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Original article

A lithostratigraphic and palaeoenvironmental framework for the late Miocene El Caracolar section (Granada Basin, Betic Cordillera, Spain) and description of decapod crustaceans☆

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ABSTRACT

The locality of El Caracolar in the Granada Basin (Central Betic Cordillera, southern Spain) has yielded a rich late Miocene assemblages composed of marine invertebrates and vertebrates, accompanied by microfossils, macroflora and trace fossils. Exposed strata consisting of sands, sandy siltstones, silty sandstones, siltstones and calcirudites are divided into four local units. Lithostratigraphically, the studied section is placed between the top of the La Peza Formation and the Quéntar Formation. Based on foraminifers, the age of units 2 and 3 is estimated to be early Tortonian (11.0–9.9 Ma), whereas units 1 and 4 do not yield any reliable biostratigraphic markers. The diverse biotic association suggests that deposition took place in a near-shore outer neritic zone of a narrow to open seaway in a mesotrophic regime, responsible for the establishment of a chemosynthetic community under (sub)tropical conditions. The palaeo-depth of the depositional setting is estimated between 70 and 130 m. We further focused on decapod crustaceans that represent the first formally reported fossil decapod assemblage from the Granada province. The faunule consists of eight genera from two assemblages representing different palaeoenvironments. The assemblage of units 1 and 4 is dominated by the ghost shrimp "*Callianassa*" cf. *almerai* and accompanied by the hermit crab *Petrochirus*, whereas the assemblage from unit 3 includes the ghost shrimp *Ctenocheles* and the brachyuran crabs *Raninoides*, *Calappa*, *Goneplax*, *Styrioplax*, and *Typilobus*. Unit 2 does not yield any identifiable decapod remains. *Styrioplax* sp. represents the first occurrence of the genus outside the Central Paratethys, substantially expanding its palaeogeographical distribution. The decapod faunule from El Caracolar shows affinities with assemblages from the Proto-Mediterranean and Paratethys. This study provides a lithostratigraphic and palaeoenvironmental framework for further palaeontological studies in this unique Western Mediterranean outcrop.

1. Introduction

Decapod crustaceans from the Iberian Peninsula are known from the Mesozoic onwards. From Portugal, occurrences are known from the Middle and Late Jurassic (Wehner, 1988; Neto de Carvalho et al., 2016) and the Early Cretaceous (Neto de Carvalho et al., 2007; Mateus et al., 2013; Neto de Carvalho, 2016). The oldest species occurrence from Spain dates back to the Middle Triassic (Vía Boada and Villalta, 1975), whereas occurrences from the next period date back primarily to the Late Jurassic (Dupuy de Lôme et al., 1956; Garassino et al., 2009a; Charbonnier et al., 2013). Cretaceous occurrences from Spain are known from the Early Cretaceous (Vía Boada, 1951; Vía Boada, 1971; Rabadà, 1993; López-Horgue, 2009; González-León et al., 2016) and from the Late Cretaceous (Van Straelen, 1934; Artal, 2008; Garassino et al., 2009b; Ossó and Díaz Isa, 2014). The most diverse fauna from that period is from the uppermost Albian (Van Straelen, 1940; Ruiz de Gaona, 1943; Vía Boada, 1981; López-Horgue et al., 1996; Fraaije

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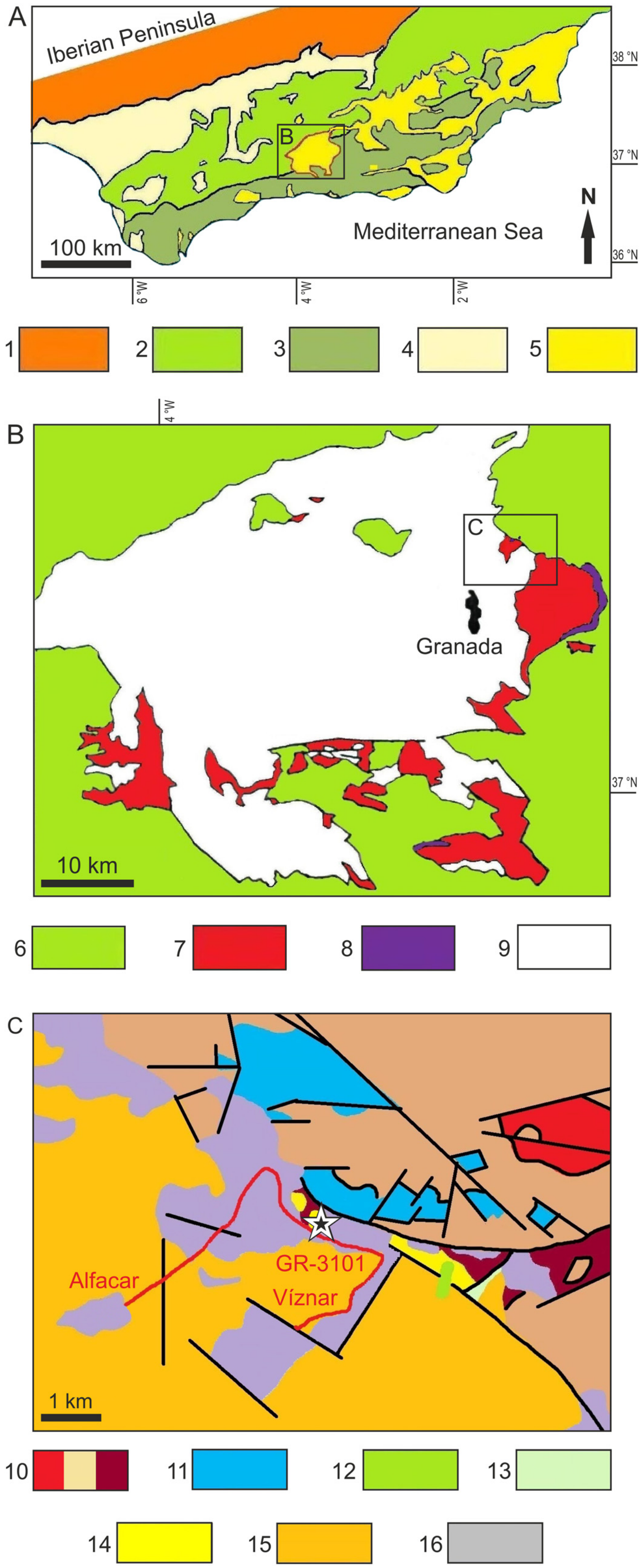

Fig. 1. Simplified geological context of the Granada Basin. The location of El Caracolar section is noted by an asterisk in C. **A, B**. Modified after Braga and Aguirre (2001). **C**. Modified after the geologic map ITGME 19-41 (sheet 1.009, Granada). **1**. Iberian Massif. **2**. Betic Cordillera (external zones). **3**. Betic Cordillera (internal zones). **4**. Atlantic Neogene basins. **5**. Mediterranean Neogene basins. **6**. Basement. **7**. Pre-upper Tortonian (Miocene) deposits. **8**. Upper Tortonian (units I–III) deposits. **9**. Turolian–Quaternary deposits (units IV–VI). **10**. Alpujárride complex. **11**. Dorsale Calcaire. **12**. Maláguide complex. **13**. Subbetic zone. **14**. Lower–upper? Tortonian deposits. **15**. Turolian deposits (Unit IV). **16**. Pliocene–Quaternary deposits (units V–VI).

et al., 2008a, 2009; Fraaije et al., 2012, 2013; Klompmaker et al., 2011a, b, c; Klompmaker et al., 2012a, b, c, Klompmaker et al., 2013, 2014, 2016; Artal et al., 2012; Klompmaker, 2013).

Cenozoic decapods from Portugal have been rarely reported (Fontannes, 1884; Veiga-Ferreira, 1954, 1958, 1961, 1965), whereas Cenozoic occurrences from Spain are well known. From the Paleogene, notably the Eocene, occurrences include numerous representatives of mostly ghost shrimps and brachyuran crabs (Vía Boada, 1959, 1969, 1970; Artal and Via, 1988; Fraaye, 1995; Ossó-Morales, 2011; Artal et al., 2006, 2013a, b, 2014, 2016; Ossó and Domínguez, 2013; Ossó et al., 2014; Artal and Hyžný, 2016). The fossil record of Neogene decapod crustaceans of Spain is also relatively rich (Vía Boada, 1932; Vía Boada, 1941; Solé and Vía Boada, 1989; Müller, 1993; García and Frontera, 1999; Artal, 2008), with most occurrences known from Catalonia. However, so far only a few contributions documented fossil decapods from the Neogene basins of southern Spain (Mayoral et al., 1998; Hyžný and Muñiz, 2012).

This paper reports on a new decapod crustacean assemblage originating from the Miocene sediments of the Granada Basin. It represents the first formal report of fossils from this area. For this reason, the stratigraphic and palaeoenvironmental setting is first described in detail, then followed by a description and discussion of the fossil decapods.

2. Geological setting

The study area is located in the Granada Basin, close to the contact between the Internal and External Zones of the Betic Cordillera, which is located in southern Spain as the westernmost segment of the European Alpine Belt (Fig. 1). The Granada Basin is a complex half-graben; its sedimentary infill has a highly molassic character (Van Houten, 1981; Rodríguez-Fernández and Sanz de Galdeano, 2006). As one of the larger intramontane basins of the Betic Cordillera, the Granada Basin formed during the early Tortonian. Its initial infilling coincided with a marine transgression that onlapped a continental relief resulting in a strong alteration due to the compressional "Terminal Serravallian" tectonic phase (Estévez et al., 1984; Sissingh, 2008) or "end Serravallian-earliest Tortonian event" (Soria, 1993). This event roughly coincided with the boundary between the second-order cycles TB2 and TB3 of the Exxon curve (Haq et al., 1987). The newly formed basin suffered rapid subsidence in response to NE-SW extension (Reicherter, 1999; Sissingh, 2008). Throughout the Neogene, the marine sedimentary infill of the Granada Basin alternated with terrestrial deposits (Fig. 2).

The post-orogenic infill of the Betic basins can be divided into six allostratigraphic units bounded by unconformities due to eustatic and/or tectonic events (Fernández et al., 1996; Viseras et al., 2004). The upper Miocene unit (Unit I) directly overlies the metamorphic basement of the Internal Zones or older Neogene units. It consists of two gradually superimposed lithological units: the lower unit (Subunit Ia) comprises temperate-like carbonates (calcirudites, calcareous sandstones, and biocalcalcarenites) deposited on an inner shelf; the upper unit (Subunit Ib) is composed of calcareous and silty-marly sediments deposited on the outer shelf or in the bathyal zone. The sequence is deepening upwards. Biocalcarenites of subunit Ia were deposited at ~8.1–7.8 Ma (i.e., during the MMi12a *G. obliquus extremus* Zone, late Tortonian) in the nearby Guadix Basin (Hüsing et al., 2010) and is characterized by a sedimentary evolution similar to that of Granada up to the

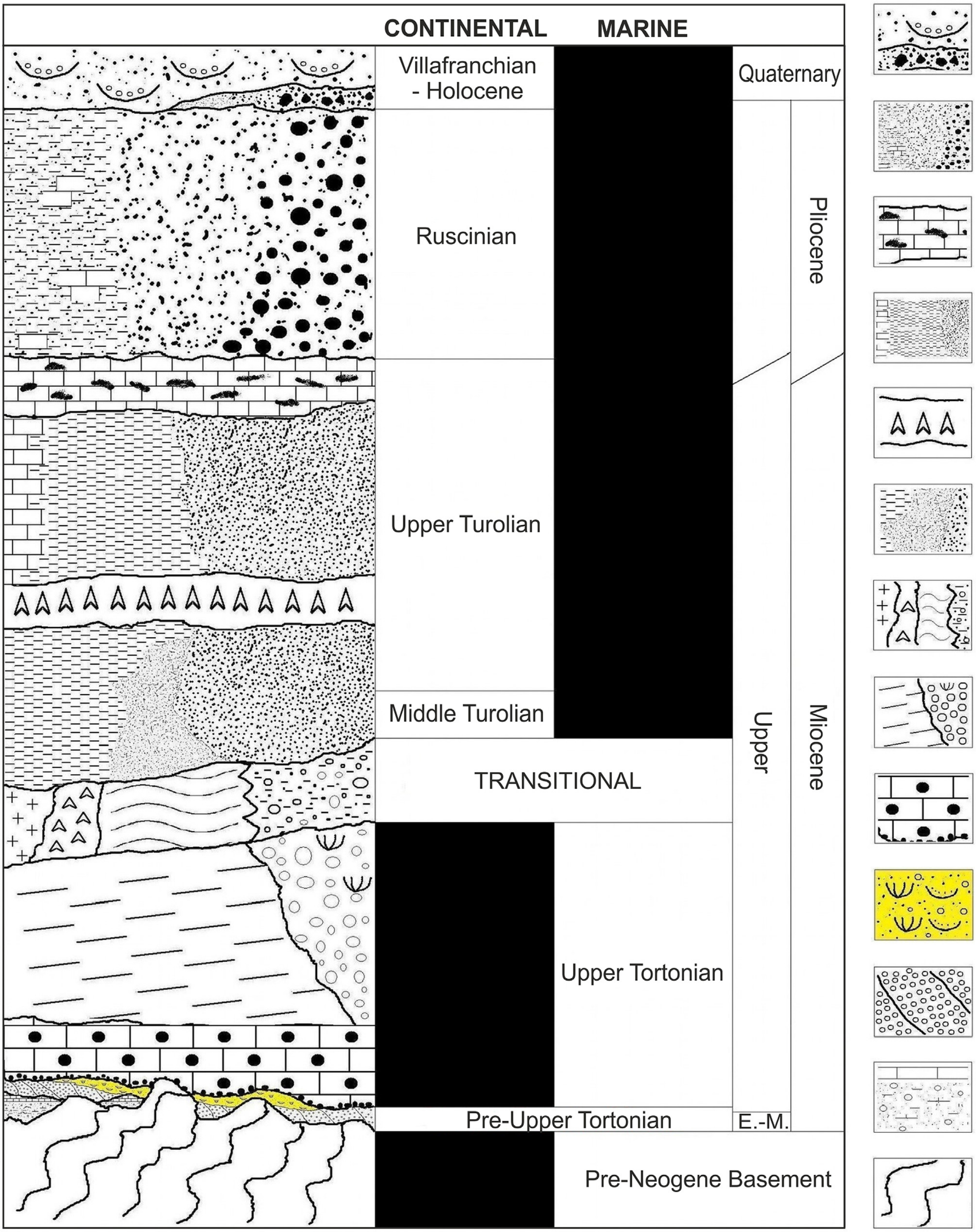

Fig. 2. Simplified lithostratigraphic scheme of the Granada Basin (Modified after García-Alix, 2006). **A**. Basement. **B**. Clastics and/or carbonates of the Alamillos, Neonumidian and Moreda formations. **C**. Clastic rocks (locally carbonates and travertines) of the La Peza Formation. **D**. Clastic rocks of the unnamed formation including the El Caracolar locality. **E**. Conglomerates, calcareous sandstones and calcarenites of the Quéntar Formation. **F**. Siltstones, marls, sandstones and conglomerates of the Quentar and Dúdar formations. **G**. Evaporites (halite, gypsum), sandstones and clastic rocks of the Pinos-Genil Formation. **H**. Clastic rocks of the Cenes-Jun Formation. **I**. Turbiditic gypsum. **J**. Clastic (and locally carbonate) rocks. **K**. Limestones with lignite intercalations. **L**. Clastic (and locally carbonate) rocks of the Alhambra Formation. **M**. Rudites, sandstones and siltstones.

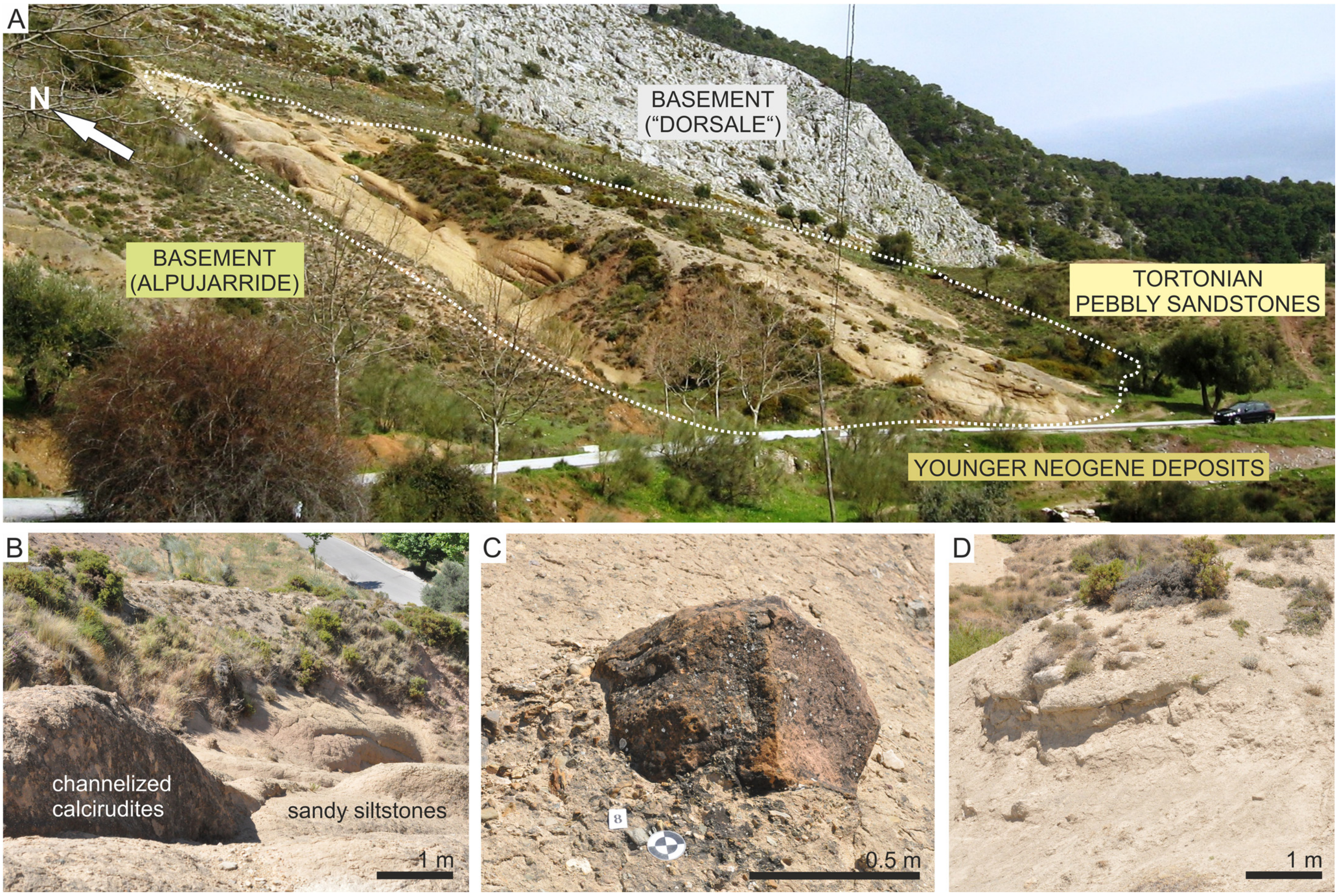

Fig. 3. Different views of the El Caracolar outcrop. **A**. Panoramic view showing the relative position of the exposed strata (area indicated with a dashed line) within a wider geological context. **B**. Field view of a channel in unit 1. **C**. Detail of a block embedded in finer sediments of unit 1. **D**. Detailed view of unit 4.

latest Tortonian (Braga et al., 2003). The transition from marine (units I–III) to continental (units IV–VI) conditions took place at the very end of the Tortonian stage (MMi12b *G. suterae* Zone, MN12 Zone) at ~7.4 Ma (García-Alix et al., 2008; Gómez-Cano et al., 2011; Corbí et al., 2012; García-Alix et al., 2013).

3. El Caracolar section

The El Caracolar locality is a natural outcrop situated in a mountainous area in the northeastern part of the Granada Basin, ~13 km NE of Granada near the villages of Alfacar and Víznar (GPS coordinates: 37° 15′N; 3° 33′ W; *ca*. 1110–1140 m a.s.l.). The road GR-3101 cuts a small portion of the outcrop (Fig. 3). Sands, sandy siltstones, silty sandstones, siltstones, biocalcarenites, and calcirudites are exposed there. Lithostratigraphically, these sediments can be ascribed to an unnamed formation intercalated between the top of the La Peza Formation (uppermost Serravallian–lowermost Tortonian; Rodríguez-Fernández, 1982) and the Quéntar Formation (lower upper Tortonian: unit I of the orogenic infill).

The basement underlying the Miocene sediments of El Caracolar can be divided into two main subunits: (*i*) Alpujárride Complex (La Plata Nappe: Paleozoic schists to the north), and (*ii*) Dorsale ("Dorsale Calcaire"), consisting of Lower Jurassic (Hettangian-Pliensbachian) non-metamorphic carbonates to the east. To the south and west, they are overlain by Neogene marine (with hermatypic corals ?late Tortonian in age) and younger continental units (?late Miocene in age), respectively.

The Miocene strata of the locality can be stratigraphically divided into four strictly local units (units 1–4, from the oldest to the youngest). These units are not equivalent to the units defined for the Granada Basin infill, but are only used for the local stratigraphy of El Caracolar. All beds dip (N140°E/20–30°SW) to the current centre of the Granada Basin, suggesting that this basin had a shape not very different from that of the present day at the beginning of the Tortonian. Aguirre (1961) already included a short taxonomic list with some of the most common taxa found at El Caracolar. Since then, the number of recognized Miocene taxa has increased. Thus far, at least 175 species have been recognized (see Appendix A), including foraminifera (hyaline and porcelanaceous forms), plants (Tracheophyta and algae), invertebrates, and vertebrates; several ichnotaxa have also been identified (Fig. 4). Bivalves are dominant among macrofossils at this locality, both in terms of number of taxa and specimens.

4. Material and methods

Units 2 and 3 were sampled for planktonic and benthonic foraminifer analyses. All samples (~500 g each) were first disaggregated and later washed over a 125 μm sieve for the study of wet-screened specimens under a binocular microscope. The macrofauna was collected during the field seasons 1994–2014. All recognizable remains were collected to ensure an unbiased analysis. Preparation of decapod specimens was done using fine needles and a pneumatic vibro-tool. Specimens were photographed either dry and uncoated or coated with ammonium chloride.

Institutional abbreviations: **MFGI**: Hungarian Geological and Geophysical Institute, Budapest, Hungary; **NHMW**: Department of

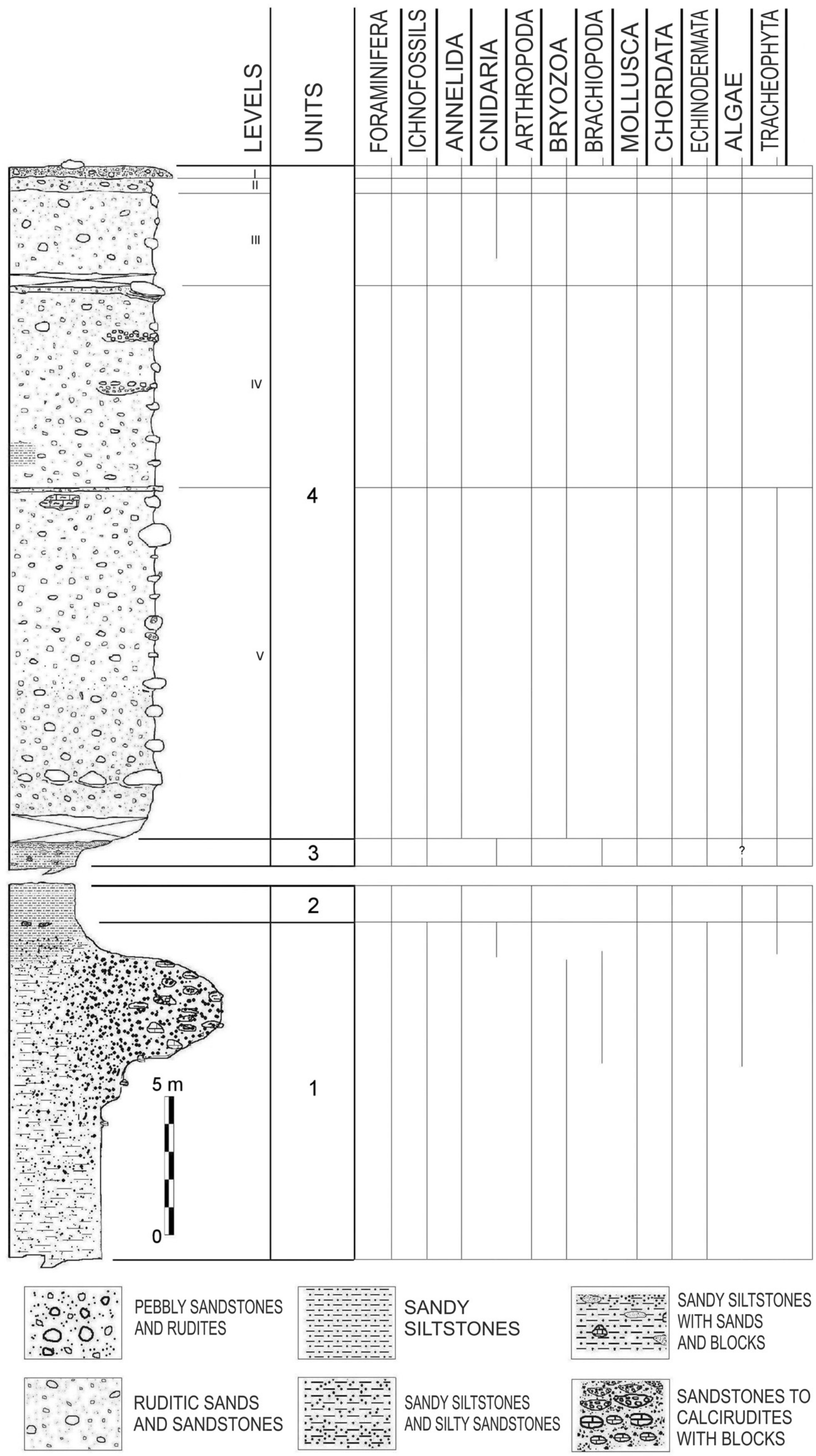

Fig. 4. Lithostratigraphic section of the El Caracolar locality, indicating the fossil content of each local unit 1–4.

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5. Systematic palaeontology

Phylum Arthropoda von Siebold, 1848
Subphylum Crustacea Brünnich, 1772
Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Infraorder Axiidea Saint Laurent, 1979
Family Ctenochelidae Manning & Felder, 1991
Subfamily Ctenochelinae Manning & Felder, 1991
Genus ***Ctenocheles*** Kishinouye, 1926

Ctenocheles sp.
Fig. 5

Material: Two isolated dactyli with preserved cuticle from units 1 (NHMW 2015/0118/0001) and 3 (NHMW 2015/0118/0002) of El Caracolar.

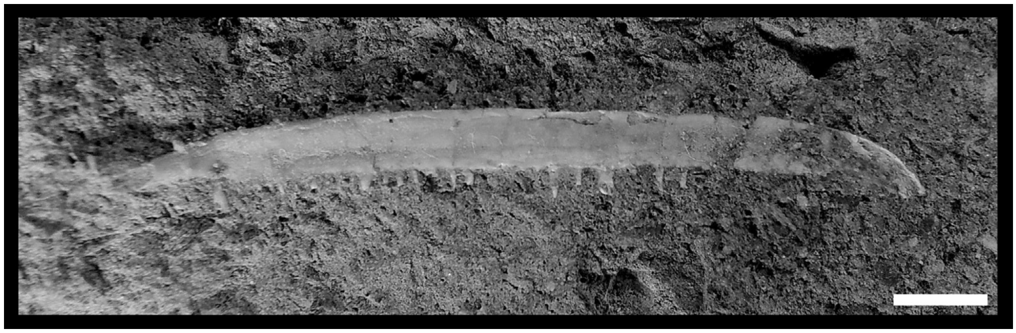

Fig. 5. *Ctenocheles* sp. from unit 1, NHMW 2015/0118/0001. Scale bar: 5.0 mm.

Fig. 6. "*Callianassa*" cf. *almerai* Müller, 1993, from unit 4. **A**. Left propodus NHMW 2015/0118/0003 in lateral (A1), mesial (A2), and ventral (A3) views. **B**. Broken left fixed finger NHMW 2015/0118/0042 in lateral view. **C**. Broken left fixed finger NHMW 2015/0118/0043 in lateral (C1) and occlusal (C2) views. **D**. Broken left fixed finger NHMW 2015/0118/0044 in lateral (D1) and ventral (D2) views. **E**. Broken left fixed finger NHMW 2015/0118/0039 in lateral (E1) and mesial (E2) views. **F**. Right dactylus NHMW 2015/0118/0021 in lateral (F1) and mesial (F2) views. **G**. Left dactylus NHMW 2015/0118/0023 in lateral (G1), mesial (G2), occlusal (G3), and dorsal (G4) views. **H**. Left dactylus NHMW 2015/0118/0026 in lateral (H1), mesial (H2), occlusal (H3), and dorsal (H4) views. **I**. Right dactylus NHMW 2015/0118/0036 in lateral (I1), mesial (I2), occlusal (I3), and dorsal (I4) views. **J**. Left dactylus NHMW 2015/0118/0009 in lateral (J1), mesial (J2), occlusal (J3), and dorsal (J4) views. **K**. Right dactylus NHMW 2015/0118/0013 in lateral (K1), mesial (K2), occlusal (K3), and dorsal (K4) views. **L**. Left dactylus NHMW 2015/0118/0010 in lateral (L1), mesial (L2), occlusal (L3), and dorsal (L4) views. All specimens represent remains of major chelae and are to scale. Scale bar: 10.0 mm.

Description: Fingers long, slender and laterally flattened, attaining same height along length. Occlusal surface armed with needle-like teeth of presumably two sizes; many have broken tips.

Remarks: The studied isolated dactyli exhibit shape and dentition typical of *Ctenocheles*. The identification of the genus in the fossil record and discussion on the taxonomically important characters at the species level were discussed by Feldmann et al. (2010), Hyžný et al. (2014), and Hyžný and Dulai (2014). Based on these studies, it is generally agreed that species-level identification is not possible if only isolated dactyli are available. This material represents the first occurrence of the genus from the Miocene of Spain; it is the youngest record of *Ctenocheles* in Europe so far.

Family Callianassidae Dana, 1852

Genus ***Callianassa*** Leach, 1814

Remarks: Since *Callianassa* Leach, 1814 *sensu* Manning and Felder (1991) and Ngoc-Ho (2003) is currently defined on the basis of soft parts, most of the fossil species of "*Callianassa*" may not fit the generic diagnosis (Hyžný and Klompmaker, 2015). Rather, fossil "*Callianassa*" represents a heterogeneous mixture of several independent genera. The material from El Caracolar exhibits affinities with *Sergio* Manning and Lemaitre, 1994 (see below), but we are hesitant to assign it to that genus because of the fragmentary nature of the material.

"*Callianassa*" cf. *almerai* Müller, 1993

Fig. 6

1993. *Callianassa almerai* nov. sp. - Müller, p. 6, fig. 2C–F.

1993. *Callianassa* sp. - Müller, p. 7, fig. 2G–H.

2010. *Callianassa almerai* Müller - Schweitzer et al., p. 33.

2011. "*Callianassa*" *almerai* Müller - Hyžný, p. 40, fig. 2–3, tables 1–2.

Material: The material from the sandy facies of unit 4 consists of isolated cheliped elements: 1 left fragmentary propodus (NHMW 2015/0118/0003), 8 left dactyli (robust morphotype; NHMW 2015/0118/0004–0011), 10 right dactyli (robust morphotype; NHMW 2015/0118/0012–0021), 8 left dactyli (slender morphotype; NHMW 2015/0118/0022–0029), 9 right dactyli (slender morphotype; NHMW 2015/0118/0030–0038), 2 left fixed fingers with smooth occlusal surface (NHMW 2015/0118/0039–0040), 1 right fixed finger with smooth occlusal surface (NHMW 2015/0118/0041), 5 left fixed fingers with denticulate occlusal surface (NHMW 2015/0118/0042–0046), 1 right fixed finger with denticulate occlusal surface (NHMW 2015/0118/0047), 1 right fixed finger embedded in the substrate (NHMW 2015/0118/0048). Most specimens retain their cuticle. The species is also present in microrudites of unit 1 (G.D.Z., pers. obs.).

Description: Major propodus rectangular; manus approximately as long as high, with prominent notch at base of fixed finger; both inner and outer surface of propodus with several tubercles at articulation with dactylus (just above the notch); fixed finger triangular in outline, not longer than manus, with occlusal margin with or without equal-sized small denticles. Dactylus of two morphotypes: stout, massive, long, and slender; stout dactylus with occlusal margin armed with teeth of unequal size, sometimes doubled, and with prominently hooked tip; slender dactylus with occlusal margin armed with equally-spaced teeth, and with gently hooked tip; upper margin of both types keeled and with spine-like protrusions at location of setal pores positioned at edge of inner lateral surface. Except two easily recognizable morphotypes of dactylus (robust and slender), several specimens exhibiting either characters of both morphotypes are present (i.e., slender with prominent hook or extremely shortened robust dactylus).

Remarks: The material from El Caracolar is left in open nomenclature because only isolated fingers and one fragmentary propodus are known, which do not allow detailed comparisons to previously published occurrences of "*Callianassa*" *almerai* from the middle Miocene of Spain (Müller, 1993) and Austria (Hyžný, 2011). The original description is based on isolated propodi; no dactyli were reported by Müller (1993). Hyžný (2011) reported on and figured articulated specimens with both major and minor chelipeds preserved. These specimens are poorly preserved, and, therefore, comparison with the El Caracolar material is difficult. However, all these occurrences share the general shape of the propodus and the presence of tubercles on both lateral surfaces below the articulation with the dactylus. These characters are shared also with another species, namely *Callianassa lusitanica* Veiga-Ferreira, 1954, from the Miocene of Portugal. Veiga-Ferreira (1965) later treated this species as *Callianassa* cf. *desmarestiana* A. Milne-Edwards, 1860. Published figures (Veiga-Ferreira, 1954: pl. 1, figs. 3, 5; Veiga-Ferreira, 1965: pl. 1, fig. 3, pl. 2, fig. 10) clearly show the presence of tubercles at the base of the fixed finger, but more details are not discernible. Re-examination of the type material is needed to resolve the taxonomic status of *C. lusitanica*.

Intraspecific variation of "C." cf. *almerai* is reminiscent of variation expressed in *Sergio* (subfamily Callichirinae). Fixed fingers with a denticulate occlusal surface are not very common in callianassid shrimps, but they have been described and figured for *Sergio guassutinga* (Rodrigues, 1971), *S. mericeae* Manning & Felder, 1995 (Rodrigues, 1971: fig. 50; Manning and Felder, 1995: figs 1d, 1h, 3h, 5c–f), and *S. sulfureus* Lemaitre & Felder, 1996 (Lemaitre and Felder, 1996: fig. 4a–b). The variation in the armature of the fixed finger of "C." cf. *almerai* is difficult to interpret in relation to the dactylar morphotypes because no articulated specimen has been recovered. Interestingly, *C. almerai* from Austria, which includes specimens that have the carpus, merus, and ischium preserved (Hyžný, 2011), shows morphological affinities with a group of genera of the subfamily Callianassinae including *Neotrypaea* Manning & Felder, 1991, *Paratrypaea* Komai and Tachikawa, 2008, and *Trypaea* Dana, 1852. A detailed revision of *C. almerai* as described by Müller (1993) including a re-examination of the original material is needed to clarify the taxonomic status of this species.

Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family Diogenidae Ortmann, 1892
Genus ***Petrochirus*** Stimpson, 1858

Petrochirus priscus (Brocchi, 1883)
Fig. 7

1883. *Pagurus priscus* nov. sp. - Brocchi, p. 7, pl. 5, fig. 9.
1928. *Petrochirus priscus* (Brocchi) - Glaessner, p. 173, 206, text-fig. 2.
1929. *Pagurus priscus* Brocchi - Lőrenthey and Beurlen, p. 34, 70, 71, pl. 3, figs. 1–2.
1954. *Petrochirus* aff. *inequalis* Rathbun - Veiga-Ferreia, p. 61, pl. 2, fig. 16.
1965. *Petrochirus* cf. *priscus* (Brocchi) - Veiga-Ferreira, p. 142, pl. 2, figs. 7, 9, 11–12.
non 1965. *Petrochirus* cf. *priscus* (Brocchi) - Veiga-Ferreira, pl. 2, fig. 8.
1984. *Petrochirus priscus* (Brocchi) - Müller, p. 59, pl. 19, fig. 5, pl. 20, figs. 1–5, pl. 21, figs. 1–3.
1998. *Petrochirus priscus* (Brocchi) - Müller, p. 12.

Material: Two fragmentary fingers with preserved cuticle from unit 4 of El Caracolar: isolated right fixed finger (NHMW 2015/0118/0049) and isolated right dactylus (NHMW 2015/0118/0050).

Description: Fingers long and robust; surface densely covered with tubercles. Occlusal surface of fixed finger armed with large molariform teeth proximally; teeth smaller distally. Dactylus with tip slightly bent downward; occlusal surface bears single row of small teeth forming cutting edge.

Remarks: Although the material is fragmentary and deformed, it exhibits characteristics typical of *Petrochirus priscus* (Brocchi,

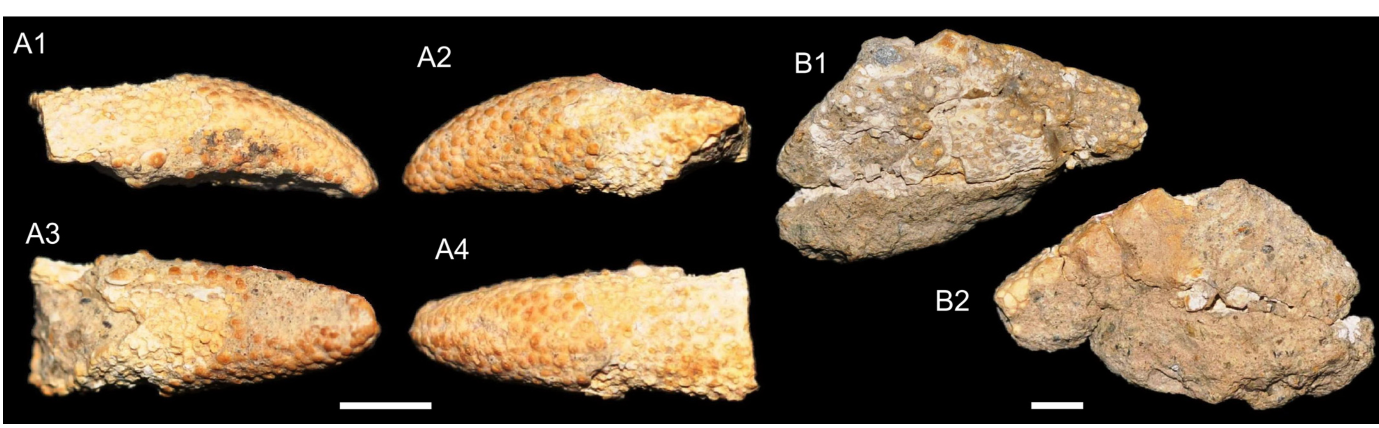

Fig. 7. *Petrochirus priscus* (Brocchi, 1883), from unit 4. **A**. Isolated left dactylus NHMW 2015/0118/0050 in mesial (A1), lateral (A2), occlusal (A3), and dorsal (A4) views. **B**. Broken right fixed finger NHMW 2015/0118/0049 in ventral (B1) and occlusal (B2) views. Scale bars: 5.0 mm.

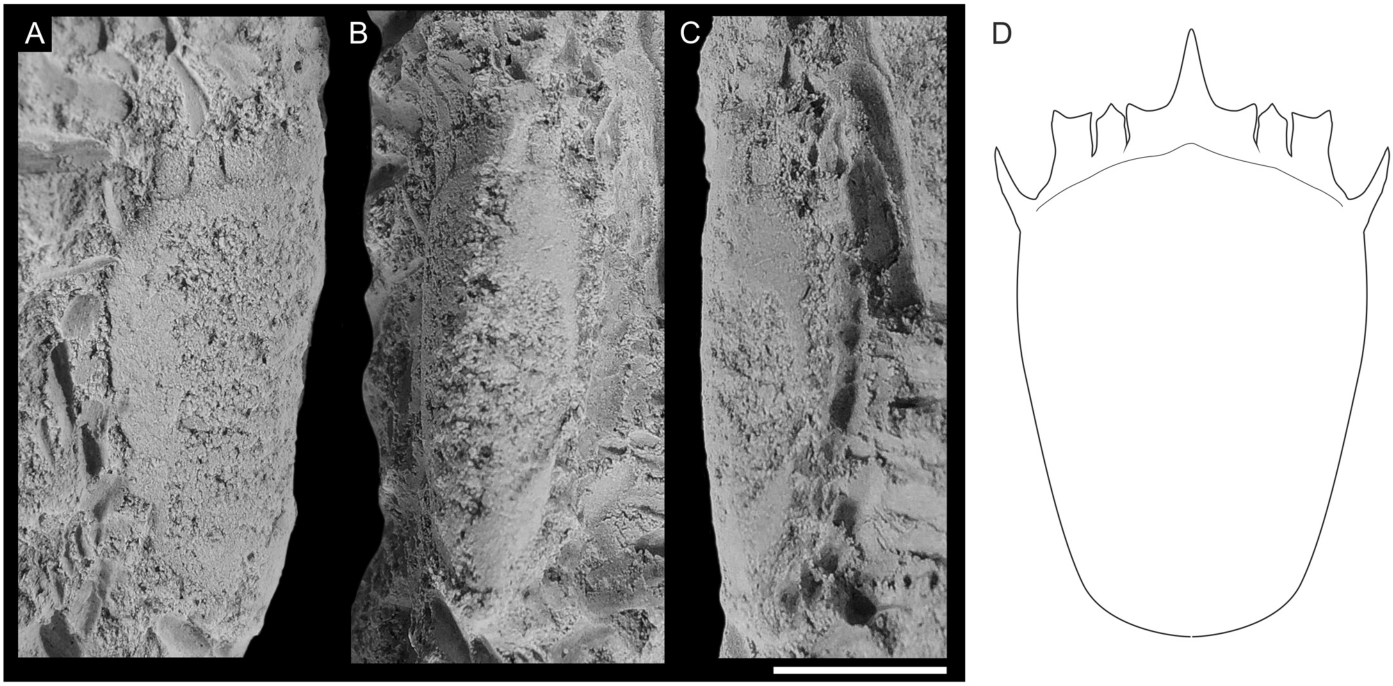

Fig. 8. *Raninoides pliocenicus* De Angeli, Garassino & Pasini, 2009, from unit 3. **A–C**. Deformed specimen NHMW 2015/0118/0051 under different angles. The specimen was covered with ammonium chloride prior the photography. **D**. Carapace reconstruction. Scale bar: 5.0 mm.

1883), namely the tuberculation on the outer surface and the molariform teeth on the occlusal surface. The cuticle, consisting of several layers, is preserved in two different modes. If the upper layer is preserved, hardly any spaces between respective rounded tubercles on the surface are observed. When the upper layer is removed, the spaces between tubercles are larger and the ornamentation is rougher. A similar preservational effect has recently been discussed by Klompmaker et al. (2015).

Petrochirus priscus has been reported from numerous Miocene localities across Europe, including Hungary (Brocchi, 1883; Lőrenthey and Beurlen, 1929; Müller, 1984), Austria (Glaessner, 1928; Müller, 1984, 1998), Romania (Müller, 1984), Slovakia (Müller, 1984), and Malta (Glaessner, 1933; Gatt, 2006). Glaessner (1928: p. 173) mentioned (but did not figure) a single left chela from the Miocene of Oued Tiflout (Morocco) attributable to *P. priscus*. Veiga-Ferreira (1954) reported *Petrochirus* aff. *inequalis* Rathbun, 1919, from the Miocene of Portugal. Later, Veiga-Ferreira (1965) examined more material and re-assigned both lots to *P.* cf. *priscus*. We refer that material together with the specimens from El Caracolar to *P. priscus*. One of the specimens (Veiga-Ferreira, 1965: pl. 2, fig. 8) clearly represents a carapace of a leucosiid crab.

Infraorder Brachyura Linnaeus, 1758
Superfamily Raninoidea De Haan, 1839
Family Raninidae De Haan, 1839
Subfamily Raninoidinae *Lőrenthey in* Lőrenthey and Beurlen, 1929
Genus ***Raninoides*** H. Milne-Edwards, 1837

Raninoides pliocenicus De Angeli, Garassino & Pasini, 2009
Fig. 8

2009. *Raninoides pliocenicus* nov. sp. - De Angeli et al., p. 171, figs. 5A–D.

Material: Two specimens from unit 3 of El Caracolar: one complete carapace (NHMW 2015/0118/0051) and one fragmentary carapace lacking anterior part (NHMW 2015/0118/0052). These specimens do not preserve cuticle.

Description: Carapace longitudinally elongated (W/L = 0.6); anterior part occupied by orbito-frontal margin. Rostrum elongated, triangular in outline. Preorbital tooth small; supraorbital margin with two deep fissures; supraorbital tooth with triangular tip; extraorbital tooth wider and tipped with two spines. Anterolateral margin with one elongated and sharply pointed spine; lateral margins nearly parallel to each other, slightly converging posteriorly; posterior margin narrower than orbito-frontal margin. Carapace regions not discernible, partly because of incompleteness of specimens.

Remarks: The more complete specimen is slightly deformed, i.e., folded longitudinally (Fig. 8). However, the number, position and outline of the orbito-frontal margin is the same as in *R. pliocenicus* from the Pliocene of Tuscany, Italy (De Angeli et al., 2009). The reconstructed outline of the carapace also matches the Italian material (De Angeli et al., 2009: fig. 5). Specimens from El Caracolar represent the second reported occurrence of the species, thereby extending its palaeogeographic and stratigraphic distribution to the early Tortonian of Spain.

Superfamily Calappoidea De Haan, 1833
Family Calappidae De Haan, 1833
Genus ***Calappa*** Weber, 1795

Calappa praelata Lőrenthey *in* Lőrenthey and Beurlen, 1929
Fig. 9

1929. *Calappa praelata* nov. sp. - Lőrenthey *in* Lőrenthey and Beurlen, p. 132, pl. 6, fig. 3.

?1954. *Calappa heberti* Brocchi - Veiga-Ferreira, p. 63, pl. 5, figs. 37, 39.

1958. *Calappa heberti* Brocchi - Veiga-Ferreira, p. 203, figs. 1–3, pl. 1, fig. 1–3.

1984. *Calappa praelata* Lőrenthey *in* Lőrenthey and Beurlen - Müller, p. 66, pl. 35, figs. 1, 2, 7.

1984. *Calappa* cf. *praelata* Lőrenthey *in* Lőrenthey and Beurlen - Müller, pl. 35, figs. 3–6.

?1993. *Calappa* sp. - Müller, p. 10.

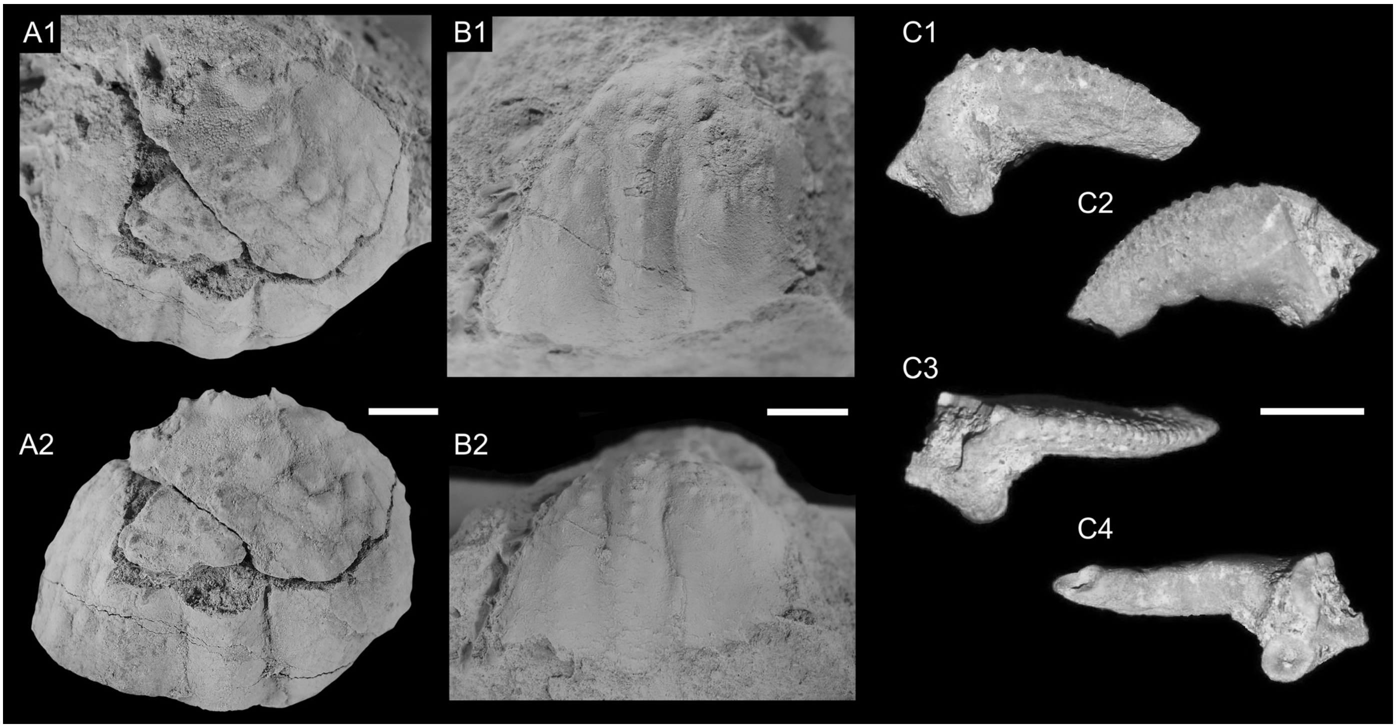

Fig. 9. *Calappa praelata* Lőrenthey *in* Lőrenthey and Beurlen, 1929, from unit 3 (A, B) and unit 4 (C). **A**. Carapace NHMW 2015/0118/0054 in fronto-dorsal (A1) and dorsal (A2) views. **B**. Carapace NHMW 2015/0118/0053 in dorsal (B1) and postero-dorsal (B2) views. **C**. Isolated right dactylus NHMW 2015/0118/0056 in lateral (C1), mesial (C2), dorsal (C3), and occlusal (C4) views. The specimens in A and B were covered with ammonium chloride prior the photography. Scale bars: 5.0 mm.

1996. *Calappa praelata* Lőrenthey *in* Lőrenthey and Beurlen - Müller, p. 9, pl. 1, fig. 11.

1998. *Calappa praelata* Lőrenthey *in* Lőrenthey and Beurlen - Müller, p. 22.

2010. *Calappa praelata* Lőrenthey *in* Lőrenthey and Beurlen - Gatt and De Angeli, p. 1329, pl. 2, fig. 2.

2012. *Calappa praelata* Lőrenthey *in* Lőrenthey and Beurlen - Pasini et al., p. 136, fig. 1.

Material: Holotype of *Calappa praelata* from Mátraverebély-Szentkút, Hungary (MFGI M.27); three specimens without cuticle from unit 3 of El Caracolar: complete carapace (NHMW 2015/0118/0053), fragmentary carapace lacking posterior part (NHMW 2015/0118/0054), carapace fragment (NHMW 2015/0118/0055); right dactylus with cuticle (NHMW 2015/0118/0056) from unit 4 of El Caracolar.

Description: Carapace strongly convex, transversely ovate in outline; anterior surface with rounded tubercles on gastro-cardiac, hepatic, and branchial regions; median regions (mesogastric, urogastric, and cardiac regions) distinctly delineated from other regions by deep longitudinal grooves, elevated area ornamented with five tubercles; posterior carapace surface nearly smooth, with faint scabrose ornamentation in posteriormost position. Front small, triangulate; anterolateral margin convex, irregularly dentate; posterolateral margin with expansions resembling blunt spines; posterior margin poorly preserved. Left dactylus granulated, with tuberculated upper margin.

Remarks: *Calappa* is a well-known genus with a distinctive carapace and rich fossil record going back into the Eocene (Schweitzer and Feldmann, 2000; Schweitzer et al., 2006). Regarding the Miocene of the Mediterranean and Paratethys, the genus is represented by several species, namely *Calappa heberti* Brocchi, 1883, *C. praelata* Lőrenthey *in* Lőrenthey and Beurlen, 1929, and *C. saheliensis* Van Straelen, 1936. The last two species are morphologically very close to each other and resemble the specimens from El Caracolar. According to Van Straelen (1936), *C. saheliensis* differs from *C. praelata* in the absence of longitudinal grooves and large tubercles in the branchial regions and the absence of a large tubercle in the middle of the carapace in *C. saheliensis*. Mayoral et al. (1998) also noted a rather smooth ornamentation on the posterior part of the carapace in *C. saheliensis* (supposedly retaining its cuticle). The specimens from El Caracolar clearly exhibit large tubercles in the branchial region and possess a large tubercle in the carapace centre. However, the posterior part of the carapace (NHMW 2015/0118/0053) exhibits only minor tuberculation; in this way, it differs slightly from the holotype of *C. praelata*. We consider this difference to represent intraspecific variation. *Calappa praelata* is known from the Miocene of the Paratethys, the Proto-Mediterranean, and the Atlantic Ocean. In the Paratethys region, it is reported from the middle Miocene of Hungary, Poland, and Austria (Müller, 1984, 1996). In the Proto-Mediterranean, it is known from the middle Miocene of Sardinia, Italy (Pasini et al., 2012), and the late Miocene (Messinian) of Malta (Gatt and De Angeli, 2010). In the Atlantic Ocean, it has been reported by Veiga-Ferreira (1954, 1958) from the late Miocene (Tortonian) of Portugal. *Calappa saheliensis* was originally described from the latest Miocene (Messinian) of Oran, Algeria (Van Straelen, 1936), but later it was also reported as *C.* cf. *saheliensis* from the early Pliocene of Sevilla, Spain (Mayoral et al., 1998).

Superfamily Goneplacoidea MacLeay, 1838
Family Chasmocarcinidae Serène, 1964
Subfamily Chasmocarcininae Serène, 1964
Genus ***Styrioplax*** Glaessner, 1969

Styrioplax sp.
Fig. 10

Material: Single articulated individual consisting of carapace and parts of venter and appendages (NHMW 2015/0118/0057); no cuticular surfaces are preserved. The specimen was found in unit 3 at El Caracolar.

Description: Carapace small with subtrapezoidal outline, approximately as long as wide, narrowing anteriorly and widest at posterolateral margin. Rostrum protruding and bilobed, broader

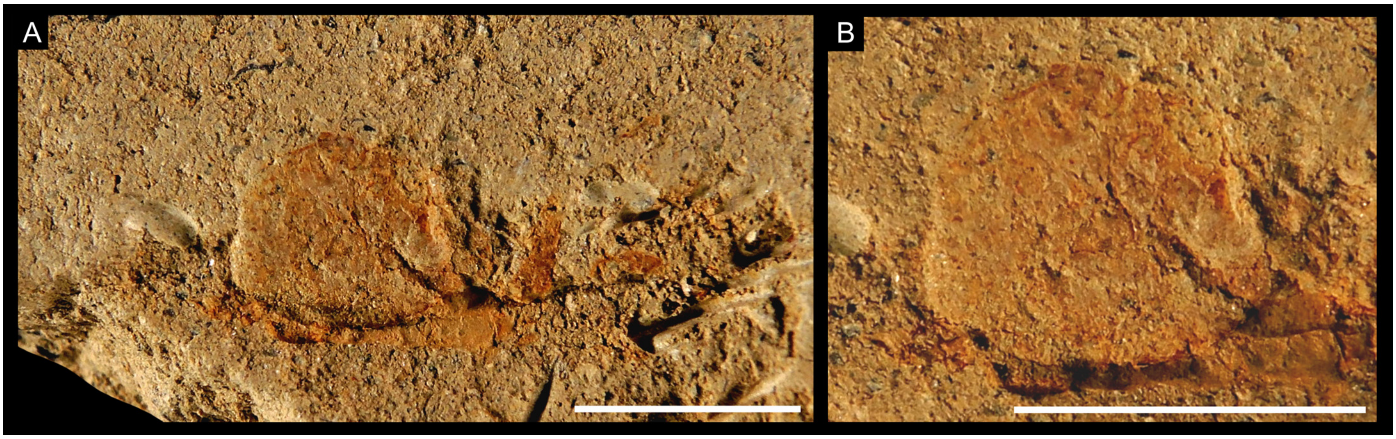

Fig. 10. *Styrioplax* sp. from unit 3. **A**. Carapace with partially preserved sternum and appendages NHMW 2015/0118/0057. **B**. Close-up view of the same specimen. Scale bars: 5.0 mm.

at base. Orbits wide and shallow. Anterolateral margins rounded and convex, lateral margins nearly parallel to each other, posterolateral margins with re-entrant (for fifth pereiopods); posterior margin straight. Carapace regions poorly to not delineated. Cardiac region relatively well visible. Gastric region separated from branchial region only posteriorly; outlines of regions form H-shaped central depressions. Parts of venter and appendages poorly preserved without any discernible details.

Remarks: The presence of a faint notch at the front, a typical character of *Styrioplax*, justifies the generic placement. The specimen is morphologically close to *Styrioplax exiguus* (Glaessner, 1928) from the early Miocene of Austria, Hungary, Slovakia, and Slovenia (Glaessner, 1928; Hyžný and Schlögl, 2011; Gašparič and Halásová, 2015; Gašparič and Hyžný, 2015; Hyžný and Gross, 2016). The preservation of the El Caracolar material is, however, insufficient to recognize details such as the granulation of the anterior portion of the carapace or the rimmed front that are typical of *S. exiguus* (Hyžný and Schlögl, 2011; Gašparič and Hyžný, 2015).

Family Goneplacidae MacLeay, 1838
Genus ***Goneplax*** Leach, 1814
Goneplax rhomboides (Linnaeus, 1758)
Fig. 11

1758. *Cancer rhomboides* nov. sp. - Linnaeus, p. 626.
1814. *Goneplax angulata* nov. sp. - Leach, p. 430.
1886. *Gonoplax* [sic.] *formosa* nov. sp. - Ristori, p. 111–114, pl. 3, fig. 11–13.
1886. *Gonoplax* [sic.] *meneghinii* nov. sp. - Ristori, p. 114–116, pl. 3, fig. 8–10.
2013. *Goneplax rhomboides* (Linnaeus) - Garassino et al., p. 359, figs. 1B–C, 2. (*cum. syn.*)

Material: A near-complete dorsal carapace (NHMW 2015/0118/0058), three fragmentary carapaces (NHMW 2015/0118/0059–0061), an isolated female pleon (NHMW 2015/0118/0062), and four poorly preserved carapaces with associated appendages (NHMW 2015/0118/0063–0066). All material originates from unit 3 and retains no cuticle.

Description: Carapace transversely trapezoidal, much wider than long (W/L = 1.2), widest at anterolateral tooth; carapace surface smooth, with two faint horizontal ridges, regions indistinct; front broad, without incision, shorter than orbits; orbits wide, expanded distally; supraorbital margin distinctly sinuous, outer orbital angle with prominent tooth; anterolateral margin with one distinct tooth. Chelipeds slightly unequal, one stouter than the other. Fingers armed with large triangular teeth; occlusal surface of stouter chela with proximal molariform teeth.

Remarks: Although most of the material from El Caracolar is rather fragmentary or poorly preserved, there is one near-complete specimen (Fig. 11) exhibiting characters typical of *Goneplax rhomboides* as discussed by Garassino et al. (2012, 2013): a transversely trapezoidal carapace that is much wider than long (widest at anterolateral tooth) and has a front that is shorter than the orbits. Its closest morphological equivalent, *Goneplax gulderi* Bachmayer, 1953, from the Miocene of Austria, Slovenia,

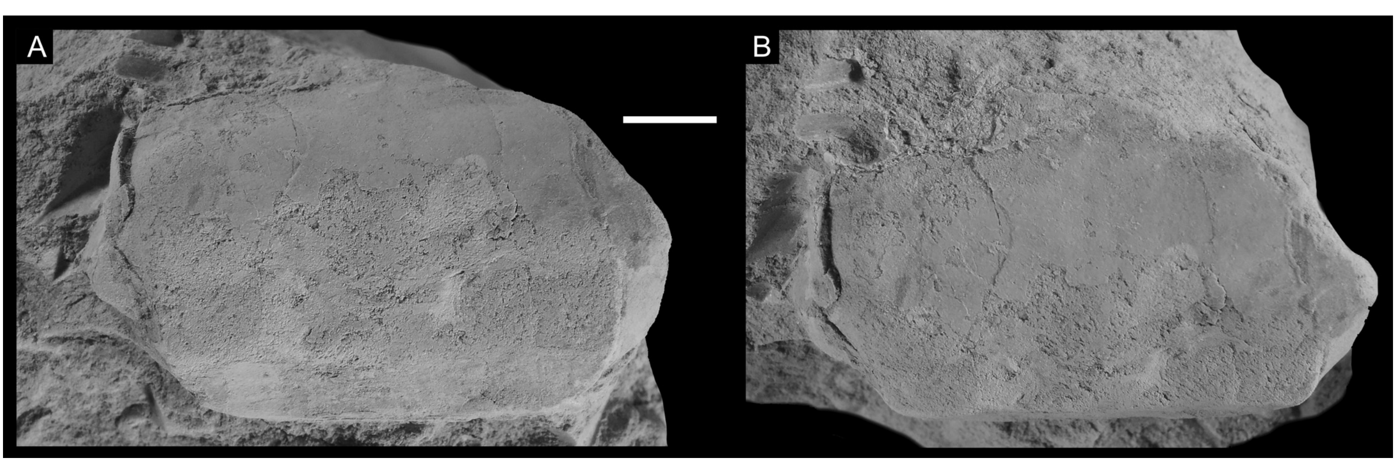

Fig. 11. *Goneplax rhomboides* (Linnaeus, 1758), from unit 3: near-complete carapace NHMW 2015/0118/0058 in dorsal (**A**) and fronto-dorsal (**B**) views. Specimen was covered with ammonium chloride prior the photography. Scale bar: 5.0 mm.

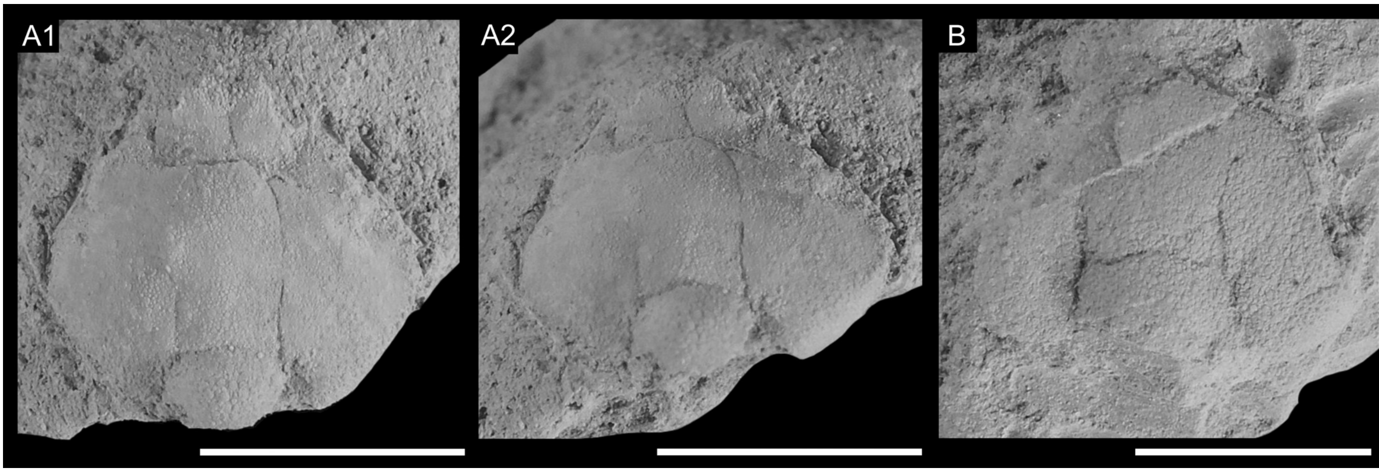

Fig. 12. *Typilobus moralejai* Müller, 1993, from unit 3. **A**. Near-complete carapace NHMW 2015/0118/0081 in dorsal (A1) and postero-dorsal (A2) views. **B**. Fragmentary carapace NHMW 2015/0118/0082. Specimens were covered with ammonium chloride prior the photography. Scale bars: 5.0 mm.

and Italy (Garassino et al., 2013; Gašparič and Hyžný, 2015), has a front that is approximately as wide as the orbits.

Goneplax has already been reported from the Miocene and early Pliocene of Spain (Vía Boada, 1948; Solé and Vía Boada, 1989; Müller, 1993; Mayoral et al., 1998), but all these occurrences were re-assigned to *Albaidaplax ispalensis* Garassino, Pasini & Castro, 2013, by Garassino et al. (2013). The material from El Caracolar exhibits orbits that strongly widen distally and with a distinctly sinuous supraorbital margin and a prominent tooth at the outer orbital angle. All these characters are characteristic for *Goneplax*, whereas *Albaidaplax* has orbits that slightly widen distally, a slightly sinuous supraorbital margin, and a short tooth at the outer orbital angle (Garassino et al., 2013). Therefore, assigning our material to *Goneplax* is warranted.

Goneplacoidea fam. indet.

Material: Isolated fixed fingers and dactyli (NHMW 2015/0118/0068–0079) from unit 3 at El Caracolar.

Remarks: The material is too fragmentary to be assigned to any brachyuran family with certainty. Some specimens show similarities to chelae of *Goneplax rhomboides*, but assignment to a lower taxonomic rank is impossible without more complete material (complete propodus).

Superfamily Leucosioidea Samouelle, 1819
Family Leucosiidae Samouelle, 1819
Genus ***Typilobus*** Stoliczka, 1871
Typilobus moralejai Müller, 1993
Fig. 12
1993. *Typilobus moralejai* nov. sp. - Müller, p. 10, figs. 4J–L.

Material: A near-complete carapace (NHMW 2015/0118/0081), a fragmentary carapace without its anterior and posterior portion (NHMW 2015/0118/0082), and a carapace fragment (NHMW 2015/0118/0083). All material originates from unit 3 and retains most of the cuticule.

Description: Carapace elliptical, strongly convex longitudinally and transversally, almost semiglobular; transverse section elliptical. Frontal margin almost straight, divided by faint notch in two halves; orbits small and circular. Lateral margins strongly convex. Posterior margin not preserved. Regions on anterior portion of carapace not defined; cardiac region elevated and delineated by distinct grooves. Entire surface of carapace covered with tiny tubercles of several sizes; tubercles on lateral margins larger, forming a serration pattern.

Remarks: These specimens conform to the original description of *Typilobus moralejai* Müller, 1993. The front seems better preserved in our material. *Typilobus moralejai* is restricted to the Miocene of Spain (Müller, 1993; this work).

The status of the genus *Typilobus* is still uncertain. Artal and Hyžný (2016) opined that it had become a catch-all taxon for accommodating fossil leucosioids with uncertain affinities. Vía Boada (1969), Müller (1993), and Feldmann et al. (2011) pointed out the heterogeneity of the genus. For the time being, we retain the species discussed above within *Typilobus*, although *T. moralejai* differs distinctly from the type species *T. granulosus* Stoliczka, 1871 as recently revised by Artal and Hyžný (2016).

Superfamily Portunoidea Rafinesque, 1815
Family indet.

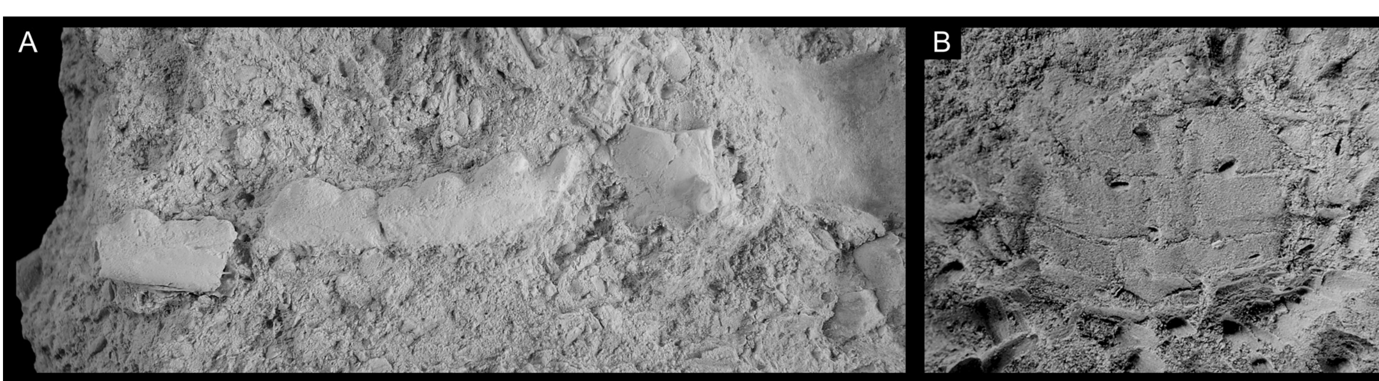

Fig. 13. Portunoidea indet. **A**. Broken fixed finger NHMW 2015/0118/0080 from unit 4. **B**. Pleonal segments with telson of a presumable female portunid crab NHMW 2015/0018/0084 from unit 3. Specimens were covered with ammonium chloride prior the photography. Scale bars: 5.0 mm.

Fig. 13

Material: Isolated fixed finger (NHMW 2015/0118/0080) from unit 4 at El Caracolar; pleonal segments (NHMW 2015/0118/0084) from unit 3.

Remarks: The material is somewhat reminiscent of *Scylla* De Haan, 1833 and *Necronectes* A. Milne-Edwards, 1881, both of which possess strong chelae with large molariform teeth. Fontannes (1884) described *Achelous delgadoi* (currently ascribed to *Portunus*; Schweitzer et al., 2010) from the Miocene of Portugal. Later, Veiga-Ferreira (1954, 1965) reported more specimens of this species as well as remains of *Neptunus granulatus* A. Milne-Edwards, 1860 (= *Neptunus monspeliensis* A. Milne-Edwards, 1860). The material from El Caracolar could possibly be ascribed to both taxa, i.e., *Scylla* and *Necronectes*. However, without better preserved material it is impossible to ascribe the specimens to a species. The pleonal segments are morphologically close to female pleons of portunoid crabs. Closer identification is not possible.

6. Results

6.1. Sedimentology and general palaeontological aspects

The composite section exposed at El Caracolar locality consists of four lithological units, usually yielding different fossil contents. In general, the biota from unit 1 is roughly similar to that of unit 4; nevertheless, there are some differences such as the restriction of crassostreid bivalve shells to unit 1 and scalpellid plates to unit 4. Callianassid remains are only found in the coarse sediments of both units. Reddish calcisiltites are characterized by a relatively high abundance of miliolids, which are exclusive to these silty sediments. Trace fossils are present in all units, except in the reddish sandy siltstones of unit 2. Rhodophyceae are absent in the finest sediments and much more common in ruditic ones. The most diverse and best preserved decapod assemblage is found in the fine siliciclastic sediments of unit 3 (see Appendix A).

Local unit 1. The oldest unit, of which the base does not crop out, is composed of well-cemented clastic sediments with an estimated thickness of 7–8 m. Greenish to yellowish silty sandstones grading laterally and stratigraphically upwards into channelized (Fig. 3B) brownish calcirudites and further into reddish silty sandstones are exposed here. Polymictic blocks are present throughout the unit, being more common and larger in coarser sediments, where they can measure > 50 cm in diameter. In the calcirudites, fossils are poorly preserved and often fragmented and/or bioeroded. In these coarse-grained sediments with poor stratification, shell fragments of *Crassostrea gryphoides* Schlotheim, 1813, are abundant, as well as calcareous red algae, shark teeth (mostly of the family Odontaspididae Müller and Henle, 1838), and echinoids (common clypeasteroids and rare echinolampadids) (Fig. 14). Other groups are represented by rather

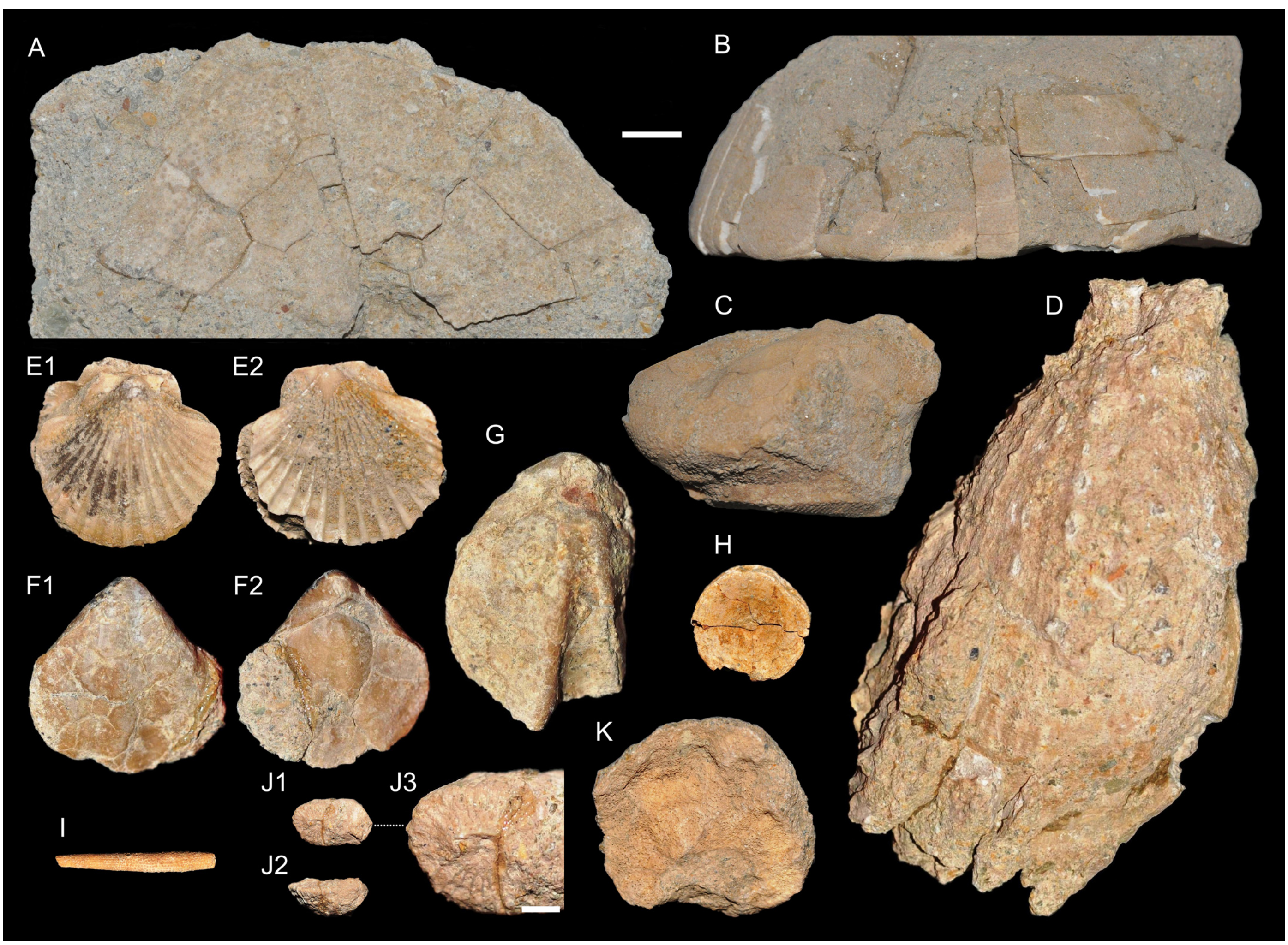

Fig. 14. Selected fossils from unit 1. **A**. *Hypsoclypus* aff. *lucae* (Desor *in* Agassiz and Desor, 1847). **B**. *Hypsoclypus* sp. **C**. *Schizaster eurynotus* Sismonda, 1842. **D**. *Spondylus* aff. *crassicosta* Lamarck, 1819. **E**. *Flabellipecten fraterculus* (Sowerby, 1841). **F**. *Maltaia* aff. *costae* (Seguenza, 1871). **G**. *Terebratula maugerii* Boni, 1933. **H**. Fish vertebra. **I**. Radiole of Cidaridae. **J**. Caryophylliidae indet. **K**. Cerioporidae indet. Scale bar: 10.0 mm for all views but J3 (1.0 mm).

common tubes of the serpulid *Ditrupa arietina* (Müller, 1776), rare terebratulid brachiopods (*Terebratula maugerii* Boni, 1933), and decapod crustaceans represented almost exclusively by the ghost shrimp "*Callianassa*" cf. *almerai*. In the sandy to silty sediments, decapod remains are very rare; the assemblage of unit 1 is dominated by the pectinids *Aequipecten seniensis* (Lamarck, 1819) and *Flabellipecten fraterculus* (Sowerby, 1841), ostreoids *Neopycnodonte navicularis* (Brocchi, 1814) and *Ostrea edulis* var. "*lamellosa*" Brocchi, 1814, and echinoids. Abundant trace fossils are almost exclusively limited to the *Entobia* (*sensu* Bromley and Asgaard, 1993) ichnofacies (coarser sediments) and *Teredolites* Leymerie, 1842 (finer sediments). Reddish sandy sediments of unit 1 pass gradually into the reddish sandy siltstones of unit 2.

Local unit 2. Fine-grained, laminated sediments attain a thickness of ~1.7 m. A moderately rich planktonic foraminifera assemblage of ~20 species has been obtained. Benthonic foraminifera are dominated by the miliolids *Triloculina* d'Orbigny, 1826 and *Quinqueloculina* d'Orbigny, 1826, as well as hyaline forms. A poorly preserved macrofauna is represented by bivalves (especially small pectinids), serpulids (well-preserved specimens of *Ditrupa arietina* Müller, 1776), echinoids (fragments of spatangoids and diademataceans), and small oxidized plant fragments. A single dactylus of an unidentified brachyuran crab is the only decapod from this unit. Occasionally, small sandy patches are present throughout the unit, similar to those commonly found in unit 3.

Local unit 3. There is a fault between units 2 and 3. The lower boundary of unit 3 cannot be observed in the field, whereas its upper part is progressively coarser and finally overlain by sediments of unit 4. The minimum thickness of unit 3 is ~1 m. It is mainly composed of massive to laminated, sand to silt-sized (siltstones, sandy siltstones, and fine sandstones), dark-coloured sediments. Macrofauna is generally rare, although some plant and echinoid fragments are immediately visible. The assemblage is dominated by echinoids (almost exclusively the spatangoids *Brissopsis* aff. *duciei* Wright, 1855 and rare specimens of *Schizaster* sp.; Fig. 15) and bivalves (mainly pectinids and anomiids). Fish scales are common and sometimes clustered. Other groups include deep-water brachiopods (Gryphinae?), deep-water corals (Stenocyathidae Stolarski, 2000), regular echinoids (radioles), and gastropods. Both planktonic and benthic foraminifera are common. Bioerosion is absent, whereas some non-bioeroding ichnofossils are locally common, but they never form dense associations. Macroflora are dominated by azonal elements of the order Poales Small, 1903, and small-sized lauroid leaves. Decapod crustaceans are represented by at least six genera including *Ctenocheles* Kishinouye, 1926, *Raninoides* Milne-Edwards, 1837, *Calappa* Weber, 1795, *Styrioplax* Glaessner, 1969, *Goneplax* Leach, 1814, and *Typilobus* Stoliczka, 1871.

Local unit 4. This unit consists of greyish heterometric (including some blocks of up to 1 m in diameter embedded in a silty-sandy matrix) and polymictic coarse siliciclastic sediments with a total thickness of 22–23 m. Bedding is hardly visible. In these coarse sediments, macrofauna is common and diverse (Fig. 16), but poorly preserved, although the best preserved ghost shrimp remains are restricted to this unit. The faunal content is roughly similar to the coarser sediments of unit 1, but the particles are less well-cemented. The macrofauna is dominated by mollusks (especially the pectinids *Aequipecten seniensis* (Lamarck, 1819), *Flabellipecten fraterculus* (Sowerby, 1841), and *Talochamys multistriata* (Poli, 1795), as well as ostreoids, mainly *Anomia ephippium* Linnaeus, 1758), echinoderms, crustaceans (callianassids and scalpellid cirripedes), and shark teeth of the families Odontaspididae and Carcharhinidae Jordan and Evermann, 1896. Benthic foraminifera are represented by very common platy nummulitids. Rhodophytes are locally abundant. Cnidarians (e.g., intermodal segments of the bamboo-coral *Keratoisis melitensis* (Goldfuss, 1826) or fragments of hermatypic corals), bryozoans, serpulids (*Ditrupa arietina*); indeterminate tetrapod bones or teleostean remains (teeth and vertebrae) are rarely found. Similar to the coarse siliciclastic sediments of unit 1, trace fossils are dominated by *Entobia* Bronn, 1838, and *Teredolites longissimus* Kelly & Bromley, 1984. Encrustation (by bryozoans and balanid barnacles) occurs rarely and affects some bivalve shells and echinoid coronas. Possible bite marks are rarely found and restricted to some shells of the scallop *A. seniensis*.

6.2. Biostratigraphy

Local unit 1. The occurrence of articulated specimens of *Flabellipecten fraterculus* suggests a Tortonian age (Cárdenas-Carreretero, 2003).

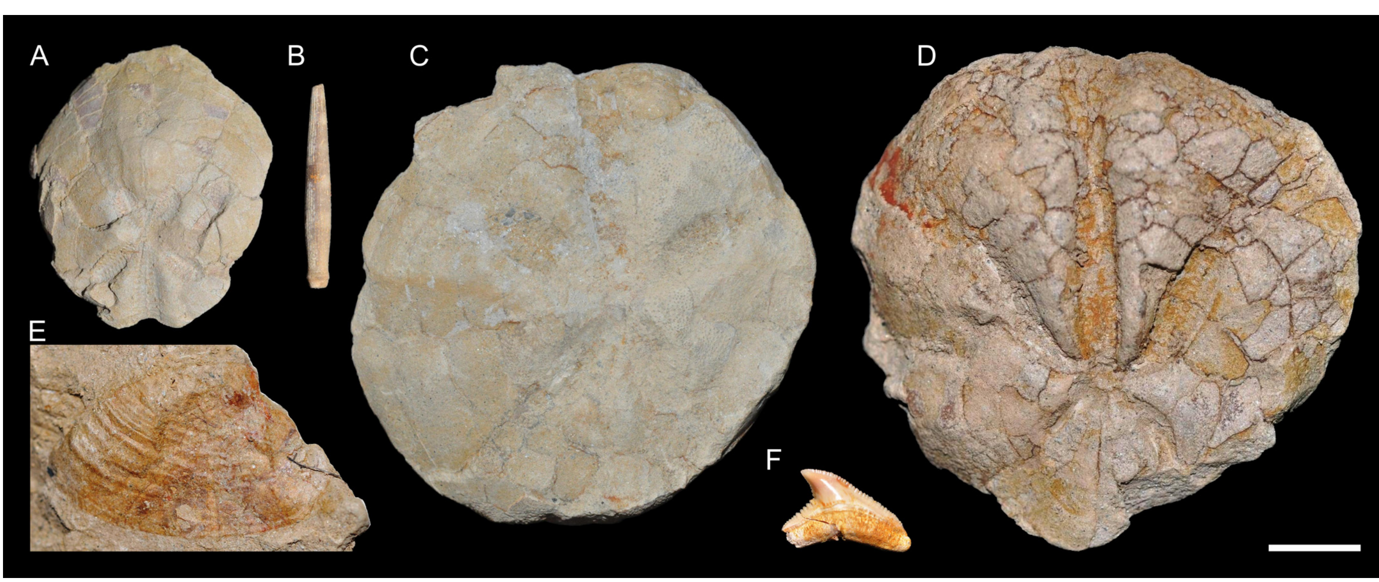

Fig. 15. Selected fossils from unit 3. **A**. *Brissopsis* sp. **B**. Radiole of *Prionocidaris* sp. **C**. *Brissopsis* aff. *duciei* Wright, 1855. **D**. *Schizaster* sp. **E**. Vesicomyidae indet. **F**. Carcharhinidae indet. Scale bar: 10.0 mm.

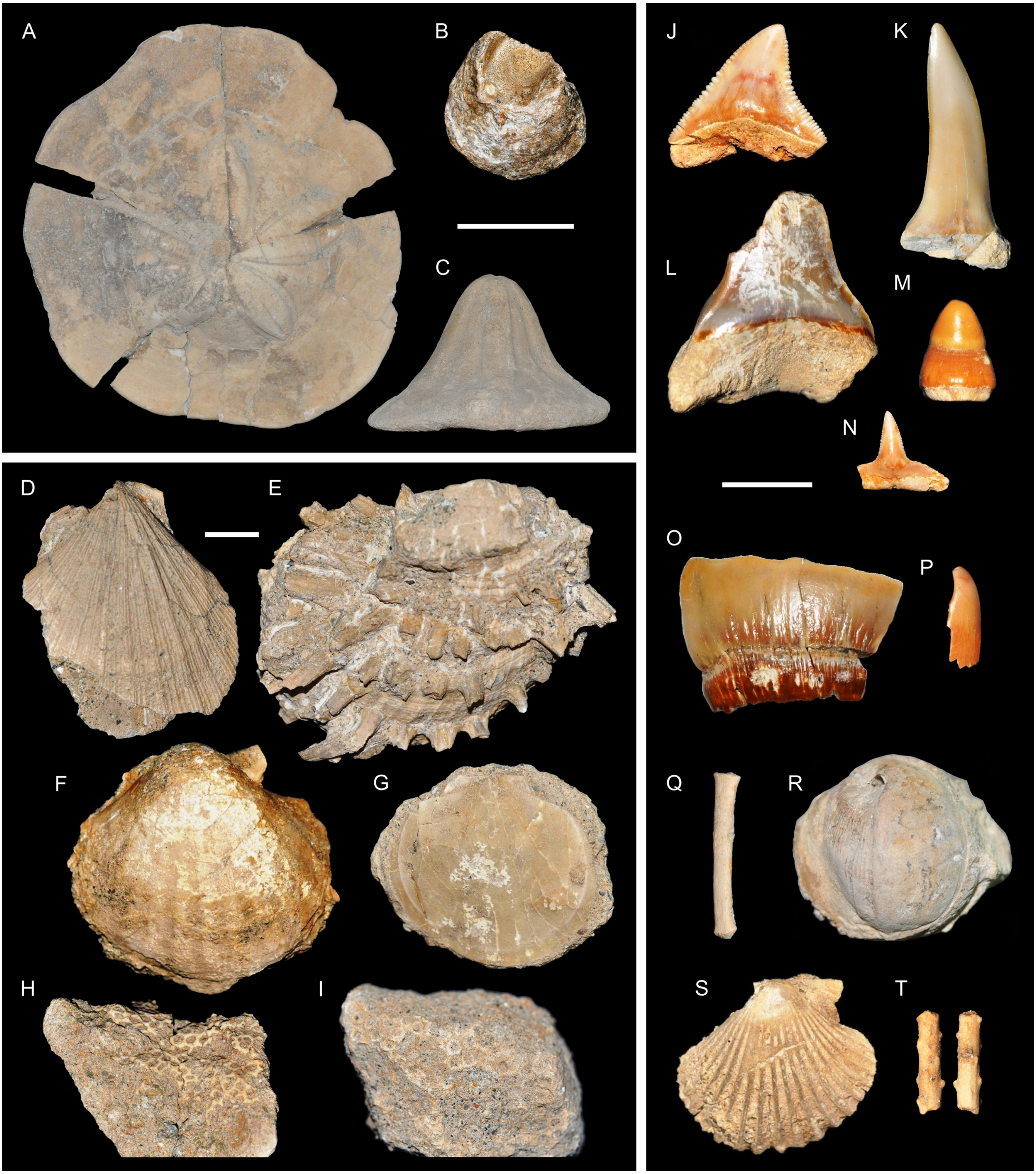

Fig. 16. Selected specimens from unit 4. **A**. Corona of *Clypeaster* forma "*marginatus*" Lamarck, 1816. **B**. *Ostrea edulis* var. *lamellosa* Brocchi, 1814. **C**. Corona of *Clypeaster* forma "*portentosus*" des Moulins, 1837. **D**. *Manupecten jakloweciana* (Kittl, 1887). **E**. *Spondylus concentricus* Bronn, 1831. **F**. *Oppenheimopecten revolutus* (Michelotti, 1847). **G**. *Amusium cristatum* (Bronn, 1827). **H**. *Reteporella* sp. **I**. Abraded fragment of an indeterminate hermatypic coral colony. **J**. *Carcharhinus obscures* (Lesueur, 1818). **K**. *Isurus* sp. **L**. *Parotodus benedeni* (Le Hon, 1871). **M**. Sparidae indet. **N**. *Carcharhinus priscus* (Brocchi, 1883). **O**. *Trigonodon jugleri* (Münster, 1846). **P**. *Balistes lerichei* Bauzà, 1949. **Q**. Internodal segment of *Keratoisis melitensis* (Goldfuss, 1826). **R**. *Jouannetia* aff. *tournoueri* Locard, 1877. **S**. *Aequipecten seniensis* (Lamarck, 1819). **T**. Incomplete radiole of *Histocidaris* aff. *rosaria*. Scale bars: 50.0 mm (A–C), 10.0 mm (D–I), 5.0 mm (J–T).

Local unit 2. A single sample contained the planktonic foraminifers *Neogloboquadrina acostaensis* (Blow, 1959), *Natlantica* Berggren, 1972, *Hirsutella* cf. *gigantea* (Blow, 1959), and *Globorotalia merotumida* Blow and Banner, 1965. Based on the presence of these taxa as well as the absence of taxa typical for the late Tortonian and Messinian (*Globorotalia humerosa* (Takayanagi and Saito, 1962), *Globigerinoides extremus*, *Globorotalia plesiotumida* Blow and Banner, 1965, and *Globorotalia mediterranea* Catalano and Sprovieri, 1969), an early Tortonian age can be estimated, i.e., 11.0–8.8 Ma (Foresi et al., 2002; Stewart, 2003; Hüsing et al., 2009; Corbí et al., 2012). According to the Mediterranean biozonation presented by Iaccarino et al. (2007), sediments of this unit may be correlated to the MMi10 *Globigerinoides obliquus* and MMi11 *Neogloboquadrina acostaensis* Biozones. Given the age of the overlying sediments, a most probable age of 11.0–9.9 Ma is inferred for this unit.

Local unit 3. The sample yielded a few specimens of neogloboquadrinids, suggesting a maximum age of *ca*. 11.8 Ma (Hilgen et al., 2000, 2003; Hüsing et al., 2009). Additionally, the abundance of *Globorotalia merotumida* indicates a maximum age of ~11 Ma (Stewart, 2003). The sample also contained some well-preserved, *in situ* specimens of *Globorotalia challengeri* Srinivasan and Kennett, 1981, a species that disappeared from the Mediterranean at 9.93–9.94 Ma (Hüsing et al., 2009). According to the biozonation of Iaccarino et al. (2007), sediments of unit 3 can be correlated with MMi10 *Globigerinoides obliquus* and the lower part of MMi11 *Neogloboquadrina acostaensis* Biozones. Thus, as for unit 2, unit 3 is also early Tortonian in age (*ca*. 11.0–9.9 Ma).

Local unit 4. No planktonic foraminifera were collected from this last unit. Nevertheless, the co-occurrence of the pectinids *Flabellipecten fraterculus* and *Pecten praebenedictus* Tourmouër *in* Dollfus and Dautzenberg, 1920, suggests a Tortonian age (Cárdenas-Carreretero, 2003; Courville and Bongrain, 2003). It is worth noting similarities between Miocene carbonatic blocks from units 1 and 4. These blocks, synchronous with the deposition of early Tortonian siliciclastic sediments, suggest development of a similar warm shallow carbonate platform.

7. Discussion

7.1. Sedimentology and biostratigraphy

Although the stratigraphic record of the late Tortonian onwards is relatively well constrained for the Granada Basin, older Neogene stratigraphy is poorly known due to the scarcity and generally poor quality of outcrops (e.g., Martín-Suárez et al., 2012). The El Caracolar section is an exception. Sediments similar to those exposed in local units 1 and 2 can be found also in outcrops ~1.5–2.0 km to the SE, near Puerto Lobo (Viznar municipality). Sediments of unit 3 seem to be unique to the vicinity of the El Caracolar section. Lithologically similar sediments to those exposed in the unit 4 are exposed ~30–35 km southward, in a small outcrop in the Murchas municipality (south-eastern Granada Basin).

Aguirre (1961) assigned the sediments exposed at El Caracolar to the "Helvetian" (= Serravallian) stage. From the 1980s onward and without biostratigraphic proxies, this locality has been considered coeval with the biocalcarenites of the Unit I of the Granada Basin infill (e.g., Braga and Aguirre, 2001; Braga et al., 2003). Recent biostratigraphic analyses focusing on planktonic foraminifers (Corbí et al., 2012) suggested an early late Tortonian age for these biocalcarenites because of the presence of *Globigerinoides extremus* Bolli and Bermúdez, 1965, and *Neogloboquadrina acostaensis* (Blow, 1959), as well as the absence of *Globorotalia suterae* Catalano & Sprovieri, 1971.

On the basis of eustatic criteria, some authors (e.g., Rodríguez-Fernández et al., 1999; Viseras et al., 2004) considered the existence of an onshore (and usually offshore too) hiatus in the Betic Cordillera corresponding to the early Tortonian. Our results corroborate with this age estimate: based on the foraminifers of unit 3, the age is early Tortonian (*ca*. 11.0–9.9 Ma).

7.2. Palaeoenvironmental interpretation

The abundance of clastic, polygenic and heterometric grains together with the barely visible and rare stratification and lamination, the presence of typically deep-water faunal elements, and the absence of taxa restricted to bathyal settings suggest that deposition took place in the outer neritic zone (*sensu* Poag, 1981, and Culver, 1988), as a part of a deltaic system (Manteca-Martínez et al., 2004), with shallower taxa and coarser sediments that were deposited due to storms and/or tectonism (i.e., earthquakes causing gravity flows; Dabrio, 1990). The occurrence of vesicomyid and thyasirid bivalves at the base of the unit 1 and throughout units 3 and 4 suggest the existence of a chemosynthetic community at the time of deposition of the sediments now exposed at El Caracolar. Chemosynthetic bivalves have also been reported from other early Tortonian localities of the Granada Basin such as Albuñuelas and Murchas (Rivas et al., 1999, and references therein). The mesotrophic conditions suggested by most if not all of the sequence are typical of early Tortonian carbonate platforms throughout the western Proto-Mediterranean Sea (Pedley et al., 1976, 1992; Pedley, 1996) or the entire Proto-Mediterranean Sea (Pomar and Hallock, 2007, 2008).

Local unit 1. The selachian association dominated by *Carcharias acutissimus* (Agassiz, 1843) and almost entirely devoid of larger pelagic forms strongly suggests deposition in a narrow inlet close to the coast for units 1 and 4 (Antunes and Balbino, 2003; Antunes and Balbino, 2004; Vialle et al., 2011). The high abundance of nummulitids, lamniform sharks, as well as ample evidence of encrustation and bioerosion throughout unit 4 is consistent with high primary productivity and with mesotrophic environments (James et al., 1999; Lescinsky et al., 2002; Marsili et al., 2007).

Local unit 2. The occurrence of miliolids dominated by *Quinqueloculina* d'Orbigny, 1826 and *Triloculina* d'Orbigny, 1826 is probably related to the existence of an open inlet in the vicinity of the coast (Norton, 1930; Lowman, 1949; Bandy and Arnal, 1960; Bandy, 1964; Luczkowska, 1974). The co-occurrence of the planktonic foraminifera *Neogloboquadrina incompta* (Cifelli, 1961), *Turborotalita quinqueloba* (Natland, 1938), and *Globigerina bulloides* d'Orbigny, 1826, points toward upwelling conditions (Bé and Tolderlund, 1971; Cifelli, 1973) during the deposition of unit 2.

Local unit 3. In this unit, the dominance of low-oxygen foraminiferal assemblages among benthic foraminifers, together with the high abundance of *G. bulloides* among planktonic ones, the presence of *Globobulimina affinis* (d'Orbigny, 1839), and some chemosynthetic bivalves (e.g., the mytilid ?*Adipicola* Dautzenberg, 1927), suggests deposition in a mesotrophic setting close to the Oxygen Minimum Zone (e.g., Fischer, 1990; Jorissen et al., 1995; Fontanier et al., 2002, 2005; Duperron, 2010; Krylova and Sahling, 2010). The presence of a vesicomyid clam close to the preserved base of unit 1 and the presence of a thyasirid bivalve on top of unit 4 suggest the existence of a chemosynthetic community throughout the whole time span of deposition of sediments at El Caracolar. The abundance in unit 3 of the foraminifer *Nonion* De Montfort, 1808, suggests relatively good connections with open marine waters (Drinia et al., 2003).

Local unit 4. The selachian association is very close to that present in unit 1. Thus, a high primary productivity in mesotrophic environments may have also dominated this unit. The presence of mollusks, the echinoid *Clypeaster* Lamarck, 1801, barnacles, serpulids, and sirenian bones indirectly suggest the extensive occurrence of seagrass meadows on the inner ramp (Hoffman, 1979; Ivany et al., 1990; Brasier, 1995; Beavington-Penney et al., 2004) at least during the deposition of unit 4.

7.3. Climate

Local unit 1. The co-occurrence of the echinoderms *Clypeaster*, *Hypsoclypus* Pomel, 1969, and *Astropecten* cf. *granulatus* Müller and Troschel, 1842, suggests a (sub)tropical climate (Ghiold and Hoffmann, 1984, 1986; Ghiold, 1989; Rowe and Gates, 1995; Slack-Smith, 1998; Zuschin and Oliver, 2003; Zuschin and Baal, 2007; Pereira, 2010). The absence of tropical forms among sharks, such as *Hemipristis* Agassiz, 1843, *Negaprion* Whitley, 1940, or *Ginglymostoma* Müller and Henle, 1838, points to subtropical rather than tropical conditions (Longbottom, 1979).

Local unit 2. No paleoclimatic indicators have been found in sediments of this unit.

Local unit 3. The benthic foraminifer *Discorbina planorbis* (d'Orbigny, 1846) is usually restricted to (sub)tropical conditions (Murray, 1991). The dominance of *Globigerina bulloides* and *Globigerinoides* spp., as well as the rarity of neogloboquadrinids and *Globorotalia scitula* (Brady, 1882), suggest that a high primary productivity resulted from the fluvial input of organic matter (and not from upwelling) in (sub)tropical conditions (Bé and Tolderlund, 1971; Boltovskoy and Wright, 1976; Bé, 1977; Bé and Hutson, 1977; Hemleben et al., 1989; Van Leeuwen, 1989; Bijma et al., 1990; Rohling et al., 1993). Macrofloral remains are restricted to mega-mesothermic (dominated by nanophyll leaves) and azonal elements, suggesting dry (sub)tropical conditions on land close to the water (McDonald et al., 2003; Popescu et al., 2010).

Local unit 4. The occurrence of the same taxa mentioned for unit 1 with the exception of the echinoid *Hypsoclypus* (absent in unit 4) and the abundance of nummulitids suggest (sub)tropical conditions. Furthermore, the abundance of the boring bivalve *Jouannetia* aff. *tournoueri* Locard, 1877, in addition to some remains of the echinoderm *Astropecten* cf. *granulatus*, suggests tropical rather than subtropical conditions (Rowe and Gates, 1995; Betzler et al., 1997).

7.4. Palaeobathymetric estimation

Water depths most likely fluctuated from 70 to 130 m, with shallowest depths probably occurring in the lowermost unit. The depth estimation is based on the macrofauna coupled with its mode of preservation. Additionally, the planktonic foraminifera zonal scheme of Iaccarino et al. (2007) within the framework of Lourens et al. (2004) was adopted.

Local unit 1. The occurrence of some bivalves (*Neopycnodonte navicularis* (Brocchi, 1814), *Pecchiolia arietina* (Brocchi, 1814), and a specimen of the family Vesicomyidae), decapods (*Ctenocheles*), cnidarians (Caryophylliidae Gray, 1847), and broken platy nummulitid foraminifers suggest a minimum depth of 70–100 m (Vaughan and Wells, 1943; Wells, 1956; Cairns, 1982; Freneix et al., 1988; Hallock and Pomar, 2008; Simone and Cunha, 2008; Krylova and Sahling, 2010; Sakai, 2011). On the other hand, the near absence of rhodoliths from finer sediments is noteworthy given their high preservation potential (Bosence, 1983); this may be related to elevated turbidity levels associated with fine-grained sediments (linked to mesotrophic to eutrophic environments), or to the final deposition in an offshore environment of depths exceeding 100–150 m (Walker et al., 1998; Rivas et al., 1999; Foster, 2001). Considering the depth of the sedimentation of the overlying unit (see below), the vertical continuity among them as well as the absence of typical or exclusive bathyal elements, a most probable palaeodepth of 70–130 m (i.e., the middle to outer neritic zone *sensu* Poag, 1981 and Culver, 1988, or the circalittoral zone *sensu* Pérès and Picard, 1964) is estimated for this unit.

Local unit 2. The absence of *Pyrgo* Defrance, 1824, and *Pyrgoella* Cushman and White, 1936, among miliolids, suggests deposition in the neritic zone (Luczkowska, 1974). Porcelanaceous foraminifera are dominated by the miliolids *Triloculina* and *Quinqueloculina*, which, in the westernmost Mediterranean Sea, thrive at depth ranges of 70–235 and 20–130 m, respectively (Milker and Schmiedl, 2012). The preservation of large quantities of these miliolids indicates limited transport of their tests (Mateu-Vicens et al., 2008). Among planktonic foraminifera, the co-occurrence of *Sphaeroidinellopsis seminulina* Schwager, 1866, and *Globorotalia merotumida* suggests a water depth exceeding 100 m (Kennett and Srinivasan, 1983; Kroon and Nederbragt, 1990; Murray, 1991; Ovechkina et al., 2010). The absence of rhodoliths is consistent with depths below 100 m (Walker et al., 1998; Foster, 2001). In conclusion, the inferred palaeodepth for this unit is 100–130 m (i.e., the outer neritic zone *sensu* Poag, 1981 and Culver, 1988, or the circalittoral zone *sensu* Pérès and Picard, 1964)

Local unit 3. The occurrence of the decapods *Raninoides*, *Ctenocheles*, *Styrioplax*, and *Goneplax* suggests outer neritic depths (Goeke, 1985; Ribes, 1989; Chen and Sun, 2002; Neumann et al., 2010; Hyžný and Schlögl, 2011; Sakai, 2011; Vaitheeswaran et al., 2013; Gašparič and Hyžný, 2015). The co-dominance of the benthic foraminifers *Globobulimina affinis*, *Cancris auriculus* (Fichtel and Moll, 1798), *Valvulineria complanata* (d'Orbigny, 1846), and *Nonion commune* (d'Orbigny, 1846) suggest depths of *ca.* 100 m, not exceeding 180 m (Rögl and Spezzaferri, 2003; Spezzaferri and Tamburini, 2007; Milker and Schmiedl, 2012; planktonic foraminifera zonal scheme based on Iaccarino et al., 2007). The presence of vesicomyid bivalves suggests a depth exceeding 100 m (Krylova and Sahling, 2010), whereas the Paratethyan occurrences of *Styrioplax* were reported from supposedly upper bathyal assemblages (Hyžný and Schlögl, 2011; Gašparič and Hyžný, 2015). Thus, the best estimate of water depth for deposition of unit 3 is 100–125 m.

Local unit 4. A water depth of 100–130 m is suggested based on the occurrence of the bivalve *Amussium cristatum* (Bronn, 1827) throughout the unit, together with the cirriped *Arcoscalpellum* Hoek, 1907, the bamboo-coral *Keratoisis melitensis* (Goldfuss, 1826) (restricted to the upper part of the unit), the cidaroid echinoid *Histocidaris* aff. *rosaria* (Bronn, 1831), the mitsukurinid shark *Mitsukurina* Jordan, 1898, and high numbers of platy nummulitids (Freneix et al., 1987; Rowe and Gates, 1995; Young, 2001; Compagno, 2001; Donovan et al., 2005; Hallock and Pomar, 2008; Chan et al., 2009). Additionally, the abundance of rhodoliths suggests depths not exceeding 100–150 m (Walker et al., 1998; Rivas et al., 1999; Foster, 2001).

7.5. Palaeobiogeographical implications of the decapod fossil assemblage

The decapods of El Caracolar show affinities with those found in the Proto-Mediterranean and the Paratethys *sensu* Harzhauser et al. (2002, 2007) (Hyžný, 2016). All reported genera except *Styrioplax* were previously known from the Miocene of Proto-Mediterranean (Veiga-Ferreira, 1965; Philippe and Secrétan, 1971; Müller, 1993; Gatt and De Angeli, 2010; Garassino et al., 2013). The occurrence of *Styrioplax* is rather surprising, suggesting either its migration from the Paratethys to the Proto-Mediterranean or *vice versa*. Based on the anti-estuarine circulation (Kroh and Harzhauser, 1999; Harzhauser et al., 2003; Báldi, 2006; Moissette et al., 2006), marine faunas migrated predominantly from the Proto-Mediterranean to the Paratethys during the middle Miocene. After Paratethyan populations were established, some seaways closed (Rögl, 1998, 1999; Popov et al., 2004), and surviving species

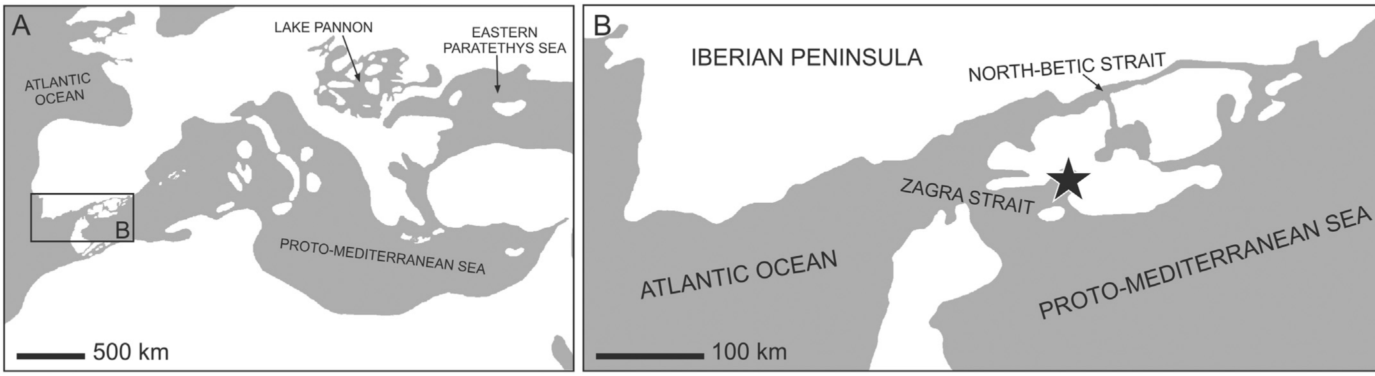

Fig. 17. Palaeogeographic reconstruction of the Proto-Mediterranean region (A) and the westernmost Proto-Mediterranean area (B) during the earliest Tortonian. **A.** Composite map modified after Rögl (1998, 1999), Magyar et al. (1999), and Paramonova et al. (2004). **B.** Map modified after Martín et al. (2014). The location of El Caracolar is indicated with an asterisk.

evolved into endemic taxa. Originally, *Styrioplax* was thought to represent such a Paratethyan endemic genus (Gašparič and Halásová, 2015; Hyžný and Gross, 2016). However, its discovery in the upper Miocene strata of Spain suggests an earlier origin in the Proto-Mediterranean. Its apparent absence in the early Miocene of the Proto-Mediterranean can be ascribed both to a collecting bias against decapods and/or to a low number of outcrops with sediments from the lower Miocene (but see Philippe and Secrétan, 1971; Fraaije et al., 2008b; De Angeli and Beschin, 2011).

The close proximity of the Granada Basin to the Atlantic Ocean (Fig. 17) is reflected in the similarities between decapod assemblages described from the middle Miocene of Portugal by Veiga-Ferreira (1958, 1965) and the assemblage of El Caracolar reported here. It has to be noted that, with the exception of *Callianassa lusitanica* (questionable status, see above) and *Portunus delgadoi*, all taxa reported from the Miocene of Portugal (Veiga-Ferreira, 1954, 1958, 1961, 1965) are also known from the Proto-Mediterranean basins. Thus, migrations between the Atlantic Ocean and the Proto-Mediterranean did occur during the early and middle Miocene. Later in the late Miocene (late Tortonian), the seaway was restricted (Corbí et al., 2012), hindering migration from the Atlantic Ocean into central-European basins. Then during the Messinian Salinity Crisis, when the marine connection was restricted, the marine faunas of the Proto-Mediterranean became severely impoverished (Hsü et al., 1978; Harzhauser et al., 2002; Krijgsman et al., 2010).

8. Conclusions

For the first time, an integrated study of sedimentological, palaeontological, and palaeoecological features of the Miocene sediments of the El Caracolar section is presented. Our evaluation of the highly diverse fossil association points toward a mesotrophic regime similar to that of other outcrops of the Granada Basin that was widespread in the Proto-Mediterranean region from the Burdigalian up to the early Tortonian. This regime was probably responsible for the presence of a varied chemosynthetic community in the Granada Basin. The analysis of the fossil content of this section suggests the predominance of (sub)tropical conditions during the time of deposition, in concordance with other roughly coeval sites (e.g., Albuñuelas patch reef) in the Granada Basin.

The allochtony of most of the fossils together with the moderate to high nutrient input, the variety of substrata and/or time-averaging were probably responsible for such an exceptionally diverse association. The high diversity of the association substantially increases the knowledge of the Tortonian in this region. Furthermore, the stratigraphic outline for this site can be a basis for further stratigraphic work on the Tortonian sediments and fossils of the Granada Basin. This association includes the first fossil decapods described for the Granada province. It resembles assemblages from southern Portugal or from the Proto-Mediterranean area, highlighting the biogeographic links with these two areas.

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Appendix A. Supplementary data

Supplementary data (taxonomic list of all fossil taxa found to date at the El Caracolar locality and their occurrence within the four sedimentological local units) associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.geobios.2017.04.003.

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