JURASSIC SEX IN THE BEACH? *MACANOPSIS* FROM THE KIMMERIDGIAN OF PRAIA DO SALGADO (PORTUGAL)

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The benefits of making it spiral

Spiral burrows are a common architecture for different organisms, such as mammals, arthropods (terrestrial and marine) and annelids (Seilacher, 2007). Despite the wide diffusion of this burrowing morphology, spiral burrows have various functions, not necessarily mutually exclusive:

1. Deposit feeding. The geometry of spiral burrows optimize the utilization of nutrients of a given sediment volume. An example is given by the spiral, branched burrows of the thalassinid shrimp *Jaxea nocturna* (Pervesler and Hohennegger, 2006). Similarly, the corkscrew spirals of *Axianassa australis* serve to allow the animals to exploit greater depths for small covered areas; regularity of spirals and spirality depends on the distribution of the organic content (Dworschak and Rodrigues, 1997).
2. Gardening and drift catching. Spiral burrows are often associated to gardening strategies. Seilacher (2007) suggests that the spiral trace fossil *Gyrolithes* may be a farming burrow. Pervesler and Hohennegger (2006) interpreted *Jaxea nocturna* as a deposit-feeder, but they also observed this shrimp taking surface material into their spiral burrow. This would suggest the coexistence of deposit feeding with gardening and/or drift catching strategies.
3. Climate refuge. Spiraled burrows are a common adaptation in hot environments, as this morphology damp thermal fluctuation (Meyer, 1999) and prevent desiccation. Such strategy against physical stress has been reported for helical burrows of mammals (Meyer, 1999) and terrestrial and semi terrestrial arthropods (Dean and Milton, 1999; Chan et al. 2006).
4. Anti-predator strategy. A helical burrow has advantages over a straight burrow as it represents a deterrent for predators (Meyer, 1999).
5. Mate attraction, copulation and incubation. Ocypodid crabs create differently shaped burrows during their life and those burrows may serve for different functions (Chan et al., 2006). Hughes (1973) reports that sexually mature males of *Ocypode saratan* dig burrows different from the “usual” ones. Intriguingly, these copulation burrows present spiral morphology and a pile of sand in front of the burrow opening.

Earliest crab-related burrows

The ichnogenus *Macanopsis* was described for the first time in Portugal (Neto de Carvalho et al., 2010), associated to a single coarse-grained sandstone unit in a tidal flat setting dominated by blue-gray micrites, showing current ripples and wrinkle marks, at the Kimmeridgian of Praia do Salgado section (Fig. 1a). This ichnogenus occurs in aggregations dominating a very low-diversity ichnoassemblage, composed by scratch marks, *Lockeia* and worm burrows, where rare *Zoophycos* also develops, in a ferruginous omission surface resulting from long exposure in the supratidal zone. *Macanopsis* consists of an upper sub-vertical cylinder-like shaft, sometimes covered with a sand pile, which becomes increasingly oblique and enlarged with depth and ends in an elongated curved chamber sub-horizontal to the bedding plane, into the underlying silty micrite (Fig. 1b). Chambers of variable diameter and elliptical cross section may be banana-shaped (closer to *Macanopsis plataniformis*) or have a broadly-elongated spiral path, with an incomplete single wide whorl (Fig. 1c), always with a dead end and scratch patterns on the burrow wall. Draft fill channel on the bottom of the burrow seems to be related with aeration of the dwelling chamber. The specimens may be the oldest record of the ichnogenus *Macanopsis* (Neto de Carvalho et al., 2010). The abundance of burrows in a single bed indicates that the tracemaking population was probably gregarious. *Macanopsis* and *Psilonichnus tubiformis* described in this area of the Lusitanian Basin may show some of the oldest crab-like fossorial behavior (see below) known from the fossil record, anticipating the establishment of most of modern crab families by the Cretaceous.

***Honeymoon* chambers?**

The function of *Macanopsis* from Praia do Salgado, with sub-horizontal spiraled chambers and gregarious behavior, may be inferred from its morphology and distribution, the sediment proprieties and the identity of the tracemaker, which was probably a brachyuran crab related with ocypodids. Indeed the presence of bioimprints suggests a tracemaker with rigid exoskeleton. In peritidal environments, decapod shrimps are among the commonest tracemakers, but their burrows are usually branched. *Macanopsis* from Praia do Salgado is more consistent with a semi-terrestrial crab trace, often consisting of simple, shallow, unbranched spiral burrows with passive infill, resulting from asymmetric digging movement of legs (Dworschak and Rodrigues, 1997). More in detail, recent ocypodid crabs dig spiral burrows with a very similar morphology to the studied *Macanopsis*. *Ocypode ceratophthalma* and *Ocypode saratan* males create spiral burrows with sand pyramids at the aperture ('reproductive burrows'; Farrow, 1971). Sand mounds are found close to, or covering shaft openings on top of the bed with *Macanopsis.* The ocypodid crabs *Macrophthalmus definitus, Macrophthalmus* sp., *Uca annulipes, Macrophthalmus pawimanus, Uca beerei* also dig spiral burrows sideward (Dworschak and Rodrigues, 1997). As for these animals the dextral coiling of *Macanopsis* spiraled chambers found may reveal handedness of the male producer (according to the major chela being the left). The scratch patterns observed on *Macanopsis* (Fig. 1d) and the enlarged dens are also consistent with bulldozing of an ocypodid tracemaker (see Seilacher, 2007, p.50; Seike and Nara, 2007). The less common presence of both crosscutting relationship and biogenic reworking suggests that producers of *Macanopsis* were territorial. It also evidences contemporary burrowing and limited heterogeneous resources. Patchiness is a common trait in many modern ocypodid crab communities (Brown and McLachlan, 1994).

Macanopsis occur within coarse grained sandstones and the presence of unlined burrow walls and bioimprints reveal that they were made in a firm and coherent sediment. These features are not fully consistent with deposit feeding and gardening behaviors, while there are no elements suggesting drift catching. Moreover, deposit feeding/gardening/drift catching is more usually associated with shrimps. *Macanopsis* was possibly made by a predator/detritus-feeder crab.

The spiral burrows of recent ocypodid crabs are morphologically similar to the studied *Macanopsis* (i.e. Chan et al., 2006, fig. 1g). Burrows shelter ocypodid crabs from heat and desiccation stress, but Chan et al. (2006) demonstrated that the vertical temperature profiles of ocypodid burrows appears similar between spiral and non-spiral burrows. For this reason, it seems that the studied *Macanopsis* might have had a thermal damping function, but this was not strictly related with the spiral morphology. On the other hand, the spiral shape might have functioned as protection against predators, which is a critical aspect in the life of crabs (Burggren and McMahon, 1988). Burrows have also a central role in the courtship and reproduction of recent ocypodid crabs:

(a) Females may choose mates based on burrow quality and for the presence of a pile of sand in front of the burrow opening. The preference for certain burrows may be linked to the quality of these burrows for breeding. For instance, relative burrow height is a good predictor of burrow collapse; moisture, ventilation and temperature of the burrow could also influence breeding (Christy and Schober, 1994). However, it should be noted that in the recent Indo-Pacific subgenera, the male also visits females' burrows (Burggren and McMahon, 1988; Kraus, 1982).

(b) Copulation often takes place underground (Burggren and McMahon, 1988). Burrows may serve also for attraction and direct defense of females before mating (Christy, 1987), until they oviposit to assure that the successful male's sperm will be used in fertilization.

Macanopsis spiral burrows could be seen in light of these neoichnological observations. Indeed Hughes (1973) describes "copulation burrows", which are spiral burrows dug by sexually mature males of *Ocypode saratan*. This morphology is intriguingly similar to those of the studied trace fossil, and therefore it could be suggested that spiral *Macanopsis* is a copulation burrow while *Psilonichnus*, also present in red beds from the same section, is mostly a domichnial burrow. This observation seems to be confirmed by Chan et al. (2006), who reports that the ghost crab *Ocypode ceratophthalma* creates burrows of different shapes (J-, Y- and spiral shaped) at different ages (spirals related only with adults). Farrow (1971) suggests that female crabs have Y-shaped burrows whilst male have spiral burrows, but this observation is disputed by many other authors (see Chan et al., 2006, Christy and Schoeber, 1994).

In conclusion, *Macanopsis* spiral burrows served as a dwelling shelter (thermal damping and anti-predator function) but it might have had a primary function as a copulation burrow, in the case of the burrows registered at the supratidal sandstone from Praia do Salgado. Studies on the burrowing morphology and behavior of recent ocypodid crabs are scarce and consequently further neoichnological research is required to confirm fully the copulation hypothesis for *Macanopsis* from Late Jurassic.

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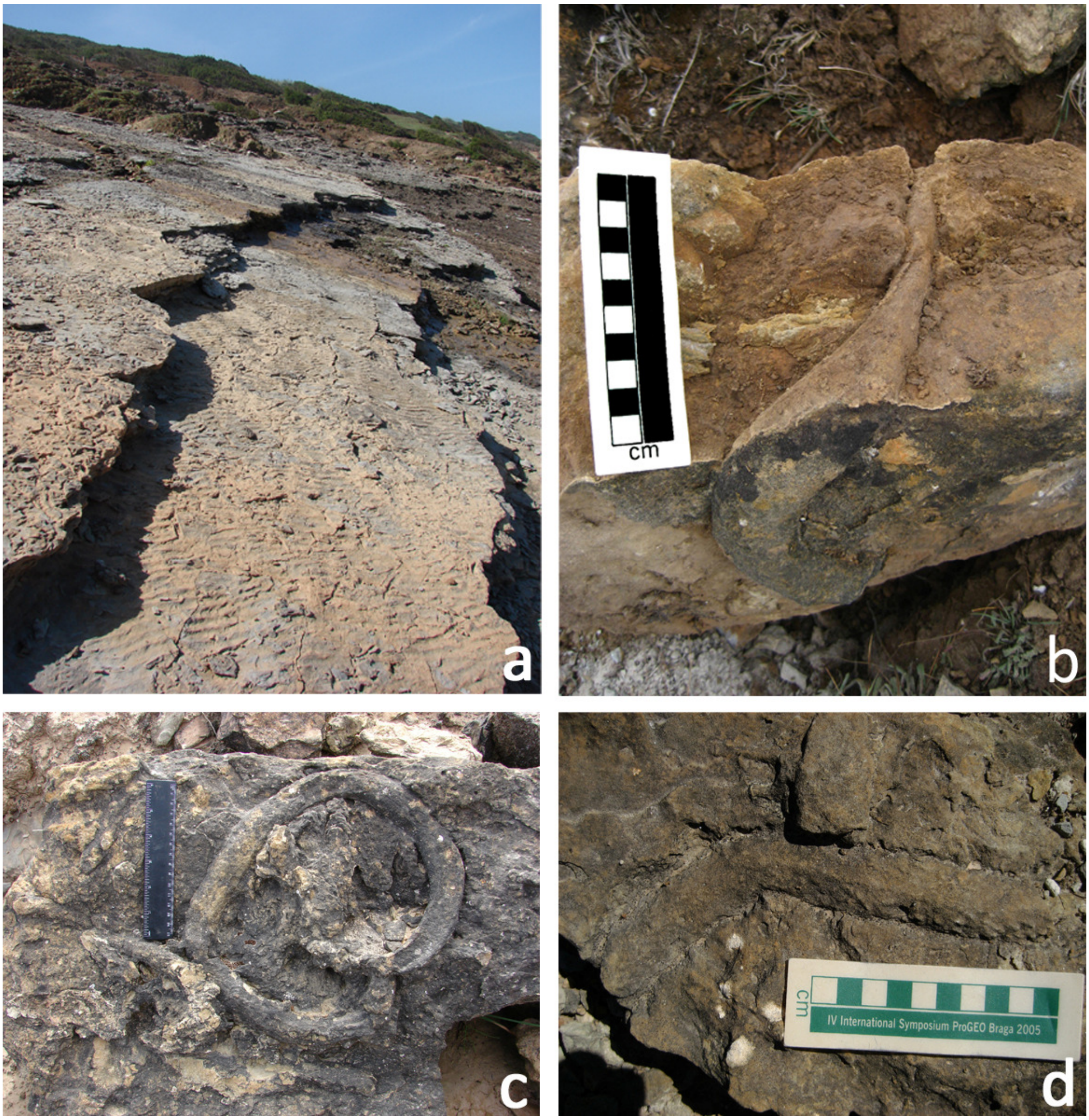

Fig. 1. *Macanopsis* burrows with spiral copulation chambers from the Kimmeridgian of Praia do Salgado. a) Tidal flat-related sequence; uppermost bed exposed is patchy bioturbated by *Macanopsis*. b) Typical morphology of *Macanopsis* in Praia do Salgado, with a vertical shaft assessing to an enlarged sub-horizontal banana-shaped to spiral den. c) Narrow spiral chamber. d) Abundant chela-prints on the wall of the basal chamber.