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Two new species of Cephalobidae from Valle de la Luna, Argentina, and observations on the genera *Acrobeles* and *Nothacrobeles* (Nematoda: Rhabditida)

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Summary - *Acrobeles emmatus* sp. n. and *Nothacrobeles lunensis* sp. n. are described from a desert valley in Argentina. *A. emmatus* sp. n. is distinct from all known species of the genus in having an "inner layer" of the cuticle undulating twice per annule. *N. lunensis* sp. n. is distinct from all other species of the genus in having a "double cuticle" as in *Seleborca* and *Triligulla*. We argue that this type of cuticular structure must have arisen independently in at least three separate lineages, and that it is insufficient as a genus character. *Seleborca* is therefore synonymized with *Acrobeles*, and *Triligulla* with *Cervidellus*. A single male of *Nothacrobeles* cf. *subtilis* is also described. It has minute tines on the probolae and a lateral field changing from four lines anteriorly to three lines posteriorly. We consider this to invalidate the genus *Namibinema*, which is therefore synonymized with *Nothacrobeles*. Tables of specific differential characters are given to the re-defined genera *Acrobeles* and *Nothacrobeles*.

Résumé - ***Deux espèces nouvelles de Cephalobidae provenant de la Vallée de la Lune, Argentine, et observations sur les genres* Acrobeles *et* Nothacrobeles *(Nematoda: Rhabditida)*** - Description est donnée d'*Acrobeles emmatus* sp. n. et de *Nothacrobeles lunensis* sp. n. provenant d'une vallée désertique d'Argentine. *A. emmatus* sp. n. se distingue de toutes les autres espèces connues du genre par la présence d'une "couche interne" de la cuticule montrant deux ondulations par anneau. *N. lunensis* sp. n. se différencie de toutes les autres espèces du genre par sa "double cuticule", semblable à celle observée chez *Seleborca* et *Triligulla*. Il est avancé que ce type de structure cuticulaire peut être apparu indépendamment dans au moins trois lignées et qu'il est donc insuffisant pour représenter un caractère générique. En conséquence, *Seleborca* et *Triligulla* sont proposés comme des synonymes mineurs d'*Acrobeles* et *Cervidellus*, respectivement. Un unique mâle de *Nothacrobeles* cf. *subtilis* est également décrit. Ses proboles sont pourvues de minuscules excroissances et le champ latéral est composé de quatre lignes antérieurement et de trois postérieurement. Ce caractère est considéré comme invalidant le genre *Namibinema* qui est donc proposé comme synonyme mineur de *Nothacrobeles*. Les diagnoses des genres *Acrobeles* et *Nothacrobeles* sont amendées et un tableau des caractères spécifiques différentiels est donné pour chacun des deux genres.

Key-words: *Acrobeles*, Argentina, key, *Namibinema*, nematode, *Nothacrobeles*, *Seleborca*, SEM, taxonomy, *Triligulla*.

Valle de la Luna or Ischigualasto Valley is an arid valley of exceptional paleontological value and natural beauty, located on the outskirts of the eastern slopes of the Andes in San Juan province, Argentina. It is one of the few formations in the world containing exposed sedimentary rock from the Middle Triassic, and is extremely rich in tetrapod fossils from this period. Because of its significance, the valley has been frequented regularly by paleontological teams, and most recently was the site of a series of expeditions organized by Dr. William Sill of The Museo de Ciencias Naturales of San Juan, in collaboration with Earthwatch. Soil samples were collected by the second author on May 5th, 1994 during one of these expeditions. Samples were taken about 10 m apart, around the roots of various xerophytes (Table 1) growing separately along one bank of a dry riverbed, next to the camping site of team 1 of Earthwatch's "Triassic Park" project. The location of this site as determined with the Global Positioning System was: altitude 1225 m, longitude 30°6'35" S and latitude 67°54'08" W.

The samples were soaked in distilled water for 6 h and then fixed with a mixture of formaldehyde 4%: glycerol 1% heated to 70°C. Nematodes were extracted with centrifugation-flotation, transferred to glycerin and mounted in double-coverslip slides at the University of Gent, Belgium.

Three females and two males of *Acrobeles emmatus* sp. n., as well as two females and two males of *Notha-*

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Table 1. *Data on the collected samples.*

Sample number	Rhizosphere of:	Soil texture	Approximate depth
1	"Algarrobo" = *Prosopis* sp., "Sampa" = *Atriplex lampa* Gill. ex Moq.	sand	30 cm
2	"Retamo" = *Bulnesia retama* (Hook.) Griseb.	sand	30 cm
3	"Pichana" = ?, "Sampa" = *Atriplex lampa* Gill. ex Moq.	sand	30 cm
4	"Yerba guanaco" = ?	sand, pebbles	10 cm

crobeles lunensis sp. n. were processed to ethanol, freeze-dried and sputter-coated with gold for examination with a Hitachi 405 scanning electron microscope (SEM) at Rothamsted Experimental Station, Harpenden, UK. Unfortunately, the specimens of *N. lunensis* did not give good results. Light microscopical (LM) photographs were taken with Nomarski optics on an Olympus BH-2. An additional *Nothacrobeles* specimen was found in a slide from Dr. G. Thorne's collection and is described here because of its relevance to genus diagnosis. The terminology of De Ley *et al.* (1995) is used for the description of the stoma. The ultrastructural composition of the cuticle is undoubtedly more complicated than suggested by its appearance under LM, and quotation marks are therefore used to mention cuticular layers as seen with LM.

*Acrobeles emmatus** sp. n.

(Figs 1-4)

MEASUREMENTS

See Table 2

DESCRIPTION

Female: Body slightly ventrally curved to C- shaped, tapering towards both extremities, occasionally clearly dorsoventrally flattened (presumably due to combined effects of incomplete rehydration and subsequent fixation). Cuticle 2.0-2.5 µm thick throughout the body, coarsely annulated, distinctly two-layered under LM. "Outer layer" simple, with annules 2.0-2.5 µm wide in neck region and 2.2-3.0 µm wide at midbody. "Inner layer" indented halfway of each annule, resulting in characteristic internal annules only half as wide as the external ones. Undulating demarcation line between "outer" and "inner layer" usually very distinct: "inner layer" often less clearly demarcated from the somatic musculature, depending on the specimen and angle of view (compare, *e.g.*, Fig. 3E with 3G). In surface view, undulations of the "inner layer" often appearing

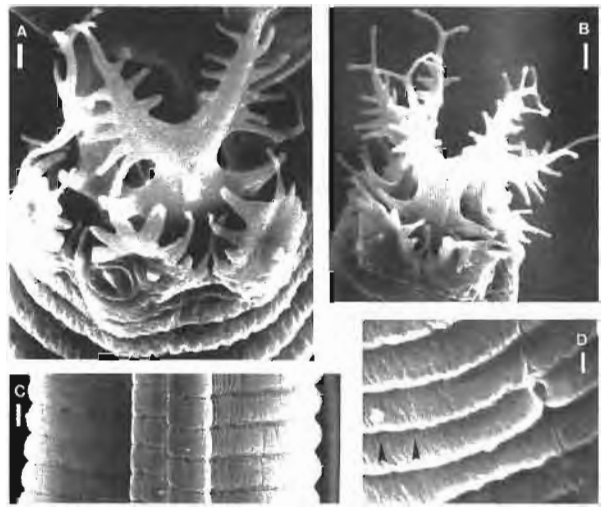

Fig. 1. Acrobeles emmatus *sp. n. electron micrographs of females. A,B: Lip region of two females from sample 1; C: Lateral field and cuticular pores; D: Cuticular pores (arrowheads) and excretory pore placed in a median incisure (Bars: A, D = 1 µm; B, C = 2 µm).*

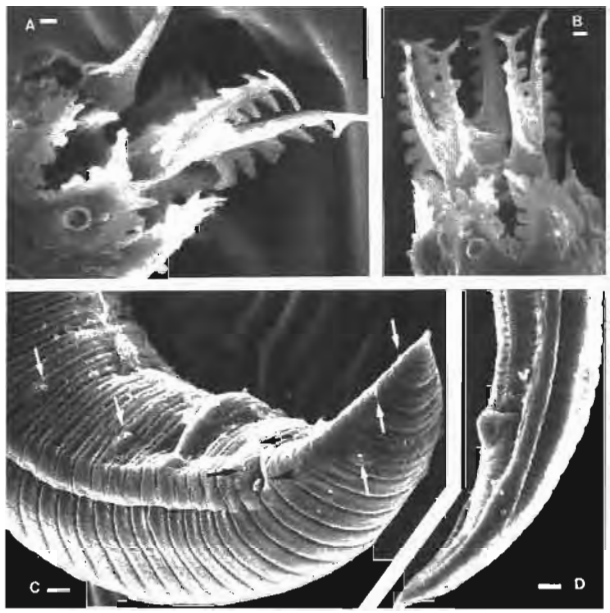

Fig. 2. Acrobeles emmatus *sp. n. electron micrographs of males. A,B: Lip region of two males from sample 3; C,D: Male tail region; arrows in C point at genital papillae, arrowhead at phasmid (Bars: A, B = 1 µm; C = 2 µm; D = 5 µm).*

* Referring to the m-shaped undulations formed by the "inner layer" of the cuticle within each annule.

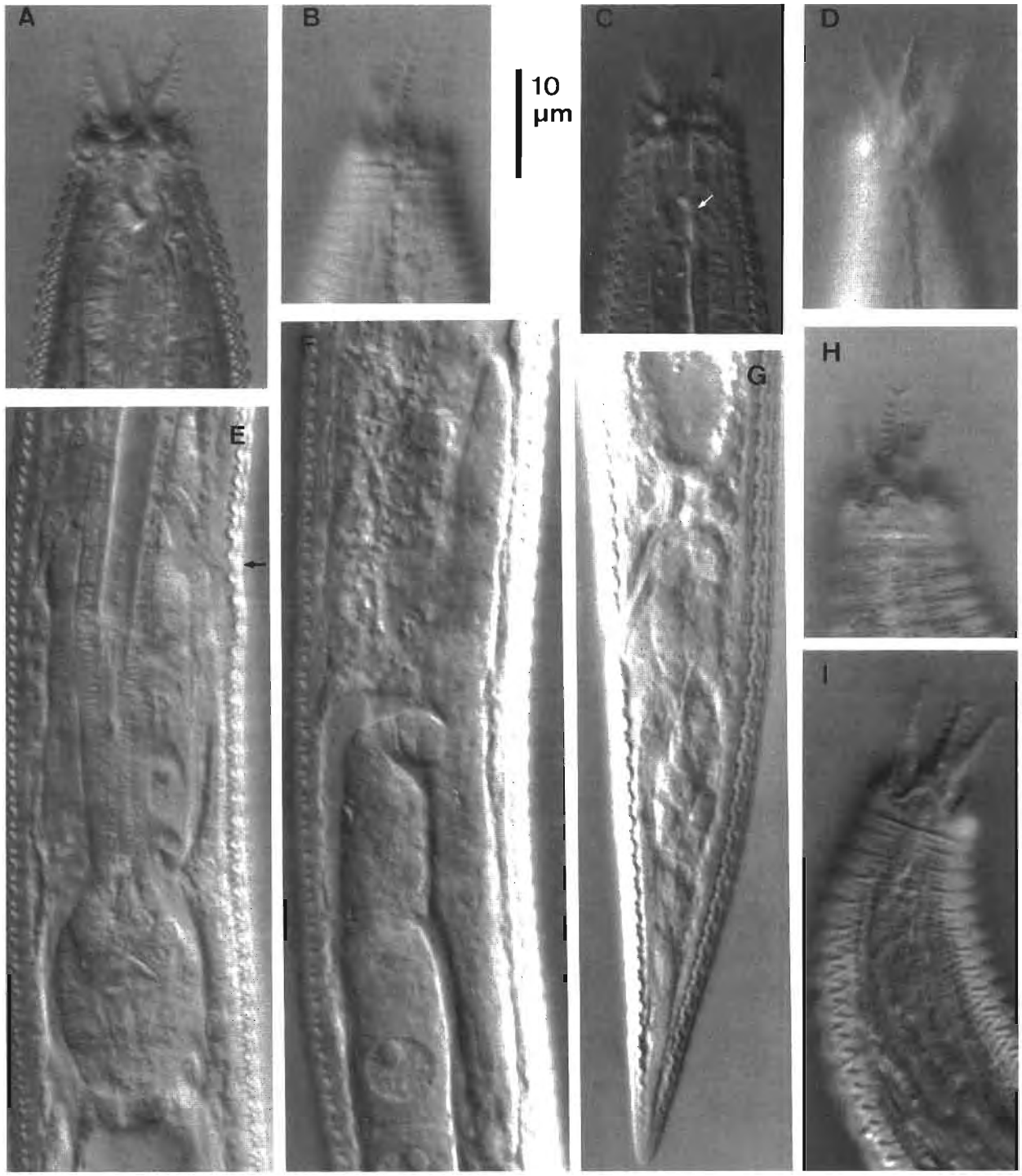

Fig. 3. *Acrobeles emmatus sp. n. photomicrographs. A-D: Lip region in surface and median view of two females from sample 1 (C,D: holotype; arrow in C points at dorsal pharyngeal gland opening); E: Posterior part of neck (arrow points at excretory pore); F: Anterior part of female reproductive system; G: Female tail; H,I: Lip region in surface view of a female (H) and male (I) from sample 3.*

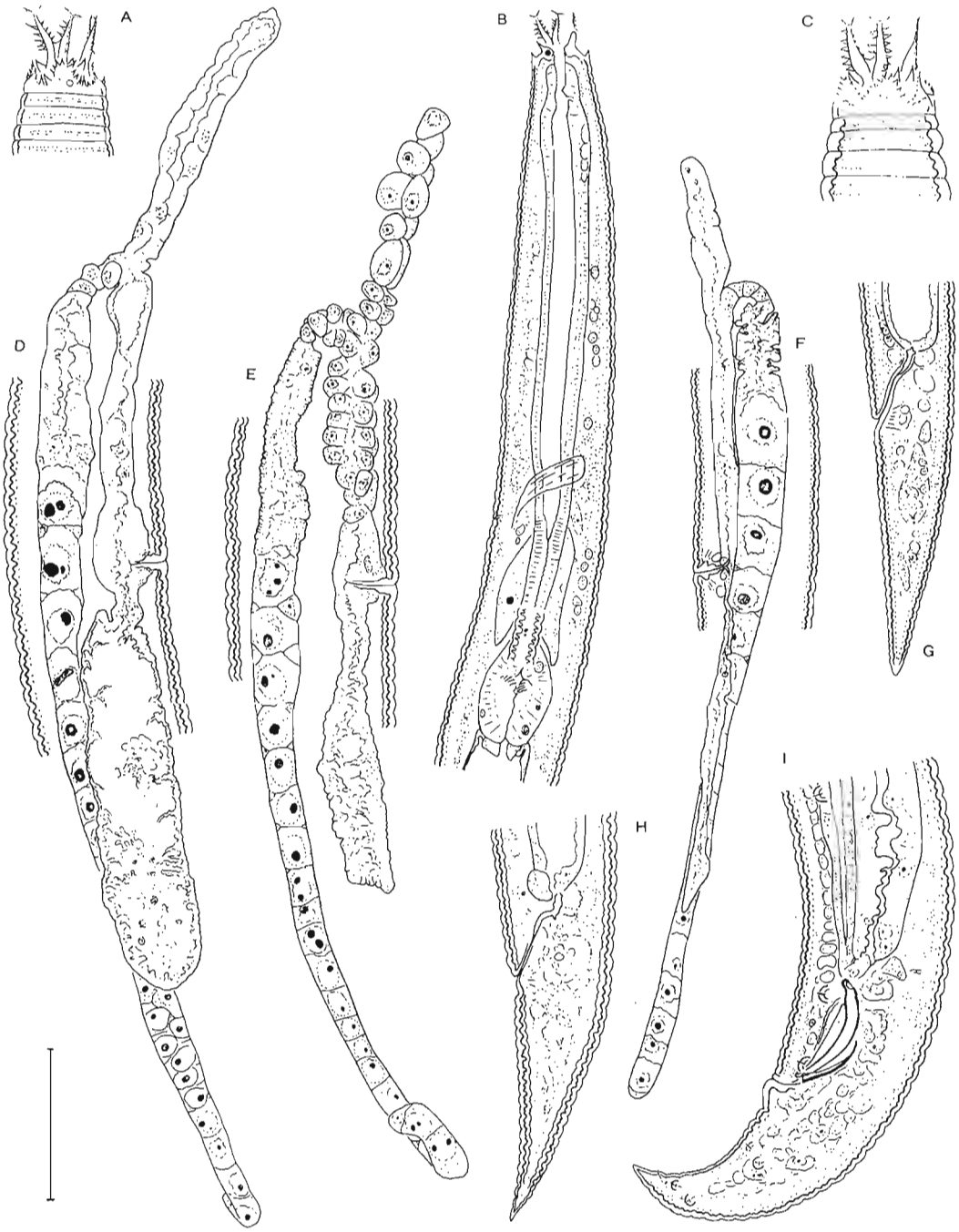

Fig. 4. Acrobeles emmatus *sp. n. A,B: Lip region and neck of holotype female; C: Lip region of female from sample 3; D-F: Female reproductive system (F is holotype); G,H: Female tail; I: Male tail (Bars: A, C = 20 µm; others = 30 µm).*

as two irregular rows per annule. Cuticle externally with longitudinal striations, these not continuous from annule to annule and only seen with SEM. Scattered cuticular pores visible with SEM between the annules and on the wings of the lateral field. Lateral field with three lines, 7.5-8.5 µm wide at mid-body

Table 2. *Measurements of holotype and paratypes of* Acrobeles emmatus *sp. n. The holotype female is from sample 1, the allotype male from sample 3 (Measurement given in µm).*

	Holotype (Fem.)	Allotype (Male)	Sample 1 (Fem.)	Sample 2 (Fem.)	Sample 2 (Male)	Sample 3 (Fem.)	Sample 3 (Male)	Sample 4
n	1	1	15	4	7	10	9	1
L	568	607	525 ± 33 (477-568)	494-600	565 ± 63 (477-653)	586 ± 30 (536-627)	599 ± 34 (536-650)	568
Body width	24	29	24 ± 1.0 (22-26)	23-25	24 ± 2.5 (21-28)	28 ± 2.2 (24-30)	28 ± 2.3 (24-30)	30
Neck length*	150	145	148 ± 4 (140-153)	143-160	148 ± 9 (134-159)	150 ± 8 (140-162)	151 ± 6 (143-159)	149
Tail length	51	47	51 ± 3.6 (44-58)	45-50	42 ± 3.4 (38-47)	50 ± 3.0 (45-54)	44 ± 3.4 (39-48)	43
Anal body width	15	20	17 ± 1.5 (15-21)	16-17	20 ± 0.8 (19-21)	19 ± 1.5 (16-21)	22 ± 1.6 (19-24)	24
a	24	21	22 ± 1.5 (19-24)	20-23	23 ± 1.9 (21-27)	21 ± 1.4 (19-23)	21 ± 1.3 (20-24)	18.9
b	3.8	4.2	3.5 ± 0.2 (3.2-3.8)	3.2-3.7	3.8 ± 0.3 (3.5-4.3)	3.9 ± 0.2 (3.6-4.4)	4.0 ± 0.1 (3.7-4.2)	3.8
c	11	13	10 ± 0.7 (9.2-11)	9.8-13	13 ± 1.3 (12-15)	11-13	13-16	13.2
c'	3.3	2.3	3.0 ± 0.3 (2.5-3.4)	2.7-3.1	2.1 ± 0.2 (1.9-2.3)	2.6 ± 0.2 (2.4-2.9)	2.0 ± 0.2 (1.7-2.3)	1.8
Stoma	11	12	11-13	11-12	11-13	11-13	11-13	11
Corpus	79	80	83 ± 2.9 (77-87)	83-87	85 ± 5.0 (78-92)	85 ± 7.0 (70-94)	85 ± 3.2 (80-89)	83
Isthmus	25	21	23 ± 2.0 (19-25)	21-23	22 ± 1.6 (20-24)	20-23	23 ± 1.4 (21-25)	20
Bulbus	21	23	20-23	21-25	22 ± 1.4 (20-24)	24 ± 1.3 (22-26)	23-25	23
Nerve ring	84	95	81 ± 6.0 (74-94)	80-95	95 ± 5.6 (88-101)	92 ± 6.3 (84-102)	92 ± 6.2 (82-99)	95
Excr. pore	90	108	90 ± 7.0 (80-102)	86-101	97 ± 6.4 (91-107)	99 ± 3.3 (94-105)	101 ± 7 (90-108)	99
Deirid	118	127	108 ± 8 (95-118)	95-113	108 ± 11 (95-123)	111 ± 7 (101-124)	117 ± 11 (102-127)	?
Nerve ring (% neck)	56	65	55 ± 4.3 (48-62)	56-61	63 ± 4.6 (58-68)	61 ± 3.9 (53-66)	61 ± 4.7 (54-66)	64
Excr. pore (% neck)	60	74	61 ± 5.6 (52-73)	59-64	64 ± 2.3 (62-67)	66 ± 4.3 (58-72)	67 ± 5.1 (58-74)	67
Deirid (% neck)	79	87	70 ± 6.9 (57-79)	62-72	71 ± 6.0 (64-77)	74 ± 6.3 (64-85)	79 ± 6.7 (71-87)	?
Phasmid	19	18	18 ± 1.5 (15-20)	14-17	16-18	18 ± 1.3 (13-18)	17-20	17
Phasmid (% tail)	38	37	34 ± 2.9 (28-38)	31-34	40 ± 3.0 (34-43)	31 ± 2.4 (27-34)	42 ± 3.7 (35-45)	39
V	56	-	56 ± 1.9 (52-59)	56-59	-	57 ± 1.9 (53-59)	-	-
G/T	34	53	34 ± 1.9 (31-37)	33-40	57 ± 3.0 (53-61)	38 ± 3.7 (32-44)	53 ± 2.6 (49-57)	47
Spermatheca/ spicules	50	26	50 ± 4.2 (45-58)	53-60	25 ± 1.6 (22-26)	55 ± 5.2 (50-64)	24-26	25
PUB/gubern.	70	13	64 ± 7.7 (53-78)	60-70	12-15	69 ± 8 (60-85)	12-14	12

End of Table 2 next page

Table 2. *(cont.).*

	Holotype (Fem.)	Allotype (Male)	Sample 1 (Fem.)	Sample 2 (Fem.)	Sample 2 (Male)	Sample 3 (Fem.)	Sample 3 (Male)	Sample 4
R	216	197	221 ± 8 (208-236)	186-229	186 ± 5 (180-194)	195 ± 6 (186-202)	188 ± 8 (173-200)	198
R_{nr}	28	26	31 ± 1.5 (28-33)	31-33	27 ± 2.4 (25-30)	29 ± 3.0 (25-35)	27 ± 1.5 (25-30)	30
R_{ex}	33	29	36 ± 1.7 (33-38)	35-38	29 ± 2.3 (25-31)	31 ± 2.0 (29-35)	28-31	32
R_{dei}	41	35	43 ± 2.3 (40-48)	44-45	33-35	36 ± 2.1 (32-40)	35 ± 1.5 (34-38)	?
R_{phar}	55	43	58 ± 3.6 (52-62)	50-62	48 ± 4.3 (42-54)	48 ± 3.6 (45-54)	44 ± 3.0 (38-47)	50
R_{phar-v}/ $R_{phar-an}$	70	138	67 ± 4.6 (58-72)	55-70	122 ± 7.3 (112-132)	61 ± 2.9 (58-66)	129 ± 7 (119-140)	133
R_{v-an}	73	-	76 ± 3.9 (70-82)	63-80	-	70 ± 3.0 (66-74)	-	-
R_{tail}	18	16	19 ± 1.3 (17-22)	16-21	-	17 ± 1.3 (16-20)	-	-

*: Neck length measured along lumen of pharynx from tips of labial probolae to base of bulbus.

(25-33% of body diameter), areolated, extending from about level of corpus to tail tip. Median lateral line visible only with SEM; "inner layer" of the cuticle causes the appearance of undulating "pseudolines" within the lateral field under LM. Lip region width (LRW) 10-13 µm; lip region weakly offset with four cephalic and six labial papillae. Amphids circular, dorsosublaterally placed. Labial probolae 7-11 µm long, straight or slightly curved, bifurcated, each prong fringed by rows of three or four tines on the inside, and four to seven tines on the outside of the bifurcation, ending in two straight apical tines. Cephalic probolae with three to six tines on each side. Larger specimens, especially those of sample 3, usually with greater numbers of tines and with all tines short and rounded; smaller specimens, especially those of sample 1, with lower numbers of tines and with some tines more elongate and more acute than the others. Tines always appearing acute under LM, undoubtedly due to their transparency. Cuticle of the cheilostom appearing as prominent "cheilorhabdia" with circular cross-section between the labial probolae. Entire stoma 0.9-1.2 LRW long, distinctly divided into cheilo-, gymno- and stegostom. Stegostom often faintly subdivided, with prominent dorsal denticle in the metastegostom and occasionally with distinct dorsal gland opening just posterior to this denticle. Corpus fusiform, 3.0-4.4 times as long as isthmus. Isthmus short, separated from corpus by a transverse marking and by the more prominent muscular fibers at its anterior end. Basal bulb spheroid to pyriform with striated transverse valves anterior to its centre. Excretory pore near corpus-isthmus junction. Posterior edge of nerve ring slightly anterior to junction of corpus and isthmus. Deirid at 5-28 µm or three to eleven annules posterior to excretory pore. Cardia small, hemispherical to conoid, 3-6 µm long. Vulva slightly posterior to middle of body, vagina occupying 22-33% of vulval body width (VBW). Female reproductive system on right side of intestine, monodelphic, prodelphic. Spermatheca offset at level of anterior flexure, outstretched. Posterior uterine branch (PUB) as long as 2.0-3.4 VBW. Ovary straight or with double flexure near tip, with 16-48 oocytes, of which 4-42 in double file. Cell walls and nuclei exceptionally clear in a few females: oviduct with two rows of four cells (n=4), spermatheca with two rows of three smaller stem cells and two rows of five larger sac cells (n=2), uterus with 30 cells arranged as follows (n=2): distally with two rows of three cells, proximally with four rows of cells, of which the dorsal two rows each consist of seven and the ventral two rows each of five cells. Tail conoid, with acute to subacute terminus. Phasmids at about one-third of tail length. Rectum 0.8-1.2 anal body widths (ABW) long.

Male: Body more strongly curved posteriorly than in the female. Labial probolae 8-12 µm long. Stoma as long as 0.9-1.1 LRW, corpus 3.4-4.2 times as long as isthmus. Deirids 5-22 µm or two to seven annules posterior to excretory pore. Reproductive system on right side of intestine, anteriorly directed. Testis reflexed over 44-64 µm. Spicules 1.0-1.4 ABW long, ventrally arcuate with broad velum and offset, rounded manubrium. Gubernaculum boat-shaped in

lateral view, half as long as spicules. Three pairs of preanal genital papillae present subventrally; one single medioventral papilla located on anterior lip of the cloacal aperture. Precloacal region with two shallow subventral cuticular grooves. Five pairs of caudal genital papillae present: three pairs near tail terminus and two pairs at one-third of tail length, just anterior to phasmids. Tail conical, ventrally curved with acute or subacute tip.

TYPE LOCALITY AND HABITAT

Sandy bank of an ephemeral river in Valle de la Luna, San Juan Province, Argentina. Holotype collected in rhizosphere of three "Algarrobos" (*Prosopis* sp.) growing together with a few "Sampas" (*Atriplex lampa* Gill. *ex* Moq). Additional specimens collected in rhizosphere of three other plant species (cf. Table 1).

TYPE SPECIMENS

Holotype female with eight female and four male paratypes deposited in the Nematode Collection of the Instituut voor Dierkunde, Universiteit Gent, Belgium; five female and three male paratypes deposited in the collection of the National Nematological Research Centre, University of Karachi, Pakistan; three female and two male paratypes deposited in the Collection Nationale de Nématodes, Muséum National d'Histoire Naturelle, Paris, France; three female and two male paratypes deposited in the collection of the Swedish Natural History Museum, Stockholm, Sweden; three female and two male paratypes deposited in the USDA Nematode Collection, Beltsville, MD, USA; three female and two male paratypes deposited in the collection of the Department of Zoology, Rand Afrikaans University, Auckland Park, South Africa.

DIAGNOSIS AND RELATIONSHIPS

Acrobeles emmatus sp. n. is distinct from all known species of the genus in its peculiar cuticular structure, with internal annules that are only half as wide as the external ones. It is also different from all known species with "double cuticle" in at least one other respect (cf. Table 4).

The new species is quite close to *A. oasiensis* Boström, 1985 in most measurements but has a distinctly longer spermatheca (45-64 µm *vs* rudimentary) and PUB (over 2 VBW *vs* less than 0.5 VBW). Males of *A. oasiensis* are unknown, but this cannot be given any diagnostic significance since Boström (1985) only found three females of *A. oasiensis*, and also because our sample 1 yielded 15 females but no males of *A. emmatus* sp. n.

Nothacrobeles lunensis* **sp. n.**

(Figs 5, 6)

MEASUREMENTS

See Table 3

DESCRIPTION

Female: Body slightly ventrally curved to spirally coiled with strongest curvature in the neck region, tapering towards both extremities, occasionally clearly dorsoventrally flattened (presumably due to combined effects of incomplete rehydration and subsequent fixation). Cuticle 1.5-2.5 µm thick throughout the body, coarsely annulated, distinctly two-layered under LM. Annulation of "inner layer" parallel to annulation of "outer layer", annules 1.8-2.2 µm wide in neck region and 1.8-2.5 µm wide at midbody. The undulating demarcation line between "outer" and "inner layer" usually very distinct, "inner layer" often less clearly demarcated from the somatic musculature, depending on the specimen and angle of view (compare, *e.g.*, Fig. 5E with 5H). Lateral field quite variable in appearance, with two or three lines under LM, with or without additional undulating "pseudolines" caused by the appearance of the "inner layer" of the cuticle. Lateral field 7.5-8.5 µm wide, (20-25% of the body width), areolated, extending from level of corpus to phasmid. Lip region 11-13 µm wide, truncate, weakly offset with four cephalic and six labial papillae. Amphids small, elliptical, dorsosublaterally placed. Labial probolae 2.0-2.5 µm high, truncate with prominent rim projecting towards the lips, bifurcated with very short prongs measuring only 1-2 µm. Lips broad with acute tip. Primary axils clearly wider and deeper than secondary axils. Two short, triangular guarding pieces sometimes visible (with Nomarski optics) in the primary axils. Minute tine-like structures sometimes visible along the rims of the lips and labial probolae (could be granules of detritus). Cuticle of the cheilostom containing inconspicuous "cheilorhabdia" with flattened, drop-shaped cross-section between the labial probolae. Entire stoma 0.5-0.6 LRW long, sometimes with distinct division into cheilo-, gymno- and stegostom. Stegostom rarely with faint subdivisions, never with prominent dorsal denticle or dorsal gland opening.

Corpus fusiform, 1.3-1.6 times as long as isthmus. Isthmus proportionally long, separated from corpus by its lesser width, transverse markings and more prominent muscular fibers at its anterior end. Basal bulb spheroid to pyriform with striated transverse valves anterior to its centre. Excretory pore and nerve ring level with anterior half of isthmus. Deirid at 2-21 µm or zero to eight annules posterior to excre-

* Referring to Valle de la Luna, the type locality.

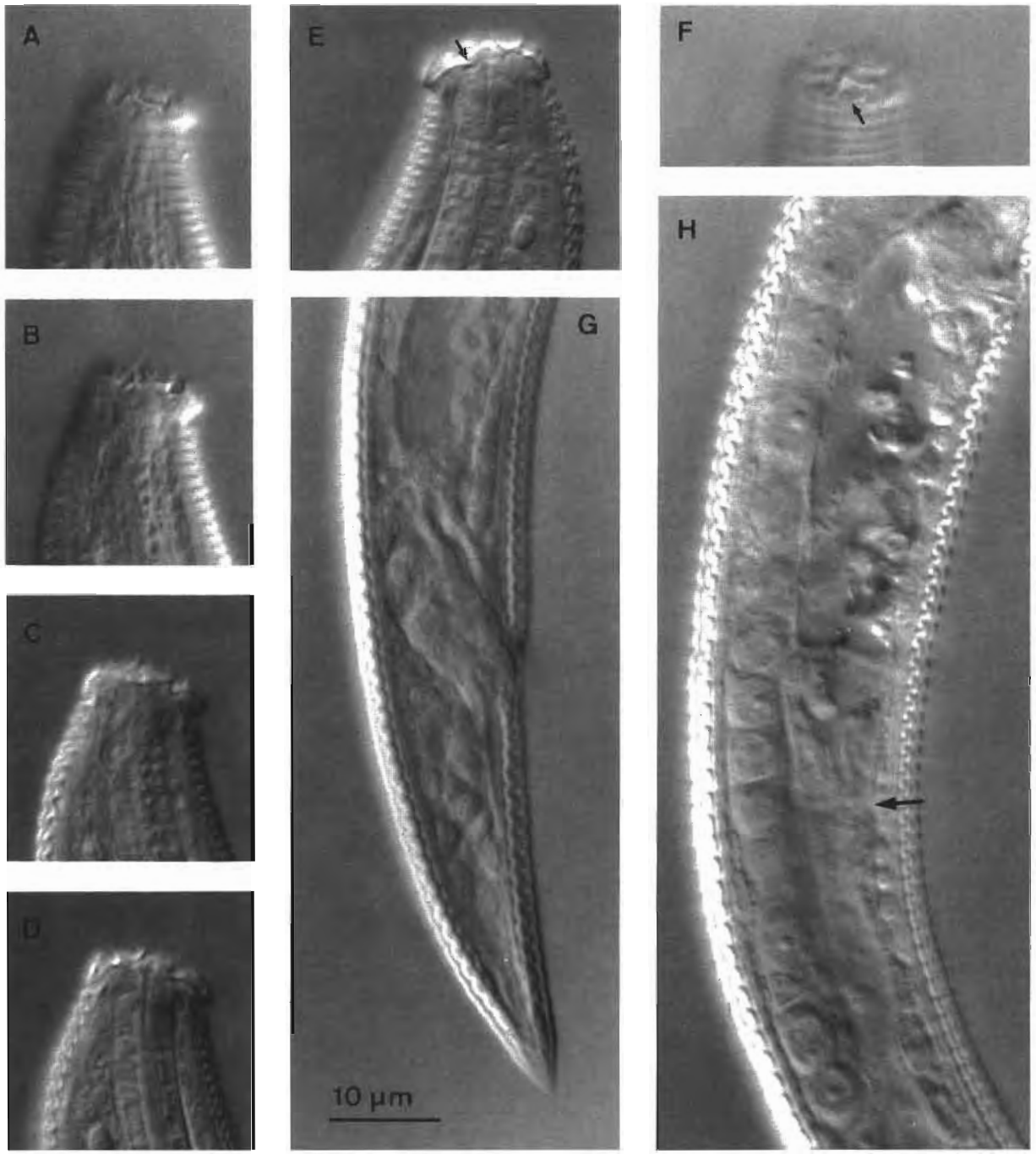

Fig. 5. Nothacrobeles lunensis *sp. n. photomicrographs of females A-D: Lip region of holotype at different levels of focus; E: Lip region in median view (arrow points at cheilorhabdion); F: Lip region in surface view (arrow points at amphid); G: Tail; H: Posterior part of reproductive system (arrow points at tip of PUB).*

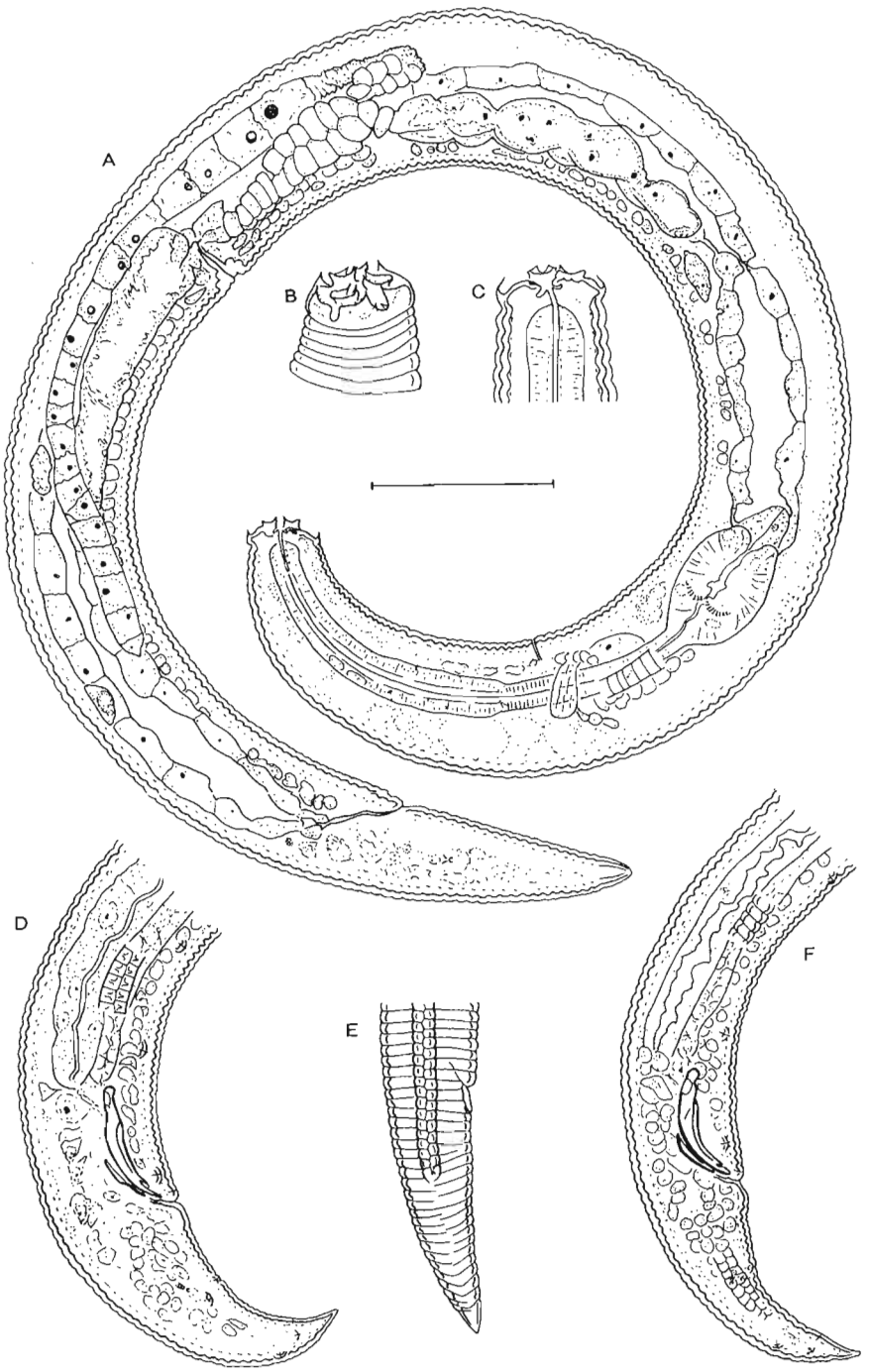

Fig. 6. Nothacrobeles lunensis *sp. n. A: Entire holotype female; B: lip region of holotype in surface view; C: Lip region of female in median view; D,F: Male tail region; E: Female tail in surface view (Bars: 3B, C = 20 µm; others = 30 µm).*

Table 3. *Measurements of holotype and paratypes of* Nothacrobeles lunensis *sp. n. and* Nothacrobeles *sp. The holotype and allotype of* N. lunensis *sp. n. are from sample 3 (Measurements given in µm).*

	Holotype (Fem.)	Allotype (Male)	Sample 2 (Fem.)	Sample 2 (Male)	Sample 3 (Fem.)	Sample 3 (Male)	*Nothacrobeles* sp (Male*)
n	1	1	5	5	14	2	1
L	447	478	452 ± 65 (373-519)	455 ± 46 (417-526)	430 ± 33 (357-475)	422-458	495
Body width	25	25	24-26	25 ± 2.2 (21-26)	23 ± 2.1 (20-26)	18-23	46
Neck length**	111	114	114 ± 6 (107-122)	109 ± 5 (100-114)	110 ± 5 (100-118)	104-115	127
Tail length	40	48	40-43	44 ± 2.3 (42-48)	42 ± 3.3 (36-48)	41-38	55
Anal body width	15	21	15-17	18-21	16 ± 1.0 (14-18)	16-18	30
a	17.9	18.9	17.8 ± 2.6 (14.3-21)	18.5 ± 1.8 (16.5-20)	18.5 ± 1.4 (15.8-21)	19-25	10.8
b	4.0	4.2	3.9 ± 0.4 (3.5-4.4)	4.1 ± 0.4 (3.7-4.7)	3.9 ± 0.2 (3.6-4.3)	4.0-4.1	3.9
c	11.1	9.9	11.0 ± 1.3 (9.3-12.2)	10.2 ± 0.9 (9.6-11.7)	10.3 ± 0.7 (9.3-11.8)	11.1-11.2	9.0
c'	2.7	2.3	2.4-2.7	2.3 ± 0.1 (2.1-2.5)	2.7 ± 0.3 (2.2-3.3)	2.2-2.5	1.8
Stoma	7	5	5.5-7.5	5-7.5	6-7.5	6	10
Corpus	45	48	48 ± 3.7 (44-52)	45 ± 3.2 (40-48)	46 ± 2.7 (42-49)	46-48	54
Isthmus	31	35	33 ± 3.0 (29-36)	32-35	32 ± 1.7 (29-34)	26-36	32
Bulbus	23	22	20-23	20-23	20-23	21-23	27
Nerve ring	60	51	54 ± 2.4 (52-57)	58 ± 5.0 (51-64)	58 ± 4.5 (50-64)	51-55	?
Excr. pore	63	63	71 ± 8.5 (60-78)	66 ± 3.0 (63-70)	63 ± 4.8 (54-70)	58-66	79
Deirid	80	77	69-70 (n=2)	79 ± 2.9 (76-82)	75 ± 5.5 (68-83)	72-74	?
Nerve ring (% neck)	54	45	47 ± 2.8 (44-51)	53 ± 5.2 (45-58)	52 ± 2.5 (49-57)	44-53	?
Excr. pore (% neck)	57	55	60 ± 6.7 (53-66)	61 ± 4.5 (55-66)	58 ± 4.9 (50-64)	50-63	62
Deirid (% neck)	72	67	63 ± 2.9 (61-65)	69 ± 1.8 (67-71)	69 ± 4.6 (62-76)	63-71	?
Phasmid	7	13	9 ± 1.8 (6.5-11)	12-15	9 ± 1.7 (7-11)	13-14	22
Phasmid (% tail)	17	28	21 ± 4.9 (15-28)	30 ± 3.4 (28-35)	20 ± 3.7 (15-26)	33-35	40
V	60	-	58-60	-	59 ± 1.9 (55-63)	-	-
G/T	40	51	42 ± 3.5 (37-46)	50 ± 2.6 (46-53)	41 ± 2.7 (35-45)	46-52	62
Spermatheca/ spicules	68	23	51 ± 9.0 (44-65)	23 ± 1.4 (20-24)	59 ± 6.4 (50-68)	20-21	34
PUB/gubern.	49	12	55 ± 11 (43-67)	11 ± 1.3 (9-13)	52 ± 6.4 (43-62)	11	21

End of Table 3 next page

Table 3. *(cont.)*

	Holotype (Fem.)	Allotype (Male)	Sample 2 (Fem.)	Sample 2 (Male)	Sample 3 (Fem.)	Sample 3 (Male)	*Nothacrobeles* sp (Male*)
R	238	232	229 ± 12 (212-245)	231 ± 10 (218-241)	232 ± 6.4 (221-242)	237-246	?
R_{nr}	30	33	30 ± 2.6 (28-33)	30 ± 2.6 (27-33)	32 ± 1.9 (30-35)	29-36	?
R_{ex}	33	35	34-37	32-35	37 ± 2.5 (33-40)	34-40	30
R_{dei}	40	42	?	41-42	43 ± 2.9 (38-48)	44-45	?
R_{phar}	60	62	57 ± 4.8 (52-64)	59 ± 6.2 (52-66)	61 ± 4.3 (54-68)	63-66	?
$R_{phar\text{-}v}$/ $R_{phar\text{-}an}$	86	155	81 ± 7.0 (75-91)	155 ± 7.5 (150-166)	81 ± 6.6 (72-92)	155-162	?
$R_{v\text{-}an}$	74	-	71 ± 7.7 (61-78)	- 17 ± 1.7	71 ± 4.0 (63-75)	-	-
R_{tail}	18	15	18-19	(15-19)	19 ± 1.8 (15-21)	18-19	19

*: Specimen visibly flattened, isthmus collapsed.
**: Neck length measured along lumen of pharynx from tips of labial probolae to base of bulbus.

tory pore. Cardia small, hemispherical to conoid, 4-6 µm long. Vulva at about three-fifths of body, vagina occupying 27-40% of VBW. Female reproductive system on right side of intestine, monodelphic, prodelphic. Spermatheca offset at level of anterior flexure, outstretched. PUB as long as 1.6-2.9 VBW. Ovary straight, with 13-20 oocytes, usually in single file (n=10). Cell walls and/or nuclei exceptionally clear in some females: oviduct with two rows of four cells (n=5), spermatheca with two rows of two smaller stem cells and two rows of five larger sac cells (n=3), uterus with four rows of six cells (n=3) and an additional double file of five cells (n=1). Tail conoid, with a subacute, slightly sclerotized terminus. Phasmids at about one-fifth to one-fourth of tail length. Rectum 0.7-1.1 ABW long.

Male: Body more strongly curved posteriorly than in the female. Lateral field sometimes with only two distinct lines on most of body, but with three lines near the phasmid. Labial probolae 2.0-2.5 µm long. Stoma as long as 0.5-0.6 LRW, corpus 1.2-1.4 times as long as isthmus. Deirids 10-16 µm or seven to eight annules posterior to excretory pore. Reproductive system on right side of intestine, anteriorly directed. Testis reflexed over 41-44 µm. Spicules 1.0-1.4 ABW long, ventrally arcuate with thin velum and with offset, rounded manubrium. Gubernaculum boat-shaped in lateral view, half as long as spicules. Three pairs of preanal genital papillae present subventrally; one single medioventral papilla located on anterior lip of the cloacal aperture. Five pairs of caudal genital papillae present: three pairs near tail terminus and two pairs at middle of tail, level with or just posterior to phasmids. Tail conical, ventrally curved with acute or subacute tip.

Type locality and habitat

Sandy bank of an ephemeral river in Valle de la Luna, San Juan Province, Argentina. Holotype collected in rhizosphere of a thicket of "Pichana" (?) with one "Sampa" (*A. lampa*). Additional specimens collected in rhizosphere of "Retamo" (*Bulnesia retama* [Hook.] Griseb.).

Type specimens

Holotype female with four female and two male paratypes deposited in the Nematode Collection of the Instituut voor Dierkunde, Universiteit Gent, Belgium; one male and four female paratypes deposited in the collection of the National Nematological Research Centre, University of Karachi, Pakistan; one male and two female paratypes deposited in the Collection Nationale de Nématodes, Muséum National d'Histoire Naturelle, Paris, France; one male and three female paratypes deposited in the collection of the Swedish Natural History Museum, Stockholm, Sweden; one male and two female paratypes deposited in the USDA Nematode Collection, Beltsville, MD, USA; one male and two female paratypes deposited in the collection of the Department of Zoology, Rand Afrikaans University, Auckland Park, South Africa.

Table 4. *Table of the specific differential characters in the genus* Acrobeles *von Linstow, 1877 (Distinctive measurements are in bold print. Ranges or characters in brackets are from sources other than the original description).*

	"Double" cuticle	♀ Rex/ position*	♀ R	PUB	♀ L (µm)	♀ c'	Spicule (µm)	Special features and other sources
A. chelatus	no	P	?	2 VBW	558-748	2.5***	34-40	labial probola tips twice bifurcated
A. annulatus	no	P	**140-153**	3 VBW (1-3 VBW)	**1050-1060 (1070)**	2.3-2.6	**43-52**	V=63-66%, phasmid precedes male caudal papillae (4)
A. sheasbyi	no	P	?	1.5-2.5 VBW	680-820	2-2.7	**41-47**	vulva sunken, cuticle tessellated
A. seelyae	no	32-35 =P	183-195	39-71 µm	540-660	2.5-3.8	26-28	vulva sunken, cuticle tessellated
A. farzanae	no	29-36 =P	175-188	1.4-2.2 VBW	700-830	2.5-2.9	42-47	tyre-like annules, phasmid precedes male caudal pap.
A. thornei	no	34*** =P	? (174-204)	? (39-78 µm)	690-800 (690-1040)	2.9*** (2.3-3.3)	? **(43-61)**	cuticle tessellated, phasmid precedes male caudal pap. (4,9)
A. canalis	no	35 =P	202	1 VBW	830-860	2.3-2.4	?	subcuticular lateral canals
A. bushmanicus	no	30-35 =P	?	1-1.5 VBW	510-520	2.4-2.8	32-38	no long tines in axils
A. taraus	no	26*** =P	?	≤ **1 VBW**	678-746	**1.3-1.4**	31-37	female tail bullet-shaped
*A. ciliatus***	no	**20-25 =M**	190 (179-198)	1.5 VBW (38-86 µm)	454-538 (410-490)	3.3*** (2.5-2.8)	26	phasmid at male caudal papillae (6, 9, 12)
A. singulus	no	**15-23 =A (13-22)**	160-190 (159-184)	≤ **1 VBW**	380-500 (340)	3-4 (3.6-4.6)	?	no long tines in axils (7,8)
A. cylindricus	no	**14 (19) =A**	? (170-172)	? **(< VBW)**	**330 (300-320)**	2.5-3 (3.2-3.4)	?	(1)
A. kotingotingus	no	?	?	**< 0.5 VBW**	785-925	2.0-3.0	36-40	annules with two rows of stripes
A. sparsus	interme-diate	P	?	**< 1 VBW**	710-850	2-3	?	
A. elaboratus	?	?	?	?	740	**1.6**	?	female phasmids adanal, outer tines curved
A. ornatus	?	?	?	?	800-850	**1.4**	?	outer tines curved, female tail < male tail
A. serricornis	?	?	?	?	615	2.1	?	cephalic probolae very slender
A. recurvus	yes	P	?	1.5 VBW	630-650	3.0-3.5	28-32	apical tines curved
A. dimorphus	yes	P	?	1.5-2 VBW	830-890	**4-5.5**	33-35	
A. complexus	yes	P (44-58)	? (237-314)	? (34-172 µm)	750-900 (590-870)	2.2 (2.0-3.7)	? (25-44)	(3,4,5,7,10,11)
A. geraerti	yes	40-62 =P	240-279	59-108 µm =1.5-3 VBW	560-640	2.1-2.9	30-34	labial probolae with minute tines

End of Table 4 next page

Table 4. *(cont.)*

	"Double" cuticle	♀ Rex/ position*	♀ R	PUB	♀ L (µm)	♀ c'	Spicule (µm)	Special features and other sources
A. welwitschiae	yes	40-47 =P	227-256	30-46 µm	440-510	2.2-3.5	**19-23**	female tail ventrally kinked
A. oasiensis	yes	38*** =P	225***	**0.5 VBW**	426-571	3	?	spermatheca minute
A. emmatus	yes	29-38 =P	186-236	53-85 µm =2.0-3.4 VBW	477-627	2.4-3.4	22-26	indentations in "inner layer" of cuticle
A. undulatus	yes	29***	?	**< 0.5 VBW**	490-650	3	?	cuticle tessellated
A. ctenocephalus	yes	**M**	?	?	500	2.3	?	phasmids adanal
A. mariannae	yes	**13-17 =A**	?	**< 1 VBW**	370-410	2.7-3.2	?	(2,3,4,7,10)
		(10-24)	(200-259)	(13-23 µm)	(410-610)	(2.3-3.5)	**(20-23)**	
A. ensicaudatus	yes	12 =A	206	< 0.5 VBW	620-684	**5.9*** **	?	female tail long, ensiform
A. timmi	yes	?	?	**< 0.5 VBW**	490-620	3-4	28-39	

*: Abbreviations used to indicate excretory pore position: P=posteriorly located; M=near middle of neck; A=anteriorly located.

**: Primary data on *A. ciliatus* are taken from the redescription by Thomas and Allen (1965).

***: Measured or counted on the relevant figure.

†: (1) Andrássy, 1984; (2) Boström, 1990; (3) De Ley *et al.*, 1990; (4) Heyns, 1969; (5) Heyns, 1995; (6) Kreis, 1930; (7) Rashid *et al.*, 1985; (8) Rashid *et al.*, 1989; (9) Rashid *et al.*, 1990*a*; (10) Rashid *et al.*, 1990*b*; (11) Steiner, 1929; (12) Yeates, 1967.

DIAGNOSIS AND RELATIONSHIPS

Nothacrobeles lunensis sp. n. differs from all other known species of the genus in having a "double cuticle".

It is closest in labial morphology and measurements to *N. scaphovulva* (Rashid & Heyns, 1990) comb. n., *N. subtilis* (Allen & Noffsinger, 1971) and *N. acrobeles* (Andrássy, 1967) Allen & Noffsinger, 1971, but differs from each of these in at least two other respects (cf. Table 5): *N. scaphovulva* has three rows of cuticular punctations per annule and a vulva set in a cuticular depression; *N. subtilis* has longer labial probolae, four lateral lines and a shorter PUB; and *N. acrobeles* has *inter alia* two rows of cuticular punctations per annule, longer labial probolae and four lateral lines.

Nothacrobeles cf. *subtilis** Allen & Noffsinger, 1971

(Fig. 7)

MEASUREMENTS

See Table 3

DESCRIPTION

Female: Not found.

Male: Body slightly ventrally curved, flattened by preservation. Cuticle 2 µm thick, coarsely annulated, under LM with a "semi-two-layered" structure (resembling that described for *Acrobeles sparsus* Heyns, 1969) and with irregular, non-refractive punctations in surface view. Annules 1.8 µm wide in neck region and 3.3 µm wide at midbody. Lateral field with four incisures at mid-body, indistinct anteriorly. Middle incisures converging gradually towards posterior end, meeting near the level of the anterior pair of genital papillae and posteriorly continuing as a single central incisure. Thus, lateral field having only three incisures in the preanal region and on the tail. Lip region 15 µm wide, truncate, weakly offset with four cephalic and six labial papillae. Amphids small, slit-shaped, dorsosublaterally placed. Labial probolae 4 µm high, stout, with prominent rim projecting towards the lips, bifurcated halfway down their length and carrying about twelve minute tines. Prongs only 2 µm long. Lips broad with acute tip and faintly corrugated anterior edge. Subdorsal primary axils narrow, with two triangular guard processes at their base. Ventral primary

* Specific name originally given as "*subtilus*" is emended into "*subtilis*" to conform with Latin orthography.

Table 5. *Table of the specific differential character in the genus* Nothacrobeles *Allen & Noffsinger, 1971 (Distinctive measurements are in bold print).*

	Prongs of lab. probolae (µm)	Lateral lines	PUB	♀ L (µm)	Spicules (µm)	Guberna-culum (µm)	Cuticle tessellated	LRW (µm)	Special features
N. lunensis	1-2	2-3	**43-67 µm =1.6-2.9 VBW**	357-519	20-24	9-13	-	11-13	"double cuticle"
N. scapho-vulva	1-2*	3	**48-62 µm**	420-620	20-34	11-19	±	12-14*	sunken vulva, annules with two rows of punctations
N. subtilis	3.5	4	11-30 µm =1 VBW	480-700	?	?	±	15*	
*N. acrobe-les***	3.3	4	?	?	36	**26**		13*	annules with two rows of punctations
N. maximus	4*-5	4	13-35 µm <1 VBW	640-870	?	?	+	17*	
N. lepidus	5*-6	4	13-21 µm <1 VBW	520-640	22-25	12-14	+	13*	
N. sheri	7*-10	4	**54-78 µm =2 VBW**	670-900	30-38	15-19	+	18*	annules with three rows of punctations
N. prominens	7*	**3**	?	600-780	35	16	-	17*	

*: Measured on relevant figure; labial probola prong length is sometimes slightly higher in the text of Allen and Noffsinger (1971) than on their relevant figure.

**: Based on redescription of holotype by Allen and Noffsinger (1971).

axil with one or two longer guard processes (not clear in lateral view). Secondary axils reduced to thin incisures. Cuticle of the cheilostom containing conspicuous "cheilorhabdia" with flattened, elliptical cross-section between the labial probolae. Entire stoma 0.7 LRW long, distinctly divided into cheilo-, gymno- and stegostom. Stegostom with prominent subdivisions, metastegostom with small dorsal denticle. Corpus slightly fusiform, 1.7 times as long as isthmus, isthmus dorsoventrally folded. Basal bulb pyriform with striated transverse valves anterior to its centre. Nerve ring and deirid not seen. Cardia indistinct. Testis reflexed over 59 µm. Spicules 1.1 (flattened!) ABW long, ventrally arcuate with broad velum and with offset, rounded or angular manubrium. Gubernaculum rod-shaped in lateral view, two-thirds as long as spicules. Three pairs of preanal genital papillae present subventrally; one single medioventral papilla located on anterior lip of the cloacal aperture. Five pairs of caudal genital papillae present: three pairs near tail terminus and two pairs at middle of tail, posterior to phasmids. Tail convex-conoid, weakly ventrally curved with acute tip.

Comments on identification

This specimen resembles in many respects both *Nothacrobeles subtilis* Allen & Noffsinger, 1971 and *N. acrobeles* (Andrássy, 1967) Allen & Noffsinger, 1971, but does not agree entirely with either, having labial probolae with shorter prongs and cephalic probolae with less prominent tines, as well as one or two ventral guard processes that are much longer than the subdorsal ones. Males of *N. subtilis* have not yet been described, and we are therefore unable to assign this single male confidently to either a known or a new species.

Locality and deposition

The single male is mounted in a slide marked "2 *Cervidellus cervus* - Richfield, Utah, shadscale soil, sept. 10, 1933". This slide also contains the neotype

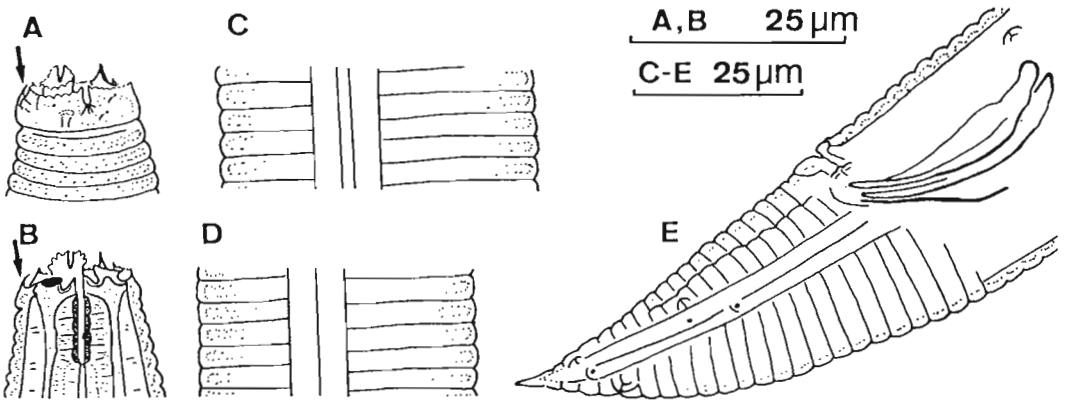

Fig. *7.* Nothacrobeles. *cf.* subtilis *Allen & Noffsinger, 1971 male. A,B: Anterior end (arrow points at enlarged ventral guard processes); C: Lateral field at mid-body; D: Lateral field in preanal region; E: Tail region.*

of *C. cervus* (Thorne, 1925) Thorne, 1937 and is kept as slide number T-489t in the USDA Nematode Collection, Beltsville, MD, USA (De Ley, unpubl.).

Discussion

Rejection of *Seleborca* and *Triligulla*

The family Cephalobidae currently contains two separate genera characterized by presence of a "two-layered" cuticle, each of which strongly resembles another genus: *Seleborca* Andrássy, 1985 is similar to *Acrobeles* von Linstow, 1877 in all respects but the cuticle, while *Triligulla* Siddiqi, 1993 fits the diagnosis of *Cervidellus* Thorne, 1937 in every major character, again except for the cuticle. Following this logic, the discovery of a new species differing from *Nothacrobeles* in this same character would have led to the proposal of a new genus for it. However, the occurrence of a "two-layered" cuticle in three different but closely related groups of species strongly suggests that this is a case of parallel evolution. The "inner layer" may provide additional protection against death from desiccation, as suggested by the distribution of the species concerned, and we think that it arose independently under similar conditions in at least three genetically similar lineages. It follows from this assumption that a "double cuticle" is a relatively easily acquired character, which may also have arisen more than once within the group of twelve species currently assigned to *Seleborca*. This strongly reduces the likelihood that these species share an exclusive common ancestry, *i.e.*, that they represent a monophyletic group.

Within current mainstream taxonomy, this phylogenetic argument could suffice to reject *Seleborca*. But there are additional, more typological grounds for its invalidity: the intermediate condition of the cuticle of *Acrobeles sparsus* Heyns, 1969 causes difficulties in its generic allocation, while the duplex annulation of the "inner layer" in *A. emmatus* sp. n. clearly represents a yet further derived condition. Another discordant species could be *A. undulatus* Loof, 1964, which is clearly depicted with undulating cuticle in Fig. 6B in Loof (1964) but was not included in *Seleborca* by Andrássy (1985). And finally, the overwhelming similarity between *Acrobeles* and *Seleborca* species in all other characters (apparent differences in the lateral field are only due to the number of visible layers in the cuticle; cf. Rashid *et al.*, 1990*a*; De Ley *et al.*, 1990) would require one character to be very significant for it to suffice for genus distinction. We feel this requirement is not met by the "double cuticle" and therefore we reject *Seleborca* and transfer all its species back to *Acrobeles* (see below). On these grounds, we also transfer the single known species of *Triligulla* to *Cervidellus*, resulting in *C. alutus* (Siddiqi, 1993) n. comb.

It should be noted that a different interpretation is theoretically possible, in which it is assumed that the "double cuticle" arose only once and therefore warrants a separate taxon (*e.g.*, subfamily) for these species. However, this is contradicted by several other characters, including not only the detailed structure of the lip region, but also, *e.g.*, the striking fact that males of *N. lunensis* sp. n. have phasmids anterior to the first two pairs of caudal papillae, a condition not found in other Cephalobidae except in *Nothacrobeles* and in some species of *Acrobeles* with "single cuticle"! In conjunction, these characters are much less likely to be parallelisms, than the cuticular structure by itself.

Another point worth making is the uncertainty about the cuticular condition of several species

described by Thorne (1925). Thus, Andrássy (1985) transferred *Acrobeles complexus* Thorne, 1925, *A. ctenocephalus* Thorne, 1925, and *A. ornatus* Thorne, 1925 to *Seleborca* (the first even as type species), but retained *A. elaboratus* Thorne, 1925 in *Acrobeles*. The lateral field and cuticular structure in cross-section of all four species was in fact illustrated rather similarly and ambiguously by Thorne (1925), and reference material of these species has to be studied to resolve their cuticular structure. More in general, a significant number of *Acrobeles* species should be re-examined to better resolve their status and diagnosis, and a better understanding of intraspecific variation in this genus should be gained. We have retained species as valid when their descriptions contain at least one difference with other species, but doubt strongly that these differences are always reliable. Thus, *A. emmatus* sp. n. varies considerably in number and length of tines on the cephalic probolae, despite the fact that the presence or absence of elongated tines in the secondary axils is traditionally used as a species character.

REJECTION OF *NAMIBINEMA*

The genus *Namibinema* was proposed by Rashid and Heyns (1990) on the basis of several differences with the then known species of *Nothacrobeles*: vulva set in a cuticular depression (*vs* flush with surrounding cuticle), labial probolae without tines (*vs* distinctly bearing tines), primary axils without guard processes (*vs* with two triangular guard processes) and lateral field with three incisures (*vs* four). However, we feel none of these differences can be retained as genus character:

- a sunken vulva is also known in *Acrobeles sheasbyi* Heyns & Hogewind, 1969, *A. seelyae* Rashid *et al.*, 1990 and an as yet undescribed species of *Cervidellus* (De Ley, unpubl.), and none of these is sufficiently different in other respects to warrant allocation to a separate genus.

- *Nothacrobeles subtilis* Allen & Noffsinger, 1971 and our single male of *Nothacrobeles* sp. have minute tines, while *Namibinema scaphovulva* Rashid & Heyns, 1990 has corrugated rims of the lips and labial probolae (cf. Fig. 2A-C in Rashid & Heyns, 1990). The difference between these conditions is far too small to support different genus allocation. Furthermore, tines are also absent (or nearly so?) in *Nothacrobeles lunensis* sp. n.

- the primary axils of *Namibinema scaphovulva* do actually contain two guard processes, as is clear on Fig. 2B, C in Rashid and Heyns (1990).

- our male *Nothacrobeles* sp. has a lateral field changing from four to three incisures (on a single animal!), while *N. lunensis* sp. n. apparently has only two or three incisures (again, sometimes on a single animal). Both conditions require SEM for absolute proof, but nevertheless significantly undermine the importance of the lateral field at genus level. In fact, most other genera of Cephalobidae include species with differing number of lateral lines, and Andrássy (1984*a*) has already transferred *Acrobeles prominens* Andrássy, 1964 to *Nothacrobeles* despite its having only three lateral lines.

In view of these considerations, both *Namibinema scaphovulva* and *Nothacrobeles lunensis* sp. n. are considered to belong in *Nothacrobeles*, and their distinctive characters are felt to be important only at species level.

Acrobeles von Linstow, 1877 = *Seleborca* Andrássy, 1985 n. syn.

DIAGNOSIS (emended)

Cephalobidae. Body small to large (L=0.3-1.1 mm). Cuticle "single" or "double", with large to very large annules, with or without longitudinal striae, punctations and/or pores. Lateral field with two or three incisures, if cuticle "double" then often with undulating internal pseudolines. **Amphids relatively distinct, circular. Labial probolae long, deeply bifurcated. Each prong with at least seven tines**, its tip usually with two elongate, separated apical tines, and its outer rim never continuing into a basal ridge. **Cephalic probolae high, triangular, separate and fringed by numerous tines**, demarcating cephalic axils that are all equally deep. Primary axils with two guarding pieces often indistinguishable from tines. Radial ridges each with one dentate process. Stoma cephalobid with distinct **cheilorhabdia that are large and spherical** in cross-section. Pharyngeal corpus cylindrical to fusiform, not distinctly swollen posteriorly, usually fixed with expanded lumen. Excretory pore position varying from very anterior to opposite basal bulb. Female reproductive system cephalobid, spermatheca and PUB small to large. Vulva flush with body, occasionally sunken. Males with three pairs of preanal papillae, five pairs of caudal papillae and one median papilla on the precloacal lip. Tails in both sexes conical, usually with acute tip. Phasmids in male usually posterior, sometimes anterior to the anteriormost caudal papillae.

TYPE SPECIES

Acrobeles ciliatus von Linstow, 1877
= *Cephalobus ciliatus* (von Linstow, 1877) de Man, 1880
= *Cephalobus (Acrobeles) ciliatus* (von Linstow, 1877) de Man, 1880
= *Acrobeles sinensis* Kreis, 1930
= *Acrobeles maeneeneus* Yeates, 1967

OTHER SPECIES

A. annulatus Heyns & Hogewind, 1969
A. bushmanicus Heyns, 1969
A. canalis Andrássy, 1985
A. chelatus Thomas & Allen, 1965
A. complexus Thorne, 1925
= *Seleborca complexa* (Thorne, 1925) Andrássy, 1985
= *Acrobeles crossotus* Steiner, 1929
A. ctenocephalus Thorne, 1925
= *Seleborca ctenocephala* (Thorne, 1925) Andrássy, 1985
A. cylindricus Ivanova, 1968
A. dimorphus Heyns & Hogewind, 1969
= *Seleborca dimorpha* (Heyns & Hogewind, 1969) Andrássy, 1985
A. elaboratus Thorne, 1925
A. emmatus sp. n.
A. ensicaudatus Thomas & Allen, 1965
= *Seleborca ensicaudata* (Thomas & Allen, 1965) Andrássy, 1985
A. farzanae Heyns, 1995
A. geraerti (Rashid, Heyns & Coomans, 1990) comb. n.
= *Seleborca geraerti* Rashid, Heyns & Coomans, 1990
A. kotingotingus Yeates, 1967
A. mariannae Andrássy, 1968
= *Seleborca mariannae* (Andrássy, 1968) Andrássy, 1985
= *Acrobeles capensis* Heyns, 1969
A. oasiensis Boström, 1985
= *Seleborca oasiensis* (Boström, 1985) Rashid, Heyns & Coomans, 1990
A. ornatus Thorne, 1925
= *Seleborca ornata* (Thorne, 1925) Andrássy, 1985
A. recurvus Heyns, 1969
= *Seleborca recurva* (Heyns, 1969) Andrássy, 1985
A. seelyae Rashid, Heyns & Coomans, 1990
A. serricephalus Thorne, 1925
A. sheasbyi Heyns & Hogewind, 1969
A. singulus Heyns, 1969
A. sparsus Heyns, 1969
A. taraus Yeates, 1967
A. thornei Heyns, 1963
A. timmi Chaturvedi & Khera, 1979
= *Seleborca timmi* (Chaturvedi & Khera, 1979) Andrássy, 1985
A. undulatus Loof, 1964
A. welwitschiae (Rashid, Heyns & Coomans, 1990) comb. n.
= *Seleborca welwitschiae* Rashid, Heyns & Coomans, 1990

SPECIES INQUIRENDAE VEL INCERTAE SEDIS

A. cephalatus (Cobb, 1901) Thorne, 1925
= *Cephalobus cephalatus* Cobb, 1901
= *Seleborca cephalata* (Cobb, 1901) Andrássy, 1985
A. ilidzensis Paesler, 1941*
A. neocephalatus Kannan, 1961
A. pachidinovae Atakhanov, 1958**
A. raoi Kannan, 1961
= *Seleborca raoi* (Kannan, 1961) Andrássy, 1985

SPECIFIC DIFFERENTIAL CHARACTERS

See Table 4.

Nothacrobeles Allen & Noffsinger, 1971

DIAGNOSIS

Cephalobidae. Body small to relatively large (L=0.4-0.9 mm). Cuticle "single" or "double", with large annules, with or without longitudinal striae and/or punctations. Lateral field with two to four incisures, if cuticle "double" then often with undulating internal pseudolines. Amphids indistinct, slit-shaped or elliptical. **Labial probolae short to long, always bifurcated**. Each prong with or without tines, its tip at most with one separated apical tine, and its outer rim always continuing into a **prominent basal ridge** located on the stem of the labial probola and protruding towards the cephalic probolae. **Cephalic probolae in pairs**, low, demarcating deep primary axils and shallow secondary axils, with or without tines. Primary axils with **two triangular guard processes** larger than any neighbouring tines. Radial ridges each with one dentate process. Stoma cephalobid with small cheilorhabdia. Pharyngeal corpus cylindrical to fusiform, not distinctly swollen posteriorly, rarely fixed with expanded lumen. Excretory pore posteriorly placed, at or near isthmus. Female reproductive system cephalobid, spermatheca and PUB small to large. Vulva flush with body, rarely sunken. Males with three pairs of preanal papillae, five pairs of caudal papillae and one median papilla on the precloacal lip. Tails in both sexes conical, usually with acute tip. **Male phasmids level with, or anterior to the anteriormost caudal papillae**.

TYPE SPECIES

Nothacrobeles sheri Allen & Noffsinger, 1971

OTHER SPECIES

N. acrobeles (Andrássy, 1967) Allen & Noffsinger, 1971

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* Apparently described from a first-stage juvenile of an *Acrobeles* species (compare with Fig. 3F in Thomas, 1965).
** This species clearly does not belong in *Acrobeles*; it could perhaps be a poorly fixed *Panagrolaimus*.

= *Zeldia acrobeles* Andrássy, 1967
N. lepidus Allen & Noffsinger, 1971
N. lunensis sp. n.
N. maximus Allen & Noffsinger, 1971
N. prominens (Andrássy, 1964) Andrássy, 1984
= *Acrobeles prominens* Andrássy, 1964
N. scaphovulva (Rashid & Heyns, 1990) comb. n.
= *Nothacrobeles scaphovulva* Rashid & Heyns, 1990
N. subtilis Allen & Noffsinger, 1971

SPECIES INQUIRENDAE

N. distinctus (Kirjanova, 1951) comb. n.*
= *Acrobeles distinctus* Kirjanova, 1951
= *Acrobeles innoxius* Kirjanova, 1951 n. sym. **

SPECIFIC DIFFERENTIAL CHARACTERS

See Table 5.

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* Examination of the male type of *A. distinctus* depicted in Fig. 9 in Kirjanova (1951) revealed the presence of distinct basal ridges on labial probolae measuring about 6 µm; specimen was too poorly preserved to decide whether it was conspecific with *N. sheri*, *N. lepidus*, or neither or both species.
** Examination of the type specimen of *A. innoxius* depicted in Fig. 6 in Kirjanova (1951) showed that this is a juvenile and not an adult female, the apparent presence of a vulva being due to cuticular irregularities (Boström & De Ley, unpubl.). Its labial probolae correspond with those of *N. distinctus* and the two species are therefore synonymized, retaining *N. distinctus* as valid name because it was described from adult specimens (recommendation 68B.4 in the International Code for Zoological Nomenclature).

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