

SYSTEMATIC STUDIES ON THE GENERA *LEPTOSOMATUM* BASTIAN, 1865 AND
LEPTOSOMATIDES FILIPJEV, 1918 (NEMATODA: LEPTOSOMATIDAE).



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Systematic studies on the genera *Leptosomatum* Bastian, 1865 and *Leptosomatides* Filipjev, 1918 (Nematoda: Leptosomatidae)

Proefschrift

ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C.C. Oosterlee,
in het openbaar te verdedigen
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Aan Toos en Theodoor

STELLINGEN

- 1 De nematodencollectie van De Man is van een dergelijke historische en wetenschappelijke waarde dat het, wegens brandgevaar, niet wenselijk is deze in een houten gebouw temidden van alcoholcollecties te bewaren.
- 2 Beheerders van collecties zouden jaarlijks een overzicht moeten publiceren waarin het onbewerkte materiaal, dat voor studie beschikbaar gekomen is, vermeld wordt.
- 3 De artefacten die Mawson bij *Leptosomatum arcticum* beschrijft, wijzen er op dat dit materiaal in een vloeistof met een te hoge osmotische waarde gefixeerd is.
Mawson, P.M., (1958). Rep. B.A.N.Z. antarct. Res. Exped. (B) 6: 315
- 4 Het verdient aanbeveling, indien men slechts één juveniel ter beschikking heeft, deze niet als een nieuwe nominale soort te presenteren.
- 5 De grote amplitude die Micoletzky geeft voor ratio 'b' van *Leptosomatum sabangense*, is vermoedelijk een gevolg van het feit dat één of meerdere exemplaren van *L. keiense* tussen dit materiaal terecht gekomen zijn.
Micoletzky, H., (1930). Vidensk. Meddr. dansk naturh. Foren. 87: 276
- 6 Het feit dat twee morfologisch nauw verwante soorten in gefixeerde toestand niet goed te onderscheiden zouden zijn is geen reden het aanduiden van een holotype achterwege te laten.
Rühm, W., (1956). Parasit. Schr. Reihe 6: 3
- 7 De beschrijving van een soort neemt in nauwkeurigheid toe indien men van de individuen afzonderlijke metingen geeft.
Dit proefschrift
- 8 De verschillen in ratio's tussen *Paraleptosomatides spiralis* en *P. elongatus* zijn vermoedelijk een gevolg van allometrische groei.
Mawson, P.M., (1956). Rep. B.A.N.Z. antarct. Res. Exped. (B) 6: 45

- 9 De redactie van een tijdschrift behoort er op toe te zien dat bij de presentatie van een nieuwe soort de aanbevelingen uit de International Code of Zoological Nomenclature opgevolgd worden, dat er een holotype aangewezen wordt en dat het typemateriaal gedistribueerd wordt over centra waar het materiaal toegankelijk is voor onderzoek.
- 10 Het gebruik van 'juveniel' ter aanduiding van een onvolwassen nematode verdient de voorkeur boven het meer gebruikelijke 'larve'.
- 11 De 'lignes chitineuses' zoals De Man die beschreef in *Leptosomatum elongatum* worden door Timm ten onrechte aangezien voor de, zoals hij ze noemt, 'six pairs of sclerotized pieces'.
De Man, J.G., (1893). Mém. Soc. zool. Fr. 6: 104,
Timm, R.W., (1953). Am. Midl. Nat. 49: 231
12. Het feit dat de ventrosublaterale slokdarmklieren in de Leptosomatinae en de Thoracostomatinae op de lippen uitmonden, krijgt in fylogenetische beschouwingen te weinig aandacht.
13. De rol van nematoden in de successie van plantengemeenschappen wordt onderschat.
14. Aan de mogelijkheden die het gebruik van nematoden als bio-indicatoren ter typering van oppervlaktewater bieden wordt in Nederland ten onrechte weinig aandacht besteed.
15. Een weidelijk jager is een inefficiënt beheerder.
16. Een 'goede morgen' bij het aanschuiven aan de koffietafel is vergelijkbaar met een nieuwjaarswens uitgesproken in de zomer.

Tom Bongers, 21 november 1984.

Systematic studies on the genera *Leptosomatum* Bastian, 1865 and *Leptosomatides* Filipjev, 1918 (Nematoda: Leptosomatidae).

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Preface

This thesis concerns the broad field of the taxonomy of marine nematodes. My interest in nematology was aroused by the late Dr. Ir. M. Oostenbrink, founder of the Department of Nematology at the Agricultural University, Wageningen and it was under his direction that this investigation was initiated. The study was continued during the interim guidance of Drs. P.A.A. Loof, Prof. Dr. J.C. Zadoks and finished under the supervision of one of my promoters Prof. Dr. Ir. A.F. van der Wal.

I wish to express my sincere gratitude to Prof. Dr. Ir. A.F. van der Wal for the opportunity he gave me to carry out the main part of this study in his laboratory and, together with Prof. Dr. A. Coomans, for their interest in the subject and sincere willingness to act as promoters.

Special thanks are also due to Drs. P.A.A. Loof for his interest in this study, and for his constructive criticism and suggestions. Without the inimitable way in which he guided me in taxonomy and without his enthusiasm, this study would not have been possible.

Only at a later stage of this study was the possibility of presenting these gathered articles as a thesis considered. At that time manuscripts of the revisions of *Leptosomatum* and *Leptosomatides*, executed in consultation of Drs. P.A.A. Loof, were almost finished.

Financial support for the investigations comprising this thesis have originated from several sources. The 'Wageningenfonds', together with the foundation 'Fonds Landbouw Export Bureau 1916/1918', made an important contribution. The printing costs of the thesis were subsidized by the 'Genootschap Noorthey'. A visit to the Smithsonian Institution, Washington D.C. was made possible, in part by a grant from that Institution. The part of this study, executed at the Zoological Institute, Leningrad, was made possible by a grant within the framework of the Cultural Exchange between the Netherlands and the U.S.S.R.

I am much indebted to Dr. T.A. Platonova for her hospitality and valuable discussions.

Some facets of this study touch other fields of study than the traditional nematode taxonomy, viz. electron-microscopy and numerical methods. Therefore it was imperative to consult with specialists in those fields of study. Colleagues of the Virology Dept. assisted me in word and deed regarding the T.E.M.-part; colleagues of the Department of Mathematics helped me with more than advice only.

Many have read and commented on parts of the manuscript including Prof. Dr. J.C. Zadoks and Drs. P.A.A. Loof, as well as Prof. Dr. E. Geraert,

Drs. Albert Otten, Ir. Theodoor Heyerman and Ir. Monique Calon. Many thanks are due to all who collected, intermediated in collecting or loaned type-specimens crucial to this study. I am specially indebted to Dr. P. Wagenaar Hummelinck who deposited his nematode-collection in Wageningen. I am sure that numerous studies will follow involving his material.

The help of the co-workers of the neighbouring departments, the Library, Photographic Service, Wordprocessing Center, Illustrating Service, Foundation for Agricultural Plant Breeding and Nematology Department is much appreciated. The author wishes to express his gratitude to the Editors of the Proceedings of the Biological Society Washington, Hydrobiologia and the Netherlands Journal of Sea Research for permission to reproduce the articles which, together, form the framework of this thesis.

Last but not least, I owe considerable appreciation for Dr. W. Duane Hope, Smithsonian Institution, Washington for his hospitality, valuable discussions, linguistic corrections, loaning specimens and moreover by his stimulating enthusiasm that encouraged me to continue the course of this study.

Chapter 1 Introduction

This study, which involves a group of marine nematodes belonging to the family Leptosomatidae, resulted from an attempt to identify nematodes that occur off the Dutch coast, especially in the sponge *Halichondria panicea*. These nematodes were originally identified as *Leptosomatum bacillatum* (Eberth, 1863). However, the identifications were questioned when atrophied males were found, a characteristic not mentioned in the original description.

Fortunately, *Leptosomatum* specimens from Kattendijke, Den Helder and Oudeschild, collected in 1970, could be studied without access to essential literature, which in the meantime had been requested and became available at a later date. As sampling data of these specimens had been lost, the only information was that provided by the labels, which revealed that the 'population' Kattendijke was represented by two samples. The first structures to which attention was drawn were the coelomocytes; the collection from Kattendijke could be divided on the basis that these cells were developed only in the specimens of one of the samples. In nematodes with developed coelomocytes, the pharynx was shorter and body diameter less than in specimens where coelomocytes were not apparent. Because the exact locations from which these samples were collected were unknown, as was the method of fixation, factors that may have played a role in their development could not be identified. Subsequently, comparable coelomocytes have been found in the Thoracostomatinae.

At least two weeks of intensive observations passed before I discovered, with 'Aha Erlebnis', that sexual dimorphism existed in the presence of the cephalic capsule. The same applies for the amphidial glands, ganglia of amphidial nerves and renette. The amphidial glands, mentioned by Eberth (1863) could, according to De Man (1893), be observed on occasion as could the swollen gland at the posterior end of the pharynx. The latter appeared to be connected to the ventral excretory pore. After an inventory of these features it appeared that the amphidial glands were never found in females and that the ventral gland, or renette, was restricted to females. Later the amphidial glands appeared to be present in all males but, at times, rather difficult to observe. A closer study of males also revealed two large cells posterior to the nerve-ring and a dimorphism in the structure of the amphidial fovea.

A need for more specimens necessitated the collecting of more sponges at Texel, from which a surprisingly high number of nematodes were obtained. Some of the females were gravid and the size of these nematodes led to the assumption that an annual cycle might occur because large, sexually mature specimens had been collected in June, whereas specimens obtained in early winter were much smaller. Based on literature, which in the meantime had become available, it seemed logical to consider these nematodes as belonging to *L. elongatum* Bastian, 1865. Their length, locality and the fact that *L. elongatum* had also been described from a sponge supported this conclusion.

The Netherlands Institute for Sea Research, Texel, offered facilities to study living nematodes where observations of nematodes moving and producing sticky threads were made. The mucus trap hypothesis and the fact that the ventrosublateral pharyngeal glands open onto the anterior end were, at the time, unknown to me; I expected the threads to be produced by the caudal glands.

The type-material of the other *Leptosomatum* species was examined to determine whether the characteristics of *L. elongatum* were also present in other species assigned to that genus. Dr. W. Duane Hope, Washington D.C. also enabled me to use the collection of unidentified *Leptosomatum* specimens of the Smithsonian Institution for this study. Dr. T.A. Platonova sent some paratypes and offered the possibility to study the holotypes and other material at the Zoological Institute in Leningrad.

In Leningrad, my attention was first attracted to those specimens identified as *L. elongatum* by Filipjev. Female specimens of this material were provided with vaginal ojectors that I had never noticed in *Leptosomatum*. The Dutch material appeared to be identical to *L. bacillatum* sensu Filipjev, 1918 from the Black Sea.

Lengthy discussions were conducted with Dr. T.A. Platonova concerning the interpretation of the structure of the cephalic capsule. At that time, I shared Timm's (1953) opinion that the cephalic capsule was composed of six pairs of sclerotized pieces. Platonova, however, was convinced that a capsule-like structure existed. Later, this capsule was examined on a ultrastructural level together with some details of the male amphids, which demonstrated the accuracy of Platonova's interpretation.

The material made available by the Smithsonian Institution included some juveniles and females of an unknown *Leptosomatum* species devoid of ocelli, that was recognized later as belonging to *Syringonomus typicus* Hope and Murphy, 1969. As no males were available I suggested to Hope that the amphidial glands might have been overlooked. He sent me a male, the existence of these glands could be confirmed.

Working from the premise that *Leptosomatum* is characterized by sexual dimorphism of the amphids and by the presence of ocelli, a number of nominal species had to be assigned to other genera. *Leptosomatum caecum* Ditlevsen, 1923 belongs to the genus generally considered as *Pseudocella*. Verification by comparison with the description and figures of *Hemipsilus trichodes* Leuckart, 1849, however, revealed that the type-species of *Pseudocella* does not agree with those species generally considered to represent *Pseudocella*. This case must be submitted to the International Commission of Zoological Nomenclature. Although *Pseudocella caeca* (Ditlevsen, 1923) becomes a homonym of *P. coeca* (Ssaweljev, 1912) it will not be renamed before *Pseudocella* is revised to avoid unnecessary synonyms.

Allgén's species *Leptosomatum groenlandicum* and *L. bathybiu* do not belong to the Leptosomatinae. The purpose of my redescriptions is to make members of these species identifiable by other taxonomists.

Dr. N. Goubault, Paris, kindly placed the type-material of *Leptosomatum magnum*, *L. roscovianum* and *L. minutum*, all Villot, 1875, at my disposal. Although these species have been transferred to other genera, re-examination and designation of lectotypes seems desirable. With the permission of Dr. Goubault, these specimens have been remounted for subsequent study.

By courtesy of Dr. D.C. Lee of the South Australian Museum Mawson's material was recently placed at my disposal. This includes *Leptosomatum articum* sensu Mawson, 1958; *Paraleptosomatides elongatus* and *P. spiralis* Mawson, 1956; *Leptosomatides antarcticus* Mawson, 1956; and *L. conisetosus* sensu Mawson, 1956 and 1958. An attempt was made to trace the types of *Leptosomatum micoletzkyi* and *Leptosomella phaustra* both Inglis, 1971, who stated that the holotypes were deposited in the Western Australian Museum and paratypes in the British Museum (Natural History). They were not deposited in either Institution. The suspicion exists that these holotypes are deposited in the South Australian Museum but they have, at this moment, not been recovered.

The results of the study on *Leptosomatum* were confirmed during a second visit to the Zoological Institute in Leningrad. In this period the species transferred to *Leptosomatides* as well as the species described in *Leptosomatides* were studied. A comparison revealed that all *Leptosomatides* species, with the exception of *L. inocellatus* Platonova, 1967, are characterized by a vaginal ovejector. Later, this ovejector was also found in *Thoracostoma* and *Deontostoma*.

Dr. R.W. Timm deposited the syntypes of *Leptosomatides reductus* Timm, 1959, previously in his personal collection, in the Collection of the Nematology Department in Wageningen. These specimens have been remounted, but could not be included in the revision of the genus *Leptosomatides*. Timm also intermediated in tracing the paratypes of *Leptosomatum ranjhai*, which have been deposited in the slide collection of the Zoological Survey of Pakistan. These slides could not be traced.

The nematode collection of Dr. P. Wagenaar Hummelinck from the Caribbean, deposited in Wageningen, and the Smithsonian Collection yielded some nematodes identical to or closely related to *Leptosomatum ranjhai* and confirmed the observations on the holo- and allotype. This material provided a firm basis for the proposal of a new genus.

To confirm the annual reproductive cycle of *L. bacillatum*, samples from sponges have been taken regularly. The results confirmed the expected reproductive cycle and, moreover, showed that *L. bacillatum*, living in conditions found in the Netherlands, continues growing after the adult stage has been reached.

The visit to the Smithsonian Institution yielded a number of *Leptosomatum* specimens not previously described. These nematodes, together with those of the Wagenaar Hummelinck-collection, new and previously described specimens are discussed in the 'numerical approach'. Material is still available for a similar study of the *Leptosomatum punctatum*-complex. Speci-

mens of that complex have been found, together with those belonging to the *L. bacillatum*-complex, in samples from Mexico, the Caribbean, Black Sea, Mediterranean and Philippines. Moreover, a new species resembling *L. punctatum*, but without precloacal papilla, has been found off Antarctica. The discovery of this new species throws doubt on the identity of *L. keiense* Micoletzky, 1930, which seems to be a mixture of two species.

It is not surprising that a study of a genus for which no type-material is available or, if available, in poor condition, causes a considerable number of taxonomic changes. The stability of the species fixed by the designation of a holotype is essential for a stable system. Type-material *must* be set aside for future investigations when describing a new species because it is not known which characteristics will prove to be of diagnostic importance.

Retrospectively, in the series of papers presented here, a distinct shifting has taken place in the value of diagnostic characters given by their numerical data in the Appendices. In the first paper, regarding the genus *Leptosomatum*, I have presented the measurements of the cephalic width, the body diameter at level of the ocelli, at level of the nerve ring, midbody width and vulva position. Later, separating the species of the *L. bacillatum*-complex, these characters have been replaced by the length and width of the cephalic capsule and diameter of the lens-like body.

Based on recent information, my conviction that the genus *Leptosomatum* may be regarded holophyletic, as stated in the first paper, wavers. To fulfil these requirements the *Leptosomatum punctatum*-complex probably deserves a separate generic status. Arguments will be given in the revision of that complex.

My intention to complete Lorenzen's classification for the Leptosomatidae as stated in the *Leptosomatum* paper does not reflect so much my preference to his newly introduced concept 'holapomorphy' (Lorenzen, 1981; emended by Lorenzen in Concepts in Nematode Systematics, 1983) but merely refers to his approach and framework established.

The term 'lens-like body' is synonymous to 'lens' as used in the first paper. Although the term lens is generally used in literature, the hyaline body in the ocelli is the sensitive part and therefore the term 'lens-like body' is preferable. A refractive body is lacking.

The term 'post-adult growth' has been used to indicate the growth after the adult stage is reached; the term 'adult growth', used in the numerical approach, is preferable.

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Tom Bongers

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.

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 α -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."¹

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-

¹ The indication "typical species" did not originally have the nomenclatorial meaning it has today. According to Stiles and Hassall (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 *Leptosomatium*.

In 1936 Chitwood described *L. elongatum* subsp. *acephalum*; 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 *Leptosomatium* and *Leptosomatides*; this will be discussed later.

Platonova (1958, 1967, 1978) published on specimens of *Leptosomatium* 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 *Leptosomatium* 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. *acephalum* Chitwood, 1936; *L. sabangense* sensu Allgén, 1942; *L. acephalum* sensu Timm, 1953; *L. bathybium* 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. bathybium*, *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 ov-ejector" 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 μm , whereas the supporting rods were no thicker than 24 and 28 μm .

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*² 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. Querfaserschicht der Cutis am Vorderende zu sehen. Palafjord, Mogilnojesees."

² *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 région 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

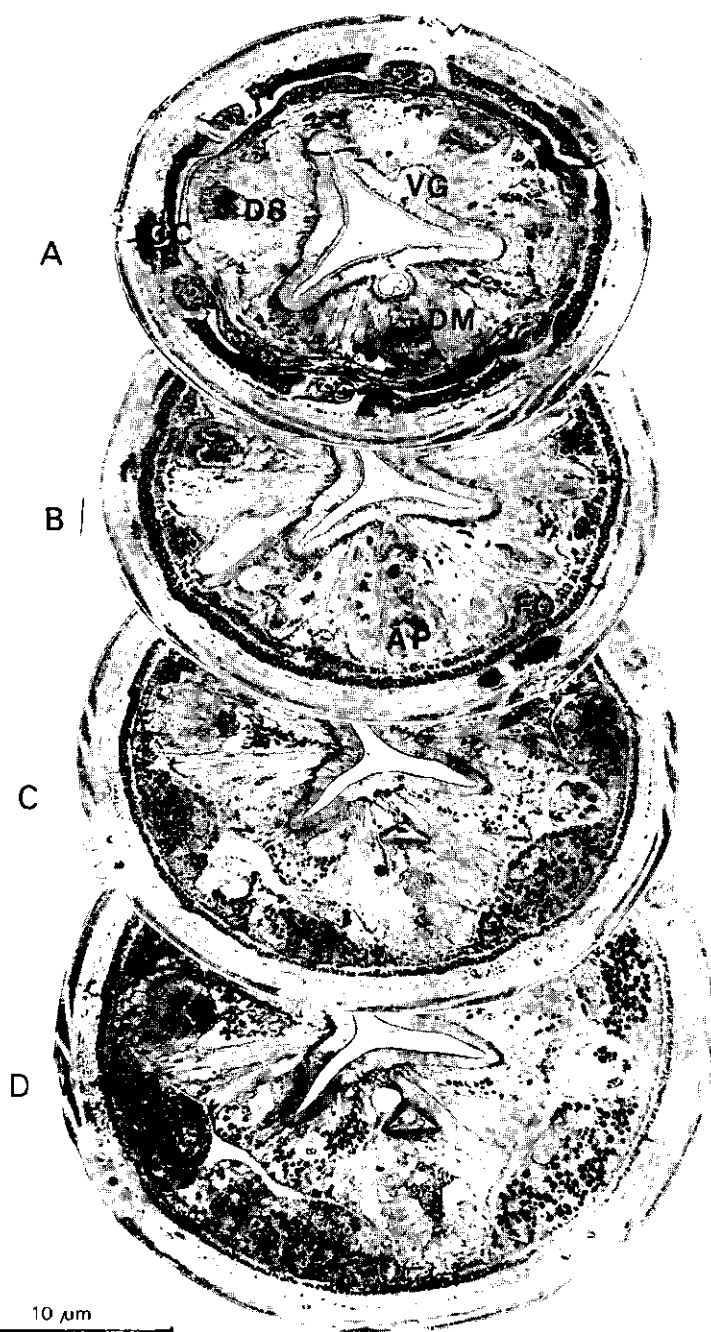


Fig. 1. Sections through cephalic capsule of female *L. bacillatum* at four different levels. A, Anterior part; B, Two microns posterior of A; C, On level of cephalic papillae; D, Through posterior part of capsule. (CC: Cephalic capsule, LG: Ventrosublateral pharyngeal gland, DM: Dilator muscles, FO: 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 μm 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 μm which opens to the exterior by a small pore. The fusus is about 15 μm in diameter, fusiform, 40 μm long, and leading to the amphidial gland (Fig. 10b). Some preliminary observations are worth mentioning.

In *L. bacillatum* the amphidial glands are 600–900 μm 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 μm : their number exceeds 500 in the posterior part of the

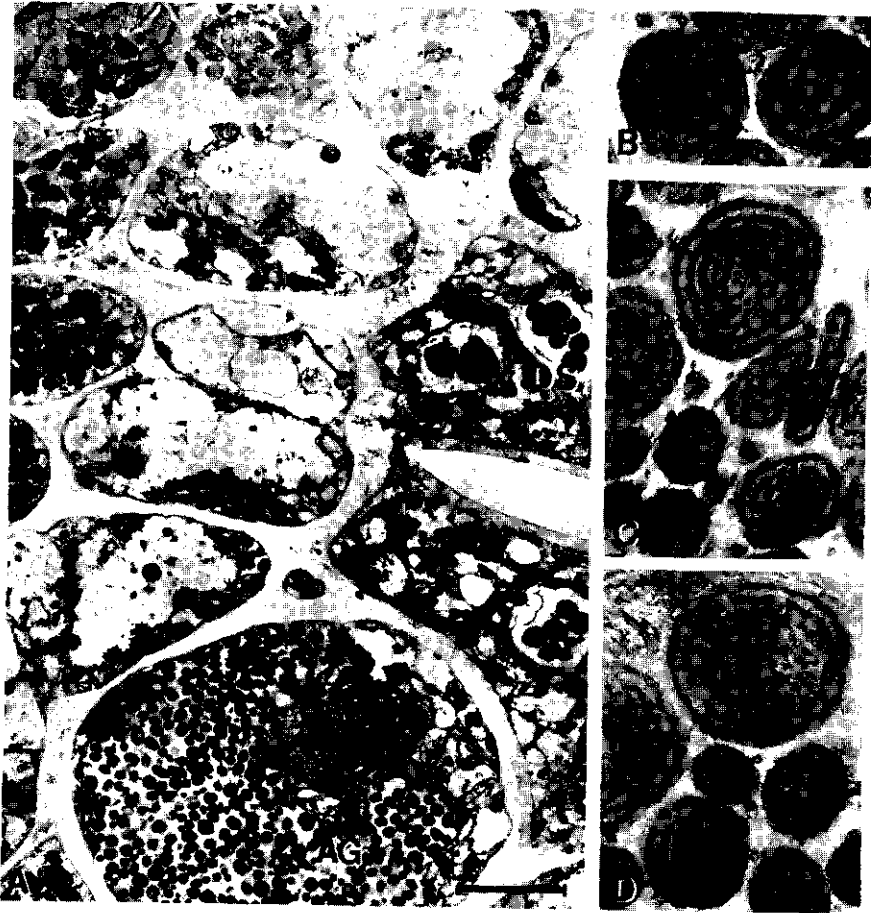


Fig. 2. A, Section through posterior end of fusus in *L. bacillatum*, male. AG: Amphidial gland, DS: Dorsal sector of pharynx. B-D, Details of microvilli. (A, 10,000 \times ; B, 100,000 \times ; C and D, 80,000 \times .)

fusos. 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 fusos 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 fusos. This means that some of the villi reach a length of at least 400 μ 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.³

Male diorchic, testes opposed and outstretched. Female amphidelphic, anti-dromic. 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 or 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.

³ 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.

Schuurmans 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 μm , whereas Sergeeva gave 94 μm ; the length of the cephalic sensilla is 1.5 and 1.25 μm 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 dependence and variability (Figs. 3–6, 8).

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

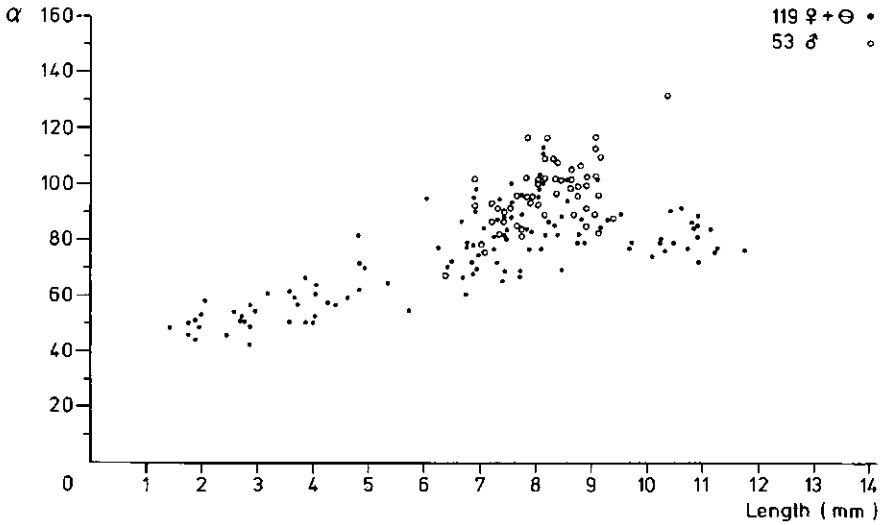


Fig. 3. Relation between ratio "a" (length/body width) and length, based on several *L. bacillatum* populations (Texel).

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

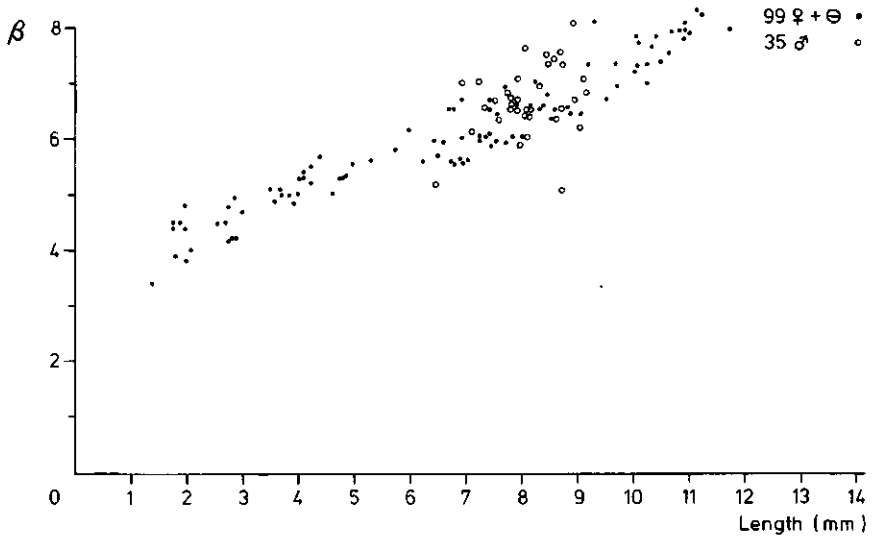


Fig. 4. Relation between ratio "b" (=length/pharynx length) and length, based on several *L. bacillatum* populations (Texel).

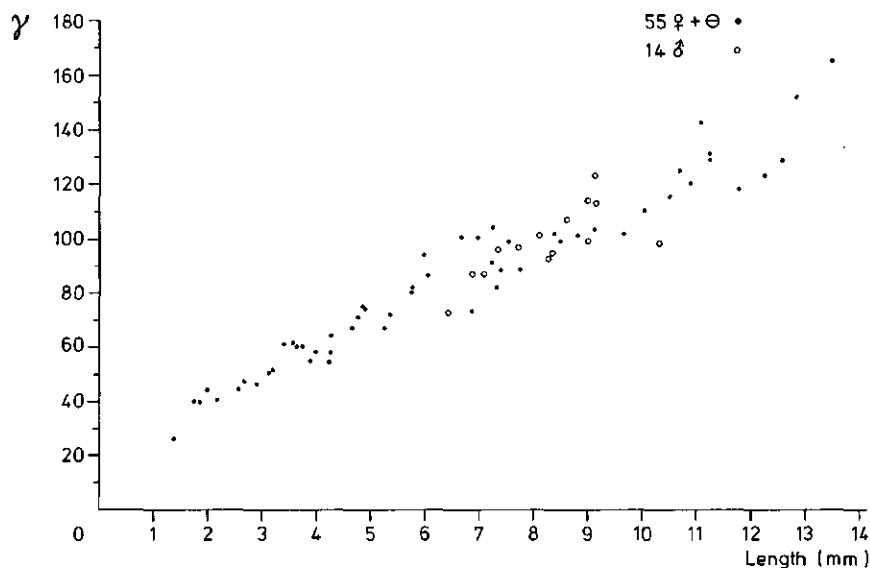


Fig. 5. Relation between ratio "c" (length/tail length) and length, based on several *L. bacillatum* populations (Texel).

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

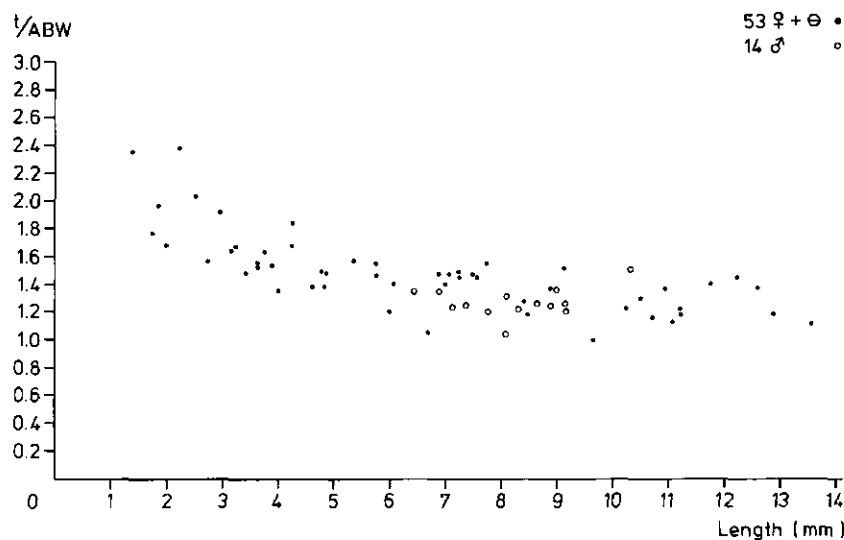


Fig. 6. Relation between "tail/anal body width" and length, based on several *L. bacillatum* populations (Texel).

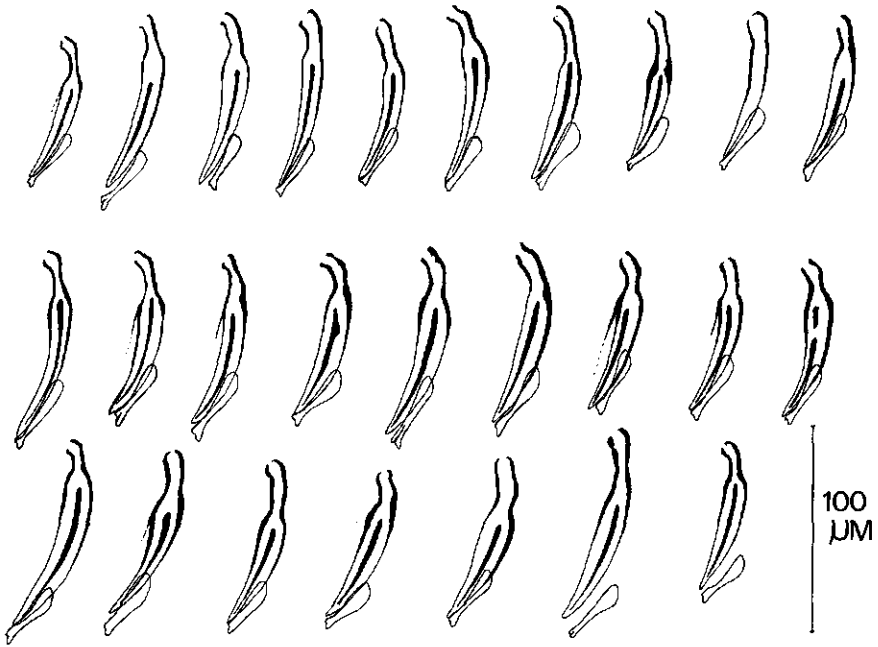


Fig. 7. Variability in spicule shape of the *L. bacillatum* population from Burghsluis.

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

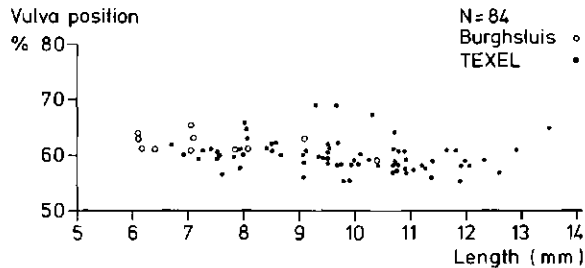


Fig. 8. Relation between V (=distance from anterior extremity to vulva $\times 100$ /body length) and length, based on several *L. bacillatum* populations from Texel.

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 μm , the more medial papillae 1–1.5 μm . 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 μm .

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.

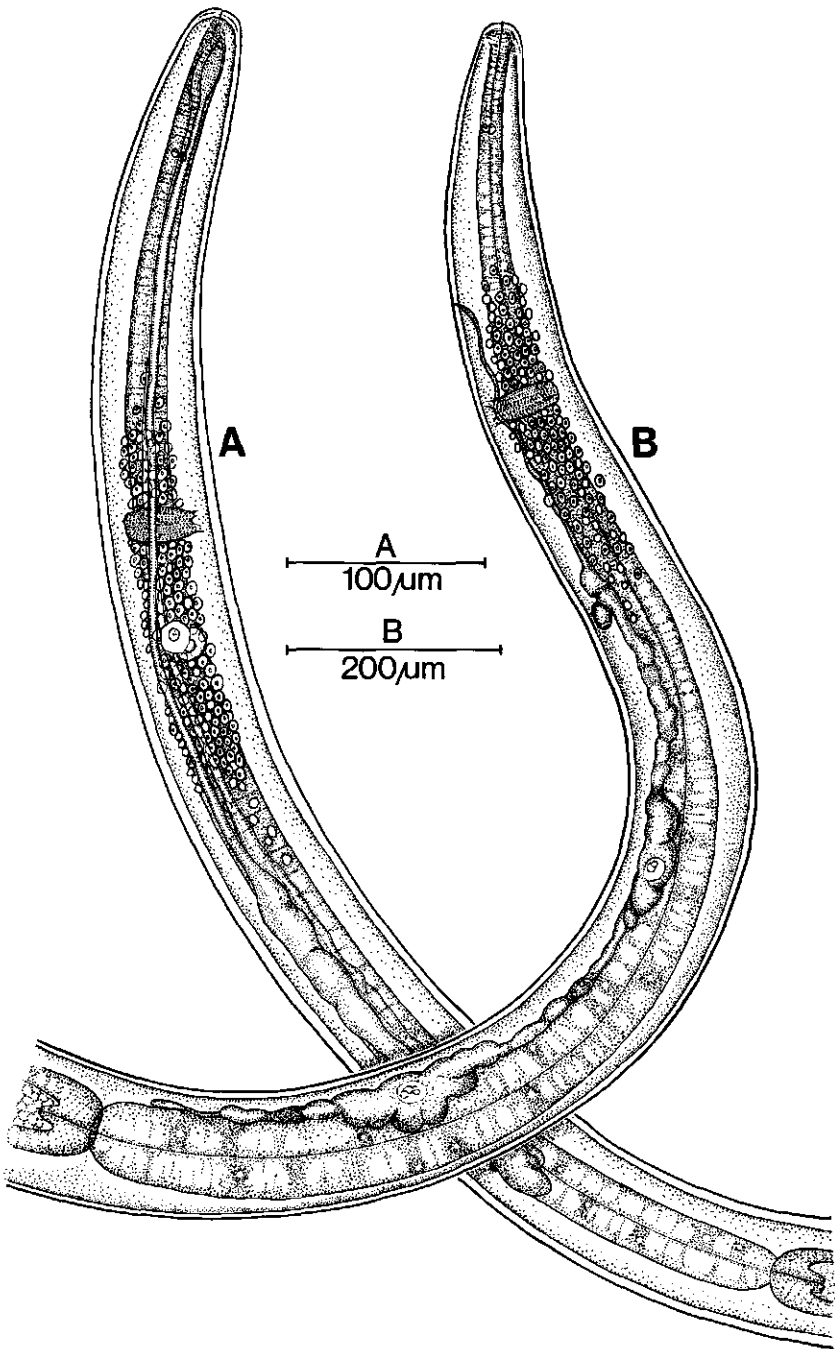


Fig. 9. *L. bacillatum* from Texel. A, Anterior end of male; B, Anterior end of female.

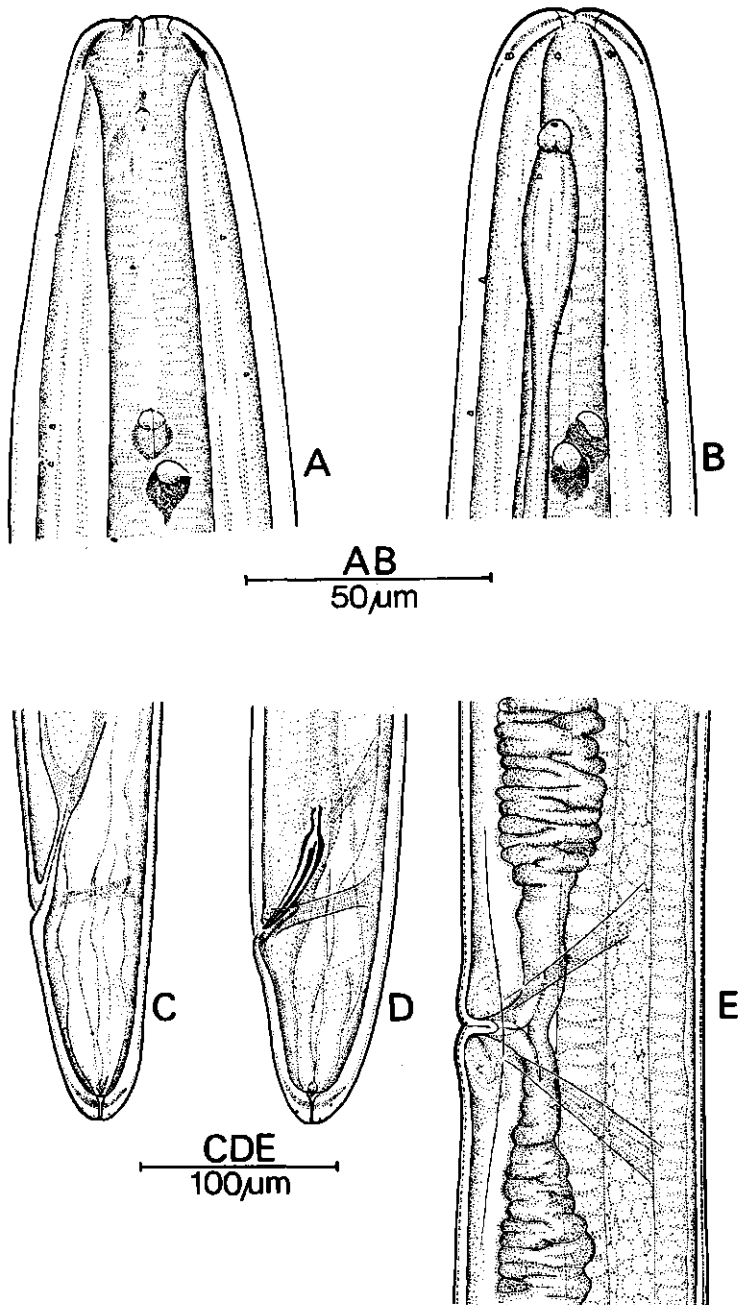


Fig. 10. *L. bacillatum*. A, Head of female, 102; B, Head of male, 76101; C, Posterior end female, 76102; D, Posterior end male, 76101; E, Vulvar region, (Burghsluis).

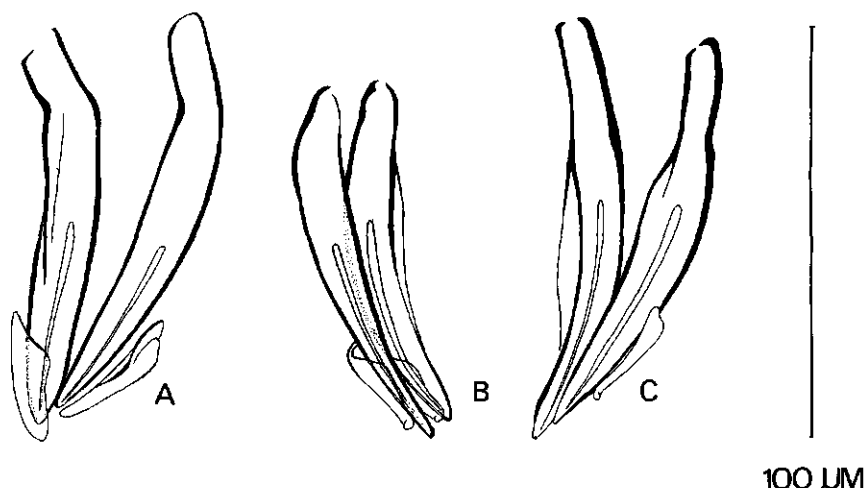


Fig. 11. A and B, Spicules *L. bacillatum* sensu Filipjev, 1918; C, Spicules holotype *L. tuapsense* Sergeeva, 1973.

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 μ m, compared with 7 μ m in *L. bacillatum*.

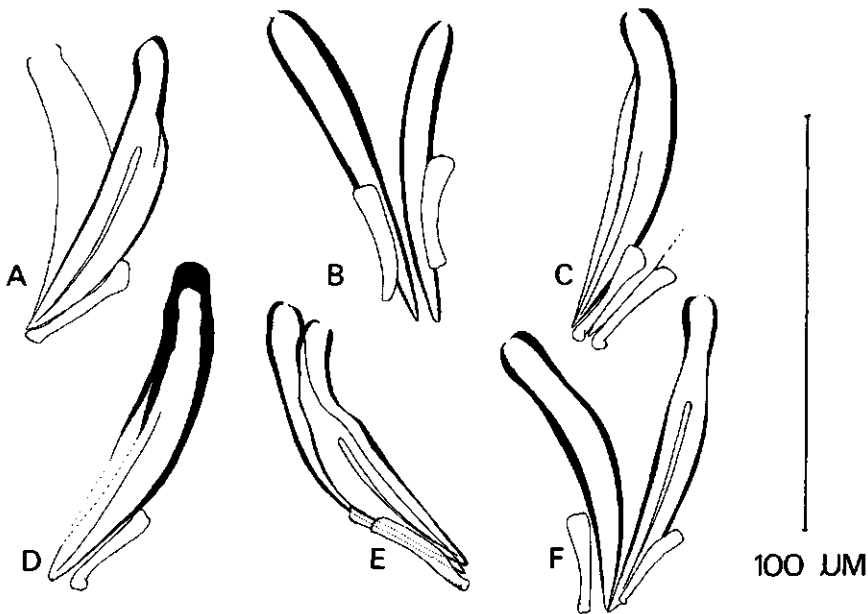


Fig. 12. Spicules. A, Holotype *L. diversum*; B, Paratype *L. diversum*; C, D and F, Paratypes *L. sachalinense*; E, Holotype *L. sachalinense*.

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 μm . 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.

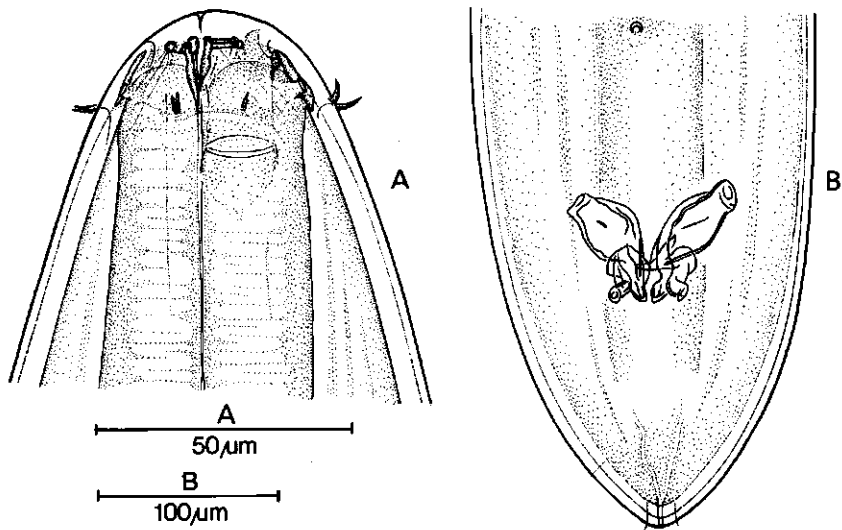


Fig. 13. *L. bathybium*. A, Head; B, Posterior end.

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" ($b = 6.3-12.9$) 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 μm , the aperture about 14 μm . The cephalic setae are vaguely visible; probably 10 setae are present; 6 μm 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 μm . In ventral view, the "papilla" is horseshoe-shaped with the open side posteriad. 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 bathybiium 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. bathybiium*" 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'j Golf,

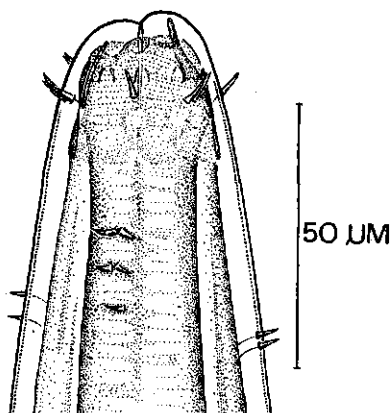


Fig. 14. Anterior end *L. caecum* Ditlevsen, 1923, Lectotype.

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. Dtl."; 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 μ m. The cervical setae do not exceed 6 μ m; their position on the left and right body halves is not alike. The lateral vulvar glands are present; the vaginal ojector 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 μ m. The cuticle thickness varies from 6 μ m at the pharyngeal base to 9 μ 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* (Ssaëljev, 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 μ 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 μ m, the amphidial aperture to 3 μ m, the fovea to 4 μ m, and the lens diameter varies from 6 to 9 μ 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 μ m, the gubernaculum 19 μ m, and the lens diameter is 9 μ 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 μ m from the anterior end; the lengths of pharynx and tail are 2950 and 270 μ m respectively. Ocelli are absent. The shortness of the gonads is remarkable; the anterior reaching a length of 478 μ m, the posterior 488 μ m. The junction of these gonads is situated 10.3 mm from the anterior end. The spicula are 160 μ 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.

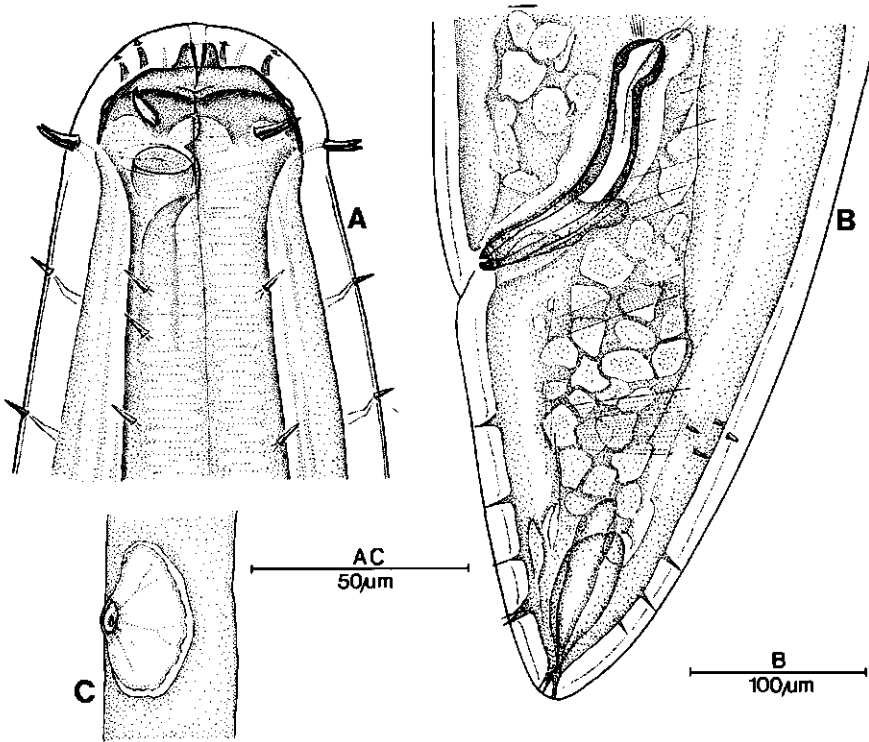


Fig. 15. *L. groenlandicum*. A, Head; B, Posterior end; C, Gland in lateral epidermal chord at level of pharynx base.

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 *Leptosomatium groenlandicum*. A new genus must be erected for these two species. At present I prefer to consider *Leptosomatium groenlandicum* a species inquirenda.

Leptosomatium 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

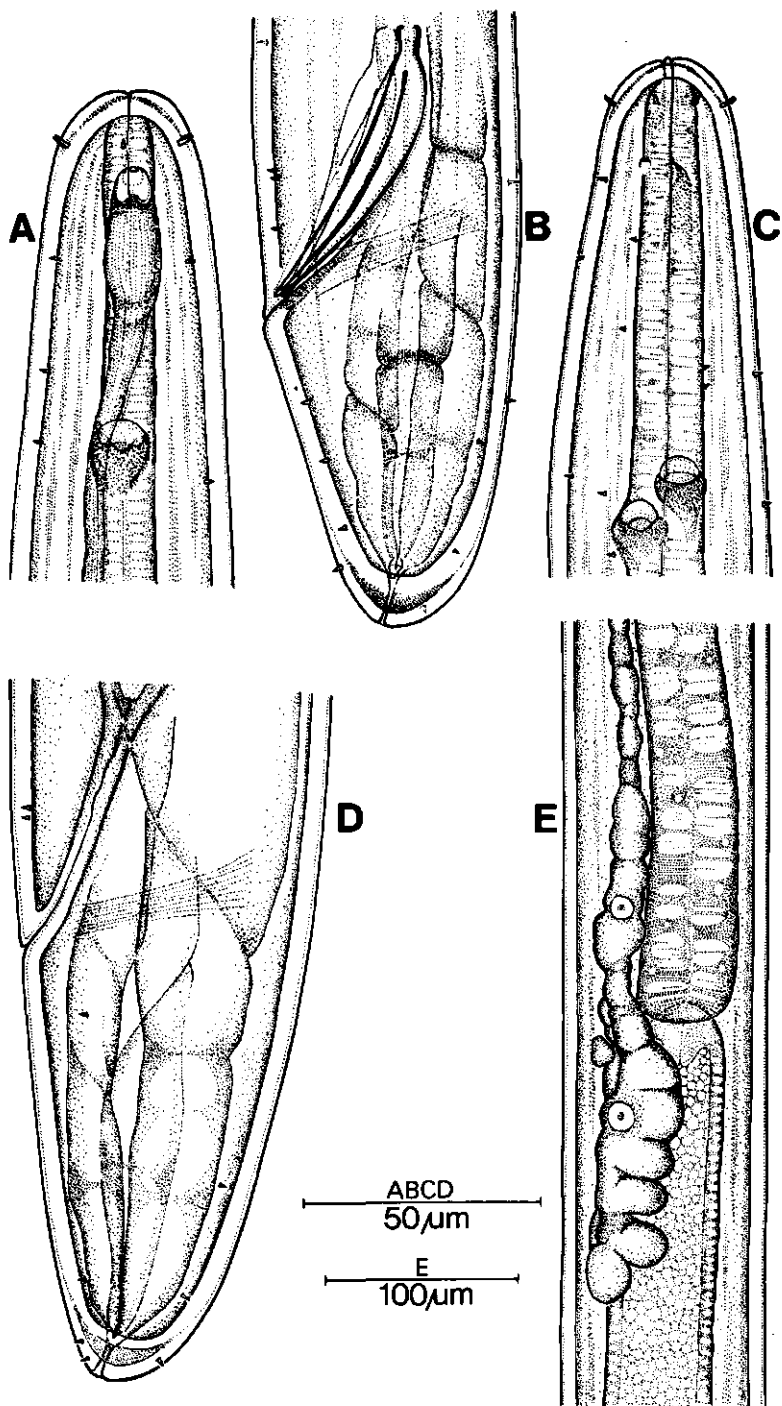


Fig. 16. *L. keiense*. A, Anterior end male; B, Posterior end male; C, Anterior end female; D, Posterior end female; E, Renette, 76047.

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 μ 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 μ 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 μ m anterior to the cloacal vent, whereas in 76049, mounted laterally, this papilla lies at 126 μ 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 μm . Male 76049 (pop. 3) has a lens of 13 μm diameter, the two males of population 2 have a lens diameter of 7 μm , but in general it varies between 9 and 11 μm .

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 μm 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 μm 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 μm long; short setae are situated over the whole body length. The amphids, 15–27 μm from the anterior end, resemble those of related species. The fovea measures 8 μm in the male and 3 μm in the female; the apertures 2 and 1 μm respectively. In one of the females (76040) the cervical pore could be detected at 227 μm from the anterior end. The spiculum length is 63–66 μm , 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 μm), 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 μm 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.

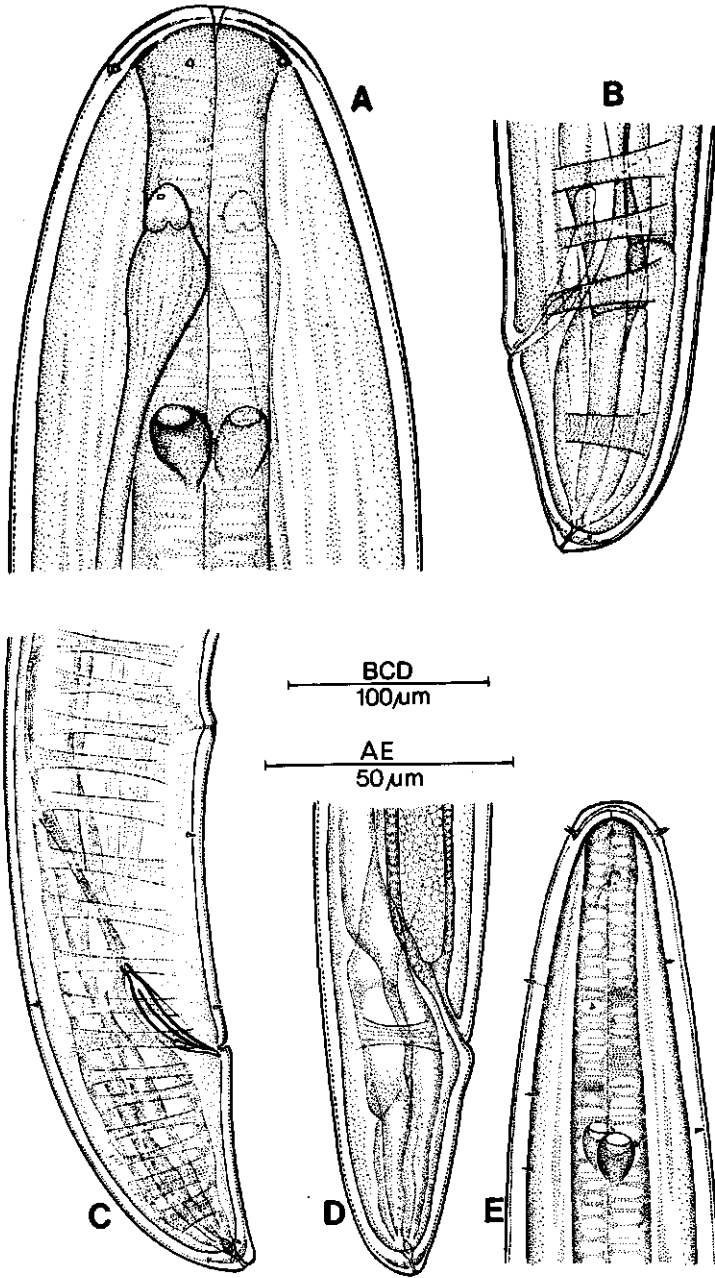


Fig. 17. *Leptosomatium kerguelense* (76056): A, Head; B, Caudal end. (C-E) *L. punctatum*: C, Caudal end of male, 1286-6; D, Caudal end of female, 1286-5; E, Anterior end of female, 76037.

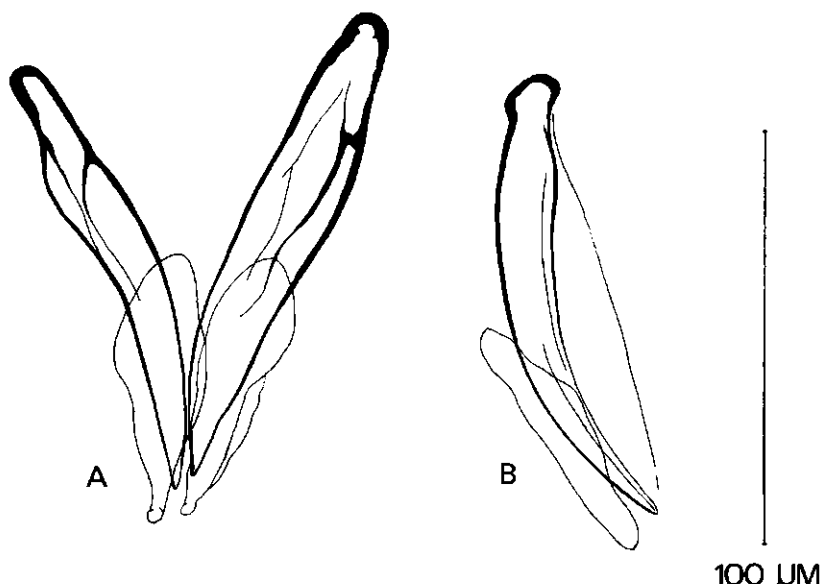


Fig. 18. Spicules *L. kerguelense*. A, Holotype; B, Paratype.

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-ocular 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 identical 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 μ m respectively. The amphidial fovea has a diameter of 5 μ m in the female and 11 μ 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 μ m with a ratio "a" of 29.06. This means that the diameter of this specimen is 240 μ 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 μ 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 μ m; longer than in this material where 3–4 μ m has been measured for the juveniles, 4, 5 for the male and 4 and 5 μ m for the females. Setae of 2–3 μ 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 μ m for the males and 4.9 μ m for the females.

The amphidial aperture and fovea in the male measure 1 and 8 μ 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 μ m, lie at 1.3 times the corresponding body width from the anterior end. The spiculum and gubernaculum length are 79 and 20 μ m, respectively. The ventromedian pre-cloacal papilla is situated at 166 μ 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 22×19 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

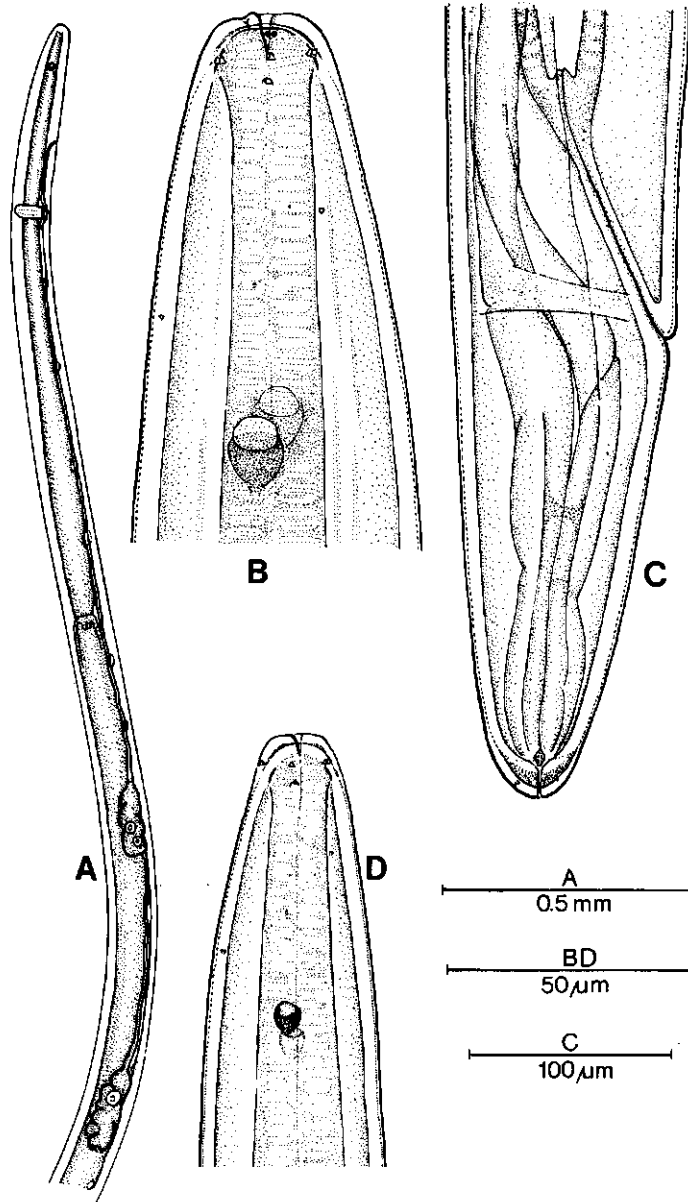


Fig. 19. Anterior end A, and head B, of *L. sp.* A; Tail C, and anterior and D, of *L. sabangense*, juvenile.

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 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 μ 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 μ m respectively. The ocelli lie at 70–86 μ m from the anterior end, the lens varies from 8 to 10 μ m. The anterior body end is very slender; the cephalic width never exceeds 30 μ m, the width at the ocelli never exceeds 60 μ 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 ranjhui* Timm, 1960, is closely related to *Pseudocella*; in *L. ranjhui*, lateral epidermal glands are also present, the pigment spots are situated anteriorly, the vaginal ovejector is absent and moreover, *L. ranjhui* 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 acrocercus* 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

| | |
|---|------------------------------------|
| <i>L. abyssale</i> Allgén, 1951 | species inquirenda |
| <i>L. acephalum</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 |

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 μ m) placed anterior to papillae. Short pharynx. Ocelli in males far anterior.
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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 μ m in diameter; pharynx short; ventromedian pre-cloacal papilla present or absent *L. keiense*
- Lens 6–7 μ 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 μ m; male rare; females big, never less than 10 μ m in length; (Southern Hemisphere) *L. clavatum*
- Cephalic capsule less than 9 μ m in length; males not rare; females often smaller than 10 μ 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. acephalum* (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. acephalum</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 | |
| F | 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. acephalum</i> , pop. 2; Mexico, Allen Point | | | | | | | | | | | | | | | | |
| F | 76110 | 7720 | 82 | 298 | 1106 | 103 | 37 | 71 | 102 | 118 | 121 | 72 | 64 | 7.0 | 75 | 56 |

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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. acephalum</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. acephalum</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. acephalum</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. acephalum</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 |

Tom Bongers

Abstract.—The results of a study of *Leptosomatides* type-material are given.

Leptosomatides conisetosus Schuurmans Stekhoven and Mawson, 1955 is transferred to *Deontostoma*; *L. antarcticus* Mawson, 1956 is considered a good species although more information is desired regarding the presence of odontia and onchia.

Leptosomatides brevisetosus Platonova, 1976, and *L. acutipapillosus* Platonova, 1976 are synonymized with *L. marinae* by Platonova (this paper). *L. caucasiensis* Sergeeva, 1973 is synonymized with *L. euxinus* Filipjev, 1918. *Leptosomatides crassus* Platonova, 1967, *L. steineri* sensu Filipjev, 1946 and *Leptosomatium elongatum* sensu Platonova, 1967 are considered identical to *L. grebnickii* (Filipjev, 1916).

Leptosomatides steineri Filipjev, 1922, and *Leptosomatium tetrophthalmum* sensu Platonova, 1967 are synonymized with *L. arcticus* (Filipjev, 1916). *L. microlaimus* (Allgén, 1957) Platonova, 1976, and *L. filiformis* (new rank) (= *L. steineri* subsp. *filiformis* Filipjev, 1946) are considered *species inquirendae*. *Leptosomatides inocellatus* Platonova, 1967 does not belong to *Leptosomatides* and is considered a *species incertae sedis*.

Additional descriptions are given in this paper. Arguments are given for transferring *Leptosomatides* to the Thoracostomatinae. In fact, the only difference from *Deontostoma* is the absence of odontia and onchia in *Leptosomatides*.

In a previous paper (Bongers 1983) the confusion concerning the separation of the genera *Leptosomatium* Bastian, 1865 and *Leptosomatides* Filipjev, 1918 was discussed, and *Leptosomatium tetrophthalmum* sensu Platonova, 1967 (*nec* Ssaweljev, 1912), *L. arcticum* Filipjev, 1916, *L. grebnickii* Filipjev, 1916 and *L. elongatum* sensu Platonova, 1967 (*nec* Bastian, 1865) were transferred to *Leptosomatides*. Based on the literature it is almost impossible to distinguish the species of *Leptosomatides*; I therefore studied the type-material of the species assigned to it. Results and additional descriptions are presented in this paper.

Material

Type-material was available for study of the following species: *Leptosomatium arcticum* Filipjev, 1916; *L. grebnickii* Filipjev, 1916; *L. tetrophthalmum* sensu Platonova, 1967; *L. elongatum* sensu Platonova, 1967; *Leptosomatides steineri* sensu Filipjev, 1946; *L. steineri* subsp. *filiformis* Filipjev, 1946; *L. crassus* Platonova, 1967; *L. inocellatus* Platonova, 1967; *L. caucasiensis* Sergeeva, 1973; *L. acutipapillosus* Platonova, 1976; *L. brevisetosus* Platonova, 1976 and *L. marinae* Platonova, 1976. In addition, the Smithsonian Institution, Washington, D.C., U.S.A. put unidentified material at my disposal.

Methods and Differential Characteristics

The specimens, many of which were in poor condition, were compared with their descriptions. In several cases the literature was almost inaccessible. Recommendations 4 and 5 appendix E of the International Code of Zoological Nomenclature (hereafter termed the Code), in which it is advised to accompany the description of a new taxon by a translation into English, French, German, Italian, or Latin, if the description is not written in one of these languages, have often not been followed. In two cases the summaries contradicted the text.

The specimens from the Smithsonian Institution had been mounted in glycerin between coverslips in aluminum frames. The other specimens had been mounted on glass slides in glycerin-gelatin and could be observed from only one side. The coverglasses on the latter slides were not supported and the nematodes were severely flattened. Several slides contained more than one species. The way in which paratypes were designated for *Leptosomatides marinae*, *L. brevisetosus*, *L. acutipapillosus* and *L. caucasiensis*, for example, does not conform to the Code and leads to confusion.

The flattening of the specimens made relative measurements valueless in so far as body width is one of the components. Often the cuticle was swollen, and the hypodermal tissue had shrunk, pulling the cervical sensilla into small craters. In my opinion, cuticle thickness is valueless as a differential character in these cases; the same holds for ratio "a" and other relative measurements. When the tail is curved strongly to the ventral side (e.g., in the males of *L. marinae*, Fig. 3) the index "c" is also valueless.

The cephalic sensilla (sensu Lorenzen 1981) are setiform in *L. antarcticus*, *L. euxinus*, and *L. reductus*, and papilliform in the remaining species. A sensillum is considered setiform when its length is twice or more its basal breadth. Cervical sensilla were present in all species examined.

The cephalic capsule is uniform in *Leptosomatides* spp. The posterior suture undulates but is never more posterior than the anterior margin of the amphid. On the outer side of this capsule a refractive layer in the cuticle can be observed, which is homologous to the lunula in the tail. Both are present in *Leptosomatides* and related genera but absent in *Leptosomatides inocellatus*, which is removed from this genus.

The amphids are uniform in structure throughout the genus *Leptosomatides*; only some size differences occur between sexes and species. The fovea, of which the diameter is presented in this paper, is circular in lateral view and the posterior margin is clearly visible, in contradiction to the fovea in female *Leptosomatium* specimens.

The ocelli are provided with a lens-like body, here termed lens, of which the diameter, in lateral view, is used in this paper. Additional pigment, posterior to the ocelli, is present in the pharynx of a number of specimens and is not species-specific. In general, the distance from lens to anterior body end varies within about 10%. The left lens lies more anterior in two-thirds of the specimens. In two aberrant specimens, belonging to *L. euxinus* and *L. marinae*, one of the ocelli lies half as far from the anterior end as the other, but this phenomenon is not characteristic for *L. euxinus* as stated by Platonova (1976).

The renette was observed in one female of *L. tetraphthalmum* sensu Platonova,

1967 and in one female of *L. marinae*. This gland is restricted to the pharyngeal region but the position of the pore has not yet been located.

The vulva lies slightly anterior to the middle of the body; a strongly developed vaginal musculature is present in all specimens throughout *Leptosomatides* and is a differentiating character from *Leptosomatium*, in which this radial musculature is absent. This ovejector, as defined by Filipjev (1916:23), is also present in *Thoracostoma* and *Deontostoma*.

Intra-cuticular granula, anterior and posterior to the vulva, and lateral vulvar glands, are present; in *L. euxinus*, however, the granula are fewer in number but distributed over a larger area. The ducts of the lateral vulvar glands were difficult to observe. Hope (1967a) described these granula and vulvar glands in, amongst others, *Thoracostoma trachygaster*. He stated that they are absent in pre-adults but in a pre-adult of *L. crassus*, slide 7016, both are present. In *L. arcticus* five to seven glands are developed, in the remaining species two to four. A small overlap exists for which I refer to the discussion of *L. marinae*. I realize that the number of glands is a doubtful distinguishing character but it is one of the few that distinguishes females of *L. marinae* and *L. arcticus*.

Filipjev (1916) described a well-developed system of sensory papillae near the vulva of *Thoracostoma denticaudatum*, and Hope (1967b) reported comparable unevennesses anterior and posterior to the vulva of *Corythostoma triaulolaimus*; these sensilla are also present in *L. marinae*.

In my opinion, Filipjev and Platonova attach unwarranted importance to the number and size of the eggs. According to Platonova (1976) *Leptosomatides crassus* can be distinguished from *L. steineri* sensu Filipjev, 1946 by the number of eggs; up to eight in the former and four in the latter. It is my opinion that size and number of eggs depend on the season and developmental stage of the female.

When males are present, the spiculum and gubernaculum shape are useful to separate the species. The gubernaculum, and to a lesser degree the spicules, may be obscured by the opaqueness of the surrounding tissue. It was impossible to ascertain if there was any difference in length between the left and right spiculum. In this paper the length of the chord is given.

Males of *L. marinae* possess two ventromedian supplements, one precloacal with alae and one postcloacal without. The anterior and posterior alae (as termed by Hope 1967a) are also present in a number of species assigned to the Thoracostomatinae.

The term "alae" to describe the refractive ribs in the ventromedian supplement is confusing. Both Hope and I agree that the introduction of another term should be postponed until more information becomes available regarding its function. Often the number of pre- and postcloacal subventral papillae shows intraspecific variability.

Historical Review

The genus *Leptosomatides*, with *L. euxinus* as type-species, was erected by Filipjev in 1918 and described as being intermediate between *Leptosomatium*, which it resembles in the structure of the anterior end, and *Deontostoma*, which it resembles in the structure of the posterior end of the male. He remarked that

Leptosomatum arcticum and *L. grebnickii*, both described by himself in 1916, might also belong to *Leptosomatides* but preferred to wait until their males should be found.

Filipjev (1921:563) transferred *Leptosomatum gracile* sensu Steiner, 1916 nec Bastian, 1865 to *Leptosomatides* and in 1922 he renamed it *Leptosomatides steineri*. In 1922, the radial musculature of the vagina wall, here termed the vaginal ovejector, was added to the generic diagnosis.

Filipjev (1946) reported *L. steineri* from the New Siberian Islands; because of its more slender body, two of the specimens were described as *L. steineri* var. *filiformis*. In 1955, Schuurmans Stekhoven and Mawson added *L. conisetosus*; one year later *L. antarcticus* was described by Mawson. Both are Antarctic forms. In 1959 Timm described the only subtropical member of this genus from the Arabian Sea as *L. reductus*.

Platonova (1967) added two species from the Kara Sea, *L. inocellatus* and *L. crassus*; Sergeeva published the description of a species from the Black Sea in 1973. Three species with papilliform cephalic sensilla from the Kuril Islands, *L. acutipapillosus*, *L. brevisetosus*, and *L. marinae*, were described by Platonova in her thesis (1976), and in the same paper, *Leptosomatum microlaimum* Allgén, 1957 was transferred to *Leptosomatides*.

Leptosomatum arcticum Filipjev, 1916, *L. grebnickii* Filipjev, 1916, *L. tetrophthalmum* sensu Platonova, 1967 nec Ssaweljev, 1912, and *L. elongatum* sensu Platonova, 1967 nec Bastian, 1865 were transferred to *Leptosomatides* by Bongers (1983).

Leptosomatides Filipjev, 1918

Leptosomatides Filipjev, 1918:50–51; 1922:98.—Platonova, 1976:69–70 [Key].

Diagnosis.—*Leptosomatidae* Filipjev, 1916. No sexual dimorphism in amphid structure; fovea round. Cephalic capsule weakly developed, posterior suture undulating; lobes never reaching beyond anterior margin of amphids. Onchia and odontia absent. Labial sensilla intracuticular; cephalic and cervical sensilla papilliform or setiform. Ocelli provided with distinct lens. Dorsal pharyngeal gland opens into pharyngeal lumen; ventrosublateral glands open at anterior end, ducts cuticularized. Renette in pharyngeal region. Caudal glands long, overlapping intestine. Lunula present. Ortho- and loxometanemes-I present.

Female gonads amphidelphic, antidromic. Vaginal ovejector present, lateral vulvar glands and intra-cuticular vulvar granules usually present. Gonads located left of intestine. Male diorchic, testes opposed and outstretched; ventral precloacal papilla and 2 subventral rows of accessory sensilla present in cloacal region. Gubernaculum with cuneus, crura present or reduced. Copulatory muscles strongly developed.

Remarks.—Discussing the labial orifices of the ventrosublateral pharyngeal glands in *Leptosomatum bacillatum*, Platonova (pers. comm.) stated that one of her students previously described these orifices in *Leptosomatides marinae*. I have also observed these orifices on the anterior end of *Syringonomus typicus* Hope and Murphy, 1969, and *Leptosomatum* species. According to Hope (1982) these openings in the mandibular grooves might be characteristic for the *Leptosoma-*

tidae. The glands, as present in the lateral hypodermal chord of, amongst others, *Cyclicolaimus* are absent in *Leptosomatides*; only in the vulvar region are such glands present. The gonads in *Leptosomatides* are situated on the left side of the intestine.

Leptosomatides antarcticus Mawson, 1956

Leptosomatides antarcticus Mawson, 1956:42, fig. 1a-e.

Diagnosis.—Cephalic sensilla setiform; 4 μ m. Amphid (fovea) 10 μ m in diameter. Ocelli 1.5 corresponding body diameters from anterior end. Spicula relatively short, 100 μ m; crura of gubernaculum present. Tail conical in both sexes. Stoma provided with tooth (?).

Type.—Syntypes: 7 ♀, 3 ♂.

Distribution.—Antarctica: Enderby Land, MacRobertson Land.

Discussion.—I was not able to obtain material of this species for comparison. Although the vulvar region is not depicted and nothing is mentioned concerning the vagina structure, this species probably belongs to *Leptosomatides*. The small tooth at the anterior end of the pharynx, however, needs confirmation. *Leptosomatides conisetosus* Schuurmans Stekhoven and Mawson, 1955, which is provided with a tooth, may have influenced this observation.

If onchia and/or odontia are present, *L. antarcticus* must be transferred to *Deontostoma*.

Regarding the figures of *L. antarcticus* and *L. conisetosus*, some confusion exists. On page 42 (Mawson 1956), fig. 1a-c is stated to represent *L. antarcticus* and fig. 2a-d *L. conisetosus*. Five illustrations, however, are given of the former and three of the latter species. Moreover, fig. 1e probably represents *L. conisetosus*. An indication of the sex of the anterior ends is missing.

An additional description of the vulva structure, amphids, precloacal papilla in the male and indication of lectotype is needed.

Leptosomatides arcticus (Filipjev, 1916), new combination

Fig. 1A, B, D

Leptosomatum arcticum Filipjev, 1916:66-68, fig. 1.

Leptosomatum gracile sensu Steiner, 1916:610-620, fig. 27a-o, nec Bastian, 1865: 145-146, figs. 158-160.

Leptosomatides steineri Filipjev, 1922:98, pro *Leptosomatides gracile* sensu Steiner, 1916:610-620, fig. 27a-o.

Leptosomatum tetraphthalmum sensu Platonova, 1967:828-829, nec Ssaweljev, 1912:124.

Nec *Leptosomatides steineri* sensu Filipjev, 1946:159, 177-178, fig. 2.

Nec *Leptosomatum arcticum* sensu Mawson, 1958:315-316, fig. 1a-c.

Diagnosis.—Cephalic sensilla papilliform; 2-3 μ m. Cephalic capsule 10-13 μ m. Fovea 8 μ m. Lens 10 μ m. Lateral vulvar glands 5-7. Intracuticular granula numerous. Males unknown.

Type.—The only syntype of *L. arcticus* is a decapitated body; *Leptosomatum gracile* sensu Steiner, 1916 could not be located. Of *L. tetraphthalmum* sensu

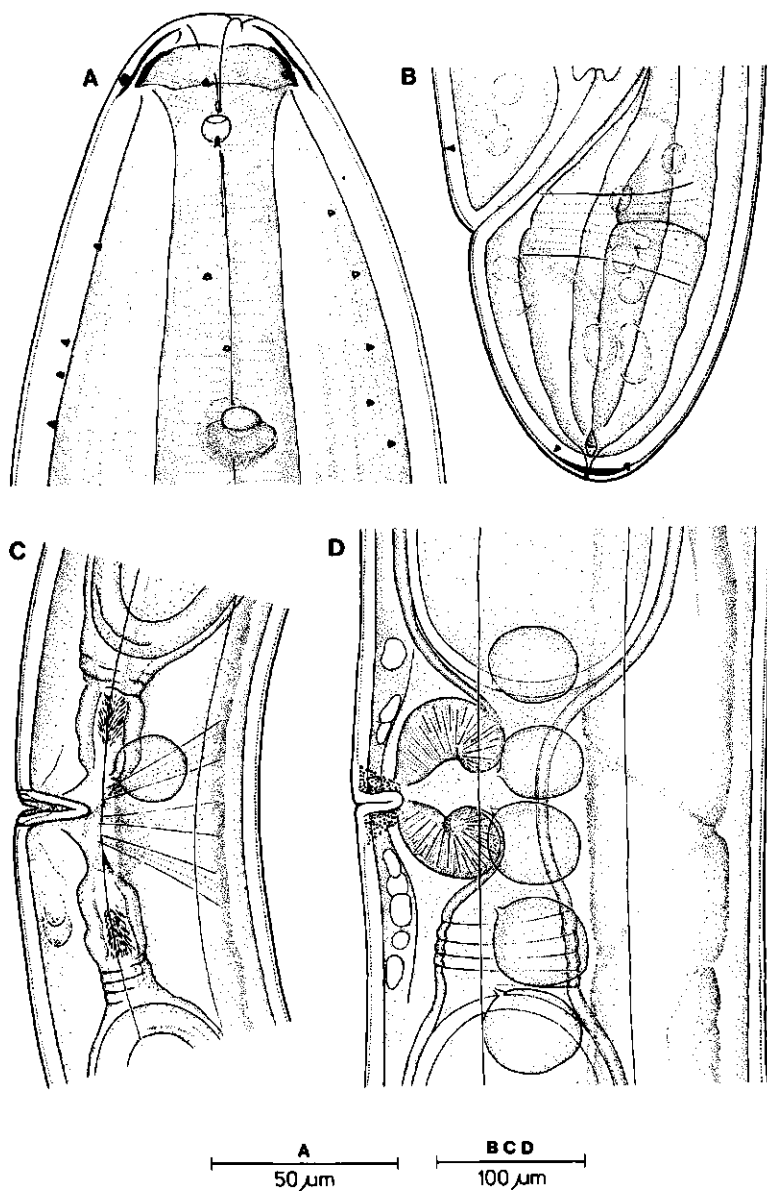


Fig. 1A, B, D. *Leptosomatides arcticus* (Filipjev, 1916) (depicted is *Leptosomatum tetrophthalmum* sensu Platonova, 1967): A, Female, anterior end; B, Female tail; C, *Leptosomatides filiformis* (Filipjev, 1946): lectotype, vulvar region; D, Vulvar region.

Platonova, 1967, 15 females are in existence. Female 5070-2, depicted in Fig. 1, whose measurements are given in the Appendix, fits the description and may be used for comparison. Slides deposited at Zoological Institute, Leningrad.

Type-locality.—Murman Coast; littoral.

Distribution.—Novaya Zemlya, Barents Sea, Kara Sea.

Discussion.—Although males are unknown, *Leptosomatum arcticum* Filipjev, 1916 has all the characters diagnostic for the females of the genus *Leptosomatides* as stated in a previous paper (Bongers 1983). The fovea comes to 8 μ m, the lens 10 μ m in lateral view. The only remaining syntype shows five lateral vulvar glands.

Leptosomatum gracile sensu Steiner, 1916 was transferred to *Leptosomatides* by Filipjev in 1921 (p. 563) and renamed *Leptosomatides steineri* in 1922.¹ Steiner described six pairs of cephalic sensilla in *L. gracile*. According to Hope (pers. comm.) this is probably not species-specific because in *Deontostoma* occasional specimens are found with six pairs of sensilla. Steiner depicted seven lateral vulvar glands; in Filipjev's specimens (1946) the number of glands never exceeds four. Therefore a distinction is drawn between Steiner's (1916) and Filipjev's (1946) material.

Leptosomatum tetrophthalmum sensu Platonova, 1967 was collected in 1915 and 1925 and was assigned to *Leptosomatum tetrophthalmum* Ssaweljev, 1912 by Filipjev. It seems plausible that Filipjev had seen Ssaweljev's material (Platonova pers. comm.) and that the specimens of Platonova were identical to those of Ssaweljev. Ssaweljev's description (1912) is quite superficial and incomplete and it is not possible to establish whether this species belongs to *Leptosomatum* or *Leptosomatides*. As no syntypes are present, this species was considered a *species inquirenda* in a previous paper.

The only existing material worth redescribing, although flattened, is *Leptosomatum tetrophthalmum* sensu Platonova, 1967. Two females have been restudied and dimensions and figures (Fig. 1) are presented in this paper. Slide 5070 bears two females collected 22-IX-1925.

Although more information is necessary regarding the male, the females can be distinguished from *L. euxinus* by the papilliform cephalic sensilla, from *L. marinae* and *L. grebnickii* by the number of lateral vulvar glands and the lens diameter, from *Leptosomatides* sp. A by the number of lateral vulvar glands.

Leptosomatides conisetosus Schuurmans Stekhoven & Mawson, 1955

Leptosomatides conisetosus Schuurmans Stekhoven & Mawson, 1955:98–100, figs. 20–22.—Mawson, 1956:42–43, fig. 2a–d; 1958b:320, fig. 5b.

This species known from Antarctica, Kerguelen Islands, and Macquarie Island,

¹ Platonova (1976) probably wrongly interpreted this paper: on the one hand she considers *L. gracile* sensu Steiner, 1916, conspecific with *L. gracile* Bastian, 1865 for which she used the figures of Steiner (1916). On the other hand, however, on page 71 she accepts *L. steineri* Filipjev, 1922 and does not refer to Steiner's paper. So, according to Platonova, *Leptosomatum gracile* sensu Steiner, 1916 and *Leptosomatides steineri* Filipjev, 1922 are not congeneric. According to Filipjev (1922), however, they are objective synonyms.

was not available for re-examination, so the discussion will be based on the original description and Mawson's papers of 1956² and 1958b.

Leptosomatides conisetosus (lapsus *conisetosum*) is characterized by a strongly developed cephalic capsule, the presence of a small tooth at the base of the funnel-shaped buccal cavity and cuticularized lips.

The shape of the cephalic capsule varies somewhat; in the holotype the lobes are short with straight edges posteriorly and semicircular spaces between the lobes. Figure 2a of Mawson's 1956 paper, however, shows a capsule with lobes broadening posteriad.

The genus *Leptosomatides* was erected as being intermediate between *Deontostoma* and *Leptosomatium* concerning the posterior and anterior end respectively. In *L. conisetosus*, however, the anterior end shows closer affinities to *Deontostoma* than to *Leptosomatium* and I herewith transfer this species to that genus as *Deontostoma conisetosum* (Schuurmans Stekhoven and Mawson, 1955), new combination.

Leptosomatides euxinus Filipjev, 1918

Fig. 2A-D

Leptosomatides euxinus Filipjev, 1918:51-54, fig. 3a-f.

Leptosomatides caucasiensis Sergeeva, 1973:1711-1712, fig. 3a-b.

Diagnosis.—Cephalic sensilla setiform: 4-5 μ m. Cephalic capsule short; 7 μ m in length. Anterior part of pharynx cuticularized. Fovea 5.5-6.5 μ m in diameter in both sexes. Lens 6-7 μ m. Vulvar glands absent (not developed?). Intracuticular vulvar granula finer and more dispersed than usual in the genus. Spiculum short; crura present, but reduced.

Holotype.—The holotype is on slides 5074 (body) and 5015 (head), Zoological Institute, Leningrad, U.S.S.R. The holotype of *L. caucasiensis* is also deposited at the Zoological Institute.

Distribution.—Black Sea.

Discussion.—The description and figures of slide 6565 given by Platonova (1976) are based on a specimen with an aberrant position of the ocelli; this phenomenon is also present in slide 7996 of *L. marinae*.

The type of *L. caucasiensis* is twisted; the precloacal papilla, in the summary erroneously stated to be absent, is visible at low magnification if the slide is turned over. According to Sergeeva (1973), the cervical setae are absent in *L. caucasiensis* and differences should exist in shape and development of spiculum and cephalic capsule respectively. These cervical setae are present. The development of the cephalic capsule is similar to that in *L. euxinus*; the caudal glands are longer than depicted, overlapping the intestine. *L. caucasiensis* Sergeeva, 1973 is herewith synonymized with *L. euxinus* Filipjev, 1918.

A slide (No. 8097) labelled "paratype" of *L. caucasiensis* (Coll. 1 Feb 1968),

² The way in which Mawson (1956) described the body proportions is not to be recommended. On page 43: "The eyes are one-fifth to one-sixth of the distance from head to nerve ring, and this latter is 1/2.7-1/3.3 of the length of the oesophagus." The length of the pharynx has to be calculated from $b = 7.2-8.8$ and $L = 14-15$. These relative measurements are almost useless.

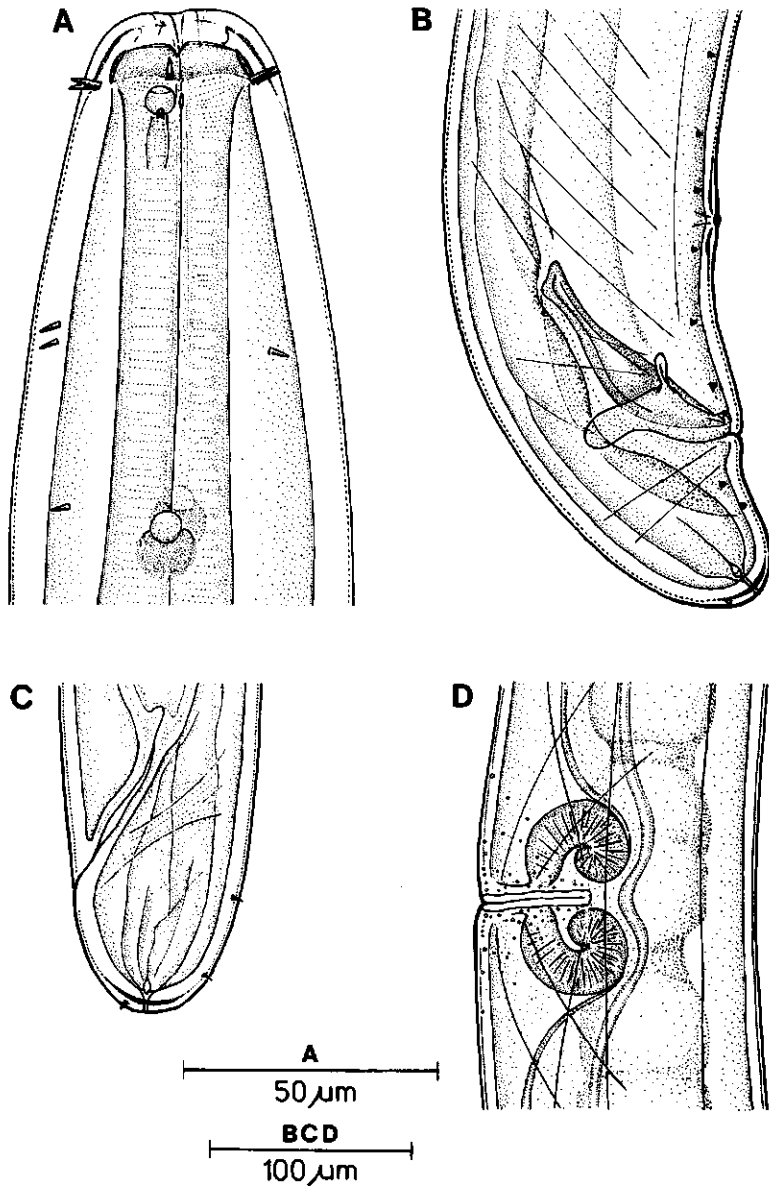


Fig. 2. *Leptosomatides euxinus* Filipjev, 1918 (depicted is *Leptosomatides caucasiensis* Sergeeva, 1973, det. Sergeeva). A, Male head; B, Male tail; C, Female tail; D, Vulvar region.

is present in the collection of the Zoological Institute, which contains a male and two female specimens in rather good condition. (The indication of slide 8097 as paratype is not valid as these specimens do not belong to the type-series.) The body dimensions of these specimens are given in the Appendix and Fig. 2 is also based on this material. The male specimen was in excellent condition and the gubernaculum structure could easily be observed. The crura are reduced; these anterior processes seem to be twisted.

In the type of *L. euxinus* I was unable to note the lateral vulvar glands. According to Filipjev (1921:405) these glands (phagocytic cells) are sometimes present, although he was unable to observe the ducts.

This species can easily be distinguished from the other species of *Leptosomatides* by the setiform cephalic sensilla, the short length of the cephalic capsule in both sexes, the ocelli, which lie at about twice the corresponding body width from the anterior end, and the c-value exceeding 120. *Leptosomatides reductus* Timm, 1959 is closely related to this species and is distinguishable by the diameter of the fovea in the male, which is about 10 μ m as opposed to 6–7 μ m in *L. euxinus*. Minor differences exist in the length of the cephalic setae and structure of spiculum.

Leptosomatides filiformis (Filipjev, 1946), new rank

Fig. 1C

Leptosomatides steineri filiformis Filipjev, 1946:159, 177–178.

Diagnosis.—Cephalic sensilla papilliform; 3 μ m. Cephalic capsule 9–11 μ m. Fovea 7 μ m. Lens 8 μ m. One lateral vulvar gland. Intracuticular granula almost absent. Uterine (?) ovejector present.

Type.—The specimen on slide 7010 is herewith designated lectotype. It is labelled: *L. steineri* var. *filiformis* ♀ det. I. N. Filipjev "SADKO," 80°16'N × 74°02'E, 26-8-1935 Karskoje more. Zoological Institute, Leningrad, U.S.S.R.

Distribution.—Northern Kara Sea (see coordinates).

Discussion.—Filipjev (1946) described a variety of *L. steineri* as subsp. *filiformis* on the basis of a more slender body. This female, and not a male as stated in the French summary, is characterized by the ratios 105, 8.0 and 105. In the collection of the Zoological Institute in Leningrad, two slides were present, 6999 and 7010, with aberrant females. The female on 7010, labelled as var. *filiformis*, was measured by me and the vulvar region figured (Fig. 1c). The body is twisted; anterior and posterior ends are oriented dorsoventrally, midbody laterally. The cuticle is considerably swollen.

The other female, labelled *L. steineri* var. *filiformis* (slide N-6999) has the same aberrant vagina structure. According to Platonova (pers. comm.) this female is 11.8 mm long with a pharynx length of 1700 μ m, tail length of 120 μ m and body width of 170 μ m.

This is a doubtful species; more information is necessary regarding the torn vaginal ovejector. The difference between this species and *L. steineri* sensu Filipjev, 1946 is not less than the differences between the other short-papilloid species and, therefore, this subspecies is raised to specific level.

Leptosomatides grebnickii (Filipjev, 1916), new combination

Leptosomatum grebnickii Filipjev, 1916:68–70, fig. 2.

Leptosomatides steineri sensu Filipjev, 1946:159, 177–178, fig. 2. *Nec* Filipjev, 1922:98 pro *Leptosomatum gracile* sensu Steiner, 1916:610–620, fig. 27a–o. — *Nec Leptosomatides steineri* subsp. *filiformis* Filipjev, 1946:159, 177–178. — Platonova, 1967:829.

Leptosomatides crassus Platonova, 1967:829–831, figs. 5–7.

Leptosomatum elongatum sensu Platonova, 1967:828. — *Nec* Bastian, 1865:145, figs. 156–157.

Diagnosis. — Cephalic sensilla papilliform 2–3 μ m. Cephalic capsule 10–13 μ m. Fovea 10 μ m in female. Lens 6 μ m. Lateral vulvar glands 2–4. Intracuticular granula numerous. Spicula uniformly curved, gubernacula with paired cunei directed posteriorly at right angles to spicula.

Type. — Head on 5778 and decapitated body on 5779. Indicated by Platonova (1976) as holotype. However, as this designation was done after the original publication, the correct designation is lectotype. Zoological Institute, Leningrad, U.S.S.R.

Type-locality. — Behring Islands.

Distribution. — New Siberian Islands, Behring, Kara and Barents Sea.

Discussion. — Platonova (1976) indicated slides 5778 and 5779 as holotype; the former slide contains the head, the latter a decapitated body of a female and a complete female. Hence the head, together with the decapitated female, represent the lectotype.

According to Filipjev (1916), *Leptosomatides grebnickii* can be distinguished from *L. arcticus* (= *Leptosomatum arcticum*) by the bigger amphids. However in the description of *L. steineri* and its variety *filiformis* by Filipjev (1946), 8 μ m is given for the diameter of the amphids (aperture?). From the text, it is impossible to conclude whether this diameter refers to the female, male, or amphids of the variety.

My measurements of the fovea of females of *L. steineri* sensu Filipjev, 1946 are 10 μ m; for the variety *filiformis* the measurement is 7 μ m; the diameter of the fovea in the male could not be stated as the anterior part of the male was twisted dorsoventrally.

Leptosomatides crassus and *Leptosomatum elongatum* sensu Platonova (det. Filipjev), both of which were described by Platonova in 1967, cannot be distinguished from *L. grebnickii*. In *Leptosomatum elongatum* sensu Platonova, the ovejector was not recorded in the more extensive description of 1976. *Leptosomatides crassus* was depicted with one short caudal gland. Both are provided with ovejector, granula, lateral vulvar glands, and long caudal glands. Slide 5761 of *L. elongatum*, collected from *Balanus porcatus* at the Murman Coast in 1923, is measured and data are presented in the Appendix.

Filipjev (1946) also described the male but as a separation is made between his *L. steineri* and its variety *filiformis*, this male might also belong to the sub-species. According to Filipjev the length of spiculum and gubernaculum are 210 and 90 μ m respectively, whereas Platonova (1976) gave 137 and 25 μ m. In both specimens, the gubernaculum and spiculum are of the *Pseudocella* type and 16–17 subventral precloacal papillae are present.

Leptosomatides grebnickii can be distinguished from *L. euxinus* by the papil-

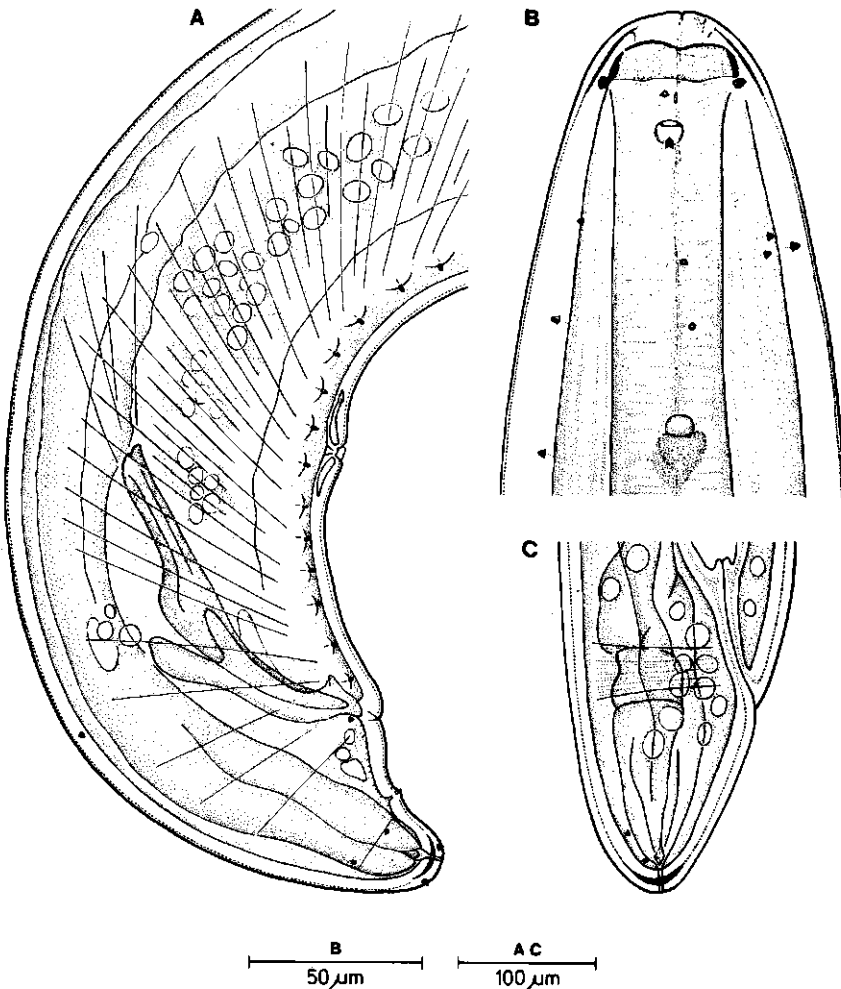


Fig. 3. *Leptosomatides marinae* Platonova, 1976. A and B, Posterior and anterior end; male paratype of *L. brevisetosus* Platonova, 1976; C, Posterior end paratype *L. marinae*.

lifiform cephalic sensilla; from *Leptosomatides arcticus*, *L. marinae* and *L. sp.* A by the size of the amphids and lens. The male is characterized by the uniformly curved spicula with paired apophyses directed posteriad at right angles to the spicula, as in *Pseudocella*, which is unique in the genus *Leptosomatides*.

Leptosomatides inocellatus Platonova, 1967

Leptosomatides inocellatus Platonova, 1967:829, figs. 3–4.

The material, on which this description was based, was collected in 1935; the nematodes were mounted in glycerin-gelatin and are rather flattened.

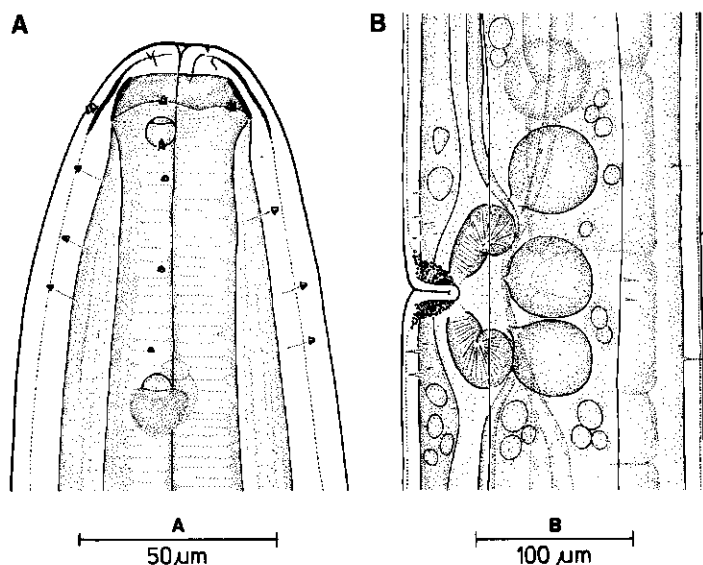


Fig. 4. *Leptosomatides marinae* Platonova, 1976. A, Anterior end, female; B, Vulvar region.

Diagnosis.—Diameter of amphidial aperture exceeds diameter of cup-shaped fovea. Vaginal musculature inconspicuous. Ocelli, intracuticular vulva granula, and lateral vulvar glands absent. Caudal glands short. Distinct glands in lateral hypodermal chord. Head structure complex; stoma probably wide.

Holotype.—Slide 7026; Zoological Institute, Leningrad.

The paratypes of *L. inoellatus* are rather variable; slide 7028 contains a nematode, provided with rather long setae compared with 7027. *Leptosomatides inoellatus*, which resembles *Leptosomatum groenlandicum* Allgén, 1954, might belong to the Platycominae. At present, however, I consider it a species *incertae sedis*.

Leptosomatides marinae Platonova, 1976

Figs. 3A–C, 4A–B

Leptosomatides marinae Platonova, 1976:70, 77–79, fig. 29.

Leptosomatides acutipapillosus Platonova, 1976:70, 75–76, fig. 27.

Leptosomatides brevisetosus Platonova, 1976:70, 76–77, fig. 28.

Diagnosis.—Cephalic papilliform sensilla 3 μ m long. Cephalic capsule 10–12 μ m in females, 7–9 μ m in males. Fovea 8–9 μ m in both sexes. Lens 8 μ m in diameter. Lateral vulvar glands 2–4. Intracuticular granula numerous. Spiculum robust, gubernaculum with crura. Ventromedian precloacal papilla provided with alae. Ventral postcloacal papilla present, vulva sensilla present.

Type.—Holotype 7880, by original designation. Zoological Institute, Leningrad, U.S.S.R.

Type-locality.—Iturup Island. Kasapka Bay, 4–5 m, in sponge.

Distribution.—Kuril Islands to East Kamchatka.

Discussion.—The holotypes of *L. acutipapillosus* and *L. brevisetosus* were provided by Platonova with an extra label with the name *L. marinae*. Therefore, in the (unpublished) opinion of Platonova, these three species are identical, with which I agree.

Following recommendation 24(A) of the Code, the name *L. marinae* is selected since it has line priority in the key on page 70.

It was impossible to decide on which specimens the description was based since the slides, labelled paratypes, contain more than 120 specimens, 40% of them provided with a question mark. These paratypes originate from 30 locations, and were collected between 1910 and 1975 from *Cystoseira*, *Laminaria*, *Balanus*, *Corallina*, *Alaria*, *Agrarum*, and sponges in the littoral zone. No slides were labelled as paratypes of *L. acutipapillosus*.

Dr. T. A. Platonova kindly gave permission to deposit one male and one female at each of the following nematode collections: Nematology Dept., Wageningen, The Netherlands; National Museum of Natural History Smithsonian Institution, Washington, D.C., U.S.A., and the South Australian Museum, Adelaide, Australia. The males, slide 6133, were labelled as paratypes of *L. brevisetosus*, collected at 9-VIII-1957, Chimushir Is. Kitabujnaja Bay from littoral rhizoids of *Laminaria*, mud, sand. The females, slide 7909, collected at Kunashir Is. 13-VII-1969 from sponges with shells, 9–10 m. The figures and dimensions given in this paper are based on these six specimens.

In 23 females of *L. marinae* the number of lateral vulvar glands was found to be 2–5 ($\bar{x} = 3.22$; $\sigma = 0.83$) in each body half.

The caudal part of the male is strongly curved; the length of the tail, the anal body width and ratio *c* are almost useless in this case. Of the subventral cloacal papillae, one or two are situated postcloacal, six to nine between cloaca and median precloacal papilla and 10–12 anterior to the ventral papilla; in general they were not conspicuous.

In one of the females, a cervical gland was present, but the pore could not be found.

Although *Leptosomatium gracile* sensu Allgén, 1954 is insufficiently described and figures of head and tail region are useless, the dimensions, placement of ocelli and number of lateral vulvar glands agree with *L. marinae*. The cephalic sensilla, capsule and amphids, however, are not described or illustrated.

The males of *L. marinae* can easily be distinguished by the precloacal papilla provided with alae. The females differ from *L. arcticus* in the number of lateral vulvar glands and the position of the ocelli; from *L. grebnickii* by the diameter of the lens and fovea, from *L. sp. A* by the diameter of the lens and tail length.

Leptosomatides microlaimus (Allgén, 1957)

Leptosomatium microlaimum Allgén, 1957:7, fig. 1a–b.

Discussion.—This species was collected at a depth of 1750 m near Spitzbergen; the type-material could not be located. It appears in the key of *Leptosomatides*, given by Platonova (1976) where it is designated *L. microlaimum* Allgén, 1957.

The absence of justification, the inappropriate gender ending, and the fact that the author's name is not enclosed in parentheses may lead to confusion. Judging from the figure, I agree with this transfer. The discrepancy in Allgén's calculations of ratio "C" and the description, which cannot be taken seriously, are reason to consider it a *species inquirenda*.

Leptosomatides reductus Timm, 1959

Leptosomatides reductus Timm, 1959:207-209, fig. 2d-e.

Diagnosis.—Cephalic setiform sensilla 6.5 μ m long. Ocelli twice corresponding body diameter from anterior end. Fovea in male 9-10.5 μ m; in female 7-7.5 μ m. Gubernaculum without crura.

Type.—Syntypes: 10 ♀, 10 ♂.

Type-locality.—Manora Island, Karachi, Arabian Sea.

Type-habitat.—Algae growing on rocks.

Discussion.—I was not able to study this material, which is deposited at the slide collection of the Pakistan Zoological Survey, Karachi. According to the description, this species resembles *L. euxinus*, but differs by the greater amphidial diameter in the male, the greater length of the cephalic setae and the absence of crura on the gubernaculum. In my opinion this is a good species.

Leptosomatides species A

Material.—Three females from the Atlantic Ocean SW of Nova Scotia. Two of them (76074 and 76075) collected at 43°40'N, 66°07'W on 10 Aug 1963 in 60 m, one female (76076), collected at 40°21'N, 67°48'W on 8 Aug 1963. These specimens are deposited in the collection of the USNM, Smithsonian Institution, Washington, D.C., U.S.A.

Description.—For general body proportions refer to the Appendix. Cephalic sensilla papilliform; 3-4 μ m. Cephalic capsule 11-13 μ m. Diameter fovea 7 μ m, lens 10 μ m. Lateral vulvar glands 3-4. Intracuticular granula numerous. Male unknown. No figures are given since the only features in which it was found to differ from *L. arcticus* are the lens diameter and the number of vulvar glands. These specimens are not named specifically as no males are present.

Key to the Species of *Leptosomatides*

1. Length of cephalic sensilla twice their basal width (setiform) 2
- Length of cephalic sensilla less than twice basal width (papilliform) ... 4
2. Ocelli 1.5 corresponding body diameters; setae 4 μ m *L. antarcticus*
- Ocelli 2 corresponding body diameters 3
3. Setae 6 μ m. Fovea in male 10 μ m *L. reductus*
- Setae 4-5 μ m. Fovea in male 6 μ m *L. euxinus*
4. Intracuticular vulva granula present 5
- Intracuticular vulva granula absent *L. filiformis*
5. Lateral vulvar glands 5-7 on each side *L. arcticus*
- Lateral vulvar glands 2-4 on each side 6
6. Lens diameter 10 μ m *L. sp. A*
- Lens diameter 8 μ m or less 7

7. Lens diameter 6 μm , crura absent, precloacal papilla without alae *L. grebnickii*
 - Lens 8 μm , crura present, precloacal papilla with alae *L. marinae*

Status of Nominal Species of *Leptosomatides*

| Species | Present status ¹ |
|--|--|
| <i>Leptosomatides acutipapillosus</i> Platonova, 1976 | Synonym of <i>L. marinae</i> |
| <i>L. antarcticus</i> Mawson, 1956 | Good species |
| <i>L. brevisetosus</i> Platonova, 1976 | Synonym of <i>L. marinae</i> |
| <i>L. caucasiensis</i> Sergeeva, 1973 | Synonym of <i>L. euxinus</i> |
| <i>L. conisetosus</i> Sch. Stekh. & Mawson, 1955 | To <i>Deontostoma</i> |
| <i>L. crassus</i> Platonova, 1967 | Synonym of <i>L. grebnickii</i> |
| <i>L. euxinus</i> Filipjev, 1918 | Good species |
| <i>L. inocellatus</i> Platonova, 1967 | Species <i>incertae sedis</i> |
| <i>L. marinae</i> Platonova, 1976 | Good species |
| <i>L. microlaimus</i> (Allg n, 1957) Platonova, 1976 | Species <i>inquirenda</i> |
| <i>L. reductus</i> Timm, 1959 | Good species |
| <i>L. steineri</i> Filipjev, 1922 | Synonym of <i>L. arcticus</i> |
| <i>L. steineri</i> sensu Filipjev, 1946 | Synonym of <i>L. grebnickii</i> |
| <i>L. steineri</i> Subsp. <i>filiformis</i> Filipjev, 1946 | <i>L. filiformis</i> , species <i>inquirenda</i> |
| <i>Leptosomatium arcticum</i> Filipjev, 1916 | <i>Leptosomatides arcticus</i> |
| <i>L. elongatum</i> sensu Platonova, 1967 | Synonym of <i>L. grebnickii</i> |
| <i>L. grebnickii</i> Filipjev, 1916 | <i>Leptosomatides grebnickii</i> |
| <i>L. tetraphthalmum</i> sensu Platonova, 1967 | Synonym of <i>L. arcticus</i> |

¹ The indication "good species" does not mean that these species are sufficiently described; more information, regarding all species is desired.

General Discussion

As far as can be determined, the genus *Leptosomatides* forms a group that includes all species with the combination of characters given in the generic diagnosis. This genus is regarded as related to *Deontostoma*. The only distinguishing characters are the reduction of the cephalic capsule and absence of onchia and/or odontia in *Leptosomatides*. More information regarding all species is needed; especially males of some species are not known. Special attention should be given to the structure of the spiculum, gubernaculum, and cloacal papillae in the male, and the intracuticular vulvar granula, lateral glands, ovejector, and sensilla in the vulvar area of the female.

Until now, the genus *Leptosomatides* has been placed in the Leptosomatinae Filipjev, 1916. In fact the only argument for this placement is the presence of a reduced cephalic capsule. *Leptosomatides* differs from the Leptosomatinae sensu stricto (*Leptosomatium* and *Syringonomus typicus* Hope and Murphy, 1969) by

the structure of the cephalic capsule, amphids, spiculum, gubernaculum, metanemes, and the presence of vulva granula, ovejector, lateral vulvar glands, median precloacal papilla, and subventral cloacal papillae. The typical sexual dimorphism in the amphids of the Leptosomatinae is absent in *Leptosomatides*. Therefore, *Leptosomatides* must be removed to the Thoracostomatinae and the diagnosis of the latter emended. The genus *Paraleptosomatides* probably also belongs to the Thoracostomatinae. In a separate paper attention will be paid to this rearrangement.

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Appendix; Measurements of Species of *Leptosomatides*

Abbreviations: S—Sex, SN—slide number, L—body length, DF—distance to fovea, DRL—distance to right lens, DLL—to left lens, DNR—distance to nerve ring, PL—pharyngeal length, CL—caudal length, CW—cephalic width, OW—body width at level of lens, NW—width at level of nerve ring, PW—width at base of pharynx, MW—maximum width, AW—anal body width and the ratio's of de Man are expressed in a, b, c and V. Dimensions are given in μm .

| S | SN | L | DF | DRL | DLL | DNR | PL | CL | CW | OW | NW | PW | MW | AW | a | b | c | V |
|--|--------|--------|----|-----|-----|-----|------|-----|----|-----|-----|-----|-----|-----|----|------|-----|----|
| <i>Leptosomatides areticus</i> (<i>Leptosomatum tetrophthalmum</i> sensu Platonova, 1967) | | | | | | | | | | | | | | | | | | |
| F | 5070-2 | 14,860 | 25 | 112 | 114 | 485 | 2531 | 179 | 54 | 114 | 168 | 216 | 279 | 187 | 53 | 5, 9 | 83 | 67 |
| F | 5070-1 | 15,110 | 23 | 116 | 119 | 493 | 2554 | 181 | 57 | 104 | — | 239 | 277 | 185 | 55 | 5, 9 | 83 | 65 |
| <i>Leptosomatides euxinus</i> (<i>L. caucasiensis</i> Sergeeva, 1973) | | | | | | | | | | | | | | | | | | |
| M | 8097-1 | 9190 | 15 | 110 | 102 | 477 | 1878 | 73 | 38 | 67 | 107 | 127 | 148 | 92 | 62 | 4, 9 | 126 | |
| F | 8097-3 | 9430 | 17 | 121 | 131 | 469 | 1944 | 77 | 40 | 68 | 103 | 129 | 156 | 81 | 91 | 6, 3 | 186 | 53 |
| F | 8097-2 | 12,450 | 16 | 125 | 114 | 481 | 1989 | 67 | 38 | 65 | 107 | 121 | 137 | 87 | 60 | 4, 9 | 122 | 60 |
| <i>Leptosomatides filiformis</i> (<i>L. steineri</i> subsp. <i>filiformis</i> Filipjev, 1946) | | | | | | | | | | | | | | | | | | |
| F | 7010 | 13,930 | 21 | 112 | 121 | 526 | 2305 | — | 57 | 108 | 135 | 137 | 160 | — | 87 | 6, 0 | — | 62 |
| <i>Leptosomatides grebnickii</i> (<i>Leptosomatum elongatum</i> sensu Platonova, 1967) | | | | | | | | | | | | | | | | | | |
| F | 5761 | 13,370 | 28 | 110 | 112 | 575 | 2734 | 178 | 52 | 95 | 132 | 170 | 204 | 152 | 66 | 4, 9 | 75 | 65 |
| <i>Leptosomatides marinae</i> (males as <i>L. brevisetosus</i> Platonova, 1976) | | | | | | | | | | | | | | | | | | |
| F | 7909-2 | 13,790 | 16 | 85 | 89 | 409 | 2350 | 144 | 41 | 77 | 111 | 141 | 177 | 121 | 78 | 5, 9 | 96 | 67 |
| F | 7909-3 | 13,860 | 22 | 89 | 92 | 409 | 2305 | 131 | 47 | 76 | 116 | 146 | 202 | 119 | 69 | 6, 0 | 106 | 66 |
| F | 7909-1 | 14,280 | 17 | 83 | 81 | 411 | 2509 | 139 | 49 | 80 | 112 | 143 | 185 | 133 | 77 | 5, 7 | 103 | 65 |
| M | 6133-3 | 17,950 | 32 | 121 | 116 | 617 | 3661 | 112 | 37 | 91 | 154 | 218 | 281 | 150 | 64 | 4, 9 | 160 | |
| M | 6133-1 | 18,810 | 27 | 135 | 139 | 658 | 3277 | 121 | 52 | 98 | 160 | 196 | 260 | 152 | 72 | 5, 7 | 155 | |
| M | 6133-2 | 19,740 | 29 | 123 | 125 | 682 | 3864 | 112 | 49 | 93 | 162 | 227 | 270 | 187 | 73 | 5, 1 | 176 | |
| <i>Leptosomatides</i> sp. A. | | | | | | | | | | | | | | | | | | |
| F | 76074 | 10,650 | 33 | 96 | 100 | 460 | 2441 | 135 | 45 | 64 | 106 | 114 | 135 | 100 | 79 | 4, 4 | 79 | 69 |
| F | 76075 | 11,290 | 29 | 96 | 108 | 485 | 2554 | 139 | 47 | 67 | 102 | 139 | 177 | 106 | 64 | 4, 4 | 81 | 68 |
| F | 76076 | 11,410 | 32 | 98 | 112 | 486 | 2418 | 129 | 52 | 77 | 116 | 125 | 185 | 123 | 62 | 4, 7 | 88 | 65 |

Chapter 4 Bionomics and reproductive cycle of the nematode *Leptosomatum bacillatum* living in the sponge *Halichondria panicea*

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by

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1. INTRODUCTION

For a taxonomic study high numbers of the nematode *Leptosomatum bacillatum* were collected from the sponge *Halichondria panicea*. Fluctuations in the composition of the population suggested an annual reproductive cycle.

The genus *Leptosomatum*, composed of large-sized marine nematodes, was revised (BONGERS, 1983) whereby *L. bacillatum* (EBERTH, 1863) and *L. elongatum* BASTIAN, 1865 were synonymized, partly because the data presented in this paper are in conflict with the main distinguishing character between *L. bacillatum* and *L. elongatum*, viz. a different length (8 to 9 and 10 to 13 mm respectively). This paper is a contribution to the knowledge of the reproductive cycle of *L. bacillatum*. The study of living specimens yielded additional biological data.

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2. MATERIAL AND METHODS

Enumeration and determination of the composition of the population was obtained from monthly samples of *Halichondria panicea*. This encrusting, cushion-shaped sponge grows on and between basalt stones of the sea dike 100 metres east of the sea water inlet of the Netherlands Institute for Sea Research (NIOZ) on the island of Texel. Sponges were hand-collected from the lower littoral by daylight during spring tide. Sampling was impossible in December 1982 due to climatic circumstances. In January the stones were covered with 2 metres of ice-floes which is quite exceptional.

After collecting, sponges were kept in sea water for 3 hours at room temperature to induce the nematodes to leave the sponge; less than 1% of the nematodes remained in the sponge, pinned by the spicules

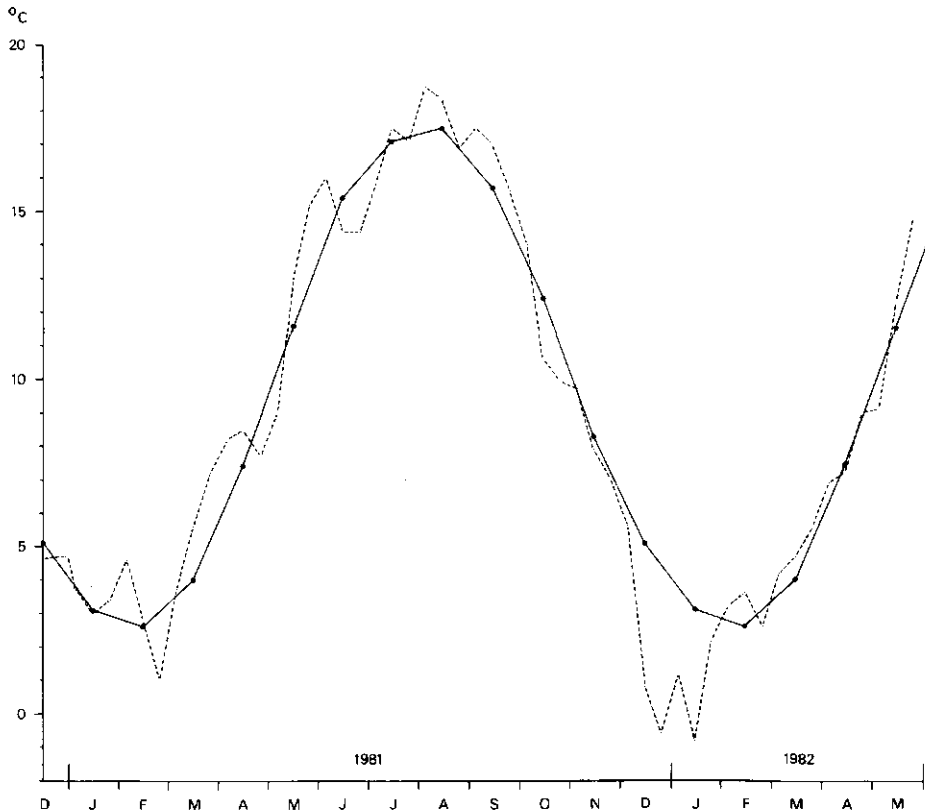


Fig. 1. Sea water temperature in period considered (dashed line) and average for the period 1951 to 1980 (solid line) at sampling locality.

of the sponges during collecting. Nematodes and sponge were subsequently fixed by adding formalin resulting in a 4% solution in sea water. After one day this solution was replaced by a glycerin-ethanol-water mixture (s_1 of SEINHURST, 1959) in which length measurements were taken. A part of each sample was transferred to glycerin. Each adult and preadult was examined at high magnification to establish whether they had already moulted and the presence of recognizable food particles in the intestine and sperm in the female reproductive system.

No quantitative samples were taken for nematodes present, with the exception of the sample of September 15, 1981, when 100 ml of sponge was collected and analyzed.

Data of temperature (Fig. 1) and salinity of the sea water were made available by RIVO, IJmuiden. The salinity at the collecting site varied between 23 and 30, reaching its maximum in summer.

3. RESULTS AND OBSERVATIONS

Six species of which more than 10 specimens were present, were found in 100 ml of sponge, collected September 15, 1981 (Table 1). Other substrata in the vicinity (mud between stones, mussels and algae) were sampled, but only yielded incidentally *Leptosomatum bacillatum* specimens.

TABLE 1

Juveniles, males and females of nematode species present in 100 ml of *Halichondria panicea*, collected September 15, 1981.

| Species | Numbers | | |
|---|---------|----|----|
| | J | M | F |
| <i>Leptosomatum bacillatum</i> (Eberth, 1863) | 877 | 16 | 43 |
| <i>Enoplus commun</i> Bastian, 1865 | 157 | 0 | 16 |
| <i>Thoracostoma coronatum</i> (Eberth, 1863) | 17 | 2 | 4 |
| <i>Pseudocella trichodes sensu auctorum, nec</i> Leuckart, 1849 | 13 | 2 | 1 |
| <i>Anticoma acuminata</i> (Eberth, 1863) | 2 | 9 | 3 |
| <i>Desmodora communis</i> (Bütschli, 1874) | 2 | 7 | 3 |

In the population studied (Table 2), juveniles hatched from July till September, the period in which the sea water temperature reaches its maximum. Females probably die after the spawning period as evidenced by the fact that females exceeding 10 mm in length become scarce, and small females are present in the colder season. Ex-

trapolating from the observed fluctuation in the population, it is concluded that juveniles reach maturity in June.

Based on Table 2 and assuming the fluctuation to be representative for a longer period, it is concluded that *L. bacillatum* has an annual reproductive cycle in which spawning takes place in late summer.

An aspect worth mentioning is the fact that juveniles exceeding 10 mm in length are rare, whereas females reach a length of 14 mm. This leads to the conclusion that females continue growing after having reached the adult stage. For males this is not the case; they do not feed as pharynx and intestine atrophy.

Leptosomatum bacillatum shows a remarkable behaviour when placed in a petri-dish with sea water immediately after collecting. The first minutes it swims upward in a rapid, undulating movement. As soon as the movements become slower, it sinks and immediately fixes itself with the caudal glands to the bottom of the dish. The nematode moves its head to the attachment point and stretches again. In doing so, a sticky thread is pulled out between the two body extremities. By circular movements of the anterior end of the body, the nematode wound thread, which became clearly visible by adhering particles, around its body. Subsequently it twisted its body so that convolutions of the thread adhered to each other, and after some minutes the nematode became invisible due to the adhering particles. I presume that this thread was formed by the excretory product of the ventrosublateral pharyngeal glands.

Due to this behaviour collecting living nematodes in the same dish appeared to be waste of time as they become entangled. After 3 hours of transport, this behaviour disappeared, however; the animals neither swam, nor secreted pharyngeal or caudal threads, perhaps because of stress.

In one case I was able to study living *L. bacillatum* specimens from a sponge (*H. panicea*) that was coloured green by the presence of symbiotic algae. In the gut of these nematodes, green algae with a diameter of 10 μm were observed. Although I studied hundreds of specimens at high magnification, mindful of identifiable food in the intestine, I have observed only an amorphous substance, probably detritus and bacteria.

Closer study also showed that sperm is incidentally present in the females observed. Two females were observed as having a second vulva. An extreme case of wound healing (genetic anomaly?) was observed in a newly hatched juvenile in which the posterior 60% of the body was lost and the wounds of both intestine and cuticle were closed. Often specimens were observed in which the posterior part was in an extreme state of decay whereas the anterior part still moved.

BIONOMICS OF LEPTOSOMATUM

TABLE 2

Numbers of *Leptosomatum bacillatum* juveniles (J), males (M), non-gravid females (F) and gravid females (F') counted monthly within millimetre length classes in samples of *Halichondria panicea* from Texel, June 1981 till May 1982.

| Date | Cat. | Length (mm) | | | | | | | | | | | | | |
|----------|------|-------------|-----|-----|-----|----|----|----|----|----|----|----|----|----|----|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| 21.06.81 | J | 0 | 0 | 6 | 10 | 19 | 10 | 10 | 5 | 1 | 0 | 0 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 4 | 3 | 1 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 12 | 16 | 14 | 7 | 4 | 3 | 1 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 0 |
| 21.07.81 | J | 20 | 6 | 4 | 4 | 4 | 7 | 9 | 8 | 0 | 0 | 0 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 2 | 5 | 7 | 8 | 7 | 3 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 1 | 11 | 5 | 7 | 9 | 4 | 2 | 0 | 0 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 17.08.81 | J | 51 | 111 | 34 | 12 | 2 | 1 | 3 | 1 | 3 | 0 | 0 | 1 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 9 | 10 | 3 | 1 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 7 | 12 | 11 | 4 | 2 | 2 | 0 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 2 | 0 | 1 | 0 | 0 | 0 |
| 15.09.81 | J | 163 | 284 | 184 | 116 | 80 | 16 | 20 | 11 | 2 | 0 | 0 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 5 | 5 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 5 | 14 | 12 | 3 | 1 | 0 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 27.10.81 | J | 10 | 70 | 79 | 48 | 43 | 18 | 14 | 5 | 0 | 1 | 1 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 7 | 2 | 0 | 0 | 1 | 1 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 03.02.82 | J | 0 | 21 | 32 | 39 | 31 | 11 | 7 | 3 | 0 | 1 | 0 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 2 | 0 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 6 | 3 | 1 | 1 | 0 | 0 | 0 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 09.03.82 | J | 0 | 16 | 32 | 21 | 16 | 17 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 3 | 5 | 4 | 1 | 0 | 0 | 0 | 0 | 0 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 23.03.82 | J | 0 | 14 | 34 | 35 | 21 | 9 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 6 | 2 | 0 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 4 | 1 | 0 | 0 | 0 | 0 | 0 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19.04.82 | J | 1 | 16 | 36 | 47 | 31 | 10 | 7 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 1 | 1 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 5 | 0 | 0 | 1 | 0 | 0 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19.05.82 | J | 0 | 7 | 32 | 35 | 49 | 29 | 22 | 12 | 1 | 0 | 0 | 0 | 0 | 0 |
| | M | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 3 | 3 | 0 | 0 | 0 | 0 | 0 |
| | F | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 7 | 2 | 0 | 0 | 1 | 1 |
| | F' | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

4. DISCUSSION

Leptosomatum elongatum BASTIAN, 1865, was originally described from an unknown sponge in crevices between stones near Falmouth. TIMM (1953) described *L. acephalatum* CHITWOOD, 1936 from *Hymeniacion heliophila* at Beaufort, N.C. *L. bacillatum* was originally described by EBERTH (1863) from "Corallen" (*Corallina*?) in the harbour of Nice. BONGERS (1983) describes populations from *Halichondria panicea* collected near Ambleteuse, France and several localities in The Netherlands, and from unknown sponges from Banyuls, France. In the collection of the Nematology Department at Wageningen specimens of *L. bacillatum* are present collected from *Codium* sp., *Polysiphonia* sp., *Cladophora* sp., *Chondrus crispus* and *Laminaria digitata*. FILIPJEV (1921) recorded numerous *Leptosomatum bacillatum* specimens (= *L. filipjevi* Schuurmans Stekhoven, 1950) from the biocoenosis of *Amphioxus* sand and of the shell bottom with *Phyllophora* in the Black Sea. These data suggest a facultative association between *Halichondria panicea* and *Leptosomatum bacillatum*. It is plausible that the sponge offers a preferred substratum to *L. bacillatum*.

The reproductive cycle of free-living nematodes reported in literature are either from field data, which are less appropriate for nematodes with asynchronous spawning periods, or from laboratory cultures in which environmental factors, such as food and light regime, are difficult to simulate. For the temperate zone with obvious seasonal temperature changes, it is usually easy to demonstrate whether an annual cycle is present or not. Relatively little is known about reproductive cycles of free-living marine nematodes. FILIPJEV (1921) recorded gravid females of *Leptosomatum bacillatum* in June-August in the Black Sea which agrees with the annual cycle reported in this paper.

According to WARWICK & BUCHANAN (1971), egg deposition in marine nematodes may be of two types. The female may store a large number of eggs in her uteri, release them in a mass and subsequently die, or lay eggs in a continuous process by which only 1 or 2 eggs per uterus mature at a time. *Leptosomatum bacillatum* belongs to the first group. In some cases one egg remains in the uterus so that even in winter gravid females are found.

Females of *L. bacillatum* continue growing after having reached the adult stage which means that length is a doubtful character in this genus, and age-dependent length is the main argument in favour of the synonymisation of *L. bacillatum* and *L. elongatum* by BONGERS (1983). FILIPJEV & MICHAJLOVA (1924) reported post-adult growth in *Enoplus communis*, and the figures of SKOOLMUN & GERLACH (1971: figs

5, 6 and 7) indicate that the phenomenon is quite common in large marine nematodes.

The observation regarding the production of sticky threads by the pharyngeal glands agrees with the mucus-trap hypothesis postulated by RIEMANN & SCHRAGE (1978). This way of feeding is most appropriate for the family Leptosomatidae as this taxon is characterized by ventrosublateral pharyngeal glands opening onto the labia (HOPE, 1982). This family comprises a.o. *Leptosomatum bacillatum*, *Thoracostoma coronatum* and *Pseudocella trichodes* which live (facultatively) in *Halichondria panicea* (Table 1). Although direct evidence is lacking, it is plausible that *Leptosomatum bacillatum* captures food in the web spun in the constant water stream generated by the sponge. It is not known whether these nematodes produce holes in the sponge by extra-corporeal digestion.

In contrast to closely related species where 90% of the females show sperm, in females of *Leptosomatum bacillatum* sperm was seldom present. In June 1977 sperm was found in 10% of the females whereas the number of fertilized females in the period June 1981 to May 1982 was almost nil. According to HOPPER & MEYERS (1966) males are quite common in natural populations of *Monhystera parelegantula*, *Chromadorina epidemos* and *Viscosia macramphida*, but under laboratory conditions males disappear and the reproductive cycle changes from amphimixis to parthenogenesis. TIETJEN (1967) reported the same for *Monhystera filicaudata*. Parthenogenesis may be more common in marine nematodes than generally accepted, even when males occur.

5. SUMMARY

Leptosomatum bacillatum (Enoplida: Leptosomatidae) occurs in high densities in the sponge *Halichondria panicea*. Previously observed fluctuations in modal length suggested an annual reproductive cycle which in this study is confirmed by monthly samplings.

Eggs are deposited in July and August and *L. bacillatum* reaches maturity after one year. Mature females continue growing, their length being season dependent. The bionomics, mucus trap hypothesis and nematode-sponge relationship are discussed.

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Abstract

Leptosomatum ranjhai Timm, 1960 can no longer be assigned to *Leptosomatum* sensu Bongers, 1983 because the sexual dimorphism in the amphids of *Leptosomatum* is absent in *L. ranjhai*. The new genus proposed for this species, *Orthophallonema*, is characterized by the presence of serially oriented lateral epidermal glands, ortho- and loxometanemes (Lorenzen, 1978), and ventral and subventral pre-cloacal sensilla in the male.

New material of *O. ranjhai* (Timm, 1960) comb. nov. is recorded from the Caribbean and a related species from Fiji is described but not named.

Introduction

In 1960 Timm described from the Arabian Sea a *Leptosomatum* species characterized by the presence of a ventral pre-cloacal supplement and subventral pre-cloacal sensilla in the male. This characteristic, according to Timm, does not seem to have been described for any other species of the genus *Leptosomatum*. Moreover, Timm described a slight blunt dorsal tooth in the stoma. This species has not been found again.

Bongers (1983) revised the genus *Leptosomatum* and emended the diagnosis. As a result, *L. ranjhai* Timm, 1960 can no longer be assigned to that genus. The sexual dimorphism, present in the amphid structure of *Leptosomatum*, is absent in *L. ranjhai*. Re-study of type-material revealed that *L. ranjhai*, moreover, is provided with short caudal glands, gland cells in the lateral chord, an ortho- and loxometanemes. These characters prevent placement of this species in the genus *Leptosomatum* and for it I propose the new genus *Orthophallonema* be erected (from orthos (= straight) and phallus (= male genital apparatus); gender: neuter).

According to Timm, the specimens, which had been cleared in lactophenol, were deposited in the slide collection of the Zoological Survey of Pakistan and in his personal collection. In 1970 the holo- and allotype were sent to Wageningen where they were remounted in glycerin. The type-specimens in Timm's personal collection have been lost (Timm, pers. comm.) and, through his kind efforts attempts have been made to locate the remaining type-specimens in the Zoological Survey. Thus far I have not succeeded in obtaining these slides and it is not known if they still exist. The generic diagnosis and additional observations presented in this paper are based on the holo- and allotype as well as on new material.

In the collection of the Smithsonian Institution, Washington, D.C., two female specimens are present that belong to this new genus and one is probably identical to Timm's species. In the Wagenaar Hummelinck collection, deposited at the Nematology Department in Wageningen, specimens are present which are considered conspecific with *Orthophallonema ranjhai* (Timm, 1960).

Orthophallonema, Genus Novum

Diagnosis: Leptosomatidae. Body long and slender. Cephalic capsule weakly developed, posterior suture only slightly visible. No sexual dimorphism in structure of cephalic capsule nor of amphids; amphids cyathiform. Internal circle (labial) of 6 sensilla intracuticular; external circle of 10 cephalic sensilla.

Dorsal pharyngeal gland opens into pharyngeal lumen; orifices of ventrosublateral pharyngeal glands on anterior end. Ondontia and onchium absent. Ocelli relatively far anterior; pigment granules diffuse, not forming a cup; lens-like body ill-defined. Excretory gland and excretory pore not observed.

Epidermal gland cells on ventral margin of lateral chord. Dorsal loxometanemes-1 present in both sexes; orthometanemes present only in males (?). Caudal glands short, convoluted and mainly restricted to caudal region. Lunula present. Gonads on left side of intestine. Female amphidelphic, gonads antidromic. Male diorchic, testes opposed and outstretched. Spermatzoa globular. Gubernaculum simply built; without appendices. Pre-cloacal ventromedian supplement and subventral pre-cloacal sensilla present. Spicula short and straight. Copulatory musculature prominent. Type-species: *Orthophallonema ranjhai* (Timm, 1960).

Re-examination of type material and discussion: Timm (1960) described a blunt dorsal tooth just behind the level of the cephalic papillae. I could not confirm the presence of a tooth in either the holotype, allotype, or the new material. It might be possible that Timm misinterpreted the pharyngeal sensory receptors, described by Hope (1982) in *Deontostoma californicum*, as the tooth in the pharyngeal lumen.

Although not described, the caudal glands in *O. ranjhai* have been depicted, more or less, as extending pre-anal. In the types, the position of these glands could not be noted, but in the new material the glands are short and comparable to those of *Pseudocella wieseri* as depicted by Hope (1967: 310).

The cephalic region resembles that in females of *Leptosomatium bacillatum*. For the interpretation of the cuticularized rods, and structure of cephalic capsule, see Bongers (1983).

The spindle-shaped swellings and cell bodies of

the proprioceptors interpreted as stretch receptor organs by Lorenzen (1978; see also Hope & Gardiner, 1982), are situated at the dorsal margin of the lateral chord, the anterior filament extends into the dorsal margin, whereas the posterior filament crosses the chord and is lost from sight above the glandular cells at the ventral margin (Fig. 1h). The posterior filaments in male 1666A-2 (see Table 1) are almost absent and these proprioceptors have to be considered dorsal orthometanemes; in male 1215-1 the proprioceptors resemble those in females.

The glandular cells on the ventral margin of the lateral chord were present in all specimens examined; 30-35 could be counted on each side of the body. In the posterior part of the males these cells are situated close together, also on the dorsal margin.

The holotype, a female, is rather flattened and in mediocre condition; the allotype is poor and broken into several parts. The position of the gonads in relation to the intestine is difficult to establish in the types. In the new material, presented in this paper, the gonads are situated to the left of the intestine in both sexes. The caudal end of the allotype is curved to the right whereas the posterior end of the male from Curaçao is curved to the left; Fig. 1g is in reverse. No addition can be given to Timm's description of the caudal end of the male; the original description is used in the diagnosis.

The number and size of eggs suggests a continuous spawning period, at least at those localities from which the present material originates. All females studied contain sperm.

The genus *Orthophallonema* resembles *Pseudocella* in the structure of vulvar region, lateral chord, diffuse ocellar pigment and caudal glands restricted to the tail. It differs from *Pseudocella* in the structure of the cephalic capsule and male genital system, and in the absence of a lens-like body in *Pseudocella*. The new genus is distinguished from *Syringonomus* and *Leptosomatium* by the absence of sexual dimorphism in the amphids, by the structure of the lateral chord, caudal glands, male genital system and ocellar pigment cup. *Orthophallonema* differs from *Leptosomatides* (see Bongers, 1983a) by the structure of the lateral chord, vulvar region and male genital system. I propose to place *Orthophallonema* in the Thoracostomatinae. The diagnosis of this subfamily has yet to be emended to

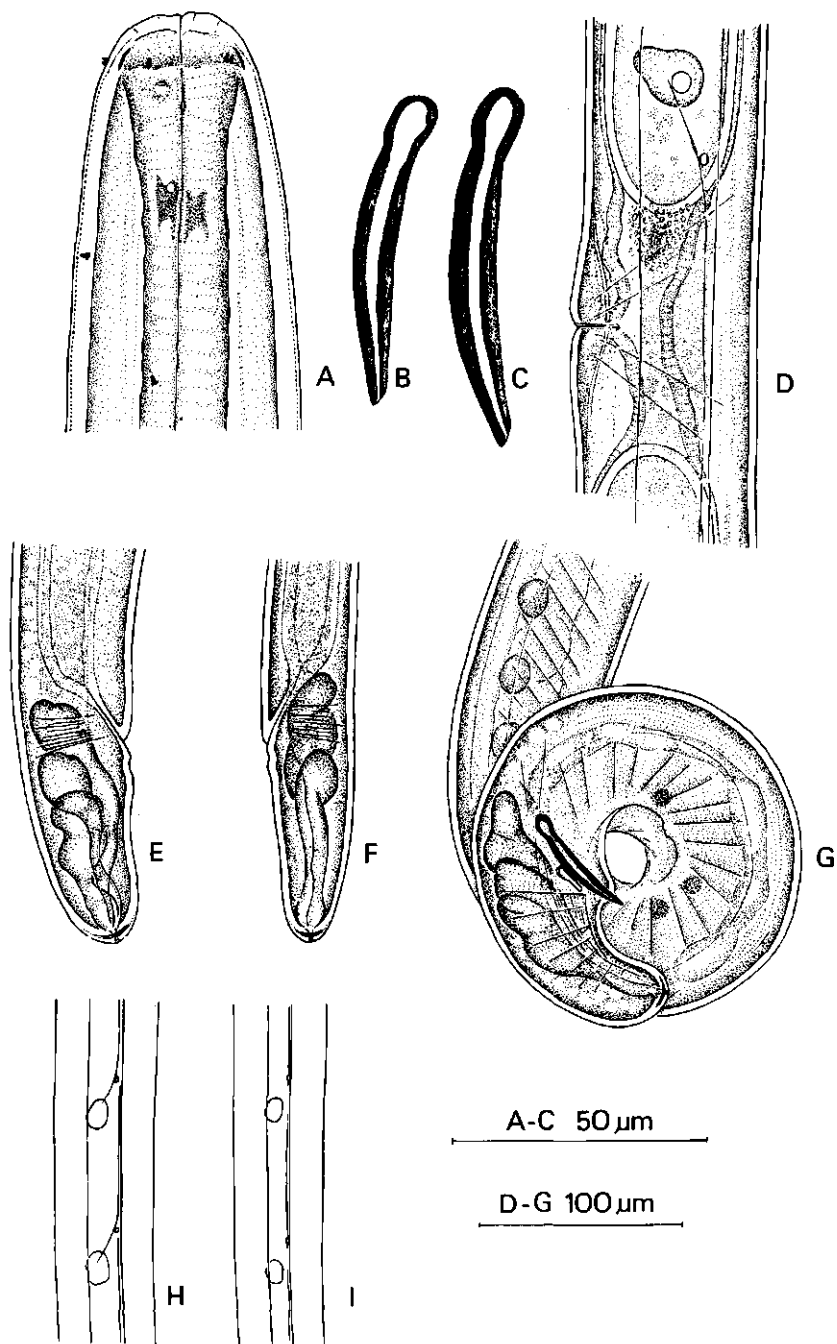


Fig. 1. A, *O. ranjhai*, anterior end female (1666A-2); B, Spiculum (1666A-1); C, Spiculum allotype; D, Vulvar region (1066A-2); E, Posterior end (1666A-2); F, *O. spec. A*, posterior end; G, *O. ranjhai*, posterior end, male (1666A-1); H, Lateral epidermal chord, female (1666A-2); I, Lateral chord, male (1666A-1) (H and I in outline).

Table 1. Numerical data new records

| S | SN | L | DNR | PL | CL | CW | NW | PW | MW | AW | a | b | c | V |
|--|------------|-------|-----|------|-----|----|----|----|-----|----|-----|------|-----|----|
| <i>Orthophallonema ranjhai</i> , pop. 1; Curaçao | | | | | | | | | | | | | | |
| ♂ | 1666A-1 | 6760 | 263 | 1031 | 68 | 27 | 57 | 66 | 62 | 48 | 102 | 6.0 | 99 | |
| ♀ | 1666A-2 | 7100 | 285 | 1183 | 92 | 31 | 63 | 77 | 86 | 54 | 82 | 6.6 | 77 | 67 |
| <i>O. ranjhai</i> , pop. 2; Aruba | | | | | | | | | | | | | | |
| ♂ | 1302-6 | 5610 | 291 | 1048 | | 26 | 51 | 77 | 55 | - | 102 | 5.4 | 43 | |
| ♀ | 1302-2 | 8350 | 277 | 1200 | 89 | 33 | 67 | 75 | 94 | 57 | 89 | 7.0 | 94 | 71 |
| ♀ | 1302-5 | 8860 | 302 | 1490 | 129 | 40 | 68 | 75 | 107 | 57 | 83 | 5.9 | 80 | 65 |
| ♀ | 1302-1 | 8920 | 354 | 1436 | 110 | 31 | 63 | 71 | 87 | 51 | 103 | 6.2 | 81 | 65 |
| ♀ | 1302-4 | 9130 | 322 | 1369 | 100 | 32 | 52 | 62 | 82 | 57 | 111 | 6.7 | 91 | 72 |
| ♀ | 1302-3 | 11090 | 333 | 1403 | 104 | 33 | 67 | 69 | 90 | 56 | 123 | 7.9 | 107 | 78 |
| <i>O. ranjhai</i> , pop. 3; Margarita | | | | | | | | | | | | | | |
| ♂ | 1216-1 | 4510 | 198 | 879 | 71 | 22 | 47 | 50 | 58 | 41 | 78 | 5.1 | 64 | |
| <i>O. ranjhai</i> , pop. 4; Los Frailes | | | | | | | | | | | | | | |
| ♀ | 1215-2 | 5980 | 218 | 1014 | 75 | 31 | 65 | 69 | 86 | 50 | 70 | 5.9 | 80 | 69 |
| ♂ | 1215-1 | 7860 | 214 | 1098 | 83 | 29 | 63 | 68 | 85 | 61 | 92 | 7.2 | 95 | |
| <i>O. ranjhai</i> , pop. 5; Mexico | | | | | | | | | | | | | | |
| ♀ | USNM 76146 | 7770 | 281 | 1132 | 98 | 28 | 64 | 72 | 87 | 79 | 89 | 6.9 | 79 | 73 |
| <i>O. spec. A</i> ; Fiji | | | | | | | | | | | | | | |
| ♀ | USNM 76145 | 8520 | 220 | 854 | 99 | 28 | 49 | 51 | 58 | 42 | 147 | 10.0 | 86 | 79 |

Abbreviations: Sex (S); specimen number (SN); length (L); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of nerve ring (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) anal body width (AW) and ratio's of de Man (a, b, c and V)

accommodate *Leptosomatides* and *Paraleptosomatides*.

Orthophallonema ranjhai (Timm, 1960), new combination

New material (Figs. 1a, b, d, e, g-i).

1. Curaçao, Awa di Oostpunt (12°08'N, 68°45'W), 30-50 m offshore; sand, *Thalassia* with *Porites*; 22 Feb. 1970. 1 ♂, 1 ♀; collected by Dr P. Wagenaar Hummelinck (for additional data see Wagenaar Hummelinck, 1977: sample 1666A). Coll. Nem. Dept., Wageningen.
2. Aruba, Druif (12°36'N, 70°05'W). Wharf of Arend Petroleum Co. 4 May 1955. 5 ♀, 1 ♂ in 15 m deep water; overgrown by *Tubastraea*, *Telastoa* and sponges; 0-2 m. Collected by Dr P. Wagenaar Hummelinck (W.H. 1302). Fixed in alcohol. Coll. Nem. Dept., Wageningen.
3. Margarita, Punta Mosquito, S of Porlamar (10°55'N, 63°55'W). 4 June 1936. 1 ♂. Sandstone and Shales; 0-1 m deep. Collected by Dr P. Wagenaar Hummelinck (W.H. 1216). Fixed in

alcohol. Coll. Nem. Dept., Wageningen.

4. Los Frailes, La Pecha, SW shore (11°13'N, 63°42'W). 19 June 1936. 1 ♂ 1 ♀. Sandy debris of igneous rock; 1-2 m. Collected by Dr P. Wagenaar Hummelinck (W.H. 1215). Coll. Nem. Dept., Wageningen.
5. Mexico, Quintana Roo; Allen Point, Ascension Bay (19°40'N, 87°30'W). 13 April 1960. 1 ♀. Collected by W. L. Schmitt. Coll. Smithsonian Inst., Wash., D.C.

These specimens, the general body measurements of which are given in Table 1, fully agree with the data as given by Timm (1960) and with my own observations on the holo- and allotype. The two specimens from Curaçao were collected in copula. The posterior part of the male fully encircled the female in the vulvar region. Numerous flattish, round sperms, with a diameter of 6 µm could be observed in both uteri.

Samples 2 and 3 have been fixed in alcohol and, therefore, hardly increase morphological knowledge. Specimens of these samples have lost their ocellar-pigment and the lens-like body can hardly be distinguished.

Description. For general body measurements see Table 1. Length cephalic capsule in optical section 5–7 μm . Length of papilliform cephalic sensilla 2–3 μm . Amphids round, cyathiform, fovea 4–5 μm , apertura 1.5 μm . Pharyngeal sensory receptors at level of amphids or slightly posterior. Tail conical with bluntly rounded terminus. Caudal glands short; in one case only one caudal gland developed. Spicula straight, 62–67 μm ; gubernaculum 13 μm . Anterior testis 4.6 mm, posterior 1.6 mm (Curaçao). Gland cells opening on ventral margin of lateral chord, measuring 13×10 till $28 \times 20 \mu\text{m}$. Cuticle 4 μm .

Orthophallonema spec. A

Material (Fig. 1f)

1. Fiji, Ndravuni Isl. ($18^{\circ}46'40''\text{S}$, $178^{\circ}31'10''\text{E}$). Coral knoll of S.E. end of Astrolabe reef, 12 m (40 ft) depth. 1 ♀. Collected by C. A. Child. 25 June, 1960. Coll. Smithsonian Inst., Wash., D.C.

Description. For general body measurements see Table 1. Cephalic capsule 4 μm . Ocelli at 27 μm from anterior end, lens diameter 3 μm . Position and structure of amphids comparable to *O. ranjhai*. Cephalic sensilla 3 μm ; setiform. Cuticula thickness 4 μm . Caudal glands short. Glandular cells large, $36 \times 32 \mu\text{m}$. Sperm present.

Discussion. This slender female ($a = 147$) differs from *O. ranjhai* by the short pharynx ($b = 10$), the vulva position (79%), the short cephalic capsule and its relatively long tail ($T/ABW = 2.4$). The cephalic sensilla are as long as in *O. ranjhai* but more slender and, therefore, setiform. Although this specimen clearly represents a new species, it is not named as the male, which will better fit to serve as holotype, is unknown.

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Chapter 6 Systematics of the *Leptosomatum bacillatum*-complex (Nematoda: Leptosomatidae); a numerical approach

INTRODUCTION

Within the genus *Leptosomatum* Bastian, 1865, at least two polytypic complexes can be distinguished viz. the *L. punctatum*- and the *L. bacillatum*-complex (Bongers, 1983). The former is characterized by the absence of a cephalic capsule in adults and juveniles and the latter by the presence of a cephalic capsule in females and juveniles. In this paper attention will be focussed on the *L. bacillatum*-complex, which according to the literature, has a worldwide distribution.

Species of the *Leptosomatum bacillatum*-complex are characterized, moreover, by papilliform sensilla, absence of median precloacal sensillum in the male and by the atrophiation of tissues in adult males. This complex is composed of *L. bacillatum* (Eberth, 1863) (syn. *L. elongatum* Bastian, 1865; *L. gracile* Bastian, 1865; *L. filipjevi* Schuurmans Stekhoven, 1950; *L. tuapsense* Sergeeva, 1973); *L. acephalatum* Chitwood, 1936; *L. clavatum* Platonova, 1958; *L. sachalinense* Platonova, 1978 (syn. *L. diversum* Platonova, 1978) and probably *L. sundaense* Bongers, 1983 (= *L. sabangense* sensu Micoletzky, 1924).

The species of this complex have relatively few distinguishing characteristics. Males are often absent in samples and, moreover, when males are present they lack the cephalic capsule and genital sensilla with their useful diagnostic characters often associated with these structures in other taxa.

Type-material has not been preserved for many of the species of this complex, especially for those described in the previous century. With hardly any exception, species cannot be distinguished by characteristics on which attention was focussed in the original descriptions. Often included among diagnostic characters are artifacts and features also present in other described species, but not included in published descriptions. The original description of *L. bacillatum* hardly includes more information than length and locality and so often when it was recollected it was described as a new nominal species. Also, the ease of artifact formation, adult growth and the phenomenon of allometric growth contributed to the number of synonyms, as did the presence of sexual dimorphism in the genus *Leptosomatum* and especially in species of the *L. bacillatum*-complex. In the past, individuals were described instead of populations. So information concerning the variability of diagnostic characteristics for species of *Leptosomatum* is scanty.

Recently, Bongers (1983a) has documented that *L. bacillatum*, under the environmental circumstances of Dutch coastal zones, has an annual reproductive cycle and, moreover, that females continue growing after having reached the adult stage, which results in an age/length relationship.

Specimens of *Leptosomatum* have not as yet been kept alive for more than one month under artificial circumstances so breeding experiments are not

yet possible, even if the practical problems of collecting and transporting of live material could be solved. Therefore the influence of temperature and food supply on variability and growth pattern cannot yet be determined.

The juvenile stages of *Leptosomatum* could not be distinguished because moulting specimens have seldom been found. Because of the continuous growth of adult females without moulting, one might expect that post-embryonic development results in a more or less continuous length increase and, moreover, a continuous increase in the dimensions of structures not replaced at moults. The only prospective characteristic to distinguish juvenile stages might concern the cephalic capsule. But in the Dutch populations, large juveniles exceed small adults in length. Body dimensions of the adults agree with those of juveniles of comparable size. Continuous growth is also believed to be evidenced by the overlapping range of measurements of total length and length and width of the cephalic capsule.

Leptosomatum bacillatum has been described or recorded from the Mediterranean, Norway, Gulf of Panama, California, Australia, Vancouver Island, Canada, Hawaii, English Channel, Argentina, Fuegian Archipelago, Falkland Islands and South Georgia as *L. bacillatum*; from the Mediterranean, English Channel, Gulf of Panama, California, Australia, Vancouver Islands, Atlantic (deep sea), Falkland Island, South Georgia, Antarctica, Barents Sea and North Sea as *L. elongatum*; from the English Channel, Jan Mayen and South Georgia as *L. gracile* and from the Black Sea as *L. filipjevi* and *L. tuapsense*. By courtesy of Prof. De Coninck, who is presently studying Allgén's material from the Swedish Antarctic Expedition, I have been able to study material recorded by Allgén (1959) as *L. bacillatum*, *L. elongatum* and *L. sabangense* from Falkland Islands. Re-examination of this material, discussed elsewhere in this paper, confirms again the shallowness of Allgén's observations and necessitates a questioning of his *Leptosomatum* records.

With the exclusion of the perpetuated misidentification of *L. elongatum* sensu Filipjev, Micoletzky's record of *L. sabangense* from the Black Sea (for both see Bongers, 1983), Schulz' (1935) record of *L. elongatum* from the Mediterranean, and Allgén's records, specimens from the Black Sea and Mediterranean have been considered, in literature, to be *L. bacillatum* sensu Eberth (1863). Likewise specimens from the English Channel and North Sea were *L. elongatum* sensu Bastian (1865).

An essential prerequisite to determine the geographic distribution of a species is a sufficient number of records based on an accurate and complete description of that species, especially with regard to those characters by which it can be distinguished from related species. These prerequisites have not been fulfilled regarding the species of the *L. bacillatum*-complex.

It is a common practice in defining nematode species to give, in addition to meristic data and descriptions of structural characteristics, the ranges for demanian ratios i.e. the ratio of each the tail length, pharynx length and body diameter to body length. Customarily, morphometric data are taken in nematode systematics without regard for allometry. According to

Micoletzky's (1930: 276) description of *Leptosomatum sabangense* Steiner, 1915, the length of females varies from 7.25 to 11.0 mm, whereas the morphometric ratio 'b' (total body length/pharynx length) varies between 6.8 and 12.6. A female of 6.8 mm with a pharynx length of 0.575 mm falls within this b-range as does a specimen with a pharynx length of 1.066 mm. Much information is lost by giving only the maximum and minimum values for calculated data of this kind, which might have been essential to separate closely related species. Because the dimensions of various body parts increase with increasing body length, valid comparisons of *Leptosomatum* specimens must be restricted to specimens of equal length. For this study juveniles are available ranging from 2.0 to 9.6 mm and adults from 4.9 to 16.9 mm in length so a method has to be devised to compare specimens of different length showing allometric growth. In this paper I will try to unravel the above-mentioned complex based upon 70 samples representing populations of the *L. bacillatum*-complex which has an almost cosmopolitan distribution.

Material

For the purpose of this study specimens were made available by the Zoological Museum, Amsterdam (ZMA), Zoological Institute, Leningrad (ZIL), Smithsonian Institution, Washington D.C. (USNM) and by the Nematology Department, Wageningen (NDW). On request, sponge-samples have been collected by Drs. Guy Boucher, Roscoff, France; C. Cazeau, Arcachon, France; Brendan O'Connor, Galway, Ireland; P. Dabinett, St.-Johns, Canada; Rudolf Evers, Utrecht, The Netherlands; Carlo Heip, Ghent, Belgium; S.Y. Hong & Y.W. Jo, Busan, Korea; J.C. Romano, Alger, Algerie; Patrick J. Schembri, B'Kara, Malta; G. Uhlig, Helgoland, Germany and Richard M. Warwick, Plymouth, England. Sponges have been identified by Rob van Soest, Amsterdam, The Netherlands.

Nematodes have been fixed for this purpose by adding formaldehyde to the sponges in seawater resulting in a final concentration of 5%; subsequently nematodes have been transferred to glycerin (Seinhorst, 1959) and mounted on Cobb slides.

Methods

Essentially, species have an almost infinite number of features by which they might be distinguished from others. Mayr, Linsley and Usinger (1953: 106) consider the number of characters to be limited only by the patience of the investigator. These discriminators are to be discovered by trial and error; a starting-point may be offered by those characteristics used in related taxa.

The diagnostic value of morphometric data increases with a decreased intraspecific variability and interspecific overlap in measurements. Ques-

tionable as useful diagnostic characters in the *L. bacillatum*-complex are a.o. the vulva position and diameter of lens-like body. The first is constant ($v\% = 60.2 \pm 3.2$; $n = 167$), but not diagnostic, whereas the latter may be diagnostic but rather variable (see sample 25). I have rejected the vulva position but included the diameter of the lens-like body as a possible diagnostic character.

Characters to be rejected, in addition to those mentioned above, are the following: Cuticle thickness because of its sensitivity to artifacts; length and position of cephalic, cervical and caudal sensilla; diameter and structure of lateral epidermal chord; diameter of ocellar pigment cup; distance from anterior end to 1). pharyngeal receptor, 2). to opening of dorsal pharyngeal gland, 3). to ventral excretory pore and 4). distance to amphids; diameter of amphidial apertura and fovea; length of rectum; mid-body width; maximum body width; structure and number of coelomocytes and metanemes; dimension of gonads; size of eggs; and position of gonads in relation to intestine. The possibility is not excluded that one of these rejected characters might be valuable in the future for distinguishing related new species.

According to the general allometric trend (see also Geraert 1978a, 1978b and 1979) the length of the various body parts tends to increase with increases in the length of the body and, therefore, it is possible to predict the average lengths of body parts for an individual of a given body length. The relationship between these measurements can be derived by means of a regression analysis, which requires a model of what is believed to be the mathematical form of the relationship. It seems appropriate to assume that the relative rate of growth of the various body parts is proportional to the relative rate of growth in body length.

In terms of instantaneous rates the assumed model is: $Y = a L^b$ where Y is the measurement of a body part, L is the length and ' a ' (allometry coefficient) and ' b ' are unknown constants. Because the allometric coefficients are derived from a sample of individuals each, they do not strictly represent patterns of growth. However, these patterns of multivariate allometry among individuals seem to account for changes in form within samples and for differences in shape between taxa. The Dutch population, sampled in other seasons, confirms this assumption. Log transformation of the 'simple allometry formula' gives $\log Y = \log a + b \log L$. These regression lines have been computed for sample 1 (Bonaire) and 2 (Texel), both consisting of 50 specimens. Comparison of parameter ' b ' showed that the proportional growth of the body parts of nematodes from these samples is not significantly different with the exception of the pharynx length ($t = -2.3$); this difference however, does not interfere with the intended method.

Specimens from site 2 (Texel) had been measured previously; from these data pharynx length is plotted logarithmically (Fig. 1) against total body length to demonstrate that the model assumed approximates the field data. These data confirm the allometric model of Jolicoeur (1963) that diverse

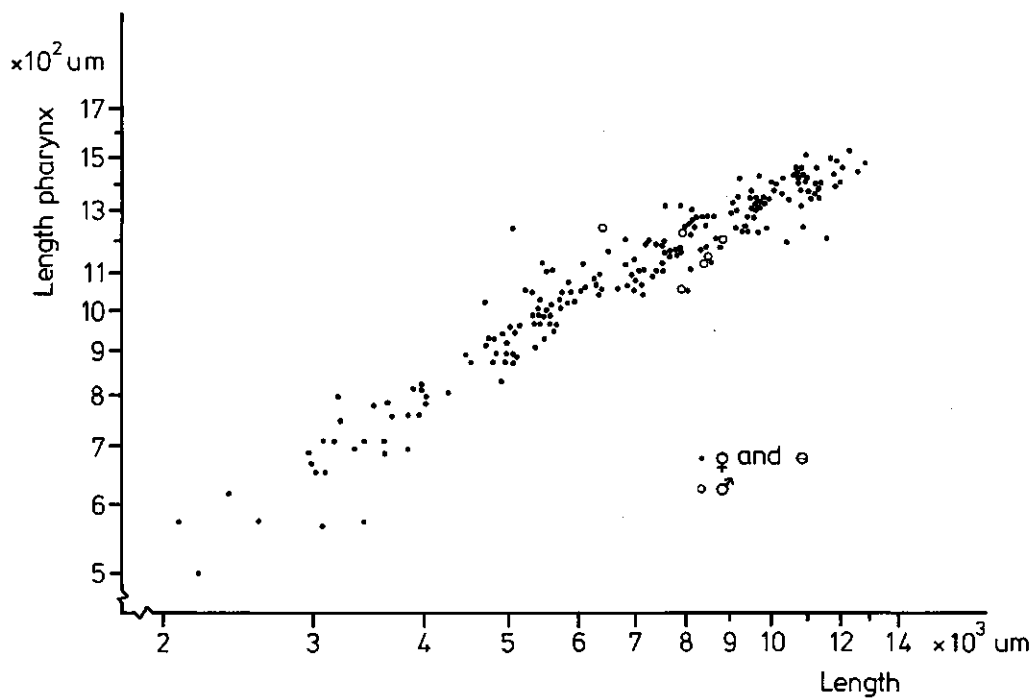


Fig. 1; Relation between log length and log pharynx length of *L. bacillatum* (S. 2; Texel).

length measurements relate loglinearly. An advantage of log transformation is, moreover, that the inhomogeneity of variance due to size variation is reduced.

A new parameter 'a' has been computed with fixed 'b' for the Dutch population (2) because this population, after having been studied previously (Bongers, 1983a), might be considered monospecific and, therefore, may serve as a reference. The dimensions of all specimens with a complete data set have been compared with the regression lines of sample 2 and log ratio's have been computed.

The log ratio (LR) of the caudal length (CL) of specimen x is defined as:

$$\begin{aligned} LR_{CL} &= \log CL_{(x)} - \log CL_{(ref.)} \\ &= \log \frac{CL_{(x)}}{CL_{(ref.)}} \end{aligned}$$

in which specimen x and the reference specimen are of equal length (Fig. 2). These log ratio's can easily be calculated for which the parameters of the reference sample (Table 1) are to be used in

$$LR_{CL} = \log \frac{CL_{(x)}}{1 \mu m} - \log a + b \log \frac{L_{(x)}}{1 \mu m}$$

Log ratio's of other characteristics (pharynx length, anal body width, length cephalic capsule etc.) can be calculated in the same way. Only natural logarithms have been used.

As a demonstration of the usefulness of the proposed method, an example will be given regarding the comparison of sample 12 (Margarita) and 2 (Texel). The length of specimens from sample 12 varies between 3,6 and 11,2 mm, the tail length from 81 - 146 μm . From sample 2 juveniles and females are available ranging from 2,2 - 13,6 mm in which the tail length varies between 52 and 101 μm . Although these tail lengths overlap, the log ratio's of sample 12 vary between 0.263 and 0.576; in sample 2 however, from -0.204 to 0.162. Perhaps it is not superfluous to state that allometric equations only apply to the range of data that they fit although written as if they applied to an infinite length range. For processing the log ratio's are assumed to show a normal distribution.

Log ratio's of 262 specimens with a complete data set, composed of 9 variables each, have been subjected to a cluster analysis to trace patterns of similarity between specimens and samples.

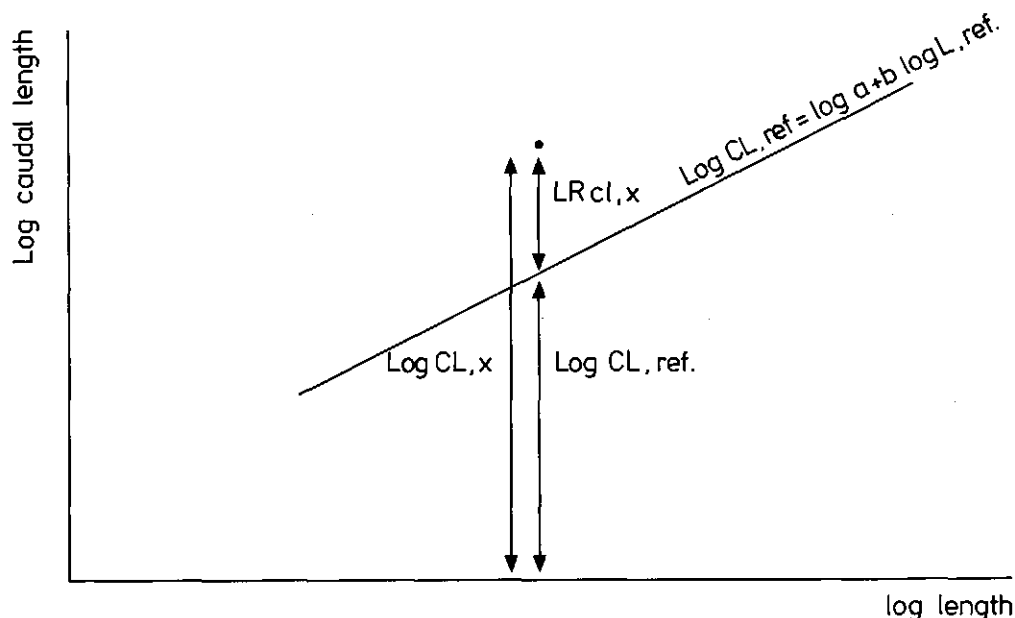


Fig. 2; Relation between caudal length of specimen x and reference sample.

The 'CLUSTAN, procedure RELOCATE' (Wishart, 1978) applied is a polythetic agglomerative technique that, by way of iterative relocations, fuses, in this case, 10 initial to 3 terminal clusters. Starting from a random/sequential allocation, initial clusters have been compared and specimens relocated depending on the square Euclidian distance to centroids of neighbouring clusters. The population is repeatedly scanned until no objects are relocated during one full scan. In the next steps, the number of clusters is reduced in every cycle by fusing the two clusters which are most similar, until 3 terminal clusters were obtained. The classification has been confirmed by an origin-determined allocation of specimens to the 10 initial clusters.

After interpretation of the classification, a discriminant analysis 'BMDP 7M' (Dixon et al., 1981) has been applied to the clusters; subsequent classification of the specimens by the functions obtained made some transfers desirable. The classification was cross validated by a randomly subdivide of the specimens with a probability 0.5. The classification functions computed for the subset were used to classify the specimens in the remaining group.

Discussing the males, an example is given of the use of classification functions for posterior probabilities.

Regarding the species and samples, full information is given of each specimen separately supported by Ferris (1983) conclusion that 'misguided efforts to reduce the length of taxonomic papers by omitting vital information about evolutionary units will forever obscure the evolutionary history and historical biogeography of nematodes.'

Of every specimen the stage or sex is given: (J)uveniles, (M)ales or (F)emales. The slide number (SN) is given for every specimen to allow restudy. The length (L) is given in microns as are the other data. The distance from anterior body end to lens-like body (DL) and nerve ring (DNR) is the distance to their anterior ends, to avoid estimations. The pharynx length (PL), caudal length (CL), body diameter at level of pharynx base (PW), anal or cloacal body width (AW) and diameter of the lens-like body are measured as usual. The length of the cephalic capsule (LCC) is difficult to determine due to its refractiveness; I have measured the refractive part, forming an angle with the longitudinal body axis. The width of the cephalic capsule (WCC) is the distance between the posterior ends of the, apparently two, refractive pieces. LD is the diameter of the lens-like body. The LD, LCC and WCC are rounded off on half microns; for computing these dimensions have been multiplied by ten. In the last column (remarks) I have indicated with a C if coelomocytes are present; with an S if sperm is present in females, G if females are gravid, P if pigment is present in the ocellar pigment cup and R stands for a developed renette. Some specimens or samples have been previously recorded (Bongers, 1983); in those cases the serial number of the sample is bracketed. Missing measurements are indicated with a point (.); in those cases that the character is absent, LCC and WCC in males, a dash (-) has been used.

Abbreviations in the sample description refer to the Institutes where the material is available for restudy (see Material). Cases that material has been fixed in alcohol, instead of formalin, are indicated. Additional information regarding samples collected by Dr. P. Wagenaar Hummelinck is given in his 1977 paper.

Results

The regression lines $Y = a + bX$ for reference sample 2, adjusted to sample 1 are given in Table 1. Standard error of estimate (S.E) of 'b' is bracketed.

Table 1. Regression lines reference sample (2).

| | a | | b | S.E. | |
|-----------|--------|---|--------|----------|-------|
| Log DL = | 1.264 | + | 0.3474 | (0.0209) | log L |
| Log DNR = | 2.434 | + | 0.3560 | (0.0188) | log L |
| Log PL = | 1.664 | + | 0.6011 | (0.0189) | log L |
| Log CL = | 1.640 | + | 0.3042 | (0.0211) | log L |
| Log PW = | -1.649 | + | 0.6863 | (0.0219) | log L |
| Log AW = | -0.584 | + | 0.5209 | (0.0219) | log L |
| Log LCC = | 1.244 | + | 0.3341 | (0.0243) | log L |
| Log LD = | 0.734 | + | 0.3611 | (0.0419) | log L |
| Log WCC = | 1.447 | + | 0.4510 | (0.0187) | log L |

For the remaining specimens involved in this study, the log ratio's have been computed.

The results of the 'CLUSTAN, procedure RELOCATE', (Wishart, 1978), are presented in Table 2 and 3. In Table 2, the clusters fused at each cycle, the coefficient at which clusters have been fused and total sum of similarities after the fusion is given.

Table 2. Clusters fused, coefficient, new number of clusters and new sum of similarities.

| Step | Clusters fused | Coeff. | Numb. Cl. | New sum sim. |
|------|----------------|--------|-----------|--------------|
| 1 | 7 and 10 | 0.40 | 9 | 103.7 |
| 2 | 5 and 8 | 0.58 | 8 | 110.5 |
| 3 | 1 and 6 | 0.61 | 7 | 111.1 |
| 4 | 5 and 9 | 0.51 | 6 | 118.4 |
| 5 | 1 and 4 | 0.58 | 5 | 123.1 |
| 6 | 1 and 7 | 0.76 | 4 | 135.2 |
| 7 | 2 and 3 | 0.73 | 3 | 147.9 |

Table 3. Results Cluster Analysis. Slide-number, Sample and cluster assigned to after fusion from 9 to 3 terminal clusters.

| SN | Sa | 9 | 8 | 7 | 6 | 5 | 4 | 3 | SN | Sa | 9 | 8 | 7 | 6 | 5 | 4 | 3 |
|----------|----|---|---|---|---|---|---|---|-------|----|---|---|---|---|---|---|---|
| 1062a-48 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3175 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-37 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3167 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-08 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3117 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-46 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3074 | 2 | 9 | 9 | 1 | 1 | 1 | 1 | 1 |
| 1062a-47 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3158 | 2 | 5 | 5 | 9 | 5 | 5 | 5 | 5 |
| 1062a-07 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3151 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-13 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3088 | 2 | 9 | 9 | 9 | 5 | 5 | 5 | 5 |
| 1062a-20 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3089 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-14 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3121 | 2 | 8 | 9 | 9 | 5 | 5 | 5 | 5 |
| 1062a-12 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3098 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-17 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3153 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-31 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3090 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-22 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3095 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-33 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3092 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-25 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3093 | 2 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| 1062a-03 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3110 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-43 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3132 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-26 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3004 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-49 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3109 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-15 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3010 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-38 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3094 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-19 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3097 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-16 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3006 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-21 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3096 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-05 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3101 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-32 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3133 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-11 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3046 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-29 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3011 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-18 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 3014 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1062a-06 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | | | | | | | | | |
| 1062a-36 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76079 | 3 | 4 | 4 | 4 | 4 | 1 | 3 | 2 |
| 1062a-28 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76080 | 3 | 3 | 3 | 3 | 2 | 2 | 2 | 2 |
| 1062a-02 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76082 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1062a-44 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76083 | 3 | 8 | 3 | 9 | 3 | 3 | 3 | 5 |
| 1062a-23 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76085 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1062a-41 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76086 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1062a-24 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76088 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1062a-35 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76089 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1062a-27 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 75115 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1062a-34 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 76114 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1062a-42 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | | | | | | | | | |
| 1062a-30 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 2165 | 4 | 9 | 9 | 9 | 1 | 1 | 3 | 2 |
| 1062a-04 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 2162 | 4 | 9 | 9 | 9 | 3 | 3 | 3 | 5 |
| 1062a-50 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 2018 | 4 | 9 | 9 | 9 | 1 | 1 | 5 | 5 |
| 1062a-01 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 2064 | 4 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| 1062a-10 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | | | | | | | | | |
| 1062a-40 | 1 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1012c | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| | | | | | | | | | 1061 | 5 | 5 | 5 | 9 | 5 | 5 | 5 | 5 |
| 3208 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 1003a | 5 | 9 | 9 | 1 | 1 | 1 | 5 | 5 |
| 3207 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 1010b | 5 | 4 | 4 | 4 | 4 | 1 | 5 | 5 |
| 3206 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 1009 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 3177 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | | | | | | | | | |
| 3216 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 1082a | 6 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 3215 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 1082c | 6 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 3128 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 1084a | 6 | 9 | 9 | 9 | 5 | 5 | 5 | 5 |
| 3168 | 2 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | | | | | | | | | |
| 3170 | 2 | 9 | 9 | 9 | 5 | 5 | 5 | 5 | | | | | | | | | |

| SN | Sa | 9 | 8 | 7 | 6 | 5 | 4 | 3 | SN | Sa | 9 | 8 | 7 | 6 | 5 | 4 | 3 |
|---------|----|---|---|---|---|---|---|---|----------|----|---|---|---|---|---|---|---|
| 1054 | 6 | 8 | 9 | 9 | 9 | 5 | 5 | 5 | 76103 | 15 | 4 | 4 | 9 | 5 | 5 | 5 | 5 |
| 1052 | 6 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 76105 | 15 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1056 | 6 | 8 | 5 | 9 | 5 | 5 | 5 | 5 | 76104 | 15 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1050 | 6 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 76102 | 15 | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1072b | 7 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 041-5 | 16 | 1 | 1 | 7 | 7 | 7 | 1 | 1 |
| 1063b | 7 | 8 | 9 | 9 | 3 | 3 | 3 | 5 | 041-2 | 16 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1064a | 7 | 8 | 5 | 9 | 5 | 5 | 5 | 5 | 041-3 | 16 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1070 | 7 | 9 | 9 | 9 | 1 | 1 | 3 | 2 | 1064a-3 | 17 | 6 | 6 | 1 | 1 | 1 | 1 | 5 |
| 1074 | 7 | 8 | 9 | 9 | 5 | 5 | 5 | 5 | 1064a-5 | 17 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1069 | 7 | 8 | 5 | 9 | 5 | 5 | 5 | 5 | 1064a-1 | 17 | 1 | 1 | 7 | 7 | 7 | 1 | 1 |
| 1577A-3 | 8 | 4 | 4 | 4 | 4 | 1 | 5 | 5 | 1064a-4 | 17 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1577A-1 | 8 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 1008a-3 | 18 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1577A-6 | 8 | 1 | 1 | 4 | 4 | 1 | 2 | 2 | 1008a-4 | 18 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1577A-2 | 8 | 4 | 4 | 3 | 3 | 3 | 2 | 2 | 1008a-2 | 18 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1577A-4 | 8 | 1 | 1 | 4 | 4 | 1 | 1 | 1 | 1008a-1 | 18 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1577A-5 | 8 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 1674-4 | 19 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1577A-7 | 8 | 1 | 1 | 4 | 4 | 1 | 2 | 2 | 1674-1 | 19 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 76103 | 9 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1674-2 | 19 | 3 | 3 | 3 | 3 | 2 | 2 | 2 |
| 76104 | 9 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1674-3 | 19 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 76105 | 9 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 1623-3 | 20 | 7 | 7 | 7 | 7 | 7 | 3 | 1 |
| 76077 | 9 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1623-2 | 20 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 76106 | 9 | 6 | 6 | 1 | 1 | 1 | 2 | 2 | 1623-1 | 20 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 76109 | 9 | 4 | 4 | 4 | 4 | 2 | 2 | 2 | 1594-2 | 21 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 76092 | 10 | 6 | 6 | 1 | 1 | 1 | 1 | 2 | 1575Aa-1 | 22 | 1 | 1 | 4 | 4 | 1 | 2 | 2 |
| 77-60 | 10 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 1575Aa-3 | 22 | 3 | 3 | 3 | 2 | 2 | 2 | 2 |
| 76094 | 10 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1575Aa-2 | 22 | 7 | 7 | 7 | 3 | 3 | 3 | 1 |
| 76096 | 10 | 3 | 3 | 3 | 2 | 2 | 2 | 2 | 1302-1 | 23 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 76097 | 10 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1302-2 | 23 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 76091 | 10 | 4 | 4 | 4 | 4 | 1 | 2 | 2 | 1302-3 | 23 | 7 | 7 | 7 | 7 | 7 | 3 | 1 |
| 1621-2 | 11 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1449-1 | 24 | 6 | 6 | 1 | 1 | 7 | 1 | 1 |
| 1621-5 | 11 | 1 | 1 | 7 | 7 | 7 | 1 | 1 | 1449-2 | 24 | 7 | 7 | 7 | 7 | 7 | 1 | 1 |
| 1621-6 | 11 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1286-1 | 25 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 1621-8 | 11 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1286-2 | 25 | 8 | 5 | 5 | 5 | 5 | 5 | 5 |
| 1621-7 | 11 | 1 | 1 | 7 | 7 | 7 | 1 | 1 | 1286-3 | 25 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| 1621-9 | 11 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1596-1 | 26 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1621-3 | 11 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1596-2 | 26 | 9 | 9 | 9 | 7 | 7 | 3 | 1 |
| 1446-2 | 12 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1596-3 | 26 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1446-6 | 12 | 1 | 1 | 7 | 7 | 7 | 1 | 1 | 1592A-2 | 27 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1446-5 | 12 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1591-2 | 28 | 1 | 1 | 4 | 4 | 1 | 1 | 1 |
| 1446-3 | 12 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1591-1 | 28 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 1446-7 | 12 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1569-2 | 29 | 9 | 9 | 2 | 2 | 2 | 2 | 2 |
| 1446-4 | 12 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1569-1 | 29 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1629-4 | 13 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1575A-1 | 30 | 1 | 1 | 2 | 2 | 2 | 2 | 2 |
| 1629-5 | 13 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1579-1 | 31 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 1629-6 | 13 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1579-2 | 31 | 6 | 6 | 1 | 1 | 1 | 1 | 1 |
| 1629-3 | 13 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | | | | | | | | |
| 1629-2 | 13 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | | | | | | | | |
| 1629-1 | 13 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | | | | | | | | | |
| 1671-6 | 14 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | | | | | | | | | |
| 1671-1 | 14 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | | | | | | | | | |
| 1671-4 | 14 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | | | | | | | | | |
| 1671-5 | 14 | 7 | 7 | 7 | 3 | 3 | 3 | 1 | | | | | | | | | |
| 1671-3 | 14 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | | | | | | | | | |
| 1671-2 | 14 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | | | | | | | | | |

| SN | Sa | 9 | 8 | 7 | 6 | 5 | 4 | 3 | SN | Sa | 9 | 8 | 7 | 6 | 5 | 4 | 3 |
|---------|----|---|---|---|---|---|---|---|--------|----|---|---|---|---|---|---|---|
| 1064c-1 | 32 | 9 | 9 | 9 | 3 | 3 | 3 | 2 | 1211a | 56 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 1064c-2 | 32 | 9 | 9 | 9 | 1 | 5 | 5 | 5 | 5800 | 57 | 4 | 4 | 4 | 4 | 1 | 2 | 2 |
| 1678-1 | 34 | 4 | 4 | 4 | 4 | 1 | 2 | 2 | 76099 | 58 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 1678-2 | 34 | 4 | 4 | 4 | 4 | 1 | 2 | 2 | 76098 | 59 | 4 | 4 | 4 | 4 | 1 | 2 | 2 |
| 1277-1 | 35 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 76100 | 60 | 1 | 1 | 4 | 4 | 1 | 2 | 2 |
| 1277-2 | 35 | 8 | 5 | 9 | 5 | 5 | 5 | 5 | 76110 | 61 | 1 | 1 | 2 | 2 | 2 | 2 | 2 |
| 370-1 | 36 | 9 | 9 | 9 | 5 | 5 | 5 | 5 | 1975-1 | 62 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 370-2 | 36 | 8 | 5 | 9 | 5 | 5 | 5 | 5 | 7369 | 63 | 3 | 3 | 3 | 2 | 2 | 2 | 2 |
| A-59 | 37 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 777-1 | 64 | 6 | 6 | 1 | 1 | 1 | 1 | 1 |
| 1708-1 | 38 | 7 | 7 | 7 | 7 | 7 | 3 | 1 | 777-2 | 65 | 6 | 6 | 1 | 1 | 1 | 2 | 2 |
| 1623A-1 | 39 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 83410 | 66 | 3 | 3 | 3 | 3 | 3 | 3 | 2 |
| 1097a | 40 | 4 | 4 | 4 | 4 | 1 | 2 | 2 | 1578-4 | 67 | 6 | 6 | 1 | 1 | 1 | 3 | 2 |
| 1555-1 | 41 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1578-5 | 67 | 6 | 6 | 1 | 1 | 1 | 3 | 2 |
| 1036a | 42 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1578-3 | 67 | 6 | 6 | 1 | 1 | 1 | 3 | 2 |
| 1038a-1 | 43 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 1578-6 | 67 | 6 | 6 | 1 | 1 | 1 | 3 | 2 |
| 1576A-1 | 44 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1578-8 | 67 | 6 | 6 | 1 | 1 | 1 | 2 | 2 |
| 1576-1 | 45 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1578-2 | 67 | 6 | 6 | 1 | 1 | 1 | 3 | 2 |
| 1653A-1 | 46 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 1578-7 | 67 | 2 | 2 | 2 | 2 | 1 | 2 | 2 |
| 1566-1 | 47 | 6 | 6 | 1 | 1 | 7 | 1 | 1 | 1578-1 | 67 | 6 | 6 | 1 | 1 | 1 | 3 | 2 |
| 1565-1 | 48 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | 1578-9 | 67 | 6 | 6 | 1 | 1 | 1 | 2 | 2 |
| 1575-1 | 49 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | Ga-16 | 68 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| 1373-1 | 51 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | Ga-03 | 68 | 8 | 9 | 9 | 3 | 3 | 3 | 2 |
| 1064b | 52 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | Ga-15 | 68 | 8 | 9 | 9 | 3 | 3 | 3 | 5 |
| 1067-1 | 53 | 6 | 6 | 1 | 1 | 1 | 1 | 1 | Ga-18 | 68 | 8 | 9 | 9 | 3 | 3 | 3 | 5 |
| 1064-1 | 54 | 7 | 7 | 7 | 7 | 7 | 1 | 1 | Ga-07 | 68 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| | | | | | | | | | Ga-19 | 68 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| | | | | | | | | | Ga-09 | 68 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| | | | | | | | | | Ga-08 | 68 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| | | | | | | | | | Ga-04 | 68 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| | | | | | | | | | Ga-05 | 68 | 8 | 5 | 9 | 5 | 5 | 5 | 5 |
| | | | | | | | | | 8878 | 69 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |

The coefficient at which clusters are fused is a measurement of similarity between clusters. An increase of the sum of similarities between clusters in two subsequent steps gives an indication of the stability of the clusters fused. From table 2 it appears that by fusing clusters 1 and 7, the new sum of similarities between clusters strongly increases, which indicates that prior to that fusion a stable clustering has been reached. Therefore, for a discriminant analysis I started with 5 clusters. In the first instance, only homogeneous samples have been compared for computing classification functions.

The first homogeneous group (see Table 3) is composed of sample 1, 11

and 18; the second composed of sample 2 (3074 omitted) and 6; the third composed of sample 3 (76079 and 76080 omitted); the fourth of sample 13 and the fifth group of sample 67 (1578-7 omitted). Although a jackknifed classification of 100% is obtained for specimens from the above mentioned samples, allocation of the remaining specimens to one of these groups yields a heterogeneous, not sample bound allocation. Sample 9 and 10 appear, in that case, to be composed of individuals allocated to each of the five groups. The heterogeneity was particularly caused by allocation to the Malta-group of single specimens from bigger samples becoming heterogeneous by this allocation.

Therefore, a more subjective way of interpretation has been chosen for which was assumed, a priori, that the groups under consideration show a limited geographic range so that a Dutch sample including one specimen which shows similarity to the Macquarie-group, is considered to represent a homogeneous sample. Sample 66 (Nice), consisting of one specimen resembling the Macquarie group if based on overall similarity, is placed in the group of cluster 5 as are the specimens of Malta (sample 67 and 69). Specimens from the Philippines have been placed in the rest-group because of their isolated geographic position as were the specimens from New Zealand.

After grouping, a preliminary discriminant analysis has been performed, which was repeated after some shifting. The grouping of the specimens is given under the description of the species. Two samples appeared to be composed of two species: sample 9 and 19.

As a control this discriminant analysis was repeated on a subset of the data obtained by selecting individuals with probabilities 0.50; the remaining specimens have subsequently been allocated to one of the groups from the random nucleus.

Comparing the analysis on complete cases and the control, differences could be found in the allocation of five specimens. Using the nucleus, the probability that 76079 was allocated to the Macquarie-group decreased from 0.60 to 0.25 and was, therefore, allocated to the Curaçao-group ($P = 0.71$). The probability that specimens 1578-8, -2, -7 and -9 were allocated to the Texel-group decreased by 0.23, 0.29, 0.45 and 0.06 respectively and, therefore, have been allocated to the Curaçao-group. On the other hand, specimens 2165 (sample 4) and 1064c-2 (sample 32) were allocated correctly by the 'random nucleus'-method, in contradiction to the complete cases method. Differences in probability were in the same order as above. One aberrant specimen is present in the material studied, namely the specimen from Malta (8878) being allocated to the Curaçao-group ($P = 1.00$) using both procedures.

The classification functions of the four groups are presented in Table 4 together with the F-values of variables to enter at each level and initial F-value. The in-product of the classification functions and corresponding log ratio's of a specimen make allocation of the specimen to one of the groups possible (an example is given on p. 123). On the basis of the initial F-value, a testing standard for group differences, the best character for

classification is determined. After removal of the character with the highest F-value, new values are calculated and the character with the highest F is subsequently removed; F-enter in Table 4 gives the highest F-value prior to each character-removal. From the initial F-value it becomes obvious that tail length, length and width of cephalic capsule and anal body width vary most between groups.

Table 4. Classification functions and F-values discriminant analysis, females & juveniles.

| Variable | Bonaire | Texel | Macquarie | Curaçao | F-enter | F-initial |
|-------------------|---------|-------|-----------|---------|---------|-----------|
| LR _{dl} | - 8.6 | 4.1 | 9.6 | 4.7 | 22.9 | 28.6 |
| LR _{dnr} | - 9.9 | 0.8 | 3.6 | 5.1 | 3.9 | 23.1 |
| LR _{pl} | -14.6 | 1.7 | 1.4 | - 8.5 | 9.4 | 19.8 |
| LR _{cl} | 80.0 | 3.6 | 56.6 | 17.5 | 601.6 | 601.6 |
| LR _{pw} | -18.5 | 2.4 | -10.8 | 7.9 | 62.1 | 63.2 |
| LR _{aw} | 3.6 | -6.9 | 20.1 | 5.1 | 9.1 | 68.7 |
| LR _{lcc} | 24.4 | 1.0 | 13.6 | 4.6 | 9.9 | 118.2 |
| LR _{ld} | 3.4 | 1.8 | 2.4 | 7.6 | 4.2 | 35.7 |
| LR _{wcc} | 16.9 | -0.9 | -15.0 | 6.6 | 26.3 | 83.2 |
| Constant | -26.8 | -1.4 | -17.9 | - 7.7 | | |

After removal of the caudal length as main classification function, the value of the length of the cephalic capsule as classification character decreases which indicates that the group with an extreme LR_{cl} is also characterized by an extreme LR_{lcc}.

After removal of each classification function, specimens are allocated according to the previously removed functions. In Table 5 the percentage correct jackknifed classification is given for each of the samples after 1 - 9 steps. From the table it results that based on LR_{cl}, LR_{pw}, LR_{dl} and LR_{wcc}, 93.8% of the specimens are correctly classified.

Table 5. Percentage correct jackknifed classification.

| Step | Variable entered | Weighted Mean | Bon. | Tex. | Mcq. | Cur. |
|------|-------------------|---------------|-------|------|-------|------|
| 1 | LR _{cl} | 81.5 | 99.0 | 87.0 | 23.5 | 56.9 |
| 2 | LR _{pw} | 89.6 | 99.0 | 94.6 | 23.5 | 84.3 |
| 3 | LR _{dl} | 92.3 | 99.0 | 94.6 | 58.8 | 86.3 |
| 4 | LR _{wcc} | 93.8 | 100.0 | 93.5 | 76.5 | 88.2 |
| 5 | LR _{lcc} | 91.2 | 99.0 | 90.2 | 76.5 | 82.5 |
| 6 | LR _{pl} | 93.1 | 98.1 | 91.3 | 88.2 | 88.2 |
| 7 | LR _{aw} | 94.6 | 99.0 | 95.7 | 100.0 | 88.2 |
| 8 | LR _{ld} | 93.5 | 99.0 | 89.1 | 94.1 | 90.2 |
| 9 | LR _{dnr} | 93.8 | 99.0 | 90.2 | 94.1 | 90.2 |

In Table 6 the classification functions after 4 steps are presented. From Table 4 and 6 it is concluded that the Bonaire-group can easily be distinguished from the Texel-group by LR_{cl}, LR_{lcc} and LR_{wcc}; from the Macquarie-group by LR_{wcc} and LR_{dl}; from the Curaçao-group by LR_{cl} and LR_{pw}. The Texel-group is to be distinguished from the Macquarie-group by LR_{cl} and LR_{aw}; from the Curaçao-group by LR_{aw}, LR_{pl} and LR_{cl}. The groups from Macquarie and Bonaire are to be distinguished by LR_{cl}, LR_{pw} and LR_{wcc}.

Table 6. Classification functions after 4 steps.

| Variable | Bonaire | Texel | Macquarie | Curaçao |
|-------------------|---------|-------|-----------|---------|
| LR _{dl} | - 7.8 | 5.0 | 18.0 | 11.5 |
| LR _{cl} | 80.3 | 2.8 | 57.8 | 18.4 |
| LR _{pw} | - 8.5 | -0.4 | 1.9 | 15.2 |
| LR _{wcc} | 25.6 | -0.1 | -5.8 | 8.2 |
| Constant | -22.4 | -1.2 | -15.9 | -6.6 |

Table 7. Variable, mean log ratio and S.E. of the four groups.

| Variable | Bonaire (100) | | Texel (92) | | Macquarie (17) | | Curaçao (51) | |
|-------------------|---------------|-------|------------|-------|----------------|-------|--------------|-------|
| | mean | S.E. | mean | S.E. | mean | S.E. | mean | S.E. |
| LR _{dl} | 0.093 | 0.076 | 0.055 | 0.110 | 0.264 | 0.135 | 0.168 | 0.112 |
| LR _{dnr} | 0.005 | 0.077 | 0.029 | 0.078 | 0.166 | 0.096 | 0.097 | 0.128 |
| LR _{pl} | -0.067 | 0.073 | 0.024 | 0.086 | 0.040 | 0.056 | -0.034 | 0.126 |
| LR _{cl} | 0.480 | 0.064 | 0.024 | 0.083 | 0.374 | 0.081 | 0.140 | 0.090 |
| LR _{pw} | 0.016 | 0.097 | -0.003 | 0.138 | 0.038 | 0.128 | 0.267 | 0.125 |
| LR _{aw} | 0.075 | 0.081 | -0.022 | 0.099 | 0.168 | 0.127 | 0.194 | 0.084 |
| LR _{lcc} | 0.376 | 0.091 | 0.035 | 0.145 | 0.218 | 0.076 | 0.216 | 0.155 |
| LR _{ld} | 0.177 | 0.132 | 0.076 | 0.221 | 0.216 | 0.120 | 0.380 | 0.133 |
| LR _{wcc} | 0.201 | 0.072 | 0.008 | 0.100 | 0.026 | 0.077 | 0.161 | 0.105 |

In Figure 3 the first canonical variable is plotted against the second. At least four groups of the *Leptosomatum bacillatum*-complex can be distinguished in this material.

The four 'groups' obtained by the cluster and verified by the discriminant analysis, are considered to represent four groups at species level. Mean log ratio's and standard errors of estimate are given in Table 7. Of these groups the Bonaire-group might represent a new species, specimens from the Texel-group are considered identical to *L. bacillatum* (Eberth, 1863), the Macquarie-group *L. clavatum* Platonova, 1958 and the Curaçao-group *L. acephalatum* Chitwood, 1936.

This analysis is based on juveniles and females; if males are assigned to that group to which the whole sample belongs, the phenomenon occurs that males are absent in the Macquarie- and Bonaire-group. Although males are absent in the Bonaire-group, 80% of the females carry sperm. In the Texel-group males are numerous, but only 10% of the females has been fertilized.

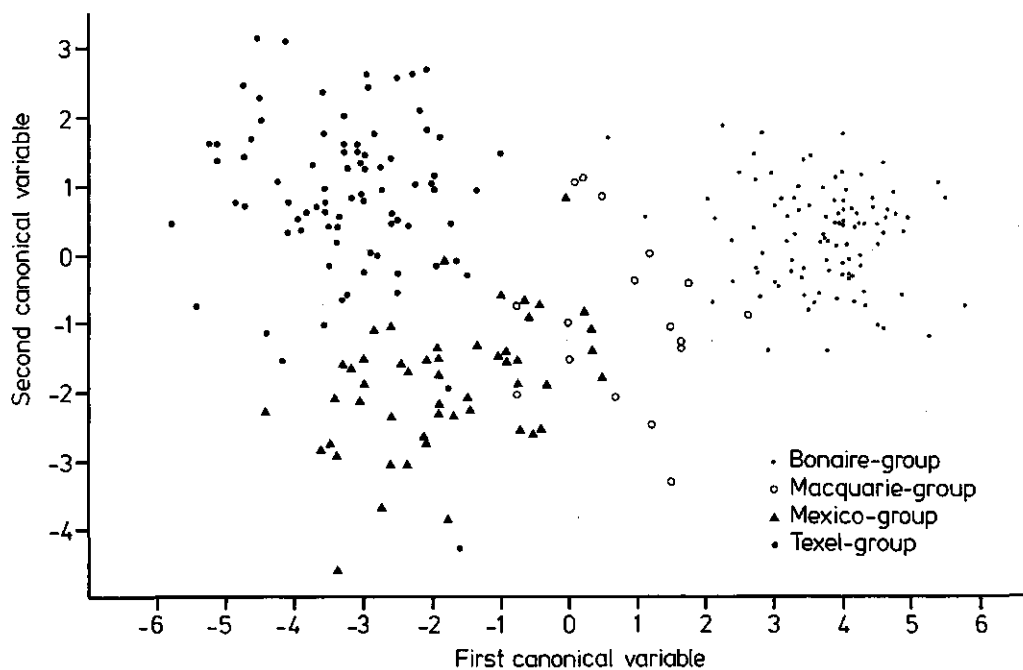


Fig. 3; Ordination of juveniles and females on the first two axes of a principal coordinates chart showing the separation of the four groups based on 9 characters.

Discussion groups obtained from cluster and discriminant analysis

Allopatric populations of the same species are not completely identical, and, in fact, even populations from the same locality may be slightly different at different seasons of the year (Mayr, Linsley and Usinger, 1953: 151). In a previous paper (Bongers, 1983a) it has been demonstrated that *L. bacillatum* has an annual reproductive cycle. Moreover, realizing that samples included in this study are heterogenous, biased and in a number of cases restricted to one specimen only, it will be obvious that an application of statistical methods may impart a false sense of precision. In discussing the samples of each of the four groups distinguished, statistical analysis will be used as a tool along with other information. For comparison of samples, the Coefficient of Difference (C.D.) will be used being a measure for joint overlap (Mayr, 1943: 102; Mayr, Linsley and Usinger, 1953: 146) in terms of the properties of the normal curve.

The Texel-group: *Leptosomatum bacillatum* (Eberth, 1863)

Specimens of the Texel-group (sample 2, 4, 5, 6, 7, 15, 25, 35 and 37) have been described in a previous paper (Bongers, 1983) whereas sample 57 represents one of the specimens described by Filipjev (1918). Some new records are presented here; sample 66 from the harbour of Nice, the type-locality of *L. bacillatum*; two samples from Malta and one from Galway, Ireland.

The log ratio's of the total group, Texel (Sample 2), Malta (S.67) and Ireland (S.68) are given by their mean and standard error of estimate together with the log ratio's of a specimen from the Black Sea (S.57) and Nice (S.66) in Table 8. The log ratio's of S.2, the reference sample, have zero mean.

Table 8. Log ratio's and standard errors for *L. bacillatum*.

| Var. | Total | n=92 | S.2 | n=38 | S.67 | n=9 | S.68 | n=10 | S.57 | S.66 |
|-------------------|--------|-------|-------|-------|--------|-------|--------|-------|--------|--------|
| | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. | | |
| LR _{dl} | 0.055 | 0.110 | 0.000 | 0.074 | 0.124 | 0.053 | 0.136 | 0.062 | 0.180 | 0.310 |
| LR _{dnr} | 0.029 | 0.078 | 0.000 | 0.059 | -0.002 | 0.043 | 0.113 | 0.068 | 0.119 | 0.131 |
| LR _{pl} | 0.024 | 0.086 | 0.000 | 0.073 | -0.002 | 0.033 | 0.093 | 0.089 | -0.053 | -0.023 |
| LR _{cl} | 0.024 | 0.083 | 0.000 | 0.089 | 0.023 | 0.055 | 0.075 | 0.062 | 0.029 | 0.057 |
| LR _{pw} | -0.003 | 0.138 | 0.000 | 0.079 | 0.170 | 0.040 | -0.179 | 0.078 | 0.258 | -0.012 |
| LR _{aw} | -0.022 | 0.099 | 0.000 | 0.083 | 0.004 | 0.044 | -0.049 | 0.055 | 0.270 | 0.026 |
| LR _{lcc} | 0.035 | 0.145 | 0.000 | 0.101 | 0.301 | 0.094 | 0.018 | 0.149 | -0.090 | 0.122 |
| LR _{ld} | 0.076 | 0.222 | 0.000 | 0.163 | 0.451 | 0.115 | 0.232 | 0.169 | 0.086 | 0.182 |
| LR _{wcc} | 0.008 | 0.100 | 0.000 | 0.072 | 0.063 | 0.055 | -0.015 | 0.078 | 0.074 | 0.004 |

The sample from Nice (66), the type-locality of *L. bacillatum*, should have been the base of comparison with other samples, but unfortunately only

one female was recovered in that sample. As this female was slightly damaged by transferring to glycerine, it will not be designated a neotype despite the efforts to take that sample.

According to Table 8, the distance from the anterior end to the lens-like body is rather constant within samples (S.E. < 0.1) but variable between samples (S.E. > 0.1). LR_{dl} of the specimens from S.57 and S.66 exceeds the mean ± 2 S.E. of sample 2; and S.66 exceeds even that of the total group. Sample 25 (Banyuls) has an LR_{dl} of 0.213 ± 0.077 resulting in a C.D. of 1.61 and a non overlap of 92% with the total group.

The distances to the nerve ring and pharynx length are rather constant within samples and within the total group. In S.66 however, the nerve ring is situated more posterior than in S.02.

The caudal length, the most diagnostic character, is rather constant within the total group. The S.E. of the total group is lower than in S.02.

The width at the pharynx base (PW) and anal width (AW) are easily influenced by flattening; the high values of these characters in S.57 are due to flattening. Sample 67 and 02 show a 92% non overlap in LR_{pw} whereas sample 67 and 68 are easily distinguishable by their LR_{pw} .

The length of the cephalic capsule (LCC) is rather constant between samples with an exception for the Malta-sample (S.67) in which LR_{lcc} has an extreme high value.

The diameter of the lens-like body is the most variable of the characters included; the highest LR_{dl} is found in the Malta-sample. The two specimens of sample 35 (Banyuls) have an extremely low LR_{dl} of -0.172 and -0.197. The width of the cephalic capsule (WCC) is rather constant within and between samples of *L. bacillatum* and variable between the groups; therefore, the width of the cephalic capsule is an important diagnostic character.

The most aberrant sample in this group is that of Malta (S.67) with an extreme LCC and LD. These values however, need confirmation by additional samples from the same locality. Should it be found that these values are not due to a fixation or mounting artifact (such e.g. as being exposed to an osmotic shock) then these specimens might represent a new species. The second sample of Malta (69) confirms the extreme diameter of the lens-like body ($LR_{ld} = 0.410$) but not the aberrant LCC.

The position of the gonads in relation to the intestine is variable in sample 02; in males the anterior and posterior testes are situated resp. to the right (R) and left (L) once and L-L twice. In females the gonad position is variable: R-L (3x), R-R (4x), L-R (6x) and L-L (8x). In other samples the same variability is observed. Therefore the use of this character, as proposed by Lorenzen (1981) for other taxa, has no value for distinction of the species of *Leptosomatum*.

Only two of the females recorded in sample 02 are gravid; 3010 carries 27 eggs in the anterior and 29 eggs in the posterior uterus, in 3011 the number of eggs comes to 27 and 20 respectively.

Female A-59 (Wimereux) contains 15 and 17 eggs; 1286-1 (Banyuls) 6 and 7; 5800 (Black Sea) 8 and 7 and 83410 (Nice) 5 and 7 eggs in the anterior and posterior uterus respectively.

The number of eggs in *L. bacillatum* exceeds the number in the other groups. The maximum number of eggs I have found in females of the Bonaire-group is 15, in the Macquarie-group 13 and 23 in the Curaçao-group (see also Timm, 1953). If only one specimen is at hand, a low number of eggs in the uterus is not diagnostic. The presence of more than 30 eggs, however, suggests that the female belongs to *L. bacillatum*.

Leptosomatum bacillatum; material studied (for numerical data see Appendix)

- (02). The Netherlands, Texel, 't Horntje (53°01'N, 4°47'E); Halichondria panicea, littoral. June 1977. R. den Ottolander. NDW.
- (04). The Netherlands, Burghsluis (51°40'N, 3°40'E). Halichondria panicea, littoral. Feb. 1978. NDW.
- (05). The Netherlands, Texel, Oudeschild (53°03'N, 4°50'E). Halichondria panicea, littoral. Nov. 1970. NDW.
- (06). The Netherlands, Kattendijke (51°33'N, 3°47'E). Halichondria panicea, littoral. Oct. 1970. NDW.
- (07). The Netherlands, Den Helder (52°58'N, 4°42'E). Polysiphonia sp. and Halichondria panicea, littoral. Nov. 1970. NDW.
- (15). N.E. England. Laminaria holdfasts at low tide on a rocky shore. R.M. Warwick. USNM.
- (25). France, Banyuls (42°29'N, 3°07'E). From unidentified sponges. June 1976. NDW.
- (35). France, Ambleteuse (50°48'N, 1°34'E). Halichondria panicea, littoral, June 1978. M. Buil. NDW.
- (37). France Wimereux (50°48'N, 1°34'E). Collected by J.G. de Man in 1890 and labelled 'Leptosomatum sp'. ZMA.
- (57). Black Sea. L. bacillatum sensu Filipjev, 1918. June 1912. ZIL.
- 66. France, Harbour of Nice (type-locality L. bacillatum). Serpulid tubes and Tunicates on cable. 10 April 1983. C. Heip. NDW.
- 67. Malta, Cominotto, Blue Lagoon. Sarcotragus spinosulus and Ircinia fasciculata; 2 m. depth. 26 June 1983. P.J. Schembri. NDW.
- 68. Ireland, Galway (53°09'07''N, 9°09'08''W). Halichondria panicea, Hymeniacion perlevis and Mycale contareni on limestone reef; littoral, (T 4-24°C; salinity 34). Sept. 1983. B. O'Connor. NDW.
- 69. Malta, St. Paul's Bay, jetty near Rxawn Point. From algae (Jania rubens and Dictyopteris tripolitana). 0-2 m. 5 Aug. 1983. P.J. Schembri. NDW.

The Macquarie-group: *Leptosomatum clavatum* Platonova, 1958.

The specimens of the Macquarie-group resemble the lectotype of *L. clavatum* Platonova, 1958 designated by Platonova in 1968 (for discussion see Bongers, 1983). Sample 36 is a new record; other samples have previously been described (Platonova 1958, 1968; Bongers, 1983). On zoogeographical grounds I have hesitated to assign the New Zealand sample (36) to this group and have preferred to place these specimens preliminary in the rest-group. After the first discriminant analysis these specimens have been allocated to the Macquarie-group and, subsequently, included among that group for the repeated discriminant analysis.

The log-ratio's of the total group and sample 3 have been given by their mean and S.E. in Table 9 together with the log ratio's of the single specimens allocated to the Macquarie-group. According to Table 9 the pharynx length, length and width of the cephalic capsule and caudal length have a

rather low S.E. The distance from anterior end to the lens-like body is a good character to distinguish *L. clavatum* from the other species of the *L. bacillatum*-complex, although the specimens of sample 36 are an exception. Especially in 370-1 the ocelli are situated far anterior. The paralectotype of *L. clavatum* (7369) is flattened resulting in a high LR_{pw} and LR_{aw} ; the length of the cephalic capsule exceeds the mean ± 2 S.E. of the total group.

Although some of the females carry sperm, no males have been found so far.

Table 9 Log ratio's and S.E. of *L. clavatum*.

| Var. | Total n=18 mean S.E. | S.3 n=10 mean S.E. | S.26 1596-1 | S.26 1596-2 | S.26 1596-3 | S.36 370-1 | S.36 370-2 | S.62 1975-1 | S.63 7369 |
|------------|-------------------------|-----------------------|----------------|----------------|----------------|---------------|---------------|----------------|--------------|
| LR_{dl} | 0.264 0.135 | 0.319 0.093 | 0.358 | 0.067 | 0.308 | 0.036 | 0.089 | 0.301 | 0.256 |
| LR_{dnr} | 0.166 0.096 | 0.217 0.103 | 0.212 | 0.077 | 0.160 | 0.045 | 0.126 | 0.137 | 0.097 |
| LR_{pl} | 0.040 0.056 | 0.039 0.054 | 0.125 | 0.020 | 0.115 | 0.126 | -0.018 | 0.016 | 0.028 |
| LR_{cl} | 0.374 0.081 | 0.380 0.115 | 0.262 | 0.336 | 0.309 | 0.288 | 0.303 | 0.428 | 0.427 |
| LR_{pw} | 0.038 0.128 | 0.042 0.108 | 0.079 | 0.009 | -0.044 | 0.039 | -0.110 | 0.020 | 0.369 |
| LR_{aw} | 0.168 0.127 | 0.201 0.113 | 0.246 | 0.144 | 0.204 | 0.042 | -0.040 | 0.020 | 0.346 |
| LR_{lcc} | 0.218 0.076 | 0.221 0.058 | 0.187 | 0.241 | 0.253 | 0.211 | 0.070 | 0.149 | 0.378 |
| LR_{ld} | 0.216 0.120 | 0.234 0.072 | 0.454 | 0.124 | 0.350 | -0.018 | 0.045 | 0.288 | 0.163 |
| LR_{wcc} | 0.026 0.077 | 0.039 0.076 | 0.140 | 0.027 | -0.102 | 0.003 | -0.028 | -0.042 | 0.020 |

L. clavatum Material; (for numerical data see Appendix)

- (03). Macquarie Isl. USARP ELTANIN STA. 1974 (54°32'S, 158°59'E). 112-124 m. 15 Feb. 1967. USNM.
- (26). Burdwood Bank (S. of Falklands). USARP ELTANIN STA. 1591. (54°39'S, 59°09'-12'W). 124 m. 14 March 1966. USNM.
- 36. New Zealand. USARP ELTANIN STA. 370 (43°22'S, 175°20'E). 95 m. 19 Nov. 1966. USNM.
- (62). Macquarie Isl. USARP ELTANIN STA. 1975 (54°29'S, 159°00'E). 443-549 m. 15 Feb. 1967. USNM.
- (63). Kerguelen. Paralectotype *L. clavatum* Platonova, 1958. 20 May 1956. Alc. ZIL.

The Bonaire-group: *L. sabangense*, *L. sundaense* or a new species?

This is a homogeneous group; with only one aberrant specimen present (S. 47; 1566-1) whose mean exceeds ± 2 S.E. for the distance to the nerve ring ($LR_{dnr} = -0.241$), the pharynx length ($LR_{pl} = 0.085$), the caudal length ($LR_{cl} = 0.236$) and the length of the cephalic capsule ($LR_{lcc} = 0.158$). This specimen is allocated to the Bonaire-group with a probability of 0.81 and to *L. bacillatum* with $P = 0.17$.

In a previous paper (Bongers, 1983) specimen 76104 of sample 9 has been considered as belonging to *L. acephalatum* Chitwood, 1936.

Discussion of systematic position.

This species, represented only by females of which the majority carries sperm, is easily distinguished by the strongly developed cephalic capsule and relatively long tail, which in a number of cases is more than twice the anal body width.

Two nominal species are known with a T/ABW of 2 in adults, viz. *L. sabangense* Steiner, 1915, and *L. sundaense* Bongers, 1983.

L. sabangense was described by Steiner (1915) as a variety of *L. elongatum* and raised to species by Filipjev (1921). This species is characterized by the cephalic capsule being situated posterior to the cephalic sensilla. Although several specimens have been allocated to this species (a.o. Steiner, 1921; Allgén, 1942, 1947, 1951 and 1959) only the juvenile described in a previous paper (Bongers, 1983) shows both the posteriorly situated capsule and tail length equaling twice the anal body width. The juvenile described by Steiner (1921) from the Caribbean has a capsule situated as usual in this genus and, therefore, it is not identical to *L. sabangense* Steiner, 1915.

L. sabangense sensu Micoletzky, 1930 nec Steiner 1915 renamed *L. sundaense* Bongers, 1983 was described as having a tail length of twice the anal body width and a cephalic capsule of 11 - 13 μm . The position of the ocelli varies from 1,21 - 3,55 cephalic diameters or 28 - 86 μm , from which the cephalic diameter can be calculated as being 23 - 24 μm ; on p. 276 Micoletzky states that the cephalic capsule measures 12 μm which is 40% of the cephalic diameter resulting in a cephalic diameter of 30 μm .

In adult females of Bonaire (sample 1) the position of the ocelli is rather constant whereas the cephalic diameter of adults varies from 31 to 42 μm . In *L. sundaense* 'ratio b' varies from 6.8 to 12.6 whereas in Bonaire-females this ratio varies between 6.9 and 9.9. According to Micoletzky (1930: 274) *L. sabangense* sensu Micoletzky and *L. keiense*, found in the same sample, can often hardly be distinguished. Bongers (1983: 837) suspects that *L. keiense* is a species-complex. The same is expected for *L. sabangense* sensu Micoletzky which may comprise one or more *L. keiense* specimens with a short pharynx. As Micoletzky's material may turn up again I postpone the naming of the species from Bonaire to avoid unnecessary synonyms.

Mean and S.E. of the log ratio's of some samples of geographical isolated populations from the Bonaire-group are given in Table 10; Bonaire (1), Curaçao (11), Margarita (12), Bahama's (16) and Saint Thomas (19).

Table 10. Log ratio's and S.E of some samples of the Bonaire-group.

| Var. | Total n=100 mean S.E. | S.1 n=47 mean S.E. | S.11 n=7 mean S.E. | S.12 n=6 mean S.E. | S.16 n=3 mean S.E. | S.19 n=3 mean S.E. |
|-------------------|--------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| LR _{dl} | 0.093 0.076 | 0.090 0.062 | 0.097 0.145 | 0.114 0.083 | 0.070 0.115 | 0.108 0.153 |
| LR _{dnr} | 0.005 0.077 | -0.017 0.064 | -0.002 0.042 | 0.034 0.043 | -0.051 0.063 | 0.050 0.134 |
| LR _{pl} | -0.067 0.073 | -0.100 0.047 | -0.060 0.070 | -0.042 0.066 | -0.096 0.067 | -0.070 0.089 |
| LR _{cl} | 0.480 0.064 | 0.492 0.041 | 0.457 0.082 | 0.483 0.077 | 0.453 0.113 | 0.355 0.096 |
| LR _{pw} | 0.016 0.097 | 0.012 0.064 | 0.198 0.057 | 0.110 0.086 | 0.098 0.127 | 0.107 0.095 |
| LR _{aw} | 0.075 0.082 | 0.074 0.059 | 0.155 0.109 | 0.172 0.128 | 0.160 0.084 | 0.104 0.090 |
| LR _{lcc} | 0.376 0.091 | 0.378 0.051 | 0.290 0.086 | 0.454 0.066 | 0.366 0.026 | 0.292 0.168 |
| LR _{ld} | 0.177 0.132 | 0.149 0.105 | 0.182 0.069 | 0.277 0.115 | 0.156 0.135 | 0.215 0.151 |
| LR _{wcc} | 0.201 0.072 | 0.226 0.043 | 0.198 0.095 | 0.180 0.031 | 0.121 0.048 | 0.118 0.055 |

Material 'Bonaire-group'; for numerical data see Appendix.

01. Bonaire, Lac, S part. Rhizophora, scanty Thalassia on sandy mud; 0 - 1½ m. 17 April 1955. P. Wagenaar Hummelinck. NDW
- (09). Mexico, Quintana Roo; N. end of Ascension Bay. At inlet behind Allen pt; on mangrove roots; Isognomon alata, Melampus, sponges, amphipods, fiddler crabs and anemones. 7 April 1960. F.C. Daiber & E.L. Bousfield. USNM
11. Curaçao. Piscadera Baai, Binnenbaai, N part. N. side of Isla de Raphael. Rhizophora with plenty of oysters and balanids. 0 - 1 m. 26 Sept. 1967. P. Wagenaar Hummelinck. NDW
12. Margarita. Punta Mangle. Very muddy lagoon with Rhizophora and Avicennia; 0 - 1 m. 11 Jan. 1964. P. Wagenaar Hummelinck. Alc. NDW
14. Curaçao. Piscadera baai, Binnenbaai, SE part, near Carmabi. Rhizophora in sand and mud. 0 - ½ m. 30 March 1970. P. Wagenaar Hummelinck. NDW
16. Bahama's. N. Bimini; N of Lerner Marine Lab-pier. 28 Aug. 1962. M.L. Jones. USNM
17. Bonaire. Lac, NE part of basin, Puito. On Rhizophora in mud with Thalassia. 0 - 1 m. 18 Nov. 1930. P. Wagenaar Hummelinck. Alc. NDW
18. Aruba. Spaans Lagoen, NW side. Roch and mud near Rhizophora. ½ - 1 m. 24 March 1970. P. Wagenaar Hummelinck. NDW
19. Saint Thomas. Benner Bay Lagoon. Rhizophora in sandy mud. 0 - 1 m. 30 April 1973. P. Wagenaar Hummelinck. Alc. NDW
20. Curaçao. Piscadera Baai, Binnenbaai, N part. NW inlet of Piscadera Chikitu. Rhizophora in muddy sand, greatly overgrown by sponges. 0 - 1 m. 26 Sept. 1967. P. Wagenaar Hummelinck. NDW
22. Bonaire. Lac, entrance of Puito, 300 m NE of Cai; mud with some Thalassia, some Halimeda. ½ - ½ m. 11 Aug. 1967. P. Wagenaar Hummelinck. NDW
23. Bonaire. Wharf of Arend Petroleum Comp., Beam of iron construction in 15 m deep water; overgrown by Tubastraea, Telesto and sponges; 0 - 2 m. 4 May 1955. P. Wagenaar Hummelinck. Alc. NDW
24. Margarita. Puente de la Restinga, E side. Concrete and rock debris in entrance of large lagoon, muddy, Rhizophora with ascidians and sponges. 11 Jan. 1964. P. Wagenaar Hummelinck. Alc. NDW
38. Curaçao. Piscadera baai, Binnenbaai. E shore, N. of destroyed area, Rhizophora on rocky shore with some mud. 0 - 1 m. 27 July 1973. P. Wagenaar Hummelinck. NDW
39. Curaçao. Piscadera Baai, Binnenbaai, N part. Muddy sand, crowded with Chione. ½ - 1 m. 26 Nov. 1967. P. Wagenaar Hummelinck. NDW
41. Bonaire. Lagoen. S shore. Sheet of water in Avicennia grove, Uca. 0 - ½ m. 19 Nov. 1967. P. Wagenaar Hummelinck. Alc. NDW
42. Curaçao. Spaanse Water, Inner Bay. New Haven, Newport Landing. On and between limestone debris in muddy lagoon 0 - 1 m 10 April 1949. P. Wagenaar Hummelinck. Alc. NDW

45. Bonaire. Lac, NE of Cai, Pariba di Cai. Mud with Rhizophora, Thalassia. 0 - ½ m. 16 Sept. 1967. P. Wagenaar Hummelinck. Alc. NDW
47. Bonaire. Lac, entrance. Secu di Sorobon, 250 m N of Sorobon Pt. Porites flat with Thalassia and Lithothamnium. 1/10 - ½ m. 21 Aug. 1967. P. Wagenaar Hummelinck. Alc. NDW
48. Bonaire. Lac, entrance. Secu di Sorobon, 250 m N of Sorobon Pt. Sandy Lithothamnium ridge, some Thalassia, Tripteneustes. ¼ - 1 m. 21 Aug. 1967. P. Wagenaar Hummelinck. NDW
49. Bonaire. Lac, entrance of Puito, 300 m NE of Cai. Soft mud with Rhizophora, Thalassia. 0 - ½ m. 11 Aug. 1967. P. Wagenaar Hummelinck. Alc. NDW
51. Bonaire. Lac, entrance. Scrobon point. Limestone with sandy debris. 0 - ½ m. 20.3 - 21.5 g Cl / l. 17 April 1955. P. Wagenaar Hummelinck. Alc. NDW
54. Bonaire. Lac, NE part of basin, Puito. On Rhizophora in soft mud, Thalassia with Cassiopea. 0 - 1½ m. 12, 16 and 19 Oct. 1930. P. Wagenaar Hummelinck. Alc. NDW

The Curaçao-group: *Leptosomatum acephalatum* Chitwood, 1936

The log ratio's of the total group, Bonaire (8), Mexico (9 & 10) and Curaçao (13) are given by mean and standard error of estimate in Table 11.

Table 11. Log ratio's *L. acephalatum*.

| Var. | Total | n=51 | S.8 | n=7 | S.9 | n=5 | S.10 | n=6 | S.13 | n=6 |
|-------------------|--------|-------|--------|-------|--------|-------|--------|-------|-------|-------|
| | mean | S.E. | mean | S.E. | mean | S.E. | mean | S.E. | mean | S.E. |
| LR _{dl} | 0.168 | 0.112 | 0.109 | 0.107 | 0.218 | 0.112 | 0.243 | 0.102 | 0.246 | 0.061 |
| LR _{dnr} | 0.097 | 0.128 | 0.092 | 0.073 | 0.005 | 0.140 | 0.120 | 0.141 | 0.175 | 0.096 |
| LR _{pl} | -0.034 | 0.126 | -0.094 | 0.054 | -0.055 | 0.051 | -0.057 | 0.080 | 0.108 | 0.034 |
| LR _{cl} | 0.140 | 0.090 | 0.159 | 0.104 | 0.152 | 0.027 | 0.157 | 0.069 | 0.046 | 0.076 |
| LR _{pw} | 0.267 | 0.125 | 0.194 | 0.143 | 0.208 | 0.121 | 0.198 | 0.132 | 0.357 | 0.073 |
| LR _{aw} | 0.194 | 0.084 | 0.133 | 0.053 | 0.213 | 0.087 | 0.148 | 0.073 | 0.244 | 0.073 |
| LR _{lcc} | 0.216 | 0.155 | 0.193 | 0.102 | 0.253 | 0.067 | 0.226 | 0.142 | 0.454 | 0.032 |
| LR _{ld} | 0.380 | 0.133 | 0.382 | 0.138 | 0.388 | 0.162 | 0.485 | 0.072 | 0.432 | 0.143 |
| LR _{wcc} | 0.161 | 0.105 | 0.075 | 0.119 | 0.153 | 0.066 | 0.165 | 0.081 | 0.309 | 0.041 |

The Mexican samples 9, 10, 58, 60 and 61 have been recorded in a previous paper (Bongers, 1983).

According to Table 3, samples 8, 9 and 10, in contradistinction to sample 13, are not allocated uniformly to one of the clusters. Sample 13 and 21 occupy a special position in the whole group. These specimens deviate at first sight by the length at which the adult stage is reached. Moreover sample 13 deviates from sample 9 by the pharynx length, length and width of the cephalic capsule. Similar to the aberrant Maltese sample, the specimens of these samples may be influenced by a shock caused by a too high osmotic value of the fixative resulting in considerable shrinkage. For the moment sample 13 and 21 are considered as belonging to the Curaçao-group, which is probably identical to *L. acephalatum* Chitwood, 1936.

Sample 27, of which the specimens are provided with extremely large lens-like bodies, is another exceptional case; more material is desired.

In general the number of specimens in the samples recorded here is rather low, the S.E. of the total group is rather high so that no specimens exceed the mean ± 2 S.E. for any of the characters.

Material; L. acephalum (for numerical data see Appendix)

08. Bonaire. Lac, Rhizophora in mud. 0 - $\frac{1}{2}$ m. 11 March 1970. P. Wagenaar Hummelinck. NDW
- (09). Mexico. Quintana Roo; N end of Ascension Bay. At inlet behind Allen Pt; on mangrove roots; Isogomon alata, Melampus, sponges, amphipods, fiddler crabs and anemones. 7 April 1960. F.C. Daiber & E.L. Bousfield. USNM
- (10). Mexico. Quintana Roo; N end of Ascension Bay. 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. 15 April 1960. E.L. Bousfield & H. Rehder. USNM
13. Curaçao. Spaanse Water, inner bay. Jan Sofat Islet. Rocky with Rhizophora in mud; 0 - 1 m. 17 Nov. 1968. P. Wagenaar Hummelinck. NDW
19. Saint Thomas. Benner Bay Lagoon. Rhizophora in sandy mud; 0 - 1 m. 30 April 1973. P. Wagenaar Hummelinck. Alc. NDW
21. Bonaire. Lac, W part. Playa Mangel Altu, 600 m W of Sorobon Pt. Sandy bottom, Thalassia flat with Halimeda. $\frac{1}{2}$ - 1 m. 23 Sept. 1967. P. Wagenaar Hummelinck. Alc. NDW
22. Bonaire. Lac, entrance of Puito, 300 m NE of Cai. Mud with Thalassia, some Halimeda. $\frac{1}{2}$ - $\frac{1}{2}$ m. 11 Sept. 1967. P. Wagenaar Hummelinck. NDW
27. Bonaire. Lac, W part of basin. Inlet S of Fogon; entrance. Muddy sand with Thalassia and Avrainvillea. $\frac{1}{2}$ - $\frac{3}{4}$ m. P. Wagenaar Hummelinck. 5 Sept. 1967. P. Wagenaar Hummelinck. Alc. NDW
28. Bonaire. Lac, W part of basin. Punta di Rancho, 500 m E of Boca Pedro. Sand on Limestone, with Thalassia and Halimeda; 0 - $\frac{1}{2}$ m. 18 Sept. 1967. P. Wagenaar Hummelinck. Alc. NDW
29. Bonaire. Lac, central part of basin, 300 m E of Palu Calbas. Sandy bottom with Thalassia, Syringodium, Halimeda, Tripterygion and Oreaster. 2 m. 11 Sept. 1967. P. Wagenaar Hummelinck. Alc. NDW
30. Bonaire. Lac, entrance of Puito, 300 m NE of Cai. Mud with Thalassia and Halimeda. 1/10 - $\frac{1}{2}$ m. 11 Sept. 1967. P. Wagenaar Hummelinck. Alc. NDW
31. Bonaire. Lac, NE Puito. Mud with Rhizophora, numerous Codakia. Cassiopea. 0 - $\frac{1}{2}$ m. 10 Sept. 1967. P. Wagenaar Hummelinck. Alc. NDW
32. Bonaire. Lac, NE part of basin, Puito. On Rhizophora in mud with Thalassia. 0 - 1 m. 17 April 1955. P. Wagenaar Hummelinck. Alc. NDW
33. Bonaire. Lac, NE part of basin, Puito. Mud with Thalassia, on Rhizophora and Avicennia. 1 m. 25 Feb. 1949. P. Wagenaar Hummelinck. NDW
34. Jamaica. Small Boat Channel, E of Port Royal. Rhizophora in mud, muddy sand with Halodule; 0 - 1 m. 7 May 1973. P. Wagenaar Hummelinck. NDW
40. Bonaire. Salinja Foensjje, seepage at wall of coral rubble; turbid water. 95 g Cl⁻/l. 18 March 1970. P. Wagenaar Hummelinck. NDW
43. Curaçao. Fuik Baai. W Part. Rock and mud with Rhizophora; 0 - 1 m. 17 April 1949. P. Wagenaar Hummelinck. Alc. NDW
44. Bonaire. Lac, muddy, with Thalassia and Halimeda. $\frac{1}{2}$ - 1 m. 16 Sept. 1967. P. Wagenaar Hummelinck. Alc. NDW
46. Bonaire. Lac, S part of basin. Muddy sand with Thalassia and Halimeda. $\frac{1}{2}$ - 1 m. 10 March 1970. P. Wagenaar Hummelinck. NDW
50. Bonaire. Lac, S of Puito. Thalassia-flat on sandy mud with Codakia. Rhizophora with Chthamalus, Cassiopea. 0 - $\frac{1}{2}$ m. 10 Aug. 1967. P. Wagenaar Hummelinck. NDW
52. Bonaire. Lac, NE part of basin, Puito. On Rhizophora in mud with Thalassia. 0 - 1 m. 17 Sept. 1948. P. Wagenaar Hummelinck. Alc. NDW
53. Bonaire. Lac, entrance, near E point of Cai. Sandflat with Thalassia. 1 $\frac{1}{2}$ - 2 m. 17 Nov. 1948. P. Wagenaar Hummelinck. Alc. NDW
56. Tortuga. Sandy reef with Acropora cervicornis. 3 - 4 m. 1 Aug. 1936. P. Wagenaar Hummelinck. NDW
58. Mexico. Quintana Roo; Ascension Bay. Along shore near Suliman Pt. On Rocks in littoral. 17 April 1960. W.L. Schmitt et al. USNM
59. Mexico. Quintana Roo; behind central part of Niccehabin Reef. 16 April 1960. W.L. Schmitt et al. USNM

60. Mexico. Quintana Roo; S and Cozumel Island. N of Pta. Santa Maria. On shore.
22 April 1960. E.L. Bousfield. USNM
61. Mexico. Quintana Roo. Allen Pt., Ascension Bay. 13 April 1960. W.L. Schmitt. USNM

Remaining specimens (Restgroup)

From the Philippines two juvenile specimens are available which are allocated to the Texel-group with a probability of 0.60 and 0.62 and to the Curaçao-group for $P = 0.36$ and 0.38 respectively. More information is necessary.

Material

64. Philippines. (05°05'N, 119°58'E). 23 Sept. 1967. E.G. Menez. USNM
65. Philippines. Pangasinan, Cangaluyan Island (16°22'N, 120°00'). 4 Sept. 1967.
E.G. Menez. USNM

Leptosomatum sachalinense Platonova, 1978

Measurements of *L. sachalinense* and *L. diversum* specimens have been made available by Dr. T.A. Platonova. In Table 12 the slide numbers are marked with -s to indicate specimens originally assigned to *L. sachalinense* and -d to indicate the type-material of *L. diversum*.

Table 12. Measurements *L. sachalinense* Platonova, 1978 and *L. diversum* Platonova, 1978

| S | SN | L µm | DL µm | DNR µm | PL µm | CL µm | AW µm | LCC µm | LD µm |
|---|--------|---------|----------|-----------|----------|----------|----------|-----------|----------|
| M | 8013-s | 6200 | 97 | 299 | 880 | 121 | 93 | - | 6.5 |
| M | 8016-d | 6650 | 85 | 295 | 896 | 97 | 94 | - | 8.0 |
| F | 8619-s | 6750 | 71 | 279 | 945 | 89 | 97 | 6.5 | 5.0 |
| M | 8614-d | 7300 | 85 | 311 | 1043 | 90 | 97 | - | 6.5 |
| F | 8617-s | 7500 | 74 | 275 | 1010 | 95 | 90 | 6.5 | 8.0 |
| F | 8018-s | 7700 | 68 | 279 | 912 | 93 | 101 | 8.0 | 6.5 |
| M | 8613-d | 8250 | 97 | 324 | 1026 | 121 | 94 | - | 6.5 |
| F | 8618-s | 8300 | 74 | 303 | 1141 | 109 | 93 | 6.5 | 5.0 |
| M | 8012-s | 8400 | 105 | 326 | 1059 | 118 | 100 | - | 5.0 |
| M | 8017-s | 10400 | 102 | 380 | 1532 | 113 | 102 | - | 6.5 |

Bongers (1983) synonymized *L. sachalinense* and *L. diversum* both described by Platonova (1978). Average log ratio's and S.E. of the females combined are presented in Table 13; and log ratio's of males in Table 14. Females of *L. sachalinense* (syn. *L. diversum*) can be distinguished from those of the Bonaire-group by the distance from anterior end to the lens-like body (DL), by their caudal length (CL) and length of the cephalic capsule (LCC); from the Macquarie-group, *L. clavatum*, by the distance to the lens-like body and length of the cephalic capsule; from the Curaçao-group, *L. acephalatum*, by the distance from anterior and to the lens-like body. The extreme high anal width may be caused by flattening.

Table 13. Mean log ratio's and S.E. of *L. sachalinense* females.

| Var. | mean | S.E. |
|-------------------|--------|-------|
| LR _{dl} | -0.093 | 0.043 |
| LR _{dnr} | 0.035 | 0.031 |
| LR _{pl} | -0.124 | 0.075 |
| LR _{cl} | 0.211 | 0.065 |
| LR _{aw} | 0.489 | 0.074 |
| LB _{lcc} | -0.001 | 0.103 |
| LR _{ld} | 0.105 | 0.275 |

Presence and distinction of males.

Males occur together with juveniles and females of the Texel- and Curaçao-group. In one case a male specimen has been found in a mixed sample containing one specimen of the Bonaire-group whereas the remaining juveniles and females belonged to the Curaçao-group (Sample 09). The males have been assigned to that species where most specimens belong to i.c.

L. acephalatum.

In Table 14 mean log ratio's and S.E. are given of males originating from the Netherlands (*L. bacillatum*), Ireland (*L. bacillatum*), Caribbean (*L. acephalatum*) and type-material of *L. sachalinense* of which the measurements were kindly made available by Dr. T.A. Platonova.

Table 14; log ratio's males and S.E.

| Var. | <u><i>L. bacillatum</i></u> S.2,4-7;n=19 | | <u><i>L. bacillatum</i></u> S.68 n=6 | | <u><i>L. acephalatum</i></u> S.8-10,27,30;n=8 | | <u><i>L. sachalinense</i></u> types; n=8 | |
|-------------------|---|-------|---|-------|--|-------|---|-------|
| | mean | S.E. | mean | S.E. | mean | S.E. | mean | S.E. |
| LR _{dl} | 0.049 | 0.077 | 0.163 | 0.032 | 0.236 | 0.136 | 0.178 | 0.074 |
| LR _{dnr} | 0.091 | 0.093 | 0.132 | 0.067 | 0.192 | 0.040 | 0.150 | 0.033 |
| LR _{pl} | 0.030 | 0.076 | 0.018 | 0.077 | -0.088 | 0.056 | -0.087 | 0.103 |
| LR _{cl} | 0.086 | 0.081 | 0.078 | 0.035 | 0.181 | 0.058 | 0.330 | 0.125 |
| LR _{pw} | -0.130 | 0.130 | -0.267 | 0.048 | -0.072 | 0.114 | . | . |
| LR _{aw} | 0.053 | 0.115 | -0.022 | 0.039 | 0.048 | 0.086 | 0.490 | 0.069 |
| LR _{ld} | 0.179 | 0.113 | 0.318 | 0.122 | 0.512 | 0.177 | 0.193 | 0.202 |

According to Table 14 these males, the types of *L. sachalinense*, can easily be distinguished by their anal body width and to a lesser degree by their caudal length. It is not known to what degree the caudal length is also influenced by flattening. Males from Galway resemble the females from that site in being slenderer than *L. bacillatum* from the Netherlands. Slight differences in spicule length exist. For the Dutch populations the average length is $85,4 \pm 4,7$; for the Irish $95,7 \pm 6,2$ and *L. acephalum* $81,1 \pm 7,1$.

The first three groups have been separated in a discriminant analysis. After 7 steps 90,9% (jackknifed) of the males are allocated correctly by the classification functions given in Table 15. Male 76108 (sample 09, *L. acephalum*) is incorrectly allocated to *L. bacillatum* (Neth.) with $P = 0.57$ whereas male Ga-12 from Galway is allocated to the Dutch group ($P = 0.53$). The most important diagnostic characters are respectively the log ratios of LD, CL, PW, PL, and DNR.

Table 15; Classification functions males after 7 steps.

| Var. | <u>L. bacill. Neth.</u> | <u>L. bacill. Ireland</u> | <u>L. acephalum</u> |
|-------------------|-------------------------|---------------------------|---------------------|
| LR _{dl} | 8.2 | 24.6 | 10.7 |
| LR _{dnr} | 10.7 | 23.5 | 37.7 |
| LR _{pl} | - 0.4 | - 4.3 | -38.0 |
| LR _{cl} | 4.8 | - 3.6 | 44.3 |
| LR _{pw} | -27.4 | -48.1 | -11.4 |
| LR _{aw} | 22.6 | 28.8 | - 4.5 |
| LR _{ld} | 12.4 | 17.8 | 35.9 |
| Const. | - 4.9 | -14.0 | -21.5 |

Although males are present in *L. bacillatum* and *L. acephalum* only 10 and 30% of the adult females respectively carries sperms; although males are absent in *L. clavatum* more than 50% of the females carries sperms. Females from the Bonaire-group had been fertilized for more than 80% and no male is present in any of the samples. Possibly males are only periodically present but as samples have been taken regularly, with the exception of February, June and December, the absence of males in the Bonaire-group remains surprising. It is possible that these males only live a few days in which they copulate and subsequently die.

An example of the use of log ratio's and classification functions.

To show the advantage of the approach presented here, consider the data given in Table 16. In sample 15 (England) a male (76101) is present, which according to the body measurements given in the traditional way, falls within the ranges of the Dutch group; the distance to the lens-like body is shorter than the comparable dimension in the Irish sample but this might be caused by the slightly smaller body length. The pharynx is slightly longer than in *L. acephalatum*. To which population should this specimen be assigned?

Table 16. Ranges measurements males of *L. bacillatum*, Dutch and Irish samples, and *L. acephalatum*; measurements male 76101 (sample 15) and accessory log ratio's.

| Var. | <i>L. bacillatum</i> Neth. n = 19 µm | <i>L. bacillatum</i> Ireland n = 6 µm | <i>L. acephalatum</i> n = 8 µm | 76101 µm | Log ratio's 76101 |
|------|--|---|--------------------------------------|-------------|----------------------|
| L | 6430 - 10370 | 8890 - 11770 | 6490 - 10650 | 8720 | |
| DL | 75 - 89 | 94 - 111 | 75 - 126 | 82 | -0.010 |
| DNR | 245 - 345 | 304 - 383 | 291 - 394 | 324 | 0.117 |
| PL | 1057 - 1417 | 1272 - 1460 | 924 - 1324 | 1342 | 0.083 |
| CL | 78 - 101 | 86 - 96 | 90 - 104 | 93 | 0.132 |
| PW | 67 - 102 | 71 - 96 | 72 - 100 | 76 | -0.247 |
| AW | 53 - 75 | 62 - 75 | 57 - 73 | 69 | 0.092 |
| LD | 5.0 - 8.0 | 6.0 - 8.5 | 6.5 - 12.5 | 6.5 | 0.164 |

The log ratio's of 76101, given in the last column of Table 16, have been calculated using Table 1. This vector written as $(-0.010, 0.117, \dots, 0.164)'$ is multiplied by the classification vectors given in Table 15 $(8.2, \dots, 12.4)'$, $(24.6, \dots, 17.8)'$ and $(10.7, \dots, 35.9)'$ and subsequently constants are subtracted in this case. This results in the values 7.73, 5.10 and -1.13 which means that the probabilities that 76101 has to be allocated to one of these groups are in the proportion of $e^{7.73}$ to $e^{5.10}$ to $e^{-1.13}$ and converted 2289.90 to 163.66 to 0.32. So the probability P that 76101 belongs to the same group as the Dutch *L. bacillatum* is 0.93, to the Irish sample P = 0.07 and to *L. acephalatum* P = 0.00 although the priori probabilities were 0.58, 0.18 and 0.24 respectively.

The *Leptosomatum bacillatum*-complex, showing a cosmopolitan distribution, comprises some species that can hardly be distinguished in the traditional way, due to their allometric growth. The use of relative measurements permits characterization of populations although high variability necessitates the availability of a series of specimens. Therefore, I recommend that new species be described only if enough material is at hand and to give measurements for each of the specimens separately because of the possibility to involve the data in subsequent studies and to make a separation into two or more species possible without the material being at hand.

The osmotic value of the fixative and way of mounting may play a bigger role in the variability of body-measurements than generally assumed, and a study of these artifacts is recommended. Because I am not sufficiently familiar with the variability and geographic range of these populations. I have restrained from describing subspecies, which may be considered in some cases (e.g. sample 67 (Malta) and 68 (Ireland) distinguishable from *L. bacillatum*, sample 13 (Curaçao) and 27 (Bonaire) from *L. acephalum* and sample 36 (New Zealand) distinguishable from *L. clavatum*) Attempts will be made in collecting additional material from these localities.

A discussion regarding the distribution of the species of the *Leptosomatum bacillatum*-complex is highly speculative due to the restricted geographical range of which samples are available and limited number of specimens in that samples. Previous records of the nominal species have to be allocated, retrospectively, to those species with which they share their geographical range because diagnostic characters were unknown in the past. Only in those cases where body-dimensions are given, can specimens be allocated to one of the species of the complex.

Steiner (1921) described a juvenile from Tortugas characterized by a tail resembling *L. elongatum* var. *sabangense* Steiner, 1915. This juvenile, 3,236 mm long, has a ratio 'c' of 44,0 and the tail length can be calculated as 73,5 μ m. Calculation of the Log ratio for the tail length, for which Table 1. is used, results in 0,20 so that this specimen has to be allocated to the Curaçao-group (Table 11.) which represents *L. acephalum*.

In some cases study of the original material might solve the problem. By courtesy of Prof. De Coninck, at present studying Allgén's material from the Swedish Antarctic Expedition, I have been able to restudy the material from the Falkland Islands identified by Allgén (1959) as *L. elongatum*, *L. bacillatum* and *L. sabangense*. This material is in poor condition; his *L. sabangense* (slide 58-10) is probably a juvenile *L. clavatum* as are the juvenile on 58-3, labelled *L. elongatum* and the female on 58-11 labelled the same. The specimens labelled *L. elongatum* numbered 40-19, 49-2, 49-7 and 58-2 belong to the species described in 1958 by Platonova as *L. kerguel-*

lense. Remarkable is the female on 40-19; this female has 54 eggs in the anterior and 48 eggs in the posterior uterus. The specimen on slide 49-1 labelled *L. bacillatum* also belongs to *L. kerguelense*. Slide 3-2 from the Fuegian Archipelago was labelled as containing two female *L. bacillatum* specimens; I have not been able to find any *Leptosomatum* specimens on this slide.

I doubt the correctness of Allgén's *Leptosomatum* identifications with the exception of his *L. bacillatum* from the Mediterranean (Allgén, 1942), which may be judged correct on the basis of locality.

Leptosomatum bacillatum is restricted to the Mediterranean Atlantic Region: the Mediterranean part of the Lusitania Province, Black Sea Province, as well as to the southern part of the Eastern Atlantic Region. According to Briggs (1974) the Boreal-Lusitania border lies at about the western entrance to the English Channel. Although I have examined large sponge samples from Roscoff (Brittany, France) and Arcachon (Bay of Biscay, France) I have not found any *Leptosomatum* nor are records known from the area south of this Boreal-Lusitania border. In fact no records are known from the Atlantic coast of Lusitania.

Leptosomatum clavatum Platonova, 1958 is restricted to the Sub Antarctic Region, which according to Briggs (1974), is affected by the West Wind Drift throughout the year that acts as an important dispersal agent. The surface temperatures are low and show only a minor amount of seasonal fluctuation (about 2°C. in winter, to 5°C. in summer).

The type-locality of *L. clavatum* is Kerguelen Island where they have been found at a dept of 50 m. Bongers (1983) described specimens from Macquarie Isl. and the Burdwood Bank. In this paper a new record off New Zealand is added of which the specimens differ only slightly from those of the type-locality. The specimens from the Swedish Antarctic Expedition collected from Falkland Islands hardly contribute to the knowledge of this species because of their poor condition.

At least two species of the *L. bacillatum*-complex occur in the tropical Western Atlantic: in the Caribbean and West Indian Provinces and the Carolina region. The northern boundary for the Carolina Region on the east coast of the United States, Cape Hatteras, is also the dividing line between the warm-temperate and tropical marine fauna's (Briggs, 1974). The type-locality of *Leptosomatum acephalatum* (Shackleford's Banks, North Carolina) is situated on this border, and with records of *L. acephalatum* being known only from the south of this boundary, I expect that for *L. acephalatum* North Carolina is the most northern region. Therefore I do not expect this species in the Western Atlantic Boreal Region. Although this region has been sampled well no records of *Leptosomatum* specimens are known: I have examined some sponge samples from Nova Scotia, but could not find any *Leptosomatum*.

The distribution of the species, which I call the Bonaire-group, depends on the identity of this species; if identical to the Indonesian *L. sundaense* or *L. sabangense* it might appear to have a pantropical distribution. If the

Bonaire-group represents a new species, it might be restricted to the tropical Western Atlantic.

The distribution of the species in the Caribbean shows a mosaic pattern; specimens of the Bonaire-group and *L. acephalatum* occur in the same sample and as the Caribbean problems of island biogeography and biotic migration routes are particularly complex, according to Hayden and Dolan (1976), more material is necessary for an analysis of the distribution pattern in this area.

Leptosomatum sachalinense is only known from the type-locality (South Sakhalin) in the Western Pacific Boreal Region.

Although *Leptosomatum* specimens are able to swim for a short period (Bongers, 1983a) dispersal seems to be a passive process; e.g. Steiner (1921) described *L. elongatum* var. *sabangense* from floating *Sargassum*. *Leptosomatum* is easily dispersed by adhering with their caudal glands to floating algae and other debris. As parthenogenetic reproduction is probably possible new populations are easily established.

SUMMARY

The *L. bacillatum*-complex, of which the species can hardly be distinguished from one another, has a cosmopolitan distribution. Allometric and adult growth, resulting in overlapping length measurements, prevent accurate comparisons of species of this complex.

Length and width measurements of the various body parts relate logarithmically. Regression coefficients of comparable data in different species are nearly identical; this opens the possibility of characterizing species by their log ratio's with respect to a reference sample. A cluster analysis followed by a discriminant analysis of about 300 female and juvenile specimens, belonging to 69 samples, gave good results. Classification functions are presented to identify females and juveniles. The best diagnostic characters to distinguish females and juveniles of the different species is the tail length and to a lesser degree the width at the level of the pharynx base, the distance to the lens-like body and width of the cephalic capsule. The diameter of the lens-like body, due to its variability, and anal body width hardly give information.

Males are only known for *L. bacillatum*, *L. acephalatum* and *L. sachalinense*. A discriminant analysis performed to distinguish two groups of *L. bacillatum* and *L. acephalatum* emphasized the diameter of the lens-like body and caudal length as the most important diagnostic characters.

The distribution of the species is discussed. New records are presented for *L. bacillatum*, *L. clavatum*, *L. acephalatum* and a species designed for the moment as the 'Bonaire-group'. Additional measurements are given of the type-material of *L. sachalinense*.

There is a strong negative correlation between the presence of males and fertilized females.

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Appendix; numerical data.

Abbr.: S, stage or Sex, J(uvenile), M(ale) and F(emale); SN, slide number; L, length; DL, distance anterior end to lens-like body; DNR, distance anterior end to nerve ring; PL, pharynx length; CL, caudal length; PW, body width at level of pharynx base; AW, anal body width; LCC, length cephalic capsule; LD, diameter lens-like body; WCC, width cephalic capsule; C, coelomocytes present; S, sperms present in female; G, gravid; P, pigment present in ocelli; R, renette developed.

| Sample | S | SN | L | DL | DNR | PL | CL | PW | AW | LCC | LD | WCC | Remarks. |
|-------------------------------------|---|------|------|----|-----|------|----|-----|----|-----|-----|------|----------|
| | | | µm | µm | µm | µm | µm | µm | µm | µm | µm | µm | |
| <u>L. bacillatum</u> (Eberth, 1863) | | | | | | | | | | | | | |
| (02) | J | 3208 | 2190 | 56 | 174 | 408 | 52 | 40 | 29 | 4.0 | 3.5 | 13.0 | |
| | J | 3207 | 2210 | 49 | 171 | 500 | 62 | 37 | 28 | 3.5 | 3.5 | 12.5 | |
| | J | 3206 | 2590 | 52 | 181 | 575 | 55 | 38 | 29 | 6.0 | 3.0 | 14.5 | |
| | J | 3177 | 3840 | 62 | 203 | 760 | 61 | 55 | 40 | 5.0 | 3.5 | 15.5 | |
| | J | 3216 | 4730 | 65 | 225 | 908 | 69 | 67 | 44 | 6.0 | 4.0 | 21.5 | |
| | J | 3215 | 4820 | 60 | 220 | 871 | 62 | 63 | 41 | 5.0 | 3.5 | 19.0 | |
| | J | 3128 | 4900 | 64 | 218 | 945 | 62 | 57 | 40 | 6.0 | 3.5 | 19.5 | |
| | J | 3127 | 4960 | 77 | 275 | 918 | 67 | 71 | 51 | 7.0 | 4.5 | . | |
| | J | 3168 | 5020 | 69 | 229 | 964 | 59 | 59 | 43 | 6.5 | 5.0 | 21.0 | C |
| | J | 3169 | 5060 | 64 | 223 | 945 | 65 | 75 | 51 | 6.0 | 5.5 | . | C |
| | J | 3176 | 5080 | 66 | 220 | 871 | 73 | 67 | 52 | 7.0 | 4.0 | . | |
| | J | 3171 | 5560 | 75 | 239 | 945 | 85 | 73 | 52 | 7.0 | 5.0 | . | C |
| | J | 3170 | 5630 | 71 | 258 | 964 | 69 | 70 | 51 | 6.5 | 6.0 | 23.0 | C |
| | J | 3175 | 5880 | 62 | 241 | 834 | 75 | 69 | 50 | 6.0 | 4.0 | 22.5 | |
| | J | 3167 | 6380 | 69 | 256 | 1057 | 62 | 69 | 50 | 6.0 | 6.0 | 23.0 | C |
| | M | 3108 | 6430 | 84 | 316 | 1242 | 89 | 89 | 66 | - | 5.5 | - | C |
| | J | 3117 | 6690 | 79 | 260 | 1057 | 77 | 77 | 52 | 6.5 | 4.5 | 23.0 | C |
| | F | 3074 | 7480 | 74 | 286 | 1112 | 86 | 99 | 66 | 8.5 | 6.0 | 27.5 | C,R |
| | J | 3119 | 7580 | 79 | 275 | 1205 | 81 | 100 | 66 | 7.0 | 6.0 | . | C |
| | F | 3158 | 7790 | 78 | 297 | 1177 | 78 | 87 | 61 | 7.0 | 5.5 | 27.0 | C |
| | J | 3116 | 8040 | 81 | 275 | 1175 | 75 | 95 | 66 | 7.0 | 5.5 | . | C |
| | M | 3106 | 8040 | 88 | 302 | 1057 | 81 | 81 | 65 | - | 7.0 | - | C |
| | J | 3154 | 8120 | 79 | 272 | 1297 | 81 | 101 | 69 | 6.5 | 5.0 | . | |
| | F | 3151 | 8160 | 79 | 291 | 1280 | 82 | 87 | 60 | 7.0 | 5.5 | 25.0 | C |
| | J | 3115 | 8470 | 78 | 284 | 1186 | 77 | 97 | 69 | 7.5 | 6.0 | . | C |
| | M | 3056 | 8750 | 89 | 310 | 1196 | 86 | 90 | 70 | - | 6.5 | - | C |
| | F | 3088 | 9090 | 97 | 315 | 1335 | 86 | 108 | 64 | 7.5 | 6.5 | 28.5 | C,R |
| | J | 3089 | 9150 | 83 | 297 | 1242 | 67 | 104 | 69 | 7.5 | 6.0 | 25.0 | C,R |
| | F | 3121 | 9210 | 90 | 320 | 1409 | 94 | 98 | 63 | 7.5 | 6.0 | 29.0 | C,R |
| | J | 3152 | 9320 | 96 | 312 | 1233 | 81 | 103 | 67 | 6.0 | 4.0 | . | C,R |

| Sample | S | SN | L | DL | DNR | PL | CL | PW | AW | LCC | LD | WCC | Remarks. |
|------------|---|-------|-------|-----|-----|------|-----|-----|----|-----|-----|------|----------|
| | | | μm | μm | μm | μm | μm | μm | μm | μm | μm | μm | |
| (02) Cont. | F | 3098 | 9340 | 87 | 289 | 1223 | 99 | 99 | 59 | 7.0 | 5.0 | 23.5 | C,R |
| | J | 3153 | 9420 | 87 | 302 | 1260 | 83 | 100 | 73 | 7.0 | 6.0 | 25.0 | C |
| | F | 3090 | 9480 | 96 | 269 | 1372 | 82 | 106 | 69 | 6.5 | 6.0 | 28.5 | C,S |
| | F | 3095 | 9490 | 81 | 302 | 1335 | 87 | 98 | 63 | 7.0 | 6.5 | 27.0 | C,R |
| | J | 3092 | 9600 | 77 | 287 | 1330 | 73 | 95 | 67 | 6.0 | 5.5 | 25.0 | C |
| | F | 3093 | 9730 | 92 | 320 | 1427 | 96 | 112 | 62 | 8.0 | 6.0 | 23.5 | C,R |
| | F | 3110 | 9790 | 85 | 287 | 1316 | 83 | 98 | 69 | 7.0 | 5.0 | 28.5 | C,S,R |
| | F | 3132 | 9920 | 78 | 278 | 1242 | 78 | 106 | 69 | 8.0 | 7.5 | 27.0 | C |
| | F | 3004 | 10020 | 88 | 305 | 1398 | 87 | 128 | 69 | 7.5 | 5.5 | 26.0 | C,S |
| | F | 3109 | 10110 | 98 | 304 | 1362 | 85 | 106 | 67 | 8.5 | 5.0 | 29.0 | C,R |
| | F | 3010 | 10670 | 94 | 310 | 1390 | 87 | 123 | 69 | 7.5 | 7.0 | 29.0 | C,G |
| | F | 3094 | 10690 | 93 | 318 | 1427 | 88 | 104 | 62 | 7.5 | 5.5 | 29.0 | C |
| | F | 3097 | 10790 | 83 | 304 | 1372 | 85 | 105 | 64 | 8.0 | 5.5 | 26.5 | C |
| | F | 3006 | 10910 | 92 | 320 | 1411 | 85 | 108 | 62 | 8.0 | 7.5 | 27.5 | C,R |
| | F | 3096 | 10960 | 79 | 310 | 1390 | 92 | 104 | 67 | 8.0 | 4.0 | 27.0 | C,R |
| | F | 3101 | 11130 | 92 | 314 | 1335 | 78 | 124 | 70 | 8.5 | 6.0 | 25.5 | C |
| | F | 3133 | 11400 | 79 | 289 | 1390 | 85 | 125 | 76 | 7.5 | 7.5 | 27.0 | C,R |
| | F | 3046 | 11780 | 92 | 330 | 1483 | 101 | 132 | 72 | 8.5 | 5.5 | 29.0 | C |
| | F | 3011 | 12630 | 94 | 306 | 1442 | 94 | 135 | 72 | 8.0 | 5.0 | 29.0 | C,G |
| | F | 3014 | 13570 | 91 | 326 | 1446 | 82 | 124 | 73 | 8.5 | 4.5 | 28.0 | C,R |
| (04) | F | 2152 | 6270 | 82 | 288 | 1123 | 81 | 81 | 58 | 6.5 | . | 23.0 | C |
| | F | 2165 | 7040 | 89 | 283 | 1251 | 89 | 100 | 62 | 6.5 | 7.5 | 27.5 | C |
| | M | 2037 | 7550 | 90 | 333 | 1192 | 93 | 83 | 65 | - | 6.0 | - | C,P |
| | F | 2162 | 7570 | 78 | 331 | 1281 | 81 | 86 | 61 | 8.5 | 6.5 | 27.0 | C |
| | M | 2008 | 7870 | 82 | 330 | 1138 | 101 | 73 | 67 | - | 6.0 | - | C,P |
| | M | 2047 | 8050 | 82 | 321 | 1288 | 87 | 79 | 75 | - | 6.5 | - | C |
| | M | 2026 | 8330 | 78 | 327 | 1225 | 89 | 86 | 73 | - | 7.5 | - | C,P |
| | M | 2077 | 9060 | 79 | 345 | 1417 | 93 | 73 | 68 | - | 6.0 | - | C |
| | F | 2018 | 9160 | 87 | 311 | 1254 | 84 | 109 | 64 | 8.5 | 6.5 | 32.0 | C,S |
| | F | 2064 | 10440 | 101 | 322 | 1336 | 98 | 106 | 72 | 8.5 | 6.5 | 26.5 | C,R |
| (05) | J | 1012c | 1370 | 47 | 149 | 407 | 52 | 25 | 22 | 3.0 | 2.5 | 12.0 | |
| | J | 1011b | 3850 | 74 | 219 | 773 | 72 | 77 | 47 | 7.5 | 4.0 | . | |
| | J | 1061 | 4260 | 63 | 227 | 896 | 66 | 53 | 36 | 6.0 | 4.5 | 20.5 | C |
| | J | 1003a | 5330 | 70 | 247 | 952 | 74 | 83 | 47 | 7.5 | 5.5 | 23.5 | C |
| | J | 1010b | 6690 | 78 | 277 | 1062 | 66 | 102 | 62 | 7.0 | 6.0 | 22.5 | C |
| | M | 1004 | 7080 | 90 | 288 | 1155 | 81 | 90 | 66 | - | 8.0 | - | C |
| | M | 1006 | 7770 | 89 | 312 | 1195 | 80 | 94 | 66 | - | 7.0 | - | C,P |
| | M | 1035 | 8040 | 86 | 335 | 1378 | 86 | 77 | 64 | - | 7.0 | - | C |
| | M | 1033 | 8920 | 95 | 336 | 1336 | 78 | 102 | 63 | - | 6.5 | - | C |
| | F | 1009 | 9350 | 78 | 274 | 1148 | 78 | 103 | 64 | 7.0 | 7.5 | 27.0 | C |
| (06) | J | 1082a | 2470 | 50 | 199 | 669 | 58 | 38 | 30 | 4.0 | 2.5 | 15.0 | |
| | J | 1082c | 2730 | 55 | 172 | 567 | 64 | 47 | 28 | 4.5 | 5.0 | 14.0 | |
| | J | 1084a | 3140 | 61 | 200 | 709 | 63 | 56 | 39 | 6.0 | 3.5 | 18.5 | |
| | J | 1054 | 5340 | 81 | 292 | 1115 | 74 | 64 | 47 | 6.0 | 4.5 | 21.0 | C |
| | M | 1055 | 7300 | 78 | 269 | 1112 | 78 | 74 | 56 | - | 6.5 | - | |
| | F | 1052 | 7540 | 75 | 271 | 1181 | 81 | 81 | 56 | 7.5 | 4.5 | 26.0 | C |
| | F | 1056 | 8130 | 83 | 283 | 1345 | 88 | 81 | 55 | 8.0 | 5.5 | 27.0 | C |
| | M | 1045 | 9080 | 89 | 245 | 1287 | 84 | 78 | 59 | - | 6.5 | - | C |
| | F | 1050 | 9120 | 78 | 286 | 1378 | 88 | 89 | 58 | 7.5 | 4.5 | 27.0 | C |
| | M | 1049 | 10370 | 75 | 306 | 1378 | 86 | 78 | 56 | - | 7.0 | - | C |
| (07) | J | 1072b | 2960 | 48 | 182 | 730 | 61 | 41 | 28 | 4.5 | 3.0 | 14.5 | |
| | F | 1063b | 6760 | 92 | 303 | 1214 | 77 | 83 | 53 | 7.5 | 6.0 | 26.0 | S |
| | F | 1064a | 7250 | 80 | 311 | 1214 | 80 | 83 | 55 | 8.5 | 4.5 | 23.0 | R |
| | M | 1065 | 7880 | 86 | 297 | 1216 | 96 | 67 | 53 | - | 6.0 | - | C |
| | M | 1073b | 7940 | 84 | 283 | 1118 | 83 | 83 | 66 | - | 6.0 | - | C |

| Sample | S | SN | L | DL | DNR | PL | CL | PW | AW | LCC | LD | WCC | Remarks. |
|------------|---|--------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|----------|
| | | | μm | μm | μm | μm | μm | μm | μm | μm | μm | μm | |
| (07) Cont. | M | 1073c | 8590 | 88 | 296 | 1166 | 86 | 83 | 59 | - | 6.5 | - | |
| | M | 1062 | 8690 | 84 | 324 | 1157 | 99 | 78 | 64 | - | 5.0 | - | |
| | F | 1070 | 8760 | 88 | 327 | 1345 | 86 | 110 | 66 | 8.5 | 7.5 | 26.0 | S |
| | F | 1074 | 10230 | 102 | 333 | 1476 | 91 | 106 | 68 | 7.5 | 6.0 | 29.0 | |
| | F | 1069 | 10870 | 108 | 342 | 1378 | 94 | 114 | 67 | 7.5 | 5.5 | 28.0 | C,R |
| (15) | J | 76103 | 6080 | 85 | 256 | 1023 | 79 | 81 | 57 | 6.0 | 6.0 | 18.5 | C |
| | F | 76105 | 7740 | 116 | 333 | 1442 | 87 | 94 | 67 | 7.5 | 6.0 | 27.0 | C |
| | M | 76101 | 8720 | 82 | 324 | 1342 | 93 | 76 | 69 | - | 6.5 | - | C,P |
| | J | 76104 | 9380 | 85 | 275 | 1167 | 83 | 86 | 61 | 6.5 | 6.0 | 21.0 | C |
| | F | 76102 | 10190 | 91 | 294 | 1305 | 108 | 92 | 66 | 6.5 | 6.5 | 24.5 | C |
| (25) | F | 1286-1 | 7620 | 102 | 288 | 1155 | 89 | 112 | 73 | 9.0 | 8.5 | 28.0 | C,G |
| | F | 1286-2 | 13490 | 109 | 376 | 1741 | 89 | 93 | 64 | 7.5 | 5.0 | 23.0 | C,R |
| | F | 1286-3 | 16890 | 135 | 415 | 1892 | 106 | 96 | 67 | 8.5 | 8.0 | 27.5 | C,P |
| (35) | F | 1277-1 | 7980 | 83 | 284 | 1048 | 79 | 95 | 64 | 7.0 | 4.5 | 21.5 | C |
| | F | 1277-2 | 8570 | 109 | 329 | 1284 | 77 | 96 | 61 | 7.5 | 4.5 | 24.5 | C |
| (37) | F | A-59 | 11560 | 89 | 279 | 1420 | 83 | 116 | 71 | 7.0 | 6.5 | 22.5 | G |
| (57) | F | 5800 | 8430 | 98 | 321 | 1147 | 83 | 123 | 81 | 6.5 | 5.0 | 27.0 | G |
| 66 | F | 3410 | 8310 | 111 | 323 | 1172 | 85 | 93 | 63 | 8.0 | 6.5 | 25.0 | C,G |
| 67 | J | 1578-4 | 2510 | 58 | 185 | 584 | 60 | 48 | 32 | 6.0 | 6.0 | 14.5 | C |
| | J | 1578-5 | 2530 | 61 | 178 | 574 | 56 | 51 | 32 | 7.0 | 5.0 | 15.0 | P |
| | J | 1578-3 | 2640 | 63 | 187 | 589 | 62 | 49 | 33 | 7.5 | 6.0 | 15.0 | C,P |
| | J | 1578-6 | 2870 | 66 | 189 | 636 | 59 | 52 | 35 | 6.5 | 5.0 | 16.0 | C,P |
| | J | 1578-8 | 3120 | 61 | 189 | 620 | 58 | 58 | 36 | 6.5 | 7.5 | 16.5 | C,P |
| | J | 1578-2 | 3210 | 64 | 206 | 682 | 65 | 56 | 37 | 7.5 | 6.0 | 17.5 | C,P |
| | J | 1578-7 | 3970 | 79 | 239 | 806 | 60 | 71 | 44 | 7.0 | 6.5 | 20.5 | C,P |
| | J | 1578-1 | 4110 | 74 | 220 | 790 | 69 | 67 | 43 | 8.0 | 6.0 | 21.0 | C,P |
| | F | 1578-9 | 7440 | 87 | 275 | 1132 | 77 | 110 | 64 | 8.0 | 8.0 | 26.0 | C,P |
| 68 | J | Ga-14 | 3270 | 63 | 216 | 785 | . | 44 | . | 6.0 | 6.0 | 16.5 | P |
| | J | Ga-16 | 5600 | 77 | 260 | 1020 | 73 | 64 | 44 | 5.5 | 7.5 | 21.0 | C,P |
| | J | Ga-20 | 6560 | 89 | 297 | 1272 | 89 | 71 | 51 | 8.0 | . | 23.5 | C,P |
| | J | Ga-03 | 7140 | 98 | 289 | 1311 | 82 | 74 | 53 | 8.5 | 7.5 | 27.0 | C,P |
| | J | Ga-15 | 7180 | 92 | 312 | 1253 | 78 | 76 | 57 | 8.5 | 6.0 | 22.0 | C,P |
| | F | Ga-18 | 7790 | 103 | 347 | 1413 | 86 | 77 | 58 | 6.0 | 7.0 | 25.5 | C,P |
| | J | Ga-07 | 8190 | 89 | 310 | 1248 | 94 | 80 | 59 | 6.5 | 6.0 | 23.0 | C,P |
| | J | Ga-19 | 8370 | 87 | 297 | 1381 | 80 | 85 | 55 | 6.0 | 6.0 | 21.5 | C,P |
| | J | Ga-09 | 8530 | 90 | 293 | 1397 | 94 | 82 | 54 | 6.5 | 6.0 | 25.0 | C,P |
| | M | Ga-12 | 8890 | 94 | 304 | 1272 | 89 | 71 | 62 | - | 6.0 | - | C,P |
| | J | Ga-17 | 8990 | 85 | 291 | 1311 | 92 | 90 | . | 7.0 | 6.5 | 25.0 | C,P |
| | M | Ga-11 | 9390 | 100 | 354 | 1460 | 86 | 83 | 62 | - | 8.5 | - | C,P |
| | J | Ga-08 | 9430 | 98 | 314 | 1327 | 87 | 94 | 69 | 7.5 | 5.5 | 24.5 | P |
| | M | Ga-02 | 9540 | 103 | 312 | 1295 | 92 | 81 | 67 | - | 8.5 | - | C,P |
| | M | Ga-01 | 9910 | 105 | 370 | 1418 | 96 | 80 | 66 | - | 8.0 | - | C,P |
| | F | Ga-06 | 10030 | 107 | 383 | 1648 | 95 | 87 | 64 | . | 8.5 | . | C,P |
| | M | Ga-13 | 10420 | 100 | 351 | 1421 | 94 | 81 | 64 | - | 8.5 | - | C,P |
| | F | Ga-04 | 10890 | 101 | 362 | 1672 | 94 | 85 | 62 | 8.5 | 5.0 | 29.0 | C,P |
| | F | Ga-05 | 11020 | 100 | 356 | 1633 | 81 | 99 | 68 | 7.0 | 6.0 | 25.5 | C,S,P |
| | M | Ga-10 | 11770 | 111 | 383 | 1319 | 94 | 96 | 75 | - | 8.5 | - | C,P |

| Sample | S | SN | L | DL | DNR | PL | CL | PW | AW | LCC | LD | WCC | Remarks. |
|-------------------------------------|---|----------|-------|-----|-----|------|-----|-----|-----|------|-----|------|----------|
| | | | µm | µm | µm | µm | µm | µm | µm | µm | µm | µm | |
| <u>L. clavatum</u> Platonova, 1958 | | | | | | | | | | | | | |
| (03) | J | 76078 | 6050 | 106 | 337 | 1115 | 106 | 87 | 73 | 8.0 | 6.0 | . | C |
| | J | 76079 | 6520 | 85 | 271 | 1014 | 94 | 85 | 67 | 7.0 | 6.0 | 22.5 | C |
| | J | 76080 | 8420 | 116 | 370 | 1352 | 128 | 125 | 99 | 9.5 | 7.0 | 29.5 | C,R |
| | F | 76082 | 11050 | 132 | 427 | 1386 | 125 | 119 | 89 | 10.0 | 8.5 | 31.5 | C |
| | F | 76083 | 12120 | 113 | 374 | 1589 | 121 | 102 | 74 | 10.0 | 7.5 | 28.0 | C |
| | F | 76084 | 12510 | 133 | 452 | 1673 | 100 | 125 | 88 | 10.5 | 8.5 | . | C,R |
| | F | 76085 | 12780 | 141 | 419 | 1606 | 142 | 127 | 92 | 10.5 | 8.0 | 33.5 | C,S,G |
| | F | 76086 | 13030 | 146 | 444 | 1741 | 146 | 125 | 94 | 10.5 | 8.0 | 33.5 | C,S,G |
| | F | 76087 | 13490 | 131 | 436 | 1639 | 152 | 146 | 99 | 10.0 | . | 31.0 | C,S,G |
| | F | 76088 | 13960 | 121 | 374 | 1758 | 142 | 134 | 93 | 11.0 | 8.5 | 33.5 | C,S,G |
| | F | 76089 | 14230 | 150 | 469 | 1656 | 139 | 150 | 92 | 10.0 | 7.5 | 31.5 | C,S,G |
| | F | 76115 | 14470 | 137 | 357 | 1642 | 156 | 148 | 102 | 11.0 | 7.5 | 33.5 | C,S,G |
| | F | 76114 | 15440 | 131 | 449 | 1712 | 150 | 137 | 98 | 10.5 | 9.5 | 30.0 | C,S,G |
| (26) | F | 1596-1 | 8210 | 116 | 349 | 1349 | 104 | 101 | 78 | 8.5 | 8.5 | 28.5 | C |
| | F | 1596-2 | 9750 | 92 | 324 | 1347 | 118 | 106 | 77 | 9.5 | 6.5 | 27.5 | C |
| | F | 1596-3 | 10970 | 122 | 367 | 1590 | 119 | 109 | 87 | 10.0 | 8.5 | 25.5 | C,S,G |
| 36 | F | 370-1 | 9080 | 81 | 306 | 1435 | 110 | 104 | 67 | 9.0 | 5.5 | 26.0 | C,S,G |
| | F | 370-2 | 9730 | 94 | 340 | 1295 | 114 | 94 | 64 | 8.0 | 6.0 | 26.0 | C,S,G |
| (62) | F | 1975-1 | 9200 | 114 | 337 | 1295 | 127 | 103 | 66 | 8.5 | 7.5 | 25.0 | C,G |
| (63) | J | 7369 | 8740 | 108 | 318 | 1271 | 125 | 141 | 89 | 10.5 | 6.5 | 26.0 | R |
| 69 | J | 8878 | 4370 | 79 | 297 | 671 | 82 | 97 | 64 | 6.5 | 6.5 | 23.0 | C |
| <u>Leptosomatum</u> spec. 'Bonaire' | | | | | | | | | | | | | |
| 01 | J | 1062a-39 | 5580 | 79 | 258 | 911 | 110 | 81 | 62 | 9.0 | 5.5 | . | C |
| | J | 1062a-48 | 6910 | 77 | 248 | 924 | 125 | 90 | 63 | 10.5 | 6.0 | 28.0 | C |
| | J | 1062a-37 | 6920 | 89 | 272 | 976 | 121 | 77 | 60 | 10.0 | 6.0 | 27.5 | C |
| | J | 1062a-09 | 7210 | 92 | 273 | 1066 | 123 | 104 | 71 | 9.5 | 6.0 | . | C |
| | J | 1062a-08 | 7360 | 80 | 278 | 976 | 125 | 79 | 56 | 10.5 | 6.0 | 27.0 | C |
| | J | 1062a-46 | 7500 | 79 | 258 | 1071 | 131 | 98 | 71 | 10.0 | 6.0 | 29.0 | C |
| | J | 1062a-47 | 7520 | 85 | 277 | 1017 | 121 | 87 | 59 | 10.0 | 5.5 | 28.0 | C |
| | J | 1062a-07 | 7560 | 88 | 291 | 1115 | 127 | 100 | 70 | 10.5 | 6.0 | 28.0 | C |
| | F | 1062a-13 | 8300 | 98 | 316 | 1207 | 135 | 102 | 73 | 10.5 | 6.5 | 34.5 | C,R |
| | F | 1062a-20 | 8440 | 96 | 237 | 1046 | 116 | 100 | 71 | 9.5 | 7.5 | 35.5 | C,R |
| | F | 1062a-14 | 8630 | 89 | 285 | 1094 | 136 | 92 | 62 | 11.0 | 6.5 | 33.5 | C,S,R |
| | F | 1062a-12 | 9500 | 96 | 285 | 1213 | 131 | 97 | 67 | 11.0 | 7.0 | 33.5 | C,S |
| | F | 1062a-17 | 9580 | 96 | 304 | 1210 | 141 | 111 | 74 | 10.5 | 6.5 | 36.0 | C,S,R |
| | F | 1062a-31 | 9580 | 92 | 310 | 1202 | 144 | 102 | 72 | 11.5 | 6.0 | 35.0 | C,S,G,R |
| | F | 1062a-22 | 9640 | 83 | 264 | 1202 | 137 | 104 | 68 | 11.5 | 6.0 | 33.5 | C,S,G |
| | F | 1062a-33 | 9960 | 104 | 343 | 1413 | 146 | 92 | 70 | 11.5 | 6.0 | 33.5 | C,S,G |
| | F | 1062a-25 | 10100 | 100 | 281 | 1228 | 150 | 103 | 74 | 12.0 | 6.0 | 35.5 | C,S,G |
| | F | 1062a-03 | 10140 | 98 | 289 | 1188 | 146 | 101 | 73 | 11.0 | 8.0 | 33.5 | C,S,G |
| | F | 1062a-43 | 10260 | 94 | 302 | 1209 | 145 | 107 | 73 | 11.5 | 6.5 | 34.0 | C,S,R |
| | F | 1062a-26 | 10290 | 94 | 308 | 1282 | 140 | 110 | 72 | 11.5 | 7.0 | 34.0 | C,S,G,R |
| | F | 1062a-49 | 10300 | 106 | 310 | 1213 | 141 | 102 | 70 | 10.0 | 8.0 | 33.5 | C,S,G,R |
| | F | 1062a-15 | 10450 | 102 | 329 | 1278 | 146 | 100 | 68 | 10.5 | 7.5 | 33.5 | C,S |
| | F | 1062a-38 | 10500 | 98 | 312 | 1300 | 144 | 112 | 73 | 12.0 | 7.0 | 34.5 | C,S,G,R |
| | F | 1062a-19 | 10700 | 89 | 301 | 1298 | 141 | 109 | 73 | 10.5 | 6.0 | 33.5 | C,S,G |
| | F | 1062a-16 | 10810 | 98 | 289 | 1169 | 129 | 114 | 74 | 11.0 | 6.0 | 35.0 | C,S,G |
| | F | 1062a-45 | 10830 | 85 | 270 | 1268 | 148 | 119 | 73 | . | 6.5 | 34.5 | C,S,G |
| | F | 1062a-21 | 10960 | 105 | 317 | 1261 | 144 | 119 | 79 | 11.5 | 8.0 | 37.5 | C,S,G |

| Sample | S | SN | L | DL | DNR | PL | CL | PW | AW | LCC | LD | WCC | Remarks. |
|------------|---|----------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|-----------|
| | | | μm | μm | μm | μm | μm | μm | μm | μm | μm | μm | |
| (01) Cont. | F | 1062a-05 | 11040 | 101 | 296 | 1269 | 135 | 113 | 74 | 11.5 | 7.0 | 34.0 | C,S,G |
| | F | 1062a-32 | 11060 | 98 | 327 | 1242 | 152 | 112 | 71 | 11.0 | 7.0 | 34.5 | C,S,G |
| | F | 1062a-11 | 11150 | 102 | 285 | 1202 | 144 | 119 | 74 | 11.5 | 7.5 | 36.0 | C,S,G |
| | F | 1062a-29 | 11190 | 101 | 319 | 1273 | 146 | 122 | 79 | 10.5 | 7.5 | 35.5 | C,S,G |
| | F | 1062a-18 | 11200 | 96 | 308 | 1332 | 149 | 112 | 71 | 10.5 | 8.5 | 35.5 | C,S,G |
| | F | 1062a-06 | 11220 | 101 | 286 | 1310 | 133 | 113 | 73 | 12.5 | 8.0 | 35.0 | C,S,G |
| | F | 1062a-36 | 11270 | 98 | 296 | 1276 | 139 | 115 | 79 | 11.5 | 8.5 | 37.5 | C,S,G |
| | F | 1062a-28 | 11360 | 94 | 310 | 1295 | 146 | 114 | 81 | 11.5 | 6.0 | 37.0 | C,S,G |
| | F | 1062a-02 | 11410 | 90 | 304 | 1286 | 148 | 126 | 81 | 11.5 | 6.0 | 38.0 | C,S,G |
| | F | 1062a-44 | 11520 | 96 | 289 | 1290 | 141 | 123 | 76 | 11.0 | 6.0 | 37.5 | C,S,G,R |
| | F | 1062a-23 | 11530 | 114 | 345 | 1330 | 149 | 127 | 83 | 11.0 | 7.0 | 36.5 | C,S,G,R |
| | F | 1062a-41 | 11580 | 104 | 347 | 1371 | 146 | 119 | 77 | 12.5 | 6.5 | 34.5 | C,S,G |
| | F | 1062a-24 | 11620 | 94 | 317 | 1378 | 152 | 116 | 77 | 11.5 | 7.5 | 36.5 | C,S,G |
| | F | 1062a-35 | 11790 | 94 | 302 | 1332 | 145 | 118 | 76 | 11.5 | 7.5 | 35.5 | C,S,G |
| | F | 1062a-27 | 12000 | 104 | 312 | 1339 | 141 | 123 | 81 | 12.0 | 7.0 | 37.5 | C,S,G |
| | F | 1062a-34 | 12130 | 102 | 327 | 1339 | 152 | 124 | 79 | 11.5 | 8.5 | 37.0 | C,S,G |
| | F | 1062a-42 | 12140 | 108 | 322 | 1380 | 148 | 127 | 82 | 11.5 | 7.0 | 37.5 | C,S,G,R |
| | F | 1062a-30 | 12160 | 96 | 314 | 1245 | 152 | 131 | 81 | 11.0 | 6.0 | 37.0 | C,S,G,R |
| | F | 1062a-04 | 12260 | 97 | 297 | 1317 | 140 | 131 | 85 | 12.5 | 6.0 | 38.5 | C,S,G |
| | F | 1062a-50 | 12260 | 102 | 327 | 1387 | 147 | 125 | 80 | 12.0 | 7.0 | 37.5 | C,S,G |
| | F | 1062a-01 | 12940 | 98 | 306 | 1319 | 150 | 129 | 88 | 11.0 | 6.5 | 35.5 | C,S,G |
| | F | 1062a-10 | 13210 | 115 | 335 | 1375 | 151 | 130 | 82 | 11.5 | 7.5 | 37.5 | C,S,G |
| | F | 1062a-40 | 13290 | 100 | 337 | 1343 | 150 | 137 | 83 | 11.5 | 8.5 | 38.0 | C,S,G |
| (09) | F | 76104 | 7200 | 95 | 272 | 997 | 133 | 98 | 68 | 10.0 | 7.0 | 34.5 | C,R |
| 11 | J | 1621-2 | 5130 | 77 | 260 | 957 | 113 | 80 | 50 | 10.0 | 6.0 | 24.5 | C,P |
| | J | 1621-5 | 6610 | 77 | 264 | 974 | 115 | 103 | 72 | 10.0 | 6.0 | 27.5 | C,P |
| | J | 1621-1 | 6750 | 83 | 285 | 1079 | 107 | 99 | 82 | 10.5 | 6.0 | . | C,P |
| | F | 1621-6 | 8280 | 102 | 300 | 1166 | 148 | 100 | 69 | 11.5 | 7.5 | 28.0 | C,S,G,P |
| | F | 1621-8 | 9360 | 102 | 304 | 1183 | 135 | 104 | 71 | 12.5 | 8.5 | 32.5 | C,S,G,P |
| | F | 1621-7 | 9850 | 87 | 287 | 1270 | 141 | 119 | 81 | 11.5 | 9.0 | 32.0 | C,S,G,P |
| | F | 1621-9 | 10460 | 94 | 316 | 1288 | 136 | 112 | 71 | 10.5 | 6.5 | 33.0 | C,S,G,P |
| | F | 1621-3 | 10980 | 110 | 322 | 1235 | 149 | 121 | 90 | 12.5 | 7.5 | 33.5 | C,S,G,P |
| | F | 1621-4 | 11000 | 100 | 310 | 1240 | 140 | 120 | 80 | 11.5 | 7.5 | 34.5 | C,S,G,P |
| 12 | J | 1446-1 | 3600 | 73 | 196 | 738 | 81 | 67 | 49 | 7.5 | 4.0 | . | C,P |
| | J | 1446-2 | 3750 | 60 | 195 | 702 | 94 | 71 | 50 | 7.5 | 5.0 | 19.0 | C,P |
| | J | 1446-6 | 6290 | 83 | 251 | 885 | 121 | 93 | 72 | 9.5 | 6.0 | 27.0 | C,P |
| | F | 1446-5 | 8360 | 87 | 270 | 1058 | 131 | 98 | 69 | 10.5 | 7.5 | 29.0 | C,S,P |
| | F | 1446-3 | 8940 | 94 | 273 | 1091 | 146 | 99 | 71 | 10.5 | 6.0 | 28.0 | C,S,G,P,R |
| | F | 1446-7 | 9050 | 100 | 313 | 1201 | 146 | 104 | 70 | 10.5 | 7.5 | 28.5 | C,S,G,P |
| | F | 1446-4 | 11210 | 79 | 277 | 1206 | 128 | 108 | 78 | 11.5 | 6.0 | 31.5 | C,S,G,P |
| 14 | F | 1671-6 | 10110 | 104 | 322 | 1409 | 146 | 116 | 81 | 12.0 | 7.5 | 35.5 | C,S,G,P |
| | F | 1671-1 | 10120 | 100 | 308 | 1392 | 146 | 123 | 81 | 12.5 | 8.5 | 34.5 | C,S,G,P |
| | F | 1671-4 | 10350 | 110 | 362 | 1444 | 139 | 104 | 71 | 11.5 | 8.5 | 33.5 | C,S,G,P |
| | F | 1671-5 | 10980 | 114 | 360 | 1470 | 135 | 87 | 64 | 12.5 | 8.0 | 32.5 | C,S,G,P |
| | F | 1671-3 | 11170 | 110 | 335 | 1479 | 144 | 127 | 83 | 12.5 | 8.5 | 37.0 | C,S,G,P |
| | F | 1671-2 | 11680 | 102 | 349 | 1444 | 150 | 133 | 83 | 12.5 | 7.0 | 36.5 | C,S,G,P |
| 16 | J | 041-4 | 4850 | 63 | 220 | 805 | 94 | 86 | 59 | 7.5 | 5.5 | . | C |
| | J | 041-1 | 6960 | 104 | 266 | 980 | 125 | 96 | 73 | 8.5 | 6.0 | . | C,R |
| | J | 041-5 | 7120 | 79 | 272 | 1032 | 119 | 107 | 60 | 9.0 | 6.5 | 29.0 | C |
| | F | 041-2 | 7280 | 92 | 285 | 1172 | 127 | 101 | 69 | 10.5 | 6.5 | 31.0 | C,S,R |
| | F | 041-3 | 11370 | 96 | 312 | 1277 | 150 | 139 | 74 | 10.0 | 6.5 | 31.5 | C,S,G,R |

| Sample | S | SN | L | DL | DNR | PL | CL | PW | AW | LCC | LD | WCC | Remarks. |
|--------|---|----------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|-----------|
| | | | μm | μm | μm | μm | μm | μm | μm | μm | μm | μm | |
| 17 | J | 1064a-2 | 3420 | 58 | 181 | 628 | . | 46 | . | 6.0 | 5.0 | 18.5 | C |
| | J | 1064a-3 | 4080 | 60 | 202 | 754 | 92 | 62 | 44 | 6.5 | 5.5 | 17.5 | C |
| | J | 1064a-5 | 5870 | 71 | 242 | 973 | 102 | 83 | 53 | 10.5 | 4.5 | 29.0 | C |
| | F | 1064a-1 | 7600 | 82 | 280 | 1021 | 135 | 103 | 75 | 12.0 | 7.5 | 32.0 | C,G,P |
| | F | 1064a-4 | 9690 | 94 | 277 | 1217 | 135 | 102 | 67 | 11.5 | 6.0 | 33.0 | C,G |
| 18 | J | 1008a-3 | 3490 | 65 | 201 | 738 | 102 | 62 | 43 | 8.5 | 4.0 | 18.5 | C,P |
| | J | 1008a-4 | 4210 | 66 | 241 | 722 | 100 | 58 | 35 | 6.5 | 4.0 | 23.0 | C,P |
| | F | 1008a-2 | 10370 | 98 | 333 | 1358 | 123 | 94 | 67 | 11.5 | 6.0 | 34.0 | C,S,P,R |
| | F | 1008a-1 | 13500 | 100 | 333 | 1415 | 146 | 120 | 75 | 10.5 | 7.5 | 32.0 | C,S,G,P,R |
| 19 | J | 1674-4 | 4560 | 62 | 224 | 823 | 94 | 69 | 50 | 9.0 | 4.5 | 21.0 | C |
| | J | 1674-1 | 6410 | 83 | 266 | 1024 | 110 | 85 | 54 | 10.0 | 6.5 | 27.0 | C |
| | F | 1674-3 | 9970 | 94 | 287 | 1099 | 134 | 108 | 73 | 8.5 | 8.5 | 29.0 | C |
| 20 | J | 1623-3 | 5030 | 83 | 258 | 922 | 110 | 74 | 52 | 8.5 | 6.5 | 25.0 | C,P |
| | F | 1623-2 | 8400 | 104 | 358 | 1375 | 126 | 89 | 60 | 11.5 | 8.5 | 31.0 | C,S,G,P |
| | F | 1623-1 | 9170 | 102 | 316 | 1340 | 133 | 102 | 75 | 9.5 | 7.5 | 35.0 | C,S,P |
| 22 | F | 1575Aa-2 | 10940 | 104 | 354 | 1409 | 147 | 107 | 68 | 10.0 | 8.0 | 30.0 | C,S,G,P |
| 23 | F | 1302-1 | 9960 | 96 | 335 | 1322 | 137 | 84 | 64 | 10.5 | 6.0 | 33.5 | C |
| | F | 1302-2 | 12070 | 94 | 350 | 1523 | 166 | 106 | 84 | 11.5 | 6.0 | 34.0 | C,S,G |
| | F | 1302-3 | 12590 | 106 | 379 | 1680 | 160 | 119 | 79 | 11.0 | 6.5 | 35.5 | C,S,G,R |
| 24 | J | 1449-1 | 7430 | 77 | 254 | 1075 | 114 | 75 | 58 | 8.5 | 7.5 | 25.0 | C,P |
| | F | 1449-2 | 7870 | 104 | 312 | 1201 | 146 | 89 | 80 | 12.5 | 6.0 | 33.0 | C,P |
| | F | 1449-3 | 8190 | . | 229 | 922 | 108 | 85 | 54 | . | . | . | C,P |
| 38 | F | 1708-1 | 11200 | 106 | 331 | 1562 | 135 | 104 | 71 | 13.0 | 8.0 | 33.5 | C,G,P |
| 39 | F | 1623A-1 | 11970 | 104 | 333 | 1288 | 146 | 108 | 83 | 10.5 | 7.5 | 32.0 | C,S,G |
| 41 | F | 1555-1 | 7340 | 75 | 324 | 1148 | 113 | 86 | 66 | 10.0 | 5.0 | 30.5 | C,S,P,R |
| 42 | J | 1036a | 5830 | 77 | 258 | 950 | 119 | 79 | 50 | 10.0 | 5.0 | 29.0 | C |
| 45 | F | 1576-1 | 10260 | 89 | 305 | 1228 | 139 | 113 | 75 | 9.5 | 8.5 | 34.0 | S,G,P,R |
| 47 | F | 1566-1 | 8960 | 98 | 229 | 1366 | 104 | 92 | 65 | 8.5 | 6.0 | 32.0 | C,S,G,P |
| 48 | F | 1565-1 | 11790 | 93 | 301 | 1382 | 131 | 100 | 76 | 10.5 | 6.0 | 31.0 | C,S,G,P |
| 49 | F | 1575-1 | 9770 | 92 | 325 | 1327 | 135 | 94 | 66 | 9.5 | 7.5 | 31.0 | C,G,P |
| 51 | J | 1373-1 | 8070 | 87 | 268 | 1115 | 114 | 92 | 62 | 9.5 | 6.0 | 28.0 | |
| 54 | J | 1064-1 | 6470 | 77 | 248 | 848 | 116 | 92 | 60 | 9.5 | 6.0 | 28.0 | C |

L. acephalum Chitwood, 1936

| | | | | | | | | | | | | | |
|----|---|---------|------|----|-----|-----|----|----|----|-----|-----|------|-----|
| 08 | J | 1577a-3 | 3150 | 60 | 193 | 609 | 69 | 66 | 40 | 5.0 | 5.5 | 14.5 | C |
| | J | 1577a-1 | 3710 | 64 | 241 | 679 | 71 | 74 | 49 | 7.0 | 6.5 | 23.0 | C |
| | J | 1577a-6 | 4460 | 71 | 233 | 731 | 73 | 88 | 52 | 7.0 | 5.5 | 21.0 | C |
| | J | 1577a-2 | 5120 | 83 | 285 | 870 | 71 | 80 | 54 | 7.5 | 7.0 | 21.0 | C |
| | J | 1577a-4 | 5790 | 69 | 268 | 783 | 93 | 88 | 60 | 7.5 | 6.0 | 23.5 | C,P |
| | J | 1577a-5 | 6020 | 92 | 300 | 940 | 77 | 79 | 57 | 8.0 | 7.0 | 21.5 | C,P |
| | J | 1577a-7 | 6040 | 79 | 277 | 922 | 97 | 95 | 63 | 8.5 | 6.5 | 23.5 | C,P |
| | M | 1577a-8 | 6490 | 97 | 291 | 940 | 99 | 75 | 57 | - | 9.5 | - | C,P |

| Sample | S | SN | L | DL | DNR | PL | CL | PW | AW | LCC | LD | WCC | Remarks. |
|--------|---|---------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|----------|
| | | | μm | μm | μm | μm | μm | μm | μm | μm | μm | μm | |
| (09) | J | 76103 | 4700 | 69 | 227 | 779 | 76 | 74 | 52 | 7.5 | 6.0 | 22.5 | C |
| | J | 76105 | 7290 | 101 | 300 | 1070 | 91 | 88 | 81 | 8.5 | 6.0 | 25.0 | C |
| | F | 76077 | 7780 | 97 | 303 | 1088 | 95 | 122 | 76 | 9.5 | 9.0 | 30.0 | C |
| | F | 76106 | 7790 | 108 | 220 | 1178 | 90 | 121 | 69 | 9.5 | 9.0 | 30.0 | C |
| | M | 76107 | 8030 | 75 | 337 | 1132 | 98 | 96 | 73 | - | 8.0 | - | C |
| | M | 76108 | 8430 | 101 | 360 | 1142 | 92 | 90 | 66 | - | 6.5 | - | C |
| | F | 76109 | 8970 | 112 | 316 | 1124 | 96 | 130 | 77 | 8.5 | 8.5 | 29.0 | C,S,G |
| (10) | J | 76092 | 4660 | 86 | 188 | 852 | 77 | 79 | 52 | 9.0 | 6.5 | 24.0 | C |
| | F | 77-60 | 6860 | 89 | 281 | 1032 | 88 | 114 | 61 | 8.0 | 8.5 | 27.5 | C |
| | M | 76093 | 7630 | 106 | 326 | 1051 | 90 | 85 | 60 | - | 9.0 | - | C |
| | F | 76094 | 7790 | 102 | 333 | 1178 | 89 | 130 | 77 | 9.0 | 9.0 | 30.0 | C |
| | M | 76095 | 7810 | 110 | 343 | 924 | 92 | 100 | 67 | - | 8.5 | - | C |
| | F | 76096 | 8090 | 118 | 341 | 1106 | 109 | 123 | 74 | 8.5 | 7.5 | 29.5 | C,S |
| | F | 76097 | 8700 | 87 | 358 | 1250 | 96 | 113 | 74 | 9.5 | 8.5 | 30.5 | C,G |
| | F | 76091 | 9860 | 110 | 343 | 1215 | 91 | 126 | 81 | 7.5 | 9.0 | 27.0 | C,G |
| 13 | J | 1629-4 | 1970 | 57 | 175 | 547 | 61 | 52 | 35 | 6.5 | 4.0 | 19.0 | C |
| | J | 1629-5 | 3900 | 77 | 237 | 864 | 67 | 75 | 50 | 9.0 | 6.0 | 23.0 | C |
| | J | 1629-6 | 4360 | 85 | 285 | 937 | 72 | 83 | 56 | 9.0 | 7.5 | 25.0 | C |
| | F | 1629-3 | 5240 | 95 | 291 | 974 | 73 | 112 | 71 | 9.5 | 6.5 | 28.0 | C,S |
| | F | 1629-2 | 5760 | 94 | 331 | 1114 | 70 | 102 | 64 | 10.0 | 8.0 | 28.0 | C,G |
| | F | 1629-1 | 5860 | 95 | 312 | 1061 | 69 | 102 | 64 | 10.0 | 8.5 | 29.0 | C |
| 19 | F | 1674-2 | 8570 | 112 | 366 | 1146 | 102 | 122 | 78 | 8.5 | 6.5 | 28.0 | C |
| 21 | J | 1594-1 | 2980 | 67 | 233 | 699 | 67 | 84 | 60 | 7.5 | 6.0 | - | C,P |
| | J | 1594-3 | 4310 | 94 | 312 | 793 | 73 | 94 | 67 | 7.5 | 7.0 | - | C,P |
| | F | 1594-2 | 4850 | 83 | 286 | 911 | 87 | 116 | 62 | 7.5 | 8.0 | 25.0 | C,S,G,P |
| 22 | F | 1575Aa1 | 7660 | 77 | 293 | 992 | 90 | 118 | 73 | 9.0 | 8.0 | 31.0 | C,P |
| | F | 1575Aa3 | 10090 | 114 | 368 | 1270 | 107 | 138 | 80 | 8.5 | 9.0 | 29.0 | C,S,G,P |
| 27 | F | 1592A-2 | 9390 | 114 | 353 | 1240 | 92 | 104 | 71 | 7.0 | 10.0 | 29.0 | C,P |
| | M | 1592A-1 | 9700 | 126 | 365 | 1209 | 94 | 81 | 60 | - | 12.5 | - | C,P |
| | M | 1592A-3 | 10650 | 119 | 394 | 1324 | 104 | 98 | 70 | - | 10.0 | - | C,P |
| 28 | J | 1591-2 | 4630 | 73 | 233 | 597 | 73 | 83 | 53 | 7.0 | 5.0 | 21.0 | C,P |
| | J | 1591-1 | 5080 | 83 | 256 | 809 | 77 | 94 | 58 | 7.5 | 6.5 | 27.0 | C,P |
| 29 | J | 1569-2 | 3380 | 56 | 191 | 989 | 69 | 83 | 58 | 6.0 | 6.0 | 17.5 | C,P |
| | F | 1569-1 | 9400 | 112 | 389 | 1193 | 96 | 108 | 73 | 7.5 | 8.5 | 29.5 | C,G,P |
| 30 | M | 1575A-2 | 7210 | 96 | 325 | 1021 | 98 | 72 | 58 | - | - | - | C,P |
| | F | 1575A-1 | 9310 | 106 | 314 | 1193 | 104 | 125 | 81 | 10.0 | 8.5 | 31.0 | C,S,P |
| 31 | J | 1579-1 | 3520 | 69 | 235 | 738 | 69 | 83 | 54 | 7.0 | 5.0 | 23.5 | C,P |
| | F | 1579-2 | 10130 | 98 | 229 | 1052 | 112 | 133 | 77 | 8.0 | 9.0 | 29.5 | C,P,R |
| 32 | J | 1064c-1 | 2730 | 62 | 220 | 703 | 67 | 54 | 35 | 6.5 | 4.0 | 16.5 | C,P |
| | J | 1064c-2 | 4180 | 63 | 219 | 1083 | 89 | 67 | 48 | 6.5 | 4.5 | 21.0 | C,P |
| 33 | J | 1066a-1 | 7630 | 89 | 297 | 989 | 71 | 112 | 82 | - | 8.5 | - | C,P |
| | J | 1066a-2 | 8850 | 112 | 330 | 1170 | 97 | 125 | 79 | - | 9.5 | 8.5 | C,P |
| 34 | J | 1678-1 | 5250 | 85 | 235 | 793 | 77 | 82 | 56 | 7.0 | 6.5 | 23.0 | C |
| | J | 1678-2 | 5790 | 87 | 254 | 805 | 90 | 106 | 73 | 4.5 | 6.0 | 23.5 | C |
| 40 | J | 1097a-1 | 5470 | 75 | 264 | 898 | 75 | 87 | 58 | 6.0 | 7.5 | 23.5 | C,P |

| Sample | S | SN | L | DL | DNR | PL | CL | PW | AW | LCC | LD | WCC | Remarks. |
|---|---|---------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|---------------|----------|
| | | | μm | μm | μm | μm | μm | μm | μm | μm | μm | μm | |
| 43 | J | 1038a-1 | 7330 | 96 | 329 | 1138 | 98 | 100 | 64 | 8.5 | 6.0 | 29.0 | C |
| 44 | F | 1576A-1 | 6630 | 94 | 302 | 989 | 75 | 114 | 73 | 8.0 | 7.5 | 30.0 | C,P |
| 46 | J | 1653A-1 | 4700 | 69 | 258 | 835 | 79 | 77 | 54 | 7.5 | 7.5 | 23.0 | C |
| 50 | F | 1578-1 | 9590 | 98 | 321 | 1130 | . | 164 | . | 7.0 | 8.5 | 31.0 | C,P |
| 52 | J | 1064-b | 3820 | 77 | 254 | 807 | 58 | 78 | 50 | 7.5 | 6.0 | 23.0 | C,P |
| 53 | J | 1067-1 | 4260 | 74 | 220 | 699 | 80 | 64 | 48 | 6.5 | 6.5 | 20.5 | C,P |
| 56 | F | 1211a | 7180 | 110 | 333 | 1083 | 83 | 110 | 65 | 9.5 | 8.5 | 28.0 | C,P |
| 58 | J | 76099 | 3430 | 65 | 322 | 562 | 70 | 87 | 53 | 5.5 | 6.0 | 18.5 | C |
| 59 | J | 76098 | 7320 | 95 | 286 | 979 | 85 | 107 | 71 | 7.0 | 7.0 | 22.0 | C,S,P |
| 60 | F | 76100 | 10170 | 87 | 316 | 1178 | 108 | 164 | 91 | 10.0 | 8.5 | 29.0 | C,R |
| 61 | F | 76110 | 7720 | 82 | 298 | 1106 | 103 | 118 | 72 | 9.5 | 8.5 | 31.0 | C,R |
| <u>Leptosomatum spec. 'Philippines'</u> | | | | | | | | | | | | | |
| 64 | J | 777-1 | 6070 | 67 | 225 | 927 | 83 | 74 | 52 | 8.0 | 7.5 | 23.0 | C,P |
| 65 | J | 777-2 | 2880 | 59 | 181 | 700 | 62 | 56 | 37 | 7.0 | 5.5 | 17.5 | C |

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Summary

Leptosomatum bacillatum, a marine nematode that occurs in high densities in the sponge *Halichondria panicea*, has an annual reproductive cycle at Dutch latitudes. During the period that the population has been studied, the smallest juveniles were present from July to September. Females continue growing after the adult stage has been reached, resulting in both 6,5 and 14 mm long females in May and June. Pre-adult males lose their cephalic capsule, which serves to adhere the pharynx, during the last moult; subsequently the somatic musculature and digestive tract starts to atrophy (Chapter 4).

The material described by de Man (1893) from the type-locality of *L. elongatum* has been compared with the Dutch nematodes and with the material described from the Black Sea by Filipjev (1918); they are identical. Because *L. elongatum* Bastian, 1865 (Syn. *L. bacillatum* (Eberth, 1863)) represents the type-species of the genus *Leptosomatum*, all species in which the character-complex (sexual dimorphism of the amphid) is absent, and which were previously considered to be a species of *Leptosomatum*, have been removed from that genus.

Males of *Leptosomatum* species differ from females and juveniles by the aberrant amphid structure expressed in long amphidial glands and obvious ganglia. In males I have never been able to observe the excretory pore or renette; the pore is always present in females, whereas the renette may or may not be present. A ventral row of coelomocytes is often present in both sexes; sometimes, however, individuals occur in which these coelomocytes are undeveloped. The function of these cells is unknown as are the factors that induce their development; the latter applies to the renette as well. An T.E.M.-study of the cephalic capsule revealed that Timm's interpretation (1953), that the capsule is composed of six pairs of sclerotised pieces, is incorrect; the capsule has to be considered a ring. The species of the genus *Leptosomatum* have neither prominent glands in the lateral chord nor a vaginal ovejector (Chapter 2).

Given the above considerations, *L. ranjhai* Timm, 1960, was at first considered a species incertae sedis. Later, when new material became available, a new genus *Orthophallonema* was erected to receive this species (Chapter 5).

L. caecum Ditlevsen, 1923 has been transferred to *Pseudocella*. Species provided with a vaginal ovejector and glands in the lateral chord of the vulvar region, i.e. *L. arcticum* and *L. grebnickii*, both Filipjev, 1916; *L. elongatum* and *L. tetrophthalmum* both sensu Platonova, 1967; and *L. gracile* sensu Allgén, 1954, have been transferred to *Leptosomatides*.

I have not been able to trace the male on which Inglis (1971) based the description of *L. micoletzkyi*. The presence of subventral precloacal papillae, shape and position of the amphid prevents placement in *Leptosomatum*. Based on the description only, it is impossible to decide to which genus it belongs and, therefore, it is considered a species incertae sedis.

More information is desired regarding *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 and *L. tetrophthalmum* Ssaweljev, 1912. These are considered species inquirenda. Although more information is desired regarding *L. sabangense* sensu Micoletzky, 1930 nec Steiner, 1915 this species was renamed as *L. sundaense* Bongers, 1983.

At present the genus *Leptosomatum* is composed of three groups. To the *L. bacillatum*-group belong *L. bacillatum* (Eberth, 1863) with its synonyms (*L. elongatum* Bastian, 1865 (the type-species); *L. gracile* Bastian, 1865; *L. tuapsense* Sergeeva, 1973; and *L. filipjevi* Schuurmans Stekhoven, 1950) *L. acephalum* Chitwood, 1936; *L. clavatum* Platonova, 1958; and *L. sachalinense* Platonova, 1978 with its synonym (*L. diversum* Platonova, 1978). This group is characterized by the absence of a cephalic capsule in the male; in females and juveniles this structure is present.

In the *L. punctatum*-group, the cephalic capsule is absent in all stages and sexes. To this group belong *L. punctatum* (Eberth, 1863), *L. keiense* Micoletzky, 1939 and possibly *L. breviceps* Platonova, 1967. The material described by Micoletzky as *L. keiense* might be composed of two species distinguishable by the presence or absence of a precloacal papilla.

The third 'group' is composed of one species only namely *L. kerguelense* Platonova, 1958 (synonym *L. crassicutis* Platonova, 1958) in which all stages and sexes are provided with a cephalic capsule. The nematodes that were considered by Mawson (1958) to represent *L. arcticum* also belong to this group.

Restudy of male paratypes of *Syringonomus typicus* Hope & Murphy, 1969 confirmed the supposition that, in addition to the characters originally described, long amphidial glands are also present in this genus. *Leptosomatum* and *Syringonomus* are closely related and should form a nominal taxon (*Leptosomatinae* ?) together (Chapter 2).

Based on the genital system the genus *Leptosomatides* is closely related to *Thoracostoma* and *Deontostoma*. Females of *Leptosomatides* can easily be distinguished from those of *Leptosomatum* by the presence of a vaginal ovejector in the former; a character hardly used in the past.

After transferring some of the *Leptosomatum* species to *Leptosomatides* the latter genus is composed of the following species: *Leptosomatides euxinus* Filipjev, 1918 (the type-species) with its synonym *L. caucasiensis* Sergeeva, 1973; *L. reductus* Timm, 1959; *L. arcticus* (Filipjev, 1916) with its synonyms *L. steineri* Filipjev, 1922 pro *Leptosomatum gracile* sensu Steiner, 1916 nec Bastian, 1865 and *Leptosomatum tetrophthalmum* sensu Platonova, 1967 nec Ssaweljev, 1912; *L. filiformis* Filipjev, 1946; *L. grebnickii* (Filipjev, 1916) with its synonyms *L. steineri* sensu Filipjev, 1946, *L. crassus* Platonova, 1967 and *Leptosomatum elongatum* sensu Platonova, 1967; *L. marinae* Platonova, 1976 with its synonyms *L. acutipapillosus* Platonova, 1976 and *L. brevisetosus* Platonova, 1976 (Plat. pers. comm.);

and finally *L. antarcticus* Mawson, 1956 which, if provided with an onchium as has been described, might belong to *Deontostoma*.

L. conisetosus Schuurmans Stekhoven & Mawson, 1955 has been placed in *Deontostoma*. More information is desired regarding *L. microlaimus* (Allgén, 1957) Platonova, 1976, and in the interim it will be considered a species inquirenda. *L. inocellatus* Platonova, 1967 does not fit in *Leptosomatides* and is considered a species incertae sedis (Chapter 3).

Special attention is paid to the *Leptosomatum bacillatum*-complex (Chapter 6). Species of this complex can hardly be distinguished with traditional methods in which allometric growth is not taken into account. If log body length is plotted against log tail length, for example, a linear function appears to exist. For every specimen the log ratio can be computed against the corresponding regression lines of a reference population. These log ratio's are not length dependant and therefore offer possibilities for a multivariate analysis. In this paper such a procedure is demonstrated resulting in a splitting of the *L. bacillatum*-complex into five groups.

Rearrangement of the genera in the family Leptosomatidae is desired. For this purpose, however, the genera must be revised and well defined. This thesis is an attempt to that study.

Samenvatting PROEFSCHRIFT: Systematische studies aan de geslachten *Leptosomatum* Bastian, 1865 en *Leptomatides* Filipjev, 1918 (Nematoda: Leptomatidae).

Leptosomatum bacillatum, een mariene nematode die in grote hoeveelheden in de spons *Halichondria panicea* voorkomt, vertoont onder Nederlandse omstandigheden een reproductie-cyclus van één jaar. De kleinste juvenielen werden in die periode dat het onderzoek duurde aangetroffen van juli tot september. Vrouwtjes blijven doorgroeien, ook na het bereiken van het volwassen stadium zodat in mei en juni in de monsters volwassen vrouwtjes van zowel 6,5 als 14 mm aangetroffen werden. Pre-adulte mannetjes verliezen hun kopkapsel, dat als aanhechtingsplaats voor de slokdarm fungeert, bij de laatste vervelling. Na deze vervelling atrofieert hun somatische musculatuur en spijsverteringsapparaat (Chapter 4).

Het materiaal dat de Man in 1893 van de type-localiteit van *L. elongatum* beschreef werd vergeleken met de Nederlandse nematoden als wel met *L. bacillatum* die Filipjev (1918) van de Zwarte Zee beschreef; verschillen werden niet gevonden. Omdat *L. elongatum* Bastian, 1865 (Syn: *L. bacillatum* (Eberth, 1863)) de typesoort van het geslacht *Leptosomatum* is, werden alle soorten waarin het kenmerkcomplex (sexueel dimorfisme in de amfiedestructuur) afwezig was en voorheen tot *Leptosomatum* gerekend werden uit dit geslacht verwijderd.

Mannetjes van de soorten uit het genus *Leptosomatum* onderscheiden zich van de vrouwtjes en juvenielen door de afwijkende structuur van de amfieden waarbij de ganglia en lange amfiedeklieren het meest opvallen. De renette noch excretieporus heb ik bij mannetjes kunnen waarnemen; de porus is bij vrouwtjes altijd aanwezig, de renette is facultatief ontwikkeld. Bij beide geslachten is er meestal een rij ventrale coelomocyten aanwezig; er komen echter individuen voor waarbij deze coelomocyten niet ontwikkeld zijn. De functie van deze cellen is onbekend evenals de factoren die de ontwikkeling van deze coelomocyten induceren. Dit laatste geldt ook voor de renette. Een elektronenmicroscopische studie van de cephale capsule heeft uitgewezen dat de opvatting van Timm (1953), dat het kopkapsel uit 6 paar gesclerotiseerde stukjes zou bestaan, onjuist is; dit kapsel moet als een ring gezien worden. De soorten van het geslacht *Leptosomatum* hebben geen opvallende klieren in het zijveld, noch is er een vaginale ovejector aanwezig (Chapter 2).

Op grond hiervan werd *L. ranjhai* Timm, 1960 in eerste instantie tot species incertae sedis verklaart. Later, toen aanvullend materiaal beschikbaar kwam, werd voor deze soort het nieuwe geslacht *Orthophallonema* opgericht (Chapter 5).

L. caecum Ditlevsen, 1923 werd naar *Pseudocella* overgebracht. De soorten met zijveldklieren in de vulvastreek en vaginale ovejector werden naar *Leptomatides* overgebracht. Dit betrof *L. arcticum* en *L. grebnickii* beide Filipjev, 1916; *L. elongatum* en *L. tetrophthalmum* beide sensu Platonova, 1967 en *L. gracile* sensu Allgén, 1954.

Het mannetje waarop Inglis (1971) *L. micoletzkyi* baseerde heb ik niet kunnen opsporen. Op grond van de aanwezigheid van subventrale precloacaal-papillen en de vorm en plaatsing van de amfiede behoort deze soort niet tot *Leptosomatum*. Waar *L. micoletzkyi* wel thuishoort is op grond van de beschrijving niet te zeggen en deze soort wordt daarom als species incertae sedis beschouwd.

Meer informatie is nodig betreffende de volgende soorten:

L. abyssale Allgén, 1951; *L. bathybiu*m 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 en *L. tetrophthalmum* Ssaweljev, 1912. Zij worden als species inquirenda beschouwd. Hoewel nog meer informatie nodig is betreffende *L. sabangense* sensu Micoletzky, 1930 nec Steiner, 1915 werd deze herbenoemd als *L. sundense* (Bongers, 1983).

Het genus *Leptosomatum* bestaat momenteel uit drie groepen. Tot de *L. bacillatum*-groep behoren *L. bacillatum* (Eberth, 1863) met als synoniemen *L. elongatum* Bastian, 1865 (de typesoort), *L. gracile* Bastian, 1865, *L. tuapsense* Sergeeva, 1973 en *L. filipjevi* Schuurmans Stekhoven, 1950; *L. acephalatum* Chitwood, 1936; *L. clavatum* Platonova, 1958 en *L. sachalinense* Platonova, 1978 met als synoniem *L. diversum* Platonova, 1978. Deze groep is o.a. gekenmerkt door de afwezigheid van een kopkapsel bij het mannetje terwijl deze bij vrouwtjes en juvenielen aanwezig zijn.

In de *L. punctatum*-groep, de tweede, is het kopkapsel afwezig bij alle stadia en sexen. Hiertoe behoren *L. punctatum* (Eberth, 1863), *L. keiense* Micoletzky, 1939 en mogelijk *L. breviceps* Platonova, 1967. Het materiaal dat Micoletzky als *L. keiense* beschreef bestaat mogelijk uit twee soorten die onderscheiden zouden kunnen worden op grond van de aan- of afwezigheid van een precloacaalpapil.

De derde 'groep' bestaat uit slechts één soort nl. *L. kerguelense* Platonova, 1958 (synoniem *L. crassicutis* Platonova, 1958) waarin alle stadia en sexen een kopkapsel bezitten. De nematoden die Mawson, 1958 tot *L. arcticum* rekende behoren eveneens tot deze soort.

Nader onderzoek aan mannetjes (paratypen) van *Syringonomus typicus* Hope & Murphy, 1969 bevestigde het vermoeden dat ook zij, naast enkele bijzondere kenmerken, in het bezit zijn van lange amfiedeklieren. *Leptosomatum* en *Syringonomus* zijn nauw aan elkaar verwant en moeten samen een taxon (*Leptosomatinae* ?) vormen (Chapter 2).

Op basis van het genitaalsysteem vertoont het geslacht *Leptosomatides* een verwantschap met de geslachten *Thoracostoma* en *Deontostoma*. Vrouwtjes van *Leptosomatides* blijken eenvoudig van die van *Leptosomatum* onderscheiden te kunnen worden door de aanwezigheid van een vaginale ovejector in de eerste, een kenmerk waaraan in het verleden nauwelijks aandacht geschonken is.

Na het overbrengen van enkele soorten van *Leptosomatum* naar *Leptosomatides* bestaat dit laatste genus uit de volgende goede soorten: *Leptosomatides*

euxinus Filipjev, 1918 (de typesoort) met als synoniem *L. caucasiensis* Sergeeva, 1973; *L. reductus* Timm, 1959; *L. arcticus* (Filipjev, 1916) met als synoniemen *L. steineri* Filipjev, 1922 pro *Leptosomatum gracile* sensu Steiner, 1916 nec Bastian, 1865 en *Leptosomatum tetrophthalmum* sensu Platonova, 1967 nec Ssaweljev, 1912; *L. filiformis* Filipjev, 1946; *L. grebnickii* (Filipjev, 1916) met als synoniemen *L. steineri* sensu Filipjev, 1946, *L. crassus* Platonova, 1967 en *Leptosomatum elongatum* sensu Platonova, 1967; *L. marinae* Platonova, 1976 met als synoniemen *L. acutipapillosus* Platonova, 1976 en *L. brevisetosus* Platonova, 1976 (Plat. pers. meded.); en tenslotte *L. antarcticus* Mawson, 1956. Indien de vermelding van de aanwezigheid van een tand in de mondholte juist blijkt te zijn, behoort deze soort tot het geslacht *Deontostoma*. Van de bovengenoemden is *L. filiformis* op soortsniveau gebracht.

L. conisetosus Schuurmans Stekhoven & Mawson, 1955 is in het geslacht *Deontostoma* geplaatst. Betreffende *L. microlaimus* (Allgén, 1957) Platonova, 1976 is meer informatie nodig, ze wordt als species inquirenda beschouwd. *L. inocellatus* Platonova, 1967 wijkt op een groot aantal kenmerken af van de overige soorten in het genus *Leptosomatides* en wordt tot de species incertae sedis gerekend (Chapter 3).

Nadere aandacht is besteed aan het *Leptosomatum bacillatum*-complex (Chapter 6). De soorten van dit complex zijn met de traditionele methoden, waarbij geen rekening wordt gehouden met de allometrische groei, nauwelijks te onderscheiden.

Indien log lichaamslengte uitgezet wordt tegen bv. log staartlengte blijkt er een rechtlijnig verband te bestaan. Van elk individu kunnen de log ratio's (gelogaritmiseerde verhoudingen) bepaald worden t.o.v. de overeenkomstige regressielijnen van een referentiepopulatie. Deze log ratio's blijken bij grote monsters niet lengte afhankelijk te zijn en bieden daarom mogelijkheden voor een statistische analyse. In dit artikel wordt een voorbeeld gegeven van een dergelijke procedure. Volgens deze methode valt het *L. bacillatum*-complex uiteen in een vijftal groepen die vervolgens besproken worden.

Een herrangschikking van de genera in de familie Leptosomatidae is wenselijk. Daartoe dienen echter eerst de genera goed gedefinieerd te worden. Dit is een aanzet daartoe.

Curriculum vitae

Bongers, Albertus Maria Theodorus (synoniem: B. Tom) werd op 26 juni 1946 te Gaanderen geboren. Na het behalen van de diploma's Mulo A en B was hij gedurende enige jaren werkzaam op de 'aaltjesafdeling' van het Bedrijfs-laboratorium voor Grond- en Gewasonderzoek te Oosterbeek, de afdeling Nematologie van de Plantenziektenkundige Dienst te Wageningen en de Vakgroep Nematologie van de Landbouwhogeschool, terwijl in de avonden een cursus voor Botanisch Analist gevolgd werd bij de STOVA te Wageningen.

In 1972 werd hem, na het afleggen van het colloquium doctum, toestemming verleend examens af te leggen aan de Landbouwhogeschool. In de doctoraal-fase van zijn biologiëstudie werden de vakken diertaxonomie, nematologie en visteelt gekozen. De praktijktijd Nematologie werd in 1978/1979 doorgebracht bij het ORSTOM in Ivoorkust. In 1979/1980 verbleef hij in het kader van een culturele uitwisseling enkele maanden op het Zoologisch Instituut te Leningrad; in 1980 keerde hij terug naar Ivoorkust voor een visteelt-onderzoek bij het CTFT te Bouaké.

Na zijn afstuderen in 1981 bood het Wageningenfonds hem de mogelijkheid het onderzoek aan de morfologie en systematiek van *Leptosomatum* uit te breiden hetgeen tenslotte enkele publicaties opleverde die de basis vormen voor zijn proefschrift.

Een gedeelte van dit onderzoek is uitgevoerd op het Smithsonian Institution te Washington D.C. en het Zoologisch Instituut te Leningrad.

Momenteel is hij werkzaam bij de vakgroep Nematologie van de Landbouwhogeschool waar hij een inventarisatie maakt van de nematodenfauna van de Nederlandse bossen.