Functional morphology, origin and phylogenetic implications of the feeding mechanism of *Tylopharynx foetida* (Nematoda: Diplogastrina)

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Summary. The buccal cavity of *Tylopharynx foetida* was examined using Nomarski optics. Video sequences of feeding worms were analysed to understand the function of stomatal structures. Comparison of mouthpart morphology and function throughout the Diplogastrina shows that the stomatal structures in *Tylopharynx* do not differ qualitatively from those of *Mononchoides* or *Neodiplogaster*. This study shows that *Tylopharynx* feeds on fungal hyphae by ripping apart the cell wall with stegostomatal teeth. The teeth are pushed out of the buccal cavity by elongation of the pharynx during each pumping cycle. This observation provides evidence for the theoretical model for pharynx function in *Ascaris* developed by Bennet-Clark (1976). The homologization of structures in *Tylopharynx* and other Diplogastrina provided a basis to reconstruct the transformations that led to the peculiarities in stoma morphology of *Tylopharynx*, such as subdorsal knobs and longitudinal protractor muscles.

Key words: Bennet-Clark model, buccal cavity, dung nematodes, protractor muscles, Tylopharyngidae.

The cow pat inhabiting nematode *Tylopharynx foetida* was first described by Bütschli (1874) as *Aphelenchus foetidus*. Bütschli (1874) interpreted the buccal cavity of *T. foetida* as a stylet and therefore had no doubts that it must belong to either of the stylet-bearing genera *Tylenchus* or *Aphelenchus*. The reason for the grouping in *Aphelenchus* was the lack of a bursa and the presence of prominent genital papillae in the male. Bütschli was nevertheless aware of similarities between *T. foetida* and "*Rhabditis*" or *Diplogaster* regarding the two bulbs of the pharynx and the pattern of male genital papillae. Micoletzky (1922), and Schneider (1939) concurred with Bütschli (1874) and grouped *Tylopharynx* within the Tylenchida. Differences between the buccal cavities of tylenchids and *Tylopharynx* shown by Goodey (1929) led Filipjev (1934) to establish the family Tylopharyngidae.

The combination of a stylet-like buccal cavity with a *Diplogaster*-like pharynx and a diplogasteroid pattern of male genital papillae was the basis for speculations about a descendence of the Tylenchida from Rhabditida (Marcinowski, 1909;

Micoletzky, 1922; Sachs, 1950; Maggenti, 1963; Zuckerman *et al.*, 1971; Andrássy, 1976).

A detailed description of the buccal morphology of *T. foetida* presented by De Ley *et al.* (1993) showed that this species possesses stomatal teeth comparable with those of Diplogastrina, rather than a stylet. As the authors did not observe live specimens, functional aspects of stomatal structures remained hypothetical. In this study the function of the structures was observed using video recordings of live specimens that fed on fungal hyphae in culture dishes. The highly specialized feeding apparatus of *Tylopharynx* has resulted from a transformation of stomatal structures as they are found in other Diplogastrina. On the basis of the cladogram published by Fürst von Lieven & Sudhaus (2000) this transformation can be reconstructed as a series of subsequent steps. Some of these steps are discussed here in more detail, providing additional descriptions of the stoma in *Butlerius filicaudatus*, *Diplogaster schneideri*, *Oigolaimella* sp., *Mononchoides* sp. 1 and *Mononchoides* sp. 2.

Table 1. Abbreviations used in text and figures.

bl	= basal lamina of pharynx	perst	= perradial strut
cheil	= cheilostom	phdilm	= pharynx dilator muscle
cl	= cuticular lining of pharynx lumen	rdg	= subdorsal ridge and stegostom-cylinder
dab	= deep adradial myofilament bundles	rst	= right subventral tooth
df	= dorsal fold	rug	= rugae
dgla	= dorsal gland ampulla	sab	= superficial adradial myofilament bundles
dldent	= dorsolateral denticle	sda	= subdorsal apodeme
dm	= dorsal adductor muscle	sdm	= subdorsal prodtractor muscle
dt	= dorsal tooth	sg	= secretory granules of dorsal gland
g/s	= border of gymno- and stegostom	stcy	= stegostom-cylinder
gym	= gymnostom	steg	= stegostom
ibrc	= interradial brace	svpl	= subventral plate
mf	= myofilaments	va	= ventral apodeme
oarcs	= outline of arcade syncytia	vm	= ventral protractor muscle
pdpl	= postdental plate		

MATERIALS AND METHODS

Species examined. *Butlerius filicaudatus* Adam, 1930: Isolated from compost, Institut für Zoologie, Freie Universität Berlin, Germany.

Diplogaster (*Diplogasteriana*) *schneideri* Paesler, 1939: Isolated from slime flux of a horse chestnut tree in Groß-Ziethen, Brandenburg, Germany.

Oigolaimella sp.: Isolated from frass of cerambycid beetles under bark sampled by M. Balke at Cyclops Mountains, Sentani, Irian Jaya, New Guinea.

Mononchoides sp. 1: Isolated by W. Sudhaus from decaying tissues of *Opuntia* sp., Madeira, Spain.

Mononchoides sp. 2: Isolated from mud taken by S. Wirth on the banks of a pond at the bottom of a gravel pit, Grunewald, Berlin, Germany.

Tylopharynx foetida (Bütschli, 1874): Isolated from cow pats sampled in Berlin-Dahlem, Germany.

Techniques. The morphology of the buccal cavity was examined in specimens that were placed on a microscope slide provided with a 0.5 mm thick layer of agar (5%). After a coverslip was applied the specimens were not able to move around, enabling them to be examined with a Zeiss Axioplan. For preparing drawings specimens were immobilized either by heat or by adding 1 μl sodium azide (1M). Sodium azide caused spontaneous contractions of myofilaments that were helpful to understand functional aspects of the buccal morphology. Drawings were made using a camera lucida.

For culturing *T. foetida*, a piece of dung was placed on a Petri dish provided with a 0.5 cm thick layer of water agar (1%). The microflora and fungal hyphae began to grow on the agar and the cow-dung inhabiting nematodes egressed from the piece of manure.

To observe the feeding behaviour of live nematodes, a small drop of water was applied on the agar in the culture dish. A coverslip was added. The agar was cut along the edges of the coverslip and the block of agar and coverslip were transferred to a microscope slide. This procedure made it possible to observe live specimens feeding on the microflora on the agar under the microscope at high magnification. The feeding movements were recorded with a video camera mounted on the microscope and the images subsequently studied in slow motion.

RESULTS

Morphology of the buccal cavity in *Tylopharynx foetida*

In the following description the revised nomenclature of De Ley *et al.* (1995) is used for stomatal structures, and abbreviations used in the text and Figures are listed in Table 1.

The stoma consists of a cheilostom, a gymnostom and a stegostom. The cheilostom represents the inner cuticle of the lips. The cuticular lining of the cheilostom is separated from the rest of the buccal cuticle by a wedge-shaped interruption on the epidermal side. The cell membrane of the anterior arcade syncytium projects into this interruption and reaches the buccal lumen (Van de Velde *et al.*, 1994; De Ley *et al.*, 1995). The cuticle of the gymnostom is surrounded by arcade
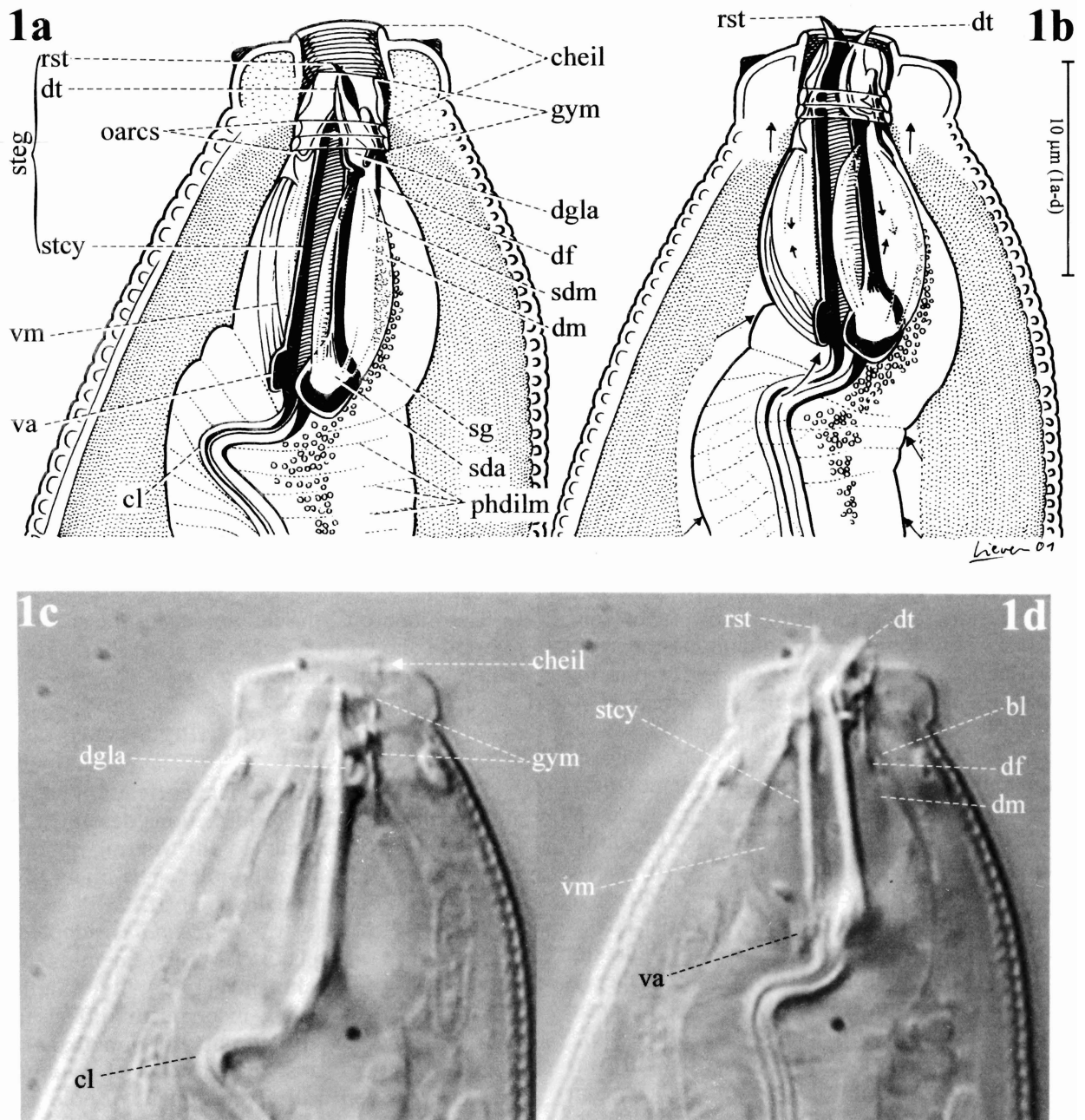
Fig. 1. *Tylopharynx foetida*, anterior end of female. The drawings in a and b combine results of microscopical observation and analysis of the video sequences shown in c and d. The video sequences show an the nematode protruding its mouthparts under the influence of NaN_3. a & c, mouthparts at rest; b & d, protrusion of gymnostom and adducted teeth. See Table 1 for explanation of the abbreviations.

syncytia. The cuticular lining of the stegostom is surrounded by pharyngeal muscle cell processes.

Cuticular structures. In *T. foetida* the cheilostom (cheil; Fig. 1a, c) forms a short tube. The apical half of the tube protrudes from the anterior end of the nematode. As the cheilostom lacks refractive cuticularizations, the posterior half is not visible. The border between the cuticular lining of the cheilostom and gymnostom, the anterior "attachment ring" mentioned by De Ley *et al.* (1993) was therefore not discernible in the light microscope. The gymnostom (gym; Fig. 1a, c) forms a tube which lies posteriorly to the cheilostom and has a shorter diameter than the latter. The walls of the gymnostom diverge posteriorly. Three thin lines encircle the base of the gymnostom. These lines possibly indicate the out-

line of the two rings of arcade syncytia (oarcs; Fig. 1a). The gymnostom is connected with the stegostom by a flexible cuticle that is folded caudally. In the dorsal sector the connecting cuticle forms a noticeable caudally orientated extension that can be seen in optical section (df; Fig. 1a, d; "tendon like structure" of Fürst von Lieven & Sudhaus, 2000). This extension most likely represents the "dorsal fold" mentioned by De Ley *et al.* (1993). Comparison with *Mononchoides* (df; Fig. 2b, 3b) and observations on the motility of the stegostom suggest that this extension is an extremely deep fold in the connecting cuticle between the gymno- and stegostom. The stegostom (steg; Fig. 1b) contains a narrow dorsal tooth (dt; Fig. 1b, d) and a narrow tooth in the right subventral sector (rst; Fig. 1b, d). The base of the dorsal tooth is hollow. The lumen of the hollow base represents a proximal extension of the duct of the dorsal gland that penetrates the dorsal tooth and is called the dorsal gland ampulla (dgla; Fig. 1a, c). Dorsal and right subventral teeth cross each other at rest (Fig 1a, c). The narrow tube (stcy; Fig. 1a, d) between the attachment of the teeth and two ball-shaped apodemes (knobs) within the pharynx is homologous with the stegostom-cylinder of *Mononchoides* (Fürst von Lieven & Sudhaus, 2000). The knobs lie in the subdorsal perradii and are called subdorsal apodemes (sda; Fig. 1a). The ventral apodeme (va; Fig. 1a, d) at the proximal end of the stegostom-cylinder mentioned by De Ley *et al.* (1993) is hardly visible with light microscopy. Other structures shown in the TEM sections of De Ley *et al.* (1993) such as the mediodorsal ridge and the ventrosublateral flange are not visible using the light microscope. In Fig. 1 De Ley *et al.* (1993) show two subdorsal keels or ridges at the proximal third of the "shaft" that merge into the subdorsal knobs, but this was not mentioned by the authors. These ridges (rdg; Fig. 12) are homologous with the "perradial struts" in other species.

Musculature. The dorsal fold (df; Fig. 1a, d) is attached to the dorsal tooth and contains the insertion of dorsal myofilaments (dm; Fig. 1a, d) that run longitudinally within the procorpus. The origin of these filaments was not discernible. Comparable bundles of myofilaments originate from the dorsal surface of the cuticular lining (cl) within the procorpus lumen and run adradially anteriorly to insert on the dorsal fold (df) in *Mononchoides* (Fig. 11a). These bundles are referred to here as "deep adradial bundles" (dab; Fig. 11a), as additional superficial adradial bundles

(sab; Fig. 11a) originate from the perradial struts (perst) in *Mononchoides*. After De Ley *et al.* (1993) the dorsal bundles in *Tylopharynx* extend "as adradial muscle bands in the procorpus". This indicates possible homology of the dorsal bands in *Tylopharynx* with the deep adradial bundles in *Mononchoides*. The assumed origin of the dorsal bands is indicated by a '?' in Figs 2a-c, 6a-d.

Each subdorsal apodeme (sda) serves as a point of attachment for a well developed longitudinal myofilament bundle (sdm; Fig. 1a; 2b, c). These subdorsal muscle bundles run anteriorly to insert on the basal lamina of the pharynx next to the dorsal fold. Fürst von Lieven & Sudhaus (2000) reported that the subdorsal muscles insert on the dorsal fold ("tendon"), but this was an observational error. The ventral knob (va) has the origin of a longitudinally orientated ventral myofilament bundle (vm; Fig. 1a, d; 2b, c) that inserts on the basal lamina of the pharynx just posterior to the connecting cuticle between the gymno- and stegostom.

The numerous muscle bundles in the subventral interradii shown by De Ley *et al.* (1993) were not visible with light microscopy.

Observations on living worms

Functional morphology. The correlation between movement and muscle contractions described here for *T. foetida* refer only to the ventral, subdorsal and dorsal myofilament bundles. The effect of the subventral muscles remains unclear.

The buccal cavity of *T. foetida* is adapted to feed on fungal hyphae. This was mentioned by Sachs (1950), Hirschmann (1952), and Sudhaus (1981), but the feeding-mechanism differs from what was expected on the assumption that *Tylopharynx* possesses a stylet. Instead of piercing a hole into the cell wall of the fungus, a hole is cut or ripped by the teeth. The dorsal tooth is adducted when the dorsal myofilaments (dm) and the subdorsal myofilaments (sdm) contract simultaneously (Fig. 2b). The dorsal filaments that insert on the dorsal fold (df) cause the adduction by pulling on the fold. The subdorsal bundles add to the adduction by bringing forward the ventral edge of the dorsal tooth base while its dorsal edge is pulled backwards. Concurrently, the subdorsal myofilaments pull back their insertion site. This retraction is transmitted to the dorsal wall of the gymnostom (gym) by indenting the pharyngeal basal lamina. Consequently, the gymnostom tilts dorsally and thus provides more space for the adduction of the dorsal tooth (Fig. 2b).
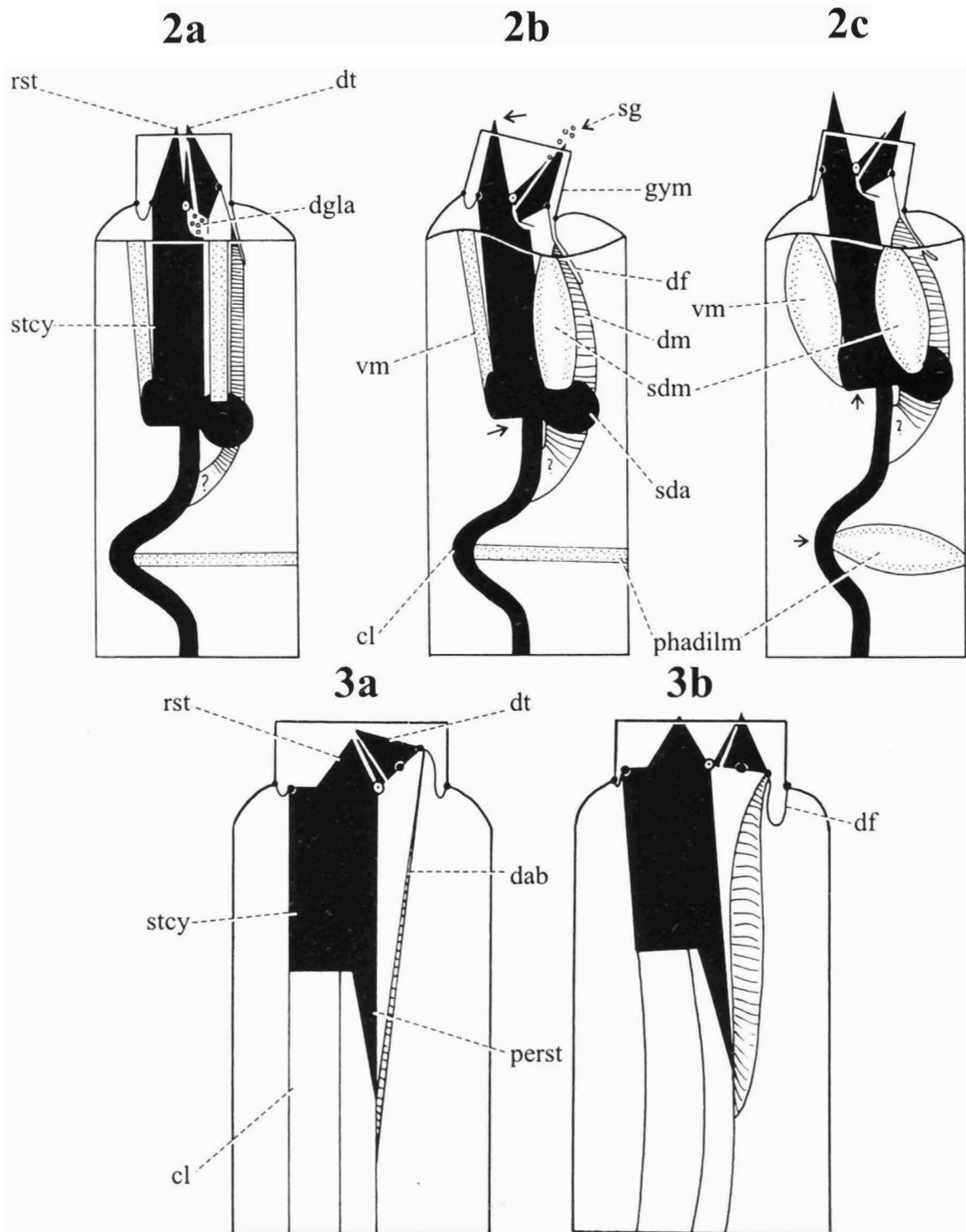
Figs. 2 and 3. Schematic reconstructions showing the motility of mouthparts. **Fig. 2.** *Tylopharynx foetida.* a, mouthparts at rest; b, adduction of teeth; c, protrusion of stegostom. **Fig. 3.** *Mononchoides* sp. 1. a, mouthparts at rest; b, adduction of teeth.
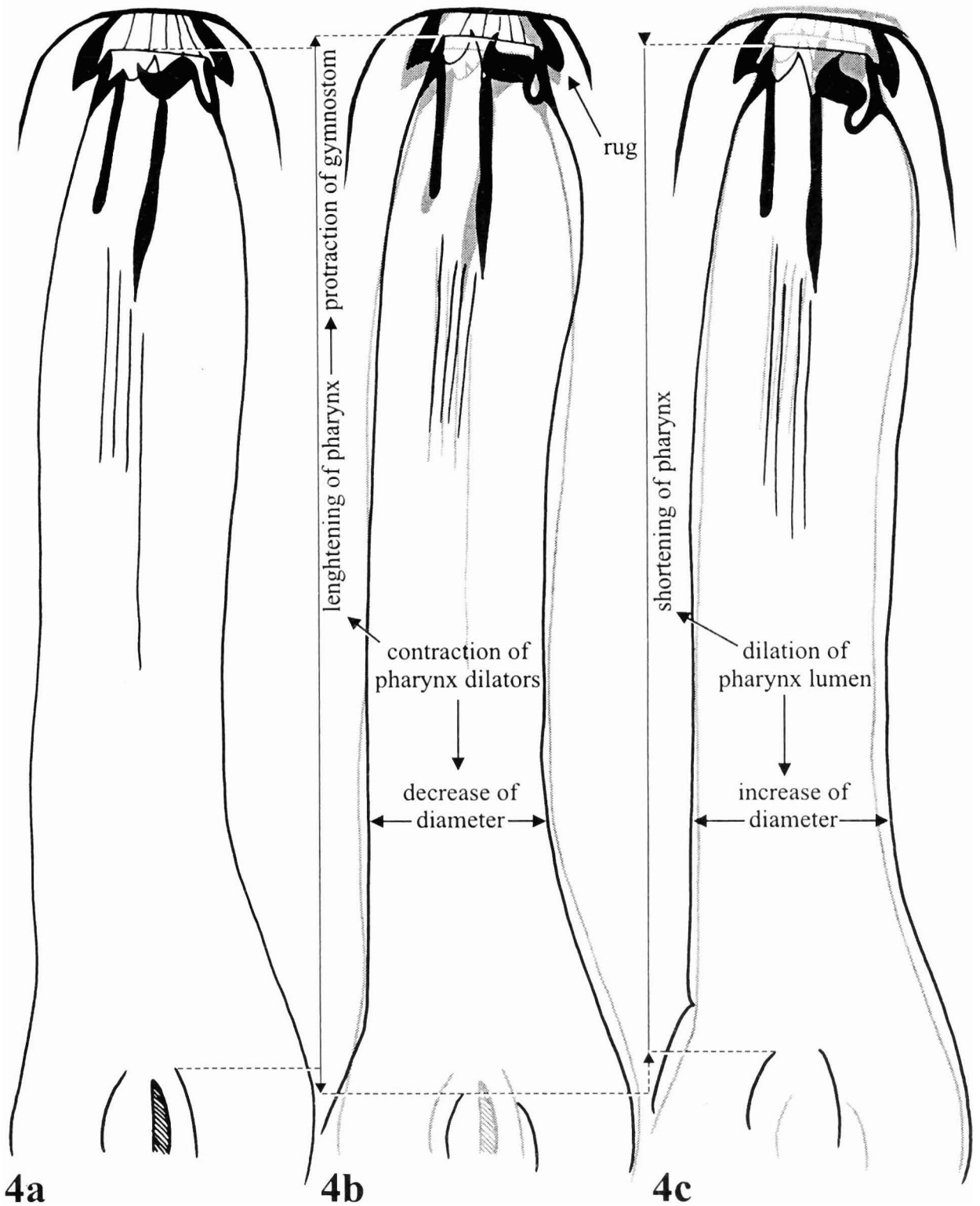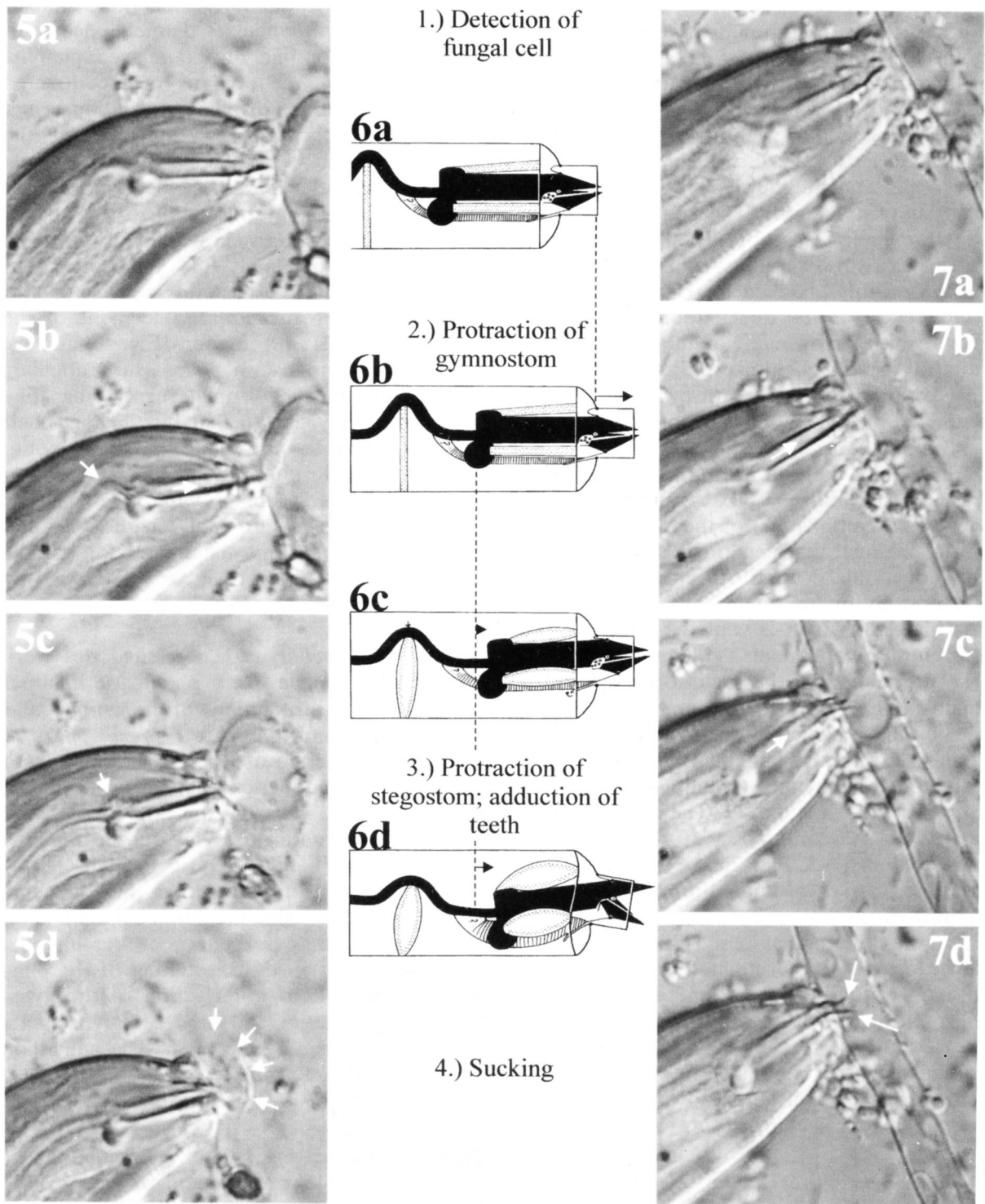
Fig. 4. Drawings of video sequences showing the changes in procorpus-length during dilation in *Mononchoides* sp. 1. a, at rest; b, just before dilation; c, dilation.

1.) Detection of
fungal cell

2.) Protraction of
gymnostom

3.) Protraction of
stegostom; adduction of
teeth

4.) Sucking

Figs. 5-7. Observations of the feeding behavior of *Tylopharynx foetida* in the culture dish. **Fig. 5a-d.** Video sequences of a worm feeding on a swollen tip of a hypha. **Fig. 6a-d.** Schematic reconstruction of the feeding process. **Fig. 7a-d.** Video sequences of a worm feeding on a hypha.

The contraction of the adductor muscles causes not only the adduction but also a tilting of the stegostom-cylinder (arrows; Fig. 2b), which tilts around an axis that runs through the base of the dorsal tooth. This tilting was postulated as a "side effect" of the adduction of the dorsal tooth by De Ley *et al.* (1993). But, whereas these authors interpreted the tilting as a "deviation" against which the tube needs to be stabilized, this side effect actually is an important prerequisite for the motility of the right subventral tooth. The caudal end of the stegostom-cylinder tilts dorsally and the part anterior to the axis tilts ventrally. As the right subventral tooth is firmly attached to the stegostom-cylinder, adduction of the dorsal tooth causes a simultaneous ventral movement of the right subventral tooth. This mechanism faciliates a synchronized movement of both teeth by using only the adductor muscles of the dorsal tooth (Fig. 2a, b).

The adduction of the dorsal tooth leads to the compression of the hollow tooth base (dgla) that probably causes secretions (sg) of the dorsal gland to flow out of the duct that penetrates the tooth.

During adduction the teeth can be pushed out of the gymnostom by protraction of the whole stegostom (Fig. 2c), which is caused by the subdorsal and ventral myofilaments (sdm and vm; Fig. 2b, c). The protraction of the stegostom pulls on the cuticular lining of the pharynx lumen (cl; Fig. 2c). Space for the protraction is provided by the following mechanism: the cuticular lining of the pharyngeal lumen is bent ventrally when the stegostom is retracted (Fig. 2a, b). The protraction is correlated with the contraction of the pharynx dilator muscles (phadilm; Fig. 2b, c) that flattens the curve of the pharyngeal lumen (arrow; Fig. 2c, 5b). Flattening of the lumen cuticula results in its elongation in the longitudinal axis. This elongation allows the stegostom to be protracted.

The motion pattern of teeth and stegostom-cylinder in *Mononchoides* (Fig. 3a, b) is similar to *Tylopharynx*, with the exception that here the stegostom can not be protracted. Protractor muscles that insert at the basal lamina of the anterior end of the pharynx are lacking in this taxon.

How do the teeth reach the hyphae? The stegostomatal teeth lie within the gymnostom. Even if they are protracted as in *Tylopharynx*, they can not reach the oral opening. To feed on sources that are too big to be sucked into the stoma-like hypae (in *Tylopharynx*), or small organisms such as ciliates and other nematodes (in *Mononchoides*), the teeth need to be brought into direct contact

with the food source. In *Tylopharynx* the detection of a fungal cell is followed by subsequent dilations of the pharynx. Each dilation results in an elongation of the pharynx while its diameter decreases (compare dotted outline of the relaxed pharynx with the outline of the pharynx with contracted dilator muscles in Fig. 1b). The elongation brings the gymnostom forwards to the level of the cheilostom (Fig. 1b, d) to enable the teeth to get in contact with the cell wall. For comparison, in *Mononchoides* sp. 1 the contraction of the dilator muscles also results in an elongation of the pharynx of about approximately 5% of the procorpus length, which results in a posterior displacement of both bulbs and an anterior displacement of the stego- and gymnostom (compare Fig. 4a and b). The protracted gymnostom pushes the cuticularized plates of the cheilostom ("rugae", rug; Fig. 4b) forwards and apart, so that they change their angle which increases the diameter of the mouth opening. The elongation of the pharynx is followed by a dilation of its lumen while the pharynx shortens to assume its original length (Fig. 4c). This observation confirms the model for the filling-cycle of the pharynx of *Ascaris* developed by Bennet-Clark (1976).

Feeding in *Tylopharynx*. The nematodes work on the walls of hyphae like a pneumatic hammer by means of ca. 7 protractions of the gymno- and stegostom per second (compare Figs 5a/b, 6a/b/c, 7a/b). Each protraction of the stegostom (Fig. 6c) is followed by the adduction of the teeth (Fig. 6d). Once they grip the cell wall they rip it apart and widen a hole large enough to suck out the contents of the fungal cell (Fig. 7c). During sucking (compare Fig. 5c and 5d) the nematodes anchor themselves in the hole by using the adducted teeth (Figs 5d, 7d). At this time relaxation of the pharynx dilators that results in the shortening of the pharynx does not lead to a retraction of the gymnostom as the anterior end of the pharynx is attached to the hyphae by the teeth. The nematode suck on the hyphae for one to two seconds.

DISCUSSION

Feeding behavior and habitat. Observations of the buccal morphology and feeding behavior of *T. foetida* suggest that this species feeds exclusively on fungal hyphae. Ingestion of bacteria was never observed. The habitat of *T. foetida* is cow pats that get populated through phoretic dauer larvae transported by *Aphodius fimetarius* (Scarabaeidae, Coleoptera; Rehfeld, 1988). In the succession of cow dung nematodes *T. foetida* appear in 14 - 36
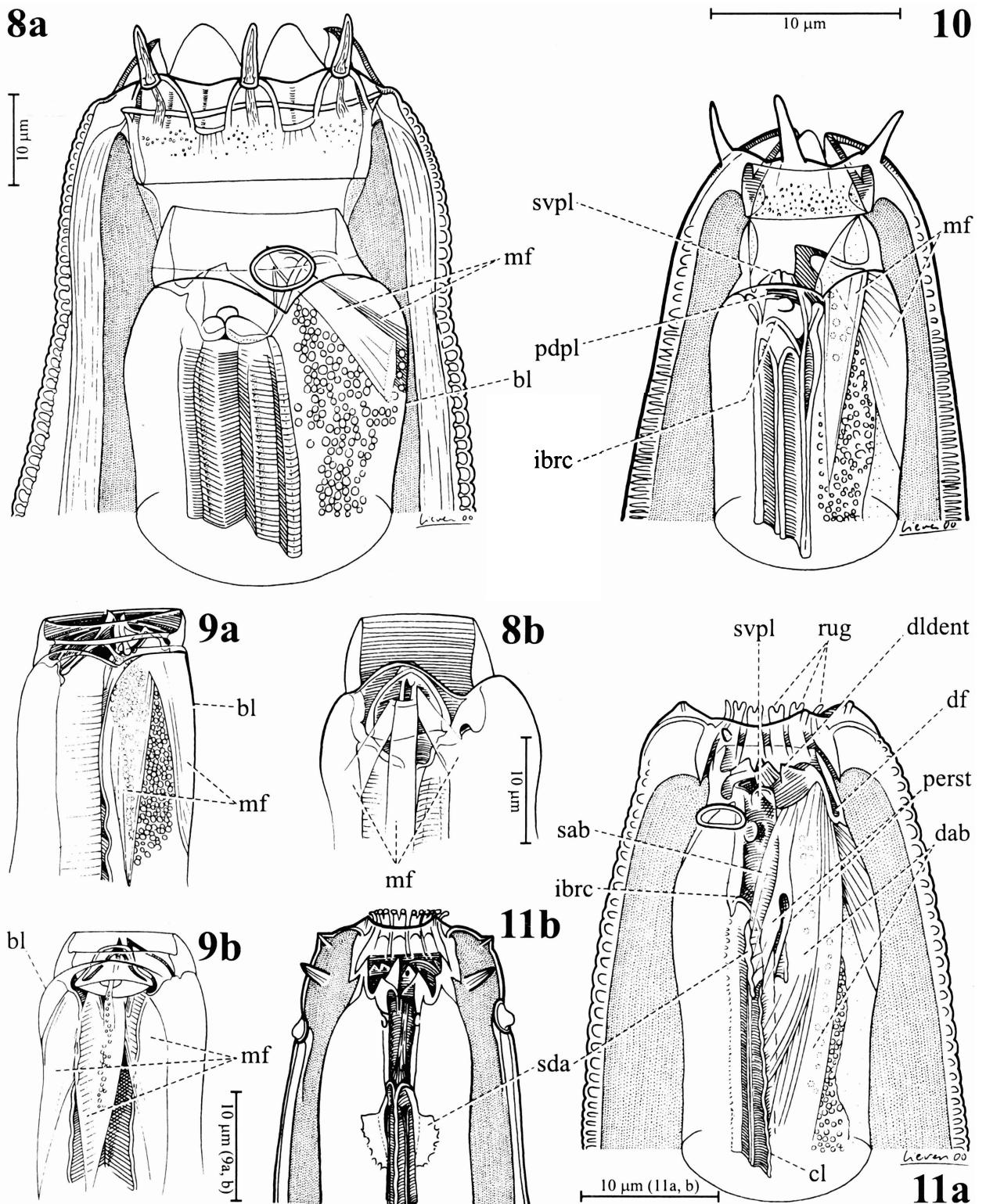
Figs. 8-11. Morphology of the stoma and procorpus in some diplogastrid species. **Fig. 8.** *Butlerius filicaudatus*, female. a, anterior end, left lateral aspect; b, anterior end of procorpus and gymnostom, dorsal aspect. **Fig. 9.** *Oigolaimella* sp., anterior end of procorpus and gymnostom. a, left lateral aspect; b, dorsal aspect. **Fig. 10.** *Diplogaster schneideri*, female, anterior end, left lateral aspect. **Fig. 11.** *Mononchoides* sp. 2. a, anterior end of female, left lateral aspect; b, anterior end of male, ventral aspect.
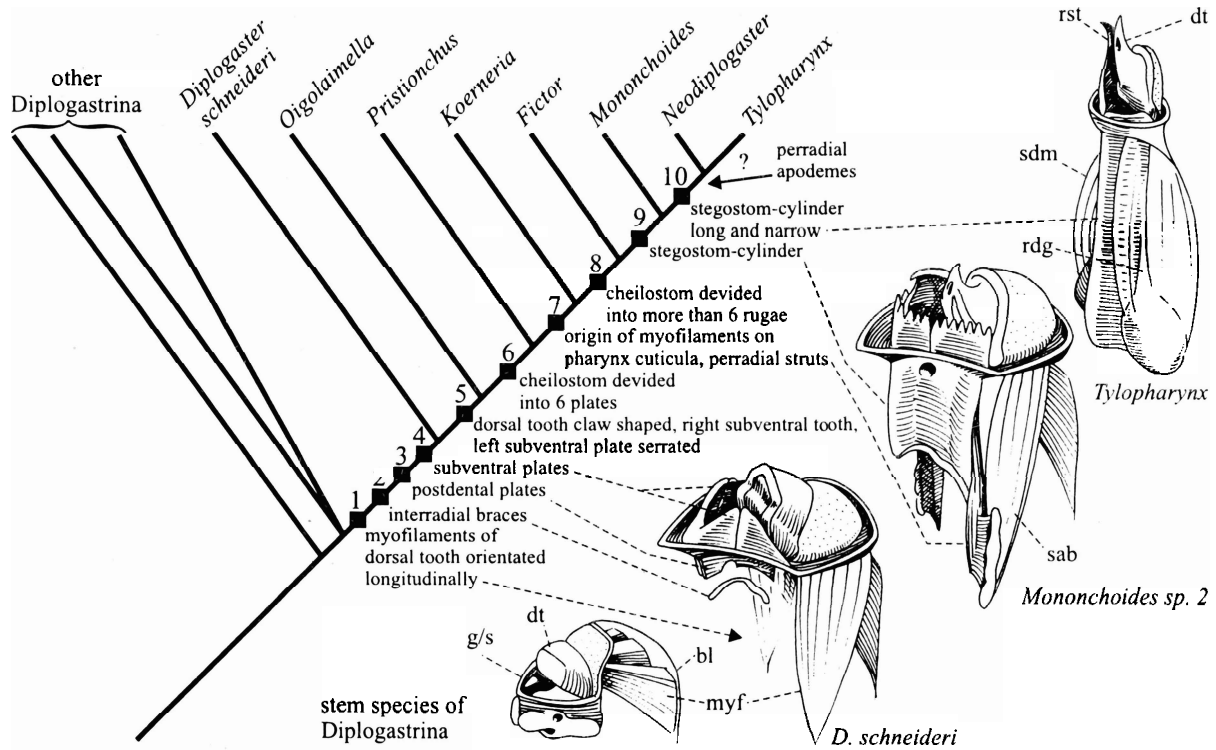
Fig. 12. Phylogenetic relationships of the claw tooth bearing diplogastrids combined with the transformation of stegostom and tooth musculature.

day old pats (Sachs, 1950). Sudhaus (1981) observed the nematodes also in 8-12 days old manure, and found them to be most abundant in 14 and 22 day old pats. The high abundance of *T. foetida* from the fourteenth day was also observed by Rehfeld (1988) and Sudhaus *et al.* (1988). According to Rehfeld (1988) the increase in population coincides with the growth phase of coprophilous fungi described by Dickinson & Underhay (1977).

Phylogenetic relationships. *Mononchoides*, from the Diplogastrina examined, is the most closely related taxon to *Tylopharynx*. In both taxa the posterior part of the stegostom forms a cylinder to which the right subventral tooth is firmly attached (Fürst von Lieven & Sudhaus, 2000). As a result of this firm attachment both taxa also share the apomorphic motion pattern of the teeth as described above (compare Figs 2 and 3). Probably the sister group of *Tylopharynx* is *Neodiplogaster* that was not examined here, as in both taxa the stegostom cylinder extends to the caudal end of the perradial struts with each having a subdorsal apodeme at

their posterior end. The subdorsal apodemes may be a second synapomorphy for *Neodiplogaster* and *Tylopharynx*, but comparable structures were also found in *Mononchoides* sp. 2 (sda; Fig. 11a, b). Other *Mononchoides* species do not possess such apodemes. Assuming homology of the apodemes in *Mononchoides* sp. 2 and *Neodiplogaster/Tylopharynx* may indicate that *Mononchoides* is a paraphylum. Another possibility is that perradial apodemes have evolved as an apomorphy of the stem species of *Mononchoides* + *Neodiplogaster* + *Tylopharynx* and were lost in some species of *Mononchoides*. The only possible apomorphic structures that could support the monophyly of *Mononchoides* are the dorsolateral denticles on the inner wall of the gymnostom (Fürst von Lieven & Sudhaus, 2000), and these are also present in *Mononchoides* sp. 2 (dldent; Fig. 11a). If *Mononchoides* is paraphyletic, the denticles must have either been lost in the stem species of *Neodiplogaster* + *Tylopharynx* or they must exist in one or the other species of *Neodiplogaster*.

The stylet and the knobs found in Tylenchida were thought to be derived from the stylet-like

buccal cavity and the stegostom-apodemes of *Tylopharynx* (Marcinowski, 1909; Micoletzky, 1922; Sachs, 1950; Maggenti, 1963; Zuckerman *et al.*, 1971; Andrássy, 1976). Rühm (1956) rejected the assumption of a closer relationship of Diplogastridae and Tylenchida *via* Tylopharyngidae because in *Tylopharynx* the pharyngeal basal lamina is attached close to the anterior end of the presumed "spear", as was correctly observed by Bütschli (1874), De Man (1884), and Sachs (1950).

The ultrastructural differences of the stoma architecture between *Tylopharynx* and Tylenchida were discussed by De Ley *et al.* (1993). The results here support the conclusion of these authors that *Tylopharynx* can not be regarded as a link between Diplogastrina and Tylenchida for the following reasons: a stylet is not present in *Tylopharynx*. Regarding the knobs, it has to be noted that the apodemes of *Tylopharynx* are located perradially (two subdorsally and one ventrally) whereas in Tylenchida the three knobs are located interradially, one dorsally and two subventrally.

These differences in the stoma architecture make it impossible to derive the tylenchid spear from the buccal cavity of *Tylopharynx*. Molecular data suggest the Tylenchida are closely related with the Cephalobidae (Blaxter *et al.*, 1998).

Some important transformations of stomatal structures in the ancestral line of *Tylopharynx*. Some striking peculiarities exist in the stoma architecture of *Tylopharynx*. These were the basis for erecting a family for *T. foetida*:

1. The stoma is mainly a narrow shaft bearing large ball-shaped apodemes at the posterior end.

2. The shaft lies within the procorpus, which means that it consists of the stegostom. In most other diplogastrid species the stegostom is a comparatively short part of the buccal cavity.

3. In contrast to the condition commonly found within the Secernentea the muscles that are attached to the stegostomatal structures run longitudinally and not transversally.

These features developed stepwise from plesiomorphic conditions within the Diplogastrina (Fürst von Lieven & Sudhaus, 2000). Examinations reported here of *Butlerius filicaudatus*, *Diplogaster schneideri*, *Oigolaimella* sp., *Mononchoides* sp.1 and *Mononchoides* sp. 2 help to reconstruct this transformation series in more detail.

The transformations occurred mainly within a monophyletic taxon substantiated by the possession of a functional unit between a claw-like dorsal tooth and a right subventral tooth. The sister taxon to this group is *Diplogaster schneideri*. The group-

ing of this species as reported by Fürst von Lieven & Sudhaus (2000) was based on weak arguments (indicated by black and white squares in Fig. 25) and should therefore be considered tentative. The position of *D. schneideri* as proposed here is supported by the following details in stegostom morphology (characters 1-4; Fig. 12):

As in all claw tooth bearing species, and contrary to all other Diplogastrina, the myofilaments (mf; Fig. 10) of the stegostomatal teeth of *D. schneideri* are orientated longitudinally.

D. schneideri possesses a cuticular ridge ("interradial brace" ibrc; Fig. 10) at the bottom of the buccal cavity in each subventral sector. Interradial braces are found in all taxa of the claw tooth bearing species except *Neodiplogaster*, *Oigolaimella* and *Tylopharynx*. The lack of the braces in these taxa is interpreted as the result of secondary loss.

The lining of the stegostom is heavily cuticularized posterior to the teeth in *D. schneideri*, to form "postdental plates" (pdpl; Fig. 10) in the subventral sectors. Homologous structures are present in all claw tooth bearing taxa, except *Oigolaimella*, where they have been secondarily lost.

In *D. schneideri* the subventral sectors of the stegostom bear "subventral plates" (svpl; Fig. 10) that are separated by an interradial incision into two adradial parts. The left subventral plate is homologous with the serrated plate in the subventral sector (svpl; Fig. 11a; not serrated in *Mononchoides* sp. 2) that occurs in all claw tooth bearing taxa except *Oigolaimella* and *Tylopharynx*. The serrated plate is always separated into two adradial parts. The right subventral plate was transformed to the right subventral tooth in the ancestral line of claw tooth bearing Diplogastrina.

Transformations of the stegostom

Musculature. A characteristic feature of a claw-like dorsal tooth, for example in *Tylopharynx*, is the longitudinal orientation of its musculature. *Butlerius filicaudatus* (Fig. 8) is a representative of Diplogastrina with oblique-transversely orientated myofilaments. In lateral view (Fig. 8a) the myofilaments (mf) can be observed originating from the basal lamina (bl) of the pharynx. In dorsal view (Fig. 8b) three portions, one dorsally and two adradially, are visible. In dorsal view of the procorpus of *Oigolaimella* sp. (Fig. 9b), a representative of Diplogastrina possessing a functional unit of claw shaped dorsal tooth and right subventral tooth, the three bundles are orientated longitudinally. Comparison of lateral (Fig. 9a) and dorsal view shows that all three bundles originate from

the basal lamina (bl) of the pharynx.

In *Mononchoides* sp. 2 (Fig. 11a) some of the adradial muscle bundles (the "deep adradial bundles", dab) originate from the dorsal side of the pharyngeal cuticular lining. Each subdorsal side of the cuticular lining is supported with a perradial strut (perst).

Phylogenetically, the shift from transversally orientated to longitudinally orientated muscles (character 1; Fig. 12) preceded the acquisition of the claw-like tooth and the right subventral tooth (character 5). Re-examination of *Diplogaster schneideri* revealed that this species, which lacks claw-like and a right subventral tooth, possesses longitudinal muscles.

The shift of the origin of adradial myofilaments from the pharyngeal basal lamina to the dorsal surface of the pharyngeal cuticular lining, and the stiffening in this region by perradial struts (character 7), occurred in the stem species of a taxon including *Koerneria*, *Fictor*, *Mononchoides*, *Neodiplogaster* and *Tylopharynx*.

In *Mononchoides* sp. 2 each strut bears a subdorsal apodeme from which the superficial adradial myofilaments originate (sda; Fig. 11a, b). This situation is similar to that found in *Tylopharynx* where the bundles attached to the apodemes are much more pronounced and lie perradially in each subdorsal radius. This suggests homology of the superficial adradial muscles (sab; Fig. 12) in *Mononchoides* and the subdorsal muscles (sdm; Fig. 12) in *Tylopharynx*.

Cuticular structures. In the ancestral line of *Mononchoides*, *Neodiplogaster* and *Tylopharynx*, the postdental plates elongated posteriorly and fused to form a stegostom-cylinder (character 9; Fig. 12). In the latter taxa the stegostom-cylinder extends further caudally than in *Mononchoides* and reaches the posterior ends of the perradial struts (character 10). Consequently, the perradial struts became part of the cylinder from which they extend as cuticular ridges as presented in the reconstruction of the buccal cavity of *Tylopharynx* by De Ley *et al.* (1993). Subsequently, the cuticularization of the region between the perradial struts completed the transformation of the stegostom in the ancestral line of *Neodiplogaster* + *Tylopharynx*.

Transformations of the cheilostom. Another important feature of *Tylopharynx* is the nematode's ability to push the gymnostom through the cheilostom that enables direct contact between teeth and fungal cell to be faciliated. In the ancestral line of *Tylopharynx* this ability possibly was obtained by interrupting the cuticularized cheilostom with longitudinal incisions that consist of flexible cuticle. The gymnostom can push apart the plates of the cheilostom when it moves forwards. The force pushing against the cheilostom is the result of the contraction of the pharynx dilator muscles that leads to an elongation of the pharynx. The association between dilation and lengthening of the pharynx is frequently observed when studying feeding nematodes (W. Sudhaus, pers. comm.; own observations). This phenomenon has been observed in representatives of *Pseudodiplogasteroides*, *Plectus* and *"Rhabditis"*. As these species are not able to protrude their buccal cavity, their pharynx length can only increase towards the posterior end. By separating the cheilostom into cuticularized plates, the elongation may be used to push the gymnostom forwards. This means that elongation as a side effect of muscle contraction can be interpreted as a preadaptation for the evolution of a protrusible stoma in the Diplogastrina. A protrusible stoma through separation of the cuticularized parts of the cheilostom evolved convergently twice within the taxon (Fürst von Lieven & Sudhaus, 2000). One of these events occurred in the stem species of *Pristionchus* and its sister group, where the cheilostom was separated into six adradial plates (character 6; Fig. 12). This condition was subject to additional transformations in the ancestral line leading to *Tylopharynx*: A further separation into narrower "rugae" (rug; Fig. 4b, 11a) occurred in the ancestor of the monophylum comprising *Fictor* and its sister group (character 8). The rugae are present in *Neodiplogaster*, but have been secondarily lost in *Tylopharynx*, where the cheilostom has no obvious cuticularisations.

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Fürst von Lieven A. Функциональная морфология, происхождение и филогенетическое значение механизма захвата пищи у *Tylopharynx foetida* (Nematoda: Diplogastrina).

Резюме. Ротовая полость *Tylopharynx foetida* исследована в микроскопе с оптикой Номарского. Для определения функций отдельных элементов проанализированы последовательные видеокадры процесса питания этих нематод. Сравнение морфологии отдельных частей ротового аппарата и их функций у различных Diplogastrina показывает, что структуры стомы *Tylopharynx* существенным образом не отличаются от таковых у *Mononchoides* и *Neodiplogaster*. Исследования показали, что *Tylopharynx* питается на гифах грибов отрывая фрагменты клеточной стенки стегостомными зубами. Последние выдвигаются из стомы за счет вытягивания пищевода в каждом из циклов засасывания пищи. Проведенные наблюдения подтверждают теоретическую модель работы пищевода у *Ascaris*, предложенную Беннетом-Кларком (Bennet-Clark, 1976). Гомологизация отдельных элементов стомы у *Tylopharynx* и других Diplogastrina дает основания для пересмотра морфологических рядов трансформации стомы у *Tylopharynx* и формирования таких структур как субдорсальные утолщения или продольные мышцы-протракторы.