

## Compound *Asterosoma ludwigae* Schlirf, 2000 from the Jurassic of the Lusitanian Basin (Portugal): conditional strategies in the behaviour of Crustacea

Formas compuestas de *Asterosoma ludwigae* Schlirf, 2000 en el Jurásico de la Cuenca Lusitánica (Portugal): estrategias condicionales en el comportamiento de Crustacea

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### Abstract

*Asterosoma ludwigae* Schlirf, 2000 is described in two sections of different age and palaeoenvironment in the Jurassic of the Lusitanian Basin. The scarce and low diversity of palaeoichnocoenoses associated with these trace fossil, as well as body fossils, indicate low oxygenation of sediment levels close to substrate-water interface. Thus, the palaeoecological significance of *Chondrites* in lithofacies preceding those with *Thalassinoides suevicus* and *Asterosoma ludwigae* (Upper Jurassic of Guincho) or in direct association with similar morphotypes (Lower Jurassic of Peniche) is emphasized. In the syn-rift, fore-reef calciturbidites of the Kimmeridgian-to-Tithonian Mem Martins Formation, an exotic palaeoichnocoenosis dominated by *Asterosoma ludwigae* in three morpho-ethological gradational stages suggests a forced opportunistic, conditional strategy for the trace maker population. However, in the “Calcários e margas de Peniche” Formation, that is coeval with the post-rifting depositional setting, *Asterosoma* is found in palaeoichnocoenoses representing equilibrium conditions. A close spatial relationship exists, in both cases, between *Asterosoma ludwigae* and the “S-O-T group” burrow networks referring to fodinichnia of possible decapod crustaceans.

**Keywords:** *Asterosoma ludwigae*, palaeoichnocoenoses, forced opportunists vs. equilibrium strategy, Jurassic, Portugal.

### Resumen

En este trabajo se describe la icnoespecie *Asterosoma ludwigae* Schlirf, 2000, que aparece en dos secciones de distinta edad y paleoambiente en el Jurásico de la Cuenca Lusitánica. Las escasas y poco diversificadas paleoicnocenosis asociadas a estos icnofósiles, así como los fósiles, indican una oxigenación baja en la interfase agua-sedimento. Por esta razón, se hace hincapié en la importancia paleoecológica de *Chondrites* en las litofacies que preceden a aquellas con *Thalassinoides suevicus* y *Asterosoma ludwigae* (Jurásico Superior de Guincho) o en asociación directa con morfotipos semejantes (Jurásico Inferior de Peniche). En el syn-rift, en las calciturbiditas de fore-reef del Kimmeridgiense-Titónico de la Formación Mem Martins, la paleoicnocenosis exótica con predominio de *Asterosoma ludwigae* en tres estadios morfoetológicos gradacionales, sugiere una estrategia condicional oportunista forzada para los organismos productores de estas estructuras. Sin embargo, en la Formación “Calcários e margas de Peniche”, contemporánea al

post-rifting, *Asterosoma* se encuentra en paleoicnocoenosis que representan condiciones de equilibrio. En ambos casos, existe una relación espacial de proximidad entre *Asterosoma ludwigae* y las redes de galerías del “grupo S-O-T”, referentes a fodinichnia de posibles crustáceos decápodos.

*Palabras clave:* *Asterosoma ludwigae*, paleoicnocoenosis, oportunistas forzados vs. estrategia de equilibrio, Jurásico, Portugal.

## 1. Introduction

The application of palaeoichnological tools in sequential stratigraphy and sedimentological studies on Portuguese Mesozoic basins, except for uncommon cases (e.g., Fürsich and Schmidt-Kittler, 1980; Fürsich, 1981), have only recently come into use in Portugal. Exceptionally, discovery of several dinosaur tracksites after the beginning of the last decade (summarized in Santos *et al.*, 1998) had here a fundamental importance. The present work shows that more detailed data on invertebrate palaeoichnocoenoses from the Portuguese Mesozoic formations are an essential complement. They display a high ichnodiversity due to a myriad of behaviours adopted by benthic communities in response to intrinsic ecological variations within different depositional environments during the North Atlantic complex rifting. The studied *Asterosoma* forms, as well as the associated palaeoichnocoenoses found in two Jurassic sequences from the Lusitanian Basin, Portugal (Fig. 1), emphasizing the occurrence of *Chondrites*, constitute examples of biotic settlement events conditioned by variations in the Redox Potential Discontinuity (RPD) at the ocean floor, resulting in the diversification of trophic behaviour assumed by their euribiont producers.

## 2. Stratigraphical sequences and palaeoichnocoenoses associated with *Asterosoma ludwigae*

### 2.1. Upper Jurassic of Praia Grande do Guincho

The Upper Jurassic succession at Guincho (Fig. 2) begins with the S. Pedro Formation, which is up to 90 m thick (Ramalho, 1971) and composed of thick limestone beds metamorphosed to marbles and calcosilicate hornfelds, alternating at the top with slaty marl layers. Thermal metamorphism was induced by the Sintra Sub-volcanic Massif (Ribeiro *et al.*, 1979). The S. Pedro Formation contains poorly preserved ammonites (Ramalho, 1971).

The Ramalhão Formation (Upper Oxfordian-Lower Kimmeridgian) succeeds the former unit (Ramalho *et al.*, 1993). It is 400-1000 m in thickness and composed of a monotonous succession of thin dark grey, locally muddy or detrital, limestone beds (2-10 cm), brown marls and slates. The predominance of fine-grained sedimentation

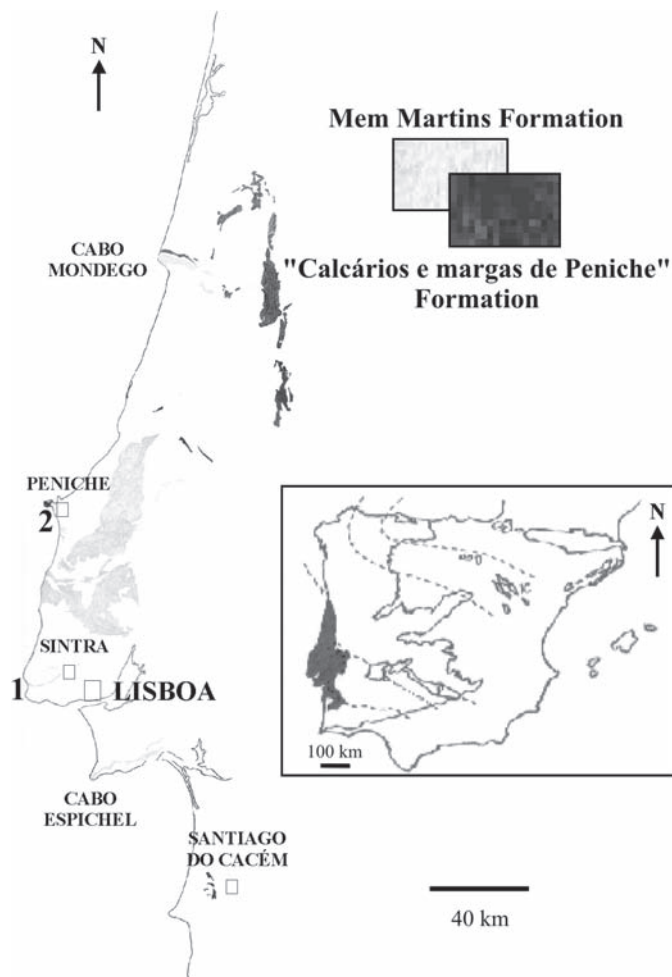


Fig. 1.- Geotectonic setting of the Lusitanian Basin in the Western Mesozoic Border (adapted from Julivert *et al.*, 1974), with particular emphasis on the “onshore” distribution of the Jurassic formations (including regional equivalents), and location of the studied outcrops. 1 - Coastal cliffs North of Praia Grande do Guincho (Sintra); 2 - Coastal outcrop of Portinho de Areia Norte (Peniche).

Fig. 1.- Situación geotectónica de la Cuenca Lusitánica en el Borde Occidental Mesozoico (adaptado de Julivert *et al.*, 1974), con énfasis particular a la distribución costera de las formaciones jurásicas (incluyendo los equivalentes regionales), y ubicación de los yacimientos estudiados. 1 - Yacimiento al Norte de la Praia Grande do Guincho (Sintra); 2 - Yacimiento de Portinho de Areia Norte (Peniche).

over crude intraclastic conglomerates and breccias, resembling Bouma (1962) intervals, type T<sub>(a) d e</sub>. These show a hemipelagic depositional environment locally influenced by debris-flows of reworked sediments in distal portions of a reefal slope to deep open sea. Fossils are rare and

of low diversity at the lower part of this sequence. They consist of ammonites and scarce trace fossils attributed to *Chondrites* isp. "type B" (cf. Osgood, 1970). *Chondrites* occurs in dark grey, marl-to-pelitic layers (Fig. 3D) and is characterized by few ramifications measuring about 10 mm wide. The upper part of this formation contains more bioturbation and intraclasts that include angular fragments of corals, molluscs, echinoids, ooids and an abundant ammonite assemblage referred to in Ramalho (1971).

The Mem Martins Formation (Fig. 1), dated as Kimmeridgian-Lower Tithonian (Ramalho, 1971), is 540 m thick and presents a basal succession of centimetric ferruginous marl beds alternating with thin beds of dark grey micritic, detrital and bioclastic limestones. Some of the beds, especially towards the top of the unit, are highly bioturbated at their bases. *Thalassinoides suevicus* (Rieth) "type B" (*sensu* Fürsich, 1981), *T. suevicus* "type A", *Megagraption irregulare* Książkiewicz meshes, *Palaeophycus tubularis* Hall (oblique burrows prevailing over the typical horizontal ones) and *Asterosoma ludwigae* Schlirf are the most relevant trace fossils (Fig. 3A-D; see also Fig. 7B-H).

Allodapic limestones are in places finely to coarsely detrital and bioclastic. Carbonate clast-supported breccia lithofacies containing algal biostromes, bryozoans, stromatoporoids and large coral reef fragments, become more important toward the top of the formation. Sequential variations along the Mem Martins Formation point to a progressive retrogradation of sedimentary conditions toward a reefal barrier with a consequent decrease in palaeobathymetry. The reef was the main source of the bioturbated sedimentation, which was mainly transported as debris-flows and rockfall, when induced by eventual seismic activity (Leinfelder, 1987). This sequence is followed by a thick series of massive limestones with interbedded ferruginous marls. In the uppermost part of the Mem Martins Formation a succession of coralline and oncoidal limestones occurs, in progressively thicker and more massive beds. These shallow water and high energy conditions point to a transition to typical reef environments at the top of Mem Martins Formation.

The overlying Farta Pão Formation consists of 400 m of thick bedded grey micritic and marly limestones culminating the Jurassic series at the Guincho section. The whole sequence shows high bioturbation levels (*Thalassinoides suevicus* "type B" dense ichnofabrics; Fig. 3A-C), with a characteristic nodular appearance of the bedding. Limestones alternate with light grey marls containing macro and microfossils typical of closed reefal lagoon environments (Ramalho, 1971).

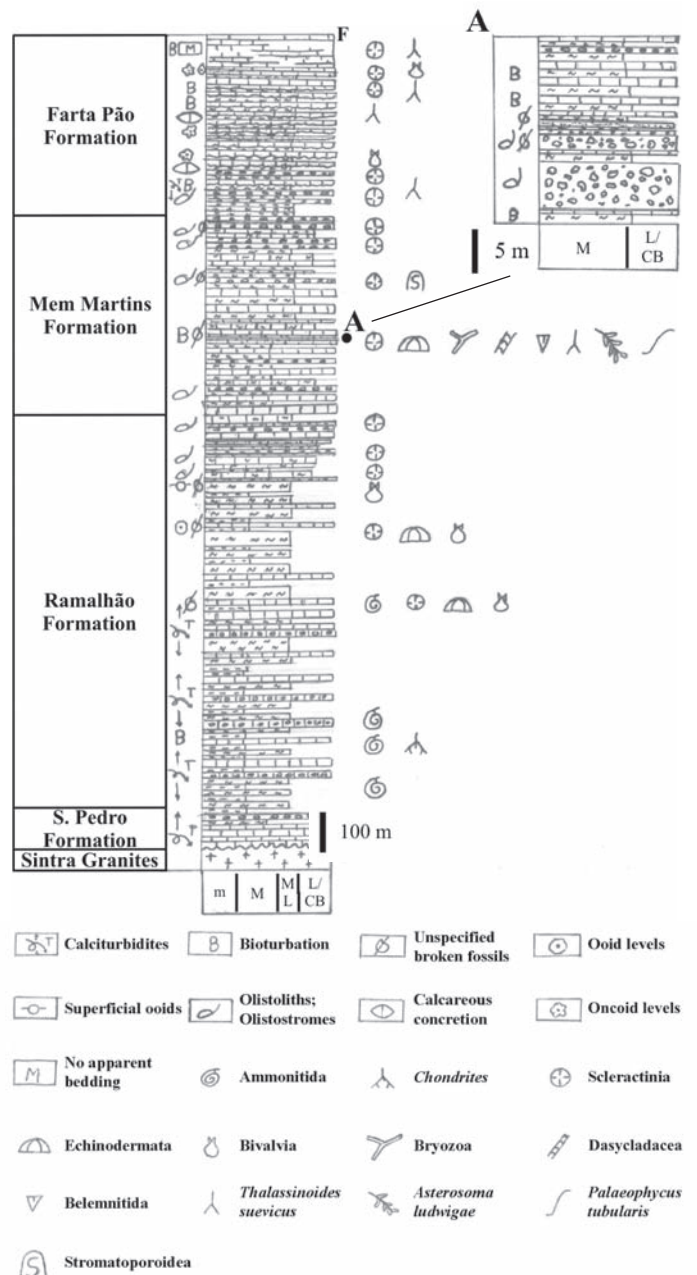


Fig. 2.- Lithofacies succession and distribution of sedimentary structures, body fossils and trace fossils of the Upper Jurassic section North of Praia Grande do Guincho. A - Detail of the proximal calciturbidite sequence including the single stratigraphic level where *Asterosoma ludwigae* occurs. Lithologic key: m - mudstones; M - marls; ML - marly limestones; L - limestones; CB - intraclastic conglomerates and breccias (including sandstone-to-microbreccia beds). U - unconformity between the Sintra intrusive granites and the sedimentary sequence; F - fault.

Fig. 2.- Sucesión de litofacies y distribución de las estructuras sedimentarias, fósiles e icnofósiles del Jurásico Superior al Norte de la Praia Grande do Guincho. A - Secuencia calciturbidítica proximal incluyendo el nivel estratigráfico donde aparece *Asterosoma ludwigae*. Leyenda litológica: m - mudstones; M - margas; ML - calizas margosas; L - calizas; CB - conglomerados intraclásticos y brechas (incluyendo capas de areniscas-microbrechas). U - inconformidad entre los granitos de Sintra y la serie sedimentaria; F - falla.

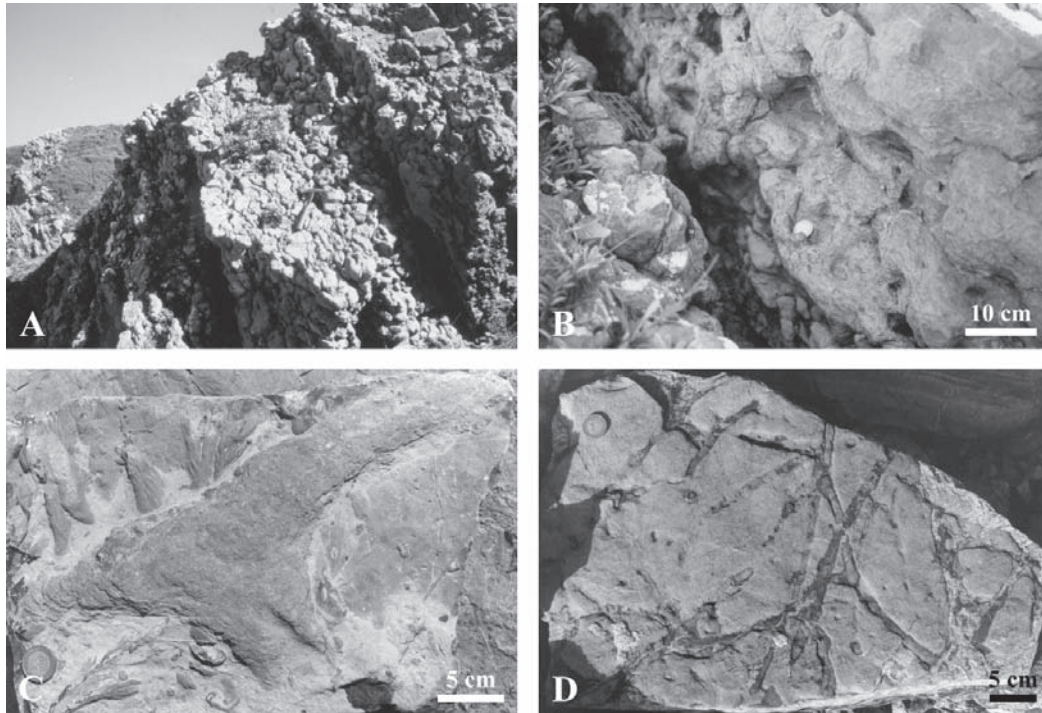


Fig. 3.- Trace fossils and ichnofabrics in the Upper Jurassic North of Guincho. A - Nodular limestones typical of lagoon facies at the top of the Jurassic sequence. B - Detail of A: note large *Thalassinoides suevicus* “type B” at the base of the limestone bed. Intense bioturbation by callianassid or glypheoid decapods results in the nodular appearance of most of the Farta Pão Formation. C - Y-shape ramification of *Thalassinoides suevicus* “type B” with the characteristic enlargement around branching point from the same stratigraphic level where *Asterosoma ludwigae* occurs. D - *Chondrites* isp. “type B” flattened and enlarged by tectonics. Figures B-D are sole views.

Fig. 3.- Icnofósiles e icnofábricas del Jurásico Superior al Norte de Guincho. A - calizas nodulares características de facies de lagoon en la parte superior de la serie jurásica. B - Detalle de A: observar los grandes *Thalassinoides suevicus* “tipo B” en la base de la capa calcárea. Bioturbación intensa por decápodos calianásidos o glifeoideos, resultando en el aspecto nodular de la mayor parte de la Formación Farta Pão. C - Ramificación en forma de Y de *Thalassinoides suevicus* “tipo B”, con el característico ensanchamiento alrededor del punto de ramificación en el mismo nivel estratigráfico donde aparece *Asterosoma ludwigae*. D - *Chondrites* isp. “tipo B” aplanados y ensanchados por la tectónica. Las figuras B-D son vistas de muro.

## 2.2. Lower Jurassic of Peniche

A Lower Jurassic marl-limestone succession containing the base of the Coimbra Formation occurs in the coastal cliffs between Papôa Peninsula and the Portinho de Areia Norte inlet (Peniche). This unit (50 m thick) is composed of sublithographic or oolitic, dolomitic and locally detrital limestones (França *et al.*, 1960). Orictocoenoses indicative of confined marine environments occur sporadically in this sequence (Mouterde, 1955). Oolitic beds suggest high energy episodes. The Sinemurian sequence is followed by a thin limestone succession (90 m thick) with subordinate ferruginous marls (Fig. 4). Mouterde (1955) attributed this basal sequence of the “Calcários e margas de Peniche” Formation (Fig. 1) to the Upper Sinemurian-Lower Pliensbachian. It is characterized by a scarce benthic assemblage containing brachiopods, gastropods, bivalves and rare belemnites. Trace fossils are common, with the ubiquitous occurrences of small *Rhizocorallium irregulare* Mayer locally appearing, in monoichnospecific associations. Moreover, *Thalassinoides*

*suevicus*, types “A and B” (*sensu* Fürsich, 1981) and, more restricted, *Spongeliomorpha sudolica* (Zaręczny), *Chondrites intricatus* (Brongniart), *Asterosoma ludwigae* and ?*Conostichus* Lesquereux (Fig. 5A-F) occur.

At the base of a decimetric light grey limestone bed, 32 m above the base of the unit, a maze of burrows attributed to *Spongeliomorpha sudolica* together with *Asterosoma ludwigae* (Fig. 8A-B) were found. They are crossed by abundant dendritic *Chondrites intricatus*, characterized by horizontal burrows, 1-2 mm wide and by a dark infill (Fig. 5F). Belemnite guards and brachiopods occasionally can also occur with trace fossils (Fig. 5C).

Towards the top of the “Calcários e margas de Peniche” Formation, marls and marly-limestones with pelagic fossils became common, and bioturbation structures progressively disappear. Those facies show high ammonite diversity (Mouterde, 1955), belemnites and nautiloids. Hence, the “Calcários e margas de Peniche” Formation shows the initial and progressive influence of the open marine Lusitanian Basin in a homoclinal ramp regime.

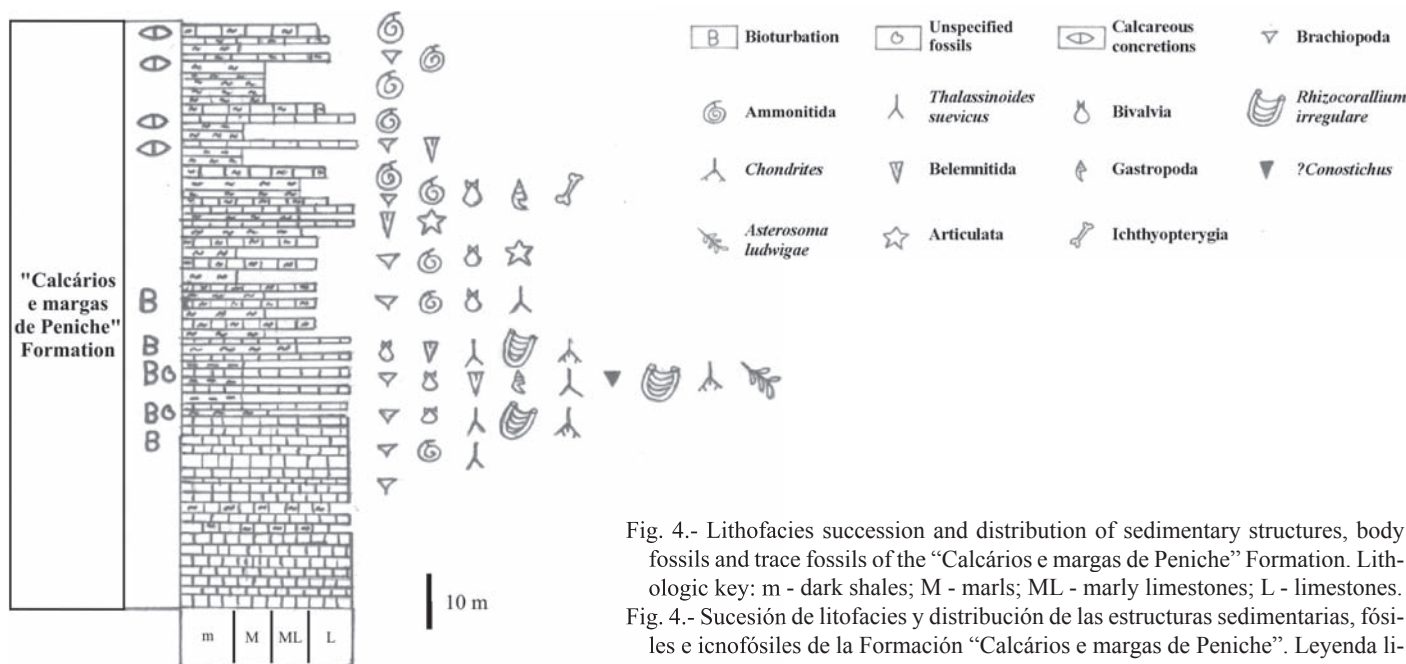


Fig. 4.- Lithofacies succession and distribution of sedimentary structures, body fossils and trace fossils of the “Calcários e margas de Peniche” Formation. Lithologic key: m - dark shales; M - marls; ML - marly limestones; L - limestones. Fig. 4.- Sucesión de litofacies y distribución de las estructuras sedimentarias, fósiles e icnofósiles de la Formación “Calcários e margas de Peniche”. Leyenda litológica: m - pizarras negras; M - margas; ML - calizas margosas; L - calizas.

### 3. Systematic ichnology

Fürsich (1973) and Pemberton and Frey (1982) recommendations were employed in the ichnotaxonomic analysis to synonymize forms interconnected in a single system, classifying it by the behaviour commonest component.

#### Ichnogenus *Asterosoma* von Otto, 1854

**Type-ichnospecies:** *Asterosoma radiciforme* von Otto, 1854

**Diagnosis:** Radial arrangement of 3 to 9 horizontal bulbous burrows starting from an axial tube, simple or budding dichotomously or in a fan-shaped pattern. Bulbs with narrow tips that might have or lack concentric *spreite* and that are connected between them by a tube positioned sub-centrally to eccentrically; ornamentation absent or constituted by striae and longitudinal to sub-angular furrows (Häntzschel, 1975; Schlirf, 2000).

#### *Asterosoma ludwigae* Schlirf, 2000

Figs. 7B-H, 8A-C

1971 - *Asterosoma radiciforme* von Otto. Chamberlain, p. 233, pl. 29, fig. 14.

1997 - *Phycodes* cf. *curvipalmatum* Pollard. Jensen, pp. 76-78, pl. 50, pl. 51, figs. 1-2.

1997 - *Phycodes palmatus* (Hall). Jensen, p. 78, pl. 50, pl. 51, figs. 1-2.

1998 - *Phycodes* isp. Schweigert, p. 13, pl. 6, fig. 1.

1998 - *Phycodes* aff. *curvipalmatus* Pollard. Schweigert, p. 13, pl. 6, fig. 2.

\*2000 - *Asterosoma ludwigae* Schlirf. Schlirf, pp. 166-168, pl. 3, figs. 1-11; text-fig. 19A-B.

2001 - *Asterosoma ludwigae* Schlirf. Neto de Carvalho and Pessoa e Costa Rodrigues, pp. 390-392, pl. 1, fig. 1a-d; pl. 2, fig. 2a-b.

**Material:** 1) GPMNHN729CC (see Fig. 7D, H) to GPMNHN734CC (see Fig. 7C, E-F) housed in the National Museum of Natural History collections, plus numerous field observations in a single limestone bed at 173 m from the base of Mem Martins Formation (Upper Kimmeridgian-Tithonian); microscopic analyses of some traces (Fig. 6A-B). 2) Field occurrences in the first 5 m of the sublithographic limestones from the basal Pliensbachian (beds 5a and lower part of 5b of Mouterde, 1955), at 30 m from the base of “Calcários e margas de Peniche” Formation.

**Emended diagnosis:** *Asterosoma* with straight or curved bulbs, circular in cross section, budding from an axial, vertical or horizontal, cylindrical burrow following a dichotomous or fan-like pattern. Bulbs are well individualized or agglutinated showing concentric or irregular *spreite* or even a massive fill. Bulb edges may show delicate digitations and sub-digitations developed between them and the bedding plane above.

**Description:** *Asterosoma ludwigae* from the Upper Jurassic North of Guincho occurs only as a convex hyporelief in the lower surface of a single limestone bed at 173 m from the formation base (Fig. 7A-B). It is excellently preserved and abundant. Six slabs were recovered. The discussed *Asterosoma* trace fossil is a cylindrical axial structure, about 3 mm in diameter arranged perpendicularly to bedding, starting from which ramifications spread at a constant angle, almost parallel to the above

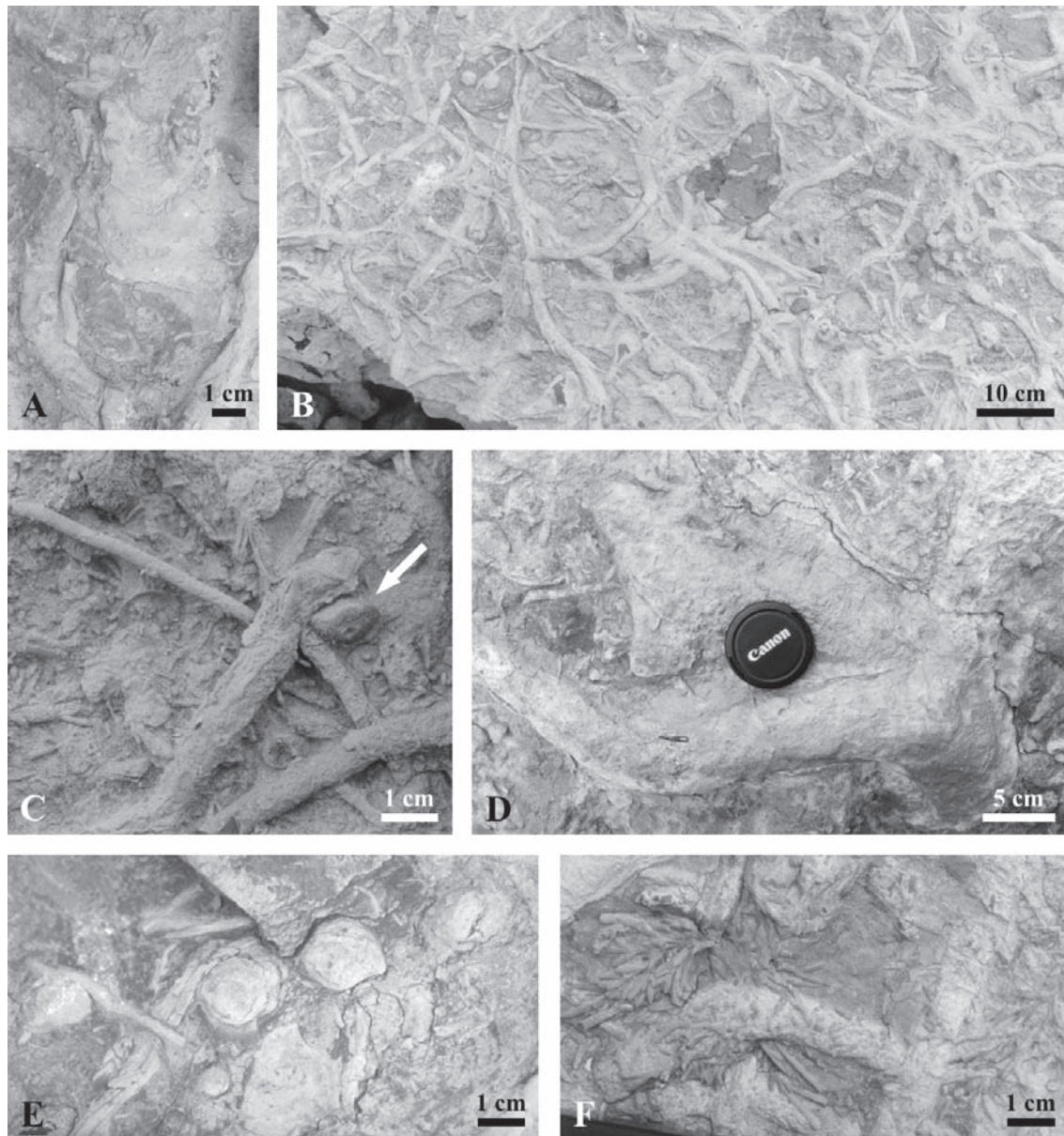


Fig. 5.- Trace fossils associated with *Asterosoma ludwigae* from the Lower Jurassic of Peniche. All figures are sole views. A - *Rhizocorallium irregulare*, vertically retrusive. B - *Spongiomorpha sudolica* constituting a complex and extense three-dimensional burrow net. C - Detail of the scratch marks on the burrow walls of *Spongiomorpha sudolica* and the co-occurrence of body fossils (arrow). D - *Thalassinoides suevicus* "type B". E - ?*Conostichus* isp. F - *Chondrites intricatus* cutting the *Thalassinoides suevicus* "type A" network.

Fig.5.- Icnofósiles asociados a *Asterosoma ludwigae* del Jurásico Inferior de Peniche. Todas las figuras son vistas de muro. A - *Rhizocorallium irregulare*, retrusivo verticalmente. B - *Spongiomorpha sudolica* constituyendo una extensa y compleja red tridimensional de galerías. C - Detalle de los bioglifos en las paredes de las galerías de *Spongiomorpha sudolica*, junto con fósiles corporales (flecha). D - *Thalassinoides suevicus* "tipo B". E - ?*Conostichus* isp. F - *Chondrites intricatus* cortando la red de *Thalassinoides suevicus* "tipo A".

limestone bedding plane, some having a greater length than others (Fig. 7D, H). Thin section analysis of the *Asterosoma*'s marly surrounding sediment revealed a pelmicrite wackestone with pyrite and a low detrital content, where the scarce bioclasts are composed of foraminifers (predominantly Quinqueloculinae) as well as ostracods and rare fragments of dasycladaceans (Fig. 6A). The burrow fill is compositionally and texturally identical to the limestone bed hosting the lower part of *Asterosoma* on

its bedding plane. In fact, thin sections of the dark grey limestone above *Asterosoma* and its fill reveal the same micritic composition with very rare pellet mounds and the absence of fossil contents. It should be stressed that pyrite enrichment and an increase of bioclasts occurs at the interface between *Asterosoma* and the marl surrounding sediment (Fig. 6A).

Three morphotypes of *Asterosoma* are distinguished. They represent gradation between ethological stages

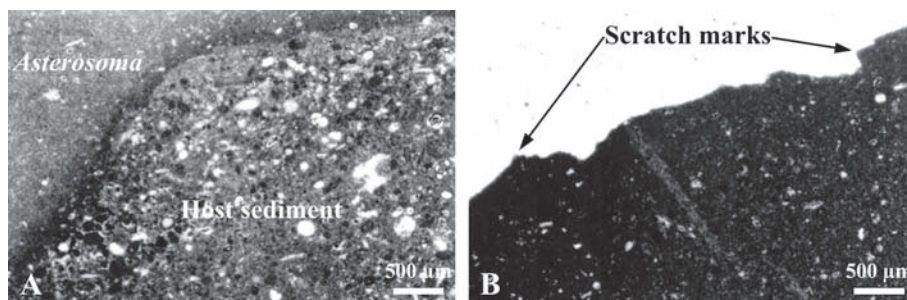


Fig. 6.- Cross-section view through *Asterosoma ludwigae*'s bulbous termination. A - Micrite infill of the trace fossil (in the upper left corner) strongly contrasts with the bioclastic sediment (containing quinqueloculinids, dasycladaceans and abundant pellets), surrounding it. B - Detail of the scratch marks that cover all *Asterosoma ludwigae* burrow surfaces. Both figures modified from Neto de Carvalho and Pessoa e Costa Rodrigues (2001).

Fig. 6.- Vista en sección de la terminación bulbosa de *Asterosoma ludwigae*. A - Relleno micrítico del icnofósil (en la parte superior izquierda), contrastando fuertemente con la matriz bioclástica que lo envuelve. B - Detalle de los bioglifos que cubren toda la superficie de la galería de *Asterosoma ludwigae*. Ambas las figuras modificadas de Neto de Carvalho y Pessoa e Costa Rodrigues (2001).

(compound forms of Pickerill, 1994), from the smallest and highly regular forms to the largest structures with burrows organized in radial bundles of highly asymmetric extensions. The small and simplest forms (1<sup>st</sup> stage morphology, Fig. 7C, H) show no more than four short burrows radiating from a central shaft normal to the bedding surface. They are in places juxtaposed or even fused together, and enlarge with distance from the central shaft. Although ramifications can develop radially, they tend to be more numerous in a single direction, which varies from structure to structure. Burrow margins show fine striae (scratch marks) starting from the central burrow zone (Fig. 6B) to the bulbs. Several cylindrical digitations are developed in the margin of the distal portion, with a diameter of 2-5 mm; those with the largest diameter can also branch (sub-digitations with a diameter of 2 mm). Digitation diameters decrease from the burrow towards the limestone sole bed. They occur whenever the radiating burrows margin does not reach the limestone bedding plane, allowing the physical contact between them. Therefore, digitation length is a function of the depth attained by the divergent bodies. These structures show some morphological similarities with the supposed "brood structures" associated to *Ophiomorpha nodosa* from Curran (1976).

The stage of largest extension and complexity of burrowing (3<sup>rd</sup> stage morphology, Fig. 7F-H) is characterized by an increase in the number of divergent burrows, organized in one to three bundles radiating from a common point (the vertical shaft was not seen in this stage), with an angle between bundles of 30°, but decreasing distally. Moreover, this stage shows burrow bundles reaching various lengths (up to 30 cm). They may be linear or slightly curved. The largest burrows, in particular, with an irregular tube width of 12 mm, have 4 to 6 pairs of bulbous terminations diverging with an average angle of

17° (standard deviation,  $s = 12^\circ$ ) in relation to the burrow orientation, disposed in a straight or slightly curved form, and showing an average long-axis length of 43.5 mm ( $s = 9.5$  mm, but with a maximum of 70 mm) and a minor axis of 22.4 mm ( $s = 3.5$  mm). Right and left bulb proportions do not differ significantly from 50:50. Bulbs become narrower and more elongate in the terminations. Longitudinal striae are present, locally criss-crossing. The curved terminations connect the structure with the lower bed surface rarely reaching an angle of 40°. In some cases, the burrows continued through the base of the limestone bed. There was no evidence of the fine digitations seen in the previously described morphotype but, owing to bulbs contacting the bedding plane, the margin of these structures was not visible. However, in a specimen it was possible to see a pronounced thinning of the bulbous structure as far as the limestone lower surface (see Fig. 9). Cylindrical burrows can still occur without the development of bulbous terminations, but showing the same budding arrangement and striae with the same geometric pattern as the one described for the 1<sup>st</sup> stage.

Intermediate structures between the two morphotypes already mentioned (2<sup>nd</sup> stage forms, Fig. 7D-E, H) show 2 to 5 radiating bulbous ramifications starting from a vertical central burrow. The central burrow is variably tilted with respect to bedding (up to 80°,  $s = 51^\circ$ ), elliptical in cross section and striated. Cylindrical digitations, like those from the 1<sup>st</sup> stage, are present along the burrows margin (Fig. 7D).

*Asterosoma ludwigae* from the Lower Jurassic of Peniche occurs in the first 5 m of the basal Pliensbachian sublithographic limestones at 30 m from the "Calcários e margas de Peniche" Formation lower boundary. Apart from their less restricted stratigraphic distribution, a few occurrences and poorer preservation, these forms of *Asterosoma* differ from those of the Upper Jurassic of Praia

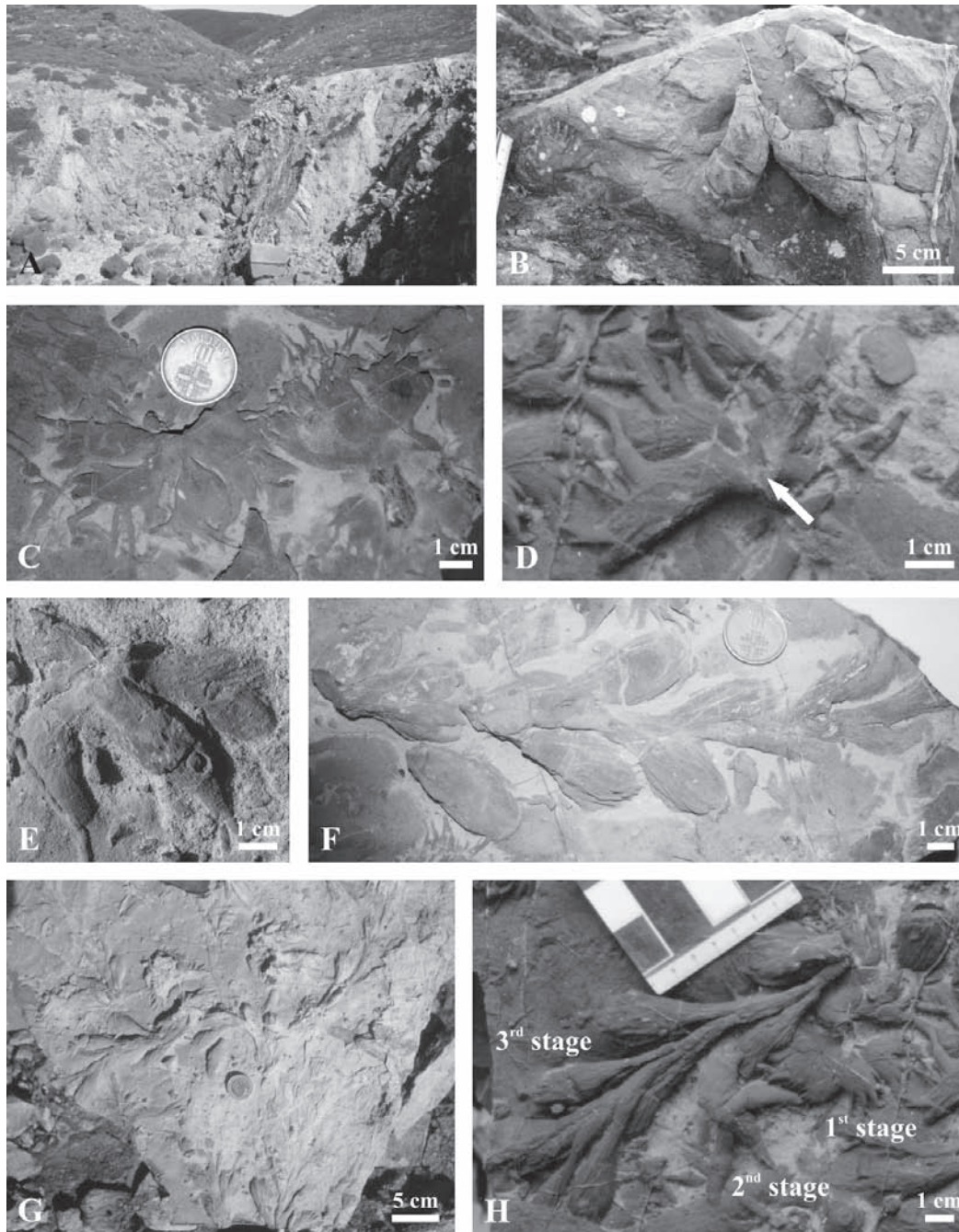


Fig. 7.- Locality and morpho-ethological stages of development in *Asterosoma ludwigae* from the Upper Kimmeridgian-Tithonian of Guincho (Mem Martins Formation). A - River mouth of the Cadaveira stream (Guincho), where a single stratigraphic level with *Asterosoma ludwigae* occurs. B - "In situ" *Asterosoma ludwigae* in convex hyporelief. C - 1<sup>st</sup> stage morphology. Large number of peripheral digitations protrudes to the limestone lower surface. GPMNHN734CC. D - 2<sup>nd</sup> stage morphology. Bulbous terminations with peripheral digitations and the connection to a possible vertical axial burrow which is not preserved (arrow). GPMNHN729CC. E - 2<sup>nd</sup> stage. GPMNHN734CC. F - Bulbous terminations of the 3<sup>rd</sup> stage. GPMNHN734CC. G - 3<sup>rd</sup> stage morphology. Two diverging ramification bundles possessing a common origin. H - The three morphological stages together in the same slab. GPMNHN729CC. Figures B to H are sole views. Figures C, E, F and H from Neto de Carvalho and Pessoa e Costa Rodrigues (2001), H modified.

Fig. 7.- Yacimiento y estadios morfoetológicos de desarrollo en *Asterosoma ludwigae* del Kimmeridgiense Superior-Tithónico de Guincho (Formación Mem Martins). A - Desembocadura del arroyo Cadaveira (Guincho), donde aparece un nivel estratigráfico con *Asterosoma ludwigae*. B - *Asterosoma ludwigae* "in situ", en hiporrelieve convexo. C - Morfología del 1<sup>er</sup> estadio. Un gran número de digitaciones periféricas sobresalen hacia la superficie inferior de la caliza. GPMNHN734CC. D - Morfología del 2<sup>o</sup> estadio. Terminaciones bulbosas con digitaciones periféricas y la conexión con una posible galería vertical axial, que no está preservada (flecha). GPMNHN729CC. E - 2<sup>o</sup> estadio. GPMNHN734CC. F - Terminaciones bulbosas del 3<sup>er</sup> estadio. GPMNHN734CC. G - Morfología del 3<sup>er</sup> estadio. Dos ramificaciones opuestas, poseyendo un origen común. H - Los tres estadios morfoetológicos en el mismo bloque. GPMNHN729CC. Las figuras B a H son vistas de muro. Las figuras C, E, F y H son de Neto de Carvalho y Pessoa e Costa Rodrigues (2001), estando la H modificada.



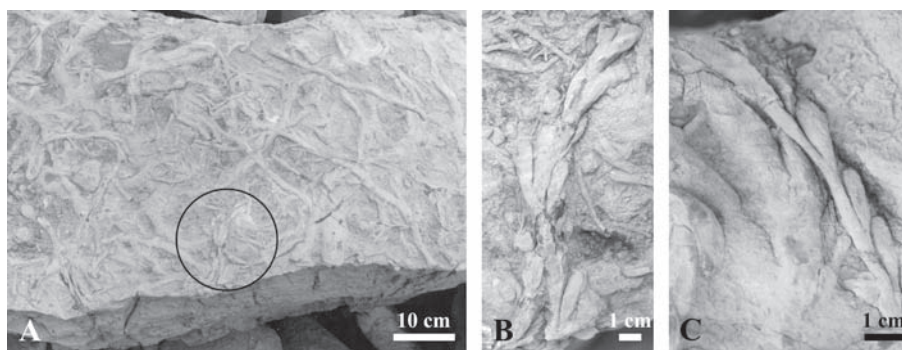


Fig. 8.- *Asterosoma ludwigae* (3<sup>rd</sup> stage morphology) from the Pliensbachian of Peniche (“Calcários e margas de Peniche” Formation). All figured forms in convex hyporelief. A - Association of *Asterosoma ludwigae* (circle) with *Spongeliomorpha sudolica*. B - Detail of *Spongeliomorpha sudolica*, revealing features in common (see text) between *Asterosoma ludwigae* and *Spongeliomorpha sudolica*. C - Asymmetrical bundle attributed to *Asterosoma ludwigae*. Figure B from Neto de Carvalho and Pessoa e Costa Rodrigues (2001).  
 Fig. 8.- *Asterosoma ludwigae* (morfología del 3<sup>er</sup> estadio) del Pliensbachense de Peniche (Formación “Calcários e margas de Peniche”). Todas las muestras se encuentran en hiporrelieve convexo. A - Asociación de *Asterosoma ludwigae* (círculo) con *Spongeliomorpha sudolica*. B - Detalle de *Spongeliomorpha sudolica*, mostrando características en común (ver texto) entre *Asterosoma ludwigae* y *Spongeliomorpha sudolica*. C - Haz asimétrico atribuido a *Asterosoma ludwigae*. La figura B es de Neto de Carvalho y Pessoa e Costa Rodrigues (2001).

Grande do Guincho by their smaller dimensions and simpler ethological patterns. Only one morphostructure resembling the well development 3<sup>rd</sup> stage forms of the Upper Jurassic was found there (Fig. 8A-C). It displays a horizontal cylindrical burrow in only one bundle, bearing striae on its surface, radiating from a single point and diverging for the left and right with terminations at an angle less than 5°. Their terminations are more cylindrical than bulbous. In these structures, lengthened bulbs are also projected from the topological burrow level above the bed’s lower surface, disappearing in the limestone. One of the trace fossils analyzed presents bulbous terminations diverging only to the left side (Fig. 8C). At Peniche, *Asterosoma* is associated with *Spongeliomorpha sudolica* mazes showing crosscutting relationships (Fig. 8A) as well as the same scratch marks pattern. However, they differ in the larger diameter of burrows attributed to *Spongeliomorpha* (average diameter = 15 mm) than in *Asterosoma* (average diameter = 6 mm).

**Discussion:** *Asterosoma* forms described in the Portuguese Jurassic differ only in their higher morphological diversity from the *Asterosoma ludwigae* holotype (3 morpho-ethological stages observed in *Asterosoma* from the Upper Jurassic of Mem Martins Formation). However, personal observations carried out in the Geologisch-Paläontologisches Institut, Universität Tübingen collections, identified structures from Grès de Châtillon Formation that are identical to the *Asterosoma ludwigae* 1<sup>st</sup> ethological stage described above. Emendation of diagnosis was needed to include the Portuguese morphological diversity.

*Asterosoma* is distinguished from the ichnogenus *Phycodes* Richter by its bulbous-shaped burrow terminations which radiate from a single axial tube, against the

dense bundles of thin cylindrical tubes which are generated distally and independently in *Phycodes* (Häntzschel, 1975; Seilacher, 2000) as result of a typically retrusive feeding system that is extremely efficient concerning the total cover of the available sediment. However, certain occurrences described by some authors (Jensen, 1997; Schweigert, 1998) and tentatively attributed to *Phycodes curvipalmatus* Pollard and *P. palmatus* (Hall), show ichnotaxobases that entirely fit in the *Asterosoma* ichnogenus and may be correlated with *Asterosoma ludwigae*, and are here placed in synonymy. There are strong resemblances between *Asterosoma* 3<sup>rd</sup> stage from the Upper Jurassic of Guincho and *Phycodes* aff. *curvipalmatus* from the Upper Kimmeridgian of Tuttlingen (Schweigert, 1998, fig. 6:2). Indeed, these occurrences are morphologically similar (e.g., bulb arrangement, striae pattern), close in age and occur in similar associated ichnocoenoses, lithofacies and palaeoenvironmental conditions (dysaerobic calciturbidites, Schweigert, pers. commun.). An *Asterosoma* described in the Mississippian-Pennsylvanian from Atoka Shale (Chamberlain, 1971) is composed of bulbs in a fan-shape arrangement radiating from a central tube, which may show ramified digitations starting from bulb edges, is similar to the 2<sup>nd</sup> morphological stage of the Portuguese Upper Jurassic forms.

#### 4. Palaeoecology of *Asterosoma ludwigae* from the Jurassic of the Lusitanian Basin: its relationships with associated palaeoichnocoenoses and orictocoenoses

##### 4.1. Upper Jurassic of Praia Grande do Guincho

The Guincho area represents during the Upper Jurassic a progressive infill of extensional, subsiding syn-rift ba-

sin that was the deepest part of the Lusitanian Basin and therefore had a relatively low terrigenous input as in the S. Pedro and Ramalhão Formations. Indeed, the fossils consist essentially of ammonites and *Chondrites*, which occur occasionally in dark grey marls of the distal fore-reef calciturbidites at the lower part of the Ramalhão Formation. Complex behaviour patterns are favoured under dysaerobic bottom conditions, where unoxidised organic matter accumulates near the water-substrate interface. The pioneering and exclusive occurrence of *Chondrites* implies an oxygen depleted environment. According to Bromley and Ekdale (1984), the presence of *Chondrites* points to a low oxygenation level on a substrate in direct contact with oxygen-deficient bottom waters, such that the possibility of substrate settlement by other benthic organisms is excluded. Rare occurrences of *Chondrites*, indicative of these conditions of episodic establishment of the *Chondrites-Zoophycos* ichnoguild (Bromley, 1990), and the important mud-carbonate sedimentation, rich in organic content and with pyrite, in contrast to a detrital, more coarsely grained sedimentation, points to the low effect of the turbiditic currents in this sector, reflecting its distal character to the reef barrier.

*Chondrites* could have been produced by polychaetes, sipunculids or even arthropods (Osgood, 1975; Savrda, 1992), although traditionally this ichnogenus is interpreted as made by sessile vermiform organisms that explored the surrounding substrate with a retractile proboscis-type organ or another tubular appendage (Simpson, 1957; Shourd and Levin, 1976). The complex horizontal pattern of anastomosing burrows with a high branching angle between branches and no apparent exits (Fig. 3D) developed in anoxic-related sediments, can be explained by the organism's extreme dependence on the oxygenation within the burrows. An alternative explanation was postulated by Seilacher (*in Savrda et al.*, 1991). Seilacher (1990) suggested that some of the commonest forms of *Chondrites* could represent channelling systems produced by sessile endobenthic organisms, like chemosymbiotic polychaetes and bivalves. These organisms would extract H<sub>2</sub>S or CH<sub>4</sub> from reducing sediments, cultivating endosymbiotic chemotrophic or denitrifier bacteria by accumulation and storage of fecal pellets for later reutilization as an energy source (a possible explanation for the observed textural and color contrast between the *Chondrites* fill and lighter sedimentary surroundings). This would be a valuable method to increase the amount and quality of available food supply wasting a minimum of energy, so vital in extreme environments like the one interpreted for the lower part of the Ramalhão Formation.

With the deposition of the Mem Martins Formation, the regressive tendency registered since the S. Pedro Forma-

tion increased, and evolved from pelagic and distal calciturbidite palaeoenvironments to a somewhat deep reefal slope setting. The reefal detrital input increases progressively towards the top of the sequence which is confirmed by the increasing calciclastic lithofacies and their maximum gravel size of about 80 cm. Bioturbation is locally intense, but with a low ichnodiversity. Occasionally, there are soles in direct contact with ferruginous marls that are highly bioturbated, with the predominance of *Thalassinoides suevicus*, and subordinate *Palaeophycus tubularis* and *Megagraption irregulare*, occurring very locally with *Asterosoma ludwigae*; *Chondrites* is totally absent while. This low diverse, but recurrent, ichnoassociation seems to be a consequence of a stressed environment. Organic-rich turbidites may have induced infaunal anoxia due to consumption of dissolved oxygen by heterotrophic bacteria. Storm or tectonically-induced wave influence on the sea bottom (reefal progradation and consequent decrease in palaeobathymetry) possibly caused oxygenation episodes which would have allowed a periodic colonization by endobenthos. However, the episodic increase of the sediment input, which enabled the preservation of organic content below local RPD (Savrda, 1992), prevented an effective and stable colonization, because of:

- a) the scarce distribution of the palaeoichnocoenoses;
- b) the dominating fodinichnia;
- c) the way of life of trace makers and a shallow tier occupation assumed for *Asterosoma*, *Thalassinoides* and *Palaeophycus*.

*Asterosoma ludwigae* found in a single bed (Fig. 6B) within a kilometric succession, in a shallow tier and with preservation of millimeter digitations and scratch marks, dominating a poorly diversified palaeoichnocoenosis, suggests precisely the colonization of an opportunist community (Vossler and Pemberton, 1988; Frey and Goldring, 1992) in a firmground after a fast organodetrital sedimentary event. Consequently there was the interstitial anoxia increase near the water/substrate interface. Occurrence of firmgrounds could be due to the development of biomats on the sea bed's surface (Gall *et al.*, 1985; Bernier *et al.*, 1991; Gaillard *et al.*, 1994). The existence of three gradational ethological stages in *Asterosoma* forms is a sign of behavioural variations, only possible with an extended occupation of the dysaerobic horizon, demonstrating a break in sedimentation. Opportunistic character of *Asterosoma* can equally be verified in Nusplingen (Germany), where Schweigert (*pers. commun.*) found horizons bioturbated by "*Phycodes* isp.", corresponding to anoxic, laminated beds, with identical features to the present example from Upper Jurassic of Guincho.

Adoption of r-selected strategies by suspension-feeders during periods of environmental stress, namely in post-

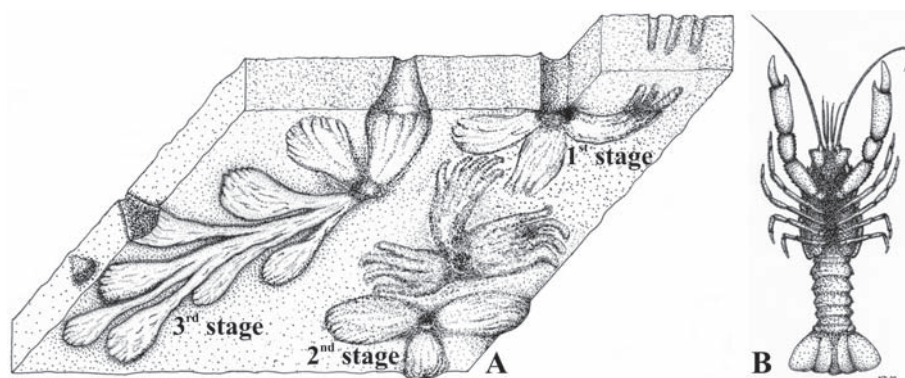


Fig. 9.- Interpretation of *Asterosoma ludwigae*. A - Sole view of three-dimensional reconstruction of the gradational morpho-ethological stages in *Asterosoma ludwigae*. B - Inferred aspect of the decapod crustacean producer.

Fig. 9.- Interpretación de *Asterosoma ludwigae*. A - Vista de muro de la reconstrucción tridimensional de los estadios morfoetológicos graduales en *Asterosoma ludwigae*. B - Aspecto inferido del crustáceo decápodo productor de *Asterosoma ludwigae*.

storm events, is well known and very common (Pember-ton and Frey, 1984; Frey, 1990). According to Buatois (pers. commun.), the opportunist occurrence of deposit-feeder trace assemblages seems to be less known. This may be due to the restriction of most previous palaeo-ichnological studies on opportunism vs. equilibrium ecology to proximal tempestites facies, where re-suspension of a great amount of organic detritus from the floor bed tends to occur. This favours the transport and settlement of typically planktonic larvae of suspension-feeders as well as their feeding methods (Frey, 1990). In distal tempestitic settings (Pember-ton and Frey, 1984; Frey, 1990), as well as in dysaerobic bottoms under the episodic influence of organic-rich sedimentary flows originating from a reef zone (such as the example from the Upper Jurassic of Guincho), low-oxygen levels did not allow the settle-ment of suspension-feeders. This way, colonization by autochthonous or allochthonous (with a planktonic lar- val stage) endobenthic depositivores who keep burrow systems in direct contact with the sea floor would be fa- voured (Ekdale and Mason, 1988). Thus, the “exotic” ho- rizon rich in *Asterosoma ludwigae* in the lower segment of the Mem Martins Formation, showing opportunistic features and dominating an ichnoassociation of low re- currence composed by crustacean (*Thalassinoides sue- vicus*) and worm (*Palaeophycus tubularis*) fodinichnia trace fossils, suggests an allochthonous origin at least for the *Asterosoma* producers, possibly transported from reef environments by gravity flows. This idea is supported by the occurrence of typical lagoon facies dasycladacean fragments and Quinqueloculininae in the same bed. This forced opportunism was favoured by:

a) the physiological adaptations of the *Asterosoma* trace maker to its typical environment, probably a reefal lagoon one;

b) the physical and geotechnical properties of the sedi- ments deposited and the frequent chemical variations of the water column (pH, salinity) due to a greater or smaller lagoon confinement induced by the reef barrier evolu- tion;

c) a typical endobenthic, detritus-feeding mode of life.

Thus, survival in this new hostile environment was at- tainable because a possible adaptation of the behavioural program genetically established which was translated into conditional strategies (*sensu* Alcock, 1998). These correspond to three different, but gradational, morpho- ethological stages on the evolution of compound burrow system fabrication. According to Alcock (1998, p. 405), generalist organisms that develop conditional strategies have the capability to change between genetic behaviour tactics depending on the environmental restrictions in- stead of reducing them to a single behavioural response under different conditions.

#### 4.2. Lower Jurassic of Peniche

During the Lower Jurassic Lusitanian Basin evolved to a post-rift progradation of open marine facies over a palaeotopography already smoothed in the basal Sine- murian, forming a large homoclinal ramp tilted from E to W. At the end of the Sinemurian-Pliensbachian, depocen- tres as in the Peniche sector were covered by a relatively shallow sea with low detrital terrigenous input. This can be verified by the dominantly marl-limestone sedimen- tation. Low diverse benthic brachiopods and gastropods prevail over nektonic forms, mainly belemnites. Brachio- pods show undamaged, articulated or loose valves, lack- ing physical abrasion or breakage (Fig. 5C), indicating a parautochthonous origin of the assemblages as well as low-energy bottom conditions. These palaeoenvironmen-

tal conditions are confirmed by the occurrence of trace fossils on the same bedding planes as the described orifices. The association of “*S-O-T* group”, *Spongiomorpha*, *Ophiomorpha* and *Thalassinoides* (Fürsich, 1973) with *Asterosoma* and *Rhizocorallium irregulare* is well known in Jurassic shallow water environments (Farrow, 1966; Fürsich, 1981; Heinberg and Birkelund, 1984; Gaillard *et al.*, 1994), being indicative of the *Cruziana* ichnofacies (*sensu* Pemberton *et al.*, 1992). Superimposition of *Chondrites intricatus* on *Thalassinoides suevicus*/*Spongiomorpha sudolica* burrow networks to *Rhizocorallium irregulare* and *Asterosoma ludwigae*, verified by cross-cutting relationships along the bedding interval for the last ichnotaxon, is attributed to slow migration of the aerobic transitional layer upwards, as a response to sedimentation (Locklair and Savrda, 1998). Producers of this form of *Chondrites* would have occupied the deepest tier, colonizing and cutting the ORIs (Oxygen-Related Ichnocoenoses *sensu* Savrda, 1992). Those were evidences of environmental equilibrium for crustaceans and other endobenthic depositivores and/or suspensivores organisms in relatively superficial tiers that were later vacated by the rise of RPD level with progressive sediment accumulation through time. This tiering reconstruction, where *Thalassinoides*/*Spongiomorpha* (in this case with *Asterosoma ludwigae*) appears in a relatively shallow tier cut by *Chondrites* that occurs in the deepest tier, is consistent with numerous other descriptions made in hemipelagic-pelagic palaeoenvironments (*e.g.* Locklair and Savrda, 1998).

### 5. Possible producers for *Asterosoma ludwigae*

Chamberlain (1971) considered that the tubular nature of burrows and their active, concentric backfill, point to a vermiform producer for *Asterosoma*. According to this author, the animal repeatedly probed into the sediment to enlarge the burrow, working vertically and laterally. Altevoigt (1968), Häntzschel (1975), Schlirf (2000) and Neto de Carvalho and Pessoa e Costa Rodrigues (2001) assumed crustacean decapods as possible producers of *Asterosoma* only by the presence of striae on its surface. “*S-O-T* group” *Spongiomorpha*, *Ophiomorpha* and *Thalassinoides* (Fürsich, 1973) ichnotaxa are usually considered as being produced by crustaceans (*e.g.*, Bromley, 1990; Ekdale, 1992). Indeed, fodinichnia open burrow systems with a typical Y-to-T ramified pattern are well known in ancient and recent environments, whose authorship is reported to Decapoda (see Glaessner, 1969; Bromley, 1990). Elements of this typically shallow water trace fossil group may occur in turbidite sequences (Crimes, 1977; Crimes *et al.*, 1981; Frey and Goldring, 1992;

Grimm and Föllmi, 1994; Tchoumatchenco and Uchman, 2001). In the Upper Jurassic of the Lusitanian Basin, a *Thalassinoides* ichnoguild dominates the lagoonal facies. Ramalho (1971) found crustacean skeletal remains associated with the microcoprolite *Favreina* Bronnimann in the upper part of the Farta Pão Formation at Guincho. Ramalho (1971, pl. 34, fig. 1) shows a pereopod with the typical morphology of fossorial decapods. In his pl. 34, fig. 4, coming from the same unit as the stratigraphic horizon of *Asterosoma ludwigae*, the author identifies a microcoprolite probably transported by turbiditic flows with typically reefal fauna. This structure, by the pore arrangement in two symmetrical groups, is similar to *Parafavreina* Bronnimann, Caron and Zaninetti, which is assumed to be anomuran excretions (Häntzschel, 1975).

*Asterosoma ludwigae* presents a considerable amount of evidences that suggest the same physiological-ethological type of producers as for the “*S-O-T* group”. The occurrences of *Asterosoma ludwigae* are associated with structures and burrow networks of *Thalassinoides suevicus*/*Spongiomorpha sudolica*, both in the Upper Jurassic of Guincho and in the Lower Jurassic of Peniche, and also occupies the same infaunal tier, as is confirmed by cross-cutting relationships. The fill and scratch marks pattern of *Asterosoma ludwigae* forms from Peniche are identical to those observed on *Spongiomorpha sudolica* burrow systems, which interact in the same relatively shallow tier (Fig. 8A). Another example of a joint occurrence of similar morphotypes can be found in the Upper Kimmeridgian from Nusplingen Lithographic Limestone (Germany) where the presence of *Thalassinoides* was attributed by Schweigert (1998) to *Glyphaea pseudoscyllarus* (Schlotheim).

Petrographic analysis of *Asterosoma ludwigae* fills does not reveal any compositional modifications that support an agrichnial behaviour. Fill sediment with identical features to the host bed indicates a passive fill of a structure open permanently to the sea floor. As in the Portuguese forms, *Asterosoma ludwigae* from the Grès de Châtillon sequence has a passive fill, which may be structured (concentric backfill) or not (*sensu* Goldring, 1996). *Asterosoma* occurrences in a pellet-rich marl horizon, but without pellets in their infills, point to a detritus feeding behaviour for the *Asterosoma* producers. For these reasons, *Asterosoma ludwigae* can be classified as an exclusive fodinichnion. The same ethological classification is commonly attributed to the “*S-O-T* group” forms (*e.g.*, Bromley, 1990; Ekdale, 1992).

Glypheoidea and other crabs like the brachyuran *Corystes* or thalassinideans present a sub-cylindrical body shape, elongated mainly in their sagittal axis. This kind of morphology is attributed to energetic optimization dur-

ing substrate penetration (cf. Savazzi, 1994). Endobenthic crabs like those mentioned typically have pereopods with distal podomeres with a sharp edge, mechanically appropriated for an infaunal mode of life. Scratch marks on the margin of *Asterosoma ludwigae* could correspond, by their morphology, to these types of appendages. Moreover, these non-penetrative, incised and sometimes criss-crossed scratch marks biogenic in origin that are not found in other trace fossils from the same ichnocoenosis, contradict the worm waste disposal hypothesis for *Asterosoma* (Chamberlain, 1971).

Digitations in the 1<sup>st</sup> and 2<sup>nd</sup> ethological stages of *Asterosoma ludwigae* from the Upper Jurassic of Guincho, connecting burrows to the bed surface (Fig. 7C, E), could be the delicate aeration structures in the most distal parts of burrow systems, preserved by substrate cohesiveness. This structural morphology, suited for survival in oxygen-depleted palaeoenvironments, could also explain the presence of *Asterosoma ludwigae* in a shallow organic-rich tier from the Upper Jurassic of Guincho. However, these peripheral digitations do not occur in the 3<sup>rd</sup> ethological stage. Despite this stage having the largest dimensions and so, presumably higher oxygen demands, the only exchanges with the surface were via the vertical opened shaft. To compensate for these apparent oxygenation difficulties, crustacean producers of these *Asterosoma* forms may have connected ramified bulbous terminations of its fodinichnion structure to the sediment surface, in order to supply oxygen to those bulbous structures considered food and/or retrocession chambers.

*Asterosoma ludwigae* stages seem to have little in common with several recent burrow systems attributed to Anomura, those more similar with the typical patterns of the "S-O-T group". However, Bromley (1990) emphasizes the existence of bundle architecture in some callianassid burrows. *Neocallichurus limosus*, a small detritus-feeding callianassid that lives on shelf muds at SE Australia, occurring in dense populations of billions of individuals, builds shallow burrows with horizontal extensions and ramifications where there are chambers connected by narrow tunnels. These callianassids are extremely dependent upon sediment consistency and texture as well as the RPD.

After the morpho-ethological interpretation and features comparison on *Asterosoma ludwigae* with the physiology and ecology of the Decapoda discussed above, it is reasonable to assume a crustacean producer for the studied specimens, particularly within Glypheoidea or Anomura (Thalassinoidea) species (Fig. 9), which were very common in Jurassic epicontinental seas (Glaessner, 1969). After all, decapods are well known by their environmental versatility (Bromley, 1990; Gibert *et al.*, 1999).

## 6. Summary and conclusions

Biodiversity is not only the result of biotic and climatic constraints, but may also reflect an explicit control of internal geodynamic mechanisms expressed by tectonics. In the Lusitanian Basin, a rift basin associated with the opening of the North Atlantic, differential subsidence rates of the Variscan basement following thermal and crustal thinning episodes associated to major rifting phases, induced pronounced topographical, and thus environmental variations, potentializing life colonization and diversification. This work synthesizes the dynamic features that allowed the adoption of several behavioural strategies expressed in ichnodiversity disparities in time and space, and which can be seen in other examples across the Lusitanian Basin (*e.g.*, Fürsich, 1981). *Asterosoma ludwigae* and their palaeoichnocoenoses are directly related with active tectono-sedimentary events where sedimentary facies were in constant flux.

Decapoda inferred as possible producers of *Asterosoma ludwigae* show the adoption of a similar behavioural strategy across disparate palaeoenvironments, as is evident in the Lower Jurassic of Peniche and in the Upper Jurassic of Guincho. In the Peniche section, *Asterosoma* is a common trace fossil along several stratigraphic horizons and is part of an equilibrium palaeoichnocoenosis, genetically related with "S-O-T group" burrow networks in a proximal offshore, under low terrigenous sedimentary rates and a low energy oxygen-rich environment. In the Guincho section, *Asterosoma* constitutes an exotic population whose producers were possible transported as plankton larvae by debris-flows, to a deep and hostile environment under the influence of the reefal slope. This forced opportunistic colonization was probably due to the innate ecophysiological abilities of *Asterosoma* producers to adapt to variable environmental conditions. Redox conditions, substrate cohesion and abundant food supply restricted *Asterosoma ludwigae* producers to a shallow tier. Behavioural evolution assumed from the three morphological gradation stages (compound forms) of *Asterosoma ludwigae* shows sequential variations in a pioneering exploration of an organic-rich substrate, from a stationary vertical burrow, whose depth was a factor of oxygen depletion, to a radial pattern, which developed through increasing structural complexity of only one to three vectorial components.

The presence of *Asterosoma ludwigae* in the Upper Jurassic of the Lusitanian Basin can be related to the doomed pioneers' model of Grimm and Föllmi (1994). The depositional environment (firmgrounds on hemipelagic deposits), transport mechanism (turbulent gravitational sedimentary flows), organism group involved

(decapod crustaceans), ephemeral colonization, and its forced exclusivity previously demonstrated are consistent with Grimm and Föllmi's theory. However, it differs from that model by different trace fossil pioneering assemblages that suggest differences in the assumed behavioural strategies. Nevertheless, this ethological differentiation is not surprising. Some endobenthic crustaceans develop conditional strategies usually modifying elements of their burrows in response to changes in environmental conditions, substrate composition and cohesiveness as well as food sources (numerous references in Grimm and Föllmi, 1994). Any single burrow is thus a result of the sum of a number of varying factors, even at a local scale.

Attribution of *Asterosoma ludwigae* trace makers to crustaceans with the morphology and ecology of fossorial decapods (glypheoids and anomurans) was discussed using all possible criteria we found, though no direct evidence of the producers inside the burrows was found. However, the same palaeoichnological criteria allowed recognition of the palaeoecological meaning of these organisms lacking a strong mineralized skeletal structure, with low preservation potential, thus enabling the knowledge of their existence and defining their palaeobiology with some accuracy.

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