Typhlorhynchus nanus Laidlaw, a kalyptorhynch turbellarian without proboscis (Platyhelminthes)

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Typhlorhynchus nanus, ectoparasite on the polychaet Nephthys scolopendroides, is shown to be a kalyptorhynch turbellarian without proboscis. Sister group of the monotypic genus Typhlorhynchus is Proschizorhynchus, both within fam. Schizorhynchidae. The proboscis of T. nanus has been lost concomitant with the transformation of the pharynx to a sucker. — The systematic rank of sister groups is briefly discussed.

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1. Introduction

Typhlorhynchus nanus Laidlaw is an ectoparasite on the polychaet Nephtys scolopendroides Chiaje. It was described by Laidlaw (1902, in part on studies by Goodrich) and later thoroughly studied by Graff (1903) and Meixner (1924: 95, footnote; 1926; 1928: 251-253). Graff (1903: 8) placed T. nanus (as Byrsophlebs nana) in the family Mesostomatidae, later (as T. nanus) in the family Byrsophlebidae (1905: 96—97). Meixner found anatomical conformities between T. nanus and the Schizorhynchia, but interpreted them in conformity with the relations between "Proxenetes" and "Trigonostomidae" and placed T. nanus in a separate family Typhlorhynchidae beside Proxenetidae and Trigonostomidae in the suborder Typhloplanoida (1938: 9), a measure already taken by Bresslau (1933, "sectio" Typhloplanoida). Curiously enough Laidlaw placed T. nanus in "Proboscidae", roughly synonymic with Kalyptorhynchia Graff, 1905, however, due to the erroneous homologization of the slender rostrum with the true proboscis of the Kalyptorhynchia.

A reconsideration of the affinity between T. nanus and the kalyptorhynch family Schizorhynchidae is based on a comparative study of T. nanus and the type species of the genus Proschizorhynchus, P. gullmarensis Karling.

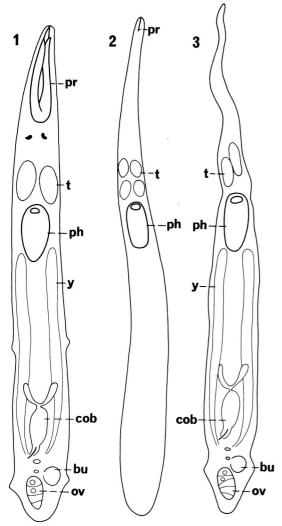
2. Material

Typhlorhynchus nanus: two slides, one with a cross-sectioned specimen, labeled "Querschn. 5 μ Hämat.-Eosin", the other with two specimens sectioned sagittally, no label. The material is still in good condition. It belongs to the University of Graz, Austria, and is evidently the basic material of Graff and Meixner (see Meixner 1924: 95, footnote).

Proschizorhynchus gullmarensis: 11 slides in the Swedish Museum of Natural History, Section of Invertebrate Zoology (SMNHI, see Karling 1950); six whole mounts, one of which designated lectotype (SMNHI No. 2802), five specimens serially sectioned.

3. Comparative anatomy of Typhlorhynchus nanus and Proschizorhynchus gullmarensis

T. nanus and P. gullmarensis have the same slender, highly changeable body shape and a similar triangular or spoon-shaped adhesive caudal end (Figs. 1, 3), features characterizing the life form of interstitial turbellarians. The caudal adhesive girdle in T. nanus consists of 10—12 (about six according to Meixner 1926: 587), in P. gullmarensis of eight adhesive spots. The medial adhesive girdle of the latter is functionally replaced in T. nanus by the pharynx (see below). T. nanus is 1—2 mm long (Graff 1903: 2), in extended condition up to 7 mm (Laidlaw 1902:



Figs. 1—3. Semidiagrammatic views of stretched specimens. — 1. Proschizorhynchus gullmarensis (after Karling 1950, fig. 9 I). 2. Neoschizorhynchus parvorostro (after Ax & Heller 1970, fig. 17A). — 3. Typhlorhynchus nanus (after Graff 1903, t. 3, fig. 1).

mp mouth piece of bursa bu bursa ca common atrium ms muscle septum cgp common genital pore ov ovary co common oviduct pore cob copulatory bulb ph pharynx cu cuticular organ proboscis genito-intestinal duct prostatic secretion glb gland bulb of pharynx seminal receptacle ST hair in the tip of the st stylet stylet str stylet retractors hb hair bundle testis tinsemination canal vagina intestine yolk glands m muscles

mo mouth

637). P. gullmarensis is about 3 mm long (Karling 1950: 16).

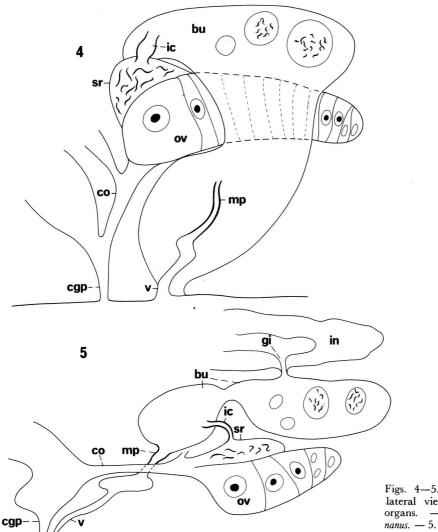
The topography of the organ systems is the same in both species, pharynx posteriorly in the anterior body half, paired testes in front of the pharynx, paired yolk glands laterally behind the pharynx, unpaired ovary in the caudal body end, two ventrocaudal genital pores — the common pore slightly in front of the vaginal pore — the male copulatory organ with paired seminal vesicles in front of the pores and further a bursa organ behind the pores.

In the body wall the epithelial cells with their irregularly lobed nuclei lack distinct limitation. The anchor cells of the adhesive organs are rounded spots without cilia and with associated bundles of gland cells in the parenchyma (see Karling 1950, fig. 9K).

The anterior body part in *T. nanus* is prolonged to a kind of highly movable rostrum (see introduction). A proboscis of kalyptorhynch type is lacking, but in the tip of the rostrum there is a pore in the body wall and behind the pore vacuolated tissue, which in a sectioned specimen contains some short threads stained as muscle fibers (Fig. 6). It cannot be excluded that juveniles have a true proboscis which will be resorbed concomitant with the separation of the rostrum from the posterior part of the body caused by the adhesion of the pharynx to the substratum.

The posterior part of the pharynx in both species is differentiated to a sac filled with glands (Fig. 7, cf. Graff 1903, t. 3, figs. 15, 16, 23; Karling 1950, fig. 10A, D). The sac is much larger in T. nanus than in P. gullmarensis. The mouth cavity and the grasping rim of the pharynx are weakly differentiated, especially in T. nanus (Fig. 8). The epithelium of the pharynx lumen lacks nuclei. A strong system of muscle fibers connects the pharynx with the body wall in T. nanus. Graff interprets these muscles in part as dilators, in part as protractors and retractors (1903: 4). The corresponding muscle system is weaker in P. gullmarensis. In T. nanus a kind of transversal diaphragm is formed by external pharynx muscles close to the frontal side of the pharynx (Fig. 8; cf. Graff 1903, fig. 23). Contraction of these muscles cause an annular constriction almost cutting off the rostrum from the rest of the body (preserved specimens). That diaphragm is not homologous with the transversal muscle septum in many Schizorhynchia, which appears to be functionally coordinated with the muscle system of the proboscis (Karling 1961: 269, 276).

There is a striking conformity in the structure of the male copulatory organ in the two species



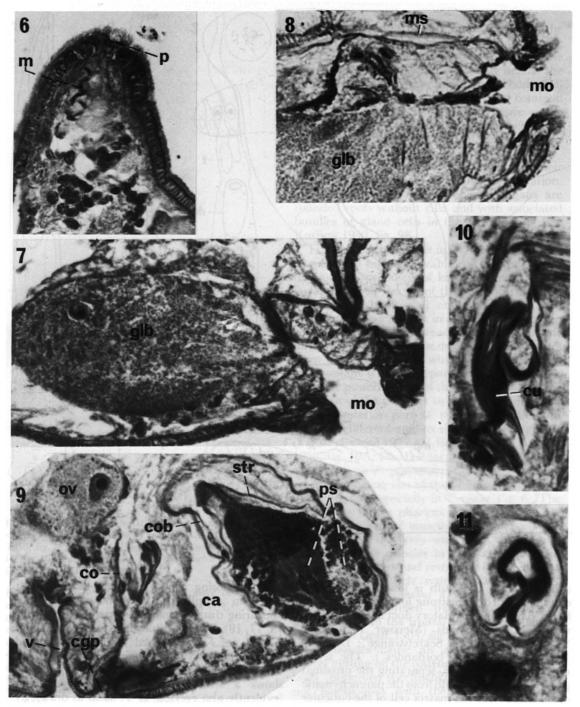
Figs. 4—5. Semidiagrammatic lateral views of female atrial organs. — 4. Typhlorhynchus nanus. — 5. Proschizorhynchus gullmarensis.

(Figs. 9, 12). The bulb is longish ellipsoidic, externally lined with strong longitudinal muscle fibers. The axial ejaculatory duct is embedded in weakly stained glands (Meixner 1926: 581: "schwach cyanophile Sekretstränge"; L'Hardy 1965: 138: "cellules bordandes"). The stylet retractors form a cone, separating the proximal prostatic part of the bulb from the parenchymatic distal tissue with the matrix cell of the cuticular apparatus, regarded by Meixner as "Bildungszelle des Muskelconus" in T. nanus (1926: 581; Karling 1950: 22).

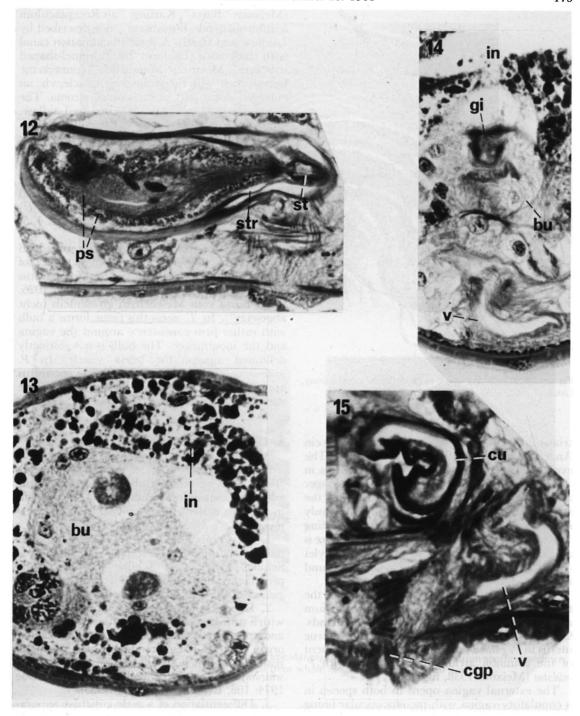
The male cuticular organ in both species is a slightly curved papilla with internal eversible

cirrus enclosing a curved needle-like stylet. It opens in a split on the concave side, thus appearing distally channel-shaped (Figs. 10, 11, 15, 17, 18). The eversible cirrus is longitudinally ribbed, in *T. nanus* lined with fine hairs and distally provided with a pair of cuticular lobes. The everted organ of *P. gullmarensis* (Fig. 19) shows a striking similarity with the organ (evidently also everted) of *T. nanus* as drawn by Goodrich (Fig. 16), but the pair of lobes is lacking.

The conformity of the cuticular organs in the two species is furthermore pronounced by new observations on whole mounts of *P. gullmarensis*. The basal part of the stylet is provided with a



Figs. 6—11. Typhlorhynchus nanus. — 6. frontal body tip, longitudinal section; 7. pharynx, sagittal section; 8. distal part of pharynx, sagittal section; 9. vagina, common atrium and male copulatory organ, sagittal section; 10. cuticular organ, sagittal section; 11. cuticular organ, cross section. Scale line = $50~\mu m$.



Figs. 12—15. Proschizorhynchus gullmarensis. — 12. male copulatory organ, sagittal section; 13. resorptive part of bursa, cross section; 14. bursa apparatus, cross section; 15. male cuticular organ, common genital pore and vagina, cross section. Scale line = $50~\mu m$ for figs 12-14, $30~\mu m$ for fig. 15.



Fig. 16. Typhlorhynchus nanus, male cuticular organ, from Laidlaw 1902, t. 35, fig. 66.

triangular plate giving it a curved shape ("wie ein Angelhaken", Graff 1913: 176 on *T. nanus*). The eversible cirrus is provided with fine hairs as in *T. nanus*, proximally very small, distally longer and agglomerated to a bundle beside the tip of the stylet (Figs. 17, 18; this bundle was previously interpreted as a papilla or a membrane, Karling 1950: 22). Previously not recorded furthermore is a fine thread emerging from the tip of the stylet (Figs. 18, 19). No corresponding structure is found in *T. nanus*.

There are no principal differences between the two species in the structure of the common atrium and the common oviduct with their glands. Contrary to my previous record there is no true uterus in *P. gullmarensis*, only a slight enlargement of the common atrium in conformity with *P. oculatus* (Meixner 1938, fig. 66).

The external vagina opens in both species in a copulatory vagina with pseudocuticular lining (Graff: "Bursa seminalis", Meixner: "Vagina", Karling: "Vaginalbursa"). A mouthpiece (Graff: "Chitinanhang der Bursa", Meixner: "Vaginalanhang der Bursa", Karling: "Mundstück") brings the alien sperm into the large bursa vesicle

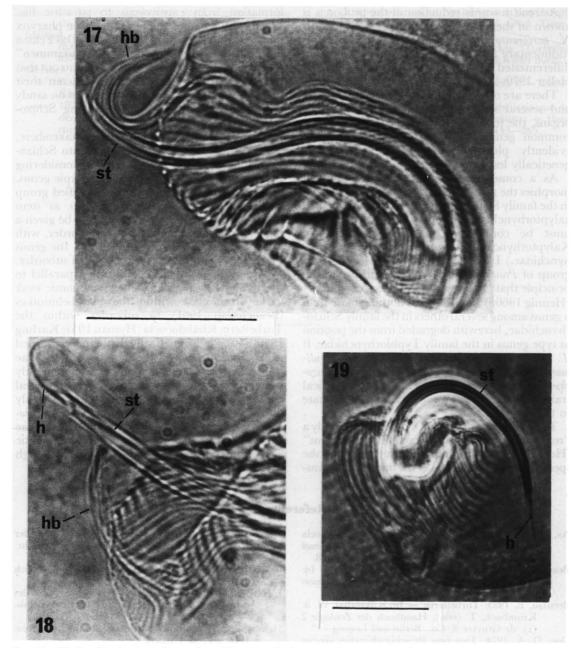
(Meixner: "Bursa", Karling: "als Receptaculum seminis dienende Bursablase", not described by Laidlaw and Graff). A short insemination canal with thick walls (Laidlaw: "short funnel-shaped structure", Meixner: "Mundstück") connects the bursa vesicle with the seminal receptacle, viz. an enlarged distal part of the ovarial stroma. The receptacle is accordingly described by Laidlaw, Graff and Meixner and exists with similar structure in P. gullmarensis, though not previously described. Excess alien sperm is resorbed in the posterior part of the bursa vesicle, this functioning as resorptive vesicle. Meixner has observed this phenomenon in T. nanus and I have now recorded it also in P. gullmarensis, where an occasional (?) genito-intestinal pore can be formed (Figs. 4, 5,

The bursa organs and the ovary are embedded in a parenchymatous tissue (mesenchyme) of which the different parts of the bursa apparatus appear as specialized derivatives (Meixner 1926: 589: "Bursa vom Mesenchym grossenteils nicht abgesetzt"). In T. nanus this tissue forms a bulb with rather firm consistence around the vagina and the mouthpiece. The bulb is not distinctly delimited against the bursa vesicle. In P. gullmarensis the distal parts of the bursa apparatus appear more distinctly delimited against the strongly vacuolated mesenchyme.

4. Discussion

Schilke's classification of the Schizorhynchia (1970) will be followed here. I interpret the following anatomical trends as synapomorphous in the two genera *Typhlorhynchus* and *Proschizorhynchus*.

- 1. Differentiation of a gland sac in the posterior part of the pharynx, described in *P. triductibus* Schilke, *P. vaginatus* Schilke (here especially prominent) and *P. nahantensis* Doe besides *P. gullmarensis* (Schilke 1970, Doe 1974).
- 2. Differentiation of a male copulatory bulb with a strong mantle of longitudinal muscle fibers and an internal cone of retractors of the cuticular organ (stylet). These trends are most distinctly realized in the subgenus *Proschizorhynchus Proschizorhynchus* Schilke (Schilke 1970: 184; Doe 1974: 108; Evdonin 1970: 324—325).
- 3. Differentiation of a male cuticular apparatus like that of *T. nanus* and *P. gullmarensis*, realized in the subgenus *P. Proschizorhynchus* (see point 2). There are only minor differences between *P. gullmarensis* and *P. triductibus* in regard to the structure of this organ. In the latter the



Figs. 17—19. Proschizorhynchus gullmarensis. — 17. male cuticular organ; 18. distal part of the same from another specimen; 19. everted male cuticular organ. — All photographs from whole mounts. Scale lines = $20 \mu m$.

stylet is smaller and the distal bundle of hairs horseshoe-shaped (Schilke 1970, fig. 21).

4. Differentiation of a bursa apparatus like that of T. nanus and P. gullmarensis, the main traits of which are a copulatory bursa with external vagina behind the common genital pore, a bursa

vesicle connected with the copulatory bursa through a mouthpiece and with the distal part of the ovary (seminal receptacle) through an insemination canal. That construction is realized with small variations in the subgenus *P. Proschizorhynchus*.

A trend towards reduction of the proboscis is known in the genus *Neoschizorhynchus* Schilke. In *N. parvorostro* Ax & Heller the proboscis is rudimentary and a posterior gland sac is weakly differentiated in the pharynx (Fig. 2, cf. Ax & Heller 1970: 36—38).

There are other conformities between *T. nanus* and several schizorhynchids, e.g. the adhesive organs, the topography of pharynx, gonads and common genital pore, but these features are evidently plesiomorphic or at least phylogenetically less important.

As a consequence of the recorded synapomorphies the genus Typhlorhynchus must be placed in the family Schizorhynchidae as the first known kalyptorhynchian without proboscis. (This fact must be considered in future diagnoses of Kalyptorhynchia, Schizorhynchia and Schizorhynchidae.) I interpret Typhlorhynchus as a sister group of *Proschizorhynchus* and, according to the principle that "sister groups must be coordinate" (Hennig 1966: 155—156), it is nothing more than a genus among several others in the family Schizorhynchidae, herewith degraded from the position as type genus in the family Typhlorhynchidae. If T. nanus reveals itself as a sister taxon of P. gullmarensis it must be placed in the genus Proschizorhynchus, but, chiefly considering the anatomical traits referred to in Neoschizorhynchus, I hesitate to take that measure.

The aberrant anatomy of *T. nanus* is evidently a "result of accelerated character development" (Hennig 1966) concomitant with the step of the species into a new niche, i.e. the nutritional trans-

formation from carnivorous to parasitic life. Within the scope of that evolution the pharynx has been transformed into a sucker. "Das Fehlen des Spaltrüssels hängt offenbar damit zusammen" (Meixner 1928: 252). Meixner also points out that the carnivorous Schizorhynchia suck out their prey and that the host of *T. nanus* lives on sandy bottom, the habitat of all free-living Schizorhynchia.

I think that the taxonomic measure taken here, i.e. the inclusion of *Typhlorhynchus* into Schizorhynchidae, will be easily accepted considering the low taxonomic level of the monotypic genus. However, suppose a large and diversified group ("T-group") evolves from *T. nanus* as stem species. Such a group would certainly be given a higher rank than genus, perhaps suborder, with the consequence that its sister group, the genus *Proschizorhynchus*, also takes the rank of suborder.

The Temnocephalida constitute a parallel to the hypothetic T-group. Their taxonomic rank varies from class within the Platyhelminthes (Beauchamp 1961) to suborder within the Turbellaria Rhabdocoela (Hyman 1951; Karling 1956: 340). Phylogenetically they can be regarded as a sister group of the family Dalyelliidae (Rhabdocoela, Dalyellioida) which consequently must be broken out from its large natural continuity to a class or a suborder, a highly dubious measure. Similarly breaking out *Proschizorhynchus* from the family Schizorhynchidae (to a suborder coordinate with the hypothetic T-group) would appear to be unrealistic though perhaps theoretically warranted.

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