# A redescription of *Ypsylonellus similis* (Thorne, 1925) Andrássy, 1984, with descriptions of some related species (Nematoda : Cephalobidae)

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**Summary** – Ypsylonellus similis is redescribed on the basis of type females, females from Spain, original specimens of Stegelletina lineata and types of S. mucronata. Both these species are synonymized with Y. similis. Other specimens from various localities are described; they are considered to represent or to be very close to Y. devimucronatus, Y. insubricus, Cervidellus servatus and C. neftasiensis. It is argued that presence or absence of longitudinal striae cannot be used to diagnose the genus Stegelletina. The structure of the cephalic axils may provide a better basis for classifying species of Stegelletina, Ypsylonellus and Cervidellus, but more species must be re-examined before taxonomic changes can be proposed.

Résumé – Redescription d'Ypsylonellus similis (Thorne, 1924) Andrássy, 1984 et description de quelques espèces voisines (Nematoda : Cephalobidae) – Ypsylonellus similis est redécrit à partir des femelles types, de femelles provenant d'Espagne, des spécimens originaux de Stegelletina lineata et des spécimens types de S. mucronata, ces deux dernières espèces étant synonymisées à Y. similis. D'autres spécimens provenant de sites variés sont également décrits; ils sont considérés comme appartenant à, ou très proches de, Y. devimucronatus, Y. insubricus, Cervidellus serratus et C. neftasiensis. Il est démontré que la présence ou l'absence de stries longitudinales ne peut être utilisée pour caractériser le genre Stegelletina. La structure des axiles céphaliques pourrait fournir une meilleure base pour la classification des espèces appartenant aux genres Stegelletina, Ypsylonellus et Cervidellus mais un plus grand nombre d'espèces doit être étudié avant de pouvoir proposer des changements taxinomiques.

Key-words : Ypsylonellus, Stegelletina, Cervidellus, Cephalobidae, taxonomy, Nematodes.

Recently, several papers have pointed out important uncertainties in the diagnosis and differentiation of the cephalobid genera *Cervidellus* Thorne, 1937, *Ypsylonellus* Andrássy, 1984 and *Stegelletina* Andrássy, 1984 (Boström, 1986, 1987, 1991; De Ley & Vandebroek, 1992). At present, it is particularly unclear how *Ypsylonellus* and *Stegelletina* can be distinguished from *Cervidellus*. Of the first genus the exact anterior morphology of the type species is uncertain, and SEM observations show that longitudinal striae, supposedly the distinctive feature of *Stegelletina*, also occur in *Cervidellus* species.

The problems in this group derive partly from the fact that many relevant species (including the type species of all three genera) were described too long ago to allow reliable taxonomic assessment in the face of current knowledge, such as is derived from e.g. SEM studies. Also, some species apparently only occur in low densities and/or less easily accessible regions, with the result that they are known only from their original description. And to make matters even worse, intraspecific variability can complicate species diagnosis even when specimens are studied and described more thoroughly (Boström, 1991, 1992).

In the last decade, six new species have been de-

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scribed in this group (Boström, 1986, 1987; Andrássy, 1987; De Clerck & De Ley, 1990; De Ley et al., 1990; De Ley & Vandebroek, 1992), and it is quite likely that a number of additional species remain to be discovered. This makes it a matter of importance that the current difficulties within and between the three genera in question are resolved, requiring the re-examination of the less well-known nominal species, and especially of the generic types. In this paper, a first step is taken towards that end, with the detailed redescription of the type species of Stegelletina : S. lineata (Thorne, 1925) Andrássy, 1984, which was found to be a junior synonym of Ypsylonellus similis (Thorne, 1925) Andrássy, 1984 and a senior synonym of S. mucronata (Loof, 1971) Andrássy, 1984. In addition, some similar forms are described and compared with two typical Cervidellus species, and a possible morphological basis for a different grouping of species is suggested.

#### Material and methods

For each species, provenance data of the examined specimens are given with their description. Because of the unclear diagnosis and validity of *Ypsylonellus* and



Stegelletina with respect to Cervidellus, species are here classified as in Andrássy (1984) – but only for formal reasons. We do not expect that this classification will be upheld by further research, but we cannot yet propose emended generic diagnoses, and have therefore used the most recently proposed allocations in order to avoid premature nomenclatorial changes. Specimens selected for SEM-study were prepared by freeze-drying and sputter-coating, and subsequently studied with a JEOL LSM-840 electron microscope. The abbreviations  $R_{ep}$  and  $R_{dei}$  are used to denote the number of ventral annules between the lip region and respectively the excretory pore and deirids.

# Ypsylonellus similis (Thorne, 1925) Andrássy, 1984

 Stegelletina lineata (Thorne, 1925) Andrássy, 1984 n. syn.
Stegelletina mucronata (Loof, 1971) Andrássy, 1984 n. syn. (Figs 1, 2)

# MATERIAL

The following specimens from Thorne's collection were studied with light microscope : two females in a slide marked "6 *Cervidellus similis* - Ft. Collins, Colo. -Dead alfalfa - July, 1924"; one female in a slide marked "3 *Stegella lineata* - Wellsville Canyon - Soil about the roots of *B. sagitta* - March 24, 1925"; one female in a slide marked "3 a *Stegella lineata* face view - Soil about roots of *Balsamohrriza sagitta* [sic] - Wellsville Hill -March 27, 1925". The females from slide 6 are syntype specimens of *Y. similis*. One female has been designated lectotype and the other paralectotype. The slide has been reclassified as slide T-494 t in the USDA Nematode Collection, Beltsville, Maryland, U.S.A. (A.M. Golden, pers. comm.).

The females in slides 3 and 3 a are not from the type locality given by Thorne (1925) for Stegelletina lineata: " soil about roots of lichens at elevation of 12 400 feet on Mount Agassiz, Uintah Mountains, Utah ". Wellsville, Utah, lies in a valley at about 130 km from the Utah mountain peaks (both are located in the Wasatch Range), and Balsamorhiza sagittata (Pursh) Nutt. is an asteracean and not a lichen. However, the female of slide 3 a was sectioned and its lip region mounted en face as in Fig. 28 a in Thorne (1925). Dr. Thorne's records do not contain further information, but he was known to examine collected specimens as soon as possible, and as his paper of 1925 actually appeared on December 24, 1925 it is very likely that the Wellsville specimens were effectively used for the original description of S. lineata (A.M. Golden, pers. comm.). We therefore consider them to be syntypes. The female of slide 3 a was reclassified as lectotype on slide T-490 t in the USDA Nematode Collection, the specimen in slide 3 (almost completely destroyed by flattening) as paralectotype on slide T-4289 p; the specimens from Mount Agassiz are lost (A.M. Golden, pers. comm.).

We have furthermore studied eight paratype females of *S. mucronata*, kept in the Nematode Collection of the Landbouwuniversiteit Wageningen, the Netherlands, in slides WT 1213 (seven females from Eskjeret, Spitzbergen) and WT 1214 (one female from Longyearbyen, Spitzbergen) and sent to us by Dr. P. A. A. Loof at our request.

Finally, we also examined specimens of Y. similis from Spain : one female collected on 21 June 1990 by Dr. R. Peña Santiago in *Quercus rotundifolia* forest from Puerto del Pinar (alt. 1560 m), Granada province; 13 females and 10 juveniles of Y. similis collected on 21 October 1986 by the third author in grassland with *Nardus stricta* in the Igüer Valley of the Pyrenees, Huesca province; and two juveniles collected by the third author on 1 July 1987 in grassland in the Sayerri Valley of the Pyrenees, Huesca province. Four females from Igüer Valley were examined with SEM.

# Measurements

See Table 1.

# DESCRIPTION

Type specimens of Y. similis (Fig. 1 B-F): Both females in relatively good condition, although treated with a red stain resulting in conspicuous nuclei but hazy organs. Body weakly ventrally arcuate. Cuticle annulated, annules 2.8-3.0 µm wide in neck region and 3.5-3.6 µm wide at mid-body, divided by longitudinal striae that are conspicuous with the light microscope and do not appear to form continuous incisures. Lateral field with three incisures, extending to tail tip. Lip region 9 µm wide; papillae and amphid not visible. Lip margins with only very faintly refractive U-shaped elements, of which there are two in the primary axils and one in the secondary axils. Primary axils with a broad base bearing a single triangular guarding piece that is slightly shorter than the lips. Secondary axils in paralectotype with a narrower base and with two inconspicuous tines, each tine being located halfway along the anterior margin of a lip. Labial probolae 3-3.5 µm high, slender-conical to filiform, with a single bifurcation close to their tip. Cheilorhabdia only very faintly refractive, granular with flattened anterior edge. Other stoma sections not discernible. Organs in neck region only discernible in lectotype : corpus 1.6 times as long as isthmus, excretory pore opposite isthmus, deirids not seen. Vulva at about two-thirds of body length, inconspicuous. PUB 12.5 µm long in paralectotype, spermatheca not seen. Ovary discernible in lectotype only, with 14 oocytes in single file and double flexure near tip. Lectotype with a single egg measuring 46 by 18  $\mu$ m. Rectum 1.3 times as long as anal body width in lectotype. Female tail conical, with ten to eleven ventral annules and an offset, ragged tip. Phasmid at 8.5- $12 \,\mu\text{m}$  from anus or  $38-45 \,\%$  of tail length.

		Y. similis *			
	Colora	Colorado, USA Spain		ain	Spitzbergen
	Lecto- type ♀	Paralec- totype 9	Huesca 7 ♀♀	Granada 1 ♀	Paratypes 8 ♀ ♀
L	448	445	371 ± 24 (347-425)	324	369 ± 23 (326-406)
Body width	22	22	19 ± 1.4 (17.5-22)	18.5	21 ± 1.3 (19-23)
Neck length	108	104	$105 \pm 2$ (101-108)	95	101 ± 3 (97-106)
Tail length	26.5	22.5	25 ± 1.8 (23-29)	21.5	27 ± 3 (23-32)
Anal width	12.5	10	10-12	10.5	11-13
а	20.4	20.2	19.1 ± 0.6 (18.2-19.8)	17.5	$17.7 \pm 1.8$ (14.8-20.3)
b	4.2	4.3	3.5 ± 4.3 (3.3-3.9)	3.4	$3.7 \pm 0.2$ (3.3-4.0)
с	16.9	19.8	$14.6 \pm 0.4$ (13.7-15.1)	15.1	$13.9 \pm 1.0$ (12.4-15.6)
c′	2.1	2.2	2.1-2.4	2.0	2.3 ± 0.3 (1.9-2.7)
Stoma	7	6	5.5-7.5	5.5	5-7.5
Corpus	49	-	47 ± 2 (45-50)	45	48 ± 2 (45-51)
Isthmus	30	-	30 ± 2 (26-33)	26	28 ± 2 (24-31)
Bulbus	18.5	19	$16 \pm 1.5$ (14-18)	14	15-17
Nerve ring	66	-	71 ± 2 (69-75)	-	72 ± 2 (68-75)
Excretory pore	73	-	78 ± 3 (76-83)	74	78 ± 3 (71-81)
Deirid	-	-	89 ± 4 (85-96)	86	92-95
N.r. (% neck)	61	-	68 ± 2 (65-71)	-	71 ± 1 (68-73)
E.p. (% neck)	68	-	75 ± 2 (72-79)	78	76 ± 3 (71-80)
Deirid (% neck)	-	-	$89 \pm 2$ (83-90)	91	90
R <sub>ep</sub>	27	-	$30 \pm 2$ (27-32)	32	30-32
$R_{dei}$	-	-	34 ± 2 (32-37)	37	35-37
Phasmid	12	8.5	9±1.4 (7-12)	6.5	11 ± 1.3 (9-13)
Phasmid (% tail)	45	38	$35 \pm 4$ (27-41)	31	$42 \pm 3$ (38-48)

**Table 1.** Measurements (in  $\mu m$ ) of Ypsylonellus similis (Thorne, 1925) Andrássy, 1984 and its junior synonym Stegelletina mucronata (Loof, 1971) Andrássy, 1984.

(Continued next page)

# Table 1. (Continued)

		Y. similis *			
	Colora	Colorado, USA		Spain	
	Lecto- type ♀	Paralec- totype ♀	Huesca 7♀♀	Granada 1 ♀	Paratypes 8 ♀ ♀
V (%)	65	66	64-66	66	65 ± 1 (63-67)
G (%)	31	-	34 ± 6 (29-47)	24	$34 \pm 4$ (28-42)
Vagina	6	-	4-6.5	6	5-6
Rectum	16	10	14 ± 1.3 (13-17)	10	$12 \pm 1.2$ (10-14)
PUB	-	12.5	$12 \pm 1.5$ (9-14)	9.5	$11 \pm 3.1$ (8-18)
Spermatheca	-	_	11-14	10	13 ± 2.5 (10-18)

\* : Original measurements recalculated from Thorne (1925) : L = 460, a = 19.2, b = 4.2, c = 15.2, c' = 2.4, V = 65 %, nerve ring at 75 % of neck.

\*\* : Original measurements from Loof (1971) : L = 320-400, a = 16-20, b = 3.3-4.1, c = 13-15, V = 63-66 % (n = 9).

Wellsville specimens of S. lineata (Fig. 1 G, H) : Condition of both specimens too poor for measuring, the paralectotype being so severely flattened that only the lip region and tail tip reveal any features, and the lectotype having been sectioned for en face view, which resulted in the collapse of the body wall of the remainder of the specimen. Body weakly arcuate in lectotype, strongly arcuate in paralectotype. Cuticle annulated, annules 3.6 µm wide at mid-body in lectotype, divided by longitudinal striae that are conspicuous with the light microscope and do not appear to form continuous incisures. Lateral field in lectotype with three incisures, extending to tail tip. Lip region 9 µm wide in this specimen, flattened and partly obscured by dirt in the other female; papillae and amphid not visible. Lip margins in both females with distinctly refractive U-shaped elements, of which there are two in the primary axils and one in the secondary axils. Primary axils with a broad base bearing a single triangular guarding piece that is slightly shorter than the lips in the paralectotype. Secondary axils with a narrower base. Lip margin too obscure to see any tines. Labial probolae  $3 \mu m$  high in paralectotype, filiform, with a single bifurcation close to their tip. Internal organs between lip region and tail not visible or measurable in either female. Tail conical, with ten ventral annules in lectotype and with an offset, ragged tip in both females. Phasmids not seen.

Type specimens of S. mucronata (Fig. 1 Q-T) : Specimens in fairly good condition, but two females clearly flattened. Body posture varying from almost straight to ventrally curved in a C-shape. Cuticle annulated, annules 2.4-2.9  $\mu$ m wide in neck region and 2.2-3.0  $\mu$ m

wide at mid-body, divided by longitudinal striae that are conspicuous with the light microscope and do not appear to form continuous incisures. Lateral field with three incisures, extending to tail tip. Lip region 9-10 µm wide, with 6 + 4 papillae and a minute, oval amphid. Lip margins with clearly refractive U-shaped elements, of which there are two in the primary axils and one in the secondary axils. Primary axils with a broad base bearing a single triangular guarding piece that is slightly shorter than the lips. Secondary axils with a narrower base, with number of tines unclear, either due to dirt on the lip region or too faint anterior margins of the lips. Labial probolae 3-3.5 µm high, conical, with a single bifurcation close to their tip. Cheilorhabdia refractive, granular. Other stoma sections not clearly refractive. Corpus 1.5-2.1 times as long as isthmus. Excretory pore opposite isthmus, deirid at five to seven annules from excretory pore (n = 2). Vulva at about two-thirds of body length, inconspicuous. PUB 8-18 µm long, i.e. 0.4-0.8 vulval body widths. Spermatheca 10-18  $\mu$ m long (n = 5). Ovary with 10-17 oocytes in single file and with or without double flexure near tip. One paralectotype with a single egg 47 µm long. Rectum 0.8-1.2 times as long as anal body width. Female tail conical, with nine to twelve ventral annules and an offset, ragged tip. Phasmid at 9-13  $\mu$ m from anus or 38-48 % of tail length.

Spanish specimens of Y. similis (Fig. 1 A, I-P; 2 A-J) : Specimens in good condition. Body weakly to strongly ventrally arcuate. Cuticle annulated, annules 2.4- $3.2 \,\mu$ m wide in neck region and  $2.1-2.5 \,\mu$ m wide at mid-body, divided by broad, irregular longitudinal striae that are conspicuous with the light microscope and do



**Fig. 1.** Ypsylonellus similis. B-F: Neck, lip regions and tails of females from Colorado (B, C, E: lectotype; D, F: paralectotype); A, O, P: Entire female and schematized lip structures of specimens from the Pyrenees (O, P based on SEM, cf. Fig. 2A-C, E); I-N: Lip region, reproductive system, neck and tail of a female from Granada (I, J are surface views from opposite sides). – Stegelletina lineata (= Y. similis). G, H: Posterior ends of females from Wellsville (G: lectotype; H: paralectotype). – Stegelletina mucronata (= Y. similis). Q-T: Lip region, neck and tail of paratype females from Spitzbergen. (Abbreviations of P are : I = primary axil, II = secondary axil, gp = guarding piece, L<sub>i</sub> = right-lateral lip, SD<sub>i</sub> = right-subdorsal lip, SV<sub>i</sub> = right-subventral lip).

not form continuous incisures. Lateral field with three incisures, extending to tail tip. Lip region 9-10  $\mu$ m wide, with 6 + 4 papillae and small, oval amphids. Lip margins with distinctly refractive U-shaped elements, of which there are two in the primary axils and one in the secondary axils. Under SEM, it can be seen that parts of the lip margins are swollen, corresponding with the posi-

tion of the refractive elements (Fig. 1 P; 2 A-C, E). Primary axils with a broad base bearing a single triangular guarding piece that is slightly shorter than the lips. Secondary axils with a narrow base and with two inconspicuous tines, each tine being located halfway along the anterior margin of a lip. A fine incisure runs down from each tine to the labial papilla posterior to it. Labial pro-



**Fig. 2.** Ypsylonellus similis from the Pyrenees. A-C, E: Lip region (arrowhead in A points at radial ridge; dorsal side is on lower left in A, left in B, upper left in C and top in E); D: Lateral field and deirid (arrowhead); F: Vulva; G, H: Tail tips. I: Tail tip and phasmid (arrowhead);  $\mathcal{J}$ : Tail in ventral view (arrowhead is at level of phasmids). (Scale bars : 2 µm in C (A, B at same scale); 4 µm in D (J at same scale); 1 µm in E (G, H at same scale) and 2 µm in F).

bolae 2.5-3.5  $\mu$ m high, slender-conical to filiform, with a single bifurcation close to their tip. Bases of labial probolae connected by tangential ridges demarcating a rounded-triangular mouth opening. Cheilorhabdia refractive, granular, rounded or flattened. Other stoma sections not or only faintly discernible. Corpus 1.5-1.7 times as long as isthmus. Excretory pore opposite isthmus. Deirids at four or five annules from excretory pore. Vulva at about two-thirds of body length, inconspicuous with light microscope, its lips with concentric wrinkles under SEM. PUB 9-14  $\mu$ m long, or 0.5-0.7 vulval body widths; spermatheca 10-14  $\mu$ m long. Oviduct with two rows of three cells (n = 3), ovary with nine to sixteen oocytes in single file and with or without double flexure near tip. No gravid females. Rectum 0.9-1.3 times as long as anal body width. Female tail conical, with nine to thirteen ventral annules and an offset, ragged tip. Phasmid at 6.5-12  $\mu$ m from anus or 27-41 % of tail length.

## Remarks

The two type specimens of Y. similis differ clearly from the females of S. lineata and S. mucronata, as well as from the Spanish specimens, in the absence of clearly refractive U-shaped sclerotizations. This is undoubtedly due to the stain with which they were treated : very faint U-shaped structures are still visible, the cheilorhabdia are also obscure, and we know from experience that in stained specimens refractiveness is usually reduced or completely effaced. While the Wellsville females of S. lineata are in very bad condition, all characters that are visible suggest that they are conspecific with Y. similis. Thorne (1925) was probably deceived by the differences in appearance caused by the staining of the latter. The types of S. mucronata differ from those of Y. similis in the slightly thicker labial probolae, but in view of the many similarities and of the variability seen in other specimens (e.g. compare thickness of labial probolae in Fig. 2 A, B), we think this does not warrant allocation to a separate species.

We therefore consider S. lineata and S. mucronata to be junior synonyms of Y. similis. This means that Y. similis becomes the type species of Stegelletina, but in view of the uncertain validity of this genus (see below) Y. similis is not transferred at this point. As redescribed here, the species is characterized by the shape of the lip region, the wide annules with deep longitudinal striae and the ragged tail tip. It appears to be a rare species, and the exact locations where it was found suggest that it is restricted to alpine soils of the northern hemisphere.

## Ypsylonellus devimucronatus (Sumenkova, 1964) Andrássy, 1984 (Fig. 3 O-S)

#### MATERIAL

We examined one female from Longyearbyen, Spitzbergen with light microscope; it is kept in slide WT 1214 of the Nematode Collection of the Landbouwuniversiteit Wageningen (slide also contains paratypes of *S. mucronata*).

Measurements

See Table 2.

Description

Female in fairly good condition. Cuticle annulated, annules  $1.9 \ \mu m$  wide in neck region,  $1.8 \ \mu m$  wide at

mid-body, without longitudinal striae under light microscope. Lateral field with three incisures, extending to tail tip. Lip region 8.5  $\mu$ m wide, with 6 + 4 papillae and small amphids. Lip margins with distinctly refractive U-shaped elements, of which there are two in the primary axils and one in the secondary axils. Primary axils with a broad base bearing a single triangular guarding piece that is about half as long as the lips. Secondary axils with a narrow base; no tines discernible but lips do appear to be indented halfway along their anterior edge. Labial probolae 3  $\mu$ m high, conical, with a single bifurcation close to their tip. Cheilorhabdia refractive, small and granular. Other stoma sections only faintly discernible. Corpus 1.8 times as long as isthmus, excretory pore opposite isthmus, deirids not seen. Vulva at about twothirds of body length, inconspicuous. PUB 19.5 µm long, or 0.8 vulval body widths; spermatheca 21 µm long. Oviduct with two rows of three cells; ovary with fourteen oocytes in single file and with a double flexure. No egg. Rectum 1.0 time as long as anal body width. Female tail conical, with 16 ventral annules and an offset, ragged tip. Phasmid at 9 µm from anus or 31 % of tail length.

## Remarks

This female agrees fairly well with the description by Sumenkova (1964), but differs in the slightly larger size  $(L = 424 \ \mu m vs \ 262-370 \ \mu m in female paratypes), pres$ ence of three lateral lines along most of the body vs four, and larger annules ( $R_{ep} = 49 vs 69$  counted on Fig. 1 c in Sumenkova, 1964; annule width 1.8-1.9 µm vs about 1.0 µm on Fig. 1 in Sumenkova, 1964). The difference in size is negligible, especially because two of the three males found by Sumenkova (1964) had  $L = 441 \,\mu m$ and  $L = 394 \,\mu m$ . The difference in lateral lines could be due to a slight separation between two wings in a lateral field still having only three incisures, rather than the presence of four true incisures. This is suggested by the fact that Sumenkova describes the female tail as having only three lateral lines instead of four. The difference in annule size, finally, might be due to incorrect representation of their width in Sumenkova (1964). Thus, the three differences found between the specimen from Spitzbergen and the description by Sumenkova (1964) need confirmation, and we therefore identify the specimen from Spitzbergen as Y. devimucronatus, until proven otherwise.

# Ypsylonellus cf. devimucronatus (Sumenkova, 1964) Andrássy, 1984 (Figs 3 I-N)

# Material

We examined the following specimens with light microscope : one female in a slide from Dr. Thorne's col-

	Y. devi- mucronatus *		Y. sp. cf. devimucronatus *		Y. sp. cf. insubricus **	
	Spitzbergen	Utah	Samos	Granada	Sen	legal
	1 ♀	1 ♀	2 º º	1 º	1 ♀	1 ਹੈ
L Body width Neck length Tail length Anal width a	424 22.5 115 29 11.5 18.8	394  104 	374-389 18-19 97-98 22 11-12 19.7-20.8	296 16.5 93 21 10 18.0	398 22.5 109 32 12.5 17 7	423 22 115 31 16.5 19.2
b	3.7	3.8	3.9-4.0	3.2	3.7	3.7
c	14.6	16.4	17.0-17.7	14.1	12.4	13.6
c'	2.5	-	1.8-2.0	2.1	2.6	1.9
Stoma	6	6	5.5-6	6	6	8.5
Corpus	61.5	50	49-52	45	62	60
Isthmus	34	26.5	26-30	22.5	26	28
Bulbus	14	17	14-15	14	16	15.5
Nerve ring	79	68	70-75	61	70	78
Excretory pore Deirid N.r. (% neck) E.p. (% neck) Deirid (% neck)	82 69 71	70 	76 80-84 71-77 77-78 82-86	64 76 66 69 82	75 91 64 69 83	80 98 68 70 85
R <sub>ep</sub>	49	39	41-42	39	34	38
R <sub>dei</sub>	-	-	47-49	47	41	46
Phasmid	9	-	5-7	9	11	16
Phasmid (% tail)	31	-	23-32	43	34	52
G (%)/Spicules Rectum/Gubernaculum PUB Spermatheca	34 12 19.5 21	- 15	23-32 13 12-13 13-16	43 10.5 11.5 11	65 37 16 21 23	20 9 -

**Table 2.** Measurements in µm of Ypsylonellus devinucronatus (Sumenkova, 1964) Andrássy, 1984; Y. sp. cf. devinucronatus and Y. sp. cf. insubricus (Steiner, 1914) Andrássy, 1984.

\* : Original measurements of Sumenkova (1964) : 9 : L = 262-370, a = 12.8-18.3, b = 3.2-4.2, c = 11.1-13.8, V = 61-67 % (n = 9); 33 : L = 333-441, a = 21.8-27.7, b = 3.3-3.7, c = 16.5-18.7, spicules = 16-20, gubernaculum = 10-13  $\mu$ m (n = 3).

\*\* : Original measurements of Steiner (1914) : 1  $\circ$  : L = 381, body width = 16, neck = 104, tail = 25, a = 24, b = 3.6, c = 15, V = 65 \%.

lection marked : "6 a *Cervidellus similis* 1  $\circ$  - Midvale, Utah 233 - March 5, 1936"; two females collected on Samos, Greece by Dr. S. Boström and described in Boström (1991); one female collected on 21 June 1990 by Dr. R. Peña Santiago in oak forest, Puerto del Pinar, Granada province, Spain.

# Measurements

See Table 2.

# Description

Specimen from Utah: Specimen in poor condition: flattened and broken slightly anterior to vulva. Body strongly ventrally arcuate in neck region, straight elsewhere. Cuticle annulated, annules 2.0  $\mu$ m wide at midbody (not measured in neck region because of curvature), without discernible longitudinal striae under light microscope. Lateral field not clear. Lip region affected by flattening. Lip margins with refractive U-shaped elements, of which there are two in the primary axils and one in the secondary axils. Primary axils with a broad base bearing a single triangular guarding piece that is slightly shorter than the lips. Secondary axils with a narrower base; tines or lip edges not seen. Labial probolae 3  $\mu$ m high, conical, with a single bifurcation close to their tip. Cheilorhabdia and other stoma sections unclear. Corpus 1.9 times as long as isthmus, excretory pore opposite isthmus, deirids not seen. Vulva at about two-thirds of body length, its lips protruding. PUB, spermatheca and ovary not discernible. Tail tip conical with ragged, offset tip. Number of ventral annules and phasmid not seen.



**Fig. 3.** Ypsylonellus cf. insubricus from Senegal. A, B: Schematized lip structures (redrawn from SEM of male, cf. Fig. 4 A-C); C: Female reproductive system; D: Neck region of female; E: Female tail; F: Male posterior end; G, H: Female anterior end. – Ypsylonellus sp. cf. devimucronatus female from Granada. I: Neck region; J-L: Lip region (J; K are views from opposite sides); M: Reproductive system; N: Tail. Y. devimucronatus female from Spitzbergen. O: Neck region; P, Q: Anterior end; R: reproductive system; S: Tail. (Abbreviations of A are: I = primary axil, II = secondary axil, gp = guarding piece, L<sub>t</sub> = right-lateral lip, SD<sub>t</sub> = right-subdorsal lip, SV<sub>t</sub> = right-subventral lip).

Specimens from Samos : Two females in good condition. Body very weakly ventrally curved. Cuticle annulated, annules 1.8-1.9  $\mu$ m wide in neck region and 1.7-1.8  $\mu$ m wide at mid-body, under light microscope without longitudinal striae. Lateral field with three incisures, extending to tail tip. Lip region 8.5-9  $\mu$ m wide, with 6 + 4 papillae and small amphids. Lip margins with distinctly refractive U-shaped elements, of which there are two in the primary axils and one in the secondary axils. Primary axils with a broad base bearing a single trian-

gular guarding piece that is slightly shorter than the lips. Secondary axils with a narrow base and probably with two inconspicuous tines. Labial probolae 3-3.5 µm high, slender-conical, with a single bifurcation close to their tip. Cheilorhabdia refractive, granular, flattened. Five more stoma sections faintly discernible. Corpus 1.7-2.0 times as long as isthmus. Excretory pore opposite isthmus. Deirids at six or seven annules from excretory pore. Vulva at about two-thirds of body length, protruding. PUB 12-12.5 µm long, or 0.6 vulval body widths; spermatheca 13-16 µm long. Ovary with twelve oocytes in single file, without double flexure. No eggs. Rectum 1.1-1.2 times as long as anal body width. Female tail conical, with ten to fifteen ventral annules and an offset, ragged tip. Phasmid at 5-7 µm from anus or 23-32 % of tail length.

Specimen from Spain : Female in fairly good condition. Body moderately ventrally curved. Cuticle annulated, annules 1.5 µm wide in neck region and 1.6 µm wide at mid-body, under light microscope without longitudinal striae. Lateral field with three incisures, extending to tail tip. Lip region 7.5  $\mu$ m wide, with 6 + 4 papillae and small amphids. Lip margins with distinctly refractive U-shaped elements, of which there are two in the primary axils and one in the secondary axils. Primary axils with a broad base bearing a single triangular guarding piece that is slightly shorter than the lips. Secondary axils with a narrow base and with two inconspicuous tines, each tine being located halfway along the anterior margin of a lip. Labial probolae 3.5 µm high, slenderconical, with a single bifurcation close to their tip. Cheilorhabdia refractive, granular, flattened. Other stoma sections not discernible. Corpus 2.0 times as long as isthmus. Excretory pore opposite isthmus, deirids at eight annules from excretory pore. Vulva at about twothirds of body length, inconspicuous. PUB 11.5 µm long, or 0.7 vulval body widths; spermatheca 11  $\mu$ m long. Ovary with eleven oocytes in single file, without double flexure. No eggs. Rectum as long as anal body width. Female tail conical, with thirteen ventral annules and an offset, ragged tip. Phasmid at 9 µm from anus or 43 % of tail length.

# Remarks

Like the female treated in the previous paragraph, these animals are undoubtedly close to Y. devimucronatus. We are not inclined to identify them as such, however, because here  $R_{ep}$  is even lower (39 vs 49 in Spitzbergen female and 69 in Fig. 1 c in Sumenkova, 1964), and also the corpus is not as slender as in the Spitzbergen female or as suggested in Fig. 1 c in Sumenkova (1964). Without certainty about the exact diagnosis of Y. devimucronatus, we prefer to leave the identification of these specimens open for now. The females from Samos were identified as Y. devimucronatus by Boström (1991), but it must be noted that his Fig. 3 gives SEMpictures that disagree with our observations of the lip region and tail of his specimens. As the samples studied by Boström (1991) contained both *Ypsylonellus* sp. cf. *devimucronatus* and *Cervidellus neftasiensis* Boström, 1986, we think there may have been a mix-up of specimens during preparation for SEM, so that the pictures in his Fig. 3 would actually be of *C. neftasiensis*. We have seen five females of *C. neftasiensis* from Samos, and their morphology under light microscope is quite consistent with this assumption.

## Ypsylonellus cf. insubricus (Steiner, 1914) Andrássy, 1984 (Figs 3 A-F; 4 A-E)

# MATERIAL

We studied one female, one male and one juvenile from nutrient-poor soil at the "Centre pour le Développement de l'Horticulture ", Cambérène, Senegal (sample 1014 : cf. De Ley, 1992) with light microscope. The male broke at one-third its length during transfer to slide (L in Table 2 was established by adding up the lengths of the two separate pieces), and its neck region was studied with SEM.

# Measurements

See Table 2.

# DESCRIPTION

Female in good condition, male broken but otherwise not visibly deformed. Cuticle annulated, annules 2.3 µm wide in neck region, 1.8-2.3 µm wide at mid-body, with shallow longitudinal striae that are only visible with SEM and do not form continuous incisures. Lateral field with three incisures under light microscope, extending to tail tip. Under SEM, however, the three incisures demarcating the two wings of each lateral field prove to be accompanied by two more incisures demarcating two gullets" that are divided by the circumferential striae of the annules. Lip region 9-9.5  $\mu$ m wide, with 6 + 4 papillae and small, oval amphids. Lip margins with distinctly refractive U-shaped elements, of which there are two in the primary axils but none in the secondary axils. Primary axils with a broad base bearing a single triangular guarding piece that is shorter than the lips. Secondary axils with a narrow base and two pairs of rounded tines. A shallow incisure runs down to the corresponding labial papilla between the tip of each lip and the tine lying next to this tip. Labial probolae 4  $\mu$ m high, conical, with a single bifurcation close to their tip. The bases of the labial probolae appear to connect with tangential and radial ridges, although these are partly hidden by the lips overhanging them (arrow in Fig. 4 E). Cheilorhabdia refractive, small and granular. Five other, lightly sclerotized stoma sections distinguishable. Corpus 2.1-2.4 times as long as isthmus. Excretory pore opposite isthmus, deirids seven to eight annules from excretory pore. Female with vulva at about two-thirds of body length, slightly protruding. PUB 21 µm long, or



**Fig. 4.** Ypsylonellus cf. insubricus male from Senegal. A-C : Lip region (dorsal side on right in A, on top in B, C); D : Lateral field; E : Mouth opening and radial ridges (arrow). (Scale bars : A-C = 1  $\mu$ m; D = 2  $\mu$ m; E : double scale of C).

0.9 vulval body widths; spermatheca 23  $\mu$ m long and filled with small sperm cells 1-2  $\mu$ m in diameter. Ovary with 22 oocytes, of which six in double file just posterior to the double flexure. No egg. Rectum 1.3 times as long as anal body width. Female tail conical, dorsally convex just anterior to the acute tip, with thirteen ventral annules. Phasmid at 11  $\mu$ m from anus or 34 % of tail length.

Male with reflexed testis tip. Manubrium of spicules slender. Genital papillae distributed as follows : two subventral pairs preanally at 35 and 61  $\mu$ m from anus, one subventral adanal pair, a single midventral papilla on the precloacal lip, two pairs of papillae on the tail between anus and phasmids, and three pairs near the narrowly rounded tail tip.

# Remarks

Our specimens agree fairly well with the original description of Y. *insubricus*, but the female from Senegal has fewer ventral tail annules (13 vs 24 on Abb. 4 in

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Steiner, 1914) a less offset tail tip, and a different lip region (Steiner, 1914 : Abb. 3 depicts a lip region with sclerotized bars instead of U's, and with filiform instead of conical labial probolae). However, the annules and tip of the tail could have been drawn incorrectly, and the lip region was very probably misinterpreted due to lower magnifications available to Dr. G. Steiner. We consider Y. insubricus a species inquirenda because its original description lacks sufficient detail to resolve its precise characters, and therefore prefer for the moment to abstain from positively identifying the Senegalese specimens as this species.

# Cervidellus serratus (Thorne, 1925) Thorne, 1937 (Figs 5 A-F)

# MATERIAL

Specimens collected in Spain by the third author : one female from *Pinus nigra* forest at Añorbe, Navarra forest

(sampled on 24 November 1986); five females from *Festuca paniculata* grassland in Igüer Valley in the Pyrenees, Huesca province (sampled on 11 March 1987); and five females from *Festuca eskia* grassland in Sayerri Valley in the Pyrenees, Huesca province (one female from a sample taken on 21 October 1986; resp. three females and one female from two samples taken on 12 May 1987). Specimens studied only with light microscope.

#### Measurements

See Table 3.

## DESCRIPTION

Condition of specimens variable. Body straight to moderately ventrally arcuate. Cuticle annulated, annules 1.7-2.3 µm in neck region and 1.5-1.7 µm wide at midbody, with faintly visible longitudinal striae under light microscope. Lateral field with three incisures, extending to phasmid. Lip region 11-13  $\mu$ m wide, with 6 + 4 papillae and inconspicuous amphid. Lip margins with thirty U-shaped refractive elements (five per axil) alternating with vaguely visible tines (five per lip), without differentiation between primary and secondary axils. Labial probolae 3.5-5 µm high, slender-conical to filiform, with a single bifurcation near tip. Cheilorhabdia granular, rounded or flattened. Other stoma sections only faintly visible. Corpus 1.9-2.2 times as long as isthmus. Excretory pore opposite isthmus, deirids at seven to ten annules from excretory pore (n = 5). Vulva at almost two-thirds of body length, inconspicuous. PUB 25-46 µm long, or 1.2-2.2 vulval body widhts; spermatheca 20-33 µm long, consisting of an anterior sac with four pairs of comparatively swollen and rounded cells (n = 7), and a posterior "stem" with eight more contiguous cells (n = 3). Oviduct with eight cells (n = 3)2), ovary with 12-21 oocytes of which none to ten in double file near tip. One female carrying a single egg measuring 51 by 18 µm. Rectum 1.0-1.4 times as long as anal body width. Tail conical, with 16-22 ventral annules and acute, confluent tip. Phasmid at 11.5-17.5 µm from anus or 37-53 % of tail length.

# Remarks

Our specimens agree with the animals described from the U.S.A. and Sweden by Boström (1986) in all respects but one : we have not found any males. This can be explained by the fact that our eleven females came from five different samples, and the reasonable assumption that females are more common than males in C. *serratus*.

## Cervidellus neftasiensis Boström, 1986 (Fig. 5 G-K)

# MATERIAL

Five females collected by the third author on 1 July 1987 from humid soil at a watering-place for cattle in

Sayerri Valley in the Pyrenees, Huesca Province, Spain (studied only with light microscope).

## Measurements

See Table 3.

# Description

Condition of specimens variable. Body straight to strongly ventrally arcuate. Cuticle annulated, annules 1.4-1.8 µm wide in neck region and 1.2-1.6 µm wide at mid-body, without visible longitudinal striae under light microscope. Lateral field with three incisures, the inner one extending slightly beyond phasmid. Lip region 10-11  $\mu$ m wide, with 6 + 4 papillae and inconspicuous amphid. Lip margins with thirty U-shaped refractive elements (five per axil) alternating with vaguely visible tines (five per lip), without differentiation between primary and secondary axils. Labial probolae 4-5 µm high, slender-conical to filiform, with a single bifurcation near tip. Cheilorhabdia granular, rounded or flattened. Other stoma sections only faintly visible. Corpus 1.7-2.3 times as long as isthmus. Excretory pore opposite isthmus, deirids at nine to eleven annules from excretory pore (n = 3). Vulva at almost two-thirds of body length, inconspicuous. PUB 11.5-17.5 µm long, or 0.5-0.7 vulval body widths; spermatheca 7.5-13 µm long, with uncertain number of cells. Oviduct cells unclear, ovary with 8-15 oocytes of which up to four in double file near tip. No gravid females. Rectum 0.8-1.3 times as long as anal body width. Tail conical, with 16-21 ventral annules and simple, acute tip. Phasmid at 12-13  $\mu$ m from anus or 39-50 % of tail length.

# Remarks

Our specimens do not agree completely with *C. neftasiensis* as originally described (from Tunisia). Thus, Boström (1986) gave body lengths of 243-290  $\mu$ m for the type specimens, while our animals have sizes of 308-377. However, Boström (1991) did identify a population with intermediate body size from Samos (L = 271-307  $\mu$ m) as *C. neftasiensis*. Another difference is the absolute size of the PUB : Boström (1986, 1991) found PUB lengths of 8-12  $\mu$ m (*vs* 11.5-17.5  $\mu$ m in our females) - although there is no difference in relative size (0.5-0.7 vulval body widths in both his and our specimens).

C. neftasiensis was originally separated from C. serratus on the basis of smaller body size (type specimens of both species resp. 243-290  $\mu$ m and 320-420  $\mu$ m long). Upon finding populations with intermediate body lengths, however, Boström (1991, 1992) provisionally differentiated between the two species on the basis of PUB length (8-12  $\mu$ m or 0.5-0.7 body widths in C. neftasiensis vs 17-37  $\mu$ m or 0.9-1.8 body widths in C. serratus).

		C. serratus		
	Añorbe, Navarra 1 ♀	Igüer Valley, Huesca 4♀♀	Sayerri Valley, Huesca 5 ♀ ♀	Sayerri Valley, Huesca 5 ♀ ♀
L	343	372-410	409 ± 20 (378-428)	333 ± 25 (308-377)
Body width	24	21-22	23-25	22 ± 2.6 (19-25)
Neck length	103	112-117	117 ± 4 (110-122)	$104 \pm 5$ (99-114)
Tail length	24	31-33	33-36	26 ± 2.7 (22-30)
Anal width	12.5	12-13	12-14	$14 \pm 1.8$ (12-17)
а	14.3	17.3-17.7	$16.9 \pm 1.2$ (15.7-18.3)	$14.9 \pm 1.0$ (13.5-16.2)
b	3.3	3.3-3.7	3.3-3.6	3.1-3.3
c	14.3	12.0-13.4	$12.0 \pm 0.9$ (10.8-12.9)	$12.8 \pm 1.1$ (11.4-14.0)
c'	1.9	2.5-2.7	$2.7 \pm 0.2$ (2.4-2.8)	$2.0 \pm 0.2$ (1.7-2.3)
Stoma	7	7-8	6-8	7-8.5
Corpus	50	57-62	58±3 (55-62)	51 ± 3 (47-55)
Isthmus	27	28-30	27-29	26 ± 1.9 (23-29)
Bulbus	15	14-16	$17 \pm 1.3$ (16-20)	15-17
Nerve ring	63	70-88	73 ± 5 (65-77)	62 ± 4 (56-69)
Excretory pore	64	78-86	81 ± 6 (73-87)	69 ± 5 (65-77)
Deirid	?	92-98	96±6 (88-102)	84 ± 7 (78-93)
N.r. (% neck)	61	62-75	62 ± 3 (58-66)	60 ± 3 (55-62)
E.p. (% neck)	62	70-74	69 ± 3 (66-74)	67 ± 3 (64-71)
Deirid (% neck)	?	82-85	82 ± 4 (79-87)	80 ± 2 (76-82)
R <sub>ep</sub>	32	37-39	34-37	36±1 (34-38)
$R_{dei}$	-	46-47	$44 \pm 2$ (42-46)	46 ± 2 (43-49)
Phasmid	12	11-14	$14 \pm 1.7$ (12-18)	12-13
Phasmid (% tail)	50	37-43	42 ± 6 (37-53)	47 ± 5 (43-53)

**Table 3.** Measurements in  $\mu m$  of Cervidellus serratus (Thorne, 1925) Thorne, 1937 and Cervidellus neftasiensis Boström, 1986 from northern Spain.

(Continued next page)

		C. serratus			
	Añorbe, Navarra 1♀	Igüer Valley, Huesca 4♀♀	Sayerri Valley, Huesca 5 ♀ ♀	Sayerri Valley, Huesca 5 Q Q	
V (%)	61	62-66	$63 \pm 2$ (61-66)	64-66	
G (%)	41	36-39	31 ± 4 (26-38)	29 ± 4 (23-35)	
Vagina	6	5	5-7	5-7	
Rectum	13	15-17	14-17	$14 \pm 1.5$ (12-16)	
PUB	46	33-35	32 ± 4 (25-36)	$14 \pm 2.4$ (11-18)	
Spermatheca	31	24-31	$26 \pm 4.6$ (20-33)	$10 \pm 2.1$ (7-13)	

#### Table 3. (Continued)



**Fig. 5.** Cervidellus serratus from Spain. A, B : Lip region; C : Tail; D : Vagina and PUB; E, F : Spermathecae. – C. neftasiensis from Spain. G, H : Lip region; I : Spermatheca;  $\mathcal{J}$  : Vagina and PUB; K : Tail.

On the basis of relative PUB length, our specimens are identified as *C. neftasiensis*. Validity of this species is supported by comparison of our specimens of *C. neftasiensis* and *C. serratus*: the latter have a clearly longer PUB (25-46  $\mu$ m or 1.2-2.2 body widths) and spermatheca (20-33  $\mu$ m), and the spermatheca is apparently also structurally different, consisting of four pairs of clearly offset cells anteriorly and four pairs of more confluent cells posteriorly in our *C. serratus vs* an uncertain number of cells that are all confluent in our *C. neftasiensis*.

A complication arises upon consideration of C. arenosus Andrássy, 1987 : this has a body length of 420440  $\mu$ m, while the PUB is said to be absent. In our opinion, body length is untrustworthy as a diagnostic feature, and in view of the intermediate specimens from Samos and from our samples, *C. arenosus* could well be conspecific with *C. neftasiensis*.

#### Discussion

Apart from highlighting some difficulties in species identification in this group of animals, our observations also throw further doubts on the status of *Stegelletina*. Thus, it now appears that the type species of the latter is synonymous with a species allocated in *Ypsylonellus* by

Andrássy (1984). Also, comparison of Y. similis (which was found to have prominent longitudinal striae under light microscope) with the other Ypsylonellus species described here (which do not have distinct longitudinal striae under light microscope) shows that they are probably quite closely related, having similar tails and lip regions. This once again suggests that presence or absence of longitudinal striae is not a valid character for genus diagnosis in this group of species (Boström, 1987). Furthermore, contrary to Fig. 28 a in Thorne (1925), the lectotype of S. lineata proves to have longitudinal striae that do not form continuous lines. This shows that it is most probably also unwarranted to diagnose Stegelletina by the presence of continuous striae.

Upon comparison of the anterior morphology of the Ypsylonellus spp. described here with e.g. our Cervidellus serratus and C. neftasiensis, we think the structure of the lip margins may be a much better diagnostic feature (see e.g. Fig. 2 A, B in Boström, 1986; Fig. 5 A, D in Rashid et al., 1989 for SEM of the last two species). Our Ypsylonellus specimens all have primary axils with a single guarding piece and no other processes along the lip margin, while the Cervidellus species have more or less symmetrical lips with five tines, or in other words primary axils containing four tines each. Under light microscope, in the first group of species each primary axil appears as two U-shaped refractive elements (corresponding with the folds of the lip margin forming the single guarding piece) and each secondary axil contains none or just one U-shaped element (tines not resulting in refractive effects). In the two *Cervidellus* species, on the other hand, both the primary and secondary axils each have five U-shaped elements under light microscope : all tines are separated from one another by refractive folds of the lip margins, resulting in the typical, serrate aspect of the lips.

It would thus seem that *Ypsylonellus* is disgnostically well-founded while all grounds for retaining Stegelletina are effaced, since both its diagnostic character (longitudinal striae) and its type species (S. lineata) are invalidated. However, a revised classification is not yet possible at this point, *i.a.* because the type species of Ypsylonellus - Y. vexilliger (de Man, 1880) Andrássy, 1984 – also needs to be re-examined to check the precise structure of its lips. This point must not be overlooked, because there is a definite possibility that Y. vexilliger is actually similar or synonymous to a Cervidellus species (P. A. A. Loof and T. Bongers, pers. comm.; De Ley, unpubl.), as is also suggested to us by de Man's descriptions and illustrations (cf. Fig. 60 in de Man, 1884). In that case, Ypsylonellus could have to be rejected and Stegelletina retained. In addition, there remain quite a number of other species to be examined and taken into account, and more time and study are needed before a solid revision of the whole group can be attempted.

A final remark must be made on oviduct structure : as far as could be discerned in our *Ypsylonellus* specimens,

the oviduct appeared to consist of three pairs of cells, while in *Cervidellus serratus* we saw four pairs. This feature could be of importance above species level, but the oviduct structure of many more Cephalobidae will have to be examined before it can be evaluated taxonomically.

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