

## REVISION OF THE GENUS *LEPTOSOMATUM* BASTIAN, 1865 (NEMATODA: LEPTOSOMATIDAE)

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*Abstract.*—The available type-material of the species of *Leptosomatum*, has been studied and compared with the type-species of the genera *Leptosomatides* (*L. euxinus* Filipjev, 1918) and *Syringonomus* (*S. typicus* Hope and Murphy, 1959).

The character complex present in *L. elongatum*, the type-species of *Leptosomatum*, sharply distinguishes the species of *Leptosomatum* from the genus *Leptosomatides*, hitherto regarded as being related to *Leptosomatum*. Females of *Leptosomatides* can be distinguished from those of *Leptosomatum* by the presence of a strongly muscularized vagina wall, here termed the vaginal ovejector. The main distinguishing character is the presence of a sexual dimorphism in the amphids of *Leptosomatum*, which is absent in *Leptosomatides*.

The species of *Leptosomatum* can be grouped into three complexes: a) The monotypic complex *L. kerguelense* Platonova, 1958 (new synonyms: *L. clavatum* Platonova, 1958 partim, *L. crassicutis* Platonova, 1958, and *L. arcticum* sensu Mawson, 1958) characterized by the presence of a cephalic capsule in both sexes. b) The *L. bacillatum*-complex composed of *L. bacillatum* (Eberth, 1863) (new synonyms: *L. elongatum* Bastian, 1865, *L. filipjevi* Schuurmans Stekhoven, 1950, and *L. tuapsense* Sergeeva, 1973), *L. sachalinense* Platonova, 1978 (new synonym: *L. diversum* Platonova, 1978), *L. acephalatum* Chitwood, 1936 and probably *L. clavatum* Platonova, 1958 partim and *L. sundaense* n.sp. for *L. sabangense* sensu Micoletzky, 1930 nec Steiner, 1915. This complex is characterized by the presence of a cephalic capsule in juveniles and females, but not in males. c) The *L. punctatum*-complex with *L. punctatum* (Eberth, 1863) (new synonyms: *L. longisetosum* Schuurmans Stekhoven, 1943 and (?) *Stenolaimus macrosoma* Marion, 1870), and *L. keiense* Micoletzky, 1930. In this complex the cephalic capsule is absent in juveniles and adults.

More information is needed regarding the species *L. abyssale* Allgén, 1951; *L. bathybium* Allgén, 1954; *L. behringicum* Filipjev, 1916; *L. breviceps* Platonova, 1967; *L. groenlandicum* Allgén, 1954; *L. indicum* Stewart, 1914; *L. pedroense* Allgén, 1947; *L. sabangense* Steiner, 1915; *L. tetrophthalmum* Ssaweljev, 1912 and *L. sundaense* new name; pro *L. sabangense* sensu Micoletzky, 1930, they are considered species inquirendae.

*Leptosomatum ranjhai* Timm, 1960, and *L. micoletzkyi* Inglis, 1970, do not belong to *Leptosomatum* and are, for the moment, considered species incertae sedis.

*L. caecum* Ditlevsen, 1923 belongs to *Pseudocella*.

*L. arcticum* Filipjev, 1916; *L. elongatum* sensu Platonova, 1967; *L. gracile* sensu Allgén, 1954; *L. grebnickii* Filipjev, 1916 and *L. tetrophthalmum* sensu Platonova, 1967 are transferred to *Leptosomatides* Filipjev, 1918.

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The genus *Leptosomatum* Bastian, 1865, which contains large-sized marine nematodes, was last revised by Filipjev (1918). Platonova (1976) published a key



and reviewed the family Leptosomatidae. According to these authors the genus is characterized by the reduced cephalic capsule and the simple gubernaculum. On this basis, females of *Leptosomatum* cannot be distinguished from those of *Leptosomatides* Filipjev, 1918. The genus now contains 31 nominal species and identification of these has become impossible.

While studying populations of a *Leptosomatum* species I observed some phenomena that appeared to be undescribed. Re-examination of type-specimens of most species revealed the presence of a character complex that clearly demarcates *Leptosomatum* from related genera. Some species that do not possess this complex had to be excluded from *Leptosomatum*, some were transferred to *Leptosomatides* and *Pseudocella*, and others must be regarded as species inquirenda.

In a series of papers, starting with the present one, I will try to raise the classification of the Leptosomatidae from the  $\alpha$ -level and to establish a classification based on holapomorphy as proposed by Lorenzen (1981). The first step is the demarcation of the genera. Lorenzen did not succeed in basing the classification of the family Leptosomatidae on holapomorphy, partly because many species descriptions are incomplete and inadequate.

Many species are synonymized, due to poor descriptions, sexual dimorphism, and post-adult growth.

In this paper I give an historical account, call attention to artifacts, give supplementary descriptions, discuss the species, and provide a key. In another paper I shall give a phylogenetic approach.

### Historical Review

The genus *Leptosomatum* was erected by Bastian (1865) who included eight species: *L. punctatum* (Eberth, 1863); *L. gracile* Bastian, 1865; *L. bacillatum* (Eberth, 1863); *L. figuratum* Bastian, 1865; *L. coronatum* (Eberth, 1863); *L. longissimum* (Eberth, 1863); *L. subulatum* (Eberth, 1863), and *L. elongatum* Bastian, 1865. The last mentioned was designated as "typical species."<sup>1</sup>

Marion (1870) transferred *L. coronatum* to *Thoracostoma*. Villot (1875) synonymized *L. figuratum* with *L. coronatum*, and described *L. roscovianum*, *L. magnum* and *L. minutum*. It was soon realized that these species did not conform to Bastian's definition of the genus: de Man (1889) made *L. magnum* type-species of his new genus *Cylicolaimus*; in 1918 Filipjev transferred *L. minutum* to the same genus and in 1927 he removed *L. roscovianum* to *Synonchus*.

Von Linstow, also, broadened the scope of *Leptosomatum*; he transferred *Thoracostoma schneideri* (Bütschli, 1874) to it and described four new species: *L. antarcticum* (1892), *L. setosum* (1896), *L. papillatum* (1903), and *L. australe* (1907); of these *L. setosum* was transferred to *Thoracostoma* by de Man (1904); *L. antarcticum* and *L. papillatum* were removed to *Deontostoma* by Filipjev (1916), and *L. australe* was considered species inquirenda by Filipjev (1918). In 1893 de Man synonymized *L. gracile* with *L. elongatum*.

The generic revision by Filipjev (1918) recognized only three of the above mentioned species, viz. *L. bacillatum*, *L. punctatum* and *L. elongatum*. In ad-

<sup>1</sup> The indication "typical species" did not originally have the nomenclatorial meaning it has today. According to Stiles and Hassal (1905), *L. elongatum* has to be considered as type by original designation.



dition four other species were included: *L. tetrophthalmum* Ssaweljev, 1912; *L. grebnickii*, *L. arcticum*, and *L. behringicum*, the latter three previously described by Filipjev in 1916. In the same paper Filipjev erected the genus *Leptosomatides*. He was somewhat uncertain about the generic placement of *L. grebnickii* and *L. arcticum* because in some respects these species resembled the type-species of *Leptosomatides*, *L. euxinus*; but as males of these two species were still unknown, he left them in *Leptosomatum*.

In 1936 Chitwood described *L. elongatum* subsp. *acephalatum*; in 1951 he reunited this form with the nominate form, but Timm (1953), in an anatomical and morphological study, raised it to specific rank.

Allgén (1947, 1951, 1954, 1954a, and 1957) described five species, which are all doubtful, being described from single specimens. Moreover he confounded *Leptosomatum* and *Leptosomatides*; this will be discussed later.

Platonova (1958, 1967, 1978) published on specimens of *Leptosomatum* identified by Filipjev in the twenties, and described some new species. In her thesis (1976) she reviewed the genus and gave a key.

Minor contributions to the taxonomy of *Leptosomatum* were made by Stewart (1914), Steiner (1915, 1916), Ditlevsen (1923), Kreis (1928), Micoletzky (1924, 1930), Schuurmans Stekhoven (1943a, 1943b, 1950), Mawson (1958), Timm (1960), Inglis (1971), and Sergeeva (1973).

### Material and Methods

The original material of the following species was studied: *L. elongatum* sensu de Man, 1893; *L. arcticum*, *L. grebnickii* and *L. behringicum* Filipjev, 1916; *L. bacillatum* (= *L. filipjevi* Schuurmans Stekhoven, 1950) and *L. punctatum* sensu Filipjev, 1918; *L. coecum* Ditlevsen, 1923; *L. elongatum* subsp. *acephalatum* Chitwood, 1936; *L. sabangense* sensu Allgén, 1942; *L. acephalatum* sensu Timm, 1953; *L. bathybiium* Allgén, 1954; *L. groenlandicum* Allgén, 1954; *L. crassicutis*, *L. kerguelense* and *L. clavatum* Platonova, 1958; *L. ranjhai* Timm, 1960; *L. breviceps* Platonova, 1967; *L. arcticum*, *L. elongatum* and *L. tetrophthalmum* sensu Platonova, 1967; *L. tuapsense* Sergeeva, 1973; *L. diversum* and *L. sachalinense* Platonova, 1978.

Of related genera, type-specimens of *Syringonomus typicus* Hope and Murphy, 1969 were studied, as well as the *Leptosomatides* collection of the Zoological Institute in Leningrad.

Furthermore 80 specimens in the collection of the Smithsonian Institution, Washington, were made available; as well as some hundreds of specimens from the Dutch coast, deposited in the nematode collection of the Nematology Department, Landbouwhogeschool, Wageningen. These latter specimens had mainly been collected from the sponge *Halichondria panicea* (Pallas, 1766), in which they occur in great densities; from 100 ml of sponge more than 900 specimens were collected. The sponges were taken off stones in the lower littoral, and immediately fixed in 5% formaldehyde. In the laboratory the nematodes were removed from the sponges. In some cases the sponges were kept in sea water for three hours, in order to allow the nematodes to leave them. They were then fixed and mounted in glycerin following the Seinhorst method (1959). The coverglasses were supported by splinters of broken coverglasses with a thickness of 0.11 mm.



The specimens of Filipjev, Platonova and Sergeeva, and also *L. bathybiium*, *L. groenlandicum*, *L. caecum*, and *L. elongatum acephalatum* had been mounted in glycerin-gelatin; for this study the three last-mentioned species were remounted. *L. elongatum* sensu de Man, 1893 and *L. ranjhai* had been remounted some years before.

Specimens from Texel, used for the E.M.-study, were collected after they had left the sponge and were subsequently fixed in an iso-osmotic 1.5% glutaraldehyde solution buffered with sodium-cacodylate at pH 7.1 for 30 minutes. The head end was excised and embedded in 1% sea water agar. These agar pieces, measuring  $1 \times 1 \times 3$  mm, were additionally fixed for one hour. Post-fixation took place in an 1% osmium tetroxide solution in 0.1 M sodium-cacodylate.

After dehydration in ethanol, the material was transferred to monomere methacrylate in which it was kept overnight. The next day the monomer was replaced by pre-polymerized methacrylate, refreshed once and polymerized for 24 hours at 50°C. Sections were stained in uranyl acetate and lead citrate.

### Notation

Cobb's formula for expressing body proportions, which was used by Filipjev (1918), is of limited use for describing dimensions of populations, because no correlations can be given. In a hypothetical case where the length of individuals in a population varies from 6 to 9 mm, information is lost when the ratio "b" is noted as 6.4–12.3. Moreover, the distribution remains indefinite. The standard deviation, which expresses the spread of the ratio, is useful only when applied to nematodes of equal length. The utility of the standard deviation is further decreased, when applied to establish significant differences between *Leptosomatum* populations, by the fact that life cycle and environmental factors influence body length.

To avoid indistinctness and to provide accurate information, body proportions are noted for each specimen separately in the Appendix. The specimens are arranged according to body length to show the relation between body length and other dimensions.

Body length was measured along the axis, which was drawn with the aid of a drawing-tube; the other, smaller measurements were taken directly with an ocular micrometer. Spicules were measured along the chord. The cephalic diameter was measured at the level of the cephalic sensilla, thickness of cuticle at level of the base of the pharynx. Pre-neural body length is distance from head end to the most anterior part of the nerve ring; length to ocelli and amphids are defined analogously. Body diameter at vulva level was measured when necessary, beside the protruding lips. The precision of the diameter of the amphid aperture is limited by focussing difficulties.

Regarding the terminology, in this paper the term "lunula" is proposed for the crescent-shaped median lamella in the tail tip, surrounding the caudal pore as described by Hope (1967:313) for *Pseudocella wieseri*. The term "vaginal ovjector" is used to indicate the strong musculature in the vaginal wall of *Deontostoma*, *Thoracostoma* and *Leptosomatides* sp. which is depicted by Steiner (1916, Taf. 30 fig. 27o, n) for what he considered to be *Leptosomatum gracile* (= *Leptosomatides steineri* Filipjev, 1922).



### Artifacts

A subject that has received little attention from taxonomists is the post-mortem phenomena caused by the fixative, the mounting medium or long-term storing. These phenomena may be advantageous—the fovea becomes more clear—but often they are disadvantageous, especially when not recognized: swelling of the cuticle, and dehydration after having been mounted for decades.

Glycerin-gelatin shrinks when dried up as do the specimens mounted in this medium, and ruptures appear. This was the case in the type-material of *L. elongatum* subsp. *acephalatum* Chitwood, 1936. On rehydration of glycerin-gelatin the medium increased in volume and ruptures disappear as a result of this swelling. The length of the nematode, which has been broken into pieces by the drying gelatin, increased by about 10%, which means that the original length has been restored. After removing superfluous gelatin, the specimen and adhering medium were dehydrated and mounted in glycerin in the usual way. Although the pieces of the nematode had not been measured, it seems acceptable that the length has been decreased by the same percentage as it increased by dehydration. This aspect of remounting is probably also applicable to the material of de Man (1893) because at present, these specimens are much smaller than originally described.

I have also observed specimens, embedded in anhydrous glycerin for a considerable time, showing signs of shrinkage although they had been dehydrated sufficiently slowly to allow the glycerin to replace the water in the tissue. This phenomenon was noted in population 1–3 of *L. bacillatum* (pp. 820 and 821). The cuticula hardly changed but the pharynx and intestine decreased considerably in length, often resulting in a rupture in the intestine. The diameter of the body decreased; this can be seen quite readily when comparing the cephalic capsule, which hardly shrinks, with the more posterior tissues. This dehydration however, gives more contrast to the fovea of the male amphid.

The type-material of *L. ranjhai* Timm, 1960 showed the same artifacts, but it is not known whether this is the result of remounting from glycerin-gelatin or of the above-mentioned factors combined.

Body width is influenced by flattening more than the other dimensions. Often it was difficult to ascertain the degree of flattening, or even whether a specimen was flattened at all. For this reason body widths are considered of minor importance.

Purposely flattening in order to bring mounted specimens within focal distance of the immersion lens is to be avoided, especially when applied to type specimens. Glass rods or other supports for the coverglasses should have at least the same diameter as the nematode body. One holotype specimen studied had a body width of 130  $\mu\text{m}$ , whereas the supporting rods were no thicker than 24 and 28  $\mu\text{m}$ .

In contrast, to soil-inhabiting nematodes, which are usually fixed after having actively passed through a cottonwool filter, marine nematodes are generally fixed together with the substrate. The fixed sample thus may contain specimens that were dead and decaying at the moment of fixation. It is, therefore, essential to be able to recognize post-mortem artifacts. For this purpose, nematodes that had died at least one day before, were fixed using 4% formaldehyde in sea water. *Leptosomatum bacillatum* showed the following artifacts: loosening and swelling of cuticular layers; loosening and retraction of the pharyngeal tissues at the anterior end. The cuticular pores became more distinct and the spicular manubrium be-



Table 1.—Differential characteristics of type-species of *Leptosomatum* and *Leptosomatides*.

	<i>Leptosomatum elongatum</i>	<i>Leptosomatides euxinus</i>
Cephalic capsule	reduced in male; poorly developed in female. Posterior suture invisible	present; posterior suture visible
Sexual dimorphism in amphids	present	absent
Renette	restricted to females	wanting
Vulvar glands in lateral hypodermal chord	absent	present
Intra-cuticular vulvar granula	absent	present
Vaginal ovejector	absent	present
Atrophy of digestive system and muscles in males	present	absent
Ventromedian precloacal papillae	absent	present
Specialized subventral pre- and postcloacal sensilla	absent	present
Spicules	short and slender	robust
Gubernaculum	dorsal wall of spicule pouches slightly cuticularized	complex; crura and cuneus present
Copulatory musculature	not extensive	strongly developed
Metanemes	loxometanemes	ortho- and loxometanemes

came clearer. The turgor disappeared, resulting in longitudinal cuticular folds at both body ends.

### The Separation of *Leptosomatum* and *Leptosomatides*

*Leptosomatides euxinus* Filipjev, 1918, and *Leptosomatum elongatum* Bastian, 1865, are the type-species of their genera. *Leptosomatum elongatum* sensu de Man, 1893 is without doubt identical with *L. elongatum* Bastian, 1865. Both type-species have been studied and compared. The two genera can be distinguished by the characters listed in Table 1.

One may wonder why Filipjev (1918) hesitated to transfer *L.-um arcticum*<sup>2</sup> and *L.-um grebnickii*, both described by him in 1916, to *Leptosomatides*. This may be explained in the following way. In 1912 Ssaweljev gave a poor description of a female, which read as follows:

“23. *Leptosomatum tetrophthalmum* n.sp. ♀—12.7; a = 60; b = 7; c = 75. Der Bau des Kopfendes ähnlich wie bei *Leptosomatum elongatum* Bastian, 1865 (de Man, 1893). Hinter den rotbraunen, kegelförmigen mit lichtbrechenden Körperchen versehenen Augen noch ein Paar heller Pigmentflecke, ähnlich wie bei den Enoplusarten. Nervenring am Ende des vorderen Oesophagusdrittels, Vulva am Ende des zweiten Körperdrittels. Querfasernschicht der Cutis am Vorderende zu sehen. Palafjord, Mogilnojesees.”

<sup>2</sup> *L.-um* and *L.-ides* are used in this section as abbreviations for *Leptosomatum* and *Leptosomatides* respectively.



No original material of Ssaweljev (1912) is present in the collection of the Zoological Institute in Leningrad but it is plausible that Filipjev saw this female (Platonova pers. comm.). In the collection, a slide is present (number 5267 dated 12-IX-1915), from the same locality identified by Filipjev as *L-um tetrophthalmum* Ssaweljev, 1912. Beside this specimen, some females are present, labelled *L-um tetrophthalmum* dated 22-IX-1925, and females, without additional eye pigment, labelled as *L-um elongatum* Bastian, 1865; both identified by Filipjev and published by Platonova (1967).

All these specimens resemble *L-ides euxines* closely in the structure of the vulvar region. Assuming that the ovejector was characteristic for the type-species of *Leptosomatium*, Filipjev could not use it, to separate the two genera.

Re-study of *elongatum* sensu Platonova, 1967 (sensu Filipjev), revealed that Filipjev was in error regarding the identity of *L-um elongatum* sensu Bastian, 1865 and de Man, 1893. *L-um elongatum* sensu Filipjev and Platonova has all the characters diagnostic for females of the genus *Leptosomatides* as have *L-um tetrophthalmum*, *L-um arcticum* and *L-um grebnickii*. These characters are absent in *L-um elongatum* sensu de Man, 1893.

This means that *L-um tetrophthalmum* sensu Platonova, 1967; *L-um elongatum* sensu Platonova, 1967 nec Bastian, 1865; *L-um arcticum* Filipjev, 1916 nec Mawson, 1958 and *L-um grebnickii* Filipjev, 1916 belong to *Leptosomatides*. They will be discussed in another paper. *L-um arcticum* sensu Mawson, 1958 will be discussed under *L. kerguelense*.

No syntypes of *L-um tetrophthalmum* Ssaweljev, 1912, are present; it must be considered a species inquirenda.

### Morphological Observations

In *L. bacillatum*, a cephalic capsule is present in females but not in males. De Man (1893) and Timm (1953) gave attention to this capsule in *L. elongatum* and the closely related *L. acephalatum* respectively. I will show that the reported difference between these two species, in structure of the cephalic capsule, does not really exist.

The supposed difference in head structure between *L. elongatum* sensu de Man, 1893 and *L. elongatum* subsp. *acephalatum* Chitwood, 1936 was the main reason for Timm (1953:230) to raise the latter to species level. For females of *L. acephalatum* Timm described "six pairs of fine sclerotized pieces, symmetrically arranged around the 'cap' of oesophageal tissue," which was presumed to be homologous to "un système de deux lignes chitineuses et très minces . . . et qui font défaut dans la region dorsale" as described by de Man (1893) in *L. elongatum*. This comparison is the result of an incorrect interpretation of de Man's paper; neither de Man's nor Timm's passage concerns the cephalic capsule.

De Man in fact described the anterior end of the ventrosublateral pharyngeal glands. He described the cephalic capsule as "une sorte de charpente chitineuse, radiairement symétrique et située à la périphérie, à laquelle s'insère évidemment l'extrémité antérieure de l'oesophage."

In whole mounts, the cephalic capsules seems to be a refractive structure that quickly disappears out of focus and, therefore, Mawson (1958) described sclerotized pieces in what she considers to be *L. arcticum* and Timm (1960) described



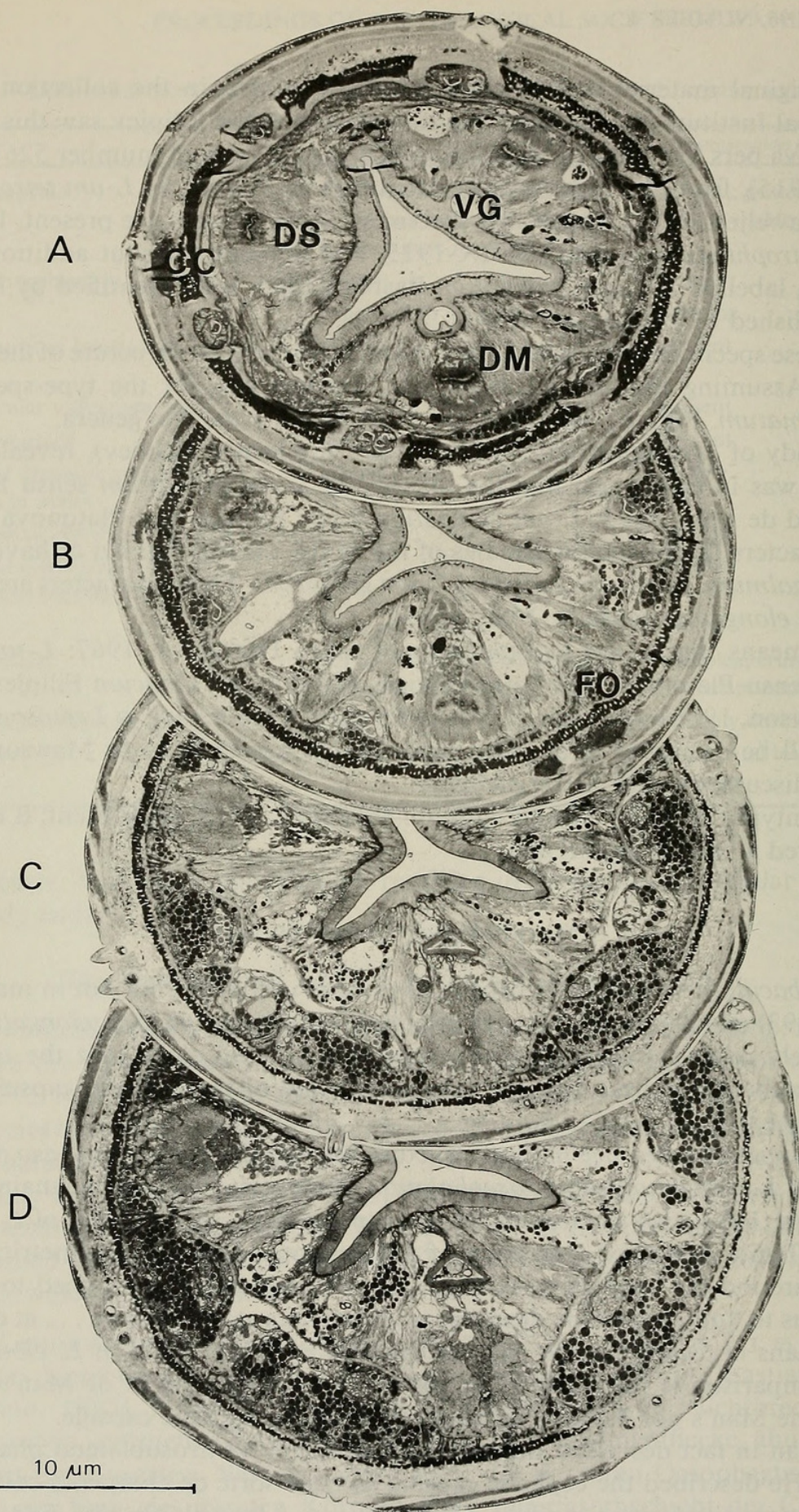


Fig. 1. Sections through cephalic capsule of female *L. bacillatum* at four different levels. A, Anterior part; B, Two microns posteriad of A; C, On level of cephalic papillae; D, Through posterior part of capsule. (CC: Cephalic capsule, LG: Ventrosublateral pharyngeal gland, DM: Dilator muscles, FO: Foramen, DS: Dorsal sector of pharynx.)



similar structures for *L. ranjhai*. Inglis (1964:289) is quite sure that what Timm (1953) is describing is the "lining of the cephalic ventricle, one component of each pair of sclerotized pieces corresponding to the musculature supplying the onchia and the other component corresponding to the radius of the oesophagus."

In Fig. 1A–D the structure of the anterior end of a female is represented spatially. Section A is cut through the anterior part of the capsule; B two microns posteriorly; C at the level of the cephalic papillae and D just in front of the posterior suture.

The cephalic capsule—the "charpente chitineuse" of de Man—is a conoid capsule; reduced but homologous to the capsule in *Leptosomatides*, *Syringonomus*, and the Thoracostomatinae. In pre-adult males this capsule is present; it disappears when the cuticle is shed during the last molt, so it is a part of the cuticle. In Fig. 1A–D this layer can be seen as an electron-dense layer that consists of radially arranged rods, 0.75  $\mu\text{m}$  in length.

The posterior suture is almost straight; the anterior is interrupted by the inner labial sensilla, but neither suture is visible in glycerin-slides. De Man (1893) depicted this rim in his Fig. 9b.

The anterior end of the pharynx is affixed to the cephalic capsule. Each sector of the pharynx contains four dilator muscles (Fig. 1 DM), paired two by two; these muscles were termed the "sclerotized pieces" by Timm (1953). The space between these bundles, the foramen (Inglis 1964), is filled by the socket cell of the labial sensilla on the inner and the pocket cell on the outer side; the latter, which is filled with electron-dense droplets, increases posteriorly in size and is pushed aside into the body-cavity at the posterior end of the cephalic capsule. The two paired bundles are separated by the pharyngeal nerves, apodemes and associated muscles, and ventrosublaterally by the pharyngeal glands. The cephalic ventricle (Inglis 1964) is absent in *Leptosomatium*.

The "secondary capsule" as depicted by Filipjev (1916, Fig. 4a) is a space, filled with a spongy tissue, between the cuticular layers; I am not certain about its ultrastructure. This space might be homologous to the lunula. These secondary capsule and lunula have been underestimated as a diagnostic character in the Leptosomatidae. In males, if the cephalic capsule is lacking, this secondary capsule (Fig. 10b) may be confused with the cephalic capsule.

In the anterior part of the pharynx I have observed one dorsal and two ventrosublateral glands. The former empties into the pharyngeal lumen; the cuticularized duct is easily observed in glycerin specimens. The ventrosublateral glands (Fig. 1 LG) open on the lips as described by Timm (1953). These ducts are also cuticularized; de Man (1893) described them as "deux lignes chitineuses" being absent in the dorsal region.

In contrast to the amphids in females and juveniles, the amphids in males are remarkable. In males the fovea is an inverted cardiform pouch with, in *L. bacillatum*, a length of 10  $\mu\text{m}$  which opens to the exterior by a small pore. The fusus is about 15  $\mu\text{m}$  in diameter, fusiform, 40  $\mu\text{m}$  long, and leading to the amphidial gland (Fig. 10b). Some preliminary observations are worth mentioning.

In *L. bacillatum* the amphidial glands are 600–900  $\mu\text{m}$  long and extend to the pharynx base. In related species with a short pharynx, the glands overlap the intestine. The posterior part is glandular and contains secretory organelles. The duct of the amphidial gland is filled with numerous microvilli (Fig. 2) with a diameter of 0.2–0.5  $\mu\text{m}$ : their number exceeds 500 in the posterior part of the



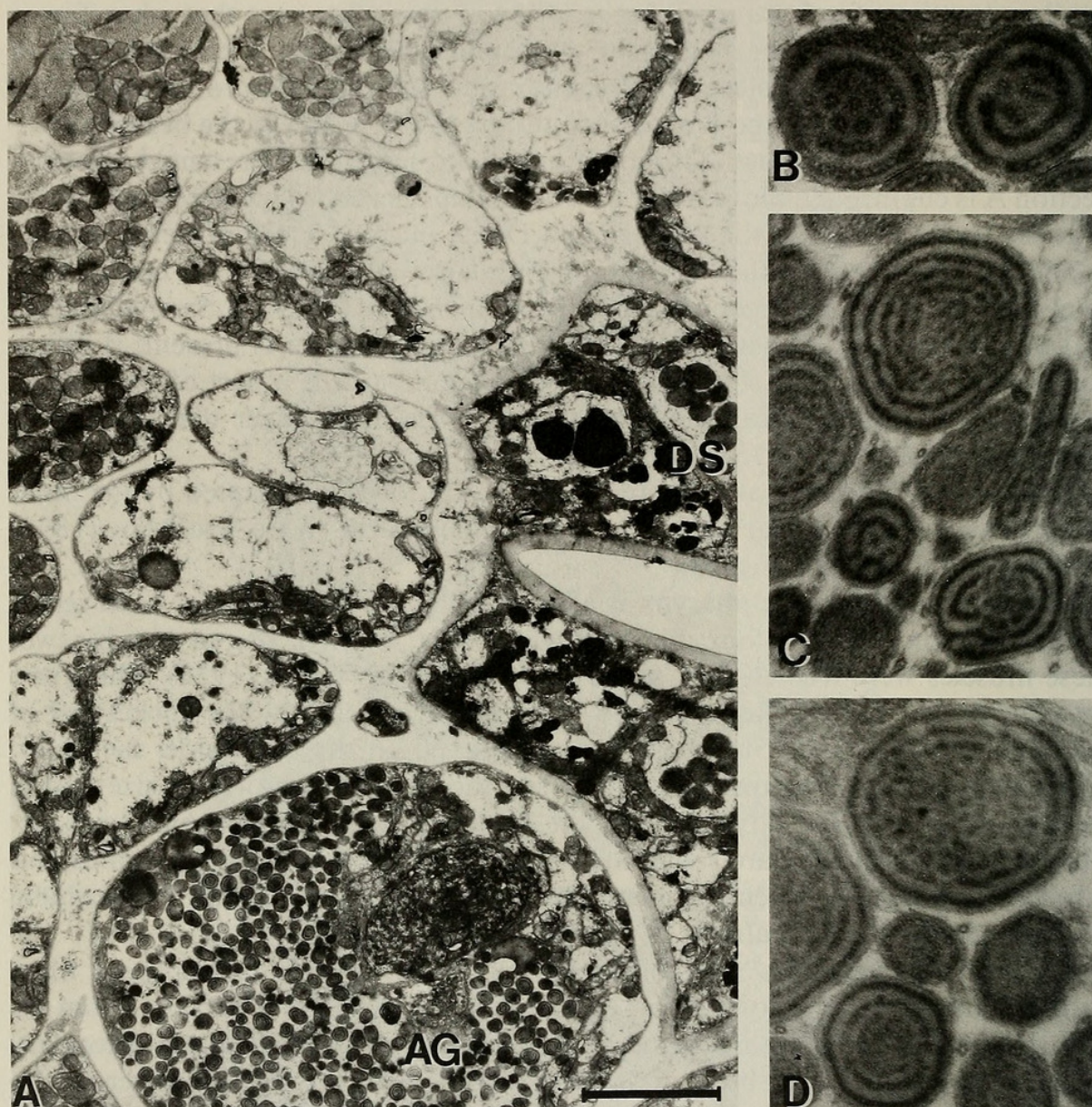


Fig. 2. A, Section through posterior end of fusus in *L. bacillatum*, male. AG: Amphidial gland, DS: Dorsal sector of pharynx. B–D, Details of microvilli. (A, 10,000 $\times$ ; B, 100,000 $\times$ ; C and D, 80,000 $\times$ .)

fuscus. Posteriorly the number decreases; at the level of the ganglia of the amphidial nerves, 50 could be counted.

These microvilli are composed of alternating electron-dense and transparent layers, the latter on the outer side. The outer two or three electron-dense layers are circular without interruptions; interiorly these layers become irregular and single fibers are present in the center. In the anterior part of the fusus the villi are enclosed in membraneous chambers that resemble the amphidial chambers in the male of *Meloidogyne incognita* (see Baldwin and Hirschmann 1973). In the fovea 14 modified cilia could be counted.

No features were observed that contradict the opinion that the villi originate in the anterior part of the fusus. This means that some of the villi reach a length of at least 400  $\mu\text{m}$ . However, as the free-floating ends of the microvilli are extended in the direction of the amphidial gland, it is difficult to imagine that, unless actively



involved in transport, the microvilli are not expelled by the excretory products of the amphidial glands. Numerous ganglia are situated anteriorly and posteriorly to the nerve ring in both sexes. In males two of them, at one corresponding body diameter behind the nerve ring, are swollen and therefore, I presume them to be the ganglia of the amphidial nerves (Fig. 9a). They are easily seen under a dissecting microscope. Under the light microscope the amphids in other species of *Leptosomatum* resemble those in *L. bacillatum*. Bastian (1865) depicted these amphidial glands in the male of *L. elongatum*.

The renette is situated ventrally in the posterior part of the pharynx and is restricted to females; in specimens with a short pharynx, "b" exceeding 8, the gland partly or wholly overlaps the intestine. The renette is not always developed, but the pore is always visible in laterally mounted females. In males I have observed neither pore nor renette, and as hundreds of males have been studied, I am certain that they are absent.

The renette in females might have been functionally replaced by the amphidial glands in males of *Leptosomatum*, although it will be difficult to prove this hypothesis.

The ventromedian cells in the pseudocoelom, here termed coelomocytes to avoid the misleading term pseudo-coelomocytes, may be present in juveniles and adults. In some populations they are developed, in others not; populations occur in which these cells are restricted to a part of the population. Further details concerning their structure and function are wanting.

Subventral pre- and postcloacal sensilla are designations for those specialized setae, often placed on hemispherical swellings of the cuticle, which differ from those in the subdorsal region, and which are functionally related to the role of the male, as depicted e.g., for *Leptosomatides inocellatus* by Platonova (1978:73). In *L. punctatum*, which is provided with cephalic setae, the setae are sparsely distributed over the whole body, just as other species with setae. They also occur in the subventral and subdorsal cloacal region.

In the lateral epidermal chords of *Cylicolaimus* (see de Man 1889a:1) glands are present; in *Pseudocella* they are more simply built, and these glands are restricted to the vulvar region in *Leptosomatides*. These glands are absent in *Leptosomatum* as are the vaginal ovejector and intra-cuticular vulva granula, which, however, are present in *Leptosomatides*.

The pre-cloacal ventromedian supplement is present in *L. punctatum* and in males of *L. keiense*. The copulatory musculature is not reduced in the former and a correlation may exist between the presence of the supplement and this musculature.

### Descriptive Section

#### *Leptosomatum* Bastian, 1865

*Phanoglene* Eberth, 1863 nec Nordmann, 1840 (Filipjev, 1918).

*Leptosomatum* Bastian, 1865:144.—de Man, 1893:102–103.—Filipjev, 1918:42–44.—Platonova, 1976:58–60.

*Type-species*.—*L. elongatum* Bastian, 1865.

*Diagnosis*.—Leptosomatinae Filipjev, 1918, with weakly developed cephalic capsule, apparent only in optical section; reduced in male or in both sexes. Somatic



tissues atrophied in males. Renette and cervical pore restricted to females, incidentally present in juveniles. Renette usually situated in pharyngeal region, but not always developed.

Sexual dimorphism expressed in structure of amphids. Males with enlarged fovea; amphidial glands strongly developed and outstretched over almost entire pharyngeal length. Pre- and postneural region of pharynx covered by numerous ganglia in both sexes. Ganglia of amphidial nerves in males much enlarged and situated at one body-diameter posterior to nerve ring.

Stoma narrow, without onchia or odontia. Labial sensilla subcuticular, cephalic and cervical sensilla seti- or papilliform. Dorsal pharyngeal gland orifice at level of amphids in pharyngeal lumen; orifices of ventrosublateral glands on anterior end; ducts cuticularized.

Ocelli provided with lens. Caudal glands long; overlapping intestine. Lunula present. Ventral row of coelomocytes usually present. Dorso- and ventrolateral orthometanemes present.<sup>3</sup>

Male diorchic, testes opposed and outstretched. Female amphidelphic, antidromic. Gubernaculum simply built; without appendices. Precloacal ventromedian supplement reduced or absent. Subventral pre- and postcloacal genital sensilla absent.

#### *Leptosomatum abyssale* Allgén, 1951

Allgén described a female, originating from a depth of 400 m from the Sagami Sea near Japan, which was not available for this study. He mentioned the shape of the amphids—small and transversely oval—as different from *L. elongatum*. It would be interesting to know whether *L. abyssale* has ocelli.

The description is absolutely inadequate; no details on the cephalic capsule, sensilla, or vulvar region are given. Until the slide is available for re-study, *L. abyssale* must be considered a species inquirenda.

#### The *Leptosomatum bacillatum* Complex

To this complex belong *L. bacillatum* (Eberth, 1863), *L. acephalatum* Chitwood, 1936, and *L. sachalinense* Platonova, 1978. These species might be conspecific, but in view of the geographical distribution and minor differences in size and ratios, I advise considering them as closely related species until well preserved material becomes available for a detailed comparison.

#### *Leptosomatum bacillatum* (Eberth, 1863) Bastian, 1865

Figs. 3–12

*Phanoglene bacillatum* Eberth, 1863:19–20.

*L. elongatum* Bastian, 1865:145.

*L. filipjevi* Schuurmans Stekhoven, 1950:27.

*L. gracile* Bastian, 1865:145–146.

*L. sabangense* sensu Allgén, 1942:8.

*L. tuapsense* Sergeeva, 1973:1710–1712.

? *L. sp.* Kreis, 1928:139.

<sup>3</sup> For terminology see Lorenzen 1978.



Nec *L. elongatum* sensu Platonova, 1967; *L. gracile* sensu Allgén, 1954. (Both belong to *Leptosomatides* and will be discussed in another paper.)

*Diagnosis.*—Cephalic and cervical sensilla papilliform. Cephalic capsule present in juveniles and females; absent in males. Ventromedian precloacal supplement absent. Caudal pore terminal. Ocelli relatively far posterior. Renette restricted to pharyngeal region.

*Distribution.*—Mediterranean, Black Sea, North Sea, (Spitsbergen ?, Vancouver Island ?, California ?, South Georgia ?, Gulf of Panama ?, Argentina ?, Lesser Antilles ?, and Falkland Islands ?).

I consider records with a question mark to be doubtful because of the numerous errors Allgén made in identifications of species of *Leptosomatum* and *Leptosomatides*. For example, *Leptosomatum microlaimum* Allgén, 1957, is a species of *Leptosomatides* and has been transferred to that genus by Platonova (1976). Specimens identified by Allgén (1954) as *Leptosomatum gracile* are doubtful as he mentions the presence of vulvar glands, which are characteristic for *Leptosomatides*. The specimens identified by Allgén as *Leptosomatum sabangense* belong, as far as can be determined, to *Leptosomatum bacillatum*. Finally, it is doubtful that Allgén has accurately identified any of the species belonging to the *Leptosomatum bacillatum*-complex, given the morphological similarity among members of that complex and the superficial nature of Allgén's work.

*Synonymy.*—Eberth (1863:20) described *L. bacillatum* as *Phanoglene bacillatum* from: "unter Corallen im Hafen von Nizza." Attempts were made to obtain material from the type-locality but harbor constructions had been carried out and in a letter dated 1980-1-22 Dr. A. Meinesz stated: "... qu'il n'y a pas de 'banc de coraux' dans le port de Nice et il n'y en a jamais eu." Recently Marc Lavaleije (pers. comm.) suggested that Eberth might have meant the calcareous alga *Corallina*. In (1878) de Man reported *L. bacillatum* from the Mediterranean, but as he did not make permanent mounts of the nematodes collected prior to 1876 (Loof 1961), only the description can be used.

Filipjev (1918) reported *L. bacillatum* from the Black Sea. These specimens are still present in the collection of the Zoological Institute in Leningrad where I was able to study them. Filipjev mentioned the presence of the opening of the gland of the accessory organ; this could not be confirmed. The amphids of the female were vaguely perceptible; presumably Filipjev depicted the male amphid in the figure of the female (Fig. 1a). In 1922 he reported gravid females with a length of 12.8 mm.

Schuermans Stekhoven (1950) renamed *L. bacillatum* sensu Filipjev, 1918, as *L. filipjevi* because Filipjev did not depict the cuticular pores on the tail tip. These pores are depicted by Eberth (1863) and were also present in the juvenile described by Schuurmans Stekhoven (1950). Examination of *L. filipjevi* Schuurmans Stekhoven, 1950 (= *L. bacillatum* sensu Filipjev, 1918) showed that the pores are present.

*Leptosomatum elongatum* Bastian, 1865, was described from Falmouth; this material has probably been lost. De Man (1893) gave a redescription based on specimens from the type-locality, and synonymized *L. elongatum* and *L. gracile*. These slides are still present in the collection of the Zoological Museum in Amsterdam, and were placed at my disposal. They are labelled:



- A 57, *Leptosomatum elongatum* B. ♀ Trefusis VI-1892. Zoöl. Museum A'dam. V. As. no. 652.
- A 58, *Leptosomatum elongatum* B. ♂♀ Trefusis VI '92. Zoöl. Museum A'dam. V. As. no. 653.
- A 58, *Leptosomatum elongatum* B. ♂♀ Trefusis VI '92. Zoöl. Museum A'dam. V. As. no. 654.
- A 59, *Leptosomatum* sp.? ♂ Wimereux 1890. Zoöl. Museum A'dam. V. As. no. 655.

The nematodes were in a rather good condition; they only showed some shrinking caused by dehydration as mentioned before, but were identical to those recently found along the Dutch coast and *L. bacillatum* sensu Filipjev, 1918.

Compared with the description, the mounted specimens of 1893 have decreased in size by approximately 30 percent. De Man was accustomed to studying specimens prior to mounting; only a part of his material was transferred to permanent slides (Loof 1961). Measurements were carried out on living specimens or on specimens recently fixed. It is known that an increase in the volume of a nematode in a hypo-osmotic environment, is expressed especially as an increase in body length. Thus de Man possibly measured his material in diluted seawater. According to Newall (1976) the length of *Enoplus brevis* increases by 40% in a 10% diluted seawater solution.

*Leptosomatum tuapsense* Sergeeva, 1973, was found to be identical to *L. bacillatum*. According to Sergeeva *L. tuapsense* differs from *L. elongatum* by the setae (?) and structure and length of the spicula. De Man (1893) mentioned a spiculum length of 98  $\mu\text{m}$ , whereas Sergeeva gave 94  $\mu\text{m}$ ; the length of the cephalic sensilla is 1.5 and 1.25  $\mu\text{m}$  respectively.

The holotype of *L. tuapsense* (slide N 8092), which is deposited in Leningrad, has been studied. The shape of the spicula, as depicted by Sergeeva, is not the lateral view; the manubrium is less cuticularized than depicted by her. The presence of a cephalic capsule could not be confirmed; she depicted the ducts of the ventrosublateral pharyngeal glands. The dimensions of the amphids have to be halved; the breadth of the fovea is one-sixth of the corresponding body diameter.

In the course of time, Sergeeva collected more material from the Black Sea, which was assigned to *L. bacillatum* (Eberth, 1863) and deposited at the Zoological Institute in Leningrad. I herewith synonymize *L. tuapsense* Sergeeva, 1973, with *L. bacillatum* (Eberth, 1863).

From the Swedish Museum for Natural History, Stockholm, three slides were placed at my disposal. They are labelled: "RMev Sthlm 3:13, 3:66, 3:82" and represent *L. sabangense* sensu Allgén, 1942:8. Although these juveniles are in a poor condition, I consider them identical to *L. bacillatum*.

Regarding *L. sp.* Kreis, 1928, more information is desired. It might belong to *L. bacillatum*; the length and ratio "c" however, need confirmation.

#### New Records

1. Den Helder, The Netherlands (52°58'N, 4°42'E); Nov 1970. 3 juv., 4 ♂ and 8 ♀, collected from *Polysiphonia* sp. and *Halichondria panicea*. Littoral. Collection Nematology Department Wageningen.
2. Kattendijke, The Netherlands (51°33'N, 3°47'E); Oct 1970. 25 juv., 15 ♂ and



- 19 ♀, collected from *Halichondria panicea*. Littoral. Collection Nematology Department Wageningen.
3. Burghsluis, The Netherlands (51°40'N, 3°40'E); Feb 1978. 200 specimens from *Halichondria panicea*. Littoral. Collection Nematology Department Wageningen.
  4. Texel, 't Horntje, The Netherlands (53°01'N, 4°47'E); Jun 1977. 230 specimens collected by Robin den Ottolander from *Halichondria panicea*. Littoral. Collection Nematology Department Wageningen.
  5. Texel, Oudeschild, The Netherlands (53°03'N, 4°50'E); Nov 1970. 55 juv. 10 ♂ and 1 ♀, collected from *Halichondria panicea*. Littoral. Collection Nematology Department Wageningen.
  6. Wimereux, France (50°48'N, 1°34'E); 1 ♀, collected by de Man in 1890 and labelled "*Leptosomatum* sp." Collection Zoological Museum Amsterdam.
  7. Ambleteuse, France (50°48'N, 1°34'E); Jun 1978. 2 ♀, collected by Michiel Buil from *Halichondria panicea*. Littoral. Collection Nematology Department Wageningen.
  8. Banyuls, France (42°29'N, 3°07'E); 3 ♀ from unknown sponges. Jun 1976. Collection Nematology Department Wageningen.
  9. N.E. England. 1 ♀ and 1 ♂; collected by R. W. Warwick from *Laminaria* holdfasts at low tide on a rocky shore. Collection Smithsonian Institution Washington, D.C.

*Discussion and Description of New Records.*—The general morphology has been described by de Man 1893 (*L. elongatum*), Filipjev 1918, and Timm 1953 (*L. acephalatum*). The ultrastructure of the cephalic capsule and amphids, has been described in a previous section.

The study of the life cycle revealed an annual cycle for the Dutch population (4) and it is reasonable that this cycle is also present in other populations in temperate zones. The eggs are deposited in July and August; the length and development of the nematodes are correlated with the sampling date. There are indications that populations collected at corresponding days in different years show significant differences in length. This may be caused by food supply and/or temperature effects.

The renette is maximally developed in autumn. In August 1978, more than 50% of the females showed a more or less developed renette, whereas in the autumn of 1981 at the same locality ('t Horntje) this gland was found in less than 10% of the specimens.

Pre-adult females of the February population from Burghsluis can have a body length between 4 and 6 mm; pre-adults of Texel (June) always exceed 6 mm in length, and these pre-adults reach a length of 8 mm. Schuurmans Stekhoven (1950) described a juvenile from Villefranche measuring 9.5 mm.

Females continue growing after having reached the adult stage; for males, there is no evidence for length increase in the adult stage. The ratios are length-dependent and therefore correlated with the seasons. The ratios of the Dutch population are plotted on graphs to show the length dependance and variability (Figs. 3–6, 8).

Newly hatched juveniles reach a length of 1.4 mm; the maximum length of



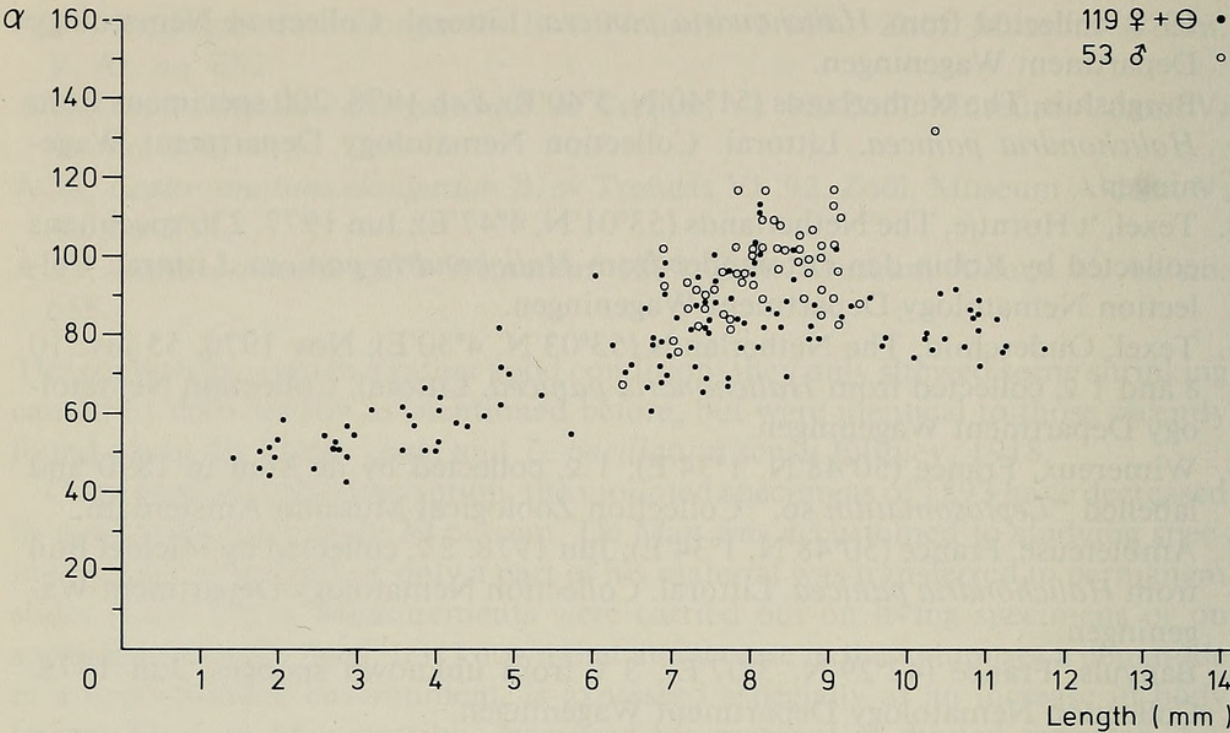


Fig. 3. Relation between ratio “a” (length/body width) and length, based on several *L. bacillatum* populations (Texel).

females from populations 2 and 3 never exceeded 12 mm. Population 4 yielded adults of 14 mm whereas one of the females from Banyuls measured 16.8 mm.

The variability of structure and length of spiculum and gubernaculum are given in Fig. 7.

The ocelli of *L. bacillatum* are placed relatively far posteriorly compared with

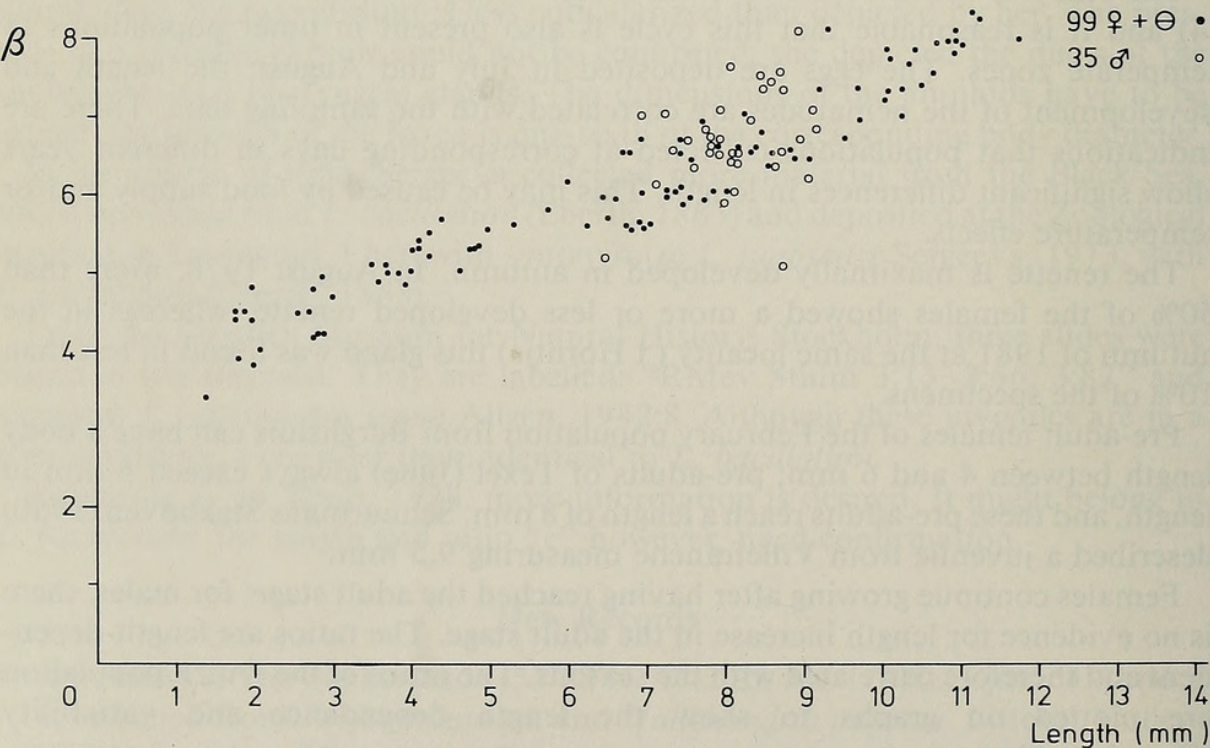


Fig. 4. Relation between ratio “b” (=length/pharynx length) and length, based on several *L. bacillatum* populations (Texel).



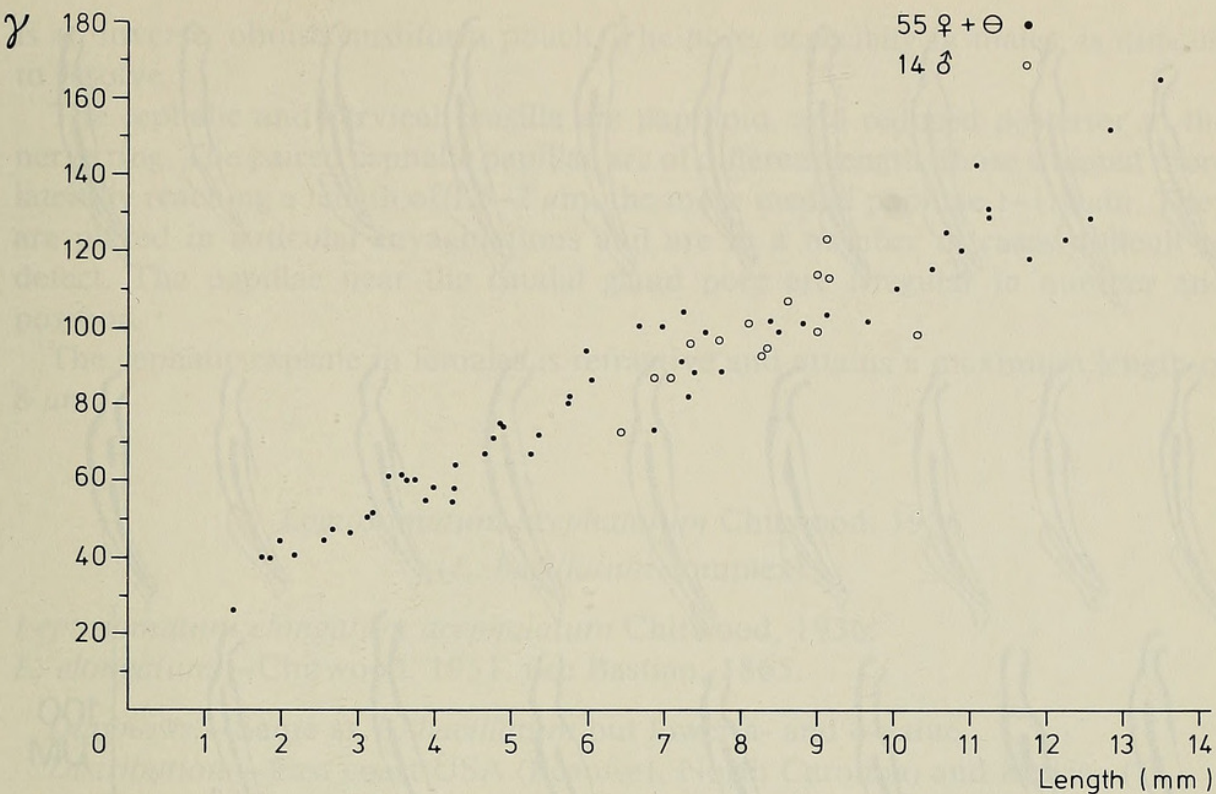


Fig. 5. Relation between ratio “c” (length/tail length) and length, based on several *L. bacillatum* populations (Texel).

*L. kerguelense* with which females could be confused. The distance from anterior end to ocelli, in the former species, is about 1.3 times the corresponding body diameter and up to 2.0 in the biggest females; in males it ranges from 1.4 to 1.7. In *L. kerguelense* the same calculation varies from 0.7 to 1.0 for females and

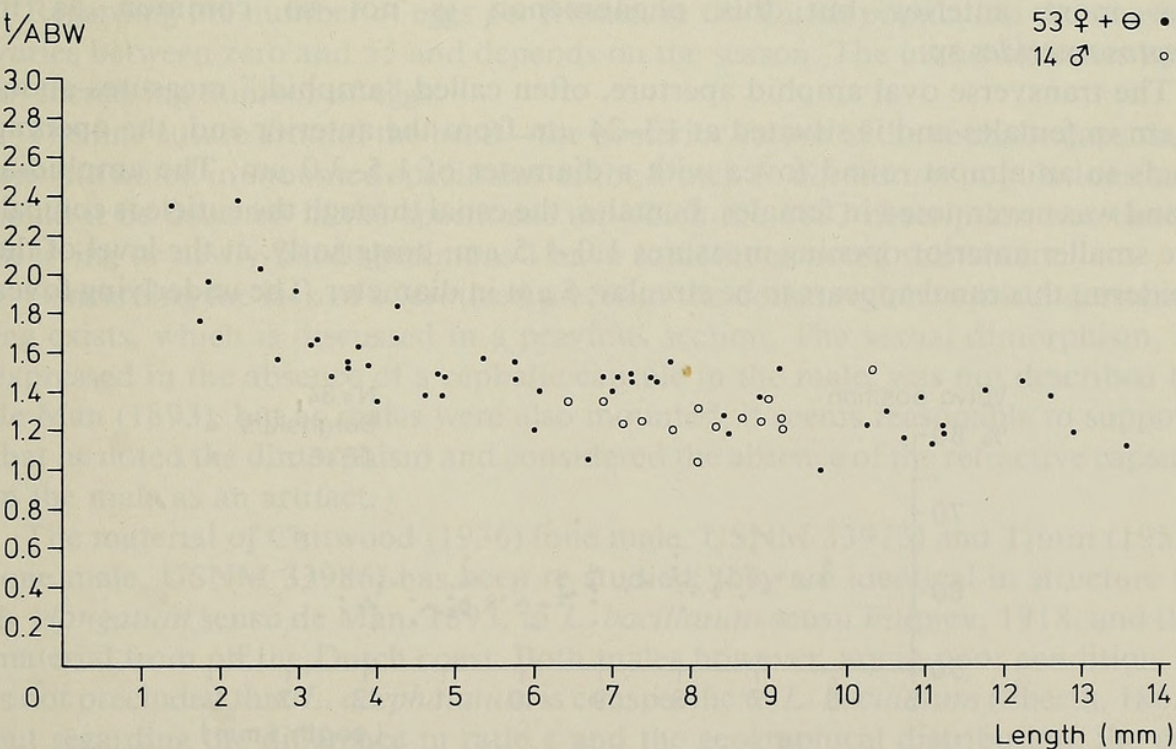


Fig. 6. Relation between “tail/anal body width” and length, based on several *L. bacillatum* populations (Texel).



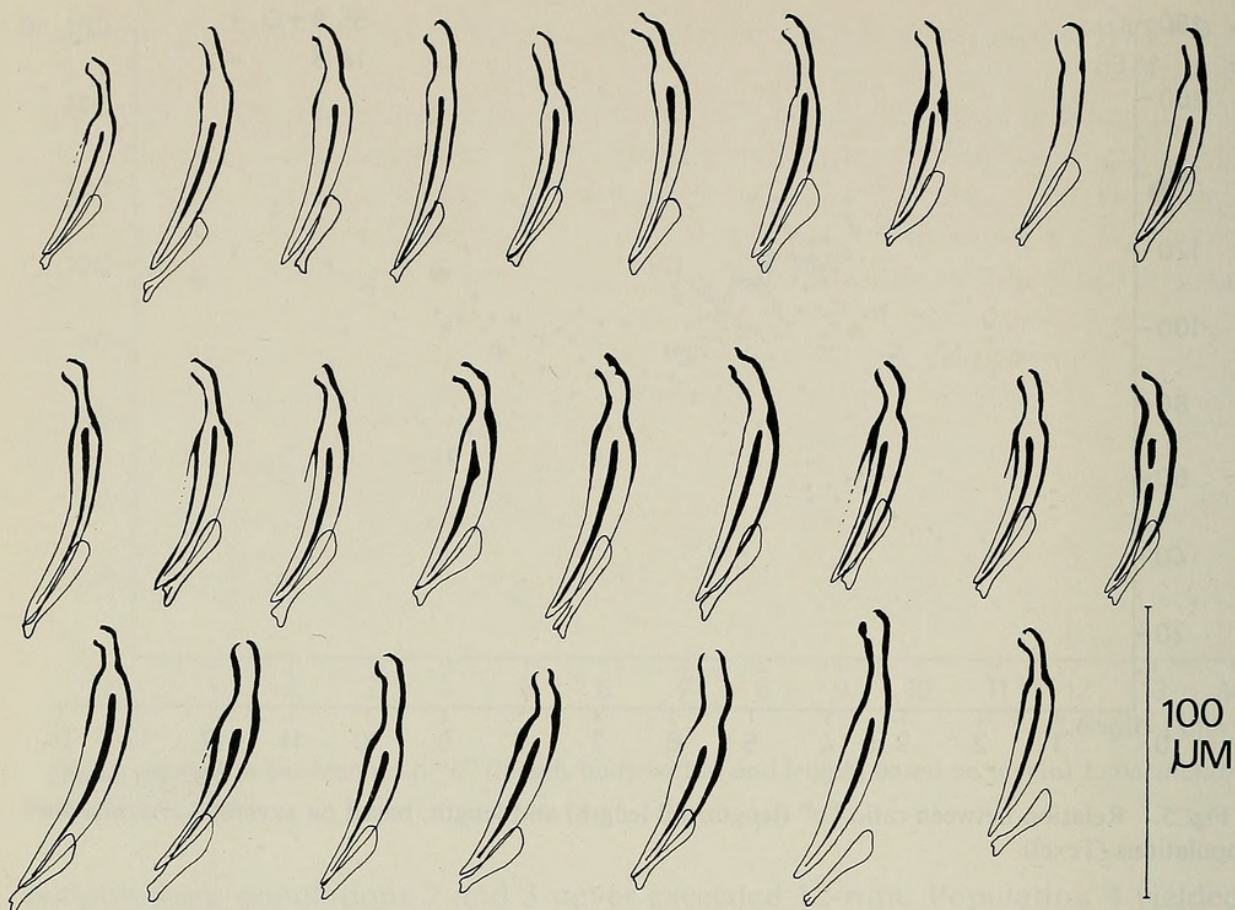


Fig. 7. Variability in spicule shape of the *L. bacillatum* population from Burghsluis.

from 0.8 to 1.1 for males. Incidentally the ocelli lie at slightly different levels—one more anterior—but this phenomenon is not so common as in *Leptosomatides* sp.

The transverse oval amphid aperture, often called “amphid,” measures about  $1\text{ }\mu\text{m}$  in females and is situated at  $13\text{--}24\text{ }\mu\text{m}$  from the anterior end; the opening leads to an almost round fovea with a diameter of  $1.5\text{--}3.0\text{ }\mu\text{m}$ . The amphidial gland was never noted in females. In males, the canal through the cuticle is conical; the smaller anterior opening measures  $1.0\text{--}1.5\text{ }\mu\text{m}$ ; posteriorly, at the level of the epiderm, this canal appears to be circular;  $5\text{ }\mu\text{m}$  in diameter. The underlying fovea

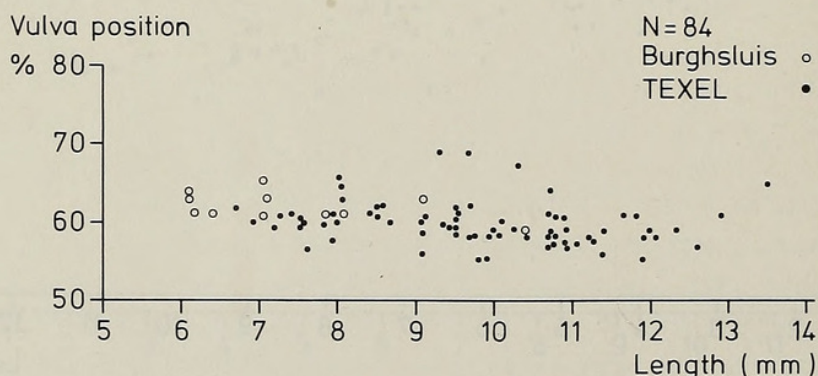


Fig. 8. Relation between  $V$  (=distance from anterior extremity to vulva  $\times 100$ /body length) and length, based on several *L. bacillatum* populations from Texel.



is an inverse, obtuse cardiform pouch. The pore, especially in males, is difficult to resolve.

The cephalic and cervical sensilla are papilloid, and reduced posterior to the nerve ring. The paired cephalic papillae are of different length; those situated more laterally reaching a length of 1.5–2  $\mu\text{m}$ , the more medial papillae 1–1.5  $\mu\text{m}$ . They are placed in cuticular invaginations and are in a number of cases difficult to detect. The papillae near the caudal gland pore are irregular in number and position.

The cephalic capsule in females is refractive and attains a maximum length of 8  $\mu\text{m}$ .

*Leptosomatum acephalatum* Chitwood, 1936

(*L. bacillatum*-complex)

*Leptosomatum elongatum acephalatum* Chitwood, 1936:

*L. elongatum*.—Chitwood, 1951, nec Bastian, 1865.

*Diagnosis*.—Same as *L. bacillatum* but lower a- and c-value.

*Distribution*.—East coast USA (Beaufort, North Carolina) and Mexico (?).

*Discussion of status*.—In 1936 Chitwood split off the variety *L. elongatum acephalatum* based on a male without cephalic capsule. In 1951 he united the variety with the nominate form after having found the female. Having studied material collected from the same sponge *Hymeniacidon heliophila*, Timm (1953) raised the variety to specific rank.

Timm's arguments were the difference in number of eggs, the fine suture around the head in de Man's specimens, the lack of sclerotized pieces in the dorsal head region, and the sexual dimorphism in head structure and size.

Regarding the number of eggs per female, in the Dutch population the number varies between zero and 55 and depends on the season. The uterus stretches with an increasing number of eggs.

The fine suture around the head—the posterior suture of the cephalic capsule—was not noted in mounted specimens of the Dutch *L. bacillatum* populations, nor could it be detected in the specimens on which the 1893 description was based. In living or newly-fixed specimens I have sometimes noted this suture.

Concerning the lack of sclerotized pieces in the dorsal region, a misunderstanding exists, which is discussed in a previous section. The sexual dimorphism, as expressed in the absence of a cephalic capsule in the male, was not described by de Man (1893), but as males were also mounted, it seems reasonable to suppose that he noted the dimorphism and considered the absence of the refractive capsule in the male as an artifact.

The material of Chitwood (1936) (one male, USNM 33973) and Timm (1953) (one male, USNM 33986) has been re-studied; they are identical in structure to *L. elongatum* sensu de Man, 1893; to *L. bacillatum* sensu Filipjev, 1918, and the material from off the Dutch coast. Both males however, are in poor condition. It is not precluded that *L. acephalatum* is conspecific to *L. bacillatum* (Eberth, 1863) but regarding the difference in ratio c and the geographical distribution, the decision to synonymize these species is postponed till more material from the type-locality becomes available.



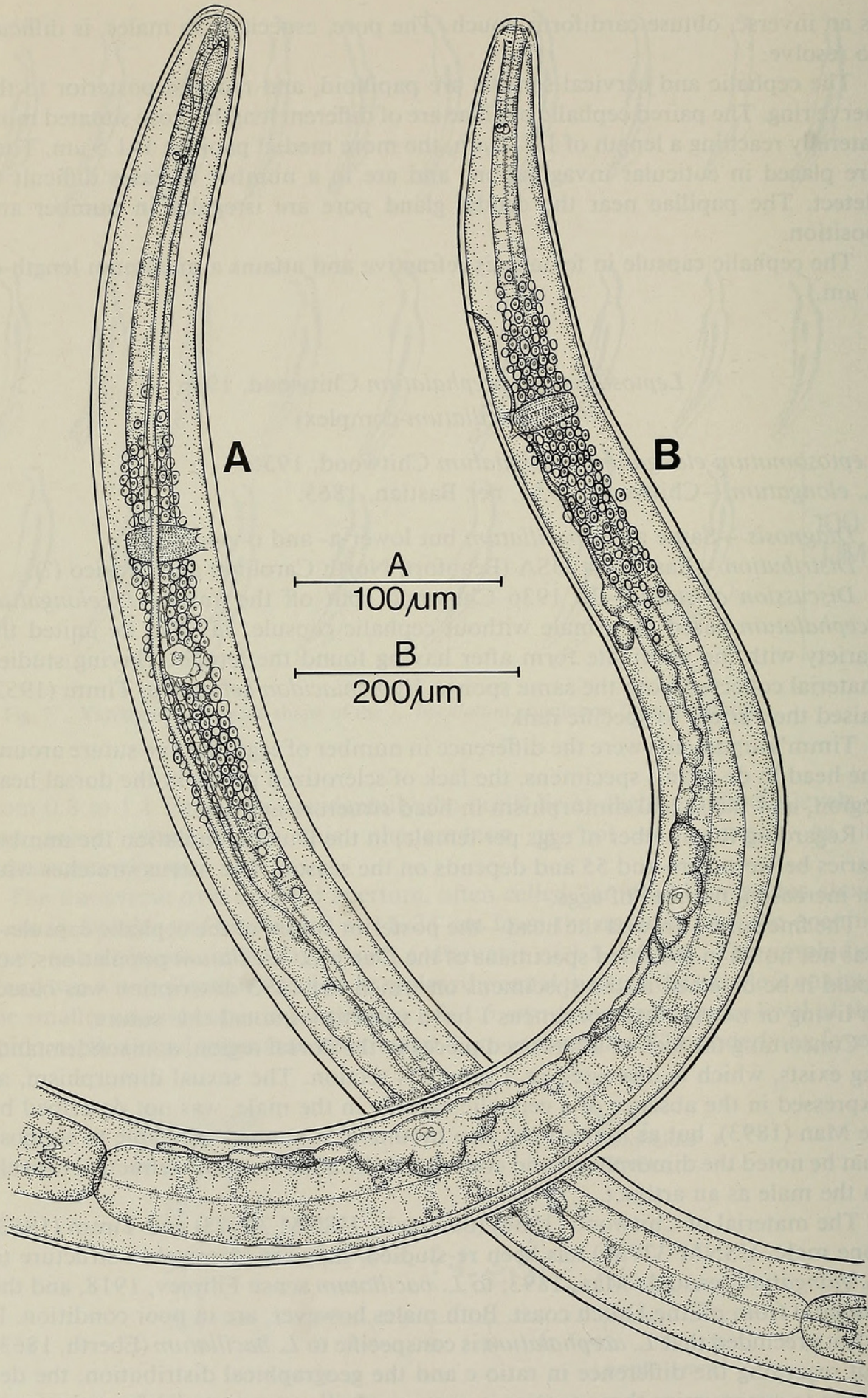


Fig. 9. *L. bacillatum* from Texel. A, Anterior end of male; B, Anterior end of female.



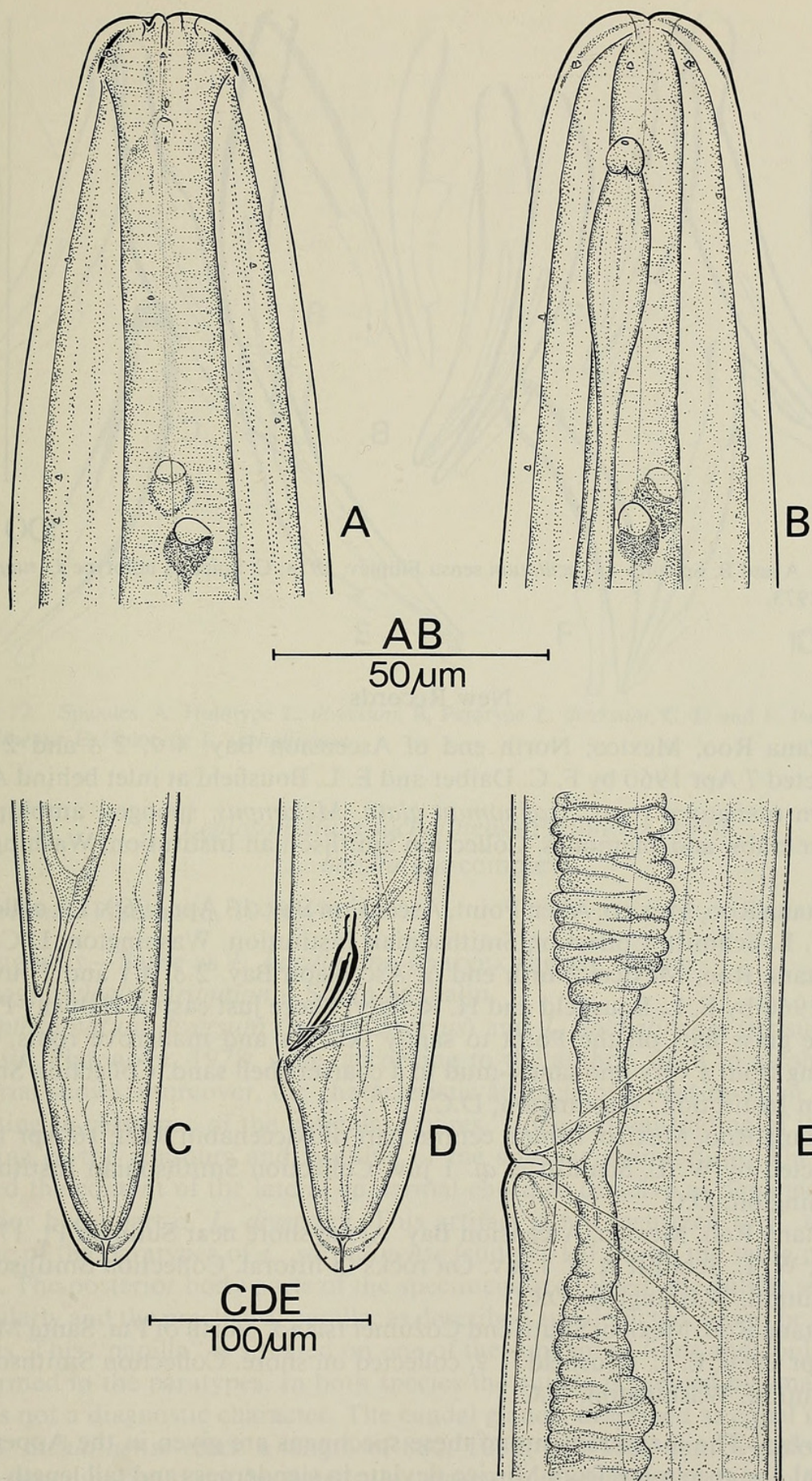


Fig. 10. *L. bacillatum*. A, Head of female, 102; B, Head of male, 76101; C, Posterior end female, 76102; D, Posterior end male, 76101; E, Vulvar region, (Burghsluis).



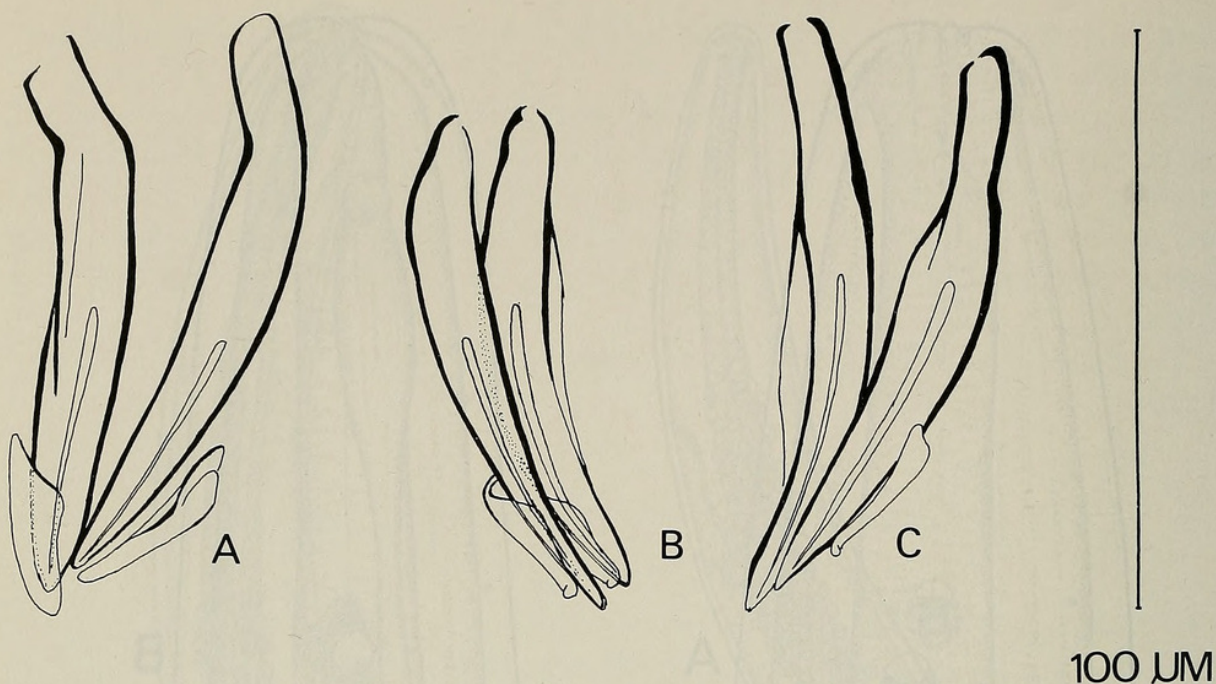


Fig. 11. A and B, Spicules *L. bacillatum* sensu Filipjev, 1918; C, Spicules holotype *L. tuapsense* Sergeeva, 1973.

#### New Records

1. Quintana Roo, Mexico; North end of Ascension Bay; 4 ♀, 2 ♂ and 2 juv. Collected 7 Apr 1960 by F. C. Daiber and E. L. Bousfield at inlet behind Allen Pt. On mangrove roots; *Isognomon alata*, *Melampus*, sponges, amphipods, fiddler crabs, and anemones. Collection Smithsonian Institution, Washington, D.C.
2. Quintana Roo, Mexico; Allen Point, Ascension Bay. 13 Apr 1960. 1 ♀, collected by W. L. Schmitt. Collection Smithsonian Institution, Washington, D.C.
3. Quintana Roo, Mexico; North end of Ascension Bay. 2 ♂, 4 ♀ and 1 juv. 15 Apr 1960 by E. L. Bousfield and H. Rehder. Shore just east of Halfway Point. Turtle grass flats off the Point to sandy beaches and mangrove roots, sand varying from a very fine sandy-mud to a coarser shell sand. Collection Smithsonian Institution, Washington, D.C.
4. Quintana Roo, Mexico; behind central part of Niccehabin Reef; 16 Apr 1960. Collected by W. L. Schmitt *et al.* 1 juv. Collection Smithsonian Institution, Washington, D.C.
5. Quintana Roo, Mexico; Ascension Bay. Along shore near Suliman Pt. 17 Apr 1960, W. L. Schmitt *et al.* 1 juv. On rocks in littoral. Collection Smithsonian Institution, Washington, D.C.
6. Quintana Roo, Mexico; South end Cozumel Island. North of Pta. Santa Maria. 22 Apr 1960. E. L. Bousfield. 1 ♀, collected on shore. Collection Smithsonian Institution, Washington, D.C.

*Remarks.*—The measurements of these specimens are given in the Appendix. In general, the specimens from Mexico deviate in slenderness and tail length from the Dutch *L. bacillatum* specimens. The diameter of the lens is 8 μm, compared with 7 μm in *L. bacillatum*.



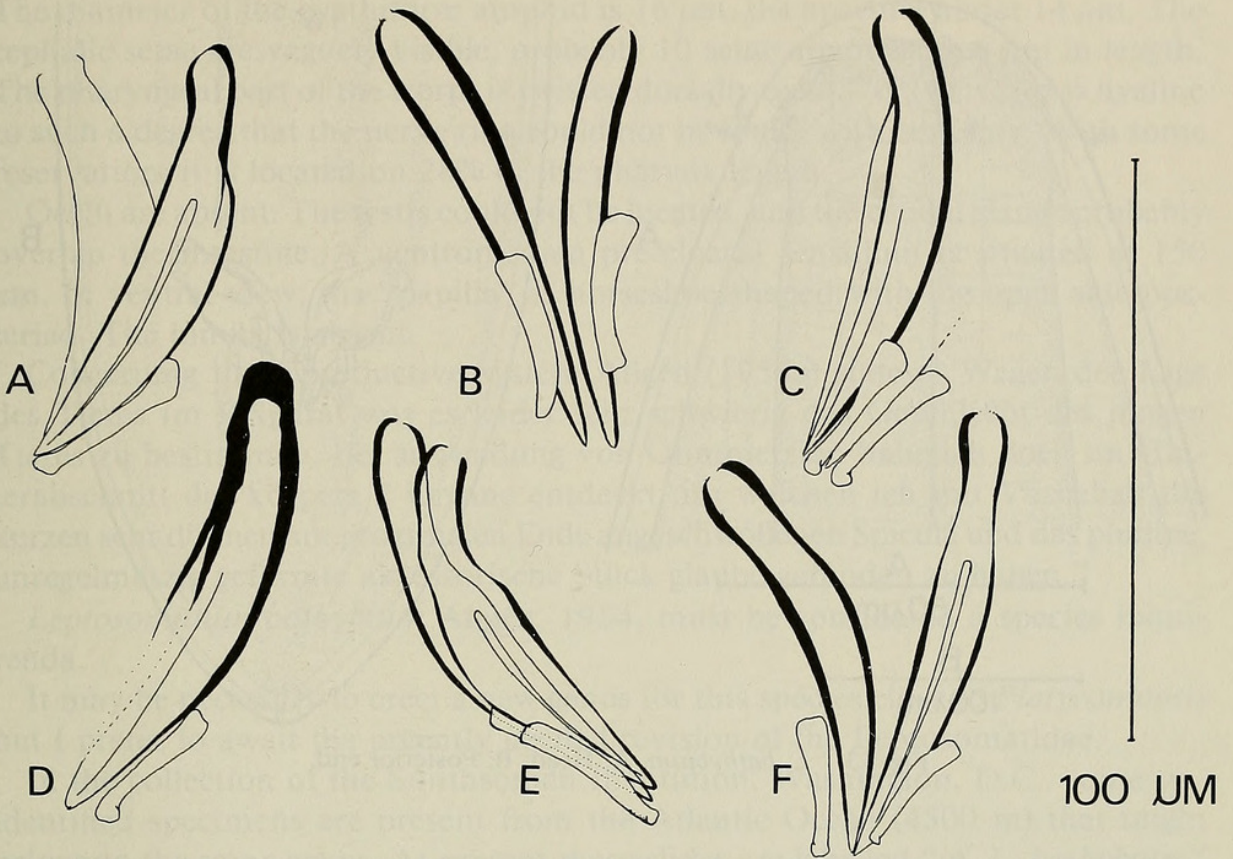


Fig. 12. Spicules. A, Holotype *L. diversum*; B, Paratype *L. diversum*; C, D and F, Paratypes *L. sachalinense*; E, Holotype *L. sachalinense*.

*Leptosomatum sachalinense* Platonova, 1978  
(*L. bacillatum*-complex)

*L. diversum* Platonova, 1978:495.

*Diagnosis*.—Same as *L. bacillatum*; pharynx slightly shorter.

*Geographical distribution*.—South Sakhalin.

*Leptosomatum diversum* (lapsus *diversus*) and *L. sachalinense* (lapsus *sachalinensis*) Platonova, 1978, were, according to the author, fixed in alcohol. This material shows, moreover, the characteristic artifacts of a post-mortem fixation, resulting in clearance of the cuticular “pores,” longitudinal folding of the body, clearing of the contours and swelling of the spicular manubrium. The alcohol caused the content of the lateral epidermal chord to dissolve as depicted for the anterior body part of *L. diversum*. This artifact is not restricted to *L. diversum* as one of the paratypes of *L. sachalinense* (slide 8013) shows the same phenomenon. The posterior body parts of the specimens are folded, the cuticle separated irregularly and the precloacal papilla, as described and depicted, has to be ascribed to this. This “papilla” is situated on one of the subventral folds and could not be confirmed in the paratypes. In both species the cuticle is pierced by small pores; this is not a diagnostic character. The caudal glands, described as equal in length for *L. sachalinense* reach a length of 880, 1090, and 1350  $\mu\text{m}$ . A difference in head structure could not be noted; this structure is identical to that in *L. bacillatum*. I herewith synonymize *L. sachalinense* and *L. diversum*. The holotype and the description of *L. sachalinense* closely agree.



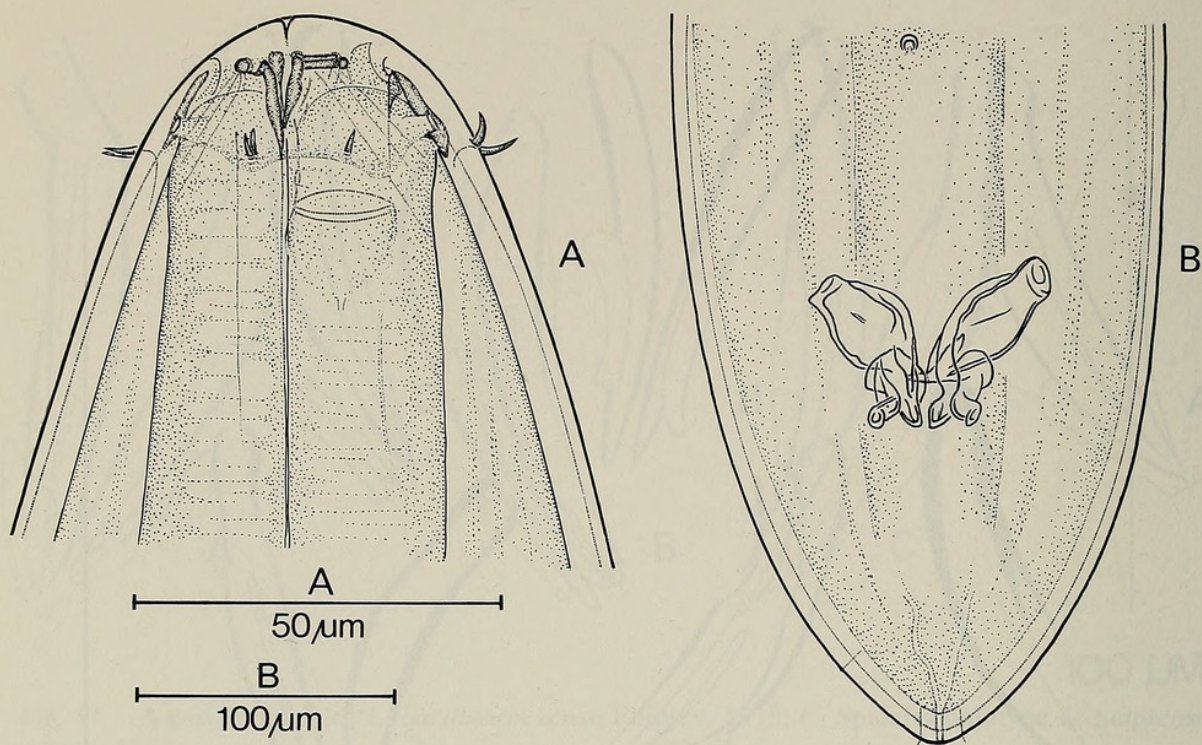


Fig. 13. *L. bathybium*. A, Head; B, Posterior end.

Ratio “b,” in the original description of *L. sachalinense* (females), has a higher maximum value than in the Dutch populations of *L. bacillatum*. However, personal examination of the paratypes revealed that the maximum value of “b” ( $b = 6.3\text{--}12.9$ ) is not as high as indicated by Platonova, and in personal communication with her, it has been determined that the datum is in error. The only feature in which *L. sachalinense* differs from *L. bacillatum* (Eberth, 1863), is the structure of the spicula; in some cases the manubrium is open, in some cases closed and heavily cuticularized (or swollen?). Although I am not able to distinguish this species from *L. bacillatum*, because of the poor condition of the first, I postpone the synonymization until more material becomes available for re-study.

*Leptosomatum bathybium* Allgén, 1954a

Fig. 13a, b

The holotype, a male from a depth of 4500 m was placed at my disposal by the Museum for Natural History at Göteborg. The type is labelled “The Swedish Deep Sea Exped. *Leptosomatum bathybium*, Allgén.”

Mounted on a slide, it could only be studied from one side. The fixation or way of mounting has caused a loss of contrast; only the cuticularized structures in cephalic and caudal region could be recognized. Moreover, the structures of the anterior region and their relative proportions could not be reconstructed due to flattening.

The interpretation of the internal head structure does not conform to the description given by Allgén (1954a). Each lip bears in the transverse plane a C-shaped cuticularized structure, the concave side medial. From the middle of these C-shaped structures, a connective piece runs to three “buccal rods” (or mandibles?) in the anterior part of the lumen. A cephalic capsule is present; the posterior suture of this capsule, which curves to produce shallow lobes, is distinguishable.



The diameter of the cyathiform amphid is 16  $\mu\text{m}$ , the aperture about 14  $\mu\text{m}$ . The cephalic setae are vaguely visible; probably 10 setae are present; 6  $\mu\text{m}$  in length. The pharyngeal part of the worm is twisted dorsally over 370°. This part is hyaline to such a degree that the nerve ring could not be found with certainty. With some reservation, it is located on 28% of the pharynx length.

Ocelli are absent. The testis could not be located, and the caudal glands probably overlap the intestine. A ventromedian pre-cloacal sensillum is situated at 150  $\mu\text{m}$ . In ventral view, the "papilla" is horseshoe-shaped with the open side posteriorly. The lunula is absent.

Concerning the reproductive system Allgén (1954a) states: "Wegen der Lage des Tieres im Präparat was es leider sehr schwierig das Geschlecht des jungen Tieres zu bestimmen. Bei anwendung von Ölimmersion habe ich doch im Hinterabschnitt des körpers 2 Organe entdeckt, im welchen ich mit Vorbehalt die kurzen sehr dünnen am proximalen Ende angeschwollenen Spicula und das plumpe, unregelmässig geformte akzessorische Stück glaube gefunden zu haben."

*Leptosomatum bathybium* Allgén, 1954, must be considered a species inquirenda.

It may be necessary to erect a new genus for this species close to *Platycomopsis* but I prefer to await the urgently needed revision of the Leptosomatidae.

In the collection of the Smithsonian Institution, Washington, D.C., some unidentified specimens are present from the Atlantic Ocean (4500 m) that might belong to the same genus. At present these slides are labelled "cf. *L. bathybium*" and are at the disposal of the next revisor.

#### *Leptosomatum behringicum* Filipjev, 1916

The material, on which the original description was based, was collected by Grebnickii in 1880 in the Bering Sea. Platonova (1976) gave a redescription in which she indicated two holotypes: 5780 and 5781. The first contains a complete female, the other a single head. Platonova and I have agreed to exclude 5781 and to designate 5780, deposited in the Zoological Institute, Leningrad, USSR, as lectotype.

Filipjev (1916) remarked that the weak color of the eye pigment was caused by alcohol used as a fixative, and that older females show traces of disintegration.

Specimen 5780 is mounted in glycerin-gelatin, situated dorsoventrally in such a way that the structure of vulva and vagina could not be determined; this difficulty was reinforced by the filled uteri. In the anterior gonad, 9 eggs are present; the posterior contains 14 eggs that are pressed against each other and have a flattened appearance.

The type-specimen of *L. behringicum* which I have examined was in such poor condition that it was impossible to obtain additional information concerning the structure of head, vagina, vulva, and lateral epidermal chord. It is impossible, therefore, to decide whether it belongs to *Leptosomatum* or *Leptosomatides*, and it has to be considered a species inquirenda.

#### *Leptosomatum breviceps* Platonova, 1967

In 1967 Platonova described a nematode from Filipjev's collection. The slide, numbered 7383, bears the superscription: VIII-1914, Barentz Sea, Kolski's Gulf,



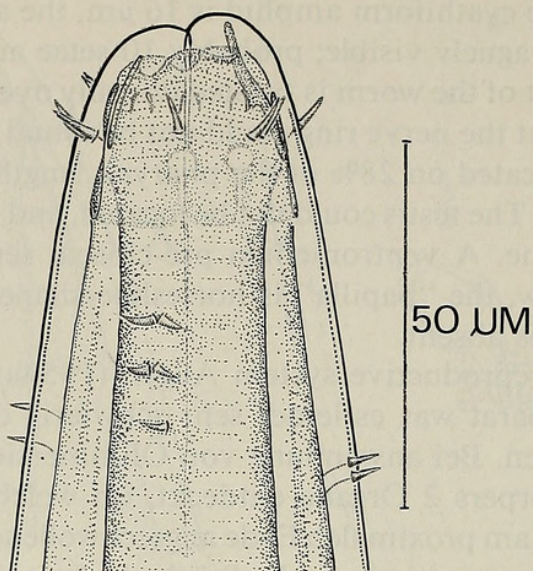


Fig. 14. Anterior end *L. caecum* Ditlevsen, 1923, Lectotype.

I. Filipjev, *L. brev.* ♀ (juv.) and is deposited in the Zoological Institute, Leningrad, USSR.

The description of 1967 and the redescription of 1976 did not mention that the description was based on a juvenile. The formation of the vulva had started, but was not completed.

The cuticular layers were split, resulting in a space of  $3.5\ \mu\text{m}$  at the anterior end and  $2\ \mu\text{m}$  at the pharyngeal base. This phenomenon might indicate that the last molt was imminent. According to Platonova's (1967) illustration, the anterior end is orientated dorsoventrally; the posterior part laterally. Both illustrations are modified. I have found that neither the anal opening nor the rectum could be observed, the tail is probably longer than described. The anterior cervical setae are slightly shorter than the cephalic setae, and they are progressively smaller posteriorly.

This specimen is extremely flattened, supported by glass-rods of  $28\ \mu\text{m}$ . The medial portion of the exteriormost cuticular layer is a more or less compact layer at the anterior end, comparable to the spongy layer in the male of *L. bacillatum*. This layer was incorrectly called "head capsule"; the anterior part of the space was termed "stoma ring." The setae are broken or partly invisible.

Having setiform cephalic sensilla, a ventrally orientated spinneret and no cephalic capsule, this juvenile resembles *L. punctatum*. As only one juvenile is known, I consider *L. breviceps* Platonova, 1967, a species inquirenda, the more so because it was found far outside the known area of *L. punctatum*.

*Leptosomatum caecum* Ditlevsen, 1923

Fig. 14

In 1923, five specimens of a nematode were collected by Ph. Dollfus near Rockall Island from a depth of 240 meters and offered to Ditlevsen for examination. Two slides were obtained from the Zoological Museum in Copenhagen, and Dr. Kirkegaard was so kind as to give permission to remount the nematodes, which had been embedded in glycerin-gelatin. One slide is labelled "Pourquoi



Pas SA 207 26 Prof. 240m. fond à Lophohelia. Dollfus. *Leptosomatum caecum* n.sp. Hj. Dittl.”; the other without indication n.sp. I have added 1342 and 1343 respectively. The dimensions of the specimens (for the abbreviations see p. 852) were as follows:

S	SN	L	DNR	PL	CL	NW	PW	MW	AW	V%
F	1342	9950	416	1528	90	88	104	132	90	60
F	1343	9660	370	1340	85	82	99	143	85	63

Each specimen has little optical contrast, but slide 1343 shows, more or less, the contours of the cephalic capsule, which resembles that of *Pseudocella* and is herewith designated as lectotype; the other female, slide 1342, is too hyaline to observe the capsule.

Ditlevsen (1923) incorrectly interpreted the position of the amphids; although rather hyaline, they are slightly perceptible and situated as usual in the lateral lacunae. I did not depict them. The cephalic setae, of which 10 are present, reach a length of 9–10  $\mu\text{m}$ . The cervical setae do not exceed 6  $\mu\text{m}$ ; their position on the left and right body halves is not alike. The lateral vulvar glands are present; the vaginal ovejector seems to be absent as are the pre- and postvulvar sensilla and groups of setae near the caudal pore. The caudal glands are short and restricted to the tail as depicted by Ditlevsen. In the lateral epidermal chord, big vacuoles or glands can be seen with a diameter of 40  $\mu\text{m}$ . The cuticle thickness varies from 6  $\mu\text{m}$  at the pharyngeal base to 9  $\mu\text{m}$  near the anal opening.

Although Filipjev probably did not examine these specimens, he suggests in a footnote (1927:94) that *L. caecum* might belong to *Pseudocella*, with which I agree.

The transferring of *L. caecum* to *Pseudocella* makes *P. caeca* (Ditlevsen, 1923) a secondary homonym to *P. coeca* (Ssacljev, 1912) according to art. 58 sub 1 of the Code. If not a synonym of one of the other nominal species in *Pseudocella*, *L. caeca* must be renamed; I propose to postpone this decision until a revision of *Pseudocella*.

#### *Leptosomatum clavatum* Platonova, 1958

*Leptosomatum kerguelense* Platonova, 1958:60–61, partim.

*Diagnosis.*—Cephalic and cervical sensilla papilliform. Cephalic capsule in female 10  $\mu\text{m}$  long. Ocelli far posterior. Ratio “c” less than in *L. bacillatum* of comparable size. Male unknown.

*Distribution.*—Kerguelen and Macquarie islands.

*Discussion.*—The identity of this species, which was found at the Kerguelen Islands, is fixed by the designation of the lectotype in 1968 (see discussion of *L. kerguelense*). Only females and juveniles are known. They differ from *L. kerguelense* by the ocelli being situated far posterior at about 1.5 corresponding body diameters from the anterior end (in the type, which is severely flattened, the pre-ocellar length hardly exceeds the corresponding body diameter), a more slender body, longer tail ( $T/ABW = 1.5$ ), and the caudal pore being situated terminally.

Slides 5836, 6013, 7346, 7365, 7369, 7371, 7372 and 7377 belong to *L. clavatum* (lectotype 5835). Because type-material of the Zoological Institute in Leningrad is not loaned, I was not able to measure the specimens in detail. The



Table 2.—Dimensions of *L. clavatum*. DF, distance to fovea; C, cuticle thickness at pharynx base. For other abbreviations see p. 852.

Sn	L	DF	DL	C	PL	CL	a	b	c	V%	Labelled as:
5835	14,420	28	109	2	1909	187	67	7.6	77	60	Allotype <i>L. clavatum</i>
5836	12,430	29	118	8	1726	129	52	7.2	96	61	Allotype <i>L. kerguelense</i>
6013	10,860	24	126	10	1411	145	46	7.7	75	59	Paratype <i>L. kerguelense</i>

measurements are presented in Table 2. Although slide 5835 is labelled as "allotype" it represents the lectotype because Platonova (1968) designated this slide as holotype.

#### *New record*

1. Macquarie Islands (54°32'S, 158°59'E); 15 Feb 1967. 3 juv., 11 ♀ and 1 ♂; 112–124 m. Collection Smithsonian Institution, Washington, D.C.

*Remarks.*—On morphological grounds, as far as is known, the population from the Macquarie Is. cannot be distinguished from *L. bacillatum*. It deviates by the body proportions i.e., the placement of the ocelli, ratio "c" and, to a lesser degree, the body width. The cephalic capsule comes to 10  $\mu$ m, the amphidial aperture to 3  $\mu$ m, the fovea to 4  $\mu$ m, and the lens diameter varies from 6 to 9  $\mu$ m.

In this population, mixed with *L. kerguelense* and *L. sp. A* (see p. 846), one male was present that also might belong to the latter. It resembles the male of *L. bacillatum*. The spiculum length is 78  $\mu$ m, the gubernaculum 19  $\mu$ m, and the lens diameter is 9  $\mu$ m in dorsoventral view. The anterior part of the single male is twisted; dimensions of the amphids cannot be given. No figures are given since the females differ only in the above-mentioned characteristics. The redescription of the lectotype and information regarding the male are wanting.

#### *Leptosomatum groenlandicum* Allgén, 1954

##### Fig. 15

The male specimen, on which the description was based, was placed at my disposal by the Swedish Museum of Natural History. It is labelled: RMev Sthlm. 37.299 East Greenland King Osc.fj.N-37. The nematode, mounted in glycerin-gelatin, was remounted because air had penetrated under the coverglass.

This male was curved in the shape of a "c." The length of 14.544 mm given by Allgén (1954), is the straight distance between the extremities. The length along the body axis came to 17.5 mm. The nerve ring is situated 580  $\mu$ m from the anterior end; the lengths of pharynx and tail are 2950 and 270  $\mu$ m respectively. Ocelli are absent. The shortness of the gonads is remarkable; the anterior reaching a length of 478  $\mu$ m, the posterior 488  $\mu$ m. The junction of these gonads is situated 10.3 mm from the anterior end. The spicula are 160  $\mu$ m long; they are ensheathed by a gubernaculum that is characterized by a dorsal outgrowth with a membranous appearance. Ten cephalic setae are present; the lateral setae are broadened. Six rows of cervical setae are visible extending to the level of the nerve ring. Subdorsal of the cloacal aperture, 4 setae could be seen. The cuticle is thick, lunula absent, and the caudal glands could hardly be observed.



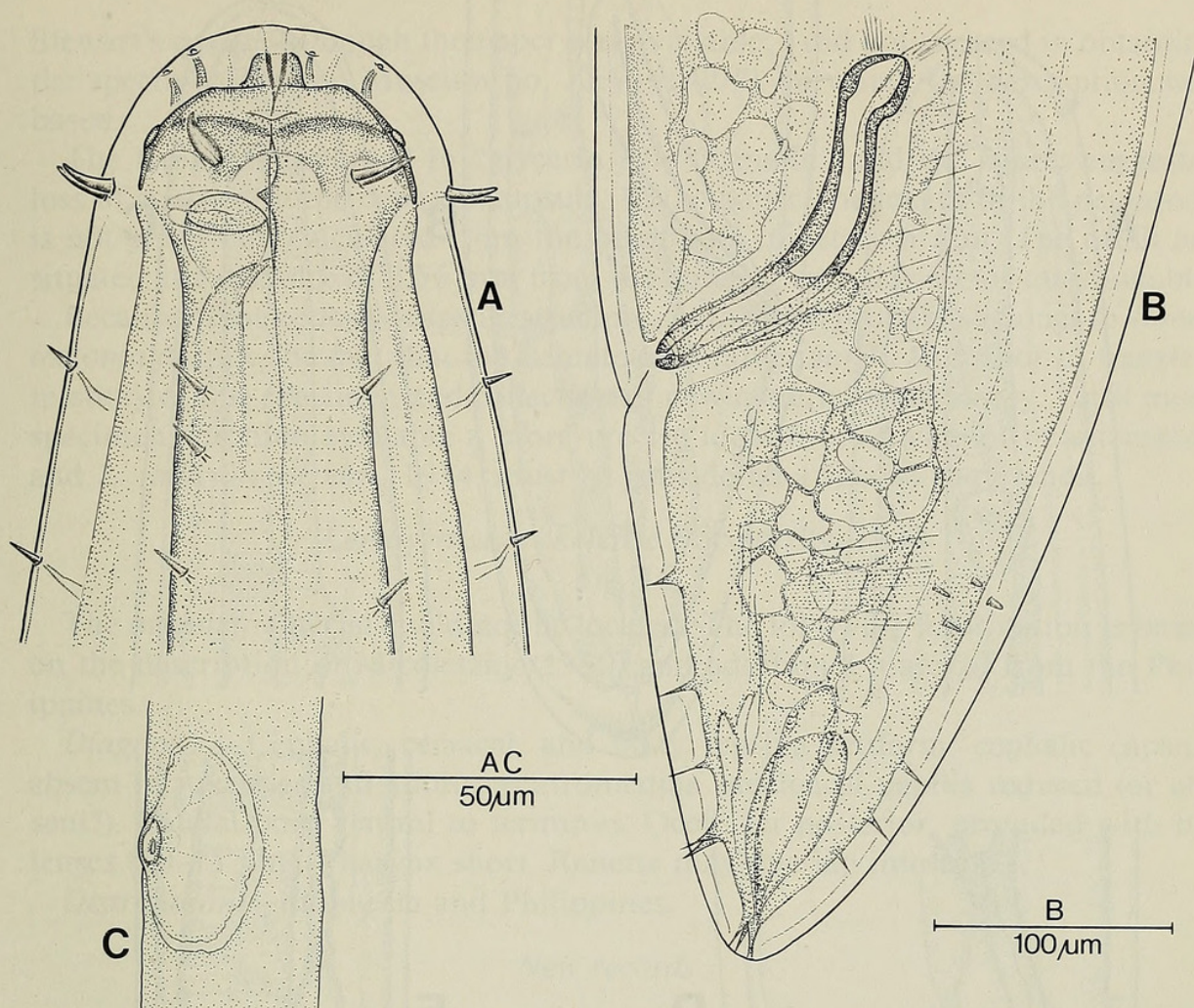


Fig. 15. *L. groenlandicum*. A, Head; B, Posterior end; C, Gland in lateral epidermal chord at level of pharynx base.

In the lateral epidermal chord, characteristic glands are present, which open to the exterior by a pore. These openings alternate dorsally and ventrally; sometimes 2 in sequence open on the same side. The presence of a coffee-bean shaped structure as described by Lorenzen (1981:136) could not be confirmed. The amphidial aperture is large and probably closed by a shield. Due to the flattening, the head structure is difficult to interpret; a cephalic capsule is present as are the cephalic ring and oesophageal capsule as termed by Inglis (1964). A tooth seems to be present in the pharyngeal lumen. More material however, is necessary for confirmation.

This male resembles *Leptosomatides inocellatus* Platonova, 1967, which differs from other *Leptosomatides* species by the absence of ocelli, lateral vulvar glands, ovejector, and lunula; and by the presence of lateral epidermal glands and amphids comparable to those of *Leptosomatum groenlandicum*. A new genus must be erected for these two species. At present I prefer to consider *Leptosomatum groenlandicum* a species inquirenda.

*Leptosomatum indicum* Stewart, 1914

This species was found in September 1903 near Chilka Lake in India. Filipjev (1921), in the additional notes on his revision, reported that he could not obtain



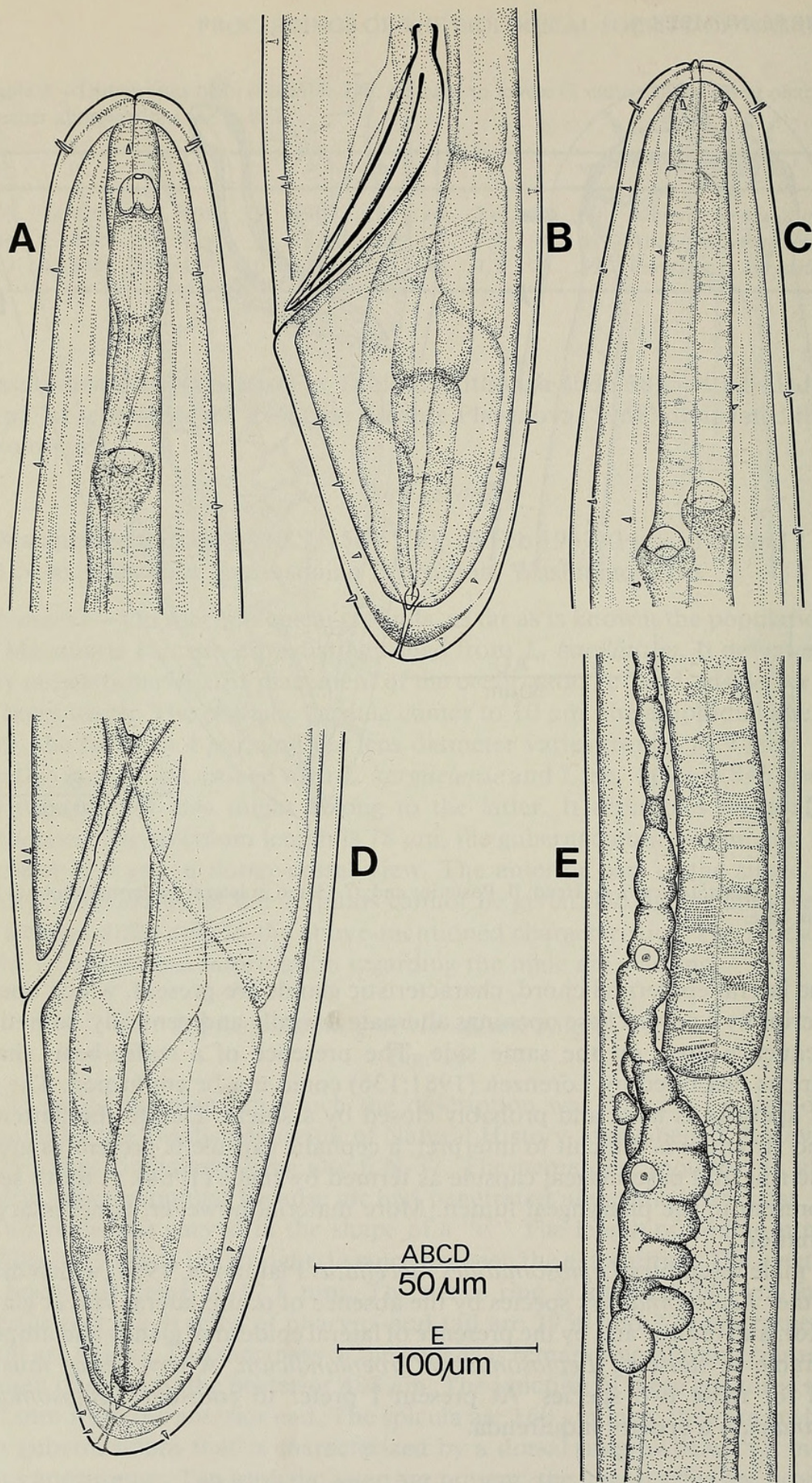


Fig. 16. *L. keiense*. A, Anterior end male; B, Posterior end male; C, Anterior end female; D, Posterior end female; E, Renette, 76047.



Stewart's paper. Although the paper was available, I did not succeed in obtaining the specimen (Indian Museum no. ZEV 6142/7) on which the description was based.

The female is mounted in "glycerin jelly-formalin" and the figures suggest a loss of contrast in the cephalic capsule. In the paper, the length of the nematode is not given but, calculated from the other data, must be 5 mm. The ocelli are situated at a distance of 0.56 mm from the anterior end; this seems questionable.

Because of the cephalic capsule structure, *L. indicum* probably belongs to *Deontostoma* despite the fact that the nematode is rather small. But prior to transfer, re-study of this specimen and collection of new material is necessary. Until more specimens become available a more precise identification cannot be attempted and *L. indicum* Stewart, 1914, must be considered a species inquirenda.

*Leptosomatum keiense* Micoletzky, 1930

Fig. 16

The original material could not be located. The following information is based on the description of Micoletzky (1930) and additional material from the Philippines.

*Diagnosis.*—Cephalic, cervical, and body sensilla setiform; cephalic capsule absent in juveniles and adults; ventromedian precloacal papilla reduced (or absent?). Caudal pore ventral to terminus. Ocelli far posterior, provided with big lenses (10–11  $\mu\text{m}$ ). Pharynx short. Renette may overlap intestine.

*Distribution.*—Indonesia and Philippines.

*New records*

Philippines; collected by E. G. Menez from algae (*Caulerpa* and *Eucheuma*). Sublittoral. Collection Smithsonian Institution, Washington, D.C.

1. Pangasinan; Telbang Cove (16°11'N, 120°03'E). 1 ♂, 1 ♀ and 1 juv. 3 Sep 1967.
2. Pangasinan; Cangaluyan Is. (16°22'N, 120°00'E). 2 ♂, 1 ♀ and 1 juv. 4 Sep 1967.
3. Salcedo, Bolic Is. (11°05'N, 125°39'E). 2 juv. and 1 ♂. 10 Sep 1967.
4. Great Santa Cruz Is. (5°52'N, 122°04'E). 1 juv. 18 Sep 1967.
5. Zamboanga; Sacol Is. (5°56'N, 122°11'E). 1 juv. 19 Sep 1967.

*Additional description and discussion.*—At first sight, this species resembles *L. punctatum* in the presence of setiform sensilla, the ventrally placed spinneret and the absence of a cephalic capsule. It can be distinguished by the greater diameter of the lens and the strong negative allometric growth of the pharynx. In some males the pre-cloacal papilla is absent.

*Leptosomatum keiense*, as described by Micoletzky, is probably a species-complex. According to Micoletzky (1930:280): "das präanal gelegene Ergänzungsorgan hatte ich nicht immer nachweisen können . . . die Augenlage ist veränderlich . . . Linsendurchmesser 5.8–6.7, selten bis 12  $\mu\text{m}$  . . . die Ausbildung des Kopfborsten zeigt individuelle Verschiedenheiten . . . b = 4.5–12.1."

The material from the Philippines shows the same variability. Males 76044 and 76045 (pop. 2), which are mounted in lateral position, do not show any trace of an accessory organ; in male 76041, mounted dorsoventrally, a papilla is present 141  $\mu\text{m}$  anterior to the cloacal vent, whereas in 76049, mounted laterally, this papilla lies at 126  $\mu\text{m}$ . Moreover, female 76040 (pop. 1) seems to be provided



with a ventromedian sensillum; this observation could not be confirmed in the other female (76046, pop. 2), which is twisted. The diameter of the lens is variable; 7–13  $\mu\text{m}$ . Male 76049 (pop. 3) has a lens of 13  $\mu\text{m}$  diameter, the two males of population 2 have a lens diameter of 7  $\mu\text{m}$ , but in general it varies between 9 and 11  $\mu\text{m}$ .

Notable is the short pharynx in one of the males ( $b = 11$ ). According to Micoletzky (1930), this phenomenon also occurs in females. In juvenile 76048, a renette is developed that extends posteriorly 700  $\mu\text{m}$  from the anterior end and overlaps the intestine. The amphidial glands in 76041, 76033, 76045 and 76049 attain lengths of 640, 800, 710 and 740  $\mu\text{m}$  respectively; in the latter the glands overlap the intestine.

The ocelli, situated at 1.5 times the corresponding body diameter from the anterior end, are provided with an intensively pigmented cup. The cephalic setae are 3.5–4.5  $\mu\text{m}$  long; short setae are situated over the whole body length. The amphids, 15–27  $\mu\text{m}$  from the anterior end, resemble those of related species. The fovea measures 8  $\mu\text{m}$  in the male and 3  $\mu\text{m}$  in the female; the apertures 2 and 1  $\mu\text{m}$  respectively. In one of the females (76040) the cervical pore could be detected at 227  $\mu\text{m}$  from the anterior end. The spiculum length is 63–66  $\mu\text{m}$ , the gubernaculum, if present, was not perceptible. Male 76045 is extensively atrophied; numerous coelomocytes of  $6 \times 4 \mu\text{m}$  could be seen throughout the body length of this male.

As stated above, *L. keiense* might be a mixture of at least two species. The ratio “pharynx length/tail length” ( $=P/T$ ) clearly separates the adults of population 2, in which  $P/T$  exceeds 12, from the remaining specimens in which  $P/T$  never exceeds 10. It is possible that the material of Micoletzky (1930) is still present and since the few specimens from the Philippines were collected at different localities, I postpone the separation, but I give some remarks regarding the specimens of population 2.

These males can be distinguished by their relatively small lenses (7  $\mu\text{m}$ ), the absence of a precloacal papilla, a slender body (“ $a$ ” = 97 and 104), a short tail (“ $c$ ” = 94 and 104), and the allometric trend less conspicuous than the other males. Ratio “ $c$ ” of the female, that has been found in the same sample, is also rather high; the lens diameter is 12  $\mu\text{m}$  in dorsoventral view. The juveniles from population 2 cannot be distinguished from those of the other localities.

*Leptosomatum kerguelense* Platonova, 1958

Figs. 17a, b, 18

*Leptosomatum crassicutis* Platonova, 1958:12–13

*Leptosomatum clavatum* Platonova, 1958:15–16 partim.

*Leptosomatum arcticum* sensu Mawson, 1965:315–316

*Diagnosis.*—Cephalic and cervical sensilla papilliform; cephalic capsule present in both sexes; ventromedian precloacal papillae absent. Caudal pore slightly ventral to terminus. Ocelli relatively far anterior. Renette restricted to pharyngeal region. Tail length equal to anal body width. Spicula long; gubernaculum reduced to 2 membranes.

*Type.*—Lectotype 5833; Zoological Institute Leningrad.



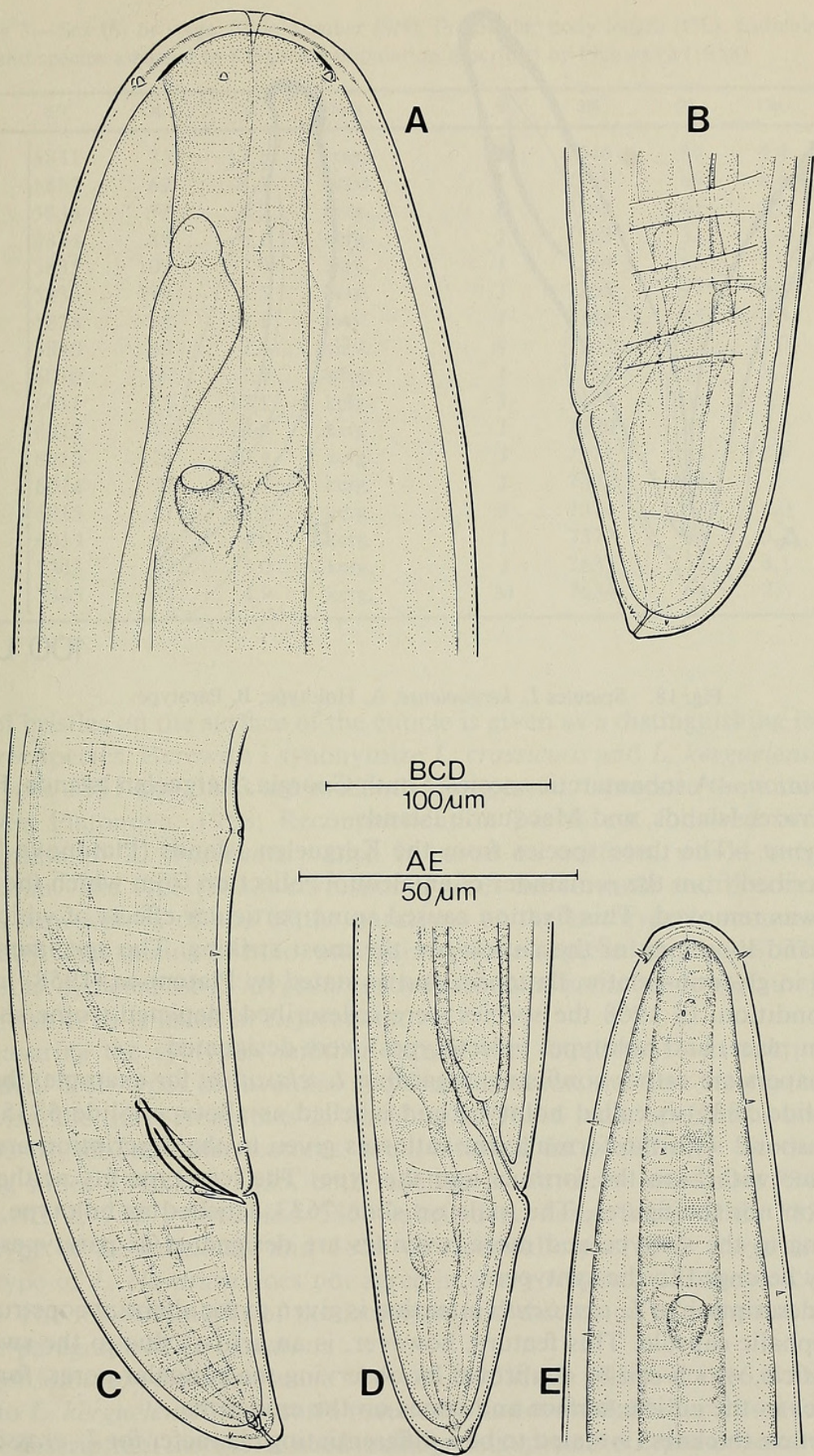


Fig. 17. *Leptosomatum kerguelense* (76056): A, Head; B, Caudal end. (C–E) *L. punctatum*: C, Caudal end of male, 1286-6; D, Caudal end of female, 1286-5; E, Anterior end of female, 76037.



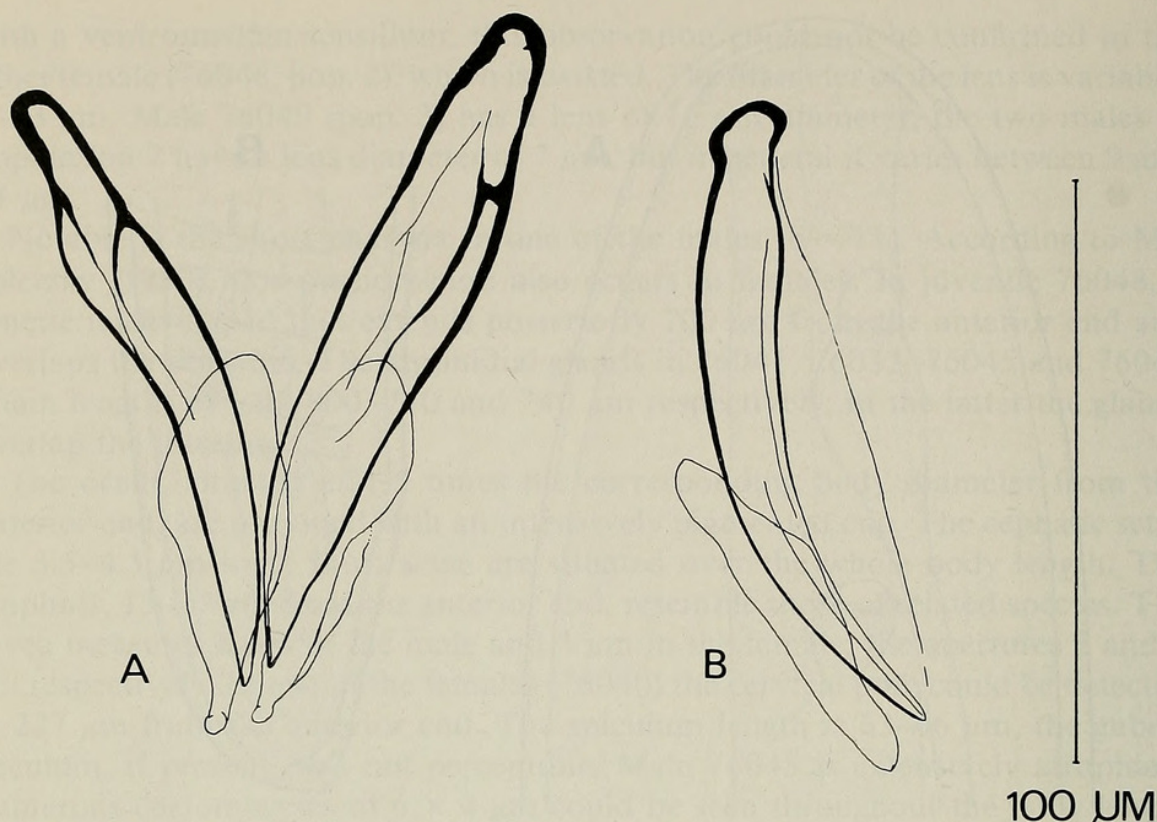


Fig. 18. Spicules *L. kerguelense*. A, Holotype; B, Paratype.

*Distribution*.—A subantarctic species: South Georgia, Kerguelen Islands, Heard Island, Crozet Islands, and Macquarie Islands.

*Synonymy*.—The three species from the Kerguelen Islands (Platonova 1958) were described from the remainder of an alcohol collection from which the macrofauna was removed. This fixation caused some particular effects of which the swelling and loosening of the cuticle are the most striking. The specimens are mounted in glycerin-gelatin, flattened, and as stated by Platonova (1958) in mediocre condition. In 1968 the species were redescribed, depicted (some shifting had taken place) and holotypes (=lectotypes) were designated.

Both papers are rather confusing; regarding *L. clavatum* for example, the lectotype (slide 5835) is called holotype and labelled as allotype. Slide 5835 does not correspond with the formula: the ratios as given in the description are also at variance with both the formula and the type. The lectotype fits neither the description nor the figures. The male on slide 7633, labelled as holotype, does not belong to the syntype and more juveniles are designated as paratypes than originally belonged to the syntypes.

In the description of *L. crassicutis* attention is given to the aberrant construction of the cephalic capsule. This feature, however, is an artifact due to the swelling of the cuticle, which can be confirmed by observing the cuticular pores, forming little holes in the cuticle surface and cones on the epidermis.

The cuticle thickness is stated to be a differentiating character for *L. crassicutis*. I have measured the cuticle at the level of the pharyngeal-intestinal junction, as did Platonova, and the pre-ocular body length. The data are given in Table 3. The cuticle thickness, which is heavily influenced by the fixative (or post-mortem fixation?), cannot be maintained as a diagnostic character for *L. crassicutis*. The



Table 3.—Sex (S) or stage, Slide number (SN), Pre-ocellar body length (OL), Cuticula thickness (Cut.) and species assigned to Kerguelen population described by Platonova (1958).

S	SN	OL	Cut.	Spec.	S	SN	OL	Cut.	Spec.
M	5831	75	12,1	crass.	J	7346	89	4,4	kerg.
F	5832	62	8,5	crass.	J	7359	69	8,4	kerg.
M	5833	73	8,5	kerg.	F	7362	65	3,2	clav.
F	5834	89	6,1	kerg.	J	7363	32	2,4	clav.
F	5835	109	2,0	clav.	J	7364	65	1,6	clav.
F	5836	118	8,5	kerg.	J	7365	97	4,0	clav.
F	5838	73	12,1	clav.	J	7366	65	5,3	clav.
F	5840	69	2,4	clav.	J	7367	32	2,0	clav.
M	6010	69	7,7	kerg.	J	7368	57	5,7	clav.
M	6011	73	12,1	kerg.	J	7369	105	5,7	clav.
F	6012	77	12,6	kerg.	J	7370	69	4,0	clav.
F	6013	126	10,1	kerg.	J	7371	93	3,6	clav.
M	6014	77	8,9	kerg.	J	7372	105	x	clav.
F	6015	77	8,1	kerg.	J	7374	57	4,0	clav.
F	6019	69	4,9	kerg.	J	7377	81	3,2	clav.
M	7343	77	13,0	kerg.	J	7633	57	8,1	clav.
J	7345	57	4,9	kerg.	M	7634	64	2,0	clav.

lack of bristles on the surface of the cuticle is given as a distinguishing feature for all three species. Herewith I synonymize *L. crassicutis* and *L. kerguelense* as their lectotypes 5831 and 5833 are evidently conspecific. I propose the name *L. kerguelense* Platonova, 1958; Recommendation 24a is not followed because the description of *L. crassicutis*, which is based on artifacts, would only lead to confusion. The type (5833) corresponds with the formula and description; the figure, however, is of one of the paratypes as the lectotype is mounted dorso-ventrally. The spicula of holo- and paratype are depicted in Fig. 18. The caudal glands, as depicted for *L. kerguelense* by Platonova, are much longer; they overlap the intestine as is usual in *Leptosomatum*.

Measuring the syntypes, another feature was found that was not previously recorded. Two types of juveniles and females occur; the first belongs to *L. kerguelense*, the other resembles *L. bacillatum*. These latter specimens are characterized by, among other features, ocelli situated far posteriorly. To this species belong slides 7346 and 5835, both labelled *L. clavatum* and slides 7365, 7369, 7371, 7372, 7377, 6013 and 5836 labelled *L. kerguelense*. Slide 5835 is the lectotype of *L. clavatum*, and 5836 the lecto-allotype of *L. kerguelense*. The lectotype of *L. clavatum* does not agree in every respect with the description of 1958. The measurements of the lectotype and discussion of its status are given in the paragraph of *L. clavatum*.

*Leptosomatum arcticum* sensu Mawson, 1958; nec Filipjev, 1916 is also indential to *L. kerguelense*. Mawson's material was not available for this study. Based on the description, there is no need to assign this species to *Leptosomatides* because structure of the gubernaculum is as in other species of *Leptosomatum*. The only difference from *L. kerguelense* is that the spiculum/gubernaculum ratio is not identical. This might be caused by artifacts or the gubernaculum may be obscured by the opaqueness of the surrounding tissue.



*New records*

1. South Georgia (53°52'S, 37°37'W). 3 ♂, 2 ♀, 1 juv. Coll. 7 Feb 1966 at a depth of 97–101 m. Collection Smithsonian Institution, Washington, D.C.
2. Macquarie Islands (54°32'S, 158°59'E). 5 Feb 1967. One pre-adult ♀. 112–124 m. Collection Smithsonian Institution, Washington, D.C.

The above-mentioned specimens of the first population are in a poor condition which may be caused by a post-mortem fixation, but they clearly belong to *L. kerguelense*. The cephalic capsule in male and female measure 4 and 6  $\mu\text{m}$  respectively. The amphidial fovea has a diameter of 5  $\mu\text{m}$  in the female and 11  $\mu\text{m}$  in the male. The construction of these amphids is identical to that in *L. bacillatum*; only slightly more robust. The tail is obtuse, caudal glands are long, and the caudal pore is shifted ventrally. Although this species is easily recognizable, a redescription from well preserved material is desirable.

*Leptosomatum micoletzkyi* Inglis, 1971

*Remarks.*—This species, described from one male, is distinguished from the species of *Leptosomatum* by the amphids, which lie at more than one cephalic diameter from the anterior end; the presence of subventral precloacal setae, and the absence of the lunula (?). Sexual dimorphism, comparable with *Leptosomatum*, seems to be absent. The spicules are slightly sinuous and end distally in blunt tips. The gubernaculum enfolds the spicules near their distal ends; proximally it forms large membranes.

The male, which was not available, does not fit any nominal genus. At present it would lead to confusion to erect a new genus for this species and I consider *L. micoletzkyi* Inglis, 1971, a species incertae sedis until the female is described.

*Leptosomatum pedroense* Allgén, 1947

Allgén (1947) described this species from a juvenile which was not available for this study. The length of this juvenile is 7120  $\mu\text{m}$  with a ratio "a" of 29.06. This means that the diameter of this specimen is 240  $\mu\text{m}$ , leading to the assumption that this juvenile is extremely flattened. This is supported by the figure of the tail. Being based on a juvenile and described insufficiently, *L. pedroense* Allgén, 1947, must be considered a species inquirenda.

*Leptosomatum punctatum* (Eberth, 1863) Bastian, 1865

Fig. 17c–e

*Phanoglene punctata* Eberth, 1863:20.

? *Stenolaimus macrosoma* Marion, 1870:17–18.—1870a:10.

*Leptosomatum longisetosum* Schuurmans Stekhoven, 1943a:4.

*Diagnosis.*—Cephalic, cervical and body sensilla setiform; cephalic capsule absent in juveniles and adults. Ventromedian precloacal supplement present. Caudal pore ventral to terminus. Ocelli relatively far posterior. Lens 6–7  $\mu\text{m}$ . Copulatory musculature relatively strongly developed.

*Distribution.*—Mediterranean, Black Sea, and Red Sea.

*Synonymy.*—Filipjev (1918) synonymized *S. macrosoma* Marion, 1870, with *L. bacillatum* (Eberth, 1863) because of Marion's statement (1870:17), "Elle ne



presente pas non plus la couronne de soies longues et robustes" in which opinion he was followed by Platonova (1976).

The argument of Filipjev, however, was based on an incorrect interpretation because Marion's (1870:17) passage had been taken out of context. The whole paragraph reads: "Le tube oesophagien se termine en effet de la même manière que celui du *Stenolaimus lepturus*, mais la tête régulièrement arrondie ne porte point de papilles. Elle ne présente pas non plus la couronne de soies longues et robustes de sa congénère; la peine si l'on remarque quelques poils courts dispersés tout le long du corps et un peu plus nombreux à la tête." In other words, *S. macrosoma* has neither papillae on its head, nor the long hairs of the preceding species *S. lepturus* (= *Anticoma acuminata* (Eberth, 1863) op. Allgén, 1942). The latter has three protruding lips to which Marion alluded and called papillae.

*Stenolaimus macrosoma* was characterized (Marion, 1870:17) by: "quelques poils courts dispersés tout le long du corps et un peu plus nombreux à la tête." Therefore, it is obvious that *S. macrosoma* is more closely related to *L. punctatum*, as the sensilla are setiform. I believe *S. macrosoma* to be identical to *L. punctatum* (Eberth, 1863).

In 1943a Schuurmans Stekhoven described *L. longisetosum* and, in the same year, illustrated it in a separate paper (1943b). I was not able to locate this specimen. According to the author, *L. longisetosum* differs from *L. punctatum* in the shape of the tail. This tail however, shows the typical shape of a juvenile of *L. punctatum*. I consider *L. longisetosum* identical with the latter.

#### New records

1. Red Sea; Ain Sukhna (29°36'N, 32°24'E). 1 ♀. Collected by W. D. Hope on 5 Jan 1967 from the intertidal sediment on the beach at El Sokhna Hotel. Various types of corals and colonial coelenterates. Collection Smithsonian Institution, Washington, D.C.
2. Banyuls; France (43°00, 3°10'E). 1 juv., 1 ♀ and 1 ♂. Deposit of unknown sponges and *Corallina*. Jun 1976. Collection Nematology Department Wageningen.

*Description and discussion.*—In general this species is smaller than *L. bacillatum*. The female from the Red Sea is only 3.6 mm long; half as long as the adults from Banyuls.

The length of the cephalic setae varies among individuals. Filipjev (1918) mentioned 6  $\mu\text{m}$ ; longer than in this material where 3–4  $\mu\text{m}$  has been measured for the juveniles, 4, 5 for the male and 4 and 5  $\mu\text{m}$  for the females. Setae of 2–3  $\mu\text{m}$  are sparsely present over the whole body length. Dr. Platonova was so kind as to remeasure the cephalic setae of Filipjev's material, and found 3.5  $\mu\text{m}$  for the males and 4.9  $\mu\text{m}$  for the females.

The amphidial aperture and fovea in the male measure 1 and 8  $\mu\text{m}$  against 2 and 3 in the female. The structure of these amphids is comparable to those in *L. bacillatum*. Eberth (1863), in his original description, probably depicted one of the amphidial glands.

The ocelli, with a lens diameter of 6–7  $\mu\text{m}$ , lie at 1.3 times the corresponding body width from the anterior end. The spiculum and gubernaculum length are 79 and 20  $\mu\text{m}$ , respectively. The ventromedian pre-cloacal papilla is situated at 166  $\mu\text{m}$  from the cloacal aperture. The tail, in both sexes, is rather long, 1.8 times the anal body width and more tapered than in *L. bacillatum*.



*Leptosomatum ranjhai* Timm, 1960

From the Arabian Sea Timm (1960) described a new species without sexual dimorphism in the head structure. The holo- and allotype were present in Wageningen in 1973 when a fire destroyed the laboratory and damaged a part of the collection. The types of *L. ranjhai* have been remounted but the contrast was almost lost which may be partly due to clearing in lactophenol.

The cephalic capsule in *L. ranjhai* is strongly developed; the posterior suture was clearly visible but the presence of cuticularized rods, surrounding the head, could not be confirmed.

The lateral epidermal chord in both sexes contains big vacuoles or glands, the structure of which could not be clarified; they measure from  $22 \times 19$  to  $34 \times 30 \mu\text{m}$  and more than 30 could be counted in one body side. Ortho- and loxometanemes-I are present. A sexual dimorphism in the amphids is absent; the structure of vagina and vulva preclude placement in *Leptosomatides*. It is necessary to erect a new genus for this species. This will be done after having compared the other genera in the Leptosomatidae and the remaining material of *L. ranjhai*.

*Leptosomatum sabangense* Steiner, 1915

Fig. 19c, d

Nec *L. sabangense* sensu Micoletzky, 1930 (= *L. sundaense* new name).

*Diagnosis*.—Cephalic and cervical sensillae papilliform. Cephalic capsule present, posterior to cephalic sensilla. Tail length twice anal body width. Caudal pore terminal. Male unknown.

*Distribution*.—Indonesia and Red Sea.

*Synonymy*.—In 1915 Steiner described *L. elongatum* var. *sabangense*, which was raised to species level by Filipjev in 1921. Steiner split off the variety because of the tail length which is twice the anal body diameter.

The figures of Steiner (1915) give another characteristic in which *L. sabangense* differs from *L. elongatum*, namely that the cephalic capsule is situated posterior to the cephalic papillae. This is depicted in both Figures 5 and 6 (Taf. 22) and confirmed in the text. This phenomenon is unique in this genus and needs confirmation.

*Leptosomatum sabangense* sensu Micoletzky, 1930, has another type of capsule, situated as usual in this genus but longer ( $11\text{--}13 \mu\text{m}$ ). The pharynx is variable in length ( $b = 6.8\text{--}12.6$ ). In the female, the ocelli are situated far posterior, in the male at less than one corresponding body diameter from the anterior end. More information is necessary concerning *L. sabangense* sensu Micoletzky, 1930 nec Steiner, 1915 which has to be renamed. I propose the name *L. sundaense* new name.

*New record*

1. Red Sea; Ain Sukhna ( $29^{\circ}36'N$ ,  $32^{\circ}24'E$ ). 1 juv. Collected by W. D. Hope 5 Jan 1967 from the intertidal sediment on the beach at El Sokhna Hotel. Various types of corals and colonial coelenterates. Collection Smithsonian Institution, Washington, D.C.

*Description*.—This juvenile is characterized by the placement of the cephalic capsule posterior to the cephalic papillae and the tail length, which is 2.16 times



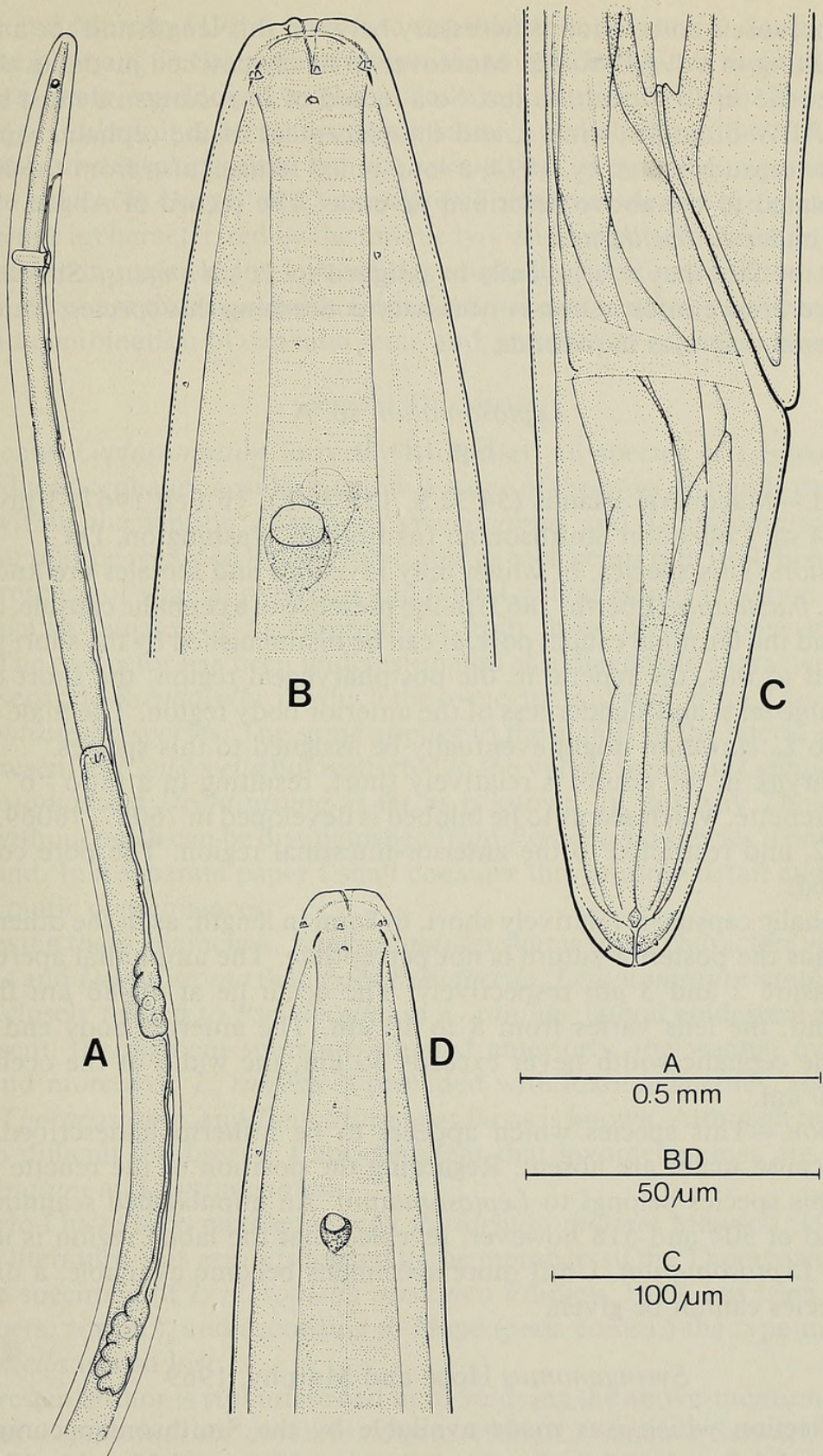


Fig. 19. Anterior end A, and head B, of *L. sp. A*; Tail C, and anterior and D, of *L. sabangense*, juvenile.

the anal body width. The measurements are given in the Appendix. Tail and cephalic end are depicted in Fig. 19c, d.

*Discussion.*—Records of *L. sabangense* which are only based on ratio c are



doubtful because a correlation is necessary between this length and the anal body width resulting in a T/ABW of 2. Moreover in newly hatched juveniles this ratio may exceed 2.5 in *L. bacillatum* too. So a record of *L. sabangense* must be based on the T/ABW of adults, ratio c, and the placement of the cephalic capsule. *L. sabangense* sensu Micoletzky, 1924, a long-tailed female, also from the Red Sea, may be related to the above described juvenile. The record of Allgén (1942) is discussed under *L. bacillatum*.

Despite the fact that at a juvenile is assigned to *L. sabangense* Steiner, 1915, in this paper, more information is necessary concerning this species, which must be considered a species inquirenda.

*Leptosomatum* sp. A

Fig. 19a, b

Material.—Macquarie Islands (54°32'S, 158°59'E); 15 Feb 1967. 3 juv. and 6 ♀; 112–124 m. Collection Smithsonian Institution, Washington, D.C.

*Description.* This species, of which only juveniles and females are known, resembles *L. bacillatum* (Eberth, 1863) in the presence of a cephalic capsule, cephalic papillae and the terminal caudal pore. It can be distinguished by the short pharynx and related to this, the renette in the postpharyngeal region, the short cephalic capsule, large lens, and slenderness of the anterior body region. The male (76081) assigned to *L. clavatum* might eventually be assigned to this species.

The pharynx in the adults is relatively short, resulting in a ratio "b" of 9.8–11.8. The renette, which seems to be bilobed is developed in 76067, 76069, 76071, and 76072, and restricted to the anterior-intestinal region. The pore could not be observed.

The cephalic capsule is relatively short, 6–8  $\mu\text{m}$  in length; as in the other species of this genus the posterior suture is not perceptible. The amphidial aperture and fovea measure 2 and 3  $\mu\text{m}$  respectively. The ocelli lie at 70–86  $\mu\text{m}$  from the anterior end, the lens varies from 8 to 10  $\mu\text{m}$ . The anterior body end is very slender; the cephalic width never exceeds 30  $\mu\text{m}$ , the width at the ocelli never exceeds 60  $\mu\text{m}$ .

*Discussion.*—This species which appears to be hitherto undescribed, is not named because males are absent. Regarding the position of the renette I doubt whether this species belongs to *Leptosomatum*. An unpublished scanning study of the head of 504 and 518 however, revealed that the labial region is identical to that in *Leptosomatum*. Until more specimens become available, a diagnosis of this species cannot be given.

*Syringonomus* Hope and Murphy, 1969

The collection which was made available by the Smithsonian comprises 4 juveniles and 4 females of *Syringonomus typicus* Hope and Murphy, 1969. The specimens were collected 20 Feb 1967 at a depth of 943–1007 m near Recife (7°58.0'S, 34°17.0'W). This species will be discussed here as this monotypic genus is closely related to *Leptosomatum*.

Dr. W. D. Hope was so kind as to send me a male and female paratype; comparison confirmed the identification of this deep-sea species. The measurements are presented in the Appendix. Little needs to be added to the description



of Hope and Murphy (1969). I wish to consider four points: (1) At the posterior end of the pharynx, in the male paratype, the amphidial glands are visible. These glands are easily overlooked as the males are not atrophied. (2) The renette is probably sexlinked; it is present in some females and absent in the male. (3) The subventral precloacal papillae are not specialized, they are comparable to the subdorsal setae. (4) Dorso- and ventrolateral orthometanemes are present.

This genus is characterized by the unique lyre-shaped pattern on, and thickening of, the cuticle in males at the level of the amphidial aperture, and the absence of ocelli. Females are distinguishable from *Leptosomatum* species by the absence of ocelli and combination of cephalic setae and presence of cephalic capsule.

### General Discussion

The genus *Leptosomatum* formerly comprised all species of Leptosomatidae with a reduced cephalic capsule, but now it is one of the most distinctly demarcated genera within the family. Together *Syringonomus* and *Leptosomatum* form a taxon that may be regarded holophyletic, just as each genus is in itself holophyletic.

The presence of vaginal ovejector and lateral vulvar glands is a good character to distinguish females of *Leptosomatides* from those of the above-mentioned genera. The ovejector has been underestimated as a diagnostic character and may serve to separate *Pseudocella*, in which the ovejector is absent, from *Thoracostoma* and *Deontostoma* species. The same applies to the glands in the lateral epidermal chord, present in *Pseudocella* but restricted to the vulvar region in *Leptosomatides*, *Thoracostoma*, and *Deontostoma* as far as is known. In this way *Thoracostoma* species without ocelli can be distinguished from *Pseudocella* species if only females are at hand. In a separate paper I shall consider this in more detail and examine the systematic consequences.

Reviewing these characters, *Leptosomatides* shares more characters with *Thoracostoma* and *Deontostoma* than does *Pseudocella*. *Leptosomatum ranjhai* Timm, 1960, is closely related to *Pseudocella*; in *L. ranjhai*, lateral epidermal glands are also present, the pigment spots are situated anteriorly, the vaginal ovejector is absent and moreover, *L. ranjhai* is provided with loxometanemes, as are *Pseudocella*, *Thoracostoma*, and *Deontostoma* as far as is known. Although metanemes are often difficult to observe, I am confident that loxometanemes are absent in *Leptosomatum* and *Syringonomus*.

Hitherto I have been unable to study *Paraleptosomatides* Mawson, 1956; judging from literature, this genus is related to the members of the Thoracostomatinae. The type-specimen of *Leptosomella acrocerca* Filipjev, 1927, has been lost (Platonova pers. comm.), and according to Hope (pers. comm.) the type-material of *Tubolaimella* is also lost.

The present author is still interested in re-studying the above-mentioned genera as well as *Leptosomatum abyssale* Allgén, 1951; *L. indicum* Stewart, 1914; *L. keiense* Micoletzky, 1930; *L. micoletzkyi* Inglis, 1971; *L. pedroense* Allgén, 1947; *L. sabangense* Steiner, 1915; *L. sabangense* sensu Micoletzky, 1930, and *L. bacillatum*, *L. elongatum*, *L. gracile* and *L. sabangense* sensu Allgén as described in several papers.

As no syntypes are present, attempts will be made to obtain material to designate neotypes for *L. bacillatum*, *L. punctatum* (both from Nice) and *L. elongatum* (Falmouth), the type-species of *Leptosomatum*.



Some taxonomists have described new species of nematodes in a very unsatisfactory manner. In addition to descriptions and illustrations often being inadequate, the rules and recommendations of the International Code of Zoological Nomenclature have not been followed consistently, especially recommendations 72b, c and d; 73d, 74a, b, c and e, as well as recommendations of Appendix E of the Code, i.e., 4, 5 and 19. Indicating paratypes to serve as reference-specimens is useful because special attention has been paid to them, but they are most useful if deposited in other collections. Care has to be taken not to flatten mounted specimens; as stated previously, it is difficult to recognize flattening, and resulting artifacts may mislead the observer.

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I should like to thank Mr. T. S. Ie and Mr. H. Lohuis for advice and assistance regarding the E.M.-part.

#### Status of Nominal Species

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<i>L. abyssale</i> Allgén, 1951	species inquirenda
<i>L. acephalatum</i> Chitwood, 1936	probably good species
<i>L. arcticum</i> Filipjev, 1916	to <i>Leptosomatides</i>
<i>L. arcticum</i> sensu Mawson, 1958	synonym of <i>L. kerguelense</i>
<i>L. australe</i> V. Linstow, 1907	species inquirenda; Filipjev, 1918
<i>L. bacillatum</i> (Eberth, 1863)	good species
<i>L. bathybium</i> Allgén, 1954	species inquirenda
<i>L. behringicum</i> Filipjev, 1916	species inquirenda
<i>L. breviceps</i> Platonova, 1967	species inquirenda
<i>L. caecum</i> Ditlevsen, 1923	to <i>Pseudocella</i>
<i>L. clavatum</i> , Platonova, 1958	probably good species
<i>L. crassicutis</i> Platonova, 1958	synonym of <i>L. kerguelense</i>
<i>L. diversum</i> Platonova, 1978	synonym of <i>L. sachalinense</i>
<i>L. elongatum</i> Bastian, 1865	synonym of <i>L. bacillatum</i>
<i>L. elongatum</i> sensu Platonova, 1967	to <i>Leptosomatides</i>
<i>L. filipjevi</i> Sch. Stekhoven, 1950	synonym of <i>L. bacillatum</i>
<i>L. gracile</i> Bastian, 1865	synonym of <i>L. bacillatum</i>
<i>L. gracile</i> sensu Allgén, 1954	to <i>Leptosomatides</i>
<i>L. grebnickii</i> Filipjev, 1916	to <i>Leptosomatides</i>
<i>L. groenlandicum</i> Allgén, 1954	species inquirenda
<i>L. indicum</i> Stewart, 1914	species inquirenda
<i>L. kerguelense</i> Platonova, 1958	good species
<i>L. keiense</i> Micoletzky, 1930	good species
<i>L. longisetosum</i> Sch. Stekhoven, 1943	synonym of <i>L. punctatum</i>
<i>L. longissimum</i> (Eberth, 1863)	species inquirenda; Filipjev, 1918
<i>L. micoletzkyi</i> Inglis, 1971	species incertae sedis
<i>L. pedroense</i> Allgén, 1947	species inquirenda
<i>L. punctatum</i> (Eberth, 1863)	good species

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Status of Nominal Species (Continued)

<i>L. ranjhai</i> Timm, 1960	species incertae sedis
<i>L. sabangense</i> Steiner, 1915	species inquirenda
<i>L. sabangense</i> sensu Micoletzky, 1930	<i>L. sundaense</i> new name
<i>L. sabangense</i> sensu Allgén, 1942	synonym of <i>L. bacillatum</i>
<i>L. sachalinense</i> Platonova, 1978	probably good species
<i>L. subulatum</i> (Eberth, 1863)	species inquirenda; Filipjev, 1918
<i>L. tetrophthalmum</i> Ssaweljev, 1912	species inquirenda
<i>L. tetrophthalmum</i> sensu Platonova, 1967	to <i>Leptosomatides</i>
<i>L. tuapsense</i> Sergeeva, 1973	synonym of <i>L. bacillatum</i>

Species inquirendae; probably belonging to *Leptosomatum*:

- L. abyssale* Allgén, 1951; Japan, Sagami Sea, 400 m depth. Resembling *L. bacillatum*.
- L. behringicum* Filipjev, 1916; Bering Sea. Resembles *L. bacillatum* but tail length equal to anal body width.
- L. breviceps* Platonova, 1967; Barents Sea. Resembles *L. punctatum*.
- L. pedroense* Allgén, 1947; San Pedro, California.
- L. sabangense* Steiner, 1915; Indonesia. Cephalic capsule posterior to papillae. Tail length twice anal body width.
- L. sundaense*; new name for *L. sabangense* sensu Micoletzky, 1930; Indonesia. Tail length twice anal body width in females, long cephalic capsule (10–12  $\mu$ m) placed anterior to papillae. Short pharynx. Ocelli in males far anterior.

Key to the Valid Nominal Species of *Leptosomatum*

- 1. Cephalic sensilla setiform; cephalic capsule absent in all sexes and stages (*L. punctatum*-complex) ..... 2
- Cephalic sensilla papilliform; cephalic capsule present in females and juveniles ..... 3
- 2. Lens 9–11  $\mu$ m in diameter; pharynx short; ventromedian pre-cloacal papilla present or absent ..... *L. keiense*
- Lens 6–7  $\mu$ m in diameter; ventromedian pre-cloacal papilla present ... *L. punctatum*
- 3. Ocelli at 1 corresponding diameter from anterior end, cephalic capsule present in male ..... *L. kerguelense*
- Ocelli at 1.5 corresponding diameter from anterior end; males, if present, without cephalic capsule ..... 4
- 4. Cephalic capsule 10  $\mu$ m; male rare; females big, never less than 10  $\mu$ m in length; (Southern Hemisphere) ..... *L. clavatum*
- Cephalic capsule less than 9  $\mu$ m in length; males not rare; females often smaller than 10  $\mu$ m ..... 5
- 5. Tail length in female twice anal body width (Indonesia) ..... *L. sundaense*
- Tail length in adults 1.5 anal body width ..... *L. bacillatum*-complex: *L. bacillatum* (Europe), *L. acephalatum* (East coast USA) and *L. sachalinense* (Sakhalin Is.)

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Appendix.—Numerical data new records.

Abbreviations: Sex (S) or stage; specimen number (SN); length (L); distance to lens (DL); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of ocelli (OW); at nerve ring level (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) and anal body width (AW).

S	SN	L	DL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
<i>L. bacillatum</i> , pop. 1; Den Helder																
J	1072-b	2960	48	182	730	61	17	28	35	41	39	28	72	4.1	49	
F	1063-b	6760	92	303	1214	77	31	58	75	83	86	53	79	5.6	88	60
F	1064-a	7250	80	311	1214	80	30	55	70	83	89	55	81	6.0	91	56
M	1065	7880	86	297	1216	96	29	52	64	67	66	53	118	6.5	82	
M	1073-b	7940	84	283	1118	83	31	53	72	83	88	66	90	7.1	96	
M	1073-c	8590	88	296	1166	86	31	58	74	83	83	59	103	7.4	100	
M	1062	8690	84	324	1157	99	30	52	74	78	86	64	101	7.5	88	
F	1070	8760	88	327	1345	86	34	66	89	110	135	66	65	6.5	102	59
F	1074	10,230	102	333	1476	91	36	66	86	106	127	68	81	6.9	112	64
F	1069	10,870	108	342	1378	94	34	64	91	114	128	67	85	7.9	116	57
<i>L. bacillatum</i> , pop. 2; Kattendijke																
J	1082-a	2470	50	199	669	58	17	30	36	38	37	30	65	3.7	43	
J	1082-c	2730	55	172	567	64	16	31	41	47	41	28	58	4.8	43	
J	1084-a	3140	61	200	709	63	22	41	52	56	52	39	56	4.4	50	
J	1054	5340	81	292	1115	74	25	45	59	64	64	47	83	4.8	72	
M	1055	7300	78	269	1112	78	28	50	71	74	80	56	91	6.6	94	
F	1052	7540	75	271	1181	81	31	55	77	81	81	56	93	6.4	93	75
F	1056	8130	83	283	1345	88	33	59	72	81	83	55	98	6.0	92	61
M	1045	9080	89	245	1287	84	31	53	70	78	80	59	114	7.1	108	
F	1050	9120	78	286	1378	88	31	53	74	89	89	58	102	6.6	104	62
M	1049	10,370	75	306	1378	86	28	52	67	78	78	56	133	7.5	121	
<i>L. bacillatum</i> , pop. 3; Burghsluis																
F	2152	6270	82	288	1123	81	33	68	75	81	81	58	77	5.6	77	59
F	2165	7040	89	283	1251	89	34	64	87	100	96	62	70	5.6	79	65
M	2037	7550	90	333	1192	93	31	56	72	83	79	65	91	6.3	81	
F	2162	7570	78	331	1281	81	33	58	78	86	81	61	88	5.9	93	58
M	2008	7870	82	330	1138	101	30	54	70	73	76	67	104	6.9	78	
M	2047	8050	82	321	1288	87	33	53	75	79	82	75	98	6.3	93	
M	2026	8330	78	327	1225	89	33	56	81	86	81	73	97	6.8	94	
M	2077	9060	79	345	1417	93	30	51	65	73	78	68	116	6.4	97	
F	2018	9160	87	311	1254	84	37	72	99	109	110	64	83	7.3	109	59
F	2064	10,440	101	322	1336	98	34	64	90	106	115	72	91	7.8	107	64



Appendix.—Continued.

Abbreviations: Sex (S) or stage; specimen number (SN); length (L); distance to lens (DL); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of ocelli (OW); at nerve ring level (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) and anal body width (AW).

S	SN	L	DL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
<i>L. bacillatum</i> , pop. 4; Texel, 't Horntje																
M	3108	6430	84	316	1242	89	30	55	77	89	95	66	68	5.2	72	
F	3074	7480	74	286	1112	86	34	63	89	99	109	66	72	7.1	91	61
F	3158	7790	78	297	1177	78	34	58	79	87	93	61	84	6.6	100	60
M	3106	8040	88	302	1057	81	31	58	75	81	86	65	93	7.6	99	
F	3024	8330	94	347	1273	91	35	67	84	97	97	67	86	6.5	92	60
M	3056	8750	89	310	1196	86	32	58	80	90	92	70	95	7.3	102	
F	3101	11,130	92	314	1335	78	31	67	93	124	132	70	84	8.3	143	57
F	3046	11,780	92	330	1483	101	34	70	96	132	152	72	78	7.9	117	61
F	3053	12,820	91	337	1464	83	35	61	91	118	146	70	88	8.8	154	61
F	3014	13,570	91	326	1446	82	34	60	91	124	136	73	100	9.4	165	65
<i>L. bacillatum</i> , pop. 5; Texel, Oudeschild																
J	1012-c	1370	47	149	407	52	13	23	28	25	24	22	55	3.4	26	
J	1011-b	3850	74	219	773	72	27	50	67	77	72	47	50	5.0	53	
J	1061	4260	63	227	896	66	23	41	53	53	53	36	80	4.8	65	
J	1003-a	5330	70	247	952	74	28	50	74	83	81	47	64	6.0	72	
J	1010-b	6690	78	277	1062	66	27	56	84	102	99	62	66	6.5	101	
M	1004	7080	90	288	1155	81	31	56	77	90	92	66	77	6.1	87	
M	1006	7770	89	312	1195	80	33	56	88	94	92	66	83	6.5	97	
M	1035	8040	86	335	1378	86	31	55	70	77	84	64	96	5.8	93	
M	1033	8920	95	336	1336	78	32	58	91	102	105	63	85	6.7	114	
F	1009	9350	78	274	1148	78	33	63	88	103	107	64	87	8.1	120	58
<i>L. bacillatum</i> , pop. 6; Wimereux																
F	A-59	11,560	89	279	1420	83	27	62	87	116	156	71	74	8.1	139	
<i>L. bacillatum</i> , pop. 7; Ambleteuse																
F	1277-1	7980	83	284	1048	79	25	52	74	95	114	64	70	7.6	101	60
F	1277-2	8570	109	329	1284	77	30	63	76	96	101	61	85	6.7	111	59
<i>L. bacillatum</i> , pop. 8; Banyuls																
F	1286-1	7620	102	288	1155	89	33	68	96	112	134	73	57	6.6	86	60
F	1286-2	13,490	109	376	1741	89	35	61	82	93	94	64	144	7.7	152	59
F	1286-3	16,890	135	415	1892	106	33	66	85	96	119	67	142	8.9	159	61
<i>L. bacillatum</i> , pop. 9; N.E. England																
M	76101	8720	82	324	1342	93	29	45	71	76	85	69	103	6.5	94	
F	76102	10,190	91	294	1305	108	32	60	83	92	113	66	90	7.8	94	59
<i>L. acephalatum</i> , pop. 1; Mexico, N.E. Asc. Bay																
J	76103	4700	69	227	779	76	25	47	64	74	73	52	64	6.0	62	
F	76104	7200	95	272	997	133	38	75	95	98	107	68	67	7.5	54	58
J	76105	7290	101	300	1070	91	31	58	82	88	112	81	65	6.8	80	
F	76113	7780	97	303	1088	95	32	59	91	122	115	76	64	7.2	82	57
F	76106	7790	108	220	1178	90	37	68	94	121	110	69	66	6.8	89	60
M	76107	8030	75	337	1132	98	35	58	81	96	118	73	68	7.1	82	
M	76108	8430	101	360	1142	92	32	60	90	90	98	66	86	7.4	92	
F	76109	8970	112	316	1124	96	34	73	98	130	140	77	64	8.0	93	57
<i>L. acephalatum</i> , pop. 2; Mexico, Allen Point																
F	76110	7720	82	298	1106	103	37	71	102	118	121	72	64	7.0	75	56



## Appendix.—Continued.

Abbreviations: Sex (S) or stage; specimen number (SN); length (L); distance to lens (DL); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of ocelli (OW); at nerve ring level (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) and anal body width (AW).

S	SN	L	DL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
<i>L. acephalatum</i> , pop. 3; Mexico, N.E. Asc. Bay																
J	76092	4660	86	188	852	77	29	54	73	79	77	52	59	5.5	61	
M	76093	7630	106	326	1051	90	32	60	77	85	92	60	83	7.3	85	
F	76094	7790	102	333	1178	89	37	70	103	130	153	77	51	6.6	88	56
M	76095	7810	110	343	924	92	34	62	81	100	99	67	78	8.5	85	
F	76096	8090	118	341	1106	109	34	70	98	123	123	74	66	7.3	73	50
F	76097	8700	87	358	1250	96	32	65	90	113	139	74	63	7.0	91	58
F	76091	9860	110	343	1215	91	30	62	96	126	147	81	67	8.1	108	54
<i>L. acephalatum</i> , pop. 4; Mexico, Niccehabin Reef																
J	76098	7320	95	286	979	85	26	52	81	107	120	71	61	7.5	86	
<i>L. acephalatum</i> , pop. 5; Mexico, Suliman Pt.																
J	76099	3430	65	322	562	70	22	45	65	87	95	53	36	6.1	49	
<i>L. acephalatum</i> , pop. 6; Mexico, S.E. Cozumel Is.																
F	76100	10,170	87	316	1178	108	40	79	117	164	193	91	53	8.6	94	51
<i>L. clavatum</i> , Macquarie Islands																
J	76078	6050	106	337	1115	106	25	69	87	87	89	73	68	5.4	57	
J	76079	6520	85	271	1014	94	25	58	81	85	102	67	64	6.4	69	
J	76080	8420	116	370	1352	128	37	64	110	125	162	99	52	6.2	66	
M	76081	8570	81	312	1014	112	27	52	73	79	87	67	99	8.5	77	
F	76082	11,050	132	427	1386	125	36	81	106	119	133	89	83	8.0	88	62
F	76083	12,120	113	374	1589	121	31	82	89	102	114	74	106	7.6	100	63
F	76084	12,510	133	452	1673	100	33	83	110	125	144	88	87	7.5	125	62
F	76085	12,780	141	419	1606	142	38	85	110	127	154	92	83	8.0	90	63
F	76086	13,030	146	444	1741	146	40	85	108	125	158	94	82	7.5	89	63
F	76087	13,490	131	436	1639	152	35	79	123	146	171	99	79	8.2	89	60
F	76088	13,960	121	374	1758	142	33	83	110	134	162	93	86	7.9	98	62
F	76089	14,230	150	469	1656	139	37	85	114	150	168	92	85	8.6	102	61
<i>L. keiense</i> , pop. 1; Philippines, Telbang Cove																
J	76039	3540	65	196	544	77	19	46	61	72	79	52	45	6.5	46	
F	76040	4970	84	256	834	90	24	44	71	87	95	58	52	6.0	55	49
M	76041	5780	71	213	689	90	32	53	71	77	74	62	75	8.4	64	
<i>L. keiense</i> , pop. 2; Philippines, Cangaluyan Is.																
J	76042	1710	42	148	406	46	16	32	44	47	48	38	36	4.2	37	
J	76043	4550	74	229	592	81	27	59	78	85	102	67	45	7.7	56	
M	76044	6180	80	273	834	66	25	44	58	64	61	55	97	7.4	94	
M	76045	6580	68	278	888	63	27	45	60	60	63	55	104	7.4	104	
F	76046	7870	67	280	979	69	25	48	71	90	114	54	69	8.0	114	
<i>L. keiense</i> , pop. 3; Philippines, Bolic Is.																
J	76047	4830	76	222	558	82	27	49	69	77	85	56	57	8.7	59	
J	76048	5610	92	256	642	98	27	64	89	105	121	71	46	8.7	57	
M	76049	7620	89	260	689	108	37	62	81	88	93	66	82	11.0	71	
<i>L. keiense</i> , pop. 4; Philippines, Gr. Santa Cruz Is.																
J	76050	4870	59	212	523	64	22	46	66	79	92	60	53	9.3	76	



Appendix.—Continued.

Abbreviations: Sex (S) or stage; specimen number (SN); length (L); distance to lens (DL); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of ocelli (OW); at nerve ring level (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) and anal body width (AW).

S	SN	L	DL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
<i>L. keiense</i> , pop. 5; Philippines, Sacol Is.																
J	76051	3770	63	182	490	75	27	53	69	78	84	59	43	7.7	50	
<i>L. kerguelense</i> , pop. 1; South Georgia																
M	76052	7150	64	452	1031	87	29	59	102	108	116	79	62	5.9	82	
J	76053	7420	69	386	1166	73	37	81	129	152	156	114	48	6.4	102	
M	76054	8530	68	345	1169	100	40	85	112	125	145	91	59	7.3	85	
F	76055	9350	67	408	1268	125	46	86	116	160	168	119	56	7.4	75	56
M	76056	10,210	77	431	1082	106	37	80	112	124	134	92	76	9.4	96	
F	76057	15,840	73	469	2315	116	36	89	141	162	201	135	79	6.8	137	59
<i>L. kerguelense</i> , pop. 2; Macquarie Islands																
J	76058	10,710	64	366	1470	107	38	68	112	146	162	106	66	7.3	100	
<i>L. punctatum</i> , pop. 1; Red Sea																
F	76037	3660	67	213	816	81	21	41	58	66	63	44	55	4.5	45	54
<i>L. punctatum</i> , pop. 2; Banyuls																
J	1286-4	2940	58	214	608	69	17	40	57	69	61	45	43	4.8	43	
F	1286-5	7600	79	321	1065	114	29	60	87	99	111	70	68	7.1	67	56
M	1286-6	7830	85	319	991	106	35	72	99	105	114	89	69	7.9	74	
<i>L. sabangense</i> ; Red Sea																
J	76038	6490	58	213	761	95	16	31	48	52	61	44	106	8.5	68	
<i>L. sp. A</i> ; Macquarie Islands																
J	76067	7610	71	267	879	98	23	46	67	77	92	62	83	8.7	78	
J	76068	8720	70	275	896	95	25	54	71	81	99	62	88	9.7	92	
J	76069	8790	74	292	930	96	21	48	67	77	83	58	106	9.5	92	
F	76070	11,100	71	284	1048	115	28	49	77	102	139	71	80	10.6	97	58
F	76071	11,830	75	366	1166	116	27	50	108	102	112	76	106	10.1	102	61
F	76072	12,150	86	325	1031	120	26	56	85	112	139	77	87	11.8	101	59
F	518	12,290	81	370	1200	116	28	52	79	94	133	71	92	10.2	106	61
F	504	12,440	87	370	1268	114	27	52	73	85	110	67	113	9.8	109	64
F	76073	14,090	75	362	1301	129	27	56	76	94	108	78	130	10.8	109	63
<i>Syringonomus typicus</i> ; Recife, Brazil																
J	76059	3310	—	239	667	79	22	—	56	66	78	60	42	5.0	42	
J	76060	3330	—	241	666	65	26	—	61	73	81	65	41	5.0	51	
F	76061	4450	—	280	881	101	34	—	70	81	95	x	47	5.1	44	68
F	76062	5050	—	321	952	104	31	—	71	88	113	90	45	5.3	49	63
F	76063	5240	—	313	904	118	34	—	74	89	116	81	45	5.8	44	60
J	76064	5360	—	297	762	95	29	—	71	82	95	79	56	7.0	56	
J	76065	5570	—	305	928	110	27	—	63	74	89	75	63	6.0	51	
F	76066	6880	—	453	1227	110	23	—	66	84	100	65	69	5.6	63	50





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