Diplogaster coprophilus n. sp. and *D. affinis* n. sp. (Nematoda, Rhabditida) from cow pats and related species, with notes on distribution, ecology and phylogeny

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SUMMARY

Diplogaster coprophilus n. sp. and *D. affinis* n. sp. from cow pats are described. *D. coprophilus* n. sp. is a sibling species of *D. bernensis* Steiner, 1914, a well known species from freshwater, which is redescribed. On the basis of type material *D. bodamicus* Micoletzky, 1922 is confirmed to be a junior synonym of *D. bernensis*. *D. anomalus* (Gagarin, 1977) n. comb. is treated as *species inquirenda*. *D. affinis* n. sp. is compared with *D. coprophages* de Man, 1876 and *D. micrurus* Weingärtner, 1955, which inhabit dung and seem to be adapted to different stages of decomposition. *D. coprophages* and *D. micrurus* are carnivourous as adults only. The drastical change from a small to a large buccal cavity during the last moult is shown. For all revised species data on distribution, ecology, biology, and phoresis are presented. All these species and *D. paraspirifer* (Zullini & Loof, 1980) n. comb. form a monophyletic group. On the basis of habitats of these species we conclude that the common ancestor was adapted to droppings of terrestrial vertebrates, and that a later evolutionary line became aquatic.

RÉSUMÉ

Diplogaster coprophilus n. sp. *and* D. affinis *n. sp. (Nematoda, Rhabditida) provenant d'excréments de bovins; espèces voisines, et notes sur la répartition, l'écologie et la phylogénie de ces espèces*

Diplogaster coprophilus n. sp. et *D. affinis* n. sp. provenant d'excréments de bovins sont décrits. *D. coprophilus* n. sp. est une espèce jumelle de *D. bernensis* Steiner, 1914, espèce dulçaquicole bien connue, qui est redécrite. L'étude du matériel type a confirmé *D. bodamicus* Micoletzky, 1922 comme synonyme mineur de *D. bernensis*. *D. anomalus* (Gagarin, 1977) n. comb. est considéré comme *species inquirenda*. *D. affinis* n. sp. est comparé à *D. coprophages* de Man, 1876 et *D. micrurus* Weingärtner, 1955 qui ont le même habitat où ils semblent adaptés à des stades de décomposition différents. Seuls les adultes de *D. coprophages* et *D. micrurus* sont carnivores. La transformation brutale de la cavité buccale, qui, d'étroite, devient beaucoup plus vaste lors de la dernière mue, est démontrée. Des données sont fournies sur l'écologie, la biologie et la phorésie des espèces étudiées. Toutes ces espèces, ainsi que *D. paraspirifer* (Zullini & Loof, 1980) n. comb., forment un groupe monophylétique. En considérant l'habitat de ces espèces, il est conclu que leur forme ancestrale commune était adaptée aux excréments des vertébrés terrestres et qu'une lignée évolutionnaire a postérieurement adopté un habitat aquatique.

Based on the thorough studies of Sachs (1950) and Gunhold (1950) the nematode fauna of cow droppings and its succession was recently studied from different aspects (Sudhaus, 1981; Sudhaus *et al.*, 1988). In the course of this study several new species were discovered. Two of the most abundant diplogastrid species are described below. One was already mentioned and figured by Sudhaus (1981) as *Diplogaster* sp. I and since then proved to be undescribed. The other has been confused hitherto with *D. bernensis* Steiner, 1914, a well known species from freshwater. The nearest relatives of both, *D. coprophages* de Man, 1876, *D. micrurus* Weingärtner, 1955 and *D. bernensis* will be revised.

***Diplogaster coprophilus* n. sp.**
(Fig. 1)

= *Diplogaster bernensis apud* Sachs, 1950; *apud* Sudhaus, 1981; *apud* Sudhaus *et al.*, 1988; *nec* Steiner, 1914.

= *Diplogaster (Paroigolaimella) bernensis apud* Weingärtner, 1955*a*; *nec* Steiner, 1914.

= *Paroigolaimella bernensis apud* Meyl, 1961 *(partim)*; *nec* Steiner, 1914.

MEASUREMENTS

See Table 1.

Table 1

Diplogaster coprophilus n. sp.
Dimensions in µm (living specimens, heat relaxed, means in brackets).

	Females	*Males*	*Ensheathed l dauerlarvae**
n	12	10	10
length	514-1 062 (778)	498-654 (559)	270-319 (305)
width	27-46 (34)	16-24 (20)	11-13 (12)
corpus	43-47 (45)	37-43 (40)	–
pharynx	83-93 (87)	72-82 (78)	79-92 (84)
tail	161-296 (242)	130-180 (160)	86-104 (98)
gonad**	135-244 (204)	194-308 (232)	–
V %	38-42 (40.4)	–	–
spicules	–	18-22 (19)	–
gubernaculum	–	9.5-13 (11)	
a	15.5-28.9 (22.4)	23.8-34.5 (28.4)	23.1-29.5 (25.7)
b	6.2-11.7 (8.9)	6.4-8.0 (7.1)	3.4-3.9 (3.6)
c	2.9-3.6 (3.2)	3.2-3.8 (3.5)	3.0-3.6 (3.1)

* Larvae ensheathed : data on body length and tail length include the cuticle of the J2, which forms the sheath.
** Measured from anterior to posterior flexure (♀), from flexure to cloaca (♂).

DESCRIPTION

Adults : A small species, slender, of whitish colour. Cuticle with faint longitudinal and transversal stripes, made up of fine dots. Distance of ten annules at midbody (fem.) 20 µm, on tail *ca.* 10 µm. No special structure in lateral field, only one longitudinal row missing. Gap between rows about 2 µm. Anterior end diameter 8.5-11 (fem.) resp. 7.5-11 µm (male), corresponding to 2-2.7 (fem.) resp. 2.2-3 (male) times width of buccal cavity. Lips closed, with six apical sensilla, in addition four sublateral ones in the male. Oval or bean-shaped amphids about 5 µm behind terminal end at level of dorsal tooth. Stoma width about 3.5-4 µm, length 7-9 (fem.) resp. 6-7 µm (male), divided into two parts of about equal dimension. Anterior ring consisting of twelve plates, visible only in disintegrating specimens, posterior rhabdions dorsally shortened, the subsequent dorsal tooth conspicuous. Subventral metarhabdions bearing small warts. Small denticle-like telorhabdions at the beginning of pharynx. Corpus occupying 50-54 % of pharynx length, diameter of median bulb 13-18 (fem.) resp. 10-12 µm (male), terminal bulb 12-17 µm wide (fem.) resp. 8.5-12 µm (male). Cervical (excretory) pore hardly visible at the end of pharynx.

Female : Anterior end to anus exactly 1.7 times distance from anterior end to vulva. Vaginal cavity especially strongly cuticularized, yellowish-brown, with plate-like margins beneath vulval lips and horseshoe-like in optical section. A bladder, measuring 8.5-14 × 5-10 µm, adhering by means of a small stalk, its position variable, sometimes directed anteriorly, sometimes posteriorly. No sperms visible in bladder, only in uterus. Gonads amphidelphic, anterior branch right of intestine, 71-149 (111) µm, posterior branch on left side, 64-123 (98) µm long, together occupying 25-32 (28) % of body length. Ovaries reflexed dorsally about 56-127 % of respective branch length. Distinct border between ovary and oviduct meandering. Maximally two cleaving eggs visible in one uterus, oviparous, but eggs laid sometimes in an advanced stage of development. Egg dimensions 43-44 × 18-19 µm. Rectum on average 14 µm long, similar to anal body width (= ABW; 12-18 µm). Rectal glands hardly observable. Tail filamentous, corresponds to 13-18 ABW (12-18 µm), phasmids 18-27 (22) µm behind anus, i.e. 1.4-1.6 ABW or 7-11 % of corresponding tail length. In one female the cuticularized vaginal structure and bladder were totally absent.

Male : Smaller than female, dead specimens not as out-stretched as females, but typically curved. Anterior end sexualdimorphic concerning sensilla as mentioned. Testis single, on the right hand side, occupying 39-47 % of body length. Ventrally reflexed part 33-61 (49) µm long, comprising 14-27 % of gonad length. Sperms spherical, diameter about 4.5 µm. In posterior body region two bands of oblique muscles extending from dorsal to ventral side, the centre of their ventral insertion at a distance of 38-43 (40) µm anterior to cloaca. Tail with nine pairs of papillae, 2 + 1/1 + 1 + 3 + 1, most of them subventral, two at level of spicules' head, no. 2 somewhat smaller than 1, no. 3 at level of cloaca difficult to see, pointing laterodorsad, no. 5 in the centre between nos 4 and 6, no. 9 directed dorsally, remnant of a bursa velum between small papillae 6-8 missing. Distance from cloaca to papilla no. 9 (just beginning of tail filament) 33-44 (39) µm, about 2-3 times ABW (13-19 µm). Spicules deeply yellow or brown, their structure extremely complex : fused to 70 % of their length, formed like a deep groove, tip slightly curved down. Ventrolaterally two outwards pointing hooks or claws. Gubernaculum linear, narrow, comprising 50-60 % of spicules' length. Precloacal lip bearing a small papilla. In one male spicules and gubernaculum were completely absent, while all caudal papillae were developed as usual.

Dauerlarva : First ensheathed, then moulting to the short-tailed dauerlarva covered by an oil-like substance. Amphid apertures conspicuous; cervical pore 54-62 (59) µm from anterior end, i.e. 66-75 % of pharynx length. ABW 9-10 µm. Tail of juvenile 3 (J3) within the old cuticle 36-44 µm long, 4-4.5 times ABW, comprising 38-48 % of J2 tail length; tail of J2 measures 6-8.5 ABW. Phasmids 12-14 µm posterior to anus.

There is no difference in pharynx length between dauerlarvae and adults. Those larvae with dimensions exceeding the span of males must be females.

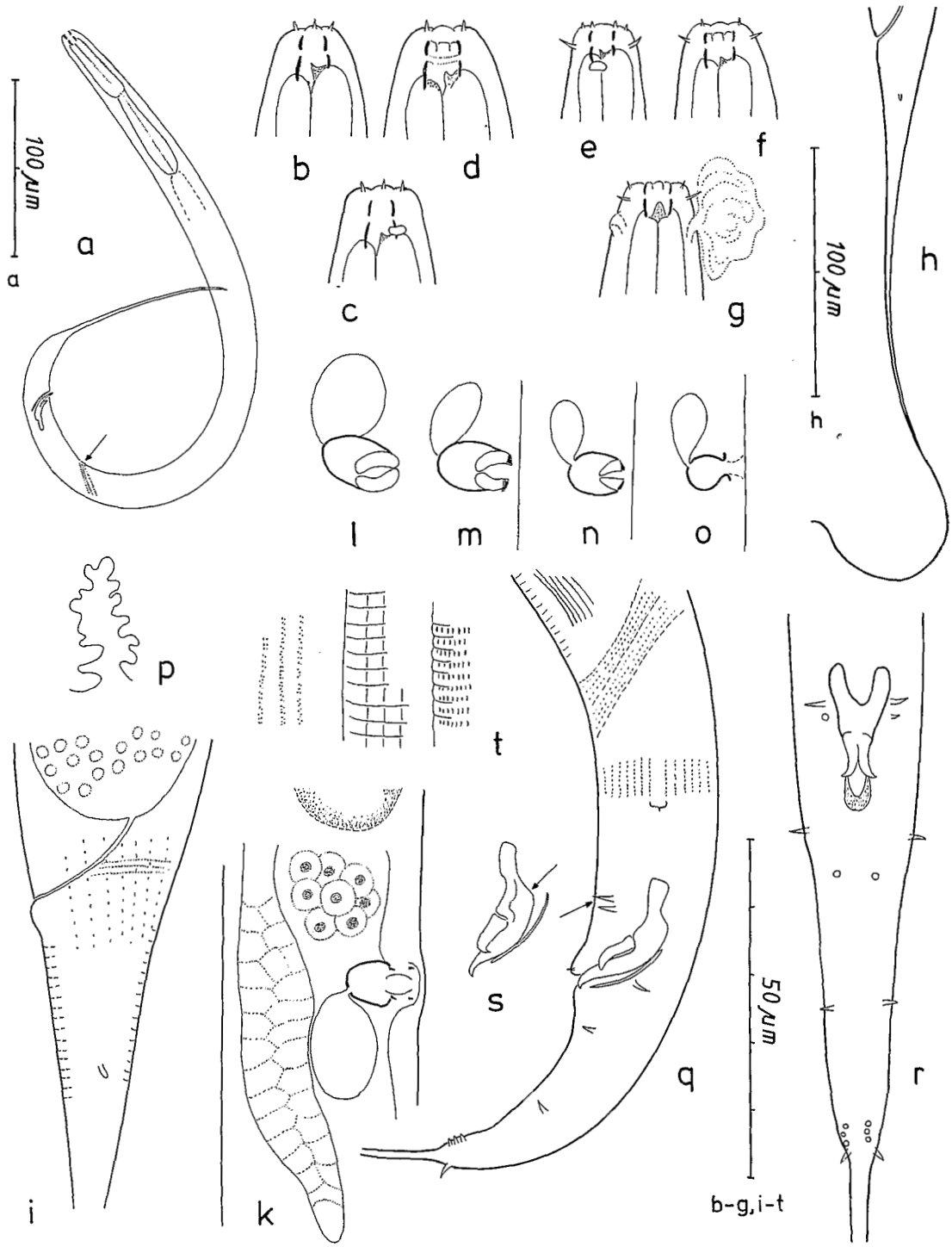

Fig. 1. *Diplogaster coprophilus* n. sp. a : typical posture of dead male; b-d : female anterior end, lateral view; c : showing amphid aperture; d : specimen disintegrating; e-g : male anterior end; e : lateral, showing amphid aperture; f : lateral, specimen disintegrating; g : ventral, gelatinous material of amphid pressed out — Female. h : tail, lateral; i : anal region, lateral; k : vaginal region, sublateral; l-o : different aspects of vaginal complex; p : borderline between ovary and oviduct — Male. q : caudal region, lateral; r : caudal region, ventral; s : spicules and gubernaculum, lateral; t : adult, different aspects of cuticle structure.

TYPE SPECIMENS

Holotype (female) catalogue N° 11022 and paratypes (males, females, immat.) N° 11023 in the collection of the Museum für Naturkunde der Humboldt-Universität (Zoologisches Museum) Berlin, GDR; other paratypes containing males and females deposited at Laboratorium voor Nematologie, Landbouwhogeschool, Wageningen, Holland; and Biologische Bundesanstalt für Land-und Forstwirtschaft (Institut für Nematologie) Münster (W-Germany).

TYPE LOCALITY AND HABITAT

Cow droppings, Berlin (West).

OTHER LOCALITIES

Also in manure from W-Germany (Berlin, surroundings of Freiburg), E-Germany (Wittenberg-Lutherstadt), Austria (near Klagenfurt), France (Esmoulières, Vosges; Bernay, Normandie), Belgium (Damme near Brugge), Great Britain (Chertsey near London, Dartmoor near Tavistock), USA (Springdale, Arkansas), and South Africa (Grahamstown). Sachs (1950) and Weingärtner (1955*a*) found this species in manure in the surroundings of Erlangen (W-Germany).

DIAGNOSIS

Stoma divided into two nearly equal parts, with dorsal tooth; amphids located at level of stoma end; vaginal cavity strongly cuticularized, horseshoe-like, with adhering bladder; spicules fused, extremely complex, without a dorsal projection; dead males typically curved.

IDENTITY

Zullini (1974), and Dassonville and Heyns (1984) were right when they doubted that the species from manure and compost examined by Weingärtner (1955*a*) was identical with *D. bernensis* from freshwater. The drawings of Weingärtner (1955*a*; reproduced in Meyl, 1961) show the typical buccal cavity and spicules (without a proximal projection) of *D. coprophilus* n. sp. She also knew *D. bernensis* from aquatic habitats, but did not realize that the nematodes from both manure and freshwater actually belonged to two different species. Because of its habitat (cow pats) we suppose that *D. coprophilus* n. sp., recorded under the name *D. bernensis*, must have been found by Sachs (1950), too.

ECOLOGY

Typical habitats are droppings of cows and horses. Once it was found in a dung ball of *Geotrupes stercorarius* (Scarabaeidae) buried beneath a cow pat (Berlin). Moreover Weingärtner (1955*a*) recorded it in compost. Sachs (1950) stated that the species (as *D. bernensis*) was rare in old cow pats (more than sixteen days) and that it was restricted to the summer season. However, we found it to be one of the most numerous species in middle-aged cow pats (5-20 days). Individuals could be recorded throughout the year at all locations studied (Sudhaus, 1981; Sudhaus *et al.*, 1988; Rehfeld, 1988; Rehfeld & Sudhaus, in press). During decomposition the species passes through two or three generations. Dauerlarvae are not waving, but must nevertheless be transported by insects to fresh droppings. Only three of 2642 beetles investigates by Sachs (1950) with regard to phoretic nematodes carried *D. coprophilus* n. sp. (two *Aphodius fimetarius*, one *A. subterraneus*, Scarabaeidae). In our studies dauerlarvae of this species were attached to only two of 53 dung beetles from the pasture (*A. fimetarius*, Scarab.; *Sphaeridium scarabaeoides*, Hydrophilidae). Furthermore we could demonstrate that it was transported by *Cercyon haemorrhoidalis* (Hydrophilidae) as well as *Sepsis cynipsea* (Sepsidae) and Sphaeroceridae (Diptera) emerging from samples of field dung. They seem to be particularly adapted to be transported by these small Diptera. Dauerlarvae aggregate close to the pupae and embark the emerging insects, where greater numbers can be observed in the genital segments. At the moment this relationship is studied in detail in our laboratory.

BIOLOGY

D. coprophilus n. sp. is a bisexual species, where males and females occur in nearly equal numbers. Altogether 47.7 % of 11 521 adults were males (data from Freiburg and Berlin). In the course of population development the sex ratio varied from 37-55 % males in samples with more than 200 adults. The copulation posture is in " spiral type " (the male coiling around the female; see Sudhaus, 1976) as usual for *Diplogaster* species. The posterior end of male coiled three times in a left spiral in relation to the female orientation. In one uterus maximally two fully developed eggs can be seen. During the studies on succession in cow pats in Berlin 3 225 females were checked : 66 % had none, 22.8 % one egg, 9.3 % two eggs, 1 % three eggs, 0.7 % four eggs and one specimen six eggs in their uteri. The anterior uterus contained 54 % of the 1 519 eggs, so that this branch seems to be somewhat more active in egg production.

***Diplogaster bernensis* Steiner, 1914**

(Fig. 2 a-m)

= *Diplogaster (Paradiplogaster) bernensis* Steiner, 1914 (Hirschmann, 1952).
= *Diplogaster (Paroigolaimella) bernensis* Steiner, 1914 (Weingärtner, 1955).
= *Diplogaster bodamicus* Micoletzky, 1922 (Fig. 2 n-v).

Table 2

Diplogaster bernensis Steiner, 1914
Dimensions in µm (living specimens, heat relaxed, means in brackets).

	Females	*Males*
n	11	10
length	658-1 339 (827)	638-910 (766)
width	23-66 (35)	18-26 (20)
corpus	66-78 (70)	53-73 (64)
pharynx	119-153 (133)	106-135 (124)
tail	109-239 (152)	92-132 (121)
gonad*	168-732 (337)	348-517 (417)
V (%)	45-59 (48.9)	–
spicules	–	22-25 (23)
gubernaculum	–	10-13 (12)
a	17.3-30.8 (24.5)	33.8-40.7 (37.1)
b	5.0-9.3 (6.1)	5.6-6.7 (6.0)
c	4.5-6.8 (5.5)	5.5-7.1 (6.3)

* See Table 1

Measurements

See Table 2.

Description

Adults : Medium sized, slender, of whitish colour. Cuticle annulated and striped by double longitudinal rows of obscure dots, except a 7-11 µm wide lateral field, extending behind phasmids on female tail. Distance of ten annules about 9 µm. Cephalic diameter 11-16 (fem.) resp. 10-13 µm (male), corresponding to 1.7-2 (fem.) resp. 1.8-2.4 (male) times of width of buccal cavity. Anterior end obtuse, six apical sensillae conspicuous, likewise the four sublateral sensillae in the male. Oval transverse openings of amphids indistinct, about one width of labial region behind anterior end, presumably somewhat more developed in male than in female. Stoma only slighgly sexual dimorphic : in female large, nearly as wide as long, about 6-9.5 µm, not clearly divided, whereas in male narrower and divided as in *D. coprophilus* n. sp., 6-7.5 µm long and 5-5.5 µm wide. Distally the twelve pantile-shaped plates more distinct than in *D. coprophilus* n. sp., metarhabdions anisomorphic, dorsally with a small anteriorly directed tooth, subventrally like a rasp provided with several denticles. Corpus length 50-58 % of pharyngeal length, width of median bulb, 12-21 (fem.) resp. 10-14 µm (male), nearly the same as of terminal bulb 12-26 µm (fem.) resp. 10-13 µm (male). Sclerotized cervical pore at 83-101 (fem.) resp. 94-122 (male) % of pharynx length somewhat conspicuous. The backwards running channel becomes visible when the specimen degenerates.

Female : Anterior end to anus corresponds to 1.2-1.8 (mostly 1.7) times distance from anterior end to vulva. The sclerotized vaginal complex nearly identical to that of *D. coprophilus* n. sp., but the " horseshoe " more knobby and not so even, the anteriorly or posteriorly directed vaginal bladder measures 13-17 × 10-11 µm*. Amphidelphic genital branches on right (anterior) and left side (posterior), 97-375 (169) respectively 99-363 (178) µm long, together occupying 25-55 (38) % of body length. Dorsally reflexed portions sometimes pass vulva region, their length about 70-114 % of respective branch. A conspicuously folded " sphincter " between ovary and oviduct. One cleaving egg in the uterus at a time, measuring 41-46 × 16-23 µm, sometimes in an advanced stage of development. Rectum 16-24 (21) µm long, three rectal glands (not observed by Liebermann, 1927), anal muscle visible, ABW 14-29 (19) µm. Tail finely tapering, about 5-11 times ABW long. A granular phasmidial gland striking, its tiny duct opening 37-60 (44) µm respectively 1.9-2.8 times ABW behind anus, about 22-31 (27) % of tail length.

Male : In contrast to *D. coprophilus* n. sp. dead specimens outstretched like females. Single testis on the left (!) side, expanding in 53-57 % of body length. The ventral flexure, 86-135 (111) µm long, occupies 20-32 % of gonad length. Sperm diameter 6.6-7 µm. Distance from centre of ventral insertion of precloacal muscle bands to cloaca 43-60 (53) µm. Arrangement of nine pairs of caudal papillae as in *D. coprophilus* n. sp. Once the first left papilla smaller than the second, whereas the opposite and normal situation on the right side. Distance between cloaca and last papilla 45-66 (61) µm, that is 3-5 times ABW, measuring 12-19 µm. Closely behind papilla 5 the granular phasmidial gland conspicuous. Spicules yellowish brown, shaped as in *D. coprophilus* n. sp. with one difference : a dorsal projection at the beginning of the fusion. Gubernaculum 45-56 % of spicules length.

Identity

The specimens correspond perfectly to the original description by Steiner (1914) based on males only. The dimensions of the body, pharynx and tail and the proximal projection of the spicules separate it distinctly from *D. coprophilus* n. sp. The same holds for the description and drawings of *Diplogaster* (resp. *Paroigolaimella*) *bernensis* male and female by Liebermann (1927), Zullini (1974, 1982), and Dassonville and Heyns

* The functions of these structures are not yet understood. Liebermann (1927) and Zullini (1974) assumed the bladder to be a *receptaculum seminis,* and Zullini (1974) claimed that it " ... appears often filled with spermatozoa... " We cannot confirm this, and the dimensions of sperms make it seem unlikely to us.

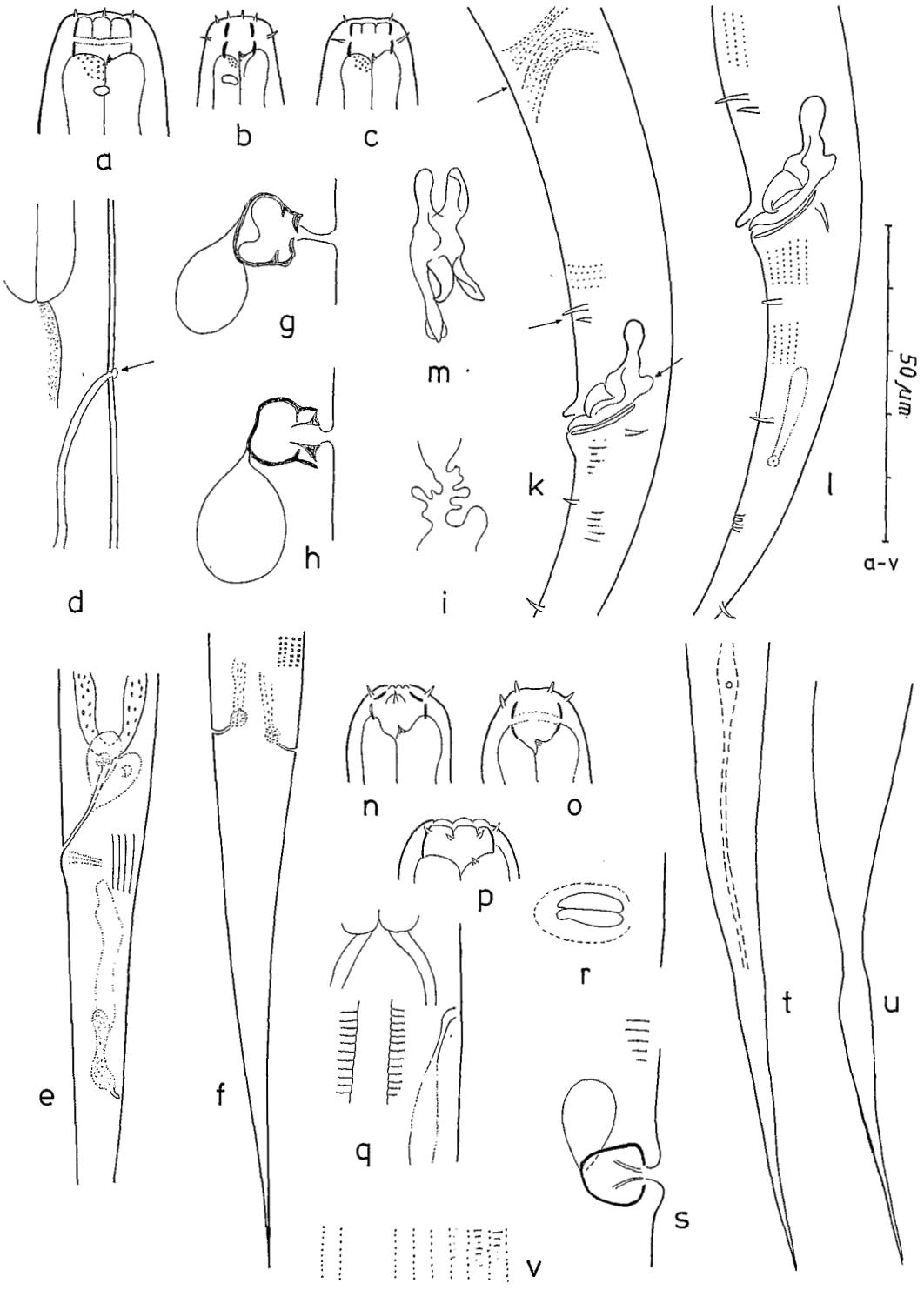

Fig. 2 a-m : *Diplogaster bernensis* Steiner, 1914. a : female anterior end, lateral; b-c : male anterior end, lateral; c : pressed on cover glass; d : male pharyngeal region, lateral, cervical pore pressed out and cervical duct widened in degenerating specimen — Female. e : caudal region, lateral; f : tail end, ventral; g-h : vaginal complex, lateral; i : transition zone between ovary and oviduct — Male. k-l : caudal region, lateral; m : spicules subventral — n-v : *D. bodamicus* Micoletzky, 1922, several different females. n-p : anterior end, lateral; q : pharyngeal region, lateral, showing cervical pore and duct and lateral field; r : vulva lips, subventral; s : vaginal complex, lateral; t : tail end, lateral; u : aberrant tail; v : cuticular pattern, showing smooth lateral field. n, q, s : holotype.

(1984) concerning the form of the vaginal cavity, female tail and spicules as well as the buccal cavity (Zullini, 1974, 1982; Dassonville & Heyns, 1984), typical cervical channel and conspicuous phasmids in the female (Liebermann, 1927), erroneously interpreted as caudal glands. If we just look at the dimensions given, *Diplogaster* (resp. *Paroigolaimella*) *bernensis* of Liebermann, 1928), Pillai and Taylor (1968), Zullini (1977), and Andrássy (1984) correspond to the species in question. On the basis of informations about the habitat, we assume that Hirschmann (1952), Weingärtner (1955, *partim*, " aquatic ", see above), Weninger (1964, 1971), Dozsa-Farkas (1965), Zullini (1975, 1976*a*, *b*), and Woombs and Laybourn-Parry (1984) also dealt with *D. bernensis*. So we contribute the following data to this species.

Liebermann (1927) was the first who synonymized *Diplogaster bodamicus* Micoletzky, 1922 with *D. bernensis*, and other authors followed her arguments (Schneider, 1939; Meyl, 1961; Zullini, 1974, lapsus in the latter case : *D. bodanicus;* Dassonville & Heyns, 1984, implicitly). However, Paramonov (1952) treated it as a valid species, Goodey (1963) declared it a *species inquirenda*, and Andrássy (1984) stated that it was identical with *D. rivalis* (Leydig, 1854). To clarify the status of *D. bodamicus*, from which only females were described and which was never found again, we studied the type slides (Nos. 8848 and 8849 in the Museum für Naturkunde in Berlin, GDR), containing five females (the sixth female was not found). The anterior end of the holotype (on No. 8849) (Fig. 2 n) was correctly depicted by Micoletzky (1922, Fig. 2). Our own measurements also correspond very well with those given by the author and fit the dimensions of *D. bernensis*. The only differences are : a longer pharynx in one case (167 µm), the " c " ratio could reach the value 8.1, and phasmids open at 37-43 % of tail. In one female the tail is swollen like a knot near the tip (Fig. 2 u). All other features agree with those of *D. bernensis*, in particular we could observe the following : plates in distal part of stoma (Fig. 2 p), pointed tooth on dorsal metarhabdion, conspicuous cervical channel (Fig. 2 q), and typical vaginal complex with a bladder adhering to a sclerotized vaginal cavity (Fig. 2 r, s). The taxonomic significance of the latter was not realized by Micoletzky (1922), who only wrote (p. 509) " vulva chitinized ". The distance from the anterior end to the anus corresponds to constantly 1.7 times the distance from the anterior end to the vulva. So there can be not doubt about the conspecificity of *D. bodamicus* and *D. bernensis*.

According to the measurements, shape of stoma, and spicules with a dorsal projection *Paroigolaimella anomala* Gagarin, 1977 from fresh-water is identical with *D. bernensis*. But the description of Gagarin (1977) shows discrepancies, so that we hesitate to synonymize it : male papillae 1 and 2 widely spaced, existence of a vestigal bursa associated with papillae 6-8, spicules smaller (only 16-18 µm long), their ventrolateral claws not drawn, gubernaculum relatively longer and forked. Some differences may stem from errors of observation [e.g. the drawing of the spicules resemble closely that of Liebermann (1927) for *D. bernensis*], but we cannot ignore subtleties of the description. We regard *Diplogaster anomalus* (Gagarin, 1977) n. comb. as *species inquirenda.*

Comparison of *D. coprophilus* n. sp. and *D. bernensis*

Both species are unique among Diplogasteridae in the complex structure of the spicules and the vaginal complex. Due to these peculiarities both species have been confused up to now. The main distinguishing characters are shown in the figures (shape of buccal cavity, form of vaginal complex, dorsal projection of spicules in *D. bernensis*). Granular phasmidial glands and cervical pore are more conspicuous in *D. bernensis*, and there is no overlap in some dimensions (length of corpus and pharynx and c-ratio in both sexes; position of vulva; length of reflexed part of testis; distance between cloaca and last caudal papilla) or nearly no overlap in others (distance between oblique muscles and cloaca; length of spicules and male tail, which is more filiform in *D. coprophilus* n. sp.). Whereas the amphids are located at level of stoma end in *D. coprophilus* n. sp., they are in a more posterior position in *D. bernensis*. Only *D. bernensis* exhibits " non-locomotive movement "; only in *D. coprophilus* n. sp. dead males are typically curved.

Distribution

The redescription of *D. bernesis* is based on a population isolated from mud of a brook near Traben-Trarbach (Mosel, FRG). Moreover we found the species in Freiburg and Sasbach (Kaiserstuhl) in polluted ditches together with *Rhabditis punctata* Cobb, 1914. Further records came from Germany (Lake Constance in Bregenz, as *D. bodamicus* Micoletzky, 1922; Dummetsweiher, Pegnitz, and Schwabach, near Erlangen : Hirschmann, 1952; Weingärtner, 1955*a*); Hungary (Budapest : Dozsa-Farkas, 1965); Czechoslowakia (Cakovice : Liebermann, 1927; Moldau near Prag : Liebermann, 1928); Austria (Traiskirchen : Weninger, 1964, 1971); Switzerland (Near Bern : Steiner, 1914); Italy (river Po at Trino Vercellese and near Caorso, and the tributary river Chiavenna : Zullini, 1974, 1975; river Seveso between Como and Milano : Zullini, 1976*a*; near Milano : Zullini, 1976*b*, 1977); England (Caton and Carnforth, Lancashire : Woombs & Laybourn-Parry, 1984); USA, Illinois (Urbana : Pillai & Taylor, 1968); and South Africa (Skinnerspruit, Pretoria : Dassonville & Heyns, 1984).

Ecology

Typical habitats are mesosaprobic and polysaprobic

waters. It was mainly found in moderately and highly polluted rivers (Liebermann, 1928; Hirschmann, 1952; Zullini, 1974, 1976; Schiemer, 1975), occurred commonly in trickling filters and effluents of waste treatment plants (Weninger, 1964, 1971; Pillai & Taylor, 1968; Zullini, 1976*b*, 1977; Woombs & Laybourn-Parry, 1984), in a sewer (Steiner, 1914), a sewer pond of a sugar factory (Liebermann, 1927), in moss and algae on a quay (Micoletzky, 1922), and sporadically on the shores of ponds (Hirschmann, 1952). The species was frequently collected among periphyton, rarely within muddy sediments (Zullini, 1974, 1975), commonly in " *Sphaerotilus*-Aufwuchs " and slime on the rocks which form filter beds (Weninger, 1964, 1971; Pillai & Taylor, 1968), once in large quantities in flooding *Leptomitus lacteus* (Hirschmann, 1952). It was also found in water from an underground source in Urbana (Pillai & Taylor, 1968) and in tap-water in Budapest (Dozsa-Farkas, 1965).

A typical behaviour of this species (in contrast to *D. coprophilus*) is the intensive " non-locomotive movement " (Anortbewegung) when disturbed in water. This habit has convergently evolved in *Rhabditis punctata*, which lives in the same habitat, and several nematodes of seaweed deposits on the shores (Sudhaus, 1976). We can interprete this behaviour as an adaptation that prevents becoming drifted away in running waters. *D. bernensis* is bacteriophagous. Once the intestine was filled with *Beggiatoa*. The nematodes could be cultured on agar plates with various bacteria as food source (Hirschmann, 1952; Pillai & Taylor, 1968; Woombs & Laybourn-Parry, 1984; own experience). Once established this species attained large numbers. It reproduced between 15 and 30 °C, whereas hatched larvae failed to mature at 10° and 32 °C, and eggs died at 35 °C (Pillai & Taylor, 1968). In the population studied by Woombs and Laybourn-Parry (1984) a continuous life-cycle was maintained at 10 °C, and juveniles transferred to 5 °C were able to reach maturity, but did not reproduce.

Biology

The species reproduces bisexually. Males and females occur approximately in a 1:1 ratio. Copulation takes place in the " spiral type ", once in a right spiral. According to Pillai and Taylor (1968) the copulation lasted 10 to 30 min, viable eggs were laid 6 to 8 h after insemination, at varying intervals with 20 min the shortest interval recorded. On average 30 eggs were laid during the first day and less than five eggs on the fourth day. During one week a single female laid 80 to 90 eggs. Reproductively active females had one or two eggs in their uteri. Usually they were laid uncleaved. The fusion of egg and sperm nuclei occurred after oviposition (Pillai & Taylor 1968). However, Micoletzky (1922, as *D. bodamicus*) declared the species to be " viviparous " as he found a female containing eight eggs and embryos (on his slides six juveniles within the eggshells in one female can be seen). Liebermann (1927) also reported " often ripe eggs and embryos within the uterus ", and after Zullini (1974) " in some females embryos may be seen in advanced developmental stage ". According to Pillai and Taylor (1968) generation time varied from 46-48 hours at 30 °C to 90-100 hours at 15 °C. Progeny of five females averaged about 18 000 after ten days at 20 °C.

***Diplogaster affinis* n. sp.**

(Fig. 3)

= *Diplogaster* sp. I *apud* Sudhaus, 1981 (Fig. 8); Sudhaus *et al.*, 1988.

Measurements

See Table 3.

Description

Adults : Of medium size, slender. Cuticle 0.4-0.5 µm, wide, with fine longitudinal and transverse striae, under high magnification resolved into fine points. Distance of ten annules about 8-11 µm. Width of labial region 11-12 (fem.) resp. 10-12 µm (male), corresponding to 2.4-3.2 times diameter of buccal cavity. Six bluntly rounded lips carrying fine apical sensilla, additionally four sublateral ones, in the male conspicious. Rather large amphid opening at level of stoma end, oval shaped, largest diameter 4.7 µm. Mouth cavity large, with parallel walls in posterior part; anterior rhabdions small, oblique, obviously subdivided into small bars, only seen once. Stoma length 5.5-7.5 (6.2) µm, width 3.6-4.5 (fem.) resp. 3.6 µm (male). Posterior rhabdions dorsally shortened, dorsal tooth very prominent; dorsal pharyngeal gland terminating in this region. No structures observed on subventral compartments. Anterior part of pharynx (corpus) 44-50 % of total pharynx length. Width of median bulb 14-16 (fem.) resp. 12-13.5 µm (male), of terminal bulb 13.5-17 µm (fem.) resp. 12-13 µm (male). Cervical (excretory) pore at 112-118 % of pharynx length.

Female : Dead specimens outstretched and often typically bent ventrally in vulva region. Vulva lips projecting, each carrying minute sensillae. Gonads amphidelphic, together occupying 36-51 (43 %) of body length. Anterior branch right of intestine, 150-243 (196) µm long; posterior branch on left side, 161-234 (192) µm long. Dorsal flexures surpassing vulva region considerably, in two cases even the opposite ovary, so that posterior flexure nearly reached pharynx end. In some females posterior flexure was reflexed once more anterior to vulva. Uterus serving as *receptaculum seminis;* sphincter between oviduct and uterus conspicuous; one to five eggs in each uterus, deposited

Table 3

Diplogaster affinis n. sp.
Dimensions in µm (living specimens, heat relaxed, means in brackets).

	Females	*Males*	*Ensheathed dauerlarvae**
n	10	10	10
length	766-1 086 (920)	473-839 (652)	288-350 (318)
width	37-62 (48)	20-35 (26)	13-17 (15)
corpus	38-44 (40)	35-38 (37)	39-44 (41)
pharynx	79-100 (88)	72-83 (77)	76-92 (81)
tail	156-227 (209)	88-122 (101)	85-119 (104)
gonad**	326-471 (393)	263-565 (427)	11-15 (12)
V %	38.6-43.6 (42)	–	–
spicules	–	19-23 (21)	–
gubernaculum	–	12-15 (14)	–
G %	–	–	42-48 (45)
a	17.3-23.5 (19.6)	16.5-29.9 (23.9)	18.8-22.9 (21.1)
b	9.1-12.1 (10.5)	6.5-10.7 (8.5)	3.5-4.2 (3.9)
c	3.8-4.9 (4.1)	4.7-7.3 (6.5)	2.7-3.6 (3.0)

* Larvae ensheathed : data on body length and tail length include the cuticle of the J2, which forms the sheath. Gonad length means length of gonad primordium; instead of vulva in % body length from the anterior end the position of the gonad primordium is given (= G %).
** See Table 1.

in an early stage of development. Egg dimension 46-56 × 21-30 µm. Vulva spherical. Length of rectum 12-16 µm, 1.1-1.5 times ABW. Rectal glands as usual. ABW 17-24 µm. Tail long and filiform corresponding to 8-12 ABW; phasmids 14-23 (20) µm behind anus, corresponding to 1-1.5 ABW, i.e. at 9-11 % of tail length.

Male : Single testis comprising 56-71 % of body length; the ventral, sometimes lateral or even dorsal flexure measuring 61-85 (77) µm, i.e. 17-23 % of length of gonad. Diameter of spherical sperms 3-4 µm. Tail with nine pairs of papillae, six posterior to cloaca. Arrangement : see Fig. 3 n, o. Papilla no. 3 laterally adcloacal, not easily visible. In one male 1st papilla was anterior to spicule knob. Unfortunately this aberrant specimen was figured by Sudhaus (1981, Fig. 8 b). In another case only a small space between papillae 1 and 2 (Fig. 3 m). Spicules yellowish, separate, proximally knobbed, widest region on shaft, distally tapering to a fine point; ventrally arcuate, the tangent on dorsal flank forming nearly a right angle with the gubernaculum. Gubernaculum not so tight to spicules, proximally boat shaped, distally straight, not bifid, 56-71 % of spicules length (measured as chord). Tail thread 1.5-3 times the distance between cloaca and last caudal papilla.

Dauerlarva : Outer cuticle of ensheathed dauerlarvae with fine longitudinal and transversal stria. Moulted J3, as usual in *Diplogaster*, exhibiting an oily surface. Anterior end rounded; width in lip region 5-6 µm; openings of amphids behind lips conspicuous; corpus 51-53 % of pharynx length; cervical pore moderately developed, 58-74 µm from anterior end, corresponding to 71-87 % of pharynx length; cardia contains a viscous material (Fig. 3 p); gonad primordium 11-15 µm long; anus hardly observable; ABW 9-11 µm; tail of J2-cuticle 9-13 times ABW; tail of J3 within the sheath 45-50 (47) µm long, 40-56 % of J2 tail length, or 4-5.5 ABW; phasmids 9-13 µm behind anus, at 19-27 % of corresponding J3 tail length. Pharynx lengths of dauerlarvae and adults are nearly identical as in *D. coprophilus* n. sp.

Type designations

Holotype (female) catalogue N° 11024 and paratypes (males, females, immat.) N° 11025 in the collection of the Museum für Naturkunde der Humboldt-Universität (Zoologisches Museum) Berlin, GDR; other paratypes containing males and females deposited at Laboratorium voor Nematologie, Landbouwhogeschool, Wageningen, Holland; and Biologische Bundesanstalt für Land- und Forstwirtschaft (Institut für Nematologie) Münster (W. Germany).

Type locality and habitat

Cow droppings, Berlin (West).

Other localities

The species was common in cow pats from Germany (Freiburg, Berlin), England (London-Chertsey) and USA (Fulton, Missouri).

Diagnosis

Stoma large, with parallel walls; dead females almost bent ventrally in vulva region; dorsal flank of spicules and gubernaculum nearly in right angle.

Ecology

It is typical for an early phase of decomposition (cow pats three to seventeen days old) and runs through few generations (Sudhaus, 1981; Sudhaus *et al.*, 1988). Dauerlarvae are waving, often adhering to one another in bundles of up to 97 individuals. They were found to be phoretic on *Aphodius fossor* (Scarab.) and *Sphaeridium bipustulatum* (Hydroph.). Because of its wide stoma the species was supposed to be predacious (Sudhaus, 1981). Up to now we could not substantiate this assumption. *D. affinis* n. sp. could be cultured on cow dung in the absence of any other species of nematodes, and adults were observed to ingest bacteria (Fig. 3 h).

Biology

The species is bisexual. When data from all studies of succession are summed up the sexual index is 56 % males (n = 275). From 494 nematodes which descended

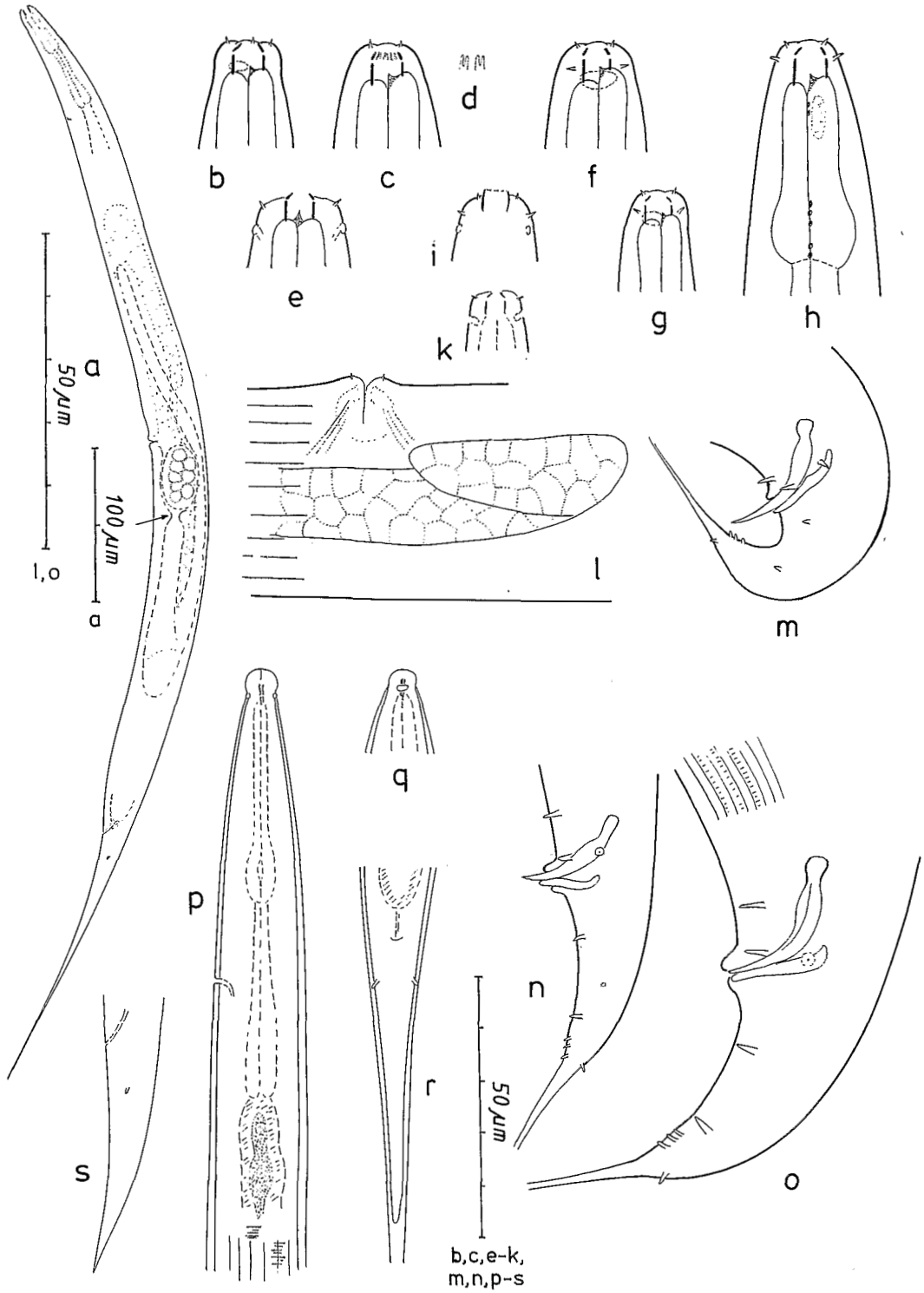

Fig. 3. *Diplogaster affinis* n. sp. a : entire female, lateral; b-c : female anterior end, lateral; b : showing amphid aperture; c : showing partitioning of the anterior mouth part; d : section of these anterior mouth structures; e : female anterior end, ventral, disintegrated, showing the amphids; f-h : male anterior end, lateral; f, g : showing amphid aperture; h : pharynx containing ingested bacteria; i, k : male anterior end, ventral, showing amphids; i : stoma and amphids pressed out; l : female vulva region, lateral, showing gonad flexure; m-o : male caudal region, lateral; m : aberrant 1st papilla; p-r : ensheathed J3; p : anterior region, lateral; q : anterior end, ventral; r : tail region, ventral; s : moulted J3 tail end, lateral.

from a single *Aphodius fossor* 46 % were males. Copulation posture " spiral type ", once in a left spiral. Each uterus contains up to five eggs at a time, sometimes developed up to an 8-cell-stage. The species is oviparous. In the succession studies in Berlin, 37 females contained two or three eggs on average, equally distributed over both genital tracts.

Comparison of *D. affinis* n. sp., *D. coprophages* and *D. micrurus*

The new species is closely related to *Diplogaster coprophages** de Man, 1876) (= *D. magnibucca* Bovien, 1937) and *Diplogaster micrurus* Weingärtner, 1955** (= *D. microcercus* Weingärtner, 1955). The main differences between these three species are shown in Fig. 4. In *D. coprophages* the buccal cavity is extraordinarily wide and barrel shaped (" globular ", Bovien 1937), the notches of the anterior part are distinct, the rasp plates of the subventral metarhabdions are conspicuous. In contrast, the stomata of *D. affinis* n. sp. and *D. micrurus* have parallel walls and the notches and rasp plates are weakly developed; in *D. affinis* n. sp. both features are hardly visible. Usually the diameter of the mouth is larger in *D. micrurus* than in *D. affinis* n. sp. if specimens of the same sex and from the same sample are compared, but this difference is not absolute. The males differ in arrangement of precloacal papillae, shape of gubernaculum and to some extent shape of spicules. The phasmids in *D. coprophages* and *D. micrurus* (usually described as papillae) are distinct between the 4th and 5th caudal papillae, but hardly visible in *D. affinis* n. sp. The arrangement of the three precloacal papillae is similar in *D. coprophages* and *D. affinis* n. sp., whereas in *D. micrurus* papilla no. 3 is shifted anterior from the level of no. 2 to the level of no. 1. Apart from the short tail thread of the male this is the main diagnostic feature of *D. micrurus*. In this species the length of the tail thread corresponds to 1.1-1.8 times the distance between the cloaca and last caudal papilla, that is somewhat longer than figured by Weingärtner (1955*a*). In males of *D. coprophages* and *D. affinis* n. sp. the tail thread is about two times as long as that of *D. micrurus*. Furthermore, *D. micrurus* can be distinguished by the proximally boat shaped, pointed gubernaculum. Typically, and in contrast to the other species, the gubernaculum in *D. coprophages* ends distally in two slightly dorsally curved spines. The longitudinal striation of the cuticle is much more distinct in *D. coprophages* and *D. micrurus* than in *D. affinis* n. sp.

Locations, habitats and ecological behaviour of *D. coprophages* and *D. micrurus*

D. coprophages is typically found in dung. De Man (1876) found it in cow pats near Leiden (Holland). Later records are from Denmark (Lyngby near Copenhagen) in cow dung (Bovien, 1937), Poland (Greiffenstein, Mühlseiffen) in dung of cows and horses (Paesler, 1946); Austria (Admont) in 2-40 days old cow pats (Paesler, 1946; Gunhold, 1950; Franz & Gunhold, 1954); W-Germany (Erlangen) in 6-46 days old cow pats (Sachs, 1950; Weingärtner, 1955*a*), dung piles (Weingärtner, 1955*a*), in the zoo in manure of fallow-deer, elephant and camel (G. Osche, archives), and in dung balls of the scarabaeid *Geotrupes* (Sachs, 1950); and in Italy (Ischia) in faeces of rabbits (Meyl, 1954). Furthermore, the species is said to have been observed in freshwater : in Italy (Ischia) in the sediment of a brook (Meyl, 1953) and in Hungary (Budapest) in drinking-water (Dozsa-Farkas, 1965). We are not convinced, that the identification of the species was correct in these cases. Additionally, Andrássy (1984) states that it was recorded from Czechoslovakia, Great Britain and Zaire.

We observed *D. coprophages* regularly in cow pats and once in fresh dung on a dung pile in W-Germany (Berlin; Osnabrück; Utzenfeld, Black Forest; Freiburg); Austria (Gössenberg, Steiermark); Spain (Torremolinos) and Australia (Ingleburn near Sydney). It is a very typical inhabitant of cow pats, occurring over several stages of decomposition (4-46 days). The waving dauerlarvae are transported by various dung beetles (Scarabaeidae, Hydrophilidae, Staphylinidae, Histeridae; a species list is given by Sachs, 1950). We observed it several times attached to *Aphodius fimetarius, A. fossor, Onthophagus coenobita, Sphaeridium scarabaeoides* and *S. bipustulatum*. The adults are carnivorous and feed on smaller nematodes, including their own juveniles, as already observed by Bovien (1937) and Sachs (1950). Therefore it is possible to rear this species on cow dung in the absence of any other species of nematodes. Bovien (1937) often found the intestine " to be stuffed with large living flagellates " that were obviously not digested.

Weingärtner (1955*a*, *b*) described *D. micrurus* from Erlangen (FRG), but did not mention the habitat. We found it in cow droppings in W. Germany (Berlin, Freiburg), Jugoslavia (Rovinj), Australia (Adelaide), USA (Springdale, Arkansas), and South Africa (Grahamstown). Additionally it is claimed to have been observed in mushrooms in the Moscow region (Sumenkowa, 1963). We believe that it is typical for manure. Adults were recorded in four to fourteen days old cow pats (Sudhaus, 1981; Rehfeld, 1988). Dauerlarvae were

* Andrássy (1984) takes the ending of the epithet to be a " lapsus ". We don't think so, because de Man (1876) used this manner of writing at two places and repeated it later (1884).

** Mostly " Weingärtner in Meyl, 1956 " is cited as author. This is because the publication of Weingärtner (1955*b*) has been overlooked. This species is not identical with *D. coprophages*, as Andrássy (1984) speculated.

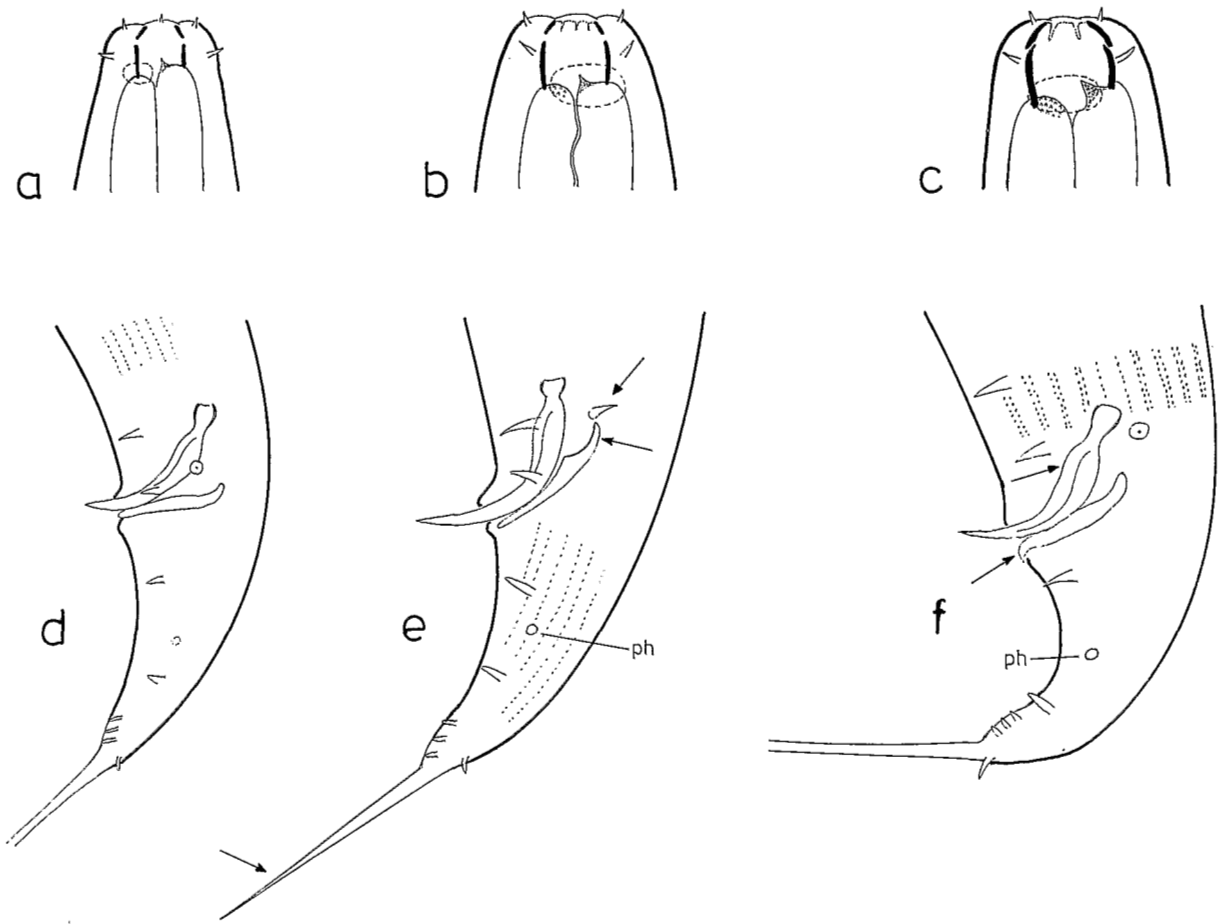

Fig. 4. Comparison of anterior and posterior end of males of *Diplogaster affinis* n. sp. (a, d), *D. micrurus* Weingärtner, 1955 (b, e) and *D. coprophages* de Man, 1876 (c, f), lateral views. ph = phasmids.

transported by coprophilous beetles (*Aphodius fossor, A. fimetarius, Sphaeridium scarabaeoides,* and one species of Histeridae). We observed adults of both sexes feeding on small nematodes. Nonetheless it was possible to culture the species on mere cow dung, possibly because of cannibalism.

It could be shown that *D. affinis* n. sp., *D. micrurus* and *D. coprophages* coexisted in the same cow dropping. The interesting question arises about the differences in their ecological niches. Our data suggest that they might show different peaks of abundance in the course of substratum decomposition. The width of the buccal cavity increases from early to late successional species (Fig. 4).

Stoma shape and nourishment

The buccal cavities of J4 stages from *D. coprophages* and *D. micrurus* resemble those of adult *D. affinis* n. sp., so that their diet may be very similar (members of the same trophic guild, presumably feeding on bacteria). The last moult of *D. coprophages* and *D. micrurus* leads in one dramatical step to the much wider buccal cavity (Fig. 5, 6), which enables the adults to be rapacious. Possibly these carnivorous stages have yet a mixed diet.

Phylogenetic discussion

Up to now there are quite different opinions on the phylogenetic relationships among the Diplogasteridae. In order to avoid contradictory alternatives in the diagnoses, what we call " *Diplogaster* " is split into about fifteen different genera (Andrássy, 1984). We prefer the use of genera in a broader sense for several reasons. First, there are no objective criteria for categories above the species level. Grouping species into one genus (or subgenus) is therefore only a matter of practical convenience. It should help to manage information on

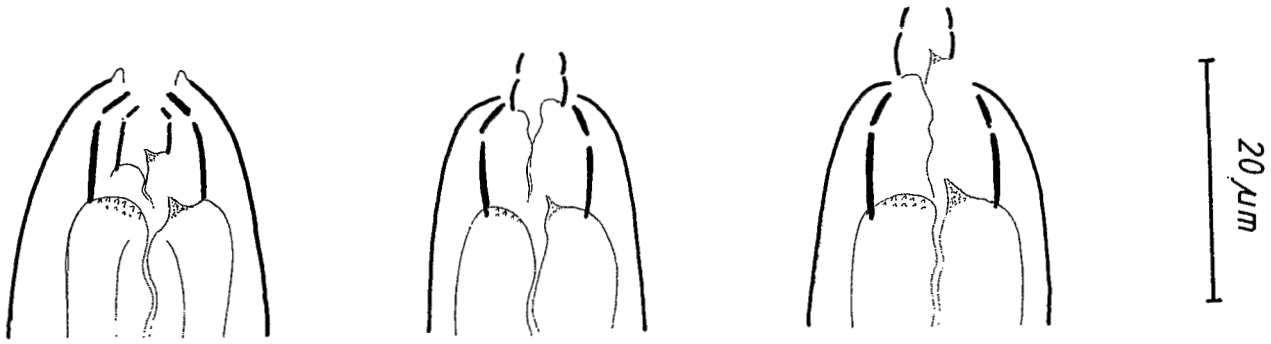

Fig. 5. Final ecdysis of *Diplogaster micrurus*-♀. The sequence shows how the J4 stoma is extruded.

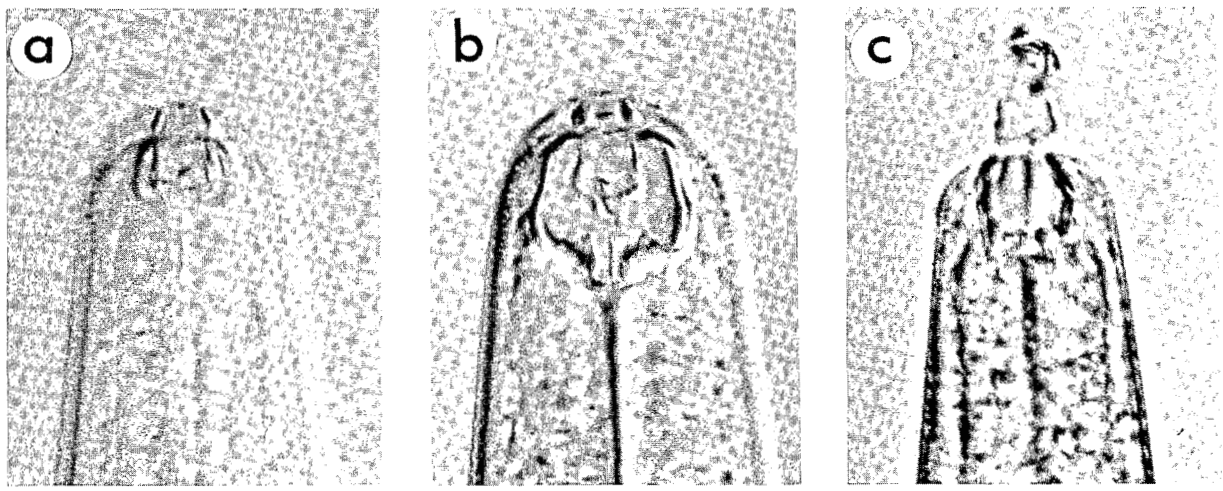

Fig. 6. Final ecdysis of *Diplogaster coprophages*. a : male; b, c : female. Note the differences between the stomata due to ontogenetic " metamorphosis " (J4 and adult stage), sexual dimorphism (a compared with b and c) and variability (b and c).

species and it should make it more easily accessible. Second, genera (or subgenera) should be monophyletic. A prerequisite for this is a phylogenetic (cladistic) analysis, which does not yet exist for *Diplogaster sensu lato*. In this stage it would be arbitrary and premature to maintain a lot of genera and subgenera.

The group of species gathered under the name *Paroigolaimella* Paramonov, 1952 might be monophyletic. This is indicated by the notching of the anterior part of the stoma (cheilostom), which forms twelve plates, and the development of warts or rasp plates on the subventral metarhabdions. These are the only characters that could be hypothesized as apomorphic. We accept the following seven species to belong to this group : *D. affinis* n. sp.; *D. anomalus* (Gagarin, 1977); *D. bernensis* Steiner, 1914; *D. coprophages* de Man, 1876; *D. coprophilus* n. sp.; *D. micrurus* Weingärtner, 1955; *D. paraspirifer* (Zullini & Loof, 1980) n. comb. Since we were not able to discern these specific characters of the stoma in *D. stresemanni* Sachs, 1950 we hesitate to include it in this group at the moment.

It is easily conceived that *D. anomalus, D. bernensis* and *D. coprophilus* n. sp. form a monophyletic group (designated as *D. bernensis*-group). Evolutionary novelties of their stem species were complex spicules, fused for more than half of their length; oblique muscles in posterior region of males; and sclerotized vaginal cavity with a bladder (these muscles and the vaginal complex have to be required for *D. anomalus*). Its sister group is not precisely known.

The species of *Paroigolaimella* live in three different habitats : *D. anomalus* and *D. bernensis* in saprobic freshwater; *D. affinis* n. sp., *D. coprophages, D. coprophilus* n. sp. and *D. micrurus* in manure; and *D. paraspirifer* in compost and dung*. It is possible to reconstruct the original habitat of the common stem species from the

* Our own records of *D. paraspirifer* are from dung piles near Goslar and Würzburg (W-Germany) and a rotting banana stem from Teneriffa (Canary Islands).

habitat distribution of these species. Whatever the sister group of the *D. bernensis*-group may be, nematodes of this outgroup as well as *D. coprophilus* n. sp. from the ingroup share the same habitat, namely manure. So the simplest assumption is that the stem species of the *D. bernensis*-group was adapted to dung, which had been available since large Amniota had evolved. In the course of speciation, the evolutionary line towards *D. bernensis* must have invaded the aquatic habitat. Since only in *D. bernensis* and *D. anomalus* the amphids are located posterior to the buccal cavity (while they lie at level of the dorsal tooth in the other species of *Paroigolaimella*), they must have been shifted backwards. We interpret this as an adaptation to the new environment.

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