

Patterns of occurrence and distribution of crustacean ichnofossils in the Lower Jurassic–Upper Cretaceous of Atlantic occidental margin basins, Portugal

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ABSTRACT:

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Crustacean ichnofossils are most abundant in the stratigraphic record of Portugal. In this paper is presented a study on crustacean ichnoassemblages from the Sinemurian to middle Cenomanian, during the opening and subsequent filling of Atlantic occidental margin basins (Lusitanian Basin and western part of Algarve Basin). *Thalassinoides* dominates the lagoonal and inner shelf facies from the late Sinemurian at least to the Turonian, generally defining all of the carbonate sequence with its dense, “nodular” ichnofabric since the Late Jurassic. A sequence is described in the lower Barremian of Cabo Espichel in which burrow mazes of *Thalassinoides suevicus* occur, containing hundreds of *Mecochirus rapax* as an obrution *lagerstätte*. The Cretaceous of the Lusitanian Basin is rich in marly limestones mottled with *Thalassinoides* but almost devoid of *Rhizocorallium*. Fairly common in dark marls and biomicrites from the Jurassic, *Rhizocorallium irregulare* locally occurs in dense monospecific fabrics. Slipper-shaped and oblique forms (*Rhizocorallium jenense*) as well as spiral and lobate forms are rhizocoralliid foraging modifications usually developed in deeper tiers than *Thalassinoides* and sometimes evidencing bioimprints in *Glossifungites* preservation. Siliciclastic facies related to rifting subsidence along major fault scarps and fan deltas/braided river depositional systems show pervasive bioturbation with *Psilonichnus tubiformis*. Another crab-style behaviour ascribed to *Macanopsis plataniformis* is described for the first time in Portugal, associated with a coarse-grained sandstone episode in a tidal flat setting from the Kimmeridgian, where monospecific brachyuran burrows were developed in a firmground.

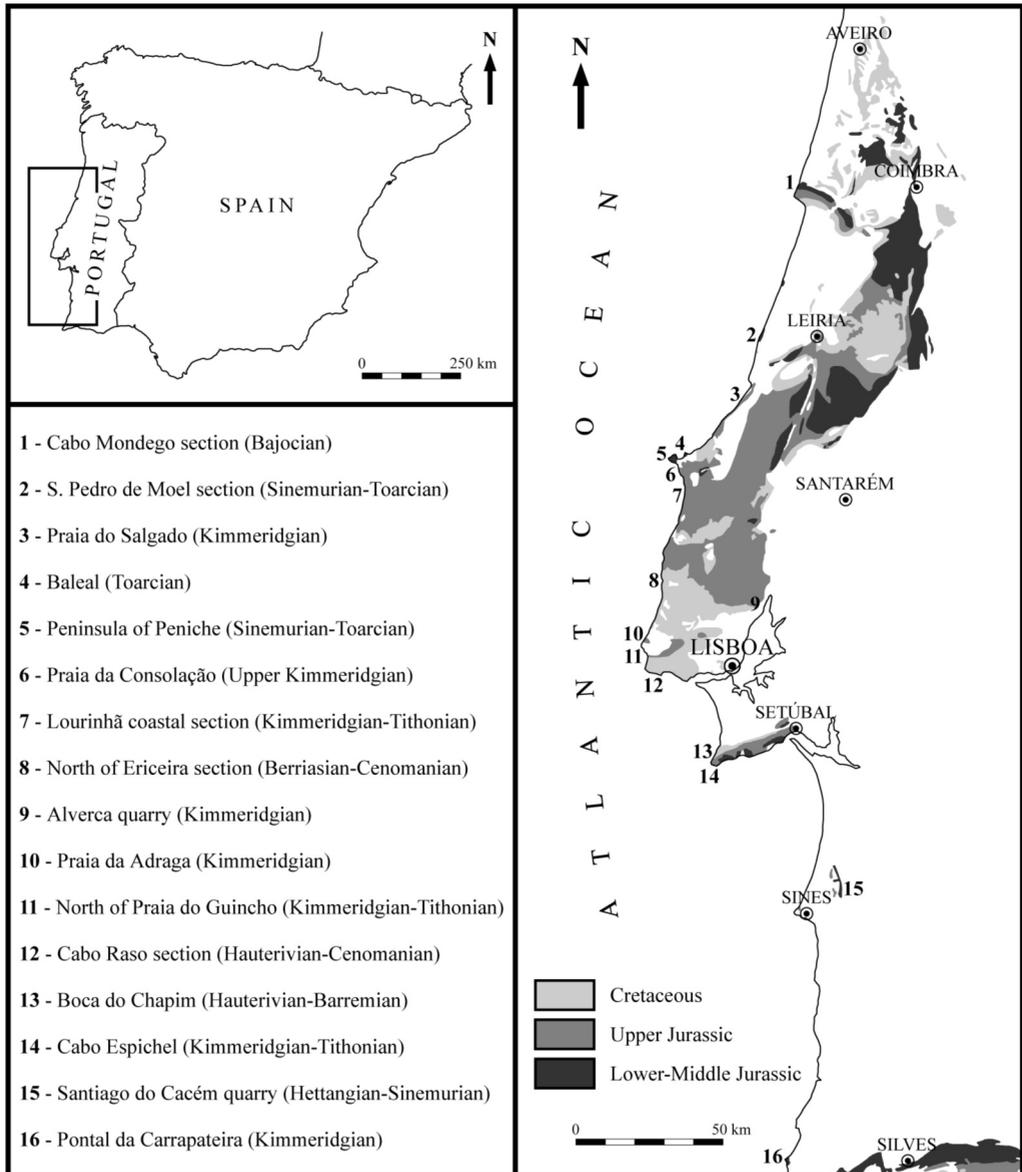
Keywords: Crustacean burrows; Stratigraphic distribution; Palaeoenvironments; Sinemurian–Cenomanian; Portugal.

INTRODUCTION

Since the Metazoan Revolution arthropods have progressively dominated all environmental settings, from air to the deep sea and the deepest soil profiles, leaving their fingerprints in practically all kinds of substrates from leaves and soupgrounds to rock-grounds and human bones. In fact, Häntzschel (1975) reported more than 70 ichnogenera attributable to arthropods, and many more have been described since then. Arthropod infaunalization became prominent especially in the Mesozoic with the radiation of crustaceans and especially malacostracans (Förster 1985;

Briggs and Clarkson 1990). The trace fossil record is dominated by permanent dwelling/feeding burrows, mostly attributed to *Thalassinoides*, occurring from fluvial to deep-sea settings. This was mainly a protective evolutionary strategy since a concealed *modus vivendi* offered protection without sacrificing mobility by resorting to a heavily armoured exoskeleton (Kluessendorf and Mikulic 1990).

The trace fossil record of crustaceans in Portugal is, not surprisingly, abundant and diversified despite being systematically studied only during the past thirty years (Wilson 1979; Fürsich and Schmidt-Kittler 1980; Fürsich 1981). The oldest record of crustaceans is that of

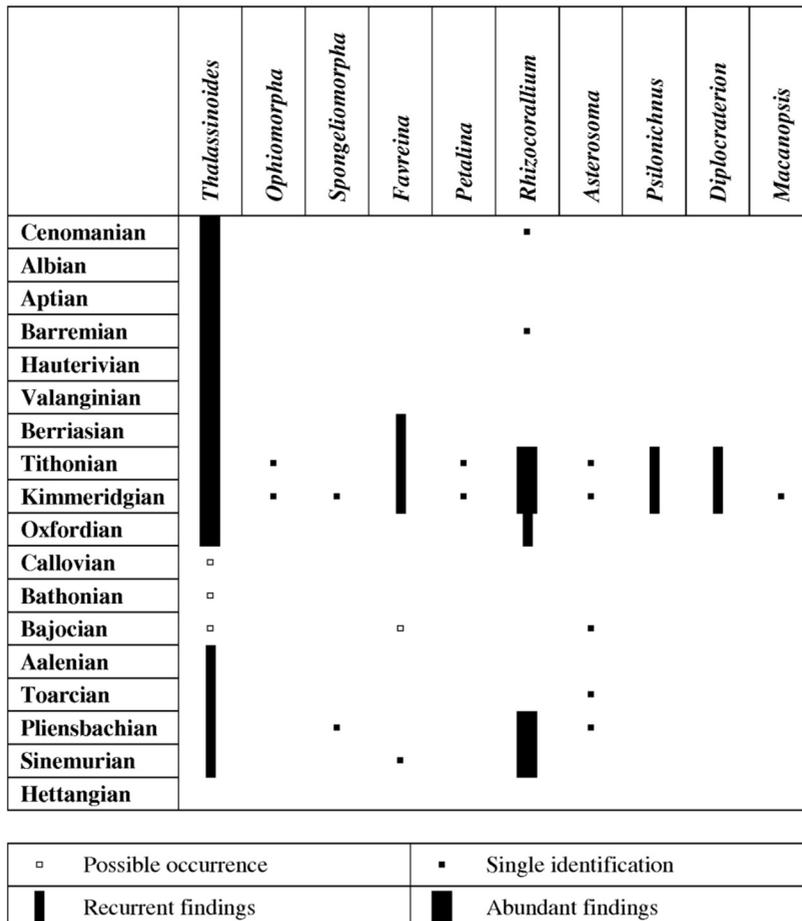


Text-fig. 1. Geological map of Atlantic occidental margin basins in Portugal with location of the main sections studied in this work. General stratigraphy adapted from Boillot and Mougénot (1978)

trackways, *Merostomichnites* (Cooper and Romano 1982; Neto de Carvalho 2003) of Floian age (Lower Ordovician). These are interpreted as phyllocarid cur-sichnia imprinted by similar foliaceous ventral appendages typical of these malacostracans (Neto de Carvalho 2003). But it is during the Mesozoic and especially after the Late Jurassic that crustacean burrows became the most representative biogenic structures (Text-fig. 1), mottling almost all marginal-marine sedimentary sequences with a characteristic nodular ichnofabric. The present work results from a thorough study of Mesozoic trace fossils in the Portuguese Atlantic-related aulacogenic basins that have been carried out by the authors since 1998. Here we present the major results of a study of crustacean-interpreted burrowing and biodepositional behaviours summarizing ten ichnogenera (Text-fig. 1). Most of the work until now has been devoted to the Lusitanian Basin, with only a few observations carried out in the westernmost part of Algarve Basin, at Pontal da Carrapateira where *Rhizocorallium* beds abound.

DEPOSITIONAL SETTING AND BIOTURBATION IN THE CONTEXT OF RIFTING BASINS ASSOCIATED WITH THE OPENING OF THE CENTRAL AND NORTH ATLANTIC

The history of the Lusitanian and Algarve basins is intrinsically determined by the processes involved in the opening of the Atlantic Ocean, by their location between this and the Tethys Ocean. The evolution and sedimentary filling of both basins were conditioned by reactivation of major tardi-Variscan oriented faults during rifting phases, delimiting strongly subsiding grabens and sub-basins. Thus, the Lusitanian Basin is a NE-SW oriented basin, 300 km long and 150 km wide (including immersed area) with carbonate and siliciclastic sequences 5 km thick; the Algarve Basin extends for a W-E length of 150 km, being up to 30 km wide and with as much as 3000 m of sedimentary fill (Azerêdo *et al.* 2003; Text-fig. 2). The first aborted rifting stage occurred in the Late Triassic in both basins. The dynamic and irregular topography that developed



Text-fig. 2. Time-abundance chart of crustacean-related ichnogenera in the Lusitanian Basin, Santiago do Cacém Sub-basin and W sector of Algarve Basin. Information compiled from fieldwork and the literature

was filled mostly during the Hettangian–Callovian megacycle. Deposition started in the Late Triassic with alluvial fan to fluvial redbeds and sabkha-related evaporitic sediments and fissural tholeiitic volcanism.

The Lusitanian and Algarve basins were opened to marine influence only after the upper Sinemurian with the installation of low-energy carbonate homoclinal ramps. Proximal ramp limestone-marl deposits in the Lusitanian Basin commonly show bioturbation with *Rhizocorallium* as in São Pedro de Moel and Peniche Peninsula sections. Small *Thalassinoides* and *Spongiomorpha* are also common. During the Toarcian–Aalenian, differentiation increased between the distal and proximal ramp with the development of hemipelagic deposits with ammonites and calciturbidite fans coming from the newborn Berlengas horst that delimited the Lusitanian Basin to the west (Duarte 1997). *Thalassinoides* is present in tide-dominated shallow marine sequences with dense ichnofabrics after the Toarcian. After the Aalenian–Bajocian transition the regressive trend increased. Most of the Lusitanian Basin was occupied by a high-energy carbonate ramp. Marginal-marine limestones were widespread during the Bajocian–Bathonian time. Distal ramp and calciturbidite deposits are only found in the Cabo Mondego and Baleal sections showing increase of ramp steepness due to fault reactivation (Azerêdo et al. 2003). The Dogger–Malm transition is marked by an angular unconformity between upper Callovian and middle Oxfordian due to tectono-eustatic causes.

The second aborted rifting stage happened in the late Oxfordian–Kimmeridgian. Sub-basins developed in strongly subsiding halfgrabens largely due to salt withdrawal, with deep block faulting and tilting. Marginal marine to terrestrial siliciclastics dominated the depositional sequence during the Late Jurassic to Early Cretaceous, punctuated only by marine transgressions from the southwest. Rapid advances of alluvial fan toes triggered by tectonic activity were followed by gradual retreat and establishment of subtropical marine conditions (Hill 1989). Fore-reef slope calciturbidites in a depocentre restricted to the Lisbon sector, reefs and mixed carbonate-siliciclastic platforms strongly influenced by terrigenous and freshwater influxes represent the most distal marine facies (Leinfelder 2001). In prodeltas or

brackish bays and confined lagoons crustacean burrows and biodepositional structures proliferated and diversified (Text-fig. 1). Large-diameter *Thalassinoides* and *Rhizocorallium* mottle most of the carbonates but are usually mutually exclusive in depauperate ichnoassemblages. *Rhizocorallium* became uncommon after the Tithonian. *Psilonichnus* ichnofacies and ichnogenus are common in marginal-marine sandstones.

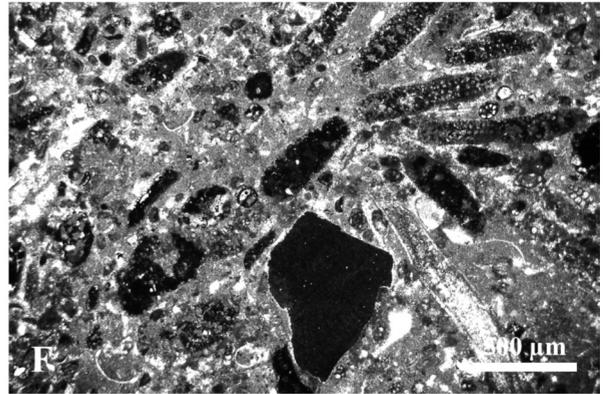
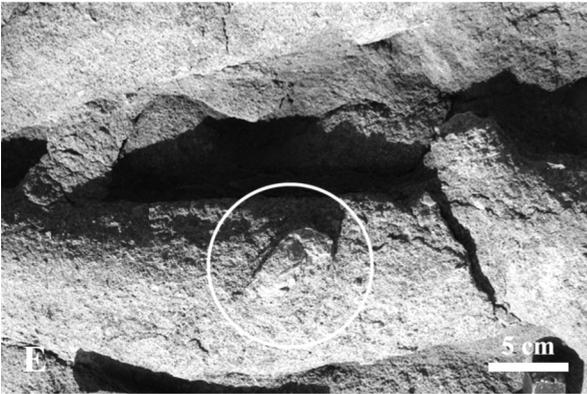
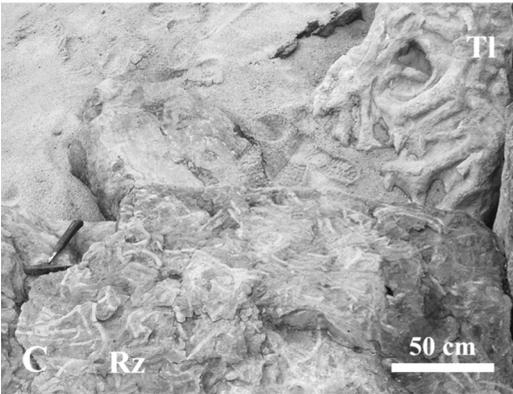
During the Early Cretaceous sedimentation was connected with a long period of thermal detumescence by crustal cooling. The Cretaceous strata of the Algarve Basin were deposited on a shallow ramp that opened to the south. Deposition occurred in open mixed platforms under the strong influence of braided and meandering river systems draining westward from the pre-Mesozoic Iberian Massif, which progressively covered the whole Lusitanian Basin (Rey et al. 2006). The rapid regression during the early Barremian is related to thermal swelling with the beginning of oceanic crust formation in the western margin of Iberia. The transition between continental break-up and passive oceanic margin in this part of the Atlantic Ocean occurred in the late Aptian (Rey et al. 2006). The definitive opening of the North Atlantic moved to west of the Berlengas horst. The Cenomanian transgression was amplified during middle Cenomanian time with inner-shelf deposition of limestones and marls having dense *Thalassinoides* ichnofabrics but rare *Rhizocorallium*. This carbonate ramp was bordered by rudist reefs during the late Cenomanian–Turonian. Sedimentary culmination occurred later in the Campanian. In the Algarve Basin post-Cenomanian non-sedimentation corresponds with a major geodynamic event that is related to the beginning of compression between Africa, Iberia and Eurasia.

REMARKS ON THE CRUSTACEAN ICHNOLOGY OF LUSITANIAN AND ALGARVE BASINS: BEHAVIOURS, POSSIBLE PRODUCERS AND OCCURRENCE TRENDS

Thalassinoides and the lobster that made it

Thalassinoides is probably the dominant arthropod burrow in the geologic record (Seilacher 1986).

Text-fig. 3. Crustacean burrows from the Mesozoic of Portugal. A – Bioclastic limestone level extending more than 200 m, highly bioturbated with wide *Thalassinoides suevicus* (Kimmeridgian, Serra da Pescaria quarry near Praia do Salgado). Partial view of the exposure; Joana Rodrigues near the pine as scale. B – Recurrence on the bedding soles of *Rhizocorallium jenense* in dense ichnofabrics from the Kimmeridgian of the Pontal da Carrapateira. C – Monospecific beds of *Rhizocorallium irregulare* (Rz) and *Thalassinoides suevicus* (Tl). The slabs are from the same unit; Kimmeridgian of Praia do Salgado). D – Coarse-grained siliciclastic filling of *Thalassinoides suevicus* with its producer (Lower Barremian, Boca do Chapim Formation, Cabo Espichel). E – Bioclastic marly limestones commonly preserve *Mecochirus rapax* within *Thalassinoides* (same section). F – Intrabiomicrosparite packstone with *Choffatella decipiens* Schlumberger and subangular quartz grains filling *Thalassinoides* (same provenance). G – Almost complete *Mecochirus rapax* in the fill of *Thalassinoides suevicus* showing preservation of long chelae and other delicate structures (same provenance). H – Bioimprints crisscrossing in the terminal tunnel of *Rhizocorallium irregulare* (Kimmeridgian, Praia do Salgado)



The *Thalassinoides* ichnognild dominates the lagoonal and inner-shelf mixed clastic-carbonate settings from the middle Oxfordian at least to the Turonian in Portugal, commonly defining the entire carbonate sequence with its related “nodular” fabric since the Late Jurassic. *Spongeliomorpha sudolica* (Zaręczny) of small diameter is common in the Lower Jurassic sequences, intergrading with narrow *Thalassinoides*. However, only during syn-rifting deposition after the middle Oxfordian did wide *Thalassinoides suevicus* (Rieth) become widespread; these burrows are linear to curving with extensive three-dimensional boxworks densely covering bedding surfaces (Text-fig. 3A). Vertical shafts of *Ophiomorpha* distinctly lined with agglutinated pelletoidal sediment are restricted to high-energy sediments from the Kimmeridgian of Cabo Espichel, whereas favreimid faecal pellets, such as *Favreina* and *Petalina*, assigned to different groups of crustaceans, are mostly found in marls and mudstones from the Kimmeridgian to early Valanginian (Schweigert et al. 1997; for summary see Neto de Carvalho and Farinha 2006).

Recently, Neto de Carvalho et al. (2007) described a sequence in the lower Barremian Boca do Chapim Formation in which burrow mazes of *Thalassinoides suevicus* contain several hundred exceptionally preserved exoskeletons of a single species, *Mecochirus rapax* (Harbort), as an obrution *lagerstatts*, (Text-figs 3D-E). The study of burrow fills indicates episodic flows of coarse-grained to clay-sized sediments from the coast and the fluvial braided system (with contributions from alluvial fans) near the lagoon sector (Text-fig. 3F). These sedimentary conditions lead to successive smothering and complete preservation of *Mecochirus* within *Thalassinoides* (Text-fig. 3G) by the flood runoff with sudden changes in the water chemistry (lowered salinity and pH; Neto de Carvalho and Viegas 2007).

Thalassinoides connections with the water-substrate interface are mostly vertical or inclined offshoots. Only a single case of *Thalassinoides* possessing helicoidal shafts has been described (Fürsich 1981). The corkscrew shape of *Gyrolithes* is thought to represent a widespread architectural adaptation to deal with extreme salinity fluctuations in Mesozoic and

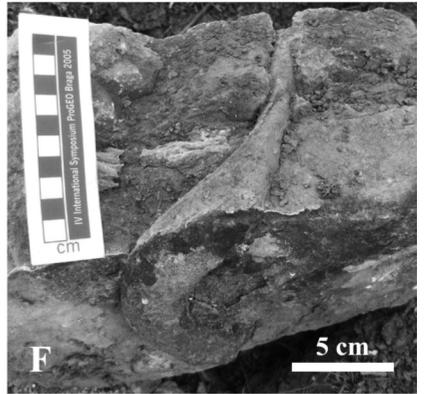
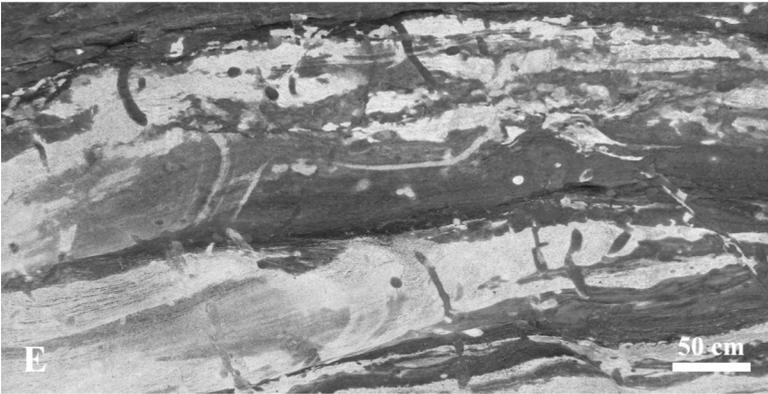
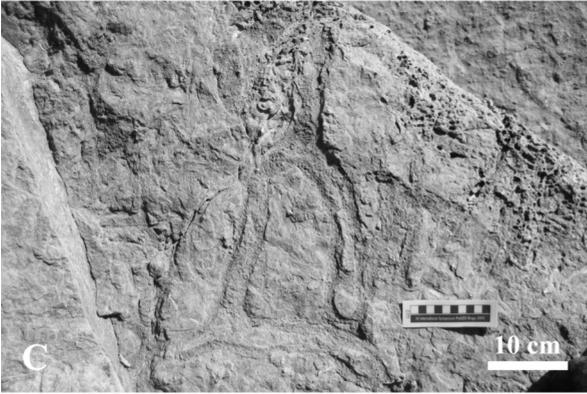
Cenozoic brackish environments (Buatois et al. 2005; Neto et al. 2007). Despite the strong confinement of Late Jurassic-Early Cretaceous lagoons in the Lusitanian Basin, the fossorial lobsters that made the *Thalassinoides* boxworks of the Boca do Chapim Formation dealt with salinity fluctuations by other means than building *Gyrolithes* shafts.

***Thalassinoides-Asterosoma* compound burrow systems**

Asterosoma ludwigae Schlirf occurs in both inner and distal ramp carbonate deposits from the Pliensbachian-Toarcian at the Peniche Peninsula and from the Bajocian of the Cabo Mondego Global Boundary Stratotype Section, as well as in confined lagoon and proximal fore-reef calciturbidites from the Santa Cruz and North of Guincho sections (Text-fig. 4D), respectively. All the environmental diversity is linked by the co-occurrence of *Asterosoma* with *Thalassinoides suevicus* and *Spongeliomorpha sudolica* networks (Neto de Carvalho and Rodrigues 2007). *Asterosoma ludwigae* shows straight or curved bulbs, circular in cross section, budding from an axial, vertical or horizontal, cylindrical burrow following a dichotomous or fan-like pattern. Three morphotypes of *Asterosoma ludwigae* are distinguished. They represent a gradation between ethological stages (compound forms) from the smallest and highly regular forms to the largest structures with burrows organized in radial bundles with highly asymmetric extensions. The fill and scratch-trace pattern of *Asterosoma ludwigae* forms are identical to those observed on *Spongeliomorpha sudolica* burrow systems, which interact in the same relatively shallow tier at the Peniche section. Scratch traces on the wall of *Asterosoma ludwigae* (Text-fig. 4D) could correspond, by their morphology, to pereopods with distal podomeres having sharp edges, mechanically appropriate for an infaunal mode of life. Moreover, these non-penetrative, incised and sometimes crisscrossed bioimprints are not found in other trace fossils from the same ichnocoenosis. *Asterosoma* occurrences in pellet-rich marls, but without pellets in their fill, point to a deposit-feeding behaviour for the crustacean producer of *Asterosoma* (see also Schlirf 2000).

Text-fig. 4. Crustacean burrows from the Mesozoic of Portugal (continued). A – Oblique displacement of slipper-shaped *Rhizocorallium jenense* in highly bioturbated sole beds (Kimmeridgian, Pontal da Carrapateira). B – Circular foraging behaviour in *Rhizocorallium irregulare* (Kimmeridgian, Praia do Salgado). C – Branching form of *Rhizocorallium irregulare* (Kimmeridgian, Praia do Salgado). D – *Asterosoma ludwigae* associated with *Thalassinoides suevicus* in the proximal calciturbidites of the Mem Martins Formation (Kimmeridgian, Guincho). E – *Psilonichmus tubiformis* in massive, coarse-grained lenticular sandstone facies, associated to transgressive surfaces (Kimmeridgian, Praia de Valmitão). F – *Macanopsis plataniformis* (Kimmeridgian, Praia do Salgado). G – Basal chamber of *Macanopsis* with cheliped imprints (Kimmeridgian, Praia do Salgado).

H – Spiral development of the basal chamber in *Macanopsis* evidencing pereopod imprints in the wall (Kimmeridgian, Praia do Salgado)



Foraging modifications in a common trace fossil: *Rhizocorallium*

Vertical and horizontal U-shaped spreite burrows are common in the Jurassic of Portugal. Postdepositional *Diplocraterion habichi* (Lisson) and protrusive *Diplocraterion parallelum* Torell may occur in washover fans in fast-aggrading medium-to fine-grained sandstones and tidal flat limestones associated with mudcracked microbial-mat crusts. They may be related to crustacean activity of suspension-feeding shrimp-like crustaceans (Fürsich 1981; Seilacher 2007) but we cannot exclude other arthropod groups or even other suspension-feeders such as various polychaetes. *Thalassinoides* and *Rhizocorallium*, the most common crustacean burrows, were mutually exclusive until the Late Jurassic (Text-fig. 3C). The Cretaceous of the Lusitanian Basin is rich in marly limestones mottled with *Thalassinoides* but almost devoid of *Rhizocorallium*. Apparently, the *Thalassinoides* makers might have replaced *Rhizocorallium* makers from their habitat almost completely. *Rhizocorallium* reflects periods of minimum disturbance and probably high influx of organic matter within the sediment (Fürsich and Schmidt-Kittler 1980). Fairly common in dark marls and biomicrites from the Jurassic, *Rhizocorallium* locally occurs in dense monospecific fabrics such as in the Kimmeridgian of the Pontal da Carrapateira, Cabo Espichel, Alverca and Praia do Salgado.

The *Glossifungites* ichnofacies (*sensu* Pemberton and Frey 1985) identifies omission surfaces dewatered by burial and subsequently exhumed as firmgrounds by scour erosion or submarine channels cutting through previously deposited sediments (Text-fig. 3B). Slipper-shaped and steeply oblique forms (*Rhizocorallium jenense* Zenker; Text-fig. 4A) are rhizocoralliid modifications usually developed in these omission surfaces or in deeper tiers than *Thalassinoides* and bearing bioimprints in *Glossifungites* preservation (Pemberton *et al.* 2004; Text-fig. 3H). Thus, in the Kimmeridgian of Praia do Salgado and Pontal da Carrapateira, rhizocoralliids were probably constructed by crustaceans, as indicated by the bifid nature of contained scratches (see also Fürsich 1981; Schlirf 2000; Seilacher 2007). *Rhizocorallium* represents a feeding behaviour showing foraging patterns of assessment and exploitation of food resources. Rhizocoralliid spreiten consist of reworked, selected bioclastic (foraminiferal) sediment. Moreover, extensive U-shaped burrows up to 70 cm long commonly develop spiral (Text-fig. 4B) and lobate forms (Text-fig. 4C). All this phenotypic differentiation (behavioural modification) in *Rhizocorallium* is caused directly by

differences in substrate tiering and cohesion as well as by resource availability and patchiness.

Earliest crab-related burrows

Fürsich (1981) described the ichnogenus *Psilonichnus* for the first time in the Kimmeridgian redbeds of Praia do Salgado, in the Lusitanian Basin. Siliciclastic facies related to rifting subsidence along major fault scarps and fan deltas/braided river depositional systems in supratidal flats show pervasive bioturbation with *Psilonichnus tubiformis* Fürsich. These simple, Y-to J-shaped, vertical cylindrical burrows were produced in shallow channels with deposition dominantly under turbulent lower-flow regime conditions, high suspended loads and frequent flooding as is observed in the Kimmeridgian sequences of Praia da Consoção, Paraia do Salgado and Praia de Valmitão (Text-fig. 4E). They are associated with transgressive surfaces as indicated by oxidation horizons and passive fill. *Psilonichnus* is generally considered as the domicion of fossorial crabs (Frey *et al.* 1984; Gingras *et al.* 2000; but see Bromley and Asgaard 1979, for possible *Psilonichnus* interpreted as made by tubificid oligochaetes), though these decapods evolved mostly during the Cretaceous and later (Carmona *et al.* 2004). *Psilonichnus* has been considered as a useful criterion for the identification of marginal-marine and quasimarine facies in the sedimentary record, and is the archetypical ichnogenus of the *Psilonichnus* ichnofacies (Frey *et al.* 1984).

The ichnogenus *Macanopsis* is here described for the first time in Portugal, associated with a coarse-grained sandstone bed in a tidal flat setting in the Kimmeridgian of Praia do Salgado. This ichnogenus dominates a low-diversity ichnoassemblage in a ferruginous firmground resulting from a transgressive surface representing subaerial exposure. *Macanopsis* consists of an upper subvertical cylindrical shaft with a distinctly lined wall, that becomes increasingly oblique with depth and ends in an elongated curved chamber horizontal to the bedding plane (Text-fig. 4F). Chambers of variable diameter may be banana-shaped (Text-fig. 4G) or have a broadly elongate circular path (Text-fig. 4H), always with a dead end. Their description fits well with *Macanopsis plataniiformis* as described by Muñoz and Mayoral (2001) from the Lower Cretaceous and upper Miocene of Spain. The specimens described herein may be the oldest record of the ichnogenus *Macanopsis*. Probably a brachyuran was the tracemaker responsible for *Macanopsis plataniiformis* domicionial structures: the basal chamber consistently shows pereiopod bioim-

prints and centimeter-sized cheliped-prints (Text-fig. 4G).

Psilonichnus and *Macanopsis* from the Lusitanian Basin may show some of the oldest crab-like fossorial behaviour known from the fossil record.

SOME CONCLUSIONS

This work presents an overview of the importance and diversification of crustacean burrowing behaviours during the Mesozoic of Portugal within the occidental margin basins, which may be related to the diversity of sedimentary environments controlled by very dynamic tectonics. Diversification of crustacean traces might also be related to latitudinal climatic control of trace fossil distribution in the marine realm during the Mesozoic break-up of Pangaea (*sensu* Goldring *et al.* 2007).

Apparently, *Thalassinoides* may have replaced the *Rhizocorallium* suite almost completely since the Late Jurassic. Early Cretaceous *Thalassinoides* were produced by fossorial deposit-feeding lobsters that were smothered and delicately preserved within their boxworks by clastic runoff into the confined, mostly brackish lagoon. Rhizocoralliid variants in analogous highly variable environments reflect foraging differentiation in climax ichnocoenoses where producer populations competed for resources leading to complication of behaviour for efficient exploitation of the environment. Compound burrows consisting of *Asterosoma ludwigae* and *Thalassinoides suevicus* are intrinsically related to diversification of mining behaviours by a single species of a still unknown crustacean. Some of the earliest crab burrows may be found in the Kimmeridgian-Tithonian from the Lusitanian Basin, allocated to the *Psilonichnus* ichnofacies and anticipating the occurrence of *Macanopsis* dwelling behaviour.

Acknowledgements

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