

The new nematode species *Poikilolaimus ernstmayri* sp. n. associated with termites, with a discussion on the phylogeny of *Poikilolaimus* (Rhabditida)*

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Summary. A new rhabditid species associated with the termite *Reticulitermes lucifugus* in Corsica is described. *Poikilolaimus ernstmayri* sp. n. is unique within "Rhabditidae" in the position of the secretory-excretory pore at the level of the median pharynx bulb. The shape of the spicules and the presence of only one pair of precloacal genital papillae differentiate *P. ernstmayri* from the otherwise similar *P. piniperdae*. The geographical and ecological distribution of the 6 *Poikilolaimus* species is reviewed, their phylogeny is discussed, and a cladogram on species level based on morphological characters is presented. The stemspecies pattern of *Poikilolaimus* is reconstructed, and 53 apo- and plesiomorphies are listed. A rudimentary bursa and an antidromously reflexed ovary are hypothesized as plesiomorphic characters. Changes of the pattern of genital papillae within *Poikilolaimus* are discussed in the framework of the phylogeny. A new formula to describe and compare this pattern is applied, which includes hypotheses on the loss of particular papillae. The sister taxon of *Poikilolaimus* is unknown. Some interesting similarities with *Myolaimus*, such as the structure of the cuticle, are discussed.

Key words: antidromously reflexed ovary, cladogram, cuticle, formula male genital papillae, Isoptera, *Myolaimus*, *Poikilolaimus*, secretory-excretory system, species description, stemspecies pattern.

During a survey of the nematodes associated with termites (Isoptera) in the Mediterranean area a new species of *Poikilolaimus* was discovered. This species is unusual within the paraphyletic "Rhabditidae" in having the pore of the secretory-excretory system positioned far anterior. This character is found in only a few other related taxa. The new species is described and integrated in the phylogenetic tree of the described species of *Poikilolaimus*. The accumulated morphological, molecular and developmental data may now be utilized to test the hypothesis of Sudhaus (1980) that *Poikilolaimus* and the *Cephaloboides-Diploscapteroides-Rhabditella* clade are sister groups.

DESCRIPTION

Poikilolaimus ernstmayri sp. n. (Figs. 1; Table 1)

Morphometry. Table 1.

Adults. Of medium length, shorter than 700 μm . Body cylindrical, stout. Body colour grey, but the anterior fifth of the intestine usually appears whitish in reflected light, or dark in transmitted light. This is due to densely packed granules in the gut cells (Fig. 1 K). Well fed worms are not transparent, as the epidermis is filled with depot

* Dedicated to Prof. Ernst Mayr on the occasion of his 100th birthday.

granules along the body extending from median bulb to at least the anus in females (Fig. 1 H) and to level of spicules in males. The stored material obscures many anatomical details. Cuticle smooth, nearly 1 μm thick, loose and inflatable, often forming papilla-like folds at concave parts of the body (Fig. 1 L). The anterior and posterior end of the body can retract into the loose cuticle (Fig. 1 K). Lateral field with two parallel lines at a distance of 1-2 μm , visible from at least the level of the median bulb to one anal body width posterior to anus or cloacal aperture, respectively. Deirids and postdeirids absent. Six lips not offset and not separated. One prominent pointed sensillum on each lip; sometimes traces of sensillae in a second circle detected. Oval amphid openings at level of anterior end of gymnostom; conspicuous in dorsal or ventral view, as are ducts; glandular and sensory complex of amphids can be traced to posterior of stoma (Fig. 1 C). A typical straight rhabditid buccal tube, twice as long as body width in the lip region, about 6-8 times as long as wide, with a pharyngeal sleeve comprising about 55 % of stoma length. Cheilostom inconspicuous. The two parts of the gymnostom can be separated by light microscopy: the process of the posterior cell of the arcade epidermis is frequently filled with granular cytoplasm, so that this part of the gymnostom appears surrounded by a conspicuous ring (Fig. 1 A); sometimes the process of the first arcade syncytium is also granulated. Stegostom proximally slightly expanded; the glottoid apparatus isomorphous but a little anisotropic (Figs 1 A, C: arrows); each sector bears two slightly curved and protruding teeth. Pharynx with median bulb and a characteristic squared or polygonal terminal bulb; diameter of median bulb comprises 73-84 % of diameter of terminal bulb. Corpus encompasses 56-60 % of pharynx length (both measured from anterior end of the body). Corpus intima with very fine transverse striations. Terminal bulb with double haustrulum and a stronger cuticularization at the beginning of the cardia; cardia well developed, opens funnel-like into the intestine. Nerve ring encircles anterior part of isthmus, often close to the median bulb. Pore of the secretory-excretory system unusually far anterior, in the region of the median bulb or even anteriorly of it, the opening conspicuously strengthened, the cuticularized duct very long, in its proximal part strongly winding, on the left hand side (Figs 1 D, E); occasionally, a secretory-excretory gland cell was observed anterior of the terminal bulb; lateral canals extending anterior of median bulb, hardly visible posteriorly.

Females. Vulva opening at midbody, circular or coffee-bean shaped in ventral view (Fig. 1 G), strongly protruding, a small copulatory plug usually present. After processing to permanent mounts the cuticle often bulges into a circular embankment around the vulva opening, never observed in living specimens. A pair of oval granulated vaginal gland cells each situated anterior and posterior of the vulva, measuring 7-9.5 x 5-7.5 μm (Figs 1 F, G: arrows). Gonads paired opposed, the anterior branch right of intestine, the posterior branch situated on the left hand side. Each branch reflexed to the dorsal side, flexures sometimes extend a little beyond the vulva. Gonads antidromous (flexure between growth zone and oviduct); beginning of uterus formed by granular cells; spermatheca not clearly differentiated, sperm also in the uterus close to the vagina. Eggs ellipsoidal, a little longer than body width; not more than 1-2 eggs in each uterus, where only a few cleavages occur. One pseudocoelomocyte distal of the anterior ovary flexure on the ventral side; two pseudocoelomocytes posterior of the posterior ovary flexure on the dorsal side. Rectum a little longer than anal body width, curved; 3 rectal gland cells inconspicuous; posterior lip of anus slightly protruding. Anterior part of tail convex dorsally, slightly concave ventrally; second half of tail conical, tapering. Phasmid openings at 49-60 % of tail length. Tail tip variable, sometimes with one or two small dorsal spines or tiny hooks (Figs 1 H, I). These hooks may serve to anchor the nematode to the substrate or the surface film of water when submersed.

Males. Testis on right side of intestine, ventrally reflexed; in two of more than 40 males the testis was on the left hand side. A ventral pseudocoelomocyte situated anterior of the flexure and another posterior of distal tip of testis. Posterior body end resembles that of female in shape, however, it is slightly cupola shaped with a tail spike bent to the ventral side (Fig. 1 N). This spike is about half as long as tail, dagger shaped; as in females, near the tip often a small dorsal rose-thorn-like projection pointing anteriorly, sometimes with tiny hooks (Figs 1 M, N). A very narrow bursa-like fold present, extending from a little anterior of cloacal opening to the last genital papilla at the base of the spine. Only six pairs of genital papillae (GP) present, grouped as 1/2+2+1, arranged in one subventral line, with exception of GP3 which is situated more ventrally and GP5 which turns to the dorsal side. GP1 very close to the cloacal aperture; GP5 at the beginning

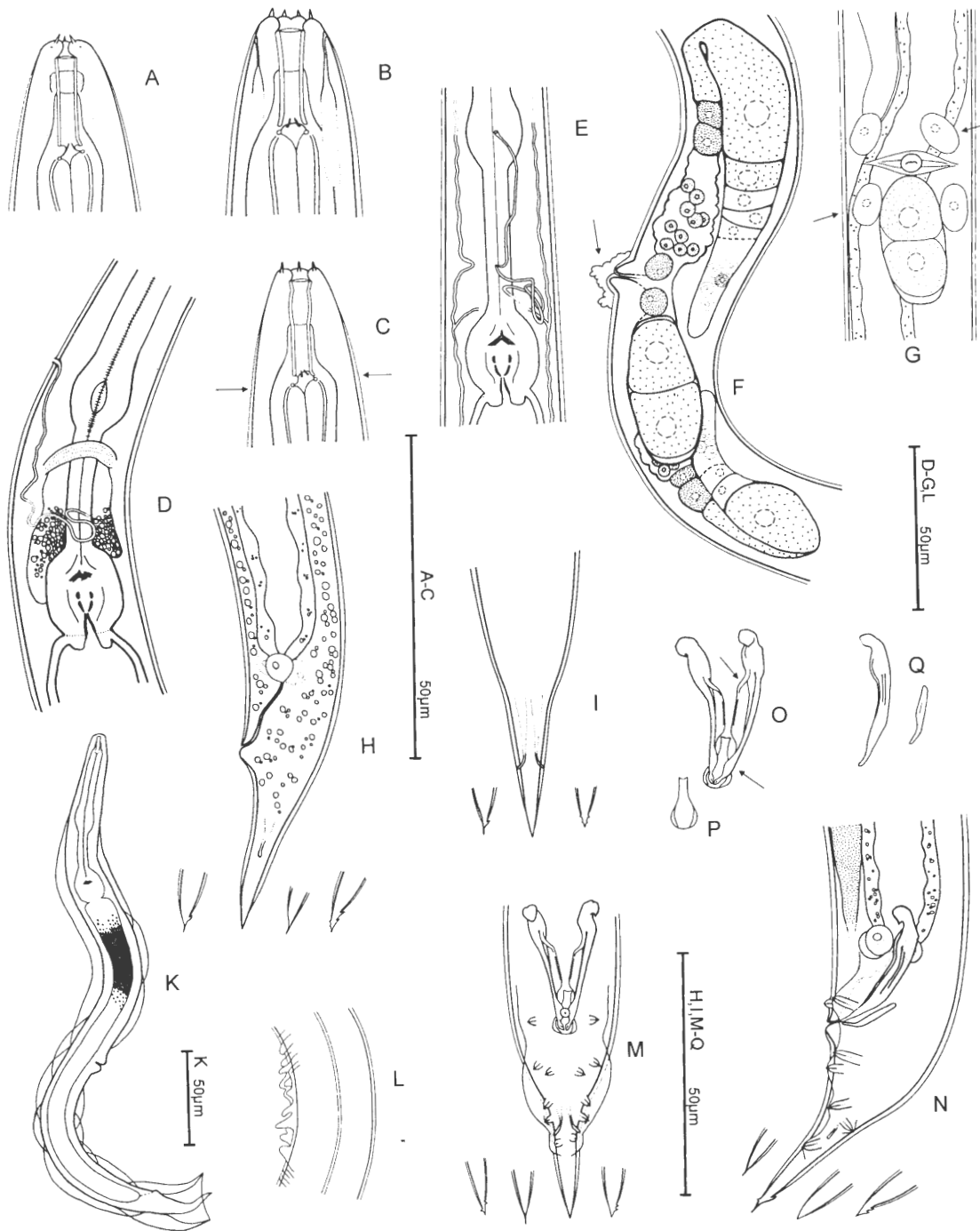


Fig. 1. *Poikilolaimus ernstmayri* sp. n. A-C: anterior end; A: male, lateral; B: female, dorsal; C: female, lateral; D-L: female; D: pharyngeal region, lateral left; E: pharyngeal region, ventral, with focus on secretory-excretory system; F: mid-body region, lateral, anterior gonad with egg moving into the oviduct, uterus with sperm, vaginal glands, vulva with mating plug (arrow); G: vulva region, ventral, with vaginal gland cells; H: posterior end, lateral, and three variations of tail tip; I: tail end, ventral, and two variations of tail tip; K: entire body, lateral, showing inflation of the cuticle and deposits of granules in anterior intestine; L: papilla-like folds of cuticle, and lateral field; M-Q: male; M: posterior end, ventral, and three variations of tail tip; N: posterior region, lateral, with three variations of tail tip; O: spicules and gubernaculum, subventral; P: gubernaculum, ventral; Q: spiculum and gubernaculum, lateral. Arrows point to significant characters mentioned in the description.

Table 1. *Poikilolaimus ernstmayri* sp. n. morphometrics (mean, standard deviation, range; all measurements in μm).

Character	10 ♀♀	10 ♂♂
Body length	584±45 (499–638)	501±44 (424–564)
Maximal body width	38±3.6 (32–43)	28±3.6 (20–32)
Width at lip region	9.4±0.9 (8.6–10.5)	8.1±0.6 (7.6–9.5)
Stoma length	18.8±1.3 (17.1–20.9)	18.5±0.8 (17.4–20.0)
Stoma width	3.1±0.3 (2.6–3.8)	2.5±0.3 (1.9–2.9)
Stegostom (pharyngeal sleeve) length	10.5±1.2 (8.6–12.4)	10.1±0.6 (9.5–11.4)
Pharynx length	153±9.2 (137–165)	146±7.9 (135–163)
Corpus length	90±6.6 (77–99)	85±4.7 (78–94)
Corpus length in % of pharynx length	58±1.2 (56–60)	58±0.8 (57–59)
Median bulb diameter	17.4±1.6 (15.2–20.0)	14.3±0.6 (13.3–15.2)
Terminal bulb diameter	22.3±2.9 (19–28.5)	18.6±1.1 (16.2–20.0)
Anterior end to excretory pore	70±6.5 (60–81)	71.0±4.2 (64–78)
Position of excretory pore in % of pharynx length	46±2.2 (41–49)	49±2.4 (43–52)
Tail length	51±5.1 (41–60)	42±5.2 (33–51)
Anal body width (ABW)	18.9±2.4 (14.3–23.8)	21.6±1.8 (18.1–23.8)
V %	54±1.5 (52–57)	
Total gonad length (from anterior to posterior flexure)	219±35.7 (161–276)	236±28.1 (202–270)
Anterior branch length	104±18.4 (81–135)	236±28.1 (202–270)
Anterior flexure length	99±30.3 (46–157)	49±6.6 (38–59)
Reflexed part in % of anterior gonad branch	95±24.2 (56–131)	20.9±2.8 (17.7–26.1)
Posterior branch length	115±19.2 (80–143)	
Posterior flexure length	89±35.5 (36–150)	
Reflexed part in % of posterior gonad branch	76±23.3 (32.5–125)	
Sperm diameter		4.1±0.2 (3.8–4.3)
Egg length	44±2.2 (41–48)	
Egg width	22.1±1.4 (20.0–23.8)	
Rectum length	22.7±1.4 (20.9–25.7)	
Ratio rectum length / ABW	1.2±0.2 (0.9–1.6)	
Anus to phasmids distance	29.2±2.8 (22.8–33.3)	23.5±3.1 (19–27.6)
Spicule length		28.8±1.0 (27.6–30.4)
Gubernaculum length		10.9±1.9 (8.6–14.3)
Gubernaculum length to spicule length (%)		38.1±7.4 (28.1–51.7)
A	15.4±0.6 (14.7–16.6)	18.3±2.0 (15.9–23.2)
B	3.8±0.1 (3.6–4.0)	3.4±0.2 (3.1–3.8)
C	11.5±0.8 (10.7–12.9)	11.9±0.8 (11–13.8)
d = c'	2.7±0.3 (2.2–3)	2.0±0.2 (1.6–2.3)

Table 2. Formula of genital papillae pattern in *Poikilolaimus*.

	Descriptive	Aligned
Hypothetical for stemspecies	v1, v2, v3 / v4, ad, v5, pd, v6, v7, ph	v1, v2, v3 / v4, ad, v5, pd, v6, v7, ph
<i>P. oxycercus</i>	v1, v2, v3 / ad, v4, pd, (v5, v6), ph	v1, v2, v3 / -, ad, v5, pd, (v6, v7), ph
<i>P. piniperdae</i>	v1, v2 / (v3, ad), v4, pd, ph	-, v2, v3 / (v4, ad), v5, -, -, pd, ph
<i>P. ernstmayri</i> sp. n.	v1 / (ad?, v2), (v3, pd), ph, v4	-, -, v3 / -, (ad?, v5), (v6, pd), ph, v7
<i>P. incisocaudatus</i>	v1 / v2, v3, v4, pd, ph?	-, -, v3 / v4, -*, v5, v6, -, pd, ph?

* - ad presumably overlooked

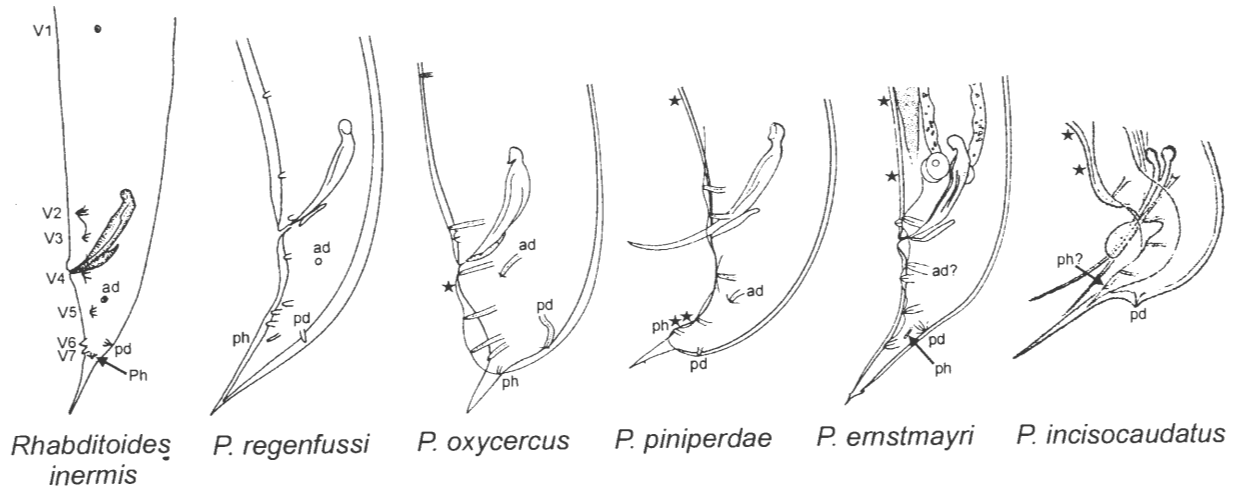


Fig. 2. Comparison of male posterior ends and patterns of genital papillae of *Rhabditoides inermis* and five species of *Poikilolaimus* (figures from left to right designated 2a to 2f in the text). v1–v7 = ventrals, ad = anterior dorsal, pd = posterior dorsal papilla, ph = phasmid, star = position, where the loss of a genital papilla is supposed. (*R. inermis* after Kiontke & Sudhaus 2000, *P. oxycercus* and *P. piniperdae panagrocercus* after Sudhaus 1980, *P. incisocaudatus* after De Coninck 1935. In the figured specimen of *P. oxycercus* v3 unusually appears a little posterior of the cloacal aperture.)

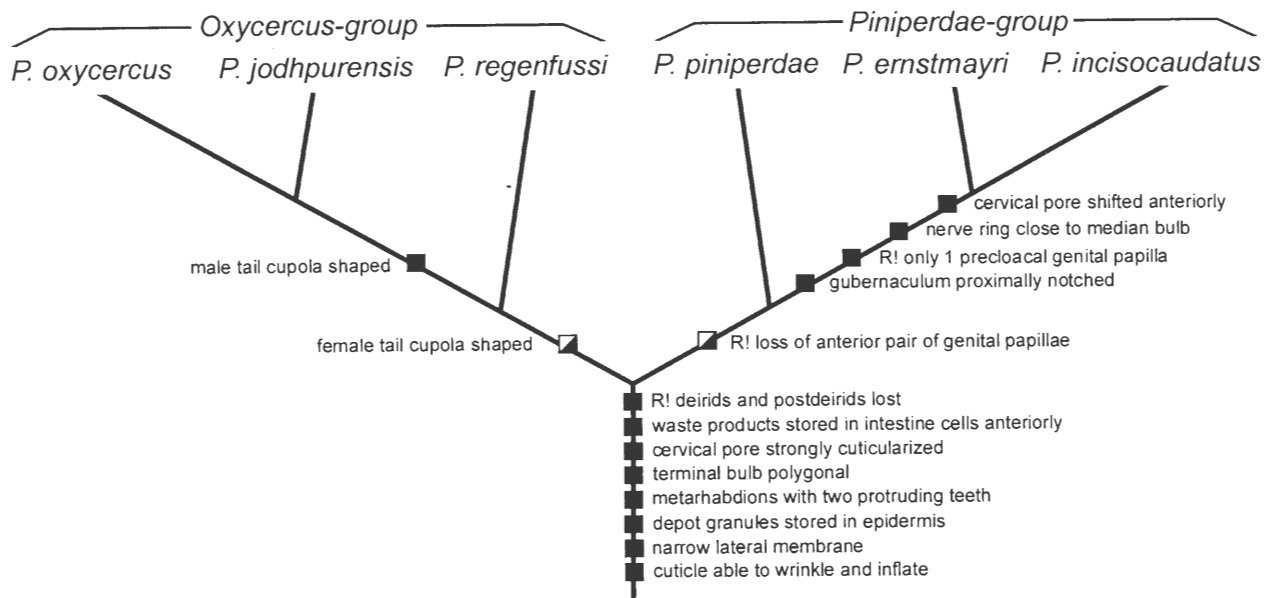


Fig. 3. Cladogram of *Poikilolaimus* species. Black squares = apomorphies; half-filled squares = apomorphies with a lower degree of confidence; R! = losses.

of spike, followed by the laterally positioned phasmid; GP6 located on the base of spike, sometimes two GP6 placed asymmetrically. Given that GP2 is the anterior dorsal papilla (ad) the formula for genital papillae (explained in the section on genital papillae) is

<v1 / (ad?, v2) (v3, pd) ph, v4>

or <v1 / (ad?, v2) (v3, pd, ph, v4)>. In one aberrant male an additional papilla was observed at spicula level anterior of papilla GP1. Posterior cloacal lip more prominent than anterior lip. The median precloacal sensillum sometimes very prominent, at short distance anterior of cloacal opening, it can be mistaken as a genital papilla; postcloacal sensilla not detected. Spicule length about one and a half cloacal body width; pale yellow; separate; slightly curved; capitulum rounded or shaped like a doves head, depending on the view (Figs 1 N, O, Q); blade proximally bulged ventrally, followed by a thin dorsal lamella and a very small ventral lamella near the tip (Fig. 1 O: arrows); both spicules thus forming a tube; terminus rounded like a probe. Gubernaculum parallel to the spicules; narrow in lateral view, slightly bulged midway; in ventral view shaped like a shoehorn, its lateral edges slightly turned up, thus forming a groove; distally blunt, proximally slightly notched (Figs 1 N, P, Q).

Differential diagnosis. *P. ernstmayri* sp. n. can be differentiated from all other described species of "Rhabditidae" by its very long cuticularized duct of the secretory-excretory system, which is proximally strongly winding and opens anterior or at the level of the median pharynx bulb, thus anterior of the nerve ring. Two pairs of granulated gland cells on either side of the vagina are conspicuous as in *P. oxycercus*. *Poikilolaimus ernstmayri* sp. n. is easily differentiated from *P. oxycercus* by a conical instead of a cupola-shaped tail. It is the only *Poikilolaimus* species where the phasmids in males are located anterior instead of posterior of the last pair of genital papillae (for *P. incisocaudatus* this is, however, not really known). Within *Poikilolaimus*, *P. ernstmayri* sp. n. can be confused only with the two smaller species (less than 650 µm body length) that do not have a cupola-shaped tail and exhibit at most 6 pairs of genital papillae (*P. piniperdae* and *P. incisocaudatus*). In contrast to *P. piniperdae*, there is only one pair of precloacal GPs (instead of two pairs) in *P. ernstmayri* sp. n., the buccal tube is always straight, the amphids are not shifted posteriorly, the nerve ring is shifted close to the median bulb, and the spicules have a different shape and are not so slender. *P. ernstmayri* sp. n. is distinct from its

sister species *P. incisocaudatus* in the relatively shorter length of stoma, female rectum, female tail, spicules and gubernaculum as well as in the shape of spicules (Fig. 2).

This new species must also be compared with the undescribed "*Rhabditis* n. sp." of Meyl (1954) that also possesses an anteriorly located secretory-excretory pore at the level of an "extremely weak" median bulb and is similar in body shape and dimensions. However, from the meagre description of only one female this species differs from *P. ernstmayri* sp. n. in the absence of a pharyngeal sleeve, the delicately annulated cuticle, a short rectum (of 3/4 anal body width) and a curiously shaped tail with a pointed spine on a conical socket, the annulations ending on the first third of the spine.

Type locality and habitat. Corsica (France) near Porto-Vecchio in wood inhabited by termites (*Reticulitermes lucifugus*) collected in March 2001 by Prof. H. Schulz-Key. The laboratory strain was designated SB346.

Type designations. Holotype (male, no. 11189) and paratypes no. 11190 deposited in the collection of the Museum für Naturkunde der Humboldt-Universität Berlin, Germany; further paratypes in Biologische Bundesanstalt für Land- und Forstwirtschaft (Institut für Nematologie) Münster, Germany; Naturhistoriska Riksmuseet Stockholm, Sweden; Plant Pathogen Interactions Division, Rothamsted Research, Harpenden, U.K.; Instituut voor Dierkunde, Gent, Belgium; Laboratorium voor Nematologie, Landbouwhogeschool, Wageningen, the Netherlands; USDA, Nematology Laboratory, Beltsville, Maryland, USA; collection of Prof. Sudhaus, Institut für Biologie der FU Berlin, Germany.

Ecology and biology. The new species was found on two occasions in samples of wood with colonies of the termite *Reticulitermes lucifugus* from Corsica. From the first sample (March 2001) the following nematodes could also be isolated: *Rhabdophanes ossiculus* Massey, 1971 (first record from Europe), *Oigolaimella kruegeri* Fürst von Lieven, 2003, *Bunonema* sp., *Panagrolaimus* sp. and *Aphelenchoides* sp. In the second sample (October 2002) *P. ernstmayri* sp. n. lived together with *Oigolaimella* sp. n., *Mesorhabditis spiculigera* (Steiner, 1936), *Oscheius* cf. *dolichura* (Schneider, 1866), *Bunonema* sp., *Cephalobus* sp., *Plectus* sp. and a species of Tylenchida. An association with termites could not be ascertained. Desiccation of the

substratum was not tolerated. Copulation follows the spiral type. Development is slow; juveniles were growing into adults in two weeks (room temperature); isolated females lived for about 40 days; only 2-3 eggs were produced daily.

The species of *Poikilolaimus* Fuchs, 1930 and their geographical and ecological distribution

In this group five described species are included: *Poikilolaimus incisocaudatus* (De Coninck, 1935), *P. jodhpurensis* (Khera, 1969), *P. oxycercus* (de Man, 1895), *P. piniperdae* Fuchs, 1930 and *P. regenfussi* (Sudhaus, 1980). In *P. piniperdae* two subspecies were differentiated: *P. piniperdae piniperdae* Fuchs, 1930 and *P. piniperdae panagrocercus* (Sudhaus, 1980). *Poikilolaimus jodhpurensis* is an inadequately described species. However, it appears from the description that synonymization with *P. oxycercus* is not justified, as Andrassy (1983) did. The differences between these sister species are listed in Sudhaus (1980).

Poikilolaimus oxycercus is cosmopolitan and lives mainly in compost-like substrates, old dung and sewage (Sudhaus, 1980). There are several records of *P. piniperdae* from Germany, Austria and Spain, found in frass of wood inhabiting beetles (Cerambycidae, Curculionidae, Lucanidae, Scolytidae: Sudhaus, 1980). We also isolated it once from wood colonized by termites in Corsica (France). Possibly the "*Poikilolaimus* sp." found associated with Scolytidae in North America by Saunders & Norris (1961) and Massey (1974) also belongs to *P. piniperdae*. From the habitat of this species a phoretic association can be expected, although no records exist. All other species were found only in one place: *P. incisocaudatus* in central Africa (Ruwenzori) under liverwort in a *Carex* swamp (De Coninck, 1935), *P. jodhpurensis* in India in the banks of a sewer (Khera, 1969), *P. regenfussi* in Sumatra in compost-like material (Sudhaus, 1980), and *P. ernstmayri* sp. n. in Corsica (France) in wood inhabited by termites.

The stemspecies pattern of *Poikilolaimus*

Using ingroup comparison a character set of the *Poikilolaimus* stemspecies was reconstructed, the character polarity was assessed by outgroup comparison. (The outgroup is the non-ingroup with respect to organisms and, therefore, encompasses all species that are not representatives of the ingroup.) The characters are listed following the order in the species description. Abbreviations:

a = apomorphic, p = plesiomorphic, np = polarity decision not possible.

- np) body shape cylindrical; body stout, plump
- a) in anterior part of intestine the cells densely packed with (presumably excretory) granules
- a) epidermis densely filled with depot granules
- a) special thick cuticle, unusually loose, inflatable, often forming transverse plaits and papilla-like structures on concave parts of the body during wriggling
- np) cuticle smooth, without inner "punctations" (struts)
- a) two parallel lateral lines forming a narrow lateral field
- a) deirids and postdeirids absent (lost)
- p) six closed lips, not offset, with prominent inner labial sensilla and tiny outer labial sensilla
- np) no cephalic sensilla discernible
- p) amphids open at the base of lips, at the level of anterior end of gymnostom
- p) stoma length two times the width of anterior body end
- p) walls of cheilostom weakly sclerotized
- p) pharyngeal sleeve (and long stegostom) present
- p) glottoid apparatus present
- a) two setose teeth protruding on each sector of the glottoid apparatus
- p) weak transverse ridges in corpus intima
- np) rather weak ellipsoidal median bulb
- a) terminal bulb polygonal
- p) double haustrulum present (posterior to the valves)
- p) nerve ring surrounds isthmus in a median position
- p) H-shaped secretory-excretory system with lateral canals present
- a) pore of the secretory-excretory system very conspicuous, strongly sclerotized
- p) secretory-excretory pore situated just behind nerve ring
- p) vulva median
- np) vulva circular
- p) female gonads paired and opposed
- p) anterior gonad branch on right side of intestine, posterior branch on left side of intestine
- np) female gonad antidromously reflexed (between ovary and oviduct)
- p) ovary flexure extends to vulva or beyond it
- p) only 1-2 eggs in uterus
- p) oviparous
- p) pseudocoelomocytes present distally of ovary flexures (anteriorly on the ventral, posteriorly on the dorsal side)
- p) length of female rectum nearly equal to anal body width

- p) female tail short, about two times anal body width
- np) anterior part of female tail dorsally convex, posterior part conical, tapering
- a) phasmids open at about three quarters of tail length
- a) one-three very tiny hooks or spines near tail tip
- p) testis on right side of intestine
- p) short testis flexure to the ventral side
- p) no appendices at *vas deferens*
- p) one ventral pseudocoelomocyte anterior of flexure and posterior of distal testis tip, each
- p) tail shape in male resembles that of female (anterior part dorsally convex), curved ventrally, with a relatively short conical spike (less than half tail length)
- np) a narrow bursa-like fold connects the genital papillae
- p) nine pairs of genital papillae (GP), three pairs precloacally
- np) the posterior dorsal GPs point to the dorsal side
- np) phasmids terminal, posterior of GPs 9
- np) formula of GPs:
v1, v2, v3 / v4, ad, v5, pd, v6, v7, ph
- p) spicules separate, yellowish, with rounded capitulum, slightly arcuate, terminus pointed
- np) gubernaculum in ventral view shaped like a shoehorn, grooved; in lateral view slipper-shaped; curvature parallel to spicules; about one third the length of the spicules
- p) gonochoristic
- np) copula in spiral type
- p) dauerlarvae do not wave
- np) they unable tolerate desiccation

The phylogenetic position of *Poikilolaimus* is unclear

There can be no doubt about the monophyly of *Poikilolaimus*. About 10 morphological characters are hypothesized to be apomorphic, listed in the stemspecies pattern. Most significant are the special cuticle, the setose teeth of the stegostom, the shape of the terminal bulb, a strongly cuticularized secretory-excretory pore, tiny hooks on the tail tip and the loss of deirids and postdeirids. However, none of the features can be hypothesized with good reasons to be synapomorphic with any other taxon, thus to suggest it as the sister taxon of *Poikilolaimus*.

Nevertheless, some of the derived characters must be discussed comparatively. A very similar cuticle, able to wrinkle and inflate, thus "very loosely fitting to the body" (Goodey, 1929) exists in *Myolaimus* (reviewed by Sudhaus, 1977), a

group of unclear phylogenetic position. This is the only known spectacular character shared by *Poikilolaimus* and *Myolaimus* apart from a polygonal terminal bulb (less significant) and perhaps spiny egg-shells (next paragraph). The inflatable cuticle possibly results from the absence of struts between the layers. Such a loose cuticle might help the nematode to escape attacks from carnivorous nematodes, in addition to the 'vigorous escape reaction' described for *P. oxycercus* by Grootaert *et al.* (1977). Even though the real function of deirids and postdeirids is unknown, it can be speculated that they were superfluous in such a slack cuticle and were completely reduced after this cuticular feature evolved. Deirids and postdeirids were independently lost in only a few other rhabditid taxa, possibly only once in a clade including *Meso-*, *Parasito-* and *Teratorhabditis* (Kiontke *et al.*, unpublished). In *Myolaimus* these sense organs also appear not to exist.

The state of the egg shell – smooth or spiny – can not be established for the stemspecies of either *Myolaimus* or *Poikilolaimus*, as to date eggs with spiny protuberances in these groups are only known from *M. stammeri* (Hirschmann, 1952) and *P. oxycercus*. Convergences are likely, and similarly sculptured egg shells were observed in "*Rhabditis filiformis*" (we question the correct identification of this species) by Chitwood & Chitwood (1950: Fig. 135C) and *Diploscapter coronatus* by Maupas (1900: plate 11, Fig. 10), Chitwood & Chitwood (1950: 181) and Thorne (1961: 460: "Eggs echinulate, but the spines are difficult to observe before deposition"). Spinulation of the outer egg layer occurs also sporadically in species of unrelated taxa like "Plectidae", Mononchidae, Tripylidae, and Physalopteridae (Chitwood & Chitwood, 1950: 180, 181, 183).

A further character that is found in *Myolaimus* and within *Poikilolaimus*, but only in *P. ernstmayri* sp. n., is the anterior position of the pore of the secretory-excretory system and the lengthening of its duct. Outgroup comparison shows that a more posterior position of this pore is the plesiomorphic condition for Secernentea and Rhabditida. Therefore, it follows from hypothesizing the anterior position of the pore to be synapomorphic in *Myolaimus* and *Poikilolaimus* that multiple reversals to a posterior position of the pore must have occurred within *Poikilolaimus*. Such a scenario is unlikely and, therefore, the anterior position of the pore is interpreted here as convergent in *P. ernstmayri* sp. n. and *Myolaimus*. The pore also shifted independently to the anterior

in *Brevibucca*, *Steinernema*, a few species of *Acrobeles* (*A. cylindricus*, *A. ensicaudatus*, *A. mariannae*), in the dubious species *Cephalobus filicaudatus* described by Cobb (1906) and in *Rhabditis* n. sp. of Meyl (1954) mentioned above. In *Caenorhabditis* Wang & Chamberlin (2004) showed that the position of the pore results from the expression of a single gene.

In the last revision, Sudhaus (1980) placed *Poikilolaimus* as the sister group of a clade encompassing *Cephaloboides*, *Diploscapteroides* and *Rhabditella* (see Kiontke, 1999a, Sudhaus & Fitch, 2001). The main arguments for this interpretation were the radial arrangement of genital papillae (posterior dorsal GPs point to the dorsal side) and the small (narrow) bursa which was then hypothesized to be vestigial. This view can not be sustained. In the course of ultrastructural investigations (De Ley *et al.*, 1995) and phylogenetic reconstructions using gene sequence data (Sudhaus & Fitch, 2001) the view on polarity of stoma characters changed, so that the existence of a glottoid apparatus and a pharyngeal sleeve are now hypothesized to be plesiomorphic for Rhabditidae. This also changed the view on the placement of taxa like *Parasitorhabditis* and *Protorhabditis*, in which a glottoid apparatus and a pharyngeal sleeve are missing. Therefore, the existence of a well developed bursa with all rays in line (as found in *Parasitorhabditis* and *Protorhabditis*) in the stemspecies of Rhabditida must be questioned as well (Sudhaus & Fitch, 2001).

According to phylogenetic analyses by K. Kiontke and D. Fitch (personal communication), using sequence data from small and large subunit ribosomal RNA genes and the gene for the largest subunit of RNA polymerase II *Poikilolaimus* is not closely related to *Rhabditella*–*Cephaloboides* (sequence data from *Diploscapteroides* do not exist). A more ancient divergence was suggested (Sudhaus & Fitch, 2001). It is not unlikely that *Poikilolaimus* represents one of the very early branches of Rhabditida. However, the molecular data and the morphological characters revised in this study do not help to identify the sister group of *Poikilolaimus*.

In this context, some developmental characters need to be considered, namely the behaviour of some of the 12 ventral epidermal precursor cells designated P(1-12).p from anterior to posterior between pharynx and rectum in females or hermaphrodites. In *Poikilolaimus oxycercus* and all species of Diplogastridae studied so far, the four cells P(1-4).p anterior and the three cells P(5-

11).p posterior to the three cells P(5-7).p which generate the vulva undergo programmed cell death early in development instead of fusing with the epidermal syncytium like in other species of Rhabditida (Sommer *et al.*, 1999). P8.p does not divide in *P. oxycercus* and Diplogastridae, whereas in other Rhabditida it divides and is a member of the competence group for vulva formation (equivalence group). P8.p also belongs to the vulva equivalence group in *P. oxycercus*, because in ablation experiments it was able to respond to inductive signals and formed part of the vulva (Sommer & Sternberg, 1996), which was also observed in two distantly related species of Diplogastridae (Sommer, 1997). It has been suggested that the epidermal fate of the anterior and posterior Pn.p cells is plesiomorphic in Rhabditida (Sommer *et al.*, 1999). Therefore, it is possible that programmed cell death of these 7 cells and a non-dividing P8.p which fuses with the epidermis are apomorphic for a clade that includes *Poikilolaimus* and Diplogastridae, though convergences can not be ruled out. Apoptosis of P(1-4).p in combination with other cell fates of the posterior Pn.p cells as observed in *Halicephalobus*, *Panagrolaimus* and *Turbatrix* is assumed to have evolved independently, because in *Panagrellus redivivus* within the same clade these cells behave as in "Rhabditidae" (Sommer *et al.*, 1999).

The antidromously reflexed female gonad and the absence of a true bursa in the stemspecies of *Poikilolaimus*

Certain characters that were accepted as secondary transformations based on the phylogenetic position of *Poikilolaimus* assumed by Sudhaus (1980) must now be discussed as possible plesiomorphies. The first is the antidromous flexure of the gonads, which is plesiomorphic in nematodes (Lorenzen, 1978, 1981; Malakhov, 1994), but unique for *Poikilolaimus* within "Rhabditidae" (Sudhaus, 1980). "Antidromously reflexed" means that the germinal and growth zone of the gonad are bent against the oviduct, contrary to homodromously reflexed where the flexure occurs within the growth zone. A homodromous flexure is characteristic for Rhabditida except *Poikilolaimus*, Bunonematidae and Diplogastridae. Also in the related Cephalobidae the gonad is antidromous. Lorenzen (1978) claimed that in antidromously reflexed gonads the oocytes upon entering the oviduct reverse their orientation so that afterwards the

opposite pole goes ahead. Malakhov (1994: 130) added that "in the region of the curve a blind process is formed" which is entered by the fully developed oocyte before its (supposed) reverse motion. It can not be ruled out that some Enoplia taxa exhibit such a movement of the oocyte. However, as was already depicted by Claus (1862: Fig. 3) for *Poikilolaimus oxycercus* (= *Anguillula brevispinus*), by Schneider (1866: Fig. 7) for *Pristionchus dentatus* or by Chitwood & Chitwood (1950: Fig. 116D, 120E) for *Chromadora* sp. and was recently shown for different Diplogastridae (Fürst von Lieven, 2001; Kiontke *et al.*, 2002), *Bunonema* sp. (Fürst von Lieven, 2001) and for *Poikilolaimus ernstmayri* sp. n. (in this paper), there is no reverse in the movement of the oocytes in the antidromous gonads of Non-Enoplia. Consequently, there is no difference in this respect to homodromous ovaries. We restricted the definition of antidromously reflexed to "female gonad reflexed at the junction of ovary and oviduct" (Fürst von Lieven & Sudhaus, 2000) and added for Diplogastridae that "the ova enter the oviduct with their proximal pole (as in a homodromously reflexed gonad)". Therefore, the evolutionary transformation between these two gonad types is not as dramatic as it appeared at the time when Lorenzen (1978) first realized the existence of the two types of reflexed female gonads. It is clear that a change from antidromous to homodromous ovaries by expansion of the growth zone occurred at least once in or within Rhabditida. A reversion to the antidromous state is difficult to imagine. Therefore it is not unlikely that an antidromous gonad is plesiomorphic in *Poikilolaimus*, Bunonematidae and in Diplogastridae.

The second character to be discussed is the absence of a true bursa velum in *Poikilolaimus*, which could also be ancestral. Only a narrow bursa-like fold connecting the genital papillae is found in all *Poikilolaimus* species except in *P. regenfussi*, where this fold is absent (Fig. 2). This fold is perhaps only a continuation of the loose cuticle between the GPs. Correlated with the absence of a bursa is the position of the anterior and posterior dorsal GPs almost lateral and not in line with the subventral GPs. This radial arrangement of papillae was already interpreted as plesiomorphic by Kiontke (1999a). Correlated with the absence of a bursa is also the spiral copulation posture, where the male coils its posterior portion around the body of the female. Thus, the stemspecies pattern of *Poikilolaimus* comes very close to the stemspecies of Rhabditida as

reconstructed in Sudhaus & Fitch (2001), having a glottoid apparatus, a pharyngeal sleeve, a median vulva, separate spicules, a rudimentary leptoderan bursa, radial arrangement of genital papillae, three pairs of GPs situated precloacally. Perhaps antidromously reflexed ovaries can now be added.

Contribution to the phylogeny of *Poikilolaimus* species and the evolution of characters

Based on the known morphological characters a phylogenetic hypothesis is proposed and depicted in a cladogram (Fig. 3) which is nearly identical to that reconstructed by Sudhaus (1980) (reprinted in Sudhaus & Fitch, 2001: 57). The *Oxycercus*-group is characterized by cupola shaped tails in the females (apomorphic), a character which according to this hypothesis evolved in a second step also in the males (compare Fig. 2, b and c). This tail shape may be correlated with an increase in body size (females are larger than males). This correlation suggests an underlying allometric program in the stemspecies of *Poikilolaimus* as was discussed by Osche (1952: 228 -230) for rhabditid tails of specimens of different sizes dependent from nourishment. *P. oxycercus* was named after the tail in both sexes described as "...bluntly rounded, with conical, pointed termination" (de Man, 1895). As the female tail in *P. regenfussi* is only slightly cupola shaped in well-fed specimens and further synapomorphies with its supposed sister taxon comprising *P. oxycercus* and *P. jodhpurensis* are unknown, the position of this species as the basal branch in the *Oxycercus*-group is not well-founded. This lineage remained plesiomorphic in the number of 8-9 pairs of genital papillae (GP) and in the location of three GPs precloacally. The position of the first GP anteriorly of the spicules head was stated as apomorphic for the *Oxycercus*-group as inferred from the assumed close relationship with *Cephaloboides*, and despite the realized similarities with *Rhabditoides* (Sudhaus, 1980). Now this character should be interpreted as plesiomorphic.

In the sister group of the *Oxycercus*-group, the *Piniperdae*-group, only 6 pairs of GPs are present. As discussed in the next section, we can assume that starting with a pattern like in *P. oxycercus* the anterior pair of genital papillae was lost and then in two lines independently a second and different pair was also lost (Fig. 2). Several arguments (listed in Fig. 3) substantiate the sister group relationship of *P. incisocaudatus* and *P. ernstmayri* sp. n., though these hypothesized synapomorphies

are in conflict with the distribution of the following three characters which are shared by *P. ernstmayri* sp. n. and *P. oxycercus*: two pairs of gland cells on either side of the vagina, a prominent single medio-ventral papilla in a short distance anteriorly of the cloacal aperture (which is reminiscent of the large precloacal sensillum in *Steinernema*), and a conspicuous shape of the capitulum of the spicules (Fig. 2). Of these characters, only the unusual vaginal glands must be taken seriously. From the cladogram they should be interpreted as symplesiomorphic, however, they are not described in any other *Poikilolaimus* species. On the other hand, convergence is possible. In Diplogastridae four vaginal saccular glands were observed in the species of *Parasitodiplogaster* (Poinar & Herre, 1991), in a species of *Mononchoides* (W. S.) as well as in *M. longicaudatus* (Jairajpuri *et al.*, 1973), and the four ventral pouches close to the vulva in *Oigolaimella ninae* (containing granular material: Fürst von Lieven, 2003) and in *Mononchoides* sp. 1 (serving as spermathecae: Kiontke, 1999b: 36) look quite similar.

Based on our cladogram we can describe a "trend" to shift the pore of the secretory-excretory system anteriorly from a position of 69-80 % of pharynx length in *P. piniperdae* via 48-65 % in *P. incisocaudatus* to 41-52 % in *P. ernstmayri* sp. n. and thus anteriorly of the nerve ring. The duct was accordingly lengthened and passes the nerve ring on the left hand side. The pore was also depicted anteriorly of the nerve ring (at about 65-70 % of pharynx length) in *P. jodhpurensis*, but not with a long strongly cuticularized duct (Khera, 1969).

Without knowing which taxa are closely related to *Poikilolaimus*, we have no good arguments to state an opinion about the body size of its stemspecies. If it was small (less than 650 µm), as we think, an increase in body size must have happened in the *Oxycercus*-group (maximum size of *P. oxycercus* female is 1800 µm). In this case it can be speculated that the apomorphic cupola shaped tail is conditioned by an increase in body size. An advantage of larger females is, that each uterus can store more than two eggs, in contrast to the small species of the *Piniperdae*-group, where it usually contains 1-2 eggs. A decrease from medium length in the stemspecies to dwarfs in the *Piniperdae*-group, however, cannot be excluded. Under that assumption the conspicuous length of spicules in *P. piniperdae panagrocercus* (34-38 µm) and in *P. incisocaudatus* (40 µm) could be interpreted as a retention of the absolute length of

spicules despite a reduction of total body size, as was suggested by Sudhaus (1980).

Transformations of the pattern of genital papillae

In our formula of genital papillae (GP), modified in long discussions with D. Fitch and K. Kiontke, the two posterior subdorsal genital papillae are designated ad (= anterior dorsal) and pd (= posterior dorsal). The other, ventrally located GPs are called v (= ventrals) and are counted from anterior to posterior as v1 to vn (in Rhabditida usually v7; Fig. 2a). Phasmids (ph) are included in this formula. Papillae that are clustered are grouped in brackets. A slash denotes the position of the cloacal opening. If all 9 pairs of GPs are present, the homologous papillae have the same designation. A problem arises if one or more GPs are absent. This is a problem of alignment. The descriptive formula is pragmatic for diagnostic purposes. We may add a question mark if we are not certain about the identity of "ad" and "pd"; and we count the ventral GPs as "v1" to "vn" initially ignoring position homology. Comparisons of related species may allow to generate hypotheses on which of the GPs are missing. In the aligned formula the position of a missing GP is indicated by a hyphen. This alignment is hypothetical as long as the loss of a certain GP cannot be demonstrated by ontogenetic studies such as the one conducted by Fitch & Emmons (1995).

In the hermaphroditic *P. regenfussi* only two of the extremely rare males could be observed (W. S.), so that the number and position of all the GPs could not be determined with certainty (Fig. 2b; the other male was depicted in Kiontke & Sudhaus, 2000: Fig. 4B). The existence of GP4 (or GP3) is uncertain. Under the assumption that it really does exist, this species has 9 pairs of genital papillae with the formula

<v1, v2, v3 / v4, ad, (v5, v6, v7) pd, ph>

or <v1, v2, v3 / v4, ad, v5, pd, (v6, v7) ph>. The exact position of "pd" could not be ascertained or is variable. Despite these uncertainties, the arrangement of genital papillae in *P. regenfussi* corresponds quite well with the pattern in *Rhabditoides inermis* (Fig. 2a) described by the formula

<v1, v2, v3 / v4, (ad, v5), pd, (v6, v7, ph)>.

The main differences are the position of papilla "v5", that is close to "ad" in *R. inermis* and very close to "v6" in *P. regenfussi*, and perhaps the position of "pd".

We can assume terminal phasmids and 9 pairs of genital papillae in an arrangement very similar to <v1, v2, v3 / v4, ad, v5, pd, v6, v7, ph> as the condition in the ancestral lineage to *Poikilolaimus*. In this pattern, as also represented in *R. inermis*, we seemingly have the first recognized example, that the developmental “default” state of “Rhabditidae” (Fitch in Sudhaus & Fitch, 2001) is realized in the male. This means that the GPs remain at the positions of their precursor cells and no migration occurs. If the observations of the GPs in *P. regenfussi* are correct, this pattern (or a pattern with the more posterior position of “pd”) should have had arisen within the ancestral lineage of *Poikilolaimus* after its divergence from its unknown sister taxon. Otherwise, one pair of papillae must have been lost in the ancestral lineage. Unfortunately, the report of 9 pairs in *P. jodhpurensis* by Khera (1969) is not reliable.

Table 2 compares the descriptive formula with a hypothesis on lost papillae (aligned formula) for *Poikilolaimus* species that do not have the full set of 9 pairs of genital papillae (compare Fig. 2). A loss of one pair of papillae occurred in *P. oxycercus*. From the usually arrangement of genital papillae in this species as

<v1, v2, v3 / ad, v4, pd, (v5, v6), ph> in comparison to *P. regenfussi* it can be assumed that the first subventral postcloacal papilla (GP4) must have been lost. To express this hypothesis, the absence of this GP is marked as a gap (–) and the aligned formula reads:

<v1, v2, v3 / –, ad, v5, pd, (v6, v7), ph>. Unfortunately, there is no support for this hypothesis by atavistic aberrations. The only aberration type in *P. oxycercus* observed so far in 3 specimens is one ectopic papilla anterior of the first genital papilla.

Comparing also the GP pattern of the other *Poikilolaimus* species, we must assume a loss of precloacal GPs in the species of the *Piniperdae*-group. According to the phylogeny presented above this means that first the most anterior pair of genital papillae (v1) was lost and in a second step the next pair (v2). The mentioned aberration of one additional anterior papilla on spicula level in *P. ernstmayri* sp. n. can be interpreted as atavistic. A derived character of this new species is that the position of the phasmids is not terminal lateral, perhaps because the last GP was shifted posterior of it. This situation is only comparable to *Rhabditoides longispina* (Kiontke & Sudhaus, 2000). These hypotheses can be tested by investigations of the development of genital papillae.

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Sudhaus W., Koch C. Новый вид нематод *Poikilolaimus ernstmayri* sp. n., ассоциированных с термитами, и обсуждение филогении *Poikilolaimus* (Rhabditida).

Резюме. Описан новый вид рабдитид, ассоциированных с термитами на Корсике. *Poikilolaimus ernstmayri* sp. n. уникален среди "Rhabditidae" по расположению секреторно-экскреторной поры на уровне метакорпального бульбуса. Форма спикул и наличие только одной пары преклоакальных папилл отличает *P. ernstmayri* от близкого по другим морфологическим признакам *P. piniperdae*. Рассмотрены географические и экологические особенности распределения 6 видов *Poikilolaimus*, обсуждается их филогения. На основании анализа морфологических признаков предложена кладограмма для видов рода. Выделены 53 апо- и плезиоморфных признака и реконструированы особенности предковой формы *Poikilolaimus*. Рудиментарная бурса и антидромные загнутые яичники рассматриваются как плезиоморфные признаки. В рамках филогенетической гипотезы обсуждаются эволюционные изменения в расположении генитальных папилл у *Poikilolaimus*. Предложена новая формула, отражающая особенности расположения генитальных папилл, позволяющая проводить сравнение между видами и учитывающая возможную потерю в эволюции отдельных пар папилл. Сестринский таксон для *Poikilolaimus* остается неизвестным. Обсуждаются интересные признаки сходства с *Myolaimus*, в том числе структура кутикулы.
