Phylogeny and evolution of the genus *Pratylenchus* according to morphological data (Nematoda: Tylenchida)

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Interspecfic variability of morphological characters and trends of character changes in the evolution of the genus *Pratylenchus* are analysed. Rows of characters (Figs 1-26) and the matrix of species and characters (Table) were composed. On the basis of the matrix, phylogenetic relations of 49 species of the genus are analysed using the PAUP software, and the consensus tree is obtained (Fig. 27). Synapomorphies (tree nodes) are described and 13 species group have been outlined. *P. coffeae* and the closely related species (including the type species *P. pratensis* (De Man) form the pratensis-coffeae group. Most of the species in the genus have the more advanced states of 9 characters (Fig. 28). Since the evolution of these characters is caused by the adaptation to the migratory endoparasitism (MEP), here is considered that the MEP-specialization was the key factor both for the formation of species diversity within the genus and for its biological progress.

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The present paper continues the analysis of classification and evolution of the genus *Pratylenchus*, started in the previous publication (Ryss, 2002). The aim of the paper is to analyse the directions of evolution of the morphological characters and, on this basis and using the PAUP phylogenetic analysis package (Swofford, 1993), to present the pattern of the phylogenetic relationships in the genus and its evolution.

Here 49 *Pratylenchus* species are analysed. The list of examined collections and other sources of material and information is given in the previous paper (Ryss, 2002). In the last paper, *Pratylenchus jordanensis* was synonymized with *P. scribneri* as a junior synonym, but here *P. jordanensis* is analysed as a separate taxon for the additional test of the correctness of this synonymy.

ROWS OF CHARACTERS USED IN PHYLOGENETIC ANALYSIS (Figs 1-26)

Rows of characters given below are similar to those used in the multientry polytomic key (Ryss, 2002), but the character states are listed here according to the directions of the evolutionary transformations in tylenchids as analysed by Ryss (1993, 1994), starting from the most primitive state assigned as 0-character state; at the same time, in the multientry key all states were numerated from 1 (see Ryss, 2002). A total of 22 characters were coded as "ordered" in the matrix of morphological characters in the NEXUS format for the subsequent processing in the phylogenetic analysis package PAUP. Characters 3, 7, 18, and 21 received the status "irreversible". Characters with their states and comments on the evolution of characters are given below.

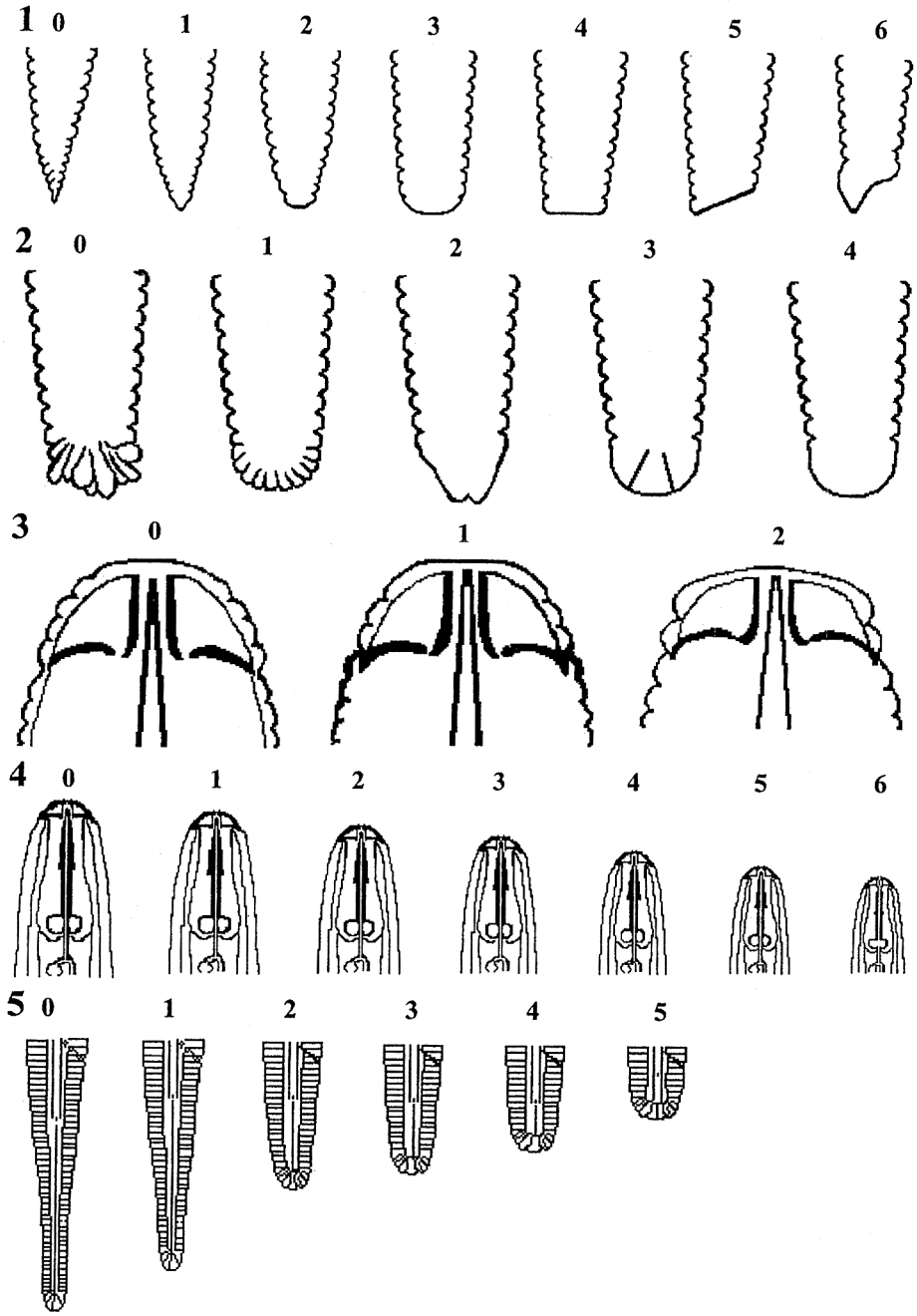
Character 1. Tail tip shape:

0, pointed or irregular;
1, conically rounded;
2, rounded;
3, spherical;
4, truncate;
5, obliquely truncate;
6, conical with heel-like dorsal outline.

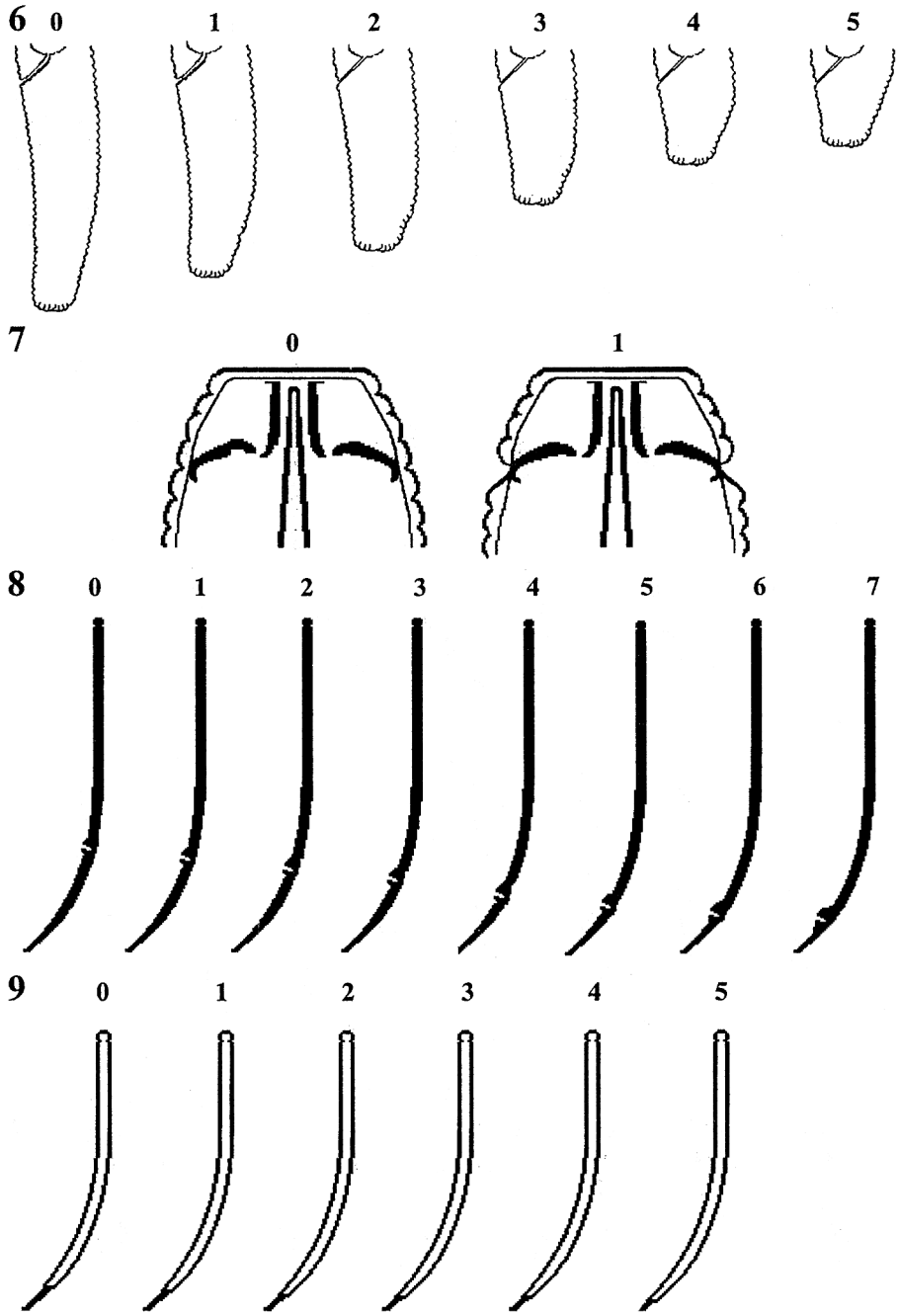
The given row of the characters corresponds to the transition from the primitive long hair-like tail of the lowest tylenchs to the blunt tail end of endoparasites.

Character 2. Tail tip annulation:

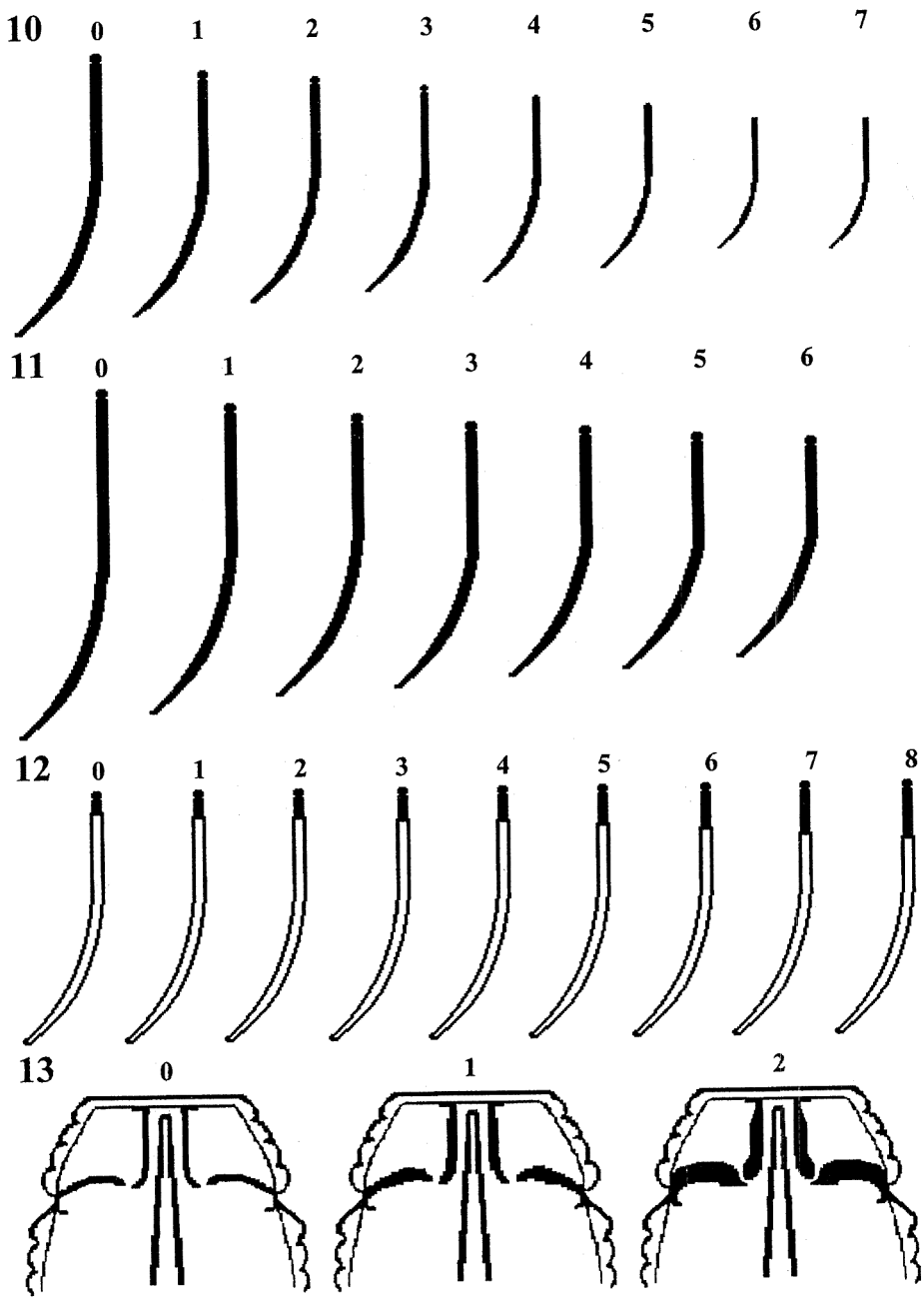
0, irregularly annulated (terminal annuli differ in width);
1, regularly annulated (terminal annuli equal in width);



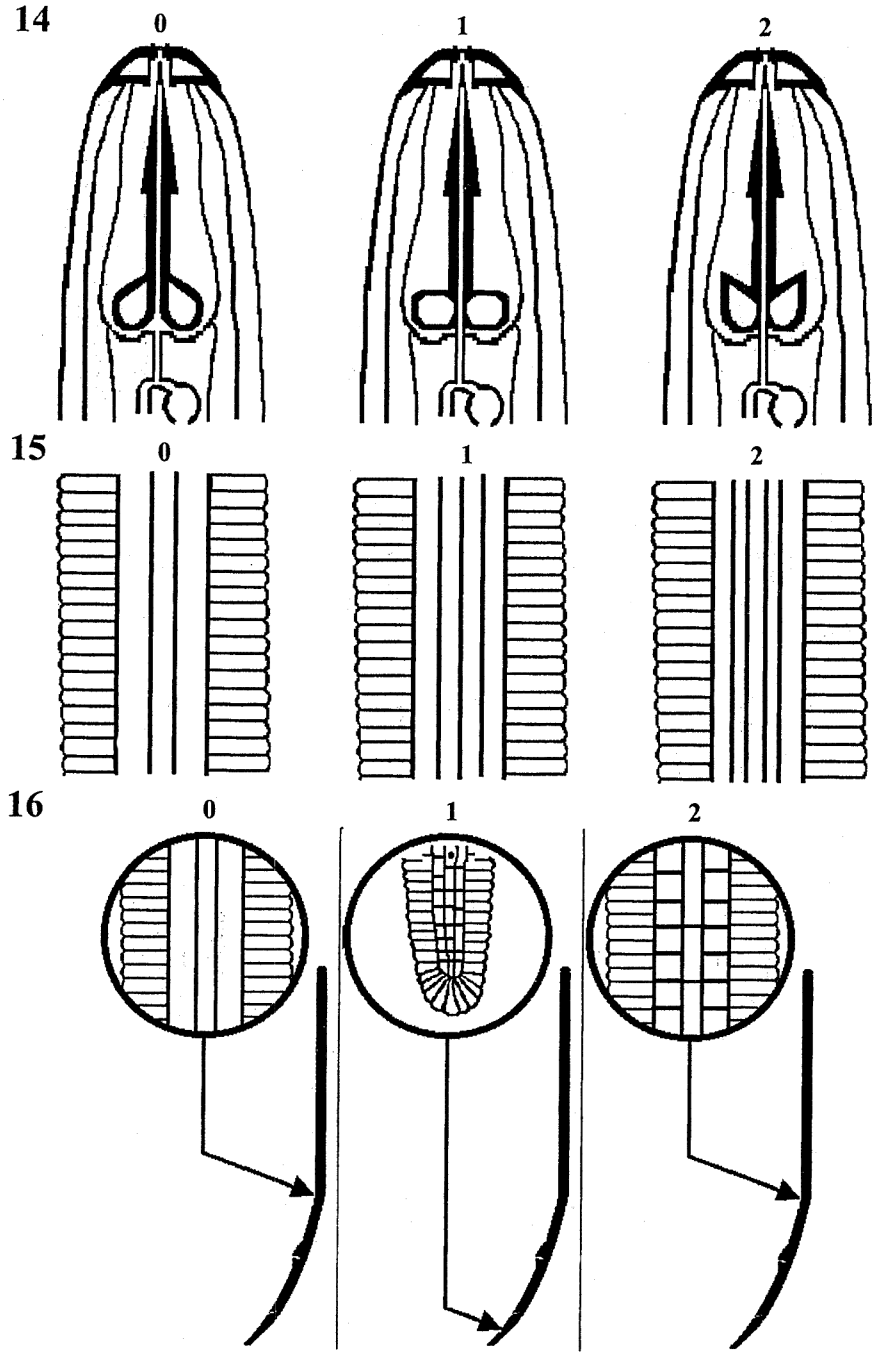
Figs 1-26. Rows of morphological characters of the genus *Pratylenchus*. Numbers of characters (1-26, to the left, bold font) and numbers of their states (0-8, along rows, standard font) correspond to the numbers of characters and character states given in the list of rows of characters.



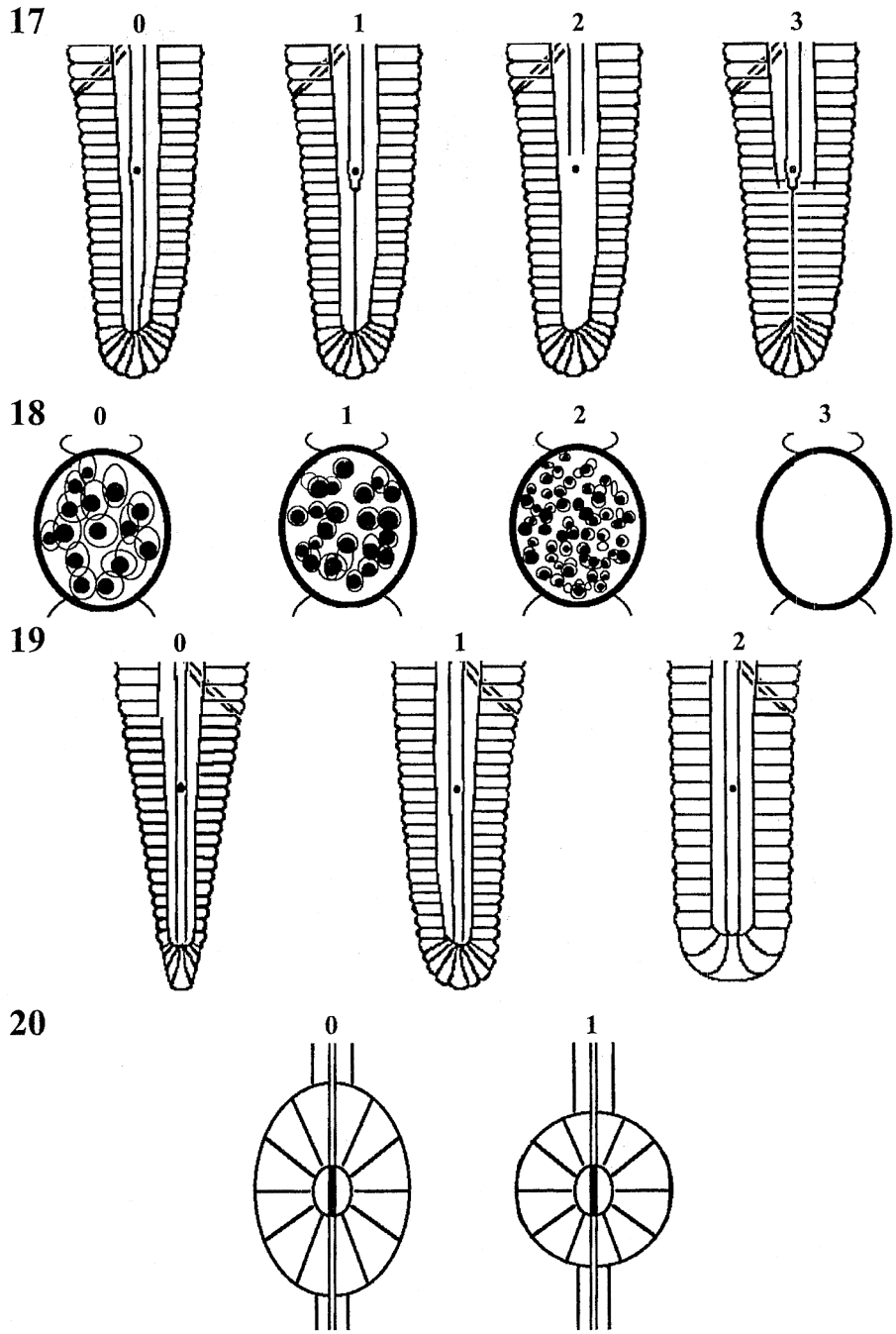
Figs 1-26. *Continued.*



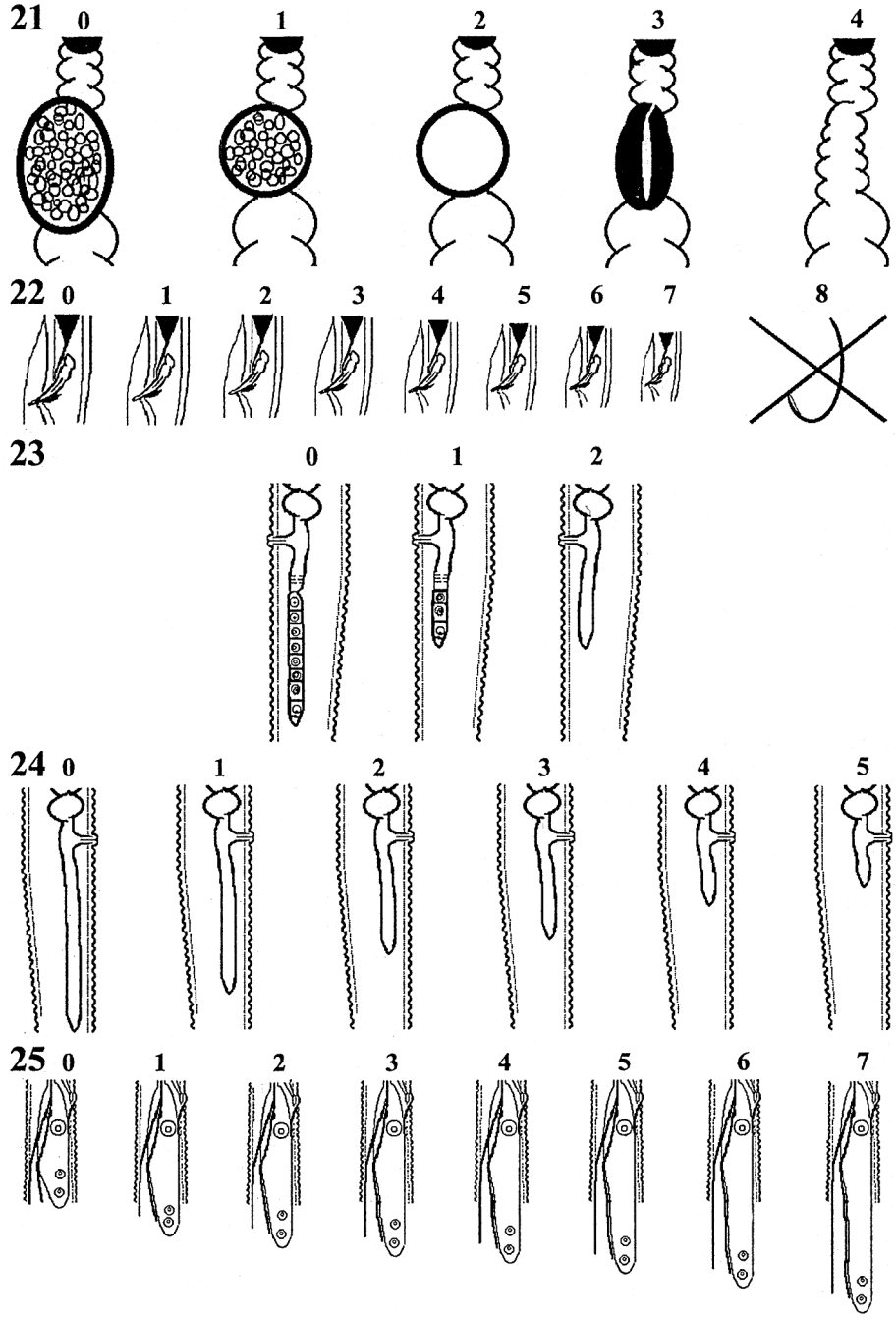
Figs 1-26. *Continued.*



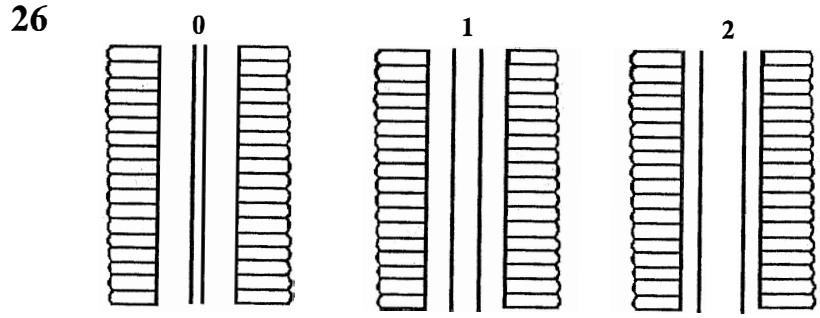
Figs 1-26. *Continued.*



Figs 1-26. *Continued.*



Figs 1-26. *Continued.*



Figs 1-26. *Continued.*

2, smooth with one or two annuli;
3, smooth with 1-2 incisures on terminus surface;
4, smooth.

Character transformation corresponds to the loss of annulation of the tail tip and to the decrease of its footing (adhesion to substratum) quality for the nematode movement, because of transition to endoparasitism.

Character 3. Head annuli:
0, four annuli;
1, three annuli;
2, two annuli.

Decrease in number of lip annuli is connected with the formation of the low and flattened lip region, which is typical for the migratory endoparasites (Paramonov, 1962, 1970; Siddiqi, 1980, 1986, 2000). Status "irreversible" is given to the character during the matrix operation in the NEXUS format.

Character 4. Stylet length:
0, 23 mm or more;
1, 20-22 μm;
2, 18-19 μm;
3, 16-17 μm;
4, 14-15 μm;
5, 13 μm;
6, 12 μm or less.

Decrease in length of the stylet and increase in size of the oesophageal glands are adaptations to endoparasitic feeding, for which the decrease of the mechanical damage of tissues is important; the latter is compensated by intensification of the secretory activity of the parasite oesophagus (Maggenti, 1971).

Character 5. Ratio of tail length to anal body width (*c'*):
0, 4.1 or more;
1, 3.5-4.0;
2, 3.0-3.4;
3, 2.5-2.9;
4, 2.0-2.4;
5, 1.9 or less.

Decrease of the tail length along with the body shortening is an adaptation to endoparasitism in the dense root tissues: the tail loses its role as the footing for the movement of worm. Squeeze between the cell walls of the host root tissue destroyed by parasite is carried out by undulation of the whole body.

Character 6. Number of tail annuli:
0, 32 or more;
1, 26-31;
2, 20-25;
3, 16-19;
4, 13-15;
5, 12 or smaller.

Decrease of the tail annuli is linked with tail shortening (see comments to Character 5).

Character 7. Cephalic region:
0, continuous, not separated from the body by marked constriction;
1, offset, separated from the body by marked constriction.

Lip region is continuous in the primitive Tylenchida (*Psilenchus*, numerous Tylenchidae). Its separation takes place independently in many Hoplolaimina (Heteroderidae, Dolichodoridae, Belonolaimidae, Pratylenchidae) and is linked with the formation solid cephalic framework (Luc & Fortuner, 1987; Ryss, 1994). The character is considered to be "irreversible", because the reversion to the primitive state 0 seems to be improbable.

Character 8. Index *V* (ratio: length of prevulval body part to body length):
0, 67 or less;
1, 68-70;
2, 71-73;
3, 74-76;
4, 77-79;
5, 80-82;

6, 83-84;
7, 85 or more.

Shift of the vulva posteriad is strongly correlated with reduction of the posterior branch of the female genital system (Paramonov, 1962, 1970; Ryss, 1987, 1988, 1993) and seems to be linked with the trend to body shortening (which is an adaptation to the migratory endoparasitism).

Character 9. Index *c* (ratio of body length to tail length):
0, 16 or less;
1, 17-18;
2, 19-22;
3, 23-25;
4, 26-28;
5, 29 or more.

Tail shortening: see comments to Character 5.

Character 10. Body length:
0, 610 μm or more;
1, 560-600 μm;
2, 510-550 μm;
3, 460-500 μm;
4, 410-450 μm;
5, 360-400 μm;
6, 320-350 μm;
7, 310 μm or less.

Decrease of the body size caused by the specialization to parasitism is one of the basic parasitic adaptations described in the textbooks on parasitology (e.g., Dogiel, 1962) and in the literature on plant parasitic nematodes (e.g., Ryss, 1987).

Character 11. Index *a* (ratio of body length to maximum body width):
0, 32 or more;
1, 29-31;
2, 27-28;
3, 25-26;
4, 22-24;
5, 18-21;
6, 17 or less.

Decrease of the relative body size is linked with adaptation to the endoparasitic life habit: see comments to Character 10.

Character 12. Index *b* (ratio of body length to oesophagus length till oesophago-intestinal valve):
0, 8.6 and more;
1, 8.3-8.5;
2, 7.6-8.2;
3, 7.1-7.5;
4, 6.6-7.0;
5, 5.9-6.5;
6, 5.6-5.8;
7, 4.7-5.5;
8, 4.6 or less.

Body grows during postembryogenesis mainly due to the elongation of its trophico-genital part. That is why *b*-value (it equals approximately 2.5 in juveniles of the 2nd stage) increases during the postembryonic development (Ryss, 1983, 1984, 1988). Tendency to the body shortening owing to the specialization to endoparasitism (see comments to Character 10) leads to the inhibition of the postembryonic growth and decrease of *b*-value.

Character 13. Cephalic framework sclerotization:
0, light;
1, moderate;
2, hard.

Enforcement of the cephalic framework is a general trend in the order Tylenchida (Paramonov, 1970; Siddiqi, 1986, 2000).

Character 14. Stylet knobs:
0, directed posteriorly;
1, directed laterally;
2, directed anteriorly.

Stylet knobs are the areas of the muscle attachment, both protractors (extending anteriad to the cephalic framework) and retractors (directed posteriad). Knobs of the lower the Hoplolaimina (*Psilenchus, Pratylenchoides*) are directed posteriad, knobs in more advanced taxa (Hoplolaimidae, Heteroderidae) are directed anteriad in connection with the enforcement of the perforation function (protraction).

Character 15. Lateral field incisures at mid-body:
0, four;
1, five;
2, six.

Incisures of the lateral field are the longitudinal constrictions between its bands. Increase in their number (initial state is 4 incisures for Secernentea taxa: Lorenzen, 1981; Ryss, 1993, 1994) means usually the increase in number of bands; it can be observed in *Pratylenchoides* and *Amplimerlinius* species, in which five and more bands extend from the excretory pore till the tail tip. However, the real increase in number of bands is not typical of pratylenchs (exceptions are *P. crenatus, P. estoniensis*, and *P. teres*, which have the real additional bands). Normally in pratylenchs the increase in number of incisures represents the simple formation of irregular folds of the lateral field near vulva, which seems to be an adaptation to expand this part of the body, functioning as egg-bearing and egg-laying area.

Character 16. Lateral field areolation:
0, absent;
1, present in tail;
2, present at mid-body.

Areolation of the lateral field (transverse lines joining the longitudinal incisures of the lateral field) is evidently a secondary character. It may be observed mostly at the narrow parts of the body (tail and excretory pore). Adaptive significance of this character is unknown.

Character 17. Lateral field incisures between phasmid and tail tip:

0, four;
1, three;
2 two;
3, one.

In primitive tylenchs, the number of incisures on tail equals to the number of those at mid-body (4), but in many pratylenchs the tail and the lateral field on tail are reduced; it leads to the decrease in number of tail incisures.

Character 18. Sperm in female spermatheca:

0, cytoplasmic, nucleus occupying 1/2 sperm diameter, which is 5 mm;
1, nuclear, nucleus occupying whole sperm diameter, which is 3 mm;
2, nuclear, nucleus occupying whole sperm diameter, which is 1 mm;
3, absent.

In the Secernentea taxa representing the outgroups to Hoplolaimina (family Anguinidae (Tylenchina) and the order Aphelenchida), the sperm cells deposited in the genital tubes of females are characterized by a significant quantity of cytoplasm; the cytoplasm considerably exceeds the sperm nucleus in volume. In pratylenchs, the cytoplasmic spermatozoids are typical only of *P. goodeyi*; significant but less quantity of cytoplasm is recorded for *P. kasari*. Sperm cells of other amphimictic pratylenchs consist of nucleus surrounded by a thin cytoplasm layer. Due to transition to parthenogenesis of the majority of *Pratylenchus* species, sperm in female spermatheca of these species is absent (see Characters 21 and 22). Character has the status "irreversible" because the return from parthenogenesis to amphimixis as well as reversion to the primitive cytoplasmic sperm, are considered to be incredible.

Character 19. Shape of tail:

0, conical;
1, subcylindrical;
2, cylindrical.

Tail shape, which is from conical to filiform in primitive Tylenchida (outgroups), is transformed into a blunt and rounded in the taxa of Hoplolaimina (Paramonov, 1963, 1969, 1970; Siddiqi, 1986, 2000; Fortuner et al., 1987-1988; Geraert & Raski, 1987) in connection with the movement in dense substrata (plant tissues, etc.).

Character 20. Shape of median bulb:

0, oval;
1, round.

Metacorpus of tylenchs is transformed into a median bulb, which functions as a pump for the plant tissues dissolved by secretions of the oesophageal glands. In endoparasites, due to the size decrease of organs performing the mechanical functions (stylet, lip region, tail, and body) the median bulb turns to be more compact still maintaining the muscle volume. Sphere is characterized by the minimum value of surface/volume ratio, and therefore the metacorpus is transformed to be spherical.

Character 21. Structure of female spermatheca:

0, filled with sperm, oval;
1, filled with sperm, round;
2, without sperm, distinct, offset, with round or oval cavity;
3, without sperm, distinct, offset, with slit-like cavity;
4, indistinct, not offset from outline of female genital tract.

Spermatheca is a sac-like structure for sperm deposition in the female genital system. Presence of sperm guarantees the permanent egg maturing and oviposition in spite of the rare copulations. Primitive Tylenchina (Tylenchidae) have an oval spermatheca. In *Pratylenchus*, the spermatheca is transformed into a compact spherical structure. In most of *Pratylenchus* species, spermatheca is reduced (states 2-4) because of the transition to parthenogenesis. Character has the status "irreversible", because the return from parthenogenesis to amphimixis is considered to be impossible.

Character 22. Spicula length:

0, 21 mm or more;
1, 20 μm;
2, 19 μm;
3, 18 μm;
4, 17 μm;
5, 16 μm;
6, 15 μm;
7, 14 μm or less;
8, males absent, spermatheca of females without sperm.

Polarity of the character reflects the decrease in size of the body and its organs and the transition to parthenogenesis. The long spicules, as in outgroups (Belonolaimidae, Psilenchidae), is a primitive state of the character. In parthenogenetic species, males are usually absent, but aberrant non-functional males rarely occur in some species (*P. neglectus, P. thornei*, and others: see Ryss et al., 1991; Ryss & Shagalina, 1992).

Character 23. Posterior genital branch differentiation:

0, 4 or more oocytes or nuclei in posterior ovary;
1, 1-3 oocytes or nuclei in posterior ovary;
2, posterior ovary or oocytes absent.

Reduction of the posterior ovary and the posterior branch of the female genital system is linked with shortening of the body (caused in pratylenchs by the endoparasitism); this tendency takes place independently in different nematode taxa (Lorenzen, 1981; Ryss, 1994).

Character 24. Posterior genital branch length:
0, 2.4 vulval diameters (45 μm) or more;
1, 2.0-2.3 vulval diameters (37-44 μm);
2, 1.7-1.9 vulval diameters (31-36 μm);
3, 1.4-1.6 vulval diameters (26-30 μm);
4, 1.1-1.3 vulval diameters (21-25 μm);
5, one vulval diameter (18-20 μm) or less.
See comments to Character 23.

Character 25. Gland lobe length:
0, 39 μm or less;
1, 40-46 μm;
2, 47-50 μm;
3, 51-55 μm;
4, 56-60 μm;
5, 61-65 μm;
6, 66-70 μm;
7, 71 μm or more.

Transformation from the tylenchoid type of oesophagus (with cardial sphincter; glands of oesophagus compact, inside of oesophagus) into the hoplolaimoid type (without cardial sphincter; gland lobe situated in the body cavity), as well as the increase of the oesophageal gland lobe in Hoplolaimina is caused by the intensification of the extra-intestinal digestion as a specialization to endoparasitism (Seinhorst, 1971; Siddiqi, 1971, 1986; Geraert, 1978; Fortuner et al., 1987-1988; Ryss, 1987, 1988).

Character 26. Central band of lateral field:
0, narrower than lateral ones;
1, equal in width to lateral ones;
2, wider than lateral ones.

The character "narrow central band of the lateral field" means that the outer bands are wider than the central one and the hypodermal chords are well developed. The latter are the frame structures for the movement by undulation. Decrease in width of the outer bands and the expansion of the central one is a secondary feature (states 1 and 20), which seems to be connected with the decrease of mobility in endoparasites.

Method of analysis of the phylogenetic relations

The above-considered rows of characters were used to construct the matrix of characters (Table). A distinctive feature of the matrix is the presence of multistate sets of characters for most of species (such polymorphic sets of characters are placed in brackets). A total of 22 characters were coded as "ordered" and 4 characters (3, 7, 18, and 21), as "irreversible", because the return from the parthenogenesis to amphimixis (characters 18 and 21) and the reverse transformation from the specialized lip region to the primitive state (characters 3 and 7) seem to be unlikely. The equal weights were assigned to all characters. The outgroup with 0-states of all characters was added to 49 nominal analysed species.

The heuristic search of the parsimonious phylogenetic trees was run and 2051 trees were obtained. On the basis of these trees (maximum tree length 1390), the consensus tree has been calculated. It consists of 95 phylogenetic events: 49 species, 1 conventional outgroup and 46 nodes. Both the Strict Consensus and the 50% Majority Rule (probability) were calculated. The latter has given the result, which is the most adequate from the points of view of a *Pratylenchus* taxonomist, and this is the reason why this tree has been used for the analysis of phylogeny and the evolution of adaptations (Fig. 27).

Phylogenetic relations and the species groups

The phylogenetic tree of the genus *Pratylenchus* (Fig. 27) includes nodes of branching each characterized by synapomorphies. Nodes are interpreted as the ancestral taxa for the following (distal) tree branches. Because of this they have the unified numeration with the terminal (recent) species of the genus *Pratylenchus*. Numeration begins from the recent 49 species and the conventional outgroup having 0-states of all characters, then includes 46 nodes numerated from the distal branches to the root of the phylogenetic tree. Thus, 96 phylogenetic events (nodes and the recent species) are present in the monophyletic (according to the initial assumption) tree of the genus. Events connected with the formation of large species groups are described here below.

Pratylenchus kasari is the most close to the conventional ancestor (outgroup). Apomorphies of this species are as follows: decrease in number of the lip annuli (Chr. 3: 0 → 1), decrease of the cytoplasm quantity in sperm cells (Chr. 18: 0 → 1), and formation of the long gland lobe of oesophagus (Chr. 25: 0 → 7). The group *P. vulnus*, *P. pseudocoffeae* and *P. ekrami* (node 95) is also close to the ancestral type. The formation of this group is connected with the following

Table. Matrix of characters of the *Pratylenchus* species. LATNAM column contains species names, columns C1-C26, the characters from 1 to 26. Number of characters and character states in cells correspond to those listed in the rows of characters. Sets of character states for polymorphic characters are given in brackets

LATNAM	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19	C20	C21	C22	C23	C24	C25	C26
alleni	2	(234)	2	4	(45)	3	1	(456)	(0123)	(456)	(2345)	(567)	0	1	0	0	(12)	2	1	1	(01)	(567)	(12)	(234)	0	1
andinus	(23)	4	1	(3456)	(45)	3	1	(45)	(12)	(123)	(01234)	(23456)	1	1	0	2	0	3	2	0	2	8	2	(2345)	(0123)	1
australis	1	4	1	(12)	(345)	2	0	(456)	(12)	(01)	(0123)	(2345)	2	1	0	0	1	3	0	0	4	8	2	(234)	(34)	1
barkati	4	1	1	2	3	3	1	(34)	(12)	(23)	(123)	(01)	1	1	0	0	0	3	1	1	2	8	2	5	6	1
bolivianus	(012)	4	(01)	(123)	(45)	(234)	1	5	(012)	(012)	(123)	(5678)	2	1	0	1	0	3	(01)	0	2	8	2	(234)	(012)	2
brachyurus	(234)	4	2	(12)	(45)	(234)	1	(67)	(0123)	(01234)	(12345)	(234567)	2	1	0	0	2	3	1	1	4	8	2	(345)	3	1
coffeae	2	(01)	2	(234)	(23)	2	1	(456)	(0123)	(01234)	(12345)	(234567)	1	1	0	0	(01)	2	(01)	(01)	0	(345)	(12)	(12345)	0	1
convallariae	2	0	1	(34)	(45)	(23)	1	(45)	(1234)	(123)	(234)	(12345)	1	1	0	0	1	2	1	1	1	(56)	2	(23)	0	1
crassi	2	4	2	(23)	4	(45)	1	(234)	(123)	4	(345)	(012)	1	1	0	0	0	2	1	1	0	(34567)	2	5	0	1
crenatus	2	1	1	(234)	(34)	(12)	1	(456)	(01234)	(12345)	(12345)	(234567)	1	0	2	0	0	3	1	1	2	8	2	3	0	1
dasi	(234)	4	1	2	2	4	1	(234)	(012)	(1234)	(1234)	(012)	1	1	0	0	0	3	1	1	2	8	2	(34)	2	1
delattrei	1	4	1	4	4	(345)	1	(234)	(12)	(345)	(345)	(78)	1	1	0	0	0	3	(01)	1	4	8	2	4	0	1
ekrami	1	4	1	(56)	(345)	(01)	0	(456)	(12345)	(01234)	(01234)	(34567)	1	0	0	0	0	2	0	(01)	0	6	1	(12)	(0123)	1
emarginatus	2	4	1	(34)	(345)	(23)	1	2	(01)	7	6	(78)	1	1	0	0	(01)	2	1	1	(01)	(67)	2	5	0	1
estoniensis	2	1	2	3	(45)	(12)	1	(567)	(012)	(3456)	(23456)	(345678)	1	2	2	0	0	3	1	0	2	8	2	(34)	0	1
exilis	2	1	1	(23)	3	(23)	1	(23)	(012)	(123)	(01)	0	1	1	0	0	0	2	1	1	1	5	2	5	3	1
fallax	2	1	1	3	(34)	(23)	1	(45)	(123)	(1234)	(01234)	(4567)	1	1	0	0	0	2	1	1	1	(567)	(12)	(34)	2	1
flakkensis	3	1	2	3	(34)	(23)	1	(234)	(01)	(1234)	(2345)	(4567)	1	1	0	0	0	2	(12)	1	1	6	(12)	3	0	1
gibbicaudatus	(234)	1	2	(34)	(12345)	(012)	1	(23)	(012)	(234)	(12345)	(34567)	1	1	0	0	(12)	3	1	1	2	3	(012)	(12345)	(12345)	1
goodeyi	6	4	0	(34)	3	(23)	1	(23)	(01)	(01234)	(0123)	(567)	1	1	0	0	(012)	0	0	1	(01)	(56)	2	(345)	0	1
hexincisus	2	4	2	(34)	5	2	1	(345)	(123)	(23456)	(12345)	(12345)	1	1	2	0	0	3	1	1	4	(45)	2	5	0	1
impar	(12)	1	2	(34)	(23)	(012)	1	(012)	(0123)	(34)	(34)	(78)	1	1	0	0	0	3	1	(01)	4	8	(12)	3	0	2
japonicus	(01)	4	2	(12)	(01234)	(12)	0	(67)	(012)	(01234)	(12345)	(23456)	1	1	0	(012)	1	3	0	1	2	8	2	(2345)	5	1
jordanensis	(12)	(34)	2	4	(234)	(23)	1	(34)	(0123)	(12345)	(0123)	(5678)	1	1	0	0	1	3	(01)	(01)	2	8	2	5	(0123)	1
kasari	0	(01)	1	(23)	(12)	0	0	(345)	(012)	(01234)	0	(23456)	1	1	(01)	0	0	1	0	0	0	(0123)	0	1	7	1
loosi	1	4	2	(234)	(23)	(123)	1	(4567)	(123)	(0123)	(012)	(3456)	1	1	(01)	0	1	2	0	1	(01)	(12345)	(12)	(45)	(01)	1
macrostylus	1	(234)	2	(01)	(234)	(23)	0	7	(0123)	(012)	4	(34567)	1	1	(01)	0	1	3	0	(01)	(234)	(678)	1	(34)	(23)	1
microstylus	(012)	4	1	6	4	3	0	(34)	(012)	(3456)	(345)	(567)	1	1	0	0	0	3	(01)	(01)	4	8	2	5	(01)	1
mulchandi	(234)	4	1	(234)	5	(34)	1	(45)	(12)	(234)	(3456)	(567)	1	2	0	0	0	3	1	1	4	8	0	3	1	1
neglectus	(45)	4	2	(234)	(45)	(34)	1	(456)	(012)	(01234)	(12345)	(34567)	1	(12)	0	0	(012)	3	(12)	1	3	8	2	5	0	1
nizamabadensis	3	1	0	2	(45)	4	0	(1234)	(1234)	(234)	(234)	(01234)	2	1	0	0	0	3	1	1	4	8	2	(45)	0	1
penetrans	1	4	1	(34)	(45)	(1234)	1	(3456)	(0123)	(01234)	(12345)	(34567)	1	1	0	(012)	0	2	(01)	1	1	(4567)	(12)	(345)	0	1
pinguicaudatus	3	4	1	(23)	(34)	2	1	(45)	(012)	(012)	(2345)	(456)	1	1	0	(012)	1	3	(12)	1	2	8	(12)	(45)	(3456)	1
pratensis	(01)	1	1	(45)	(34)	(12)	1	(34)	(12)	(1234)	(01234)	(567)	1	1	0	0	(012)	2	(01)	0	0	(234)	2	(345)	1	1
pseudocoffeae	(1234)	4	(12)	(234)	(345)	(23)	1	(456)	(12)	(01234)	(01234)	(45678)	1	(12)	0	2	(01)	2	(012)	0	0	(23456)	1	(12345)	(567)	1
pseudopratensis	(234)	4	(01)	(45)	(45)	(345)	1	(345)	(23)	(2345)	(12345)	(3456)	1	1	(01)	0	0	2	1	1	0	(4567)	2	5	0	1
ranjani	(34)	4	0	(34)	5	(012)	0	(345)	(012)	(0123)	(0123)	(78)	1	1	0	0	0	3	(12)	1	4	8	2	(12)	(12)	2
scribneri	2	4	2	(34)	(34)	(12)	1	(345)	(012)	(01234)	(12345)	(23456)	1	1	(01)	0	(01)	3	(12)	(01)	2	8	2	(345)	0	1
sefaensis	(234)	(34)	1	(34)	(345)	(23)	1	(45)	(123)	(2345)	(123)	(4567)	1	1	0	0	1	3	1	0	2	(567)	1	(2345)	(01)	(12)
sensillatus	(34)	4	1	(34)	(345)	(234)	1	(45)	(2345)	(01)	(012)	(123)	1	1	0	1	(01)	3	(12)	0	4	8	0	(2345)	(01234)	(12)
similis	2	1	2	(56)	3	3	1	(34567)	(0123)	(345)	(12345)	8	1	1	0	0	0	2	(01)	(01)	0	7	2	1	0	2
subranjani	(12345)	(01)	1	(23)	(123)	(012)	0	(45)	(01)	(12345)	(01234)	(234567)	1	(12)	0	(12)	(012)	3	(01)	0	(34)	8	2	(0123)	(01234)	1
sudanensis	(34)	4	1	(34)	(2345)	(23)	1	(23)	(0123)	(12345)	(1234)	(34567)	1	1	(01)	0	1	2	1	1	(01)	(34)	2	(345)	0	1
teres	2	1	1	(23)	(45)	(12)	1	(1234)	(01234)	(45)	(45)	8	1	(12)	2	0	3	3	1	(01)	4	8	2	5	4	1
thornei	4	4	1	(23)	3	(123)	0	(2345)	(123)	(0123)	(0123)	(23456)	1	1	0	0	0	3	2	(01)	(34)	0	(12)	(345)	0	1
unzenensis	(34)	0	1	(34)	(1234)	(012)	0	(34)	0	(345)	(1234)	(567)	1	1	0	(12)	(012)	2	(01)	0	0	7	2	(2345)	(01234)	1
vulnus	1	4	(01)	(23)	(234)	(12)	0	(456)	(01234)	(0123)	(012)	(34567)	1	1	0	0	(012)	2	0	0	0	(12345)	1	(01)	(34)	0
wescolargicus	2	4	(01)	(23)	(34)	3	1	(45)	(123)	(0123)	(0123)	(4567)	2	2	0	(12)	1	3	1	0	2	8	2	5	(012)	1
zeae	1	4	1	(34)	2	1	0	(123)	(012)	(01234)	(12345)	(23456)	1	1	0	0	0	3	0	(01)	3	8	2	(2345)	(1234)	1

events: shift of vulva backwards (8: 3 → 4), decrease of cytoplasm quantity in sperm cells (18: 0 → 2), and elongation of the oesophageal gland lobe (25: 0 → 3). Within this group, *P. vulnus* is the most primitive species, from which *P. pseudocoffeae* and *P. ekrami* differ in the following synapomorphies (node 94): decrease in number of the lip annuli (3: 0 → 1), decrease of the stylet length (4: 3 → 4), and shortening of the male spicules (22: 5 → 6).

The next group originated from the ancestor species of *Pratylenchus* is a phylogenetic stock of all other species of the genus. They are characterized by the following synapomorphies (node 93): change of the tail shape from conical to rounded (1: 1 → 2), decrease in number of the tail annuli (6: 1 → 2), shortening of the body (10: 0 → 2), decrease of the relative body size (11: 0 → 1; 12: 4 → 5), transition to the spherical metacorpus (20: 0 → 1), and reduction of the posterior branch of the female genital system (23: 1 → 2; 24: 1 → 4). *P. goodeyi* is the most primitive species in this group. Other species (node 92) are characterized by the following synapomorphies: shift of vulva backwards (8: 3 → 4), decrease of the cytoplasmic part in sperm cells to a thin layer surrounding the sperm nucleus (18: 0 → 2), and change of tail shape from conical to subcylindrical (19: 0 → 1).

Node 92 gives an origin for two groups. The smaller one is very interesting (node 91), as it includes *P. pratensis* (the type species of the genus) and *P. coffeae*, an intensively studied species of agricultural importance. Node 91 is characterized by the following synapomorphies: decrease in number of the lip annuli (3: 0 → 1), separation of the lip region (7: 0 → 1), and reduction of the incisures of the lateral field on tail (17: 0 → 1). The results prove that the "coffeae group" studied by the participants of several international projects does not exist in *Pratylenchus*, because *P. coffeae* and the closely related species have no distinct hiatus from the species that are close to the type species of the genus.

The largest group branching from node 92 includes all other pratylenchs (node 86) with the following synapomorphies: decrease in number of the tail annuli (6: 2 → 3), decrease of the relative body size (11: 1 → 3), and shortening of the male spicules (22: 5 → 6). The group splits itself into two large groups: nodes 64 and 85. There are the following apomorphies for node 64: decrease of the relative tail length (5: 3 → 4), normal (10: 2 → 4) and relative (11: 3 → 4) shortening of the body.

Node 85 (which includes the most primitive species *P. thornei*) is characterized by the following changes: transformation of conical tail into a blunt (1: 2 → 3) and short one (9: 1→ 2), and transition to parthenogenesis accompanied by the loss of sperm in spermatheca (18: 2 → 3; 21: 0 → 2). Two subrgroups take origin from node 84, namely nodes 83 and 76. Node 83 is characterized by the following changes: decrease in number of lip annuli (3: 0 → 1) and considerable elongation of the oesophageal gland lobe (25: 0 → 3). Within this node, the separation of the lip region is typical of the pinguicaudatus-dasibarkati group (node 82, 7: 0 → 1), whereas the brachyurus-australis group (77) is marked by the following apomorphies: heavy sclerotized cephalic framework (13: 1 → 2) and the final reduction of the spermatheca till its complete fusion with other part of the female genital tube (21: 2 → 4). Node 76 has as apomorphy the decrease of the relative tail length (5: 3 → 4). This node gives an origin to two others, 75 and 71. Apomorphies of node 75 are shortening of the body (10: 2 → 3) and reduction of the spermatheca (21: 2 → 4). Within this branch, node 74 (delattrei-microstylus-mulchandi-ranjani) is separated with two apomorphies: decrease of the stylet length (4: 3 → 4) and elongation of the oesophagus (12: 5 → 7). Node 71 is characterized by two apomorphies: separation of the lip region (7: 0 → 1) and shortening of the posterior branch of the female genital system (24: 4 → 5). Node 70 branches out within the last group (*P. neglectus, P. scribneri* with its junior synonym *P. jordanensis*, and *P. hexincisus*) with the following changes: decrease in number of the lip annuli (3: 0 → 2) and shortening of the stylet (4: 3 → 4). The other node within group 71 unites *P. andinus, P. sefaensis, P. sensillatus, P. bolivianus* and *P. wescolargicus* (68) with the following changes: shift of the vulva posteriad (8: 4 → 5), development of the lateral field areolation (16: 0 → 1) and transformation of the median bulb into a spherical one (20: 1 → 0). *P. bolivianus* and *P. wescolargicus* (67) are characterized by the sclerotization of the cephalic framework (13: 1 → 2), whereas *P. andinus, P. sefaensis* and *P. sensillatus* (66), by the decrease in number of the lip annuli (3: 0 → 1).

Node 64 is the last large set of species. Groups 63 and 60 take their origin from this node. For the penetrans group (63: *P. penetrans, P. pseudopratensis, P. crassi,* and *P. emarginatus*), the following two transformations are important: separation of the lip region (7: 0 → 1) and decrease of the relative body length (11: 4 → 5). Node 60 is characterized by decrease in number of the lip annuli (3: 0 → 1). The group conval-

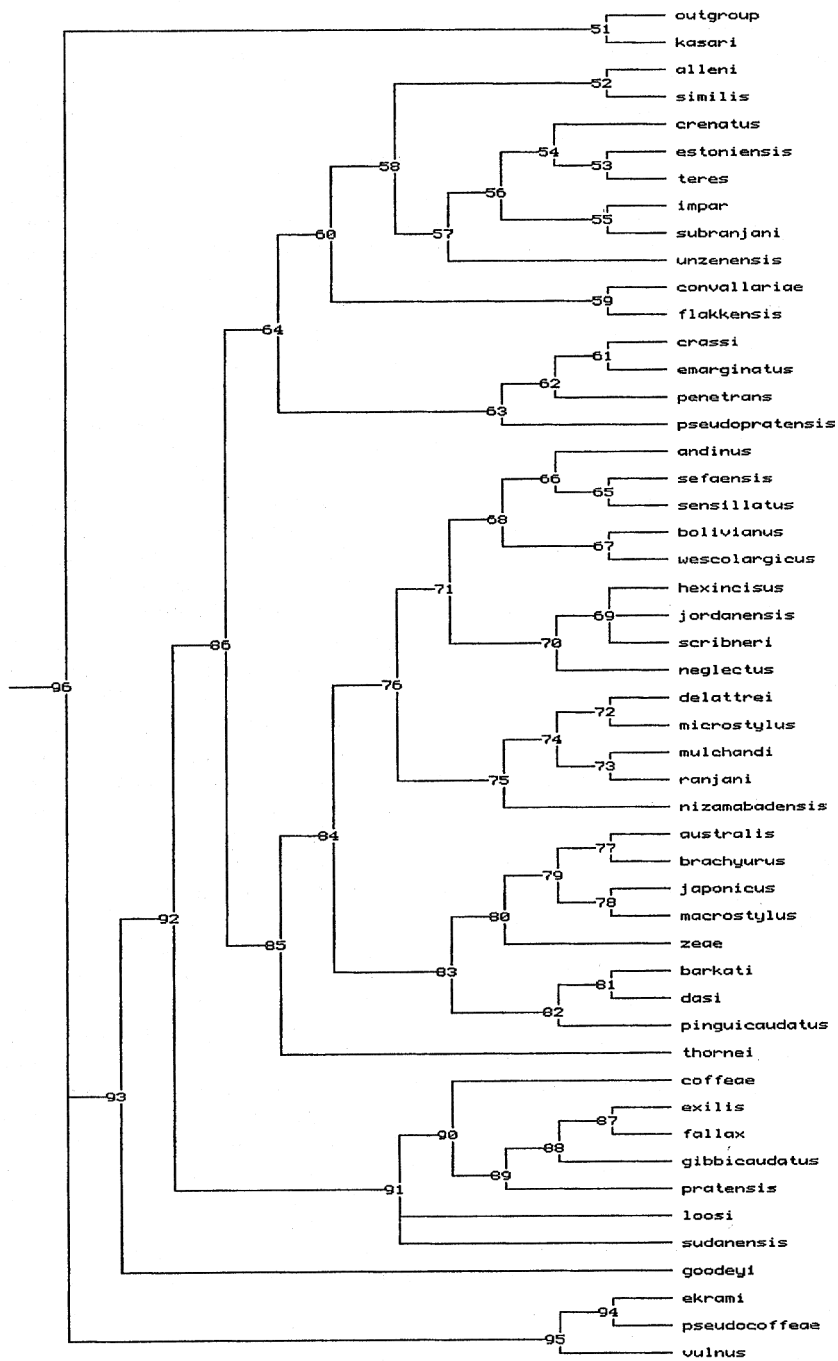


Fig. 27. Cladogram of the genus *Pratylenchus* (PAUP, 50% Majority Rule Consensus Tree).

lariae-flakkensis (59) has two apomorphies: separation of the lip region (7: 0 → 1) and change of the spermatheca shape from oval to spherical (21: 0 → 1). The other branch (58) has two apomorphies: increase in the relative length of oesophagus (12: 5 → 7) and shortening of the male spicules (22: 6 → 7). Nodes 52 and 57 originate from branch 58. *P. alleni* and *P. similis* (52) have the following transformations: decrease in number of the lip annuli (3: 1 → 2), shortening of the stylet (4: 3 → 4) and separation of the lip region from the body (7: 0 → 1).

In branch 57, the group crenatus-estoniensis-teres-impar-subranjani (56) is characterized by apomorphies connected with the transition to parthenogenesis (18: 2 → 3; 21: 0 → 2, 22: 7 → 8). For *P. impar* and *P. subranjani* (55), the reduction of spermatheca is typical (21: 2 → 3), whereas *P. crenatus, P. estoniensis* and *P. teres* (54) are characterized by the separation of the lip region (7: 0 → 1) and increase in number of the lateral field incisures (15: 0 → 2). *P. estoniensis* and *P. teres* are joined by the following changes: increase in the relative length of oesophagus (12: 7 → 8), shift of the stylet knobs anteriad (14: 1 → 2), and shortening of the posterior branch of the female genital system (24: 3 → 4).

According to the cladogram (Fig. 27) and the foregoing analysis, the following species groups can be outlined within the genus *Pratylenchus*:

1. alleni (node 52): *P. alleni, P. similis.*
2. crenatus (node 54): *P. crenatus, P. estoniensis, P. teres.*
3. subranjani (node 55): *P. impar, P. subranjani.*
4. flakkensis (node 59): *P. flakkensis, P. convallariae.*
5. penetrans (node 63): *P. crassi, P. emarginatus, P. penetrans, P. pseudopratensis.*
6. sefaensis (node 66): *P. andinus, P. sefaensis, P. sensillatus.*
7. bolivianus (node 67): *P. bolivianus, P. wescolargicus.*
8. scribneri (node 70): *P. scribneri* (with its junior synonym *P. jordanensis*), *P. hexincisus, P. neglectus.*
9. delattrei (node 75): *P. delattrei, P. microstylus, P. mulchandi, P. ranjani, P. nizamabadensis.*
10. brachyurus (node 80): *P. brachyurus, P. australis, P. macrostylus. P. japonicus, P. zeae.*
11. pinguicaudatus (node 82): *P. pinguicaudatus, P. barkati, P. dasi.*
12. pratensis-coffeae (node 91): *P. pratensis, P. coffeae, P. exilis, P. fallax, P. loosi, P. sudanensis, P. gibbicaudatus.*
13. vulnus (node 95): *P. vulnus, P. ekrami, P. pseudocoffeae.*

Species not included in the groups: *P. kasari, P. unzenensis, P. thornei, P. goodeyi.*

Evidence of the biological progress in the genus *Pratylenchus*

Definition of the *biological progress* of a taxon includes the large number of its species, large area of its distribution and the general development of its morpho-biological features. The analysis of state frequencies of some characters shows that the biological progress takes place within the genus *Pratylenchus*. The most advanced states of some characters are present in the majority of the *Pratylenchus* species (Fig. 28). These characters and states are listed below: sperm in female spermatheca (character 18: 92% of pratylenchs species have the most advanced states of this character, located in the diagram to the right of the median of character states); ratio of tail length to anal body width (*c'*) (character 5: 82 % of species are characterized by the advanced states); length of posterior genital branch (character 24: 76% of species); cephalic region (character 7: 74% of species); index *b* (character 12: 72% of species); spicule length (character 22: 70% of species); differentiation of posterior genital branch (character 23: 64% of species); shape of median bulb (character 20: 60% of species); and tail tip annulation (character 2: 59% of species).

The diagram (Fig. 28) displays the trends of transition to the parthenogenesis in the genus (character 18), shortening of the body due to the inhibition of the postembryonic individual growth (character 12; *b*-value decreases in the postembryonic development, see Ryss, 1983, 1984, 1988), shortening of the tail and decrease of its adhesion to substratum (characters 5 and 2), accelerated reduction of the posterior part of the female genital system (characters 24 and 23), separation of the lip region (character 7) and transformation from the oval to spherical metacorpus (character 20). Reduction of the posterior genital branch in females is the consequence of shortening of the body (Ryss, 1981, 1988, 1993, 1994). The decrease in body length and the decrease of footing role of the tail are adaptations to migratory parasitism of pratylenchs. The parthenogenesis is also an adaptation, which makes the reproduction within roots easier. Separation of the lip region is connected with its enforcement, because the cephalic framework is the base for the protractor muscles of the stylet. Forma-

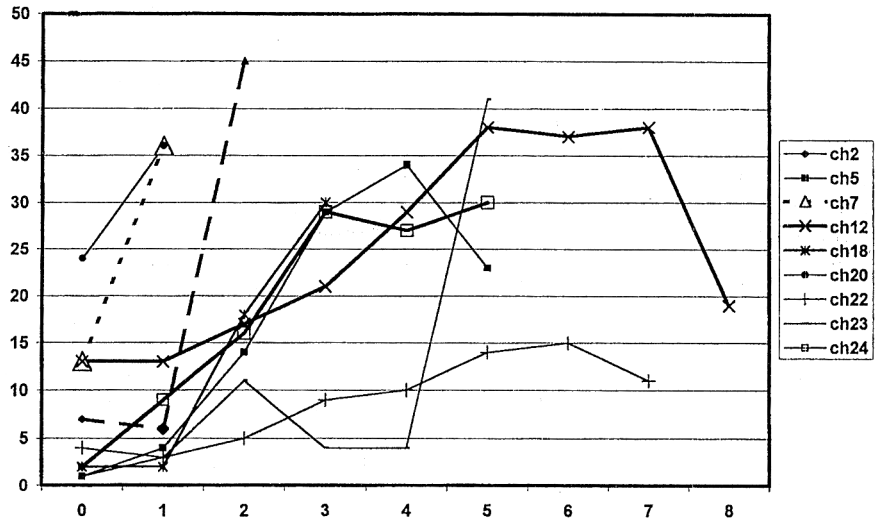


Fig. 28. Diagram of state frequencies of some characters in species of the genus *Pratylenchus*. Ordinate: number of species with the corresponding character state; abscissa: values 0-8 identical to the character states in the rows of characters. Styles of the graphics lines are shown to the right in the diagram legend (in rectangular frame); ch2, ch5, ch7... are the character 2, character 5, etc., respectively, where the character numbers correspond to those in the list of characters.

tion of the spherical median bulb corresponds to the increase of the sucking role of the anterior part of the oesophagus. As stated above, the frequency pattern of the character states within the genus demonstrates the increase of adaptations to the migratory endoparasitism. According to the analysis of the *Pratylenchus* phylogeny and the morphological changes in evolution, these adaptations have been developed independently in different phylogenetic lines of pratylenchs.

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