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Functional morphology and ethology of decapod crustaceans gathered by *Thalassinoides* branched burrows in Mesozoic shallow water environments

Every part of a burrow has an important and specific function with regard to the ecology and trophism of the burrower. It goes from the guarantee of the oxygenation and irrigation of the tunnels to the protection of the organism or the storing of organic material for feeding (Nickell & Atkinson, 1995). Regarding modern thalassinoid burrows, presence of surface mounds, vertical development of tunnels, geometry of the section of tunnels and horizontal galleries, presence of chambers and of organic debris within the burrows, number and type of apertures on the seafloor, presence of exhalant tunnels and Y- or U-shaped burrow in vertical section, are generally considered as the most important characteristics for ethological characterization of the burrow and of the trace-maker (Nickell & Atkinson, 1995). Some of these features can be recovered also in the trace fossil *Thalassinoides*, usually considered a fossil counterpart of modern thalassinoid burrows, and they allow one to formulate hypotheses about the trophism of the trace maker. This can be particularly useful in those cases in which body-fossil remains of the burrowers are completely absent and a direct comparison between the morphology of ancient and modern organisms is not possible. Ecologic considerations are here applied to Pliensbachian and Albian *Thalassinoides* developed in the lagoonal deposits of the Trento carbonate platform (Rotzo Member, Calcarei Grigi Formation, northern Italy) and in the outer shelf deposits of the Sácaras Formation (Serra Gelada, Alicante Province southeastern Spain), respectively. Different morphotypes of *Thalassinoides* were identified in these two areas, mainly on the basis of dimensions of the branches, diameter of the turning chamber and development and geometry of the maze. Even if *Thalassinoides* like burrows are nowadays produced also by worms and fishes, we consider crustaceans to be the most probable trace makers of the studied *Thalassinoides*. For a detailed discussion of the geological setting, palaeoenvironmental models, and ichnology concerning the studied areas see Avanzini (1998), Giannetti (2004), Giannetti & Monaco (2002), Masetti *et al.* (1998), Masetti & Posenato (2002), Monaco (2000a, 2000b), Monaco & Garassino (2001), Monaco & Giannetti (2001, 2002), Winterer & Bosellini (1981), and Zempolich (1993) for the Calcarei Grigi Formation, and Caracuel *et al.* (2002), Castro (1998), Giannetti *et al.* (2005), Monaco *et al.* (2005), Vilas *et al.* (1982), and Yébenes (1996) for the Sácaras Formation and references therein.

In the Rotzo Member, three types of *Thalassinoides suevicus* Rieth 1932 (*Thalassinoides* type I to type III, from the smallest to the largest form) and another form type of *Thalassinoides* isp. (type IV) were identified.

Thalassinoides suevicus type I is a small burrow, with a diameter ranging from 2 cm to 5 cm. Branches are thin and circular in section. Turning chambers are not particularly developed. Mazes are regular and geometrical in shape and developed only on the horizontal plane. Burrows are mud-filled and their surface is smooth. When these burrows are in tiered with the other forms of *Thalassinoides*, they occupy the upper tier.

In *Thalassinoides suevicus* type II, the diameter of branches ranges from 5 cm to 10 cm and diameter of turning chambers ranges from 6 cm to 10 cm. Branches are long and form geometrical, sometimes pentagonal mazes. The external surface is smooth and lining is absent. Mudstone or bioclastic wackestone fills the burrows. Bioclasts can be minutely fragmented and grouped in the internal part of the burrow. This is the most frequently observed type of *Thalassinoides* in the studied sections.

Thalassinoides suevicus type III is one of the largest *Thalassinoides* form. Its diameter ranges between 10 cm and 16 cm, and the diameter of the turning chamber is up to 22 cm. Branches are squat with respect to the morphology of the whole burrow and bifurcate at regular angles. The outer surface is smooth and the filling is made of bioclastic wackestones/packstones. Mottled concentrations of minutely fragmented bioclasts can be present in the central part of the burrow, in correspondence to the lumen. This form always occupies the deepest tiers.

In *Thalassinoides* type IV the diameter of the branches can reach 16 cm. The outer surface is mammillary, with small mounds distributed without particular orientation with respect to the burrow. Branches are short, subcircular in section and mazes are irregularly developed. On the outer surface, crinoids and other bioclasts are frequently grouped. Bioclastic wackestone fills the burrows.

Other cylindrical burrows, indicated as *Thalassinoides?* isp., exhibit simple tubes up to 80 cm in length, are gently arched, 6 to 8 cm in diameter, and show short aborted branches, without turning chambers. These traces are very similar in horizontal plane view to those illustrated by BROMLEY (1990). These atypical, branched tunnels are very different from I-II-III-IV types described above, and are analogous to some burrows of stomatopods from the Seychelles Islands. For their morphological and taphonomic characteristics these simple cylindrical tubes

are not closely related to burrows of shrimps or other decapods, but resemble to those of carnivorous crustaceans (stomatopods, Malacostraca), indicated as active predators, now populating the shallow waters mainly of tropical and subtropical seas.

In the Sácaras Formation, we identified three types of *Thalassinoides suevicus* Rieth 1932 (*Thalassinoides* type A to type C) and another poorly branched form (*Thalassinoides* type D), resembles the *Thalassinoides*? isp. described for the Rotzo Member, while the type IV is very rare.

Thalassinoides suevicus type A is a small burrow, with a maximum diameter of 5 cm. Turning chambers are present but not particularly developed. It does not show laterally developed mazes, but only burrows with short branches developed only on the horizontal plane. Burrows are mud-filled and their surface is smooth. Similarly to the Rotzo examples, these burrows can be frequently observed tiered with the other forms of *Thalassinoides* and they are placed in the most superficial layers.

In *Thalassinoides suevicus* type B, branch diameter ranges from 6 cm to 8 cm, turning chambers, can reach a diameter of 9 cm. Regular mazes can be well developed on the horizontal plane. The outer surface is smooth, lining is absent and filling is homogenous and made up of bioclastic wackestone.

Thalassinoides suevicus type C is the largest *Thalassinoides* form, with a mean diameter of around 8 cm, and up to 12 cm in size for the turning chamber. When tiering is present, this form is always located in the deepest layers. Filling is homogeneous and made up of bioclastic wackestone.

Thalassinoides isp. type D is a very large, horizontally developed burrow, following an irregular zigzag path. It is up to 1 m long, with a diameter ranging between 10 cm and 14 cm and a circular to slightly elliptical section. It does not show true branching, but only short protrusions, extending in correspondence of the bending point of the burrow. This trace resembles *Thalassinoides*? isp. of Calcarei Grigi. Filling is generally homogeneous and is made up of fine-grained calcarenites or by bioclastic wackestone/packstone, according to the lithology of the host rock.

The following interpretation of the trophism of the trace makers and of the ecological significance of the different *Thalassinoides* forms are based on the model proposed by Nickell & Atkinson (1995; fig. 3, p. 195) for modern *Thalassinoides*-like burrows, considering the main features common for both, modern and fossil burrows. The 12 diagnostic features suggested by Nickell & Atkinson (1995) and their ecological significance are here briefly examined.

1) Surface mounds. They are produced by the trace-maker removing sediment from the burrow and transporting it to the surface. Surface mounds formed after the construction of the burrow are indicative of deposit feeding trophic mode. Cone-shaped, muddy mounds, locally crossed by narrow vertical shafts are represented by a few specimens in the Rotzo Member and are completely absent in the Sácaras Formation, maybe due to the higher intensity of bottom currents.

2) Horizontal mazes (it replaces the "tightly layered lattice" feature of Nickell & Atkinson, 1995). They suggest the intense exploitation of the sediment by a deposit

feeder. Although all the studied *Thalassinoides* are horizontally developed, this feature is particularly characteristic of *Thalassinoides* type II, forming geometrical mazes widely developed at the base of the beds. As suggested by Suchanek *et al.* (1986), laterally extended mazes would allow the trace makers to maximize the capture of organic material when the substratum has a low nutritional value. This probably could be related to different rates of nutrient input within the sediment in the various phases of evolution of the lagoon.

3) Deep burrows. Depth of the burrow development within the substratum can indicate the importance of surface sediments as a nutritional source for the trace-maker. The deeper the maze is developed within the sediment, the less the trace maker depends directly on organic materials and current destruction present on the seafloor. Due to the absence of vertical tunnels and to the vertical distribution of the different *Thalassinoides* types within the beds, we have hypothesized that the studied *Thalassinoides*, and in particular the smallest forms, were probably developed at a shallow depth within the substratum. This would indicate a quite strong dependence of the trace makers on organic material present on the seafloor (surface deposit feeders or omnivorous scavengers). We must consider the possibility that parts of burrows were eroded by bottom currents and depth of burrowing within the substratum could have been therefore underestimated. This consideration is particularly important in the Serra Gelada section, where burrows are developed in a relative high-energy environment.

4) Sub-circular tunnel cross section. According to Nickell & Atkinson (1995), sub-circular tunnels occur in established burrows, after the phase of exploitation, and are the result of crustacean movement. Oval or irregular shapes are less suitable for efficient water flow than a perfectly circular cross-section (Nickell & Atkinson, 1995). The narrowing in cross section, as occurs in some *Thalassinoides*? isp. (such as in some modern burrows of stomatopods), is another characteristic which is not ideal to water flow. According to this hypothesis, the occupant of the burrow would be strongly dependent on the surface sediments as a nutritional source and less to current flows. With the exception of *Thalassinoides* type IV, all the studied *Thalassinoides* both in the Calcarei Grigi and in the Sácaras Formation have a sub-circular cross section or narrowing, thus confirming the hypothesis suggested by the other characters that the primary nutritional source was the organic material present on the seafloor rather than that transported passively by current flow within the tunnels.

5) Chambered burrows. Chambers can have different purposes: they can be used for sub-surface deposit feeding or to store coarse grained material and fragmented bioclasts, found within the substratum or coming from the sea-floor. Another purpose maybe the change the direction of crustacean by 180°, by performing a somersault followed by a roll around the body axis, as observed in modern examples of thalassinoides. Therefore, the sub-spherical shape of chambers maybe important to recognize behaviour patterns, in the relationship with characteristics of the substrate (Monaco & Giannetti, 2002). In *Thalassinoides* type III, type IV and secondarily in *Thalassinoides* type II of the Calcarei Grigi Formation and type B and C of the Sácaras Formation, turning chambers are particularly

developed and large. Stored coarse grained material such as fragments of crinoids, coated grains and large bivalves, algae and foraminifers were sometimes observed, in particular in *Thalassinoides* type IV.

6) Organic detritus in burrows. Organic detritus in burrows can be the result of scavenging on the surface, but also of passive falling of material within an open burrow. In the fossil record, the different origin of organic detritus can be sometimes identified through taphonomic and sedimentologic criteria. In modern *Thalassinoides*-like burrows, organic material is also used by the crustacean to cultivate micro-organisms for nutritional purposes. Organic detritus in burrows is particularly abundant in *Thalassinoides* type III and type IV.

7) Oblique tunnels were very rarely recorded in the studied sections (in some *Thalassinoides* ? isp.) and therefore they are not considered here.

8) Burrow openings, tubular tempestites. In the studied sections, burrow openings can be directly observed only rarely. Their existence can be deduced by the presence of tubular tempestites inside the bed, but their number, dimensions and density cannot be defined. The presence of many burrow openings would indicate a continuous and necessary contact of the trace maker with the seafloor, for deposit feeding or scavenging.

9) Funnel-shaped openings. According to Nickell & Atkinson (1995), the presence of funnel-shaped openings would facilitate the capture of prey or any other nutritional particles, as they fall down to the sides of the funnel and into the burrow. In the studied section, this feature is represented only by a specimen from the Rotzo Member. The funnel is asymmetric in shape, the back being nearly vertical and the front being flattened probably due to the continuous movement of the trace maker. The bottom of the funnel is connected to a short vertical tunnel, which is not directly related to a preserved *Thalassinoides* maze.

10) Narrow exhalant shaft. The presence of a narrow exhalant shaft indicates the necessity of current generation. This feature was observed only in one cone-shaped mound in the Rotzo Member, but its origin is uncertain.

11) U- or Y- shaped burrows in vertical section. This feature, typical of many modern thalassinoidan burrow systems (Bromley, 1990), was not observed in the studied fossil *Thalassinoides* and therefore it is not considered here.

12) Circular tunnel cross section. Their presence would facilitate the water flow within and through the burrow. Due to the importance of a constant water flow through the burrow, circular tunnel cross sections are present also in burrows produced by primarily deposit feeders and therefore this cannot be considered diagnostic of a particular trophic mode (Nickell & Atkinson, 1995). In the studied sections this feature is only rarely represented in *Thalassinoides* type II and in the largest *Thalassinoides* type III, mainly where mazes are well preserved and regularly developed.

In summary, features representing sediment processing and storage of material for nutritional and maintenance purposes are the most common in the *Thalassinoides* of the Rotzo Member.

The only characteristic shared by the five *Thalassinoides* forms is the horizontal development of the burrows. Branches with a sub-circular section are typical of *Thalassinoides suevicus* type I, type II, and type III. Enlarged chambers are absent in *Thalassinoides suevicus*

type I and *Thalassinoides*? isp., present in type II and type III and well developed in type IV.

According to the scheme proposed by Nickell & Atkinson (1995), the most commonly observed features in all the *Thalassinoides* of the Calcarei Grigi Formation indicate intense sediment processing. In *Thalassinoides suevicus* type II, type III, and especially in the type IV, storage of organic material (chambered burrows and organic detritus in burrows, characters 5 and 6) is also evidenced. The presence of organic detritus is represented by coarse-grained to fine-grained crushed bioclasts within *Thalassinoides suevicus* type II, type III, and type IV. It indicates both biogenic sorting and storage of bioclastic debris coming from the seafloor and fallen down or transported into the burrow. The local concentration of coarse-grained fragmented shells in *Thalassinoides* type IV, is probably due to the need of the trace maker to maintain other parts of burrow free from debris.

Vertical tunnels and apertures on the seafloor (characters 8, 9 and 12) are very rarely observed and it is sometimes impossible to state if vertical tunnels are not preserved due to sedimentologic or diagenetic processes or if they were really poorly developed in the burrows. Actually, we have no evidences of deep burrows with a U- or Y- shaped vertical morphology. We have hypothesized, therefore, that mazes were burrowed on horizontal planes only at shallow depth in the substratum. The few evidences of vertical tunnels and of exhalant shafts are difficult to relate to *Thalassinoides* mazes. The presence of tubular tempestites inside the beds proves the existence of direct apertures on the seafloor, even if only the horizontal part of the filled burrows can be usually observed. The only clearly observable vertical element has a circular section (character 12), but it is an isolated feature. This tunnel closely resembles the burrows of modern crustaceans and therefore we have considered it separately. In the category of the vertical elements, we have considered also inhalant and exhalant shafts, represented in the Rotzo Member only by an unclear example. Actually, shafts are so small that they could be produced also by worms. These rare vertical elements indicate the presence of suspension feeders, whose primary nutritional source is the water column, and of surface deposit feeders. According to the scheme proposed by Nickell & Atkinson (1995), all the studied *Thalassinoides* belong to the category of the sub-surface deposit feeders (searching for organic particles within the substratum) and secondarily to that of the omnivorous scavengers (Vaugelas, 1990), which ingest organic debris present on the seafloor and deriving from other animals and algae.

Similar interpretations can be proposed for the *Thalassinoides* studied in the Sácaras Formation, even if only four of the twelve characters described by Nickell & Atkinson (1995), namely those related the horizontal development of the burrow (characters 2-5), are well preserved. The problem concerns the vertical development of the burrows, because we have neither direct nor indirect proofs of the existence of vertical tunnels (except *Ophiomorpha* specimens of calcarenites at the top of parasequences of Serra Gelada, see Monaco *et al.*, 2007) and of the type and number of apertures on the seafloor. Anyway, we can hypothesize the presence at least of some vertical tunnels linking the biggest *Thalassinoides*, placed in the deepest tiers within

the sediment, to the seafloor. Intense bioturbation of the more superficial tiers probably obliterated them.

All the studied *Thalassinoides* are horizontally developed (*horizontal mazes*, character 2) and show a sub-circular cross section (character 4), both characters indicative of intense sediment processing.

Presence of enlarged chambers (as in *Thalassinoides suevicus* type B and in *Th. suevicus* type C, character 5) could indicate storage of organic material for feeding purposes or changes in the direction of locomotion. Concentration of skeletal remains (character 6) is rarely observed, due to the high bioclastic content of the host rock and of the burrow filling. Because of the absence of vertical tunnels, we cannot formulate hypotheses about conditions of irrigation and importance of the water column for nutritional purposes (characters 7-12). It is evident that burrowers were closely dependent on nutrients present within and on the substratum as the main

feeding source. Therefore, they can be included in the trophic categories of the sub-surface deposit feeders and secondarily in those of the surface deposit feeders and of the omnivorous scavengers.

This is only a first step in the ecological analysis of the *Thalassinoides* trace fossils and of the trophism of their trace-makers. However, an approach which considers the functional morphology of the parts making up modern *Thalassinoides*-like burrows can be useful for understanding of the ecological meaning of ancient burrows produced by extinct crustaceans and can give further information for a more complete paleoenvironmental reconstruction (Monaco *et al.*, 2007). However, this method has to be refined, elaborating a detailed model which compares different types of *Thalassinoides* in different environmental contexts and considering also the functional morphology of modern branched burrows produced not only by crustacean decapods but also by other organisms.

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