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Burrows of Jaxea nocturna NARDO in the Gulf of Trieste.

With 3 Text-Figures, 4 Tables, and 4 Plates.

Peter Pervesler & Peter C. Dworschak.

Abstract.

[PERVESLER, P. & DWORSCHAK, P. C. (1985): Burrows of Jaxea nocturna NARDO in the Gulf of Trieste. — Senckenbergiana marit., 17 (1/3): 33-53, 3 figs., 4 tabs., 4 pls.; Frankfurt a. M.]

Three resin casts of the burrows of the thalassinidean shrimp Jaxea nocturna were made in situ between 12 and 17 m depth in the Gulf of Trieste. The burrow shape is a spiral with a horizontal extension between 0.3 and 1.1 m^2 reaching to a depth between 53 and 90 cm. Dip and trend angle analysis showed a characteristic orientation of these burrows. Additional information on study sites, sediments and associated fauna is given. The biology of this shrimp is discussed.

Kurzfassung.

[PERVESLER, P. & DWORSCHAK, P. C. (1985): Bauten von Jaxea nocturna NARDO im Golf von Triest. — Senckenbergiana marit., 17 (1/3): 33-53, 3 Abb., 4 Tab., 4 Taf.; Frankfurt a. M.]

Drei Bauten des thalassiniden Krebses Jaxea nocturna wurden im Golf von Triest zwischen 12 und 17 m Tiefe mit Kunstharz ausgegossen. Alle drei Bauten zeigen die Form einer Spirale mit einer horizontalen Ausdehnung zwischen 0,3 und 1,1 m² und reichen in Tiefen zwischen 53 und 90 cm. Sie weisen eine ausgeprägte Orientierung auf. Zusätzliche Informationen zum Untersuchungsgebiet, dessen Sedimente und die vorkommende Fauna werden angeführt. Im Anschluß wird die Biologie dieses Krebses diskutiert.

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Introduction.

Decapod burrows are conspicuous features of recent and fossil marine sediments. Comparison of recent and fossil lebensspuren helps to interpret fossil environments. In summer 1983 and 1984, studies on recent lebensspuren were carried out in the Gulf of Trieste (Northern Adriatic). Resin casts of burrows were made in depths between 7 and 25 m. In addition to burrow replicas of several crustaceans, molluscs and polychaetes, this yielded three large casts which could be identified as burrows of the thalassinidean shrimp *Jaxea nocturna* NARDO (Pl. 1 figs. 1-3). This paper deals with the description of these burrows.

Environmental Setting.

The Gulf of Trieste is the northeastern-most section of the Adriatic Sea (Fig. 1). It is part of a paleoalluvial plain which was drowned during a postglacial transgression. The maximum water depth in the central part of the Gulf does not exceed 25 m. In the Northwest, between Grado and Duino, the Gulf is bordered by a shallow-water zone; here the 10 m isobath may come to lie as far as 3 km offshore. This shallow zone is influenced by the freshwater inflow of the Isonzo. The steeper coast between Duino and Trieste is a spur of the karst; here the 10 m isobath lies 250 m offshore. The steep coast in the southeastern part of the Gulf is interrupted by shallow bays. The rivers flowing into this area are the Dragonja and the Risano. The sediments are sandy pelites and pelites of terrigenous origin, which are dispersed uniformly off the mouths of the rivers and accumulate in the protected basin of the Gulf (BRAMBATI & VENZO 1967; BRAMBATI & CIABATTI & FANZUTTI & MARABINI & MAROCCO 1983).

Positions A and C.

Position A is located two kilometers northwest of the Laboratorio di Biologia Marina, Sorgenti di Aurisina (Fig. 1). The beach is 20 m wide and ends landward in a steep rock-cliff. The intertidal zone is characterized by pebbles and cobbles. A zone of boulders densely populated by *Paracentrotus lividus* reaches from the low water line to a depth of 4 m. Following this is a 10 to 20 m broad meadow of the seagrass *Cymodocea nodosa* which extends to a depth of 6 m. At this depth a zone of bare sandy pelite begins which extends to a depth of 9 m, 200 m offshore. This zone is characterized by numerous burrow openings of *Upogebia pusilla*. Following this is a zone consisting of clayey silt (Tab. 1) characterized by burrow openings of *Squilla mantis* and *Upogebia tipica* and holes occupied by gobiids. Conspicuous faunal elements here include Actiniaria, Ophiuridae, Scaphopoda, Pectinoidea, *Aporrhais pes-pelecani* and *Spirographis spalanzani*. The first resin cast of *Jaxea nocturna* (Jx 1: Pl. 1 fig. 3, Pl. 2 figs. 4-5) was made in this zone at 12 m in July, 1983.



Fig. 1. Map of the Gulf of Trieste showing locations where resin casts were made (A, C, Aurisina: Jx 1 and Jx 3; B, Bay of Strunjan: Jx 2) and specimens of *Jaxea nocturna* collected (positions 1 and 7 according to STACHOWITSCH 1984).

Abb. 1. Der Golf von Triest. Lage der Positionen, an denen Kunstharzausgüsse angefertigt (A, C, Aurisina: Jx 1 und Jx 3; B, Bucht von Strunjan: Jx 2) und Exemplare von Jaxea nocturna aufgesammelt wurden (Positionen 1 und 7, nach STACHOWITSCH 1984).

Position C lies 1 km further offshore than Position A and is similar to the latter. The third resin cast of *Jaxea nocturna* (Jx 3: Pl. 4 figs. 8-10) was made in this zone at 14 m in September, 1984.

Position B.

Position B is located in the Bay of Strunjan, which lies 3 km east of Piran (Fig. 1). In its inner part the Bay contains a small tidal flat consisting of muddy fine sand populated by *Callianassa tyrrhena*, *Upogebia pusilla*, *Gastrana fragilis*, *Tellina*

tenuis, Bornia sebetia, enteropneusts and numerous polychaetes. Below the low water line a dense meadow of the seagrass Cymodocea nodosa extends to a depth of 8 m. This is followed by a typical muddy bottom community (Avčin & MEITH-Avčin & VUKOVIČ & VRIŠER 1974). Characteristic for the muddy bottom in about 9 m depth were numerous holes, probably Squilla mantis-burrows, holes occupied by gobiids, as well as the sea-star Astropecten aranciacus, Holothuria tubulosa and Schizaster canaliferus. About 1 km from the tidal flat a water depth of 17 m is reached. Here, the bottom consists of very soft turbid mud showing numerous large mounds, 20-30 cm high and 40-50 cm in diameter.

The second resin cast of *Jaxea nocturna* (Jx 2: Pl. 3 figs. 6-7) was made here in September, 1983. Several resin casts of *Upogebia tipica*-burrows were also made nearby. The surrounding sediment is a clayey silt (Tab. 1).

Positions 1, 7, and 9.

Positions 1, 7, and 9 are located northeast of Piran (Fig. 1). The muddy bottom in 20 m (Pos. 9), 22 m (Pos. 7) and 25 m (Pos. 1) is populated by a high biomass epibenthic community mainly consisting of the filter-feeding genera *Ophiothrix*, *Reniera* and *Microcosmus* (ORM-community, FEDRA & ÖLSCHER & SCHERÜBEL & STACHOWITSCH & WURZIAN 1976). During a mass mortality event in September 1983 (STACHOWITSCH 1984), several infaunal species — some of them previously not recorded for this area — emerged from their burrows.

One of these species was *Jaxea nocturna*. The data on those specimens sampled by hand during a 20 minute diving period at positions 1 and 7 are summarized in Tab. 2. At position 9 which was in an advanced state of mass mortality, only disintegrated specimens could be recognized. Characteristic bottom features at all positions included numerous large mounds. The sediment is a firm mud with many shell particles (Tab. 1).

Material and Methods.

Jaxea nocturna NARDO 1847 belongs within the infraorder Thalassinidea of the family Laomediidae. This family comprises 5 genera with 11 extant and one fossil species; these are listed in Tab. 3 along with their size, geographical and bathymetric distribution, and type of sediment in which they occur.

Information on the biology of *J. nocturna* is meager; accounts stating that it lives in burrows which the animal digs itself and the reported nocturnal activity are based on the original decription of NARDO (1847).

All in situ investigations were carried out using SCUBA. Casts of burrows were made by the "SHINN-method" (SHINN 1968; FARROW 1975) using an epoxy resin (CIBA Araldit GY 257 with hardener HY 830 and HY 850, 25 : 7 : 8 parts by weight). The components were mixed from preweighed lots on board. The mixture was filled into a 10 l plastic petrol can with screw cap immediately before the dive. On the bottom, metal rings (3 cm high, 11 or 15 cm in diameter) were placed around the selected holes and the resin poured in. After 48 hours the resin cast could be dug out. Before removal, an arrow pointing north was scratched into the resin in the rings. Table 1. Sieve and pipette analysis data of sediments inhabited by *Jaxea nocturna.* — Gulf of Trieste, northern Adriatic Sea.

		%	weight	
μm	Φ	А	В	1 and 7*)
>1000	0	-	_	6.5
500	1	-	-	2.0
250	2	-	-	4.0
125	3		-	8.0
63	4	-	_	13.5
32	5	4.0	7.5	8.0
16	6	11.4	19.9	58 (< 32 μm)
8	7	11.4	13.5	
4	8	17.4	16.7	
2	9	16.7	14.0	
<2	>9	39.1	28.4	
	Md 🖣 —	- 8.3	7.5	-

*) after FEDRA (1977).

Table 2. Sex and size of specimens of *Jaxea nocturna* collected at positions 1 and 7, Gulf of Trieste, northern Adriatic Sea. — tl – total length from tip of rostrum to the end of telson; cl – carapace length.

Tabelle 2. Angaben zu den Exemplaren von *Jaxea nocturna*, die bei den Positionen 1 und 7 aufgesammelt wurden. Golf von Triest, nördliche Adria. — tl – Gesamtlänge; cl – Carapaxlänge.

Position	Depth m	Date	Sex	tl mm	cl mm	Remarks
1	25	830918	ď	44	17.0	
			ç	46	18.8	
			Ŷ	47	18.2	ovigerous, orange eggs
1	25	830919	ୖ	46	17.8	
			Ŷ	45	17.5	ovigerous, eyed eggs
7	22	830921	Ŷ	49	19.4	plumose setae on pleopods

cı – carapace ıengtn.						
T ab elle 3. Übersicht der Arten der Familie Laone Sedimentart. — tl – Gesamtlänge; cl – Carapaxlänge.	ediida	e, mit .	Angaben zur ihrer	Größe, geogi	aphischen und	bathymetrischen Verteilung sowie
Species	Size	E E	Geographical distribution	Depth	Sediment	References
Laomedia astacina DE HAAN 1849	cl	24	Japan, Korea India	intertidal	muddy sand	SAKAI (1962), OHSHIMA (1967), UTASHIRO (1973)
Laomedia healyi YALDWYN & WEAR 1970	cl	28	Australia	intertidal	soft mud	YALDWYN & WEAR (1972)
Jaxea nocturna NARDO 1847	tl 8	-60	Atlantic Mediterranean	15-250 m	sandy mud	PESTA (1918), BOUVIER (1940), Holthuis & Gottlieb (1958), Garcia Raso (1983)
Jaxea novaezelandia WEAR & YALDWYN 1966	cl	13	New Zealand	3.6-22 m	soft mud	WEAR & YALDWYN (1966)
Jaxea kuemehi BACHMAYER 1954	c]	9	Austria, Miocene			BACHMAYER (1954)
Naushonia crangonoides KINGSLEY 1897	tl	34	Cape Cod	shallow water	muddy sand	GOSNER (1979)
Naushonia perrieri (NOBILI 1904)	tl	16	Red Sea			NOBILI (1904)
Naushonia macginitiei (GLASSEL 1938)	tl	18	California	intertidal	among stones	GLASSEL (1938)
Naushonia portoricensis (RATHBUN 1901)	tl	14	Cuba	intertidal	among stones	RATHBUN (1901)
Naushonia panamensis MARTIN & ABELE 1982	t.l	14.7	Panama Eastern Pacific	intertidal	pnm	MARTIN & ABELE (1982)
Axianassa intermedia SCHMITT 1924	cl	8.5	Curaçao	creek	pnu	SCHMITT (1924)
Laurentiella heterocheir LE LOEUFF & INTES 1974	tl	25	Guinea	20-25 m	muddy sand	LE LOEUFF & INTES (1974)

T a b l e 3. Species of the family Laomediidae: size, geographical and bathymetric distribution, and sediment in which they occur. — tl – total length;

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In the laboratory, the resin casts were positioned in their original orientation and the dip and trend angles determined with a Clar-compass. The casts were then weighed, photographed and measured with sliding calipers. Grain size analysis was performed according to BUCHANAN & KAIN (1971).

Results.

Burrow Shape.

Burrows of J. nocturna are figured in Pls. 2-4. All three burrows have two main openings at the sediment surface. In [x 1 both entrances (14 cm apart) were flush with the surface and funnel-shaped with a diameter of about 10 cm at the surface and 4 cm in 5 cm sediment depth (Pl. 2 figs. 4-5). In Jx 2 one entrance (diameter 1.5 cm) opened on top of a mound (about 20 cm high and 40 cm in diameter); the second entrance, 15 cm from the first, was funnel-shaped and located at the foot of the mound (Pl. 3 figs. 6-7). In Jx 3 (Pl. 4 figs. 8-10) one entrance (diameter 2.6 cm) opened on top of a mound (20 cm high and 30 cm in diameter); the second entrance, 55 cm from the first, was funnel-shaped. In 18 cm depth a short branch (2 cm in diameter) leads from the shaft of the first opening to the surface. From both main entrances, nearly vertical (75 to 85° dip angle) shafts with circular cross-sections (1.6 to 3.5 cm) lead to a depth of about 30 cm. At this depth the burrow becomes more horizontal (dip angles of 15 to 25°), the two arms turning in opposite directions (Ix 1 and Ix 3). After several turns at nearly right angles both arms join in a depth of about 45 cm. Burrow diameter in this part is elliptical (3 to 4 cm \times 1.5 to 2 cm). In Jx 1 there are 2 to 3 swollen chambers (6 to 8 cm \times 2 to 4 cm) at different sediment depths. One of these branches leads into a T-shaped large chamber (Pl. 2 fig. 4, left corner). After joining, the burrow follows the form of a spiral continuing the direction of one of the arms (Jx 1 and Jx 2). Three more swollen chambers in different sediment depths are linked by a gently sloping tunnel with elliptical crosssection. In its deepest part, the tunnel of Jx 1 becomes thinner and circular in crosssection before it ends blindly. In Jx 2 the form of the spiral is also recognisable, although less prominently than in Jx 1. Chambers at different sediment depths are broader than in Jx 1. The burrow does not continue after the joining of the two arms in Jx 3, but the spiral form of the whole system can also be recognised. Jx 1 and Ix 2 have the form of a dextral spiral, whereas Ix 3 turns to the left.

Burrow Dimensions.

The dimensions of the three burrows are summarized in Tab. 4. The total length of the entombed animal in Jx 1 is about 50 mm and in Jx 3 about 60 mm as estimated from chela length (Pl. 1 fig. 3).

Burrow Wall.

As judged from resin cast surfaces, the burrow wall is knobby and rough on roofs and smooth to slightly rippled on floors. Smoothness of floors in the chambers of Jx 2 is due to incomplete filling of the burrow (Pl. figs. 6-7). Several smaller burrows (2 to 10 mm in diameter), probably of polychaetes, branch off in some chambers. Shells of *Aporrhais pes-pelecani, Clamys* sp., *Turitella communis,* Scaphopoda and *Amphictene* can be found in the entrance shafts.

	Jx 1	Jx 2	Jx 3
	648	381	257
Horizontal extension (cm)	110 x 100	90 x 85	66 x 44
Total depth (cm)	90	85	53
Volume (cm³)	4300	> 1980	2710
Surface (cm ²)	6700	> 3600	3020

Table 4. Dimensions of burrows of Jaxea nocturna. - Gulf of Trieste, northern Adriatic Sea.

Tabelle 4. Abmessungen der Bauten von Jaxea nocturna. - Golf von Triest, nördliche

Orientation.

Dip and trend angles from successive parts of the burrows were measured. Frequency distributions of burrow parts according to their dip angles are figured in Fig. 2. Burrow parts with slight inclination contribute much more to overall orientation of the system than steep parts. Orientation analysis by means of circular histograms reveal preferred trend angles within the burrows of J. nocturna. Such frequency distributions can be explained by two overlying axial distributions after "von Mises" (HOHENEGGER & PERVESLER in press). The mean vectors of these two axial distributions in Ix 1 (Pl. 2 figs. 4-5) enclose an angle of nearly 90° (Fig. 3).

Discussion.

The complex burrow system of Jaxea nocturna is unlikely to be confused with the burrows of other animals occuring in the same area: Upogebia tipica-burrows are Y-shaped (DWORSCHAK unpublished data) and similar to burrows of U. pusilla (DWORSCHAK 1983). Squilla mantis constructs simple, flat, U-shaped burrows, and burrows of Gobius sp. are simple conical short shafts with many attached burrows of smaller size (PERVESLER unpublished data). Characteristic for burrows of J. nocturna are the following features: (1) two main entrances, vertical shafts with circular cross-section reaching to a depth of about 30 cm, then becoming more horizontal and meeting after several branchings; (2) gently sloping and horizontal parts with elliptical cross-section showing sinuous, rough roofs and more flattened, ridged floors; (3) a generally spiral configuration; (4) a branching of nearly 100° and (5) several flattened, wide-elongated chambers at different sediment depths.

Even on the sediment surface, burrows of J. nocturna can be distinguished from burrow openings of other animals: Upogebia tipica-burrows open in 2 holes, 3 to 12 cm apart and 6 to 12 mm in diameter, which are flush with the sediment surface. The burrow opening of Squilla mantis is also flush with the surface, shows sharp edges and has a diameter from 40 to 50 mm. The second hole can often be recognised at a distance of about 1 m from the first; in some cases an animal is

Adria.



Fig. 2. Frequency distribution of burrow parts according to their dip angles. -100% = total length of burrow, see Tab. 3.

Abb. 2. Häufigkeitsverteilung der in den Bauten vorkommenden Neigungswinkel. — 100% = Gesamtlänge des jeweiligen Baus, siehe Tab. 3.

present. Burrows of *Gobius* sp. — which seem to be abandoned burrows of other animals (e. g. *Squilla*) — have crater-like openings, and the inhabitant can bee seen in nearly all cases. The funnel-shaped opening of *J. nocturna*-burrows are very similar to the latter, but can be distinguished by the absence of the fish. More obvious than the first opening is the second, which is located on top of a mound 20 to 30 cm high and 30 to 40 cm at its base. Although this mound is missing in Jx 1, it seems to be a characteristic surface feature of *J. nocturna*-burrows.

Mounds, which can be attributed to burrows of *J. nocturna* occur on positions A and B in densities of 8 to $9/100 \text{ m}^2$. On position 1 near Piran, density of mounds



Fig. 3. Circular histogram of trend angles measured at Jx 1. — r_1 , r_2 mean vectors; s_1 , s_2 standard deviations.

Abb. 3. Kreishistogramm der Einfallswinkel, die an Jx 1 gemessen wurden. — r1, r2 mittlere Vektoren; s1, s2 Standardabweichungen.

could be estimated to be up to $20/100 \text{ m}^2$; mounds occur in groups of 1 to 5 in a 4 m² area. These findings indicate that *J. nocturna* is more common in the Gulf of Trieste than previously recorded by faunal surveys performed with grabs. Only one specimen has been found in the Gulf of Piran (MANNING & ŠTEVČIĆ 1982). AVČIN & VRIŠER (1983), however, state that the species is common. *J. nocturna* was not represented in the samples collected in the Italian part of the Gulf of Trieste (OREL & MENNEA 1969).

It is evident from the resin casts that *J. nocturna* is a burrowing animal. Previously, the burrowing habit of sublittoral laomediids was assumed from indirect evidence such as general facies and diurnal/nocturnal collecting ratios (NARDO 1847; PESTA 1918; WEAR & YALDWYN 1966). Further investigation is necessary to determine whether the capture of trawled specimens only at night is due to emergence of animals from their burrows or to the presence of the animal near the entrance during the night.

Gut content analysis, general burrow shape and the poor fit of the animal's diameter to burrow diameter indicate deposit feeding in *J. nocturna*. The mine-like construction of the burrows (large chambers in different sediment depths) suggests that the animal selectively seeks sediment layers which may be rich in organic matter.

Considering the dimension of the burrow, the question arises as to how the animal effects an exchange between burrow water and overlying water. If we assume a similar pumping rate for *J. nocturna* as has been measured for *U. pusilla* — in this case 0.5 ml s⁻¹ for Jx 1 with tl = 50 mm and 0.85 ml s⁻¹ for Jx 3 with tl = 60 mm (DwORSCHAK 1981) — *J. nocturna* would have to spend 14 to 40 times more time than *U. pusilla* for pumping to exchange burrow water. Furthermore, as burrow diameter is greater than animal diameter and pleopod area is approximately 4 times smaller than in *U. pusilla*, pumping rates in *J. nocturna* would be expected to be even lower. Thus, passive ventilation as is induced by water flow over burrows with two openings at different levels (VOGEL & BRETZ 1972) may play an important role in the exchange of burrow water.

Characteristic orientation of burrows are known for many supralittoral (e.g. FREY & MAYOU 1971; CHAKRABARTI 1981) and sublittoral crustaceans (e.g. ATKIN-SON 1974) as well as for fossil burrows of probable crustacean origin (HOHENEGGER & PERVESLER in press). Further investigation is necessary to determine which parameters are responsible for such orientation patterns in *J. nocturna*.

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Plate 1.

Jaxea nocturna NARDO. — Bar is 1 cm.

- Fig. 1. Ovigerous female with a total length of 46 mm, collected at Pos. 1, Aurisina, Italy, September 1983, Lateral view.
- Fig. 2. Same as Fig. 1., dorsal view.
- Fig. 3. Close-up of resin cast Jx 1, Aurisina, Pos. A, with entombed animal. Position marked by arrows in Pl. 2 fig. 4-5, viewed from below. Note shell of Corbula gibba to the right.

Tafel 1.

Jaxea nocturna NARDO. — Maßstab 1 cm.

- Fig. 1. Eiertragendes Weibchen, Gesamtlänge von 46 mm, Seitenansicht. Aurisina, Pos. 1, Golf von Triest, Italien.
- Fig. 2. Wie Fig. 1., von dorsal.
- Fig. 3. Nahaufnahme des Kunstharzausgusses Jx 1 mit dem eingeschlossenen Tier. Aurisina, Pos. A. — Die Stelle, auf die die Pfeile in Taf. 2 Fig. 4-5 weisen, von unten gesehen. Rechts neben dem Tier eine leere Schale von Corbula gibba.



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Plate 2.

Burrow of Jaxea nocturna. — Resin cast Jx 1, Aurisina, Pos. A, 12 m depth. Diameter of rings 11 cm. Arrows indicate position of entombed animal; arrow scratched into resin of inflow-ring marks orientation.

Fig. 4. View from above.

Fig. 5. Oblique view.

Tafel 2.

Bau von Jaxea nocturna. — Kunstharzausguß Jx 1, Aurisina, Pos. A, 12 m Tiefe. Durchmesser der Metallringe 11 cm. Die Pfeile weisen auf die Lage des miteingegossenen Tieres. Der im Harz des Eingießringes eingeritzte Pfeil markiert die Nordrichtung.

Fig. 4. Ansicht von oben.

Fig. 5. Schrägansicht.



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Plate 3.

Burrow of Jaxea nocturna. — Resin cast Jx 2, Bay of Strunjan, Pos. B, 17 m depth. Diameter of inflow-ring 11 cm.

Fig. 6. View from above.

Fig. 7. Oblique view.

Tafel 3.

Bau von Jaxea nocturna. — Kunstharzausguß Jx 2, Bucht von Strunjan, Pos. B, 17 m Tiefe. Durchmesser des Eingießringes 11 cm.

Fig. 6. Ansicht von oben.

Fig. 7. Schrägansicht.



Plate 4.

Burrow of Jaxea nocturna. — Resin cast Jx 3, Aurisina, Pos. C, 14 m depth. Diameter of inflow-ring 15 cm. Arrows indicate position of entombed animal.

- Fig. 8. First side view.
- Fig. 9. View from above.

Fig. 10. Second side view.

Tafel 4.

Bau von Jaxea nocturna. — Kunstharzausguß Jx 3, Aurisina, Pos. C, 14 m Tiefe. Durchmesser des Eingießpfropfens 15 cm. Die Pfeile weisen auf die Lage des miteingegossenen Tieres.

Fig. 8. Erste Seitenansicht.

Fig. 9. Ansicht von oben.

Fig. 10. Zweite Seitenansicht.





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