

Redescription of *Cervidellus vexilliger* (de Man, 1880) Thorne, 1937 (Nematoda : Cephalobidae) and taxonomical consequences

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Summary – *Cervidellus vexilliger*, presently the type species of the genus *Ypsylonellus*, is redescribed and a neotype selected from specimens in a sample collected at the type locality: the Haagse Bos, the Netherlands. The sample also yielded a second very similar species, agreeing with the diagnosis of *C. neftasiensis*. The original description of *C. vexilliger* and the new specimens described from the type locality, suggest that *C. vexilliger* is conspecific with *C. serratus*. *C. serratus* is therefore synonymized with *C. vexilliger* and *Ypsylonellus* is synonymized with *Cervidellus*. Differential diagnoses and a provisional classification of the genera *Cervidellus* and *Stegelletina* are presented.

Résumé – **Redescription de *Cervidellus vexilliger* (de Man, 1880) Thorne, 1937 (Nematoda : Cephalobidae) et implications taxonomiques** – *Cervidellus vexilliger*, actuellement espèce type du genre *Ypsylonellus*, est redécrit et un néotype est désigné parmi les spécimens d'un échantillon collecté dans la localité type: Haagse Bos, Pays-Bas. Une autre espèce très proche, correspondant à la diagnose de *C. neftasiensis*, était également présente dans cet échantillon. La description originale de *C. vexilliger* et les nouveaux spécimens provenant de la localité type suggèrent que *C. vexilliger* est conspécifique de *C. serratus*. *C. serratus* est donc synonymisé avec *C. vexilliger* et *Ypsylonellus* est synonymisé avec *Cervidellus*. Des diagnoses différentielles et une classification provisoire sont proposées pour les genres *Cervidellus* et *Stegelletina*.

Key-words : *Cervidellus*, nematodes, SEM, *Stegelletina*, taxonomy, *Ypsylonellus*.

Two recent papers have reported on the detailed organisation of the anterior region in different species of the genus *Ypsylonellus* Andrassy, 1984 (Boström, 1993; De Ley *et al.*, 1994). The pattern of elements in the lip region of *Ypsylonellus* was found to be clearly different from that of some species of *Cervidellus* Thorne, 1937 and *Stegelletina* Andrassy, 1984, described with the aid of scanning electron microscope (SEM) in recent years (Boström, 1986, 1987; De Clerck & De Ley, 1990; De Ley *et al.*, 1990; De Ley & Vandebroek, 1992). These findings established *Ypsylonellus* as a genus of separate status.

However, as De Ley *et al.* (1994) pointed out, the type species of *Ypsylonellus*, *Y. vexilliger* (de Man, 1880) Andrassy, 1984, remained to be re-examined, and there were reasons to believe that *Y. vexilliger* is conspecific with a species of *Cervidellus* (P. A. A. Loof and T. Bongers, pers. comm.). The type material of *C. vexilliger* is unfortunately lost (P. A. A. Loof, pers. comm.), so a new sampling had to be performed at the type locality: the " Haagse Bos ", the Netherlands.

As de Man's original descriptions (1880, 1884) of *Cephalobus vexilliger* are not easily obtained, his more extensive description (in German) and drawings of 1884 are therefore reproduced here in *facsimile* (Figs 1, 2). The description of *C. vexilliger* can thus be com-

pared with the species found in the type locality and described here.

This paper is part of an ongoing revision of the genera *Cervidellus*, *Ypsylonellus* and *Stegelletina*. Re-examination of the type specimens of many other species is required to resolve the taxonomy of these genera, and thus only a provisional classification is presented.

On 24 April 1993, approximately 1 dm³ of soil was collected from the Haagse Bos, the Netherlands, by the second author. The soil was extracted by centrifugation (one half of the sample with Ludox AS and the other half with MgSO₄). This sample yielded two very similar species. One is redescribed here as *Cervidellus vexilliger* (de Man, 1880) Thorne, 1937, and the other identified as *C. neftasiensis* Boström, 1986. The implications on specific and generic diagnoses are discussed. Live specimens were either immediately fixed with a hot formalin/glycerin (4:1) solution or transferred to 1 % water agar plates sprinkled with soil particles. Establishment of cultures on agar was not successful. Fixed specimens were transferred to and mounted in anhydrous glycerin. For SEM studies, four females, two males and two juveniles of *C. vexilliger* and three females of *C. neftasiensis* were selected. They were prepared by freeze-drying, sputter-coated and subsequently studied with a JEOL LSM-840 SEM. Scale bars in the electronmicrographs are as pro-

vided by the SEM, and can have an error of up to 10 %. Specimens are known to shrink during preparation for SEM, and especially near the two body ends where dimensions may be reduced by as much as 30 %. Apparent disagreement between LM measurements and SEM appearance is due to the combination of these distortions, and not to measurement errors. The abbreviations R_{ep} and R_{dei} are used to denote the number of ventral annules between the lip region and the excretory pore and deirids, respectively.

***Cervidellus vexilliger* (de Man, 1880)**

Thorne, 1937

- = *Cephalobus vexilliger* de Man, 1880
 = *Cephalobus (Acrobeles) vexilliger* (de Man, 1880) de Man, 1921
 = *Acrobeles vexilliger* (de Man, 1880) Thorne, 1925
 = *Ypsylonellus vexilliger* (de Man, 1880) Andrassy, 1984 (Figs 3, 4, 5, 6A-B)

MEASUREMENTS

See Table 1.

DESCRIPTION

Female: Body generally slightly arcuate ventrad or almost straight. Cuticle annulated, annules 1.5–2.1 μm wide in neck region, 1.4–1.8 μm at mid-body. Lateral field with three incisures, of which the middle one stops at or anterior to the phasmid, and the two outer ones extend somewhat further. Lip region 10–13 μm wide, with 6 + 4 papillae and two amphids. Lip margins with 30 U-shaped refractive elements (five per axil) alternating with rounded tines (five per lip) that are only faintly visible with LM. Central tine with apical incisure. No differentiation between primary and secondary axils. Labial probolae 4–5.5 μm high, slender-conical with a single bifurcation in the anterior one-fourth. Cheil-rhabdia granular, rounded; other stomatal elements less clearly discernible. Corpus 2.1–2.9 times longer than isthmus. Excretory pore opposite isthmus. Vulva at about two-thirds of body length, vulval lips slightly or conspicuously protruding. Two females each carrying one intra-uterine egg measuring $39 \times 15 \mu\text{m}$ and $47 \times 20 \mu\text{m}$, respectively. Post-vulval uterine branch (PUB) 21–47 μm long, or 0.9–1.9 body widths (BW). Spermatheca 27–48 μm long, consisting of sixteen cells: eight smaller, contiguous cells that form a proximal stem and eight larger, offset cells that form a swollen distal sac or cluster. Sperm, if present, is found within the distal part. Rectum about one anal body width (ABW) long. Tail conoid with a pointed, acute terminus. Phasmids with wide opening and distinct pouch, at 39–50 % of tail length.

Male: Body generally slightly arcuate ventrad. Cuticle annulated, annules 1.5–1.9 μm wide in neck region, 1.3–1.6 μm at midbody. Lateral field with three incisures,

Table 1. Measurements (in μm) of *Cervidellus vexilliger* (de Man, 1880) Thorne, 1937 and *Cervidellus neftasiensis* Boström, 1986 from "Haagse Bos", the Netherlands.

	Neotype	<i>C. vexilliger</i>		<i>C. neftasiensis</i>
		48 females	14 males	8 females
Body length	356	368 \pm 3 (326–411)	344 \pm 7 (289–388)	307 \pm 5 (285–323)
Body width	21	23 \pm 0.2 (20–25)	21 \pm 0.3 (19–22)	20 \pm 0.5 (17–22)
Pharynx length	96	98 \pm 1 (87–101)	93 \pm 1.4 (85–99)	94 \pm 1 (88–101)
Tail length	32	32 \pm 0.3 (27–35)	33 \pm 0.7 (28–36)	26 \pm 0.4 (24–27)
V-A/T*	3.1	3.1 \pm 0.03 (2.4–3.5)		3.2 \pm 0.06 (3.0–3.5)
Anal body width	14	14 \pm 0.1 (12–15)	16 \pm 0.2 (14–17)	12 \pm 0.3 (11–13)
a	17	16 \pm 0.3 (15–17)	17 \pm 0.3 (15–19)	16 \pm 0.3 (15–17)
b	3.7	3.8 \pm 0.02 (3.5–4.1)	3.7 \pm 0.04 (3.4–3.9)	3.3 \pm 0.07 (3.1–3.7)
c	11.1	11.6 \pm 0.1 (10.5–12.9)	10.6 \pm 0.2 (10.0–12.3)	12.0 \pm 0.2 (11.5–12.9)
c'	2.3	2.4 \pm 0.02 (1.9–2.6)	2.0 \pm 0.05 (1.7–2.3)	2.2 \pm 0.04 (2.0–2.3)
V (%)	65	65 \pm 0.1 (63–66)		65 \pm 0.2 (65–66)
T (%)			59 \pm 0.8 (56–63)	
stoma	7	7.1 \pm 0.1 (6–8)	6.7 \pm 0.1 (6–7)	6.3 \pm 0.3 (5–7)
corpus	55	59 \pm 0.5 (55–65)	58 \pm 0.7 (54–60)	53 \pm 1 (48–58)
isthmus	25	24 \pm 0.4 (19–28)	23 \pm 0.5 (21–24)	27 \pm 1.5 (23–32)
bulbus	16	16 \pm 0.2 (14–19)	15 \pm 0.2 (14–17)	15 \pm 0.3 (14–16)
nerve ring	63	63 \pm 0.6 (55–69)	60 \pm 1.7 (55–67)	58 \pm 1.5 (54–67)
excretory pore	69	71 \pm 0.7 (60–79)	65 \pm 2.6 (50–76)	62 \pm 1.1 (57–64)
deirid	82	86 \pm 0.8 (76–94)	81 \pm 4.0 (60–91)	75 \pm 1.4 (69–81)
R_{ep}	32	34 \pm 0.3 (29–37)	33 \pm 0.5 (30–34)	32 \pm 1.0 (29–37)
R_{dei}	39	42 \pm 0.4 (38–47)	41 \pm 0.6 (38–43)	40 \pm 1.0 (36–43)
phasmid (% tail)	50	45 \pm 0.4 (39–50)	54 \pm 0.8 (51–59)	36 \pm 2.0 (32–44)
PUB	30	34 \pm 1 (21–47)		11 \pm 1 (5–15)
PUB/BW	1.4	1.5 \pm 0.04 (0.9–1.9)		0.6 \pm 0.04 (0.3–0.7)
spermatheca	30	34 \pm 1 (27–48)		11 \pm 1 (7–16)
spicules			19 \pm 0.3 (18–21)	
gubernaculum			12 \pm 0.2 (12–13)	

* Distance vulva to anus divided by tail length.

9. *Cephalobus vexilliger* d. M.

Taf. XV, Fig. 60.

 $\delta\varnothing$ 0,42 mm., $\alpha = 14-18$. $\beta = 3\frac{1}{4}-3\frac{1}{2}$, $\gamma = 11-13$.

Diese kleine sonderbare Art hat ein sehr plumptes Vorkommen, mit sehr wenig verschmälertem Vorderende. Die Cuticula ist geringelt, mit schmaler Seitenmembran. Das Kopfende (Fig. 60a, 60b) ist sehr niedrig und breit, ein wenig abgesetzt, und aus (6) peripherischen Lappen gebildet, welche in einen kurzen Dorn auslaufen; gleich um die Mundöffnung, auf der breiten Vorderfläche des Kopfeudes stehen 3 (oder 6) steife, in zwei Ästchen auslaufende Borstchen. Ausserdem beobachtet man in der medianen Lage am Kopfende vier submedian verlaufende Linien (Fig. 60b), deren Bedeutung zweifelhaft blieb. Die Mundhöhle ist sehr klein, nicht tief, übrigens wie bei den typischen Cephaloben gebaut. Auch der Oes. verhält sich ganz typisch: in seinem vorderen Theile ist er breiter, verschmälert sich dann nach hinten und endigt mit verhältnissmässig grossem Bulbus, der einen kräftigen Klappenapparat enthält; die Darmwand ist ziemlich grobkörnig. Der Gefässporus liegt in geringer Entfernung vor dem Bulbus, auf gleicher Höhe des Nervenringes, welcher deutlich ist. Die weibl., etwas hervorragende Geschlechtsöffnung befindet sich beim Anfang des letzten Körperdrittheils; es giebt einen hinteren Ast des Uterus, und der vordere Theil streckt sich weit nach vorn hin aus. Beim Weibchen ist der Schwanz (Fig. 60c) kegelförmig, zugespitzt, mit dreieckiger, spitzer Ausführungsröhre einer Schwanzdrüse und mit einer lateralen Papille in der Mitte. Die Spicula (Fig. 60d) sind sblank, gebogen, mit stabförmigem accessorischem Stücke versehen. Am Schwanz des Männchens, welcher mehr oder weniger gleichgestaltet ist wie beim Weibchen, fand ich zwei laterale Papillen, die eine etwas hinter der Mitte, die andere ein wenig vor dem Ende des Schwanzes (Fig. 60e).

Fundort und Lebensweise. Diese eigenthümliche, seltene Art lebt nicht nur im sandigen Dünenboden meines Vaterlandes, sondern auch in der feuchten, humusreichen Erde des Waldes. Das Thierchen bewegt sich lebhaft und beide Geschlechter sind gleich bäufig.

Geographische Verbreitung. Bis jetzt nirgendwo sonst beobachtet.

Fundzeit. In den Monaten Januar und October wurde er geschlechtsreif angetroffen.

[Translation: 9. *Cephalobus vexilliger* d.M. – Taf. XV, Fig. 60. – $\delta\varnothing$ 0.42 mm., $\alpha = 14-18$. $\beta = 3\frac{1}{4}-3\frac{1}{2}$. $\gamma = 11-13$. – This small peculiar species has a very stout appearance, with very slightly narrowed anterior end. The cuticle is annulated, with narrow lateral fields. The head end (Fig. 60a, 60b) is very low and wide, slightly offset, and composed of (6) peripheral flaps, which extend in a short thorn; just around the mouth opening, on the broad anterior surface of the head end stand 3 (or 6) stiff small bristles extending into two small branches. Besides these, one observes in the median position on the head end four submedially running striae (Fig. 60b), whose significance remain uncertain. The stoma is very small, not deep, otherwise built as in the typical cephalob. The oesophagus also appears quite typical: it is broad in its anterior part, narrows posteriorly and ends with a relatively large bulb, containing a strong valvular apparatus; the intestinal wall is rather coarse-grained. The excretory pore lies at a small distance in front of the bulb, at the same level as the nerve ring, which is conspicuous. The female's slightly protruding genital opening is found at the beginning of the last third of the body; there is a posterior uterine branch, and the anterior part extends far anteriorly. The tail of the female is (Fig. 60c) conoid, pointed, with a triangular, pointed duct of a tail gland and with a lateral papilla in the middle. The spicules (Fig. 60d) are slender, arcuate, supplied with bar-shaped accessory pieces. On the male tail, which is more or less similar in shape to that in the female, I found two lateral papillae, one somewhat behind the middle, the other somewhat in front of the tail end (Fig. 60e). – Locality and way of life. This strange, rare species lives not only in sandy dune soil of my country, but also in the moist, humus-rich forest soil. The small animals move lively and both sexes are equally numerous. – Geographical distribution. So far nowhere else observed. – Time of finding. In the months of January and October found sexually mature].

Fig. 1. Fac-simile of the description of *Cephalobus vexilliger* de Man, 1880 (from de Man, 1884), and translation.

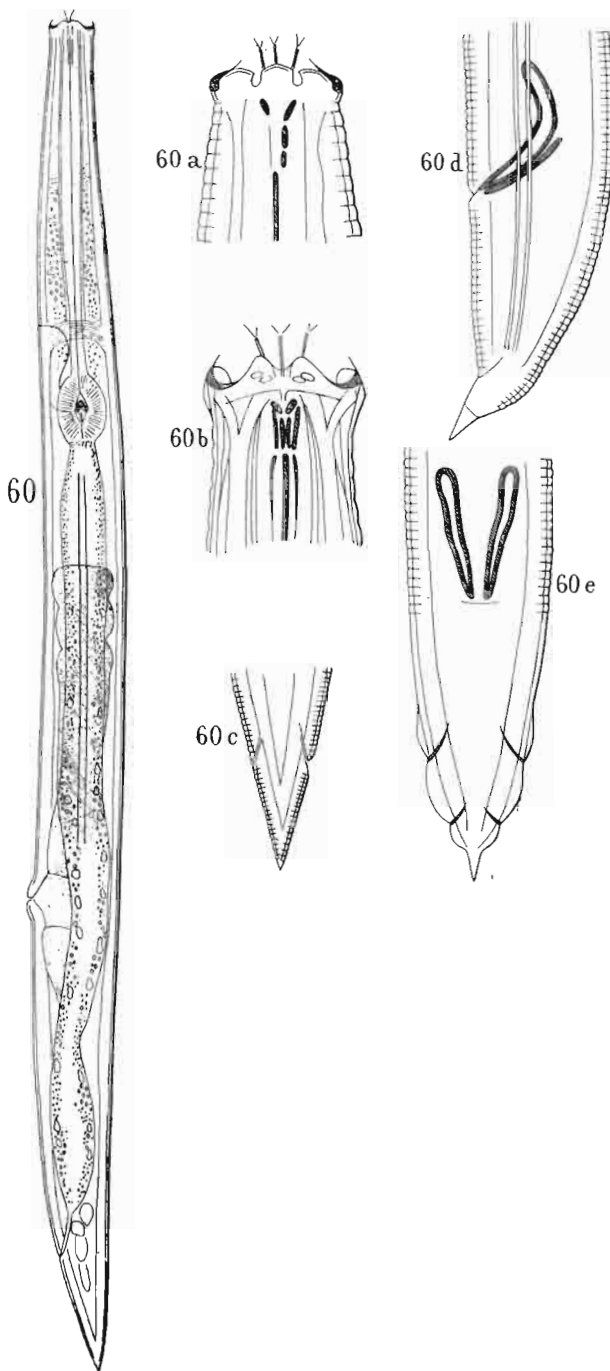


Fig. 2. Fac-simile reproduction of the original drawings of *Cephalobus vexilliger* (from de Man, 1884 : Fig. 60).

the two outer ones extending posterior to phasmid. Lip region 10-12 μm wide, with papillae and amphids. Labial probolae 4-5 μm high. Corpus 2.3-2.7 times longer than isthmus. Testis reflexed in anterior part. Spicules arcuate ventrad with slender, rounded manubrium and

slightly recurved tip; gubernaculum lineate in lateral view, 0.7-0.9 times ABW long. Tail conoid, ending in an offset 4-6 μm long mucro. Phasmids with wide opening and distinct pouch, at 51-59 % of tail length. Papillae distributed as follows : three subventral preanal pairs; a single midventral papilla on anterior cloacal lip; one lateral pair and one sublateral pair anterior to phasmid; three pairs (one subdorsal, one lateral and one subventral) near tail tip.

TYPE SPECIMENS

The topotypes are deposited as follows : Neotype female with twelve female and five male topotypes in the Landbouwniversiteit, Wageningen, the Netherlands; fifteen female and four male topotypes in the USDA Nematode Collection, Beltsville, Maryland, USA; fifteen female and three male topotypes in Sektionen för Evoltebratzoologi, Naturhistoriska Riksmuseet, Stockholm, Sweden; twelve female and three male topotypes on slides, plus five female and two male topotypes on SEM stubs in the Nematode Collection of the Instituut voor Dierkunde, Universiteit Gent, Belgium.

TYPE HABITAT AND LOCALITY

Brown soil covered by leaf litter. Vegetation consisting of mixed deciduous trees and a sparse herb layer. Sample taken in the Haagse Bos at 75 m SE from the junction of the Benoordenhoutse Weg with the Laan Van Clingendael, The Hague, The Netherlands.

Cervidellus neftasiensis Boström, 1986 (Figs 6C-N, 7)

MEASUREMENTS

See Table 1.

DESCRIPTION

Female : Body generally slightly arcuate ventrad. Cuticle annulated, annules 1.4-1.8 μm wide in neck region, 1.3-1.6 μm at mid-body. Lateral field with three incisures that usually extend nearly to tail tip, but occasionally stop at phasmid (the latter condition seen in three of the females with light microscope, in one female with SEM : Figs 6M, N; 7F). Lip region 9-11 μm wide, with 6 + 4 papillae and two amphids. Lip margins as described above for *C. vexilliger*, but central tine without apical incisure, and elongate tines present in primary axils in one of three scanned females. Labial probolae 3.5-4 μm high, slender-conical with a single bifurcation in the anterior one-fourth. Cheilorhabdia granular, rounded; other stomatal elements faintly visible. Corpus 1.5-2.5 times the length of isthmus. Excretory pore opposite isthmus. Vulva at about 2/3 of body length. Vulval lips slightly protruding. PUB 5-15 μm long, corresponding to 0.3-0.7 BW. Spermatheca 7-16 μm long, usually too small for separate cells to be distinguishable, but with ten nuclei faintly visible in three females. Rectum about one anal body width long. Tail conoid with

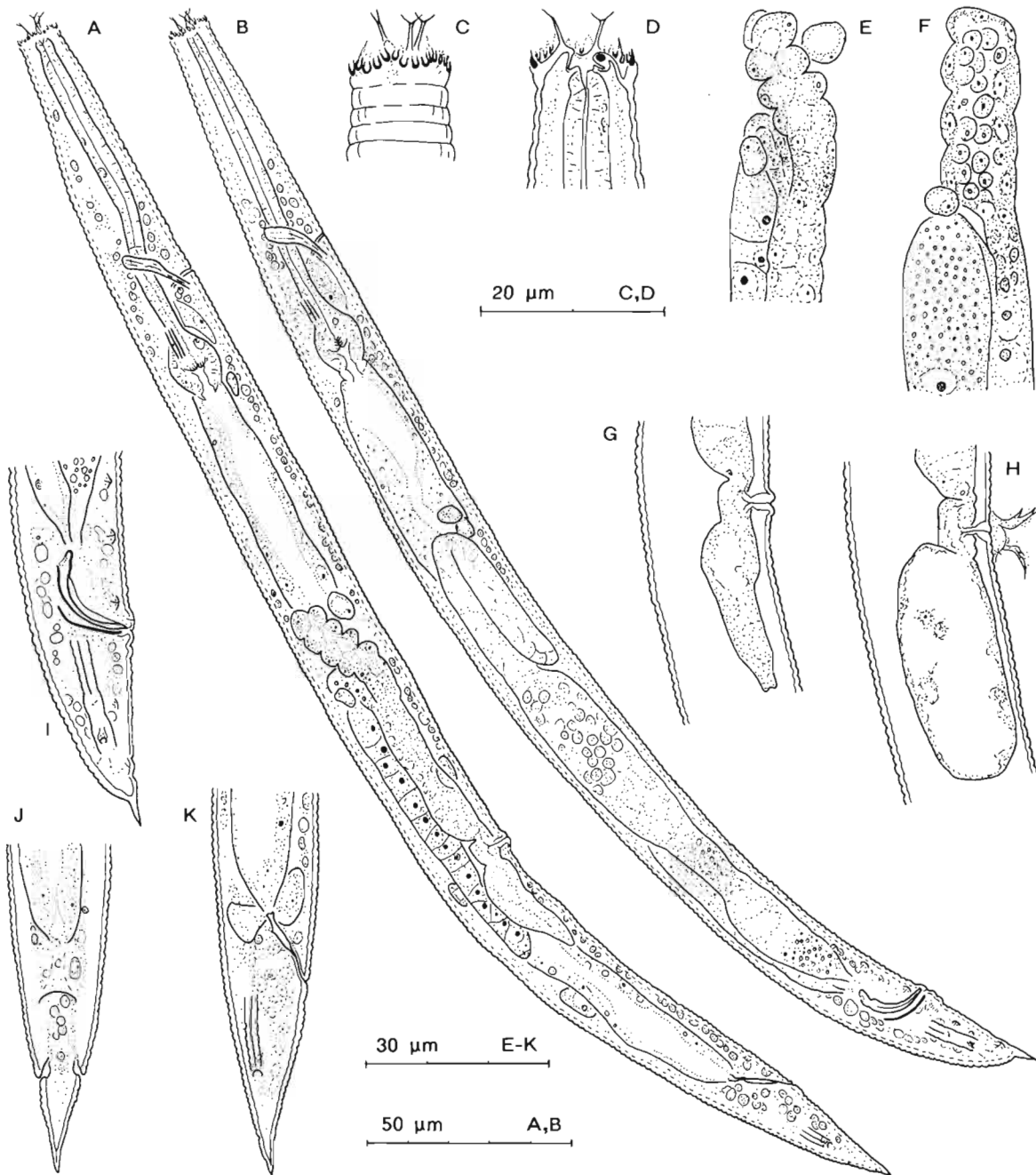


Fig. 3. *Cervidellus vexilliger* from the "Haagse Bos", the Netherlands. *A*: Neotype female; *B*: Male; *C-D*: Lip region; *E-F*: Variability in shape of spermatheca; *G-H*: Variability in shape of post-ovulval uterine branch; *I*: Male tail, lateral view; *J-K*: Female tail (*J*: ventral view; *K*: lateral view).

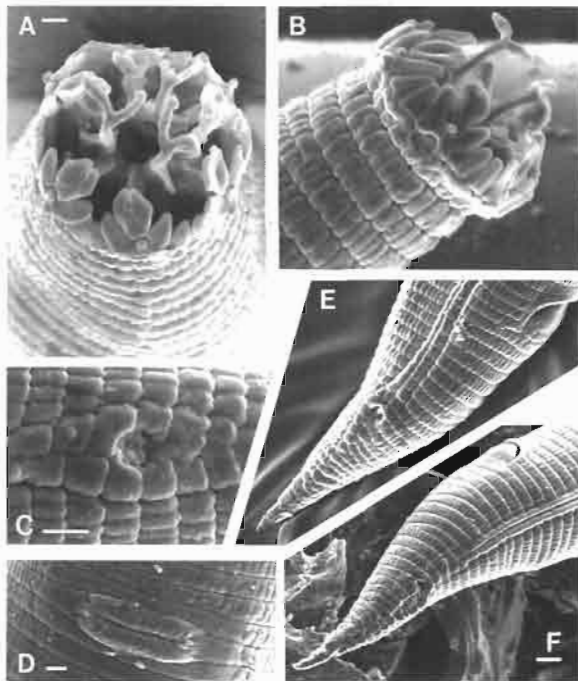


Fig. 4. *Cervidellus vexilliger* from the “Haagse Bos”, the Netherlands. A-B: Lip region; C: Phasmid; D: Vulva; E-F: Female tail, lateral view. (Scale bars: A-D, F = 1 μ m; in E same as in F).

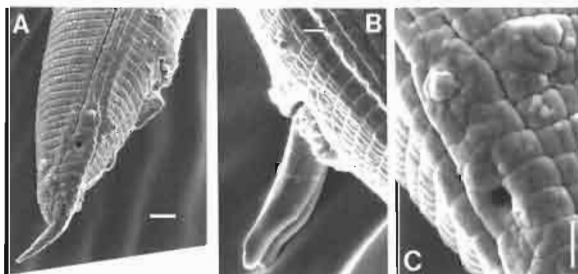


Fig. 5. *Cervidellus vexilliger* from the “Haagse Bos”, the Netherlands. A: Male tail, lateral view; B: Spicules; C: Phasmid. (Scale bars: A = 2 μ m; B-C = 1 μ m).

pointed, acute terminus. Phasmids with narrow opening and small pouch, at 32-44 % of tail length.

Discussion

DE MAN'S DESCRIPTION OF *C. VEXILLIGER*

The essential problem with the descriptions (1880, 1884) and drawings (1884) of *C. vexilliger* by de Man is that, except for tail shape, they do not contain sufficient detail to compare confidently with data derived from SEM and better optics. Thus, to identify his species unequivocally is impossible, and anyone who wishes to clarify its true morphology must resort to more or less speculative interpretations of his drawings. Neverthe-

less, the exact morphology of *C. vexilliger* must be resolved, because it has direct importance for two different sets of taxonomic problems: the validity of the genus *Ypsylonellus*, and the validity of the species *Cervidellus serratus* (Thorne, 1925) Thorne, 1937.

The most important features relevant to these problems are the following: de Man (1884: Fig. 60) depicted a fairly stout body shape ($a = 14-18$) with a slightly expanded anterior end (calculated by us to be about 14 μ m wide) and a conoid tail ($c = 11-13$) with acute tip. The lip region, described as “low and wide, slightly offset and made up from six fringes each ending in a short thorn”, cannot be interpreted in detail. The lip margins are drawn with weakly arcuate refringent bands (Fig. 60a, b), probably due to limited resolution of the microscope available to de Man. Around the stoma opening, three (or six) stiff terminally bifurcated small bristles (labial probolae) are found. The pharynx is typically cephalobid with a b-value of 3.25-3.5. The drawing of the female gonad (Fig. 60) shows a “globular” structure at or near the level of anterior flexure, which may correspond with the swollen cells of a spermatheca. The post-vulval region, as described in de Man's description and shown in his Fig. 60, suggests presence of a posterior part of the uterus (PUB), but cannot be interpreted reliably as it could as well pertain to a gonad flexure instead.

AGREEMENT BETWEEN THE TOPOTYPES AND THE ORIGINAL DESCRIPTION OF *C. VEXILLIGER*

In the sample from the Haagse Bos, specimens of two very similar species of *Cervidellus* were found. They are described above as *C. vexilliger* and *C. neftasiensis*. Females of both species could be distinguished by different size and structure of spermatheca and post-vulval uterine branch, different width of the phasmid opening, presence or absence of apical incisure on the central tine, and usually also by the extent of the lateral field on the tail. The males present could not clearly be allocated to two different species. We assume that they all belong to *C. vexilliger*, because the males have wide phasmid openings and also because no *C. neftasiensis* females contained sperm, while some *C. vexilliger* females did.

The specimens collected from the type locality of *C. vexilliger* are in sufficient agreement with de Man's descriptions and drawings (1880, 1884) to be identified and redescribed as *C. vexilliger*. The specimens described by de Man are somewhat larger (420 μ m vs 289-411 μ m) with a longer pharynx ($b = 3.25-3.5$ vs 3.4-4.1) than the newly collected specimens. However, body width ($a = 14-18$ vs 15-19) and tail length ($c = 11-13$ vs 10-13) overlap. The lip region of *C. vexilliger*, as shown by de Man (Fig. 60a, b), does not agree perfectly with the specimens from Haagse Bos, which have typically “serrated” lip margins, consisting of six groups of five contiguous refractive “U”-shaped elements (one group per axil). It is, however, likely that de

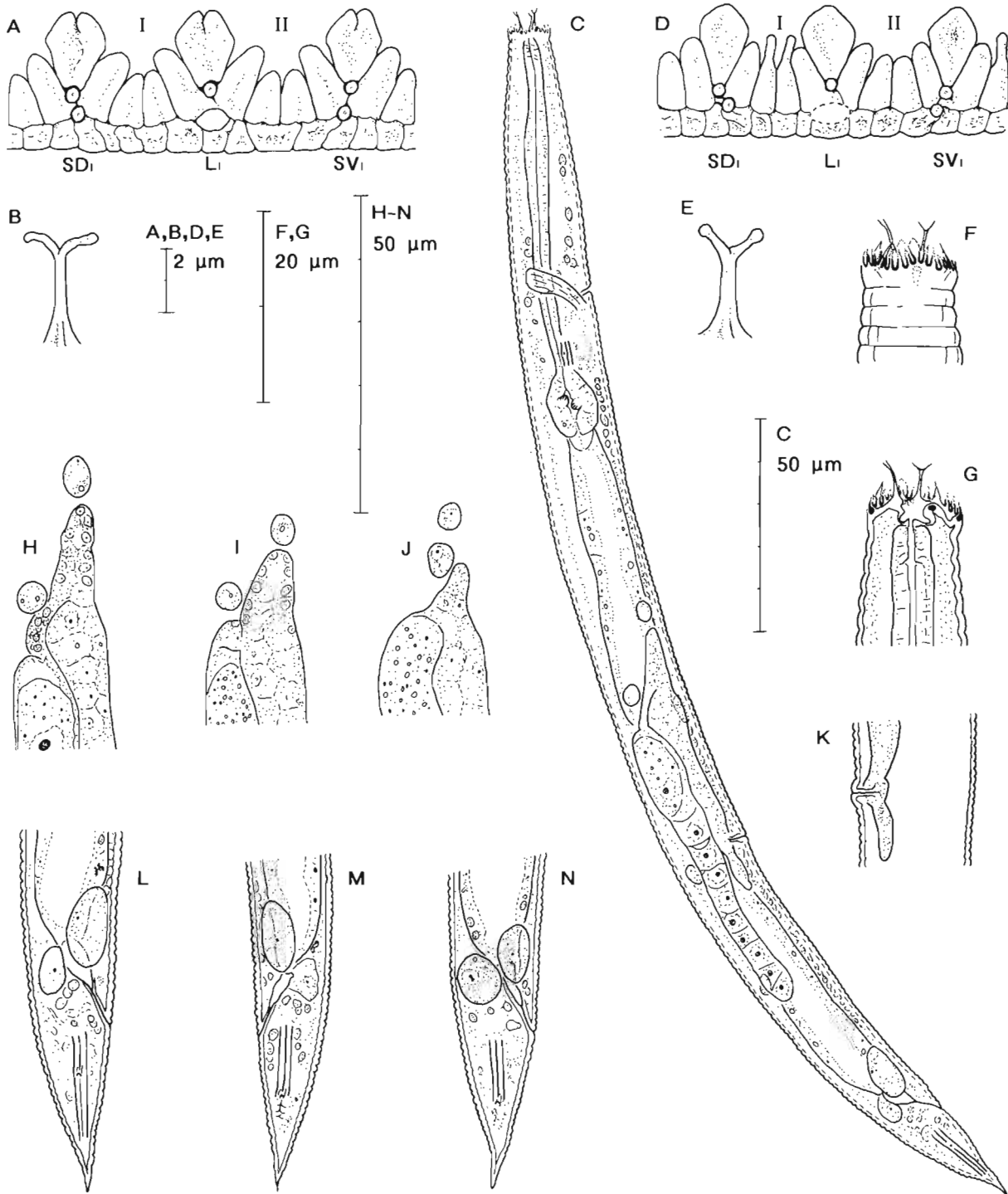


Fig. 6. *Cervidellus vexilliger* from the "Haagse Bos", the Netherlands. *A*: Schematized lip structure; *B*: Labial probola. *Cervidellus neftasiensis* from the "Haagse Bos", the Netherlands. *C*: Female; *D*: Schematized lip structures; *E*: Labial probola; *F-G*: Lip region; *H-J*: Variability in shape of spermatheca; *K*: Post-vulval uterine branch; *L-N*: Variability in shape of female tail, lateral view. (Abbreviations of *A* and *D* are: I = primary axil, II = secondary axil, L₁ = left-lateral lip, SD₁ = left-subdorsal lip, SV₁ = left-subventral lip).

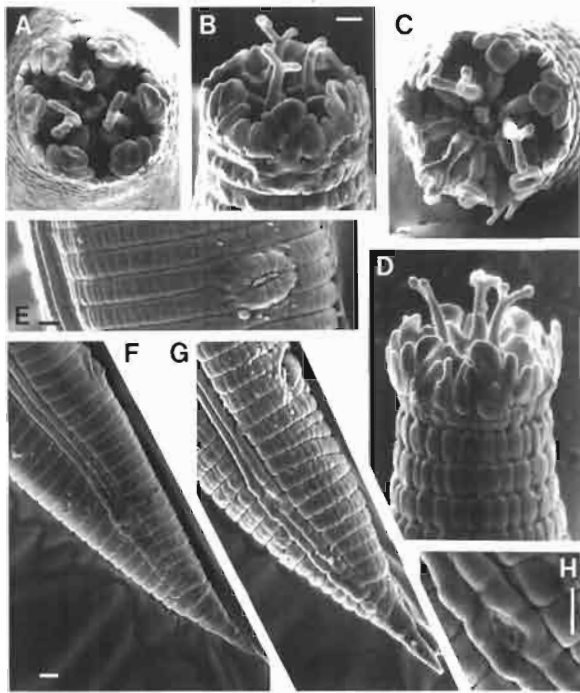


Fig. 7. *Cervidellus neftasiensis* from the "Haagse Bos", the Netherlands. A-D: Lip region; E: Vulva; F-G: Tail, lateral view; H: Phasmid. (Scale bars: B, E, F, H = 1 μ m; in A, C, D same as in B; in G same as in F).

Man's drawings correspond to this type of lip margin, because the groups of contiguous U's do form weakly arcuate refringent bands when seen with low magnification. The globular structure interpreted as a spermatheca corresponds well with the swollen multicellular spermatheca in the topotypes. As pointed out above, the post-vulval region is difficult to interpret on de Man's Fig. 60, but presence of a PUB in de Man's description would agree with the newly collected specimens. The conical female tail and male tail with mucro in specimens from Haagse Bos agree quite well with de Man's description and drawings (Fig. 60c-e). The evidence thus supports identification of our material from Haagse Bos as *C. vexilliger*.

SYNONYMIZATION OF *C. VEXILLIGER* WITH *C. SERRATUS* AND COMPARISON WITH SPECIES OF *YPSYLONELLUS*

The females of the population of *C. vexilliger* described here agree well with the diagnosis of the species *C. serratus* (Thorne, 1925) Thorne, 1937. The original descriptions and drawings of *C. vexilliger* by de Man (1880, 1884) also suggest that these two species are conspecific and *C. serratus* is therefore synonymized with *C. vexilliger*. Apart from being in agreement with the original description by Thorne (1925), our speci-

mens of *C. vexilliger* also agree with more recent descriptions of *C. serratus* by Boström (1986, 1992) and De Ley *et al.* (1994).

C. vexilliger was chosen by Andrassy (1984) as type species of the problematical genus *Ypsylonellus* and we must therefore discuss the possibility that *C. vexilliger* does not resemble either *C. serratus* or *C. neftasiensis*, but rather some of the other species placed in *Ypsylonellus* by Andrassy (1984). For this purpose, we will compare the description and drawing of *C. vexilliger* by de Man (1880, 1884) with the morphology of *C. serratus* on the one hand, and the better-known *Ypsylonellus* species on the other. At present, two species of *Ypsylonellus* have been studied in detail: *Y. devimucronatus* (Sumenkova, 1964) Andrassy, 1984 and *Y. similis* (Thorne, 1925) Andrassy, 1984 (see Boström 1991, 1993; De Ley *et al.*, 1994). We will refer to these as "the *similis*-group".

The main differentiating characters for *C. serratus* and the *similis*-group are the organization of the lip region and the shape of the female tail: *i*) the former has the typically "serrated" lip margins, consisting of six groups of five contiguous refractive "U"-shaped elements (one group per axil), while the latter has three pairs of refractive U's (one per primary axil), usually alternating with three additional U's (a single one per secondary axil); *ii*) the former has a conical female tail with pointed tip, while the latter has a mucronate to "ragged" female tail tip.

The following features in the original description of *C. vexilliger* and in our description are relevant to its distinction from the *similis*-group:

- De Man's (1884) drawings of the lip region (Fig. 60a, b) correspond more closely to a *serratus*-type lip margin, because the groups of contiguous U's in this type do form weakly arcuate refringent bands when seen with low magnification. By contrast, the *similis*-type lip region appears to have vertical refringent rods (cf. drawings of *Y. insubricus* by Steiner, 1914 and *Y. similis* by Thorne, 1925). Also, de Man's Fig. 60 shows an animal with relatively broad lip region: if $L = 420 \mu\text{m}$ (as given in de Man's description), then its lip region has a diameter of 14 μm , which agrees much better with *C. serratus* (10-13 μm) than with the *similis*-group (lip region width 7.5-10 μm in all relevant species in De Ley *et al.*, 1994).

- According to de Man (1880), *C. vexilliger* has a = 14-18. Measurements of *C. serratus* compiled from recent descriptions (Boström, 1986, 1992; De Ley *et al.* 1994) give a = 11-20, and the bisexual species from Haagse Bos has a = 15-19. By contrast, species from the *similis*-group are more slender, with a = 17-26.

- The globular structure near the anterior flexure of the female gonad (de Man, 1884: Fig. 60) may well correspond with the swollen spermatheca cells of *C. serratus* and the specimens from Haagse Bos (see Fig. 3F), while it does not resemble the structure of this gonad region in members of the *similis*-group (cf. Boström, 1991; De Ley *et al.*, 1994).

– It is tempting to interpret Fig. 60 in de Man (1884) as showing a long PUB, unlike the short PUB found in the *similis*-group. However, his drawing could instead represent a double flexure of the ovary tip, and is therefore equivocal on this point.

– The tail shapes shown for males and females of *C. vexilliger* by de Man (1884 : Fig. 60, 60c-e) agree with those described for *C. serratus* (cf. e.g. Fig. 1E, F in Boström, 1986) and found in our material from Haagse Bos, while differing clearly from those known in males and females of the *similis*-group (Boström, 1993; De Ley *et al.*, 1994).

The above arguments show that the weight of evidence is well in favour of a synonymy of *C. vexilliger* with *C. serratus* and that the latter is well distinguished from any species presently in the genus *Ypsylonellus*. Further facts in support of this possibility are that neither Dr. P. A. A. Loof, nor Dr. T. Bongers, nor we ourselves have found any *Ypsylonellus*-like specimens in the Netherlands. On the other hand, *C. serratus* has been found frequently in Dutch samples, i.a., from Wernhout, a locality from which de Man (1921) again reported *C. vexilliger* (De Ley, unpubl.).

DIFFERENTIATION BETWEEN *C. SERRATUS* AND *C. NEFTASIENSIS*

As *C. vexilliger* is synonymized with *C. serratus*, but not with *C. neftasiensis* from Haagse Bos, the following arguments for differentiation between the two latter species are presented :

– The size of *C. vexilliger* as originally described (L = 420 µm; de Man, 1880) overlaps with known range in *C. serratus* (300-428 µm), but not in *C. neftasiensis* (241-377 µm).

– *C. neftasiensis* usually has a proportionally slightly longer pharynx (b = 3.0-3.7) but compiled measurements of *C. serratus* (3.2-4.0) include de Man's values (3.25-3.5) completely.

– *C. neftasiensis* (like the species from the *similis*-group) has a short spermatheca without swollen cells. Observed at lower magnification, the spermatheca is either invisible or visible as a short projection ventrally at the point where the oviduct forms the anterior gonad flexure. *C. serratus*, by contrast, has a "grape" - shaped spermatheca with swollen cells that frequently matches de Man's drawing (Fig. 60) of the gonad quite well at low magnification.

– De Man's drawings of the male and female tail in ventral view (Fig. 60c, e) show clear phasmids, which we would expect for *C. serratus* but not necessarily *C. neftasiensis*.

– The fairly common presence of males of *C. serratus* suggests that this is de Man's species, as he included males in his description. Males of *C. neftasiensis* were not found in Haagse Bos, and are only known from the original description of this species.

Conclusions

We are convinced that *C. vexilliger* is neither synonymous nor close to any species from the *similis*-group, mostly because of differences in tail shape as shown by de Man (1884 : Fig. 60c-e). Overall, the case for synonymy of *C. vexilliger* with *C. serratus*, rather than *C. neftasiensis*, is less overwhelming. But this can hardly be expected given the great resemblance between these two species. Note that in either case *Ypsylonellus* must be synonymized with *Cervidellus*, unless sufficient reasons would be found to separate *C. serratus* and/or *C. neftasiensis* from the type of *Cervidellus*, *C. cervus* (Thorne, 1925) Thorne, 1937. We have already re-examined types of *C. cervus*, and did not find any such reasons.

It follows from this that *Ypsylonellus* is rejected and the species presently classified in the genus have to be placed elsewhere. De Ley *et al.* (1994) showed that the type species of *Stegelletina*, *S. lineata* (Thorne, 1925) Andrassy, 1984, is a junior synonym of *Y. similis* (Thorne, 1925) Andrassy, 1984. Since the validity of the status of *Stegelletina* was uncertain, they chose not to transfer *Y. similis* to that genus. However, as *Ypsylonellus* is now rejected, *Stegelletina* will be retained as a valid genus and rediagnosed to harbour some of the species presently in *Ypsylonellus*.

At the moment, it is not possible to give a more permanent classification of the genera *Cervidellus* and *Stegelletina*. Therefore we present only a provisional classification and differential diagnoses, which are likely to change considerably in the years to come as more type specimens are re-examined.

Cervidellus Thorne, 1937

DIAGNOSIS

Labial probolae bifurcated at one to three levels. Primary cephalic axils with even number of tines, sometimes including two guarding pieces. Tail tip of both sexes acute.

TYPE SPECIES

Cervidellus cervus (Thorne, 1925) Thorne, 1937
= *Acrobeles cervus* Thorne, 1925

OTHER SPECIES

Cervidellus cancellatus (Thorne, 1925) n. comb.
= *Acrobeles cancellatus* Thorne, 1925
= *Stegella cancellata* (Thorne, 1925) Thorne, 1937
= *Stegelleta cancellata* (Thorne, 1925) Thorne, 1938
= *Stegelletina cancellata* (Thorne, 1925) Andrassy, 1984
Cervidellus capraeolus (De Ley *et al.*, 1990) n. comb.
= *Stegelletina capraeola* De Ley *et al.*, 1990
Cervidellus doorsselaeri (De Clerk & De Ley, 1990) n. comb.
= *Stegelletina doorsselaeri* De Clerk & De Ley, 1990

- Cervidellus hamatus* Thorne, 1937
Cervidellus laticollaris (De Ley & Vandebroek, 1992) n. comb.
= *Stegelletina laticollaris* De Ley & Vandebroek, 1992
Cervidellus neftasiensis Boström, 1986
Cervidellus rarus (Nesterov, 1969) n. comb.
= *Stegelleta rara* Nesterov, 1969
= *Stegelletina rara* (Nesterov, 1969) Andrassy, 1984
Cervidellus spitzbergensis Boström, 1987
Cervidellus vexilliger (de Man, 1880) Thorne, 1937
= *Cephalobus vexilliger* de Man, 1880
= *Cephalobus (Acrobeles) vexilliger* (de Man, 1880) de Man, 1921
= *Acrobeles vexilliger* (de Man, 1880) Thorne, 1925
= *Ypsylonellus vexilliger* (de Man, 1880) Andrassy, 1984
= *Acrobeles serratus* Thorne, 1925
= *Cervidellus serratus* (Thorne, 1925) Thorne, 1937
= *Acrobeles serricephalus* Thorne, 1925
= *Cervidellus serricephalus* (Thorne, 1925) Thorne, 1937.

SPECIES INQUIRENDAE

- Cervidellus arenosus* Andrassy, 1987 (1)*
Cervidellus kerguelensis (Steiner, 1916) Thorne, 1937
= *Cephalobus vexilliger kerguelensis* Steiner, 1916
= *Acrobeles vexilliger kerguelensis* (Steiner, 1916) Thorne, 1925
= *Ypsylonellus kerguelensis* (Steiner, 1916) Andrassy, 1984

***Stegelletina* Andrassy, 1984**

DIAGNOSIS

Labial probolae bifurcated at one level. Primary cephalic axils with one guarding piece and no other tines. Female tail tip mucronate, male tail tip rounded, acute or mucronate.

TYPE SPECIES

- Stegelletina similis* (Thorne, 1925) n. comb.
= *Acrobeles similis* Thorne, 1925
= *Cervidellus similis* (Thorne, 1925) Thorne, 1937
= *Ypsylonellus similis* (Thorne, 1925) Andrassy, 1984
= *Acrobeles lineatus* Thorne, 1925
= *Stegella lineata* (Thorne, 1925) Thorne, 1937
= *Stegelleta lineata* (Thorne, 1925) Thorne, 1938
= *Stegelletina lineata* (Thorne, 1925) Andrassy, 1984
= *Stegelleta mucronata* Loof, 1971

- = *Stegelletina mucronata* (Loof, 1971) Andrassy, 1984

OTHER SPECIES

- Stegelletina argentinica* (Andrassy, 1963) Andrassy, 1984
= *Stegelleta argentinica* Andrassy, 1963
Stegelletina devimucronata (Sumenkova, 1964) n. comb.
= *Cervidellus devimucronatus* Sumenkova, 1964
= *Ypsylonellus devimucronatus* (Sumenkova, 1964) Andrassy, 1984

SPECIES INQUIRENDAE

- Stegelletina ankyra* (Thorne, 1925) n. comb. (2)
= *Acrobeles ankyrus* Thorne, 1925
= *Cervidellus ankyrus* (Thorne, 1925) Thorne, 1937
= *Ypsylonellus ankyrus* (Thorne, 1925) Andrassy, 1984
Stegelletina insubrica (Steiner, 1914) n. comb. (3)
= *Cephalobus insubricus* Steiner, 1914
= *Cephalobus (Acrobeles) insubricus* (Steiner, 1914) de Man, 1921
= *Acrobeles insubricus* (Steiner, 1914) Thorne, 1925
= *Cervidellus insubricus* (Steiner, 1914) Thorne, 1937
= *Ypsylonellus insubricus* (Steiner, 1914) Andrassy, 1984

***Species incertae sedis vel inquirendae* (4)**

- Acrobelophis distinctus* (Kirjanova, 1951) Andrassy, 1984
= *Acrobeles distinctus* Kirjanova, 1951
= *Chiloplacus distinctus* (Kirjanova, 1951) Andrassy, 1959
= *Cervidellus distinctus* (Kirjanova, 1951) Goodey, 1963
Acrobelophis innoxius (Kirjanova, 1951) Andrassy, 1984
= *Acrobeles innoxius* Kirjanova, 1951
= *Cervidellus innoxius* (Kirjanova, 1951) Meyl, 1961
Acrobelophis insons (Kirjanova, 1951) Andrassy, 1984
= *Acrobeles insons* Kirjanova, 1951
= *Cervidellus insons* (Kirjanova, 1951) Meyl, 1961
Acrobelophis serenus (Kirjanova, 1951) Andrassy, 1984
= *Acrobeles serenus* Kirjanova, 1951
= *Chiloplacus serenus* (Kirjanova, 1951) Andrassy, 1969
= *Cervidellus serenus* (Kirjanova, 1951) Goodey, 1963
Cervidellus anatolicus Gadea, 1978 (5)

* (1), (2)... : see " Notes " below.

- Cervidellus desertus* (Kirjanova, 1951) Goodey, 1963
= *Acrobeles desertus* Kirjanova, 1951
Ypsylonellus desidiosus (Kirjanova, 1951) Andrassy, 1984
= *Acrobeles desidiosus* Kirjanova, 1951
= *Cervidellus desidiosus* (Kirjanova, 1951) Meyl, 1961
Ypsylonellus habibullae (Erzhanova, 1964) Andrassy, 1984 (6)
= *Cervidellus habibullae* Erzhanova, 1964
Ypsylonellus manifestus (Kirjanova, 1951) Andrassy, 1984
= *Acrobeles manifestus* Kirjanova, 1951
= *Cervidellus manifestus* (Kirjanova, 1951) Meyl, 1961

NOTES

- (1) *C. arenosus* is in our opinion probably a synonym of *C. vexilliger* or *C. neftasiensis*.
(2) *S. ankyra* could be a senior synonym of *S. similis*.
(3) *S. insubrica* could be a senior synonym of *S. devimucronata* since the morphology of the latter agrees with the former when observed under low magnification. However, De Ley *et al.* (1994) described a female specimen from Senegal that resembles the original description of *S. insubrica* by Steiner (1914), but is definitely not conspecific with *S. devimucronata*.
(4) None of the species described by Kirjanova (1951) can be accurately placed because of the very short original descriptions and schematic drawings. For the same reason they are of doubtful specific validity.
(5) *C. anaticus* was originally described by Gadea (1978) as having three differently shaped labial probolae without information on the fine structure of the primary cephalic axils.
(6) *Y. habibullae* was originally described by Erzhanova (1964) as lacking labial probolae and having a rounded tail tip.

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