

A revision of the genus *Pseudacrobeles* Steiner, 1938 (Nematoda : Cephalobidae). Part 2. Subgenus *Bunobus* subgen. n., problematical species, discussion and key

Paul DE LEY*, Mohammad Rafiq SIDDIQI** and Sven BOSTRÖM***

* Instituut voor Dierkunde, Ledeganckstraat 35, 9000 Gent, Belgium

** International Institute of Parasitology, 395a Hatfield Road, St. Albans, Herts. AL4 0XU, England, and

*** Zoo. Tax. Naturhistoriska Riksmuseet, Box 50007, 104 05 Stockholm, Sweden.

Accepted for publication 9 September 1992.

Summary – *Bunobus* subgen. n. is proposed under the genus *Pseudacrobeles* for four species which were found to lack cephalic and labial probolae, and which have subdorsal and subventral lips more developed than the laterals. Three of these species, *P. pulcher*, *P. loofi* and *P. pseudolatus*, were previously placed in *Heterocephalobus* and are now transferred. The fourth is new: *P. cruzi* sp. n., very close to *P. pulcher* and *P. loofi*. The male of *P. pulcher* is described for the first time. The consequences on classification of the revised diagnosis of *Pseudacrobeles* (given in Part 1 of this revision) are discussed. *Heterocephalobus basilogoodeyi*, *H. bisimilis*, *H. elongatus*, *H. eurystoma*, *H. eximius*, *H. latus*, *H. loczyi*, *H. longicaudatus*, *H. multicinctus* and *H. nannus* are considered *species inquirendae* and/or *incertae sedis*. *Heterocephalobus magnificus* is transferred to *Heterocephalobellus*. Panagrocephalinae becomes a synonym of Cephalobinae with the rejection of *Panagrocephalus*. Acrolobinae subfam. n. is proposed for the genera *Acrolobus*, *Panagroteratus* and *Teratolobus*, being characterized by six deeply offset, flap-like lips and a cephalobid stoma. S.E.M. pictures of three *Bunobus* species are given, as well as a key for the redefined genus *Pseudacrobeles*, which is argued to represent the least derived group within Cephalobinae.

Résumé – Révision du genre *Pseudacrobeles* Steiner, 1938. Partie 2. Sous-genre *Bunobus* subgen. n., espèces problématiques, discussion et clé – *Bunobus* subgen. n. est proposé pour rassembler dans le genre *Pseudacrobeles*, quatre espèces dépourvues de probolae céphaliques ou labiales et dont les lèvres subdorsales et subventrales sont plus développées que les latérales. Trois de ces espèces, *P. pulcher*, *P. loofi* et *P. pseudolatus* appartenaient primitivement au genre *Heterocephalobus*; la quatrième, *P. cruzi* sp. n., est très proche de *P. pulcher* et *P. loofi*. Le mâle de *P. pulcher* est décrit pour la première fois. Les conséquences de la révision diagnostique de *Pseudacrobeles* sur la classification sont discutées. *Heterocephalobus basilogoodeyi*, *H. bisimilis*, *H. elongatus*, *H. eurystoma*, *H. eximius*, *H. latus*, *H. loczyi*, *H. longicaudatus*, *H. multicinctus* et *H. nannus* sont considérés comme *species inquirendae* et (ou) *incertae sedis*. *Heterocephalobus magnificus* est transféré au genre *Heterocephalobellus*. Le genre *Panagrocephalus* étant rejeté, la sous-famille des Panagrocephalinae devient un synonyme mineur des Cephalobinae. La sous-famille des Acrolobinae subfam. n. – caractérisée par des lèvres foliacées très en relief et un stoma de type Céphalobide – est proposée pour grouper les genres *Acrolobus*, *Panagroteratus* et *Teratolobus*. Des photographies au MEB de trois espèces de *Bunobus* sont données, de même qu'une clé du genre *Pseudacrobeles* ainsi redéfini. Il est considéré comme le moins évolué du groupe des Cephalobinae.

Key-words : (*Bunobus*), *Pseudacrobeles*, *Heterocephalobellus*, *Panagrocephalus*, *Acrolobus*, *Panagroteratus*, *Teratolobus*, Nematoda, Cephalobidae, morphology, taxonomy.

This is the second and final part of our study on the genus *Pseudacrobeles* Steiner (1938). The previous part (De Ley *et al.*, 1993), which will henceforth be referred to as "Part 1", presented and emended diagnosis for the genus, as well as the proposal of the subgenus *Pseudacrobeles*, for which a diagnosis, list of species and species descriptions were given. In addition, a superspecies was proposed for the type species *P. variabilis* and its closest relatives. We refer to this same paper for details on previous publications, methods, terminology, and a list of samples studied (Table 1 in Part 1). In this paper, a new subgenus is proposed for four species with aberrant lip region, and extensive discussions are given dealing with problematical species, diagnostic aspects of

characters, and several taxonomic and phylogenetic aspects. Following the synonymisation of *Panagrocephalus* Andrassy, 1967 with *Pseudacrobeles* (cf. Part 1), the subfamily Panagrocephalinae is synonymized with Cephalobinae. The new subfamily Acrolobinae is proposed to accommodate three genera linking Cephalobinae with Panagrolaimidae. Our material did not allow us to clarify relationships between *Pseudacrobeles* and the two related genera, *Cephalobus* Bastian, 1865 and *Eucephalobus* Steiner, 1936, which both have chronological priority to *Pseudacrobeles*. What is clear, however, is that *Pseudacrobeles* is as complicated a genus as any other in Cephalobidae, and that further studies are required for reassessment of this difficult group of species.

Subgenus *Bunobus* * subgen. n.

DIAGNOSIS

As for the genus *Pseudacrobeles*, but with the following restrictions: Lip region always with bilateral symmetry. Subdorsal and subventral lips separate, rounded, larger than lateral lips. Labial and cephalic probolae completely absent. Tail always elongate, conical, with acute tip.

TYPE SPECIES

Pseudacrobeles (Bunobus) pulcher (Loof, 1964) comb. n.

= *Eucephalobus pulcher* Loof, 1964 syn. n.
 = *Heterocephalobus pulcher* (Loof, 1964) Andr ssy, 1967 syn. n.

OTHER SPECIES

P. (B.) cruzi sp. n.
P. (B.) loofi (Andr ssy, 1967) comb. n.
 = *Heterocephalobus loofi* Andr ssy, 1967 syn. n.
P. (B.) pseudolatus (Hern ndez, 1990) comb. n.
 = *Heterocephalobus pseudolatus* Hern ndez, 1990 syn. n.

Table 1. Measurements in μm of *Pseudacrobeles (Bunobus) pulcher* (Loof, 1964) comb. n.

	Types (Nigeria & Venezuela)			Brazil	Burkina-Faso	India (I10, I11 I12, I14, I30)		Indonesia
	Loof (1964) 4 ♀♀	our measurements holo ♀	1 para ♀	(B4, B1857) 2 ♀♀	(BF) 1 ♀	7 ♀♀	1 ♂	(IN) 1 ♀
L	530-590		560	550-590	615	560-675	565	535
body width			21	24-27	27	24-30	18	21
pharynx length	141*	132	141	146-143	155	125-154	152	138
tail length	106*		98	98-101	98	92-111	45	94
anal width	11*		13	13-15	15	13-15	19	11
a	24-30		26	20-25	23	22-25	31	25
b	3.9-4.3		4.0	3.8-4.0	4.0	4.1-4.5	3.7	3.9
c	5.6-6.1		5.7	5.6-5.8	6.2	5.5-6.2	12.6	5.7
c'	9		7.5	6.7-7.5	6.6	6.8-7.4	2.4	8.5
stoma	13*	12	13	13-14	14	12-16	14	14
corpus	83*	76	82	84-89	96	77-93	90	86
isthmus	25*	25	27	24-30	26	21-30	30	24
bulbus	17*	17	18	15-18	18	14-17	16	13
corpus: isthmus	3.5	3.0	3.0	2.8-3.7	3.7	2.9-3.9	3.0	3.6
nerve ring	116*	83	90	66-95	101	85-105	99	
excretory pore	101*	87	95	75-96	105	84-103	99	96
deirid	109*		110	84-108	118	95-119	114	108
n.r. (% pharynx)	82*	63	64	46-65	65	62-69	65	
e.p. (% pharynx)	72*	66	67	52-66	68	67-69	65	67
deirid (% pharynx)	77*		78	59-74	76	73-78	75	
R _{an} (annuli)	47*		36	36-39	38	40-44	42	
R _{ep} (annuli)	40*		38	39	38	38-43	42	38
R _{dei} (annuli)	44*		44	43-44	44	44-49	48	
phasmid	22*	20	20	20-21	19	17-26	24	18
phasmid (% tail)	21-23		20	18-23	54	19		
cuticle thickn.			2.0	1.5	2.0	1.5	2.0	2.0
annule width	2.4		2.2	2.3-2.6	2.6	2.2-2.7	2.6	2.0
V (%)/flexure	56-58		56	55-57	55	54-58	45	57
G (%)/T (%)			29	31-33	33	27-33	51	31
vagina/spicules		8	8	8-11	7	8-11	22	8
rectum/gubernaculum		15	22	18-21	23	17-22	14	19
PUB/spike		20	15	20-24	26	17-24	0	16
spermatheca/mucro		24	27	31-45	30	20-44	0	

* Measured on Fig. 3 in Loof (1964) - see remarks in text on position of nerve ring.

* From the Greek word *βουνος* (hill), referring to the dome-shaped lips, combined with the last letters of *Cephalobus*.

Table 2. Measurements in μm of *Pseudacrobeles (Bunobus) loofi* (Andrássy, 1968) comb. n., *P. (B.) cruzi* sp. n., *P. (Bunobus) sp.* and *Heterocephalobus kaczanowskii* (Brzeski, 1960) Brzeski, 1961.

	<i>P. (B.) loofi</i>		<i>P. (B.) cruzi</i>			<i>Pseudacrobeles (Bunobus) sp.</i>	<i>Heterocephalobus kaczanowskii</i>
	Paraguay (types)* 4 ♀♀	Galápagos (G8, G13, G14, G17) 15 ♀♀	Galápagos G5 6 ♀♀	Galápagos G2f 1 ♀	Tanzania (T45) 2 ♀♀	Spain (S) 1 ♂	Poland (P) 1 paratype ♀
L	400-430	295-400	480-575	505	590-600	390	945
body width	18**	11-18	21-27	25	26-30	18	
pharynx length	114**	95-116	130-145	125	138-142	120	239
tail length	77-83**	46-81	90-111	105	110-116	35	80
anal width	9-11**	6-9	11-13	13	13-14	13	
a	22-24	20-30	22-25	20	20-23	22	
b	3.7-3.8	3.1-3.7	3.7-4.2	4.0	4.2-4.3	3.3	4.0
c	5.2-5.4	4.4-6.8	4.9-5.5	4.8	5.1-5.5	11	12
c'	8-10	5.4-10.7	8.0-9.4	8.1	8.1-8.9	2.7	
stoma	10-11	8-11	13-14	12	12-14	12	16
corpus	56**	50-62	71-82	75	82-83	64	155
isthmus	28**	20-31	27-32	24	27-28	32	42
bulbus	14-15	10-15	15-18	15	17-19	12	26
corpus : isthmus	2.5-2.8***	1.9-2.7	2.2-2.9	3.1	2.9-3.1	2.0	3.7
nerve ring	69**	39-70	75-91	80	97-98	72	
excretory pore	69**	48-75	77-96	87	98-101	76	
deirid		57-86	86-118	102	109-118		
n.r. (% pharynx)	61**	42-63	58-65	64	69-70	60	
e.p. (% pharynx)	61**	49-68	59-68	70	71	63	
deirid (% pharynx)		57-76	66-80	87	66-83		
R _{nr} (annuli)		64-65	48-54	48	50-52	47	
R _{sp} (annuli)		58-65	50-54	49	51-52	49	
R _{dei} (annuli)		65-75	55-63	58	57-60		
phasmid	18**	8-19	16-19	22	18-25	20	
phasmid (% tail)	< 25	14-27	15-19	21	22	57	
cuticle thickness	0.7-0.8	0.5-1	1-1.5	1.0	1.0-1.5	1.0	
annule width	1.4-1.6	0.9-1.2	1.3-1.6	-	1.6-1.7	1.1	2.5
V (%) / flexure	56-57	52-60	56-58	56	55-56	41	62
G (%) / T (%)		16-28	21-27	26	25-27	44	
vagina/spicules	5**	3-6	6-9	7	7-10	20	
rectum/gubernaculum	18**	12-17	15-20	16	19-23	12	26
PUB/spike	11**	2-10	13-19	14	14-18	0	52
spermatheca/mucro		3-9	17-20	18	19-20	0	

* Measurements by Andrásy (1968), except:

** Measured on Abb. 3 in Andrásy (1968).

*** Corpus : isthmus = 2.0 in Abb. 3B in Andrásy (1968)!

***Pseudacrobeles (Bunobus) pulcher*
(Loof, 1964) comb. n.**

(Figs 1 A-J; 2 A-C)

MATERIAL

Specimens were studied from B4 (1 ♀); B1857 (1 ♀); BF (1 ♀); I10 (1 ♀); I11 (2 ♀♀); I12 (1 ♀); I14 (1 ♀); I30 (4 ♀♀, 1 ♂); IN (1 ♀); N (1 paratype ♀); V (holo-

type ♀). Two specimens from I30 were studied with SEM.

MEASUREMENTS

See Table 1.

DESCRIPTION

Cephalic and labial probolae absent. Lateral lips strongly reduced, subventral and subdorsal lips sep-

arate, broadly rounded, connected by four tangential ridges. Lip region with bilateral symmetry, only four lips visible with light microscope. Cheilorhabdia bar-shaped in optical section. Second stoma section as wide and refractive as cheilostome. Nerve ring lying at two-thirds to base of corpus. Excretory pore from two annules anterior to three annules posterior to trailing edge of nerve ring. Deirid 4-6 annules posterior to excretory pore. Females with PUB 0.6-1.2 body widths long. One gravid specimen with single egg $48 \times 22 \mu\text{m}$. Rectum 1.2-2 ABW. Female tail tip slightly refractive, subacute to carrying a minute knob. Male tail without spike. Spicules $3.5 \mu\text{m}$ wide, 1.2 ABW long. Gubernaculum with *cornua crurum* moderately distinct.

JUSTIFICATION OF DETERMINATION

This species is easily recognized by its prominent annulation. The specimens agree well with the original description in all respects but one. Loof (1964) described and illustrated it with nerve ring lying at the base of the isthmus, but we always found it anterior to the corpus/isthmus-junction, both in the specimens from other localities as well as in the type material (albeit only indistinctly in the holotype). Loof (1964) did not specify the number of distinct lips, but observations with both SEM and light microscope always show four (Figs 1 A, B; 2 A, B). The male of the species has not been described before.

Pseudacrobeles (Bunobus) loofi (Andrássy, 1968) comb. n.

(Fig. 1 K-U; 2 G-J)

MATERIAL

Specimens were studied from G5 (1 ♀, 1J), G8 (1 ♀), G11 (1 ♀, 2JJ), G13 (6 ♀♀, 3JJ), G14 (14 ♀♀, 7JJ) and G17 (1 ♀). One female and one juvenile were studied with SEM. We were unable to examine type material.

MEASUREMENTS

See Table 2.

DESCRIPTION

Cephalic and labial probolae absent. Subventral and subdorsal lips separate, rounded but with slightly angular aspect caused by labial papillae; lateral lips less developed, usually still visible with light microscope, but in some specimens not discernible at all. Mouth opening hexagonal in female (Fig. 2 J), convex-triangular in juvenile (Fig. 2 H), in both connected with six short radial striae intercalating between the lips. True liplets (i.e. separate cuticular flaps) appear to be absent, however. Cheilorhabdia bar-shaped in optical section. Second stoma section similar to cheilostome in width but slightly less refractive. Nerve ring lying at three-fifths of corpus to base of corpus. Excretory pore from level of, to three annules posterior to, trailing edge of nerve ring. Deirid

6-12 annules posterior to excretory pore. PUB 0.3-0.9 corresponding body widths long. Rectum 1.4-2.4 ABW long. Female tail tip clearly refractive, always carrying a minute knob or hook. No adult or juvenile males found.

JUSTIFICATION OF DETERMINATION

The specimens from the Galápagos do not agree perfectly with the original description by Andrássy (1968), having narrower annules ($0.9-1.2$ vs $1.4-1.6 \mu\text{m}$), a shorter PUB ($0.1-0.3$ vs $2/3-3/4$ body widths) and a usually relatively longer pharynx ($b = 3.1-3.7$ vs $3.7-3.8$). Also, Andrássy (1968) did not specify the presence of a refractive hook- or knob-shaped tip for *P. (B.) loofi*, and as can be expected from the larger number of specimens measured, the material from the Galápagos exhibits much wider ranges in many measurements. This is especially true for tail length: one female (from G14) had a tail only $46 \mu\text{m}$ long ($c' = 5.4$), in another it was $53 \mu\text{m}$ long ($c' = 7.6$), and in the remainder $60-81 \mu\text{m}$ ($c' = 7.6-10.7$) without pronounced gaps.

We have identified our material as *P. (B.) loofi* because we think the differences noted may well be due to variability, e.g. we found *P. (B.) pulcher* with or without knobbed tail tip. We also took into account contrasts with the specimens described below as new species *P. (B.) cruzi*. These are very similar to *P. (B.) loofi* too, and in fact the type specimens of *P. (B.) loofi* as described by Andrássy (1968) are intermediate between the new species and our *P. (B.) loofi* in several respects (Table 2). Our evidence suggests that the latter two groups of specimens are indeed separate species, exhibiting several morphological differences (see below) while co-occurring in sample G5. We therefore estimated which of the two was most likely to represent *P. (B.) loofi* and, not having types of this species at our disposition, mainly based our conclusions on the fact that Andrássy (1968, 1970) described and illustrated the lip region of *P. (B.) loofi* as having lateral lips well distinguishable with light microscope. The specimens described above usually have a similar lip region, and are therefore considered to be, probably, *P. (B.) loofi*.

We consider the specimens described as *Heterocephalobus loofi* in Rashid *et al.* (1989) to be probably *P. (P.) [v.] variabilis* (see Part 1), while the animals identified as *H. loofi* by Zell (1987) might actually belong to *P. (B.) cruzi* sp. n.

*Pseudacrobeles (Bunobus) cruzi** sp. n.

(Fig. 1 V-DD; 2 D-F)

MEASUREMENTS

See Table 2.

* The specific epithet was chosen both in reference to Isla Santa Cruz as well as in honor of Mr. C. Cruz, whose help as guide was instrumental in the collection of the Galápagos samples.

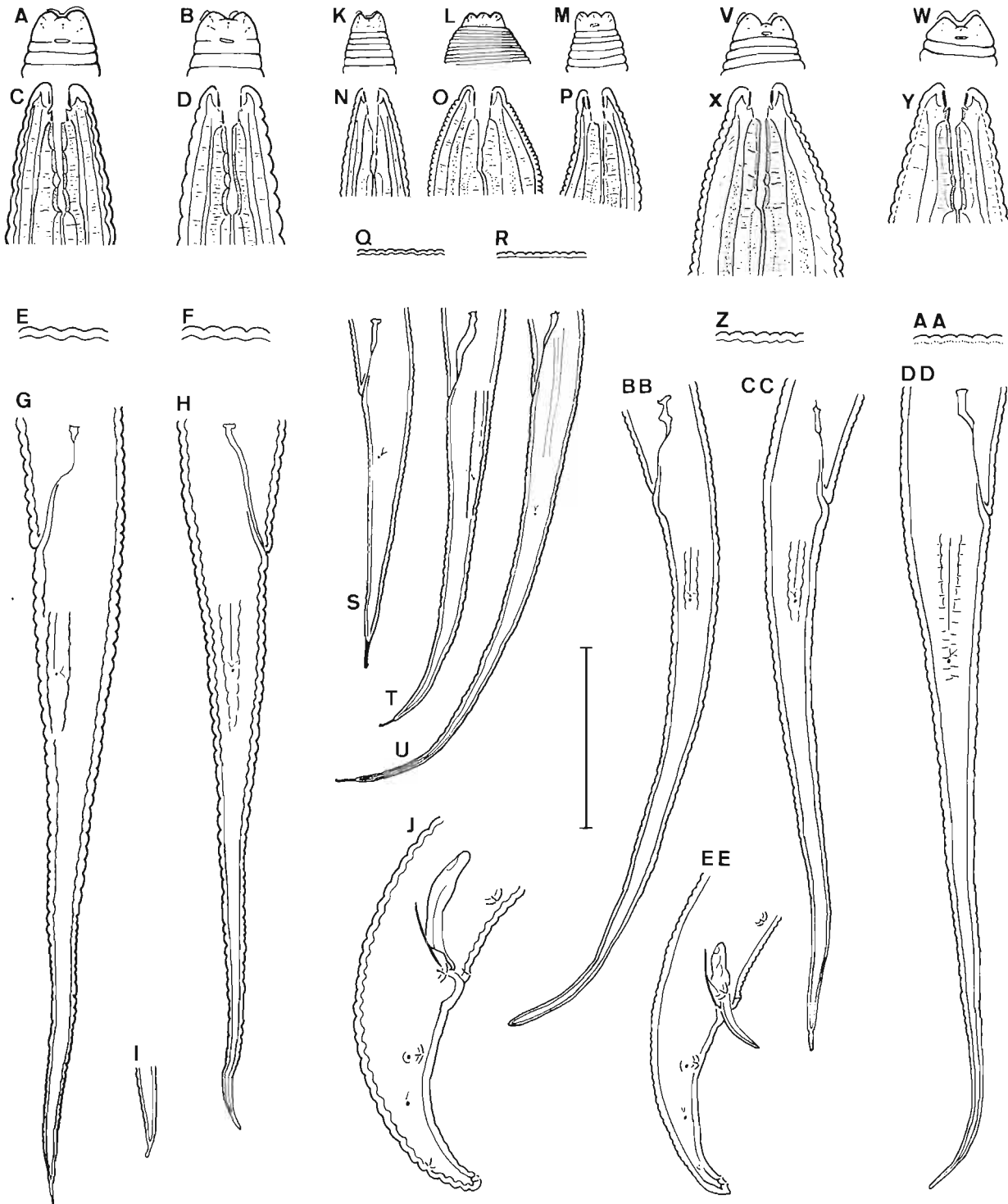


Fig. 1. *Pseudacrobeles (Bunobus) pulcher* (Loof, 1964) comb. n. A, C, F, J : Male from India (I30); B, D : Paratype female from Nigeria; E, H : Female from Brazil (B1857); G, I : From India (I11, resp. I30). - *P. (B.) loofi* (Andrássy, 1968) comb. n. K, N, S : From Isla Floreana (K, N from G13; S from G14); L, O, Q, T : From Isla Fernandina (G17); M, P, R, U : From Isla Santa Cruz (G8). - *P. (B.) cruzi* sp. n. V, X, Z, BB, CC : From Isla Santa Cruz (G5); W, Y, AA, DD : From Tanzania (T45). - *Pseudacrobeles (Bunobus)* sp. : EE : male from Spain. (Scale bar = 30 μ m for tails, 20 μ m for rest.)

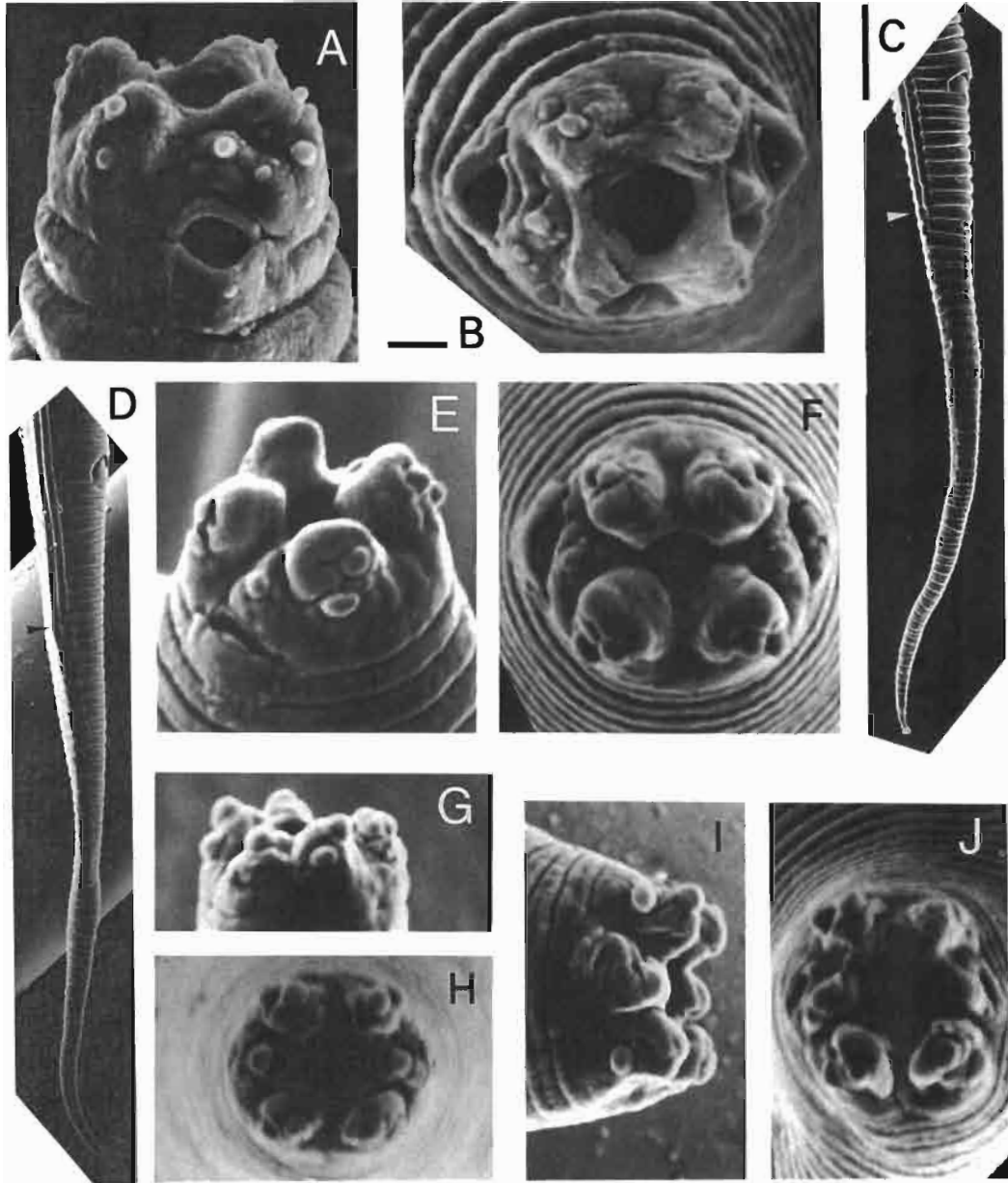


Fig. 2. *Pseudacrobeles (Bunobus) pulcher* (Loof, 1964) comb. n. A-C : Female from India (I30). – *P. (B.) cruzi* sp. n.; D-F : Female from Isla Santa Cruz (G5). – *P. (B.) loofi* (Andrássy, 1968) comb. n. from Isla Santa Cruz (G5); G, H : Juvenile; I, J : Female. Dorsal side is up in B, F, I, J and on left in A, E, G. Arrowheads in C, D point at phasmid (Scale bar of B is 1 μ m and applies to all lip regions. Scale bar = 10 μ m for C and D.)

DESCRIPTION

Cephalic and labial probolae absent. Lateral lips low, hardly visible with light microscope; subventral and subdorsal lips separate, conical-blunt. No tangential ridges or radial striae. Lip region with bilateral symmetry, showing only four lips with light microscopy. Cheilorhabdia bar-shaped in optical section. Second stoma section slightly narrower than cheilostome, wider and more refractive than subsequent sections. Nerve ring lying at base of corpus to anterior end of isthmus. Excretory pore 0-2 annules posterior to trailing edge of nerve ring. Deirid 5-9 annules posterior to excretory pore. PUB 0.5-0.9 body widths long. Rectum 1.1-1.8 ABW long. Female tail tip slightly refractive, sharp or somewhat irregular. Male not found.

DIFFERENTIAL DIAGNOSIS

P. (B.) cruzi differs from the specimens determined by us as *P. (B.) loofi* i.a. in its more prominent subventral and subdorsal lips (Figs 1 K-M, V-W; 2 E, I), larger size (L = 480-600 vs 295-400 μm), lower R_{ep} (50-54 vs 58-65) and R_{dei} (55-63 vs 65-75), longer stoma (12-14 vs 8-11 μm), longer PUB (13-19 vs 2-10 μm) and wider annuli (1.3-1.7 vs 0.9-1.2 μm). It differs from *P. (B.) loofi* as originally described in having lateral lips absent versus still discernible with light microscope, larger size (L = 480-600 vs 400-430 μm), longer stoma (12-14 vs 10-11 μm), thicker cuticle (0.7-0.8 vs 1.0-1.5 μm) and proportionally usually shorter rectum (1.1-1.8 vs 1.7-2 ABW). It differs from *P. (B.) pulcher* in higher R_{ep} (50-54 vs 38-43) and R_{dei} (55-63 vs 43-49), narrower annuli (1.3-1.7 vs 2.0-2.7 μm) and proportionally usually slightly longer tail ($c = 4.8-5.5$ vs 5.5-6.2). With SEM, another difference is the absence of tangential ridges (Fig. 2 A, B, E, F). It can be distinguished from *P. (B.) pseudolatus* i.a. by the female tail (tip tapering vs dorsally convex, $c = 4.8-5.5$ vs 8.4-9.4, $c' = 8.0-9.4$ vs 4.2-4.5), vulva position (V = 55-58 vs 61-63 %) and female body slenderness ($a = 20-25$ vs 15-18).

TYPE LOCALITY AND HABITAT

Humid soil around roots of *Scalesia*, 3 m west of road Isla Baltra-Santa Rosa at 670 m altitude, northern slope of Isla Santa Cruz, Galápagos Archipelago, Ecuador (G5).

OTHER LOCALITIES AND DISTRIBUTION OF TYPE MATERIAL

Specimens were studied from G2f (1♀, 1J); G5 (8♀, 9 juv.); G7 (1♀, 3 juv.); G15 (2♀) and T45 (2♀). The female from G7 and two juveniles from G5 were studied with SEM. The material is distributed among collections as follows: holotype ♀ and paratype ♀ in the Muséum National d'Histoire Naturelle, Paris, France; six paratype ♀♀ in the Instituut voor Dierkunde, Universiteit Gent, Belgium; two paratype ♀♀ (from Tanzania) in the International Institute of Parasit-

ology, St Albans, UK; one paratype ♀ in the Department of Systematic Zoology and Ecology of the Eötvös Loránd University, Budapest, Hungary; one paratype ♀ in the USDA Nematode Collection, Beltsville, USA.

JUSTIFICATION OF DETERMINATION

Allocation of these specimens to a new species, despite overall resemblance to *P. (B.) loofi* as originally described, is based mostly on lip region shape. In view of the great variability of this character encountered in *P. (P.) [v.] variabilis* (cf. Part 1), this would appear to be a poor criterion, but we saw no lateral lips with light microscope in all 27 specimens (adult and juvenile) studied, from five different localities. The same rigidity was observed in the clearly closely related species *P. (B.) pulcher*, and we therefore assume that the lip region is much less variable in these two species. Furthermore (see above) we found specimens with *P. (B.) loofi*-like lip region that most probably represent a different species. There also is some biometric support for distinction, although admittedly slight. Re-examination of the type material of *P. (B.) loofi* is still desirable to clarify relationships with our specimens, as we may well be dealing with yet another species complex.

We also examined a single male *P. (Bunobus)* sp. from Spain (sample S) that corresponds rather well with the male one would expect for *P. (B.) cruzi*, but has lower values than the females for a number of measurements (Table 2). Without females from the same locality it is better not assigned to a species at present.

Discussion

1. SPECIES INQUIRENDAE VEL INCERTAE SEDIS

As explained in section 5 of this discussion, *Heterocephalobus* Brzeski, 1960 is considered *genus inquirendum*. The following species were placed in the genus by Andrassy (1967a, 1984), but should in our opinion be re-examined before transferring them to *Pseudacrobeles* or any other genus. Species are listed under their original names.

Acrobeles bisimilis Thorne, 1925 is depicted by Thorne (1925: Fig. 8 b) with a lip region similar to that of *Eucephalobus*. As the delineation of this genus from *Pseudacrobeles* and others needs investigation (see discussion), allocation of the species is uncertain at present.

Cephalobus elongatus de Man, 1880: While the validity of this species is not questioned, its position cannot be ascertained at present. Fig. 57 b in de Man (1884) depicts the female tail of this species with a lateral field extending over two-thirds of its length, while not showing the phasmid position. Pending on resolution of the delineation of *Cephalobus*, *Eucephalobus*, *Heterocephalobus* and *Pseudacrobeles*, the species could belong to any of these genera (see below and in discussion).

Cephalobus latus Cobb, 1906: The original descrip-

tion contains three elements which suggest that this species belongs in Rhabditidae instead of in Cephalobidae: *i*) $V = 50\%$, approached only by cephalobids with extremely slender tail (e.g. Tables 1, 2); *ii*) "... the anterior half [of the pharynx] being upon the average one-half, while the posterior half is only one-fourth as wide as the... neck", suggesting a corpus: isthmus-junction halfway the pharynx; *iii*) "The sexual organs are double and reflexed" (Cobb, 1906). The allocation of the species to Cephalobidae is mainly due to the "re-description" in Thorne (1937), but there is no indication that this was based on specimens representing Cobb's species.

Cephalobus longicaudatus Bütschli, 1873 was described very succinctly by Bütschli (1873) from juveniles only. Since then different authors have identified a range of different Rhabditida as being this species (e.g. a cephalobid in de Man, 1884; a panagrolaimid in Liebermann, 1927; a rhabditid in Steiner, 1936b). None of these authors report having examined Bütschli's material, and from the original description it cannot be deduced which nematodes are really concerned. It must be noted that several of the species included here in *Pseudacrobeles* fit Bütschli's description.

Cephalobus loczyi von Daday, 1894: The description of this species in von Daday (1897) contains some peculiar features, while giving too few details on other points to allow allocation to a genus with any confidence. The male posterior end depicted in Fig. 24 in von Daday (1897) has a spicule only 0.8 ABW long, which is proportionally quite small for Cephalobidae. The lip regions shown in his Figs 22, 23 and 25 appear to have been studied at too low a magnification to allow deduction of its true configuration, while Fig. 22 and 23 both show a nerve ring lying much more anterior than usual in the family. The pharynx is described and illustrated as having a clearly swollen corpus, suggesting placement in *Acrobeloides* (Cobb, 1924) Thorne, 1937, but all these features need confirmation before reliable conclusions can be drawn.

Cephalobus multicinctus Cobb, 1893: Andrassy (1984) considered this a probable synonym of *C. elongatus* (see above), but as with *C. longicaudatus* the original description actually leaves room for synonymy with a number of the species treated here.

Eucephalobus nannus Steiner, 1936 appears ill-placed in Cephalobidae: $V = 53$, with stoma and pharynx as shown in Fig. 8 in Steiner (1936a) reminiscent of Panagrolaimidae (the apparent division of the stoma wall in rhabdia is actually due to Steiner's habit of representing cuticular annulation: cf. e.g. Fig. 25 B in Steiner, 1936b). The single type specimen appears to be lost (Morgan Golden, pers. comm.). We have checked remaining material of the sample from which Steiner isolated the species, but found no specimens complying fully to his description. However, we did encounter nu-

merous *Panagrolaimus* specimens, the adults of which were much bigger than the 340 μm reported for *E. nannus*, but did resemble Steiner's illustrations rather well. Considering the taxonomical complexity of *Panagrolaimus* and the fact that Steiner would have to have made a series of errors for his description to apply to these animals, we will refrain from definite conclusions at this point. The *Panagrolaimus* specimens have been reclassified in the USDA Nematode Collection as *Eucephalobus nannus?* on slides G-10150 to G-10174.

Heterocephalobus basilogoodeyi Brzeski, 1961 was transferred to *Acrobeloides* by Andrassy (1984) because of the swollen pharyngeal corpus (cf. Fig. 3 in Brzeski, 1961). Its lateral field apparently has only two incisures (Fig. 5 in Brzeski, 1961) and extends to the sharp tail tip. These characters constitute a mixture of features found in *Acrobeloides*, *Cephalobus*, *Eucephalobus* and *Heterocephalobus* – genera that are poorly delineated at present. The precise structure of the lip region is unclear, and the species cannot be placed adequately in a genus without elucidation of these points.

Heterocephalobus eurystoma Andrassy, 1967 has a lip region that suggests its belonging in *Eucephalobus* (Abb. 12 a, b in Andrassy, 1967a). However, the definition and diagnosis of this genus needs further investigation (see discussion).

Heterocephalobus eximius Mukhina, 1981 has a lateral field with four incisures, one or two of these extending well posterior to the phasmid (Fig. 54 D, E in Mukhina, 1981). The pharynx has a slender corpus three times as long as the isthmus. The second stoma section is as wide as the cheilostome – it was actually interpreted as being part of this by Mukhina (1981). Three rounded lips are drawn and reported. The number of lateral lines of the species supports its validity, but adds to difficulties in generic allocation due to the uncertain diagnostic value of the extent of the lateral field on the tail (cf. *Cephalobus elongatus* and *H. kaczanowskii*).

Heterocephalobus kaczanowskii (Brzeski, 1960) Brzeski, 1961 is the original type species of *Heterocephalobus*, but was synonymized with *C. elongatus* (now *H. elongatus*) by Andrassy (1967a). We have examined a female and a juvenile paratype, both in poor condition, the female being clearly flattened. Measurements are given in Table 2. The lateral field has three incisures, and appears to extend far on the tail in the juvenile (unclear in female). The lip region has triradiate symmetry, with low, ridge-like labial probolae and without cephalic probolae (Fig. 4 B). The second stoma section is almost as wide as the cheilostome, but not as refractive (Fig. 4 C). Nerve ring, excretory pore, deirid and phasmid could not be seen. The female tail is conical, with an acute, slightly dorsally convex tip (Fig. 4 A). These specimens support Andrassy's synonymization of the species, but unfortunately do not resolve its generic position, phasmid and lateral field being unclear on the tail. Partly

because of this, the status of Brzeski's genus with respect to *Pseudacrobeles* becomes doubtful (see section 5 below).

We refer to Andr ssy (1984) for an additional list of *species inquirendae* that have been placed in *Heterocephalobus* at one time or another. A last species that must be mentioned is *H. magnificus* Andr ssy, 1987, which is rather slender with long pharynx and PUB, being quite reminiscent of *Heterocephalobellus brasiliensis* Rashid *et al.* (1985) and *H. potamiensis* Bostr m, 1991. We therefore propose *Heterocephalobellus magnificus* (Andr ssy, 1987) comb. n. = *Heterocephalobus magnificus* Andr ssy, 1987 syn. n. It is worth noting that *Heterocephalobellus* can be diagnosed by the fact that the PUB extends well posterior to the ovary tip, a feature known for no other Cephalobidae.

2. DIAGNOSTIC ASPECTS OF SOME CHARACTERS

Our material allows some remarks to be made on the application of a number of morphological features in the diagnosis of species in this group of cephalobids.

Lip region: Considerable variation in lip region has already been reported for several Cephalobidae in cultures raised in different conditions (Anderson, 1965, 1968; Anderson & Hooper, 1970, 1971). Rashid *et al.* (1985) reported similar variation in their field population of *P. (P.) [v.] tabacum*, and we encountered this phenomenon yet again in *P. (P.) [v.] variabilis* from Brazil and Tanzania (Part 1 : Fig. 3 B-F, H-L). Presence or absence of well-developed probolae is clearly not a reliable species character in representatives of several genera. However, there do seem to be differences in the potential for variation between different populations, and these may well be linked to genetic differences (Bostr m & Gydemo, 1983).

In our material character variability was inconsistent, depending on the populations considered. For instance, within the superspecies *P. (P.) [variabilis]* we found populations of *P. (P.) [v.] variabilis* with highly variable lip regions, while in *P. (P.) [v.] baloghi* it varied only between conditions of setiform *versus* stub-shaped cephalic probolae, and in *P. (P.) [v.] macrocystis* all animals have fully ornate lip regions. Also, the four species of the subgenus *Bunobus* were never found to exhibit labial or cephalic probolae. The precise shape of the lip region appears to be much more constant in this small group, although some variation is still possible in *P. (B.) loofi*. It seems acceptable to use the lip region in characterization of certain species after all, and in the case of *Bunobus* we have even used it as subgeneric character (see section 8 below).

Structure of anterior end of stoma: The shape of the cheilorhabdia in lateral view appeared to be useful in separating populations and species – which, considering their size, illustrates the difficulties within this group. We distinguished comma-, bar- and granule-shaped types (Fig. 3 H-J), although we certainly did encounter

intermediates, as well as variation encompassing two types in one population. However, the cheilorhabdia are not correlated with body size, and no group appeared to exhibit all three types. Thus, *P. (P.) [v.] macrocystis* and *P. (P.) [v.] variabilis* have different cheilorhabdia in spite of their similar measurements. The appearance of the second stoma section offers an additional helpful character, but one must often observe carefully just to see the section itself, let alone compare it to the cheilostome and the subsequent sections. Also, distortions or deformations in the stoma do occur (Figs 3 L, 5 D in Part 1) and it is necessary to examine this structure in lateral view to allow correct comparison.

Corpus : isthmus ratio and isthmus length: The anterior end of the isthmus may cause confusion, as the muscle fibers in its first 5 μm are often more prominent than in surrounding tissue (Fig. 3 A), and may even be fixed during contraction when surrounding fibers are not (Fig. 3 B, C). Functionally this suggests a slightly independent role of this region and biometrically it means one must be careful in determining the exact location of the corpus-isthmus junction, since slight errors may greatly influence the corpus : isthmus-ratio. A remark should be made with respect to Andr ssy (1968) : the ratio given for *P. (B.) loofi* in the text (2.5-2.8) does not agree with his Abb. 3 B, where it is only 2.0. Possibly, he included the stoma when measuring the corpus. Andr ssy (1970, Abb. 3) depicts another specimen with corpus : isthmus = 2.1.

Position of nerve ring, excretory pore and deirid: These three characters are widely used at species level in taxonomy of Cephalobidae and other Rhabditida. They are usually expressed in function of their general proximity to the subdivisions of the pharynx, and less commonly as an absolute distance (from the anterior end) or a percentage (of pharynx length). We have encountered considerable variability in these characters in several species, in some cases with nerve ring percentages ranging over 20 % or more (Table 3). This variability is apparently partly due to the great flexibility of the pharynx and the body cuticle. Indeed, the most anterior positions of nerve ring, excretory pore and deirid are found in specimens fixed in strongly arcuate position and/or with contracted cervical musculature (compare Fig. 3 D-G, D'-G'), conditions accompanied by tell-tale deformations such as a widened region of strongly compressed annules below the lip region (Figs 1 L, O, V, X; 3 F, G) and a collapsed isthmus (Fig. 3 F, G).

This means that the conventional methods for measuring the positions of nerve ring, excretory pore and deirid can only be applied reliably in specimens fixed in relaxed body postures. Fortunately, as excretory pore and deirid are fixed to the cuticle, the numbers of annules separating them from the lip region are not affected by distortive fixation. Counting these numbers is therefore to be recommended for much more wide-

Table 3. Comparison of variability in positions of nerve ring, excretory pore and deirid as determined by different methods of measurement in different specimens of four species of *Pseudacrobeles* Steiner, 1938.

species :		<i>P. (B.) pulcher</i>			<i>P. (B.) loofi</i>			<i>P. (P.) [v.] baloghi</i>			<i>P. (P.) [v.] macrocystis</i>			
sex & locality :		♀B1857	♂I30	♀I14	♀G17	♀G8	♀G14	♂G4	♀G18	♀G18	♀T41	♀T41	♀T41	♀T45
drawn in Fig. :		-	1 A, C	-	1 I, K	1 J, L	-	-	-	3 L, M	3 G	3 F	3 E	3 D
µm from	nerve ring	66	99	86	48	61	70	72	87	76	81	91	111	123
anterior	excretory pore	75	99	84	53	62	75	77	87	81	79	98	118	126
end	deirid	84	114	95	62	72	86	90	102	87	88	111	128	138
µm from	nerve ring	31	3	0	16	5	0	22	14	8	42	44	22	3
corpus/	excretory pore	25	5	4	14	6	-3	18	13	3	46	40	17	4
isthmus*	deirid	16	-10	-7	6	-4	-13	6	0	-3	37	27	7	-7
% of	nerve ring	46	65	69	44	55	61	53	59	62	-	49	58	68
pharynx	excretory pore	52	65	67	49	56	65	56	59	66	-	53	63	69
length**	deirid	59	75	76	57	65	74	66	69	71	-	60	67	76
annules	nerve ring	36	42	40	61	61	63	63	56	54	62	63	65	58
from lip	excretory pore	39	42	42	62	61	65	65	56	57	59	65	67	59
region	deirid	43	48	45	70	71	73	74	63	62	66	73	74	64

* Negative values indicate positions *posterior* to junction corpus/isthmus.

** Dashes indicate pharynx could not be measured (due to collapsed isthmus).

spread application in cephalobid taxonomy. The nerve ring, being flexible and connected with nerves as well as with the cuticle, is more variable in position by its nature (see also Anderson, 1968), and therefore less reliable even with annule counts. This being said, except for the *Bunobus* populations ranges of annule counts tended to overlap considerably between related forms. *P. (B.) pulcher* is nevertheless distinguishable from all other *Pseudacrobeles* species by its R_{ep} of 38-43 – the only case we encountered of a species unequivocally recognizable by a single character! Also, annule counts are evidently correlated with annule widths, and it is no surprise that the *Bunobus* populations diverge in annule width as well as R_{ep} and R_{dei} .

Spermatheca : In the females of most species we examined, the length of the spermatheca when filled with sperm did not exceed 45 µm, and separate spermatozoa of 2-4 µm diameter could be seen within (Fig. 3 N). Larger spermathecae (Fig. 3 O-Q) were only found in some of the females identified as *P. (P.) [v.] macrocystis*, and here also the sperm cells sometimes appear to be packed so close that only their nuclei are distinguishable (Fig. 3 P). A truly enormous spermatheca (104 µm!), which also contained two fibrillar masses in addition to faintly distinguishable sperm, was found in one female from Cameroon (Fig. 3 Q). This was probably a pathological condition, but spermatheca lengths up to 77 µm do appear to be naturally possible within the species. Spermatheca length is obviously diagnostically very sus-

pect, both because of the great structural flexibility of the organ and because it cannot be applied to young females. On the other hand, it is peculiar that such large spermathecae are found in only one form of *Pseudacrobeles*. Anderson and Hooper (1970) found a maximum spermatheca length of 52 µm in 66 females of *C. pers-egnis*. We have encountered similar sizes in other cephalobid genera only very occasionally, and think it may be a useful species character at population level. Species status of *P. (P.) [v.] macrocystis* is not based on this feature alone (see section 3 below), but in part.

Female tail : A number of aspects of the female tail structure can be distinguished. We will consider tail length, number of ventral annules and tail tip shape. Female tail length is useful in the characterization and allocation of populations, but it must be noted that slight errors of measurement can considerably influence the calculated c' , mainly because of the large percentual error on anal body width. Also, intraspecific variability should not be underestimated (e.g. Fig. 1 S-U).

The number of annules ventrally on the tail appears to have diagnostic value in short-tailed cephalobids, but in long-tailed forms the annulation tends to be too irregular for general use. It is often simply impossible to count annules precisely with light microscopy, because the annulation fades out gradually towards the tail tip. An extreme example is provided by one *P. (B.) pulcher* female, which had only about seventeen distinct ventral tail annules, against 36-53 in the other eleven females

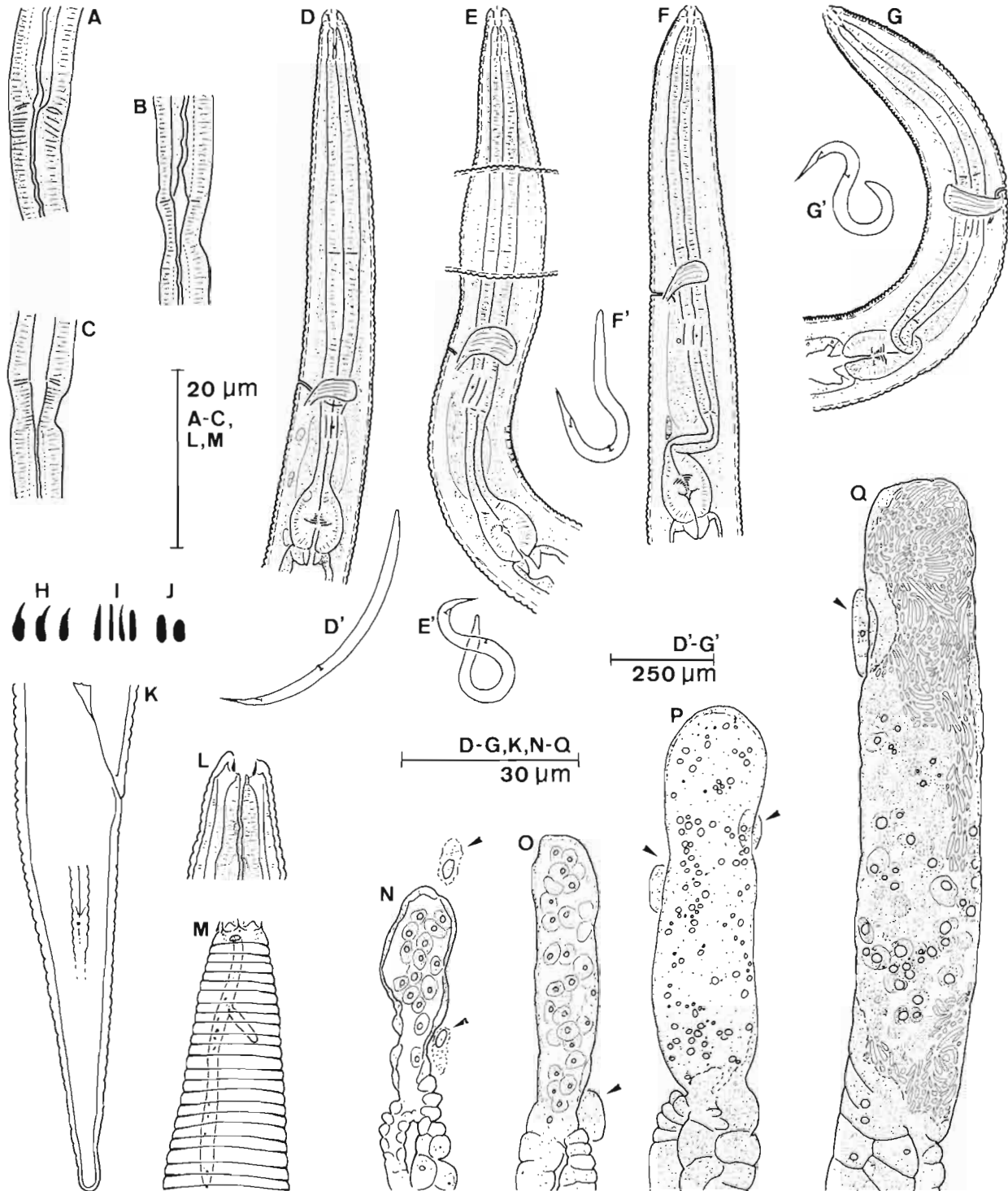


Fig. 3. Morphology of *Pseudacrobeles*, with some examples of presumed artefacts. A-C: Anterior end of isthmus in *P. (P.) [v.] baloghi*; D-G, D'-G': Position of nerve ring, excretory pore and deirid in *P. (P.) [v.] macrocystis* specimens with different body curvature (D'-G'), lip region retraction and isthmus collapse (see Table 3); H-J: Different types of cheilorhabdion shapes: comma (H), bar (I), granule (J); K: *P. (P.) [v.] macrocystis* female tail with blunt tip, probably as a result from wound healing; L, M: *P. (P.) [v.] baloghi* female with fungal infection via amphid, probably explaining narrow second stoma section (L); N-Q: spermatheca of fertilized *P. (P.) [v.] variabilis* (N) compared with spermathecae in *P. (P.) [v.] macrocystis* females (O-Q). Q is probably pathological. Arrowheads point at accompanying coelomocytes.

Table 4. Ranges and intervals of some quantitative characters in *Cephalobus persegnis* Bastian, 1865, *Eucephalobus striatus* (Bastian, 1965) Thorne, 1937 and *Pseudacrobeles (P.) [variabilis]* (Steiner, 1936) Steiner, 1938 (all measurements in μm).

Character	<i>C. persegnis</i> 66♀♀, 55♂♂*		<i>E. striatus</i> 50♀♀, 18♂♂**		<i>P. (P.) [variabilis]</i> 138♀♀, 86♂♂	
	range	interval	range	interval	range	interval
L	494-862	368	376-640	264	380-795	415
body width	18-42	24	17-37	20	15-37	22
pharynx length	132-203	71	116-141	35	105-205	100
tail length ♀♀	30-47	17	36-57	21	46-100	54
tail length ♂♂	32-48	16	33-47	13	20-53	33
a	20-31	11	17-39	22	16-30	14
b	3.3-5.6	2.3	3.1-5.2	2.1	3.0-5.0	2.0
c ♀♀	14-20	6	8.9-15	6.1	5.4-9.9	4.5
c ♂♂	14-20	6	9-13	9	8.4-21	12.6
c' ♀♀	1.5-3.3	1.8	2.3-4.7	2.4	3.5-8.7	5.0
c' ♂♂	1.7-2.6	0.9	2.1-3.2	1.1	1.7-3.7	2.0
stoma	10-14	4	10-14	4	9-16	7
corpus	91-132	41	74-91	27	63-135	72
isthmus	22-34	12	24-35	11	16-33	17
bulbus	15-23	8	14-19	5	13-24	11
nerve ring	89-133	44	76-99	23	72-131	59
excretory pore	89-149	50	83-106	23	66-129	63
deirid	102-162	60	92-132	40	83-146	63
phasmid ♀♀	13-31	18	15-28	13	8-27	19
phasmid ♀♀ (% tail)	35-65	20			11-36	25
annule width	1.3-2.4	1.1	1.3-3.2	1.9	0.9-2.3	2.4
V (%)	61-70	9	55-67	12	57-66	9
rectum	15-25	10	15-27	12	15-30	15
PUB	16-47	31	7-16	9	4-38	34
spermatheca	15-52	37	14-37	23	3-77	74
testis flexure	46-112	66	31-60	29	32-67	35
spicules	18-28	10	16-23	7	15-27	12
gubernaculum	8-14	6	11-15	4	8-15	7
spike	0	0	2-7	5	0-20	20

* Measurements from Anderson & Hooper (1970) - no SD or SE given.

** Measurements from Anderson & Hooper (1971) - no SD or SE given.

measured of this species. Furthermore, this character is partly correlated with tail length, and does not necessarily tell more than c, c' or absolute tail length. For these reasons, we have not relied on tail annule counts.

The tail tip is simply sharp-tapering in most specimens and species of *Pseudacrobeles*, but can occasionally be offset into a mucro, or even into a sclerotized drumstick- or hook-shaped terminus. Considering the variation encountered within single populations, one should remain cautious, but we have the impression that the hook-shaped tail tip of our *P. (B.) loofi* specimens is a useful character in diagnosis, and even in phylogenetic reconstruction (see section 8 below). The dorsally con-

vex tail of *P. (P.) laevis* and *P. (B.) pseudolatus* also may be good characters. However, bluntly rounded tail tips can occur, perhaps occasionally resulting from wound healing (Fig. 3 K), but also from less obvious environmental influences. Marinaro-Palmisano (1967) encountered blunt-tailed specimens of *P. (P.) pauciannulatus* in proportions approaching 50% in nutrient-poor cultures. Strictly speaking, the sharpness of the tail tip is an unreliable character, therefore, both for species and genera.

Male tail: Because of the presence of genital papillae and the possible occurrence of a spike consisting of a cuticular and pseudocoelomic component, the male tail

offers some extra possibilities for characterization when compared to that of the female. Counting of ventral annules, conversely, is usually quite impossible with the light microscope. We have concentrated mostly on spike and mucro, because they offer such striking variations and also because they are incorporated within measurements such as c , c' , tail length and phasmid (%) without revealing similar patterns. For instance, *P. (P.) [v.] anadelphus* males have $c' = 1.4-1.5$ with very short spike (Andrássy, 1967 b), while *P. (P.) [v.] variabilis* males from South-Carolina have $c' = 2.1-2.4$ with similar spike. Conversely, the single male found of *P. (B.) pulcher* has $c' = 2.4$ without any spike, while *P. (P.) [v.] macrocystis* males from Malaysia on average have $c' = 2.5$ with a spike of $10 \mu\text{m}$. We have not measured positions of male genital papillae (neither caudal nor precloacal) because we were not led to expect distinct patterns upon comparison of our drawings of male tails. Male tail shape is important in the diagnosis of two species: *P. (P.) anadelphus* is different from all species described in this paper in its male $c' = 1.4-1.5$; *P. (P.) [v.] baloghi* males typically have a spike of $16-20 \mu\text{m}$ long, exceeding that of all others studied. However, the two males from G4, with $10-11 \mu\text{m}$ long spike, are at odds with this diagnosis.

General conclusions: There are no easy criteria for determination or classification in *Pseudacrobeles*. All characters exhibit overlapping ranges and/or intergrading states for many species, so that distinct gaps between similar populations occur only exceptionally. Also, for many characters, both qualitative (lip region, tail tip) and quantitative (Table 4), great differences are possible within one species. From a strictly diagnostic point of view, where each taxon should be perfectly distinguishable from all others of the same rank, we would probably have to reduce the number of species and genera in this group to a fraction of the present number, and discard most characters as having too great a potential for intraspecific variation to be trustworthy. However, other evidence suggests that morphological divergence in speciation can lag well behind on physiological and genomic divergence (e.g. Butler *et al.*, 1981; Riley *et al.*, 1989). The sum of these conflicting observations is, that there are no easy rules for distinction of species on the basis of morphology, that each case must be carefully examined and considered in its own right, and that conclusions always remain assumptions instead of certainties.

3. PROPOSAL OF A SUPERSPECIES FOR *P. VARIABILIS*

Steiner (1936b) did not explain his choice of specific epithet for his new species, but it now proves to have been prophetic: his specimens are part of an extremely variable group, that cannot be adequately separated in truly discrete subgroups. Lip region structure varies considerably within single populations, cheilorhabdion shapes form a continuum from one population to another,

and the few gaps between different populations in male tail structure are traversed by the males from G4. Thus, one should place these specimens together in a taxon of species-group rank. On the other hand, we feel this group should not be treated simply as a species, for three reasons: *i*) Some of the samples studied (T9, T41, T45 and T46) contained two forms that could be separated into two discrete groups (when only considering these samples) on the basis of anterior stoma structure supported by cuticle thickness, annule width, spicule width, slenderness of female tail and lip region structure. This suggests the co-occurrence of two different species. Because the form with comma-shaped cheilorhabdia does not agree well with any described species, it was considered to represent a separate species, *P. (P.) [v.] macrocystis*. *ii*) Nominal species *P. (P.) [v.] baloghi* can still be distinguished from *P. (P.) [v.] variabilis* by the longer spike of "typical" males ($16-20 \mu\text{m}$ vs $0-9 \mu\text{m}$). The two males from G4 reduce this gap, with spike lengths of 10 and $11 \mu\text{m}$, but we have not found conclusive evidence of synonymy of the two species in the form of a truly overlapping and intergrading population. We assume that the G4 males represent an intermediate stage between very close species and are *ipso facto* not easily assignable. *iii*) Nominal species *P. (P.) [v.] tabacum* is very close to *P. (P.) [v.] variabilis*, to the point where overlap between the two occurs at least slightly for all characters. However, we have not synonymized the species, due to three divergencies: the short isthmus ($16-21 \mu\text{m}$), relatively short pharynx ($b = 4.0-5.0$) and occurrence of bar- to granule-shaped cheilorhabdia. Compounding data of *P. (P.) [v.] variabilis*, *P. (P.) [v.] baloghi* and *P. (P.) [v.] macrocystis*, we find that for a total of 198 specimens examined, the isthmus is $20-33 \mu\text{m}$ long, $b = 3.0-4.3$ and granule-shaped cheilorhabdia never occur.

We have opted for proposal of a superspecies to formalize our impression that all these specimens represent a species complex. This complicates taxonomical nomenclature, especially in combination with the use of subgenera. However, in this group and at this point of knowledge we actually feel such complication is a positive factor instead of a nuisance: taxonomy of these animals simply is not clear-cut, and classification should reflect this fact. Admittedly, our evidence is not unequivocal. Thus, one would expect wider variability to occur in a superspecies than in a related species. Comparison of the total ranges of quantitative characters of *P. (P.) [v.] variabilis* with the ranges given in Anderson and Hooper (1970, 1971) in *Cephalobus persegnis* and *Eucephalobus striatus* shows that there are indeed a number of wider ranges in the superspecies (Table 4), most notably in pharynx length, corpus length, isthmus length, characters associated with length of male or female tail, spermatheca length and positions of nerve ring, excretory pore and deirid. Of these features, however, the latter three are definitely unreliable when measured as the

absolute distance from the anterior end (see section 2 above). Also, spermatheca length and characters associated with female tail length are suspect – as the female tail of *P. (P.) [variabilis]* is longer on average than that of *C. persegnis* or *E. striatus*, absolute variation of tail length may well be correlated with tail length itself. Finally, considerably more specimens were measured of *P. (P.) [variabilis]* than of the other two species, and this alone may explain the observed wider ranges.

4. DELINEATION OF *PSEUDACROBELES* FROM *CEPHALOBUS* AND *EUCEPHALOBUS*

According to our emended diagnosis, distinction of *Pseudacrobeles* from *Cephalobus* is based on only one character: in females of *Pseudacrobeles* the lateral field extends only to the phasmid, in females of *Cephalobus* it extends to the tail tip. The validity of this criterion remains to be examined. As appears from Marinari-Palmisano (1967), tail tip shape (sharp vs blunt) cannot be

used as a strictly dichotomous criterion. Delineation of *Pseudacrobeles* from *Eucephalobus* is even more difficult. At present, it can only be based on the lip region: *Eucephalobus* has more or less sharply bifurcate labial probolae, while those of *Pseudacrobeles* are flat ridges or small knobs (or absent in one specimen from B1861 – see Part 1). Also, no setiform cephalic probolae have as yet been found in *Eucephalobus* – but without S.E.M. *Pseudacrobeles* with setiform cephalic probolae is sometimes hardly distinguishable from *Eucephalobus* with bifurcate labial probolae (compare Fig. 2 A, K; 4 A, E in Part 1 with Fig. 4 L, N in this article). It is also interesting to know that *Eucephalobus* contains species both with sharp and with blunt female tail, and species both with and without lateral fields extending to the tail tip. More details on problems with *Eucephalobus* can be found in Boström (1985). It is quite possible that the distinctions at genus level between *Cephalobus*, *Eucephalobus* and *Pseudacrobeles* will break down in the future. In

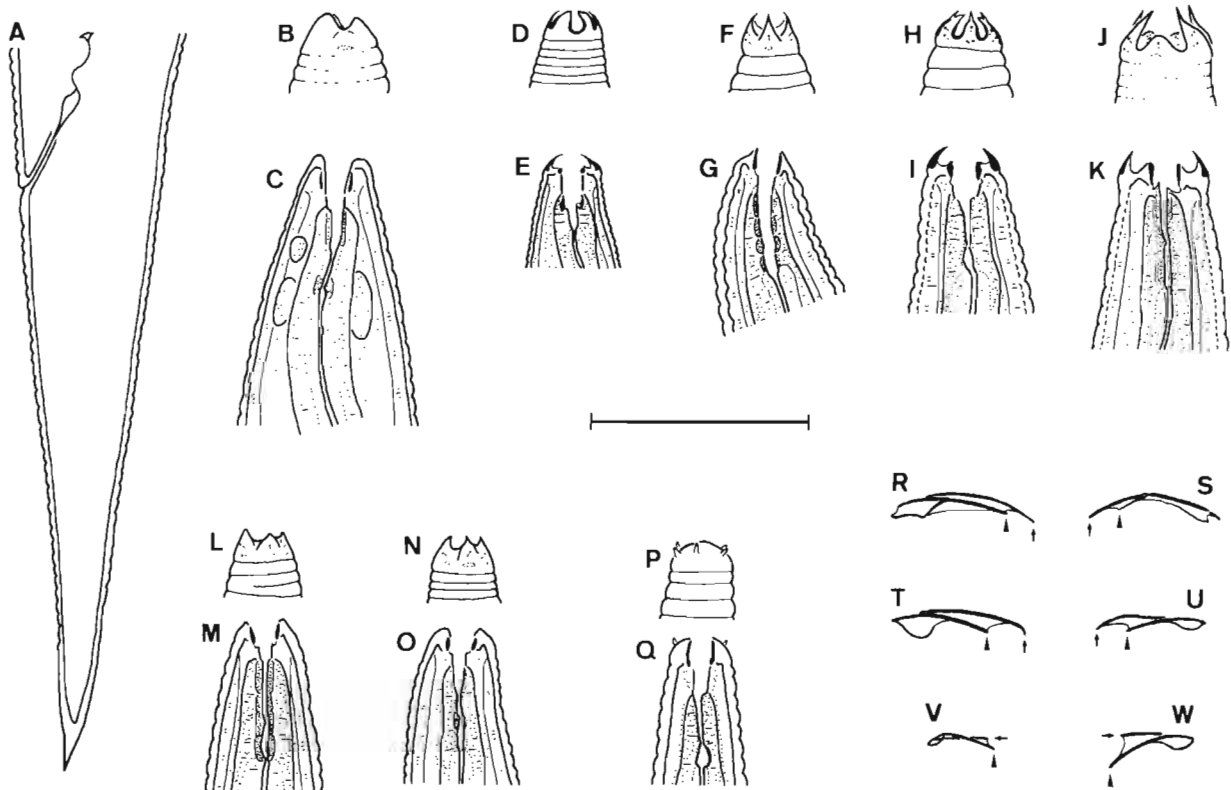


Fig. 4. Some species related to *Pseudacrobeles*. A-C: Paratype female of *Heterocephalobus kaczanowskii* (Brzeski, 1960) Brzeski, 1961; D, E: Paratype of *Panagrobetium minimum* Andrassy, 1986; F, G, W: Paratypes of *Panagrotetratus occultus* De Ley & Coomans, 1990; H, I, V: *Teratolobus regulus* Andrassy, 1968 from Brazil; J, K, U: *Acrolobus emarginatus* (de Man, 1880) Boström, 1985 from Sweden; L, M: *Eucephalobus oxyuroides* (de Man, 1876) Steiner, 1936 from Belgium; N, O: *Eucephalobus hooperi* Marinari-Palmisano, 1967 from Isla Fernandina (G18); P, Q, T: *Macrolaimellus longicauda* (Rashid et al., 1985) Rashid & Geraert, 1987 from South Africa; R: *Pseudacrobeles (Bunobus) pulcher* (Loof, 1964) comb. n. from India (I30); S: *P. (P.) [v.] macrocystis* De Ley & Siddiqi, 1991 from Cameroon. Arrows in R-W point at *cuneus*, arrowheads at one of the two *cornua crurum*. (Scale bar = 30 μ m for A, 20 μ m for rest.)

Table 5. Lattice key to the species of the genus *Pseudacrobeles* Steiner, 1938 and some related species *inc. sed.* (distinctive character states in bold print).

	Shape cheilo-rhabdia	Aspect second section	Cephalic probolae	n° lips visible with LM	c (♀♀)	c' (♀♀)	Phasmid in % tail (♀♀)	c' (♂♂)	Spike (µm)	Corpus isthmus	L (♀♀) (µm)	Special features
Subgenus <i>Pseudacrobeles</i>												
<i>P. [variabilis]</i>												
<i>P. [v.] tabacum</i>	bar to granule	as third section	absent to seta	3 or 6	7.6-10	4.1-4.8	27-36	2.1-2.6	2-3	4.1-5.1	535-690	isthmus 16-21 µm long, b = 4.0-5.0
<i>P. [v. variabilis]</i>	bar	varies	absent to seta	3 or 6	5.4-9.6	4.6-8.7	12-32	1.7-2.9	0-9	2.5-4.5	440-795	
<i>P. [v.] baloghi</i>	bar to comma	as chei-lostome	stub to seta	6	7.1-9.2	3.5-6.4	18-31	2.8-3.7	(10-) 16-20	2.9-4.2	400-620	spermatheca often longer than 45 µm
<i>P. [v.] macrocystis</i>	comma	as chei-lostome	seta	6	7.1-9.9	3.7-5.8	11-31	1.8-2.9	4-13	2.8-4.7	525-785	
<i>P. anadelphus</i>	comma	as chei-lostome	seta	6	8.0-9.4	3.9-4.8	< 20	1.4-1.5	< 5*	5.0-5.5	660-740	
<i>P. laevis</i>	bar	between the two	absent (to seta?)	3	11-14	3.1-3.8	33-42	2.1-2.3	1-3	3.2-4.2	595-705	
<i>P. pauciammulatus</i>	bar to granule	as third section	absent	3	8.5-14	3.0-4.9	± 40	autotoke	autotoke	2.5*	385-653	tail with 22-26 ventral annules
<i>P. teres</i>	granule	as third section	absent	3	11-12	4.0-4.3	27*	unknown	unknown	4.1-4.5	735-740	
Subgenus <i>Bunobus</i>												
<i>P. pulcher</i>	bar	as chei-lostome	absent	4	5.5-6.2	6.6-9	18-23	2.4	0	2.8-3.9	530-675	R _{op} = 38-43
<i>P. loofi</i>	bar	as chei-lostome	absent	4 or 6	4.4-6.0	(5-) 7-11	14-27	unknown	unknown	1.9-2.8	295-430	R _{op} = 58-65
<i>P. pseudolatus</i>	bar**	as chei-lostome**	absent**	4**	8.4-9.4	4.2-4.5	± 30	2.3-2.5	4-6	?	410-470	R _{op} = 52-54**; tip ♀ tail dors. convex
<i>P. cruzi</i>	bar	as chei-lostome	absent	4	4.9-5.5	8.0-9.4	15-22	unknown	unknown	2.2-3.1	480-600	R _{op} = 50-54
Genus <i>inquirendum</i> <i>Heterocephalobus</i> : species <i>incertae sedis</i>												
<i>H. basilogoodeyi</i>	granule	?	absent	?	13-20	2.5	41*	unknown	unknown	?	440-450	lateral field reaching tail tip
<i>H. elongatus</i>	bar	?	absent	3	14-15	4.1*	?	2.3*	< 5*	?	900	
<i>H. eurystoma</i>	bar	as chei-lostome?	absent	6	10-12	3.5-3.8	± 40	2.2-2.4	< 5*	3.5-3.7	490-670	PUB 1.3-1.5 body widths long
<i>H. eximius</i>	bar	as chei-lostome	absent	3	12	3.1	47	unknown	unknown	3	650	lateral field with 4 incisures
<i>H. kaczanowskii</i>	bar	as chei-lostome	absent	3	12-15	4.6*	?	2.2*	< 5*	3.7	600-945	= <i>H. elongatus</i> ?

* Measured on relevant figure(s) in original description.

** Our observations on paratypes.

that case, it could still be appropriate to retain *Pseudacrobeles* and *Bunobus* as subgenera of e.g. senior genus *Cephalobus*. Our range of material did not reveal information relevant to this problem, and further study is clearly required.

5. DOUBTFUL STATUS OF *HETEROCEPHALOBUS*

As explained in Part I, *P. (P.) [v.] variabilis* has three lateral incisures, and not five as stated by Andr ssy (1984). Also, intraspecific variation of the lip region extends from "typical" for *Pseudacrobeles* (i.e. with relatively well-developed labial and cephalic probolae) to "typical" for *Heterocephalobus* (i.e. without cephalic probolae and with very low labial probolae) in two *Pseudacrobeles* species (*P. (P.) [v.] tabacum* and *P. (P.) [v.] variabilis*) as well as in *Cephalobus persegnis* (cf. Anderson & Hooper, 1970). Rashid *et al.* (1989) also reported a population determined as *P. (P.) paucianmulatus* from Krakatau with well-developed head structures, a feature not described originally by Marinari-Palmisano (1967). Thus, *Heterocephalobus* as defined by Andr ssy (1967a, 1984) is a synonym of *Pseudacrobeles*.

However, the original definition of *Heterocephalobus* by Brzeski (1960, 1961) was not based on the above points, but on lateral fields supposedly extending to the tail tip in both sexes. In all our material where this feature was visible, the lateral field never extended over more than the anterior half of the tail, and the middle incisure never passed the phasmid (one slight exception in Fig. 3 K). Unfortunately, in the paratypes of *H. kaczanowskii* we could not definitely ascertain this character, but we do consider it possible that the lateral field extends well beyond the middle of the tail, contrary to Andr ssy (1967a). For one thing, this seemed to be the case in the juvenile paratype, and for another Fig. 57b in de Man (1884) of *H. elongatus*, probable senior synonym of *H. kaczanowskii*, clearly depicts the lateral field as extending over two-thirds of the female tail. No clues exist to the position of the phasmid. Intermediate species or species with variable extent of the lateral field have not yet been reported (but see remark above on *Eucephalobus*), and the lateral field could be a good character to set *H. kaczanowskii* (or *H. elongatus*) apart from *Pseudacrobeles* after all. However, the point is that in that case no difference would be left between *Heterocephalobus* and senior genus *Cephalobus*. Thus, validity of *Heterocephalobus* is not disproven, but clearly very doubtful: it is tied up with elucidation of the relationships between *Pseudacrobeles* and *Cephalobus* in such a way that it will probably have to be rejected whatever the outcome of this other problem.

6. REJECTION OF *PANAGROCEPHALUS*

As with *Heterocephalobus*, the diagnostic differences hitherto used to distinguish between *Panagrocephalus* and *Pseudacrobeles* are invalid. *Pseudacrobeles* has three lateral lines and not five, and there really is no structural

difference between the stoma of *P. (P.) anadelphus*, former type species of *Panagrocephalus*, and that of *P. (P.) [v.] variabilis*. As in all Cephalobidae hitherto examined by us (De Ley & Siddiqi, 1991) as well as *P. (P.) anadelphus*, *P. (P.) [v.] variabilis* has a stoma section in between cheilostome and the stoma parts covered by pharyngeal tissue. As in *P. (P.) anadelphus*, this stoma section is usually wider and more refractive than the posterior sections. The minute differences between *P. (P.) anadelphus* and *P. (P.) [v.] variabilis* in cheilorhabdion shape and actual width of the second section are bridged by *P. (P.) [v.] baloghi* and *P. (P.) [v.] macrocystis*. In addition, these two species are so hard to distinguish already from *P. (P.) [v.] variabilis*, that separate status of *P. (P.) anadelphus* above species level is clearly unwarranted.

7. REJECTION OF PANAGROCEPHALINAE AND PROPOSAL OF A NEW SUBFAMILY

Synonymization of the genus *Panagrocephalus* with *Pseudacrobeles* leads directly to synonymization of the subfamily Panagrocephalinae Andr ssy, 1976 with Cephalobinae Filipjev, 1934. However, Panagrocephalinae contained some additional genera which do probably represent a lineage distinct from that of Cephalobinae (cf. De Ley & Coomans, 1990): *Teratolobus* Andr ssy, 1968, *Acrolobus* Bostr m, 1985 and *Panagroteratus* Andr ssy, 1986. We think these genera should be set apart and propose a new subfamily for them:

Acrolobinae subfam. n.

DIAGNOSIS

Cephalobidae. Lips separated from each other by six clefts. Labial probolae absent, cephalic probolae absent or short-setiform. Male (as far as known) with gubernaculum with prominent *cornua crurum* that may extend anterior to the *cuneus* in lateral view.

TYPE GENUS

Acrolobus Bostr m, 1985.

A. emarginatus (de Man, 1880), Bostr m, 1985 (type and only species).

OTHER GENERA

Panagroteratus Andr ssy, 1986.

P. hamatus Andr ssy, 1986 (type species)

P. baloghi Andr ssy, 1986

P. occultus De Ley & Coomans, 1990

Teratolobus Andr ssy, 1968 = *Pseudocephalobus* Joshi, 1972

T. regulus Andr ssy, 1968 (type species)

T. indicus (Joshi, 1972) Rashid *et al.*, 1985

= *Pseudocephalobus indicus* Joshi, 1972

Acrolobus is chosen as type genus because we consider it to be a derived form within the subfamily, and also because it is the only genus of which we have been able to examine the specimens used for original proposal of

that genus. Differentiation of Acrolobinae from other subfamilies is based on the following points :

– The subfamily Acrobelinae Thorne, 1937 was already synonymized with Cephalobinae by Boström (1988) and Rashid *et al.* (1989). Our findings on lip region variability support this view.

– The subfamily Alirhabditinae Suryawanshi, 1971 was placed in Cephalobidae by Rashid *et al.* (1985) on the basis of the cephalobid structure of the reproductive organs of *Alirhabditis indica* Suryawanshi, 1971, single representative of the group (we do not consider *Macrolaimellus* Andrassy, 1966 as belonging here). This species has a tubular stoma, covered only in its proximal half by thin pharyngeal tissue, and a narrow lip region, amalgamated into a disc and apparently devoid of any probolae or clefts. Confusion with Acrolobinae is impossible and relationships seem rather distant. Because of the stoma, we are actually more inclined to consider the family Alirhabditidae Suryawanshi, 1971 as valid, within Cephaloidea as proposed by Ali *et al.* (1973).

– The subfamily Cephalobinae Filipjev, 1934 is considered to encompass Cephalobidae which usually have labial probolae, and if these are absent then the lips are not separated by clefts (see section 8 for explanation of this elaborate specification). In male Cephalobinae the gubernaculum has *cornua crurum*, but these are only rarely distinct in lateral view and never extend beyond the cuneus (Fig. 4 R, S).

– The subfamily Kirjanoviinae Andrassy, 1976 contains two monotypic genera, *Kirjanovia* Ivanova, 1969 and *Acromoldavicus* Nesterov, 1970 and presents particular problems. In both genera, the lips are so deeply separated that they can be said to be “stalked”, and the mouth is surrounded by pointed to triangular labial probolae (see Boström, 1989 for SEM of *Acromoldavicus*). Males have been described with “normal” gubernacula in both genera (but presence of *cornua crurum* is easily overlooked!). The stoma of *Acromoldavicus* is quite aberrant from that of Cephalobinae, being narrow-tubular with very small granular cheilorhabdia and no other distinct rhabdia. *Kirjanovia* seems closer to Cephalobinae in this respect, but its stoma is wide throughout and lacks distinct rhabdia proximally. The combination of stalked lips and aberrant stoma structure(s) supports Andrassy's allocation of *Kirjanovia* and *Acromoldavicus* to a separate subfamily, and also allocation of *Acrolobus*, *Teratolobus* and *Panagroteratus* to their own subfamily, in turn. Further study is clearly needed, however.

– The subfamily Macrolaiminae Sanwal, 1971 must be mentioned – although placed currently (Andrassy, 1984) in suborder Teratocephalina Andrassy, 1974, family Chambersiellidae (Thorne, 1937) Sanwal, 1957 – because of close similarities between *Macrolaimellus longicauda* (Rashid *et al.*, 1985) Rashid & Geraert, 1987

and such species as *Panagroteratus baloghi*, *Pseudacrobeles (B.) loofi* and *P. (P.) [v.] variabilis*. We do not agree with the allocation of *Macrolaimellus* to Alirhabditinae as proposed by Rashid *et al.* (1985) because of differences in stoma and lip structure, but we do agree that *Macrolaimellus* is close to Cephalobinae. In fact, comparison of SEM of *M. longicauda* (Fig. 8 A, B in Rashid *et al.*, 1989) with our pictures of *P. (B.) loofi* (Fig. 2 G-J) suggests very close phylogenetic affinities between these three. Also, we have examined the gubernaculum of the male *M. longicauda* described from Namibia by Rashid and Heyns (1990) and found distinct *cornua crurum* as in Acrolobinae (Fig. 4 T). The only character allowing satisfactory distinction of Macrolaiminae at subfamily level, both from Cephalobinae and Acrolobinae, appears to be the presence of setiform labial sensilla. Fig. 8 A, B in Rashid *et al.* (1989) shows that even this difference need not be pronounced. We will not propose any specific alteration to the position of Macrolaiminae and Chambersiellidae at this point, because we have not seen enough relevant material to make confident suggestions about the other genera of this family.

– The subfamily Metacrobelineae Andrassy, 1974 is not considered justified, as the “aberrant” stoma reported in De Ley *et al.* (1990) for *Metacrobeles* Loof, 1962 proves to be as in Cephalobinae (De Ley & Siddiqi, 1991). The very posterior vulva position of *Metacrobeles* is a good genus character, but does not justify a separate subfamily. As suggested in Boström (1988), Metacrobelineae is synonymized with Cephalobinae.

– The subfamily Panagrolaiminae Thorne, 1937 is closely connected with Acrolobinae through *Panagrobelus* Thorne, 1939 and especially *Panagrobelum* Andrassy, 1984, genera which have a similar lip region, and of which the latter seems intermediate between Panagrolaimidae and Acrolobinae in stoma structure (Abb. 1a in Andrassy, 1960; Fig. 6 A in Andrassy, 1986). We examined a paratype female of *P. minimum* Andrassy, 1986 sent to us by Dr. I. Andrassy, and interpret the stoma structure as depicted in Fig. 4 E. Upon comparison of the generic diagnoses, differentiation of *Panagrobelum* from *Panagroteratus* is only possible through two, relatively minor characters: *Panagrobelum* has the phasmids in the posterior half of the female tail and altogether lacks a PUB. The phasmids were not clear in the specimen of *P. minimum* studied by us, but we did see a small PUB, and the diagnosis of *Panagrobelum* should therefore be revised. Re-examination of type species *P. topayi* (Andrassy, 1960) Andrassy, 1984 is required to resolve the position of the genus, but on the basis of our observations of the stoma of *P. minimum* we assume it is correctly placed in Panagrolaiminae. The other genera of Panagrolaiminae (as defined in Andrassy, 1984) are sufficiently distinct from Acrolobinae in stoma, pharynx, gonads and male copulatory structures to avoid confusion.

8. NEW EVALUATION OF *PSEUDACROBELES* AND JUSTIFICATION OF THE SUBGENUS *BUNOBUS*

As redefined and reorganized here, *Pseudacrobeles* is much less rare and contains many more species than hitherto assumed. It is now shown to be quite common throughout the tropics, if not in densities then at least in geographical range, and it also occurs in some regions at higher latitudes (the United States and Spain). Apart from the locations already noted in this revision, additional records of the genus are from Peru and New Caledonia, specimens from which countries were sent to us by Dr. I. Andr ssy (two females from each locality that could not be identified further than *P. (P.) [variabilis]* in the absence of males).

With respect to phylogenetic evaluation of its morphology, we consider *Pseudacrobeles* to exhibit the least derived characters within Cephalobinae. This can be deduced from comparisons with representatives of several outgroups, viz. species of the genera *Macrolaimellus* (Macrolaiminae), *Panagrobeltum* (Panagrolaiminae), *Panagroteratus* and *Teratolobus* (both Acrolobinae). The following similarities between these species exist :

- Body 0.3–0.6 mm long.
- Lip region hexaradiate, with six radial clefts between the lips (in *M. longicauda* these are reduced to indentations separating liplets).
- Stoma sections not enveloped by pharyngeal musculature are clearly wider and have more refractive walls than the posterior ones.
- Lateral field with two or three incisures.
- Female tail at least three ABW long, and often much longer (c' up to twelve).
- Male tail also relatively long (c' between 3 and 4), usually with long spike (10–14 µm in *Teratolobus regulus*, 20.5 µm in *Macrolaimellus longicauda* and 8.5 µm in *Panagrobeltum topayi*).
- In both sexes the tail tip can be straight-sharp, hooked or harpoon-shaped, but never bluntly rounded.

In effect, this adds up to a reconstruction of the hypothetical ancestor of Cephalobinae. The female characters in this reconstruction come very close to our *P. (B.) loofi*, and in fact these specimens only diverge in the lip region with weak bilateral instead of hexaradial symmetry, and six radial striae instead of true clefts between the lips. Presence of a hooked tail tip is also noteworthy, contrasting with nearly all other Cephalobinae (e.g. resembling tips only found again here and there in *P. (P.) [v.] variabilis*, *P. (P.) [v.] baloghi* and *P. (B.) pulcher* (see Figs 1 B; 4 Y, Z in Part 1; Fig. 1 I in this article). Interestingly, such tail tips are relatively common in Chambersiellidae. The presence or absence of cephalic probolae in the “ancestral cephalobin” is uncertain, because these occur in *Teratolobus regulus* and *Panagroteratus occultus*, but not in *Macrolaimellus* or *Bunobus*, and only in some *P. (P.) [v.] variabilis* specimens.

With respect to the lip region, Bostr m (1988) and

Rashid *et al.* (1989) considered Cephalobinae as always having labial probolae. However, our SEM data now show that intraspecific variation can include other conditions. The specimen of *P. (P.) [v.] variabilis* from B1861 with apparently six liplets (cf. Part 1) co-occurred with two others which were found to have three labial probolae instead – but we must admittedly remain cautious because of bad fixation. The specimens of *P. (P.) [v.] variabilis* from T41 (cf. Fig. 3 B–F, H–L in Part 1) yield a smooth transition series, and include forms where the dorsal labial probola is little more than a merged pair of subdorsal lips (Part 1 : Fig. 3 E, F, K, L) and a “monstrosity” (Part 1 : Fig. 3 C, I). *Bunobus* specimens lack probolae, but are quite close to *P. (P.) [v.] variabilis* in all other respects. For these reasons, we think it is no longer appropriate to consider labial probolae as a *conditio sine qua non* for Cephalobinae. This complicates diagnosis : Cephalobinae can still be distinguished from Acrolobinae in lacking deep clefts between the lips, but more derived Cephalobinae such as *Cervidellus* Thorne, 1937 and *Acrobeles* von Linstow, 1877 can have clearly separated lips, albeit of different structure (a case of homoplasy?). Thus, Cephalobinae have to be diagnosed by specifying that, if labial probolae are absent, then the lips are not separated by clefts. What our material also accentuates, is that the phylogenetic origin of the labial probolae may be a combination of liplet fusion (suggested by the B1861 specimens) and lip fusion (cf. T41 series).

Species of the subgenus *Pseudacrobeles* fit relatively well into a putative evolutionary line towards *Cephalobus*, beginning with *P. (P.) [variabilis]* and ending with *P. (P.) paucianmulatus*, showing reduction of female tail length, appearance of labial probolae and reduction of the second stoma section. *P. (B.) cruzi*, *P. (B.) loofi*, *P. (B.) pseudolatus* and *P. (B.) pulcher* do not fit into this line, but rather appear to have maintained a plesiomorphic condition of the second stoma section, while developing an alternative lip region structure (paratypes of *P. (B.) pseudolatus* were checked for these features) that lacks probolae altogether. Because of this, we think these animals do not have the genetic and/or ontogenetic potential to develop them, and within a subfamily where such a diversity and complexity of probolae has evolved, the complete absence of these structures deserves recognition in classification. On the other hand, the delineation of this little group from its closest relatives – and especially of *P. (B.) loofi* from *P. (P.) [v.] variabilis* – is not at all easy, and allocation to a separate subgenus within the least derived genus of Cephalobinae therefore seems the best solution. The (usually) pronounced bilateral symmetry of the lip region, with subdorsal and subventral lips all separate from each other, may be an autapomorphy of this subgenus, derived from the ancestral state independently from the triradiate type with labial probolae.

Acknowledgments

The authors wish to thank the following people for kindly sending them material on request: Dr. I. Andrassy, Dr. I. Armendariz, Dr. M. Hernández, Dr. A. M. Golden, Dr. P.A.A. Loof and Dr. G. Winiszewska. We are also grateful to Mrs. F. De Cuyper for translation of Mukhina (1981). The first author is research assistant with the National Fund for Scientific Research of Belgium, and is indebted to the N.F.S.R. for a travel grant to visit the International Institute of Parasitology during preparation of this paper. The second author, likewise, is grateful to the British Council for support to visit the Instituut voor Dierkunde. The third author gratefully acknowledges support from the Swedish Natural Science Research Council (NFR).

References

- ALI, S. M., SURYAWANSHI, M. V. & CHISTY, K. Z. (1973). Two new species of *Drilocephalobus* Coomans & Goodey, 1965 (Nematoda: Drilocephalobidae n. fam.) from Marathwada, India, with a revised classification of the superfamily Cephaloboidea (Paramonov, 1956) Paramonov, 1962. *Nematologica*, 19, 308-317.
- ANDERSON, R. V. (1965). *Acrobeloides uberrinus* n. sp., with a note on morphologic variation within soil and bacteria-reared populations. *Proc. helminth. Soc. Wash.*, 32: 232-235.
- ANDERSON, R. V. (1988). Variation in taxonomic characters of a species of *Acrobeloides* (Cobb, 1924) Steiner and Buhrer, 1933. *Canad. J. Zool.*, 46: 309-320.
- ANDERSON, R. V. & HOOPER, D. J. (1970). A neotype for *Cephalobus persegnis* Bastian, 1865, redescription of the species, and observations on variability in taxonomic characters. *Canad. J. Zool.*, 48: 457-469.
- ANDERSON, R. V. & HOOPER, D. J. (1971). A neotype for *Eucephalobus striatus* (Bastian, 1865) Thorne, 1937 (Nematoda) and redescription of the species from topotypes and their progeny. *Canad. J. Zool.*, 49: 451-459.
- ANDRÁSSY, I. (1960). *Panagrobelus topayi* n. sp., eine neue Nematoden-Art aus Kenya. *Zool. Anz.*, 164: 195-198.
- ANDRÁSSY, I. (1967a). Die Unterfamilie Cephalobinae (Nematoda: Cephalobidae) und ihre Arten. *Acta zool. Acad. Sci. hung.*, 13: 1-37.
- ANDRÁSSY, I. (1967b). Nematoden aus Chile, Argentinien und Brasilien, gesammelt von Prof. Dr. H. Franz. *Opusc. zool. Bpest.*, 7: 3-34.
- ANDRÁSSY, I. (1968). Fauna Paraguayensis 2. Nematoden aus den Galeriewäldern des Acaray-Flusses. *Opusc. zool. Bpest.*, 8: 167-315.
- ANDRÁSSY, I. (1970). Freilebende Nematoden aus Vietnam. *Opusc. zool. Bpest.*, 10: 5-31.
- ANDRÁSSY, I. (1984). *Klasse Nematoda (Ordnungen Monhysterida, Desmoscolecida, Araeolaimida, Chromadorida, Rhabditida)*. Stuttgart, Gustav Fischer Verlag, 509 p.
- ANDRÁSSY, I. (1986). Fifteen new nematode species from the Southern Hemisphere. *Acta zool. hung.*, 32: 1-33.
- BOSTRÖM, S. (1985). A scanning electron microscope study of three species of *Eucephalobus* Steiner, 1936 (Nematoda: Cephalobidae). *Nematologica*, 30 (1984): 131-139.
- BOSTRÖM, S. (1988). *Morphological and systematic studies of the family Cephalobidae (Nematoda: Rhabditida)*. University of Stockholm, Doctoral Thesis, 34 p.
- BOSTRÖM, S. (1989). A scanning electron microscope study of juveniles of *Acromoldavicus* Nesterov (Nematoda: Cephalobidae) from Greece. *Nematol. mediterr.*, 17: 27-29.
- BOSTRÖM, S. & GYDEMO, R. (1983). Intraspecific variability in *Acrobeloides nanus* (de Man) Anderson (Nematoda: Cephalobidae) and a note on external morphology. *Zool. Scripta*, 12: 245-255.
- BRZESKI, M. (1960). *Cephalobus (Heterocephalobus) Kaczanowskii* subgen. nov., sp. nov. (Nematoda: Cephalobidae). *Bull. Acad. pol. Sci., Cl. II (Sér. Sci. biol.)*, 8: 163-165.
- BRZESKI, M. (1961). Revision of the genus *Heterocephalobus* Brzeski, 1960 n. grad. (Nematoda, Cephalobidae). *Bull. Acad. pol. Sci., Cl. II (Sér. Sci. biol.)*, 9: 97-100.
- BUTLER, M. H., WALL, S. M., LUEHRSEN, K. R., FOX, G. E. & HECHT, R. M. (1981). Molecular relationships between closely related strains and species of nematodes. *J. molecular Evol.*, 18: 18-23.
- BÜTSCHLI, O. (1873). Beiträge zur Kenntnis der freilebenden Nematoden. *Nova Acta Ksl. Leop.-Carol. D. Akad. Naturforsch.*, 36: 1-144.
- COBB, N. A. (1906). Freelifving nematodes inhabiting the soil about the roots of cane and their relation to root diseases. *Bull. Hawaiian Sugar Planters' Assoc. Exp. Stat.*, 5: 163-195.
- VON DADAY, E. (1897). Die freilebenden Süßwasser-Nematoden Ungarns. *Zool. Jahrb.*, 10: 91-134.
- DE LEY, P. & COOMANS, A. (1990). Terrestrial Nematodes of the Galápagos Archipelago I: Three Rhabditida from Isla Fernandina. *Bull. K. belg. Inst. Natuurw. schapp., Biol.*, 60: 5-22.
- DE LEY, P., COOMANS, A. & GERAERT, E. (1990). *Meta-crobeles tessellatus* sp. n., second species of a rare genus (Nematoda: Rhabditida). *Nematologica*, 35 (1989): 25-36.
- DE LEY, P. & SIDDIQI, M. R. (1991). Description of *Pseudacrobeles macrocystis* sp. n., with some new observations on the morphology of Cephalobidae (Nematoda). *Afro-Asian J. Nematol.*, 1: 31-40.
- DE LEY, P., SIDDIQI, M. R. & BOSTRÖM, S. (1993). A revision of the genus *Pseudacrobeles*. Part 1. Subgenus *Pseudacrobeles* grad. n. *Fund. appl. Nematol.*, 16: 219-238.
- LIEBERMANN, A. (1927). Die freilebenden Nematoden der Cakovicer Zuckerfabriksteiche. *Int. Revue gesamten Hydrobiol. Hydrograph.*, 17: 10-187.
- LOOF, P.A.A. (1964). Free-living and plant-parasitic nematodes from Venezuela. *Nematologica*, 10: 201-300.
- DE MAN, J. G. (1884). *Die frei in der reinen Erde und im Süßen Wasser lebenden Nematoden der niederländischen Fauna*. Leiden, 206 p.
- MARINARI-PALMISANO, A. (1967). Contributo alla conoscenza di alcuni nematodi dei generi *Rhabditoides*, *Eucephalobus*, *Heterocephalobus*. *Redia*, 50: 289-308.

- MUKHINA, T. I. (1981). Fauna nematod zamanikhi Primorskogo kraja. In : *Svobodnozh. fitopat. Nematody Fauny Dalnego Vostoka*. Vladivostok : 41-156.
- RASHID, F., GERAERT, E. & SHARMA, R. D. (1985). Morphology, taxonomy and morphometry of some Cephalobidae (Nematoda : Rhabditida) from Brazil, with descriptions of two new genera and four new species. *Nematologica*, 30 (1984) : 251-298.
- RASHID, F., GERAERT, E., COOMANS, A. & SUATMADJI, W. (1989). Cephalobidae from the Krakatau region (Nematoda : Rhabditida). *Nematologica*, 34 (1988) : 125-143.
- RASHID, F. & HEYNS, J. (1990). *Chiloplacus* and *Macrolaimelus* species from South West africa/Namibia (Nematoda : Cephalobidae). *Phytophylactica*, 22 : 189-199.
- RILEY, I. T., REARDON, T. B. & MCKAY A. C. (1989). Electrophoretic resolution of species boundaries in seed-gall nematodes, *Anguina* spp. (Nematoda : Anguinidae), from some graminaceous hosts in Australia and New Zealand. *Nematologica*, 34 (1988) : 401-411.
- STEINER, G. (1936a). Opuscula miscellanea nematologica, III. *Proc. helminth. Soc. Wash.*, 3 : 16-22.
- STEINER, G. (1936b). Opuscula miscellanea nematologica, IV. *Proc. helminth. Soc. Wash.*, 3 : 74-80.
- STEINER, G. (1938). Opuscula miscellanea nematologica, VII. *Proc. helminth. Soc. Wash.*, 5 : 35-40.
- THORNE, G. (1925). The genus *Acrobeles* von Linstow, 1887. *Trans. microsc. Soc.*, 44 : 171-210.
- THORNE, G. (1937). A revision of the nematode family Cephalobidae Chitwood and Chitwood, 1934. *Proc. helminth. Soc. Wash.*, 4 : 1-16.
- ZELL, H. (1987). Nematoden eines Buchenwaldbodens 9. Die Cephaloben (Nematoda, Rhabditida). *Carolinea*, 45 : 121-134.