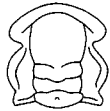


A modern analogue for the trace fossil *Gyrolithes*: burrows of the thalassinidean shrimp *Axianassa australis*

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LETHAIA



Dworschak, P.C. & Rodrigues, S. de A. 1997 04 15: A modern analogue for the trace fossil *Gyrolithes*: burrows of the thalassinidean shrimp *Axianassa australis*. *Lethaia*, Vol. 30, pp. 41–52. Oslo. ISSN 0024-1164.

The tidal flats at Praia do Araça, Brazil have muddy siliciclastic sediments on the surface and a layer of heavily packed shells down to 30–40 cm depth. The most obvious element of the infauna is the thalassinidean shrimp *Axianassa australis*. Several animals were captured with a yabby pump. Burrow openings were characterized by a low mound (1–2 cm high and 10–30 cm in diameter at the base) with one or two simple holes nearby (20–70 cm away). Counts along two transects showed a mean density of *Axianassa* burrow openings of 1.4 m⁻² (range: 0–7), mounds ranged in density from 0 to 3 m⁻² (mean 1.25). Three nearly complete (and several incomplete) resin casts showed a unique burrow shape, with spiral shafts leading to wide horizontal galleries from which several evenly proportioned corkscrew-shaped spirals branched off, leading to further horizontal galleries at greater sediment depths. Burrows had up to 15 such spirals and a total length of over 8 m. The total burrow depth was between 106 and 130 cm. The role of the spirals and the similarity of *Axianassa* burrows to the trace fossil *Gyrolithes* are discussed. □ *Thalassinidea*, *AXIANASSA*, *spiral burrows*, *trace fossils*, *GYROLITHES*, *Brazil*.

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Crustaceans are among the most important burrowers in intertidal and shallow subtidal sediments. A number of trace fossils have been attributed to crustaceans, mainly stomatopods, crabs, lobsters and mud-shrimps (e.g., Frey *et al.* 1984; Pemberton *et al.* 1984; Bromley 1990). Of these (seven ichnogenera), three are of particular interest: *Ophiomorpha* Lundgren, characterized by burrows with a knobby outer wall lining; *Thalassinoides* Ehrenberg, characterized by burrows with a three-dimensional network of smooth-walled cylindrical components of variable diameter with Y- to T-shaped branches; and *Gyrolithes* Saprota characterized by burrows with a regular spiral form. *Gyrolithes* has a world-wide distribution, ranging from marine deposits of Jurassic through Miocene (Gernant 1972; Bromley & Frey 1974; Häntzschel 1975; Christiansen & Curran 1995). A recent analogue of *Ophiomorpha* can be found in the burrows of the thalassinidean shrimp *Callichirus major*, which is characteristic of beaches along the Atlantic coast of the Americas. Burrows of *Thalassinoides* form are made in modern environments by a number of marine organisms, including cerianthid anemones, enteropneusts, and fish, but most importantly

by decapod crustaceans, primarily thalassinidean shrimps (Myrow 1995). Modern spiral burrows similar to *Gyrolithes* have only been reported for capitellid polychaetes (Powell 1977). Häntzschel (1934, 1935) argued that *Gyrolithes* had most probably been made by polychaetes, but the majority of palaeontologists have interpreted these spirals to be the burrows of decapods (e.g., Kilpper 1962; Gernant 1972; Bromley & Frey 1974; Mayoral 1986; Christiansen & Curran 1995).

Among the burrowing decapods, the Thalassinidea are of greatest importance; this group lives almost exclusively in burrows. Many intertidal and shallow-subtidal sediment substrates are inhabited by large numbers of members of the species-rich families Upogebiidae and Callianassidae. The genus *Axianassa* has been placed alternately in the families Axianassidae (established by Schmitt 1924) and Laomediiidae (Rodrigues & Shimizu 1992) and, until recently, was thought to be quite rare. Up to 1990, only five specimens representing two species had been recorded. The number of specimens was increased to nine with the description of three more species by Kensley & Heard (1990). The description of *Axianassa australis* from

Brazil by Rodrigues & Shimizu (1992) was based on six specimens and increased the number of species to six.

The present work reports on the results of a study of the burrowing crustaceans of intertidal and shallow subtidal habitats around São Sebastião, São Paulo, Brazil, which revealed a relatively large population of *Axianassa australis* at the tidal flat at Araça. Yabby-pump sampling yielded a total of nine specimens. Resin casting of the burrows resulted in several incomplete and three nearly complete burrow replicas, which all showed a unique shape closely resembling *Gyrolithes*. This paper describes these unusual burrows and considers the possible methods of construction and the possible functions of the spirals.

Study site

Praia do Araça is situated south of the town of São Sebastião, São Paulo, Brazil (Fig. 1). Here there is a bay about 600 m wide and 350 m deep, measured from the line between Ponta do Araça in the south and the corner of the pier in the north. There are two rocky outcrops in the middle of the bay. From the more southern of the two rocks, a bank measuring 100 m long and ca. 80 cm above low water level and consisting mainly of mollusc shells stretches to the inner side of the bay. The inner edges of the bay and the south end of the bank support a sparse growth of mangrove trees. The present investigations were carried out in an area north of the bank, which was exposed during low tide (Fig. 2). The tides are semidiurnal, and the mean tidal range is 1.5 m.

The sediment at the surface is soft, whereas the deeper sediment layers show compacted shell accumulations. The sediment depth in which the shell accumulations began ranged between 10 cm near the shell bank and 30 cm in the middle of the tidal flat. At the site of the resin casts and the sediment core the accumulation started at 17 cm depth.

The surface sediment (0–11 cm deep in the core) consists of silty, very fine sand with 17.7% silt and 8.7% clay, an organic content (wet oxidation) of 7.9%, and a carbonate content of 9.8%. At 22–33 cm depth, the sediment consists of 12.2% particles larger than 4 mm, mainly of mollusc shells and shell fragments (Fig. 3). The remaining sediment is a medium sand with only 5.5% silt, an organic content of 6.6% and a carbonate content of 21.6%.

Most of the shells were of bivalves, mainly the venerid *Anomalocardia brasiliensis* (Gmelin) and the lucinid *Phacoides pectinatus* (Gmelin). A few shells were from gastropods, mainly *Cerithium muscarum* Say and *Bulla ?striata* Brugière.

Other important infaunal organisms living in this tidal flat were the stomatopod *Lysiosquilla scabricauda* (Lamarck), the polychaetes *Diopatra cf. cuprea* (Bosc) and *Chaetopterus variopedatus* (Renier), an unidentified

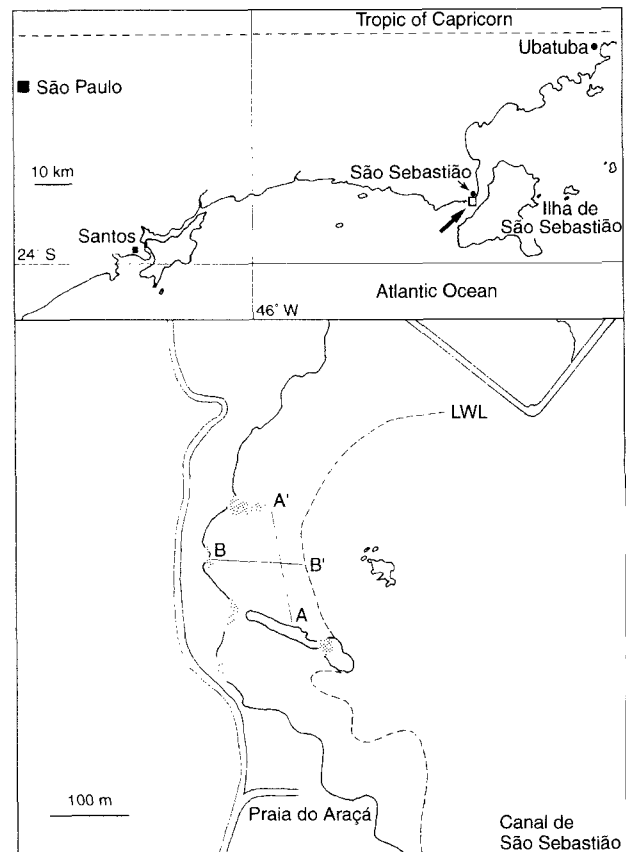


Fig. 1. Map showing the study site. LWL: low-water line on April 28th, 1994; dotted areas: mangroves; A–A' and B–B': transects. Modified after Rodrigues (1966) and Rodrigues & Rocha (1993)



Fig. 2. View north on Praia do Araça.

neriid and a terebellomorph, the bivalves *Anomalocardia brasiliensis* (Gmelin), *Tagelus plebeius* (Lightfoot) and *Phacoides pectinatus* (Gmelin) (= *Lucina jamaicensis*), a sipunculid (?*Sipunculus nudus* L.), an echiurid, a new species of nemertean (Wolfgang Senz, personal communication), the tanaidacean *Kalliapseudes* sp., and an as yet unidentified species of alpheid shrimp (which probably lives in the burrows of *Axianassa*; see Felder *et al.* 1995). Near

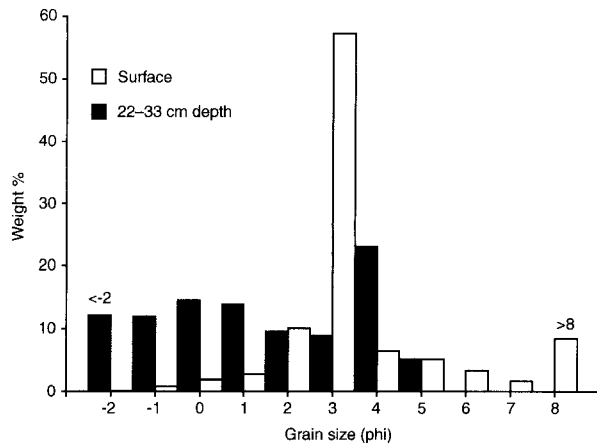


Fig. 3. Grain-size distribution of sediments from the tidal flat at Praia do Araça as percent weight retained on sieve. White columns: sediment at the surface (0–11 cm); black columns: sediment at a depth between 22 and 33 cm.

the rocks, a specimen of the thalassinidean shrimp *Upogebia omissa* Gomes Correa was captured.

Material and methods

Axianassa australis (Fig. 4A) was described recently by Rodrigues & Shimizu (1992). It was collected from mangrove mud in Valença, Bahia, Brazil, and was first captured at the tidal flat at Araça in 1985. Animal density was estimated by counting holes and mounds in a 1 m² frame along two transects, one across the bay, the other from the mangrove trees to the low water line nearly at right angles to the first (Fig. 1).

Animals were captured with a yabby pump similar to that described by Rodrigues (1966). Preserved specimens were deposited in the Naturhistorisches Museum, Wien (NHMW) and in the Muséum National d'Histoire Naturelle, Paris (MNHM). Sediment samples were obtained using the yabby pump as a corer and were analysed using the methods outlined by Buchanan (1984).

Resin casting was done *in situ* using an epoxy resin (see Pervesler & Dworschak 1985). Initial attempts to cast mounds resulted in only short casts of vertical shafts (5–20 cm deep). In subsequent attempts, suction was exerted at the mounds with a small yabby pump and resin poured into those holes by visibly responding to the suction. A slow-setting mixture of the resin (Araldite GY257:HY830:HY850 in proportions by weight of 20:9:3, which needs 4–6 days hardening time, instead of 25:7:8 with a hardening time of 2 days) yielded the most complete casts. For reference, three casts were deposited in the Naturhistorisches Museum, Wien (NHMW).

The terminology used for description of the spirals follows that of Gernant (1972) and Bromley & Frey (1974).

Results

Appearance of openings and density

At the sediment surface, burrow openings of *A. australis* are characterized by low mounds, 0.5–1.5 cm high and 3–27 cm in diameter at their base (Fig. 4B, D). These mounds are grey to black in colour, in contrast to the surrounding brown, ripple-marked sediment surface. In some cases, faecal pellets were found among the sediment forming the mound (Fig. 4C). When the burrow openings were submerged, suspended sediment blown out of the opening by the pumping activity of the shrimp could be seen. This pumping activity was also observed during low tide, when the receding water formed typical rill marks on the mounds (Fig. 4B, D) and murky water filled the troughs of the ripple marks (Fig. 4C, D). Most of the mounds had a small opening on top (0.5–1.4 cm in diameter) while some had the shape of a crater (2–3 cm in diameter). Near to the mound, at a distance between 10 and 49 cm, a second opening was visible, which was either a simple hole (Fig. 4B) or a funnel 2–3 cm deep, measuring 1.2–3.6 cm in diameter at the surface and narrowing to 0.5–0.9 cm (Fig. 4C). These openings became visible when suction with the yabby pump was exerted at the mound opening.

The density of burrow openings attributed to *A. australis* ranged between 0 and 8 m⁻² (means 1.35 and 1.68 for the first and second transect, respectively). Mounds occurred at a density of between 0 and 5 m⁻² (means 1.22 and 1.27), and simple holes at a density of between 0 and 4 m⁻² (means 1.17 and 1.5).

In most cases, only one specimen was captured when applying suction to a mound and then to the corresponding second opening. In one case a male–female pair was obtained. Females outnumbered males, and all females except one were ovigerous. The measurements of all nine specimens of *A. australis* are summarized in Table 1.

Burrow shape and dimensions

Burrows of *A. australis* follow a general pattern (Figs. 5, 6). From both the hole and the mound site (marked with h and m in Figs. 5A–D and 6A–B), a vertical shaft (7–12 mm in diameter, circular in cross section) leads to a depth between 13 and 30 cm (Table 2). At this depth, it either leads after a short whorl (Fig. 5A, C) into a wide tunnel or continues as a wide spiral shaft (Fig. 6A, B), sometimes with a series of chambers at depths between 30 and 60 cm, which opens into a wide tunnel. This wide tunnel occurs at depths between 13 and 60 cm from which one or two regular, vertical spirals branch off. These spirals lead either to other (less wide) tunnels made at greater sediment depth, or up to the surface (Fig. 5C, F). Several other

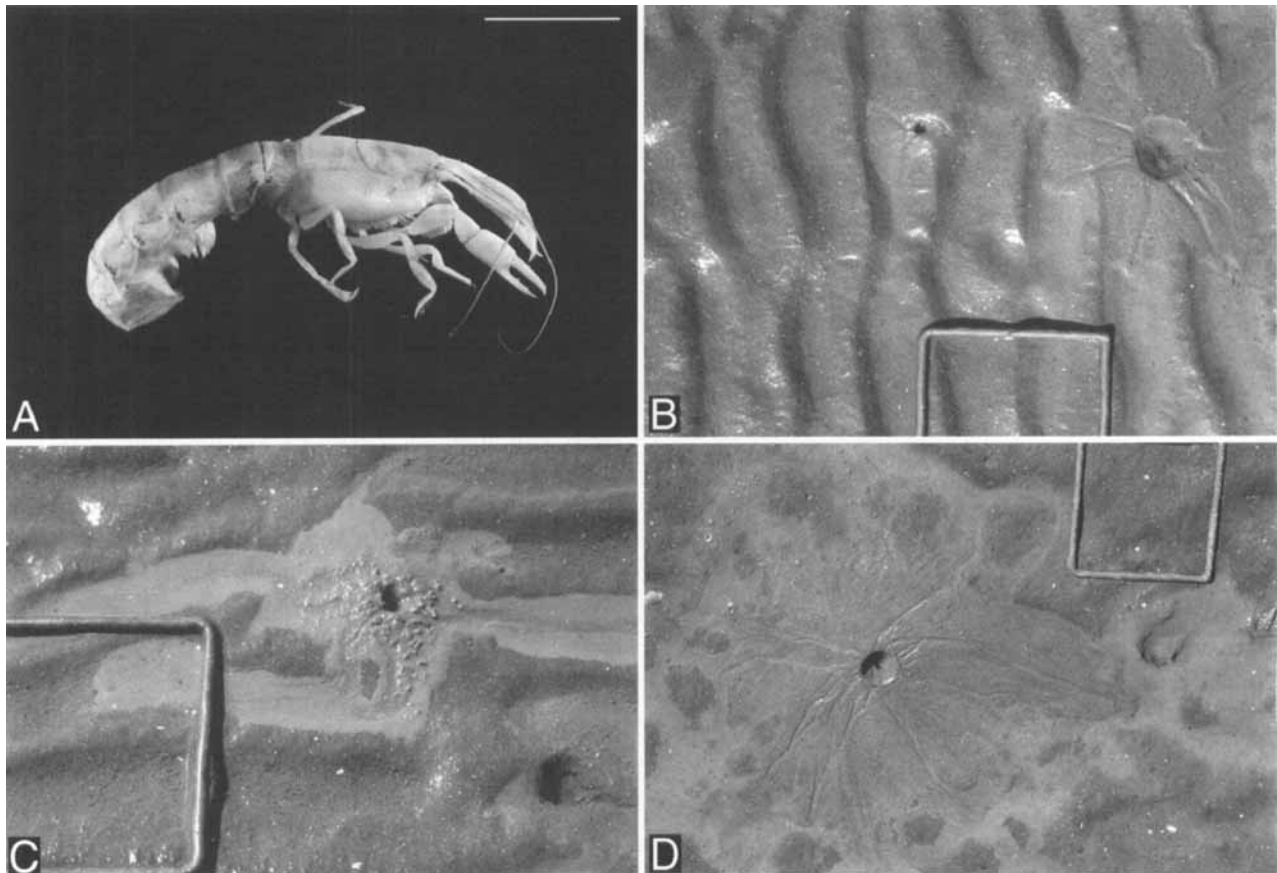


Fig. 4. □A. Specimen of *Axianassa* (female, NHMW 8452) in side view; scale is 1 cm. Photo A. Schumacher. □B–D. Burrow openings of *A. australis*; frame is 10×10 cm.

Table 1. Measurements (in mm) of *Axianassa australis* specimens collected at Praia do Araça with a yabby pump; sex, f: female, fo: ovigerous female, m: male; TL: total length; CL: carapace length; CW: carapace width; si: side of major cheliped, r: right, l: left; PLma: length of major cheliped; PWma: width of major cheliped; PLmi: length of minor cheliped; PWmi: width of minor cheliped; Museum in which specimens have been deposited (NHMW: Naturhistorisches Museum in Wien; MNHN: Muséum National d'Histoire Naturelle Paris).

Date	Sex	TL	CL	CW	si	PLma	PWma	PLmi	PWmi	Museum
940425	f	35	10.5	6.0	l	4.6	2.8	3.6	2.5	NHMW 8452
940425	f	37	11.2	5.8	l	5.0	3.6	4.5	3.0	MNHN-Th 1292
940425	fo	33	9.9	5.0						NHMW 8470
940425	m	18	7.2	3.3	l	4.0	3.4	3.6	2.5	NHMW 8455
940425	fo	38	11.3	6.0	l	5.0	2.9	3.6	2.5	MNHN-Th 1292
940425	fo	43	12.2	7.2	l	5.5	3.7	4.7	3.2	NHMW 8469
940426	m	40	11.5	7.4	r	6.0	4.8			NHMW 8453
940426	fo	38	12.2	6.9				4.6	2.7	NHMW 8454
940426	f	36	12.3	7.2	l			4.2	2.9	NHMW 8456

spirals are linked by another series of tunnels. In the case of cast 940430 (Fig. 5E), two parallel spirals branch off the tunnel at 13 cm depth, and another pair of parallel spirals was present in greater sediment depths (Fig. 5F). Both left and right turning spirals can be present in a single burrow (see Table 2).

The tunnels are either straight or curved, and occur with or without side branches. In cross-sections the tunnels are circular or elliptical when the roof is more arched than the bottom or triangular to pear-shaped (see cross-sections in Figs. 5A, C and 6A). The length of these tunnels ranges from 10 to 40 cm. The irregular shape of the

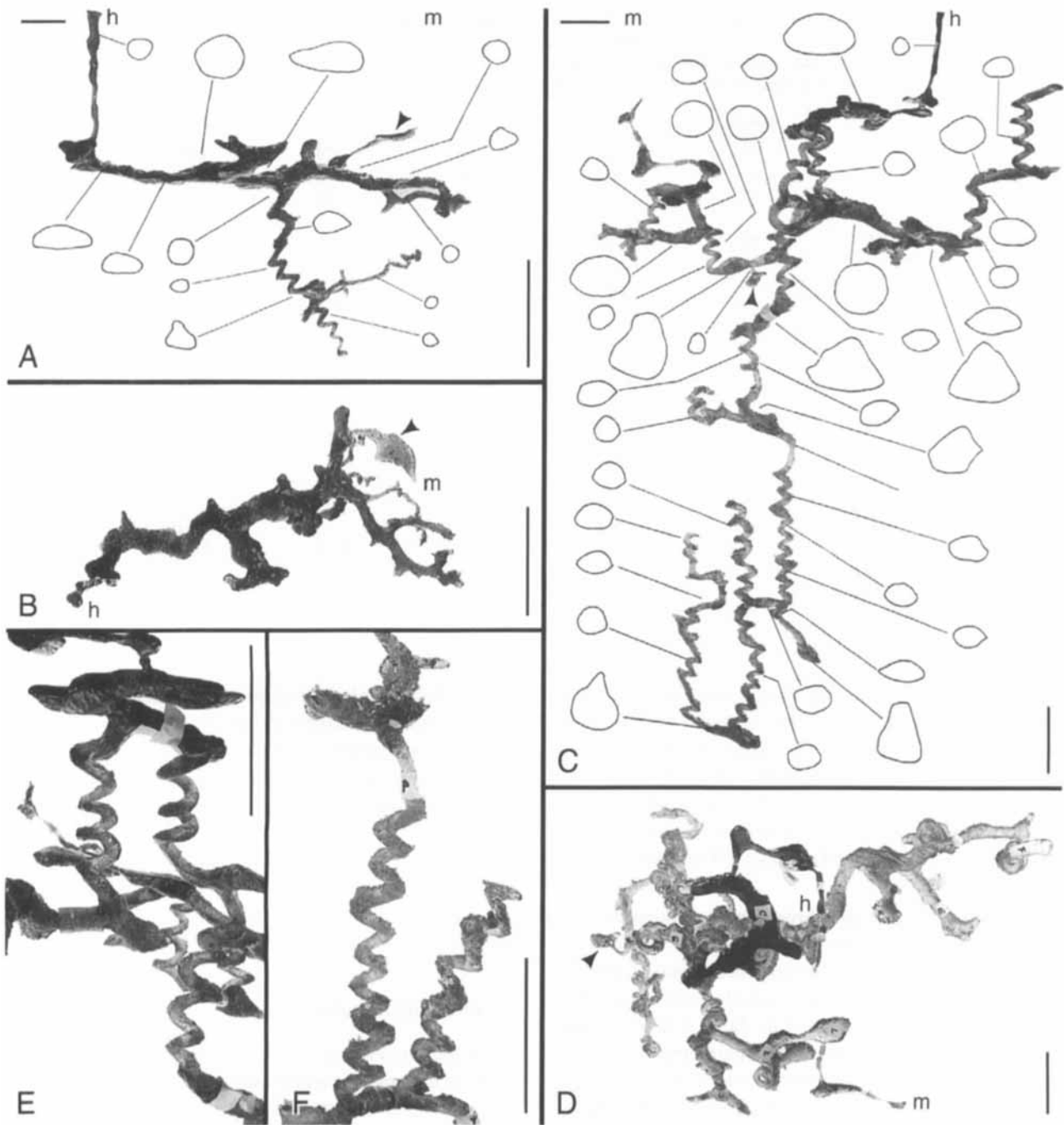


Fig. 5. Burrows of *A. australis*. □A. Cast 940427/1 (NHMW 13723) in side view. □B. Same cast viewed from above. □C. Cast 940430 (NHMW 13724) in side view. □D. Same cast viewed obliquely from above. □E. Detail of C showing upper parallel spirals, the left one turning left down, the right one turning right down. □F. Detail of C showing lower parallel spirals, both turning down to the left; note rougher roofs compared to the upper spirals. m: mound site; h: hole (funnel) site. Arrow shows position where an animal was entombed. Vertical scale (for resin casts) is 10 cm; horizontal scale (for cross-sections in A and C) is 2 cm.

tunnels can be seen particularly when the casts are viewed from above (Figs. 5B, D, 6B). The dip angle of the tunnels ranges between 0° and 30° .

The burrows in the regular 'corkscrew spirals' have an elliptical cross-section, and the roof is more arched than the bottom. The outside of these burrows is more acute

than the rounded inner side and sometimes forms a keel running along the outside of the spirals (see Fig. 5E). The dip angle of the burrow within these spirals ranges from 20° to 40° .

No complete animals were entombed by the resin. In 940427/1 two chelipeds (PLma = 3.3 mm; PLmi = 2.5

Table 2. Measurements of *Axiomassa australis* burrow casts. W: weight; TL: total length; T1st: depth of first (wide) spiral; TU: depth of U; TG: total depth; V: burrow volume (calculated from density of resin); left: number of spirals turning down to the left; right: number of spirals turning down to the right; A: distance of openings; HE: horizontal extension; BH: burrow height; BW: burrow width; SH: spiral height; CD: outer coil diameter; L: 'length' of the spiral, i.e. the vertical extension of one entire spiral between separate tunnels and side branches.

	940427/1	940427/2	940427/3	940427/4	940428	940430	940501
W [g]	186	177	150	92	179	1605	1572
TL [cm]	182	119	148	94	180	1020	809
T1st [cm]	13	15	18	32	28	12	36
TU [cm]	13					33	81
TG [cm]	34	62	62	67	79	106	130
A [cm]	31					40	20
HE [cm]	40	44	37	50	44	70	80
V [cm ³]	135.8	129.2	109.5	67.2	130.7	1171.5	1147.5
left	2		1			9	2
right	1		1		2	6	5
remarks	chelae	incomplete	incomplete	incomplete	incomplete	chela	
<i>tunnels:</i>							
BH [mm]	9–18		10–18			11–27	10–29
BW [mm]	15–29		13–37			14–30	19–36
<i>spirals:</i>							
BH [mm]	6–11.5		11			8–14	10–15
BW [mm]	6–11.5		14			10–18	15–23
SH [mm]	13–27		28		21–27	17–40	16–35
CD [mm]	12–22		24		18–24	28–37	38–60
L [cm]	6–10				7	8–25	7–30

mm) and part of the cephalothorax were caught in the resin (see arrows in Fig. 5A, B). In cast 940430/1 only one cheliped (presumably the major; PLma = 7 mm) was entombed (see arrows in Fig. 5C, D). From the measurements of the chelipeds the total length of the inhabitants was calculated to be between 21 and 23 mm in the small cast (940427/1) and ca. 50 mm in the large cast (940430/1).

The dimensions of the three complete burrows and four incomplete burrows are summarized in Table 2. Measurements of the partly entombed animals indicate that the burrow dimensions are related to animal size. The mean burrow width of the spirals shows a more regular cross-section than the tunnels. This parameter was therefore chosen as the independent variable in calculating regressions of the mean spiral radius, mean spiral height, and mean coil diameter in relation to the mean burrow width (Fig. 7).

The inner coil diameter ranged from 0 to 10 mm. Because of the complex shape and varying diameter of the burrows, no exact calculations of the burrow surface have been made. Very rough estimates indicate a surface of more than 0.5 m² for the largest burrow.

Properties of the burrow wall

The burrows are unlined, and the walls of the tunnels and spirals are irregular and rough. In several places imprints of shells and shell fragments are visible, and in some cases

entire shells have been embedded in the resin (Fig. 6C, D). The floors of the tunnels and spirals are smooth. The gradation from tunnels to spirals often has paired ridges or furrows (rounded, 0.5 mm high/deep, 5 mm wide) on the floor running in the direction of the burrow segment over a distance of 10 cm (Fig. 6D).

During excavation of the casts it was observed that the burrow wall of the spirals was a light brown colour (indicating that it was oxidized), compared to the surrounding black to grey colour characteristic of reduced sediment.

Burrowing behaviour

In a laboratory aquarium, *A. australis* made only feeble attempts to construct a new burrow. Over a period of four days the specimen created only a slight depression at the sediment surface.

Discussion

Recent and fossil spiral burrows

This is the first report of a symmetrical 'corkscrew spiral' in an extant species of burrowing shrimp. All burrows of thalassinideans can at least occasionally have burrow components with a more-or-less spiral shape (e.g., Dworschak 1983; Bromley 1990). A spiral is even present in the Y-shaped burrows of the suspension-feeding Upo-

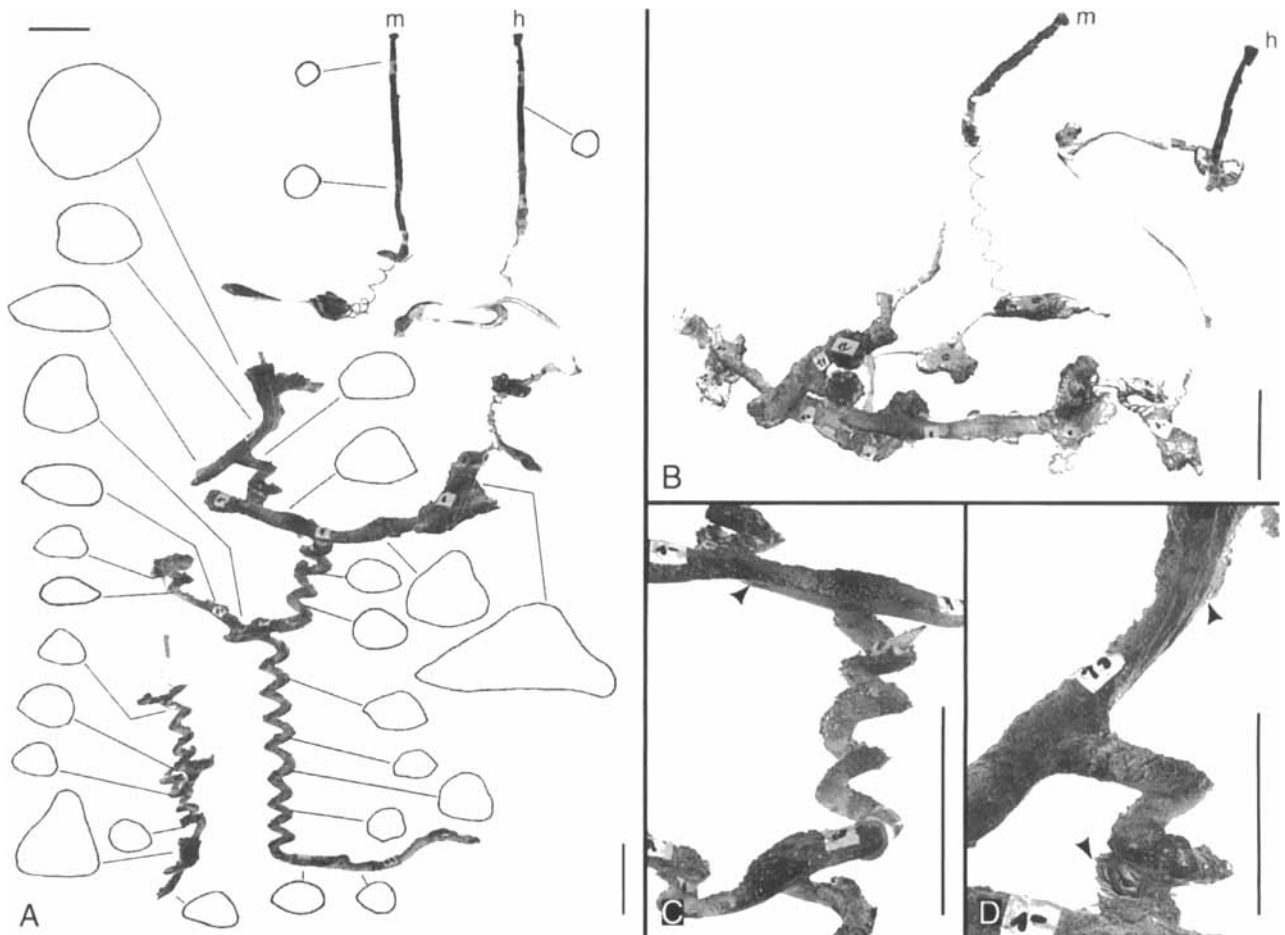


Fig. 6. Resin cast 950501 (NHMW 13725) of an *A. australis* burrow. □A. Side view with superimposed outlines of cross-sections. □B. Viewed from above. □C. Detail of spiral showing embedded gastropod shell; note keel on sides of the tunnels (arrow). □D. Detail of tunnel with furrows on the floor (arrow up) and packed bivalve shells within spiral whorl (arrow down). m: burrow opening showing mound; h: burrow opening showing hole; burrow below upper shafts incompletely filled and partly reconstructed with wire. Vertical scale (for resin casts) is 10 cm; horizontal scale (for cross-sections in A) is 2 cm.

gebiidae (Dworschak 1983). However, in such cases the spiral is generally wide with branching blind tunnels (e.g., in *Glypturus acanthochirus*; Dworschak & Ott 1993) and often has of a series of chambers linked by a shaft. This latter pattern is seen in the burrows of the callianassid *Callianassa bouvieri* (Dworschak & Pervesler 1988) and in the laomediid *Jaxea nocturna* (Pervesler & Dworschak 1985).

The spiral burrows of *Axianassa* are very similar in shape and dimensions to the trace fossils *Gyrolithes* (Fig. 8). The shape and dimensions of these trace fossils, however, vary considerably. The burrow cross-section has been described as either circular (Kilpper 1962; Gernant 1972; Christiansen & Curran 1995) or elliptical (Mansfield 1927, 1930; Mayoral 1986; Föllmi & Grimm 1990; Grimm & Föllmi 1994). An elliptical cross-section has been interpreted to be due to early compaction (Stenzel *et al.* 1957). However, the elliptical cross-section of the burrows of *Axianassa* is most probably due to the natural burrowing actions of the animals and not to non-biological forces such as compaction.

Fig. 7 shows three dimensions of selected fossil and recent spiral burrows plotted in relation to the burrow width of the spirals. All burrow widths in the spirals of *Axianassa* burrows from Brazil fall within the range of those reported for *Gyrolithes*. A spiral cast taken in Belize (probably of an *Axianassa* species) was found to have a much wider burrow. Spiral height was found to be a linear function of burrow width in *Axianassa* burrows (line b in Fig. 7). The spiral height of fossil burrows is smaller than in *Axianassa* burrows of comparable burrow width in the case of small specimens, but larger in spiral burrows of greater burrow width (line c' in Fig. 7). The coil diameter of spirals in *Axianassa* burrows was not found to be linearly related to burrow width, but showed logarithmic relation with coil diameter in spirals showing a smaller increase with increasing burrow width (line c in Fig. 7). Nearly all fossil spiral burrows have a larger coil diameter than the spirals of *Axianassa* burrows of comparable burrow width. This is mainly due to the fact that some of the *Gyrolithes* have a much wider inner coil diameter – e.g.,

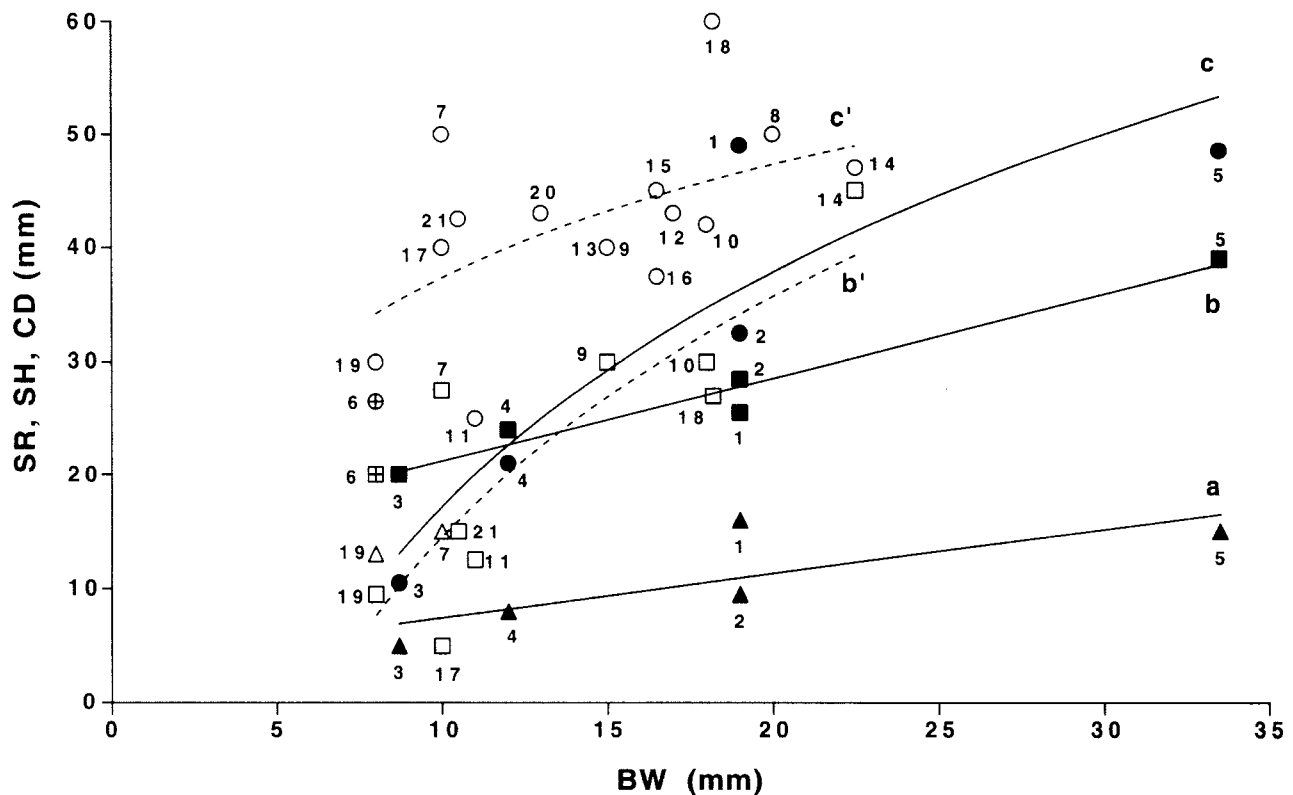


Fig. 7. Dimensions of modern and fossil spiral burrows. *Axianassa* burrows: filled symbols, solid lines; *Notomastus lobatus*: crossed symbols; *Gyrolithes*: open symbols, dashed lines. Mean burrow width (BW); mean spiral radius (SR, triangles, a: $SR = 0.3847BW + 3.6053$, $r^2 = 0.6133$); mean spiral height (SH, quadrats, b: $SH = 0.7373BW + 13.804$, $r^2 = 0.9614$; b': $SH = 29.675 \ln BW - 53.74$, $r^2 = 0.706$); mean coil diameter (CD, circles, c: $CD = 29.85 \ln BW - 51.571$, $r^2 = 0.8193$; c': $CD = 14.289 \ln BW + 4.4614$, $r^2 = 0.2723$). Sources: 1–4: this study; 1: cast 940501; 2: cast 940430; 3: cast 940427; 4: cast 940428. 5: burrow cast, probably of *Axianassa* from Carrie Bow Cay, Belize (Dworschak, unpublished). 6: *Notomastus lobatus*, intertidal, North Carolina (Powell 1974, Fig. 2). 7: *Gyrolithes davreuxi*, Upper Cretaceous, Belgium (Bromley & Frey 1974, Fig. 1). 8: *Gyrolithes*, Oligocene, Germany (von Ammon 1900 ex Gernant 1972, Table 1). 9: *Gyrolithes marylandicus*, Miocene, St. Mary's Formation, Maryland (Mansfield 1927, Pl. 3:2). 10: *Gyrolithes clarki*, Miocene, Monterey Group, California (Mansfield 1930, Pl. 2:1). 11: *Gyrolithes mexicana*, Cretaceous, Mexico (Mansfield 1930, Pl. 1:3). 12: *Gyrolithes*, Eocene, Stone City Beds, Texas (Stenzel *et al.* 1957 ex Gernant 1972, Table 1). 13: *Gyrolithes cf. marylandicus*, Miocene, Braunkohlenformation, Germany (Kilpper 1962). 14: *Gyrolithes*, Miocene, Borneo (Keij 1965, Fig. 29/3). 15, 16: *Gyrolithes marylandicus* (Gernant 1972, Table 1 and Pl. 1:1). 17: *Gyrolithes*, Miocene, Brazil (Fernandes & Assis 1980). 18: *Gyrolithes vidali*, Pliocene, Spain (Mayoral 1986, Table 1). 19: *Gyrolithes*, Oligocene–Miocene, San Gregorio Formation, Baja California (Föllmi & Grimm 1990, Fig. 2B). 20: *Gyrolithes marylandicus*, Miocene, St. Mary's Formation, Maryland (Christiansen & Curran 1995 and Allen Curran, personal communication, 1995). 21: *Gyrolithes*, Oligocene–Miocene, San Gregorio Formation, Baja California (Grimm & Föllmi 1994, Figs. 6B and 10). Dimensions given as mean value of ranges mentioned in text or measured from figures in original publications.

up to 3 cm in *Gyrolithes davreuxi* (Bromley & Frey 1974) – than the spirals of *Axianassa* burrows, where the inner coil diameter is zero in most cases.

Recent spiral burrows of similar size have also been reported by Powell (1977) for a polychaete (*Notomastus* sp.) from tidal flats in North Carolina. A much smaller spiral burrow (burrow diameter 3 mm, coil diameter 1.6 cm) oriented obliquely or horizontally was observed for another capitellid polychaete, *Heteromastus latericus*, from the North Sea near Helgoland (Hertweck & Reineck 1966; Reineck *et al.* 1967). Members of the polychaete family Paraonidae (*Paraonis fulgens*, *Aricidea fragilis*) also make spiralled, corkscrew-like structures in the deeper parts of their burrows (Röder 1971; Ruppert & Fox 1988). In *Paraonis fulgens* these spirals lie in a horizontal plane (Röder 1971). According to Ruppert & Fox (1988), the

enteropneust *Saccoglossus kowalevskii* from tidal flats in North Carolina constructs helical U-shaped burrows.

Spiral burrows have been observed in a number of brachyuran crabs (for a review, see Vannini, 1980). Some adult male ocypodid crabs, e.g., *Ocyopode saratan* (Al-Kholy 1958; Magnus 1961; Linsenmair 1965, 1967) and *O. ceratophthalma* (Farrow 1971), dig spiral burrows associated with sand pyramids ('reproductive burrows'). Other ocypodid crabs, e.g., *Macrophthalmus definitus* (Verwey 1930), *Macrophthalmus* sp. (Farrow 1971), *Uca annulipes* and *Macrophthalmus parvimanus* (Braithwaite & Talbot 1972), and *Uca beebei* (Christy & Schober 1994), also dig spiral burrows. These crab burrows, however, have an incomplete single, wide whorl (up to 60 cm coil diameter in *Ocyopode*) with a circular cross-section, and a much larger burrow diameter (up to 10 cm) when com-

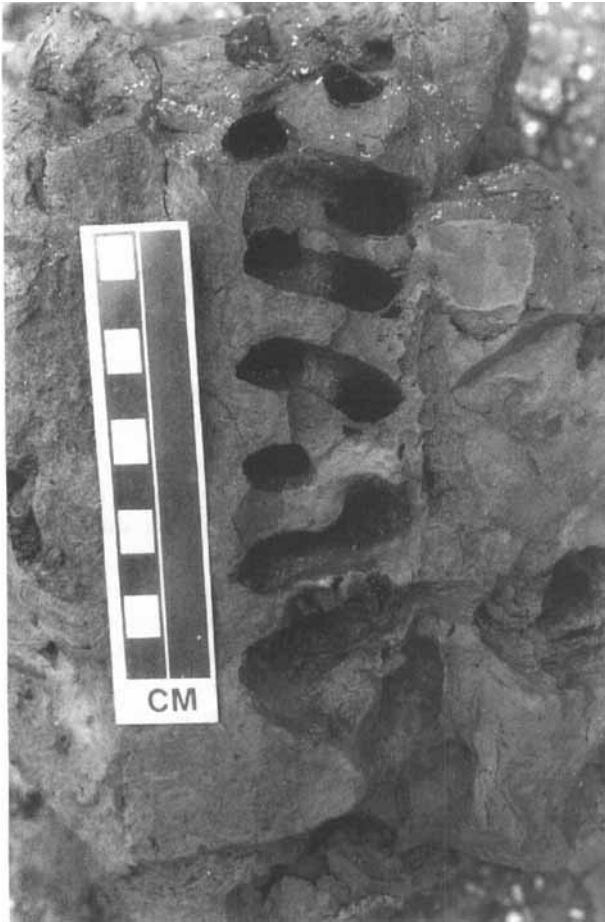


Fig. 8. Trace fossil *Gyrolithes marylandicus*, Little Cove Point Member of St. Mary's Formation (Miocene) of Maryland, USA. Photo H.A. Curran.

pared with the fossil spiral burrows described under the ichnogenus *Gyrolithes*.

Of the above-mentioned modern spiral burrows, only that of *Notomastus* would qualify as *Gyrolithes*.

Intergradational morphologies among fossil and recent burrows

Intergradation among the trace fossils *Gyrolithes*, *Ophiomorpha*, *Spongeliomorpha* and *Thalassinoides* has been reported a number of times by palaeontologists (see Fürsich 1973; Bromley & Frey 1974; Mayoral 1986; Bromley 1990). It has been explained either by the presence of morphologically different burrow parts (in a burrow produced by a particular species) or by the co-occurrence of several different burrowing species in a particular sedimentary setting. Studies on recent burrowing crustaceans, particularly thalassinidean shrimp, indicate that the burrows have a wide diversity, both in their morphology and in their function (see Nickell & Atkinson 1995). For example, the burrows of *A. australis* show three dis-

tinct burrow parts: vertical shafts, branched horizontal tunnels, and regular corkscrew spirals. On the basis of comparative morphology alone, the corkscrew spirals would be referred to the ichnogenus *Gyrolithes*, while the irregular branched horizontal tunnels would be referred to the ichnogenus *Thalassinoides* (Frey *et al.* 1984). Furthermore, in addition to *A. australis*, there are a number of other burrowing organisms found in this tidal flat. In the 1960s, several species of callinassid shrimp were collected at this location (Rodrigues 1966, 1971), including *C. major* which was also collected in 1994, 200 m south of the tidal flat. The burrows of *C. major* are one of the recent analogues for the trace fossil *Ophiomorpha* (Weimer & Hoyt 1964; Frey *et al.* 1978). Stomatopods (*Squilla* sp.) have also been observed to construct burrows with agglutinated walls and a knobby exterior which are similar to *Ophiomorpha* (Vaugelas 1991). *Alachosquilla floridensis* (Manning) is common in the subtidal of Baia do Segredo (Coelho 1995) and Praia de Barequeçaba (which are both bays south of Praia do Araçá) and constructs a burrow with an agglutinated wall (Dworschak, unpublished). Another stomatopod, *Lysiosquilla scabricauda*, is commonly found in the tidal flat in Brazil, where *A. australis* lives. In the mangrove channel of Twin Cays (Belize), where a spiral burrow most probably made by *Axianassa* was found, there were also burrows made by alpheid shrimps and by the callinassid *Glypturus acanthochirus* (Dworschak & Ott 1993).

Construction of the spirals

In addition to speculation on the identity of the organisms responsible for constructing spiral burrows, theories have been presented on how such burrows may have been constructed. Toots (1963) discussed several possible mechanisms and considered this burrow shape to be the result of asymmetric digging movements. Another model of construction of *Gyrolithes* was presented by Mayoral (1986), who considered the paired striae on the outside of the whorls to be scratch marks of a presumed crab's chelipeds.

A number of works dealing with the burrowing behaviour of decapods have been reviewed by Atkinson & Taylor (1988). Thalassinideans construct burrows mainly by excavation. Sediment is loosened with the first two pairs of pereopods and is carried in a basket formed by the setae of these first two pairs of appendages (MacGinitie 1930; Sankolli 1963; Devine 1966; Rodrigues 1966; LeGall 1969; Thompson, 1972; Ott *et al.* 1976; Rodrigues & Hödl 1990). The sediment removed during the construction of a new burrow is first brought to the surface. Later, the sediment is transported to other parts of the burrow, where it is placed in blind tunnels or incorporated into the burrow wall. A different mode of sediment transport has been observed in the laomediid *Jaxea nocturna* by Nickell &

Atkinson (1995), which bulldozes sediment between its chelipeds. This method of sediment transport by carrying sediment on the chelae and pushing with the outside of the chelae has been observed to be typical of burrowing alpheid shrimp (Magnus 1967; review in Karplus, 1987). Bulldozing may be responsible for the ridges and furrows seen on the burrow floor at transitions from the spiral section to tunnels in the burrow casts of *Axianassa*.

In the burrowing ocypodid crabs, the direction of the spiral is related to the handedness of the animal. The burrow spiral runs clockwise or counterclockwise, according to whether the small chela is the left or the right one (Linsenmair 1967; Farrow 1971). Ocypodids loosen sediment with the walking legs and carry it between the minor cheliped and the second and third walking leg of the same side (Vannini 1980). These animals always dig sideways and always enter the burrow with their minor cheliped first.

Handedness may also be a factor in the construction of spiral burrows in the thalassinideans. In *Axianassa*, however, there is not a great difference in size between the major and minor cheliped (see Table 1). In addition, both left- and right-turning spirals are found in the same burrow (see Table 2). Callianassids have a more pronounced difference between their major and minor chelipeds, but both left- and right-turning spirals have been observed in a single burrow inhabited by a single animal, e.g., in *Callianassa bouvieri* (Dworschak & Pervesler 1988; Dworschak, unpublished).

The trace fossil *Daimonhelix*, known as the 'Devil's corkscrew', have spirals of a much larger dimension than *Gyrolithes*. However, the 'Devil's corkscrew' has been attributed to the work of terrestrial beavers (*Palaeocastor*), which made the burrows by a series of right- or left-handed incisor strokes (Martin 1994).

Recently, Föllmi & Grimm (1990) and Grimm & Föllmi (1994) attempted to interpret the occurrence of *Gyrolithes* and *Thalassinoides* in laminated sediments associated with event beds. They proposed the theory of 'doomed pioneers', whereby thalassinidean shrimps were carried within gravity flows to a deeper but more oxygen-poor environment, where they reworked extensively the laminated sediments with no other sign of bioturbation. These authors speculated on the origins of spiral burrows: (a) the burrows are made by a 'decapod amputee' (which lost its large cheliped during transport), (b) variations in the coiling direction of spiral burrows may reflect the normal sexual dimorphism of differential cheliped enlargement, and (c) the transport of an enrolled crustacean may have disturbed the statocyst balance system, making the animal dizzy, which resulted in it digging a spiral burrow. None of these conditions would provide a satisfactory explanation for the means of construction of the spiral burrow of *Axianassa* described in the present work.

Functional morphology of *AXIANASSA* burrows

The burrows of *Axianassa australis*, with their unique corkscrew spirals, cannot readily be classified using existing models, such as the one proposed by Griffis & Suchanek (1991). They defined six burrow types, based on the absence or presence of (1) sediment mounds, (2) seagrass in chambers or the burrow lining and (3) a simple 'U' shaped burrow design, and attribute the types to one of the three general trophic modes (deposit feeding, drift catching and filter/suspension feeding). Using the alternative approach proposed by Nickell & Atkinson (1995), features such as 'surface mound', 'deep burrow', and 'sub-circular tunnel cross section' found in *Axianassa* burrows are indicative of sediment processing for feeding or for burrow expansion and repair. This would infer that these animals are deposit feeders utilizing sub-surface sediments.

The compact sediment and the relatively weak ability for reburrowing observed in aquaria indicate that at least the deeper parts of *Axianassa* burrows are quite permanent. The occurrence of mounds with freshly expelled sediment and the ventilation activity observed during both water coverage at high tide and exposure at low tide indicate that sediment is removed from the deeper layers, either for burrow expansion or for the repair of collapsed parts of the upper burrow.

A close fit between animal size and burrow diameter is indicative of suspension feeding, as in upogebiids (Dworschak 1983) and suspension feeding callianassids, e.g., *Callichirus major* (Rodrigues 1966; Rodrigues & Hödl 1991). A close fit is necessary for effective ventilation of the burrow, for both respiratory and feeding purposes (Dworschak 1981, 1987). Deposit-feeding callianassids and axiids such as *Axiopsis serratifrons* (Dworschak & Ott 1993) and laomediids do not fit tightly in their burrows. They have a large relative burrow diameter and may turn around anywhere in it. The extreme case is *Jaxea nocturna* (Pervesler & Dworschak 1985), where animals with a total length of 5 cm and a body diameter of less than 1 cm dig a burrow 3–4 cm wide and 1.5–2 cm high. Here, gently sloping burrow segments (with dip angles of between 0° and 30°) connect with even larger (6–8 cm wide, 2–4 cm high) chambers.

Deposit feeding (rather than suspension feeding) is implied by the poor fit of *A. australis* to its burrow dimensions (see Tables 1 and 2). This poor fit would make movement in vertical shafts, and especially bulldozing of sediment, impossible. The corkscrew spirals found in the burrows of *A. australis* may therefore serve to allow the animals to burrow to greater depths, with gently sloping burrow floor in order to exploit deeper sediment layers rich in organic matter.

Thalassinidean burrows with large chambers in different sediment depths (such as those of *Jaxea nocturna*)

suggest that animals selectively seek sediment layers rich in organic matter (Pervesler & Dworschak 1985). A tightly layered lattice (such as is found in the burrows of *Callianassa subterranea*) is considered to represent the maximal exploitation of a given volume of sediment by the animal, with the depth of the lattices indicating the thickness of the layers rich in organic matter (Nickell & Atkinson 1995). The regular spirals in the burrows of *Axianassa* offer an optimum of accessible surface area in a given volume of sediment. This indicates that organic matter is more or less evenly distributed over the entire sediment layer in which the spirals occur.

It should be noted that the above explanations for the function of the spirals are tentative and not intended to provide a complete answer. Direct observations of the burrowing and feeding behaviour of *A. australis*, together with a study of the spatial distribution of organic matter in the sediment, will undoubtedly help to clarify the function of the unusual spiral burrows.

Recently, Darryl Felder (personal communication, September, 1996) has hypothesized an anti-predator function for spirals in the burrows of *Axianassa* sp. that he cast in south Florida. Experimental work is being designed by him to test this.

Environmental significance of *AXIANASSA* burrows

Little is known about the biology and ecology of *Axianassa*. Five of the known six species have been reported to occur from the intertidal zone, with only one species, *A. arenaria*, living in deeper water (38 m; Kensley & Heard 1990). The sediment in which the *Axianassa* were found ranged from intertidal stones on rocky and gravelly beaches (for *A. miniieri*) to sand or sandy silt (for *A. jamaicensis* and *A. arenaria*), to muddy sand or mud (for *A. intermedia* and *A. australis*) (Kensley & Heard 1990; Rodrigues & Shimizu 1992). *Axianassa australis* has been reported to occur at, or near to, mangroves (Rodrigues & Shimizu 1992; this study), and several specimens of undescribed species of *Axianassa* have been collected in the Caribbean and the Gulf of Mexico from mangrove environments (Felder *et al.* 1995; Darryl Felder, personal communication, 1994). A cast similar to those of *A. australis* was made in a mangrove channel in Belize (Dworschak, unpublished). The genus *Axianassa* therefore seems to occur mainly in poorly oxygenated sediments in protected environments.

Acknowledgements. – Financial support was given to PCD within the frame of the Convenio between the University of Vienna and the University of São Paulo. Part of the resin was provided by courtesy of Ciba-Geigy Brasil. We are grateful to the entire staff of CEBIMar for their hospitality during our stay in São Sebastião. Our thanks are due to Ms. Vania R. Coelho and Mr. Paulo Pezzuto for help during field work, to Drs. Allen Curran and Darryl Felder for unpublished information, and to Dr. Jörg A. Ott for critical reading of the manuscript. Dr. Neil Cumberlidge helped to improve the English. We also thank Drs. R. James A. Atkinson and H. Allen Curran for their constructive comments.

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