that the lower unit shows more intense burrowing, whereas in the upper one the evidence of bottom reworking by waves is more evident. As described below, Subunit IIIa corresponds to fossiliferous level N2, which yielded the following bivalves: *Hoernesia socialis* (Schlotheim), *Neoschizodus orbicularis* (Bronn), *Myophoria vulgaris* (Schlotheim), *Neoschizodus laevigatus* (Goldfuss), and *Pleuromya elongata* (Schlotheim). Subunit IIIc, that correspond to fossiliferous level N3, also yielded all those taxa, and additionally *Burmesia posteroradiata* Cox, *Elegantinia* aff. *elegans* (Dunker), and *Unionites fassaensis* (Wissman).

The unit rests on the hardened surface that marks the top of the previous unit and records a substantial change in depositional conditions. The bottom agitation that had dominated the underlying unit gave way to a low-energy muddy sedimentation, with well-oxygenated bottoms, possibly located in more distal settings in the carbonate ramp system (middle ramp environments), in which infaunal species (*Myophoria*, *Neoschizodus*, and *Unionites*) and the endobyssate bivalve *Hoernesia* could live. All these bivalves were suspension feeders and shallow/deep burrowers. Those areas were deep enough to be uninfluenced by currents but occasionally affected by the action of storm waves.

The upper limit of Unit-III is outlined by a sharp stratigraphic surface showing evidence of moderate erosion (Fig. 3 h). It abruptly separates the former sedimentary facies of low-energy well-oxygenated seafloor, in middle ramp environments, from grainy dolostone facies, deposited in very shallow and agitated environments (inner ramp) (Fig. 3 i). These facies dominate the first meters of the overlaying unit, before changing into a thick succession of peritidal facies (> 40 m).

4 Paleontological remarks

A total of eight bivalve species and four ichnospecies were identified, taxonomically classified, and subjected to preliminary description (Table 1). All specimens are housed at the Museo de la Universitat de València de Historia Natural (MUVHN). The fossils herein analyzed were collected in the levels labelled N0 to N3 in the stratigraphic column of Fig. 2.

Bivalvia Linnnaeus, 1758
Order Trigonioida Dall, 1889
Superfamily Trigonioidea Lamarck, 1819
Family Myophoridae Bronn, 1849

Genus *Myophoria* Bronn in Alberti, 1834
Myophoria vulgaris (Schlotheim, 1822)
Figures 4a–c and 5g–i.

Specimens. More than 125 specimens (levels N1, N2, N3, these corresponding to stratigraphic Unit-II, and Unit-III, subunits IIIa and IIIc respectively, Fig. 2). MGUV 3795-001, MGUV 3897, MGUV 3952-001.

Description. Internal mold of a medium-sized, trigonal-shaped bivalve shell, posteriorly truncated. Equivalve and

Table 1 Specimen abundance of bivalve species and ichnospecies recorded in the Serra section

SERRA Anisian species		Unit/level/number of specimens				Total
		Unit I	Unit II	Unit III		
		N0	N1	N2	N3	
Bivalves	*Burmesia posteroradiata* Cox				1	1
	Elegantinia aff. *elegans* (Dunker)				2	2
	Hoernesia socialis (Schlotheim)		15	64	21	100
	Myophoria vulgaris (Schlotheim)		24	50	53	127
	Neoschizodus orbicularis (Bronn)			3	2	5
	Neoschizodus laevigatus (Goldfuss)			13	34	47
	Pleuromya elongata (Schlotheim)			6	4	10
	Unionites fassaensis (Wissman)				15	15
Ichnofossils	*Planolites* isp.			7	5	12
	Oravaichnium isp.			1		1
	Thalasinoides isp.				1	1
	Taenidium isp.	1				1

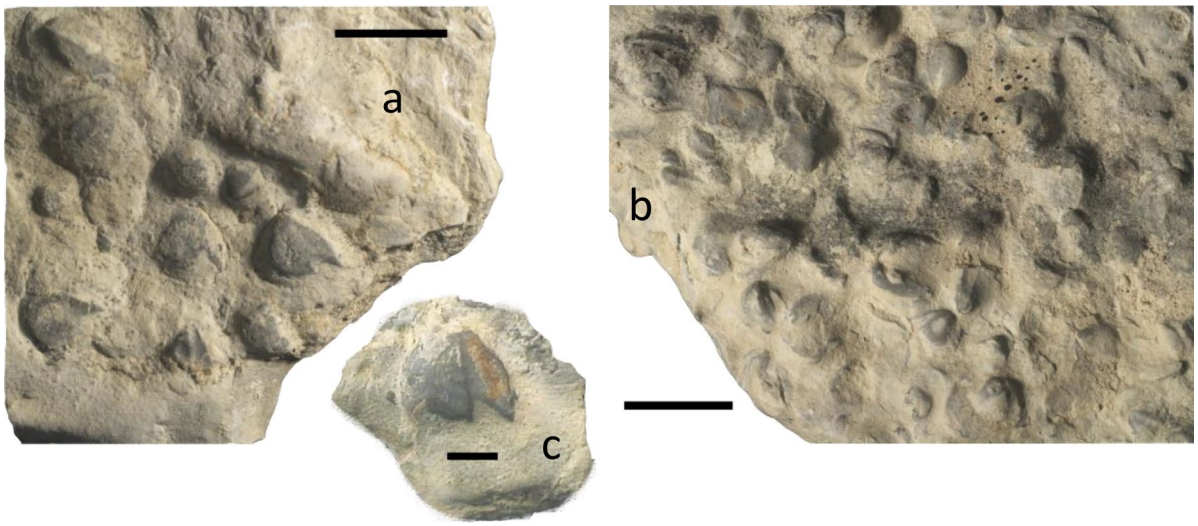


Fig. 4 **a, b** Upper surface of shell bed (N1) showing several internal cast of *Myophoria vulgaris* MGUV 3952-001 and *Hoernesia socialis* MGUV 3962-001. **c** Left valve internal cast of *Myophoria vulgaris* (N0) MGUV 3795-001. Scale bar = 5 mm. Photos by AM-A

moderately convex, but inequilateral. Beaks prosogyrous. The shell length is approximately equal to the shell height. Anterior margin tightly curved, ventral margin rounded. The right valve exhibits two prominent radial ribs. The posterior rib, located near the shell margin, extends from the umbo to the posterior extremity of the ventral margin. The anterior rib runs from the umbo to the central portion of the ventral margin. The marginal carina divides the shell into two distinct regions: a posterior dorsal area (corselet) and an anterior region. Fine commarginal ribbing is preserved on parts of the shell surface.

Taxonomic and biogeographic remarks. Márquez-Aliaga (1985) conducted a comprehensive study on *Myophoria* from the Iberian Peninsula and the Catalonian Coastal Range. The abundance of specimens recovered from the three stratigraphic levels (see Table 1) confirms the presence of *Myophoria vulgaris*, a cosmopolitan species known from the Middle Triassic. The examined material closely resembles specimens illustrated by Lerman (1960) from the Anisian of Ramon (Israel), and by Klug et al. (2005) from the Trochitenkalk Formation (Anisian, lower Upper Muschelkalk) in Neckarrems, Germany. *Myophoria vulgaris* is a characteristic Anisian bivalve of the Alpine Tethyan realm (Diener, 1923). Its stratigraphic range spans the entire Muschelkalk succession, from the Röt to the Keuper formations, within the Germanic Basin (Schmidt, 1928).

Genus *Elegantinia* Waagen, 1906
Elegantinia aff. *elegans* (Dunker, 1849)
Figure 5j–l

Specimens. 2 specimens (level N3, stratigraphic subunit IIIc, Fig. 2). MGUV 3943, MGUV 9944.

Description. Shell medium sized, slightly longer than high, subtrigonal, inequilateral, and moderately inflated. The anterior and ventral margins are broadly rounded, while the posterior margin is distinctly truncated. Umbo prominent, orthogyrous and positioned anteriorly, beak not visible. A prominent marginal carina extends from the umbo to the postero-ventral margin. The surface of the right valve displays three radial ribs and a distinct groove in the corselet area. Several well-developed commarginal ribs are observed in the anterior region. The material comprises two specimens, one internal mold and one incomplete external mold. The former is particularly well preserved, retaining the original shell material, with both valves slightly gaping; the left valve is largely intact. This specimen was recovered from one of the limestone nodules frequently found at the second stratigraphic level, along with the corresponding external cast of the better-preserved valve.

Taxonomic and biogeographic remarks. The morphological features of the specimen are consistent with those of *Elegantinia elegans*. However, due to the limited number of specimens (only one confidently assignable individual), a definitive taxonomic assignment cannot be made. Moreover, the notable morphological variability reported for *Elegantinia elegans* in various publications (e.g., Márquez-Aliaga, 1985) further complicates precise identification. *E. elegans* is widely distributed in the Muschelkalk deposits of the Germanic Basin and has also been reported from Anisian strata in Romania and China (Friesenbichler et al., 2021). Its stratigraphic range extends from the base of the Olenekian to the top of the Ladinian.

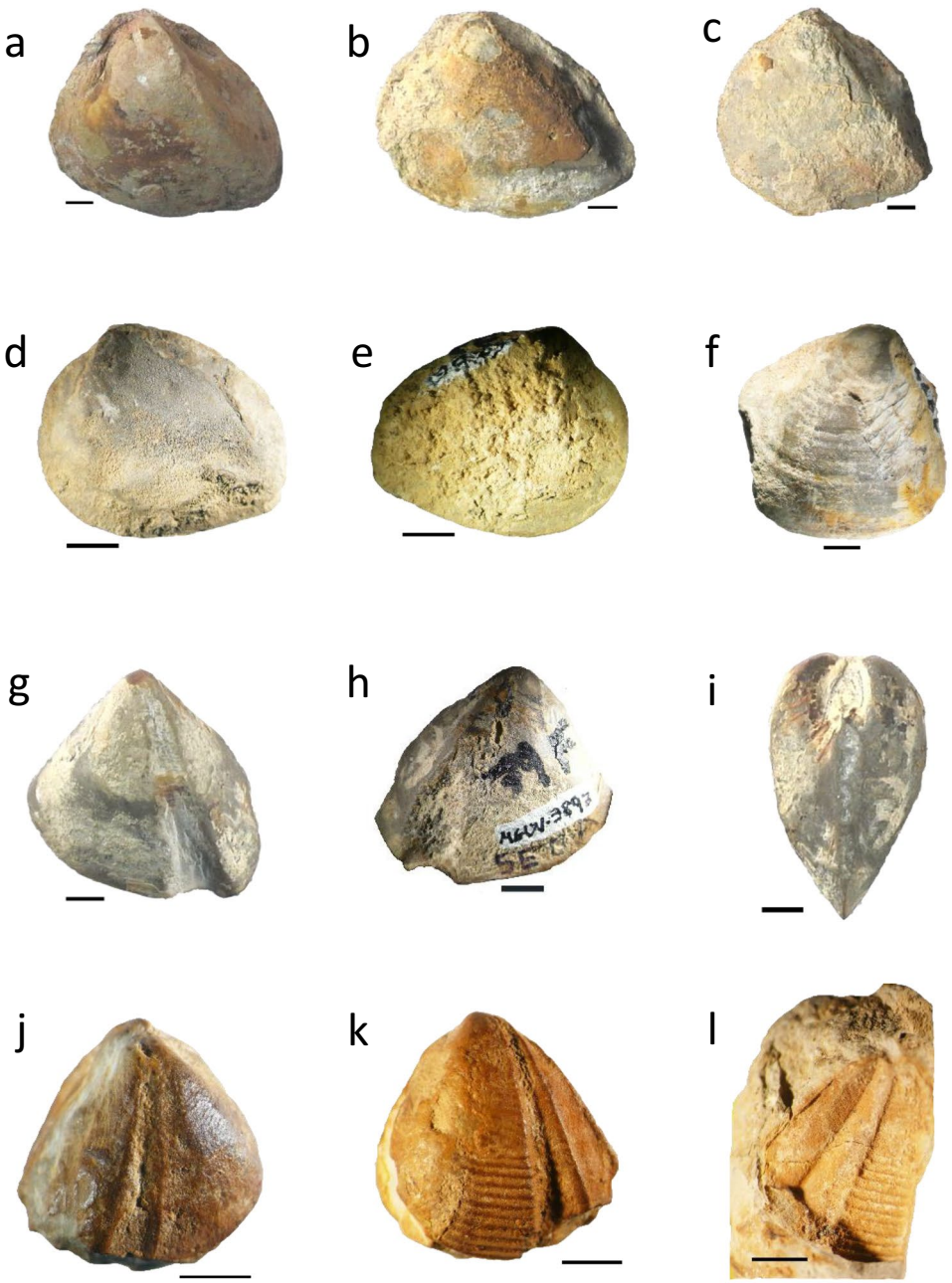


Fig. 5 **a, c** Right valve internal cast of *Neoschizodus laevigatus* (N3) MGUV 3900 and MGUV 3931. **b** Left valve internal cast of *Neoschizodus laevigatus* (N2) MGUV 3930; **d** Left valve internal cast of *Neoschizodus orbicularis* (N2) MGUV 3975. **e** Right valve internal cast of *Neoschizodus orbicularis* (N3) MGUV 3897. **f** Right valve internal cast of *Neoschizodus orbicularis* MGUV 3974. **g** Left valve internal cast of *Myophoria vulgaris* (N2) MGUV 3897. **h** Right view of the same specimen and **i** dorsal view same specimen. **j** Internal cast right valve and **k** left valve with preserved shell sowing radial and commarginal ornamentation of *Elegantinia* aff. *elegans* (N3) MGUV 3943. **l** Left valve external cast of *Elegantinia* aff. *elegans* (N3), MGUV 9944. Scale bar = 5 mm. Photos by AM-A

Genus *Neoschizodus* Giebel, 1855
Neoschizodus laevigatus (Goldfuss in Zieten, 1830)
Figure 5a–c

Specimens. About fifty specimens (levels N2 and N3, these corresponding to stratigraphic Unit-III subunits IIIa and IIIc respectively, Fig. 2). MGUV 3900, MGUV 3930, MGUV 3931.

Description. Specimen medium to large in size, subtrigonal in outline. Equivalve, inequilateral, and moderately convex. The shell length slightly exceeds the umbo-pallial diameter. The anterior margin is rounded with tight curvature, while the ventral margin exhibits a broad, continuous curvature extending toward the posterior region. The posterior margin is truncated and straight, lacking an escutcheon. The umbo is well developed, orthogyrous, and situated in an anterior position. The anterior adductor muscle scar is small and elliptical. The anterior region of the shell surface is convex, sharply interrupted by a straight, pronounced, and very acute ridge, which runs obliquely toward the ventral margin, forming a relatively sharp angle at the intersection. The marginal carina transitions into a broader posterior area. Shell fragments lack distinct ornamentation but exhibit fine growth lines with filamentous

appearance, irregularly spaced. All studied specimens (over 50) are internal molds of closed shells, showing variable sizes. In some examples, only a single valve is visible. Specimens are present throughout all stratigraphic levels of Unit III, with the best-preserved and largest examples occurring in level N3.

Taxonomic and biogeographic remarks. This species is highly abundant in both the Germanic and Alpine Triassic successions and is closely related to several morphologically similar taxa, some of which have been regarded as synonyms by Márquez-Aliaga (1985). The material studied here closely resembles specimens figured by Klug et al. (2005) from the Trochitenkalk Formation (Anisian) at Neidenfels, Germany. Cox (1924) documented numerous comparable specimens from the Wadi Hesban locality in the Jordan Valley (northeastern edge of the Dead Sea), within an Anisian Muschelkalk assemblage. The species is also common in the lower Ladinian strata of Ramon (Israel), as reported by Lerman (1960). Overall, it is a widespread and abundant species throughout the Middle Triassic (Schmidt, 1928).

Neoschizodus orbicularis Brownn, 1837
Figure 5d–f

Specimens. Five specimens (levels N2 and N3, corresponding to stratigraphic subunits IIIa and IIIc respectively, Fig. 2). MGUV 3897, MGUV 3974, MGUV 3975.

Description. Internal molds of bivalve shells with elliptical to subcircular outlines, with a maximum length of approximately 15 mm. Inequivalve and variably inequilateral. Umbones are slightly prosogyrous. The posterior adductor muscle scar is centrally located but poorly defined. No radial ornamentation is present. Both valves display a characteristically smooth surface; in some areas where the original shell is preserved, fine growth lines are visible.

Taxonomic and biogeographic remarks. The specimens examined closely resemble those illustrated by Wurm (1911, pl. VI, fig. 5) from the lower Muschelkalk facies of Aragón (Saviñán, Zaragoza), as well as those figured by Schmidt (1928, figs. 43, 435), Lerman (1960, pl. 1, figs. 14–15), and Klug et al. (2005) from the Lower Muschelkalk of Nussloch (Germany). This taxon is characteristic of the Anisian stage and is widely distributed throughout the Tethyan realm.

Order Pholadomyoida Newell, 1965
Superfamily Pholadomyoidea King, 1844
Family Burmesiidae Healey, 1908

Genus *Burmesia* Healey, 1908
Burmesia posteroradiata Cox, 1924
Figure 6g, h.

Specimens. One specimen (Level N3, Subunit IIIc, Fig. 2). MGUV 3976.

Description. Body fossil medium-size bivalve shell, equivalve, with moderate convexity and inaequilateral. Elongate-ovate in outline. Hinge line elongate, rounded anteriorly. The umbo is situated slightly anterior to the midline and rises above the posterior portion of the hinge margin. The shell surface can be divided into two distinct regions by an imaginary line extending ventrally and anteriorly from the umbo. The anterior region is ornamented with prominent concentric undulations (commarginal ornamentation), while the posterior region displays more than ten radial ribs, extending toward the posterior hinge margin. These ribs are most densely packed in the central portion of the shell.

Taxonomic and biogeographic remarks. Cox (1924) originally described the species *posteroradiata*, tentatively assigning it to the genus *Burmesia*, though he also noted its morphological affinity with the genus *Pholadomya*, based on material from Wadi Ayun Musa, located in the northeastern sector of the Dead Sea. The species is considered rare, and no additional references to it have been found in the subsequent literature. The current specimen, being the only individual recovered from a well-studied stratigraphic section, further supports the rarity and potential significance of this taxon. Cox (1924) assigned a Carnian age to *Burmesia posteroradiata* from Wadi Ayun Musa. However, more recent studies (Márquez-Aliaga & Hirsch, 1988) place the age of the Triassic marine limestones of the Jordan Valley within the Olenekian to Anisian interval.

Family Pleuromydae Dall, 1900
Genus *Pleuromya* Agassiz, 1842
Pleuromya elongata (Schlotheim, 1822)

Figures 6d–f and 7c, e.

Specimens. Ten specimens (levels N2, N3, Subunits IIIa and IIIc of Unit-III, Fig. 2). MGUV 3983, MGUV 3984, MGUV 16890.

Description. Internal mold of a small-sized bivalve shell. The valves are equivalve and exhibit moderate convexity, which is most pronounced beneath the umbo. Outline elongate-elliptical. The shell height represents approximately 30% of the shell length. The shell is markedly inequilateral. The anterior margin is broadly rounded and transitions smoothly into the slightly curved ventral margin, which exhibits a subtle indentation beneath the umbo. The posterior margin is short, sub-rectilinear, and oriented obliquely—almost orthogonally—with respect to the ventral margin. The anterior dorsal margin is very short and oblique, while the posterior dorsal margin is elongated and curved, featuring a shallow depression beginning immediately behind the umbo and forming a broad posterior projection.

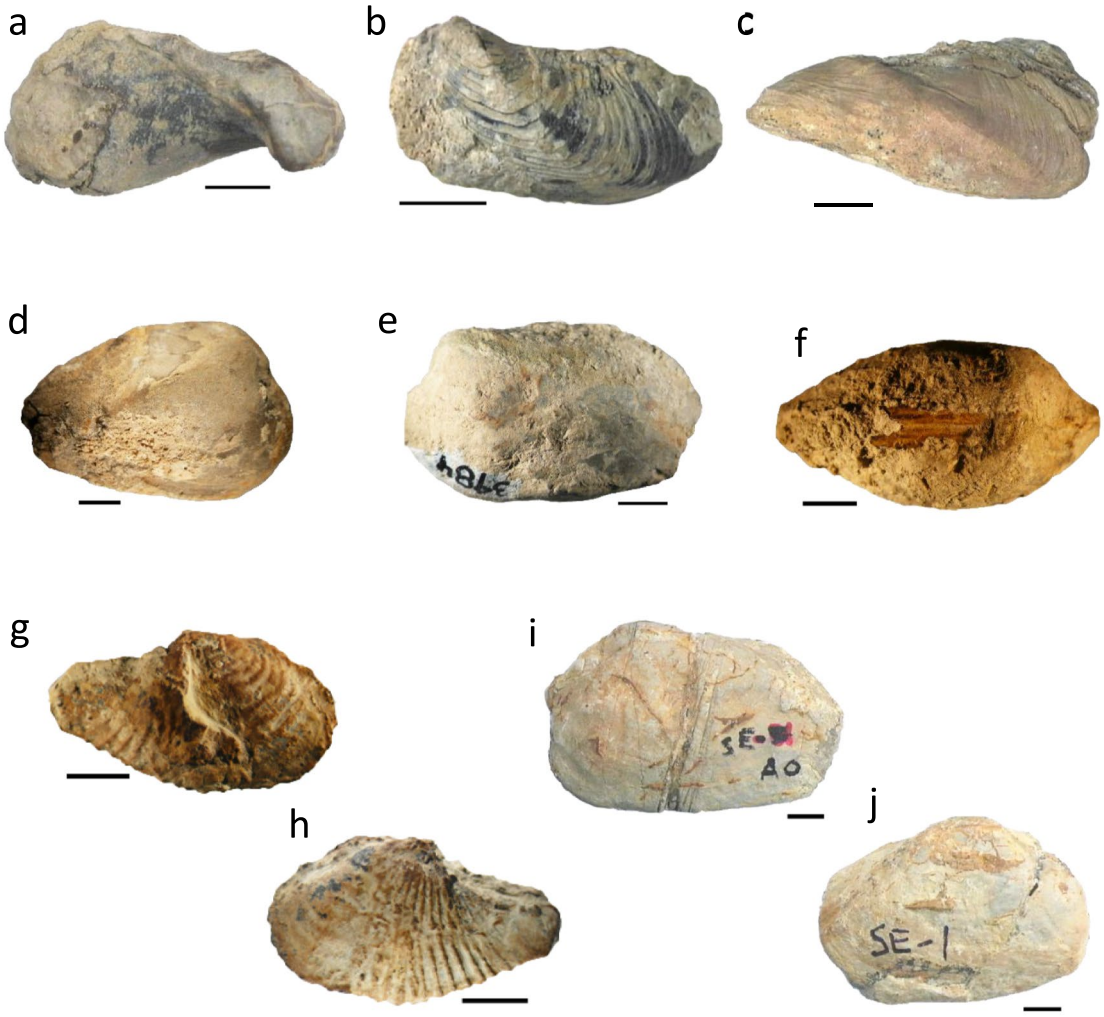


Fig. 6 **a** Right valve internal cast with part of the preserved shell of *Hoernesia socialis* (N2) MGUV 3287. **b** Body fossil left valve, note the preserved shell growing line of *Hoernesia socialis* (N2) MGUV 3289. **c** Body fossil left valve with the preserved shell of *Hoernesia socialis* (N3) MGUV 3286. **d** Right valve internal cast of *Pleuromya elongata* (N2) MGUV 3983. **e** and **f** Left valve internal cast and dorsal view of *Pleuromya elongata* (N3) MGUV 3984. **g**, **h** Body fossil right and left valves view showing the radial and commarginal ornamentation of *Burmesia posteroradiata* (N3) MGUV 3976. **i** Left valve internal cast of *Unionites fassaensis* (N3) MGUV 3904. **j** Right valve internal cast of *Unionites fassaensis* (N3) MGUV 3906. Scale bar = 5 mm. Photos by AM-A

Umbo in anterior position, broad, rounded and with the apex recurved toward the dorsal margin. The valve surface exhibits a shallow radial depression, irregular in pattern and not deeply incised, extending from the umbo to the ventral margin. No distinct ornamentation is preserved; however, numerous growth lines of varying thickness and irregular arrangement are present.

Taxonomic and biogeographic remarks. The earliest reference to this form appears in Wurm (1911), who described several species of *Pleuromya* —then assigned to *Myacites*— from the lower Muschelkalk facies of Boquete de Tranquera and Royuela (Zaragoza and Teruel, Iberian Range) (p. 118, pl. VI, figs. 24, 27, 28). In the Catalan Coastal Range, Llopis and Villalta (1935) reported several species and varieties of *Pleuromya* from the 'Trochitenkalk' levels at Aiguafreda (Barcelona), considering these fossils as evidence that the Muschelkalk deposits of Catalonia correspond to the Germanic Facies. Later, Virgili (1958) described and illustrated additional *Pleuromya* specimens from the Aiguafreda, Farell, and Centelles sections (Barcelona), within the lower Muschelkalk facies (MI sensu Virgili, *op. cit*.) (p. 487, pl. 10, figs. 1, 3, 4).

Order Pterioida Newell, 1965
Superfamily Pterioidea Gray, 1847
Family Bakevellidae King, 1850

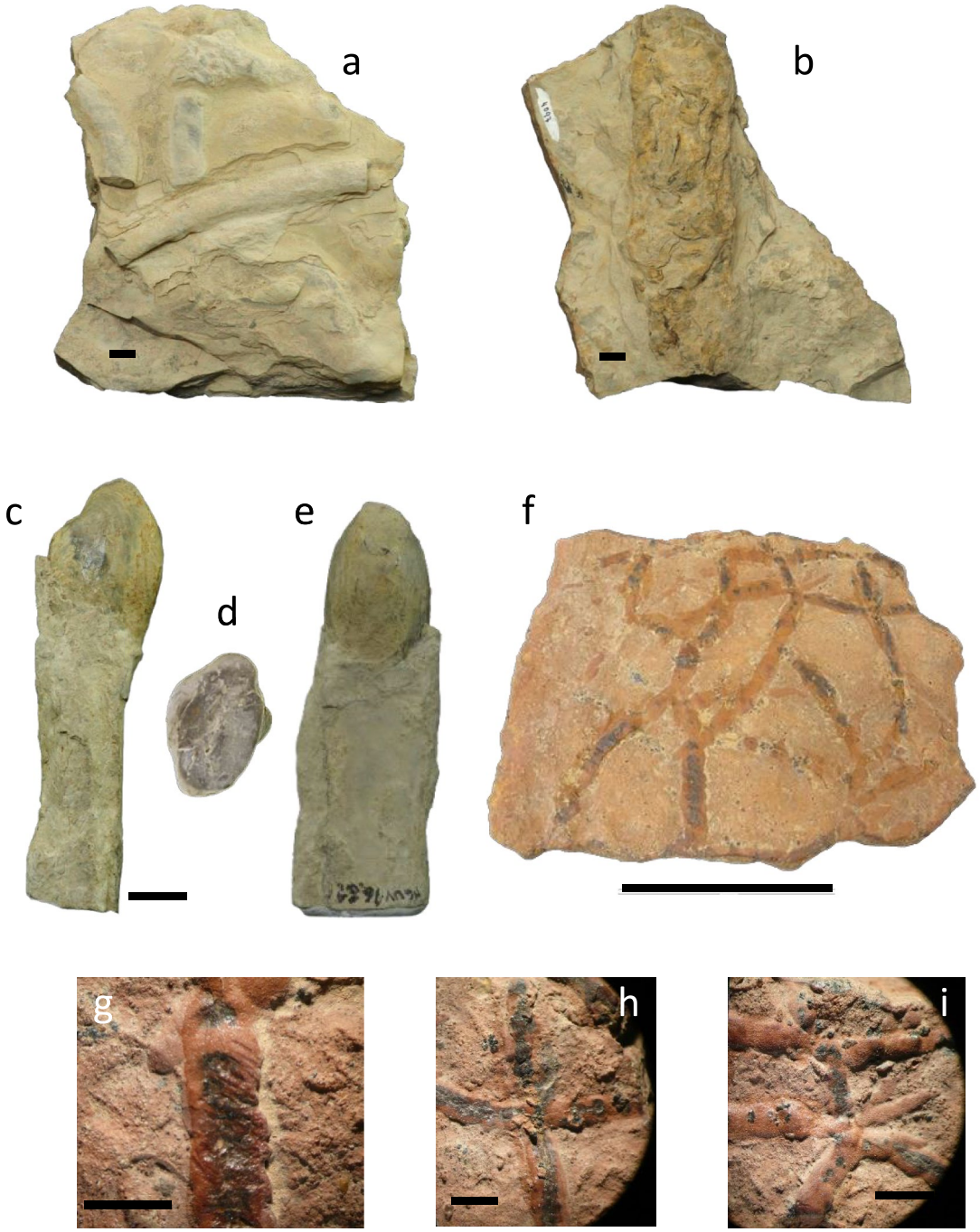


Fig. 7 **a** *Planolites* isp. preserved as full relief (MGUV 3666), several specimens tubular shaped and oriented parallel to the bedding plane. **b** Fragment of *Thalassinoides* isp. MGUV 4097. **c, e** *Oravaichnium* with *Pleuromya* MGUV 16890, **d** subquadrate cross-section of *Oravaichnium*. **f** *Taenidium* isp. preserved as full relief (MGUV 3660). **g–i** Details of the meniscate backfill of *Taenidium* isp. Scale bars = 10 mm (**a–e**), 5 cm (**f**), 5 mm (**g–i**)

Genus *Hoernesia* Laube, 1866
Hoernesia socialis (Schlotheim, 1823)
Figure 6a–c.

Specimens. About one hundred specimens (levels N1, N2 and N3, Unit-II and subunits IIIa and IIIc of Unit-III, Fig. 2). MGUV 3962-001, MGUV 3286, MGUV 3287, MGUV 3289.

Description. Medium-sized bivalve shell, trapezoidal-elongated, slightly oblique and inequilateral. Extremely inequivalve. Left valve strongly convex, with a broad and prominently projecting umbonal region, while right valve

slightly convex to nearly concave. In some specimens, the shell edges do not lie in the same plane due to the torsion of the valves. The beak is positioned anteriorly. The posterior wing is not clearly differentiated from the rest of the valve; the angle between the dorsal margin and the umbo-pallial diameter is approximately 30 degrees. The ventral margin is gently curved, and the posterior margin shows a closed, rounded curvature. A smooth, blunt keel extends along the left valve from the umbo to the posterior extremity. The shell surface is devoid of radial ornamentation, though both valves exhibit numerous irregularly spaced growth lines.

Shell microstructure and preservation. Optical and electron microscopy studies conducted by De Renzi and Márquez-Aliaga (1980) and further detailed by Márquez-Aliaga (1985) indicate that the shell of *Hoernesia* was originally bimineralic, consisting of an outer calcitic layer with a typical prismatic microstructure, and an inner aragonitic layer. Both layers have undergone diagenetic replacement, primarily by dolomite. The preserved calcitic prisms are oriented orthogonally to the shell surface and display visible growth increments. The original aragonitic inner layer is no longer present, having been replaced at an early diagenetic stage by sparry calcite cement.

Taxonomic and biogeographic remarks. In the Iberian Peninsula, *Hoernesia* has been reported from the Ladinian strata of Mallorca, particularly in the Canet section (Esporlas), within the so-called "Virglorian Muschelkalk" (Anisian), which is characterized by the presence of abundant *Planolites* and occurs below limestone beds bearing *Daonella lommeli* (Darder, 1914). Hinkelbein (1969) recorded *H.* cf. *socialis* from Barranco Cazulla near Royuela (Teruel), as well as *Hoernesia* sp. from Arcos de las Salinas (Teruel), though he expressed uncertainty about the genus presence in the Middle Triassic of the Iberian Range. Vía-Boada et al. (1977) illustrated a specimen as *Hoernesia socialis* (pl. 2, fig. 6) from the Longobardian of Mont-ral (Tarragona); however, this specimen is more appropriately assigned to *Bakevellia costata*. Outside the Iberian Peninsula, *Hoernesia* is frequently recorded from the Ladinian of Sardinia (Italy) (Posenato, 2002; Stori et al., 2024), as well as in the Anisian of Recoaro (Italy) (Mostler, 1976), Upper Silesia (Poland) (Kaim, 1997), Niesen (Germany) (McGowan & Smith, 2006), and the Anisian succession of the Mecsek Mountains in Hungary (Foster & Sebe, 2017). Overall, *Hoernesia socialis* exhibits a broad stratigraphic and geographic range throughout the Middle Triassic (Schmidt, 1928).

Order Unioida Stoliczka, 1871
Superfamily Anthracosioidea Amalizky, 1892
Family Anthracosiidae Amalizky, 1892

Genus *Unionites* Wissmann, 1841
Unionites fassaensis (Wissmann, 1841)
Figure 6i, j

Specimens. Fifteen specimens (levels N2 and N3, respectively belonging to subunits IIIa and IIIc of Unit-III, Fig. 2). MGUV 3904, MGUV 3906.

Description. Internal and composite molds of a small-sized bivalve shell. Equivalve, subelliptical in outline, with prosogyrous umbones projecting prominently above the dorsal margin. Beaks positioned approximately at the anterior 40% or less of the dorsal margin. Posterodorsal margin is nearly straight, while the anterior margin is smoothly rounded. Due to preservation limitations, internal features and shell sculpture are not discernible.

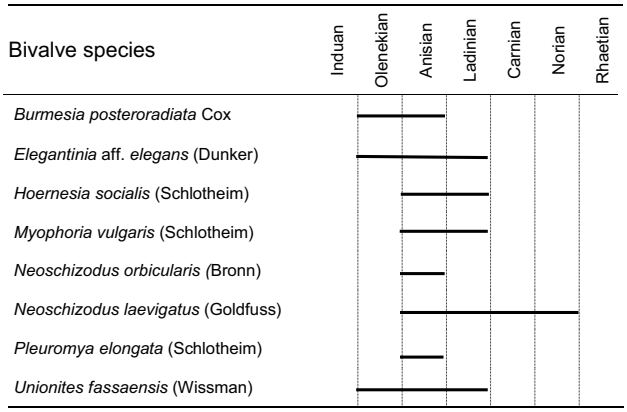
Taxonomic and biogeographic remarks. Most records of Early and Middle Triassic *Unionites* are based primarily on external shell morphology, which provides limited diagnostic value for confident genus-level identification. *Unionites fassaensis* is among the most frequently reported bivalve species from this interval. Its broad geographical distribution and apparent abundance may, at least in part, is attributed to its imprecise taxonomic characterization (Hofmann et al., 2014). In the Middle East, *Anodontophora fassaensis* was cited by Lerman (1960) from the Anisian strata of the Ramon section in southern Israel and Sinai. He further noted that in Germany, the stratigraphic range of this species extends from the Röth to the Lettenkohle formations, corresponding to the Spathian through late Ladinian, with a concentration in the Middle Triassic.

The summary diagram (Table 2) illustrates the stratigraphic age range associated with the Serra bivalve assemblage. It also supports the Anisian age attribution of the Muschelkalk deposits from the study area.

Ichnofossils

Following the end-Permian extinction, biodiversity experienced a substantial decline, with the marine infaunal

Table 2 Stratigraphic range of the identified bivalve species in western Tethys realm



domain particularly affected. This led to a notable reduction in both the abundance and diversity of ichnofossils (e.g., Twitchett, 1999). Compared to other time intervals, the Middle Triassic ichnofauna remains relatively understudied (Knaust, 2007), and it is especially poorly documented in the eastern Iberian Peninsula (but see Baeza-Carratalá et al., 2024). In contrast, the Anisian ichnofauna has been more thoroughly investigated in other regions, such as the Germanic Basin (e.g., Knaust, 1998, 2007; Stachacz & Matysik, 2020; Stachacz et al., 2022), southern Poland (Jaglarz & Uchman, 2010), or southwestern China (Feng et al., 2017).

Ichnogenus *Planolites* Nicholson, 1873
Planolites isp.
Figure 7a

Specimens. Multiple specimens were observed in the field, with twelve collected from levels N2 and N3, corresponding respectively to subunits IIIa and IIIc of Unit-III (Fig. 2). MGUV 3666.

Description. These trace fossils are characterized as unbranched, cylindrical burrows, varying from straight to slightly curved in morphology. They exhibit no internal structure and are typically oriented parallel or slightly oblique to the bedding plane. The burrow infill is massive and texturally distinct from the surrounding matrix. Burrow diameters range from 7 to 15 mm, with the maximum recorded length reaching up to 90 mm. The traces are preserved in full relief, and overlapping of individual burrows is frequently observed in outcrop.

Ichnological interpretation. These features are attributed to *Planolites*, a simple and morphologically non-diagnostic trace fossil known to be produced by a broad range of infaunal organisms. Potential tracemakers include vermiform animals such as annelids, hemichordates, and priapulids, in addition to various arthropods and mollusks. *Planolites* is interpreted as a feeding trace (fodinichnion), resulting from the activity of deposit feeders that actively backfilled their burrows while foraging within unconsolidated sediments (Fillion & Pickerill, 1990; Pemberton & Frey, 1982). This ichnotaxon is known to occur across a wide variety of depositional settings and ichnofacies, highlighting its ecological generalism and the functional simplicity of its production.

Ichnogenus *Oravaichnium* Plička & Uhrová, 1990
Oravaichnium isp.
Figure 7c–e

Specimens. A single specimen was recovered (level N2, Unit-III). MGUV 16890. https://sketchfab.com/3d-models/siphonichnus-isp-d0cb26d37d52436182eea3df1daeff34.

Description. Straight, unbranched burrow with a subquadrate cross-section, homogeneous fill, and smooth margins. Maximum cross-section is 17 mm and minimum 12 mm wide, and 23 mm high. The bivalve *Pleuromya* is located on the burrow top.

Ichnological Interpretation. The trace fossils described herein clearly falls within the category of animal behavior that Seilacher (2007) defined as mortichnia or taphoglyphs (term most commonly used for vertebrates; Sarjeant, 1975). An unsuccessful escape attempt, leaving the clam's shell at the top of the trace, can be interpreted simultaneously as both a mortichnion and a fugichnion (Pokorný et al., 2024).

Oravaichnium was initially described from Eocene beds of the Carpathian Mountains (Plička & Uhrová, 1990), but later reported from Muschelkalk (Anisian) beds of Poland and Germany (Stachacz et al., 2022) and Spain (Baeza-Carratalá et al., 2024), and is attributed to the activity of bivalves.

Ichnogenus *Taenidium* Heer, 1877
Taenidium isp.
Figure 7f–i

Specimens. A single specimen was recovered (level N0, Unit-I). MGUV 3660.

Description. The trace fossil consists of cylindrical burrows that range from straight to sinuous in morphology, unlined, and exhibiting successive secondary branching. Cross-sections are circular to ellipsoidal, and the overall orientation of the burrows is subparallel to the bedding plane. The burrow fill is compositionally distinct from the host rock and characterized by meniscate structures that are well-defined, densely packed, and heterogeneous in appearance. Burrow widths vary between 3 and 9 mm, with a maximum observed length of 95 mm. The traces are preserved in full relief on the upper bedding surfaces, and overlapping among individual burrows is uncommon. The studied specimen reveals evidence of active backfilling with microcoprolites, supporting its attribution to *Taenidium* isp.

Ichnological Interpretation. The meniscate backfill structures of *Taenidium* are generally interpreted as the product of sediment ingestion, compaction, and posterior excretion by deposit-feeding organisms (Fürsich, 1974), classifying this ichnotaxon as a feeding trace (fodinichnion). Alternative interpretations suggest that sediment may have been displaced around the organism during locomotion, with little or no ingestion (Bradshaw, 1981; Bromley & Asgaard, 1975). A hybrid mechanism involving both physical displacement and biological processing has also been proposed (Bromley & Asgaard, 1975), reflecting a complex interplay between behavioral and sedimentary processes during trace formation. *Taenidium* is a widely distributed ichnogenus typically associated with continental to marginal marine environments

influenced by episodic flooding and subaerial exposure. Such settings are characteristic of the *Scoyenia ichnofacies*. The tracemakers are inferred to be deposit-feeding organisms, most likely annelids or crustaceans (Ros-Franch et al., 2021).

Ichnogenus *Thalassinoides* Ehrenberg, 1944
Thlassinoides isp.
Figure 7b

Specimens. A single specimen was collected (level N3, subunit IIIc, Fig. 2). MGUV 4097.

Description. Due to its incomplete preservation, this fragmentary trace lacks diagnostic features such as horizontal branching and bifurcation that would allow a more confident ichnotaxonomic assignment. Nonetheless, it represents a horizontal trace fossil, with notable accumulations of bioclasts (shell fragments) at its basal surface. The specimen consists of a solitary, cylindrical, straight burrow fragment with unlined walls and passive fill. The burrow measures approximately 13 cm in preserved length, with a diameter of 6 cm. The infill is lithologically distinct from the surrounding host sediment.

Ichnological interpretation. This structure is interpreted as a dwelling trace (domichnion), potentially produced by deposit- or suspension-feeding organisms, most likely decapod crustaceans such as thalassinidean shrimp and frequently found in shallow water environments (Myrrow, 1995). In certain contexts, similar burrow morphologies may also reflect feeding behavior (fodinichnia) or locomotion (pascichnia), depending on the overall architecture and ichnological context. Although incomplete, the morphology and paleoenvironmental setting are consistent with the ichnogenus *Thalassinoides*.

5 Discussion

The bivalve assemblage is stratigraphically located at the lower levels of the Muschelkalk facies succession of the Serra section. That interval records the first marine transgression in Iberia within the framework of the Alpine cycle, and its study allow for progress in the knowledge of the paleogeographic, tectonic and biogeographic patterns that defined the sedimentary basins during the Middle Triassic.

5.1 Paleogeography and tectonic context

During Middle Triassic times, Pangea experienced definitive changes in the frame of its disintegration, leading to the creation of large marine corridors that would end up in the separation of the mega-continent into smaller ones already throughout the Jurassic. These episodes were marked by the closure of the Paleo-Tethys and the rapid development of the Neo-Tethys due to the northward movement of Cimmeria and the paleogeographic consequences linked to this displacement. The underlying causes of Pangea instability started just after the mega-continent final consolidation at the early stages of the Permian, and are related to a change in the polarity of drag forces that were exerted by asthenosphere convection on the overlying lithosphere (Ziegler, 1990). Therefore, different rift systems were developed or reactivated with important refill of continental sediments during the Early Triassic (McCann et al., 2006). It was accompanied by short-lived build-up of regional tensional stresses that gave rise to wrench deformations along fault systems that resulted in important regional erosive surfaces and unconformities, in continental basins (Borruel-Abadía et al., 2015; Bourquin et al., 2011; Ziegler, 1988). During the early Middle Triassic, the western Tethys domain was furrowed by the southward development of these long tectonic lineaments by means of rift branches that crossed Central and Western Europe, an activity that was accompanied by the northward drift of the Gondwana-derived Cimmerian continent (McCann et al., 2006; Sengör, 1984). These lineaments were running parallel to the contemporaneous Lagonegro trough, that formed the western margin of the Italo-Dinarid (Apulia) block (Wood, 2005) until reaching the Morocco Massif (Ziegler, 1990).

During the early Anisian, the activity of these systems provoked hundreds of meters of subsidence in continental western peri-Tethys basins, as eastern Iberia, and Majorca, Minorca and Sardinia islands (Arche & López-Gómez, 1996; Cassinis et al., 2003; Vargas et al., 2009) and the first marine connections in these basins during the late Anisian (Escudero-Mozo et al., 2015; Stori et al., 2022, 2024). These conditions also provoked increased water runoff and fertilization in shallow marine areas that resulted in an increase of biodiversity (Foster & Sebe, 2017; Posenato, 2019). As result, both lineaments and fertilization favored the development of corridors and westward migration of marine fauna in the Tethys. This migration reached NE Iberia for the first time in the late Anisian (Escudero-Mozo, 2015; Escudero-Mozo et al., 2015) where shallow marine deposits were accumulated by the first time since Carboniferous times, conclusions which are consistent with those reached in this paper.

5.2 Comparative regional studies on bivalve fauna

In the Catalonian Coastal Ranges, Llopis and Villalta (1935) described *Myophoria vulgaris* (Schlotheim), *M. intermedia* Schauroth, *Pleuromya elongata* (Schlotheim), and other bivalves from Aiguafreda, near Montseny. They noted that this assemblage represents a shallow-marine fauna identical

to that of northern Germany in the lower Muschelkalk, preserved within Germanic facies deposits. Subsequently, Virgili (1958) reported similar Anisian bivalve assemblages from Aiguafreda, Figaró, El Farell, and Olesa. More recently, a synthesis of the Triassic of eastern Iberia by Escudero-Mozo et al. (2015) reaffirmed these Anisian associations and provided updated insights into their paleogeographic context.

Recently, Anisian deposits have been described in the external zones of the Betic Range (Pérez-Valera et al., 2023). These deposits, originating from the Atalayas section (Murcia, Spain), contain an abundant bivalve assemblage, including *Myophoria vulgaris* (Schlotheim), *Neoschizodus orbicularis* (Bronn), *Neoschizodus laevigatus* (Goldfuss), *Unionites* sp. aff. *fassaensis* (Wissmann), and *Pleuromya* aff. *elongata* (Schlotheim), among others. This association exhibits notable similarities to the Serra association described in this study.

5.3 Alpine and Germanic Middle Triassic bivalve faunas

Cox (1924), in his study of Mediterranean Triassic geology, documented several bivalves from sections of the Jordan Valley, near the Dead Sea. He described various fossil associations and illustrated several specimens. Based on his descriptions, we have identified species that are also present in our studied section. *Reubenia hesbanensis* Cox, 1924 (pl. I, fig. 6a, b, c) is now regarded to belong to *Hoernesia socialis* (Schlotheim), while *Myophoria transversa* (Bornemann) (Cox, 1924, pl. II, fig. 11) is identified as *M. vulgaris* Schlotheim. Additionally, Cox described the new species *Burmesia? posteroradiata*, which we recognize as a valid species also present in our materials. These species, along with *Coenothyris vulgaris* (Schlotheim) and *Beneckeia* sp., led Cox to classify the assemblage as belonging to the early Middle Triassic (Anisian), a period frequently associated with the Germanic Muschelkalk.

Lerman (1960) conducted a study on Triassic bivalves from the Ramon area (Negev, southern Israel). The following species were identified from the fossiliferous beds (T1): *Beneckeia* sp., *Lingula tenuissima* Bronn, *Myalina beneckei* Brotzen, *Myophoria vulgaris* (Schlotheim), *M. intermedia* Schauroth, *Neoschizodus orbicularis* (Bronn), *Gervillia joleaudi* Schmidt, *Enantiostreon difforme* (Schlotheim), and *Trigonodus tenuidentatus* sp. nov. The presence of *Beneckeia* sp. and *N. orbicularis* (Bronn) indicates that these strata correspond to the Anisian stage (=early Muschelkalk). Species of *Beneckeia* are known to occur in the Upper Buntsandstein and Lower Muschelkalk formations of Germany and Upper Silesia. Additionally, they have been recorded in Bulgaria and Wadi Hesban in Transjordan.

In Bulgaria, *Pleuromya elongata* (Schlotheim) and *Myophoria orbicularis* (Bronn) have been reported from the Tolbouhin section and are recognized as common species in Germany (Encheva, 1969). In the Pelsonian deposits of Belogradchik, *Myophoria vulgaris* (Schlotheim), *Hoernesia socialis* (Schlotheim), *Unionites fassaensis* (Wissmann), and *Pleuromya* sp. were identified by Márquez-Aliaga (1985). Subsequently, Budurov et al. (1993) conducted a comprehensive study of the fossil record, establishing a stratigraphic correlation between the eastern and western regions of the Tethys, specifically between Bulgaria and Spain.

Anisian bivalves in Spain have been recorded in multiple localities within the Catalonian Coastal Ranges (Centelles, Farell, Olesa, Pallejà, and Begues) and the Iberian Ranges (Serra and Chelva). The main assemblage consists of *Hoernesia socialis* (Schlotheim), *Myophoria vulgaris* (Schlotheim), *Pleuromya musculoides* (Schlotheim), *P. elongata* (Schlotheim), and *Unionites muensteri* (Wissmann). A comparable assemblage has been documented in the upper Anisian (Illyrian) deposits of Bulgaria, particularly in the Belogradchik and Golo-Bardo sections. These findings highlight the cosmopolitan nature of Anisian bivalves, which are present in both the Tethyan and Germanic realms.

The Middle Triassic deposits of the Mecsek Mountains (southern Hungary) contain bivalve assemblages that are widely distributed across both the Germanic and Alpine provinces in shallow marine environments. The Bertalanhegy Member of the Zuhánya Formation, dated to the Anisian, has yielded the most diverse bivalve fauna, including *Pleuromya elongata* (Schlotheim), *Hoernesia socialis* (Schlotheim), *Neoschizodus laevigatus* (Goldfuss), and *Lyriomyophoria elegans* (Dunker), among others (Szente, 1997). These species are also commonly found in the Serra study section.

Assemblages highly similar to those studied have been reported from the Lower Muschelkalk of the Germanic Triassic in the "lowlands" of Poland (Senkowiczowa, 1985). More recently, *Myophoria vulgaris* (Schlotheim) has been identified in the Lower Muschelkalk deposits of Raciborowice Górne (southwestern Poland), associated with abundant trace fossils such as *Planolites* (Chrząstek, 2013).

In the Lower Muschelkalk of the Winterswijk Formation (eastern Netherlands), stratigraphic levels with abundant *Myophoria vulgaris* (Schlotheim) have been reported, along with the presence of *Hoernesia socialis* (Schlotheim), *Myophoria orbicularis* (Bronn), and *Pleuromya elongata* Schlotheim (Oosterink, 1981). Stratigraphically, the Muschelkalk sequence in the Winterswijk area is assigned to the Bithynian substage of the Anisian stage (lower Middle Triassic) (Oosterink & Winkelhorst, 2013). More recently, a comprehensive study on the invertebrate assemblages of this formation highlighted that the most common bivalve species in the Muschelkalk are *Myophoria vulgaris* (Schlotheim),

Myophoria cf. *germanica* Hohenstein, and *Neoschizodus orbicularis* (Bronn). These species occur throughout the stratigraphic column, reaching over 96% of all bivalve specimens, and even up to 99% in certain levels. Less common taxa include *Gervillia modiolaeformis* Giebel, *Hoernesia socialis* (Schlotheim), *Pleuromya brevis* (Assmann), and *Homomya althausi* (Alberti). The presence of *Neoschizodus orbicularis* (Bronn) in the uppermost part of the section suggests a possible correlation with the Illyrian substage of the Anisian (Eldijk et al., 2019).

There are limited data on the bivalve assemblages of the Germanic Muschelkalk from the lower Bithynian to the lower Aegean-Illyrian interval. Klug et al. (2005) reported the presence of *Myophoria vulgaris* (Schlotheim), *Neoschizodus laevigatus* (Goldfuss), *N. orbicularis* (Bronn), and *Trigonodus sandbergeri* (Alberti). According to Mahler and Sell (1993), the stratigraphic horizon characterized by the co-occurrence of *Myophoria vulgaris* (Schlotheim) and *Costatoria costata* (Zenker), previously documented in the Röth Formation of Upper Silesia, has also been identified in Mainfranken. The *vulgaris/costata* bed represents an isochronous layer present in both the Germanic Basin and the Tethys Realm. These aspects are very important, since the fauna now described does not belong to the Sephardi domain, which suggests that the paleogeographic connections for the arrival of the fauna of this domain to the shallow marine environments of eastern Iberia were probably still closed.

Applying sequence stratigraphic concepts, Aigner and Bachmann (1992) described the Lower Muschelkalk as a transgressive surface, characterized by siltstones, shales, and dolomite beds containing *Myophoria vulgaris* (Schlotheim) and *Costatoria costata* (Zenker). In contrast, higher in the sequence, the Middle Muschelkalk of the South Germanic region exhibits a regressive, progradational character, with *Myophoria orbicularis* (Bronn) as a characteristic taxon.

5.4 Environmental and ecological significance

The reduced ichnodiversity observed may reflect environmentally stressful conditions, such as limited water circulation and high salinity—factors frequently recorded in the Western Tethys during the early Middle Triassic (Jaglarz & Uchman, 2010; Knaust & Costamagna, 2012).

Strata dominated by *Planolites* traces have been interpreted as indicative of shallow subtidal settings (Pérez-López et al., 2021). In the Catalan Coastal Ranges, dense but low-diversity *Planolites* assemblages have been linked to environmentally restricted conditions within Ladinian ramp carbonates (Mercedes-Martín & Buatois, 2021). Similarly, in the Middle Triassic carbonates of the Tatra Mountains (Western Carpathians), such associations have been attributed to hypersaline depositional environments (Jaglarz & Uchman, 2010).

The bivalve assemblage displays a predominance of shallow infaunal taxa, both in terms of abundance and diversity, reflecting adaptation to high-energy, nearshore marine settings (Stanley & Perissoratis, 1977). The endobyssate species—such as *Hoernesia socialis*, one of the most common taxa—are well represented as well as deep burrower taxa (*Burmesia* and *Pleuromya*).

The presence of meniscate ichnofossil *Taenidium* in Unit-I (level N0) reflects a well-documented increase in bioturbation activity within the primary sedimentary fabric that began in the Triassic. Ichnofossils with fecal-filled structures similar to those found here have been recorded in the Anisian of China (Luo et al., 2017) and are described for the first time in the Iberian Peninsula for this age.

These materials display the earliest signs of biotic recovery in the southeastern Iberian Basin following the end-Permian mass extinction, marked by the re-establishment of infaunal tiering, and may represent an early indicator of the forthcoming "Mesozoic Lacustrine Revolution" (Buatois et al., 2016).

6 Conclusions

This study highlights the exceptional Middle Triassic (Anisian) bivalve assemblage from the Serra stratigraphic section (Sierra Calderona, Valencia, Spain). This fossil record developed during the installation of a carbonate ramp in the SE Iberian Basin in response to the first major marine transgression of the Triassic in the western Tethys domain. Simultaneous marine incursions into the peri-Tethys area occurred in association with the southward propagation of active rift systems in this area. This marine connection allowed us to compare the bivalve fauna associations with others described in neighboring peri-Tethys (Paleotethys) basins from the early Middle Triassic.

Sedimentary facies of the Serra section show a variety of environments that define the installation of a carbonate ramp in the area including coastal shabkha, carbonate tidal flats, subtidal agitated areas and shallow mid-ramp settings. The assemblages of bivalve fossils were found in facies corresponding to well-oxygenated shallow-marine (mid ramp) environments, characterized by low energy conditions excepting moderate action of waves during storms. They include *Hoernesia socialis* (Schlotheim), *Myophoria vulgaris* (Schlotheim), *Pleuromya elongata* (Schlotheim), *Unionites fassaensis* (Wissmann), and *Neoschizodus laevigatus* (Goldfuss), an Anisian bivalve assemblage. Additionally, the ichnofauna of the site is first described and studied, including the ichnogenera *Planolites*, *Oravaichnium Taenidium* and *Thalassinoides*. The abundance and diversity of burrowing bivalves, together with the presence of trace fossils, represent a soft-bottom organism association indicative

of a shallow-water environment. These environments probably reflect for this area the conditions of maximum marine flooding during the first broad transgressive episode that occurred in the Middle Triassic in Iberia. This contribution helps to understand the complex stratigraphy of the Middle Triassic in Muschelkalk facies in the Levantine area of Iberia, which is largely conditioned by the lack of precise dating.

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Declarations

Conflict of interest We declare that there are no conflicts of interest between ourselves and the research being submitted for publication in the journal.

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