

# A revision of the genus *Pseudacrobeles* Steiner, 1938 (Nematoda : Cephalobidae)<sup>(1)</sup>. Part 1. Subgenus *Pseudacrobeles* grad. n.

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**Summary** – Major changes are proposed to the composition of the genus *Pseudacrobeles* on the basis of numerous specimens from several species, mainly from tropical and subtropical countries. In the first part of this revision, the diagnosis of the genus is emended. The subgenus *Pseudacrobeles* grad. n. is proposed, characterized by the occurrence of labial probolae in all its species, and of cephalic probolae in some. The genus *Panagrocephalus* is considered a junior synonym of genus and subgenus *Pseudacrobeles*; *Panagrocephalus anadelphus* and *P. baloghi* are transferred, and *P. anadelphus impervius* is synonymized with *P. baloghi*. The genus *Heterocephalobus* is considered *genus inquirendum* because of its unsatisfactory diagnostic characters. *Heterocephalobus laevis*, *H. pauciannulatus*, *H. tabacum* and *H. teres* are transferred to genus and subgenus *Pseudacrobeles*. The type species of the genus and subgenus, *Pseudacrobeles (P.) variabilis*, was found to be part of a very variable group which could not be divided easily but did appear to represent several species. The superspecies *P. (P.) [variabilis]* is proposed for this group, comprising of the species *P. (P.) [v.] baloghi*, *P. (P.) [v.] macrocystis*, *P. (P.) [v.] tabacum* and *P. (P.) [v.] variabilis*. Intraspecific variability of the lip region in *P. (P.) [v.] variabilis* is shown as seen with SEM.

**Résumé – Révision du genre *Pseudacrobeles* Steiner, 1938 (Nematoda : Cephalobidae). Part. 1. Sous-genre *Pseudacrobeles* grad. n.** – Fondés sur l'étude de nombreux spécimens appartenant à différentes espèces provenant principalement des régions tropicales et subtropicales, d'importants changements dans la composition du genre *Pseudacrobeles* sont proposés. Dans cette première partie, la diagnose du genre est amendée; le sous-genre *Pseudacrobeles* grad. n. – caractérisé par la présence de probolae labiales chez toutes ses espèces et de probolae céphaliques chez certaines – est proposé; le genre *Panagrocephalus* est considéré comme un synonyme mineur du genre et sous-genre *Pseudacrobeles* auquel sont transférés *Panagrocephalus anadelphus* et *P. baloghi*, cependant que *P. anadelphus impervius* est considéré comme un synonyme mineur de *P. baloghi*. Par suite des insuffisances de sa diagnose, le genre *Heterocephalobus* est considéré comme *genus inquirendum*. *Heterocephalobus laevis*, *H. pauciannulatus*, *H. tabacum* et *H. teres* sont transférés au genre et sous-genre *Pseudacrobeles*. L'espèce type du genre et sous-genre, *Pseudacrobeles (P.) variabilis* est tenue pour l'un des éléments d'un groupe à notables variations lequel ne peut être aisément divisé tout en représentant apparemment plusieurs espèces. La superespèce *P. (P.) [variabilis]* est proposée pour ce groupe qui comprend les espèces *P. (P.) [v.] baloghi*, *P. (P.) [v.] macrocystis*, *P. (P.) [v.] tabacum* et *P. (P.) [v.] variabilis*. La variabilité intraspécifique de la région labiale chez *P. (P.) [v.] variabilis* est démontrée à l'aide de photographie au M.E.B.

**Key-words** : *Pseudacrobeles*, *Heterocephalobus*, *Panagrocephalus*, Nematoda, Cephalobidae, morphology, taxonomy.

Steiner described *Acrobeles variabilis* in 1936 and subsequently erected the monotypic genus *Pseudacrobeles* for it in 1938. Until very recently, this seemed to be both an uncommon and small genus : no other species were added, and it was reported again only twice, from Zaire (Geraert, 1962) and from Australia (Sauer & Annells, 1985). Although various authors described some very similar forms, these were consistently placed in other genera (Andrássy, 1967b, 1968; Rashid *et al.*, 1985, 1989; Boström, 1990; De Ley & Coomans, 1990). We have examined a range of new and old material from numerous locations, and encountered many specimens

of some nine species belonging to the genus. One of these species was considered new and described as *P. macrocystis* by De Ley and Siddiqi (1991). The sum of our material revealed that *Pseudacrobeles* was incorrectly conceived until now : it actually has a widespread distribution, consists of at least twelve species, and is taxonomically exceedingly confusing.

Our material also prompted us to investigate the validity of the genera *Heterocephalobus* Brzeski, 1960 and *Panagrocephalus* Andrássy, 1967. The diagnosis of *Heterocephalobus* has undergone some changes since its establishment by Brzeski, first as a subgenus in 1960 and

<sup>(1)</sup> This article was announced as in press in *Afro-Asian J. Nematol.* in the references of De Ley and Siddiqi (1991).

then as a genus in 1961, but according to the most recent formulation (Andrássy, 1984), it can be distinguished from *Pseudacrobeles* by its head shape (low-rounded *vs* carrying six setose processes) and lateral field (three incisures *vs* five). Andrásy (1984) listed thirteen species as belonging to *Heterocephalobus*, with *H. elongatus* (de Man, 1880) Andrásy, 1967 [= *Cephalobus* (*H.*) *kaczanowskii* Brzeski, 1960], as type species. Three more species were added after 1984 (Rashid *et al.*, 1985; Andrásy, 1987; Hernández, 1990). Andrásy (1984) differentiated *Panagrocephalus* from *Pseudacrobeles* by its stoma structure (prostome wide and not covered by the pharyngeal collar, *vs* the opposite condition) and lateral field (three incisures *vs* five). Apart from type species *P. anadelphus* Andrásy, 1967 the genus contains one other species: *P. baloghi* Andrásy, 1968. Recently, De Ley and Coomans (1990) described a new subspecies, *P. anadelphus impervius*.

On the basis of our study, no criteria remain for upholding the genus *Panagrocephalus*, which is therefore rejected, while *Heterocephalobus* is considered *genus inquirendum*. In total, nine species are transferred to *Pseudacrobeles*. Also, the genus is considered to consist of two subgenera.

As the description of all the species studied and the justification of all the proposed changes would have resulted in a very large single paper, it was considered better to divide the revision in two parts. This first part emends the diagnosis of *Pseudacrobeles*, proposes the subgenus *Pseudacrobeles* grad. n., lists the species of this subgenus and presents descriptions of those which we studied. The second part (De Ley *et al.*, 1993) will include the diagnosis, species list and species descriptions of a new subgenus, as well as a key to the genus, a list of *species inquirendae* and/or *incertae sedis*, and an extensive discussion. This complementary sequel of the present article will henceforth be referred to as « Part 2 ». The new subgenus proposed in it is not yet named here in order to avoid nomenclatorial complications.

## Material and methods

Table 1 lists the samples from which specimens were used for measurement and description, together with available data on these samples. Details on numbers and samples of origin of the specimens are given per species prior to each relevant description. S.E.M. observations were made with a JEOL LSM-840 microscope from specimens submitted to critical point drying and sputter-coating.

The emphasis of this study lies strongly on the correction of the diagnosis of some taxa, and descriptions are therefore restricted to diagnostic aspects of characters. Also, they are written so as to minimize overlap with tables and diagnoses, and are based only on specimens seen by us. Species diagnoses based on other populations as well as ours (e.g. type material not available to

us) are given in the form of a lattice key in Part 2. For more details on the morphology of this group of animals we refer especially to De Ley and Siddiqi (1991).

Terminology of head structures follows Rashid *et al.* (1989). For clarity's sake, we must specify that in this revision cephalic probolae refers to the six apical cuticular outgrowths that can occur on the lips, but not to the lips themselves. For stoma structure, a different nomenclature is used than that of Steiner (1933): apart from the cheilostome, stoma sections are referred to by counting from anterior to posterior, and a total of six sections is distinguished (cf. De Ley & Siddiqi, 1991). The shape of the cheilorhabdia in lateral view is described with the terms comma-, bar- or granule-shaped (as depicted respectively in Figs 4 H-J, 4 F-G and 7 O-P; see Part 2). To measure the positions of nerve ring, excretory pore and deirid, we have (among other methods) counted the number of ventral annules. The abbreviations  $R_{nr}$ ,  $R_{cp}$  and  $R_{dei}$  are used for the respective values thus obtained. "Postvulval uterine branch" is abbreviated as PUB, "anal body widths" as ABW. In descriptions, we use the word "spike" for that part of the male tail extending posterior to the posteriormost pair of genital papillae. "Mucro" is reserved for the cuticular terminal end of the tail, irrespective of its being clearly offset from the remainder of the spike or not. Thus, the length of the spike equals that of the mucro plus the length of body cavity extending posterior to the posteriormost papillae (Figs 4 P-T, 6 D). The term *cornua crurum* is introduced for the anterior extensions of the *crura* of the gubernaculum that occur in some Cephalobidae. When present, these are visible in lateral view as a pair of refractive lines lying anterolateral to the single line formed by the dorsal surface of the *cuneus* of the gubernaculum. They may even extend beyond the proximal end of the *cuneus* (Fig. 5 G in De Ley & Coomans, 1990; see Part 2).

Line drawings follow some conventions. All drawings are based on lateral views, except when stated otherwise. Each drawing of a lip region in surface view is accompanied by one of the lip region and stoma in median view from the same specimen (e.g. Fig. 1 D, F). Sections of cuticle (e.g. Fig. 1 H) are drawn at mid-body along a length representing 10  $\mu$ . Phasmid and lateral field on female tails are drawn to the degree that they were visible.

We do not comment on, or compare with descriptions in Andrásy (1967a), because we have not seen his specimens and because their descriptions were apparently not based on type material.

## Genus *Pseudacrobeles* Steiner, 1938

= *Panagrocephalus* Andrásy, 1967 syn. n.

### DIAGNOSIS (EMENDED)

Cephalobinae Filipjev, 1934. Lateral field with three incisures, fading out at or near the phasmid. Lip region

**Table 1.** Sample specifications.

Country	Sample Collector	Date	Vegetation	Soil	Location	Kept at *	Remarks	
Brazil	B4	?	?	Gladiolus	?	Bahia State	LW	Slide nº 7057
	B1160	R. D. Sharma	1974-76	<i>Theobroma cacao</i> L. cv. Comum	Medium	Faz. Asonara Dois, Gandu Bahia State	IvD	
	B1225	R. D. Sharma	1974-76	<i>Theobroma cacao</i> L. cv. Comum	Light- Sandy	Faz. Futurosa, Belmonte Bahia State	IvD	
	B1226	R. D. Sharma	1974-76	<i>Nicotiana tabacum</i> L.	Light	Sítio Pracinha, Muriúba BR 101, Bahia State	IvD	
	B1651	R. D. Sharma	1974-76	<i>Cocos nucifera</i> L.	Sandy	Faz. Crasto, Estância, Sergipe State	IvD	
	B1857	R. D. Sharma	1974-76	<i>Theobroma cacao</i> L. cv. Comum	Sandy	Faz. Modelo, Itamaraju, Bahia State	IvD	
	B1861	R. D. Sharma	1974-76	<i>Citrus sinensis</i> Osbeck.	Loamy	SUDAP-Estação Exp. do Buquim, Sergipe State	IvD	
Burkina Faso	BF	S. D. Sharma	VII.87	Groundnut	?	?	IIP	
Cameroon	C	?	??90	Forest	?	?	IIP	Sample coded 45/90
Ecuador	G2f	K. Desender	?V.91	Fern-sedge zone	?	Alt. 850 m, Cerro Azul, Isabela	IvD	
	G4	A. Coomans	12.II.88	Grasses (clearance in scalesia forest)	Crumbly brown	N slope, alt. 670 m, 15 m east of road, Santa Cruz	IvD	
	G5	A. Coomans	12.II.88	Scalesia forest	Crumbly brown	N slope, alt. 670 m, 3 m west of road, Santa Cruz	IvD	
	G7	A. Coomans	15.II.88	Fern-sedge zone	Crumbly reddish	Cerro Crocker, alt. 860 m, 1.5 m N of hut, Santa Cruz	IvD	
	G8	A. Coomans	15.II.88	Fern-sedge zone	Crumbly brown	S slope Cerro Crocker, alt. 700 m, Santa Cruz	IvD	
	G11	A. Coomans	19.II.88	Grasses	Humid, grey	SW slope, alt. 180 m, Casetas Tortuga, Santa Cruz	IvD	
	G13	A. Coomans	21.II.88	Herbs and grasses in scalesia forest	Humid	Near finca Claudio Cruz, alt. 350 m, Floreana	IvD	
	G14	A. Coomans	21.II.88	Grasses in guava orchard	?	Finca Claudio Cruz, alt. 350 m, Floreana	IvD	
	G17	A. Coomans	26.II.88	Arid zone	Rather humid	SW slope, alt. 200 m, foot Cerro Verde, Fernandina	IvD	
G18	A. Coomans	27.II.88	Fern-sedge zone	Humid	SW slope, alt. 800 m, Fernandina	IvD		
India	I10	P. Speyer	?	Grape	?	Hassan	LW	Slide nº 8310
	I11	P. Speyer	?	Banana	?	Bangalore	LW	Slide nº 8332
	I12	P. Speyer	?	Banana	?	Coinbatore	LW	Slide nº 8386
	I14	B. G. Narayanaswamy	?	French bean	?	Bangalore	LW	Slide nº 9561
	I30	M. Ramaswamy	??87	Groundnut	?	Citrus Improvement Project Tirupati, Andhra Pradesh	IIP	Sample coded 30/87
Indonesia	IN	?	?	Citrus	?	Garut	LW	Slide nº 7369

**Table 1.** Sample specifications (*continued*).

Country	Sample	Collector	Date	Vegetation	Soil	Location	Kept at *	Remarks
Kenya	K	N. Wedell	??85	Grasses, <i>Eucalyptus</i>	Clayey, silty	Othaya, plot 348	NR	
Malaysia	M1	Kueh Tiong Kheng	??87	<i>Piper nigrum</i>	?	Durin 3 <sup>rd</sup> Division, Sarawak	IIP, IvD USDA, NR	Sample coded 32/87
	M2	Kueh Tiong Kheng	??89	? herb 139	?	John Brodie, Telok Sabang, Samarahan	IIP, NR	Sample coded 29/89
Nigeria	N	K. Lakshmi Unny	??63	<i>Manihot utilissima</i> Pohl.	?	Umudike	LW	Slide n° 3512
Poland	P	A. Kaczanowski	25.IX.58	?	?	Dzieskanów Leśny, Polonia cent. 75A	PAS	Slides NT-16, NT-18 poorly preserved
Spain	S	I. Armendáriz	16.IV.86	<i>Pinus nigra</i> , <i>Bursus</i> , <i>Quercus</i> , grasses	?	Locality * Eslava *, Navarra, coord. 30TXN21	UdN	Slide n° VIIIe P1 004
Tanzania	T4b	J. Bridge	21.II.83	Cooking banana	?	Farm Katambo Muoshezi, Bukoba Urban, Bukoba	IIP	
	T9	J. Bridge	22.II.83	Cooking banana	?	Nyanga, Bukoba	IIP	
	T26	J. Bridge	25.II.83	Cooking banana	?	Kashekya, Gera Ward, Bukoba	IIP	
	T41	J. Bridge	28.II.83	Highlevel cooking banana	?	Farm Tevazias Tadeo, Buganguzi	IIP	
	T45	J. Bridge	22.II.84	<i>Coffea robusta</i>	?	Field VCE, cult. & breed, line, Lyamungu Res. Station	IIP	
	T46	J. Bridge	22.II.84	<i>Coffea robusta</i>	?	Field 39, Lyamungu Res. Station	IIP	
USA	US1	Diehl	30.VII.38	<i>Glomidium vesicarium</i>	?	U.S.Pl. Introd. Garden, Savannah, Georgia	USDA	Slide n° T-458t, very flattened
	US2	Taylor	1.VIII.38		?	Lumberton experiments Savannah, Georgia	USDA	Slides T-4216p & T-4217p, very poor
	US3	D. Harshman	??90	Culture raised from corn field sample	?	Coll. Agric. Sc., Clanson University, S-Carolina	IIP	
	US7	G. Thorne	27.II.36	Decaying daffodil with <i>Ditylenchus</i>	?	Brookings, Oregon	USDA	Slide n° T-452t, very poor
	US47	W. D. Courtney	10.XII.47	Wild strawberry bed	?	Waldport, Oregon	USDA	Slides T-4193p & T-4194p
Venezuela	V	M. Oostenbrink	1.III.64	Fallow plot formerly planted with cucumber	Very dry	Cagua	LW	Slide n° 3539, poorly preserved

\* : Collections abbreviated as follows : IIP = International Institute of Parasitology, St Albans, UK; IvD = Instituut voor Dierkunde, Gent, Belgium; LW = Landbouwwuniversiteit Wageningen, The Netherlands; NR = Naturhistoriska Riksmuseet, Stockholm, Sweden; PAS = Polish Academy of Sciences, Warsaw, Poland; UdN = Universidad de Navarra, Pamplona, Spain.

with hexaradial, triradial or bilateral symmetry and bearing 6 + 4 papilliform sensillae. Amphids small slits or oval pores at bases of lateral lips. Lips separate or amalgamated; lateral lips may be reduced. Cephalic probolae absent to short-setiform. Labial probolae absent to

low knobs or ridges. Radial ridges absent, tangential ridges present or absent. Mouth opening circular to triangular, occasionally with small radial striae separating small liplet-like structures but never extending deeply between the lips. Stoma with six sets of sclerotizations.

Cheilorhabdions comma-, bar- or granule-shaped in optical section; cheilostome wide. Appearance of second stoma section in lateral view varying from being as wide as cheilostome and having sclerotized rhabdia, to being as narrow as third section and having inconspicuous rhabdia. Third to sixth sections at rest clearly narrower than cheilostome. Females with PUB usually developed, never surpassing ovary tip. Female tail sharp or blunt, conical, from 2.5 to 10 ABW long. Male tail with or without mucro, with or without extension of the body core beyond the posteriormost papillae. Gubernaculum with *cornua crurum* never prominent.

## TYPE SUBGENUS

*Pseudacrobeles* Steiner, 1938.

## OTHER SUBGENUS

See Part 2.

**Subgenus *Pseudacrobeles* Steiner, 1938**

## DIAGNOSIS

As for the genus, but with the following restrictions: Lip region predominantly triradiate, very occasionally with hexaradiate or bilateral symmetry. Labial probolae present in all species, but perhaps not in all individuals: if apparently absent then all lips low, amalgamated. Cephalic probolae present or absent.

## TYPE SPECIES

*Pseudacrobeles (Pseudacrobeles) [variabilis] variabilis* (Steiner, 1936) Steiner, 1938.

## OTHER SPECIES

- P. (P.) anadelphus* (Andrássy, 1967) comb. n.  
= *Panagrocephalus anadelphus* András-sy, 1967 syn. n.  
= *Panagrocephalus anadelphus anadelphus* András-sy, 1967 (in De Ley & Coomans, 1990) syn. n.
- P. (P.) laevis* (Thorne, 1937) comb. n.  
= *Eucephalobus laevis* Thorne, 1937 syn. n.  
= *Heterocephalobus laevis* (Thorne, 1937) András-sy, 1967 syn. n.
- P. (P.) pauciannulatus* (Marinari-Palmisano, 1967) comb. n.  
= *Heterocephalobus pauciannulatus* Marinari-Palmisano, 1967 syn. n.
- P. (P.) teres* (Thorne, 1937) comb. n.  
= *Eucephalobus teres* Thorne, 1937 syn. n.  
= *Heterocephalobus teres* (Thorne, 1937) András-sy, 1967 syn. n.
- P. (P.) [variabilis] baloghi* (Andrássy, 1968) comb. n.  
= *Panagrocephalus baloghi* András-sy, 1968 syn. n.  
= *Panagrocephalus anadelphus impervius* De Ley & Coomans, 1990 syn. n.
- P. (P.) [variabilis] macrocystis* De Ley & Siddiqi, 1991.

*P. (P.) [variabilis] tabacum* (Rashid *et al.*, 1985) comb. n.

= *Heterocephalobus tabacum* Rashid *et al.*, 1985 syn. n.

Note: *P. (P.) variabilis*, *P. (P.) baloghi*, *P. (P.) macrocystis* and *P. (P.) tabacum* are considered to form a species complex, for which the superspecies name *P. (P.) [variabilis]* (Steiner, 1936) Steiner, 1938 is proposed here. A diagnosis is given below.

**Superspecies *Pseudacrobeles (Pseudacrobeles) variabilis***

(Steiner, 1936) Steiner, 1938

(Fig. 1-6; 7 K-Y)

## DIAGNOSIS

Body 0.4-0.8 mm long. Cheilorhabdia bar-, granule- or comma-shaped. Second stoma section varying from similar to third section in width and refractiveness, to similar to cheilostome in both respects. Lip region very variable. Corpus: isthmus ratio 2.5-5.1. Female tail with  $c' = 3.5-8.7$ . Male tail with spike 0-20  $\mu\text{m}$  long, mucro 0-15  $\mu\text{m}$  long and  $c' = 1.7-3.7$ . Spicules 15-27  $\mu\text{m}$  long and 2.5-4.5  $\mu\text{m}$  wide. Gubernaculum 8-15  $\mu\text{m}$  long.

***Pseudacrobeles (P.) [v.] variabilis***

(Steiner, 1936) Steiner, 1938

(Fig. 1; 2; 3 B-F, H-L; 6 A)

## MATERIAL

Specimens from the following samples were measured: B1225 (4 ♀♀, 4 ♂♂); B1651 (8 ♀♀, 2 ♂♂); B1861 (1 ♀, 3 ♂♂); K (5 ♀♀, 6 ♂♂); T9 (2 ♀♀, 2 ♂♂); T26 (1 ♀, 1 ♂); T41 (3 ♀♀, 3 ♂♂); T45 (5 ♀♀, 4 ♂♂); T46 (6 ♀♀, 3 ♂♂); US1 (1 ♀); US2 (2 ♀♀, 4 ♂♂); US3 (7 ♀♀, 6 ♂♂). The four specimens from B1861, as well as 4 ♀♀ and 3 ♂♂ from T46, were prepared for SEM. The specimens from Brazil broke up during this procedure, so that determination of sex became impossible. The type material of the species (from Jacksonville, Florida) is probably lost (M. Golden, pers. comm.). The female from US1 has been reclassified in the USDA Nematode Collection as lectotype on slide T-458t, specimens from US2 as paralectotypes on slides T-4216p and T-4217p.

## MEASUREMENTS

See Tables 2, 3.

## DESCRIPTION

Cephalic probolae varying from distinctly setiform to completely absent. Labial probolae varying from small but distinct knobs, to flat ridges formed by partially fused lips. Tangential ridges varying from present to absent. Lip region usually with triradiate symmetry, but sometimes with a bilateral component caused by shape

**Table 2.** Measurements in  $\mu\text{m}$  of *Pseudacrobeles* (*P.*) [*v.*] *variabilis* (Steiner, 1936) Steiner, 1938 from the U.S.A.

	Florida* (types)		Georgia (US1 & US2)		South Carolina (US3)	
	? ♀♀	? ♂♂	3 ♀♀	4 ♂♂	7 ♀♀	6 ♂♂
L	650-670	650-670	500-745	450-575	620-795	520-605
body width			25	22	21-30	23-28
pharynx length			130-174	130-140	170-185	162-166
tail length	100 **	35 **	62-78	20-32	86-99	35-39
anal width	19 **	23 **	13	12-15	12-16	16-19
a	17-18	19	20	24	25-30	22-23
b	4.0	4.0-4.3	3.7-4.3	3.5-3.9	3.6-4.3	3.2-3.6
c	7.3-8.0	18-20	8.0-9.6	14-21	6.6-8.9	13-17
c'	5.3 ** - 5.7 ***	1.7 **	4.8	1.7-2.1	5.8-7.2	2.1-2.4
stoma	13-16 **	13-16 **	11-14	12-13	13-15	12-15
corpus			81-114	89	107-122	98-107
isthmus			21-26	22	24-31	26-27
bulbus			18-24	14-19	18-21	16-19
corpus : isthmus	3.1 ***	3.1 ***	3.9-4.4	4.0	3.6-4.5	3.6-4.2
nerve ring			92-112	?	92-105	96-106
excretory pore			66-116	83-98	99-120	104-118
deirid			112	96	114-135	121-126
n.r. (% pharynx)	59 ***	59 ***	54-64	?	54-61	64-69
e.p. (% pharynx)			51-67	64-70	58-69	62-71
deirid (% pharynx)	62 ***	62 ***	66	74	67-76	74-77
R <sub>nr</sub> (annuli)	66 ***	66 ***	50	?	57-71	61-67
R <sub>ep</sub> (annuli)			52-53	57	61-67	57-65
R <sub>dei</sub> (annuli)	70 ***	70 ***	60	?	68-75	72-75
phasmid	22 **	17 **	16-19	13-21	17-24	20-26
phasmid (% tail)	22 **	50 **	21-31	55-67	19-28	57-68
cuticle thickness			1.5	?	1.5-2.0	1.0-1.5
annule width			?	?	1.5-2.2	1.3-1.8
V (%) / flexure	60-61		61	50	57-61	49-60
G (%) / T (%)			25-30	41	21-32	48-58
vagina/spicules		22 **	8	19-23	7-10	19-22
rectum/gubernaculum	19 **		20-27	10-12	18-26	11
PUB/spike		2 **	16-31	0?	19-35	0-4
spermatheca/mucro		2 **	23-36	0?	6-40	0-4

\* : Measurements from Steiner (1936), except :

\*\* : Measured on Fig. 23 in Steiner (1936),

\*\*\* : Measured on Fig. 13 in Steiner (1938; scales apparently incorrect!).

differences between the lateral lips and the others, and also between the dorsal labial probola and the subventrals. One specimen from B1861 apparently with six rudimentary liplets instead of labial probolae, resulting in a hexaradially symmetrical lip region under SEM. This specimen was severely damaged, however, and for this reason is not shown. Cheilorhabdia bar-shaped in optical section. Second stoma section varying from intermediate between cheilostome and posterior sections in width and degree of sclerotization, to similar to cheilostome. Nerve ring lying at four fifths to base of corpus.

Excretory pore from two annules anterior to five annules posterior to trailing edge of nerve ring. Deirid 4-12 annules posterior to excretory pore. Females with PUB 0.5-1.6 body widths long and rectum 1.2-2.0 ABW. Male tail with body cavity extending for 0-1.5  $\mu\text{m}$  into spike. Spicules 2.5-4  $\mu\text{m}$  broad, 1.1-1.6 ABW long.

#### JUSTIFICATION OF DETERMINATION

The specimens from Georgia (US1 and US2) were determined as *P. variabilis* by Steiner (M. Golden, pers. comm.). The material from US3 originated from South

**Table 3.** Measurements in  $\mu\text{m}$  of *Pseudacrobeles* (*P.*) [*v.*] *variabilis* (Steiner, 1936) Steiner, 1938 from Brazil, Kenya and Tanzania.

	Brazil (B1225, B1651 & B1861)		Kenya (K)		Tanzania (T9, T26, T41, T45, T46)	
	13 ♀♀	9 ♂♂	22 ♀♀*	6 ♂♂*	17 ♀♀	13 ♂♂
L	440-650	385-545	450-570	380-440	465-610	445-620
body width	15-26	16-23	18-24	17-20	20-27	19-24
pharynx length	125-163	125-144	120-143	105-126	127-160	121-161
tail length	69-100	25-38	55-71	27-34	61-89	32-46
anal width	10-14	12-17	11-14	14-17	11-15	14-19
a	24-29	21-29	21-28	21-25	20-28	23-26
b	3.4-4.1	3.1-3.8	3.4-4.1	3.5-3.8	3.6-4.1	3.5-4.1
c	5.4-7.2	13.3-16.4	6.9-8.9	12-14	6.8-8.4	12.0-16.0
c'	5.7-8.7	1.9-2.7	4.6-5.8	2.1-2.4	4.7-7.1	1.9-2.9
stoma	9-13	9-12	11-13	11-13	12-15	12-15
corpus	76-106	73-91	85-99	72-90	74-105	68-103
isthmus	20-28	20-26	20-27	20-23	23-28	23-28
bulbus	14-20	14-17	15-18	13-18	15-18	13-20
corpus : isthmus	2.7-4.5	3.1-4.1	3.5-4.4	3.7-4.2	2.7-4.0	2.5-4.0
nerve ring	78-102	78-103	81-95 **	76-90 **	88-107	80-105
excretory pore	82-105	81-106	81-100 **	80-100 **	89-107	80-105
deirid	95-118	92-112	90-113 **	86-106 **	98-118	95-122
n.r. (% pharynx)	61-64	61-75	60-68 **	67-70 **	62-72	61-71
e.p. (% pharynx)	58-68	65-77	60-72 **	71-75 **	64-75	62-75
deirid (% pharynx)	70-78	73-81	67-78 **	77-95 **	71-85	72-83
R <sub>w</sub> (annuli)	63-72	59-70	60 **	55-60 **	54-63	54-63
R <sub>cp</sub> (annuli)	64-75	62-71	62 **	60-66 **	55-66	57-66
R <sub>de</sub> (annuli)	70-85	70-80	73 **	64-73 **	61-73	65-73
phasmid	8-23	14-22	13-18 **	14-17 **	12-23	14-23
phasmid (% tail)	12-23	55-64	18-32	40-50	17-27	35-60
cuticle thickness	0.5-1.0	0.5-1.0	?	?	1.0-1.5	0.5-1.5
annule width	1.1-1.7	0.9-1.6	1.5-2.0	1.5-2.0	1.3-1.9	1.3-1.8
V (%) / flexure	57-61	32-52	60-64	36-47 **	59-63	39-62
G (%) / $\Gamma$ (%)	22-34	40-51	31-33 **	54-60 **	26-35	46-60
vagina/spicules	5-9	15-22	?	18-20	5-9	18-24
rectum/gubernaculum	15-23	8-12	17-19	8-10	16-23	9-12
PUB/spike	13-38	1-5	12-19	?	11-23	1-9
spermatheca/mucro	6-41	?	21-42	3-6	20-40	0-8

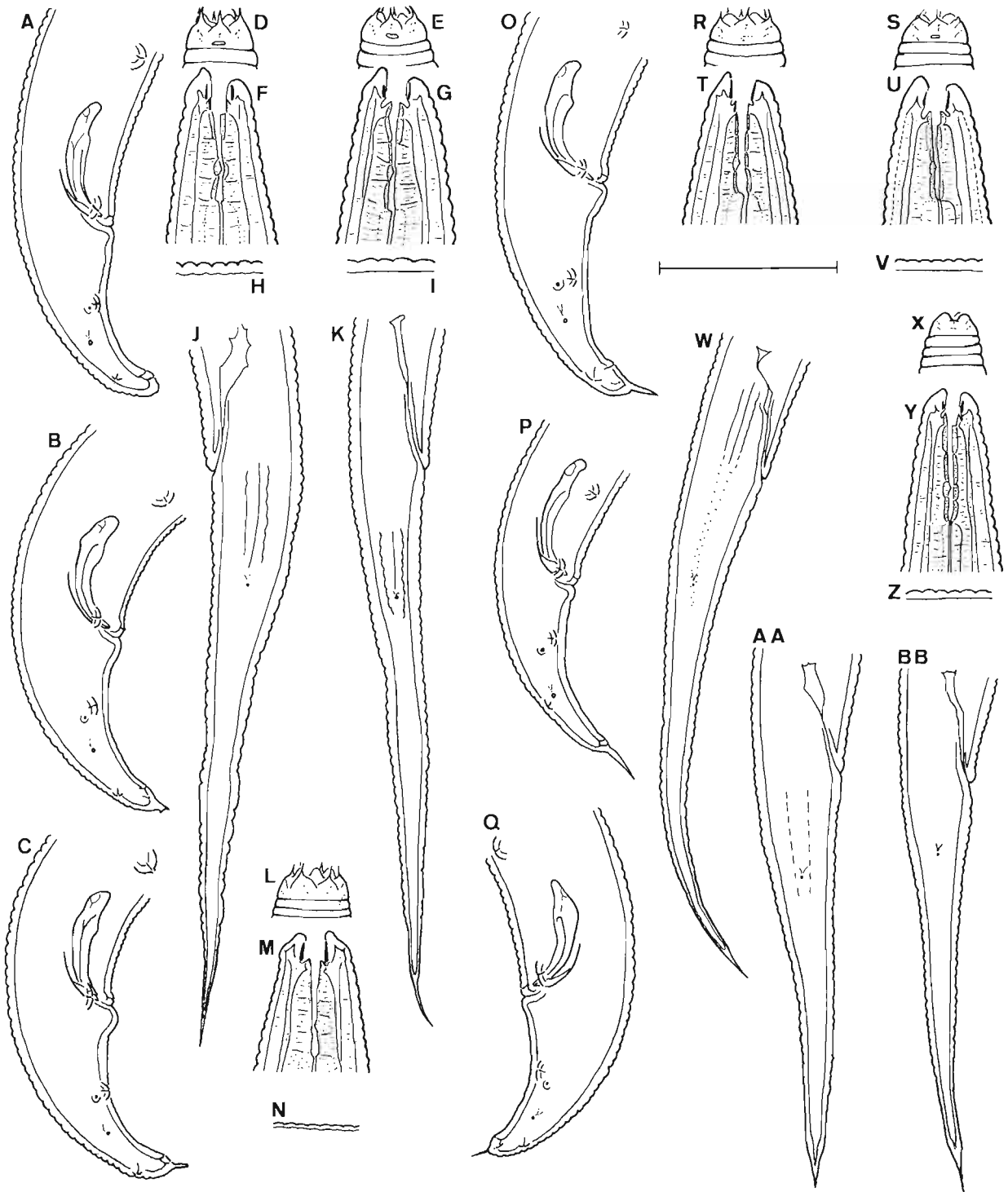
\* : All measurements from Boström (1990 &amp; unpubl.), except :

\*\* : Measured on re-examined specimens (5 ♀♀ and 6 ♂♂).

Carolina, as did the specimens described in Steiner (1938), and corresponds closely to the descriptions of Steiner (1936, 1938). The specimens from Brazil, Tanzania and Kenya were smaller on average, and displayed a greater variability in many respects (especially in lip region structure), but we could not identify any more or less consistently distinctive character apart from the more subcylindrical tail shape of Brazilian males (Fig. 2 G, H, N, V, W). Rashid *et al.* (1989) described a population from Krakatau as *Heterocephalobus loofi*, expressing some doubts on their own identification, however, and mentioning that at first they thought it was

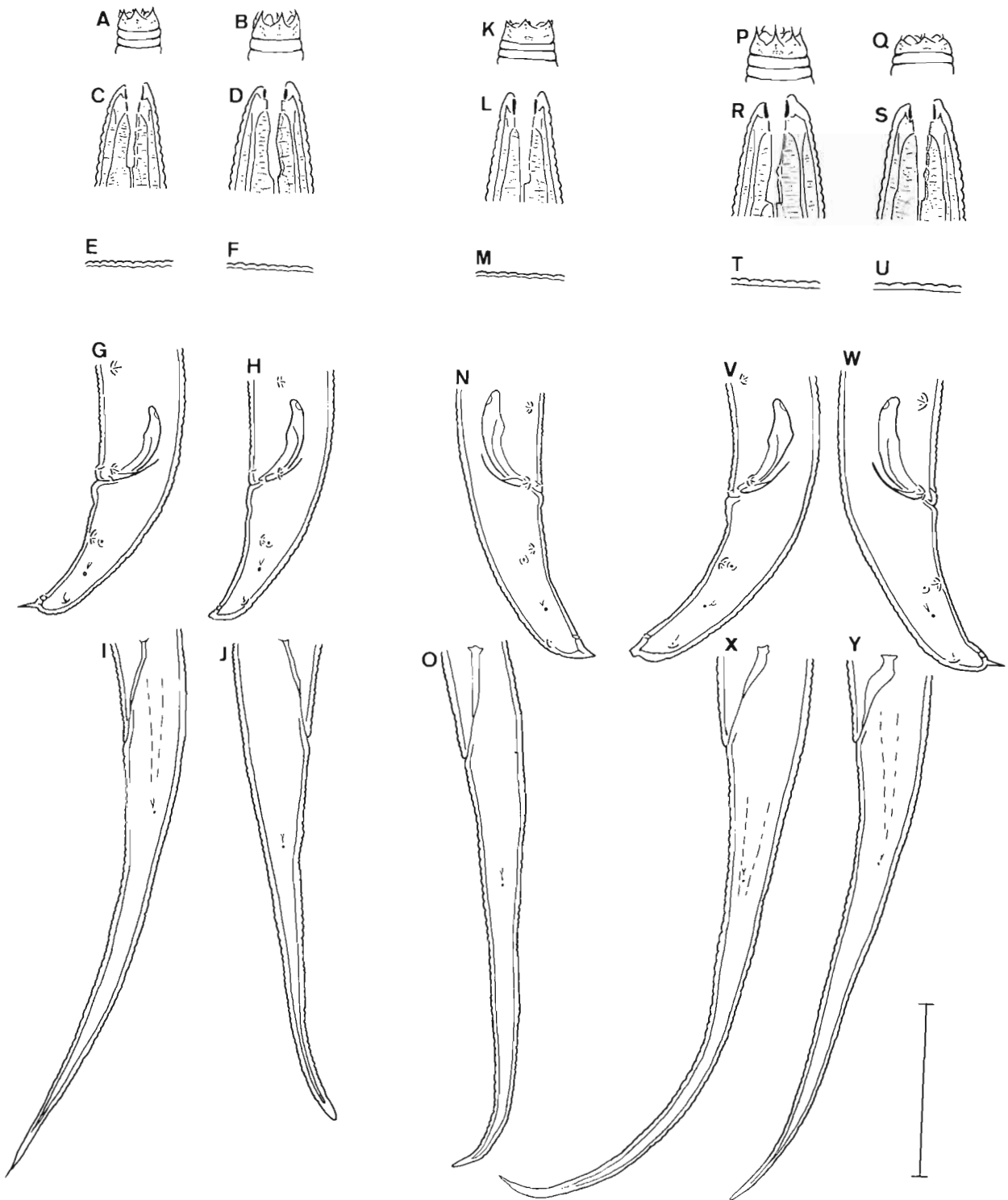
*Eucephalobus oxyuroides*. We have not seen these specimens, but consider it likely that they also represent *P. variabilis*, because of the long female tail ( $c' = 6.7-10.7!$ ) and the short spike on the male tail. Also, all specimens of *P. variabilis* from Brazil studied by us were previously determined as *E. oxyuroides* by Rashid *et al.* (1985). The material from Kenya was tentatively identified as *Heterocephalobus latus* in Boström (1990). As discussed in Part 2, *H. latus* (Cobb, 1906) Andrassy, 1967 is now considered *species inquirenda et incertae sedis*.

It should be noted that Steiner (1938) described the lateral field of *P. variabilis* as "bordered and separated



**Fig. 1.** *Pseudacrobeles (P.) [v.] variabilis* (Steiner, 1936) Steiner, 1938. A-K : From South Carolina (US3); L-N : From Georgia (US1); O-BB : From Tanzania (T9 : R-U, W; T41 : V, BB; T46 : X-AA) (Scale bar = 30  $\mu$ m for tails; 20  $\mu$ m for rest).





**Fig. 2.** *Pseudacrobeles (P.) [v.] variabilis* (Steiner, 1936) Steiner, 1938, from Brazil (B1225 : A-J; B1861 : K-O; B1651 : P-Y) (Scale bar = 30  $\mu$ m for tails; 20  $\mu$ m for rest).

by three wings which end near the phasmid". In current terminology three wings would correspond with four incisures, while Andr ssy (1984) even diagnosed *Pseudacrobeles* as having five incisures. However, comparison of Steiner's figures (Fig. 13 C, D in Steiner, 1938) with the sentence quoted and with our material (including his

own specimen from US1) clearly show that Steiner was describing a lateral field with three incisures. This refutes one of the supposed differences between *Pseudacrobeles* and both *Heterocephalobus* and *Panagrocephalus* (cf. introduction and Part 2).

**Table 4.** Measurements in  $\mu\text{m}$  of *Pseudacrobeles (P.) [variabilis] baloghi* (Andr ssy, 1968) comb. n. and *P. (P.) [v.] tabacum* (Rashid et al., 1985) comb. n.

	<i>P. (P.) [v.] baloghi</i>								<i>P. (P.) [v.] tabacum</i> (types from Brazil : B1226)			
	Paraguay		Gal�pagos						Measurements of Rashid et al. (1985)		our measurements	
	(types *) 1 ♀	2 ♂♂	Fernandina (G18) 14 ♀♀	420-490 8 ♂♂	Santa Cruz (G4) 1 ♀	400-420 2 ♂♂	Santa Cruz (G8) 7 ♀♀	475 1 ♂	13 ♀♀	13 ♂♂	5 ♀♀	5 ♂♂
L	560	490-510	400-570	420-490	585	400-420	485-620	475	550-690	490-600	535-660	510-565
body width	30**		19-30	20-25	24	17-18	20-29	18			23-31	22
pharynx length			123-158	136-157	162	135-139	147-169	140	121-148	116-133	122-145	115-131
tail length	60**	48**	49-69	48-52	70	39	65-79	52	61-75	34-40	60-75	36-42
anal width	18**	15**	9-15	14-18	12	13-14	10-18	14			13-18	16-17
a	19	26-27	16-23	18-24	24	23	21-24	26	23-29	22-29	21-25	21-25
b	3.4	3.4-3.7	3.0-3.7	3.0-3.4	3.6	3.3-3.4	3.3-3.7	3.4	4.2-5.0	4.0-4.5	4.3-4.9	4.0-4.6
c	9.2	10-16	7.3-8.8	8.4-9.8	8.4	10.4-10.7	7.1-8.1	9.0	7.6-10	13-16	8.6-9.5	13-15
c'	3.5	3.0-3.3	4.3-6.1	2.9-3.7	5.6	2.8-3.0	4.2-6.4	3.6			4.1-4.8	2.1-2.6
stoma	14**	13-14	11-13	12-13	12	12	12-14	12	10-13		10-13	10-12
corpus			63-84	82-104	104	72-84	89-105	85			80-98	75-86
isthmus			21-30	24-29	25	23-27	24-28	26			16-19	16-21
bulbus			15-21	15-20	19	15	15-21	15			15-16	13-15
corpus : isthmus	4	4	2.9-3.7	3.2-3.5	4.2	3.2-3.7	3.3-4.2	3.3			4.5-5.1	4.1-4.7
nerve ring			72-95	81-91	93	72-84	86-99	83			90-107	89-95
excretory pore			79-100	82-90	102	76-85	85-108	87	94-108		91-113	93-105
deirid			83-135	94-108	113	90-97	99-122	95			106-126	104-115
n.r. (% pharynx)			53-64	52-61	57	53-60	58-63	59			73-74	70-77
e.p. (% pharynx)	± 50	± 50	55-66	54-62	63	56-61	56-65	62			74-78	75-81
deirid (% pharynx)			63-87	61-72	70	66-70	67-72	67			86-91	82-90
R <sub>1</sub> (annuli)			51-59	55-58	69	63-71	55-65	60			50-57	51-57
R <sub>2</sub> (annuli)			55-59	51-59	71	65-71	58-69	60			51-57	52-60
R <sub>3</sub> (annuli)			62-66	60-66	83	74-82	64-70	66			60-66	58-66
phasmid	12**	14**	10-17	13-19	21	15-17	13-20	17	16-20		18-27	19-28
phasmid (% tail)	20**	29**	19-25	28-37	31	38-42	18-27	33		35-37***	27-36	55-65
cuticle thickness	1.2	1.2	1.0-1.5	1.0-1.5	1.0	1.0	1.0-1.5	1.0	1		1.0-1.5	1.0-1.5
annule width	1.7-2.0	1.7-2.0	1.4-2.0	1.4-1.9	1.6	1.4	1.4-2.2	1.4	1.5-2.0		2.0-2.2	1.6-2.0
V (% flexure)	63		60-64	41-56	60	36	59-63	37	59-64		58-64	51-67
G <sub>1</sub> (%T) (%)			21-37	46-56	36	42-46	20-30	44		52-71	30-39	49-52
vagina/spicules	9**	19-22	5-9	19-24	7	19-21	5-9	19		21-25	7-11	22-24
rectum/gubernaculum	22**	10-11	15-23	10-12	21	9-11	20-24	11		11-14	20-23	11-14
PUB/spike	15**	18-19**	4-18	16-20	21	10-11	13-18	20	25-30		22-31	2-3
spermatheca/mucro		6-7**	3-44	7-15	38	6-7	15-23	9	22-40		30-38	1-2

\* : All measurements by Andr ssy (1968), except :  
 \*\* : Measured on Abb. 5 in Andr ssy (1968).  
 \*\*\* : Apparently measured from tail tip instead of from anus.

***Pseudacrobeles (P.) [v.] baloghi***  
(Andrássy, 1968) comb. n.

(Figs 4, 6 B, D)

**MATERIAL**

Specimens were measured from the following samples: G4 (1 ♀, 2 ♂♂); G8 (7 ♀♀, 1 ♂); G18 (14 ♀♀, 8 ♂♂). Two ♂♂ and one ♀ from G18 were studied with SEM. We have not seen type specimens of *P. baloghi* (from Paraguay). Type specimens of *Panagrocephalus anadelphus impervius* were re-examined and compared with more specimens obtained from the original and other samples from the Galápagos.

**MEASUREMENTS**

See Table 4.

**DESCRIPTION**

Cephalic probolae stubby to distinctly setiform. Labial probolae small but distinct knobs. Tangential ridges seen in two males and two females hitherto studied with SEM. Lip region with triradiate symmetry. Cheilorhabdia bar- to comma-shaped in optical section. Second stoma section nearly as wide as cheilostome, with distinctly refractive walls. Nerve ring lying at three fifths to base of corpus. Excretory pore from two annules anterior to six annules posterior to trailing edge of nerve ring. Deirid 5-9 annules posterior to excretory pore. Females with PUB 0.3-0.7 body widths long and rectum 1.3-2.2 ABW. Male tail with body core extending in spike for 4-11 µm. Spicules 2.5-3.5 µm wide, 1.2-1.5 ABW long.

**JUSTIFICATION OF DETERMINATION**

All females from the Galápagos have a more slender tail than the single female described in Andrássy (1968):  $c' = 4.2-6.4$  vs 3.5. However, Andrássy (1970) described another female from Vietnam with  $c' = 4.5$ , and it is indeed reasonable to expect that intraspecific variability bridges the gap. Both the female from Paraguay and Vietnam had a short mucro on the tail (Andrássy, 1968, 1970), which was usually not true for the material we studied, but we encountered mucro-like tail tips in some specimens of many of the *Pseudacrobeles* populations studied (e.g. Figs 1 K, BB; 4 U, AA; 5 T, DD). It seems unwarranted to consider this a good character to distinguish species.

The single male from G8 agrees well with the original description, especially in tail shape, while the eight males from G18 form a series, with the spike being made up more and more by the mucro at the expense of the postpapillar body core (Fig. 4 P-T). The allotype of *Panagrocephalus anadelphus impervius* fits neatly into this series (cf. Fig. 3 G in De Ley & Coomans, 1990), and no clear grounds are left to distinguish this taxon from *Pseudacrobeles baloghi*. We therefore propose synonymy. The two males from G4 are problematical, being intermediate between *P. baloghi*, *P. macrocystis* and *P. va-*

*riabilis*. They provide grounds for the concept of these species as a complex (see Part 2).

***Pseudacrobeles (P.) [v.] tabacum***  
(Rashid *et al.*, 1985) comb. n.

(Fig. 7 K-Y)

**MATERIAL**

Type specimens were studied from B1226. 5 ♀♀ (including holotype) and 5 ♂♂ of reasonable quality were measured. No SEM.

**MEASUREMENTS**

See Table 4.

**DESCRIPTION**

Cephalic probolae absent to distinctly setiform. Labial probolae from low ridges to distinct knobs. Lip region with triradiate symmetry. Cheilorhabdia bar- to granule-shaped in optical section. Second stoma section never as wide and refractive as cheilostome. Nerve ring lying at base of corpus to anterior end of isthmus. Excretory pore 0-4 annules posterior to trailing edge of nerve ring. Deirid 5-9 annules posterior to excretory pore. Females with PUB 0.9-1.3 body widths long and rectum 1.1-1.6 ABW. Male tail with body core extending in spike for 1 µm. Spicules 3.5-4 µm wide, 1.3-1.4 ABW long.

***Pseudacrobeles (P.) [v.] macrocystis***  
**De Ley & Siddiqi, 1991**

(Fig. 3 A, G; 5; 6 C)

**MATERIAL**

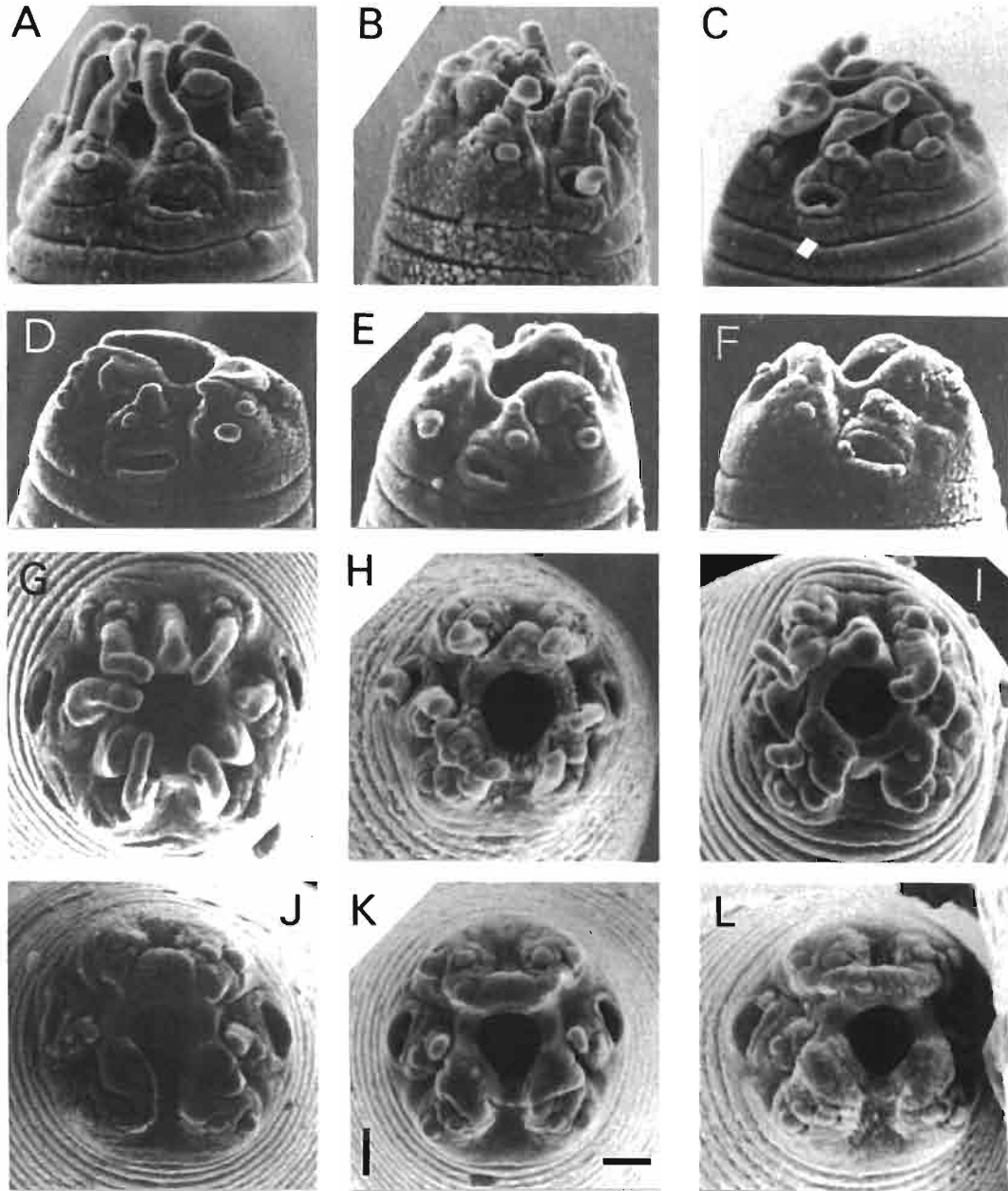
Specimens from the following samples have been measured: B1160 (1 ♀, 2 ♂♂); B1857 (2 ♀♀, 1 ♂); C (2 ♀♀, 1 ♂); T4b (2 ♂♂); T9 (2 ♀♀); T41 (9 ♀♀, 2 ♂♂); T45 (5 ♀♀, 3 ♂♂); T46 (1 ♂). The male from T46 was examined with SEM. We have also studied the type material (17 ♀♀ and 1 ♂ from M1, 13 ♀♀ and 12 ♂♂ from M2). To keep the datasets separate, however, the description does not include data of the type specimens.

**MEASUREMENTS**

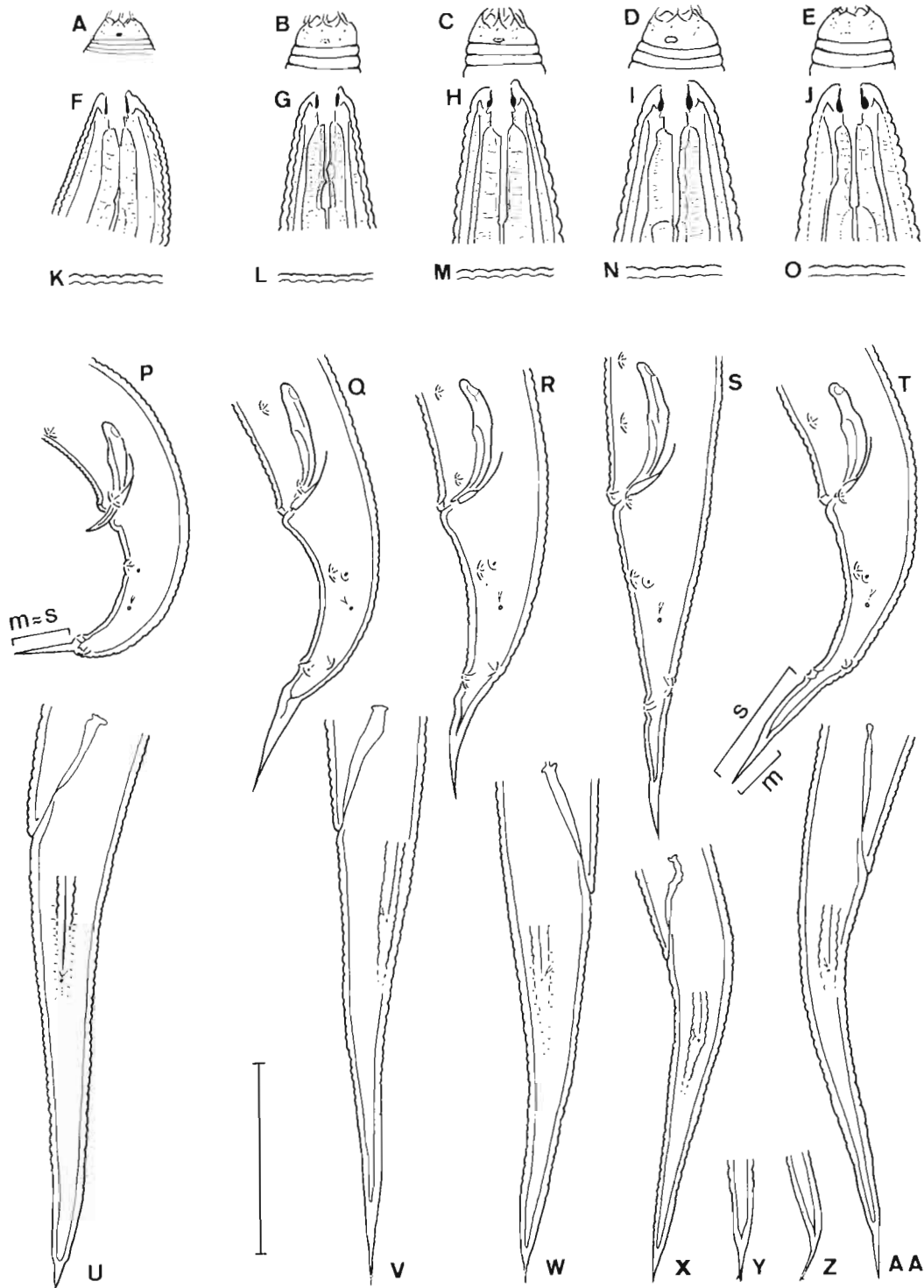
See Table 5.

**DESCRIPTION**

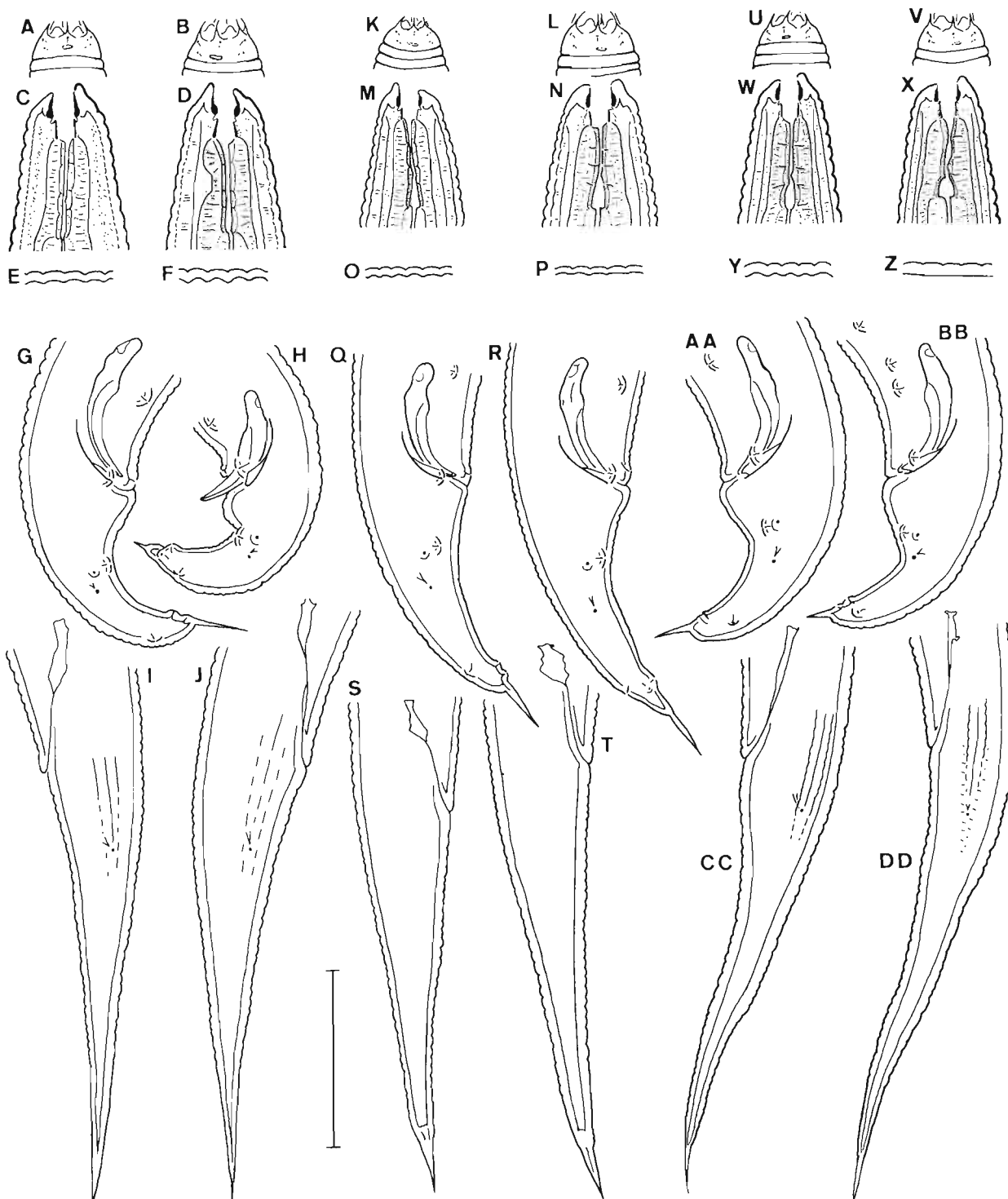
Cephalic probolae distinctly setiform. Labial probolae small but distinct knobs. Tangential ridges present in male shown in Fig. 3 A, G. Lip region with triradiate symmetry. Cheilorhabdia comma-shaped in optical section. Second stoma section similar to cheilostome in width and refractiveness. Nerve ring lying at three-fifths to base of corpus. Excretory pore from three annules anterior to seven annules posterior to trailing edge of nerve ring. Deirid 5-9 annules posterior to excretory pore. Females with PUB 0.5-0.9 body widths long and



**Fig. 3.** *Pseudacrobeles* (*P.*) [*v.*] *macrocystis* De Ley & Siddiqi, 1991. A, G : from T41. *P.* (*P.*) [*v.*] *variabilis* (Steiner, 1936) Steiner 1938; B-F, H-L : from T41 (Dorsal side is left on A-C, E, F; right on D; up on G-L).



**Fig. 4.** *Pseudacrobeles* (*P.*) [*v.*] *baloghi* (Andrássy, 1968) comb. n. A, F, P, U : From Isla Santa Cruz (G4); D, E, I-K, N, O, T, Y-AA : From Isla Santa Cruz (G8); B, C, G, H, L, M, Q-S, V-X : From Isla Fernandina (G18) (Scale bar = 30  $\mu$ m for tails, 20  $\mu$ m for rest).



**Fig. 5.** *Pseudacrobeles* (*P.*) [*v.*] *macrocystis* De Ley & Siddiqi, 1991. A-J : From Tanzania (T41 : A, C, H, I; T45 : B, D-G, J); K-T : From Malaysia (all from M1); U-DD : From Brazil (B1160 : V, X-AA, DD; B1857 : U, W, BB, CC) (Scale bar = 30  $\mu$ m for tails, 20  $\mu$ m for rest).

**Table 5.** Measurements in  $\mu\text{m}$  of *Pseudacrobeles (P.) [v.] variabilis macrocystis* De Ley & Siddiqi, 1991.

	Malaysia* (M1, M2)		Brazil (B1160, B1857)		Cameroon (C)		Tanzania (T4b, T9, T41, T45, T46)	
	30 ♀♀	13 ♂♂	3 ♀♀	3 ♂♂	2 ♀♀	1 ♂	16 ♀♀	8 ♂♂
L	525-670	505-605	600-705	555-605	670-700	595	575-785	485-690
body width	19-32	22-27	24-34	23-26	30-31	26	25-37	22-34
pharynx length	153-174	144-160	158-191	151-167	182-192	158	165-205	155-192
tail length	57-76	42-53	74-80	35-42	83-87	37	74-89	36-49
anal width	10-18	17-21	14-17	19-20	17	19	15-23	16-24
a	21-29	20-25	20-26	24	22-23	23	17-26	20-26
b	3.3-4.2	3.4-4.1	3.1-3.9	3.5-3.7	3.7	3.8	3.3-4.0	3.3-3.8
c	8.5-9.9	11-14	7.6-9.6	14-17	8.1	16	7.1-9.8	13-16
c'	3.7-5.8	2.2-2.9	4.4-5.7	1.8-2.1	4.9-5.1	2.0	3.8-5.5	1.8-2.4
stoma	13-16	12-15	12-16	12-13	15-16	14	14-16	13-16
corpus	91-109	86-94	100-122	93-104	115-126	97	104-135	99-123
isthmus	23-32	23-30	26-29	27-28	25-28	27	27-33	23-33
bulbus	18-23	17-21	19-23	15-21	21-22	17	19-24	18-23
corpus : isthmus	3.0-4.2	2.8-3.9	3.8-4.2	3.4-3.7	4.5-4.6	3.6	3.4-4.7	2.7-4.4
nerve ring	101-115	93-113	101-108	99-109	117	105	79-131	89-126
excretory pore	103-117	96-115	97-113	102-115	117-118	109	78-129	101-123
deirid	114-135	107-128	109-133	116-125	127-131	113	91-146	111-140
n.r. (% pharynx)	64-71	65-72	53-65	61-66	61-64	66	49-67	60-69
e.p. (% pharynx)	65-73	65-73	51-66	62-71	61-65	69	53-69	62-73
deirid (% pharynx)	72-82	72-82	57-75	71-81	68-70	72	60-81	67-83
R <sub>w</sub> (annuli)	58-68	58-63	56-62	52-58	58-62	59	55-67	52-63
R <sub>sp</sub> (annuli)	58-66	59-64	56-58	53-59	59-65	59	56-68	57-63
R <sub>st</sub> (annuli)	64-74	66-73	63-66	70-64	65-68	64	63-76	62-70
phasmid	13-22	16-23	9-11	12-17	14-17	12	9-17	13-21
phasmid (% tail)	20-31	36-45	12-14	30-47	16-20	32	11-21	33-47
cuticle thickness	1.5-2.0	1.5-2.0	2.0	1.5	1.5-2.0	1.5	1.5-2.0	1.0-2.0
annule width	1.6-2.2	1.6-2.0	1.9-2.0	2.0-2.3	2.1-2.2	2.0	1.8-2.3	1.5-2.2
V (%)/flexure	61-66	37-52	60-62	46-56	62-63	58	58-64	50-64
G (%)/T (%)	18-36	37-52	26-34	45-54	28-40	49	29-39	42-60
vagina/spicules	6-10	20-24	10	24-27	5-7	22	6-10	22-26
rectum/gubernaculum	17-25	10-14	23-28	13-15	22	13	21-30	12-14
PUB/spike	11-23	8-13	20-22	4-8	20-22	7	18-26	4-13
spermatheca/mucro	7-77	7-10	24-33	3-6	36-104	6	10-65	1-10

\* : Measurements from De Ley & Siddiqi (1991).

rectum 1.3-1.7 ABW. Male tail with body cavity extending for 1-2.5  $\mu\text{m}$  in spike. Male of Fig. 6 C with a pair of minute submedian cuticular stubs on the anterior lip of the cloacal opening. These stubs were not seen clearly with light microscope in any specimen. Spicules 3.5-4.5  $\mu\text{m}$  wide, 1.1-1.5 ABW long.

#### JUSTIFICATION OF DETERMINATION

The specimens from Brazil, Cameroon and Tanzania differ from the type populations in several respects : the more arcuate and angular ventral contour of the male tail (Fig. 5 G, H, Q, R, AA, BB), the more slender

female tail terminus (Fig. 5 I, J, S, T, CC, DD), the usually longer female tail (74-89 *vs* 57-76  $\mu\text{m}$ ) and the relatively more anterior phasmid in females (at 11-21 *vs* 20-31 %). As the delineation of all these specimens from *P. (P.) [v.] baloghi* is not an easy matter (see Part 2), we nevertheless prefer to consider them as a single species to limit possible confusion. Females with spermathecae longer than 45  $\mu\text{m}$  (never occurring in other species) were found from Cameroon (1 ♀ out of 2) and Tanzania (5 ♀♀ out of 16), but not from Brazil (3 ♀♀ studied). In the types, this feature occurred in 17 females out of 30.

**Table 6.** Measurements in  $\mu\text{m}$  of *Pseudacrobeles (P.) laevis* (Thorne, 1937) comb. n. and *Pseudacrobeles (P.) teres* (Thorne, 1937) comb. n.

	<i>P. (P.) laevis</i>				<i>P. (P.) teres</i>	
	Utah* (types)		Oregon (US47)		Oregon (US7)	
	? ♀♀	? ♂♂	6 ♀♀	7 ♂♂	? ♀♀	1 ♂♂
L	700	700	595-705	595-685	740	735
body width			22-28	22-27		
pharynx length			159-182	163-189		178
tail length			46-57	36-40		62
anal width			12-16	16-18		14
a	24	29	25-28	25-29	25	
b	3.9	4.0	3.4-3.8	3.4-3.7	4.1	4.1
c	11-14	15	12-14	17	11	12
c'	3.6 **	2.3 **	3.1-3.8	2.1-2.3	4.0 **	4.3
stoma			12-15	14-15		12
corpus			97-122	100-120		115
isthmus			29-33	30-36		28
bulbus			18-21	16-20		21
corpus : isthmus	3.4 **	3.4 **	3.3-4.2	3.2-3.5	4.5	4.1
nerve ring			96-111	83-119		110
excretory pore			100-115	88-117		107
deirid			117-121	117		
n.r. (% pharynx)	63 **	63 **	54-63	51-65		62
e.p. (% pharynx)	64 **	64 **	55-65	54-64		60
deirid (% pharynx)	73 **	73 **	64-70	65		
R <sub>nr</sub> (annuli)	81 **	81 **	63-67	60-66		
R <sub>ep</sub> (annuli)	81 **	81 **	62-71	60-67		
R <sub>dei</sub> (annuli)	90 **	90 **	71-77	75		
phasmid			12-20	16-20		
phasmid (% tail)	33 **	50 **	34-42	42-52	27 **	
cuticle thickness			1.0-1.5	1.0-1.5		
annule width			1.5-2.0	1.7-2.1		
V (%) / flexure	63		61-66	27-74	62	61
G (%) / T (%)	33	42	29-35	45-60	29	35
vagina/spicules			7-10	21-25		
rectum/gubernaculum			17-24	10-14		17
PUB/spike			29-45	1-3		34
spermatheca/mucro			24-43	0-2		

\* : Measurements from Thorne (1937) – number of specimens unknown – except :

\*\* : Measured on Fig. 3 in Thorne (1937).

The specimens from Brazil were, judging by the slide labels, variously identified as *Eucephalobus oxyuroides* or *Heterocephalobus multincinctus* by Rashid *et al.* (1985).

***Pseudacrobeles (Pseudacrobeles) laevis*  
(Thorne, 1937) comb. n.**

(Fig. 7 A-J)

**MATERIAL**

Specimens were studied from US47 (6 ♀♀, 6 ♂♂).

This material was determined by Thorne as *Eucephalobus teres* (!); it is reclassified as such in the USDA Nematode Collection on slides T-4193p and T-4194p. No SEM.

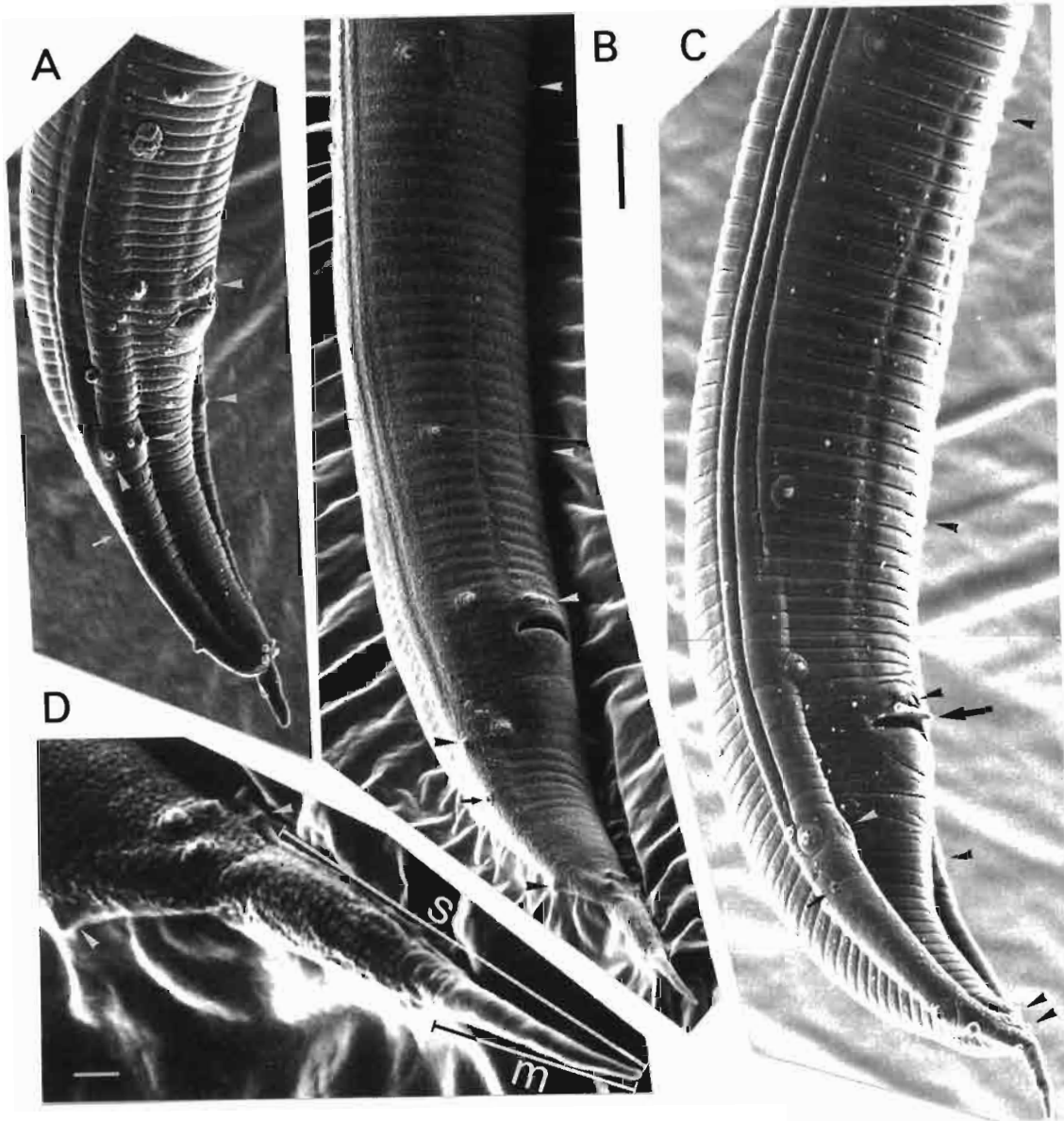
**MEASUREMENTS**

See Table 6.

**DESCRIPTION**

Lateral field not clear. Cephalic probolae absent. Labial probolae low, ridge-like. Lip region with triradiate





**Fig. 6.** *Pseudacrobeles* (*P.*) [*v.*] *variabilis* (Steiner, 1936) Steiner 1938. A : From Tanzania (T41). *P.* (*P.*) [*v.*] *baloghi* (Andrássy, 1968) comb. n.; B, D : From Isla Fernandina (G18). – *Pseudacrobeles* (*P.*) [*v.*] *macrocystis* De Ley & Siddiqi, 1991; C : From Tanzania (T41). Arrowheads point at less clear papillae, arrow in C points at preloacal cuticular stubs. “s” = spike, “m” = mucro (Scale bar = 5  $\mu$ m for A, B, C; 1  $\mu$ m for D).

symmetry. Cheilorhabdia bar-shaped in optical section. Second stoma section narrower than cheilostome, its walls slightly refractive. Nerve ring lying at four fifths to base of corpus. Excretory pore from one annule anterior to four annules posterior to trailing edge of nerve ring. Deirid four to ten annules posterior to excretory pore. Females with PUB 1.2-1.6 body widths long. Rectum 1.1-1.7 ABW. Tip of female tail dorsally convex. Male tail with body core extending into spike for 0-1  $\mu\text{m}$ . Spicules 3-4.5  $\mu\text{m}$  wide, 1.2-1.5 ABW long.

#### JUSTIFICATION OF DETERMINATION

Although Thorne (1937) determined this material himself as *Eucephalobus teres* (see below), it actually corresponds even more closely to his original description and especially his Fig. 3 G-K of *E. laevis* (cf. Table 6; Fig. 7 A-J).  $R_{\text{nr}}$ ,  $R_{\text{ep}}$  and  $R_{\text{dei}}$  differ, but it is possible that these were not drawn accurately on Fig. 3 in Thorne (1937). While our specimens did not show the lateral field clearly, Thorne (1937, Fig. 3 K) shows three incisures ending at the phasmid. The animals can be distinguished from most species described here by the dorsally convex female tail tip and by the anterior stoma structure. They resemble *Heterocephalobus elongatus* (de Man, 1880) Andrassy, 1967 closely in these and other respects, but the female tail is proportionally slightly shorter ( $c' = 3.1-3.8$  vs 4.1 on Fig. 57 in de Man, 1884) and its tip more convex. As there is no detailed description available of *H. elongatus* (see Part 2), *E. laevis* is considered valid for the time being, and transferred to *Pseudacrobeles*.

#### *Pseudacrobeles (Pseudacrobeles) teres* (Thorne, 1937) comb. n.

#### MATERIAL

The single remaining type specimen was studied (from US7, 1 ♀). It is reclassified as lectotype in the USDA Nematode Collection (slide T-452t).

#### MEASUREMENTS

See Table 6.

#### DESCRIPTION

Lateral field not clear. Cephalic and labial probolae not discernible. Cheilorhabdia appear bar-shaped in optical section. Second stoma section narrower than cheilostome, its walls not refractive. Nerve ring lying at six sevenths of corpus. Excretory pore level with anterior edge of nerve ring. Deirid not seen. Female rectum 1.2 ABW long, but ABW may have been affected by flattening. No males.

#### REMARKS

The condition of the lectotype is too poor to allow confident assumptions to be made on the validity of this species. Our observations do not match the original description with respect to the shape of the cheilorhabdia :

Fig. 3 P in Thorne (1937) shows granular cheilorhabdia, while we discerned bar-shaped ones in the lectotype. This may be due to bad preservation, with fading out of the real cheilorhabdia and darkening of the cheilostome walls, and we therefore follow Thorne's drawing in the key in Part 2.

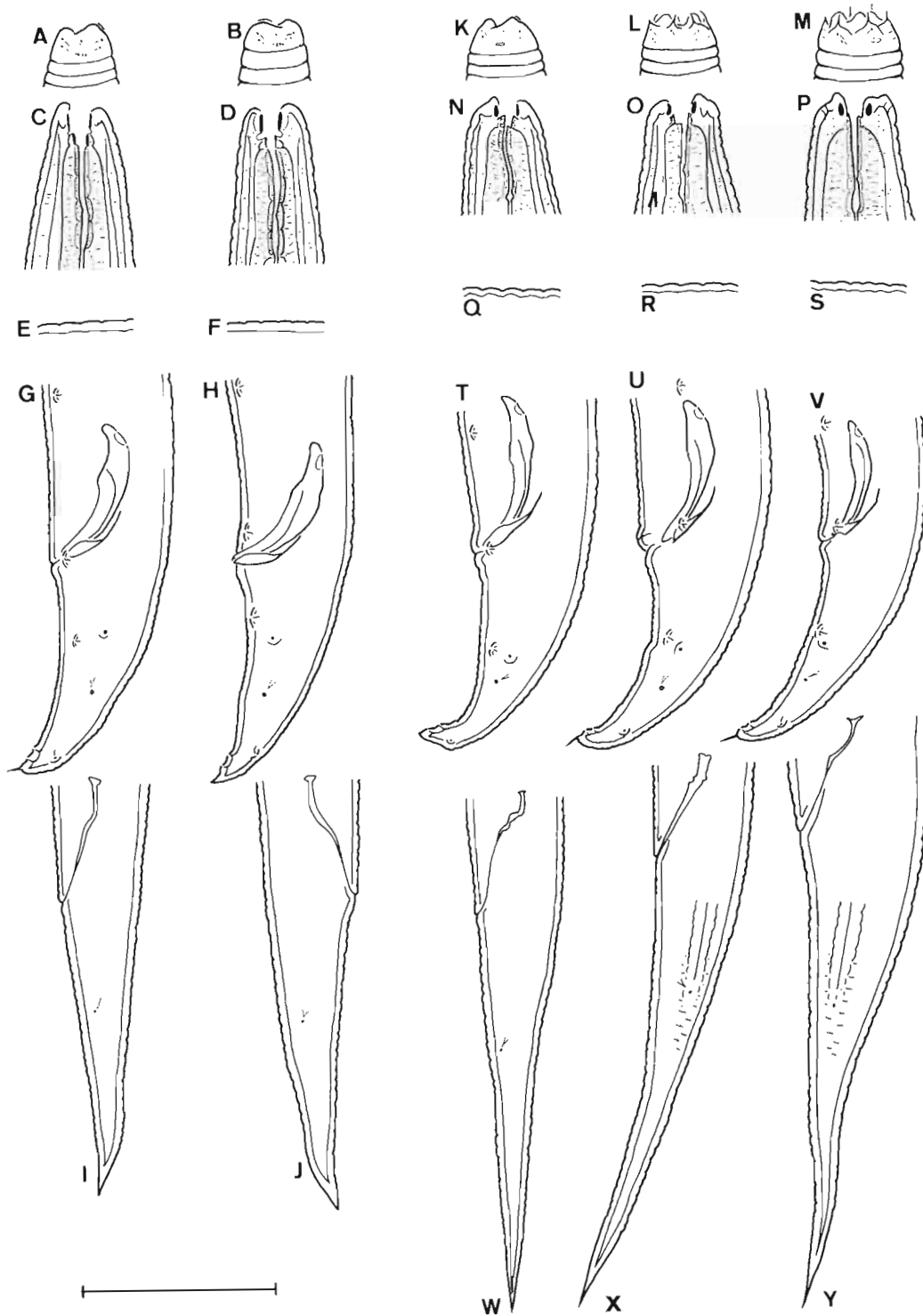
Topotypes are needed to clarify the status of the species, especially because there are three likely candidates for synonymy. Firstly, *P. (P.) [v.] variabilis* is only slightly different in female tail length ( $c = 5.4-9.6$  in all our material vs 11-12 in *P. (P.) teres*;  $c' = 4.6-8.7$  vs 4.0-4.3) and in width of the second stoma section. Secondly, *P. (P.) laevis* is different only in tip shape and  $c'$  (3.1-3.8 vs 4.0-4.3) of the female tail, but not clearly in  $c$  or corpus : isthmus-ratio (Table 6). Thirdly, *P. (P.) [v.] tabacum* females only differ in having a corpus : isthmus-ratio of 4.5-5.1 (vs 4.1-4.5 in *P. (P.) teres*),  $c = 7.6-10$  (vs 11-12) and excretory pore at 74-78 % of pharynx (vs 60 % in lectotype of *P. (P.) teres*). For the present, we have retained the species as valid in this paper because of the few formal distinctions that can still be made with other species. Although the lateral field was deteriorated beyond recognition in the lectotype, the species is transferred to *Pseudacrobeles* because Thorne (1937, Fig. 3 Q) depicts the female tail with lateral field ending at the phasmid. However, he also drew only two incisures, a character needing verification.

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**Fig. 7.** *Pseudacrobeles (P.) laevis* (Thorne, 1937) comb. n.; A-J : From Oregon (US7). – *Pseudacrobeles (P.) [v.] tabacum* (Rashid *et al.*, 1985) comb. n. K-Y : type specimens from Brazil (B1226; M, P, S, Y : holotype), M, P in ventrosublateral view (Scale bar = 30  $\mu$ m for tails, 20  $\mu$ m for rest).

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