Morphology and ecology of the kalyptorhynch *Typhlopolycystis rubra* (Plathelminthes), an inmate of lugworm burrows in the Wadden Sea

U. Noldt¹ & K. Reise²

¹II. Zoologisches Institut und Museum der Universität Göttingen; Berliner Straße 28, D-3400 Göttingen, FRG ²Biologische Anstalt Helgoland, Litoralstation List; D-2282 List/Sylt, FRG

ABSTRACT: *Typhlopolycystis rubra*, a new species of the taxon Polycystididae (Plathelminthes, Kalyptorhynchia), is described. The red species is characterized by copulatory hard structures which consist of a proximal girdle and 2 similar sized stylets. *T. rubra* occurs in intertidal sand near the island of Sylt in the North Sea. Here, it is virtually confined to the lowest parts of lugworm (*Arenicola marina*) burrows, where it aggregates in the coarse grained sand around the feeding pocket areas. This is an extremely narrow spatial niche within the sulfide layer of sediment. Population size over a period of 7 years is the most constant one among all species of Plathelminthes living on the tidal flat. The ability of *T. rubra* to endure unsuitable conditions inside a cyst may contribute to this remarkably low population variability.

INTRODUCTION

Current conjectures on the number of existing species go up to 30 or 40 million (see Lewin, 1983; Wilson, 1985; May, 1986). Of these, approximately 1.7 million have been described, and knowledge on behaviour or ecological requirements is probably limited to < 1 % of the real number. Particularly with regard to ecology, it seems doubtful whether generalizations based on such a small fraction can achieve high reliability.

For example, the benthos in the Wadden Sea has been characterized as poor in species, dominated by a few strong populations which are well adapted to this harsh environment (cf. Beukema, 1976; Wolff, 1983). However, this conclusion is mainly based on the tidal flat fauna that can be retained by a 1-mm sieve. Equally detailed studies on meiofauna or on benthic diatoms would presumably arrive at a completely different statement. With every new species, new phenomena of general interest may be discovered.

Here we report on a new species of free-living Plathelminthes ("Turbellaria") which is predictably found in the lowest parts of lugworm (*Arenicola marina*) burrows. Of all Plathelminthes on a sandy tidal flat near the island of Sylt, it has shown the most constant population size over the last seven years; yet its spatial niche is one of the smallest. This robin worm is capable of encystment, which is a novel phenomenon of free-living Plathelminthes living in the sulfide system of tidal flats.

Typhlopolycystis rubra was formerly referred to as *Typhlopolycystis* sp. in Reise (1983a, 1983b; 1984; 1985) and Scherer (1985).

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MATERIAL AND METHODS

The type locality is a sandy lugworm flat in the lower tidal zone of the eastern part of Königshafen, island of Sylt (see Reise, 1984; Figs 2, 3). In June 1984 thirty specimens were collected. 20 serial sections were prepared and stained with Delafield's iron hematoxylin. 5 specimens were preserved as whole mounts (embedded in polyvinyl-lactophenol). The holotype is one sagittal series (P1991). Paratypes (P1992–P2000) include 6 other serial sections and 3 whole mounts. The material is deposited at the Zoological Museum of the University of Göttingen.

Burrows of the lugworm were dug up with a spade. Samples of 2 cm^3 each were obtained from the region of the feeding pocket and the horizontal gallery. These small samples were simply diluted with filtered seawater, partitioned over a set of about 12 petri dishes, and specimens were picked up with a pipette under the dissecting microscope. No sieves were used and only live material was investigated.

MORPHOLOGY

General morphology

The smallest free-living individual encountered attained a length of 0.45 mm, and the largest one up to 1.6 mm. On average, length is 1.0 mm and maximum width is 0.15 mm. When crawling, the body is elongated; while swimming, individuals contract. All movements are very slow.

Most of the 516 individuals found at the type locality are bright red, a few pale or brownish. About one third were found curled up within spherical cysts of 0.4 to 0.5 mm in diameter. Cysts consist of a transparent mucus layer with adhering detritus, $CaCO_3$ -needles from dissolved mussel shells, and sand grains. Repeated probing with a needle caused the animals to break through the mucus envelope, to crawl or swim away leaving the empty cyst behind. Bright light and increased temperature under the dissecting microscope also induced animals to leave their cysts.

Large adhesive glands (cgl) are located in the posterior part of the body (Fig. 1). Other adhesive organs are lacking. A few tactile cilia are present at the anterior body tip. The epidermis and the cilia form layers of 6 μ m width. The basal lamina is 3.0 μ m (medial body) to 4.5 μ m (body tips) thick. The epidermal nuclei are scattered, the minute pigment granules are concentrated in the periphery of the epidermis. The subepidermal musculature consists of a fine internal longitudinal and an external circular muscle layer. One pair of pigmented eyes is located in the anterior region of the brain. Two basophilic frontal glands (fgl) with fine secretion granules lie caudally to the brain.

Proboscis

The proboscis (Figs 2, 5) is 250–280 μ m long (\triangleq about 1/5 of the body length). In live specimens 25–35 μ m are recorded for the apex, 100–110 μ m for the proboscis cone, and 125–150 μ m for the proboscis bulb. The proboscis pouch is characterized by a high basophilic epithelium (e₃). The nuclei are concentrated in the medial part. A sphincter surrounds the orifice of the proboscis pouch. In the posterior part of the pouch a fine circular muscle layer (cm₃) is located beneath the layer of longitudinal muscles (lm_2). Caudally to the sphincter 4 bundles of dilatator muscles (di), composed of several fibers, insert. The retractors of the pouch (rpp) arise at about the level of the apex.

At the juncture (j), the pouch epithelium is demarcated by the high acidophilic cone epithelium (e_1). The apex epithelium (e_2) is weakly stained. In both the apex and the proboscis cone, there is an underlying circular musculature (cm_2). The proboscis bulb is externally lined with 50 strong, regularly distributed longitudinal muscles (lm_1 ; rectangular in cross-section). Internally, beneath the basal lamina of the bulb, a strong circular musculature (cm_1) makes up about 1/10 of the proboscis diameter. In cross-section, numerous cone retractor muscles (rc) are concentrated in the central part of the proboscis (Figs 2, 17, 18). Six bundles of fixator muscles (fi) insert at the medial proboscis bulb and run rostrad to the integument. Between those insertions the 6 longitudinal packages of mantle cells (mc) are located. Each package contains up to 12 nuclei. Caudally to the fixator muscles 3 pairs of proboscis retractors (rpr) arise, each one composed of 3–5 strong fibers. Acidophilic proboscis glands (pgl) are situated caudally to the brain and empty into the proboscis node. At the node, 4 pairs of protractors (pro) insert. They run anteriad and insert at the basal lamina of the body at the level of the proboscis tip.

Pharynx rosulatus

The pharynx is located in the medial body third. The diameter is $170-200 \mu m$ (live observation). The mouth opening is displaced frontally, the bulb itself is inclined from the dorsoventral axis. Three types of pharyngeal glands exist (Fig. 3). About 20 acidophilic glands (gl₁) with medium size secretion granules are located peripherally and empty close to the pharynx lip. With openings dorsal to the former, 8 basophilic glands (gl₂) with larger secretion are mainly located in the proximal bulb. Fine basophilic secretion of an unknown number of the third gland type (gl₃) is discharged into the medial pharynx lumen. The pharynx epithelium is generally thin (e₃), but papillate (e₂), when the bulb is contracted.

The circular musculature is composed of 35-40 external muscles (cme), about 20 muscles on the ventral part of the pharynx lip, 20-25 internal muscles (cmi), and about 10 muscles beneath the 4 pairs of cuticular knobs (ck). There is no concentration of circular fibres at the distal part of the pharynx lip. A thick longitudinal muscle layer (lm₂) is found; a thin hardened epithelial layer, however, is lacking. 38 internal longitudinal fibres (lmi) insert distally at the lip and proximally beneath the cuticular knobs. The external longitudinal fibres (lme) are fine. In sagittal sections, the number of radial fibres (rm) is about 25; in horizontal sections 40 fibres are found (Figs 3, 20).

From the junction between the pharynx lip and the pharynx pouch ("Kontaktrand"), an indeterminable number of protractor muscles (php) runs ventrad to the integument. Ventrally, one pair of rostral and caudal lacunae (la) join the pharynx pouch (Figs 3, 19). Each lacuna contains 3 large nuclei; however, a glandular matrix is lacking. The pharynx pouch is lined with a thin epithelium (e_1) devoid of nuclei and covered by a fine longitudinal muscle layer (lm_1). The mouth opening is surrounded by a sphincter. The short esophagus is demarcated from the intestine by medially located, eosinophilic gland cells (mg), which may project into the proximal pharynx lumen.







Genital organs

The long unpaired testis lies caudally to the pharynx bulb. A short, muscle-free deferent duct (vd in Fig. 10) leads to the seminal vesicle which is 150-200 µm long and 40-50 µm in diameter. The vesicle is septated interiorly and covered by thin longitudinal muscle fibres. It opens subterminally into the copulatory bulb (Figs 6, 10). Lined with spirally arranged musculature, the copulatory bulb is 60-70 µm long and 30-40 µm in diameter. The seminal duct (ds), which lacks musculature, runs acentrically on a slightly winding course through the ovoid bulb.

Three prostatic fascicles (ksf) with differently stained, but similar size secretion, lie in the copulatory bulb (Figs 10, 11, 21). The nucleated parts of the glands are located externally of the bulb. Some nucleated glands with intensively stained acidophilic secretion enter the terminal end of the accessory gland organ (av). This bulb is up to 60 µm long and lined with spirally arranged musculature. The fine muscle-free duct (w in

Figs 1–3. Typhlopolycystis rubra. 1. Organization (combined). 2. Anterior body (reconstruction from				
horizontal sections; proboscis contracted, left side cut off). 3. Rosulate pharynx (reconstruction from				
sagittal sections)				
Abbreviations in the figures				
	a	apex of proboscis	lme	external longitudinal muscles
	ac	genital atrium	lmi	internal longitudinal muscles
	ast	accessory stylet	mc	mantle cells
	av	accessory prostatic vesicle	mg	Mignot's glands
	b	copulatory bursa	mgd	male genital duct
	bl	basal lamina	mo	mouth opening
	bu	proboscis bulb	pe	pigmented eyes
	cer	brain	pgl	proboscis gland
	cgl	caudal adhesive glands	ph	rosulate pharynx
	ci	cilia	$_{\rm php}$	protractors of pharynx
	ck	cuticular knobs	pht	pharynx pouch
	cm_n	circular muscles	pro	protractors of proboscis
	cme	external circular muscles	prp	proboscis pouch
	cmi	internal circular muscles	rc	retractors of proboscis cone
	со	proboscis cone	rm	radial muscles
	cob	copulatory bulb	ro	opening of proboscis pouch
	di	dilatator muscles	грр	retractors of proboscis pouch
	ds	seminal duct	rpr	retractors of proboscis
	en	epithelium	TS	seminal receptacle
	ep	epidermis	s	sphincter
	es	esophagus	sm	spiral muscles
	fgd	female genital duct	st	stylet
	fgl	frontal glands	stg	stylet girdle
	fi	fixator muscles	t	testis
	g	germarium, germocyte	ut	uterus
	gln	glands	vc	vacuol
	go	gonopore	vd	deferent duct
	h	copulatory hard structures	vi	vitellaria, vitellocyte
	in	intestinum	vs	seminal vesicle
	j	juncture of proboscis	w	muscle-free duct
	ksf	prostatic fascicle	х	diverticulum
	la	lacuna of pharynx pouch	Y	germovitelloduct
	lmn	longitudinal muscles	z	uterine papillae



Figs 4–8. *Typhlopolycystis rubra.* 4. Specimen with egg-capsule. 5. Proboscis. 6. Copulatory organ. 7 and 8. Seminal receptacle. Scales: Fig. 6: 50 µm; Fig. 8: 20 µm

Figs 10, 11) runs acentrically in the copulatory bulb and enters the accessory stylet proximally.

The copulatory hard structures (Figs 9, 23, 24) consist of a proximal closed girdle (stg), a sheath-like prostatic stylet (st), and a tubiform, pointed accessory stylet (ast). Both



Figs 9–15. Typhlopolycystis rubra. 9. Copulatory hard structures (left: sections a-e, from different serial sections). 10. Copulatory bulb (combined). 11–13. Copulatory bulb and male genital duct with copulatory hard structures (cross-sections). 14. Seminal receptacle (sagittal section). 15. Uterus (cross-section). Scales: Fig. 9, Figs 11–14: 30 μm; Fig. 10: 50 μm; Fig. 15: 20 μm

tips are bent distally. The overall length of the copulatory hard structures is $105-120 \mu m$. The diameter of the girdle is $38-44 \mu m$, the proximal rim is thicker than the distal parts. In cross-section the rim is irregularly shaped (section a in Fig. 9). The girdle is split on one side. The resulting cleft becomes wider distally. Proximally, one part of the girdle is separated by a thin wall (section b). In cross-section, it is angular and represents the upper part of the $80-90 \mu m$ long accessory stylet. Within the accessory stylet there is only the fine outlet of the accessory organ (Figs 10, 12). The diameters of the accessory stylet are 7.5 μm (proximally) and 2–3 μm (distally at the level of section e). The wall opposite the cleft splits further distad (approximately at the level of section c) to form the sheath-like stylet. Only a small, thin non-hardened septum covers the distal parts of the prostatic fascicles and the fine seminal duct (Figs 12, 13). In sections, a partly hardened ridge is observed on the inside of the stylet sheath (section d in Fig. 9; Fig. 13). The walls of the distal stylet form a sheath, in which the accessory stylet may be embedded (Fig. 9, section e). Thus, the stylet serves as a guide for the accessory stylet.

At the proximal rim of the hard structure the musculature of the copulatory bulb and of the male genital duct inserts. The male canal is characterized by a strong circular muscle layer, a thin epithelium lacking nuclei, and an external longitudinal musculature (Figs 11–13). At the transition of the male genital canal and the common atrium a rostral diverticulum (x in Fig. 16) with unknown function is found. Ventrally to the diverticulum the uterus opens into the atrium. The uterus has a longitudinal muscle tunic and is distally surrounded by a strong sphincter. In cross-sections, the uterus stalk is ovoid; the proximal uterus is flattened. At the level of the sphincter, acidophilic uterine glands (gl₁) open; the basophilic glands (gl₂) empty proximad from the sphincter. The thin nucleated uterus epithelium is characterized by 2 large dorsal papillae (z; Figs 15, 16, 22). The common genital opening is surrounded by a strong sphincter. The egg-capsules found in 2 specimens measured $300 \times 200 \ \mu m$ (Fig. 4). No egg-filament was detected.

The short, distally sphinctered female genital duct has a thin epithelium. Dorsally, the female canal receives a minute germovitelloduct (y in Fig. 16). The short paired

Fig. 16. Typhlopolycystis rubra. Genital organs (reconstruction from sagittal sections). Scale: 50 µm

Figs 17-22. Typhlopolycystis rubra. 17 and 18. Proboscis. 19. Pharynx pouch with lacuna. 20. Pharynx bulb. 21. Copulatory bulb. 22. Uterus. (All cross-sections, except 17, sectioned longitudinally). All scales: 30 μm

vitelloducts open ventrally of the germarium. The proximal part of the germarium is bent anteriad. Further distad the female genital canal communicates with the seminal receptacle (Figs 7, 8, 14). The 70–85 μ m long spindle-like receptacle is characterized by a strong distal sphincter. Proximally, it is covered by thin spiral fibres which derive from the sphincter. The fine tip of the receptacle is located near the intestinal cells. There is no indication for a pore or duct in the terminal part of the seminal receptacle. Ventrocaudally, the atrium receives the large copulatory bursa, which is also closed with a small sphincter. Distally, the bursa consists of a homogenous, basophilic tissue with numerous nuclei and few spaces. Proximally, there are large spaces filled with alien sperm (Fig. 16).

The vitellaria extend from the proboscis to the caudal adhesive glands. Near the pharynx, the vitellocytes of both sides are adjacent to one another. In one cross-section of the body the vitellaria formed a longitudinal cylinder.

Discussion

Copulatory hard structures consisting of a proximal closed girdle, which splits into a prostatic stylet and an accessory stylet, are the specific character of the *Typhlopolycystis* species. Until now, 4 species have been described: *T. coeca, T. mediterranea, T.*

Figs 23 and 24. Typhlopolycystis rubra. Copulatory hard structures. Scales: 20 μm

coomansi and *T. schockaerti* (see Karling, 1956; Brunet, 1965; Schilke, 1970a; Schockaert & Karling, 1975; Karling, 1978).

The new species *T. rubra* is characterized by the longest copulatory hard structures within the taxon *Typhlopolycystis*. Furthermore, both stylets are of almost equal length, whereas in the previously described *Typhlopolycystis* species the accessory stylet is longer than the prostatic stylet. In *T. rubra* both stylet tips are gradually curved, a feature found in *T. mediterranea* as well. In *T. coeca, T. coomansi* and *T. schockaerti* the accessory stylets are straight, tubiform, and taper distally. In *T. coeca* and *T. rubra* the copulatory bulb is lined with spirally arranged muscles and contains 3 prostatic fascicles. However, in *T. coeca* there are only 2 different types of secretion. In both species the prostatic glands enter the copulatory bulb subterminally in different places (see Karling, 1956; Fig. 87).

The probosces of the *Typhlopolycystis* species are large. The relative length of the proboscis compared to the body length is: 1:3 in *T. coeca* and *T. mediterranea*, 1:4 to 1:3 in *T. coomansi*, 1:5 in *T. rubra*, and 1:6 in *T. schockaerti*. The proboscis of *T. rubra* differs from that of *T. coeca*, which was studied by Schockaert (1972/1973). There are 50 external longitudinal muscles lining the bulb in *T. rubra* (30 in *T. coeca*). The circular muscle layer of the proboscis bulb is thicker in *T. coeca*.

With respect to the female genital organs, the new species is characterized by 2 features. (1) There are 2 large epithelial papillae in the uterus, located dorsally and proximally to the uterus stalk. (2) The seminal receptacle is distally surrounded by a large sphincter. With the exception of *T. schockaerti* a spindle-like seminal receptacle has been found in all *Typhlopolycystis*-species. The receptacles are lined with spirally arranged musculature; however, a large sphincter is lacking in *T. coeca, T. mediterranea, T. coomansi* (see Karling, 1956; Fig. 89; Brunet, 1965; Fig. 11.2; Schockaert & Karling, 1975; Fig. 43).

ECOLOGY

Distribution and dynamics

At the type locality, a total of 2780 samples of 2 cm³ were taken from various microsites of the oxic surface layer and the sulfide layer below, and particularly alongside lugworm burrows. There are no records from the surface layer where most other species of free-living Plathelminthes occur. All individuals found at type locality were 8 to 16 cm below the surface, in the sediment immediately surrounding the feeding pocket area or the horizontal gallery of lugworm burrows (*Arenicola marina* L.). The only exceptions are a single individual in the head shaft sediment at 6 to 7 cm depth, and another one in an experimental aggregate of the tellinid clam *Macoma balthica* (L.) at a depth of 3 to 4 cm below the surface (Fig. 25; see Reise, 1983a).

Thus, *T. rubra* is virtually confined to the lowest part of lugworm burrows where it lives in coarse-grained sand. This layer of coarse particles is generated by the lugworm population (cf. Baumfalk, 1979). Surface material slides down the head shafts of burrows. Only small particles are ingested in the feeding pocket and are recycled to the surface, while coarse material accumulates at the base of burrows. The size-frequency distribution of the quartz grains is bimodal. Modes are at 0.3 and 1.2 mm of particle diameter. In addition to sand, there are also mollusc shells (mainly *Hydrobia* and small *Ceras*-

Fig. 25. Distribution (left) and dynamics (right) of *Typhlopolycystis rubra* on a sandy tidal flat with lugworm burrows. Boxes indicate positions of 2 cm³ samples taken from normal sediment (central column), from head and tail shaft, feeding pocket and gallery. Numbers refer to individuals found in 70 samples from June 1980 to June 1986. Layer of coarse sand is indicated. Individuals in 52 cm³ from all positions are given (right) for *T. rubra* and the sum of all free-living Plathelminthes to show interannual variability

toderma), calcium-carbonate needles from dissolved mussel shells, and organic aggregates mostly 50 μ m in diameter. *T. rubra* lives among these particles and distinctly aggregates at the feeding pocket areas.

A total of 97 species of free-living Plathelminthes has been encountered on the lugworm flat where *T. rubra* is abundant. The spatial niche of *T. rubra* is very small compared to these other species. Most of them populate micro-habitats at the surface or occur over a wide depth range within the sediment, particularly alongside lugworm burrows. There are only two other species, *Mariplanella frisia* Ax & Heller, 1970 and *Gyratricella attemsi* (Graff, 1913), which are abundant near the feeding pockets and do not occur anywhere else on this tidal flat.

Notwithstanding an unusually narrow spatial niche, *T. rubra* exhibits the least interannual variability of all free-living Plathelminthes at the site (Fig. 25). Every June from 1980 to 1986, 10 samples of 2 cm³ were taken from each of the 26 micro-sites, including feeding pockets and galleries of lugworm burrows. Based on this set of data, the average density in 10 cm³ of pocket sand was 31 (range 19 to 40) and in galleries 2 (range 1 to 6). The coefficient of temporal variation was 0.24 for *T. rubra* while the other species (n = 56 with \geq 7 individuals) range from 0.37 to 2.65, with an average of 1.25. A significantly positive Spearman rank correlation of abundance over the 7 years exists only with *Gyratricella attemsi*, a species which is also confined to the feeding pockets.

Seasonally, *T. rubra* was abundant in June and October (26 individuals in 10 cm^3 of pocket sand) but rare in February (1 in 10 cm^3). This may indicate an overwintering in the

Fig. 26. Size-frequency distribution from June `and October 1980. Size classes are given in 0.1 mm length intervals; frequency refers to individuals in 40 cm³ of pocket and gallery sand of lugworm burrows. Most young of June have attained maturity in October

egg stage within cocoons. However, size-frequency distributions of young and mature individuals in June and October (Fig. 26) suggest a persistent population throughout the year, with mature individuals surviving the winter.

DISCUSSION

The known distribution of *Typhlopolycystis rubra* is rather limited. In spite of intensive research on the distribution of Kalyptorhynchia (Hoxhold, 1974; Noldt, 1985, 1986; Schilke, 1970a, 1970b), and free-living plathelminth species in general (Armonies, 1987; Ax, 1977; Dittmann & Reise, 1985; Hellwig, 1987; Wehrenberg & Reise, 1985; Xylander & Reise, 1984), in various littoral zones and sediments near the island of Sylt, it has been found in only two sandy tidal flats near lugworm burrows (Reise, 1984; Scherer, 1985).

This insular distribution is in contrast to the wide habitat spectra of macrofaunal species on tidal flats in the Wadden Sea (see Dankers & Beukema, 1981). Another striking feature is the low between-year variability of the population density in *T. rubra*. In fact, it

has the lowest rate of all free-living plathelminth species on the sand flat investigated. Although the feeding pockets may be almost unaffected by the short-term physical variability of the tidal environment, it is nevertheless subject to unpredictable behavior of the lugworm individuals. They may interrupt feeding or pumping, change the position of their feeding pockets, or even move out of the sediment (Beukema & de Vlas, 1979; Krüger, 1971).

This irregularly deprives *T. rubra* of essential living conditions. The feeding pocket area is supplied by the lugworm with sediment from the surface, with oxic water pumped into the burrow, with mucus and excreted metabolites. This combination may cause a gardening effect for the microbiota (Hylleberg, 1975) and attracts meiofauna (Reise & Ax, 1979; Reise, 1983b, 1984; Scherer, 1985). In the coarse grained sediment surrounding the feeding pocket, *T. rubra* will be safe from accidental ingestion, since lugworms take up only small particles (see Baumfalk, 1979). Encystment offers a possibility to endure periods of anoxia with high sulfide concentrations or when prey is absent. Thus, the ability of encystment may explain in part the observed constancy of population size.

The activity of lugworms generally ceases at low temperatures (Krüger, 1964), and then feeding pockets lose their attraction for meiofauna (Scherer, 1985). We assume that during winter, cysts of *T. rubra* are scattered throughout the coarse-grained, subsurface layer of the sediment, irrespective of the position of lugworm burrows. This might cause the low numbers of *T. rubra* in samples taken in February.

Encystment is a rare phenomenon in marine species of free-living Plathelminthes (Meixner, 1938). Recently, Armonies (1986) discovered that 11 species living in supralittoral salt marshes endure unfavorable conditions by encystment. He found that factors like humidity, salinity, temperature, and oxygen determine whether cysts are left or not. Here we report encystment for a species living in the sulfide layer of marine sediments. Cysts are easily detected because the red individuals are visible through the transparent envelope. Cysts of uncolored species, if present, probably went unnoticed.

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